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Effects of group size and population size on the evolutionary stability of cooperation

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Evolutionary game theory has classically been developed under the implicit assumption of an infinite population. Exact analytical results for finite populations are rare, and those that exist apply to situations in which strategy sets are discrete. We rigorously analyse a standard model for the evolution of cooperation (the multi-player continuous-strategy snowdrift game) and show that in many situations in which there is a cooperative evolutionarily stable strategy (ESS) if the population is infinite, there is no cooperative ESS if the population is finite (no matter how large). In these cases, contributing nothing is a globally convergently stable finite-population ESS, implying that apparent evolution of cooperation in such games is an artefact of the infinite population approximation. The key issue is that if the size of groups that play the game exceeds a critical proportion of the population then the infinite-population approximation predicts the wrong evolutionary outcome (in addition, the critical proportion itself depends on the population size). Our results are robust to the underlying selection process.

1. Introduction

Many evolutionary games assume—for mathematical convenience—that populations are infinitely large (e.g.

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[1–7]). This assumption is sometimes justified on the grounds that '[p]opulations which stay numerically small quickly go extinct by chance fluctuations' [8, §2.1]. Of course, all real populations are finite, and important differences in evolutionary dynamics between finite and infinite populations have been demonstrated [9–15].

In spite of the technical challenges of working with finite populations, some exact analytical results have been obtained for games with discrete strategy sets [9,12,14–16], notably also in structured populations [17–24]. However, most existing finite-population results rely on approximate analytical methods and simulations [11,15,25–29]. For example, a diffusion approximation is often employed for its analytical convenience [1,27,30]; such approximations are useful, but have limitations (e.g. some real populations may be better-described using non-diffusive processes [31]).

Almost all existing finite-population results involve discrete strategy sets, such as when individuals must choose between making a fixed positive contribution to a public good, or nothing at all (e.g. [9,12,14–16]). Yet, many traits are better described on a continuum (e.g. allocation of time or effort to a communal task); consequently, evolutionary games involving continuous strategy sets are widely applicable, and they have been extensively studied using infinite-population models [32]. Moreover, to our knowledge, almost all existing results for finite populations assume a particular selection process—almost always the Moran process, and occasionally the Wright–Fisher process [33,34] (with few exceptions, e.g. [35,36]).

Here, we present mathematically rigorous results for finite-population evolutionary games with continuous strategy sets. We consider a standard model for exploring the evolution of cooperation—the continuous multi-player snowdrift game [3]—which has previously been studied in infinite populations using exact analysis and simulations [3,7,37–39] and in finite populations using approximations and simulations [11,29,40,41]. We focus on a subclass of the snowdrift game, which we refer to as the natural snowdrift game (NSG) because its definition excludes parameter regions that are not biologically sensible. For the NSG in finite populations, we characterize all evolutionarily stable strategies (ESSs) and expose the roles of group size and population size in determining the evolutionary stability of cooperation.

An important outcome of our analysis is that we rigorously identify critical differences in the predictions of evolutionary games in finite and infinite populations. The NSG always has at least one ESS, the non-cooperative (defection) ESS, regardless of whether the population is finite or infinite. When played in an infinite population, the NSG always has a second (cooperative) ESS [42], but we find conditions under which there is no cooperative ESS when it is played in finite populations. This qualitative difference in predictions for finite and infinite populations can occur no matter how large the finite population is, and is universal in the sense that it is independent of the selection process (a notion we clarify at the end of §2 and define rigorously in [43,44]). To our knowledge, there are no other examples in the literature of qualitatively different dynamics in finite and infinite populations that persist for arbitrarily large populations and are independent of the selection process; other studies that demonstrate such differences (e.g. [45]) are restricted to particular selection processes. Our results underline the need to model real populations as explicitly finite in size.

The results we present are supported by formal mathematical theorems, which we state in §3 and prove in §5 and appendices A and B.

2. Terminology

The *snowdrift game* is an abstraction of the situation in which a group of individuals encounters a snowdrift that blocks their path. We suppose that n players are drawn from a population of self-interested individuals (n is the *group size*), and that each player chooses how much to contribute to a public good—e.g. snow cleared off the path—from which all group members benefit. A focal individual contributing x incurs a cost C(x) that depends only on its own contribution, whereas

its benefit $B(\tau) \ge 0$ depends on the *total good* τ contributed by the group as a whole. The focal individual's *payoff*—which is interpreted as a change in fitness—is then

$$W(x, \tau) = B(\tau) - C(x).$$
 (2.1)

If *x* is a continuous variable, as we assume here, the game is said to be continuous. Positive contributions represent *cooperative strategies*, and individuals who contribute nothing are said to *defect*. If the population is finite and contains *N* individuals, then for convenience we refer to the ratio G = N/n as the *number of groups*; however, we *do not* assume that the population is simultaneously subdivided into groups of *n* individuals (and in particular, *G* need not be an integer).

To avoid mathematical complexities that are not relevant to the biological issues that concern us, and to ensure that the fitness function in equation (2.1) is biologically sensible, we impose a few natural conditions on the cost and benefit functions and refer to the *natural snowdrift game* (NSG; see §5a). The NSG was introduced in [42], where it was shown that—when played in infinite populations—the game always has a cooperative ESS. Cost, benefit and fitness functions for an NSG example are shown in figure 1.

Traditionally, an *evolutionarily stable strategy (ESS)* is one such that, when adopted by the entire population, a single mutant individual playing a different strategy cannot invade the population [46]. Because the phenotypic changes caused by mutations are often small, local ESSs are of particular interest: a population of individuals playing a *local ESS* is resistant to the invasion of a single individual playing a slightly different strategy. A strategy is *convergently stable* if a population playing a different strategy evolves toward it [47]; convergence can be either global or local.

In infinite populations, the theory of adaptive dynamics [2,8,48] identifies a *singular strategy* as one at which the selection gradient, $\partial_x W(x, x + (n - 1)X)|_{x=X}$, vanishes [49, table 1]; for an NSG, this reduces to

$$B'(nX) - 1 = 0. (2.2)$$

A singular strategy for which the mutant fitness is concave near the singular strategy is a local ESS.¹ Local convergent stability of singular strategies is also defined via a condition on the local fitness difference (see table 1 of [2]).

The definition of singular strategies can be extended to finite populations: the defining feature of a singular strategy is that when it is played by a resident population, directional selection (equation (A 4a)) vanishes²; for an NSG, this condition reduces to

$$\frac{N-n}{N-1}B'(nX) - 1 = 0.$$
(2.3)

The finite-population extension of the concept of evolutionary stability is more involved, because it must account for the fact that selection can favour fixation of a mutant strategy, even if selection opposes its invasion [9]. Thus, the standard definition of an evolutionary stable strategy in a finite population (ESS_N [9]) requires that selection oppose both invasion by, and fixation of, mutant strategies. In addition, the presence of one or more mutants in a finite population has a non-negligible effect on the fitness of residents (whereas finitely many mutants cannot affect the mean fitness of residents in an infinite population).

Fixation probabilities depend on the *selection process* [43], i.e. the stochastic process by which differences in fitnesses of individuals playing different strategies generate changes in the frequencies of strategies in the population over time.³ As a result, the strategies that are

¹We assume throughout this paper that the strategy space is one-dimensional.

 $^{^{2}}$ See definition 4.3.5 and appendix 4.C of [50] for a more general exposition of evolutionarily singular strategies, from which it follows that the derivative in equation (A 4a) must vanish.

³In [43], we rigorously define and study selection processes. These are Markov processes describing the evolution of populations in which there are two types of individuals, there are no mutations, and at any time, the number of individuals of the type that has a higher mean fitness is expected to increase. The Moran and Wright–Fisher processes are particular examples of selection processes.



Figure 1. Example cost, benefit and fitness functions for a natural snowdrift game (NSG, defined in §5a). (*a*) The cost function is simply C(x) = x. (*b*) The benefit function $B(\tau)$ is given in §5 equation (5.5); parameter values are L = 10, k = 1, m = 1.5, $\tau_{turn} = 15$. (*c*) Fitness is shown for three situations involving groups of n = 2 individuals. (i) Residents cooperate and contribute the ESS_N (light green, $X_{res} = 9.63$), (ii) Residents cooperate but contribute less than the ESS_N (medium green, $X_{res} = 5$). (iii) Residents defect, i.e. contribute nothing (dark green, $X_{res} = 0$). Resident strategies are indicated by dotted vertical lines in the same colour as the associated fitness function. In the case of defecting residents, a focal individual's fitness function does not depend on the group size (*n*) and has a local maximum at the maximizing total good ($\tau_{max} = 19.3$, thin grey vertical line).

evolutionarily stable in finite populations depend on the selection process. Variants of the Moran and Wright–Fisher processes [33,51,52] are commonly assumed, but are idealizations that do not exactly describe realistic populations (e.g. [31]). We are spared this complication in this paper because, for the games we consider, every ESS_N is a *universal* ESS_N [44, §5], that is, all ESS_N s are evolutionarily stable irrespective of the selection process [43]. Consequently, we need not specify the population-genetic processes underlying selection, and we obtain general results about evolutionary stability. We use the term *universal* more generally to indicate that a property or statement holds for any selection process.

