

Regular Phase in a Model of Microtubule Growth

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Abstract. We study a continuous-time stochastic process on strings made of two types of particles, whose dynamics mimics the behaviour of microtubules in a living cell; namely, the strings evolve via a competition between (local) growth/shrinking as well as (global) hydrolysis processes. We show that the velocity of the string end, which determines the long-term behaviour of the system, depends analytically on the growth and shrinking rates. We also identify a region in the parameter space where the velocity is a strictly monotone function of the rates. The argument is based on stochastic domination, large deviations estimates, cluster expansions and semi-martingale techniques.

KEYWORDS: microtubules, phase transition, birth-and-death process, stochastic domination, coupling, cluster expansions

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1. Introduction

We consider a stochastic model on semi-infinite strings introduced by Antal et al. [1] as a model of microtubules, which evolve via a competition between (local) growth/shrinking and (global) hydrolysis. The model was rigorously studied in [5], where, in particular, its long-term behaviour was described in terms of velocity. The purpose of the present paper is to study dependence of the velocity v on the growth (λ^+, λ^-) and shrinking (μ) rates. We show that the limiting velocity v analytically depends on these rates in the positive orthant of \mathbb{R}_+^3 , and prove that it is strictly monotone in the region $\lambda^- \geq \lambda^+$. Notice that this monotonicity property is not universal; indeed, for some values of the growth rates in the complementary region $\lambda^- < \lambda^+$, increasing the shrinking

rate forces the velocity to change its sign at least three times [4]. This feature is a dynamical analogue of the so-called re-entrant transition for the Ising model, observed in [11].

1.1. The model

Informally, the model can be described as follows [1]: we consider semi-infinite strings made of two types of symbols, \oplus and \ominus (and containing at most a finite number of \oplus 's), whose dynamics is as follows:

$$\begin{array}{llll}
 |\dots\oplus\rangle & \mapsto & |\dots\oplus\oplus\rangle & \text{rate } \lambda^+, \\
 |\dots\ominus\rangle & \mapsto & |\dots\ominus\oplus\rangle & \text{rate } \lambda^-, \\
 |\dots\ominus\rangle & \mapsto & |\dots\rangle & \text{rate } \mu, \\
 |\dots\oplus\dots\rangle & \mapsto & |\dots\ominus\dots\rangle & \text{rate } 1.
 \end{array} \tag{1.1}$$

In words, the strings can grow by adding a \oplus symbol on the right end with rate λ^+ (if the current right end is \oplus) or λ^- (if the current right end is \ominus) and can shrink by removing the extreme \ominus symbol on the right end with rate μ ; in addition, each \oplus symbol hydrolyses (i.e., irreversibly converts into a \ominus symbol) with rate 1, independently of all other symbols.

In [5] it has been shown that the long-term behaviour of this stochastic dynamical system can be described in terms of velocity v . The purpose of this paper is to study analytic and monotonicity properties of v .

We now formally define the model and fix notations to be used in the remainder of the paper. Let $\{\oplus, \ominus\}$ be a two-symbol alphabet, and let $\mathcal{S} = \cup_{k \geq 0} \{\oplus, \ominus\}^k$ denote the collection of all finite strings, including the empty one. For $\mathbf{s} \in \mathcal{S}$, we use $\|\mathbf{s}\|$ to denote the number of \oplus symbols in \mathbf{s} , and write $|\mathbf{s}|$ for the total number of symbols in \mathbf{s} (i.e., its length). If $\mathbf{s}' = s'_k \dots s'_1$ and $\mathbf{s}'' = s''_l \dots s''_1$ are two finite strings in \mathcal{S} , we write $\mathbf{s}'\mathbf{s}''$ for the concatenated string $s'_k \dots s'_1 s''_l \dots s''_1$ of $k+l$ symbols. Further, we call a *head* any word belonging to the set

$$\mathcal{W} = \{\emptyset\} \cup \{\mathbf{w} = \oplus\mathbf{s} \text{ with } \mathbf{s} \in \mathcal{S}\} \subset \mathcal{S},$$

so that every non-empty head \mathbf{w} is a finite string whose left-most symbol is \oplus . Of course, every string $\mathbf{s} \in \mathcal{S}$ can be converted into the corresponding (possibly empty) head,

$$\mathbf{s} \mapsto \mathbf{w} \equiv \langle \mathbf{s} \rangle \in \mathcal{W}, \tag{1.2}$$

by deleting all its \ominus symbols on the left end. It is convenient to decompose

$$\mathcal{W} = \mathcal{W}_+ \cup \mathcal{W}_-,$$

where \mathcal{W}_+ contains all heads \mathbf{w} of the form $\mathbf{w} = \mathbf{w}'\oplus$ (i.e., ending with a \oplus symbol), and \mathcal{W}_- contains all remaining heads (i.e., the empty head \emptyset and all non-empty heads \mathbf{w} ending with \ominus , $\mathbf{w} = \mathbf{w}''\ominus$).

Since every string under consideration contains at most a finite number of \oplus 's, the state of the system can be described by specifying its head $\mathbf{w}_t = w_k(t) \dots w_0(t)$ and the position $x_t \in \mathbb{Z}$ of its right-most symbol $w_0(t)$. The dynamics, informally described in (1.1) above, turns the process

$$\mathbf{y}_t \equiv (x_t, \mathbf{w}_t), \quad t \geq 0, \quad (1.3)$$

into a continuous-time Markov process with values in $\mathcal{Y} \equiv \mathbb{Z} \times \mathcal{W}$. One can show [5] that the component \mathbf{w}_t on its own is a positive recurrent continuous-time Markov chain in \mathcal{W} ; in particular, $\mathbb{P}(|\mathbf{w}_t| < \infty \text{ for all } t \geq 0) = 1$. As a result, starting from any initial condition $\mathbf{y}_0 = (x_0, \mathbf{w}_0) \in \mathcal{Y}$ the trajectory of the process \mathbf{y}_t is well defined (and remains in \mathcal{Y}) for all $t \geq 0$ (with probability one). Without loss of generality we may and often shall assume that \mathbf{y}_t starts from the configuration with empty head located at the origin,

$$\mathbf{y}_0 = (x_0, \mathbf{w}_0) = (0, \emptyset). \quad (1.4)$$

Let λ^+ , λ^- and μ be fixed positive constants. We now formally describe the dynamics (1.1) of the process \mathbf{y}_t : for arbitrary non-empty heads $\mathbf{w}' \in \mathcal{W}_+$, $\mathbf{w}'' \in \mathcal{W}_-$ and $\mathbf{w} \in \mathcal{W}$, the attachment, detachment and conversion moves are defined as

$$\begin{array}{lll} (x, \mathbf{w}') & \mapsto & (x+1, \mathbf{w}' \oplus), \quad \text{rate } \lambda^+, \\ (x, \mathbf{w}'') & \mapsto & (x+1, \mathbf{w}'' \oplus), \quad \text{rate } \lambda^-, \\ (x, \emptyset) & \mapsto & (x+1, \oplus), \quad \text{rate } \lambda^-, \\ (x, \mathbf{w} \ominus) & \mapsto & (x-1, \mathbf{w}), \quad \text{rate } \mu, \\ (x, \emptyset) & \mapsto & (x-1, \emptyset), \quad \text{rate } \mu, \\ (x, \mathbf{w}) & \mapsto & (x, \langle \hat{\mathbf{w}} \rangle), \quad \text{rate } 1, \end{array}$$

where $\langle \hat{\mathbf{w}} \rangle$ is obtained from \mathbf{w} by replacing one of its \oplus symbols with the \ominus symbol (and then contracting some \ominus symbols on the left, if necessary; recall (1.2)). Notice that as a result of the last move the number $\|\mathbf{w}\|$ of \oplus symbols in \mathbf{w} will decrease by one, $\|\langle \hat{\mathbf{w}} \rangle\| = \|\mathbf{w}\| - 1$, and, if the left-most \oplus symbol in \mathbf{w} transforms into \ominus , the resulting head will be shorter, $|\langle \hat{\mathbf{w}} \rangle| < |\mathbf{w}|$, or might even become empty, $\langle \hat{\mathbf{w}} \rangle = \emptyset$.

