Prisoner’s Dilemma cellular automata revisited: evolution of cooperation under environmental pressure

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Abstract. We propose an extension of the evolutionary Prisoner’s Dilemma cellular automata, introduced by Nowak and May [14], in which the pressure of the environment is taken into account. This is implemented by requiring that individuals need to collect a minimum score $U_{\text{min}}$, representing indispensable resources (nutrients, energy, money, etc.) to prosper in this environment. So the agents, instead of evolving just by adopting the behaviour of the most successful neighbour (who got $U_{\text{msn}}$), also take into account if $U_{\text{msn}}$ is above or below the threshold $U_{\text{min}}$. If $U_{\text{msn}} < U_{\text{min}}$ an individual has a probability of adopting the opposite behaviour from the one used by its most successful neighbour. This modification allows the evolution of cooperation for payoffs for which defection was the rule (as it happens, for example, when the sucker’s payoff is much worse than the punishment for mutual defection). We also analyse a more sophisticated version of this model in which the selective rule is supplemented with a "win-stay, lose-shift" criterion. The cluster structure is analyzed and, for this more complex version we found power-law scaling for a restricted region in the parameter space.
1. Introduction

Cooperation among animals, either within or between species, is widespread throughout nature [1]-[7]. This presents a puzzle for Darwinists since, according to Darwin’s theory, the rule among animals should be competition, not cooperation.

Attempting to understand the evolution of cooperation, Maynard Smith and Price [8] applied game theory to interactions between competing individuals of the same species that use different strategies for survival. They found that in situations like combat, in which each individual must decide whether or not to escalate the fight without knowing his opponent’s decision, the interests of both combatants are best served if both decide not to escalate the fight.

$2 \times 2$ games (2 players making a choice between 2 alternatives), which showed their usefulness in Economics and Social Sciences [5], constitute also a basic tool to model the conflict/cooperation situations in Biology [9]. Furthermore, the marriage of Game Theory and Darwinian evolution gave rise to a new branch of game theory, namely evolutionary game theory [10].

In particular one of such games is the Prisoner’s Dilemma (PD), now well established as a useful tool for studying cooperative interactions among self-interested agents. The PD game comes from an experimental setup designed by the researchers at the RAND Corporation M. Dresher and M. Flood. The game refers to an imaginary situation in which two suspects are arrested near the scene of a crime. The police don’t have enough evidence to convict the pair on the principal charge. The two prisoners are held in separate cells and offered a deal: If one testifies implicating the other in the principal crime will go free, while the other, if remains silent, will receive 10 years in prison. If they both testify against each other, each will receive 5 years. Finally, if they both remain silent, they will both be convicted by a minor crime and serve one year. What’s the rational choice for each prisoner? To remain silent (cooperate with your partner) or to confess (not to cooperate)? The “dilemma” faced by the prisoners is that, whatever the other does, each is better off confessing than remaining silent. But the outcome obtained when both confess is worse for each than the outcome they would have obtained if both had remained silent. This puzzle illustrates a conflict between individual and group rationality. A group whose members pursue rational self-interest may all end up worse off than a group whose members act contrary to rational self-interest. Formulated in its general form the PD game involves two players each confronting two choices: cooperate (C) or defect (D) and each makes his choice without knowing what the other will do. The possible outcomes for the interaction of both agents are: 1) they can both cooperate: (C,C) and get the “reward” for mutual cooperation $R$, 2) they can both defect: (D,D) and get the ”punishment” for mutual defection or 3) one of them cooperates and the other defects: (C,D); in that case the one who played C gets the ”sucker’s payoff” $S$ while agent who played D gets the ”temptation to defect” $T$. The following payoff matrix summarizes the payoffs for row actions when confronting with column actions:

$$M = \begin{pmatrix} (R, R) & (S, T) \\ (T, S) & (P, P) \end{pmatrix},$$

with the four payoffs obeying the inequalities:

$$T > R > P > S.$$
Clearly it pays more to defect: if your opponent defects, and you cooperate you will end up with the worst payoff. On the other hand, even if your opponent cooperates, you should defect because in that case your payoff is $T$ which is higher than $R$. In other words, independently of what the other player does, defection D yields a higher payoff than cooperation and is the dominant strategy for rational agents. Nevertheless, reasoning that way both agents get $P$ which is worst than $R$.

