

Evolutionary Dynamics of Collective Action

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Abstract. In the natural world, performing a given task which is beneficial to an entire group requires the cooperation of several individuals of that group who often share the workload required to perform the task. The mathematical framework to study the dynamics of collective action is game theory. We study the evolutionary dynamics of cooperators and defectors in a population in which groups of individuals engage in N -person, non-excludable public goods games. We analyze the N -person Prisoner's dilemma (NPD), where the collective benefit increases proportional to the cost invested, and the N -person Snowdrift game (NSG), where the benefit is fixed but the cost is shared among those who contribute. We impose the existence of a threshold which must be surpassed before collective action becomes successful, and discuss the evolutionary dynamics in infinite and finite populations. In infinite populations, the introduction of a threshold leads, in both dilemmas, to a unified behavior, characterized by two interior fixed points. The fingerprints of the interior fixed points are still traceable in finite populations, despite evolution remaining active until the population reaches a monomorphic end-state. As the group size and population size become comparable, we find that spite dominates, making cooperation unfeasible.

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1. Introduction

The last decades have witnessed the discovery of key insights into the emergence and sustainability of cooperation at different levels of organization [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17]. Special attention has been paid to two-person dilemmas such as the Prisoner's Dilemma (PD) [18, 19], the Snowdrift Game (SG) [20] and the Stag-Hunt game (SH) [16], which constitute powerful metaphors to

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describe conflicting situations often encountered in the natural and social sciences [5, 16]. Many real-life situations, however, are associated with collective action based on joint decisions made by a group often involving more than 2 individuals. This is the case, for instance, in the upper primates, where problems of collective action are recurrent [2, 21]. These types of problems are best dealt-with in the framework of N -person games [22, 23, 24, 25, 26, 27, 28]. The crossover from two-person games to N -person games brings along additional difficulties, similar to what one observes in the physical sciences when moving from the study of interactions between two particles and those involving many particles. The impact of this additional complexity in the context of biology has been well captured by the words of W.D. Hamilton [29]:

“The theory of many person games may seem to stand to that of two-person games in the relation of sea-sickness to a headache.”

The prototypical example of a Public Goods Game (PGG) is captured by the so-called N -person PD (NPD). It involves a group of N individuals, who can be either Cooperators (C) or Defectors (D). Cs contribute a cost “ c ” to the public good, whereas Ds refuse to do so. After all individuals are given the chance to contribute, the accumulated contribution is multiplied by an enhancement factor “ F ”, and the total amount is equally shared among all individuals of the group. In other words, if there are k Cs in a group of N individuals, Ds end up with kFc/N , whereas Cs only get $kFc/N - c$, that is, in mixed groups Cs are always worse off than Ds.

Group hunting provides an excellent example of this type of setting. From lionesses in Etosha National Park, Namibia [30], to Chimpanzees in the Tai forest [31] and African wild dogs [32], group hunting, being ubiquitous, usually requires, to be effective, the joint action of at least a minimum number of animals. Of course, the more individuals participate, the more effective the hunting will be. In animals, other collective actions, such as lions defending a kill against a pack of hyenas, can also be seen as generalized Stag Hunt games [33]. In human affairs we also find collective action problems that can be viewed as generalized Stag hunts, not only in literal hunts such as the whale hunts discussed in [34], but also in international relations [35] and macroeconomics [36].

Despite their abundance, N -person generalizations of the Prisoner’s Dilemma and the Stag-Hunt games do not exhaust the spectrum of collective action dilemmas encountered in the natural and social phenomena. Indeed, generalized snow-drift games appear all too often. In the standard SG, two individuals are driving on a road which is blocked by a snowdrift. To proceed with their journey home, the snow must be removed. Three possibilities occur: No-one shovels, and hence no-one gets home: The two drivers cooperate and shovel, and both get home, each one sharing the workload of shoveling the snow. If only one driver decides to shovel, both get home despite one driver incurring the entire cost of snow shoveling. If we define the benefit of getting home as b and the cost of shoveling as c , then if both drivers cooperate and shovel, each gets $b - c/2$. If both defect, no one gets

anything: 0. If one cooperates and the other defects, the Cooperator (C) gets $b - c$ while the defector (D) gets b . Assuming, as usual, that the benefit is greater than the cost, we get a payoff ranking characteristic of a chicken, hawk-dove or snowdrift dilemma [6]. The generalization of this game to a public goods game involving N players is straightforward. To remain with the previous example, we can imagine that the snowdrift occurs at a cross-road where N drivers meet. Again, all want to go home (getting all the same benefit b), but perhaps not all are willing to shovel. If all shovel, then each gets $b - c/N$. But if only k individuals shovel (C), they get $b - c/k$ whereas those who defect by refusing to shovel get home for free and get b .

Similar to group hunting, however, it is often the case that no common benefit is produced unless its cost is shared by a minimum threshold of cooperating individuals. In keeping with the metaphor introduced above, the fact that individuals have a finite capacity of clearing the snow, may lead to the requirement of a minimum threshold of people to cooperate (shovel) so that the road is cleared.

The existence of thresholds in NSG abounds. For example, not all Amish need to participate in the construction of a church for the church to be built (see, e.g., the movie *Witness*, directed by P. Weir (1985)). Yet, the more contribute the better, since the effort to be invested by each member of the construction group will be smaller. On the other hand, the cost of building a church cannot be provided by a single individual. In this example, the public good is the church. Note, further, that the size of the church, or the benefits of having one, do not necessarily increase with the number of individuals that worked on it. Similar settings apply whenever individuals act collectively to setup sandbag levees to prevent river flooding.

