Branching processes in random environment, frequent mutations in eco-evolution and evolution of sexual preferences

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Chapter 1

References and organization of the manuscript

This report presents a synthesis of my work since the end of my PhD, as well as some open questions I would like to explore. The primary objective that guides my research is to develop new probabilistic models taking better into account the interactions and diversity of individuals in populations and ecosystems, to understand better their dynamics. My research has so far focused on the development and theoretical study of individual-based stochastic models with interactions and variable environments. These models, mainly applied to the study of population dynamics, were motivated by questions in genetics, ecology and evolution. The manucript consists of three chapters. Each of them begins with an introduction and a detailed bibliography on the theme addressed, and ends with a description of the perspectives that follow from the work presented.

The following references, written during the course of my PhD thesis, will not be discussed:

- [BPS13]: V. Bansaye, J-C. Pardo, C. Smadi, On the extinction of continuous state branching processes with catastrophes, *Electronic Journal of Probability*, 18, 2013,
- [Sma15]: C. Smadi, An eco-evolutionary approach of adaptation and recombination in a large population of varying size, *Stochastic Processes and their Applications*, 125(5), 2015
- [BSS17]: R. Brink-Spalink, C. Smadi, Genealogies of two linked neutral loci after a selective sweep in a large population of stochastically varying size, *Advances in Applied Probability*, 49(1), 2017.

The works presented in Chapter 2 mainly address the following question: does the population under study survive with positive probability, and if not, what is its extinction rate at large times? The framework is that of branching processes in random environment. All individuals die and give birth independently of each other, and with a law depending on the current environment in which the population is living. The main assumption is that the random environment has independent and identically distributed (iid) increments, and is thus given by a random walk or a Lévy process depending on whether the time is discrete or continuous. We will also mention some works where

the law of the random environment depends on the population state (but for a class of possible environments much smaller). The following references will be described or mentioned in Chapter 2 of this manuscript:

- [PPS16]: S. Palau, J-C. Pardo, C. Smadi, Asymptotic behaviour of exponential functionals of Lévy processes with applications to random processes in random environment, *ALEA Lat. Am. J. Probab. Math. Stat.*, 13(2), 2016,
- [DSV20]: C. Dong, C. Smadi, V.A. Vatutin, Critical branching processes in random environment and Cauchy domain of attraction, *ALEA Lat. Am. J. Probab. Math. Stat.*, 17(2), 2020,
- [BPS21]: V. Bansaye, J-C. Pardo, C. Smadi, Extinction rate of continuous state branching processes in critical Lévy environments, *ESAIM: Probability and Statistics*, 25, 2021,
- [MS21]: A. Marguet, C. Smadi, Long time behaviour of continuous-state nonlinear branching processes with catastrophes, *Electronic Journal of Probability*, 26, 2021.
- [MS20]: A. Marguet, C. Smadi, Parasite infection in a cell population with deaths, *arXiv preprint arXiv:2010.16070*, 2020,
- [Sma22]: C. Smadi, Parasite infection in a cell population with deaths and reinfections, *MathS in Action*, 2022.

Chapter 3 deals with eco-evolutionary models with mutations frequent enough that the time scales of ecology and evolution cannot be separated. We will see that it may give rise to various and sometime unexpected evolutionary trajectories. This chapter will be based on the following references:

- [Sma17]: C. Smadi, The effect of recurrent mutations on genetic diversity in a large population of varying size, *Acta Applicandae Mathematicae*, 149(1), 2017,
- [BS17]: S. Billiard, C. Smadi, The interplay of two mutations in a population of varying size: a stochastic eco-evolutionary model for clonal interference, *Stochastic Processes and their Applications*, 127(3), 2017,
- [BCS19]: A. Bovier, L. Coquille, C. Smadi, Crossing a fitness valley as a metastable transition in a stochastic population model, *The Annals of Applied Probability*, 29(6), 2019,
- [BS20]: S. Billiard, C. Smadi, Stochastic dynamics of three competing clones: Conditions and times for invasion, coexistence, and fixation, *The American Naturalist*, 195(3), 2020,
- [GCS21]: A. Gonzalez Casanova, C. Smadi, Multidimensional Λ-Wright-Fisher processes with general frequency-dependent selection, *Journal of Applied Probability*, 57, 2021,
- [CKS21]: L. Coquille, A. Kraut, C. Smadi, Stochastic individual-based models with power law mutation rate on a general finite trait space, *Electronic Journal of Probability*, 26, 2021.

The last chapter will be concerned with mating preferences. Up to now, I mainly explored the questions of evolution and ecological implications of assortative mating, but I recently got interested in the case of disassortative mating, on the occasion of the PhD Thesis of Ludovic Maisonneuve. The following works will be described in Chapter 4:

- [CCLS18]: C. Coron, M. Costa, H. Leman, C. Smadi, A stochastic model for speciation by mating preferences, *Journal of Mathematical Biology*, 76(6), 2018,
- [SLL18]: C. Smadi, H. Leman, V. Llaurens, Looking for the right mate in diploid species: How does genetic dominance affect the spatial differentiation of a sexual trait?, *Journal of Theoretical Biology*, 447, 2018,
- [CCL+19]: C. Coron, M. Costa, F. Laroche, H. Leman, C. Smadi, Emergence of homogamy in a two-loci stochastic population model, *ALEA Lat. Am. J. Probab. Math. Stat.*, 2020
- [MBJ+21]: L. Maisonneuve, T. Beneteau, M. Joron, C. Smadi, V. Llaurens, When do opposites attract? A model uncovering the evolution of disassortative mating, *The American Naturalist*, 198, 2021,
- [MSL22]: L. Maisonneuve, C. Smadi, V. Llaurens, Evolutionary origins of sexual dimorphism: Lessons from female-limited mimicry in butterflies, *Evolution*, 2022
- [MSL21]: L. Maisonneuve, M. Elias, C. Smadi, V. Llaurens, The limits of evolutionary convergence in sympatry: reproductive interference and developmental constraints leading to local diversity in aposematic signals, bioRxiv, 2021,

Finally, the following references will not be addressed in this document, in order to maintain a coherent picture and to limit the size of the manuscript:

- [SV16]: C. Smadi, V.A. Vatutin, Reduced two-type decomposable critical branching processes with possibly infinite variance, *Markov Processes and Related Fields*, 21(2), 2016,
- [VABS18]: M. Voinson, A. Alvergne, S. Billiard, C. Smadi, Stochastic dynamics of an epidemic with recurrent spillovers from an endemic reservoir, *Journal of Theoretical Biology*, 457, 2018,
- [LSA+19]: F. Lavallée, C. Smadi, I. Alvarez, B. Reineking, F-M. Martin, F. Dommanget, S. Martin, A stochastic individual-based model for the growth of a stand of Japanese knotweed including mowing as a management technique, *Ecological Modelling*, 413, 2019,
- [CSKC19]: T. Cordonnier, C. Smadi, G. Kunstler, B. Courbaud, Asymmetric competition, ontogenetic growth and size inequality drive the difference in productivity between two-strata and one-stratum forest stands, *Theoretical Population Biology*, 130, 2019,
- [SV21a]: C. Smadi, V.A. Vatutin, Critical branching processes in random environment with immigration: survival of a single family, *Extremes*, 24(3), 2021,

- [SV21b]: C. Smadi, V.A. Vatutin, Critical branching processes in random environment with immigration: the size of the only surviving family, *Branching Processes and Related Issues*, Collected papers. On the occasion of the 75th birthday of Andrei Mikhailovich Zubkov and 70th birthday of Vladimir Alekseevich Vatutin, 2022.
- [VSB22]: M. Voinson, C. Smadi, S. Billiard, How does the host community structure affect the epidemiological dynamics of emerging infectious diseases?, *Ecological Modelling*, 472, 2022.

Chapter 2

Extinction of branching processes in random environment

2.1 Branching processes in random environment

2.1.1 Galton-Watson processes

These processes have their origin in the study of the extinction probabilities of family names in Great Britain in the nineteenth century. The following presentation is inspired by the work of Athreya and Ney [AN72]. Let ξ be an integer-valued random variable with law

$$\mathbb{P}(\xi = k) = p_k, \quad k \geq 0,$$

and Y_n be the population size at time n. The generation $n+1$ is composed of the descendants of the individuals of the generation n, and conditionally to Y_n, the individual $(1 \leq i \leq Y_n)$ of the generation n generates $\xi(i,n)$ descendants where the variables $\xi(i,n)$ and $\xi(j,n)$ are independent if $i \neq j$, and of the same law as ξ, which can be written as follows:

$$Y_{n+1} = \sum_{i=1}^{Y_n} \xi_{(i,n)}.$$

This procedure is then iterated, the variables $\xi(i,n)$ being independent of the variables $\xi(j,p)$ for $i \neq j$ or $p \neq n$. The Markov chain $(Y_n, n \geq 0)$ is called Galton-Watson process. If $Y(x)$ is a Galton-Watson process with an initial number of individuals $Y_0 = x$, we have the branching property which follows directly from the definition of the process:

$$Y(x+y) \stackrel{\mathcal{L}}{=} Y^{(1)}(x) + Y^{(2)}(y)$$

where $Y^{(1)}$ and $Y^{(2)}$ are independent copies of Y and $\stackrel{\mathcal{L}}{=}$ stands for equality in law. In terms of modelling, this property implies the absence of competition between individuals. It is therefore well suited when considering small populations or populations with access to a large amount of resources.

In the absence of precision, we will assume that $Y_0 = 1$. For $s \in [0,1]$, the generating function f of the random variable ξ is defined by:

$$f(s) := \mathbb{E}[s^\xi] = \sum_{i=0}^{\infty} p_i s^i, \quad s \in [0,1].$$

We then notice that for any $(s,n) \in [0,1] \times \mathbb{N}$,

$$\mathbb{E}[s^{Y_{n+1}}] = \mathbb{E}[\mathbb{E}[s^{Y_{n+1}}|Y_n]] = \mathbb{E}[\mathbb{E}[s^{\xi_{(1,n)}+\xi_{(2,n)}+\ldots+\xi_{(Y_n,n)}}|Y_n]] = \mathbb{E}[f(s)^{Y_n}],$$

which entails, by iterating:

$$\mathbb{E}[s^{Y_n}] = f^{(n)}(s) = \underbrace{f \circ f \ldots \circ f}_{\text{n times}}, \quad (s,n) \in [0,1] \times \mathbb{N}.$$

The moments of the process, when they exist, can be expressed using the derivatives of f:

$$\mathbb{E}[Y_1] = f'(1) \quad \text{and} \quad \mathbb{E}[Y_n] = (f^{(n)})'(1) = (f'(1))^n,$$

which leads to the following definition which will be justified later.

Definition 2.1.1. *If $\ln f'(1)$ is strictly less than 0, equal to 0, or strictly greater than 0, then the process is called subcritical, critical or supercritical respectively.*

This classification is equivalent to distinguishing processes that on average decrease, remain stable or increase. We restrict ourselves to the case $p_0 + p_1 < 1$; f is then strictly convex and increasing over $[0,1]$. Let q be the smallest root of f on $[0,1]$. It is equal to 1 in the subcritical and critical cases, and is strictly less than 1 in the supercritical case. This root will indicate the long time behaviour of the process.

Proposition 2.1.2. *The subcritical and critical processes almost surely die out. The supercritical process gets extinct with probability $q < 1$, where q is the smallest root of $x \mapsto f(x) - x$ on $[0,1]$.*

Knowing the probability of extinction, a natural question is to look at the extinction rates of processes that almost certainly die out, and at the long-time behaviour of processes that survive. The Markov chain

$$W_n := f^{-n}(1) Y_n, \quad n \in \mathbb{N}$$

is a non-negative martingale, and thus almost surely converges to a non-negative random variable W. The law of W can then give us information about the long-time behaviour of a supercritical process when it does not get extinct. We have the following possibilities for the long time survival probability of the process (we exclude the trivial case when the process is deterministic).

Theorem 2.1.3.

- *Subcritical process: If $\ln f'(1) < 0$ and $\mathbb{E}[Y_1 \ln^+ Y_1] < \infty$, there exists a finite constant c such that*

$$\mathbb{P}(Y_n > 0) \sim c(f'(1))^n, \quad (n \to \infty).$$

- *Critical process: If* $\ln f'(1) = 0$,

$$\mathbb{P}(Y_n > 0) \sim \frac{2}{nVar(Y_1)}, \quad (n \to \infty).$$

- *Supercritical process: If* $\ln f'(1) > 0$ *and* $\mathbb{E}[Y_1 \ln^+ Y_1] < \infty$, *then* $\mathbb{E}[W] = 1$, *and*

$$\mathbb{P}(W = 0) = \mathbb{P}(\exists n \in \mathbb{N}, Y_n = 0 | Y_0 = 1) = q.$$

2.1.2 Galton-Watson processes in random environment

In the Galton-Watson process, the law of birth is the same for each generation, which means that the population lives in a constant environment. In the early 1970s, Smith and Wilkinson [SW69] and later Athreya and Karlin [AK71b, AK71a] sought to understand the effect of the environment on population dynamics. They introduced variability in birth laws reflecting environmental variability over generations. In the case of a population of annual plants, this variability may reflect the variability in sunshine, rainfall or pollination rate from one year to the next, variables that have a great influence on the quantity of offspring produced by the plants. These processes have subsequently been studied by many authors. We refer to [BGK05, VDS13] or the recent monograph [KV17] for known results on critical and sub-critical processes (see Definition 2.1.4). We also refer to [BB11, BB13, Böi14] for results concerning the supercritical case. We will limit our presentation to the monotype case and to iid environments.

A Galton-Watson process $(Z_n, n \in \mathbb{N})$ in a random environment (GWRE) can be described in terms of its generating functions $(f_n, n \in \mathbb{N})$. The state of the environment at time $n-1$ is denoted $\mathcal{E}_n$. Associated with this state is a sequence of real numbers $(p_k^{(n)}, k \in \mathbb{N})$ where $p_k^{(n)}$ is the probability that an individual of the generation $n-1$ produces k descendants in the generation n. We thus obtain:

$$f_n(s) := \mathbb{E}[s^{Z_n} | \mathcal{E}_n, Z_{n-1} = 1] = \sum_{k=0}^{\infty} p_k^{(n)} s^k, \quad (s, n) \in [0,1] \times \mathbb{N}.$$

The generating functions of the inhomogeneous Markov chain $(Z_n, n \in \mathbb{N})$ corresponding to the sequence of population sizes in the environment $(\mathcal{E}_1, ..., \mathcal{E}_n, ...)$ are then obtained by iterating the successive generating functions:

$$\mathbb{E}[s^{Z_n} | \mathcal{E}_1, ..., \mathcal{E}_n] = f_1 \circ f_2 \circ ... \circ f_n(s), \quad (s, n) \in [0,1] \times \mathbb{N}.$$

Therefore, the average of the population size Z_n in the environment $(\mathcal{E}_1, ..., \mathcal{E}_n)$ is:

$$\mathbb{E}[Z_n | \mathcal{E}_1, ..., \mathcal{E}_n] = f_1'(1)...f_n'(1) =: e^{S_n}, \quad n \in N, \tag{2.1}$$

where the random walk S_n is defined by:

$$S_0 = 0, \quad S_n = \ln f_1'(1) + ... + \ln f_n'(1), \quad n \in \mathbb{N}. \tag{2.2}$$

The simplest example of GWRE is the fractional linear case, characterized by the generating functions

$$f_n(s) = r_n + (1 - r_n) \frac{t_n s}{1 - (1 - t_n)s},$$

where the parameters (r_n, t_n) describing the state of the environment at generation $n-1$ are in $[0,1) \times (0,1]$ for any integer n. In this case, the probability of survival to time n of the Markov chain $(Z_n, n \in \mathbb{N})$ can be expressed by:

$$\mathbb{P}(Z_n > 0 | \mathcal{E}_1, ..., \mathcal{E}_n) = \left(e^{-S_n} + \sum_{k=1}^{n} \frac{1-t_k}{1-r_k} e^{-S_{k-1}} \right)^{-1}. \tag{2.3}$$

Equality (2.3) implies that under certain moment conditions, the probability of survival of the process, $\mathbb{P}(Z_n > 0 | \mathcal{E}_1, ..., \mathcal{E}_n)$, is governed by the minimum of the random walk $(S_n, n \in \mathbb{N})$ defined in (2.2). Indeed the right-hand side of (2.3) has the order of $\exp(\min(S_0, S_1, ..., S_n))$. We will see that the random walk $(S_n, n \in \mathbb{N})$ is intimately linked to the long time behaviour of the process $(Z_n, n \in \mathbb{N})$. But before specifying more precisely this relation, we may already notice that:

$$\begin{aligned} \mathbb{P}(Z_n > 0) = \mathbb{P}\left(\mathbb{P}(Z_n > 0 | \mathcal{E}_1, ..., \mathcal{E}_n)\right) &= \mathbb{P}\left(\min_{0 \le i \le n} \mathbb{P}(Z_i > 0 | \mathcal{E}_1, ..., \mathcal{E}_n \right) \\ &\le \mathbb{P}\left(\min_{0 \le i \le n} \mathbb{E}[Z_i | \mathcal{E}_1, ..., \mathcal{E}_n] \right) \\ &= \mathbb{E}[\exp(\min(S_0, S_1, ..., S_n))], \end{aligned} \tag{2.4}$$

where we applied Markov inequality, Equality (2.1) and Definition (2.2). If the random walk $(S_n, n \in \mathbb{N})$ is not degenerate (i.e. we exclude the case $S \equiv 0$), it has only three possible a.s. behaviours at infinity [Fel71]: $\lim_{n\to\infty} S_n = +\infty$, $\lim_{n\to\infty} S_n = -\infty$, and $\limsup_{n\to\infty} S_n = -\liminf_{n\to\infty} S_n = +\infty$, which correspond respectively to cases $\mathbb{E}[\ln f_1'(1)] < 0$, > 0, and $= 0$ when $\mathbb{E}[|\ln f_1'(1)|] < \infty$. In the rest of this presentation and for the sake of simplicity we will restrict ourselves to the case where $\ln f_1'(1)$ is integrable. It is possible to define a classification for GWRE's similar to the Definition 2.1.1:

Definition 2.1.4. *If $\mathbb{E}[\ln f_1'(1)]$ is strictly less than 0, equal to 0, or strictly greater than 0, the Galton-Watson process in a random environment is called subcritical, critical or supercritical.*

Inequality (2.4) is sufficient to show that the process $(Z_n, n \in \mathbb{N})$ almost certainly gets extinct in subcritical and critical cases. We have in fact the equivalent of Theorem 2.1.3:

Proposition 2.1.5 (Theorem 3.1 [SW69]). *Subcritical and critical processes get extinct almost surely. The supercritical process survives with a positive probability if $\mathbb{E}[|\ln(1 - f_1(0))|] < \infty$.*

The condition $\mathbb{E}[|\ln(1 - f_1(0))|] < \infty$ excludes the possibility that a sequence of "catastrophic" environments leads to the death of the population within a few generations.

Finally, we have the following equivalent of Theorem 2.1.3 concerning the extinction rate of the critical case and the long time behaviour of the supercritical process in the case of survival:

Theorem 2.1.6 ([AK71a, Kap74, Koz76, GK01]).

- *Critical process: If $\mathbb{E}[\ln f_1'(1)] = 0$, $0 < Var[\ln f_1'(1)] < \infty$ and $f_1'(1)$ has a non-lattice distribution, there are positive finite constants c_1 and c_2 such that*

$$\mathbb{P}(Z_n > 0) \sim c_1 \mathbb{P}(\min(S_0, ..., S_n) \ge 0) \sim \frac{c_2}{\sqrt{n}}, \quad (n \to \infty).$$

- *Supercritical process: If* $\mathbb{E}[Z_1 \ln Z_1 / f_1'(1)] < \infty$ *and* $\mathbb{E}[\ln f_1'(1)] > 0$, *then the martingale* $(Z_n \exp(-S_n), n \in \mathbb{N})$ *has a non-zero finite limit on the non-extinction event of the process:*

$$\lim_{n\to\infty} Z_n e^{-S_n} = W \quad a.s., \quad \mathbb{P}(W > 0) = \mathbb{P}(\forall n \in \mathbb{N}, Z_n > 0 | Z_0 = 1) > 0.$$

The behaviour of the subcritical process is more complex in the case of GWREs than in the case of conventional Galton-Watson processes. Knowing that $\mathbb{E}[\ln f_1'(1)] < 0$ is not sufficient to deduce the behaviour of the process in long time. The extinction rate in the subcritical case has been studied, in more and more general cases by Dekking [Dek87], D'Souza and Hambly [DH97], Guivarch and Liu [GL01], and finally by Geiger, Kersting and Vatutin [GKV03]. The heuristic that we will present to understand the origin of the different sub-cases is inspired by [BGK05]. We recall the definition (2.2) of the random walk $(S_n, n \in \mathbb{N})$ and we suppose that there exists $\varepsilon > 0$ such that $\mathbb{E}[e^{(1+\varepsilon)S_1}] < \infty$. We introduce, for $\beta \in [0,1]$, the probability $\mathbb{P}^{(\beta)}$ via:

$$\begin{aligned}\mathbb{E}^{(\beta)}[\phi(\mathcal{E}_1, ..., \mathcal{E}_n, Z_1, ..., Z_n)] &:= \mathbb{E}[\phi(\mathcal{E}_1, ..., \mathcal{E}_n, Z_1, ..., Z_n) e^{\beta S_n}] \left(\mathbb{E}[e^{\beta S_n}]\right)^{-1} \\ &= (\mathbb{E}[e^{\beta S_1}])^{-n} \mathbb{E}[\phi(\mathcal{E}_1, ..., \mathcal{E}_n, Z_1, ..., Z_n) e^{\beta S_n}],\end{aligned}$$

for a positive function ϕ. The probability of survival at time n can be expressed as a function of this new probability: for all $\beta \in \mathbb{R}_+$ such that $\mathbb{E}[e^{\beta S_1}] < \infty$,

$$\mathbb{P}(Z_n > 0) = (\mathbb{E}[e^{\beta S_1}])^n \mathbb{E}^{(\beta)}[\mathbb{P}(Z_n > 0 | \mathcal{E}_1, ..., \mathcal{E}_n) e^{-\beta S_n}].$$

We now continue the heuristic by admitting that $\mathbb{P}(Z_n > 0 | \mathcal{E}_1, ..., \mathcal{E}_n)$ is of the order of $e^{\min(S_0, S_1, ..., S_n)}$, and we are interested in the limit behaviour of the expectation:

$$\mathbb{E}[e^{\min(S_0, S_1, ..., S_n)}] = (E[e^{\beta S_1}])^n \mathbb{E}^{(\beta)}[e^{\min(S_0, S_1, ..., S_n) - \beta S_n}].$$

We will then look for a real β such that the last term does not have an exponential growth or decrease. The term $\mathbb{E}[\exp(\beta S_1)]$ will then give the exponential decrease of the probability of survival, and the term $\mathbb{E}^{(\beta)}[e^{\min(S_0, S_1, ..., S_n) - \beta S n}]$ its polynomial decrease. We can already exclude the case $\beta > 1$. Indeed in the subcritical case the random walk $(S_n, n \in \mathbb{N})$ drifts towards minus infinity and the term $\min(S_0, S_1, ..., S_n) - \beta S_n$ drifts towards infinity for all $\beta > 1$. Hence we look for $\beta \in [0,1]$. We will see that we can distinguish three cases according to the behaviour of the function $\beta \mapsto \mathbb{E}[\exp(\beta S_1)]$ on the interval $[0,1]$. This function is well defined under our hypotheses and even admits a first and a second derivatives on $[0,1]$ which have for expressions :

$$\partial_\beta \mathbb{E}[\exp(\beta S_1)] = \mathbb{E}[S_1 \exp(\beta S_1)], \quad \partial_{\beta\beta} \mathbb{E}[\exp(\beta S_1)] = \mathbb{E}[S_1^2 \exp(\beta S_1)] > 0.$$

It is thus a convex function which reaches its minimum in $\tau \in (0,1)$ if $\mathbb{E}[S_1 \exp(S_1)] > 0$ and in 1 if $\mathbb{E}[S_1 \exp(S_1)] \leq 0$. We will therefore consider successively the different signs that $\mathbb{E}[S_1 \exp(S_1)]$ can take.

- $\mathbb{E}[S_1 \exp(S_1)] > 0$: Then $\beta \mapsto \mathbb{E}[\exp(\beta S_1)]$ reaches its minimum on $[0,1]$ in $\tau \in (0,1)$, and $0 = \mathbb{E}[S_1 e^{\tau S_1}] = \mathbb{E}[e^{\tau S_1}] \mathbb{E}^{(\tau)}[S_1]$. The random walk $(S_n, n \in \mathbb{N})$ has a null expectation and a finite variance under $\mathbb{P}^{(\tau)}$. The only possibility for $\min(S_0, S_1, ..., S_n) - \tau S_n$ to be close

to 0 is that $\min(S_0, S_1, ..., S_n)$ and τS_n are close to 0. The event $\{S_0, ..., S_{n-1} \geq 0, S_n \leq 0\}$ has a probability of order $n^{-3/2}$ under $\mathbb{P}^{(\tau)}$ (see [Épp79] Equation C of the Theorem for the non-lattice case, and [AD99] for the lattice case). Therefore,

$$\mathbb{E}^{(\tau)}[e^{\min(S_0,S_1,...,S_n)-\tau S_n}] \asymp n^{-3/2}$$

is expected in this case.

- $\mathbb{E}[S_1 \exp(S_1)] = 0$: Then in the same way, $\mathbb{E}^{(1)}[S_1] = 0$ and $\min(S_0, S_1, ..., S_n) - S_n$ is close to 0 if $(S_n, n \in \mathbb{N})$ reaches its minimum on $\{0, ..., n\}$ near n. As the probability of the event $\{S_0, ..., S_{n-1} \geq S_n\}$ is of order $n^{-1/2}$ under $\mathbb{P}^{(1)}$ (Equation (7.12) Chapter XII of [Fel71]) we expect:
$$\mathbb{E}^{(1)}[e^{\min(S_0,S_1,...,S_n)-S_n}] \asymp n^{-1/2}.$$

- $\mathbb{E}[S_1 \exp(S_1)] > 0$: Then $\mathbb{E}^{(1)}[S_1] < 0$ and $\min(S_0, S_1, ..., S_n) - S_n$ remains bounded since $(S_n, n \in \mathbb{N})$ drifts to minus infinity under the probability $\mathbb{P}^{(1)}$. We will thus have:
$$\mathbb{E}^{(1)}[e^{\min(S_0,S_1,...,S_n)-S_n}] \asymp const.$$

A rigorous treatment of this heuristic leads to the following asymptotics for the probability of survival in the subcritical case (recall that $S_1 = \ln f'(1)$).

Theorem 2.1.7 ([GKV03]). *We consider the subcritical case, $\mathbb{E}[\ln f_1'(1)] < 0$, and introduce*

$$\tau := argmin_{\beta \in (0,1)} \mathbb{E}[f_1'(1)^\beta].$$

Under additional moment assumptions we have the following asymptotics, where c denotes a positive finite constant whose value can change from one line to another:

- *Strong subcritical case: If $\mathbb{E}[f_1'(1) \ln f_1'(1)] < 0$, then $\tau = 1$ and*
$$\mathbb{P}(Z_n > 0) \sim c(\mathbb{E}[f_1'(1)])^n, \quad (n \to \infty).$$

- *Intermediate subcritical case: If $\mathbb{E}[f_1'(1) \ln f_1'(1)] = 0$, then $\tau = 1$ and*
$$\mathbb{P}(Z_n > 0) \sim c(\mathbb{E}[f_1'(1)])^n n^{-1/2}, \quad (n \to \infty).$$

- *Weak subcritical case: If $0 < \mathbb{E}[f_1'(1) \ln f_1'(1)] < \infty$, then $\tau \in (0, 1)$ and*
$$\mathbb{P}(Z_n > 0) \sim c(\mathbb{E}[f_1'(1)^\tau])^n n^{-3/2}, \quad (n \to \infty).$$

Hence when the variability of the environment is small, the extinction probability is similar to the one of the subcritical Galton-Watson process. For an average growth rate $\mathbb{E}[Z_1|Z_0 = 1] = \mathbb{E}[\ln f_1'(1)] < 0$, the exponential extinction rate depends on the law of the environment only if the environment is sufficiently variable, more precisely when $\mathbb{E}[f_1'(1) \ln f_1'(1)] > 0$. In order to see that the variability of the environment is linked to this inequality it can be noted that for this inequality to be satisfied $f'(1)$ must take large values. Moreover, since $\mathbb{E}[\ln f'(1)]$ is negative in the subcritical case, $f'(1)$ must also take small values.

2.1.3 Continuous state branching processes

Continuous state branching processes (CSBPs) are the analog in continuous time and space of Galton-Watson processes. They were introduced by Jirina [Jivr58] and studied by many authors. Let us mention in particular [Lam67a, Lam67b, Gre74, Gri74, Bin76] for the first works on the subject, and [Kyp06, Li10] for recent reviews. A CSBP $Y = (Y_t, t \in \mathbb{R}_+)$ is a strong Markov process with values in $\mathbb{R}_+$ and which satisfies the branching property. Y admits 0 and ∞ as absorbing points, and $\mathbb{P}_x$ denotes the law of the process starting from x. Lamperti [Lam67b] has shown that CSBPs are the only possible scaling limits of Galton-Watson processes and that, conversely, any CSBP can be obtained as such a scaling limit.

Here again for the sake of simplicity we will assume that $(Y_t, t \in \mathbb{R}_+)$ admits a first moment. The branching property of the process implies that its Laplace exponent has the form:

$$\mathbb{E}_x[e^{-\theta Y_t}] = e^{-x u_t(\theta)}, \quad (x, t, \theta) \in \mathbb{R}_+^3, \tag{2.5}$$

where ([Sil68]) the function $(u_t(\theta), (t, \theta) \in \mathbb{R}_+^2)$ is the unique solution to the differential equation:

$$\frac{\partial}{\partial t} u_t(\theta) + \psi(u_t(\theta)) = 0, \quad u_0(\theta) = \theta, \tag{2.6}$$

where for $\lambda \geq 0$,

$$\psi(\lambda) = \lambda \psi'(0+) + \gamma^2 \lambda^2 + \int_{(0,\infty)} (e^{-\lambda z} - 1 + \lambda z) \mu(dz), \tag{2.7}$$

for $\psi'(0+) \in \mathbb{R}$, $\gamma \geq 0$ and μ is a measure with support in $(0, \infty)$ that satisfies $\int_{(0,\infty)} (z \wedge z^2) \mu(dz) < \infty$. The function ψ is the branching mechanism associated to Y and (2.7) is called the Lévy-Khintchine formula.

CSBPs are spectrally positive, with jumps representing macroscopic birth events (an infinitesimal individual gives birth to a sufficiently large number of infinitesimal individuals to be visible macroscopically).

A CSBP can also be defined via a stochastic differential equation, a representation that we will use later:

Theorem 2.1.8 ([FL10]). *The process $(Y_t, t \in \mathbb{R}_+)$ is the unique strong solution to the equation*

$$Y_t = Y_0 - \psi'(0+) \int_0^t Y_s ds + \int_0^t \sqrt{2\gamma^2 Y_s} dB_s + \int_0^t \int_0^\infty \int_0^{Y_{s^-}} z \tilde{N}_0(ds, dz, du), \tag{2.8}$$

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

Remark 2.1.9. We have considered the case where Y admits a first moment. This implies in particular that $\int_{(0,\infty)} (z \wedge z^2) \mu(dz) < \infty$, which allows to also compensate large jumps and brings out the drift term g which governs the long time behaviour of the process. In the general case we only have $\int_{(0,\infty)} (1 \wedge z^2) \mu(dz) < \infty$ and we only may compensate jumps smaller than 1.

The branching mechanism ψ uniquely determines the law of the CSBP Y. It is a convex function null at 0. Its shape depends on the sign of $\psi'(0)$.

From (2.5) and (2.6) we may prove that:

$$\mathbb{E}_x[Y_t] = xe^{-\psi'(0+)t}.$$

We then have the analog of Definitions 2.1.1 and 2.1.4.

Definition 2.1.10. *If $\psi'(0+)$ is strictly greater than 0, equal to 0, or strictly less than 0, the CSBP Y is called subcritical, critical or supercritical, respectively.*

The extinction event is defined by:

$$Ext := \left\{ \lim_{t\to\infty} Y_t = 0 \right\}, \tag{2.9}$$

which leads to the analog of Propositions 2.1.2 and 2.1.5.

Proposition 2.1.11. *The subcritical and critical processes almost surely die out. The supercritical process survives with positive probability. More precisely,*

$$\mathbb{P}_x(Ext) = e^{-x\Phi(0)}, \quad \forall x > 0,$$

where $\Phi(0)$ is the strictly positive root of ψ.

In the case of CSBPs, a distinction must be made between two events, extinction and absorption of the process. The first was defined in (2.9), the second corresponds to the case where the process reaches 0 in finite time:

$$Abs := \{\exists t < \infty, Y_t = 0\}. \tag{2.10}$$

These two events do not necessarily coincide. For example the CSBP $Y = (Y_0 e^{-t}, t \geq 0)$ satisfies for every $x \in \mathbb{R}_+^\star$, $\mathbb{P}_x(Ext) = 1$ and $\mathbb{P}_x(Abs) = 0$. So we can have extinction and not absorption. On the other hand, if the probability that the process is absorbed is positive, the events of absorption and extinction coincide almost surely:

$$\begin{aligned}\mathbb{P}_x(Abs) > 0, \forall x > 0 &\Leftrightarrow Abs = Ext \quad p.s.\\ &\Leftrightarrow \psi(\infty) = \infty \text{ and } \int^\infty ds\psi(s) < \infty.\end{aligned}$$

CSBPs are therefore more complex objects than Galton-Watson processes. In particular, the determination of their extinction rate is problematic since they can tend towards 0 without cancelling out. One class of CSBPs however is well known: stable CSBPs. For $\beta \in (0,1)$, their jump measure μ (see Theorem 2.1.8) is given by:

$$\mu(dx) = \frac{c_\beta \beta(\beta+1)}{\Gamma(1-\beta)x^{\beta+2}}, \quad x > 0, \tag{2.11}$$

where c_β is a positive and finite constant (the case $\beta = 1$ corresponds to Feller diffusion (a Brownian part and no jump)). The differential equation (2.6) can be explicitly solved and one can obtain an explicit expression of the extinction rate (see e.g. Proposition 4 of [BPS13]):

$$\mathbb{P}_{x_0}(Y_t > 0) = 1 - \exp\left(-x_0 \left(c_\beta \beta \int_0^t e^{\beta\psi'(0+)s} ds \right)^{-1/\beta} \right).$$

This allows us to derive the following analog of Theorem 2.1.3 (the result for the critical case can be found in [KP08] p.12).

Theorem 2.1.12. *Let $Y = (Y_t, t \geq 0)$ be a stable CSBP with $\beta \in (0,1)$:*

1. *If $g = 0$ (critical case)*
$$\mathbb{P}_{x_0}(Y_t > 0) \sim \frac{x_0}{(c_\beta \beta t)^{1/\beta}}, \quad (t \to \infty).$$

2. *If $g < 0$ (subcritical case)*
$$\mathbb{P}_{x_0}(Y_t > 0) \sim x_0 \left(\frac{|\psi'(0+)|}{c_\beta}\right)^{1/\beta} e^{-\psi'(0+)t} = x_0 \left(\frac{|\psi'(0+)|}{c_\beta}\right)^{1/\beta} (\mathbb{E}_1[Y_1])^t, \quad (t \to \infty).$$

In particular in the case $\beta = 1$ (Feller diffusion) we get an extinction rate similar to that of a Galton-Watson process in the critical case:

$$\mathbb{P}_{x_0}(Y_t > 0) \sim \frac{x_0}{\gamma^2 t}, \quad (t \to \infty).$$

This is a consequence of the fact that Feller diffusion is a scaling limit of Galton-Watson process sequences whose reproduction law has a finite variance. If

$$\mathcal{Y}_t^{(n)} := \frac{1}{n} Y^{(n)}_{\lfloor nt \rfloor}, \quad t \geq 0$$

where $(Y^{(n)}, n \in \mathbb{N})$ is a sequence of GW processes with reproduction law ξ and satisfying $Y_0^{(n)} = n$ and $Var(Y_1^{(n)}) < \infty$ for all $n \in \mathbb{N}$, then $(\mathcal{Y}_t^{(n)}, t \in [0,T])$ converges in law when n tends towards infinity (here T is a positive real) towards a Feller diffusion on the interval $[0,T]$.