A possible way out for this dilemma is to play the game repeatedly. In this iterated Prisoner’s Dilemma (IPD), in which condition (1) is supplemented with the condition:

$$2R > S + T,$$

there are several strategies that outperform the dominant one-shot ‘always D’ strategy and lead to some non-null degree of cooperation. The tournaments organized by Axelrod [5, 11] in the 80s were very illuminating. He invited researchers from different fields to contribute a strategy, in the form of a computer program, to play the Prisoner’s Dilemma against each other and themselves repeatedly. Each strategy specified whether to cooperate or defect based on the previous moves of both the strategy and its opponent. The programs were then ranked according to the total payoff accumulated. The winning program, was also the simplest: ‘TIT FOR TAT’ (TFT), which plays C on the first move, and on all subsequent moves copies the choice of its opponent on the previous move. In an ecological approach [12], the scores from round two were used to calculate the relative frequencies of the strategies in a hypothetical population. The strategies were then submitted to each subsequent round in proportion to their cumulative payoff in the previous round. In the long run, TFT outcompeted its rivals and went to fixation. Axelrod and Hamilton [11] used these ecological competition between strategies as a basis for their analysis of the evolution of reciprocal altruism. This model is applicable in two opposite situations: on the one hand, in the case of higher animals, which can distinguish between their various opponents in order to reciprocate [13], discouraging thus defection. On the other hand, in the case of very simple organisms who have only one opponent in its lifetime.

Nowak and May [14] found another way to escape from the dilemma: the incorporation of territoriality in evolutionary game theory favours cooperation. The authors proposed simple cellular automata (CA) for general ecological systems involving indiscriminating organisms who play against several opponents (their neighbours). They neglected all strategical complexities or memories of past encounters considering unconditional cellular automata i.e. agents using unconditional strategies (each cell is either in a C or D state), as opposed to the conditional ones like TFT, the simpleton [15] or PAVLOV [16] "win-stay, lose-shift", etc. Cells simply play repeatedly with their neighbours and in the next round or generation adopt the state of the most successful cell of their neighbourhood (the one that collected the highest score among the cell itself and its neighbours). Coexistence of both states or behaviours were found for a simplified version of the PD in which the punishment $P$ is equal to the sucker’s payoff $S$, implying then a ”weak dilemma” (maximum punishment i.e. the minimum possible value of $P$). Taking $R = 1$ and $P = S = 0$ allows to parameterise the payoff matrix in terms of just the parameter $T$. Szabó

‡ Indeed this is the frontier between the PD game and another interesting game, called chicken by game theorists and Hawk-Dove (H-D) game by evolutionary biologists, in which the punishment for mutual defection is the worst payoff i.e. $T > R > S > P$. 

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The text continues with more details on the evolution of cooperation, strategies, and ecological models.
and Töke [17] slightly modified the Nowak-May (N-M) model with the addition of randomness: players are chosen to update their states randomly by copying the state of one of its neighbours with a probability depending on the payoff difference. They measured the fraction of cooperators $c$ for different values of the temptation to defect $T$ and found a continuous transition from $c = 1$ to $c = 0$ as $T$ increases. A problem with these simple spatial games is that if $P$ is augmented until it becomes non negligible compared with the reward $R$ then cooperation disappears and all the individuals end playing D.

An alternative to go beyond weak dilemmas is to consider more sophisticated players, with $m$-steps memory and strategies involving conditional probabilities, as Lindgren and Nordahl [18] did. They considered payoff matrices parameterised in terms of two parameters, $T/R$ and $P/R$ ($S = 0$), and found the evolution of cooperation for payoff matrices beyond "weak" dilemmas. However, pursuing as much generality as possible without sacrificing the simplicity, which is part of the N-M model beauty, in this paper we explore a different approach. Our starting point is realising that, interesting as it is, the N-M model lacks a fundamental ingredient, namely that of the stress exerted by the environment on the individuals. This is a crucial factor in order to explain the emergence of cooperation between self-interested individuals even when they are very simple (without requiring long term memory nor distinguishing "tags" nor access to sophisticated strategies and, of course, no rational behaviour).

