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The evolution of cooperation in heterogeneous networks when opponents can be distinguished

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Abstract

Cooperation has been widely studied in the context of evolutionary games on graphs. Usually the players are set on the nodes of a network and adopt the same strategy, cooperation or defection, against all of their neighbors. In heterogeneous networks, it was shown that cooperation is highly sustained, although when the cumulative payoff is normalized by the connectivity, the cooperation is severely weakened. Here, we study the evolution of cooperation in heterogeneous networks when it is possible to adopt different strategies against different opponents. We study numerically different types of heterogeneous networks, including scale-free networks, that differ in the extent of the role of the highly connected nodes, usually called hubs. The remarkable result is that cooperation is maintained irrespective of whether the payoff is the total one or the normalized one, and, in spite of such blindness, we still find that the topology has a strong effect. When the presence of the hubs is more prominent, we find that the cooperation level decreases for synchronous update but remains almost unchanged for the asynchronous update. It is also shown that cooperation is robust against errors in the update rule.

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1. Introduction

Cooperation is a widespread behavior that is present from the simplest unicellular to the more complex multicellular organisms [1–8]. The core of the cooperation act is to pay a cost to bestow a benefit on another individual. Evolutionary theory came up to explain the ultimate causes of cooperative traits [9]. Why is cooperation widespread if it is so costly to their bearers? In the case of non-human animals, kin selection gives good ultimate explanations,

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because if the cooperator helps a relative, as the cooperator and the recipient of the help are genetically similar, it helps the transfer of the cooperative gene to the next generation [1, 7, 10, 12, 11]. But humans also cooperate with strangers [7]. Humans have developed remarkable mechanisms to sustain cooperation, like the reciprocity mechanism. Reciprocity means that what an individual does depends on what others do to it directly or indirectly. Direct reciprocity means that I choose what to do to you depending on what you do to me [13]. Indirect reciprocity means that my behavior toward you also depends on what you do to others [14]. One of the most simple strategies that can perform reciprocity is ‘tit for tat’ (TFT) strategy, where the players do whatever the co-player did in the previous round. This simple strategy was first proposed in Axelrod’s tournaments, where TFT was the greatest winner [13, 15]. In the context of reciprocity, punishment and reward are also present in human behavior and are good proximate explanations for cooperation [16–18]. Note that all of the reciprocity strategies assume the ability of discriminating the co-players in such a way that cooperative traits receive different treatments when compared to the non-cooperative traits.

Genetic inheritance is part of the mechanism of the cooperative trait evolution. But one of the remarkable features that the humans have developed is the ability of cultural transmission [7, 19]. Humans have developed a cognitive support that allows them to learn with others and to imitate the successful individuals. This means that if a successful individual can be imitated, natural selection favors the cognitive capacity that allows the imitation of the best, since those that are able to learn perform better than those that are not able to learn [19]. Therefore cooperation can also spread by cultural transmission, like the process of imitating the best [19, 20]. But social learning is not the only way to learn. Individuals can also learn from their own experience, e.g., by changing the strategy if the current one is no longer satisfying [21, 22]. One of the most successful strategies that has been studied is the ‘win-stay-lose-shift’ strategy [21]. In this strategy, each individual has an aspiration level and changes its strategy if the current payoff is below the aspiration level. It has also been shown that ‘win-stay-lose-shift’ strategy outperforms TFT [21].

The imitation process is a model of the reproduction of strategies. When a successful individual is imitated, it means that somebody imitated the strategy that the successful individual is adopting. It does not mean that the successful individuals generated offspring. It is just a cultural transmission. In the context of cultural transmission, the social network of interactions is an important factor to be studied [23]. From simple interaction networks, like the square lattices [24–26], to complex interaction networks, like scale-free networks [27–29], it was shown that cooperation is maintained in the imitation process. Scale-free networks are claimed to be a unifying framework for the evolution of cooperation [27]. The properties of the scale-free networks [30, 31], like the connectivity degree correlation, the clustering coefficient or the assortative degree, have strong effect in the evolution of cooperation [32, 28, 29]. In these networks, the initial condition has also a strong effect. If the hubs are initially defectors, the final cooperation level is low. On the other hand, if the hubs are initially cooperators, the final cooperation level is high [33]. It was also shown that the transition from random to scale-free networks is followed by an increase in the cooperation level [34]. All of these results support the assumption that the topology of the interaction network has an important effect in the evolution of cooperation. In the great part of these models, the success is measured in terms of the cumulative payoff. In scale-free networks, the hubs can have a huge cumulative payoff just because they have many interactions. If the cumulative payoff is divided by the connectivity of the node, in other words, if the effective payoff is used, the advantage of scale-free networks is weakened [35]. It is as if the scale-free network was a regular network. The asymmetry introduced in the cumulative payoff due to the heterogeneity has also been addressed in a different way by limiting the number of interactions that a node can establish

