LINES OF DESCENT IN THE DETERMINISTIC MUTATION-SELECTION MODEL WITH PAIRWISE INTERACTION

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ABSTRACT. We consider the mutation-selection differential equation with pairwise interaction and establish the corresponding ancestral process, which is a specific random tree and a variant of the ancestral selection graph. To make this object tractable, we prune the tree upon mutation, thus reducing it to its informative parts. The hierarchies inherent in the tree are encoded systematically via ternary trees with weighted leaves; this leads to the stratified ancestral selection graph. The latter is dual to the mutation-selection equation and provides a stochastic representation of its solution. It also allows to reveal the genealogical structures inherent in the bifurcations of the equilibria of the differential equation. Furthermore, we establish constructions, again based on the stratified ancestral selection graph, that allow to trace back the ancestral lines into the distant past and obtain explicit results about the ancestral population in the case of unidirectional mutation.

1. INTRODUCTION

Models of population genetics describe the evolution of biological populations under the interplay of various processes such as mutation, selection, recombination, and migration. Traditionally, they come in two categories, deterministic and stochastic. Deterministic approaches assume that the population is so large that a law of large numbers applies so that random fluctuations may be neglected; the resulting models are (ordinary or partial) differential equations or (discrete-time) dynamical systems, which describe the evolution in the usual forward direction of time. This has led to an elaborate body of theory, which is comprehensively surveyed in the monograph by Bürger [8]. In contrast, stochastic approaches take into account the fluctuations due to finite population size; the resulting stochastic processes have a firm place in probability theory. Here, the corresponding *ancestral processes*, which describe the ancestry of a sample of individuals from a population at the present, play an eminent role. Their study gives rise to duality relations and random genealogies, which yield deep insight and serve as versatile tools to investigate the model in question. This area of research is comprehensively surveyed in the monograph by Durrett [15].

The deterministic models of population genetics are related to their stochastic counterparts via a dynamical law of large numbers (also known as mean-field limit). Nevertheless, they have largely led separate lives for many decades. Recently, however, a beginning has been made to build new bridges between them by introducing the genealogical picture into the deterministic equations [3, 4, 6, 9]. The corresponding ancestral processes remain random even in the deterministic limit, since they describe the history of a finite sample of individuals. They lead to stochastic representations of the solutions of the deterministic equations and shed new light on both their dynamics and asymptotic behaviour. For example, for the so-called haploid mutation-selection equation with unidirectional mutation, the bifurcation structure of the equilibria of the ordinary differential equation (ODE) was recovered in terms of the asymptotic properties of a variant of the ancestral selection graph (ASG); the latter is a central concept for the study of genealogies with selection [21, 30]. Furthermore, by tracing back the ancestral lines, the corresponding equilibria and bifurcations in the distant past could be elucidated, thus characterising the ancestors of today's equilibrium population [4, 6].

Our goal in this article is to extend these results to the case with interaction between individuals. In the aforementioned haploid mutation-selection equation, individuals reproduce independently of each other; we will now explore the case of pairwise interaction, where the reproduction rate of an individual depends on the type of a partner chosen uniformly from the population. Biologically, this is a special case

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of what is known as frequency-dependent selection, which also occurs in evolutionary game theory (see, e.g., [18]). The resulting equation is also equivalent to the so-called diploid mutation-selection equation, which describes individuals that carry two copies of the genetic information rather than one as in the haploid case.

The mutation-selection equation with interaction has a higher degree of nonlinearity than the haploid one, and a richer bifurcation structure. In particular, one observes bistability in certain parameter regions; this is absent in the haploid case. While this is well known in the forward direction of time, the corresponding ancestral processes are largely unexplored territory. We will therefore first have to establish appropriate concepts. Starting from ideas in [29], we will extend the ASG to the case with pairwise interaction. In the deterministic limit, the resulting construction will be a specific random tree. To make this object tractable, we will *prune* the tree upon mutation, thus reducing it to its informative parts. The hierarchies inherent in the tree will play a crucial role and will be encoded systematically via ternary trees with weighted leaves; this will lead to the *stratified ASG*. The latter will serve as dual to the forward process and provide a stochastic representation of the solution of the mutation-selection equation. It will also be our workhorse to reveal the genealogical structures inherent in the bifurcations of the equilibria of the ODE. Indeed, it will turn out that the random genealogical trees have very different properties in the various parameter regimes. Furthermore, we will establish constructions, again based on the stratified ASG, that allow to trace back the ancestral lines into the distant past and obtain explicit results about the ancestral population in the biologically relevant case of unidirectional mutation.

We would like to mention related work by Mach et al. [26], who study a large class of ODEs that arise as mean-field limits of interacting particle systems on the complete graph. Their study relies crucially on recursive tree processes. As an example, Mach et al. [26] (see also [25]) treat the cooperative branching model with deaths, which corresponds to a special case of our mutation-selection model with interaction. The analyses via recursive tree processes and the stratified ASG provide complementary insight into the behaviour of the model. Mach et al. [26] compare their work with ours in detail in their Section 2.1. We will spell out the similarities and differences as we go along.

The article is organised as follows. In Sect. 2, we recapitulate the two-type mutation-selection differential equation with interaction, along with its equilibrium and bifurcation structure. We then (Sect. 3) turn to its finite-population counterpart, namely the two-type Moran model with mutation, selection, and pairwise interaction; it turns into the differential equation in the deterministic limit. The Moran model has a graphical representation as an interacting particle system, which we use to recapitulate the ASG with interaction for the finite system. In Sect. 4, the law of large numbers is applied to this ASG and yields the ancestral process corresponding to the deterministic equation. The stratified ASG is introduced in Sect. 5, and some of its fundamental properties are proved. The core of the results are found in Sect. 6 and 7. Sect. 6 establishes the connection between the stratified ASG and the deterministic model in the form of a duality relation and provides a stochastic representation of the solution of the differential equation. In this way, the bifurcation structure in the case of unidirectional mutation is recovered by genealogical means. Finally, Sect. 7 establishes the constructions to trace back an ancestral line into the distant past; these are the stratified ASG with immune line and the forest of stratified ASGs. We use them to derive the ancestral type distribution under unidirectional mutation, both over time and at stationarity.

2. The mutation-selection equation with interaction

We consider a deterministic model for the evolution of a population subject to mutation, selection, and a special form of frequency-dependent selection that we call pairwise interaction. More precisely, the population is composed of two types, type 0 and type 1. We will refer to type 0 as the fit or beneficial type and to type 1 as the unfit or deleterious type. Both types reproduce at a so-called *neutral* (that is, type-independent) rate of 1. On top of this, type 0 has a selective advantage, that is, an additional reproduction rate. This has two contributions: one that is independent of the current type distribution in the population and one that depends on it. We refer to the former as selection and to the latter as frequency-dependent selection. The rate of selective reproduction is s > 0. The rate of frequencydependent selective reproduction is $\gamma(1 - y(t; y_0))$, where $\gamma \ge 0$ is the interaction parameter and $y(t; y_0)$ denotes the proportion of type 1 at time t given that the proportion at time 0 was $y_0 \in [0, 1]$. The interaction is called *pairwise* because it depends on y in a linear way; this reflects the dependence on the type of one randomly-chosen partner in the Moran model, as will become clear in Sect. 3. Both types may mutate at rate u > 0, where with probability ν_0 (or ν_1) the resulting type is 0 (is 1). Throughout, we assume $\nu_0, \nu_1 \ge 0$ and $\nu_0 + \nu_1 = 1$. It is implied throughout that the population is so large that random fluctuations may be neglected. If the initial frequency of type 1 is $y_0 \in [0, 1]$, then $y(t; y_0)$ evolves deterministically as the solution of the initial value problem (IVP)

$$\frac{dy}{dt}(t) = -y(t)(1-y(t))[s+\gamma(1-y(t))] + u\nu_1(1-y(t)) - u\nu_0y(t) =: F(y(t)),$$

$$y(0) = y_0, \quad \text{for } y_0 \in [0,1].$$
(2.1)

We speak of the ODE as the mutation-selection equation with interaction. The form of the mutation terms is obvious; the reproduction term describes that type-0 individuals selectively reproduce at overall rate $(1 - y(t))[s + \gamma(1 - y(t))]$ and thus reduce the relative frequency of type-1 individuals according to their current proportion y(t). The neutral reproduction does not enter the equation since its net contribution is -(1 - y(t))y(t) + y(t)(1 - y(t)) = 0; as a matter of fact, therefore, the same ODE results for any neutral reproduction rate $c \ge 0$. In principle, the solution of (2.1) can be expressed explicitly in terms of the roots of F by standard methods, but we refrain from doing this here.

Remark 2.1. We have introduced the interaction in terms of frequency-dependent selection, but an alternative interpretation corresponds to a diploid population with two allelic types subject to mutation and selection; the ODE is then usually termed the diploid mutation-selection equation. The diploid genotypes are then given by the pairs $(i, j), i, j \in \{0, 1\}$, and their reproduction rates w_{ij} are $w_{00} = 1 + 2s + \gamma$, $w_{01} = w_{10} = 1 + s$, and $w_{11} = 1$. This choice of parameters corresponds to the case where allele 0 is (partially) recessive, that is, it needs another 0 to fully play out its selective advantage (see also [5]).

Remark 2.2. The general form of the mutation-selection equation goes back to Wright [37] and is intensively discussed by Crow and Kimura [11]. They understand it as a simplistic model for the evolution of a population under the forces of mutation, (frequency-dependent) selection and migration; and note that it is suited for an approximation of a large population with constant environmental factors [11]. We consider a special case in which there is no migration, only two allelic types, and our special form of frequency-dependent selection.

Remark 2.3. For a special choice of parameters, the ODE (2.1) corresponds to the mean-field limit (or law of large numbers) of the cooperative branching model on the complete graph as investigated by Mach et al. [26] (see also [25]). More precisely, our notation translates to their case by interchanging the roles of type 0 and 1 and by setting $\gamma = \alpha$, u = 1, $\nu_0 = 0$, $\nu_1 = 1$, and s = 0. This leads to the mean-field equation [26, Eq. (1.36)].

Equilibria and bifurcation structure. To understand the asymptotic behaviour of the mutationselection equation, we analyse the equilibria \bar{y} , namely the (real) roots of F in (2.1), along with their stability. Since $F(0) \ge 0$ and $F(1) \le 0$, the unit interval (which is the biologically relevant domain) is positive invariant under the flow and there exists at least one root of F in [0, 1]. Let \hat{y}_{∞} and \check{y}_{∞} be the smallest and largest root of F in [0, 1], respectively. The conditions on the boundary, together with the fact that F is a polynomial, imply that \hat{y}_{∞} and \check{y}_{∞} are attracting from the left and right, respectively, provided they are in (0, 1). We initially concentrate on the case $\nu_0 = 0$, in which expressions for the roots simplify significantly. We first extend (2.1) to all of \mathbb{R} and consider *all* equilibria and later specialise to those that lie in the unit interval. We will consider the mutation rate as the bifurcation parameter; it will be convenient to identify two specific threshold values for it.

Definition 2.4. For $\gamma > 0$ and s > 0, let

$$\hat{u} := s$$
 and $\check{u} := \frac{1}{\gamma} \left(\frac{s+\gamma}{2} \right)^2$. (2.2)



FIGURE 1. The equilibria \bar{y} of (2.1) as a function of u/s for $\nu_0 = 0$ and s = 1/30. The left, middle, and right panels correspond to $\gamma = 0$, $\gamma = 1/40$, and $\gamma = 1/10$, respectively. Black lines: stable. Grey lines: unstable.

In particular, $\hat{u} \leq \check{u}$.

If $\nu_0 = 0$, the right-hand side of (2.1) reduces to

$$F(y) = (y - 1)G(y)$$
(2.3)

with $G(y) = -\gamma y^2 + (s + \gamma)y - u$. Hence, the equilibria of (2.3) are

$$\bar{y}_1 = 1 \tag{2.4}$$

together with the real roots of G. Namely,

• for $\gamma = 0$ and $u \in [0, \infty)$,

$$\bar{y}_2 = \frac{u}{s} \tag{2.5}$$

(see Fig. 1, left);

• for $\gamma > 0$ and $u \in [0, \check{u}]$,

$$\bar{y}_2 = \frac{1}{2} \left(1 + \frac{s}{\gamma} - \sqrt{\sigma} \right) \quad \text{and } \bar{y}_3 = \frac{1}{2} \left(1 + \frac{s}{\gamma} + \sqrt{\sigma} \right),$$
(2.6)

where

$$\sigma := \left(1 + \frac{s}{\gamma}\right)^2 - 4\frac{u}{\gamma} \tag{2.7}$$

(see Fig. 1, middle and right).

Remark 2.5. Note that if $\gamma > 0$, then $u \leq \check{u}$ is equivalent to $\sigma \geq 0$. So, for $\gamma > 0$ and $u \in (\check{u}, \infty)$, the polynomial G has no real roots and \bar{y}_1 is the only equilibrium.

In order to determine the stability (still for $\nu_0 = 0$), note that

$$F'(y) = G(y) + (y - 1)G'(y),$$

where $G'(y) = -2\gamma y + s + \gamma$. Then,

- $F'(\bar{y}_1) = G(1) = s u$, so \bar{y}_1 is stable (unstable) for $u < s \ (u > s)$.
- $F'(\bar{y}_2) = (\bar{y}_2 1)G'(\bar{y}_2) = \gamma \sqrt{\sigma}(\bar{y}_2 1)$, so \bar{y}_2 is stable (unstable) if $\bar{y}_2 < 1$ ($\bar{y}_2 > 1$).
- $F'(\bar{y}_3) = (\bar{y}_3 1)G'(\bar{y}_3) = -\gamma\sqrt{\sigma}(\bar{y}_3 1)$, so \bar{y}_3 is stable (unstable) if $\bar{y}_3 > 1$ ($\bar{y}_3 < 1$).

We summarise this analysis in the following result.

Proposition 2.6. Let $\nu_0 = 0$ and $s, \gamma, u > 0$. If $\sigma \ge 0$, the ODE (2.1) has equilibria \bar{y}_1 , \bar{y}_2 , and \bar{y}_3 given in (2.4)–(2.6). The corresponding stability is summarised in the following table (where bold indicates equilibria that are stable in [0, 1]).

	$s > \gamma$		$s = \gamma$		$s < \gamma$	
	$\sigma = 0$	$\sigma > 0$	$\sigma = 0$	$\sigma > 0$	$\sigma = 0$	$\sigma > 0$
$u < \hat{u}$	—	$0 < \bar{\mathbf{y}}_2 < \bar{y}_1 < \bar{y}_3$	—	$0 < \bar{\mathbf{y}}_2 < \bar{y}_1 < \bar{y}_3$	—	$0 < \bar{\mathbf{y}}_2 < \bar{y}_1 < \bar{y}_3$
$u = \hat{u}$	_	$\bar{\mathbf{y}}_1 = \bar{y}_2 < \bar{y}_3 = s/\gamma$	$ar{\mathbf{y}_1} = ar{\mathbf{y}_2} = ar{\mathbf{y}_3}$	_	_	$0 < \bar{\mathbf{y}}_2 = s/\gamma < \bar{y}_1 = \bar{y}_3$
$u > \hat{u}$	$\bar{\mathbf{y}}_1 < \bar{y}_2 = \bar{y}_3$	$\bar{\mathbf{y}}_1 < \bar{y}_2 < \bar{y}_3$			$\frac{1}{2} < \bar{y}_2 = \bar{y}_3 < \bar{\mathbf{y}}_1$	$0 < \bar{\mathbf{y}}_2 < \bar{y}_3 < \bar{\mathbf{y}}_1$

If $\sigma < 0$, \bar{y}_1 is the only equilibrium and it is stable.

As described in [5], we can identify the following bifurcation phenomena with u as the bifurcation parameter. For all $s, \gamma > 0$, there is an exchange of stability (also known as transcritical bifurcation) at $u = \hat{u}$ of \bar{y}_1 and \bar{y}_2 . When u surpasses the critical value \hat{u} , then \bar{y}_1 (\bar{y}_2) switches from unstable (stable) to stable (unstable). For $s < \gamma$, there is an additional saddle-node bifurcation at $u = \check{u}$. There, the equilibria \bar{y}_2 and \bar{y}_3 (one stable, one unstable) collide and both vanish. If $\hat{u} = \check{u}$, we see a pitchfork bifurcation, where the unstable \bar{y}_1 passes through the collision point of \bar{y}_2 and \bar{y}_3 and becomes stable. (We refer the interested reader to Guckenheimer and Holmes [17] for a general account of bifurcation theory for equilibria of ODEs.)

The equilibria directly lead to the asymptotic behaviour, which we now consider for $y_0 \in [0, 1]$. Let $y(t; y_0)$ be the solution of (2.1) with $\nu_0 = 0$ and $s, \gamma, u > 0$. By the monotonicity of $y(\cdot; y_0)$, we infer that

$$y_{\infty}(y_0) := \lim_{t \to \infty} y(t; y_0) \tag{2.8}$$

exists and is always an equilibrium. The asymptotic type frequencies are characterised in the following corollary, which is a direct consequence of Remark 2.5 together with Proposition 2.6.

Corollary 2.7. Let $y_0 \in [0, 1]$, $\nu_0 = 0$, and $s, \gamma > 0$.

(i) If either $u < \hat{u}$ or $(s < \gamma \text{ and } u = \hat{u})$,

$$y_{\infty}(y_0) = \begin{cases} \bar{y}_2, & \text{if } y_0 \in [0, 1), \\ \bar{y}_1, & \text{if } y_0 = \bar{y}_1. \end{cases}$$

(ii) If $s < \gamma$ and $u \in (\hat{u}, \check{u}]$,

$$y_{\infty}(y_0) = \begin{cases} \bar{y}_2, & \text{if } y_0 \in [0, \bar{y}_3), \\ \bar{y}_3, & \text{if } y_0 = \bar{y}_3, \\ \bar{y}_1, & \text{if } y_0 \in (\bar{y}_3, \bar{y}_1]. \end{cases}$$

(iii) If either $u > \check{u}$ or $(s \ge \gamma \text{ and } u \in [\hat{u}, \check{u}])$, then for all $y_0 \in [0, 1]$,

$$y_{\infty}(y_0) = \bar{y}_1$$

Remark 2.8. If $s < \gamma$ and $u = \check{u}$, we have $\bar{y}_2 = \bar{y}_3$ and

$$y_{\infty}(y_0) = \begin{cases} \bar{y}_2, & \text{if } y_0 \in [0, \bar{y}_2], \\ \bar{y}_1, & \text{if } y_0 \in (\bar{y}_2, \bar{y}_1]. \end{cases}$$

Clearly, the equilibria $\bar{y}_i = \bar{y}_i(s, \gamma, u, \nu_0)$ $(i \in \{1, 2, 3\})$ are functions of s, γ, u and ν_0 . The asymptotic type frequency $y_{\infty}(y_0) = y_{\infty}(y_0, s, \gamma, u, \nu_0)$ furthermore depends on y_0 . By a straightforward application of L'Hôpital's rule, we see that \bar{y}_2 is continuous in γ at 0.

Corollary 2.9. For s, u > 0 and $\nu_0 = 0$,

$$\lim_{\gamma \to 0} \bar{y}_2(s,\gamma,u,0) = \frac{u}{s}.$$

In particular,

$$\lim_{\gamma \to 0} y_{\infty}(y_0, s, \gamma, u, 0) = \begin{cases} \min\{\frac{u}{s}, 1\}, & \text{if } y_0 \in [0, 1), \\ 1, & \text{if } y_0 = 1. \end{cases}$$

Let us recapitulate from [5] the biological implications of Corollary 2.7. For $\gamma \leq s$, the fit type persists in the population for $u < \hat{u}$, but is lost for $u \ge \hat{u}$; this happens for any positive initial value and is an instance of the so-called error threshold [16]. For $\gamma > s$, one has again persistence for $u < \hat{u}$ and loss for $u > \check{u}$ for any positive initial value. But in the bistable regime (\hat{u}, \check{u}) , the fit type will only persist if its initial frequency is at least $1 - \bar{y}_3$; otherwise it will be lost. In particular, a beneficial mutant arising in small frequency in a population that is otherwise unfit will not be able to establish itself.



FIGURE 2. Equilibria of (2.1) evaluated numerically as functions of u/s for $\nu_0 = 1/100$ and s = 1/30. The left, middle, and right cases correspond to $\gamma = 0$, $\gamma = 1/60$, and $\gamma = 4/15$, respectively. Black lines: stable. Grey lines: unstable.

Finally, let us briefly discuss the case $\nu_0 \in (0, 1)$ (we do not explicitly consider the limiting case $\nu_0 = 1$; the biologically reasonable regime is $0 < \nu_0 \ll 1$, and $\nu_0 = 0$ is often a reasonable approximation). Since F is then a cubic polynomial, explicit expressions for its roots are in principle available. In particular, a stability analysis as in the case $\nu_0 = 0$ is possible. But due to the length of expressions and the many case distinctions, we refrain from doing so. Nevertheless, by Budan's theorem [7], we can deduce a bound for the number of real roots in [0, 1].

Proposition 2.10. Let $u, \gamma > 0$ and $\nu_0 \in (0, 1)$. If $u < \hat{u}$ or $(\gamma < s \text{ and } u \ge \hat{u})$, then F has exactly one root in [0, 1].

Proof. Note first that if $u, \gamma > 0$ and $\nu_0, \nu_1 \in (0, 1)$, then 0 and 1 are not roots of F. Recall that $F(y) = -\gamma y^3 + (2\gamma + s)y^2 - (\gamma + s + u)y + u\nu_1$. Define

$$F^+(y) := F(y+1) = -\gamma y^3 + (s-\gamma)y^2 + (s-u)y - u\nu_0.$$

Denote by o_F and o_{F^+} the number of sign changes of the coefficients of F and F^+ , respectively. Then, $o_F = 3$ and

$$o_{F^+} = \begin{cases} 2, & \text{if } u < \hat{u} \text{ or } (\gamma < s \text{ and } u \ge \hat{u}), \\ 0, & \text{if } s < \gamma \text{ and } u \ge \hat{u}. \end{cases}$$

Denote by r the number of roots of F in (0, 1). Now, Budan's theorem states that $r \leq o_F - o_{F^+}$. On the other hand, we know from the discussion at the beginning of this section that there is at least one root in [0, 1].

Remark 2.11. If (2.1) has three equilibria in [0, 1], then the equilibrium in the middle is unstable. To see this, note that F is positive before \hat{y} and negative after \check{y} . Since there is an equilibrium in the middle, F must have a positive derivative at this point.

In contrast to $\nu_0 = 0$, if $\nu_0 \in (0, 1)$, neither y = 0 nor y = 1 are equilibria and so both types coexist independently of y_0 , see also Fig. 2. Yet, the asymptotic behaviour may again depend on y_0 . After this discussion of the deterministic mutation-selection equation, we now turn to its stochastic counterpart.

