

GROUP-SIZE DIVERSITY IN PUBLIC GOODS GAMES

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Public goods games are models of social dilemmas where cooperators pay a cost for the production of a public good while defectors free ride on the contributions of cooperators. In the traditional framework of evolutionary game theory, the payoffs of cooperators and defectors result from interactions in groups formed by binomial sampling from an infinite population. Despite empirical evidence showing that group-size distributions in nature are highly heterogeneous, most models of social evolution assume that the group size is constant. In this article, I remove this assumption and explore the effects of having random group sizes on the evolutionary dynamics of public goods games. By a straightforward application of Jensen's inequality, I show that the outcome of general nonlinear public goods games depends not only on the average group size but also on the variance of the group-size distribution. This general result is illustrated with two nonlinear public goods games (the public goods game with discounting or synergy and the N -person volunteer's dilemma) and three different group-size distributions (Poisson, geometric, and Waring). The results suggest that failing to acknowledge the natural variation of group sizes can lead to an underestimation of the actual level of cooperation exhibited in evolving populations.

KEY WORDS: Cooperation, game theory, Jensen's inequality, prisoner's dilemma, public goods game, variance.

Social dilemmas are situations in which there is a conflict between individual and collective interests. In game theory terms, social dilemmas are defined as games with at least one Pareto inefficient Nash equilibrium (Kollock 1998; Archetti and Scheuring, in press): an alternative outcome making at least one player better off without reducing any other player's payoff is possible, but no player has the incentive to change their behavior. Such tension between the individual and the collective interest is encountered at all levels of biological organization, from the production of enzymes in microorganisms (Turner and Chao 1999; Gore et al. 2009) to predator inspection (Pitcher 1991), sentinel behavior (Clutton-Brock et al. 1999), and cooperative hunting (Packer and Ruttan 1988) in social vertebrates. Pollution, human overpopulation, overexploitation of fisheries (Hardin 1968), the use of public transportation (Van Vugt et al. 1996), and the production of open-source software (Hippel and Krogh 2003) are typical examples of the kind of social dilemmas faced by contemporary human societies.

Many social dilemmas are related to the production of public goods, defined as common resources that are simultaneously nonexcludable (no individual can be excluded from its consumption) and nonrivalrous (one individual's use of the public good does not diminish its availability to another individual) (Samuelson 1954; Pindyck and Rubinfeld 2001). Public goods games (PGGs) are simple models of public goods dilemmas, used by both experimental economists (Kagel and Roth 1995) and theoreticians (Hamburger 1973; Fox and Guyer 1978; Sigmund 2010). In general, a PGG can be described by a benefit function $B(i, N)$ and a cost function $C(i, N)$, where i is the number of cooperators (Cs) in a group of size N (Archetti and Scheuring, in press). Only Cs pay the cost $C(i, N)$ whereas both Cs and defectors (Ds) get the benefit $B(i, N)$. This leads to payoffs for Ds and Cs being, respectively, given by $P_D(i, N) = B(i, N)$ and $P_C(i, N) = B(i, N) - C(i, N)$.

By far, the most well-known PGG is the N -person Prisoner's Dilemma, hereafter NPD (Hamburger 1973). The NPD involves

a group of N individuals where C s contribute a cost $c > 0$ to the public good, whereas D s contribute nothing. All contributions are added together, multiplied by an enhancement factor $1 < r < N$, and then shared among all the individuals of the group. This gives $B(i, N) = rci/N$ for the benefit function and $C(i, N) = c$ for the cost function. The NPD is the archetypal example of a social dilemma because its only Nash equilibrium (all players defect) is evidently Pareto inefficient: everybody ends up getting nothing, but if everybody had cooperated, each individual would have obtained $c(r - 1) > 0$. Moreover, defection is dominant, so that each individual is better off defecting no matter what their coplayers do, that is, $P_D(i, N) > P_C(i + 1, N)$. The fact that defection is dominant prevents cooperation from evolving when groups form randomly (Nunney 1985). (Note, however, that if $r > N$ cooperation dominates defection, there is no social dilemma, and cooperation evolves).

A great deal of effort in evolutionary biology has been devoted to the study of mechanisms allowing for the evolution of cooperation in the NPD, such as kin selection (Hamilton 1964; Grafen 1985; Frank 1998; Grafen 2009) and reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Nowak and Sigmund 2005), which can all be understood as different ways of creating and maintaining positive assortment between C s (Lehmann et al. 2006; Fletcher and Doebeli 2009). Voluntary participation (Hauert et al. 2002), punishment of noncontributors (Boyd and Richerson 1992) and rewards to contributors (Hauert 2010) have also been proposed as alternative mechanisms to promote cooperation in the NPD.

Despite its theoretical importance, it is clear that the NPD is only a very specific case of PGG, characterized by a linear benefit function and by the fact that defection is the dominant strategy. Other social dilemmas may depart from these assumptions, as it has been well understood in the social sciences (Schelling 1978; Taylor and Ward 1982; Hirshleifer 1983; Kollock 1998) and recognized in theoretical evolutionary biology (Maynard Smith 1965; Charnov and Krebs 1975; Cohen and Eshel 1976; Matessi and Jayakar 1976; Boyd and Richerson 1988; Dugatkin 1990; Motro 1991) for decades. Recently, several works in evolutionary game theory have focused on PGGs with nonlinear payoff functions, bringing to the fore alternatives to the NPD for modeling social dilemmas (Bach et al. 2006; Hauert et al. 2006b; Zheng et al. 2007; Pacheco et al. 2009; Souza et al. 2009; Archetti 2009a,b; Archetti and Scheuring 2011, in press). The most important result from this heterogeneous collection of works is that removing the assumptions of dominant defection and linearity on which the NPD is based has important consequences on the resulting evolutionary dynamics. Stable and unstable interior fixed points may appear in the replicator dynamics of nonlinear PGGs, leading to the coexistence of C s and D s or to bistability between coopera-

tive and defective equilibria. In these cases, cooperation can be maintained without the need of invoking reciprocity, punishment, voluntary participation, rewards, or any of the mechanisms generally proposed to generate assortment in the NPD (Archetti and Scheuring, in press).

For reasons of parsimony, it is common to consider the group size N as constant when investigating the evolutionary dynamics of PGGs. Natural and social systems, however, often exhibit high levels of group-size heterogeneity. Indeed, the group-size distributions of several species, including social amoeba (Fortunato et al. 2003), tuna fish and sardinellas (Bonabeau and Dagorn 1995), buffaloes (Sinclair 1977), antelopes (Wirtz and Lörcher 1983), bison (Lott and Minta 1983), lions (Schaller 1972), wolves (Rodman 1981), killer whales (Baird and Dill 1996), and humans (Zipf 1949; James 1953; Newman 2001) have been reported to be heavily skewed, and in many cases well approximated by power-law distributions (Bonabeau and Dagorn 1995; Bonabeau et al. 1999; Sjöberg et al. 2000; Newman 2001; Niwa 2003). Heterogeneous group-size distributions are also expected to arise from simple stochastic models of aggregation and grouping (Cohen 1971; Okubo 1986; Bonabeau et al. 1999; Duerr and Dietz 2000; Niwa 2003).