The basic idea is that individuals need to collect, when playing with their $z$ neighbours, a payoff above certain threshold $U_{\text{min}}$ in order to prosper. In an ecosystem $U_{\text{min}}$ represents the minimal resources (nutrients, energy, etc.) without which organisms die; in economics it may correspond to some threshold below which the business is no longer profitable, etc. Thus, although D players are the most successful for $P - S$ large enough, when $U_{\text{min}} > z(P - S)$ they cannot achieve the critical payoff if surrounded by an entire neighbourhood of D’s and so some of them will be replaced by C players.

We use a normalized payoff matrix with $R = 1$ and $S = 0$. Besides the 3 parameters: $U_{\text{min}}, T$ and $P$ we include a probability $p$ for players of adopting the behaviour that is the opposite of the one used by the most successful neighbour ($\text{msn}$). In the simplest model version an individual has a probability of behaving different from the $\text{msn}$ if the score of the $\text{msn}$ is below $U_{\text{min}}$. This simple recipe allows the evolution of cooperation even when the punishment $P$ is relatively soft i.e. when the sucker’s payoff is much worse than the payoff for mutual defection ($P >> S$). Furthermore, it gives rise to states of universal cooperation. We also consider a more sophisticated hybrid model version in which the selective rule of copying the behaviour of the $\text{msn}$ is supplemented with a "win-stay, lose-shift" criterion. That is, individuals also take into account if their own scores $U$ are below or above $U_{\text{min}}$ to update their behaviour. This version, although more complex, seems well-grounded since it is widely known that Pavlovian strategies play a central role in animal behaviour [19]-[23]. Moreover, the remarkable experiments conducted by Milinski and Wedekind [24],[25] revealed that, humans engaged in social dilemma games use by far strategies of the kind of "win-stay, lose-shift".

For the different model versions, we explore a subspace of the space of parameters \{\(T, P, U_{\text{min}}, p\)\} measuring the fraction of cooperators and quantities characterizing the resulting cluster structure.
2. The Basic Model

The players, which can adopt only two unconditional strategies or behaviours when playing with their neighbours: cooperate (C) or defect (D), are thus represented by binary state cells of a two dimensional automaton. In this work we restrict ourselves to square grids and two types of neighbourhood: a) von Neumann neighbourhood, consisting of the $z = 4$ first neighbouring cells of a given cell, and b) Moore neighbourhood, formed by the $z = 8$ cells surrounding a given cell. Typical grid sizes range from $50 \times 50$ to $500 \times 500$. Periodic boundary conditions are used. The score $U$ of a given player is the sum of all the payoffs it collects against its neighbours. Tables 1 and 2 summarize the different scores for a player depending on the number of C cells in its neighbourhood. The dynamic is synchronous: all the agents update their states simultaneously at the end of each lattice sweep.

|       | 4C, 0D | 3C, 1D | 2C, 2D | 1C, 3D | 0C, 4D |
|-------|--------|--------|--------|--------|--------|
| C     | 4      | 3      | 2      | 1      | 0      |
| D     | 4T     | 3T + P | 2T + 2P | T + 3P | 4P     |

Table 1. Score $U$ for a player depending on its state C (row 1) or D (row 2) and the number of C and D agents in its neighbourhood for the $z = 4$ case.

|       | 8C, 0D | 7C, 1D | 6C, 2D | 5C, 3D | 4C, 4D | 3C, 5D | 2C, 6D | 1C, 7D | 0C, 8D |
|-------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| C     | 8      | 7      | 6      | 5      | 4      | 3      | 2      | 1      | 0      |
| D     | 8T     | 7T + P | 6T + 2P | 5T + 3P | 4T + 4P | 3T + 5P | 2T + 6P | T + 7P | 8P     |

Table 2. The same as Table 1 but for $z = 8$ neighbours.

In the CA of ref. [14] natural selection is implemented very simply: each agent or player adopts the state of the most successful neighbour (msn) who got $U_{msn}$. Here, if $U_{msn}$ is below the threshold $U_{min}$, we allow the individuals to adopt the opposite state with a probability $p$. The rationale for this is that blindly copying the most successful neighbour, when its score doesn’t reach a critical threshold, may not be, in the long run, the most efficient strategy from an evolutionary point of view.