3. The Moran model with interaction

The 2-type Moran model with mutation, selection, and pairwise interaction describes the evolution of a haploid population of a finite number N of individuals in continuous time. Each individual has a type, which is either 0 or 1. As before, we refer to type 0 as the fit or beneficial type, whereas type 1 is unfit or deleterious. When an individual reproduces, its single offspring inherits the parent's type and replaces a uniformly chosen individual, thereby keeping the population size constant. Individuals of type 1 reproduce at rate 1, whereas individuals of type 0 reproduce at rate $1 + s + \gamma(N - k)/N$ with $s, \gamma > 0$ and k the current number of type-1 individuals. The selective advantage of type 0 has two contributions: a part that is independent of the current type distribution and occurs at rate s per fit individual; and a part that depends on the frequency of the fit type and is encoded by the parameter γ . More precisely,

a fit individual chooses uniformly at rate γ a partner from the population. If the partner is fit (unfit), then the type-0 individual does (not) reproduce. Each individual mutates at rate u; the type after the event is i with probability ν_i , $i \in \{0, 1\}$. We assume throughout that u > 0 and $\nu_0, \nu_1 \ge 0$ with $\nu_0 + \nu_1 = 1$.

Let now $Y_t^{(N)}$ be the (random) number of type-1 individuals at time t in a population of size N. The process $Y^{(N)} = (Y_t^{(N)})_{t \ge 0}$ is a continuous-time Markov chain with transition rates

$$q_{Y^{(N)}}(k,k+1) = k\frac{N-k}{N} + (N-k)u\nu_1, \quad q_{Y^{(N)}}(k,k-1) = k\frac{N-k}{N}\left(1+s+\gamma\frac{N-k}{N}\right) + ku\nu_0, \quad (3.1)$$

where $k \in \{0, ..., N\}$. There are no other transitions.

The Moran model with interaction has a well-known graphical representation as an interacting particle system, see Fig. 3. Here, individuals are represented by pieces of horizontal lines. Time runs from left to right in the figure. Reproduction events are depicted by arrows between the lines. If a parent (at the tail of an arrow) places offspring via the arrow, the offspring inherits the parent's type and replaces the individual at the tip. We decompose reproduction events into neutral, selective, and interactive ones. Neutral arrows appear at rate 1/N per ordered pair of lines; selective arrows appear at rate s/N per ordered pair. Interactive arrows occur at rate γ/N per ordered pair of lines and are always accompanied by a checking arrow whose tail shares the tail of the interactive arrow; but whose tip is connected to a uniformly chosen line. That is, these arrow pairs occur at rate γ/N^2 per triple of lines. All types of arrows (including the interactive/checking pairs) are laid down via Poisson point processes independently of each other. The rules for their use are as follows. Neutral arrows are used by all types; selective arrows are used only by individuals of type 0. Interactive arrows are used by the individual at its tail if and only if both this individual and the one at the tip of the checking arrow are of type 0.

Mutation events are depicted by crosses and circles on the lines. A circle (cross) indicates a mutation to type 0 (type 1), which means that the type on the line is 0 (is 1) after the mutation. This occurs at rate $u\nu_0$ (at rate $u\nu_1$) on every line, again by way of independent Poisson point processes. Note that it is no restriction to describe mutation in this parent-independent way; indeed, in the two-type case, the rates can always be parametrised in this way. Given a realisation of the particle system and an initial type configuration (that is, a type assigned to each line at t = 0), we can read off the types on the lines at all later times t > 0. The distribution of the initial types and the law of the graphical elements (arrows, circles, and crosses) are independent of each other.

Remark 3.1. The Moran model with interaction can be translated into the cooperative branching process on a complete graph [25, Ch. I.1.2.3, Ch. I.2.1] (see also [26]) by interchanging the roles of type 0 and 1 and by setting $s = \nu_0 = 0$ and u = 1. A deleterious mutation then corresponds to a death event and an interactive arrow to a cooperative branching event. Other variants of such dynamics may be found in [28, 31, 33].

Remark 3.2. Graphical representations are available for a comprehensive class of interacting particle systems, see e.g. Sturm and Swart [34, Sect. 5.2].

The ancestral selection graph in the Moran model with interaction. The ancestral selection graph (ASG) was introduced by Krone and Neuhauser [21] and Neuhauser and Krone [30] in order to study genealogies in population models with selection. It was extended by Neuhauser [29] to a model of minority advantage, a special case of interactive selection. Following these lines, we now describe the ASG for the Moran model with interaction (cf. Fig. 3). Our starting point is a realisation of the graphical representation of the Moran model in the time interval [0,t] for some time t > 0, to which we refer as the present. We pick an untyped sample (that is, no types have been assigned to the individuals) at present and trace back the lines of its *potential influencers*; backward time will be denoted by r, where r = 0 corresponds to forward time t and r = t corresponds to forward time 0. We call individuals potential influencers if their type has an influence on the type of the sampled individuals where, at this stage, we only take into account the information contained in the reproduction events, and ignore the



FIGURE 3. A realisation of the Moran interacting particle system (thin lines) for a population of size N = 5 and the embedded ASG (bold lines) for a sample of size 1. Time runs forward in the Moran model (\rightarrow) and backward in the ASG (\leftarrow). A bullet marks the joint tails of the interactive and the checking arrows.

additional information due to mutation. The arrows in the representation change the number of potential influencers and their respective locations. The ASG is composed of the lines of these potential influencers. Assume there are currently n lines in the ASG. When a neutral arrow joins two lines in the current set, a *coalescence event* takes place, i.e. the two lines merge into the single one at the tail of the arrow and the number of lines in the graph decreases by one (see Fig. 4). Since neutral arrows appear at rate 1/N per ordered pair of lines, coalescence events occur at rate n(n-1)/N in our ASG of size n. When a line in the current set is hit by an arrow that emanates from a line that is currently not in the graph, a *relocation event* occurs; i.e. the ASG continues with the *incoming branch* (the line at the tail of the arrow) and the number of lines in the graph does not change. Relocation events occur at rate n(N-n)/N.



FIGURE 4. Coalescence event (left) and relocation event (right).

When a selective arrow hits the current set of lines, the hit individual has two potential parents, namely the individual at the incoming branch, and the one at the *continuing branch* (the one to the left of the tip). Which of these is the true parent of the individual at the *descendant branch* (the one to the right of the tip) depends on the type at the incoming branch, but for the moment we work without types. This means that we must trace back both potential parents; we say the selective event remains *unresolved*. These events can be of two types: a *bifurcation*^{*} *event* if the selective arrow emanates from an line outside the current set of lines, and a *simple collision event* if the selective arrow links two lines in the graph (see Fig. 5). The former increases the number of lines in the graph by one and, since selective arrows appear at rate s/N per ordered pair of lines, occurs at rate sn(N - n)/N in our ASG of size n. The latter does not change the number of lines in the ASG and occurs at rate sn(n - 1)/N.



FIGURE 5. Bifurcation (left) and simple collision (right).

When an interactive arrow hits a line in the ASG, the individual that is hit has two influencers, the individual at the incoming branch and the individual at the continuing branch. The true parent depends

^{*}That is a binary branching. Not to be confused with bifurcations in the context of dynamical systems, such as the transcritical and saddle node bifurcations in Sect. 2.

9

on the types of the individuals at the incoming and checking branches; but as before, we work without types. The resulting additional unresolved reproduction events can now be of three types: a trifurcation if both the incoming and the checking arrows emanate from lines currently not in the ASG; a collisionbifurcation event if either the incoming or the checking line, but not both of them, emanate from outside the current set of lines; and a *double collision event* if the incoming and the checking branches are currently in the graph (see Fig. 6). Since interactive arrow pairs occur at rate γ/N^2 per ordered triple of lines, in our ASG of size n a trifurcation occurs at rate $\gamma n(N-n)(N-n-1)/N^2$, a collision-bifurcation at rate $\gamma n(n-1)(N-n)/N^2$, and a double collision at rate $\gamma n(n-1)(n-2)/N^2$. Note that all arrows can also point to their own tails. In contrast to the original ASG (that is, without interaction), not all potential influencers are necessarily potential ancestors. Namely, the individual on the checking line is, in general, not ancestral; but its type may have an influence on the type of the sampled individual. We generally refer to bifurcations and trifurcations as branching events. The number of lines in the ASG decreases by one in a coalescence event, increases by one in a bifurcation or collision-bifurcation event, increases by two in a trifurcation event, and remains unchanged in simple collision, double collision and relocation events. As in the Moran model, beneficial and deleterious mutations are superimposed on the lines at rate $u\nu_0$ and $u\nu_1$, respectively. The resulting object is called the *untyped ASG*; this refers to the fact that the initial types have not yet been assigned and the consequences of mutations are still unresolved.



FIGURE 6. From left to right: trifurcation, collision-bifurcation with incoming branch already in ASG, collisionbifurcation with checking branch already in ASG, double collision.

Once the untyped ASG has been constructed, the true ancestry of the initial sample is obtained after assigning types to all lines in the ASG at forward time 0, that is, backward time t, without replacement from an exchangeable distribution at time 0 and propagating the types up to time t as follows. Mutation circles and crosses on the ASG turn the type on that line to a type 0 or type 1, respectively (this also includes the possibility of no type change, i.e. the mutations are silent). Now that the types are known, the bifurcation and trifurcation events can be resolved. At every selective event, the individual at the incoming branch is the ancestor if it is of type 0; otherwise the individual at the continuing branch is the ancestor. This hierarchy will be called the *pecking order*. Note that the descendant is of type 1 if and only if both the incoming and the continuing branch are of type 1. At every interactive event, the individual at the incoming branch is the ancestor if it is of type 0 and if the individual at the checking branch is also fit. Otherwise, the individual at the continuing line is the ancestor. Under these rules, the types of the sampled individuals are recovered together with their ancestry.

4. MUTATION-SELECTION EQUATION AS A LIMIT OF THE MORAN MODEL

Let us now relate the Moran model to the mutation-selection equation. To this end, we study the asymptotic behaviour of $Y^{(N)}/N$ as $N \to \infty$ without rescaling of parameters or time. This corresponds to the strong selection–strong interaction–strong mutation (sssism) limit. The following result provides the asymptotic behaviour of the stochastic process $Y^{(N)}/N$ and its connection to the deterministic model in the form of a dynamical law of large numbers.

Proposition 4.1. Assume that $\lim_{N\to\infty} Y_0^{(N)}/N = y_0 \in [0,1]$. Then, for all $\varepsilon > 0$ and $t < \infty$, we have

$$\lim_{N\to\infty} P\left(\sup_{\xi\leqslant t}\left|\frac{Y^N_\xi}{N}-y(\xi;y_0)\right|>\varepsilon\right)=0,$$

where $y(\cdot; y_0)$ is the solution of the IVP (2.1), i.e. $Y^{(N)}/N$ converges to $y(\cdot; y_0)$ uniformly on compact time intervals in probability.



FIGURE 7. Bifurcation of a descendant line (D) into the continuing line (C) and the incoming line (I) along with the propagation of types according to the pecking order.

Proof. The function F of (2.1) is Lipschitz continuous in [0,1]. We have $F(0) = u\nu_1 \ge 0$ and $F(1) = -u\nu_0 \le 0$. Hence, the initial value problem (2.1) has a unique solution $y(\cdot; y_0)$ from $[0, \infty)$ to [0, 1]. Note that we can rewrite the rates of $Y^{(N)}$ as $q_{Y^{(N)}}(k, k + \ell) = Nq\left(\frac{k}{N}, \ell\right)$ for $\ell \in \mathbb{Z} \setminus \{0\}$, where $q : [0, 1] \times \mathbb{Z} \setminus \{0\} \to \mathbb{R}$ is given by

$$q(y,1) = y(1-y) + (1-y)u\nu_0, \quad q(y,-1) = y(1-y)(1+s+\gamma(1-y)) + yu\nu_1,$$

together with $q(y, \ell) = 0$ for $|\ell| > 1$. Since q is continuous, $(Y^{(N)})_{N \ge 1}$ is a density-dependent family of Markov chains. Thus,

$$\sup_{y \in [0,1]} \sum_{\ell} |\ell| q(y,\ell) < \infty \quad \text{and} \quad \lim_{d \to \infty} \sup_{y \in [0,1]} \sum_{|\ell| > d} |\ell| q(y,\ell) = 0.$$
(4.1)

The desired result follows as an application of the law of large numbers for density-dependent families of Markov chains by Kurtz [22, Thm. 3.1]. \Box

Remark 4.2. In the absence of interactions ($\gamma = 0$), the previous result coincides with Cordero [10, Prop. 3.1].

The connection of the two forward processes provides a way to establish an ancestral picture for the mutation-selection equation. We start with the ancestral picture of the stochastic model and consider the same limit that connects the forward processes.

The ancestral selection graph in the strong selection-strong interaction-strong mutation limit (sssism-limit). The connection between the Moran model and the mutation-selection equation provided by Proposition 4.1 yields a way to construct the ASG in the deterministic model: We just let $N \to \infty$ in the ASG of the Moran model. The resulting process will still be stochastic. Before we embark on this, note first that, since we assign types to the ASG in an exchangeable manner, when tracing back ancestries with the ASG in the Moran model, the relocation events do not affect the distribution of types, and so we can ignore them. For the same reason, we can assign a particular order to the lines in the ASG without changing the type distribution. Hence, we proceed as in [23] (see also [6, 9]) and construct the ASG directly in a lookdown-like manner. This means that the lines are placed on consecutive levels, starting at level 1, according to a hierarchy reminiscent of the lookdown construction [13, 14]. We do not rely on this particular construction for the results that follow, but it helps the intuition and, in particular, makes it easier to visualise the process. Since the rates of coalescence, simple collision, double-collision, and collision-bifurcation events vanish as N tends to infinity (they are $\mathcal{O}(1/N)$ per ordered pair of lines). these events will be absent in the asymptotic ASG, i.e. we will only see bifurcations, trifurcations, and mutations. In particular, the ASG of an initial sample of n individuals is distributed as n independent copies of an ASG started with a single individual. Thus, we can restrict ourselves to the evolution of an ASG starting with a single line. Let us first explain the ordering of the lines used in the construction

FIGURE 8. Trifurcation of the descendant line (D) into the continuing line (C), the checking line (J), and the incoming line (I) along with the associated pecking order (\star stands for an arbitrary type.)



FIGURE 9. Propagating types across mutation events (note the parent independence).

of the ASG. At backward time r = 0, we place the single initial individual at level 1. A bifurcation at level i in the ASG is represented by a horizontal open arrowhead at level i (see Fig. 7). The incoming branch emanates from the arrowhead and takes level i. All the lines at levels $\ge i$ are shifted one level upwards. This includes the descendant line, which then continues on level i + 1 as the continuing line. A trifurcation event at level i in the ASG is represented by an interactive arrowhead inscribed into an open square at level i (see Fig. 8). The incoming line emanates from the square at level i, the checking line emanates from the square and is placed at level i + 1, and all the lines at levels $\ge i$ are shifted two levels upwards. Again, this includes the descendant line, which continues as the continuing line on level i+2.

Each line in the ASG independently bifurcates at rate s, thus increasing the number of lines by one. Each line trifurcates at rate γ independently of the others and independently of bifurcations. A trifurcation increases the number of lines by two. In addition, each line mutates to type 0 at rate $u\nu_0$ and to type 1 at rate $u\nu_1$ (see Fig. 9). Mutations occur independently on each line and independently of all the other events.

To determine the true ancestry of the sample at present, we independently sample the type for each line at forward time 0 according to $(1 - y_0, y_0)$ and propagate the types up to forward time t using the same rules as in the finite Moran model. These rules are illustrated in Figs. 7–9. A visualisation of the ASG in some time interval [0, t] is depicted in Fig. 12.

Remark 4.3. We will often identify an ASG starting with n lines with the collection $\mathcal{A} = (\mathcal{A}(i))_{i \in [n]}$, where $\mathcal{A}(i)$ denotes the ASG associated with the *i*-th line.

Consider now a realisation \mathcal{A}_t of the ASG in the time interval [0, t]. For $y_0 \in [0, 1]$, we denote by $H(\mathcal{A}_t, y_0)$ the probability that all lineages at the present are unfit if the initial type distribution is given by $(1-y_0, y_0)$. A natural way of computing $H(\mathcal{A}_t, y_0)$ is to determine first those assignments of types to the lines that lead to an unfit descendant and then to evaluate the probability of observing these assignments if we independently sample according to $(1 - y_0, y_0)$. The next lemma summarises some elementary properties of the function H.

Lemma 4.4. Let A_t be a realisation of the ASG in [0,t] starting with n lines and, for $i \in \{1,...,n\}$, let $A_t(i)$ the ASG in [0,t] associated with the *i*-th line. Then, for all $y_0 \in [0,1]$,

$$H(\mathcal{A}_t, y_0) = \prod_{i=1}^n H(\mathcal{A}_t(i), y_0).$$

Moreover, for n = 1, if T_{\star} is the time of the first event in \mathcal{A}_t , then

- (1) if the event at time T_{\star} is a deleterious mutation, then $H(\mathcal{A}_t, y_0) = 1$.
- (2) if the event at time T_{\star} is a beneficial mutation, then $H(\mathcal{A}_t, y_0) = 0$.
- (3) if the event at time T_{\star} is a selective branching, we denote by $\mathcal{A}^{1}_{T_{\star},t}$ and $\mathcal{A}^{2}_{T_{\star},t}$ the ASGs starting from the continuing and incoming line, respectively, at time T_{\star} and ending at time t. Then

$$H(\mathcal{A}_{t}, y_{0}) = H(\mathcal{A}_{T_{\star}, t}^{1}, y_{0})H(\mathcal{A}_{T_{\star}, t}^{2}, y_{0}).$$

(4) if the event at time T_{\star} is a trifurcation, we denote by $\mathcal{A}^{1}_{T_{\star},t}$, $\mathcal{A}^{2}_{T_{\star},t}$, and $\mathcal{A}^{3}_{T_{\star},t}$ the ASGs starting from the continuing, incoming, and checking line, respectively, at time T_{\star} and ending at time t. Then,

$$H(\mathcal{A}_{t}, y_{0}) = H(\mathcal{A}_{T_{\star}, t}^{1}, y_{0}) \left[H(\mathcal{A}_{T_{\star}, t}^{2}, y_{0}) + H(\mathcal{A}_{T_{\star}, t}^{3}, y_{0}) - H(\mathcal{A}_{T_{\star}, t}^{2}, y_{0}) H(\mathcal{A}_{T_{\star}, t}^{3}, y_{0}) \right].$$

Remark 4.5. Let us at this point make a connection to Mach et al. [26]. In their context, deleterious mutations and trifurcations are captured by the local maps dth ('deaths') and cob ('cooperative branchings'), respectively. Hence, if $s = \nu_0 = 0$, $H(\mathcal{A}_t, y_0)$ corresponds to the concatenation of their higher-level maps dth and cob, respectively. In particular, (1) and (4) of our Lemma 4.4 agree with [26, Eq. (1.84)].

Proof of Lemma 4.4. The lines in the ASG do not interact, so the first result follows by independence. Now fix n = 1. For (1) and (2), note that if the first event is a mutation, the type of the line at time r = 0 is independent of the type assignment at time r = t due to parent independence (cf. Fig. 9). If the first event is a selective event, the individual at time 0 is of type 1 if and only if the two lines involved in the event are of type 1. This leads to (3). If the first event is an interactive event, the individual at time r = 0 is of type 1 if and only if the continuing line is unfit and either the checking or the incoming line is unfit. This leads to (4).

5. The stratified ASG

Quite generally there are two approaches to compute the function H. The natural way is to determine first the type assignments to the lines in the ASG that lead to an unfit descendant and then to evaluate the probability of observing these assignments if we independently sample according to $(1 - y_0, y_0)$. This is the approach pursed by Mach [25], but the general idea is also present in the work of Dawson and Greven [12]. In contrast, we aim at resolving for any positive initial value all information contained in the tree on the spot. This leads to a reduction and pruning of the tree. A subsequent reorganization leads to a stratification of the ASG into distinct regions. This is the topic of the current section.

5.1. Motivation: The case without interaction. In the absence of interaction and mutation, a sampled individual is of type 1 if and only if all its potential ancestors are of type 1; this follows from a simple generalisation of the pecking order and holds regardless of the tree structure. A mutation determines the type of the line on which it occurs, so this line need not be traced back further and hence can be pruned. Moreover, if a beneficial mutation occurs on a line that is not yet pruned, the type of the descendant will be fit such that we can stop reading the ASG, and we send the process to a cemetery point Δ . This reasoning gave rise to the killed ASG [6]. Its line-counting process $R = (R_r)_{r \ge 0}$ is a Markov process on $\mathbb{N}_0 \cup {\Delta}$ with transition rates

$$q_{B}(k, k+1) = ks, \quad q_{B}(k, k-1) = ku\nu_{1}, \quad q_{B}(k, \Delta) = ku\nu_{0}, \qquad k \in \mathbb{N}_{0}.$$

Absorption of R in 0 implies that all individuals in the sample are of type 1; whereas absorption of R in Δ implies that at least one individual in the sample is fit. The process R is in moment duality with the mutation-selection model without interaction (see [6, Thm.2]), that is we have

$$y(t;y_0)^n = E_n [y_0^{R_t}]. (5.1)$$

5.2. Reducing the interactive ASG. In the interactive case, a single fit line does not necessarily lead to a fit sampled individual (see Fig. 8), and hence we cannot use the same reasoning as in the non-interactive case. In particular, counting lines is not sufficient; rather, the tree structure plays an eminent role. A first step to circumvent this problem is to get rid of the mutation events present in the ASG. As in the non-interactive case, a mutation on a line in the ASG determines the effect of that line on the type of the sampled individual, and, therefore, we need not trace back its ancestry any further. In addition, the type assigned to the line by the mutation will propagate (forward in time), resolving on its way some of the selective and/or interactive events it encounters, by following the local rules presented in the previous section. A particularly interesting situation occurs when the first event after a trifurcation is a deleterious mutation in the corresponding continuing line. In this case, the type of the descendant line depends only on the type of the incoming and the checking lines. For this reason, we consider a new type of event, which we call *interactive bifurcation* and which corresponds to an interactive event where the continuing line is pruned due to a deleterious mutation. Moreover, we denote as *generalised ASG* an ASG consisting of selective and interactive bifurcations, trifurcations, and mutations. The following notions of reduction and pruning permit to resolve the local effects of mutations in a generalised ASG.



FIGURE 10. 1-step pruning described by (1.a)-(1.d)

Definition 5.1 (Reduction and pruning). Let \mathcal{A} be a generalised ASG. The reduced ASG of \mathcal{A} , denoted by $\chi(\mathcal{A})$, is obtained by removing from \mathcal{A} all the sub-ASGs arising to the left of mutation events. We refer to $\overline{\mathcal{A}}$ as a reduced ASG if there exists some generalised ASG \mathcal{A} such that $\overline{\mathcal{A}} = \chi(\mathcal{A})$. Assume that $\chi(\mathcal{A})$ contains at least one branching event and at least one mutation event. If m denotes a mutation event in $\chi(\mathcal{A})$, we call $\rho_m(\mathcal{A})$ the 1-step pruning of $\chi(\mathcal{A})$ at m and define it as follows (cf. Figs. 10 and 11).

