The ancestral selection graph for a Λ -asymmetric Moran model

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Abstract

Motivated by the question of the impact of selective advantage in populations with skewed reproduction mechanims, we study a Moran model with selection. We assume that there are two types of individuals, where the reproductive success of one type is larger than the other. The higher reproductive success may stem from either more frequent reproduction, or from larger numbers of offspring, and is encoded in a measure Λ for each of the two types. Our approach consists of constructing a Λ -asymmetric Moran model in which individuals of the two populations compete, rather than considering a Moran model for each population. Under certain conditions, that we call the "partial order of adaptation", we can couple these measures. This allows us to construct the central object of this paper, the Λ -asymmetric ancestral selection graph, leading to a pathwise duality of the forward in time Λ -asymmetric Moran model with its ancestral process. Interestingly, the construction also provides a connection to the theory of optimal transport. We apply the ancestral selection graph in order to obtain scaling limits of the forward and backward processes, and note that the frequency process converges to the solution of an SDE with discontinous paths. Finally, we derive a Griffiths representation for the generator of the SDE and use it to find a semi-explicit formula for the probability of fixation of the less beneficial of the two types.

Keywords: Moran model, ancestral selection graph, duality, Λ -coalescent, fixation probability, optimal transport 2020 MSC: 92D15, 60J28, 60J90

1. Introduction

There is a deep connection between the ancestry of a population and the dynamics of its genetic configuration. Mathematical population genetics exploits and formalises this connection, see for example [9] for an overview. Its most classical instance is the moment duality relation between the block counting process of the Kingman coalescent and the Wright Fisher diffusion, which relates the past and future of a population that evolves on absence of selection and in which the number of offsprings of a mother is of a smaller order of magnitude than the population size.

This connection between the past and the future is ubiquitous and occurs in many biologically inspired mathematical models. For example, the ancestry of populations with skewed offspring distributions have been modelled by Λ -coalescents or multiple merger coalescents [27, 30] different from the Kingman coalescent, but which still have a moment dual, namely the Λ -Fleming Viot process (see [3, 5, 6]). Skewed offspring distributions occur in populations where the number of offspring of one mother can be of the order of magnitude of the population size. It is believed that they may be

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relevant for certain marine species such as the Atlantic cod, where one mother may lay millions of eggs. See e.g. [1, 11] and references therein for a more detailed discussion.

In the presence of weak selection, for example when one type of individuals reproduces slightly faster than the others, it is cumbersome to formally connect the ancestry and the forward in time changes in a population configuration. Remarkably, there is a notion of potential ancestry that overcomes this difficulty for populations in the universality class of the Kingman coalescent: The celebrated ancestral selection graph (ASG) of Krone and Neuhauser [22, 25]. Heuristically, in a population with only two types, Krone and Neuhauser were able to describe the number of potential ancestors of a sample as a branching coalescing process. Under the rule that an individual is of the selective type if at least one of its ancestors has selective advantage, the forward in time propagation of types can be specified in terms of the potential ancestry and the types at time zero. As a consequence, the frequency of individuals with selective disadvantage is a Markov process, which is moment dual to the process of the number of potential ancestors (backward in time). The graphical construction of the ancestral selection graph is very strong and provides a pathways duality relation of the forward and backward processes, which for example links fixation probabilities with the ancestral process, see e.g. [28, 21].

However, the classical ancestral selection graph couldn't capture genetic dynamics of a population of, say, cods in which a subpopulation is capable of reproducing faster, as this leads to selective events individually affecting large portions of the population. What is then a good model for populations with skewed offspring distributions in the presence of selection? This was one of the main motivating questions of work by Griffiths, Etheridge and Taylor [8], see also Etheridge and Griffiths [7]. These authors showed that the process of potential ancestors in this case should be a nonlinear branching and coalescing process. They equipped their model with parent independent mutation and found a duality in terms of the stationary distribution of the forward process, in the case that the stationary distribution exists. They also spelled out the reason for this mysterious nonlinear branching.

Furthermore, it was theorised by Gillespie [15, 16] that subpopulations with different reproduction mechanisms competing in a sequential sampling experiment (for example, in the Lenski experiment [23, 18]) lead to different macroscopic behaviours, which scale beyond the Wright Fisher diffusion universality class. A detailed mathematical analysis of these *asymmetric* models models was carried out in [4]. What does it mean that one subpopulation has selective advantage over another if they have very different reproduction behaviour? Can one compare the strategy of the cod with the strategy of the rabbit?

The goal of the present paper is to revisit the motivating questions of [8] and [15] to give a graphical representation of a Moran model with Λ -reproduction in the presence of selection and asymetry, following the structure of the ancestral selection graph. Our representation provides a pathways duality between what we will call below the Λ -asymmetric Moran model and its ancestral line counting process, from which the generator duality can be derived. Contrary to Etheridge, Griffiths and Taylor we don't need to start from the invariant distribution in our construction and therefore don't need to include mutations in the model. Moreover, and probably most importantly, our construction works without previously assigning types to the individuals, since we can construct the ancestral selection graph independently, in the spirit of Neuhauser and Krone.

Our construction is based on a coupling of the measures governing the reproduction mechanisms of two subpopulations, which has connections to the theory of optimal transport. However, not every pair of measures can be used to construct a Λ -ancestral selection graph, and we provide explicit sufficient conditions. This is done by introducing the *partial order of adaptation* and showing that a pair of measures that is comparable with respect to this partial order can be coupled to construct an ancestral selection graph.

Finally, we derive a representation inspired by Griffiths [19] for the processes that arise as scaling limits of our Λ -Moran model with selection. As an application we compute a recursion for the fixation probabilities.

The paper is organised as follows. In the next section, we will define the Λ -asymmetric Moran model and provide the generator of its frequency process. In Section 3 we will state the central

coupling lemma and construct the ancestral selection graph. Using this construction, we will consider the ancestral process and show our duality result in Section 4. The coupling lemma will be proved and discussed in Section 5. Finally, we will discuss scaling limits in Section 6, and fixation probabilities via Griffith's representation in Section 7.

2. Λ -asymmetric Moran model

In this section, we define our main object of interest, the Λ -asymmetric Moran model. It is related to the Moran model with viability selection of Etheridge, Griffiths and Taylor [8], but in the present paper we restrict ourselves to the case of only two types, and we don't include mutation.

We consider a continuous time Moran model with fixed population size N. The two types will be denoted by + and -, we write $\tau(i,t) \in \{+,-\}$ for the type of individual $i \in [N] = \{1,...,N\}$ at time $t \ge 0$. Denote by $\mathcal{M}[0,1]$ the set of finite measures on [0,1] equipped with the Borel sigma field. Fix measures $\Lambda^+, \Lambda^- \in \mathcal{M}[0,1]$. These measures will provide the reproduction rates and the strength of the selection at a reproductive event. We write $\|\Lambda^{\tau}\|$ for the total mass of the measure $\Lambda^{\tau}, \tau \in \{-,+\}$.

Definition 2.1 (A-asymmetric Moran model). Each of the N individuals reproduces independently at rate $N^{-1} \| \Lambda^{\tau(i,t)} \|$ if it has currently type $\tau(i,t)$. If at time t individual i reproduces, then the selective strenght of the reproductive event is provided as a random variable Y sampled independently of everything else from the probability measure $\Lambda^{\tau(i,t)}/\| \Lambda^{\tau(i,t)} \|$. Conditional on Y, each of the N-1individuals in $[N] \setminus \{i\}$ participates in the reproduction event with probability Y, meaning that the participating individuals die and are replaced by offspring of the reproducing individuals, carrying the type of individual i.

Remark 2.2. In [8], a Moran model including viability selection was defined in a similar manner. There, individuals reproduce at fixed rate λ and produce a number of offspring, among which only some of the children survive to maturity. The probability of an individual of type τ to have b mature offspring is given as $p_{\tau b} = \sum_{a=b}^{N-1} r_a v_{\tau ab}$, with r_a the number of children, and $v_{\tau ab}$ the probability that b out of a children survive to maturity. In particular $v_{\tau ab} = \int_{[0,1]} {a \choose b} p^b (1-p)^{a-b} \nu_{\tau}(dp)$ for some probability measure ν_{τ} may be considered. This corresponds to our model if we set $\Lambda^{\tau} = \lambda \nu_{\tau}$ and $r_{N-1} = 1$. As it stands, our model doesn't directly lead to an interpretation in terms of viability selection. On the other hand, we can at least implicitly incorporate various selective mechanisms in our finite measures Λ^{τ} . See also Example 3.3 below for an interpretation of the Λ -measures in some special cases.

Moran models with other types of Λ reproduction undergoing selection have been investigated by Schweinsberg and studied further by Bah and Pardoux and Ged [31, 32, 2, 14]. However, the role of the Λ measure in these works differs from our construction.

We denote by

$$X_t^N = \frac{1}{N} \sum_{i=1}^N \mathbb{1}_{\{\tau((t,i)) = -\}}, \qquad t \ge 0$$

the frequency at time t of individuals of type –, which will later be the less fit type. Clearly the process $X^N = (X_t^N)_{t\geq 0}$ is a piecewise continuous Markov chain with state space $\{0, 1/N, ..., (N-1)/N, 1\}$. Its transitions are given by

$$x \mapsto \begin{cases} x + \frac{k}{N} & \text{at rate } x \int_0^1 {\binom{(1-x)N}{k}} y^k (1-y)^{(1-x)N-k} \Lambda^-(dy), \quad k = 1, ..., (1-x)N \\ x - \frac{k}{N} & \text{at rate } (1-x) \int_0^1 {\binom{xN}{k}} y^k (1-y)^{xN-k} \Lambda^+(dy), \quad k = 1, ..., xN. \end{cases}$$

In other words, upon a reproduction event of a type – individual, which happens at a total rate of $x \|\Lambda^{-}\|$ in the population, the strength y of the reproduction is determined according to the measure $\Lambda^{-}/\|\Lambda^{-}\|$ (thus the total mass $\|\Lambda^{-}\|$ cancels out in the expression of the transition rate). Then, independently with probability y, each of the N-1 non-reproducing individuals dies and is replaced by an offspring of type –. With probability 1-y it remains. Only a replacement of a type + individual

by an offspring of type – leads to an increase in type – individuals, thus there are (1-x)N individuals that may swap type from + to – at such an event. The number of individuals switching type from + to – is thus binomial with success probability y and N(1-x) trials. A reproduction of a type + individuals works vice versa. See Figure 1 for an example.

