AN ECO-EVOLUTIONARY APPROACH OF ADAPTATION AND RECOMBINATION IN A LARGE POPULATION OF VARYING SIZE

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Abstract. We identify the genetic signature of a selective sweep in a population described by a birth-and-death process with density dependent competition. We study the limit behaviour for large $K$, where $K$ scales the population size. We focus on two loci: one under selection and one neutral. We distinguish a soft sweep occurring after an environmental change, from a hard sweep occurring after a mutation, and express the neutral proportion variation as a function of the ecological parameters, recombination probability $r_K$, and $K$. We show that for a hard sweep, two recombination regimes appear according to the order of $r_K \log K$.

1. Introduction

There are at least two different ways of adaptation for a population: selection can either act on a new mutation (hard selective sweep), either on preexisting alleles that become advantageous after an environmental change (soft selective sweep). New mutations are sources of diversity, and hard selective sweep was until recently the only considered way of adaptation. Soft selective sweep allows a faster adaptation to novel environments, and its importance is growing in empirical and theoretical studies (Prezeworski, Coop and Wall [27], Barrett and Schluter [2]). These distinct selective sweeps entail different genetic signatures in the vicinity of the newly fixed allele, and the multiplication of genetic data available allows to detect these signatures in current populations as described by Peter, Huerta-Sanchez and Nielsen [25]. To do this in an effective way, it is necessary to identify accurately the signatures left by these two modes of adaptation.

In this work, we consider a sexual haploid population of varying size, modeled by a birth and death process with density dependent competition. The ability to survive and reproduce of each individual depends on its own genotype and on the population state. More precisely, each individual is characterized by some ecological parameters: birth rate, intrinsic death rate and competition kernel describing the competition with other individuals depending on their genotype. The differential reproductive success of individuals generated by their interactions entail progressive variations in the number of individuals carrying a given genotype. This process, called natural selection, is a key mechanism of evolution. Such eco-evolutionary approach has been introduced by Metz and coauthors in [24] and made rigorous in the seminal paper of Fournier and Méléard [18]. Then it has been developed by Champagnat and coauthors [5, 6, 7, 8, 9], and Méléard and Tran [23] for the haploid asexual case and by Collet, Méléard and Metz [10] and Coron [11, 12] for the diploid sexual case. The recent work of Billiard and coauthors [4] studies the dynamics of a two-locus model in an haploid asexual population. Following these works, we introduce a parameter $K$ called carrying capacity which scales the population size, and study the limit behavior for large $K$. But unlike them, we focus on two loci in a sexual haploid population and take into account the recombination process.
account recombinations: one locus is under selection and has two possible alleles $A$ and $a$ and the second one is neutral with allele $b_1$ or $b_2$. When two individuals give birth, either a recombination occurs with probability $r_K$ and the newborn inherits one allele from each parent, or he is the clone of one parent.

We first focus on soft selective sweep occurring after a change in the environment (new pathogen, environmental catastrophe, occupation of a new ecological niche,...). We assume that before the change the alleles $A$ and $a$ were neutral and represented both a positive fraction of the population, and that in the new environment the allele $a$ becomes favorable and goes to fixation. We can divide the selective sweep in two periods: a first one where the population process is well approximated by the solution of a deterministic dynamical system, and a second one where $A$-individuals are near extinction, the deterministic approximation fails and the fluctuations of the $A$-population size become predominant. We give the asymptotic value of the final neutral allele proportions as a function of the ecological parameters, recombination probability $r_K$ and solutions of a two-dimensional competitive Lotka-Volterra system.

We then focus on hard selective sweep. We assume that a mutant $a$ appears in a monomorphic $A$-population at ecological equilibrium. As stated by Champagnat in [5], the selective sweep is divided in three periods: during the first one, the resident population size stays near its equilibrium value, and the mutant population size grows until it reaches a non-negligible fraction of the total population size. The two other periods are the ones described for the soft selective sweep. Moreover, the time needed for the mutant $a$ to fix in the population is of order $\log K$. We prove that the distribution of neutral alleles at the end of the sweep has different shapes according to the order of the recombination probability per reproductive event $r_K$ with respect to $1/\log K$. More precisely, we find two recombination regimes: a strong one were $r_K \log K$ is large, and a weak one were $r_K \log K$ is bounded. In both recombination regimes, we give the asymptotic value of the final neutral allele proportions as a function of the ecological parameters and recombination probability $r_K$. In the strong recombination regime, the frequent exchanges of neutral alleles between the $A$ and $a$-populations yield an homogeneous neutral repartition in the two populations and the latter is not modified by the sweep. In the weak recombination regime, the frequency of the neutral allele carried by the first mutant increases because it is linked to the positively selected allele. This phenomenon, called genetic hitch-hiking by Maynard Smith and Haigh [29], has been studied by many authors. Maynard Smith and Haigh [29] and Stephan and coauthors [30] use deterministic models for the change in the frequency of the selected allele. Kaplan and coauthors [20] and Barton [3] present more precise models taking into account the randomness of the first and third periods of the mutant invasion. Durrett and Schweinsberg [14, 28], Etheridge and coauthors [16], Pfaffelhuber and Studeny [26], and Leocard [21] describe the population process by a structured coalescent and finely study genealogies of neutral alleles during the sweep. Eriksson and coauthors [15] describe a deterministic approximation for the growth of the favored allele frequency during a sweep, which leads to more accurate approximation than previous models for large values of the recombination probability. Unlike our model, in all these works, the population size is constant and the individuals’ “selective value” does not depend on the population state, but only on the individuals’ genotype.

The structure of the paper is the following. In Section 2 we describe the model, review some results of Champagnat in [5] about the two-dimensional population process when we do not consider the neutral locus, and present the main results. In Section 3 we state a semimartingale decomposition of neutral proportions, key tool in the different proofs. Section 4 is devoted to the proof for the soft sweep. It relies on a comparison of the population process with a four dimensional dynamical system. In Section 5 we describe a coupling of the population process with two birth and death processes widely use in Sections 6 and 7, respectively devoted to the proofs for
the strong and the weak recombination regimes of hard sweep. The proof for the weak regime requires a fine study of the genealogies in a structured coalescent process during the first phase of the selective sweep. We use here some ideas developed in [28]. Finally in Appendix we state technical results.

This work stems from the papers of Champagnat [5] and Schweinsberg and Durrett [28]. In the sequel, \( c \) is used to denote a positive finite constant. Its value can change from line to line but it is always independent of the integer \( K \) and the positive real number \( \epsilon \). The set \( \mathbb{N} := \{1, 2, \ldots \} \) denotes the set of positive integers.

2. Model and main results

We introduce the sets \( \mathcal{A} = \{A, a\}, \mathcal{B} = \{b_1, b_2\} \), and \( \mathcal{E} = \{A, a\} \times \{b_1, b_2\} \) to describe the genetic background of individuals. The state of the population will be given by the four dimensional Markov process \( N^{(z,K)} = (N^{(z,K)}(t), (\alpha, \beta) \in \mathcal{E})_{t \geq 0} \) where \( N^{(z,K)}(t) \) denotes the number of individuals with alleles \((\alpha, \beta)\) at time \( t \) when the carrying capacity is \( K \in \mathbb{N} \) and the initial state is \((zK)\) with \( z = (z_{\alpha \beta}, (\alpha, \beta) \in \mathcal{E}) \in \mathbb{R}^\mathcal{E} \). We recall that \( b_1 \) and \( b_2 \) are neutral, thus ecological parameters only depend on the allele, \( A \) or \( a \), carried by the individuals at their first locus. There are the following:

- For \( \alpha \in \mathcal{A} \), \( f_\alpha \) and \( D_\alpha \) denote the birth rate and the intrinsic death rate of an individual carrying allele \( \alpha \).
- For \((\alpha_1, \alpha_2) \in \mathcal{A}^2 \), \( C_{\alpha_1, \alpha_2} \) represents the competitive pressure felt by an individual carrying allele \( \alpha_1 \) from an individual carrying allele \( \alpha_2 \).
- \( K \in \mathbb{N} \) is a parameter rescaling the competition between individuals. It can be interpreted as a scale of resources or area available, and is related to the concept of carrying capacity, which is the maximum population size that the environment can sustain indefinitely. In the sequel \( K \) will be large.
- \( r_K \) is the recombination probability per reproductive event. When two individuals with respective genotypes \((\alpha_1, \beta_1)\) and \((\alpha_2, \beta_2)\) in \( \mathcal{E} \) give birth, the newborn individual, either is a clone of one parent and carries alleles \((\alpha_1, \beta_1)\) or \((\alpha_2, \beta_2)\) with probability \((1 - r_K) / 2\), or has a mixed genotype \((\alpha_1, \beta_2)\) or \((\alpha_2, \beta_1)\) with probability \( r_K / 2 \).

We will use, for every \( n = (n_{\alpha \beta}, (\alpha, \beta) \in \mathcal{E}) \in \mathbb{Z}^\mathcal{E}_+ \) and \((\alpha, \beta) \in \mathcal{E} \), the notations

\[
n_a = n_{\alpha b_1} + n_{\alpha b_2}, \quad n_\beta = n_{\alpha \beta} + n_{\bar{\alpha} \beta}, \quad \text{and} \quad |n| = n_A + n_a = n_{b_1} + n_{b_2}.
\]

Let us now give the transition rates of \( N^{(z,K)} \) when \( N^{(z,K)}(t) = n \in \mathbb{Z}^\mathcal{E}_+ \). An individual can die either from a natural death or from competition, whose strength depends on the carrying capacity \( K \). Thus death rate of individuals \( (\alpha, \beta) \in \mathcal{E} \) is given by:

\[
d^A_{\alpha \beta}(n) = [D_\alpha + C_{\alpha A} n_A / K + C_{\alpha a} n_a / K] n_{\alpha \beta}.
\]

An individual carrying allele \( \alpha \in \mathcal{A} \) produces gametes with rate \( f_\alpha \), thus the relative frequencies of gametes available for reproduction are \( p_{\alpha \beta}(n) = f_\alpha n_{\alpha \beta} / (f_A n_A + f_a n_a) \), \((\alpha, \beta) \in \mathcal{E} \). When an individual gives birth, he chooses his mate uniformly among the gametes available. Then the probability of giving birth to an individual of a given genotype depends on the parents (the couple \((ab_2, ab_1)\) is not able to generate an individual \(Ab_1\)). We detail the computation of \( b^K_{\alpha \beta}(n) \):

\[
b^K_{\alpha \beta}(n) = f_A n_{\alpha b_1} p_{\alpha b_1} + p_{\alpha b_1} / 2 + p_{ab_1} / 2 + (1 - r_K) p_{ab_2} / 2 + f_A n_{\alpha b_2} p_{ab_2} / 2 + r_K p_{ab_1} / 2 + f_a n_{ab_1} (1 - r_K) p_{ab_1} / 2
\]

\[
= f_A n_{\alpha b_1} + r_K f_A f_a (n_{ab_1} n_{ab_2} - n_{ab_1} n_{ab_2}) / (f_A n_A + f_a n_a).
\]

If we denote by \( \bar{\alpha} \) (resp. \( \bar{\beta} \)) the complement of \( \alpha \) in \( \mathcal{A} \) (resp. \( \beta \) in \( \mathcal{B} \)), we obtain in the same way:

\[
b^K_{\bar{\alpha} \bar{\beta}}(n) = f_a n_{\bar{\alpha} \bar{b}_1} + r_K f_a f_A n_{\bar{\alpha} \bar{b}_1} n_{\bar{\alpha} \bar{b}_2} - n_{\bar{\alpha} \bar{b}_1} n_{\bar{\alpha} \bar{b}_2} n_{\alpha \beta} / (f_A n_A + f_a n_a), \quad (\alpha, \beta) \in \mathcal{E}.
\]
The definitions of death and birth rates in (2.1) and (2.2) ensure that the number of jumps is finite on every finite interval, and the population process is well defined.

When we focus on the dynamics of traits under selection $A$ and $a$, we get the process $(N^\alpha_a, N^\beta_a)$. It has been studied by Champagnat in [5] and its death and birth rates, which are direct consequences of (2.1) and (2.2), satisfy:

$$(2.3) \quad d^K_\alpha(n) = \sum_{\beta \in \mathcal{B}} d^K_{\alpha\beta}(n) = \left[D_a + C_{a,A} \frac{N_A}{K} + C_{a,a} \frac{N_a}{K}\right] n_a, \quad b^K_\alpha(n) = \sum_{\beta \in \mathcal{B}} b^K_{\alpha\beta}(n) = f_\alpha n_a, \quad \alpha \in \mathcal{A}.$$  

Champagnat has proved that under some conditions the rescaled population process $(N^\alpha_A/K, N^\beta_A/K)$ is well approximated by the following dynamical system,

$$(2.4) \quad \dot{n}^{(z)}_\alpha = (f_\alpha - D_a - C_{a,A} n^{(z)}_A - C_{a,a} n^{(z)}_a) n^{(z)}_\alpha, \quad n^{(z)}_\alpha(0) = z_\alpha, \quad \alpha \in \mathcal{A}.$$  

More precisely Theorem 3 (b) in [5] states that for every compact subset $B \subset (\mathbb{R}^{A \times \mathcal{B}})^* \times (\mathbb{R}^{A \times \mathcal{B}})^*$ and finite real number $T$, we have for any $\delta > 0$,

$$(2.5) \quad \lim_{k \to \infty} \sup_{z \in B} \left( \sup_{0 \leq t \leq T, \alpha \in \mathcal{A}} |N^\alpha_A(t)/K - n^{(z)}_\alpha(t)| \geq \delta \right) = 0.$$  

Moreover, if we assume

$$(2.6) \quad f_A > D_A, \quad f_a > D_a, \quad \text{and} \quad f_A - D_a > (f_A - D_A) \sup \left\{ C_{a,A}/C_{A,A}, C_{a,a}/C_{A,a} \right\},$$  

then the dynamical system (2.4) has a unique attracting equilibrium $(0, \tilde{n}_a)$ for initial condition $z$ satisfying $z_\alpha > 0$, and an unstable steady state $(\tilde{n}_A, 0)$ where

$$(2.7) \quad \tilde{n}_a = \frac{f_a - D_a}{C_{a,a}} > 0, \quad \alpha \in \mathcal{A}.$$  

Hence, Assumption (2.6) avoids the coexistence of alleles $A$ and $a$, and $\tilde{n}_a$ is the equilibrium density of a monomorphic $\alpha$-population per unit of carrying capacity. This implies that when $K$ is large, the size of a monomorphic $\alpha$-population stays near $\tilde{n}_a K$ for a long time (Theorem 3 (c) in [5]). Moreover, if we introduce the invasion fitness $S_{aa}$ of a mutant $\alpha$ in a population $\tilde{a}$,

$$(2.8) \quad S_{aa} = f_a - D_a - C_{a,a} \tilde{n}_a, \quad \alpha \in \mathcal{A},$$  

it corresponds to the per capita growth rate of a mutant $\alpha$ when it appears in a population $\tilde{a}$ at its equilibrium density $\tilde{n}_\alpha$. Assumption (2.6) is equivalent to

**Assumption 1.** *Ecological parameters satisfy*

$$\tilde{n}_A > 0, \quad \tilde{n}_a > 0, \quad \text{and} \quad S_{Aa} < 0 < S_{A\tilde{a}}.$$  

Under Assumption 1, with positive probability, the $A$-population becomes extinct and the $a$-population size reaches a vicinity of its equilibrium value $\tilde{n}_a K$.