- (1) If m is a deleterious mutation and
 - (a) the event preceding m is a selective branching, we remove the arrow and the line segment between the two events, and we connect the other line involved in the branching to the descendant line.
 - (b) the event preceding m is a trifurcation and the line involved in the mutation is incoming (resp. checking) to this event, we remove the line segment between the two events, the sub-ASG arising from the checking (resp. incoming) line, and the interactive arrow.
 - (c) the event preceding m is a trifurcation and the line involved in the mutation is continuing to this event, we remove the line segment between the two events, thus transforming the trifurcation into an interactive bifurcation.
 - (d) the event preceding m is an interactive bifurcation, we remove the sub-ASG arising from the interactive event and replace the interactive event by a deleterious mutation.
- (2) If m is a beneficial mutation and
 - (a) the event preceding m is a selective branching and the line involved in the mutation is continuing (resp. incoming), we remove the sub-ASG arising from the incoming (resp. continuing) line and connect the remaining line to the descendant line.
 - (b) the event preceding m is a trifurcation and the line involved in the mutation is incoming (resp. checking) to this event, we remove the sub-ASG arising from the incoming (resp. checking) line and connect the checking (resp. incoming) line to the continuing line via a selective arrow.
 - (c) the event preceding m is a trifurcation and the line involved in the mutation is continuing to this event, we remove the sub-ASGs arising from the checking and incoming lines.
 - (d) the event preceding m is an interactive bifurcation and the line involved in the mutation is incoming (resp. checking) to this event, we remove the line segment between the two events and connect the checking (resp. incoming) line to the descendant line.

We call $\hat{\mathcal{A}}$ a pruning of \mathcal{A} if $\hat{\mathcal{A}} = \mathfrak{X}(\mathcal{A})$ or if it is obtained by successive 1-step prunings of $\mathfrak{X}(\mathcal{A})$. Moreover, a pruning of \mathcal{A} is called *total* if it is composed of a generalised ASG without mutations and/or a collection of lines ending in mutation events. We write $\mathcal{A} \sim \circ$ if \mathcal{A} consists of a single line ending in a beneficial mutation. Similarly, we write $\mathcal{A} \sim \times$ if \mathcal{A} consists of a single line ending in a deleterious mutation.

Remark 5.2. Note that a 1-step pruning reduces the number of events in a reduced ASG at least by one. Therefore, a total pruning is obtained after a finite number of 1-step prunings.

Remark 5.3. If \mathcal{A} is a generalised ASG, then $\mathfrak{X}(\mathcal{A})$ is, by construction, embedded into \mathcal{A} (in the obvious way). Similarly, if $\overline{\mathcal{A}}$ is a reduced ASG and $\rho_m(\overline{\mathcal{A}})$ is a 1-step pruning of it, then the lines of $\rho_m(\overline{\mathcal{A}})$

can be embedded into $\bar{\mathcal{A}}$. However, the type of the connections between lines can differ between $\rho_m(\bar{\mathcal{A}})$ and $\bar{\mathcal{A}}$ (see Fig. 12). This identification of lines will be used implicitly all along in this section.

We extend the definition of H to generalised ASGs by adding the rule that in an interactive bifurcation the descendant line is fit if and only if both checking and incoming lines are fit. For a reduced ASG in [0, t], we assign types to the lines that are present at time r = t (the lines ending before time t get their types from the corresponding mutation events). Next, we propagate types in the usual way. Hence, we can also extend the definition of H to reduced ASGs.

Remark 5.4. The statement of Lemma 4.4 remains true if A_t is a reduced ASG or a generalised ASG in [0, t]. Moreover, points (1), (2), (3) and (4) are complemented by

(5) if the event at time T_{\star} is an interactive bifurcation, we denote by $\mathcal{A}^2_{T_{\star},t}$ and $\mathcal{A}^3_{T_{\star},t}$ the ASGs starting at time T_{\star} from the incoming and checking line, respectively. Then,

$$H(\mathcal{A}_t, y_0) = H(\mathcal{A}_{T_{\star}, t}^2, y_0) + H(\mathcal{A}_{T_{\star}, t}^3, y_0) - H(\mathcal{A}_{T_{\star}, t}^2, y_0)H(\mathcal{A}_{T_{\star}, t}^3, y_0).$$

The next lemma states that reduction and pruning do not change the value of H.

Lemma 5.5. The function H is invariant under reduction and 1-step prunings.

Proof. Let \mathcal{A} be a generalised ASG in [0, t] consisting of n lines at time t, denoted by $\ell_1, ..., \ell_n$. Let $I \subset {\ell_1, ..., \ell_n}$ be the subset of lines that are also present in $\mathfrak{A}(\mathcal{A})$ at time t. By Lemma 4.4, we can without loss of generality assume that \mathcal{A} starts with one line. For $x := (x_i)_{i \in [n]} \in {\{0, 1\}}^n$, we denote by $v(x) \in {\{0, 1\}}$ the type of the single line present at time 0 in \mathcal{A} if at time t, for each $i \in [n]$, line ℓ_i is assigned type x_i . From construction, if $y := (y_i)_{i \in [n]}, z := (z_i)_{i \in [n]} \in {\{0, 1\}}^n$ are such that $y_i = z_i$ for all $i \in I$, then v(y) = v(z). Therefore, H is invariant under reduction.

We prove that H is invariant under 1-step prunings by induction on the number of branching events in the corresponding ASG. First, assume that \mathcal{A}_t is a reduced ASG in [0, t] consisting of one branching event and at least one mutation. We have to show that for every mutation event m on a line of \mathcal{A}_t , $H(\mathcal{A}_t, y_0) = H(\rho_m(\mathcal{A}_t), y_0)$. We prove this in the case that the branching is a trifurcation, m is deleterious and occurs in the continuing line, all the other cases are analogous. Using the notation of Lemma 4.4-(4), $\mathcal{A}_{T_t,t}^1 \sim \times$, and therefore $H(\mathcal{A}_{T_t,t}^1, y_0) = 1$. Hence, using Lemma 4.4-(4) and Remark 5.4, we get

$$H(\mathcal{A}_t, y_0) = H(\mathcal{A}_{T_\star, t}^2, y_0) + H(\mathcal{A}_{T_\star, t}^3, y_0) - H(\mathcal{A}_{T_\star, t}^2, y_0) H(\mathcal{A}_{T_\star, t}^3, y_0) = H(\rho_m(\mathcal{A}_t), y_0).$$

Now, we assume that the result is true for reduced ASGs containing at most k branchings. Let \mathcal{A}_t be a reduced ASG in [0, t] consisting of k + 1 branchings and at least one mutation. We have to show that, for every mutation event m on a line of \mathcal{A}_t , $H(\mathcal{A}_t, y_0) = H(\rho_m(\mathcal{A}_t), y_0)$. Assume that the first event in \mathcal{A}_t is a trifurcation, m is beneficial and occurs in the region arising from the checking line. If $\mathcal{A}_{T_*,t}^3 \sim \circ$, using the notation of Lemma 4.4-(4), then $H(\mathcal{A}_{T_*,t}^3, y_0) = 0$. Thus, using Lemma 4.4-(3,4), we obtain

$$H(\mathcal{A}_{t}, y_{0}) = H(\mathcal{A}_{T_{\star}, t}^{1}, y_{0})H(\mathcal{A}_{T_{\star}, t}^{2}, y_{0}) = H(\rho_{m}(\mathcal{A}_{t}), y_{0}),$$



FIGURE 11. 1-step pruning described by (2.a)-(2.d)



FIGURE 12. A realisation of the ASG \mathcal{A}_t in the ssism-limit in the time interval [0, t] (grey and black, left and right), its reduced ASG $\mathfrak{X}(\mathcal{A})$ (black, left), and its total pruning $\hat{\mathcal{A}}$ (black, right).

which proves the result in this case. Now, assume that $\mathcal{A}_{T_{\star},t}^3$ contains at least one branching. In this case, $\rho_m(\mathcal{A}_t)$ is obtained by replacing $\mathcal{A}_{T_{\star},t}^3$ by $\rho_m(\mathcal{A}_{T_{\star},t}^3)$ in \mathcal{A}_t . Moreover, since $\mathcal{A}_{T_{\star},t}^3$ contains at most k branchings, applying the induction hypothesis, we deduce that $H(\mathcal{A}_{T_{\star},t}^3, y_0) = H(\rho_m(\mathcal{A}_{T_{\star},t}^3), y_0)$. Therefore, Lemma 4.4-(4) yields

$$H(\mathcal{A}_{t}, y_{0}) = H(\mathcal{A}_{T_{\star,t}}^{1}, y_{0}) \left[H(\mathcal{A}_{T_{\star,t}}^{2}, y_{0}) + H(\mathcal{A}_{T_{\star,t}}^{3}, y_{0}) - H(\mathcal{A}_{T_{\star,t}}^{2}, y_{0}) H(\mathcal{A}_{T_{\star,t}}^{3}, y_{0}) \right]$$

= $H(\mathcal{A}_{T_{\star,t}}^{1}, y_{0}) \left[H(\mathcal{A}_{T_{\star,t}}^{2}, y_{0}) + H(\rho_{m}(\mathcal{A}_{T_{\star,t}}^{3}), y_{0}) - H(\mathcal{A}_{T_{\star,t}}^{2}, y_{0}) H(\rho_{m}(\mathcal{A}_{T_{\star,t}}^{3}), y_{0}) \right]$
= $H(\rho_{m}(\mathcal{A}_{t}), y_{0}),$

which proves the result in this case. The remaining cases are analogous.

Remark 5.6. Two total prunings are not necessarily identical. See for example Fig. 13.

Lemma 5.7. Let A_t be a realisation of the ASG in [0, t], starting with one line. Two total prunings of A_t are either identical or both consist of a single line ending in the same type of mutation.

Proof of Lemma 5.7. We proceed by induction on the number of events in the ASG. The statement is trivially true for any ASG consisting of exactly one event. Let us assume that the statement holds true for any ASG consisting of at most n events. Let \mathcal{A}_t be an ASG consisting of exactly n + 1 events and let T_{\star} be the time to the first event on \mathcal{A}_t .

If the event at time T_{\star} is a mutation, then $\mathfrak{X}(\mathcal{A}_t)$ is a single line ending at the corresponding mutation at time T_{\star} . Hence, $\mathfrak{X}(\mathcal{A}_t)$ is the unique total pruning of \mathcal{A}_t . The result follows in this case.

For the remaining cases, we denote by $\rho^1(\mathcal{A}_t)$ and $\rho^2(\mathcal{A}_t)$ two total prunings of \mathcal{A}_t . If the event at time T_* is a selective branching, we denote by $\mathcal{A}_{T_*,t}^1$ and $\mathcal{A}_{T_*,t}^2$ the ASGs arising at time T_* from the continuing and incoming line, respectively. For $i, j \in \{1, 2\}$, we denote by $\rho^i(\mathcal{A}_{T_*,t}^j)$ the reduced ASG obtained by pruning $\mathcal{A}_{T_*,t}^j$ according to ρ^i ignoring the prunings associated with events that are not in $\mathcal{A}_{T_*,t}^j$. If $\rho^1(\mathcal{A}) \sim \circ$, then, by construction, there is $i \in \{1, 2\}$ such that $\rho^1(\mathcal{A}_{T_*,t}^i) \sim \circ$. In particular, $\rho^1(\mathcal{A}_{T_*,t}^i)$ is a total prunings of $\mathcal{A}_{T_*,t}^i$, and by the induction hypothesis, if $\overline{\mathcal{A}}$ is a total pruning of $\mathcal{A}_{T_*,t}^i$, then $\overline{\mathcal{A}} \sim \circ$. Hence, if $\rho^2(\mathcal{A}_{T_*,t}^i) \approx \circ$, then $\rho^2(\mathcal{A}_{T_*,t}^i)$ can not be a total pruning and therefore has to contain at least two lines and at least one mutation. Thus, $\rho^2(\mathcal{A}_{T_*,t}^j) \sim \circ$, for $j \in \{1,2\} \setminus \{i\}$, such that $\rho^2(\mathcal{A}_t) \sim \circ$, and



FIGURE 13. Resolving first the first (second) mutation from the left leads to the total pruning on the left (right). Note the difference in length of the line segment to the beneficial mutation after pruning.

the result follows in this case. On the other hand, if $\rho^2(\mathcal{A}_{T_{\star},t}^i) \sim \circ$, then $\rho^2(\mathcal{A}_t) \sim \circ$, and the result also follows.

We assume now that $\rho^1(\mathcal{A}_t) \approx 0$. In this case, $\rho^2(\mathcal{A}_t) \approx 0$. Therefore, for $i, j \in \{1, 2\}$, $\rho^i(\mathcal{A}_{T_\star,t}^j)$ either has no mutations or $\rho^i(\mathcal{A}_{T_\star,t}^j) \sim \times$. In particular, $\rho^i(\mathcal{A}_{T_\star,t}^j)$ is a total pruning of $\mathcal{A}_{T_\star,t}^i$, for $i, j \in \{1, 2\}$. The induction hypothesis yields that $\rho^1(\mathcal{A}_{T_\star,t}^i) = \rho^2(\mathcal{A}_{T_\star,t}^i)$, for $i \in \{1, 2\}$. Thus, either $\rho^1(\mathcal{A}_t) = \rho^2(\mathcal{A}_t)$ or $\rho^1(\mathcal{A}_t) \sim \times \sim \rho^2(\mathcal{A}_t)$. The result in the case of an interactive event at time T_\star follows in a similar way.

The previous result supports the following definition.

Definition 5.8 (Pruned ASG). Let \mathcal{A}_t be a realisation of the ASG in the time interval [0, t] starting with one line. The pruned ASG associated with \mathcal{A}_t , denoted by $\rho(\mathcal{A}_t)$, is defined as follows. Let $\overline{\mathcal{A}}_t$ be a total pruning of \mathcal{A}_t . If $\overline{\mathcal{A}}_t \sim \times$, we set $\rho(\mathcal{A}_t) := \emptyset$. If $\overline{\mathcal{A}}_t \sim \circ$, we set $\rho(\mathcal{A}_t) := \Delta$, where Δ denotes a cemetery point. In the remaining case, we set $\rho(\mathcal{A}_t) := \overline{\mathcal{A}}_t$. Moreover, if $\mathcal{A}_t := (\mathcal{A}_t(i))_{i \in [n]}$ is a realisation of the ASG in the time interval [0, t] starting with n lines, then the pruned ASG associated with \mathcal{A}_t is given by

$$\rho(\mathcal{A}_t) := \begin{cases} \Delta, & \text{if } \rho(\mathcal{A}_t(i)) = \Delta \text{ for some } i \in [n], \\ \emptyset, & \text{if } \rho(\mathcal{A}_t(i)) = \emptyset \text{ for all } i \in [n], \\ (\rho(\mathcal{A}_t(i)))_{i \in I_n}, & \text{otherwise}, \end{cases}$$

where $I_n := \{i \in [n] : \rho(\mathcal{A}_t(i)) \neq \emptyset\}.$

We set $H(\Delta, y_0) := 0$ and $H(\emptyset, y_0) := 1$, for $y_0 \in [0, 1]$.

Lemma 5.9. For any realisation \mathcal{A} of the ASG in a finite interval, we have

$$H(\mathcal{A}, y_0) = H(\rho(\mathcal{A}), y_0), \qquad y_0 \in [0, 1].$$

Proof. It follows by iterating Lemma 5.5.

5.3. Stratifying the ASG. The pruned ASG permits to get rid of the mutation events in the ASG. The next step is to partition or *stratify* the pruned ASG into sub-regions within which types propagate as in the non-interactive case. To this end, we say that two lines in a generalised ASG belong to the same region if they are connected only by means of selective arrows. A single trifurcation gives rise to two new regions, which originate from the checking and incoming lines. Each region may give rise to subregions due to subsequent trifurcations. In this way, the line at the origin of a given region is assigned type 1 if and only if all the lines sharing this region are assigned type 1, and at any trifurcation point involving a line in this region (where the affected line is by definition continuing) either the incoming or the checking line is assigned type 1. Interactive bifurcations will be treated analogously. In this way, it will be enough to keep track of the sizes of the regions and of the tree structure inherent to the connections between them. In order to encode this information, we introduce the notion of weighted ternary trees.

In what follows, a rooted tree will be an undirected, acyclic, connected graph in which we identify a special vertex that is called the root. A ternary tree is a rooted tree in which each vertex has either no children or three distinguishable children that we call left, middle, and right child, respectively. We denote by Ξ the set of all ternary trees. For a ternary tree $\tau \in \Xi$, we denote by V_{τ} the set of its vertices and by $L_{\tau} \subseteq V_{\tau}$ the set of its leaves. A weighted ternary tree is a pair $\mathcal{T} = (\tau, m_{\tau})$, where $\tau \in \Xi$ and $m_{\tau} : L_{\tau} \to \mathbb{N}_0$. We denote by Υ the set of weighted ternary trees. We write \widehat{m} for the weighted ternary tree that consists only of a root of weight n.

For a given realisation of the ASG, we will associate a weighted ternary tree such that: (1) the leaves of the weighted ternary tree encode the different regions in the corresponding pruned ASG, (2) the underlying tree structure provides the connections between the regions, and (3) the weight of a leaf corresponds to the number of lines in the associated region.

Definition 5.10 (Stratified ASG). Let \mathcal{A}_t be a generalised ASG in [0, t]. The stratified ASG associated with \mathcal{A}_t , denoted by $S(\mathcal{A}_t) \in \Upsilon_* := \Upsilon \cup \{\Delta\}$, is defined as follows. If $\rho(\mathcal{A}_t) = \emptyset$, we set $S(\mathcal{A}_t) := \overline{0}$. If $\rho(\mathcal{A}_t) = \Delta$, we set $S(\mathcal{A}_t) := \Delta$. Assume now that $\rho(\mathcal{A}_t) \notin \{\emptyset, \Delta\}$. If there are no interactive events



FIGURE 14. Building blocks of the pruned ASG and their associated stratified ASG.

in $\rho(\mathcal{A}_t)$, we set $S(\mathcal{A}_t) := {}^{(m)}$, where *m* is the number of lines present at time *t* in $\rho(\mathcal{A}_t)$. In the remaining case, we denote by $\mathcal{A}_{T_{\star},t}^2$ and $\mathcal{A}_{T_{\star},t}^3$ the sub-ASGs arising at the first interactive event in $\rho(\mathcal{A}_t)$ from the checking and incoming lines, respectively. Moreover, we denote by \mathcal{A}_t^1 the generalised ASG obtained by removing $\mathcal{A}_{T_{\star},t}^2$ and $\mathcal{A}_{T_{\star},t}^3$ from $\rho(\mathcal{A}_t)$. Thus, $S(\mathcal{A}_t)$ is defined recursively by joining the roots of $S(\mathcal{A}_t^1)$, $S(\mathcal{A}_{T_{\star},t}^2)$ and $S(\mathcal{A}_{T_{\star},t}^3)$ to a new node $\hat{\rho}$, so that they play the role of the left, middle, and right child of $\hat{\rho}$, respectively.

Remark 5.11. If \mathcal{A}_t is a generalised ASG in [0, t] with $\rho(\mathcal{A}_t) \notin \{\emptyset, \Delta\}$, there is a natural way to associate with any line present at time t in $\rho(\mathcal{A}_t)$ a leaf in $S(\mathcal{A}_t)$. If there are no interactive events in $\rho(\mathcal{A}_t)$, all the lines at time t in $\rho(\mathcal{A}_t)$ are associated with the root. Otherwise, using the notation in Definition 5.10, we proceed recursively by associating, for $i \in \{1, 2, 3\}$, the lines of \mathcal{A}_t^i present at time t with the leaves of $S(\mathcal{A}_t^i)$. This construction will play an important role in Lemma 5.15.

It remains to explain how to compute the probability $H(\mathcal{A}, y_0)$ on the basis of $S(\mathcal{A})$.

Definition 5.12. We define $\mathcal{H}: \Upsilon_{\star} \times [0,1] \to [0,1]$ recursively. First, we set for $y_0 \in [0,1]$,

$$\mathcal{H}(\underline{n}, y_0) := y_0^n, \quad n \in \mathbb{N}_0, \quad \text{and} \quad \mathcal{H}(\Delta, y_0) := 0.$$

For $\mathcal{T} = (\tau, m_{\tau}) \in \Upsilon$ having at least three leaves, we denote by κ^1, κ^2 , and κ^3 the left, middle and right child of the root of τ , and we define recursively

$$\mathcal{H}(\mathcal{T}, y_0) := \mathcal{H}(\mathcal{T}_{\kappa^1}, y_0) \left[\mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) + \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) \right].$$
(5.2)

The next theorem shows that the stratified ASG together with the function \mathcal{H} is the right object to encode the probability that the initial lineages in an ASG are all unfit.

Theorem 5.13. For any realisation \mathcal{A}_t of the ASG in [0, t], we have

$$H(\mathcal{A}_t, y_0) = \mathcal{H}(S(\mathcal{A}_t), y_0), \qquad \forall y_0 \in [0, 1].$$

Proof. From Lemma 5.9, it is enough to prove that for any realisation \mathcal{A}_t of the ASG in [0, t], we have

$$H(\rho(\mathcal{A}_t), y_0) = \mathcal{H}(S(\mathcal{A}_t), y_0), \qquad \forall y_0 \in [0, 1].$$

$$(5.3)$$

If $\rho(\mathcal{A}_t) \in \{\emptyset, \Delta\}$, the result follows from the definition. Now we assume that $\rho(\mathcal{A}_t) \notin \{\emptyset, \Delta\}$, and we proceed by induction on the number m of interactive events present in $\rho(\mathcal{A}_t)$. For m = 0, iterating Lemma 4.4-(1), we obtain that $H(\rho(\mathcal{A}_t), y_0) = y_0^n$, where n is the number of lines present in $\rho(\mathcal{A}_t)$ at time t. In addition, by definiton $S(\mathcal{A}_t) = \widehat{(n)}$, and hence $\mathcal{H}(S(\mathcal{A}_t), y_0) = y_0^n$, and the result follows in this case. Now we assume that (5.3) holds for any ASG such that the corresponding pruned ASG consists of at most m interactive events. Assume that \mathcal{A}_t is such that $\rho(\mathcal{A}_t)$ contains exactly m + 1 interactive events. As in Definition 5.10, we denote by $\mathcal{A}_{T_{\star,t}}^2$ and $\mathcal{A}_{T_{\star,t}}^3$ the sub-ASGs arising at the first interactive event in $\rho(\mathcal{A}_t)$ from the checking and incoming line, respectively, and by \mathcal{A}_t^1 the generalised ASG obtained by removing $\mathcal{A}_{T_{\star,t}}^2$ and $\mathcal{A}_{T_{\star,t}}^3$ from $\rho(\mathcal{A}_t)$. By construction, \mathcal{A}_t^1 and $\mathcal{A}_{T_{\star,t}}^i$ ($i \in \{2,3\}$) contain at most m interactive events, and therefore from the induction hypothesis $H(\rho(\mathcal{A}_t^1), y_0) = \mathcal{H}(S(\mathcal{A}_t^1), y_0)$ and $H(\rho(\mathcal{A}_{T_{\star,t}}^i), y_0) = \mathcal{H}(S(\mathcal{A}_{T_{\star,t}}^i), y_0)$ ($i \in \{2,3\}$). Hence, the result follows by using Lemma 4.4 (or Remark 5.4 in the case of an interactive bifurcation) and the definition of $S(\mathcal{A}_t)$ and \mathcal{H} .



