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Convergence of generalized urn models to non-equilibrium attractors

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Abstract

Generalized Polya urn models have been used to model the establishment dynamics of a small founding population consisting of k different genotypes or strategies. As population sizes get large, these population processes are well-approximated by a mean limit ordinary differential equation whose state space is the k simplex. We prove that if this mean limit ODE has an attractor at which the temporal averages of the population growth rate is positive, then there is a positive probability of the population not going extinct (i.e. growing without bound) and its distribution converging to the attractor. Conversely, when the temporal averages of the population growth rate are negative along this attractor, the population distribution does not converge to the attractor. For the stochastic analog of the replicator equations which can exhibit non-equilibrium dynamics, we show that verifying the conditions for convergence and non-convergence reduces to a simple algebraic problem. We also apply these results to selection–mutation dynamics to illustrate convergence to periodic solutions of these population genetics models with positive probability.

Keywords: Markov chains; Urn models; Replicator equation; Selection–mutation dynamics; Non-equilibrium attractors

1. Introduction

Biological invasions, where a species is introduced in a novel habitat, are occurring repeatedly throughout the world and often start with small founding population. Whether or not these

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founding populations establish or go extinct in their new environment depends on a diversity of factors including local environmental conditions, demographic stochasticity, genetic diversity of the founding population, and nonlinear feedbacks between individuals in the founding population. One commonly used approach to understanding the roles of the first two factors is modeling the dynamics of establishment with branching processes [2]. This approach assumes that individuals survive, grow, and reproduce independently of one another and has provided fundamental insights into fixation of beneficial alleles [8], the build up of biodiversity on islands [11], the viability of endangered populations [15], and the evolution of disease emergence in novel host populations [1,12]. However, even when populations are at low abundance, individuals may interact with one another (e.g. finding or competing for mates in sexually reproducing populations) and thereby violate the assumption of independence of these classical branching processes. When these interactions occur between different types of individuals, they lead to frequency-dependent feedbacks on the population dynamics.

To account for these frequency-dependent interactions within a founding population, Schreiber [13] introduced a class of generalized urn models which were studied more extensively by Benaïm et al. [5]. These models consider an urn containing a finite number of balls (the population) of different colors (the different genotypes or phenotypes). At each stage, balls of possibly different colors can be added or removed from the urn, modeling deaths, births, or changes of state due to interactions between individuals.

Two key questions about these Markov processes are (a) when is there a positive probability that the population never goes extinct (i.e. the population establishes)? and (b) on the event of non-extinction, what can be said about the long-term frequency dynamics? To address these questions, Schreiber [13] introduced a mean limit ordinary differential equation (ODE) on the simplex (corresponding to all possible population frequencies) associated with the urn models. Using these mean field ODEs Benaïm et al. [5] proved: (i) if the population is expected to grow uniformly in the neighborhood of an attractor of this mean limit ODE, then with positive probability the population never goes extinct and the frequencies of the population converge to this attractor (see Theorem 2 next section); (ii) conversely if the population is expected to decrease uniformly in the neighborhood of a given set, then convergence toward this set occurs with probability zero (see Theorem 3 next section). As the expected growth rate of the population typically varies along non-equilibrium attractors, these two results, however, are most useful for equilibrium attractors of the mean limit ODE.

Here, we study the case where the underlying mean limit ODE admits non-equilibrium attractors with non-constant growth rates. As we show in the applications section, this case arises quite naturally in stochastic models for evolutionary games and population genetics. We extend the results of Benaïm et al. [5] to a more general framework (see Theorems 4 and 5 in Section 3). Most notably, we replace the assumption of uniform positive (respectively, negative) population growth near the attractor with the assumption that the temporal average of the population growth rate is positive (respectively, negative) for initial conditions near the attractor (see assumptions (7) and (8)).

The remainder of this paper is organized as follows. In next section, we define the class of generalized urn models, and recall the main results of Benaïm et al. [5]. We also discuss the stochastic approximation methods, and briefly explain how they were used to derive these results. In Section 3, we state and prove our main results: convergence with positive probability toward an attractor with average positive growth and non-convergence to an invariant set with negative average growth. Section 4 is devoted to applications to evolutionary games and population genetics. The proofs of some technical estimates are given in the Appendix.