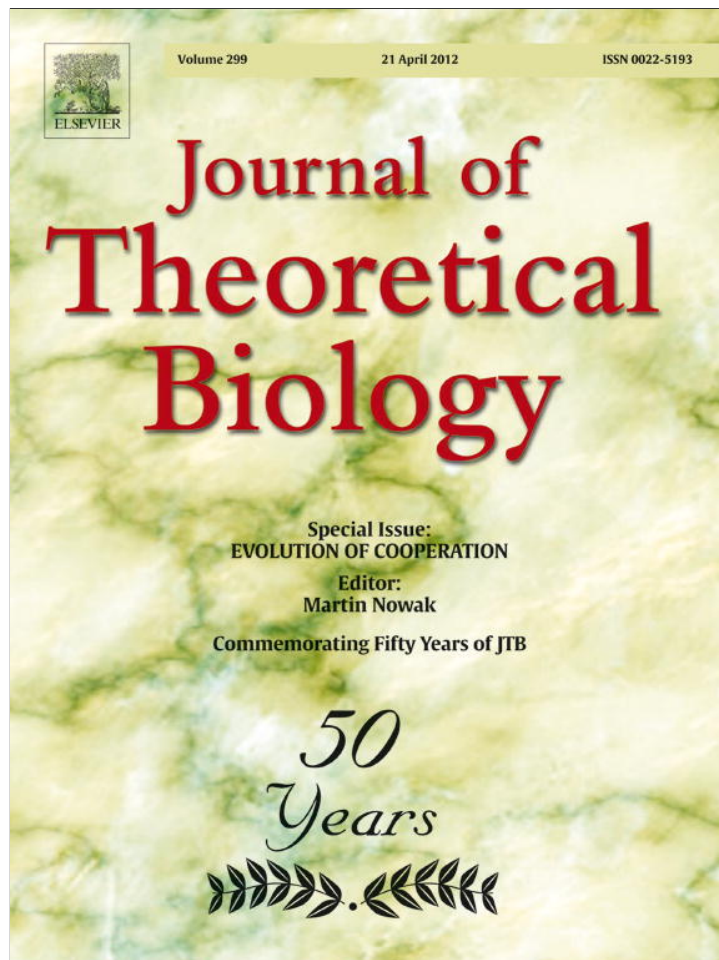


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

## Journal of Theoretical Biology

journal homepage: [www.elsevier.com/locate/yjtbi](http://www.elsevier.com/locate/yjtbi)

## Review: Game theory of public goods in one-shot social dilemmas without assortment

Marco Archetti<sup>a</sup>, István Scheuring<sup>b,\*</sup>

<sup>a</sup> Faculty of Business and Economics, University of Basel, Peter Merian-Weg 6, CH-4002 Basel, Switzerland

<sup>b</sup> Research Group of Theoretical Biology and Ecology, Department of Plant Taxonomy and Ecology, Eötvös University, Pázmány P. s. 1/C, 1117, Budapest, Hungary

## ARTICLE INFO

Available online 24 June 2011

**Keywords:**

Cooperation  
Public good  
Social dilemma  
Game theory  
Mixed equilibrium

## ABSTRACT

We review the theory of public goods in biology. In the  $N$ -person prisoner's dilemma, where the public good is a linear function of the individual contributions, cooperation requires some form of assortment, for example due to kin discrimination, population viscosity or repeated interactions. In most social species ranging from bacteria to humans, however, public goods are usually a non-linear function of the contributions, which makes cooperation possible without assortment. More specifically, a polymorphic state can be stable in which cooperators and non-cooperators coexist. The existence of mixed equilibria in public goods games is a fundamental result in the study of cooperation that has been overlooked so far, because of the disproportionate attention given to the two- and  $N$ -person prisoner's dilemma. Methods and results from games with pairwise interactions or linear benefits cannot, in general, be extended to the analysis of public goods. Game theory helps explain the production of public goods in one-shot,  $N$ -person interactions without assortment, it leads to predictions that can be easily tested and allows a prescriptive approach to cooperation.

© 2011 Elsevier Ltd. All rights reserved.

### 1. Social dilemmas in biology

Social dilemmas are situations in which the optimal behavior of an individual contrasts with the optimal outcome for the group: in game theory this means that the situation at hand can be described by a game in which at least one equilibrium is Pareto inefficient: an alternative outcome is possible in which at least one player could have a higher payoff without reducing any other player's payoff (a Pareto improvement is possible; hence the *inefficiency*); no one, however, has an incentive to change their behavior (hence the *equilibrium*). This conflict between individual and collective success is found at all levels of biological organization, from genes to societies.

At the level of genes, conflict occurs because the optimal strategy for a gene is not necessarily the optimal strategy for the organism. Segregation distorter genes, for example, promote their own spread to the next generation by disrupting meiosis even if this can have deleterious consequences for the organism and can lead entire populations to extinction (Hurst et al., 1996; Burt and Trivers, 2006). Genes that initiate recombination can evolve for their own benefit by exploiting the DNA repair machinery to induce a damage on the homolog (Archetti, 2003;

Friberg and Rice, 2008). Genes that are expressed when maternally derived and genes that are expressed when paternally derived, as is the case with genomic imprinting, are in conflict over the allocation of nutrients to the fetus, and certain diseases during pregnancy can be interpreted as a result of these genetic conflicts (Haig, 1993, 2000). DNA sequences of genes expressed during development can evolve to be hypersensitive to mutations if this improves their likelihood to be transmitted to the next generation, even if this makes the organism more vulnerable to somatic mutations (Archetti, 2006, 2009a).

At the level of societies, conflict occurs because the optimal strategy for an individual is not necessarily the optimal strategy for the group. In unicellular organisms that secrete extracellular enzymes, non-producers can exploit the enzymes produced by producers without paying the cost (Crespi, 2001; Velicer, 2003). A similar problem occurs in vertebrates with cooperative hunting, where the prey is distributed evenly among the hunters independently of the investment in effort (Packer et al., 1990; Stander, 1991; Creel, 1997; Bednarz, 1988) or in the case of alarm calls against predators, where only individuals that give the alarm pay the cost, while the benefit of the alarm is distributed among all individuals in the group (Clutton-Brock, 1999; Beauchamp, 2003; Searcy and Nowicki, 2005). The most complex social dilemmas occur at the level of human interactions: typical examples are food sharing, cooperative war and hunting in hunter-gatherers (Boehm, 1999) and the contribution to public services like taxes, or the

\* Corresponding author.

E-mail address: [shieazsf@ludens.elte.hu](mailto:shieazsf@ludens.elte.hu) (I. Scheuring).

exploitation of natural resources (Hardin, 1968; Bergstrom et al., 1986; Kollock, 1998) in modern societies.

Most of the major transitions in evolution can be considered solutions to social dilemmas, that is transitions from individual-optimizing states to group-optimizing states of evolutionary units (Maynard Smith and Szathmary, 1995).

While the evolution of cooperation is still often presented as a major unsolved problem in evolutionary theory, it is understood that the creation of positive assortment between cooperators can maintain cooperation. Assortment can be brought about by genetic relatedness, which can arise because of kin discrimination, limited dispersal or greenbeard mechanisms (Hamilton, 1963, 1964; Michod, 1982; Frank, 1998; Grafen, 1984, 1985, 2006, 2009) or by repeated interactions (Axelrod and Hamilton, 1981; Nowak, 2006) that allow reciprocation, reputation and punishment. Kin selection and repeated interactions provide general solutions to the problem of the evolution of cooperation. There are many cases, however, in which cooperation exists in one-shot interactions without relatedness or other forms of assortment. How do we explain these cases?

Before discussing cooperation in social dilemmas we define cooperation by reviewing briefly the problem in pairwise interactions.

## 2. 2-Person games

2-Person games with 2 strategies ( $2 \times 2$  games) are often used in game theory to understand the strategic nature of an interaction. Because they are often easy to understand and described using intuitive stories, they have been often adopted (and often abused) by biologists to describe scenarios that involve conflict and cooperation.

Consider the game described in Fig. 1: two individuals are engaged in a pairwise interaction; each can Cooperate (C) or Defect (D); the cost paid by a cooperator is  $c$ , while the reward (or benefit) of cooperation for both is  $r_1c$  if only one cooperates, and  $r_2c$  if two cooperators interact ( $r_1 > 0$ ,  $r_2 > 1$ ). There is no cost and no benefit for mutual defection. Depending on the parameters  $r_1$ ,  $r_2$ , and  $c$  there are four possible games.

*No conflict:* If  $r_2 - r_1 > 1$  and  $r_1 > 1$  Cooperate is a dominant strategy and the only stable equilibrium is mutual cooperation (CC), which is Pareto-efficient. This is a game of *No Conflict*. There is no problem in explaining cooperation here.

*Prisoner's Dilemma:* If  $r_2 - r_1 < 1$ ,  $r_1 < 1$ , Defect is a dominant strategy and the only stable equilibrium is mutual defection (DD), which is Pareto-inefficient (mutual cooperation CC would give a higher payoff to both players). This game is the *Prisoner's Dilemma* (PD) discovered by Flood and Dresher in 1950 and described by Tucker in the same year (Tucker, 1950). The problem with cooperation here is to explain how to escape from the inefficient stable equilibrium of mutual defection. The problem described by

the PD is the one that most studies on the evolution cooperation try to explain, often with the implicit, mistaken assumption that this is the only type of social dilemma.

*Chicken:* If  $r_2 - r_1 < 1$  and  $r_1 > 1$  CC (mutual cooperation) is better than CD (cooperating while the other player defects), but DC (defecting while the other player cooperates) is better than CC, and DD is the worst possible outcome. This is an anti-coordination game, with two asymmetric equilibria in pure strategies (DC and CD) and one symmetric equilibrium in mixed strategies. Because the asymmetric equilibria require coordination, the natural outcome is usually considered the symmetric mixed-strategy equilibrium; at this equilibrium the probability of playing Cooperate is  $(r_1 - 1)/(2r_1 - r_2)$ . This game was called *Chicken* by Russell (1959) before being properly defined as a game by Rapoport and Chammah (1966); it was named *Hawk-Dove* by Maynard Smith and Price (1973) in their seminal paper on the logic of animal conflicts; it is called *Snowdrift game* (SD; after Sugden, 1986) in the field of the evolution of cooperation (the only difference in that in the snowdrift game the cost is usually diluted on both individuals in case of mutual cooperation). The problem with cooperation here is different from the PD; cooperators and defectors can coexist; the problem is to explain how to increase the number of cooperators and thus the average fitness of the population.