Let us now present the main results of this paper. We introduce the extinction time of the $A$-population, and the fixation event of the $a$-population. For $(z, K) \in \mathbb{R}^\mathcal{B}_+ \times \mathbb{N}$:

$$(2.9) \quad T_{\text{ext}}^{(z,K)} := \inf \left\{ t \geq 0, N^\alpha_A(t) = 0 \right\}, \quad \text{and} \quad \text{Fix}^{(z,K)} := \left\{ T_{\text{ext}}^{(z,K)} < \infty, N^\beta_a(T_{\text{ext}}^{(z,K)}) > 0 \right\}.$$  

We are interested in the neutral allele proportions. We thus define for $t \geq 0$,

$$(2.10) \quad p^{(z,K)}_{a,\beta}(t) = \frac{N^{(z,K)}_{a,\beta}(t)}{N^{(z,K)}_\alpha(t)}, \quad (\alpha, \beta) \in \mathcal{B}, \ K \in \mathbb{N}, \ z \in \mathbb{R}^\mathcal{B}_+.$$
the proportion of alleles $\beta$ in the $\alpha$-population at time $t$, with the convention $0/0 = 0$. More precisely, we are interested in these proportions at the end of the sweep, that is at time $T_{\text{ext}}^{(z,K)}$ when the last $A$-individual dies. We then introduce the neutral proportion at this time:

$$\varphi^{(z,K)}_{\alpha,b_1} = p^{(z,K)}_{\alpha,b_1}(T_{\text{ext}}^{(z,K)}).$$

We first focus on soft selective sweep. We assume that the alleles $A$ and $a$ were neutral and coexisted in a population with large carrying capacity $K$. At time $0$, an environmental change makes the allele $a$ favorable (in the sense of Assumption (1)). Before stating the result, let us introduce the function $F$, defined for every $(z, r, t) \in (\mathbb{R}_+^\alpha)^* \times [0, 1] \times \mathbb{R}_+^{\alpha}$ by

$$F(z, r, t) = \int_0^t r f_A f_a n^{(z)}_A(s) \exp \left( - r f_A f_a \int_0^s n^{(z)}_A(u) + n^{(z)}_a(u) \, du \right) ds,$$

where $(n^{(z)}_A, n^{(z)}_a)$ is the solution of the dynamical system (2.4). We notice that $F : t \in \mathbb{R}_+ \to F(z, r, t)$ is non-negative and non-decreasing. Moreover, if we introduce the function $h : (z, r, t) \in (\mathbb{R}_+^\alpha)^* \times [0, 1] \times \mathbb{R}_+ \to r f_A f_a \int_0^t n^{(z)}_A(s) \exp \left( - r f_A f_a \left( n^{(z)}_A(s) + n^{(z)}_a(s) \right) \right) ds$ non-decreasing in time, then

$$0 \leq F(z, r, t) \leq \int_0^t \partial_s h(z, r, s) e^{-h(z, r, s)} ds = e^{h(z, r, 0)} - e^{-h(z, r, t)}.$$

Thus $F(z, r, t)$ has a limit in $[0, 1]$ when $t$ goes to infinity and we can define

$$F(z, r) := \lim_{t \to \infty} F(z, r, t) \in [0, 1].$$

In the case of soft sweep, the selected allele gets to fixation with high probability. More precisely, Champagnat proved the following asymptotic result in [5]: under Assumption 1,

$$\lim_{K \to \infty} \mathbb{P}(\text{Fix}^{(z,K)}) = 1, \quad \forall z \in \mathbb{R}_+^{A \times \mathbb{R}} \times (\mathbb{R}_+^{A \times \mathbb{R}})^*.$$

We consider the soft selective sweep with recombination probability $r_K$ satisfying:

**Assumption 2.**

$$\lim_{K \to \infty} r_K = r \in [0, 1].$$

Then recalling (2.11) we get the following result whose proof is deferred in Section 4:

**Theorem 1.** Let $z$ be in $\mathbb{R}_+^{A \times \mathbb{R}} \times (\mathbb{R}_+^{A \times \mathbb{R}})^*$ and Assumptions 1 and 2 hold. Then on the fixation event $\text{Fix}^{(z,K)}$, the proportion of alleles $b_1$ when the $A$-population becomes extinct (time $T_{\text{ext}}^{(z,K)}$) converges in probability:

$$\lim_{K \to \infty} \mathbb{P}\left( \left| \varphi^{(z,K)}_{\alpha,b_1} - \left( \frac{Z_{Ab_1}}{Z_A} F(z, r) + \frac{Z_{Ab_1}}{Z_a} (1 - F(z, r)) \right) \right| > \epsilon \right) = 0, \quad \forall \epsilon > 0.$$

The neutral proportion at the end of the soft sweep is thus a weighted mean of initial proportions in populations $A$ and $a$. In particular, soft sweep is responsible for a diminution of the number of neutral alleles with very low or very high proportions in the population, as remarked in [27]. We notice that the weight $F(z, r)$ does not depend on the initial neutral proportions. It only depends on $r$ and on the dynamical system (2.4) with initial condition $(n_A(0), n_a(0)) = (z_A, z_a)$.

Now we focus on hard selective sweep: a mutant $a$ appears in a large population and gets to fixation. We assume that the mutant appears when the $A$-population is at ecological equilibrium, and carries the neutral allele $b_1$. In other words, recalling Definition (2.7), we assume:

**Assumption 3.** There exists $z_{Ab_1} \in [0, \tilde{n}_A]$ such that $\Lambda^{(z,K)}(0) = [z^{(K)}K]^{+}$ with $z^{(K)} = (z_{Ab_1}, \tilde{n}_A - z_{Ab_1}, K^{-1}, 0)$. 


In this case, the selected allele gets to fixation with positive probability. More precisely, Champagnat proved the following asymptotic result in [5]: under Assumptions 1 and 3,

\[
\lim_{K \to \infty} P(\text{Fix}^{(z,K),K}) = \frac{S_{\alpha A}}{f_{\alpha a}}.
\]

In the case of strong selective sweep we will distinguish two different recombination regimes:

**Assumption 4.** Strong recombination

\[
\lim_{K \to \infty} r_{K} \log K = \infty.
\]

**Assumption 5.** Weak recombination

\[
\limsup_{K \to \infty} r_{K} \log K < \infty.
\]

Recall (2.11). Then we have the following results whose proofs are deferred in Sections 6 and 7:

**Theorem 2.** Suppose that Assumptions 1 and 3 hold. Then on the fixation event \(\text{Fix}^{(z,K)}\) and under Assumption 4 or 5, the proportion of alleles \(b_{1}\) when the \(A\)-population becomes extinct (time \(T_{\text{ext}}^{(z,K)}\)) converges in probability. More precisely, if Assumption 4 holds,

\[
\lim_{K \to \infty} P\left(1_{\text{Fix}^{(z,K)}} \left| \mathcal{G}^{(z,K),K}_{a,b_{1}} - \frac{Z_{A}b_{1}}{Z_{A}} > \varepsilon \right. \right) = 0, \quad \forall \varepsilon > 0,
\]

and if Assumption 5 holds,

\[
\lim_{K \to \infty} P\left(1_{\text{Fix}^{(z,K)}} \left| \mathcal{G}^{(z,K),K}_{a,b_{1}} - \left[ \frac{Z_{A}b_{1}}{Z_{A}} + \frac{Z_{A}b_{2}}{Z_{A}} \exp \left( - \frac{f_{\alpha a}r_{K} \log K}{S_{\alpha A}} \right) \right] \right| > \varepsilon \right) = 0, \quad \forall \varepsilon > 0.
\]

As stated in [5], the selective sweep has a duration of order \(\log K\). Thus, when \(r_{K} \log K\) is large, a lot of recombinations occur during the sweep, and the neutral alleles are constantly exchanged by the populations \(A\) and \(a\). Hence in the strong recombination case, the sweep does not modify the proportion of neutral alleles. On the contrary, when \(r_{K}\) is of order \(1/\log K\) the number of recombinations undergone by a given lineage does not go to infinity, and the frequency of the neutral allele \(b_{1}\) carried by the first mutant \(a\) increases. This phenomenon is called genetic hitchhiking [29]: the selective sweep leads to a diminution of diversity around the selected allele.

**Remark 1.** The limits in the two regimes are consistent in the sense that

\[
\lim_{r_{K} \log K \to \infty} \frac{Z_{A}b_{2}}{Z_{A}} \exp \left( - \frac{f_{\alpha a}r_{K} \log K}{S_{\alpha A}} \right) = 0.
\]

Moreover, let us notice that we can easily extend the results of Theorems 1 and 2 to a finite number of possible alleles \(b_{1}, b_{2}, ..., b_{l}\) on the neutral locus.

3. A semi-martingale decomposition

The expression of birth rate in (2.2) shows that the effect of recombination depends on the recombination probability \(r_{K}\) and also on the population state via the term \(n_{\alpha \beta}n_{a \beta} - n_{\alpha \beta}n_{a \beta}\). This quantity is linked with the linkage disequilibrium of the population, which is the occurrence of some allele combinations more or less often than would be expected from a random formation of haplotypes (see [13] Section 3.3 for an introduction to this notion or [22] for a study of its structure around a sweep). Proposition 1 states a semi-martingale representation of the neutral allele proportions.

**Proposition 1.** Let \((\alpha, z, K)\) be in \(\mathcal{A} \times (\mathbb{R}^{+})^{*} \times \mathbb{N}\). The process \((P_{a,b_{1}}^{(z,K)}(t), t \geq 0)\) defined in (2.10) is a semi-martingale and we have the following decomposition:

\[
P_{a,b_{1}}^{(z,K)}(t) = P_{a,b_{1}}^{(z,K)}(0) + M_{a}^{(z,K)}(t) + r_{K}f_{\alpha a} \int_{0}^{t} \frac{N_{a}^{(z,K)}N_{a}^{(z,K)} - N_{a}^{(z,K)}N_{a}^{(z,K)}}{(N_{a}^{(z,K)} + 1)} dt,
\]

where...

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where the process \((M_{\alpha}^{z,K}(t), t \geq 0)\) is a martingale bounded on every interval \([0, t]\) whose quadratic variation is given by (3.7).

To enlighten the presentation in remarks and proofs we shall mostly write \(N\) instead \(N^{(z,K)}\).

**Remark 2.** The process \(N_{ab_1}N_{ab_2} - N_{ab_1}N_{ab_2}\) will play a major role in the dynamics of neutral proportions. Indeed it is a measure of the neutral proportion disequilibrium between the \(A\) and \(a\)-populations as it satisfies:

\[
N_{A}N_{a}(P_{A,b_1} - P_{a,b_1}) = N_{ab_2}N_{Ab_1} - N_{ab_1}N_{Ab_2}.
\]

**Proof of Proposition 1.** In the vein of Fournier and Méléard [18] we represent the population process in terms of Poisson measure. Let \(Q(ds, d\theta)\) be a Poisson random measure on \(\mathbb{R}^2_+\) with intensity \(dsd\theta\), and \((e_{a,b}(\alpha, \beta) \in \mathcal{A})\) the canonical basis of \(\mathbb{R}^\mathcal{A}\). According to (2.3) a jump occurs at rate \(\sum_{(a,b) \in \mathcal{A}}(b_{a,b}^K(N) + d_{a,b}^K(N)) = f_{A}N_{a} + d_{F}^K(N) + f_{A}N_{A} + d_{F}^K(N).\) We decompose on possible jumps that may occur: births and deaths for \(a\)-individuals and births and deaths for \(A\)-individuals. Itô’s formula with jumps (see [19] p. 66) yields for every function \(h\) measurable and bounded on \(\mathbb{R}^2_+\):

\[
h(N(t)) = h(N(0)) + \int_0^t \left\{ \sum_{s \in \mathcal{A}} \left[ h(N(s^-) + e_{a,b}(s)) \right] \right\} \int_{\mathcal{A}} dQ(ds, d\theta).
\]

Let us introduce the functions \(\mu_{K}^a(N, s, \theta)\) defined for \(\alpha \in \mathcal{A}\) and \((s, \theta)\) in \(\mathbb{R}_+ \times \mathbb{R}_+\) by,

\[
\mu_{K}^a(N, s, \theta) = \frac{N_{ab_2}(s)}{(N_a(s) + 1)N_a(s)} \int_{(0,\theta) \in \mathcal{A}} dQ(ds, d\theta) + \frac{N_{ab_1}(s)}{(N_a(s) + 1)N_a(s)} \int_{(\theta, 0) \in \mathcal{A}} dQ(ds, d\theta).
\]

with the convention \(0/0 = 0\). Then we can represent the neutral allele proportions \(P_{a,b_1}\) as,

\[
P_{a,b_1}(t) = P_{a,b_1}(0) + \int_0^t \int_{\mathcal{A}} \mu_{K}^a(N, s, \theta) Q(ds, d\theta), \quad t \geq 0.
\]

A direct calculation gives

\[
\mu_{K}^a(N, s, \theta)d\theta = \int_{\mathcal{A}} dQ(ds, d\theta).
\]

Thus if we introduce the compensated Poisson measure \(\tilde{Q}(ds, d\theta) = Q(ds, d\theta) - dsd\theta\), then \(M_{a}(t) = \int_0^t \int_{\mathcal{A}} \mu_{K}^a(N, s, \theta) \tilde{Q}(ds, d\theta)\) is a local martingale. By construction the process \(P_{a,b_1}\) has values in \([0,1]\) and as \(r_K \leq 1\),

\[
\sup_{s \leq t} |r_K f_{A}f_{a} \int_0^s \frac{N_{ab_1}N_{ab_2} - N_{ab_1}N_{ab_2}}{(N_a(s) + 1)(f_{A}N_A + f_{A}N_a)} | \leq r_K f_{a} t \leq f_{a} t, \quad t \geq 0.
\]
Thus $M_\alpha$ is a square integrable pure jump martingale bounded on every finite interval with quadratic variation
\begin{equation}
\langle M_\alpha \rangle_t = \int_0^t \int_{\mathbb{R}^+} \left( \mu^K_\alpha(N, s, \theta) \right)^2 d s d \theta
\end{equation}
\begin{equation}
= \int_0^t \left\{ P_{a,b_1}(1 - P_{a,b_1}) \left[ \left( D_a + \frac{C_{a,a}}{K} N_a + \frac{C_{a,a}}{K} N_\tilde{a} \right) \left( \frac{N_a + 2 N_\tilde{a}}{(N_a + 1)^2} \right) \right] + \frac{f_a N_a}{(N_a + 1)^2} + \frac{r f_a f_a (N_{a_{b_1}} N_{a_{b_2}} - N_{a_{b_1}} N_{a_{b_2}})(1 - 2 P_{a,b_1})}{(N_a + 1)^2(f_a N_a + f_a N_\tilde{a})} \right\}.
\end{equation}

This ends up the proof of Proposition 1. \hfill \Box

**Remark 3.** Let us mention two properties of the functions $\mu^K_\alpha$, defined in (3.4), which will be useful in the sequel. Firstly by definition we have for all $(s, \theta)$ in $\mathbb{R}_+ \times \mathbb{R}_+$,
\begin{equation}
\mu^K_\alpha(N, s, \theta) = 0.
\end{equation}
Secondly, the convention $0/0 = 0$ yields the following equality for $\alpha \in \mathcal{A}$ and all $(s, \theta)$ in $\mathbb{R}_+ \times \mathbb{R}_+$,
\begin{equation}
\mu^K_\alpha(N, s, \theta) \mathbb{1}_{N_a(s) \geq 1} = \mu^K_\alpha(N, s, \theta).
\end{equation}
For sake of simplicity we will use more often the second notation, but in Section 6 the first notation will also be useful.

Lemma 3.1 states properties of the quadratic variation widely used in the forthcoming proofs. We introduce a compact interval containing the equilibrium size of the $A$-population,
\begin{equation}
I^K_\varepsilon := \left[ K \left( \bar{N}_A - 2 \varepsilon \frac{C_{A,a}}{C_{A,A}} \right), K \left( \bar{N}_A + 2 \varepsilon \frac{C_{A,a}}{C_{A,A}} \right) \right],
\end{equation}
and the stopping times $T^K_\varepsilon$ and $\bar{T}^K_\varepsilon$, which denote respectively the hitting time of $[\varepsilon K]$ by the mutant population and the exit time of $I^K_\varepsilon$ by the resident population,
\begin{equation}
T^K_\varepsilon := \inf \left\{ t \geq 0, N^K_a(t) = \{ \varepsilon K \} \right\}, \quad \bar{T}^K_\varepsilon := \inf \left\{ t \geq 0, N^K_a(t) \notin I^K_\varepsilon \right\}.
\end{equation}

**Lemma 3.1.** For $\nu < \infty$, there exists a finite $C(v)$ such that $(N^K_A(t), N^K_a(t)) \in [0, v K]^2$ implies
\begin{equation}
\frac{d}{dt} \langle M^{(z,K)}_\alpha \rangle_t = \int_{\mathbb{R}^+} \left( \mu^K_\alpha(N^{(z,K)}_a, t, \theta) \right)^2 d \theta \leq C(v) \mathbb{1}_{N_a(t) \geq 1} \frac{\bar{N}_A(t)}{N_a(t)}, \quad \alpha \in \mathcal{A}.
\end{equation}
Under Assumptions 1 and 3, there exist $k_0 \in \mathbb{N}$, $\varepsilon_0 > 0$ and a pure jump martingale $\bar{M}$ such that for $\varepsilon \leq \varepsilon_0$ and $t \geq 0$,
\begin{equation}
e^{\frac{2 \kappa}{k_0 + 1}} \int_{T^K_\varepsilon}^{\bar{T}^K_\varepsilon} \left[ \mu^K_\alpha(N^{(z,K)}_a), t \wedge T^K_\varepsilon \wedge \bar{T}^K_\varepsilon, \theta \right]^2 d \theta \leq (k_0 + 1) C \left( \bar{N}_A + 2 \varepsilon \frac{C_{A,a}}{C_{A,A}} \right) \bar{M}_{t \wedge T^K_\varepsilon \wedge \bar{T}^K_\varepsilon},
\end{equation}
and
\begin{equation}
E \left[ \bar{M}_{t \wedge T^K_\varepsilon \wedge \bar{T}^K_\varepsilon} \right] \leq \frac{1}{k_0 + 1}.
\end{equation}

**Proof.** Equation (3.12) is a direct consequence of (3.7). To prove (3.13) and (3.14), let us first notice that according to Assumption 1, there exists $k_0 \in \mathbb{N}$ such that for $\varepsilon$ small enough and $k \in \mathbb{Z}_+$,
\begin{equation}
f_a(k_0 + k - 1) - (D_a + C_{a,a} \bar{N}_A + \varepsilon C_{a,a} + 2 C_{A,a} C_{A,A} / C_{A,A})(k_0 + k + 1) \geq \frac{S_{A,a}}{2}.
\end{equation}
This implies in particular that for every $t < T^K_\varepsilon \wedge \bar{T}^K_\varepsilon$,
\begin{equation}
\frac{f_a N_a(t)(N_a(t) + k_0 - 1) - d_a N_a(t)(N_a(t) + k_0 + 1)}{(N_a(t) + k_0 - 1)(N_a(t) + k_0 + 1)} \geq \frac{S_{A,a} N_a(t)}{2(N_a(t) + k_0 + 1)} \geq \frac{S_{A,a} \mathbb{1}_{N_a(t) \geq 1}}{2(k_0 + 1)},
\end{equation}
where the death rate $d_a$ has been defined in (2.3). For sake of simplicity let us introduce the process $X$ defined as follows:

$$X(t) = \frac{\mathbb{1}_{N_a(t) \geq 1}}{N_a(t) + K_0} \exp \left( \frac{S_{d_A t}}{2(k_0 + 1)} \right), \quad \forall t \geq 0.$$ 

Applying Itô’s formula with jumps we get for every $t \geq 0$:

$$X(t) = \tilde{M}(t) + \int_0^t \tilde{M}(s) \, ds,$$

where the martingale $\tilde{M}$ has the following expression:

$$\tilde{M}(t) = \frac{1}{k_0 + 1} + \int_0^t \int_{\mathbb{R}_+} Q(ds, d\theta) \mathbb{1}_{N_a(s) \geq 1} \exp \left( \frac{S_A t}{2(k_0 + 1)} \right) \frac{Q_{\alpha \beta}(s)}{N_a(s) + k_0 + 1} \leq \frac{1}{N_a(s) + k_0 + 1}.$$

Thanks to (3.15) the integral in (3.16) is nonpositive. Moreover, according to (3.12), for $t \leq T^K \land T^K$, we introduce a deterministic time $T^K$ after which the solution $(n^{(2)}_A, n^{(2)}_a)$ of the dynamical system (2.4) is close to the stable equilibrium $(0, \bar{a})$:

$$n^{(2)}_A(t) \geq \min \left\{ s \geq 0, \forall t \geq s, (n^{(2)}_A(t), n^{(2)}_a(t)) \in [0, \epsilon^2 / 2] \times [\bar{a} - \epsilon / 2, \infty) \right\}.$$

Once $(n^{(2)}_A, n^{(2)}_a)$ has reached the set $[0, \epsilon^2 / 2] \times [\bar{a} - \epsilon / 2, \infty)$ it no more escapes from it. Moreover, according to Assumption 1 on stable equilibrium, $T^K(z)$ is finite.