It has been shown in [5] that for any fixed collection of positive rates λ^+ , λ^- and μ the limit

$$v = \lim_{t \rightarrow \infty} \frac{x_t - x_0}{t} \quad (1.5)$$

exists with probability one. Here we study analytic and monotonicity properties of the limiting velocity v .

1.2. Results

As a function of the positive rates λ^+ , λ^- , and μ , the velocity $v = v(\lambda^+, \lambda^-, \mu)$ has the following properties.

Theorem 1.1. *The velocity $v = v(\lambda^+, \lambda^-, \mu)$ is an analytic function of the rates.*

Theorem 1.2. *Let $\lambda^- \geq \lambda^+$. Then v is a strictly monotone function of the rates λ^+ , λ^- , and μ , with partial derivatives $\partial_{\lambda^+} v > 0$, $\partial_{\lambda^-} v > 0$, and $\partial_{\mu} v < 0$.*

Remark 1.1. One can show [4] that in the complementary region $\lambda^- < \lambda^+$ the velocity v is not everywhere monotone, and, moreover, exhibits an interesting behaviour when increasing the shrinking rate μ leads to a faster growth (i.e., increases the velocity v).

It is interesting to notice that the process \mathbf{w}_t is a particular case of a random grammar (see, e.g., [6–8] and references there). Indeed, the first three moves in (1.1) are of left linear type and the last move there is of context-free type. Of course, since the process \mathbf{w}_t is positive recurrent [5], this is a rather simple case of a random grammar. The emphasis of the present paper is on studying the velocity (1.5), which itself is a long-term characteristic of the coordinate component x_t , an additive functional of jumps of the process $(\mathbf{w}_t)_{t \geq 0}$.

The remainder of the paper is organised as follows. Theorems 1.1 and 1.2 are respectively proved in Sections 2 and 3. A cluster expansion result used in the proof of Theorem 1.2 is proved in Appendix 3.2. Our study of perturbations for continuous-time processes is based upon a variety of discrete and continuous techniques including large deviations, cluster expansions, coupling and semi-martingale estimates.

2. Analyticity of the velocity: Proof of Theorem 1.1

The model under consideration has the following renewal property [5]: if the rates λ^+ , λ^- and μ are fixed, and the dynamics starts from the initial condition $\mathbf{y}_0 = (0, \mathbf{w})$, then the Markov process $(\mathbf{y}_t)_{t \geq 0}$ is recurrent in that its \mathbf{w}_t component keeps revisiting the state \emptyset . Moreover, if $0 \leq \tilde{\tau}_0 < \tilde{\tau}_1 < \dots$ are the moments of consecutive returns to the empty-head state, and $\tilde{\mathbf{y}}_\ell \equiv \mathbf{y}_{\tilde{\tau}_\ell} = (\tilde{x}_\ell, \emptyset)$, then the differences $(\tilde{x}_\ell - \tilde{x}_{\ell-1}, \tilde{\tau}_\ell - \tilde{\tau}_{\ell-1})$, $\ell > 0$, are independent and identically distributed. By the strong law of large numbers, the velocity v of the active end of the microtubule exists and satisfies $v = \mathbf{E}(\tilde{x}_1 - \tilde{x}_0) / \mathbf{E}(\tilde{\tau}_1 - \tilde{\tau}_0)$ [5, Cor.1.1]; of course, for the empty-head initial conditions (1.4) one has $\tilde{x}_0 = \tilde{\tau}_0 = 0$.

Let $\tilde{\kappa}_1$ be the number of jumps until the process \mathbf{y}_t first returns to the empty-head state. Fix an arbitrary collection of rates $(\lambda^+, \lambda^-, \bar{\mu}) \in \mathbb{R}_+^3$ and choose $\delta_0 \in (0, \bar{\mu})$. It has been shown in [5, Sect.2.2] that if $\mathbf{E}[z^{\tilde{\kappa}_1} \exp\{\bar{s}\tilde{\tau}_1\}] < \infty$ for some $\bar{z} > 1$ and $\bar{s} > 0$, then also $\mathbf{E}[z^{\tilde{x}_1} \exp\{\bar{s}\tilde{\tau}_1\}] < \infty$. Moreover, a careful inspection of the proof of Proposition A.1 in [5] shows that

$$\limsup_{K \rightarrow \infty} \sup \mathbf{E}[z^{\tilde{x}_1} e^{s\tilde{\tau}_1} \mathbf{1}\{\tilde{\kappa}_1 > K\}] = 0,$$

where the inner supremum is taken over $0 < z < \bar{z}$, $s < \bar{s}$, $|\lambda^+ - \bar{\lambda}^+| < \delta_0$, $|\lambda^- - \bar{\lambda}^-| < \delta_0$, $|\mu - \bar{\mu}| < \delta_0$, with possibly smaller $\delta_0 > 0$. Since for every $K \geq 1$ the expectation $\mathbb{E}[z^{\tilde{x}_1} e^{s\tilde{\tau}_1} \mathbb{1}\{\tilde{\kappa}_1 \leq K\}]$ is a finite analytic function of the rates $(\lambda^+, \lambda^-, \mu)$ as well as the parameters z and s in the region described above, the expectation $\Phi_0(z, s) \equiv \mathbb{E}[z^{\tilde{x}_1} e^{s\tilde{\tau}_1}]$ is also analytic there. This implies that the averages

$$\mathbb{E}\tilde{x}_1 \equiv \frac{d}{dz} \Phi_0(z, s) \Big|_{(1,0)}, \quad \mathbb{E}\tilde{\tau}_1 \equiv \frac{d}{ds} \Phi_0(z, s) \Big|_{(1,0)}$$

are analytic functions for such values of the rates, and thus everywhere in \mathbb{R}_+^3 . Finally, as $\tilde{\tau}_1 > 0$ is a non-degenerate random variable, we deduce that $\mathbb{E}\tilde{\tau}_1 > 0$ for all positive values of rates, and therefore the velocity $v = \mathbb{E}\tilde{x}_1/\mathbb{E}\tilde{\tau}_1$ is an analytic function of the rates λ^+ , λ^- , and μ in \mathbb{R}_+^3 .

