The effective strength of selection in random environment

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Abstract

We analyse a family of two-types Wright-Fisher models with selection in a random environment and skewed offspring distribution. We provide a calculable criterion to quantify the impact of different shapes of selection on the fate of the weakest allele, and thus compare them. The main mathematical tool is duality, which we prove to hold, also in presence of random environment (quenched and in some cases annealed), between the population’s allele frequencies and genealogy, both in the case of finite population size and in the scaling limit for large size. Duality also yields new insight on properties of branching-coalescing processes in random environment, such as their long term behaviour.

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1 Introduction: coordinated branching and its relation to selection

In population genetics the selective fitness of a species, or an allele, is widely thought to be permeable to the influence of environmental factors which may vary randomly in time: in certain generations, the population may be subject to particularly stressful external conditions (extreme temperatures, cataclysms, abrupt invasions of pathogens, hurricanes etc) making the selective advantage of some allelic types unusually more pronounced than in other generations. This could be due to a better ability to secure resources, or to a lower sensitivity to stress, or to various other reasons [12, 18, 28, 27].

Thus if we consider a population comprising only two allelic types 0 and 1, say, where type 1 is assumed to be always fitter than type 0, it is intuitively clear that the possible occurrence of such “cataclysmic”generations would enhance the probability of extinction of type 0, compared to the neutral case where both types have equal fitness. It is, however, less obvious if rare but strong selective events put type 0 more at risk of extinction than a small but constant-in-time selective pressure. The problem is reminiscent of similar questions arising in experimental biology, where, for example, some detrimental substance (antibiotic) is inoculated in a population of bacteria, and there is an interest in determining whether a constant administration of the substance in low concentration dosage is more effective at wiping out the population, than a more occasional inoculation with higher dosages of varying concentration [36]. This paper aims to study the long term effect of rare selective events and quantify how big and frequent cataclysms owed to random environment must be in order to wipe out a family as effectively
as constant weak selection in a steady environment.

We will focus on a wide class of population models with selection and possibly highly skewed offspring distribution (known as Lambda-Wright-Fisher models). We will construct a discrete-time, individual-based population model, following an approach first proposed in \cite{20}. For a population with constant size \( N \in \mathbb{N} \), we will define a suitable Wright-Fisher random graph, where the notion of selection is associated to the idea that, at each generation, every individual choose a random number of potential parents from the previous generation and inherit the fittest type among those found in their sampled pool. In a population of size \( N \), at each generation \( g \in \mathbb{Z} \), selection is thus parametrised by the probability distribution \( Q \), say, of the vector of pool sizes \( K_g = \{ K_g(i) : i = 1, \ldots, N \} \). The distribution of \( Q \) will depend on time, through a sequence of \([0,1]\)-valued random variables indexed by \( \mathbb{Z} \), representing the time-varying random environment.

The selection mechanism thus is fully specified in terms of the (time-varying) distribution of pool sizes of potential parents, but the actual impact of selection depends also on how each individual chooses the actual labels of the potential parent to include in each such pool, and this choice is in turn affected by whether or not, at any given generation, the population undergoes an extreme reproductive event (or Lambda-event). In generations without extreme reproductive events, all individuals will sample the labels of their potential parents independently at random; in those with extreme reproduction, choices made by distinct individuals may be correlated. The occurrence and size of extreme reproductive events at each generation will be modelled by an additional, independent sequence of \([0,1]\) random variables indexed by \( \mathbb{Z} \).

The construction summarised above (and described in full details in Section 2.1) shows clearly how the fate of the weak allele frequency is intrinsically linked to the population’s ancestry.

In models with selection in deterministic environment, a well-established method to study such a link is based on the notion of duality, which has attracted the interest of an increasing number of researchers in a variety of areas of probability \cite{17,25,35}, including population genetics \cite{9,13,20,23,33}: If \( X = (X(t) : t \geq 0) \) and \( Z = (Z(t) : t \geq 0) \) are two stochastic processes, respectively with state space \( E \) and \( F \), then \( X \) and \( Z \) are said to be dual to each other with respect to the duality function \( h : E \times F \rightarrow \mathbb{R} \) if, for every \((x,y) \in E \times F\),

\[
\forall t \geq 0 : \quad \mathbb{E}[h(X(t),y) \mid X(0) = x] = \mathbb{E}[h(x,Z(t)) \mid Z(0) = y]. \tag{1}
\]

We will extend the use of duality to analyse population models with time-varying random environment. We will show in Lemma \ref{lem:quenched_duality} that, for finite \( N \), a quenched relation of duality similar to (1) holds conditionally on the environment’s sample path, when \( X \) describes the forward-in-time process of 0-allele frequencies; \( Z \) the corresponding backward-in-time ancestral process, tracking the number of surviving potential ancestral lineages; \( h \) is an appropriate generalisation of the so-called sampling duality function originally proposed in \cite{33} and later adapted by \cite{20} to models with deterministic selection.

We will then focus on models where the environment evolves according to an i.i.d. process. In this case, it turns out that duality also holds in an annealed form (i.e. unconditionally on the environment). Then, taking the population size \( N \) to infinity and rescaling time suitably, we will prove in Lemma \ref{lem:annealed_duality} that, with the choice \( h(x,n) = x^n \), an annealed moment duality relation of the form (1) holds between the two processes in the scaling limit.
The limit ancestral process $Z$ will evolve as a continuous-time Markov chain with state space $\mathbb{N} \cup \{\infty\}$, with positive jumps from $n$ to $n+k$ occurring at rate

$$
\int_{[0,1]} \mathbb{P}\left(\sum_{j=1}^{n} K_{y,j} = n + k\right) \frac{\Lambda_{y}(dy)}{\mathbb{E}[K_{y,1} - 1]} + wn\delta_{1,k}
$$

(2)

for $k \in \mathbb{N}$ and with negative jumps from $n$ to $n-k$ occurring at rate

$$
\int_{(0,1]} \left(\frac{n}{k+1}\right) y^{k+1}(1-y)^{n-k-1} \frac{\Lambda_{y}(dy)}{y^2} + \sigma (n^{\frac{1}{2}}) \delta_{1,k}
$$

(3)

for all $k \in \{1,\ldots,n-1\}$, where $w \geq 0$ is a constant, $\Lambda_{y}$ and $\Lambda_{z}$ are two finite measures with no atoms in 0 and, for each $y \in [0,1]$, $\{K_{y,j}\}_{j \in \mathbb{N}}$ is an iid family of $\mathbb{N} \cup \{\infty\}$-valued random variables with common distribution $Q(y)$ parametrised by $y \in [0,1]$. We will refer to $Z = (Z(t) : t \geq 0)$ as to the branching-coalescing process in random environment (BCRE). Positive jumps are driven by $\Lambda_{y}$ and correspond to a lineage branching off into one actual and one or more virtual parental lineages, as an effect of selective pressure, whereas negative jumps, driven by $\Lambda_{z}$, correspond to two or more lineages coalescing into a common ancestor, as an effect of pure genetic drift. The constant $w$ is responsible for the classical form of weak genic selection, acting constantly and deterministically in time. Correspondingly, $\sigma$ is a weight associated to the classical Kingman dynamic (binary mergers, i.e. non-extreme reproduction). The measures $\Lambda_{y}$ and $\Lambda_{z}$ are the intensities of two poisson processes governing the occurrence and size of rare selective events (cataclysms) and of the extreme reproduction events, respectively. Loosely speaking, for every $y \in [0,1]$, $Q(y)$ represents the distribution of the size of the pool of potential parents which a typical individual in the limit population will come up with when the environment has value $y$. The choice of $Q$ is arbitrary as long as it satisfies a minimal key condition of integrability, as explained later on in Section 1.1.

As for the forward-in-time allele frequency process, we will prove that a scaling limit approximation of the 0-allele frequency evolution is described by a jump-diffusion process $(X(t) : t \geq 0)$ arising as the unique strong solution to the SDE

$$
dX(t) = \int (\mathbb{E}[X(t^-)^{K_y}] | X(t^-) - X(t^-)) \mathcal{N}_y(dt,dy) - wX(t)(1-X(t))dt
\begin{align*}
&+ c \int \int z(1_{u \leq X(t^-)}) - X(t^-)) \mathcal{N}_z(dt,dz,du) \\
&+ \sigma \sqrt{X(t)(1-X(t))} dB(t)
\end{align*}
$$

(4)

where: $(B(t) : t \geq 0)$ is a standard Brownian motion; $\mathcal{N}_y$ is a Poisson point measure on $[0,\infty] \times [0,1]$ with intensity $ds \otimes (\mathbb{E}[K_{y} - 1])^{-1} \mathbb{1}_{[0,1]} \Lambda_{y}(dy)$, with $K_{y} \equiv K_{y,1}$, $\Lambda_{y}(dy)$ and $w$ exactly as in (2); $\mathcal{N}_z$ is a Poisson point measure on $[0,\infty] \times [0,1] \times [0,1]$ with intensity $ds \otimes z^{-2} \Lambda_{z}(dz) \otimes du$, with $\Lambda_{z}(dz)$ exactly as in (3). We will refer to the process $X$ as the two-type Fleming-Viot process with weak and rare selection (FVWRS). Note that for $c = 0$ this process was introduced Bansaye, Caballero and Méléard in [4]. The classical Wright-Fisher diffusion process with genic selection is obtained when $c = 0$ and $\mathcal{N}_z([0,\infty] \times [0,1]) = 0$.

Coming back to our motivating problem (comparing the impact of rare selective shocks with that of constant weak selection), it turns out that it is not sufficient to compare the total intensity $\alpha_{x} = \Lambda_{x}([0,1])$ of rare selective events against the rate $w$ of (classical) weak selection: it is necessary to take into account also information about the actual “shape” of rare selection, reflecting the
specific action of the random environment. We will show in Section 3 that all the needed additional information is sufficiently summarised by the parameter

\[ \alpha^* := \mathbb{E} \left[ \frac{1}{1 + \mathbb{E}[K_{Y^*}] - 1 | Y^*]} \right], \]

where \( Y^* \) is a random variable with distribution \( \alpha^{-1}_s \Lambda_s \), \( K_{Y^*} \) has distribution \( Q(Y^*) \) and \( V \) is a uniform random variable in \([0, 1]\), independent of all the other variables. We will thus refer to \( \alpha^* \) as the shape of rare selection.

We will demonstrate that the correct way to measure the effective strength of selection, combining the effect of both rare and weak selection, is via the quantity

\[ \alpha_{\text{Eff}} := \alpha_s \alpha^* + w. \] (5)

In Theorem 3.2 we will find a critical value \( \beta^* \) for the total selection \( \alpha_{\text{Eff}} \), separating regimes leading to almost sure ultimate extinction \( (\alpha_{\text{Eff}} > \beta^*) \), from regimes where the weaker type 0 has a chance to survive and fixate \( (\alpha_{\text{Eff}} < \beta^*) \). This extends results by Foucart \[14\] and Griffiths \[21\] who independently discovered this threshold for the case of classic weak selection. While Foucart works with the branching coalescing process, Griffiths introduces a helpful representation of the generator of the diffusion process and combines this with a Lyapunov-function approach. We propose (Section 3.2) an extension of Griffiths’ approach to find a critical value for population models solving (4). A non-trivial step in this endeavour requires closing a gap in \[21\], which we have achieved with our Lemma 3.6. This Lemma also covers the case analysed by Griffiths and can be extended to include the models in \[20\].

The critical value \( \beta^* \) for \( \alpha_{\text{Eff}} \) does not depend on the selection parameters, nor on the environment. This has interesting and, to some extent, counter-intuitive implications for our motivating problem, when comparing the intensity \( \alpha_s \) of strong rare selection against the intensity \( w \) of weak selection. In a model with purely rare selective events \( (w = 0) \), the effective critical threshold for \( \alpha_s \) to guarantee extinction is given by the ratio \( \beta^*/\alpha^* \geq \beta^* \). This implies that, given the same genetic drift parameter measure \( \Lambda_s \), a higher minimum level of rare selective intensity \( \alpha_s \) is required to guarantee extinction, compared to a model with purely constant weak selection \( (\alpha_s = 0) \) for which \( \beta^* \) is still the actual threshold for \( w \). Note that due to the form of the shape parameter \( \alpha^* \), this is the case even for choices of intensity measures \( \Lambda_s \) typically favouring large “cataclysms”, from which we would expect a faster pressure towards extinction. For a comparison among specific examples of rare selection mechanisms see Remark 3.4.

Although random environment was introduced a few decades back both in the literature of branching processes (e.g. \[3, 39\]) and in population genetics models (\[28, 27\]), it is currently attracting a renewed interest in both communities (see \[1, 5, 10, 16, 15, 22\] in the context of branching processes and \[4, 8, 10, 24\] in the context of population genetics). While the present paper draws its main motivation from open problems about selection in population genetics, it is our opinion that the above-mentioned duality property is also interesting from the point of view of the theory of branching (and coalescing) processes in a random environment. In the present work, Lemma 2.14 shows that not only does the key Condition \[1\] (see below Section 1.1) ensure strong existence of the solution of Equation (4), but it also implies conservativeness of the BCRE defined by (2)-(3), and this time in presence of both coalescence and random environment. This result is a beautiful consequence of moment duality and can thus be extended to the processes
studied in [20], in [19] and to any other scenario where the the moment dual of a BPRE has the Feller property. We believe that the results and methods in this paper could help to shed further light on the connections between these two families and it is plausible that several of the results presented here can be extended to other types of non-iid environmental processes.

1.1 A key condition on the parameters of rare selection

The action of rare selection in random environment is parametrised by two objects: the rare selection mechanism is given by a kernel $Q = \{Q(y) : y \in [0, 1]\}$ where, for every $y$, $Q(y)$ is a distribution on $\mathbb{N} \cup \{\infty\}$; the random environment itself is determined by a measure $\mu$ on $[0, 1]$, the space of parameters of $Q$, whose one-to-one relation with $\Lambda_s$ we now explain. As a central assumption for all our results, we will require that the kernel $Q$ and the measure $\mu$ satisfy the following condition:

**Condition 1.** The kernel $Q$ and the measure $\mu$ satisfy

$$\int_{[0,1]} \mathbb{E}[K_y - 1] \mu(dy) < \infty,$$

where $K_y$ is a $(\mathbb{N} \cup \{\infty\})$-valued random variable with distribution $Q(y)$.

In addition, for the sake of simplicity we will also always assume that $Q(y) = \delta_1$ if and only if $y = 0$. Note that Condition 1 implies the representation $\mu = \mu(\{0\}) \delta_0 + \mu^+\delta_1$ where $\mu^+$ has density $y \mapsto (\mathbb{E}[K_y - 1])^{-1} \mathbb{1}_{[0,1]}(y)$ with respect to a finite measure which we denote $\Lambda_s$. It will become apparent, however, that the atom in zero of $\mu$ has no effect on the selection mechanism, hence we will assume, without loss of generality, $\mu(\{0\}) = 0$. Since $\mu$ and $\Lambda_s$ are suitably equivalent, we will make use of both representations.

The choice of $[0,1]$ as parameter space for $Q(y)$ is entirely arbitrary and one can replace it with any general parameter space $\mathcal{Y}$. The use of $[0,1]$ has the advantage of being rich enough and interpretable, encompassing most known models of non-balancing selection. For example, by setting $Q(y)$ to be the Geometric distribution on $\mathbb{N}$ with parameter $1 - y$ for $y \in [0, 1]$ and $Q(1) \equiv \delta_{\{\infty\}}$, and choosing $\Lambda_s = a\delta_{y^*}$, ($y^* \in [0, 1]$) one recovers known moment dualities for populations in constant environment: For $a = 1$ and $y^* = 0$, the model is neutral (no selection), in which case the ancestry is described by a coalescent with multiple collisions [34, 37] with merger sizes governed by the parameter measure $\Lambda_c$ and the frequency process is the two-type Fleming-Viot process [7]. For $a = y^* \rightarrow 0$ the model specialises to the haploid weak selection model, whose genealogy is given by the Ancestral Selection Graph of [31] and its dual is the Wright-Fisher diffusion with weak selection [29]. If, in addition, $c = 0$ the model reduces to Kingman’s coalescent process [30] with the Wright-Fisher diffusion as its dual [29]. With random environment (non-degenerate $\Lambda_s$), the duality property [11] has not been established before. The duality implies that the allele 0 will become extinct with probability one if and only if its ancestral process does not admit a stationary distribution, which happens when the action of coalescing events occurs at a sufficiently fast time scale to ultimately outperform the action of branching events (see later on Remark 3.1).
1.2 Outline of the paper

The paper is structured as follows. We begin, in Section 2.1, with the construction of the Wright-Fisher graph with selection in random environment incorporating the possible occurrence of highly skewed offspring distributions (Lambda reproduction mechanism); we will also define the frequency process of the 0-allele and the so-called block-counting process of the ancestry of a sample. Subsequently, we prove the quenched and annealed sampling duality results. Section 2.2 establishes the two-type Fleming-Viot process with selection \( X \) as the scaling limit of the frequency process of the 0-allele, if the environment is chosen to be \( iid \). Section 2.3 begins with the duality of \( X \) and the branching coalescing process in random environment \( Z \) and its implication of conservativeness of \( Z \). Duality is then also used to prove that \( Z \) arises as the scaling limit of the block-counting process of the ancestry of the finite Wright-Fisher graph. The long-term behaviour of the scaling limits and their dependence on the strength of selection is then analysed in Section 3 subdivided in the result for \( X \) in Section 3.1 and its translation through duality for \( Z \) in Section 3.3.