First we compare the population process with a four dimensional dynamical system on the time interval $[0, T^K(z)]$. Then we study this dynamical system and get an approximation of the neutral proportions at time $T^K(z)$. Finally, we state that during the A-population extinction period, this proportion stays nearly constant.

### 4. Proof of Theorem 1

In this section we suppose that Assumptions 1 and 2 hold. For $\epsilon \leq C_{a,A}/C_{a,A} \land 2|S_{d_A}|/C_{a,A}$ and $z \in (\mathbb{R}^4_+ \times \mathbb{R}^4_+ \times \mathbb{R}^4_+ \times \mathbb{R}^4_+)$ we introduce a deterministic time $t^K(z)$ after which the solution $(n^{(2)}_A, n^{(2)}_a)$ of the dynamical system (2.4) is close to the stable equilibrium $(0, \bar{a})$:

$$t^K(z) := \inf \{ s \geq 0, \forall t \geq s, (n^{(2)}_A(t), n^{(2)}_a(t)) \in [0, \epsilon^2 / 2] \times [\bar{a} - \epsilon / 2, \infty) \}.$$

We denote by $n^{(2)}_A = (n^{(2)}_a, (\alpha, \beta) \in \mathcal{E})$ the solution of

$$\dot{n}^{(2)}_a = \left( f_a - (D_a + C_{a,A} n^{(2)}_A + C_{a,a} n^{(2)}_a) \right) n^{(2)}_a + rf_A f_a \left( n^{(2)}_a - n^{(2)}_a n^{(2)}_a - n^{(2)}_A n^{(2)}_a \right), \quad (\alpha, \beta) \in \mathcal{E},$$

with initial condition $n^{(2)}_A(0) = z \in \mathbb{R}^4_+$. Then we have the following comparison result:

**Lemma 4.1.** Let $z$ be in $\mathbb{R}^4_+$ and $\epsilon$ be in $\mathbb{R}^*_+$. Then we have the following comparison result:

$$\lim_{K \to \infty} \sup_{s \leq t^K(z)} \| N^{(z;K)}(s) / K - n^{(2)}(s) \| = 0 \quad a.s.$$
Proof. The proof relies on a slight modification of Theorem 2.1 p. 456 in Ethier and Kurtz [17]. According to (2.1) and (2.2), the rescaled birth and death rates

\[
\tilde{b}_{ab}^K(n) = \frac{1}{K} b_{ab}^K(Kn) = f_a n_{ab} + r_K f_a f_A \frac{n_{ab} n_{ab} - n_{ab} n_{ab}}{f_A n_A + f_a n_a}, \quad (a, \beta) \in \mathcal{E}, n \in \mathbb{N}_0^\varepsilon,
\]

and

\[
\tilde{d}_{ab}^K(n) = \frac{1}{K} d_{ab}^K(Kn) = [D_a + C_{a,A} n_A + C_{a,a} n_a] n_{ab}, \quad (a, \beta) \in \mathcal{E}, n \in \mathbb{N}_0^\varepsilon,
\]

are Lipschitz and bounded on every compact subset of \( \mathbb{N}_0^\varepsilon \). The only difference with [17] is that \( \tilde{b}_{ab}^K \) depends on \( K \) via the term \( r_K \). Applying Itô’s formula with jumps we get:

\[
\frac{N^{(z,K)}(t)}{K} = \left[ \frac{|z|}{K} - z \right] + \text{Mar} \ t^{(z,K)}(t) + \int_0^t \sum_{(a,\beta) \in \mathcal{E}} e_{ab} \left( \tilde{b}_{ab}^K \left( \frac{N^{(z,K)}(s)}{K} \right) - \tilde{d}_{ab}^K \left( \frac{N^{(z,K)}(s)}{K} \right) \right) ds,
\]

where \( \text{Mar} \ t^{(z,K)} \) is a martingale, and we recall that \((e_{ab}, (a, \beta) \in \mathcal{E})\) is the canonical basis of \( \mathbb{R}_+^\mathcal{E} \). If we denote by \( \tilde{b}_{ab}^\infty \) the function

\[
\tilde{b}_{ab}^\infty(n) = f_a n_{ab} + r_f f_a f_A \frac{n_{ab} n_{ab} - n_{ab} n_{ab}}{f_A n_A + f_a n_a}, \quad (a, \beta) \in \mathcal{E}, n \in \mathbb{N}_0^\varepsilon,
\]

we get

\[
n^{(z)}(t) = z + \int_0^t \sum_{(a,\beta) \in \mathcal{E}} e_{ab} \left( \tilde{b}_{ab}^\infty \left( n^{(z)}(s) \right) - \tilde{d}_{ab}^\infty \left( n^{(z)}(s) \right) \right) ds.
\]

Hence we have for every \( t \leq t_z(z) \),

\[
\frac{N^{(z,K)}(t)}{K} - n^{(z)}(t) \leq \left| \frac{|z|}{K} - z \right| + \text{Mar} \ t^{(z,K)}(t) + \int_0^t \sum_{(a,\beta) \in \mathcal{E}} \left| \tilde{b}_{ab}^\infty \left( n^{(z)}(s) \right) - \tilde{b}_{ab}^K \left( n^{(z)}(s) \right) \right| ds
\]

\[
+ \int_0^t \sum_{(a,\beta) \in \mathcal{E}} \left| \tilde{b}_{ab}^K - \tilde{d}_{ab}^\infty \right| \left( \frac{N^{(z,K)}(s)}{K} \right) - \left( \tilde{b}_{ab}^K - \tilde{d}_{ab}^\infty \right) \left( n^{(z)}(s) \right) \right| ds,
\]

and there exists a finite constant \( M \) such that

\[
\frac{N^{(z,K)}(t)}{K} - n^{(z)}(t) \leq \frac{1}{K} + \left| \text{Mar} \ t^{(z,K)}(t) \right| + |r - r_K| Mt_z(z) + M \int_0^t \left| \frac{N^{(z,K)}(s)}{K} - n^{(z)}(s) \right| ds.
\]

But following Ethier and Kurtz, we get

\[
\lim_{K \to \infty} \sup_{z \in t_z(z)} \left| \text{Mar} \ t^{(z,K)} \right| = 0, \quad \text{a.s.},
\]

and we end the proof by using Assumption 2 and Gronwall’s Lemma. \( \square \)

Once we know that the rescaled population process is close to the solution of the dynamical system (4.2), we can study this latter.

Lemma 4.2. Let \( z \) be in \( \mathbb{R}_+^\mathcal{E} \) such that \( z_A > 0 \) and \( z_a > 0 \). Then \( n^{(z)}(t) \) and \( n_{ab}^{(z)}(t) \) have a finite limit when \( t \) goes to infinity, and there exists a positive constant \( \varepsilon_0 \) such that for every \( \varepsilon \leq \varepsilon_0 \),

\[
\left| \frac{n_{ab}^{(z)}(\infty)}{n_a^{(z)}(\infty)} - \frac{n_{ab}^{(z)}(t_z(z))}{n_a^{(z)}(t_z(z))} \right| \leq \frac{2 f_a \varepsilon^2}{n_A |S_{aA}|}.
\]

Proof. Assumption 1 ensures that \( n_a^{(z)}(t) \) goes to \( \bar{n}_a \) at infinity. If we define the functions

\[
p_{a,b}^{(z)} = n_{ab}^{(z)} / n_a^{(z)}, \quad \alpha \in \mathcal{A}, \quad \text{and} \quad g_{ab}(z) = p_{A,b}^{(z)} - p_{a,b}^{(z)},
\]

\[
\lim_{t \to \infty} \sup_{z \in t_z(z)} \left| \text{Mar} \ t^{(z,K)} \right| = 0, \quad \text{a.s.},
\]

and we end the proof by using Assumption 2 and Gronwall’s Lemma. \( \square \)
we easily check that \( \phi : (n^{(z)}_A, n^{(z)}_{Ab}, n^{(z)}_{ab_1}, n^{(z)}_{ab_2}) \rightarrow (n^{(z)}_A, n^{(z)}_{a}, g^{(z)}_1, p^{(z)}_{a,b}) \) defines a change of variables from \( \mathbb{R}^4_{+} \times [0, 1] \) and (4.2) is equivalent to:

\[
\begin{align*}
\dot{n}^{(z)}_A &= (f_A - (D_A + C_{A,a}n^{(z)}_A + C_{a,a}n^{(z)}_a))n^{(z)}_A, \quad \alpha \in \mathcal{A} \\
\dot{g}^{(z)}_1 &= -g^{(z)}_1 \left( \frac{f_A f_A n^{(z)}_A + n^{(z)}_a}{(f_A n^{(z)}_A + f_A n^{(z)}_a)} \right) \\
\dot{p}^{(z)}_{a,b} &= g^{(z)}_1 \left( \frac{f_A f_A n^{(z)}_A}{(f_A n^{(z)}_A + f_A n^{(z)}_a)} \right),
\end{align*}
\]

with initial condition \((n^{(z)}_A(0), n^{(z)}_{a}(0), g^{(z)}_1(0), p^{(z)}_{a,b}(0)) = (z_A, z_{Ab}, z_{a}/z_{A} - z_{ab_1}/z_{a} - z_{ab_2}/z_{a})\). Moreover, a direct integration yields

\[
p^{(z)}_{a,b}(t) = p^{(z)}_{a,b}(0) - (p^{(z)}_{a,b}(0) - p^{(z)}_{a,b}(0)) F(z, r, t),
\]

where \( F \) has been defined in (2.12). According to (2.13), \( F(z, r, t) \) has a finite limit when \( t \) goes to infinity. Hence \( p^{(z)}_{a,b} \) also admits a limit at infinity. Let \( \epsilon \equiv |S_{Aa}|/C_{A,a} \wedge C_{a,a} \wedge C_{A,a} \wedge \bar{n}_{a}/2 \), and \( t_{\epsilon}(z) \) defined in (4.1). Then for \( t \geq t_{\epsilon}(z) \),

\[
\bar{n}^{(z)}_A(t) = (f_A - D_A - C_{A,a}(\bar{n}_a - \epsilon/2))n^{(z)}_A(t) \leq S_{Aa}n^{(z)}_A(t)/2 < 0.
\]

Recalling that \( r \leq 1 \) and \( |g(t)| \leq 1 \) for all \( t \geq 0 \) we get:

\[
|p^{(z)}_{a,b}(\infty) - p^{(z)}_{a,b}(t_{\epsilon}(z))| \leq \int_{t_{\epsilon}(z)}^{\infty} \frac{f_A f_A n^{(z)}_A + n^{(z)}_a}{f_A n^{(z)}_A + f_A n^{(z)}_a} \leq \frac{f_A \epsilon^2}{\bar{n}_a} \int_{0}^{\infty} e^{S_{Aa}t/2} ds \leq \frac{2f_A \epsilon^2}{\bar{n}_a |S_{Aa}|},
\]

which ends up the proof. \( \square \)

### 4.2. \( A \)-population extinction.

The deterministic approximation (4.2) fails when the \( A \)-population size becomes too small. We shall compare \( N_A \) with birth and death processes to study the last period of mutant invasion. We show that during this period, the number of \( A \) individuals is so small that it has no influence on the neutral proportion in the \( a \)-population, which stays nearly constant. Before stating the result, we recall Definition (2.9), introduce the compact set \( \Theta \):

\[
\Theta := \{ z \in \mathbb{R}_+^{4	imes[0,1]} | z_0 \leq \epsilon^2 \quad {\text{and}} \quad |z_a - \bar{n}_a| \leq \epsilon \},
\]

the constant \( M'' = 3 + (f_A + C_{A,a})/C_{a,a} \) and the stopping time:

\[
S^K_{\epsilon}(z) := \inf \left\{ t \geq 0, N^{(z,K)}_A(t) > \epsilon K \text{ or } |N^{(z,K)}_A(t) - \bar{n}_aK| > M''\epsilon K \right\}.
\]

**Lemma 4.3.** Let \( z \) be in \( \Theta \). Then under Assumption 1, there exist two positive finite constants \( c \) and \( \epsilon_0 \) such that for \( \epsilon \leq \epsilon_0 \),

\[
\limsup_{K \to \infty} \mathbb{P} \left( \sup_{t \leq T_{\epsilon,K}^0} \left| p^{(z,K)}_{a,b}(t) - p^{(z,K)}_{a,b}(0) \right| > \epsilon \right) \leq ce.
\]

**Proof.** Let \( z \) be in \( \Theta \) and \( Z^\epsilon \) be a birth and death process with birth rate \( f_A \), death rate \( D_A + (\bar{n}_a - M''\epsilon)C_{A,a} \), and initial state \( \epsilon^2K \). Then on \( [0, S^K_{\epsilon}(z)] \), \( N_A \) and \( Z^\epsilon \) have the same birth rate, and \( Z^\epsilon \) has a smaller death rate than \( N_A \). Thus according to Theorem 2 in [5], we can construct the processes \( N \) and \( Z^\epsilon \) on the same probability space such that:

\[
N_A(t) \leq Z^\epsilon(t), \quad \forall t \leq S^K_{\epsilon}(z).
\]

Moreover, if we denote by \( T_{\epsilon}^0 \) the extinction time of \( Z^\epsilon \), \( T_{\epsilon}^1 := \inf \{ t \geq 0, Z^\epsilon(t) = 0 \} \), and recall that

\[
f_A - D_A - (\bar{n}_a - M''\epsilon)C_{A,a} = S_{Aa} + M''C_{A,a} \epsilon - S_{Aa}/2 < 0, \quad \forall \epsilon < |S_{Aa}|/(2M''C_{A,a}),
\]

we get according to (A.10) that for \( z \leq \epsilon^2 \) and \( L(\epsilon, K) = 2 \log K/|S_{Aa} + M''\epsilon C_{A,a}| \),

\[
\mathbb{P}_{|z|K} \left( T_{\epsilon}^1 \leq L(\epsilon, K) \right) \geq \exp \left[ |z|K \left[ \log(K^2 - 1) - \log(K^2 - f_A(D_A + (\bar{n}_a - M''\epsilon)C_{A,a})^{-1}) \right] \right].
\]

Thus:

\[
\lim_{K \to \infty} \mathbb{P}_{|z|K} \left( T_{\epsilon}^1 < L(\epsilon, K) \right) = 1.
\]
Moreover, Equation (A.4) ensures the existence of a finite $c$ such that for $\varepsilon$ small enough,

\begin{equation}
\mathbb{P}\left(L(\varepsilon, K) < S_{c}^{K}(z)\right) \geq 1 - c\varepsilon.
\end{equation}

Equations (4.11) and (4.12) imply

\begin{equation}
\liminf_{K \to \infty} \mathbb{P}\left(T_{0}^{1} < L(\varepsilon, K) < S_{c}^{K}(z)\right) \geq 1 - c\varepsilon
\end{equation}

for a finite $c$. According to Coupling (4.9) he have the inclusion $\{T_{0}^{1} < L(\varepsilon, K) < S_{c}^{K}(z)\} \subset \{T_{ext}^{K} < L(\varepsilon, K) < S_{c}^{K}(z)\}$. Adding (4.13) we finally get:

\begin{equation}
\liminf_{K \to \infty} \mathbb{P}(T_{ext}^{K} < L(\varepsilon, K) < S_{c}^{K}(z)) \geq 1 - c\varepsilon.
\end{equation}

Recall the martingale decomposition of $P_{a,b_{1}}$ in (3.1). To bound the difference $|P_{a,b_{1}}(t) - P_{a,b_{1}}(0)|$ we bound independently the martingale $M_{a}(t)$ and the integral $|P_{a,b_{1}}(t) - P_{a,b_{1}}(0) - M_{a}(t)|$. On the other hand Doob’s Maximal Inequality and Equation (3.12) imply:

\begin{equation}
\mathbb{P}\left(\sup_{t \leq L(\varepsilon, K) \wedge S_{c}^{K}(z)} |M_{a}(t)| > \frac{\varepsilon}{2}\right) \leq \frac{4C_{a} + \varepsilon}{\varepsilon^{2}} \mathbb{P}\left(\frac{C_{a}}{L(\varepsilon, K)} \leq S_{c}^{K}(z)\right).
\end{equation}

On the other hand the inequality $|N_{a,b_{1}}N_{a,b_{2}} - N_{a,b_{1}}N_{a,b_{2}}| \leq N_{a}N_{a}$ yields for $t \geq 0$

\begin{equation}
\left|\int_{0}^{t \wedge S_{c}^{K}(z)} \frac{f_{a}\bar{f}_{a}a(N_{a,b_{1}}N_{a,b_{2}} - N_{a,b_{1}}N_{a,b_{2}})}{(N_{a} + 1)(f_{a}N_{a} + f_{a}N_{a})} ds\right| \leq \int_{0}^{t \wedge S_{c}^{K}(z)} \frac{f_{a}N_{a}}{(\bar{n}_{a} - \varepsilon \varepsilon M''t)}.
\end{equation}

Hence decomposition (3.1), Markov’s Inequality, and Equations (4.9), (A.8) and (4.10) yield

\begin{equation}
\mathbb{P}\left(|(P_{a,b_{1}} - M_{a})(t \wedge S_{c}^{K}(z)) - P_{a,b_{1}}(0)| > \frac{\varepsilon}{2}\right) \leq \frac{2f_{a}E_{2}}{\varepsilon(\bar{n}_{a} - \varepsilon \varepsilon M'')} \int_{0}^{t \wedge S_{c}^{K}(z)} e^{-S_{c}^{K}(z)/2} ds \leq \frac{4f_{a}E_{2}}{(\bar{n}_{a} - \varepsilon \varepsilon M'')} |

Taking the limit of (4.15) when $K$ goes to infinity and adding (4.16) end the proof.

