Public goods games in populations with fluctuating size

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ABSTRACT

Many mathematical frameworks of evolutionary game dynamics assume that the total population size is constant and that selection affects only the relative frequency of strategies. Here, we consider evolutionary game dynamics in an extended Wright–Fisher process with variable population size. In such a scenario, it is possible that the entire population becomes extinct. Survival of the population may depend on which strategy prevails in the game dynamics. Studying cooperative dilemmas, it is a natural feature of such a model that cooperators enable survival, while defectors drive extinction. Although defectors are favored for any mixed population, random drift could lead to their elimination and the resulting pure-cooperator population could survive. On the other hand, if the defectors remain, then the population will quickly go extinct because the frequency of cooperators steadily declines and defectors alone cannot survive. In a mutation–selection model, we find that (i) a steady supply of cooperators can enable long-term population survival, provided selection is sufficiently strong, and (ii) selection can increase the abundance of cooperators but reduce their relative frequency. Thus, evolutionary game dynamics in populations with variable size generate a multifaceted notion of what constitutes a trait's long-term success.

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1. Introduction

The emergence of cooperation is a prominent research topic in evolutionary theory. The problem is usually formulated in such a way that it pays to exploit cooperators, yet the payoff to one cooperator against another is greater than the payoff to one defector against another (Axelrod and Hamilton, 1981). In spite of this conflict of interest, cooperation is broadly observed in nature, and various mechanisms have been put forth to explain its evolution (Nowak, 2006a). In fact, the question of how cooperators may proliferate in social situations is one of the main concerns of evolutionary game theory, a framework that models cooperation and defection as strategies of a game.

Evolutionary game-theoretic models typically involve a number of assumptions. In this study, we are concerned with two potentially restrictive ones: (i) the population size is infinite or (ii) the population size is finite but fixed and unaffected by evolution. While the classical replicator equation (Taylor and Jonker, 1978; Hofbauer et al., 1979; Hofbauer and Sigmund, 1998) can be used to model large populations that fluctuate in size (Hauert et al.,

2006), replicator dynamics capture only the relative frequencies of the strategies. Even stochastic models that account for populations of any finite size, such as the Moran model or the Wright–Fisher model and their game-theoretic extensions, usually require the number of players to remain fixed over time (Moran, 1958; Nowak et al., 2004; Taylor et al., 2004; Lieberman et al., 2005; Ohtsuki et al., 2006; Taylor et al., 2007; Szabó and Fáth, 2007; Tarnita et al., 2009a; Nowak et al., 2009; Hauert and Imhof, 2012; Débarre et al., 2014). Here, we explore the evolutionary dynamics of cooperation in social dilemmas when the population can fluctuate in size and even go extinct.

Branching processes have a rich history in theoretical biology [see Kimmel and Axelrod, 2015] and are a natural way to model populations that vary in size. A number of recent works have considered non-constant population size within evolutionary game theory. Hauert et al. (2006) treat ecological dynamics in evolutionary games by modifying the replicator equation to account for population density and show that fluctuating density can lead to coexistence between cooperators and defectors. Melbinger et al. (2010) illustrate how the decoupling of stochastic birth and death events can lead to transient increases in cooperation. By allowing a game to influence carrying capacities, Novak et al. (2013) demonstrate that variable density regulations can change

the stability of equilibria relative to the replicator equation. Furthermore, demographic fluctuations can act as a mechanism to promote cooperation in public goods games (Constable et al., 2016) and indefinite coexistence (as opposed to fixation) in coexistence games (Ashcroft et al., 2017). Fluctuating size in a Lotka–Volterra model also leads to different growth rates for isolated populations of cooperators and defectors (Huang et al., 2015), and even when the two competing types are neutral at the equilibrium size, fluctuations can still give one type a selective advantage over the other (Chotibut and Nelson, 2017). When traits have the same growth rate, these fluctuations also affect a mutant's fixation probability (Czuppon and Traulsen).

Here, we develop a branching-process model based on the Wright–Fisher process (Fisher, 1930; Wright, 1931) for a population with non-overlapping generations in which trait values of offspring are sampled from the previous generation depending on the success of individuals (parents) in a sequence of interactions (Ewens, 2004; Imhof and Nowak, 2006). Success is quantified in terms of payoffs, which come from a game and represent competition between the different types, or strategies. Usually, the Wright–Fisher process is defined such that every subsequent generation has exactly the same size as the first generation. We consider a variant of this model for populations that fluctuate in size, in which each individual has a Poisson-distributed number of surviving offspring, with an expected value determined by payoffs from interactions in a game.

Recently, Houchmandzadeh (2015) considered a model similar to the one we study here, but under the assumption that the population size in the next generation, $N(x)$, is a deterministic function of the fraction of cooperators in the present generation, x. The update rule then has essentially two stages: (i) determine the population size of the next generation, $N(x)$, and (ii) sample $N(x)$ offspring from the previous generation using the standard Wright–Fisher rule. In contrast, the model we treat has a stochastic population size that does not need to be prespecified. Moreover, it depends on the numbers of both cooperators and defectors in the current generation, not just on the fraction of cooperators. As mentioned above, we also allow for the possibility that the entire population goes extinct.

We use the public goods game to study the evolution of cooperation in an unstructured population. Cooperators maintain a shared resource or public good, with a cost, w, to their fecundity. Defectors neither help maintain the public good nor incur a cost. The resource is distributed evenly among all individuals in the population, but its per-capita effect on fecundity can be greater than the per-capita cost of its production (Sigmund, 2010). A multiplication factor, $R > 1$, quantifies this return on the investment made by cooperators toward production of the good. In this model, everyone is better off when the whole population consists of cooperators, but defectors can benefit from cooperation without paying the cost.

We show that when the population size can fluctuate, selection can be essential for the survival of the population as a whole. In our model, population growth and decline are influenced by the public goods game but also by a baseline reproductive capacity, f_N, which is the same for all individuals and which primarily acts to constrain runaway growth. Even when cooperators are less frequent than defectors in the mutation–selection equilibrium, there can be an optimal cost of cooperation, w^*, depending on f_N, at which (i) the population does not immediately go extinct, with the numbers of cooperators and defectors each fluctuating around equilibrium values, and (ii) the frequency of cooperators is maximized subject to (i). In other words, cooperation can be favored by selection at a positive cost of cooperation when there is demographic stochasticity, which marks a departure from the behavior of models with fixed size.

Furthermore, even when the population would survive due to the baseline reproductive capacity alone, selection can increase the number of cooperators while at the same time decreasing their frequency. In models where the population size is assumed to be fixed, cooperators are less frequent than defectors if and only if cooperators are less abundant than defectors. However, this equivalence breaks down when the population size can fluctuate because the frequency of a strategy is determined by both its abundance and the population size. Thus, the evolutionary success of a strategic type depends on more than just the strategy.

2. Description of the model

We use the term "reproductive capacity" rather than "fitness" [see Doebeli et al., 2017] to refer to the expected number of offspring of an individual. In a growing population, the average reproductive capacity is greater than one. In a shrinking population, it is less than one. In a population of fixed size or a population at its carrying capacity, the average reproductive capacity is equal to one. If different individuals in the same population have different reproductive capacities, some individuals have a selective advantage over others.

2.1. Update rule

We assume that individuals reproduce asexually, so our model corresponds to a model of haploid genetic transmission. In the standard Wright–Fisher process, the population has fixed size, N. Thus, in a game with two strategies, C ("cooperate") and D ("defect"), the state of the population is determined by number of cooperators, x_C, or by their relative frequency, x_C/N. If $F_C = F_C(x_C)$ and $F_D = F_D(x_C)$ give the reproductive capacities of cooperators and defectors, respectively, in the state with x_C cooperators, then the probability of transitioning to the state with y_C cooperators (provided $0 \leqslant y_C \leqslant N$) is

$$\mathbf{P}(y_C \mid x_C) = \binom{N}{y_C} \left(\frac{x_C F_C}{x_C F_C + (N - x_C) F_D} \right)^{y_C}$$
$$\times \left(\frac{(N - x_C) F_D}{x_C F_C + (N - x_C) F_D} \right)^{N - y_C}. \tag{1}$$

In other words, the cooperators in one generation are sampled from the previous generation according to a binomial distribution with mean $N x_C F_C / (x_C F_C + (N - x_C) F_D)$. One biological interpretation for this transition rule is the following: Each player in one generation produces a large number of gametes from which the surviving offspring in the next generation are selected. These offspring are sampled at random, weighted by the success of the parents in competitive interactions, subject to a constant population size.

In treating populations that fluctuate in size, we drop the assumed dependence that $y_D = N - y_C$ which is implied above, but continue to hold that generations are non-overlapping. Let $F_C = F_C(x_C, x_D)$ and $F_D = F_D(x_C, x_D)$ give the reproductive capacities of cooperators and defectors, respectively, when the current generation is in state (x_C, x_D). We assume that the number of offspring per individual follows a Poisson distribution, with parameter F_C for cooperators and parameter F_D for defectors. The probability of transitioning from state (x_C, x_D) to state (y_C, y_D) in one generation is then

$$\mathbf{P}(y_C, y_D \mid x_C, x_D) = \left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!} \right) \left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!} \right). \tag{2}$$

Eq. (2) reduces to Eq. (1) when the population size is fixed and equal to N (see Haccou et al., 2005 and also Appendix A.)

The transition probabilities of Eqs. (1)–(2) do not take into account errors in strategy transmission, i.e. mutations. In what

follows, we assume that when an individual reproduces, the offspring acquires a random strategy with probability $u \geqslant 0$. Thus, with probability $1 - u$, the offspring acquires the strategy of the parent and with probability u, becomes either a cooperator or a defector (uniformly at random). For simplicity (and by convention [e.g. see Tarnita et al., 2009b]), we assume symmetric mutation, with $C \rightarrow D$ as likely as $D \rightarrow C$.

Using the binomial distribution with parameter q and density function $b_q(n, k) := \binom{n}{k} q^k (1 - q)^{n-k}$, the mutation rate, u, is incorporated into the transition rule defined by Eq. (2) as follows:

$$\mathbf{P}^u(y_C, y_D \mid x_C, x_D) = \sum_{z_C=0}^{y_C+y_D} \mathbf{P}(z_C, y_C + y_D - z_C \mid x_C, x_D)$$

$$\times \sum_{k=\max\{0, z_C-y_C\}}^{\min\{z_C, y_C\}} b_{u/2}(z_C, k) b_{u/2}(y_C + y_D - z_C, k + y_C - z_C). \quad (3)$$

In words, we sum over all transitions defined by Eq. (2) such that, after mutations are accounted for, there are y_C cooperators and y_D defectors. Note that mutations themselves do not affect the population size.

