

# Instability of cooperation in finite populations

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## Abstract

Evolutionary game theory has been developed primarily under the implicit assumption of an infinite population. We rigorously analyze a standard model for the evolution of cooperation (the multi-player 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 artifact 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.

cooperation | public goods games | evolutionary game theory

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## 1 Introduction

Many evolutionary games assume—for mathematical convenience—that populations are infinitely large (*e.g.*, (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 two-player games with discrete strategy sets (9, 12, 14–16). However, most existing finite-population results rely on approximation methods and simulations (11, 15, 17–21). Notably, almost all 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, evolutionary games involving continuous strategy sets (*e.g.*, allocating time or effort to a communal task) are both widely applicable and extensively studied using infinite-population models (22). Moreover, to our knowledge, all existing results for finite populations depend on a choice of selection process (*e.g.*, Moran or Wright-Fisher (23, 24)).

Here, we present mathematically rigorous results that identify critical differences in the predictions of evolutionary games in finite and infinite populations. We focus on 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, 25–27) and in finite populations using approximations and simulations (11, 21, 28, 29).

We show that evolutionary outcomes in finite and infinite populations can be dramatically different. In particular, for a class of snowdrift games for which a cooperative ESS exists in infinite populations (30), we find conditions under which there is no cooperative ESS when 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 (31). 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.*, (32)) are restricted to particular selection processes.

The results we present are supported by formal mathematical theorems, which we state in [Results](#) and prove in [Methods](#) and [Supporting Information](#).

## 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  $B(\tau)$  depends on the **total good**  $\tau$  contributed by the group as a whole. The focal individual’s **payoff**—which is interpreted as a

62 change in fitness—is then

$$63 \quad W(x, \tau) = B(\tau) - C(x). \quad (1)$$

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

70 To avoid mathematical complexities that are not relevant to the biological issues that  
71 concern us, we impose a few natural conditions on the cost and benefit functions and refer  
72 to the **natural snowdrift game** (NSG; see [Methods §5.1](#)). The NSG was introduced in  
73 (30), where it was shown that—when played in infinite populations—the game always has  
74 a cooperative ESS. Cost, benefit and fitness functions for an NSG example are shown in  
75 figure 1.

76 Traditionally, an **evolutionarily stable strategy (ESS)** is one such that, when adopted  
77 by the entire population, a single mutant individual playing a different strategy cannot in-  
78 vade the population (33). Because the phenotypic changes caused by mutations are often  
79 small, local ESSs are of particular interest: a population of individuals playing a **local ESS**  
80 is resistant to the invasion of a single individual playing a slightly different strategy. A  
81 strategy is **convergently stable** if a population playing a different strategy evolves toward  
82 it (34); convergence can be either global or local.

83 In infinite populations, the theory of adaptive dynamics (2, 8, 35) identifies a **singular**  
84 **strategy** as one at which the selection gradient,  $\partial_x W(x, x + (n-1)X)|_{x=X}$ , vanishes (36,  
85 Table 1); for an NSG, this reduces to

$$86 \quad B'(nX) - 1 = 0. \quad (2)$$

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

91 The definition of singular strategies can be extended to finite populations: The defining  
92 feature of a singular strategy is that when it is played by a resident population, directional  
93 selection vanishes; for an NSG, this condition reduces to

$$94 \quad \frac{N-n}{N-1} B'(nX) - 1 = 0, \quad (3)$$

96 [see definition 4.3.5 of (37) and equation (28)]. The finite-population extension of the concept  
97 of evolutionary stability is more involved, because it must account for the fact that selection  
98 can favour fixation of a mutant strategy, even if selection opposes its invasion (9). Thus,  
99 the standard definition of an evolutionary stable strategy in a finite population (**ESS<sub>N</sub>**  
100 (9)) requires that selection oppose both invasion by, and fixation of, mutant strategies. In  
101 addition, the presence of one or more mutants in a finite population has a non-negligible  
102 effect on the fitness of residents (whereas finitely many mutants cannot affect the mean  
103 fitness of residents in an infinite population).

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

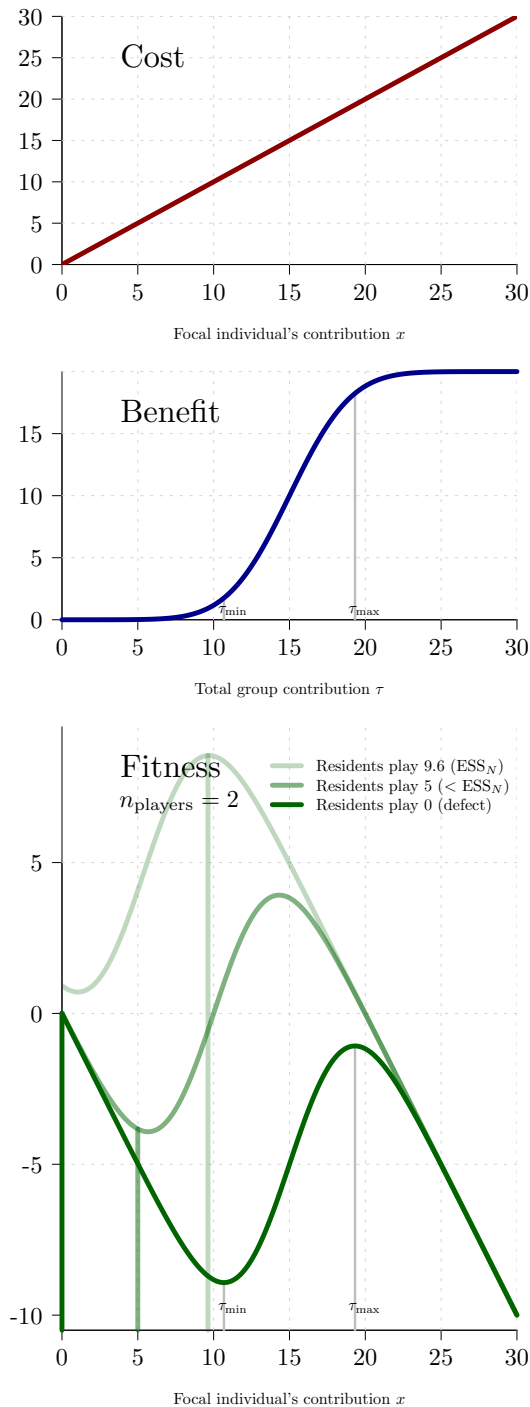


Figure 1: Example cost, benefit and fitness functions for a natural snowdrift game (NSG, defined in [Methods §5.1](#)). *Top panel:* The cost function is simply  $C(x) = x$ . *Middle panel:* The benefit function  $B(\tau)$  is given in [Methods](#) equation (23); parameter values are  $L = 10$ ,  $k = 1$ ,  $m = 1.5$ ,  $\tau_{\text{turn}} = 15$ . *Bottom panel:* Fitness is shown for three situations involving groups of  $n = 2$  individuals. (i) Residents cooperate and contribute the ESS<sub>N</sub> (light green,  $X_{\text{res}} = 9.63$ ) (ii) Residents cooperate but contribute less than the ESS<sub>N</sub> (medium green,  $X_{\text{res}} = 5$ ). (iii) Residents defect, *i.e.*, contribute nothing (dark green,  $X_{\text{res}} = 0$ ). Resident strategies are indicated by 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).

104 Fixation probabilities depend on the **selection process** (31), *i.e.*, the stochastic process  
105 by which differences in fitnesses of individuals playing different strategies generate changes in  
106 the frequencies of strategies in the population over time. As a result, the strategies that are  
107 evolutionarily stable in finite populations depend on the selection process. Variants of the  
108 Moran and Wright-Fisher processes (23, 38, 39) are commonly assumed, but are idealizations  
109 that do not exactly describe realistic populations (*e.g.*, (40)). We are spared this complication  
110 in this paper because, for the games we consider, every ESS is a **universal ESS**, that is, all  
111 ESSs are evolutionarily stable irrespective of the selection process. Consequently, we need  
112 not specify the population-genetic processes underlying selection, and we obtain general  
113 results about evolutionary stability. We use the term **universal** more generally to indicate  
114 that a property or statement holds for any selection process.

### 115 3 Results

116 **ESSs in infinite populations.** As we have previously shown (30), if an NSG (*Methods*  
117 *§5.1*) is played in an infinite population then there are always two (and only two) ESSs:

118 **defect:** contribute nothing ( $x = 0$ ), or

119 **cooperate:** make a positive contribution that is inversely proportional to the group size  
120  $n$  ( $x = X_{\infty}^* > 0$ ).

121 Both ESSs are global, and both are locally convergently stable [theorem 4.1 of (30)]. At  
122 the cooperative ESS, everyone contributes an equal share of the amount that maximizes  
123 individual fitness given that everyone contributes equally. In terms of this **maximizing**  
124 **total good**  $\tau_{\max}$  (see *Methods* §5.1 and figure 1), the cooperative ESS is

$$125 \quad X_{\infty}^* = \frac{\tau_{\max}}{n}. \quad (4)$$

126 **ESSs in finite populations.** In a finite population, NSGs do not necessarily have a coop-  
127 erative ESS<sub>N</sub>, and when they do it is not necessarily possible to find an explicit formula for  
128 evolutionarily stable cooperation levels in terms of the parameters of an NSG (nevertheless,  
129 cooperative ESS<sub>N</sub>s are always easy to find numerically within the interval (6) identified in  
130 the following theorem).

