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Donald A. Dawson • Andreas Greven

# Spatial Fleming-Viot Models with Selection and Mutation



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# Abstract

The monograph constructs a rigorous framework to analyse some phenomena in evolutionary theory of populations arising due to the combined effects of migration, selection and mutation in a spatial stochastic population model, namely the evolution towards fitter and fitter types through punctuated equilibria. The discussion is based on some new methods, in particular multiple scale analysis, nonlinear Markov processes and their entrance laws, atomic measure-valued evolutions and new forms of duality (for state-dependent mutation and multitype selection) which are used to prove ergodic theorems in this setting and are applicable for many other questions and renormalization analysis to analyse some phenomena (stasis, punctuated equilibrium, failure of naive branching approximations, biodiversity) which occur due to the combination of rare mutation, mutation, resampling, migration and selection and require mathematically to bridge between (in the limit) separating time and space scales.

Consider the following spatial multitype population model. The state of a single colony is described by a probability measure on some countable type space, the geographic space is modelled by a set of colonies and the colonies (or demes) are labelled with the countable hierarchical group  $\Omega_N = Z^{\otimes N}$ , with  $Z$  the cyclic group of order  $N$ . This set mimics  $\mathbb{Z}^2$  as  $N \rightarrow \infty$ . The stochastic dynamics is given by a system of interacting measure-valued diffusions and the driving mechanisms include resampling (pure genetic drift) as diffusion term, migration, selection and mutation as drift terms. Resampling is modelled in each colony by the usual Fleming–Viot diffusion. The haploid selection is based on a fitness function on the space of types, and the mutation is type-dependent and has the feature that fitter types are more stable against deleterious mutation and fitter types appear through rare mutation. The evolution starts from one basic type. The model belongs to a class of processes which have been constructed via a well-posed martingale problem by Dawson and Greven (Electron. J. Probab. **4**, paper no. 4, 181, 1999).

The goal of the monograph is to determine the long-time behaviour of the process in terms of a sequence of quasi-equilibria developing in longer and longer time scales with increasing fitness levels. This is in contrast with the more familiar single

equilibrium that develops as time tends to infinity. In particular we show that the combination of mutation, selection and migration leads to the following new effects.

We show that the evolution to fitter types is governed by the immigration of rare mutants from distant locations and subsequent conquest of the colonies, which is possible due to the greater stability of the fitter mutants against further deleterious mutation which gives them a quasi-selective advantage. We describe in detail how the transition from the quasi-equilibrium on one level of fitness to the next occurs.

Since we have a spatial system this transition is taking place in different time scales. We identify five phases (corresponding to specific time-space scales) of the transitions from one quasi-equilibrium to the next, each of which we explicitly describe asymptotically.

Starting in a quasi-equilibrium of a certain level, we get some rare mutations somewhere in space creating a droplet of colonies of fitter types of exponentially growing size and total mass which later dominate everywhere in space. We describe the droplet by means of a random atomic measure and identify the limiting dynamic in terms of processes driven by Poisson random measures. This dynamic allows us to identify the random growth factor (reflecting the randomness of the rare events) and the deterministic exponential growth rate. We next determine the time scale at which the global emergence and fixation by rare mutants occurs on the level of components and blockaverages and describe the limiting dynamics on the various levels. The emergence is of a stochastic nature which makes the subsequent phase of fixation on the next higher level random. A key object for fixation is the random entrance law of a nonlinear evolution equation (McKean–Vlasov equation).

After fixation we see a neutral evolution on the higher level before, after a very long time, finally the new quasi-equilibrium on the higher level is reached.

In addition to the process describing the current population, we construct the historical process giving the information on the complete family structure of the population alive at time  $t$ . The genealogical structure of the population arising in our model depends on the migration mechanism, which determines whether we have local biodiversity or a local monoancestor situation, in other words whether the local population asymptotically includes one or countably many high level mutant families.

The method of analysis is a hierarchical renormalization scheme based on a sequence of spatial scales combined with different types of sequences of time scales, together with a limit  $N \rightarrow \infty$  (in  $\Omega_N$ ) which corresponds to a separation of several natural time scales of the model. These separating multiscales are connected by working with entrance laws.

Due to mutation the structure of the limiting dynamics is quite different from models previously studied with renormalization techniques, and new methods are developed in this monograph to handle the present situation. We introduce and use for this purpose a new class of dual processes to derive expressions for the moment measures which allow us to treat selection and type-dependent mutation and also allows us to prove stronger ergodic theorems than previously known for diffusion models involving migration, selection, mutation and resampling.

**Keywords.** Atomic measure-valued processes, Biodiversity, Droplet formation, Duality, Interacting Fleming–Viot processes, Mutation, Punctuated equilibrium, Random entrance law, Random McKean–Vlasov equation, Rare mutant, Renormalization, Selection

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