FIGURE 15. From left to right: ternary tree τ with leftmost leaf ℓ_{τ}^1 and root κ_{τ} ; the tree $\tau_{a_v}^C$ that arises if we remove from τ all the descendants of a_v ; the restriction τ_v of τ to the subtree induced by v; the concatenation $\tau_{a_v}^C \otimes_{a_v} \tau_v$ of $\tau_{a_v}^C$ with τ_v at leaf a_v . Note that the labels do not indicate the weights here.

5.4. The stratified ASG process. In what follows, \mathcal{A}_{∞} denotes a random realisation of the ASG in $[0, \infty)$ and, for $r \ge 0$, \mathcal{A}_r denotes its restriction to [0, r]. In this section we aim to describe the evolution of the process $(S(\mathcal{A}_r))_{r\ge 0}$. We first introduce some notation and operations on weighted ternary trees, which will serve as building blocks to describe the transitions of this process.

Fix $\mathcal{T} := (\tau, m_{\tau}) \in \Upsilon$. We denote by κ_{τ} and ℓ_{τ}^{1} the root and the leftmost leaf of τ , respectively. For $v \in V_{\tau} \setminus {\kappa_{\tau}}$, a_{v} is the parent of v and a_{v}^{\star} is either v if v is not the left child of its parent, or the youngest ancestor of v that is not the left child of its parent. In particular, $a_{l^{\perp}}^{\star} = \kappa_{\tau}$.

For $v \in V_{\tau}$, $\tau_v \in \Xi$ is the subtree of τ that contains v and all its descendants such that v is the root of τ_v . We write $\mathcal{T}_v = (\tau_v, m_{\tau_v}) \in \Upsilon$ for the ternary tree τ_v with weights given by the restriction of m_{τ} to L_{τ_v} , see also Fig. 15. Similarly, τ_v^C is the tree that arises from τ by removing all the descendants of v. The analogous weighted ternary tree is $\mathcal{T}_v^C = (\tau_v^C, m_{\tau_v^C})$, where

$$m_{\tau_v^C}(l) = \begin{cases} m_\tau(l), & \text{if } l \neq v, \\ 0, & \text{if } l = v. \end{cases}$$

For $\ell \in L_{\tau}$ and $\bar{\tau} \in \Xi$, we define $\tau \otimes_{\ell} \bar{\tau} \in \Xi$ as the tree that arises by concatenating $\bar{\tau}$ to τ at the leaf ℓ , see Fig. 17. In particular, the corresponding set of leaves is $L_{\tau \otimes_{\ell} \bar{\tau}} = (L_{\tau} \setminus \{\ell\}) \cup L_{\bar{\tau}}$. For $\bar{\mathcal{T}} = (\bar{\tau}, m_{\bar{\tau}}) \in \Upsilon$, the concatenation of $\bar{\mathcal{T}}$ at a leaf ℓ of \mathcal{T} is defined as $\mathcal{T} \otimes_{\ell} \bar{\mathcal{T}} = (\tau \otimes_{\ell} \bar{\tau}, m_{\tau} \otimes_{\ell} m_{\bar{\tau}})$, where

$$m_{\tau} \otimes_{\ell} m_{\bar{\tau}} = \begin{cases} m_{\tau}(l), & \text{if } l \in L_{\tau} \setminus \{\ell\}, \\ m_{\bar{\tau}}(l), & \text{if } l \in L_{\bar{\tau}} \setminus \{\ell_{\bar{\tau}}^1\}, \\ m_{\tau}(\ell) + m_{\bar{\tau}}(l), & \text{if } l = \ell_{\bar{\tau}}^1. \end{cases}$$

The total weight of \mathcal{T} is

$$M(\mathcal{T}) := \sum_{v \in L_{\tau}} m_{\tau}(v).$$
(5.4)



FIGURE 16. The weighted ternary tree in the middle arises if we apply the ' \circ '-operation at the dashed leaf in the left tree. The weighted ternary tree of the right arises if we apply the ' \times '-operation at the dotted leaf in the left tree. The labels indicate the weights of the leaves.



FIGURE 17. Concatenation of two trees at a given leaf. Note that the labels do not indicate weights here. The weight of leaf $\tilde{\ell}^1$ in the right tree is the weight of ℓ^1 plus the weight of $\tilde{\ell}^1$ in the middle tree.

We denote by b_{ℓ} the youngest ancestor of ℓ that is either the left child of its parent, or that is not the left child of its parent but where the parent has left child b_{ℓ}^1 such that $M(\tau_{b_{\ell}^1}) > 0$, or which is the root. Denote by $\Psi \in \Xi$ the ternary tree with three leaves. Moreover, we set $\Psi^* = (\Psi, m_{\Psi}) \in \Upsilon$ as the ternary tree Ψ with left leaf of weight 0 and middle and right leaf of weight 1. The following transformations will play the role of transitions of the process $(S(\mathcal{A}_r))_{r\geq 0}$ (see Figs. 16–18).

Definition 5.14 (Transformations of weighted ternary trees). For $\mathcal{T} = (\tau, m_{\tau}) \in \Upsilon$ and $\ell \in L_{\tau}$, we define $\mathcal{T}^{\ell}_{\Upsilon}, \mathcal{T}^{\ell}_{\Psi}, \mathcal{T}^{\ell}_{\times}, \mathcal{T}^{\ell}_{\circ} \in \Upsilon_{\star}$ as follows.

- $\mathcal{T}^{\ell}_{\Upsilon} := (\tau^{\ell}_{\Upsilon}, m_{\tau^{\ell}_{\Upsilon}})$ with $\tau^{\ell}_{\Upsilon} := \tau, m_{\tau^{\ell}_{\Upsilon}}(\ell) := m_{\tau}(\ell) + 1$ and $m_{\tau^{\ell}_{\Upsilon}}(l) := m_{\tau}(l)$ for $l \neq \ell$.
- $\mathcal{T}^{\ell}_{\Psi} := (\tau^{\ell}_{\Psi}, m_{\tau^{\ell}_{\Psi}})$ with $\tau^{\ell}_{\Psi} := \tau \otimes_{\ell} \Psi$ and $m_{\tau^{\ell}_{\Psi}} := m_{\tau} \otimes_{\ell} m_{\Psi^{\star}}$.
- $\mathcal{T}^{\ell}_{\times} := (\tau^{\ell}_{\times}, m_{\tau^{\ell}_{\times}})$ where
 - if $m_{\tau}(\ell) > 1$ or ℓ is the left child of its parent, then $\tau_{\times}^{\ell} := \tau$, $m_{\tau_{\times}^{\ell}}(\ell) := m_{\tau}(\ell) 1$ and $m_{\tau_{\times}^{\ell}}(l) := m_{\tau_{\times}^{\ell}}(\ell) = m_{\tau_{\times}^{\ell}}(\ell) = m_{\tau_{\times}^{\ell}}(\ell)$ $m_{\tau}(l)$ for $l \neq \ell$.
 - if $m_{\tau}(\ell) = 1, \ \ell$ is not the left child of its parent, and b_{ℓ} is not the root, then we set $\mathcal{T}_{\times}^{\ell} :=$ $\mathcal{T}^C_{a_{b_\ell}} \otimes_{a_{b_\ell}} \mathcal{T}_{b_\ell^1}.$
 - if $m_{\tau}(\ell) = 1$, ℓ is not the left child of its parent, and b_{ℓ} is the root, then $\mathcal{T}_{\times}^{\ell} := 0$.

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• \mathcal{T}^{\ell}_{\circ} := (\tau^{\ell}_{\circ}, m_{\tau^{\ell}_{\circ}}) where
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- if $\ell \neq \ell_{\tau}^1$, denote by v and w the two children of $a_{a_{\ell}^{\star}}$ other than a_{ℓ}^{\star} ordered from left to right. Then we set, $\mathcal{T}^{\ell}_{\circ} := \left(\mathcal{T}^{C}_{a_{a_{\ell}}^{\star}} \otimes_{a_{a_{\ell}}^{\star}} \mathcal{T}_{v}\right) \otimes_{\ell^{1}_{(\tau_{v})}} \mathcal{T}_{w}.$ • if $\ell = \ell^{1}_{\tau}$, we set $\mathcal{T}^{\ell}_{\circ} := \Delta$.

Lemma 5.15. Let \mathcal{A}_t be a realisation of the ASG in [0, t]. Assume that $\rho(\mathcal{A}_{r-}) \notin \{\emptyset, \Delta\}, r \in (0, t]$, and that at time r a line present in $\rho(\mathcal{A}_{r-})$ is affected by an event in \mathcal{A}_r . If the affected line is associated to leaf $\ell \in S(\mathcal{A}_{r-})$ and the event corresponds to a

- (1) branching, then $S(\mathcal{A}_r) = (S(\mathcal{A}_{r-}))^{\ell}_{\gamma}$.
- (2) trifurcation, then $S(\mathcal{A}_r) = (S(\mathcal{A}_{r-}))^{\ell}_{\Psi}$.
- (3) deleterious mutation, then $S(\mathcal{A}_r) = (S(\mathcal{A}_{r-1}))^{\ell}_{\times}$.
- (4) beneficial mutation, then $S(\mathcal{A}_r) = (S(\mathcal{A}_{r-1}))_{\alpha}^{\ell}$.

Proof. We prove the lemma for case (3). For the other cases the proof works analogously. We proceed by induction on the number k of interactive events present in $\rho(\mathcal{A}_{r-})$. For k=0, we have that $S(\mathcal{A}_{r-}) = 0$. where n denotes the number of lines present at time $r - \ln \rho(\mathcal{A}_{r-})$. In particular, all the lines present at time $r - \text{ in } \rho(\mathcal{A}_{r-})$ are associated with the root κ . Hence, $(S(\mathcal{A}_{r-}))_{\times}^{\kappa} = (j)$, where j := n-1. In addition, $\rho(\mathcal{A}_r)$ does not contain interactive events and consists of j lines at time r. Therefore, $S(\mathcal{A}_r) = (j)$, which proves the result for k = 0. Now, we assume the result is true whenever $\rho(\mathcal{A}_r)$ contains at most k interactive events. If $\rho(\mathcal{A}_{r-})$ contains exactly k+1 interactive events, we denote by \mathcal{A}_{v}^{2} and \mathcal{A}_{v}^{3} , for v=ror $v = r^{-}$, the sub-ASGs arising at the first interactive event in $\rho(\mathcal{A}_v)$ from the checking and incoming line, respectively. Moreover, we denote by \mathcal{A}_v^1 the generalised ASG obtained by removing \mathcal{A}_v^2 and \mathcal{A}_v^3



FIGURE 18. Stratified ASG process. The dotted leaf is the leaf affected by the operation associated with the subsequent transition arrow. Here, the labels in the leaves indicate their respective weight.

from $\rho(\mathcal{A}_v)$. Let us assume that the line affected by the event is in \mathcal{A}_{r-}^2 (the other cases follow in a similar way). If $\rho(\mathcal{A}_r^2) = \emptyset$, then $\rho(\mathcal{A}_r) = \rho(\mathcal{A}_r^1)$. In particular, $S(\mathcal{A}_r) = S(\mathcal{A}_r^1) = S(\mathcal{A}_{r-}^1)$. In addition, by the induction hypothesis $S(\mathcal{A}_{r-}^2)_{\times}^{\ell} = S(\mathcal{A}_r^2) = (0)$, and hence $S(\mathcal{A}_{r-})_{\times}^{\ell} = S(\mathcal{A}_{r-}^1) = S(\mathcal{A}_r)$. It remains to prove the result in the case where $\rho(\mathcal{A}_r^2) \neq \emptyset$. In this case, $S(\mathcal{A}_v)$, for v = r or v = r-, is the weighted ternary tree obtained by joining from left to right $S(\mathcal{A}_v^1)$, $S(\mathcal{A}_v^2)$ and $S(\mathcal{A}_v^3)$ to a new root κ . By construction $S(\mathcal{A}_r^i) = S(\mathcal{A}_{r-}^i)$ for $i \in \{1,3\}$, and by the induction hypothesis, $S(\mathcal{A}_r^2) = S(\mathcal{A}_{r-})_{\times}^{\ell}$.

Definition 5.16 (Stratified ASG process). The stratified ASG process $\mathscr{T} = (\mathscr{T}(r))_{r \ge 0}$ is the continuoustime Markov chain with values in Υ_{\star} and, for any $\mathcal{T} = (\tau, m_{\tau}) \in \Upsilon$ and $\ell \in L_{\tau}$, transition rates,

$$q_{\mathscr{T}}(\mathcal{T},\mathcal{T}^{\ell}_{\mathsf{Y}}) := sm_{\tau}(\ell), \qquad q_{\mathscr{T}}(\mathcal{T},\mathcal{T}^{\ell}_{\psi}) := \gamma m_{\tau}(\ell), \qquad q_{\mathscr{T}}(\mathcal{T},\mathcal{T}^{\ell}_{\mathsf{X}}) := u\nu_{1}m_{\tau}(\ell), \qquad q_{\mathscr{T}}(\mathcal{T},\mathcal{T}^{\ell}_{\mathsf{o}}) := u\nu_{0}m_{\tau}(\ell)$$

The states 0 and Δ are absorbing.

The infinitesimal generator of \mathscr{T} is then given by

$$\mathcal{G}_{\mathscr{T}}f(\mathcal{T}) = \mathcal{G}_{\Upsilon}f(\mathcal{T}) + \mathcal{G}_{\Psi}f(\mathcal{T}) + \mathcal{G}_{\times}f(\mathcal{T}) + \mathcal{G}_{\circ}f(\mathcal{T}),$$
(5.5)

where for $\mathcal{T} = (\tau, m_{\tau})$

$$\mathcal{G}_{\Upsilon}f(\mathcal{T}) := \sum_{\ell \in L_{\tau}} m_{\tau}(\ell) \big[f(\mathcal{T}_{\Upsilon}^{\ell}) - f(\mathcal{T}) \big], \quad \mathcal{G}_{\Psi}f(\mathcal{T}) := \sum_{\ell \in L_{\tau}} m_{\tau}(\ell) \big[f(\mathcal{T}_{\Psi}^{\ell}) - f(\mathcal{T}) \big], \\
\mathcal{G}_{\times}f(\mathcal{T}) := \sum_{\ell \in L_{\tau}} m_{\tau}(\ell) \big[f(\mathcal{T}_{\times}^{\ell}) - f(\mathcal{T}) \big], \quad \mathcal{G}_{\circ}f(\mathcal{T}) := \sum_{\ell \in L_{\tau}} m_{\tau}(\ell) \big[f(\mathcal{T}_{\circ}^{\ell}) - f(\mathcal{T}) \big].$$
(5.6)

The following result implies that the stratified ASG process is, in distribution, equal to the stratified ASG associated with a realisation of an ASG.

Theorem 5.17. If $S(\mathcal{A}_0) = \mathscr{T}(0)$, then we have

$$(S(\mathcal{A}_r))_{r \ge 0} \stackrel{(d)}{=} (\mathscr{T}(r))_{r \ge 0}.$$

Proof. Note that by construction $S(\mathcal{A}_r)$ is only affected by the events happening to the lines in $\rho(\mathcal{A}_r)$ at time r. Since the number of lines in $\rho(\mathcal{A}_r)$ that are associated with a given leaf $\ell \in S(\mathcal{A}_r) =: (\tau_r, m_r)$ is $m_r(\ell)$, the result follows as a direct application of Lemma 5.15.

6. Type distribution via stratified ASG

In this section we aim to connect the solution of the deterministic mutation-selection equation (2.1) with the stratified ASG, both over time and at stationarity. The formal relation will be given as a duality with respect to the function \mathcal{H} of Definition 5.12. In a first step, we study the effect of the generator of \mathscr{T} on \mathcal{H} for a fixed initial frequency of unfit types $y_0 \in [0, 1]$.

Lemma 6.1. For every $\mathcal{T} \in \Upsilon_{\star}$, we have $\mathcal{H}(\mathcal{T}, \cdot) \in \mathcal{C}^1([0, 1], \mathbb{R})$. Moreover, for any $y_0 \in [0, 1]$,

$$\mathcal{G}_{\Upsilon}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = -sy_0(1 - y_0)\frac{\partial\mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0), \quad \mathcal{G}_{\Psi}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = -\gamma y_0(1 - y_0)^2\frac{\partial\mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0), \quad \mathcal{G}_{\chi}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = y_0u\nu_0\frac{\partial\mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0). \quad (6.1)$$

Proof. See Appendix A.

The next result establishes the aforementioned duality between the solution of the mutation-selection equation and the stratified ASG.

Theorem 6.2. The stratified ASG $(\mathscr{T}(t))_{t\geq 0}$ and the solution $(y(t; y_0))_{t\geq 0}$ of the IVP (2.1) satisfy the duality relation

$$\mathcal{H}(\mathcal{T}, y(t; y_0)) = E_{\mathcal{T}}[\mathcal{H}(\mathscr{T}(t), y_0)] \quad for \quad y_0 \in [0, 1], \ \mathcal{T} \in \Upsilon_{\star}.$$
(6.2)

In particular, for t > 0 and $y_0 \in [0, 1]$,

$$y(t; y_0) = E_{\widehat{(1)}}[\mathcal{H}(\mathscr{T}(t), y_0)].$$
(6.3)

Remark 6.3. If $s = \nu_0 = 0$ and u = 1, our theorem resembles [25, Prop. I.2.1.4]. But, as mentioned in the beginning of Sect. 5, the two processes dual to the ODE are conceptually different.

Proof of Theorem 6.2. We consider $(y(t; y_0))_{t \ge 0}$ as a (deterministic) Markov process on [0, 1] with generator given by

$$\mathcal{G}_F g(\tilde{y}) = F(\tilde{y}) \frac{\partial g}{\partial y}(\tilde{y}) \tag{6.4}$$

for $g \in \mathcal{C}^1([0,1],\mathbb{R})$. Using Lemma 6.1, we deduce that

$$\mathcal{G}_{\mathscr{T}}\mathcal{H}(\cdot,\tilde{y})(\mathcal{T}) = \mathcal{G}_F\mathcal{H}(\mathcal{T},\cdot)(\tilde{y}) \text{ for } \mathcal{T} \in \Upsilon_{\star} \text{ and } \tilde{y} \in [0,1].$$

Since \mathcal{H} is continuous, the result follows from Liggett [24, Thm. 3.42] (or Jansen and Kurt [19, Prop. 1.2]).

Eventually, we want to recover the asymptotic behaviour of the forward process in terms of the backward process by taking $t \to \infty$ in (6.3). Note that in the case $\gamma = 0$, the stratified ASG is equivalent to a birth-death process with killing (which occurs at rate $u\nu_0$). Since birth-death processes either absorb or grow to ∞ (see Karlin and McGregor [20]), the same holds true for the stratified ASG in this parameter regime; see also Baake et al. [6, Lem. 5]. For the general case, we denote the time of absorption in 0and Δ by

$$T_{(0)} := \inf \left\{ r > 0 : \mathscr{T}(r) = \overset{(0)}{=} \right\} \quad \text{and} \quad T_{\Delta} := \inf \{ r > 0 : \mathscr{T}(r) = \Delta \},$$

respectively. Denote by

$$T_{\rm abs} := \min\{T_{(0)}, T_{\Delta}\}.$$

The next result generalises the previous idea to the case $\gamma > 0$.

Proposition 6.4. On $\{T_{abs} = \infty\}$, we have that $\lim_{r\to\infty} M(\mathscr{T}(r)) = \infty$.

Proof. If $\gamma = 0$, $M(\mathscr{T}(r)) \to \infty$ is only possible if $\nu_0 = 0$. In this case $(\mathscr{T}(r))_{r \ge 0}$ is a classical birth-death process and the result follows by standard theory; see [6, Lem. 5 - (iii)] for details. Hence, assume $\gamma > 0$. By Theorem 5.17, we can directly work on the basis of a random realisation of an ASG \mathcal{A}_{∞} in $[0, \infty)$. Denote by $\bar{a} := P(T_{abs} = \infty \mid S(\mathcal{A}_0) = (1))$. For any r > 0, we will construct on $\{T_{abs} = \infty\}$ a set $\hat{\mathcal{A}}_r \subseteq \rho(\mathcal{A}_r)$ with the following properties. All the lines in $\hat{\mathcal{A}}_r$ end at time r and the restriction of $\hat{\mathcal{A}}_{r'}$ to [0, r] is $\hat{\mathcal{A}}_r$ for any $r \leq r'$. Informally, this means that $\hat{\mathcal{A}}_r$ consists of paths in $\rho(\mathcal{A}_r)$ that persist indefinitely as $r \to \infty$. Set $\hat{\mathcal{A}}_0 = \mathcal{A}_0$. If at time r there is a selective event in a line that is in $\hat{\mathcal{A}}_{r-}$, we continue the paths that are not on the line of the selective event until time r. We extend the path on the line with the selective event by the lines that persist indefinitely arising from the branching event. On $\{T_{abs} = \infty\}$, there will be at least one such line. If at time r there is an interactive event on a line that is in $\hat{\mathcal{A}}_r$. An interactive event on each line in \mathcal{A}_r occurs at rate γ . With probability $\bar{a}^2(1 - d_1)$ the incoming and the checking line both persist indefinitely. In particular, a lower bound for the rate at which $\hat{\mathcal{A}}_r$ increases by one is

$$\gamma \frac{(1-d_1)\bar{a}^2}{1-(1-\bar{a})^3}.$$

Clearly, $|\hat{\mathcal{A}}_r| \to \infty$ as $r \to \infty$. Since we are working on $\{T_{abs} = \infty\}$, we have that $|\hat{\mathcal{A}}_r| \leq M(S(\mathcal{A}_r))$ and the result follows.

We now deduce the main properties of the process $(H(\mathscr{T}(r), y_0))_{r \ge 0}$.

Theorem 6.5. Let $T_1 < T_2 < T_3 < \cdots < T_{n+1}$ be the successive jump times of \mathscr{T} . For $y_0 \in [0, 1]$,

$$E[\mathcal{H}(\mathscr{T}(T_{n+1}), y_0) \mid \mathscr{T}(T_n)] = \mathcal{H}(\mathscr{T}(T_n), y_0) + \frac{F(y_0)}{(s+\gamma+u)M(\mathscr{T}(T_n))} \frac{\mathcal{H}(\mathscr{T}(T_n), y)}{\partial y}(y_0), \tag{6.5}$$

with $F(\cdot)$ from (2.1) and $M(\mathscr{T}(T_n))$ from (5.4). Furthermore,

- If $F(y_0) > 0$, then $(\mathcal{H}(\mathcal{T}(r), y_0))_{r \ge 0}$ is a bounded submartingale.
- If $F(y_0) = 0$, then $(\mathcal{H}(\mathcal{T}(r), y_0))_{r \ge 0}$ is a bounded martingale.
- If $F(y_0) < 0$, then $(\mathcal{H}(\mathscr{T}(r), y_0))_{r \ge 0}$ is a bounded supermartingale.

In particular, $\mathcal{H}_{\infty}(y_0) := \lim_{r \to \infty} \mathcal{H}(\mathscr{T}(r), y_0) \in [0, 1]$ exists almost surely.