per round [36]. Although the total payoff seems to be more realistic [37], the effective payoff might be a valid update rule in the cultural evolution scenario. A player interacting with a hub might recognize that the huge payoff of the hub is not due to its strategy only, but due to the large number of interactions. The effective payoff might be thought of as an increase in the rationality of the players.

A simple model was recently introduced to study the evolution of cooperation. It takes into account the possibility of distinguishing the opponents, the social and the individual learning, the effects of the interaction network and an implicit punishment [38]. Instead of adopting a single strategy against all of the opponents, each individual can adopt a different strategy against each opponent. An individual imitates the strategy of the more successful players and changes the strategy in the interaction that gives the worst payoff by the imitated one. When the players are placed in a square lattice, a ring and a fully connected network, it is shown that cooperation can be maintained even if the tendency to defect is high. For the fully connected network, this result was also corroborated by a new mean-field approximation [39].

In this work, we analyze the effects of the total and the effective payoff in the evolution of cooperation in heterogeneous networks within the model where it is possible to distinguish the opponents. Here, we consider networks generated by an algorithm developed by Krapivsky and Redner [40, 41]. By tuning a single parameter, this algorithm generates networks that vary from random grown networks to networks where all nodes are connected to a single subset of nodes. The nodes in this subset are called hubs. For an intermediate value of the control parameter, the scale-free network introduced by Barabási and Albert [31] is recovered. We find the remarkable result that cooperation is maintained irrespective of whether the payoff is the total one or the effective one. It should be stressed that within the usual models, cooperation is severely weakened in heterogeneous networks with the effective payoff. This work is organized as follows. In the following section, we present our model in detail. The results are discussed in section 3 and we summarize our results in the last section.

2. The model

We use the prisoner dilemma as the scenario for the cooperation problem and set the players on the nodes of a network of size N . The usual models with structured populations set a single strategy to each player, namely, cooperation (C) and defection (D). If a focal player j interacts with k_j neighbors, its strategy is just $S_j = C$ or $S_j = D$. It adopts the same strategy against all of the k_j opponents, where k_j is the connectivity degree of node j . In the model where it is possible to distinguish the opponents, the focal player j adopts a set of strategies, $\{S_{j,1}, \dots, S_{j,k_j}\}$, where $S_{j,v} \in \{C, D\}$ is the strategy that player j adopts against the neighbor v . So the focal player j has k_j interactions. If in one of these interactions, the focal player j plays C against an opponent who is playing D , we denote this interaction as (C, D) (the first entry is the strategy of the focal player j and the second entry is the opponent strategy).

In a simplified version of the prisoner dilemma payoff [23], both players receive 1 upon mutual cooperation and ϵ upon mutual defection; the defector receives b if the other cooperates, and the cooperator receives 0 if the other defects. The tendency to defect is given by b ($b \geq 1$), and ϵ is small ($\epsilon \ll 1$). Each individual plays one round of the game with each of its neighbors and earns a cumulative payoff. The total payoff is just the cumulative payoff and the effective payoff is given by the cumulative payoff over the connectivity of the node. The total and the effective payoff are two different ways to measure the success. We study the evolution of cooperation in these two different scenarios. In the first one, everyone uses the total payoff and in the second one everyone uses the effective payoff. When two players interact, we assume that they have the information of (i) the total, or the effective, and of (ii) the strategy they

are using against each other. In the total payoff scenario, each player randomly chooses one neighbor and compares its total payoff with the opponent's one. If the opponent's total payoff is bigger than its own one, it imitates the strategy that the opponent is using against it with probability p_{tot} proportional to the difference between the total payoffs, ΔP_{tot} , namely

$$p_{\text{tot}} = \frac{|\Delta P_{\text{tot}}|}{bk_{\text{max}}},$$

where k_{max} is the highest connectivity degree among the connectivities of the focal player and of the opponent. Here b ensures the proper normalization. On the other hand, if the opponent's total payoff is lower than or equal to its own one, the focal player remains with the same strategies. In the effective payoff scenario, the rule is the same except that the imitation takes place with probability p_{eff} proportional to the difference of the effective payoffs ΔP_{eff} , namely

