Mathematical Biosciences Institute Lecture Series 1.4
Stochastics in Biological Systems

Vincent Bansaye · Sylvie Méléard

Stochastic Models for Structured Populations

Scaling Limits and Long Time Behavior

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Volume 1: Stochastics in Biological Systems

Stochasticity is fundamental to biological systems. While in many situations the system can be viewed as a large number of similar agents interacting in a homogeneously mixing environment so the dynamics are captured well by ordinary differential equations or other deterministic models. In many more situations, the system can be driven by a small number of agents or strongly influenced by an environment fluctuating in space or time. Stochastic fluctuations are critical in the initial stages of an epidemic; a small number of molecules may determine the direction of cellular processes; changing climate may alter the balance among competing populations. Spatial models may be required when agents are distributed in space and interactions between agents form a network. Systems evolve to become more robust or co-evolve in response to competitive or host-pathogen interactions. Consequently, models must allow agents to change and interact in complex ways. Stochasticity increases the complexity of models in some ways, but may smooth and simplify in others.

Volume 1 provides a series of lectures by well-known international researchers based on the year on Stochastics in Biological Systems which took place at the MBI in 2011-2012.

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Mathematical Biosciences Institute Lecture Series
Volume 1: Stochastics in Biological Systems

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Stochastic Models for Structured Populations
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ISSN 2364-2297 ISSN 2364-2300 (electronic)
Mathematical Biosciences Institute Lecture series
ISBN 978-3-319-21710-9 ISBN 978-3-319-21711-6 (eBook)
DOI 10.1007/978-3-319-21711-6

Library of Congress Control Number: 2015945107

Mathematics Subject Classification (2010): 60J80, 60J75, 60G57, 60H10, 92D25, 92D15

Springer Cham Heidelberg New York Dordrecht London

Printed on acid-free paper

Springer International Publishing AG Switzerland is part of Springer Science+Business Media (www.springer.com)

To
Marius, Margot, Martin

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Chapter 1
Introduction

This course concerns the stochastic modeling of population dynamics. In the first part, we focus on monotype populations described by one-dimensional stochastic differential equations with jumps. We consider their scaling limits for large populations and study the long time behavior of the limiting processes. It is achieved, thanks to martingale properties, Poisson measure representations, and stochastic calculus. These tools and results will be used and extended to measure-valued processes in the second part. The latter is dedicated to structured populations, where individuals are characterized by a trait belonging to a continuum.

In the first section, we define birth and death processes with rates depending on the state of the population and recall some long time properties based on recursion equations. A pathwise representation of the processes using Poisson point measures is introduced, from which we deduce some martingale properties. We represent the carrying capacity of the underlying environment through a scaling parameter $K \in \mathbb{N}$ and state our results in the limit of large K. Depending on the demographic rates, the population size renormalized by K is approximated either by the solution of an ordinary differential equation or by the solution of a stochastic differential equation. The proofs are based on martingale properties and tightness-uniqueness arguments. When the per individual death rate is an affine function of the population size, in the limit we obtain either a so-called logistic equation or a logistic Feller diffusion process. The long time behavior of these limiting dynamics is studied. Assuming a constant per capita death rate leads to a Feller diffusion which satisfies the branching property: two disjoint subpopulations evolve independently. In that case, specific tools using Laplace transforms can be used. We extend this class of processes by adding jumps, which may be due either to demographic stochasticity or to environmental stochasticity. We consider them separately and we characterize their finite dimensional laws and long time behavior using the branching property, the generator and martingale properties. First, we focus on Continuous State Branching Processes, which arise as scaling limits of branching processes when the individuals may have a very large number of offspring. This gives rise to a jump term whose

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_1

rate is proportional to the size of the population. Using the Lamperti transform, we can then both describe their scaling limits and classify the long time behavior: extinction, absorption at 0 or exponential growth to infinity. The second class of jump processes models random environmental catastrophes, which kill a random fraction of the population. The continuous state process can be obtained as a limit of discrete particle systems, where the demographic dynamics of the population and the environmental catastrophes occur on different timescales. Now, only the *quenched* branching property holds and the long time behavior of the Laplace exponent is more subtle. We recover the three usual regimes, subcritical, critical, and supercritical, but the subcritical case is split into three sub-cases leading to different asymptotics for the survival probability.

The second part concerns structured populations whose individuals are characterized by a type taking values in a continuum. Two main examples are developed. The first one models Darwinian evolution where the type is an heritable trait subject to selection and mutation. The second case describes cell division with parasite infection and the type of a cell is the amount of parasites it carries. In both cases, the mathematical model is a measure-valued Markov process with jumps. Therefore, we develop some stochastic tools for such processes and use a pathwise representation driven by Poisson point measures to obtain martingale properties. We consider different approximations of the process, depending on the parameter K, which as before scales the population size but now also the demographic rates. The limiting theorems are proved using compactness-uniqueness arguments and the semimartingale decomposition of the measure-valued processes.

In the first two subsections, the population model includes mutations, which may occur during each birth event with some positive probability. The mutant inherits a random perturbation of the ancestor's trait. The individuals compete for resources and the individual death rate depends on the whole population trait distribution, leading to nonlinearities in the limit. In the large population case, the limiting equation is a nonlinear integro-differential equation. In the allometric case, when the demographic rates are much larger but the mutation amplitude is very small in an appropriate scale, the limiting object can be either a nonlinear reaction-diffusion equation or a nonlinear super-process. The latter is a continuous measure-valued process whose law is characterized by martingale properties. Simulations show the qualitative differences between the trait supports for these different asymptotics. It means that a change of scales in the parameters leads to quite different evolutive scenarios. Let us point out that the classical models for population dynamics in an ecological or mutational framework can thus be explained from the birth and death processes describing the evolution of the population at the level of the individuals.

In the last two subsections, we describe two-level models motivated by cell division dynamics. First, we consider a finite population of dividing cells. The cells are infected by parasites which may influence their division rates. The parasites are more abundant and reproduce and die faster than the cells and their growth is modeled by a Feller diffusion. When the cells divide, the parasite load is randomly shared in the two daughter cells. Following a random cell lineage (by keeping one daughter cell at random at each division) makes appear a Feller diffusion with catastrophes. When studying the number of infected cells for large times, we obtain different regimes depending on the positivity or not of a parameter based on the division rate, the parasite splitting law and the parasite growth rate. Finally, we consider the long time behavior of a structured population when the genealogical tree is a branching process. It allows multiple offspring and deaths. Between the branching events, the individual traits evolve independently following a Markov process. The ergodicity of a well-chosen one-dimensional auxiliary Markov process allows to prove the convergence of the trait distribution within the population when time goes to infinity.

Notation

For a Polish space E, $\mathcal{P}(E)$ denotes the space of probability measures on E.

The spaces $C_b^2(\mathbb{R})$, $C_b^2(\mathbb{R}_+)$, $C_b^2(\mathbb{R}^d)$ are the spaces of bounded continuous functions whose first and second derivatives are bounded and continuous, resp. on $\mathbb{R}$, $\mathbb{R}_+$, $\mathbb{R}^d$.

In all what follows, C denotes a constant real number whose value can change from one line to the other.

Acknowledgements The authors wish to warmly thank Amandine Véber for the reading of the manuscript and her suggestions.

Part I
Discrete Monotype Population Models and One-dimensional Stochastic Differential Equations

In the first chapter, we concentrate on one-dimensional models for population dynamics. After recalling the main properties of the birth and death processes, we study different scaling limits using a martingale approach. Then we investigate the long time behavior of some classes of limiting processes, in the case of large reproduction events or random environment using the branching property.

Chapter 2
Birth and Death Processes

2.1 Definition and non-explosion criterion

Definition 2.1. A **birth and death process** is a pure jump Markov process whose jump steps are equal to ±1. The transition rates are as follows:

$$\begin{cases} i \to i+1 & \text{at rate} \;\; \lambda_i \\ i \to i-1 & \text{at rate} \;\; \mu_i, \end{cases}$$

$(\lambda_i)_{i\in\mathbb{N}^*}$ and $(\mu_i)_{i\in\mathbb{N}^*}$ being two sequences of positive real numbers and $\lambda_0 = \mu_0 = 0$.

In this case, the infinitesimal generator is the matrix $(Q_{i,j})$ defined on $\mathbb{N} \times \mathbb{N}$ by

$$Q_{i,i+1} = \lambda_i \, , \; Q_{i,i-1} = \mu_i \, , \; Q_{i,i} = -(\lambda_i + \mu_i) \, , \;\; Q_{i,j} = 0 \text{ otherwise.}$$

The global jump rate for a population with size $i \geq 1$ is $\lambda_i + \mu_i$. After a random time distributed according to an exponential law with parameter $\lambda_i + \mu_i$, the process increases by 1 with probability $\frac{\lambda_i}{\lambda_i+\mu_i}$ and decreases by -1 with probability $\frac{\mu_i}{\lambda_i+\mu_i}$. If $\lambda_i + \mu_i = 0$, the process is absorbed at i.

Recall that if $P(t) = (P_{i,j}(t)), t \in \mathbb{R}_+$ denotes the transition semigroup of the process, then

$$P_{i,i+1}(h) = \lambda_i \, h + o(h) \, ; P_{i,i-1}(h) = \mu_i \, h + o(h) \, ; P_{i,i}(h) = 1 - (\lambda_i + \mu_i) \, h + o(h).$$

Examples. The constant numbers λ, μ, ρ, c are positive.

1) The Yule process corresponds to the case $\lambda_i = i\lambda, \;\; \mu_i = 0$.
2) The branching process or linear birth and death process : $\lambda_i = i\lambda, \;\; \mu_i = i\mu$.
3) The birth and death process with immigration : $\lambda_i = i\lambda + \rho, \;\; \mu_i = i\mu$.

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_2

4) The logistic birth and death process : $\lambda_i = i\lambda,\ \mu_i = i\mu + c\, i(i-1)$.

The following theorem characterizes the non-explosion in finite time of the process. In this case, the process will be defined and will have a.s. finite value at any time $t \in \mathbb{R}_+$.

Theorem 2.2. *Suppose that $\lambda_i > 0$ for all $i \geq 1$. Then the birth and death process has almost surely an infinite lifetime if and only if the following series diverges:*

$$\sum_{i\geq 1}\left(\frac{1}{\lambda_i} + \frac{\mu_i}{\lambda_i\lambda_{i-1}} + \cdots + \frac{\mu_i\cdots\mu_2}{\lambda_i\cdots\lambda_2\lambda_1}\right) = +\infty. \tag{2.1}$$

Corollary 2.3. *If for any i, $\lambda_i \leq \lambda\, i$, with $\lambda > 0$, the process is well defined on $\mathbb{R}_+$.*

Remark 2.4. One can check that the birth and death processes mentioned in the examples above satisfy this property and are well defined on $\mathbb{R}_+$.

Proof of Theorem 2.2. Let $(T_n)_n$ be the sequence of jump times of the process and $(S_n)_n$ the sequence of the inter-jump times,

$$S_n = T_n - T_{n-1}, \quad \forall n \geq 1; \quad T_0 = 0, \quad S_0 = 0.$$

We define $T_\infty = \lim_n T_n$. The process doesn't explode almost surely and is well defined on $\mathbb{R}_+$ if and only if for any $i \geq 1$, $\mathbb{P}_i(T_\infty < +\infty) = 0$.

The proof consists in showing that the process doesn't explode almost surely if and only if the unique non-negative and bounded solution $x = (x_i)_{i\in\mathbb{N}}$ of $Qx = x$ is the null solution. This proof is actually achieved for any integer valued pure jump Markov process. We will then see that it is equivalent to (2.1) for birth and death processes.

For any $i \geq 1$, we set $h_i^{(0)} = 1$ and for $n \geq 1$,

$$h_i^{(n)} = \mathbb{E}_i(\exp(-T_n)) = \mathbb{E}_i\left(\exp(-\sum_{k=1}^{n} S_k)\right).$$

We have

$$\mathbb{E}_i\left(\exp\left(-\sum_{k=1}^{n+1} S_k\right)\Big|S_1\right) = \exp(-S_1)\, \mathbb{E}_i\left(\mathbb{E}_{X_{S_1}}\left(\exp(-\sum_{k=1}^{n} S_k)\right)\right),$$

by the Markov property, the independence of S_1 and X_{S_1} and since the jump times of the shifted process are $T_n - S_1$. Moreover,

$$\mathbb{E}_i\left(\mathbb{E}_{X_{S_1}}\left(\exp(-\sum_{k=1}^{n} S_k)\right)\right) = \sum_{j\neq i}\mathbb{P}_i(X_{S_1} = j)\, \mathbb{E}_j\left(\exp(-\sum_{k=1}^{n} S_k)\right)$$

$$= \sum_{j \neq i} \frac{Q_{i,j}}{q_i} \, h_j^{(n)},$$

where $q_i = \sum_{j \neq i} Q_{i,j}$. Therefore, for all $n \geq 0$,

$$h_i^{(n+1)} = \mathbb{E}_i \left(\mathbb{E}_i \left(\exp(-\sum_{k=1}^{n+1} S_k) \big| S_1 \right) \right) = \sum_{j \neq i} \frac{Q_{i,j}}{q_i} \, h_j^{(n)} \, \mathbb{E}_i(\exp(-S_1)).$$

Since $\mathbb{E}_i(\exp(-S_1)) = \int_0^\infty q_i e^{-q_i s} e^{-s} ds = \frac{q_i}{1+q_i}$, we finally obtain that

$$h_i^{(n+1)} = \sum_{j \neq i} \frac{Q_{i,j}}{1 + q_i} \, h_j^{(n)}. \tag{2.2}$$

Let $(x_i)_i$ be a non-negative solution of $Qx = x$ bounded by 1. We get $h_i^{(0)} = 1 \geq x_i$ and thanks to the previous formula, we deduce by induction that for all $i \geq 1$ and for all $n \in \mathbb{N}$, $h_i^{(n)} \geq x_i \geq 0$. Indeed if $h_j^{(n)} \geq x_j$, we get $h_i^{(n+1)} \geq \sum_{j \neq i} \frac{Q_{i,j}}{1+q_i} x_j$. As x is solution of $Qx = x$, it satisfies $x_i = \sum_j Q_{i,j} \, x_j = Q_{i,i} x_i + \sum_{j \neq i} Q_{i,j} x_j = -q_i x_i + \sum_{j \neq i} Q_{i,j} x_j$, thus $\sum_{j \neq i} \frac{Q_{i,j}}{1+q_i} x_j = x_i$ and $h_i^{(n+1)} \geq x_i$.

If the process doesn't explode almost surely, we have $T_\infty = +\infty$ a.s. and $\lim_n h_i^{(n)} = 0$. Making n tend to infinity in the previous inequality, we deduce that $x_i = 0$. Thus, in this case, the unique non-negative and bounded solution of $Qx = x$ is the null solution.

Let us now assume that the process explodes with a positive probability. Let $z_i = \mathbb{E}_i(e^{-T_\infty})$. There exists i such that $\mathbb{P}_i(T_\infty < +\infty) > 0$ and for this integer i, $z_i > 0$. Going to the limit with $T_\infty = \lim_n T_n$ and $T_n = \sum_{k=1}^n S_k$ yields $z_j = \lim_n h_j^{(n)}$. Making n tend to infinity proves that z is a non-negative and bounded solution of $Qz = z$, with $z_i > 0$. It ensures that the process doesn't explode almost surely if and only if the unique non-negative and bounded solution $x = (x_i)_{i \in \mathbb{N}}$ of $Qx = x$ is $x = 0$.

We apply this result to the birth and death process. We assume that $\lambda_i > 0$ for $i \geq 1$ and $\lambda_0 = \mu_0 = 0$. Let $(x_i)_{i \in \mathbb{N}}$ be a non-negative solution of the equation $Qx = x$. For $n \geq 1$, introduce $\Delta_n = x_n - x_{n-1}$. Equation $Qx = x$ can be written $x_0 = 0$ and

$$\lambda_n x_{n+1} - (\lambda_n + \mu_n) x_n + \mu_n x_{n-1} = x_n \ , \ \forall n \geq 1.$$

Setting $f_n = \dfrac{1}{\lambda_n}$ and $g_n = \dfrac{\mu_n}{\lambda_n}$, we get

$$\Delta_1 = x_1 \ ; \ \Delta_2 = \Delta_1 \, g_1 + f_1 \, x_1 \ ; \ \ldots \ ; \ \Delta_{n+1} = \Delta_n \, g_n + f_n \, x_n.$$

Remark that for all n, $\Delta_n \geq 0$ and the sequence $(x_n)_n$ is non-decreasing. If $x_1 = 0$, the solution is zero. Otherwise we deduce that

$$\Delta_{n+1} = f_n x_n + \sum_{k=1}^{n-1} f_k \, g_{k+1} \cdots g_n \, x_k \; + \; g_1 \cdots g_n \, x_1 .$$

Since $(x_k)_k$ is non-decreasing and defining $r_n = \dfrac{1}{\lambda_n} + \displaystyle\sum_{k=1}^{n-1} \dfrac{\mu_{k+1} \cdots \mu_n}{\lambda_k \lambda_{k+1} \cdots \lambda_n} + \dfrac{\mu_1 \cdots \mu_n}{\lambda_1 \cdots \lambda_n}$, it follows that $r_n \, x_1 \leq \Delta_{n+1} \leq r_n \, x_n$, and by iteration

$$x_1(1 + r_1 + \cdots + r_n) \leq x_{n+1} \leq x_1 \prod_{k=1}^{n} (1 + r_k).$$

Therefore we have proved that the boundedness of the sequence $(x_n)_n$ is equivalent to the convergence of $\sum_k r_k$ and Theorem 2.2 is proved. ☐

2.2 Kolmogorov equations and invariant measure

Let us recall the Kolmogorov equations (see, for example, Karlin-Taylor[47]).

Forward Kolmogorov equation: for all $i, j \in \mathbb{N}$,

$$\begin{aligned} \frac{dP_{i,j}}{dt}(t) &= \sum_k P_{i,k}(t) \, Q_{k,j} = P_{i,j+1}(t) Q_{j+1,j} + P_{i,j-1}(t) Q_{j-1,j} + P_{i,j}(t) Q_{j,j} \\ &= \mu_{j+1} P_{i,j+1}(t) + \lambda_{j-1} P_{i,j-1}(t) - (\lambda_j + \mu_j) P_{i,j}(t). \end{aligned} \tag{2.3}$$

Backward Kolmogorov equation: for all $i, j \in \mathbb{N}$,

$$\begin{aligned} \frac{dP_{i,j}}{dt}(t) &= \sum_k Q_{i,k} \, P_{k,j}(t) = Q_{i,i-1} P_{i-1,j}(t) + Q_{i,i+1} P_{i+1,j}(t) + Q_{i,i} P_{i,j}(t) \\ &= \mu_i P_{i-1,j}(t) + \lambda_i P_{i+1,j}(t) - (\lambda_i + \mu_i) P_{i,j}(t). \end{aligned} \tag{2.4}$$

Let us define for all $j \in \mathbb{N}$ the probability measure

$$p_j(t) = \mathbb{P}(X(t) = j) = \sum_i \mathbb{P}(X(t) = j | X_0 = i) \mathbb{P}(X(0) = i) = \sum_i \mathbb{P}(X(0) = i) P_{i,j}(t).$$

A straightforward computation shows that the forward Kolmogorov equation (2.3) reads

$$\frac{dp_j}{dt}(t) = \lambda_{j-1} \, p_{j-1}(t) + \mu_{j+1} \, p_{j+1}(t) - (\lambda_j + \mu_j) \, p_j(t). \tag{2.5}$$

This equation is useful to find an invariant measure, that is a sequence $(q_j)_j$ of non-negative real numbers with $\sum_j q_j < +\infty$ and satisfying for all j,

$$\lambda_{j-1}\, q_{j-1} + \mu_{j+1}\, q_{j+1} - (\lambda_j + \mu_j)\, q_j = 0.$$

2.3 Extinction criterion - Extinction time

Some of the following computation can be found in [47] or in [2], but they are finely developed in [9].

Let T_0 denote the extinction time and $u_i = \mathbb{P}_i(T_0 < \infty)$ the probability to see extinction in finite time starting from state i.

Conditioning by the first jump $X_{T_1} \in \{-1, +1\}$, we get the following recurrence property: for all $i \geq 1$,

$$\lambda_i u_{i+1} - (\lambda_i + \mu_i)u_i + \mu_i u_{i-1} = 0 \tag{2.6}$$

This equation can also be easily obtained from the backward Kolmogorov equation (2.4). Indeed

$$u_i = \mathbb{P}_i(\exists t > 0, X_t = 0) = \mathbb{P}_i(\cup_t\{X_t = 0\}) = \lim_{t\to\infty} P_{i,0}(t),$$

and

$$\frac{dP_{i,0}}{dt}(t) = \mu_i P_{i-1,0}(t) + \lambda_i P_{i+1,0}(t) - (\lambda_i + \mu_i)P_{i,0}(t).$$

Let us solve (2.6). We know that $u_0 = 1$. Let us first assume that for a state N, $\lambda_N = 0$ and $\lambda_i > 0$ for $i < N$. Define $u_i^{(N)} = \mathbb{P}_i(T_0 < T_N)$, where T_N is the hitting time of N. Thus $u_0^N = 1$ et $u_N^N = 0$. Setting

$$U_N = \sum_{k=1}^{N-1} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k},$$

straightforward computations using (2.6) yield that for $i \in \{1, \cdots, N-1\}$

$$u_i^{(N)} = (1 + U_N)^{-1} \sum_{k=i}^{N-1} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} \quad \textit{and in particular} \;\; u_1^{(N)} = \frac{U_N}{1 + U_N}.$$

For the general case, let N tend to infinity. We observe that extinction will happen (or not) almost surely in finite time depending on the convergence of the series $\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}$.

Theorem 2.5. *(i) If* $\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} = +\infty$*, then the extinction probabilities* u_i *are equal to* 1*. Hence we have almost-sure extinction of the birth and death process for any finite initial condition.*

(ii) If $\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} = U_\infty < \infty$*, then for* $i \geq 1$,

$$u_i = (1 + U_\infty)^{-1} \sum_{k=i}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}.$$

There is a positive probability for the process to survive for any positive initial condition. □

Application of Theorem 2.5 to the binary branching process (linear birth and death process): any individual gives birth at rate λ and dies at rate μ. The population process is a binary branching process and individual lifetimes are exponential variables with parameter $\lambda + \mu$. An individual either gives birth to 2 individuals with probability $\frac{\lambda}{\lambda+\mu}$ or dies with probability $\frac{\mu}{\lambda+\mu}$.

Applying the previous results, one gets that when $\lambda \leq \mu$, i.e. when the process is sub-critical or critical, the sequence $(U_N)_N$ tends to infinity with N and there is extinction with probability 1. Conversely, if $\lambda > \mu$, the sequence $(U_N)_N$ converges to $\frac{\mu}{\lambda-\mu}$ and straightforward computations yield $u_i = (\mu/\lambda)^i$.

Application of Theorem 2.5 to the logistic birth and death process. Let us assume that the birth and death rates are given by

$$\lambda_i = \lambda\, i\, ; \;\; \mu_i = \mu\, i + c\, i(i-1). \tag{2.7}$$

The parameter c models the competition pressure between two individuals. It's easy to show that in this case, the series $\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}$ diverges, leading to the almost sure extinction of the process. Hence the competition between individuals makes the extinction inevitable.

Let us now come back to the general case and assume that the series $\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k}$ diverges. The extinction time T_0 is well defined and we wish to compute its moments.

We use the standard notation

$$\pi_1 = \frac{1}{\mu_1} \; ; \; \pi_n = \frac{\lambda_1 \dots \lambda_{n-1}}{\mu_1 \dots \mu_n} \qquad \forall n \geq 2.$$

Proposition 2.6. *Let us assume that*

$$\sum_{k=1}^{\infty} \frac{\mu_1 \cdots \mu_k}{\lambda_1 \cdots \lambda_k} = \sum_n \frac{1}{\lambda_n \pi_n} = +\infty. \tag{2.8}$$

Then

(i) For any $a > 0$ and $n \geq 1$,

$$G_n(a) = \mathbb{E}_{n+1}(\exp(-aT_n)) = 1 + \frac{\mu_n + a}{\lambda_n} - \frac{\mu_n}{\lambda_n} \frac{1}{G_{n-1}(a)}. \tag{2.9}$$

(ii) $\mathbb{E}_1(T_0) = \sum_{k\geq 1} \pi_k$ and for every $n \geq 2$,

$$\mathbb{E}_n(T_0) = \sum_{k\geq 1} \pi_k + \sum_{k=1}^{n-1} \frac{1}{\lambda_k \pi_k} \sum_{i \geq k+1} \pi_i = \sum_{k=1}^{n-1} \left(\sum_{i \geq k+1} \frac{\lambda_{k+1} \dots \lambda_{i-1}}{\mu_{k+1} \dots \mu_i} \right).$$

Proof. (i) Let τ_n be a random variable distributed as T_n under $\mathbb{P}_{n+1}$ and consider the Laplace transform of τ_n. Following [3, p. 264] and by the Markov property, we have

$$\tau_{n-1} \overset{(d)}{=} \mathbf{1}_{\{Y_n=-1\}} \mathcal{E}_n + \mathbf{1}_{\{Y_n=1\}} \left(\mathcal{E}_n + \tau_n + \tau'_{n-1} \right)$$

where Y_n, $\mathcal{E}_n$, τ'_{n-1} and τ_n are independent random variables, $\mathcal{E}_n$ is an exponential random variable with parameter $\lambda_n + \mu_n$ and τ'_{n-1} is distributed as τ_{n-1} and $\mathbb{P}(Y_n = 1) = 1 - \mathbb{P}(Y_n = -1) = \lambda_n/(\lambda_n + \mu_n)$. Hence, we get

$$G_{n-1}(a) = \frac{\lambda_n + \mu_n}{a + \lambda_n + \mu_n} \left(G_n(a) G_{n-1}(a) \frac{\lambda_n}{\lambda_n + \mu_n} + \frac{\mu_n}{\lambda_n + \mu_n} \right)$$

and (2.9) follows.

(ii) Differentiating (2.9) at $a = 0$, we get

$$\mathbb{E}_n(T_{n-1}) = \frac{\lambda_n}{\mu_n} \, \mathbb{E}_{n+1}(T_n) + \frac{1}{\mu_n}, \quad n \geq 1.$$

Following the proof of Theorem 2.5, we first deal with the particular case when $\lambda_N = 0$ for some $N > n$, $\mathbb{E}_N(T_{N-1}) = \frac{1}{\mu_N}$ and a simple induction gives

$$\mathbb{E}_n(T_{n-1}) = \frac{1}{\mu_n} + \sum_{i=n+1}^{N} \frac{\lambda_n \dots \lambda_{i-1}}{\mu_n \dots \mu_i}.$$

We get $\mathbb{E}_1(T_0) = \sum_{k=1}^{N} \pi_k$ and writing $\mathbb{E}_n(T_0) = \sum_{k=1}^{n} \mathbb{E}_k(T_{k-1})$, we deduce that

$$\mathbb{E}_n(T_0) = \sum_{k=1}^{N} \pi_k + \sum_{k=1}^{n-1} \frac{1}{\lambda_k \pi_k} \sum_{i=k+1}^{N} \pi_i.$$

In the general case, let $N > n$. Thanks to (2.8), T_0 is finite and the process a.s. does not explode in finite time for any initial condition. Then $T_N \to \infty$ $\mathbb{P}_n$-a.s., where we use the convention $\{T_N = +\infty\}$ on the event where the process does not attain N. The monotone convergence theorem yields

$$\mathbb{E}_n(T_0; T_0 \le T_N) \underset{N\to+\infty}{\longrightarrow} \mathbb{E}_n(T_0).$$

Let us consider a birth and death process X^N with birth and death rates $(\lambda_k^N, \mu_k^N : k \ge 0)$ such that $(\lambda_k^N, \mu_k^N) = (\lambda_k, \mu_k)$ for $k \ne N$ and $\lambda_N^N = 0, \mu_N^N = \mu_N$.

Since $(X_t : t \le T_N)$ and $(X_t^N : t \le T_N^N)$ have the same distribution under $\mathbb{P}_n$, we get

$$\mathbb{E}_n\left(T_0; T_0 \le T_N\right) = \mathbb{E}_n\left(T_0^N; T_0^N \le T_N^N\right),$$

which yields

$$\mathbb{E}_n(T_0) = \lim_{N\to\infty} \mathbb{E}_n\left(T_0^N; T_0^N \le T_N^N\right) \le \lim_{N\to\infty} \mathbb{E}_n\left(T_0^N\right),$$

where the convergence of the last term is due to the stochastic monotonicity of T_0^N with respect to N under $\mathbb{P}_n$. Using now that T_0^N is stochastically smaller than T_0 under $\mathbb{P}_n$, we have also

$$\mathbb{E}_n(T_0) \ge \mathbb{E}_n(T_0^N).$$

We deduce that

$$\mathbb{E}_n(T_0) = \lim_{N\to\infty} \mathbb{E}_n(T_0^N) = \lim_{N\to\infty} \sum_{k=1}^{N} \pi_k + \sum_{k=1}^{n-1} \frac{1}{\lambda_k \pi_k} \sum_{i=k+1}^{N} \pi_i,$$

which ends up the proof. □

Exercise. *Assume* (2.8)*. Show that for every* $n \geq 0$,

$$\mathbb{E}_{n+1}(T_n^2) = \frac{2}{\lambda_n \pi_n} \sum_{i \geq n} \lambda_i \pi_i \, \mathbb{E}_{i+1}(T_i)^2;$$

$$\mathbb{E}_{n+1}(T_n^3) = \frac{6}{\lambda_n \pi_n} \sum_{i \geq n} \lambda_i \pi_i \, \mathbb{E}_{i+1}(T_i) \, \mathrm{Var}_{i+1}(T_i).$$

2.4 Trajectorial representation of birth and death processes

We consider as previously a birth and death process with birth rates $(\lambda_n)_n$ and death rates $(\mu_n)_n$. We write $\lambda_n = \lambda(n)$ and $\mu_n = \mu(n)$, where $\lambda(.)$ and $\mu(.)$ are two functions defined on $\mathbb{R}_+$. We assume further that there exist $\bar{\lambda} > 0$ and $\bar{\mu} > 0$ such that for any $x \geq 0$,

$$\lambda(x) \leq \bar{\lambda}\, x \quad ; \quad \mu(x) \leq \bar{\mu}(1 + x^2). \tag{2.10}$$

This assumption is satisfied for the logistic case where $\lambda(x) = \lambda\, x$ and $\mu(x) = cx(x-1) + \mu\, x$.

Assumption (2.10) is a sufficient condition ensuring the existence of the process on $\mathbb{R}_+$, as observed in Corollary 2.3.

Proposition 2.7. *On the same probability space, we consider a Poisson point measure* $N(ds, du)$ *with intensity* $ds du$ *on* $\mathbb{R}_+ \times \mathbb{R}_+$ *(see Appendix). We also consider a random variable* Z_0 *independent of* N *and introduce the filtration* $(\mathcal{F}_t)_t$ *given by* $\mathcal{F}_t = \sigma(Z_0, N((0,s] \times A), s \leq t, A \in \mathcal{B}(\mathbb{R}_+))$.

The left-continuous and right-limited non-negative Markov process $(Z_t)_{t \geq 0}$ *defined by*

$$Z_t = Z_0 + \int_0^t \int_{\mathbb{R}_+} \left(\mathbf{1}_{\{u \leq \lambda(Z_{s-})\}} - \mathbf{1}_{\{\lambda(Z_{s-}) \leq u \leq \lambda(Z_{s-}) + \mu(Z_{s-})\}} \right) N(ds, du) \tag{2.11}$$

is a birth and death process with birth (resp. death) rates $(\lambda_n)_n$ *(resp.* $(\mu_n)_n$*).*

If for $p \geq 1$, $\mathbb{E}(Z_0^p) < +\infty$, *then for any* $T > 0$,

$$\mathbb{E}\big(\sup_{t \leq T} Z_t^p\big) < +\infty. \tag{2.12}$$

Proof. For $n \in \mathbb{N}$, let us introduce the stopping times

$$T_n = \inf\{t > 0, Z_t \geq n\}.$$

For $s \leq t$, we have

$$Z^p_{s\wedge T_n} = Z^p_0 + \int_0^{s\wedge T_n} ((Z_{s-}+1)^p - Z^p_{s-})\mathbf{1}_{\{u\leq\lambda(Z_{s-})\}} N(ds,du)$$
$$+ \int_0^{s\wedge T_n} ((Z_{s-}-1)^p - Z^p_{s-})\mathbf{1}_{\{\lambda(Z_{s-})\leq u\leq\lambda(Z_{s-})+\mu(Z_{s-})\}} N(ds,du).$$

The second part of the r.h.s. is non-positive and the first part is increasing in time, yielding the upper bound

$$\sup_{s\leq t} Z^p_{s\wedge T_n} \leq Z^p_0 + \int_0^{t\wedge T_n} ((Z_{s-}+1)^p - Z^p_{s-})\mathbf{1}_{\{u\leq\lambda(Z_{s-})\}} N(ds,du).$$

Since there exists $C > 0$ such that $(1+x)^p - x^p \leq C(1+x^{p-1})$ for any $x \geq 0$ and by (2.10), we get

$$\mathbb{E}(\sup_{s\leq t} Z^p_{s\wedge T_n}) \leq \mathbb{E}(Z^p_0) + C\,\bar\lambda\,\mathbb{E}\left(\int_0^{t\wedge T_n} Z_s\,(1+Z^{p-1}_s)\,ds\right)$$
$$\leq \bar C\left(1 + \int_0^t \mathbb{E}(\sup_{u\leq s\wedge T_n} Z^p_u)\,ds\right),$$

where $\bar C$ is a positive number independent of n. Since the process is bounded by n before T_n, Gronwall's Lemma implies the existence (for any $T > 0$) of a constant number $C_{T,p}$ independent of n such that

$$\mathbb{E}\big(\sup_{t\leq T\wedge T_n} Z^p_t\big) \leq C_{T,p}. \tag{2.13}$$

In particular, the sequence $(T_n)_n$ tends to infinity almost surely. Indeed, otherwise there would exist $T_0 > 0$ such that $\mathbb{P}(\sup_n T_n < T_0) > 0$. Hence $\mathbb{E}\big(\sup_{t\leq T_0\wedge T_n} Z^p_t\big) \geq n^p\,\mathbb{P}(\sup_n T_n < T_0)$, which contradicts (2.13). Making n tend to infinity in (2.13) and using Fatou's Lemma yield (2.12). □

Remark that given Z_0 and N, the process defined by (2.11) is unique. Indeed it can be inductively constructed. It is thus unique in law. Let us now recall its infinitesimal generator and give some martingale properties.

