Evolutionary dynamics of collective action in *N*-person stag hunt dilemmas

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In the animal world, collective action to shelter, protect and nourish requires the cooperation of group members. Among humans, many situations require the cooperation of more than two individuals simultaneously. Most of the relevant literature has focused on an extreme case, the *N*-person Prisoner's Dilemma. Here we introduce a model in which a threshold less than the total group is required to produce benefits, with increasing participation leading to increasing productivity. This model constitutes a generalization of the two-person stag hunt game to an *N*-person game. Both finite and infinite population models are studied. In infinite populations this leads to a rich dynamics that admits multiple equilibria. Scenarios of defector dominance, pure coordination or coexistence may arise simultaneously. On the other hand, whenever one takes into account that populations are finite and when their size is of the same order of magnitude as the group size, the evolutionary dynamics is profoundly affected: it may ultimately invert the direction of natural selection, compared with the infinite population limit.

1. INTRODUCTION

During recent years, evolutionary game theory has been able to provide key insights into the emergence and sustainability of cooperation at different levels of organization (Axelrod & Hamilton 1981; Maynard-Smith 1982; Axelrod 1984; Boyd & Richerson 1985; Hofbauer & Sigmund 1998; Skyrms 2001, 2004; Macy & Flache 2002; Hammerstein 2003; Nowak & Sigmund 2004; Nowak *et al.* 2004; Santos & Pacheco 2005; Nowak 2006; Ohtsuki *et al.* 2006; Santos *et al.* 2006). The most popular and studied game has been the two-person Prisoner's Dilemma (PD). However, other social dilemmas, such as the snowdrift game (Sugden 1986) or the stag hunt (SH) (Skyrms 2004) game also constitute powerful metaphors for many situations routinely encountered in the natural and social sciences (Macy & Flache 2002; Skyrms 2004).

In particular, the SH game constitutes the prototypical example of the social contract, and one can identify instances of SH games in the writings of, for example, Rousseau, Hobbes and Hume (Skyrms 2004). Maynard-Smith & Szathmáry (1995) have discussed the social contracts implicit in some of the major transitions of evolution. After framing most of the discussion in terms of the PD, they remarked that perhaps the SH (their rowing game) is a better model. In a SH there is an equilibrium in which both players cooperate as well as one in which both defect.

Whenever collective action of groups of individuals is at stake, *N*-person games are appropriate. Recent literature has focused on *N*-person Prisoner's Dilemmas (NPDs) in the form of provision of Public Goods games (PGG; Kollock 1998; Hauert *et al.* 2002, 2006, 2007; Brandt *et al.* 2006; Milinski *et al.* 2006, 2008; Rockenbach & Milinski 2006; Santos *et al.* 2008). The prototypical example of a PGG is captured by the so-called 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 were *k* Cs in a group of *N* individuals, Ds end up with kFc/N, whereas Cs only get $kFc/N - c$, i.e. in mixed groups Cs are always worse off than Ds. If *F* is smaller than *N*, to cooperate is always disadvantageous against any combination of actions by other group members. In this sense, we have an NPD. Evolutionary game theory directly leads to the tragic outcome in which everybody ends up defecting, hence foregoing the public good. When the group is a mere pair of individuals, this dilemma reduces to the two-person PD.

Consider, however, group hunts of three or four lionesses in Etosha National Park, Namibia (Stander 1992). 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. It is not possible with one or two participants,

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but it is with three and is even better with four. This is not a generalized PD, but a generalized SH. It is a SH because, unlike the PD, 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 (Boesch 2002) and African wild dogs (Creel & Creel 1995). In animals, other collective actions, such as lions defending a kill against a pack of hyenas, can also be seen as generalized SH games (Maynard-Smith & Szathmáry 1995).

In human affairs, we also find collective action problems that can be viewed as generalized SHs, not only in literal hunts such as the whale hunts discussed in Beding (2008), but also in international relations (Jervis 1978) and macroeconomics (Bryant 1994).