Hence, as with the NPD, the need for collective coordination in the NSG introduces a behavioral tension common to conventional coordination games [15, 16]: if the others do their work, it might be profitable to do it as well; otherwise you definitely gain from *opting out*.

Mathematically, this means that for a given group of size N , we define a threshold $1 \leq M \leq N$ such that only when the number k of Cs in the group is at least M ($k \geq M$) a public good is achieved. In all cases, a cost c must be paid before a common benefit b is produced. For the NPD, the benefit increases with the cost invested. For the NSG, the benefit is fixed but the cost is shared among those that contribute. In Table 1 we summarize the payoffs of Cs and Ds in any case (as usual in N -person games, $k = 0$ means no cost is expended and no benefit is produced).

We shall assume a population of size Z , from which groups of size N are randomly sampled. Let us first study the conventional limit in which $Z \rightarrow \infty$, under deterministic replicator dynamics. Subsequently, we shall consider stochastic dynamics in finite populations. The fitness of individuals is determined by their payoff collected when engaging in N -person PGG, requiring at least $0 < M < N$ individuals to produce any public good at all. We shall find that requiring a minimum threshold of cooperators to produce a benefit leads to the appearance of both coexistence and coordination features in an otherwise defector dominance game (NPD), and to coordination features in an otherwise coexistence game (NSG).

Game	NPD		NSG	
	C	D	C	D
$1 \leq k < M$	$-c$	0	$-\frac{c}{M}$	0
$M \leq k$	$\frac{Fkc}{N} - c$	$\frac{Fkc}{N}$	$b - \frac{c}{k}$	b

TABLE 1. Payoff values Π_C and Π_D for the *NPD* and *NSG*.

Hence, we obtain a richer evolutionary dynamics scenario in infinite populations, which, at least qualitatively, brings about a unified picture of N -person games with a threshold. We find that this scenario remains qualitatively valid whenever we remove the approximation of assuming infinite populations, although the stochastic dynamics only ends whenever a monomorphic composition of the population is reached. Nonetheless, for small populations and/or group sizes spanning nearly the entire population, we observe the “spite” effect first noted by Hamilton in 1970, and which works against cooperation [37].

2. Evolutionary dynamics of PGGs in infinite populations

Let us assume a very large population, a fraction x of which is composed of Cs, the remaining fraction $(1 - x)$ being Ds. Let groups of N individuals be sampled randomly from the population. Such a random sampling leads to groups whose composition follows a binomial distribution. The fitness of the Ds is given by

$$f_D = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} \Pi_D(k), \quad (2.1)$$

whereas the average fitness of Cs is given by

$$f_C = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} \Pi_C(k+1), \quad (2.2)$$

Π_C and Π_D are defined in Table 1 for each of the games. The evolutionary dynamics is given by the replicator equation [4],

$$\dot{x} = x(1-x)(f_C - f_D) \quad (2.3)$$

following that there exists an interior fixed point, x^* , whenever $Q(x^*) = f_C(x^*) - f_D(x^*) = 0$.

2.1. N -person PD with thresholds in infinite populations

For the *NPD*, with a given threshold M , the payoff of Defectors and Cooperators can be explicitly written as (see Table 1) $\Pi_D = (kFc/N)\theta(k-M)$ and $\Pi_C = \Pi_D - c$,

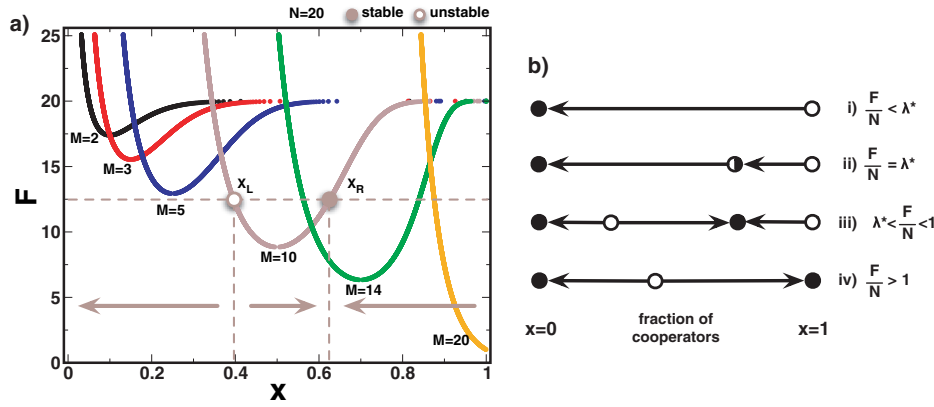


FIGURE 2.1. a) Interior fixed points of the replicator equation for N -person PD games with coordination threshold. The curves provide the location of the critical values of the fraction of cooperators (x_L, x_R) at which $f_C = f_D$. For each value of F (defining a horizontal line), the critical values are given by the intersection of this line with each curve (one curve for given fixed M and $N = 20$). Scenarios with none, one and two interior fixed points are possible as detailed in the right panel. b) Dynamics of N -person PD in infinite populations with coordination threshold. Empty circles represent unstable fixed points; full circles represent stable fixed points and arrows indicate the direction of evolution by natural selection.