In this article, I study the effects of introducing variable group sizes in the replicator dynamics of PGGs. I do so by assuming that group size is a random variable with a prescribed probability distribution. In contrast to other models of social evolution featuring diverse group sizes, the model presented here does not involve (1) changes in group size caused by changes in behavior (Lehmann et al. 2006), (2) individual group size preferences (Avilés 2002; van Veelen et al. 2010; Powers et al. 2011), (3) time-varying group-size distributions with fluctuating mean values (Eshel 1977; Szathmáry 1993; Hauert et al. 2002, 2006a, 2008; Mathew and Boyd 2009; Parvinen 2010) nor (4) network-structured populations (Santos et al. 2008; Santos and Pacheco 2011). Rather, it is based on the following assumptions: (1) group-size distributions are exogenously determined, (2) C s and D s have the same tendency to aggregate (no particular preference for a given group size), (3) group-size distributions are static, and (4) the population is well mixed. The motivation behind these simpler assumptions is to explore to which extent the sole fact of having diverse but static group-size distributions can affect the evolutionary dynamics of PGGs in the absence of assortment of strategies resulting from differential grouping tendencies or population structure.

With the above-mentioned assumptions, the general model presented in this article is closely related to the models of intrademic group selection by Cohen and Eshel (1976) and Matessi and Jayakar (1976), who also studied evolutionary PGGs with constant and random group sizes. However, my approach

contrasts with these works in various respects. First, I make explicit use of a general result in probability theory (Jensen’s inequality) for investigating when and how the evolutionary dynamics under random group sizes are expected to be different from those under constant group sizes. Second, I consider group-size distributions going beyond the Poisson distribution used by Cohen and Eshel (1976). Finally, I illustrate the general results with different social dilemmas, namely the public goods with discounting or synergy (PGGDS) (Hauert et al. 2006b) and the N-person volunteer’s dilemma (NVD) (Diekmann 1985; Archetti, 2009a,b).

My model is also related to recent work by Brännström et al. (2011), who studied the consequences of fluctuating group sizes for the evolution of cooperation in continuous PGGs. The authors analyzed general classes of PGGs with payoff functions that do not explicitly depend on group size and derived general conditions for group-size diversity to promote/hinder cooperation in the framework of adaptive dynamics (Metz et al. 1996). In this work, I focus instead on the effects of group-size diversity on PGGs with payoff functions that explicitly depend on group size, in the framework of the replicator dynamics for two discrete strategies: *D*s that contribute $c = 0$ and *C*s that contribute $c > 0$. This choice allows direct comparison with recent works on evolutionary PGGs that consider the same setup (replicator dynamics of *C*s and *D*s), but assume that the group size is constant (Hauert et al. 2006b; Zheng et al. 2007; Pacheco et al. 2009; Souza et al. 2009; Archetti, 2009a,b; Archetti and Scheuring 2011).

The Model

Consider a very large and well-mixed population consisting of a fraction x of *C*s and $1 - x$ of *D*s, where groups of N individuals are formed randomly by binomial sampling. For now, assume that the group-size N is constant, so that $N = n$ with probability equal to one. Then, the probability that a given individual finds itself in a group where j of the other $n - 1$ individuals are *C*s is given by

$$\binom{n-1}{j} x^j (1-x)^{n-1-j}.$$

In each group with j other *C*s, *C*s receive a payoff $P_C(j + 1, n)$ and *D*s a payoff $P_D(j, n)$. Therefore, the average payoff of a *C* and a *D* are given, respectively, by

$$f_C(x, n) = \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} P_C(j + 1, n),$$

and

$$f_D(x, n) = \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} P_D(j, n).$$

In the framework of evolutionary game theory, the change in frequency of cooperators can be described by the replicator dynamics (Taylor and Jonker 1978; Hofbauer and Sigmund 1998)

$$\dot{x} = x(1-x)f(x, n), \tag{1}$$

where $\dot{x} = dx/dt$ and

$$f(x, n) = f_C(x, n) - f_D(x, n).$$

As mentioned above, the analysis of equation (1) for different PGGs has been extensively carried out for the case of constant group sizes (Boyd and Richerson 1988; Dugatkin 1990; Hauert et al. 2006b; Zheng et al. 2007; Pacheco et al. 2009; Souza et al. 2009; Archetti, 2009a,b; Archetti and Scheuring 2011).

To introduce group-size diversity, suppose now that N is no longer a constant but a random variable with support $n \in \{n_{\min}, n_{\min} + 1, \dots, n_{\max}\}$ and probability mass function $p_n = \Pr(N = n)$, so that $\sum_{n=n_{\min}}^{n_{\max}} p_n = 1$. The mean value of N is given by $\mu_N = \mathbb{E}[N] = \sum_n p_n n$ and its variance by σ_N^2 . Assume that $n_{\min} \geq 2$ as to exclude “groups” of size one where by definition there is no social dilemma. Finally, denote by $\mathbb{E}[g(N)] = \sum_n p_n g(n)$ the expected value of the function $g(N)$. Then, by the law of total probability, the average payoff of a *C* and a *D* can be written as

$$F_C(x, N) = \sum_n q_n f_C(x, n),$$

and

$$F_D(x, N) = \sum_n q_n f_D(x, n),$$

where $q_n = np_n/\mu_N$ is the probability that an individual joins a group of size n . The replicator dynamics becomes

$$\dot{x} = x(1-x)F(x, N), \tag{2}$$

where

$$\begin{aligned} F(x, N) &= F_C(x, N) - F_D(x, N) = \sum_n q_n f(x, n) \\ &= \frac{1}{\mu_N} \mathbb{E}[Nf(x, N)]. \end{aligned} \tag{3}$$

Notice that the standard case where group size is constant is recovered from equation (2) by assuming that N is distributed according to the degenerate distribution, that is, a distribution with probability mass function $p_n = \delta(n, \mu_N)$, where $\delta(x, y)$ is the Kronecker delta function, so that $\delta(x, y) = 1$ if $x = y$

and $\delta(x, y) = 0$ otherwise. In this case, the replicator dynamics reduces to

$$\dot{x} = x(1 - x)f(x, \mu_N). \tag{4}$$

Let us now assume that N is distributed according to a non-degenerate distribution, so that $\sigma_N^2 > 0$. Then, it is clear from equations (2), (3), and (4) that, for a given x , group-size diversity will lead to a dynamical scenario which is more favorable to cooperation than the one obtained if N is constant whenever $F(x, N) > f(x, \mu_N)$. This last expression leads to

$$\mathbb{E}[Nf(x, N)] > \mu_N f(x, \mu_N). \tag{5}$$

I now make use of Jensen’s inequality (see Jensen [1906] for the original paper, Gillespie [1977] for a classic application to evolutionary biology, and Ruel and Ayres [1999] for a review and applications to ecology), a well-established result in probability theory stating that the average of a nonlinear function $\mathbb{E}[g(X)]$ is different from the function evaluated at the average $g(\mathbb{E}[X])$. In particular, $\mathbb{E}[g(X)] > g(\mathbb{E}[X])$ if $g(x)$ is strictly convex ($d^2g(x)/dx^2 > 0$) and $\mathbb{E}[g(X)] < g(\mathbb{E}[X])$ if $g(x)$ is strictly concave ($d^2g(x)/dx^2 < 0$). By a straightforward application of Jensen’s inequality, the condition given by equation (5) is true if

$$h(x, n) \equiv nf(x, n)$$

is strictly convex in n , that is, if $\partial^2h/\partial n^2 > 0$.

From this, it is clear that the NPD is essentially unaffected by group-size diversity. Indeed, it can be easily shown that for this game $h(x, n)$ reduces to $c(r - n)$, which is a linear function of n . Thus, $F(x, N) = f(x, \mu_N)$ so that the replicator dynamics of the NPD is invariant with respect to changes of the group-size distribution preserving its average value.