3. Results

(a) ESSs in infinite populations

As we have previously shown [42], if an NSG (§5a) is played in an infinite population then there are always two (and only two) ESS:

defect: contribute nothing (x = 0), or *cooperate*: make a positive contribution that is inversely proportional to the group size n ($x = X_{\infty}^* > 0$).

Both ESSs are global, and both are locally convergently stable (theorem 4.1 of [42]). At the cooperative ESS, everyone contributes an equal share of the amount that maximizes individual fitness given that everyone contributes equally. In terms of this *maximizing total good* τ_{max} (see §5a and figure 1), the cooperative ESS is

$$X_{\infty}^{*} = \frac{\tau_{\max}}{n}.$$
(3.1)

(b) ESSs in finite populations

In a finite population, NSGs do not necessarily have a cooperative ESS_N , and when they do it is not necessarily possible to find an explicit formula for evolutionarily stable cooperation levels in terms of the parameters of an NSG (nevertheless, cooperative ESS_N s are always easy to find numerically within the interval (3.3) identified in the following theorem).

Theorem 3.1 (Existence and universality of stable cooperation levels in the natural snowdrift game). Consider a finite population (of N individuals) that is subject to selection resulting from groups of n individuals playing an NSG (defined in §5a). A strategy X is singular if and only if

$$B'(nX) = 1 + \frac{n-1}{N-n},$$
(3.2)

and any such strategy X lies in the open interval

$$\left(\frac{\tau_{\min}}{n}, \frac{\tau_{\max}}{n}\right), \tag{3.3}$$

(hence, from (3.1), $X < X_{\infty}^{*}$).

Necessary condition for ESS_N: Any cooperative ESS_N (X > 0) satisfies both equation (3.2) and

$$B^{\prime\prime}(nX) \le 0. \tag{3.4}$$

Sufficient condition for universal ESS_N : If X satisfies equation (3.2) and

$$B''(nX) < 0,$$
 (3.5)

then X is a universal ESS_N that is (universally) locally convergently stable.

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 X^*_{∞} and X^*_N



15

population size N

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ESS_Ns in large populations: If $B''(\tau_{max}) \neq 0$ and the group size n is either fixed, or satisfies $n(N)/N \xrightarrow{N \to \infty} 0$, then for any sufficiently large population size N, there is a universal ESS_N $X = X_N^*$ satisfying equation (3.5). Moreover, $X_N^* \to X_\infty^*$ as $N \to \infty$.

While the evolutionarily stable cooperation levels in finite and infinite populations are never exactly the same, theorem 3.1 shows that the difference is negligible in sufficiently large populations if as the population size $N \rightarrow \infty$, groups become a vanishingly small proportion of the population (cf. figure 2). However, if group size is not sufficiently small relative to the total population size then evolutionary predictions from finite population models differ qualitatively from the predictions for infinite ones: it may actually be impossible for cooperation to evolve at all. This is formalized in the next theorem.

Theorem 3.2 (ESS_Ns of the natural snowdrift game). Consider a finite population (of N individuals) that is subject to selection resulting from groups of n individuals playing an NSG (defined in §5a with fitness W defined by equation (5.2)). Let m denote the maximal marginal fitness, i.e.

$$m \equiv \max_{\tau \ge 0} \left(\frac{\partial W}{\partial x} \right) = \max_{\tau \ge 0} \left(B'(\tau) - 1 \right).$$
(3.6)

Then m > 0 and there is a **critical maximal marginal fitness** threshold,

$$m_{\rm c} = \frac{N-1}{N-n} - 1, \tag{3.7}$$

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such that⁴

$$m > m_{c} \implies \begin{cases} Generically, at least one cooperative local \\ ESS_{N} (X = X_{N}^{*} > 0) exists that is \\ universal and universally \\ locally convergently stable. \\ In addition, defection is (universally) \\ a locally convergently stable ESS_{N}. \end{cases}$$

$$m = m_{c} \implies \begin{cases} Generically, no cooperative ESS_{N} exists. \\ Defection is (universally) globally evolutionarily \\ stable and locally convergently stable. \end{cases}$$

$$and \quad m < m_{c} \implies \begin{cases} No cooperative ESS_{N} exists. \\ Defection is (universally) globally evolutionarily \\ stable and locally convergently stable. \end{cases}$$

$$(3.8a)$$

$$(3.8b)$$

$$(3.8b)$$

$$(3.8c)$$

This theorem predicts qualitatively different evolutionary outcomes, depending on the maximal marginal fitness (*m*): equation (3.7) gives the critical maximal marginal fitness above which a cooperative ESS_N exists, and below which defection is the only ESS_N . Theorem 3.2 thus connects the maximal marginal fitness—a property of the fitness function that relates investments in the communal task to fitness benefits—with properties of the population of interacting agents: the population size (*N*), the number of players in a group (*n*) and the number of groups (*G* = *N*/*n*).

Equation (3.7) expresses the critical maximal marginal fitness in terms of a given population size and given group size. To clarify the roles of group size and number of groups in the evolution of cooperation, it is useful to think instead of the maximal marginal fitness (*m*) as given (i.e. as a fixed property of the strategic interaction) and one of *n* or *G* as also fixed. Then, in the inequality $m > m_c$ (see (3.8*a*)), we can replace m_c by the expression on the right-hand size of equation (3.7), and solve for a critical number of groups (*G*_c) or critical group size (*n*_c).

(f) ESS conditions in relation to the number of groups (G) with group size (n) fixed

Condition (3.8a) can be expressed equivalently as

$$G > G_{\rm c} \equiv 1 + \frac{1}{m} \left(1 - \frac{1}{n} \right),$$
 (3.9)

i.e. the number of groups *G* must be greater than G_c , the minimum number of groups that are needed to support stable cooperation if the group size is *n*. For any given number of players in a group (*n*), if we multiply (3.9) by *n* we see that cooperation cannot evolve—i.e. no cooperative ESS_N exists—*unless* the population size is *greater than* a critical population size,⁵

$$N > N_{\min} \equiv n + \frac{n-1}{m}.$$
(3.10)

Figure 2 illustrates this result for the particular NSG specified by the benefit function shown in figure 1. Put another way, for a given group size n, if the population size N is too small then there is no cooperative ESS_N, but if N is sufficiently large then there is a (universal) cooperative ESS_N. For any given population size N, there are group sizes n and benefit functions $B(\tau)$ that yield $N_{\min} > N$, so a qualitative difference between the evolutionary outcomes in finite and infinite populations can occur for any population size N.

⁴In (3.8*a*), 'generically' means excluding the unlikely possibility of singular strategies also being inflection points of B(nX); in (3.8*b*), it excludes the possibility of the marginal benefit $B'(\tau)$ being constant in a neighbourhood of arg max $B'(\tau)$.

⁵Condition (c) in the definition of the NSG (§5a) implies that m > 0, so N_{\min} is always well defined in (3.10).

(g) ESS conditions in relation to group size (n) with the number groups (G) fixed

Rearranging condition (3.8*a*) again, we can write

$$n < n_{\rm c} \equiv \begin{cases} \frac{1}{1-m(G-1)} & \text{if } m < \frac{1}{(G-1)}, \\ \infty & \text{otherwise,} \end{cases}$$
(3.11)

i.e. for cooperation to evolve, the group size n must be less than n_c , the maximum size of groups that support cooperation in a population divided into G groups⁶. Multiplying (3.11) by G and rearranging, we obtain

$$N < N_{\max} \equiv \begin{cases} \frac{G}{1-m(G-1)} & \text{if } m < \frac{1}{(G-1)}, \\ \infty & \text{otherwise,} \end{cases}$$
(3.12)

i.e. if the number of groups is fixed (and smaller than 1 + 1/m) then in order for a cooperative ESS_N to exist, the population size must be *less than* the threshold in (3.12), as illustrated in figure 3.

(h) Lack of ESS_N for any population size

It is even possible that there is a cooperative ESS if the population is infinite, but no cooperative ESS_N for any finite population size N. This is easy to verify for an NSG as follows. As noted above, an NSG always has an infinite-population cooperative ESS (3.1). An ESS_N exists if and only if (3.8*a*) (or (3.11) or (3.9)) is satisfied. Rearranging inequality (3.9) (or equation (3.7)), we can write, equivalently,

$$m > m_{\rm c} \equiv \frac{1 - (G/N)}{G - 1},$$
 (3.13)

i.e. there is a cooperative ESS_N if and only if the maximum marginal fitness *m* exceeds the threshold m_c (exactly the same threshold that appears in equation (3.7), but expressed here in terms of *G* rather than *n*). Suppose now that the population is divided into a given number of groups, $G \ge 2$. There must be at least two individuals in each group, so $N \ge 2G$ and hence $G/N \le 1/2$. Consequently, for *any possible population size* N, we have

$$m_{\rm c} \ge \frac{1}{2(G-1)}.$$
 (3.14)

Therefore, there is a simple, sufficient condition that precludes evolutionary stability of cooperation for an NSG played in any finite population: if the benefit function is such that

$$m < \frac{1}{2(G-1)} \tag{3.15}$$

then no cooperative ESS_N exists, and defection is the only ESS_N , no matter how large the population size *N*. When the game defined by the same cost and benefit functions is played in an *infinite* population, defection remains an ESS, but in addition, there is also a cooperative ESS (regardless of the group size *n*).⁷ Given *G*, it is easy to satisfy (3.15) since the only other constraint on *m* is that it must be positive; for example, equation (5.5) below can be used to construct a benefit function satisfying (3.15).