respectively, where the Heaviside step function $\theta(x)$ is equal to 1 whenever $x \geq 0$ and equal to 0 otherwise. The introduction of a threshold ($M > 1$) leads to a symmetry breaking of the sampling, which does not allow a closed form expression for the fitness. Thus, the determination of the possible interior equilibrium points, i.e., the zeros of $Q(x)$ has to be done numerically. However, a great deal of information can be obtained without solving explicitly for $Q(x) = 0$. Indeed, as shown in [38], introducing Π_C and Π_D above in Eqs. (2.1) and (2.2) leads to

$$\begin{aligned}
 Q(x) &= f_C(x) - f_D(x) \\
 &= c \left(\frac{F}{N} - 1 \right) \\
 &\quad - c \frac{F}{N} (1-x)^{N-M} \sum_{k=0}^{M-1} \binom{N-1}{k} (1-M\delta_{k,M-1}) x^k (1-x)^{M-1-k}.
 \end{aligned}$$

In what follows, we shall strictly assume that $N \geq 2$. For most of the time, we shall assume that $1 < M \leq N$; the degenerate cases can be handled as well, and

the reader is referred to [38] for details. Let

$$\begin{aligned} R(x) &= \sum_{k=M}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} + M \binom{N-1}{M-1} x^{M-1} (1-x)^{N-M} \\ &= x^{M-1} \left(\sum_{k=M}^{N-1} \binom{N-1}{k} x^{k-M+1} (1-x)^{N-1-k} + M \binom{N-1}{M-1} (1-x)^{N-M} \right). \end{aligned} \quad (2.4)$$

Since,

$$1 = 1^{N-1} = (x + 1 - x)^{N-1} = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k},$$

we have that

$$Q(x) = -c(1 - \lambda R(x)), \quad (2.5)$$

with $\lambda = F/N$.

Lemma 2.1. *The polynomial R defined above satisfies*

1. $R(0) = 0$;
2. $R(1) = 1$;
3. $R(x) > 0$, $x \in (0, 1)$;
4. Let $x^* = M/N$. Then we have that $R'(x) > 0$ for $0 \leq x < x^*$, and $R'(x) < 0$ for $x^* < x < 1$. In particular, $R'(x^*) = 0$, and x^* is a point of maximum of R with $R(x^*) > 1$.

Proof. First, notice that 1., 2. and 3. are straightforward from the form of the polynomial $R(x)$; cf. (2.4).

To prove 4., we let $k = N - 1 - k'$, and on noting that

$$\binom{N-1}{N-1-k'} = \binom{N-1}{k'},$$

we may write

$$\begin{aligned} R(x) &= x^{M-1} \left[\sum_{k'=0}^{N-M-1} \binom{N-1}{k'} x^{N-M-k'} (1-x)^{k'} + M \binom{N-1}{M-1} (1-x)^{N-M} \right] \\ &= x^{N-1} \left[\sum_{k'=0}^{N-M-1} \binom{N-1}{k'} \left(\frac{1-x}{x} \right)^{k'} + M \binom{N-1}{M-1} \left(\frac{1-x}{x} \right)^{N-M} \right]. \end{aligned}$$

Let

$$z = \frac{1-x}{x}.$$

Then, we have that

$$z' = -\frac{1}{x^2} = -\frac{1}{x}(z+1)$$

Thus,

$$R(x) = x^{N-1}p(z), \quad \text{with } p(z) = \sum_{i=0}^{N-M} a_i z^i,$$

where

$$a_i = \binom{N-1}{i}, \quad 0 \leq i < N-M \quad \text{and} \quad a_{N-M} = M \binom{N-1}{M-1}$$

We now compute R' :

$$\begin{aligned} R'(x) &= (N-1)x^{N-2}p(z) - x^{N-2}p'(z)(z+1) \\ &= x^{N-2}[(N-1)p(z) - (z+1)p'(z)] \\ &= x^{N-2} \left[(N-1) \sum_{i=0}^{N-M} a_i z^i - \sum_{i=1}^{N-M} i a_i z^i - \sum_{i=1}^{N-M} i a_i z^{i-1} \right] \\ &= x^{N-2} \left[(N-1)a_0 - a_1 + (N-1) \sum_{i=1}^{N-M} a_i z^i - \sum_{i=1}^{N-M} i a_i z^i - \sum_{i=2}^{N-M} i a_i z^{i-1} \right]. \end{aligned}$$

Since $a_0 = 1$ and $a_1 = N-1$, and writing $i = i+1$ in the last sum, we find that

$$\begin{aligned} R'(x) &= x^{N-2} \left[(N-1) \sum_{i=1}^{N-M} a_i z^i - \sum_{i=1}^{N-M} i a_i z^i - \sum_{i=1}^{N-M-1} (i+1) a_{i+1} z^i \right] \\ &= x^{N-2} S(z), \end{aligned}$$

where

$$\begin{aligned} S(z) &= \sum_{i=1}^{N-M-2} [(N-1-i)a_i - (i+1)a_{i+1}] z^i \\ &\quad + [M a_{N-M-1} - (N-M)a_{N-M}] z^{N-M-1} + (M-1)a_{N-M} z^{N-M}. \end{aligned}$$