Theorem 2.8. *Let us assume that* $\mathbb{E}(Z^p_0) < \infty$, *for* $p \geq 2$.

(i) The infinitesimal generator of the Markov process Z is defined for any bounded measurable function ϕ *from* $\mathbb{R}_+$ *into* $\mathbb{R}$ *by*

$$L\phi(z) = \lambda(z)(\phi(z+1) - \phi(z)) + \mu(z)(\phi(z-1) - \phi(z)).$$

(ii) For any measurable function ϕ such that $|\phi(x)| + |L\phi(x)| \leq C(1 + x^p)$, the process M^ϕ defined by

$$M_t^\phi = \phi(Z_t) - \phi(Z_0) - \int_0^t L\phi(Z_s)ds \tag{2.14}$$

is a left-limited and right-continuous (càdlàg) $(\mathcal{F}_t)_t$-martingale.

(iii) The process M defined by

$$M_t = Z_t - Z_0 - \int_0^t (\lambda(Z_s) - \mu(Z_s))ds \tag{2.15}$$

is a square-integrable martingale with quadratic variation

$$\langle M \rangle_t = \int_0^t (\lambda(Z_s) + \mu(Z_s))ds. \tag{2.16}$$

Remark that the drift term of (2.15) involves the difference between the birth and death rates (i.e., the growth rate), while (2.16) involves the sum of both rates. Indeed the drift term describes the mean behavior whereas the quadratic variation reports the random fluctuations.

Proof. (i) is well known.

(ii) Dynkin's theorem implies that M^ϕ is a local martingale. By the assumption on ϕ, all the terms of the r.h.s. of (2.14) are integrable. Therefore M^ϕ is a martingale.

(iii) We first assume that $\mathbb{E}(Z_0^3) < +\infty$. By (2.10), we may apply (*ii*) to both functions $\phi_1(x) = x$ and $\phi_2(x) = x^2$. Hence $M_t = Z_t - Z_0 - \int_0^t (\lambda(Z_s) - \mu(Z_s))ds$ and $Z_t^2 - Z_0^2 - \int_0^t \big(\lambda(Z_s)(2Z_s + 1) - \mu(Z_s)(1 - 2Z_s)\big)ds$ are martingales. The process Z is a semi-martingale and Itô's formula applied to Z^2 gives that $Z_t^2 - Z_0^2 - \int_0^t 2Z_s\big(\lambda(Z_s) - \mu(Z_s)\big)ds - \langle M \rangle_t$ is a martingale. The uniqueness of the Doob-Meyer decomposition leads to (2.16). The general case $\mathbb{E}(Z_0^2) < +\infty$ follows by a standard localization argument. □

Chapter 3
Scaling Limits for Birth and Death Processes

If the population is large, so many birth and death events occur that the dynamics becomes difficult to describe individual per individual. Living systems need resources in order to survive and reproduce and the biomass per capita depends on the order of magnitude of these resources. We introduce a parameter $K \in \mathbb{N}^* = \{1, 2, \ldots\}$ scaling either the size of the population or the total amount of resources. We assume that the individuals are weighted by $\frac{1}{K}$.

In this section, we show that depending on the scaling relations between the population size and the demographic parameters, the population size process will be approximate either by a deterministic process or by a stochastic process. These approximations will lead to different long time behaviors.

In the rest of this section, we consider a sequence of birth and death processes Z^K parameterized by K, where the birth and death rates for the population state $n \in \mathbb{N}$ are given by $\lambda_K(n)$ and $\mu_K(n)$. Since the individuals are weighted by $\frac{1}{K}$, the population dynamics is modeled by the process $(X^K_t, t \geq 0) \in \mathbb{D}(\mathbb{R}_+, \mathbb{R}_+)$ with jump amplitudes $\pm\frac{1}{K}$ and defined for $t \geq 0$ by

$$X^K_t = \frac{Z^K_t}{K}. \tag{3.1}$$

This process is a Markov process with generator

$$L_K\phi(x) = \lambda_K(Kx)\big(\phi(x + \frac{1}{K}) - \phi(x)\big) + \mu_K(Kx)\big(\phi(x - \frac{1}{K}) - \phi(x)\big). \tag{3.2}$$

Therefore, adapting Proposition 2.7 and Theorem 2.8, one can easily show that if $\lambda_K(n) \leq \bar{\lambda} n$ (uniformly in K) and if

$$\sup_K \mathbb{E}((X^K_0)^3) < +\infty, \tag{3.3}$$

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_3

then

$$\sup_K \mathbb{E}(\sup_{t\le T}(X_t^K)^3) < +\infty, \tag{3.4}$$

and for any $K \in \mathbb{N}^*$, the process

$$M_t^K = X_t^K - X_0^K - \frac{1}{K}\int_0^t (\lambda_K(Z_s^K) - \mu_K(Z_s^K))ds \tag{3.5}$$

is a square-integrable martingale with quadratic variation

$$\langle M^K\rangle_t = \frac{1}{K^2}\int_0^t (\lambda_K(Z_s^K) + \mu_K(Z_s^K))ds. \tag{3.6}$$

3.1 Deterministic approximation - Malthusian and logistic equations

Let us now assume that the birth and death rates satisfy the following assumption:

$$\begin{aligned}&\lambda_K(n) = n\lambda\left(\frac{n}{K}\right);\ \mu_K(n) = n\mu\left(\frac{n}{K}\right),\ \text{where the functions}\\ &\lambda \text{ and } \mu \text{ are non-negative and Lipschitz continuous on } \mathbb{R}_+,\\ &\lambda(x) \le \bar\lambda \quad ; \quad \mu(x) \le \bar\mu(1+x).\end{aligned} \tag{3.7}$$

We will focus on two particular cases:

The linear case: $\lambda_K(n) = n\lambda$ and $\mu_K(n) = n\mu$, with $\lambda, \mu > 0$.
The logistic case: $\lambda_K(n) = n\lambda$ and $\mu_K(n) = n(\mu + \frac{c}{K}n)$ with $\lambda, \mu, c > 0$.

By (3.3), the population size is of the order of magnitude of K and the biomass per capita is of order $\frac{1}{K}$. This explains that the competition pressure from one individual to another one in the logistic case is proportional to $\frac{1}{K}$.

We are interested in the limiting behavior of the process $(X_t^K, t \ge 0)$ when $K \to \infty$.

Theorem 3.1. *Let us assume* (3.7), (3.3) *and that the sequence* $(X_0^K)_K$ *converges in law (and in probability) to a real number* x_0. *Then for any* $T > 0$, *the sequence of processes* $(X_t^K, t \in [0,T])$ *converges in law (and hence in probability), in* $\mathbb{D}([0,T],\mathbb{R}_+)$, *to the continuous deterministic function* $(x(t), t \in [0,T])$ *solution of the ordinary differential equation*

$$x'(t) = x(t)(\lambda(x(t)) - \mu(x(t)))\ ; x(0) = x_0. \tag{3.8}$$

In the linear case, the limiting equation is the Malthusian equation

$$x'(t) = x(t)(\lambda - \mu).$$

In the logistic case, one obtains the logistic equation

$$x'(t) = x(t)(\lambda - \mu - c\,x(t)). \tag{3.9}$$

These two equations have different long time behaviors. In the Malthusian case, depending on the sign of $\lambda - \mu$, the solution of the equation tends to $+\infty$ or to 0 as time goes to infinity, modeling the explosion or extinction of the population. In the logistic case and if the growth rate $\lambda - \mu$ is positive, the solution converges to the carrying capacity $\dfrac{\lambda - \mu}{c} > 0$. The competition between individuals yields a regulation of the population size.

Proof. The proof is based on a compactness-uniqueness argument. More precisely, the scheme of the proof is the following:

1) Uniqueness of the limit.
2) Uniform estimates on the moments.
3) Tightness of the sequence of laws of $(X_t^K, t \in [0,T])$ in the Skorohod space. We will use the Aldous and Rebolledo criteria.
4) Identification of the limit.

Thanks to Assumption (3.7), the uniqueness of the solution of equation (3.8) is obvious. We also have (3.4). Therefore it remains to prove the tightness of the sequence of laws and to identify the limit. Recall (see, for example, [30] or [43]) that since the processes $(X_t^K = X_0^K + M_t^K + A_t^K)_t$ are semimartingales, tightness will be proved as soon as we have

(i) The sequence of laws of $(\sup_{t\leq T} |X_t^K|)$ is tight,
(ii) The finite variation processes $\langle M^K \rangle$ and A^K satisfy the Aldous conditions.

Let us recall the Aldous condition (see [1]): let $(Y^K)_K$ be a sequence of $\mathcal{F}_t$-adapted processes and τ the set of stopping times for the filtration $(\mathcal{F}_t)_t$. The Aldous condition can be written: $\forall \varepsilon > 0$, $\forall \eta > 0$, $\exists \delta > 0$, K_0 such that

$$\sup_{K\geq K_0} \sup_{S,S'\in\tau; S\leq S'\leq (S+\delta)\wedge T} \mathbb{P}(|Y_{S'}^K - Y_S^K| > \varepsilon) \leq \eta.$$

Let us show this property for the sequence $(A^K)_K$. We have

$$\mathbb{E}(|A_{S'}^K - A_S^K|) \leq \mathbb{E}\left(\int_S^{S'} X_s^K |\lambda(X_s^K) - \mu(X_s^K)| ds\right)$$

$$\leq C\mathbb{E}\left(\int_S^{S'} (1 + (X_s^K)^2)ds\right) \quad \text{by (3.7)}$$
$$\leq C\,\delta\,\mathbb{E}\left(\sup_{s\leq T}(1 + (X_s^K)^2)\right)$$

which tends to 0 uniformly in K as δ tends to 0. We use a similar argument for $(\langle M^K\rangle)_K$ to conclude for the tightness of the laws of $(X^K)_K$. Prokhorov's Theorem implies the relative compactness of this family of laws in the set of probability measures on $\mathbb{D}([0,T],\mathbb{R})$, leading to the existence of a limiting value Q.

Let us now identify the limit. The jumps of X^K have the amplitude $\frac{1}{K}$. Since the mapping $x \to \sup_{t\leq T}|\Delta x(t)|$ is continuous from $\mathbb{D}([0,T],\mathbb{R})$ into $\mathbb{R}_+$, then the probability measure Q only charges the subset of continuous functions. For any $t > 0$, we define on $\mathbb{D}([0,T],\mathbb{R})$ the function

$$\psi_t(x) = x_t - x_0 - \int_0^t (\lambda(x_s) - \mu(x_s))\, x_s ds.$$

The assumptions yield

$$|\psi_t(x)| \leq C \sup_{t\leq T}(1 + (x_t)^2)$$

and we deduce the uniform integrability of the sequence $(\psi_t(X^K))_K$ from (3.4). The projection mapping $x \to x_t$ isn't continuous on $\mathbb{D}([0,T],\mathbb{R})$ but since Q only charges the continuous paths, we deduce that $X \to \psi_t(X)$ is Q-a.s. continuous, if X denotes the canonical process. Therefore, since Q is the weak limit of a subsequence of $(\mathcal{L}(X^K))_K$ (that for simplicity we still denote $\mathcal{L}(X^K)$) and using the uniform integrability of $(\psi_t(X^K))_K$, we get

$$\mathbb{E}_Q(|\psi_t(X)|) = \lim_K \mathbb{E}(|\psi_t(X^K)|) = \lim_K \mathbb{E}(|M_t^K|).$$

But

$$\mathbb{E}(|M_t^K|) \leq \left(\mathbb{E}(|M_t^K|^2)\right)^{1/2}$$

tends to 0 by (3.6), (3.7), and (3.4). Hence the limiting process X is the deterministic solution of the equation

$$x(t) = x_0 + \int_0^t x_s(\lambda(x_s) - \mu(x_s))ds.$$

That ends the proof. □

3.2 Stochastic approximation - Feller and logistic Feller diffusions

Let us now assume that

$$\lambda_K(n) = n\,(\gamma K n + \lambda)\,;\ \mu_K(n) = n\left(\gamma K n + \mu + \frac{c}{K}n\right), \tag{3.10}$$

where γ, λ, μ, c are non-negative constants and $\lambda > \mu$. The coefficient $\gamma > 0$ is called the allometry coefficient. Such population model describes the behavior of small individuals which are born or die very fast. As we will see in the next theorem, this assumption changes the qualitative nature of the large population approximation.

Theorem 3.2. *Assume* (3.10) *and* (3.3) *and that the random variables* X_0^K *converge in law to a square-integrable random variable* X_0*. Then for any* $T > 0$*, the sequence of processes* $(X_t^K, t \in [0,T])$ *converges in law, in* $\mathbb{D}([0,T],\mathbb{R}_+)$*, to the continuous diffusion process* $(X_t, t \in [0,T])$ *solution of the stochastic differential equation*

$$X_t = X_0 + \int_0^t \sqrt{2\gamma X_s}dB_s + \int_0^t X_s(\lambda - \mu - cX_s)ds. \tag{3.11}$$

In this case, the limiting process is stochastic. Indeed there are so many birth and death jump events that the stochasticity cannot completely disappear. Hence the term $\sqrt{2\gamma X_t}dB_t$ models the demographic stochasticity. Its variance is proportional to the renormalized population size. When $c = 0$, we get the Feller diffusion equation

$$dX_t = \sqrt{2\gamma X_t}dB_t + X_t(\lambda - \mu)dt. \tag{3.12}$$

If $c \neq 0$, Equation (3.11) is called by extension the logistic Feller diffusion equation (see Etheridge [29] and Lambert [51]).

Proof. Here again the proof is based on a uniqueness-compactness argument.

Let us first prove the uniqueness in law of a solution of (3.11). We use a general result concerning one-dimensional stochastic differential equations (see Ikeda-Watanabe [41] p.448). The diffusion and drift coefficients are of class C^1 and non-zero on $(0, +\infty)$ but can cancel at 0. So Equation (3.11) is uniquely defined until the stopping time $T_e = T_0 \wedge T_\infty$ where T_0 is the hitting time of 0 and T_∞ the explosion time. Furthermore, 0 is an absorbing point for the process. In the particular case where $c = 0$ (no interaction), the process stays in $(0, \infty)$ or goes to extinction almost surely (see Subsection 4.1 and Proposition 4.7. When $c > 0$, the process goes to extinction almost surely, as recalled below.

Lemma 3.3. *For any* $x > 0$*,* $\mathbb{P}_x(T_e = T_0 < +\infty) = 1$ *if* $c > 0$*.*

Proof of Lemma 3.3. Recall Ikeda-Watanabe's results in [41] (see also Shreve-Karatzas [45] Prop. 5.32). Let Y_t denote the solution of the one-dimensional stochastic differential equation $dY_t = \sigma(Y_t)dB_t + b(Y_t)dt$. Let us introduce the two functions:

$$\Lambda(x) = \int_1^x \exp\left(-\int_1^z \frac{2b(y)}{\sigma^2(y)}dy\right) dz;$$
$$\kappa(x) = \int_1^x \exp\left(-\int_1^z \frac{2b(y)}{\sigma^2(y)}dy\right) \left(\int_1^z \exp\left(\int_1^\eta \frac{2b(y)}{\sigma^2(y)}dy\right) \frac{d\eta}{\sigma^2(\eta)}\right) dz.$$

Then there is equivalence between the two following assertions:

(a) For any $y > 0$, $\mathbb{P}_y(T_e^Y = T_0^Y < +\infty) = 1$.
(b) $\Lambda(+\infty) = +\infty$ and $\kappa(0^+) < +\infty$.

In our case, straightforward computations allow us to show that (b) is satisfied by the solution of (3.11) as soon as $c \neq 0$. □

Let us now prove that there exists a constant $C_{1,T}$ such that

$$\sup_{t\le T}\sup_K \mathbb{E}((X_t^K)^3) \le C_{1,T}, \tag{3.13}$$

where $C_{1,T}$ only depends on T. Following the proof of Theorem 2.8 (*iii*), we note that

$$(X_t^K)^3 - (X_0^K)^3 - \int_0^t \Big\{\gamma K^2 X_s^K\Big((X_s^K + \frac{1}{K})^3 + (X_s^K - \frac{1}{K})^3 - 2(X_s^K)^3\Big)$$
$$+\lambda K X_s^K\Big((X_s^K + \frac{1}{K})^3 - (X_s^K)^3\Big) + (\mu K + cX_s^K)X_s^K(X_s^K - \frac{1}{K})^3 - (X_s^K)^3\Big\} ds$$

is a martingale. Therefore, using that $(x + \frac{1}{K})^3 + (x - \frac{1}{K})^3 - 2x^3 = \frac{6}{K^2}x$ and (3.4), a localization argument and Gronwall's inequality, we get (3.13).

Hence, we may deduce a pathwise second order moment estimate:

$$\sup_K \mathbb{E}\big(\sup_{t\le T}(X_t^K)^2\big) \le C_{2,T}, \tag{3.14}$$

where $C_{2,T}$ only depends on T. Indeed, we have

$$X_t^K = X_0^K + M_t^K + \int_0^t X_s^K(\lambda - \mu - cX_s^K)ds,$$

where M^K is a martingale. Then, there exists $C'_T > 0$ with

$$\mathbb{E}\big(\sup_{s\le t}(X_s^K)^2\big) \le C'_T\left(\mathbb{E}((X_0^K)^2) + \sup_{s\le t}\mathbb{E}((X_s^K)^2) + \mathbb{E}\big(\sup_{s\le t}(M_s^K)^2\big)\right),$$

and by Doob's inequality,

$$\mathbb{E}\big(\sup_{s\leq t}(M_s^K)^2\big) \leq C\mathbb{E}(\langle M^K\rangle_t) = C\mathbb{E}\left(\int_0^t \big(2\gamma X_s^K + \frac{X_s^K}{K}(\lambda+\mu+cX_s^K)\big)ds\right).$$

Finally Gronwall's Lemma and (3.13) allow to get (3.14). The proof of the tightness follows as in the proof of Theorem 3.1.

Let us now identify the limit. We consider a limiting value Q. Remark once again that since the mapping $x \to \sup_{t\leq T}|\Delta x(t)|$ is continuous from $\mathbb{D}([0,T],\mathbb{R})$ into $\mathbb{R}_+$, then Q charges only the continuous paths. For any $t>0$ and $\phi\in C_b^2$, we define on $\mathbb{D}([0,T],\mathbb{R})$ the function

$$\psi_t^1(x) = \phi(x_t) - \phi(x_0) - \int_0^t L\phi(x_s)\,ds,$$

where $L\phi(x) = \gamma\, x\,\phi''(x) + ((\lambda-\mu)x - cx^2)\,\phi'(x)$. Note that $|\psi_t^1(x)| \leq C \int_0^T(1+x_s^2)ds$, which implies the uniform integrability of the sequence $(\psi_t^1(X^K))_K$ by (3.4).

Let us prove that the process $(\psi_t^1(X), t\geq 0)$ is a Q-martingale. That will be true as soon as $\mathbb{E}_Q(H(X)) = 0$ for any function H defined as follows:

$$H(X) = g_1(X_{s_1})\cdots g_k(X_{s_k})(\psi_t^1(X) - \psi_s^1(X)),$$

for $0\leq s_1\leq\cdots\leq s_k\leq s<t$ and $g_1,\cdots,g_k\in C_b(\mathbb{R}_+)$.

Now, $\phi(X_t^K)$ is a semimartingale and

$$\phi(X_t^K) = \phi(X_0^K) + M_t^{K,\phi} + \int_0^t L_K\phi(X_s^K)ds,$$

Moreover $|L_K\phi(x) - L\phi(x)| \leq \dfrac{C}{K}(1+x^2)$ and

$$\mathbb{E}(|L_K\phi(X_s^K) - L\phi(X_s^K)|) \leq \frac{C}{K}\mathbb{E}(\sup_{s\leq T}(1+|X_s^K|^2)). \tag{3.15}$$

We denote by $\psi_t^K(X)$ the similar function as $\psi_t^1(X)$ with L replaced by L_K.

The function H_K will denote the function similar to H with ψ_t^1 replaced by ψ_t^K. We write

$$\mathbb{E}_Q(H(X)) = \mathbb{E}_Q(H(X) - H_K(X)) + \big(\mathbb{E}_Q(H_K(X)) - \mathbb{E}(H_K(X^K))\big) + \mathbb{E}(H_K(X^K)).$$

The third term is zero since $(\psi_t^K, t\geq 0)(X^k)$ is a martingale. It's easy to prove the convergence to 0 of the first term using (3.15). The second term tends to 0 by continuity and uniform integrability. Hence we have proved that under Q the limiting process satisfies the following martingale problem: for any $\phi\in C_b^2$, the process $\phi(X_t) - \phi(X_0) - \int_0^t L\phi(X_s)ds$ is a martingale. We know further that for any $T > 0$, $\mathbb{E}(\sup_{t\leq T}(X_t)^2) < +\infty$. It remains to show that under Q, (X_t) is the unique solution of (3.11). Such point is standard and can be found, for example, in Karatzas-Shreve [45] but we give a quick proof. Applying the martingale problem to $\phi(x) = x$, then $\phi(x) = x^2$, we get that X_t is a square-integrable semimartingale and that $X_t = X_0 + M_t + \int_0^t X_s(\lambda - \mu - cX_s)X_s\,ds$ and the martingale part M_t has quadratic variation $\int_0^t 2\gamma X_s ds$. Then a representation theorem is used to conclude. Indeed, let us increase the probability space and consider an auxiliary space $(\Omega', \mathcal{A}', \mathbb{P}')$ and a Brownian motion W defined on the latter. On $\Omega \times \Omega'$, let us define

$$B_t(\omega, \omega') = \int_0^t \frac{1}{\sqrt{2\gamma X_s(\omega)}} \mathbf{1}_{\{X_s(\omega)\neq 0\}} dM_s(\omega) + \int_0^t \mathbf{1}_{\{X_s(\omega)=0\}} dW_s(\omega').$$

It's obvious that the processes B_t and $B_t^2 - t$ are continuous martingales on the product probability space. Then B is a Brownian motion by the Lévy's characterization. In addition, we compute

$$\mathbb{E}\left(\left(M_t - \int_0^t \sqrt{2\gamma X_s} dB_s\right)^2\right) = \mathbb{E}\left(\int_0^t \mathbf{1}_{\{X_s(\omega)=0\}} d\langle M\rangle_s\right) = 0.$$

Thus, $M_t = \int_0^t \sqrt{2\gamma X_s} dB_s$, which ends the proof. □

3.3 Selection strategy in random environments

In (3.11), the stochastic term is demographic in the sense that, as seen in the previous section, it comes from a very high number of births and deaths. Another stochastic term can be added to the deterministic equation to model a random environment. In Evans, Hening, and Schreiber [34], the authors consider the population abundance process $(Y_t, t \geq 0)$ governed by the stochastic differential equation

$$dY_t = Y_t(r - cY_t) + \sigma Y_t dW_t\ ,\ Y_0 > 0, \tag{3.16}$$

where $(W_t)_{t\geq 0}$ is a standard Brownian motion.

The growth rate has a stochastic component whose σ^2 is the infinitesimal variance. The process is well defined and has an explicit form which can be checked using Itô's formula:

$$Y_t = \frac{Y_0 \exp\left((r - \frac{\sigma^2}{2})t + \sigma W_t\right)}{1 + Y_0 \frac{r}{c} \int_0^t \exp\left((r - \frac{\sigma^2}{2})s + \sigma W_s\right) ds}.$$

Then $Y_t \geq 0$ for all $t \geq 0$ almost surely.

The authors deduce the long time behavior of the process depending on the sign of $r - \frac{\sigma^2}{2}$. We refer to [34] for the proof.

Proposition 3.4. *1. If* $r - \frac{\sigma^2}{2} < 0$*, then* $\lim_{t\to\infty} Y_t = 0$ *almost surely.*

2. If $r - \frac{\sigma^2}{2} = 0$*, then* $\liminf_{t\to\infty} Y_t = 0$ *almost surely,* $\limsup_{t\to\infty} Y_t = \infty$ *almost surely and* $\lim_{t\to\infty} \frac{1}{t}\int_0^t Y_s ds = 0$ *almost surely.*

3. If $r - \frac{\sigma^2}{2} > 0$*, then* $(Y_t)_t$ *has a unique stationary distribution which is the law* $\Gamma(\frac{2r}{\sigma^2} - 1, \frac{\sigma^2}{2c}) = \Gamma(k, \theta)$*, with density* $x \longrightarrow \frac{1}{\Gamma(k)\theta^k} x^{k-1} e^{-\frac{x}{\theta}}$.

Of course, a challenge is to consider a mixed model with demographic stochasticity and random environment, consisting in adding the term $\sqrt{Y_t} dB_t$ to the r.h.s. of (3.16). Some work has been developed in this sense in [12] in the case without interaction $c = 0$. Modeling branching processes in random environment will be the aim of Chapter 5.

Chapter 4
Continuous State Branching Processes

In this part, we consider a new class of stochastic differential equations for monotype populations, taking into account exceptional events where an individual has a large number of offspring. We generalize the Feller equation (3.12) obtained in Subsection 3.2 by adding jumps whose rates are proportional to the population size. The jumps are driven by a Poisson point measure, as already done in Subsection 2.4. This class of processes satisfies the branching property: the individuals of the underlying population evolve independently. Combining this property with the tools developed in the first part, we describe finely the processes, their long time behavior, and the scaling limits they come from.

4.1 Definition and examples

Definition 4.1. Let $r \in \mathbb{R}$, $\gamma \geq 0$ and μ be a σ-finite measure on $(0, \infty)$ such that $\int_0^\infty \big(h \wedge h^2\big)\mu(dh)$ is finite. Let $N_0(ds, dh, du)$ be a Poisson point measure on $\mathbb{R}_+^3$ with intensity $ds\mu(dh)du$ and $\tilde{N}_0$ its compensated measure. Let B be a standard Brownian motion independent of N_0 and Z_0 a square-integrable random variable independent of N_0 and B.

The Continuous State Branching process (CSBP) Z with characteristic triplet (r, γ, μ) is the unique non-negative strong solution in $\mathbb{D}(\mathbb{R}_+, \mathbb{R}_+)$ of the following stochastic differential equation

$$Z_t = Z_0 + \int_0^t rZ_s ds + \int_0^t \sqrt{2\gamma Z_s} dB_s + \int_0^t \int_0^\infty \int_0^\infty \mathbf{1}_{\{u \leq Z_{s-}\}} h \tilde{N}_0(ds, dh, du), \tag{4.1}$$

The difficulties in the proof of the existence and uniqueness come from the term $\sqrt{Z_t}$ (which is non-Lipschitz for Z close to 0). We refer to Fu and Li [36] for a general framework on the existence and uniqueness of such equations. In the forthcoming

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_4

Proposition 4.5 and Section 4.5, the Lamperti representation and scaling limits of discrete branching processes will be proved to actually provide alternative ways to construct and identify CSBP.

We recall from the previous section that the term $\sqrt{2\gamma Z_s}dB_s$ corresponds to continuous fluctuations of the population size, with variance proportional to the number of individuals. The last term describes the jumps of the population size whose rate at time s is proportional to the size Z_{s-} and the distribution proportional to the measure μ. The jump term appears in the scaling limit when the individuals reproduction law charges very large numbers (the second moment has to be infinite, see Section 4.5). The case $\mu(dz) = cz^{-(1+\alpha)}dz$ ($\alpha \in (1,2)$) plays a particular role (see below), since the corresponding CSBP is then a stable process. We stress that in the definition given above the jumps appear only through the compensated Poisson measure, which uses the integrability assumption on μ. Thus, the drift term rZ_s can be seen as the sum of the drift term of a Feller diffusion and the drift term due to the mean effect of the jumps.

4.2 Characterization and properties

Let Z be a CSBP with characteristic triplet (r, γ, μ). It's a Markov process.

Proposition 4.2. *The infinitesimal generator of Z is given by: for every $f \in C_b^2(\mathbb{R}_+)$,*

$$\mathcal{A}f(z) = rzf'(z) + \gamma zf''(z) + \int_0^\infty \Big(f(z+h) - f(z) - hf'(z)\Big)z\mu(dh).$$

We refer to the Appendix for complements on the semi-martingale decomposition. We note from the expression of $\mathcal{A}$ that the function $z \to z^2$ doesn't belong (in general) to the domain of the generator. But one can prove that C^2 functions with two first derivatives bounded belong to the domain. It can be achieved by monotone convergence using non-decreasing sequences of functions $g_n \in C_b^2$ such that $\| g_n' \|_\infty + \| g_n'' \|_\infty$ is bounded and there exists $C > 0$ such that

$$|\mathcal{A}f(z)| \le C\left(\| f' \|_\infty + \| f'' \|_\infty\right) z$$

for every $z \ge 0$.

Exercise. *Prove that $\mathbb{E}_z(Z_t) = z\exp(rt)$ for any $t, z \ge 0$ and that $(\exp(-rt)Z_t : t \ge 0)$ is a martingale. What can you say about the long time behavior of Z_t? What is the interpretation of r ?*

Hint: One can use the two-dimensional Itô formula.

We give now the key property satisfied by our class of processes. If necessary, we denote by $Z^{(z)}$ a CSBP starting at z.

Proposition 4.3. *The process Z satisfies the branching property, i.e.*

$$Z^{(z+\tilde{z})} \overset{d}{=} Z^{(z)} + \tilde{Z}^{(\tilde{z})} \qquad (z, \tilde{z} \in \mathbb{R}_+),$$

where Z et $\tilde{Z}$ are independent CSBPs with the same distribution.

Then the Laplace transform of Z_t is of the form

$$\mathbb{E}_z\Big[\exp(-\lambda Z_t)\Big] = \exp\{-zu_t(\lambda)\}, \qquad \textit{with } \lambda \geq 0,$$

for some non-negative function u_t and any $z \geq 0$.

Proof. To simplify the notation, we write $X_t = Z_t + Z'_t$, where $Z_0 = z$, $Z'_0 = \tilde{z}$ and Z and Z' are two independent CSBP. The process X satisfies a.s. :

$$\begin{aligned} X_t = X_0 + \int_0^t rX_s ds + \int_0^t \sqrt{2\gamma Z_s} dB_s + \sqrt{2\gamma Z'_s} dB'_s \\ + \int_0^t \int_0^\infty \int_0^{Z_{s-}} h\tilde{N}_0(ds, dh, du) + \int_0^t \int_0^\infty \int_0^{Z'_{s-}} h\tilde{N}'_0(ds, dh, du) \end{aligned} \tag{4.2}$$

where B and B' are two independent Brownian motions and N_0 and N'_0 are two independent Poisson point measures on $\mathbb{R}_+^3$ with intensity $ds\mu(dh)du$. We introduce the real valued process B'' defined by

$$B''_t = \int_0^t \mathbf{1}_{\{X_s>0\}} \frac{\sqrt{2\gamma Z_s} dB_s + \sqrt{2\gamma Z'_s} dB'_s}{\sqrt{2\gamma X_s}} + \int_0^t \mathbf{1}_{\{X_s=0\}} dB_s$$

and note that B'' is a Brownian motion by Lévy Theorem since it is a continuous local martingale with quadratic variation equal to t. We also define the random point measure N''_0 on $\mathbb{R}_+^3$ by

$$N''_0(ds, dh, du) = N_0(ds, dh, du)\mathbf{1}_{\{u \leq Z_{s-}\}} + \widehat{N'_0}(ds, dh, du),$$

where $\widehat{N'_0}$ is the random point measure on $\mathbb{R}_+^3$ given by $\widehat{N'_0}(A \times B \times [h_1, h_2]) = N'_0(A \times B \times [h_1 - Z_{s-}, h_2 - Z_{s-}])$. The random measure N''_0 is also a Poisson point measure with intensity $ds\mu(dh)du$ since N_0 and N'_0 are independent. Adding that (4.2) can be rewritten as

$$X_t = X_0 + \int_0^t rX_s ds + \int_0^t \sqrt{2\gamma X_s} dB''_s + \int_0^t \int_0^\infty \int_0^{X_{s-}} h\tilde{N}''_0(ds, dh, du),$$

the process X is a CSBP with initial condition $z + \tilde{z}$.