4.3. End of the proof of Theorem 1. Recall Definitions (2.9) and (4.1). We have:

\begin{align*}
\left|p_{a,b_{1}}^{(\varepsilon,K)}(T_{ext}^{(\varepsilon,K)}) - p_{a,b_{1}}^{(\varepsilon,K)}(\infty)\right| &\leq \left|p_{a,b_{1}}^{(\varepsilon,K)}(T_{ext}^{(\varepsilon,K)} - p_{a,b_{1}}^{(\varepsilon,K)},(z)) - p_{a,b_{1}}^{(\varepsilon,K)}(\infty)\right| \leq \left|p_{a,b_{1}}^{(\varepsilon,K)}(T_{ext}^{(\varepsilon,K)} - p_{a,b_{1}}^{(\varepsilon,K)}(\infty)\right|.
\end{align*}

To bound the two last terms we use respectively Lemmas 4.1 and 4.2. For the first term of right hand side, (2.5) ensures that with high probability, $N_{a,b_{1}}(t_{e}(z)) \in \Theta$ and $t_{e}(z) < T_{ext}^{(\varepsilon,K)}$. Lemma 4.3, Equation (3.14) and Markov’s Inequality allow us to conclude that for $\varepsilon$ small enough

\begin{equation}
\limsup_{K \to \infty} \mathbb{P}(\exists t_{e}(z), \exists a,b_{1} \left| p_{a,b_{1}}^{(\varepsilon,K)}(T_{ext}^{(\varepsilon,K)} - p_{a,b_{1}}^{(\varepsilon,K)}(\infty)\right| > 3\varepsilon) \leq c\varepsilon,
\end{equation}

for a finite $c$. It is equivalent to the convergence in probability, which concludes the proof.

5. A COUPLING WITH TWO BIRTH AND DEATH PROCESSES

In Sections 6 and 7 we suppose that Assumptions 1 and 3 hold and we denote by $N^{K}$ the process $N^{K}$. As it will appear in the proof of Theorem 2 the first period of mutant invasion, which ends at time $T_{K}$ when the mutant population size hits $[\varepsilon K]$, is the most important for the neutral proportion dynamics. Indeed, the neutral proportion in the $a$-population has already reached its final value at time $T_{K}^{K}$. Let us describe a coupling of the process $N^{K}$ with two birth and death processes which will be a key argument to control the growing of the population $a$ during the first period. To this aim we recall Definition (3.11) and define for $\varepsilon < S_{a,b_{1}}/(2C_{a,b_{1}}C_{A,a}/C_{A,a} + C_{a,b})$,

\begin{equation}
s_{-}(\varepsilon) := \frac{S_{a,b_{1}}}{f_{a}} - \frac{2C_{a,b_{1}}C_{A,a}}{f_{a}C_{A,a}} + \frac{C_{a,b_{1}}C_{A,a}}{f_{a}C_{A,a}}, \quad s_{+}(\varepsilon) := \frac{S_{a,b_{1}}}{f_{a}} + \frac{2C_{a,b_{1}}C_{A,a}}{f_{a}C_{A,a}}.
\end{equation}
Definitions (2.3) and (2.8) ensure that for $t < T^K_t \land T^K_{\tilde{t}}$,
\begin{equation}
(5.2) \quad f_a(1-s_\varepsilon) \leq \frac{d^K_a(N^K(t))}{N^K_a(t)} = f_a - S_{Aa} + \frac{C_{a,A}}{K}(N^K_A(t) - \bar{r}_A K) + \frac{C_{a,a}}{K} N^K_a(t) = f_a(1-s_\varepsilon),
\end{equation}
and following Theorem 2 in [5], we can construct on the same probability space the processes $Z^\varepsilon_{-}$, $N^K$ and $Z^\varepsilon_{+}$ such that almost surely:
\begin{equation}
(5.3) \quad Z^\varepsilon_{-}(t) \leq N^K_a(t) \leq Z^\varepsilon_{+}(t), \quad \text{for all } t < T^K_t \land T^K_{\tilde{t}},
\end{equation}
where for $* \in \{-, +\}$, $Z^\varepsilon_{*}$ is a birth and death process with initial state 1, and individual birth and death rates $f_a$ and $f_a(1-s_\varepsilon)$. We want to prove convergences on the fixation event $\text{Fix}^K$, defined in (2.9). Inequality (A.6) allows us to restrict our attention to the conditional probability measure:
\begin{equation}
(5.4) \quad \hat{\mathbb{P}}(.) = \mathbb{P}(T^K_t \leq \tilde{T}^K_{\tilde{t}}).
\end{equation}
To study expectations ($\hat{\mathbb{E}}$) and variances ($\hat{\text{Var}}$) associated with this probability measure, we express the event $(\hat{T}^K_t \leq \tilde{T}^K_{\tilde{t}})$ in a form easier to handle. More precisely, if we introduce the events:
\begin{equation}
(5.5) \quad \mathcal{L}^K_{\varepsilon} := \left\{ f_a(1-s_\varepsilon) \leq \frac{d^K_a(N^K(t))}{N^K_a(t)} \leq f_a(1-s_\varepsilon), \forall t \leq T^K_{\varepsilon} \right\}, \quad \mathcal{H}^K_{\varepsilon} := \{ N^K_A(t) \in I^K_{\varepsilon}, \forall t \leq T^K_{\varepsilon} \},
\end{equation}
then we can check that
\begin{equation*}
\{ T^K_t \leq \tilde{T}^K_{\tilde{t}} \} = \{ T^K_{\varepsilon} < \infty, \mathcal{L}^K_{\varepsilon}, \mathcal{H}^K_{\varepsilon} \}.
\end{equation*}
The term $T^K_{\varepsilon} < \infty$ is due to the almost sure finiteness of $\tilde{T}^K_{\tilde{t}}$. Indeed the extinction time of a birth and death process with competition is almost surely finite.

6. PROOF OF THEOREM 2 IN THE STRONG RECOMBINATION REGIME

We distinguish the three periods of the selective sweep: (i) rare mutants and resident population size near its equilibrium value, (ii) quasi-deterministic period governed by the dynamical system (2.4), and (iii) $A$-population extinction. First we prove that at time $T^K_{\varepsilon}$ proportions of $b_1$ alleles in the populations $A$ and $a$ close to $z^{b_1}_{A A}/z^{b_1}_A$. Once the neutral proportions are the same in the two populations, they do not evolve anymore until the end of the sweep.

**Lemma 6.1.** There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $\varepsilon \leq \varepsilon_0$:
\begin{equation}
\limsup_{K \to \infty} \mathbb{E} \left[ \mathbb{E}^K_{T^K_{\varepsilon} \land \tilde{T}^K_{\tilde{t}}} \left\{ \left| p^K_{A,a_{b_1}}(T^K_{\varepsilon}) - \frac{z^{b_1}_{A b_1}}{z^{b_1}_A} \right| + \left| p^K_{A,a_{b_1}}(T^K_{\varepsilon}) - p^K_{a,a_{b_1}}(T^K_{\varepsilon}) \right| \right\} \right] \leq c \varepsilon.
\end{equation}

**Proof.** First we bound the difference between the neutral proportions in the two populations, $|p_{A,b_1}(t) - p_{A,b_1}(t)|$, then we bound $|p_{A,a_{b_1}}(t) - z^{b_1}_{A b_1}/z^{b_1}_A|$. For sake of simplicity we introduce:
\begin{equation}
G(t) := p_{A,a_{b_1}}(t) - p_{A,b_1}(t) = \frac{N^{A_{a_{b_1}}}(t)N^{A_{b_1}}(t) - N^{A_{b_1}}(t)N^{A_{a_{b_1}}}(t)}{N^A(t)N^A(t)}, \quad \forall t \geq 0,
\end{equation}
\begin{equation*}
Y(t) = \mathbb{E}^{(\varepsilon)}_{[|N_{A_{a}}(t)| \geq 1, N_{a}(t) \geq 1]} G^2(t) e^{rK_1(f_a \land f_a)t}, \quad \forall t \geq 0.
\end{equation*}
Recalling (3.8) and applying Itô's formula with jumps we get
\begin{align*}
Y(t \land T^K_{\varepsilon} \land \tilde{T}^K_{\tilde{t}}) &= Y(0) + \tilde{\mathbb{M}}_{t \land T^K_{\varepsilon} \land \tilde{T}^K_{\tilde{t}}} + rK \int_0^t \mathbb{1}_{s < T^K_{\varepsilon} \land \tilde{T}^K_{\tilde{t}}} \left( f_a \land f_a - H(s) \right) Y(s) ds \\
&\quad + \int_0^t \mathbb{1}_{s < T^K_{\varepsilon} \land \tilde{T}^K_{\tilde{t}}} e^{rK_1(f_a \land f_a)s} ds \int_{\mathbb{R}_+} \left[ \mu^K_A(N, s, \theta) \right]^2 + \left( \mu^K_a(N, s, \theta) \right)^2 \mathbb{1}_{[N_{a}(t) \geq 1, N_{a}(t) \geq 1]} d\theta,
\end{align*}
where $\tilde{\mathbb{M}}$ is a martingale with zero mean, and $H$ is defined by
\begin{equation}
H(t) = \frac{2f_a f_A N_a(t)N_a(t)}{f_A N_A(t) + f_a N_a(t)} \left[ \frac{1}{N_A(t) + 1} + \frac{1}{N_a(t) + 1} \right], \quad t \geq 0.
\end{equation}
In particular we can check that for all \( s \geq 0 \) we have \( Y(s)H(s) \geq (f_A \wedge f_a)Y(s) \). Equations (3.12) and (3.13) give bounds for the integrals \( \int (\mu^K_s)^2, \alpha \in \mathcal{A} \), and adding (3.14) we obtain:

\[
\begin{align*}
\mathbb{E}[Y(t \wedge T^K \wedge \tilde{T}^K)] & \leq 1 + \frac{C(n_A + 2\varepsilon C_{A,a}/C_{A,A})}{\Xi} e^{\varepsilon R_x(f_A \wedge f_a)t} \\
&+ \int_0^t (k_0 + 1) C\left(\frac{C_{A,a}}{C_{A,A}}\right) \mathbb{E}\left[|N^{z\wedge e_t} \wedge \tilde{T}^K| \right] e^{\left(R_x(f_A \wedge f_a) - \frac{S_{A,a}}{2(1+1)}\right)ds} \\
&\leq c\left(1 + \frac{1}{K}\right) e^{\varepsilon R_x(f_A \wedge f_a)t} + e^{\left(R_x(f_A \wedge f_a) - \frac{S_{A,a}}{2(1+1)}\right)ds},
\end{align*}
\]

(6.3)

where \( c \) is a finite constant which can be chosen independently of \( \varepsilon \) and \( K \) if \( \varepsilon \) is small enough and \( K \) large enough. Combining Equation (3.1), Cauchy-Schwarz Inequality, and Equations (3.12) and (6.3) we get for every \( t \geq 0 \),

\[
\mathbb{E}\left[\left|P_{A,b_i}(t \wedge T^K \wedge \tilde{T}^K) - \frac{[z_{A,h_i}]}{[z_{A,K}]}\right|\right] \leq \mathbb{E}\left[\left|M_{A}(t \wedge T^K \wedge \tilde{T}^K)\right|\right] + \frac{\varepsilon R_x f_a}{\Xi} \int_0^t \mathbb{E}\left[1_{s < T^K \wedge \tilde{T}^K} |G(s)1_{N(n_i(s)) \leq 1/N(n_i(s)) \leq 1}|\right] ds \\
\leq \mathbb{E}\left[\left|M_{A}(t \wedge T^K \wedge \tilde{T}^K)\right|\right] + c r K e^{\int_0^t \mathbb{E}\left[1_{s < T^K \wedge \tilde{T}^K} |G(s)1_{N(n_i(s)) \leq 1/N(n_i(s)) \leq 1}|\right] ds} \\
\leq c\left(\sqrt{t/K} + \varepsilon \int_0^t \left(\varepsilon R_x(f_A \wedge f_a)s + \frac{1}{K} + e^{-S_{A,a}/2(k_0 + 1)}\right) d s\right),
\]

(6.4)

where \( c \) is finite. A simple integration then yields the existence of a finite \( c \) such that:

\[
\mathbb{E}\left[\left|P_{A,b_i}(t \wedge T^K \wedge \tilde{T}^K) - \frac{[z_{A,h_i}]}{[z_{A,K}]}\right|\right] \leq c\left(\sqrt{t/K} + \varepsilon \left[1 + \frac{t}{\sqrt{K}}\right]\right).
\]

But according to Coupling (5.3) and limit (A.11) we have the asymptotic behavior

\[
\lim_{K \to \infty} \mathbb{P}(T^K \geq 2S_{A,a}\log K | T^K \leq \tilde{T}^K) = 0,
\]

(6.5)

Hence applying (6.4) at time \( t = 2S_{A,a}\log K \) and using (A.3) and (6.5), we bound the first term in the expectation. The second bound is obtained in the same way. \( \square \)

The following Lemma states that during the second period, the neutral proportion stays constant in the \( a \)-population.

**Lemma 6.2.** There exist two positive finite constants \( c \) and \( c_0 \) such that for \( \varepsilon \leq c_0 \):

\[
\limsup_{K \to \infty} \mathbb{E}\left[\left|T^K_{t_\varepsilon} \right| \left|P_{A,b_i}(T^K_{t_\varepsilon} + t_\varepsilon(\frac{N^K(t)}{K})) - \frac{[z_{A,h_i}]}{[z_{A,K}]}\right|\right] \leq c_\varepsilon.
\]

**Proof.** Let us introduce, for \( \varepsilon \in \mathbb{R}_{+}^\delta \) and \( \varepsilon > 0 \) the set \( \Gamma \) and the time \( t_\varepsilon \) defined as follows:

\[
\Gamma := \left\{ z \in \mathbb{R}_{+}^\delta, z_A \in \left[\bar{n}_A - 2\varepsilon C_{A,a}, \bar{n}_A + 2\varepsilon C_{A,a}\right], z_a \in \left[\frac{\varepsilon}{2}, \frac{3\varepsilon}{2}\right]\right\}, \quad t_\varepsilon := \sup\{t_\varepsilon(z), z \in \Gamma\},
\]

(6.6)

where \( t_\varepsilon(z) \) has been defined in (4.1). According to Assumption 1, \( t_\varepsilon < \infty \), and

\[
I(\Gamma, \varepsilon) := \inf_{z \in \Gamma} \inf_{t \leq t_\varepsilon} \left|N^{z, K}(t), n^{z, a}_A(t)\right| > 0,
\]

and we can introduce the stopping time

\[
L^{K}(z) = \inf\{t \geq 0, (N^{z, K}(t), n^{z, a}_A(t)) \in \left.I(\Gamma, \varepsilon)K/2, (\bar{n}_A + \bar{n}_a)K\right|^2\}
\]

(6.7)

Finally, we denote by \( (\mathcal{F}^K_t, t \geq 0) \) the canonical filtration of \( N^K \). Notice that on the event \( \{T^K \leq \tilde{T}^K\} \), \( N(T^K) / K \in \Gamma \), thus \( t_\varepsilon(N(T^K)) / K \leq t_\varepsilon \). The semi-martingale decomposition (3.1) and the
The definition of $G$ in (6.1) then twice the Strong Markov property and the Cauchy-Schwarz Inequality yield:

\[
\mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} \left| P_{n, A} \left( T_e^K + t_e \left( N(T_e^K) \right) K \right)^{L_e^K \left( (N(T_e^K)) K \right)} - P_{n, A} (T_e^K) \right| \right] \\
\leq \mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} |M_\varepsilon (T_e^K + t_e \left( N(T_e^K) \right) K) - M_\varepsilon (T_e^K)| + f_\varepsilon \int_{t_e^K}^{T_e^K + t_e \left( N(T_e^K) \right) K} \left| G \right| |\mathcal{F}_{t^*}^{K_e^K} \right] \\
\leq \mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} \left| (M_\varepsilon (T_e^K + t_e \left( N(T_e^K) \right) K)) - (M_\varepsilon (T_e^K)) \right| |\mathcal{F}_{t^*}^{K_e^K} \right] + f_\varepsilon \sqrt{t_e} \mathbb{E}^{1/2} \left[ \int_{t_e^K}^{T_e^K + t_e \left( N(T_e^K) \right) K} \left| G \right|^2 |\mathcal{F}_{t^*}^{K_e^K} \right].
\]

To bound the first term of the right hand side we use Strong Markov property, Equation (3.12) and the definition of $L_e^K$ in (6.7). We get

\[
\mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} \mathbb{E}^{1/2} \left[ \left( M_\varepsilon (T_e^K + t_e \left( N(T_e^K) \right) K)) - (M_\varepsilon (T_e^K)) \right) |\mathcal{F}_{t^*}^{K_e^K} \right] \right] \leq \frac{2t_e C(\tilde{n}_A + \tilde{n}_A)}{\Gamma (\varepsilon) K^2}.
\]