Hence, the generator of the frequency process of the Λ -asymmetric Moran model acts on bounded measurable functions $f: [0, 1] \rightarrow [0, 1]$ as

$$\mathcal{B}^{N}f(x) = x \|\Lambda^{-}\|\mathbb{E}\left[f\left(x + \frac{1}{N}\operatorname{Binom}(N(1-x), Y^{-})\right) - f(x)\right] + (1-x)\|\Lambda^{+}\|\mathbb{E}\left[f\left(x - \frac{1}{N}\operatorname{Binom}(Nx, Y^{+})\right) - f(x)\right].$$

Here, $x \in [N_0] := \{0, 1/N, ..., (N-1)/N, 1\}$, and the expectation is taken with respect to the random variables Y^- resp. Y^+ , which are distributed according to the probability measures $\Lambda^-/\|\Lambda^-\|$ resp. $\Lambda^+/\|\Lambda^+\|$.

3. Partial order of adaptation, and the Λ -asymmetric ancestral selection graph

The next aim is to construct an ancestral selection graph corresponding to the Λ -asymmetric Moran model defined in the previous section. We will give a graphical representation which forward in time provides a construction of the Λ -asymmetric Moran model, and backward in time gives the ancestry of a sample of such a population. Our construction differs from the graphical representation of Etheridge, Griffiths and Taylor in several ways. In particular, the construction works for any assignment of types to the individuals, and it doesn't need an invariant distribution. It thus provides a pathwise construction of the duality found in [8], see Corollary 4.6 below.

As a trade-off, it only works for measures Λ^- and Λ^+ that are ordered in a relatively general way, that we call the partial order of adaptation. This assumption will allow us to construct a coupling that will play a crucial role in the construction. It turns out that this coupling also provides an interesting connection with the theory of optimal transport, as we will explain later.

Definition 3.1 (The partial order of adaptation). For any pair of finite measures on [0,1], we say that $\mu_0 \leq \mu_1$ if for every $x \in [0,1]$ it holds that $\mu_0[x,1] \leq \mu_1[x,1]$.

Proposition 3.2. The partial order of adaptation is a partial order on the finite measures of [0, 1].

Proof. Let μ_0, μ_1, μ_2 be finite measures in [0, 1]. It is immediate that $\mu_0 \leq \mu_0$, so the relation is reflexive. If $\mu_0 \leq \mu_1$ and $\mu_1 \leq \mu_0$, then for every $x \in [0, 1], \mu_0[x, 1] = \mu_1[x, 1]$, which in turns implies that $\mu_0 = \mu_1$. Finally, if $\mu_0 \leq \mu_1$ and $\mu_1 \leq \mu_2$, or every $x \in [0, 1], \mu_0[x, 1] \leq \mu_1[x, 1] \leq \mu_2[x, 1]$, which implies that $\mu_0 \leq \mu_2$.

In terms of the measures Λ^+ , Λ^- we used above in the construction of the Λ -asymmetric Moran model, the partial order of adaptation, which is known as the partial order of stochastic domination in other contexts, is readily interpreted in terms of the selective advantage of the reproduction mechanisms. In our simplistic setting, we say that a mutation *contributes to the adaptation* or that it is a *selective mutation* if it increases the reproduction rate or the typical number of offsprings per reproduction event, or both.

Example 3.3. Indeed, $\Lambda^{-} \leq \Lambda^{+}$ in particular in the following cases:

- 1. (Faster reproduction) if $\Lambda^+ = (1 + \alpha)\Lambda^-$ for some $\alpha > 0$.
- 2. (Bigger reproductive events) There exists a function $s : [0,1] \mapsto [0,1]$ such that $s(x) x \ge 0$ and $\Lambda^{-}(s(A)) = \Lambda^{+}(A)$.



Figure 1: A realisation of the Λ -asymmetric frequency process. Filled dots represent the reproducing individuals, filled squares the offspring. In the first reproductive event, a type + individual has three children, in the second one a type - individual has three children, and in the last event a type - individual has no offspring. The role of selection in this construction will be discussed later in Section 3, cf. also Figure 2.

In the first case, in particular $\|\Lambda^+\| = (1 + \alpha)\|\Lambda^-\|$, hence we are in the situation of the classical ancestral selection graph by Krone and Neuhauser [22, 25]. The second case is satisfied for example if $\Lambda^- = \delta_a$ and $\Lambda^+ = \delta_b$, with $0 \le a \le b \le 1$ where Λ^- generates reproductive events of size a, and Λ^+ of size b.

The crucial step in our construction is the following coupling lemma. It turns out that if the finite measures Λ^- and Λ^+ we used in our construction of the Λ -asymmetric Moran models are ordered accourding to the partial order of adaptation, we can equivalently consider a Moran model constructed from just one measure Λ that contains the information of a particular coupling of the pair (Λ^- , Λ^+).

Lemma 3.4 (Adaptation coupling). Let $\Delta = \{(y, z) \in [0, 1]^2 : y + z \in [0, 1]\}$ and consider two finite measures Λ^+, Λ^- on [0, 1]. If $\Lambda^- \leq \Lambda^+$, in the sense of Definition 3.1 then there exists a finite measure Λ^1 on Δ and two finite measures $\Lambda^{+,1}$ and $\Lambda^{+,2}$ on [0, 1] such that $\Lambda^+ = \Lambda^{+,1} + \Lambda^{+,2}$, and such that the following are satisfied:

- $\Lambda^{-}(A) = \Lambda^{1}(\{(y, z) : y \in A\})$ for any $A \in \mathcal{B}([0, 1])$.
- $\Lambda^{+,1}(A) = \Lambda^1(\{(y,z) : y + z \in A\})$ for any $A \in \mathcal{B}([0,1])$.
- $\Lambda^+(A) = \Lambda(\{(y, z) : y + z \in A\})$, where the measure Λ on Δ is defined by

$$\Lambda(dy, dz) = \Lambda^1(dy, dz) + \delta_0(dy) \otimes \Lambda^{+,2}(dz).$$

In particular, if $\|\Lambda^-\| = \|\Lambda^+\|$, then we can take $\Lambda^+ = \Lambda^{+,1}$, $\Lambda = \Lambda^1$, and the measure ρ on $[0,1]^2$ defined by

$$\rho(A \times B) = \Lambda(\{(y, z) : y \in A, y + z \in B\}), \qquad A, B \in \mathcal{B}([0, 1]),$$

is a coupling of Λ^- and Λ^+ such that $\rho\{(y,z): y > z\} = 0$.

We refer to the measure Λ as the adaptation coupling of (Λ^-, Λ^+) , although strictly speaking, only the measure ρ is a coupling. The proof of Lemma 3.4 is postponed to Section 5 below. The idea behind it may be interpreted as splitting the measure Λ^+ into two parts $\Lambda^{+,1}$ and $\Lambda^{+,2}$, where the mass of $\Lambda^{+,1}$ is transported to Λ^- , and $\Lambda^{+,2}$ contains the excess of mass. In this sense, $\Lambda^{+,1}$ corresponds to the case of bigger reproductive events of Example 3.3, while $\Lambda^{+,2}$ is related to the α in case 1 of this example. The idea of mass transport is also further discussed in Section 5.

Remark 3.5. By the definition of Λ as in Lemma 3.4, we note that for any measurable function $f: [0,1] \mapsto [0,1]$ such that f(0) = 0,

$$\int_{\Delta} f(y) \Lambda(dy,dz) = \int_{[0,1]} f(y) \Lambda^-(dy), \ and \ \int_{\Delta} f(y+z) \Lambda(dy,dz) = \int_{[0,1]} f(z) \Lambda^+(dz).$$

With this coupling, we can now construct the Λ -asymmetric ancestral selection graph. In order to make the construction more transparent, we first provide an alternative description of the Λ -asymmetric Moran model, using the above partial order of adaptation. Assume that the measures Λ^+ and Λ^- satisfy $\Lambda^- \leq \Lambda^+$. Let Λ be its adaptation coupling in the sense of Lemma 3.4. This means that the random variable Y that was sampled in Definition 2.1 according to either Λ^+ or Λ^- , depending on the type of the reproducing individual, can now be sampled instead as a pair (Y, Z)according to Λ from Δ , such that individuals are replaced with probability Y if a type – individual reproduces, and individuals are replaced with probability Y + Z if a type + individual reproduces. The rates of the frequency process can thus be rewritten as (cf. Remark 3.5)

$$x \mapsto \begin{cases} x + \frac{k}{N} & \text{at rate } x \int_{\Delta} {\binom{(1-x)N}{k}} y^k (1-y)^{(1-x)N-k} \Lambda(dy, dz), \quad k = 1, \dots (1-x)N \\ x - \frac{k}{N} & \text{at rate } (1-x) \int_{\Delta} {\binom{xN}{k}} (y+z)^k (1-(y+z))^{xN-k} \Lambda(dy, dz), \quad k = 1, \dots Nx \end{cases}$$

and the generator becomes

$$\begin{aligned} \mathcal{B}^{N}f(x) &= x \int_{\Delta} \mathbb{E}\left[f\left(x + \frac{1}{N}\mathrm{Binom}(N(1-x), y)\right) - f(x)\right]\Lambda(dy, dz) \\ &+ (1-x) \int_{\Delta} \mathbb{E}\left[f\left(x - \frac{1}{N}\mathrm{Binom}(Nx, y+z)\right) - f(x)\right]\Lambda(dy, dz). \end{aligned}$$

We are now ready to define the central object of this paper, which is the ancestral selection graph for the Λ -asymmetric Moran model. We give a construction in the spirit of Neuhauser and Krone in terms of a Poisson process driven by the adaptation coupling measure Λ .

Definition 3.6 (Λ -asymmetric ancestral selection graph, ASG). Consider a Poisson processes M^N with values in $\mathbb{R}_+ \times [0,1] \times [N] \times \Delta \times [0,1]^N$ and intensity measure $dt \times dm \times \Lambda(dy, dz) \times du_1 \times du_2 \dots \times du_N$, where dm denotes the uniform measure on [N]. Each point $(t,i) \in \mathbb{R} \times [N]$, represents the *i*-th individual alive at time t.

- We say that at time t there is a neutral arrow between i and j if there is a point $(t, i, y, z, u_1, u_2, ..., u_N) \in M^N$ such that $u_j \in [0, y]$.
- We say that at time t there is a selective arrow between i and j if there is a point $(t, i, y, z, u_1, u_2, ..., u_N) \in M^N$ such that $u_j \in [0, y+z]$.

The ancestral selection graph is then given by $(\mathbb{R}_+ \times [N], M^N)$.

In the graphical representation of the ancestral selection graph, as usual, individuals are represented by lines, and reproductive events are denoted by arrows, where the arrow starts at the reproducing individual, and the tip points to the line of (potential) offspring. Here we represent the reproducing individuals by filled dots, the individuals at the tips of neutral arrows by filled squares, and the individuals at the tips of selective arrows by squares with a question mark, see Figure 2. Neutral and



Figure 2: The realisation of the Λ -asymmetric frequency process from Figure 1 now in terms of the coupling construction. Neutral arrows are black with filled squares at the tips, selective arrows grey with question marks at the tips. Individuals of type + may reproduce through any arrow, individuals of type - only through neutral arrows. Therefore some of the arrows weren't present in Figure 1, where the measures applied to determine the reproduction depended on the type of the reproducing individuals.

selective arrows may occur at the same time. Observe that formally we can have both neutral and selective arrows from i to itself, but they won't have an effect on the frequency process.