We refer to the process with transitions governed by Eqs. (2)–(3) as a "Wright–Fisher branching process". Branching processes of this sort have been treated elsewhere [see (Haccou et al., 2005)], notably with Poisson-distributed offspring counts but frequency-independent reproductive capacities (Haccou and Iwasa, 1996). Branching processes have also been considered in models with both density-dependent (Lambert, 2005) and frequency-dependent (Wild, 2011; Bao and Wild, 2012) reproductive capacities. We consider a Wright–Fisher branching process in which the reproductive capacities of cooperators and defectors in Eqs. (2)–(3) are equal to a baseline reproductive capacity times a factor which depends on the outcome of a public goods game.

2.2. Baseline reproductive capacity

The standard Wright–Fisher model, and variants like that in Houchmandzadeh (2015), assume that population regulation is very strong or deterministic. This may be a good approximation for large populations and those close to carrying capacity [but see (Chotibut and Nelson, 2017)]. However, fully stochastic treatments are warranted for populations that fluctuate in size and may go extinct. In the Wright–Fisher branching process we consider, population regulation is achieved through a balance of players' payoffs in an evolutionary game and a baseline reproductive capacity which represents all other ecological factors. The dynamics depend on the numbers of cooperators and defectors, not just on their relative frequencies. The baseline reproductive capacity is a function of the total population size and is the same for every individual. It captures the ecological constraints which keep populations from growing without limit.

Let f_N be the per-capita reproductive capacity (again, the expected number of offspring) applicable to all individuals when the population size is N. We assume that f_N is a non-increasing function of the population size, N, so that larger populations lead (in general) to lower per-capita reproductive capacities due to ecological constraints. This baseline reproductive capacity is the fluctuating-size analogue of the "background fitness" that is typically used in models with fixed population size (Nowak et al., 2009).

While the baseline reproductive capacity does not vary from player to player, it can depend on the number of players in the population, N. If there are limited resources and reproduction slows as the population grows, then f_N is a decreasing function of N. An example we consider is $f_N = c_K + r \left(1 - \frac{N}{K}\right)$ for some c_K, r, and K. In this case, r reflects the growth rate when the population is

small, and c_K gives the reproductive capacity when the population has size $N = K$. To ensure f_N is non-negative, we set $f_N = 0$ whenever $c_K + r \left(1 - \frac{N}{K}\right) \leqslant 0$. A second example we consider is one in which the baseline reproductive capacity is constant up to a threshold value of N and decreasing thereafter, specifically with $f_N = 1 + r$ if $N \leqslant K$ and $f_N = (1+r) K/N$ if $N > K$ for some r and K. For both of these functions, f_N decays to 0 as $N \rightarrow \infty$ (see Fig. 1).

2.3. Public goods game

Consider a game with two strategies, C ("cooperate") and D ("defect"), and suppose that a defector does nothing and a cooperator incurs a cost, w, representing a fraction of his or her baseline reproductive capacity, f_N, in order to contribute to the provision of a public good. The public good is distributed evenly among all N players in the population (Sigmund, 2010). Finally, a multiplication factor, $R > 1$, quantifies the return on investment in this shared resource (Chen et al., 2012).

The reproductive capacities of cooperators and defectors in state (x_C, x_D) are given by

$$F_C(x_C, x_D) = \left(1 - w + wR \frac{x_C}{x_C + x_D}\right) f_{x_C+x_D}; \quad (4a)$$

$$F_D(x_C, x_D) = \left(1 + wR \frac{x_C}{x_C + x_D}\right) f_{x_C+x_D}. \quad (4b)$$

When $w \ll 1$, the contribution of this game to reproductive capacity is small. On the other hand, when $w = 1$, cooperators expend their entire baseline reproductive capacity contributing to the public good. Unlike in many evolutionary games in populations of fixed size, where w represents selection strength and quantifies relative differences between traits, here the cost of cooperation admits an intuitive biological interpretation: cooperators sacrifice a fraction w of their expected number of offspring in hopes of seeing a return.

For a neutral population whose dynamics are governed only by the non-increasing baseline reproductive capacity, f_N, if $f_1 < 1$ then the time to extinction will be relatively short. In contrast, if $f_1 > 1$ the population will have a positive growth rate until N becomes large enough that $f_N < 1$. Then the population will reach a stochastic carrying capacity and fluctuate around this size, possibly for considerable time. (For the two classes of baseline reproductive capacities we consider here, this carrying capacity need not be exactly K; see Appendix A). We will refer to situations of this sort as "metastable" because all the populations we consider would eventually go extinct. According to Eq. (4), payoffs from the public goods game can increase reproductive capacities, with the possibility of positive population growth rates even if $f_1 < 1$. Due to our choice of non-increasing functions for f_N (that decay to 0 as N grows), this will lead to metastable states but never to unbounded growth of the population.

3. Evolutionary dynamics of the Wright–Fisher branching process

Let $\mathbf{E}_{(x_C, x_D)}[y_C]$ and $\mathbf{E}_{(x_C, x_D)}[y_D]$ denote the expected numbers of cooperators and defectors in the next generation given x_C cooperators and x_D defectors in the current generation. In this section, we are mainly interested in the existence of metastable equilibria, which are defined as states, (x_C^*, x_D^*), such that

$$\mathbf{E}_{(x_C^*, x_D^*)}[y_C] = x_C^*; \quad (5a)$$

$$\mathbf{E}_{(x_C^*, x_D^*)}[y_D] = x_D^*. \quad (5b)$$

Populations will fluctuate around these states for some time, although extinction is inevitable. The time to extinction depends on
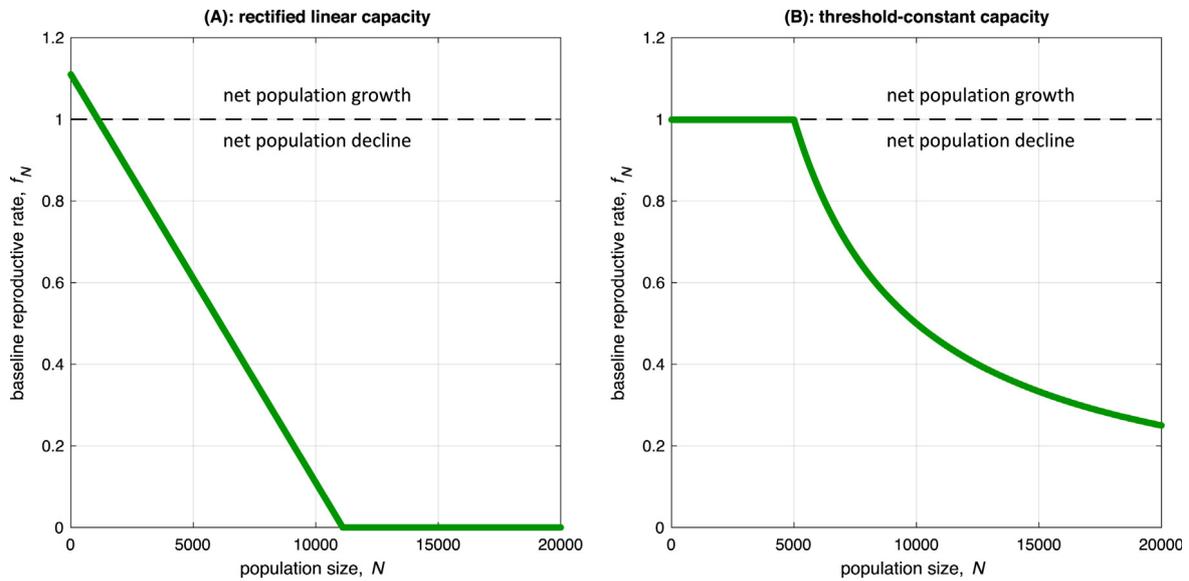
Fig. 1. Two examples of baseline reproductive capacities, f_N. In (A), $f_N = \max\left\{0, c_K + r\left(1 - \frac{N}{K}\right)\right\}$ for $c_K = 1.1$, $r = 0.01$, and $K = 100$. This function decreases linearly to 0 and remains at 0 for all sufficiently large N since the reproductive capacity is (by definition) non-negative. This function is called "rectified" linear because of the constraint that $f_N \geqslant 0$. In (B), $f_N = (1 + r)\min\left\{1, \frac{K}{N}\right\}$ for $r = -0.001$ and $K = 5000$. The reproductive capacity is held constant and equal to $1 + r$ whenever $1 \leqslant N \leqslant K$. When the population size is greater than K, the resources contributing to reproductive capacities are no longer abundant and must be divided up among the individuals in the population, which gives the expression $f_N = (1 + r)\frac{K}{N}$ for $N \geqslant K$. This function is called "threshold-constant" because it is constant up to the threshold population size $N = K$. Note that in (A), when the population size is initially small, there is net population growth since $f_1 > 1$. In (B), $f_N < 1$ for every N, so any population evolving according to this function alone will (on average) shrink in the direction of extinction. This immediate extinction could be prevented by choosing $r > 0$ instead of $r < 0$ as in (B).

the population's carrying capacity (see below and Appendix C). Even when the population eventually goes extinct with probability 1, it can take extremely long to do so.

We are particularly interested in the case when a population of defectors cannot survive for long on their own but a population of cooperators can. While a population of defectors evolves according to f_N, a population of cooperators evolves according to the reproductive capacity $(1 + w(R - 1))f_N$, which can be greater than 1 even when $f_N < 1$. In polymorphic populations, cooperators and defectors have reproductive capacities given by $F_C(x_C, x_D)$ and $F_D(x_C, x_D)$ in Eq. (4), which are functions of x_C and x_D, but also depend on the baseline reproductive capacity, f_N, the cost of cooperation, w, and the multiplication factor for the public good, R. We also consider situations in which a population of defectors can reach a metastable carrying capacity, i.e. when $f_1 > 1$. In this case, we are interested in the effects that w and R can have on the numbers of cooperators and defectors in polymorphic metastable states.

