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16

**Abstract**

17 Cooperation is ubiquitous in the world surrounding us, from bacteria to Human  
18 interactions. In Humans, cooperation is often associated with various group decisions,  
19 resulting from their complex web of interrelated interests, associations or preferences.  
20 The existence of such social structures not only opens the opportunity of having diverse  
21 behaviors depending on the individuals' social position, but also for a dynamical  
22 allocation of contributions depending on the returns obtained from each group. Here, we  
23 address these issues by studying the evolution of cooperation under Public Goods Games  
24 in the framework of Evolutionary Game Theory where cooperative players are able to  
25 distribute their donations to their liking. As a result, cooperation is greatly enhanced  
26 when the community structure is described by homogeneous graphs, as cooperators  
27 become able to support cooperative groups and retaliate against those with poor  
28 achievements by withdrawing donations from them. Whenever the underlying network  
29 becomes complex enough to add diversity to the distribution of group sizes, directed  
30 investments do not optimize the emergence of cooperation, but they do enhance its  
31 robustness against the invasion of a minority of free-riders. We define a robustness index  
32 and show that directed investments expand the robustness of cooperation by about 50%.

33 **Keywords:** evolutionary game theory; public goods game; structured populations;  
34 evolution of cooperation; complex networks.

35

## 36 **1 Introduction**

37 Cooperation is a key feature of self-organized systems, occurring at all scales and levels  
38 of complexity (Hardin, 1968; Taylor, 1982; Axelrod, 1984; Trivers, 1985; Maynard-  
39 Smith and Szathmáry, 1995; Sigmund, 1995; Barrett, 2007; Sigmund, 2010). Despite  
40 this, the reasons behind its ubiquity remain an open, and challenging, quest in several  
41 areas of science. To address this issue, different models were built in the framework of  
42 evolutionary game theory (Maynard-Smith, 1982; Sigmund, 2010) to try to reproduce the  
43 emergence of cooperation amongst selfish individuals, using different mechanisms to  
44 achieve this goal. In this quest, the role of higher levels of individual cognition has  
45 remained elusive. In the present paper, we show that an additional layer of individual  
46 complexity may provide a major contribution to the emergence and robustness of  
47 cooperation and investigate how the evolutionary advantage of such complexity is tightly  
48 connected with the way in which the population is structured.

49 For this purpose, we study the  $N$ -person Prisoner's Dilemma, better known as a Public  
50 Goods Game (**PGG**) of cooperation (Hardin, 1968; Kollock, 1998; Barrett, 2007;  
51 Sigmund, 2010). **PGGs** constitute the primary tool in evolutionary game theory to  
52 investigate the emergence of cooperation in group interactions. In this game,  $N$   
53 participants can decide to donate or not an amount to the public good. An individual is  
54 considered to be a cooperator (**C**), if she donates; otherwise she is a defector (**D**). The  
55 donations are collected in a common pot and multiplied by a factor  $r$  ( $r > 1$ ). The resulting  
56 sum is subsequently shared equally among the members of the group independently of  
57 their contribution. Hence, in a mixed group of  $N$  individuals, refusing to contribute to a

58 common good assures the highest individual payoff. Thus, if all participants are rational,  
59 individuals refuse to donate, falling into the Tragedy of the Commons (Hardin, 1968).

60 Among the many mechanisms (Nowak, 2006; West et al., 2007) suggested to avoid this  
61 negative outcome, such as repeated interactions (Trivers, 1971), reward and punishment  
62 mechanisms (Sigmund et al., 2001; Fehr and Gächter, 2002; de Quervain et al., 2004;  
63 Sigmund et al., 2010; Szolnoki and Perc, 2010), reputation systems (Nowak and  
64 Sigmund, 2005; Ohtsuki and Iwasa, 2006), voluntary participation (Brandt et al., 2006),  
65 etc., most assume large populations and a well-mixed interaction pattern in which every  
66 player interacts equally likely with everyone else. While the well-mixed limit may be  
67 valid for small populations, spatial constraints or complex networks of contacts often  
68 shape the interactions within large-scale societies. This feature has been initially  
69 addressed by means of regular lattices and graphs, exploring the role of space in the  
70 emergence of collective behaviors (Nowak and May, 1992; Nowak et al., 1994; Szabó  
71 and Hauert, 2002; Szabó et al., 2005; Ohtsuki et al., 2006; Szabó and Fáth, 2007; Taylor  
72 et al., 2007). More recently, our increasing understanding of real interactions structures  
73 (Doreian and Stokman, 1997; Barabási and Albert, 1999; Watts, 1999; Amaral et al.,  
74 2000; Dorogotsev and Mendes, 2003; Newman, 2003) has led to a general analysis of  
75 evolutionary dynamics in a broad range of topologies (Santos and Pacheco, 2005; Vukov  
76 and Szabó, 2005; Santos et al., 2006; Gómez-Gardeñes et al., 2007; Szabó and Fáth,  
77 2007; Santos et al., 2008).