From the graphical reperesentation and the Poisson point process construction we can derive the frequency process. Heuristically, at an arrival of the Poisson process, the reproducing individual i is chosen uniformly at random, and the reproductive strenght is determined by the measure Λ . The uniform values u_j then determine whether individual j participates in a neutral or selective reproduction event. After introducing types, type + will be propagated (that is, the individual at the tip of the arrow will be replaced) both through neutral and selective arrows, while type - will be propagated only through neutral arrows. Hence we can construct the frequency process from the ASG by distributing types at time t = 0, and propagating them forward in time according to the arrows on the ASG.

Proposition 3.7. The frequency process constructed from the Λ -asymmetric ancestral selection graph by propagating type + through both neutral and selective arrows, and type - through neutral arrows only, is the same as the frequency process of the Λ -asymmetric Moran model.

We will give a more formal definition of the frequency process and a proof of this result below.

Remark 3.8. Note that it's straightforward to extend our construction to include parent independent mutations just as the classical ASG can be modified easily to incorporate them. Generalising our construction to multiple types would require a careful application of the order of adaptation and is left for future work.

4. Ancestral process, sampling function and duality

In this section we will formalize the connection between the Λ -asymmetric Moran model and the ancestral selection graph from Definition 3.6. We will also define the ancestral line counting process and state its pathwise sampling duality with the frequency process.

We start by introducing suitable forward and backward filtrations. For any subset of individuals $S \subset [N]$ and any time $T \in \mathbb{R}_+$ we will write $S_T = \{(T, i) : i \in S\}$. We think of S_T as a (random) sample of individuals taken at time T. We will follow the construction detailed in [17] and define the forward and backward filtrations of our ancestral selection graph.

Definition 4.1. Let $(\mathbb{R}_+ \times [N], M^N)$ be the Λ -asymmetric ancestral selection graph, and let S_T be a sample as defined above.

- Let \mathcal{F}_t^T denote the sigma algebra generated by S_T and the restriction of M^N to [T, T+t]. Then $\{\mathcal{F}_t^T\}_{t>0}$ is the forward filtration.
- Let \mathcal{P}_t^T denote the sigma algebra generated by S_T and the restriction of M^N to [T, T-t]. Then $\{\mathcal{P}_t^T\}_{t\geq 0}$ is the backward filtration.

The ancestral selection graph is particularly useful as a construction that can be used both forward and backward in time. In order to utilize this, we now introduce the notion of ancestral path in the ancestral selection graph, which will go backward in time.

Definition 4.2. Let $t, s \in \mathbb{R}_+, i, j \in [N]$. An ancestral path going from (t + s, i) to (t, j) is the graph of a cadlag function $f : [t, t + s] \mapsto [N]$ such that:

- 1. f(t) = j, f(t+s) = i.
- 2. If $f(u^-) = k \neq f(u) = l$ then there is an arrow (neutral or selective) in the ancestral selection graph M^N from (u, k) to (u, l).
- 3. If there is an arrow from (u, k) to (u, l), then $f(u^{-}) \neq l$.

We say that an individual (t, j) is a potential ancestor of (t + s, i) if there exists an ancestral path going from (t + s, i) to (t, j) and in this case we write $(t, j) \sim (t + s, i)$.

Graphically, it is easy to understand the concept of potential ancestor and of ancestral paths (see Figure 3).

Note that, as opposed to the Moran model, an individual in this model can have many potential ancestors at any given time in its past. Moreover, recall that we introduced neutral and selective arrows, which correspond to the measures Λ^+ and Λ^- in our original definition of the Λ -asymmetric Moran model, where individuals of type + have a selective advantage by reproducing according to Λ^+ and individuals of type - reproduce according to Λ^- , with $\Lambda^- \leq \Lambda^+$. This means that if we assign type - to all individuals of a sample S_T taken at time T, and type + to the individuals of S_T^c , then an individual i at time T + s is of type + if and only if there exists an ancestral path from (T + s, i) to at least one individual in S_T^c . In this case, we write $\tau((s, i)) = +$. Otherwise, if all the potential ancestors of (T + s, i) at time T belong to S_T , we write $\tau((T + s, i)) = -$.

We therefore formally define the frequency process in the Λ -asymmetric ancestral selection graph by assigning types -, + to all individuals at time T > 0, and denote by $X^{N,T} = \{X_t^{N,T} : t \ge T\}$ the frequency of type - individuals at time t > T. Thus,

$$X_t^{N,T} = \frac{1}{N} \sum_{i=1}^N \mathbb{1}_{\{\tau((t,i)) = -\}}, \qquad t \ge T,$$

where $\tau(t, i)$ is constructed as explained above using the ancestral lines of the ASG.

By construction, it is straightforward to check that the process $(X_t^{N,T})_{t>T}$ satisfies

$$X_{t}^{N,T} = X_{T}^{N,T} + \sum_{i=1}^{N} \int_{t}^{T} \int_{\Delta} \int_{[0,1]^{N}} 1_{\{\tau(s,i)=-\}} \frac{1}{N} \sum_{j=1}^{N} 1_{\{\tau(s,j)=+,u_{j} \leq y\}} M^{N}(di, ds, dy, dz, du) - \sum_{i=1}^{N} \int_{t}^{T} \int_{\Delta} \int_{[0,1]^{N}} 1_{\{\tau(s,i)=+\}} \frac{1}{N} \sum_{j=1}^{N} 1_{\{\tau(s,j)=-,u_{j} \leq y+z\}} M^{N}(di, ds, dy, dz, du), \quad t \geq T.$$
(1)



Figure 3: The possible ancestries of two different samples, using the realisation of the Λ -asymmetric ancestral selection graph from Figure 2. On the left, the potential ancestry of a sample of four individuals (of type -) is represented, on the right the ancestry of two individuals (of type +). We see that if at a reproductive event, lines from individuals with a filled square (black arrows) are alway merged with the reproducing line (filled circle), where for question marks (grey arrows), both lines are continued.

Proposition 4.3. Fix $x \in [0,1]$ and assume that $X_T^{N,T} = x$, then the process $X^{N,T}$ is a $\{\mathcal{F}_t^T\}_{t\geq 0}$ measurable continuous-time Markov chain with values in $[N_0]/N$, and its infinitesimal generator $\mathcal{B}^{N,T}$ is given for any $f \in \mathcal{C}^2([0,1])$ by

$$\mathcal{B}^{N,T}f(x) = x \int_{\Delta} \mathbb{E}\left[f\left(x + \frac{1}{N}\operatorname{Binom}(N(1-x), y)\right) - f(x)\right] \Lambda(dy, dz) + (1-x) \int_{\Delta} \mathbb{E}\left[f\left(x - \frac{1}{N}\operatorname{Binom}(Nx, y+z)\right) - f(x)\right] \Lambda(dy, dz).$$
(2)

Proof. The first statement of the proposition follows from (1). Now, using (1) and an application of Itô's formula we obtain for any $f \in C^2([0, 1])$ and $t \ge T$

$$\begin{split} f(X_t^{N,T}) &= f(X_T^{N,T}) \\ &+ \sum_{i=1}^N \int_T^t \int_\Delta \int_{[0,1]^N} \left[f\left(X_{s-}^{N,T} + \mathbf{1}_{\{\tau(s,i)=-\}} \frac{1}{N} \sum_{j=1}^N \mathbf{1}_{\{\tau(s,j)=+,u_j \le y\}} \right) - f(X_{s-}^{N,T}) \right] M^N(di,ds,dy,dz,du) \\ &+ \sum_{i=1}^N \int_T^t \int_\Delta \int_{[0,1]^N} \left[f\left(X_{s-}^{N,T} - \mathbf{1}_{\{\tau(s,i)=+\}} \frac{1}{N} \sum_{j=1}^N \mathbf{1}_{\{\tau(s,j)=-,u_j \le y+z\}} \right) - f(X_{s-}^{N,T}) \right] M^N(di,ds,dy,dz,du). \end{split}$$

Taking expectations in the previous identity gives for $t \ge T$

$$\mathbb{E}\left[f(X_t^{N,T})\right] = \mathbb{E}[f(X_T^{N,T})]$$

$$+ \mathbb{E}\left[\int_T^t \int_{\Delta} \int_{[0,1]^N} \frac{1}{N} \sum_{i=1}^N \mathbf{1}_{\{\tau(s,i)=-\}} \left[f\left(X_{s-}^{N,T} + \frac{1}{N} \sum_{j=1}^N \mathbf{1}_{\{\tau(s,j)=+,u_j \le y\}}\right) - f(X_{s-}^{N,T})\right] ds \Lambda(dy, dz) du$$

$$+ \mathbb{E}\left[\int_{T}^{t} \int_{\Delta} \int_{[0,1]^{N}} \frac{1}{N} \sum_{i=1}^{N} \mathbb{1}_{\{\tau(s,i)=+\}} \left[f\left(X_{s-}^{N,T} - \frac{1}{N} \sum_{j=1}^{N} \mathbb{1}_{\{\tau(s,j)=-,u_{j} \leq y+z\}}\right) - f(X_{s-}^{N,T}) \right] ds \Lambda(dy, dz) du$$

$$= \mathbb{E}[f(X_{T}^{N,T})] + \mathbb{E}\left[\int_{T}^{t} \int_{\Delta} X_{s-}^{N,T} \left[f\left(X_{s-}^{N,T} + \frac{1}{N} \operatorname{Binom}(N(1 - X_{s-}^{N,T}), y)\right) - f(X_{s-}^{N,T}) \right] ds \Lambda(dy, dz) \right]$$

$$+ \mathbb{E}\left[\int_{T}^{t} \int_{\Delta} \int_{[0,1]^{N}} (1 - X_{s-}^{N,T}) \left[f\left(X_{s-}^{N,T} - \frac{1}{N} \operatorname{Binom}(NX_{s-}^{N,T}, y+z)\right) - f(X_{s-}^{N,T}) \right] ds \Lambda(dy, dz) \right].$$

$$(3)$$

Finally, by differentiating (3) and taking t = 0 we obtain (2).

Proof of Proposition 3.7. The generator $\mathcal{B}^{N,T}$ has no true dependence on T, but only on the cardinality of the sample S_T of indivduals of type -, which gives the initial frequency $|S_T|/N$ of individuals of type -. Comparing $\mathcal{B}^{N,T}$ and \mathcal{B}^N shows that they are equal, hence the processes they generate are equal in distribution.