131 **Theorem 1** (Existence and universality of stable cooperation levels in the natural snowdrift  
132 game). *Consider a finite population (of  $N$  individuals) that is subject to selection resulting*  
133 *from groups of  $n$  individuals playing an NSG [defined in *Methods* §5.1]. A strategy  $X$  is*  
134 *singular if and only if*

$$135 \quad B'(nX) = 1 + \frac{n-1}{N-n}, \quad (5)$$

136 *and any such strategy  $X$  lies in the open interval*

$$137 \quad \left( \frac{\tau_{\min}}{n}, \frac{\tau_{\max}}{n} \right). \quad (6)$$

138 **Necessary condition for  $ESS_N$ :** Any cooperative  $ESS_N$  ( $X > 0$ ) satisfies both equa-  
 139 tion (5) (which implies  $X < X_\infty^*$ ) and

$$140 \quad B''(nX) \leq 0. \quad (7)$$

141 **Sufficient condition for universal  $ESS_N$ :** If  $X$  satisfies equation (5) and

$$142 \quad B''(nX) < 0, \quad (8)$$

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

144  **$ESS_N$ s in large populations:** If  $B''(\tau_{\max}) \neq 0$  and the group size  $n$  is either fixed, or  
 145 satisfies  $\frac{n(N)}{N} \xrightarrow{N \rightarrow \infty} 0$ , then for any sufficiently large population size  $N$ , there is a universal  
 146  $ESS_N$   $X = X_N^*$  satisfying inequality (8). Moreover,  $X_N^* \rightarrow X_\infty^*$  as  $N \rightarrow \infty$ .

147 While the evolutionarily stable cooperation levels in finite and infinite populations are never  
 148 exactly the same, theorem 1 shows that the difference is negligible in sufficiently large pop-  
 149 ulations if as the population size  $N \rightarrow \infty$ , groups become a vanishingly small proportion of  
 150 the population (cf. figure 2). However, if group size is not sufficiently small relative to the  
 151 total population size then evolutionary predictions from finite population models differ qual-  
 152 itatively from the predictions for infinite ones: it may actually be impossible for cooperation  
 153 to evolve at all. This is formalized in the next theorem.

154 **Theorem 2** ( $ESS_N$ s of the natural snowdrift game). Consider a finite population (of  $N$   
 155 individuals) that is subject to selection resulting from groups of  $n$  individuals playing an  
 156 NSG [defined in Methods §5.1 with fitness  $W$  defined by equation (20)]. Let  $m$  denote the  
 157 **maximal marginal fitness**, i.e.,

$$158 \quad m \equiv \max_{\tau \geq 0} \left( \frac{\partial W}{\partial x} \right) = \max_{\tau \geq 0} \left( B'(\tau) - 1 \right). \quad (9)$$

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

$$160 \quad m_c = \frac{N-1}{N-n} - 1, \quad (10)$$

such that<sup>†</sup>

$$m > m_c \quad \Longrightarrow \quad \begin{cases} \text{Generically, at least one cooperative local } ESS_N \text{ (} X = \\ X_N^* > 0 \text{) exists that is } \textit{universal} \text{ and universally locally} \\ \text{convergently stable. In addition, defection is (univer-} \\ \text{sally) a locally convergently stable } ESS_N. \end{cases} \quad (11a)$$

$$m = m_c \quad \Longrightarrow \quad \begin{cases} \text{Generically, no cooperative } ESS_N \text{ exists. Defection is} \\ \text{(universally) globally evolutionarily stable and locally} \\ \text{convergently stable.} \end{cases} \quad (11b)$$

$$m < m_c \quad \Longrightarrow \quad \begin{cases} \text{No cooperative } ESS_N \text{ exists. Defection is (universally)} \\ \text{globally evolutionarily and convergently stable.} \end{cases} \quad (11c)$$

<sup>†</sup>In (11a), “generically” means excluding the unlikely possibility of singular strategies also being inflection points of  $B(nx)$ ; in (11b), it excludes the possibility of the marginal benefit  $B'(\tau)$  being constant in a neighbourhood of  $\arg \max B'(\tau)$ .

161 This theorem predicts qualitatively different evolutionary outcomes, depending on the max-  
 162 imal marginal fitness ( $m$ ): Equation (10) gives the critical maximal marginal fitness above  
 163 which a cooperative ESS<sub>N</sub> exists, and below which defection is the only ESS<sub>N</sub>. Theorem 2  
 164 thus connects the maximal marginal fitness—a property of the fitness function that relates  
 165 investments in the communal task to fitness benefits—with properties of the population of  
 166 interacting agents: the population size ( $N$ ), the number of players in a group ( $n$ ), and the  
 167 number of groups ( $G = N/n$ ).

168 Equation (10) expresses the critical maximal marginal fitness in terms of a given popula-  
 169 tion size and given group size. To clarify the roles of group size and number of groups in the  
 170 evolution of cooperation, it is useful to think instead of the maximal marginal fitness ( $m$ ) as  
 171 given (*i.e.*, as a fixed property of the strategic interaction). Then, in the inequality  $m > m_c$   
 172 [see (11a)], we can replace  $m_c$  by the expression on the right hand side of Equation (10), and  
 173 solve for a critical number of groups ( $G_c$ ) or critical group size ( $n_c$ ).

174 **ESS conditions in relation to the number of groups ( $G$ ).** Condition (11a) can be  
 175 expressed equivalently as

$$176 \quad G > G_c \equiv \frac{m+1}{m+(1/N)} = 1 + \frac{1}{m} \left(1 - \frac{1}{n}\right), \quad (12)$$

177 *i.e.*, the number of groups  $G$  must be greater than  $G_c$ , the minimum number of groups that  
 178 support cooperation in a population of size  $N$  (or in groups of  $n$  players). For any given  
 179 number of players in a group ( $n$ ), if we multiply inequality (12) by  $n$  we see that cooperation  
 180 cannot evolve—*i.e.*, no cooperative ESS<sub>N</sub> exists—*unless* the population size is *greater than*  
 181 a critical population size<sup>‡</sup>,

$$182 \quad N > N_{\min} \equiv n + \frac{n-1}{m}. \quad (13)$$

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

190 **ESS conditions in relation to group size ( $n$ ).** Rearranging condition (11a) again, we  
 191 can write

$$192 \quad n < n_c \equiv \frac{mN+1}{m+1} = \begin{cases} \frac{1}{1-m(G-1)} & \text{if } m < 1/(G-1), \\ \infty & \text{otherwise.} \end{cases} \quad (14)$$

193 *i.e.*, for cooperation to evolve, the group size  $n$  must be less than  $n_c$ , the maximum size of  
 194 groups that support cooperation in a population of size  $N$  (or a population divided into  $G$

<sup>‡</sup>Condition (c) in the definition of the NSG (§5.1) implies that  $m > 0$ , so  $N_{\min}$  is always well-defined in (13).

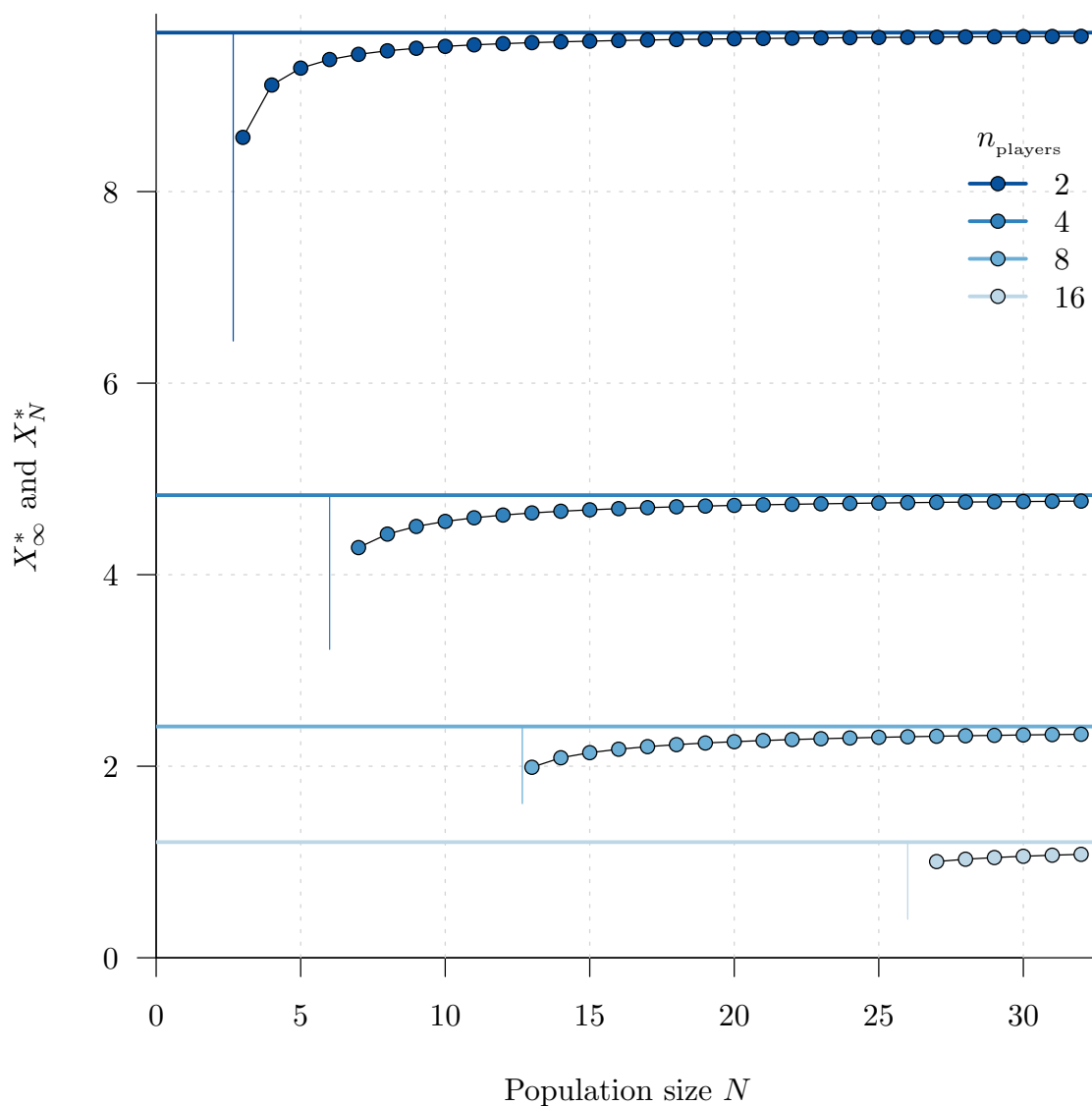


Figure 2: Evolutionarily stable strategies in the natural snowdrift game (*Methods* §5.1, with the sigmoidal benefit function shown in figure 1). For several group sizes ( $n$ ), the infinite population ESS ( $X_\infty^*$ , equation (4)) is shown as a horizontal line, and the finite population ESS ( $X_N^*$ ) is shown with dots as a function of population size  $N$ . The vertical line segments indicate the critical population size threshold ( $N_{\text{min}}$ , inequality (13)). A cooperative ESS $_N$  exists if and only if  $N > N_{\text{min}}$ .



