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Fluctuation driven fixation of cooperative behavior

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ABSTRACT

Cooperative behaviors are defined as the production of common goods benefitting all members of the community at the producer's cost. They could seem to be in contradiction with natural selection, as non-cooperators have an increased fitness compared to cooperators. Understanding the emergence of cooperation has necessitated the development of concepts and models (inclusive fitness, multilevel selection, etc.) attributing deterministic advantages to this behavior. In contrast to these models, we show here that cooperative behaviors can emerge by taking into account only the stochastic nature of evolutionary dynamics: when cooperative behaviors increase the population size, they also increase the genetic drift against non-cooperators. Using the Wright–Fisher models of population genetics, we compute exactly this increased genetic drift and its consequences on the fixation probability of both types of individuals. This computation leads to a simple criterion: cooperative behavior dominates when the relative increase in population size caused by cooperators is higher than the selection pressure against them. This is a purely stochastic effect with no deterministic interpretation.

1. Introduction

One form of cooperative behaviors can be defined as the production of a common good by an individual that benefits everybody in the community. Such behavior has a cost in terms of fitness, as the producer devotes part of its resources to this task. To early evolutionary biologists, cooperative behaviors seemed to be in contradiction with natural selection (Sober and Wilson, 1999; Dugatkin, 2006): since selection acts on individuals, a non-cooperator has a higher fitness than a cooperator and will always invade the community. Cooperative behaviors however, specially in microbial world, are widespread. A few examples of such behaviors are light production in *Vibrio fisheri* (Visick and Ruby, 2006), siderophore production in *Pseudomonas aeroguinosa* (West and Buckling, 2003; Harrison and Buckling, 2009), stalk formation by *Dictyostelium discoidum* (Kessin, 2001; Foster et al., 2004), decreased virulence in many pathogen-host systems (Diggle, 2010). All these cases are examples of a *production of common good* by an individual benefiting every individual in the community. More generally, these behaviors can be seen as particular cases of Niche Construction (Odling-smee et al., 2013).

Researchers have investigated the deterministic advantages that these kinds of behaviors could confer on individuals. The major schools along this line of investigation are inclusive fitness (Hamilton, 1964; Michod, 1982; Gardner et al., 2011) and multilevel selection (Lewontin, 1970; Wilson, 1983; Silva and Fontanari, 1999a; Traulsen and Nowak, 2006) and their associated variants (Nowak, 2006), although the relative merits of these concepts are sometimes hotly debated (Lehmann et al., 2007; Nowak et al., 2010; Abbot et al., 2011). These models have been extended to take into account finite size populations and stochastic effects. However, the emergence of cooperative behavior in these model is due to deterministic advantages (see Section 5). Throughout this article, "deterministic advantages" refers to factors which affects the *fitness* of an individual; "deterministic formulation" refers to models where fluctuations are neglected and a simple differential equation (such as (1)) is used to describe the dynamics of the population.

The aim of this article is not to discuss the relevance of these models, which have been documented in a large number of books and articles. The fact that cooperative behaviors are so widespread, however, behooves us to search for simple mechanisms to explain their emergence. I intend in this article to show that cooperative behaviors, by the simple act of increasing the population size, give an advantage to cooperators. The origin of this advantage is not deterministic, but has to be sought in the stochasticity of evolutionary dynamics. Note that the counterintuitive effect of stochasticity (favoring the *a priori* disadvantaged type) has been shown in spatially extended populations (van Baalen and Rand, 1998; Shnerb et al., 2000; Perc, 2006; Perc and Szolnoki, 2008), where space is supposed to play the crucial role (van Baalen and Rand, 1998). We show in this paper that this phenomenon can take place even in well mixed populations and space plays then the role of an amplification factor (see Section 5).

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Evolution is an interplay between deterministic causes broadly called fitness, and random events such as sampling between generations. An advantageous mutant does not spread with certainty but has only a greater probability of invading the community and of being fixed. This probability, called the fixation probability, is the relevant quantity to weight deterministic versus stochastic causes (Patwa and Wahl, 2008).

Consider an asexual population of fixed size N, with two types of individuals A and S, where S types have a constant positive excess relative fitness s compared to A. The deterministic differential equation describing the variation of the proportion $x = N_A/N$ of the A type is (Ewens, 2004):

$$\frac{dx}{dt} = -sx(1-x) \tag{1}$$

and leads to the disappearance of A individuals ($x \to 0$).

Going beyond the deterministic approach, one can solve the full stochastic dynamics of such a model and extract the invasion capacity of these two types, i.e. the fixation probability π_1^i of one individual of type i introduced into a population consisting entirely of the other type. In the framework of the Wright–Fisher, for a population of fixed size N, in the small selection pressure limit $Ns \ll 1$ (see Ewens (2004) and the exact derivations in Eq. (10)):

$$\pi_1^A = \frac{1}{N} - s \tag{2}$$

$$\pi_1^S = \frac{1}{N} + s \tag{3}$$

Therefore, if $s > 0$ then $\pi_1^S > \pi_1^A$ and type S individuals have a higher invasion capacity than type A individuals. In this case, the ratio of invasion capacities has the same information content as the deterministic approach: both lead to the conclusion that $s > 0$ favors the S type. The equivalence between these two approaches has led researchers to investigate the existence of *deterministic* advantages that could favor the cooperators (A individuals) against non-cooperators (S individuals) even though s, the *bare* fitness of S (or equivalently, the cost of altruism to A) is positive.

