



## The joker effect: Cooperation driven by destructive agents

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### ABSTRACT

Understanding the emergence of cooperation is a central issue in evolutionary game theory. The hardest setup for the attainment of cooperation in a population of individuals is the Public Goods game in which cooperative agents generate a common good at their own expenses, while defectors “free-ride” this good. Eventually this causes the exhaustion of the good, a situation which is bad for everybody. Previous results have shown that introducing reputation, allowing for volunteer participation, punishing defectors, rewarding cooperators or structuring agents, can enhance cooperation. Here we present a model which shows how the introduction of rare, malicious agents – that we term jokers – performing just destructive actions on the other agents induce bursts of cooperation. The appearance of jokers promotes a rock-paper-scissors dynamics, where jokers outbeat defectors and cooperators outperform jokers, which are subsequently invaded by defectors. Thus, paradoxically, the existence of destructive agents acting indiscriminately promotes cooperation.

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### 1. Introduction

In the recent Hollywood movie *The Dark Knight* (2008) the comic character known as the Joker jeopardizes a whole society spreading chaos and destruction with no aim of benefit at it. The situation is so critical that even the mob is willing to cooperate with honest people to stop this nonsensical catastrophe. This fiction provides a visual metaphor of how an event like this can force exploiters of society to collaborate temporarily to fight the common enemy. Society is an emergent structure resulting from the cooperation among its members, and exploiters need society to survive, even if they do not contribute to it. Thus they are specially sensitive to the destruction of society precisely because, being selfish agents, society is their only source of survival. The appearance of the Joker provides a strong incentive for cooperation.

Beside situations like the one depicted by the Joker metaphor, the importance of the inclusion of malicious agents on the game is also illustrated in other scenarios. Here are a few examples. Temporary coalitions of rival parties are constantly formed whenever a common enemy arises, only to restore their old rivalry once this enemy has been wiped out. During the Second World War U.S.A. and U.S.S.R. were allied in fighting Hitler, but they got engaged in the Cold War for decades after the danger of Nazism had been ruled out. It is also well known that strong

affective links between humans are created when they face a common difficult situation. Biology is another source of potential examples. For instance, it has been shown that the perception of an increase in the risk of predation can induce cooperative behavior in some bird species (Krams et al., 2010). Indeed, prey species frequently form groups to increase the survival rate against predator attacks (Hamilton, 1971; Krebs and Davies, 1993). In some cases, this has been proven to happen even in the absence of kinship among its members, as in the collective defense of spiny lobsters (Lavalli and Herrnkind, 2009).

The existence of these temporary coalitions for defense against a common danger in rational and irrational agents alike calls for an evolutionary explanation. In this article we propose a stylized evolutionary game (Hofbauer and Sigmund, 1998) aimed at studying theoretically this enhancement of cooperation driven by the emergence of purely destructive agents. The game does not try to model any specific situation, but it proposes an abstract setting in which the role of the indiscriminate destructive action of these agents in enhancing cooperation is made clear. Our model is a modification of the standard Public Goods (PG) game (Groves and Ledyard, 1977), the  $n$ -players version of Prisoner's Dilemma and a paradigm of the risk of exploitation faced by cooperative behavior (Hardin, 1968). It has been shown that several mechanisms involving reputation (Milinski et al., 2005), allowing for volunteer participation (Hauert et al., 2002a, 2002b), punishing defectors (Fehr and Gächter, 1999, 2000), rewarding cooperators (Sigmund et al., 2001) or structuring agents (Szabó and Hauert, 2002; Wakano et al., 2009; Hauert et al., 2008), can

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enhance cooperation. Here, we present a different mechanism for the enhancement of cooperation based on the existence of evil agents. The game involves  $n$  players who belong to one out of three different types: cooperators, who contribute to the public good at a cost for themselves; defectors, who free-ride the public good at no expense; and jokers, who do not participate in the public good – hence obtain no benefit whatsoever – and only inflict damage to the public good. Groups are formed randomly, and each player's strategy is established before the group is selected. Hence, players have no memory. Remarkably, the appearance of jokers promotes a rock-paper-scissors dynamics, where jokers outbeat defectors and cooperators outperform jokers, which are subsequently invaded by defectors. In contrast to previous models (Hauert et al., 2002a,b), the cycles induced by jokers are limit cycles, i.e., attractors of the dynamics, and exist in the presence of mutations; these properties make them robust evolutionary outcomes. Therefore, paradoxically, the existence of destructive agents acting indiscriminately promotes cooperation.