195 groups<sup>§</sup>). Multiplying inequality (14) by  $G$  and rearranging, we obtain

$$196 \quad N < N_{\max} \equiv \begin{cases} \frac{G}{1-m(G-1)} & \text{if } m < 1/(G-1), \\ \infty & \text{otherwise,} \end{cases} \quad (15)$$

197 *i.e.*, if the number of groups is fixed (and smaller than  $1+1/m$ ) then in order for a cooperative  
198 ESS<sub>N</sub> to exist, the population size must be *less than* the threshold in inequality (15), as  
199 illustrated in figure 3.

200 **Lack of ESS<sub>N</sub> for any population size.** It is even possible that there is a cooperative  
201 ESS if the population is infinite, but no cooperative ESS<sub>N</sub> for any finite population size  
202  $N$ . This is easy to verify for an NSG as follows. As noted above, an NSG always has an  
203 infinite-population cooperative ESS (4). An ESS<sub>N</sub> exists if and only if inequality (11a) [or  
204 inequality (14) or inequality (12)] is satisfied. Rearranging inequality (12) [or equation (10)],  
205 we can write, equivalently,

$$206 \quad m > m_c \equiv \frac{1 - (G/N)}{G - 1}, \quad (16)$$

207 *i.e.*, there is a cooperative ESS<sub>N</sub> if and only if the maximum marginal fitness  $m$  exceeds  
208 the threshold  $m_c$  (exactly the same threshold that appears in equation (10), but expressed  
209 here in terms of  $G$  rather than  $n$ ). Suppose now that the population is divided into a given  
210 number of groups,  $G \geq 2$ . There must be at least two individuals in each group, so  $N \geq 2G$   
211 and hence  $G/N \leq 1/2$ . Consequently, for *any possible population size*  $N$ , we have

$$212 \quad m_c \geq \frac{1}{2(G-1)}. \quad (17)$$

213 Therefore, if the benefit function is such that

$$214 \quad m < \frac{1}{2(G-1)} \quad (18)$$

215 then no cooperative ESS<sub>N</sub> exists, no matter how large the population size  $N$ . Yet, when the  
216 game defined by the same cost and benefit functions is played in an *infinite* population, a  
217 cooperative ESS exists (regardless of the group size  $n$ ). Given  $G$ , in the example of the NSG  
218 defined using equation (23), it is easy to satisfy inequality (18) since the only constraint on  
219  $m$  is that it must be positive.

220 Above, we have considered populations divided into a given number of groups. Alter-  
221 natively, we could consider groups of a given size ( $n$ ), and ask whether it is possible for a  
222 public goods game to have a cooperative ESS if the population is infinite but no cooperative  
223 ESS<sub>N</sub> for any finite population size. As we show elsewhere, NSGs do not have this property,  
224 but there are snowdrift games that *do* have it (41).

225 **Confirmation with both selection and mutation.** Lastly, in figure 4 we complement  
226 our rigorous analyses with individual-based simulations of finite populations in which indi-  
227 viduals undergo both selection and mutation (see appendix 5.2 for details). Simulations such

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<sup>§</sup>Note 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<sub>N</sub> for any number of players  $n$ .

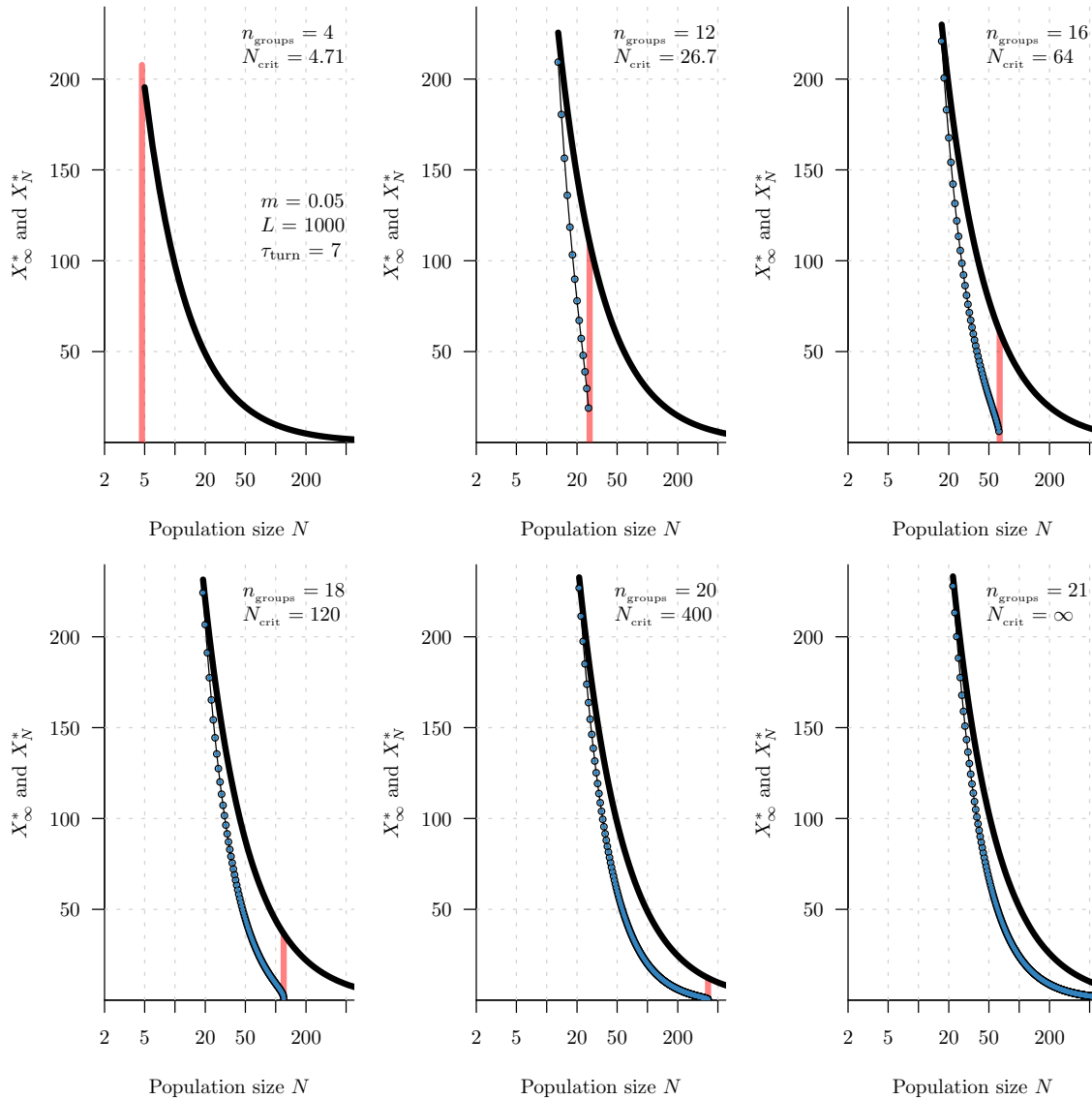


Figure 3: Evolutionarily stable strategies in the natural snowdrift game ([Methods §5.1](#)), with the sigmoidal benefit function  $B(\tau)$  given in [Methods](#) equation (23); parameter values are  $L = 1000$ ,  $k = 1$ ,  $m = 0.05$ ,  $\tau_{\text{turn}} = 7$ . For several numbers of groups ( $G$ ), the infinite population ESS ( $X_{\infty}^*$ , equation (4)) is shown as a curve, and the finite population ESS ( $X_N^*$ ) is shown with dots as a function of population size  $N$ . For each number of groups, the minimum population considered is  $N = G + 1$ . The vertical line segments indicate the critical population size threshold ( $N_{\text{max}}$ , inequality (15)), below which a cooperative ESS<sub>N</sub> exists (in contrast to the situation in which the group size  $n$  is fixed and an ESS<sub>N</sub> exists only above a critical population size; *cf.* figure 2).

228 as these confirm that rigorous game-theoretical analyses—which are based on selection acting  
229 with only two types in the population—correctly predict evolutionary outcomes in realistic  
230 populations in which each individual can, in principle, be playing a different strategy.

## 231 4 Discussion

232 We have seen that the evolutionary dynamics of the class of natural snowdrift games (NSGs,  
233 defined in [Methods §5.1](#)) are different when played in finite *vs.* infinite populations. Since all  
234 real populations are finite, it is important to understand how inferences based on infinite-  
235 population analyses of the multi-player snowdrift game (*e.g.*, ([3](#), [30](#), [42](#))) might be affected.  
236 More generally, under what circumstances are infinite-population analyses of the evolution  
237 of cooperation likely to lead to invalid inferences about real populations?

238 We have shown that there are games for which it is *possible* that cooperation can evolve in  
239 an infinite population but not in any finite population (no matter how large). This extreme  
240 possibility emphasizes that inferences drawn from infinite population analyses should always  
241 be regarded cautiously.