Back to the lionesses in Etosha National Park, two individuals are not enough for a cooperative hunt, three can be successful and four even more so. The average pay-off of an individual depends on the number of participants and may vary according to species and environment. Much empirical evidence supports a U-shaped function for average meat per participant across a number of species, but it is controversial whether this remains true when energetic costs of the hunt are taken into account (Creel & Creel 1995; Packer & Caro 1997).

Here we focus on games where there is a threshold (M) for participants below which no public good is produced. We do not make the general assumption that total participation gives each individual the highest pay-off. For instance, we include the possibility of 'three in a boat, two must row' (Taylor & Ward 1982; Ward 1990), a generalization of the SH game to three players, where contributions of two out of three players are required for the success of the joint venture. If two others row, there is an incentive to free ride; but if one other rows, there is an incentive to jump in and contribute. There may be an analogue in cooperative hunting by lions in richer environments where prides are larger and the participation of the entire group is not so helpful.

We shall start by investigating the evolutionary dynamics of Cs and Ds in the traditional setting of evolutionary game theory, i.e. infinite well-mixed populations evolving. The fitness of individuals is determined by their pay-off collected when engaging in an N-person stag hunt (NSH) dilemma requiring at least $M < N$ individuals to produce any public good at all. We shall find that the NSH game leads to richer and more interesting evolutionary dynamics scenarios than the corresponding NPD. Subsequently, we investigate the implications of taking into account the fact that populations are finite. Evolutionary dynamics for large finite populations was pioneered in economics by Young (1993) and by Kandori *et al.* (1993). The focus here is on the limiting effect of mutation as it becomes infrequent. Owing to mutation evolutionary dynamics becomes an ergodic Markov chain (Nowak *et al.* 2004). In the classic SH, it is shown that the population spends almost all its time at the non-cooperative equilibrium.

Evolutionary dynamics of a growing (or shrinking) finite population with random deaths is modelled in Schreiber (2001) and by Benaim *et al.* (2004). Either a strategy or the whole population can wander into extinction, but if this does not happen the trajectory of the growing population comes to approximate that of the replicator dynamics.

We shall focus on a (possibly small) well-mixed population of fixed size Z without mutation. The dynamics will be a Markov process, with the only possible end states—the absorbing states—being monomorphisms. When the population is large the dynamics approximates the replicator dynamics in the medium run, but it will eventually end up in one of the absorbing states. Thus, it may spend a long time near a stable polymorphic equilibrium of the associated mean-field dynamics before eventually being absorbed by a monomorphism. For small populations where population size is close to group size, there is also the 'spite' effect first noted by Hamilton (1970), which works against cooperation.

2. RESULTS

(a) *Evolutionary dynamics in infinite populations*

Let us assume an infinite, well-mixed population, a fraction x which is composed of Cs, the remaining fraction $(1-x)$ being Ds, and let us further assume that the groups of N individuals are sampled randomly from the population. As shown in appendix A, random sampling of individuals leads to groups whose composition follows a binomial distribution (Hauert *et al.* 2006), which also establishes the average fitness of Cs (f_C) and Ds (f_D). In each N-individual group with k Cs, the fitness of Ds is given by $\Pi_D(k) = (kFc/N)\theta(k-M)$, where the Heaviside step function ($\theta(x)$ satisfies $\theta(x<0)=0$ and $\theta(x\geq0)=1$. The corresponding fitness of Cs is given by $\Pi_C(k) = \Pi_D(k) - c$.

The time evolution of the fraction of cooperators x in the population is given by the replicator equation,

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

It is straightforward to show that, for the NPD ($M=0$), the right-hand side of the replicator equation will be positive (and hence, the fraction of cooperators will steadily increase) whenever $F > N$, since $f_C - f_D \sim (F/N) - 1$ (appendix A). On the other hand, whenever $F < N$, $f_C - f_D < 0$ for $x \in [0, 1]$, and cooperators have no evolutionary chance.