The paper is organized as follows. Section 2 exposes the model and shows the existence of cycles. Section 3 analyzes the dynamics for infinite populations, and Section 4 compares the joker model with other RPS dynamics.

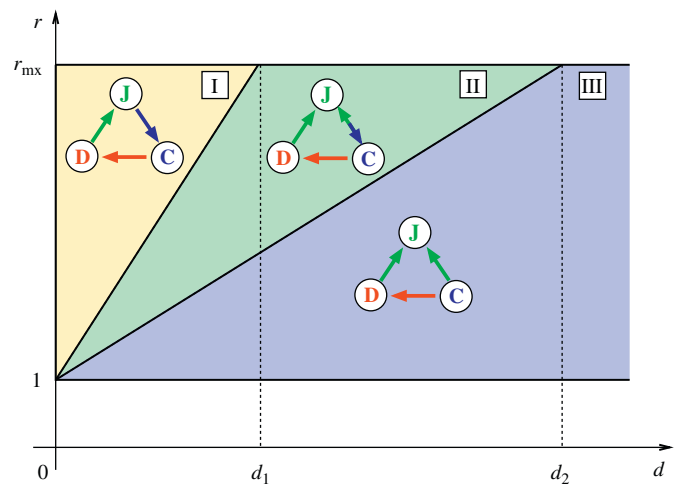
## 2. A Public Good game with jokers: existence of limit cycles

The PG game works as usual: every cooperator yields a benefit  $b=rc$  ( $r > 1$ ) to be shared by cooperators and defectors alike, at a cost  $c$  for herself (this cost can be set to  $c=1$  without loss of generality: all other payoffs are given in units of  $c$ ), and defectors produce no benefit at all but get their share of the public good. As for the new agents (jokers), every joker inflicts a damage  $-d < 0$  to be shared equally by all non-jokers and gets no benefit. In a given game  $0 \leq m \leq n$  denotes the number of cooperators,  $0 \leq j \leq n$  the number of jokers, and  $n-m-j \geq 0$  the number of defectors;  $S=n-j$  expresses the number of non-jokers. In this group, the payoff of a defector will be  $\Pi_D(m,j) = (rm-dj)/S$ , and that of a cooperator  $\Pi_C = \Pi_D - 1$ . Then, in each group, defectors will always do better than cooperators. Jokers' payoff is always 0.

A usual requirement of PG games is that  $r < n$ . Without this requirement the solution in which all  $n$  players are defectors is no longer a Nash equilibrium—hence the dilemma goes away. As shown later, the evolutionary dynamics for infinite populations yields the same constraint, i.e., if  $r < n$  the dynamics asymptotically approaches the tragedy of the commons. However, this is no longer true for finite populations, where the upper bound of  $r$  for which the tragedy of the commons takes place grows as  $M$ , the population size, decreases. In this case the tragedy of the commons arises whenever  $r < r_{\max} = n(M-1)/(M-n)$  (see Appendix A; notice in passing that for a population of  $M=n$  individuals, the evolutionary dynamics yields a tragedy of the commons for every  $r > 1$ ).

An invasion analysis provides the clue as to why a rock-paper-scissors (RPS) cycle is to be expected when jokers intervene in the game. We shall assume that we have a population of  $M$  players of the same type and will consider putative mutations of one individual to any of the other two types. The mutation will thrive if the average payoff of the mutant after many interactions overcomes the average payoff of a non-mutant player. The result of this analysis (see Appendix A) is summarized in Fig. 1, which represents the three different patterns of invasion that can be observed within the region of interest  $1 < r < r_{\max}$ ,  $d > 0$ :

- I. *Rock-paper-scissors cycle*: It arises whenever  $r > 1+(n-1)d$ . This condition expresses the fact that a single cooperator gets a positive payoff in spite of the damage inflicted by  $n-1$



**Fig. 1.** Dynamics of invasions in a Public Goods game with jokers. The axes represent the gain factor  $r$  of the Public Goods game (i.e., the payoff each cooperator yields to the public good) and the “damage”  $d > 0$  that every joker inflicts on the public good. The tragedy of the commons occurs for  $1 < r < r_{\max} = n(M-1)/(M-n)$  (see text), which includes the dilemmatic region  $1 < r < n$  characteristic of PG games. Different colors are assigned to different invasion patterns: Light blue corresponds to a region where J invades both C and D (III); light green corresponds to a region where neither C nor J invades each other (there is bistability on the J–C line) but D invades C and is in turn invaded by J, so again everything ends up in J (II); finally, light yellow corresponds to a region where D invades C, J invades D, but C invades J back, thus generating a rock-paper-scissors cycle (I). The latter behavior is the essence of the *Joker effect*. The equations of the straight lines separating the three regions are (from top to bottom)  $r = 1 + (n-1)d$  and  $r = 1 + d/(M-1)$ . Notice that this scheme is valid for arbitrary  $n > 1$ . Also, for fixed  $r$ , all three regions are crossed upon varying  $d$ , whereas vice versa is only true provided  $d < d_1 = M/(M-n)$ . The Joker effect does not occur if  $d > d_1$ . For large populations,  $M \gg 1$ , the region for the rock-paper-scissors cycle simplifies to  $n > r > 1 + (n-1)d$  and  $d < 1$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