3.1. Selection dynamics (without mutation)

When the initial numbers of cooperators and defectors are small, stochastic effects have a profound influence over the long-run composition of the population. We show in Appendix B that any non-zero metastable equilibrium must be monomorphic (all-cooperator or all-defector) for the update rule defined by Eq. (2). Although defectors generally have larger growth rates than cooperators in mixed populations, they can go extinct quickly in small populations, which, in turn, can permit cooperators to prosper. For example, suppose that defectors cannot survive on their own ($f_1 < 1$), which means that any population of defectors shrinks, on average, from one generation to the next. If any population of cooperators grows, due to the multiplication factor $R > 1$, then the only populations that persist beyond a short time horizon are those composed entirely of cooperators. Therefore, cooperators have a type of survivorship bias. Fig. 2 illustrates this phenomenon,

showing that defectors often outcompete cooperators (approximately 85% of the time) when both are in the population (A), but once one type goes extinct, the population must consist of just cooperators in order to survive for any considerable length of time (B). These simulations are done with the baseline capacity $f_N = \max\left\{0, c_K + r\left(1 - \frac{N}{K}\right)\right\}$, where $c_K = 0.99$, $r = 0.01$, and $K = 100$; cost of cooperation $w = 0.1$; and multiplication factor $R = 2.0$.

3.2. Mutation–selection dynamics

A common way to quantify the evolutionary success of cooperators is to introduce strategy mutations and study the frequency of cooperators in the mutation–selection equilibrium (Tarnita et al., 2009b; Antal et al., 2009a; Tarnita et al., 2011). Mutations indicate errors in the transmission (either cultural or genetic) of the two strategies (cooperation and defection) and can be small (Nowak, 2006b; Wu et al., 2011) or large (Traulsen et al., 2009) depending on their interpretation. The success of cooperation is quantified by its average frequency in the population over many generations. In a population of cooperators and defectors under neutral drift (i.e. without selective differences between the two types), cooperators are indistinguishable from defectors and are equally frequent in the mutation–selection equilibrium. If selection brings the cooperator frequency above 1/2, then selection is said to favor cooperation. By this metric, selection typically disfavors cooperation in unstructured populations (Tarnita et al., 2009b).

If the population size is static and the update rule is that of the Wright–Fisher process, Eq. (1), then the baseline reproductive capacity appearing in Eq. (4), f_N, cancels out. Only the relative fitnesses of cooperators and defectors matters. The dynamics are then captured in the relative frequencies of cooperators and defectors. Since cooperators are always less frequent than defectors when the intensity of selection, w, is positive, selection unambiguously disfavors cooperators relative to defectors. This result can be seen in Fig. 3(D)–(F), in which results are shown for three different values of w. These simulations were generated using a
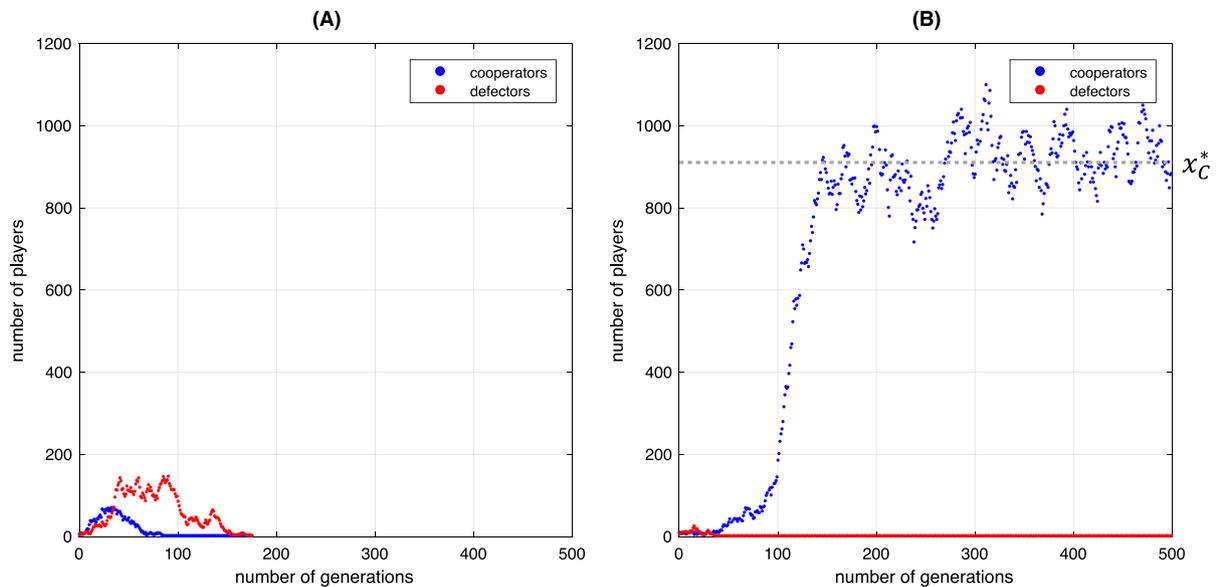
(A) **(B)**

Fig. 2. Dynamics of the Wright–Fisher branching process in the absence of mutation. The baseline reproductive capacity is given by $f_N = \max\left\{0, c_K + r\left(1 - \frac{N}{K}\right)\right\}$, where $c_K = 0.99$, $r = 0.01$, and $K = 100$. The initial population consists of just 5 cooperators and 5 defectors. Approximately 15% (rounded to the nearest percentage) of runs result in the behavior of panel (B), with defectors going extinct and cooperators reaching their carrying capacity. The remaining runs resemble panel (A), with almost-immediate extinction of the entire population. Without mutation, any metastable equilibrium is necessarily monomorphic; since defectors cannot survive on their own ($f_1 < 1$), it follows that only all-cooperator states can be observed as the long-run outcome of these initial conditions. Notably, while defectors go extinct in fewer than 200 generations in (A), in (B) the population of cooperators thrives even after 10^9 generations (although it goes extinct, eventually, with probability 1). To demonstrate the initial ascent of cooperators, we include here only the first 500 generations. Parameters: $u = 0$, $w = 0.1$, and $R = 2.0$.

multiplication factor of $R = 2.0$ and a mutation rate of $u = 0.01$. That selection favors defectors is a standard property of many social dilemmas in unstructured populations; additional mechanisms (such as spatial structure) must typically be present in order for cooperators to outperform defectors (Nowak et al., 2009).

When the population size can fluctuate and u is the probability that a mutation occurs, then the dynamics are governed by Eq. (3). Here, it is still the case that selection decreases the frequency of cooperators relative to defectors. On the other hand, the population can quickly go extinct if selection is not sufficiently strong, which we illustrate in Fig. 3(A)–(C) with $R = 2.0$, $u = 0.01$, and $f_N = (1 + r) \min\left\{1, \frac{K}{N}\right\}$ with $r = -0.001$ and $K = 5000$. Thus, cooperation can be favored in such situations because it protects against extinction.

One key difference from models with fixed population size is that, in a branching process, the population either grows unboundedly or eventually goes extinct (Jagers and Klebaner, 2012; Hamza et al., 2015). That is, if the population remains bounded in size, then the only true stationary state is extinction. Despite this behavior capturing the long-run dynamics of the process, there can also exist metastable equilibria in which the process persists prior to population extinction. We show in Appendix C that the persistence time grows exponentially in K [see also (Jagers and Klebaner, 2011; Faure and Schreiber, 2014; Schreiber, 2017)], meaning that if $\mathbf{E}[\tau_K]$ is the expected number of generations prior to extinction after starting in the quasi-stationary distribution, then there exists $c > 0$ (independent of K) for which $\mathbf{E}[\tau_K] \geqslant e^{cK}$.

More informally, if $\left(x_C^*, x_D^*\right)$ is a metastable equilibrium and σ denotes standard deviation, then

$$\sigma_{(x_C^*, x_D^*)}[y_C] / \mathbf{E}_{(x_C^*, x_D^*)}[y_C] = \frac{1}{\sqrt{x_C^*}}; \qquad (6a)$$

$$\sigma_{(x_C^*, x_D^*)}[y_D] / \mathbf{E}_{(x_C^*, x_D^*)}[y_D] = \frac{1}{\sqrt{x_D^*}}. \qquad (6b)$$

Therefore, the fluctuations around a metastable equilibrium constitute only small fractions of x_C^* and x_D^* when x_C^* and x_D^* are sufficiently large (see Appendix B for further details). Since x_C^* and x_D^*

grow with K, and since the fluctuations in x_C^* and x_D^* are on the order of $\sqrt{x_C^*}$ and $\sqrt{x_D^*}$, respectively, the expected amount of time until deviations from the mean destroy the population, i.e. deviates so far as to hit $(x_C, x_D) = (0, 0)$, grows rapidly in K. Fig. 4 shows the quasi-stationary distributions of x_C and x_D that result from fluctuations around metastable equilibria, such as those shown in Fig. 3(C).

The dynamics of this public goods game result from the balance among three factors: mutation, selection, and population survival. Although long-term population survival can be achieved by increasing the cost of cooperation, w, it can also be destroyed by decreasing the mutation rate, u. In Appendix B, we show that for any $N \geqslant 1$ and any non-zero mutation rate and cost of cooperation, there exists a critical multiplication factor, R_N^*, such that the population is supported at a metastable equilibrium consisting of at least N players whenever $R > R_N^*$. In general, the harmful effect (population extinction) of either low costs of cooperation or low mutation rates can be mitigated by increasing the return on investment in the public good.

Selection can also increase cooperator abundance while decreasing their relative frequency (Fig. 5). This phenomenon is a consequence of the fact that the presence of cooperators can change the carrying capacity of population. That abundance and frequency can move in opposite directions is unique to models with variable population size and presents an interesting question about the definition of cooperator success. We show in Appendix B that the fraction of cooperators present in a metastable equilibrium is independent of f_N and depends on just u, w, and R. Thus, when u, w, and R are fixed, defectors claim a fixed fraction (at least 1/2) of the total population, which means that cooperators are disfavored relative to defectors. However, based on population growth alone, cooperators could be considered to be favored by selection in an absolute sense because their abundance is an increasing function of the cost of cooperation, w.