On noting that

$$\binom{L}{j+1} = \frac{L-j}{j+1} \binom{L}{j}, \quad (2.6)$$

we obtain, for $1 \leq i < N-M$, that

$$a_{i+1} = \frac{N-1-i}{i+1} a_i.$$

Hence,

$$\sum_{i=1}^{N-M-2} [(N-1-i)a_i - (i+1)a_{i+1}] z^i = 0.$$

Also, we have

$$M a_{N-M-1} - (N-M)a_{N-M} = M \binom{N-1}{M} - (N-M) \binom{N-1}{M-1},$$

which on calling upon (2.6) yields

$$\begin{aligned} M \binom{N-1}{M} - (N-M) \binom{N-1}{M-1} &= (N-M) \binom{N-1}{M} - (N-M) \binom{N-1}{M-1} \\ &= -(N-M)(M-1) \binom{N-1}{M-1}. \end{aligned}$$

Thus, we write

$$S(z) = z^{N-M-1} \binom{N-1}{M-1} [-(N-M)(M-1) + M(M-1)z]$$

which yields

$$R'(x) = x^{M-1}(1-x)^{N-M-1} \binom{N-1}{M-1} [-(N-M)(M-1) + M(M-1)z] \quad (2.7)$$

For $x \in (0, 1)$, (2.7) vanishes at

$$z^* = \frac{N-M}{M} = \frac{1-M/N}{M/N}.$$

Since

$$z = \frac{1-x}{x}$$

is one-to-one.

$$x^* = \frac{M}{N}.$$

Also, from (2.7), we see that

1. for $0 < z < z^*$, $R'(x) < 0$;
2. for $z > z^*$, $R'(x) > 0$

Furthermore, $z = (1-x)/x$ is monotonically decreasing and maps $(0, 1)$ in $(0, \infty)$ (thus reversing the orientation), which yields that $0 < z < z^*$ corresponds to $x^* < x < 1$ and $z > z^*$ corresponds to $0 < x < x^*$.

This proves 4. □

Using the information provided by Lemma 2.1, we have

Theorem 2.2. *Let $\lambda^* = 1/R(x^*)$. Then we have that $0 < \lambda^* < 1$. Moreover, we have that $Q(x)$ satisfies:*

1. For $\lambda < \lambda^*$ there are no roots in $(0, 1)$;
2. For $\lambda = \lambda^*$ there exists one double root at $x = x^*$;
3. For $\lambda^* < \lambda \leq 1$ there are two simple roots $\{x_L, x_R\}$, with $x_L \in (0, x^*)$ and $x_R \in (x^*, 1]$.
4. For $\lambda > 1$ there is only one root in $(0, x^*)$.

From Theorem 2.2, we can infer the complete evolutionary dynamics of the system. Thus, if $F < \lambda^*N$, no interior equilibrium is possible. For $F = \lambda^*N$, $x = M/N$ is an unstable equilibrium. For

$$\lambda^* < \frac{F}{N} < 1,$$

we have the existence of two equilibria. The leftmost equilibrium is always less than M/N and it is unstable. On the other hand, the rightmost equilibrium is always greater than M/N , and it is stable. The reader is referred to [38] for the detailed proofs.

Overall, the analysis above shows that the properties of $Q(x)$ lead to a very interesting dynamics of the replicator equation, with possibly two interior fixed points (x_L and x_R), as illustrated in Fig. 2.1, for $N = 20$, different values of $1 < M \leq 20$ and variable F . Note, in particular, that the fact that $R'(x_L) > 0$ and $R'(x_R) < 0$ [38] allows us to classify immediately x_L as an unstable fixed point whereas x_R , if it exists, corresponds to a stable fixed point, as illustrated also in Fig. 2.1. Moreover, when $F/N = R(M/N)^{-1}$, M/N is the unique interior and unstable fixed point.

Between these two limiting values of F , and given the nature of the interior fixed points x_L and x_R , one can easily conclude that below x_L all individuals will ultimately forego the public good. Conversely, for all $x > x_L$, the population will evolve towards a mixed equilibrium defined by x_R , corresponding to a stable fixed point of the associated replicator equation (even if, initially, $x > x_R$). Similar to the N -person PD, whenever $F/N < R(M/N)^{-1}$, $f_C(x) < f_D(x)$, for all $x \in (0, 1)$, which means that all individuals will end up foregoing the public good.

2.2. N -person SG with thresholds in infinite populations

For the NSG, we may formally write the payoffs in Table 1 in the form

$$\Pi_D(k) = b\theta(k - M) \quad (2.8)$$

for the payoff of a defector in the group and

$$\Pi_C(k) = \Pi_D(k) - \frac{c}{k}\theta(k - M) - \frac{c}{M}(1 - \theta(k - M)) \quad (2.9)$$

for the payoff of a cooperator in the same group. Under these assumptions, one can show that $Q(x)$ now reads [39]

$$Q(x) = \frac{c}{xN} \left\{ N \frac{b}{c} \binom{N-1}{M-1} x^M (1-x)^{N-M} - \left[1 + \sum_{k=0}^{M-1} \binom{N}{k} x^k (1-x)^{N-k} \left(\frac{k}{M} - 1 \right) \right] \right\}.$$

Although the polynomial Q in this case is quite distinct from the NPD case, we can show similar results for the internal fixed points. More precisely, let $\gamma = c/b$.