$$p_{\text{eff}} = \frac{|\Delta P_{\text{eff}}|}{b}.$$

If imitation takes place, in both scenarios the new strategy replaces the strategy used in one of the interactions that gives the worst payoff. If more than one interaction gives the worst payoff, a random one among these poor interactions is chosen. The worst pairwise payoff of the focal player is given by the interaction (C, D) , followed by (D, D) , (C, C) and (D, C) , because in these interactions the focal player earns 0, ϵ , 1 and b , respectively. For example, this means that if the focal player has m (C, D) interactions and a defection strategy is imitated, a random interaction among these m (C, D) interactions is replaced by (D, D) . We consider synchronous and asynchronous updates. In the synchronous update, every player carries out the update process simultaneously. In the asynchronous update, first an individual is randomly chosen and carries out the update process. After this individual update, the cumulative payoffs are updated, and other individual is randomly chosen to update its strategies. A time step, the Monte Carlo step (MCS), in the asynchronous update consists of N of such individual processes.

To study the influence of the population structure, we consider three types of networks: a random grown network, the Barabasi and Albert scale-free network and a super-hub network. These networks are generated using the Redner and Kaprivsky algorithm [40]. It is an algorithm of growing networks. It starts with six nodes each linked to two nodes (self-connection is not allowed), which is the appropriated initial condition [41]. At each time step, a new node x comes up with two links. The nodes to which the new node is attached are called the antecessors of the new node. The new node randomly chooses two nodes, namely y_1 and y_2 . With probability $1 - r$, the new node connects to y_1 and, with the same probability, to y_2 . But with probability r , each of the links is rewired to the antecessor of y_1 and y_2 . The three types of heterogeneous networks are obtained by tuning the parameter r . In random grown networks we set $r = 0.0$, so the new nodes are randomly linked to the old nodes and the degree distribution has an exponential distribution. For $r = 0.5$, we have the Barabasi and Albert scale-free network [28] and the degree distribution follows a power law. There are a few nodes having lots of links while others have a few links. In the super-hub network, we set $r = 1.0$ and all of the new nodes are linked to the initial nodes. In this paper, we analyze a population of size $N = 100$ because of the huge time to reach the equilibrium configurations. We performed simulations for larger networks up to $N = 1000$ for some parameters and the results remain qualitatively unchanged. Note that the process of growing the network is used just to generate the network. We do not consider co-evolution of the growing network and the evolutionary game [42].

We made simulations with initial conditions where each individual has a probability of 0.5 to cooperate in each interaction. The cooperativity in the population is measured by the average fraction of cooperation (F_c) in the population. If $n_c(i, t)$ is the quantity of C strategies used by

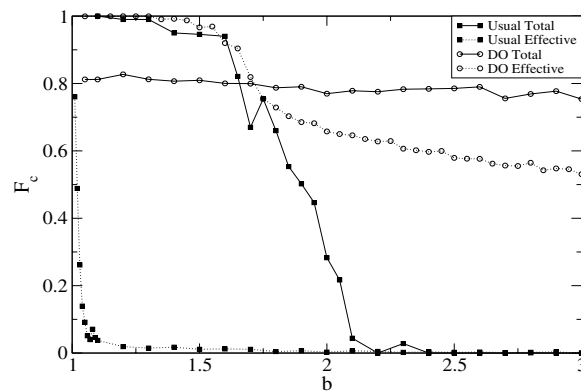


Figure 1. Fraction of cooperation as a function of b in the Usual and in the DO model for $r = 0.5$. The results are shown for the total and the effective payoff with synchronous update.

the player i at time t , the cooperation fraction of player i is given by $f_c(i, t) = n_c(i, t)/k_i$. Then we discard the transient time needed to reach the stationary state and make a time average of $f_c(i, t)$ over 1000 MCS. The average fraction of cooperation (F_c) is given by

$$F_c = \frac{1}{N} \sum_{i=1}^N f_c(i),$$

where $f_c(i)$ is the time average of $f_c(i, t)$ in the stationary state. A second average is made over 100 different samples. We take b values in the range $1 < b \leq 3$ and consider $\epsilon = 0.001$. We call the model where it is possible to distinguish the opponents the ‘DO model’ and the usual model where the players adopt a single strategy the ‘Usual model’.