78 In a networked population, nodes represent individuals, whereas links represent shared  
79 goals, investments or exchanges. In an N-person interaction setting, neighborhoods define  
80 a network of overlapping groups (Szabó and Hauert, 2002; Santos et al., 2008), defining

81 not only who interacts with whom, but also the universe of possible role models of each  
82 individual. With the help of this powerful and general population structure metaphor,  
83 many different communities can be modeled and the outcome of the strategies' evolution  
84 is highly dependent on the underlying topology. During the evolutionary process, every  
85 player is involved in  $(k+1)$  game-interactions, where  $k$  is the number of acquaintances  
86 (neighbors) of the given player. The group interactions take place in the  $(k+1)$  groups  
87 centered on the neighbors and on the focal player (see Figure 1A). The total payoff of a  
88 player is gained from these  $(k+1)$  games (Szabó and Hauert, 2002; Santos et al., 2008).

89 In the simplest setting (Santos et al., 2008), cooperators donate a fixed cost  $c$  to every  
90 **PGG** they participated. However this assumption may be unrealistic in situations where  
91 players participate in a large number of interactions, as it is very unlikely that players  
92 have such a huge amount of resources at their disposal at any time. Limited resources  
93 may add the limitation that all players have the same amount to invest, which will be  
94 equally shared amongst all the groups (Santos et al., 2008; Pacheco et al., 2009). This  
95 means that cooperators donate  $c/(k+1)$  to every group. This modification has a big impact  
96 when the interaction graph is heterogeneous, as we will discuss later. However for regular  
97 networks where the number of neighbors is the same for every node, this principle is  
98 equivalent to the traditional case with a rescaling of the cost  $c$  by a factor of  $1/(k+1)$ .  
99 Nevertheless fixing the available resources for the players raises new opportunities: what  
100 if cooperators could decide themselves how to distribute their donations amongst the  
101 groups they interact with?

102 Such a cooperator opens up a whole avenue of new strategies, from random ones where  
103 cooperators just randomly contribute to the different groups, to strategies where

104 cooperators can take past events, decisions or incomes into account before deciding about  
105 the amount to contribute to each collective endeavor. Using this idea, we shall address the  
106 role played by this additional speck of complexity, and consider cooperators that donate  
107 to different groups proportionally to the income previously received from each given  
108 group (see Figure 1B). Individuals assess how large is the share they obtained from each  
109 group and, in the next generation, they donate the corresponding fraction of  $c$  to this  
110 group. As detailed in Section 2, this strategy is reactive and inherently assumes that  
111 players can keep track of their payoffs from immediate past events, i.e., they have some  
112 kind of short-term memory. As group profits are generated solely from donations of  
113 cooperators, this strategy rewards groups with higher cooperative standards. From this  
114 point of view, this strategy can be seen as a form of direct reciprocity (Trivers, 1971) in  
115 group interactions. For this reason, we shall refer to this type of behavior as *reactive*  
116 *strategies*.

## 117 **2 Methods**

118 To have a clearer understanding of the results, here we give a more thorough description  
119 of the model details. Players are located on the nodes of a graph. The edges of the graph  
120 define who interacts with whom and who can imitate whom. Each individual engages in  
121  $k+1$  **PGG** games where  $k$  is the number of her neighbors. The **PGG** groups are defined  
122 by the central player and her neighbors, i.e., a given player is member of his own and his  
123 neighbors' group (Figure 1A). Players gain their accumulated payoff from these  
124 interactions in each generation. There are two available strategies: defectors (**D**) do not  
125 donate to the public good, while cooperators (**C**) donate the cost  $c$ . For the different