We find that it will be more appropriate to study

$$p(x, \gamma) = N \binom{N-1}{M-1} x^M (1-x)^{N-M} - \gamma \left[1 + \sum_{k=0}^{M-1} \binom{N}{k} x^k (1-x)^{N-k} \left(\frac{k}{M} - 1 \right) \right].$$

$p(x, \gamma)$ has the same interior roots as $Q(x)$, and we made the dependence on γ explicit. Notice also that $p(x, \gamma)$ implies the same dynamics for the Replicator equation as that implied by $Q(x)$ in $(0, 1)$ up to a time rescaling. We then have the following result

Theorem 2.3. *There exists $0 < \bar{\gamma}$ and $0 < \bar{x} < 1$ such that, if*

1. $\bar{\gamma}/\gamma < 1$, *then the evolutionary dynamics has no interior equilibria.*
2. $\bar{\gamma}/\gamma = 1$, *then \bar{x} is a unique interior equilibrium.*
3. $\bar{\gamma}/\gamma > 1$, *then there are two interior equilibria $x_L < \bar{x} < x_R$. Moreover, x_L is always an unstable equilibrium point, while x_R is always a stable point.*

In order to prove Theorem 2.3, it turns out that is more convenient to determine what γ will render a given $x \in (0, 1)$ an interior point, rather than determining what x are equilibria for a given γ . Let us define

$$\Gamma(x) = \begin{cases} 0, & x = 0, \\ N \binom{N-1}{M-1} \frac{x^M (1-x)^{N-M}}{1 + \sum_{k=0}^{M-1} \binom{N}{k} x^k (1-x)^{N-k} \left(\frac{k}{M} - 1 \right)}, & 0 < x \leq 1. \end{cases} \quad (2.10)$$

Then $\Gamma : [0, 1] \rightarrow \mathbb{R}$ is continuous in $[0, 1]$ and differentiable in $(0, 1)$. Also, by solving for γ the equation $p(x, \gamma) = 0$, it is straightforward to verify that we have the identity

$$p(x, \Gamma(x)) = 0. \quad (2.11)$$

Ultimately, $\Gamma(x)$ is responsible for the existence of a cost-to-benefit ratio at which a given interior x can become an equilibrium of the replicator dynamics. The critical value \bar{x} corresponds to the first interior equilibrium which emerges when $c/b = \bar{\gamma}$ and which divides the unit interval into two pieces, in which the stable and unstable equilibria remain confined whenever $c/b < \bar{\gamma}$. The thrust of the argument is to study the number of solutions of $\Gamma(x) = \gamma$, for a given γ , which then can be used to prove Theorem 2.3. In order to achieve our goal, we establish a series of results about Γ . In what follows, we shall assume $N > 2$ and $1 < M < N$.

Proposition 2.4. *There is a unique $\bar{x} \in (0, 1)$ such that $\Gamma'(\bar{x}) = 0$. Such \bar{x} will be the unique point of global maximum for Γ .*

Proposition 2.5. *Let $\bar{\gamma} = \Gamma(\bar{x})$, with \bar{x} given above. Then the equation $\Gamma(x) = \gamma$ has*

1. *two solutions, x_L and x_R , for $\gamma < \bar{\gamma}$. Moreover $x_L \in [0, \bar{x})$ and $x_R \in (\bar{x}, 1]$.*
2. *one solution for $\gamma = \bar{\gamma}$;*
3. *no solution for $\gamma > \bar{\gamma}$.*

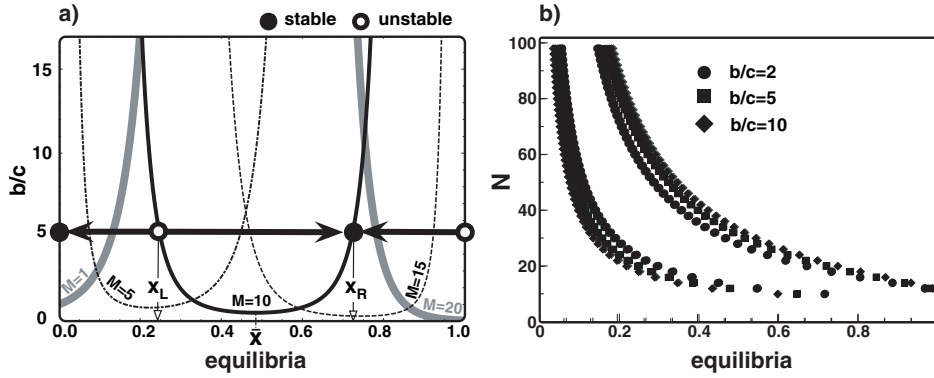


FIGURE 2.2. Equilibria of the N -person Snowdrift Game with threshold. We assume infinite, well-mixed populations, fix the group size at $N = 20$ and vary the threshold M above which cooperation leads to a common benefit b . The total cost involved is c . In a) we show how the occurrence of a threshold leads to the appearance of at most 2 interior fixed points x_L and x_R , which can be found via the intersection of a horizontal line with the appropriate curve (illustrated for $M = 10$); in this case, the leftmost root is always an unstable fixed point whereas the rightmost corresponds to stable fixed point, as illustrated by the horizontal arrows (see main text for details). For a given M/N , there is a critical value $\bar{\gamma}$ for the critical cost-to-benefit ratio c/b below which the 2 interior roots discussed above always exist. In panel b) we show how these interior fixed points scale with variable group size N for some values of the b/c ratio indicated. For $\bar{\gamma}b < c$ no interior fixed points exist and defectors dominate unconditionally, whereas for $\bar{\gamma}b = c$ the only root corresponds to an unstable fixed point.