3. Monotonicity of the velocity: Proof of Theorem 1.2

Here we prove the main result of this note — Theorem 1.2. Our argument consists of two main steps, and we illustrate the idea in the case of varying λ^+ , with the argument for $\partial_{\lambda^-} v$ and $\partial_{\mu} v$ being similar. Let $\mathbf{y}'_t = (x'_t, \mathbf{w}'_t)$ and $\mathbf{y}''_t = (x''_t, \mathbf{w}''_t)$ be two copies of the process with rates $(\lambda', \lambda^-, \mu)$ and $(\lambda'', \lambda^-, \mu)$ respectively, where $\lambda' = \lambda^+ + \delta$ and $\lambda'' = \lambda^+$ with small $\delta > 0$. First, using Lemma 3.1 below, we construct a monotone coupling, which preserves the following stochastic order: if $\mathbf{y}'_0 = (x'_0, \emptyset)$ and $\mathbf{y}''_0 = (x''_0, \emptyset)$ with $x'_0 \leq x''_0$, then $x'_t \leq x''_t$ for most $t \geq 0$. We then use large deviation bounds together with the cluster expansion estimate from Proposition A.1 below to show that, for some constant $c > 0$ and all $\delta > 0$ small enough, the inequality

$$v(\lambda^+ + \delta, \lambda^-, \mu) - v(\lambda^+, \lambda^-, \mu) \geq c\delta > 0 \quad (3.1)$$

holds with probability one. By analyticity of v , this implies that $\partial_{\lambda^+} v > 0$ with probability one. With a bit of extra work, one can even derive an “explicit” expression for this derivative, see below.

3.1. A coupling lemma

Let $\mathbf{y}'_t = (x'_t, \mathbf{w}'_t)$ and $\mathbf{y}''_t = (x''_t, \mathbf{w}''_t)$ be two copies of the process \mathbf{y}_t with the empty-head initial condition (1.4) and the respective rates $(\lambda', \lambda^-, \mu)$ and $(\lambda'', \lambda^-, \mu)$, where $\lambda' = \lambda^+$ and $\lambda'' = \lambda^+ + \delta$ with some small $\delta > 0$. We can think of the process \mathbf{y}''_t as a perturbation of \mathbf{y}'_t , by subjecting the latter to an additional Poisson process of intensity $\delta > 0$ of attempts to attach a \oplus symbol on the right end of \mathbf{w}_t (which will be successful only if $\mathbf{w}_t \in \mathcal{W}_+$). Let t_0 be the (random) moment of the first such successful arrival. We then have $\mathbf{y}'_t \equiv \mathbf{y}''_t$ for $t \in [0, t_0)$ and

$$\mathbf{y}'_{t_0} = (x_{t_0}, \mathbf{w}_{t_0}), \quad \mathbf{y}''_{t_0} = (x_{t_0} + 1, \mathbf{w}_{t_0} \oplus), \quad (3.2)$$

with some $\mathbf{w}_{t_0} \in \mathcal{W}_+$. Let $0 \leq \tau_0'' < \tau_1'' < \dots$ be the consecutive moments when the process \mathbf{y}_t'' enters an empty-head configuration,

$$\mathbf{y}_{\tau_k''} = (x_{\tau_k''}, \emptyset).$$

In what follows we shall see that the main contribution to the left-hand side of (3.1) comes from those “excursions” $[\tau_{k-1}'', \tau_k'']$ which contain a single successful \oplus arrival of the additional $\text{Poi}(\delta)$ stream. When combined with the cluster estimate from Proposition A.1 below, this observation can even be used to derive an “explicit” description of the partial derivative $\partial_{\lambda^+} v$.

By the strong Markov property, given (3.2), the future behaviour of the pair of processes $(\mathbf{y}_t', \mathbf{y}_t'')_{t \geq t_0}$ is independent of the past behaviour, $t < t_0$. By shifting the time origin, we thus can study a single “truncated” excursion for the pair $(\mathbf{y}_t', \mathbf{y}_t'')_{t \geq 0}$ with initial conditions

$$\mathbf{y}'_0 = (x, \mathbf{w}), \quad \mathbf{y}''_0 = (x + 1, \mathbf{w} \oplus), \quad \mathbf{w} \in \mathcal{W}_+. \quad (3.3)$$

Of course, when studying $\partial_{\lambda^-} v$ or $\partial_{\mu} v$ one has to respectively consider the initial conditions

$$\mathbf{y}'_0 = (x, \mathbf{w}), \quad \mathbf{y}''_0 = (x + 1, \mathbf{w} \oplus), \quad \mathbf{w} \in \mathcal{W}_-, \quad (3.4)$$

(with respective rates $(\lambda^+, \lambda', \mu)$ and $(\lambda^+, \lambda'', \mu)$, where $\lambda' = \lambda^-$, $\lambda'' = \lambda^- + \delta$ for some small $\delta > 0$) or the initial conditions

$$\mathbf{y}'_0 = (x, \mathbf{w}), \quad \mathbf{y}''_0 = (x + 1, \mathbf{w} \ominus), \quad \mathbf{w} \in \mathcal{W}, \quad (3.5)$$

(with respective rates $(\lambda^+, \lambda^-, \mu')$ and $(\lambda^+, \lambda^-, \mu'')$, where $\mu' = \mu + \delta$, $\mu'' = \mu$ for some small $\delta > 0$).

The key result of this section — Lemma 3.1 below — essentially states that with any of the three initial conditions listed above, at the moment τ_1'' of the first visit to the empty-state configuration by the process \mathbf{y}_t'' we have $x_{\tau_1''}'' \geq x_{\tau_1''}'$; moreover, one can show that the expectation of the difference $x_{\tau_1''}'' - x_{\tau_1''}'$ is in fact positive (so that the estimate (3.1) follows from the ergodic theorem). We notice that arguments similar to those used in [5] show that τ_1'' has exponential moments in a neighbourhood of the origin; therefore, for $\delta > 0$ very small, the main contribution to the difference $x_{\tau_1''}'' - x_{\tau_1''}'$ comes from the excursions having no additional \oplus arrivals from the $\text{Poi}(\delta)$ stream. It is thus important to understand the impact of the initial conditions (3.3)–(3.5) on the dynamics of the process \mathbf{y}_t . We do this by constructing a maximal parallel coupling of the pair $(\mathbf{y}_t', \mathbf{y}_t'')$ of two copies of \mathbf{y}_t with the *same set of rates* $(\lambda^+, \lambda^-, \mu)$ but starting from the initial conditions of the type (3.3)–(3.5). The corresponding result is presented in Lemma 3.1 below, but before stating it we need to introduce some additional notation.

Every configuration $(x, \mathbf{w}) \in \mathcal{Y}$, where $\mathbf{w} = w_{|\mathbf{w}|-1} \dots w_1 w_0$, is in one-to-one correspondence with the related semi-infinite string $\bar{\mathbf{s}} = \dots \bar{s}_{x-2} \bar{s}_{x-1} \bar{s}_x$, namely,

$$\bar{s}_{x-k} = w_k, \quad k = 0, \dots, |\mathbf{w}| - 1, \quad \text{and} \quad \bar{s}_{x-k} \equiv \ominus, \quad k \geq |\mathbf{w}|.$$

Of course, every two semi-infinite strings $\bar{\mathbf{s}}'$ and $\bar{\mathbf{s}}''$ can have only a finite number of positions for which they differ. For the argument below it is convenient to allow any two such strings to run “in parallel for as long as they can”, and thus it is natural to extract their maximal common right-most part. This idea is formally introduced as follows, see Figure 1 below.

