

Emergence of collective action under coordination dilemmas

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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. Here we describe the dynamics of collective action using the framework of game theory. In particular, 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 discuss both infinite and finite populations, imposing the existence of a threshold above which collective action is materialized. In infinite populations, the introduction of a threshold leads to a rich dynamics, characterized by two interior fixed points. The fingerprints of the interior fixed points remain effective in finite populations, despite evolution leading the population inexorably to a monomorphic end-state. Whenever the group size and population size become comparable, we find that spite sets in, rendering cooperation unfeasible in both cases.

1 Introduction

The last decades have witnessed the discovery of key insights into the emergence and sustainability of cooperation at different levels of organization [1–10]. Special attention has been paid to two-person dilemmas such as the Prisoner’s Dilemma (PD), the Snowdrift Game (SG) [11] and the Stag-Hunt game (SH) [10], which constitute powerful metaphors to describe conflicting situations often encountered in the natural and social sciences [10]. Many real-life situations, however, are associated with collective action based on joint decisions made by a group often involving more than two individuals. This is the case, for instance, in the upper primates, where problems of collective action are recurrent [2, 12]. These types of problems are best dealt-with in the framework of N-person games [13–18]. Describing the evolutionary dynamics of many-person games provides a richer scenario of possibilities, and an intrinsic additional complexity, as captured by the words of late W. D. Hamilton [19]:

“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 Prisoner's dilemma (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.

However, consider, for instance, group hunts of 3 or 4 lionesses in Etosha National Park, Namibia [20]. Two lionesses, the wings, attack a group of prey from either side panicking them to run forward. They run right into one or two other lionesses, positioned as centres, who are waiting for them. This kind of hunt is highly successful. However, if analyzed in more detail, one immediately recognizes that the hunt is unfeasible with only one or two participants, but it becomes feasible with three and even better with four. In other words, this is no longer a NPD, as one needs a minimum threshold of participants to achieve a public good. Instead, this example configures what one may call a generalized, or N -person, stag-hunt game, in the sense that there is a cooperative equilibrium where if others do their part, it is best for you to do yours as well. Variations on this kind of cooperative hunting have been observed in other species, such as Chimpanzees in the Tai forest [21] and African wild dogs [22]. 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 [23]. 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 [24], but also in international relations [25] and macroeconomics [26].

Here, 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 other words, a cost cM must be paid before a common benefit is produced, which, if achieved, this benefit increases with the additional investments. Formally, we can summarize the payoff of a D under this modified dilemma, in groups with k Cs, as $\Pi_D(k) = \frac{Fkc}{N}\theta(k - M)$, where the Heaviside step function $\theta(x)$ is equal to 1 whenever $x \geq 0$ and equal to 0 otherwise. As before, the payoffs of Cs can be written as $\Pi_C(k) = \Pi_D(k) - c$.

We shall assume a population of size Z , from which groups of size N are randomly sampled. We shall 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. Hence, we obtain a richer evolutionary dynamics scenario in infinite populations, which, in connection with similar results obtained for other dilemmas

[27], 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 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 [28] in 1970, and which works against cooperation.

2 Evolutionary Dynamics 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 [17]. The fitness of the Ds is given by

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

whereas the average fitness of Cs is given by

$$f_C = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} \Pi_C(k+1), \quad (2)$$

where we impose that the binomial coefficients satisfy $\binom{k}{j} = 0$ if $k < 0$. Π_C and Π_D are defined above, and depend both on the group size (N) and the coordination threshold (M). The evolutionary dynamics is given by the replicator equation [4],

$$\dot{x} = x(1-x)(f_C - f_D) \quad (3)$$

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

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, introducing Π_C and Π_D above in Eqs. (1) and (2) leads to

$$Q(x) = c \left(\frac{F}{N} - 1 \right) - c \frac{F}{N} (1-x)^{N-M} \sum_{k=0}^{M-1} \binom{N-1}{k} (1-M\delta_{k,M-1}) x^k (1-x)^{M-1-k}.$$