Proof. We first prove (6.5). Fix $n \in \mathbb{N}$ and $\mathcal{T} = (\tau, m_{\tau})$. Note that

$$\begin{split} E[\mathcal{H}(\mathscr{T}(T_{n+1}), y_0) - \mathcal{H}(\mathscr{T}(T_n), y_0) \mid \mathscr{T}(T_n) = \mathcal{T}] \\ &= E\left[\sum_{\ell \in L_{\tau}} \sum_{\star \in \{\Upsilon, \Psi, \times, \circ\}} \mathbf{1}_{\{\mathscr{T}(T_{n+1}) = \mathcal{T}^{\ell}_{\star}\}} \big(\mathcal{H}(\mathscr{T}(T_{n+1}), y_0) - \mathcal{H}(\mathscr{T}(T_n), y_0)\big) \mid \mathscr{T}(T_n) = \mathcal{T}\right] \\ &= \sum_{\ell \in L_{\tau}} \sum_{\star \in \{\Upsilon, \Psi, \times, \circ\}} \big(\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0)\big) P\big(\mathscr{T}(T_{n+1}) = \mathcal{T}^{\ell}_{\star} \mid \mathscr{T}(T_n) = \mathcal{T}\big). \end{split}$$

Then,

$$(s+\gamma+u)M(\mathcal{T})P\big(\mathscr{T}(T_{n+1}) = \mathcal{T}^{\ell}_{\star} \mid \mathscr{T}(T_n) = \mathcal{T}\big) = \begin{cases} m_{\mathcal{T}}(\ell)s, & \text{if } \star = \Upsilon, \\ m_{\mathcal{T}}(\ell)\gamma, & \text{if } \star = \Psi, \\ m_{\mathcal{T}}(\ell)u\nu_1, & \text{if } \star = \times, \\ m_{\mathcal{T}}(\ell)u\nu_0, & \text{if } \star = \circ. \end{cases}$$

In particular,

$$\sum_{\ell \in L_{\tau}} \sum_{\star \in \{\Upsilon, \Psi, \times, \circ\}} \left(\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0) \right) P\left(\mathscr{T}(T_{n+1}) = \mathcal{T}^{\ell}_{\star} \mid \mathscr{T}(T_n) = \mathcal{T}\right) = \frac{\mathcal{G}_{\mathscr{T}} \mathcal{H}(\cdot, y_0)(\mathcal{T})}{(s + \gamma + u)M(\mathcal{T})}.$$

Recall that we consider $y(t; y_0)$ as the (deterministic) Markov process with generator \mathcal{G}_F (see (6.4)). By Lemma 6.1,

$$\frac{\mathcal{G}_{\mathscr{T}}\mathcal{H}(\cdot,y_0)(\mathcal{T})}{(s+\gamma+u)M(\mathcal{T})} = \frac{\mathcal{G}_F\mathcal{H}(\mathcal{T},\cdot)(y_0)}{(s+\gamma+u)M(\mathcal{T})} = \frac{F(y_0)}{(s+\gamma+u)M(\mathcal{T})}\frac{\partial\mathcal{H}(\mathcal{T},y)}{\partial y}(y_0)$$

such that the first result follows. We proceed to prove the second statement. For r < t we denote the number of jumps of $\mathcal{H}(\mathscr{T}, y_0)$ in the time interval [r, t) by $N_{r,t}$. If $N_{r,t} = k$, let T_i^k be the time of the *i*-th jump $(1 \leq i \leq k)$ with $T_0^k = r$. Then,

$$\begin{split} E[\mathcal{H}(\mathscr{T}(t), y_0) &- \mathcal{H}(\mathscr{T}(r), y_0) \mid \mathcal{H}(\mathscr{T}(r), y_0)] \\ &= \sum_{k=0}^{\infty} E\Big[\mathbf{1}_{\{N_{r,t}=k\}} \Big(\mathcal{H}\big(\mathscr{T}(t), y_0\big) - \mathcal{H}\big(\mathscr{T}(r), y_0\big)\Big) \mid \mathcal{H}\big(\mathscr{T}(r), y_0\big)\Big] \\ &= \sum_{k=0}^{\infty} \sum_{l=1}^{k} E\Big[\mathbf{1}_{\{N_{r,t}=k\}} \Big(\mathcal{H}\big(\mathscr{T}(T_l^k), y_0\big) - \mathcal{H}\big(\mathscr{T}(T_{l-1}^k), y_0\big)\Big) \mid \mathcal{H}\big(\mathscr{T}(r), y_0\big)\Big] \\ &= \sum_{k=0}^{\infty} \sum_{l=1}^{k} E\Big[\mathbf{1}_{\{N_{r,t}=k\}} E\Big[\mathcal{H}(\mathscr{T}(T_l^k), y_0) - \mathcal{H}\big(\mathscr{T}(T_{l-1}^k), y_0\big) \mid \mathscr{T}(T_{l-1}^k)\big] \mid \mathcal{H}(\mathscr{T}(r), y_0)\Big] \end{split}$$

where in the last step we used the tower property for conditional expectations and the fact that

$$\sigma(\mathcal{H}(\mathscr{T}(r), y_0)) \subseteq \sigma(\mathscr{T}(T_{l-1}^k)),$$

where $\sigma(X)$ denotes the σ -algebra generated by X. But,

$$E[\mathcal{H}(\mathscr{T}(T_l^k), y_0) - \mathcal{H}(\mathscr{T}(T_{l-1}^k), y_0) \mid \mathscr{T}(T_{l-1}^k)] = \frac{F(y_0)}{(s+\gamma+u)M\big(\mathscr{T}(T_{l-1}^k)\big)} \frac{\partial \mathcal{H}(\mathscr{T}(T_{l-1}^k), y)}{\partial y}(y_0),$$

where $(s + \gamma + u)M(\mathscr{T}(T_{l-1}^k))$ and $(\partial \mathcal{H}(\mathscr{T}(T_{l-1}), y)/\partial y)(y_0)$ are non-negative and $F(y_0)$ is either greater, equal, or less than 0. The second statement follows. In particular, $(\mathcal{H}(\mathscr{T}(r), y_0))_{r \ge 0}$ is a non-negative bounded sub/super-martingale. Hence, an straightforward application of the Doob's martingale convergence theorem yields the last result.

Note that $\mathcal{H}_{\infty}(y_0) = 1$ on $\{T_{(0)} < \infty\}$ for any $y_0 \in [0,1]$. Similarly, $\mathcal{H}_{\infty}(y_0) = 0$ on $\{T_{\Delta} < \infty\}$ for any $y_0 \in [0,1]$. In particular, conditionally on $\{T_{abs} < \infty\}$, $\mathcal{H}_{\infty}(y_0)$ is a Bernoulli random variable. If \mathscr{T} is not absorbed, the analysis of $\mathcal{H}_{\infty}(y_0)$ is more involved. But, unless y_0 is an unstable equilibrium of (2.1), the result is the same. This is the content of next proposition.

Proposition 6.6. If y_0 is not an unstable equilibrium of (2.1), then $\mathcal{H}_{\infty}(y_0)$ is a Bernoulli random variable with parameter $y_{\infty}(y_0)$.

Remark 6.7. Let us make a link to [26] and endogeny (see [1, 27] for the notion of endogeny). It follows from [26, Prop. 15] together with [27, Thm. 5] (alternatively, [26, Prop. 16]) that if y_0 is an equilibrium of (2.1), then $\mathcal{H}_{\infty}(y_0)$ is Bernoulli if and only if the recursive tree process corresponding to y_0 is endogenous. In particular, Proposition 6.6 implies that in our setup, the recursive tree processes corresponding to stable equilibria are always endogenous. An alternative way to recover Proposition 6.6 is via [26, Prop. 19, see also Sect. 2.1] (alternatively, [1, Lem. 15]).

For $s = \nu_0 = 0$ and u = 1, Proposition 6.6 can be also recovered from [26, Theorem 17]. Moreover, if y_0 is an unstable equilibrium, Mach et al. [26, Lemma 18] determine the first and second moments of $\mathcal{H}_{\infty}(y_0)$. This permits to infer that $\mathcal{H}_{\infty}(y_0)$ is not Bernoulli. Furthermore, they complement the result by numerical evaluation of the distribution function [26, Figure 2].

Proof of Proposition 6.6. Fix $y_0 \in [0, 1]$ such that it is not an unstable equilibrium of (2.1). In particular, $y_{\infty}(y_0)$ is then attracting (from at least on side) and, therefore, $F'(y_{\infty}(y_0)) \leq 0$. Consider a realisation of $(\mathscr{T}(r))_{r \geq 0}$ of the stratified ASG process. Denote by $T_{\Upsilon}, T_{\Psi}, T_{\circ}$, and T_{\times} the time of the first selective, interactive, beneficial mutation, and deleterious mutation event, respectively. Let $T = \min\{T_{\Upsilon}, T_{\Psi}, T_{\circ}, T_{\times}\}$. For sufficiently large r > 0,

$$\begin{aligned} \mathcal{H}(\mathscr{T}(r), y_0) &= \mathbf{1}_{\{T=T_{\vee}\}} + \mathbf{1}_{\{T=T_{\vee}\}} \mathcal{H}(\mathscr{T}^1(r-T), y_0) \mathcal{H}(\mathscr{T}^2(r-T), y_0) + \mathbf{1}_{\{T=T_{\Psi}\}} \mathcal{H}(\mathscr{T}^3(r-T), y_0) \\ &\times \left[\mathcal{H}(\mathscr{T}^4(r-T), y_0) + \mathcal{H}(\mathscr{T}^5(r-T), y_0) - \mathcal{H}(\mathscr{T}^4(r-T), y_0) \mathcal{H}(\mathscr{T}^5(r-T), y_0) \right], \end{aligned}$$

where $\mathscr{T}^1, \mathscr{T}^2, \mathscr{T}^3, \mathscr{T}^4$, and \mathscr{T}^5 are independent stratified ASGs all of which are started with a single line. Taking the limit $r \to \infty$ yields,

$$\mathcal{H}_{\infty}(y_0) = \mathbf{1}_{\{T=T_{\times}\}} + \mathbf{1}_{\{T=T_{\vee}\}} \mathcal{H}^1_{\infty}(y_0) \mathcal{H}^2_{\infty}(y_0) + \mathbf{1}_{\{T=T_{\psi}\}} \mathcal{H}^3_{\infty}(y_0) [\mathcal{H}^4_{\infty}(y_0) + \mathcal{H}^5_{\infty}(y_0) - \mathcal{H}^4_{\infty}(y_0) \mathcal{H}^5_{\infty}(y_0)].$$

In particular, for every $G \in \mathcal{C}([0, 1], \mathbb{R})$, we have

$$E[G(\mathcal{H}_{\infty}(y_{0}))] = P(T = T_{\times})E[G(1)] + P(T = T_{\circ})E[G(0)] + P(T = T_{\gamma})E\Big[G\big(\mathcal{H}_{\infty}^{1}(y_{0})\mathcal{H}_{\infty}^{2}(y_{0})\big)\Big] + P(T = T_{\psi})E\Big[G\big(\mathcal{H}_{\infty}^{3}(y_{0})\big[\mathcal{H}_{\infty}^{4}(y_{0}) + \mathcal{H}_{\infty}^{5}(y_{0}) - \mathcal{H}_{\infty}^{4}(y_{0})\mathcal{H}_{\infty}^{5}(y_{0})\big]\big)\Big].$$
(6.6)

Note that X is a Bernoulli random variable if and only if E[X(1-X)] = 0. Choosing G(x) = x(1-x) in (6.6) and using independence, we obtain

$$E(y_0) - V(y_0) = \frac{s}{u+s+\gamma} \left(E(y_0) - V(y_0) \right) \left(E(y_0) + V(y_0) \right) + \frac{\gamma}{u+s+\gamma} \left(E(y_0) - V(y_0) \right) \left(V(y_0)^2 + V(y_0)(2 - 3E(y_0)) + E(y_0)(2 - E(y_0)) \right),$$
(6.7)

where $E(y_0) := E[\mathcal{H}_{\infty}(y_0)]$ and $V(y_0) := E[\mathcal{H}_{\infty}(y_0)^2]$. By the duality, $E(y_0) = y_{\infty}(y_0)$ and hence $E(y_0)$ is an equilibrium of (2.1) for which, by assumption, we have $F'(E(y_0)) \leq 0$. Furthermore, $\mathcal{H}_{\infty}(y_0) \in [0, 1]$ and hence

$$0 \leqslant V(y_0) = E\left[\mathcal{H}_{\infty}(y_0)^2\right] \leqslant E\left[\mathcal{H}_{\infty}(y_0)\right] = E(y_0)$$

Equation (6.7) is equivalent to

$$(E(y_0) - x)p(E(y_0), x) = 0,$$

where

$$p(E(y_0), x) = s(E(y_0) + x) + \gamma(x^2 + x(2 - 3E(y_0)) + E(y_0)(2 - E(y_0))) - (u + s + \gamma).$$

Note that

$$p(E(y_0), 0) = s(E(y_0) - 1) + \gamma(E(y_0)(2 - E(y_0)) - 1) - u \leq -u$$

and $p(E(y_0), E(y_0)) = F'(E(y_0))$. In particular, since $p(E(y_0), x)$ is a quadratic polynomial with positive quadratic term in $x, p(E(y_0), x) \neq 0$ for all $x \in [0, E(y_0))$. Altogether, this implies $V(y_0) = E(y_0)$. \Box

For $n \in \mathbb{N} \cup \{0\}$, we denote the probability of absorption in 0 of the stratified ASG started in n by

$$w_n := P(T_{(0)} < \infty \mid \mathscr{T}(0) = \overset{(n)}{=}),$$

and $w_{\Delta} := 0$. Similarly, we denote the probability of *not* getting absorbed in Δ of the stratified ASG process started in (n) by

$$d_n := P(T_\Delta = \infty \mid \mathscr{T}(0) = \overset{(n)}{=}),$$

and $d_{\Delta} := 0$. By definition, we have $w_n \leq d_n$, for all n. Moreover, we define for $y_0 \in [0, 1]$,

$$p(y_0) := E\left[\mathbf{1}_{\{T_{(0)} = \infty\}} \mathcal{H}_{\infty}(y_0) \mid \mathscr{T}(0) = \textcircled{1}\right].$$

Note that in the case in which y_0 is not an unstable equilibrium, it follows by Proposition 6.6 that

$$p(y_0) = P(\mathcal{H}_{\infty}(y_0) = 1, T_{\textcircled{0}} = \infty \mid \mathscr{T}(0) = \textcircled{1}).$$

If the stratified ASG process absorbs in (0), then the descendant is of type 1. On the other hand, if the stratified ASG process absorbs in Δ , then the descendant is of type 0. In both cases this is independent of the sampling probability y_0 at the leaves. There are parameter regions where $w_1 = d_1$, so these are the only possibilities. If the stratified ASG grows to ∞ , which occurs if $d_1 > w_1$, the type depends on y_0 . We will examine this in detail in what follows. Recall from Sect. 2 that we denote the smallest and largest equilibrium of (2.1) in [0, 1] by \hat{y}_{∞} and \check{y}_{∞} , respectively.

Theorem 6.8. For any $y_0 \in [0, 1]$, we have

$$y_{\infty}(y_0) = w_1 + p(y_0). \tag{6.8}$$

In particular, $\hat{y}_{\infty} = w_1$ and $\check{y}_{\infty} = d_1$. Furthermore, the two following statements are equivalent:

- (i) $P(T_{\text{abs}} < \infty \mid \mathscr{T}(0) = (1)) = 1$,
- (ii) $\hat{y}_{\infty} = w_1 = d_1 = \check{y}_{\infty}$ is the unique equilibrium in [0, 1].

In both cases, w_1 is stable.

Remark 6.9. Theorem 6.8 in combination with the facts collected at the beginning of Sect. 2 implies that w_1 is never unstable. Furthermore, if $\nu_0 > 0$, then d_1 is not unstable.

Proof of Theorem 6.8. We decompose $\mathcal{H}(\mathscr{T}(t), y)$ according to $\{T_{\textcircled{0}} < \infty\}$ and $\{T_{\textcircled{0}} = \infty\}$. More precisely, starting from the duality,

$$y(t;y_0) = E_{\widehat{\mathbb{I}}}[\mathcal{H}(\mathscr{T}(t),y_0)\mathbf{1}_{\{T_{\widehat{\mathbb{I}}}<\infty\}}] + E_{\widehat{\mathbb{I}}}[\mathcal{H}(\mathscr{T}(t),y_0)\mathbf{1}_{\{T_{\widehat{\mathbb{I}}}=\infty\}}].$$
(6.9)

Since $\mathcal{H}(\underline{0}, y_0) = 1$, the first term in (6.9) converges to w_1 as $t \to \infty$. By Theorem 6.5, the second term of (6.9) converges to $p(y_0)$ as $t \to \infty$, thus proving (6.8). Since $\mathcal{H}_{\infty}(0) = 0$ on $\{T_{\underline{0}} = \infty\}$, $\mathcal{H}_{\infty}(1) = 1$ on $\{T_{\Delta} = \infty\}$, and $\mathcal{H}_{\infty}(1) = 0$ on $\{T_{\Delta} < \infty\}$, then

$$p(0) = 0$$
 and $p(1) = P(T_{(0)} = \infty, T_{\Delta} = \infty) = d_1 - w_1$

Since p is increasing, we deduce that $\hat{y}_{\infty} = w_1$ and $\check{y}_{\infty} = d_1$. Note that under (i), $p(y_0) = 0$ for all $y_0 \in [0, 1]$, and hence the stability of w_1 follows in this case by taking the limit when $t \to \infty$ in (6.9). Finally, the equivalence between (i) and (ii) follows using the identity

$$P(T_{\textcircled{0}} = \infty, T_{\Delta} = \infty) = d_1 - w_1.$$

We denote the domain of attraction of an equilibrium y_{∞} by

$$\operatorname{Attr}(y_{\infty}) := \left\{ y_0 \in [0,1] : \lim_{t \to \infty} y(t;y_0) = y_{\infty} \right\}$$

and refine the statement of Proposition 6.6.

Corollary 6.10. If $y_0 \in Attr(w_1)$, then a.s.

$$\mathcal{H}_{\infty}(y_0) = \begin{cases} 0, & \text{if } T_{\textcircled{0}} = \infty, \\ 1, & \text{if } T_{\textcircled{0}} < \infty. \end{cases}$$

If $y_0 \in Attr(d_1)$, then a.s.

$$\mathcal{H}_{\infty}(y_0) = \begin{cases} 0, & \text{if } T_{\Delta} < \infty, \\ 1, & \text{if } T_{\Delta} = \infty. \end{cases}$$

Remark 6.11. For $y_0 \in \{w_1, d_1\}$, Corollary 6.10 makes the endogeny of the underlying recursive tree process corresponding to y_0 explicit.

Remark 6.12. Note that $\operatorname{Attr}(w_1) = \operatorname{Attr}(d_1)$ if and only if $w_1 = d_1$. By Theorem 6.8, $w_1 = d_1$ if and only if $P(T_{(0)} = \infty, T_{\Delta} = \infty) = 0$.

Proof of Corollary 6.10. If $y_0 \in Attr(w_1)$, then by definition $w_1 = y_{\infty}(y_0)$ and together with Theorem 6.8,

$$w_1 = y_{\infty}(y_0) = w_1 + p(y_0),$$

which implies that $p(y_0) = 0$ and the first statement follows. Now assume that $P(\mathcal{H}_{\infty}(y_0) = 1 | T_{\Delta} = \infty) < 1$. In this case also $E[\mathcal{H}_{\infty}(y_0) | T_{\Delta} = \infty] < 1$. On the other hand, if $y_0 \in \text{Attr}(d_1)$, then by Theorem 6.8

 $d_1 = y_{\infty}(y_0) = w_1 + p(y_0) = E[\mathbf{1}_{\{T_{\Delta} = \infty\}} \mathcal{H}_{\infty}(y_0)] = d_1 E[\mathcal{H}_{\infty}(y_0) \mid T_{\Delta} = \infty] < d_1,$

which is a contradiction.

Proposition 6.13. If $P(T_{abs} = \infty \mid \mathscr{T}(0) = \textcircled{1}) > 0$, we have that

$$y_c := \inf \left\{ y_0 \in [0,1] : P(\mathcal{H}_{\infty}(y_0) = 1 \mid T_{abs} = \infty, \ \mathscr{T}(0) = \textcircled{1}) = 1 \right\}$$
$$= \sup \left\{ y_0 \in [0,1] : P(\mathcal{H}_{\infty}(y_0) = 0 \mid T_{abs} = \infty, \ \mathscr{T}(0) = \textcircled{1}) = 1 \right\}.$$

Furthermore, $y_c \in [w_1, d_1]$.

Proof. Define $y^{(1)} := \inf\{y_0 \in [0,1] : P(\mathcal{H}_{\infty}(y_0) = 1 \mid T_{abs} = \infty, \mathscr{T}(0) = (1) = 1\}$ and $y^{(0)} := \sup\{y_0 \in [0,1] : P(\mathcal{H}_{\infty}(y_0) = 0 \mid T_{abs} = \infty, \mathscr{T}(0) = (1) = 1\}$. By the properties of sup and inf, $y^{(0)} \leq y^{(1)}$. By Theorem 6.8, $w_1 \leq d_1$ are equilibria and $y_{\infty}(y^{(0)}), y_{\infty}(y^{(1)}) \in [w_1, d_1]$. By definition of sup and inf and $p(y_0)$, we have that for all $\varepsilon > 0$ the inequalities $w_1 < y_{\infty}(y^{(0)} + \varepsilon)$ and $d_1 > y_{\infty}(y^{(1)} - \varepsilon)$ hold. Assume $y^{(0)} < y^{(1)}$. In particular, for $y_0 \in (y^{(0)}, y^{(1)})$, we have that $w_1 < y_{\infty}(y_0) < d_1$. Since (2.1) has at most three equilibria, for all $y_0 \in (y^{(0)}, y^{(1)})$ we have $y_{\infty}(y_0) \equiv c$ for some c in (w_1, d_1) . But then, c, which is enclosed by w_1 and d_1 , is stable. This contradicts the findings from Remark 2.11. By Corollary 6.10, it follows that $y_c \in [w_1, d_1]$.

Corollary 6.14. (1) If $P(T_{abs} = \infty | \mathscr{T}(0) = \textcircled{1}) = 0$, then $w_1 = d_1$ is the unique equilibrium of (2.1) in [0,1] and it is stable.

(2) If $P(T_{abs} = \infty \mid \mathscr{T}(0) = (1) > 0$ and $y_c = d_1$, then w_1 and d_1 are the only equilibria of (2.1) [0,1] with $Attr(w_1) = [0, d_1)$ and $Attr(d_1) = [d_1, 1]$.

- (3) If $P(T_{abs} = \infty \mid \mathscr{T}(0) = \textcircled{1}) > 0$ and $y_c = w_1$, then w_1 and d_1 are the only equilibria of (2.1) in [0, 1] with $Attr(w_1) = [0, w_1]$ and $Attr(d_1) = (w_1, 1]$.
- (4) If $P(T_{abs} = \infty \mid \mathscr{T}(0) = (1)) > 0$ and $w_1 < y_c < d_1$, then $w_1 < y_{\infty}(y_c) < d_1$ are the only equilibria of (2.1) [0,1] with w_1 and d_1 being stable and $y_{\infty}(y_c)$ being unstable.