3. The results

First let us state a fundamental feature of the model that does not depend on the topology nor on the synchronicity of the update. We state that any interaction of type (C, C) will never be replaced by (D, C) . Suppose that a focal player imitates a defection strategy of the opponent. This means that the focal player has at least one (C, D) or (D, D) interaction. These interactions furnish the payoff 0 and ϵ that are smaller than that of a (C, C) interaction, namely 1. It follows that (C, C) will never be replaced. This proves the existence of a lower bound for the fraction of cooperation given by the initial fraction of mutual cooperation. One can see that mutual cooperation is never destroyed and every exploitation is punished when a defection is imitated. Once the exploitations are punished, the dynamics of the synchronous and the asynchronous update becomes different. In the synchronous update, it is possible to have a (D, D) to (C, C) transition whenever two players make a (D, D) to (C, D) transition in their shared (D, D) interaction. This is an essential feature of the synchronous model. This kind of transition does not take place in the asynchronous update.

The heterogeneous networks are claimed to help the emergence of cooperation. But in the usual models with the effective payoff, the benefits of the heterogeneity are smoothed and the dynamics is similar to the dynamics in regular graphs [35]. The first remarkable result of the DO model is that cooperation is maintained independently if the payoff is the total one or the effective one. Figure 1 shows the simulation results for the Usual model and the DO model with both the cumulative and effective payoffs for $r = 0.5$ and synchronous update.

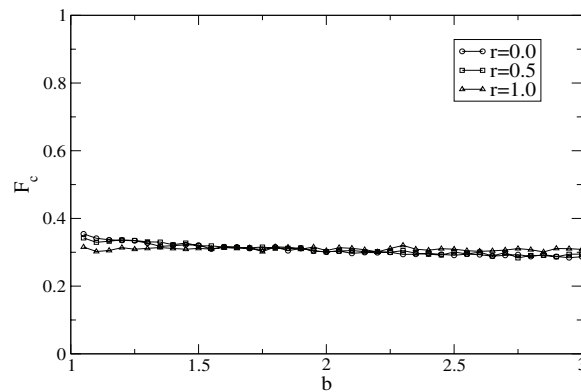


Figure 2. Fraction of cooperation as a function of b in the DO model for $r = 0.0$, $r = 0.5$ and $r = 1.0$. The results are shown for the effective payoff with asynchronous update.

One can see that in the DO model the effective payoff actually provides higher levels of cooperation than the total payoff for low b values, although for large b values the opposite happens. Indeed it was shown for the DO model in a regular lattice that cooperations dominate the population for low b values and cooperation decreases for large b values [38]. So even though with effective payoff the network behaves like a regular network, cooperation is still maintained in the heterogeneous networks even for large b values. The asynchronous update has a weak dependence on the topology, as can be seen in figure 2. The cooperation fraction cannot go far away from the initial distribution of mutual cooperation, because of the absence of the (D, D) to (C, C) transition. The cooperation level remains at constant levels that does not depend much on b nor on r . So let us focus on the analysis of the synchronous update in the rest of this paper.

Another remarkable result is that in the DO model with total payoff, the fraction of cooperation does not depend much on b , while with the effective payoff the fraction of cooperation decreases as b increases. The reason for such b independence is related to the fact that with total payoff the most connected nodes have a major impact in the dynamics. The hubs have the largest payoffs and are always imitated, while they seldom imitate others. So the equilibrium distribution depends much more on the distribution of strategies in the hubs than on b . On the other hand, with effective payoff the hubs do not have any privilege concerning the cumulative payoff anymore.

The main topological feature is the presence of the most connected nodes, namely the hubs, that is controlled by the parameter r . Figure 3 shows the dependence of the fraction of cooperation on r for $b = 1.05$ and $b = 2.0$. One can see that as r increases, the cooperation decreases. For r close to 1, the network can be approximated by a star. The star is a network of size N where $N - 1$ nodes, the non-hubs, are connected to a central node, the hub. Figure 4 illustrates a star network. With the total payoff, the hub is always imitated but it never imitates anybody. So if the non-hub is facing a C , this C will be imitated by the non-hub, and if the non-hub is facing a D , this D will be imitated by the non-hub. The final outcome is the initial distribution of cooperation of the hub, which in the present simulations is of 50% of cooperation. With the effective payoff, the hub has no longer any prevalence and only the initial mutual cooperation is maintained in the star. So if r is close to 1, the cooperation fraction is lower with the effective payoff.