Furthermore, the branching property ensures that for $\lambda > 0$,

$$\mathbb{E}_{z+z'}\Big[\exp(-\lambda Z_t)\Big] = \mathbb{E}_z\Big[\exp(-\lambda Z_t)\Big]\mathbb{E}_{z'}\Big[\exp(-\lambda Z_t)\Big]$$

which yields the linearity of the Laplace exponent (taking the logarithm). $\square$

Combining Propositions 4.2 and 4.3, we characterize the finite dimensional distributions of a CSBP.

Corollary 4.4 (Silverstein [61]). *Let $\lambda > 0$. The Laplace exponent $u_t(\lambda)$ is the unique solution of*

$$\frac{\partial}{\partial t} u_t(\lambda) = -\psi(u_t(\lambda)), \qquad u_0(\lambda) = \lambda, \tag{4.3}$$

where ψ is called the branching mechanism associated with Z and is defined by

$$\psi(\lambda) = -r\lambda + \gamma\lambda^2 + \int_0^\infty \left(e^{-\lambda h} - 1 + \lambda h\right)\mu(dh). \tag{4.4}$$

Proof. Applying Propositions 4.2 and 4.3 and defining $z \to f_\lambda(z) := \exp(-\lambda z) \in C_b^2(\mathbb{R}_+)$, we get $P_t f_\lambda(z) = \exp(-z u_t(\lambda))$ and

$$\frac{\partial}{\partial t} P_t f_\lambda(1) = \mathcal{A} P_t f_\lambda(1) = -\frac{\partial u_t(\lambda)}{\partial t}\exp(-u_t(\lambda)).$$

Thus computing the generator for the function $z \to \exp(-z u_t(\lambda))$ yields the result. $\square$

An alternative proof of this result can be given by using Itô's formula to prove that $(\exp(-v_{T-t}(\lambda) Z_t) : t \in [0, T])$ is a martingale if and only if v is the solution of (4.3). This idea will be extended to the random environment in the next section.

Exercise. *1) Check that for any $\lambda > 0$ and $t > 0$, $u_t(\lambda)$ is the unique solution of the integral equation*

$$\int_{u_t(\lambda)}^{\lambda} \frac{1}{\psi(v)}\, dv = t.$$

2) Compute $u_t(\lambda)$ for a Feller diffusion and deduce from it the extinction probability.

4.3 The Lamperti transform

The following result is fundamental for the trajectorial and long time study of CSBPs, since it allows to see these processes (whose dynamics are multiplicative) as the time change of some Lévy processes (which are well-known additive random processes). We recall that a Lévy process is a càdlàg process with stationary independent increments.

Proposition 4.5 (Lamperti [52, 53]). *Let Y be a Lévy process defined by*

$$Y_t := y_0 + rt + \gamma B_t + \int_0^t \int_0^\infty h\tilde{N}(ds, dh),$$

where $r \in \mathbb{R}$, $\gamma \geq 0$, N is a Poisson point measure on $\mathbb{R}_+^2$ with intensity $ds\mu(dh)$, $\tilde{N}$ its compensated measure and $\int_0^\infty \left(h \wedge h^2\right)\mu(dh) < \infty$. Writing Y^+ for the process Y killed when it reaches 0, the equation

$$Z_t = Y^+_{\int_0^t Z_s ds} \tag{4.5}$$

has a unique solution Z for $t \geq 0$. This process Z is càdlàg and distributed as the CSBP with characteristic (r, γ, μ) started at y_0.

In particular, when $\mu(dz) = cz^{-(1+\alpha)}dz$ ($r = 0, \gamma = 0$), we recover the stable Lévy processes. A converse statement is given in the last part of this section. It relies on the expression $Y_t = Z_{\gamma_t}$ with $\gamma_t = \inf\{u : \int_0^u \beta(Z_s)ds > t\}$.

To prove Proposition 4.5, we use the following lemma, which we derive from Chapter 6 (random time changes) of Ethier & Kurtz [30].

Lemma 4.6. *Let X be a càdlàg process from $\mathbb{R}_+$ to $\mathbb{R}_+$ and β be a non-negative continuous function on $\mathbb{R}_+$. We define $A_t := \int_0^t 1/\beta(X_u)du$ and assume that*

$$\lim_{t\to\infty} A_t = +\infty, \qquad \inf\{t \geq 0 : A_t = +\infty\} = \inf\{t \geq 0 : \beta(X_t) = 0\} \quad a.s.$$

(i) There exists a unique function τ from $\mathbb{R}_+$ to $[0, \inf\{t \geq 0 : \beta(X_t) = 0\})$ which is solution of the equation $A_{\tau_t} = t$.
(ii) The process Z defined by $Z_t := X_{\tau_t}$ for $t \geq 0$ is the unique solution of $Z_t = X_{\int_0^t Z_s ds}$ for $t \geq 0$.
(iii-Martingale problem) If $(f(X_t) - \int_0^t g(X_s)ds : t \geq 0)$ is an $(\mathcal{F}_t^X)_t$ martingale, then $(f(Z_t) - \int_0^t \beta(Z_s)g(Z_s)ds : t \geq 0)$ is an $(\mathcal{F}_t^Z)_t$ martingale.

Proof. *(i)* simply comes from the fact that $t \to A_t$ is an increasing bijection from $[0, T)$ to $\mathbb{R}_+$, with $T := \inf\{t \geq 0 : \beta(X_t) = 0\}$.
(ii) is deduced from (i) by noticing that

$$A_{\tau_t} = t \ \ (t \geq 0) \iff \tau_t' = \beta(Z_t) \text{ a.e.} \iff \tau_t = \int_0^t \beta(Z_s)ds \ \ (t \geq 0)\ . \tag{4.6}$$

(Take care of the regularity of the processes).

To prove (*iii*), we first check that $\{\tau_s \leq t\} = \{A_t \geq s\} \in \mathcal{F}_t^X$. The optional sampling theorem ensures that if $f(X_t) - \int_0^t g(X_s)ds$ is an $(\mathcal{F}_t^X)_t$ martingale, then $f(X_{\tau_t}) - \int_0^{\tau_t} g(X_s)ds = f(Z_t) - \int_0^t g(Z_s)\tau_s' ds$ is an $(\mathcal{F}_{\tau(t)}^Y)_t$ martingale. Recalling from (4.6) that $\tau_s' = \beta(X_{\tau_s}) = \beta(Z_s)$ a.e, we get the result. □

Proof of Proposition 4.5. The existence and uniqueness of the problem (4.5) come from Lemma 4.6 (*i*) and (*ii*) with $X = Y^+$ and $\beta(x) = x$. Indeed, we first note that $\mathbb{E}(Y_1) \in (-\infty, \infty)$ and the following law of large numbers holds: $Y_t/t \to \mathbb{E}(Y_1)$ a.s. Then $\int_0^\infty 1/Y_s^+ ds = \infty$ a.s. Let us now check that the first time at which A_t is infinite is the first time at which Y^+ reaches 0. The fact that $\inf\{t \geq 0 : Y_t^+ = 0\} \leq \inf\{t \geq 0 : A_t = \infty\}$ is obvious. To get the converse inequality, we denote by T the non-decreasing limit of the stopping times $T_\epsilon = \inf\{t \geq 0 : Y_t \leq \epsilon\}$ for $\epsilon \to 0$ and prove that $Y_T = 0$ on the event $\{T < \infty\}$ (quasi-left continuity). For that purpose, we use

$$\mathbb{E}\left(f(Y_{T\wedge t}) - f(Y_{T_\epsilon \wedge t}) - \int_{T_\epsilon \wedge t}^{T\wedge t} Qf(Y_s)ds \middle| \mathcal{F}_{T_\epsilon \wedge t}\right) = 0.$$

for $f \in C_b^2(\mathbb{R}_+)$, where we have denoted by Q the generator of Y:

$$Qf(y) := rf'(y) + \gamma f''(y) + \int_0^\infty \Big(f(y+h) - f(x) - hf'(y)\Big)\mu(dh).$$

Then

$$\lim_{\epsilon \to 0} \mathbb{E}(f(Y_{T\wedge t})|\mathcal{F}_{T_\epsilon \wedge t}) = f(0),$$

and using some non-negative function $f \in C_b^2(\mathbb{R}_+)$ which coincides with x^2 in a neighborhood of 0, we obtain $Y_{T\wedge t} = 0$ on $\{T < \infty\}$.

To check that the process given by (4.5) is indeed a CSBP, we use again the generator Q of Y. Lemma 4.6 (*iii*) ensures that for $f \in C_b^2(\mathbb{R}_+)$,

$$f(Z_t) - \int_0^t Z_s Qf(Z_s)ds$$

is a martingale. It identifies the distribution of the càdlàg Markov process Z via its generator $\mathcal{A}f(z) = zQf(z)$. More precisely, the uniqueness of the martingale problem is required here to ensure the uniqueness of the distribution of the process and we refer to Ethier & Kurtz [30], Theorem 4.1 in Section 4 for a general statement. In our particular case, the proof can be made directly using the set of functions $f_\lambda(z) = \exp(-\lambda z)$. Indeed, the independence and stationarity of the increments of Y ensure the branching property of Z. One can then follow the proof of Corollary 4.4 to derive $\mathbb{E}_z(\exp(-\lambda Z_t))$ from $\mathcal{A}$ and identify the finite dimensional distributions of Z. □

4.4 Long time behavior

In this section, the characteristic triplet (r, γ, μ) is assumed to be non-identical to 0, to avoid the degenerate case where Z is a.s. constant.

Proposition 4.7. *(i-unstability) With probability one, Z_t tends to 0 or to ∞ as $t \to \infty$.*
(ii-extinction probability) Denoting by η the largest root of ψ, we have

$$\mathbb{P}_z(\lim_{t\to\infty} Z_t = 0) = \exp(-z\eta) \qquad (z \geq 0).$$

In particular, extinction occurs a.s. if and only if $r = -\psi'(0) \leq 0$.
(iii-absorption probability) $\mathbb{P}(\exists t > 0 : Z_t = 0) > 0$ if and only if $\int^\infty 1/1\psi(x)$ $dx < \infty$.

As an illustration, which is left as an exercise, check that the CSBPs with characteristics $(r, 0, 0)$ and $(0, 0, x^{-2}1_{[0,1]}(x)dx)$ have positive extinction probability but null absorption probability. For stable CSBPs (including the Feller diffusion), extinction and absorption coincide.

Proof. (i) is a consequence of the Lamperti representation given in Proposition 4.5. Indeed a non-degenerate Lévy process Y either goes to $+\infty$, $-\infty$ or oscillates between $+\infty$ and $-\infty$ and we stress that Y is killed at 0 in the Lamperti transform. So

$$\left\{\int_0^\infty Z_s ds = \infty\right\} \subset \left\{Z_t \overset{t\to\infty}{\longrightarrow} 0\right\} \cup \left\{Z_t \overset{t\to\infty}{\longrightarrow} \infty\right\}.$$

Adding that

$$\left\{\int_0^\infty Z_s ds < \infty\right\} \subset \left\{Z_t \overset{t\to\infty}{\longrightarrow} Y_{\int_0^\infty Z_s ds} \text{ and } \int_0^\infty Z_s ds < \infty\right\} \subset \left\{Z_t \overset{t\to\infty}{\longrightarrow} 0\right\}$$

ends up the proof.

Concerning the extinction (ii), we first use (i) to write $\exp(-Z_t) \to \mathbf{1}_{\{\lim_{t\to\infty} Z_t = 0\}}$ as $t \to \infty$. By the bounded convergence theorem, $\mathbb{E}_z(\exp(-Z_t)) \to \mathbb{P}_z(\lim_{t\to\infty} Z_t = 0)$. Moreover, $\mathbb{E}_z(\exp(-Z_t)) = \exp(-zu_t(1))$ by Proposition 4.3. Noting that the branching mechanism ψ is convex (and non-trivial), it is positive for $z > \eta$ and negative for $0 < z < \eta$. Thus, $u_t(1) \to \eta$ as $t \to \infty$ and $\mathbb{P}_z(\lim_{t\to\infty} Z_t = 0) = \exp(-z\eta)$.

Let us finally deal with the absorption (iii). We note that $\mathbb{P}_z(Z_t = 0) = \lim_{\lambda\to\infty} \exp(-zu_t(\lambda)) = \exp(-zu_t(\infty))$ and recall from Proposition 4.4 that

$$\int_{u_t(\lambda)}^{\lambda} \frac{1}{\psi(u)} du = t.$$

If $u_t(\lambda)$ is bounded for $\lambda > 0$ (with some fixed t), then $\int^{\infty} 1/\psi < \infty$ (by letting $\lambda \to \infty$). Conversely the fact that $u_t(\infty) < \infty$ is bounded for $t \geq 0$ forces $\int^{\infty} 1/\psi(x)dx = +\infty$ (by letting λ and then t go to ∞). $\square$

4.5 Scaling limits

In this section, we obtain the CSBP as a scaling limit of Galton-Watson processes. We recall that a Galton-Watson process X with reproduction law ν is defined by

$$X_{n+1} = \sum_{i=1}^{X_n} L_{i,n},$$

where $(L_{i,n} : i \geq 1, n \geq 0)$ are i.i.d random variables with common distribution ν.

Let us associate a random walk with this process, denoted by S. It is obtained by summing the number of offspring of each individual of the Galton-Watson tree as follows:

$$S_0 := Z_0, \quad S_{k+1} := S_k + L_{k-A_n+1,n} - 1$$

for each $k \in [A_n, A_{n+1})$ and $n \geq 0$, where $A_n := \sum_{j=0}^{n-1} X_j$. Thus the increments of the random walk S are distributed as ν shifted by -1. This random walk S satisfies $S_{A_{n+1}} - S_{A_n} = \sum_{i=1}^{X_n}(L_{i,n} - 1) = X_{n+1} - X_n$, so that

$$X_n = S_{A_n} = S_{\sum_{i=0}^{n-1} X_i}, \tag{4.7}$$

which yields the discrete version of the Lamperti time change. It both enlightens the Lamperti transform in the continuous setting (Proposition 4.5) and allows us to prove the following scaling limit.

Theorem 4.8. *Let X^K be a sequence of Galton-Watson processes with reproduction law ν_K and $[Kx]$ initial individuals. We consider the scaled process*

$$Z_t^K = \frac{1}{K} X^K_{[v_K t]} \qquad (t \geq 0),$$

where $(v_K)_K$ is a sequence tending to infinity. Denoting by S^K the random walk associated with Z^K, we assume that

$$\frac{1}{K} S^K_{[K v_K .]} \Rightarrow Y,$$

where Y is a Lévy process. Then $Z^K \Rightarrow Z$, where Z is the CSBP characterized by (4.5).

The Feller diffusion case ($\mu = 0$) is the only possible limit of Galton-Watson processes with bounded variance (see [38]). It comes from the convergence of $(S_{[K^2t]}/K : t \geq 0)$ to a Brownian motion under second moment assumption. More generally, the stable case with drift $\psi(\lambda) = -r\lambda + c\lambda^{\alpha+1}$ (α in $(0, 1]$) corresponds to the class of CSBPs which can be obtained by scaling limits of Galton-Watson processes with a fixed reproduction law (i.e., $\nu_K = \nu$).

Several proofs of this theorem can be found. One can use a tightness argument and identify the limit thanks to the Laplace exponent. Such a proof is in the same vein as the previous section and we refer to [38] for details. As mentioned above, the proof can also be achieved using discrete Lamperti transform (4.7) with an argument of continuity. This argument can be adapted from Theorem 1.5 chapter 6 in Ethier-Kurtz [30]:

Lemma 4.9. *Let Y be a Lévy process killed at 0 and β a continuous function. Assume that $Y^K \Rightarrow Y$, where Y^K is a càdlàg process from $\mathbb{R}_+$ to $\mathbb{R}_+$ and define the process Z^K as the solution of $Z_t^K = Y^K_{\int_0^t \beta(Z_s^K)ds}$. Then $Z^K \Rightarrow Z$.*

4.6 On the general case

What is the whole class of branching processes in the continuous setting? What is the whole class of scaling limits of Galton-Watson processes? These two classes actually coincide and extend the class of CSBPs with finite first moment (called conservative CSBPs) we have considered above.

Theorem 4.10 ([18, 53]). *The càdlàg Markov processes Z which take values in $[0, \infty]$ and satisfy the branching property are in one to one correspondence with Lévy processes Y with no negative jumps, through the equation*

$$Z_t = Y^+_{\int_0^t Z_s}.$$

Such a process Z is still characterized by a triplet (r, γ, μ), with $r \in \mathbb{R}, \gamma \in \mathbb{R}_+$ but the measure μ on $\mathbb{R}_+$ only satisfies that

$$\int_0^\infty \left(1 \wedge z^2\right)\mu(dz) < \infty.$$

More specifically, the Laplace exponent u_t of Z, which uniquely determines the finite dimensional distributions, is the unique solution of

$$\frac{\partial u_t(\lambda)}{\partial t} = -\psi(u_t(\lambda)), \qquad u_0(\lambda) = \lambda,$$

where

$$\psi(\lambda) := -r\lambda + \gamma\lambda^2 + \int_0^\infty (e^{-\lambda h} - 1 + \lambda h \wedge h^2)\mu(dh).$$

More generally, the results given above can be extended. Thus, the expression of the generator $\mathcal{A}$ remains valid and Z is given by the following SDE (see Proposition 4 in [18])

$$Z_t = Z_0 + \int_0^t rZ_s ds + \int_0^t \sqrt{2\gamma Z_s} dB_s + \int_0^t \int_0^1 \int_0^{Z_{s-}} h\tilde{N}_0(ds, dh, du) \\ + \int_0^t \int_1^\infty \int_0^{Z_{s-}} hN_0(ds, dh, du),$$

where B is a standard Brownian motion, $N_0(ds, dz, du)$ is a Poisson random measure on $\mathbb{R}_+^3$ with intensity $ds\mu(dz)du$ independent of B, and $\tilde{N}_0$ is the compensated measure of N_0.

We stress that the class of CSBPs obtained now yields the (only possible) scaling limits of Galton-Watson processes (or more generally discrete space continuous time branching processes) [18, 52, 53].

A new phenomenon appears in the non-conservative case: the process may explode in finite time [37].

Proposition 4.11. *The CSBP Z blows up with positive probability, which means that $\mathbb{P}_1(Z_t = \infty) > 0$ for some $t \geq 0$, if and only if*

$$\psi'(0+) = -\infty \quad \text{and} \quad \int_0 \frac{ds}{\psi(s)} > -\infty.$$

In this section, we have focused on the size of the population Z_t. The scaling limits actually provide a natural notion of genealogy for the limiting object, see [27]. An other point of view, using the flow of subordinators which comes by letting the initial size vary, has been exhibited recently by Bertoin and Le Gall [11]. Finally, let us mention that several extensions of CBSPs have been considered. In particular, for CSBPs with immigration, we refer to [36] for the SDEs characterization and to [17] for the Lamperti transform.

Chapter 5
Feller Diffusion with Random Catastrophes

We deal now with a new family of branching processes taking into account the effect of the environment on the population dynamics. It may cause random fluctuations of the growth rate [12, 33] or catastrophes which kill a random fraction of the population [7].

Here, we are focusing on a Feller diffusion with catastrophes, in order to simplify the study and fit with the motivations given in Chapter 8. We aim at highlightening new behaviors due to the random environment and we refer to Subsection 5.4 for extensions and comments on (more general) CSBPs in random environment.

5.1 Definition and scaling limit

We consider the Feller diffusion (3.12) and add some random catastrophes, whose rates are given by a function τ and whose effect on the population size are multiplicative and given by some random variable F taking values in $[0,1]$. This process Y is defined as the solution of the following SDE:

$$Y_t = y_0 + \int_0^t rY_s ds + \int_0^t \sqrt{2\gamma Y_s} dB_s - \int_0^t \int_0^\infty \int_0^1 \mathbb{1}_{u \le \tau(Y_{s-})} \big(1-\theta\big) Y_{s-} N_1(ds, du, d\theta)$$

where B and N_1 are, respectively, a Brownian motion and a Poisson point measure on $\mathbb{R}_+ \times \mathbb{R}_+ \times (0,1]$ with intensity $ds\, du\, \mathbb{P}(F \in d\theta)$, which are independent.

Thus, the random variable F is the intensity of the catastrophes. We assume that $\mathbb{P}(F > 0) = 1$ and $\mathbb{P}(F \in (0,1)) > 0$ to avoid absorption by a single catastrophe. Similarly, we also assume that

$$\mathbb{E}(\log(F)) > -\infty.$$

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_5

The rate τ at which the catastrophes occur may depend on the population size. We refer to Chapter 8 for motivations for cell division. More generally, the fact that τ is increasing is relevant when the catastrophe is actually a regulation of the population dynamics. We may think about the effect of a treatment for an infected population or invasive species or protocols for web treatment of tasks such as TCP, etc.

Following Section 3.2, the process can be constructed as a scaling limit, which enlightens the two timescales involved in the dynamics, namely the timescale of the demography of the population and that of the catastrophes. It is achieved by considering a linear birth and death process Y_t^K starting from $[Ky]$ individuals. Its individual birth and death rates are given by $\lambda + K\gamma$ and $\mu + K\gamma$. Moreover the process Y^K jumps with rate $\tau(n/K)$ from n to $[\theta n]$ where θ is chosen randomly following the distribution F. More precisely

$$Y_t^K = [Ky] + \int_0^t \int_0^\infty \left(\mathbb{1}_{u \le Y^K_{s-}(\lambda+K\gamma)} - \mathbb{1}_{Y^K_{s-}(\lambda+K\gamma) \le u \le Y^K_{s-}(\lambda+K\gamma+\mu+K\gamma)}\right) N_0(ds,du)$$

$$- \int_0^t \int_0^\infty \mathbb{1}_{u \le \tau(Y^K_{s-}/K)} (Y_{s-} - [\theta Y_{s-}]) N_1(ds,du,d\theta).$$

Then $(Y_t^K/K : t \ge 0)$ converges weakly to $(Y_t : t \ge 0)$ as $K \to \infty$, see [5] for more details. Taking the integer part of the population size after a catastrophe is convenient when proving the convergence of the scaling limit via tightness and limiting martingale problem. Other models in discrete space would yield the same limiting object. For example, each individual could be killed independently with probability F when a catastrophe occurs. We also recall from the previous sections that scaling limits of other processes, such as Galton Watson processes, lead to the Feller diffusion.

5.2 Long time behavior when catastrophes occur at a constant rate

In this section, we assume that $\tau(.) = \tau$ is constant and the successive catastrophes can be represented by a Poisson point process $\{(T_k, F_k) : k \ge 0\}$ on $\mathbb{R}_+ \times [0,1]$ with intensity $\tau dt d\mathbb{P}(F \in d\theta)$. The long time behavior of Y can be guessed thanks to the following heuristic :

$$Y_t \approx Z_t . \Pi_{T_k \le t} F_k$$

where Z is a Feller diffusion with parameters (r, γ) and all the catastrophes during the time interval $[0,t]$ have been postponed at the final time. We recall from Section 4.2 that Z_t is equal to $e^{rt} M_t$ where M is a martingale. We prove in this section (see the two forthcoming theorems) that Y_t behaves as $\exp(rt)\Pi_{T_k\leq t}F_k = \exp(K_t)$ as t goes to infinity, where

$$K_t := rt + \sum_{T_k\leq t}\log F_k = rt + \int_0^t\int_0^1 \log(\theta)N_1(ds,[0,\tau],d\theta),$$

with $N_1(ds,[0,\tau],d\theta)$ a Poisson point measure with intensity $\tau ds\mathbb{P}(F\in d\theta)$ and K a Lévy process. It turns out that the asymptotic behavior of Feller diffusions with catastrophes will be inherited from the classification of long time behavior of Lévy processes. First, we check that

$$\bar{Y}_t := \exp(-K_t)Y_t$$

is a continuous local martingale, which extends the result of Section 4.2 to random environment.

Lemma 5.1. *The process* $(\bar{Y}_t : t\geq 0)$ *satisfies the SDE*

$$\bar{Y}_t = y_0 + \int_0^t e^{-K_s/2}\sqrt{2\gamma\bar{Y}_s}dB_s. \tag{5.1}$$

Proof. Since for every $t\in\mathbb{R}_+$, $0\leq Y_t\leq X_t$, where X_t is a Feller diffusion, all the stochastic integrals that we write are well defined. Applying the two-dimensional Itô's formula with jumps to $F(K_t,Y_t)=\bar{Y}_t$, with $F(x,y)=\exp(-x)y$, we get

$$\begin{aligned}\bar{Y}_t =& x_0 + \int_0^t e^{-K_s}\left[rY_sds + \sqrt{2\gamma Y_s}dB_s\right] - \int_0^t rY_se^{-K_s}ds\\ &+\int_0^t\int_0^\infty\int_0^1\left(Y_se^{-K_s} - Y_{s\_}e^{-K_{s}-}\right)\mathbb{1}_{u\leq\tau}N_1(ds,du,d\theta)\\ =& x_0+\int_0^t e^{-K_s}\sqrt{2\gamma Y_s}dB_s + \int_0^t\int_0^\infty\int_0^1 \bar{Y}_{s-}\left(\theta e^{-\log(\theta)}-1\right)\mathbb{1}_{u\leq\tau}N(ds,du,d\theta)\\ =& x_0+\int_0^t e^{-K_s}\sqrt{2\gamma Y_s}dB_s.\end{aligned}$$

Then $(\bar{Y}_t : t\geq 0)$ satisfies the SDE (5.1). □

We now state the absorption criterion.

Theorem 5.2. *(i) If* $r\leq\mathbb{E}(\log(1/F))\tau$, *then* $\mathbb{P}(\exists t>0 : Y_t=0)=1$.
(ii) Otherwise, $\mathbb{P}(\forall t\geq 0 :\ Y_t>0)>0$.

For the proof, we first consider the quenched process, conditioned by the environment $\mathcal{F}^{N_1}$. Indeed the transformation $Y_{t-}\to xY_{t-}=Y_t$ preserves the branching property of the Feller diffusion. The Feller diffusion then undergoes deterministic catastrophes given by the conditional Poisson point measure N_1.

Lemma 5.3 (Quenched characterization).

(i) *Conditionally on* $\mathcal{F}^{N_1}$ *and setting for* $t_0, \lambda \geq 0$ *and* $t \in [0, t_0]$,

$$u(t,y) = \exp\left(-\frac{\lambda y}{\gamma\lambda \int_t^{t_0} e^{-K_s} ds + 1}\right).$$

The process $(u(t, \bar{Y}_t) : 0 \leq t \leq t_0)$ *is a bounded martingale.*

(ii) *For all* $t, \lambda, y_0 \geq 0$,

$$\mathbb{E}_{y_0}\left(\exp(-\lambda \bar{Y}_t) \mid \mathcal{F}^{N_1}\right) = \exp\left(-\frac{\lambda y_0}{\gamma\lambda \int_0^t e^{-K_s} ds + 1}\right). \tag{5.2}$$

Exercise. *Prove that conditionally on* $\mathcal{F}^{N_1}$, *Y satisfies the branching property.*

One may write a direct proof following Proposition 4.3 or use Lemma 5.3 (ii).

We stress that the non-conditional (*annealed*) branching property does not hold. Formally, the quenched process can be defined on the probability space $(\Omega, \mathcal{F}, \mathbb{P}) := (\Omega_e \times \Omega_d, \mathcal{F}_e \otimes \mathcal{F}_d, \mathbb{P}_e \otimes \mathbb{P}_d)$ by using a Poisson Point process $N_1(w) = N_1(w_e, w_d) := N_1(w_e)$ for catastrophes and a Brownian motion $B_t(w) = B_t(w_e, w_d) := B_t(w_d)$ for the demographic stochasticity. Thus, the process Y conditioned on the environment $\mathcal{F}^{N_1} = \sigma(K_s) = \sigma(\mathcal{F}_e)$ (quenched process) is given by $Y(w_e, .)$ $\mathbb{P}_e$ a.s.

Proof. Let us work conditionally on $\mathcal{F}^{N^1}$. Using Itô's formula for a function $u(t,y)$ which is differentiable by parts with respect to t and infinitely differentiable with respect to y, we get

$$\begin{aligned} u(t, \bar{Y}_t) = u(0, y_0) + &\int_0^t \left[\frac{\partial u}{\partial s}(s, \bar{Y}_s) + \frac{\partial^2 u}{\partial y^2}(s, \bar{Y}_s)\gamma \bar{Y}_s e^{-K_s}\right] ds \\ &+ \int_0^t \frac{\partial u}{\partial y}(s, \bar{Y}_s) e^{-K_s/2}\sqrt{2\gamma \bar{Y}_s dB_s}. \end{aligned}$$

The function u has been chosen to cancel the finite variation part, i.e. it satisfies

$$\frac{\partial u}{\partial s}(s,y) + \frac{\partial^2 u}{\partial y^2}(s,y)\gamma y e^{-K_s} = 0 \qquad (s, y \geq 0).$$

Then the process $(u(t, \bar{Y}_t) : 0 \leq t \leq t_0)$ is a local martingale bounded by 1 and thus a real martingale and (i) holds. We deduce that

$$\mathbb{E}_{y_0}\left(u(t_0, \bar{Y}_{t_0}) \mid \mathcal{F}^{N_1}\right) = u(0, \bar{Y}_0),$$

which gives (ii). □

Before proving Theorem 5.2, we deal with the functional of the Lévy process involved in the extinction.

Lemma 5.4. *If* $r \leq \tau\mathbb{E}(\log(1/F))$*, then* $\liminf_{t\to\infty} K_t = -\infty$ *and* $\int_0^\infty \exp(-K_s)ds = +\infty$ *a.s.*

Otherwise, $\lim_{t\to\infty} K_t = +\infty$ *and* $\int_0^\infty \exp(-K_s)ds < +\infty$ *a.s.*

Proof. If $r \leq \tau\mathbb{E}(\log(1/F))$, then $\mathbb{E}(K_1) \leq 0$ and the Lévy process K_t either goes to $-\infty$ or oscillates. In any case, the sequence of stopping times

$$T_0 := 0, \qquad T_k := \inf\{t \geq T_{k-1} + 1 : K_t \leq 0\} < +\infty$$

is finite for $k \geq 0$. Then,

$$\begin{aligned} \int_0^\infty \exp(-K_s)ds &\geq \sum_{k\geq 1} \int_{T_k}^{T_k+1} \exp(-K_s)ds \\ &\geq \sum_{k\geq 1} \int_0^1 \exp(-(K_{T_k+s} - K_{T_k}))ds =: \sum_{k\geq 1} X_k, \end{aligned}$$

where X_k are non-negative (non-identically zero) i.i.d. random variables. Then $\int_0^\infty \exp(K_s)ds = +\infty$ a.s. Conversely if $r > \tau\mathbb{E}(\log(1/F))$, there exists $\epsilon > 0$ such that $\mathbb{E}(K_1) - \epsilon > 0$ and $K_t - \epsilon t$ goes to $+\infty$ a.s. Then

$$L := \inf\{K_s - \epsilon s : s \geq 0\} > -\infty \quad \text{a.s.}$$

and $\int_0^\infty \exp(\epsilon s)ds = +\infty$ yields the result. □

Proof of Theorem 5.2. Integrating (5.2), we get by bounded convergence that

$$\lim_{t\to\infty} \mathbb{E}_{y_0}(\exp(-\lambda \bar{Y}_t)) = \mathbb{E}_{y_0}\left(\exp\left(-\frac{\lambda y_0}{\gamma\lambda \int_0^\infty \exp(-K_s)ds + 1}\right)\right).$$

The process $(\bar{Y}_t : t \geq 0)$ converges in distribution as $t \to +\infty$ to $\bar{Y}_\infty$ whose distribution is specified by the right-hand side of the above limit. Letting $\lambda \to +\infty$, we get by bounded convergence:

$$\mathbb{P}_{y_0}(\bar{Y}_\infty = 0) = \mathbb{E}_{y_0}\left(\exp\left(-\frac{y_0}{\gamma \int_0^\infty \exp(-K_s)ds}\right)\right). \tag{5.3}$$

Recalling from Lemma 5.1 that $(\bar{Y}_t : t \geq 0)$ is a non-negative local martingale, we obtain by Jensen's inequality that $(\exp(-\bar{Y}_t) : t \geq 0)$ is a positive sub-martingale bounded by 1. We deduce that the convergence towards $\bar{Y}_\infty$, which is possibly infinite, also holds a.s.