4. Discussion

Public goods games have been used to model conflicts of interest ranging from cooperation in microorganisms (Craig MacLean

Dynamic population size (Wright–Fisher branching process)

Constant population size (Wright–Fisher process)
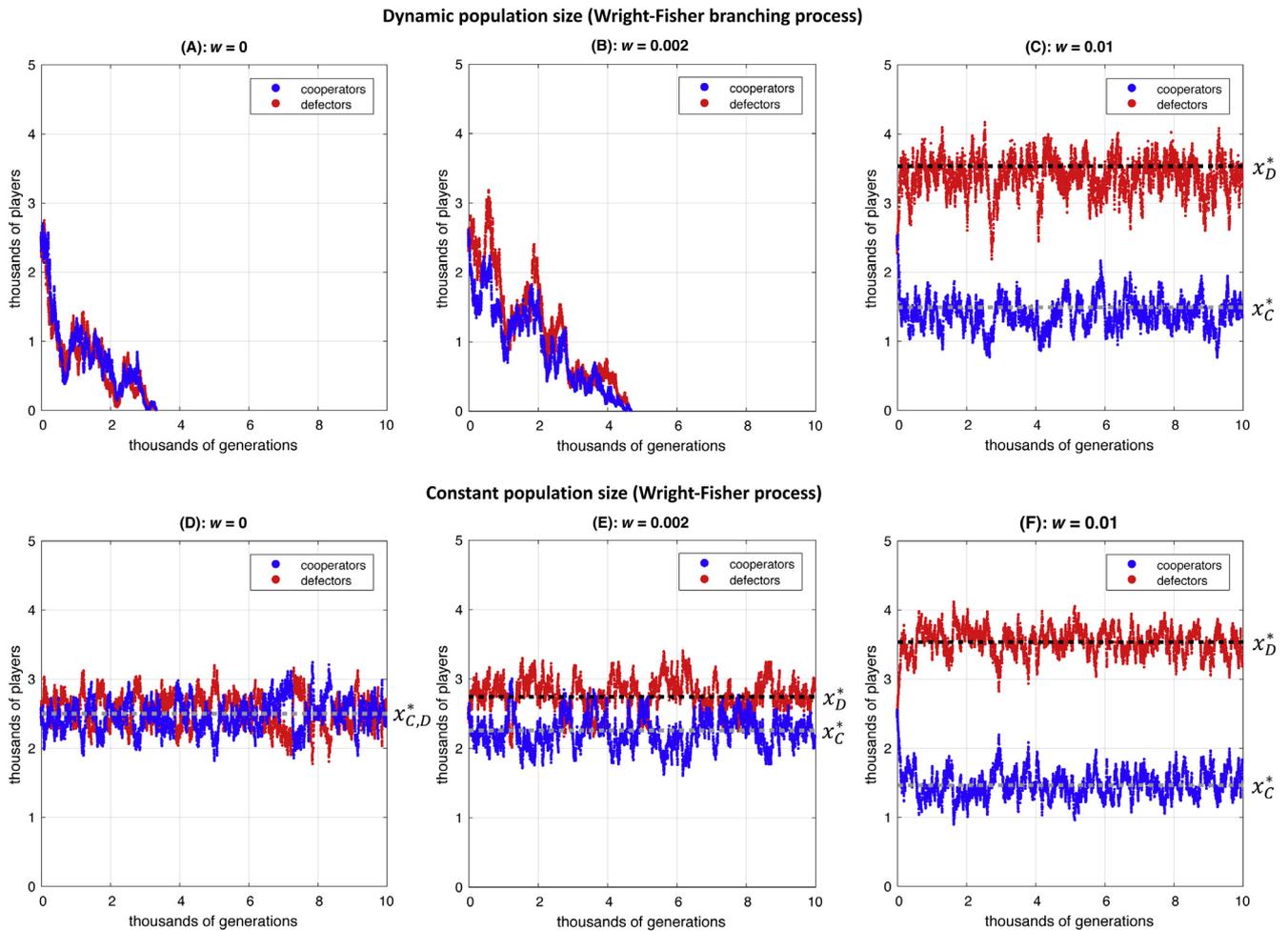

Fig. 3. Mutation–selection dynamics for the Wright–Fisher branching process (panels (A)–(C)) and the Wright–Fisher process with constant population size (panels (D)–(F)). The baseline reproductive capacity is $f_N = (1 + r) \min\left\{1, \frac{K}{N}\right\}$, where $r = -0.001$ and $K = 5000$, although this is relevant only for (A)–(C) since the population size is held fixed in (D)–(F). In all panels, the population initially consists of 2500 cooperators and 2500 defectors, the strategy mutation rate is $u = 0.01$, and the multiplication factor for the public goods game is $R = 2.0$. In the top row, the population size can fluctuate over time; in the bottom row, it is held constant at 5000 players. In (A) and (D), there are no selective differences between cooperators and defectors ($w = 0$). In (B) and (E), a cooperator sacrifices a small fraction, $w = 0.002$, of his or her baseline reproductive capacity in order to provide the community with a benefit. In (C) and (F), cooperators sacrifice a larger portion, $w = 0.01$, of their reproductive capacity when provisioning a public good. While the population is artificially prevented from going extinct in (D)–(F), it can go extinct in (A)–(C) and does so quickly when the cost of cooperation is too small (panels (A) and (B)) since $f_1 < 1$. Although increasing the cost of cooperation tends to decrease the frequency of cooperators relative to defectors, a sufficient amount of selection is necessary for the survival of the population as a whole. Therefore, there is an optimal cost of cooperation, w^*, falling between 0.002 and 0.01, that maximizes the frequency of cooperators subject to survival of the population.

and Brandon, 2008; Czárán and Hoekstra, 2009; Cordero et al., 2012; Sanchez and Gore, 2013; Allen et al., 2013), to alarm calls in monkeys (Seyfarth et al., 1980; Clutton-Brock, 2016), sentinel behavior in meerkats (Clutton-Brock et al., 1999), and large-scale human efforts aimed at combating climate change (Milinski et al., 2006; Jacquet et al., 2013) and pollution (Ehmke and Shogren, 2008). Due to its linearity and close relationship to the prisoner's dilemma, the public goods game we consider is sometimes called the "*N*-person prisoner's dilemma" (Archetti and Scheuring, 2012). Provided $1 \leqslant R \leqslant N$, this game presents a conflict of interest between the group and the individual that can be reduced to a sequence of $N - 1$ prisoner's dilemma interactions (Hauert and Szabó, 2003). However, the analysis and interpretation of a single public goods game is somewhat more straightforward than that of a series of prisoner's dilemma interactions when the population size fluctuates over time.

In populations of fixed size, extinction is impossible and defectors can survive without the support of cooperators. This point marks perhaps the most prominent feature of classical models in evolutionary game theory that breaks down when the population size can fluctuate over time. When populations vary in size and

defectors cannot sustain themselves on their own, cooperators must be present and selection must be sufficiently strong in order to maintain the existence of the population (Fig. 3). Furthermore, when the population size is assumed to be fixed, selection decreases the frequency of cooperators if and only if it decreases the number, or abundance, of cooperators. In fluctuating populations, selection can decrease the frequency of cooperators while increasing their abundance (Fig. 5).

We have referred to w as the "cost of cooperation" because of its interpretation as the expected fraction of offspring that must be sacrificed in order to cooperate. However, we note that because this fraction of an individual's baseline reproductive capacity is shared across the population, larger w also means a greater effect of cooperation (similar to the return, R). Further, if $w = 0$ then the population is identical to a population of defectors. In standard Wright–Fisher processes, f_N is irrelevant and it is common to rewrite the terms in Eq. (4) as $F_C = 1 + w\pi_C$ and $F_D = 1 + w\pi_D$, and to refer to w the "strength" (Antal et al., 2009a; Chastain et al., 2014; Allen et al., 2017) or "intensity" of selection (Nowak et al., 2004; Wu et al., 2010, 2013). When the population size is held
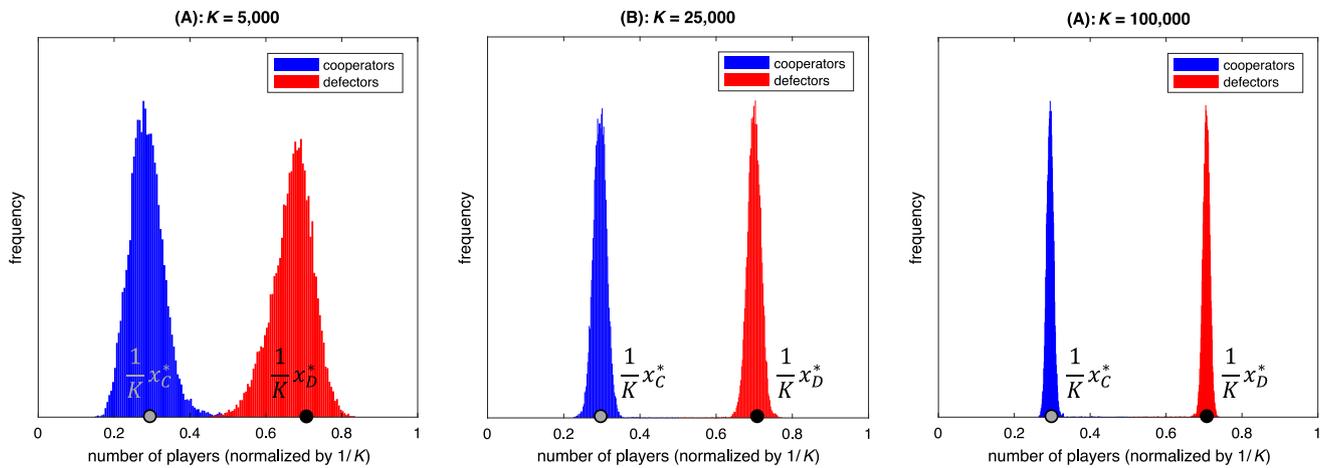
Fig. 4. Simulation of the quasi-stationary distribution for several values of K. Here, K enters in the baseline reproductive capacity, $f_N = (1 + r) \min \left\{ 1, \frac{K}{N} \right\}$, where $r = -0.001$. In each panel, cooperators and defectors are each initialized at an equal abundance of $K/2$. The plots are histograms for cooperator (blue) and defector (red) abundance over the first 25 000 generations. The equilibrium fraction of cooperators, p, depends on only u, w, and R and is the same for all panels. Therefore, the peaks are centered at $x_C^*/K = 0.999x \left(1 + w (R - 1) x\right) \approx 0.2954$ for cooperators and $x_D^*/K = 0.999 \left(1 - x\right) \left(1 + w (R - 1) x\right) \approx 0.7066$ for defectors (see Appendix B). As K grows, this quasi-stationary distribution converges to the Dirac measure centered on $(0.2954, 0.7066)$. Parameters: $u = w = 0.01$ and $R = 2.0$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
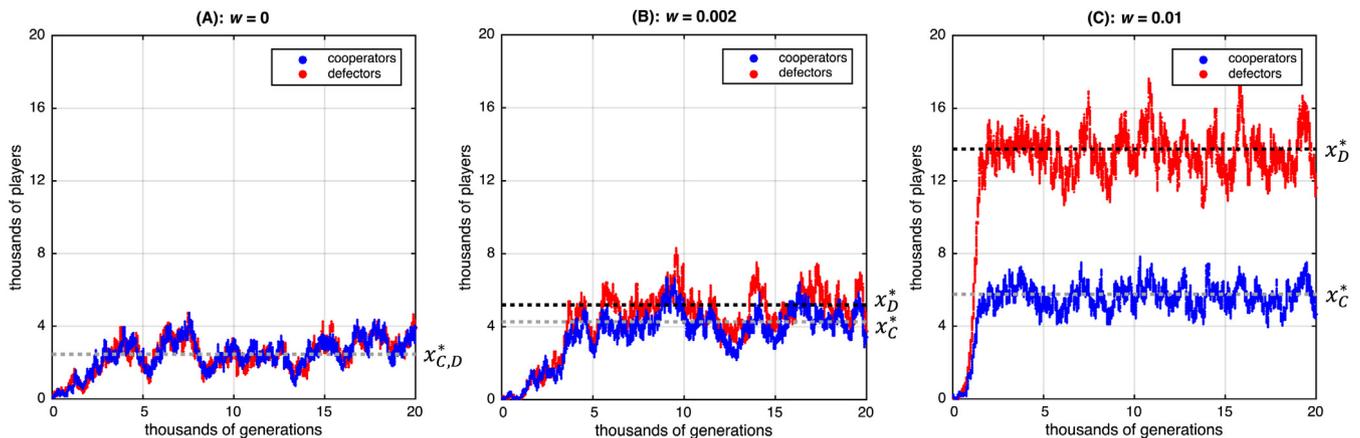