Proof. The first claim is already part of Theorem 6.8. The second and third claims follow from Proposition 6.13 and Theorem 6.8. The last claim follows by Proposition 6.13, Theorem 6.8, and Remark 2.11. \Box

Let us discuss how Corollary 6.14 relates to the forward picture. In (1) the stratified ASG absorbs almost surely such that the type of the descendant is independent of the sampling probability y_0 , which results in a unique equilibrium in [0, 1]. Its (global) stability reflects the independence of the sampling step. In (2) to (4), the stratified ASG may also grow to ∞ in which case the sampling probability y_0 becomes relevant. In (2) and (3), $y_c \in \{w_1, d_1\}$ such that $[0, 1] = \operatorname{Attr}(w_1) \dot{\cup} \operatorname{Attr}(d_1)$, whereas in (4), $y_c \in (w_1, d_1)$ such that $[0, 1] = \operatorname{Attr}(w_1) \dot{\cup} \{y_c\} \dot{\cup} \operatorname{Attr}(d_1)$. Corollary 6.10 describes the type of the descendant when the leaves in an infinite stratified ASG are sampled according to $y_0 \in \operatorname{Attr}(w_1) \cup \operatorname{Attr}(d_1)$: for $y_0 \in \operatorname{Attr}(w_1)$ $(y_0 \in \operatorname{Attr}(d_1))$ the descendant is of type 1 (of type 0) almost surely. For $y_0 = y_c$, the probability of an unfit descendant on non-absorption of the stratified ASG is given by $p(y_c)$. In the remainder of this section, we concentrate on the case $\nu_0 = 0$, where we can make more explicit statements.

Corollary 6.15. If $\nu_0 = 0$, then $w_1 = \min\{\bar{y}_2, 1\}$ and $d_1 = 1$. In particular, $w_1 = d_1$ if and only if we are in one of the following parameter regimes

(1) $\sigma < 0$, (2) $\sigma = 0$, $u = s = \gamma$, (3) $\sigma \ge 0$, $u \ge \hat{u}$, and $s > \gamma$.

Proof. The corollary is a direct consequence of Theorem 6.8 together with Proposition 2.6.

Let us now connect the genealogical backward picture in the case $\nu_0 = 0$ with the bifurcation structure described in Sect. 2.

- (i) By the analysis of the forward picture, if either $u < \hat{u}$ or $(s < \gamma \text{ and } u = \hat{u}), y_{\infty}(y_0) \in [0, 1)$ unless $y_0 = 1$. The genealogical picture in this case is as follows. Either the backward process absorbs in a state in which all lines vanished due to deleterious mutations (probability $w_1 < 1$); or, by Proposition 6.4, the number of lines tends to ∞ and, as a consequence of Corollary 6.10, the ordering of these lines is such that the sum of the sampling probabilities of valid type assignments does not have positive mass.
- (ii) If either $u > \check{u}$ or $(s \ge \gamma \text{ and } u \in [\hat{u}, \check{u}])$, then $y_{\infty}(y_0) = 1$ for all $y_0 \in [0, 1]$. By Theorem 6.8, this corresponds to the backward process absorbing in ⁽¹⁾ almost surely and the sampled individual is unfit regardless of y_0 .
- (iii) If $s < \gamma$ and $u = \check{u}$, both w_1 and 1 are attracting from the left, i.e. $y_{\infty}(y_0) = w_1$ for $y_0 \in [0, w_1]$ and $y_{\infty}(y_0) = 1$ for $y_0 \in (w_1, 1]$. By the same arguments as in case (i), we have the following backward picture. If the process does not absorb, which occurs with probability $w_1 < 1$, the number of lines tends to ∞ . Whether or not the sum of the sampling probabilities of valid type assignments has positive mass depends on the initial type frequency. If $y_0 \leq \bar{y}_2$, the mass is zero and if $y_0 > \bar{y}_2$ the mass is 1.
- (iv) If $s < \gamma$ and $u \in (\hat{u}, \check{u})$, there exist three equilibria in [0,1]. By arguments similar to case (i), the backward picture is as follows. If the process does not absorb, where absorption occurs with probability $w_1 < 1$, the number of lines tends to ∞ . Whether or not the sum of the sampling probabilities of valid type assignments has positive mass depends on the initial type frequency. If $y_0 < \bar{y}_3$, the mass is zero and if $y_0 > \bar{y}_3$ the mass is 1.

In the cases (i), (ii), and (iii), where the outcome depends on y_0 , the question arises whether a more detailed analysis of the stratified ASG can be made that explains the dependence on y_0 in terms of the tree structure. This can be done in the case $u < \check{u}$, where w_1 is the smallest solution of

$$-\gamma y^{2} + (s+\gamma)y - u = 0, \qquad (6.10)$$

i.e. $w_1 = (1 + s/\gamma - \sqrt{\sigma})/2$; see (2.3) and (2.6). Let us rederive this expression in terms of the stratified ASG. To do so, we analyse $1 - w_1$, which is the survival probability of the stratified ASG started in \bigcirc .

Define $\tilde{\gamma} := \gamma(1 - w_1)$ as well as

$$a := 1 - \frac{u}{s}$$
 and $b = \frac{u}{s} \frac{\gamma}{s + \tilde{\gamma} - u}$

Note that, by a straightforward calculation, we can rewrite (6.10) (with $y = w_1$) as a quadratic equation in $1 - w_1$, namely

$$b(1-w_1)^2 - (1-w_1) + a = 0. (6.11)$$

Using the solution formula and the series expansion of the square root at 1 leads to

$$1 - w_1 = \frac{1 - \sqrt{1 - 4ab}}{2b} = \frac{1}{2b} \sum_{n=1}^{\infty} \frac{(2n)!}{(2n - 1)(n!)^2} a^n b^n.$$

A straightforward calculation then leads to the following result for which we will subsequently provide an additional probabilistic proof.

Proposition 6.16. For $u < \hat{u}$, we have

$$1 - w_1 = \sum_{n=0}^{\infty} C_n a^{n+1} b^n, \tag{6.12}$$

where C_n is the nth Catalan number.

Probabilistic proof. Note that the number of lines inside a continuing region (i.e. only the lines that are connected to the initial line of the region by selective arrows) behaves like a simple birth-death process with birth rate s and death rate u. Recall that this process dies out with probability u/s and grows to ∞ with probability 1 - u/s (note that we consider here the parameter regime $u < \hat{u} = s$, so $u/s \in [0, 1)$). Hence, a is the probability that the leftmost leaf in the stratified ASG does not reach weight 0. On the other hand, (6.10) is equivalent to

$$y = \frac{u}{s} - \frac{u}{s} \frac{\gamma(1-y)}{s+\gamma(1-y)}.$$

Using the fact that w_1 is a solution of the above, a straightforward calculation yields the survival probability of the entire tree as

$$1 - w_1 = \frac{s + \tilde{\gamma} - u}{s + \tilde{\gamma}}.\tag{6.13}$$

In what follows, we work on the basis of an ASG in the time interval $[0, \infty)$ that is started with one line. Here, we refer to a region either as the entire ASG or as the ASG arising from the incoming or checking line in a trifurcation. We call a trifurcation in an ASG successful if both the associated checking and incoming lines give rise to ASGs that have non-absorbing stratified ASGs (note that, if one of them absorbs, both lines will be pruned in the long run, see the argument in the proof of Proposition 6.4). We say that a region survives without the help of trifurcations if the leftmost leaf of its associated stratified ASG does not reach weight 0; otherwise we say that the region goes extinct without trifurcations. On the other hand, we say that a region survives due to trifurcations if its stratified ASG does not absorb but its leftmost leaf reaches weight 0. Denote by π the probability that, conditional on the ASG going extinct without the help of trifurcations, the ASG goes extinct. We claim that $\pi = s/(s + \tilde{\gamma})$. Indeed, conditional on the event that the ASG goes extinct without trifurcations, the weight of the leftmost leaf evolves as a birth-death process with birth rate u and death rate s; see Lemma A.2. Hence, a first-step decomposition of π leads to

$$(\gamma(1 - w_1)^2 + s + u)\pi = s + u\pi^2.$$

In the parameter regime we consider here, the solution is unique in [0, 1] and is given by $s/(s + \tilde{\gamma})$, which proves the claim. In particular, the probability that the ASG survives due to trifurcations is

$$\frac{u}{s}(1-\pi) = \frac{u}{s}\frac{\gamma(1-w_1)^2}{s+\tilde{\gamma}-u} = b(1-w_1)^2,$$

where we used (6.13). The probability that the incoming and checking lines of a successful trifurcation both survive without the help of trifurcations is $a^2/(1-w_1)^2$. Hence, a^2b is the probability that the ASG survives due to trifurcations and the incoming and the checking line of the first successful trifurcation



FIGURE 19. Ways of the stratified ASG process to survive (and then grow to infinite size) if $\nu_0 = 0$. The label ∞ in a leaf means that the region survives without the help of trifurcations. For an ASG that survives without the help of trifurcations, there is $C_0 = 1$ binary tree (left). For n = 1 there is $C_1 = 1$ binary tree (middle). For n = 2 there are $C_2 = 2$ binary trees (right). The solid lines correspond to the binary trees.

survive without the help of trifurcations.

We now partition the event of non-absorption of the stratified ASG according to the possible ways the stratified ASG may survive. We do this by associating to every such stratified ASG a binary tree \mathcal{B} . We start with the binary tree with one leaf β . If the ASG survives without the help of trifurcations, we set $\mathcal{B} = \beta$. If not, we add two leaves β_1 and β_2 that are associated with the incoming and checking region in the first successful trifurcation, respectively. If one of these regions survives without the help of trifurcations, the corresponding leaf stops branching. Otherwise, we attach to it two new leaves and continue this procedure in a recursive way. By construction, \mathcal{B} is a binary Galton-Watson tree with offspring distribution $p_2 = a/(1 - w_1)$ and $p_0 = 1 - p_2$. A straightforward calculation, which uses (6.11), shows that $p_0 > p_2$ and hence \mathcal{B} is almost surely finite (on the event of non-absorption). Let N be the random number of bifurcations. In the previous construction a branching corresponds to a successful trifurcation in a region of the reduced ASG that goes extinct without trifurcations and a leaf corresponds to a region that survives without the help of trifurcations; see Fig. 19. By a simple induction argument on the number of bifurcations n in the binary tree, one can show that the probability that the ASG corresponds to a given binary tree with n+1 leaves is $a^{n+1}b^n$. Indeed, we have already proved that for n=0 this probability is a and for n=1 it is a^2b . By construction, computing the probability for a tree with n+1 bifurcations amounts to replacing a leaf by a tree with one bifurcation, which entails replacing a factor a by a factor a^2b . Since there are C_n binary trees with n+1 leaves,

$$P(T_{(0)} = \infty, N = n) = C_n a^{n+1} b^n.$$

Summing over the possible values of N leads to (6.12).

Assume that the binary tree associated with a realisation of the stratified ASG has n leaves. Each leaf corresponds to a region that survives without trifurcations and therefore, the leftmost leaf in the corresponding stratified ASG has infinite weight. Hence, if $y_0 < 1$, the descendant is of type 0 almost surely. If $y_0 = 1$, the descendant is of type 1. We thus also have a purely genealogical proof of the first case in Corollary 6.10.

If $u \ge \hat{u}$, by a straightforward comparison with a simple birth-death process, each leaf in the stratified ASG eventually reaches weight 0 almost surely. However, for $u \in [\hat{u}, \check{u}]$ the stratified ASG can survive by escaping via trifurcations the effects of absorbing leaves. The analysis of the underlying tree structures is more difficult and we leave the details to future work.

7. Ancestral type distribution via stratified ASG

So far we have been concerned with a randomly chosen individual at present and determined its type via the stratified ASG. Let us now change perspective and consider the type of the *ancestor*, at time r before the present, of our current individual. It will turn out that this can also be tackled by means of a construction that builds on the stratified ASG. Indeed the specific structure of our reduced and pruned trees will be essential.



FIGURE 20. A new perspective on the pLD-ASG: from the immune line emerge three independent killed ASGs. They are R_1 (...), R_2 (--), and R_3 (--) at times T_1, T_2 , and T_3 . Here, R_2 has absorbed before backward time t, but R_1 and R_3 have not.

In the Moran model and its diffusion limit, all individuals at present originate from a single individual in the distant past, see also [21, 29]. This individual is called the common ancestor. In the diffusion limit, the ancestral type distribution can be characterised in terms of a solution of a boudary value problem, see [35]. In the deterministic limit, the ancestries are all disjoint, so the notion of a common ancestor does not make sense. In line with Cordero [9] (see also [6]), we call the type of the ancestor living at backward time r of a generic individual from the population at present the ancestral type at backward time r and denote it by J_r . We abbreviate the probability for J_r to be unfit, conditional on the type distribution of the population at backward time r being $(1 - y_0, y_0)$, by $g_r(y_0) := P_{y_0}(J_r = 1)$.

7.1. Ancestral type distribution without interaction. In the absence of interaction, a pruned version of the ASG, which is called the pruned lookdown ASG (pLD-ASG), is a tool to determine the ancestral type distribution (see [23] and [6] for details and [4] for a review). Let us recall this construction in the strong selection-strong mutation limit (without interaction), see Fig. 20. The pLD-ASG starts from a single individual. The lines of the graph correspond to the potential ancestors and are assigned consecutive levels, starting at level 1. If a line is hit by a selective arrow, its level is increased by one and at the same time all lines above it are shifted up one level; thereby making space for the incoming line, which then occupies the former level of the line it hit. If the first event on a line that does not occupy the top level is a deleterious mutation, we can conclude that it will not be ancestral, since it will, at a later time, play the role of an unsuccessful incoming line, for its type is 1 due to the mutation. We therefore prune this line at the time of the mutation event. The line occupying the top level is exempt from the pruning since, regardless of its type, this line will be ancestral if all lines below it are non-ancestral. We call this line the immune line. If a line that is not the top line has a mutation to type 0, we can cut away all lines above it, because this line will, at some stage, be incoming to all lines above it. It will, due to the beneficial mutation, be successful in all these selection events. If the top line is hit by a mutation to type 0, this does not have an effect. This reasoning gives rise to the line-counting process of the pLD-ASG $L = (L_r)_{r \ge 0}$ as a continuous-time Markov chain on \mathbb{N} with transition rates

$$q_L(n,n+1) = ns, \quad q_L(n,n-1) = (n-1)u\nu_1 + \mathbf{1}_{\{n>1\}}u\nu_0, \quad q_L(n,n-j) = u\nu_0, \qquad n \in \mathbb{N},$$

where $j \in \{2, ..., n-1\}$. The convenient feature of the above construction is that the original individual has an unfit ancestor if and only if all potential ancestors in the pLD-ASG are unfit. The above reasoning leads to

$$g_r(y_0) = \sum_{n=1}^{\infty} P(L_r = n \mid L_0 = 1) y_0^n.$$
(7.1)

As a warm-up for the case with interaction, we introduce a different perspective on the pLD-ASG without interaction and without beneficial mutation ($\nu_0 = 0$). In this case, we can separate the pLD-ASG into two parts. The first part is the immune line, which gives rise to new lines at rate s. Since it is not pruned upon deleterious mutations, it persists indefinitely. The lines that emerge from the immune line evolve independently and each of them is the origin of a killed ASG (we have recalled its definition in the beginning of Sect. 5.1). The collection of these mutually independent killed ASGs forms the second part.

Under this new perspective, an ancestor is unfit if and only if 1) at the time of sampling, an unfit type is associated with the immune line, and 2) all killed ASGs emerging from it are unfit at the time of their origin. We will see that the independence of the killed ASGs, the duality (5.1), and standard properties of Poisson processes permit to derive the following generalisation of [6, Thm.23] to finite time horizons.

Proposition 7.1. Let $\nu_0 = 0$ and $\gamma = 0$. Then

$$g_r(y_0) = y_0 \exp\left(-s \int_0^r \left(1 - y(\xi; y_0)\right) d\xi\right), \qquad y_0 \in [0, 1].$$
(7.2)

In particular,

$$g_r(y_0) = \begin{cases} y_0 \frac{u - s \, y(r; y_0)}{u - s y_0}, & \text{if } y_0 \in [0, 1) \setminus \{\frac{u}{s}\}, \\ y_0 \, \exp(-rs(1 - y_0)), & \text{if } y_0 \in \{\frac{u}{s}, 1\}. \end{cases}$$
(7.3)

Furthermore, $g_{\infty}(y_0) = \lim_{r \to \infty} g_r(y_0)$ exists and is given as follows.

(i) If
$$s = 0$$
, $g_{\infty}(y_0) = y_0$ for all $y_0 \in [0, 1]$
(ii) If $u \leq \hat{u}$, $g_{\infty}(y_0) = \begin{cases} 0, & \text{if } y_0 \in [0, 1), \\ 1, & \text{if } y_0 = 1. \end{cases}$
(iii) If $u > \hat{u}$, $g_{\infty}(y_0) = y_0 \frac{u-s}{u-sy_0}$.

Proof. The proof of (7.2) is given in the next section in a more general setting (see proof of Theorem 7.9). Given (7.2), (7.3) follows by standard integration techniques. To see this, consider $y_0 < u/s$. Then $y(r; y_0)$ increases and hence

$$-s\int_0^r \left(1 - y(\xi, y_0)\right)d\xi = \int_{y_0}^{y(r;y_0)} \frac{-s}{u - s\eta}d\eta = \ln\left(\frac{u - sy(r;y_0)}{u - sy_0}\right).$$

where we substituted $y(\xi; y_0) = \eta$. Together with (7.2) this leads to (7.3). We can proceed similarly for $y_0 \in (u/s, 1)$. For $y_0 \in \{u/s, 1\}$, one has $y(r; y_0) \equiv y_0$ and the result follows. (i)–(iii) are a consequence of (7.3) together with the form of $y_{\infty}(y_0)$ from Corollary 2.7 if $\gamma = 0$.

Let us use Proposition 7.1 to once more make the connection with the deterministic dynamics. Note that $s(1-y(t; y_0))$ is the mean reproduction rate per individual in the model underlying (2.1) if the neutral reproduction rate is set to 0; so $\int_0^t s(1-y(\xi; y_0))d\xi$ is the integrated growth intensity per individual up to time t, and

$$f(t) = \exp\left(\int_0^t s(1 - y(\xi; y_0))d\xi\right)$$

is the size of the population at (forward) time t relative to its size at time 0 if absolute frequencies rather than proportions are considered. More precisely, the absolute frequencies of type 0 and type 1 at time t are $y(t; y_0)f(t)$ and $(1 - y(t; y_0))f(t)$ times the initial population size, respectively. This fact is well known in deterministic population genetics because it allows to transform the nonlinear equation (2.1) into a linear system, see Thompson and McBride [36]. In our context, the key is to think in terms of the integrated offspring size. Since type-1 individuals neither reproduce nor mutate, their absolute frequency remains constant at y_0 times the initial population size, while the total population size grows by a factor of f(t). It is therefore clear that the proportion of unfit ancestors in the population at time t is $y_0/f(t)$, in line with (7.2).

7.2. Ancestral type distribution with interaction: stratified ASG with immune line ($\nu_0 = 0$). In the remainder of this article, we assume that $\nu_0 = 0$ (hence $\nu_1 = 1$). The main argument that led to the representation of the ancestral type distribution in the context of (7.1) was that, if $\gamma = 0$, the ancestor is unfit if and only if all individuals in the pLD-ASG are unfit. Therefore, the line-counting process L is sufficient, and the individual killed ASGs need not be considered. For $\gamma > 0$, we can not expect a similar statement to hold. For example, already after a single trifurcation, the ancestor can be unfit, even though the individual on the incoming line is fit (an unfit continuing *or* checking line suffices TODO:Why or?). However, it is possible to generalise the new perspective mentioned before Proposition 7.1 and

illustrated in Fig. 20. Namely, we add trifurcations to the picture as pairs of ASGs emerging from the immune line and argue in the same way as before; that is, an ancestor is unfit if and only if 1) at the time of sampling, an unfit type is associated with the immune line, 2) all ASGs emerging from it via selection events are unfit at the time of their origin, and 3) at each interaction event on the immune line, at least one of the origins of the ASGs arising from either the incoming or checking line is unfit. 2) and 3) are satisfied if none of the selective and interactive arrows hitting the immune line is used. Using the results from Sect. 6, we can validate 2) and 3) by means of stratified ASGs started with one (incoming) line and stratified ASGs started in Ψ^* (one checking and one incoming line). Let us start to make this precise.

Definition 7.2. Consider a realisation \mathcal{A}_t of the ASG in the time interval [0, t] starting with a single line at time 0. We call the *immune line* of \mathcal{A}_t the line that is continuing to all the bifurcation and trifurcation events. The *stratified ASG with immune line* associated with \mathcal{A}_t is defined by $S_*(\mathcal{A}_t) := S(\mathcal{A}_t^*)$, where \mathcal{A}_t^* is the ASG \mathcal{A}_t after deletion of all the deleterious mutations on its immune line. By construction the immune line is now always relevant and is associated with the leftmost leaf of the corresponding stratified ASG. We define $H_*(\mathcal{A}_t, y_0)$ as the probability that the initial line has an unfit ancestor at backward time t, given that the type distribution at backward time t is $(1 - y_0, y_0)$.

Proposition 7.3. For any realisation A_t of the ASG in [0, t] started with a single line, we have

$$H_{\star}(\mathcal{A}_t, y_0) = \mathcal{H}(S_{\star}(\mathcal{A}_t), y_0), \qquad \forall y_0 \in [0, 1], t > 0.$$

Proof. Note that a type assignment to the lines of \mathcal{A}_t at time r = t corresponds to an unfit ancestor at time t of the single individual at time 0 if and only if the same assignment of types on the lines of \mathcal{A}_t^* leads to an unfit individual at time 0. Hence, $H_*(\mathcal{A}_t, y_0) = H(\mathcal{A}_t^*, y_0)$. Moreover, Theorem 5.13 yields $H(\mathcal{A}_t^*, y_0) = \mathcal{H}(S(\mathcal{A}_t^*), y_0)$ because \mathcal{A}_t^* is a realisation of an ASG. Since by definition $S_*(\mathcal{A}_t) = S(\mathcal{A}_t^*)$, the result follows.

We can also define the stratified ASG with immune line in a Poissonian manner without a realisation of the ASG.

Definition 7.4. We define the stratified ASG process with immune line as the continuous-time Markov chain $\mathscr{T}_{\star} = (\mathscr{T}_{\star}(r))_{r \ge 0}$ on Υ with transition rates

 $q_{\mathscr{T}_{\star}}(\mathcal{T},\mathcal{T}^{\ell}_{\mathsf{Y}}) = sm_{\tau}(\ell), \qquad q_{\mathscr{T}_{\star}}(\mathcal{T},\mathcal{T}^{\ell}_{\psi}) = \gamma m_{\tau}(\ell), \qquad q_{\mathscr{T}_{\star}}(\mathcal{T},\mathcal{T}^{\ell}_{\mathsf{X}}) = u\nu_1 \big(m_{\tau}(\ell) - \mathbf{1}_{\ell^{1}_{\tau}}(\ell)\big).$

The process \mathscr{T}_{\star} has no absorbing states. As in the case without interaction, we do not insist on starting the process with a single line, i.e. with state (1), but one should keep in mind that if we start the process in a state $\mathcal{T} \in \Upsilon$ with $M(\mathcal{T}) = n$ for some n > 1, the process does not describe the relation of potential influencess of n individuals.