For the second term, Strong Markov property and Itô's formula with jumps yield

\[
\mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} \mathbb{E}^{1/2} \left[ \int_{t_e^K}^{T_e^K + t_e \left( N(T_e^K) \right) K} G^2 |\mathcal{F}_{t^*}^{K_e^K} \right] \right] \\
\leq \sqrt{t_e} \sup_{z \in \Gamma, t \leq t_e} \mathbb{E} \left[ G^2 (t \wedge L_e^K(z)) - G^2 (0) \right] |N(0) = [zK]| + \mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} |G(T_e^K)| \right] \\
\leq \sqrt{t_e} \sum_{a \in \mathcal{A}} \int_{0}^{\tilde{t}_e^K} \mathbb{E} \left[ (M_\varepsilon (a_Z)) d\varepsilon + \mathbb{1}_{t^* \leq \tilde{t}_e^K} |G(T_e^K)| \right].
\]

Equations (3.12) and Lemma 6.1 finally lead to

\[
\mathbb{E}\left[\mathbb{1}_{t^* \leq \tilde{t}_e^K} \mathbb{E}^{1/2} \left[ \int_{t_e^K}^{T_e^K + t_e \left( N(T_e^K) \right) K} G^2 |\mathcal{F}_{t^*}^{K_e^K} \right] \right] \leq \sqrt{t_e} \left( \frac{B t_e C(\tilde{n}_A + \tilde{n}_A)}{\Gamma (\varepsilon) K^2} \right)^{1/2} + o_K (1)
\]

where $o_K (1)$ denotes a function of $K$ going to 0 at infinity. Moreover (2.5) ensures that

\[
\mathbb{P}\left( T_e^K \leq \tilde{t}_e^K \wedge L_e^K \left( N(T_e^K) \right) K \right) \leq t_e \left( N(T_e^K) \right) K \right) \mathbb{P}\left( \left( N(T_e^K) \right) K \right) \rightarrow K \rightarrow \infty 0,
\]

where $\Theta$ has been defined in (4.7). Adding Equations (6.8), (6.9), (6.10) and Lemma 6.1, we finally end the proof of Lemma 6.2.

\[\square\]

**Proof of Theorem 2 in the strong recombination regime.** Let us focus on the $A$-population extinction period. We have thanks to Strong Markov property:

\[
\mathbb{P}\left(\mathbb{1}_{N(T_e^K + t_e (N(T_e^K)/K)) \in \Theta} \left| P_{n, A} (T_e^K) - P_{n, A} (T_e^K + t_e \left( N(T_e^K) \right) K) \right| > \sqrt{e} \right) \\
\leq \sup_{z \in \Theta} \mathbb{P}\left( \left| P_{n, A} (T_e^K) - P_{n, A} (0) \right| > \sqrt{e} \right) |N(0) = [zK]|.
\]

But Equation (2.5) yields $\mathbb{P}(N(T_e^K + t_e (N(T_e^K)/K)) / K \in \Theta | N(T_e^K) / K \in \Gamma) \rightarrow K \rightarrow \infty 1$, and $\{T_e^K \leq \tilde{t}_e^K \} \subset \{N(T_e^K) / K \in \Gamma\}$. Adding Equation (A.6) and Lemma 6.2, Triangle inequality allows us to conclude that for $\epsilon$ small enough

\[
\limsup_{K \rightarrow \infty} \mathbb{P}\left( \left| P_{n, A} (T_e^K) - \frac{z A h_i}{z A} \right| > \sqrt{e} \right) |\text{Fix}^K| \leq c \epsilon.
\]

As $\mathbb{P} (\text{Fix}^K) \rightarrow K \rightarrow \infty S_{A A} / f_a > 0$, it is equivalent to the claim of Theorem 2 in the strong regime. \[\square\]
7. Proof of Theorem 2 in the Weak Recombination Regime

In this section we suppose that Assumptions 3 and 5 hold. We first focus on the neutral proportion in the \( a \) population at time \( T^K_\epsilon \). The idea is to consider the neutral alleles at time \( T^K_\epsilon \) and follow their ancestral lines back until the beginning of the sweep, to know whether they are descended from the first mutant or not. Two kinds of event can happen to a neutral lineage: coalescences and m-recombinations (see Section 7.1); we show that we can neglect the coalescences and the occurrence of several m-recombinations for a lineage during the first period. Therefore, our approximation of the genealogy is the following: two neutral lineages are independent, and each of them undergoes one recombination with an \( A \)-individual during the first period with probability \( 1 - \exp(-r_f a \log K / \log a) \). If it has undergone a recombination with an \( A \)-individual, it can be an allele \( b_1 \) or \( b_2 \). Otherwise it is descended from the first mutant and is an allele \( b_1 \).

To get this approximation we follow the line presented by Schweinsberg and Durrett in [28]. In this paper, the authors describe the population dynamics by a variation of Moran model with two loci and recombinations. In their model, the population size is constant and each individual has a constant selective advantage, 0 or \( s \). In our model the size is varying and the individual’s ability to survive depends on the population state. After the study of the first period we check that the second and third periods have little influence on the neutral proportion in the \( a \)-population.

7.1. Coalescence and m-recombination times. Let us introduce the jump times of the stopped Markov process \((N^K(t), t \leq T^K_\epsilon)\), \(0 := t^K_0 < t^K_1 < \ldots < t^K_m := T^K_\epsilon\), where \( J^K \) denotes the jump number of \( N^K \) between 0 and \( T^K_\epsilon \), and the time of the \( m \)-th jump is:

\[
t^K_m = \inf\{t > t^K_{m-1}, N^K(t) \neq N^K(t^K_{m-1})\}, \quad 1 \leq m \leq J^K.
\]

Let us sample two individuals uniformly at random at time \( T^K_\epsilon \) and denote by \( \beta_p \) and \( \beta_q \) their neutral alleles. We want to follow their genealogy backward in time and know at each time between 0 and \( T^K_\epsilon \) the types (\( A \) or \( a \)) of the individuals carrying \( \beta_p \) and \( \beta_q \).

We say that \( \beta_p \) and \( \beta_q \) coalesce at time \( t^K_m \) if they are carried by two different individuals at time \( t^K_m \) and by the same individual at time \( t^K_{m-1} \). In other words the individual carrying the allele \( \beta_p \) (or \( \beta_q \)) at time \( t^K_m \) is a newborn and has inherited his neutral allele from the individual carrying allele \( \beta_q \) (or \( \beta_p \)) at time \( t^K_{m-1} \). The jump number at the coalescence time is denoted by

\[
TC^K(\beta_p, \beta_q) := \begin{cases} 
\sup\{m \leq J^K, \beta_p \text{ and } \beta_q \text{ coalesce at time } t^K_m\}, & \text{if } \beta_p \text{ and } \beta_q \text{ coalesce} \\
-\infty, & \text{otherwise.}
\end{cases}
\]

We say that \( \beta_p \) m-recombines at time \( t^K_m \) if the individual carrying the allele \( \beta_p \) at time \( t^K_m \) is a newborn, carries the allele \( a \in \mathcal{A} \), and has inherited his allele \( \beta_p \) from an individual carrying allele \( \tilde{a} \). In other words, a m-recombination is a recombination which modifies the selected allele connected to the neutral allele. The jump numbers of the first and second (backward in time) m-recombinations are denoted by:

\[
TR^K_1(\beta_p) := \begin{cases} 
\sup\{m \leq J^K, \beta_p \text{ m-recombines at time } t^K_m\}, & \text{if there is at least one m-recombination} \\
-\infty, & \text{otherwise,}
\end{cases}
\]

\[
TR^K_2(\beta_p) := \begin{cases} 
\sup\{m < TR^K_1(\beta_p), \beta_p \text{ m-recombines at time } t^K_m\}, & \text{if there are at least two m-recombinations} \\
-\infty, & \text{otherwise.}
\end{cases}
\]

Let us now focus on the probability for a coalescence to occur conditionally on the state of the process \((N^K_A, N^K_a)\) at two successive jump times. We denote by \( \bar{p}^{K,N}(n) \) the probability that the genealogies of two random neutral alleles associated respectively with alleles \( a_1 \) and \( a_2 \in \mathcal{A} \) at time \( t^K_m \) coalesce at this time conditionally on \((N^K_A(t^K_{m-1}), N^K_a(t^K_{m-1})) = n \in \mathbb{N}^2\) and on the birth of an individual carrying allele \( a_1 \in \mathcal{A} \) at time \( t^K_m \). Then we have the following result:
Lemma 7.1. For every \( n = (n_A, n_\bar{a}) \in \mathbb{N}^2 \) and \( \alpha \in \mathcal{A} \), we have:
\[
(7.1) \quad p_{cK}^{\alpha}(n) = \frac{2}{n_\bar{a}(n_\alpha + 1)} \left( 1 - \frac{r_Kf_\bar{a}n_\bar{a}}{f_\bar{a}n_\bar{a} + f_\alpha n_\alpha} \right) \quad \text{and} \quad p_{aK}^{\alpha}(n) = \frac{r_Kf_\alpha}{(n_\alpha + 1)(f_\bar{a}n_\bar{a} + f_\alpha n_\alpha)}.
\]

Proof. We only state the expression of \( p_{aK}^{\alpha}(n) \), as the calculations are similar for \( p_{cK}^{\alpha}(n) \). If there is a m-recombination, we cannot have the coalescence of two neutral alleles associated with allele \( \alpha \) at time \( \tau^K_m \). With probability \( 1 - r_Kf_\bar{a}n_\bar{a}/(f_\bar{a}n_\bar{a} + f_\alpha n_\alpha) \) there is no m-recombination and the parent giving its neutral allele carries the allele \( \alpha \). When there is no m-recombination, two individuals among those, who carry allele \( \alpha \) also carry a neutral allele which was in the same individual at time \( \tau^K_{m-1} \). We have a probability \( 2/n_\bar{a}(n_\alpha + 1) \) to pick this couple of individuals among the \( (n_\alpha + 1) \alpha \)-individuals.

Remark 4. A m-recombination for a neutral population associated with an \( \alpha \) allele is a coalescence with an \( \bar{a} \) individual. Thus if we denote by \( p_{cK}^{\alpha}(n) \) the probability that an \( \alpha \)-individual, chosen at random at time \( \tau^K_m \), is the newborn and underwent a m-recombination at his birth, conditionally on \( (N^K_A(\tau^K_{m-1}), N^K_\bar{a}(\tau^K_{m-1})) = n \in \mathbb{N}^2 \) and on the birth of an individual \( \alpha \) at time \( \tau^K_m \) we get
\[
(7.2) \quad p^{\alpha}(n) = n_\bar{a}p^{\alpha}_{aK}(n) = \frac{n_\bar{a}r_Kf_\bar{a}}{(n_\alpha + 1)(f_\bar{a}n_\bar{a} + f_\alpha n_\alpha)}.
\]
Moreover, if we recall the definition of \( I^K_\alpha \) in (3.10), we notice that there exists a finite constant \( c \) such that for \( k < [\varepsilon K] \),
\[
(7.3) \quad (1 - ce)^{r_K/K + 1} \leq \inf_{n_\bar{a} \in I^K_\alpha} \sup_{n_\alpha \in I^K_\alpha} p^{\alpha}_{aK}(n_\alpha,k) \leq \sup_{n_\alpha \in I^K_\alpha} p^{\alpha}_{aK}(n_\alpha,k) \leq \frac{r_K}{k + 1}.
\]

7.2. Jumps of mutant population during the first period. We want to count the number of coalescences and m-recombinations in the lineages of the two randomly chosen neutral alleles \( \beta_p \) and \( \beta_\bar{a} \). By definition, these events can only occur at a birth time. Thus we need to study the upcrossing number of the process \( N^K_\alpha \) before \( T^K_\alpha \) (Lemma 7.2). It allows us to prove that the probability that a lineage is affected by two m-recombinations or that two lineages coalesce, and then (backward in time) are affected by a m-recombination are negligible (Lemma 7.3). Then we obtain an approximation of the probability that a lineage is affected by a m-recombination (Lemma 7.4), and finally we check that two lineages are approximately independent (Equation (7.20)). The last step consists in controlling the neutral proportion in the population \( A \) (Lemma 7.5). Indeed it will give us the probability that a neutral allele which has undergone a m-recombination is a \( b_1 \) or a \( b_2 \).

Let us denote by \( \xi^K_\alpha \) the jump number of last visit to \( k \) before the hitting of \( [\varepsilon K] \),
\[
(7.4) \quad \xi^K_\alpha := \sup\{m \leq \lfloor K \rfloor, N^K_\alpha(\tau^K_m) = k\}, \quad 1 \leq k \leq [\varepsilon K].
\]
This allows us to introduce for \( 0 < j \leq k < [\varepsilon K] \) the number of upcrossings from \( k \) to \( k + 1 \) for the process \( N^K_\alpha \) before and after the last visit to \( j \):
\[
(7.5) \quad U^{(K,1)}_{j,k} := \#\{m \in [0, \ldots, \xi^K_\alpha - 1], (N^K_\alpha(\tau^K_m), N^K_\bar{a}(\tau^K_{m+1})) = (k, k + 1)\},
\]
\[
(7.6) \quad U^{(K,2)}_{j,k} := \#\{m \in [\xi^K_\alpha, \ldots, K - 1], (N^K_\alpha(\tau^K_m), N^K_\bar{a}(\tau^K_{m+1})) = (k, k + 1)\}.
\]
We also introduce the number of jumps of the \( A \)-population size when there are \( k a \)-individuals and the total number of upcrossings from \( k \) to \( k + 1 \) before \( T^K_\alpha \):
\[
(7.7) \quad H^K_k := \#\{m < \lfloor K \rfloor, N^K_\alpha(\tau^K_m) = N^K_\bar{a}(\tau^K_{m+1}) = k\},
\]
\[
(7.8) \quad U^K_k := U^{(K,1)}_{j,k} + U^{(K,2)}_{j,k} = \#\{m < \lfloor K \rfloor, (N^K_\alpha(\tau^K_m), N^K_\bar{a}(\tau^K_{m+1})) = (k, k + 1)\}.
\]
The next Lemma states moment properties of these jump numbers. Recall Definition (5.1). Then
Lemma 7.2. There exist two positive and finite constants $\varepsilon_0$ and $c$ such that for $\varepsilon \leq \varepsilon_0$, $K$ large enough and $1 \leq j < \lfloor \varepsilon K \rfloor$, we have

\begin{equation}
\hat{E}[H^K_j] \leq \frac{12f_{A}\tilde{n}_A K}{s^2(\varepsilon) f_{a,j}}, \quad \lambda_\varepsilon := \frac{(1 - s_-(\varepsilon))^3}{(1 - s_+(\varepsilon))^2} \in (0, 1), \quad \hat{E}[(U^{(K,1)}_{j,k})^2] \leq \frac{4\lambda^{k-j}_\varepsilon}{s^2(\varepsilon)(1 - s_+(\varepsilon))},
\end{equation}

(7.9)

\begin{equation}
\hat{E}[(U^{2}_j)^2] \leq \frac{2}{s^2(\varepsilon)}, \quad \left| \text{Cov}(U^{(K,2)}_{j,k}, U^{(K,1)}_j) \right| \leq c(\varepsilon + (1 - s_-(\varepsilon))^{k-j}),
\end{equation}

and

(7.10)

\begin{equation}
r_K \sum_{k=1}^{\lfloor \varepsilon K \rfloor - 1} \frac{\hat{E}[U^K_j]}{k + 1} - \frac{f_{a}\log K}{s_{a,A}} \leq c\varepsilon.
\end{equation}

(7.11)

This Lemma is widely used in Sections 7.3 and 7.4. Indeed, we shall decompose on the possible states of the population when a birth occurs, and apply Equations (7.1) and (7.2) to express the probability of coalescences and m-recombinations at each birth event. The proof of Lemma 7.2 is quite technical and is postponed to Appendix B.

7.3. Negligible events. The next Lemma bounds the probability that two m-recombinations occur in a neutral lineage and the probability that a couple of neutral lineages coalesce and then m-recombine when we consider the genealogy backward in time.