126 simulation scenarios, cooperators use slightly different strategies. In the unconditional,  
 127 unconstrained case (UUC), they donate the cost  $c$  to every group they participate in. In  
 128 the unconditional, constrained case (UCC), when the amount of donation per player is  
 129 fixed to  $c$ , they donate to all their groups equally, i.e., all groups' pot receive  $c/(k+1)$ . In  
 130 the conditional, reactive case (CRC), cooperators are allowed to redistribute their  
 131 donations, and they donate proportional to the payoffs they received from the given group  
 132 in the previous simulation step. Hence, if a cooperator received payoff  $p_i$  from his  $i$ th  
 133 group at a given time (see Introduction and Fig. 1) then she will donate  $(c \cdot p_i)/P$  in the  
 134 next round, where  $P = \sum_{j=1}^{k+1} p_j$ . In the first round of the simulation, cooperators donate  
 135 equally to the groups. The same happens if a defector imitates a cooperator and she had  
 136 zero total payoff ( $P=0$ ) in the previous round.

137 Simulations start from a random initial condition where the concentration of cooperators  
 138 and defectors is equal. Having different initial conditions (e.g. fewer cooperators at the  
 139 start) does not really influence the stationary distributions. The average values are  
 140 decreased slightly because of the cases when cooperator clusters cannot form and  
 141 cooperation vanishes at the initial transitional period due to the low initial cooperator  
 142 frequency. We use synchronous update: In each simulation time step, we update the  
 143 payoff for every player, and then randomly pick a neighbor ( $y$ ) for every player ( $x$ ).  
 144 Player  $x$  can adopt the strategy of player  $y$  with a probability given by the so called pair-  
 145 wise comparison rule:  $W(x \leftarrow y) = \frac{1}{1 + e^{(P_x - P_y)/K}}$ , where  $P_x$  and  $P_y$  are the total payoff of  
 146 players  $x$  and  $y$  while  $K$  is characterizing the amount of errors in decision making. After  
 147 calculating the possible strategy imitations, we update the strategy of every player at the

148 same time.

149 The final outcome of evolution and cooperation is obtained from extensive computer  
150 simulations performed on the following network topologies: We consider paradigmatic  
151 examples of homogeneous and heterogeneous network structures. For the former class we  
152 consider a square lattice with von Neumann neighborhood structure and periodic  
153 boundary conditions. For the latter class, we explore the effects of topological  
154 heterogeneity using Barabási-Albert scale-free networks (Barabási and Albert, 1999),  
155 generated by the combination of growth and linear preferential attachment. This leads to  
156 distributions of group sizes and number of games played by each player that follows the  
157 degree distribution of the network, i.e., a power-law. After 2000 initial generations, we  
158 average the strategy concentrations over the population during 10000 generations. Each  
159 result is obtained from 100 runs from different random initial conditions and in the case  
160 of heterogeneous networks, from 10 different network realizations. We investigated the  
161 strong selection regime and used  $K=0.04$ . The qualitative behavior of the system is the  
162 same for higher  $K$  values (we tested it up to  $K=1.0$ ), the ranking among the different  
163 strategies remains the same so the conclusions are valid for those parameter values too. In  
164 the case of the homogeneous networks, higher  $K$  shifts the threshold above which  
165 cooperation can be maintained to higher multiplication values as among these conditions  
166 defectors can break in to the cooperator cluster more easily due to the higher noise. For  
167 heterogeneous networks, the thresholds are about the same but the transition from the full  
168 defector state to full cooperation is sharper, isolated, small islands of the minority  
169 strategy are consumed due to the higher noise.

### 170 3 Results and Discussion

171 Figure 2 shows the results for the unconditional cooperative strategy (UUC) and the  
 172 reactive cooperative strategy (CRC) on the square lattice (see Fig. 1A) as a homogeneous  
 173 interaction network (note that, in this case, UUC and UCC lead to the same results). The  
 174 fraction of cooperators is plotted as a function of the normalized multiplicative factor  
 175  $\eta=r/(k+1)$ , where  $k=4$  for the square lattice with von Neumann-neighborhood. In infinite,  
 176 well-mixed populations, full defection is replaced by full cooperation at  $\eta \geq 1$ , as in this  
 177 case, a single cooperator can provide positive payoff for the whole group. Under spatial  
 178 reciprocity, the threshold happens for significantly lower values of  $\eta$ . There is also  
 179 formally a lower threshold at  $\eta \leq 1/(k+1)$ , in which case even full cooperation results in  
 180 negative payoffs, that is, cooperation becomes impossible among these conditions.