jokers and, therefore, being a cooperator pays (jokers get no payoff whatsoever).

- II. *Joker-cooperator bistability*: If  $1 + d/(M-1) < r < 1 + (n-1)d$  neither jokers nor cooperators can invade each other. Nonetheless defectors always invade cooperators, and jokers always invade defectors, so eventually only jokers survive, either because they are initially a majority or indirectly through the emergence of defectors.
- III. *Joker invasion*: If  $r < 1 + d/(M-1)$  jokers will invade any homogeneous population, so a homogeneous population of jokers is the only stable solution. Notice that this region disappears for large populations ( $M \rightarrow \infty$ ) because  $r > 1$ .

The RPS cycle  $C \rightarrow D \rightarrow J \rightarrow C$  occurring in region I is the essence of the Joker effect.

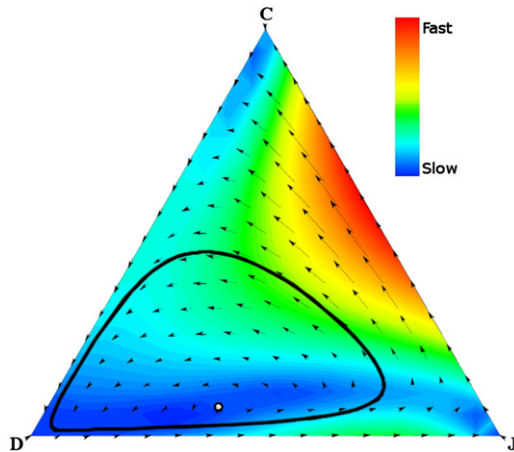
## 3. Infinite populations

We can gain further insight into this effect by studying a replicator-mutator dynamics (Maynard Smith, 1982). We assume a very large population in which the three types are present at time  $t$  in fractions  $x$  (cooperators),  $y$  (defectors), and  $z = 1 - x - y$  (jokers). Agents interact with the whole population by engaging in the above described game within groups of  $n$  randomly chosen individuals (Hauert et al., 2006). Average payoffs of a cooperator, a defector, and a joker are denoted  $P_C(x,z)$ ,  $P_D(x,z)$ , and  $P_J(x,z)$ , respectively. Assuming individuals of a given type mutate to any other type at a rate  $\mu \ll 1$ , the replicator-mutator equations for

this system will be

$$\begin{aligned} \dot{x} &= x(P_C - \bar{P}) + \mu(1 - 3x), \\ \dot{y} &= y(P_D - \bar{P}) + \mu(1 - 3y), \\ \dot{z} &= z(P_J - \bar{P}) + \mu(1 - 3z), \end{aligned} \tag{1}$$

where  $\bar{P} = xP_C + yP_D + zP_J$  is the mean payoff of the population at a given time. Explicit expressions for  $P_C$ ,  $P_D$ , and  $P_J$  can be obtained



**Fig. 2.** The Joker effect in public goods games for large, well-mixed populations. The simplex describes the replicator-mutator dynamics, Eq. (1), for a population of cooperators, defectors and jokers with parameter values satisfying  $n > r > 1 + (n-1)d$ , for which a rock-paper-scissor dynamics is expected (yellow region in Fig. 1). When mutation rates are small, the only equilibrium is a repeller (white dot), and trajectories end up in a stable limit cycle (black line). Thus the presence of jokers induces periodically a burst of cooperators. Cooperators abound during short time spans, as shown by the small fraction of cooperators in the equilibrium point. Parameters:  $n=5$ ,  $r=3$ ,  $d=0.4$  and  $\mu=0.005$ . (Images generated using a modified version of the Dynamo Package (Sandholm and Dokumaci, 2007)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