Let $\bar{\mathbf{s}}' = \dots \bar{s}'_{x'-2} \bar{s}'_{x'-1} \bar{s}'_{x'} \sim (x', \mathbf{w}')$ and $\bar{\mathbf{s}}'' = \dots \bar{s}''_{x''-2} \bar{s}''_{x''-1} \bar{s}''_{x''} \sim (x'', \mathbf{w}'')$ be two semi-infinite strings with $x' \leq x''$. We first define

$$k_r = \max \{k \geq 0 : k < \max(|\mathbf{w}'|, |\mathbf{w}''|) \text{ and } w'_j = w''_j \text{ for all } j = 0, \dots, k\}$$

if the set of j 's under consideration is not empty, and then put

$$\mathbf{s}_r = \mathbf{s}_r' = \mathbf{s}_r'' = w'_{k_r} \dots w'_1 w'_0 \equiv \bar{s}'_{x'-k_r} \dots \bar{s}'_{x'-1} \bar{s}'_{x'};$$

alternatively, we declare $k_r = -1$ and write $\mathbf{s}_r = \mathbf{s}_r' = \mathbf{s}_r'' = \emptyset$. Informally, \mathbf{s}_r is the maximal common part of $\bar{\mathbf{s}}'$ and $\bar{\mathbf{s}}''$ on the right, if they were translated to end at the same position $x \in \mathbb{Z}$ (notice that if $|\mathbf{w}'| < |\mathbf{w}''|$, one might have $|\mathbf{w}'| < |\mathbf{s}_r| < |\mathbf{w}''|$, i.e., the maximal common part \mathbf{s}_r of $\bar{\mathbf{s}}'$ and $\bar{\mathbf{s}}''$ on the right can be longer than the shorter of the two heads; indeed, if $\mathbf{w}' = \emptyset$ and $\mathbf{w}'' = \oplus \ominus$, we have $\mathbf{s}_r = \ominus$).

We next define

$$k_l = \min \{k > k_r : \bar{s}'_{x'-j} = \bar{s}''_{x''-j} \text{ for all } j \geq k\},$$

which always exists as any two semi-infinite strings coincide for all positions far enough to the left. Let $\hat{\mathbf{s}}$ be the maximal common part of $\bar{\mathbf{s}}'$ and $\bar{\mathbf{s}}''$ on the left,

$$\hat{\mathbf{s}} = \dots \bar{s}'_{x'-k_r-2} \bar{s}'_{x'-k_r-1}.$$

If $\|\hat{\mathbf{s}}\| > 0$, i.e., $\hat{\mathbf{s}}$ contains \oplus symbols, we apply the contraction operator (1.2) to extract the shortest sub-head $\mathbf{w}_1 = \langle \hat{\mathbf{s}} \rangle$ of $\hat{\mathbf{s}}$; otherwise $\hat{\mathbf{s}}$ contains no \oplus symbols, and we put $\mathbf{w}_1 = \emptyset$.

Finally, we define the “central parts” of $\bar{\mathbf{s}}'$ and $\bar{\mathbf{s}}''$ via

$$\mathbf{s}_c' = \bar{s}'_{x'-k_r+1} \dots \bar{s}'_{x'-k_l-1} \quad \text{and} \quad \mathbf{s}_c'' = \bar{s}''_{x''-k_r+1} \dots \bar{s}''_{x''-k_l-1},$$

with the tacit assumption that if any of the index intervals above is empty then the corresponding \mathbf{s}_c string equals \emptyset by definition.

With this construction, the canonical form (1.3) of the semi-infinite string $\bar{\mathbf{s}}'$ becomes $(x', \mathbf{w}') \equiv (x', \mathbf{w}_1 \mathbf{s}_c' \mathbf{s}_r)$, whereas that of $\bar{\mathbf{s}}''$ becomes $(x'', \mathbf{w}'') \equiv$

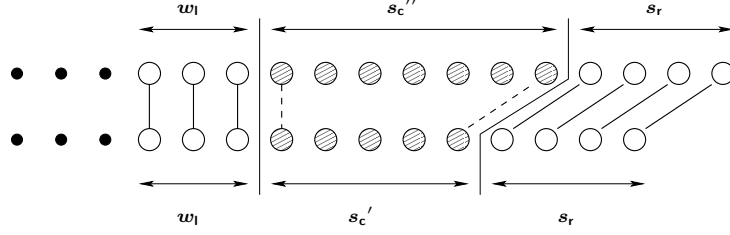


Figure 1. Parallel decomposition of two semi-infinite strings: symbols connected with solid lines are identical in both strings, symbols connected with dashed lines are distinct. If \mathbf{s}_c' is empty but \mathbf{s}_c'' is not, the right-most symbol in \mathbf{s}_c'' is different from that in \mathbf{w}_1 . If $\mathbf{s}_c' = \mathbf{s}_c'' = \emptyset$, we have $\mathbf{w}_1 = \emptyset$ and thus $\mathbf{s}_r \equiv \mathbf{w}$.

$(x'', \mathbf{w}_1 \mathbf{s}_c'' \mathbf{s}_r)$. When the values x' and x'' are not important, we abbreviate this representation to

$$[\mathbf{w}_1 \mathbf{s}_c'' \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_c' \mathbf{s}_r] \quad (3.6)$$

and drop any of the components which is empty. Notice that the relative shift $x'' - x'$ of these strings can be deduced from (3.6) via $x'' - x' = |\mathbf{s}_c''| - |\mathbf{s}_c'|$.

For the strings corresponding to (3.3)–(3.5), one can see that $\mathbf{s}_c' = \emptyset$ and \mathbf{s}_c'' is a one-symbol string, $|\mathbf{s}_c''| = 1$, with $\mathbf{s}_c'' = \oplus$ in (3.3)–(3.4) and $\mathbf{s}_c'' = \ominus$ in (3.5). Moreover if \mathbf{w} in (3.3) ends with exactly k symbols \oplus , i.e., can be written as $\mathbf{w} = \hat{\mathbf{w}} \oplus_k$ with $\hat{\mathbf{w}} \in \mathcal{W}_-$, then

$$\mathbf{w}_1 = \hat{\mathbf{w}}, \quad \mathbf{s}_c' = \emptyset, \quad \mathbf{s}_c'' = \oplus, \quad \mathbf{s}_r = \oplus_k;$$

so that the representation (3.6) becomes $[\hat{\mathbf{w}} \oplus \oplus_k : \hat{\mathbf{w}} \oplus_k]$, with possibly empty sub-head $\hat{\mathbf{w}} \in \mathcal{W}_-$. Similarly, for the configuration described in (3.4) with $\mathbf{w} \in \mathcal{W}_-$,

$$\mathbf{w}_1 = \mathbf{w}, \quad \mathbf{s}_c' = \emptyset, \quad \mathbf{s}_c'' = \oplus, \quad \mathbf{s}_r = \emptyset,$$

and (3.6) becomes $[\mathbf{w} \oplus : \mathbf{w}]$, with possibly empty $\mathbf{w} \in \mathcal{W}_-$. Finally, if the head \mathbf{w} in (3.5) ends with exactly m symbols \ominus , i.e., $\mathbf{w} = \hat{\mathbf{w}} \ominus_m$ with $\hat{\mathbf{w}} \in \mathcal{W}_+$, then

$$\mathbf{w}_1 = \hat{\mathbf{w}}, \quad \mathbf{s}_c' = \emptyset, \quad \mathbf{s}_c'' = \ominus, \quad \mathbf{s}_r = \ominus_m,$$

which is written as $[\hat{\mathbf{w}} \ominus \ominus_m : \hat{\mathbf{w}} \ominus_m]$ with $\hat{\mathbf{w}} \in \mathcal{W}_+$, and if $\mathbf{w} \in \mathcal{W}_+$, then

$$\mathbf{w}_1 = \mathbf{w}, \quad \mathbf{s}_c' = \emptyset, \quad \mathbf{s}_c'' = \ominus, \quad \mathbf{s}_r = \emptyset,$$

and gives $[\mathbf{w} \ominus : \mathbf{w}]$ with $\mathbf{w} \in \mathcal{W}_+$; of course, the trivial case of $\mathbf{w} = \emptyset$ in (3.5) gives just $[\ominus : \emptyset]$. Notice that in all these cases we have $\|\mathbf{s}_c''\| \leq |\mathbf{s}_c''| = 1$.