181 The results in Fig. 2 show that reactive cooperative strategy (CRC, red circles)  
 182 successfully outcompetes defectors for a wide range of parameters when compared with  
 183 unconditional cooperators (blue squares), while managing to achieve mixed, dynamical  
 184 coexistence with them under rather unfavorable conditions. By dividing their donations  
 185 among successful groups, cooperators are able to support the emergence of cooperative  
 186 clusters by “directed” contributions to fellow cooperator groups. Moreover, these  
 187 individuals are able to withdraw help from the most defective groups, located at the edges  
 188 of the cooperative clusters. So the reactive cooperative strategy could be considered as a  
 189 mix of two mechanisms: *reciprocity* towards good, generous neighbors/groups and  
 190 *punishment* with the withdrawal of donations from defective neighbors. As a result,  
 191 whenever the conditions are not too adverse, the cooperative clusters can grow and they  
 192 will almost always take over the whole community. In the coexistence region, due to the

193 lower multiplication factor, cooperator clusters gain and loose territories dynamically  
194 while the strategy concentrations slightly fluctuate around the average. We have  
195 investigated other regular networks, such as the kagome-lattice (Syôzi, 1951) and the  
196 one-dimensional ring-graph (Watts, 1999) to filter out possible “square lattice”-specific  
197 features but the results were qualitatively the same on all of them: the overall level of  
198 cooperation was very significantly increased with the introduction of a small level of  
199 complexity (CRC). Similar qualitative results are also obtained for other values of the  
200 intensity of selection, here associated with the parameter  $K$ .

201 The picture is different when the interaction graph is described by a heterogeneous  
202 network. In this case different players will have, in general, different number of  
203 neighbors. Consequently, fixing the maximum amount of contribution for unconditional  
204 cooperators is no longer a mere rescaling issue — in fact, it has a huge impact on the final  
205 outcome of evolution (Santos et al., 2008; Pacheco et al., 2009). Blue squares in Figure 3  
206 show the results on a scale-free network when cooperators donate  $c$  to every group they  
207 are part of (UUC). Cooperation becomes viable in a considerably wide range even if  
208 cooperators in a central role have to invest a big amount. The key of the success of  
209 cooperation is that the complex interaction network made the payoff distribution  
210 heterogeneous and this gave an opportunity for cooperators to outplay defectors: central  
211 cooperators can collect a high income due to the many groups they are part of and can  
212 turn most of their neighbors to cooperators while if a defector ends up in a central role,  
213 she will turn her followers to defectors, decreasing her own payoff and after a while  
214 loosing the “leading” position. However for lower  $\eta$ , the establishment of cooperation is  
215 hindered by the fact that highly connected individuals (hubs) have to invest a huge

216 amount which can be non-remunerative in a partly defective environment. Fixing the total  
217 amount of donation of each individual (UCC) can be of assistance to this problem, as  
218 shown with the green triangles. Indeed, in (Santos et al., 2008; Pacheco et al., 2009) it has  
219 been argued that it is not the amount given what is important but the act of giving.

220 Unlike the situation observed in homogeneous networks, the introduction of reactive  
221 cooperators (CRC) does not boost cooperation further (red circles in Fig. 3). Apparently,  
222 the additional complexity in the strategy does not add up to the effects already induced by  
223 the scale-free interaction network, associated with the heterogeneous payoff distribution  
224 In other words, the network structure may by itself dispense the need to develop highly  
225 cognitive capabilities. Differently, a heterogeneous allocation of donations may open a  
226 window to smarter ways of cheating in a heterogeneous network context.

227 On the other hand one expects that additional skills may enhance the aptitude of  
228 Cooperators to protect themselves against Defectors, which may play a different role  
229 depending on the composition of the population. Up to now we have been discussing the  
230 viability of cooperation to emerge from an equal distribution of cooperators and  
231 defectors. But how stable is cooperation once established? In the following we investigate  
232 the robustness of the cooperative community against defector invasion attempts. To this  
233 end, and after an initial transient period, in every generation we replace a given amount of  
234 the population by defectors. It turns out that reactive cooperators can withstand defector  
235 attacks far more successfully. Figure 4 shows that even for extreme defector inflow  
236 values as high as 10% of the population in every generation, cooperation survives with  
237 the help of this more sophisticated strategy. We can define a numerical index to compare  
238 the robustness of cooperation in different scenarios by calculating the integral below the

239 surfaces in Fig. 4. The ratio of the integrals  $\Omega_{\text{CRC}}/\Omega_{\text{UCC}}=1.46$  shows that the reactive  
240 cooperative strategy (CRC) is almost 1.5 times more successful in defending itself than  
241 the unconditionally equal cooperators (UCC).