In order to understand the impact of r when r is not close to 1, it is worthy to look at the dynamics. Let us first look at the dynamics of the effective payoff. In the time evolution,

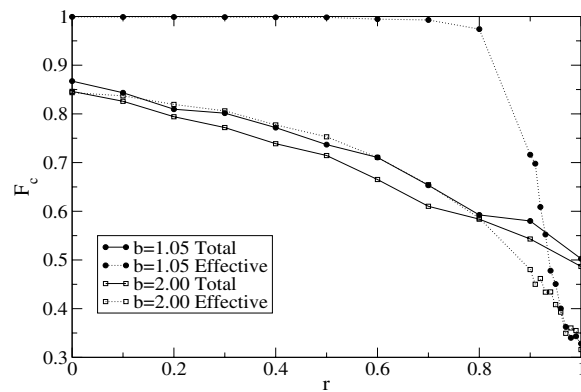


Figure 3. Fraction of cooperation as a function of r in the Usual and in the DO model for $r = 0.5$. The results are shown for the total and the effective payoff with synchronous update.

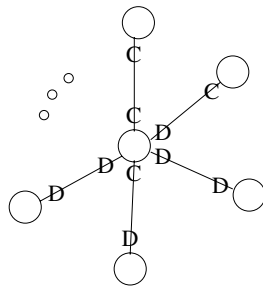


Figure 4. A star network with an initial distribution of 50% of cooperation.

initially large part of the exploitations are punished and the interactions of the type (C, D) become (D, D) , with all initial (C, C) maintained. Once this happens, the nodes with large connectivity have a payoff around $1/4$ and the nodes with low connectivity may have larger payoffs. For instance, if a node with two interactions has one (C, C) and one (D, D) , its payoff is equal to $1/2$. The next step necessary to have a cooperation boosting is the transition from (D, D) to (C, C) . In such a transition, two nodes should have the opportunity to imitate a C strategy and replace the same (D, D) interaction. But as r increases, we expect that the large part of the nodes are connected to the hubs. So one of the nodes needed to make the (D, D) to (C, C) transition is likely to be a non-hub that wants to imitate a C strategy adopted by a hub. But this imitation will not take place, because the hubs have smaller payoff at this stage. But as r decreases toward zero, it is more likely to have a (D, D) to (C, C) transition and the cooperation fraction increases. The argument for the total payoff is similar, except for the fact that now the hubs have the largest payoffs. To see that this argument is indeed valid in the case of the more complex networks studied here, we define an auxiliary measure. First let us rank the nodes by their connectivity. The node ranked in the first position is the node with the highest connectivity and the node ranked in the last position has the lowest connectivity. Let A_i be the fraction of cooperation available to be imitated by the node in the rank i . The measure A_i is given by the fraction of opponents adopting C against the node in the rank i that has a larger payoff than the payoff of the node in the rank i . In such kind of interactions, the C

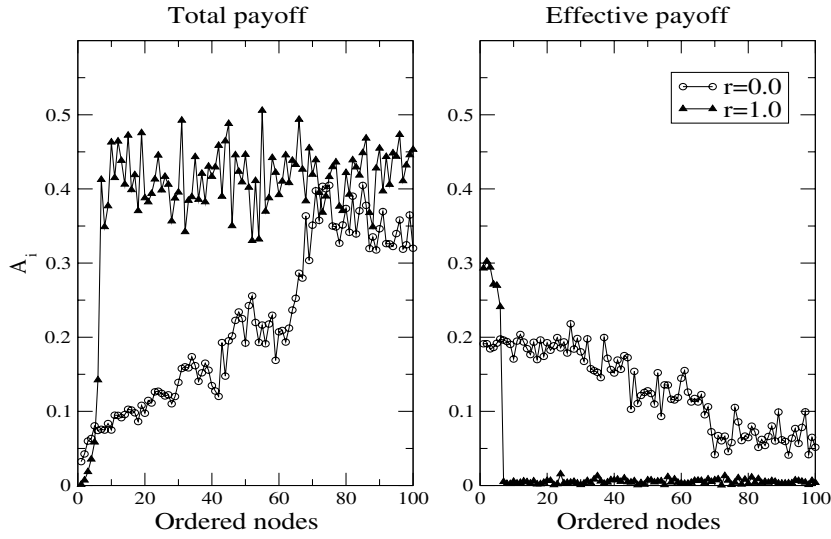


Figure 5. Fraction of interactions with cooperative strategies available for imitation (A_i). The rank of the nodes is represented in the horizontal axis. The rank equal to 1 represents the highest connectivity and the rank equal to 100 represents the lowest connectivity. The defection tendency used here is $b = 2.0$. The result is shown for synchronous update.

strategy is a good option to be imitated by the node in the rank i . We averaged the A_i measure in the first 10^4 MCS and plotted the average of A_i for all ranks. The results for $r = 0.0$ and $r = 1.0$ are shown in figure 5. If we look at A_i , we can see that the distinction between the six most connected nodes and the others is weaker for $r = 0.0$ than for $r = 1.0$. Restating the argument, we see that the probability that two nodes imitate simultaneously a C strategy is higher as r is close to zero in the networks studied here, which makes cooperation increase when r approaches zero. So these results corroborate the argument given above.