*Stag Hunt:* If  $r_2 - r_1 > 1$  and  $r_1 < 1$  CC is better than DD, and both DD and CC give better results than lack of coordination (CD or DC). This is a coordination game, with two symmetric equilibria in pure strategies (DD and CC). It is usually called the *Stag-Hunt game* after the verbal account by Rousseau (Samuelson, 1997; Skyrms, 2004) and is also known as *Assurance game* (in the social sciences) or *Security Dilemma* (in international relations). It has received little attention in evolutionary biology. The problem with cooperation here is to shift from the risk-dominant equilibrium (DD) to the payoff-dominant equilibrium (CC).

These games are not just random example of  $2 \times 2$  conflict games but are closely related and define the most common situations of conflict. While their relatedness is not evident from the classical taxonomy of  $2 \times 2$  games (Rapoport and Guyer 1966), it is clear from a topological classification (Robinson and Goforth, 2005) and from the payoff matrix defined in Fig. 1. It is important to keep in mind that the problem of cooperation is different in the four  $2 \times 2$  games above.

## 3. N-person games

2-Person games can be helpful as starting points for modeling social dilemmas if we assume multiple pairwise interactions. Conflicts in real biological situations, however, generally occur among more than two individuals simultaneously. In order to study social dilemmas we must move from games with pairwise interactions to  $N$ -person games, that is games of collective action in which the payoff of an individual depends on what all other individuals in the group are doing. The difference between 2- and  $N$ -person games is sometimes surprisingly easy to miss, and this mistake can be deeply misleading as we shall see.

The problem of cooperation in  $N$ -person games can generally be defined as a collective action problem for the production of a public good. A *public good* is any good (benefit) that is simultaneously non-excludable (nobody can be excluded from its consumption) and non-rivalrous (use of the benefit by one individual does not diminish its availability to another individual). In practice, in most cases public goods are not purely non-excludable (*club goods*) and non-rivalrous (*common goods*) but can be considered such; an alarm call against a predator can be considered a pure public good; breathing reduces the availability of

	Cooperate	Defect
Cooperate	$r_2c - c$	$r_1c$
Defect	$r_1c - c$	0

Fig. 1. Payoff matrix of a generalized  $2 \times 2$  conflict game. Each cell shows the payoffs for the two players (top right: column; bottom left: row);  $c (> 0)$  is the cost paid by a cooperator (C);  $r_i$  scales the benefit (in units of  $c$ ) when there are  $i$  cooperators in the interaction;  $r_1 > 0$ ,  $r_2 > 1$ .

oxygen to others, but air can be approximated to a public good; natural resources and enzyme production in bacteria are generally common goods. When we refer to “public goods” games, therefore, sometimes the public good is in fact a common good.

### 3.1. *N*-person prisoner's dilemma

It took more than 20 years after the discovery of the prisoner's dilemma to develop analogous *N*-person games. Although Olson (1965) and Hardin (1968) were clearly describing *N*-person social dilemmas and the basic problem had already been put forward by Samuelson (1954) and, in retrospect, by Hume (1739) and undoubtedly others, an *N*-person version of the PD appeared relatively late in the literature (Hamburger, 1973; Fox and Guyer, 1978). The *N*-person Prisoner's Dilemma (NPD) is usually described as follows: individuals can be cooperators (volunteers) or defectors (cheaters); cooperators pay a contribution *c*, whereas defectors do not; all contributions are summed, the sum multiplied by a reward factor *r* (> 1), and then redistributed to all individuals (both cooperators and defectors). Thus if there are *i* cooperators among *N* participants, the payoff of a defector is

$$P_D(i) = \frac{rci}{N}.$$

Similarly the payoff of a cooperator is

$$P_C(i) = \frac{rci}{N} - c = P_D(i) - c.$$

For *N*=2 the game is equivalent to the PD if *r*<2 (see Fig. 1).

Let us assume that groups of *N* individuals are formed at random, *without any assortment*: any focal individual finds *j* cooperators in a group of *N* (including self) individuals with the same probability  $f_j(x)$ , where *x* is the frequency of cooperators in the population. Thus the fitness of an individual playing *Defection* (*D*) is

$$W_D = \sum_{j=0}^{N-1} f_j(x) \frac{rcj}{N}, \quad (1)$$

and the fitness of an individual playing *Cooperation* (*C*) is

$$W_C = \sum_{j=0}^{N-1} f_j(x) \left[ \frac{rc(j+1)}{N} - c \right] = W_D + \frac{rc}{N} - c. \quad (2)$$

Comparing  $W_C$  and  $W_D$  it is easy to see that if  $r/N > 1$ , then *C* dominates *D* and there is no social dilemma; *C* is the only ESS. Conversely if  $r/N < 1$ , *D* dominates *C*, therefore *D* is the only ESS; the average fitness is zero at this ESS, which is smaller than  $(r-1)c$ , the average fitness in case of total cooperation (the equilibrium is Pareto-inefficient).

### 3.2. *Tragedy of the commons*

The NPD leads to complete absence of cooperation. This is the starting point of most studies on the evolution of cooperation: it is usually stated that because defection is the only stable equilibrium, social dilemmas lead to what Hardin (1968) famously called the “tragedy of the commons”. In Hardin's example a group of herders whose cows graze a common parcel of land have a self interest in putting as many cows as possible onto the land, even if the common is damaged as a result, because the herder receives all the benefits from the additional cows, while the cost due to damage to the common is shared by the entire group; yet if all herders make this selfish decision, the common is destroyed.

The NPD has become so prominent in the study of cooperation, and Hardin's metaphor so famous, that it can be hard to see how

misleading they can be in many cases. Unfortunately it seems a common misunderstanding that all social dilemmas are NPD's and that they all lead to the “tragedy of the commons”. The misunderstanding was pointed out by Kollock (1998) in the social sciences; Maynard Smith and Szathmáry (1995) made a similar remark, but the idea that public goods games are equivalent to the NPD seems to persist in evolutionary biology (Rankin et al., 2007). In fact, as we will see, social dilemmas exist that are as different from the NPD as the 2-person PD is different from Chicken or the Stag Hunt game. This has very important consequences for the study of social evolution, because these games have very different equilibria.

### 3.3. *The N*-person snowdrift game

Consider the so-called *N*-person snowdrift game (NSD) (Zheng et al., 2007). The name derives from the fact that, as in the SD, the cost of cooperation is diluted among the cooperators. Therefore the payoffs for an individual playing *Cooperation* and for one playing *Defection* are, respectively

$$P_C(i) = rc - \frac{c}{i} \text{ for } 1 \leq i \leq N$$

and

$$P_D(i) = \begin{cases} rc & \text{if } 1 \leq i \leq N-1 \\ 0 & \text{if } i = 0 \end{cases}, \quad (3)$$

where *i* is the number of cooperators in the group and  $rc=b$  is the benefit of cooperation in units of cost. In infinite, well-mixed population, cooperators will be in coexistence with defectors; however, the frequency of cooperators decreases roughly according to  $1/N$  at the ESS (Zheng et al., 2007). Consequently, the difference between the maximal fitness (everybody cooperates) and the fitness at the evolutionary equilibrium increases with *N* and the frequency of cooperators is negligible if *N* is in the order of hundreds (Zheng et al., 2007).

The cost here is a non-linear decreasing function (see Eq. (3)) rather than a constant (as in the NPD); the NPD and the NSD behave differently, except if *N* is large. Non-linearity in the benefit (that is the public good itself), however, has even more dramatic effects, as we will show in the next sections.

### 3.4. *Why non-linearity?*

Insisting on non-linearity might seem only a mathematical exercise of scarce interest to a biologist. There are two reasons to focus on non-linear benefits.

First, empirically, non-linear public goods are by far more common than linear public goods in biology. In microbes, for example, when cooperation is based on the expression of specific molecules like replication enzymes in viruses (Turner and Chao, 2003), adhesive polymers (Rainey and Rainey, 2003) and antibiotic resistance in bacteria (Lee et al., 2010) or invertase in yeast (Gore et al., 2009), the effect of enzyme production, and thus the level of benefit, is generally a saturating function of its concentration (Hemker and Hemker, 1969); moreover, if the speed limiting enzyme reaction is catalyzed by an oligomer enzyme with cooperative active centers then effect of the enzyme will be a sigmoid function of enzyme concentration (Ricard and Noat, 1986). Similarly, if a metabolic pathway is controlled by signal metabolites through an enzyme cascade, the product of the metabolism follows a highly non-linear switch-on switch-off behavior, which is a function of signal concentration (e.g. Mendes, 1997; Eungdamrong and Iyengar, 2004). Examples of non-linear benefits in social behavior are cooperative hunting (Packer et al., 1990; Stander, 1991; Creel, 1997; Bednarz, 1988; Yip et al., 2008), cooperative nesting and breeding (Rabenold,



1984) in vertebrates and the formation of fruiting bodies in social amoebas (Bonner, 2008). On the contrary, to our knowledge, no linear public goods have been reported, apart from artificial public goods in experimental settings for behavioral experiments (e.g. Fehr and Gintis, 2007).

Second, theoretically, the shape of the public good function is the very definition of a social dilemma; insisting on linearity would be equivalent to insisting that the PD captures all cases of 2-person interactions, which of course is not the case (Maynard Smith and Szathmáry, 1995; Kollock, 1998).