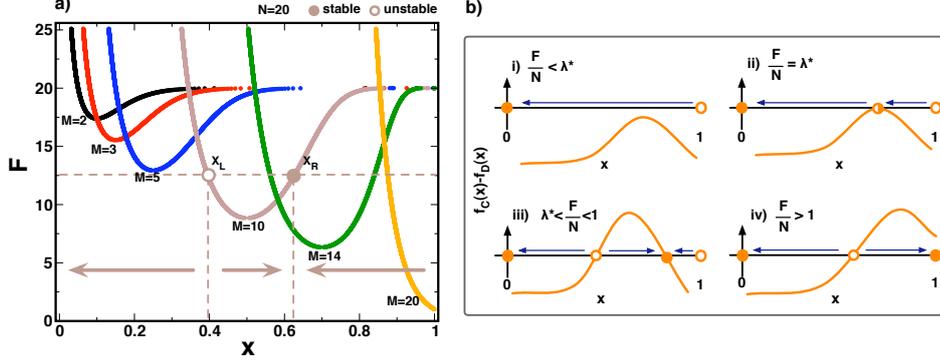


Fig. 1. a) Interior fixed points of the replicator equation for N -person PD games with coordination threshold. The curves provide the location of the critical values of the fraction of cooperators (x_L, x_R) at which $f_C = f_D$. For each value of F (defining a horizontal line), the critical values are given by the intersection of this line with each curve (one curve for given M and $N = 20$). Scenarios with none, one and two interior fixed points are possible as detailed in the lower 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. For each case, the solid (orange) lines represent the typical shape of the function $f_C(x) - f_D(x)$. The quantity $\lambda^* = R(M/N)$ corresponds to the value of F at which the minimum of each curve in a), for fixed M , is reached.

In what follows, we shall strictly assume that $N \geq 2$ and $1 < M < N$. Let

$$\begin{aligned}
 R(x) &= \sum_{k=M}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} + M \binom{N-1}{M-1} x^{M-1} (1-x)^{N-M} \quad (4) \\
 &= x^{M-1} \left(\sum_{k=M}^{N-1} \binom{N-1}{k} x^{k-M+1} (1-x)^{N-1-k} + M \binom{N-1}{M-1} (1-x)^{N-M} \right).
 \end{aligned}$$

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

$$Q(x) = -c(1 - \lambda R(x)), \quad (5)$$

with $\lambda = F/N$.

Lemma 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. (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

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

Let $z = \frac{1-x}{x}$, we have that $z' = -\frac{1}{x^2} = -\frac{1}{x}(z+1)$. Thus,

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

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' :

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

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

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

where

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

On noting that

$$\binom{L}{j+1} = \frac{L-j}{j+1} \binom{L}{j}, \quad (6)$$

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 $Ma_{N-M-1} - (N-M)a_{N-M} = M\binom{N-1}{M} - (N-M)\binom{N-1}{M-1}$, which on calling upon (6) yields

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

Thus, we can write

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

which yields

$$R'(x) = x^{M-1}(1-x)^{N-M-1}\binom{N-1}{M-1} [-(N-M)(M-1) + M(M-1)z] \quad (7)$$

For $x \in (0, 1)$, (7) vanishes at $z^* = \frac{N-M}{M} = \frac{1-M/N}{M/N}$. Since $z = \frac{1-x}{x}$, $x^* = \frac{M}{N}$. Also, from (7), we see that

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

Also, $z = (1-x)/x$ 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 1, we have

Theorem 1. *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 1, we can infer the 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 a 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 [29] 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. 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 $R'(x_R) < 0$ 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. 1. Moreover, when $F/N = R(M/N)$, 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 $F/N < R(M/N)$, $f_C(x) < f_D(x)$, for all $x \in (0, 1)$, which means that all individuals will end up foregoing the public good.

3 Evolutionary Dynamics 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

$$f_C(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k-1}{j} \binom{Z-k}{N-j-1} \Pi_C(j+1) \quad (8)$$

and

$$f_D(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k}{j} \binom{Z-k-1}{N-j-1} \Pi_D(j) \quad (9)$$

respectively.

The fraction of cooperators is no longer a continuous variable, varying in steps of $1/Z$. We adopt a stochastic birth-death process [30] combined with the pairwise comparison rule [31] 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)

$$p = \frac{1}{1 + e^{-\beta(f_A - f_B)}}. \quad (10)$$

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 $Z \rightarrow \infty$ [31]. For arbitrary β , the quantity corresponding to the right hand side