Let us now consider the NSH, where $1 < M \leq N$. Let us assume that the return from the public good increases linearly with the number k of Cs, inasmuch as $k \geq M$. In view of the previous definitions, whenever $k < M$ no public good is produced, and hence Ds have a pay-off of zero whereas Cs have a pay-off of $-c$. The evolutionary dynamics of Cs and Ds in the NSH game with a minimum threshold M can again be studied by analysing the sign of $f_C - f_D$. We may write (see the electronic supplementary material)

$$f_C - f_D \equiv Q(x) = -c\left[1 - \frac{F}{N}R(x)\right],$$

where the polynomial $R(x)$ and its properties have been defined in appendix A, whereas the details are provided in the electronic supplementary material. In a nutshell, the properties of $Q(x)$ lead to very interesting dynamics of the replicator equation, with possibly two interior fixed points (x_L and x_R, with $x_L \leq x_R$), as illustrated in figure 1, for $N=20$, different values of $1 < M \leq 20$ and variable F.
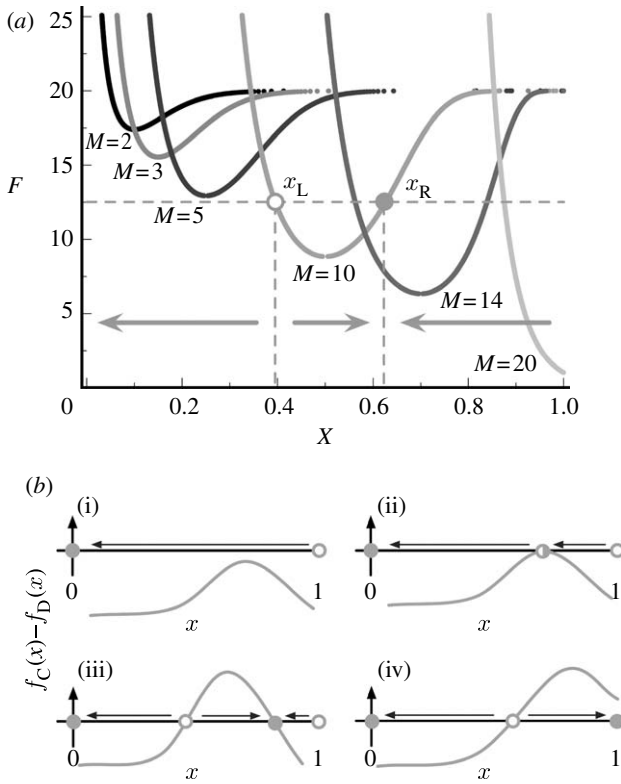
Figure 1. (*a*) Interior fixed points of the replicator equation for NSH games. The curves provide the location of the critical values of the fraction of cooperators ($x^* = \{x_L, x_R\}$) at which $f_C(x^*) = f_D(x^*)$. For each value of F (defining a horizontal line), the x^* values are given by the intersection of this line with each curve (one curve for given, fixed M, $N=20$). Scenarios with none, one and two interior fixed points are possible as detailed in (*b*(i–iv)): dynamics of NSH in infinite populations. Open circles represent unstable fixed points; filled circles represent stable fixed points and arrows indicate the direction of evolution by natural selection. For each case, the solid curves represent the typical shape of the function $f_C(x) - f_D(x)$. The quantity $\lambda^* = R(M/N)$ is defined in appendix A and corresponds to the value of F at which the minimum of each curve in (*a*) for fixed M is reached. (i) $F/N < \lambda^*$, (ii) $F/N = \lambda^*$, (iii) $\lambda^* < F/N < 1$ and (iv) $F/N > 1$.

Note, in particular, the fact that $R'(x_L) > 0$ and $R'(x_R) < 0$ (electronic supplementary material) 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 also illustrated in figure 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, $x > x_R$). 'Three in a boat' provides the simplest possible case of this scenario. Similar to the NPD, whenever $F/N < R(M/N)$, $f_C(x) < f_D(x)$ for all x, which means that all individuals will end up foregoing the public good.