2.1.4 Continuous state branching processes in Lévy random environment

The construction of CSBPs as scaling limits of Galton-Watson processes raises a natural question. Is it possible, like for the Galton-Watson processes, to immerse a CSBP in a random environment, in order to take into account the variability of the living and reproductive conditions of the (infinitesimal) individuals constituting the modelled populations? Here the question is more delicate. Indeed, to make the environment vary in a discrete framework we consider a new reproduction law at each discrete time step (or generation). In the continuous time case, the environment can vary in multiple ways: continuously, abruptly, more or less frequently, with a variable amplitude...

We will focus on the case where the environment can be described by a Lévy process, similarly as in the case of BPREs where the environment could be described by the random walk S. Such CSBPs in Lévy random environment can be obtained as scaling limits of BPREs. Historically, the existence of branching diffusions in Brownian environments constructed as scaling limits of Galton-Watson processes in random environment has been conjectured by Keiding [Kei75] and rigorously established by Kurtz [Kur78]. Recent work [BS15, BCM19] has focused on the scaling limits of a large class of branching processes in variable environments (in particular a reproduction law that could have infinite variance, bottlenecks, interactions between individuals,...), and the authors of these works obtained, among other processes, a large class of CSBPs in Lévy environments.

Like CSBPs (recall (2.8)), the class of CSBPREs we will consider can be seen as solutions to SDEs. This is the point of view we will adopt for the study of their extinction rate. The realization

of generalized branching processes (with interactions, immigration, bottlenecks,...) in variable environments as the only strong solution of SDEs is currently the subject of much work (see for example [PP18, HLX18, FL20]). The proofs of these results are generalizations of techniques introduced by Li and co-authors (see for example [FL10, DL12, LP12]). We will not need to apply these results in their full generality, and so we present only the case of interest for us, namely the case of a branching process (without additional interactions or immigration) with a finite expectation in a random environment given by a Lévy process.

Let $(\Omega^{(b)}, \mathcal{F}^{(b)}, (\mathcal{F}_t^{(b)})_{t\geq 0}, \mathbb{P}^{(b)})$ be a filtered probability space satisfying the usual hypothesis and introduce a $(\mathcal{F}_t^{(b)})$-adapted standard Brownian motion $B^{(b)} = (B_t^{(b)}, t \geq 0)$ and an independent $(\mathcal{F}_t^{(b)})$-adapted Poisson random measure $N^{(b)}(\mathrm{d}s, \mathrm{d}z, \mathrm{d}u)$ defined on $\mathbb{R}_+^3$, with intensity $\mathrm{d}s\mu(\mathrm{d}z)\mathrm{d}u$. The measure μ is concentrated on $(0, \infty)$ and we assume that

$$\int_{(0,\infty)} (z \wedge z^2)\mu(\mathrm{d}z) < \infty, \tag{2.12}$$

which guarantees non-explosivity. We denote by $\widetilde{N}^{(b)}$ the compensated measure of $N^{(b)}$.

Following Theorem 2.1.8, we can define a CSBP $Y = (Y_t, t \geq 0)$ as the unique strong solution of the SDE

$$Y_t = Y_0 - \psi'(0^+)\int_0^t Y_s\mathrm{d}s + \int_0^t \sqrt{2\gamma^2 Y_s}\mathrm{d}B_s^{(b)} + \int_0^t \int_{(0,\infty)} \int_0^{Y_{s-}} z\widetilde{N}^{(b)}(\mathrm{d}s, \mathrm{d}z, \mathrm{d}u). \tag{2.13}$$

For the random environment, we consider now $(\Omega^{(e)}, \mathcal{F}^{(e)}, (\mathcal{F}_t^{(e)})_{t\geq 0}, \mathbb{P}^{(e)})$ a filtered probability space satisfying the usual hypothesis and a $(\mathcal{F}_t^{(e)})$-Lévy process $K = (K_t, t \geq 0)$ which is defined as follows

$$K_t = \alpha t + \sigma B_t^{(e)} + \int_0^t \int_{\mathbb{R}\setminus(-1,1)} (e^z - 1)N^{(e)}(\mathrm{d}s, \mathrm{d}z) + \int_0^t \int_{(-1,1)} (e^z - 1)\widetilde{N}^{(e)}(\mathrm{d}s, \mathrm{d}z), \tag{2.14}$$

where $\alpha \in \mathbb{R}$, $\sigma \geq 0$, $B^{(e)} = (B_t^{(e)}, t \geq 0)$ denotes a $(\mathcal{F}_t^{(e)})$-adapted standard Brownian motion and $N^{(e)}(\mathrm{d}s, \mathrm{d}z)$ is a $(\mathcal{F}_t^{(e)})$-adapted Poisson random measure on $\mathbb{R}_+ \times \mathbb{R}$ with intensity $\mathrm{d}s\pi(\mathrm{d}y)$, which is independent of $B^{(e)}$. The measure π is concentrated on $\mathbb{R} \setminus \{0\}$ and fulfills the following integral condition

$$\int_{\mathbb{R}} (1 \wedge z^2)\pi(\mathrm{d}z) < \infty.$$

The population size has no impact on the dynamics of the environment and we are considering independent processes for demography and environment. More precisely, we work now on the product space $(\Omega, \mathcal{F}, (\mathcal{F})_{t\geq 0}, \mathbb{P})$, where $\Omega = \Omega^{(e)} \times \Omega^{(b)}$, $\mathcal{F} = \mathcal{F}^{(e)} \otimes \mathcal{F}^{(b)}$, and $\mathcal{F}_t = \mathcal{F}_t^{(e)} \otimes \mathcal{F}_t^{(b)}$ for $t \geq 0$, $\mathbb{P} = \mathbb{P}^{(e)} \otimes \mathbb{P}^{(b)}$ and we make the direct extension of $B^{(b)}$, $N^{(b)}$, $B^{(e)}$, $N^{(e)}$ and K to Ω by projection respectively on $\Omega^{(b)}$ and $\Omega^{(e)}$. In particular, $(B^{(e)}, N^{(e)})$ is independent of $(B^{(b)}, N^{(b)})$.

Letting $Z_0 \in [0, \infty)$ a.s., a CSBP in a Lévy environment Z can be defined as the unique nonnegative strong solution of the following SDE,

$$\begin{aligned} Z_t =& Z_0 - \psi'(0^+)\int_0^t Z_s\mathrm{d}s + \int_0^t \sqrt{2\gamma^2 Z_s}\mathrm{d}B_s^{(b)} \\ &+ \int_0^t \int_{(0,\infty)} \int_0^{Z_{s-}} z\widetilde{N}^{(b)}(\mathrm{d}s, \mathrm{d}z, \mathrm{d}u) + \int_0^t Z_{s-}\mathrm{d}K_s. \end{aligned} \tag{2.15}$$

The only difference with the SDE (2.13) is the addition of the environmental impact via the last term. According to He et al. [HLX18] and Palau and Pardo [PP18], under our assumptions, pathwise uniqueness and strong existence hold for (2.15).

2.2 Asymptotic behaviour of exponential functionals of Lévy processes

This part is based on a work in collaboration with S. Palau and J-C. Pardo [PPS16], which concerns the long-time behaviour of a class of exponential functionals of Lévy processes. One application of the results of this paper, which was the motivation for this study, concerns the extinction rate of stable CSPBs in Lévy environment. Let us first present this link.

2.2.1 Extinction rate of stable CSBPs in Lévy environment

We are interested in the case where the branching mechanism is stable, that is to say

$$\psi(\lambda) = c_\beta \lambda^{\beta+1}, \qquad \lambda \in \mathbb{R},$$

for some $\beta \in (0,1]$ and $c_\beta > 0$. We call its associated CSBP a self-similar CSBP. We can define a self-similar CSBP in a Lévy random environment as the unique non-negative strong solution to the SDE

$$Z_t = Z_0 + \mathbf{1}_{\{\beta=1\}} \int_0^t \sqrt{2c_\beta Z_s}\mathrm{d}B_s^{(b)} + \mathbf{1}_{\{\beta\neq 1\}} \int_0^t \int_0^\infty \int_0^{Z_{s-}} z\widetilde{N}^{(b)}(\mathrm{d}s,\mathrm{d}z,\mathrm{d}u) + \int_0^t Z_{s-}\mathrm{d}K_s, \tag{2.16}$$

where $N^{(b)}$ has intensity $\mu(dz)dsdu$ and μ has been defined in (2.11).

In what follows, we introduce the auxiliary Lévy process

$$\bar{K}_t = \bar{\alpha}t + \sigma B_t^{(e)} + \int_0^t \int_{(-1,1)} v\widetilde{N}^{(e)}(\mathrm{d}s,\mathrm{d}v) + \int_0^t \int_{\mathbb{R}\setminus(-1,1)} vN^{(e)}(\mathrm{d}s,\mathrm{d}v), \tag{2.17}$$

where

$$\bar{\alpha} = \alpha - \frac{\sigma^2}{2} - \int_{(-1,1)} (e^v - 1 - v)\pi(\mathrm{d}v). \tag{2.18}$$

Similarly as in [BT11, BPS13], using Itô's formula with jumps, we can compute explicitely the Laplace transform of $Z_t e^{-\bar{K}_t}$. It provides a closed formula for the probability of survival of Z. More precisely, for all $z, \lambda > 0$ and $t \geq 0$,

$$\mathbb{E}_z\Big[\exp\Big\{-\lambda Z_t e^{-\bar{K}_t}\Big\}\Big|\bar{K}\Big] = \exp\left\{-z\left(\lambda^{-\beta} + \beta c_\beta \int_0^t e^{-\beta K_u}\mathrm{d}u\right)^{-1/\beta}\right\}. \tag{2.19}$$

Letting λ go to ∞ and taking the expectation, we get

$$\mathbb{P}_z\Big(Z_t > 0\Big) = \mathbb{E}\left[1 - \exp\left\{-z\left(\beta c_\beta \int_0^t e^{-\beta \bar{K}_u}\mathrm{d}u\right)^{-1/\beta}\right\}\right] \qquad \text{a.s.}$$

As a consequence, to obtain the extinction rate for large t, we need to study the asymptotics of the expectation of an exponential functional of a Lévy process.

2.2.2 Asymptotic behaviour of exponential functionals of Lévy processes

We are interested in studying the exponential functional of $\bar{K}$, defined by

$$I_t(\bar{K}) := \int_0^t e^{-\bar{K}_s} \mathrm{d}s, \qquad t \geq 0.$$

There is a vast literature about exponential functionals of Lévy processes drifting to $+\infty$ or killed at an independent exponential time $\mathbf{e}_q$ with parameter $q \geq 0$, see for instance [BLM08, BY05, PRvS+13]. In such cases, $I_\infty(\bar{K})$ or $I_{\mathbf{e}_q}(\bar{K})$ is finite almost surely with an absolute continuous density. Most of the known results on $I_\infty(\bar{K})$ and $I_{\mathbf{e}_q}(\bar{K})$ are related to the knowledge of their densities or the behaviour of their tail distributions. We refer to [BLM08, BY05, KPS+12, PRvS+13], and the references therein, for more details about these facts.

We are interested in the case when the Lévy process $\bar{K}$ does not drift to $+\infty$ and is not killed, in other words when $I_t(\bar{K})$ does not converge almost surely to a finite random variable, as t goes to ∞. More precisely, one of our aims is to study the asymptotic behaviour of

$$\mathbb{E}\Big[F\big(I_t(\bar{K})\big)\Big] \qquad \text{as} \qquad t \to \infty,$$

where F is a function which, at infinity, is non-increasing and has polynomial decay, under some exponential moment conditions on $\bar{K}$. We find five regimes that depend on the shape of the Laplace exponent ϕ (see definition in Equation (2.20)).

Before presenting the results of [PPS16], I would like to mention a work by Li and Xu [LX18], done in parallel and with very similar results. Li and Xu used in their proofs fluctuation theory for Lévy processes and the knowledge of Lévy processes conditioned to stay positive. Our approach is based on a discretization of the exponential functional of Lévy processes and on the asymptotic behaviour of functionals of semi-direct products of random variables which was described by Guivarc'h and Liu [GL01].

Let ϕ be the Laplace exponent of $\bar{K}$:

$$\phi(\lambda) = \log \mathbb{E}e^{\lambda \bar{K}_1}, \qquad \lambda \in [0, \theta^+), \tag{2.20}$$

where

$$\theta^+ := \sup\{\lambda > 0 : \phi(\lambda) < \infty\}. \tag{2.21}$$

Assume that θ^+ is positive. Then ϕ is well defined on the interval (θ^-, θ^+), where

$$\theta^- := \inf\{\lambda < 0 : \phi(\lambda) < \infty\}. \tag{2.22}$$

The function ϕ is convex, belongs to $C^\infty(\theta^-, \theta^+)$ and $\phi(0) = 0, \phi'(0+) \in [-\infty, \infty)$ and $\phi''(\lambda) > 0$, for $\lambda \in (\theta^-, \theta^+)$. As a consequence, either ϕ is positive on $(0, \theta^+)$ or it may have another root on this interval. In the latter scenario, ϕ has at most one global minimum on $(0, \theta^+)$. Whenever such a global minimum exists, we denote by τ the position where it is reached.

For the sake of readability, we introduce the notation

$$\mathcal{E}_F(t) := \mathbb{E}\left[F(I_t(\bar{K}))\right],$$

where F belongs to a particular class of continuous functions on $\mathbb{R}_+$ that we will now introduce. Let $\mathbf{k}$ be a positive constant. We will consider functions F satisfying one of the following conditions: there exists $x_0 \geq 0$ such that $F(x)$ is non-increasing for $x \geq x_0$, and

(A1) $F(x) = cx^{-p}$, $c \in (0, \infty)$ or F satisfies

$$F(x) = \mathbf{k}(x+1)^{-p}\Big[1 + (1+x)^{-\varsigma}h(x)\Big], \qquad \text{for all } x > 0,$$

where $0 < p \leq \tau$, $\varsigma \geq 1$ and h is a Lipschitz function which is bounded.

(A2) $F(x) = cx^{-p}$, $c \in (0, \infty)$ or F is an Hölder function with index $\alpha > 0$ satisfying

$$F(x) \leq \mathbf{k}(x+1)^{-p}, \qquad \text{for all } x > 0,$$

with $p > \tau$.

Notice that

$$0 < p \leq \tau \Longrightarrow \phi'(p) \leq 0$$

whereas

$$p > \tau \Longrightarrow \phi'(p) > 0.$$

Then we have the five following possible asymptotic regimes.

Theorem 2.2.1. *Assume that $0 < p < \theta^+$ and recall that we are in the stable case with $\beta \in (0, 1]$.*

i) If $\phi'(0+) > 0$ and F is a positive and continuous function which is bounded,

$$\lim_{t\to\infty} \mathcal{E}_F(t) = \mathcal{E}_F(\infty).$$

*ii) If $\phi'(0+) = 0$, F satisfies (**A2**) and $\theta^- < 0$, then there exists a positive constant c_3 such that*

$$\lim_{t\to\infty} \sqrt{t}\mathcal{E}_F(t) = c_3.$$

iii) Suppose that $\phi'(0+) < 0$, and thus τ exists:

*a) If F satisfies (**A1**) and $\phi'(p) < 0$ ($p < \tau$), then there exists a finite constant c_1 such that:*

$$\lim_{t\to\infty} e^{-t\phi(p)}\mathcal{E}_F(t) = \lim_{t\to\infty} e^{-t\phi(p)}\mathbf{k}\mathbb{E}\left[I_t(\bar{K})^{-p}\right] = \mathbf{k}c_1.$$

*b) If F satisfies (**A1**), $\phi'(p) = 0$ ($p = \tau$) and $\phi''(p) < \infty$, then there exists a positive constant c_2 such that,*

$$\lim_{t\to\infty} \sqrt{t}e^{-t\phi(p)}\mathcal{E}_F(t) = \lim_{t\to\infty} \sqrt{t}e^{-t\phi(p)}\mathbf{k}\mathbb{E}\left[I_t(\bar{K})^{-p}\right] = \mathbf{k}c_2.$$

*c) If F satisfies (**A2**), $\phi'(p) > 0$ $(p > \tau)$ and $\tau + p < \theta^+$ then there exists a positive constant c_4 such that*

$$\lim_{t\to\infty} t^{3/2} e^{-t\phi(\tau)} \mathcal{E}_F(t) = c_4.$$

We will give the ideas of the proofs for the cases $ii)$ and $iii-a)$ because these two cases cover the range of techniques needed to prove the other cases. The idea is to study the asymptotic behaviour of $\mathcal{E}_F(n/q)$ for q fixed and n large, and then to use the monotonicity of F at infinity to deduce the asymptotic behaviour of $\mathcal{E}_F(t)$ when t goes to infinity. To do so, we use a key result due to Guivarc'h and Liu that we recall now:

Theorem 2.2.2 (see Theorem 2.1 in [GL01]). *Let $(a_n, b_n)_{n\geq 0}$ be a $\mathbb{R}_+^2$-valued sequence of i.i.d. random variables such that $\mathbb{E}[\ln a_0] = 0$. Assume that $b_0/(1-a_0)$ is not constant a.s. and define*

$$A_0 := 1, \quad A_n := \prod_{k=0}^{n-1} a_k \quad \text{and} \quad B_n := \sum_{k=0}^{n-1} A_k b_k, \qquad \text{for} \quad n \geq 1.$$

Let η, κ, ϑ be three positive numbers such that $\kappa < \vartheta$, and $\tilde{\phi}$ and $\tilde{\psi}$ be two positive continuous functions on $\mathbb{R}_+$ such that they do not vanish and for a constant $C > 0$ and for every $a > 0$, $b \geq 0$, $b' \geq 0$, we have

$$\tilde{\phi}(a) \leq C a^{\kappa}, \quad \tilde{\psi}(b) \leq \frac{C}{(1+b)^{\vartheta}}, \quad \text{and} \quad |\tilde{\psi}(b) - \tilde{\psi}(b')| \leq C|b-b'|^{\eta}.$$

Moreover, assume that

$$\mathbb{E}\left[a_0^{\kappa}\right] < \infty, \quad \mathbb{E}\left[a_0^{-\eta}\right] < \infty, \quad \mathbb{E}\left[b_0^{\eta}\right] < \infty \quad \text{and} \quad \mathbb{E}\left[a_0^{-\eta} b_0^{-\vartheta}\right] < \infty.$$

Then, there exist two positive constants $c(\tilde{\phi}, \tilde{\psi})$ and $c(\tilde{\psi})$ such that

$$\lim_{n\to\infty} n^{3/2} \mathbb{E}\left[\tilde{\phi}(A_n)\tilde{\psi}(B_n)\right] = c(\tilde{\phi}, \tilde{\psi}) \qquad \text{and} \qquad \lim_{n\to\infty} n^{1/2} \mathbb{E}\left[\tilde{\psi}(B_n)\right] = c(\tilde{\psi}).$$

In order to apply this result, we fix $q > 0$ and define the sequence $q_n = n/q$, for $n \geq 0$. For $k \geq 0$, we also define

$$\widetilde{K}_u^{(k)} = \bar{K}_{q_k+u} - \bar{K}_{q_k}, \qquad \text{for} \quad u \geq 0,$$
$$a_k = e^{-\widetilde{K}^{(k)}_{q_{(k+1)}-q_k}} \qquad \text{and} \qquad b_k = \int_0^{q_{(k+1)}-q_k} e^{-\widetilde{K}_u^{(k)}} \mathrm{d}u. \tag{2.23}$$

Hence, (a_k, b_k) is a $\mathbb{R}_+^2$-valued sequence of i.i.d. random variables. Observe that

$$a_0 = e^{-\bar{K}_{1/q}} \qquad \text{and} \qquad \frac{b_0}{1-a_0} = \frac{I_{1/q}(\bar{K})}{1-e^{-\bar{K}_{1/q}}},$$

which are not constant a.s. as required by Theorem 2.2.2. Moreover, we have

$$\int_{q_i}^{q_{i+1}} e^{-\bar{K}_u} \mathrm{d}u = e^{-\bar{K}_{q_i}} b_i = \prod_{k=0}^{i-1} a_k b_i = A_i b_i,$$

where A_i is defined as in Theorem 2.2.2. The latter identity implies

$$I_{q_n}(\bar{K}) = \sum_{i=0}^{n-1} \int_{q_i}^{q_{i+1}} e^{-\bar{K}_u} \mathrm{d}u = \sum_{i=0}^{n-1} A_i b_i := B_n.$$

In other words, we have all the objects required to apply Theorem 2.2.2.

ii) Assume that $\phi'(0+) = 0$. We take $0 < \eta < \alpha$ and $d_p > 1$ such that $-\theta^-/d_p < p$ and $\theta^- < -\eta < \eta + p < \theta^+$, and let

$$(\eta, \kappa, \vartheta) = \left(\eta, \frac{-\theta^-}{d_p}, p\right).$$

We can check that the moment conditions of Theorem 2.2.2 hold for the couple (a_0, b_0). Therefore the asymptotic behaviour of $\mathcal{E}_F(q_n)$ for large n, follows from a direct application of Theorem 2.2.2, and there exists a positive constant $c(q)$ such that

$$\sqrt{n}\mathcal{E}_F(q_n) \sim c(q), \qquad \text{as} \quad n \to \infty.$$

To get our result, we take a positive real number t. Since the mapping $s \mapsto \mathcal{E}_F(s)$ is non-increasing, we get

$$\sqrt{t}\mathcal{E}_F(t) \leq \sqrt{t}\mathcal{E}_F(\lfloor qt \rfloor / q) = \sqrt{\frac{t}{\lfloor qt \rfloor}}\sqrt{\lfloor qt \rfloor}\mathcal{E}_F(\lfloor qt \rfloor / q).$$

Similarly

$$\sqrt{t}\mathcal{E}_F(t) \geq \sqrt{t}\mathcal{E}_F((\lfloor qt \rfloor + 1)/q) = \sqrt{\frac{t}{\lfloor qt \rfloor + 1}}\sqrt{\lfloor qt \rfloor + 1}\mathcal{E}_F((\lfloor qt \rfloor + 1)/q).$$

Therefore

$$\sqrt{t}\mathcal{E}_F(t) \sim c(q)q^{-1/2}, \qquad \text{as } t \to \infty.$$

Moreover, we deduce that $c(q)q^{-1/2}$ is positive and does not depend on q. Hence we denote this constant by c_3. This concludes the proof of point ii).

iii − a) Assume now that $\phi'(0) < 0$ and introduce the exponential change of measure known as the Esscher transform. According to Theorem 3.9 in Kyprianou [Kyp06], for any λ such that $\phi(\lambda) < \infty$, we can perform the following change of measure

$$\left.\frac{d\mathbb{P}^{(\lambda)}}{d\mathbb{P}}\right|_{\mathcal{F}_t} = e^{\lambda \bar{K}_t - \phi(\lambda)t}, \qquad t \geq 0 \tag{2.24}$$

where $(\mathcal{F}_t)_{t\geq 0}$ is the natural filtration generated by $\bar{K}$ which is naturally completed. Moreover, under $\mathbb{P}^{(\lambda)}$ the process $\bar{K}$ is still a Lévy process with Laplace exponent given by

$$\phi_\lambda(z) = \phi(\lambda + z) - \phi(\lambda), \qquad z \in \mathbb{R}.$$

Now recall from Lemma II.2 in [Ber96] that the time reversal process $(K_t - K_{(t-s)^-}, 0 \leq s \leq t)$ has the same law as $(K_s, 0 \leq s \leq t)$. Then

$$e^{-K_t} I_t(-K) = e^{-K_t}\int_0^t e^{K_{t-s}}ds = \int_0^t e^{-(K_t - K_{t-s})}ds \overset{(d)}{=} \int_0^t e^{-K_s}ds = I_t(K); \tag{2.25}$$

Hence

$$I_t(\bar{K}) \overset{(\mathcal{L})}{=} e^{-\bar{K}_t} I_t(-\bar{K}), \qquad t \geq 0,. \tag{2.26}$$

As a consequence, using the Esscher transform (2.24), with $\lambda = p$, we obtain

$$\mathbb{E}\left[I_t(\bar{K})^{-p}\right] = \mathbb{E}\left[e^{p\bar{K}_t} I_t(-\bar{K})^{-p}\right] = e^{t\phi(p)}\mathbb{E}^{(p)}\left[I_t(-\bar{K})^{-p}\right], \qquad t \geq 0. \tag{2.27}$$

We can show that the decreasing function $t \mapsto \mathbb{E}^{(p)}[I_t(-\bar{K})^{-p}]$ is finite for all $t > 0$. Recall that under the probability measure $\mathbb{P}^{(p)}$, the process $\bar{K}$ is a Lévy process with mean $\mathbb{E}^{(p)}[\bar{K}_1] = \phi'(p) \in (-\infty, 0)$. Then, according to Theorem 1 in [BY05], $\mathbb{E}^{(p)}[I_t(-\bar{K})^{-p}]$ converges to $\mathbb{E}^{(p)}[I_\infty(-\bar{K})^{-p}]$, as t increases.

Hence the asymptotic behaviour is proven if we show that

$$\mathcal{E}_F(t) \sim \mathbf{k}\mathbb{E}\left[I_t(\bar{K})^{-p}\right], \quad \text{as} \quad t \to \infty.$$

Since $\phi'(p) < 0$, there is $\varepsilon > 0$ such that $p(1+\varepsilon) < \theta^+$, $\phi(p(1+\varepsilon)) < \phi(p)$ and $\phi'((1+\varepsilon)p) < 0$. Hence, from Lemma A.2 in [PPS16], we deduce that there is a constant M such that

$$\left|F\left(I_t(\bar{K})\right) - \mathbf{k} I_t(\bar{K})^{-p}\right| \leq M I_t(\bar{K})^{-(1+\varepsilon)p}. \tag{2.28}$$

In other words, it is enough to prove

$$\mathbb{E}\left[I_t(\bar{K})^{-(1+\varepsilon)p}\right] = o(e^{t\phi(p)}), \quad \text{as} \quad t \to \infty. \tag{2.29}$$

From the Esscher transform (2.24) with $\lambda = (1+\varepsilon)p$, we deduce

$$\mathbb{E}\left[I_t(\bar{K})^{-(1+\varepsilon)p}\right] = \mathbb{E}\left[e^{p(1+\varepsilon)\bar{K}_s} I_t(-\bar{K})^{-(1+\varepsilon)p}\right] = e^{t\phi(p)}e^{t\phi_p(\varepsilon p)}\mathbb{E}^{((1+\varepsilon)p)}\left[I_t(-\bar{K})^{-(1+\varepsilon)p}\right].$$

We can prove that $\mathbb{E}^{((1+\varepsilon)p)}[I_t(-\bar{K})^{-(1+\varepsilon)p}]$ is finite for all $t > 0$ and as before, we can deduce that $\mathbb{E}^{((1+\varepsilon)p)}[I_t(-\bar{K})^{-(1+\varepsilon)p}]$ has a finite limit, as t goes to ∞. We conclude by observing that $\phi_p(\varepsilon p)$ is negative implying that (2.29) holds. We complete the proof of point iii)-a) by observing that (2.28) and (2.29) yield

$$\mathbb{E}[F\left(I_t(\bar{K})\right)] \sim \mathbf{k}\mathbb{E}[I_t(\bar{K})^{-p}], \quad t \to \infty.$$

We now present two applications of Theorem 2.2.1 different from the asymptotics of survival probability. In Section 2.4 we will present more general results on the extinction rate of CSBP in Lévy environment in the critical case.

2.2.3 Applications

Explosion rate of stable CSBP in Lévy environment

Let $\beta \in (-1, 0)$ and $c_\beta < 0$. According to Palau and Pardo [PP18], we can define a self-similar branching process whose dynamics is affected by a Lévy random environment as the unique non-negative strong solution of the stochastic differential equation

$$Z_t = Z_0 + \int_0^t \int_0^\infty \int_0^{Z_{s-}} z N^{(b)}(\mathrm{d}s, \mathrm{d}z, \mathrm{d}u) + \int_0^t Z_{s-}\mathrm{d}K_s,$$

where N and K are as in (2.16), and μ is still given by (2.11), except that c_β is taken negative as $\beta \in (-1, 0)$. Recall (2.19): for all $z, \lambda > 0$ and $t \geq 0$,

$$\mathbb{E}_z\left[\exp\left\{-\lambda Z_t e^{-\bar{K}_t}\right\}\middle|\bar{K}\right] = e^{-z\left(\lambda^{-\beta} + \beta c_\beta \int_0^t e^{-\beta\bar{K}_u}\mathrm{d}u\right)^{-1/\beta}}.$$

The event of *explosion* at fixed time t, is given by $\{Z_t = \infty\}$. Letting λ go to 0, we deduce

$$\mathbb{P}_z\left(Z_t < \infty \middle| \bar{K}\right) = \exp\left\{-z\left(\beta c_\beta \int_0^t e^{-\beta \bar{K}_u} \mathrm{d}u\right)^{-1/\beta}\right\} \qquad \text{a.s.} \tag{2.30}$$

Recall that when there is no environment, a self-similar CB-process explodes at time t with probability $1 - \exp\{-z(\beta c_\beta t)^{-1/\beta}\}$. Under the presence of a Lévy random environment three different regimes appear for the asymptotic behaviour of the non-explosion probability, as in the case of extinction probability. A direct application of Theorem 2.2.1 gives the explicit rate of decay in these three cases. We refer the interested reader to Proposition 2.1 in [PPS16].

Mean population size for a logistic model in Lévy environment

We now consider an extension of the competition model introduced in Evans et al. [EHS15] and studied by Palau and Pardo [PP18]. Following [PP18], we define a logistic process with competition in a Lévy random environment, $(Z_t, t \geq 0)$, as the unique strong solution to the SDE

$$Z_t = Z_0 + \int_0^t Z_s(r - kZ_s)\mathrm{d}s + \int_0^t Z_{s-}\mathrm{d}K_s$$

where $r > 0$ is the drift, $k > 0$ is the competition, and the environment K is given by the Lévy process defined in (2.14). Moreover, the process Z satisfies the Markov property and we have

$$Z_t = Z_0 e^{\bar{K}_t}\left(1 + kZ_0 \int_0^t e^{\bar{K}_s}\mathrm{d}s\right)^{-1}, \qquad t \geq 0,$$

where K is the Lévy process defined in (2.17). Applying Theorem 2.2.1, we may obtain the possible asymptotic behaviours of $\mathbb{E}_z[Z_t]$, where we recall that $\mathbb{P}_z$ denotes the law of Z starting from z. We refer the interested reader to Proposition 2.3 [PPS16] for their expressions.

2.3 Critical Galton-Watson processes in random environment and Cauchy domain of attraction

2.3.1 Beyond explicit expressions of the survival probability

In the previous section, we saw that the probability of extinction of a CSBP in a Lévy environment could be expressed as the expectation of an exponential functional of the Lévy process associated with the random environment, if the branching mechanism of the CSBP is stable. Unfortunately, apart from the stable case, we have no explicit formula for the probability of extinction of CSBPs in Lévy environment, and alternative strategies must be found to study the rate of extinction. The strategy I will present now was developed by Afanasyev and coauthors in [AGK+05] in the discrete case. Recall notations of Section 2.1.2. In [AGK+05], the authors focus on the critical case, more precisely on the case were the random walk S is oscillating and satisfies the so-called Spitzer's condition (with $\rho \in (0, 1)$, see below) which is a well-known assumption in fluctuation theory of random walk (and Lévy processes). They state pathwise relationships between the dynamics of the

BPRE and the random walk driving the random environment on the survival event. More precisely, they prove that the survival of the process is strongly related to its survival up to the time when the random environment reaches its running infimum. Then, they decompose its paths into two parts, the pre-infimum and post-infimum processes. If the process survives until the time when the random environment reaches its running infimum, then it has a positive probability to survive after this time and, consequently, it evolves in a "favorable" environment.

In a publication with C. Dong and V.A. Vatutin [DSV20], we have extended these results to the case where the branching process satisfies the Spitzer condition for $\rho = 0$ or 1. To do this we used recent results on fluctuations of random walks in the Cauchy domain of attraction, derived first in [Ber19] and then in [KR19] under weaker conditions. The next subsection is dedicated to the presentation of this work.

2.3.2 Critical Galton-Watson processes in random environment and Cauchy domain of attraction

Recall the definition of the random walk $(S_n, n \in \mathbb{N})$ in (2.2). We assume that it satisfies the Doney-Spitzer condition:

$$\lim_{n\to\infty} \frac{1}{n} \sum_{m=1}^{n} \mathbf{P}\left(S_m > 0\right) =: \rho. \tag{2.31}$$

According to Bertoin and Doney [BD97], this condition is equivalent to

$$\lim_{n\to\infty} \mathbf{P}\left(S_n > 0\right) =: \rho.$$

The case $\rho \in (0,1)$ has been studied by Afanasyev and coauthors in [AGK+05]. Under some mild additional assumptions they proved the following equivalent for the survival probability of the population at large times n,

$$\mathbf{P}(Z_n > 0) \sim \frac{l(n)}{n^{1-\rho}}, \tag{2.32}$$

where $l(.)$ is a slowly varying function at infinity. In [DSV20] we complemented (2.32) by considering the asymptotic behaviour of $\mathbf{P}(Z_n > 0)$ as $n \to \infty$ in the cases $\rho = 0$ and $\rho = 1$.

Before stating the main results of [DSV20], let us introduce some notation and a set of assumptions on the law of the random walk S. The main assumption is that S is in the domain of attraction of a stable law with parameter 1. It means that there exist a slowly varying function at infinity $\mathfrak{l}(\cdot)$, and two nonnegative numbers p and q, with $p + q = 1$, such that

$$\mathbf{P}\left(X_1 > x\right) \sim p\frac{\mathfrak{l}(x)}{x} \quad \text{and} \quad \mathbf{P}\left(X_1 < -x\right) \sim q\frac{\mathfrak{l}(x)}{x}, \quad x \to \infty, \tag{2.33}$$

where for the sake of readability, $X_i = \ln f_i'(1)$ (recall notations in Section 2.1.2).

We can show that S satisfies the Doney-Spitzer condition with $\rho = 0$ (resp. $\rho = 1$) in the case $p > q$ (resp. $p < q$). Let us introduce two scaling sequences which play the main role in the asymptotic behaviour of various quantities related to the random walk S. The first sequence,

$\{a_n, n \in \mathbb{N}\}$, satisfies, as $n \to \infty$ the relation

$$\frac{\mathfrak{l}(a_n)}{a_n} \sim \frac{1}{n}. \tag{2.34}$$

Note that the sequence $\{a_n, n \in \mathbb{N}\}$ is regularly varying with parameter 1 as $n \to \infty$ (see [Sen76]). We can thus rewrite it as

$$a_n = n\mathfrak{l}_1(n) \tag{2.35}$$

where $\mathfrak{l}_1(.)$ is a slowly varying function. The second sequence, $\{h_n, n \in \mathbb{N}\}$, is specified by

$$h_n := n\mu\left(a_n\right) \text{ where } \mu(x) = \mathbf{E}\left[X_1 \mathbf{1}_{\{|X_1| \leq x\}}\right], \tag{2.36}$$

and $\mathbf{1}$ is the indicator function. In addition, we suppose that

$$\mu := \mathbf{E}\left[X_1\right] = 0. \tag{2.37}$$

As in [AGK+05], we need to impose restrictions on the standardized truncated second moment of the environment, namely:

$$\zeta_k(a) := \sum_{y=a}^{\infty} y^2 f_k(y) / \left(\sum_{y=0}^{\infty} y f_k(y)\right)^2, \tag{2.38}$$

for $a, k \in \mathbb{N}$. The moment condition depends on the value of ρ in the Doney-Spitzer condition (2.31).