Using Lemma 5.4, we obtain that the probability of the event

$$\{\liminf_{t\to\infty} Y_t = 0\} = \{\liminf_{t\to\infty} e^{K_t}\bar{Y}_t = 0\}$$

is either one or less than one depending on $r \le \tau\mathbb{E}(\log(1/F))$ or $r > \tau\mathbb{E}(\log(1/F))$. Moreover, the absorption probability of the Feller diffusion is positive (see Section 4.2) and the Markov property ensures that Y is a.s. absorbed on the event $\{\liminf_{t\to\infty} Y_t = 0\}$. It ends the proof. □

Let us note that the a.s. convergence relies here on the fact that $(\exp(-\bar{Y}_t) : t \ge 0)$ is a bounded sub-martingale. This method can be adapted to study the long time behavior of a conservative CSBP instead of using the Lamperti transform (see Chapter 4). We describe now the speed at which the absorption occurs. The random environment makes three asymptotic regimes appear in the subcritical case.

Theorem 5.5 (Growth and speed of extinction, [7]). *We assume that* $\mathbb{E}((\log F)^2) < \infty$.

a/ If $r < \tau\mathbb{E}(\log(1/F))$ (subcritical case)*, then*

- *(i) If* $\tau\mathbb{E}(F\log F) + r < 0$ (strongly subcritical regime)*, then there exists* $c_1 > 0$ *such that for every* $y_0 > 0$,

$$\mathbb{P}_{y_0}(Y_t > 0) \sim c_1 y_0 e^{t(r+\tau[\mathbb{E}(F)-1])}, \qquad as \quad t \to \infty.$$

- *(ii) If* $\tau\mathbb{E}(F\log F) + r = 0$ (intermediate subcritical regime)*, then there exists* $c_2 > 0$ *such that for every* $y_0 > 0$,

$$\mathbb{P}_{y_0}(Y_t > 0) \sim c_2 y_0 t^{-1/2} e^{t(r+\tau[\mathbb{E}(F)-1])}, \qquad as \quad t \to \infty.$$

- *(iii) If* $\tau\mathbb{E}(F\log F) + r > 0$ (weakly subcritical regime)*, then for every* $y_0 > 0$, *there exists* $c_3 > 0$ *such that*

$$\mathbb{P}_{y_0}(Y_t > 0) \sim c_3 t^{-3/2} e^{t(r+\tau[\mathbb{E}(F^{\chi})-1])}, \qquad as \quad t \to \infty,$$

where χ *is the root of* $\mathbb{E}(F^{\chi}\log F) + r$ *on* $(0,1)$.

b/ If $r = \tau\mathbb{E}(\log(1/F))$ (critical case)*, then for every* $y_0 > 0$*, there exists* $c_4 > 0$ *such that*

$$\mathbb{P}_{y_0}(Y_t > 0) \sim c_4 t^{-1/2}, \qquad as \quad t \to \infty.$$

c/ If $r > \tau\mathbb{E}(\log(1/F))$ (supercritical case)*, then there exists a finite r.v. W such that*

$$e^{-K_t}Y_t \xrightarrow[t\to\infty]{} W \quad a.s., \qquad \{W = 0\} = \left\{\lim_{t\to\infty} Y_t = 0\right\}.$$

The asymptotic results *a/ −b/* rely on the study of $\mathbb{P}(Y_t > 0) = \mathbb{E}\left(f\left(\int_0^t e^{-\beta K_s} ds\right)\right)$, for $t \to \infty$, where f has a polynomial decay when $x \to \infty$ and here $\beta = 1$. It is linked to the asymptotic distribution of $I_t = \inf\{K_s : s \leq t\}$ and the different asymptotics appear for $\mathbb{P}(I_t \geq x)$ when $t \to \infty$. The proof in [7] uses a discretization of $\int_0^t \exp(-\beta K_s) ds$ of the form $\sum_{i=0}^n \Pi_{j=0}^i A_i$ and the different regimes are inherited from local limit theorems for semi-direct products [55].

5.3 Monotone rate of catastrophes

We first deal with increasing rates, which are relevant for the applications on cell infection developed in the second part.

Proposition 5.6. *We assume that τ is a non-decreasing function.*

(i) If there exists $y_1 \geq 0$ such that $r \leq \mathbb{E}(\log(1/F))\tau(y_1)$, then

$$\mathbb{P}\Big(\exists t > 0,\ Y_t = 0\Big) = 1.$$

(ii) If $r > \mathbb{E}(\log(1/F)) \sup_{x \geq 0} \tau(x)$, then $\mathbb{P}(\forall t \geq 0 :\ Y_t > 0) > 0$.

Heuristically, if $r \leq \mathbb{E}(\log(1/F))\tau(y_1)$, as soon as $Y \geq y_1$, the division rate is larger than $r(y_1)$ and Theorem 5.2 (*i*) ensures that the process is pushed back to y_1. Eventually, it reaches zero by the strong Markov property, since each time it goes below y_1, it has a positive probability to reach 0 before time 1.

The proof can be made rigorous by using a coupling with a Feller diffusion with catastrophes occurring at constant rate $\tau(y_1)$. Finally, we note that the case

$$r > \mathbb{E}(\log(1/F))\tau(x) \quad \textit{for every} \ \ x \geq 0; \qquad r = \mathbb{E}(\log(1/F)) \sup_{x \geq 0} \tau(x)$$

remains open.

Let us now consider the case when τ is non-increasing. The asymptotic behavior now depends on

$$\tau_* = \inf_{x \geq 0} \tau(x). \tag{5.4}$$

Proposition 5.7. *We assume that r is a non-increasing function.*

(i) If $r \leq \mathbb{E}(\log(1/F))\tau_*$, then $\mathbb{P}\Big(\exists t > 0,\ Y_t = 0\Big) = 1$.

(ii) Else, $\mathbb{P}(\forall t > 0,\ Y_t > 0) > 0$.

The proof is easier in that case and we refer to [5] for details.

5.4 Further comments : CSBPs in random environment

We have studied a particular case of continuous state branching processes in random environment. It can be extended in several ways. A general construction of Feller diffusions in random environment has been provided by Kurtz [50]. It relies on the scaling and time change

$$Y_t = \exp(M_t) Z_{\tau_t}, \qquad \textit{where } \tau_t = \int_0^t \exp(-M_s) A_s ds,$$

M is a càdlàg process and Z is a Feller diffusion and A is non-decreasing and absolutely continuous w.r.t. Lebesgue measure.

In the case where $M_t = K_t$ and $A_t = \gamma t$, this construction leads to the Feller diffusion with catastrophes. When M_t is a Brownian motion and $A_t = \gamma t$, we obtain a Feller diffusion in a Brownian environment. Its asymptotic behavior is close to the one of Feller diffusion with catastrophes and can be found in [12, 40]. It uses the explicit expression of the density of some functional of Brownian motion involved in the Laplace exponent of the process.

The construction of Kurtz has been extended by Borovkov [15] to the case where A is no more absolutely continuous. The time change can also be generalized to the stable case but does not hold for general CSBPs in random environment. We refer to [8] for the quenched construction without second moment assumption, as a scaling limit, when M has finite variations. Let us mention [7] for the asymptotic study of CSBPs with catastrophes, which extends the asymptotic results given in Section 5.2. New asymptotic behaviors appear for the process, which may oscillate in $(0,\infty)$ in the critical regime.

A possible generalization of our results is the combination of Brownian fluctuations of the drift and catastrophes

$$Y_t = y_0 + \int_0^t Y_{s-} dM_s + \int_0^t \sqrt{2\gamma_s Y_s} dB_s - \int_0^t \int_{\mathbb{R}_+ \times [0,1]} \mathbb{1}_{u \le \tau(Y_{s-})} \big(1-\theta\big) Y_{s-} N_1(ds, du, d\theta),$$

where $dM_s = r_s ds + \sigma_e dB^e_s$ and N_1 is a Poisson Point Process with intensity $ds\, du\, \mathbb{P}(F \in d\theta)$ and both are independent of B. Such stochastic differential equations both integrate small fluctuations and dramatic random events due to the environment. Finding a general approach to deal with the long time behavior of CSBPs in random environment is an open and delicate question.

Part II
Structured Populations and Measure-valued Stochastic Differential Equations

In this chapter the individuals are characterized by some quantitative traits. Therefore the population is described by a random point measure with support on the trait space. We first study the measure-valued process modeling the population dynamics including competition and mutation events. We give its martingale properties and determine some scaling limits. Then we consider the particular case of cell division with parasite infection and the Markov processes indexed by continuous time Galton-Watson trees.

Chapter 6
Population Point Measure Processes

6.1 Multitype models

In the previous sections, the models that we considered described a homogeneous population and could be considered as toy models. A first generalization consists in considering multitype population dynamics. The demographic rates of a subpopulation depend on its own type. The ecological parameters are functions of the different types of the individuals competing with each other. Indeed, we assume that the type has an influence on the reproduction or survival abilities, but also on the access to resources. Some subpopulations can be more adapted than others to the environment.

For simplicity, the examples that we consider now deal with only two types of individuals. Let us consider two sub-populations characterized by two different types 1 and 2. For $i = 1, 2$, the growth rates of these populations are r_1 and r_2. Individuals compete for resources either inside the same species (intra-specific competition) or with individuals of the other species (inter-specific competition). As before, let K be the scaling parameter describing the capacity of the environment. The competition pressure exerted by an individual of type 1 on an individual of type 1 (resp. type 2) is given by $\frac{c_{11}}{K}$ (resp. $\frac{c_{21}}{K}$). The competition pressure exerted by an individual of type 2 is, respectively, given by $\frac{c_{12}}{K}$ and $\frac{c_{22}}{K}$. The parameters c_{ij} are assumed to be positive.

By similar arguments as in Subsection 3.1, the large K-approximation of the population dynamics is described by the well-known competitive Lotka-Volterra dynamical system. Let $x_1(t)$ (resp. $x_2(t)$) be the limiting renormalized type 1 population size (resp. type 2 population size). We get

$$\begin{cases} x_1'(t) = x_1(t)\,(r_1 - c_{11}\,x_1(t) - c_{12}\,x_2(t)); \\ x_2'(t) = x_2(t)\,(r_2 - c_{21}\,x_1(t) - c_{22}\,x_2(t)). \end{cases} \tag{6.1}$$

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_6

This system has been extensively studied and its long time behavior is well known. There are 4 possible equilibria: the unstable equilibrium $(0, 0)$ and three stable ones: $(\frac{r_1}{c_{11}}, 0)$, $(0, \frac{r_2}{c_{22}})$ and a non-trivial equilibrium (x_1^*, x_2^*) given by

$$x_1^* = \frac{r_1 c_{22} - r_2 c_{12}}{c_{11} c_{22} - c_{12} c_{21}} \; ; \; x_2^* = \frac{r_2 c_{11} - r_1 c_{21}}{c_{11} c_{22} - c_{12} c_{21}}.$$

Of course, the latter is possible if the two coordinates are positive. The (unique) solution of (6.1) converges to one of the stable equilibria, describing either the fixation of one species or the co-existence of both species. The choice of the limit depends on the signs of the quantities $r_2 c_{11} - r_1 c_{21}$ and $r_1 c_{22} - r_2 c_{12}$ which, respectively, quantify the invasion ability of the subpopulation 2 (resp. 1) in a type 1 (resp. type 2) monomorphic resident population.

One could extend (6.1) to negative coefficients c_{ij}, describing a cooperation effect of species j on the growth of species i. The long time behavior can be totally different. For example, the prey–predator models have been extensively studied in ecology (see [39], Part 1). The simplest prey–predator system

$$\begin{cases} x_1'(t) = x_1(t)\,(r_1 - c_{12}\,x_2(t)); \\ x_2'(t) = x_2(t)\,(c_{21}\,x_1(t) - r_2), \end{cases} \tag{6.2}$$

with $r_1, r_2, c_{12}, c_{21} > 0$, has periodic solutions.

Stochastic models have also been developed, based on this two type-population model. Following the previous sections, a first point of view consists in generalizing the logistic Feller stochastic differential equation to this two-dimensional framework. The stochastic logistic Lotka-Volterra process is then defined by

$$\begin{cases} dX_1(t) = X_1(t)\,(r_1 - c_{11}\,X_1(t) - c_{12}\,X_2(t))\,dt + \sqrt{\gamma_1 X_1(t)}dB_t^1; \\ dX_2(t) = X_2(t)\,(r_2 - c_{21}\,X_1(t) - c_{22}\,X_2(t))\,dt + \sqrt{\gamma_2 X_2(t)}dB_t^2, \end{cases}$$

where the Brownian motions B^1 and B^2 are independent and give rise to the demographic stochasticity (see Cattiaux-Méléard [20]). Another point of view consists in taking account the environmental stochasticity (see Evans, Hening, Schreiber [34]).

Of course, we could also study multi-dimensional systems corresponding to multi-type population models. In what follows we are more interested in modeling the case where the types of the individuals belong to a continuum. That will allow us to add mutation events where the offspring of an individual may randomly mutate and create a new type.

6.2 Continuum of types and measure-valued processes

Even if the evolution appears as a global change in the state of a population, its basic mechanisms, mutation and selection, operate at the level of individuals. Consequently, we model the evolving population as a stochastic system of interacting individuals, where each individual is characterized by a vector of phenotypic trait values. The trait space $\mathcal{X}$ is assumed to be a closed subset of $\mathbb{R}^d$, for some $d \geq 1$.

We will denote by $M_F(\mathcal{X})$ the set of all finite non-negative measures on $\mathcal{X}$. Let $\mathcal{M}$ be the subset of $M_F(\mathcal{X})$ consisting of all finite point measures:

$$\mathcal{M} = \left\{ \sum_{i=1}^{n} \delta_{x_i},\ n \geq 0, x_1, \ldots, x_n \in \mathcal{X} \right\}.$$

Here and below, δ_x denotes the Dirac mass at x. For any $\mu \in M_F(\mathcal{X})$ and any measurable function f on $\mathcal{X}$, we set $\langle \mu, f \rangle = \int_{\mathcal{X}} f d\mu$.

We wish to study the stochastic process $(Y_t, t \geq 0)$, taking its values in $\mathcal{M}$, and describing the distribution of individuals and traits at time t. We define

$$Y_t = \sum_{i=1}^{N_t} \delta_{X_t^i}, \tag{6.3}$$

$N_t = \langle Y_t, 1 \rangle \in \mathbb{N}$ standing for the number of individuals alive at time t, and $X_t^1, \ldots, X_t^{N_t}$ describing the individuals' traits (in $\mathcal{X}$).

We assume that the birth rate of an individual with trait x is $b(x)$ and that for a population $\nu = \sum_{i=1}^{N} \delta_{x^i}$, its death rate is given by $d(x, C * \nu(x)) = d(x, \sum_{i=1}^{N} C(x - x^i))$. This death rate takes into account the intrinsic death rate of the individual; it does not depend not only on its phenotypic trait x but also on the competition pressure exerted by the other individuals alive, modeled by the competition kernel C. Let $p(x)$ and $m(x,z)dz$ be, respectively, the probability that an offspring produced by an individual with trait x carries a mutated trait and the law of this mutant trait.

Thus, the population dynamics can be roughly summarized as follows. The initial population is characterized by a (possibly random) counting measure $\nu_0 \in \mathcal{M}$ at time 0, and any individual with trait x at time t has two independent random exponentially distributed "clocks": a birth clock with parameter $b(x)$, and a death clock with parameter $d(x, C * Y_t(x))$. If the death clock of an individual rings, this individual dies and disappears. If the birth clock of an individual with trait x rings, this individual produces an offspring. With probability $1 - p(x)$ the offspring carries the same trait x; with probability $p(x)$ the trait is mutated. If a mutation occurs, the mutated offspring instantly acquires a new trait z, picked randomly according to the mutation step measure $m(x,z)dz$. When one of these events occurs, all individuals' clocks are reset to 0.

We are looking for a $\mathcal{M}$-valued Markov process $(Y_t)_{t\geq 0}$ with infinitesimal generator L, defined for all real bounded functions ϕ and $\nu \in \mathcal{M}$ by

$$\begin{aligned} L\phi(\nu) = & \sum_{i=1}^{N} b(x^i)(1-p(x^i))(\phi(\nu+\delta_{x^i})-\phi(\nu)) \\ & + \sum_{i=1}^{N} b(x^i)p(x^i)\int_{\mathcal{X}}(\phi(\nu+\delta_z)-\phi(\nu))m(x^i,z)dz \\ & + \sum_{i=1}^{N} d(x^i, C*\nu(x^i))(\phi(\nu-\delta_{x^i})-\phi(\nu)). \end{aligned} \tag{6.4}$$

The first term in (6.4) captures the effect of births without mutation, the second term the effect of births with mutation, and the last term the effect of deaths. The density-dependence makes the third term nonlinear.

6.3 Path construction of the process

Let us justify the existence of a Markov process admitting L as infinitesimal generator. The explicit construction of $(Y_t)_{t\geq 0}$ also yields two side benefits: providing a rigorous and efficient algorithm for numerical simulations (given hereafter) and establishing a general method that will be used to derive some large population limits (Chapter 7).

We make the biologically natural assumption that the trait dependency of birth parameters is "bounded," and at most linear for the death rates. Specifically, we assume

Assumption 6.1. *There exist constants* $\bar{b}$, $\bar{d}$, $\bar{C}$, *and* α *and a probability density function* $\bar{m}$ *on* $\mathbb{R}^d$ *such that for each* $\nu = \sum_{i=1}^{N}\delta_{x^i}$ *and for* $x, z \in \mathcal{X}$, $\zeta \in \mathbb{R}$,

$$b(x) \leq \bar{b}, \quad d(x,\zeta) \leq \bar{d}(1+|\zeta|),$$

$$C(x) \leq \bar{C},$$

$$m(x,z) \leq \alpha\,\bar{m}(z-x).$$

These assumptions ensure that there exists a constant $\hat{C}$, such that for a population measure $\nu = \sum_{i=1}^{N}\delta_{x^i}$, the total event rate, obtained as the sum of all event rates, is bounded by $\hat{C}N(1+N)$.

Let us now give a pathwise description of the population process $(Y_t)_{t\geq 0}$. We introduce the following notation.

Notation 1. Let $\mathbb{N}^* = \mathbb{N}\backslash\{0\}$. Let $H = (H^1, \dots, H^k, \dots) : \mathcal{M} \mapsto (\mathbb{R}^d)^{\mathbb{N}^*}$ be defined by $H\left(\sum_{i=1}^n \delta_{x_i}\right) = (x_{\sigma(1)}, \dots, x_{\sigma(n)}, 0, \dots, 0, \dots)$, where σ is a permutation such that $x_{\sigma(1)} \preccurlyeq \dots \preccurlyeq x_{\sigma(n)}$, for some arbitrary order $\preccurlyeq$ on $\mathbb{R}^d$ (for example, the lexicographic order).

This function H allows us to overcome the following (purely notational) problem. Choosing a trait uniformly among all traits in a population $\nu \in \mathcal{M}$ consists in choosing i uniformly in $\{1, \dots, \langle \nu, 1\rangle\}$, and then in choosing the individual *number* i (from the arbitrary order point of view). The trait value of such an individual is thus $H^i(\nu)$.

We now introduce the probabilistic objects we will need.

Definition 6.1. Let $(\Omega, \mathcal{F}, P)$ be a (sufficiently large) probability space. On this space, we consider the following four independent random elements:

(i) a $\mathcal{M}$-valued random variable Y_0 (the initial distribution),
(ii) Poisson point measures $N_1(ds, di, d\theta)$, and $N_3(ds, di, d\theta)$ on $\mathbb{R}_+ \times \mathbb{N}^* \times \mathbb{R}^+$, with the same intensity measure $ds\left(\sum_{k\geq 1} \delta_k(di)\right) d\theta$ (the “clonal” birth and the death Poisson measures),
(iii) a Poisson point measure $N_2(ds, di, dz, d\theta)$ on $\mathbb{R}_+ \times \mathbb{N}^* \times \mathcal{X} \times \mathbb{R}^+$, with intensity measure $ds\left(\sum_{k\geq 1} \delta_k(di)\right) dzd\theta$ (the mutation Poisson point measure).

Let us denote by $(\mathcal{F}_t)_{t\geq 0}$ the canonical filtration generated by these processes.

We finally define the population process in terms of these stochastic objects.

Definition 6.2. Assume (H). A $(\mathcal{F}_t)_{t\geq 0}$-adapted stochastic process $Y = (Y_t)_{t\geq 0}$ is called a population process if a.s., for all $t \geq 0$,

$$
\begin{aligned}
Y_t = Y_0 &+ \int_{[0,t]\times\mathbb{N}^*\times\mathbb{R}+} \delta_{H^i(Y_{s-})} \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}}\, \mathbf{1}_{\{\theta\leq b(H^i(Y_{s-}))(1-p(H^i(Y_{s-})))\}} N_1(ds, di, d\theta)\\
&+ \int_{[0,t]\times\mathbb{N}^*\times\mathcal{X}\times\mathbb{R}+} \delta_z \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}}\, \mathbf{1}_{\{\theta\leq b(H^i(Y_{s-}))p(H^i(Y_{s-}))\, m(H^i(Y_{s-}),z)\}} N_2(ds, di, dz, d\theta)\\
&- \int_{[0,t]\times\mathbb{N}^*\times\mathbb{R}+} \delta_{H^i(Y_{s-})} \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}} \mathbf{1}_{\{\theta\leq d(H^i(Y_{s-}),C*Y_{s-}(H^i(Y_{s-})))\}} N_3(ds, di, d\theta)
\end{aligned}
\tag{6.5}
$$

Let us now show that if Y solves (6.5), then Y follows the Markovian dynamics we are interested in.

Proposition 6.3. *Assume Assumption 6.1 holds and consider a solution* $(Y_t)_{t\geq 0}$ *of* (6.5) *such that* $\mathbb{E}(\sup_{t\leq T}\langle Y_t, \mathbf{1}\rangle^2) < +\infty$, $\forall T > 0$. *Then* $(Y_t)_{t\geq 0}$ *is a Markov process. Its infinitesimal generator L is defined by* (6.4). *In particular, the law of* $(Y_t)_{t\geq 0}$ *does not depend on the chosen order* $\preccurlyeq$.

Proof. The fact that $(Y_t)_{t\geq 0}$ is a Markov process is classical. Let us now consider a measurable bounded function ϕ. With our notation, $Y_0 = \sum_{i=1}^{\langle Y_0,1\rangle} \delta_{H^i(Y_0)}$. A simple computation, using the fact that a.s., $\phi(Y_t) = \phi(Y_0) + \sum_{s\leq t}(\phi(Y_{s-} + (Y_s - Y_{s-})) - \phi(Y_{s-}))$, shows that

$$\begin{aligned}\phi(Y_t) = \phi(Y_0) + &\int_{[0,t]\times\mathbb{N}^*\times\mathbb{R}+} \big(\phi(Y_{s-} + \delta_{H^i(Y_{s-})}) - \phi(Y_{s-})\big)\, \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}} \\ &\qquad \mathbf{1}_{\{\theta\leq b(H^i(Y_{s-}))(1-p(H^i(Y_{s-})))\}} N_1(ds,di,d\theta) \\ &+ \int_{[0,t]\times\mathbb{N}^*\times\mathcal{X}\times\mathbb{R}+} (\phi(Y_{s-} + \delta_z) - \phi(Y_{s-}))\, \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}} \\ &\qquad \mathbf{1}_{\{\theta\leq b(H^i(Y_{s-}))p(H^i(Y_{s-}))\, m(H^i(Y_{s-}),z)\}} N_2(ds,di,dz,d\theta) \\ &+ \int_{[0,t]\times\mathbb{N}^*\times\mathbb{R}+} \big(\phi(Y_{s-} - \delta_{H^i(Y_{s-})}) - \phi(Y_{s-})\big)\, \mathbf{1}_{\{i\leq\langle Y_{s-},1\rangle\}} \\ &\qquad \mathbf{1}_{\{\theta\leq d(H^i(Y_{s-}),C*Y_{s-}(H^i(Y_{s-})))\}} N_3(ds,di,d\theta).\end{aligned}$$

Taking expectations, we obtain

$$\begin{aligned}&\mathbb{E}(\phi(Y_t)) = \mathbb{E}(\phi(Y_0)) \\ &\quad + \int_0^t \mathbb{E}\Big(\sum_{i=1}^{\langle Y_s,1\rangle} \Big\{ \big(\phi(Y_s + \delta_{H^i(Y_s)}) - \phi(Y_s)\big)\, b(H^i(Y_s))(1 - p(H^i(Y_s))) \\ &\quad + \int_{\mathcal{X}} (\phi(Y_s + \delta_z) - \phi(Y_s))\, b(H^i(Y_s))p(H^i(Y_s))\, m(H^i(Y_s),z)dz \\ &\quad + \big(\phi(Y_s - \delta_{H^i(Y_s)}) - \phi(Y_s)\big)\, d(H^i(Y_s), C * Y_s(H^i(Y_s)))\Big\}\Big)ds\end{aligned}$$

Differentiating this expression at $t = 0$ leads to (6.4). □

Let us show the existence and some moment properties for the population process.

Theorem 6.4. (i) *Assume Assumption 6.1 holds and that* $\mathbb{E}(\langle Y_0, 1\rangle) < \infty$. *Then the process* $(Y_t)_{t\geq 0}$ *defined in Definition 6.2 is well defined on* $\mathbb{R}_+$.
(ii) *If furthermore for some* $p \geq 1$, $\mathbb{E}(\langle Y_0, 1\rangle^p) < \infty$, *then for any* $T < \infty$,

$$\mathbb{E}(\sup_{t\in[0,T]} \langle Y_t, 1\rangle^p) < +\infty. \tag{6.6}$$

Proof. We first prove (ii). Consider the process $(Y_t)_{t\geq 0}$. We introduce for each n the stopping time $\tau_n = \inf\{t \geq 0,\ \langle Y_t, 1\rangle \geq n\}$. Then a simple computation using Assumption 6.1 shows that, dropping the non-positive death terms,

$$\begin{aligned}\sup_{s\in[0,t\wedge\tau_n]}\langle Y_s,1\rangle^p &\le \langle Y_0,1\rangle^p\\&+\int_{[0,t\wedge\tau_n]\times\mathbb{N}^*\times\mathbb{R}+}((\langle Y_{s-},1\rangle+1)^p-\langle Y_{s-},1\rangle^p)\,\mathbf{1}_{\{i\le\langle Y_{s-},1\rangle\}}\\&\qquad\mathbf{1}_{\{\theta\le b(H^i(Y_{s-}))(1-p(H^i(Y_{s-})))\}}N_1(ds,di,d\theta)\\&+\int_{[0,t\wedge\tau_n]\times\mathbb{N}^*\times\mathcal{X}\times\mathbb{R}+}((\langle Y_{s-},1\rangle+1)^p-\langle Y_{s-},1\rangle^p)\,\mathbf{1}_{\{i\le\langle Y_{s-},1\rangle\}}\\&\qquad\mathbf{1}_{\{\theta\le b(H^i(Y_{s-}))p(H^i(Y_{s-}))\,m(H^i(Y_{s-}),z)\}}N_2(ds,di,dz,d\theta).\end{aligned}$$

Using the inequality $(1+x)^p-x^p\le C_p(1+x^{p-1})$ and taking expectations, we thus obtain, the value of C_p changing from one line to the other,

$$\begin{aligned}\mathbb{E}(\sup_{s\in[0,t\wedge\tau_n]}\langle Y_s,1\rangle^p)&\le C_p\left(1+\mathbb{E}\left(\int_0^{t\wedge\tau_n}\bar{b}\,(\langle Y_{s-},1\rangle+\langle Y_{s-},1\rangle^p)\,ds\right)\right)\\&\le C_p\left(1+\mathbb{E}\left(\int_0^{t}(1+\langle Y_{s\wedge\tau_n},1\rangle^p)\,ds\right)\right).\end{aligned}$$

The Gronwall Lemma allows us to conclude that for any $T<\infty$, there exists a constant $C_{p,T}$, not depending on n, such that

$$\mathbb{E}(\sup_{t\in[0,T\wedge\tau_n]}\langle Y_t,1\rangle^p)\le C_{p,T}. \tag{6.7}$$

First, we deduce that τ_n tends a.s. to infinity. Indeed, if not, one may find $T_0<\infty$ such that $\epsilon_{T_0}=P(\sup_n\tau_n<T_0)>0$. This would imply that $\mathbb{E}\left(\sup_{t\in[0,T_0\wedge\tau_n]}\langle Y_t,1\rangle^p\right)\ge\epsilon_{T_0}n^p$ for all n, which contradicts (6.7). We may let n go to infinity in (6.7) thanks to the Fatou Lemma. This leads to (6.6).

Point (i) is a consequence of point (ii). Indeed, one builds the solution $(Y_t)_{t\ge0}$ step by step. One only has to check that the sequence of jump instants T_n goes a.s. to infinity as n tends to infinity. But this follows from (6.6) with $p=1$. □

6.4 Examples and simulations

Let us remark that Assumption 6.1 is satisfied in the case where

$$d(x,C*\nu(x))=d(x)+\alpha(x)\int_{\mathcal{X}}C(x-y)\nu(dy), \tag{6.8}$$

and b, d, and α are bounded functions.

In the case where moreover, $p \equiv 1$, this individual-based model can also be interpreted as a model of “spatially structured population,” where the trait is viewed as a spatial location and the mutation at each birth event is viewed as dispersal. This kind of models has been introduced by Bolker and Pacala [13, 14] and Law et al. [54], and mathematically studied by Fournier and Méléard [35]. The case $C \equiv 1$ corresponds to a density-dependence in the total population size.

Later, we will consider the particular set of parameters, taken from Kisdi [49] and corresponding to a model of asymmetric competition:

$$\mathcal{X} = [0,4], \quad d(x) = 0, \quad \alpha(x) = 1, \quad p(x) = p,$$
$$b(x) = 4 - x, \quad C(x-y) = \frac{2}{K}\left(1 - \frac{1}{1 + 1.2\exp(-4(x-y))}\right) \tag{6.9}$$

and $m(x,z)dz$ is a Gaussian law with mean x and variance σ^2 conditioned to stay in $[0,4]$. As we will see in Chapter 7, the constant K scaling the strength of competition also scales the population size (when the initial population size is proportional to K). In this model, the trait x can be interpreted as body size. Equation (6.9) means that body size influences the birth rate negatively, and creates asymmetrical competition reflected in the sigmoid shape of C (being larger is competitively advantageous).

Let us give now an algorithmic construction of the population process (in the general case), giving the size N_t of the population and the trait vector $\mathbf{X}_t$ of all individuals alive at time t.

At time $t = 0$, the initial population Y_0 contains N_0 individuals and the corresponding trait vector is $\mathbf{X}_0 = (X_0^i)_{1 \le i \le N_0}$. We introduce the following sequences of independent random variables, which will drive the algorithm.

- The type of birth or death events will be selected according to the values of a sequence of random variables $(W_k)_{k \in \mathbb{N}^*}$ with uniform law on $[0,1]$.
- The times at which events may be realized will be described using a sequence of random variables $(\tau_k)_{k \in \mathbb{N}}$ with exponential law with parameter $\hat{C}$.
- The mutation steps will be driven by a sequence of random variables $(Z_k)_{k \in \mathbb{N}}$ with law $\bar{m}(z)dz$.

We set $T_0 = 0$ and construct the process inductively for $k \ge 1$ as follows.

At step $k-1$, the number of individuals is N_{k-1}, and the trait vector of these individuals is $\mathbf{X}_{T_{k-1}}$.

Let $T_k = T_{k-1} + \dfrac{\tau_k}{N_{k-1}(N_{k-1}+1)}$. Notice that $\dfrac{\tau_k}{N_{k-1}(N_{k-1}+1)}$ represents the time between jumps for N_{k-1} individuals, and $\hat{C}(N_{k-1}+1)$ gives an upper bound of the total rate of events affecting each individual.

At time T_k, one chooses an individual $i_k = i$ uniformly at random among the N_{k-1} alive in the time interval $[T_{k-1}, T_k)$; its trait is $X^i_{T_{k-1}}$. (If $N_{k-1} = 0$, then $Y_t = 0$ for all $t \ge T_{k-1}$.)

- If $0 \leq W_k \leq \dfrac{d(X^i_{T_{k-1}}, \sum_{j=1}^{I_{k-1}} C(X^i_{T_{k-1}} - X^j_{T_{k-1}}))}{\hat{C}(N_{k-1}+1)} = W^i_1(\mathbf{X}_{T_{k-1}})$, then the chosen individual dies, and $N_k = N_{k-1} - 1$.
- If $W^i_1(\mathbf{X}_{T_{k-1}}) < W_k \leq W^i_2(\mathbf{X}_{T_{k-1}})$, where

$$W^i_2(\mathbf{X}_{T_{k-1}}) = W^i_1(\mathbf{X}_{T_{k-1}}) + \frac{[1 - p(X^i_{T_{k-1}})]b(X^i_{T_{k-1}})}{\hat{C}(N_{k-1}+1)},$$

  then the chosen individual gives birth to an offspring with trait $X^i_{T_{k-1}}$, and $N_k = N_{k-1} + 1$.
- If $W^i_2(\mathbf{X}_{T_{k-1}}) < W_k \leq W^i_3(\mathbf{X}_{T_{k-1}}, Z_k)$, where

$$W^i_3(\mathbf{X}_{T_{k-1}}, Z_k) \quad = \quad W^i_2(\mathbf{X}_{T_{k-1}}) \; + \; \frac{p(X^i_{T_{k-1}})b(X^i_{T_{k-1}})\, m(X^i_{T_{k-1}}, X^i_{T_{k-1}} + Z_k)}{\hat{C}\bar{m}(Z_k)(N_{k-1}+1)},$$

  then the chosen individual gives birth to a mutant offspring with trait $X^i_{T_{k-1}} + Z_k$, and $N_k = N_{k-1} + 1$.
- If $W_k > W^i_3(\mathbf{X}_{T_{k-1}}, Z_k)$, nothing happens, and $N_k = N_{k-1}$.