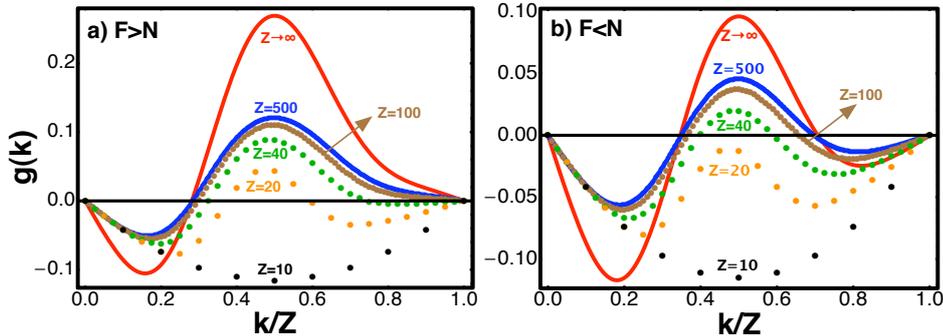


Fig. 2. Behaviour of $g(k)$ for a N -person PD game with coordination threshold $M = 5$ in a population of variable size Z and fixed group size $N = 10$. a) Since $F = 12 > N$, the game becomes a pure coordination game in infinite populations. In finite populations, however, it strongly depends on Z : 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. 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.

of the replicator equation, specifying the *gradient of selection*, is given in finite populations by [31]

$$g(k) \equiv T^+(k) - T^-(k) = \frac{k}{Z} \frac{Z - k}{Z} \tanh\left\{\frac{\beta}{2}[f_C(k) - f_D(k)]\right\} \quad (11)$$

The right hand side of $g(k)$ is similar to the replicator equation, only that the (non-linear) pairwise comparison [31] defined in Eq. 10 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 [31], 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.

Whenever $M = 0$ we may write

$$f_C(k) - f_D(k) = c \left[\frac{F}{N} \left(1 - \frac{N-1}{Z-1} \right) - 1 \right] \quad (12)$$

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 $F = N(1 - \frac{N-1}{Z-1})^{-1}$.

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. 1). In finite populations the possible scenarios are depicted in the upper panel of Fig. 2. Clearly, for small population sizes, cooperators are always disadvantageous. With increasing Z , however, one approaches the replicator dynamics scenario (see Fig. 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. 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 lower panel of Fig. 2.

4 Discussion

In sections 2 and 3 we show how the generalized version of the N-person Prisoner's dilemma can converge to a completely new evolutionary scenario in the presence of coordination thresholds. 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, which determines a threshold for cooperative collective action. The other, at higher frequency of cooperators, is a stable fixed point, and hence determines the final frequency of cooperators in the population, assuming the coordination threshold is overcome. Moreover, the dilemma converges to a pure coordination game whenever the coordination threshold approaches the group size. Moreover, 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. Once the simplifying assumption of an infinite population size is abandoned, the evolutionary dynamics of the NPD game is 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 and of the game parameters, in accord with the so-called “spite“ effect first described by Hamilton. 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.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 $\lambda^* = R(M/N)$ defined above, 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. Finally, for $F < M$ cooperators have no chance irrespective of the population size. Such strong size dependence, with an impact which is stronger for smaller population sizes, can be directly traced back to the fact that, for smaller populations, the hypergeometric sampling of individuals into groups significantly deviates from binomial sampling. This, in turn, reflects the intuition that, in small populations, choices are reduced, and this must influence the overall evolutionary dynamics.

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 [3] to the salvation of the planet against environmental hazards[32, 33], 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 contribution to *ECCS 2010*, we discuss 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. This analysis has focused in the most studied collective dilemmas: the N-person prisoner’s dilemma. 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. It is also important to note that the new qualitative dynamical picture showed here remain valid whenever other N-person games are considered. For instance, often the collective benefit remains constant with the increase of the number of cooperators and, instead, costs of cooperation are shared by those who contribute. Such scenario is nicely characterized by a N-person Snowdrift game, which, as shown in [27], provides the same dynamical framework — with a coordination and co-existence fixed points — as the one picture here. Hence, 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 co-existence game), the existence of a coordination threshold is able to produce an unifying framework associated with a generalized stag-hunt game. 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 co-existence 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 re-inforce 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.

References

- [1] Axelrod, R., Hamilton, W.: The evolution of cooperation. *Science* **211**(4489) (1981) 1390–6
- [2] Boyd, R., Richerson, P.: *Culture and the Evolutionary Process*. University of Chicago Press (1985)
- [3] Bowles, S.: *Microeconomics: Behavior, Institutions and Evolution*. Princeton University Press (2003)
- [4] Hofbauer, J., Sigmund, K.: *Evolutionary Games and Population Dynamics*. Cambridge Univ. Press, Cambridge, UK (1998)
- [5] Maynard-Smith, J.: *Evolution and the Theory of Games*. Cambridge University Press, Cambridge (1982)
- [6] Nowak, M.: Five rules for the evolution of cooperation. *Science* **314**(5805) (2006) 1560–3
- [7] Santos, F., Pacheco, J., Lenaerts, T.: Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc Natl Acad Sci U S A* **103**(9) (2006) 3490–4
- [8] Santos, F., Santos, M., Pacheco, J.: Social diversity promotes the emergence of cooperation in public goods games. *Nature* **454**(7201) (2008) 213–6
- [9] Pacheco, J.M., Santos, F.C., Chalub, F.A.C.C.: Stern-judging: A simple, successful norm which promotes cooperation under indirect reciprocity. *PLoS Computational Biology* **2**(12) (2006) e178