Lemma 7.3. There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $K \in \mathbb{N}$ and $\varepsilon \leq \varepsilon_0$,

\begin{equation*}
\hat{P}\left( TR_2^K(\beta_p) \neq -\infty \right) \leq \frac{c}{\log K}, \quad \text{and} \quad \hat{P}\left( 0 \leq TR_1^K(\beta_p) \leq TC^K(\beta_p, \beta_q) \right) \leq \frac{c}{\log K}.
\end{equation*}

Proof. By definition, the neutral allele $\beta_p$ is associated with an allele $a$ at time $T^K_{\varepsilon}$s. If there are at least two m-recombinations it implies that there exists a time between 0 and $T^K_{\varepsilon}$ at which $\beta_p$ has undergone a m-recombination when it was associated with an allele $A$. We shall work conditionally on the stopped process $(N_A(t^K_{m}), m \leq J^K)$ and decompose according to the $a$-population size when this m-recombination occurs. We get the inclusion:

\begin{equation*}
\{ TR_2^K(\beta_p) \neq -\infty \} \subset \bigcup_{k=1}^{\lfloor \varepsilon K \rfloor - 1} \bigcup_{m=1}^{J^K} \left\{ TR_2^K(\beta_p) = m, N_A(t^K_{m-1}) = N_A(t^K_{m}) = k \right\}.
\end{equation*}

We recall the definition of $I^K_{\varepsilon}$ in (3.10). Thanks to Equations (7.2) and (7.9), we get:

\begin{equation*}
\hat{P}(TR_2^K(\beta_p) \neq -\infty) \leq \sum_{k=1}^{\lfloor \varepsilon K \rfloor - 1} \sup_{n,A \in I^K_{\varepsilon}} p^{I^K_{\varepsilon}}_{A}(n,A,k) \hat{E}[H^K_k] \leq \frac{12r_K \tilde{n}_A \varepsilon}{s^2(\varepsilon)(\tilde{n}_A - 2\varepsilon C_{A,a}/C_{A,a})^2}.
\end{equation*}

The Assumption 5 on weak recombination completes the proof of the first inequality in Lemma 7.3. The proof of the second one is divided in two steps, presented after introducing the notations

\begin{equation*}
(\alpha \beta_m) := \{ \text{the neutral allele } \beta_m \text{ is associated with the allele } \alpha \text{ at time } t^K_m \}, \quad \alpha \in \mathcal{A}, \quad m \leq J^K
\end{equation*}

and

\begin{equation*}
(\alpha_1 \beta_m, \alpha_2 \beta_m) := (\alpha_1 \beta_m) \cap (\alpha_2 \beta_m), \quad (\alpha_1, \alpha_2) \in \mathcal{A}^2, \quad m \leq J^K
\end{equation*}

First step: We show that the probability that $\beta_p$ is associated with an allele $A$ at the coalescence time is negligible. We first recall the inclusion,

\begin{equation*}
\{ TC^K(\beta_p, \beta_q) \neq -\infty, (A\beta_m)_{TC^K(\beta_p, \beta_q)} \} \subset \bigcup_{k=1}^{\lfloor \varepsilon K \rfloor - 1} \bigcup_{m=1}^{J^K} \left\{ TC^K(\beta_p, \beta_q) = m, N_A(t^K_{m-1}) = k, (A\beta_m) \right\}.
\end{equation*}
and decompose on the possible selected alleles associated with $\beta_q$ and on the type of the newborn at coalescence time. Using Lemma 7.1, Equations (7.9) and (7.10), and $r_K \leq 1$, we get

\begin{equation}
\hat{\phi}(T^{K,K}_C(\beta_p, \beta_q)) \neq -\infty, (A\hat{\rho}_p)_{TC^K(\beta_p, \beta_q)}
\end{equation}

\begin{equation}
\leq \sum_{k=1}^{[eK]-1} \left| \sup_{n_a \in I_k} p_{AA}(n_a, k) + \sup_{n_a \in I_k} p_{aA}(n_a, k) \right| \vec{E}[\hat{H}^{K}_k] + \sup_{n_a \in I_k} p_{AA}(n_a, k) \vec{E}[U^{K}_k] \leq \frac{e}{K} \sum_{k=1}^{[eK]-1} \frac{1}{k},
\end{equation}

for a finite $c$, which is of order $\log K/K$.

**Second step:** Then, we focus on the case where $\beta_p$ and $\beta_q$ are associated with an allele $a$ at coalescence time. The inclusion

\{ $N_a(\tau^K_C(\beta_p, \beta_q)) = k, (a\beta_p, a\beta_q)_{TC^K(\beta_p, \beta_q)} \subseteq \bigcup_{m=1}^{j^K} \{ T^{K,K}_C(\beta_p, \beta_q) = m, N_a(\tau^K_{m-1}) = k, (a\beta_p, a\beta_q)_m \}$,

and Equations (7.1) and (7.10) yield for every $k \in \{1, \ldots, [eK] - 1\}:

\begin{equation}
\hat{\phi}(N_a(\tau^K_C(\beta_p, \beta_q))) = k, (a\beta_p, a\beta_q)_{TC^K(\beta_p, \beta_q)} \leq \sup_{n_a \in I_k} p_{AA}(n_a, k) \vec{E}[U^{K}_k] \leq \frac{4}{s^2(\varepsilon)(k(k+1))},
\end{equation}

If $\beta_p$ and $\beta_q$ coalesce then undergo their first m-recombination when we look backward in time, and if the $\alpha$-population has the size $k$ at the coalescence time, it implies that the m-recombination occurs before the $\epsilon^K_k$-th jump when we look forward in time. For $k, l \leq [eK]$,

\begin{equation}
\hat{\phi}\left[ N_a(\tau^K_{TC(\beta_p)}) = l, 0 \leq T^{K,K}_C(\beta_p) \leq T^{K,K}_C(\beta_p, \beta_q), N_a(\tau^{K,K}_C(\beta_p, \beta_q)) = k, (a\beta_p, a\beta_q)_{TC^K(\beta_p, \beta_q)} \right] \leq \sup_{n_a \in I_k} p_{AA}(n_a, l) \left[ \eta_{k,l}(1) + \eta_{k,l}(U^{K}_l) \right] \leq \frac{2r_K}{(l+1)s^2(\varepsilon)} \left[ \frac{2s_K}{s^2(\varepsilon)(1-s(\varepsilon))} + 1 \right],
\end{equation}

where the last inequality is a consequence of (7.3), (7.9) and (7.10). The two last equations finally yield the existence of a finite $c$ such that for every $K \in \mathbb{N}$:

\begin{equation}
\hat{\phi}(0 \leq T^{K,K}_C(\beta_p) \leq T^{K,K}_C(\beta_p, \beta_q), (a\beta_p, a\beta_q)_{TC^K(\beta_p, \beta_q)}) \leq cr_K \sum_{k,l=1}^{[eK]} \frac{\eta_{k,l}(1) + \eta_{k,l}(U^{K}_l)}{k(k+1)(l+1)} \leq cr_K,
\end{equation}

which ends up the proof of Lemma 7.3 with Assumption 5. 

**7.4. Probability to be descended from the first mutant.** We want to estimate the probability for the neutral lineage of $\beta_p$ to undergo no m-recombination.

**Lemma 7.4.** There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $\varepsilon \leq \varepsilon_0$:

\begin{equation}
\limsup_{K \to \infty} \left| \hat{\phi}(T^{K,K}_C(\beta_p)) = -\infty \right| - \exp\left( -\frac{f(\varepsilon) \log K}{S_{\hat{\rho}_p}} \right) \leq c\varepsilon.
\end{equation}

**Proof.** We introduce $\hat{\rho}^K_{\alpha}$, the conditional probability that the neutral lineage of $\beta_p$ m-recombines at time $\tau^K_m$, given $(N_{\alpha}(\tau^K_n), N_{\alpha}(\tau^K_n), n \neq m)$ and given that it has not m-recombined during the time interval $[\tau^K_m, T^{K}_m)$. The last condition implies that $\beta_p$ is associated with an allele $a$ at time $\tau^K_m$.

\begin{equation}
\rho^K_m := \eta_{N_{\alpha}(\tau^K_m), N_{\alpha}(\tau^K_m)}(1) p_{aA}(N_{\alpha}(\tau^K_m), N_{\alpha}(\tau^K_m) - 1).
\end{equation}

We also introduce $\eta^K$, the sum of these conditional probabilities for $1 \leq m \leq j^K$:

\begin{equation}
\eta^K := \sum_{m=1}^{j^K} \rho^K_m.
\end{equation}

We want to give a rigorous meaning to the sequence of equivalents:

\begin{equation}
\hat{\phi}\left( T^{K,K}_C(\beta_p) = -\infty \right) \left( N_{\alpha}(\tau^K_m), N_{\alpha}(\tau^K_m) \right) \leq j^K \prod_{m=1}^{j^K} (1 - \rho^K_m) \sim \prod_{m=1}^{j^K} \exp(-\rho^K_m) \sim \exp(-\eta^K).
\end{equation}
when \( K \) goes to infinity. Jensen and Triangle inequalities and the Mean Value Theorem imply

\[
\hat{\mathbb{E}} \left[ \frac{1}{2} \right] \mid \beta_p \mid = -\infty \mid (N_A(\tau^K_m), N_a(\tau^K_m))_{m \leq k^*} \mid - e^{-\frac{\alpha_{rK} \log K}{\alpha_A}} \mid \leq \sum_{k=1}^{\lfloor \varepsilon \rfloor} \sup_{n_a \in l_k^*} \left( p^{\beta_p}(n_A, k) \right)^2 \hat{\mathbb{E}}[U^K_k] \leq \frac{\pi^2 r^2 K}{30^2 (\varepsilon)},
\]

where \( I^K_k \) has been defined in (3.10) and the last inequality follows from (7.3) and (7.10). To bound the second term, we need to estimate \( \hat{\mathbb{E}}[\eta^K] \). Inequality (7.3) implies

\[
\left( 1 - \varepsilon \right) r^K K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{U^K_k}{k + 1} \leq \eta^K \leq r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{U^K_k}{k + 1}.
\]

Adding (7.11) we get that for \( \varepsilon \) small enough,

\[
\limsup_{K \to \infty} \left| \exp(-\hat{\mathbb{E}}[\eta^K]) - \exp \left(-\frac{r^K \alpha_{rK} \log K}{S_{aA}} \right) \right| \leq c \varepsilon.
\]

The bounding of the last term of (7.13) requires a fine study of dependences between upcrossing numbers before and after the last visit to a given integer by the mutant population size. In particular, we widely use Equation (7.10). We observe that \( \hat{\mathbb{E}}[\eta^K - \hat{\mathbb{E}}[\eta^K]] \leq (\hat{\text{Var}}[\eta^K])^{1/2} \), but the variance of \( \eta^K \) is quite involved to study and according to Assumption 5 and Equations (7.15) and (7.10),

\[
\left| \hat{\text{Var}}[\eta^K] - \hat{\text{Var}} \left( r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{U^K_k}{k + 1} \right) \right| \leq c \varepsilon \hat{\mathbb{E}} \left[ r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{U^K_k}{k + 1} \right] \leq c \varepsilon r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{1}{k + 1} \frac{1}{(k + 1)(l + 1)} \leq c \varepsilon,
\]

for a finite \( c \). Let \( k \leq l < [\varepsilon K] \), and recall that by definition, \( U^K_l = U^K_{l,1} + U^K_{l,2} \). Then we have

\[
\hat{\text{Cov}}(U^K_l, U^K_l) \leq \hat{\mathbb{E}}[(U^K_l)^2] \hat{\mathbb{E}}[(U^K_{l,1})^2]^{1/2} + \left| \hat{\text{Cov}}(U^K_l, U^K_{l,2}) \right|.
\]

Applying Inequalities (7.9) and (7.10) and noticing that \( (1 - s_\varepsilon) ) \leq \lambda_{l,1/2} < 1 \) (see proof of Lemma 7.2 in Appendix B) lead to

\[
\hat{\text{Cov}}(U^K_l, U^K_l) \leq c(\lambda_{l,1/2}^{l-k} + \varepsilon + (1 - s_\varepsilon)^{(l-k)}) \leq c(\lambda_{l,1/2}^{l-k} + \varepsilon)
\]

for a finite \( c \). We finally get:

\[
\hat{\text{Var}} \left( r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{U^K_k}{k + 1} \right) \leq 2r^K \sum_{k=1}^{\lfloor \varepsilon \rfloor} \frac{1}{k + 1} \sum_{l=k}^{\lfloor \varepsilon \rfloor} \frac{\hat{\text{Cov}}(U^K_l, U^K_l)}{l + 1} + \varepsilon \leq cr^K \varepsilon \log^2 K,
\]

where we used (7.18) for the second inequality. Applying Jensen’s Inequality to the left hand side of (7.13) and adding Equations (7.14), (7.16), (7.17) and (7.19) complete the proof of Lemma 7.4. \( \square \)

We finally focus on the dependence between genealogies of \( \beta_p \) and \( \beta_q \). Following [28] pp. 1622 to 1624 in the case \( J = 1 \), we can prove that for \( d \) in \( [0, 1, 2] \),

\[
\limsup_{K \to \infty} \left| \hat{\mathbb{P}}(\mathcal{V}_{TR^K_p} \cap \mathcal{V}_{TR^K_p}^c = 0) + \hat{\mathbb{P}}(\mathcal{V}_{TR^K_q} \cap \mathcal{V}_{TR^K_q}^c = 0) = d \right| \leq \left( 1 - e^{-\frac{\alpha_{rK} \log K}{\alpha_A}} \right) d \left( e^{-\frac{\alpha_{rK} \log K}{\alpha_A}} \right)^{-2 - d} \leq c \varepsilon.
\]
In particular we use here the weak dependence between two neutral lineages stated in Lemma 7.3 and the probability to descend from the first mutant for $\beta_p$ and $\beta_q$ obtained in Lemma 7.4.

7.5. **Neutral proportion at time** $T^K_\varepsilon$. According to Lemma 7.3 and Equation (7.20), it is enough to distinguish two cases for the randomly chosen neutral allele $\beta_p$: either its lineage has undergone one m-recombination, or no m-recombination. In the second case, $\beta_p$ is a $b_1$. In the first one, the probability that $\beta_p$ is a $b_1$ depends on the neutral proportion in the $A$ population at the coalescence time. We now state that this proportion stays nearly constant during the first period.

**Lemma 7.5.** There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $\varepsilon \leq \varepsilon_0$,

$$\limsup_{K \to \infty} \mathbb{P} \left( \sup_{t \in T^K_\varepsilon} \left| P^K_{A,b_1}(t) - \frac{Z_{Ab_1}}{Z_A} \right| > \sqrt[3]{\varepsilon}, T^K_\varepsilon < \infty \right) \leq c \varepsilon^{1/3}.$$

Lemma 7.5 whose proof is postponed to Appendix B, allows us to state the following lemma.

**Lemma 7.6.** There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $\varepsilon \leq \varepsilon_0$,

$$\limsup_{K \to \infty} \mathbb{P} \left( \left| P^K_{A,b_2}(T^K_\varepsilon) - \left( 1 - \exp \left( - \frac{f_a r_K \log K}{S_{aA}} \right) \right) \frac{Z_{Ab_2}}{Z_A} \right| > \varepsilon^{1/3} \right) \leq c \varepsilon^{1/3}.$$

**Proof.** $\beta_i, i \leq \varepsilon K \}$ denotes the neutral alleles carried by the $a$-individuals at time $T^K_\varepsilon$ and $A^K_2(i) := \{\beta_i \text{ has undergone exactly one m-recombination and is an allele } b_2\}$. If $\beta_i$ is a $b_2$, either its genealogy has undergone one m-recombination with an individual $Ab_2$, either it has undergone more than two m-recombinations. Thus

$$0 \leq N^K_{a,b_2}(T^K_\varepsilon) - \sum_{i=1}^{\lfloor \varepsilon K \rfloor} A^K_2(i) \leq \sum_{i=1}^{\lfloor \varepsilon K \rfloor} \mathbb{I}_{TR^K_\varepsilon(\beta_i) \neq -\infty}.$$

Moreover, the probability of $A^K_2(i)$ depends on the neutral proportions in the $A$-population when $\beta_i$ m-recombines. For $i \leq \lfloor \varepsilon K \rfloor$,

$$\limsup_{K \to \infty} \mathbb{P} \left( \mathbb{I}_{[P^K_{A,b_2}(T^K_\varepsilon)]} \geq 0, TR^K_2(\beta_i) = -\infty, \sup_{t \in T^K_\varepsilon} \left| P^K_{A,b_1}(t) - \frac{Z_{Ab_1}}{Z_A} \right| \leq \sqrt[3]{\varepsilon}, \frac{Z_{Ab_2}}{Z_A} \leq \sqrt[3]{\varepsilon} \right) \leq c \varepsilon^{1/3}.$$

Lemma 7.5 and Equation (A.5) ensure that $\limsup_{K \to \infty} \mathbb{P} \left( \sup_{t \in T^K_\varepsilon} \left| P^K_{A,b_2}(t) - \frac{Z_{Ab_2}}{Z_A} \right| > \sqrt[3]{\varepsilon} \right) \leq c \varepsilon^{1/3}$, and Lemmas 7.3 and 7.4 that $\sqrt[3]{\varepsilon} \leq c \varepsilon^{1/3}$. It yields:

$$\limsup_{K \to \infty} \mathbb{P} \left( \mathbb{I}_{[P^K_{A,b_2}(T^K_\varepsilon)]} \geq 0, TR^K_2(\beta_i) = -\infty, \sup_{t \in T^K_\varepsilon} \left| P^K_{A,b_1}(t) - \frac{Z_{Ab_1}}{Z_A} \right| \leq \sqrt[3]{\varepsilon}, \frac{Z_{Ab_2}}{Z_A} \leq \sqrt[3]{\varepsilon} \right) \leq c \varepsilon^{1/3}$$

for a finite $c$. Adding (7.21) we get:

$$\limsup_{K \to \infty} \mathbb{E} \left[ \mathbb{I}_{[P^K_{a,b_2}(T^K_\varepsilon)]} \left( 1 - \exp \left( - f_a r_K \log K / S_{aA} \right) \right) (1 - \frac{Z_{Ab_2}}{Z_A}) \right] \leq c \sqrt{\varepsilon}.$$

In the same way, using the weak dependence between lineages stated in (7.20), we prove that

$$\limsup_{K \to \infty} \mathbb{E} \left[ \left| P^K_{a,b_2}(T^K_\varepsilon) \right| (1 - \exp \left( - f_a r_K \log K / S_{aA} \right))^2 (1 - \frac{Z_{Ab_2}}{Z_A})^2 \right] \leq c \sqrt{\varepsilon}. $$

This implies, adding (7.22) that

$$\limsup_{K \to \infty} \mathbb{E} \mathbb{V} \left[ P^K_{a,b_2}(T^K_\varepsilon) \right] \leq c \sqrt[3]{\varepsilon}. $$

We end the proof by using Chebyshev’s Inequality.

7.6. **Second and third periods.** Now we prove that during the second period the neutral proportion in the $A$ population remains nearly constant. This is due to the short duration of this period, which does not go to infinity with the carrying capacity $K$.