A different picture emerges in the case of nonlinear PGGs, because nonlinearities in payoff functions translate into functions h that are nonlinear in n and, by Jensen’s inequality, into $F(x, N) \neq f(x, \mu_N)$. In particular, the more diverse the group-size distribution and the more nonlinear the function h , the larger the deviation of the gradient of selection of the replicator dynamics from its mean-value approximation $F(x, N) \approx f(x, \mu_N)$. Indeed, we can write (see Appendix 1)

$$F(x, N) \approx \underbrace{f(x, \mu_N)}_{\text{mean-value approximation}} + \frac{1}{2} \underbrace{\frac{\partial^2 h(x, \mu_N)}{\partial n^2}}_{\text{nonlinearity}} \times \underbrace{\frac{\sigma_N^2}{\mu_N}}_{\text{group-size diversity}}. \tag{6}$$

Equation (6) neatly shows the combined effects of nonlinearity and group-size diversity on the replicator dynamics and further clarifies the predictions of Jensen’s inequality: for a given x ,

group-size diversity favors cooperation if and only if h is strictly convex in n ($\partial^2h(x, \mu_N)/\partial n^2 > 0$). Whenever h is nonlinear, so that $\partial^2h(x, \mu_N)/\partial n^2 \neq 0$, the promotion or hindering of cooperation is more important the larger the nonlinearity of h (as measured by $|\partial^2h(x, \mu_N)/\partial n^2|$) and the larger the diversity of the group-size distribution (as measured by the variance-to-mean ratio σ_N^2/μ_N).

In the following, I illustrate this general result with two particular cases of nonlinear PGGs: PGGDS and the NVD. I explicitly model the group-size distributions by making use of (truncated) Poisson, geometric, and Waring distributions, which greatly differ in their variance-to-mean ratios (see Fig. 1). These distributions frequently arise as the result of simple aggregation processes (Coleman and James 1961; Cohen 1971; Okubo 1986; Duerr and Dietz 2000) and are good models of animal group-size distributions. The Waring distribution (Irwin 1968) exhibits power-law behavior for large values of the random variable (i.e., if N is a Waring variate, $\Pr(N = n) \propto n^{-\alpha}$ for large values of n), hence it can be used to model grouping based on preferential attachment (Barabási and Albert 1999), whereby larger groups are preferentially chosen by joining individuals. A mathematical description of these probability distributions is given in Appendix 2.

PUBLIC GOODS GAME WITH DISCOUNTING OR SYNERGY (PGGDS)

In the PGGDS (Hauert et al. 2006b), the first C in the group contributes a value b to produce a public good, the second C contributes wb and so on, to the i th C which contributes $w^{i-1}b$. The public good is then shared equally among the members of the group. The benefit function is thus given by

$$B(i, n) = \frac{b(1 + w + w^2 + \dots + w^{i-1})}{n} = \frac{b(1 - w^i)}{n(1 - w)},$$

whereas the cost function is given by $C(i, n) = c$ (each C pays a fixed cost c). For $w = 1$, the NPD is recovered as a special case when $b = rc < nc$. If $0 < w < 1$, the benefit function is decelerating (benefits are discounted) whereas if $w > 1$, it is accelerating (benefits are synergistically enhanced).

With these definitions we obtain after little algebra:

$$f(x, n) = \frac{b}{n}(1 - x + wx)^{n-1} - c, \tag{7}$$

and

$$F(x, N) = \frac{b}{\mu_N} \mathbb{E}[(1 - x + wx)^{N-1}] - c. \tag{8}$$

Let us denote by $\gamma = c/b$ the cost-to-benefit ratio, and define $\gamma_1 = 1/\mu_N$ and

$$\gamma_2 = \mathbb{E}[w^{N-1}]/\mu_N. \tag{9}$$

Then, as shown in the left panel of Figure 2, four different dynamical scenarios can be distinguished (see Appendix 3 for the

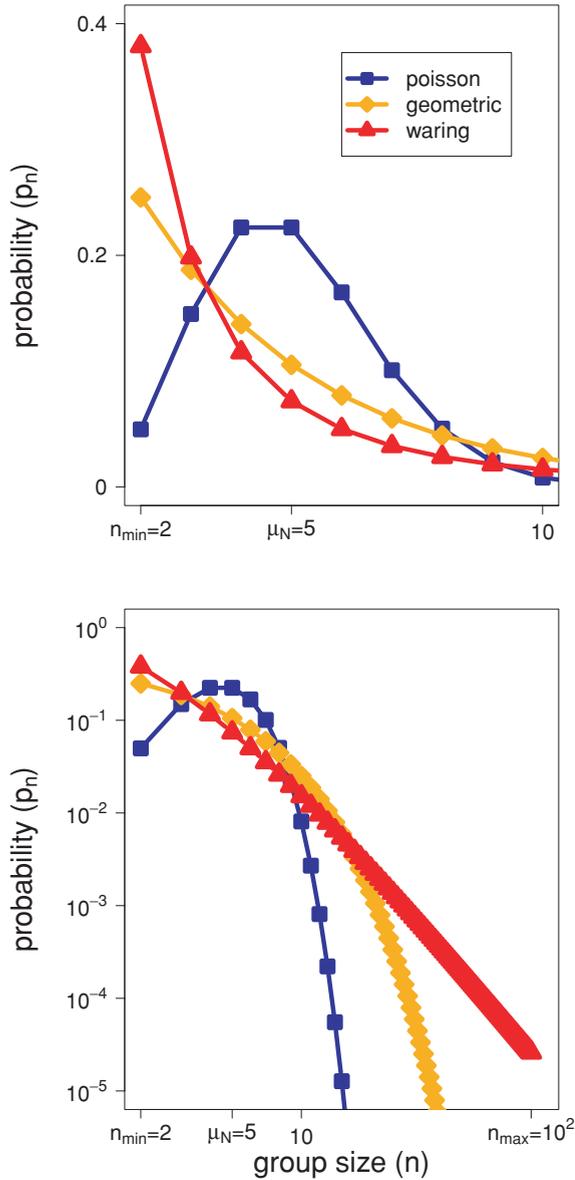


Figure 1. Examples of the nondegenerate group-size distributions used in this study: Poisson, geometric, and Waring. Parameters: $n_{\min} = 2$, $n_{\max} = 100$, and $\mu_N = 5$. Top panel. Plots of the probability mass functions. Bottom panel. Log-log plots of the probability mass functions. For large values of n , the Waring distribution used in this study exhibits power-law behavior with exponent $\alpha = 3$, that is, $p_n \propto n^{-\alpha}$ with $\alpha = 3$.

derivation):

- (1) If $\gamma > \gamma_1$ and $\gamma > \gamma_2$, the only stable fixed point is $x_0 = 0$, and defection is dominant.
- (2) If $\gamma_2 < \gamma < \gamma_1$, there is an interior fixed point x_F , which is stable, while both $x_0 = 0$ and $x_1 = 1$ are unstable. C s and D s coexist at a polymorphic equilibrium with a proportion x_F of C s.

- (3) If $\gamma < \gamma_1$ and $\gamma < \gamma_2$ the only stable fixed point is $x_1 = 1$, and cooperation is dominant.
- (4) If $\gamma_1 < \gamma < \gamma_2$, the interior fixed point x_F is unstable and both $x_0 = 0$ and $x_1 = 1$ are stable. There is bistability: C s and D s cannot invade each other and the population evolves either to $x_0 = 0$ or $x_1 = 1$ depending on the initial conditions.