2 Modeling Selection in random environment

In this section we generalise the Wright-Fisher discrete graph with selection, originally introduced in [20], in order to include random environment. We then prove quenched duality between the corresponding ancestral graph and 0-allele frequency process.

2.1 The discrete ancestral selection graph with random environment

We begin by constructing an individual-based, finite-population model extending [20] to encompass randomly varying selection. Consider a population of fixed, finite size \( N \in \mathbb{N} \), with discrete, non-overlapping generations indexed by \( g \in \mathbb{Z} \). Denote: \( [N] := \{1, \ldots, N\} \) and \( V_N := \mathbb{Z} \times [N] \). Each individual in the history of the population is identified by a point \( v = (g, i) \in V_N \), and we will write \( g(v) = g \) and \( i(v) = i \) to indicate, respectively, the generation of \( v \) and its label in \( [N] \). Negative and positive values of \( g \) will then index past and future generations, respectively, with respect to an arbitrarily chosen “present generation” \( g = 0 \).

\( V_N \) is the (deterministic) set of vertices of what is to become our random graph. The randomness, of course, lies in the ancestral relations: an edge will be drawn between any two vertices where one vertex is a potential parent of the other. The random ancestry will have to incorporate two features: a possibly skewed offspring distribution, on one hand, and selection in a random environment, on the other. The environment influencing selection is modelled as a sequence of random variables \( Y = (Y_g : g \in \mathbb{Z}) \) taking values in a given measurable state space \( \mathcal{Y} \) indexing a probability kernel \( Q = \{Q(y, \cdot) : y \in \mathcal{Y}\} \), that is: for every \( y \in \mathcal{Y} \), \( Q(y) = Q(y, \cdot) \) is a probability distribution on \( \mathbb{N} \cup \{\infty\} \) and, denoting with \( \mathcal{R} \) the Borel sigma-algebra of \( \mathbb{N} \cup \{\infty\} \) with respect to the discrete metric, for every \( A \in \mathcal{R} \), \( y \mapsto Q(y, A) \) is measurable. \( Q \) will effectively play the role of a selection parameter. As mentioned in the Introduction, throughout this paper we will take \( \mathcal{Y} = [0, 1] \) for convenience. Given the kernel \( Q : [0, 1] \times \mathcal{R} \to [0, 1] \) and the
random environment process \( \bar{Y} = (Y_g : g \in [0, 1]) \), we assign to each individual \( v = (g, i) \in V_N \) independently a random number of potential parents \( K_v \). Given \( Y_g = y \), the random variables \( K_{(g,i)} \), \( i \in [N] \), are assumed to be conditionally iid with common distribution \( Q(y) \). Given the whole trajectory of the environment process \( \bar{Y} = \bar{y} \) the vectors \( \{K_{(g,i)} : i \in [N]\} \), \( g \in \mathbb{Z} \), are conditionally independent.

Let us now introduce highly skewed offspring distribution, responsible for correlation in how the individuals choose parents from the \( N \) vertices in the previous generation. Let \( \Lambda \) be a distribution on \([0, 1]\) with \( \Lambda([0]) = 0 \) and let \( c \in [0, 1] \). We introduce an iid process \( (C_g : g \in \mathbb{Z}) \) with values in \([0, 1]\) which, at each generation \( g \), will determine the strength of correlation among choice of parental labels made by distinct individuals. We assume that at each \( g \), \( C_g \) has distribution

\[
(1 - c)\delta_0 + c\Lambda(dz).
\]

The interpretation is that, at each generation \( g \), with probability \( 1 - c \), the individuals make uncorrelated choices of their own pool of potential parents (strength \( C_g = 0 \)) and, with probability \( c \), the choices are no longer independent and the strength of correlation \( C_g \) is governed by \( \Lambda \).

Now, denote with \( \mathcal{U} \) the discrete uniform distribution on \([N]\) and let \( I_g \) be a random variable with distribution \( \mathcal{U} \).

The population then reproduces as follows. At each generation \( g \in \mathbb{Z} \), every individual \( v = (g, i) \in V \) chooses \( K_{(g,i)} \) potential parents from among the \( N \) individuals in the previous generation \( g - 1 \). The labels of the potential parents are chosen with replacement from \([N]\) as iid random variables with distribution

\[
C_g I_g + (1 - C_g)\mathcal{U}.
\]

In other words, the whole population at generation \( g \), collectively marks a special label \( I_g \) picked uniformly from \( \{1, \ldots, N\} \). Then every individual \( v = (i, g) \) will flip \( K_v \) iid coins with a random bias \( C_g \). Whenever any such coin returns a success, the individual from generation \( g - 1 \) with special label \( I_g \) is chosen as potential parent for \( v \); for all coins returning failure, the potential parent is picked uniformly at random, independently of all other random variables.

Ultimately each individual potential parent is, marginally, uniformly chosen from \([N]\). Notice that, since choices are made with replacement, the actual number of distinct labels, chosen an individual \( v \in V_N \) as potential parents, might be less than \( K_v \). Repeated choices will be invisible to the graph, i.e. no multiple edges will be drawn between any two distinct vertices. See Figure ?? for an illustration of the mechanisms. We assume that all the above random variables are defined on the same underlying probability space \((\Omega, \mathcal{F}, \mathbb{P})\).

With this, we obtain the definition of the Wright-Fisher graph with selection in random environment with skewed offspring distribution. We denote by \([w, v]\) the directed edge from \( w \) to \( v \), for \( w, v \in V_N \).

**Definition 2.1.** For every \( N \in \mathbb{N} \) let \( \bar{Y} = (Y_g)_{g \in \mathbb{Z}} \) be a \([0, 1]\)-valued process, \( Q : [0, 1] \times \Omega \rightarrow [0, 1] \) a probability kernel, \( c \in [0, 1] \), and \( \Lambda \) a distribution on \([0, 1]\).

The Wright-Fisher graph with selection \( Q \) in random environment \( \bar{Y} \) and skewed offspring distribution governed by \( \Lambda - \) denoted \( \text{WF}(N, \bar{Y}, Q, c, \Lambda) \) – is given by the graph

\[
G_N = G_N(\omega) = (V_N, E_N(\omega)), \quad \omega \in \Omega
\]

with deterministic set of vertices \( V_N \), and random set of edges \( E_N = E_N(\omega) \) formed by the rule: \([u, v]\) is an edge of \( E_N \) if and only if \( u \) is a potential parent of \( v \).
On a given Wright-Fisher graph $WF(N, \bar{Y}, Q, c, \Lambda)$, we introduce the two-point type space $\{0, 1\}$, where 0 will be the weak (less fit) type and 1 the strong (fitter) type. We assign arbitrarily types 0 or 1 to all the individuals in a fixed generation $g_0 \in \mathbb{Z}$, chosen to be the starting generation of our process. (This is only specified when necessary.)

The mechanism of inheritance is modelled as follows: in each subsequent generation, every individual will take on the type of its fittest potential parent, that is: it will inherit type 0 if and only if all its potential parents are of type 0. Clearly, this mechanism describes the advantage of the fitter type 1 and selection is fully explained in terms of multiple parents choice.

This rule assigns types to all vertices in $\{v \in V_N \mid g(v) \geq g_0\}$. Let $\xi(v) \in \{0, 1\}$ denote the type of $v$ and define $[N]_0 := \{0, \ldots, N\}$, $[N]_0/N := \{0, 1/N, \ldots, 1\}$. Note that for every $g$ the vector of types $(\xi(g, i) : i \in [N])$ is exchangeable.

The population’s allele frequencies dynamics and the correspondic backward-in-time genealogy can be both obtained as functions of the same $WF(N, \bar{Y}, Q, c, \Lambda)$ graph.

**Definition 2.2.** The 0-allele frequency process started in $g_0 \in \mathbb{Z}$ in a Wright-Fisher graph $WF(N, \bar{Y}, Q, c, \Lambda)$ is the $[N]_0/N$-valued process $X^{N,g_0} = (X^{N,g_0}(g) : g \geq g_0)$ describing the proportion of 0-alleles in each generation $g \geq g_0$:

$$X^{N,g_0}(g) := \frac{1}{N} \sum_{v : g(v) = g} (1 - \xi(v)), \quad g \geq g_0.$$

Notice that the distribution of $X^{N,g_0}$ depends on the initial distribution of types only through the resulting frequency of types.

**Remark 2.3.** Our graph encompasses several models of allele frequency evolution already known in the population genetics literature. Let us focus on the cases without skewed offspring distribution, i.e. $c \equiv 0$. A key role is played by the choice of geometric kernels $Q$ given, for every $y \in [0, 1]$, by

$$Q(y) = \sum_{i=1}^{\infty} y^{i-1}(1 - y)\delta_i =: \text{Geo}(1 - y)$$

and $Q(1) := \delta_{\infty}$. Indeed, with such a choice of $Q$, if $\bar{Y}$ is taken to be a constant, deterministic process, that is, for some $y \in [0, 1]$, $Y_g = y$ for every $g \in \mathbb{Z}$, then $X^{N,g_0}$ reduces to the ordinary Wright-Fisher model with selection parameter $y$ (see [20], Example 2.3). If, with the same choice of $Q$, the environment $\bar{Y} = (Y_g : g \in \mathbb{Z})$ is the $N$-th instance of a sequence of processes in the domain of attraction of a spectrally negative Lévy process $\bar{Y}$, then it can be shown that the frequency process $X^{N,g_0}$ falls within a class of Wright-Fisher models with selection with random environment recently introduced in [4].

The ancestry in a $WF(N, \bar{Y}, Q, c, \Lambda)$ graph is defined as follows. An individual $(g(v) - r, i) \in V_N$ living $r \geq 1$ generations before $v$ is called a potential ancestor of $v$, if there exists a path in $(V_N, E_N)$ connecting $v_0 := (g(v) - r, i)$ to $v_r := v$, that is: there exist $v_1, \ldots, v_{r-1} \in V_N$ such that $[v_l, v_{l+1}] \in E_N$ for every $l = 0, \ldots, r - 1$. Denote by $A^N(v)$ the set of all such ancestors of $v$. For $n \in [N]$, the potential ancestry of the sample $\{v_1, \ldots, v_n\}$ is the set

$$A^n := \bigcup_{j=1}^{n} A^N(v_j).$$

Now, given an arbitrary collection $\bar{v} = \{v_1, \ldots, v_n\} \subseteq \{g_0\} \times [N]$ of distinct individuals chosen from generation $g_0 \in \mathbb{Z}$, the potential ancestors of the sample $\{v_1, \ldots, v_n\}$ alive $l$ generations back in time are the vertices in the set

$$A^N(\bar{v}) := \{w \in A^N(v_1, \ldots, v_n) \mid g(w) = g_0 - l\}.$$
**Definition 2.4.** Let \( \bar{v} \subseteq \{g_0\} \times [N] \) be a sample of individuals from generation \( g_0 \). The block-counting process of the ancestry of \( \bar{v} \) is the \([N]_0 \subset \mathbb{N}_0\)-valued Markov chain \( Z_{\bar{v}}^{N,g_0} = (Z_{\bar{v}}^{N,g_0}(g) : g \leq g_0) \) defined by \( Z_{\bar{v}}^{N,g_0}(g) := |\bar{v}| \) and

\[
Z_{\bar{v}}^{N,g_0}(g) := |A_{g_0-g}(\bar{v})|, \quad g \leq g_0,
\]

where \( |A| \) denotes the cardinality of the set \( A \).

Note that the distribution of \( Z_{\bar{v}}^{N,g_0} \) actually depends on \( \bar{v} \) only through the sample size \( |\bar{v}| \). We omit the subscript \( \bar{v} \) when there is no danger of confusion.

Both processes \( X^{N,g_0} \) and \( Z^{N,g_0} \) need the additional time-parameter \( g_0 \) to indicate where they are anchored with respect to the absolute time, i.e. the time of the random environment \( \bar{Y} = (Y_g)_{g \in \mathbb{Z}} \). Observe also, that the quantities \( X^{N,g_0}(g) \) and \( Z^{N,g_0}(g) \) actually depend on the random environment \( \bar{Y} \) only through the variables \( Y_{g_0+1}, \ldots, Y_g \) and \( Y_{g+1}, \ldots, Y_{g_0} \) respectively.

For these two processes we can now prove the so-called sampling duality property for Wright-Fisher graphs, stated in a quenched form, i.e. conditionally on a realisation of the random environment \( \bar{Y} \). For every \( y \in [0,1] \), denote with \( \varphi_y \) the probability generating function of the distribution \( Q(y) : \)

\[
\varphi_y(x) := \mathbb{E}[x^K_y].
\]

Let \( U \sim \Lambda \) and for each \( x \in [0,1] \) let \( B_x \) be Bernoulli with success parameter \( 1 - x \), both independent of any other randomness in the model.

**Lemma 2.5.** Let \( X^N \) and \( Z^N \) be, respectively, the 0-allele frequency process and the ancestral process of a Wright-Fisher graph \( WF(N, \bar{Y}, \bar{Q}, c, \Lambda) \).

Define the function \( H : [0,1] \times N_0 \times \mathbb{Z} \times [0,1]^2 \rightarrow [0,1] \) by

\[
H(x,n;g,y) := (1-c)(\varphi_y(x))^n + c \mathbb{E}\left[(\varphi_y((1-U)x + U(1-B_x))^n\right).
\]

Then, for all \( x \in [N]_0/N, n \in [N]_0 \) and \( r < s \), \( \mathbb{P}\)-a.s.

\[
\mathbb{E}\left[H\left(X^{N,r}(s-1), n; s, \bar{Y}^{N}; r = x, \bar{Y}\right) \mid X^{N,r}(r) = x, \bar{Y}\right] = \mathbb{E}\left[H\left(x, Z^{N,s}(r+1); r + 1, \bar{Y}\right) \mid Z^{N,s}(s) = n, \bar{Y}\right].
\]

**Remark 2.6.**

(i) The equality (7) establishes a “sampling duality”, since the duality function \( H(x,n;g,y) \) is precisely the probability, under the environment \( \bar{y} = (y_g)_{g \in \mathbb{Z}} \), of sampling \( n \) individuals of type 0 from generation \( g \), given that the 0-type frequency was \( x \) in the previous generation. This will be more apparent in the proof of Lemma 2.5.

(ii) For \( c = 0 \), i.e. with no skewed offspring distribution, and any choice of \( \bar{Q} \) and \( \bar{Y} \) resulting in \( K_v = 1 \) almost surely for every \( v \in V_N \), the equality (7) reduces to the well-known moment duality between the \( N \)-finite Wright-Fisher allele frequency process and the corresponding block-counting process of the genealogy [33]. This is the case, for example, when \( \bar{Q} \) is, at each generation, geometric with parameter equal to 0.

(iii) For arbitrary \( c \) and \( \bar{Q} \), but constant, deterministic environment, the sampling duality for Wright-Fisher graphs with selection was proved in Proposition 2.9 in [20].
Similarly, recalling the independent variables $U$ and $Y$, we may assume that the sample in generation $s$ consists of the individuals with the labels $1, \ldots, n$ and therefore

$$p(\bar{Y}; x) := P((s, 1), \ldots, (s, n) \text{ are all of type 0} | X^{N,r}(s) = x, \bar{Y}).$$

We first calculate $p(\bar{Y}; x)$ by considering the types of the potential parents chosen by $(s, 1), \ldots, (s, n)$. All equalities between random variables in the following hold $\mathbb{P}$-a.s. Recall that each individual $(s, i)$ will be of the weak type 0, if and only if in each of its $K_{(s,i)}$ (independent) attempts it chooses a weak potential parent. Observe:

(i) In a generation $s$ without skewed offspring distribution, for each $i = 1, \ldots, N$ the probability for $(s, i)$ to be weak, conditional on the frequency of the weak type in the previous generation is

$$E\left[\left[X^{N,r}(s-1)\right]^{K(s,i)} | X^{N,r}(s-1), X^{N,r}(r) = x, \bar{Y}\right].$$

Denote this probability by $p_1(X^{N,r}(s-1), \bar{Y}; x)$.

(ii) In a generation with skewed offspring distribution, recall that $I_s$ denotes the favoured individual (special marked label) collectively chosen at time $s$ and $\xi(I_s)$ its type. By construction, the distribution of $\xi(I_s)$ conditional on the frequency of weak in the previous generation is Bernoulli with parameter $1 - X^{N,r}(s-1)$. Hence, in such a generation, the conditional probability for $(s, i)$ to be weak, conditional on the frequency of the weak type in the previous generation is, by (9),

$$E\left[(1 - U_s)X^{N,r}(s-1) + U_s(1 - \xi(I_s))\right]^{K(s,i)} | X^{N,r}(s-1), X^{N,r}(r) = x, \bar{Y}.$$ 

Denote this probability by $p_2(X^{N,r}(s-1), \bar{Y}, x)$.