Fluctuations and random events can however be more subtle and alter the equivalence between deterministic and stochastic modeling. In particular, we can have $\pi_1^S < \pi_1^A$ *even when* $s > 0$, without any hidden deterministic advantage. This is the case of a cooperative behavior that increases the *population size*.

Biologically, the dependence of population size on the number of cooperators happens for example in situations where individuals compete for limited resources and two strategies are possible: an economic use of the resources leading to high population size but low growth rate or a dispendious use of resources leading to high growth rate but low population size (known as "the tragedy of the common" (Hardin, 1968)). In the microbial word, this phenomenon (called high yield versus high rate) is common where individuals can have two strategies, for example for ATP synthesis (respiration versus fermentation in yeast) (Pfeiffer et al., 2001; MacLean and Gudelj, 2006; MacLean, 2008) and competition in biofilms where a high yield mutant give rise to larger biofilm, even though it has a lower growth rate (Kreft, 2004). Rainey and Rainey (Rainey and Rainey, 2003) have studied another case, where the production of a polymeric molecule by the cooperator type leads to large decrease in growth rate but higher densities.

A similar observation was performed by Chuang et al. in an engineered microbial system (Chuang et al., 2009) where two type of bacteria were competing in an antibiotic containing media. One type (called producers, *i.e.* cooperators, A) was designed to produce an anti-biotic resistance molecule; the resources used to produce this molecule would reduce the growth rate (fitness) of this type. The other type of bacteria (called non producers, *i.e.* non cooperators, S) was designed not to produce the anti-biotic resistance molecule and would therefore have a higher growth rate compared to producers. The common good in this case is the anti-biotic resistance molecule. In a culture composed only of the S type, no common good is available and the population reaches a low density. In a population composed only of A type, the common good is abundant and the population reaches a high density. In a mixed population, the final population density would reach an intermediate level. However, because non producers have a higher relative growth rate, they always increase their proportion during one growth cycle.

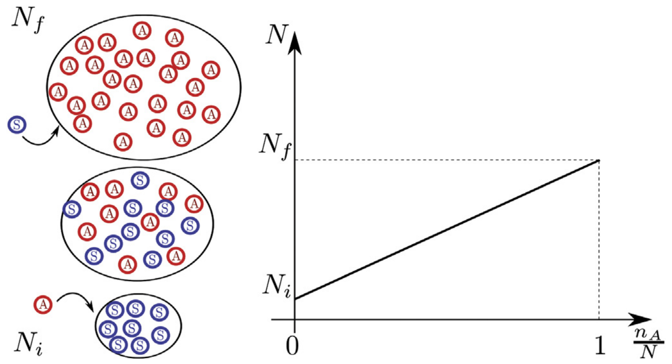

Fig. 1. Scheme of a cooperative behavior where the population size N of the habitat is an increasing function of the proportion x of type A individuals: $N = N(x)$. For a habitat formed of only S type individuals, $N(0) = N_i$. When only A individuals are present, $N(1) = N_f$, where $N_f > N_i$. The invasion capacity of each type is defined as the fixation probability of one i type introduced into a community formed only of type j.

Consider a system where the population size is a function of the proportion of cooperators, varying between N_i when only S type is present and N_f where only A type is present, with $N_i < N_f$ (Fig. 1). We suppose that S types have a constant excess relative fitness $s > 0$. The deterministic Eq. (1) does not change and will again lead to the A's extinction. The stochastic dynamic however can be different. When one A mutant is introduced in a population of S, the initial population size is N_i; on the other hand, when one S type is introduced in a population of A, the initial population size is N_f. Using expressions (2) and (3) as a back of the envelope estimation of the invasion capacity of both types therefore yields (an exact derivation is given in the following section):

$$\pi_1^A = \frac{1}{N_i} - s \tag{4}$$

$$\pi_1^S = \frac{1}{N_f} + s \tag{5}$$

We observe that we can have $\pi_1^S < \pi_1^A$ even though $s > 0$, if

$$2s < \frac{1}{N_i} - \frac{1}{N_f}$$

If the *selection pressure* against cooperators is smaller than the relative variation in the population size due to cooperators, then the latter type is favored and has a higher invasion capacity. This is a purely stochastic effect with no deterministic counterpart and is due to the fact that cooperators increase the genetic drift of non-cooperators.

We had previously shown the existence of this effect using a two dimensional Markov chain approach of a generalized Moran model (Houchmandzadeh and Vallade, 2012). This approach however is mathematically intricate and only approximate solutions could be obtained at small selection pressure. The effect however can be understood in a much simpler way using a classical Wright–Fisher (WF) model of population genetics, which I develop in the following sections, where very general results can be obtained. The WF model