



Effects of population growth on the success of invading mutants

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ABSTRACT

Understanding if and how mutants reach fixation in populations is an important question in evolutionary biology. We study the impact of population growth has on the success of mutants. To systematically understand the effects of growth we decouple competition from reproduction; competition follows a birth–death process and is governed by an evolutionary game, while growth is determined by an externally controlled branching rate. In stochastic simulations we find non-monotonic behaviour of the fixation probability of mutants as the speed of growth is varied; the right amount of growth can lead to a higher success rate. These results are observed in both coordination and coexistence game scenarios, and we find that the ‘one-third law’ for coordination games can break down in the presence of growth. We also propose a simplified description in terms of stochastic differential equations to approximate the individual-based model.

1. Introduction

When and how mutants spread in wildtype populations is an important question in population dynamics; answering it has implications in bacterial evolution, cancer initiation, viral dynamics and for the understanding of social phenomena (Maddamsetti et al., 2015; Nowak, 2006; Altrock et al., 2015; Castellano and Fortunato, 2009). While the behaviour of populations has traditionally been described mostly with deterministic models (Hofbauer and Sigmund, 1998; Smith, 1982), it is increasingly recognised that the fate of invading mutants can be influenced by random genetic drift. Work from recent decades reflects this shift in modelling, and much current research is concerned with the properties of stochastic evolution in finite populations (Nowak, 2006; Traulsen and Hauert, 2009; Ewens, 2004; Goel and Richter-Dyn, 1974; Taylor et al., 2004; Bladon et al., 2010).

Mathematical models of stochastic evolution typically describe a population of individuals who can each be of one of several types or species. In the simplest scenario one considers the spread of mutant individuals in a wildtype population. Often the interactions between species follow a birth–death process; individuals of one type may generate offspring at the expense of other individuals who are removed from the population, such that the total population size is conserved. These events occur stochastically and their rates are determined by the relative reproductive fitnesses of the different species; these fitnesses in

turn depend on the composition of the population (Nowak, 2006; Traulsen and Hauert, 2009). Evolutionary game theory is a commonly-used framework for describing these frequency-dependent dynamics. Fixation probabilities and mean fixation times can be computed for these stylised models using techniques from the theory of stochastic processes (Gardiner, 2009; van Kampen, 2007; Ewens, 2004; Altrock and Traulsen, 2009; Antal and Scheuring, 2006).

More recently, work has also focused on models with populations of dynamic size. Melbinger et al. have investigated the impact that demography has on the spread of cooperation in the prisoners dilemma game (Melbinger et al., 2010; Cremer et al., 2011, 2012). Other evolutionary game formats have also been studied in populations of time-dependent size (Novak et al., 2013; Chotibut and Nelson, 2015; Huang et al., 2015; Li et al., 2015; Constable et al., 2016). In these models growth is limited by an overall carrying capacity. The effect of population growth has also been considered in host–parasite interactions (Papkou et al., 2016), and in spin systems (Morris and Rogers, 2014). Other work specifically focuses on range expansions in space (Hallatschek et al., 2007).

In such models that combine selection and growth, an interesting interplay between the underlying deterministic dynamics and intrinsic noise is to be expected. For example, consider a scenario where the deterministic flow has a stable fixed point for non-zero numbers of both types of individual. For infinite populations noise can be neglected, and

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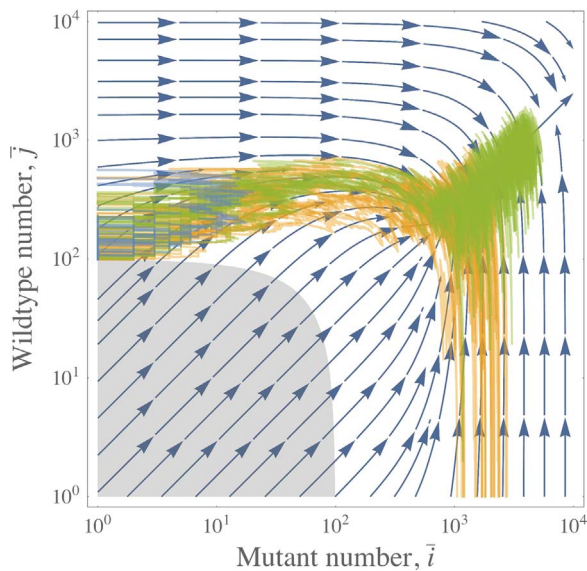


Fig. 1. Stochastic trajectories of a single mutant in a growing population subject to coexistence-game dynamics. Trajectory colours indicate the outcome of extinction, fixation, or indefinite coexistence. Background arrows are the deterministic flow field, as described in Section 3. Data shown is for selection strength $\beta=0.1$, payoff matrix (15) with fixed point $x^*=0.8$, initial population size $N_0=100$, and power-law population growth with exponent $\gamma=0.4$

the deterministic flow leads to the indefinite coexistence of two species. In finite populations, however, extinction of one of the two types can and will occur as these phenomena are driven by the intrinsic noise. A growing population presents an interesting intermediate case; if its initial size is small, demographic stochasticity shapes the outcome in the early phases (in populations of size N , intrinsic noise has an amplitude of order $N^{-1/2}$ relative to deterministic selection). As the population grows the relative strength of the noise gradually reduces, and in the latter stages deterministic flow dominates over random drift. This can lead to outcomes of fixation or extinction, or indefinite coexistence, as highlighted in Fig. 1. The speed of growth determines how long intrinsic noise is relevant before the deterministic flow takes over. The purpose of our work is to investigate this in more detail and to characterise the outcome of evolution for different speeds of population growth.