We may thus identify the two frequency processes $(X_t^N)_{t\geq 0}$ and $(X_t^{N,T})_{t\geq T}$ with $X_0^N = |S_T|/N$, and call it the frequency process associated with the Λ - asymmetric ancestral selection graph.

One of the big advantages of the Λ -ancestral selection graph is that it also allows for a $\{\mathcal{P}_t^T\}_{t\geq 0}$ measurable ancestral process, the ancestral line counting process, which satisfies a duality relation with the frequency process.

Definition 4.4 (Ancestral process). Fix a sample S_T of individuals at some time $T \in \mathbb{R}$. The ancestral line counting process $(A_t^{N,T})_{0 \le t \le T}$ of a sample taken at time T is given by

$$A_t^{N,T} = \sum_{i=1}^N \mathbb{1}_{\{(T-t,i)\sim(T,j), \text{ for some } (T,j)\in S_T\}}, \qquad t\in[0,T].$$

Hence by definition $A_t^{N,T}$ counts the number of potential ancestors living at time $t \in [0,T]$ of individuals from the sample S_T .

Proposition 4.5. The process $(A_t^{N,T})_{0 \le t \le T}$ is a $\{\mathcal{P}_t\}_{t \ge 0}$ measurable continuous-time Markov chain with values in [N] starting at $A_0^{N,T} = |S_T|$ and transition rates

$$n \mapsto \begin{cases} n-k & \text{at rate } \frac{n}{N} \int_{\Delta} \binom{n-1}{k} y^k (1-y)^{n-1-k} \Lambda(dy, dz), \quad k=1,...,n-1 \\ n-k+1 & \text{at rate } (1-\frac{n}{N}) \int_{\Delta} \binom{n}{k} y^k (1-y)^{n-k} \Lambda(dy, dz), \quad k=2,...,n \\ n+1 & \text{at rate } (1-\frac{n}{N}) \int_{\Delta} [(1-y)^n - (1-y-z)^n] \Lambda(dy, dz). \end{cases}$$

Since again the process doesn't depend on T but only on $|S_T|$, we drop the T from the notation and call $(A_t^N)_{t>0}$ the ancestral line counting process or process of potential ancestors.

Proof. Measurability is clear, as well as the initial value. In order to understand the rates, we consider the graphical representation and go backward from sampling time T. If we have currently n potential ancestors, then the next event backward in time is one of the following three cases (cf. Figure 4):

1. From one of the *n* potential ancestors, *k* neutral arrows emerge and hit *k* of the remaining n-1 lines of potential ancestors. In that case, the *k* lines coalesce with the reproducing line, reducing the number of potential ancestors by *k*. According to the construction of the ancestral selection graph, this happens at rate $\frac{n}{N} \int_{\Delta} {\binom{n-1}{k}} y^k (1-y)^{n-1-k} \Lambda(dy, dz)$, leading to the first line in the above transition rates. There might be selective arrows at the same event, but these don't change the number of potential ancestors, since in that case both lines continue to be potential ancestors.

- 2. From one of the N n lines that don't currently belong to the set of potential ancestors there are neutral arrows to $k \ge 2$ out of the *n* current potential ancestors. In that case those *k* lines merge, but the line of the reproducing individual is added to the set of potential ancestors. This happens at rate $(1 \frac{n}{N}) \int_{\Delta} {n \choose k} y^k (1 y)^{n-k} \Lambda(dy, dz)$.
- 3. From one of the N n lines outside the current set of potential ancestors there is a selective arrow to at least one of the n individuals from the current set of ancestors, while at the same time there are no neutral arrows to any of the n current ancestors in the sample. In that case, the reproducing line is added to the set of potential ancestors, while all the other lines remain. This happens at rate $(1 \frac{n}{N}) \int_{\Delta} [(1 y)^n (1 y z)^n] \Lambda(dy, dz)$, since $(1 y)^n (1 y z)^n$ is the probability that there are no neutral arrows to individuals of the ancestal process, while there is at least one selective arrow.

There are no further events in the graphical construction that could change the number of potential ancestors. $\hfill \Box$

For $x \in [N_0]/N$, $n \in [N]$, and $t \ge 0$ we define the sampling function $S_t(x,n)$ as follows. Let $\{u_i\}_{i\in[n]}$ be a uniformly sampled subset of [N] of size n, and let $S_t(x,n)$ be the probability that all individuals in the sample $S_t = \{(u_i, t)\}$ are of type – conditional on the initial frequency of type – individuals at time 0 is x. Note that for t = 0

$$S_0(x,n) = \prod_{i=1}^n \frac{Nx+1-i}{N+1-i}.$$

Observe that for fixed n and large N is of order $x^n + O(1/N)$, a fact that we will use in Proposition 6.5 below.

Now, using the graphical representation, for any t > 0 we can write $S_t(x, n)$ in terms of $S_0(x, n)$ and A_t^N started at $A_0^N = n$. Recall that an individual at time t has type – if and only if all its potential ancestors at time 0 have type –. Thus the probability that n individuals sampled at time t is given in terms of the number of potential ancestors of these individuals, and we obtain

$$S_t(x,n) = \mathbb{E}[S_0(x, A_t^N) | A_0^N = n] = \mathbb{E}_n[S_0(x, A_t^N)].$$

Here, \mathbb{E} denotes the expectation with respect to the law of the ancestral selection graph, and \mathbb{E}_n the expectation with respect to the Markov chain $(A_t^N)_{t\geq 0}$ started at n. Similarly, we can write $S_t(x, n)$ in terms of $S_0(x, n)$ and X_t^N started at $X_0^N = x$ as

$$S_t(x,n) = \mathbb{E}[S_0(X_t^N, n) \,|\, X_0 = x] = \mathbb{E}_x[S_0(X_t^N, n)].$$

Hence we have shown

Corollary 4.6. The processes $(X_t^N)_{t\geq 0}$ and $(A_t^N)_{t\geq 0}$ are dual with respect to the duality function S_0 , that is,

$$\mathbb{E}_x[S_0(X_t^N, n)] = \mathbb{E}_n[S_0(x, A_t^N)] \quad \forall t \ge 0, x \in [N_0]/N, n \in \mathbb{N}.$$

5. Proof of the coupling lemma, and optimal transport connection

We are now going to prove the adaptation coupling that lies at the heart of our construction, and discuss its connection to the theory of optimal transport.

Proof of Lemma 3.4. Step 1.- First assume that $\Lambda^+[0,1] = \Lambda^-[0,1] = c^{-1}$. By assumption we know that $\Lambda^-[0,x] - \Lambda^+[0,x] \ge 0$ for any $x \in [0,1]$. Therefore by a version of Strassen Theorem (see (3) in [24]) there exists two random variables Z^- and Z^+ on a probability space such that

$$Z^- \sim c\Lambda^-(\cdot),$$
 and, $Z^+ \sim c\Lambda^+(\cdot),$



Figure 4: The three possible types of transitions of the ancestral process. On the left, the reproducing individuals belongs to the current sample, there is one neutral and two selctive arrow. The line of the individual at the end of the neutral arrow is discarded, resp. merges with the reproducing line, while the lines with a question mark (selective) remain. In the middle, the reproducing individuals doesn't belong to the current sample, there are two neutral and two selctive arrows. The line of the reproducing individual is thus added, the lines of the individuals at the end of a neutral arrow are discarded, resp. merge with the reproducing line. On the right, only selective arrows are present, where the incoming lines are kept, but the reproducing line is added. We therefore see a branching.

and $Z^- \leq Z^+$ a.s. Here ~ means that the random variable is distributed according to the respective probability mesure. Moreover, the joint distribution of (Z^-, Z^+) , is given as follows

$$\mathbb{P}\left((Z^{-}, Z^{+}) \in A\right) = \mathbb{P}\left((F_{-}^{-1}(U), F_{+}^{-1}(U)) \in A\right), \qquad A \in \mathcal{B}([0, 1]^{2}),$$

where F_{-} (resp. F_{+}) is the distribution function of the random variable Z^{-} (resp. Z^{+}) and U is a unifom random variable on [0, 1]. Hence, let us define the following kernel in Δ

$$\Lambda(A) := c^{-1} \mathbb{P}\left((Z^-, (Z^+ - Z^-)) \in A \right), \quad \text{for any } A \in \mathcal{B}(\Delta).$$

Then we note that for any Borel set $B \subset [0, 1]$

$$\Lambda(B \times [0,1]) = c^{-1} \mathbb{P}\left((Z^-, Z^+ - Z^-) \in B \times [0,1] \right) = c^{-1} \mathbb{P}(Z^- \in B) = \Lambda^-(B),$$

additionally

$$\Lambda\left(\{(y,z): y+z \in A\}\right) = c^{-1}\mathbb{P}\left(Z^{-} + Z^{+} - Z^{-} \in A\right) = c^{-1}\mathbb{P}\left(Z^{+} \in A\right) = \Lambda^{+}(A).$$

Step 2.- Now we assume that $\|\Lambda^-\| < \|\Lambda^+\|$. The fact that $\Lambda^- \leq \Lambda^+$ implies that for any $x \in [0, 1]$,

$$\Lambda^{-}([x,1]) \le \Lambda^{+}([x,1]).$$
(4)

Without loss of generality let us assume that Λ^- is a probability measure on [0, 1], as the general case follows by normalizing the measure Λ^- .

We define $x^* = \sup\{x \in [0, 1] : \Lambda^+([x, 1]) \ge 1\}$, then

(i) If $\Lambda^+([x^*,1]) = 1$ we define the measures $\Lambda^{+,1}(A) = \Lambda^+(A \cap [x^*,1])$ and $\Lambda^{+,2}(A) = \Lambda(A \cap [0,x^*))$ for any $A \in \mathcal{B}([0,1])$.

(ii) if $\Lambda^+([x^*, 1]) > 1$ then we have that $\Lambda^+([x^*, 1]) - \Lambda^+((x^*, 1]) > 0$ which implies that $\Lambda^+(\{x^*\}) > 0$. In this case we define $B := \Lambda^+([x^*, 1]) - \Lambda^+((x^*, 1]), C := 1 - \Lambda^+((x^*, 1])$ and

$$\Lambda^{+,1}(A) = \Lambda^+((x^*, 1] \cap A) + C\delta_{x^*}(A).$$

Then if we denote $D := \Lambda^+([x^*, 1]) - 1$

$$\Lambda^{+}(A) = \Lambda^{+}((x^{*}, 1] \cap A) + \Lambda^{+}([0, x^{*}) \cap A) + B\delta_{x^{*}}(A)$$

= $\Lambda^{+}((x^{*}, 1] \cap A) + \Lambda^{+}([0, x^{*}) \cap A) + C\delta_{x^{*}}(A) + D\delta_{x^{*}}(A)$
= $\Lambda^{+,1}(A) + \Lambda^{+,2}(A),$ (5)

where $\Lambda^{+,2}(A) = \Lambda^{+}([0, x^{*}) \cap A) + D\delta_{x^{*}}(A).$

By construction we have that $\Lambda^+ = \Lambda^{+,1} + \Lambda^{+,2}$ and that

$$\Lambda^{+,1}[0,1] = \Lambda^+((x^*,1]) + C = \Lambda^+((x^*,1]) + 1 - \Lambda^+((x^*,1]) = 1$$

Additionally, assume that $\Lambda^+([x^*, 1]) > 1$ and consider $x \in [0, 1]$ such that $x > x^*$ then

$$\Lambda^{+,1}([x,1]) = \Lambda^+([x,1]) \ge \Lambda^-[x,1],$$

where the last inequality follows from (4). If we consider that $x \leq x^*$ we obtain

$$\Lambda^{+,1}([x,1]) = \Lambda^+((x^*,1]) + 1 - \Lambda^+((x^*,1]) = 1 \ge \Lambda^-([x,1]).$$

Hence, $\Lambda^{-} < \Lambda^{+,1}$. The case in which $\Lambda_{1}([x^{*}, 1]) = 1$ follows analogously.