242 The infinite-population approximation is *likely* to predict incorrect evolutionary outcomes  
243 if the number of individuals playing the game (the group size,  $n$ ) is substantial relative to  
244 the total population size ( $N$ ). Exactly what “substantial” means will depend on the game  
245 in question and the population size; we have specified this threshold precisely for NSGs in  
246 inequality ([14](#)). Evolutionary predictions derived from infinite population analyses can be  
247 incorrect for finite populations of any size (figure [2](#) and theorem [2](#)). The origin of such  
248 erroneous inferences is that finite groups (no matter how large) are always negligible in  
249 size compared to an infinite underlying population, but not compared to a finite underlying  
250 population.

251 Intuition for how different predictions arise in finite and infinite populations can be  
252 developed by considering a thought experiment in which the population (of size  $N$ ) is *si-*  
253 *multaneously* divided into  $G$  groups that play the game. If a single mutant invades the  
254 resident population, the probability that a randomly chosen group contains the mutant is  
255  $1/G$ . If the population size were then increased by adding more and more groups of the  
256 same size ( $G \rightarrow \infty$ , keeping  $n$  fixed), then the effect of the mutant on the residents would  
257 be “infinitely diluted” (the mutant would have a negligible effect on residents’ fitnesses as  
258  $N \rightarrow \infty$ ). If, instead, the population size were increased by adding individuals to the  
259 existing groups (without increasing the number of groups) then the probability that a ran-  
260 domly selected group contains the mutant would not change; however, in this version of the  
261 thought experiment, the limit  $N \rightarrow \infty$  entails the size of each group also becoming infinitely  
262 large.

263 Adaptive dynamics, which has been extensively used in the study of evolutionary dynam-  
264 ics [*e.g.*, ([3](#), [42](#), [43](#)), as well as ([44](#)) and references therein], relies on an infinite-population  
265 approximation ([8](#)). Previous work has presented reasonable arguments to justify this ap-  
266 proximation (*e.g.*, ([35](#))) and reported general agreement between adaptive dynamics and  
267 stochastic simulations of finite populations (see ([45](#)) for a review). In addition, specific  
268 agreement has been noted ([15](#)) between the finite- and infinite-population evolutionary dy-  
269 namics of the multi-player snowdrift game with *discrete* strategies. These results appear to  
270 contrast those presented here, though ([15](#)) did observe that defectors prevail when the group

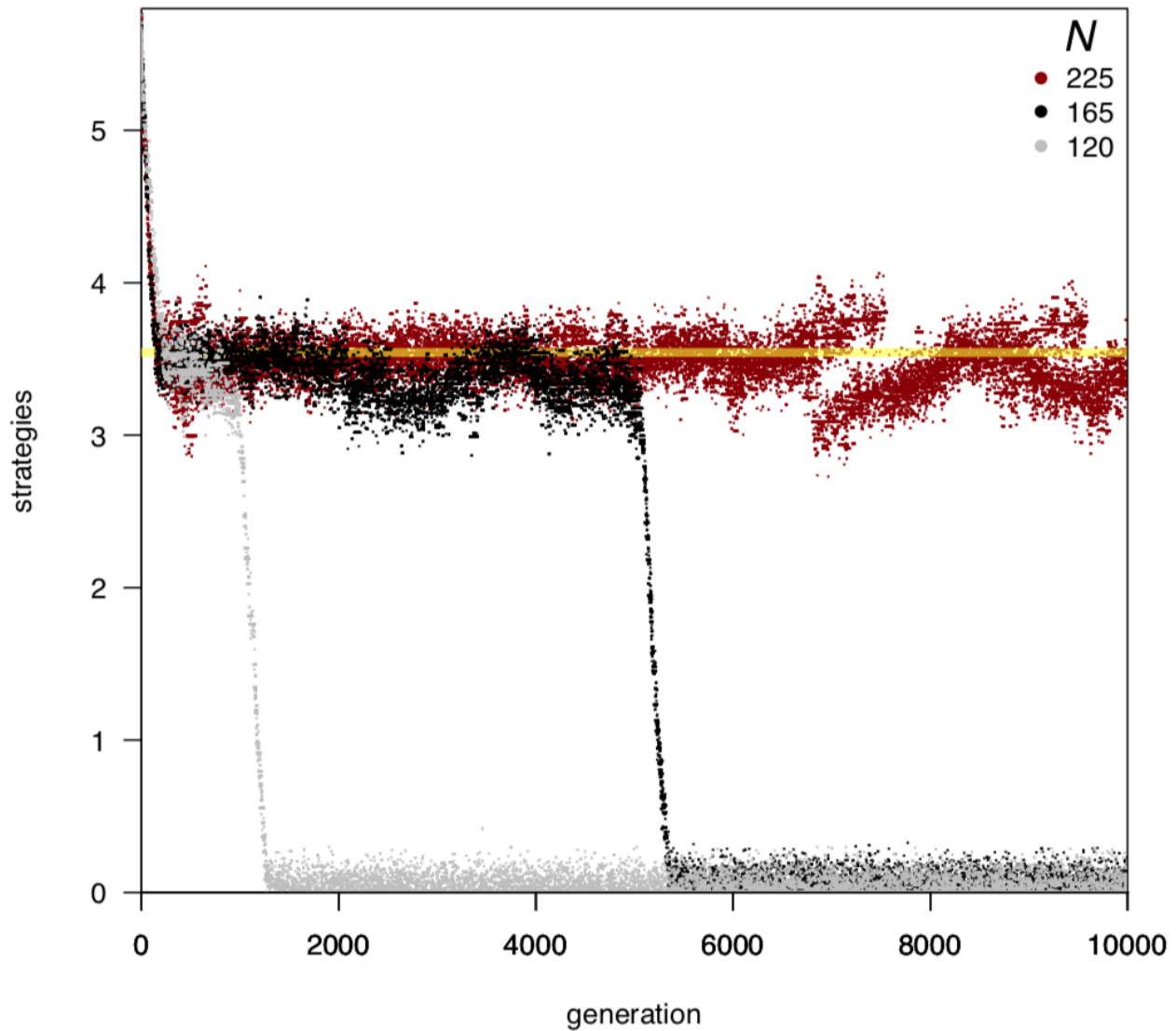


Figure 4: Individual-based simulations (details in appendix 5.2) of populations playing an NSG with cost and benefit functions as in figure 1 and group size  $n = 15$ , for population sizes  $N = 225$  (red), 165 (black) and 120 (grey). The horizontal axis is the number of generations elapsed, and the 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  $\text{ESS}_N$ ; for  $N > 155$ , a cooperative  $\text{ESS}_N$  is predicted at  $X^* = 3.54$  (marked with a horizontal yellow line). The ESS for an infinite population playing this game is  $X_\infty^* = 3.56$ . Note in these simulations, the mutation rate is high enough that populations contain more than two strategies at any given generation (in contrast to our rigorous mathematical analysis of dimorphic populations).

271 size approaches the population size (even in situations in which cooperators and defectors  
272 can coexist in an infinite population). In other work, there has been a focus on situations in  
273 which the group size is much smaller than the population size, which reduces the chance of  
274 discovering discrepancies between finite and infinite population evolutionary predictions.

275 Our analysis of the class of natural snowdrift games is rigorous (theorems 1 and 2), and  
276 our conditions for existence of a cooperative  $\text{ESS}_N$  are **universal** (in the sense of being en-  
277 tirely independent of the selection process). Broadly, our results indicate that approximating  
278 large populations by infinite ones may generate misleading conclusions. In particular, infer-  
279 ences based on adaptive dynamics are not necessarily applicable to real (finite) populations.  
280 There is a general need to reevaluate the theoretical justification for approximating large  
281 populations by infinite ones, and to derive clear conditions for when such approximations  
282 are useful.

## 283 5 Methods

### 284 5.1 The natural snowdrift game (NSG)

285 This biologically motivated version of the **continuous snowdrift game** (§2) was introduced  
286 in (30). We consider a population of individuals that are identical except (possibly) with  
287 respect to the strategy (contribution level) adopted when playing the snowdrift game. In  
288 particular, there is no age, spatial, social or other structure in the population. Evolution  
289 affects only the contribution levels of individuals, so at any time the population is completely  
290 characterized by the set of strategies present in the population and the numbers of individuals  
291 (or population proportions) playing each strategy. An individual's fitness is determined  
292 entirely by its payoff from the continuous snowdrift game played in groups of  $n$  individuals.  
293 We say that this population plays a **natural snowdrift game** (NSG) if, in addition, the  
294 cost and benefit functions have the following properties (which are satisfied by the example  
295 shown in figure 1):

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

$$298 \qquad C(x) = x. \qquad (19)$$

299 Thus, the focal individual's fitness is

$$300 \qquad W(x, \tau) = B(\tau) - x, \qquad (20)$$

301 where  $\tau$  is the total contribution in the focal individual's group.

- 302 (b) The benefit  $B(\tau)$  is a *smooth* function of the total contribution  $\tau$  (more precisely,  $B''(\tau)$   
303 exists for all  $\tau \geq 0$ ).

- 304 (c) There exist total contribution levels  $\tau_{\min}$  and  $\tau_{\max}$  ( $0 \leq \tau_{\min} < \tau_{\max}$ ) such that  $B(\tau) - \tau$   
305 decreases for  $\tau < \tau_{\min}$  and  $\tau > \tau_{\max}$  and increases for  $\tau_{\min} < \tau < \tau_{\max}$ . Consequently,  
306 given condition (a), if only one member of a group contributes anything then that  
307 individual's fitness [take  $x = \tau$  in equation (20)] is locally minimized (maximized) if  
308 its contribution is  $x = \tau_{\min}$  ( $\tau_{\max}$ ).

309 (d) There is a net fitness cost to an individual who contributes  $\tau_{\max}$  when all other  
 310 group members contribute nothing,

$$B(\tau_{\max}) < C(\tau_{\max}), \quad (21)$$

311 but there is a net incremental fitness benefit for contributing  $\tau_{\max}/n$  if other group  
 312 members contribute that amount,

$$313 \quad B(\tau_{\max}) - B\left((n-1)\frac{\tau_{\max}}{n}\right) > C\left(\frac{\tau_{\max}}{n}\right). \quad (22)$$

314  
 315 In an infinite population, condition (c) implies that  $\tau_{\max}/n$  and 0 are the only local  
 316 ESSs (30). Adding condition (d) guarantees that they are both global ESSs [0 via and  
 317 condition (21) and  $\tau_{\max}/n$  via condition (22); see (30)].