Then, at any time $t \geq 0$, the number of individuals and the population process are defined by

$$N_t = \sum_{k \geq 0} 1_{\{T_k \leq t < T_{k+1}\}} N_k, \qquad Y_t = \sum_{k \geq 0} 1_{\{T_k \leq t < T_{k+1}\}} \sum_{i=1}^{N_k} \delta_{X^i_{T_k}}.$$

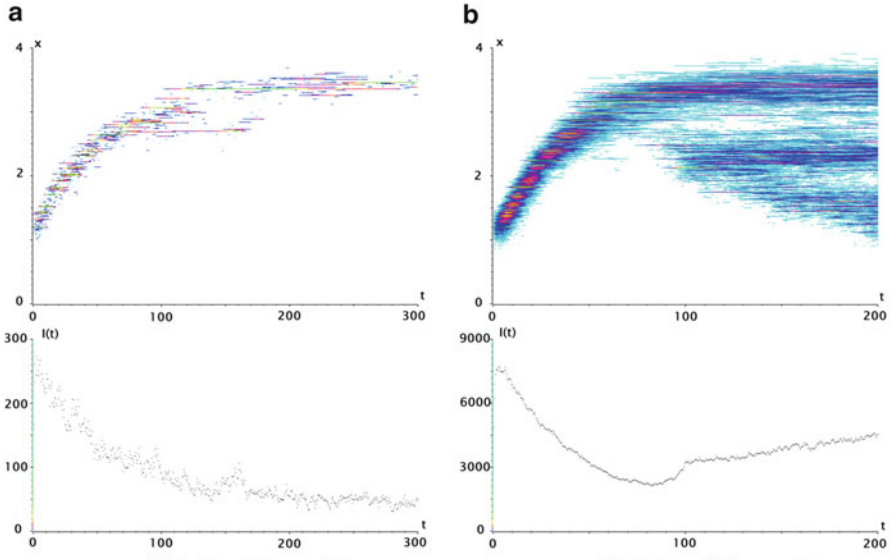
The simulation of Kisdi's example (6.9) can be carried out following this algorithm. We can show a very wide variety of qualitative behaviors depending on the value of the parameters σ, p and K.

In the following figures (cf. Champagnat-Ferrière-Méléard [21]), the upper part gives the distribution of the traits in the population at any time, using a grey scale code for the number of individuals holding a given trait. The lower part of the simulation represents the dynamics of the total population size N_t.

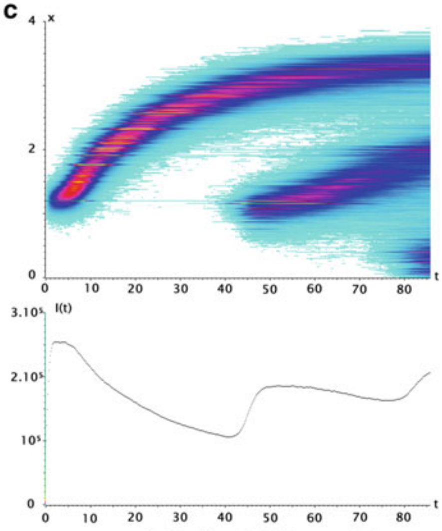
These simulations will serve to illustrate the different mathematical scalings described in Chapter 7. In Fig. 6.1 (a)–(c), we see the qualitative and quantitative effects of increasing scalings K, from a finite trait support process for small K to a wide population density for large K. The simulations of Fig. 6.2 involve birth and death processes with large rates (see Section 7.2) given by

$$b(x) = K^\eta + b(x) \quad \text{and} \quad d(x, \zeta) = K^\eta + d(x) + \alpha(x)\zeta$$

and small mutation step σ_K. There is a noticeable qualitative difference between Fig. 6.2 (a) where $\eta = 1/2$, and Fig. 6.2 (b) where $\eta = 1$. In the latter, we observe

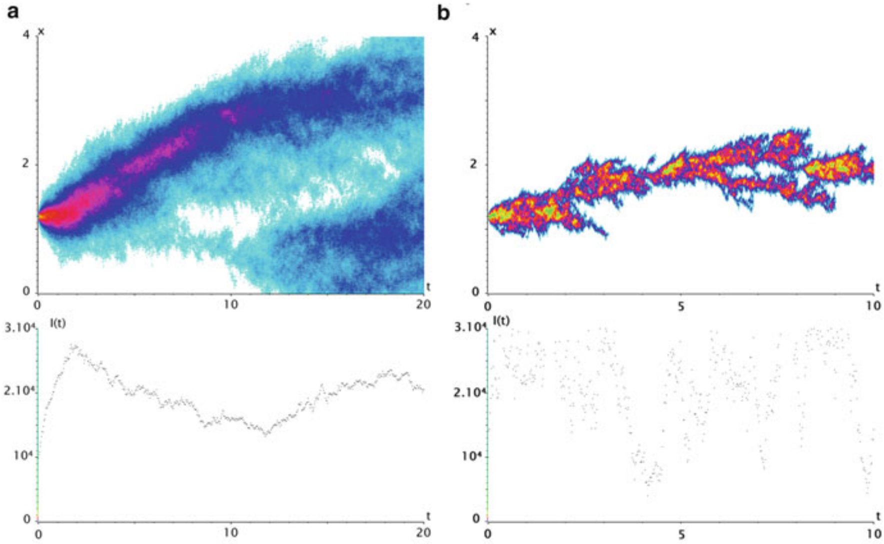


$p = 0.03,\ K = 100,\ \sigma = 0.1.$ $p = 0.03,\ K = 3000,\ \sigma = 0.1.$



$p = 0.03,\ K = 100000,\ \sigma = 0.1.$

Fig. 6.1 Numerical simulations of trait distributions (upper panels, darker means higher frequency) and population size (lower panels). The initial population is monomorphic with trait value 1.2 and contains *K* individuals. (**a**–**c**) Effect of increasing the system size (measured by the parameter *K*).



$p = 0.3,\ K = 10000,\ \sigma = 0.3/K^{\eta/2},\ \eta = 0.5.$ $p = 0.3,\ K = 10000,\ \sigma = 0.3/K^{\eta/2},\ \eta = 1.$

Fig. 6.2 Numerical simulations of trait distributions (upper panels, darker means higher frequency) and population size (lower panels) for accelerated birth and death and concurrently increased parameter K. The parameter η (between 0 and 1) relates the acceleration of demographic turnover to the increase of system size K. (**a**) Case $\eta = 0.5$. (**b**) Case $\eta = 1$. The initial population is monomorphic with trait value 1.2 and contains K individuals.

strong fluctuations in the population size and a finely branched structure of the evolutionary pattern, revealing a new form of stochasticity in the large population approximation.

6.5 Martingale Properties

We give some martingale properties of the process $(Y_t)_{t\geq 0}$, which are the key point of our approach.

Theorem 6.5. *Suppose Assumption 6.1 holds and that for some* $p \geq 2$, $E(\langle Y_0, 1\rangle^p) < \infty$.

(i) *For all measurable functions* ϕ *from* $\mathcal{M}$ *into* $\mathbb{R}$ *such that for some constant C, for all* $\nu \in \mathcal{M}$, $|\phi(\nu)| + |L\phi(\nu)| \leq C(1 + \langle \nu, 1\rangle^p)$, *the process*

$$\phi(Y_t) - \phi(Y_0) - \int_0^t L\phi(Y_s)ds \tag{6.10}$$

is a càdlàg $(\mathcal{F}_t)_{t\geq 0}$*-martingale starting from* 0.

(ii) *Point (i) applies to any function* $\phi(\nu) = \langle \nu, f \rangle^q$, *with* $0 \le q \le p-1$ *and with* f *bounded and measurable on* $\mathcal{X}$.

(iii) *For such a function* f, *the process*

$$M_t^f = \langle Y_t, f \rangle - \langle Y_0, f \rangle - \int_0^t \int_{\mathcal{X}} \left\{ \Big((1-p(x))b(x) - d(x, C * Y_s(x)) \Big) f(x) \right.$$
$$\left. + p(x)b(x) \int_{\mathcal{X}} f(z)\, m(x,z)dz \right\} Y_s(dx)ds \tag{6.11}$$

is a càdlàg square-integrable martingale starting from 0 *with quadratic variation*

$$\langle M^f \rangle_t = \int_0^t \int_{\mathcal{X}} \left\{ \Big((1-p(x))b(x) - d(x, C * Y_s(x)) \Big) f^2(x) \right.$$
$$\left. + p(x)b(x) \int_{\mathcal{X}} f^2(z)\, m(x,z)dz \right\} Y_s(dx)ds. \tag{6.12}$$

Proof. The proof follows the proof of Theorem 2.8. First of all, note that point (i) is immediate thanks to Proposition 6.3 and (6.6). Point (ii) follows from a straightforward computation using (6.4). To prove (iii), we first assume that $E\left(\langle Y_0, 1\rangle^3\right) < \infty$. We apply (i) with $\phi(\nu) = \langle \nu, f \rangle$. This gives us that M^f is a martingale. To compute its bracket, we first apply (i) with $\phi(\nu) = \langle \nu, f \rangle^2$ and obtain that

$$\langle Y_t, f \rangle^2 - \langle Y_0, f \rangle^2 - \int_0^t \int_{\mathcal{X}} \left\{ \Big((1-p(x))b(x)(f^2(x) + 2f(x)\,\langle Y_s, f \rangle) \right.$$
$$+ d(x, C * Y_s(x))(f^2(x) - 2f(x)\,\langle Y_s, f \rangle) \Big)$$
$$\left. + p(x)b(x) \int_{\mathcal{X}} (f^2(z) + 2f(z)\,\langle Y_s, f \rangle)\, m(x,z)dz \right\} Y_s(dx)ds \tag{6.13}$$

is a martingale. On the other hand, we apply the Itô formula to compute $\langle Y_t, f \rangle^2$ from (6.11). We deduce that

$$\langle Y_t, f \rangle^2 - \langle Y_0, f \rangle^2 - \int_0^t 2\,\langle Y_s, f \rangle \int_{\mathcal{X}} \left\{ \Big((1-p(x))b(x) - d(x, C * Y_s(x)) \Big) f(x) \right.$$
$$\left. + p(x)b(x) \int_{\mathcal{X}} f(z) m(x,z)dz \right\} Y_s(dx)ds - \langle M^f \rangle_t \tag{6.14}$$

is a martingale. Comparing (6.13) and (6.14) leads to (6.12). The extension to the case where only $E\left(\langle Y_0, 1\rangle^2\right) < \infty$ is straightforward by a localization argument, since also in this case, $E(\langle M^f \rangle_t) < \infty$ thanks to (6.6) with $p = 2$. □

Chapter 7
Scaling limits for the individual-based process

As in Chapter 2, we consider the case where the system size becomes very large. We scale this size by the integer K and look for approximations of the conveniently renormalized measure-valued population process, when K tends to infinity.

For any K, let the set of parameters C_K, b_K, d_K, m_K, p_K satisfy Assumption 6.1. Let Y_t^K be the counting measure of the population at time t. We define the measure-valued Markov process $(X_t^K)_{t\geq 0}$ by

$$X_t^K = \frac{1}{K} Y_t^K .$$

As the system size K goes to infinity, we need to assume the

Assumption 7.1. *The parameters C_K, b_K, d_K, m_K, and p_K are continuous, $\zeta \mapsto d(x,\zeta)$ is Lipschitz continuous for any $x \in \mathcal{X}$ and*

$$C_K(x) = \frac{C(x)}{K}.$$

A biological interpretation of this renormalization is that larger systems are made up of smaller individuals, which may be a consequence of a fixed amount of available resources to be partitioned among individuals. Indeed, the biomass of each interacting individual scales like $1/K$, and the interaction effect of the global population on a focal individual is of order 1. The parameter K may also be interpreted as scaling the amount of resources available, so that the renormalization of C_K reflects the decrease of competition for resources.

The generator $\tilde{L}^K$ of $(Y_t^K)_{t\geq 0}$ is given by (6.4), with parameters C_K, b_K, d_K, m_K, p_K. The generator L^K of $(X_t^K)_{t\geq 0}$ is obtained by writing, for any measurable function ϕ from $M_F(\mathcal{X})$ into $\mathbb{R}$ and any $\nu \in M_F(\mathcal{X})$,

$$L^K\phi(\nu) = \partial_t \mathbb{E}_\nu(\phi(X_t^K))_{t=0} = \partial_t \mathbb{E}_{K\nu}(\phi(Y_t^K/K))_{t=0} = \tilde{L}^K\phi^K(K\nu)$$

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_7

where $\phi^K(\mu) = \phi(\mu/K)$. Then we get

$$\begin{aligned} L^K\phi(\nu) = K\int_{\mathcal{X}} & b_K(x)(1-p_K(x))(\phi(\nu+\frac{1}{K}\delta_x)-\phi(\nu))\nu(dx) \\ &+K\int_{\mathcal{X}}\int_{\mathcal{X}} b_K(x)p_K(x)(\phi(\nu+\frac{1}{K}\delta_z)-\phi(\nu))\, m_K(x,z)dz\nu(dx) \\ &+K\int_{\mathcal{X}} d_K(x,C*\nu(x))(\phi(\nu-\frac{1}{K}\delta_x)-\phi(\nu))\nu(dx). \end{aligned} \tag{7.1}$$

By a similar proof as that carried out in Section 6.5, we may summarize the moment and martingale properties of X^K.

Proposition 7.1. *Assume that for some* $p \geq 2$, $\mathbb{E}(\langle X_0^K, 1\rangle^p) < +\infty$.

(1) *For any* $T > 0$, $\mathbb{E}\big(\sup_{t\in[0,T]}\langle X_t^K, 1\rangle^p\big) < +\infty$.
(2) *For any bounded and measurable function* ϕ *on* M_F *such that* $|\phi(\nu)| + |L^K\phi(\nu)| \leq C(1+\langle \nu,1\rangle^p)$, *the process* $\phi(X_t^K) - \phi(X_0^K) - \int_0^t L^K\phi(X_s^K)ds$ *is a càdlàg martingale.*
(3) *For each measurable bounded function* f, *the process*

$$\begin{aligned} M_t^{K,f} &= \langle X_t^K,f\rangle - \langle X_0^K,f\rangle \\ &\quad -\int_0^t\int_{\mathcal{X}} (b_K(x)-d_K(x,C*X_s^K(x)))f(x)X_s^K(dx)ds \\ &\quad -\int_0^t\int_{\mathcal{X}} p_K(x)b_K(x)\Big(\int_{\mathcal{X}} f(z)m_K(x,z)dz - f(x)\Big)X_s^K(dx)ds \end{aligned}$$

is a square-integrable martingale with quadratic variation

$$\begin{aligned} \langle M^{K,f}\rangle_t = \frac{1}{K}\Big\{ & \int_0^t\int_{\mathcal{X}} p_K(x)b_K(x)\Big(\int_{\mathcal{X}} f^2(z)\, m_K(x,z)dz - f^2(x)\Big)X_s^K(dx)ds \\ &+\int_0^t\int_{\mathcal{X}} (b_K(x)+d_K(x,C*X_s^K(x)))f^2(x)X_s^K(dx)ds\Big\}. \end{aligned} \tag{7.2}$$

The search of tractable limits for the semimartingales $\langle X^K,f\rangle$ yields different choices of scalings for the parameters. In particular, we obtain a deterministic or stochastic approximation, depending on the quadratic variation of the martingale term given in (7.2).

7.1 Large-population limit

We assume here that $b_K = b$, $d_K = d$, $p_K = p$, $m_K = m$. We also assume that $\mathcal{X}$ is a compact subset of $\mathbb{R}^d$ and we endow the measure space $M_F(\mathcal{X})$ with the weak topology.

Theorem 7.2. *Assume Assumptions 6.1 and 7.1 hold. Assume moreover that* $\sup_K E(\langle X_0^K, 1\rangle^3) < +\infty$ *and that the initial conditions* X_0^K *converge in law and for the weak topology on* $M_F(\mathcal{X})$ *as K increases, to a finite deterministic measure* ξ_0.

Then for any $T > 0$, *the process* $(X_t^K)_{t\geq 0}$ *converges in law, in the Skorohod space* $\mathbb{D}([0,T], M_F(\mathcal{X}))$, *as K goes to infinity, to the unique deterministic continuous function* $\xi \in C([0,T], M_F(\mathcal{X}))$ *satisfying for any bounded* $f : \mathcal{X} \to \mathbb{R}$

$$\langle \xi_t, f\rangle = \langle \xi_0, f\rangle + \int_0^t \int_{\mathcal{X}} f(x)[(1-p(x))b(x) - d((x, C * \xi_s(x))]\xi_s(dx)ds$$
$$+ \int_0^t \int_{\mathcal{X}} p(x)b(x) \left(\int_{\mathcal{X}} f(z)\, m(x,z)dz \right) \xi_s(dx)ds \tag{7.3}$$

The proof of Theorem 7.2 is left to the reader. It can be adapted from the proofs of Theorem 7.4 and 7.6 below, or obtained as a generalization of Theorem 3.1. This result is illustrated by the simulations of Figs. 6.1 (a)–(c).

Main Examples:

(1) A density case.

Proposition 7.3. *Suppose that* ξ_0 *is absolutely continuous with respect to Lebesgue measure. Then for all* $t \geq 0$, ξ_t *is absolutely continuous with respect to Lebesgue measure and* $\xi_t(dx) = \xi_t(x)dx$, *where* $\xi_t(x)$ *is the solution of the functional equation*

$$\partial_t \xi_t(x) = [(1-p(x))b(x) - d(x, C * \xi_t(x))]\, \xi_t(x)$$
$$+ \int_{\mathbb{R}^d} m(y,x)p(y)b(y)\xi_t(y)dy \tag{7.4}$$

for all $x \in \mathcal{X}$ *and* $t \geq 0$.

Some people refer to $\xi_t(.)$ as the population number density.

Proof. Consider a Borel set A of $\mathbb{R}^d$ with Lebesgue measure zero. A simple computation allows us to obtain, for all $t \geq 0$,

$$\langle \xi_t, \mathbf{1}_A\rangle \leq \langle \xi_0, \mathbf{1}_A\rangle) + \bar{b} \int_0^t \int_{\mathcal{X}} \mathbf{1}_A(x)\xi_s(dx)ds$$
$$+ \bar{b} \int_0^t \int_{\mathcal{X}} \int_{\mathcal{X}} \mathbf{1}_A(z)m(x,z)dz\xi_s(dx)ds.$$

By assumption, the first term on the RHS is zero. The third term is also zero, since for any $x \in \mathcal{X}$, $\int_{\mathcal{X}} \mathbf{1}_A(z)m(x,z)dz = 0$. Using Gronwall's Lemma, we conclude that $\langle \xi_t, \mathbf{1}_A \rangle = 0$ and then, the measure $\xi_t(dx)$ is absolutely continuous w.r.t. Lebesgue measure. One can easily prove from (7.3) that the density function $\xi_t(.)$ is solution of the functional equation (7.4). □

(2) The mean field case. The case of structured populations with $d(x, C * \xi(x)) = d + \alpha\, C * \xi(x)$ with constant rates b, d, α is meaningful, and has been developed in a spatial context where the kernel C describes the resources available (see, for example, [49]). In this context, (7.3) leads to the following equation on the total mass $n_t = \langle \xi_t, 1 \rangle$:

$$\partial_t n_t = (b-d)n_t - \alpha \int_{\mathcal{X}\times\mathcal{X}} C(x-y)\xi_t(dx)\xi_t(dy). \tag{7.5}$$

This equation is not closed in $(n_t)_t$ and presents an unresolved hierarchy of nonlinearities. In the very particular case of uniform competition where $C \equiv 1$ (usually called "mean-field case"), there is a "decorrelative" effect and we recover the classical mean-field logistic equation of population growth:

$$\partial_t n_t = (b-d)n_t - \alpha n_t^2.$$

(3) Monomorphic and dimorphic cases with no mutation. We assume here that the mutation probability is $p = 0$. Without mutation, the trait space is fixed at time 0.

(a) Monomorphic case: All the individuals have the same trait x. Thus, we can write $X_0^K = n_0^K(x)\delta_x$, and then $X_t^K = n_t^K(x)\delta_x$ for any time t. In this case, Theorem 7.2 recasts into $n_t^K(x) \to n_t(x)$ with $\xi_t = n_t(x)\delta_x$, and (7.3) reads

$$\frac{d}{dt}n_t(x) = n_t(x)\big(b(x) - d(x, C(0)n_t(x))\big), \tag{7.6}$$

When $d(x, C * \xi(x)) = d + \alpha\, C * \xi(x)$, we recognize the logistic equation (3.9).

(b) Dimorphic case: The population consists in two subpopulations of individuals with traits x and y, i.e. $X_0^K = n_0^K(x)\delta_x + n_0^K(y)\delta_y$ and when K tends to infinity, the limit of X_t^K is given by $\xi_t = n_t(x)\delta_x + n_t(y)\delta_y$ satisfying (7.3), which recasts into the following system of coupled ordinary differential equations:

$$\begin{aligned} \frac{d}{dt}n_t(x) &= n_t(x)\big(b(x) - d(x, C(0)n_t(x) + C(x-y)n_t(y))\big) \\ \frac{d}{dt}n_t(y) &= n_t(y)\big(b(y) - d(y, C(0)n_t(y) + C(y-x)n_t(x))\big). \end{aligned} \tag{7.7}$$

When $d(x, C * \xi(x)) = d + \alpha\, C * \xi(x)$, we obtain the competitive Lotka-Volterra system (6.1).

7.2 Large-population limit with accelerated births and deaths

We consider here an alternative limit of large population, combined with accelerated birth and death. This may be useful to investigate the qualitative differences of evolutionary dynamics across populations with allometric demographies (larger populations made up of smaller individuals who reproduce and die faster, See [19, 22]).

Here, we assume that $\mathcal{X} = \mathbb{R}^d$. Let us denote by M_F the space $M_F(\mathbb{R}^d)$. It will be endowed with the weak topology (the test functions are continuous and bounded). We will also consider the vague topology (the test functions are compactly supported). We assume that the dominant terms of the birth and death rates are proportional to K^η while preserving the demographic balance. That is, the birth and death rates satisfy

Assumption 7.2.

$$b_K(x) = K^\eta \gamma(x) + b(x), \quad d_K(x,\zeta) = K^\eta \gamma(x) + d(x,\zeta).$$

The allometric effect (smaller individuals reproduce and die faster) is parametrized by a positive and bounded function r and by a real number $\eta \in (0,1]$. A detailed discussion of the biological meaning of these parameters in terms of allometry and life-history can be found in [21]. Observe that η is a parameter scaling the speed of acceleration of the birth and death rates when $K \to \infty$ (births and deaths occur faster for larger η) and that the individual growth rate $b_K - d_K$ stays bounded from above. In other words, the timescale of population growth is assumed to be slower than the timescale of individuals' births and deaths. As in Section 7.1, the interaction kernel C is renormalized by K. Using similar arguments as in Section 7.1, the process $X^K = \frac{1}{K} Y^K$ is now a Markov process with generator

$$\begin{aligned} L^K\phi(\nu) = K &\int_{\mathbb{R}^d} (K^\eta\gamma(x) + b(x))(1 - p_K(x))(\phi(\nu + \frac{1}{K}\delta_x) - \phi(\nu))\nu(dx) \\ &+ K \int_{\mathbb{R}^d} (K^\eta\gamma(x) + b(x))p_K(x) \int_{\mathbb{R}^d} (\phi(\nu + \frac{1}{K}\delta_z) \\ &- \phi(\nu))\, m_K(x,z)dz\nu(dx) + K \int_{\mathbb{R}^d} (K^\eta\gamma(x) \\ &+ d(x, C * \nu(x)))(\phi(\nu - \frac{1}{K}\delta_x) - \phi(\nu))\nu(dx). \end{aligned}$$

As before, for any measurable functions ϕ on M_F such that $|\phi(\nu)| + |L^K\phi(\nu)| \leq C(1 + \langle \nu, 1\rangle^3)$, the process

$$\phi(X^K_t) - \phi(X^K_0) - \int_0^t L^K\phi(X^K_s)ds \tag{7.8}$$

is a martingale. In particular, for each measurable bounded function f, we obtain

$$\begin{aligned} M_t^{K,f} &= \langle X_t^K, f\rangle - \langle X_0^K, f\rangle \\ &- \int_0^t \int_{\mathbb{R}^d} (b(x) - d(x, C * X_s^K(x)))f(x)X_s^K(dx)ds \\ &- \int_0^t \int_{\mathbb{R}^d} p_K(x)(K^\eta \gamma(x) + b(x))\Big(\int_{\mathbb{R}^d} f(z)m_K(x,z)dz - f(x)\Big)X_s^K(dx)ds \end{aligned} \tag{7.9}$$

is a square-integrable martingale with quadratic variation

$$\begin{aligned} \langle M^{K,f}\rangle_t = \frac{1}{K}\Big\{ &\int_0^t \int_{\mathbb{R}^d} (2K^\eta\gamma(x) + b(x) + d(x, C * X_s^K(x)))f^2(x)X_s^K(dx)ds \\ &+ \int_0^t \int_{\mathbb{R}^d} p_K(x)(K^\eta\gamma(x) + b(x))\Big(\int_{\mathbb{R}^d} f^2(z)m_K(x,z)dz - f^2(x)\Big)X_s^K(dx)ds\Big\}. \end{aligned} \tag{7.10}$$

In what follows, the variance of the mutation distribution m_K is of order $1/K^\eta$. That will ensure that the deterministic part in (7.9) converges. In the large-population renormalization (Section 7.1), the quadratic variation of the martingale part was of order $1/K$. Here, it is of order $K^\eta \times 1/K$. This quadratic variation will thus stay finite provided that $\eta \in (0, 1]$, in which case tractable limits will result. Moreover, this limit will be zero if $\eta < 1$ and nonzero if $\eta = 1$, which will lead to deterministic or random limit models, as stated in the two following theorems.

We assume here that the mutation rate is fixed, so that mutation events appear more often as a consequence of accelerated births. We assume

Assumption 7.3. (1) $p_K = p$.

(2) *The mutation step density $m_K(x,z)$ is the density of a random variable with mean x, variance–covariance matrix $\Sigma(x)/K^\eta$ (where $\Sigma(x) = (\Sigma_{ij}(x))_{1\le i,j\le d}$) and with third moment of order $1/K^{\eta+\varepsilon}$ uniformly in x ($\varepsilon > 0$). (Thus, as K goes to infinity, mutant traits become more concentrated around their progenitors).*

(3) *$\sqrt{\Sigma}$ denotes the symmetric square root matrix of Σ and the function $\sqrt{\Sigma}\,\gamma\, p$ is Lipschitz continuous.*

The main example is when the mutation density is the vector density of independent Gaussian variables with mean x and variance $\sigma^2(x)/K^\eta$:

$$m_K(x,z) = \left(\frac{K^\eta}{2\pi\sigma^2(x)}\right)^{d/2} \exp\left(-K^\eta|z-x|^2/2\sigma^2(x)\right) \tag{7.11}$$

where $\sigma^2(x)$ is positive and bounded over $\mathbb{R}^d$.

Then the convergence results of this section can be stated as follows.

Theorem 7.4. (1) *Assume that Assumptions 6.1–7.3 hold and that* $0 < \eta < 1$. *Assume also that the initial conditions* X_0^K *converge in law and for the weak topology on* M_F *as* K *increases, to a finite deterministic measure* ξ_0 *and that*

$$\sup_K \mathbb{E}(\langle X_0^K, 1\rangle^3) < +\infty. \tag{7.12}$$

Then, for each $T > 0$, *the sequence of processes* (X^K) *belonging to* $\mathbb{D}([0,T], M_F)$ *converges (in law) to the unique deterministic function* $(\xi_t)_{t\geq 0} \in C([0,T], M_F)$ *satisfying: for each function* $f \in C_b^2(\mathbb{R}^d)$,

$$\begin{aligned}\langle \xi_t, f\rangle = \langle \xi_0, f\rangle &+ \int_0^t \int_{\mathbb{R}^d} (b(x) - d(x, C * \xi_s(x))) f(x) \xi_s(dx) ds \\ &+ \int_0^t \int_{\mathbb{R}^d} \frac{1}{2} p(x)\gamma(x) \sum_{1\leq i,j\leq d} \Sigma_{ij}(x) \partial_{ij}^2 f(x) \xi_s(dx) ds,\end{aligned} \tag{7.13}$$

where $\partial_{ij}^2 f$ *denotes the second-order partial derivative of* f *with respect to* x_i *and* x_j $(x = (x_1, \ldots, x_d))$.

(2) *Assume moreover that there exists* $c > 0$ *such that* $\gamma(x)p(x)s^*\Sigma(x)s \geq c||s||^2$ *for any* x *and* s *in* $\mathbb{R}^d$. *Then for each* $t > 0$, *the measure* ξ_t *has a density with respect to Lebesgue measure.*

Observe that the limit (7.13) is independent of $\eta \in (0,1)$. As will appear in the proof, this comes from the fact that the growth rate $b_K - d_K$ is independent of η and that the mutation kernel $m_K(x,z)$ compensates exactly the dispersion in the trait space induced by the acceleration of the births with mutations.

Remark 7.5. In case (2), Eq. (7.13) may be written as

$$\partial_t \xi_t(x) = \big(b(x) - d(x, C * \xi_t(x))\big)\xi_t(x) + \frac{1}{2} \sum_{1\leq i,j\leq d} \partial_{ij}^2 (\gamma p \Sigma_{ij} \xi_t)(x). \tag{7.14}$$

Observe that for the example (7.11), this equation writes

$$\partial_t \xi_t(x) = \big(b(x) - d(x, C * \xi_t(x))\big)\xi_t(x) + \frac{1}{2} \Delta(\sigma^2 \gamma p\, \xi_t)(x). \tag{7.15}$$

Therefore, Eq. (7.15) generalizes the Fisher reaction-diffusion equation known from classical population genetics (see, e.g., [16]).

Theorem 7.6. *Assume that Assumptions 6.1–7.3 hold and that* $\eta = 1$. *Assume also that the initial conditions* X_0^K *converge in law and for the weak topology on* M_F *as* K *increases, to a finite (possibly random) measure* X_0, *and that* $\sup_K E(\langle X_0^K, 1\rangle^3) < +\infty$.

Then, for each $T > 0$, the sequence of processes (X^K) converges in law in $\mathbb{D}([0,T], M_F)$ to the unique (in law) continuous superprocess $X \in C([0,T], M_F)$, defined by the following conditions:

$$\sup_{t\in[0,T]} \mathbb{E}\left(\langle X_t, 1\rangle^3\right) < \infty, \tag{7.16}$$

and for any $f \in C_b^2(\mathbb{R}^d)$,

$$\begin{aligned}\bar{M}_t^f = \langle X_t, f\rangle - \langle X_0, f\rangle - \frac{1}{2}\int_0^t \int_{\mathbb{R}^d} p(x)\gamma(x) \sum_{1\le i,j\le d} \Sigma_{ij}(x)\partial^2_{ij} f(x) X_s(dx)ds \\ - \int_0^t \int_{\mathbb{R}^d} f(x)\left(b(x) - d(x, C * X_s(x))\right) X_s(dx)ds \end{aligned} \tag{7.17}$$

is a continuous martingale with quadratic variation

$$\langle \bar{M}^f\rangle_t = 2\int_0^t \int_{\mathbb{R}^d} \gamma(x) f^2(x) X_s(dx)ds. \tag{7.18}$$

Remark 7.7. (1) The limiting measure-valued process X appears as a generalization of the one proposed by Etheridge [29] to model spatially structured populations.

(2) The equations characterizing the above process X can be formally rewritten as

$$\partial_t X_t(x) = \Big(b(x) - d(x, C * X_t(x))\Big) X_t(x) + \frac{1}{2}\sum_{1\le i,j\le d} \partial^2_{ij}(\gamma\, p\, \Sigma_{ij} X_t)(x) + \dot{M}_t$$

where $\dot{M}_t$ is a random fluctuation term, which reflects the demographic stochasticity of this fast birth and death process, that is, faster than the accelerated birth and death process which led to the deterministic reaction-diffusion approximation (7.15).

(3) As developed in Step 1 of the proof of Theorem 7.6 below, a Girsanov's theorem relates the law of X_t and the one of a standard super-Brownian motion, which leads us to conjecture that a density for X_t exists only when $d = 1$, as for super-Brownian motion.

These two theorems are illustrated by the simulations of Figs. 6.2 (a) and (b).

Proof of Theorem 7.4. **(1)** We divide the proof in six steps. Let us fix $T > 0$.