Noting that by construction $\|\Lambda^{+,1}\| = \|\Lambda^{-}\| = 1$, we have by Step 1 that there exists a measure Λ^{1} on Δ such that $\Lambda^{-}(A) = \Lambda^{1}(\{(y,z) : y \in A\})$ and $\Lambda^{+,1}(A) = \Lambda^{1}(\{(y,z) : y + z \in A\})$. And, by (5) we get for any $A \in \mathcal{B}(\Delta)$

$$\Lambda(A) = \Lambda^{+,1}(A) + (\delta_0 \otimes \Lambda^{+,2}) \left(\{ (y,z) : y+z \in A \} \right) = \Lambda^{+,1}(A) + \Lambda^{+,2}(A) = \Lambda^+(A)$$

Keeping in mind the proof of Lemma 3.4, we will now show that the representation of the frequency process by means of the coupling ρ introduced in Lemma 3.4 minimizes the number of potential ancestors in the construction of the Λ -asymmetric ancestral graph given in Definition 3.6 in the case in which Λ^- and Λ^+ are probability measures.

To be more precise, denote for $n \in \mathbb{N}$.

$$c(y,z) := (1-y)^n - (1-z)^n, \qquad y,z \in [0,1]^2,$$

and consider the following optimal transport problem, consisting in finding a probability measure γ^* on $[0,1]^2$ such that the following infimum is achieved

$$V(n,\Lambda^{-},\Lambda^{+}) := \inf\left\{\int_{[0,1]^2} c(y,z)\gamma(dy,dz) : \gamma \in \Gamma(\Lambda^{-},\Lambda^{+})\right\},\tag{6}$$

where $\Gamma(\Lambda^-, \Lambda^+)$ is the set of probability measures on $[0, 1]^2$ with marginals Λ^-, Λ^+ on [0, 1].

We first note that by construction

$$\int_{\Delta} \left[(1-y)^n - (1-y-z)^n \right] \Lambda(dy, dz) = \int_{[0,1]^2} \left[(1-y)^n - (1-z)^n \right] \rho(dy, dz) = \mathbb{E} \left[c(Z^-, Z^+) \right], \quad (7)$$

where Z^-, Z^+ , given in the proof of Lemma (3.4), satisfy that $(Z^-, Z^+) = (F_-^{-1}(U), F_+^{-1}(U))$.

On the other hand, the function c satisfies the "Monge" conditions, i.e. c is continuous and satisfies that for $y' \ge y$ and $z' \ge z$

$$c(y', z') - c(y, z') - c(y', z) - c(y, z) = 0.$$

Hence, as in Section 7.1 in [29] we have that the solution to the optimization problem given in (6) is given by a measure γ^* with distribution $F^*(y, z) := \min\{F_-(y), F_+(z)\}$ for $y, z \in [0, 1]^2$, or in terms of random variables, γ^* is the distribution function of the random vector $(F_-^{-1}(U), F_+^{-1}(U))$, where U a uniform random variable.

Hence comparing with (7) we obtain that $\gamma^* = \rho$ and therefore the measure ρ from our coupling is the solution to the minimisation problem (6) i.e.

$$V(n,\mu_1,\mu_2) = \int_{[0,1]^2} \left[(1-y)^n - (1-z)^n \right] \rho(dy,dz)$$

for each $n \in \mathbb{N}$. In that sense, the adaptation coupling ρ minimises the number of selective arrows resp. the number of potential ancestors.

6. Scaling Limits

In this section we will study the scaling limit of the frequency process associated to the Λ -asymmetric ancestral selection graph introduced in Section 3. We start by showing that the limiting object is well defined, which is the content of the next result.

Proposition 6.1. Assume that Λ is a measure on $\Delta = \{(y, z) \in [0, 1]^2 : y + z \in [0, 1]\}$ such that

$$\int_{\Delta} (y^2 + z) \Lambda(dy, dz) < \infty.$$
(8)

Then, for any $x \in [0,1]$ there exists a unique strong solution $Y = \{Y_t : t \ge 0\}$ to the following stochastic differential equation

$$Y_{t} = x + \int_{0}^{t} \int_{0}^{1} \int_{\Delta} \left(y(1 - Y_{s-}) \mathbf{1}_{\{u \le Y_{s-}\}} - (y + z) Y_{s-} \mathbf{1}_{\{u \ge Y_{s-}\}} \right) \mathbf{1}_{\{Y_{s-} \in [0,1]\}} \tilde{N}(ds, du, dy, dz) - \int_{\Delta} z \mu(dy, dz) \int_{0}^{t} (1 - Y_{s-}) Y_{s-} \mathbf{1}_{\{Y_{s-} \in [0,1]\}} ds,$$
(9)

where N is a Poisson random measure on $(0, \infty) \times [0, 1] \times \Delta$ with intensity measure $dt \times du \times \Lambda(dy, dz)$ and $\tilde{N}(ds, du, dy, dz) := N(ds, du, dy, dz) - dsdu\Lambda(dy, dz)$ denotes the compensated random measure associated to N. We refer to the process Y as the Λ -asymmetric frequency process.

Proof. Let us denote for $(x, y, z, u) \in [0, 1] \times \Delta \times [0, 1]$

$$g(x, y, z, u) := y(1 - x)\mathbf{1}_{\{u < x\}} - (y + z)x\mathbf{1}_{\{u \ge x\}}$$

For fixed $(y, z, u) \in \Delta \times [0, 1]$ we have

$$x + g(x, y, z, u) = \begin{cases} y + x(1 - y) & \text{if } u < x, \\ x(1 - (y + z)) & \text{if } u \ge x. \end{cases}$$
(10)

First, we note that for fixed $(y, z, u) \in \Delta \times [0, 1]$

$$0 \le x + g(x, y, z, u) = x + y(1 - x)\mathbf{1}_{\{u < x\}} - (y + z)x\mathbf{1}_{\{u \ge x\}} \le 1.$$

Hence, by a modification of Proposition 2.1 in [13] (see also Corollary 6.2 in [26]) we obtain that $\mathbb{P}(Y_t \in [0, 1] \text{ for all } t \ge 0) = 1.$

On the other hand, (10) implies that for fixed $(y, z, u) \in \Delta \times [0, 1]$ the mapping $x \mapsto x + g(x, y, z, u)$ is non-decreasing for $x \in [0, 1]$.

Denote for $x \in [0, 1]$

$$b(x) := \left(\int_{\Delta} z\Lambda(dy, dz)\right) x(1-x).$$

Then, for $x_1, x_2 \in [0, 1]$

$$|b(x_1) - b(x_2)| = |x_2(1 - x_2) - x_1(1 - x_1)| \int_{\Delta} z\Lambda(dy, dz) \le 2 \int_{\Delta} z\Lambda(dy, dz) |x_2 - x_1|.$$
(11)

Similarly, for $x_1, x_2 \in [0, 1]$

$$|g(x_1, y, z, u) - g(x_2, y, z, u)| = y(x_2 - x_1) \mathbf{1}_{\{u \le x_1 \land x_2\}} - (y(1 - x_2) + (y + z)x_1) \mathbf{1}_{\{x_1 \le u \le x_2\}} + (y(1 - x_1) + (y + z)x_2) \mathbf{1}_{\{x_2 \le u \le x_1\}} - (y + z)(x_1 - x_2) \mathbf{1}_{\{x_1 \lor x_2 \le u\}}.$$
(12)

Using (12) we obtain for $x_1, x_2 \in [0, 1]$

$$\int_{\Delta} \int_{0}^{1} |g(x_{1}, y, z, u) - g(x_{2}, y, z, u)|^{2} du \Lambda(dy, dz)
\leq \int_{\Delta} \int_{0}^{1} \left[y^{2} |x_{2} - x_{1}|^{2} \mathbf{1}_{\{u \leq x_{1} \wedge x_{2}\}} + (y(1 - x_{2}) + (y + z)x_{1})^{2} \mathbf{1}_{\{x_{1} \leq u \leq x_{2}\}}
+ (y(1 - x_{1}) + (y + z)x_{2})^{2} \mathbf{1}_{\{x_{2} \leq u \leq x_{1}\}} + (y + z)^{2} |x_{1} - x_{2}|^{2} \mathbf{1}_{\{x_{1} \vee x_{2} \leq u\}} \right] du \Lambda(dy, dz)
\leq 6 |x_{2} - x_{1}| \int_{\Delta} (y^{2} + z) \Lambda(dy, dz).$$
(13)

Finally we note that for $x \in [0, 1]$

$$|b(x)|^2 = \left(\int_{\Delta} z\Lambda(dy, dz)\right)^2 x^2 (1-x)^2 \le \left(\int_{\Delta} z\Lambda(dy, dz)\right)^2 x^2,\tag{14}$$

and

$$\int_{\Delta} \int_{0}^{1} |g(x, y, z, u)|^{2} du \Lambda(dy, dz) = \int_{\Delta} \int_{0}^{1} \left[y^{2} (1 - x)^{2} \mathbf{1}_{\{u < x\}} + (y + z)^{2} x^{2} \mathbf{1}_{\{u \ge x\}} \right] du \Lambda(dy, dz)$$

$$\leq \int_{\Delta} \left[y^{2} (1 - x)^{2} x + x^{2} (y + z)^{2} (1 - x) \right] \Lambda(dy, dz)$$

$$\leq (1 + x^{2}) \int_{\Delta} (y^{2} + z) \Lambda(dy, dz).$$
(15)

Therefore, there exists K > 0 such that for $x \in [0, 1]$

$$|b(x)|^{2} + \int_{\Delta} \int_{0}^{1} |g(x, y, z, u)|^{2} du \Lambda(dy, dz) \le K(1 + |x|^{2}).$$
(16)

Hence using (11), (13) and (15) together with the fact that the mapping $x \mapsto x + g(x, y, z, u)$ is nondecreasing for $x \in [0, 1]$, we obtain by a slight modification of Theorem 5.1 in [26] that there exists a unique strong solution to (9). **Remark 6.2.** Note that if the weaker condition

$$\int_{\Delta} (y+z)\Lambda(dy,dz) < \infty,$$

holds, then the process Y, solution to the SDE given in (9), can be described as the solution to the simpler SDE given by

$$Y_t = x + \int_0^t \int_\Delta \int_0^1 \left(y(1 - Y_{s-}) \mathbf{1}_{\{u \le Y_{s-}\}} - (y + z) Y_{s-} \mathbf{1}_{\{u \ge Y_{s-}\}} \right) \mathbf{1}_{\{Y_{s-} \in [0,1]\}} N(ds, du, dy, dz).$$

In the following result we derive the convergence of the frequency processes associated to the Λ ancestral selection graph introduced in Section 3. In doing so we need to take some care in dealing with the possible singularity at 0 of the measure Λ . To this end, we will apply a truncation procedure at 0, and study a sequence of frequency processes Y^N that correspond to the truncated Λ -measures.