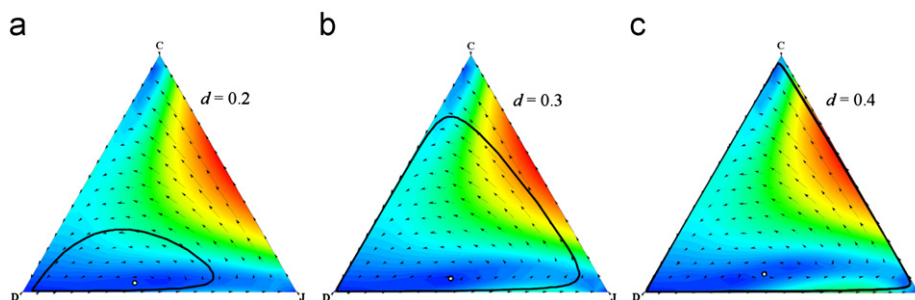
by averaging over all samples of groups of  $n$  players extracted from a population containing  $Mx$  cooperators,  $My$  defectors, and  $Mz$  jokers, in the limit of very large populations ( $M \rightarrow \infty$ ); the derivation can be found in Appendix B. Let us recall that the parameters of the game in the infinite population limit satisfy  $1 < r < n$  and  $d > 0$ ; the first condition enforces the public goods dilemma, and the second one implies that jokers beat defectors in the absence of cooperators, because defectors receive the damage inflicted by jokers thus obtaining a negative payoff.

The stability analysis of the dynamical system (1) recovers the picture displayed in Fig. 1 (taking  $M \rightarrow \infty$ ). When  $r < 1 + (n-1)d$  the system is in region II. The only stable equilibrium is a population of only jokers and any trajectory of (1) is asymptotically attracted to it. Thus, in this region the destructive power of jokers is high enough to wipe out the populations of both cooperators and defectors. But the most interesting situation takes place when

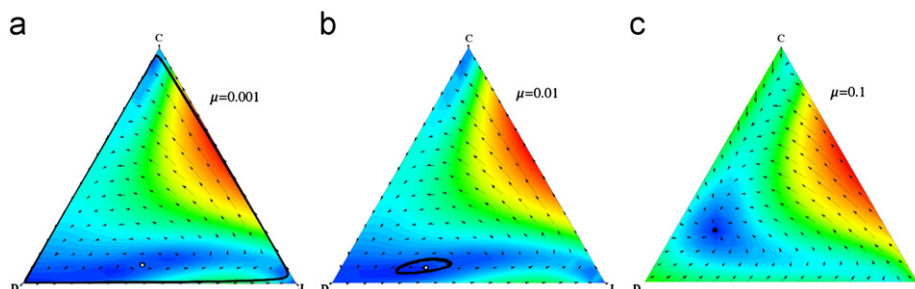
$$r > 1 + (n-1)d, \tag{2}$$

i.e., in region I. In the absence of mutations the dynamical system (1) has three saddle points at the corners of the simplex as well as an unstable mixed equilibrium (see Appendix C). As a consequence, the attractor of the system is the heteroclinic orbit  $C \rightarrow D \rightarrow J \rightarrow C$ . The period is infinite because the system delays more and more around the saddle points. When mutations occur the corners of the simplex are no longer equilibria, and one is left with the interior fixed point, which for small mutations is a repeller (see Appendix C). Since trajectories are confined within the closed region of the simplex, they are attracted to a stable limit cycle for any  $r > 1$  (a direct consequence of the Poincaré–Bendixon theorem, Simmons and Krantz, 2006), as shown in Fig. 2.

The size of the cycle depends on the parameter values. It grows as  $d$  increases – i.e., when jokers play a more important role (Fig. 3) – and as the mutation rate decreases (Fig. 4). For both, large values of  $d$  (compatible with condition (2)) and very small mutations, the cycle closely follows the boundaries of the simplex



**Fig. 3.** Replicator-mutator dynamics as a function of the damage  $d$  inflicted by jokers. For a fixed mutation rate, the size of the cycles increases as the damage increases. Parameters:  $n=5$ ,  $r=3$  and  $\mu=0.001$ .



**Fig. 4.** Replicator-mutator dynamics as a function of the mutation rate  $\mu$ . (a) For very small mutation rates cycles approach the boundary of the simplex. (b) As  $\mu$  increases, the cycle amplitude decreases and, above a critical value (typically,  $\mu_c \approx 0.01$ ), cycles disappear in a Hopf bifurcation yielding a stable mixed equilibrium (c) Parameters:  $n=5$ ,  $r=3$  and  $d=0.4$ .