We consider two possible variants:

(i) Simplest variant: Conditional copying the most successful neighbour.

If $U_{msn} \geq U_{min}$, the player copies the state of its msn. Otherwise, if $U_{msn} < U_{min}$, the player has a probability $p$ of adopting the opposite state.

(ii) Variant 1 + death of organisms.

This variant contemplates the possibility that organisms that don’t reach the threshold $U_{min}$ die and some cells remain unoccupied. The rules are the same as above except that in the case when $U_{msn} < U_{min}$, instead of adopting the strategy of the msn, the player dies with probability $1 - p$ leaving an empty cell. An empty cell updates its state copying the one of its msn with probability
Prisoner’s Dilemma revisited: evolution of cooperation under pressure

1 − p (adopting the opposite behaviour with probability p). Finally, an empty cell surrounded by empty cells remains unoccupied in the next round.

It turns out that, for both variants of the model, the system reaches a steady state with a definite value $c$ for the fraction of agents playing C after a transient. The duration of the transient depends on the lattice size and the neighbourhood. For instance for a 50 × 50 lattice and $z = 8$ it last typically between 100 and 200 rounds.

To avoid dependence on the initial conditions, the measures correspond to averages over an ensemble of 100 systems with arbitrary initial conditions. The standard deviation is about 7 percent so this averages are quite representative.

Here, we present results for a subspace of the parameter space \{T, P, U_{min}, p\}. We choose definite values for the punishment $P$ and the probability parameter $p$, specifically: $P = 0.5$§ and $p = 0.1$. The temptation parameter $T$ is varied between 1 and 2. A threshold $U_{min} > zP$ is required in order to avoid the all D state; on the other hand $U_{min} > zT$ doesn’t make sense since no one can reach this threshold. Thus, the parameter space reduces to the square plane $T - U_{min}$ delimited by $1 \leq T \leq 2$ and $zP \leq U_{min} \leq zT$.

After a transient, the steady or asymptotic fraction of C agents $c$ is computed for a grid of points in the $T-U_{min}$ plane using lattices of relatively modest size: 50 × 50. Similar results hold for 100 × 100 lattices or bigger.

![Figure 1](image_url)

Figure 1. Asymptotic frequency of cooperators for the simplest model, for $p = 0.1$, (a) $z=4$ neighbours and (b) $z=8$ neighbours.

Figures 1a and 1b corresponding to the first model variant show a similar dependence on frequency of cooperators with $T$ and $U_{min}$. Note that, when $U_{min} > zP$, the fraction of cooperators raises from zero to a non negligible value regardless of $T$.

§ This value of the punishment implies a non weak dilemma and, both for $z = 4$ or $z = 8$, leads to $c = 0$ when simulating the model of ref. [13].
of the value of $T$. The explanation of this is simple: a D agent surrounded by D's gets a score $zP$ that is below the surviving threshold, and thus has a probability $p$ of becoming C in the next round. Basically three regions can be distinguished in the plots:

- A **stepladder region** emerges from the right border $U_{\text{min}} = zP$.
- For not too large values of $T$ and $U_{\text{min}}$ there is a high peak of cooperation, delimited to the left by $U_{\text{min}} = zR = z$ (when all the cells play C).
- Finally, beyond $U_{\text{min}} = zR = z$, $c$ reaches a plateau delimited by the straight line $U_{\text{min}}(T) = zT$ ($U_{\text{min}}$ greater than $zT$ is an unreachable score in the game we are considering).

To understand the peak of cooperation it is illuminating to consider a small deviation of $T$ from 1: $T = 1 + \epsilon$. Therefore, for $z = 8$ and $P = 0.5$ the Table 2 becomes the Table 3. For $U_{\text{min}}$ greater than 6, the only D agents which can achieve the minimum $U_{\text{min}}$ are the ones surrounded by at least 4 C's (see row 2 of Table 3), so cooperation grows dramatically. This corresponds to $\epsilon \lesssim 0.16$ (for increasing values of $\epsilon$, D agents surrounded by less than 4 C's will survive and we cannot expect great values for $c$). When $U_{\text{min}} = 8\epsilon$ drops abruptly since even C agents surrounded entirely by other C's cannot survive anymore.