Above, we have considered populations divided into a given number of groups. Alternatively, we could consider groups of a given size (n), and ask whether it is possible for a public goods game to have a cooperative ESS if the population is infinite but no cooperative ESS_N for any finite population size. As we show elsewhere, NSGs do not have this property, but there are snowdrift games that do have it [44].

⁶Note that n_c is always finite for a given population size, but when the number of groups *G* is fixed and larger than 1 + 1/m, then there is an ESS_N for any number of players *n*.

⁷Note, however, that the group size $n \to \infty$ as the number of groups $G \to \infty$, and while the cooperative equilibrium X_{∞}^* exists in the infinite population limit for any finite number of groups G, it tends to 0 as $G \to \infty$.



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Figure 3. ESSs in the NSG (§5a), with the sigmoidal benefit function $B(\tau)$ given in §5 equation (5.5); parameter values are L = 1000, k = 1, m = 0.05, $\tau_{turn} = 7$. For several numbers of groups (*G*), the infinite population ESS (X_{∞}^* , equation (3.1)) is shown as a black curve, and the finite population ESS_N (X_N^*) is shown with blue dots as a function of population size *N*. For each number of groups, the minimum population size considered is N = G + 1. The red vertical line segments indicate the critical population size threshold (N_{max} , (3.12)), *below* which a cooperative ESS_N exists (in contrast to the situation in which the group size *n* is fixed and an ESS_N exists only *above* a critical population size; cf. figure 2).

(i) Confirmation with both selection and mutation

Lastly, in figure 4 we complement our rigorous analyses with individual-based simulations of finite populations in which individuals undergo both selection and mutation (see §5b for details). Simulations such as these confirm that rigorous game-theoretical analyses—which are based on selection acting with only two types in the population—correctly predict evolutionary outcomes in realistic populations in which each individual can, in principle, be playing a different strategy.

4. Discussion

We have seen that the evolutionary dynamics of the class of natural snowdrift games (NSGs, defined in §5a) are different when played in finite versus infinite populations. Since all real populations are finite, it is important to understand how inferences based on infinite-population analyses of the multi-player snowdrift game (e.g. [3,42,53]) might be affected. More generally,



Figure 4. Individual-based simulations (details in §5b) of populations playing an NSG with cost and benefit functions as in figure 1 and group size n = 15, for population sizes N = 225 (red), 165 (black) and 120 (grey). The values of the additional parameters required to simulate using algorithm 1 (§5b) were nRep = 10, $nGen = 10^4$, $x_{max} = 6$, $\mu_x = 5.5$, $\sigma_x = 0.1$, $p_{mut} = 0.005$, $\sigma = 0.1$, l = -0.3, u = 0.3. The horizontal axis is the number of generations elapsed, and the vertical axis is the strategy (contribution level) of each individual in the population. The strategies present in the population in each generation are plotted on a vertical line intersecting the horizontal axis at the corresponding point. For N = 120, defecting is the unique, globally convergently stable ESS_N; for N > 155, a cooperative ESS_N X_N^* (B 21) is predicted, and specifically $X_{165}^* = 3.53$ and $X_{225}^* = 3.54$ (marked with a horizontal yellow line). The ESS for an infinite population playing this game is $X_{\infty}^* = 3.56$. In these simulations, the mutation rate is high enough—i.e. the probability p_{mut} is large enough—that populations contain more than two strategies at any given generation (in contrast to our rigorous mathematical analysis of dimorphic populations). Nonetheless, for population sizes N > 155, for which a cooperative ESS_N is predicted, we see evidence for its existence. With the width (σ) of the truncated Normal distribution of mutation effect sizes used here (cf. algorithm 1, §5b), the simulation with the largest population size (N = 225) would eventually leave the vicinity of the cooperative ESS_N and settle at the non-cooperative ESS_N. A narrower distribution of mutation step sizes (smaller σ) would increase the probability that any population with size N > 155 would remain in the basin of attraction of the cooperative ESS_N for a longer period.

under what circumstances are infinite-population analyses of the evolution of cooperation likely to lead to invalid inferences about real populations?

We have shown that there are situations in which cooperation in the snowdrift game can evolve in an infinite population but not in any finite population (no matter how large). This extreme possibility emphasizes that inferences drawn from infinite population analyses should be regarded cautiously when applied to groups that are relatively large compared with the population size. Other models may or may not have parameter regimes in which cooperation can evolve only if the population is infinite, but it is important to be aware of the possibility that the infinite-population approximation might predict incorrect evolutionary outcomes if the number of individuals playing the game (the group size, n) is substantial relative to the total population size (N). Exactly what 'substantial' means will depend on the game in question and the population size⁸; we have specified this threshold precisely for NSGs in (3.11). Evolutionary predictions derived from infinite population analyses can be incorrect for finite populations of any size (figure 2 and theorem 3.2). The origin of such erroneous inferences is that finite groups (no matter how large) are always negligible in size compared to an infinite underlying population, but not compared to a finite underlying population. This highlights the fact that, when evaluating

⁸In fact, to underscore the dependence of 'substantial' on the game, note that it is possible to construct snowdrift games for which 'substantial' can be any desired quantity. More precisely, for any given group and population sizes it is possible to choose quadratic cost and benefit functions (as used in, e.g. [3]) such that the infinite population approximation yields the wrong evolutionary outcome [44].

whether an infinite-population approximation is appropriate, it is important to consider whether and how the group size changes as the (finite) population size is increased.

Intuition for how different predictions arise in finite and infinite populations can be developed by considering a thought experiment in which the population (of size N) is simultaneously divided into G groups that play the game. If a single mutant invades the resident population, the probability that a randomly chosen group contains the mutant is 1/G. If the population size were then increased by adding more and more groups of the same size ($G \rightarrow \infty$, keeping *n* fixed), then the effect of the mutant on the residents would be 'infinitely diluted' (the mutant would have a negligible effect on residents' fitnesses as $N \to \infty$). This example is illustrative of a more general difference between well-mixed finite and infinite populations: it can be shown that in a well-mixed population containing both mutants and residents, on average, mutants interact with fewer mutants, and residents interact with more mutants in a finite population than in an infinite one. This difference between the environments experienced by—and thus payoff functions of residents in finite and infinite populations gives rise to the difference in evolutionary outcomes. If, instead, the population size were increased by adding individuals to the existing groups (without increasing the number of groups) then the probability that a randomly selected group contains the mutant would not change; however, in this version of the thought experiment, the limit $N \rightarrow \infty$ entails the size of each group also becoming infinitely large.

Adaptive dynamics, which has been extensively used in the study of evolutionary dynamics (e.g. [3,53,54], as well as [55] and references therein), relies on an infinite-population approximation [8]. Previous work has presented reasonable arguments to justify this approximation (e.g. [48]) and reported general agreement between adaptive dynamics and stochastic simulations of finite populations (see [56] for a review). In addition, specific agreement has been noted [15] between the finite- and infinite-population evolutionary dynamics of the multi-player snowdrift game with *discrete* strategies. These results appear to contrast with those presented here, though [15] did observe that defectors prevail when the group size approaches the population size (even in situations in which cooperators and defectors can coexist in an infinite population). In other work, there has been a focus on situations in which the group size is much smaller than the population size, which reduces the chance of discovering discrepancies between finite and infinite population evolutionary predictions.

Our analysis of the class of natural snowdrift games is rigorous (theorems 3.1 and 3.2), and our conditions for existence of a cooperative ESS_N are universal (in the sense of being entirely independent of the selection process [43]). These exact results for the finite-population NSG, together with exact results for the infinite-population NSG [42], make it easy to identify differences in predictions when the game is played in finite versus infinite populations. For the NSG, we have found that the infinite-population approximation yields the wrong evolutionary outcome for group sizes that are substantial relative to the population size. More broadly, our results indicate that approximating large populations by infinite ones (as in the classical adaptive dynamics framework [8]) has the potential to generate misleading conclusions. There is a general need to reevaluate the theoretical justification for approximating large populations by infinite ones, and to derive clear conditions for when such approximations are valid.