For constant group sizes, the conditions found by Hauert et al. (2006b) are recovered, namely, $\gamma_2 = w^{\mu_N-1}/\mu_N$, and $x_F = x_f$, with

$$x_F = x_f = \frac{1 - (\gamma\mu_N)^{1/(\mu_N-1)}}{1 - w}.$$

For random group sizes, we have

$$\frac{\partial^2 h(x, n)}{\partial n^2} = b(1 - x + wx)^{n-1} \ln^2(1 - x + wx),$$

which is greater than zero for all $x \in (0, 1)$, for all $w \neq 1$ and for all n . Hence, by Jensen's inequality, $F(x, N) \geq f(x, \mu_N)$ for all x , with strict equality only in the case where the group-size distribution is degenerate or when $w = 1$. This means that group-size diversity systematically promotes cooperation in the PG-GDS with respect to the case of constant group sizes for both discounted and synergistically enhanced benefits. In particular, since w^n is a convex function of n , Jensen's inequality gives $\gamma_2 = \mathbb{E}[w^{N-1}]/\mu_N > w^{\mu_N-1}/\mu_N$. As a result, the introduction of group-size diversity makes the regions of dominant cooperation and of bistability grow at the expense of the regions of coexistence and dominant defection, respectively. Moreover, it is clear that $F(x, N) > f(x, \mu_N)$ for all x implies that $x_F > x_f$ for $w < 1$ and $x_F < x_f$ for $w > 1$. Hence, group-size diversity translates into a larger fraction of C s when there is coexistence (see the top panel of Fig. 3), and into a larger basin of attraction for the C equilibrium when cooperation and defection are bistable (see the bottom panel of Fig. 3). Overall, the degree of cooperation (given by the fraction of C s at equilibrium or by the size of the basin of attraction of $x_1 = 1$) in the case of random group sizes is always greater than or equal to the respective degree of cooperation in the case of constant group sizes, for any point in the parameter space (see the right panel of Fig. 2).

For an arbitrary n_{\max} , the critical value γ_2 can be directly calculated from its defining series $\gamma_2 = \frac{1}{w\mu_N} \sum_n p_n w^n$, and the fixed point x_F can be found by numerically solving $F(x_F, N) = \frac{1}{\mu_N} \sum_n p_n n f(x_F, n) = 0$. This is the approach I used for calculating the data shown in Figures 2 and 3. These calculations can be cumbersome for large values of n_{\max} . In such cases, it is more convenient to have closed-form expressions for γ_2 and $F(x, N)$. These can be obtained exactly in the limit $n_{\max} \rightarrow \infty$ if the expected values converge (see Appendix 4) or approximated

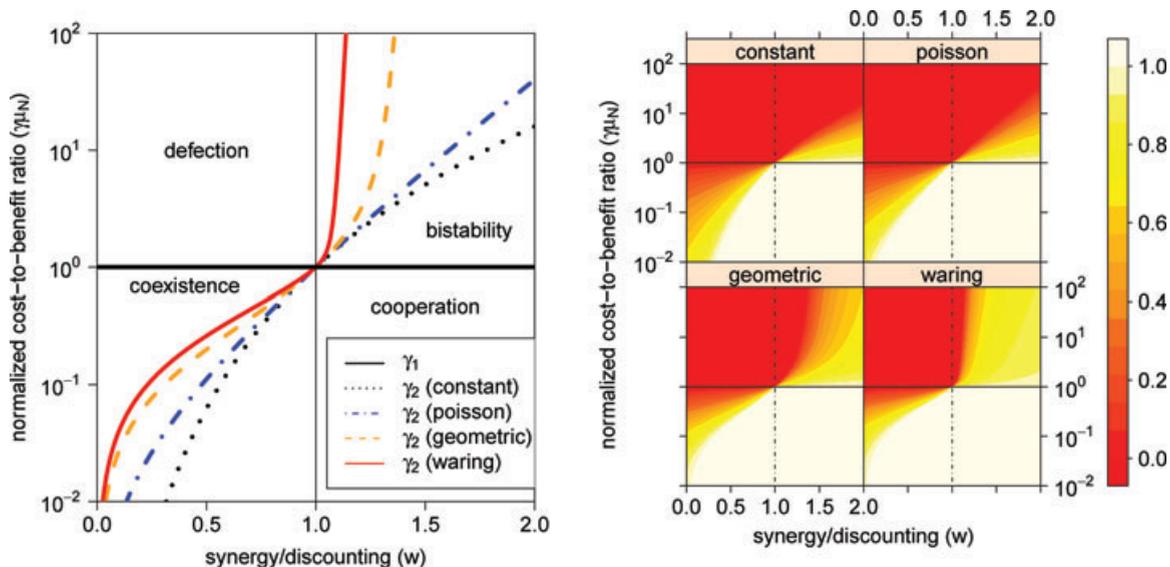


Figure 2. Phase diagram and degree of cooperation in the PGGDS for the different group-size distributions. Left panel. Phase diagram illustrating the four different dynamical regimes (defection, coexistence, cooperation, and bistability). Right panel. Degree of cooperation for the different group-size distributions. The degree of cooperation is given by the fraction of Cs at equilibrium, except in the bistability region where it is given by the size of the basin of attraction of the cooperative equilibrium. Parameters: $n_{\min} = 2$, $n_{\max} = 100$, $\mu_N = 5$.

using equation (6) to obtain

$$\gamma_2 \approx \frac{w^{\mu_N-1}}{\mu_N} \left[1 + \frac{\ln^2(w)\sigma_N^2}{2} \right],$$

and

$$F(x, N) \approx \frac{b}{\mu_N} (1 - x + wx)^{\mu_N-1} \left[1 + \frac{\ln^2(1 - x + wx)\sigma_N^2}{2} \right] - c.$$

N-PERSON VOLUNTEER’S DILEMMA (NVD)

In the NVD (Diekmann 1985; Archetti, 2009a,b), each individual in a group of size n must decide whether to volunteer to provide a public good or not. If at least k players volunteer to pay a cost c , everyone receives a benefit b . Thus $B(i, n) = b\theta(i - k)$, where $\theta(x)$ is the Heaviside step function, such that $\theta(x < 0) = 0$ and $\theta(x \geq 0) = 1$, and $C(i, n) = c$. Here, I explore the simple case where $k = 1$. Note that this case has sometimes been called N -person snowdrift game (van Veelen and Nowak 2012).

With $k = 1$, we find

$$f(x, n) = b(1 - x)^{n-1} - c,$$

and

$$F(x, N) = \frac{b}{\mu_N} \mathbb{E}[N(1 - x)^{N-1}] - c. \tag{10}$$

Note that f is a monotonically decreasing function of x for $n \geq 1$, which implies that $F = \sum_n q_n f(x, n)$ is also a monotonically decreasing function of x , because $q_n \geq 0 \forall n$. Additionally,

since $F(0, N) = b - c > 0$ and $F(1, N) = -c < 0$, the only stable state of the replicator dynamics is the fixed point $x_F \in (0, 1)$, so that Cs and Ds coexist at a polymorphic equilibrium with a proportion x_F of Cs. In the general case of random group sizes, x_F can be found by numerically solving $F(x_F, N) = 0$. In the case of constant group sizes, x_F reduces to (Archetti 2009b)

$$x_F = x_f = 1 - \gamma^{1/(\mu_N-1)}, \tag{11}$$

where $\gamma = c/b$ is the cost-to-benefit ratio. Note that the proportion of Cs at equilibrium is inversely proportional to the cost-to-benefit ratio.