| $8C,0D$ | $7C,1D$ | $6C,2D$ | $5C,3D$ | $4C,4D$ | $3C,5D$ | $2C,6D$ | $1C,7D$ | $0C,8D$ |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| C     | 8     | 7     | 6     | 5     | 4     | 3     | 2     | 1     | 0     |
| D     | 8.0 + 8\epsilon | 7.5 + 7\epsilon | 7.0 + 6\epsilon | 6.5 + 5\epsilon | 6.0 + 4\epsilon | 5.5 + 3\epsilon | 5 + 2\epsilon | 4.5 + \epsilon | 4 |

**Table 3.** Same as Table 2 for $T = 1 + \epsilon$, $P = 0.5$

The stepladder structure for $z = 8$ (a similar analysis holds for $z = 4$) can be easily explained considering the scores for D agents of Table 2. As long as $U_{\text{min}}$ increases each D agent needs more C agents in its surroundings in order to achieve the threshold. So cooperation grows with $U_{\text{min}}$ by steps at the values mentioned before: $U_{\text{min}} = T + 7P$, $U_{\text{min}} = 2T + 6P$ and so on, which correspond to straight lines with different slopes in the $(T, U_{\text{min}})$ plane. Finally, when $U_{\text{min}} > 8T$ the minimum required is above any agent’s possible score, then the fraction of agents C one time step further will be given by

$$c(t+1) = p f_D + (1-p)f_C,$$

where $f_D$ stands for the fraction of agents (C and D) whose most successful neighbour is a D-cell and $f_C$ is the fraction of agents (C and D) whose most successful neighbour is a C-cell. As none of the agents achieves the threshold, the state of all of them is updated with probability $p$ to a state opposite to the one of the msn. For small values of $p$, $f_C \approx 0$ (since a C agent needs to be surrounded by a minimum number of C agents to be the most successful), $f_D \approx 1$ and finally $c \approx p$. This explains why the height of the plateau coincides with the probability $p$.

The landscape that emerges from the second model variant (see Fig. 2a and Fig. 2b) is very similar to the one produced by the first variant.

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\[\|\text{At least in the considered } T \text{ interval: } 1 < T < 2.\]

\[\&\text{Besides } p = 0.1, \text{ we checked this also for } p = 0.2 \text{ and } p = 0.3\]
3. Hybrid Model: Natural Selection Complemented with a Pavlovian Criterion.

A relevant input for an agent to assess its performance in a game is the comparison of its own score $U$ with $U_{\text{min}}$. If it is above $U_{\text{min}}$, then the agent’s behaviour may be worth keeping even if it is not the most successful in the neighbourhood. The behaviour updating rule thus becomes more sophisticated and instead of the previous rule we have:

(i) If $U^{\text{msn}} < U_{\text{min}}$: The player adopts the opposite state of its $msn$ but now with probability $1 - p$.

(ii) If $U^{\text{msn}} \geq U_{\text{min}}$: There are two alternatives depending on its score $U$:

- If $U < U_{\text{min}}$, the player keeps its state with probability $p$ (adopts the state of its $msn$ with probability $1 - p$).
- If $U \geq U_{\text{min}}$ the player keeps its state with probability $1 - p$ (adopts the state of its $msn$ with probability $p$).

Therefore, this model interpolates between the ordinary evolutionary recipe of copying the most successful neighbour and the "win-stay, lose-shift" criterion of the game analysed in detail by Herz [26].

3.1. Frequency of cooperators

Again, the system reaches a steady state with a definite value $c$ for the fraction of agents playing $C$ after a transient. This hybrid model produces qualitatively similar results, but there are remarkable modifications in the landscape shown in Fig. 3.
Firstly, we observe a strong increase in $c$ for all the parameter space surrounding the peak zone. In particular, note the height of the plateau and the step formation. Secondly, most part of the plateau is replaced by steeply "cliffs". Figure 3 shows the fraction of cooperators for $T = 1.6, z = 8$. Between $zP(=4)$ and $zR(=8)$, the fraction $c$ increases almost monotonously with $U_{\text{min}}$. However, once $U_{\text{min}}=8$ is reached, the fraction of cooperators falls down drastically. This is due to the fact that C agents surrounded entirely by C’s can no longer survive and turn into D agents with probability $1-p = 0.9$. Since some of the D agents still have a payoff above $U_{\text{min}}$, they survive to the next round, so cooperation fraction should decrease. As long as $U_{\text{min}}$ increases, more C’s are necessary in the neighbourhood of a D for this agent to keep its strategy, so cooperation would increase again.