(*b*) *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 (see

appendix B). The fraction of cooperators is no longer a continuous variable, varying in steps of $1/Z$. We adopt a stochastic birth–death process (Karlin & Taylor 1975) combined with the pairwise comparison rule (Traulsen *et al.* 2006, 2007*a*,*b*) 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),

$$p \equiv \frac{1}{1 + \exp(-\beta(f_A - f_B))}.$$

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 $Z \to \infty$ (Traulsen *et al.* 2006, 2007*a*,*b*). The pairwise comparison rule is similar to the so-called logit rule (Sandholm in press), according to which an individual A is selected with a probability proportional to $e^{f_A/\eta}$; here the noise parameter η plays the role of the temperature above; in fact, both processes share the same fixation probabilities, despite leading to different evolutionary dynamics equations.

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 (Traulsen *et al.* 2006, 2007*a*,*b*)

$$g(k) \equiv T^+(k) - T^-(k) = \frac{k}{Z}\frac{Z-k}{Z}\tanh\left\{\frac{\beta}{2}\left[f_C(k) - f_D(k)\right]\right\}. \tag{2.1}$$

The right-hand side of $g(k)$ is similar to the replicator equation, only that the pairwise comparison 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 (Traulsen *et al.* 2006, 2007*a*,*b*), 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 ($k/Z=0$ or $k/Z=1$). 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 $M=0$ (NPD) we may write (see appendix B)

$$f_C(k) - f_D(k) = c\left[\frac{F}{N}\left(1 - \frac{N-1}{Z-1}\right) - 1\right], \tag{2.2}$$

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 $f_C(k) - f_D(k) = -c$ and cooperators have no chance irrespective of the value of the enhancement factor. This contrasts with the result in infinite, well-mixed populations ($Z \to \infty$), 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.
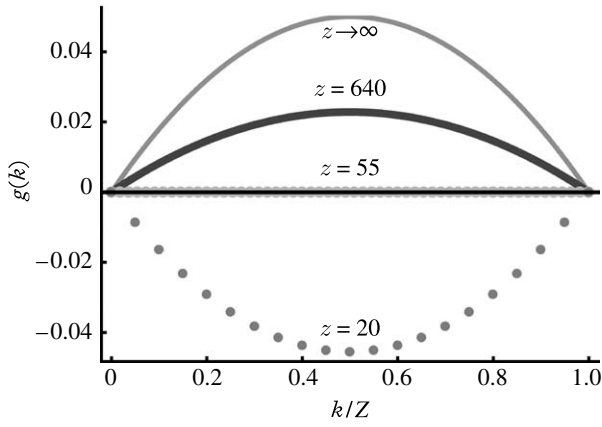
Figure 2. Behaviour of an $g(k)$NPD game in which $F > N$. We plot $g(k)$ as a function of the (discrete) frequency of cooperators k/Z, for different values of the population size Z as indicated. Given that $F = 12$ and $N = 10$, for $Z = 55$, $g(k) = 0$ for all k, as depicted. Hence, selection is neutral and evolution proceeds via random drift, which means that the fixation probability of k Cs (or Ds) is simply k/Z. For values of Z below $Z = 55$, Cs are disadvantageous, whereas for values above $Z = 55$ Cs become advantageous, irrespective of the initial fraction of Cs initially present in the population, which corresponds to the evolutionary dynamics scenario in an infinite, well-mixed population.

Given the independence of $f_C - f_D$ on k in finite populations, for a given population size there is a critical value of F for which selection is neutral, and above which cooperators will win the evolutionary race. From the two equations above, this critical value reads

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

In figure 2, we show the Z-dependence of $g(k)$ for fixed group size $N = 10$ and fixed $F = 12$ leading to a critical population size $Z = 55$.

Let us now discuss the NSH with $1 < M < N \le Z$. 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. 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 (see appendix B).

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. figure 1). The possible scenarios are depicted in figure 3a.