Finally, the recently introduced concept of the *Social Efficiency Deficit* (SED) [57,58] captures the 'opportunity cost' that an evolving population experiences, in comparison to what players could attain at the social optimum. Because evolutionary outcomes can differ between finite and infinite populations, an interesting direction for future inquiry would be to compare the different SEDs experienced in these two settings.

5. Methods

(a) The natural snowdrift game

This biologically motivated version of the continuous snowdrift game (§2) was introduced in [42].

We consider a population of individuals that are identical except (possibly) with respect to the strategy (contribution level) adopted when playing the snowdrift game. In particular, there is no age, spatial, social or other structure in the population. Evolution affects only the contribution levels of individuals, so at any time the population is completely characterized by the set of strategies present in the population and the numbers of individuals (or population proportions) playing each strategy. Fitnesses are determined entirely by payoffs from the continuous snowdrift game played in groups of *n* individuals. We say that this population plays a *natural snowdrift game* (NSG) if, in addition, the cost and benefit functions have the following properties (which are satisfied by the example shown in figure 1):

(a) The cost to the focal individual of a contribution *x* is measured in units of its impact on this individual's fitness, that is,

$$C(x) = x. \tag{5.1}$$

Thus, the focal individual's fitness is

$$W(x,\tau) = B(\tau) - x, \tag{5.2}$$

where τ is the total contribution in the focal individual's group.

- (b) The benefit $B(\tau)$ is a *smooth* function of the total contribution τ (more precisely, $B''(\tau)$ exists for all $\tau \ge 0$).
- (c) There exist total contribution levels τ_{\min} and τ_{\max} ($0 \le \tau_{\min} < \tau_{\max}$) such that $B(\tau) \tau$ decreases for $\tau < \tau_{\min}$ and $\tau > \tau_{\max}$ and increases for $\tau_{\min} < \tau < \tau_{\max}$. (See [42, 2] for the biological motivation for this assumption, the key aspect of which is that the marginal cost of an increase in contribution eventually outweighs its benefit.) Consequently, given condition (a), if only one member of a group contributes anything then that individual's fitness [take $x = \tau$ in equation (5.2)] is locally minimized (maximized) if its contribution is $x = \tau_{\min}(\tau_{\max})$.
- (d) There is a net fitness cost to an individual who contributes τ_{max} when all other group members contribute nothing,

$$B(\tau_{\max}) < C(\tau_{\max}),\tag{5.3}$$

but there is a net incremental fitness benefit for contributing τ_{max}/n if other group members contribute that amount,

$$B(\tau_{\max}) - B\left((n-1)\frac{\tau_{\max}}{n}\right) > C\left(\frac{\tau_{\max}}{n}\right).$$
(5.4)

In an infinite population, condition (c) implies that τ_{max}/n and 0 are the only local ESSs [42]. Adding condition (d) guarantees that they are both global ESSs (0 via (5.3) and τ_{max}/n via (5.4); see [42]).

(i) Benefit function used for numerical examples

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For the purpose of making example graphs and running simulations, we have used sigmoidal benefit functions. The biological motivation for this is that one would expect a nonlinear increase in the ease of passing the barrier as more snow is cleared, but eventually there can be no further benefit from additional work because all the snow has been cleared.

Specifically, for any integer k > 0 and real numbers m > 0, L > 0 and $\tau_{turn} \ge 0$, consider the benefit function

$$B(\tau) = L \operatorname{erf}_{2k}\left((m+1)\frac{\Gamma(1/(2k))}{2kL}(\tau - \tau_{\operatorname{turn}})\right), \quad \tau \ge 0,$$
(5.5)

where $\operatorname{erf}_{\ell}(x)$ is the generalized error function [59] of order ℓ ,

$$\operatorname{erf}_{\ell}(x) = \frac{\ell}{\Gamma(1/\ell)} \int_0^x e^{-t^{\ell}} dt, \qquad (5.6)$$

and $\Gamma(x)$ is the gamma function (equation (B 4*a*)). We analyse this flexible class of sigmoidal benefit functions in appendix B, where we show that the parameters *L* and τ_{turn} are the horizontal

asymptote and the inflection point, respectively, k controls the 'width' of the sigmoid⁹, and m + 1is the maximal marginal benefit (so that *m* is the maximal marginal fitness that results from this functional form, justifying our notation).

Figure 1 shows the benefit function (5.5) for particular values of k, m, L and τ_{turn} , together with the corresponding fitness function (5.2) that results if residents defect, or—in groups of two individuals—if residents play the infinite population ESS (equation (3.1)). Based on equation (5.5), in appendix B we derive explicit formulae for τ_{\min} , τ_{\max} , and X_{∞}^* and X_{N}^* (in terms of *m*, *L*, τ_{turn}) and k).

The class of sigmoids based on generalized error functions is much more flexible than the more common 'logistic' sigmoid used by Molina & Earn [42] and Cornforth et al. [53] (which is based on shifting, and horizontally and vertically stretching, the hyperbolic tangent function, tanh(x)). Whereas the maximum slope, horizontal asymptote and position of the inflection point uniquely determine the 'width' of a logistic sigmoid, the generalized error function allows the width to be set independently via the parameter k (see equation (B14)).

Individual-based simulations (b)

The three individual-based simulations shown in figure 4 (for population sizes N = 120 (grey), 165 (black) and 225 (red)) were run using algorithm 1 (§5b), which we implemented in an R [60] package. In the following description, we denote the normal distribution truncated to the interval (l, u) by TruncNormal (μ, σ, l, u) . It is assumed that values of the following parameters have been set:

- Parameters (k, m, L and τ_{turn}) of the benefit function (5.5).
- Group size (*n*) and population size (*N*), such that G = N/n is an integer.
- Number of repetitions of the NSG between reproductive events (*nRep*).
- Maximum number of generations to evolve (nGen).
- Upper bound for contribution level (x_{max}).
- Mean (μ_x) and standard deviation (σ_x) of an underlying Normal(μ_x, σ_x) distribution of strategies; the initial strategies $(x_i, i=1,...,N)$ are to be sampled from TruncNormal $(\mu_x, \sigma_x, 0, x_{\max})$.
- Mutation probability (p_{mut}) per individual per generation.
- Standard deviation (σ) of an underlying Normal (0, σ) distribution of the strategy changes caused by mutations, and upper and lower bounds on mutation sizes, (l, u); when an individual playing strategy x mutates, its new strategy is sampled from TruncNormal $(x, \sigma, \max\{0, x - l\}, \min\{x_{\max}, x + u\})$, so that the mutation is within the interval [*l*, *u*] and the mutated strategy is in $[0, x_{max}]$.

Data accessibility. Code used to produce the figures in this manuscript (in particular, the evolvr R package) is attached as ESM. The latest version of the evolvr R package can be found from the GitHub repository: https:// github.com/davidearn/evolvr [61]. Version 0.0.3 is provided in electronic supplementary material [62].

Declaration of Al use. We have not used AI-assisted technologies in creating this article.

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⁹More precisely, for a given maximal marginal fitness (m) and horizontal asymptote (L), k controls the distance between the benefit function's inflection point (τ_{turn}) and the total contribution at which the marginal benefit is half of its maximum.

Algorithm 1. Individual-based simulation algorithm.

1: $x_i \leftarrow \text{TruncNormal}(\mu_x, \sigma_x, 0, x_{\max}), i = 1, \dots, N$ ▷ randomly sample initial strategies 2: *iGen* \leftarrow 1 ⊳ generation counter 3: while *iGen* < *nGen* and not all x_i 's are identical **do** ▶ evolve to *nGen* or fixation 4: Compute fitnesses: 5: $W_i \leftarrow 0$, $i=1,\ldots,N$ ▷ initialize individual fitnesses **for** *iRep* \leftarrow 1 to *nRep* **do** ▶ estimate fitness from *nRep* interactions 6: 7: Permute (x_1, \ldots, x_N) \triangleright randomly assign individuals into groups of size *n* $\tau_j \leftarrow \sum_{k=1}^n x_{k+(j-1)n}, \quad j=1,\ldots,G$ \triangleright total contribution in group *j* 8: $W_i \leftarrow W_i + W(x_i, \tau_{\lceil i/n \rceil}), \quad i = 1, \dots, N$ 9: \triangleright individual fitness via (5.2), (5.5) 10: end for 11: $W_i \leftarrow W_i - \min\{W_i : 1 \le j \le N\} + 1$ ▷ shift fitnesses so minimum is 1 Selection by Wright-Fisher process: 12: $\tilde{x} \leftarrow \text{unique}(x)$ ▷ subset of unique strategies 13: $n_{\text{uniq}} \leftarrow \text{dimension}(\tilde{x})$ 14: ▶ number of unique strategies $\widetilde{W}_{\ell} \leftarrow \sum_{\{i: x_i = \tilde{x}_\ell\}} W_i,$ $\ell = 1, \ldots, n_{\text{uniq}}$ 15: total fitness of each unique strategy $\tilde{p}_{\ell} \leftarrow \widetilde{W}_{\ell} / \sum_{\ell=1}^{n_{\text{uniq}}} \widetilde{W}_{\ell},$ $\ell = 1, \ldots, n_{\text{uniq}}$ 16: normalized total fitness 17: $(N_1, \ldots, N_{n_{\text{uniq}}}) \leftarrow \text{Multinom}(N; \tilde{p}_1, \ldots, \tilde{p}_{n_{\text{uniq}}})$ ▷ how many \tilde{x}_{ℓ} in next generation $x \leftarrow (\underbrace{\tilde{x}_1, \dots, \tilde{x}_1}_{N_1 \text{ times}}, \underbrace{\tilde{x}_2, \dots, \tilde{x}_2}_{N_2 \text{ times}}, \dots, \underbrace{\tilde{x}_{n_{\text{uniq}}}, \dots, \tilde{x}_{n_{\text{uniq}}}}_{N_{n_{\text{uniq}}} \text{ times}})$ 18: ▷ new population 19: Mutation: 20: for i = 1 to N do 21: $u \leftarrow \text{Uniform}[0, 1]$ ▷ random uniform deviate 22: if $u < p_{mut}$ then \triangleright mutate with probability p_{mut} 23: $x_i \leftarrow \text{TruncNormal}(x_i, \sigma, \max\{0, x_i - l\}, \min\{x_{\max}, x_i + u\})$ ⊳ random shift end if 24: 25: end for 26: $iGen \leftarrow iGen + 1$ 27: end while