Lemma 7.5. Let $\nu_0 = 0$. For any $r \ge 0$ and $y_0 \in [0, 1]$, we have

$$g_r(y_0) = E_{\bigcirc}[\mathcal{H}(\mathscr{T}_{\star}(r), y_0)].$$

Proof. Let \mathcal{A}_r denote a random realisation of the ASG in [0, r] of a generic individual at time 0. From the definition of g_r and the tower property for conditional expectations, we obtain

$$g_r(y_0) = P_{y_0}(J_r = 1) = E_{\widehat{1}}[E_{y_0}[1_{\{J_r = 1\}} \mid \mathcal{A}_r]] = E_{\widehat{1}}[H_{\star}(\mathcal{A}_r, y_0)]$$

The result follows from Proposition 7.3 and the fact that by construction $S_{\star}(\mathcal{A}_r)$ and $\mathscr{T}_{\star}(r)$ have the same distribution.

Let us now try and understand the ancestral distribution from the perspective of the immune line (as in Sect. 7.1). Consider a realisation \mathcal{A}_t of the ASG in [0, t] starting with a single line at r = 0. Note that the ancestor at time t of the single line at time 0 is unfit if and only if the ancestor is the immune line and this is unfit at time t. The immune line is the ancestor if it succeeds at all the selective and interactive events it encounters. We know from Sect. 5 that in order to decide if the immune line succeeds at a given selective event it is enough to look at the stratified ASG arising from the corresponding incoming line. Similarly, the immune line succeeds at a given interactive event if either the incoming or checking line is unfit, and this can be decided by looking at the stratified ASG starting with Ψ^* arising from these lines,



FIGURE 21. From the immune line there emerge independent stratified ASGs started either in (1) or Ψ^* . Here, $\mathscr{T}_1^{\mathbb{O}}$, $\mathscr{T}_2^{\mathbb{O}}$ and $\mathscr{T}_3^{\mathbb{O}}$ emerge at times $T_1^{\mathbb{O}}$, $T_2^{\mathbb{O}}$, and $T_3^{\mathbb{O}}$, respectively. $\mathscr{T}_1^{\Psi^*}$ and $\mathscr{T}_2^{\Psi^*}$ emerge at times $T_1^{\Psi^*}$, respectively.

where the checking and incoming lines are assigned to the middle and right leaves of Ψ^* , respectively. This idea motivates the following definition.

Definition 7.6. Consider a realisation \mathcal{A}_t of the ASG in the time interval [0, t] starting with a single line at time 0. The *forest of stratified ASGs* associated with \mathcal{A}_t is the collection

$$\mathcal{F}(\mathcal{A}_t) := \left(\left(\mathscr{T}_i^{\textcircled{1}}(t), T_i^{\textcircled{1}} \right)_{i=1}^N, \left(\mathscr{T}_i^{\psi^*}(t), T_i^{\psi^*} \right)_{i=1}^M \right),$$

where

- (1) N is the number of selective events on the immune line of \mathcal{A}_t and $0 \leq T_1^{\textcircled{O}} < \cdots < T_N^{\textcircled{O}} \leq t$ are the successive times at which they occur.
- (2) For $i \in \{1, ..., N\}$, $\mathscr{T}_i^{(0)}(t)$ is the stratified ASG associated with the ASG (in the time interval $[T_i^{(0)}, t]$) arising from the incoming line at the selective event occurring at time $T_i^{(0)}$.
- (3) M is the number of interactive events on the immune line of \mathcal{A}_t and $0 \leq T_1^{\bigcup^*} < \cdots < T_M^{\bigcup^*} \leq t$ are the successive times at which they occur.
- (4) For $i \in \{1, ..., M\}$, $\mathscr{T}_i^{\psi^*}(t)$ is the stratified ASG associated with the ASG (in the time interval $[T_i^{\psi^*}, t]$) arising from the checking and incoming lines at the interactive event occurring at time $T_i^{\psi^*}$, with checking and incoming lines being assigned to the middle and right leaves of Ψ^* , respectively.

See Fig. 21 for an illustration.

Proposition 7.7. Let $\nu_0 = 0$. Using the notation from Definition 7.6, we have

$$H_{\star}(\mathcal{A}_{t}, y_{0}) = y_{0} \prod_{i=1}^{N} \mathcal{H}(\mathscr{T}_{i}^{(0)}(t), y_{0}) \prod_{j=1}^{M} \mathcal{H}(\mathscr{T}_{j}^{\psi^{\star}}(t), y_{0}), \quad y_{0} \in [0, 1].$$
(7.4)

Proof. We know that the ancestor at backward time t of the single lineage at time 0 is unfit if and only if the ancestor is the immune line and this one is unfit at time t; the latter is the case with probability y_0 . In addition, the immune line is the ancestor at time t if it succeeds at all the selective and interactive events involved. The immune line succeeds at the selective event happening at time $T_i^{\textcircled{0}}$ if and only if the corresponding incoming line is of type 1; this occurs with probability $\mathcal{H}(\mathscr{T}_i^{\textcircled{0}}(t), y_0)$. The immune line succeeds at the interactive event $T_j^{\Downarrow^*}$ if and only if either the checking or the incoming line is of type 1; this occurs with probability $\mathcal{H}(\mathscr{T}_j^{\Downarrow^*}(t), y_0)$. The result follows from the independence of the corresponding stratified ASGs.

We can also construct the forest of stratified ASGs in a Poissonian manner.

Definition 7.8. Let $\mathcal{N} := (\mathcal{N}_r)_{r \geq 0}$ and $\mathcal{M} := (\mathcal{M}_r)_{r \geq 0}$ be two independent homogeneous Poisson processes with rate *s* and γ , respectively. Let $(T_i^{(1)})_{i \in \mathbb{N}}$ and $(T_i^{\psi^*})_{i \in \mathbb{N}}$ be the successive arrival times of \mathcal{N} and \mathcal{M} , respectively. Furthermore, we invoke two independent collections of independent stratified ASG processes $(\mathscr{T}_i^{(0)})_{i \in \mathbb{N}}$ and $(\mathscr{T}_i^{\psi^*})_{i \in \mathbb{N}}$. In the first collection all the stratified ASGs start at (1), and in the second one all the stratified ASGs start at Ψ^* . The *forest of stratified ASGs* process $\mathscr{I} = (\mathscr{I}(r))_{r \geq 0}$ is then defined by setting

$$\mathscr{I}(r) := \left(\left(\mathscr{T}_i^{(1)}(r - T_i^{(1)}), T_i^{(1)} \right)_{i=1}^{\mathcal{N}_r}, \left(\mathscr{T}_i^{\psi^\star}(r - T_i^{\psi^\star}), T_i^{\psi^\star} \right)_{i=1}^{\mathcal{M}_r} \right), \quad r \ge 0.$$

Theorem 7.9. Let $\nu_0 = 0$. Then,

$$g_r(y_0) = y_0 \exp\left(-\int_0^r \left(1 - y(\xi; y_0)\right) \left(s + \gamma(1 - y(\xi; y_0))\right) d\xi\right), \qquad y_0 \in [0, 1].$$
(7.5)

Theorem 7.9 is connected to the deterministic dynamics in the same way as (7.2). This time, $(1 - y(t; y_0))(s + \gamma(1 - y(t; y_0)))$ is the mean reproduction rate per individual (if the neutral reproduction rate is 0), and

$$f(t) = \exp\left(\int_0^t \left(1 - y(\xi; y_0) \left((s + \gamma(1 - y(\xi; y_0))\right)\right) d\xi\right)$$

is the size of the population at time t relative to its initial size in terms of absolute frequencies. This leads to a simple generalisation of Thompson's trick that allows to transform the mutation-selection equation into a system with a lower degree of nonlinearity. We do not spell this out here but rather focus on the integrated offspring size again. With the same argument as before, the proportion of unfit ancestors in the population at time t is $y_0/f(t) = g_r(y_0)$, in line with the theorem.

Theorem 7.9 permits to derive explicit expressions for $g_r(y_0)$ by means of classical integration techniques, which results in the following corollary.

Corollary 7.10. Let $\nu_0 = 0, \gamma > 0$, and $\bar{y}_1, \bar{y}_2, \bar{y}_3, \sigma$ be given as in (2.4), (2.6) and (2.7). For $y_0 \in \{\bar{y}_1, \bar{y}_2, \bar{y}_3\} \cap [0, 1]$, we have

$$g_r(y_0) = y_0 \exp\left(-r(1-y_0)(s+\gamma(1-y_0))\right)$$

For $y_0 \in [0, 1] \setminus \{\bar{y}_1, \bar{y}_2, \bar{y}_3\}$ and (i) $\sigma > 0$,

$$g_r(y_0) = y_0 \left(\frac{\bar{y}_2 - y(r; y_0)}{\bar{y}_2 - y_0}\right)^{\frac{\bar{y}_3}{\sqrt{\sigma}}} \left(\frac{\bar{y}_3 - y_0}{\bar{y}_3 - y(r; y_0)}\right)^{\frac{\bar{y}_2}{\sqrt{\sigma}}},\tag{7.6}$$

$$g_r(y_0) = y_0 \frac{y(r; y_0) - \bar{y}_2}{y_0 - \bar{y}_2} \exp\left(-\bar{y}_2 \frac{y(r; y_0) - y_0}{(y(r; y_0) - \bar{y}_2)(y_0 - \bar{y}_2)}\right),\tag{7.7}$$

(iii) $\sigma < 0$,

(*ii*) $\sigma = 0$,

$$g_{r}(y_{0}) = y_{0}\sqrt{\frac{u - y(r; y_{0})\left(s + \gamma\left(1 - y(r; y_{0})\right)\right)}{u - y_{0}\left(s + \gamma\left(1 - y_{0}\right)\right)}}}\exp\left(-\frac{1}{\sqrt{-\sigma}}\left(1 + \frac{s}{\gamma}\right)\right) \times \left[\arctan\left(2\frac{y(r; y_{0}) - \frac{1}{2}\left(1 + \frac{s}{\gamma}\right)}{\sqrt{-\sigma}}\right) - \arctan\left(2\frac{y_{0} - \frac{1}{2}\left(1 + \frac{s}{\gamma}\right)}{\sqrt{-\sigma}}\right)\right]\right).$$
(7.8)

The proof of the corollary is postponed to the appendix.

Proof of Theorem 7.9. By Proposition 7.3, Lemma 7.5, Proposition 7.7 and the Poissonian construction of the forest of stratified ASGs, we obtain

$$g_r(y_0) = y_0 E \bigg[\prod_{i=1}^{\mathcal{N}_r} \mathcal{H} \big(\mathscr{T}_i^{(\underline{0})}(r - T_i^{(\underline{0})}), y_0 \big) \bigg] E \bigg[\prod_{j=1}^{\mathcal{M}_r} \mathcal{H} \big(\mathscr{T}_j^{\psi^\star}(r - T_j^{\psi^\star}), y_0 \big) \bigg].$$

We begin by considering the first non-trivial factor. Then,

$$E\left[\prod_{i=1}^{N_r} \mathcal{H}(\mathscr{T}_i^{(0)}(r-T_i^{(0)}), y_0)\right] = \sum_{n=0}^{\infty} P(\mathcal{N}_r = n) E_n\left[E\left[\prod_{i=1}^n \mathcal{H}(\mathscr{T}_i^{(0)}(r-T_i^{(0)}), y_0) \mid (T_i^{(0)})_{i=1}^n\right]\right],$$
(7.9)

where by $E_n[\cdot]$ we denote the expectation conditional on $\mathcal{N}_r = n$. Now, we use the well-known connection between Poisson processes and the uniform distribution. Conditional on $\mathcal{N}_r = n$, the arrival times of \mathcal{N} have the same distribution as an ordered independent sample of size n from the uniform distribution on [0,r] [32, Thm. 2.4.6]. Since $E[\prod_{i=1}^{n} \mathcal{H}(\mathscr{T}_{i}^{(\underline{0})}(r-T_{i}^{(\underline{0})}), y_{0}) \mid (T_{i}^{(\underline{0})})_{i=1}^{n}]$ is a function that is symmetric in the arrival times of the Poisson process, we can deduce that

$$E_n\left[E\left[\prod_{i=1}^n \mathcal{H}(\mathscr{T}_i^{\textcircled{0}}(r-T_i^{\textcircled{0}}), y_0) \mid (T_i^{\textcircled{0}})_{i=1}^n\right]\right] = E\left[\prod_{i=1}^n \mathcal{H}(\mathscr{T}_i^{\textcircled{0}}(U_i), y_0)\right],\tag{7.10}$$

since $r - U_i$ is again uniform on [0, r]. Moreover, $(\mathscr{T}_i^{(1)}(U_i))_{i=1}^n$ are independent, and hence

$$E\left[\prod_{i=1}^{n} \mathcal{H}(\mathscr{T}_{i}^{(1)}(U_{i}), y_{0})\right] = E\left[\mathcal{H}(\mathscr{T}_{i}^{(1)}(U_{i}), y_{0})\right]^{n} = \left(\frac{1}{r} \int_{0}^{r} E_{\xi}\left[\mathcal{H}(\mathscr{T}_{i}^{(1)}(\xi), y_{0})\right] d\xi\right)^{n} = \left(\frac{1}{r} \int_{0}^{r} y(\xi, y_{0}) d\xi\right)^{n},$$
(7.11)

where we used the duality result in Theorem 6.2. Combining (7.10) and (7.11) into (7.9) and using the fact that \mathcal{N}_r is Poisson distributed with parameter sr yields

$$E\bigg[\prod_{i=1}^{N_r} \mathcal{H}\big(\mathscr{T}_i^{(1)}(r-T_i^{(1)}), y_0\big)\bigg] = \sum_{n=0}^{\infty} \frac{(sr)^n}{n!} e^{-sr}\bigg(\frac{1}{r} \int_0^r y(\xi, y_0) d\xi\bigg)^n = \exp\bigg(-s \int_0^r (1-y(\xi, y_0)) d\xi\bigg).$$

Next, we consider the second non-trivial factor. In a similar way, we obtain

$$E_m \bigg[\prod_{j=1}^m \mathcal{H} \big(\mathscr{T}_j^{\psi^\star}(r - T_j^{\psi^\star}), y_0 \big) \bigg] = E_m \bigg[H(\mathscr{T}_1^{\psi_\star}(U_1), y_0) \bigg]^m = \Big\{ 2E \big[H(\mathscr{T}^{\bigcirc}(U), y_0) \big] - E \big[H(\mathscr{T}^{\bigcirc}(U), y_0)^2 \big] \Big\}^m$$

Hence,

$$E\bigg[\prod_{j=1}^{\mathcal{M}_r} H\big(\mathscr{T}_j^{\Psi^\star}(r-T_j^\star), y_0\big)\bigg] = \exp\bigg(-\gamma \int_0^r \big(1-y(\xi;y_0)\big)^2 d\xi\bigg).$$

Altogether, we obtain (7.5).

Taking the limit $r \to \infty$, we obtain the analogue to [6, Thm. 23] in the case with interaction and in the absence of beneficial mutations.

Corollary 7.11. Let $\nu_0 = 0$ and $\gamma > 0$. Then we have $g_{\infty}(1) = 1$. For $y_0 \in [0, 1)$ and (i) $\sigma > 0$, we have

$$g_{\infty}(y_0) = \mathbf{1}_{\{y_0 > \bar{y}_3\}} y_0 \left(\frac{1 - \bar{y}_2}{y_0 - \bar{y}_2}\right)^{\frac{\bar{y}_3}{\sqrt{\sigma}}} \left(\frac{y_0 - \bar{y}_3}{1 - \bar{y}_3}\right)^{\frac{\bar{y}_2}{\sqrt{\sigma}}},\tag{7.12}$$

(ii) $\sigma = 0$, we have

$$g_{\infty}(y_0) = \mathbf{1}_{\{y_0 > \bar{y}_3\}} y_0 \frac{1 - \bar{y}_2}{y_0 - \bar{y}_2} \exp\left(-\bar{y}_2 \frac{1 - y_0}{(1 - \bar{y}_2)(y_0 - \bar{y}_2)}\right),\tag{7.13}$$

(iii) $\sigma < 0$, we have

$$g_{\infty}(y_0) = y_0 \sqrt{\frac{u-s}{u-y_0s}} \exp\left(-\frac{1}{\sqrt{-\sigma}} \left(1+\frac{s}{\gamma}\right) \left[\arctan\left(\frac{1-\frac{s}{\gamma}}{\sqrt{-\sigma}}\right) - \arctan\left(2\frac{y_0 - \frac{1}{2}\left(1+\frac{s}{\gamma}\right)}{\sqrt{-\sigma}}\right)\right]\right).$$
(7.14)
Proof Combining Corollary 2.7 with Corollary 7.10 yields the result

Proof. Combining Corollary 2.7 with Corollary 7.10 yields the result.

At last, we consider the ancestral type distribution at equilibrium, i.e. $(1 - g_{\infty}(y_{\infty}(y_0)), g_{\infty}(y_{\infty}(y_0)))$. The following corollary extends the expression for $g_{\infty}(y_{\infty}(y_0))$ from [6, Sect.6] to the case $\gamma > 0$.

Corollary 7.12. Let $\nu_0 = 0$ and $s, \gamma \ge 0$. Then we have $g_{\infty}(y_{\infty}(1)) = 1$. For all $y_0 \in [0, 1)$, (i) if $s \ge \gamma$, then

$$g_{\infty}(y_{\infty}(y_0)) = \begin{cases} 0, & \text{if } u < \hat{u}, \\ 1, & \text{if } u \geqslant \hat{u}. \end{cases}$$

$$(7.15)$$

(ii) if $s < \gamma$ and $u < \hat{u}$, then $g_{\infty}(y_{\infty}(y_0)) \equiv 0$. (iii) if $s < \gamma$ and $u \in [\hat{u}, \check{u}]$, then

$$g_{\infty}(y_{\infty}(y_0)) = \begin{cases} 0, & \text{if } y_0 \leq \bar{y}_3, \\ 1, & \text{if } y_0 > \bar{y}_3. \end{cases}$$
(7.16)

(iv) If $s < \gamma$ and $u > \check{u}$, then $g_{\infty}(y_{\infty}(y_0)) \equiv 1$.



FIGURE 22. The ancestral type distribution at equilibrium for the parameter regimes from Fig. 1. Dotted lines: equilibria \bar{y} . White background: $(u/s, y_0)$ s.t. $g_{\infty}(y_{\infty}(y_0)) = 0$. Grey background: $(u/s, y_0)$ s.t. $g_{\infty}(y_{\infty}(y_0)) = 1$.

Proof of Corollary 7.12. In the following, we throughout use Corollaries 2.7 and 7.11. For $y_0 = 1$, we have $y_{\infty}(1) = 1$ and hence $g_{\infty}(y_{\infty}(1)) = 1$. For the remainder, fix $y_0 \in [0, 1)$. If $s \ge \gamma$ and $u < \hat{u}$, we have that $y_{\infty}(y_0) < 1$ such that $g_{\infty}(y_{\infty}(y_0)) = 0$. For $s \ge \gamma$ and $u \ge \hat{u}$, $y_{\infty}(y_0) = 1$ and hence $g_{\infty}(y_{\infty}(y_0)) = 1$. This leads to (i). If $s < \gamma$ and $u < \hat{u}$, then $y_{\infty}(y_0) < 1$ and hence $g_{\infty}(y_{\infty})(y_0) = 1$ and hence $g_{\infty}(y_{\infty})(y_0) \equiv 0$. Similarly, $s < \gamma$ and $u > \check{u}$, then $y_{\infty}(y_0) = 1$ and hence $g_{\infty}(y_{\infty})(y_0) \equiv 1$. Altogether, (ii) and (iv) follow. For (iii), note that when $s < \gamma$ and $u \in [\hat{u}, \check{u}]$, then $y_{\infty}(y_0) < 1$ for $y_0 \le \bar{y}_3$ and $y_{\infty}(y_0) = 1$ for $y_0 > \bar{y}_3$. \Box

Let us explain the underlying genealogical picture. Assume $y_0 \in [0, 1)$. Note that, since the immune line persists indefinitely, the number of lines does not absorb.

- If $u < \hat{u}$, each stratified ASG that emerges from the immune line grows to ∞ with probability $1 - w_1$ by Proposition 6.4. Note that, by the discussion at then end of Sect. 6, $w_1 < 1$. By Corollary 6.10, in this parameter regime a stratified ASG with infinite mass will always lead to a fit descendant provided the potential ancestors are sampled from a population with a positive frequency of fit types. In particular, one of the stratified ASGs emerging from the immune line grows to ∞ and then leads to a fit ancestor.
- If $u > \check{u}$ or $(u \in [\hat{u}, \check{u}]$ and $s \ge \gamma)$, we have, by the discussion at the end of Sect. 6, that $y_{\infty}(y_0) \equiv 1$. In particular, all potential ancestors in the forest of stratified ASGs are unfit.
- If $u \in [\hat{u}, \check{u}]$ and $s < \gamma$, the situation is different. Here, each stratified ASG that emerges from the immune line may grow to ∞ with probability $1 - w_1$ by Proposition 6.4. Note that, by the discussion at the end of Sect. 6, $w_1 < 1$. But now the probability for an unfit ancestor depends crucially on y_0 , and we recover the bistability from Sect. 2. The two equilibria of (2.1) lead to an asymptotic frequency of unfit types that is either < 1 or 1. If $y_0 \in [0, \bar{y}_3)$ (recall $\bar{y}_3 = \bar{y}_3(u, s, \gamma)$ is a function of the parameters) then $y_{\infty}(y_0) = w_1$, so that by Corollary 6.10 each of the stratified ASGs with infinite mass leads to a fit descendant. One of these descendants then is the fit ancestor. If $y_0 \in (\bar{y}_3, 1]$, then $y_{\infty}(y_0) = 1$ and all the potential ancestors are unfit. In particular, the total mass of the stratified ASG is irrelevant. In the case $y_0 = \bar{y}_3$, we have $E[\mathcal{H}_{\infty}(y_0)] < 1$ by Corollary 6.14 such that one of the infinite stratified ASGs leads to a fit descendant and hence to a fit ancestor, see also Fig. 22 (right).

For $y_0 \in [0,1)$, $g_{\infty}(y_{\infty}(\cdot))$ is constant if $s \ge \gamma$ or $(s < \gamma \text{ and } u \notin [\hat{u}, \check{u}])$. If $s < \gamma$ and $u \in [\hat{u}, \check{u}]$, \bar{y}_3 is the critical value above which $g_{\infty}(y_{\infty}(y_0))$ jumps from 0 to 1.

APPENDIX A. REMAINING PROOFS

The following identities will be useful in what follows.

Lemma A.1. Let $\mathcal{T} = (\tau, m) \in \Upsilon$.