Fix a measure Λ on Δ such that $\int_{\Delta} (y^2 + z) \Lambda(dy, dz) < \infty$, an initial frequency $x \in [0, 1]$ and a number $\alpha \in (0, 1/2)$. For each $N \in \mathbb{N}$ we define the truncated frequency process $Y^N = (Y_t^N)_{t \geq 0}$ with initial value $Y_0^N = \lfloor xN \rfloor / N$ as the frequency process of an asymmetric Λ -Moran model with reproduction mechanism

$$\Lambda^{(N)}(A) := \int_{\Delta^N} 1_A(y, z) \Lambda(dy, dz),$$

where

$$\Delta^N:=\{(y,z)\in\Delta:y^2>1/N^\alpha\}.$$

Note that the measure $\Lambda^{(N)}$ is a finite measure on Δ , indeed by the definition of Δ^N we have

$$\Lambda^{(N)}(\Delta) = \Lambda(\Delta^N) \le N^{\alpha} \int_{\Delta} (y^2 + z) \Lambda(dy, dz) < \infty.$$

Hence Y^N is well defined. We will now show the convergence of the sequence of process $(Y^N)_{N\in\mathbb{N}}$ as the total size of the population N grows to infinity to the Λ -asymmetric frequency process Y defined in Proposition 6.1.

Proposition 6.3. The sequence $(Y^N)_{n \in \mathbb{N}}$ converges weakly in $\mathbb{D}([0,T],[0,1])$ to a limit Y, where Y is the Λ -asymmetric frequency process given in (9).

Proof. We recall that the infinitesimal generator \mathcal{B}^N of the process Y^N is given for any $f \in \mathcal{C}^2([0,1])$ by

$$\begin{aligned} \mathcal{B}^{N}f(x) &= \int_{\Delta^{N}} \left\{ \frac{\lfloor xN \rfloor}{N} \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N} B_{N} \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \\ &+ \left(1 - \frac{\lfloor xN \rfloor}{N} \right) \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N} \tilde{B}_{N} \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \Lambda(dy, dz), \end{aligned}$$

where $B_N := \text{Binom}\left(N\left(1 - \frac{\lfloor xN \rfloor}{N}\right); y\right)$ and $\tilde{B}_N := \text{Binom}\left(\lfloor xN \rfloor; y+z\right)$. Now, for any $f \in \mathcal{C}^2([0,1])$ and $x \in [0,1]$ we have by Taylor's Theorem that

$$f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - f\left(\frac{\lfloor xN \rfloor}{N}\right) - (f(x+(1-x)y) - f(x))$$
$$= R\left(\frac{\lfloor xN \rfloor}{N}, \frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - R(x, x+(1-x)y).$$
(17)

where $R(u, v) := \int_{u}^{v} f'(t) dt$.

Now, we note that

$$R\left(\frac{\lfloor xN \rfloor}{N}, \frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - R(x, x + (1-x)y) = \int_{\frac{\lfloor xN \rfloor}{N}}^{\frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N} f'(t)dt - \int_x^{x + (1-x)y} f'(t)dt$$
$$\leq \int_{\frac{\lfloor xN \rfloor}{N}}^x f'(t)dt + \int_{x + (1-x)y}^{\frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N} f'(t)dt.$$
(18)

Therefore, using (18)

$$\left| R\left(\frac{\lfloor xN \rfloor}{N}, \frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - R(x, x + (1 - x)y) \right| \\
\leq \|f'\|_{[0,1]} \left| x - \frac{\lfloor xN \rfloor}{N} \right| + \|f'\|_{[0,1]} \left| \frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N - x - (1 - x)y \right| \\
= \|f'\|_{[0,1]} \frac{1}{N} + \|f'\|_{[0,1]} \left| (1 - y) \left(\frac{\lfloor xN \rfloor}{N} - x \right) + \frac{1}{N}B_N - \left(1 - \frac{\lfloor xN \rfloor}{N} \right) y \right| \\
\leq \|f'\|_{[0,1]} \frac{1}{N} + \|f'\|_{[0,1]} \left[\frac{1}{N}(1 - y) + \left| \frac{1}{N}B_N - \left(1 - \frac{\lfloor xN \rfloor}{N} \right) y \right| \right], \quad (19)$$

where $\|g\|_{[0,1]} := \sup_{x \in [0,1]} |g(x)|$ for any $g \in \mathcal{C}^2([0,1])$. On the other hand, we note that

$$\mathbb{E}\left[\left|\frac{1}{N}B_N - \left(1 - \frac{\lfloor xN \rfloor}{N}\right)y\right|^2\right] = \frac{1}{N^2}\mathbb{E}\left[\left|B_N - N\left(1 - \frac{\lfloor xN \rfloor}{N}\right)y\right|^2\right] = \frac{1}{N}\left(1 - \frac{\lfloor xN \rfloor}{N}\right)y(1-y),$$

and by the Cauchy-Schwarz inequality we have

$$\mathbb{E}\left[\left|\frac{1}{N}B_N - \left(1 - \frac{\lfloor xN \rfloor}{N}\right)y\right|\right] = \left[\frac{1}{N}\left(1 - \frac{\lfloor xN \rfloor}{N}\right)y(1-y)\right]^{1/2}.$$

Hence, by taking expectations on (19), we can find a constant $C_f > 0$ only dependent on f such that

$$\mathbb{E}\left[\left|R\left(\frac{\lfloor xN \rfloor}{N}, \frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - R(x, x + (1-x)y)\right|\right] = C_f\left(\frac{1}{N} + \frac{1}{N^{1/2}}y^{1/2}\right).$$
 (20)

Hence, by (17) together with (20) there exists a constant $C_f > 0$ only dependent on f such that

$$\left| f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N}B_N\right) - f\left(\frac{\lfloor xN \rfloor}{N}\right) - \left(f(x + (1 - x)y) - f(x)\right) \right| \le C_f\left(\frac{1}{N} + \frac{1}{N^{1/2}}y^{1/2}\right).$$
(21)

Very similarly we can deal with the other term in the generator involving \tilde{B}_N , and after the same kind of calculations as before we arrive at

$$\left| f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N}\tilde{B}_N\right) - f\left(\frac{\lfloor xN \rfloor}{N}\right) - \left(f(x - x(y + z)) - f(x)\right) \right| \le \tilde{C}_f\left(\frac{1}{N} + \frac{1}{N^{1/2}}(y + z)^{1/2}\right).$$
(22)

Using (21) together with (22) we obtain, for $x \in [0, 1]$,

$$\sup_{x \in [0,1]} \left| \int_{\Delta^{N}} \left\{ x \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N} B_{N} \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] + (1-x) \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N} \tilde{B}_{N} \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \Lambda(dy, dz)
- \int_{\Delta} \left\{ x f(x+y(1-x)) + (1-x) f(x-(y+z)x) - f(x) \right\} \Lambda(dy, dz)
\leq 2(C_{f} + \tilde{C}_{f}) \frac{1}{N^{1/2}} \int_{\Delta^{N}} \Lambda(dy, dz)
+ \sup_{x \in [0,1]} \int_{\Delta \setminus \Delta^{N}} \left| x f(x+y(1-x)) + (1-x) f(x-(y+z)x) - f(x) \right| \Lambda(dy, dz).$$
(23)

Expanding the integrand in the right-hand side of (23) gives

$$\begin{aligned} |xf(x+y(1-x)) + (1-x)f(x-(y+z)x) - f(x)| &= \left| x \int_{x}^{x+y(1-x)} \frac{f''(t)}{2} (x+y(1-x)-t) dt \right. \\ &+ (1-x) \int_{x}^{x-(y+z)x} \frac{f''(t)}{2} (x-(y+z)x-t) dt - x(1-x)zf'(x) \right| \\ &\leq \frac{\|f''\|_{[0,1]}}{4} \left(x(1-x)^2 y^2 + (1-x)(y+z)^2 x^2 \right) + \|f'\|_{[0,1]} x(1-x)z \leq K_f(y^2+z), \end{aligned}$$

$$(24)$$

where K_f is positive constant only dependent on f. Hence, using (24) in (23)

$$\begin{split} \lim_{n \to \infty} \sup_{x \in [0,1]} \left| \int_{\Delta^N} \left\{ x \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N} B_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \\ &+ (1-x) \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N} \tilde{B}_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \Lambda(dy, dz) \\ &- \int_{\Delta} \left\{ x f(x+y(1-x)) + (1-x) f(x-(y+z)x) - f(x) \right\} \Lambda(dy, dz) \right| \\ &\leq \lim_{n \to \infty} \left[(C_f + \tilde{C}_f) \frac{1}{N^{1/2-\alpha}} \int_{\Delta} (y^2 + z) \Lambda(dy, dz) + K_f \int_{\Delta \setminus \Delta^N} (y^2 + z) \Lambda(dy, dz) \right] = 0. \end{split}$$

$$(25)$$

Finally, we note that

$$\lim_{N \to \infty} \sup_{x \in [0,1]} \left| \int_{\Delta^N} \left\{ \frac{\lfloor xN \rfloor}{N} \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N} B_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \\
+ \left(1 - \frac{\lfloor xN \rfloor}{N} \right) \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N} \tilde{B}_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \\
- \int_{\Delta^N} \left\{ x \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} + \frac{1}{N} B_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] + (1 - x) \mathbb{E} \left[f\left(\frac{\lfloor xN \rfloor}{N} - \frac{1}{N} \tilde{B}_N \right) - f\left(\frac{\lfloor xN \rfloor}{N} \right) \right] \right\} \\
\leq \lim_{N \to \infty} 2 \|f\|_{[0,1]} \frac{1}{N^{1-\alpha}} \int_{\Delta} (y^2 + z) \Lambda(dy, dz) = 0.$$
(26)

Following the steps of Proposition 4.2 in [4] we have that the infinitesimal generator \mathcal{B} of the Λ -asymmetric frequency process Y is given for any $f \in \mathcal{C}^2([0,1])$ and $x \in [0,1]$ by

$$\mathcal{B}f(x) = \int_{\Delta} \left[xf(x+y(1-x)) + (1-x)f(x-(y+z)x) - f(x) \right] \Lambda(dy,dz), \qquad x \in [0,1].$$
(27)

Hence, by (25) together with (26) we obtain that $\mathcal{B}^N f \to \mathcal{B}$ as $n \to \infty$ uniformly in [0, 1]. Therefore, Theorem 17.25 in [20] implies that $Y^N \to Y$ as $n \to \infty$ weakly in the space $\mathbb{D}([0, T], [0, 1])$.