Fig. 5. Mutation–selection dynamics when a population of defectors can sustain itself at a positive carrying capacity ($f_1 > 1$). The baseline reproductive capacity is $f_N = \max \left\{ 0, c_K + r \left(1 - \frac{N}{K}\right) \right\}$, where $c_K = 1$, $r = 0.001$, and $K = 5000$. In each panel, the population starts out with 100 cooperators and 100 defectors. In (A), $w = 0$ and cooperators are indistinguishable from defectors. The population grows to a metastable equilibrium with roughly equal frequencies of cooperators and defectors; $\left(x_C^*, x_D^*\right) = (2500, 2500)$. In (B), the cost of cooperation is positive ($w = 0.002$) and defectors begin to outnumber cooperators; $\left(x_C^*, x_D^*\right) \approx (4287, 5219)$. At the metastable equilibrium, however, cooperators in (B) slightly outnumber cooperators in (A). In (C), the cost of cooperation is increased to $w = 0.01$ and the gap between cooperator and defector abundance widens; $\left(x_C^*, x_D^*\right) \approx (5806, 13890)$. Although cooperators are less frequent than defectors in (C), they are more abundant in (C) than they were in (A) and (B), suggesting that their abundance is favored by selection even though their relative frequency is not. Parameters: $u = 0.01$ and $R = 2.0$.

constant in our model, w corresponds exactly to this well-known notion of selection intensity.

That the frequencies of cooperators relative to defectors in the metastable equilibria of Figs. 3(C), 3(F), and 5(C) are all the same is not a coincidence. The fraction of cooperators, p, present at a metastable equilibrium is independent of the baseline reproductive capacity, f_N, and depends on only the mutation rate, u; the cost of cooperation, w; and the multiplication factor for the public goods game, R. The population size at a metastable equilibrium, however, does depend on f_N. In Appendix B, we give an explicit formula for p and a condition for the existence of a non-zero metastable equilibrium in terms of f_N, w, R, and p.

In the absence of mutation, either cooperators or defectors must be extinct in any metastable equilibrium. Although defectors outperform cooperators in a mixed population, a population of cooperators reaches a higher carrying capacity and persists at this size for a longer time than does a population of defectors. Small populations of cooperators have a distinct advantage over their all-defector counterparts due to larger growth rates. In particular,

quick extinction is less likely for all-cooperator populations than it is for all-defector populations, reflecting observations of Huang et al. (2015) and Waite et al. (2015) for related models.

Unlike in the models of Houchmandzadeh and Vallade (2012) and Houchmandzadeh (2015), the population size in our model is not a deterministic function of the fraction of cooperators. Rather, it is a random quantity derived from the collective offspring pool of the parental generation. The population size at time $t + 1$ depends on both the number of cooperators *and* the number of defectors at time t.

A framework more similar to ours is that of Behar et al. (2016), which uses stochastic differential equations to model the numbers of producers and non-producers of a common resource. Both numbers increase when small but eventually non-producers drive the population to extinction. Analogous to the possible role of mutations described here, Behar et al. (2016) allow migration to reseed populations with producers. A metastable equilibrium may then occur in the total population even as each local population experiences boom and bust cycles. Our focus here has been on

treating baseline reproductive dynamics as an exogenous feature and understanding on how these may be perturbed by a game to allow a variety of different carrying capacities to emerge depending on the parameters of the model.

Since population size can fluctuate in our model, one could also allow the multiplication factor of the public good, represented here by R, to change with N. If this multiplication factor gets weaker as N grows, then one observes dynamics similar to those here even if f_N is independent of N. Viewing R as a function of N presents an alternative way to model populations that cannot have unbounded growth due to environmental constraints. Another extension of our model could involve asymmetric mutation rates with, for example, $C \rightarrow D$ mutations more likely than $D \rightarrow C$. Although the importance of asymmetric mutation in population models is well-established (Eigen et al., 1988; Durrett and Schmidt, 2008; Arnoldt et al., 2012), we do not expect this would cause any qualitative changes in the results reported here unless the asymmetry was very extreme.

Incorporating dynamic population size into classical evolutionary models complicates the analysis of their dynamics. Notably, how one measures the evolutionary success of cooperators is not as unambiguous here as it is in models with fixed population size. We have shown that selection can favor cooperator abundance despite disfavoring cooperator frequency, and that even though cooperators are exploited by defectors, they can be crucial to the survival of the population as a whole.

Acknowledgments

Appendix A. Wright–Fisher branching process

A.1. Update rule

Suppose that the population is unstructured but allowed to vary in size. For simplicity, assume that we are dealing with a symmetric game with two strategies, C ("cooperate") and D ("defect"). A state of the population is then uniquely defined by a pair, (x_C, x_D), where x_C and x_C are the number of players using C and D, respectively. The population size is $N = x_C + x_D$, which can vary over time.

Suppose that the reproductive capacities of cooperators and defectors in state (x_C, x_D) are given by functions $F_C = F_C(x_C, x_D)$ and $F_D = F_D(x_C, x_D)$, respectively. That is, the reproductive capacities are frequency-dependent and determined by the number of each type of player in the population. We define reproductive capacity as the expected number of surviving offspring of an individual over its lifetime. Ours is therefore an "absolute" interpretation of reproductive capacity. We assume a reproductive mechanism in which the number of offspring is Poisson-distributed with mean equal to the parent's reproductive capacity. Therefore, the probability of transitioning from (x_C, x_D) to (y_C, y_D) over a single generation in this "Wright–Fisher branching process" is

$$\mathbf{P}_{\text{WFB}}(y_C, y_D \mid x_C, x_D) = \left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!} \right)$$
$$\times \left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!} \right). \tag{7}$$

As in the standard Wright–Fisher process, we assume that generations are non-overlapping.

Remark 1. If the population size is static and fixed at N, then, for $x_C + x_D = y_C + y_D = N$,

$\mathbf{P}_{\text{WFB}}(y_C, y_D \mid x_C, x_D ; \text{ fixed population size})$

$$= \frac{\left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!} \right) \left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!} \right)}{\sum_{z_C + z_D = N} \left(\frac{(x_C F_C)^{z_C} e^{-x_C F_C}}{z_C!} \right) \left(\frac{(x_D F_D)^{z_D} e^{-x_D F_D}}{z_D!} \right)}$$

$$= \frac{\left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!} \right) \left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!} \right)}{\frac{1}{N!} \sum_{z_C + z_D = N} N! \left(\frac{(x_C F_C)^{z_C} e^{-x_C F_C}}{z_C!} \right) \left(\frac{(x_D F_D)^{z_D} e^{-x_D F_D}}{z_D!} \right)}$$

$$= \frac{\left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!} \right) \left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!} \right)}{\frac{1}{N!} (x_C F_C + x_D F_D)^N e^{-(x_C F_C + x_D F_D)}}$$

$$= \frac{N!}{y_C! y_D!} \left(\frac{x_C F_C}{x_C F_C + x_D F_D} \right)^{y_C} \left(\frac{x_D F_D}{x_C F_C + x_D F_D} \right)^{y_D}$$

$$= \mathbf{P}_{\text{WF}}(y_C \mid x_C), \tag{8}$$

recovering the classical transition rule based on binomial sampling (Haccou et al., 2005). Therefore, the update rule defined by Eq. (7) may be thought of as a generalization of the classical, frequency-dependent Wright–Fisher process.

A.2. Reproductive capacities and selection

In the absence of selection, each player in a population of size N has a reproductive capacity determined by a baseline reproductive capacity, f_N. We consider the following two functional forms for f_N, examples of which are depicted in Fig. 1 in the main text.

A.2.1. Rectified linear

One natural way to model reproductive capacity is as a linear function of the population size, N. In this case, we can write $f_N = \max \left\{ 0, c_K + r \left(1 - \frac{N}{K} \right) \right\}$ for some parameters c_K, r, and K. We refer to f_N as a "rectified" linear reproductive capacity since it piecewise-linear with the constraint $f_N \geqslant 0$ for every N. Note that $f_{N^*} = 1$ when $N^* = K \left(1 - \frac{1}{r} (1 - c_K) \right)$. Therefore, N^* may be interpreted as the (neutral) carrying capacity of the population since, when $f_{N^*} = 1$, each individual is replaced by one offspring on average. Note that K itself is not necessarily the neutral carrying capacity for this form of f_N.

A.2.2. Threshold-constant

If the reproductive capacity is constant, then every player expects to produce $1 + r$ offspring that survive into the next generation, where $r \geqslant -1$. We assume that this growth is eventually bounded by environmental constraints, so we set $f_N = (1 + r) \min \{1, K/N\}$ for some K. We refer to f_N as a "threshold-constant" reproductive capacity since it is constant up to a threshold ($N = K$) and then decreasing to 0 beyond K. When $r < 0$, there is no solution to $f_N = 1$ since $f_N \leqslant 1 + r < 1$ for each N. When $r > 0$, we have $f_{(1+r)K} = 1$, so $N^* = (1 + r) K$ is the neutral carrying capacity of the population.