Condition A. ($\rho = 0 \leftrightarrow p > q$) There exist $a \in \mathbb{N}$ and $\beta > 0$ such that

$$\mathbf{E}[\zeta_1^{\beta}(a)] < \infty \quad \text{and} \quad \mathbf{E}[U(X_1)\zeta_1^{\beta}(a)] < \infty,$$

where U is the renewal function associated with the strict descending ladder epochs of $\mathcal{S}$,

$$\gamma_0 := 0, \quad \gamma_{j+1} := \min\left(n > \gamma_j : S_n < S_{\gamma_j}\right), \quad j \in \mathbb{N}_0 := \mathbb{N} \cup \{0\}, \tag{2.39}$$

and is defined by

$$U(x) := \sum_{j=0}^{\infty} \mathbf{P}(S_{\gamma_j} \geq -x), \quad x > 0, \quad U(0) = 1, \quad U(x) = 0, \quad x < 0. \tag{2.40}$$

Condition B. ($\rho = 1 \leftrightarrow p < q$) There exist $a \in \mathbb{N}$ and $\beta > 0$ such that

$$\mathbf{E}\left[\left(\log^+ \zeta_1(a)\right)^{1+\beta}\right] < \infty \quad \text{and} \quad \mathbf{E}\left[U(X_1)\left(\log^+ \zeta_1(a)\right)^{1+\beta}\right] < \infty.$$

Recall that the moment condition in [AGK+05] under the Doney-Spitzer condition (2.31) with $\rho \in (0,1)$ was the existence of $\beta > 0$ and $a \in \mathbb{N}$ such that:

$$\mathbf{E}\left[\left(\log^+ \zeta_1(a)\right)^{1/\rho+\beta}\right] < \infty \quad \text{and} \quad \mathbf{E}\left[U(X_1)\left(\log^+ \zeta_1(a)\right)^{1+\beta}\right] < \infty.$$

Our **Condition B** is thus a natural extension of the moment condition to the case $\rho = 1$. In contrast, such a natural extension for $\rho = 0$ would have made appear an infinite exponent for the logarithm

and we could not obtain a moment condition on the logarithm only. Notice however that we can take β as small as we want in **Condition A.**

Last, for technical reasons, we need an assumption which will be used for the case $p > q$ only.

Condition C. There exists an integer-valued function $g(x) = e^{o(x)},\ x \to \infty$, such that

$$\sum_{j=1}^{\infty} 1/\Lambda(g(j)) < \infty,$$

where Λ is a slowly varying function (see the proof of Proposition 12 in [KR19]) defined by

$$\Lambda\left(\frac{1}{1-s}\right) = \exp\left(\sum_{k=1}^{\infty} \frac{\mathbf{P}(S_k \geq 0)}{k} s^k\right), \quad s \in [0,1). \tag{2.41}$$

As previously mentioned, the survival of a Galton-Watson process in random environment is essentially determined by its survival until the moment when the associated random walk S reaches its infimum. Let us introduce the running infimum of the random walk S:

$$L_n := \min\{S_0, S_1, ..., S_n\},\ n \in \mathbb{N}_0. \tag{2.42}$$

Depending on the relative positions of p and q (defined in (2.33)) or equivalently on the value of ρ (0 or 1) we have the two following possible asymptotics for the survival probability of the process Z:

Theorem 2.3.1. *Assume that Conditions (2.33) and (2.37) hold.*

- *If $p > q$, and **Conditions A** and **C** hold then there exists a constant $K_1 \in (0, \infty)$ such that, as $n \to \infty$*

$$\mathbf{P}(Z_n > 0) \sim K_1 \mathbf{P}(L_n \geq 0) \sim K_1 \frac{\mathfrak{l}_2(n)}{n}, \tag{2.43}$$

  where $\mathfrak{l}_2(.)$ is a function slowly varying at infinity.

- *If $p < q$ and **Condition B** holds then there exists a constant $K_2 \in (0, \infty)$ such that, as $n \to \infty$*

$$\mathbf{P}(Z_n > 0) \sim K_2 \mathbf{P}(L_n \geq 0) \sim K_2 \mathfrak{l}_3(n),$$

  where $\mathfrak{l}_3(.)$ is a function slowly varying at infinity.

Hence, despite the irregular behaviour of the associated random walk S (a null expectation but a probability converging to 1 to be positive (resp. negative)), the asymptotic behaviour of the survival probability is, except for the slowly varying function, the limit of the one obtained in [AGK+05] by taking $\rho = 0$ or 1 instead of $\rho \in (0,1)$.

We will now give an idea of the proof. We will only mention the case $p > q$, as the proof of the case $p < q$ is very similar. As we have said, the survival of the population at time n is intimately related with the minimum of the random walk S before time n, L_n. If this minimum is too small, the population has experienced very bad conditions and died out with a probability close to one.

We thus need to focus on trajectories of the random walk S with an exceptionally high minimum, which is equivalent to trajectories which reach their minimum at the beginning of the trajectory. Following [AGK+05], we thus divide the survival probability of the population process at a time $n \in \mathbb{N}$ into three terms as follows:

$$\begin{aligned}\mathbf{P}\left(Z_n > 0\right) &= \sum_{k=0}^{n} \mathbf{P}\left(Z_n > 0; \tau_n = k\right) \\ &= \sum_{k=0}^{N} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right] + \sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right] \\ &\quad + \sum_{k=n\varepsilon+1}^{n} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right], \end{aligned} \tag{2.44}$$

for some $N \in \mathbb{N}$ to be precised later on, and a small positive ε, and where the $f_{0,n}$'s correspond to iterations of probability generating functions defined as follows: for $0 \leq k \leq n-1$, $0 \leq s \leq 1$,

$$f_{k,n}(s) := f_{k+1}(f_{k+2}(\ldots(f_n(s))\ldots))$$

and $f_{n,n}(s) := s$. The variable τ_n in (2.44) denotes the first time when the random walk S reaches its minimum before time n:

$$\tau_n := \min\left\{j \leq n : S_j = L_n\right\}.$$

We will prove that the second and third terms become negligible when n goes to infinity for N large enough and ε small enough. Using that

$$1 - f_{0,k}(0) = \mathbb{P}(Z_k \geq 1 | f_0, ..., f_k) \leq \mathbb{E}[Z_k | f_0, ..., f_k] = e^{S_k}$$

by definition of the random walk S, we can bound as follows the second term in the right hand side of (2.44)

$$\begin{aligned}\sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right] &\leq \sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[1 - f_{0,k}(0); \tau_n = k\right] \\ &= \sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[1 - f_{0,k}(0); \tau_k = k\right] \mathbf{P}\left(L_{n-k} \geq 0\right) \\ &\leq \sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[e^{S_k}; \tau_k = k\right] \mathbf{P}\left(L_{n-k} \geq 0\right). \end{aligned}$$

By the duality principle for random walks and estimates for the extrema of the random walk S (see Lemma 2.6 in [DSV20], we may prove that

$$\mathbf{E}\left[e^{S_k}; \tau_k = k\right] \leq c\frac{1}{ka_k} \sim c\frac{1}{k^2 \mathfrak{l}_1(k)},$$

which entails

$$\begin{aligned}\sum_{k=N+1}^{n\varepsilon} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right] &\leq \mathbf{P}\left(L_{n(1-\varepsilon)} \geq 0\right) \sum_{k=N+1}^{\infty} \frac{1}{k^2 \mathfrak{l}_1(k)} \\ &\leq C\frac{\mathbf{P}\left(L_{n(1-\varepsilon)} \geq 0\right)}{a_N}, \end{aligned}$$

where we used recent results on the fluctuations of S (see [Ber19, KR19]).

Now we focus on the last term of (2.44). Similarly as for the second part, we have the following series of inequalities, where the value of the finite constant C may change from line to line and may depend on ε:

$$\begin{aligned}\sum_{k=n\varepsilon+1}^{n} \mathbf{E}\left[1-f_{0,n}(0);\tau_n=k\right] &\leq C\sum_{k=n\varepsilon+1}^{n}\frac{1}{k^2\mathfrak{l}_1(k)}\mathbf{P}\left(L_{n-k}\geq 0\right)\\ &\leq C\frac{\mathfrak{l}_2(n)}{n^2\mathfrak{l}_1(n)}=o\left(\frac{1}{n^{3/2}}\right),\end{aligned} \tag{2.45}$$

where $\mathfrak{l}_2$ is a function slowly varying at infinity.

The last step of the proof consists in evaluating the first term of the right hand side of (2.44). To relate this term to the value of the running infimum of the random walk S giving the random environment, we now introduce a change of measure. Recall the definition of the renewal function U in (2.40). One of its fundamental properties is the identity (see, for instance, [Koz77, BD94])

$$\mathbf{E}\left[U(x+X);X+x\geq 0\right]=U(x),\quad x\geq 0,$$

where X is distributed as X_1. This property has often been used to construct changes of probability measures (see for instance [GK01]), and we will use such a construction in our proof.

Denote by $\mathcal{F}$ the filtration consisting of the $\sigma-$algebras $\mathcal{F}_n$ generated by the random variables $S_0,...,S_n$ and $Z_0,...,Z_n$. Taking into account $U(0)=1$ (cf. (2.40)) we may introduce the probability measures $\mathbf{P}_n^+$ on the σ-fields $\mathcal{F}_n$ by means of the densities

$$d\mathbf{P}_n^+ \;:=\; U(S_n)I_{\{L_n\geq 0\}}\,d\mathbf{P},$$

using that $(U(S_n)I_{\{L_n\geq 0\}}, n\in\mathbb{N})$ Because of the martingale property the measures are consistent, i.e., $\mathbf{P}_{n+1}^+|\mathcal{F}_n=\mathbf{P}_n^+$. Therefore, there exists a probability measure $\mathbf{P}^+$ on the σ-field $\mathcal{F}_\infty:=\bigvee_n\mathcal{F}_n$ such that

$$\mathbf{P}^+|\mathcal{F}_n \;=\; \mathbf{P}_n^+\,,\quad n\geq 0\,. \tag{2.46}$$

We note that (2.46) can be rewritten as

$$\mathbf{E}^+\left[Y_n\right] \;=\; \mathbf{E}[Y_nU(S_n);L_n\geq 0] \tag{2.47}$$

for every $\mathcal{F}_n$–measurable non-negative random variable Y_n. This change of measure is the well-known Doob h-transform from the theory of Markov processes. In particular, under $\mathbf{P}^+$ the process S becomes a Markov chain with state space $\mathbb{R}_0^+$ and transition kernel

$$P^+(x;dy) \;:=\; \frac{1}{U(x)}\mathbf{P}\left(x+X\in dy\right)U(y)\,,\quad x\geq 0\,.$$

In our context, we can show that $\mathbf{P}^+$ can be realised as the limit of the probability of the process conditioned to live in a nonnegative environment (in the sense that the running infimum is null). It is the content of the next lemma, and will allow us to link the survival probability of the population process to the probability for the running infimum to be null, to end the proof of Theorem 2.3.1.

Lemma 2.3.2. *(compare with Lemma 2.5 in [AGK+05]) Assume that Conditions (2.33) and (2.37) hold. For $k \in \mathbb{N}$ let Y_k be a bounded real-valued $\mathcal{F}_k$–measurable random variable. Then, as $n \to \infty$,*

$$\mathbf{E}[Y_k \mid L_n \geq 0] \;\to\; \mathbf{E}^+ Y_k \,.$$

More generally, let $Y_1, Y_2, \ldots$ be a uniformly bounded sequence of real-valued random variables adapted to the filtration $\mathcal{F}$, which converges $\mathbf{P}^+$–a.s. to some random variable Y_∞. Then, as $n \to \infty$,

$$\mathbf{E}[Y_n \mid L_n \geq 0] \;\to\; \mathbf{E}^+ Y_\infty \,.$$

We may now study the first term in the rhs of (2.44). We have

$$\sum_{k=0}^{N} \mathbf{E}\left[1 - f_{0,n}(0); \tau_n = k\right] = \sum_{k=0}^{N} \mathbf{E}\left[1 - f_{k,n}^{Z_k}(0); \tau_k = k, L_{k,n} \geq 0\right]$$

where

$$L_{k,n} = \min_{k \leq j \leq n} \left(S_j - S_k\right).$$

Using Lemma 2.3.2 and the independency and homogeneity of the environmental components we conclude that for $k \leq N$,

$$\begin{aligned}
\mathbf{E}\left[1 - f_{k,n}^{Z_k}(0); \tau_k = k, L_{k,n} \geq 0\right] &= \sum_{j=1}^{\infty} \mathbf{P}\left(Z_k = j, \tau_k = k\right) \mathbf{P}\left(L_{n-k} \geq 0\right) \mathbf{E}\left[1 - f_{0,n-k}^{j}(0) | L_{n-k} \geq 0\right] \\
&\sim \mathbf{P}\left(L_n \geq 0\right) \sum_{j=1}^{\infty} \mathbf{P}\left(Z_k = j, \tau_k = k\right) \mathbf{E}^+\left[1 - f_{0,\infty}^{j}(0)\right]
\end{aligned}$$

as $n \to \infty$. The last step consists in showing that

$$\mathbf{E}^+\left[1 - f_{0,\infty}^{j}(0)\right] > 0.$$

The proof of this fact is technical and justifies the introduction of **Condition C**. We refer to [DSV20]. Finally, letting first n to infinity, then ε to zero and, finally, N to infinity we prove (2.43).

2.4 Extinction rate of continuous state branching processes in critical Lévy environments

In this section, I focus again on the continuous case. I will present a work in collaboration with V. Bansaye and J.C. Pardo [BPS21] aiming at relaxing the assumption made in [PPS16] that the branching mechanism is stable. In this case we do not have an explicit expression of the probability of survival as an exponential functional of the Lévy process giving the environment. We focus on the critical case, more precisely on oscillating Lévy environments satisfying the Spitzer's condition with $\rho \in (0,1)$ (see assumption **(H1)** below). To do so, we use two main tools in our arguments: fluctuation theory and the asymptotic behaviour of exponential functionals of Lévy processes satisfying Spitzer's condition. We follow the point of view of Afanasyev et al. [AGK+05] in the discrete time setting, described in the previous section, to deduce pathwise relationships between

the dynamics of the CSBP in random environment and the Lévy process driving the random environment on the survival event. As we will see below, the global picture stays unchanged compared to [AGK+05] but new difficulties arise in the continuous space setting. For instance, the state 0 can be polar and the process might become very close to 0 but never reach this point. To focus on the absorption event, we use Grey's condition which guarantees that 0 is accessible. Another difficulty arises at the upper bound for the probability of survival. Indeed, in the discrete setting, to bound the probability of survival we can use the fact that the probability that the process survives at times when the environment reaches a local minimum is equal to the probability that the current population size is bigger or equal than 1 at times when the environment reaches a local minimum. Then Chebyshev or Markov inequality helps to obtain a suitable upper bound. In the continuous setting, this strategy is not helpful. To overcome these difficulties, we impose some assumptions on the branching mechanism and on the environment.

Recall notation of Section 2.1.4. In the discrete setting, we have seen that the survival of the population is intimately related with the trajectories of the random walk S, which is such that the process $(Z_n e^{-S_n}, n \in \mathbb{N})$ is a martingale. In the continuous setting, the equivalent of this random walk is obtained by a modification of the Lévy process K defined in (2.14). If we consider the Lévy process $\bar{K}$ defined as in (2.17), but with

$$\overline{\alpha} := \alpha - \psi'(0+) - \frac{\sigma^2}{2} - \int_{(-1,1)} (e^z - 1 - z)\pi(\mathrm{d}z), \tag{2.48}$$

($\psi'(0+)$ was equal to 0 when we defined $\bar{\alpha}$ in (2.18)), we obtain the following statement.

Proposition 2.4.1. *For $\mathbb{P}^{(e)}$ almost every $w^{(e)} \in \Omega^{(e)}$,*

$$\left(\exp\{-\overline{K}_t(w^{(e)},.)\}Z_t(w^{(e)},.) : t \geq 0\right)$$

is a $(\Omega^{(b)}, \mathcal{F}^{(b)}, \mathbb{P}^{(b)})$-martingale and for any $t \geq 0$ and $z \geq 0$,

$$\mathbb{E}_z[Z_t \mid K] = ze^{\overline{K}_t}, \qquad \mathbb{P}\text{-a.s.}$$

2.4.1 Properties of the Lévy environment

For simplicity, we denote by $\mathbb{P}_x^{(e)}$ (resp. $\mathbb{E}_x^{(e)}$) the probability (resp. expectation) associated to the process $\overline{K}$ starting from $x \in \mathbb{R}$, and we use the notation $\mathbb{P}^{(e)}$ for $\mathbb{P}_0^{(e)}$ (resp. $\mathbb{E}$ for $\mathbb{E}_0$), i.e.

$$\mathbb{P}_x^{(e)}(\overline{K}_t \in B) = \mathbb{P}^{(e)}(\overline{K}_t + x \in B), \qquad \text{for} \quad B \in \mathcal{B}(\mathbb{R}).$$

We assume in the sequel that $\overline{K}$ is not a compound Poisson process.

In what follows and as in the discrete case, we assume a *Spitzer's condition*, i.e.

$$(\mathbf{H1}) \qquad \frac{1}{t}\int_0^t \mathbb{P}^{(e)}(\overline{K}_t \geq 0)\mathrm{d}t \longrightarrow \rho \in (0,1), \qquad \text{as} \quad t \to \infty.$$

This condition implies that $\overline{K}$ oscillates and implicitly, from Proposition 2.4.1, that the process Z is in the critical regime. According to Bertoin and Doney [BD97] condition **(H1)** is equivalent to

$$\mathbb{P}^{(e)}(\overline{K}_t \geq 0) \longrightarrow \rho \in (0,1), \qquad \text{as} \quad t \to \infty.$$

Spitzer's condition is a key condition to understand the tail distribution of first passage times (see (2.51) for instance). Notice that if Spitzer's condition holds and $\bar{K}$ has a finite variance, then necessarily $\rho = 1/2$. Examples of Lévy processes satisfying Spitzer's condition are the standard Brownian motion, and stable processes where $\rho \in (0,1)$ plays the role of the positivity parameter. Furthermore, any symmetric Lévy process satisfies Spitzer's condition with $\rho = 1/2$ and any Lévy process in the domain of attraction of a stable process with positivity parameter $\rho \in (0,1)$ as $t \to \infty$, satisfies Spitzer's condition.

Our arguments on the survival event rely on the running infimum of $\overline{K}$, here denoted by $I = (I_t, t \geq 0)$ where

$$I_t = \inf_{0 \leq s \leq t} \overline{K}_s, \qquad t \geq 0. \tag{2.49}$$

To be more precise, we use fluctuation theory of Lévy processes reflected at their running infimum. The reflected process $\overline{K} - I$ is a Markov process with respect to the filtration $\mathcal{F}^{(e)}$ and whose semigroup satisfies the Feller property (see for instance Proposition VI.1 in the monograph of Bertoin [Ber96]). We denote by $\widehat{L}$ the local time of $\overline{K} - I$ at 0 in the sense of Chapter IV in [Ber96]. Similarly to the discrete framework [AGK+05], the asymptotic analysis and the role of the initial condition involve the renewal function $\widehat{V}$ which is defined, for all $x \geq 0$, as follows

$$\widehat{V}(x) := \mathbb{E}^{(e)}\left[\int_{[0,\infty)} \mathbf{1}_{\{I_t \geq -x\}} \mathrm{d}\widehat{L}_t\right]. \tag{2.50}$$

The renewal function $\widehat{V}$ is subadditive, continuous and increasing and satisfies $\widehat{V}(x) \geq 0$ for $x \geq 0$ and $\widehat{V}(x) > 0$ for $x > 0$. Under Spitzer's condition (see Theorem VI.18 in Bertoin [Ber96]) the asymptotic behaviour of the probability that the Lévy process $\overline{K}$ remains positive, i.e. $\mathbb{P}_x^{(e)}(I_t > 0)$ for $x > 0$, is regularly varying at ∞ with index $\rho - 1$,

$$\mathbb{P}_x^{(e)}(I_t > 0) \sim \widehat{V}(x) t^{\rho-1} \ell(t), \quad \text{as} \quad t \to \infty, \tag{2.51}$$

where ℓ is a slowly varying function at infinity.

2.4.2 Extinction rate of CSBPs in critical Lévy environments

We need some assumptions to control the effect of the environment on the event of survival. The following moment assumption is needed to guarantee the non-extinction of the process under favorable environments,

(**H2**) $$\int^{\infty} \theta \ln^2(\theta) \mu(\mathrm{d}\theta) < \infty.$$

The above condition is similar to $x \ln x$ moment condition on the measure μ, used in Proposition 2 in [PP17] to determine that the probability of survival of CSBP processes under Lévy environments that drift to $+\infty$, is positive.

As we will see below, Spitzer's condition (**H1**) and assumption (**H2**) are sufficient conditions to provide a lower bound for the survival probability. In order to get the upper bound, further assumptions on the branching mechanism and the environment are required. Let

$$\psi_0(\lambda) := \psi(\lambda) - \lambda \psi'(0+), \qquad \text{for} \quad \lambda \geq 0, \tag{2.52}$$

and assume that there exists $\beta \in (0,1]$, $\theta^+ > 1$ and $C > 0$ such that

$$(\mathbf{H3}) \qquad \psi_0(\lambda) \geq C\lambda^{1+\beta}, \quad \text{for } \lambda \geq 0.$$

Assumption **(H3)** allows us to control the absorption of the process for bad environments and in particular, it guarantees that $\psi_0(\lambda)$ satisfies the so-called Grey's condition, i.e.

$$\int^{\infty} \frac{\mathrm{d}z}{\psi_0(z)} < \infty, \tag{2.53}$$

which is a necessary and sufficient condition for absorption of CSBPs, see for instance [Gre74]. Recently, He et al. [HLX18] have shown that this condition is also necessary and sufficient for CSBPs in a Lévy environment to get absorbed with positive probability (see Theorem 4.1 in [HLX18]). In our case since the process $\overline{K}$ oscillates and Grey's condition (2.53) is satisfied then absorption occurs a.s. according to Corollary 4.4 in [HLX18].

We may now state the main result of [BPS21].

Theorem 2.4.2. *Assume that assumptions* $(\mathbf{H1}) - (\mathbf{H3})$ *hold. Then there exists a positive function* c *such that for any* $z > 0$,

$$\mathbb{P}_z(Z_t > 0) \sim c(z)\mathbb{P}_1^{(e)}(I_t > 0) \sim c(z)\widehat{V}(1)t^{\rho-1}\ell(t), \quad \text{as} \quad t \to \infty,$$

where ℓ *is the slowly varying function introduced in* (2.51).

We point out that we only need assmptions $(\mathbf{H1})$ and $(\mathbf{H2})$ to ensure that the probability of survival of the process Z satisfies

$$\mathbb{P}_z(Z_t > 0) \geq c(z)\mathbb{P}_1^{(e)}(I_t > 0) \sim \widehat{V}(1)c(z)t^{\rho-1}\ell(t), \quad \text{as} \quad t \to \infty. \tag{2.54}$$

Let us now give an idea of the proof of Theorem 4.1.2, which is similar in spirit to the proof of the discrete case in [AGK+05], as we have explained above.

We will study the event of survival at time t, $\{Z_t > 0\}$ in three different situations that depend on the behaviour of the infimum of the environment. To be more precise, we split the survival event as follows: for $z, x > 0$,

$$\begin{aligned}\mathbb{P}_z(Z_t > 0) = \mathbb{P}_{(z,x)}(Z_t > 0, I_t > 0) \\ + \mathbb{P}_{(z,x)}(Z_t > 0, -y < I_t \leq 0) + \mathbb{P}_{(z,x)}(Z_t > 0, I_t \leq -y),\end{aligned} \tag{2.55}$$

where $y > 0$ will be chosen later on. In other words, to deduce our result, we study such events separately for t sufficiently large.

Similarly as in the discrete setting, the first term is the leading term and can be studied via a change of measure which lies on the martingale property of the renewal function. We can construct the law of a CSBP in a Lévy environment conditioned to stay positive as a Doob-h transform. To be more precise, for $\Lambda \in \mathcal{F}_t$ and $x, z > 0$, we define

$$\mathbb{P}^{\uparrow}_{(z,x)}(\Lambda) := \frac{1}{\widehat{V}(x)}\mathbb{E}_{(z,x)}\left[\widehat{V}(\overline{K}_t)\mathbf{1}_{\{I_t \geq 0\}}\mathbf{1}_{\Lambda}\right] \tag{2.56}$$

(reminiscent of (2.47)). The term *Lévy environment conditioned to stay positive* in definition (2.56) is justified from the following convergence result, reminiscent of Lemma 2.3.2:

Lemma 2.4.3. *Assume that Spitzer's condition* **(H1)** *holds and let $z, x > 0$. For $t \geq 0$ and $\Lambda \in \mathcal{F}_t$, we have*

$$\lim_{s\to\infty} \mathbb{P}_{(z,x)}(\Lambda | \overline{K}_u > 0, 0 \leq u \leq s) = \mathbb{P}^{\uparrow}_{(z,x)}(\Lambda).$$

Moreover if $(H_t, t \geq 0)$ is a uniformly bounded process which is adapted to $(\mathcal{F}_t, t \geq 0)$ and such that it converges to H_∞, as $t \to \infty$, $\mathbb{P}^{\uparrow}_{(z,x)}$-almost surely, then

$$\lim_{t\to\infty} \mathbb{P}_{(z,x)}\left[H_t | \overline{K}_u > 0, 0 \leq u \leq t\right] = \mathbb{P}^{\uparrow}_{(z,x)}\left[H_\infty\right].$$

In particular, let us introduce the events $\mathcal{S}_t = \{Z_t > 0\}$, and $\mathcal{S}_\infty = \{\forall s \geq 0,\ Z_s > 0\}$ and the r.v.'s $Y_t = \mathbf{1}_{\mathcal{S}_t}$ and $Y_\infty = \mathbf{1}_{\mathcal{S}_\infty}$. Since Y_t converges to Y_∞, $\mathbb{P}^{\uparrow}_{(z,x)}$-almost surely, as t goes to ∞, we can apply Lemma 2.4.3, which yields

$$\begin{aligned}\mathbb{P}_{(z,x)}(Z_t > 0, I_t > 0) &= \mathbb{P}_{(z,x)}(Z_t > 0 | I_t > 0)\mathbb{P}^{(e)}_x(I_t > 0)\\ &\sim \mathbb{P}^{\uparrow}_{(z,x)}(\forall s \geq 0,\ Z_s > 0)\mathbb{P}^{(e)}_x(I_t > 0), \qquad \text{as} \quad t \to \infty.\end{aligned}$$

We can prove (technical) that

$$\mathbb{P}^{\uparrow}_{(z,x)}(\forall s \geq 0,\ Z_s > 0) > 0.$$

Using (2.51) we deduce

$$\mathbb{P}_{(z,x)}(Z_t > 0, I_t > 0) \sim c(z,x)\mathbb{P}^{(e)}_x(I_t > 0) \sim c(z,x)V(x)t^{-(1-\rho)}\ell(t), \quad \text{as} \quad t \to \infty,$$

where ℓ is a slowly varying function at ∞, introduced in (2.51).

Hence to prove Theorem 4.1.2, we just need to prove that the two last terms in the right hand side of (2.55) are negligible with respect to the first term.

Let us take $\varepsilon, z, x > 0$ and $\delta \in (0,1)$. We will show that for t and y large enough, we have

$$\mathbb{P}_{(z,x)}(Z_t > 0, I_{t-\delta} < -y) \leq \varepsilon \mathbb{P}_{(z,x+y)}(Z_t > 0, I_{t-\delta} > 0). \tag{2.57}$$

According to Proposition 2 in [PP18] for $s \in [0,t]$, the functional $v_t(s,\lambda,\overline{K})$ is the unique solution of the backward differential equation

$$\frac{\partial}{\partial s} v_t(s,\lambda,\overline{K}) = e^{\overline{K}_s}\psi_0(v_t(s,\lambda,\overline{K})e^{-\overline{K}_s}), \qquad v_t(t,\lambda,\overline{K}) = \lambda, \tag{2.58}$$

which implies that the quenched survival probability satisfies

$$\mathbb{P}_{(z,x)}(Z_t > 0 | \overline{K}) = 1 - e^{-zv_t(0,\infty,\overline{K}-x)}. \tag{2.59}$$

From assumption **(H3)** and definition (2.58), we obtain that for $s \leq t$ and $\lambda \geq 0$,

$$\frac{\partial}{\partial s} v_t(s,\lambda e^{-x},\bar{K}-x) \geq Ce^{\overline{K}_s - x}\left(v_t(s,\lambda e^{-x},\overline{K}-x)e^{-\overline{K}_s+x}\right)^{\beta+1} = Cv_t^{\beta+1}(s,\lambda e^{-x},\overline{K}-x)e^{-\beta(\overline{K}_s-x)}.$$

This yields

$$\frac{1}{v_t^\beta(0,\lambda e^{-x},\overline{K}-x)} - \frac{1}{\lambda^\beta} \geq \beta C\mathcal{I}_t(\beta(\overline{K}-x)),$$

where

$$\mathcal{I}_t(\beta(\overline{K}-x)) := \int_0^t e^{-\beta(\overline{K}_s-x)}\mathrm{d}s.$$

Letting λ go to ∞, we obtain

$$v_t(0,\infty,\overline{K}-x) \leq \left(\beta C\mathcal{I}_t(\beta(\overline{K}-x))\right)^{-1/\beta}. \tag{2.60}$$

Using (2.59) and (2.60), we get the following upper bound

$$\begin{aligned}\mathbb{P}_{(z,x)}(Z_t>0, I_{t-\delta}<-y) &\leq \mathbb{E}_x^{(e)}\left[\left(1-e^{-z\left(\beta C\mathcal{I}_t(\beta(\overline{K}-x))\right)^{-1/\beta}}\right)\mathbf{1}_{\{I_{t-\delta}<-y\}}\right]\\ &= \mathbb{E}^{(e)}\left[\left(1-e^{-z\left(\beta C\mathcal{I}_t(\beta(\overline{K}))\right)^{-1/\beta}}\right)\mathbf{1}_{\{I_{t-\delta}<-y-x\}}\right]. \end{aligned}\tag{2.61}$$

For simplicity, we introduce the notation $\tilde{y}=y+x$. Hence from the property of independent increments of $\overline{K}$, we get the following sequence of inequalities, for $t\geq 3t_2$ (where $t_2<\infty$ is defined in [BPS21]),

$$\begin{aligned}&\mathbb{E}^{(e)}\left[\left(1-e^{-zC_\beta\left(\mathcal{I}_t(\beta(\overline{K}))\right)^{-1/\beta}}\right), \tau_{-\tilde{y}}\leq t-\delta\right]\\ &\quad\leq \mathbb{E}^{(e)}\left[\left(1-e^{-zC_\beta\left(\int_{\tau_{-\tilde{y}}}^t e^{-\beta\overline{K}_s}\mathrm{d}s\right)^{-1/\beta}}\right)\mathbf{1}_{\{\tau_{-\tilde{y}}\leq t-\delta\}}\right]\\ &\quad\leq \mathbb{E}^{(e)}\left[\left(1-\exp\left\{-zC_\beta e^{-\tilde{y}}\left(\int_0^{t-\tau_{-\tilde{y}}} e^{-\beta\left(\overline{K}_{\tau_{-\tilde{y}}+u}-\overline{K}_{\tau_{-\tilde{y}}}\right)}\mathrm{d}s\right)^{-1/\beta}\right\}\right)\mathbf{1}_{\{\tau_{-\tilde{y}}\leq t-\delta\}}\right]\\ &\quad\leq \mathbb{E}^{(e)}\left[\left(1-e^{-zC_\beta e^{-\tilde{y}}\left(\mathcal{I}_{\frac{t+t_2}{2}}(\beta\overline{K})\right)^{-1/\beta}}\right)\right]\\ &\qquad+\mathbb{E}^{(e)}\left[\left(1-e^{-zC_\beta e^{-\tilde{y}}\left(\mathcal{I}_\delta(\beta\overline{K})\right)^{-1/\beta}}\right)\right]\mathbb{P}^{(e)}\left(\frac{t-t_2}{2}<\tau_{-\tilde{y}}\leq t-\delta\right).\end{aligned}$$

Next, using results of [PS18], Potter's Theorem and consequences of the Spitzer condition, we may finally obtain (2.57). This part is technical and we refer to [BPS21] for more details.

Hence we deduce

$$\begin{aligned}\mathbb{P}_z(Z_t>0) &= \mathbb{P}_{(z,x)}(Z_t>0, I_{t-\delta}>0)\\ &\qquad+\mathbb{P}_{(z,x)}(Z_t>0, -y<I_{t-\delta}\leq 0)+\mathbb{P}_{(z,x)}(Z_t>0, I_{t-\delta}\leq -y)\\ &\leq \mathbb{P}_{(z,x+y)}(Z_t>0, I_{t-\delta}>0)+\varepsilon\mathbb{P}_{(z,x+y)}(Z_t>0, I_t>0)\\ &\leq \mathbb{P}_{(z,x+y)}(Z_{t-\delta}>0, I_{t-\delta}>0)+\varepsilon\mathbb{P}_{(z,x+y)}(Z_t>0, I_t>0)\\ &\leq \left(\frac{\mathbb{P}_{(z,x+y)}(Z_{t-\delta}>0, I_{t-\delta}>0)}{\mathbb{P}_{(z,x+y)}(Z_t>0, I_t>0)}+\varepsilon\right)\mathbb{P}_{(z,x+y)}(Z_t>0, I_t>0),\end{aligned}$$

which allows us to obtain that for every $\varepsilon>0$, there exists $y'>0$ such that for t large enough

$$\mathbb{P}_{(z,y')}(Z_t>0, I_t>0)\leq \mathbb{P}_z(Z_t>0)\leq (1+\varepsilon)\mathbb{P}_{(z,y')}(Z_t>0, I_t>0).$$

But we have also proved that

$$\mathbb{P}_{(z,y')}(Z_t > 0, I_t > 0) \sim c(z,y')\mathbb{P}^{(e)}_{y'}(I_t > 0) \sim c(z,y')\widehat{V}(y')t^{-(1-\rho)}\ell(t), \quad \text{as} \quad t \to \infty,$$

and implicitly, we deduce

$$\mathbb{P}_z(Z_t > 0) \sim c(z,y')\mathbb{P}^{(e)}_{y'}(I_t > 0) \sim c(z,y')\widehat{V}(y')t^{-(1-\rho)}\ell(t).$$

This completes the proof.

2.5 Perspectives

I have recently started to focus, in a collaboration with A. Marguet, on a general class of branching Markov processes, in which the birth and death rates of individuals may depend on a trait that changes over time [MS21, MS20, Sma22]. The application we have been particularly interested in is the case of a cell population infected by parasites. Each cell contains a certain quantity of parasites (its trait), which can evolve according to a very general dynamic, and the division and death rates of the cells can depend on this quantity of parasites.