To address this issue we explicitly decouple the between-species interactions – birth–death dynamics in the form of a two-player two-strategy evolutionary game – from the reproduction dynamics leading to population growth. We consider evolutionary scenarios described by the well-known cases of the dominance, coordination, and coexistence games (Traulsen and Hauert, 2009), as described in Section 2.1. Growth in our model is governed by an externally-controlled per-capita reproduction rate, $\Gamma(N, t)$, which may depend on the current population size and/or have an explicit time dependence as described in Section 2.2. This rate is not frequency-dependent, such that the growth process itself does not favour any of the two species – selection is controlled only by the between-species interactions. By varying the growth law independently from the selection dynamics, we can systematically test the effect of population growth on the evolutionary outcome. This is much harder to do in models in which growth and selection are combined, as the growth law then ‘emerges’ from the population itself and cannot easily be controlled externally.

2. Model definitions

We consider a well-mixed, growing population of discrete individuals. Each member of the population can be one of two types, A or B . We will refer to species A as the ‘mutant’ type, and B as the ‘wildtype’. The state of the population at any time can be described by the pair of

variables (i, N) . In our notation $i(t)$ is the number of individuals of type A (mutants), and $N(t)$ is the total number of individuals in the population at a given time t . The number of individuals of type B (wildtypes) can be written as $j(t) = N(t) - i(t)$. Generally we are interested in the fate of a single mutant in a population of wildtype individuals. For the dynamics we consider two types of discrete events: Competition between the species, and growth of the population.

2.1. Competition

Competition (or selection) in our model is governed by transitions of the type $(i, N) \rightarrow (i \pm 1, N)$, i.e. replacement of an individual by another of the opposite type without increasing the population size through a birth–death process. We use the framework of evolutionary game theory to describe these interactions (Nowak, 2006; Traulsen and Hauert, 2009). When two individuals interact, the likelihood for one type to succeed over the other is characterised by the individuals’ expected payoffs within the population. These are written as $\pi_A(i, N)$ and $\pi_B(i, N)$ respectively for members of the two types; their precise form will be defined below. In our model the rates at which these selection events happen are given by

$$\begin{aligned} (i, N) \rightarrow (i + 1, N): \quad T_{i,N}^+ &= \frac{i(N-i)}{N} g(\pi_A, \pi_B) \\ (i, N) \rightarrow (i - 1, N): \quad T_{i,N}^- &= \frac{i(N-i)}{N} g(\pi_B, \pi_A). \end{aligned} \quad (1)$$

This follows the lines, for example, of Bladon et al. (2010); Traulsen and Hauert (2009). The detailed mechanics of these birth–death events are governed by the competition kernel $g(\cdot, \cdot)$. Generally, this kernel will be an increasing function of the first argument, and decreasing in the second. For our investigation we use the common choice

$$g(\pi_A, \pi_B) = \frac{1}{1 + \exp[-\beta(\pi_A - \pi_B)]}, \quad (2)$$

which is sometimes referred to as the ‘Fermi process’ (Traulsen and Hauert, 2009; Bladon et al., 2010; Altrock and Traulsen, 2009). The parameter $\beta \geq 0$ is the intensity of selection: For $\beta = 0$ evolution is neutral with no selection bias in favour of either species, for non-zero values of β the payoffs determine the direction of selection.

We focus on the case of frequency-dependent selection; the expected payoffs of the two species depend on the current composition of the population. As is often done in the existing literature (see e.g. (Nowak, 2006)) we assume that $\pi_A(i, N)$ and $\pi_B(i, N)$ are determined by the following payoff matrix and functions:

$$\begin{array}{cc} \begin{array}{cc} A & B \\ A & a \quad b, \\ B & c \quad d \end{array} & \begin{array}{l} \pi_A(i, N) = \frac{i-1}{N-1}a + \frac{N-i}{N-1}b, \\ \pi_B(i, N) = \frac{i}{N-1}c + \frac{N-i-1}{N-1}d. \end{array} \end{array} \quad (3)$$

The parameter a describes the payoff an individual of type A receives from an interaction with another individual of type A . Parameter b is the payoff to A when interacting with an individual of type B . Parameters c and d follow similarly.

For these interactions alone (i.e. without changes in population size), the deterministic dynamics can be described by the so-called replicator equation (Hofbauer and Sigmund, 1998). Writing $x(t) = \langle i(t)/N(t) \rangle = \langle i(t) \rangle / N$, where $\langle \cdot \rangle$ represents an average over infinitely many realisations of the stochastic process, and assuming that higher-order moments factorise (e.g. $\langle i^2 \rangle = \langle i \rangle^2$), we have

$$\dot{x} = x(1-x)[g(\bar{\pi}_A, \bar{\pi}_B) - g(\bar{\pi}_B, \bar{\pi}_A)]. \quad (4)$$

Here $g(\bar{\pi}_A, \bar{\pi}_B)$ [$g(\bar{\pi}_B, \bar{\pi}_A)$] is the (effective) fitness of type A [B], where $\bar{\pi}_A(x) = xa + (1-x)b$ and $\bar{\pi}_B(x) = xc + (1-x)d$. The choice of the payoff matrix elements a, b, c , and d determines the shape of the selection bias. Our analysis below focuses on several types of games, representing the different structures that can arise. These include cases in which one species strictly dominates the other (Eq. (4) has no fixed points for

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