### 318 5.1.1 Benefit function used for numerical examples

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

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

$$325 \quad B(\tau) = L \operatorname{erf}_{2k} \left( (m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}}) \right), \quad \tau \geq 0, \quad (23)$$

326 where  $\operatorname{erf}_{\ell}(x)$  is the generalized error function (46) of order  $\ell$ ,

$$327 \quad \operatorname{erf}_{\ell}(x) = \frac{\ell}{\Gamma(1/\ell)} \int_0^x e^{-t^{\ell}} dt, \quad (24)$$

328 and  $\Gamma(x)$  is the gamma function [equation (50a)]. We analyze this flexible class of sigmoidal  
 329 benefit functions in appendix B, where we show that the parameters  $L$  and  $\tau_{\text{turn}}$  are the  
 330 horizontal asymptote and the inflection point, respectively,  $k$  controls the “width” of the  
 331 sigmoid<sup>¶</sup>, and  $m+1$  is the maximal marginal benefit (so that  $m$  is the maximal marginal  
 332 fitness that results from this functional form, justifying our notation).

333 Figure 1 shows the benefit function (23) for particular values of  $k$ ,  $m$ ,  $L$  and  $\tau_{\text{turn}}$ , together  
 334 with the corresponding fitness function (20) that results if residents defect, or—in groups  
 335 of two individuals—if residents play the infinite population ESS [equation (4)]. Based on  
 336 equation (23), in appendix B we derive explicit formulae for  $\tau_{\min}$ ,  $\tau_{\max}$ , and  $X_{\infty}^*$  and  $X_N^*$  (in  
 337 terms of  $m$ ,  $L$ ,  $\tau_{\text{turn}}$  and  $k$ ).

338 The class of sigmoids based on generalized error functions is much more flexible than  
 339 the more common “logistic” sigmoid used by (30, 42) (which is based on shifting, and hor-  
 340 izontally and vertically stretching, the hyperbolic tangent function,  $\tanh(x)$ ). Whereas the  
 341 maximum slope, horizontal asymptote and position of the inflection point uniquely deter-  
 342 mine the “width” of a logistic sigmoid, the generalized error function allows the width to be  
 343 set independently via the parameter  $k$  [see equation (60)].

<sup>¶</sup>More precisely, for a given maximal marginal fitness ( $m$ ) and horizontal asymptote ( $L$ ),  $k$  controls the distance between the benefit function’s inflection point ( $\tau_{\text{turn}}$ ) and the total contribution at which the marginal benefit is half of its maximum.

## 344 5.2 Individual-based simulations

345 The three individual-based simulations shown in figure 4 [for population sizes  $N = 120$   
346 (grey), 165 (black) and 250 (red)] were run using algorithm 1, which we implemented in an  
347 R (47) package. In the following description, we denote the normal distribution truncated  
348 to the interval  $(l, u)$  by `TruncNormal` $(\mu, \sigma, l, u)$ . It is assumed that values of the following  
349 parameters have been set:

- 350 • Parameters  $(k, m, L$  and  $\tau_{\text{turn}}$ ) of the benefit function (23).
- 351 • Group size  $(n)$  and population size  $(N)$ , such that  $G = N/n$  is an integer.
- 352 • Number of repetitions of the NSG between reproductive events  $(n_{\text{reps}})$ .
- 353 • Maximum number of generations to evolve  $(nGen)$ .
- 354 • Upper bound for contribution level  $(x_{\text{max}})$ .
- 355 • Mean  $(\mu_x)$  and standard deviation  $(\sigma_x)$  of an underlying `Normal` $(\mu_x, \sigma_x)$  distribu-  
356 tion of strategies; the initial strategies  $(x_i, i = 1, \dots, N)$  are to be sampled from  
357 `TruncNormal` $(\mu_x, \sigma_x, 0, x_{\text{max}})$ .
- 358 • Mutation probability  $(p_{\text{mut}})$  per individual per generation.
- 359 • Standard deviation  $(\sigma)$  of an underlying `Normal` $(0, \sigma)$  distribution of the strategy  
360 changes caused by mutations, and upper and lower bounds on mutation sizes,  $(l, u)$ ;  
361 when an individual playing strategy  $x$  mutates, its new strategy is sampled from  
362 `TruncNormal` $(x, \sigma, \max\{0, x - l\}, \min\{x_{\text{max}}, x + u\})$ , so that the mutation is within  
363 the interval  $[l, u]$  and the mutated strategy is in  $[0, x_{\text{max}}]$ .

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**Algorithm 1** Individual-based simulation algorithm