The strategy that we used to study these processes consists in introducing a one-dimensional auxiliary process, also known as spinal process, whose dynamics provides information on the dynamics of the whole cell population, via a Many-to-One formula (see [BDMT11] and references therein). Introducing a spinal decomposition and using a Many-to-One formula is a classical method to obtain information on the distribution of a trait in a structured branching population. It consists in distinguishing a particular line of descent in the population, and to prove that the dynamics of the trait along this particular lineage is representative of the dynamics of the trait of a typical individual in the population, *i.e.* an individual picked uniformly at random. In particular, we refer to [GB03, HH09, BDMT11, Clo17, Mar16, Mar19] for general results on these topics in the continuous-time case. In our case, the auxiliary process takes the form of a non-linear branching process evolving in a random environment; here the amount of parasites in a cell line undergoes a negative jump when a cell divides, producing a 'catastrophe', which, unlike the branching processes in Lévy environment I have discussed in this chapter, has a rate of arrival that may depend on the amount of parasites.

Such an example suggests a more general question: could we build a general framework to study branching processes having both a structure and a dynamic depending on a time varying environment? An even more general question would be to add interactions between individuals, a motivating example being for instance competition for food or space. A first work concerning interactions recently apppeared ([Ban21]). Here again, the main tool is the construction of a spinal process. The construction of general spinal processes taking into account structure, time varying environment and interactions thus appears as a challenging research direction for the next few years.

I have recently started two collaborations related to these questions.

2.5.1 Long time behaviour of bacterial consortia

Bacterial consortia are everywhere and take part in the functioning of many living systems; The human microbiota is a striking example of this. The study of these microbiota has thus various applications.

We recently began a collaboration with E. Cinquemani, L. Coquille, A. Leclercq Samson and A. Marguet to better understand the role of individual and environmental stochasticities on the long-time behaviour of these consortia. The PhD thesis of C. Medous, cosupervised with L. Coquille and A. Marguet from October 2021, will focus on the probabilistic study of structured branching processes with interactions (see [Ban21] for a recent work in this direction). This PhD project will have as a starting point a prototypical example of cooperating populations of *E. Coli*: A producer grows on glucose and synthesizes a heterologous protein, excreting acetate as a byproduct that is toxic in high concentration; a cleaner species scavenges acetate from the environment, thus favouring the growth and protein synthesis of the producer (note that this consortium has been observed in naturally evolving *E. Coli* populations). The aim is also to study questions of inference, with data at the population scale available at the Université Grenoble Alpes.

2.5.2 Consequences and evolution of somatic mutations in plants

In plants, growth is fueled by cell divisions occurring in meristems. Each shoot is produced by an apical meristem and may bear axillary meristems, which grow out to become the apical meristems of new shoots upon activation. As meristematic cells generate all the tissues constituting the shoot, any mutation occurring in a meristematic cell will be present in all the cells it gave rise to, leading to genetic mosaicism within individual plants. Importantly, meristems also give rise to reproductive structures, which implies that somatic mutations occurring during growth may end up in gametes and thus be transmitted to the offspring. In a collaboration with T. Lesaffre, we would like to study the evolution of the mutation rate in plants, and the consequences of somatic mutations accumulation for plants evolution in species with contrasting life-histories.

Chapter 3

When mutations are not so rare

3.1 Eco-evolutionnary framework

3.1.1 Adaptive dynamics

The biological theory of adaptive dynamics aims at studying the interplay between ecology and evolution through the modelling of three basic mechanisms: heredity, mutations, and competition. Selection results from the interactions between individuals, notably the competition for resources, but also many other effects (predation, symbiosis, parasitism, mutualism,...). Adaptive dynamics was first developed in the 1990ies, partly heuristically, by Metz, Geritz, Bolker, Pacala, Dieckmann, Law, and coauthors [MGM$^+$95, DL96, GMKM97, BP97, BP99, DL00]. A rigorous derivation of the theory was achieved over the last decade in the context of stochastic individual-based models, where the evolution of a population of individuals characterised by their phenotypes under the influence of the evolutionary mechanisms of birth, death, mutation, and ecological competition in an inhomogeneous "fitness landscape" is described as a measure valued Markov process [FM04]. Using various scaling limits involving large population size, small mutation rates, and small mutation steps, key features described in the biological theory of adaptive dynamics, in particular the canonical equation of adaptive dynamics, the trait substitution sequence, and the polymorphic evolution sequence were recovered, see [CFB01, Cha06, FM04, CFM08, CM11, BBC17]. Extensions of those results for more structured populations were investigated, for example, in [Tra08, Lem16].

The classical theories of evolution can be broadly classified into two branches: population dynamics, that focuses on ecology, i.e. on the dynamics of population sizes as a result of interactions between individuals and species, and population genetics, that focuses on individual genotypes and the genealogical structure of populations. Population dynamics models are often deterministic, and do not take into account trait variability inside species. Population genetics models are usually stochastic and most of the time assume a constant population size. But taking into account varying population sizes as well as stochasticity is necessary if we aim at better understanding phenomena involving small populations, such as mutational meltdown [CMPR13], invasion of a mutant population [Cha06], evolutionary suicide and rescue [AAB17], population extinction time [CCM16, CCLS18], or recovery phenomena [BCM$^+$16, BCN18]. Adaptive dynamics is to a certain extent a combination of both population dynamics and population genetics. An important

assumption of adaptative dynamics, that we will discuss later on, is the separation of the time scales of ecology and evolution, which implies a small mutation rate.

A fundamental concept in the study of populations is the fitness of the different individuals constituting these populations. Fitness is a concept with different meanings, which is still the object of many discussions (see e.g. [MNG92] or Chapter 8 of [Ewe12]). In adaptive dynamics, the fitness of individuals with a specific trait does not only depend on this trait, but also on the state of the entire population, as a result of competition and other interactions. In fact, if a population is in ecological equilibrium, then all co-existing traits have zero fitness (i.e. they do not grow or shrink). Under the assumption of separation of time scales, the only relevant fitness parameter is then the so-called *invasion fitness*, which is the exponential growth rate of a mutant born with a given trait in the presence of the current equilibrium population, and will be rigorously defined in the next subsection.

3.1.2 Model

We now describe the general model we will consider in this chapter. Specific questions on particular cases will be studied in Sections 3.2 to 3.4, and we will treat the general case in Section 3.5.

We consider an individual-based Markov process that models the evolution of a haploid, asexually reproducing population. The space of possible traits is given by the vertices of a (possibly directed) finite graph $\mathcal{G} = (V, E)$.

For all traits $v, w \in V$ and every $K \in \mathbb{N}$, we introduce the following parameters:

- $b_v \in \mathbb{R}_+$, the birth rate of an individual of trait v,
- $d_v \in \mathbb{R}_+$, the (natural) death rate of an individual of trait v,
- $c^K_{v,w} = c_{v,w}/K \in \mathbb{R}_+$, the competition imposed by an individual of trait w onto an individual of trait v,
- $\mu_K \in [0, 1]$, the probability of mutation at birth,
- $m(v, \cdot) \in \mathcal{M}_p(V)$, the law of the trait of a mutant offspring produced by an individual of trait v.

The process N^K describes the state of the population, where $N^K_v(t)$ denotes the number of individuals of trait $v \in V$ alive at time $t \geq 0$. We assume that edges in E mark the possibility of mutation and hence $m(v, w) > 0$ if and only if $(v, w) \in E$.

Moreover, we assume that, for every $v \in V$, $c_{v,v} > 0$. The parameter K is scaling the competitive pressure and, through this self-competition, fixes the equilibrium size of the population to the order of K. K is sometimes called *carrying capacity* and can be interpreted as a scaling parameter for the available sources of food or space.

As a consequence of our parameter definitions, the process N^K is characterised by its infinitesimal generator:

$$\mathcal{L}^K\phi(N) = \sum_{v\in V}(\phi(N+\delta_v)-\phi(N))\left(N_v b_v(1-\mu_K)+\sum_{w\in V}N_w b_w \mu_K m(w,v)\right) + \sum_{v\in V}(\phi(N-\delta_v)-\phi(N))N_v\left(d_v+\sum_{w\in V}c^K_{v,w}N_w\right), \tag{3.1}$$

where $\phi : \mathbb{N}^V \to \mathbb{R}$ is measurable and bounded. Such processes have been explicitely constructed in terms of Poisson random measures in [FM04].

Due to the scaling of the competition c^K, the equilibrium population is of order K. We will essentially focus on cases where the mutation probability μ_K tends to zero as $K \to \infty$. In these cases, the process N^K/K converges (on finite time intervals) to the mutation-free Lotka-Volterra system (3.2) involving all initial coexisting resident traits. When K is large enough, the macroscopic traits (i.e. whose population size is of order K) interact on any finite time interval according to the corresponding mutation-free Lotka-Volterra system (see Chapter 11, Theorem 2.1 in [EK09] for the proof of this law of large numbers): Let $\mathbf{v} \subset V$, then the mutation-free Lotka-Volterra system associated to $\mathbf{v}$ is

$$\dot{n}_w(t) = \left(b_w - d_w - \sum_{v\in\mathbf{v}} c_{w,v}n_v(t)\right)n_w(t), \quad w \in \mathbf{v},\ t \geq 0. \tag{3.2}$$

For a subset $\mathbf{v} \subset V$ of traits, we denote by $\bar{n}(\mathbf{v}) \in \mathbb{R}_+^V$ the unique equilibrium of the Lotka-Volterra system (3.2), when it exists, and where to simplify notations, we extend it by $\bar{n}_w(\mathbf{v}) = 0$ for $w \notin \mathbf{v}$. In the case where $\mathbf{v} = \{v\}$, we obtain from classical results on Lotka-Volterra models (see [Cha06] for instance)

$$\bar{n}_v(v) = (b_v - d_v)/c_{v,v} \vee 0.$$

If $\mathbf{v}$ denotes the set of macroscopic traits, we call the traits $v \in \mathbf{v}$ such that $\bar{n}_v(\mathbf{v}) > 0$ *resident*.

The approximate rate at which a mutant of trait w grows in a population of coexisting resident traits $\mathbf{v}$ is called *invasion fitness* and is denoted by $f_{w,\mathbf{v}}$, where

$$f_{w,\mathbf{v}} := b_w - d_w - \sum_{v\in\mathbf{v}} c_{w,v}\bar{n}_v(\mathbf{v}). \tag{3.3}$$

If $f_{w,\mathbf{v}} > 0$, the trait w is called *fit*. If $f_{w,\mathbf{v}} < 0$, the trait w is called *unfit*. In case $\mathbf{v}$ is reduced to a singleton, we will also write f_{wv} without the comma, for the sake of readability.

3.1.3 Mutation rates

The class of models described in the previous section has first been studied in the original context of separation between evolutionary and ecological time scales. That is in the joint limit of large populations and rare mutations such that a mutant either dies out or fixates before the next mutation occurs. Mathematically this amounts to considering a probability of mutation satisfying

$$\mu_K \ll 1/K\ln K \quad \text{as } K \to \infty. \tag{3.4}$$

Indeed, as we have explained before, a mutant arriving in a population at equilibrium first grows with a Malthusian parameter given by its invasion fitness (recall definition 3.3). It thus takes a time of order $\ln K$ to reach a population size of order K, or dies in a time much smaller than $\ln K$. Once it has a size of order K it interacts with the other populations whose sizes are of order K according to the Lotka-Volterra dynamical system (3.2), which reaches its equilibrium in a time of order 1. Hence if the mutation rates satisfy (3.4), every new mutant population has time either to die, or to reach a new (maybe coexisting with populations of different traits) equilibrium with a population size of order K, before the arrival of the next mutation. We will call this regime "rare mutation regime" in the sequel. The description of the succession of mutant invasions in this regime, on the mutation time scale $1/K\mu_K$, in a monomorphic [Cha06] or polymorphic [CM11] asexual population gives rise respectively to the so-called *Trait Substitution Sequence* or *Polymorphic Evolution Sequence*.

When adaptation is due to successive selective sweeps, with at most two competing types of individuals at a given time, the adaptation rate is proportional to the population size, the mutation rate, and the effect of mutation on fitness. This is, however, not true in large clonal populations: evolution experiments with microorganisms show that multiple strains compete in a population at a given time even though they were started with a single strain. In large clonal populations, mutations arise at a rate higher than they invade and go to fixation, resulting in a large number of competing clones. It has dramatic consequences on adaptation rate, which is generally slower: it is proportional to a power of the logarithm of the population size, a phenomenon generally called "clonal interference" or "concurrent mutations regime" [GL98, Neh13]. Clonal interference has been observed in bacteria, viruses, yeasts, and cancer tumors (e.g., [MGME99, dVR06, HSHK06, GM12, LRH+13, LBV+15]).

Even though the theory about invasion and fixation rates when multiple clones compete is advanced in population genetics literature, it is based on important simplifying assumptions: population size is a fixed parameter, and mutations are supposed to have transitive effects - that is, mutations affect only the reproduction rates of clones and not the competitive interactions between individuals within or between clonal strains. Such assumptions hinder the possibility of stable coexistence of several strains in a single population in a well-mixed homogeneous environment, where long-term coexistence and nonlinear dynamics are common ([LBD11, MLB15, GMB+17, BCM+18]). Unpredicted evolutionary dynamics has been explained by varying mechanisms. Lang and coauthors [LBD11] observed different replicates of yeast evolution experiments, where a lineage showed two successive frequency peaks that they explained by the occurrence of a third cryptic mutation affecting a preexisting lineage. Several other experiments showed coexistence of different clonal strains in the long term, which was interpreted as evidence of frequency-dependent selection ([RT98, MSNMF06, LBD11, MLB15, GMB+17, BCM+18]). Good et al [GMB+17] in particular showed that the observed long-term coexistence of different clonal strains cannot be due to clonal interference only. In [RSTA94] and [KWK+14] the long-term coexistence of three lineages derived by mutation from a single initial Escherichia coli clone in a chemostat was observed. The authors explained it with cooperative interactions rather than competitive interactions.

Intransitive competitive interactions are of particular interest in the context of large clonal populations since evolution experiments with microorganisms show complex dynamics even in uniform environments with a few shared resources (often a single one). Different mechanisms can

underlie intransitivity for competitive interactions: trade-offs, life-history traits change between developmental stages, variability in efficiency in the use of different resources, or space (reviewed in [Gal17]). Experimental studies have shown that intransitive competitive interactions commonly occur in plants, bacteria, fungi, protists, corals, and lizards, in some cases both within and between species (see for instance [SL96, AL99, TA90, NHK11, FHG17, Gal17, SLB+18]).

Theoretical works have shown that intransitive competitive interactions can promote coexistence, even in the simplest models (e.g., the Lotka-Volterra competitive model [ML75, ZZ03, GZLA17]). However, all theoretical works studying the effect of competitive interactions on coexistence, including intransitivity, have used two types of criteria: either the invasibility of a species when all others are at equilibrium (e.g., [Doe02, GZLA17, GMH18]) or the stability of the equilibrium of a community of species (e.g., [BJMSA16]). These models have three important drawbacks. First, they implicitly assume a large number of individuals of the different species, which, on the one hand, hinders considering fixation as a possible final state and, on the other hand, does not give insights into the probability of invasion of a mutant or immigrant. Second, as shown by the evolution experiments, there is no particular reason why the community should be at equilibrium when a mutant or an immigrant enters into a population. Investigating the conditions for the invasion of a rare species or clonal strain assuming that the community is at equilibrium might thus not capture the whole complexity of the dynamics. For instance, the time at which a mutant or immigrant enters a population can dramatically affect the final state of the population. Third, they generally do not consider the particular case of a community derived from a single strain by mutations (see, however, [GMH18]).

These drawbacks have motivated several of my research projects. I have been interested in models of populations with intransitive competitive interactions and mutation rates high enough that new mutants appear before the population is at equilibrium. These works, conducted alone [Sma17], in collaboration with a biologist [BS17, BS20], or in collaboration with mathematicians [BCS19, CKS21], are the subject of this chapter.

3.2 Stochastic dynamics of three competing clones

In a work in collaboration with Sylvain Billiard [BS17, BS20], we explored a mutation regime where only few types of individuals (denoted clones) are present in the population. We assume that the initial population is at equilibrium and that two successive mutants (or immigrants) appear. The second mutant arrives in the population before the equilibrium between the initial population and the first mutant population is reached. We focus on this case with only three competing clones for the sake of simplicity, but the case with a limited number (that is to say which does not go to infinity with the population size) of clones can be handled with the same mathematical tools. We (i) showed that multiple dynamics and final states are possible depending on mutational effects on fitness and the time separating mutations, (ii) gave precise approximations of invasion and fixation times and invasion probability, and (iii) explored the likelihood of the different dynamics and final states depending on prior distributions of parameters.

Before presenting our results, I will recall what happens when one mutant arrives in a monomorphic

population at equilibrium. This case has been studied in detail by Champagnat in [Cha06] and we refer to this paper for the proofs.

3.2.1 One mutant

Recall notations of Section 3.1.2. Denote by 0 the type of the resident population which is initially at equilibrium, and by 1 the mutant type. We assume that the mutants 1 are beneficial when rare. In other words

$$N^K(0) = \lfloor \bar{n}_0 K \rfloor \mathbf{e}_0 + \mathbf{e}_1 \text{ and } f_{10} > 0.$$

We can distinguish three phases in the mutant invasion: an initial phase in which the fraction of mutant-individuals does not exceed a small and fixed value $\varepsilon > 0$ and where the dynamics of the wild-type population is nearly undisturbed by the invading type. A second phase where both types account for a non-negligible percentage of the population and where the dynamics of the population can be well approximated by the system (3.2) with types 0 and 1. And finally a third phase where either the roles of the types are interchanged and the wild-type population is near extinction (when $\bar{n}_0, \bar{n}_1 > 0$, and $f_{01} < 0 < f_{10}$), or the two types stay close to their coexisting equilibrium (when $\bar{n}_0, \bar{n}_1 > 0$, $f_{10}, f_{01} > 0$ and $c_{0,0}c_{1,1} \neq c_{0,1}c_{1,0}$). The duration of the invasion process is of order $\ln K$ with a deterministic phase which only lasts an amount of time of order 1. More precisely, during the first phase, when the population 1 has a size smaller than $\lfloor \varepsilon K \rfloor$, this latter can be approximated by a supercritical birth and death process, with respective individual birth and death rates

$$b_1 \text{ and } d_1 + \frac{c_{1,0}}{K}\bar{n}_0 K = b_1 - f_{10} < b_1.$$

Hence from well known properties of supercritical birth and death processes (see [AN72] for example) we know that with a probability close to f_{10}/b_1 the 1-population size reaches the value $\lfloor \varepsilon K \rfloor$ in a time of order $\ln K / f_{10}$ for large K. The second phase can be approximated by the dynamical system (3.2) with types 0 and 1 and the system takes a time of order 1 to get close to

- $(N_0^K, N_1^K) = (\lfloor \bar{n}_{01}^{(0)} K \rfloor, \lfloor \bar{n}_{01}^{(1)} K \rfloor)$ (if $f_{01} > 0$, where $(\bar{n}_{01}^{(0)}, \bar{n}_{01}^{(1)})$ is the unique positive equilibrium of (3.2))
- or to $(N_0^K, N_1^K) = (\lfloor \varepsilon^2 K \rfloor, \lfloor \bar{n}_1 K \rfloor)$ (if $f_{01} < 0$).

Finally, if $f_{01} > 0$ the sizes of the populations 0 and 1 stay close to their coexisting equilibrium $(\lfloor \bar{n}_{01}^{(0)} K \rfloor, \lfloor \bar{n}_{01}^{(1)} K \rfloor)$ during a time of order e^{VK} for a positive V and if $f_{01} < 0$ the dynamics of the 0-population size is comparable to a subcritical birth and death process, with respective individual birth and death rates

$$b_0 \text{ and } d_0 + \frac{c_{0,1}}{K}\bar{n}_1 K = b_0 + |f_{01}| > b_0.$$

Hence it gets extinct almost surely, in a time close to $\ln K / |f_{01}|$.

3.2.2 Two mutants: surprising dynamics

To summarize, for large K, the first and third phases have a duration of order at least $\ln K$ and the second phase has a duration of order 1. Hence if a second mutation (with type 2) appears during

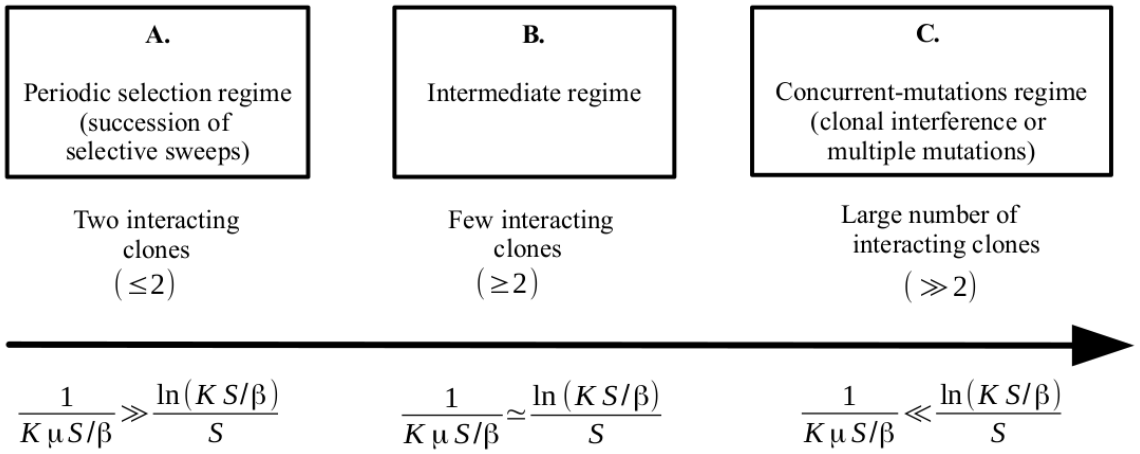

Figure 3.1: The different regimes of mutation-selection in finite clonal populations. The number of clones competing in a population at a given time depends on the rate of favorable mutations μ, the effect of mutations on fitness S, population size K and individual reproduction rate b. **A.** At most two different clones compete. **B.** A few competing clones. **C.** A large number of competing clones.

the sweep, this occurs with high probability during the first or the third phase. We denote by $\alpha \ln K$ the time of occurrence of the second mutation and we distinguish three cases:

- Either the mutation 2 occurs during the first phase of the mutant 1 invasion and the 1-population size reaches $\lfloor \varepsilon K \rfloor$ before the 2-population
- Or it occurs during the first phase but the invasion fitness $f_{20} > 0$ is large enough for the 2-population to reach size $\lfloor \varepsilon K \rfloor$ before the 1-population
- Or it occurs during the third phase.

The time of occurrence of the second mutation is a parameter in our model, $\alpha \ln K$, while it is a random variable in natural and experimental conditions, depending on the mutation rate. We expect that the dynamics observed in our model and described hereafter are most probable only under the condition that the mutation rate is neither too high, otherwise much more than three mutants would co-occur in the population, nor too low, otherwise the dynamics essentially consist in the competition between two mutants. Since the total time taken by a beneficial mutant 1 to invade a resident population is of order $\ln K$ and that the total number of individuals is of order K, we expect the dynamics that we describe when the probability of beneficial mutation per reproductive event is of order $1/(K \ln K)$. The regime we are studying is represented in Figure 3.1

In [BS17, BS20], we explored all the possible dynamics in the presence of two successive clones. Here, we will only highlight the surprising behaviours we may obtain, and illustrate them by numerical simulations. We will not provide the assumptions under which these behaviours happen, for the sake of readability.

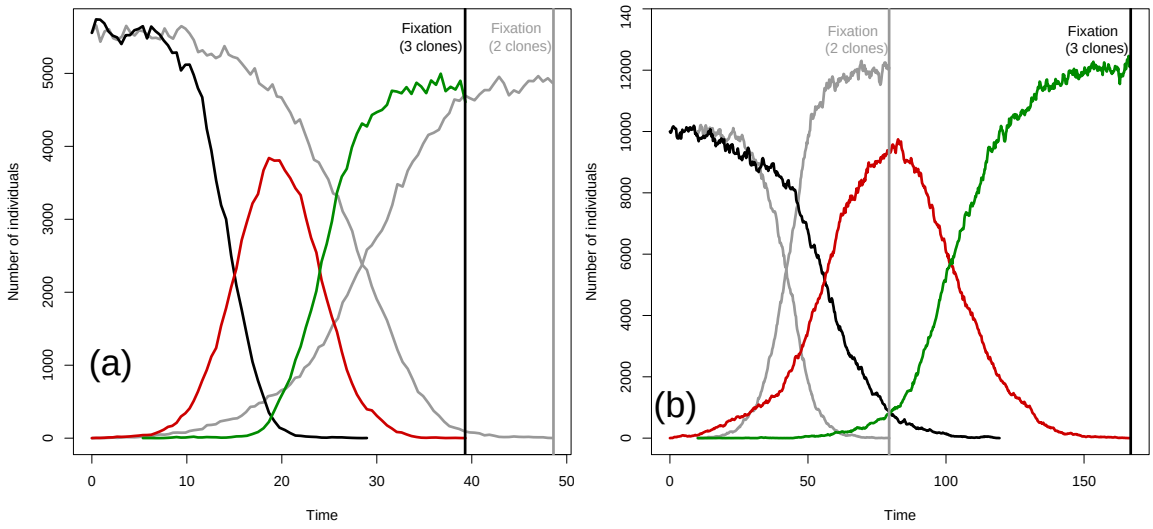

Figure 3.2: Different possible dynamics: simulations of the stochastic process. Black: Resident clone; red: clone 1, green: clone 2. (a) Clonal assistance: fixation of clone 2 is faster with clone 1 than without (compare gray and colored curves); (b) Clonal hindrance: fixation of clone 2 is slower with clone 1 than without (compare gray and colored curves)

Does clonal interference speed up or slow down invasion?

In population genetic models of clonal interference, the authors concluded that the presence of other mutants slowed down the invasion of the fittest mutant as it had to outcompete some individuals fitter than the wild type individuals [Mul32, Mul64, GL98, dVR06]. In our individual based model, the result of the competition between two mutant subpopulations depends on the population state, and the interplay between different mutations can take various forms. For some values of the parameters, clonal interference does indeed slow down the invasion of a beneficial mutant. The presence of the mutation 1 may not modify the invasion probability of the mutation 2 and the final state of the population, but however slow down the invasion of the second one (see example in Fig. 3.2(b)). But due to the non-transitive phenotypic interactions that our model is able to take into account, the presence of the first mutant can also speed up the invasion of the second one, without modifying its invasion probability and the final state of the population. This is illustrated in Fig. 3.2(a).

When do beneficial mutations annihilate adaptation?

Another interesting phenomenon can happen in our model: the occurrence of the second mutation can annihilate the effects of the first one and lead to the final fixation of the wild type population 0 which would have been outcompeted by the first mutation alone. Such a phenomenon is not possible in case of transitive fitnesses, as in this setting $f_{10} > 0$ and $f_{21} > 0$ necessarily imply $f_{20} > 0$. Such a dynamics is illustrated in Fig. 3.3(d).

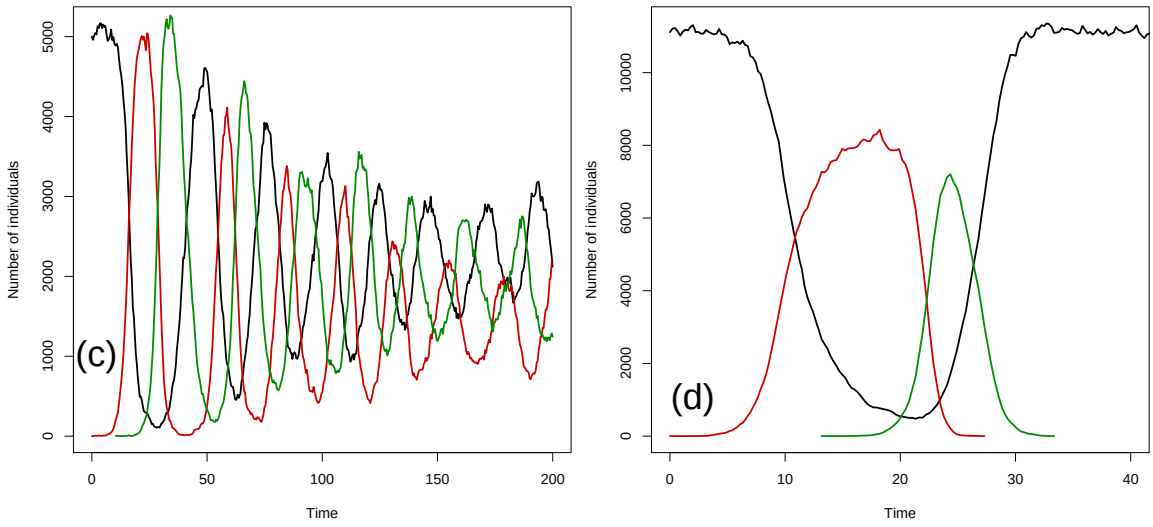

Figure 3.3: Same colors as in Figure 3.2. (c) An example of clonal coexistence: Rock-Paper-Scissor dynamics. (d) Annihilation of adaptation: Clone 0 gets finally fixed after the successive invasions of clones 1 and 2.

At the origin of the Rock-Paper-Scissors cycles

Rock-Paper-Scissors (RPS) is a children's game where rock beats scissors, which beat paper, which in turn beats rock. Such competitive interactions between morphs or species in nature can lead to cyclical dynamics, and have been documented in various ecological systems [BJ79, TA90, SL96, KRFB02, KR04, CWA09, NHK11]. Let us present one example ([SL96]). It is concerned with pattern of sexual selection on some male lizards. Males are associated to their throat colours, which have three morphs. Type 0 individuals (orange throat) are polygamous and very aggressive. They control a large territory. Type 1 individuals (dark-blue throat) are monogamous. They control a smaller territory. Finally type 2 individuals (prominent yellow stripes on the throat, similar to receptive females) do not engage in female-guarding behaviour but roam around in search of sneaky matings. As a consequence of these different strategies, the type 0 outcompetes the type 1 (because males are more aggressive), which outcompetes the type 2 (as males of type 1 are able to control their small territory and guard their female), which in turn outcompetes the type 0 (as males of type 0 are not very efficient in defending their territory, having to split their efforts on several females).

Neumann and Schuster [38] modelled such interactions by a three dimensional competitive Lotka-Volterra system. In particular they proved that migrations or recurrent mutations were not necessary ingredients to obtain limit cycles, as it was assumed in previous models (see [CHP02, SK13] for example). They studied the long time behaviour of the system but payed little attention to initial conditions, only assuming "the presence of all three strains in one homogeneous medium". But the question of initial conditions is crucial. Indeed, how to explain the appearance of such cycles whereas when only two strains are present one of them is outcompeted by the other one and disappears? Our simple model provides a framework explaining how a cyclical RPS dynamics emerges in an ecological system thanks to the interplay of two successive mutations. Such a

	Lower invasion probability ($f_{21} < f_{20}$ or $f_{201} < f_{20}$)	**Higher invasion probability** ($f_{21} > f_{20}$ or $f_{201} > f_{20}$)
Polymorphism	Soft clonal coexistence	Hard clonal coexistence
Fixation		
- Faster fixation	Soft clonal assistance	Hard clonal assistance
- Slower fixation	Soft clonal hindrance	Hard clonal hindrance

Table 3.1: Categories of possible dynamics.

dynamics is illustrated in Fig. 3.3(c).

3.2.3 Likelihood of possible outcomes

We saw that a large variety of dynamics can be observed when three clones compete. The dynamics can vary regarding their final states or invasion and fixation times. Our model allows us to predict each possible case given any set of ecological parameters and the time when clone 2 enters the population. How competition between three clones affects dynamics can be synthesized into six categories (Table 3.1), depending on (i) the final state (fixation or stable coexistence), (ii) how the invasion probability of clone 2 is affected relative to the case with only two interacting clones (compare the invasion fitnesses f_{20} and f_{21}, for instance), and (iii) how the fixation time of clone 2 is affected (longer or shorter compared with the case with two competing clones). We introduce the following terms to describe the six possible categories of dynamics: "clonal coexistence", when clonal interaction promotes the maintenance of polymorphism; "clonal assistance" versus "clonal hindrance", when the fixation time of clone 2 is shortened or increased; and "soft" versus "hard", when the invasion probability of clone 2 is lower versus higher than with only two competing clones.

It is, however, difficult to have an overview of the likelihood of a particular dynamics, its final state, and duration since the parameter space has many dimensions. We now aim to explore the parameter space assuming prior distributions on the parameter space, and we aim especially at quantifying the likelihood of the different possible final states. The complexity of the model can be reduced by defining new parameters: $r_i = b_i - d_i$, the net individual reproductive rate of clone i, and $\tilde{c}_{i,j} = c_{i,j}/c_{j,j}$, the ratio of the between- and within-clone competitive interactions. In bacteria, yeasts, and some eukaryotes, fitness is generally estimated as the initial growth rate (at low density) of mutants (see table 2 in [ML06] and the appendix in [MGML12]). We thus assumed that the effect of mutations on the growth rate of clone i follows a Fisher's geometric model. Given that the net reproduction rate of clone 0 is r_0, we assumed that the reproductive rate of clone i is $r_i = r_0 + x_i$, with x_i the effect of mutation drawn in a shifted negative gamma distribution (an approximation of a Fisher's geometric model [ML06]). Note that when mutation 2 enters the population during the second stochastic phase, mutation 2 is assumed to occur in the most frequent population at equilibrium: $r_2 = r_1 + x_2$ when mutant 1 is more frequent than mutant 0, $r_2 = r_0 + x_2$ otherwise.

There is, to our knowledge, no theoretical or empirical consensus on the distribution of mutation

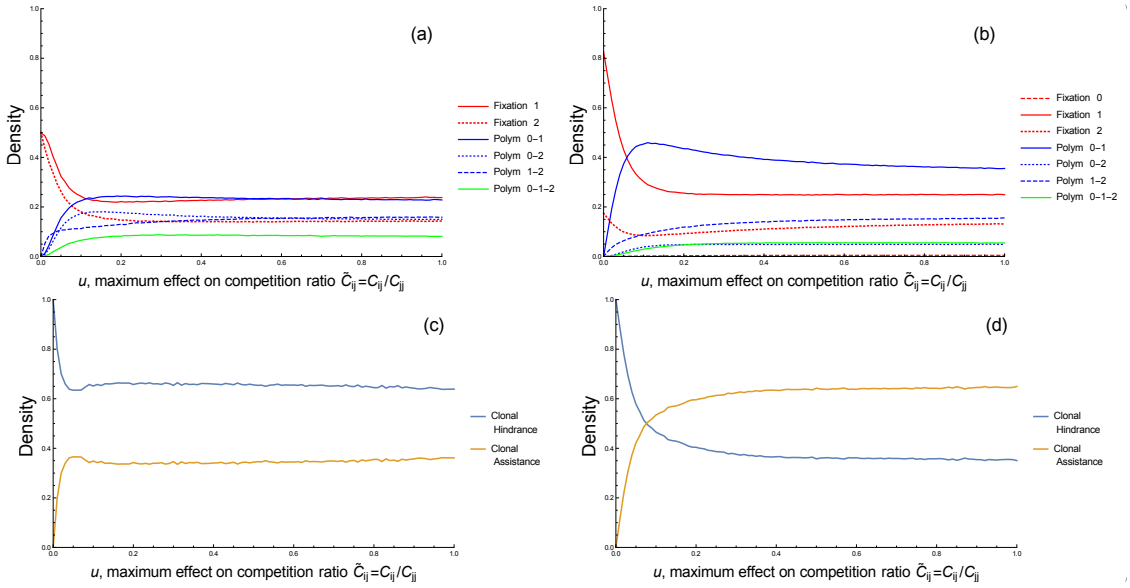

Figure 3.4: Posterior probability when competition coefficient is drawn in a uniform distribution. Left and right columns: clone 2 enters in the first or third phase of the dynamics, respectively. (a)-(b) Final states; (c)-(d) Clonal hindrance *vs.* clonal assistance. The growth rate of clone 0 $r_0 = 2$ is supposed to be at 50% from the optimum in a Fisher's Geometric adaptive landscape (see text for details). The ratio of competitive abilities $\widetilde{c}_{i,j} = c_{i,j}/c_{j,j}$ between clones i and j are drawn in a uniform distribution with range $[1-u, 1+u]$.

effects on the competitive abilities $\tilde{c}_{i,j}$. Without any knowledge about the distribution of competitive abilities, we simply assumed that the ratio of competitive interactions $c_{i,j}$ follows a uniform distribution in the interval $[1-u, 1+u]$, with $0 \leq u \leq 1$. Note that when $u = 0$, all $\tilde{c}_{i,j} = 1$ and invasion fitnesses are necessarily transitive, while if $u > 0$, non-transitivity can occur. As u increases, the variance of the competitive ratio $\tilde{c}_{i,j}$ also increases, that is, the more different the competitive interactions between mutants can be. Finally, we assumed that the time when clone 2 enters the population $\alpha \ln K$ is uniformly distributed and occurs during either the first or the third phase of the dynamics. We randomly drew 10^6 different sets of parameters in such prior distributions. The posterior distribution of the final states was estimated as its proportion observed among the 10^6 random parameter sets.