For random group sizes, we have

$$\frac{\partial^2 h(x, n)}{\partial n^2} = b(1 - x)^{n-1} \ln(1 - x)[n \ln(1 - x) + 2], \tag{12}$$

which is less than zero if $n < \eta(x)$ and greater than zero if $n > \eta(x)$, with $\eta(x) = -2/\ln(1 - x)$. Figure 4 shows a plot of $\eta(x)$. Note that $\eta(x) \rightarrow \infty$ as $x \rightarrow 0$ and $\eta(x) \rightarrow 0$ as $x \rightarrow 1$. Thus, the domain of convexity of h in n decreases as $x \rightarrow 0$ and increases as $x \rightarrow 1$. Moreover, n_{\min} and n_{\max} determine values $x_R = 1 - e^{-2/n_{\min}}$ and $x_L = 1 - e^{-2/n_{\max}}$ such that h is concave in n for all $n \in [n_{\min}, n_{\max}]$ if $x < x_L$ and convex in n for all $n \in [n_{\min}, n_{\max}]$ if $x > x_R$. Hence, by Jensen’s inequality, $F(x, N) \leq f(x, \mu_N)$ for $x \leq x_L$ and $F(x, N) \geq f(x, \mu_N)$ for $x \geq x_R$. Intuitively, this should translate into more cooperation than in the constant group-size case for low cost-to-benefit ratios (where Cs are common at equilibrium) and less cooperation than in the constant group-size case for high cost-to-benefit ratios (where Cs are rare at equilibrium). This prediction is confirmed

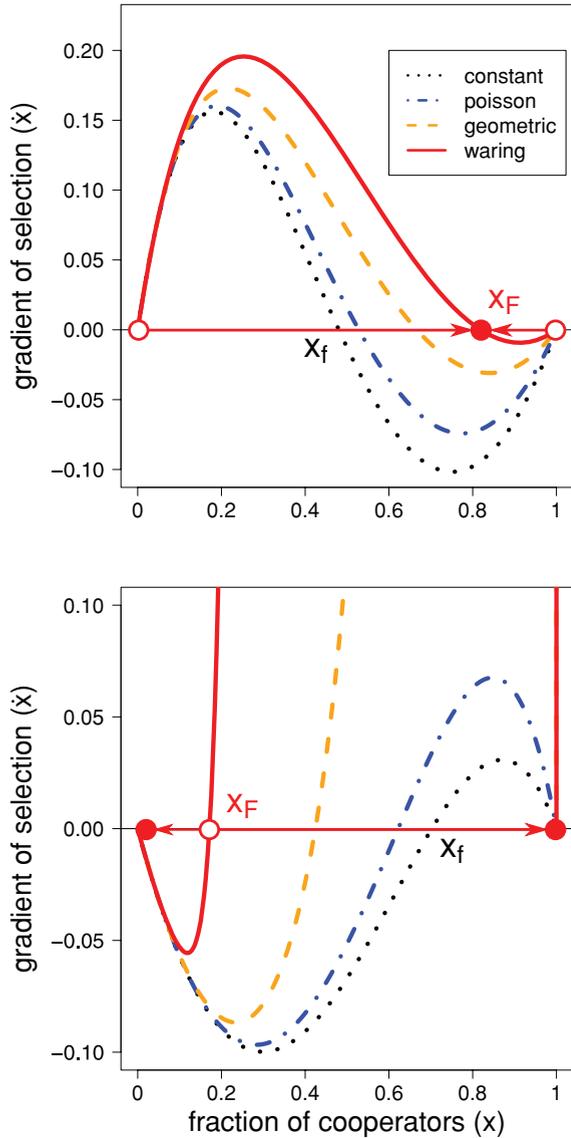


Figure 3. Effects of group-size diversity in the PGGDS. Top panel. Evolutionary dynamics for $w = 0.5$, $c = 1$, and $b = 15$ ($\gamma\mu_N = 1/3$). Coexistence: $x_F > x_f$. Bottom panel. Evolutionary dynamics for $w = 1.5$, $c = 1$, and $b = 1.5$ ($\gamma\mu_N = 10/3$). Bistability: $x_F < x_f$. Parameters: $n_{\min} = 2$, $n_{\max} = 100$, $\mu_N = 5$.

in Figure 5, which shows the stable equilibrium x_F for different group-size distributions with $\mu_N = 5$, $n_{\min} = 2$ and $n_{\max} = 100$, and the replicator dynamics for $\gamma = 1/20$ and $\gamma = 2/5$. It is clear from these results that group-size diversity favors cooperation up to a critical cost-to-benefit ratio γ^* , above which cooperation is disfavored. Note, however, that the effect of group-size diversity seems to be more pronounced when promoting than when hindering cooperation. The exact value of γ^* depends on the particular group-size distribution, but it can be well approximated (see Appendix 5) by

$$\gamma^* \approx e^{-2(\mu_N-1)/\mu_N},$$

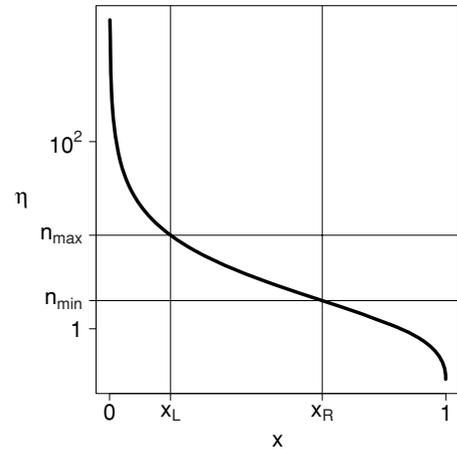


Figure 4. Plot of $\eta(x) = -2/\ln(1-x)$. Note that n_{\min} and n_{\max} determine values $x_R = 1 - e^{-2/n_{\min}}$ and $x_L = 1 - e^{-2/n_{\max}}$ such that $n < \eta(x)$ for all $n_{\min} < n < n_{\max}$ if $x < x_L$ and $n > \eta(x)$ for all $n_{\min} < n < n_{\max}$ if $x > x_R$. Note the logarithmic scale of the y-axis. Here, $n_{\min} = 2$ and $n_{\max} = 10$.

which leads to $\gamma^* \approx 0.2019$ for $\mu_N = 5$, in good agreement with the results shown in Figure 5.

Appendix 6 gives closed-form expressions for $F(x, N)$ in the limit when $n_{\max} \rightarrow \infty$. In this limit, and in the particular case of the geometric distribution, an analytical expression for x_F can also be derived (see eq. 16 in Appendix 6). Finally, and for general n_{\max} , $F(x, N)$ can also be approximated using equation (6) so that

$$F(x, N) \approx b(1-x)^{\mu_N-1} \times \left\{ 1 + \ln(1-x)[\mu_N \ln(1-x) + 2] \frac{\sigma_N^2}{2\mu_N} \right\} - c.$$

Discussion

The evolution of cooperation in sizable groups has been traditionally studied by investigating the evolutionary dynamics of the NPD and other PGGs under the assumption that the group size is constant. In the research presented in this article, I relaxed this assumption and showed that although group-size diversity leaves the linear NPD unaffected, it can lead to qualitative and quantitative changes in the evolutionary dynamics of more general, nonlinear PGGs.