As stated before, the initial mutual cooperations are never destroyed. As a direct consequence, the initial condition has a strong impact on the equilibrium fraction of cooperation. Now instead of cooperating with 50%, let each player cooperate with its neighbors with probability given by p_0 . The probability of a mutual cooperation between two players is given by p_0^2 and, as p_0 increases, it is expected that the fraction of cooperation at equilibrium also increases. Figure 6 shows the fraction of cooperation in the DO model with the total and the effective payoff. The networks with low r have a higher fraction of cooperation. So again, the more a network centered around the hubs the harder it is to have cooperation in the DO model. In another analysis, it was noted for the Usual model [33] that the initial condition adopted by the hubs has a strong impact on the final outcome. We also performed simulations for different initial conditions adopted by the hubs. Note that in the algorithm used to generate the networks studied here, there is a set of six initial nodes that attract most of the links when r becomes close to 1. Keeping the other nodes with initial probability of cooperation equal to 0.5, we set three different initial conditions for the six initial nodes: (i) AllC, cooperation in all of the interactions; (ii) HalfC, cooperation with probability 0.5 in each interaction; (iii) AllD, defection in all of the interactions. For $r = 0.5$ and $r = 1.0$, the equilibrium fraction of cooperation with the total and the effective payoff for $b = 2.0$ is shown in table 1. Note that if the hubs are initially more cooperative, the final outcome is also more cooperative. The opposite happens if the hubs are initially more defective. Although the cooperation decreases if r increases, for the same r , if the hubs are more cooperative, the cooperation is higher.

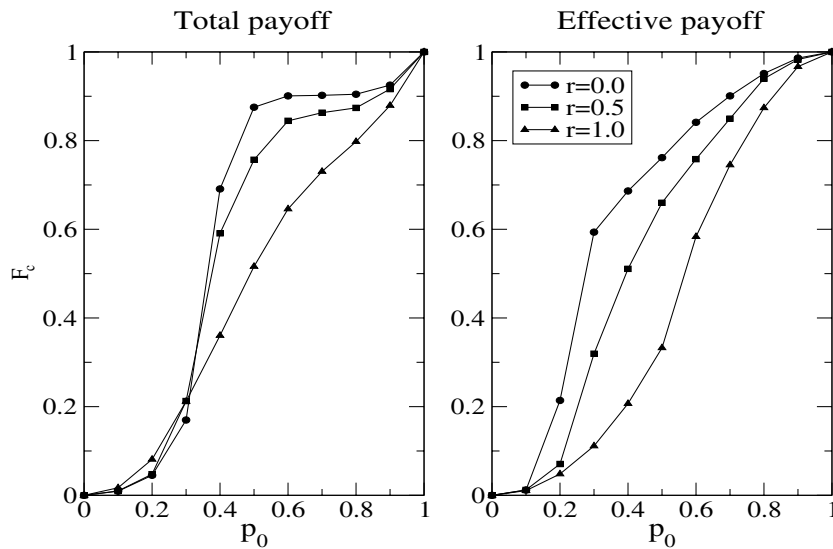


Figure 6. Fraction of cooperation at the equilibrium for different initial conditions (p_0) in the DO model for $b = 2.0$ and synchronous update.

Table 1. Fraction of cooperation for different initial conditions adopted by the six initial nodes used to grow the network. The initial conditions are (i) AllC, where they adopt cooperation in all of the interactions, (ii) HalfC, where they adopt cooperation with probability 0.5 and (iii) AllD, where they adopt defection in all of the interactions. The values for the total and the effective payoff for $b = 2.0$ and synchronous update are shown.