Conditionally on $Y_s$ the random variables $K_{(s,1)}, \ldots, K_{(s,n)}$ are independent and identically distributed with distribution $Q(Y_s)$. Hence, for any $\tilde{x} \in [0, 1]$ 

$$\mathbb{E}[\tilde{x}^{\sum_{i=1}^n K(s,i)} | \bar{Y}] = \left(\mathbb{E}[\tilde{x}^{K(s,i)} | \bar{Y}]\right)^n = \left(\mathbb{E}[\varphi_{Y_s}(\tilde{x}) | \bar{Y}]\right)^n = \left(\varphi_{Y_s}(\tilde{x})\right)^n. \quad (8)$$

Similarly, recalling the independent variables $U$ and $B_{\tilde{x}}$ introduced in Lemma 2.5

$$\mathbb{E}\left[(1 - U)\tilde{x} + U(1 - B_{\tilde{x}})\sum_{i=1}^n K(s,i) | \bar{Y} \right] = \mathbb{E}\left[(\varphi_{Y_s}((1 - U)\tilde{x} + U(1 - B_{\tilde{x}})))^n | \bar{Y}\right] \quad (9)$$
Since $K_{(s,1)}, \ldots, K_{(s,n)}$ are also independent of $X^{N,r}_x(r)$, $X^{N,r}_x(s-1)$, $U_s$ and $\xi(I_s)$, this implies

$$p(Y;x) = (1-c)E \left[p_1(X^{N,r}_x(s-1), Y;x) \right] + c E \left[p_2(X^{N,r}_x(s-1), Y;x) \right]$$

On the other hand, we can calculate the $p(Y^N)$ by looking at the number of potential ancestors of the sample in generation $r + 1$: these too need to be all of the weak type 0 in order for our sample to be of type 0. This in turn is only possible if all their potential ancestors in the previous generation $r$ are of the weak type. Hence

$$p(Y;x) = \mathbb{P}(A^N_{N,r-1}(\{(s,1), \ldots, (s,n)\}) \text{ are all of type } 0 | X^{N,r}_x(r) = x, Y)$$

The number of potential ancestors of $(s,1), \ldots, (s,n)$ in generation $r + 1$ is

$$|A^N_{N-r-1}(\{(s,1), \ldots, (s,n)\})| = Z^{N,s}(r + 1)$$

And the frequency of the weak type 0 in generation $r$ is, by assumption, equal to $x$. Since each of the individuals in $A^N_{N-r-1}(\{(s,1), \ldots, (s,n)\})$ chooses its potential parents independently, as before, the sought probability can be expressed as

$$p(Y;x) = (1-c)E \left[ x^{\sum_{i=1}^{N,s}(r+1)} K_{(r+1,i)} | Z^{N,s}_x(s) = n, Y \right]$$

where, again, we have profited from the fact that, conditionally on $Y$, the vector $(K_{(r+1,i)} : i \in [N])$ has iid coordinates and is independent of $Z^{N,s}(r + 1)$ and $Z^{N,s}(s)$, along with the observations $\mathcal{S}$ and $\mathcal{B}$ with $s$ replaced by $(r + 1)$. 

The next Proposition shows that a similar duality property holds in an annealed form (i.e. unconditionally on the environment $Y$) when the environment is described by an iid process. With the choice of an iid environment, the distributions of $X^N$ and $Z^N$ do not depend on the specific choice of starting time $g_0$, whence we will assume most of the times, without loss of generality, this to be $g_0 = 0$ and omit the corresponding superscript. To abbreviate the terms, we write

$$\mathbb{P}_x(\cdot) := \mathbb{P}(\cdot | Z^{N,g_0}(g_0) = n) \quad \text{and} \quad P_x(\cdot) := \mathbb{P}(\cdot | X^{N,g_0}(g_0) = x)$$

for any $x \in [N]_0/N$ and $n \in [N]_0$.
Proposition 2.7. Assume that the random environment $\bar{Y} = (Y_g)_{g \in \mathbb{Z}}$ is a sequence of iid random variables with common distribution $\mu$. Define the function $H_\mu : [0, 1] \times \mathbb{N} \to [0, 1]$ by

$$H_\mu(x, n) := E[H(x, n; 0, \bar{Y})]$$

$$= (1 - c)E[\varphi_{Y_0}(x)^n] + c \ E \left[ \varphi_{Y_0} \left( (1 - U)x + U(1 - B_0) \right)^n \right],$$

where $H$ is the duality function defined in Lemma 2.2. Then for all $x \in \lfloor N \rfloor_0 / \mathbb{N}$, $n \in \mathbb{N}_0$ and $g \geq 0$

$$E_x \left[ H_\mu \left( X^{N,0}(g), n \right) \right] = E_n \left[ H_\mu(x, Z^{N,0}(-g)) \right].$$

Proof. The idea of the proof is the same as for Lemma 2.5, but we have to take the iid environment carefully into account. Let $g \geq 0$. First note that, by identity in distribution,

$$H_\mu(x, n) = E[H(x, n; 1, \bar{Y})]$$

$$= (1 - c)E[\varphi_{Y_1}(x)^n] + c \ E \left[ \varphi_{Y_1} \left( (1 - U)x + U(1 - B_0) \right)^n \right]$$

$$= E[H(x, n; g + 1, \bar{Y})]$$

$$= (1 - c)E[\varphi_{Y_{g+1}}(x)^n] + c \ E \left[ \varphi_{Y_{g+1}} \left( (1 - U)x + U(1 - B_0) \right)^n \right]$$

and with the new notation

$$E_n \left[ H_\mu(x, Z^{N,0}(-g)) \right] = E_n \left[ H_\mu(x, Z^{N,g+1}(1)) \right].$$

We again seek to determine the same probability, except that this time we do not condition on the random environment, i.e. we search

$$p(x) := \mathbb{P}_x ((g + 1, 1), \ldots, (g + 1, n) \text{ are all of type } 0)$$

As before, this probability can, on one hand, be expressed using $X^{N,0}(g)$ as

$$p(x) = (1 - c)E_x \left[ (X^{N,0}(g))^{\sum_{i=1}^{g+1} K_{(g+1,i)}} \right]$$

$$+ c \ E_x \left[ (1 - U_{g+1})X^{N,0}(g) + U_{g+1}(1 - \xi(I_{g+1})) \right]^{\sum_{i=1}^{g+1} K_{(g+1,i)}}$$

$$= (1 - c)E_x \left[ \varphi_{Y_{g+1}}(X^{N,0}(g))^n \right]$$

$$+ c \ E_x \left[ \varphi_{Y_{g+1}} \left( (1 - U_{g+1})X^{N,0}(g) + U_{g+1}(1 - B_{X^{N,n}(g)}) \right)^n \right]$$

$$= E_x \left[ H_\mu(X^{N,0}(g), n) \right].$$

For the second equality we used that $(K_{(g+1,1)}, \ldots, K_{(g+1,n)}, Y_{g+1})$ and $X^{N,0}(g)$ are independent, and that conditional on $Y_{g+1}$ the $K_{(g+1,1)}, \ldots, K_{(g+1,n)}$ are iid, which in particular implies for any $\bar{x} \in [0, 1]$

$$E[\bar{x}^{\sum_{i=1}^{g+1} K_{(g+1,i)}}] = E[E[\bar{x}^{K_{(g+1,1)}} | Y]^n] = E[\varphi_{Y_{g+1}}(\bar{x})^n]$$

and likewise

$$E[\left( (1 - U)\bar{x} + U(1 - B_{\bar{x}}) \right)^{\sum_{i=1}^{g+1} K_{(g+1,i)}}] = E \left[ E \left[ \left( (1 - U)\bar{x} + U(1 - B_{\bar{x}}) \right)^{K_{(g+1,1)}} | U, B_{\bar{x}}, \bar{Y} \right]^n \right]$$

$$= E \left[ E \left[ \varphi_{Y_{g+1}}(\left( (1 - U)\bar{x} + U(1 - B_{\bar{x}}) \right)^n \right] \right]
Note that the random variables $K_{g+1,1}, \ldots, K_{g+1,n}$ are normally only conditionally independent, given a realisation of $Y_{g+1}$, which is why we cannot, in the unconditioned case, write the duality function as a product of expectations. On the other hand, we can calculate the same probability $p$ considering the ancestry with $Z^{N,g+1}(1)$ through

\[
p(x) = (1-c)\mathbb{E}[\sum_{i=1}^{N^{g+1}(1)} K_{1,i} + c \mathbb{E}_x \left[ \left((1-U_1)x + U_1(1-\xi(I_1))\right) \sum_{i=1}^{N^{g+1}(1)} K_{1,i} \right]]
\]

\[
= (1-c)\mathbb{E}_x \left[ \varphi_Y(x) Z^{N,g+1}(1) \right] + c \mathbb{E}_x \left[ \varphi_Y(x(1-U_1)x + U_1(1-\tilde{B})) Z^{N,g+1}(1) \right]
\]

\[
= \mathbb{E}[H_\mu(x, Z^{N,g+1}(1))]
\]

where we again profited from the independence of $Z^{N,g+1}(1)$ and $(K_{1,1}, \ldots, K_{1,N}, \tilde{Y})$ and the observations \[14\] and \[15\] with $g+1$ replaced by 1. Hence, we have proven

\[
\mathbb{E}_x \left[ H_\mu \left( X^{N,0}(g), u \right) \right] = \mathbb{E}_n \left[ H_\mu(x, Z^{N,g+1}(1)) \right]
\]

which together with \[13\] completes the proof. \[\square\]

2.2 Forward scaling limit in iid environment: rare selection

From now on we will focus solely on models with iid random environment. We will now study the asymptotic behaviour as the population size $N$ goes to infinity. In order to attain an interesting scaling limit process, selection must scale to zero either in its intensity, as in the classical weak selection model, or in its frequency, for so-called rare selection, corresponding to occasional catastrophic selective events. Recall all the notation of Section \[11\]. We will study existence of a continuous-time Markov process $X = (X(t) : t \geq 0)$ defined as the solution to the SDE

\[
dX(t) = \int (\mathbb{E}[X(t^-)K_y | X(t^-)] - X(t^-)) \mathcal{N}_z(dt, dy) - wX(t)(1-X(t))dt + c \int \int z(1_{u \leq X(t^-)}) - X(t^-)) \mathcal{N}_\epsilon(dt, dz, du) + \sigma \sqrt{X(t)}(1-X(t))dB(t)
\]

(16)

where $(B(t) : t \geq 0)$ is a Brownian motion, $\mathcal{N}_\epsilon$ is a Poisson point measure on $[0,\infty] \times [0,1]$ with intensity $ds \otimes z^{-2} \Lambda\epsilon(z)dz \otimes du$, where $\Lambda\epsilon$ is a distribution on $[0,1]$ with no atom in 0, $c, w \geq 0$, $\mathcal{N}_z$ is a Poisson point measure on $[0,\infty] \times [0,1]$ with intensity $ds \otimes \mu(dy)$ and $K_y$ is an $\mathbb{N} \cup \{\infty\}$-valued random variable with distribution $Q(y)$ parametrised by $y \in [0,1]$.

Note that, if $X$ exists, the compensator of $N_\epsilon$ is zero and Condition \[11\] guarantees that the compensator of $N_\epsilon$ is finite. As a result, $X$ solves the martingale problem associated with the generator $\mathcal{A}$, given by

\[
\mathcal{A}f(x) = \int_{[0,1]} \left[ f(\mathbb{E}[xK^*_y]) - f(x) \right] \mu(dy) - wx(1-x)f'(x)
\]

\[
+ \int_{[0,1]} \left\{ x[f(x(1-z) + z) - f(x)] + (1-x)[f(x(1-z)) - f(x)] \right\} \frac{1}{z^2} \Lambda\epsilon(z)dz
\]

\[
+ \sigma x(1-x)\frac{f''(x)}{2}
\]

(17)

for every $C_2$ function $f : [0,1] \rightarrow \mathbb{R}$.
Lemma 2.8. Assume Condition 7. Then there exists a unique strong solution to (16).

Definition 2.9. For a distribution $\Lambda_1$ on $[0, 1]$ with $\Lambda_1(\{0\}) = 0$, a measure $\mu$ on $[0, 1]$ and a kernel $Q$ satisfying Condition 1 and constants $w, c, \sigma \geq 0$, define the two-type Fleming-Viot process with weak and rare selection (FVWRS) parametrised by $Q$, $\mu$ and $w$ and $\Lambda_1$, $c$ and $\sigma$ as the unique strong solution $X = (X(t) : t \geq 0)$ to (16).

Proof of Lemma 2.8. For the case without the third summand in the generator (16) the statement of Lemma 2.8 was already proved in [4] Cor. 3.3. For the general case, the proof is an application of Theorem 5.1 in [32], of which we only need to verify conditions 3a), 3b) and 5a). Using the notation of [32], in our case the relevant functions are $\sigma(x) = \sqrt{\sigma x(1 - x)}1_{[0, 1]}(x)$, $b(x) = wx(1 - x)$, $g_0(x, (z, u)) = z(1_{[0, x]}(u) - x)1_{[0, 1]}(x)$ for $U_0 = [0, 1]^2$ and $g_1(x, y) = E[x^{K_y} - x_1]1_{[0, 1]}(x)$ for $U_1 = [0, 1]$. All conditions are easy to check for $g_0$ and were shown for $b$ and $\sigma$ in Equation (3.9) and (26) of [20], respectively, so we only need to concern ourselves with the selection component $g_1$.

Note that $\frac{\partial g_1}{\partial y}(x, y) = [E[K_y x^{K_y - 1} - 1]] \leq E[K_y - 1]$, for all $x \in [0, 1]$. Then, by the mean value theorem, for any $x_1, x_2 \in [0, 1]$

$$\int_{[0, 1]} |g_1(x_1, x) - g_1(x_2, x)| \mu(dy) \leq |x_1 - x_2| \int_{[0, 1]} E[K_y - 1] \mu(dy)$$

Since the integral is finite by Condition 1 this gives us condition 3a) of [32]. The observation above also shows that $\frac{\partial g_1}{\partial x}$ is $(\mu(dy) \otimes dx)$-integrable on $[0, 1] \times [0, 1]$, because

$$\int_{[0, 1] \times [0, 1]} \left| \frac{\partial g_1}{\partial x}(x, y) \right| \mu(dy) \otimes dx \leq \int_{[0, 1]} E[K_y - 1] \mu(dy) < \infty,$$

whence we can use Fubini’s Theorem and, using the fact that $g_1(x, y)^2 \leq |g_1(x, y)|$,

$$\int_{[0, 1]} (g_1(x, y))^2 \mu(dy) \leq \int_{[0, 1]} \int_{[0, x]} \left| \frac{\partial g_1}{\partial s}(s, y) \right| ds \mu(dy) \leq x \int_{[0, 1]} E[K_y - 1] \mu(dy)$$

for $x \in [0, 1]$, which yields the estimates for condition 5a) of [32].

We have now all the elements to prove the convergence of the 0-allele frequency process in the Wright-Fisher graph to the solution $X = (X(t) : t \geq 0)$ of (16). For clarity, we will first focus on the case of pure rare selection, i.e. with $w = 0$. In the pre-limit model, the parameters $\mu, c$ and the random environment process $Y$ will now be indexed by the corresponding population size $N$: $\mu_N, c_N, Y^N$. We will choose an iid environment with a distribution $\mu_N$ assigning a large weight on the event of no selection (hence we have rare selection) but such that, when selection occurs, its strength does not scale with $N$.

Theorem 2.10. Let $(\rho_N)_{N \in \mathbb{N}}$ be a sequence of positive numbers converging to 0.

For a constant $\sigma \in [0, \infty]$ assume

$$\lim_{N \to \infty} \rho_N^{-1} N^{-1} = \sigma. \quad (18)$$

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Let $\Lambda_c$ be a distribution on $[0, 1]$ with $\Lambda_c(\{0\}) = 0$ and $(c_N)_{N \in \mathbb{N}}$ a sequence in $[0, 1]$ converging to 0. For an $\alpha \in (0, 1/2)$ define

$$\Lambda^\alpha_N(du) := u^{-2} \mathbb{1}_{[1-\alpha, 1]}(u) \Lambda_c(du) \quad \text{and} \quad \Lambda^\alpha_N := \frac{1}{\Lambda^\alpha_N([0, 1])} \Lambda^\alpha_N$$

and assume that for a constant $c \in [0, \infty[$,

$$\lim_{N \to \infty} \rho^{-1}_N \frac{c_N}{\Lambda^\alpha_N([0, 1])} = c. \quad (19)$$

Let $Q$ be a probability kernel from $[0, 1]$ to $\mathbb{N} \cup \{\infty\}$ and $\mu$ a measure in $[0, 1]$ such that Condition 1 holds. In particular, $\mu$ is $\sigma$-finite, so let $(I_N)_{N \in \mathbb{N}}$ be an increasing sequence of sets such that we can define finite measures

$$\gamma_N(\cdot) := \mu(\cdot \cap I_N) \quad \text{and} \quad \bar{\gamma}_N := \frac{1}{\gamma_N([0, 1])} \gamma_N$$

and such that $\gamma_N([0, 1]) \rho_N$ converges to 0.

Lastly, assume

$$\lim_{N \to \infty} \gamma_N([0, 1]) c_N = 0. \quad (20)$$

For each $N \in \mathbb{N}$, let $X^N$ be the 0-allele frequency process started in 0 in a WF$(N, Y^N, Q, c_N, \Lambda^\alpha_N)$ graph as introduced in Definition 2.2, where $Y^N = (Y^N_g)_{g \in \mathbb{Z}}$ is an iid environment with common distribution

$$\bar{\mu}_N := (1 - \gamma_N([0, 1]) \rho_N) \delta_0 + \gamma_N([0, 1]) \rho_N \bar{\gamma}_N.$$

If $X^N_0 \xrightarrow{w} x \in [0, 1]$, as $N \to \infty$,

$$(X^N(\lfloor \rho^{-1}_N t \rfloor) : t \geq 0) \implies (X(t) : t \geq 0),$$

where $X = (X(t) : t \geq 0)$ is the two-type Fleming-Viot process with rare selection, i.e. the unique strong solution to (16) (for $w = 0$) started in $X_0 = 0$.