Step 1 Let us first show the uniqueness of a solution of the equation (7.13). To this aim, we define the mild equation associated with (7.13). It is easy to prove that if ξ is a solution of (7.13) satisfying $\sup_{t\in[0,T]}\langle \xi_t, 1\rangle < \infty$, then for each test function $\psi_t(x) = \psi(t,x) \in C_b^{1,2}(\mathbb{R}_+ \times \mathbb{R}^d)$, one has

$$
\begin{aligned}
\langle \xi_t, \psi_t \rangle = \langle \xi_0, \psi_0 \rangle &+ \int_0^t \int_{\mathbb{R}^d} (b(x) - d(x, C * \xi_s(x)))\psi(s,x)\xi_s(dx)ds \\
&+ \int_0^t \int_{\mathbb{R}^d} (\partial_s \psi(s,x) + \frac{1}{2}\gamma(x)p(x) \sum_{i,j} \Sigma_{ij}(x)\partial^2_{ij}\psi_s(x))\xi_s(dx)ds.
\end{aligned}
\tag{7.19}
$$

Now, since the function $\sqrt{\Sigma\,\gamma\,p}$ is Lipschitz continuous, we may define the transition semigroup (P_t) with infinitesimal generator $f \mapsto \frac{\gamma p}{2} \sum_{i,j} \Sigma_{ij}\partial^2_{ij} f$.

Then, for each function $f \in C^2_b(\mathbb{R}^d)$ and fixed $t > 0$, choosing $\psi(s,x) = P_{t-s}f(x)$ yields

$$
\langle \xi_t, f \rangle = \langle \xi_0, P_t f \rangle + \int_0^t \int_{\mathbb{R}^d} (b(x) - d(x, C * \xi_s(x)))P_{t-s}f(x)\xi_s(dx)ds, \tag{7.20}
$$

since $\partial_s \psi(s,x) + \frac{1}{2}\gamma(x)p(x)\sum_{i,j}\Sigma_{ij}(x)\partial^2_{ij}\psi_s(x) = 0$ for this choice.
We now prove the uniqueness of a solution of (7.20).
Let us consider two solutions $(\xi_t)_{t\geq 0}$ and $(\bar{\xi}_t)_{t\geq 0}$ of (7.20) satisfying $\sup_{t\in[0,T]} \langle \xi_t + \bar{\xi}_t, 1 \rangle = A_T < +\infty$. We consider the variation norm defined for μ_1 and μ_2 in M_F by

$$
||\mu_1 - \mu_2|| = \sup_{f \in L^\infty(\mathbb{R}^d),\ ||f||_\infty \leq 1} |\langle \mu_1 - \mu_2, f \rangle|. \tag{7.21}
$$

Then, we consider some bounded and measurable function f defined on $\mathcal{X}$ such that $||f||_\infty \leq 1$ and obtain

$$
\begin{aligned}
|\langle \xi_t - \bar{\xi}_t, f \rangle| \leq &\int_0^t \left| \int_{\mathbb{R}^d} [\xi_s(dx) - \bar{\xi}_s(dx)]\,(b(x) - d(x, C * \xi_s(x)))\,P_{t-s}f(x) \right| ds \\
&+ \int_0^t \left| \int_{\mathbb{R}^d} \bar{\xi}_s(dx)(d(x, C * \xi_s(x)) - d(x, C * \bar{\xi}_s(x)))P_{t-s}f(x) \right| ds.
\end{aligned}
\tag{7.22}
$$

Since $||f||_\infty \leq 1$, then $||P_{t-s}f||_\infty \leq 1$ and for all $x \in \mathbb{R}^d$,

$$
|(b(x) - d(x, C * \xi_s(x)))P_{t-s}f(x)| \leq \bar{b} + \bar{d}(1 + \bar{C}A_T).
$$

Moreover, d is Lipschitz continuous in its second variable with Lipschitz constant K_d. Thus we obtain from (7.22) that

$$
|\langle \xi_t - \bar{\xi}_t, f \rangle| \leq \left[\bar{b} + \bar{d}(1 + \bar{C}A_T) + K_d A_T \bar{C}\right] \int_0^t ||\xi_s - \bar{\xi}_s|| ds. \tag{7.23}
$$

Taking the supremum over all functions f such that $||f||_\infty \leq 1$, and using Gronwall's Lemma, we finally deduce that for all $t \leq T$, $||\xi_t - \bar{\xi}_t|| = 0$. Uniqueness holds.

Step 2 Next, we would like to obtain some moment estimates. First, we check that for any $T > 0$,

$$\sup_K \sup_{t \in [0,T]} \mathbb{E}\big(\langle X_t^K, 1\rangle^3\big) < \infty. \tag{7.24}$$

To this end, we use (7.8) with $\phi(\nu) = \langle \nu, 1\rangle^3$. (To be completely rigorous, one should first use $\phi(\nu) = \langle \nu, 1\rangle^3 \wedge A$ and let A tend to infinity). Taking expectation, we obtain that for all $t \geq 0$, all K,

$$\begin{aligned}&\mathbb{E}\left(\langle X_t^K, 1\rangle^3\right) = \mathbb{E}\left(\langle X_0^K, 1\rangle^3\right)\\&+ \int_0^t \mathbb{E}\bigg(\int_{\mathbb{R}^d} \bigg([K^{\eta+1}\gamma(x) + Kb(x)] \bigg\{ [\langle X_s^K, 1\rangle + \frac{1}{K}]^3 - \langle X_s^K, 1\rangle^3 \bigg\}\\&\{K^{\eta+1}\gamma(x) + Kd(x, C * X_s^K(x))\} \bigg\{ [\langle X_s^K, 1\rangle - \frac{1}{K}]^3\\&- \langle X_s^K, 1\rangle^3 \bigg\} \bigg) X_s^K(dx) \bigg) ds.\end{aligned}$$

Dropping the non-positive death term involving d, we get

$$\begin{aligned}\mathbb{E}(\langle X_t^K, 1\rangle^3) \leq + \int_0^t \mathbb{E}\bigg(\int_{\mathbb{R}^d} \bigg(& K^{\eta+1}\gamma(x) \bigg\{ [\langle X_s^K, 1\rangle + \frac{1}{K}]^3\\&+ [\langle X_s^K, 1\rangle - \frac{1}{K}]^3 - 2\langle X_s^K, 1\rangle^3 \bigg\}\\&+ Kb(x) \bigg\{ [\langle X_s^K, 1\rangle + \frac{1}{K}]^3 - \langle X_s^K, 1\rangle^3 \bigg\} \bigg) X_s^K(dx) \bigg) ds.\end{aligned}$$

But for all $x \geq 0$, all $\epsilon \in (0, 1]$, $(x + \epsilon)^3 - x^3 \leq 6\epsilon(1 + x^2)$ and $|(x + \epsilon)^3 + (x - \epsilon)^3 - 2x^3| = 6\epsilon^2 x$. We finally obtain

$$\mathbb{E}\left(\langle X_t^K, 1\rangle^3\right) \leq \mathbb{E}\left(\langle X_0^K, 1\rangle^3\right) + C \int_0^t \mathbb{E}\left(\langle X_s^K, 1\rangle + \langle X_s^K, 1\rangle^2 + \langle X_s^K, 1\rangle^3\right) ds.$$

Assumption (7.12) and Gronwall's Lemma allow us to conclude that (7.24) holds.

Next, we wish to check that

$$\sup_K \mathbb{E}\big(\sup_{t\in[0,T]} \langle X_t^K, 1\rangle^2\big) < \infty. \tag{7.25}$$

Applying (7.9) with $f \equiv 1$, we obtain

$$\langle X_t^K, 1\rangle = \langle X_0^K, 1\rangle + \int_0^t \int_{\mathcal{X}} \big(b(x) - d(x, C * X_s^K(x))\big)\, X_s^K(dx)ds + M_t^{K,1}.$$

Hence

$$\sup_{s\in[0,t]} \langle X_s^K, 1\rangle^2 \le C\bigg(\langle X_0^K, 1\rangle^2 + \bar{b} \int_0^t \langle X_s^K, 1\rangle^2 ds + \sup_{s\in[0,t]} |M_s^{K,1}|^2\bigg).$$

Thanks to (7.12), the Doob inequality and Gronwall's Lemma, there exists a constant C_t not depending on K such that

$$\mathbb{E}\big(\sup_{s\in[0,t]} \langle X_s^K, 1\rangle^2\big) \le C_t \left(1 + \mathbb{E}\left(\langle M^{K,1}\rangle_t\right)\right).$$

Using now (7.10), we obtain, for some other constant C_t not depending on K,

$$\mathbb{E}\left(\langle M^{K,1}\rangle_t\right) \le C \int_0^t \left(\mathbb{E}\left(\langle X_s^K, 1\rangle + \langle X_s^K, 1\rangle^2\right)\right) ds \le C_t$$

thanks to (7.24). This concludes the proof of (7.25).

Step 3 We first endow M_F with the vague topology, the extension to the weak topology being handled in Step 6 below. To show the tightness of the sequence of laws $Q^K = \mathcal{L}(X^K)$ in $\mathcal{P}(\mathbb{D}([0,T], (M_F, v)))$, it suffices, following Roelly [59], to show that for any continuous bounded function f on $\mathbb{R}^d$, the sequence of laws of the processes $\langle X^K, f\rangle$ is tight in $\mathbb{D}([0,T], \mathbb{R})$. To this end, we use the Aldous criterion [1] and the Rebolledo criterion (see [43]). We have to show that

$$\sup_K \mathbb{E}\big(\sup_{t\in[0,T]} |\langle X_t^K, f\rangle|\big) < \infty, \tag{7.26}$$

and the Aldous condition, respectively, for the predictable quadratic variation of the martingale part and for the drift part of the semimartingales $\langle X^K, f\rangle$. Since f is bounded, (7.26) is a consequence of (7.25): let us thus consider a couple (S, S') of stopping times satisfying a.s. $0 \le S \le S' \le S + \delta \le T$. Using (7.10) and (7.25), we get for constants C, C'

$$\mathbb{E}\left(\langle M^{K,f}\rangle_{S'} - \langle M^{K,f}\rangle_S\right) \le C\mathbb{E}\left(\int_S^{S+\delta} \left(\langle X_s^K, 1\rangle + \langle X_s^K, 1\rangle^2\right) ds\right) \le C'\delta.$$

In a similar way, the expectation of the finite variation part of $\langle X^K_{S'},f\rangle - \langle X^K_S,f\rangle$ is bounded by $C'\delta$.
Hence, the sequence $(Q^K = \mathcal{L}(X^K))$ is tight in $\mathcal{P}(\mathbb{D}([0,T],(M_F,v)))$.

Step 4 We want to get a convergence result with M_F endowed with the weak topology. To this aim, as in [44] Lemmas 4.2 and 4.3, we use a sequence of functions which will help to control the measures outside the compact sets.

Lemma 7.8. *There exists a sequence of $C^2_b(\mathbb{R})$-functions $(f_n)_n$, even and non-decreasing on $\mathbb{R}_+$, with $f_0 = 1$ and such that*

$$f_n = 0 \text{ on } [-(n-1); n-1] \text{ ; } f_n = 1 \text{ on } [-n;n]^c$$

and satisfying

$$\lim_{n\to\infty} \limsup_{K\to\infty} \mathbb{E}\left(\sup_{t\le T}\langle X^K_t, f_n\rangle\right) = 0. \tag{7.27}$$

We refer to [44] for the proof of Lemma 7.8.

Step 5 Let us now denote by Q the weak limit in $\mathcal{P}(\mathbb{D}([0,T],(M_F,v)))$ of a subsequence of (Q^K) which we also denote by (Q^K). Let $X = (X_t)_{t\ge 0}$ a process with law Q. We remark that by construction, almost surely,

$$\sup_{t\in[0,T]} \sup_{f\in L^\infty(\mathbb{R}^d), \|f\|_\infty \le 1} |\langle X^K_t, f\rangle - \langle X^K_{t-}, f\rangle| \le 1/K.$$

Since, for each f in a countable measure-determining set of continuous and compactly supported functions on $\mathbb{R}$, the mapping $\nu \mapsto \sup_{t\le T} |\langle \nu_t, f\rangle - \langle \nu_{t-}, f\rangle|$ is continuous on $\mathbb{D}([0,T],(M_F,v))$, one deduces that Q only charges the continuous processes from $[0,T]$ into (M_F,v). Let us now endow M_F with the weak convergence topology and check that Q only charges the continuous processes from $[0,T]$ into (M_F,w), and that the sequence (Q^K) in $\mathcal{P}(\mathbb{D}([0,T],(M_F,w))$ converges weakly to Q. For this purpose, we need to control the behavior of the total mass of the measures. We employ the sequence (f_n) of smooth functions introduced in Lemma 7.8 which approximate the functions $\mathbf{1}_{\{|x|\ge n\}}$. For each $n \in \mathbb{N}$, the continuous and compactly supported functions $(f_{n,l} \overset{\text{def}}{=} f_n(1-f_l))_{l\in\mathbb{N}}$ increase to f_n, as $l\to\infty$. Continuity of the mapping $\nu \mapsto \sup_{t\le T}\langle \nu_t, f_{n,l}\rangle$ on $\mathbb{D}([0,T],(M_F,v))$ and its uniform integrability deduced from (7.25) imply the bound

$$\mathbb{E}\left(\sup_{t\le T}\langle X_t, f_{n,l}\rangle\right) = \lim_{K\to\infty} \mathbb{E}\left(\sup_{t\le T}\langle X^K_t, f_{n,l}\rangle\right) \le \liminf_{K\to\infty}\mathbb{E}\left(\sup_{t\le T}\langle X^K_t, f_n\rangle\right).$$

Taking the limit, $l \to \infty$, in the left-hand side, in view of the monotone convergence theorem and respectively, (7.25) and Lemma 7.8, one concludes that for $n = 0$,

$$\mathbb{E}\left(\sup_{t\le T}\langle X_t, 1\rangle\right) = \mathbb{E}\left(\sup_{t\le T}\langle X_t, f_0\rangle\right) < +\infty \tag{7.28}$$

and for general n,

$$\lim_{n\to\infty} \mathbb{E}\left(\sup_{t\le T}\langle X_t, f_n\rangle\right) = 0. \tag{7.29}$$

As a consequence one may extract a subsequence of the sequence $(\sup_{t\le T}\langle X_t, f_n\rangle)_n$ that converges a.s. to 0 under Q, and the set $(X_t)_{t\le T}$ is tight Q-a.s. Since Q only charges the continuous processes from $[0, T]$ into (M_F, v), one deduces that Q also only charges the continuous processes from $[0, T]$ into (M_F, w).
According to Méléard and Roelly [56], to prove that the sequence (Q^K) converges weakly to Q in $\mathcal{P}(\mathbb{D}([0, T], (M_F, w))$, it is sufficient to check that the processes $(\langle X^K, 1\rangle = (\langle X_t^K, 1\rangle)_{t\le T})_K$ converge in law to $\langle X, 1\rangle \overset{\text{def}}{=} (\langle X_t, 1\rangle)_{t\le T}$ in $\mathbb{D}([0, T], \mathbb{R})$. For a Lipschitz continuous and bounded function F from $\mathbb{D}([0, T], \mathbb{R})$ to $\mathbb{R}$, we have

$$\begin{aligned}\limsup_{K\to\infty} |\mathbb{E}(F(\langle \nu^K, 1\rangle) - F(\langle X, 1\rangle)| &\le \limsup_{n\to\infty}\ \limsup_{K\to\infty} |\mathbb{E}(F(\langle X^K, 1\rangle) - F(\langle X^K, 1-f_n\rangle))| \\ &\quad + \limsup_{n\to\infty}\limsup_{K\to\infty} |\mathbb{E}(F(\langle X^K, 1-f_n\rangle) - F(\langle X, 1-f_n\rangle))| \\ &\quad + \limsup_{n\to\infty} |\mathbb{E}(F(\langle X, 1-f_n\rangle) - F(\langle X, 1\rangle))|.\end{aligned}$$

Since $|F(\langle X, 1-f_n\rangle) - F(X, 1\rangle)| \le C\sup_{t\le T}\langle X_t, f_n\rangle$, Lemma 7.8 and (7.29), respectively, imply that the first and the third terms in the r.h.s. are equal to 0. The second term is 0 in view of the continuity of the mapping $\nu \mapsto \langle \nu, 1-f_n\rangle$ in $\mathbb{D}([0, T], (M_F, w))$.

Step 6 The time $T > 0$ is fixed. Let us now check that almost surely, the process X is the unique solution of (7.13). Thanks to (7.28), it satisfies $\sup_{t\in[0,T]}\langle X_t, 1\rangle < +\infty$ a.s., for each T. We fix now a function $f \in C_b^3(\mathbb{R}^d)$ (the extension of (7.13) to any function f in C_b^2 is not hard) and some $t \le T$. For $\nu \in C([0, T], M_F)$, denote

$$\Psi_t^1(\nu) = \langle \nu_t, f\rangle - \langle \nu_0, f\rangle - \int_0^t \int_{\mathbb{R}^d} (b(x) - d(x, C * \nu_s(x)))f(x)\nu_s(dx)ds,$$

$$\Psi_t^2(\nu) = -\int_0^t \int_{\mathbb{R}^d} \frac{1}{2} p(x)\gamma(x) \sum_{i,j} \Sigma_{ij}(x)\partial_{ij}^2 f(x)\nu_s(dx)ds. \tag{7.30}$$

Our aim is to show that

$$\mathbb{E}\left(|\Psi_t^1(X) + \Psi_t^2(X)|\right) = 0, \tag{7.31}$$

implying that X is solution of (7.19).
By (7.9), we know that for each K,

$$M_t^{K,f} = \Psi_t^1(X^K) + \Psi_t^{2,K}(X^K),$$

where

$$\Psi_t^{2,K}(X^K) = -\int_0^t \int_{\mathbb{R}^d} p(x)(K^\eta \gamma(x) + b(x)) \times \left(\int_{\mathbb{R}^d} f(z)m_K(x,z)dz - f(x)\right) X_s^K(dx)ds. \tag{7.32}$$

Moreover, (7.25) implies that for each K,

$$\mathbb{E}\left(|M_t^{K,f}|^2\right) = \mathbb{E}\left(\langle M^{K,f}\rangle_t\right) \le \frac{C_f K^\eta}{K} \mathbb{E}\left(\int_0^t \left\{\langle X_s^K, 1\rangle + \langle X_s^K, 1\rangle^2\right\} ds\right) \le \frac{C_{f,T} K^\eta}{K}, \tag{7.33}$$

which goes to 0 as K tends to infinity, since $0 < \eta < 1$. Therefore,

$$\lim_K \mathbb{E}(|\Psi_t^1(X^K) + \Psi_t^{2,K}(X^K)|) = 0.$$

Since X is a.s. strongly continuous (for the weak topology) and since $f \in C_b^3(\mathbb{R}^d)$ and thanks to the continuity of the parameters, the functions Ψ_t^1 and Ψ_t^2 are a.s. continuous at X. Furthermore, for any $\nu \in \mathbb{D}([0,T], M_F)$,

$$|\Psi_t^1(\nu) + \Psi_t^2(\nu)| \le C_{f,T} \sup_{s\in[0,T]} \left(1 + \langle \nu_s, 1\rangle^2\right). \tag{7.34}$$

Hence using (7.24), we see that the sequence $(\Psi_t^1(X^K) + \Psi_t^2(X^K))_K$ is uniformly integrable, and thus

$$\lim_K \mathbb{E}\left(|\Psi_t^1(X^K) + \Psi_t^2(X^K)|\right) = \mathbb{E}\left(|\Psi_t^1(X) + \Psi_t^2(X)|\right). \tag{7.35}$$

We have now to deal with $\Psi_t^{2,K}(X^K) - \Psi_t^2(X^K)$. The convergence of this term is due to the fact that the measure $m_K(x,z)dz$ has mean x, variance $\Sigma(x)/K^\eta$, and third moment bounded by $C/K^{\eta+\varepsilon}$ ($\varepsilon > 0$) uniformly in x. Indeed, if $Hf(x)$ denotes the Hessian matrix of f at x,

$$\begin{aligned}
&\int_{\mathbb{R}^d} f(z) m_K(x,z)dz \\
&= \int_{\mathbb{R}^d} \Big(f(x) + (z-x)\cdot\nabla f(x) \\
&\quad + \frac{1}{2}(z-x)^* Hf(x)(z-x) + O((z-x)^3)\Big) m_K(x,z)dz \\
&= f(x) + \frac{1}{2}\sum_{i,j}\frac{\Sigma_{ij}(x)}{K^\eta}\partial^2_{ij}f(x) + o(\frac{1}{K^\eta}).
\end{aligned} \tag{7.36}$$

where $K^\eta o(\frac{1}{K^\eta})$ tends to 0 uniformly in x (since f is in C_b^3), as K tends to infinity. Then,

$$\begin{aligned}
\Psi_t^{2,K}(X^K) = -\int_0^t \int_{\mathbb{R}^d} p(x)(K^\eta\gamma(x) + b(x))\times \\
\times \left(\frac{1}{2}\sum_{i,j}\frac{\Sigma_{ij}(x)}{K^\eta}\partial^2_{ij}f(x) + o(\frac{1}{K^\eta})\right) X_s^K(dx)ds,
\end{aligned}$$

and

$$|\Psi_t^{2,K}(X^K) - \Psi_t^2(X^K)| \le C_f\big(\sup_{s\le T} < X_s^K, 1 > \big)\left(\frac{1}{K^\eta} + K^\eta o(\frac{1}{K^\eta})\right).$$

Using (7.25), we conclude the proof of (7.31) and Theorem 7.4 **(1)**.
Let us now prove the point **(2)**. The non-degeneracy property $\gamma(x)p(x)s^*\Sigma(x)s \ge c\|s\|^2 > 0$ for each $x, s \in \mathbb{R}^d$ implies that for each time $t > 0$, the transition semigroup $P_t(x,dy)$ introduced in Step 1 of this proof has for each x a density function $p_t(x,y)$ with respect to Lebesgue measure. Then if we come back to the mild equation (7.20), we can write

$$\begin{aligned}
\int_{\mathbb{R}^d} f(x)\xi_t(dx) = \int_{\mathbb{R}^d}\left(\int_{\mathbb{R}^d} f(y)p_t(x,y)dy\right)\xi_0(dx) \\
+ \int_0^t\int_{\mathbb{R}^d}(b(x) - d(x, C*\xi_s(x)))\left(\int_{\mathbb{R}^d} f(y)p_{t-s}(x,y)dy\right)\xi_s(dx)ds.
\end{aligned}$$

Using the fact that the parameters are bounded, that $\sup_{t\leq T}\langle \xi_t, 1\rangle < +\infty$ and that f is bounded, we can apply Fubini's theorem and deduce that

$$\int_{\mathbb{R}^d} f(x)\xi_t(dx) = \int_{\mathbb{R}^d} H_t(y)f(y)dy$$

with $H \in L^\infty([0,T], L^1(\mathbb{R}^d))$. We deduce that ξ_t has a density with respect to Lebesgue measure for each time $t \leq T$.
Equation (7.14) is then the dual form of (7.13). □

Proof of Theorem 7.6. We use a similar method as the one of the previous theorem. Steps 2, 3, 4, and 5 of this proof can be achieved exactly in the same way. Therefore, we only have to prove the uniqueness (in law) of the solution to the martingale problem (7.16)–(7.18) (Step 1), and that any accumulation point of the sequence of laws of X^K is solution to (7.16)–(7.18) (Step 6).

Step 1 This uniqueness result is well known for the super-Brownian process (defined by a similar martingale problem, but with $b = d = 0$, $\gamma = p = 1$ and $\Sigma = \mathrm{Id}$, cf. [59]). Following [29], we may use the version of Dawson's Girsanov transform obtained in Evans and Perkins [31] (Theorem 2.3), to deduce the uniqueness in our situation, provided the condition

$$\mathbb{E}\left(\int_0^t \int_{\mathbb{R}^d} [b(x) - d(x, C * X_s(x))]^2 X_s(dx)ds\right) < +\infty$$

holds. This is easily obtained from (7.16) since the coefficients are bounded.

Step 6 Let us now identify the limit. Let us call $Q^K = \mathcal{L}(X^K)$ and denote by Q a limiting value of the tight sequence Q^K, and by $X = (X_t)_{t\geq 0}$ a process with law Q. Because of Step 5, X belongs a.s. to $C([0,T], (M_F, w))$. We want to show that X satisfies the conditions (7.16), (7.17), and (7.18). First note that (7.16) is straightforward from (7.25). Then, we show that for any function f in $C_b^3(\mathbb{R}^d)$, the process $\bar{M}_t^f$ defined by (7.17) is a martingale (the extension to every function in C_b^2 is easy). We consider $0 \leq s_1 \leq \ldots \leq s_n < s < t$, some continuous bounded maps $\phi_1, \ldots \phi_n$ on M_F, and our aim is to prove that, if the function Ψ from $\mathbb{D}([0,T], M_F)$ into $\mathbb{R}$ is defined by

$$\begin{aligned}\Psi(\nu) = \phi_1(\nu_{s_1})\ldots\phi_n(\nu_{s_n})\Big\{&\langle \nu_t, f\rangle - \langle \nu_s, f\rangle \\ &- \int_s^t \int_{\mathbb{R}^d}\Big(\frac{1}{2}p(x)\gamma(x)\sum_{i,j}\Sigma_{ij}\partial^2_{ij}f(x) \\ &+ f(x)\,[b(x) - d(x, C * \nu_u(x))]\Big)\nu_u(dx)du\Big\},\end{aligned} \tag{7.37}$$

then

$$\mathbb{E}\left(|\Psi(X)|\right) = 0. \tag{7.38}$$

It follows from (7.9) that

$$0 = \mathbb{E}\left(\phi_1(X^K_{s_1})\dots\phi_n(X^K_{s_n})\left\{M^{K,f}_t - M^{K,f}_s\right\}\right) = \mathbb{E}\left(\Psi(X^K)\right) - A_K, \tag{7.39}$$

where A_K is defined by

$$\begin{aligned}A_K = \mathbb{E}\Big(\phi_1(X^K_{s_1})\dots\phi_n(X^K_{s_n})\int_s^t\int_{\mathbb{R}^d}p(x)\Big\{b(x)\Big[\int_{\mathbb{R}^d}(f(z)-f(x))m_K(x,z)dz\Big]\\ +\gamma(x)K\Big[\int_{\mathbb{R}^d}(f(z)-f(x)-\sum_{i,j}\frac{\Sigma_{ij}(x)}{2K}\partial^2_{ij}f(x))m_K(x,z)dz\Big]\Big\}X^K_u(dx)du\Big).\end{aligned}$$

Using (7.36), we see that A_K tends to zero as K grows to infinity and using (7.25), that the sequence $(|\Psi(X^K)|)_K$ is uniformly integrable, so

$$\lim_K \mathbb{E}\left(|\Psi(X^K)|\right) = \mathbb{E}\left(|\Psi(X)|\right). \tag{7.40}$$

Collecting the previous results allows us to conclude that (7.38) holds, and thus $\bar{M}^f$ is a martingale.

We finally have to show that the bracket of $\bar{M}^f$ is given by (7.18). To this end, we first check that

$$\begin{aligned}\bar{N}^f_t &= \langle X_t,f\rangle^2 - \langle X_0,f\rangle^2 - \int_0^t\int_{\mathbb{R}^d}2\gamma(x)f^2(x)X_s(dx)ds\\ &-2\int_0^t\langle X_s,f\rangle\int_{\mathbb{R}^d}f(x)\left[b(x)-d(x,C*X_s(x))\right]X_s(dx)ds\\ &-\int_0^t\langle X_s,f\rangle\int_{\mathbb{R}^d}p(x)\gamma(x)\sum_{i,j}\Sigma_{ij}(x)\partial^2_{ij}f(x)X_s(dx)ds\end{aligned} \tag{7.41}$$

is a martingale. This can be done exactly as for $\bar{M}^f_t$, using the semimartingale decomposition of $\langle X^K_t,f\rangle^2$, given by (7.8) with $\phi(\nu) = \langle\nu,f\rangle^2$. On the other hand, Itô's formula implies that

$$\begin{aligned}\langle X_t,f\rangle^2 - \langle X_0,f\rangle^2 - \langle\bar{M}^f\rangle_t - \int_0^t\langle X_s,f\rangle\int_{\mathbb{R}^d}\gamma(x)p(x)\sum_{i,j}\Sigma_{ij}(x)\partial^2_{ij}f(x)X_s(dx)ds\\ -2\int_0^t\langle X_s,f\rangle\int_{\mathbb{R}^d}f(x)\big[b(x)-d(x,C*X_s(x))\big]X_s(dx)ds\end{aligned}$$

is a martingale. Comparing this formula with (7.41), we obtain (7.18). □

Chapter 8
Splitting Feller Diffusion for Cell Division with Parasite Infection

We now deal with a continuous time model for dividing cells which are infected by parasites. We assume that parasites proliferate in the cells and that their lifetimes are much shorter than the cell lifetimes. The quantity of parasites $(X_t : t \geq 0)$ in a cell is modeled by a Feller diffusion (see Chapter 3 and Definition 4.1). The cells divide in continuous time at rate $\tau(x)$ which may depend on the quantity of parasites x that they contain. When a cell divides, a random fraction F of the parasites goes in the first daughter cell and a fraction $(1 - F)$ in the second one. More generally, splitting Feller diffusion may model the quantity of some biological content which grows (without resource limitation) in the cells and is shared randomly when the cells divide (for example, proteins, nutriments, energy or extrachromosomal rDNA circles in yeast).

Let us give some details about the biological motivations. The modeling of parasites sharing is inspired by experiments conducted in Tamara's Laboratory where bacteria E-Coli have been infected with bacteriophages. These experiments show that a heavily infected cell often shares in a heavily infected cell and a lightly infected cell. Thus we are interested in taking into account unequal parasite splitting and we do not make restrictive (symmetry) assumptions about the distribution of F. We aim at quantifying the role of asymmetry in the infection. Without loss of generality, we assume that F is distributed as $1 - F$ and we say that the sharing is asymmetric when its distribution is not closely concentrated around $1/2$.

This splitting diffusion is a "branching within branching" process, in the same vein as the multilevel model for plasmids considered by Kimmel [48]. In the latter model, the cells divide in continuous time at a constant rate and the number of parasites is a discrete quantity which is fixed at the birth of the cell: the parasites reproduce 'only when the cells divide.' Moreover the parasites sharing is symmetric.

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_8

Let us describe briefly our process and we refer to Subsection 7.1 for a precise construction and definition. We denote by $\mathfrak{I} := \cup_{n\geq 0}\{1,2\}^n$ the usual labeling of a binary tree and by $n(di)$ the counting measure on $\mathfrak{I}$. We define $V_t \subset \mathfrak{I}$ as the set of cells alive at time t and N_t the number of cells alive at time t: $N_t = \#V_t$. For $i \in V_t$, we denote by $X_t^i \in \mathbb{R}_+$ the quantity of parasites in the cell i at time t.

The population of cells at time t including their parasite loads is modeled by the random point measure on $\mathbb{R}_+$:

$$Z_t(dx) = \sum_{i\in V_t} \delta_{X_t^i}(dx), \tag{8.1}$$

and the dynamics of Z is described as follows.

1. A cell with load x of parasites divides into two daughters at rate $\tau(x)$, where for some $p \geq 1$ and any $x \geq 0$, $\tau(x) \leq \bar{\tau}(1+x^p)$.
2. During the division, the parasites are shared between the two daughters: Fx parasites in one cell (chosen at random) and $(1-F)x$.
3. Between two divisions, the quantity of parasites in a cell follows a Feller diffusion process (see (3.12)), with diffusion coefficient $\sqrt{2\gamma x}$ and drift coefficient rx, r and γ being two real numbers, $\gamma > 0$.

Let us give a pathwise representation of the Markov process $(Z_t, t \geq 0)$. Let $(B^i, i \in \mathfrak{I})$ be a family of independent Brownian motions (BMs) and let $N(ds, du, di, d\theta)$ be a Poisson point measure (PPM) on $\mathbb{R}_+ \times \mathbb{R}_+ \times \mathfrak{I} \times [0,1]$ with intensity $q(ds, dv, di, d\theta) = ds\, dv\, n(di)\, \mathbb{P}(F \in d\theta)$ independent of the BMs. We denote by $(\mathcal{F}_t : t \geq 0)$ the canonical filtration associated with the BMs and the PPM. Then, for every $(t,x) \mapsto f(t,x) \in C_b^{1,2}(\mathbb{R}_+ \times \mathbb{R}_+, \mathbb{R})$ (the space of bounded functions of class C^1 in t and C^2 in x with bounded derivatives),

$$\begin{aligned}\langle Z_t, f\rangle = {} & f(0,x_0) + \int_0^t \int_{\mathbb{R}_+} \left(\partial_s f(s,x) + rx\partial_x f(s,x) + \gamma x \partial^2_{xx} f(s,x)\right) Z_s(dx)\, ds \\ & + M_t^f + \int_0^t \int_{\mathbb{R}_+\times\mathfrak{I}\times[0,1]} \mathbb{1}_{i\in V_{s-},\, u\leq \tau(X^i_{s-})} \Big(f(s, \theta X^i_{s-}) \\ & + f(s,(1-\theta)X^i_{s-}) - f(s, X^i_{s-}) \Big) N(ds, du, di, d\theta),\end{aligned} \tag{8.2}$$

where x_0 is the load of parasites in the ancestor cell $\emptyset$ at $t = 0$ and

$$M_t^f = \int_0^t \sum_{i\in V_s} \sqrt{2\gamma X_s^i}\, \partial_x f(s, X_s^i)\, dB_s^i \tag{8.3}$$

is a continuous square-integrable martingale with quadratic variation:

$$\langle M^f\rangle_t = \int_0^t \int_{\mathbb{R}_+} 2\gamma x (\partial_x f(s,x))^2\, ds\, Z_s(dx). \tag{8.4}$$

Remark 8.1. The existence and uniqueness of a solution of (8.2) are obtained from an adaptation of Subsection 5.3. (See also the next subsection for an approximation proof of the existence and [5] for details).