When $U_{\text{min}} > 8T$ the equation (3) is replaced by

$$c(t+1) = (1-p)f_D + pc(t).$$

(4)

Hence, in the steady state ($c(t+1) = c(t)$) we have the solution $c = f_D$.

3.2. Cluster structure

An additional novelty of this model, connected with the greater richness in the $c$ landscape (see Fig. 3), is the cluster structure which exhibits power law scaling for a restricted region in the $T-U_{\text{min}}$ plane (for the basic model no power-laws were found). In this subsection we analyse the cluster structure and spatial patterns in the three different regions of the plane $T-U_{\text{min}}$ identified in the previous subsection. We present results for the $z = 8$ Moore neighbourhood, since it is the one that exhibits more clear cut results. Fig. 4 shows snapshots of the steady state at four representative points.
in the \( T - U_{\text{min}} \) plane: (a) \([T=1.5, U_{\text{min}}=11.9]\) belonging to the plateau \((c \simeq 0.75)\), (b) \([T=1.06, U_{\text{min}}=6.9]\) belonging to the peak \((c \simeq 0.91)\), (c) \([T=1.2, U_{\text{min}}=5.5]\) at the side of the peak \((c \simeq 0.5)\) and (d) \([T=1.6, U_{\text{min}}=7.5]\) belonging to the stepladder region \((c \simeq 0.4)\).

For \([T=1.5, U_{\text{min}}=11.9]\), although fraction of cooperators is stable the spatial patterns change constantly as a consequence of the transition rules. One of these patterns is shown in Fig. 5.a. For \([T=1.06, U_{\text{min}}=6.9]\), giant stable clusters dominate the lattice as expected from the high level of cooperation in that region as shown in Fig. 5.b. At the side of the cooperation peak there are spatial stable structures of clusters as the ones shown in Fig. 5.c. When we move away from the peak into the region bounded between \(2T + 6P, AT + 4P\) and \(U_{\text{min}} = 8\) scale invariance emerges: clusters of all size occur as can be seen from Fig. 5.d for \(T = 1.6\) and \(U_{\text{min}} = 7.5\). In this case we are in presence of constantly changing spatial patterns again. Histograms of the size distribution of clusters for the four above points in the \( T - U_{\text{min}} \) plane are shown in Fig. 6.

The histogram 6.b shows that only exist (giant) clusters for a narrow interval of sizes. As we move to regions in the phase space with lower values of \(c\), a greater diversity of sizes occur (see Figs. 6.a and 6.c) until 6.d clearly shows a power law distribution with exponent \(-1.6357 \pm 0.0001\). Power laws are the signature of organization into a critical state. It indicates that the system exhibits the highest pattern of diversity: there are few large structures and many smaller clusters. This power-law scaling emerges only for a very reduced region in the plane \( T - U_{\text{min}} \) in the vicinity of the point \([T = 1.6, U_{\text{min}} = 7.5]\). In that sense this scale-free behaviour seems more to ordinary critical phenomena (second order phase transitions), where a fine-tuning of the control parameters is required, than to the much more robust self-organized criticality (SOC).

We also explored the correlation function in this region and found a scaling with distance \(r\) proportional to \(\frac{\xi}{r}\). Fig. 7 shows this function for the point \([T = 1.6, U_{\text{min}} = 7.5]\) where the correlation length \(\xi\) takes the value 2.95.
Figure 5. Steady state cooperation maps for the $z = 8$ hybrid model (with $p=0.1$) for: (a) $T = 1.5, U_{\text{min}} = 11.9$ (b) $T = 1.06, U_{\text{min}} = 6.9$ (c) $T = 1.2, U_{\text{min}} = 5.5$ (d) $T = 1.6, U_{\text{min}} = 7.5$. Black cells correspond to C agents and white cells to D agents. The mean frequency of cooperators corresponding to each map is (a) $c = 0.75$ (b) $c = 0.91$ (c) $c = 0.50$ (d) $c = 0.40$.