Figure 3.4 shows the posterior probability of the dynamics and final states when mutation 2 enters the population during the first or third phase of the dynamics, assuming that the competition abilities are drawn in a uniform distribution. When the variance of the distribution of $\tilde{c}_{i,j}$ is small, all clones have similar competitive abilities ($\tilde{c}_{i,j} \sim 1$); that is, invasion fitnesses are mostly transitive. We naturally recover predictions from population genetics models: the likeliest scenario is the fixation of either mutant 1 or mutant 2 (Fig. 3.4c, 3.4d). Rapidly, when the variance of the uniform distribution increases, polymorphic final states become the likeliest. When the effect of mutation on competitive abilities becomes large (u increases), the likelihood of all dynamics rapidly reaches a plateau. Our results suggest that nontransitive fitnesses are mostly expected to occur when several

clones are interacting as soon as mutations affect their competitive abilities. This further supports that clonal coexistence is likely to occur even when considering only competitive interactions. Finally, our results show that RPS dynamics and back-to-the-initial-state dynamics are unlikely. Comparing the left and right columns in figure 3.4 shows that the time at which clone 2 enters the population only marginally affects the dynamics and the final states. Interestingly, comparing the final states between cases with two or three interacting clones shows that more polymorphic final states are expected when three clones are interacting, even though the difference is small. Whether increasing the number of interacting clones could promote the maintenance of polymorphism even more is an open question.

Finally, Figures 3.4(c) and 3.4(d) show the likelihood of clonal hindrance versus clonal assistance (sensu Table 3.1). Clonal hindrance is the most probable when the competitive abilities are similar between clones (small u). However, when the difference between competitive abilities increases (large u), the likelihood of clonal assistance increases. When clone 2 enters the population during the third phase of the dynamics, clonal assistance is even likelier than clonal hindrance. Globally, our results thus suggest that clonal hindrance might indeed be an important factor affecting the adaptation rate, but clonal assistance can be as important given that nontransitive fitnesses are possible.

3.3 The effect of recurrent mutations on genetic diversity

Recurrent mutations are a common phenomenon in population genetics [Hal33]. They may cause diseases [SXF+06, EXN+07, RGC+07], or reduce the fitness of an individual in a given environment [RSB+03]. They may also be at the origin of the fixation of a new genotype. The selective sweeps are then called "soft sweeps", as multiple copies of the selected allele contribute to a substitution [HP05]. The other possibility is hard sweep, when selection acts on a new mutation. Soft sweeps allow a faster adaptation to novel environments, and their importance is growing in empirical and theoretical studies. Messer and Petrov [MP13] review a lot of evidence that soft sweeps are common in a broad range of organisms. Hard and soft sweeps entail different footprints in DNA in the vicinity of the newly fixed allele, called genetic signatures, and the accumulation of genetic data available allows one to detect these signatures in current populations (see for instance [NHBG96, TRR+07, NNS+07, SBM+09] or references in [WPM14]). To do this in an effective way, it is necessary to identify accurately the signatures left by these different modes of adaptation.

In [Sma17], I studied the genetic signature left by a selective sweep induced by recurrent mutations at a given locus from an allele A to an allele a under positive selection (i.e. $f_{aA} > 0$), depending on the mutation frequency. I distinguished several scales for the mutation probability per reproductive event, which entail distinct genetic signatures.

Let us describe the model under consideration. We focus on one locus with alleles in $\mathcal{A} := \{A, a\}$. Let $\bar{\alpha}$ denote the complementary type of α in $\mathcal{A}$: when an α individual gives birth, the newborn is of type α with a probability $1 - \mu_K^{\alpha\bar{\alpha}}$, and of type $\bar{\alpha}$ with a probability $\mu_K^{\alpha\bar{\alpha}}$. We will consider the three following mutation scales for $\alpha \in \mathcal{A}$:

Assumption 1.

$$\mu_K^{a\bar{a}} \sim \lambda^{a\bar{a}} K^{-1}, \quad K \to \infty, \quad \lambda^{a\bar{a}} \in \mathbb{R}_+^*.$$

Assumption 2.

$$\mu_K^{a\bar{a}} \sim \lambda^{a\bar{a}} K^{-1+\beta}, \quad K \to \infty, \quad \lambda^{a\bar{a}} \in \mathbb{R}_+^*, \quad \beta \in (0,1).$$

Assumption 3.

$$\mu_K^{a\bar{a}} \sim \lambda^{a\bar{a}}, \quad K \to \infty, \quad \lambda^{a\bar{a}} \in (0,1).$$

Under Assumption 1, the mutation rate at the population scale is of order one. This is the usual scaling for diffusion approximations and it has been widely studied with the constant population assumption (see for instance [KO78, Gri80, Nag83]). In the second regime, the product of mutation rate and population size increases as a power law. Under the last assumption, mutations are frequent and the population is large. The highest mutation rates have so far been reported in viruses: for example $1.5\ 10^{-3}$ mutations per nucleotide, per genomic replication in the single-stranded RNA phage $Q\beta 10$ [Dra93], $2.5\ 10^{-3}$ mutations per site and replication cycle in Chrysanthemum chlorotic mottle viroid [GEFS09], or $4.1\ 10^{-3}$ mutations per base per cell in HIV-1 virus [CGG+15]. Moreover, existing measures of mutation rate focus only on mean rates [DSH08]. In particular, some sites may have a higher mutation rate that what is measured. Besides, several mutations may generate the same phenotypic change [VDBS+13], leading to higher effective mutation rates. Viruses can also have very high population sizes (for example up to 10^{12} RNA viruses in an organism [MHGC04]), and it seems reasonable to consider such sizes as infinite as an approximation. Hence the parameter range covered by Assumption 3 could be relevant for such viruses. As we will see in the sequel, this is the only regime where back mutations (from a to A) have a macroscopic effect on the pattern of allelic diversity.

As we will see, under Assumption 1, several mutant populations are growing simultaneously, and we can approximate the diversity of a individuals at the end of the sweep. In the second case, the a mutants are so numerous that with a probability close to one, two individuals sampled uniformly at the end of the sweep will be descended from two different a mutants. Finally, under Assumption 3, the distribution of the alleles a and A in the population converges to a deterministic limit distribution.

In order to study the process in detail and discriminate between distinct haplotypes (i.e. the genetic materials transmitted by the successive mutants generated from A), we make a distinction between the descendants of the successive mutants generated from A. Let T_i denote the time of birth of the ith mutant of type a, and $N_i^K(t)$ the size of its descendance at time t. In particular,

$$N_i^K(t) = 0 \quad \forall t < T_i \quad \text{and} \quad N_a^K(t) = \sum_{i \in \mathbb{N}} N_i^K(t), \quad \forall t \geq 0.$$

The state of the population process at time $t \geq 0$ is now represented by the vector

$$(N_A^K(t), N_1^K(t), N_2^K(t), ...).$$

Note that this representation is well defined as the number of mutations is almost surely finite in every time interval under our assumptions.

For the sake of simplicity, we assume that at time 0, the A-population is at its monomorphic equilibrium and that the first mutant has just appeared, that is to say

$$N^K(0) = (\lfloor \bar{n}_A K \rfloor, 1). \tag{3.5}$$

We define the end of the sweep T_F^K as the time at which all ancestral A type individuals have died out, i.e. all remaining A-individuals are descendants of an a-individual via a back mutation. Then using usual couplings with branching processes, we can show that under Assumption $i \in \{1, 2\}$, if we denote $(\beta_1, \beta_2) = (0, \beta)$,

$$\frac{T_F^K}{\ln K}\left(\frac{(1-\beta_i)}{f_{aA}} + \frac{1}{|f_{Aa}|}\right)^{-1} \underset{K\to\infty}{\to} 1, \quad \text{in probability.}$$

We are interested in the effect of selective sweeps by recurrent mutations on the genetic diversity. This diversity will be expressed in terms of the distribution of mutant haplotypes $(N_1^K(t), N_2^K(t), ...)$ at the end of the sweep. In other words, we want to know if a-individuals sampled at the end of the sweep originate from the same or from distinct a-mutant individuals. In order to describe the haplotype distribution, we introduce the so called GEM distribution, named after Griffiths, Egen and McCloskey:

Definition 3.3.1. *Let ρ be positive. The infinite sequence of random variables $(P_i, i \geq 1)$ has a GEM distribution with parameter $\rho > 0$ if for every $i \geq 1$,*

$$P_i \overset{\mathcal{L}}{=} B_i \prod_{j=1}^{i-1}(1 - B_j),$$

where $(B_i, i \geq 1)$ is a sequence of i.i.d. random variables with law Beta$(1, \rho)$ whose density with respect to the Lebesgue measure is

$$\rho(1-x)^{\rho-1}\mathbf{1}_{[0,1]}(x).$$

We are now able to describe the relative proportions of the different haplotypes at the end of the sweep (plus a time negligible with respect to K):

Theorem 3.3.2. *For $i \geq 1$ and $t \geq 0$, denote by $N_a^{(i),K}(t)$ the size at time t of the ith oldest family among the mutant populations having survived until time t. Let f_K be a positive function such that $f_K = o(K)$ and*

$$\mathcal{T}_K := T_F^K + f_K.$$

Then,

1. *Under Assumption 1,*

$$(N_a^K(\mathcal{T}_K))^{-1}(N_a^{(1),K}(\mathcal{T}_K), N_a^{(2),K}(\mathcal{T}_K), ...) \underset{K\to\infty}{\to} (P_1, P_2, P_3...), \quad \textit{in law,}$$

   where $(P_i, i \geq 1)$ has a GEM distribution with parameter $b_A \bar{n}_A \lambda^{aA}/b_a$.

2. *Under Assumption 2,*

$$(N_a^K(\mathcal{T}_K))^{-1}(N_a^{(1),K}(\mathcal{T}_K), N_a^{(2),K}(\mathcal{T}_K), ...) \underset{K\to\infty}{\to} (0, 0, 0...), \quad \textit{in probability,}$$

where for $x \in \mathbb{R}^{\mathbb{N}}$, $\|x\| = \sup_{i\in\mathbb{N}} |x_i|$.

As a consequence, the relative haplotype proportions at the end of the sweep essentially differ depending on the mutation probability scale.

The proof of Theorem 3.3.2 consists in two steps. First, during a time long but negligible with respect to the sweep duration $\ln K$ we couple the different subpopulations issued from different mutants with independent birth and death processes with the same law (birth rate b_a and death rate $d_a + c_{a,A}\bar{n}_A$). We use known results on birth and death processes to deduce the relative proportions of these different mutant populations. We then construct martingales and prove that these relative proportions stay almost constant until the end of the sweep.

Theorem 3.3.2 allows us to answer the following question: what is the probability that two individuals sampled uniformly at random at time $\mathcal{T}_K$ are identical by descent, or in other words originate from the same individual alive at time 0? To answer this question, we need to define an equivalence relation between two sampled individuals i and j:

$$i \sim j \iff \Big\{\text{there is no mutation in the lineages of } i \text{ and } j \text{ sampled at time } \mathcal{T}_K \text{ before their more recent common ancestor (backward in time)}\Big\}.$$

We do not indicate the dependence on $\mathcal{T}_K$ for the sake of readability but it will be clear in the statement of the results. Note that the probability of the event $i \sim j$ does not depend on the labeling of a-individuals at time $\mathcal{T}_K$ as they are exchangeable. The following result is a direct consequence of Theorem 3.3.2:

Corollary 3.3.3. *Assume* (4.2.1). *Then,*

1. *Under Assumption 1,*

$$\lim_{K\to\infty} \mathbb{P}(i \sim j, \forall\ a\text{-individuals } i \text{ and } j \text{ sampled uniformly at random at time } \mathcal{T}_K) = \frac{1}{1 + 2\bar{n}_A b_A \lambda^{Aa}/b_a}.$$

2. *Under Assumption 2,*

$$\lim_{K\to\infty} \mathbb{P}(i \sim j, \forall\ a\text{-individuals } i \text{ and } j \text{ sampled uniformly at random at time } \mathcal{T}_K) = 0.$$

When the mutation probabilities per reproductive event are of order one, we get a deterministic limit via a direct application of Theorem 2.1 p. 456 in Ethier and Kurtz [EK09] (recall (3.2)): let $T > 0$; under Assumption 3 and when $K \to \infty$, the process

$$(N_A^K(t)/K, N_a^K(t)/K, 0 \le t \le T)$$

converges in probability for the uniform norm to the deterministic solution of

$$\begin{cases} \dot{n}_A = (b_A(1-\lambda^{Aa}) - D_A - C_{A,A}n_A - C_{A,a}n_a)n_A + b_a\lambda^{aA}n_a, & n_A(0) = z_A(0) \\ \dot{n}_a = (b_a(1-\lambda^{aA}) - D_a - C_{a,A}n_A - C_{a,a}n_a)n_a + b_A\lambda^{Aa}n_A, & n_a(0) = z_a(0). \end{cases} \tag{3.6}$$

The dynamical system (3.6) may admit different types of fixed points that are described in Figure 3.5. We may prove that this dynamical system has different possible properties, depending on the

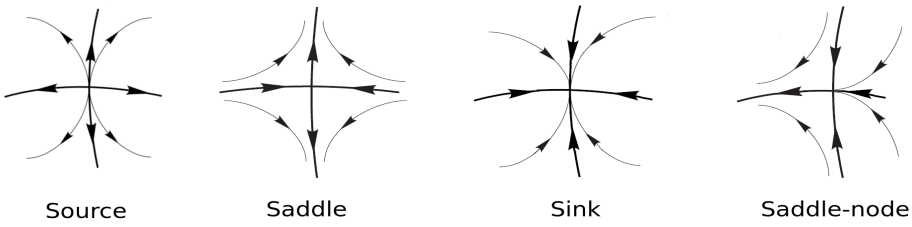

Figure 3.5: The different types of fixed points of system (3.6) (adapted from Figure 2.13 in [DLA06]).

values of some functions of the system parameters. We will not give the technical conditions here but only list these behaviours:

Theorem 3.3.4. *The dynamical system (3.6) has no periodic orbit in $\mathbb{R}_+^2$ and admits at least two fixed points in $\mathbb{R}_+^2$: $(0,0)$, and at least one fixed point in $(\mathbb{R}_+^*)^2$. Moreover,*

- *either there is only one fixed point in $(\mathbb{R}_+^*)^2$ (with an explicit expression),*
- *or there are two fixed points in $(\mathbb{R}_+^*)^2$ (with an explicit expression)*
- *or there are three fixed points in $\mathbb{C}^2$ (with an explicit expression), and as a consequence, there is one, two, or three fixed points in $(\mathbb{R}_+^*)^2$.*

When there is one fixed point in $(\mathbb{R}_+^*)^2$, it is a sink, when there are two fixed points, one of them is a sink, and the second one a saddle-node, and when there are three fixed points, either there are two sinks and one saddle, or there are two saddle-nodes and a sink.

To prove the absence of periodic orbits we use Dulac's Theorem, and to find the equilibrium points and their nature, we apply Cardano's Method as well as known results on sectorial decomposition.

We can also obtain some convergence results for the dynamical system under some specific conditions on the parameters that we will not describe here. We refer to [Sma17] for details.

3.4 Crossing a fitness valley

Until now we focused on mutants with positive invasion fitnesses: each mutant had an initial positive growth rate and thus a positive probability to invade. But there may be traits with positive invasion fitness that can be reached only through *several* consecutive mutation steps [LOPA03, CBM06]. The purpose of the work [BCS19] in collaboration with A. Bovier and L. Coquille was to analyse precisely how such an escape from a stable singularity happens in various scaling regimes.

We proved that three essentially different dynamics may occur. In the first one, the mutation probability is so large that many mutants (a number of order μK) are created in a time of order 1. In this case the fixation time scale is dominated by the time needed for a successful mutant to invade

(which is of order $\ln(1/\mu)$). The second scenario occurs if the mutation probability is smaller, but large enough so that a fit mutant will appear before the resident population dies out. In this case the fixation time scale is exponentially distributed and dominated by the time needed for the first successful mutant to be born. The last possible scenario is the extinction of the population before the emergence of the fit mutant, which occurs when the mutation probability is very small (smaller than e^{-CK} for a constant C to be made precise later).

Recall notations of Section 3.1.2 and in particular (3.1). We assume that there are $L+1$ types in the population, denoted $\{0, 1, ..., L\}$ and that the *mutation kernel* may take the two following forms

$$m_{ij}^{(1)} = \delta_{i+1,j} \quad \text{or} \quad m_{ij}^{(2)} = \frac{1}{2}(\delta_{i+1,j} + \delta_{i-1,j}), \tag{3.7}$$

where $\delta_{i,j}$ is the Kronecker delta (1 if $i = j$, 0 otherwise).

We are interested in the situation where $\bar{n}_0 > 0$, $f_{i0} < 0$, $1 \leq i \leq L-1$, $f_{L0} > 0$, and $f_{0L} < 0$. Under these assumptions, all mutants created by the initial population initially have a negative growth rate, and thus tend to die out. However, if by chance such mutants survive long enough to give rise to further mutants, such that eventually an individual will reach the trait L, it will found a population at this trait that, with positive probability, will grow and eliminate the resident population through competition. Our purpose is to analyse precisely how this process happens. The process that we want to describe can be seen as a manifestation of the phenomenon of *metastability* (see, e.g., the recent monograph [BDH16] and references therein). The initial population appears stable for a long time and makes repeated attempts to send mutants to the trait L, which will eventually be reached and take over the entire population. Apart from scaling the population size by taking the carrying capacity $K \uparrow \infty$, we are also interested in the limit of small mutation probabilities, $\mu = \mu_K \downarrow 0$, with possibly simultaneous time rescaling. This gives rise to essentially different asymptotics, depending on how μ tends to zero as a function of K. To be more precise, our assumptions are the following:

Assumption 4.

- *Viability of the resident population:* $\bar{x}_0 > 0$.
- *Fitness valley: All traits are unfit with respect to 0 except L:*

$$f_{i0} < 0, \text{ for } i \in \{1, ..., L-1\} \text{ and } f_{L0} > 0. \tag{3.8}$$

- *All traits are unfit with respect to L:*

$$f_{iL} < 0, \text{ for } i \in \{0, ..., L-1\}. \tag{3.9}$$

- *The following fitnesses are different:*

$$f_{i0} \neq f_{j0} \text{ and } f_{iL} \neq f_{jL}, \text{ for all } i \neq j. \tag{3.10}$$

Note that conditions (3.10) are imposed in order to lighten the analysis of the deterministic system. Similar results are probably true without these assumptions.

3.4.1 Deterministic limit $(K, \mu) \to (\infty, \mu)$, then $\mu \to 0$

The first regime we are interested in is the case when μ is small but does not scale with the population size. From a biological point of view, this corresponds to high mutation probabilities.

Theorem 3.4.1. *Suppose that Assumption 4 holds. Take as initial condition*

$$x^\mu(0) = (\bar{x}_0, 0, \dots, 0). \tag{3.11}$$

Then, for $i \in \{0, ..., L\}$, as $\mu \to 0$, uniformly on bounded time intervals,

$$\frac{\log\left[x_i^\mu\left(t \cdot \log\left(1/\mu\right)\right)\right]}{\log(1/\mu)} \to x_i(t), \tag{3.12}$$

where $x_i(t)$ is piece-wise linear. More precisely,

1. *in the case of 1-sided mutations, $m_{ij} = m_{ij}^{(1)}$, for $i \in \{0, L-1\}$,*

$$x_i(t) = \begin{cases} -i, & \text{for } 0 \le t < L/f_{L0}, \\ -i - (t - L/f_{L0}) \min_{k \in [|0,i|]} |f_{kL}|, & \text{for } t > L/f_{L0}, \end{cases} \tag{3.13}$$

and

$$x_L(t) = \begin{cases} -L + f_{L0}t, & \text{for } 0 \le t < L/f_{L0}, \\ 0, & \text{for } t > L/f_{L0}. \end{cases} \tag{3.14}$$

2. *in the case of 2-sided mutations, $m_{ij} = m_{ij}^{(2)}$: consider the sequence $\{i_1, \dots, i_r\}$ of "fitness records", defined recursively by $i_1 = 0$, $i_k = \min\{i \in \{0, L-1\} : f_{iL} < f_{i_{k-1}L}\}$,*

$$x_i(t) = \begin{cases} -i \vee (-L - (L-i) + f_{L0}t), & \text{for } 0 \le t < L/f_{L0}, \\ -(L-i) \vee \max_{k \in \{0,i\}}\{-i - |f_{kL}|(t - L/f_{L0})\} \\ \qquad \vee \max_{k \in \{1,r\}}\{-i_k - |i - i_k| - |f_{i_kL}|(t - L/f_{L0})\}, & \text{for } t > L/f_{L0}. \end{cases} \tag{3.15}$$

Moreover,

$$\left(x_0^\mu(t\log(1/\mu)), x_L^\mu(t\log(1/\mu))\right) \to \begin{cases} (\bar{x}_0, 0), & \text{for } 0 \le t < L/f_{L0}, \\ (0, \bar{x}_L), & \text{for } t > L/f_{L0}. \end{cases} \tag{3.16}$$

The shape of $x(t) := (x_0(t), \dots, x_L(t))$ can be seen on Figures 3.6 and 3.7 in the 1-sided and 2-sided cases, respectively.

In the 1-sided case, the rescaled deterministic process $x(t)$ can be explained as follows: In the first phase, the 0-population stays close to $\bar{n}_0$ until the L-population reaches order one. As competition between the populations of type i and j for $i, j \neq 0$ is negligible in comparison to competition between type i and type 0, for $i \in \{1, ..., L\}$, the i-population first stabilises around $O(\mu^i)$ in a time of order $o(1)$, then the L-population, starting from a size $O(\mu^L)$, grows exponentially with rate f_{L0} until reaching order one (which takes a time L/f_{L0}) while the other types stay stable.

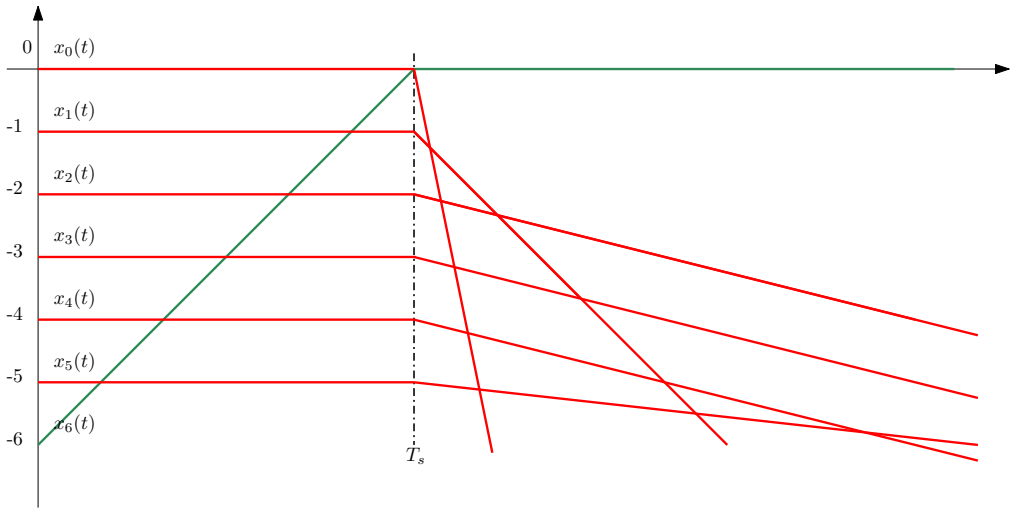

Figure 3.6: Graph of $x(t)$ in the 1-sided case $m_{ij} = m_{ij}^{(1)}$ for $L = 6$ and $f_{60} = 1, (f_{06}, f_{16}, f_{26}, f_{36}, f_{46}, f_{56}) = (-5, -1, -0.25, -1.5, -2, -0.05)$.

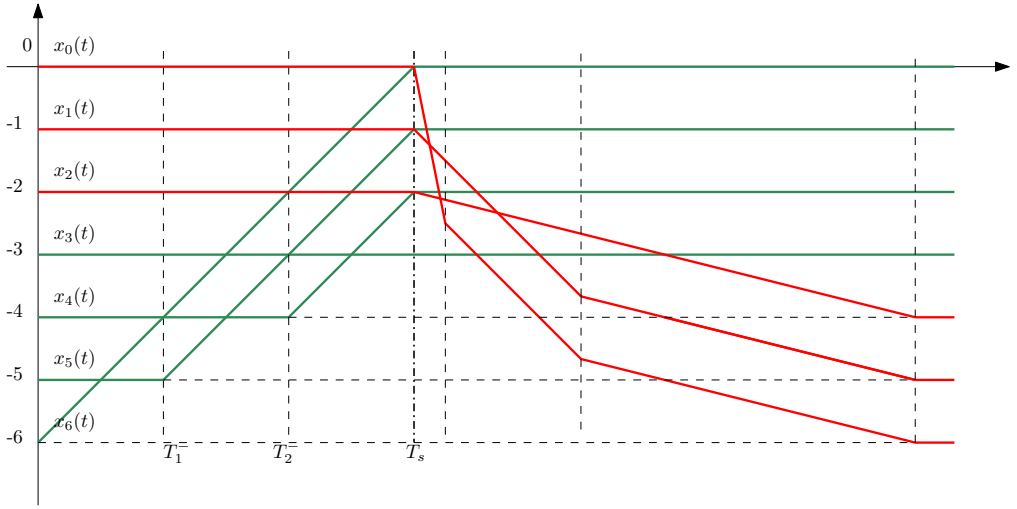

Figure 3.7: Graph of $x(t)$ in the 2-sided case $m_{ij} = m_{ij}^{(2)}$ for $L = 6$ and $f_{60} = 1, (f_{06}, f_{16}, f_{26}) = (-5, -1, -0.25)$.

Next, a swap between populations 0 and L (two-dimensional Lotka-Volterra system) is happening in a time of order $o(1)$, and finally, for $i \neq L$, the i-population decays exponentially from $O(\mu^i)$ with a rate given by the lowest (negative) fitness of its left neighbours, $(\min_{j\in[|0,i|]} |f_{jL}|)$ while the L-population approaches its equilibrium density $\bar{n}_L$. To understand the rate of decrease during the last phase, let us consider only the 0- and 1- populations. The competition exerted by populations $j \in \{0, ..., L-1\}$ on the 0- and 1-populations is negligible with respect to the competition exerted by the L-population, which has a size of order 1. As a consequence, x_0^μ has a dynamics close to this of the solution to:

$$\dot{\tilde{x}}_0(t) = f_{0L}\tilde{x}_0(t),$$

that is to say, $x_0(t) \approx x_0(0)e^{f_{0L}t}$, and x_1 has a dynamics close to this of the solution to:

$$\dot{\tilde{x}}_1(t) = f_{1L}\tilde{x}_1(t) + \mu\tilde{x}_0(t) = f_{1L}\tilde{x}_1(t) + \mu\tilde{x}_0(0)e^{f_{0L}t},$$

that is to say

$$x_1(t) \approx x_1(0)e^{f_{1L}t} + \mu\frac{x_0(0)}{f_{0L} - f_{1L}}\left(e^{f_{0L}t} - e^{f_{1L}t}\right).$$

From this heuristics we get that

$$\begin{aligned} x_1^\mu(t\log(1/\mu)) &\approx x_1^\mu(0)\mu^{|f_{1L}|t} + \mu\frac{x_0^\mu(0)}{|f_{1L}| - |f_{0L}|}\left(\mu^{|f_{0L}|t} - \mu^{|f_{1L}|t}\right) \\ &= \mu\left(C_1\mu^{|f_{1L}|t} + \frac{C_0}{|f_{1L}| - |f_{0L}|}\left(\mu^{|f_{0L}|t} - \mu^{|f_{1L}|t}\right)\right), \end{aligned} \tag{3.17}$$

where C_0 and C_1 are of order 1. We thus see that the leading order is $\mu^{1+\inf\{|f_{0L}|,|f_{1L}|\}t}$. Reasoning in the similar way for the other populations yields that the leading order for the variation of the i-population size ($i \in \{0, ..., L-1\}$) is $\mu^{i+\inf\{|f_{0L}|,|f_{1L}|,...,|f_{iL}|\}t}$.

In the 2-sided case, a modification of the order of magnitude of the i-population (for $i \neq L$) happens due to backward mutations. The reasoning is similar to the heuristics we have just described, except that mutants from the i-population ($i \in \{1, ..., L\}$) might also have an impact on the decrease rate of the $(i-1)$-population. This is the case if $x_i^\mu / x_{i-1}^\mu \geq C/\mu$, for a positive constant C. Under this condition the number of type-$(i-1)$ individuals produced by mutations of type i-individuals has the same order as the type-$(i-1)$ population size.

3.4.2 Stochastic limit $(K, \mu) \to (\infty, 0)$

When the mutation probability is small, the dynamics and time scale of the invasion process depend on the scaling of the mutation probability per reproductive event, μ, with respect to the carrying capacity K. We consider in this section mutation probabilities with two possible forms. Either,

$$\mu = f(K)K^{-1/\alpha}, \quad \text{with} \quad \alpha \geq 1 \quad \text{and} \quad |\ln f(K)| = o(\ln K), \tag{3.18}$$

or

$$\mu = o(1/K). \tag{3.19}$$

For simplicity, we now only consider the mutation kernel $m_{ij}^{(1)} = \mu\delta_{i+1,j}$.

In a time of order one, there will be of order $K\mu^i$ mutants of type i, provided that this number is larger than 1. In particular, there will be of order $K\mu^L$ fit L-mutants at time one, if $L/\alpha < 1$. This is the regime of large mutation probability. In this case, the time for the L-population to hit a size of order K is of order $\ln K$. We obtain a precise estimate of this time, as well as of the time for the trait L to outcompete the other traits under the same assumptions. Let us introduce

$$t(L, \alpha) := \frac{L}{\alpha}\frac{1}{f_{L0}} + \sup\left\{\left(1 - \frac{i}{\alpha}\right)\frac{1}{|f_{iL}|}, 0 \leq i \leq L-1\right\}.$$

We proved in [BCS19] that it takes a time of order $t(L, \alpha)\ln K$ for the L-population to outcompete the other populations and enter in a neighbourhood of its monomorphic equilibrium size $\bar{n}_L K$. Once

this has happened, it stays close to this equilibrium for at least a time e^{KV}, where V is a positive constant. In fact the constant $t(L,\alpha)$ can be intuitively computed from the deterministic limit. Indeed, for $\alpha > L$, we prove that the system performs small fluctuations around the deterministic evolution studied above: the i-population first stabilises around $O(K\mu^i)$ in a time of order one, then the L-population grows exponentially with rate f_{L0} until reaching order K (super-critical branching process, needs a time close to $L\ln K/\alpha f_{L0}$) while the other types stay stable. The swap between populations 0 and L then takes a time of order one, and finally, for $i \neq L$, the i-population decays exponentially from $O(K\mu^i)$ to extinction with a rate given by the lowest (negative) fitness of its left neighbours (sub-critical branching process, needs a time close to $(\sup_{j\in[|0,i|]}(1-j/\alpha)/|f_{jL}|)\ln K$). Thus the time until extinction of all non-L populations is close to $t(L,\alpha)\ln K$.

Next we consider the case of small mutation probability, when $L/\alpha > 1$. In this case, there is no L-mutant at time one, and the fixation of the trait L happens on a much longer time scale.

We define, for $0 < \rho < 1$,

$$\lambda(\rho) := \sum_{k=1}^{\infty} \frac{(2k)!}{(k-1)!(k+1)!}\rho^k\,(1-\rho)^{k+1}\,, \tag{3.20}$$

and, for $\lfloor\alpha\rfloor + 1 \leq i \leq L-1$, we set $\rho_i := b_i/(b_i + d_i + c_{i0}\bar{x}_0)$.

We also introduce for $v \geq 0$ the first time the L-population reaches the size $\lfloor vK\rfloor$,

$$T_v^{(K,i)} := \inf\{t \geq 0, X_i(t) = \lfloor vK\rfloor\}, \tag{3.21}$$

and the time needed for the populations at all sites but L to get extinct,

$$T_0^{(K,\Sigma)} := \inf\Big\{t \geq 0, \sum_{0\leq i\leq L-1} X_i(t) = 0\Big\}. \tag{3.22}$$

Then we have

Theorem 3.4.2. *Assume that* (3.18) *holds,* $\alpha \notin \mathbb{N}$ *and* $1 <\alpha < L$. *Then there exist two positive constants* ε_0 *and* c, *and two exponential random variables* E_- *and* E_+ *with parameters*

$$(1+c\varepsilon)\frac{\bar{x}_0 b_0 ... b_{\lfloor\alpha\rfloor}}{|f_{10}|...|f_{\lfloor\alpha\rfloor 0}|}\frac{f_{L0}}{b_L}\prod_{i=\lfloor\alpha\rfloor+1}^{L-1}\lambda(\rho_i) \qquad \textit{and} \qquad (1-c\varepsilon)\frac{\bar{x}_0 b_0 ... b_{\lfloor\alpha\rfloor}}{|f_{10}|...|f_{\lfloor\alpha\rfloor 0}|}\frac{f_{L0}}{b_L}\prod_{i=\lfloor\alpha\rfloor+1}^{L-1}\lambda(\rho_i),$$

such that, for every $\varepsilon \leq \varepsilon_0$,

$$\liminf_{K\to\infty} \mathbb{P}\left(E_- \leq \left(T^{(K,L)}_{\bar{x}_L-\varepsilon} \vee T_0^{(K,\Sigma)}\right) K\mu^L \leq E_+\right) \geq 1 - c\varepsilon. \tag{3.23}$$

The typical trajectories of the process are as follows: mutant populations of type i, for $1 \leq i \leq \lfloor\alpha\rfloor$, reach a size of order $K\mu^i \gg 1$ in a time of order $b_{i-1}\ln K/f_{i0}$ (they are well approximated by birth-death processes with immigration and their behaviour is then close to the deterministic limit), and mutant populations of type i, for $\lfloor\alpha\rfloor + 1 \leq i \leq L$, describe a.s. finite excursions, whose a proportion of order μ produces a mutant of type $i+1$. Finally, every L-mutant has a probability f_{L0}/b_L to produce a population which outcompetes all other populations. The term $\lambda(\rho_i)$ is the

expected number of individuals in an excursion of a subcritical birth and death process of birth rate b_i and death rate $d_i + c_{i0}\bar{x}_0$ excepting the first individual. Hence $\mu\lambda(\rho_i)$ is the approximated probability for a type i-population ($\lfloor\alpha\rfloor + 1 \leq i \leq L-1$) to produce a mutant of type $i+1$, and the overall time scale can be recovered as follows:

1. The last 'large' population is the $\lfloor\alpha\rfloor$-population, which reaches a size of order $K\mu^{\lfloor\alpha\rfloor}$ after a time which does not go to infinity with K.