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```

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

```

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## 513 SUPPORTING INFORMATION

### 514 A Proofs

#### 515 A.1 Analysis of the natural snowdrift game (NSG; §5.1) in a finite 516 population

517 Our main results are stated in theorems 1 and 2 (§3). Before developing the proofs in detail,  
518 it is useful to note that:

- 519 •  $\tau_{\min} > 0$  (where  $\tau_{\min}$  is defined in assumption (c) of the definition of the NSG, §5.1).  
520 To see this, suppose that  $\tau_{\min} = 0$ . Then assumption (c) implies that  $B(\tau_{\max}) \geq \tau_{\max}$ ,  
521 contradicting assumption (d).
- 522 • The benefit function  $B(\tau)$  is twice-differentiable. This follows from assumption (b) in  
523 the definition of the NSG (§5.1).
- 524 •  $B'(\tau_{\min}) = B'(\tau_{\max}) = 1$ ,  $B'(\tau) > 1$  for  $\tau_{\min} < \tau < \tau_{\max}$ , and  $B'(\tau) < 1$  otherwise [these  
525 properties of  $B(\tau)$  follow from assumption (c)]. Consequently,  $m > 0$  and  $B''(\tau_{\max}) \leq 0$ .

##### 526 A.1.1 The mean fitness difference between mutants and residents

527 Consider a population of  $N$  individuals, comprised of  $M_p$  mutants who play  $x$  and  $N - M_p$   
528 residents who play  $X$ , and denote the proportion of mutants in the population by  $\epsilon = M_p/N$ .  
529 Suppose that groups of  $n$  individuals are randomly sampled from this population without  
530 replacement, which implies that the number of mutants in each such group is hypergeomet-  
531 rically distributed with parameters  $N$ ,  $M_p$  and  $n$  (37, 48); thus, the probability of  $k$  mutants  
532 occurring in a random sample of  $n$  individuals is

$$533 \Pr(M_g = k) = \frac{\binom{N-M_p}{n-k} \binom{M_p}{k}}{\binom{N}{n}}. \quad (25)$$

534 Suppose, moreover, that a focal individual is selected from the population by first sampling a  
535 group of  $n$  individuals, and then selecting one of the members of this group. Lastly, suppose  
536 for simplicity that individual fitnesses are given by the payoffs from a single round of the  
537 NSG played in such randomly selected groups#. We show elsewhere (37, eq. 4.61, p. 137)  
538 that the expected difference between the mutant and resident fitnesses is then

$$539 \delta \bar{W}_\epsilon(x, X) = X - x + \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p}{k}}{\binom{N-1}{n-1}} \left( \frac{kN - M_p n}{M_p(N - M_p)} \right) B(kx + (n - k)X). \quad (26)$$

#Equation (26) 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.

541 Differentiating equation (26) yields

$$\begin{aligned}
 542 \quad \partial_x \delta \bar{W}_\epsilon(x, X) &= -1 + \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p}{k}}{\binom{N-1}{n-1}} \frac{kN - M_p n}{M_p(N - M_p)} k B'(kx + (n - k)X) \\
 543 \quad &= -1 + \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} B'(kx + (n - k)X) \quad (27) \\
 544
 \end{aligned}$$

545 Differentiating with respect to  $x$  and setting  $x = X$ , we find (37, pp. 138–139)

$$546 \quad \partial_x \delta \bar{W}_\epsilon(x, X)|_{x=X} = -1 + \frac{N - n}{N - 1} B'(nX), \quad (28a)$$

$$547 \quad \partial_x^2 \delta \bar{W}_\epsilon(x, X)|_{x=X} = \frac{N - n}{N - 1} \left( \frac{N - 2n}{N - 2} + 2 \frac{(n - 1)}{N - 2} N \epsilon \right) B''(nX). \quad (28b) \\
 548$$

549 From these expressions we see that

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

552 We will exploit these facts below.

### 553 A.1.2 Evolutionary and convergent stability of defection

554 **Lemma 3** (Evolutionary stability of defection). *If the NSG (§ 5.1) is played in a finite*  
 555 *population then not contributing ( $X = 0$ ) is a locally convergently stable  $ESS_N$  for any*  
 556 *selection process. Moreover, if the population and group sizes are the same ( $N = n$ , so the*  
 557 *entire population plays the game together) then defecting is the unique  $ESS_N$  and is globally*  
 558 *evolutionarily and convergently stable.*

559 *Proof.*  $B'(0) < 1$  because  $B(\tau) - \tau$  decreases for  $0 \leq \tau < \tau_{\min}$ , so using equation (28a),

$$560 \quad \partial_x \delta \bar{W}_\epsilon(x, 0)|_{x=0} = \frac{N - n}{N - 1} B'(0) - 1 < 0. \quad (29) \\
 561$$

562 Because  $\partial_x \delta \bar{W}_\epsilon(x, X)|_{x=X}$  is continuous in  $X$ ,

$$563 \quad \partial_x \delta \bar{W}_\epsilon(x, X)|_{x=X} < 0, \quad (30) \\
 564$$

565 for  $X$  sufficiently small. From Theorem 4.3.9 in (37), it follows that  $X = 0$  (defection)  
 566 is convergently stable, and selection opposes invasion of mutants contributing a sufficiently  
 567 small but positive amount,  $x > 0$ . To establish that  $X = 0$  is evolutionarily stable, observe  
 568 that equation (29) implies that  $\delta \bar{W}_\epsilon(x, 0) < 0$  for sufficiently small  $x$ , so such mutants are  
 569 selected against, regardless of their proportion ( $\epsilon$ ) in the population. Thus, corollary 5.4 of  
 570 (31) implies that selection also opposes the fixation of such mutants.

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

### 578 A.1.3 Proof of theorem 1

579 Inserting equation (28a) into the definition of an evolutionarily singular strategy (definition  
580 4.3.5 of (37)) implies that cooperative singular strategies are characterized by equation (5).  
581 Any solution of equation (5) must satisfy  $nX_N^* \in (\tau_{\min}, \tau_{\max})$ , because the right hand side of  
582 equation (5) is greater than 1 and, as noted above, if  $\tau \notin (\tau_{\min}, \tau_{\max})$  then  $B'(\tau) \leq 1$ .

583 **Necessary condition for ESS<sub>N</sub>:** Suppose that  $X$  solves equation (5) but  $B''(nX) >$   
584  $0$ . Plugging equation (5) into equation (28a) gives  $\partial_x \delta \bar{W}_\epsilon(x, X)|_{x=X} = 0$ . Rearranging  
585 equation (28b), we have

$$586 \quad \partial_x^2 \delta \bar{W}_\epsilon(x, X)|_{x=X} = \frac{N-n}{N-1} \left( 1 + 2 \frac{(n-1)}{N-2} (N\epsilon - 1) \right) B''(nX) \quad (31)$$

588 so  $\partial_x^2 \delta \bar{W}_\epsilon(x, X)|_{x=X}$  is increasing in  $\epsilon$  and positive for any  $\epsilon \geq 1/N$  (*i.e.*, any mixed popu-  
589 lation). Thus, when mutants play  $x$  sufficiently close to  $X$ ,  $\partial_x \delta \bar{W}_\epsilon(x, X)|_{x=X}$  is negative for  
590  $x < X$  and positive for  $x > X$ ; hence, since  $\delta \bar{W}_\epsilon(X, X) = 0$ , we must have  $\delta \bar{W}_\epsilon(x, X) > 0$   
591 for any  $x$  that is near but not equal to  $X$  (and this is true for any number of mutants  
592  $M_p = 1, \dots, N-1$ ). Corollary 5.4 of (31) then implies that selection favours the fixation of  
593 such mutants, so  $X$  is not an ESS<sub>N</sub>, regardless of the selection process. Thus, if  $X_N^* > 0$  is  
594 an ESS<sub>N</sub> then it cannot be that  $B''(nX) > 0$ , *i.e.*, inequality (7) holds.

595 **Sufficient condition for universal ESS<sub>N</sub>:** The sufficient condition for local universal  
596 evolutionary and convergent stability follows immediately from theorem 4.D.1 of (37) and  
597 equation (28).

598 **ESS<sub>N</sub>s in large populations:** Suppose that  $B''(\tau_{\max}) \neq 0$  and consider the equation

$$599 \quad f(X, y) = B'(nX) - y = 0. \quad (32)$$

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

$$601 \quad \partial_X f(X, y)|_{(X,y)=(\tau_{\max}/n,1)} = B''(\tau_{\max}) \neq 0, \quad (33)$$

602 from the implicit function theorem (49, Theorem 12.40), there exists a differentiable function  
603  $X(y)$  defined in a neighbourhood of  $y = 1$ , such that  $X(1) = \tau_{\max}/n$  and

$$604 \quad f(X(y), y) = yB'(nX(y)) - y = 0. \quad (34)$$

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

$$606 \quad \frac{n(N)}{N} \xrightarrow{N \rightarrow \infty} 0.$$

607 If we define  $y_N := 1 + \frac{n-1}{N-n}$  then  $y_N \rightarrow 1$ , so for all sufficiently large population sizes  $N$ ,  
608 equation (34) can be solved implicitly for  $X_N^* := X(y_N)$ . Such  $X_N^*$  then solve equation (5),  
609 and  $X_N^* \xrightarrow{N \rightarrow \infty} X_\infty^*$  because  $X(y)$  is continuous. Recalling that  $B''(\tau_{\max}) \leq 0$  and  $B''(\tau_{\max}) \neq$   
610  $0$  by assumption, we have  $B''(\tau_{\max}) < 0$ , so for sufficiently large  $N$ ,  $B''(nX_N^*) < 0$ . Theorem  
611 4.D.1 of (37) then implies that for sufficiently large  $N$ ,  $X_N^*$  is a universal local ESS<sub>N</sub> and is  
612 locally convergently stable.  $\square$

#### 613 A.1.4 Proof of theorem 2

614 First, note that  $X = 0$  is always a locally convergently stable  $\text{ESS}_N$  (lemma 3). From  
 615 Corollary 4.3.8 of (37), selection opposes invasion of a cooperative resident strategy  $X > 0$   
 616 by sufficiently similar mutant strategies only if  $X$  is singular, which (using equation (28a))  
 617 occurs *iff*  $X$  satisfies

$$618 \quad B'(nX) = 1 + \frac{n-1}{N-n}. \quad (35)$$

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

621 **Case  $m > m_c$ .** Because  $B'(\tau_{\max}) = 1$  and  $B'(nX)$  is a continuous function of  $X$  on the  
 622 interval  $[\tau_{\min}/n, \tau_{\max}/n]$ , it follows from the intermediate value theorem (49) that equa-  
 623 tion (5) has a solution in this interval. Let  $\mathcal{S}$  be the set of singular strategies, *i.e.*,  
 624 solutions of equation (5),