Finally, the following asymptotic result allows an approximate determination of \bar{x} .

Proposition 2.6. *Let $x_0 = \frac{M}{N}$ and assume that*

$$0 < \epsilon = \frac{N - M}{N} \ll 1$$

Then, we have that

$$\bar{x} = x_0 - \frac{x_0^M}{M} \binom{N}{M-1} \epsilon^{N-M+1} + \mathcal{O}(\epsilon^{N-M+2}).$$

Therefore, when the threshold is comparable in order to the size of the group, we have that while the critical equilibrium is not quite M/N , it is quite close to it. We refer the interested reader to [39] for detailed proofs.

As in the case of the NPD, the exact position of the roots of $Q(x)$ in the NSG regime may be cumbersome to find analytically, but are easy to compute numerically. Fig. 2.2 pictures the position of the interior roots of $Q(x)$ for a fixed group size of $N = 20$ and variable threshold values of M (right panel).

For each value of M there is a critical benefit-to-cost value b/c above which two interior fixed points emerge. These can be found in Fig. 2.2 by drawing a horizontal line at a fixed b/c – its intersection with the appropriate curve for a given threshold M provides the location of the points.

As shown above and illustrated in Fig. 2.2, one root corresponds to an unstable fixed point (x_L) and the other to a stable fixed point (x_R) inducing a coexistence between Cs and Ds. This means there is a range of values of x ($x_L < x < x_R$), in which Cs are favored against Ds ($f_C(x) > f_D(x)$). When $x > x_L$, the system will always evolve to the mixed configuration given by x_R , and below x_L all individuals will end up refusing to contribute to the public good.

3. Evolutionary dynamics of PGGs in finite populations

Let us focus on a well-mixed population of size Z in the absence of mutations. Sampling of individuals is no longer binomial, following a hypergeometric distribution. Consequently, the average fitness of Cs and Ds can now be written as

$$f_C(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k-1}{j} \binom{Z-k}{N-j-1} \Pi_C(j+1) \quad (3.1)$$

and

$$f_D(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k}{j} \binom{Z-k-1}{N-j-1} \Pi_D(j) \quad (3.2)$$

respectively.

The fraction of cooperators is no longer a continuous variable, varying in steps of $1/Z$. We adopt a stochastic birth-death process [40] combined with the pairwise comparison rule [41, 42, 43] in order to describe the evolutionary dynamics of Cs (and Ds) in a finite population. Under pairwise comparison, two individuals from the population, A and B are randomly selected for update (only the selection of mixed pairs can change the composition of the population). The strategy of A will replace that of B with a probability given by the Fermi function (from statistical physics)

$$p = \frac{1}{1 + e^{-\beta(f_A - f_B)}}. \quad (3.3)$$

The reverse will happen with probability $1 - p$. The quantity β , which in physics corresponds to an inverse temperature, controls the intensity of selection: For $\beta \ll 1$ selection is weak, and one recovers the replicator equation in the limit $Z \rightarrow \infty$ [41, 42, 43]. For arbitrary β , the quantity corresponding to the right-hand

side of the replicator equation, specifying the *gradient of selection*, is given in finite populations by [41, 42, 43]

$$g(k) \equiv T^+(k) - T^-(k) = \frac{k}{Z} \frac{Z-k}{Z} \tanh \left\{ \frac{\beta}{2} [f_C(k) - f_D(k)] \right\} \quad (3.4)$$

The right-hand side of $g(k)$ is similar to the replicator equation, only that the (non-linear) pairwise comparison [41, 42, 43] defined in Eq. 3.3 leads to the appearance of the hyperbolic tangent of the fitness difference, instead of the fitness difference. This has implications in the characteristic evolutionary times, which now depend on β [41, 42, 43], but not in what concerns the roots of $g(k)$. Importantly, the evolutionary dynamics in finite populations will only stop whenever the population reaches a monomorphic state ($k = 0$ or $k = Z$). Hence, the sign of $g(k)$, which indicates the direction of selection, is important in that it may strongly influence the evolutionary time required to reach any of the absorbing states.

3.1. N -person PD with thresholds in finite populations

Whenever $M = 0$ (NPD without the requirement to coordinate to obtain collective benefits) we may write

$$f_C(k) - f_D(k) = c \left[\frac{F}{N} \left(1 - \frac{N-1}{Z-1} \right) - 1 \right] \quad (3.5)$$

which is independent of k being, however, population and group size dependent. This means frequency independent selection. In particular, whenever the size of the group equals the population size, $N = Z$, we have that $f_C(k) - f_D(k) = -c$ and cooperators have no chance irrespective of the value of the enhancement factor. This contrasts with the result in infinite, well-mixed populations ($Z \rightarrow \infty$), where to play C would be the best option whenever $F > N$. For finite populations, the possibility that group size equals population size leads to the demise of cooperation. Moreover, given the independence of $f_C(k) - f_D(k)$ on k in finite populations, for a given population size, it is straightforward to obtain a critical value of F for which selection is neutral, and above which cooperators will win the evolutionary race. From the equations above this critical value reads $F = N \left(1 - \frac{N-1}{Z-1} \right)^{-1}$.