### 3.5. Non-linear N-person games

We define a general social dilemma using an N-person public goods game described by a benefit  $\beta(i)$  and a cost  $\gamma(i)$ . We assume that  $\beta(i)$  increases monotonically with the number of cooperators ( $i$ ), while  $\gamma(i)$  decreases monotonically with  $i$  (this allows to include the case of constant functions). The number of interacting individuals (group size)  $N$  is a fixed variable of the game (we discuss later some models in which  $N$  varies as well). Thus the payoffs for Defection ( $D$ ) and for Cooperation ( $C$ ) are respectively

$$P_D(i) = \beta(i),$$

$$P_C(i) = \beta(i) - \gamma(i).$$

Therefore the average fitness of a defector and a cooperator are, respectively

$$W_D = \sum_{j=0}^{N-1} f_j(x) P_D(j)$$

and

$$W_C = \sum_{j=0}^{N-1} f_j(x) P_C(j+1)$$

where  $f_j(x)$  is the probability of interacting with  $j$  cooperators and  $x$  is the frequency of cooperators. We consider very large well-mixed populations with no assortment: assuming that the  $N$  interacting individuals are selected from this population randomly

$$f_j(x) = \binom{N-1}{j} x^j (1-x)^{N-1-j}.$$

We assume that individuals adopt pure strategies  $C$  and  $D$ , thus the change in frequency of cooperators can be described by the replicator dynamics

$$\dot{x} = x(1-x)(W_C - W_D). \quad (4)$$

We are interested in the fixed points ( $x_1=0$ ,  $x_2=1$  and the solutions of  $W_C=W_D$  in the interval  $x \in [0,1]$ ) and their stability in Eq. (4).

### 3.6. Discounted and synergistic benefits

In an important but unfortunately neglected paper, Motro (1991) studied some non-linear models of cooperation in N-person social dilemmas. He started with the assumptions defined above, except that he did not use a dynamical description like the replicator dynamics, but simply searched for the ESS's of the game. He determined ESS's in the case of convex (synergistically enhanced or super-additive) and concave (discounted or sub-additive) benefit function, that is when  $\beta(i+1) - \beta(i) = \delta(i) > 0$  is an increasing or decreasing function of  $i$ ;  $\gamma(i) = c$  as in the NPD. It can be shown that the ESS's are

$$x^* = \begin{cases} 1 & \text{if } c \leq \delta(0) \\ 0 \text{ and } 1 & \text{if } \delta(0) < c < \delta(N-1) \\ 0 & \text{if } c \geq \delta(N-1) \end{cases}$$

for the convex benefit function, and

$$x^* = \begin{cases} 1 & \text{if } c \leq \delta(N-1) \\ \hat{x} \in (0,1) & \text{if } \delta(N-1) < c < \delta(0), \\ 0 & \text{if } c \geq \delta(0) \end{cases}, \quad (5)$$

for the concave case. In agreement with the conclusions of the NPD, Motro (1991) showed that if the maximal increase of benefit that can be achieved by a cooperator is not bigger than the cost of cooperation ( $c$ ), then the only ESS is defection ( $x^*=0$ ). Conversely, if the cost of cooperation is not bigger than any increase of benefit for an added cooperator then the only ESS is cooperation ( $x^*=1$ ). If neither of these (trivial) cases are valid then both complete cooperation and defection are ESS (convex benefit function) or coexistence of cooperators and defectors is the only ESS (concave benefit function). We note here that if  $x^*$  is an ESS, then it is also a stable fixed point of the replicator dynamics (Hofbauer and Sigmund 1998, 2003) thus Motro's results are adequate even if we focus on the dynamical description of the dilemma. Furthermore,  $\hat{x}$  can define either a mixed ESS or an evolutionary stable polymorphic state in the ESS analysis (Motro, 1991), while the replicator dynamics is generally applied to pure strategies (but see Taylor, 1979; Cressmann and Hofbauer, 2005; Archetti and Scheuring, 2011).

More recently Hauert et al. (2006a) considered a more specific, synergistically enhanced or discounted benefit function in a similar game. They used a constant rate of enhancing or discounting effect by assuming that the first cooperator provides benefit  $b$ , the second one  $b\omega$ , the  $j$ -th one  $b\omega^{j-1}$ , thus

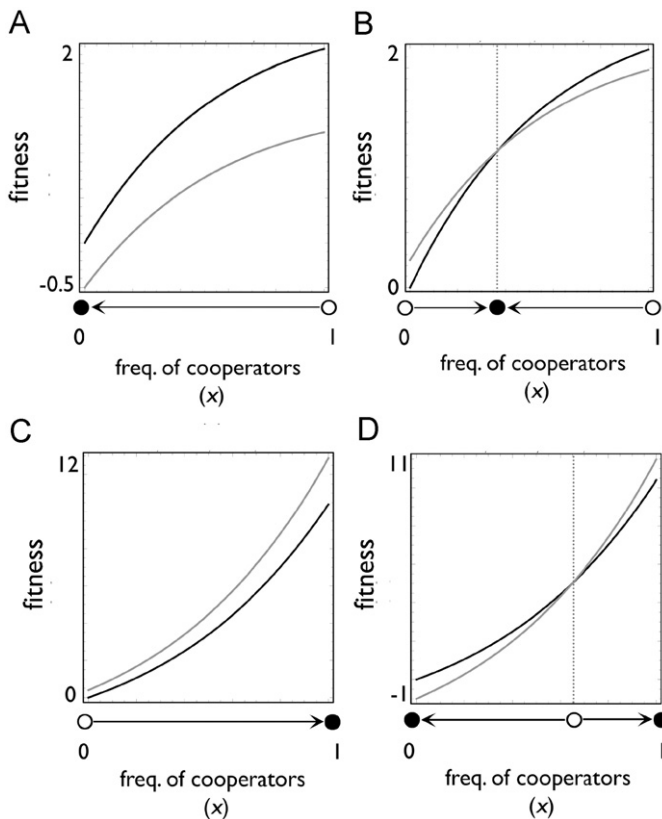
$$\beta(i) = \frac{b}{N} (1 + \omega + \omega^2 + \dots + \omega^{i-1}) = \frac{b}{N} \frac{1 - \omega^i}{1 - \omega}, \quad (6)$$

while  $\gamma(i) = c$ , as above. For  $\omega > 1$   $\beta(i)$  increases faster than linear (convex), thus cooperators interact synergistically, for  $\omega < 1$  it increases in a sub-additive manner (concave), so there is a discounting effect. For  $\omega = 1$  we recover the classical linear NPD game with  $b=rc$  (see Eq. (1)). Assuming only pure strategies and replicator dynamics in an infinite well mixed population and substituting Eq. (6) into Eq. (4) beside the trivial fixed points ( $x_1=0$ ,  $x_2=1$ ) the nontrivial fixed point can be computed explicitly

$$x^* = \frac{1 - (cN/b)^{1/(N-1)}}{1 - \omega} = \frac{1 - (N/r)^{1/(N-1)}}{1 - \omega}. \quad (7)$$

Depending on whether  $x^*$  is within the (0,1) interval or not, and on whether  $x^*$  is stable or unstable fixed point of (4), four different solutions can be distinguished (Hauert et al., 2006a).

- (i)  $N/r > 1$  and  $N/r > \omega^{N-1}$ : the only stable fixed point is  $x_1=0$  in  $[0,1]$  (Fig. 2A). This parameter range corresponds to the NPD game since there  $r/N < 1$  and  $\omega=1$  by definition and to  $c \geq \delta(N-1)$  for the convex or  $c \geq \delta(0)$  for the concave benefit function in Motro's model.
- (ii)  $1 > N/r > \omega^{N-1}$ :  $x^* \in (0,1)$  is stable while  $x_1=0$  and  $x_2=1$  are unstable (Fig. 2B), which is a special case of  $\delta(N-1) < c < \delta(0)$  in Motro's model. Here rare strategies invade, thus this case structurally is identical to the NSD game, but note that while the discounting effect of benefit has a crucial role in this model, discounting of cost is responsible for the coexistence of cooperators and defectors in the traditional NSD game.
- (iii)  $N/r < 1$  and  $N/r < \omega^{N-1}$ : cooperators have higher fitness than defectors for every  $x \in [0,1]$  (Fig. 2C). Thus there is no social dilemma: all individuals will be cooperators at equilibrium, independently of the initial ratio of  $C$  and  $D$  strategies. In Motro's model this happens if  $c \leq \delta(0)$  for convex or  $c \geq \delta(0)$  for concave benefit function.
- (iv)  $1 < N/r < \omega^{N-1}$ :  $x_1=0$  and  $x_2=1$  equilibria are stable, and the inner fixed point  $x^*$  is unstable. Thus depending on the initial



**Fig. 2.** Equilibria with synergistic effects. Fitness for a cooperator ( $W_C$ , gray) and for a defector ( $W_D$ , black) as a function of the frequency of cooperators ( $x$ ) for different values for the parameters in the model defined by (6). Circles show the equilibria, stable (full) or unstable (empty); arrows show the change in frequency of cooperators according to the replicator dynamics.  $N=10$ . (A)  $c/b=1/5$ ,  $\omega=0.8$ . (B)  $c/b=1/20$ ,  $\omega=0.8$ . (C)  $c/b=1/50$ ,  $\omega=1.2$ . (D)  $c/b=3/10$ ,  $\omega=1.2$ .

conditions the population evolves either to  $D$  or  $C$  (Fig. 2D), which was observed by Motro (1991) as well for convex benefit function if  $\delta(0) < c < \delta(N-1)$ .

The intuitive explanation is that if the benefit of the public good is a discounting function of  $x$ , then  $W_D$  increases with  $x$  more quickly than  $W_C$  (Fig. 2A and B); cooperators on average experience higher amounts of public goods than defectors, but this difference is less and less pronounced as the frequency of cooperators increases. If the benefit is synergistic, instead, the advantage of higher levels of public goods for the cooperators increases with  $x$ ; therefore  $W_C$  increases with  $x$  more quickly than  $W_D$  (Fig. 2C and D). In summary, Hauert et al., (2006a) achieve qualitatively the same conclusion as Motro (1991), but their model is more tractable and shows clearer connection among the different cases. Frank (2010) emphasizes the role of non-linearity in maintaining cooperation using similar power law cost and benefit functions.