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Appendix A. Proofs

(a) Analysis of the natural snowdrift game (NSG, §5a) in a finite population

Our main results are stated in theorems 3.1 and 3.2 (§3). Before developing the proofs in detail, it is useful to note that:

- $\tau_{\min} > 0$ (where τ_{\min} is defined in assumption (c) of the definition of the NSG, §5a). To see this, suppose that $\tau_{\min} = 0$. Then assumption (c) implies that $B(\tau_{\max}) - \tau_{\max} \ge B(0) - 0 \ge 0$, so $B(\tau_{\max}) \ge \tau_{\max}$, contradicting assumption (d).
- The benefit function B(τ) is twice-differentiable [assumption (b) in the definition of the NSG (§5a)].
- $B'(\tau_{\min}) = B'(\tau_{\max}) = 1$, $B'(\tau) > 1$ for $\tau_{\min} < \tau < \tau_{\max}$, and $B'(\tau) \le 1$ otherwise [these properties of $B(\tau)$ follow from assumption (c)]. Consequently, m > 0 [cf. equation (3.6)] and $B''(\tau_{\max}) \le 0$.

(i) The mean fitness difference between mutants and residents

Consider a population of *N* individuals, comprised of M_p mutants who play *x* and $N - M_p$ residents who play *X*, and denote the proportion of mutants in the population by $\epsilon = M_p/N$. Suppose that groups of *n* individuals are randomly sampled from this population without replacement, which implies that the number of mutants in each such group is hypergeometrically distributed with parameters *N*, M_p and *n* [50,63]; thus, the probability that the number of mutants M_g in a randomly sampled group of *n* individuals is *k* is given by

$$\Pr(M_{g} = k) = \frac{\binom{N - M_{p}}{n - k}\binom{M_{p}}{k}}{\binom{N}{n}}.$$
(A 1)

Suppose, moreover, that a focal individual is selected from the population by first sampling a group of n individuals, and then selecting one of the members of this group. Lastly, suppose for simplicity that individual fitnesses are given by the payoffs from a single round of the NSG played in such randomly selected groups.¹⁰ We show elsewhere [50, eqn. 4.61, p. 137] that the expected difference between the mutant and resident fitnesses is then

$$\delta \overline{W}_{\epsilon}(x,X) = X - x + \sum_{k=0}^{n} \frac{\binom{N-M_{\rm p}}{n-k}\binom{M_{\rm p}}{k}}{\binom{N-1}{n-1}} \left(\frac{kN - M_{\rm p}n}{M_{\rm p}(N - M_{\rm p})}\right) B(kx + (n-k)X).$$
(A 2)

Differentiating equation (A 2) yields

$$\partial_{x}\delta\overline{W}_{\epsilon}(x,X) = -1 + \sum_{k=0}^{n} \frac{\binom{N-M_{p}}{n-k}\binom{M_{p}}{k}}{\binom{N-1}{n-1}} \frac{kN - M_{p}n}{M_{p}(N - M_{p})} kB'(kx + (n-k)X)$$
$$= -1 + \sum_{k=0}^{n} \frac{\binom{N-M_{p}}{n-k}\binom{M_{p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_{p}n}{N - M_{p}} B'(kx + (n-k)X),$$
(A 3)

and setting *x* = *X*, we find [50, pp. 137–138]

$$\partial_x \delta \overline{W}_{\epsilon}(x, X)|_{x=X} = -1 + \frac{N-n}{N-1} B'(nX). \tag{A4a}$$

Similarly, differentiating equation (A 2) with respect to *x* and setting x = X yields

$$\partial_x^2 \delta \overline{W}_{\epsilon}(x,X)|_{x=X} = \frac{N-n}{N-1} \left(\frac{N-2n}{N-2} + 2\frac{(n-1)}{N-2} N\epsilon \right) B''(nX). \tag{A4b}$$

From these expressions, we see that

$$- \partial_x \delta \overline{W}_{\epsilon}(x, X)|_{x=X} \text{ is independent of } \epsilon, \text{ and} - \partial_x^2 \delta \overline{W}_{\epsilon}(x, X)|_{x=X} \text{ is linear in } \epsilon.$$

We will exploit these facts below.

(ii) Evolutionary and convergent stability of defection

Lemma A.1 (Evolutionary stability of defection). *If the* NSG (§5*a*) *is played in a finite population then not contributing* (X = 0) *is a locally convergently stable* ESS_N *for any selection process. Moreover, if the population and group sizes are the same* (N = n, *so the entire population plays the game together) then defecting is the unique* ESS_N *and is globally evolutionarily and convergently stable.*

¹⁰Equation (A 2) remains valid if individual fitnesses are obtained by averaging payoffs from an arbitrary (either fixed or random) number of rounds of the NSG, as long as groups are selected independently in each round.

Proof. B'(0) < 1 because $B(\tau) - \tau$ decreases for $0 \le \tau < \tau_{\min}$, so using equation (A 4*a*),

$$\partial_x \delta \overline{W}_{\epsilon}(x,0)|_{x=0} = \frac{N-n}{N-1} B'(0) - 1 < 0.$$
(A5)

Because $\partial_x \delta \overline{W}_{\epsilon}(x, X)|_{x=X}$ is continuous in X, for X sufficiently small,

$$\partial_x \delta W_\epsilon(x, X)|_{x=X} < 0. \tag{A6}$$

From theorem 4.3.9 in [50], it follows that X = 0 (defection) is convergently stable, and selection opposes invasion of mutants contributing a sufficiently small but positive amount, x > 0. To establish that X = 0 is evolutionarily stable, observe that equation (A 5) implies that $\delta W_{\epsilon}(x, 0) < 0$ for sufficiently small x, so such mutants are selected against, regardless of their proportion (ϵ) in the population. Thus, corollary 5.4 of [43] implies that selection also opposes the fixation of such mutants.

Now suppose groups constitute the entire population, i.e. N = n. Then, for any resident strategy X > 0 and any number of mutants $M_p \in \{1, 2, ..., N - 1\}$, mutants contributing less than residents to the public good ($0 \le x < X$) have a higher payoff than residents; hence defection is the unique ESS_N and is globally convergently stable. Defection is also globally evolutionarily stable because for any mutant strategy x > 0 and any number of mutants ($M_p < N$), residents obtain a higher payoff than mutants (because they receive the same benefit without paying a cost).

(iii) Proof of theorem 3.1

Inserting equation (A 4a) into the definition of an evolutionarily singular strategy (definition 4.3.5 of [50]) implies that cooperative singular strategies are characterized by equation (3.2). Any solution of equation (3.2) must satisfy $nX_N^* \in (\tau_{\min}, \tau_{\max})$, because the right-hand side of equation (3.2) is greater than 1 and, as noted above, if $\tau \notin (\tau_{\min}, \tau_{\max})$ then $B'(\tau) \leq 1$.

Necessary condition for ESS_N: Suppose that X solves equation (3.2) but B''(nX) > 0. Plugging equation (3.2) into equation (A 4a) gives $\partial_x \delta W_{\epsilon}(x, X)|_{x=X} = 0$. Rearranging equation (A 4b), we have

$$\partial_x^2 \delta \overline{W}_{\epsilon}(x,X)|_{x=X} = \frac{N-n}{N-1} \left(1 + 2\frac{(n-1)}{N-2}(N\epsilon - 1) \right) B''(nX), \tag{A7}$$

so $\partial_x^2 \delta \overline{W}_{\epsilon}(x, X)|_{x=X}$ is increasing in ϵ and positive for any $\epsilon \ge 1/N$ (i.e. any mixed population). Thus, when mutants play x sufficiently close to X, $\partial_x \delta \overline{W}_{\epsilon}(x, X)|_{x=X}$ is negative for x < X and positive for x > X; hence, since $\delta \overline{W}_{\epsilon}(X, X) = 0$, we must have $\delta \overline{W}_{\epsilon}(x, X) > 0$ for any x that is near but not equal to X (and this is true for any number of mutants $M_p = 1, \ldots, N-1$). Corollary 5.4 of [43] then implies that selection favours the fixation of such mutants, so X is not an ESS_N , regardless of the selection process. Thus, if $X_N^* > 0$ is an ESS_N then it cannot be that B''(nX) > 0, i.e. (3.4) holds.