Recall that, due to the iid property of the environment, the distribution of $X^N$ does not depend on the starting time-point $g_0 = 0$.

Observe also, that the mechanisms for skewed offspring distribution and rare selection are very similar. The role of $c_N$ in the skewed offspring distribution is played by $\gamma_N([0, 1]) \rho_N$ for rare selection: they both describe the probability of an extreme, but rare event. In both cases we truncate a possibly infinite measure $- y^{-1} \Lambda_c(dy)$ and $\mu$ respectively – to obtain distributions for the finite population model. The analogue of assumption (19) for the case of rare selection also holds trivially as it is given by

$$\rho^{-1}_N \frac{\gamma_N([0, 1]) \rho_N}{\gamma_N([0, 1])} = 1$$

The role of assumption (20) becomes more clear when rewritten as

$$\lim_{N \to \infty} \frac{\gamma_N([0, 1]) \rho_N c_N}{\rho_N} = 0$$

which uncovers that (20) ensures that the probability of both rare events occurring simultaneously converges to 0 sufficiently quickly, in the appropriate time rescaling. Such an assumption simplifies the proof and it could be possibly weakened but this is beyond the scope of this paper.
Using the independence of \( f(x) \) for a given initial frequency \( X_N \) depending on \( X \) conditioning on the four possible cases reflecting occurrence vs non-occurrence of selection or multiple mergers. To this end, starting without loss of generality from generation \( g_0 = 0 \), let \( B_t \) and \( B_s \) be the random variables indicating whether selection, resp. multiple mergers occur in the first time-step. By construction of the reproduction mechanism, they are independent Bernoulli random variables with success parameter \( c_N \) and \( \rho_N \gamma_N \{0, 1\} \) respectively. For \( C_2 \) functions \( f : [0, 1] \to \mathbb{R} \) the generator then acts according to the rule

\[
A_N f(x) := \rho_N^{-1} \mathbb{E}_x \left[ f(X_N^N) - f(x) \right] = \rho_N^{-1} \left( 1 - \rho_N \gamma_N \{0, 1\} \right)(1 - c_N) \left( \frac{1}{2N} x^2 f''(x) + O \left( \frac{1}{N^2} \right) \right) + \rho_N \gamma_N \{0, 1\}(1 - c_N) \mathbb{E}_x \left[ f(X_N^N) - f(x) \right] B_t = 1, B_s = 0 \\
+ \rho_N \gamma_N \{0, 1\}(1 - c_N) \mathbb{E}_x \left[ f(X_N^N) - f(x) \right] B_t = 0, B_s = 1 \\
+ \rho_N \gamma_N \{0, 1\}(1 - c_N) \mathbb{E}_x \left[ f(X_N^N) - f(x) \right] B_t = 1, B_s = 1 \right) 
\] (21)

The first summand corresponds to the standard neutral Wright-Fisher model without multiple mergers, hence assumption \( (18) \) implies the convergence to the first component of the generator given in \( (17) \).

Since the last expectation is bounded, assumption \( (20) \) implies that the last summand vanishes as \( N \to \infty \), so we only need to calculate carefully the remaining two summands:

For the first of these two – the case of only skewed offspring distribution – observe that, since \( B_t = 1, B_s = 0 \), by virtue of the reproduction mechanism \( (6) \), for a given initial frequency \( X_0^N = x \), strength of correlation (multiple mergers) \( C_1^N = u \in [0, 1] \) and type \( B = b \in \{0, 1\} \) of the favoured parent, \( X_N^N \) is simply a Binomial random variable with parameters \( N \) and \( (1 - u)x + u(1 - b) \). Also note that given \( X_0^N = x \), \( B = \) a Bernoulli random variable with success parameter \( 1 - x \).

Apply Taylor’s expansion to \( f \) around \((1 - u)x + u(1 - b)\). We obtain, for an \( \eta \) depending on \( X_1^N, C_1^N, B \) and \( x \),

\[
\mathbb{E}_x \left[ f(X_1^N) - f(x) \right] B_t = 1, B_s = 0 = \mathbb{E}_x \left[ f((1 - C_1^N)x + C_1^N(1 - B)) - f(x) \right] B_t = 1, B_s = 0 \\
+ \mathbb{E}_x \left[ \frac{1}{2} f''(\eta)(X_N^N - (1 - C_1^N)x - C_1^N(1 - B))^2 \right] B_t = 1, B_s = 0
\]

Using the independence of \( U_1^N \), \( B_t \), and \( B_s \), we obtain can rewrite the first term:

\[
\rho_N^{-1} c_N \mathbb{E}_x \left[ f((1 - C_1^N)x + C_1^N(1 - B)) - f(x) \right] B_t = 1, B_s = 0 \\
= \rho_N^{-1} c_N \left. \int_{[0, 1]} (xf((1 - u)x + u) + (1 - x)f((1 - u)x) - f(x)) \frac{1}{u^2} \mathbb{P}_{([-\alpha, \alpha])}^N(du) \right|_{\alpha = 0} \\
\overset{N \to \infty}{\longrightarrow} c \int_{[0, 1]} (xf((1 - u)x + u) + (1 - x)f((1 - u)x) - f(x)) \frac{1}{u^2} \Lambda_x(du).
\]
The convergence in the last step follows from (19) and is uniform in \(x \in [0, 1]\). Using the conditional variance of \(NX_1^N\) given \(C_1^N\) and \(B\) allows us to estimate

\[
\begin{aligned}
|\mathbb{E}_x \left[ \frac{1}{2} f''(\eta) \left( X_1^N - (1 - C_1^N) x - C_1^N (1 - B) \right)^2 \right]_{B_\varepsilon = 1, B_s = 0} | \\
\leq \frac{1}{2} \sup_{z \in [0, 1]} |f''(z)| \mathbb{E}_x \left[ \frac{N (1 - (1 - C_1^N) x - C_1^N (1 - B)) \left( (1 - C_1^N) x + C_1^N (1 - B) \right)}{N^2} \right] | \\
= \frac{1}{2} \sup_{z \in [0, 1]} |f''(z)| \frac{1}{N \Lambda_N([0, 1])} \\
\times \left| \int_{[N \to 1]} \mathbb{E}_x \left[ (1 - (1 - u)x - u(1 - B)) \left( (1 - u)x + u(1 - B) \right) \right] \frac{1}{u^2} \Lambda_\varepsilon(du) \right| \\
\leq \frac{1}{2} \sup_{z \in [0, 1]} |f''(z)| \frac{1}{N \Lambda_N([0, 1])} N^{2\alpha - 1}.
\end{aligned}
\]

In the second step we simply used the independence of \(C_1^N\) and \(B\) as well as the definition of \(\Lambda_N\). Since the expectation in the integrand is not greater than 1, the last inequality holds because \(\Lambda_\varepsilon\) is a distribution. Since we chose \(\alpha < 1/2\), assumption (19) implies that this term vanishes. Note that also this bound is uniform in \(x \in [0, 1]\).

In the same spirit as for the skewed offspring distribution, given that we only observe rare selection, i.e. \(B_\varepsilon = 0, B_s = 1\), the distribution of \(NX_1^N\) conditioned on a strength of selection \(Y_1^N = y \in [0, 1]\) is again binomial with parameters \(N\) and \(\mathbb{E}[X^K_\varepsilon]\). Applying Taylor in this point one obtains for an \(\eta\) depending on \(X_1^N, Y_1^N\) and \(x\):

\[
\mathbb{E}_x \left[ f(X_1^N) - f(x) \right]_{B_\varepsilon = 0, B_s = 1} \\
= \mathbb{E}_x \left[ f(\mathbb{E}[X^K_\varepsilon | Y_1^N]) - f(x) \right]_{B_\varepsilon = 0, B_s = 1} \\
+ \mathbb{E}_x \left[ \frac{1}{2} f''(\eta)(X_1^N - \mathbb{E}[X^K_\varepsilon | Y_1^N])^2 \right]_{B_\varepsilon = 0, B_s = 1}.
\]

Again, using the conditional variance of \(NX_1^N\) given \(Y_1^N\), we estimate

\[
\begin{aligned}
\mathbb{E}_x \left[ \frac{1}{2} f''(\eta)(X_1^N - \mathbb{E}[X^K_\varepsilon | Y_1^N])^2 \right]_{B_\varepsilon = 0, B_s = 1} \\
\leq \frac{1}{2} \max_{z \in [0, 1]} f''(z) \frac{1}{N} \mathbb{E}_x \left[ \mathbb{E}[X^K_\varepsilon | Y_1^N](1 - \mathbb{E}[X^K_\varepsilon | Y_1^N]) \right]_{B_\varepsilon = 0, B_s = 1} \\
\leq \frac{1}{2} \max_{z \in [0, 1]} f''(z) \frac{1}{N}
\end{aligned}
\]

since the last expectation is bounded by 1. Since \(\rho_N \gamma_N([0, 1])\) vanishes, assumption (18) proves that this term also vanishes in the limit.

To calculate the first expectation on the other hand, note that conditioned on \(B_s = 1, Y_1^N\) is distributed according to \(\gamma_N\). Hence,

\[
\gamma_N([0, 1]) \mathbb{E}_x \left[ f(\mathbb{E}[X^K_\varepsilon | Y_1^N]) - f(x) \right]_{B_\varepsilon = 0, B_s = 1} \\
= \gamma_N([0, 1]) \int_{[0, 1]} (f(\mathbb{E}[X^K_\varepsilon]) - f(x)) \gamma_N(dy) \\
= \int_{[0, 1]} (f(\mathbb{E}[X^K_\varepsilon]) - f(x)) \mu(dy) \xrightarrow{N \to \infty} \int_{[0, 1]} (f(\mathbb{E}[X^K_\varepsilon]) - f(x)) \mu(dy).
\]

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To see that this convergence is uniformly in \( x \in [0,1] \), recall \( \text{(Q)} \) and observe that using the Mean-Value-theorem

\[
\left| \int_{[0,1]} \left( f(\mathbb{E}[x^K_y]) - f(x) \right) 1_{I_y}(y) \mu(dy) \right|
= \left| \int_{[0,1]} \left( f(\mathbb{E}[x^K_y]) - f(x) \right) 1_{I_y}(y) \frac{1}{\mathbb{E}[K_y - 1]} \Lambda_y(dy) \right|
\leq \max_{z \in [0,1]} |f'(z)| \int_{[0,1]} |\mathbb{E}[x^K_y] - x| 1_{I_y}(y) \frac{1}{\mathbb{E}[K_y - 1]} \Lambda_y(dy).
\]

Since \( K_y \) only takes integer values, as observed in the proof of Lemma \( \text{(2.8)} \), \( |\mathbb{E}[x^K_y] - x| \leq \mathbb{E}[K_y - 1] \) and the claim follows since \( \Lambda_y \) is a distribution.

Therefore we have proven that the assumptions of the theorem ensure \( \mathbb{A}^N f \to \mathbb{A} f \) uniformly on the compact \([0,1] \). Hence, using Theorem 19.28 in \( \text{[26]} \) we conclude the desired weak convergence.

**Remark 2.11 (\( \Lambda \)-selection).** Recall from the introduction in Section \( \text{(2.1)} \) that the measure \( \Lambda_x \), is a distribution on \([0,1] \) with no atom in 0 which describes the extreme events resulting from a skewed offspring distribution through \( y^{-2} \Lambda_x(dy) \) and recall also from the discussion after Condition \( \text{(Q)} \) that \( \Lambda_x \) is likewise a finite measure on \([0,1] \) with no atom in 0 describing the selection mechanism through \( \mu(dy) = (\mathbb{E}[K_y - 1])^{-1} 1_{(0,1]}(y) \Lambda_y(dy) \). The extent of the parallels between these two mechanisms becomes more transparent with the following observations. If for a sequence \( \Lambda^n_x, n \in \mathbb{N}, \) of such distributions we have \( \Lambda^n_x \overset{w}{\to} \sigma \delta_0, \) as \( n \to \infty, \) then also

\[
\int_{[0,1]} \left\{ x [f(x(1-z) + z) - f(x)] + (1-x) [f(x(1-z)) - f(x)] \right\} \frac{1}{z^2} \Lambda^n_x(dz)
\overset{n \to \infty}{\to} \sigma x(1-x) f''(x) \frac{2}{2}.
\]

For this reason it is common to find in the literature the interpretation that identifies \( \Lambda_x(\{0\}) \) with the intensity \( \sigma \) of the “Wright-Fisher noise” or, as will be seen later, of the “Kingman component” of the dual coalescence-mechanism (see for example \( \text{[38]} \) or, in a spatial set-up, in \( \text{[6]} \)).

Naturally, the question arises whether an analogous interpretation holds for the selection mechanism. Let \( \Lambda^n_x, n \in \mathbb{N} \) be a sequence of finite measure on \([0,1] \) such that \( \Lambda^n_x \overset{w}{\to} w \delta_0 \) as \( n \to \infty \) in the Prohorov-metric for a \( w > 0 \). Let \( A^n_x \) be the summand in the generator responsible for the rare selection mechanism induced by \( \Lambda^n_x \). Consider the kernel given by \( Q(y) = (1-y) \delta_1 + y \delta_2, \) \( y \in [0,1] \), i.e. the mechanism with at most binary branching. Then Condition \( \text{(Q)} \) holds automatically and implies that \( \mu \) has density \( 1/y \) with respect to \( \Lambda^n_x \) on \([0,1] \).

Applying Taylor’s expansion around \( x \) reveals

\[
A_x f(x) = \int_{[0,1]} \left\{ f(x) - x(1-x)y f'(x) + \mathcal{O}(y^2) - f(x) \right\} \frac{1}{y} \Lambda^n_x(dy)
\overset{n \to \infty}{\to} -wx(1-x)f''(x)
\]

which is the component responsible for genic (weak) selection in \( \text{(17)} \). The same result holds true for the choice of geometric \( Q \) (see Remark \( \text{(2.3)} \) and one might believe this to be true for every general kernel. However, we do not believe this
to hold. The following conditions on the kernel $Q = (Q(y) : y \in [0, 1])$, ensure convergence of the generator for rare selection to the generator of genic (weak) selection in the set-up above: Assume $y \mapsto Q(y, A)$ is continuous for every $A \in \mathcal{R}$ and that

$$\lim_{y \downarrow 0} \frac{\mathbb{P}(K_y \geq 2)}{\mathbb{E}[K_y - 1]} < \infty \quad \text{and} \quad \lim_{y \downarrow 0} \frac{\mathbb{P}(K_y = 2)}{\mathbb{E}[K_y - 1]} = 1. \quad (22)$$

Indeed, for such $Q$ (also satisfying Condition 1) using Taylor’s expansion around $x$ we see

$$\int_{[0, 1]} [f(\mathbb{E}[x^{K_y}]) - f(x)] \mu(dy) = \int_{[0, 1]} [f(\mathbb{E}[x^{K_y}]) - f(x)] \frac{1}{\mathbb{E}[K_y - 1]} \Lambda^n_x(dy)$$

$$= \int_{[0, 1]} (\mathbb{E}[x^{K_y}] - x) f'(x) \frac{1}{\mathbb{E}[K_y - 1]} \Lambda^n_x(dy) + o(1)$$

$$= - \int_{[0, 1]} \sum_{k=2}^\infty \sum_{l=0}^{k-2} \frac{1}{\mathbb{E}[K_y - 1]} \Lambda^n_x(dy) x(1-x) f'(x) + o(1)$$

$$\xrightarrow{n \to \infty} w x(1-x) f'(x).$$

The first and second condition in (22) are used to justify the “$+o(1)$” in the second and fourth equality respectively. For the third equality we used that $x^k - x = -x(1-x)^{k-2} x^l$ for any $k \in \mathbb{N}$ and $x \in [0, 1]$. We conjecture that these conditions are also necessary and that if one only assumes the first condition in (22), then the limit belongs to the family of diffusions related to frequency dependent selection studied in [20].

We may, however, also obtain the diffusion with weak selection from the particle system directly. In order to obtain both weak and rare selection simultaneously, we have to carefully design our random environment. $\mu$ will still be responsible for the rare mechanism only. The kernel of distributions will now consist of distributions from two sets: a general one describing the rare selection and a set of geometric distributions describing weak selection. As before, in the particle system we will have to ensure to rarely make use of the former, while we weaken the effect of the latter as $N \to \infty$. In order to accomodate the different scalings of the mechanisms without overcomplicating notation, we exceptionally allow the environment to take values in $[-1, 1]$.

**Theorem 2.12.** Retain all the assumptions and notation of Theorem 2.10. For a sequence $(w_N)_{N \in \mathbb{N}}$ in $[0, 1]$ and a constant $w \in [0, \infty)$ assume

$$\lim_{N \to \infty} \rho^{-1}_N w_N = w.$$

Let $\tilde{Q} := (Q(y) : y \in [-1, 0])$ be such that $Q(y) = \text{Geo}_N(1+y)$, for $y \in [-1, 0]$.

For each $N \in \mathbb{N}$, let $X^N$ be the $\Theta$-allele frequency process in a $WF(N, Y^N, \tilde{Q}, c_N, \tilde{A}_N^\gamma)$ graph and iid $[-1,1]$-valued environment $Y^N$ with common distribution

$$\mu_N := (1 - \gamma_N([0, 1])\rho_N) \delta_{-w_N} + \gamma_N([0, 1])\rho_N \tilde{A}_N^\gamma.$$

Then, if $X_0^N \xrightarrow{w} x \in [0, 1]$, as $N \to \infty$,

$$(X^N([\rho_N^{-1} t]) : t \geq 0) \Rightarrow (X(t) : t \geq 0),$$

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where \( X = (X(t) : t \geq 0) \) is the two-type Fleming-Viot process with weak and rare selection, i.e. the unique strong solution to (21) with \( X_0 = x \).