	Total payoff		Effective payoff		
	$r = 0.5$	$r = 1.0$	$r = 0.5$	$r = 1.0$	
AllC	0.77	0.76	AllC	0.77	0.76
HalfC	0.76	0.51	HalfC	0.66	0.32
AllD	0.26	0.00	AllD	0.59	0.00

In the DO model it is assumed that the players are able to distinguish the opponents and to keep track of what strategies are being played with each opponent. As in the case of reputation effects, if the reciprocator fails to recognize the defectors, cooperation no more thrives [43]. What happens to the cooperation fraction at the equilibrium if there is some probability of misjudgment of the worst interaction in the DO model? Let us suppose that with probability w , the focal player replaces a random strategy instead of the strategy in the interaction that gives the worst payoff. If $w = 0$, the original DO model is recovered and if $w = 1$ the replacement is completely random. We consider $w \in \{0, 0.001, 0.01, 0.1\}$ and again the fraction of cooperation in the equilibrium is measured. The results for $b = 1.05$ and for $b = 3.0$ in the DO model with effective payoff are shown in figures 7 and 8, respectively. Note that for $b = 1.05$ cooperation is robust against misjudgment, while for $b = 3.0$ it is not. With the total payoff, the results are similar. Note that in the presence of misjudgments, the mutual cooperations can be broken. In order to have cooperation, the rate of recovery of the mutual cooperation must be higher than the rate of D imitation. But the rate of D imitation is higher for large b values, which makes the cooperation non-robust against misjudgments in the region of large b . In the same way, we saw that for r close to 1, it is hard to recover

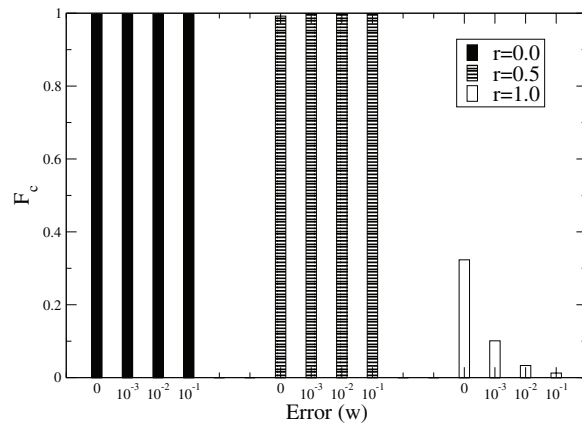


Figure 7. Fraction of cooperation at the equilibrium in the DO model with effective payoff for $b = 1.05$ in the presence of errors for the synchronous update. The results are shown for $r = 0.0$, $r = 0.5$ and $r = 1.0$.

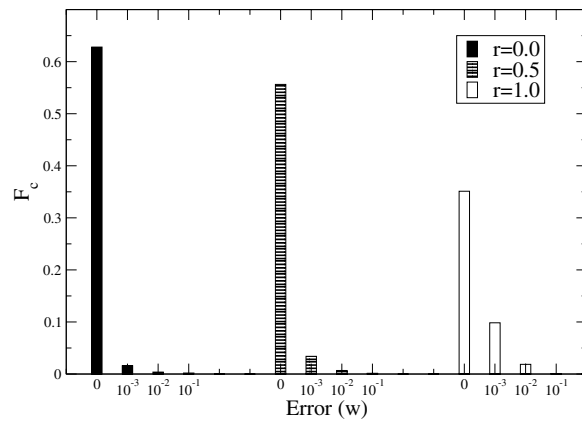


Figure 8. Fraction of cooperation at the equilibrium in the DO model with effective payoff for $b = 3.0$ in the presence of errors for the synchronous update. The results are shown for $r = 0.0$, $r = 0.5$ and $r = 1.0$.

mutual cooperations from (D, D) interactions. So, even for low b values, as r increases, the cooperation is less robust.

4. Conclusion

The mechanism of adopting different strategies against different opponents with strategy evolution given by the imitation rule and the replacement of the worst strategy is a simple mechanism that keeps cooperation alive. This mechanism has the general property of keeping the initial mutual cooperation and of punishing the exploiters. The remarkable feature of this model is that cooperation in heterogeneous topologies is maintained at high levels with both the total and the effective payoff, a phenomenon that does not occur in the usual models with the effective payoff. On the other hand, by changing the parameter r in the synchronous update, we found that the more the nodes centered around a few highly connected nodes, the lower the cooperation fraction. We also showed that the initial fraction of cooperation strongly shapes

the final outcome. In the asynchronous case, we showed that the network topology has a weak effect. As the last result, we showed that in the presence of misjudgments in the determination of the worst interaction, the cooperation fraction at equilibrium is robust for low b values. To conclude, we stress that, although in the usual model cooperation is severely weakened in the case of effective payoff, in the DO model cooperation is kept alive even for high b values in both cases.