(1) Let $k \in \mathbb{N}$ and $m_{\tau}^{(k)} : L_{\tau} \to \mathbb{N} \cup \{0\}$ be defined by $m_{\tau}^{(k)}(\ell) := m_{\tau}(\ell) + \mathbf{1}_{\{\ell = \ell_{\tau}^1\}} k$. In addition, we set $\mathcal{T}^{(k)} := (\tau, m_{\tau}^{(k)})$. Then, we have

$$\mathcal{H}(\mathcal{T}^{(k)}, y_0) = y_0^k \mathcal{H}(\mathcal{T}, y_0), \quad y_0 \in [0, 1].$$

(2) For all $\widetilde{\mathcal{T}} \in \Upsilon$ and $y_0 \in [0,1]$, we have

$$\mathcal{H}(\mathcal{T} \otimes_{\ell^1_{ au}} \widetilde{\mathcal{T}}, y_0) = \mathcal{H}(\mathcal{T}, y_0) \, \mathcal{H}(\widetilde{\mathcal{T}}, y_0) \, \mathcal{H}(\widetilde{\mathcal{T}, y_$$

Proof.

(1) We fix $k \in \mathbb{N}$ and proceed by induction on $|L_{\tau}|$. If $\mathcal{T} = \widehat{(n)}$, then $\mathcal{T}^{(k)} = \widehat{(j)}$ with j = n + k, and the assertion follows from the definition of \mathcal{H} . Assume the assertion is true for all $\widetilde{\mathcal{T}} = (\widetilde{\tau}, m_{\widetilde{\tau}})$ with $|L_{\widetilde{\tau}}| < |L_{\tau}|$. We have to show that the assertion remains true for \mathcal{T} . Let $\kappa^1, \kappa^2, \kappa^3$ be the left, middle, and right child of the root of \mathcal{T} . Since the leftmost leaf of \mathcal{T}_{κ^1} is ℓ^1_{τ} , the induction hypothesis implies that the assertion holds true for \mathcal{T}_{κ^1} , i.e.

$$\mathcal{H}(\mathcal{T}_{\kappa^1}^{(k)}, y) = y^k \,\mathcal{H}(\mathcal{T}_{\kappa^1}, y)$$

The result then follows via Eq. (5.2).

(2) We fix $\tilde{\mathcal{T}} = (\tilde{\tau}, \tilde{m}) \in \Upsilon$ and proceed by induction on $|L_{\tau}|$. If $\mathcal{T} = \widehat{(m)}$, then $\mathcal{T} \otimes_{\ell_{\tau}^{1}} \tilde{\mathcal{T}} = \tilde{\mathcal{T}}^{(n)}$, and the result follows from assertion (1). Assume the result is true for all $\bar{\mathcal{T}} = (\bar{\tau}, m_{\bar{\tau}})$ with $|L_{\bar{\tau}}| < |L_{\tau}|$. We have to show that the result remains true for \mathcal{T} . Let $\kappa^{1}, \kappa^{2}, \kappa^{3}$ be the left, middle, and right child of the root of \mathcal{T} . The induction hypothesis applied to $\mathcal{T}_{\kappa^{1}}$ yields

$$\mathcal{H}(\mathcal{T}_{\kappa^1} \otimes_{\ell^1_{\tau}} \widetilde{\mathcal{T}}, y_0) = \mathcal{H}(\mathcal{T}_{\kappa^1}, y_0) \, \mathcal{H}(\widetilde{\mathcal{T}}, y_0)$$

Moreover, since $(\mathcal{T} \otimes_{\ell_{\tau}^{1}} \widetilde{\mathcal{T}})_{\kappa^{1}} = \mathcal{T}_{\kappa^{1}} \otimes_{\ell_{\tau}^{1}} \widetilde{\mathcal{T}}, (\mathcal{T} \otimes_{\ell_{\tau}^{1}} \widetilde{\mathcal{T}})_{\kappa^{2}} = \mathcal{T}_{\kappa^{2}} \text{ and } (\mathcal{T} \otimes_{\ell_{\tau}^{1}} \widetilde{\mathcal{T}})_{\kappa^{3}} = \mathcal{T}_{\kappa^{3}}, \text{ the result follows by Eq. (5.2).}$

Proof of Lemma 6.1. Fix $\mathcal{T} = (\tau, m) \in \Upsilon_{\star}$ and $y_0 \in [0, 1]$. We want to show that

$$\mathcal{G}_{\Upsilon}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = -sy_0(1-y_0)\frac{\partial\mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0),\tag{A.1}$$

$$\mathcal{G}_{\psi}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = -\gamma y_0 (1 - y_0)^2 \frac{\partial \mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0), \tag{A.2}$$

$$\mathcal{G}_{\times}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = (1 - y_0)u\nu_1 \frac{\partial \mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0), \tag{A.3}$$

$$\mathcal{G}_{\circ}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = y_0 u \nu_0 \frac{\partial \mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0).$$
(A.4)

We proceed by induction on the size of the underlying tree. First note that, since $\mathcal{H}((n), y_0) = y_0^n$, we have $(\partial \mathcal{H}((n), \cdot)/\partial y)(y_0) = ny_0^{n-1}$. In addition,

$$\begin{aligned} \mathcal{G}_{\Upsilon} \mathcal{H}(\cdot, y_0)(\widehat{n}) &= ns(y_0^{n+1} - y_0^n) = -sy_0(1 - y_0)ny_0^{n-1}, \\ \mathcal{G}_{\Psi} \mathcal{H}(\cdot, y_0)(\widehat{n}) &= n\gamma(y_0^n(y_0 + y_0 - y_0^2) - y_0^n) = -\gamma y_0(1 - y_0)^2 ny_0^{n-1}, \\ \mathcal{G}_{\times} \mathcal{H}(\cdot, y_0)(\widehat{n}) &= nu\nu_1(y_0^{n-1} - y_0^n) = (1 - y_0)u\nu_1 ny_0^{n-1}, \\ \mathcal{G}_{\circ} \mathcal{H}(\cdot, y_0)(\widehat{n}) &= nu\nu_0(0 - y_0^n) = -y_0u\nu_0 ny_0^{n-1}. \end{aligned}$$

Hence (A.1), (A.2), (A.3), and (A.4) hold true for $\mathcal{T} = \widehat{m}$. Now, we fix $\mathcal{T} = (\tau, m_{\tau}) \in \Upsilon$ and we assume that (A.1), (A.2), (A.3) and (A.4) hold true for all $\widetilde{\mathcal{T}} = (\tilde{\tau}, \tilde{m}_{\tilde{\tau}}) \in \Upsilon$ with $|L_{\tilde{\tau}}| < |L_{\tau}|$. We aim to prove that they remain true for \mathcal{T} . Let us denote by κ^1, κ^2 , and κ^3 the left, middle, and right child of the root

of \mathcal{T} . From Definition 5.12 and the chain rule,

$$\frac{\partial \mathcal{H}(\mathcal{T}, y)}{\partial y}(y_0) = \frac{\partial \mathcal{H}(\mathcal{T}_{\kappa^1}, y)}{\partial y}(y_0) \left[\mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) + \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) \right] \\
+ \mathcal{H}(\mathcal{T}_{\kappa^1}, y_0) \left[\frac{\partial \mathcal{H}(\mathcal{T}_{\kappa^2}, y)}{\partial y}(y_0) \left(1 - \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0)\right) + \frac{\partial \mathcal{H}(\mathcal{T}_{\kappa^3}, y)}{\partial y}(y_0) \left(1 - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0)\right) \right].$$
(A.5)

We claim that for each $\star \in \{\Upsilon, \Psi, \times, \circ\}$, we have

(1) for $\ell \in L_{\tau_{\kappa^1}}$,

 $\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0) = \Big(\mathcal{H}\big((\mathcal{T}_{\kappa^1})^{\ell}_{\star}, y_0\big) - \mathcal{H}\big(\mathcal{T}_{\kappa^1}, y_0\big)\Big)\Big[\mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) + \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0)\mathcal{H}(\mathcal{T}_{\kappa^3}, y_0)\Big],$ (2) for $\ell \in L_{\tau_{-2}}$,

$$\gamma_{\kappa^2}$$

$$\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0) = \mathcal{H}(\mathcal{T}_{\kappa^1}, y_0)(1 - \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0)) \Big(\mathcal{H}\big((\mathcal{T}_{\kappa^2})^{\ell}_{\star}, y_0\big) - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0) \Big),$$

(3) for $\ell \in L_{\tau_{\nu^3}}$,

$$\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0) = \mathcal{H}(\mathcal{T}_{\kappa^1}, y_0)(1 - \mathcal{H}(\mathcal{T}_{\kappa^2}, y_0)) \Big(\mathcal{H}\big((\mathcal{T}_{\kappa^3})^{\ell}_{\star}, y_0\big) - \mathcal{H}(\mathcal{T}_{\kappa^3}, y_0) \Big).$$

Assume that the claim is true. Denote by

$$q_{\star} = s \mathbf{1}_{\{\star=\Upsilon\}} + \gamma \mathbf{1}_{\{\star=\Psi\}} + u \nu_1 \mathbf{1}_{\{\star=\times\}} + u \nu_1 \mathbf{1}_{\{\star=\circ\}}$$

Since

$$\mathcal{G}_{\star}\mathcal{H}(\cdot, y_0)(\mathcal{T}) = \sum_{i \in \{1, 2, 3\}} \sum_{\ell \in L_{\tau_{\kappa^i}}} q_{\star} m(\ell) (\mathcal{H}(\mathcal{T}^{\ell}_{\star}, y_0) - \mathcal{H}(\mathcal{T}, y_0)),$$

we infer that

$$\begin{aligned} \mathcal{G}_{\star}\mathcal{H}(\cdot,y_{0})(\mathcal{T}) &= \mathcal{G}_{\star}\mathcal{H}(\cdot,y_{0})(\mathcal{T}_{\kappa^{1}})\Big[\mathcal{H}(\mathcal{T}_{\kappa^{2}},y_{0}) + \mathcal{H}(\mathcal{T}_{\kappa^{3}},y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{2}},y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}},y_{0})\Big] \\ &+ \mathcal{H}(\mathcal{T}_{\kappa^{1}},y_{0})\Big[\big(1 - \mathcal{H}(\mathcal{T}_{\kappa^{3}},y_{0})\big)\mathcal{G}_{\star}\mathcal{H}(\cdot,y_{0})(\mathcal{T}_{\kappa^{2}}) + (1 - \mathcal{H}(\mathcal{T}_{\kappa^{2}},y_{0}))\mathcal{G}_{\star}\mathcal{H}(\cdot,y_{0})(\mathcal{T}_{\kappa^{3}})\Big]. \end{aligned}$$

Applying the induction hypothesis to \mathcal{T}_{κ^1} , \mathcal{T}_{κ^2} and \mathcal{T}_{κ^3} , the previous identity together with (A.5) permit to show that (A.1), (A.2), (A.3) and (A.4) hold true for \mathcal{T} . It remains to prove the claim.

For $\star \in \{\Upsilon, \Psi\}$, the claim follows easily by Definition 5.12 and noting that for $i \in \{1, 2, 3\}$ and $\ell \in L_{\tau_{\kappa^i}}, \mathcal{T}^{\ell}_{\star}$ is constructed from \mathcal{T} by replacing \mathcal{T}_{κ^i} with $(\mathcal{T}_{\kappa^i})^{\ell}_{\star}$. But for the latter the induction hypothesis applies. In the following cases, the tree changes only in one subtree of one of the children of the root and therefore we can apply the same argument. We are in these cases if $\star = \times$ and

- if $m_{\tau}(\ell) > 1$ or ℓ is the left child of its parent,
- if $m_{\tau}(\ell) = 1, \ell$ is not the left child of its parent, and b_{ℓ} is the left child of its parent,
- if $m_{\tau}(\ell) = 1$, ℓ is not the left child of its parent, and b_{ℓ} is not the left child of its parent and it is not the root,

or if $\star = \circ$ and

- if ℓ is not a middle or right child of the root,
- if ℓ is a left child and $a_{a_{\ell}^{\star}}$ is not the root.

We treat the remaining cases separately. For $\star = \times$, $m_{\tau}(\ell) = 1$, ℓ is not the left child of its parent, and b_{ℓ} is the root, we have that $\mathcal{T}_{\times}^{\ell} = 0$. In particular, $\mathcal{H}(\mathcal{T}_{\times}^{\ell}, y_0) = 1$ for all $y_0 \in [0, 1]$. Furthermore, since b_{ℓ} is the root, $\ell \in T_{\kappa^2}$ or $\ell \in T_{\kappa^3}$, because otherwise κ^1 would be an ancestor of ℓ and it would be a left child of the root. Furthermore, $\mathcal{H}(\mathcal{T}_{\kappa^1}, y_0) = 1$, because $\sum_{v \in L_{\tau_{(b_1)}}} m_{\tau}(v) = 0$ (since otherwise b_{ℓ}^1 is not

the root). Again, by Definition 5.12, we can deduce that for $\ell \in \mathcal{T}_{\kappa^2}$,

$$\begin{aligned} \mathcal{H}(\mathcal{T}_{\times}^{\ell}, y_{0}) - \mathcal{H}(\mathcal{T}, y_{0}) &= 1 - H(\mathcal{T}, y_{0})) \\ &= 1 - \left[\mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0}) + \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0})\right] \\ &= (1 - \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}))[1 - \mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})] \\ &= \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})(1 - \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}))[\mathcal{H}((\mathcal{T}_{\kappa^{2}})_{\times}^{\ell}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})]. \end{aligned}$$

We can proceed in a similar way if $\ell \in \mathcal{T}_{\kappa^3}$. The last case is $\star = \circ$ and ℓ is a child of the root. If ℓ is the middle child of the root, i.e. $\ell = \kappa^2$, then $(\mathcal{T}_{\ell})^{\ell}_{\circ} = \Delta$. By the definition of $\mathcal{T}^{\ell}_{\circ}$, we have

$$\mathcal{T}^{\ell}_{\circ} = \left(\mathcal{T}^{C}_{\kappa_{\tau}} \otimes_{\kappa_{\tau}} \mathcal{T}_{\kappa^{1}} \right) \otimes_{\ell^{1}_{\tau_{\kappa^{1}}}} \mathcal{T}_{\kappa^{3}}$$

By Lemma A.1, $\mathcal{H}\left((\mathcal{T}_{\kappa_{\tau}}^{C} \otimes_{\kappa_{\tau}} \mathcal{T}_{\kappa^{1}}) \otimes_{\ell_{\tau_{\kappa^{1}}}^{1}} \mathcal{T}_{\kappa^{3}}, y_{0}\right) = \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}).$ Therefore, using Definition 5.12

$$\begin{aligned} \mathcal{H}(\mathcal{T}^{\ell}_{\circ}, y_{0}) - \mathcal{H}(\mathcal{T}, y_{0}) &= \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})[\mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0}) + \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) \\ &= \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0}) \big(1 - \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0})\big) [-\mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})]. \end{aligned}$$

We can proceed in a similar way if $\ell \in \mathcal{T}_{\kappa^3}$. It remains to prove the case in which ℓ is the left child of its parent and $a_{a_{\ell}^{\star}}$ is the root. Assume $a_{\ell}^{\star} = \kappa^2$. Then, $(\mathcal{T}_{\kappa^2})_{\circ}^{\ell} = \Delta$. Again, $\mathcal{T}_{\circ}^{\ell} = (\mathcal{T}_{\kappa_{\tau}}^C \otimes_{\kappa_{\tau}} \mathcal{T}_{\kappa^1}) \otimes_{\ell_{\tau_{\kappa^1}}} \mathcal{T}_{\kappa^3}$. Once more, we apply Lemma A.1 and we use Definition 5.12, such that

$$\begin{aligned} \mathcal{H}(\mathcal{T}^{\ell}_{o}, y_{0}) - \mathcal{H}(\mathcal{T}, y_{0}) &= \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0})[\mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0}) + \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0}) - \mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})\mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0})] \\ &= \mathcal{H}(\mathcal{T}_{\kappa^{1}}, y_{0}) \big(1 - \mathcal{H}(\mathcal{T}_{\kappa^{3}}, y_{0})\big) [-\mathcal{H}(\mathcal{T}_{\kappa^{2}}, y_{0})]. \end{aligned}$$

We can proceed in a similar way if $a_{\ell}^{\star} = \kappa^3$. Altogether, this proves the claim.

Proof of Corollary 7.10. We apply classical integration theory. Recall that \bar{y}_2 and \bar{y}_3 are the roots of the polynomial $y \mapsto u - y(s + \gamma(1 - y))$. First, we consider the case $\sigma > 0$ in which \bar{y}_2 and \bar{y}_3 are both real (recall from (2.6)). We want to treat $u \leq s$ in which case $\bar{y}_2 < \bar{y}_1 < \bar{y}_2$. For $y_0 < \bar{y}_2$, $y(r; y_0)$ is increasing. By substituting $\eta = y(\xi, y_0)$ and partial fraction expansion, we obtain

$$\begin{split} &-\int_{0}^{r} \left(1-y(\xi;y_{0})\right) \left(s+\gamma(1-y(\xi;y_{0}))\right) d\xi \\ &=-\int_{y_{0}}^{y(r;y_{0})} \frac{s+\gamma(1-\eta)}{u-\eta(s+\gamma(1-\eta))} d\eta \\ &=-\frac{1}{\gamma} \frac{s+\gamma(1-\bar{y}_{2})}{\bar{y}_{3}-\bar{y}_{2}} \int_{y_{0}}^{y(r;y_{0})} \frac{1}{\bar{y}_{2}-\eta} d\eta + \frac{1}{\gamma} \frac{s+\gamma(1-\bar{y}_{3})}{\bar{y}_{3}-\bar{y}_{2}} \int_{y_{0}}^{y(r;y_{0})} \frac{1}{\bar{y}_{3}-\eta} d\eta \\ &=\frac{1}{\gamma} \frac{s+\gamma(1-\bar{y}_{2})}{\bar{y}_{3}-\bar{y}_{2}} \log\left(\frac{\bar{y}_{2}-y(r;y_{0})}{\bar{y}_{2}-y_{0}}\right) - \frac{1}{\gamma} \frac{s+\gamma(1-\bar{y}_{3})}{\bar{y}_{3}-\bar{y}_{2}} \log\left(\frac{\bar{y}_{3}-y(r;y_{0})}{\bar{y}_{3}-y_{0}}\right). \end{split}$$

Note that, $s/\gamma + (1-\bar{y}_2) = \bar{y}_3$, $s/\gamma + (1-\bar{y}_3) = \bar{y}_2$, and $\bar{y}_3 - \bar{y}_2 = \sqrt{\sigma}$ such that the claim follows. A similar argument applies, if $\bar{y}_1 > y_0 > \bar{y}_2$; only then $y(r; y_0)$ is decreasing. If $y_0 \in \{\bar{y}_1, \bar{y}_2\}$, then $y(\cdot; y_0) \equiv y_0$ such that

$$-\int_0^r \left(1 - y(\xi; y_0)\right) \left(s + \gamma(1 - y(\xi; y_0))\right) d\xi = -r(s + \gamma(1 - y_0))y_0.$$

If $\sigma > 0$ and $\gamma > s$, we can proceed similarly. The only subtlety lies in the monotonicity of $y(r; y_0)$ depending on y_0 . For $\sigma = 0$, we have $\bar{y}_2 = \bar{y}_3$ and $y(r; y_0)$ is increasing for all $y_0 \in [0, 1]$. Hence,

$$-\int_{y_0}^{y(r;y_0)} \frac{s + \gamma(1-\eta)}{u - \eta(s + \gamma(1-\eta))} d\eta = \int_{y_0}^{y(r;y_0)} -\frac{s + \gamma(1-\bar{y}_2)}{\gamma(\eta-\bar{y}_2)^2} + \frac{1}{\eta-\bar{y}_2} d\eta$$
$$= \bar{y}_2 \left(\frac{1}{y(r;y_0) - \bar{y}_2} - \frac{1}{y_0 - \bar{y}_2}\right) + \log\left(\frac{y(r;y_0) - \bar{y}_2}{y_0 - \bar{y}_2}\right)$$

At last, we treat the case $\sigma < 0$. Again, $y(r; y_0)$ is increasing. Here,

$$-\int_{y_0}^{y(r;y_0)} \frac{s+\gamma(1-\eta)}{u-\eta(s+\gamma(1-\eta))} d\eta$$

= $\frac{1}{2} \int_{y_0}^{y(r;y_0)} \frac{-(s+\gamma)+2\gamma\eta}{u-(s+\gamma)\eta+\gamma\eta^2} - \frac{1}{2} \int_{y_0}^{y(r;y_0)} \frac{s+\gamma}{u-(s+\gamma)\eta+\gamma\eta^2} d\eta$
= $\frac{1}{2} \log \left(\frac{u-y(r;y_0)(s+\gamma(1-y(r;y_0)))}{u-y_0(s+\gamma(1-y_0))} \right) - \frac{1}{2} \int_{y_0}^{y(r;y_0)} \frac{s+\gamma}{u-(s+\gamma)\eta+\gamma\eta^2} d\eta$

In the last term, we substitute $\mu = \varphi(\eta) := 2(\eta - \frac{1}{2}(1 + \frac{s}{\gamma}))/\sqrt{-\sigma}$ and we obtain

$$-\frac{1}{2}\int_{y_0}^{y(r;y_0)} \frac{s+\gamma}{u-(s+\gamma)\eta+\gamma\eta^2} d\xi = -\frac{1}{\sqrt{-\sigma}} \left(1+\frac{s}{\gamma}\right) \int_{\varphi(y_0)}^{\varphi(y(r;y_0))} \frac{1}{1+\mu^2} d\mu$$
$$= -\frac{1}{\sqrt{-\sigma}} \left(1+\frac{s}{\gamma}\right) \left[\arctan\left(\varphi(y(r;y_0))\right) - \arctan\left(\varphi(y_0)\right)\right].$$
ends the proof of Corollary 7.10.

This ends the proof of Corollary 7.10.

Lemma A.2. Let $Z = (Z_t)_{t \ge 0}$ be a binary Galton-Watson process with birth rate λ and death rate μ with $\mu < \lambda$. Let $\hat{Z} = (\hat{Z}_t)_{t \ge 0}$ be the same Galton-Watson process but conditioned to not die out. Then the transition rates of \hat{Z} are given by

$$q_{\hat{Z}}(n, n-1) = \lambda n, \qquad q_{\hat{Z}}(n, n+1) = \mu n$$

This is the continuous-time version of the classical discrete-time result (see Athreya and Ney [2, Thm. 3, 12.3]).

Proof. Consider a binary Galton-Watson process $Z = (Z_t)_{t \ge 0}$ with birth rate λ and death rate μ . The extinction probability of Z is given by $h(n) := P(Z_{\infty} = 0 \mid Z_0 = n) = (\mu/\lambda)^n$. By Doob's h-transform the rates of \hat{Z} are given by

$$q_{\hat{Z}}(n,n-1) = q_Z(n,n-1)\frac{h(n-1)}{h(n)} = \lambda n, \qquad q_{\hat{Z}}(n,n+1) = q_Z(n,n+1)\frac{h(n+1)}{h(n)} = \mu n.$$

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