**Proof.** The proof is exactly analogous to that of Theorem 2.10. As done there, one can condition, with the help of suitable Bernoulli random variables, on whether or not now rare selection or multiple mergers occur. For the first summand in (21), however, one now calculates

\[
\mathbb{E}_x [f(X^N_t) - f(x)] B_t = 0, B_s = 0
\]

\[
= -w_N \frac{x(1 - x)}{1 - x w_N} f'(x) + \frac{1}{2 N} x(1 - x) f''(x) \frac{1 - w_N}{(1 - x w_N)^2} + O(w_N^2) + O(N^{-2})
\]

(doiing a Taylor expansion around \( x \)). The three other summands coincide with those in the proof of Theorem 2.10 and the claim follows.

2.3 Moment duality and convergence to the branching coalescing process in random environment

As foreshadowed in the introduction, there is a genealogical process arising as before Condition 1, the BCPRE Lemma 2.14.

**Definition 2.13.** For a distribution \( \Lambda_c \) on \([0, 1]\) with \( \Lambda_c(\{0\}) = 0 \) and for a measure \( \mu \) on \([0, 1]\) and a kernel \( Q \) satisfying Condition 4, define the branching coalescing process in random environment \( Z = (Z(t) : t \geq 0) \) with branching intensity \((Q, \mu, w)\) and coalescing intensity \((\Lambda_c, c, \sigma)\) as the continuous time \(\mathbb{N} \cup \{\infty\}\)-valued Markov chain with positive jumps from \( n \in \mathbb{N} \) to \( n + k \) at rate

\[
\int_{[0, 1]} \mathbb{P} \left( \sum_{j=1}^{n} K_{y,j} = n + k \right) \mu(dy) + w n \delta_{1, k}
\]

(where \( K_{y,1}, \ldots, K_{y,n} \) are iid with distribution \( Q(y) \)) and with negative jumps from \( n \) to \( n - k \in \mathbb{N} \) occurring at rate

\[
c \int_{[0, 1]} \binom{n}{k+1} \frac{y^{k+1} (1 - y)^{n-k-1} \Lambda_c(dy)}{y^2} + \sigma \left( \frac{n}{2} \right) \delta_{1, k},
\]

and entrance law \( \mathbb{E}^{\infty}[x^{Z_t}] := \mathbb{P}_x (X(t) = 1) \), where \((X(t) : t \geq 0)\) is the two-type Fleming-Viot process with rare and weak selection parametrised by \( Q, \mu, w \) and \( \Lambda_c, c \) and \( \sigma \).

Before we prove the duality, we will now see that \( Z \) is conservative, i.e. actually takes values in \( \mathbb{N} \) when started in an element of \( \mathbb{N} \) and that it is Feller with respect to the topology of the harmonic numbers. Denote \( C \) the set of continuous functions from the metric space \( \mathbb{N} \cup \{\infty\} \) with \( d(n, m) = |\frac{1}{m} - \frac{1}{n}| \) to itself.

**Lemma 2.14.** Under Condition 4, the BCPRE \( Z = (Z(t) : t \geq 0) \) given in Definition 2.13 is Feller with respect to the topology of the harmonic numbers on \( \mathbb{N} \cup \{\infty\} \) and conservative. More precisely,

\[
\forall n \in \mathbb{N}, \quad \forall t \geq 0 : \quad \mathbb{E}^{n}[Z_t] < \infty.
\]

**Proof.** To prove that \( Z \) is Feller we will show that the semigroup \( P_t f(n) = \mathbb{E}_n[f(Z_t)] \) sends \( C \) to \( C \). All the other properties of a Feller semigroup can be verified. Consider the process \( (B_t^{(i,j)}) := (B_t^{(1,i)}, B_t^{(2,j)}, \ldots, B_t^{(i,j)}) \) with starting
condition \((B^{(1,l)}_0, B^{(2,l)}_0, ..., B^{(l,l)}_0) = (1, 1, ..., 1)\) rates from \((n_1, ..., n_l)\) with \(n_1 \in \mathbb{N}\) and \(n_i \in \mathbb{N}_0\) for \(i = 2, ..., l\) to \((n_1 + k_1, ..., n_l + k_l)\) at rate

\[
\int_{[0,1]} \prod_{i=1}^l \mathbb{P} \left( \sum_{j=1}^{n_i} K_{y,j} = n_i + k_i \right) \mu(dy) + \sum_{i=1}^l \alpha_i \delta_{e_i}(k_i, ..., k_l)
\]

and from \((n_1, ..., n_l)\) to \((n_1 - k_1, ..., n_l - k_l) + c(\bar{k})\), where \(\bar{k} = (k_1, ..., k_l)\) and \(c(\bar{k}) = c_r\) if and only if \(k_r > 0\) and \(k_j = 0\) for \(al j < r\), occurring at rate

\[
c \int_{[0,1]} \prod_{i=1}^l \left( \frac{n_i}{k_i} \right) y^{k_i} (1-y)^{n_i-k_i} \sum_{i=1}^l \frac{\alpha_i}{y^2} + \left( \frac{n_i}{2} \right) \delta_{e_i}(k_i, ..., k_l) + \sum_{i=1}^l \sum_{j=1}^{i-1} n_i n_j \delta_{e_i+e_j}(k_i, ..., k_l).
\]

Note that the rates are consistent and thus \((B_t) := (B^{(1,l)}_t) := (B^{(1,1)}_t, B^{(1,2)}_t, ...)\) can now be constructed by Kolmogorov extension Theorem. This is a Coupling of \(Z_t\) started with different initial conditions. Indeed, if we denote \(Z^{(n)}_t := Z_t|_{Z_0 = n}\), then in distribution \(Z^{(n)}_t := \sum_{i=1}^n B^{(i)}_t\) and \(Z^{(\infty)}_t := \sum_{i=1}^\infty B^{(i)}_t\). Observe that

\[
\mathbb{E}_n[f(Z_t)] - \mathbb{E}_\infty[f(Z_t)] = \mathbb{E}_n[f(\sum_{i=1}^n B^{(i)}_t)] - f(\sum_{i=1}^\infty B^{(i)}_t)
\]

This can be bounded by

\[
\mathbb{E}_n[f(\sum_{i=1}^n B^{(i)}_t) - f(\infty)] \sum_{i=1}^\infty B^{(i)}_t = \infty + \mathbb{E}_n[f(\sum_{i=1}^n B^{(i)}_t) - f(\sum_{i=1}^\infty B^{(i)}_t)] \sum_{i=1}^\infty B^{(i)}_t < \infty.
\]

Note that the first summand vanishes when \(n\) tends to infinity because \(f\) is a continuous function. If \(\sum_{i=1}^\infty B^{(i)}_t < \infty\) then there exist a random natural number \(n(t)\) such that \(\sum_{i=1}^n B^{(i)}_t = 1\) for all \(n > n(t)\). This implies that the second summand tends to zero as \(n\) tends to infinity, this implies that

\[
\lim_{n \to \infty} \mathbb{E}_n[f(Z_t)] - \mathbb{E}_\infty[f(Z_t)] = 0
\]

in turns, this imply that \(P_t f\) is continuous, which allow us to conclude that \(Z_t\) is a Feller process.

Let \(W_t\) be the process with the same branching mechanism than \(Z\) but with no coalescence. It is clear that stochastically \(W_t > Z_t\). Now we use Dynkin’s formula on the function \(f_m(n) = n1_{\{n < m\}}\) to observe that

\[
f_m(W_t) = \int_0^{\tau_m} \int_{[0,1]} \mathbb{P} \left( \sum_{j=1}^{W_s} K_{y,j} = k \right) \left[ f_m(k) - f_m(W_s) \right] \mu(dy) + w W_s \mu[1_{\{f_m(W_s+1) - f_m(W_s)\}]} ds
\]

is a martingale. Also, by Fubini, \(\mathbb{E}_n[W_t] = \lim_{n \to \infty} \mathbb{E}_n[f_m(W_t)]\) and observing that the identity is bigger than \(f_m\)

\[
\mathbb{E}_n[f_m(W_t)] - n \leq \mathbb{E}_n[\int_0^{\tau_m} \int_{[0,1]} \mathbb{P} \left( \sum_{j=1}^{W_s} K_{y,j} = k \right) \left[ k - W_s \right] \mu(dy) + w W_s ds]
\]

Note that

\[
\mathbb{E}_n[\int_{[0,1]} \mathbb{P} \left( \sum_{j=1}^{W_s} K_{y,j} = k \right) \left[ k - W_s \right] \mu(dy)] = \mathbb{E}_n[W_s] \int_{[0,1]} \left[ K_{y,j} - 1 \right] \mu(dy)
\]
Assumption one and the above formulae imply that
\[ E_n[W_t] \leq n + \int_0^t E_n[W_s] \left( \int_{[0,1]} (K_{y,j} - 1) \mu(dy) + w \right). \]
Gronwall’s inequality implies that \( E_n[W_t] < \infty \) and stochastic domination that \( E_n[Z_t] < \infty \), which finishes the proof.

Now that we know that \( Z \) is Feller, we can prove it is the moment dual of \( X \).

**Lemma 2.15** (Moment duality). Under Condition 1 let \( X = (X(t) : t \geq 0) \) be the two-type \( \Lambda \)-process with rare and weak selection solution to (16) and let \( Z = (Z(t) : t \geq 0) \) be the branching coalescing process in random environment from Definition 2.13.
For any \( x \in [0,1], n \in \mathbb{N} \cup \{\infty\} \) and \( t \geq 0 \) we have
\[ E_x[X(t)^n] = E^n[x^{Z(t)}]. \]

**Proof.** The case \( n = \infty \) holds by the choice of the entrance law. By the Markov property, for every other \( n \), the proof can be done by calculating the generator applied to the function(s) \( f_x(n) := f^n(x) := x^n \). Recall the generator \( \mathcal{A}_x \) of \( X \) from (17) and let \( \mathcal{B}_x \) be the generator of \( Z \).
Since the moment duality relations between the Wright-Fisher diffusion and the Kingman coalescent, between the \( \Lambda \)-jump diffusion and the \( \Lambda \)-coalescents and between binary branching and the logistic ODE are well-known [7], the additive structure of the generator allows us to only consider the component of the generators responsible for rare selection, which we denote by \( \mathcal{A}_x \) and \( \mathcal{B}_x \) respectively. For any \( y \in [0,1] \) and \( n \in \mathbb{N} \) let \( K_{y,j} \) for \( j = 1, \ldots, n \) be iid with distribution \( Q(y) \). Then, for any \( x \in [0,1] \) and \( n \in \mathbb{N}_0 \)
\[ \mathcal{A}_x f^n(x) = \int_{[0,1]} \left\{ (E[x^{K_y}])^n - x^n \right\} \mu(dy) \]
\[ = \int_{[0,1]} \left\{ E[x^{\sum_{j=1}^n K_{y,j}}] - x^n \right\} \mu(dy) \]
\[ = \int_{[0,1]} \left[ \sum_{k=n}^\infty x^k \mathbb{P}\left( \sum_{j=1}^n K_{y,j} = k \right) - x^n \right] \mu(dy) \]
\[ = \int_{[0,1]} \left[ \sum_{k=n}^\infty \mathbb{P}\left( \sum_{j=1}^n K_{y,j} = k \right) (x^k - x^n) \right] \mu(dy) = \mathcal{B}_x f_x(n) \]
Since we know that \( X \) is a Markov solutions to the martingale problem associated to \( \mathcal{A}_x \) and Lemma 2.14, \( Z \) is Feller, the moment duality between \( X \) and \( Z \) follows immediately (see e.g. Proposition 6.1 in [11]).

As an important application of duality, we will prove the Feller property for the process \( X \), which is a simple consequence of \( Z \) being conservative and was already used in the proof of Theorem 2.12.

**Lemma 2.16.** Under Condition 1 the two-type Fleming-Viot-process with weak and rare selection defined in Definition 2.13 is Feller.

**Proof.** Let \( f(x) := x^n \) for fixed \( n \in \mathbb{N}_0 \). Let \( (\hat{P}_t)_{t \geq 0} \) be the semigroup generated by \( \mathcal{A} \) given in (17). Then, using the moment duality from Lemma 2.15
\[ \hat{P}_t f(x) = E_x[f(X(t))] = E_x[X(t)^n] = E^n[x^{Z(t)}]. \]
Note that, since $Z$ is conservative, $x \mapsto x^{Z(t)}(\omega)$ is continuous for all $x \in [0,1]$ for $\mathbb{P}$-almost all $\omega \in \Omega$. Hence, by bounded convergence and using duality again

$$\lim_{x \to 0} \tilde{P}_t f(x) = \lim_{x \to 0} \mathbb{E}^x[x^{Z(t)}] = \mathbb{E}^x[\tilde{x}^{Z(t)}] = \mathbb{E}_x[X(t)^N] = \tilde{P}_t f(\tilde{x})$$

for all $\tilde{x} \in [0,1]$. Therefore, for every $t \geq 0$, $\tilde{P}_t$ maps monomials to continuous functions. By the linearity of the expectation this also holds for polynomials and by the Stone-Weierstrass-Theorem we have proven the claim.

As a second and important consequence of the moment duality, we are now able to prove the missing convergence of the ancestral process to the BCPRE from Definition 2.13.

**Theorem 2.17.** Assume the conditions of Theorem 2.12 and let $Z^N$ be the ancestral process on the Wright-Fisher graph with selection in random environment and multiple mergers $WF(N,Y^N,Q \cup \check{Q},c_N,\Lambda_k)$ for an iid environment $Y^N = (Y^N_\theta)_{\theta \in \mathbb{Z}}$ with common distribution $\mu_N := (1-\gamma_N([0,1])\rho_N)\delta_{-w_N} + \gamma_N([0,1])\rho_N\gamma_N$.

Then

$$(Z^N \left([-\lceil \rho_N^{-1}t \rceil]\right)) : t \geq 0 \implies (Z(t) : t \geq 0),$$

where $Z = (Z(t) : t \geq 0)$ is the branching coalescing process in random environment given in Definition 2.13, when we equip $\mathbb{N}$ with the topology of the harmonic numbers, by considering the distance $d(m,n) = |\frac{1}{m} - \frac{1}{n}|$ for $n,m \in \mathbb{N} \cup \{\infty\}$ with $\frac{1}{\infty} := 0$.

**Proof.** The key in this proof is to show that the discrete semigroup $P^N$ of $(Z^N\left([-\lceil \rho_N^{-1}t \rceil]\right)) : t \geq 0$ converges for any $t > 0$ strongly to the semigroup $P$ of $Z := (Z(t) : t \geq 0)$, when applied to functions of the form $f_\lambda(n) = e^{-\lambda n}$, $\lambda > 0$. Since $Z$ is Feller by Proposition 2.14 and the functions $f_\lambda$ are dense in the set of functions that are continuous and vanish at infinity in this topology, this implies weak convergence by Theorem 19.28, (ii) of [26].