### 3.7. Threshold effects

The above results show that introducing non-linearity (discounting and synergistic effect) leads to more diverse results than in the NPD. While cases (i) and (iii) (Fig. 2A and C) lead qualitatively to the same results as the NPD (depending on  $N/r$  either complete defection (i) or cooperation (iii) is the ESS), cases (ii) and (iv) can lead to two stable equilibria (complete defection and complete cooperation; case (iv), Fig. 2D) or one internal equilibrium (coexistence of cooperation and defection; case (ii), Fig. 2B).

The models analyzed so far, however, cover only part of the possible biological scenarios. It is possible that the benefit increases synergistically at low frequencies of cooperators and with decreasing returns as the frequency of cooperators increases, because of some saturating effect. The simplest  $\beta(i)$  function with the above described characteristics is the (Heaviside) step function with a lower value below a critical number of cooperators and a higher value above the threshold. Using a step function for  $\beta(i)$  Bach et al. (2001, 2006) studied the obvious extension of the 2-person PD, a 3-person game in which at least two cooperators are necessary to obtain the benefit of cooperation, that is

$$\beta(i) = \begin{cases} 0 & \text{if } i \leq 1 \\ b & \text{otherwise} \end{cases} \quad \text{and } \gamma(i) = c. \quad (8)$$

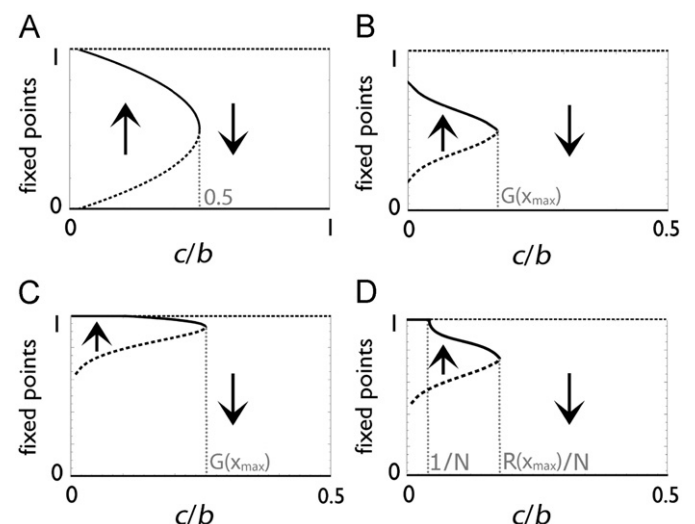
The virtue of this model is that the fixed points of Eq. (4) and their stability can be computed analytically, although the benefit function is non-linear.  $x_1=0$  is a stable and  $x_2=1$  is an unstable fixed point here like in the 2-person PD game. However, if  $c/b < 1/2$  there exist an inner unstable fixed point of (4)

$$x_-^* = \frac{1}{2} - \frac{1}{2} \sqrt{1 - \frac{2c}{b}},$$

and an inner stable fixed point

$$x_+^* = \frac{1}{2} + \frac{1}{2} \sqrt{1 - \frac{2c}{b}}.$$

The dynamics can be represented by a bifurcation diagram as a function of  $c/b$  ( $=1/r$ ) (Fig. 3A). Two important new characteristics emerge from this model that are absent in the NPD: a population evolves to a state where cooperators and defectors coexist if  $c/b < 1/2$  and the initial fraction of cooperators is higher than  $x_-^*$ , otherwise the population evolves to pure defection. The bifurcation diagram depicted in Fig. 3A shows also the hysteresis effect: if the system is originally at  $x_+^*$  and  $c/b$  increases above  $1/2$ , a subsequent reduction of  $c/b$  will not make the system go back to  $x_+^*$  since  $x_1=0$  is also a stable fixed point.



**Fig. 3.** Equilibria with threshold effects. Bifurcation diagrams of the replicator dynamics for the 3-person game in which the benefit is defined by (8) (A); for the  $N$ -person game in which the benefit is defined by (9) with  $N=20$ ,  $s=2$  and  $k=10$  (B) or  $k=18$  (C); and for the  $N$ -person game in which the benefit is defined by (12) with  $k=15$  (D). Fixed points are plotted as a function of the cost/benefit ratio  $c/b$  ( $=1/r$ ). Stable fixed points are represented by solid lines and unstable ones by dashed lines. Arrows indicate the direction of motion from characteristically different initial states. See text for more information about the bifurcation points and the functions  $G$  and  $R$ .

### 3.8. Volunteer's dilemma

We can now consider a more general  $N$ -person game in which at least  $k$  ( $\leq N$ ) cooperators are necessary to produce the public good, while the cost of cooperation is constant. Using our notation

$$\beta(i) = \begin{cases} 0 & \text{if } i < k \\ b & \text{otherwise} \end{cases} \quad \text{and } \gamma(i) = c. \quad (9)$$

The threshold game defined by (9) is sometimes called Volunteer's Dilemma if  $k=1$  (VD; Diekmann, 1985) or Teamwork Dilemma if  $k > 1$  (Myatt and Wallace, 2009; see also Palfrey and Rosenthal, 1984). We will call VD any  $N$ -person game in which at least  $k$  ( $\leq N$ ) cooperators are necessary to produce the public good; the public good is produced if at least  $k$  individuals pay a contribution  $c$ . The dilemma is that each individual would rather avoid the cost of volunteering and exploit the public goods produced by others, but if the public good is not produced everybody pays a cost higher than that of volunteering. It can be shown easily that for  $k=1$  there is only one stable fixed point  $x^*_+ = 1 - (c/b)^{1/(N-1)}$  (Archetti, 2009b, c). If  $k=N$  then  $x^*_+ = (c/b)^{1/(N-1)}$  and since  $G(x)$  is monotonously increasing in  $[0,1]$   $x_1=0$  and  $x_2=1$  are stable fixed points: at equilibrium either everybody defects or everybody volunteers.

For  $N > k > 1$  Bach et al. (2006) show that under certain conditions the dynamics is qualitatively similar to that of the 3-person threshold game:  $c/b$  must be smaller than

$$G(x_{max}) = \binom{N-1}{k-1} x_{max}^{k-1} (1-x_{max})^{N-k}$$

for the existence of inner unstable ( $x^*_-$ ) and stable ( $x^*_+$ ) fixed points, where  $x_{max} = (k-1)/(N-1)$  is the value of  $x$  for which  $G(x)$  is maximal. Otherwise the only stable fixed point is pure defection ( $x=0$ ; Fig. 3B and C). Thus the inner fixed points are the solutions of  $G(x) - c/b = 0$ . Bach et al. (2006) give conditions under which internal equilibria exist. Archetti (2009b,c) finds the frequency of cooperators at equilibrium with and without relatedness, and Archetti and Scheuring (2011) find an analytical solution that yields a good approximation for large groups

$$x^*_\pm = x_{max} \pm \sqrt{\frac{2x_{max}(1-x_{max})}{N-1} \left[ 1 - \frac{c}{bG(x_{max})} \right]}$$

For very large  $N$  these solutions can be approximated by  $x^*_\pm = (k-1)/(N-1)$ .

The VD shows that public goods games can have different results depending on the cost of cooperation ( $c$ ) and on the amount of volunteers required for the production of the public good ( $k$ ). Pure Defect is stable (Fig. 4A) if  $c$  is large; if  $c$  is not too large and the public good is produced at an intermediate frequency of cooperation, pure Defect is still stable but a polymorphic equilibrium also exists in which Defect and Cooperate coexist (Fig. 4B); the frequency of cooperators at equilibrium increases as  $k$  approaches  $N$  (Fig. 4C). If the public good is produced only when  $k=N$  both pure Defect and pure Cooperate can be stable depending on the initial conditions.

### 3.9. Variations of the VD

A variation of the game defined in (9) is to allow the cost of cooperation to be inversely related to the number of cooperators as in the NSD game, that is either

$$\gamma(i) = c/i, \quad (10)$$

or

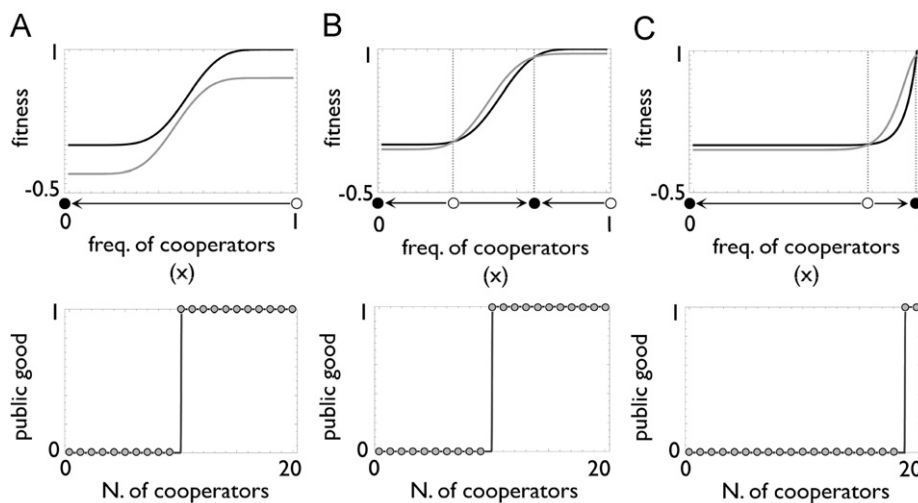
$$\gamma(i) = \begin{cases} c/k & \text{if } 1 < i < k \\ c/i & \text{otherwise} \end{cases}, \quad (11)$$

while  $\beta(i)$  is defined as in (9). These systems behave qualitatively like system (9); defection is the only stable fixed point of (4) if  $c/b$  is larger than a critical value and an inner unstable ( $x^*_-$ ) and a stable ( $x^*_+$ ) fixed point exist if  $c/b$  is below this critical value (Sousa et al., 2009).