I have shown that the replicator dynamics of nonlinear PGGs depend not only on the average group size but also on the variance of the group-size distribution and on the convexity of the function $h = nf(x, n)$ (see eq. 6). Indeed, the evolution of cooperation is promoted (hindered) with respect to the case of constant group sizes when h is convex (concave) in the group-size n , the more the larger the variance of the group-size distribution. In the PGGDS, h is always strictly convex and, consequently, group-size diversity systematically leads to dynamical scenarios more favorable to the evolution of cooperation than what is obtained under

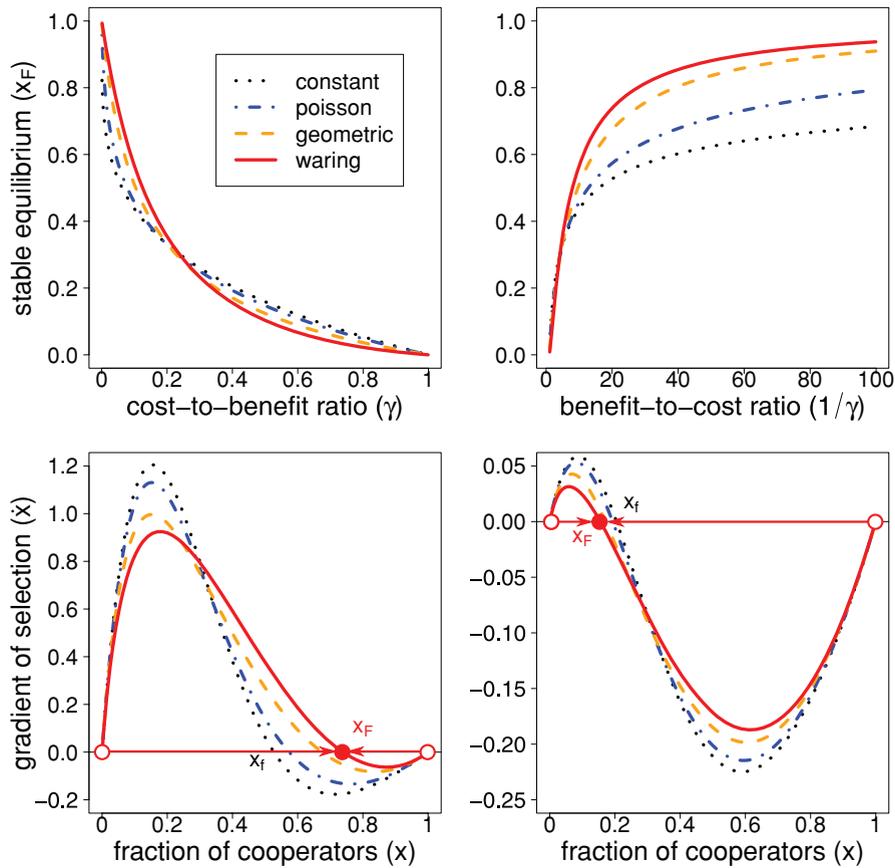


Figure 5. Effects of group-size diversity in the NVD dilemma. Stable equilibria shown as a function of the cost-to-benefit ratio $\gamma = c/b$ (top left) are also shown as a function of the benefit-to-cost ratio b/c (top right) to emphasize the promotion of cooperation for low values of γ . Bottom left. Evolutionary dynamics for $c = 1$ and $b = 20$ ($\gamma = 0.05$). Bottom right. Evolutionary dynamics for $c = 1$ and $b = 2.5$ ($\gamma = 0.4$). Parameters: $n_{\min} = 2$, $n_{\max} = 100$, $\mu_N = 5$.

the assumption of constant group sizes. Specifically, the introduction of variable group sizes enlarges the zones of the parameter space where the cooperative equilibrium is stable, increases the proportion of Cs at stable polymorphic equilibria when Cs and Ds coexist, and leads to larger basins of attraction of the cooperative equilibrium when the replicator dynamics is bistable. In the NVD, h is convex when Cs are common and concave when Cs are rare. As a result, group-size diversity can either promote or hinder cooperation with respect to the case where all groups are of the same size depending on the cost-to-benefit ratio: there is promotion for low cost-to-benefit ratios and hindering for high cost-to-benefit ratios. Overall, I have shown that the degree of cooperation in PGGs can be underestimated by focusing only on the average group size, especially if the group-size distribution is highly heterogeneous.

In the model presented here, the evolutionary dynamics of the NPD is independent of the level of group-size diversity. Consequently, cooperation cannot evolve in the NPD for any group-size distribution. This result, which can be shown to agree with results stemming from patch-structured models where group-size diver-

sity is endogenously determined (Lehmann et al. 2006; Alizon and Taylor 2008), contrasts with the results of other models of social evolution featuring variable group sizes where cooperation has been shown to be viable under the NPD (Hauert et al. 2002, 2006a; Santos et al. 2008). The reason behind such seeming discrepancy is to be found in the additional assumptions made in these works, which are not made in the model presented here: (1) fluctuating average group sizes resulting from voluntary participation (Hauert et al. 2002) or ecological feedback (Hauert et al. 2006a) that make the PGG to alternate between an NPD ($1 < r < \mu_N$) and a game with no conflict ($r > \mu_N$), and (2) assortment of strategies via network structure (Santos et al. 2008). Simply introducing variance in the group-size distribution does not make the average group size fluctuate over time nor introduces assortment; as a result, cooperation can not be made possible in the NPD by group-size diversity alone.

Contrastingly, group-size diversity can promote the evolution of cooperation with respect to the case where the group size is constant in nonlinear PGGs. This has been demonstrated here for the specific cases of the PGGDS (cooperation promoted for the

whole of the parameter space, except when $w = 1$ where the NPD is recovered) and the NVD (promotion of cooperation for low cost-to-benefit ratios). As mentioned above, the resulting promotion of cooperation does not derive from any kind of assortment, but solely from the interaction between the nonlinearity of public good functions and the variability of group sizes. Such interaction is nicely captured by Jensen's inequality, a somewhat counterintuitive result in probability theory stating that the average of a nonlinear function does not equal the function of the average. This is not the first time that a statistical phenomenon which is apparently paradoxical is associated with models of social evolution. Many readers will be familiar with Simpson's paradox (Simpson 1951; Blyth 1972; Bickel et al. 1975): the reversal of a correlation present in different groups when the groups are combined which has been often invoked to explain the evolution of cooperation (Sober and Wilson 1998; Hauert et al. 2002, 2006a; Chuang et al. 2009). In the model of nonlinear PGGs with variable group sizes studied here, both Simpson's paradox and Jensen's inequality are at work. Simpson's paradox manifests itself in the fact that, for both the PGGDS and the NVD, cooperation is disfavored in each mixed group ($P_C(i, n) - P_D(i, n) < 0$ for all n and all $0 < i < n$), but it can be favored globally ($f_C(x, n) > f_D(x, n)$ for at least some x) and hence evolutionarily viable. Jensen's inequality is brought about by the variation in group size and the nonlinearity of payoff functions, so that cooperation is promoted with respect to the constant case if $h = nf(x, n)$ is convex in n . Considered together, Simpson's paradox and Jensen's inequality help us understand mathematically the apparent paradox of the evolution of cooperation in variable group-structured populations of individuals facing social dilemmas.

For the sake of parsimony, I have based my analysis on the standard replicator dynamics, which relies on the assumption that the evolving population is of infinite size. Recent work on evolutionary game theory has suggested ways of taking into account the finite nature of real populations, replacing the deterministic replicator equation by frequency-dependent stochastic processes (Rousset and Billiard 2000; Nowak et al. 2004). Initially developed for studying two-person games, the theory has been extended to take into account multiplayer games as well (Kurokawa and Ihara 2009; Gokhale and Traulsen 2010). Preliminary results suggest that the effects of group-size diversity on the evolutionary dynamics of multiplayer games in finite populations can be studied in much the same way as it has been done here for the case of infinite populations, that is, by checking the convexity (in the group-size n) of functions of the form $h = nf(n)$, where f is a function ruling the dynamic behavior of the system. It is worth pointing out, however, that the effects of group-size diversity in finite populations can be sometimes qualitatively different from those arising in infinite populations. Further work along these lines is in progress.