$$625 \quad \mathcal{S} = \left\{ X \mid B'(nX) = 1 + \frac{n-1}{N-n} \right\}. \quad (36)$$

626 Note that from theorem 1,  $\mathcal{S} \subset (\tau_{\min}/n, \tau_{\max}/n)$ . Denote the largest solution of equa-  
 627 tion (35) by  $X_N^*$ , *i.e.*,

$$628 \quad X_N^* = \max \mathcal{S} \quad (37)$$

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

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

$$634 \quad B'(n\tilde{X}) > B'(nX_N^*) = 1 + \frac{n-1}{N-n}. \quad (38)$$

635 From the intermediate value theorem, there exists  $X \in \mathcal{S}$  such that

$$636 \quad X > \tilde{X} > X_N^* = \max \mathcal{S}, \quad (39)$$

637 a contradiction.

638 Thus  $B''(nX_N^*) < 0$  and  $C''(X) = 0$ , so theorems 4.D.1 and 4.3.9 of (37) imply that  
 639  $X_N^*$  is a local  $\text{ESS}_N$  and is locally convergently stable.

640 **Case  $m = m_c$ .** Suppose, in order to derive a contradiction, that  $X > 0$  is a cooperative  
 641  $\text{ESS}_N$ . From theorem 1,  $X$  must solve equation (35) so, from the definition of  $m_c$  in  
 642 equation (10),

$$643 \quad B'(nX) = \frac{N-1}{N-n} = m_c + 1. \quad (40)$$

---

<sup>||</sup>We need to avoid the situation in which singular strategy  $X_N^*$  is also an inflection point of  $B(nx)$ . This occurs when  $nX_N^*$  is both a critical point and an inflection point of  $B(x) - (N-1)x/(N-n)$ , which is generically *not* the case.



644 Suppose further that  $\arg \max B'(\tau)$  does not contain an interval (*i.e.*, the marginal  
 645 benefit  $B'$  is not maximal for an interval of total contributions  $\tau$ ), which happens  
 646 generically. Then, any total contribution in  $\arg \max B'(\tau)$  is a local maximum of  $B'(\tau)$ .  
 647 It follows that if  $x < X$  and  $x$  is sufficiently close to  $X$ , then

$$648 \quad B'(x + (n-1)X) < \frac{N-1}{N-n}, \quad (41)$$

649 and therefore from equation (27),

$$650 \quad \begin{aligned} \partial_x \delta \bar{W}_\epsilon(x, X) &= -1 + \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} B'(kx + (n-k)X) \\ 651 \quad &< -1 + \left( \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} \right) \frac{N-1}{N-n}, \end{aligned} \quad (42)$$

653 which, together with the identity (37, equation (4.63), p. 138),

$$654 \quad \sum_{k=0}^n \frac{\binom{N-K}{n-k} \binom{K-1}{k-1}}{\binom{N-1}{n-1}} \left( \frac{kN - Kn}{N - K} \right) = \frac{N-n}{N-1}, \quad (43)$$

655 implies that  $\partial_x \delta \bar{W}_\epsilon(x, X) < 0$ . Hence, similar to [an argument](#) in the proof of theorem 1,  
 656 since  $\delta \bar{W}_\epsilon(X, X) = 0$ , we must have  $\delta \bar{W}_\epsilon(x, X) > 0$  for any  $x$  that is slightly less than  
 657 but not equal to  $X$  (and this is true for any number of mutants  $M_p = 1, \dots, N-1$ ).  
 658 Consequently, selection favours the invasion and replacement of  $X$  by any such  $x$ , so  
 659  $X$  is not evolutionarily stable.

660 To see that defection is globally evolutionarily stable, substitute  $X = 0$  in equation (27)  
 661 to get

$$662 \quad \partial_x \delta \bar{W}_\epsilon(x, 0) = -1 + \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} B'(kx). \quad (44)$$

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

$$665 \quad \partial_x \delta \bar{W}_\epsilon(x, 0) \leq -1 + \left( \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} \right) (m_c + 1) = 0, \quad (45)$$

667 where we have used equations (10) and (43) in the last equality. Thus,  $\delta \bar{W}_\epsilon(x, 0)$  is  
 668 non-decreasing in  $x$ . Moreover, if  $x < \tau_{\min}/n$ , then  $B'(kx) < 1$  for all  $k = 0, \dots, n$ , so  
 669 similarly, equations (43) and (44) imply that  $\partial_x \delta \bar{W}_\epsilon(x, 0) < 0$ . Because  $\delta \bar{W}_\epsilon(0, 0) = 0$ ,  
 670 it follows that  $\delta \bar{W}_\epsilon(x, 0) < 0$  for all  $x > 0$  (regardless of the proportion of mutants  
 671 in the population). Thus, from (31, corollary 5.4), when residents defect, selection  
 672 opposes invasion and fixation of any mutants.

673 **Case  $m < m_c$ .** In this case, equation (5) has no solution, and no cooperative ESS<sub>N</sub> exists.

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

$$676 \quad B'(\tau) < 1 + \frac{n-1}{N-n} = \frac{N-1}{N-n}, \quad \text{for all } \tau \geq 0. \quad (46)$$

677 Then, using equations (27), (46) and equation (4.63) on p.138 of (37), it follows that

$$678 \quad \begin{aligned} \partial_x \delta \bar{W}_\epsilon(x, X) &< -1 + \left( \sum_{k=0}^n \frac{\binom{N-M_p}{n-k} \binom{M_p-1}{k-1}}{\binom{N-1}{n-1}} \cdot \frac{kN - M_p n}{N - M_p} \right) \frac{N-1}{N-n} \\ 679 \quad &= -1 + \left( \frac{N-n}{N-1} \right) \left( \frac{N-1}{N-n} \right) = 0, \end{aligned}$$

681 so  $\delta \bar{W}_\epsilon(x, X)$  decreases with  $x \geq 0$  for any  $X \geq 0$ . Thus, from (31, corollary 5.4),  
 682 defection ( $X = 0$ ) is a globally evolutionarily and convergently stable strategy.  $\square$

## 683 B Analysis of the benefit function used for numerical 684 examples

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

### 688 B.1 Sigmoids using generalized error functions

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

$$690 \quad B(\tau) = L \operatorname{erf}_{2k} \left( (m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}}) \right), \quad \tau \geq 0, \quad (47)$$

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

$$692 \quad \operatorname{erf}_\ell(x) = \frac{\ell}{\Gamma(1/\ell)} \int_0^x e^{-t^\ell} dt. \quad (48)$$

693 This class of functions generalizes the the error function,  $\operatorname{erf}$ , which is recovered for  $\ell = 2$   
 694 or, equivalently,  $k = 1$ ; see § B.2.

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

$$698 \quad \operatorname{erf}_\ell(x) = \frac{1}{\Gamma(1/\ell)} \int_0^{x^\ell} z^{\frac{1}{\ell}-1} e^{-z} dz = \frac{1}{\Gamma(1/\ell)} \left( \Gamma\left(\frac{1}{\ell}\right) - \Gamma\left(\frac{1}{\ell}, x^\ell\right) \right), \quad (49)$$

699

700 where

$$701 \quad \Gamma(s) = \int_0^{\infty} t^{s-1} e^{-t} dt, \quad (50a)$$

$$702 \quad \Gamma(s, x) = \int_x^{\infty} t^{s-1} e^{-t} dt, \quad (50b)$$

703

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

707 **Parameter meanings:** Because equation (49) implies

$$708 \quad \lim_{x \rightarrow \infty} \text{erf}_{\ell}(x) = 1, \quad (51)$$

709 it follows that

$$710 \quad \lim_{x \rightarrow \infty} B(x) = L. \quad (52)$$

711 We show below that the inflection point of  $B$  (47) is  $\tau_{\text{turn}}$ , and that the maximal marginal  
712 fitness given the benefit function  $B$  is  $m$ .

713 From the integral definition of the generalized error function [equation (48)]

$$714 \quad \frac{d \text{erf}_{\ell}(x)}{dx} = \frac{\ell}{\Gamma(1/\ell)} e^{-x^{\ell}}, \quad (53a)$$

$$715 \quad \frac{d^2 \text{erf}_{\ell}(x)}{dx^2} = -\frac{\ell}{\Gamma(1/\ell)} \ell x^{\ell-1} e^{-x^{\ell}}, \quad (53b)$$

716

717 so

$$718 \quad B'(\tau) = \frac{\sqrt{\pi}L}{\Gamma(2k)\Gamma(1/(2k))} (m+1) \frac{\Gamma(1/(2k))}{2kL} \frac{(2k)!}{\sqrt{\pi}} \exp\left(-\left[(m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}})\right]^{2k}\right)$$

$$719 \quad = (m+1) \exp\left(-\left[(m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}})\right]^{2k}\right), \quad (54a)$$

$$720 \quad B''(\tau) = -2k \left[(m+1) \frac{\Gamma(1/(2k))}{2kL}\right]^{2k} (\tau - \tau_{\text{turn}})^{2k-1}$$

$$721 \quad \times (m+1) \exp\left(-\left[(m+1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}})\right]^{2k}\right)$$

$$722 \quad = -2k \left[(m+1) \frac{\Gamma(1/(2k))}{2kL}\right]^{2k} (\tau - \tau_{\text{turn}})^{2k-1} B'(\tau). \quad (54b)$$

723

---

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

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

$$727 \max_{\tau \geq 0} B'(\tau) = B'(\tau_{\text{turn}}) = m + 1, \quad (55)$$

728 so from equation (9), the maximal marginal fitness is

$$729 \max_{\tau \geq 0} \left( \frac{\partial W}{\partial x} \right) = \max_{\tau \geq 0} B'(\tau) - 1 = m. \quad (56)$$

730 **The minimizing and maximizing total goods:** Since  $B'(\tau)$  is monotonic on each of  
 731 the intervals,  $(-\infty, \tau_{\text{turn}})$  and  $(\tau_{\text{turn}}, \infty)$  and  $B'(\tau)$  is even, for any  $b \in B'(\mathbb{R}_{\geq 0}) = (0, m + 1]$ ,  
 732 we can find two real values of  $\tau$  for which  $B'(\tau) = b$  (although one of these values may  
 733 be negative and therefore biologically irrelevant, because total contributions to the public  
 734 good cannot be negative). To find these values of total contribution  $\tau$ , we set  $B'(\tau) = b$  in  
 735 equation (54a), and get

$$736 \log \frac{m + 1}{b} = \left[ (m + 1) \frac{\Gamma(1/(2k))}{2kL} (\tau - \tau_{\text{turn}}) \right]^{2k}, \quad (57)$$

$$737 \tau = \tau_{\text{turn}} \pm \frac{2kL}{(m + 1) \Gamma(1/(2k))} \sqrt[2k]{\log \frac{m + 1}{b}}. \quad (58)$$

739 To find  $\tau_{\text{max}}$  and  $\tau_{\text{min}}$ , we substitute  $b = B'(\tau) = 1$  in equation (58) and, noting that  $B''(\tau)$   
 740 changes sign from positive to negative at  $\tau_{\text{turn}}$ , we have

$$741 \tau_{\text{min}} = \tau_{\text{turn}} - \frac{2kL}{(m + 1) \Gamma(1/(2k))} \sqrt[2k]{\log(m + 1)}, \quad (59a)$$

$$742 \tau_{\text{max}} = \tau_{\text{turn}} + \frac{2kL}{(m + 1) \Gamma(1/(2k))} \sqrt[2k]{\log(m + 1)}, \quad (59b)$$

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

$$744 \Delta\tau = \tau_{\text{max}} - \tau_{\text{min}} = \frac{4kL}{(m + 1) \Gamma(1/(2k))} \sqrt[2k]{\log(m + 1)}. \quad (60)$$

