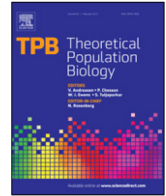




Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpb

Public goods games in populations with fluctuating size

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ARTICLE INFO

Article history:

Received 10 September 2017

Available online xxxxx

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 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 applied branching processes 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

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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 model (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 (Houchmandzadeh, 2015). 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 $0 \leq y_C \leq N$) is

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

In other words, the cooperators in one generation are sampled from the previous generation according to a binomial distribution with mean $Nx_C F_C / (x_C F_C + (N - x_C) F_D)$. 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. Then the probability of transitioning from state (x_C, x_D) to state (y_C, y_D) in one generation is

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

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 $u \geq 0$. Thus,

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