In addition to studying finite populations, the work presented in this article can be extended in several ways. First, more general social dilemmas can be explored. In the case of the NVD, for instance, I limited myself to the case where one volunteer is sufficient for providing the public good. More generally, however, one can assume that the minimal number of volunteers required for providing the public good in a group of size n is any integer $1 \leq k \leq n$. For the extreme case where $k = n$ (mathematically equivalent to a weakest-link N -person stag hunt game [Hirshleifer 1983; Skyrms 2004; van Veelen and Nowak 2012]), one obtains the same results as for the case $k = 1$ analyzed here, up to the replacement $x \leftrightarrow 1 - x$. The resulting evolutionary dynamics is one characterized by bistability, with one internal unstable equilibrium standing between the basins of attraction of the two pure stable equilibria. As in the case $k = 1$, group-size diversity can be shown to promote (hinder) cooperation with respect to what is obtained when groups are of equal sizes for low (high) cost-to-benefit ratios. Indeed, the results for $k = n$ can be obtained from those shown in the top panels of Figure 4 for $k = 1$ by reinterpreting the y -axis as showing the size of the basin of attraction of the cooperative equilibrium. The cases with $1 < k < n$ are more difficult to analyze, as they can give rise to replicator dynamics with two internal equilibria, and should be addressed in future work.

Yet another possibility is to explore the effects of group-size diversity in games where cost functions are decreasing functions in the number of C s, as when the cost for providing the public good is assumed to be shared among C s. Also, augmenting the NPD with reciprocity, punishment or rewarding leads to nonlinear payoff functions and thus to evolutionary game dynamics susceptible of being influenced by group-size diversity. Finally, individual variation resulting from development or ecology can be modeled by letting costs and benefits be random variables with prescribed probability distributions. Such individual variation can be taken into account independently of or together with group-size variation and explored by making use of Jensen's inequality in a similar way as the one proposed in this article.

Recent theoretical and empirical research has suggested that nonlinear social dilemmas and heterogeneous group-size distributions are the rule rather than the exception in the organization of social and biological systems (Bonabeau et al. 1999; Archetti and Scheuring, in press). As demonstrated here, the simultaneous presence of nonlinearity and group-size variance greatly enrich the evolutionary dynamics of N -person games and open up unexpected opportunities for the evolution and maintenance of cooperation in biological and social systems.

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Appendix 1

SECOND-ORDER APPROXIMATION FOR $F(x, N)$

Expanding $h(x, n) = nf(x, n)$ as a Taylor series about $n = \mu_N$, we obtain

$$h(x, n) = \sum_{k=0}^{\infty} \frac{h^{(k)}(x, \mu_N)}{k!} (n - \mu_N)^k,$$

where $h^{(k)}(x, \mu_N)$ is the k th partial derivative of h in n evaluated at $n = \mu_N$. Writing this expression as a function of the random variable N , taking the expected value and dividing both sides by

μ_N , we obtain

$$\begin{aligned}
 F(x, N) &= \sum_{k=0}^{\infty} \frac{h^{(k)}(x, \mu_N) \mathbb{E}[(N - \mu_N)^k]}{\mu_N k!} \\
 &= f(x, \mu_N) + \frac{h^{(2)}(x, \mu_N) \mathbb{E}[(N - \mu_N)^2]}{2\mu_N} \\
 &\quad + \sum_{k=3}^{\infty} \frac{h^{(k)}(x, \mu_N) \mathbb{E}[(N - \mu_N)^k]}{\mu_N k!},
 \end{aligned}$$

which, assuming $\mathbb{E}[(N - \mu_N)^k]/(\mu_N k!) \approx 0$ for $k \geq 3$, gives equation (6) in the main text.

Appendix 2

GROUP-SIZE DISTRIBUTIONS

I assume that the group-size N is a random variable with support $n \in \{n_{\min}, n_{\min} + 1, \dots, n_{\max}\}$. The distribution of N is given by truncating a random variable K distributed according to a Poisson, geometric, or Waring distribution, so that

$$p_n = \Pr(N = n) = \frac{\phi_{n-n_{\min}}}{\sum_{n=n_{\min}}^{n_{\max}} \phi_{n-n_{\min}}},$$

with $\phi_k = \Pr(K = k)$. Table A1 shows the formulas for the probability mass function ϕ_k , the generating function $\sum_{k=0}^{\infty} \phi_k z^k$, the mean μ_K , the variance σ_K^2 , and the variance-to-mean ratio σ_K^2/μ_K , for different choices of the distribution of K . For the Waring distribution, I set $\rho = 2$ so that, for large k , the distribution approximates a power-law $\Pr(K = k) \propto k^{-\alpha}$ with exponent $\alpha = 3$. The free parameters (λ for the Poisson distribution, p for the geometric distribution, and a for the Waring distribution) are calculated to set the value μ_N . For finite n_{\max} , this means (numerically) solving the equation $\sum_n n p_n = \mu_N$. For $n_{\max} \rightarrow \infty$, we have $\mathbb{E}[N] = \mathbb{E}[K] + n_{\min}$ so that the free parameters can be easily set so that $\mu_K = \mu_N - n_{\min}$.

The functions $F(x, N)$ resulting from the two specific cases of nonlinear PGGs analyzed in this article depend on expressions of the form $\mathbb{E}[z^N]$ or $\mathbb{E}[Nz^N]$ (see eqs. 8 and 10). When $n_{\max} \rightarrow \infty$, $p_n = \phi_{n-n_{\min}}$, and we can write such expressions as

functions of the generating function of the variable K . Indeed

$$\mathbb{E}[z^N] = \sum_{n=n_{\min}}^{\infty} p_n z^n = \sum_{k=0}^{\infty} p_{k+n_{\min}} z^{k+n_{\min}} = z^{n_{\min}} \sum_{k=0}^{\infty} \phi_k z^k, \tag{A1}$$

and

$$\begin{aligned}
 \mathbb{E}[Nz^N] &= \sum_{n=n_{\min}}^{\infty} p_n n z^n \\
 &= \sum_{k=0}^{\infty} p_{k+n_{\min}} (k + n_{\min}) z^{k+n_{\min}} \\
 &= z^{n_{\min}} \left(\sum_{k=0}^{\infty} \phi_k k z^k + n_{\min} \sum_{k=0}^{\infty} \phi_k z^k \right) \\
 &= z^{n_{\min}} \left(z \frac{d}{dz} \sum_{k=0}^{\infty} \phi_k z^k + n_{\min} \sum_{k=0}^{\infty} \phi_k z^k \right). \tag{A2}
 \end{aligned}$$

I shall make use of equations (A1) and (A2) to write closed-form expressions for $F(x, N)$ for the PGGDS (Appendix 4) and the NVD (Appendix 6).

Appendix 3

DYNAMICAL SCENARIOS IN THE PGGDS

For the PGGDS, $f(x, n)$ is given by equation (7) and $F(x, N)$ by equation (8). Taking the derivative of $f(x, n)$ with respect to x , we obtain

$$\frac{\partial f(x, n)}{\partial x} = \frac{b(n-1)(w-1)[1-x+wx]^{n-2}}{n},$$

which, for $n > 1$, is equal to zero for $w = 1$, negative for $w < 1$ and positive for $w > 1$. Then, for a fixed value of w , $f(x, n)$ is a monotone function of x in $[0, 1]$. This means that $F(x, N) = \sum_n q_n f(x, n)$ is also a monotone function of x in $[0, 1]$, because $q_n \geq 0 \forall n$. Moreover, $F(0, N) = b/\mu_N - c$ and $F(1, N) = b\mathbb{E}[w^{N-1}]/\mu_N - c$. Therefore, the replicator dynamics given by equation (2) can have at most one fixed point x_F in $(0, 1)$, and this when $F(0, N)$ and $F(1, N)$ are of opposite sign. We thus have the following four scenarios:

1. $F(0, N) < 0$ and $F(1, N) < 0$. Hence, $F(x, N) < 0 \forall x$ (only $x_0 = 0$ is stable).