Clearly, for small population sizes, cooperators are always disadvantageous. With increasing Z, however, one approaches the replicator dynamics scenario (coordination game), despite the fact that, e.g. for $Z = 20$, convergence towards the absorbing state at 100 per cent 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 $g(k)$.
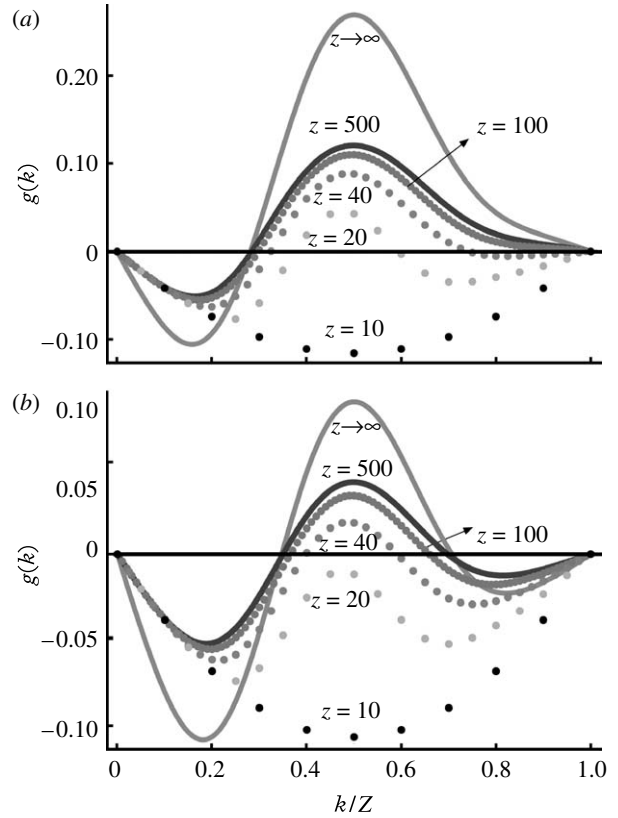
Figure 3. Behaviour of $g(k)$ for a NSH game in a population of variable size Z and fixed group size $N = 10$, and $M = 5$. (a) Since $F = 12 > N$, the game becomes a pure coordination game in infinite populations. In finite populations, however, it strongly depends on Z: for $Z = N$, Cs are always disadvantageous and evolutionary dynamics leads mostly to 100 per cent Ds. For $Z = 20$ (and using a terminology which is only correct for $Z \to \infty$), 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: 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 now exhibits two interior fixed points in infinite populations (dark grey curve). Similar to (a), for small Z Cs are disadvantageous for all k. Unlike (a), however, now the 'interior fixed points' emerge together for a critical population size, and remain for larger population sizes.

Whenever $F < N$, yet above the critical limit below which Cs become disadvantageous for all x in figure 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 Z_{CRIT}, as illustrated in figure 3b.

3. DISCUSSION

In this paper, we extend the range of PGG to systems where a minimum of coordinated collective action is required to achieve a public good. By doing so, we generalized the two-person SH game to N-person games. 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. The one at the lower frequency of cooperators is always an unstable fixed point, which determines a threshold for cooperative collective action.

Table 1. Interior roots of $g(k)$ for the NSH. One distinguishes two groups of interior roots of $g(k)$ which depend on how $F(>M)$ compares with N. When $F>N$, one approaches the infinite population size limit indirectly, in the sense that there is a first population threshold Z_1 above which two interior roots emerge, one of them disappearing above a second threshold Z_2. This scenario contrasts with that associated with $M<F<N$, for which there is a threshold Z_C at which two interior roots emerge, smoothly approaching the infinite limit with increasing population size Z (we used $\tilde{x}_L$ and $\tilde{x}_R$ to distinguish the roots for finite populations from those defined for infinite population).

