



The interplay of two mutations in a population of varying size: A stochastic eco-evolutionary model for clonal interference

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Received 11 May 2015; received in revised form 4 May 2016; accepted 27 June 2016

Available online 5 July 2016

Abstract

Clonal interference, competition between multiple beneficial mutations, has a major role in adaptation of asexual populations. We provide a simple stochastic model of clonal interference taking into account a wide variety of competitive interactions. The population evolves as a three-type birth-and-death process with type dependent competitions. This allows us to relax the classical assumption of transitivity between mutations, and to predict genetic patterns, such as coexistence of several mutants or emergence of Rock–Paper–Scissors cycles, which were not explained by existing models. In addition, we call into questions some classical preconceived ideas about fixation time and fixation probability of competing mutations.

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MSC: 92D25; 60J80; 60J27; 92D15; 92D10

Keywords: Eco-evolution; Clonal interference; Birth and death processes; Lotka–Volterra systems; Couplings; Population genetics

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Introduction

From the works of the ‘great trinity’ of Fisher [20,21], Wright [47] and Haldane [24] the questions of fixation probability and fixation time of new beneficial mutations have been widely studied. These are indeed fundamental questions if we aim at understanding how and how fast a population can adapt to a changing environment, the dynamics of genetic diversity, or the long term behaviour of ecological systems.

The first models of adaptation in asexual populations postulated that the beneficial mutations were rare enough for populations to evolve sequentially by rapid fixations of a positively selected mutation alternating with long periods with no mutation (see [40] for a review of these models). However, various empirical evidences [17,32,33] show that in large asexual populations, several mutations can co-occur, which especially can lead to a competition between beneficial mutations. This phenomenon is known as clonal interference [23], and has a major importance for adaptation of asexual populations, such as bacteria and other prokaryotes, yeasts and other fungi, or cancers. Consequently in recent years there has been a growing interest in developing experimental studies and theoretical models to analyse clonal interference [2,23,17,8,16,31,32].

Most models investigating how clonal interference might affect the probability and time of fixation of beneficial mutations, and thus adaptation, made two important but limiting assumptions: first population sizes are constant and independent of the fitness of the individuals, and second, fitnesses only depend on the type of the mutations and not on the state of the population, i.e. fitnesses are assumed transitive. However, as emphasized by Nowak and Sigmund [39], there is a reciprocal feedback between adaptation and environmental changes because of ecological interactions between individuals, especially competition. Mutation with the highest fitness invades the population, but its fitness might depend on the density of the other mutations present in the population and might thus change during the course of adaptation. Thus, fitnesses are not necessarily transitive, i.e. selection can be frequency dependent, and phenomena such as cyclical dynamics or stable coexistence can occur. Interestingly, non-transitivity of fitnesses has been documented empirically in asexual populations [41,30].

In this paper we aim at providing and studying a simple stochastic model taking into account the wide variety of competitive interactions which can be found in nature. We show that type dependent competitive interactions are able to generate ecological patterns which are observed but not explained by conventional models. In particular we relax the classical assumption of transitivity between the different mutations (see the discussion in Section 2.1) and call into questions some classical preconceived ideas about clonal interference (see Propositions 3, 5 and 6). To model precisely the interactions between individuals we extend the model introduced in [9] where the author only considered the occurrence of one mutation. The population dynamics, described in Section 1, is a multitype birth and death Markov process with density-dependent competition. Individuals are characterized by ecological parameters depending on their genetic type and governing their growth rate and competition with other individuals. As a consequence, the ‘‘fitness’’ of an individual depends on the population state and is not an intrinsic characteristic of individuals. We reflect the carrying capacity of the underlying environment by a scaling parameter $K \in \mathbb{N}$ and state results in the limit for large K .

Such an eco-evolutionary approach has been introduced by Metz and coauthors [34] and has been made rigorous in the probabilistic setting in the seminal paper of Fournier and Méléard [22]. Then it has been developed by Champagnat, Méléard and coauthors (see [9,11,10] and references therein) for the haploid asexual case, by Smadi and coauthors [45,5] for the haploid sexual case, and by Collet, Méléard and Metz [12] and Coron and coauthors [14,13] for the diploid sexual

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