One can now couple two copies, \mathbf{y}_t' and \mathbf{y}_t'' , of the process \mathbf{y}_t with initial conditions (3.6) in such a way that the common \mathbf{w}_1 -parts and \mathbf{s}_r -parts perform identical moves in both processes, which we refer to as the *maximal parallel*

coupling. An important feature of this coupling is that if $\mathbf{s}_c' = \emptyset$, the structure (3.6) with $\mathbf{s}_c'(t) = \emptyset$ is preserved for all future times (though the actual sub-strings might vary); moreover, the inequality $|\mathbf{s}_c''(t)| \geq |\mathbf{s}_c''| - 1$ holds for all $t \geq 0$. We will show below that if $\mathbf{s}_c' = \emptyset$, the maximal parallel dynamics reaches a state of the type $[\tilde{\mathbf{s}}_c \tilde{\mathbf{s}}_r : \tilde{\mathbf{s}}_r]$ with $\tilde{\mathbf{s}}_c = \ominus_m$ for some $m \geq 0$, i.e., the coupling event occurs, in which both semi-infinite strings become identical but shifted by $|\tilde{\mathbf{s}}_c| \geq 0$ symbols relative to each other. From that moment onwards, the maximal parallel dynamics constructed in the proof below will preserve the shift of \mathbf{y}'_t relative to \mathbf{y}''_t .

Lemma 3.1. *Let $\lambda^- \geq \lambda^+$. For every initial condition of the type $[\mathbf{w}_1 \mathbf{s}_c \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_r]$ with $\mathbf{w}_1 \in \mathcal{W}$ and $\mathbf{s}_c, \mathbf{s}_r \in \mathcal{S}$ satisfying $\|\mathbf{s}_c\| \leq 1$ and $|\mathbf{s}_c| \geq 1$, there exists a coupling of \mathbf{y}'_t and \mathbf{y}''_t resulting in a coupling event with relative shift of length at least $|\mathbf{s}_c| - 1 \geq 0$.*

Proof. We proceed by induction in $\|\mathbf{w}_1\| \geq 0$ and show that the statement of the lemma holds for all initial conditions $[\mathbf{w}_1 \mathbf{s}_c \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_r]$ with $\|\mathbf{s}_c\| \leq 1$ and $|\mathbf{s}_c| > 0$.

If $\|\mathbf{w}_1\| = 0$ (i.e., $\mathbf{w}_1 = \emptyset$), we start by considering the following partial case:

$$\mathbf{w}_1 = \mathbf{s}_r = \emptyset, \quad \mathbf{s}_c = \ominus_m \oplus, \quad m \geq 0, \quad (3.7)$$

i.e., at time $t \geq 0$ we have $\mathbf{y}'_t = (x', \oplus)$, $\mathbf{y}''_t = (x'', \emptyset)$ with $x' - x'' = |\mathbf{s}_c| = m + 1 > 0$. Consider four independent exponential random variables

$$\zeta_1 \sim \text{Exp}(\lambda^- - \lambda^+), \quad \zeta_2 \sim \text{Exp}(1), \quad \zeta_3 \sim \text{Exp}(\mu), \quad \zeta_4 \sim \text{Exp}(\lambda^+)$$

and put $\zeta = \min(\zeta_1, \zeta_2, \zeta_3, \zeta_4)$. Here and below, the distribution $\text{Exp}(0)$ describes non-negative random variables ζ' which are infinite with probability one (and thus the event $\zeta = \zeta'$ has probability zero). The first transition in the joint model occurs after time ζ and is as follows:

- If $\zeta = \zeta_1$, then a \oplus symbol attaches to the second string,

$$\mathbf{y}'_{t+\zeta} = (x', \oplus), \quad \mathbf{y}''_{t+\zeta} = (x'' + 1, \oplus),$$

and thus from that moment onwards both processes will run in parallel with relative shift $x' - x'' - 1 = |\mathbf{s}_c| - 1 \geq 0$.

- If $\zeta = \zeta_2$, then the \oplus symbol hydrolyses,

$$\mathbf{y}'_{t+\zeta} = (x', \emptyset), \quad \mathbf{y}''_{t+\zeta} = (x'', \emptyset),$$

thus finishing the current cycle with relative shift $|\mathbf{s}_c| > 0$.

- If $\zeta = \zeta_3$, then the extreme \ominus symbol leaves the second string,

$$\mathbf{y}'_{t+\zeta} = (x', \oplus), \quad \mathbf{y}''_{t+\zeta} = (x'' - 1, \emptyset),$$

i.e., we revisit the initial condition (3.7) with $m \geq 0$ increased by one.

- If $\zeta = \zeta_4$, then single \oplus symbols attach to both strings,

$$\mathbf{y}'_{t+\zeta} = (x' + 1, \oplus\oplus), \quad \mathbf{y}''_{t+\zeta} = (x'' + 1, \oplus),$$

thus giving a canonical pair with

$$\mathbf{w}_1 = \emptyset, \quad \mathbf{s}_c = \ominus_m \oplus, \quad \mathbf{s}_r = \oplus.$$

In the last case, from the moment $t + \zeta$ both strings will develop in parallel until the time $\tau_c \wedge \tau_r$, where

$$\tau_c \stackrel{\text{def}}{=} \min \{s \geq t + \zeta : \mathbf{s}_c(s) = \ominus_{m+1}\}, \quad \tau_r \stackrel{\text{def}}{=} \min \{s \geq t + \zeta : \mathbf{s}_r(s) = \emptyset\}.$$

In the first case (i.e., when $\tau_c < \tau_r$) we arrive at the coupling event $[\ominus_{m+1}\tilde{\mathbf{s}}_r : \tilde{\mathbf{s}}_r]$ after which the system will develop in parallel (with horizontal shift $m + 1$). On the other hand, if $\tau_r < \tau_c$ the system revisits the initial configuration $[\ominus_m \oplus : \emptyset]$, recall (3.7). Since on every visit to a state of the type (3.7) (i.e., $\|\mathbf{w}_1\| = \|\mathbf{s}_r\| = 0$, $\|\mathbf{s}_c\| = 1$) the hydrolysis of the only \oplus symbol occurs with probability $1/(1 + \mu + \lambda^-)$, it is immediate to deduce that the coupling event occurs after a random time with finite exponential moments in a neighbourhood of the origin.

As the argument above also covers the case $[\mathbf{s}_c \mathbf{s}_r : \mathbf{s}_r]$ with $\mathbf{s}_r \neq \emptyset$, the claim of the lemma holds for all canonical pairs $[\mathbf{w}_1 \mathbf{s}_c \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_r]$ with $\mathbf{w}_1 = \emptyset$ and \mathbf{s}_c satisfying $\|\mathbf{s}_c\| \leq 1$, $|\mathbf{s}_c| > 0$.