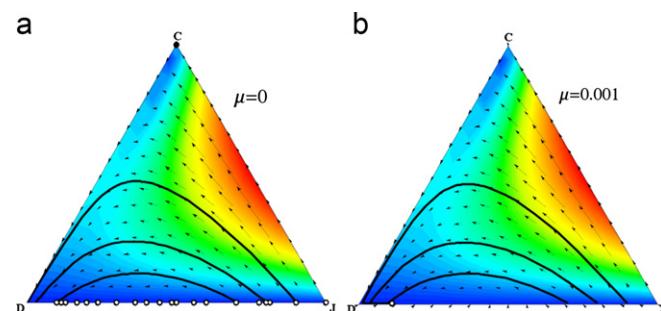
(see Fig. 4a). By increasing the mutation rate (typically over 0.01), cycles disappear in a Hopf bifurcation yielding a stable mixed equilibrium (Figs. 4b–c).

#### 4. Discussion and conclusions

This evolution has some resemblances with the effect of volunteering in a PG game (Hauert et al., 2002a,b), but the two games are fundamentally different. This can be told from the dynamic behavior of the system. In both cases, the existence of a third agent which does not participate in the game is the ultimate reason why cooperators periodically thrive through a rock-paper-scissor dynamics. However, while the loners game leads to neutrally stable cycles around a center, trajectories in the Joker model are attracted by the heteroclinic cycle C–D–J–C. The difference is even more striking if mutations are included. Mutations replace the cycles in the loner model by a stable mixed equilibrium. In contrast, in the Joker model mutations substitute the heteroclinic orbit by a stable limit cycle, which undergoes a transition (Hopf bifurcation) to a stable mixed equilibrium above a threshold mutation rate.

These two scenarios can be understood from the analysis of general RPS games (Hofbauer and Sigmund, 1998). There are three situations: (a) orbits are attracted towards an asymptotically stable mixed equilibrium (the case of the loners game with mutations), (b) orbits cycle around a neutrally stable mixed equilibrium (the case of the loners game without mutations), and (c) orbits go away from an unstable mixed equilibrium and approach the heteroclinic orbit defined by the border of the simplex (the case of the Joker game without mutations). If mutations are added to the latter type of RPS games, limit cycles and a Hopf bifurcation upon increasing the mutation rate are also found (Mobilia, 2010). Limit cycles are robust to perturbations and have a well-defined amplitude irrespective of the initial fractions of players (as long as it is not at the border of the simplex). Therefore, they are true attractors of the dynamics, and can thus be regarded as a robust evolutionary outcome, in contrast to neutrally stable cycles.

In contrast to loners, which do not participate in the game but receive a benefit outside of it, jokers do not receive any benefit at all and cause damage to players. Both loner and joker models coincide – in the absence of mutations – when the damage inflicted by jokers and the benefit obtained by loners are both zero. In this case both become simply non-participants in the game, and the only effect they produce is a reduction in the effective number of players in the game, which is not enough to induce an oscillatory dynamics (see Fig. 5). In other words, the appearance of the RPS cycle which periodically increases the population of cooperators in the presence of jokers can only



**Fig. 5.** Replicator-mutator dynamics for  $d=0$ . If jokers are just passive agents cooperators go extinct. (a)  $\mu=0$ . The system ends up in a point of the line DJ with a majority of defectors. (b)  $\mu=0.001$ . Mutation generates one single stable state made up mostly by defectors. Parameters:  $n=5$ ,  $r=3$  and  $d=0$ .

happen, remarkably, provided  $d > 0$ , i.e., if jokers are truly destructive agents.

In this letter we have shed light on a still unexplored aspect of evolutionary game theory (the presence of a destructive strategy) in the prototypical PG game. We have shown, both theoretically and by numerical simulations, that the addition of purely destructive agents (jokers) to a standard PG game has, paradoxically, a positive effect on cooperation. Bursts of cooperators are induced through the appearance of a RPS cycle in which jokers beat defectors, who beat cooperators, who beat jokers in succession. The evolutionary dynamics provoked by the Joker, with periods of cooperation, defection and destruction of the PG, may help understand the appearance of cognitive abilities that allow individuals to foresee the destructive periods, promoting in advance the necessary cooperation to avoid them.

We have proven this “Joker effect” to occur both in finite and infinite populations, discarding the possibility of its being an artificial size-depending phenomenon. Further research is required to ascertain the scope of the constructive role of destruction in general settings. This provides a new framework for the evolution of cooperation that may find important implications in social, biological, economical, and even philosophical contexts, and that is worth exploring either with different variants of this game or with new, more specific games accounting for indiscriminate destruction.