Since fitness increases linearly with the number of cooperators in the classical NPD game another possible modification of the benefit function would be that the public good increases linearly but only above a threshold (Pacheco et al., 2009), that is

$$\beta(i) = \begin{cases} 0 & \text{if } i < k \\ \frac{bi}{N} & \text{otherwise} \end{cases} \quad \text{and } \gamma(i) = c. \quad (12)$$

Depending on the parameters of the model three characteristically different solutions can be distinguished. Similar to the VD where  $G(x)$  has a central role in the qualitative behavior, here the maximal value of  $R(x)$  classifies the solutions (for the definition of  $R(x)$  see Pacheco et al., 2009). If  $c/b \geq R(x_{max})/N > 1/N$  the only stable fixed point is pure defection ( $x_1 = 0$ ), which is a similar but less strict condition for the dominance of Defect than in the NPD.



**Fig. 4.** Equilibria, fitness and the public good in the volunteer's dilemma. Top: fitness for a cooperator ( $W_C$ , gray) and for a defector ( $W_D$ , black) as a function of the frequency of cooperators ( $x$ ); circles show the equilibria, stable (black) or unstable (white); arrows show the change in frequency of cooperators. Bottom: the public good defined by (9) as a function of the number of cooperators (the continuous lines are only for guidance; the public good exists only for integer values of  $N$ —the gray dots).  $N=20$ . (A)  $c/b=3/10$ ,  $k=10$ . (B)  $c/b=5/100$ ,  $k=10$ . (C)  $c/b=5/100$ ,  $k=19$ .

In the region where  $R(x_{max})/N > c/b > 1/N$ , beside  $x_1$ , an unstable  $x_2^*$  and a stable  $x_3^*$  fixed point emerge in the  $(0,1)$  interval; if  $c/b < 1/N$  then  $x_3^*$  will be larger than one, thus complete cooperation ( $x_2 = 1$ ) will be the second stable fixed point (Fig. 3D). Interestingly,  $x_{\pm}^* \approx k/N$  for large  $N$  in these models as well (Zheng et al., 2007; Sousa et al., 2009; Pacheco et al., 2009).

The presence of a threshold in these games means that benefit function  $\beta(i)$  is strictly convex for  $i \leq k$  and concave for  $i > k$ . Thus if there is a fixed point in the convex region then it is unstable and if there is a fixed point in the concave region then it is stable (compare Fig. 2B and D with Fig. 4B and C).

### 3.10. From the prisoner's dilemma to the volunteer's dilemma

As we will show below most of the models described so far are special cases of the general public goods game that we describe in this section (Archetti and Scheuring (2011)). We only assume that the benefit is a monotonously increasing saturating function of the individual contributions. As a simple analytical representation the public good function is given by

$$\beta(i) = b \frac{\alpha(i) - \alpha(0)}{\alpha(N) - \alpha(0)}, \quad (13)$$

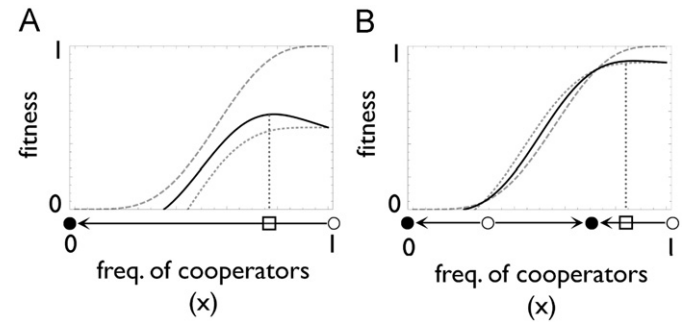
where  $\alpha(i) = (1 + \exp[s(k-i)])^{-1}$ .

Changing the parameters  $k$  (the position of the inflection point) and  $s$  (the steepness of the function at the inflection point, that is the synergistic effect of volunteering) this model can generate all the cases described above, including increasing returns ( $k \rightarrow N$ ) and diminishing returns ( $k \rightarrow 0$ ) and it can be used to model the VD ( $s \rightarrow \infty$ ) and the NPD ( $s \rightarrow 0$ ). Changing the steepness of the public good function ( $s$ ) changes the position of the mixed equilibria only slightly unless the function is approximately linear ( $s \rightarrow 0$ , that is if the game is an NPD). Therefore many social dilemmas can be approximated by the VD (Fig. 5), whereas the NPD is a very special case (a formal proof is in Archetti and Scheuring (2011)) and by no means the rule in public goods games.

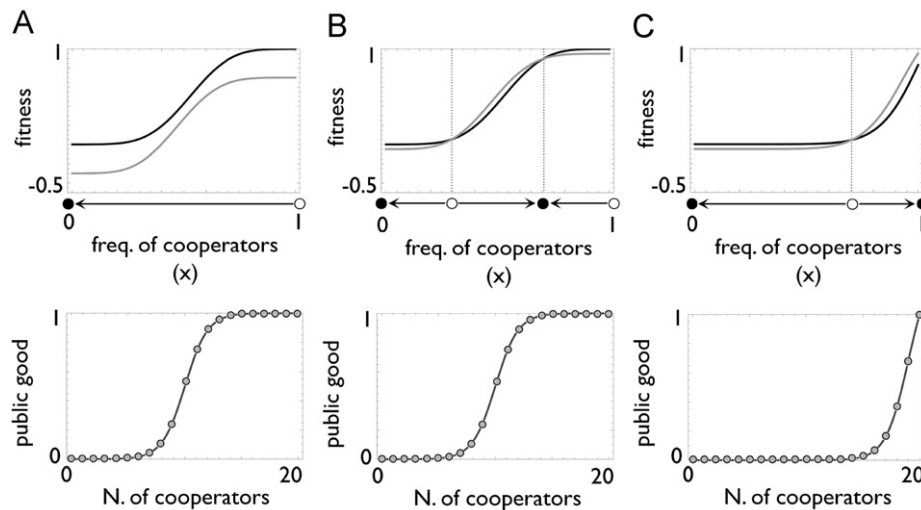
Changing the cost of cooperation  $c$  and the shape of the public good function ( $s$  and  $k$ ) can lead to different results: pure Defect is stable (Fig. 5A) if  $c$  is large and/or the public good is linear or almost linear; pure Cooperate and pure Defect (Fig. 5C) are stable if the benefit starts to increase only for very high frequencies of

cooperation; in this case which equilibrium will be reached depends on the initial conditions of the system. In most cases, however, if  $c$  is not too high and the public good is non-linear, both pure Defection and a mixed equilibrium with Defection and Cooperate (Fig. 5B) are possible: it is possible, therefore, that cooperation is maintained at intermediate levels in the absence of any additional force (relatedness or other forms of assortment, iterations).

The frequency of cooperators  $x_3^*$  at the polymorphic equilibrium is not necessarily the frequency  $x_M$  that maximizes fitness (and of course not necessarily the frequency that maximizes the production of the public good); however  $x_3^*$  and  $x_M$  can be very close to each other and fitness at  $x_3^*$  can be close to fitness at  $x_M$  (Fig. 6). In order to move the equilibrium state even closer to the group optimum, beside non-linearity in public goods multilevel selection (a specific form of assortment) must be assumed (e.g.: Frank, 2010; Boza and Számádó, 2010). The production of the public good improves for very high (close to  $N$ ) or very low (close to 1) values of  $k$  (Fig. 7) (Archetti, 2009c). Although, as we have seen, the existence of the polymorphic equilibrium depends on the  $c/b$  ratio, if this equilibrium does exist, the amount of public

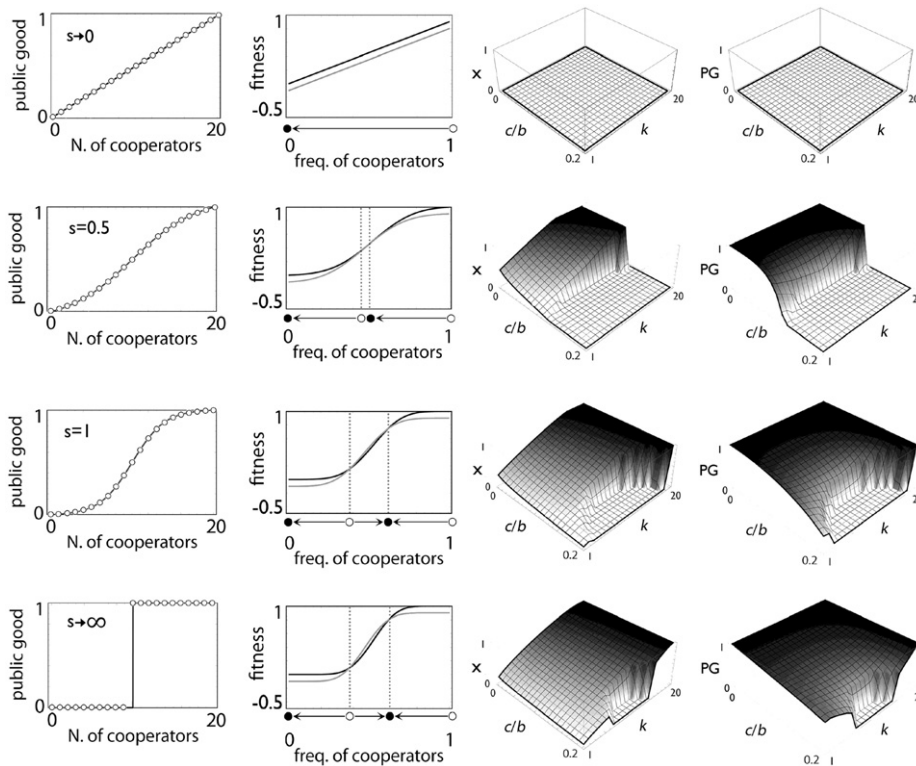


**Fig. 6.** Fitness is maximized at an intermediate frequency of cooperators, and can be close to fitness at equilibrium. The gray lines show the fitness for a cooperator ( $W_C$ , the dotted line), for a defector ( $W_D$ , the dashed line) and for the mixed strategy ( $W_{eq} = xW_C + (1-x)W_D$ , the black line) as a function of the frequency of cooperators ( $x$ ).  $N=10$ ,  $b=1$ ,  $s=10$ ;  $k=5$ . Circles show the equilibria, stable (full) or unstable (empty); arrows show the change in frequency of cooperators. The gray square shows the value of  $x$  for which the mixed strategy has the highest fitness ( $W_{max}$ ). (A)  $c=0.5$ ; there is no mixed equilibrium. (B)  $c=0.1$ ;  $W_{eq}$  is close to  $W_{max}$  and the frequency of cooperators is close to the frequency required for  $W_{max}$ .