We turn now to verifying the inductive step. Suppose that the claim of the lemma has been proved for all canonical pairs $[\mathbf{w}_1 \mathbf{s}_c \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_r]$ with $\|\mathbf{s}_c\| \leq 1$ and $\mathbf{w}_1 \in \mathcal{W}$ satisfying $\|\mathbf{w}_1\| \leq k$. Starting from the initial conditions

$$[\mathbf{w}_1 \mathbf{s}_c \mathbf{s}_r : \mathbf{w}_1 \mathbf{s}_r] \quad \text{with} \quad \|\mathbf{w}_1\| = k + 1, \quad (3.8)$$

we introduce the following stopping times (notice that the numbers $\|\mathbf{w}_1(s)\|$ and $\|\mathbf{s}_c(s)\|$ of \oplus symbols in the internal blocks do not increase when \mathbf{s}_r is not empty)

$$\begin{aligned} \tau_1 &= \min \{s > t : \|\mathbf{w}_1(s)\| = k\}, \\ \tau_c &= \min \{s > t : \|\mathbf{s}_c(s)\| = 0\}, \\ \tau_r &= \min \{s > t : \mathbf{s}_r(s) = \emptyset\}, \end{aligned}$$

and put $\bar{\tau} = \min(\tau_1, \tau_c, \tau_r)$. Three cases are possible ($\bar{\tau} = \tau_1$, $\bar{\tau} = \tau_c$, and $\bar{\tau} = \tau_r$), which will be considered separately.

Case I: if $\bar{\tau} = \tau_1$, then the claim of the lemma follows from the induction hypothesis.

Case II: if $\bar{\tau} = \tau_c$, we arrive at a canonical pair

$$[\mathbf{w}'_1 \ominus_{m+1} \mathbf{s}'_r : \mathbf{w}'_1 \mathbf{s}'_r] \quad (3.9)$$

with some $\mathbf{s}_r' \neq \emptyset$ and $\mathbf{w}_1' \in \mathcal{W}_+$ such that $\|\mathbf{w}_1'\| = \|\mathbf{w}_1\| = k + 1$ (in fact \mathbf{w}_1' is just \mathbf{w}_1 with all its \ominus symbols on the right, if any, removed). We now denote:

$$\tau_1' = \min \{s > \tau_c : \|\mathbf{w}_1'(s)\| = k\}, \quad \tau_r' = \min \{s > \tau_c : \mathbf{s}_r'(s) = \emptyset\}.$$

If $\tau_1' < \tau_r'$, the the claim of the lemma follows from the induction hypothesis. On the other hand, if $\tau_1' > \tau_r'$, we arrive at a canonical pair of the type

$$[\mathbf{w}_1' \ominus_{m+1} : \mathbf{w}_1'], \quad \mathbf{w}_1' \in \mathcal{W}_+, \quad (3.10)$$

and investigate the effect of all possible moves out of this configuration. To this end, consider four independent exponential random variables

$$\zeta_1 \sim \text{Exp}(k + 1), \quad \zeta_2 \sim \text{Exp}(\mu), \quad \zeta_3 \sim \text{Exp}(\lambda^+), \quad \zeta_4 \sim \text{Exp}(\lambda^- - \lambda^+),$$

and put $\zeta = \min(\zeta_1, \zeta_2, \zeta_3, \zeta_4)$. The first transition in the joint model occurs after time ζ and is given by

- If $\zeta = \zeta_1$, then one of the \oplus symbols in \mathbf{w}_1' hydrolyses, and the result follows from the induction hypothesis.
- If $\zeta = \zeta_2$, then the extreme \ominus symbol leaves the longer string. If \mathbf{s}_c becomes empty (when $m = 0$), both strings become identical and we arrive at the coupling event (with zero shift). Otherwise the configuration becomes $[\mathbf{w}_1' \ominus_m : \mathbf{w}_1']$ with $\mathbf{w}_1' \in \mathcal{W}_+$, i.e., of the type (3.10).
- If $\zeta = \zeta_3$, then individual \oplus symbols attach to both strings, so that the new configuration has heads $\mathbf{w}_1' \ominus_{m+1} \oplus$ and $\mathbf{w}_1' \oplus$ with $\mathbf{w}_1' \in \mathcal{W}_+$, i.e., we revisit a state of the type (3.8).
- If $\zeta = \zeta_4$, a \oplus symbol attaches to the longer string and we arrive at the configuration with heads $\mathbf{w}_1' \ominus_{m+1} \oplus$ and \mathbf{w}_1' , i.e.,

$$[\mathbf{w}_1'' \mathbf{s}_c'' \mathbf{s}_r'' : \mathbf{w}_1'' \mathbf{s}_r'']$$

with $\|\mathbf{s}_r''\| \geq 1$, $\|\mathbf{s}_c\| = 1$ and $\|\mathbf{w}_1''\| < \|\mathbf{w}_1'\|$, so that the result follows from the induction hypothesis.

Case III: if $\bar{\tau} = \tau_r$, we arrive at a canonical pair

$$[\mathbf{w}_1' \mathbf{s}_c' : \mathbf{w}_1'] \quad \text{with} \quad \|\mathbf{s}_c'\| = 1, \quad |\mathbf{s}_c'| = |\mathbf{s}_c|. \quad (3.11)$$

If $\|\mathbf{w}_1'\| < \|\mathbf{w}_1\|$, the result follows from the induction hypothesis. We thus consider the case when $\|\mathbf{w}_1'\| = \|\mathbf{w}_1\|$ (so that \mathbf{w}_1' and \mathbf{w}_1 can only differ by the number of \ominus symbols on the right end) and observe that the condition $\mathbf{s}_r' = \emptyset$ implies that in the pair (3.11) the right-most symbols of \mathbf{s}_c' and \mathbf{w}_1' are different.

Case IIIa: Let $\mathbf{w}_1' \in \mathcal{W}_-$, in other words

$$\mathbf{y}'_{\bar{\tau}} = (x', \mathbf{w}_1' \ominus_m \oplus), \quad \mathbf{y}''_{\bar{\tau}} = (x'', \mathbf{w}_1'), \quad x' - x'' = |\mathbf{s}_c'| = m + 1.$$

This state corresponds to the canonical representation

$$[\mathbf{w}_1'' \ominus_{l+m} \oplus : \mathbf{w}_1'' \ominus_l], \quad \mathbf{w}_1'' \in \mathcal{W}_+, \quad l > 0, \quad (3.12)$$

and we study the effect of a single step of the joint dynamics from this state. To this end, consider five independent exponential random variables

$$\begin{aligned} \zeta_1 &\sim \text{Exp}(1), & \zeta_2 &\sim \text{Exp}(\|\mathbf{w}_1''\|), & \zeta_3 &\sim \text{Exp}(\mu), \\ \zeta_4 &\sim \text{Exp}(\lambda^+), & \zeta_5 &\sim \text{Exp}(\lambda^- - \lambda^+) \end{aligned}$$

and put $\bar{\zeta} = \min(\zeta_1, \zeta_2, \zeta_3, \zeta_4, \zeta_5)$. The first transition in the joint model occurs after time $\bar{\zeta}$ and is given by