Let $A^N := \{A_t^N : t > 0\}$ denote the ancestral process associated to the frequency process Y^N defined in Proposition 6.3. In the next result we show the convergence of the sequence of processes $(A^N)_{N \in \mathbb{N}}$ as the total size of the population N grows to infinity.

Proposition 6.4. The sequence $(A^N)_{N \in \mathbb{N}}$ converges weakly in $\mathbb{D}([0,T],\mathbb{N})$ to a limit A, where A is a continuous-time Markov chain with values in \mathbb{N} , whose generator has the following transition rates

$$m \mapsto \begin{cases} m-k+1 & \text{at rate } \int_{\Delta} {m \choose k} y^k (1-y)^{m-k} \Lambda(dy, dz), \quad k=2, ..., m \\ m+1 & \text{at rate } \int_{\Delta} [(1-y)^m - (1-y-z)^m] \Lambda(dy, dz). \end{cases}$$

Proof. Fix $m \in \mathbb{N}$. Using that $|(1-y)^m - (1-y-z)^m| \le mz$, for $y, z \in \Delta$ we obtain that (8) together with dominated convergence gives

$$\lim_{N \to \infty} \left(1 - \frac{m}{N} \right) \int_{\Delta^N} \left[(1 - y)^m - (1 - y - z)^m \right] \Lambda(dy, dz) = \int_{\Delta} \left[(1 - y)^m - (1 - y - z)^m \right] \Lambda(dy, dz).$$

On the other hand, for $k \ge 2$, by (8) and dominated convergence

$$\lim_{N \to \infty} \left(1 - \frac{m}{N} \right) \int_{\Delta^N} \binom{m}{k} y^k (1 - y)^{m-k} \Lambda(dy, dz) = \int_{\Delta} \binom{m}{k} y^k (1 - y)^{m-k} \Lambda(dy, dz).$$

By the definiton of Δ^N we note that dominated convergence gives

$$\lim_{N \to \infty} \frac{m}{N} \int_{\Delta^N} my (1-y)^{m-1} \Lambda(dy, dz) \le \lim_{N \to \infty} m^2 \frac{1}{N^{1-\alpha/2}} \int_{\Delta^N} y^2 \Lambda(dy, dz) = 0.$$

Similarly, for $k \ge 2$, proceeding as in the previous identities we get

$$\lim_{N \to \infty} \frac{m}{N} \int_{\Delta^N} \binom{m}{k} y^k (1-y)^{m-k} \Lambda(dy, dz) = 0.$$

Therefore, by Problem 3(ii) in [10] we obtain the result.

As expected we show in the next result that the processes Y and A are moment duals. To this end, we note that the infinitesimal generator \mathcal{A} of the process A is given for any $f : \mathbb{N} \to \mathbb{N}$ by

$$\mathcal{A}f(n) = \sum_{k=1}^{n} (f(n-k+1) - f(n)) \int_{\Delta} \binom{n}{k} y^{k} (1-y)^{n-k} \Lambda(dy, dz) + (f(n+1) - f(n)) \int_{\Delta} [(1-y)^{n} - (1-y-z)^{n}] \Lambda(dy, dz).$$
(28)

Proposition 6.5. Consider the Λ -asymmetric frequency process Y defined in Proposition 6.1 and the ancestry process A with rates given in Proposition 6.4. Then the processes Y and A are moment duals, i.e. for any $x \in [0, 1]$ and $n \in \mathbb{N}$

$$\mathbb{E}_x\left[Y_t^n\right] = \mathbb{E}_n\left[x^{A_t}\right], \quad \text{for all } t > 0.$$

Proof. We will consider \mathbb{N} endowed with the discrete topology and $\mathbb{N} \times [0, 1]$ with the product topology. We denote for every fixed $x \in [0, 1]$, $H(n, x) = x^n$, which is bounded and continuous. In addition, for every fixed $k \in \mathbb{N}$, $H(k, x) = x^k$ is continuous. Therefore, we conclude that $H : \mathbb{N} \times [0, 1] \mapsto [0, 1]$ is continuous.

We observe that $H(\cdot, n)$ is a polynomial in [0, 1] for fixed $n \in \mathbb{N}$. This fact clearly implies that $H(\cdot, n) \in \mathcal{C}^2([0, 1])$ and hence it lies in the domain of the generator \mathcal{B} of the Λ -asymmetric frequency process Y as in (27). Therefore, the process

$$H(n, Y_t) - \int_0^t \mathcal{B}H(n, Y_s) ds,$$

is a martingale.

Additionally, we have that for fixed $x \in [0, 1]$ the function $H(\cdot, x)$ lies in the domain of the generator \mathcal{A} , which implies that the process

$$H(A_t, x) - \int_0^t \mathcal{A}H(A_s, x) ds,$$

is also a martingale.

We will compute $\mathcal{B}H(n, x)$ for $x \in [0, 1]$ and $n \in \mathbb{N}$, then using (27)

$$\mathcal{B}H(n,x) = \int_{\Delta} \left[x(x+y(1-x))^n + (1-x)(x-(y+z)x)^n - x^n \right] \Lambda(dy,dz), \ x \in [0,1], n \in \mathbb{N}.$$
(29)

We note that

$$x(x+y(1-x))^{n} = x\sum_{k=0}^{n} \binom{n}{k} y^{k} x^{n-k} (1-y)^{n-k} = x^{n+1}(1-y)^{n} + \sum_{k=1}^{n} \binom{n}{k} y^{k} x^{n-k+1} (1-y)^{n-k}.$$

Additionaly,

$$(1-x)(x-(y+z)x)^n = (x^n - x^{n+1})(1-y-z)^n,$$

and finally

$$x^{n} = x^{n}(1-y)^{n} + x^{n} \sum_{k=1}^{n} \binom{n}{k} y^{k}(1-y)^{n-k}.$$

Hence, using the previous identities gives

$$x(x+y(1-x))^{n} + (1-x)(x-(y+z)x)^{n} - x^{n} = \sum_{k=2}^{n} \binom{n}{k} y^{k} (1-y)^{n-k} (x^{n-k+1} - x^{n}) + (x^{n+1} - x^{n}) \left[(1-y)^{n} - (1-y-z)^{n} \right].$$
(30)

Using (30) in (29) we obtain

$$\mathcal{B}H(n,x) = \sum_{k=2}^{n} (x^{n-k+1} - x^n) \int_{\Delta} \binom{n}{k} y^k (1-y)^{n-k} \Lambda(dy, dz) + (x^{n+1} - x^n) \int_{\Delta} \left[(1-y)^n - (1-y-z)^n \right] \Lambda(dy, dz) = \mathcal{A}H(n,x).$$

Finally an application of Proposition 6.1 in [4] gives the result.

7. Griffiths representation and the probability of fixation

We motivate our next result by recalling a result for the two-type Λ -Fleming Viot process, which is defined as the solution to the SDE

$$Z_{t} = y + \int_{0}^{t} \int_{0}^{1} \int_{\Delta} \left(y(1 - Z_{s-}) \mathbf{1}_{\{u \le Z_{s-}\}} - yZ_{s-} \mathbf{1}_{\{u \ge Z_{s-}\}} \right) \mathbf{1}_{\{Z_{s-} \in [0,1]\}} \tilde{N}(ds, du, dy) - \int_{0}^{t} s(1 - Z_{s-}) Z_{s-} \mathbf{1}_{\{Z_{s-} \in [0,1]\}} ds, \quad t \ge 0.$$

Independently and using different techniques, Foucart [12] and Griffiths [19] obtained explicit conditions for the ttwo-type Λ -Fleming Viot process to be absorbed at 0 almost surely, or to be absorbed in either of the boundaries $\{0,1\}$ with positive probability. In particular, they observed that for every Λ it is always possible to find a small enough selection parameter s such that $\mathbb{P}(\lim_{t\to\infty} Z_t = 1)\mathbb{P}(\lim_{t\to\infty} Z_t = 0) > 0$. Foucart uses a duality technique which relies on the observation that the Λ -Fleming Viot process can be absorbed at 1 if and only if its dual, that we denote $(F_t)_{t\geq 0}$, is positive recurrent. The process $(F_t)_{t\geq 0}$ coalesces like the block counting process of the Λ -coalescent and branches at rate ns. In our model, the dual process is given by the ancestral line counting process $(A_t)_{t\geq 0}$. It coalesces at the same rate and branches at rate $\int_0^1 \int_0^1 \left[(1-y)^{n-1} - (1-y-z)^{n-1}\right] \Lambda(dy, dz)$ which is smaller than ns for all n > n(s), for some $n(s) \gg 1$, which exists for every s. This implies that $(F_t)_{t\geq 0}$ reflected in n(s) stochastically dominates $(A_t)_{t\geq 0}$. In turn this implies that $(A_t)_{t\geq 0}$ is positive recurrent. A duality argument allows to conclude that the limiting frequency process $(Y_t)_{t\geq 0}$ in equation (6.1) fullfils $\mathbb{P}(\lim_{t\to\infty} Y_t = 1)\mathbb{P}(\lim_{t\to\infty} Y_t = 0) > 0$.