Sufficient condition for universal ESS_N : The sufficient condition for local universal evolutionary and convergent stability follows immediately from theorem 4.D.1 of [50] and equation (A4).

ESS_N**s in large populations:** Suppose that $B''(\tau_{max}) \neq 0$ and consider the equation

$$f(X, y) = B'(nX) - y = 0.$$
 (A8)

Noting that $f(\tau_{\max}/n, 1) = 0$ and that

$$\partial_X f(X, y)|_{(X, y) = (\tau_{\max}/n, 1)} = B''(\tau_{\max}) \neq 0,$$
 (A9)

from the implicit function theorem [64, Theorem 12.40], there exists a differentiable function X(y)defined in a neighbourhood of y = 1, such that $X(1) = \tau_{max}/n$ and

$$f(X(y), y) = yB'(nX(y)) - y = 0.$$
 (A 10)

Now suppose that the group size *n* is either fixed, or varies with population size but satisfies

$$\frac{n(N)}{N} \xrightarrow{N \to \infty} 0.$$

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If we define $y_N := 1 + (n-1)/(N-n)$ then $y_N \xrightarrow{N \to \infty} 1$, so for all sufficiently large population sizes N, equation (A 10) can be solved implicitly for $X_N^* := X(y_N)$. Such X_N^* then solve equation (3.2), and $X_N^* \xrightarrow{N \to \infty} X_\infty^*$ because X(y) is continuous. Recalling that $B''(\tau_{\max}) \le 0$ and $B''(\tau_{\max}) \ne 0$ by assumption, we have $B''(\tau_{\max}) < 0$, so for sufficiently large N, $B''(nX_N^*) < 0$. Theorem 4.D.1 of [50] then implies that for sufficiently large N, X_N^* is a universal local ESS_N and is locally convergently stable.

(iv) Proof of theorem 3.2

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First, note that X = 0 is always a locally convergently stable ESS_N (lemma A.1). From corollary 4.3.8 of [50], selection opposes invasion of a cooperative resident strategy X > 0 by sufficiently similar mutant strategies only if X is singular, which (using equation (A 4*a*)) occurs *iff* X satisfies

$$B'(nX) = 1 + \frac{n-1}{N-n}.$$
 (A 11)

Because B'(nX) > 1 only if $\tau_{\min}/n < X < \tau_{\max}/n$, if a cooperative ESS_N exists then it must lie in this interval.

Case $m > m_c$. Because $B'(\tau_{max}) = 1$ and B'(nX) is a continuous function of X on the interval $[\tau_{min}/n, \tau_{max}/n]$, it follows from the intermediate value theorem [64] that equation (3.2) has a solution in this interval. Let S be the set of singular strategies, i.e. solutions of equation (3.2),

$$S = \left\{ X \left| B'(nX) = 1 + \frac{n-1}{N-n} \right\}.$$
(A 12)

Note that from theorem 3.1, $S \subset (\tau_{\min}/n, \tau_{\max}/n)$. Denote the largest solution of equation (A 11) by X_N^* , i.e.

$$X_N^* = \max \mathcal{S} \tag{A13}$$

(this maximum exists because the continuity of B'(nX) on a closed interval implies $\sup S \in S$).

Generically,¹¹ $B''(nX_N^*) \neq 0$. We claim that $B''(nX_N^*) < 0$. To see this, suppose, in order to derive a contradiction, that $B''(nX_N^*) > 0$. Then, B'(nX) increases in a neighbourhood of X_N^* , so there exists \tilde{X} such that $X_N^* < \tilde{X} < \tau_{\max}/n$ and

$$B'(n\tilde{X}) > B'(nX_N^*) = 1 + \frac{n-1}{N-n}.$$
 (A 14)

From the intermediate value theorem, there exists $X \in S$ such that

$$X > \tilde{X} > X_N^* = \max \mathcal{S},\tag{A15}$$

a contradiction.

Thus $B''(nX_N^*) < 0$ and C''(X) = 0, so theorems 4.D.1 and 4.3.9 of [50] imply that X_N^* is a local ESS_N and is locally convergently stable.

Case $m = m_c$. Suppose, in order to derive a contradiction, that X > 0 is a cooperative ESS_N. From theorem 3.1, *X* must solve equation (A 11) so, from the definition of m_c in equation (3.7),

$$B'(nX) = \frac{N-1}{N-n} = m_{\rm c} + 1. \tag{A16}$$

Suppose further that $\arg \max B'(\tau)$ does not contain an interval (i.e. the marginal benefit B' is not maximal for an interval of total contributions τ), which happens

generically. Then, any total contribution in $\arg \max B'(\tau)$ is a local maximum of $B'(\tau)$. It follows that if x < X and x is sufficiently close to X, then

$$B'(x+(n-1)X) < \frac{N-1}{N-n},$$
 (A 17)

and therefore from equation (A 3),

$$\partial_{x}\delta\overline{W}_{\epsilon}(x,X) = -1 + \sum_{k=0}^{n} \frac{\binom{N-M_{p}}{n-k}\binom{M_{p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_{p}n}{N - M_{p}} B'(kx + (n-k)X)$$

$$< -1 + \left(\sum_{k=0}^{n} \frac{\binom{N-M_{p}}{n-k}\binom{M_{p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_{p}n}{N - M_{p}}\right) \frac{N-1}{N-n'},$$
(A 18)

which, together with the identity [50, eqn (4.63), p. 138],

$$\sum_{k=0}^{n} \frac{\binom{N-K}{n-k}\binom{K-1}{K-1}}{\binom{N-1}{n-1}} \left(\frac{kN-Kn}{N-K}\right) = \frac{N-n}{N-1},$$
(A 19)

implies that $\partial_x \delta \overline{W}_{\epsilon}(x, X) < 0$. Hence, similar to an argument in the proof of theorem 3.1, since $\delta \overline{W}_{\epsilon}(X, X) = 0$, we must have $\delta \overline{W}_{\epsilon}(x, X) > 0$ for any x < X sufficiently close to X (and this is true for any number of mutants $M_p = 1, ..., N - 1$). Consequently, selection favours the invasion and replacement of X by any such x, so X is not evolutionarily stable.

To see that defection is globally evolutionarily stable, substitute X = 0 in equation (A 3) to get

$$\partial_x \delta \overline{W}_{\epsilon}(x,0) = -1 + \sum_{k=0}^n \frac{\binom{N-M_{\rm p}}{n-k}\binom{M_{\rm p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_{\rm p}n}{N - M_{\rm p}} B'(kx).$$
(A 20)

Noting that for all x > 0, $B'(kx) \le m_c + 1$, we have

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$$\partial_{x}\delta\overline{W}_{\epsilon}(x,0) \leq -1 + \left(\sum_{k=0}^{n} \frac{\binom{N-M_{p}}{n-k}\binom{M_{p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN-M_{p}n}{N-M_{p}}\right)(m_{c}+1) = 0, \tag{A 21}$$

where we have used equations (3.7) and (A 19) in the last equality. Thus, $\delta W_{\epsilon}(x, 0)$ is non-decreasing in *x*. Moreover, if $x < \tau_{\min}/n$, then B'(kx) < 1 for all k = 0, ..., n, so similarly, equations (A 19) and (A 20) imply that $\partial_x \delta W_{\epsilon}(x, 0) < 0$. Because $\delta W_{\epsilon}(0, 0) = 0$, it follows that $\delta W_{\epsilon}(x, 0) < 0$ for all x > 0 (regardless of the proportion of mutants in the population). Thus, from [43, corollary 5.4], when residents defect, selection opposes invasion and fixation of any mutants.

Case $m < m_c$. In this case, equation (3.2) has no solution, and no cooperative ESS_N exists.

To see that defection (X = 0) is globally evolutionarily and convergently stable, observe first that $m < m_c$ implies

$$B'(\tau) < 1 + \frac{n-1}{N-n} = \frac{N-1}{N-n}, \text{ for all } \tau \ge 0.$$
 (A 22)

Then, using equations (A 3), (A 22) and equation (4.63) on p.138 of [50], it follows that

$$\partial_x \delta \overline{W}_{\epsilon}(x, X) < -1 + \left(\sum_{k=0}^n \frac{\binom{N-M_{\rm p}}{n-k} \binom{M_{\rm p}-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_{\rm p}n}{N-M_{\rm p}} \right) \frac{N-1}{N-n} = -1 + \left(\frac{N-n}{N-1} \right) \left(\frac{N-1}{N-n} \right) = 0,$$

so $\delta W_{\epsilon}(x, X)$ decreases with $x \ge 0$ for any $X \ge 0$. Thus, from [43, corollary 5.4], defection (X = 0) is a globally evolutionarily and convergently stable strategy.