- If $\bar{\zeta} = \zeta_1$, the right-most \oplus symbol in \mathbf{y}'_t hydrolyses, so that we arrive at the canonical pair $[\mathbf{w}_1'' \ominus_{l+m+1} : \mathbf{w}_1'' \ominus_l]$, i.e., we revisit a state of the type (3.9).
- If $\bar{\zeta} = \zeta_2$, the total number of \oplus symbols in \mathbf{w}_1'' decreases by one, so that the result follows from the induction hypothesis.
- If $\bar{\zeta} = \zeta_3$, the extreme \ominus symbol leaves \mathbf{y}''_t . If the string \mathbf{y}''_t still ends with \ominus symbol, we revisit a configuration of the type (3.12) with $l > 0$. Alternatively, $l = 0$, and we arrive at a configuration whose canonical representation $[\mathbf{w}_1''' \mathbf{s}_c''' \mathbf{s}_r''' : \mathbf{w}_1''' \mathbf{s}_r''']$ satisfies $\|\mathbf{w}_1'''\| < \|\mathbf{w}_1''\|$, so that the result follows from the induction hypothesis.
- If $\bar{\zeta} = \zeta_4$, a \oplus symbol attaches to both strings and we revisit a state of the type (3.8).
- If $\bar{\zeta} = \zeta_5$, a \oplus symbol attaches to the shorter string, so that we arrive at the configuration with heads $\mathbf{w}''_t \ominus_{l+m} \oplus$ and $\mathbf{w}''_t \ominus_l \oplus$, where $\mathbf{w}''_t \in \mathcal{W}_+$, i.e., we revisit a state of the type (3.9) with $|\mathbf{s}_c|$ decreased by one. Notice, that if $m = 0$, both heads become identical and we arrive at a coupling event with zero shift.

This finishes our discussion of the case (3.12).

Case IIIb: Let $\mathbf{w}_1' \in \mathcal{W}_+$, in other words

$$\mathbf{y}'_{\bar{\tau}} = (x', \mathbf{w}_1' \mathbf{s}_c'), \quad \mathbf{y}''_{\bar{\tau}} = (x'', \mathbf{w}_1'), \quad x' - x'' = |\mathbf{s}_c'| = |\mathbf{s}_c|, \quad (3.13)$$

where $\mathbf{s}_c' \in \mathcal{S}_-$ (i.e., the right-most symbol of \mathbf{s}_c' is \ominus) contains exactly a single \oplus symbol, $\|\mathbf{s}_c'\| = 1$. Consider five independent exponential random variables,

$$\begin{aligned} \zeta_1 &\sim \text{Exp}(1), & \zeta_2 &\sim \text{Exp}(\|\mathbf{w}_1'\|), & \zeta_3 &\sim \text{Exp}(\mu), \\ \zeta_4 &\sim \text{Exp}(\lambda^+), & \zeta_5 &\sim \text{Exp}(\lambda^- - \lambda^+) \end{aligned}$$

and put $\bar{\zeta} = \min(\zeta_1, \zeta_2, \zeta_3, \zeta_4, \zeta_5)$. The first transition in the joint model occurs after time $\bar{\zeta}$ and is given by

- If $\bar{\zeta} = \zeta_1$, then the only \oplus symbol in \mathbf{s}_c' hydrolyses, and we arrive at a state of the type (3.9) with $\mathbf{s}_r' = \emptyset$.
- If $\bar{\zeta} = \zeta_2$, then one of the \oplus symbols in \mathbf{w}_l' hydrolyses, so that the result follows from the induction hypothesis.
- If $\bar{\zeta} = \zeta_3$, then the extreme \ominus symbol in \mathbf{s}_c' departs; as a result, we either stay in the same class (3.13) of configurations (with $\mathbf{s}_c'' \in \mathcal{S}_-$), or the right-most symbol in \mathbf{s}_c'' becomes \oplus , thus leading to the canonical representation of the form $[\mathbf{w}_l'' \mathbf{s}_c'' \mathbf{s}_r'' : \mathbf{w}_l'' \mathbf{s}_r'']$ with $\|\mathbf{w}_l''\| < \|\mathbf{w}_l'\|$, so that the result follows from the induction hypothesis.
- If $\bar{\zeta} = \zeta_4$, single \oplus symbols attach to both strings, so that we revisit the initial state of the type (3.8).
- If $\bar{\zeta} = \zeta_5$, then a \oplus symbol attaches to the longer string, thus leading to the canonical pair $[\mathbf{w}_l'' \mathbf{s}_c'' \mathbf{s}_r'' : \mathbf{w}_l'' \mathbf{s}_r'']$ with $\|\mathbf{w}_l''\| < \|\mathbf{w}_l'\|$ and $\|\mathbf{s}_c''\| \geq 1$, so that the result follows from the induction hypothesis.

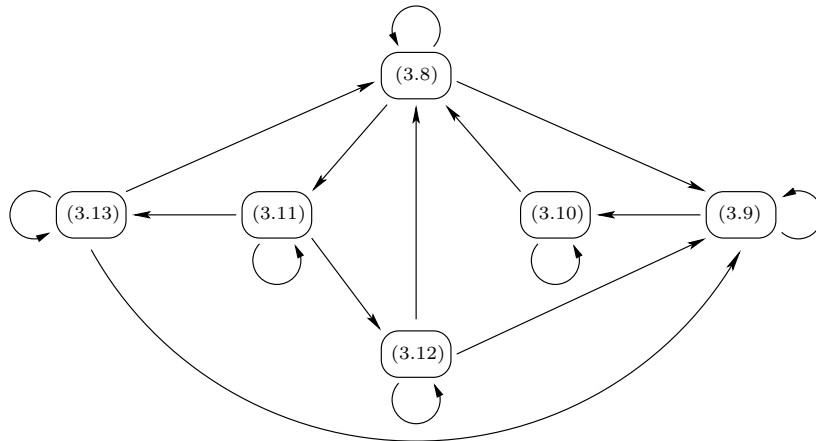


Figure 2. Connections between classes of configurations in the proof of Lemma 3.1; additionally, from every class the “induction hypothesis” class can be reached.

This finishes the list of possible classes of configurations and the connections between them. The whole structure is summarised in Figure 2, which for simplicity does not show the “inductive hypothesis” class of states and the

corresponding transitions; the latter can be reached from any of the nodes of the diagram.

With the induction step verified, the claim of Lemma 3.1 follows. \square

3.2. Strict monotonicity of the velocity

Fix positive rates λ^+ , λ^- , μ , and arbitrary $\delta_0 > 0$. Our aim is to show that if $\lambda^+ \leq \lambda^-$ and δ_0 is small enough, then for some constant $c = c(\lambda^+ + \delta_0, \lambda^-, \mu) > 0$ and all $\delta \in (0, \delta_0)$ the inequality (3.1),

$$v(\lambda^+ + \delta, \lambda^-, \mu) - v(\lambda^+, \lambda^-, \mu) \geq c\delta > 0,$$

holds with probability one. As explained above, this implies positivity of the corresponding partial derivative $\partial_{\lambda^+} v$ and, in particular, strict monotonicity of $v(\cdot, \lambda^-, \mu)$ as a function of λ^+ . Of course, similar arguments apply to other partial derivatives of interest, $\partial_{\lambda^-} v$ and $\partial_{\mu} v$.

Since x_t is a functional of the Markov chain \mathbf{w}_t , our arguments are close in spirit to the proof of the Ergodic theorem for Markov chains, see e.g., [10].

Let $0 = \tilde{\tau}_0^\delta < \tilde{\tau}_1^\delta < \tilde{\tau}_2^\delta < \dots$ be the consecutive moments when the process \mathbf{y}_t'' with rates $(\lambda^+ + \delta, \lambda^-, \mu)$ enters a state with empty head, $\mathbf{w}_{\tilde{\tau}_j^\delta} = \emptyset$. Denote by $\tilde{\ell}_t^\delta$ the total number of complete excursions by time t ,

$$\tilde{\ell}_t^\delta = \max\{j \geq 0 : \tilde{\tau}_j^\delta \leq t\}.$$

Since the duration of an individual excursion has finite exponential moments in a neighbourhood of the origin [5], and the lengths of the individual excursions are independent and identically distributed with positive mean $\mathbf{E}[\tilde{\tau}_1^\delta]$, by the strong law of large numbers,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \tilde{\ell}_t^\delta = \mathbf{E}[\tilde{\tau}_1^\delta]$$

and, hence, $\tilde{\ell}_t^\delta \rightarrow \infty$ as $t \rightarrow \infty$, with probability one.