Notice that between two jumps, $\langle Z_t, f\rangle = \sum_{i\in V_t} f(X_t^i)$ and Itô's formula explains the second and third terms of (8.2). The fourth term (driven by the PPM) models the division events with the random sharing of parasites.

Proposition 8.2. *The total quantity of parasites* $X_t = \int_{\mathbb{R}_+} x Z_t(dx)$ *is a Feller diffusion (defined in* (3.12)*) with drift* rx *and diffusion coefficient* $\sqrt{2\gamma x}$ *starting from* x_0*. As a consequence,*

$$\forall t \in \mathbb{R}_+,\ \mathbb{E}_{x_0}(X_t) = x_0 e^{rt} < +\infty, \quad \mathbb{P}_{x_0}(\exists t \geq 0 :\ X_t = 0) = \exp(-rx_0/\gamma). \quad (8.5)$$

Proof. We remark that X_t can be written $X_t = x_0 + \int_0^t rX_s ds + M_t$ where M is a continuous square-integrable martingale with quadratic variation $\int_0^t 2\gamma X_s ds$. The representation theorem explained in the proof of Theorem 3.2 allows us to conclude. The properties (8.5) follow by classical arguments. □

8.1 Approximation by scaling limit

Inspired by the previous sections, we are looking for discrete approximations of the continuous model defined in (8.2), where each cell hosts a discrete parasite population. Let us introduce, as previously, the scaling parameter K. Let us describe the approximating model. The initial cell contains $[Kx_0]$ parasites. The parasites reproduce asexually with the individual birth and death rates $K\gamma + \lambda,\ K\gamma + \mu$, where $\lambda, \mu > 0$ satisfy $\lambda - \mu = r > 0$. The cell population is fully described by the point measure

$$\bar{Z}_t^K(du, dx) = \sum_{i\in V_t} \delta_{(i, X_t^{K,i})}(du, dx)$$

where $X_t^{K,i}$ is the number of parasites renormalized by K in the cell i at time t. This representation allows to keep a record of the underlying genealogy, which is useful in the forthcoming proofs. It also provides a closed equation to characterize the process $\bar{Z}$ (and derive Z). Notice that an alternative representation has been given in Chapter 7 by ordering the atoms $X_t^{K,i}$ for $i \in V_t$.

Let N^0 and N^1 be two independent PPMs on $\mathbb{R}_+ \times \mathcal{X}_0 := \mathbb{R}_+ \times \mathfrak{I} \times \mathbb{R}_+$ and $\mathbb{R}_+ \times \mathcal{X}_1 := \mathbb{R}_+ \times \mathfrak{I} \times \mathbb{R}_+ \times [0,1]$ with intensity measures $ds n(di) du$ and $ds\, n(di) du\, \mathbb{P}(F \in d\theta)$. We associate N^1 with the births and deaths of parasites, while N^2 corresponds to the cell divisions. The discrete space process is the unique strong solution of

$$\begin{aligned}\bar{Z}_t^K &= \delta_{(\emptyset,[Kx_0]/K)} \\ &+ \int_0^t \int_{\mathcal{X}_0} N^0(ds,di,du)\mathbb{1}_{i\in V_{s-}} \Big[\Big(\delta_{(i,X_{s-}^{K,i}+1/K)} - \delta_{(i,X_{s-}^{K,i})}\Big)\mathbb{1}_{u\le\lambda_K X_{s-}^{K,i}} \\ &\qquad + \Big(\delta_{(i,X_{s-}^{K,i}-1/K)} - \delta_{(i,X_{s-}^{K,i})}\Big)\mathbb{1}_{\lambda_K X_{s-}^{K,i}<u\le(\lambda_K+\mu_K)X_{s-}^{K,i}}\Big]. \\ &+ \int_0^t \int_{\mathcal{X}_1} N^1(ds,di,du,d\theta)\mathbb{1}_{i\in V_{s-}}\mathbb{1}_{u\le\tau(X_{s-}^{K,i})}\Big(\delta_{(i1,[\theta K X_{s-}^{K,i}]/K)} \\ &\qquad + \delta_{(i2,X_{s-}^{K,i}-[\theta K X_{s-}^{K,i}]/K)} - \delta_{(i,X_{s-}^{K,i})}\Big),\end{aligned} \tag{8.6}$$

where we set $\lambda_K = K(\lambda + K\gamma), \mu_K = K(\mu + K\gamma)$. We recall from Sections 4.5 and 5.1 that other discrete models would lead to the same continuous limiting object. For example, the parasites could be shared following a binomial distribution whose parameter is picked according to $\mathbb{P}(F \in d\theta)$.

Proposition 8.3. *Assume that there exists an integer $p \geq 1$ and a positive $\bar{\tau} > 0$ such that for all $x \in \mathbb{R}_+$, $0 \leq \tau(x) \leq \bar{\tau}(1 + x^p)$. Then, the sequence $(Z^K : n \in \mathbb{N}^*)$ defined in (8.6) converges in distribution in $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\mathbb{R}_+))$ as $K \to +\infty$ to the process Z defined in (8.2)–(8.4).*

The proof can be found in the Appendix of [5]. It follows the scheme of proof developed in the previous section, namely control of the moments and tightness and identification of the limit via the martingale problem for $< \bar{Z}_t^K, f >$. The additional regularities on the division rate τ are required to control the difference between the microscopic process (8.6) and its approximation (8.2)–(8.4).

Exercise. *Write the measure-valued equation which characterizes the limiting process $\bar{Z}_t(du, dx) = \sum_{i\in V_t} \delta_{(i,X_t^i)}(du, dx)$.*

8.2 Recovery criterion when the division rate is constant

We now consider the case where the infection does not influence the division rate and $\tau(.) = \tau$. We say that the organism recovers when the proportion of infected cells becomes negligible compared to the population of cells.

Theorem 8.4. *(i) If $r \leq 2\tau\mathbb{E}(\log(1/F))$, then the organism recovers a.s.:*

$$\lim_{t\to+\infty} \frac{\#\{i \in V_t : X_t^i > 0\}}{N_t} = 0 \quad a.s.$$

(ii) If $r > 2\tau\mathbb{E}(\log(1/F))$ then the parasites proliferate in the cells as soon as the parasites do not become extinct in the sense that

$$\Big\{\limsup_{t\to+\infty}\frac{\#\{i\in V_t : X_t^i \geq e^{\kappa t}\}}{N_t} > 0\Big\} = \{\forall t>0 :\ X_t > 0\} \quad a.s. \tag{8.7}$$

for every $\kappa < r - 2\tau\mathbb{E}(\log(1/F))$*. The probability of this event is* $1 - \exp(-rx_0/\gamma)$.

The factor 2 in the criterion comes from a bias phenomenon in continuous time. It appears in the following result shedding light on an auxiliary Markov process, namely the infection process X with catastrophes occurring at the accelerated rate 2τ. This factor 2 'increases the probability of recovery' in the sense that the amount of parasites in a random cell lineage (which can be obtained by keeping one cell at random at each division) may go to infinity with positive probability whereas the organism recovers a.s.

Since the division rate is constant, the process $(N_t, t \geq 0)$ is a simple linear (branching) birth process (called Yule process). Then $\mathbb{E}(N_t) = \exp(\tau t)$ and we define

$$\gamma_t(dx) := \mathbb{E}(Z_t(dx))/\mathbb{E}(N_t) = e^{-\tau t}\mathbb{E}(Z_t(dx)).$$

The dynamics of γ_t is given by the following result.

Lemma 8.5. *The family of probability measures* $(\gamma_t, t \geq 0)$ *is the unique solution of the following equation: for* $f \in C_b^{1,2}(\mathbb{R}_+^2, \mathbb{R})$ *and* $t \in \mathbb{R}_+$ *(and* $f_t(.) = f(t,.)$*):*

$$\langle \nu_t, f_t\rangle = f_0(x_0) + \int_0^t \int_{\mathbb{R}_+} \big(\partial_s f_s(x) + rx\partial_x f_s(x) + \gamma x \partial_{xx}^2\, f_s(x)\big)\, \nu_s(dx)ds.$$

$$+\, 2\tau \int_0^t \int_{\mathbb{R}_+} \int_0^1 [f_s(\theta x) - f_s(x)]\, \mathbb{P}(F \in d\theta)\nu_s(dx)ds \tag{8.8}$$

Proof of Lemma 8.5. Let $t \in \mathbb{R}_+$ and $(f : (s,x) \mapsto f_s(x)) \in C_b^{1,2}(\mathbb{R}_+^2, \mathbb{R})$. Using (8.2) with $(s,x) \mapsto f_s(x)e^{-\tau s}$ entails:

$$\begin{aligned}
&\langle e^{-\tau t}Z_t(dx), f_t\rangle = \langle Z_t(dx), e^{-\tau t}f_t\rangle \\
&= f_0(x_0) + \int_0^t \int_{\mathbb{R}_+} \Big(rx\partial_x f_s(x) + \gamma x \partial_{xx}^2 f_s(x) - \tau f_s(x) + \partial_s f_s(x)\Big) e^{-\tau s} Z_s(dx)\, ds \\
&+ \int_0^t \int_{\mathbb{R}_+\times\mathfrak{I}\times[0,1]} \mathbb{1}_{i\in V_{s-}}\, \mathbb{1}_{u\leq\tau}\Big[f_s(\theta X_{s-}^i) + f_s((1-\theta)X_{s-}^i) - f_s(X_{s-}^i)\Big] e^{-\tau s} N(ds, du, di, d\theta) \\
&+ M_t^f
\end{aligned}$$

where M_t^f is a continuous square-integrable martingale started at 0. Taking the expectation and using the symmetry of the distribution of F with respect to $1/2$:

$$\begin{aligned}\langle\gamma_t, f_t\rangle = & f_0(x_0) + \int_0^t \int \big(rx\,\partial_x f_s(x) + \gamma x\,\partial^2_{xx} f_s(x) + \partial_s f_s(x)\big)\,\gamma_s(dx)ds \\ & + \int_0^t \int_{\mathbb{R}_+\times[0,1]} 2\tau\,[f_s(\theta x) - f_s(x)]\,\mathbb{P}(F\in d\theta)\gamma_s(dx)ds. \end{aligned} \tag{8.9}$$

Let us prove that there is a unique solution to (8.8). We follow Step 1 of the proof of Theorem 7.4 and let $(\nu^1_t, t\geq 0)$ and $(\nu^2_t, t\geq 0)$ be two probability measures solutions of (8.8). The total variation distance between ν^1_t and ν^2_t is

$$\|\nu^1_t - \nu^2_t\|_{TV} = \sup_{\substack{\phi\in C_b(\mathbb{R}_+,\mathbb{R})\\ \|\phi\|_\infty\leq 1}} |\langle\nu^1_t,\phi\rangle - \langle\nu^2_t,\phi\rangle|. \tag{8.10}$$

Let $t\in\mathbb{R}_+$ and $\varphi\in C^2_b(\mathbb{R}_+,\mathbb{R})$ with $\|\varphi\|_\infty\leq 1$. We denote by $(P_s : s\geq 0)$ the semi-group associated with the Feller diffusion started at $x\in\mathbb{R}_+$: $P_s\varphi(x) = \mathbb{E}_x(\varphi(X_s))$. Notice that $\|P_{t-s}\varphi\|_\infty\leq\|\varphi\|_\infty\leq 1$. By (8.9) with $f_s(x) = P_{t-s}\varphi(x)$, the first term equals 0 and

$$\begin{aligned}\big|\langle\nu^1_t - \nu^2_t,\varphi\rangle\big| = & \left|2\tau\int_0^t\int_{\mathbb{R}_+}\int_0^1 \Big(P_{t-s}\varphi(\theta x) - P_{t-s}\varphi(x)\Big)\mathbb{P}(F\in d\theta)(Y^1_s - \nu^2_s)(dx)\,ds\right| \\ \leq & 4\tau\int_0^t \|\nu^1_s - \nu^2_s\|_{TV}ds.\end{aligned}$$

Since $C^2_b(\mathbb{R}_+,\mathbb{R})$ is dense in $C_b(\mathbb{R}_+,\mathbb{R})$ for the bounded pointwise topology, taking the supremum in the l.h.s. implies that: $\|\nu^1_t - \nu^2_t\|_{TV}\leq 4\tau\int_0^t\|\nu^1_s - \nu^2_s\|_{TV}ds$. Gronwall's Lemma ensures that $\|\nu^1_t - \nu^2_t\|_{TV} = 0$, which ends up the proof. □

We can then interpret γ_t as the marginal distribution (at time t) of an auxiliary process $(Y_t, t\geq 0)$.

Proposition 8.6. *For all $f\in C^2_b(\mathbb{R}_+,\mathbb{R})$ and $t\in\mathbb{R}_+$,*

$$\langle\gamma_t, f\rangle = e^{-\tau t}\mathbb{E}\Big(\sum_{i\in V_t} f(X^i_t)\Big) = \mathbb{E}(f(Y_t)), \tag{8.11}$$

where $(Y_t, t\geq 0)$ is a Feller branching diffusion with catastrophes with rate 2τ and distribution given by F. Moreover,

$$\mathbb{E}\left(\#\{i\in V_t : X^i_t > 0\}\right) = e^{\tau t}\mathbb{P}(Y_t > 0). \tag{8.12}$$

Proof. One can describe the dynamics of $t \to \gamma_t(f_t) = \mathbb{E}(f_t(Y_t))$ thanks to Itô's formula and check that it satisfies (8.8). Uniqueness of the solution of this equation yields (8.11). We can then apply (8.11) with $f(x) = \mathbb{1}_{x>0}$ by taking a monotone limit of C_b^2 functions to get (8.12). □

Proof of Theorem 8.4. Let us first prove the convergence in probability in (i). We denote by $V_t^* = \{i \in V_t : X_t^i > 0\}$ the set of infected cells and by $N_t^* = \#V_t^*$ its cardinality. By Theorem 5.2, under the assumption (i), $(Y_t, t \geq 0)$ dies in finite time a.s. Thus $\langle \gamma_t, \mathbb{1}_{x>0} \rangle$ converges in $\mathbb{L}^1$ and hence in probability to 0. Moreover the non-negative martingale $N_t/\exp(\tau t)$ tends a.s. to a non-negative random variable W. In addition, the $\mathbb{L}^2$-convergence can be easily obtained and is left to the reader. Therefore, $\mathbb{P}(W > 0)$ and then $W > 0$ a.s. One could actually even show that W is an exponential random variable with mean 1. Then

$$\lim_{t\to+\infty} \frac{N_t^*}{N_t} = \lim_{t\to+\infty} \frac{N_t^*}{e^{\tau t}} \frac{e^{\tau t}}{N_t} = 0 \quad \textit{in probability.} \tag{8.13}$$

It remains to show that the convergence holds a.s, which is achieved by checking that

$$\sup_{s\geq 0} N_{t+s}^*/N_{t+s} \overset{t\to\infty}{\longrightarrow} 0 \quad \textit{in probability.} \tag{8.14}$$

Indeed, let us denote by $V_{t,s}(i)$ the set of cells alive at time $t+s$ and whose ancestor at time t is the cell $i \in V_t$. Then $(\#V_{t,s}(i), s \geq 0)$ are i.i.d. random processes for $i \in V_t$ distributed as $(N_s, s \geq 0)$. We have

$$N_{t+s}^* \leq \sum_{i\in V_t^*} \#V_{t,s}(i) \leq e^{\tau s} \sum_{i\in V_t^*} M_t(i) \quad \text{a.s.}$$

where $M_t(i)$ are i.i.d random variables distributed like $M := \sup\{e^{-\tau s}N_s, s \geq 0\}$. Similarly,

$$N_{t+s} \geq \sum_{i\in V_t} \#V_{t,s}(i) \geq e^{\tau s} \sum_{i\in V_t} I_t(i) \quad \text{a.s.,}$$

where $I_t(i)$ are i.i.d. random variables distributed like $I := \inf\{e^{-\tau s}N_s, s \geq 0\}$. We add that $\mathbb{E}(M) < \infty$ since the martingale $e^{-\tau s}N_s$ is bounded in $\mathbb{L}^2$. Moreover $\mathbb{E}(I) \in (0, \infty)$ so that

$$\frac{N_t^{*-1} \sum_{i\in V_t^*} M_t(i)}{N_t^{-1} \sum_{i\in V_t} I_t(i)}$$

is stochastically bounded (or tight) for $t \geq 0$. Using that $N_t^*/N_t \to 0$ when $t \to +\infty$ in probability yields (8.14). This ensures the a.s. convergence of $R_t = N_t^*/N_t$ to 0, using that $\mathbb{P}(\limsup_{t\to\infty} R_t \geq \epsilon) \leq \lim_{t\to 0} \mathbb{P}(\sup_{s\geq 0} R_{t+s} \geq \epsilon) = 0$.

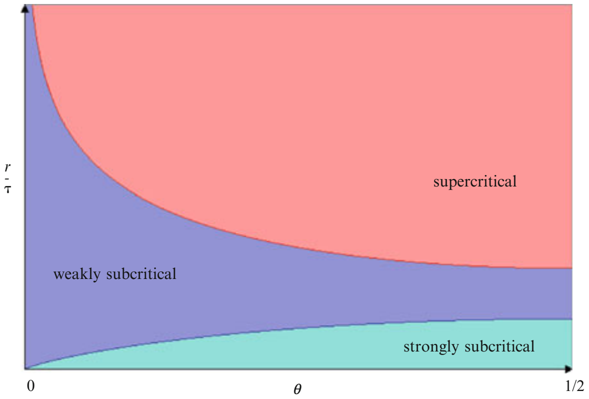


Fig. 8.1 Asymptotic regimes for the mean number of infected cells when $\mathbb{P}(F = \theta) = \mathbb{P}(F = 1 - \theta) = 1/2$ and $\theta \in (0, 1)$.

The proof of (*ii*) is similar. One can first note thanks to Section 5.2 that $\mathbb{P}(Y_t \geq \exp(\kappa t))$ has a positive limit and prove that

$$\left\{ \limsup_{t \to +\infty} \frac{\#\{i \in V_t : X_t^i \geq e^{\kappa t}\}}{N_t} > 0 \right\}$$

has a positive probability. To check that this latter event coincides with $\{\forall t > 0 : X_t > 0\}$, a zero-one law is involved, which is inherited from the branching property by a standard argument. □

Asymptotic regimes for the speed of infection. Combining Theorem 5.5 and Proposition 8.11 yield different asymptotic regimes for the mean number of infected cells $\mathbb{E}(N_t^*)$. They are plotted in Figure 8.1 when the sharing F of parasites is deterministic. We stress that it differs from the discrete analogous model [4]. In the supercritical regime, the number of infected cells and the number of cells are of the same order. In the strongly subcritical regime, the number of infected cells and the parasite loads are of the same order. In the weakly subcritical regime, the number of infected cells is negligible compared to the number of cells and the amount of parasites.

8.3 Some first results for a monotonic rate of division

The asymptotic study of such processes with a non-constant rate of division is the object of recent works (see [23, 25] and works in progress). Let us simply mention some relevant consequences of the previous results for non-decreasing rate τ.

8.3.1 A sufficient condition for recovery

We assume either that τ is non-decreasing and there exists $x_1 > 0$ such that $\tau(x_1) < \tau(0)$ or that $\tau(0) > \tau(x)$ for any $x > 0$. The second case means that the non-infected cells divide faster than the infected ones. Let us recall from Proposition 5.6 in Section 5.3 the notation

$$\tau_* := \inf\{\tau(x) : x \geq 0\}.$$

Proposition 8.7. *If* $r \leq \tau_* \mathbb{E}(\log 1/(\min(F, 1-F)))$*, the organism recovers a.s.*

We only give the idea of the proof and refer to [5] for more details. Let us follow a cell lineage by starting from the initial cell and choosing the less infected cell at each division. The infection along this lineage is a Feller diffusion with catastrophes whose distribution is $\min(F, 1-F)$ and the catastrophe rate is τ. We know from Section 5.3 when the infection in such a cell line becomes extinct a.s. Then one uses that the population of non-infected cells is growing faster than the population of cells infected by more than x_1 parasites.

8.3.2 An example of moderate infection

We assume here that $\tau(x)$ is an increasing function of the parasite load. This means that the more the cell is infected, the faster it divides. Low infected cells divide slower and may even stop dividing if $\tau(0) = 0$. That's why a new regime appears here, between recovery and proliferation of the parasites, where a positive fraction of cells is infected but the quantity of parasites inside remains bounded. We then say that the infection is *moderate*. Let us provide an example where the infection is indeed moderate: the organism does not recover but the parasites do not proliferate in the cells.

$$F = 1/2 \text{ a.s.}, \quad \tau(x) = 0 \text{ if } x < 2 \text{ and } \tau(x) = \infty \text{ if } x \geq 2.$$

Indeed, as soon as the quantity of parasites in a cell reaches 2, the cell divides and the quantity of parasites in each daughter cell is equal to one. The parasites do not proliferate in the cells since the parasite load in each cell is less than 2.

We now fix the growth rate of parasites r such that the probability that the Feller diffusion $(X_t, t \geq 0)$ reaches 0 before 2 is strictly less than $1/2$. Then the number of infected cells follows a supercritical branching process and grows exponentially with positive probability. Conditionally on this event, the proportion of infected cells doesn't tend to zero since the non-infected cells do not divide. Thus the organism doesn't recover.

Chapter 9
Markov Processes along Continuous Time Galton-Watson Trees

In this section, we consider measure-valued processes associated with a discrete genealogy given by a branching process. These processes describe a structured population where individuals are characterized by a trait. We focus on the case where the branching rate is constant and the number of offspring belongs to $\mathbb{N}$. During the life of an individual, its trait dynamics is modeled by a general Markov process. More precisely, the individuals behave independently and

1. Each individual lives during an independent exponential time of parameter τ and then gives birth to a random number of offspring whose distribution is given by $(p_k, k \geq 0)$.
2. Between two branching events, the trait dynamics of an individual follows a càdlàg strong Markov process $(X_t)_{t\geq 0}$ with values in a Polish space $\mathcal{X}$ and infinitesimal generator L with domain $D(L)$. Here again, we can assume that $\mathcal{X} \subset \mathbb{R}^d$.
3. When an individual with trait x dies, the distribution of the traits of its offspring is given by $(P^{(k)}(x, dx_1, \ldots, dx_k) : k \geq 1)$, where k is the number of offspring.

Let us note that an individual may die without descendance when $p_0 > 0$. Moreover, when X is a Feller diffusion and $p_2 = 1$, we recover the splitting Feller diffusion of Chapter 8. In the general case, the process X is no longer a branching process and the key property for the long time study of the measure-valued process will be the ergodicity of a well-chosen auxiliary Markov process.

A vast literature can be found concerning branching Markov processes and special attention has been payed to Branching Brownian Motion from the pioneering work of Biggins [10] about branching random walks, see, e.g., [28, 60] and the references therein. More recently, non-local branching events (with jumps occurring at the branching times) and superprocesses limits corresponding to small and rapidly branching particles have been considered and we refer, e.g., to the works of Dawson et al. and Dynkin [26].

V. Bansaye, S. Méléard, *Stochastic Models for Structured Populations*, Mathematical Biosciences Institute Lecture Series 1.4, DOI 10.1007/978-3-319-21711-6_9

9.1 Continuous Time Galton-Watson Genealogy

The genealogy of the population is a branching process with reproduction at rate τ and offspring distribution given by $(p_k, k \geq 0)$. We assume that the population arises from a single ancestor $\{\emptyset\}$. Roughly speaking, the genealogy is obtained by adding i.i.d. exponential life lengths (with parameter τ) to a (discrete) Galton-Watson tree. Let us give some details on this construction, which will be useful in the sequel. We define $\mathbf{I} := \{\varnothing\} \cup \bigcup_{n\geq 1}(\mathbb{N}^*)^n$, which we endow with the order relation $\preceq$: $u \preceq v$ if there exists $w \in \mathbf{I}$ such that $v = (u, w)$. For example, the individual $(2, 3, 4)$ is the fourth child of the third child of the second child of the root $\emptyset$. We denote by $(A(i), i \in \mathbf{I})$ i.i.d. random variables with distribution p. The discrete genealogy $\mathcal{I}$ is the random subset of $\mathbf{I}$ obtained by keeping the individuals which are born:

$$\mathcal{I} := \cup_{q\geq 0}\{(i_1, \ldots, i_q) : \forall k = 1, \ldots, q,\ i_k \leq A((i_1, \ldots, i_{k-1}))\},$$

where by convention the first set in the right-hand side is $\{\emptyset\}$. We consider now a sequence $(l_i, i \in \mathbf{I})$ of exponential random variables, so that l_i is the lifetime of the individual $i \in \mathcal{I}$ and

$$\alpha(i) = \sum_{j\prec i} l_j \quad \text{and} \quad \beta(i) = \sum_{j\preceq i} l_j = \alpha(i) + l_i, \tag{9.1}$$

with the convention $\alpha(\emptyset) = 0$, are the birth and death times of $i \in \mathcal{I}$. We assume that the offspring distribution p has a finite second moment and that

$$m = \sum_{k\geq 0} k p_k > 1 \ \text{(supercriticality)}.$$

Let us denote by $V_t \subset \mathcal{I}$ the set of individuals alive at time t :

$$V_t := \{i \in \mathcal{I} : \alpha(i) \leq t < \beta(i)\}, \qquad \text{and as before } N_t = \#V_t.$$

The supercriticality assumption on the reproduction law implies the persistence of the process with positive probability.

Proposition 9.1. *The population size process* $(N_t, t \geq 0)$ *survives with positive probability. Moreover, for any* $t \geq 0$,

$$\mathbb{E}(N_t) = \exp(\tau(m-1)t) \tag{9.2}$$

and

$$\frac{N_t}{\mathbb{E}(N_t)} \xrightarrow{t\to\infty} W \quad \text{a.s. and in } \mathbb{L}^2,$$

where $W \in \mathbb{R}_+$ *is positive on the survival event.*

The proof uses the generator of N and the martingale $N_t/\mathbb{E}(N_t)$. It is left to the reader.

The continuous time Galton-Watson genealogy $\mathcal{T}$ is defined as the (random) subset of $\mathcal{I} \times \mathbb{R}_+$ such that $(i,t) \in \mathcal{T}$ if and only if $i \in V_t$.

We define now the branching Markov process along this genealogy $\mathcal{T}$. We use the shift operator θ for such trees and $\theta_{(i,t)}\mathcal{T}$ is the subtree of $\mathcal{T}$ rooted in (i,t).

Definition 9.2. Let $X = (X_t, t \geq 0)$ be a càdlàg $\mathcal{X}$-valued strong Markov process and $\mu \in \mathcal{P}(\mathcal{X})$. Let $(P^{(k)}(x, dx_1 \ldots dx_k), k \geq 1)$ be a family of transitions probabilities from $\mathcal{X}$ to $\mathcal{X}^k$.

The continuous time branching Markov process $X_{\mathcal{T}} = (X_t^i, (i,t) \in \mathcal{T})$ indexed by $\mathcal{T}$, the underlying trait dynamics X and starting distribution μ, is defined conditionally on $\mathcal{T}$ recursively as follows:

(i) $X^\emptyset = (X_t^\emptyset, t \in [0, \beta(\emptyset)))$ is distributed as $(X_t, t \in [0, \beta(\emptyset)))$ with X_0 distributed according μ.
(ii) Conditionally on $X^\emptyset$, the initial traits of the first generation of offspring $(X^i_{\alpha(i)}, 1 \leq i \leq A(\emptyset))$ are distributed as $P^{(A(\emptyset))}(X^\emptyset_{\beta(\emptyset)}, dx_1 \ldots dx_{A(\emptyset)})$.
(iii) Conditionally on $X^\emptyset$, $A(\emptyset)$, $\beta_\emptyset$ and $(X^i_{\alpha(i)}, 1 \leq i \leq A(\emptyset))$, the tree-indexed Markov processes $(X^{ij}_{\alpha(i)+t}, (j,t) \in \theta_{(i,\alpha(i))}\mathcal{T})$ for $1 \leq i \leq A(\emptyset)$ are independent and, respectively, distributed as X with starting distribution $\delta_{X^i_{\alpha(i)}}$.

There is no spatial structure on the genealogical tree and without loss of generality, we assume that the marginal measures of $P^{(k)}(x, dx_1 \ldots dx_k)$ are identical. It can be achieved simply by a uniform permutation of the traits of the offspring.

Following the previous sections, we give a pathwise representation of the point measure-valued process defined at time t by

$$Z_t = \sum_{i \in V_t} \delta_{X_t^i}. \tag{9.3}$$

The dynamics of Z is given by the following stochastic differential equation. Let $N(ds, di, dk, d\theta)$ be a Poisson point measure on $\mathbb{R}_+ \times \mathbf{I} \times \mathbb{N} \times [0,1]$ with intensity $\tau ds n(di) p(dk) d\theta$ where $n(di)$ is the counting measure on $\mathbf{I}$ and $p(dk) = \sum_{l \in \mathbb{N}} p_l \delta_l(dk)$ is the offspring distribution. Let L be the infinitesimal generator of X. Then for test functions $f : (t,x) \mapsto f_t(x)$ in $C_b^{1,0}(\mathbb{R}_+ \times \mathcal{X}, \mathbb{R})$ such that $\forall t \in \mathbb{R}_+, f_t \in D(L)$, we have

$$\begin{aligned} \langle Z_t, f_t \rangle = {} & f_0(X_0^\emptyset) + \int_0^t \int_{\mathbb{R}_+} (Lf_s(x) + \partial_s f_s(x))\, ds Z_s(dx) + M_t^f \\ & + \int_0^t \int_{\mathbf{I} \times \mathbb{N} \times [0,1]} \mathbf{1}_{\{i \in V_{s-}\}} \left(\sum_{j=1}^k f_s(F_j^{(k)}(X^i_{s_-}, \theta)) - f_s(X^i_{s_-}) \right) N(ds, di, dk, d\theta), \end{aligned} \tag{9.4}$$

where M_t^f is a martingale and $(F_j^{(k)}(x, \Theta) : j = 1 \ldots k)$ is a random vector distributed like $P^{(k)}(x, dx_1 \ldots dx_k)$ when Θ is uniform in $[0,1]$.

9.2 Long time behavior

We are now interested in studying the long time behavior of the branching Markov process Z. We will show that it is deduced from the knowledge of the long time behavior of a well-chosen one-dimensional auxiliary Markov process. In particular, the ergodicity of the auxiliary process will give a sufficient condition in the applications, to obtain a limit as time goes to infinity.

Let us recall from Proposition 9.1 that the expectation at time t and the long time behavior of the population size process N are known.

9.2.1 *Many-to-one formula*

We introduce the auxiliary Markov process Y with infinitesimal generator given by

$$Af(x) = Lf(x) + \tau m \int_{\mathcal{X}} \big(f(y) - f(x)\big) Q(x, dy)$$

for $f \in D(L)$ and

$$Q(x, dy) := \frac{1}{m} \sum_{k \geq 0} k p_k P^{(k)}(x, dy \mathcal{X}^{k-1}).$$

In words, Y follows the dynamics of X with additional jumps at rate τm whose distribution is given by the size biased transition probability measure Q.

Proposition 9.3. *For $t \geq 0$ and for any non-negative measurable function $f \in \mathcal{B}(\mathbb{D}([0,t], \mathcal{X}))$ and $t \geq 0$, we have*

$$\mathbb{E}_\mu \left(\sum_{i \in V_t} f(X_s^i,\ s \leq t) \right) = \mathbb{E}(N_t)\, \mathbb{E}_\mu(f(Y_s,\ s \leq t)) = e^{\tau(m-1)t}\, \mathbb{E}_\mu(f(Y_s,\ s \leq t)), \tag{9.5}$$

where (with a slight abuse) X_s^i is the trait of the ancestor of $i \in V_t$ living at time s.

To prove such a formula in the particular case $f(x_s, s \leq t) = f(x_t)$, one can use Itô's calculus and follow Section 8.2 and conclude with a monotone class argument. Here we prove the general statement using the following Girsanov type formula. In the rest of this section, the random jumps $\tilde{T}_k$ and T_k of the Poisson point processes on $\mathbb{R}^+$ that we consider are ranked in increasing order.