242 Finally, it is also noteworthy that different cognitive skills and levels of complexity can  
243 have an impact in several emerging features of the population beyond the levels of  
244 cooperation. In Fig. 5 we portray the wealth (here understood as fitness) distribution of  
245 the population in a fully cooperative community, that is, we compute how the total  
246 income is divided among the individuals. It is known (Santos et al., 2008) that donating a  
247 fixed cost per individual results in less poor and more rich people than in the case of  
248 donating a fixed cost per game. With the advent of reactive cooperators, society becomes  
249 more “fair”, individuals are shifted from the poor regions to the “middle class”. This can  
250 be also shown by the Gini coefficient  $G$  (Gini, 1912), which measures inequality of a  
251 distribution ( $G=0$  for maximum equality and  $G=1$  for total inequality):  $G$  is 0.30 for the  
252 reactive cooperators (CRC) and 0.38 for the UCC. The few, very poor individuals are  
253 victims of the randomly built scale-free interaction network: they belong to an  
254 unfortunate neighborhood that condemns them to lower payoffs.

## 255 **4 Conclusions**

256 We investigated the emergence of cooperation in Public Goods Games from the point of  
257 view of individual complexity. We found that increasing the complexity of the cooperator  
258 strategy can help to establish and maintain cooperation in different environments. When  
259 the interaction network is homogeneous, described by regular graphs, the introduction of  
260 a more complex, reactive cooperator strategy (CRC) helped to improve the performance

261 of cooperators to a great extent. However if the interaction network itself is complex and  
262 heterogeneous, as in the case of a scale-free graph, then the additional complexity in  
263 strategy (CRC) does not positively take effect on the spreading range but renders  
264 established cooperation more robust against defector invasion.

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344  
345

346 **Figure legends**

347 **Figure 1. Public Goods Game on graphs. A.** Players are participating in  $(k+1)$  games in  
348 every generation. Colored bubbles show the PGG groups in which the central (orange)  
349 player is participating while the  $p_i$  values show the payoff she gains from the  
350 corresponding groups. **B.** Reactive behavior of CRC cooperators: colored bars show the  
351 orange player's payoff-share gained from each group (with a given color) compared to  
352 the player's total payoff. In the next generation, cooperators divide their contribution to  
353 the public good according to their previous income.

354 **Figure 2. Results of additional cooperator complexity on the square lattice:** the  
355 fraction of cooperators as a function of the normalized multiplicative factor ( $\eta$ ) for the  
356 different cooperator strategies. The incipient cognitive abilities of CRC cooperators make  
357 it possible to prevail under much worse conditions. Red circles show the concentration of  
358 CRC cooperators when the donations are given proportional to the payoff from the  
359 groups, while blue squares show the results of the traditional case (UUC or, equivalently,  
360 UCC), where the donations are shared equally. We used a square lattice of size  
361  $Z=100 \times 100$  as an example of a homogeneous interaction structure, with nearest neighbor  
362 (von Neumann) interactions ( $k=4$ ) and with periodic boundary conditions.

363

364 **Figure 3. Cooperation level with scale-free networks as interaction structures.** The  
365 different symbols show the fraction of cooperators with different model setups as a  
366 function of the normalized multiplicative factor ( $\eta$ ). For heterogeneous, scale-free  
367 networks,  $\eta$  is calculated using the average connectivity ( $\langle k \rangle = 4$ ) of the graph. Blue  
368 squares stand for the UUC cooperators, green triangles for the UCC cooperators, while  
369 red circles indicate the CRC cooperators. The definition of the strategies is given in the  
370 Methods. Scale-free networks (size of  $Z=1000$  and average degree of  $\langle k \rangle = 4$ ) were  
371 generated using the Barabási-Albert algorithm (Barabási and Albert, 1999).