Besides the size distribution of clusters, the relationship between the perimeter and the area of the clusters provides useful information on their geometry. The area $A$ of a cluster is the number of all connected cells with a given strategy (C or D) and its perimeter $\ell$ is defined as the number of cells that form its boundary (those cells of the cluster with at least one neighbour not belonging to it). We compute the mean perimeter $\ell(A)$ for a given area $A$ averaging over all the perimeters of clusters with given area $A$. Plots of $\ell$ vs. $A$ for the four $T, U_{\text{min}}$ points treated before are shown in Fig. 8.

Figure 8b is consistent with the very narrow range of sizes of C clusters observed in Fig. 6b (something similar happens for Fig. 6a but without a clear dependence of perimeter with area). In Fig. 8d -which corresponds to a power law in size distribution as shown in Fig. 6d- the mean perimeter scales linearly with the area. From this linearity it follows that the ratio of perimeter to interior (being the interior $A - \ell(A)$) becomes independent of the cluster size. The coefficient of the line $\ell(A)$ is $0.8369 \pm 0.0001$. This result differs greatly from the square root dependence of $\ell$ with $A$ expected for regular geometry and is an indicator of the ramified structure of clusters (see Fig. 8d).
4. Discussion

We have shown how cooperation among self-interested individuals can emerge from evolution in PD games, involving quite arbitrary payoff matrices (instead of just weak dilemmas), using the simplest possible agents: unconditional strategists, without long term memory and without distinguishing "tags". This allows the applicability of the model to a wide variety of contexts from natural to social sciences.

The main idea was to include the influence of the environment exerting pressure on individuals to cooperate even when the punishment for defecting is relatively soft. This is implemented by requiring a minimum score $U_{\text{min}}$ necessary for agents to carry on vital functions. In particular, for moderate values of the temptation to defect $T$, there is an intermediate range of values of $U_{\text{min}}$ that maximizes cooperation among self-interested agents producing a state of "universal cooperation".

Our findings might be connected with questions in evolutionary genetics like the effects of deleterious mutations on fitness. Mutations, in spite of being the ultimate engine for evolution, in general have a negative effect on fitness. It has been widely accepted that these deleterious fitness effects are, on average, magnified in stressful
Figure 7. Correlation between C agents as a function of distance for $[T = 1.6, U_{\text{min}} = 7.5]$; values obtained in simulations (▽) and theoretical fitting $\alpha e^{-\frac{\xi}{r}}$ (where $\xi = 2.95$) in solid line.

environments. Recent experimental measures of growth rates of E.coli mutants under a diverse set of environmental stresses suggest just the opposite: the effects of deleterious mutations can sometimes be ameliorated in stressful environments [27]. A possibility is that C-inclined organisms may be regarded as deleterious mutants in the case of no stress which can take over the population under some (appropriate) degree of stress.

It is worth remarking that the more sophisticated model, that results when supplementing the ordinary evolutionary recipe of copying the most successful neighbour with a Pavlovian "win-stay, lose-shift" criterion, exhibits two relevant properties. The first is global optimisation i.e. it enhances the cooperation level. The second is the emergence of power-law scaling in the size distribution for clusters of C-agents. Power-laws were also found in a different study of cellular automata playing the PD game with Pavlovian strategies [28]. However, in that case, this scaling behaviour is much more robust than the one we found here which holds only for quite reduced region in the $T - U_{\text{min}}$ plane.

The effect of requiring a threshold has been analysed in social sciences. For instance, in relation to reinforcement learning by Borgers and Sarin [29], [30], although treatment is quite different. Indeed, this threshold represents an aspiration level and may improve the decision maker’s long-run performance.

To conclude, we envisage some future extensions of this (these) model (models). For instance to explore the effect of heterogeneities, in the environment (a landscape dependent $U_{\text{min}}$ function) or in the agents (different payoff matrices, different types of individuals, etc.). In addition, the spatial networks observed in nature are in general not uniform square lattices like the ones considered here. So another interesting direction that seems worth studying is to consider more realistic network topologies, for example scale free [31] or small worlds networks [32].
Acknowledgments

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Prisoner's Dilemma revisited: evolution of cooperation under pressure

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