A.2.3. Selection

In a game with strategies C and D, let $\pi_C(x_C, y_C)$ and $\pi_D(x_C, x_D)$ be the total payoffs to C and D, respectively, when there are x_C cooperators and x_D defectors. If the population size is fixed, then a payoff of π is typically converted to a fitness of f by defining $f = 1 + w\pi$, where w is the "selection strength" [see Antal et al., 2009a, b]. This perturbation approach has even been extended to asymmetric games played between different populations (Veller and Hayward, 2016). While our setup is somewhat different, we maintain this convention of using payoffs from a game to perturb

reproductive capacities. In particular, if w is a parameter representing the intensity of selection, then the reproductive capacities of cooperators and defectors are given by

$$F_C(x_C, x_D) := \left(1 + w\pi_C(x_C, x_D)\right)f_{x_C+x_D}; \tag{9a}$$

$$F_D(x_C, x_D) := \left(1 + w\pi_D(x_C, x_D)\right)f_{x_C+x_D}, \tag{9b}$$

respectively. In other words, the baseline reproductive capacity, $f_{x_C+x_D}$, is perturbed by the game according to the strength of selection, w. In order to maintain non-negative reproductive capacities, w must be sufficiently small. In the next section, we consider a public goods game in which w has a clear biological interpretation.

Appendix B. Dynamics of the public goods game

In the public goods game, a cooperator sacrifices a fraction, w, of his or her baseline reproductive capacity in order to contribute to a public good. This contribution is enhanced by a factor of $R > 1$ and then distributed evenly among all of the players in the population. In terms of the payoff function in Eq. (9a), we have $\pi_C(x_C, x_D) = R\left(\frac{x_C}{x_C+x_D}\right) - 1$ and $\pi_D(x_C, x_D) = R\left(\frac{x_C}{x_C+x_D}\right)$ as well as Eq. (4) in the main text.

B.1. Metastable equilibria

Consider a population evolving according to the update rule of Eq. (3). As noted in the main text, such a branching process either grows without bound or eventually goes extinct. Even when the population has an extinction probability of 1, there can be so-called "metastable" states (or "equilibria") around which the population fluctuates for many generations. While a quasi-stationary distribution for the process describes the distribution of strategy abundances prior to extinction, a metastable equilibrium describes the mean(s) around which these strategy counts fluctuate. We are interested in when these metastable equilibria exist and how they are influenced by the parameters of the model.

Let $\mathbf{E}_{(x_C,x_D)}[y_C]$ (resp. $\mathbf{E}_{(x_C,x_D)}[y_D]$) be the expected abundance of cooperators (resp. defectors) in the next generation given x_C cooperators and x_D defectors in the current generation. Formally, a metastable equilibrium for this process is a state at which $\mathbf{E}_{(x_C^*,x_D^*)}[y_C] = x_C^*$ and $\mathbf{E}_{(x_C^*,x_D^*)}[y_D] = x_D^*$. That is, cooperator and defector abundances each remain unchanged (on average) at a metastable equilibrium. We use the term "metastable" because the population fluctuates around this state but eventually goes extinct. We discuss extinction time in Appendix C. First, we derive the metastable equilibria for public goods games.

B.1.1. Derivation of metastable equilibria

Let u be the strategy-mutation rate. With probability $1 - u$, an offspring acquires the strategy of the parent. With probability u, the offspring takes on one of C and D uniformly at random. In state (x_C, x_D), the expected number of cooperators in the next generation is

$$\begin{aligned}
\mathbf{E}_{(x_C,x_D)}[y_C] &= \sum_{(y_C,y_D)} \mathbf{P}_{\text{WFB}}(y_C, y_D \mid x_C, x_D) \\
&\quad \times \left(\left(1 - \frac{u}{2}\right)y_C + \left(\frac{u}{2}\right)y_D\right) \\
&= \sum_{(y_C,y_D)} \left(\frac{(x_C F_C)^{y_C} e^{-x_C F_C}}{y_C!}\right)\left(\frac{(x_D F_D)^{y_D} e^{-x_D F_D}}{y_D!}\right) \\
&\quad \times \left(\left(1 - \frac{u}{2}\right)y_C + \left(\frac{u}{2}\right)y_D\right) \\
&= \left(1 - \frac{u}{2}\right)x_C F_C + \left(\frac{u}{2}\right)x_D F_D. \tag{10}
\end{aligned}$$

Similarly, the expected number of defectors in the next generation is $\left(\frac{u}{2}\right)x_C F_C + \left(1 - \frac{u}{2}\right)x_D F_D$. Therefore, the system of equations we need to solve in order to find a metastable equilibrium is

$$x_C = \left(1 - \frac{u}{2}\right)x_C F_C + \left(\frac{u}{2}\right)x_D F_D; \tag{11a}$$

$$x_D = \left(\frac{u}{2}\right)x_C F_C + \left(1 - \frac{u}{2}\right)x_D F_D. \tag{11b}$$

In other words, it must be true that

$$\begin{aligned}
x_C &= \Big[\left(1 - \frac{u}{2}\right)x_C\left(1 + w\pi_C(x_C, x_D)\right) \\
&\quad + \left(\frac{u}{2}\right)x_D\left(1 + w\pi_D(x_C, x_D)\right)\Big]f_{x_C+x_D}; \tag{12a}
\end{aligned}$$

$$\begin{aligned}
x_D &= \Big[\left(\frac{u}{2}\right)x_C\left(1 + w\pi_C(x_C, x_D)\right) \\
&\quad + \left(1 - \frac{u}{2}\right)x_D\left(1 + w\pi_D(x_C, x_D)\right)\Big]f_{x_C+x_D}. \tag{12b}
\end{aligned}$$

These equations are trivially satisfied when $x_C = x_D = 0$ (population extinction). There can also be solutions to Eq. (12) with $x_C \neq 0$ or $x_D \neq 0$; we give a condition for the existence of non-zero solutions below.

Remark 2. If $u = 0$, then Eq. (12) reduces to the system

$$x_C = \left(1 + w\pi_C(x_C, x_D)\right)x_C f_{x_C+x_D}; \tag{13a}$$

$$x_D = \left(1 + w\pi_D(x_C, x_D)\right)x_D f_{x_C+x_D}. \tag{13b}$$

If x_C and x_D satisfy this system and $x_C, x_D \neq 0$, then

$$\left(1 + w\pi_C(x_C, x_D)\right)f_{x_C+x_D} = \left(1 + w\pi_D(x_C, x_D)\right)f_{x_C+x_D} = 1. \tag{14}$$

Therefore, either $w = 0$ and $f_{x_C+x_D} = 1$ or $w \neq 0$ and $\pi_C(x_C, x_D) = \pi_D(x_C, x_D)$. However, for the public goods game, it is always the case that $\pi_C(x_C, x_D) < \pi_D(x_C, x_D)$ when $x_C > 0$, so it must be true that $w = 0$ and $f_{x_C+x_D} = 1$. Thus, if $u = 0$ and $w > 0$, then any solution satisfies $x_C = 0$ or $x_D = 0$. In other words, in the absence of mutation, selection forces the extinction of at least one strategy.

Similarly, if $u > 0$ and there is a solution (x_C, x_D) with $x_C = 0$, then one obtains $x_D F_D = 0$ from Eq. (11a) and $x_D = 0$ from Eq. (11b). For a similar reason, if there is solution with $x_D = 0$, then it must also be true that $x_C = 0$. Thus, if (x_C, x_D) is a non-zero solution to Eq. (12) with $u > 0$, then $x_C > 0$ and $x_D > 0$.

Lemma 1. If $u > 0$, then there exists $p \in (0, 1)$ such that any non-zero solution to Eq. (12), (x_C, x_D), satisfies $\frac{x_C}{x_C+x_D} = p$. In other words, the fraction of cooperators is the same in any solution to Eq. (12).

Proof. If (x_C, x_D) is a solution to Eq. (12) with $x_C, x_D \geqslant 0$ and $x_C + x_D > 0$, then $p := \frac{x_C}{x_C+x_D}$ can be expressed in terms of the payoff functions by Eq. (15) as given in Box I. Since $\pi_C(x_C, x_D) = R\left(\frac{x_C}{x_C+x_D}\right) - 1$ and $\pi_D(x_C, x_D) = R\left(\frac{x_C}{x_C+x_D}\right)$, Eq. (15) is equivalent to

$$\begin{aligned}
\varphi(p) &:= 2(1 - uR)wp^2 + (uw(R + 1) - 2u - 2w)p + u \\
&= 0. \tag{16}
\end{aligned}$$

Since $\varphi(p)$ is (at most) quadratic, $\varphi(0) = u$, and $\varphi(1) = -u(1 - w + Rw)$, we see that if $u > 0$, then there is a unique solution to Eq. (15) that falls within $[0, 1]$, and, furthermore, this solution is in $(0, 1)$. Explicitly, p is given by Eq. (17) (which is given in Box II) if $R \neq 1/u$ and $w \neq 0$, and $p = u/(2u + (1 - u)w)$ if $R = 1/u$ or $w = 0$, which completes the proof. $\square$

From the proof of Lemma 1, we see that if $u = 0$, then either (i) $w = 0$ and every $p \in [0, 1]$ is a solution to Eq. (15) or (ii) $w > 0$ and the only solutions to Eq. (15) are $p = 0$ and $p = 1$. For any $u \in [0, 1]$, the fraction of cooperators in a non-zero metastable

$$p = \frac{x_C}{x_C + x_D}$$

$$= \frac{\left(1 - \frac{u}{2}\right) x_C \left(1 + w\pi_C \left(x_C, x_D\right)\right) + \left(\frac{u}{2}\right) x_D \left(1 + w\pi_D \left(x_C, x_D\right)\right)}{x_C \left(1 + w\pi_C \left(x_C, x_D\right)\right) + x_D \left(1 + w\pi_D \left(x_C, x_D\right)\right)}$$

$$= \frac{\left(1 - \frac{u}{2}\right) \left(\frac{x_C}{x_C + x_D}\right) \left(1 + w\pi_C \left(\frac{x_C}{x_C + x_D}, \frac{x_D}{x_C + x_D}\right)\right) + \left(\frac{u}{2}\right) \left(\frac{x_D}{x_C + x_D}\right) \left(1 + w\pi_D \left(\frac{x_C}{x_C + x_D}, \frac{x_D}{x_C + x_D}\right)\right)}{\left(\frac{x_C}{x_C + x_D}\right) \left(1 + w\pi_C \left(\frac{x_C}{x_C + x_D}, \frac{x_D}{x_C + x_D}\right)\right) + \left(\frac{x_D}{x_C + x_D}\right) \left(1 + w\pi_D \left(\frac{x_C}{x_C + x_D}, \frac{x_D}{x_C + x_D}\right)\right)}$$

$$= \frac{\left(1 - \frac{u}{2}\right) p \left(1 + w\pi_C \left(p, 1 - p\right)\right) + \left(\frac{u}{2}\right) (1 - p) \left(1 + w\pi_D \left(p, 1 - p\right)\right)}{p \left(1 + w\pi_C \left(p, 1 - p\right)\right) + (1 - p) \left(1 + w\pi_D \left(p, 1 - p\right)\right)}. \tag{15}$$