372 **Figure 4. Robustness against defector inflow on scale-free networks.** Color codes  
373 show the cooperator concentration for different defector inflow rates as a function of  $\eta$ .  
374 After a transient period, a given amount of players were randomly replaced by defectors  
375 in every generation and the concentration values were calculated during the subsequent  
376  $10^4$  generations under continuous defector inflow. The left panel (4A) displays the results  
377 for the case when cooperators share their donations equally (UCC), while the right panel  
378 (4B) shows them for the more complex, reactive cooperator strategy (CRC). CRCs are  
379 more robust against the invasion of a minority of free-riders, specially for large  $\eta$  and  
380 defectors inflow rates.

381 **Figure 5. Wealth distribution in fully cooperative populations for the different**

382 **cooperative strategies.** Red bars stand for the cognitive cooperator strategy (CRC) while  
383 striped bars show the distribution for the “equal” cooperators (UCC). CRC cooperators  
384 lead to less poor and more rich individuals. Both distributions were obtained from an  
385 average over 10 different network realizations with a size of  $Z=10^3$ .

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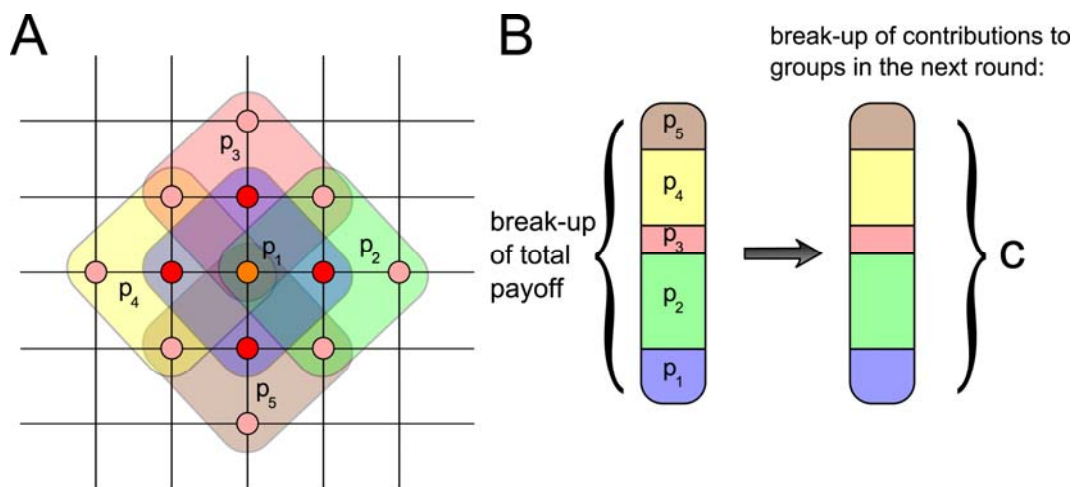
**Highlights:**

- We study the evolution of cooperation in the framework of Public Goods Games.
  - Cooperative players are able to distribute their donations to their liking.
  - Directed investments greatly enhance cooperation on homogeneous graphs.
  - Established cooperation is robust against the invasion of free-riders.
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Fig. 1



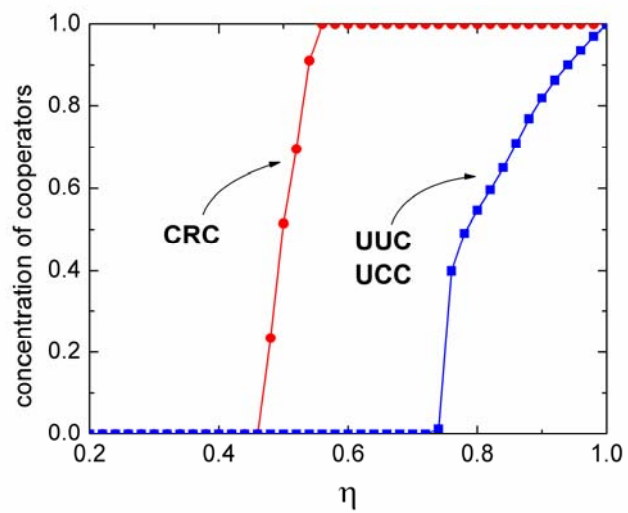
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Fig. 2