Appendix B. Analysis of the benefit function used for numerical examples

In this appendix, we define the class of sigmoidal benefit functions that we have used to illustrate our results, and derive a variety of analytical formulae that we have found useful when working with these functions.

(a) Sigmoids using generalized error functions

For any integer k > 0 and real m > 0, L > 0 and $\tau_{turn} \ge 0$, consider the benefit function

$$B(\tau) = L \operatorname{erf}_{2k}\left((m+1)\frac{\Gamma(1/(2k))}{2kL}(\tau - \tau_{\operatorname{turn}})\right), \quad \tau \ge 0,$$
(B1)

where $\operatorname{erf}_{\ell}(x)$ is the generalized error function of order ℓ ,

$$\operatorname{erf}_{\ell}(x) = \frac{\ell}{\Gamma(1/\ell)} \int_0^x e^{-t^{\ell}} \mathrm{d}t.$$
 (B2)

This class of functions generalizes the error function, erf, which is recovered for $\ell = 2$ or, equivalently, k = 1; see §(b) below.

Expressing generalized error functions using gamma functions: It is sometimes convenient to express $\operatorname{erf}_{\ell}$ in terms of gamma functions. For x > 0, the transformation $z = t^{\ell}$ ($t = z^{1/\ell}$ and $dt = z^{1/(\ell-1)}dz/\ell$) gives

$$\operatorname{erf}_{\ell}(x) = \frac{1}{\Gamma(1/\ell)} \int_{0}^{x^{\ell}} z^{(1/\ell)-1} e^{-z} dz = \frac{1}{\Gamma(1/\ell)} \left(\Gamma\left(\frac{1}{\ell}\right) - \Gamma\left(\frac{1}{\ell}, x^{\ell}\right) \right), \tag{B3}$$

where

$$\Gamma(s) = \int_0^\infty t^{s-1} e^{-t} dt \tag{B4a}$$

and

$$\Gamma(s,x) = \int_{x}^{\infty} t^{s-1} e^{-t} dt, \qquad (B4b)$$

are the gamma,¹² and upper incomplete gamma functions, respectively. Note that we are only interested in generalized error functions of even order ($\ell = 2k$), which are odd functions of *x*.

Parameter meanings: Because equation (B3) implies

$$\lim_{x \to \infty} \operatorname{erf}_{\ell}(x) = 1, \tag{B5}$$

it follows that

$$\lim_{x \to \infty} B(x) = L. \tag{B6}$$

We show below that the inflection point of *B* (equation (B1)) is τ_{turn} , and that the maximal marginal fitness given the benefit function *B* is *m*.

From the integral definition of the generalized error function (equation (B2))

$$\frac{\operatorname{derf}_{\ell}(x)}{\operatorname{d}x} = \frac{\ell}{\Gamma(1/\ell)} e^{-x^{\ell}}$$
(B7*a*)

and

$$\frac{d^2 \mathrm{erf}_{\ell}(x)}{dx^2} = -\frac{\ell}{\Gamma(1/\ell)} \ell x^{\ell-1} \,\mathrm{e}^{-x^{\ell}},\tag{B7b}$$

¹²For any positive integer k, $\Gamma(k) = (k - 1)!$.

 $B'(\tau) = \frac{\sqrt{\pi}L}{\Gamma(2k)\Gamma(1/(2k))} (m+1) \frac{\Gamma(1/(2k))}{2kL} \frac{(2k)!}{\sqrt{\pi}}$ $\times \exp\left(-\left[(m+1)\frac{\Gamma(1/(2k))}{2kL}(\tau-\tau_{\text{turn}})\right]^{2k}\right)$ $= (m+1) \exp\left(-\left[(m+1)\frac{\Gamma(1/(2k))}{2kL}(\tau - \tau_{\text{turn}})\right]^{2k}\right),$ (B 8a) $B''(\tau) = -2k \left[(m+1) \frac{\Gamma(1/(2k))}{2kL} \right]^{2k} (\tau - \tau_{\rm turn})^{2k-1}$ $\times (m+1) \exp\left(-\left[(m+1)\frac{\Gamma(1/(2k))}{2kL}(\tau-\tau_{\rm turn})\right]^{2k}\right)$ $= -2k \left[(m+1) \frac{\Gamma(1/(2k))}{2kL} \right]^{2k} (\tau - \tau_{\rm turn})^{2k-1} B'(\tau).$ (B8b)

Consequently, τ_{turn} is the unique solution of $B''(\tau) = 0$, and is thus the only inflection point. $B'(\tau)$ is always positive, and hence $B(\tau)$ is monotonically increasing. However, $B''(\tau) > 0$ for $\tau < \tau_{turn}$ and $B''(\tau) < 0$ for $\tau > \tau_{turn}$, and hence

$$\max_{\tau \ge 0} B'(\tau) = B'(\tau_{\text{turn}}) = m + 1, \tag{B9}$$

so from equation (3.6), the maximal marginal fitness is

$$\max_{\tau \ge 0} \left(\frac{\partial W}{\partial x}\right) = \max_{\tau \ge 0} B'(\tau) - 1 = m.$$
(B10)

The minimizing and maximizing total goods: Since $B'(\tau)$ is monotonic on each of the intervals, $(-\infty, \tau_{turn})$ and (τ_{turn}, ∞) and $B'(\tau)$ is even, for any $b \in B'(\mathbb{R}_{>0}) = (0, m+1]$, we can find two real values of τ for which $B'(\tau) = b$ (although one of these values may be negative and therefore biologically irrelevant, because total contributions to the public good cannot be negative). To find these values of total contribution τ , we set $B'(\tau) = b$ in equation (B 8a), and get

$$\log \frac{m+1}{b} = \left[(m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\rm turn}) \right]^{2k}$$
(B11)

and

so

$$\tau = \tau_{\rm turn} \pm \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\frac{m+1}{b}}.$$
 (B12)

To find τ_{max} and τ_{min} , we substitute $b = B'(\tau) = 1$ in equation (B 12) and, noting that $B''(\tau)$ changes sign from positive to negative at τ_{turn} , we have

$$\tau_{\min} = \tau_{turn} - \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}$$
(B13a)

and

$$\tau_{\max} = \tau_{turn} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)},$$
(B13b)

and the distance between the location of the fitness minimum and maximum is

$$\Delta \tau = \tau_{\max} - \tau_{\min} = \frac{4kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}.$$
 (B14)

The infinite-population cooperative ESS: Equation (3.1) then gives

$$X_{\infty}^{*} = \frac{\tau_{\max}}{n} = \frac{1}{n} \left(\tau_{turn} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)} \right).$$
(B15)

Using $B'(\tau_{max}) = 1$ and equation (B 13*b*) in equation (B 8*b*), we have

$$B''(\tau_{\max}) = B''(nX_{\infty}^{*}) = -2k \left[\frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} (\tau_{\max} - \tau_{turn})^{2k-1}$$
$$= -2k \left[\frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} \left(\frac{2kL}{(m+1)\Gamma(1/(2k))} \right)^{2k-1}$$
$$\times (\log(m+1))^{(2k-1)/2k}$$
$$= -\Gamma\left(\frac{1}{2k}\right) \frac{m+1}{L} (\log(m+1))^{1-(1/2k)}.$$
(B16)

Using equation (B1) and the fact that erf_{2k} is odd,

$$B(\tau_{\max}) - B(\tau_{\min}) = 2L \operatorname{erf}_{2k} \left(\sqrt[2k]{\log(m+1)} \right).$$
 (B17)

Singular and evolutionarily stable cooperative strategies in finite populations: In a finite population of size *N*, a singular strategy X_N^* of the NSG is a solution of equation (3.2), that is,

$$B'(nX_N^*) = 1 + \frac{n-1}{N-n} = \frac{N-1}{N-n},$$
(B18)

so equation (B12) implies that at the ESS, the total contribution must be one of

$$\tau = \tau_{\rm turn} \pm \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)}.$$
 (B 19)

There are therefore two singular strategies,

$$X_{N\pm}^{*} = \frac{1}{n} \left(\tau_{\text{turn}} \pm \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)} \right).$$
(B 20)

Similarly to τ_{\min} and τ_{\max} , $B''(nX_{N+}^*) > 0$ and $B''(nX_{N-}^*) < 0$, so from theorem 3.1, the unique ESS_N is

$$X_N^* = \frac{1}{n} \left(\tau_{\text{turn}} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)} \right).$$
(B21)