746 **The infinite-population cooperative ESS:** Equation (4) then gives

$$747 X_{\infty}^* = \frac{\tau_{\text{max}}}{n} = \frac{1}{n} \left( \tau_{\text{turn}} + \frac{2kL}{(m + 1) \Gamma(1/(2k))} \sqrt[2k]{\log(m + 1)} \right). \quad (61)$$

748 Using  $B'(\tau_{\text{max}}) = 1$  and equation (59b) in equation (54b), we have

$$749 b_{\text{curve}} := B''(\tau_{\text{max}}) = B''(nX_{\infty}^*) = -2k \left[ \frac{(m + 1) \Gamma(1/(2k))}{2kL} \right]^{2k} (\tau_{\text{max}} - \tau_{\text{turn}})^{2k-1}$$

$$750 = -2k \left[ \frac{(m + 1) \Gamma(1/(2k))}{2kL} \right]^{2k} \left( \frac{2kL}{(m + 1) \Gamma(1/(2k))} \right)^{2k-1} (\log(m + 1))^{\frac{2k-1}{2k}}$$

$$751 = -\Gamma \left( \frac{1}{2k} \right) \frac{m + 1}{L} (\log(m + 1))^{1 - \frac{1}{2k}}. \quad (62)$$

752

753 Using equation (47) and the fact that  $\text{erf}_{2k}$  is odd,

$$754 \quad B(\tau_{\max}) - B(\tau_{\min}) = 2L \text{erf}_{2k} \left( \sqrt[2k]{\log(m+1)} \right). \quad (63)$$

755

756 **Singular and evolutionarily stable cooperative strategies in finite populations:**  
 757 In a finite population of size  $N$ , a singular strategy  $X_N^*$  of the NSG is a solution of equa-  
 758 tion (5), that is,

$$759 \quad B'(nX_N^*) = 1 + \frac{n-1}{N-n} = \frac{N-1}{N-n}. \quad (64)$$

760 so equation (58) implies that at the ESS, the total contribution must be one of

$$761 \quad \tau = \tau_{\text{turn}} \pm \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)}. \quad (65)$$

762

763 There are therefore two singular strategies,

$$764 \quad X_{N\pm}^* = \frac{1}{n} \left( \tau_{\text{turn}} \pm \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)} \right). \quad (66)$$

765 Similarly to  $\tau_{\min}$  and  $\tau_{\max}$ ,  $B''(nX_{N+}^*) > 0$  and  $B''(nX_{N-}^*) < 0$ , so from theorem 1, the unique  
 766 ESS<sub>N</sub> is

$$767 \quad X_N^* = \frac{1}{n} \left( \tau_{\text{turn}} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)} \right). \quad (67)$$

768 **The curvature of the benefit function at the ESS<sub>N</sub>:** Similar to equation (62), we  
 769 have

$$770 \quad B''(nX_N^*) = -2k \left[ \frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} (nX_N^* - \tau_{\text{turn}})^{2k-1} \frac{N-1}{N-n} \quad (68)$$

$$771 \quad = -2k \left[ \frac{(m+1)\Gamma(1/(2k))}{2kL} \right]^{2k} \left( \frac{2kL}{(m+1)\Gamma(1/(2k))} \right)^{2k-1}$$

$$772 \quad \times \left( \log\left((m+1)\frac{N-n}{N-1}\right) \right)^{\frac{2k-1}{2k}} \frac{N-1}{N-n}$$

$$773 \quad = -(m+1) \frac{N-1}{N-n} \frac{\Gamma(1/(2k))}{L}$$

$$774 \quad \times \left( \log\left((m+1)\frac{N-n}{N-1}\right) \right)^{\frac{2k-1}{2k}}. \quad (69)$$

775

776 **Condition for the fitness difference having a minimum when a single mutant**  
 777 **defects and residents play the ESS:** To guarantee that when a single mutant invades a  
 778 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 (or equivalently, the contribution of the nonfocal individuals—all residents—must be less than the minimizing total good  $\tau_{\min}$ ),

$$\tau_{\min} - \frac{n-1}{n}\tau_{\max} > 0. \quad (70)$$

Using equations (59b) and (60), this is equivalent to  $\tau_{\max} > n\Delta\tau$ , or

$$\begin{aligned} n < \frac{\tau_{\max}}{\Delta\tau} &= \frac{\tau_{\text{turn}}}{\frac{4kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}} + \frac{1}{2} \\ &= \tau_{\text{turn}} \frac{m+1}{4kL} \frac{\Gamma(1/(2k))}{\sqrt[2k]{\log(m+1)}} + \frac{1}{2}. \end{aligned} \quad (71)$$

Rewriting this condition in terms of the horizontal asymptote  $L$ ,

$$L < \frac{\tau_{\text{turn}}(m+1)}{2k(2n-1)} \frac{\Gamma(1/(2k))}{\sqrt[2k]{\log(m+1)}}. \quad (72)$$

**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.

$$\begin{aligned} \Delta\Psi &= \left[ B(\tau_{\max}) - \frac{\tau_{\max}}{n} \right] - \left[ B(\tau_{\min}) - \left( \tau_{\min} - \frac{n-1}{n}\tau_{\max} \right) \right] \\ &= B(\tau_{\max}) - B(\tau_{\min}) - (\tau_{\max} - \tau_{\min}) \\ &= B(\tau_{\max}) - B(\tau_{\min}) - \Delta\tau, \end{aligned} \quad (73)$$

so using equations (60) and (63), we have

$$\Delta\Psi = 2L \operatorname{erf}_{2k} \left( \sqrt[2k]{\log(m+1)} \right) - \frac{4kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}. \quad (74)$$

**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 (70), the distance between the fitness extrema is

$$\frac{\tau_{\max}}{n} - \left( \tau_{\min} - \frac{n-1}{n}\tau_{\max} \right) = \tau_{\max} - \tau_{\min} = \Delta\tau. \quad (75)$$

Equations (60) and (74) then yield

$$\begin{aligned} \frac{\Delta\Psi}{\Delta\tau} &= \frac{2L \operatorname{erf}_{2k} \left( \sqrt[2k]{\log(m+1)} \right)}{\frac{4kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}} - 1 \\ &= (m+1) \frac{\Gamma(1/(2k))}{2k} \frac{\operatorname{erf}_{2k} \left( \sqrt[2k]{\log(m+1)} \right)}{\sqrt[2k]{\log(m+1)}} - 1, \end{aligned} \quad (76)$$

812 which only depends on the maximal marginal fitness,  $m$  (and the order of the generalized  
813 error function,  $2k$ ). Note also that using equation (48) and L'Hôpital's rule (49),

$$814 \quad \lim_{x \rightarrow 0} \frac{\operatorname{erf}_\ell(x)}{x} = \lim_{x \rightarrow 0} \frac{\ell}{\Gamma(1/\ell)} e^{-x^\ell} = \frac{\ell}{\Gamma(1/\ell)}, \quad (77)$$

815 so

$$816 \quad \lim_{m \rightarrow 0} \frac{\Delta\Psi}{\Delta\tau} = 0. \quad (78)$$

817 In addition, equation (49) implies that for any  $x > 0$ ,

$$818 \quad \lim_{k \rightarrow \infty} \operatorname{erf}_\ell(x) = 1, \quad (79)$$

819 (because  $\Gamma(x) \rightarrow \infty$  as  $x \rightarrow 0$ , and  $\Gamma(\frac{1}{\ell}, x^\ell)$  is bounded), and

$$820 \quad \lim_{x \rightarrow 0} x\Gamma(x) = \lim_{x \rightarrow 0} \Gamma(x+1) = 1, \quad (80)$$

821 so we have

$$822 \quad \lim_{k \rightarrow \infty} \frac{\Delta\Psi}{\Delta\tau} = m. \quad (81)$$

823 **The ratio of ESSs in infinite and finite populations:** Using equations (60), (61) and  
824 (67),

$$\begin{aligned} 825 \quad \frac{X_\infty^*}{X_N^*} &= \frac{\tau_{\text{turn}} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log(m+1)}}{\tau_{\text{turn}} + \frac{2kL}{(m+1)\Gamma(1/(2k))} \sqrt[2k]{\log\left((m+1)\frac{N-n}{N-1}\right)}} \\ 826 \quad &= \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{\frac{\log\left((m+1)\frac{N-n}{N-1}\right)}{\log(m+1)}}}} \\ 827 \quad &= \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{1 + \frac{\log\left(\frac{N-n}{N-1}\right)}{\log(m+1)}}}}. \quad (82) \end{aligned}$$

829 Rewriting the population size as  $N = nG$ ,

$$830 \quad \frac{X_\infty^*}{X_N^*} = \frac{2\tau_{\text{turn}} + \Delta\tau}{2\tau_{\text{turn}} + \Delta\tau \sqrt[2k]{1 + \frac{\log\left(\frac{G-1}{G-\frac{1}{n}}\right)}{\log(m+1)}}}}. \quad (83)$$

831  
832 We see that the ratio  $X_\infty^*/X_N^* \rightarrow 1$  as  $G \rightarrow \infty$  with  $n$  fixed. However,  $X_\infty^*/X_N^*$  approaches  
833 a (finite) value greater than 1 as  $n \rightarrow \infty$  with  $G$  fixed (assuming  $X_N^*$  exist for all  $N$ ; see  
834 inequality (15)).

## 835 B.2 Sigmoid using standard error-function

836 In the special case  $k = 1$  (i.e.,  $\ell = 2$ ), since  $\Gamma(1/2) = \sqrt{\pi}$ , equation (47) reduces to

$$837 \quad B(\tau) = L \operatorname{erf} \left( (m+1) \frac{\sqrt{\pi}}{2L} (\tau - \tau_{\text{turn}}) \right), \quad \tau \geq 0. \quad (84)$$

838 Then, setting  $k = 1$  in equation (85) gives the maximizing and minimizing total goods,

$$839 \quad \tau_{\min} = \tau_{\text{turn}} - \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}}, \quad (85a)$$

$$840 \quad \tau_{\max} = \tau_{\text{turn}} + \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}}, \quad (85b)$$

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

$$843 \quad \Delta\tau = \tau_{\max} - \tau_{\min} = 4 \frac{L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}}. \quad (86)$$

844 Equation (61) then gives

$$845 \quad X_{\infty}^* = \frac{1}{n} \left( \tau_{\text{turn}} + \frac{2L}{m+1} \sqrt{\frac{\log(m+1)}{\pi}} \right), \quad (87)$$

846 and equation (62) becomes

$$847 \quad b_{\text{curve}} = B''(\tau_{\max}) = -\frac{m+1}{L} \sqrt{\pi \log(m+1)}. \quad (88)$$

849 From equation (63),

$$850 \quad B(\tau_{\max}) - B(\tau_{\min}) = 2L \operatorname{erf} \left( \sqrt{\log(m+1)} \right). \quad (89)$$

852 Equation (67) gives the unique ESS<sub>N</sub>:

$$853 \quad X_N^* = \frac{1}{n} \left( \tau_{\text{turn}} + \frac{2L}{m+1} \sqrt{\frac{\log((m+1)^{\frac{N-n}{N-1}})}{\pi}} \right), \quad (90)$$

854 and equation (68) becomes

$$855 \quad B''(nX_N^*) = -\frac{m+1}{L} \sqrt{\pi \log \left( (m+1)^{\frac{N-n}{N-1}} \right)}. \quad (91)$$

856 Condition (71), which guarantees that when a single mutant invade a population playing  
857 the ESS, the fitness difference has both a minimum and a maximum (as a function of the  
858 mutant strategy), reduces to

$$859 \quad n < \tau_{\max} / \Delta\tau = \frac{\tau_{\text{turn}}}{4} \frac{m+1}{L} \sqrt{\frac{\pi}{\log(m+1)}} + \frac{1}{2}, \quad (92)$$

860



861 the PED,  $\Delta\Psi$  (equation (74)) becomes

$$862 \quad \Delta\Psi = 2L \operatorname{erf}\left(\sqrt{\log(m+1)}\right) - 4\frac{L}{m+1}\sqrt{\frac{\log(m+1)}{\pi}}, \quad (93)$$

863

864 and the mean fitness slope (equation (76)) between the extrema reduces to

$$865 \quad \frac{\Delta\Psi}{\Delta\tau} = \frac{m+1}{2}\sqrt{\frac{\pi}{\log(m+1)}}\operatorname{erf}\left(\sqrt{\log(m+1)}\right) - 1. \quad (94)$$

866