Here, instead of formalising the previous argument, we will exploit Griffiths' technique in order to compute a semi-explicit expression for the probability of fixation of type – individuals in a Λ asymmetric frequency process. To this end, we will start by obtaining an alternative expression for its generator \mathcal{B} , given in (27), following the ideas of Theorem 1 in [19]. This is given in the next result. We define the measure $\tilde{\Lambda}$ on the simplex Δ by

$$\tilde{\Lambda}(dy, dz) := (y^2 + z)\Lambda(dy, dz).$$

Proposition 7.1. Let \mathcal{B} be the infinitesimal generator of a Λ -asymmetric frequency process as in (27). Let U, V, Y, Z be independent random variables, such that V has a uniform distribution on [0,1], U has density 2u with respect to the Lebesgue measure, and (Y, Z) is distributed according to $\tilde{\Lambda}/\|\tilde{\Lambda}\|$. Then, for any $f \in \mathcal{C}^2([0,1])$,

$$\mathcal{B}f(x) = \frac{\|\tilde{\Lambda}\|}{2}x(1-x)\mathbb{E}\left[f''(x(1-UY)+UYV)\frac{Y^2}{Z+Y^2} - 2f'(x-xY-xZV)\frac{Z}{Z+Y^2}\right].$$

Proof. Using that V has a uniform distribution on [0, 1] we obtain that

$$\begin{split} \mathbb{E}\left[f''(x(1-UY)+UYV)\frac{Y^2}{Z+Y^2}\right] &= \mathbb{E}\left[\frac{Y^2}{Z+Y^2}\int_0^1 f''(x(1-UY)+UYv)dv\right] \\ &= \mathbb{E}\left[\frac{Y}{Z+Y^2}\left[f'(x(1-UY)+UY)-f'(x(1-UY))\right]\frac{1}{U}\right] \\ &= \mathbb{E}\left[\frac{2}{Z+Y^2}\left(\frac{f(x(1-Y)+Y)-f(x)}{1-x}+\frac{f(x(1-Y))-f(x)}{x}\right)\right] \\ &= \frac{2}{\|\tilde{\Lambda}\|}\int_{\Delta}\left[\frac{f(x(1-y)+y)-f(x)}{1-x}+\frac{f(x(1-y))-f(x)}{x}\right]\frac{\tilde{\Lambda}(dy,dz)}{z+y^2}. \end{split}$$
(31)

where in the third equality we used that U has density given by 2u on [0, 1].

In a similar way, we obtain

$$\mathbb{E}\left[\frac{Z}{Z+Y^2}f'(x-xY-xZV)\right] = -\mathbb{E}\left[\frac{Z}{Z+Y^2}\left(f(x-xZ-xY)-f(x-xY)\right)\frac{1}{xZ}\right]$$
$$= -\frac{1}{\|\tilde{\Lambda}\|}\int_{\Delta}\left[\frac{f(x-xy-xz)-f(x-xy)}{x}\right]\frac{\tilde{\Lambda}(dy,dz)}{z+y^2}.$$
(32)

Therefore, using (31) and (32) we obtain for $x \in [0, 1]$

$$\begin{split} \frac{\|\tilde{\Lambda}\|}{2} x(1-x) \mathbb{E} \left[f''(x(1-UY)+UYV) \frac{Y^2}{Z+Y^2} - 2f'(x-xZV) \frac{Z}{Z+Y^2} \right] \\ &= \int_{\Delta} \left[x(f(x(1-y)+y)-f(x)) + (1-x)(f(x(1-y)) - f(x))] \frac{\tilde{\Lambda}(dy,dz)}{z+y^2} \right. \\ &+ \int_{\Delta} (1-x) \left[f(x(1-y-z)) - f(x(1-y)) \right] \frac{\tilde{\Lambda}(dy,dz)}{z+y^2} \\ &= \int_{\Delta} \left[x(f(x(1-y)+y) - f(x)) + (1-x)(f(x(1-y-z)) - f(x))) \right] \frac{\tilde{\Lambda}(dy,dz)}{z+y^2} \\ &= \mathcal{B}f(x). \end{split}$$

Denote by p(x) for $x \in [0, 1]$ the probability of fixation of type – in the A-asymmetric frequency process, where x denotes the initial frequency of type – individuals. Since p is a harmonic function for the generator \mathcal{B} , we see from the previous proposition that it satisfies for $x \in (0, 1)$

$$\mathbb{E}\left[p''(x(1-UY)+UYV)\frac{Y^2}{Z+Y^2}-2p'(x-xY-xZV)\frac{Z}{Z+Y^2}\right] = 0,$$
(33)

with boundary conditions given by p(0) = 0 and p(1) = 1.

We note that

$$\mathbb{E}\left[p''(x(1-UY)+UYV)\frac{Y^2}{Z+Y^2}\right] = \mathbb{E}\left[\frac{p'(x(1-W)+W)-p'(x(1-W))}{W}\frac{Y^2}{Z+Y^2}\right],$$
(34)

with W := UY.

In order to find the solution to (33), following [19], we will consider polynomials of the form

$$h_n(x) = \sum_{r=0}^n a_{n,r} x^r,$$
(35)

with $h_0(x) = 1$.

Then, we will prove that we can take a choice of coefficients $\{a_{n,r}\}_{0 \le r \le n}$ such that

$$\mathbb{E}\left[\frac{h_n(x(1-W)+W) - h_n(x(1-W))}{W}\frac{Y^2}{Z+Y^2}\right] = n\mathbb{E}\left[h_{n-1}\left(x(1-Y-ZV)\right)\frac{Z}{Z+Y^2}\right].$$
 (36)

with the choice

$$a_{n,n} = \prod_{i=1}^{n-1} \frac{\mathbb{E}\left[(1 - Y - ZV)^i \frac{Z}{Z + Y^2} \right]}{\mathbb{E}\left[(1 - W)^i \frac{Y^2}{Z + Y^2} \right]}, \qquad n = 0, 1 \dots$$
(37)

for the diagonal elements. Indeed, by (35)

$$\mathbb{E}\left[\frac{h_n(x(1-W)+W) - h_n(x(1-W))}{W} \frac{Y^2}{Z+Y^2}\right] = \mathbb{E}\left[\frac{Y^2}{Z+Y^2} \sum_{r=0}^n \frac{a_{n,r}}{W} \left[(x(1-W)+W)^r - (x(1-W))^r\right]\right]$$
$$= \sum_{r=1}^n a_{n,r} \sum_{j=0}^{r-1} \binom{r}{j} \mathbb{E}\left[(1-W)^j W^{r-j-1} \frac{Y^2}{Z+Y^2}\right] x^j$$
$$= \sum_{j=0}^{n-1} \sum_{r=j+1}^n \binom{r}{j} \mathbb{E}\left[(1-W)^j W^{r-j-1} \frac{Y^2}{Z+Y^2}\right] a_{n,r} x^j.$$

Hence in order for (36) to hold we need that

$$\sum_{j=0}^{n-1} \sum_{r=j+1}^{n} \binom{r}{j} \mathbb{E}\left[(1-W)^j W^{r-j-1} \frac{Y^2}{Z+Y^2} \right] a_{n,r} x^j = \sum_{j=0}^{n-1} n a_{n-1,j} \mathbb{E}\left[(1-Y-ZV)^j \frac{Z}{Z+Y^2} \right] x^j$$

or equivalently that

$$a_{n-1,j} = \sum_{r=j+1}^{n} {\binom{r}{j}} \frac{\mathbb{E}\left[(1-W)^{j} W^{r-j-1} \frac{Y^{2}}{Z+Y^{2}} \right]}{n \mathbb{E}\left[(1-Y-ZV)^{j} \frac{Z}{Z+Y^{2}} \right]} a_{n,r}.$$
(38)

Following the discussion in [19], we can determine the coefficients $\{a_{n,j}\}_{j=0}^{n-1}$ of the polynomial h_n , from the coefficients $\{a_{n-1,j}\}_{j=0}^n$ of the polynomial h_{n-1} . Indeed, we can take $a_{n,n}$ as in (37) and then, using (38), recursively obtain $a_{n,j}$ for $j = n - 1, \ldots, 0$. We notice that the coefficient $a_{n,0}$ can be chosen arbitrary, and will be specified later in the construction of the probability of fixation p.

Now let us return to the probability of fixation p, where for the first derivative p'(x) we make the ansatz

$$p'(x) = A \sum_{n=1}^{\infty} 2^n c_n h_{n-1}(x),$$
(39)

with p(1) = 1 and p(0) = 0. Using (39) in (33), together with (34) and (36) gives

$$\mathbb{E}\left[\frac{p'(x(1-W)+W)-p'(x(1-W))}{W}\frac{Y^2}{Z+Y^2}-2p'(x(1-Y-ZV))\frac{Z}{Z+Y^2}\right]$$

= $A\sum_{n=1}^{\infty} 2^n c_n(n-1)\mathbb{E}\left[h_{n-2}\left(x(1-Y-ZV)\right)\frac{Z}{Z+Y^2}\right]-2A\sum_{n=1}^{\infty} 2^n c_n\mathbb{E}\left[h_{n-1}\left(x(1-Y-ZV)\right)\frac{Z}{Z+Y^2}\right]$

By choosing $c_n = \frac{1}{(n-1)!}$, for $n \in \mathbb{N}$, we obtain

$$\mathbb{E}\left[\frac{p'(x(1-W)+W) - p'(x(1-W))}{W} \frac{Y^2}{Z+Y^2} - 2p'(x(1-Y-ZV))\frac{Z}{Z+Y^2}\right]$$

= $A\sum_{n=2}^{\infty} \frac{2^n}{(n-2)!} \mathbb{E}\left[h_{n-2}\left(x(1-Y-ZV)\right)\frac{Z}{Z+Y^2}\right] - A\sum_{n=1}^{\infty} \frac{2^{n+1}}{(n-1)!} \mathbb{E}\left[h_{n-1}\left(x(1-Y-ZV)\right)\frac{Z}{Z+Y^2}\right] = 0$

Hence, p is a solution to (33). Now, by integrating (39) we obtain that

$$p(x) = A \sum_{n=1}^{\infty} \int_0^x \frac{2^n}{(n-1)!} h_{n-1}(u) du.$$

So if we choose $\{h_n(0)\}_{n\geq 1}$ such that

$$\int_{0}^{1} nh_{n-1}(u)du = 1,$$

then by the fact that p(1) = 1 and p(0) = 0 we obtain that

$$1 = p(1) - p(0) = A \sum_{n=1}^{\infty} \frac{2^n}{n!} \int_0^1 nh_{n-1}(u) du = A(e^2 - 1),$$

and hence $A = (e^2 - 1)^{-1}$.

So putting the pieces together we have that

$$p(x) = (e^2 - 1)^{-1} \sum_{n=1}^{\infty} \frac{2^n}{n!} H_n(x),$$

where $H_n(x) := \int_0^x n h_{n-1}(u) du$, and $\{h_n\}_{n \ge 1}$ satisfies (36).

The previous discussion leads to the following main result of this section.

Proposition 7.2. The fixation probability of type - individuals is given by

$$p(x) = (e^2 - 1)^{-1} \sum_{n=1}^{\infty} \frac{2^n}{n!} H_n(x), \qquad x \in [0, 1],$$

where the polynomials $\{H_n\}_{n=0}^{\infty}$ are given by

$$H_n(x) = \int_0^x nh_{n-1}(u)du, \qquad x \in [0,1]$$

with $\{h_n\}_{n=0}^{\infty}$ given in (35), (37), and (38) and the constants $\{h_n(0)\}_{n=0}^{\infty}$ chosen so that

$$\int_0^1 nh_{n-1} = 1.$$

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