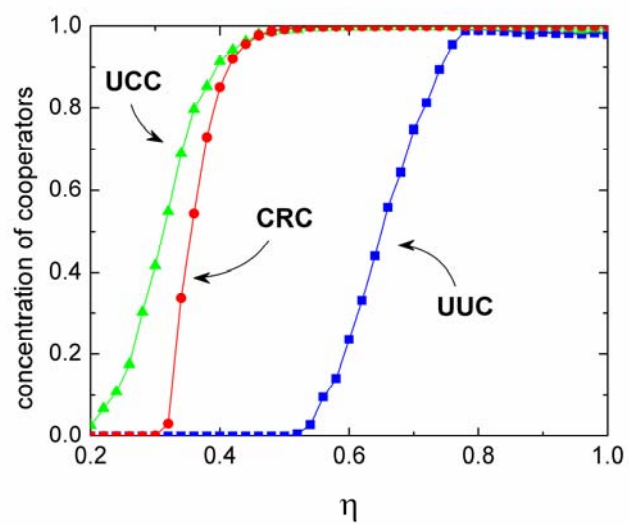
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Fig. 3



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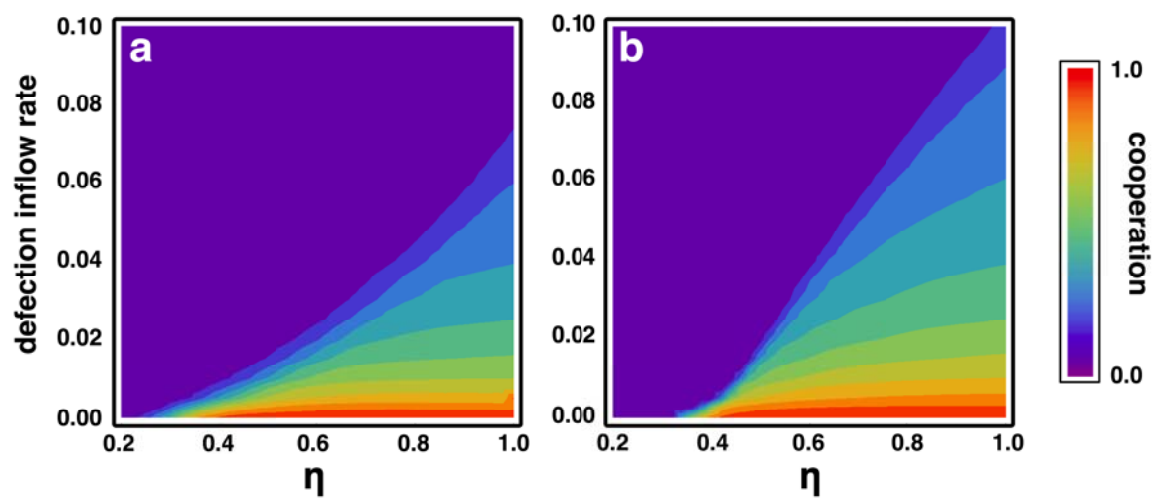
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Fig. 4



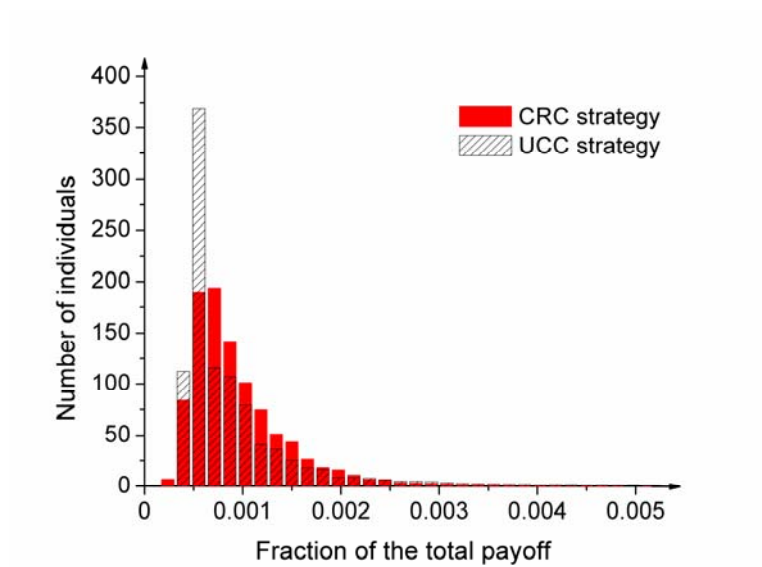
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Fig. 5



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