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References

- [1] West S A, Griffin A S and Gardner A 2007 *Curr. Biol.* **17** R661
- [2] Griffin A S, West S A and Buckling A 2004 *Nature* **430** 1024
- [3] Strassmann J E, Zhu Y and Queller D C 2000 *Nature* **408** 965
- [4] Ratnieks F L W and Wenseleers T 2008 *Trends Ecol. Evol.* **23** 45
- [5] Sharp S P, McGowan A, Wood M J and Hatchwell B J 2005 *Nature* **434** 1127
- [6] Clutton-Brock T H *et al* 2000 *Proc. R. Soc. B* **267** 301
- [7] Boyd R 2006 *Science* **314** 1555
- [8] Fehr E and Fischbacher U 2003 *Nature* **425** 785
- [9] Tinbergen N 2005 *Anim. Biol.* **55** 297
- [10] Hamilton W D 1964 *J. Theor. Biol.* **7** 1
- [11] Jansen V A A and van Baalen M 2006 *Nature* **440** 663
- [12] Riolo R L, Cohen M D and Axelrod R 2001 *Nature* **414** 441
- [13] Axelrod R and Hamilton W D 1981 *Science* **211** 1390
- [14] Nowak M A and Sigmund K 2005 *Nature* **437** 1291
- [15] Axelrod R 1984 *The Evolution of Cooperation* (New York: Basic Books)
- [16] Fehr E and Gächter S 2002 *Nature* **415** 137
- [17] Boyd R, Gintis H, Bowles S and Richerson P J 2003 *Proc. Natl Acad. Sci. USA* **100** 3531
- [18] Sigmund K, Hauert C and Nowak M A 2001 *Proc. Natl Acad. Sci. USA* **98** 10757
- [19] Henrich J and Henrich N 2006 *Cogn. Syst. Res.* **7** 220
- [20] Ohtsuki H, Hauert C, Lieberman E and Nowak M A 2006 *Nature* **441** 502
- [21] Nowak M A and Sigmund K 1993 *Nature* **364** 56
- [22] Posch M 1999 *J. Theor. Biol.* **198** 183
- [23] Szabó G and Fáth G 2007 *Phys. Rep.* **446** 97
- [24] Nowak M A, Bonhoeffer S and May R M 1994 *Int. J. Bifurcat. Chaos* **4** 33
- [25] Szabó G, Vukov J and Szolnoki A 2005 *Phys. Rev. E* **72** 047107
- [26] Nakamaru M, Matsuda H and Iwasa Y 1997 *J. Theor. Biol.* **184** 65
- [27] Santos F C and Pacheco J M 2005 *Phys. Rev. Lett.* **95** 098104
- [28] Assenza S, Gómez-Gardeñes J and Latora V 2008 *Phys. Rev. E* **78** 017101
- [29] Rong Z, Li X and Wang X 2007 *Phys. Rev. E* **76** 027101
- [30] Boccaletti S, Latora V, Moreno Y, Chavez M and Hwang D-U 2006 *Phys. Rep.* **424** 175
- [31] Barabási A L and Albert R 1999 *Science* **286** 509
- [32] Pusch A, Weber S and Porto M 2008 *Phys. Rev. E* **77** 036120
- [33] Chen X, Fu F and Wang L 2008 *Phys. Lett. A* **372** 1161
- [34] Gómez-Gardeñes J, Campillo M, Floría L M and Moreno Y 2007 *Phys. Rev. Lett.* **98** 108103
- [35] Szolnoki A, Perc M and Danku Z 2008 *Physica A* **387** 2075
- [36] Poncela J, Gómez-Gardeñes J and Moreno Y 2011 *Phys. Rev. E* **83** 057101
- [37] Santos F C and Pacheco J M 2006 *J. Evol. Biol.* **19** 726
- [38] Wardil L and da Silva J K L 2009 *Eur. Phys. Lett.* **86** 38001
- [39] Wardil L and da Silva J K L 2010 *Phys. Rev. E* **81** 036115
- [40] Krapivsky P L and Redner S 2001 *Phys. Rev. E* **63** 066123
- [41] Krapivsky P L and Redner S 2002 *J. Phys. A: Math. Gen.* **35** 9517
- [42] Perc M and Szolnoki A 2010 *BioSystems* **99** 109
- [43] Sigmund K 2010 *The Calculus of Selfishness* (Princeton, NJ: Princeton University Press)