**Lemma 7.7.** There exist two positive finite constants $c$ and $\varepsilon_0$ such that for $\varepsilon \leq \varepsilon_0$,

$$\limsup_{K \to \infty} \mathbb{P} \left( \sup_{t \in T^K_\varepsilon} \left| p^K_{A,b_1}(t) - P^K_{A,b_1}(T^K_\varepsilon) \right| > \varepsilon^{1/3} \right) \leq c \varepsilon^{1/3}.$$
Proof. Let us introduce the stopping time $V^K_K$: 
\[ V^K_K := \inf \{ t \geq 0, \sup_{s \leq t} \mathbb{E}\{ \epsilon | M^K_a(T^K_a + t) - M^K_a(T^K_a) | > \sqrt{\epsilon} \} \}. \]

Recall the definition of $t^*_K$ in (6.6) and that $(\mathcal{F}^K_t, t \geq 0)$ denotes the canonical filtration of $N^K$. Strong Markov property, Doob's Maximal Inequality and Equation (3.12) yield:
\[ \mathbb{P}\{ T^K_t \leq \tilde{T}^K_t, \sup_{s \leq \tilde{T}^K_t} | M^K_a(T^K_a + s) - M^K_a(T^K_a) | > \sqrt{\epsilon} \} \]
\[ = \mathbb{E}\{ \mathbb{E}\{ | M^K_a(T^K_a + s) - M^K_a(T^K_a) | > \sqrt{\epsilon} | \mathcal{F}^K_t \} \} \leq \frac{c(\epsilon)}{\epsilon^K}, \]

where $c(\epsilon)$ is finite. But according to Equation (2.5) with $\delta = \epsilon^3$, \( \lim \sup_{K \to \infty} \mathbb{P}\{ V^K_t < \epsilon^K | T^K_t \leq \tilde{T}^K_t \} = 0 \). Moreover, Equations (3.1) and (3.3) imply for every $t \geq 0$
\[ \sup_{s \leq \tilde{T}^K_t} | P^K_a(T^K_a + s) - P^K_a(T^K_a) | \leq \sup_{s \leq \tilde{T}^K_t} | M^K_a(T^K_a + s) - M^K_a(T^K_a) | + r_K t^*_K. \]

As $r_K$ goes to 0 under Assumption 5, we finally get:
\[ \lim_{K \to \infty} \mathbb{P}\{ \sup_{s \leq \tilde{T}^K_t} | P^K_a(T^K_a + s) - P^K_a(T^K_a) | > \sqrt{\epsilon}, T^K_t \leq \tilde{T}^K_t \} = 0. \]

Adding Lemma 4.3 ends the proof of Lemma 7.7.

7.7. End of the proof of Theorem 2 in the weak recombination regime. Thanks to Lemmas 7.6 and 7.7 we get that for $\epsilon$ small enough,
\[ \lim_{K \to \infty} \mathbb{P}\{ \sup_{s \leq \tilde{T}^K_t} | P^K_a(T^K_a + s) - P^K_a(T^K_a) | > \sqrt{\epsilon}, T^K_t \leq \tilde{T}^K_t \} = 0. \]

APPENDIX A. TECHNICAL RESULTS

We first present some results stated in [5]. We recall Definitions (2.8), (2.9), (4.7), (4.8), (3.11) and (6.6) and that the notation $K$ refers to processes that satisfy Assumption 3. Proposition 2 is a direct consequence of Equations (42), (71), (72) and (74) in [5]:

Proposition 2. There exist two positive finite constants $M_1$ and $\epsilon_0$ such that for every $\epsilon \leq \epsilon_0$
\[ \lim_{K \to \infty} \mathbb{P}\{ | N^K(T_{ext}) - K \bar{N}_a | > \epsilon K | \text{Fix}^K \} = 0, \quad \text{and} \quad \lim_{K \to \infty} \mathbb{P}\{ T^K_t < \epsilon^K \} - \frac{S_{aA}}{f_a} \leq M_1 \epsilon. \]

Moreover there exists $M_2 > 0$ such that for every $\epsilon \leq \epsilon_0$, the probability of the event
\[ F^K_\epsilon = \{ T^K_t \leq \tilde{T}^K_t, N^K_A(T^K_a + t) < \frac{\epsilon^2 K}{2}, | N^K_a(T^K_a + t) - \bar{N}_a | < \frac{\epsilon K}{2} \} \]
 satisfies
\[ \lim_{K \to \infty} \mathbb{P}\{ F^K_\epsilon \} \geq \lim_{K \to \infty} \mathbb{P}\{ F^K_\epsilon \} \geq \frac{S_{aA}}{f_a} - M_2 \epsilon, \]

and if $z \in \Theta$, then there exist $V > 0$ and $c < \infty$ such that:
\[ \lim_{K \to \infty} \mathbb{P}(S^K(z) > e^{VK}) \geq 1 - \epsilon c. \]
Thanks to these results we can state the following Lemma, which allows us to focus on the event \( T^K_e \leq \tilde{T}^K_e \) rather than on \( \text{Fix}^K \) in Section 7.

**Lemma A.1.** There exist two positive finite constants \( c \) and \( \varepsilon_0 \) such that for every \( \varepsilon \leq \varepsilon_0 \)
\[
\limsup_{K \to \infty} \mathbb{P}(T^K_e < \infty, \tilde{T}^K_e > \tilde{T}^K_e) \leq c \varepsilon,
\]
and
\[
\limsup_{K \to \infty} \left[ \mathbb{P}([T^K_e \leq \tilde{T}^K_e] \setminus \text{Fix}^K) + \mathbb{P}(\text{Fix}^K \setminus [T^K_e \leq \tilde{T}^K_e]) \right] \leq c \varepsilon.
\]

**Proof.** From Equation (A.1), we deduce that for \( \varepsilon < \tilde{n}_d/2 \)
\[
\lim_{K \to \infty} \mathbb{P}(T^K_e = \infty | \text{Fix}^K) \leq \lim_{K \to \infty} \mathbb{P}\left( \left| N^K_d(T^{\text{ext}}_e) - K\tilde{n}_d \right| > \varepsilon K | \text{Fix}^K \right) = 0.
\]
Adding (2.15) we get that \( \lim_{K \to \infty} \mathbb{P}(T^K_e = \infty, \text{Fix}^K) = 0 \). The equality
\[
\mathbb{P}(T^K_e < \infty, T^K_e > \tilde{T}^K_e) = \mathbb{P}(T^K_e < \infty) + \mathbb{P}(T^K_e > \tilde{T}^K_e) - \mathbb{P}(T^K_e = \infty, \text{Fix}^K)
\]
with Equations (A.1) and (A.3) ends the proof of (A.5). From Equation (2.14) we deduce that \( \lim_{K \to \infty} \mathbb{P}(\text{Fix}^K | T^K_e \leq \tilde{T}^K_e) = 1 \). We end the proof of (A.6) thanks to Equations (A.7) and (A.5).

We also recall some results on birth and death processes which proofs can be found in Equations 3.1 in [28] and in [1] p 109 and 112.

**Proposition 3.** Let \( Z = (Z_t)_{t \geq 0} \) be a birth a death process with birth and death rates \( b \) and \( d \). For \( i \in \mathbb{Z}^+ \), \( T_i = \inf\{t \geq 0 : Z_t = i\} \) and \( \mathbb{P}_i \) (resp. \( \mathbb{E}_i \)) is the law (resp. expectation) of \( Z \) when \( Z_0 = i \). Then
- For \( i \in \mathbb{N} \) and \( t \geq 0 \),
  \[
  \mathbb{E}_i(Z_t) = i e^{(b - d) t}.
  \]
- For \( (i, j, k) \in \mathbb{Z}_+^3 \) such that \( j \in (i, k) \),
  \[
  \mathbb{P}_i(T_k < T_j) = \frac{1 - (d/b)^{j-i}}{1 - (d/b)^{k-i}}.
  \]
- If \( 0 < d < b \) for every \( i \in \mathbb{Z}^+ \) and \( t \geq 0 \),
  \[
  \mathbb{P}_i(T_0 \leq t) = \left( \frac{d(1 - e^{(d-b)t})}{b - d e^{(d-b)t}} \right)^i.
  \]
- If \( 0 < d < b \), on the non-extinction event of \( Z \), which has a probability \( 1 - (d/b)^{2\tilde{n}} \), the following convergence holds:
  \[
  T_N / \log N \to (1 - d/b)^{-1}, \text{ a.s.}
  \]
For \( 0 < s < 1 \), if \( \tilde{Z}^{(s)} \) denotes a random walk with jumps \( \pm 1 \) where up jumps occur with probability \( 1/(2-s) \) and down jumps with probability \( (1-s)/(2-s) \), we denote by \( \mathbb{P}^{(s)}_i \) the law of \( \tilde{Z}^{(s)} \) when the initial state is \( i \in \mathbb{N} \) and introduce for every \( a \in \mathbb{R}_+ \), the stopping time
\[
\tau_a := \inf\{n \in \mathbb{Z}_+ : \tilde{Z}_n^{(s)} = |a|\}.
\]
We also introduce for \( \varepsilon \) small enough and \( 0 \leq j, k < |\varepsilon K| \), the quantities
\[
q^{(s_1, s_2)}_{j, k} := \frac{\mathbb{P}^{(s_1)}_{k+1}(\tilde{T} \leq \tau_k)}{\mathbb{P}^{(s_1)}_{k+1}(\tilde{T} < \tau_j)} = \frac{s_1}{1 - (1 - s_1)^{|\varepsilon K| - j}} \frac{1 - (1 - s_2)^{|\varepsilon K| - j}}{1 - (1 - s_2)^{|\varepsilon K| - j}} - s_1, 0 < s_1, s_2 < 1,
\]
whose expressions are direct consequences of (A.9). Let us now state two technical results. The first one is necessary to get Lemma 7.5. The second one helps us to control upcrossing numbers of the process \( N^K_a \) before reaching the size \( |\varepsilon K| \).
Lemma A.2. • Let $D, C, F, G$ and $H$ be measurable events such that $D \subset C \subset F$. Then we have $P(\mathcal{H} \cap (C \cup D)) - P(\mathcal{H} \cap D) \leq P(\mathcal{F}) - P(D) + P(\mathcal{G} \setminus C)$.

- For $a \in [0,1/2]$, $(s_1, s_2) \in [a, 1 - a]^2$, and $0 \leq j \leq k < \lfloor eK \rfloor$,

$$q_{0,k}^{(s_1, s_2)} \geq s_1 \wedge s_2 \quad \text{and} \quad \left| \frac{1}{q_{k,l}^{(s_1, s_2)}} - \frac{1}{q_{j,l}^{(s_2, s_1)}} \right| \leq \frac{2(1 + 1/s_2)}{ea^l \log(1 - a)} |s_2 - s_1| + \frac{1 - s_2^{l+1-k}}{s_2^2}.$$  

(A.14)

**Proof.** The proof of the first result is left to the reader. The first part of (A.14) is a direct consequence of Definition (A.13). Let $a$ be in $[0,1/2]$ and consider functions $f_{a,\beta} : x \mapsto (1 - x^\alpha)/(1 - x^\beta)$, $(a, \beta) \in \mathbb{N}^2$, $a \in [a, 1 - a]$. Then for $x \in [a, 1 - a]$,

$$\|f_{a,\beta}\|_{\infty} \leq 2(ea^2 \log(1 - a))^{-1}.$$  

From Equation (A.9), we get for $0 < s < 1$ and $0 \leq j < \lfloor eK \rfloor$,

$$\left| P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j) - P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j) \right| = \frac{(1 - (1 - s)k^{-j})(1 - (1 - s)k^{-j} - (1 - s)\lfloor eK \rfloor^{-j})}{(1 - (1 - s)\lfloor eK \rfloor^{-j})(1 - (1 - s)\lfloor eK \rfloor^{-j})} \leq (1 - s)^{l+1-k} s^{-2}.$$  

(A.16)

Triangle Inequality leads to:

$$\left| \frac{1}{q_{k,l}^{(s_1, s_2)}} - \frac{1}{q_{j,l}^{(s_2, s_1)}} \right| = \left| \frac{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_k)}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} - \frac{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_k)}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} \right| \leq \left| \frac{1}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} - \frac{1}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} \right| \left| P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_k) \right|$$

$$+ \left| \frac{1}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} - \frac{1}{P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_j)} \right| \left| P^{(s)}_{l+1}(\tau_{\lfloor eK \rfloor} < \tau_k) \right|$$

Noticing that $P_{l+1}^{(s_1)}(\tau_{\lfloor eK \rfloor} < \tau_j)$ $\geq P_{l+1}^{(s_2)}(\tau_{\lfloor eK \rfloor} < \tau_j)$ $= P_{l+1}^{(s_2)}(\tau_\infty < \tau_0) = s_2$, and using (A.16) and the Mean Value Theorem with (A.15), we get the second part of (A.14). \( \square \)

**APPENDIX B. PROOFS OF LEMMAS 7.2 AND 7.5**

**Proof of Equation (7.10).** In the whole proof, the integer $n_\alpha$ denotes the state of $N_\alpha$ at some time smaller than $T^K_\alpha$ and thus belongs to $I^K_\alpha$ which has been defined in (3.10). $P_{(n_\alpha, n_a)}$ (resp. $\hat{P}_{(n_\alpha, n_a)}$) denotes the probability $P$ (resp. $\hat{P}$) when $(N_\alpha(0), N_a(0)) = (n_\alpha, n_a) \in \mathbb{Z}_+^2$. We introduce for $u \in \mathbb{R}_+$ the hitting time of $[u]$ by the process $N_\alpha$:

$$\sigma^K_\alpha = \inf\{t \geq 0, N^K_\alpha(t) = [u] \}.$$  

(B.1)

Let $(i, j, k)$ be in $\mathbb{Z}_+^3$ with $j < k < \lfloor eK \rfloor$. Between jumps $\zeta^K_\alpha$ and $J^K$ the process $N_a$ necessarily jumps from $k$ to $k + 1$. Then, either it reaches $\lfloor eK \rfloor$ before returning to $k$, either it again jumps from $k$ to $k + 1$ and so on. Thus we approximate the probability that there is only one jump from $k$ to $k + 1$ by comparing $U^{(k,2)}_{j,k}$ with geometrically distributed random variables. As we do not know the value of $N_\alpha$ when $N_a$ hits $k + 1$ for the first time, we take the maximum over all the possible values in $I^K_\alpha$. Recall Definition (5.5). We get:

$$\hat{P}(U^{(k,2)}_{j,k} = 1|U^K_j = i) = \sup_{n \in \mathbb{N}} \hat{P}_{(n_\alpha, n_a)}(T^K_\alpha < \sigma^K_\alpha|T^K_\alpha < \sigma^K_\alpha, U^K_j = i)$$

$$= \sup_{n \in \mathbb{N}} \hat{P}_{(n_\alpha, n_a)}(T^K_\alpha < \sigma^K_\alpha|T^K_\alpha < \sigma^K_\alpha, U^K_j = i, I^K_\alpha, \mathcal{H}^K_\alpha).$$
The value of $U^K_j$ is correlated with the value of $N_A$ when $N_a$ hits $k + 1$. But here we take the maximum over all the possible values of $N_A$. Hence the value of $U^K_j$ has no influence on the last probability and we can ignore it. We thus obtain the inequality:

$$
\hat{\Pr}(U^{(K,2)}_{j,k} = 1 | U^K_j = i) \leq \sup_{n,a \in I^K} \frac{\Pr^{(n,a,k+1)}(T^K_e < \sigma^K_k \mid \mathcal{L}^K_e, \mathcal{H}^K_e)}{\Pr^{(n,a,k+1)}(T^K_e < \sigma^K_j \mid \mathcal{L}^K_e, \mathcal{H}^K_e)}.
$$

Definition (5.5) allows us to compare these conditional probabilities with the probabilities of the same events under $\Pr^{(s_+ \epsilon,c)}$ and $\Pr^{(s_- \epsilon,c)}$, namely sup $\Pr^{(n,a,k+1)}(T^K_e < \sigma^K_k \mid \mathcal{L}^K_e, \mathcal{H}^K_e) \leq \Pr^{(s_+ \epsilon,c)}(T^K_e < \tau_k)$, and inf $\Pr^{(n,a,k+1)}(T^K_e < \sigma^K_j \mid \mathcal{L}^K_e, \mathcal{H}^K_e) \geq \Pr^{(s_- \epsilon,c)}(T^K_e < \tau_j)$. Then

$$
\hat{\Pr}(U^{(K,2)}_{j,k} = 1 | U^K_j = i) \leq \frac{\Pr^{(s_+ \epsilon,c)}(T^K_e < \tau_k)}{\Pr^{(s_- \epsilon,c)}(T^K_e < \tau_j)} = q^{(s_+ \epsilon,c,s_- \epsilon,c)}_{j,k}.
$$

In an analogous way we show that $\hat{\Pr}(U^{(K,2)}_{j,k} = 1 | U^K_j = i) \geq q^{(s_+ \epsilon,c,s_- \epsilon,c)}_{j,k}$. We deduce that we can construct two geometrically distributed random variables $G_1$ and $G_2$, possibly on an enlarged space, with respective parameters $q^{(s_+ \epsilon,c,s_- \epsilon,c)}_{j,k}$, and construct two random variables $G_1' \overset{d}{=} G_1$ and $G_2' \overset{d}{=} G_2$ such that

$$
G_1 \leq U^{(K,2)}_{j,k} \leq G_2.
$$

For the same reasons we obtain $q^{(s_+ \epsilon,c,s_- \epsilon,c)}_{j,k} \leq \hat{\Pr}(U^{(K,2)}_{j,k} = 1) \leq q^{(s_+ \epsilon,c,s_- \epsilon,c)}_{j,k}$, and again we can construct two random variables $G_1' \overset{d}{=} G_1$ and $G_2' \overset{d}{=} G_2$ such that

$$
G_1' \leq U^{(K,2)}_{j,k} \leq G_2'.
$$

Recall that $U_{0,k} = U^K_k$. Hence taking $j = 0$ and adding the first part of Equation (A.14) give the first inequality of (7.10). According to Definition (5.1), for $\epsilon$ small enough, $|s_+ \epsilon - s_- \epsilon| \leq \epsilon c$ for a finite $c$. Hence Equations (B.2), (B.3) and (A.14) entail the existence of a finite $c$ such that for $\epsilon$ small enough $|\hat{E}[U^{(K,2)}_{j,k}] | U^K_j = i) - \hat{E}[U^{(K,2)}_{j,k}] | U^K_j = i) | \leq \epsilon c + (1 - s_- \epsilon)^{k+1-j}/s^2_\epsilon$. Thus according to the first part of Equation (7.10),

$$
\left| \hat{\text{Cov}}(U^{(K,2)}_{j,k}, U^K_j) \right| \leq \sum_{i \in \mathbb{N}^a} i \hat{\Pr}(U^K_j = i) \left| \hat{E}[U^{(K,2)}_{j,k}] | U^K_j = i) - \hat{E}[U^{(K,2)}_{j,k}] | U^K_j = i) \right| \leq \frac{2}{s^2_\epsilon} \left( \epsilon c + \frac{(1 - s_- \epsilon)^{k+1-j}}{s^2_\epsilon} \right),
$$

where we use that $U^K_j \leq (U^K_j)^2$. This ends up the proof of (7.10).