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#### Appendix A. Finite populations: invasion analysis

We shall consider the situation in which in a homogeneous population of  $M$  individuals with the same strategy  $Y$ , one of them mutates (changes) to a different type  $X$ . The new individual will invade provided its average payoff after many interactions,  $P_X$ , is larger than the average payoff of a  $Y$  individual, i.e.,  $P_X > P_Y$ . Average payoffs can be evaluated as follows. The population is made of one  $X$  player and  $M-1$   $Y$  players. Thus, when playing the game, the  $X$  player will always interact with  $n-1$   $Y$  players. Therefore

$$P_X = \Pi_X(1X, (n-1)Y). \quad (\text{A.1})$$

On the other hand, the  $n-1$  opponents of a  $Y$  player can be of just two types: either all  $n-1$  are  $Y$  players, or  $n-2$  are  $Y$  players and one is the single  $X$  player. The latter situation occurs with probability  $(n-1)/(M-1)$ . Therefore, the average payoff of a  $Y$  player will be

$$P_Y = \Pi_Y(nY) \frac{M-n}{M-1} + \Pi_Y(1X, (n-1)Y) \frac{n-1}{M-1}. \quad (\text{A.2})$$

Next we derive the invasion conditions for homogeneous populations of three types of players. In this new scenario we must

consider the six different situations arising from the pair interactions that can be formed:

(A) 1D+(M-1)C.

$$P_C = r - 1 - \frac{r(n-1)}{nM-1}, \quad P_D = r - \frac{r}{n}. \tag{A.3}$$

The tragedy of the commons occurs when defectors overcome cooperators, i.e.,  $P_D > P_C$ . This happens iff

$$r < n \frac{M-1}{M-n}. \tag{A.4}$$

We will henceforth assume (A.4) to hold. This condition contains the dilemmatic region  $1 < r < n$  of PG games. In the limit  $M \rightarrow \infty$ , the inequality (A.4) reduces to  $r < n$  and both, the conditions for the dilemma and the tragedy of the commons coincide.

(B) 1C+(M-1)D.

$$P_C = \frac{r}{n} - 1, \quad P_D = \frac{r(n-1)}{nM-1}. \tag{A.5}$$

Because of (A.4)  $P_D > P_C$ , so C never invades D.

(C) 1J+(M-1)C.

$$P_C = r - 1 - \frac{d}{M-1}, \quad P_J = 0. \tag{A.6}$$

Since  $P_J > P_C$  iff

$$r < 1 + \frac{d}{M-1}, \tag{A.7}$$

then J invades C iff (A.7) holds.

(D) 1C+(M-1)J.

$$P_C = r - (n-1)d - 1, \quad P_J = 0. \tag{A.8}$$

Since  $P_C > P_J$  iff

$$r > 1 + (n-1)d, \tag{A.9}$$

then C invades J iff (A.9) holds.

(E) 1D+(M-1)J.

$$P_D = -(n-1)d, \quad P_J = 0. \tag{A.10}$$

As long as  $d > 0$  we will have  $P_J > P_D$ , then D never invades J.

(F) 1J+(M-1)D.

$$P_D = -\frac{d}{M-1}, \quad P_J = 0. \tag{A.11}$$

As long as  $d > 0$  we will have  $P_J > P_D$ , then J always invades D.

Fig. 1 illustrates the different regions of interest in this game. The most interesting one is that in which there is a rock-paper-scissor rotation between C, D, and J, which corresponds to

$$1 < r < n \frac{M-1}{M-n}, \quad 0 < d < \frac{r-1}{n-1}. \tag{A.12}$$

### Appendix B. Infinite populations: average payoffs

We evaluate here the average payoffs  $P_x$  obtained by each strategy ( $i=C, D, J$ ) in this game when the population is very large. These functions will determine the dynamics of the population through the replicator equation. As before, sample groups of  $n$  individuals playing the game are randomly formed, and it is assumed that each player is sampled a large number of times before payoffs are compared in order to update strategies. The payoff for a given strategy is, therefore, proportional to the average payoff that a player using this strategy obtains playing against the whole population. This average payoff will depend

only on the player's strategy and the composition of the population, described by a fraction  $x$  of cooperators,  $z$  of jokers and  $y = 1 - x - z$  of defectors. Notice that  $P_J = 0$  for any composition of the population, so only cooperators' and defectors' payoffs need to be calculated.