Let us now discuss the NPD with $1 < M < N \leq Z$. Whenever $N = Z$, the result is easily inferred from the NPD above – all individuals in the population will ultimately forego the public good. This will happen, in finite populations, irrespective of the existence (or not) of a threshold M . However, whenever $N < Z$ the threshold brings about a strong disruption of the finite population dynamics, which we illustrate numerically, given the unappealing look of the analytical equations.

Let us start with the case in which $F > N$, that is, the regime for which we obtain a pure coordination game with a single (unstable) fixed point in the replicator dynamics equation (cf. Fig. 2.1). In finite populations the possible scenarios are depicted in the left panel of Fig. 3.1. Clearly, for small population sizes, cooperators are always disadvantageous. With increasing Z , however, one approaches

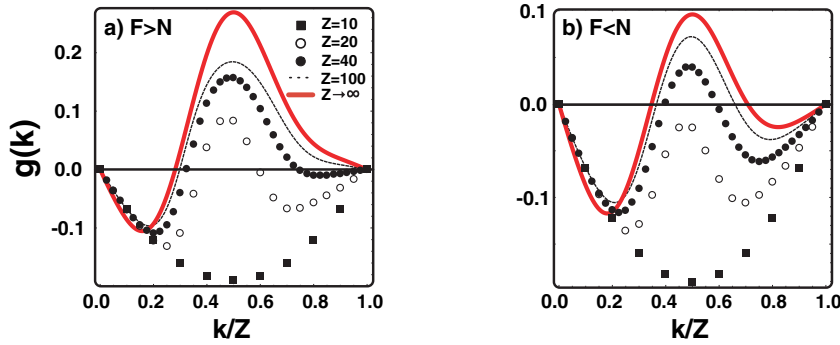


FIGURE 3.1. Behaviour of $g(k)$ for a N -person PD game with coordination threshold $M = 5$ in a population of variable size Z and fixed group size $N = 10$. a) Since $F = 12 > N$, the game becomes a pure coordination game in infinite populations. In finite populations, however, it strongly depends on Z : For $Z = N$, Cs are always disadvantageous and evolutionary dynamics leads mostly to 100% Ds. For $Z = 20$ (and using a terminology which is only correct for $Z \rightarrow \infty$), we obtain a profile for $g(k)$ evidencing the emergence of a coordination point and a coexistence point. For increasingly large Z (e.g., $Z = 40$), the coexistence point disappears and we recover the behaviour of the replicator dynamics (see Fig. 2.1: Selection favours Cs above a given fraction k/Z and Ds below that fraction which, in turn, depends on the population size. b) Since $F = 8 < N$, the game exhibits now 2 interior fixed points in infinite populations (red curve). Similar to a), for small Z Cs are disadvantageous for all k . Unlike a), however, now two interior fixed points emerge together for a critical population size, and remain for larger population sizes.

the replicator dynamics scenario (see Fig. 2.1), despite the fact that, e.g., for $Z = 20$, convergence towards the absorbing state at 100% Cs is hindered because Cs become disadvantageous for large k . Indeed, for this population size, Cs are advantageous only in a small neighbourhood of $k/Z = 0.5$, being disadvantageous both for smaller and larger values of k/Z . In other words, and despite the fact that evolution will stop only at $k = 0$ or $k = Z$, the time it takes to reach an absorbing state will depend sensitively on the population size, given the occurrence (or not) of interior roots of $g(k)$.

Whenever $F < N$, yet above the critical limit below which Cs become disadvantageous for all x in Fig. 2.1, we observe that for small population sizes Cs are always disadvantageous, and the two interior fixed points of the replicator dynamics equation only manifest themselves above a critical population size, as illustrated in the right panel of Fig. 3.1.

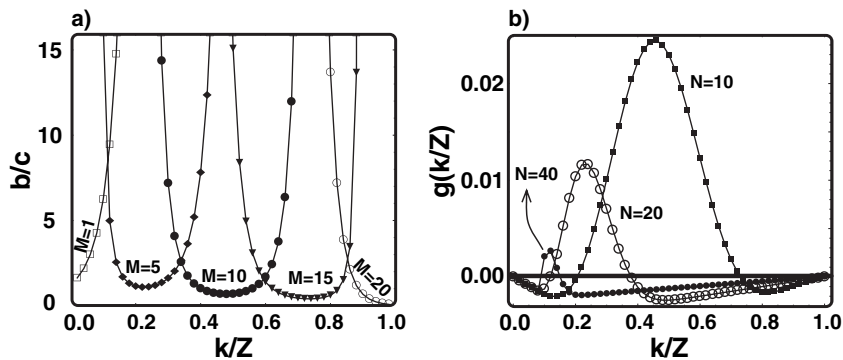


FIGURE 3.2. a) Equilibria of the N -person snowdrift game with threshold in finite populations. Population size is $Z = 50$ and group size is $N = 20$. We vary the threshold M above which cooperation leads to a common benefit b . For each k/Z we show the corresponding b/c at which $g(k) = 0$ (cf. Eq. (13)). Whenever the population size is large compared to group size, selection in finite populations is qualitatively similar to that in infinite populations. b) Effect of group size in the evolution of cooperation. We plot $g(k)$ as a function of the fraction of cooperators k/Z , for $b/c = 5$. We fixed the population size at $Z = 50$ and the threshold at $M = 5$, while varying the group size N . As the group size approaches the population size, the range of values of k/Z for which cooperation is advantageous ($g(k) > 0$) is reduced.