Lemma 9.4. *Let $\{(\tilde{T}_k, \tilde{A}_k) : k \geq 0\}$ be a Poisson point process with intensity $\tau m\, ds\, \tilde{p}(dk)$ on $\mathbb{R}_+ \times \mathbb{N}$, where*

$$\tilde{p}(\{k\}) = k p_k / m.$$

Then, for any $t \geq 0$ and $q \geq 0$ and any non-negative measurable function g on $(\mathbb{R}_+ \times \mathbb{N})^{q+1}$:

$$\begin{aligned}
&\mathbb{E}\left(g((\tilde{T}_k, \tilde{A}_k) : k \leq q)\mathbb{1}_{\tilde{T}_q \leq t < \tilde{T}_{q+1}}\right) \\
&\quad = \mathrm{e}^{-\tau(m-1)t}\,\mathbb{E}\left(g((T_k, A_k) : k \leq q)\mathbf{1}_{\{T_q \leq t < T_{q+1}\}} \prod_{k \leq q} A_k\right),
\end{aligned}$$

where $\{(T_k, A_k) : k \geq 0\}$ is a Poisson point process on $\mathbb{R}_+ \times \mathbb{N}$ with intensity $\tau\, ds\, p(dk)$. Thus, for any measurable non-negative function h,

$$\begin{aligned}
&\mathbb{E}\left(h((\tilde{T}_k, \tilde{A}_k) : k \geq 0,\ \tilde{T}_k \leq t)\right) \\
&\quad = \mathrm{e}^{-\tau(m-1)t}\,\mathbb{E}\left(h((T_k, A_k) : k \geq 0,\ T_k \leq t) \prod_{T_k \leq t} A_k\right). \qquad (9.6)
\end{aligned}$$

Proof. Let $q \geq 0$ and remark that

$$g((\tilde{T}_k, \tilde{A}_k) : k \leq q) = G_q(\tilde{T}_0, \tilde{T}_1 - \tilde{T}_0, \ldots, \tilde{T}_q - \tilde{T}_{q-1}, \tilde{A}_0, \tilde{A}_1, \ldots, \tilde{A}_q),$$

for some non-negative functions $(G_q, q \in \mathbb{N})$. Using that $\tilde{T}_0$ and $(\tilde{T}_{k+1} - \tilde{T}_k : k \geq 0)$ are i.i.d. exponential random variables with parameter τm, we deduce that

$$\begin{aligned}
&\mathbb{E}[g((\tilde{T}_k, \tilde{A}_k) : k \leq q)\mathbb{1}_{\tilde{T}_q \leq t < \tilde{T}_{q+1}}] \\
&= \int_{\mathbb{R}_+^{q+2}} \sum_{n_0, \ldots, n_q} (\tau m)^{q+2}\, \mathrm{e}^{-\tau m(t_0 + \ldots + t_{q+1})}\, G_q(t_0, \ldots, t_q, n_0, \ldots, n_q) \\
&\qquad\qquad \times \prod_{k=0}^{q} \frac{p_{n_k} n_k}{m}\, \mathbb{1}_{\{\sum_{k=0}^{q} t_k \leq t < \sum_{k=0}^{q+1} t_k\}} dt_0 \ldots dt_{q+1} \\
&= \int_{\mathbb{R}_+^{q+1}} \sum_{n_0, \ldots, n_q} \tau^{q+1}\, \mathrm{e}^{-\tau t}\, G_q(t_0, \ldots, t_q, n_0, \ldots, n_q)\, \mathrm{e}^{-\tau(m-1)t} \\
&\qquad\qquad \times \prod_{k=0}^{q} n_k\, p_{n_k}\, \mathbb{1}_{\{\sum_{k=0}^{q} t_k \leq t\}} dt_0 \ldots dt_q,
\end{aligned}$$

which yields the first result. The second one is obtained by summing over q and forgetting the last point of the PPP. □

Proof of Proposition 9.3. We give here the main steps of the proof. We recall that the random variables $(A(i), l(i))$ have been defined for $i \in \mathbf{I}$. Let us now introduce the point process describing the birth times and number of offspring of the ancestral lineage of i:

$$\Lambda^i := \{(\beta(j), A(j)) : j \preceq i\} \qquad (i \in \mathbf{I}).$$

We stress that for any $q \geq 0$, the processes $((X^i, \Lambda^i), i \in (\mathbb{N}^*)^q)$ corresponding to individual labels with length q, are identically distributed (but dependent). They are distributed like (X', Λ_q), where

- $\Lambda_q = \{(T_k, A_k) : k \leq q\}$ and $\mathit{\Lambda} = \{(T_k, A_k) : k \geq 0\}$ is a Poisson point process on $\mathbb{R}_+ \times \mathbb{N}$ with intensity $\tau ds p(dk)$ (with T_k ranked in increasing order).
- Conditionally on $\Lambda = \{(t_k, n_k) : k \geq 0\}$ for $n_k \geq 1$, X' is the time non-homogeneous Markov process such that
  - at time t_i, X' jumps and the transition probability is given by $P^{(n_i)}(x, dy\mathcal{X}^{n_i-1})$;
  - during the time intervals $[t_i, t_{i+1})$, the infinitesimal generator of X' is L.

We denote by $|i|$ the length of the label i. We can now compute

$$\begin{aligned}
&\sum_{i\in\mathbf{I}} \mathbb{E}_\mu\big(g(\Lambda^i)f(X^i_s : s \leq t)\mathbf{1}_{\{i\in V_t\}}\big) \\
&= \sum_{i\in\mathbf{I}}\sum_{q\in\mathbb{N}} \mathbf{1}_{\{|i|=q\}}\mathbb{E}_\mu\big(g(\Lambda^i)\mathbb{E}_\mu(f(X^i_s : s \leq t)|\Lambda^i)\mathbf{1}_{\{\alpha(i)\leq t<\beta(i);\ \forall k=1,\ldots,q:\ A(i_1,\ldots,i_{k-1})\geq i_k\}}\big) \\
&= \sum_{i\in\mathbf{I}}\sum_{q\in\mathbb{N}} \mathbf{1}_{\{|i|=q\}}\mathbb{E}_\mu\big(g(\Lambda_q)\mathbb{E}_\mu(f(X'_s : s \leq t)|\Lambda)\mathbf{1}_{\{T_{q-1}\leq t<T_q;\ \forall k=0,\ldots,q-1:\ A_k\geq i_{k+1}\}}\big) \\
&= \sum_{i\in\mathbf{I}}\sum_{q\in\mathbb{N}} \mathbb{1}_{\{|i|=q\}}\mathbb{E}_\mu\big(F_f(\Lambda_q)\mathbf{1}_{\{T_{q-1}\leq t<T_q;\ \forall k=0,\ldots,q-1:\ A_k\geq i_{k+1}\}}\big),
\end{aligned}$$

where we have denoted $F_f(\Lambda^q) = g(\Lambda^q)\mathbb{E}_\mu(f(X'_s : s \leq t)|\Lambda^q)$ and used the convention $T_{-1} = 0$. Adding that

$$\begin{aligned}
&\sum_{q\in\mathbb{N}}\sum_{i\in\mathbf{I}} \mathbf{1}_{\{|i|=q\}}F_f(\Lambda_q)\mathbb{1}_{\{T_{q-1}\leq t<T_q;\ \forall k=0,\ldots,q-1:\ A_k\geq i_{k+1}\}} \\
&\quad = \sum_{q\in\mathbb{N}} F_f(\Lambda_q)\#\{i \in \mathbf{I} : |i| = q,\ \forall k = 0, \ldots, q-1 : i_{k+1} \leq A_k\}\mathbb{1}_{T_{q-1}\leq t<T_q} \\
&\quad = F_f((T_k, A_k) : k \geq 0, T_k \leq t) \prod_{T_k\leq t} A_k
\end{aligned}$$

and using (9.6) and (9.2), we get

$$\sum_{i\in\mathbf{I}} \mathbb{E}_\mu\big(g(\Lambda^i)f(X^i_s : s \le t)\mathbf{1}_{\{i\in V_t\}}\big) = \mathbb{E}_\mu\left(F_f((T_k,A_k) : k \ge 0, T_k \le t)\prod_{T_k\le t} A_k\right)$$
$$= e^{\tau(m-1)t}\mathbb{E}_\mu\left(F_f((\tilde{T}_k,\tilde{A}_k) : k \ge 0, T_k \le t)\right).$$

Finally, we combine the definitions of X' and Y to conclude, recalling that $\{(\tilde{T}_k,\tilde{A}_k) : k \ge 0\}$ is a Poisson point process with intensity $\tau m ds\tilde{p}(dk)$. ☐

9.2.2 Law of large numbers

Let us now describe the asymptotic distribution of traits within the population (see [6] for details).

Theorem 9.5. *Assume that for some bounded continuous function f, the auxiliary process satisfies*

$$\mathbb{E}_x(f(Y_t)) \overset{t\to\infty}{\longrightarrow} \pi(f) \tag{9.7}$$

for every $x \in \mathcal{X}$ and π a probability measure on $\mathcal{X}$.

Then, for every probability distribution μ on $\mathcal{X}$,

$$\lim_{t\to\infty} \frac{\mathbb{1}_{\{N_t>0\}}}{N_t}\sum_{i\in V_t} f\big(X^i_t\big) = \mathbb{1}_{\{W>0\}}\pi(f) \tag{9.8}$$

in $\mathbb{P}_\mu$ probability.

This result implies in particular that for such a function f,

$$\lim_{t\to+\infty} \mathbb{E}\big[f(X^{U(t)}_t) \,|\, N_t > 0\big] = \pi(f), \tag{9.9}$$

where $U(t)$ stands for an individual chosen at random in the set V_t of individuals alive at time t.

Condition (9.7) deals with the ergodic behavior of Y and will be obtained for regular classes of functions f, see below for an example.

Main ideas of the proof. Let f be a non-negative function bounded by 1 and define

$$G^i_t := f(X^i_t) - \pi(f)$$

and let us prove that

$$A_t := \mathbb{E}\left(\left(\sum_{i\in V_t} G_t^i\right)^2\right) \ll \mathbb{E}(N_t)^2$$

Indeed we can write $A_t = B_t + C_t$, where

$$B_t := \mathbb{E}\left(\sum_{i\in V_t}(G_t^i)^2\right) \quad \text{and} \quad C_t := \mathbb{E}\left(\sum_{i\neq j\in V_t} G_t^i G_t^j\right).$$

We easily remark from (9.2) that $B_t \leq \mathbb{E}(N_t) \ll \mathbb{E}(N_t)^2$. Let us now deal with C_t and use the most recent common ancestor of i and j:

$$C_t = \mathbb{E}\left(\sum_{\substack{u,(u,k_1),(u,k_2)\in\mathcal{I},\\ k_1\neq k_2}} \mathbf{1}_{\{\beta(u)<t\}}\,\mathbb{E}\left(\sum_{i\in V_t:i\succeq(u,k_1)}\sum_{j\in V_t:j\succeq(u,k_2)} \mathbb{E}\left(G_t^iG_t^j\middle|\,\beta(u),X_{\beta(u)}^{(u,k_1)},X_{\beta(u)}^{(u,k_2)}\right)\right)\right)$$

The key point is that on the event $\{\beta(u) < t,\ (u,k_1) \in \mathcal{I}, (u,k_2) \in \mathcal{I}\}$,

$$\begin{aligned}&\sum_{i\in V_t:i\succeq(u,k_1)}\sum_{j\in V_t:j\succeq(u,k_2)} \mathbb{E}\left(G_t^iG_t^j\middle|\,\beta(u),X_{\beta(u)}^{(u,k_1)},X_{\beta(u)}^{(u,k_2)}\right)\\ &\qquad= \sum_{i\in V_t:i\succeq(u,k_1)} \mathbb{E}\left(G_t^i\middle|\,\beta(u),X_{\beta(u)}^{(u,k_1)}\right) \times \sum_{j\in V_t:j\succeq(u,k_2)} \mathbb{E}\left(G_t^j\middle|\,\beta(u),X_{\beta(u)}^{(u,k_2)}\right)\end{aligned}$$

by the branching property. Moreover the many-to-one formula (9.5) ensures that

$$\sum_{i\in V_t:i\succeq uk_1} \mathbb{E}\left(G_t^i\middle|\,\beta(u),X_{\beta(u)}^{(u,k_1)}\right) = \mathbb{E}(N_t)\mathbb{E}_{X_{\beta(u)}^{(u,k_1)}}\left(f(Y_{t-\beta(u)}) - \mu(f)\right)$$

on the event $\{\beta(u) < t,\ (u,k_1) \in \mathcal{I}, (u,k_2) \in \mathcal{I}\}$. The convergence (9.7) ensures that the second term in the right-hand side tends to zero for $\beta(u)$ fixed. This convergence depends on the initial condition. Nevertheless this difficulty can be overcome by proving (see [6]) that the common ancestor of two individuals lives almost-surely at the beginning of the continuous time Galton-Watson tree. This fact also allows to sum over $(u,k_1) \in \mathcal{I}, (u,k_2) \in \mathcal{I}$ and obtain that $C_t \ll \mathbb{E}(N_t)^2$ by dominated convergence arguments. Recalling that $N_t/\mathbb{E}(N_t)$ converges to W in $\mathbb{L}^2$ yields the result. □

9.3 Application to splitting diffusions

For the sake of simplicity, we assume in this section that the branching events are binary ($p(dk) = \delta_2(dk)$), so that the genealogical tree is the Yule tree. We describe a population of infected cells undergoing a binary division, as in the previous chapter for constant division rates. When a division occurs, a random fraction F is inherited by a daughter cell and the rest by the other daughter cell. But in contrast with the previous chapter, the process X may not be a branching process, which allows, for example, to take into account resources limitation for the parasites living in the cell. Here, X is a diffusion with infinitesimal generator

$$Lf(x) = r(x)f'(x) + \frac{\sigma(x)^2}{2}f''(x)$$

We refer to [6] for other applications, such as cellular aging.

The infinitesimal generator of the auxiliary process Y is characterized for $f \in \mathcal{C}_b^2(\mathbb{R}, \mathbb{R})$ by:

$$Af(x) = r(x)f'(x) + \frac{\sigma(x)^2}{2}f''(x) + 2\tau \int_0^1 \big(f(\theta x) - f(x)\big)\mathbb{P}(F \in d\theta). \tag{9.10}$$

Proposition 9.6. *Assume that Y is a Feller process which is irreducible, i.e. there exists a probability measure ν on $\mathbb{R}$ such that for any measurable set B and $x \in \mathbb{R}$,*

$$\nu(B) > 0 \Rightarrow \int_0^\infty \mathbb{P}_x(Y_t \in B)dt > 0.$$

Assume also that there exists $K \geq 0$, such that for every $|x| \geq K$, $r(x) \leq \tau'|x|$ for some $\tau' < \tau$.

Then, Y is ergodic with stationary probability π and we have

$$\frac{\mathbb{1}_{\{N_t>0\}}}{N_t}\#\{i \in V_t : X_t^i \in A\} \overset{t\to\infty}{\longrightarrow} \pi(A)$$

for every Borelian set A such that $\pi(\partial A) = 0$ and ∂A is the boundary of A.

Proof. Once we check that Y is ergodic, the second part comes from Theorem 9.5. The ergodicity of Y is based on Theorems 4.1 of [57] and 6.1 of [58]. Since Y is Feller and irreducible, the process Y admits a unique invariant probability measure π and is exponentially ergodic provided there exists a positive measurable function V such that $\lim_{x\to\pm\infty} V(x) = +\infty$ and for which:

$$\exists c > 0,\ d \in \mathbb{R},\ \forall x \in \mathbb{R},\ AV(x) \leq -cV(x) + d. \tag{9.11}$$

For $V(x) = |x|$ regularized on an ε-neighborhood of 0 ($0 < \varepsilon < 1$), we have:

$$\forall |x| > \varepsilon,\ AV(x) = \mathrm{sign}(x)r(x) + 2\tau|x|\mathbb{E}(F-1) = \mathrm{sign}(x)r(x) - \tau|x|, \tag{9.12}$$

as the distribution of F is symmetric with respect to $1/2$. Then, by assumption, there exist $\eta > 0$ and $K > \varepsilon$ such that

$$\forall x \in \mathbb{R},\ AV(x) \le -\eta V(x) + \Big(\sup_{|x|\le K} |r(x)| + \tau K\Big)\mathbb{1}_{\{|x|\le K\}}. \tag{9.13}$$

This implies (9.11) and the geometric ergodicity gives us that

$$\exists \beta > 0,\ B < +\infty,\ \forall t \in \mathbb{R}_+,\ \forall x \in \mathbb{R}, \quad \sup_{g\,/\,|g(u)|\le 1+|u|} \big|\mathbb{E}_x(g(Y_t)) - \langle \pi, g\rangle\big| \le B(1+|x|)\,\mathrm{e}^{-\beta t}.$$

The proof is complete. ☐

9.4 Some extensions

Following Chapter 3, we could consider a model for cell division with parasites where the growth of parasites is limited by the resources for the cells. The Markovian dynamics of the parasite population size could be described by a logistic Feller diffusion process. Since this process goes to extinction almost surely (or to a finite positive limit if the process is deterministic), Proposition 9.6 may be applied to derive the asymptotic distribution of the infection among the cell population. The construction of the model and the proofs are left to the reader.

On the other hand, let us note that the many-to-one formula (9.5) holds for f depending on time. Therefore the large numbers law (Theorem 9.5) can be extended to the case where Y isn't ergodic as soon as we can find some renormalization g_t such $g_t(Y_t)$ satisfies (9.7). We refer to [6] for an application when X is a branching Lévy process and in particular we recover the classical central limit theorem for branching Brownian motions.

Appendix A
Poisson point measures

In this appendix, we summarize the main definitions and results concerning the Poisson point measures. The reader can consult the two main books by Ikeda-Watanabe [41] and by Jacod-Shiryaev [42] for more details.

Definition A.1. Let $(E, \mathcal{E})$ be a measurable space and μ a σ-finite measure on this space. A (homogeneous) Poisson point measure N with intensity $\mu(dh)dt$ on $\mathbb{R}_+ \times E$ is a $(\mathbb{R}_+ \times E, \mathcal{B}(\mathbb{R}_+) \otimes \mathcal{E})$-random measure defined on a probability space $(\Omega, \mathcal{F}, \mathbb{P})$ which satisfies the following properties:

1. N is a counting measure: $\forall \hat{A} \in \mathcal{B}(\mathbb{R}_+) \otimes \mathcal{E}$, $\forall \omega \in \Omega$, $N(\omega, \hat{A}) \in \mathbb{N} \cup \{+\infty\}$.
2. $\forall \omega \in \Omega$, $N(\omega, \{0\} \times E) = 0$: no jump at time 0.
3. $\forall \hat{A} \in \mathcal{B}(\mathbb{R}_+) \otimes \mathcal{E}$, $\mathbb{E}(N(\hat{A})) = \nu(\hat{A})$, where $\nu(dt, dh) = \mu(dh)dt$.
4. If $\hat{A}$ and $\hat{B}$ are disjoint in $\mathcal{B}(\mathbb{R}_+) \otimes \mathcal{E}$ and if $\nu(\hat{A}) < +\infty$, $\nu(\hat{B}) < +\infty$, then the random variables $N(\hat{A})$ and $N(\hat{B})$ are independent.

The existence of such a Poisson point measure with intensity $\mu(dh)dt$ is proven in [42], for any σ-finite measure μ on $(E, \mathcal{E})$.

Let us remark that for any $A \in \mathcal{E}$ with $\mu(A) < \infty$ the process defined by

$$N_t(A) = N((0, t] \times A)$$

is a Poisson process with intensity $\mu(A)$.

Definition A.2. The filtration $(\mathcal{F}_t)_t$ generated by N is given by

$$\mathcal{F}_t = \sigma(N((0, s] \times A), \forall s \leq t, \forall A \in \mathcal{E}).$$

If $\hat{A} \in (s, t] \times \mathcal{E}$ and $\nu(\hat{A}) < \infty$, then $N(\hat{A})$ is independent of $\mathcal{F}_s$.

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Let us first assume that the measure μ is finite on $(E, \mathcal{E})$. Then $(N_t(E), t \geq 0)$ is a Poisson process with intensity $\mu(E)$. The point measure is associated with a compound Poisson process. Indeed, let us write

$$\mu(dh) = \mu(E)\,\frac{\mu(dh)}{\mu(E)},$$

the decomposition of the measure μ as the product of the jump rate $\mu(E)$ and the jump amplitude law $\frac{\mu(dh)}{\mu(E)}$. Let us fix $T > 0$ and introduce $T_1, \ldots, T_\gamma$ the jump times of the process $(N_t(E), t \geq 0)$ between 0 and T. We know that the jump number γ is a Poisson variable with parameter $T\mu(E)$. Moreover, conditionally on γ, $T_1, \ldots, T_\gamma$, the jumps $(U_n)_{n=1,\ldots,\gamma}$ are independent with the same law $\frac{\mu(dh)}{\mu(E)}$. We can write in this case

$$N(dt, dh) = \sum_{n=1}^{\gamma} \delta_{(T_n, U_n)}.$$

Therefore, one can define for any measurable function $G(\omega, s, h)$ defined on $\Omega \times \mathbb{R}_+ \times E$ the random variable

$$\int_0^T \int_E G(\omega, s, h) N(\omega, ds, dh) = \sum_{n=1}^{\gamma} G(\omega, T_n, U_n).$$

In the following, we will forget the ω. Let us remark that $T \longrightarrow \int_0^T \int_E G(s, h)\, N(ds, dh)$ is a finite variation process which is increasing if G is positive. A main example is the case where $G(\omega, s, h) = h$. Then

$$X_T = \int_0^T \int_E h\, N(ds, dh) = \sum_{n=1}^{\gamma} U_n = \sum_{s \leq T} \Delta X_s$$

is the sum of the jumps between 0 and T.

Our aim now is to generalize the definition of the integral of G with respect to N when $\mu(E) = +\infty$. In this case, one can have an accumulation of jumps during the finite time interval $[0, T]$ and the counting measure N is associated with a countable set of points:

$$N = \sum_{n \geq 1} \delta_{(T_n, U_n)}.$$

We need additional properties on the process G.

Since μ is σ-finite, there exists an increasing sequence $(E_p)_{p \in \mathbb{N}}$ of subsets of E such that $\mu(E_p) < \infty$ for each p and $E = \cup_p E_p$. As before we can define $\int_0^T \int_{E_p} G(s, h) N(ds, dh)$ for any p.

We introduce the predictable σ-field $\mathcal{P}$ on $\Omega \times \mathbb{R}_+$ (generated by all left-continuous adapted processes) and define a predictable process $(G(s,h), s \in \mathbb{R}_+, h \in E)$ as a $\mathcal{P} \otimes \mathcal{E}$ measurable process.

Theorem A.3. *Let us consider a predictable process G(s, h) and assume that*

$$\mathbb{E}\left(\int_0^T \int_E |G(s,h)|\mu(dh)ds\right) < +\infty. \tag{A.1}$$

1) *The sequence of random variables* $\left(\int_0^T \int_{E_p} G(s,h)N(ds,dh)\right)_p$ *is Cauchy in* $\mathbb{L}^1$ *and converges to a* $\mathbb{L}^1$*-random variable that we denote by* $\int_0^T \int_E G(s,h)N(ds,dh)$. *It's an increasing process if G is non-negative. Moreover, we get*

$$\mathbb{E}\left(\int_0^T \int_E G(s,h)N(ds,dh)\right) = \mathbb{E}\left(\int_0^T \int_E G(s,h)\mu(dh)ds\right)$$

2) *The process* $M = (\int_0^t \int_E G(s,h)N(ds,dh) - \int_0^t \int_E G(s,h)\mu(dh)ds, t \leq T)$ *is a martingale.*

   The random measure

$$\tilde{N}(ds,dh) = N(ds,dh) - \mu(dh)ds$$

   is called the compensated martingale-measure of N.

3) *If we assume moreover that*

$$\mathbb{E}\left(\int_0^T \int_E G^2(s,h)\mu(dh)ds\right) < +\infty, \tag{A.2}$$

   then the martingale M is square-integrable with quadratic variation

$$\langle M\rangle_t = \int_0^t \int_E G^2(s,h)\mu(dh)ds.$$

Let us remark that when (A.1) holds, the random integral $\int_0^t \int_E G(s,h)N(ds,dh)$ can be defined without the predictability assumption on G but the martingale property of the stochastic integral $\int_0^t \int_E G(s,h)\tilde{N}(ds,dh)$ is only true under this assumption.

We can improve the condition under which the martingale (M_t) can be defined. The proof of the next theorem is tricky and consists in studying the $\mathbb{L}^2$-limit of the sequence of martingales $\int_0^t \int_{E_p} G(s,h)\tilde{N}(ds,dh)$ as p tends to infinity. Once again, this sequence is Cauchy in $\mathbb{L}^2$ and converges to a limit which is a square-integrable martingale. Let us recall that the quadratic variation of a square-integrable martingale M is the unique predictable process $\langle M\rangle$ such that $M^2 - \langle M\rangle$ is a martingale.

Theorem A.4. *Let us consider a predictable process G(s, h) satisfying* (A.2). *Then the process* $M = (\int_0^t \int_E G(s,h)\tilde{N}(ds,dh), t \leq T)$ *is a square-integrable martingale with quadratic variation*

$$\langle M\rangle_t = \int_0^t \int_E G^2(s,h)\mu(dh)ds.$$

If (A.2) is satisfied but not (A.1), the definition of M comes from a $\mathbb{L}^2$-limiting argument, as for the usual stochastic integrals. In this case the quantity $\int_0^t \int_E G(s,h)N(ds,dh)$ isn't always well defined and we are obliged to compensate.

Example. Let $\alpha \in (0,2)$. A symmetric α-stable process S can be written

$$S_t = \int_0^t \int_{\mathbb{R}} h\mathbf{1}_{\{0<|h|<1\}}\tilde{N}(ds,dh) + \int_0^t \int_{\mathbb{R}} h\mathbf{1}_{\{|h|\geq 1\}}N(ds,dh), \tag{A.3}$$

where $N(ds,dh)$ is a Poisson point measure with intensity $\mu(dh)ds = \frac{1}{|h|^{1+\alpha}}dhds$. There is an accumulation of small jumps and the first term in the r.h.s. of (A.3) is defined as a compensated martingale. The second term corresponds to the big jumps, which are in finite number on any finite time interval.

If $\alpha \in (1,2)$, then $\int h \wedge h^2\mu(dh) < \infty$ and the process is integrable. If $\alpha \in (0,1)$, we only have that $\int 1 \wedge h^2\mu(dh) < \infty$ and the integrability of the process can fail.

Let us now consider a stochastic differential equation driven both by a Brownian term and a Poisson point measure. We consider a random variable X_0, a Brownian motion B and a Poisson point measure $N(ds,dh)$ on $\mathbb{R}_+ \times \mathbb{R}$ with intensity $\mu(dh)ds$. Let us fix some measurable functions b and σ on $\mathbb{R}$ and $G(x,h)$ and $K(x,h)$ on $\mathbb{R}\times\mathbb{R}$.

We consider a process $X \in \mathbb{D}(\mathbb{R}_+,\mathbb{R})$ such that for any $t > 0$,

$$\begin{aligned} X_t = X_0 &+ \int_0^t b(X_s)ds + \int_0^t \sigma(X_s)dB_s \\ &+ \int_0^t \int_{\mathbb{R}} G(X_{s-},h)N(ds,dh) + \int_0^t \int_{\mathbb{R}} K(X_{s-},h)\tilde{N}(ds,dh). \end{aligned} \tag{A.4}$$

To give a sense to the equation, one expects that for any $T > 0$,

$$\mathbb{E}\left(\int_0^T \int_{\mathbb{R}} |G(X_s,h)|\mu(dh)ds\right) < +\infty \ ; \ \mathbb{E}\left(\int_0^T \int_{\mathbb{R}} K^2(X_s,h)\mu(dh)ds\right) < +\infty.$$

We refer to [41] Chapter IV-9 for general existence and uniqueness assumptions (generalizing the Lipschitz continuity assumptions asked in the case without jump).

Let us assume that a solution of (A.4) exists. The process X is a left-limited and right-continuous semimartingale. A standard question is to ask when the process $f(X_t)$ is a semimartingale and to know its Doob-Meyer decomposition. For a smooth function f, there is an Itô's formula generalizing the usual one stated for continuous semimartingales.

Recall (cf. Dellacherie-Meyer VIII-25 [24]) that for a function $a(t)$ with bounded variation, the change of variable formula gives that for a C^1-function f,

$$f(a(t)) = f(a(0)) + \int_{(0,t]} f'(a(s))da(s) + \sum_{0<s\le t} (f(a(s)) - f(a(s^-)) - \Delta a(s) f'(a(s^-))).$$

We wish to replace a by a semimartingale. We have to add smoothness to f and we will get two additional terms in the formula because of the two martingale terms. As in the continuous case, we assume that the function f is C^2.

Theorem A.5 (see [41] Theorem 5.1 in Chapter II). *Let f a C^2-function. Then $f(X)$ is a semimartingale and for any t,*

$$\begin{aligned} f(X_t) = f(X_0) &+ \int_0^t f'(X_s)b(X_s)ds + \int_0^t f'(X_s)\sigma(X_s)dB_s \\ &+ \frac{1}{2}\int_0^t f''(X_s)\sigma^2(X_s)ds \\ &+ \int_0^t \int_{\mathbb{R}} (f(X_{s-} + G(X_{s-},h)) - f(X_{s-}))N(ds,dh) \\ &+ \int_0^t \int_{\mathbb{R}} (f(X_{s-} + K(X_{s-},h)) - f(X_{s-}))\tilde{N}(ds,dh) \\ &+ \int_0^t \int_{\mathbb{R}} \big(f(X_s + K(X_s,h)) - f(X_s) - K(X_s,h)f'(X_s)\big)\, \mu(dh)ds. \end{aligned} \tag{A.5}$$

Corollary A.6. *Under suitable integrability and regularity conditions on b, σ, G, K and μ, the process X is a Markov process with extended generator: for any C^2-function f, for $x \in \mathbb{R}$,*

$$\begin{aligned} Lf(x) = b(x)f'(x) + \frac{1}{2}\sigma^2(x)f''(x) &+ \int_{\mathbb{R}} (f(x + G(x,h)) - f(x))\, \mu(dh) \\ &+ \int_{\mathbb{R}} \big(f(x + K(x,h)) - f(x) - K(x,h)f'(x)\big)\, \mu(dh). \end{aligned} \tag{A.6}$$

Example. Let us study the case where

$$X_t = X_0 + \int_0^t b(X_s)ds + \int_0^t \sigma(X_s)dB_s + S_t,$$

where S is the stable process introduced in (A.3). Let us consider a C^2-function f. Then $f(X)$ is a semimartingale and writes

$$\begin{aligned}
f(X_t) &= f(X_0) + M_t + \int_0^t f'(X_s)b(X_s)ds + \frac{1}{2}\int_0^t f''(X_s)\sigma^2(X_s)ds \\
&\quad + \int_0^t \int_{\mathbb{R}} (f(X_{s-} + h\mathbf{1}_{\{|h|>1\}}) - f(X_{s-}))\frac{1}{|h|^{1+\alpha}} dhds \\
&\quad + \int_0^t \int_{\mathbb{R}} \big(f(X_{s-} + h\mathbf{1}_{\{|h|\le 1\}}) - f(X_{s-}) \\
&\quad - h\mathbf{1}_{\{|h|\le 1\}} f'(X_{s-})\big) \frac{1}{|h|^{1+\alpha}} dhds \\
&= f(X_0) + M_t + \int_0^t f'(X_s)b(X_s)ds + \frac{1}{2}\int_0^t f''(X_s)\sigma^2(X_s)ds \\
&\quad + \int_0^t \int_{\mathbb{R}} \big(f(X_{s-} + h) - f(X_{s-}) - h\mathbf{1}_{\{|h|\le 1\}} f'(X_{s-})\big) \frac{1}{|h|^{1+\alpha}} dhds,
\end{aligned}$$

where M is a martingale.

Let us come back to the general case and apply Itô's formula (A.7) to $f(x) = x^2$:

$$\begin{aligned}
X_t^2 = X_0^2 &+ \int_0^t 2X_s b(X_s)ds + \int_0^t 2X_{s-}\sigma(X_{s-})dB_s + \int_0^t \sigma^2(X_s)ds \\
&+ \int_0^t \int_{\mathbb{R}} (2X_{s-}G(X_{s-}, h) + (G(X_{s-}, h))^2)N(ds, dh) \\
&+ \int_0^t \int_{\mathbb{R}} (2X_{s-}K(X_{s-}, h) + (K(X_{s-}, h))^2)\tilde{N}(ds, dh) \\
&+ \int_0^t \int_{\mathbb{R}} (K(X_{s-}, h))^2 \mu(dh)ds.
\end{aligned} \tag{A.7}$$

On the other hand, since

$$X_t = X_0 + M_t + A_t,$$

where M is square-integrable and A has finite variation, then

$$X_t^2 = X_0^2 + N_t + \int_0^t 2X_{s-}dA_s + \langle M \rangle_t.$$

Doob-Meyer's decomposition allows us to identify the martingale parts and the finite variation parts in the two previous decompositions and therefore

$$\langle M \rangle_t = \int_0^t \sigma^2(X_s)ds + \int_0^t \int_{\mathbb{R}} (G^2(X_{s-}, h) + K^2(X_{s-}, h))\mu(dh)ds.$$

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