The convergence of the semigroups will prove to be a consequence of the convergence in Theorem 2.10 using the moment duality from Lemma 2.10 for $X$ and $Z$ and the sampling duality from Proposition 2.7 for $X^N$ and $Z^N$. First, observe that the sampling duality approximates the moment duality for large $N$ for our choice of $\mu_N$: conditioning on the choice of distribution for $Y^N_\theta$, we can rewrite the sampling duality function in the notation of Proposition 2.4 as

$$H^N_{\mu_N}(x,n) = (1 - c_N)\mathbb{E}[\varphi^N_{Y^N}(x)^n] + c_N\mathbb{E}[\varphi^N_{Y^N}(1-U)x + U(1-B_x))^n]$$

$$= (1 - c_N)(1-\rho_N\gamma_N([0,1]))x^n \left(1 - \frac{w_N}{1 - xw_N}\right)^n + \mathbb{E}[\varphi^N_{Y^N}(x)^n \mid Y^N_\theta \sim \gamma_N|\rho_N\gamma_N([0,1]) + O(c_N)]$$

$$= (1 - c_N)(1-\rho_N\gamma_N([0,1]))x^n \left(1 - \frac{w_N}{1 - xw_N}\right)^n + O(\rho_N\gamma_N([0,1])) + O(c_N)$$

$$= x^n \left(1 - \frac{w_N}{1 - xw_N}\right)^n + O(\rho_N\gamma_N([0,1])) + O(c_N)$$

where we crudely estimated the expectations and the expression in the first summand by 1. Note that this way the convergence of the remainder terms is uniform.
in $n$ and $x$. Then the sampling duality can be written as

$$
\mathbb{E}^n \left[ x^{Z_N(-g)} \left( \frac{1 - w_N}{1 - x w_N} \right)^{-Z_N(-g)} \right]
= \mathbb{E}_x \left[ \left( X_N(g) \right)^n \left( \frac{1 - w_N}{1 - X_N(g) w_N} \right)^n \right] + O(\rho N \gamma_N([0, 1])) + O(c_N)
$$

which we can rearrange to

$$
\mathbb{E}^n \left[ x^{Z_N(-g)} \right] = \mathbb{E}_x \left[ \left( X_N(g) \right)^n \left( \frac{1 - w_N}{1 - X_N(g) w_N} \right)^n \right] + O(\rho N \gamma_N([0, 1])) + O(c_N)
$$

Note that the function $h_N : [0, 1] \to [0, 1]$, $h_N(x) := x^n \left( \frac{1 - w_N}{1 - x w_N} \right)^n$, is continuous and bounded and converges uniformly to $h(x) := x^n$. In addition, the sequence is decreasing in $n$. Hence, the weak convergence of $X_N([\rho_N^{-1} t]) \to X(t)$ from Theorem 2.10 implies

$$
\mathbb{E}_x \left[ \left( X_N([\rho_N^{-1} t]) \right)^n \left( \frac{1 - w_N}{1 - X_N([\rho_N^{-1} t]) w_N} \right)^n \right] \xrightarrow{N \to \infty} \mathbb{E}_x[X(t)^n]
$$

for any $t \geq 0$ and any $x \in [0, 1]$, uniformly in $n$, which takes care of the first summand. For the second, consider the functions $\tilde{h}_{N,x} : [0, 1] \to [0, 1]$, $\tilde{h}_{N,x}(u) := \exp \left( u^{-1} \log \left( \frac{x - \frac{1 - w_N}{1 - x w_N}}{\frac{1 - w_N}{1 - x w_N}} \right) \right) \mathbb{I}_{[0]}(u)$ and note that by Dini’s Theorem this converges to $\tilde{h}_x(u) := \exp(u^{-1} \log(x)) \mathbb{I}_{[0]}(u) = x^{(u^{-1})} \mathbb{I}_{[0]}(u)$ uniformly over all $u \in [0, 1]$. This allows us to estimate

$$
0 \leq \mathbb{E}^n \left[ x^{Z_N(-g)} \left( 1 - \left( \frac{1 - w_N}{1 - x w_N} \right)^{-Z_N(-g)} \right) \right]
\leq \sup_{k \in \mathbb{N}} \mathbb{E}^n \left[ x^k \left( 1 - \left( \frac{1 - w_N}{1 - x w_N} \right)^k \right) \right]
\leq \sup_{u \in [0, 1]} (\tilde{h}_x(u) - \tilde{h}_{N,x}(u)) \xrightarrow{N \to \infty} 0
$$

for any $g \in \mathbb{Z}$ and $x \in [0, 1]$. Note that this convergence is again uniformly in $n$. Therefore, rescaling time and taking the limits in (23) we obtain

$$
\lim_{N \to \infty} \mathbb{E}^n \left[ x^{Z_N(-[\rho_N^{-1} t])} \right] = \mathbb{E}_x[X(t)^n]
$$

for every $t \geq 0$ and $x \in [0, 1]$, uniformly in $n \in \mathbb{N}_0$. Now to prove convergence of the semigroups fix $t > 0$ and $\lambda > 0$. Define $x := e^{-\lambda t}$ and observe that, using the observations above and the moment duality from Lemma 2.15,

$$
P^N_t f_\lambda(n) = \mathbb{E}_n[f_\lambda(Z_N(-[\rho_N^{-1} t]))] = \mathbb{E}_n[x^{Z_N(-[\rho_N^{-1} t])}]
\xrightarrow{N \to \infty} \mathbb{E}_x[X(t)^n] = \mathbb{E}_n[x^{Z(t)}] = P_t f_\lambda(n),
$$

uniformly in $n$, which completes the proof.
3 Long term behaviour

Throughout this section assume $Q$ and $\mu$ to be such that Condition 1 holds. In order to avoid trivialities, assume also that $\mu([0,1]) + w + c + \sigma > 0$.

Taking a closer look at (16), we see that the two-type FV-process for rare and/or weak selection $X = (X(t) : t \geq 0)$ is a (bounded) supermartingale, since the last two terms – corresponding to the neutral genetic drift – each yield martingales, while the first two terms – corresponding to selection – give a downward drift and downward jumps, respectively. Hence converges $P$-a.s. to a random variable, which we will name $X_\infty$. The distribution of this random variable is not only of mathematical interesting, but of biological relevance as it encodes the probabilities of fixation or extinction of the weak allele or, a priori, coexistence of the two types traced. As expected, coexistence can be ruled out almost surely, in this case as a direct consequence of the duality between $X$ and the branching coalescing process in random environment $Z$, which also describes how the the weak allele’s chance of survival (and thus fixation) depends on the ergodic properties of $Z = (Z(t) : t \geq 0)$, as we point out in the following remark.

**Remark 3.1.** Applying the same arguments as in Lemma 4.7 of [20], the duality obtained in Lemma 2.15 implies:

(i) If $Z$ is positive recurrent, then it has a unique invariant distribution $\nu$ and

$$\forall x \in [0,1] : P_x (X_\infty \in \cdot) = (1 - \varphi_\nu(x))\delta_0 + \varphi_\nu(x)\delta_1,$$

where $\varphi_\nu$ is the probability generating function of $\nu$.

(ii) If, on the other hand, $Z$ is not positive recurrent, then

$$\forall x \in [0,1] : P_x (X_\infty = 0) = 1.$$

In particular, we always know $X_\infty \in \{0,1\} P_x$-a.s. for any $x \in [0,1]$.

Note also that the dichotomy implies that if there exists an $x \in [0,1]$ such that $P_x (X_\infty = 0) < 1$, then this holds for all $x \in [0,1]$.

Naturally, the question arises how the chances of survival of the weak allele depend on the strength of selection. We answer this with Theorem 3.2 below and can use the above observations to consequently deduce the ergodic behaviour of the branching coalescing process in random environment in Corollary 3.8.

3.1 Probability of fixation of the weak allele

The mechanisms of selection and genetic drift compete in their influence on the probability of fixation (or extinction) of the weak allele. The strength of the genetic drift is characterised by $\sigma$ and the pair $c$ and

$$\beta^* := \frac{1}{2} \mathbb{E} \left[ \frac{1}{W(1-W)} \right],$$

respectively. Here, $W := Y^c U$, where $Y^c \sim \Lambda_c$, $U$ has density $2u$ on $[0,1]$ and they are independent.

Analogously, the strength of weak selection is given by $w$ and that of rare selection by the pair $\alpha_s := \Lambda_s([0,1])$ and

$$\alpha^* := \mathbb{E} \left[ \frac{1}{1+V \mathbb{E} [K_{Y_s} - 1 | Y^s]} \right],$$

respectively. Here, $W := Y^c U$, where $Y^c \sim \Lambda_c$, $U$ has density $2u$ on $[0,1]$ and they are independent.
where $V$ is uniform on $[0,1]$ and $Y_s \sim \alpha_s^{-1} \Lambda_s([0,1])$ and they are independent.

As formalised in the following theorem, if the total strength of selection is sufficiently strong, it overcomes the genetic drift and the weak allele will become extinct almost surely. If not, it retains a positive probability of survival even in the presence of selection.

**Theorem 3.2.** Let $X = (X(t) : t \geq 0)$ be the two-type FV-process for weak and rare selection given by (16) for a $\sigma$-finite $\mu$. Define

$$p(x) := \mathbb{P}_x (X_\infty = 0)$$

to be the probability of extinction of the weak allele 0, given we start with a frequency $x \in [0,1]$.

Assume $\beta^* < \infty$.

(i) If $\alpha_s \alpha^* + w < \beta^*$, then for all $x \in [0,1]: p(x) < 1$.

(ii) If $\alpha_s \alpha^* + w > \beta^*$, then for all $x \in [0,1]: p(x) = 1$.

$\beta^*$ is the threshold identified for weak selection as defined with this representation in Equation (26) in [21] and coincides with the threshold in [14]. Note that, given Condition 1, the assumption of Theorem 3.2 is the assumption of Theorem 3 in [21], which also treats the critical case. In particular under this condition, $W$ can not have an atom at zero and hence $\sigma = 0$ in this result for both weak and rare selection $X$. Let us stress that [14] succeeds to also cover the case of $\beta^* = \infty$.

**Remark 3.3.** In the case studied in [12] lizards with long fingers have a selective advantage whenever their habitat is hit by a hurricane, as their enhanced ability to hold on prevents them from being - literally - blown away. A generation under the influence of a hurricane can be modelled as a two-type Wright-Fisher model with selection in a random environment, taking $K_y \sim Q(y)$ to be geometric with parameter $1 - y$ and adapt the distribution of $Y_s$, to model the frequency and intensity of hurricanes. Theorem 3.2 now gives conditions for which the individuals with long fingers will go to fixation almost surely, and thus help us to understand how pulses of selection shape the evolution of lizards in particular and all forms of life in general.

**Remark 3.4.** The strength of rare selection is determined by both the kernel $Q = (Q(y) : y \in [0,1])$ and the measure $\mu$, respectively $\Lambda_s$. Two relevant examples are the case of geometric $Q$

$$Q_{geo}(y) = \sum_{i=1}^{\infty} (1 - y)y^{i-1} \delta_i$$

through its connection to weak selection (see Remark 2.3) and the case of binary $Q$

$$Q_{bin}(y) = (1 - y)\delta_1 + y\delta_2$$

as the simplest branching mechanism. In these cases we obtain

$$\alpha_{geo}^* := \mathbb{E} \left[ \frac{1}{1 + V Y_s^*} \right] \quad \text{and} \quad \alpha_{bin}^* := \mathbb{E} \left[ \frac{1}{1 + V Y_s^*} \right].$$

Observe that, given the same choice of $\Lambda_s$, $\alpha_{geo}^* \leq \alpha_{bin}^*$ and we say that the effective strength of rare selection is larger in the binary case, than in the geometric case, since this, of course, implies $\alpha_s \alpha_{geo}^* \leq \alpha_s \alpha_{bin}^*$. 

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Theorem 3.2 is obtained as a combination of two observations: Lemma 3.5 establishes the connection between the threshold and the integrability in time of the expected frequency of the weak allele. Lemma 3.6 explains that, if the frequency process converges to 0 almost surely, then it does so quickly, in the sense that its expectation is integrable over time. Indeed, we will prove that in this case, the expectation decays exponentially.

Lemma 3.5. Let \( X = (X(t) : t \geq 0) \) be the two-type FV-process for weak and rare selection given by (10). Assume \( \beta^* < \infty \).

(i) If \( \alpha_s \alpha^* + w < \beta^* \), then there exists an \( \bar{x} \in [0, 1] : \int_{[0, \infty]} \mathbb{E}_x[X(s)]ds = \infty \).

(ii) If \( \alpha_s \alpha^* + w > \beta^* \), then for all \( x \in [0, 1] : \int_{[0, \infty]} \mathbb{E}_x[X(s)]ds < \infty \).

Lemma 3.6. Let \( X = (X(t) : t \geq 0) \) be the two-type FV-process for weak and rare selection given by (10) for a \( \sigma \)-finite \( \mu \). For any \( x \in [0, 1] : \)

\[
\int_{[0, \infty]} \mathbb{E}_x[X(s)]ds < \infty \iff \mathbb{P}_x(X_\infty = 0) = 1.
\]

Given these observations the proof of Theorem 3.2 is straightforward.

Proof of Theorem 3.2. Assuming \( \alpha_s \alpha^* + w < \beta^* \), Lemma 3.5 (i) and Lemma 3.6 imply the existence of an \( \bar{x} \in [0, 1] \) such that \( \mathbb{P}_x(X_\infty = 0) < 1 \). Therefore, we are in case (i) of Remark 3.1 from which we may conclude that \( \mathbb{P}_x(X_\infty = 0) < 1 \) for all \( x \in [0, 1] \) which proves (i). (ii) is immediate from Lemmas 3.5 (ii) and 3.6.

The proof of Lemma 3.5 is quite delicate in that it requires analysis of a suitable Lyapunov function and is thus postponed to Section XXX. We proceed with the proof of Lemma 3.6 first. The result itself can be explained with the following intuition: If one believes that the sample heterozygosity \( \mathbb{E}_x[X(t)(1 - X(t))] \) decays exponentially over time for any \( x \in [0, 1] \) as it does in the classical case, the assumption \( \mathbb{P}_x(X_\infty = 0) = 1 \) means that the term \( 1 - X(t) \) cannot contribute to this decay, hence \( \mathbb{E}_x[X(t)] \) should decay exponentially, as we will indeed prove.

The idea of the proof is to obtain a geometric bound for the analogous quantity in the finite population size model. This will be done by estimating the probability that a uniformly chosen individual and an individual of the strong type picked from the same generation have a disjoint ancestry. A crucial observation for this estimate is that the assumption \( \mathbb{P}_x(X_\infty = 0) = 1 \) implies an infinite genealogy of strong individuals, which will allow us to sample the strong individual uniformly and independently of the first individual.

Proof of Lemma 3.6. Since we know that the limit for \( t \to \infty \) of \( X(t) \) exists and takes values in \( \{0, 1\} \) \( \mathbb{P}_x \)-a.s. for any \( x \in [0, 1] \), the implication \( \Rightarrow \) is immediate.

The converse \( \Leftarrow \), however, requires more care. Let us first consider the case where \( \sigma + c = 0 \), i.e. there is no genetic drift. Since we assumed the process not to be constant, we know \( \alpha_s \alpha^* + w > 0 \), and by Lemma 3.5 (ii) \( \int_{[0, \infty]} \mathbb{E}_x[X(s)]ds < \infty \) (for all \( x \in [0, 1] \)), which suffices for \( \Leftarrow \).

Assume now that \( \sigma + c > 0 \). The proof is split in three steps and uses that \( (X(t))_{t \geq 0} \) is the (appropriately rescaled) weak limit of a finite particle system \( (X^N(g))_{g \in \mathbb{N}_0} \), as observed in Theorem 2.1.2. (Without loss of generality we let the time-index of \( X^N \) start in \( g_0 = 0 \) and hence omit the additional superscript.) Since \( (X^N(g))_{g \in \mathbb{N}_0} \) is a Markov chain on a finite state-space...
with two absorbing states 0 and 1, it will be absorbed in finite time, hence
\(X^N(\infty) := \lim_{N \to \infty} X^N(g) \in \{0, 1\}\) exists \(\mathbb{P}_x\)-a.s. for any \(x \in [N]_0/N\).

Fix \(x \in [0, 1]\) rational. All \(N\) appearing henceforth are assumed to be such that \(x \in [N]_0/N\).

**Step 1:** We begin by proving that the assumption \(\mathbb{P}_x(X_\infty = 0) = 1\) in particular implies

\[
\lim_{N \to \infty} \mathbb{P}_x(X^N(\infty) = 0) = 1. \quad (26)
\]

Recall the duality from Proposition 27

\[
\mathbb{E}^n[H_{\mu^N}(x, Z^N(-g))] = \mathbb{E}_x[H_{\mu^N}(X^N(g), n)]
\]

for any \(n \in \mathbb{N}\). The map \(\bar{x} \mapsto H_{\mu^N}(\bar{x}, n)\) is continuous and bounded (for any \(n \in \mathbb{N}_0\)) with \(H_{\mu^N}(0, n) = 0\) and \(H_{\mu^N}(1, n) = 1\) therefore

\[
\lim_{g \to \infty} \mathbb{E}_x[H_{\mu^N}(X^N(g), n)] = \mathbb{P}_x(X^N(\infty) = 1). \quad (27)
\]

Since for fixed \(N \in \mathbb{N}\) the state space of \((Z^N(-g))_{g \in \mathbb{N}_0}\) is finite, it has an invariant distribution which we will denote \(\nu^N\) and assume to be defined on \(\mathbb{N}_0\). Let \(\mathbb{E}^{\nu^N}\)

denote the expectation under the law of the process with initial distribution \(\nu^N\). Then, using again the duality

\[
\mathbb{E}^{\nu^N}[H_{\mu^N}(x, Z^N(-g))] = \sum_{n \in \mathbb{N}_0} \nu^N(n) \mathbb{E}^n[H_{\mu^N}(x, Z^N(-g))]
\]

\[
= \sum_{n \in \mathbb{N}_0} \nu^N(n) \mathbb{E}_x[H_{\mu^N}(X^N(g), n)]
\]

\[
\xrightarrow{g \to \infty} \mathbb{P}_x(X^N(\infty) = 1),
\]

by (27) as the sum is actually finite and \(\nu^N\) a distribution. However, the left-hand-side does actually not depend on \(g\), since \(\nu^N\) is precisely the invariant distribution. Therefore we can substitute the limit by an equality and obtain the representation

\[
\sum_{n \in \mathbb{N}_0} \nu^N(n) \mathbb{E}_x[H_{\mu^N}(X^N(g), n)] = \mathbb{P}_x(X^N(\infty) = 1) \quad (28)
\]

for any \(g \in \mathbb{N}_0\). One can check that for any \(N \in \mathbb{N}\), \(\bar{x} \in [0, 1]\) and \(n \in \mathbb{N}_0\)

\[H_{\mu^N}(\bar{x}, n) \leq H_{\mu^N}(\bar{x}, 1)\]

and that \(\bar{x} \mapsto H_{\mu^N}(\bar{x}, 1)\) converges to the identity map \(\bar{x} \mapsto \bar{x}\) uniformly in \([0, 1]\).

By the latter, the weak convergence of \(X^N([\rho^{-1}_N t])\) to \(X(t)\) implies

\[
\mathbb{E}_x[H_{\mu^N}(X^N([\rho^{-1}_N t]), 1)] \xrightarrow{N \to \infty} \mathbb{E}_x[X(t)]
\]

for every \(t \geq 0\). Thus, using (28) with \(g = [\rho^{-1}_N t]\) and the observations above

\[
0 \leq \limsup_{N \to \infty} \mathbb{P}_x(X^N(\infty) = 1) = \limsup_{N \to \infty} \sum_{n \in \mathbb{N}_0} \nu^N(n) \mathbb{E}_x[H_{\mu^N}(X^N([\rho^{-1}_N t]), n)]
\]

\[
\leq \limsup_{N \to \infty} \mathbb{E}_x[H_{\mu^N}(X^N([\rho^{-1}_N t]), 1)] \sum_{n \in \mathbb{N}_0} \nu^N(n)
\]

\[
= \mathbb{E}_x[X(t)]
\]

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for any $t \geq 0$, where the last equality follows from the fact that $\sum_{n \in \mathbb{N}_0} \nu^n(n) = 1$. Under the assumption $\mathbb{P}_x(X_{\infty} = 0) = 1$, however, the right-hand-side converges to 0, as $t \to \infty$, and since the left-hand-side does not depend on $t$, we have proven (20).