Table A1. Probability mass function (ϕ_k), generating function ($\sum_{k=0}^{\infty} \phi_k z^k$), mean (μ_K), variance (σ_K^2), variance-to-mean ratio (σ_K^2/μ_K), and parameters for the three choices of K used in this study. For the Waring distribution, $\Gamma(x)$ is the gamma function, and ${}_2F_1(a, b; c; z)$ is $\sum_{k=0}^{\infty} \frac{(a)_k (b)_k z^k}{(c)_k k!}$ is the Gauss hypergeometric function, where $(a)_k = a(a+1) \dots (a+k-1) = \Gamma(a+k)/\Gamma(a)$ is the Pochhammer symbol.

	ϕ_k	$\sum_{k=0}^{\infty} \phi_k z^k$	μ_K	σ_K^2	σ_K^2/μ_K	Parameters
Poisson	$\frac{\lambda^k e^{-\lambda}}{k!}$	$e^{\lambda(z-1)}$	λ	λ	1	$\lambda > 0$
Geometric	$(1-p)^k p$	$\frac{p}{1-(1-p)z}$	$\frac{1-p}{p}$	$\frac{1-p}{p^2}$	$\frac{1}{p} > 1$	$0 < p < 1$
Waring	$\frac{\rho \Gamma(\rho+a) \Gamma(k+a)}{\Gamma(a) \Gamma(k+\rho+a+1)}$	$\frac{\rho}{\rho+a} {}_2F_1(a, 1; \rho+a+1; z)$	$\frac{a}{\rho-1}$	∞	∞	$\rho > 0, a > 0$

2. $F(0, N) > 0$ and $F(1, N) < 0$. Hence, $F(x, N) > 0$ for $x < x_F$ and $F(x, N) < 0$ for $x > x_F$ ($x_0 = 0$ and $x_1 = 1$ are unstable; x_F exists and is stable).
3. $F(0, N) > 0$ and $F(1, N) > 0$. Hence, $F(x, N) > 0 \forall x$ (only $x_1 = 1$ is stable).
4. $F(0, N) < 0$ and $F(1, N) > 0$. Hence, $F(x, N) < 0$ for $x < x_F$ and $F(x, N) > 0$ for $x > x_F$ ($x_0 = 0$ and $x_1 = 1$ are stable; x_F exists and is unstable).

Defining γ , $\gamma_1 = 1/\mu_N$ and $\gamma_2 = \mathbb{E}[w^{N-1}]/\mu_N$, the scenarios given in the main text are recovered.

Appendix 4

CLOSED-FORM EXPRESSIONS FOR γ_2 AND $F(x, N)$ IN THE LIMIT $n_{\max} \rightarrow \infty$ (PGGDS)

Here, I calculate closed-form expressions for γ_2 and $F(x, N)$ in the limit $n_{\max} \rightarrow \infty$ for the PGGDS.

Poisson distribution

From equations (8), (9), (A1), and the expression for the generating function of the Poisson distribution (see Table A1), we obtain after little algebra

$$F(x, N) = \frac{b}{\mu_N} (1 - x + wx)^{n_{\min}-1} e^{\lambda(w-1)x} - c,$$

and

$$\gamma_2 = \frac{w^{n_{\min}-1}}{\mu_N} e^{\lambda(w-1)},$$

with $\lambda = \mu_N - n_{\min}$. The previous expressions are valid for all w , because the generating function of the Poisson distribution converges for all z .

Solving $F(x_F, N) = 0$, we obtain

$$x_F = \frac{(n_{\min} - 1)W\left(\frac{\lambda(\gamma\mu_N e^\lambda)^{1/(n_{\min}-1)}}{n_{\min} - 1}\right) - \lambda}{\lambda(w - 1)}, \quad (A3)$$

where W is the Lambert W -function, that is, the inverse function of $f(W) = We^W$.

Geometric distribution

We obtain

$$F(x, N) = \frac{bp(1 - x + wx)^{n_{\min}-1}}{\mu_N[1 - (1 - p)(1 - x + wx)]} - c,$$

and

$$\gamma_2 = \frac{pw^{n_{\min}-1}}{\mu_N[1 - (1 - p)w]},$$

with $p = 1/(\mu_N - n_{\min} + 1)$. These expressions are valid only for $w < 1/(1 - p)$, because the generating function of the geometric distribution converges only for $z < 1/(1 - p)$. For $n_{\min} = 2$,

$F(x_F, N) = 0$ can be solved analytically, yielding

$$x_F = \frac{p(1 - \gamma\mu_N)}{(1 - w)[p(1 - \gamma\mu_N) + \gamma\mu_N]}.$$

Waring distribution

We obtain

$$F(x, N) = \frac{2b(1 - x + wx)^{n_{\min}-1}}{\mu_N(a + 2)} {}_2F_1(a, 1; a + 3; 1 - x + wx) - c,$$

and

$$\gamma_2 = \frac{2w^{n_{\min}-1}}{\mu_N(a + 2)} {}_2F_1(a, 1; a + 3; w),$$

with $a = \mu_N - n_{\min}$. ${}_2F_1(a, b; c; z)$ is the Gauss hypergeometric function (see Table A1). The previous expressions are valid only for $w < 1$, because the generating function of the geometric distribution converges only for $z < 1$.

Appendix 5

AN APPROXIMATION FOR γ^* IN THE NVD

Let us define the critical value γ^* as the cost-to-benefit ratio such that $x_F = x_f$. The exact value of γ^* will depend on the particular group-size distribution. However, a useful approximation for γ^* can be found in the following way. From equations (6) and (12), we have that $F(x_F(\gamma^*), N) \approx f(x_f(\gamma^*), \mu_N)$, if

$$\frac{\partial^2 h(x_f, \mu_N)}{\partial n^2} = b(1 - x_f)^{\mu_N-1} [\mu_N \ln(1 - x_f) + 2] = 0.$$

Solving for x_f , we obtain $x_f(\gamma^*) \approx 1 - e^{-2/\mu_N}$. Finally, comparing this with equation (11) and solving for γ^* , we obtain the approximation given in the main text.

Appendix 6

CLOSED-FORM EXPRESSIONS FOR $F(x, N)$ IN THE LIMIT $n_{\max} \rightarrow \infty$ (NVD)

Here, I calculate closed-form expressions for $F(x, N)$ in the limit $n_{\max} \rightarrow \infty$ for the NVD.

Poisson distribution

From equations (10), (A2), and the expression for the generating function of the Poisson distribution (see Table A1), we obtain after little algebra

$$F(x, N) = \frac{b}{\mu_N} (1 - x)^{n_{\min}-1} e^{-\lambda x} [n_{\min} + \lambda(1 - x)] - c,$$

with $\lambda = \mu_N - n_{\min}$.

Geometric distribution

We obtain

$$F(x, N) = \frac{b}{\mu_N} \frac{(1-x)^{n_{\min}-1} p [n_{\min} - (n_{\min} - 1)(1-p)(1-x)]}{[1 - (1-p)(1-x)]^2} - c,$$

with $p = 1/(\mu_N - n_{\min} + 1)$. For $n_{\min} = 2$, $F(x_F, N) = 0$ can be solved analytically, yielding

$$x_F = \frac{1}{1-p} \left(\sqrt{\frac{p}{p + \gamma \mu_N (1-p)}} - p \right). \quad (\text{A4})$$

Waring distribution

We obtain

$$F(x, N) = \frac{b(1-x)^{n_{\min}-1}}{\mu_N} \frac{a(1-x)}{\rho + a + 1}^2 \times F_1(a + 1, 2; \rho + a + 2; 1-x) + \frac{b(1-x)^{n_{\min}-1}}{\mu_N} \frac{n_{\min} \rho}{\rho + a}^2 \times F_1(a, 1; \rho + a + 1; 1-x) - c,$$

with $a = \mu_N - n_{\min}$.