Z	$M<F<N$	Z	$N<F$
$N\leq Z<Z_C$	—	$N\leq Z<Z_1$	—
$N<Z_C<Z$	$\tilde{x}_L, \tilde{x}_R$	$N<Z_1<Z<Z_2$	$\tilde{x}_L, \tilde{x}_R$
$Z\to\infty$	x_L, x_R	$N<Z_1<Z_2<Z$	$\tilde{x}_L$
		$Z\to\infty$	x_L

The other, at a higher frequency of cooperators, is a stable fixed point, and hence determines the final frequency of cooperators in the population, assuming that the coordination threshold is overcome. Besides this most interesting regime, there are also the possible outcomes of no cooperation or of a pure coordination game with a threshold that 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 NSH game is profoundly affected, mostly when the population size is comparable with the group size (see table 1 for a summary). In this regime, one observes an overlap of the different scenarios obtained 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 of Z_1, above which the interior roots of $g(k)$ emerge, which constitute the finite-population analogues of x_L and x_R in infinite populations (cf. figure 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, i.e. $F<N$ but yet above the critical value $\lambda^* = R(M/N)$ defined in appendix A and the electronic supplementary material, cooperators are always disadvantageous; however, above a critical population size (Z_C) the interior roots of $g(k)$ emerge simultaneously and the evolutionary dynamics approach 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 that 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.

In this work we have always assumed that the benefit returned by the PGG scales linearly with the amount contributed. This need not be the case, and it is possible to find examples in which a nonlinear return paradigm would be more appropriate. Hence, it will prove interesting to

understand in which way deviations from a linear return will affect evolutionary game dynamics, mostly in finite populations. Work along these lines is in progress.

APPENDIX A. REPLICATOR DYNAMICS IN INFINITE POPULATIONS

We assume an infinite, well-mixed population, where x denotes the fraction of Cs, and $(1-x)$ the fraction of Ds. Groups of N individuals are sampled randomly from the population and engaged in an NSH game. As referred to in §1, the NSH requires a minimum threshold of $M>1$ ($M\leq N$) individuals for a public good to be produced whereas the NPD is obtained whenever $M=0$. As a result, the average fitness of Ds in this population (as usual, we identify here fitness with pay-off) is given by

$$f_D(x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} \Pi_D(k), \quad (A1)$$

whereas the average fitness of Cs is given by

$$f_C(x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} \Pi_C(k+1), \quad (A2)$$

where $\Pi_C(k)$ ($\Pi_D(k)$) are the fitness of a C (D) in a group of N individuals, k of which are Cs. Random sampling of individuals leads to groups whose composition follows a binomial distribution. In an N-individual group with Cs the fitness of Ds is given by

$$\Pi_D(k) = \frac{kFc}{N}\theta(k-M),$$

and that of Cs by

$$\Pi_C(k) = \Pi_D(k) - c,$$

where the Heaviside step function $\theta(x)$ satisfies $\theta(x<0)=0$ and $\theta(x\geq 0)=1$. Hence, each C pays a fixed cost when engaging in a PGG, and the value of the public good increases linearly with the number k of Cs, inasmuch as $k\geq M$. In view of the previous definitions, whenever $k<M$ no public good is produced, and hence Ds have a pay-off of zero whereas Cs have a pay-off of $-c$.

For the NPD ($M=0$), we readily obtain from equations (A1) and (A2) that $f_C - f_D \sim (F/N) - 1$ and cooperation becomes the preferred option whenever $F>N$. Whenever $F<N$, $f_C - f_D < 0$ for $x \in [0, 1]$, and cooperators have no evolutionary chance.

Whenever $M>1$ and $k<M$, the situation is similar to the NPD: Cs remain disadvantageous in mixed groups. Whenever $k\geq M$, some public good is produced and now $\Pi_D(k) = (kFc/N)$ whereas $\Pi_C(k) = \Pi_D(k) - c$.