**Proof of Equation (7.9).** Definitions (2.3) and (5.5) ensure that if $n,a \in I^K$,

$$
\hat{\Pr}_{\langle n,a,k \rangle}(N_a(d t) = k + 1) = \frac{\Pr^{(n,a,k)}(T^K_e < \infty \mid N_a(d t) = k + 1, \mathcal{L}^K_e, \mathcal{H}^K_e)}{\Pr^{(n,a,k)}(T^K_e < \infty \mid \mathcal{L}^K_e, \mathcal{H}^K_e)} = \frac{\Pr^{(s_+ \epsilon,c)}(T^K_e < \tau_0)}{\Pr^{(s_- \epsilon,c)}(T^K_e < \tau_0)} f_a k(d t + o(d t))
$$

$$
= \frac{1 - (1 - s_- \epsilon)^{k+1}}{1 - (1 - s_- \epsilon)^{\epsilon K}} f_a k(d t + o(d t)) \geq s^2_\epsilon f_a k(d t + o(d t)),
$$
and
\[
\hat{p}_{(n_\varepsilon,k)}(N_{nA}(dt) \neq n_A) \leq \frac{P_{(n_\varepsilon,k)}[N_{nA}(dt) \neq n_A| \mathcal{G}_d]}{P_{(n_\varepsilon,k)}[N_{nA}(dt) \neq n_A| \mathcal{H}_d]} \\
\leq (1 + ce)2f_{\varepsilon}n_AK(dt + o(dt)).
\]

for a finite \(c\), where we use (A.9) and that \(D_{A} + C_{A,A}n_A = f_{A}\). Thus for \(\varepsilon\) small enough:
\[
\hat{p}(N_{\varepsilon}(t_{k+1}^+) \neq N_{\varepsilon}(t_{k}^+)|N_{\varepsilon}(t_{k}^+) = k) \geq \frac{s_{\varepsilon}^2(\varepsilon)f_{\varepsilon}k}{3f_{\varepsilon}n_AK}.
\]

If \(D^K_k\) denotes the downcrossing number from \(k\) to \(k - 1\) before \(T^K_{\varepsilon}\), then under the probability \(\hat{p}\), we can bound \(U^K_{\varepsilon} + D^K + H^K_{\varepsilon}\) by the sum of \(U^K_{\varepsilon} + D^K\) independent geometrically distributed random variables \(G^K\) with parameter \(s_{\varepsilon}^2(\varepsilon)f_{\varepsilon}k/3f_{\varepsilon}n_AK\) and \(H^K_{\varepsilon} \leq \sum_{1 \leq i < 0}U^K_{\varepsilon} + D^K(G^K - 1)\). Let us notice that if \(k \geq 2\), \(D^K_{k-1} = U^K_{k-1} - 1\), and \(D^K_1 = 0\). Using the first part of (7.10) twice we get
\[
\mathbb{E}[H^K_{\varepsilon}] \leq \left(\frac{4}{s_{\varepsilon}^2(\varepsilon)} - 1\right)\left(\frac{3f_{\varepsilon}n_AK}{s_{\varepsilon}^2(\varepsilon)f_{\varepsilon}k - 1}\right),
\]
which ends up the proof of the first inequality in (7.9).

As the mutant population size is not Markovian we cannot use symmetry and Strong Markov property to control the dependence of jumps before and after the last visit to a given state as in [28]. Hence we describe the successive excursions of \(N_{nA}(\varepsilon)\) above a given level to get the last inequality in (7.9). Let \(U_{j,k}(i)\) be the number of jumps from \(k\) to \(k + 1\) during the \(i\)th excursion above \(j\). We first bound the expectation \(\mathbb{E}[(U_{j,k}(i))^2]\). During an excursion above \(j\), \(N_{\varepsilon}\) hits \(j + 1\), but we do not know the value of \(N_{\varepsilon}\) at this time. Thus we take the maximum value for the probability when \(n_A\) belongs to \(I_{\varepsilon}^K\), and \(\hat{p}(U_{j,k}(i) \geq 1) \leq \sup_{n_A \in I_{\varepsilon}^K} \hat{p}(j+1,n_A)|\sigma_{k+1}^j < \sigma_j^K < T^K_{\varepsilon})\). Then using Coupling (5.3) and Definitions (5.4) and (5.5) we obtain
\[
\hat{p}(U_{j,k}(i) \geq 1) \leq \sup_{n_A \in I_{\varepsilon}^K} \frac{P_{(j+1,n_A)}(T^K_{\varepsilon} < \infty|\sigma_{k+1}^j < \sigma_j^K < T^K_{\varepsilon}, \mathcal{G}_d^K, \mathcal{H}_d^K)}{P_{(j+1,n_A)}(T^K_{\varepsilon} < \infty|\sigma_{k+1}^j < \sigma_j^K < T^K_{\varepsilon}, \mathcal{G}_d^K, \mathcal{H}_d^K)} \\
\leq \frac{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{\varepsilon} < \tau_j^0)}{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{\varepsilon} < \tau_j^0)}\frac{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{k+1}^j < \tau_{j+1}^j)}{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{k+1}^j < \tau_{j+1}^j)} \\
\leq \frac{(1 - s_{\varepsilon}(\varepsilon))^{k+1-j}}{s_{\varepsilon}(\varepsilon)(1 - s_{\varepsilon}(\varepsilon))}.
\]

Moreover if \(U_{j,k}(i) \geq 1\), \(N_{\varepsilon}\) necessarily hits \(k\) after its first jump from \(k\) to \(k + 1\), and before its return to \(j\). Using the same techniques as before we get:
\[
\hat{p}(U_{j,k}(i) = 1|U_{j,k}(i) \geq 1) \geq \inf_{n_A \in I_{\varepsilon}^K} \hat{p}(n_A,k)|\sigma_j^K < \sigma_{k+1}^j < T^K_{\varepsilon}) \geq \frac{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{\varepsilon} < \tau_j^0)}{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{\varepsilon} < \tau_j^0)}\frac{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{k+1}^j < \tau_{j+1}^j)}{P_{j}(s_{\varepsilon}(\varepsilon)|\tau_{k+1}^j < \tau_{j+1}^j)},
\]
which yields
\[
\hat{p}(U_{j,k}(i) = 1|U_{j,k}(i) \geq 1) \geq s_{\varepsilon}(\varepsilon)s_{\varepsilon}(\varepsilon)(1 - s_{\varepsilon}(\varepsilon))^{k-j} \geq s_{\varepsilon}(\varepsilon)(1 - s_{\varepsilon}(\varepsilon))^{k-j}.
\]
Furthermore, given that $\tilde{U}_{j,k}^{(i)}$ is non-null, $\tilde{U}_{j,k}^{(i)}$ is smaller than a geometrically distributed random variable with parameter $q = \frac{1}{2}(1 - s_+(e)/(1 - s_-(e)))^{k-j}$. In particular,

$$\mathbb{E}\left[(\tilde{U}_{j,k}^{(i)})^2\right] \leq \frac{2}{q^2} \frac{2}{s'_e(e)(1 - s_+(e))} \leq \left(\frac{1 - s_+(e)}{1 - s_-(e)}\right)^{2(k-j)}.$$

Adding Equations (B.5) and recalling that $|s_+(e) - s_-(e)| \leq \epsilon$ for $c$ finite and $\epsilon$ small enough yield

$$\mathbb{E}\left[(O_{j,k}^{(i)})^2\right] \leq \frac{2\lambda_{\epsilon}^{k-j}}{s'_e(e)(1 - s_+(e))}, \quad \text{where} \quad \lambda_{\epsilon} := \frac{(1 - s_+(e))^3}{(1 - s_-(e))^2} < 1.$$

Using that for $n \in \mathbb{N}$ and $(x_i, 1 \leq i \leq n) \in \mathbb{R}^n$, $(\sum_{1 \leq i \leq n} x_i)^2 \leq n^2 \sum_{1 \leq i \leq n} x_i^2$ and that the number of excursions above $j$ before $T^K_j$ is $U_j^K - 1$, we get

$$\mathbb{E}\left[(U_j^{(i)})^2\right] \leq \mathbb{E}\left[|U_j^K - 1|\right] \frac{2\lambda_{\epsilon}^{k-j}}{s'_e(e)(1 - s_+(e))} \leq \frac{4\lambda_{\epsilon}^{k-j}}{s'_e(e)(1 - s_+(e))},$$

where we use the first part of Equation (7.10). This ends the proof of Equation (7.9). \hfill \square

**Proof of Equation (7.11).** Definition (A.13), Inequality (B.3) and Equation (A.9) yield:

$$r_K \sum_{k=1}^{[\epsilon K]} \frac{\mathbb{E}[U^K_j]}{k + 1} \geq r_K \sum_{k=1}^{[\epsilon K]} \left(\frac{k+1}{s'_e(e)(1 - s_+(e))}\right)^{-1} \leq r_K (A - B) \frac{r_K f_a \log K}{S_a a}.$$

with

$$A := \sum_{k=1}^{[\epsilon K]} \frac{1 - (1 - s_-(e))^k}{k + 1}, \quad \text{and} \quad B := (1 - s_+(e))^{[\epsilon K]} \sum_{k=1}^{[\epsilon K]} \frac{1 - (1 - s_-(e))^k}{k + 1}.$$

For large $K$, $A = \log(\epsilon K) + O(1)$. Moreover, Lemma 3.5 in [28] ensures that for $u > 1$ there exists $D(u) < \infty$ such that $\frac{1}{\epsilon_k} u^{k} \leq D(u) u^{(K)} / |eK|$. This implies that $B \leq \frac{c}{|eK|}$ for a finite $c$. Finally, by definition, for $\epsilon$ small enough, $|S_{aA} / f_a - s_+(e)| \leq \epsilon c$ for a finite constant $c$. This yields

$$r_K \sum_{k=1}^{[\epsilon K]} \frac{\mathbb{E}[U^K_j]}{k + 1} \geq (1 - \epsilon c) r_K f_a \frac{\log K}{S_a a},$$

for a finite $c$ and concludes the proof for the lower bound. The upper bound is obtained in the same way. This concludes the proof of Lemma 7.2. \hfill \square

**Proof of Lemma 7.5.** We use Coupling (5.3) to control the growing of the mutant population during the first period of invasion, and the semi-martingale decomposition in Proposition 1 to bound the fluctuations of $M_A$. The hitting time of $[eK]$ and non-extinction event of $Z^*_e$ are denoted by:

$$T^*_e, K = \inf\{t \geq 0, Z^*_e(t) = [eK]\}, \quad \text{and} \quad F^*_e = \left\{Z^*_e(t) \geq 1, \forall t \geq 0\right\}, \quad * \in \{-, +\}.$$

From (5.3) we get $\mathcal{D} = \{F^-_e, T^-_K \leq \tilde{T}_K \} \subset \mathcal{E} = \{T^-_K < \infty, T^-_K \leq \tilde{T}_K \} \subset \mathcal{F} = \{T^+_K < \infty, T^-_K \leq \tilde{T}_K \}$. Lemma A.2 with $\mathcal{G} = \{T^-_K > \tilde{T}_K\}$ and $\mathcal{H} = \{\sup_{t \leq T^-_K} |P_{A_{b_i}}(t) - z_{A_{b_i}}| > \sqrt{\epsilon}\}$ yields:

$$\|P(\mathcal{H}, F^-_e, T^-_K) - P(\mathcal{H}, T^-_K < \infty)\| \leq \|P(T^+_K < \infty) - P(F^-_e)\| + P(T^+_K < \infty, T^-_K > \tilde{T}_K).$$

But thanks to Equation (A.9) we get that $\mathbb{P}(T^+_K < \infty) - \mathbb{P}(F^-_e) = s_+(e)/(1 - (1 - s_-(e))^{k-j}) - s_-(e)$, and (5.1) and (A.5) lead to:

$$\limsup_{K \to \infty} \mathbb{P}(T^+_K < \infty) - \mathbb{P}(F^-_e) + \mathbb{P}(T^-_K < \infty, T^-_K > \tilde{T}_K) \leq \epsilon c.$$

It allows us to focus on the probability $\mathbb{P}(\mathcal{H}, F^-_e, T^-_K \leq \tilde{T}_K)$. We recall that $|N_{A\beta_i} - N_{A\beta_i} - N_{A\beta_i} - N_{A\beta_i}| \leq N_{A\beta_i}$, and that Assumption 5 holds. Then (3.1) and (3.11) imply for $\epsilon$ small enough

$$\sup_{t \leq T^+_K \wedge \tilde{T}_K} \left|P_{A_{b_i}}(t) - \frac{z_{A_{b_i}}}{z_A} - M_A(t)\right| \leq r_K f_a \frac{\epsilon K}{T^+_K} \sup_{t \leq T^+_K \wedge \tilde{T}_K} \left\{\frac{N_a(t)}{N_a(t)}\right\} \leq \frac{r_K f_a \epsilon K}{n_A - 2\epsilon C_{A,a}/C_{A,A}} \leq \frac{c e K}{\log K}.$$
Moreover, $F^- \cap \{T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \} \subset F^- \cap \{T^K_\varepsilon \leq T^{-,K}_\varepsilon \}$. Thus we get
\[
\mathbb{P} \left( \sup_{t \leq T^K_\varepsilon} \left| P_{A,b_1}(t) - \frac{Z_{A\varepsilon}b_1}{Z_A} - M_A(t) \right| > \frac{\sqrt{\varepsilon}}{2}, F^-_\varepsilon, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \right) \leq \mathbb{P} \left( \frac{\varepsilon \ell_{T^{-,K}_\varepsilon}}{\log K} > \sqrt{\varepsilon}/2, F^-_\varepsilon \right).
\]

Finally, Equation (A.11) ensures that $\lim_{K \to \infty} T^{-,K}_\varepsilon / \log K = s_-/(\varepsilon)^{-1}$ a.s. on the non-extinction event $F^-_\varepsilon$. Thus for $\varepsilon < s_-(\varepsilon)/2c$,
\[
(B.9) \quad \lim_{K \to \infty} \mathbb{P} \left( \sup_{t \leq T^K_\varepsilon} \left| P_{A,b_1}(t) - \frac{Z_{A\varepsilon}b_1}{Z_A} - M_A(t) \right| > \frac{\sqrt{\varepsilon}}{2}, F^-_\varepsilon, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \right) = 0.
\]

To control the term $|M_A|$, we introduce the sequence of real numbers $t_K = (2 \ell_a \log K)/S_{A\varepsilon}$:
\[
\mathbb{P} \left( \sup_{t \leq T^K_\varepsilon} |M_A(t)| > \frac{\sqrt{\varepsilon}}{2}, F^-_\varepsilon, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \right) \leq \mathbb{P} \left( \sup_{t \leq t_K} |M_A(t)| > \frac{\sqrt{\varepsilon}}{2}, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \wedge t_K \right) + \mathbb{P}(T^K_\varepsilon > t_K, F^-_\varepsilon).
\]

Equation (5.1) yields for $\varepsilon$ small enough, $t_K,s_-(\varepsilon)/\log K > 3/2$. Thus thanks to (A.11) we get,
\[
\lim_{K \to \infty} \mathbb{P}(T^K_\varepsilon > t_K, F^-_\varepsilon) \leq \lim_{K \to \infty} \mathbb{P}(T^{-,K}_\varepsilon > t_K, F^-_\varepsilon) = 0.
\]

Applying Doob's maximal inequality to the submartingale $|M_A|$ and (3.12) we get:
\[
\mathbb{P} \left( \sup_{t \leq t_K} |M_A(t)| > \sqrt{\varepsilon}/2, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \wedge t_K \right) \leq \mathbb{P} \left( \sup_{t \leq t_K} |M_A(t \wedge T^K_\varepsilon \wedge \tilde{T}^K_\varepsilon)| > \sqrt{\varepsilon}/2 \right) \leq \frac{4}{\varepsilon} \mathbb{E} \left[ (M_A)_{t_K \wedge T^K_\varepsilon \wedge \tilde{T}^K_\varepsilon} \right] \leq \frac{c t_K}{K},
\]

which goes to 0 at infinity. Adding Equation (B.9) leads to:
\[
\lim_{K \to \infty} \mathbb{P} \left( \sup_{t \leq T^K_\varepsilon} \left| P_{A,b_1}(t) - \frac{Z_{A\varepsilon}b_1}{Z_A} - M_A(t) \right| > \frac{\sqrt{\varepsilon}}{2}, F^-_\varepsilon, T^K_\varepsilon \leq \tilde{T}^K_\varepsilon \right) = 0.
\]

Finally, Equations (B.7) and (B.8) complete the proof of Lemma 7.5.

\[\Box\]

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