#### B.1. Defectors

The average payoff of a defector is

$$P_D = \left\langle \frac{rm-dj}{S} \right\rangle, \tag{B.1}$$

where the symbol  $\langle \dots \rangle$  denotes an average over samples of  $n-1$  opponents randomly selected from the population. The average  $\langle m/S \rangle$  can be obtained as in Hauert et al. (2002b), yielding

$$\left\langle \frac{m}{S} \right\rangle = \frac{x}{1-z} \left( 1 - \frac{1-z^n}{n(1-z)} \right).$$

Since  $j = n - S$ , the second term in Eq. (B.1) can be written as  $n \langle 1/S \rangle - 1$ , where

$$\left\langle \frac{1}{S} \right\rangle = \sum_{s=1}^n \binom{n-1}{s-1} (1-z)^{s-1} z^{n-s} \frac{1}{s},$$

the factor in front of  $1/S$  in the summation being the probability of having  $S-1$  non-jokers in a group of  $n-1$  randomly chosen players. By using the identity  $a \binom{n-1}{a-1} = b \binom{n}{a}$ , the latter expression becomes

$$\left\langle \frac{1}{S} \right\rangle = \frac{1-z^n}{n(1-z)}.$$

Joining the two averages one gets the average payoff of a defector,

$$P_D = r \frac{x}{1-z} \left( 1 - \frac{1-z^n}{n(1-z)} \right) - d \left( \frac{1-z^n}{1-z} - 1 \right), \tag{B.2}$$

the first term arising from the exploitation of cooperators and the second one being the damage inflicted by jokers.

#### B.2. Cooperators

The difference  $P_D - P_C$  can be written as

$$P_D - P_C = \left\langle 1 - \frac{r}{S} \right\rangle, \tag{B.3}$$

because in a group of  $S-1$  opponents switching from cooperation to defection yields a payoff increment of  $1 - r/S$ : the defector's payoff gets reduced by  $r/S$  because there is one cooperator less in the group, but adds 1 to her payoff because she does not pay the cost of cooperating (Hauert et al., 2002b). The average in the r.h.s. of Eq. (B.3) just contains  $\langle 1/S \rangle$ , thus yielding

$$P_D - P_C = 1 - \frac{r}{n} \frac{1-z^n}{1-z}. \tag{B.4}$$

Finally, from Eqs. (16) and (18) one gets

$$P_C = r \frac{x}{1-z} \left( 1 - \frac{1-z^n}{n(1-z)} \right) + \frac{r}{n} \frac{1-z^n}{1-z} - 1 - d \left( \frac{1-z^n}{1-z} - 1 \right). \tag{B.5}$$

### Appendix C. Infinite populations: proof of existence of limit cycles

To complete the proof that the system ends up in a limit cycle it remains to show that the interior equilibrium of Eq. (1) is a

repeller, i.e., its two eigenvalues have positive real parts. The interior equilibrium and its stability can be evaluated in the limit of small mutation rates, the one we are interested in. In this case, one can neglect the dependence of  $\mu$  in the position of the fixed point. We are thus faced with the solution of the dynamical system (1) without the mutation term. The calculation becomes simple for  $n=2$ , and tractable for  $n > 3$ . The proofs are treated separately in the next subsections.

C.1. Interior fixed point for  $n=2$

The interior fixed point  $(x_0, y_0, z_0)$  satisfies  $P_C = P_D = 0$ . According to Eq. (B.4), the first equality requires  $(1 + z_0)r = 2$ , yielding

$$z_0 = \frac{2-r}{r}.$$

Since  $n = 2 > r > 1$ , one has  $0 < z_0 < 1$ , as it should. The second equality,  $P_D = 0$ , produces

$$x_0 = 2d \frac{2-r}{r^2}.$$

Condition  $r > 1 + d$  from expression (2) guarantees that  $0 < x_0 < 1$  and  $0 < y_0 = 1 - x_0 - z_0 < 1$ . In order to analyze the stability of this equilibrium, we consider frequencies  $x$  and  $z$  as the independent variables of the two-dimensional system. To prove that the equilibrium is a repeller it suffices to show that the trace and determinant of the Jacobian matrix at the fixed point are both positive. For  $n=2$ , Eq. (1) become

$$\dot{x} = -\frac{1}{2}x(2dz^2 - rz + 2 - r - 2x + rx), \tag{C.1}$$

$$\dot{z} = z[(1-r)x + dz(1-z)]. \tag{C.2}$$

The Jacobian matrix in the interior equilibrium is

$$\begin{pmatrix} \frac{d(2-r)^2}{r^2} & \frac{d(2-r)(r^2 + 4dr - 8d)}{r^3} \\ -\frac{(2-r)(r-1)}{r} & \frac{d(2-r)(3r-4)}{r^2} \end{pmatrix}, \tag{C.3}$$

whose trace,  $T$ , and determinant,  $D$ , are

$$T = \frac{2d(2-r)(r-1)}{r^2} > 0, \tag{C.4}$$

$$D = \frac{d(r-2)^2(r^2 + r(d-1) - 2d)}{r^3} > 0. \tag{C.5}$$

$T$  is positive because  $n = 2 > r > 1$ . To prove that the determinant is positive, we should realize that the second bracket in its expression can be written as  $r(r-1) - d(2-r)$ , which is larger than  $2(r-1)^2 > 0$  because  $r > 1 + d$ .