2. The $\lfloor\alpha\rfloor$-population produces an excursion of an $(\lfloor\alpha\rfloor+1)$-population at a rate of order $K\mu^{\lfloor\alpha\rfloor+1}$, which has a probability of order μ to produce an excursion of an $(\lfloor\alpha\rfloor+2)$-population, and so on,

giving the order $K\mu^L$.

3.4.3 On the extinction of the population

One of the key advantages of stochastic logistic birth and death processes on constant size processes when dealing with population genetics issues is that we can compare the time scale of mutation processes and the population lifetime. In particular, for the case of fitness valley crossing, we can show that if the mutation probability μ is too small, the population gets extinct before the birth of the first mutant of type L.

The quantification of the lifetime of populations with interacting individuals is a tricky question (see [CCM16, CCM19] for recent results) and we were not able to determine necessary and sufficient conditions for the L-mutants to succeed in invading before the population extinction. However, we were able to provide some necessary conditions, and some sufficient conditions (see [BCS19] for details).

3.5 Power law mutation rate on a general finite trait space

We saw in the previous section that interesting phenomena may occur when we relax the evolutionary and ecological time scales separation and focus on power law mutation rates. We thus decided to study this class of mutation rates in a collaboration with L. Coquille and A. Kraut. The mutation rate μ_k is thus given by:

$$\mu_K = K^{-1/\alpha}, \quad \text{for } \alpha > 0. \tag{3.24}$$

The space of possible traits is given by the vertices of a (possibly directed) finite graph $\mathcal{G} = (V, E)$, and mutations are towards nearest neighbours in the graph $\mathcal{G}$. We start with a macroscopic initial condition (that is to say of order K) and we are interested in the stochastic process given by the large population limit under the mutation rate (3.24). In [CKS21] we describe the time evolution of the orders of magnitude of each sub-population on the $\ln K$ time scale, as K tends to infinity. We show that the limiting process is deterministic, given by piecewise affine continuous functions, which are determined by an algorithm describing the changes in the fitness landscape due to the succession of new resident or emergent types. Moreover, we give a precise description of this algorithm for any

finite graph $\mathcal{G}$. We refer the interested reader to Theorem 2.2 and Proposition 2.3 in [CKS21].

Our proof heavily relies on couplings of the original process with logistic birth and death processes with non-constant immigration, and the analysis of the later simpler processes on the $\ln K$ time scale. This approach was developed by Champagnat, Méléard and Tran in [CMT19]. They considered an individual-based model for the evolution of a discrete population performing horizontal gene transfer and mutations on $V = [0,4] \cap \delta\mathbb{N}, \delta > 0$. Their goal was to analyse the trade-off between natural selection, which drives the population to higher birth-rates, and transfer, which drives the population to lower ones. Under the mutation rate (3.24), they exhibited parameter regimes where different evolutionary outcomes appear, in particular evolutionary suicide and emergence of a cyclic behaviour. As in the present paper, their results characterized the time evolution of the orders of magnitude of each sub-population on the $\ln K$ time scale, which are shown to be piecewise affine continuous functions whose slopes are given by an algorithm describing the succession of phases when a given type is dominant or resident. Their proofs provided us with the main ingredients needed for our results. However, the graph structure they chose simplifies the inductions and we have to generalise their approach to treat the case of more general graphs.

Recall notations of Section 3.1.2. It is convenient to describe the population size of a certain trait $v \in V$ by its K-exponent. For $t \geq 0$,

$$\beta_v^K(t) := \frac{\ln(1 + N_v^K(t \ln K))}{\ln K}, \tag{3.25}$$

which is equivalent to $N_v^K(t \ln K) = K^{\beta_v^K(t)} - 1$. Since the population size is restricted to order K by the competition, β_v^K ranges between 0 and 1, as $K \to \infty$.

Mutants can be produced along (directed) edges of the graph. We denote by $d(v,w)$ the graph distance, i.e. the length of the shortest (directed) path from v to w in $\mathcal{G} = (V,E)$. For a subset $\mathbf{v} \subset V$ we define

$$d(\mathbf{v},w) := \min_{v \in \mathbf{v}} d(v,w) \quad \text{and} \quad d(w,\mathbf{v}) := \min_{v \in \mathbf{v}} d(w,v).$$

We now present some non intuitive behaviours of the population process, which stem from the mutation scale or the generality of the mutational graph that we allow for. They are direct applications of Theorem 2.2 and Proposition 2.3 in [CKS21]. Several examples are built on directed graphs. Although this is not a necessary condition to obtain the desired phenomena, it allows a simplified study (especially of the decay phases). We first introduce some notations for the sake of readability.

Definition 3.5.1. *Let $w, v \in V$ and $\boldsymbol{v} \subset V$. We write*

1. *$w > \boldsymbol{v}$ if and only if $f_{w,\boldsymbol{v}} > 0$, that is if w can invade in $\boldsymbol{v}$,*
2. *$w < \boldsymbol{v}$ if and only if $f_{w,\boldsymbol{v}} < 0$, that is if w cannot invade in $\boldsymbol{v}$,*
3. *$w \gg v$ (or $v \ll w$) if and only if $f_{w,v} > 0$ and $f_{v,w} < 0$, that is if w can invade in v and fixate,*
4. *$w \equiv v$ if and only if $f_{w,v} > 0$ and $f_{v,w} > 0$, that is if w and v can coexist,*
5. *$w \frown v$ if and only if $f_{w,v} < 0$ and $f_{v,w} < 0$, that is if w and v can neither invade in each other.*

3.5.1 Back mutations before adaptation

In the following, we build an example where the ancestry of the resident population comes from back mutations from an ancestral trait, even if the mutations happening in between are not deleterious.

Example 1. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.8 where $V = \{0,1,2,3\}$ and $E = \{[0,1],[1,2],[2,0],[0,3]\}$. Let $\alpha > 2$, an initial condition given by $(\bar{n}(0),0,0,0)$ and a fitness landscape given by*

$$0 \ll 1 \ll 2, \quad 3 \frown 0, \quad 3 \frown 1$$
$$0 \equiv 2, \quad 3 > \{0,2\}, \quad 2 < 3 \tag{3.26}$$
$$f_{2,0} < 2f_{1,0} \tag{3.27}$$
$$f_{0,1} \geq f_{3,1}, \quad f_{2,0} \leq f_{1,0} \tag{3.28}$$
$$i_1 := \frac{1-1/\alpha}{f_{0,1}} < \frac{-(1-4/\alpha)}{f_{2,1}} =: i_2 \tag{3.29}$$

In this case, on the $\ln K$ time scale, the rescaled macroscopic population jumps from traits $0-1-2$ then to coexistence between 0 and 2, followed by the invasion and fixation of 3 which is produced with high probability, due to Condition (3.29), by individuals of type 0 which have the sequence $0-1-2$ as ancestry. In other words, the final resident individuals of trait 3, although they can be produced by individuals of trait 0 directly, come from a sequence of mutations which went around the loop $0-1-2$ of $\mathcal{G}$. Conditions (3.26), summarized on Figure 3.8, imply phase portrait number 8 in the classification of Zeeman [Zee93]. Condition (3.27) ensures that trait 1 becomes resident before 2. Condition (3.28) is not necessary but allows to simplify the setting. The exponents are drawn on Figure 3.8.

Note that this scenario can also happen in the rare mutation regime considered in [Cha06] (for example $\alpha \in (0,1)$): the average waiting time until a mutant of type 1 appears is then of order $O(1/K\mu_K) = O(K^{-1+1/\alpha}) \gg \ln K$. Once it has appeared, it survives with positive probability and the succession of invasions and fixations above takes place on the $\ln K$ time scale, separated by mutation events on the $K^{-1+1/\alpha}$ time scale. What is new in our case is that such a scenario can still take place for higher mutation rates than the ones considered in [Cha06], and on a $\ln K$ time scale.

3.5.2 Non-intuitive mutational pathways in the high mutation framework

Longer or shorter path than expected

If evolution and mutation time scales are separated (i.e. in the rare mutation regime of [Cha06] for instance), mutations occur one at a time, and the number of successive resident traits from the wild type to the type gathering k successively beneficial mutations is k. This is not necessarily the case if mutations are faster, in which case it is possible to observe either more or less resident traits, as the following examples show.

Example 2. *Let us consider the directed graph $\mathcal{G}$ depicted on Figure 3.9, where $V = \{00,01,10,11\}$ and $E = \{[00,01],[00,10],[01,11],[10,11]\}$. Let $\alpha > 2$, an initial condition given by $(\bar{n}_{00},0,0,0)$ and a fitness*

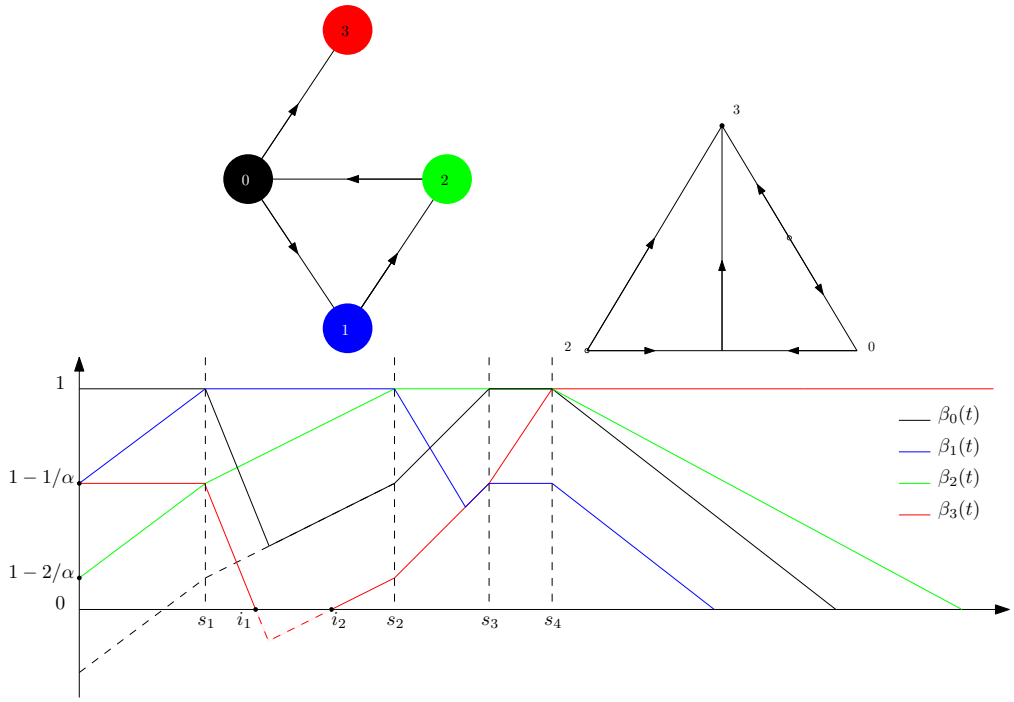

Figure 3.8: Graph $\mathcal{G}$, phase portrait of traits 0-2-3, and exponents $\beta(t)$ of Example 1.

landscape given by

$$
\begin{aligned}
&00 \ll 01 \ll 10 \ll 11, \quad \textit{and} \quad 01 \ll 11 \\
&10, 11 \frown 00 \\
&f_{11,00} < f_{01,00} \qquad (3.30)\\
&f_{10,01} > f_{11,01} \qquad (3.31)
\end{aligned}
$$

In this case, in the rare mutation regime, the rescaled macroscopic population jumps along $00 - 01 - 11$.

In our mutation regime, the rescaled macroscopic population jumps along $00 - 01 - 10 - 11$ on the $\ln K$ time scale. The exponents are drawn on Figure 3.9. Note that Condition (3.30) ensures that 11 does not invade before 01; it is not necessary but allows to simplify the setting. Condition (3.31) ensures that 11 does not invade before 10.

Example 3. *Let us consider the directed graph $\mathcal{G}$ depicted on Figure 3.9, where $V = \{00, 01, 10, 11\}$ and $E = \{[00, 01], [00, 10], [01, 11], [10, 11]\}$. Let $\alpha > 2$, an initial condition given by $(\bar{n}_{00}, 0, 0, 0)$ and a fitness landscape given by*

$$
\begin{aligned}
&01 > 00, \quad 11 \gg 00 \\
&10 < 00 \qquad (3.32)\\
&01, 10 < 11 \\
&\frac{2}{f_{11,00}} < \frac{1}{f_{01,00}} \qquad (3.33)
\end{aligned}
$$

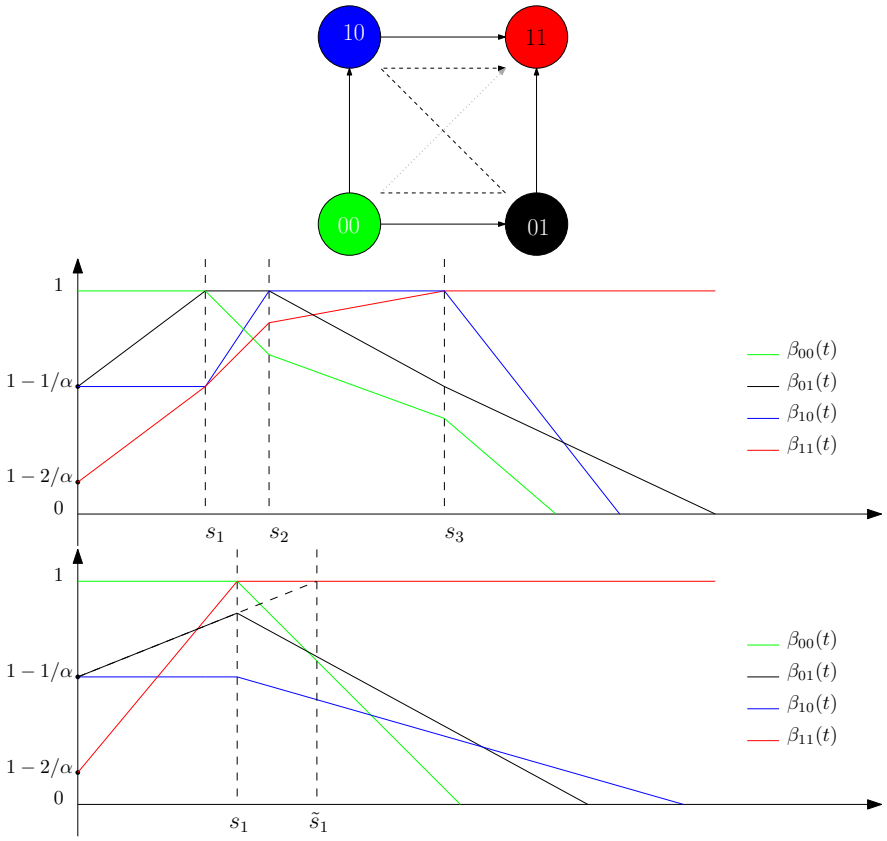

Figure 3.9: Graph $\mathcal{G}$ and exponents $\beta(t)$ for Examples 2 and 3.

In this case, in the rare mutation regime, the rescaled macroscopic population still jumps along $00-01-11$, under the additional assumption that $f_{11,01}>0$.

In our mutation regime, the rescaled macroscopic population directly jumps from 00 to 11 on the $\ln K$ time scale. More precisely, the exponents are drawn on Figure 3.9. Condition (3.33) ensures that 11 fixates before 01. Condition (3.32) is not necessary but allows to simplify the setting.

Price of anarchy

We build an example where adding a new possible mutation path to a fit trait increases the time until it appears macroscopically.

Example 4. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.10, where $V=\{1,2a,2b,3\}$ and the edge set is either $E_1=\{[1,2a],[2a,3],[2b,3],[3,2b]\}$ or*
$E_2=\{[1,2a],[2a,3],[2b,3],[2a,2b],[3,2b]\}$. Let $\alpha>3$, an initial condition given by $(\bar{n}_1,0,0,0)$ and a fitness landscape given by

$$1\ll 2a\ll 3,\quad \textit{and}\quad 2a\ll 2b \tag{3.34}$$

$$1<2b,\quad \textit{and},\quad 1,2b<3$$

$$f_{2a,1}\geq f_{3,1},f_{2b,1},\quad \textit{and}\quad \frac{1}{f_{2b,2a}}<\frac{1}{f_{3,2a}}<\frac{2}{f_{2b,2a}} \tag{3.35}$$

$$0<f_{3,2b}<f_{3,2a}. \tag{3.36}$$

In this case, if the edge set is E_1, the rescaled macroscopic population jumps along traits $1-2a-3$ in a time t_1 on the $\ln K$ time scale. But if the edge set is E_2, the population jumps along $1-2a-2b-3$ and the time to reach 3 is $t_2>t_1$. More precisely, the exponents are drawn on Figure 3.10. Condition (3.35) ensures that $2b$ invades first when the edge set is E_2 but not when it is E_1, in other words β_{2b} reaches 1 before β_3 if started at $1-1/\alpha$ but not at $1-2/\alpha$. And Condition (3.36) enlarges the time of fixation of 3. Note that the first inequality in Condition (3.35) is not necessary but allows to simplify the second one. In the rare mutation regime we can observe this phenomenon on the mutation time scale, but only with probability strictly smaller than 1, since both $2b$ and 3 are fit with respect to $2a$ and can both invade with positive probability once they are produced.

Counter cycle

Example 5. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.11, where $V=\{1,2,3\}$ and the edge set is $E=\{[1,2],[2,3],[3,1]\}$. Let $\alpha>2$, an initial condition given by $(\bar{n}(1),0,0)$ and a fitness landscape given by*

$$1\gg 2,\quad 2\gg 3,\quad 3\gg 1.$$

In this case, the rescaled macroscopic population jumps along traits $1-3-2$ (in the clockwise sense) although the mutations are directed counterclockwise. More precisely, the exponents are drawn on Figure 3.11. Moreover, if Conditions (3.37) below are fulfilled the period is shorter and shorter, an acceleration takes place, as it is depicted on Figure 3.11.

$$f_{2,3}>-f_{1,3}\quad f_{1,2}>-f_{3,2}\quad f_{3,1}>-f_{2,1}. \tag{3.37}$$

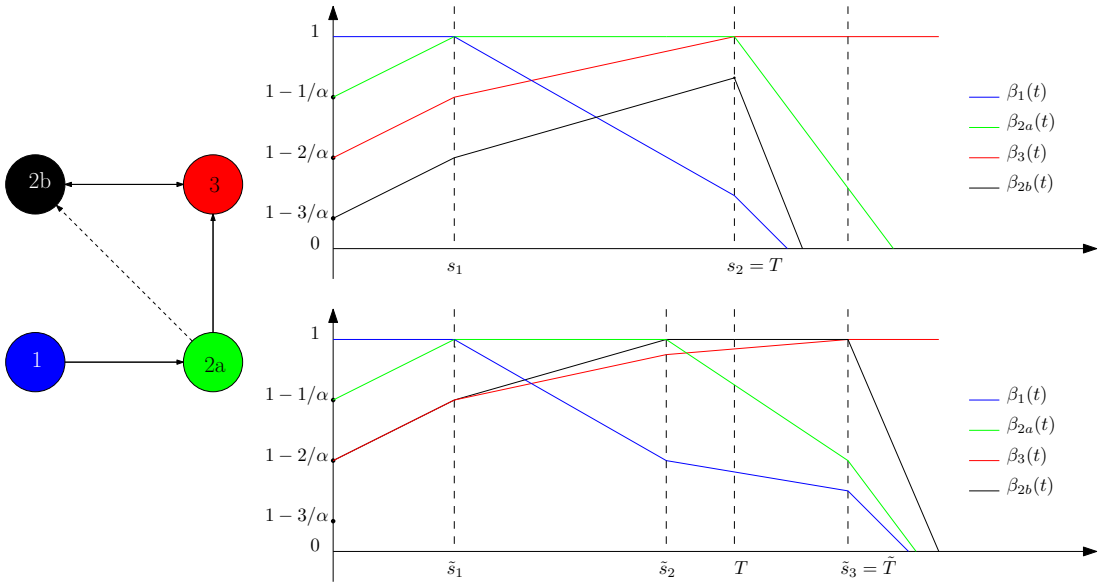

Figure 3.10: Graph $\mathcal{G}$ and exponents $\beta(t)$ for Example 4, with edge set E_1 (above) and E_2 (below).

Note that in the rare mutation regime, with the chosen parameters, there would be no evolution since $2 < 1$. Moreover, there are no parameters such that counter cyclic or accelerating behaviours could arise.

3.5.3 Arbitrary large jumps on the $\ln K$-time scale

A natural question to ask is if the "cut-off" α restricts the range of the jumps, on the $\ln K$ time-scale, to traits which are at a distance less than α. The answer is no, as the following example shows.

Example 6. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.12, where $V = \{0,1,2,3,4\}$ and $E = \{[0,1],[1,2],[2,3],[3,4]\}$. Let $\alpha \in (3,4)$, an initial condition given by $(\bar{n}_0, 0, \dots, 0)$ and a fitness landscape given by*

$$\begin{gathered} 1,2 < 0, \quad 3,4 > 0, \quad 0,1,2,3 < 4 \\ \frac{1}{f_{4,0}} + \frac{-1+4/\alpha}{f_{3,0}} < \frac{3/\alpha}{f_{3,0}} \end{gathered} \tag{3.38}$$

In this case, the cut-off is in between traits 3 and 4 (meaning that $K\mu_K^i \to 0$ for $i > 3$) thus population of trait 4 vanishes at time 0. However, the rescaled macroscopic population jumps from trait 0 to trait 4 in a time

$$s_1 = \frac{-1+4/\alpha}{f_{30}} + \frac{1}{f_{40}}$$

on the $\ln K$ time scale. More precisely, the exponents are drawn on Figure 3.12. Condition (3.38) ensures that trait 4 fixates before trait 3.

It is easy to generalize this example to construct jumps to any distance L larger than α, by taking larger and larger fitnesses after the negative fitness region. The condition implying emergence of

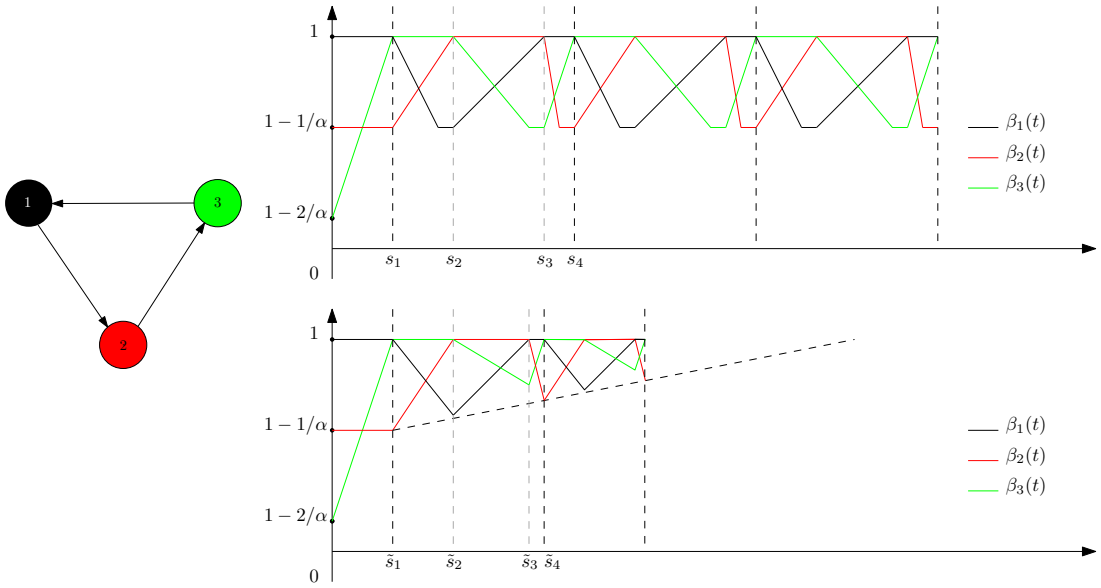

Figure 3.11: Graph $\mathcal{G}$ and exponents $\beta(t)$ for Example 5, without Assumption 3.37 (above) and with Assumption 3.37 (below).

trait L is then a little more technical to write, since one has to compute the time for the piecewise affine function $\beta_L(t)$ (with multiple slope-breaks) to reach 1 before the other traits. Example 6 constitutes the simplest non-trivial example of this phenomenon.

Example 7. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.13, where $V = \{0,1,2,3,4,5\}$ and $E = \{[0,1],[1,2],[2,3],[3,4],[4,5]\}$. Let $\alpha \in (3,4)$, an initial condition given by $(\bar{n}_0, 0, \dots, 0)$ and a fitness landscape given by*

$$\begin{aligned} &1,2 < 0, \quad 3,4,5 > 0, \quad 0,1,2,3,4 < 5 \\ &f_{3,0} < f_{4,0} < f_{5,0} \quad \textit{and} \quad \frac{-1+4/\alpha}{f_{3,0}} + \frac{-4/\alpha+5/\alpha}{f_{4,0}} + \frac{1}{f_{5,0}} < \frac{3/\alpha}{f_{3,0}}. \end{aligned} \tag{3.39}$$

In this case, the cut-off is in between traits 3 and 4 (meaning that $K\mu_K^i \to 0$ for $i > 3$) thus population of trait 4 and 5 vanishes at time 0. However, the rescaled macroscopic population jumps from trait 0 to trait 5 in a time

$$s_1 = \frac{-1+4/\alpha}{f_{3,0}} + \frac{-4/\alpha+5/\alpha}{f_{4,0}} + \frac{1}{f_{5,0}}$$

on the $\ln K$ time scale. More precisely, the exponents are drawn on Figure 3.13. Condition (3.39) ensures that trait 5 fixates before traits 3 and 4. The first inequality is not needed but allows to simplify the second one. The dotted lines in the figures allow to construct the points where some exponents become positive.

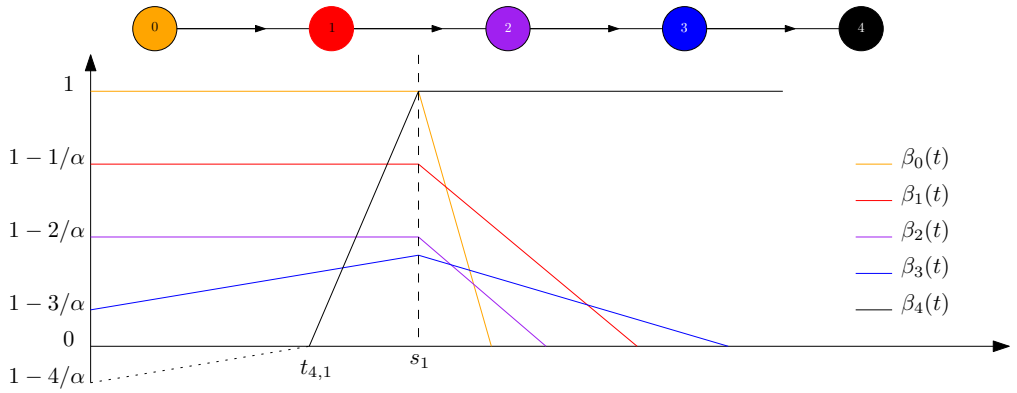

Figure 3.12: Graph $\mathcal{G}$ and exponents $\beta(t)$ for Example 6.

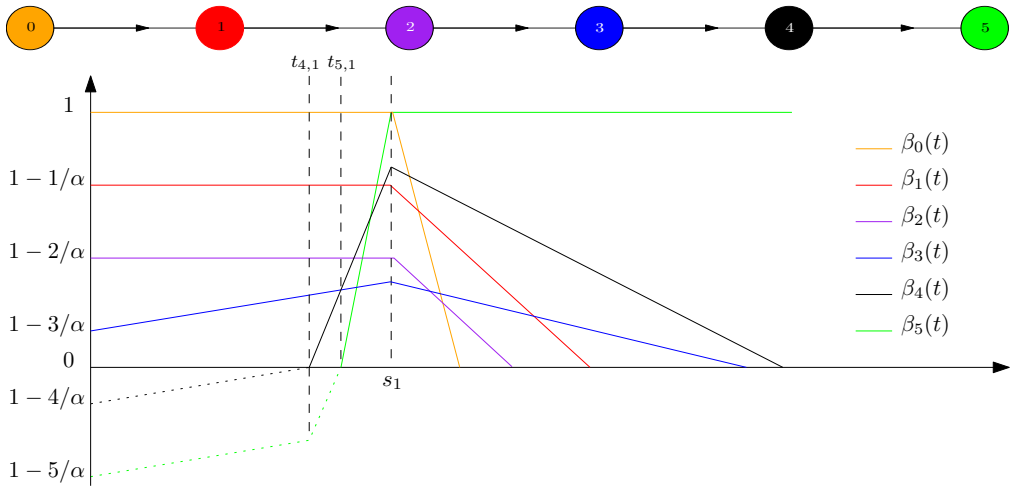

Figure 3.13: Graph $\mathcal{G}$ and exponents $\beta(t)$ for Example 7.

3.5.4 Effective random walk across fitness valleys

2 effective sites

Example 8. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.14, where $V = \{0, 1a, 1b, i\}$ and $E = \{[0,i],[i,1a],[1a,1b],[i,1b]\}$. We suppose that whenever there are several outgoing edges from a vertex v, the mutation kernel is uniform among the nearest neighboring vertices. Let $\alpha \in (0,1)$, an initial condition given by $(\bar{n}_0, 0, \dots, 0)$ and a fitness landscape given by*

$$1a \gg 0 \gg 1b \gg 1a$$
$$i < 0, \quad i < 1a, \quad i < 1b.$$

In this case, according to [BCS19], the time to cross the fitness valley is of order $O(1/K\mu_K^2) = O(K^{-1+2/\alpha}) \gg \ln K$, thus the first mutant of type $1a$ will appear on this time scale, and will invade with positive probability. Then, in a time of order $O(\ln K)$, type $1b$ fixates, and one has to wait again a time of order $O(K^{-1+2/\alpha})$ until the appearance of the next mutant of type 0. Thus, on the time scale $O(K^{-1+2/\alpha})$, the population process converges to a jump process between the two states 0 and $1b$ with positive jump rates although the fitness $f_{1b,0}$ is negative. More precisely, recall the definition of $\lambda(\rho)$ in (3.20) and define for $(i,j) \in \mathcal{G}^2$,

$$\rho_{i,j} := \frac{b_i}{b_i + d_i + c_{ij}\bar{n}_j}$$

Theorem 3.5.2. *As $K \to \infty$, the following convergence holds*

$$(N_0^K, N_{1b}^K)(tK^{-1+2/\alpha}) \Rightarrow \bar{n}_{X_t}\delta_{X_t}$$

for finite dimensional distributions, where X_t is a continuous time Markov chain on $\{0, 1b\}$ with transition rates

$$r_{0\to 1b} = \frac{\bar{n}_0 b_0}{|f_{i0}|}\lambda(\rho_{i,0})\frac{f_{1a,0}}{b_{1a}} \quad \text{and} \quad r_{1b\to 0} = \frac{\bar{n}_{1b} b_{1b}}{|f_{i,1b}|}\lambda(\rho_{i,1b})\frac{f_{0,1b}}{b_0}.$$

3 effective sites

Example 9. *Let us consider the graph $\mathcal{G}$ depicted on Figure 3.14. We suppose that whenever there are several outgoing edges from a vertex v, the mutation kernel is uniform among the nearest neighbouring vertices. Let $\alpha \in (0,1)$, an initial condition given by $(\bar{n}_0, 0, \dots, 0)$ and a fitness landscape given by*

$1a \gg 0$	$2a \gg 0$	$2a \gg 1b$
$1b \gg 1a$	$2b \gg 2a$	$1a \gg 2b$
$0 \gg 1b$	$0 \gg 2b$	$1b \gg 2b$
$i < 0$	$j < 0$	$k < 1a,\ k < 1b$
$i < 1a,\ i < 1b$	$j < 2a,\ j < 2b$	$k < 2a,\ k < 2b$

Thus, following [BCS19], on the time scale $O(K^{-1+2/\alpha})$, the population process converges to a jump process between the three states $\{0, 1b, 2b\}$ with positive jump rates. More precisely,

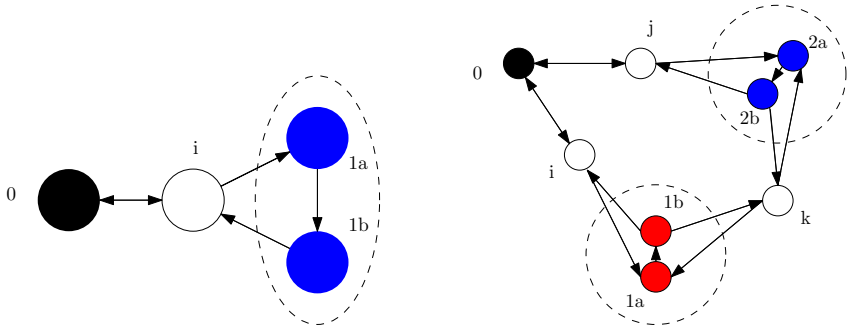

Figure 3.14: Graph $\mathcal{G}$ of Examples 8 and 9.

Theorem 3.5.3. *As $K \to \infty$, the following convergence holds*

$$(N_0^K, N_{1b}^K, N_{2b}^K)(tK^{-1+2/\alpha}) \Rightarrow \bar{n}_{X_t}\delta_{X_t}$$

for finite dimensional distributions, where X_t is a continuous time Markov chain on $\{0, 1b, 2b\}$ with transition rates:

$$\begin{aligned}
r_{0\to 1b} &= \frac{\bar{n}_0 b_0/2}{|f_{i0}|}\lambda(\rho_{i,0})\frac{f_{1a,0}}{b_{1a}}, & r_{1b\to 0} &= \frac{\bar{n}_{1b} b_{1b}/2}{|f_{i,1b}|}\lambda(\rho_{i,1b})\frac{f_{0,1b}}{b_0}\\
r_{0\to 2b} &= \frac{\bar{n}_0 b_0/2}{|f_{j0}|}\lambda(\rho_{j,0})\frac{f_{2a,0}}{b_{2a}}, & r_{2b\to 0} &= \frac{\bar{n}_{2b} b_{2b}/2}{|f_{j,2b}|}\lambda(\rho_{j,2b})\frac{f_{0,2b}}{b_0}\\
r_{1b\to 2b} &= \frac{\bar{n}_{1b} b_{1b}/2}{|f_{k,1b}|}\lambda(\rho_{k,1b})\frac{f_{2a,1b}}{b_{2a}}, & r_{2b\to 1b} &= \frac{\bar{n}_{2b} b_{2b}/2}{|f_{k,2b}|}\lambda(\rho_{k,2b})\frac{f_{1a,2b}}{b_{1a}}.
\end{aligned}$$

3.6 Perspectives

The effects of frequent changes in the phenotypes of individuals within populations, whether due to mutations or reversible switches during an individual's lifetime, have been the subject of increasing interest in the literature in recent years. I would be interested in exploring some of the questions raised in these works.

3.6.1 Effects and evolution of high mutation rates

I would like to continue studying the consequences of high mutation rates on evolutionary trajectories. In particular, I have not studied certain biological mechanisms that are of great importance in the evolution of populations, and whose modelling has recently made progress in the context of random processes (in eco-evolution or population genetics). I am thinking in particular of the horizontal gene transfer between bacteria [CMT19], and the mechanisms of dormancy [BT20].