Box I.

$$p = \frac{uw\left(R + 1\right) - 2u - 2w + \sqrt{u^2 w^2 R^2 + 2u^2 w^2 R + 4u^2 wR - 4uw^2 R + u^2 w^2 - 4u^2 w + 4u^2 - 4uw^2 + 4w^2}}{4\left(uR - 1\right) w}. \tag{17}$$

Box II.

equilibrium is independent of the baseline reproductive capacity, f_N. However, the existence of a metastable equilibrium and the size of the population at such an equilibrium both depend on the baseline reproductive capacity. Suppose that $x_C = pN$ and $x_D = (1 - p) N$ satisfy Eq. (12), where $p \in [0, 1]$ is a fraction of cooperators that satisfies Eq. (15). From Eq. (12),

$$p = \left[\left(1 - \frac{u}{2}\right) p \left(1 + w\pi_C \left(p, 1 - p\right)\right) \right.$$
$$\left. + \left(\frac{u}{2}\right) (1 - p) \left(1 + w\pi_D (p, 1 - p)\right)\right] f_N; \tag{18a}$$

$$1 - p = \left[\left(\frac{u}{2}\right) p \left(1 + w\pi_C (p, 1 - p)\right) \right.$$
$$\left. + \left(1 - \frac{u}{2}\right) (1 - p) \left(1 + w\pi_D (p, 1 - p)\right)\right] f_N, \tag{18b}$$

which, in turn, holds if and only if the total population size, N satisfies

$$f_N = \frac{1}{1 + w\left(R - 1\right) p}. \tag{19}$$

The right-hand-side of Eq. (19) is independent of f_N, and once this quantity is calculated, it is straightforward to check for any f_N whether there exists N for which Eq. (19) holds. If f_N is strictly monotonic, then there exists at most one N that satisfies this equation. For other types of baseline reproductive capacities, there might be several such N that satisfy Eq. (19) (resulting in several non-zero metastable equilibria).

In addition to the simulations described in the main text, Figs. 6–7 demonstrate further effects of model parameters on metastable equilibria.

Lemma 2. *If $u \in (0, 1)$ and $w \neq 0$, then p is a strictly increasing function of R with $p \uparrow 1/2$ as $R \to \infty$.*

Proof. Since the polynomial defined by Eq. (16) satisfies $\varphi(0) = u$ and $\varphi(1/2) = -w(1 - u)/2$, we see that the solution to $\varphi(p) = 0$ that falls within $[0, 1]$ is actually at most $1/2$. Moreover, we can

write

$$\varphi_R(p) := \varphi(p) = 2(uR - 1)wp \left(\frac{1}{2} - p\right)$$
$$- \left((1 - u) w + 2u\right)p + u, \tag{20}$$

where, notably, only the coefficient of $p \left(\frac{1}{2} - p\right)$ depends on R. Thus, if $R_1 < R_2$ and p_1 satisfies $\varphi_{R_1}(p_1) = 0$, then $\varphi_{R_2}(p_1) > 0$. Since $\varphi(1/2) < 0$, the unique solution to $\varphi_{R_2}(p_2) = 0$ satisfies $p_2 > p_1$, thus p is an increasing function of R. That $p \uparrow 1/2$ as $R \to \infty$ follows immediately from taking the limit of Eq. (17). $\square$

Theorem 1. *Suppose that $f_N \downarrow 0$ as $N \to \infty$. If $u \neq 0$ and $w \neq 0$, then, for each $N \geqslant 1$, there is a critical multiplication factor, $R_N^* \geqslant 1$, which is the minimum multiplication factor for which there exists a non-zero metastable equilibrium supporting a population size of at least N whenever $R \geqslant R_N^*$.*

Proof. Since $p \uparrow 1/2$ as $R \to \infty$, we see that $\frac{1}{1+w(R-1)p} \downarrow 0$ as $R \to \infty$. Let

$$R_N^* := \inf \left\{ R \geqslant 1 \mid f_{N'} = \frac{1}{1 + w\left(R - 1\right) p} \text{ for some } N' \geqslant N \right\}. \tag{21}$$

Since $f_N \downarrow 0$ as $N \to \infty$, we have $R_N^* < \infty$. If $R \geqslant R_N^*$ and N' satisfies $f_{N'} = \frac{1}{1+w(R_N^*-1)p}$, then $(x_C^*, x_D^*) = (pN', (1 - p) N')$ is a metastable equilibrium by Eq. (18). Furthermore, if $R \geqslant R_N^*$, then

$$\frac{1}{1 + w\left(R - 1\right) p} \leqslant \frac{1}{1 + w\left(R_N^* - 1\right) p}, \tag{22}$$

and it follows that any solution to $f_{N''} = \frac{1}{1+w(R-1)p}$ satisfies $N'' \geqslant N' \geqslant N$, as desired. $\square$

Remark 3. If $\inf_{N \geqslant 1} f_N > 0$, then Theorem 1 need not hold. For example, whenever R is sufficiently large and $w \neq 0$, we have $\frac{1}{1+w(R-1)p} < \inf_{N \geqslant 1} f_N$, so no value of N satisfies Eq. (19).

B.1.2. Variance

In state (x_C, x_D), the expected squared number of cooperators in the next generation is
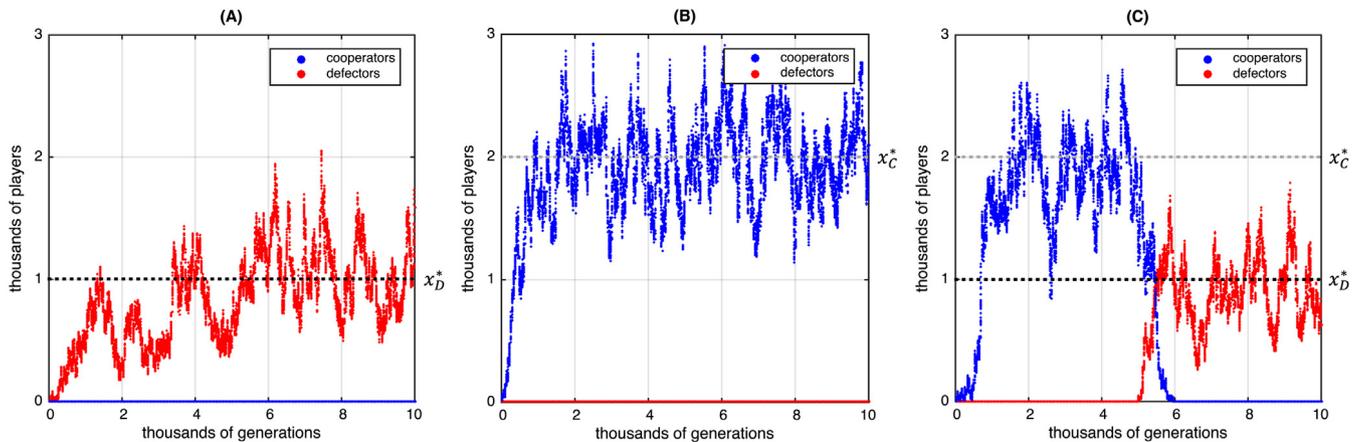
Fig. 6. Evolutionary game dynamics when there is no mutation and the baseline reproductive capacity, f_N, is defined by $f_N = \max\left\{0, c_K + r\left(1 - \frac{N}{K}\right)\right\}$, where $c_K = 1$, $r = 0.005$, and $K = 1000$. The multiplication factor for the public goods game is $R = 1.5$ and the cost of cooperation is $w = 0.01$. In (A), the population is initialized with no cooperators and 10 defectors. The defectors grow until they reach their carrying capacity of 1000 and then persist at this metastable equilibrium ($f_1 \geqslant 1$). In (B), the population is initialized with 10 cooperators and no defectors. The cooperators then grow in abundance until they reach their carrying capacity of approximately 2000 players. It is immediate from panels (A) and (B) that groups of cooperators perform better than groups of defectors since selection allows them to reach a higher carrying capacity. In (C), the population is initialized with 10 cooperators and no defectors, and the population then proceeds to reach its carrying capacity. After 5000 generations, an additional 10 defectors are introduced into the population, which disrupts the metastable equilibrium reached by the all-cooperator population. Defectors then outcompete and replace cooperators and finally reach their carrying capacity, which, as in (A), is significantly lower than the carrying capacity of an all-cooperator population.
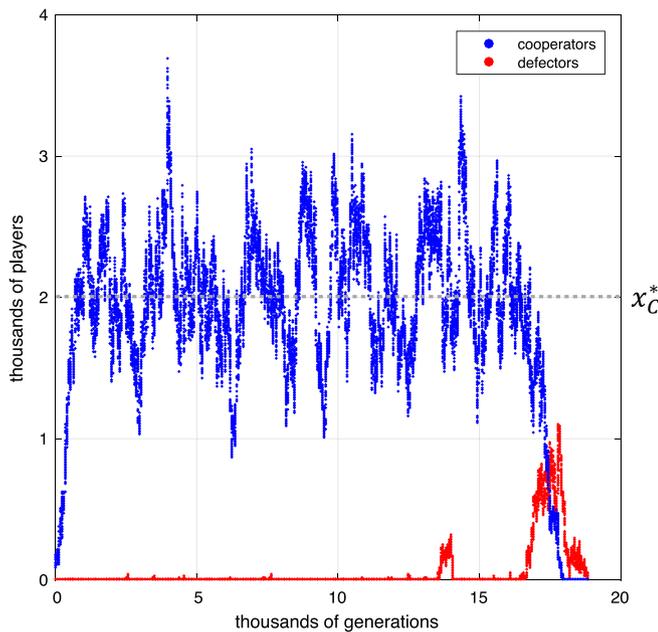