**Fig. 5.** Equilibria, fitness and the public good in the generalized public goods game. Top: fitness for a cooperator ( $W_C$ , gray) and for a defector ( $W_D$ , black) as a function of the frequency of cooperators ( $x$ ); circles show the equilibria, stable (black) or unstable (white); arrows show the change in frequency of cooperators. Bottom: the public good defined by (13) as a function of the number of cooperators (the continuous lines are only for guidance; the public good exists only for integer values of  $N$ —the gray dots).  $N=20$ ,  $s=1$ . (A)  $c/b=3/10$ ,  $k=10$ . (B)  $c/b=5/100$ ,  $k=10$ . (C)  $c/b=5/100$ ,  $k=19$ .





**Fig. 7.** Cooperation in one-shot social dilemmas, from the prisoner's dilemma to the volunteer's dilemma. For different values of  $s$  the 2-dimensional plots show the public good as a function of the number of cooperators (the continuous lines are only for guidance; the public good exists only for integer values of  $N$ —the gray dots) and fitness for cooperators ( $W_C$ , gray) and for defectors ( $W_D$ , black) as a function of the frequency of cooperators ( $x$ ).  $N=20$ ,  $c/b=1/10$ ,  $k=10$ . Circles show the equilibria, stable (black) or unstable (white); arrows show the change in the frequency of cooperators. The  $N$ -person prisoner's dilemma corresponds to  $s \rightarrow 0$ . The volunteer's dilemma corresponds to  $s \rightarrow \infty$ . The 3-dimensional plots show the frequency of cooperators ( $x$ ) at equilibrium and the public good (PG) at equilibrium, as a function of the cost/benefit ratio of cooperation  $c/b$  and the parameter  $k$  (the position of the inflection point in the public goods function; the number of volunteers required for the production of the public good in the volunteer's dilemma).

good produced is affected only slightly by the value of  $c$  (Fig. 7). A similar result, not shown here (see Archetti, 2009b,c), holds for relatedness: while higher relatedness facilitates existence of the mixed equilibrium, if the mixed equilibrium exists, the amount of public good produced is affected only marginally by relatedness.

### 3.11. More elaborate assumptions

We have assumed a monotonously increasing function for the public good, but a non-monotonous function with a maximum at  $i^*$  ( $0 < i^* < N$ ) has a biological relevance as well (for example overproduction of enzymes may be harmful). In this case the public good starts to decrease if  $i$  is greater than a critical value, which trivially leads to coexistence of defectors and cooperators. Other possible, more elaborate assumption are described in this section.

#### 3.11.1. Finite population size

The results we have discussed so far are based on a dynamic analysis in infinitely large, well mixed populations. Non-linear public goods games in finite, well mixed populations have also been studied recently (Pacheco et al., 2009; Souza et al., 2009). In this case the fraction of cooperators is no longer a continuous variable, thus sampling follows a hypergeometric distribution. The classical deterministic replicator dynamics is replaced by a stochastic birth–death process combined with a pairwise update rule determined by the fitness differences of the compared individuals (see also Traulsen et al., 2006, 2007 for details). Evolutionary dynamics are roughly similar in finite populations to the dynamics of the corresponding infinite models, however

the picture is modulated further. Most importantly if population size is below a critical level, then cooperation is always disadvantageous (naturally this is the case if  $N$  equals population size). Furthermore, in a finite population the dynamics is inherently stochastic, consequently without any mutation there are only two end points of the process: either everybody cooperates or everybody defects (Pacheco et al., 2009; Souza et al., 2009). Thus even if there is a stable inner fixed point, cooperators and defectors coexist only temporarily. However, since the system remains in this temporal metastable state for a very long time even in relatively small populations (Antal and Scheuring, 2006) this latter difference between the infinite and finite model can practically be neglected.

#### 3.11.2. Density dependence

We have assumed (as is usually assumed in the NPD) that fitness does not depend on the density of the population and that the number of interacting individuals  $N$  is constant. It is reasonable, however, to imagine that if fitness decreases (for example because the population is dominated by defectors) population density will decrease too and  $N$  will change. In a density dependent model of the NPD game Hauert et al. (2006b) showed that cooperators can be maintained because they are favored when density decreases (since then  $r/N > 1$  on average); then density can increase (because replication rate is high) and when  $r/N < 1$  this leads to the spread of defectors which causes again a reduction in density. In short, if the expected group size  $\langle N \rangle$  on average is equal to the multiplication factor  $r$ , cooperators and defectors have the same fitness and can coexist. This ecological feedback leads qualitatively to the case depicted in Fig. 1B: at low

frequency of cooperators  $W_C > W_D$ , while the reverse is true for high frequency of cooperators and thus  $\langle N \rangle$ . An extended version of this model (Parvinen, 2010) that allows cooperation to be an evolving variable from the never cooperating (*Defect*) to the always cooperating strategy (*Cooperate*), shows that the linear public goods function used by Hauert et al. (2006b) leads to a structurally unstable model. By using a non-linear public good function with an inflexion point (like the generalized public goods game described above), instead, then population evolves to a coexistence of highly cooperative and highly defective types. That is, coexistence of cooperators and defectors is observed in a more elaborated ecological model if the public goods function is non-linear.

### 3.11.3. Non-compulsory participation

Taking part in the public goods game is compulsory in the standard NPD and in our generalized  $N$ -person game. But if a third so-called *Loner* strategy (L) is introduced, which does not participate in the game and gets a fixed positive payoff instead, the result of the NPD changes dramatically. If the population is dominated by cooperators then defectors can invade (since  $r/N < 1$ ); if the frequency of defectors is high, however, the frequency of loners can increase (because their fitness is higher than the fitness of defectors if there are only some cooperators); as the frequency of loners increases, effective group size  $N$  decreases (similar to the density dependent model described above) and when  $r/N > 1$  on average, cooperators can spread. This rock-scissors-paper type game can maintain the coexistence of C, D and L strategies (Hauert et al., 2002, but see Mathew and Boyd, 2009; Semmann et al., 2003 for an experimental test). Naturally there is no possibility to play the *Loner* strategy in many situations (e.g. microbial cooperation), while individuals really can choose to be loners in other cases (e.g. cooperative hunting).

All in all, although finite population size, density dependence or more elaborate sets of strategies make the result more diverse, the main result of the generalized public goods game does not change: cooperators and defectors can coexist at equilibrium.

## 4. Discussion

### 4.1. Coexistence of cooperators and defectors

Social dilemmas are described in game theory by  $N$ -person games. The widely used NPD predicts that public goods can be produced in the presence of some form of assortment. The prominence of the NPD in the literature on the evolution of cooperation has obscured the fact that most social dilemmas are, in fact, not NPD's. Many public goods in biology, ranging from microbial to human conflicts, are non-linear functions of the individual contributions. If this is the case, cooperation can be stable without any form of assortment. More specifically, a polymorphic equilibrium can be stable in which cooperators and non-cooperators coexist. At this equilibrium fitness can be close to its maximum and the production of the public good can be high.

For the benefit of the reader that may have got lost or intentionally skipped the mathematics in the previous sections, the reason why cooperators and defectors coexist in non-linear public goods games can be explained intuitively as follows.

Consider first a public good that is produced if and only if at least 1 individual contributes to its production. Why do cooperators (producers) and defectors (non-producers) coexist? Because if nobody else cooperates the best strategy for a rational individual is to cooperate (because not producing the public good is worse than paying the cost of volunteering); but if someone else

cooperates the best strategy is to defect (the public good is produced anyway and the cost of volunteering is spared). The result is that, not knowing what the others are doing, the best strategy is to cooperate with a certain probability (which, as we have seen, depends on the cost/benefit ratio and on group size). The result is an inefficient production of the public good, but the public good is produced nonetheless, with no need of assortment.

Now consider the next step: the public good is produced if and only if at least  $k$  individuals volunteer to pay a small cost; similar to the  $k=1$  case, if less than  $k$  other individuals volunteer, then the best strategy is to volunteer, but if  $k$  or more other individuals already volunteer the cost of volunteering would be wasted, as the public good would be produced anyway. Again, the best strategy is to volunteer with a probability that is a function of the cost/benefit ratio, group size and  $k$ .

The next step is to allow the public good to be a smooth sigmoid function rather than a step function; when the steepness of this function is high the public good is almost a step function, as in the VD with  $k > 1$  (see Fig. 7) and the result is similar to the VD; again, volunteering with a probability. As we have seen, coexistence of cooperators and defectors is possible as long as the cost of volunteering is not too high; as the public good approaches a linear function this critical cost decreases, and when the public good is linear (as in the NPD) no coexistence is possible.

### 4.2. Relatedness, assortment and iterations are not necessary for the production of public goods

The existence of a mixed equilibrium in which cooperators and defectors coexist is the main result that emerges from the analyses of non-linear public goods we have reviewed. This result is independent from any type of assortment. In other words, cooperation (or, more precisely, the coexistence of cooperation and defection) in public goods games does not require positive assortment (for example kin recognition, population viscosity or iterations), unless the cost of the contribution is very high. In simple words, there is no need to invoke kin selection or repeated interactions, that is any type of positive assortment of cooperators. This is in stark contrast with the result of the NPD in which no cooperation is possible in the absence of some form of assortment. The logic of game theory and the predictions of the  $N$ -person games we have reviewed, are sometimes surprisingly easy to miss.