C.2. Interior fixed point for  $n > 3$

We use the same procedure as in the previous case. The fraction of jokers  $z_0$  of the interior equilibrium arises from  $P_C = P_D$ , namely Eq. (B.4). Once it is found,  $x_0$  follows from  $P_D = 0$ , c.f. Eq. (B.2).

C.2.1. Calculation of  $z_0$

$z_0$  is obtained as the solution to

$$1 - \frac{r}{n} \frac{1-z^n}{1-z} = 0, \tag{C.6}$$

which is equivalent to

$$\sum_{i=0}^{n-1} z^i = n/r. \tag{C.7}$$

The latter equation has exactly one solution, namely the crossing of the polynomial in the l.h.s of Eq. (C.7) with the constant  $n/r > 1$ .

Since  $r > 1$ , this occurs at  $0 < z_0 < 1$ , consistent with the meaning of  $z_0$ . There is no analytical solution to Eq. (C.6) for arbitrary  $n$ . There exists, however, a simple analytical solution in the limit of large  $n$ , which is indeed an excellent approximation for all  $n > 3$ . It can be obtained neglecting  $z^n$  as compared to 1 in (C.6), which leads to

$$z_0 \approx 1 - \frac{r}{n}. \tag{C.8}$$

Since  $r < n$ , one has, of course,  $0 < z_0 < 1$ . For consistence,  $z_0^n = (1 - (r/n))^n \approx e^{-r} \ll 1$ , which holds, say, for  $r > 3$ . Notice that if  $r \ll n$  the equilibrium approaches all J, so that cycles get very close to this state in this limit.

C.2.2. Calculation of  $x_0$

Let us impose  $P_D = 0$ . Introducing (C.6) into (B.2) one finds

$$x_0 \approx \frac{d}{r-1} \left( \frac{n}{r} - 1 \right) (1 - z_0). \tag{C.9}$$

Conditions  $d > 0$ ,  $n > r > 1$ , and  $r > 1 + (n-1)d$  yield  $0 < x_0 < 1$  and  $0 < x_0 + z_0 < 1$ , so that the three fractions are smaller than 1. Substituting  $z_0$  from expression (C.8) into (C.9) one finally obtains

$$x_0 \approx \frac{d}{r-1} \left( 1 - \frac{r}{n} \right). \tag{C.10}$$

C.2.3. Stability of the interior equilibrium

We need to determine the Jacobian matrix for the equilibrium  $(x_0, z_0)$  given by (C.9) and (C.8). The dynamical system (1) can be written as

$$\begin{aligned} \dot{x} = & -\frac{x}{n(1-z)^2} (-r + n - rnxz - dnx^{n+1} + 2nxz \\ & - nxz^2 - 2nz + rx - rxz^n + dnx^2 - nx + rz^n \\ & + nz^2 + rz - rz^{n+1} + rnxz^2 + dnx^{n+2} - dnx^3) \end{aligned} \tag{C.11}$$

$$\dot{z} = -(-dz + rx + dz^n - x)z. \tag{C.12}$$

The first equation is very cumbersome. Fortunately, as already explained, in the limit of large  $n$  and if  $r > 3$  one can neglect terms of order  $z^n$  and above. Using expressions (C.8) and (C.10), the Jacobian matrix  $J$  can be written as  $J = Yd(n-r)/n$ , where

$$Y = \begin{pmatrix} \frac{n-r}{r} & \frac{nr(r-1) + d(r-n)(r^2 - r + n)}{r^2(r-1)^2} \\ -\frac{r-1}{d} & 2 \end{pmatrix}. \tag{C.13}$$

(Notice that the factor  $d(n-r)/n > 0$ .) As the diagonal elements of this matrix are positive, the trace is positive. Also  $Y_{zx} < 0$  and, as we show next,  $Y_{xz} > 0$ , therefore, the determinant turns out to be positive, and the interior equilibrium is a repeller. To see that  $Y_{xz} > 0$  we must show that the numerator is positive. This can be shown by writing it as

$$nr(r-1) + d(r-n)(r^2 - r + n) > (r-1)^2 \frac{(n-r)^2 + nr}{n-1} > 0.$$

The first inequality follows from condition  $r-1 > (n-1)d$ .

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