**Step 2:** Step 1 now allows us to condition on the event of extinction of the finite-population process (for $N$ sufficiently large). Denote by $\bar{\mathbb{P}}^N_x$ the probability measure obtained from $\mathbb{P}_x$ by conditioning on $\{X^N(\infty) = 0\}$. Let $T^N_0$ be the time to extinction of $X^N$, i.e.

$$T^N_0 := \inf \{g \geq 0 \mid X^N(g) = 0\}.$$  

Hence, we are precisely conditioning on $T^N_0$ being finite. By definition of $T^N_0$, any individual in a generation after $T^N_0$ is of the strong type 1. Recall from Definition 2.4 that we denote by $A^N_l(w)$ the potential ancestors of an individual $w$ alive $l$ generations back in time (counting from $g(w) \in \mathbb{N}_0$, the generation of $w$). Analogously, define the **strong potential ancestors** of $w$ in the typed process alive $l$ generations back

$$SA^N_l(w) := \{v \in A^N_l(w) \mid v \text{ is of type } 1\}, \quad l = 0, \ldots, g(w).$$

Note that $SA^N_l(w) = \emptyset$ if, and only if, $w$ is of the weak type 0.

Fix a generation $g \geq 0$. We want to prove a geometric bound on $\bar{\mathbb{P}}^N_{x}[X^N(g)]$.

First, note that for $I$ uniform on $[N]$ and independent of all other randomness in the model, we can express

$$\bar{\mathbb{P}}^N_{x}[X^N(g)] = \bar{\mathbb{P}}^N_{x}((g, I) \text{ is of type } 0).$$

We will use the fact that, for an individual from generation $g$ to be of the weak type 0, its ancestry must be disjoint from the strong ancestry of any strong individual in the same generation $g$ (which we know to exist $\bar{\mathbb{P}}^N_{x}$-a.s.). However, in order to estimate the probability of this event, said individual must be chosen with care.

Let $J$ be another random variable uniform on $[N]$, independent of any other randomness and use it to choose uniformly at random an individual from the first generation not before $g$ in which the strong type has fixated:

$$W := \{\max\{g, T^N_0\}, J\}.$$  

Like all individuals in his generation, $W$ is of the strong type 1. $SA^N_{\max\{g, T^N_0\}}(W)$ are its strong potential ancestors alive in generation $g$. Consequently, choose $W'$ uniformly at random (independently of all other randomness) among those $SA^N_{\max\{g, T^N_0\}}(W)$. Then $W'$ is by definition a strong individual in generation $g$. Due to exchangeability of the underlying ancestral process, however, its label $i(W')$ is uniform on $[N]$ and independent of $I$, the label of $(g, I)$, the first individual we chose.

As remarked, for $(g, I)$ to be of the weak type 0, its ancestry $A^N_l((g, I))$ must be, in particular, disjoint from the (non-empty) strong ancestry $SA^N_l(W')$ of $W'$, for every previous generation, allowing us to estimate

$$\bar{\mathbb{P}}^N_{x}((g, I) \text{ is of type } 0) \leq \bar{\mathbb{P}}^N_{x} \left( \forall l = 0, \ldots, g : A^N_l((g, I)) \cap SA^N_l(W') = \emptyset \right).$$

The probability for two given individuals to find a common ancestor of any type in the previous generation, can be estimated from above by the probability $p_N$ for this same event with the selection mechanism “turned off”, whereby each
individual always samples one and only one parent. A close look at the parent-
choosing mechanism described in Section 2.1 reveals that
\[ p_N = \frac{(1 - c_N) + m_1 c_N + m_2 c_N}{N} \]  
(29)
for some positive, finite constants \( m_1 \) and \( m_2 \). Since we constructed \( W' \) and \((g, I)\) such that they are both uniform on \([N]\) and independent, by exchangeability and independence of the generations we can use this estimate for every generation and obtain
\[
\mathbb{E}_x^N[X^N(g)] \leq \mathbb{E}_x^N(\forall l = 0, \ldots, g : A^N((g, I)) \cap SA^N(W') = \emptyset) \\
\leq (1 - p_N)^g \left(1 - \frac{1}{N}\right),
\]
where the last factor is the probability of the two individuals \((g, I)\) and \(W'\) not being identical.

**Step 3:** All that remains to be done is to translate this bound into a bound for the scaling limit. Since the identity map is bounded and continuous on \([0, 1]\), Theorem 2.12 implies
\[
\mathbb{E}_x[X^N(\lfloor \rho_N^{-1} t \rfloor)] \xrightarrow{N \to \infty} \mathbb{E}_x[X(t)]
\]
for any \( t \geq 0 \). At the same time, since \( \lim_{N \to \infty} \mathbb{P}_x(X_N(\infty) = 0) = 1 \) by step 1, using bounded convergence, we see
\[
\left| \mathbb{E}_x[X(t)] - \mathbb{E}_x[X^N(\lfloor \rho_N^{-1} t \rfloor)] \right| \\
\leq \left| \mathbb{E}_x[X(t)] - \mathbb{E}_x[X^N(\lfloor \rho_N^{-1} t \rfloor)] \right| \\
= \left| \mathbb{E}_x \left[ X^N(\lfloor \rho_N^{-1} t \rfloor) \left(1 - \frac{\mathbb{1}(X_N(\infty) = 0)}{\mathbb{P}_x(X_N(\infty) = 0)}\right) \right] \right| \\
\xrightarrow{N \to \infty} 0.
\]
Therefore the estimate from step 2 yields
\[
\mathbb{E}_x[X(t)] = \lim_{N \to \infty} \mathbb{E}_x[X^N(\lfloor \rho_N^{-1} t \rfloor)] \leq \lim_{N \to \infty} (1 - p_N)^{\lfloor \rho_N^{-1} t \rfloor}
\]
for every \( t \geq 0 \). Under the assumptions of Lemma 2.10, \( \lim_{N \to \infty} p_N \rho_N^{-1} = \sigma + m_1 c > 0 \), and therefore
\[
\mathbb{E}_x[X(t)] \leq \lim_{N \to \infty} (1 - p_N)^{\lfloor \rho_N^{-1} t \rfloor} = \exp(- (\sigma + m_1 c) t)
\]
which in turn implies \( \int_0^\infty \mathbb{E}_x[X(s)] ds < \infty \).

Finally we remove the assumption of rationality on \( x \). Thus, let \( x \in [0, 1] \) and assume \( \mathbb{P}_x(X_\infty = 0) = 1 \). By Remark 3.1 we may therefore choose an \( \tilde{x} \in [x, 1] \) rational, such that \( \mathbb{P}_{\tilde{x}}(X_\infty = 0) = 1 \). For such \( \tilde{x} \) we have just proven that \( \int_0^\infty \mathbb{E}_\tilde{x}[X(s)] ds < \infty \). The claim follows since \( \mathbb{E}_x[X(t)] \leq \mathbb{E}_\tilde{x}[X(t)] \) for every \( t \geq 0 \).

The proof of Lemma 3.5 follows the idea of the proof of Theorem 3 in [21], but we extend and formalise the arguments. The key is a representation of the generator \( A \) (equation (17)) of \( X \), in the spirit of [21], given in the following Lemma:
Lemma 3.7 (Griffiths representation). The generator $A$ of $X$ can be written as

$$Af(x) = \frac{1}{2} x(1-x) f''(x) + \frac{1}{2} x(1-x)E [f''(x(1-W) + VW)] - \alpha x(1-x) f'(x)$$

$$- \alpha x(1-x)E \left[ \frac{1}{E[K_{Y^*} - 1 | Y^*]} \times \left. f' \left( x - x(1-x) V E \left[ \sum_{l=0}^{K_{Y^*}-2} x^l | Y^* \right] \right) \right] ,$$

for every $x \in [0,1]$, and $V$, $W$ and $Y^*$ chosen as in (24) and (25).

It will be convenient to consider the summands of the generator individually. Therefore, we denote by $A_\alpha$ the part of the generator describing the rare selection mechanism, i.e.

$$A_\alpha f(x) := \int_{[0,1]} (f(E[x^{K_{Y^*}}]) - f(x)) \frac{1}{E[K_y - 1]} \Lambda_\alpha(dy)$$

and the part describing the coordinated random genetic drift as

$$A_c f(x) := Af(x) - \frac{1}{2} x(1-x) f''(x) + \alpha x(1-x) f'(x) - A_\alpha f(x).$$

Recall that we abbreviate $\alpha_\alpha := \Lambda_\alpha([0,1])$.

Proof. It is sufficient to find the correct representations for $A_c$ and $A_\alpha$. Theorem 1 in [21] already states

$$A_c f(x) = \frac{1}{2} x(1-x) E [f''(x(1-W) + VW)].$$

On the other hand, in the spirit of the proof of said theorem, we can calculate

$$A_\alpha f(x) = \int_{[0,1]} (f(E[x^{K_{Y^*}}]) - f(x)) \frac{1}{E[K_y - 1]} \Lambda_\alpha(dy)$$

$$= \int_{[0,1]} (f(x + E[x^{K_{Y^*}}]) - f(x)) \frac{1}{E[K_y - 1]} \Lambda_\alpha(dy)$$

$$= \int_{[0,1]} \int_{[0,1]} E[x^{K_{Y^*}} - x] f'(x + uE[x^{K_{Y^*}} - x]) du \frac{1}{E[K_y - 1]} \Lambda_\alpha(dy)$$

$$= -\alpha \int_{[0,1]} \int_{[0,1]} x(1-x) E \left[ \sum_{l=0}^{K_{Y^*}-2} x^l \right] \frac{1}{E[K_y - 1]}$$

$$\times f'(x + uE[x^{K_{Y^*}} - x]) du \frac{\Lambda_\alpha(dy)}{\Lambda_\alpha([0,1])}$$

$$= -\alpha x(1-x) E \left[ \frac{1}{E[K_{Y^*} - 1 | Y^*]} \times f' \left( x - x(1-x) V E \left[ \sum_{l=0}^{K_{Y^*}-2} x^l | Y^* \right] \right) \right].$$

We used once again the simple observation that $x^k - x = -x(1-x) \sum_{l=0}^{k-2} x^l$ for any $k \in \mathbb{N}$ and $x \in [0,1]$ if we interpret the empty sum as zero. □
3.2 Proof of Lemma 3.5 via Lyapunov functions

We are now ready to turn to the last missing proof, that of Lemma 3.5. We use the same Lyapunov approach as in [21] to attain slightly weaker conclusions than [21] in that extra care was needed to avoid the risk of some illegal exchanges of expectation and integration. Lemma 3.6 crucially helps circumventing such issues and guarantees our final result.

Proof of Lemma 3.5. Let \( \kappa \in \mathbb{R} \) and \( N \in \mathbb{N} \) and consider the functions \( f_{N, \kappa} : [0, 1] \rightarrow \mathbb{R} \) defined as

\[
f_{N, \kappa}(x) := \sum_{n=1}^{N} \frac{1}{n} x^n - \kappa x.
\]

Note that for \( N \rightarrow \infty \) the sum converges to \(-\log(1-x)\), but for each finite \( N \) they have convenient integrability properties which will allow us to use these functions for a Lyapunov-type argument to prove both parts of the theorem.

We begin with a few observations on these functions and the generators applied to them. Their first derivative is

\[
f'_{N, \kappa}(x) = \sum_{n=1}^{N} x^{n-1} - \kappa = \begin{cases} \frac{1}{N} & \text{if } x \neq 1, \\ N - \kappa & \text{if } x = 1. \end{cases}
\]

Since the calculations are simple, but tedious, we consider the parts of the generator separately for clarity, using their representations given in Lemma 3.7. Recall that the assumption \( \beta^* < \infty \) implies \( \sigma = 0 \).

Taking the expectation with respect to \( V \) in the second equality, then plugging in the definition of the derivative we obtain the following expression:

\[
\mathcal{A}_c f_{N, \kappa}(x) = \frac{1}{2} x(1-x) \mathbb{E} \left[ f'_{N, \kappa}(x(1-W) + VW) \right] \\
= \frac{1}{2} x(1-x) \mathbb{E} \left[ \frac{1}{W} (f'_{N, \kappa}(x(1-W) + W) - f'_{N, \kappa}(x(1-W))) \right] \\
= x \frac{1}{2} (1-x) \mathbb{E} \left[ \frac{1}{W} \left( \frac{1 - (x(1-W) + W)^N}{1 - (x(1-W) + W)} - \frac{1 - (x(1-W))^N}{1 - x(1-W)} \right) \right].
\]

Note that the expression \( f'_{N, \kappa}(1) \) can only occur for \( x = 1 \) and since in this case the right-hand-side is 0 if we assume something in the spirit of \( 0 \cdot \infty = 0 \), we take the liberty to write this expression for all \( x \in [0, 1] \).

Following the same reasoning we obtain a similar expression for the coordinated selection term for any \( x \in [0, 1] \):

\[
\mathcal{A}_s f_{N, \kappa}(x) \\
= -\alpha_s x(1-x) \mathbb{E} \left[ \frac{K_{Y*}-2}{\mathbb{E}[K_{Y*} - 1 \mid Y^s]} \frac{1}{\mathbb{E}[K_{Y*} - 1 \mid Y^s]} \times f'_{N, \kappa}(x + V \mathbb{E}[x_{K_{Y*}} - x \mid Y^s]) \right] \\
= -\alpha_s x(1-x) \mathbb{E} \left[ \sum_{l=0}^{K_{Y*}-2} x^l \mid Y^s \right] \frac{1}{\mathbb{E}[K_{Y*} - 1 \mid Y^s]}
\]
Let $\mathcal{A}_\mathcal{N}f_{N,\kappa}(x)$ be such that $\mathcal{A}_\mathcal{N}f_{N,\kappa}(x) = x\mathcal{A}_\mathcal{N}f_{N,\kappa}(x)$. From these expressions, we can deduce bounds for

$$\tilde{\mathcal{A}}f_{N,\kappa}(x) := \mathcal{A}_\mathcal{N}f_{N,\kappa}(x) - w(1-x)f'_{N,\kappa}(x) + \tilde{\mathcal{A}}_\mathcal{N}f_{N,\kappa}(x)$$

that are monotone in $N$.

We obtain a lower bound, by omitting certain positive terms in $\tilde{\mathcal{A}}f_{N,\kappa}$ as follows: For $x < 1$, define

$$a(N,x,\kappa) := \frac{1}{2}(1-x)\mathbb{E} \left[ \frac{1}{W} \left( 1 - \frac{(1-W)W^N}{1-x} - \frac{1}{1-x} \right) \right]$$

$$-w(1-x) \left( \frac{1}{1-x} - \kappa \right)$$

$$-\alpha_a(1-x)\mathbb{E} \left[ \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{\mathbb{E}[K_{V^*} - 1 | Y^a]} \times \left( \frac{1}{1-x} \left( 1 + x\mathbb{E} \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{1 + x\mathbb{E} \sum_{l=0}^{K_{V^*}-2} x^l | Y^a} \right) \right) \right]$$

$$+ \kappa w(1-x) + \kappa \alpha_a(1-x)\mathbb{E} \left[ \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{\mathbb{E}[K_{V^*} - 1 | Y^a]} \times \left( \frac{1}{1-x} \left( 1 + x\mathbb{E} \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{1 + x\mathbb{E} \sum_{l=0}^{K_{V^*}-2} x^l | Y^a} \right) \right) \right]$$

Then, trivially $\tilde{\mathcal{A}}f_{N,\kappa}(x) \geq a(N,x,\kappa)$ for any $x \in [0,1]$ (and $N \in \mathbb{N}, \kappa \in \mathbb{R}$).

We rearrange the terms of $a$ to obtain a more convenient form. Separating the terms that do/do not depend on $N$ and $\kappa$, then canceling several $(1-x)$-terms in a second step

$$a(N,x,\kappa) = \frac{1}{2}(1-x)\mathbb{E} \left[ \frac{1}{(1-W)(1-x)(1-x)(1-W)} \right]$$

$$-\frac{1}{2}(1-x)\mathbb{E} \left[ \frac{(x(1-W) + W)^N}{W(1-W)(1-x)} \right] - w$$

$$-\alpha_a(1-x)\mathbb{E} \left[ \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{\mathbb{E}[K_{V^*} - 1 | Y^a]} \times \left( \frac{1}{1-x} \left( 1 + x\mathbb{E} \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{1 + x\mathbb{E} \sum_{l=0}^{K_{V^*}-2} x^l | Y^a} \right) \right) \right]$$

$$+ \kappa w(1-x) + \kappa \alpha_a(1-x)\mathbb{E} \left[ \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{\mathbb{E}[K_{V^*} - 1 | Y^a]} \times \left( \frac{1}{1-x} \left( 1 + x\mathbb{E} \frac{\sum_{l=0}^{K_{V^*}-2} x^l | Y^a}{1 + x\mathbb{E} \sum_{l=0}^{K_{V^*}-2} x^l | Y^a} \right) \right) \right]$$

$$-\frac{1}{2}\mathbb{E} \left[ \frac{(x(1-W) + W)^N}{W(1-W)} \right].$$
By extending \( g(N, 1, \kappa) := -w - \alpha_s \alpha^* \), we do indeed obtain

\[
\bar{A} f_{N, \kappa}(x) \geq \underline{g}(N, x, \kappa)
\]  

(30)

for all \( N \in \mathbb{N} \), \( \kappa \in \mathbb{R} \) and \( x \in [0, 1] \).