For example in *Salmonella typhimurium* a fraction of pathogen cells dies in the cellular lysis process that leads to producing toxins, which is beneficial only for the cells that do not produce the toxin (Paton, 1996; Voith and Ballard, 2005); these cooperative and defecting behaviors are probably the stochastically emerging alternative phenotypes of the same genotype (Kaern et al., 2005). Ackermann et al. (2008) studied the evolutionary dynamics of self-destructive cooperative pathogens. In the framework of the NPD they show that coexistence of self-destructive and defective phenotypes is evolutionary stable only if deme selection (a specific kind of assortment) is present. However, they show that the public good in their system is a discounting function of the frequency of the self-destructive type (see their Fig. 2D). As we have shown, this is a case of non-linear public goods, in which coexistence of cooperators and defectors is possible even without assortment (Fig. 2B). We must at least be cautious against interpreting experimental observations of coexistence of cooperators and defectors as the result of assortment.

The problem is not just about ascribing cooperation to assortment, but it extends to other specific predictions. Consider one of the most cited examples of cooperation in microbes: the production of invertase in yeast. Invertase catalyzes the hydrolysis of

sucrose into glucose and fructose (yeast can also metabolize sucrose but metabolism of glucose is more efficient); yeast cells that secrete invertase are considered cooperators, while non-producers are considered defectors because they can use the invertase produced by the cooperators. This system was initially described as a PD (Greig and Travisano, 2004). The invertase produced by one individual, however, is available to all its neighbors; there are no pairwise interactions, this is an  $N$ -person game. A recent paper (Gore et al., 2009) described, instead, invertase production as a SD game, thus potentially explaining the coexistence of cooperators and defectors. Clearly however, again, yeast cells are not engaged in a SD (that is a 2-person game). It is unfortunate that such basic misunderstandings still populate the literature on the evolution of cooperation; while the mistake may pass unnoticed in Gore et al. (2009), because the SD has a mixed equilibrium like the  $N$ -person game, it can be misleading. Elaborating on Gore et al. (2009); MacLean et al. (2010) observe that the SD game is not appropriate to describe cooperation in yeast because, although cooperators and defectors coexist, maximum group benefit in their experimental system occurs when an intermediate frequency of defectors is present rather than (as predicted by the SD game) when everybody cooperates. A similar result (maximum growth occurs when the two types are mixed) is found by Lee et al. (2010) in a bacterial system. MacLean et al. (2010) dismiss game theory and resort to systems biology (which must invoke assortment again to explain cooperation). Their result (maximum group benefit at an intermediate frequency of defectors), however, is surprising for game theory only if one uses the predictions of the 2-person SD (in which the optimal group benefit is when everybody cooperates). The problem, instead, is a collective action problem, which should be described by an  $N$ -person public goods game. And, as we have seen, in a public goods game not only is coexistence of cooperators and defectors possible, but the optimal group benefit is at intermediate frequencies of cooperators. There is no reason to dismiss game theory if one uses the predictions of the right game.

#### 4.3. Game theory is the key to the study of cooperation

After a huge interest in the 80s, it seems that evolutionary biologists have recently lost confidence in game theory. It is often stated (more in private discussions than in print) that, although the PD and the SD were useful in understanding the basic problem, game theory is no longer useful in the study of cooperation because it cannot explain the details of real, complex biological systems, and that we should resort to other methods like inclusive fitness techniques or systems biology. This is an unfortunate belief and, as we have seen, incorrect. Game theory, of course, is not just a collection of toy games like the PD: it is the branch of mathematics that studies strategic behavior, and as such it is the most appropriate method to study conflict and cooperation. The prominence of kin selection theory on the study of cooperation in biology has led to the prominence of inclusive fitness techniques as a method of analytical investigation in the study of cooperation. Game theory, however, remains essential in the study of public goods. It should be enough to point out that all the studies mentioned above that discover the coexistence of cooperators and defectors are game-theoretic studies.

Game theory is important also because it gives predictions in which costs and benefits have a straightforward interpretation and could be measured using an appropriate experimental system. Experiments with microbes have been used widely to test social evolution theory. The main problem with current experimental approaches is that, while relatedness can be measured and varied, measuring quantitatively costs and benefits is tricky, and manipulating them is challenging. This has allowed, so far,

only qualitative tests. While Hamilton's rule can always be invoked, Chuang et al. (2010) show that its predictive value is limited when the public good is non-linear, because the parameters  $c$  and  $b$  lose their interpretation as phenotypic properties defined at the level of individuals. In the models we described here, instead,  $b$  and  $c$  have a straightforward interpretation and can be measured easily, for example using the new synthetic *Escherichia coli* system developed by the laboratory of S. Leibler (Chuang et al., 2010): the cost  $c$  is simply the growth difference between producers and non-producers, when having access to the same amount of *Rhl* autoinducer (the public good) and the benefit  $b$  is the growth improvement for both producers and non-producers as a function of the amount of *Rhl*.

Finally, game theory is important because it can suggest practical ways to improve public goods, that is a prescriptive approach to cooperation. In a situation of conflict one wants to devise ways to increase cooperation. Assortment (including relatedness) does this by changing the game from one in which defection is the only stable equilibrium to one in which cooperation can be stable. Likewise repeated interactions facilitate cooperation by changing the game to one in which cooperation can be stable. Clearly, however, relatedness or iterations cannot normally be imposed by the players or by an external authority, and therefore are not practical solutions for social dilemmas; they only offer a descriptive solution to the problem. It would be interesting, instead, to understand how rational, self-interested individuals can improve cooperation in public goods games. A discussion on this topic seems premature here; we only note that there are various ways to improve the production of public goods at a mixed equilibrium (for example reducing one's ability to contribute—see Archetti, 2011a) that are absent in the NPD.

## 5. Conclusion

In the social sciences it has been clear for a long time that the NPD is not the only type of social dilemma (Kollock, 1998). Evolutionary biology instead has developed a theory of public goods that has, for way too long, insisted on the prisoner's dilemma and, as a consequence, on relatedness, spatial structure or other ways to create assortment to explain cooperation. As we have shown, the results of games with pairwise interactions or linear benefits cannot be extended to all  $N$ -person games. The existence of mixed equilibria in public goods games is a fundamental result in the study of cooperation, which has been overlooked so far in evolutionary biology. The fact that at this mixed equilibrium a certain amount of cooperation exists irrespective of additional forces, might seem to spoil, suddenly, the mystery of the evolution of cooperation. We do not believe it actually makes the study of cooperation less interesting. Indeed, it allows a prescriptive approach to public goods that is still largely unexplored. Game theory provides clear predictions that can be easily tested in experimental systems.

## Acknowledgments

We thank L.D. Hurst, G. Noldeke, E. Szathmáry and D.W. Yu for discussion. This work was partly supported by TECT BIOCONTRACT project under contract numbers NN71700 (SI).

## References

- Ackermann, M., Stecher, B., Freed, N.E., Songhet, P., Hardt, W.D., Doebeli, M., 2008. Self-destructive cooperation mediated by phenotypic noise. *Nature* 454, 987–990.

