



Splitting trees with neutral mutations at birth

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Abstract

We consider a population model where individuals behave independently from each other and whose genealogy is described by a chronological tree called splitting tree. The individuals have i.i.d. (non-exponential) lifetime durations and give birth at constant rate to clonal or mutant children in an infinitely many alleles model with neutral mutations.

First, to study the allelic partition of the population, we are interested in its frequency spectrum, which, at a fixed time, describes the number of alleles carried by a given number of individuals and with a given age. We compute the expected value of this spectrum and obtain some almost sure convergence results thanks to classical properties of Crump–Mode–Jagers (CMJ) processes counted by random characteristics.

Then, by using multitype CMJ-processes, we get asymptotic properties about the number of alleles that have undergone a fixed number of mutations with respect to the ancestral allele of the population.

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1. Introduction

We consider a general branching model with neutral mutations occurring at birth. We suppose that individuals carry alleles, have i.i.d. (and not necessarily exponential) life lengths and give

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birth at constant rate b during their lives to children who can be mutants with probability p or clones of their parents with probability $1 - p$. We are working with an infinite alleles model, that is, when a mutation occurs, the allele of the mutant child was never encountered before. Moreover, mutations are neutral because they do not imply advantages or disadvantages (all individuals have identically distributed dynamics).

Without mutation, the model is linked to a genealogical tree called *splitting tree* [16,17,26]. Moreover, if $\Xi(t)$ denotes the number of alive individuals at time t , the process $\Xi := (\Xi(t), t \geq 0)$ is a *Crump–Mode–Jagers process* (or general branching process) [21] which is binary (births occur singly) and homogeneous (constant birth rate).

We are first interested in the allelic partition of the population and more precisely in properties of the *frequency spectrum* $(M_t^{i,a}, i \geq 1)$ where $M_t^{i,a}$ is the number of distinct alleles carried by exactly i individuals at time t and that appeared after time $t - a$ (or equivalently the alleles whose ages are less than a at time t). Roughly speaking, this spectrum classifies the different alleles depending on their ages and on their sizes.

This kind of question was first studied by Ewens [14] who discovered the well known ‘sampling formula’ named after him and which describes the law of the allelic partition for a Wright–Fisher model with neutral mutations. In our model, we cannot get a counterpart of the Ewens’ sampling formula in the sense that we cannot compute the joint law of $(M_t^{i,a}, i \geq 1)$ for fixed $0 < a \leq t$. However, we obtain two kinds of results concerning the frequency spectrum $(M_t^{i,a}, i \geq 1)$. We first compute the expected value of the number of alleles carried by i individuals at time t and with age a . When the process Ξ is supercritical, we also obtain the asymptotic behaviors of the frequency spectrum and of the relative abundances of alleles as $t \rightarrow \infty$ on the survival event of Ξ .

Similar models to ours have been studied in the literature. In [18], Griffiths and Pakes study the case of a Bienaymé–Galton–Watson process where children can independently be mutants with a given probability: the authors obtained asymptotic results about the number of alleles and the frequency spectrum at generation n as $n \rightarrow \infty$. In [30], Pakes gets analogous properties concerning continuous-time Markov branching processes. In particular, his formula of the expected frequency spectrum can be seen as a counterpart of ours, stated in Section 3.1. These two works [18,30] have recently been used by Kimmel and coworkers in several articles. In [24], the authors are interested in the evolution of parts of DNA called Alu sequences. They model the evolution of these sequences using the infinite-alleles branching process of [18] with a linear-fractional offspring distribution. In [37], the authors consider the model of Pakes [30] and they especially obtain an explicit expression of the limiting mean frequency spectrum in the particular case of birth and death processes and they also study the variance frequency spectrum.

In the two articles [3,4], Bertoin considers an infinite alleles model with neutral mutations in a subcritical or critical Bienaymé–Galton–Watson process where individuals independently give birth to a random number of clonal and mutant children according to the same joint distribution. In [3], he defines a tree of alleles where all individuals of a common allele are gathered in clusters and specifies the law of the allelic partition of the total population by describing the joint law of the sizes of the clusters and the numbers of their mutant children. In [4], Bertoin obtains the convergence of the sizes of allelic families for a large initial population and a small mutation rate.

Recent results have been obtained about splitting trees with mutations. In [11], Delaporte studies sequences of splitting trees with general and neutral mutations occurring at birth and investigates scaling limits in a regime of large population size and rare mutations. In two related

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