Fig. 7. Mutation–selection dynamics with drastically reduced mutation rates. The parameters used here are $u = 0.00001$, $w = 0.005$, and $R = 2.0$. The baseline reproductive capacity is $f_N = \max\left\{0, c_K + r\left(1 - \frac{N}{K}\right)\right\}$, where $c_K = 0.995$, $r = 0.005$, and $K = 2000$. The population is initialized with 100 cooperators and no defectors, and the cooperators then grow to reach their carrying capacity. Although small clusters of defectors are occasionally introduced through mutation, cooperators can resist invasion for a short period of time. Eventually, defectors invade and replace cooperators, and the population goes extinct due to the fact that defectors cannot survive on their own ($f_1 < 1$).

$$\mathbf{E}_{(x_C, x_D)}\left[y_C^2\right] = \sum_{(y_C, y_D)} \mathbf{P}_{\mathrm{WFB}}\left(y_C, y_D \mid x_C, x_D\right) m_2, \quad (23)$$

where

$$m_2 = \sum_{a=0}^{y_C} \sum_{b=0}^{y_D} (a+b)^2 \binom{y_C}{a}\left(1 - \frac{u}{2}\right)^a \left(\frac{u}{2}\right)^{y_C - a} \binom{y_D}{b}$$
$$\times \left(1 - \frac{u}{2}\right)^{y_D - b}\left(\frac{u}{2}\right)^{b}.$$

$$= \left(1 - \frac{u}{2}\right) y_C \left(1 + \left(1 - \frac{u}{2}\right)(y_C - 1)\right) + 2\left(\frac{u}{2}\right)$$
$$\times \left(1 - \frac{u}{2}\right) y_C y_D + \left(\frac{u}{2}\right) y_D \left(1 + \left(\frac{u}{2}\right)(y_D - 1)\right). \quad (24)$$

It follows from a straightforward calculation that

$$\mathbf{E}_{(x_C, x_D)}\left[y_C^2\right] = \left[\left(1 - \frac{u}{2}\right)(x_C F_C) + \left(\frac{u}{2}\right)(x_D F_D)\right]$$
$$+ \left[\left(1 - \frac{u}{2}\right)(x_C F_C) + \left(\frac{u}{2}\right)(x_D F_D)\right]^2$$
$$= \mathbf{E}_{(x_C, x_D)}\left[y_C\right] + \mathbf{E}_{(x_C, x_D)}\left[y_C\right]^2. \quad (25)$$

Therefore, $\mathbf{Var}_{(x_C, x_D)}\left[y_C\right] = \mathbf{E}_{(x_C, x_D)}\left[y_C\right]$, and, similarly, $\mathbf{Var}_{(x_C, x_D)}\left[y_D\right] = \mathbf{E}_{(x_C, x_D)}\left[y_D\right]$. Thus,

$$\sigma_{(x_C, x_D)}\left[y_C\right] / \mathbf{E}_{(x_C, x_D)}\left[y_C\right] = \frac{1}{\sqrt{\mathbf{E}_{(x_C, x_D)}\left[y_C\right]}}; \quad (26a)$$

$$\sigma_{(x_C, x_D)}\left[y_D\right] / \mathbf{E}_{(x_C, x_D)}\left[y_D\right] = \frac{1}{\sqrt{\mathbf{E}_{(x_C, x_D)}\left[y_D\right]}}, \quad (26b)$$

which both approach 0 as $\mathbf{E}_{(x_C, x_D)}\left[y_C\right]$ and $\mathbf{E}_{(x_C, x_D)}\left[y_D\right]$ get large.

Appendix C. Extinction time for branching games

We now characterize the extinction time for our model, inspired by techniques used in classical branching processes [see (Jagers and Klebaner, 2011; Faure and Schreiber, 2014; Schreiber, 2017)]. Let $x = (x_C/K, x_D/K)$ be normalized quantities of cooperators and defectors, where $K > 0$ parametrizes the baseline reproductive capacity, f_N. Let

$$A(x) := \begin{pmatrix} (1-u)F_C(xK) & uF_D(xK) \\ uF_C(xK) & (1-u)F_D(xK) \end{pmatrix}, \quad (27)$$

and consider the map, ϕ, defined by

$$\phi : \mathbb{R}_{\geqslant 0}^2 \longrightarrow \mathbb{R}_{\geqslant 0}^2$$
$$: x \longmapsto A(x)x. \quad (28)$$

Since F_C and F_D are bounded, so too is ϕ.

We consider the normalized Markov chain $X_t^K = (C_t/K, D_t/K)$, where C_t and D_t are the number of cooperators and defectors at time t, respectively. Write $p_K(x, y) = \mathbf{P}\left[X_{t+1}^K = y \mid X_t^K = x\right]$

for the transition kernel. The transition probabilities are Poisson-distributed with mean given by the matrix $A(x)$. Note that $p_K(\mathbf{0}, y) = 0$ for all $y \neq \mathbf{0}$ since $\mathbf{0}$ is an absorbing state.

A measure $\mu_K \in \Delta(\mathbb{R}^2_{\geq 0} - \mathbf{0})$ is a quasi-stationary distribution for p_K if there exists $\lambda_K \in (0, 1)$ such that

$$\int_{x \in \mathbb{R}^2_{\geq 0} - \mathbf{0}} p_K(x, E) \, d\mu_K(x) = \lambda_K \mu_K(E). \tag{29}$$

for all $E \subseteq \mathbb{R}^2_{\geq 0} - \mathbf{0}$. We denote the extinction time, i.e. the time until the chain is absorbed at the state $\mathbf{0}$, by τ_K. Note that, if we start distributed according to a quasi-stationary distribution, μ_K, then the probability of being absorbed in the next step is $1 - \lambda_K$ since

$$
\begin{aligned}
\mathbf{P}\left[X^K_{t+1} = \mathbf{0} \mid X^K_t \sim \mu_K\right] &= \int_{x \in \mathbb{R}^2_{\geq 0} - \mathbf{0}} p_K(x, \mathbf{0}) \, d\mu_K(x) \\
&= \int_{x \in \mathbb{R}^2_{\geq 0} - \mathbf{0}} \left(1 - p_K(x, \mathbb{R}^2_{\geq 0} - \mathbf{0})\right) d\mu_K(x) \\
&= 1 - \lambda_K. \tag{30}
\end{aligned}
$$

Moreover, if not absorbed in the next time step, the chain remains distributed according to μ_K. Therefore, the extinction time τ_K is a geometric random variable with parameter $1 - \lambda_K$, and $\mathbf{E}[\tau_K] = 1/(1 - \lambda_K)$, where $\mathbf{E}[\tau_K]$ denotes the expected value of τ_K when the chain is initially distributed according to μ_K.

Proposition 1. *There exists $c > 0$, independent of K, such that $\mathbf{E}[\tau_K] \geq e^{cK}$.*

Proof. For the model considered in the main text, ϕ has a unique fixed point, x^*, with $\phi(x^*) = x^*$. Moreover, this fixed point is an attractor. (One can show that the normalized quasi-stationary distribution μ_K converges weakly to δ_{x^*} as $K \to \infty$.) Therefore, there exists $\delta > 0$ and an open set, U, containing x^* such that $N_\delta(\phi(\overline{U})) \subseteq U$, where for $E \subseteq \mathbb{R}^2_{\geq 0} - \mathbf{0}$, the δ-neighborhood of E is defined as

$$N_\delta(E) := \left\{ y \in \mathbb{R}^2_{\geq 0} - \mathbf{0} \mid \inf_{x \in E} \|y - x\| < \delta \right\}. \tag{31}$$

By definition of the quasi-stationary distribution, μ_K, we have

$$
\begin{aligned}
\lambda_K \mu_K(U) &= \int_{x \in \mathbb{R}^2_{\geq 0} - \mathbf{0}} p_K(x, U) \, d\mu_K(x) \\
&\geq \int_{x \in U} p_K(x, U) \, d\mu_K(x) \\
&\geq \mu_K(U) \inf_{x \in \overline{U}} p_K(x, U) \\
&= \mu_K(U) \left(1 - \sup_{x \in \overline{U}} p_K(x, U^c)\right). \tag{32}
\end{aligned}
$$

For $x \in \overline{U}$, $\phi(x) \in \phi(\overline{U})$, which implies that $N_\delta(\phi(x)) \subset N_\delta(\phi(\overline{U})) \subset U$. Therefore,

$$
\begin{aligned}
\lambda_K &\geq 1 - \sup_{x \in \overline{U}} p_K(x, U^c) \\
&\geq 1 - \sup_{x \in \overline{U}} p_K(x, N_\delta(\phi(x))^c). \tag{33}
\end{aligned}
$$

To complete the proof, we bound $p_K(x, N_\delta(\phi(x))^c)$ via a large-deviation estimate based on the Chernoff–Cramer method. If Z is a Poisson random variable with mean $\phi(x)K$, then

$$
\begin{aligned}
p_K(x, N_\delta(\phi(x))^c) &= \mathbf{P}\left[X^K_{t+1} \notin N_\delta(\phi(x)) \mid X^K_t = x\right] \\
&= \mathbf{P}\left[\left|X^K_{t+1} - \phi(x)\right| > \delta \mid X^K_t = x\right] \\
&= \mathbf{P}\left[|Z - \phi(x)K| > \delta K\right]. \tag{34}
\end{aligned}
$$

Using Markov's inequality and the Poisson moment-generating function, we see that

$$\mathbf{P}[Z > (\phi(x) + \delta)K] \leq \frac{\mathbf{E}\left[e^{tZ}\right]}{e^{t(\phi(x)+\delta)K}} = \frac{e^{\phi(x)K(e^t - 1)}}{e^{t(\phi(x)+\delta)K}}. \tag{35}$$

As a function of t, the minimum of $\frac{e^{\phi(x)K(e^t-1)}}{e^{t(\phi(x)+\delta)K}}$ is at $t^* = \log(1 + \delta/\phi(x))$. Since the function $g(y) := \log(1 + \delta/y)(y + \delta) - \delta$ satisfies $g(y) > 0$ and $g'(y) < 0$ for all $y > 0$, we have

$$\mathbf{P}[Z > (\phi(x) + \delta)K] \leq e^{-g(\phi(x))K} \leq e^{-g(m)K}, \tag{36}$$

where $m = \max_{x \in \mathbb{R}^2_{\geq 0}} \phi(x)$. It follows that with $c := g(m)$,

$$\mathbf{E}[\tau_K] = \frac{1}{1 - \lambda_K} \geq e^{cK}, \tag{37}$$

which completes the proof. $\square$

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