- [10] Skyrms, B.: *The Stag Hunt and the Evolution of Social Structure*. Cambridge University Press (2004)
- [11] Sugden, R.: *The economics of rights, co-operation and welfare*. Basil Blackell, Oxford, UK (1986)
- [12] Boehm, C.: *Hierarchy un the Forest: The Evolution of Egalitarian Behavior*. Harvard University Press (1999)
- [13] Hardin, G.: The tragedy of the commons. *Science* **162**(5364) (1968) 1243–8
- [14] Schelling, T.C.: Hockey helmets, concealed weapons, and daylight saving: A study of binary choices with externalities. *J. Conflict Resolution* **17**(381) (1973)
- [15] Boyd, R., Richerson, P.J.: The evolution of reciprocity in sizable groups. *J Theor. Biol.* **132** (1988)
- [16] Kollock, P.: Social dilemmas: The anatomy of cooperation. *Annu. Rev. Sociol.* **24** (1998) 183–214
- [17] Hauert, C., Michor, F., Nowak, M., Doebeli, M.: Synergy and discounting of cooperation in social dilemmas. *J Theo Bio* **239**(2) (2006) 195–202
- [18] Hauert, C., Traulsen, A., Brandt, H., Nowak, M., Sigmund, K.: Via freedom to coercion: The emergence of costly punishment. *Science* **316**(5833) (2007) 1905 – 1907
- [19] Hamilton, W.: Biosocial anthropology. In: *Biosocial anthropology*. Malaby Press, London (1975) 133–155
- [20] Stander, P.: Cooperative hunting in lions - the role of the individual. *Behavioral Ecology and Sociobiology* **29**(6) (1992) 445–454
- [21] Boesch, C.: Cooperative hunting roles among tai chimpanzees. *Human Nature-an Interdisciplinary Biosocial Perspective* **13**(1) (2002) 27–46–
- [22] Creel, S., Creel, N.: Communal hunting and pack size in african wild dogs, *lycaonpictus*. *Animal Behaviour* **50** (1995) 1325–1339–
- [23] Maynard-Smith, J., Szathmáry, E.: *The Major Transitions in Evolution*. Freeman, Oxford (1995)
- [24] Beding, B.: The stone-age whale hunters who kill with their bare hands (2008)
- [25] Jervis, R.: Cooperation under the security dilemma. *World Politics* **30** (1978) 167–214
- [26] Bryant, J.: Coordination theory, the stag hunt and macroeconomics. In: *Problems of Coordination in Economic Activity*, Dorcrecht:Kluwer (1994) –
- [27] Souza, M.O., Pacheco, J.M., Santos, F.C.: Evolution of cooperation under n-person snowdrift games. *Journal of Theoretical Biology* **260**((4)) (2009) 581–588
- [28] Hamilton, W.: Selfish and spiteful behaviour in an evolutionary model. *Nature* **228** (1970) 1218–1220
- [29] Pacheco, J.M., Santos, F.C., Souza, M.O., Skyrms, B.: Evolutionary dynamics of collective action in n-person stag-hunt dilemmas. *Proceedings of the Royal Society B: Biological Sciences* **276**(1655) (2009)
- [30] Karlin, S., Taylor, H.: *A first course in Stochastic Processes*. Volume 2nd edition. Academic, London (1975)
- [31] Traulsen, A., Nowak, M., Pacheco, J.: Stochastic dynamics of invasion and fixation. *Phys Rev E Stat Nonlin Soft Matter Phys* **74**(1 Pt 1) (2006) 011909
- [32] Milinski, M., Semmann, D., Krambeck, H., Marotzke, J.: Stabilizing the earth’s climate is not a losing game: Supporting evidence from public goods experiments. *Proc Natl Acad Sci U S A* **103**(11) (2006) 3994–3998
- [33] Milinski, M., Sommerfeld, R., Krambeck, H., Reed, F., Marotzke, J.: The collective-risk social dilemma and the prevention of simulated dangerous climate change. *Proc Natl Acad Sci U S A* **105**(7) (2008) 2291–2294