- Antal, T., Scheuring, I., 2006. Fixation of strategies for an evolutionary game in finite populations. *Bull. Math. Biol.* 68, 1923–1944.
- Archetti, M., 2003. A selfish origin for recombination. *J. Theor. Biol.* 223, 335–346.
- Archetti, M., 2006. Genetic robustness and selection at the protein level for synonymous codons. *J. Evol. Biol.* 19, 353–365.
- Archetti, M., 2009a. Survival of the steepest: hypersensitivity to mutations as an adaptation to soft selection. *J. Evol. Biol.* 22, 740–750.
- Archetti, M., 2009b. The volunteer's dilemma and the optimal size of a social group. *J. Theor. Biol.* 261, 475–480.
- Archetti, M., 2009c. Cooperation as a volunteer's dilemma and the strategy of conflict in public goods games. *J. Evol. Biol.* 22, 2192–2200.
- Archetti, M., 2011. A strategy to increase cooperation in the volunteer's dilemma: reducing vigilance improves alarm calls. *Evolution* 65, 885–892.
- Archetti, M., Scheuring, I., 2011. Coexistence of cooperation and defection in public goods games. *Evolution* 65, 1140–1148.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Bach, L.A., Bentzen, S., Alsner, J., Christiansen, F.B., 2001. An evolutionary-game model of tumour-cell interactions: possible relevance to gene therapy. *Eur. J. Cancer* 37, 2116–2120.
- Bach, L.A., Helvik, T., Christiansen, F.B., 2006. The evolution of  $n$ -player cooperation—threshold games and ESS bifurcations. *J. Theor. Biol.* 238, 426–434.
- Beauchamp, G., 2003. Group-size effects on vigilance: a search for mechanisms. *Behav. Proc.* 63, 111–121.
- Bednarz, J.C., 1988. Cooperative hunting Harris' hawks (*Parabuteo unicinctus*). *Science* 239, 1525–1527.
- Bergstrom, T., Blume, L., Varian, H., 1986. Private provision of public goods. *J. Public Econ.* 29, 25–49.
- Boehm, C., 1999. *Hierarchy in the forest*. Harvard University Press, Cambridge, MA.
- Bonner, J.T., 2008. *The Social Amoeba*. Princeton University Press, Princeton, NJ.
- Boza, G., Számadó, S., 2010. Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in threshold public good games. *BMC Evol. Biol.* 10, 336.
- Burt, A., Trivers, R., 2006. *Genes in Conflict*, Cambridge MA. Harvard University Press.
- Chuang, J.S., Rivoire, O., Leibler, S., 2010. Cooperation and Hamilton's rule in a simple synthetic microbial system. *Mol. Syst. Biol.* 398. doi:10.1038/msb.2010.57.
- Clutton-Brock, T.H., 1999. Selfish sentinels in cooperative mammals. *Science* 284, 1640–1644.
- Creel, S., 1997. Cooperative hunting and group size: assumptions and currencies. *Anim. Behav.* 54, 1319–1324.
- Crespi, B.J., 2001. The evolution of social behavior in microorganisms. *Trends Ecol. Evol.* 16, 178–183.
- Cressman, R., Hofbauer, J., 2005. Measure dynamics on one dimensional continuous trait space: theoretical foundations for adaptive dynamics. *Theor. Popul. Biol.* 67, 47–59.
- Diekmann, A., 1985. Volunteer's Dilemma. *J. Conflict Resolution* 29, 605–610.
- Eungdamrong, N.J., Iyengar, R., 2004. Modeling cell signaling networks. *Biol. Cell* 96, 355–362.
- Fehr, E., Gintis, H., 2007. Human motivation and social cooperation: experimental and analytical foundations. *Annu. Rev. Sociol.* 33, 43–64.
- Fox, J., Guyer, M., 1978. Public Choice and cooperation in  $N$ -person Prisoner's Dilemma. *J. Conflict Resolut.* 22, 469–481.
- Frank, S., 2010. A general model of public goods dilemma. *J. Evol. Biol.* 23, 1245–1250.
- Frank, S.A., 1998. *Foundations of Social Evolution*, Princeton, NJ. Princeton University Press.
- Friberg, U., Rice, W.R., 2008. Cut thy neighbor: cyclic birth and death of recombination hotspots via genetic conflict. *Genetics* 179, 2229–2238.
- Gore, J., Youk, H., van Oudenaarden, A., 2009. Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459, 253–256.
- Grafen, A., 1984. Natural selection, kin selection and group selection. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology* second ed. Blackwell, Oxford, UK, pp. 62–84.
- Grafen, A., 1985. A geometric view of relatedness. *Oxford Surv. Evol. Biol.* 2, 28–89.
- Grafen, A., 2006. Optimisation of inclusive fitness. *J. Theor. Biol.* 238, 541–563.
- Grafen, A., 2009. Formalizing Darwinism and inclusive fitness theory. *Philos. Trans. R. Soc. B* 364, 3135–3141.
- Greig, D., Travisano, M., 2004. The Prisoner's Dilemma and polymorphism in yeast SUC genes. *Proc. R. Soc. London Ser. B* 27, S25–S26.
- Haig, D., 1993. Genetic conflicts in human pregnancy. *Q. Rev. Biol.* 68, 495–532.
- Haig, D., 2000. The kinship theory of genomic imprinting. *Annu. Rev. Ecol. Syst.* 31, 9–32.
- Hamburger, H., 1973.  $N$ -person prisoners dilemma. *J. Math. Sociol.* 3, 27–48.
- Hamilton, W.D., 1963. The evolution of altruistic behavior. *Am. Nat.* 97, 354–356.
- Hamilton, W.D., 1964. The genetical evolution of social behaviour. *J. Theor. Biol.* 7, 1–52.
- Hardin, G., 1968. The tragedy of the commons. *Science* 162, 1243–1248.
- Hauert, C., De Monte, S., Hofbauer, J., Sigmund, K., 2002. Volunteering as red queen mechanism for cooperation in public goods games. *Science* 296, 1129–1132.
- Hauert, C., Holmes, M., Doebeli, M., 2006a. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proc. R. Soc. B* 273, 2565–2570.
- Hauert, C., Michor, F., Nowak, M.A., Doebeli, M., 2006b. Synergy and discounting in social dilemmas. *J. Theor. Biol.* 239, 195–202.
- Hemker, H.C., Hemker, P.W., 1969. General kinetics of enzyme cascades. *Proc. Roy. Soc. B* 173, 411–420.
- Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press.
- Hofbauer, J., Sigmund, K., 2003. *Evolutionary game dynamics*. *Bull. Am. Mat. Soc.* 40, 479–519.
- Hume, D., 1739. *A Treatise of Human Nature*.
- Hurst, L.D., Atlan, A., Bengtsson, B.O., 1996. Genetic conflicts. *Q. Rev. Biol.* 71, 317–364.
- Kaern, M., Elston, T.C., Blake, W.J., Collins, J.J., 2005. Stochasticity in gene expression: from theories to phenotypes. *Nat. Rev. Genet.* 6, 451–464.
- Kollock, P., 1998. Social dilemmas: the anatomy of cooperation. *Annu. Rev. Sociol.* 24, 183–214.
- Lee, H.H., Molla, M.N., Cantor, C.R., Collins, J.J., 2010. Bacterial charity work leads to population-wide resistance. *Nature* 467, 82–86.
- MacLean, R.C., Fuentes-Hernandez, A., Greig, D., Hurst, L.D., Gudelj, I., 2010. A mixture of “cheats” and “co-operators” can enable maximal group benefit. *PLoS Biol.* 8. doi:10.1371/journal.pbio.1000486 e1000486.
- Mathew, S., Boyd, R., 2009. When does optional participation allow the evolution of cooperation? *Proc. Roy. Soc. B* 276, 1167–1174.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- Maynard Smith, J., Szathmáry, E., 1995. *The major transitions in evolution*. Freeman, San Francisco.
- Mendes, P., 1997. Biochemistry by numbers: simulation of biochemical pathways with Gepasi 3. *Trends Biochem. Sci.* 22, 361–363.
- Michod, R.E., 1982. The Theory of Kin Selection. *Annu. Rev. Ecol. Syst.* 13, 23–55.
- Motro, U., 1991. Co-operation and defection: playing the field and ESS. *J. Theor. Biol.* 151, 145–154.
- Myatt, D.P., Wallace, C., 2009. Evolution, teamwork and collective action: Production targets in the private provision of public goods. *Econ. J.* 119, 61–90.
- Nowak, M.A., 2006. *Evolutionary Dynamics*, Cambridge, MA. Harvard University Press.
- Olson, M., 1965. *The Logic of Collective Action: Public Goods and the Theory of Groups*, Cambridge, MA. Harvard University Press.
- Pacheco, J.M., Santos, F.C., Souza, M.O., Skyrms, B., 2009. Evolutionary dynamics of collective action in  $N$ -person stag hunt dilemmas. *Proc. Roy. Soc. B* 276, 315–321.
- Packer, C., Scheel, D., Pusey, A.E., 1990. Why lions form groups: food is not enough. *Am. Nat.* 136, 1–19.
- Palfrey, T.R., Rosenthal, H., 1984. Participation and the provision of public goods: a strategic analysis. *Journal of Public Economics* 24, 171–193.
- Parvinen, K., 2010. Adaptive dynamics of cooperation may prevent the coexistence of defectors and cooperators and even cause extinction. *Proc. Roy. Soc. B* 277 (1693), 2493–2501.
- Paton, J.C., 1996. The contribution of pneumolysin to the pathogenicity of *Streptococcus pneumoniae*. *Trends Microbiol.* 4, 103–106.
- Rabenold, K.N., 1984. Cooperative enhancement of reproductive success in tropical wren societies. *Ecology* 65, 871–885.
- Rainey, P.B., Rainey, K., 2003. Evolution of co-operation and conflict in experimental bacterial populations. *Nature* 425, 72–74.
- Rankin, D.J., Bargum, K., Kokko, H., 2007. The tragedy of the commons in evolutionary biology. *Trends Ecol. Evol.* 12, 643–651.
- Rapoport, A., Chammah, A.M., 1966. The game of chicken. *Am. Behav. Sci.* 10, 10–28.
- Robinson, D., Goforth, D., 2005. *The Topology of the 2 × 2 Games: a New Periodic Table*. Routledge.
- Ricard, J., Noat, G., 1986. Catalytic efficiency, kinetic co-operativity of oligometric enzymes and evolution. *J. Theor. Biol.* 123, 431–451.
- Russell, B.W., 1959. *Common Sense and Nuclear Warfare*. George Allen and Unwin, London.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication*. Princeton University Press, Princeton, NJ.
- Samuelson, L., 1997. *Evolutionary Games and Equilibrium Selection*. MIT Press.
- Samuelson, P.A., 1954. The pure theory of public expenditure. *Rev. Econ. Stat.* 36, 387–389.
- Semmann, D., Krambeck, H.J., Milinski, M., 2003. Volunteering leads to rock-paper-scissors dynamics in a public goods game. *Nature* 425, 390–393.
- Souza, M.O., Pacheco, J.M., Santos, F.C., 2009. Evolution of cooperation under  $N$ -person snowdrift games. *J. Theor. Biol.* 260, 581–588.
- Stander, P.E., 1991. Foraging dynamics of lions in semi-arid environment. *Can. J. Zool.* 70 (8–21).
- Skyrms, B., 2004. *The Stag Hunt and Evolution of Social Structure*. Cambridge University Press, Cambridge.
- Sugden, R., 1986. *The Economics of Rights, Cooperation and Welfare*. Blackwell, Oxford.
- Taylor, P.D., 1979. Evolutionarily stable strategies with two types of player. *J. Appl. Probab.* 16, 76–83.
- Traulsen, A., Nowak, M.A., Pacheco, J.M., 2006. Stochastic dynamics of invasion and fixation. *Phys. Rev. E* 74 011909.
- Traulsen, A., Pacheco, J.M., Nowak, M.A., 2007. Pairwise comparison and selection temperature in evolutionary game dynamics. *J. Theor. Biol.* 244, 349–356.
- Tucker, A., 1950. A two-person dilemma. In: Rasmusen, E., *Readings in Games and Information*. Oxford, Blackwell, 2001, pp. 7–8.



- Turner, P.E., Chao, L., 2003. Escape from prisoner's dilemma in RNA phage  $\Phi 6$ . *Am. Nat.* 161, 497–505.
- Velicer, G.J., 2003. Social strife in the microbial world. *Trends Microbiol.* 11, 330–337.
- Voth, D.E., Ballard, J.D., 2005. Clostridium difficile toxins: mechanism of action and role in disease. *Clin. Microbiol. Rev.* 18, 247–263.
- Yip, E.C., Powers, K.S., Aviles, L., 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. *PNAS* 105, 11818–11822.
- Zheng, D.F., Yin, H.P., Chan, C.H., Hui, P.M., 2007. Cooperative behavior in a model of evolutionary snowdrift games with  $N$ -person interactions. *Euthorophys. Lett.* 80, 18002.