Another issue I would like to focus on is the evolution of mutation rates. One of the results of the work I have just presented in this chapter is that high mutation rates allow evolutionary trajectories that could not occur if mutation rates were an order of magnitude lower. But the multiplication of evolutionary trajectories is not necessarily beneficial. It might be interesting to study in which cases high mutation rates are favoured or, on the contrary, counter-selected.

3.6.2 Eco-evolution and population genetics

Another issue I would like to explore in the coming years is the links between population genetics models and eco-evolution models. A first natural direction of research is to try to build models aiming for the generality of adaptive dynamics and the tractability of population genetics. We have started to do this in a collaboration with A. Gonzalez Casanova [GCS21]. Our method consisted in generalizing the idea of Krone and Neuhauser [KN97], and Gonzalez Casanova and Spano [GCS18], who represented the selection by allowing individuals to sample several potential parents in the previous generation before choosing the 'strongest' one, by allowing individuals to use any rule to choose their parent.

Another natural question is to try to make links between population genetics models and eco-evolution models via duality relations, in order to deduce properties of a model of one type from properties of a model of another type. We have begun to explore such relationships in a collaboration with A. Gonzalez Casanova and A. Wakolbinger. Starting from a population genetics model of Muller's ratchet, we have shown a duality relationship with competitive birth and death models, to which recent work has been devoted, in particular the question of survival times and distance to the quasistationary distribution [CCM16, CCM19].

Chapter 4

Evolution and consequences of mating preferences

In the last chapter of this manuscript, we are also interested on questions about evolution. We come back to the rare mutation regime of adaptive dynamics, and focus on mating preferences.

Sexual selection is an important part of the theory of evolution [JR09]. This term appeared in Charles Darwin's theory along with natural and artificial selections. This selection was first viewed as interfering with natural selection as it may explain the existence of traits disadvantaged by natural selection such as spectacular ornaments. Now this type of selection is much studied and is seen as a key element in trait and species diversifications. One hypothesis arising from Fisher idea is that mate choice evolves indirectly in response to selection acting of mating cues [Fis30, Lan81, Ros17]. As mate choice evolves, the sexual selection acting on mating cues changes generating feedback loops between selection on choice and mating cues such as runaway processes.

Mate choice is a process that leads to a bias in reproduction investment towards individuals carrying certain traits (called mating cues) [Edw14]. For example, females of *Heliconius* butterflies frequently show mating bias toward males with certain wing pattern [JNCM01, MCN14]. Mating bias can be expressed before (see example in the fiddler crab *Uca annulipes* [BP96]) or after (see example in the scorpionfly *Harpobittacus nigriceps* [Tho83]) mating. However, this definition of mate choice is broader than active discrimination and includes numerous mechanisms that lead to non random reproduction investment such as mechanical constraints [Bar90], molecular mechanisms [Cis99, HM03], allochronic isolation (different times of flowering [WWV+05, SAL+06], different arrival dates [HDW04, BFF+05]) or spatial segregation [BC00].

Mate choice is associated whit many costs. They generate a direct selection on mate preference (see [Pom87] for a review of these costs) that limits their evolution. For example, choosy individuals can pay a fitness cost because they refuse mating opportunities (that strongly limits the evolution of preference in theoretical studies [SB06, KH08]). Moreover the mechanism underlying mate choice may require specialized morphological, physiological and cognitive changes (see [Ros17] for a review), that may induce specific metabolic costs. For instance, in the self-incompatibility system in the genus *Brassica*, mate choice involves a specialized receptor-ligang association [HM03], so that

the evolution of self-incompatibility is associated with metabolic costs implied by the production of the specific proteins. Mate choice can also increase the investment in mate searching, because a choosy individual needs to sample several mates to find a suitable one. This increased sampling effort can be costly in time [KH67], in energy (as empirically estimated in antilopes [BWJR05]) and may increase predation risk, for instance in patrolling animals [HKB12]. In addition, the evolution of mate preferences can involve supplementary costs associated with the rebuttal. In the fly species *Musca domestica*, males jump on females' back to initiate mating and choosy females have to kick unpreferred males to avoid mating [Sac64]. Despite the numerous associated costs, mate choice has been observed in many species (see [Ros17]) suggesting that some positive effects should increase the fitness of choosy individuals. Fitness advantages linked to mate choice would then promote its evolution: these advantages can be direct, therefore improving the fitness of the chooser [Wag11] (because of beneficial sexually transmitted infections [SM15], by decreasing risk of pre-copulatory cannibalism [PR09], ...). But indirect fitness benefits linked to the quality of offspring might also promote the evolution of mate preferences on certain cues.

Once mate preferences are established in the population, they generate sexual selection on the traits exhibited by individuals during courtship, that may drive the evolution of extravagant traits in males, following a fisherian runaway [Fis30, O'D80, Lan81]. The evolution of mate preferences thus involves complex evolutionary processes where preferences co-evolve with the cues displayed by the chosen individuals. This co-evolution has been observed in natural populations [GS11, HMSP12] and in experimental studies [BC99, MP02], underpinning the importance of sexual selection feedbacks on the evolution of mate preferences.

The different selective regimes acting on traits involved in mate choice can drive the evolution of different types of mate preferences. Assortative mating for instance, *i.e.* preferential crosses between individuals displaying a same phenotype, is common in nature (see [JBK13] for a review in animals). The strength of assortative mating can be measured as the correlation between male and female phenotypes or genotypes across mated pairs [JBK13, Wri21, RA06]. In natural populations of certain species, this coefficient can also be negative, resulting from disassortative mating, whereby individuals tend to mate preferentially with partners exhibiting a trait different from their own [JBK13]. The selection regimes enabling the evolution of assortative *vs.* disassortative matings are strikingly different. For example, natural selection can enhance reproductive success between individuals sharing trait similarity, as in the Australian frog, *Uperoleia laevigata* where heavier males hamper oviposition and lighter males do not produce enough sperm to fertilize the whole clutch, which promotes the evolution of assortative mating [Rob90]. Contrastingly, direct selection favouring dissimilar cue mating promotes disassortative preferences (see [IF03] for a theoretical study). The indirect selection acting on mating cues can also shape the evolution of assortative and disassortative mate preferences. Disruptive selection whereby different mating cues are favoured in different habitats for instance, can promote assortative preferences that tend to increase the number of locally adapted offspring [Kir00, KR02, DD99, Die04, Gav04, OSN08, BHK12, dCBK08]. In contrast, selection conferring fitness advantages to intermediate phenotypes is often thought to promote disassortative mating [KS98, KN04]. Nevertheless, the selection regimes enabling the evolution of disassortative mating are much less studied than the selective pressures involved in the evolution of assortative mating, extensively investigated in the context of speciation [Gav04].

Indeed, understanding mechanisms underlying speciation remains a central question in evolutionary biology; more particularly understanding the origin of isolating barriers that prevent gene flow among populations or within a population. Ecological speciation has been largely studied, highlighting the relations between sexual selection and speciation, and demonstrating negative links [SB14, SB15] as well as beneficial ones [Bou01]. Lande [Lan81] is the first one to have popularized the idea of sexual selection promoting speciation. Then numerous authors have dealt with it in depth [Wu85, TB95, HTY99, vDDW04, Rit07, PKM+08]. Furthermore, biological examples of speciation that involve well studied mechanisms of sexual selection are numerous and well documented, as the case of Hawaiian cricket *Laupala* [Ott89, SP02, MS05], Amazonian frog *Physalaemus* [BFD+07], or the cichlid fish species of Lake Victoria [STM+08]. The role of so-called 'magic' or 'multiple effect' traits, which associate both adaptation to a new ecological niche and a mate preference as enhancer of speciation has been evidenced in many experimental studies [MWB+12] as well as theoretical ones [LK88, VDNH98]. However, identifying the role of sexual selection itself as trigger of speciation without ecological adaptation has received less attention [Gav14]. In Section 4.1 we will introduce and study mathematically a stochastic model accounting for the stopping of gene flow between two subpopulations by means of sexual preference only, and in Section 4.2.1, we will explore the conditions under which such a mating preference may invade a population of individuals mating uniformly at random.

A meta-analysis carried out on more than 1,116 cases of assortative or disassortative mating in animals reveals that disassortative mating is rare compared to assortative mating [JBK13]. Cases of disassortative mating have been documented, as for instance the MHC locus in humans and mice, where females prefer males with a genotype different from their own [WSBP95], the plumage coloration in the white throated sparrow [Thr75], or the wing colour pattern in the mimetic butterfly *Heliconius numata* [CLPPJ17]. In those cases, heterozygote advantage has been reported [JCW+21], so that disassortative mating may increase the offspring fitness. Ihara and Feldman [IF03] also showed that disassortative mating can be promoted when matings of pairs with different phenotypes are more fertile. Other theoretical studies have focused on the effect of disassortative mating on the persistence of variations at the cue locus, illustrating the fact that this mate preference may limit the purging at the cue locus [KF68, FL69, IF03]. These results suggest that the evolution of disassortative preferences is likely to depend on the natural selection acting at the cue locus but also on complex feedbacks between cue polymorphism and mate choice. The aim of Section 4.2.2 will be to explore the conditions enabling the evolution of disassortative mating.

4.1 The effect of assortative mating on speciation

In this section, I will present the work [CCLS18], realized in a collaboration with C. Coron, M. Costa and H. Leman, in which we assumed a population of individuals mating assortatively and wanted to understand the effect of this mating preference on the stopping of gene flow, necessary to lead to a speciation event.

We consider a population of hermaphroditic haploid individuals characterized by their genotype at one multi-allelic locus, and by their position on a space that is divided in several patches.

This population is modeled by a multi-type birth and death process with competition, which is ecologically neutral in the sense that individuals with different genotypes are not characterized by different adaptations to environment or by different resource preferences. However, individuals reproduce sexually according to mating preferences that depend on their genotype: two individuals having the same genotype have a higher probability to mate. In addition to this sexual preference, individuals can migrate from one patch to another, at a rate depending on the frequency of individuals carrying the other genotype and living in the same patch. Examples of animals migrating to find suitable mates are well documented [Sch88, HWE+07].

4.1.1 Two similar patches

The class of models considered is similar to the one introduced in Section 3.1.2, except that individuals reproduce sexually and thus the birth rates are more complex. Each individual carries an allele belonging to the genetic type space $\mathcal{A} := \{A, a\}$, and lives in a patch i in $\mathcal{I} = \{1, 2\}$. We denote by $\mathcal{E} = \mathcal{A} \times \mathcal{I}$ the type space, by $(\mathbf{e}_{\alpha,i}, (\alpha, i) \in \mathcal{E})$ the canonical basis of $\mathbb{R}^{\mathcal{E}}$, and recall that $\bar{\alpha}$ is the complement of α in $\mathcal{A}$. The population is modeled by a multi-type birth and death process with values in $\mathbb{N}^{\mathcal{E}}$. More precisely, we denote by $n_{\alpha,i}$ the current number of α-individuals in the patch i and by $\mathbf{n} = (n_{\alpha,i}, (\alpha, i) \in \mathcal{E})$ the current state of the population. The birth rate is the consequence of the following mechanisms: at a rate $B > 0$, any individual encounters another individual uniformly at random in its deme. Indeed, all the individuals are assumed to be ecologically and demographically equivalent, thus the probability that they are at the same place at the same time is uniform. Mathematically, the probability of encountering an individual of genotype α' in the patch i writes

$$\frac{n_{\alpha',i}}{n_{\alpha,i} + n_{\bar{\alpha},i}}, \tag{4.1}$$

at the time of the encounter. Then the probability that the encounter leads to a successful mating with the birth of an offspring is $b\beta/B \leq 1$ if the two individuals carry the same genotype, and $b/B \leq 1$ otherwise. As a consequence, the birth rate of individuals with genotype α in the deme i is equal to

$$\begin{aligned} \lambda_{\alpha,i}(\mathbf{n}) =& b\left(n_{\alpha,i}\beta\frac{n_{\alpha,i}}{n_{\alpha,i} + n_{\bar{\alpha},i}} + \frac{1}{2}n_{\alpha,i}\frac{n_{\bar{\alpha},i}}{n_{\alpha,i} + n_{\bar{\alpha},i}} + \frac{1}{2}n_{\bar{\alpha},i}\frac{n_{\alpha,i}}{n_{\alpha,i} + n_{\bar{\alpha},i}}\right) \\ =& bn_{\alpha,i}\frac{\beta n_{\alpha,i} + n_{\bar{\alpha},i}}{n_{\alpha,i} + n_{\bar{\alpha},i}}. \end{aligned} \tag{4.2}$$

The parameter $\beta > 1$ represents the "mating preference" as two encountering individuals have a probability β times larger to mate and give birth to a viable offspring if they carry the same allele $\alpha \in \mathcal{A}$. Note that, in our model, the preference does not only bias the distribution of genotypes among mating partners but also affects the rate of mating for choosy individuals, unlike what is assumed in standard (population genetics) sexual selection models [Lan81, Kir82].

The death rate of α-individuals in the patch i writes

$$d^K_{\alpha,i}(\mathbf{n}) = \left(d + \frac{c}{K}(n_{\alpha,i} + n_{\bar{\alpha},i})\right) n_{\alpha,i}. \tag{4.3}$$

The individual intrinsic death rate d is assumed to be non negative and less than b:

$$0 \leq d < b. \tag{4.4}$$

The death rate definition (4.3) implies that all the individuals are ecologically equivalent: the competition pressure does not depend on the alleles carried by the two individuals involved in an event of competition for food or space. Last, the migration of α-individuals from patch $\bar{i} = \mathcal{I} \setminus \{i\}$ to patch i occurs at a rate

$$\rho_{\alpha,\bar{i}\to i}(\mathbf{n}) = p\left(1 - \frac{n_{\alpha,\bar{i}}}{n_{\alpha,\bar{i}} + n_{\bar{\alpha},\bar{i}}}\right) n_{\alpha,\bar{i}} = p\frac{n_{\alpha,\bar{i}} n_{\bar{\alpha},\bar{i}}}{n_{\alpha,\bar{i}} + n_{\bar{\alpha},\bar{i}}}, \tag{4.5}$$

(see Figure 4.1). The individual migration rate of α-individuals is proportional to the frequency of

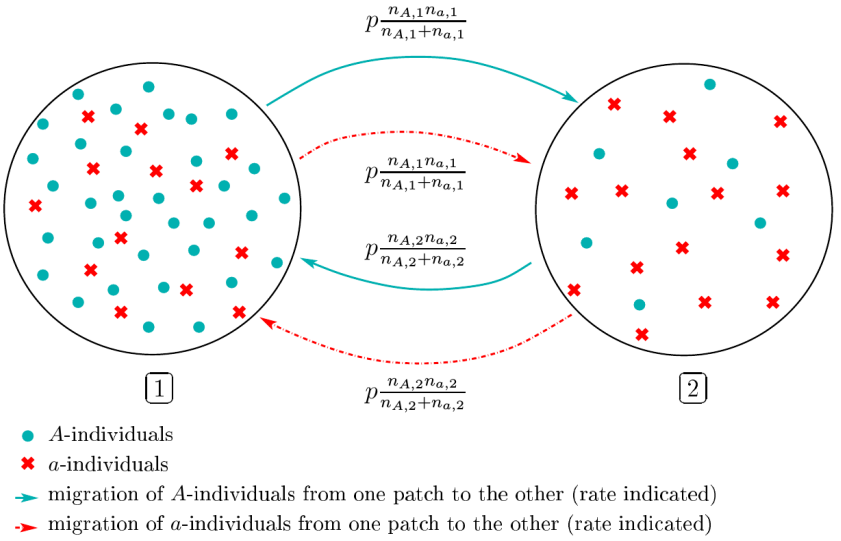

Figure 4.1: Migrations of A- and a-individuals between the patches.

$\bar{\alpha}$-individuals in the patch. This reflects the fact that individuals prefer being in an environment with a majority of individuals of their own type. In particular, if all the individuals living in a patch are of the same type, there is no more migration outside this patch. Remark that the migration rate from patch $\bar{i}$ to i is equal for A- and a-individuals, hence to simplify notation, we denote

$$\rho_{\bar{i}\to i}(\mathbf{n}) = \rho_{A,\bar{i}\to i}(\mathbf{n}) = \rho_{a,\bar{i}\to i}(\mathbf{n}).$$

The community is therefore represented at every time $t \geq 0$ by a stochastic process with values in $\mathbb{R}^{\mathcal{E}}$:

$$(\mathbf{N}^K(t), t \geq 0) = (N^K_{\alpha,i}(t), (\alpha, i) \in \mathcal{E}, t \geq 0),$$

whose transitions are, for $\mathbf{n} \in \mathbb{N}^{\mathcal{E}}$ and $(\alpha, i) \in \mathcal{E}$:

$$\begin{array}{rcll} \mathbf{n} & \longrightarrow & \mathbf{n} + \mathbf{e}_{\alpha,i} & \text{at rate} \quad \lambda_{\alpha,i}(\mathbf{n}), \\ & \longrightarrow & \mathbf{n} - \mathbf{e}_{\alpha,i} & \text{at rate} \quad d^K_{\alpha,i}(\mathbf{n}), \\ & \longrightarrow & \mathbf{n} + \mathbf{e}_{\alpha,i} - \mathbf{e}_{\alpha,\bar{i}} & \text{at rate} \quad \rho_{\bar{i}\to i}(\mathbf{n}). \end{array}$$

In the sequel, we will assume that the initial population sizes $(N^K_{\alpha,i}(0), (\alpha,i) \in \mathcal{E})$ are of order K. As a consequence, we consider a rescaled stochastic process $(\mathbf{N}^K(t)/K, t \geq 0)$, which (as in the previous Chapter by an application of [EK09], Chapter 11, Theorem 2.1) will be comparable to a solution of the dynamical system

$$\begin{cases} \frac{d}{dt}z_{A,1}(t) = z_{A,1}\left[b\frac{\beta z_{A,1}+z_{a,1}}{z_{A,1}+z_{a,1}} - d - c(z_{A,1}+z_{a,1}) - p\frac{z_{a,1}}{z_{A,1}+z_{a,1}}\right] + p\frac{z_{A,2}z_{a,2}}{z_{A,2}+z_{a,2}} \\ \frac{d}{dt}z_{a,1}(t) = z_{a,1}\left[b\frac{\beta z_{a,1}+z_{A,1}}{z_{A,1}+z_{a,1}} - d - c(z_{A,1}+z_{a,1}) - p\frac{z_{A,1}}{z_{A,1}+z_{a,1}}\right] + p\frac{z_{A,2}z_{a,2}}{z_{A,2}+z_{a,2}} \\ \frac{d}{dt}z_{A,2}(t) = z_{A,2}\left[b\frac{\beta z_{A,2}+z_{a,2}}{z_{A,2}+z_{a,2}} - d - c(z_{A,2}+z_{a,2}) - p\frac{z_{a,2}}{z_{A,2}+z_{a,2}}\right] + p\frac{z_{A,1}z_{a,1}}{z_{A,1}+z_{a,1}} \\ \frac{d}{dt}z_{a,2}(t) = z_{a,2}\left[b\frac{\beta z_{a,2}+z_{A,2}}{z_{A,2}+z_{a,2}} - d - c(z_{A,2}+z_{a,2}) - p\frac{z_{A,2}}{z_{A,2}+z_{a,2}}\right] + p\frac{z_{A,1}z_{a,1}}{z_{A,1}+z_{a,1}}, \end{cases} \tag{4.6}$$

denoted by

$$(\mathbf{z}^{(\mathbf{z^0})}(t), t \geq 0) = (z^{(\mathbf{z^0})}_{\alpha,i}(t), (\alpha,i) \in \mathcal{E})_{t\geq 0}$$

when starting from $\mathbf{z}(\mathbf{0}) = \mathbf{z^0} \in \mathbb{R}^{\mathcal{E}}_+$.

When K is large, this convergence result allows one to derive the global behaviour of the population process $\mathbf{N}^K$ from the behaviour of the dynamical system (4.6). Therefore, a fine study of (4.6) is carried out in [CCLS18]. In particular a long-time convergence of the dynamical system (4.6) toward a stable equilibrium of interest, when starting from an explicit subset of $\mathbb{R}^{\mathcal{E}}_+$ is proven. To state this latter, we need to introduce the parameter

$$\zeta := \frac{\beta b - d}{c}, \tag{4.7}$$

which corresponds to the equilibrium size of the α-population for the dynamical system (4.6), in a patch with no $\bar{\alpha}$-individuals, and to define the subset of $\mathbb{R}^{\mathcal{E}}_+$

$$\mathcal{D} := \{\mathbf{z} \in \mathbb{R}^{\mathcal{E}}_+, z_{A,1} - z_{a,1} > 0, z_{a,2} - z_{A,2} > 0\}, \tag{4.8}$$

and the positive real number

$$p_0 = \frac{\sqrt{b(\beta-1)[b(3\beta+1)-4d]} - b(\beta-1)}{2}. \tag{4.9}$$

Notice that under Assumption (4.4) and as $\beta > 1$,

$$p_0 < b(\beta+1) - 2d.$$

Finally, for $p < b(\beta+1) - 2d$, we introduce the set

$$\mathcal{K}_p := \left\{\mathbf{z} \in \mathcal{D},\ \{z_{A,1}+z_{a,1},\ z_{A,2}+z_{a,2}\} \in \left[\frac{b(\beta+1)-2d-p}{2c}, \frac{2b\beta-2d+p}{2c}\right]\right\}. \tag{4.10}$$

Then we have the following result:

Theorem 4.1.1. *Let $p < p_0$. Then*

i/ Any solution to (4.6) which starts from $\mathcal{D}$ converges to the equilibrium $(\zeta, 0, 0, \zeta)$.

ii/ If the initial condition of (4.6) lies in $\mathcal{K}_p$, there exist two positive constants k_1 and k_2, depending on the initial condition, such that for every $t \geq 0$,

$$\|\mathbf{z}(t) - (\zeta, 0, 0, \zeta)\| \leq k_1 e^{-k_2 t}.$$

Symmetrical results hold for the equilibria $(0, \zeta, \zeta, 0)$, $(\zeta, 0, \zeta, 0)$ and $(0, \zeta, 0, \zeta)$.

Note that the limit reached depends on the genotype which is initially in majority in each patch, since the subset $\mathcal{D}$ is invariant under the dynamical system (4.6). Secondly, when $p = 0$, the results of Theorem 4.1.1 can be proven easily since the two patches are independent from each other. The difficulty is thus to prove the result when $p > 0$. Our arguments allow us to deduce an explicit constant p_0 under which we have convergence to an equilibrium with reproductive isolation between patches. However, we are not able to deduce a rigorous result for all p. Indeed, when p increases, there is more mixing between the two patches which makes the model difficult to study. Nevertheless simulations suggest that the result stays true.

Let us now present the main result of [CCLS18] on the probability and the time needed for the stochastic process $\mathbf{N}^K$ to reach a neighbourhood of the equilibria $(\zeta, 0, 0, \zeta)$ or $(0, \zeta, \zeta, 0)$.

Theorem 4.1.2. *Assume that $\mathbf{N}^K(0)/K$ converges in probability to a deterministic vector $\mathbf{z^0}$ belonging to $\mathcal{D}$, with $(z^0_{a,1}, z^0_{A,2}) \neq (0, 0)$. Introduce the following bounded set depending on $\varepsilon > 0$:*

$$\mathcal{B}_\varepsilon := [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K] \times \{0\} \times \{0\} \times [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K].$$

Then there exist three positive constants ε_0, C_0 and m, and a positive constant V depending on (m, ε_0) such that if $p < p_0$ and $\varepsilon \leq \varepsilon_0$,

$$\lim_{K\to\infty} \mathbb{P}\left(\left| \frac{T^K_{\mathcal{B}_\varepsilon}}{\ln K} - \frac{1}{b(\beta - 1)} \right| \leq C_0 \varepsilon,\ \mathbf{N}^K\left(T^K_{\mathcal{B}_\varepsilon} + t\right) \in \mathcal{B}_{m\varepsilon}\ \forall t \leq e^{VK} \right) = 1, \tag{4.11}$$

where $T^K_{\mathcal{B}}$, $\mathcal{B} \subset \mathbb{R}^{\mathcal{E}}_+$ is the hitting time of the set $\mathcal{B}$ by the population process $\mathbf{N}^K$.
Symmetrical results hold for the equilibria $(0, \zeta, \zeta, 0)$, $(\zeta, 0, \zeta, 0)$ and $(0, \zeta, 0, \zeta)$.

This theorem gives the order of magnitude of the time to reproductive isolation between the two patches (given by $T^K_{\mathcal{B}_\varepsilon}$), as a function of the population size scaling factor K. This isolation time is infinite when considering the dynamical system (4.6) for which K is equal to infinity. Note that the time needed to reach the reproductive isolation is inversely proportional to $\beta - 1$ which suggests that the system behaves differently for $\beta = 1$ (see [CCLS18] for a study of this special case). Moreover, the time does not depend on the parameter p. Intuitively, this can be understood as follows: the time needed to reach a neighbourhood of the state $(\zeta, 0, 0, \zeta)$ is of order 1 (recall Theorem 4.1.1.ii/), and from this neighbourhood the time needed for the complete extinction of the a-individuals in the patch 1 and the A-individuals in the patch 2 is much longer, it is of order $\ln K$ (according to (4.11)). During this second phase, the migrations between the two patches are already balanced, which entails the independence with respect to p. Furthermore, the constant does not depend on d and c since there is no ecological difference between the two types and the

two patches: during the second phase, the natural birth rate of the a-individuals in the patch 1 is approximately b since the patch 1 is almost entirely filled with A-individuals, and their natural death rate can be approximated by $d + c\zeta = b\beta$ where the term $c\zeta$ comes from the competition exerted by the A-individuals. Thus, their natural growth rate is approximately $b - b\beta$ which only depends on the birth parameters.

Note that Theorem 4.1.2 gives not only an estimation of the time to reach a neighbourhood of the limit, but also it proves that the dynamics of the population process stays a long time in the neighbourhood of equilibria $(\zeta, 0, 0, \zeta)$ or $(0, \zeta, \zeta, 0)$ after this time.

Finally, the assumption $(z^0_{a,1}, z^0_{A,2}) \neq (0, 0)$ is necessary to get the lower bound in (4.11). Indeed, if $(z^0_{a,1}, z^0_{A,2}) = (0, 0)$, the set $\mathcal{B}_\varepsilon$ is reached faster, and thus only the upper bound still holds. In this case, the speed to reach the set $\mathcal{B}_\varepsilon$ will depend on the speed of convergence of the sequence $(N^K_{a,1}/K, N^K_{A,2}/K)$ to the limit $(0, 0)$. In the trivial example where $(N^K_{a,1}/K, N^K_{A,2}/K) = (0, 0)$, $T^K_{\mathcal{B}}$ will be of order 1 which is the time needed for the processes $N^K_{A,1}/K$ and $N^K_{a,2}/K$ to reach a neighbourhood of the equilibrium ζ.

4.1.2 Ideas of the proofs

The first step of the proof consists in finding the equilibrium points of the dynamical system (4.6) and determining their stability. This is achieved by classical methods.

The second step of the proof consists in proving Theorem 4.1.1. To do that, we first prove that any trajectory reaches the compact set $\mathcal{K}_p$ in finite time, and stays in this set. Then, we introduce the function $V : \mathcal{D} \to \mathbb{R}$:

$$V(\mathbf{z}) = \ln\left(\frac{z_{A,1} + z_{a,1}}{z_{A,1} - z_{a,1}}\right) + \ln\left(\frac{z_{a,2} + z_{A,2}}{z_{a,2} - z_{A,2}}\right), \tag{4.12}$$

which is well defined as $\mathcal{D}$ is invariant under the dynamical system (4.6). It characterizes the dynamics of (4.6) on $\mathcal{K}_p$, and we may prove that V is a Lyapunov function if p smaller than p_0. This allows to prove that the solutions to (4.6) converge to $(\zeta, 0, 0, \zeta)$ exponentially fast as soon as their trajectory reaches the set $\mathcal{K}_p$.

Finally, we need to study the extinction phase, when one type has a population size of order smaller than K. This is achieved by couplings with subcritical multitype birth and death processes, in the spirit of [Cha06].

4.1.3 Generalisations of the model

Until now we considered a simple model to understand the key drivers of spatial segregation between patches. In fact, our findings are robust and we may generalise the model and show that we can relax several assumptions and still get spatial segregation between patches.

Differences between patches

We assumed that the patches were ecologically equivalent in the sense that the birth, death and competition rates b, d and c, respectively, did not depend on the label of the patch $i \in \mathcal{I}$. In fact we

could make these parameters depend on the patch, and denote them b_i, d_i and c_i, $i \in \mathcal{I}$. In the same way, the sexual preference β_i and the migration rate p_i could depend on the label of the patch $i \in \mathcal{I}$. As a consequence, the dynamical system (4.6) becomes

$$\begin{cases} \frac{d}{dt}z_{A,1}(t) = z_{A,1}\left[b_1\frac{\beta_1 z_{A,1}+z_{a,1}}{z_{A,1}+z_{a,1}} - d_1 - c_1(z_{A,1}+z_{a,1}) - p_1\frac{z_{a,1}}{z_{A,1}+z_{a,1}}\right] + p_2\frac{z_{A,2}z_{a,2}}{z_{A,2}+z_{a,2}} \\ \frac{d}{dt}z_{a,1}(t) = z_{a,1}\left[b_1\frac{\beta_1 z_{a,1}+z_{A,1}}{z_{A,1}+z_{a,1}} - d_1 - c_1(z_{A,1}+z_{a,1}) - p_1\frac{z_{A,1}}{z_{A,1}+z_{a,1}}\right] + p_2\frac{z_{A,2}z_{a,2}}{z_{A,2}+z_{a,2}} \\ \frac{d}{dt}z_{A,2}(t) = z_{A,2}\left[b_2\frac{\beta_2 z_{A,2}+z_{a,2}}{z_{A,2}+z_{a,2}} - d_2 - c_2(z_{A,2}+z_{a,2}) - p_2\frac{z_{a,2}}{z_{A,2}+z_{a,2}}\right] + p_1\frac{z_{A,1}z_{a,1}}{z_{A,1}+z_{a,1}} \\ \frac{d}{dt}z_{a,2}(t) = z_{a,2}\left[b_2\frac{\beta_2 z_{a,2}+z_{A,2}}{z_{A,2}+z_{a,2}} - d_2 - c_2(z_{A,2}+z_{a,2}) - p_2\frac{z_{A,2}}{z_{A,2}+z_{a,2}}\right] + p_1\frac{z_{A,1}z_{a,1}}{z_{A,1}+z_{a,1}}. \end{cases} \tag{4.13}$$

The set $\mathcal{D}$ is still invariant under this new system and the solutions to (4.13) with initial conditions in $\mathcal{D}$ reach in finite time the invariant set

$$\mathcal{K}'_p := \left\{\mathbf{z} \in \mathcal{D},\ z_{A,i}+z_{a,i} \in \left[\frac{b_i(\beta_i+1)-2d_i-p_i}{2c_i}, \zeta_i + \frac{p_{\bar{i}}}{2c_i},\ i \in \mathcal{I}\right]\right\},$$

where

$$\zeta_i := \frac{b_i\beta_i - d_i}{c_i}.$$

As $\mathcal{D}$ is invariant under (4.13), we can define the function V as in (4.12). Its first order derivative is

$$\frac{d}{dt}V(\mathbf{z}(t)) = -\sum_{i=1,2}\frac{z_{A,i}z_{a,i}}{z_{A,i}+z_{a,i}}\left[\frac{2b_i(\beta_i-1)+2p_i}{z_{A,i}+z_{a,i}} - \frac{2p_i}{z_{A,\bar{i}}+z_{a,\bar{i}}}\right].$$

As a consequence, we can prove similar results to Theorems 4.1.1 and 4.1.2 under the assumption that p_1 and p_2 satisfy

$$p_i c_{\bar{i}}(2c_i\zeta_i + p_{\bar{i}}) < c_i(b_i(\beta_i-1)+p_i)(b_{\bar{i}}(\beta_{\bar{i}}+1) - 2d_{\bar{i}} - p_{\bar{i}}),\ \text{for } i \in \mathcal{I},$$

and where the constant in front of the time $\ln K$ is no more $1/b(\beta-1)$ but $1/\omega_{1,2}$ with

$$\omega_{1,2} = \frac{1}{2}(b_1(\beta_1-1)+p_1+b_2(\beta_2-1)+p_2) - \frac{1}{2}\sqrt{(b_1(\beta_1-1)+p_1-b_2(\beta_2-1)-p_2)^2+4p_1p_2}.$$

Here, note that the constant does depend on all the parameters. Indeed, since there is no ecological neutrality between the two patches, there are no simplifications and balancings as in the previous model.

Migration

The migration rates under consideration increase when the genetic diversity increases. Indeed, let us consider

$$H_T^{(i)} := 1 - \left[\left(\frac{n_{A,i}}{n_{A,i}+n_{a,i}}\right)^2 + \left(\frac{n_{a,i}}{n_{A,i}+n_{a,i}}\right)^2\right]$$

as a measure of the genetic diversity in the patch $i \in \mathcal{I}$. Note that $H_T^{(i)} \in [0, 1/2]$ is known as the "total gene diversity" in the patch i (see the article by [Nei75] for instance) and is widely used as a measure of diversity. When we express the migration rates in terms of this measure, we get

$$\rho_{\alpha,\bar{i}\to i}(n) = p\frac{n_{A,i}n_{a,i}}{n_{A,i}+n_{a,i}} = \frac{p}{2}(n_{A,i}+n_{a,i})H_T^{(i)}.$$

Hence we can consider that the migration helps the speciation. We may prove that we can get the same kind of result when we consider an arbitrary form for the migration rate if this latter is symmetrical and bounded. We thus consider a more general form for the migration rate. More precisely,

$$\rho_{\alpha,\bar{i}\to i}(n) = p(n_{A,\bar{i}}, n_{a,\bar{i}}),$$

and we assume

$$p(n_{A,\bar{i}}, n_{a,\bar{i}}) = p(n_{a,\bar{i}}, n_{A,\bar{i}}) \quad \text{and} \quad p(n_{A,\bar{i}}, n_{a,\bar{i}}) \frac{n_{A,\bar{i}} + n_{a,\bar{i}}}{n_{A,\bar{i}} n_{a,\bar{i}}} < p_0,$$

where p_0 has been defined in (4.9). Note that the second condition on the function p imposes that as one of the population sizes goes to 0, then so does the migration rate. In particular, this condition ensures that the points $(\zeta, 0, 0, \zeta)$, $(0, \zeta, \zeta, 0)$, $(0, \zeta, 0, \zeta)$ and $(\zeta, 0, \zeta, 0)$ are still equilibria of the system. Theorems 4.1.1 and 4.1.2 still hold with this new definition for the migration rate.