3.2. N -person SG with thresholds in finite populations

In Fig. 3.2a, we show how the qualitative behavior of selection under stochastic dynamics in finite populations mimics closely that already encountered in the previous section (cf. Fig. 2.2), associated with deterministic dynamics in infinite populations. Although the population will always fixate in one of the two *absorbing states* ($k = 0$ and $k = Z$ in the absence of mutations), selection will act to drive the population toward a composition reflecting the rightmost root of $g(k)$, which constitutes the deepest point of the basin of attraction of the evolutionary dynamics.

On the other hand, as the group size approaches the population size the previous basin of attraction is reduced. In Fig. 3.2b we show a typical behavior of $g(k)$ as a function of the fraction of cooperators k/Z for fixed population size $Z = 50$, threshold $M = 5$ and different group sizes N . As N increases, cooperation becomes increasingly unfeasible – in the limit when $N \rightarrow Z$, cooperators have no chance and defectors dominate unconditionally. Moreover, for a given b/c ratio, the existence of a finite population analogue of a stable root of $g(k)$ (in infinite populations) occurs for values of the frequency k/Z of cooperators which decrease as N increases. This has been first noted by Hamilton [37] and reflects the occurrence of “spite” which works against cooperation, as illustrated in Fig. 3.2.

4. Discussion

We showed how generalizing the conventional versions of the *NPD* and *NSG* dilemmas by introducing thresholds below which collective action is unfeasible leads to the emergence of an entirely new evolutionary scenario. Irrespectively of the game played, in infinite, well-mixed populations, the existence of a threshold opens the possibility for the appearance of two interior fixed points in the replicator equation (x_L and x_R). The one at lower frequency of cooperators is always an unstable fixed point (coordination), which determines a threshold for cooperative collective action. The other, at higher frequency of cooperators, is a stable fixed point (coexistence), and hence determines the final frequency of cooperators in the population, assuming the coordination threshold is overcome. Moreover, both dilemmas converge to a pure coordination game whenever the coordination threshold approaches the group size.

In the particular case of the *NSG* with a given threshold M and group size N , there is always a critical cost-to-benefit ratio c/b above which the two interior roots discussed above emerge. The same qualitative behavior can be observed in finite populations. However, as soon as the group size approaches the population size, cooperation becomes increasingly unfeasible.

In the *NPD*, besides the above-mentioned regime with two interior roots, there are also the possible outcomes of no cooperation or of a pure coordination game, which depends sensitively on the minimum number of cooperators M in a group of N individuals required to produce any public good. In finite populations, the evolutionary dynamics of the *NPD* game may be profoundly affected, mostly when the population size (Z) is comparable to the group size (N). In this regime, one observes an overlap of the different scenarios observed in infinite populations. Hence, for $Z = N$, cooperators are always disadvantageous, irrespective of the existence or not of a threshold. For $Z > N$, the direction of selection in a finite population is strongly size dependent. For fixed $F > N$, there is a critical value, Z_1 , above which the interior roots of $g(k)$ emerge, which constitute the finite-population analogs of x_L and x_R in infinite populations (cf. Fig. 2.1). Above a second critical value, Z_2 , x_R disappears, and one ends up with a coordination game. For $M < F < N$ and a small population size, that is, $F < N$ but yet above the critical value $\lambda^* = R(M/N)^{-1}$ defined in section 2.1, cooperators are always disadvantageous; however, above a critical population size (Z_C) the interior roots of $g(k)$ emerge simultaneously and the evolutionary dynamics approaches that observed in infinite populations.

5. Conclusions

Unlike two-person games, current models of collective action have typically overlooked the necessity of some form of coordination among individuals, pervasive in biological and social collective dilemmas. From social organization [17] to the salvation of the planet against environmental hazards [44, 45], examples abound

where a minimum number of individuals, which does not necessarily equal the entire group, must simultaneously cooperate before any outcome (or public good) is produced.

In this chapter we investigate the predictions of evolutionary game theory in both finite and infinite populations, whenever a minimum threshold of individuals must cooperate simultaneously in a group before any viable public good is achieved. We have concentrated on two of the most important collective dilemmas: the N -person snowdrift game (NSG) [39] and N -person prisoner's dilemma (NPD) [38]. In doing so, we uncover a new framework in which the advantage or not of cooperators depends sensitively on group and population size, as well as on the threshold for collective action. Such interplay leads to rich evolutionary scenarios, impossible to anticipate based on the traditional assumption of infinite populations, providing valuable insights into the variety and complexity of many person social dilemmas, inescapable especially among humans.

In addition, it is noteworthy that irrespectively of the distinctive features of the N -person Prisoner's dilemma (a defector's dominance dilemma) and the N -person Snowdrift game (a coexistence game), the existence of a coordination threshold is able to produce a unifying framework associated with a generalized stag-hunt game [38]. Moreover, the necessity of coordination is shown to increase the equilibrium fraction of cooperators, even if this enhancement comes together with a strong dependence on the initial level of cooperation, since coexistence between cooperators only emerges when a minimum number of cooperators is already present in the population. This result is of particular relevance given that the existence of coordination thresholds constitutes a rule, rather than the exception. Finally, our results reinforce the idea that even minor differences in the nature of collective rewards and/or costs can have a profound effect in the final outcome of evolution.

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