The curvature of the benefit function at the ESS_N: Similar to equation (B16), we have

$$B''(nX_N^*) = -2k \left[\frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} (nX_N^* - \tau_{turn})^{2k-1} \frac{N-1}{N-n}$$
(B 22)
$$= -2k \left[\frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} \left(\frac{2kL}{(m+1)\Gamma(1/(2k))} \right)^{2k-1}$$
$$\times \left(\log\left((m+1)\frac{N-n}{N-1}\right) \right)^{(2k-1)/2k} \frac{N-1}{N-n}$$
$$= -(m+1)\frac{N-1}{N-n} \frac{\Gamma(1/(2k))}{L}$$
$$\times \left(\log\left((m+1)\frac{N-n}{N-1}\right) \right)^{(2k-1)/2k}.$$
(B 23)

Condition for the fitness difference having a minimum when a single mutant defects and residents play the ESS: To guarantee that when a single mutant invades a population playing the ESS, the fitness difference has both a minimum and a maximum (as a function of the mutant strategy), we need the mutant contribution that minimizes fitness to be positive; equivalently, the total contribution of the non-focal individuals—all of whom are residents—must be less than the minimizing total good τ_{min} . Thus,

$$\tau_{\min} - \frac{n-1}{n} \tau_{\max} > 0. \tag{B24}$$

Using equations (B 13*b*) and (B 14), this is equivalent to $\tau_{max} > n\Delta\tau$, or

$$n < \frac{\tau_{\max}}{\Delta \tau} = \frac{\tau_{turn}}{(4kL/(m+1)\Gamma(1/(2k))) \sqrt[2k]{\log(m+1)}} + \frac{1}{2}$$
$$= \tau_{turn} \frac{m+1}{4kL} \frac{\Gamma(1/(2k))}{\sqrt[2k]{\log(m+1)}} + \frac{1}{2}.$$
(B 25)

Rewriting this condition in terms of the horizontal asymptote L,

$$L < \frac{\tau_{\text{turn}}(m+1)}{2k(2n-1)} \frac{\Gamma(1/(2k))}{\sqrt[2k]{\log(m+1)}}.$$
 (B26)

The payoff extrema difference: We now calculate the payoff extrema difference (PED), $\Delta \Psi$, that is, the difference between a mutant's local minimum and maximum fitnesses when residents contribute the infinite-population ESS.

$$\Delta \Psi = \left[B(\tau_{\max}) - \frac{\tau_{\max}}{n} \right] - \left[B(\tau_{\min}) - \left(\tau_{\min} - \frac{n-1}{n} \tau_{\max} \right) \right]$$
$$= B(\tau_{\max}) - B(\tau_{\min}) - (\tau_{\max} - \tau_{\min})$$
$$= B(\tau_{\max}) - B(\tau_{\min}) - \Delta \tau, \qquad (B27)$$

so using equations (B14) and (B17), we have

$$\Delta \Psi = 2L \operatorname{erf}_{2k} \left(\sqrt[2k]{\log(m+1)} \right) - \frac{4kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}.$$
(B 28)

The mean fitness slope: To choose parameter values that generate a fitness difference with a distinct peak at the ESS (when residents play the ESS), we would like to find the mean fitness slope between the extrema, i.e. the ratio of the PED, $\Delta \Psi$, and the distance between the fitness extrema as a function of our parameters. To that end, using equation (B24), the distance between the fitness extrema is

$$\frac{\tau_{\max}}{n} - \left(\tau_{\min} - \frac{n-1}{n}\tau_{\max}\right) = \tau_{\max} - \tau_{\min} = \Delta\tau.$$
(B29)

Equations (B14) and (B28) then yield

$$\frac{\Delta\Psi}{\Delta\tau} = \frac{2L \operatorname{erf}_{2k} \left(\sqrt[2k]{\log(m+1)} \right)}{(4kL/(m+1)\Gamma(1/(2k))) \sqrt[2k]{\log(m+1)}} - 1$$
$$= (m+1)\frac{\Gamma(1/(2k))}{2k} \frac{\operatorname{erf}_{2k} \left(\sqrt[2k]{\log(m+1)} \right)}{\frac{2k}{\log(m+1)}} - 1, \tag{B 30}$$

which depends only on the maximal marginal fitness, m (and the order of the generalized error function, 2k). Note also that using equation (B2) and L'Hôpital's rule [64],

$$\lim_{x \to 0} \frac{\text{erf}_{\ell}(x)}{x} = \lim_{x \to 0} \frac{\ell}{\Gamma(1/\ell)} e^{-x^{\ell}} = \frac{\ell}{\Gamma(1/\ell)},$$
(B31)

$$\lim_{m \to 0} \frac{\Delta \Psi}{\Delta \tau} = 0. \tag{B32}$$

so

In addition, equation (B 3) implies that for any x > 0,

$$\lim_{\ell \to \infty} \operatorname{erf}_{\ell}(x) = 1, \tag{B33}$$

(because $\Gamma(x) \to \infty$ as $x \to 0$, and $\Gamma(1/\ell, x^{\ell})$ is bounded), and

$$\lim_{x \to 0} x \Gamma(x) = \lim_{x \to 0} \Gamma(x+1) = 1,$$
(B 34)

so we have

$$\lim_{k \to \infty} \frac{\Delta \Psi}{\Delta \tau} = m. \tag{B35}$$

The ratio of ESSs in infinite and finite populations: Using equations (B14), (B15) and (B21),

$$\frac{X_{\infty}^{*}}{X_{N}^{*}} = \frac{\tau_{\text{turn}} + (2kL/(m+1)\Gamma(1/(2k))) \sqrt[2k]{\log(m+1)}}{\tau_{\text{turn}} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)}}
= \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{(\log((m+1)((N-n)/(N-1)))/\log(m+1))}}
= \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{(\log((N-n)/(N-1))/\log(m+1))}}.$$
(B 36)

Rewriting the population size as N = nG,

$$\frac{X_{\infty}^*}{X_N^*} = \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{1 + \log((G-1)/(G-(1/n)))/\log(m+1)}}.$$
(B 37)

We see that the ratio $X_{\infty}^*/X_N^* \to 1$ as $G \to \infty$ with *n* fixed. However, X_{∞}^*/X_N^* approaches a (finite) value greater than 1 as $n \to \infty$ with *G* fixed (assuming X_N^* exist for all *N*; see (3.12)).

(b) Sigmoid using standard error-function

In the special case k = 1 (i.e. $\ell = 2$), since $\Gamma(1/2) = \sqrt{\pi}$, equation (B1) reduces to

$$B(\tau) = L \operatorname{erf}\left((m+1)\frac{\sqrt{\pi}}{2L}(\tau - \tau_{\operatorname{turn}})\right), \quad \tau \ge 0.$$
(B 38)

Then, setting k = 1 in equation (B 13) gives the maximizing and minimizing total goods,

$$\tau_{\min} = \tau_{\text{turn}} - \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}},\tag{B39a}$$

and

$$\tau_{\max} = \tau_{turn} + \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}},\tag{B39b}$$

and the distance between the location of the fitness minimum and maximum is

$$\Delta \tau = \tau_{\max} - \tau_{\min} = 4 \frac{L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}}.$$
 (B 40)

Equation (B15) then gives

$$X_{\infty}^{*} = \frac{1}{n} \left(\tau_{\text{turn}} + \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}} \right),$$
 (B41)

and equation (B16) becomes

$$B''(\tau_{\max}) = -\frac{m+1}{L} \sqrt{\pi \log(m+1)}.$$
 (B42)

From equation (B17),

$$B(\tau_{\max}) - B(\tau_{\min}) = 2L \operatorname{erf}\left(\sqrt{\log(m+1)}\right).$$
(B43)

Equation (B 21) gives the unique ESS_N :

$$X_N^* = \frac{1}{n} \left(\tau_{\text{turn}} + \frac{2L}{m+1} \sqrt{\frac{\log((m+1)((N-n)/(N-1)))}{\pi}} \right),$$
 (B44)

and equation (B 22) becomes

$$B''(nX_N^*) = -\frac{m+1}{L}\sqrt{\pi \log\left((m+1)\frac{N-n}{N-1}\right)}.$$
 (B45)

Condition (B 25), which guarantees that when a single mutant invades a population playing the ESS, the fitness difference has both a minimum and a maximum (as a function of the mutant strategy), reduces to

$$n < \frac{\tau_{\max}}{\Delta \tau} = \frac{\tau_{turn}}{4} \frac{m+1}{L} \sqrt{\frac{\pi}{\log(m+1)}} + \frac{1}{2},$$
 (B46)

the PED, $\Delta \Psi$ (equation (B 28)) becomes

$$\Delta \Psi = 2L \operatorname{erf}\left(\sqrt{\log(m+1)}\right) - 4\frac{L}{m+1}\sqrt{\frac{\log(m+1)}{\pi}},\tag{B47}$$

and the mean fitness slope (equation (B 30)) between the extrema reduces to

$$\frac{\Delta\Psi}{\Delta\tau} = \frac{m+1}{2}\sqrt{\frac{\pi}{\log(m+1)}}\operatorname{erf}\left(\sqrt{\log(m+1)}\right) - 1.$$
 (B48)

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