Number of patches

We restricted our attention to the case of two patches, but we can consider an arbitrary number $N \in \mathbb{N}$ of patches. We assume that all the patches are ecologically equivalent but that the migrant individuals have a probability to migrate to an other patch which may depend on the geometry of the system. Moreover, we allow the individuals to migrate outside the N patches. In other words, for $\alpha \in \mathcal{A}$, $i \leq N$, $j \leq N+1$ and $\mathbf{n} \in (\mathbb{N}^{\mathcal{A}})^N$,

$$\rho_{\alpha,i\to j}(\mathbf{n}) = p_{ij} \frac{n_{A,i} n_{a,i}}{n_{A,i} + n_{a,i}},$$

where the "patch" $N+1$ denotes the outside of the system.
As a consequence, we obtain the following limiting dynamical system for the rescaled process, when the initial population sizes are of order K in all the patches: for every $1 \leq i \leq N$,

$$\begin{aligned}
\frac{dz_{A,i}(t)}{dt} &= z_{A,i} \left[b \frac{\beta z_{A,i} + z_{a,i}}{z_{A,i} + z_{a,i}} - d - c(z_{A,i} + z_{a,i}) - \sum_{j \neq i, j \leq N+1} p_{ij} \frac{z_{a,i}}{z_{A,i} + z_{a,i}} \right] \\
&\quad + \sum_{j \neq i, j \leq N} p_{ji} \frac{z_{A,j} z_{a,j}}{z_{A,j} + z_{a,j}} \\
\frac{dz_{a,i}(t)}{dt} &= z_{a,i} \left[b \frac{\beta z_{a,i} + z_{A,i}}{z_{A,i} + z_{a,i}} - d - c(z_{A,i} + z_{a,i}) - \sum_{j \neq i, j \leq N+1} p_{ij} \frac{z_{A,i}}{z_{A,i} + z_{a,i}} \right] \\
&\quad + \sum_{j \neq i, j \leq N} p_{ji} \frac{z_{A,j} z_{a,j}}{z_{A,j} + z_{a,j}}.
\end{aligned} \tag{4.14}$$

For the sake of readability, we introduce the two following notations:

$$p_{i\to} := \sum_{j \neq i, j \leq N+1} p_{ij} \quad \text{and} \quad p_{i\leftarrow} := \sum_{j \neq i, j \leq N} p_{ji}.$$

Let N_A be an integer smaller than N which gives the number of patches with a majority of individuals of type A. We can assume without loss of generality that

$$z_{A,i}(0) > z_{a,i}(0), \text{ for } 1 \le i \le N_A, \quad \text{and} \quad z_{A,i}(0) < z_{a,i}(0), \text{ for } N_A + 1 \le i \le N.$$

Let us introduce the subset of $(\mathbb{R}_+^{\mathcal{A}})^N$

$$\mathcal{D}_{N_A,N} := \{\mathbf{z} \in (\mathbb{R}_+^{\mathcal{A}})^N, z_{A,i} - z_{a,i} > 0 \text{ for } i \le N_A \quad \text{and} \quad z_{a,i} - z_{A,i} > 0 \text{ for } i > N_A\}.$$

We assume that the sequence $(p_{ij})_{i,j\in\{1,..,N\}}$ satisfies: for all $i \in \{1,..,N\}$,

$$p_{i\to} < b(\beta+1) - 2d \text{ and } \frac{b(\beta-1)+p_{i\to}}{2cz + p_{i\leftarrow}} - \sum_{j\neq i, j\le N+1} \frac{p_{ij}}{b(\beta+1) - 2d - p_{j\to}} > 0. \tag{4.15}$$

Then we have the following result.

Theorem 4.1.3. *We assume that Assumption (4.15) holds. Let us assume that $\mathbf{Z}^K(0)$ converges in probability to a deterministic vector $\mathbf{z^0}$ belonging to $\mathcal{D}_{N_A,N}$ with $(z^0_{a,1}, z^0_{A,2}) \neq (0,0)$. Introduce the following bounded set depending on $\varepsilon > 0$:*

$$\mathcal{B}_{N_A,N,\varepsilon} := \Big([(\zeta-\varepsilon)K, (\zeta+\varepsilon)K] \times \{0\}\Big)^{N_A} \times \Big(\{0\} \times [(\zeta-\varepsilon)K, (\zeta+\varepsilon)K]\Big)^{N-N_A}.$$

Then there exist three positive constants ε_0, C_0 and m, and a positive constant V depending on (m, ε_0) such that if $\varepsilon \le \varepsilon_0$,

$$\lim_{K\to\infty} \mathbb{P}\left(\left|\frac{T^K_{\mathcal{B}_\varepsilon}}{\ln K} - \frac{1}{b(\beta-1)}\right| \le C_0\varepsilon, \mathbf{N}^K\left(T^K_{\mathcal{B}_{N_A,N,\varepsilon}} + t\right) \in \mathcal{B}_{N_A,N,m\varepsilon}\ \forall t \le e^{VK}\right) = 1,$$

where $T^K_{\mathcal{B}}$, $\mathcal{B} \subset \mathbb{R}_+^{\mathcal{E}}$ is the hitting time of the set $\mathcal{B}$ by the population process $\mathbf{N}^K$.

The proof is really similar to the one for two patches. To handle the deterministic part of the proof, we first show that for every initial condition on $\mathcal{D}_{N_A,N}$, the solution of (4.14) reaches the set

$$\mathcal{K}_{N_A,N} := \left\{\mathbf{z} \in \left((\mathbb{R}_+^*)^{\mathcal{A}}\right)^N, \{z_{A,i} + z_{a,i}\} \in \left[\frac{b(\beta+1) - 2d - p_{i\to}}{2c}, \zeta + \frac{p_{i\leftarrow}}{2c}\right] \forall i \le N\right\} \cap \mathcal{D}_{N_A,N}.$$

in finite time, and that this set is invariant under (4.14). Then, we conclude with the Lyapunov function

$$\mathbf{z} \in \mathcal{K}_{N_A,N} \mapsto \sum_{i\le N_A} \ln\left(\frac{z_{A,i}+z_{a,i}}{z_{A,i}-z_{a,i}}\right) + \sum_{N_A<i\le N} \ln\left(\frac{z_{a,i}+z_{A,i}}{z_{a,i}-z_{A,i}}\right).$$

4.1.4 The effect of diploidy

Finally, in a collaboration with H. Leman and V. Llaurens, we explored the effects of genetic architecture on the stopping of gene flow, by studying the case of diploid individuals. The population dynamics is then very dependent on the behaviour of heterozygotes. We contrasted two assumptions:

(1) Preference expressed towards heterozygotes is intermediate between assortative and disassortative mating (COD 1) ($\beta > 1$ for pairs (AA, AA), (aa, aa) and (Aa, Aa), $(\beta+1)/2$ for pairs (AA, Aa) and (aa, Aa), and 1 for pairs (AA, aa)) and migration rate varies accordingly because the decision to leave the patch depends on the lack of preferred partners in the patch.

(2) Heterozygotes express no preference towards any partners (COD2), the preference parameter is thus β for pairs (AA, AA) and (aa, aa), and 1 for all other pairs. Because of this lack of preference, heterozygotes have no reason to look for suitable mate and thus do not migrate.

Our results show that trajectories of diploid populations assuming codominance between alleles depart from equilibria observed in the haploid model. Notably, migration limits the probability of population differentiation in the diploid model which was not observed in haploids. Because migration depends on the number of individuals with different phenotypes, population differentiation is quickly achieved in the haploid model because of a rapid decrease of migration as soon as differentiation starts, until a complete isolation of the two populations, which fixed different alleles. In the diploid model however, when the two alleles are codominant, the presence of heterozygotes with intermediate phenotypes promotes migration even when populations are initially differentiated, and frequently leads to the fixation of a single allele throughout both connected populations. The discrepancy observed here between haploid and diploid assumptions highlights the need to consider the effect of ploidy in spatially-structured models of trait evolution, because the presence of an intermediate phenotype can interfere in the differentiation process.

Depending on the assumption regarding codominance, the resulting equilibrium slightly differed. The absence of preference of heterozygotes for their own phenotypes (hypothesis COD2) can promote polymorphism of the trait under sexual selection, notably when populations are initially uneven. These heterozygotes do not migrate and reproduce equally with any genotypes. When they initially occur in significant proportion within populations, they promote migration of homozygous genotypes and limit fixation of the initially predominant allele. This contrasts with the co-dominance drawn from hypothesis COD1, where heterozygotes can migrate and are half as preferred by homozygotes. In this case, fixation of a single allele throughout both populations is always achieved when the same allele is predominant in both populations initially. Heterozygote behaviour is therefore a key parameter in the dynamics of population differentiation in mating traits.

4.2 Evolution to sexual preferences

4.2.1 Evolution to assortative mating

As explained in the introduction of this chapter, mating preferences come with costs: for instance, they decrease the number of potential partners, and this decrease depends on the composition of the population. In a work in collaboration with C. Coron, M. Costa, F. Laroche and H. Leman, we studied the conditions enabling the evolution of assortative preferences in a population where individuals initially choose their mate uniformly at random.

We suppose that a mutation arises in the population: individuals carrying the mutation (denoted P) have a higher (resp. smaller) reproductive success when mating with individuals of the same (resp. different) phenotype than individuals without the mutation (denoted p).

We consider a population of individuals that reproduce sexually and compete with each other for a common resource. Individuals are haploid and are characterized by their genotype at two loci

located on different chromosomes. Locus 1 presents two alleles, denoted by A and a, and codes for phenotypes, as in the previous section. Locus 2 presents two alleles denoted by P and p, and codes for assortative mating, which is defined relatively to the first locus. The genotype of each individual belongs to the set $\mathcal{G} := \{AP, Ap, aP, ap\}$ and the state of the population is characterized at each time t by a vector in $\mathbb{N}^4$ giving the respective numbers of individuals carrying each of these four genotypes. The dynamics of this population is thus modeled by a multi-type birth-and-death process

$$(N^K(t), t \geq 0) := (N^K_{AP}(t), N^K_{Ap}(t), N^K_{aP}(t), N^K_{ap}(t), t \geq 0)$$

with values in $\mathbb{N}^4$. As before and because we focus on the role of reproduction, the death rate of an individual does not depend on its genotype, and is the same as in (4.3). More precisely, when the population is in state $\mathbf{n} = (n_{AP}, n_{Ap}, n_{aP}, n_{ap}) \in \mathbb{N}^4$ with size $n = n_{AP} + n_{Ap} + n_{aP} + n_{ap}$, then the rate at which the population looses an individual with genotype $i \in \mathcal{G}$, is equal to

$$d_i(\mathbf{n}) = n_i \left(d + \frac{c}{K} n\right), \tag{4.16}$$

with $d \in \mathbb{R}^+$, $c > 0$ and $K > 0$. Moreover, the rate $b_i(n)$ at which an individual with genotype $i \in \mathcal{G}$ is born, is defined by

$$\begin{aligned}
b_{AP}(\mathbf{n}) &= b\left[n_{AP} + \frac{1}{n}\left(\beta_1 n_{AP}\left(n_{AP} + \frac{n_{Ap}}{2}\right) - \beta_2\left(n_{AP}\left(n_{aP} + \frac{n_{ap}}{4}\right) + n_{Ap}\frac{n_{aP}}{4}\right)\right) + \frac{\Delta_{aP}}{2n}\right] \\
b_{Ap}(\mathbf{n}) &= b\left[n_{Ap} + \frac{1}{n}\left(\beta_1 n_{Ap}\frac{n_{AP}}{2} - \beta_2\left(n_{Ap}\frac{n_{aP}}{4} + n_{AP}\frac{n_{ap}}{4}\right)\right) - \frac{\Delta_{aP}}{2n}\right] \\
b_{aP}(\mathbf{n}) &= b\left[n_{aP} + \frac{1}{n}\left(\beta_1 n_{aP}\left(n_{aP} + \frac{n_{ap}}{2}\right) - \beta_2\left(n_{aP}\left(n_{AP} + \frac{n_{Ap}}{4}\right) + n_{ap}\frac{n_{AP}}{4}\right)\right) - \frac{\Delta_{aP}}{2n}\right] \\
b_{ap}(\mathbf{n}) &= b\left[n_{ap} + \frac{1}{n}\left(\beta_1 n_{ap}\frac{n_{aP}}{2} - \beta_2\left(n_{ap}\frac{n_{AP}}{4} + n_{aP}\frac{n_{Ap}}{4}\right)\right) + \frac{\Delta_{aP}}{2n}\right],
\end{aligned} \tag{4.17}$$

where

$$\Delta_{aP} := n_{aP} n_{Ap} - n_{AP} n_{ap}.$$

The parameter $b(1+\beta_1)$ with $b > 0$ and $\beta_1 \geq 0$ is the rate at which any individual (called first parent) reproduces (it corresponds to the product $b\beta$ of the previous section), the second parent being chosen uniformly in the population. Each reproduction leads to the birth of a new individual with probability $1/(1+\beta_1)$ when the first parent carries allele p, with probability 1 if the first parent carries allele P and both parents carry the same allele at locus 1, and with probability $(1-\beta_2)/(1+\beta_1)$ if the first parent carries allele P and the two parents carry different alleles at locus 1 (hence $(1-\beta_2)b$ would correspond to the parameter b of the previous section). The parameters β_1 and β_2 respectively quantify benefits and penalties for homogamous individuals.

We will make the following assumptions on the parameters:

1. $b > d$
2. $\beta_1 \geq 0$

3. $0 \leq \beta_2 \leq 1$

The first assumption ensures that a population of individuals mating uniformly at random is not doomed to a rapid extinction because of a natural death rate larger than the birth rate under uniform random mating. The second (resp. third) assumption means that choosy individuals have a higher (resp. smaller) probability to give birth when mating with an individual with the same (resp. different) trait (A or a).

We assume that at time 0, all individuals mate uniformly at random (no sexual preference, all individuals carry allele p), and that the population size is close to its long time equilibrium, $(b-d)K/c$ (see page 88 for details). A mutant (or a migrant) appears in the population, with genotype αP, where $\alpha \in \mathcal{A} := \{A, a\}$. The goal of our Theorem 4.2.1 is to study a step in Darwinian evolution, that consists in the progressive invasion of the new allele P and loss of initial allele p in the population. The proof of this theorem relies on the study of three phases in the population dynamics trajectories (mutant survival or extinction, mean-field phase, and resident allele extinction). The statement of Theorem 4.2.1 requires the introduction of several quantities that we define now.

Our first goal is to determine conditions under which the mutant population has a positive probability to survive and invade the resident population. In order to answer this question, and as we have done in the previous chapter, we will compare the mutant population with a branching process during the first times of the invasion: as long as the mutant population size is negligible with respect to the carrying capacity K, the dynamics of the resident population will not be affected by the presence of the mutants and will stay close to its initial state. In other words, the size and proportions of the resident population will remain almost constant and the dynamics of the mutant population will be close to the dynamics of the process $\bar{\mathbf{N}} = (\bar{N}_A, \bar{N}_a)$, which is a bi-type branching process with the following transition rates:

$$\begin{array}{lll} (\bar{N}_A, \bar{N}_a) \to (\bar{N}_A + 1, \bar{N}_a) & \text{at rate} & \bar{\beta}_{AA}\bar{N}_A + \bar{\beta}_{aA}\bar{N}_a \\ (\bar{N}_A, \bar{N}_a) \to (\bar{N}_A, \bar{N}_a + 1) & \text{at rate} & \bar{\beta}_{Aa}\bar{N}_A + \bar{\beta}_{aa}\bar{N}_a \\ (\bar{N}_A, \bar{N}_a) \to (\bar{N}_A - 1, \bar{N}_a) & \text{at rate} & b\bar{N}_A \\ (\bar{N}_A, \bar{N}_a) \to (\bar{N}_A, \bar{N}_a - 1) & \text{at rate} & b\bar{N}_a, \end{array} \tag{4.18}$$

where for $\alpha \in \mathcal{A}$, $\bar{\alpha} \in \mathcal{A} \setminus \{\alpha\}$,

$$\bar{\beta}_{\alpha\alpha} := \frac{b}{2}\left(1 + (\beta_1 + 1)\rho_\alpha - \frac{\beta_2}{2}\rho_{\bar{\alpha}}\right), \quad \bar{\beta}_{\alpha\bar{\alpha}} := \frac{b}{2}\left(1 - \frac{\beta_2}{2}\right)\rho_{\bar{\alpha}}, \tag{4.19}$$

and

$$\rho_A := \lim_{K\to\infty} \frac{N^K_{Ap}(0)}{N^K_p(0)} \quad \text{and} \quad \rho_a := 1 - \rho_A = \lim_{K\to\infty} \frac{N^K_{ap}(0)}{N^K_p(0)} \tag{4.20}$$

are the initial proportions in the resident population. The rates of this branching process have been obtained by considering the dynamics of (N^K_{AP}, N^K_{aP}) described by (4.16) and (4.17) when

$$(N^K_{Ap}, N^K_{ap}) = (K\rho_A\frac{b-d}{c}, K(1-\rho_A)\frac{b-d}{c}),$$

$N^K = K\frac{b-d}{c}$ and the second order terms in N^K_{AP} and N^K_{aP} are neglected. We denote the extinction probabilities of the process $\bar{\mathbf{N}}$ by

$$q_\alpha := \mathbb{P}(\exists t < \infty, \bar{\mathbf{N}}(t) = 0 | \bar{\mathbf{N}}(0) = \mathbf{e}_\alpha), \tag{4.21}$$

$\alpha \in \mathcal{A}$, $\mathbf{e}_A = (1,0)$ and $\mathbf{e}_a = (0,1)$, meaning that the process starts with only one individual of type A or a. Classical results of branching process theory (see [AN72]) ensure that these extinction probabilities correspond to the smallest solution to the system of equations

$$\begin{aligned} u_A(s_A, s_a) &:= b(1-s_A) + \bar{\beta}_{AA}(s_A^2 - s_A) + \bar{\beta}_{Aa}(s_A s_a - s_A) = 0 \\ u_a(s_A, s_a) &:= b(1-s_a) + \bar{\beta}_{aa}(s_a^2 - s_a) + \bar{\beta}_{aA}(s_A s_a - s_a) = 0. \end{aligned} \tag{4.22}$$

Moreover, the branching process $\bar{\mathbf{N}}$ is supercritical (i.e. q_A and q_a are not equal to one) if and only if its mean matrix

$$J := \begin{pmatrix} \bar{\beta}_{AA} - b & \bar{\beta}_{Aa} \\ \bar{\beta}_{aA} & \bar{\beta}_{aa} - b \end{pmatrix} \tag{4.23}$$

has a positive eigenvalue, that is to say if and only if

$$\beta_1 > \beta_2 \quad \text{or} \quad \rho_A(1-\rho_A) < \frac{\beta_1(\beta_2+2)}{2(\beta_1+\beta_2)(\beta_1+2)}. \tag{4.24}$$

We denote by λ the maximal eigenvalue of (4.23), which is thus positive when (4.24) holds and which will be of interest to quantify the time before invasion. Notice that J can be written as b times a matrix only depending on $(\rho_A, \beta_1, \beta_2)$. As a consequence, λ can be written $\lambda = b\tilde{\lambda}(\rho_A, \beta_1, \beta_2)$. We will use this notation in Theorem 4.2.1 to make appear the dependence on the parameters.

If the mutant population invades and its size reaches order K with K large, the population dynamics enters a second phase during which it is well approximated (again by an application of [EK09], Chapter 11, Theorem 2.1) by a mean field process. More precisely, if we define the rescaled process

$$(\mathbf{Z}^K(t), t \geq 0) := \left(\frac{N^K_{AP}(t)}{K}, \frac{N^K_{Ap}(t)}{K}, \frac{N^K_{aP}(t)}{K}, \frac{N^K_{ap}(t)}{K}, t \geq 0 \right),$$

then it will be close to the solution of the dynamical system

$$\dot{z}_i = b_i(\mathbf{z}) - (d + cz)z_i, \quad i \in \mathcal{G}, \tag{4.25}$$

where $z = z_{AP} + z_{Ap} + z_{aP} + z_{ap}$ is the total rescaled population size and the functions $(b_i, i \in \mathcal{G})$ have been defined in Equation (4.17). This dynamical system has a unique solution, as the vector field is locally Lipschitz and that the solutions do not explode in finite time [Chi06]. We will denote by

$$(\mathbf{z}^{(\mathbf{z}^0)}(t), t \geq 0) = (z_{AP}(t), z_{Ap}(t), z_{aP}(t), z_{ap}(t), t \geq 0)$$

this unique solution starting from $\mathbf{z}(0) = \mathbf{z}^0 \in \mathbb{R}^4_+$.

Notice that when there are only individuals of type p in the population (no sexual preferences), the dynamical system (4.25) is

$$\begin{cases} \dot{z}_{Ap} = z_{Ap}(b - d - c(z_{Ap} + z_{ap})) \\ \dot{z}_{ap} = z_{ap}(b - d - c(z_{Ap} + z_{ap})). \end{cases}$$

This system admits an infinity of equilibria:

- $(z_{Ap}, z_{ap}) = (0, 0)$, which is unstable
- $(z_{Ap}, z_{ap}) = (\rho(b-d)/c, (1-\rho)(b-d)/c)$ for all $\rho \in [0, 1]$, which are non hyperbolic.

However, if we consider the equation giving the dynamics of the total population size $z = z_{Ap} + z_{ap}$, we get

$$\dot{z} = z(b - d - cz).$$

Its solution, with a positive initial condition, converges to its unique stable equilibrium, $(b-d)/c$. That is why we will assume that the initial population size, before the arrival of the mutant, is $(b-d)K/c$.

A fine study of the dynamics of the solutions to (4.25) with our particular initial conditions, that is to say few individuals mating assortatively at the beginning and a majority of A (or a) in both resident and mutant populations allow us to show that the dynamical system converges to an equilibrium where some of the variables $z_i, i \in \mathcal{G}$ are equal to 0. When the population size of these i becomes too small (of order smaller than K before rescaling), the mean fields approximation stops being a good approximation, and we will again compare the dynamics of the small population sizes with these of branching processes (now subcritical). The birth and death rates of these branching processes will then provide the time to extinction of these small populations.

Combining all these steps, we are able to describe the invasion/extinction dynamics of the mutant population, which is the subject of Theorem 4.2.1. Before stating it, we need to introduce some last notations: a set of interest for the rescaled process $\mathbf{Z}^K$, for any $\mu > 0$

$$S_\mu := \left[\frac{b(1+\beta_1) - d}{c} - \mu, \frac{b(1+\beta_1) - d}{c} + \mu \right] \times \{0\} \times \{0\} \times \{0\}, \tag{4.26}$$

a stopping time describing the time at which $\mathbf{Z}^K$ reaches this set,

$$T_{S_\mu} := \inf\{t \geq 0, \mathbf{Z}^K(t) \in S_\mu\}, \tag{4.27}$$

as well as a stopping time which gives the first time when the rescaled P-mutant population size reaches any threshold (from below or above): for any $\varepsilon \geq 0$,

$$T_\varepsilon^P := \inf\left\{ t > 0, N_P^K(t) = \lfloor \varepsilon K \rfloor \right\}, \tag{4.28}$$

where $\lfloor x \rfloor$ is the integer part of x. Note that these stopping times depend on the scaling parameter K. However, to avoid cumbersome notations, we drop the K dependency.

Theorem 4.2.1. *Assume that* $\lambda \neq 0$,

$$\left(Z^K_{Ap}(0), Z^K_{ap}(0)\right) \underset{K\to\infty}{\to} \left(\rho_A \frac{b-d}{c}, (1-\rho_A)\frac{b-d}{c}\right)$$

in probability with $\rho_A > 1/2$ *and that for some* $\alpha \in \mathcal{A}$

$$\left(N^K_{\alpha P}(0), N^K_{\bar{\alpha} P}(0)\right) = (1,0).$$

Then there exists a Bernoulli random variable B *with parameter* $1-q_\alpha$ *(recall (4.21)) such that for any* $0 < \mu < (b(1+\beta_1)-d)/c$*:*

$$\lim_{K\to\infty} \left(\frac{T_{S_\mu} \wedge T^P_0}{\ln K}, \mathbf{1}_{\{T_{S_\mu} < T^P_0\}}\right) = B \times \left(\frac{1}{b\tilde{\lambda}(\rho_A, \beta_1, \beta_2)} + \frac{2}{b\beta_1}, 1\right), \tag{4.29}$$

where the convergence holds in probability.
Moreover,

$$\mathbf{1}_{\{T^P_0 < T_{S_\mu}\}} \left|\left| \frac{Nbf^K(T^P_0)}{K} - (0, \rho_A, 0, 1-\rho_A)\frac{b-d}{c} \right|\right|_1 \underset{K\to\infty}{\longrightarrow} 0 \qquad \textit{in probability,} \tag{4.30}$$

where $\|\cdot\|_1$ *stands for the* L^1-*norm.*

Notice that if condition (4.24) does not hold, $q_\alpha = 1$, and the convergence in (4.29) is an almost sure convergence to $(0,0)$ meaning that the mutant population dies out in a time smaller than $\ln K$. In this case, the allelic proportions in the resident population do not vary. Condition (4.24) gives two possible sufficient conditions for the mutant population to invade with positive probability. The first one imposes that the trade-off between the advantage for homogamous reproduction (β_1) and the loss for heterogamous reproduction (β_2) has to be favourable enough. The second condition requires a low level of initial allelic diversity at locus 1 (alleles A and a). In particular, even if the advantage for homogamy is very low, very asymmetrical initial conditions (ρ_A close to 0 or 1) will ensure the invasion of the mutation with positive probability. As expected, these conditions are the same as the conditions for the approximating branching process $\bar{\mathbf{N}}$ defined on page 86 to be supercritical. In fact, the random variable B is the indicator of survival of a version of $\bar{\mathbf{N}}$ coupled with the mutant process.

Let us emphasize that our result ensures that when the mutant population invades (whatever allele a or A the first mutant carries), then the final population is monomorphic, and all individuals carry the allele a or A which was in the majority in the resident $p-$population. Only the mutant invasion probability depends on the allele carried by the first P individual.

The study of the population process is more involved than in the previous references on similar questions (see for instance [Cha06, CM11, BS17]) because the initial state of the population is not an hyperbolic equilibrium, since alleles A and a are initially neutral. As a consequence, the fluctuations around the initial state may be substantial and are strongly influenced by the presence of mutants, even in a small number. We thus cannot use the classical large deviation theory [DE97], and we need to study the dynamics of the types altogether. Moreover, again unlike in [Cha06, CM11, BS17]

but similarly as in [CCLS18], the dynamical system arising as the limit of the rescaled population after the invasion phase admits many (stable and unstable) fixed points and we need to identify precisely the four dimensional zone reached by the rescaled population process after the invasion phase in order to determine the convergence point of the dynamical system.

We were not able to obtain an explicit formula in general for the extinction probability q_a of the assortative mating mutation, solution of (4.22). However, in the particular case when there are only A- or a-individuals in the population before the arrival of the mutant, we can derive the invasion probability.

Proposition 4.2.2. *Assume that there are only A individuals before the arrival of the mutant ($\rho_A = 1$). In this case,*

$$q_A = \frac{2}{2+\beta_1}$$

and

$$q_a = \frac{1}{2-\beta_2}\left(\frac{6-\beta_1\beta_2+4\beta_1-\beta_2}{2+\beta_1} - \sqrt{\left(\frac{6-\beta_1\beta_2+4\beta_1-\beta_2}{2+\beta_1}\right)^2 - 4(2-\beta_2)}\right).$$

Results obtained with the help of the software Mathematica show a complex dependency with respect to parameters. We performed numerical simulations of the extinction probabilities (q_A, q_a) using Newton approximation scheme starting from $(0,0)$. We computed the values of q_A as a function of ρ_A for different values of β_1 and β_2. Using the symmetry of our model, we have that $q_a(\rho_A) = q_A(1-\rho_A)$. We observe on Figure 4.2 that q_A is a continuous function of ρ_A but that it is not differentiable near criticality.

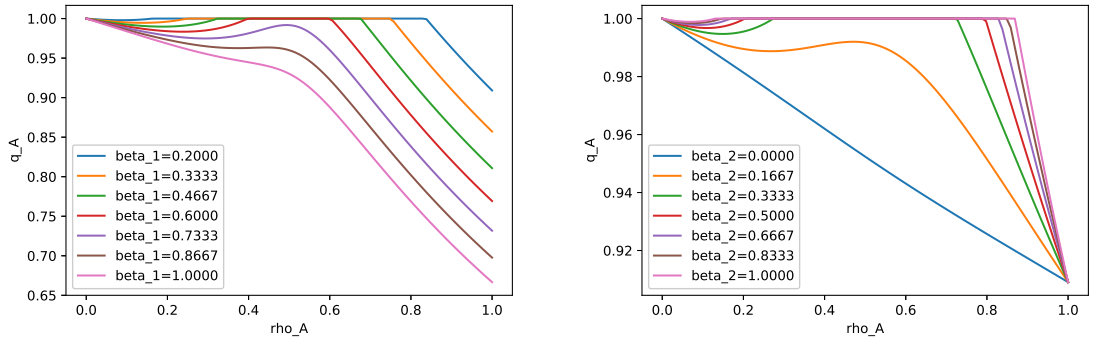

Figure 4.2: Values of q_A as a function of ρ_A for different values of β_1 and β_2. On the left, β_2 is fixed to 0.7 and β_1 varies. On the right β_1 is fixed to 0.2 and β_1 varies. In both cases $b = 1$.

4.2.2 Evolution to disassortative mating

I have been cosupervising the PhD thesis of L. Maisonneuve with V. Llaurens since September 2019. His first research work was devoted to the study of the conditions allowing the evolution of disassortative mating. I will briefly present his results, described in the article [MBJ+21].

Following the theoretical framework developed by [OSN08], we investigate the evolution of disassortative mating by assuming a diploid sexual species with balanced sex ratio, and considering two loci C and P. The locus C controls for a trait used as a mating cue and the locus P for the mate preference. We consider two different alleles, a and b, at locus C so that $\mathcal{G}_C = \{aa, ab, bb\}$ is the set of possible genotypes at this locus. This locus C can be under different viability selection regimes. At the mating preference locus P, we assume two alleles: a resident allele M and a mutant allele m. The set of possible genotypes at locus P is thus $\mathcal{G}_P = \{MM, Mm, mm\}$. The two loci recombine with probability r at each birth event. We consider a constant population and discrete time model and follow the genotypes frequencies over time.

We assume females to be the choosy sex [dCBK08, GB98, KH08, Lan81, OSN08], so that males can mate with any accepting female. We assume a balanced sex-ratio and consider that the frequencies of females and males with a given genotype are equal [dCBK08, GB98, OSN08].

We use the Quasi-Linkage-Equilibrium (QLE) analysis results presented in [OSN08]. This approach is valid when the selection coefficients, the strength of choosiness as well as costs of assortment are small relative to recombination. Under this hypothesis the genetic associations (linkage disequilibria and departures from Hardy-Weinberg) are small. This approach allows to obtain mathematical expressions of allele frequency changes at the cue and preference loci from the Hardy-Weinberg equilibrium. This method highlights the key evolutionary mechanisms shaping the evolution of allele frequencies at these loci. In particular, we assume that the mutant allele m increases disassortative preference, and investigate the evolutionary forces acting on this allele. When the hypothesis of weak selection is relaxed, we use numerical simulations to explore the evolutionary stable level of strength of disassortative mating.

I will just highlight some of the findings and refer the interested reader to [MBJ+21] for more precise results.

Predicted selection regimes promoting disassortative mating match empirical observations

Our results show that disassortative mating is promoted either (1) when heterozygotes at cue locus are in average fitter that homozygotes or (2) when viability selection on cue favors the rarest cue allele. These selection regimes promoting disassortative mating are opposed to the selection regimes promoting assortative mating, such as homozygote advantage at cue locus or viability selection on cue favoring the most common allele [OSN08]. Interestingly, our simulations also show that higher levels of disassortative mating are promoted when one cue allele is dominant. The dominance relationship can indeed decrease sexual selection and relative cost of choosiness impairing the evolution of disassortative preferences. Simulations also highlight that higher levels of disassortative mating are promoted when the dominant allele is disfavored when homozygous. This effect is consistent with the observed cases of disassortative mating. For instance the butterfly *Heliconius numata* displays a strong disassortative mating based on wing-pattern phenotype (in a tetrad experiment, 3/4 of the realized crosses were involving disassortative pairs) [CLPPJ17]. In this species, the variation in wing-pattern morphs is controlled by a supergene with three main haplotypes [JFJ+11]. The dominant haplotypes are associated with a low survival of homozygous larvae [JCW+21]. This case of disassortative mating seems to gather the conditions pinpointed

by our model to enable the evolution of higher levels of disassortative mating. Similarly, in the white-throated sparrow *Zonotrichia albicollis* an almost strict disassortative mating based on plumage morphs (white or tan) has been reported [Thr75]. Two supergene haplotypes (here referred to as t and w) control this variation in plumage coloration. Individuals with tt genotype have a tan coloration whereas individuals carrying tw and ww genotypes have a white coloration. However the dominant haplotype w is associated with strong genetic load, generating homozygote disadvantage in ww individuals [TBK+16]. Individuals with white coloration may be advantaged over tan individuals because they invest less into parental care [KF83], generating an advantage of heterozygotes tw over homozygotes tt. Here the dominant cue allele is again associated with a strong disadvantage when homozygous, which, according to our results, strongly favors the emergence of disassortative preferences.

Negative feedback in the evolution of disassortative mating contrasts with the evolution of assortative mating

A striking result from our analyses stems from the role of sexual selection generated by disassortative preferences on its evolution, which contrasts with the evolutionary dynamics of assortative mating. Our results confirm that the sexual selection generated by disassortative mating often limits its own spread, as already mentioned by Nuismer et al. [NOB08]. Indeed, the disassortative mating allele is generally associated with heterozygotes at the cue locus. Individuals with such allelic combinations tend to preferentially mate with homozygotes, generating sexual selection disfavoring heterozygotes at the cue locus. However, this sexual selection acting against heterozygotes depends on the distribution of cue allele frequency. Similarly, the evolution of assortative mating is thought to be limited by sexual selection [OSN08]. However, this negative effect of sexual selection decreases when the proportion of homozygotes at the cue locus is high. Assortative mating usually produces more homozygotes than random mating: a decrease in the level of heterozygosity at the cue locus is thus expected when assortative preferences are spreading within a population. During the evolution of assortative mating, the negative effect of sexual selection on the evolution of assortative mating decreases as the proportion of homozygote increases. The evolution of disassortative mating may therefore be more severely impaired by sexual selection than the evolution of assortative mating.

4.3 Perspectives

The study of questions related to the evolution of sexual preferences in an eco-evolutionary framework, where we take into account both the variation in the composition of populations (genetic, spatial, phenotypic, ...) and the variation in the sizes of sub-populations with different traits (which are consequences of each other) is quite recent. This framework allows a better understanding of the interactions between different evolutionary forces, and many questions remain to be explored. I am continuing to study some of these questions, notably in collaboration with V. Llaurens of the Museum National d'Histoire Naturelle.

4.3.1 Convergent evolution and reproductive interference

During the PhD thesis of L. Maisonneuve, we explore more generally the question of the evolution of mating preferences and their interaction with other ecological processes. In particular, one of our current subjects of interest is the evolutionary consequence of interactions between evolutionary convergence and reproductive interaction. In some cases, as mimicry for instance, it can be advantageous for a species to resemble another species. However, when males of different species resemble each other too much, females may suffer from reproductive interference, generated by erroneous mating attempts with heterospecific males. We aim at studying the interplay of such opposite evolutionary directions and some of their consequences, as sexual dimorphism for instance [MSL21, MSL22].

4.3.2 Eco-evolutionary models of disassortative mating

In the continuation of my previous work, in collaboration with C. Coron, M. Costa, H. Leman and V. Llaurens, I am also exploring various questions related to sexual preferences, using eco-evolutionary models. For instance, we would like to understand how much disassortative mate choices increase the number of cues maintained within populations, depending on the relative fitness advantages associated with the different heterozygous combinations.

The evolution of mate preferences has been shown to depend on the genetic architecture underlying mate choice. In a recent review on the evolution of assortative mating, [KSM+18] distinguished two main mechanisms: (1) Matching model, whereby crosses preferentially occur between individuals displaying the same cue (2) Preference/trait model, where preference alleles control attraction toward a given cue, independently from the trait displayed by the chooser. These two mechanisms generate different evolutionary fates for both cue and preference variations. We would like to contrast the effects of these two mechanisms.

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