Note that we can estimate

\[
|\underline{g}(N, x, \kappa)| \leq \beta^* + w + \alpha_s + w + |\kappa| \alpha_s + \beta^* < \infty
\]

and the right-hand-side does not depend on \( x \) nor \( N \).

In a similar fashion we define an upper bound by omitting certain negative terms: For \( x < 1 \), define

\[
\overline{g}(N, x, \kappa) := \frac{1}{2} (1 - x) E \left[ \frac{1}{W(1 - x)} \right] - w(1 - x) \left( 1 - \frac{x^N}{1 - x} \right) - \alpha_s (1 - x) E \left[ \sum_{l=0}^{K_N - 2} x^l | Y^s \right] \frac{1}{E[K_N - 1 | Y^s]} \times \left( \frac{1 - (x - x(1 - x) V E \left[ \sum_{l=0}^{K_N - 2} x^l | Y^s \right])^N}{1 - (x - x(1 - x) V E \left[ \sum_{l=0}^{K_N - 2} x^l | Y^s \right])^N} - \kappa \right)
\]

and extend it by \( \overline{g}(N, 1, \kappa) := \beta^* \). As before, by definition,

\[
\bar{A} f_{N, \kappa}(x) \leq \overline{g}(N, x, \kappa)
\]  

(31)

for all \( N \in \mathbb{N} \), \( \kappa \in \mathbb{R} \) and \( x \in [0, 1] \). In addition, if we recall that \(-x(1 - x) \sum_{l=0}^{N} x^l = x^N - x \), we can simply estimate

\[
|\overline{g}(N, x, \kappa)| \leq \beta^* + w + w|\kappa| + \alpha_s |\kappa| + \alpha_s \alpha^* < \infty
\]

and the right-hand-side does not depend on \( x \) nor \( N \).

In particular, combining the above observations, we now know that

\[
|\bar{A} f_{N, \kappa}(x)| \leq 2 \beta^* + (2 + |\kappa|) w + (1 + |\kappa| + \alpha^*) \alpha_s < \infty
\]

uniformly in \( N \in \mathbb{N} \) and \( x \in [0, 1] \). Therefore

\[
\left( f_{N, \kappa}(X(t)) - f_{N, \kappa}(X(0)) - \int_{[0, t]} \bar{A} f_{N, \kappa}(X(s)) ds \right)_{t \geq 0}
\]
is a Martingale and we know
\[
E_x[f_{N,\kappa}(X(t))] - f_{N,\kappa}(x) = \int_{[0,t]} E_x[Af_{N,\kappa}(X(s))]ds
\]
holds for all \(N \in \mathbb{N}, \kappa \in \mathbb{R}, x \in [0,1]\) and \(t \geq 0\).

Before we turn to the proof of the two statements of the lemma, we draw a
first helpful conclusion: Under the assumption of \(\beta^* < \infty\), (32) implies that for
any \(x \in [0,1]\) and any \(t \geq 0\) the probability of the weak allele having reached
fixation is zero, i.e.
\[
P_x(X(t) = 1) = 0.
\]
(33)

If this were not the case there would exist \(\bar{x} \in [0,1]\) and \(\bar{t} > 0\) such that
\[
P_{\bar{x}}(X(\bar{t}) = 1) > 0.
\]
For this choice of parameters
\[
E_{\bar{x}}[f_{N,0}(X(\bar{t}))] - f_{N,0}(\bar{x}) \geq P_{\bar{x}}(X(\bar{t}) = 1)
\]
On the other hand, (32) implies
\[
E_{\bar{x}}[f_{N,0}(X(\bar{t}))] - f_{N,0}(\bar{x}) = \int_{[0,\bar{t}]} E_x[Af_{N,\kappa}(X(s))]ds
\]
for any \(N \in \mathbb{N}\), which is a contradiction and proves the claim.

Indeed, since \(1\) is an absorbing state the sets \(\{X_t = 1\}\) are increasing in \(t \geq 0\)
and therefore we have actually proven that the fixation time is almost surely
infinite, but we will not use this here.

We are now ready to tackle the lemma itself.

**Proof of (i):** Assume \(\alpha_s\alpha^* + w < \beta^*\). Equivalently, \(\beta^* - w - \alpha_s\alpha^* > 0\).
For this part we will work with the lower bound \(a\). Note that parts of the first
and third summand of \(a\) converge (e.g. by bounded convergence) to the critical
values as \(x\) tends to 1:
\[
\frac{1}{2} E \left[ \frac{1}{(1-W)(1-x(1-W))} \right] \xrightarrow{x \to 1} \beta^*
\]
and
\[
E \left[ \sum_{l=0}^{K_{Y^*} - 2} x_l^l \left| Y^* \right| \right] \xrightarrow{x \to 1} \alpha^*
\]
whence we may choose an \(x_0 \in [0,1]\) such that for all \(x \geq x_0\)
\[
\frac{1}{2} E \left[ \frac{1}{(1-W)(1-x(1-W))} \right] - \frac{1}{2} \alpha_s E \left[ \sum_{l=0}^{K_{Y^*} - 2} x_l^l \left| Y^* \right| \right] \geq \beta^* - w - \alpha_s\alpha^* =: \delta > 0.
\]
We use $\kappa$ to control the remaining $x \leq x_0$. Hence, fix $\kappa_0 \geq 0$ sufficiently large such that

$$\kappa_0 w(1 - x_0) + \kappa_0 \alpha_2(1 - x_0) \mathbb{E} \left[ \sum_{i=0}^{K_{Y^+} - 2} x_i^2 \left| Y^s \right| \frac{1}{\mathbb{E}[K_{Y^+} - 1 | Y^s]} \right]$$

$$\geq w + \alpha_2 - \frac{1}{2} \mathbb{E} \left[ \frac{1}{1 - W} \right] + \delta. \quad (34)$$

Note that $(1 - x_0) \sum_{i=0}^{k-2} x_i = 1 - x_0^{k-1}$, thus the left-hand-side is decreasing in $x$ and therefore (34) actually holds for all $x \leq x_0$.

Combined, we obtain for all but the last summand of $\mathfrak{g}$: For all $x \in [0, 1]$

$$\frac{1}{2} \mathbb{E} \left[ \frac{1}{(1 - W)(1 - x(1 - W))} \right] - w$$

$$- \alpha_2 \mathbb{E} \left[ \sum_{i=0}^{K_{Y^+} - 2} x_i^2 \left| Y^s \right| \frac{1}{\mathbb{E}[K_{Y^+} - 1 | Y^s]} \right]$$

$$+ \kappa_0 w(1 - x) + \kappa_0 \alpha_2(1 - x) \mathbb{E} \left[ \sum_{i=0}^{K_{Y^+} - 2} x_i^2 \left| Y^s \right| \frac{1}{\mathbb{E}[K_{Y^+} - 1 | Y^s]} \right]$$

$$\geq \delta$$

which in turn implies

$$\mathfrak{g}(N, x, \kappa_0) \geq \delta - \frac{1}{2} \mathbb{E} \left[ \frac{(x(1 - W) + W)^N}{W(1 - W)} \right]$$

for all $N \in \mathbb{N}$ and all $x \in [0, 1]$.

All these estimates serve to control the right-hand-side of (32). While we were able to do the previous estimates for deterministic $x$, the last term will be tackled using bounded convergence after substituting $X(s)$ for $x$ in the expressions above. In order to obtain a contradiction, assume

$$\forall x \in [0, 1] \int_{0, \infty} \mathbb{E}_x[X(s)] ds < \infty, \quad (35)$$

which in particular implies that for any $x \in [0, 1] \mathbb{P}_x(X_\infty = 1) = 0$ and therefore

$$X_{\sup} := \sup_{t \in [0, \infty]} X(t) < 1 \quad \mathbb{P}_x\text{-a.s.} \quad (36)$$

Without loss of generality we may assume $(X(t))_{t \geq 0}$ and $W$ to be independent and we can estimate

$$\mathbb{E}_x[X(s)\mathfrak{g}(N, X(s), \kappa_0)] \geq \mathbb{E}_x \left[ X(s) \left( \delta - \frac{(X(s)(1 - W) + W)^N}{W(1 - W)} \right) \right]$$

$$\geq \mathbb{E}_x \left[ X(s) \left( \delta - \frac{(X_{\sup}(1 - W) + W)^N}{W(1 - W)} \right) \right] \quad (37)$$

for all $N \in \mathbb{N}$. Using bounded convergence and (36) we see that the right-hand-side converges

$$\mathbb{E}_x \left[ X(s) \left( \delta - \frac{(X_{\sup}(1 - W) + W)^N}{W(1 - W)} \right) \right] \xrightarrow{N \to \infty} \delta \mathbb{E}_x[X(s)] > 0.$$
Assumption (35) allows us to use bounded convergence again, to estimate
\[
\lim_{N \to \infty} \int_{[0, \infty]} \mathbb{E}_x [X(s)g(N, X(s), \kappa_0)] \, ds \\
\geq \lim_{N \to \infty} \int_{[0, \infty]} \mathbb{E}_x \left[ X(s) \left( \delta - \frac{(X_{\text{sup}}(1 - W) + W)^N}{W(1 - W)} \right) \right] \, ds \\
= \delta \int_{[0, \infty]} \mathbb{E}_x [X(s)] \, ds := \delta > 0
\]
for any \( x \in [0, 1] \). Recalling that \( a \) was designed as a lower bound (and using (33)) this yields that for every \( x \in [0, 1] \) there exists an \( N_0 = N_0(x) \) such that for every \( N \geq N_0 \)
\[
\int_{[0, \infty]} \mathbb{E}_x [A f_{N, \kappa_0}(X(s))] \, ds = \int_{[0, \infty]} \mathbb{E}_x \left[ X(s) A f_{N, \kappa_0}(X(s)) \right] \, ds \\
\geq \int_{[0, \infty]} \mathbb{E}_x [X(s) \alpha(N, X(s), \kappa_0)] \, ds \geq \frac{\delta}{2} > 0. \quad (38)
\]
Now choose \( \bar{x} \) sufficiently close to 1, such that
\[
\log(1 - \bar{x}) + \kappa_0 \bar{x} < -1.
\]
Then choose \( \bar{N} \geq N_0(\bar{x}) \) sufficiently large such that
\[
- \sum_{n=1}^{\bar{N}} \frac{1}{n} \bar{x}^n + \kappa_0 \bar{x} < -\frac{1}{2}.
\]
Recall that assumption (35) in particular implies \( P_x(X_\infty = 0) = 1 \) and therefore
\[
\lim_{t \to \infty} \mathbb{E}_x [f_{\bar{N}, \kappa_0}(X(t))] - f_{\bar{N}, \kappa_0}(\bar{x}) = 0 - \sum_{n=1}^{\bar{N}} \frac{1}{n} \bar{x}^n + \kappa_0 \bar{x}.
\]
Together with equation (32) and (38) this implies
\[
- \frac{1}{2} > \lim_{t \to \infty} \mathbb{E}_x [f_{\bar{N}, \kappa_0}(X(t))] - f_{\bar{N}, \kappa_0}(\bar{x}) = \lim_{t \to \infty} \int_{[0, t]} \mathbb{E}_x [A f_{\bar{N}, \kappa_0}(X(s))] \, ds \geq \frac{\delta}{2} > 0,
\]
which clearly is a contradiction.

Hence, we have proven that assuming \( \alpha_x \alpha^* + w < \beta^* \), we know
\[
\exists \bar{x} \in [0, 1] \quad \int_{[0, \infty]} \mathbb{E}_x [X(s)] \, ds = \infty.
\]

**Proof of (ii):** Assume \( \alpha_x \alpha^* + w > \beta^* \). Equivalently \( \beta^* - w - \alpha_x \alpha^* < 0 \). For this part we will work with the upper bound \( \alpha \) which can be rearranged to
\[
\alpha(N, x, \kappa) = \beta^* - w - \alpha_x \mathbb{E} \left[ \sum_{l=0}^{K_{\alpha^*} - 2} x^l \mid Y^a \right] \frac{1}{\mathbb{E}[K_{\alpha^*} - 1 \mid Y^a]} \\
\times \frac{1}{1 + x \mathbb{E} \left[ \sum_{l=0}^{K_{\alpha^*} - 2} x^l \mid Y^a \right]} \\
+ w \kappa(1 - x) + \alpha_x \kappa(1 - x) \mathbb{E} \left[ \sum_{l=0}^{K_{\alpha^*} - 2} x^l \mid Y^a \right] \frac{1}{\mathbb{E}[K_{\alpha^*} - 1 \mid Y^a]}
\]

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Again, we control the remaining $\sum_{l=0}^{K_{v^*}-2} x^l \mid Y^s$ and thereby convergence, for all $x$. Therefore there exists an $x \in [0, 1]$ such that for all $x \geq x_0$

$$\beta^* - w - \alpha_s \beta^* \leq \frac{\beta^* - w - \alpha_s \beta^*}{2} = -\delta < 0.$$ 

Again, we control the remaining $x$ with the help of $\kappa$. Choose $\kappa_0 \leq 0$ with $|\kappa_0|$ sufficiently large such that

$$w\kappa_0(1 - x_0) + \alpha_s \kappa_0(1 - x_0) \leq -\beta^* - \delta.$$ 

Since the left-hand-side is increasing in $x$ (recall that $\kappa_0 \leq 0$), the estimate actually holds for all $x \in [0, x_0]$. Thus we now know that for all $x \in [0, 1]$ we can bound the first five summands of $\pi$ by

$$\beta^* - \alpha_s \beta^* \leq \alpha_s (1 - x) \leq -\delta < 0.$$ 

Note that we also find a simple bound for the last two summands and thereby obtain

$$\pi(N, x, \kappa_0) \leq -\delta + w_x^N + \alpha_s x^N$$

for all $x \in [0, 1]$ and $N \in \mathbb{N}$. We will return to this estimate below.

In order to obtain a contradiction, assume

$$\exists x \in [0, 1] \int_{[0, \infty]} \mathbb{E}_x [X(s)] ds = \infty.$$ 

Fix one such $x$ for the remainder of the proof. By monotone (or bounded) convergence,

$$\mathbb{E}_x [X(s)(-\delta + (w + \alpha_s)X(s)^N)]$$
\[
\frac{N \to \infty}{\int_{[0,t]} \mathbb{E}_x[AF_{N,x\alpha}(X(s))]ds} \leq \int_{[0,t]} \mathbb{E}_x[X(s)(N-X(s),\kappa_0)]ds
\]
\[
\leq \int_{[0,t]} \mathbb{E}_x[X(s)(-\delta + (w + \alpha_x)X)^N]ds
\]
\[
\frac{N \to \infty}{\int_{[0,t]} \mathbb{E}_x[X(s)]ds < 0.}
\]

By assumption (10) we may choose \( t > 0 \) such that
\[
\int_{[0,t]} \mathbb{E}_x[X(s)]ds \geq -\frac{4\log(1-x) - \kappa_0 x}{\delta}
\]
and by (22) an \( \bar{N} = \bar{N}(t) \) such that
\[
\int_{[0,t]} \mathbb{E}_x[AF_{\bar{N},x\alpha}(X(s))]ds \leq 2(\log(1-x) + \kappa_0 x).
\]

Now that we have the right-hand-side under control, we turn to the left-hand-side of (22) Remembering that \( \kappa_0 \leq 0 \), we crudely estimate
\[
\mathbb{E}_x[f_{N,x\alpha}(X(t))] - f_{N,x\alpha}(x) = \sum_{n=1}^{N} \frac{1}{n} \mathbb{E}_x[X(t)^n] - \kappa_0 \mathbb{E}_x[X(t)] - \sum_{n=1}^{N} \frac{1}{n} x^n + \kappa_0 x
\]
\[
\geq - \sum_{n=1}^{N} \frac{1}{n} x^n + \kappa_0 x \geq \log(1-x) + \kappa_0 x
\]
which is a contradiction to (22) given (13).

\section{Ergodicity of the branching coalescing process in random environment}

As characterised in Remark 3.1 the chance of survival of the weak allele has a direct correspondence to the ergodic behaviour of the branching coalescing process in random environment \((Z(t) : t \geq 0)\). Hence, the following is a corollary or Theorem 3.2

\begin{corollary}
Let \( Z = (Z(t) : t \geq 0) \) be the coordinated branching coalescing process from Definition 2.13 for a \( \sigma \)-finite \( \mu \). Assume \( \beta^* < \infty \). Then
\begin{enumerate}[(i)]
\item If \( \alpha_x \alpha^* + w < \beta^* \), then \( Z \) is positive recurrent.
\item If \( \alpha_x \alpha^* + w > \beta^* \), then \( \mathbb{P}(Z(t) \leq M) \to 0 \), as \( t \to \infty \), for all \( M \in \mathbb{N} \) i.e. \( Z \) is null-recurrent or transient.
\end{enumerate}
In the case of (i), the generating function of \( \nu \) is given by \( \varphi_\nu(x) = \mathbb{P}_x(X_{\infty} = 1) \).
\end{corollary}
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