The evolutionary dynamics of Cs and Ds in the NSH game with a minimum threshold M can be studied by analysing again the sign of $f_C - f_D$. We may write

$$f_C(x) - f_D(x) \equiv Q(x) = -c\left[1 - \frac{F}{N}R(x)\right],$$

Table 2. Nature and number of fixed points of replicator dynamics. Given the definition of $\lambda^* = R(M/N)$, we identify the fixed points of the replicator dynamics, as well as their nature, for the different regimes associated with the possible values of the ratio F/N. Besides the trivial endpoints $\{0,1\}$, we also identify possible interior fixed points $\{x_L, x_R\}$ satisfying $x_L \in (0, M/N)$ and $x_R \in (M/N, 1)$ (see main text for additional details).

	$F/N < \lambda^*$	$F/N = \lambda^*$	$\lambda^* < F/N \le 1$	$1 < F/N$
stable	0	0	$0, x_R$	$0,1$
unstable	1	$M/N, 1$	$x_L, 1$	x_L

(see the electronic supplementary material) where

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

The roots of $Q(x)$ in $(0,1)$ determine whether the replicator equation exhibits interior fixed points. In the electronic supplementary material, we prove several properties of the polynomial $R(x)$. In particular, let us define $\lambda^* = R(M/N)$. Then (i) for $(F/N) < \lambda^*$ for there are no roots for $x \in (0,1)$; (ii) for $(F/N) = \lambda^*$, M/N is a double root in $(0,1)$; (iii) for $(F/N) < 1$, there is only one simple root $x_L \in (0, M/N)$; and (iv) whenever $\lambda^* < (F/N) \le 1$ there are two simple roots $\{x_L, x_R\}$, with $x_L \in (0, M/N)$ and $x_R \in (M/N, 1)$. The implications of $R(x)$ in the evolutionary dynamics of the population are illustrated in figure 1b and summarized in table 2.

The fact that $R'(x_L) > 0$ and $R'(x_R) < 0$ (see the electronic supplementary material) allow us to classify immediately x_L as an unstable fixed point whereas x_R, if it exists, corresponds to a stable fixed point. Moreover, when $(F/N) = \lambda^*$, M/N is always an unstable fixed point.

APPENDIX B. PAIRWISE COMPARISON IN FINITE POPULATIONS

We consider now a finite well-mixed population of size Z, individual fitness resulting from engaging in an NSH. The average fitness of Cs and Ds now becomes a function of the (discrete) fraction k/Z of Cs in the population, and can be written as (hypergeometric sampling) (Hauert *et al.* 2007)

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

and

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

respectively, where we impose that the binomial coefficients satisfy $\binom{k}{j} = 0$ if $k < 0$.

We adopt a stochastic birth–death process (Karlin & Taylor 1975) combined with the pairwise comparison rule (Traulsen *et al.* 2006, 2007a,b) introduced before in §2b, in order to describe the evolutionary dynamics of Cs (and

Ds) in a finite population. Given that we have k Cs in the population, the probability that, in a given time step, the number of Cs increases (decreases) by one is given by the transition probabilities

$$T^\pm(k) = \frac{k}{Z}\frac{Z-k}{Z}\frac{1}{1+\exp(\mp\beta[f_C(k)-f_D(k)])},$$

where β specifies the intensity of selection.

For finite populations, the quantity corresponding to the right-hand side of the replicator equation, specifying the 'gradient of selection', is given by (Traulsen *et al.* 2006, 2007a,b) $g(k)$ defined in equation (2.1) in §2b, and its interior roots are the roots of $f_C(k) - f_D(k)$. Since $\Pi_D(k) = (kFc/N)\theta(k-M)$ and $\Pi_C(k) = \Pi_D(k) - c$, we may explicitly write equation (2.2) of §2b for $f_C(k) - f_D(k)$ (see also the electronic supplementary material), whenever $M = 0$, *which is independent of k* being, however, *population and group size dependent.*

Whenever $M > 1$ and $Z = N$, the result is easily inferred from the NPD case. For $1 < M < N < Z$, the threshold brings about a strong disruption of the finite population dynamics, the analytical treatment of which is cumbersome. Numerically, however, the situation is easy to understand in light of the previous discussion. Consequently, figure 3 was computed numerically using a direct implementation of the equations in MATHEMATICA.

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