We think of \mathbf{y}_t'' as the process \mathbf{y}_t' with rates $(\lambda^+, \lambda^-, \mu)$ subjected to an additional Poisson stream of arrivals of \oplus symbols at rate $\delta > 0$. Every excursion $(\tilde{\tau}_{j-1}^\delta, \tilde{\tau}_j^\delta)$ of \mathbf{y}_t'' can now be classified according to the number of successful arrivals of the $\text{Poi}(\delta)$ stream during the corresponding time interval. Define the following disjoint events

$$\begin{aligned} \mathbf{N}_j &= \{\text{no } \delta\text{-arrivals during the } j\text{th excursion}\}, \\ \mathbf{S}_j &= \{\text{single } \delta\text{-arrival during the } j\text{th excursion}\}, \\ \mathbf{D}_j &= \{\text{two or more } \delta\text{-arrivals during the } j\text{th excursion}\}, \end{aligned}$$

and consider the corresponding increments

$$\begin{aligned} x_t^{\text{N}} &= \sum (x''_{\tilde{\tau}_j^\delta} - x''_{\tilde{\tau}_{j-1}^\delta}) \mathbb{1}\{\text{N}_j\}, & x_t^{\text{S}} &= \sum (x''_{\tilde{\tau}_j^\delta} - x''_{\tilde{\tau}_{j-1}^\delta}) \mathbb{1}\{\text{S}_j\}, \\ x_t^{\text{D}} &= x_t'' - x_t^{\text{N}} - x_t^{\text{S}} = \sum (x''_{\tilde{\tau}_j^\delta} - x''_{\tilde{\tau}_{j-1}^\delta}) \mathbb{1}\{\text{D}_j\} + (x_t'' - x''_{\tilde{\ell}_t^\delta}), \end{aligned}$$

where each sum runs for all $j = 1, \dots, \tilde{\ell}_t^\delta$. Of course, during the type-N excursions the behaviour of \mathbf{y}''_t coincides with that of \mathbf{y}'_t , whereas during the type-S excursions the increment of \mathbf{y}''_t is not smaller than the increment of \mathbf{y}'_t during the same time interval, recall Lemma 3.1. On the other hand, the total increment x_t^{D} is bounded above by the total number of jumps of the process \mathbf{y}''_t during the corresponding time intervals, which by comparison with the related birth-and-death process [5, Sect. 2] can be estimated as in Proposition A.2 below. We now use these observations to derive the target inequality (3.1).

First, let $\tilde{\tau}_t^{\text{N}}$ be the total duration of all type-N excursions up to time t ,

$$\tilde{\tau}_t^{\text{N}} = \sum (\tilde{\tau}_j^\delta - \tilde{\tau}_{j-1}^\delta) \mathbb{1}\{\text{N}_j\},$$

with the sum running for all $j = 1, \dots, \tilde{\ell}_t^\delta$. Then the long-term density

$$p^{\text{N}} = \lim_{t \rightarrow \infty} \frac{1}{t} \tilde{\tau}_t^{\text{N}}$$

exists with probability one. Consequently the following almost sure limit exists

$$\lim_{t \rightarrow \infty} \frac{1}{t} x_t^{\text{N}} = v p^{\text{N}}, \quad (3.14)$$

with v being the velocity of the process \mathbf{y}'_t .

Next, let $\tilde{\tau}_t^{\text{S}}$ and $\tilde{\ell}_t^{\text{S}}$ be the total duration and the number of all type-S excursions up to time t ,

$$\tilde{\tau}_t^{\text{S}} = \sum (\tilde{\tau}_j^\delta - \tilde{\tau}_{j-1}^\delta) \mathbb{1}\{\text{S}_j\}, \quad \tilde{\ell}_t^{\text{S}} = \sum \mathbb{1}\{\text{S}_j\},$$

with the sums running for all $j = 1, \dots, \tilde{\ell}_t^\delta$. It is straightforward to check existence of the following almost sure limits

$$p^{\text{S}} = \lim_{t \rightarrow \infty} \frac{1}{t} \tilde{\tau}_t^{\text{S}}, \quad \ell^{\text{S}} = \lim_{t \rightarrow \infty} \frac{1}{t} \tilde{\ell}_t^{\text{S}}.$$

By a single-trajectory bound one can show that in fact $\ell^{\text{S}} > c\delta$ for some constant $c = c(\lambda^+ + \delta_0, \lambda^-, \mu) > 0$ and all $\delta \in (0, \delta_0)$. On the other hand, the coupling Lemma 3.1 implies that if $[\tilde{\tau}_{j-1}^\delta, \tilde{\tau}_j^\delta)$ is a type-S excursion, then the relative shift of the increments of the processes \mathbf{y}''_t and \mathbf{y}'_t during this time interval,

$$\xi_j = (x''_{\tilde{\tau}_j^\delta} - x''_{\tilde{\tau}_{j-1}^\delta}) - (x'_{\tilde{\tau}_j^\delta} - x'_{\tilde{\tau}_{j-1}^\delta}),$$

is a non-negative random variable with finite positive expectation, $\mathbf{E}\xi_j \in (0, \infty)$ (indeed, ξ_j is stochastically bounded by the total number of jumps $\tilde{\kappa}_\delta$ of the process \mathbf{y}_t'' during a single excursion, and the latter has finite exponential moments in a neighbourhood of the origin). A straightforward adaptation of the previous argument shows that, with probability one,

$$\lim_{t \rightarrow \infty} \frac{1}{t} x_t^S = vp^S + \ell^S \mathbf{E}\xi \geq vp^S + A_1 \delta, \quad (3.15)$$

for some positive constant $A_1 = A_1(\lambda^+ + \delta_0, \lambda^-, \mu)$.

Finally, the remaining increment, $x_t^D = x_t'' - x_t^N - x_t^S$, is not bigger than the total number of jumps of the process \mathbf{y}_t'' not included in type-N or type-S excursions. By Proposition A.2, we deduce that

$$\lim_{t \rightarrow \infty} \frac{1}{t} |x_t^D| \leq A_2 \delta^2, \quad (3.16)$$

with probability one, where $A_2 = A_2(\lambda^+ + \delta_0, \lambda^-, \mu)$ is a positive constant.

Combining (3.14)–(3.16) and Corollary A.1, we finally deduce that with probability one,

$$\lim_{t \rightarrow \infty} \frac{1}{t} x_t'' \geq v + A_1 \delta - A_3 \delta^2,$$

with some constant $A_3 = A_3(\lambda^+ + \delta_0, \lambda^-, \mu) > 0$. It remains to choose δ_0 to satisfy $2A_3\delta_0 < A_1$. With this choice of parameters the target estimate (3.1) follows.

A straightforward adaptation of the previous argument proves the analogues of the inequality (3.1) with varying λ^- or μ . The proof of Theorem 1.2 is finished.

Appendix A. Density estimate for birth-and-death processes with immigration

For fixed $\lambda > 0$ and $\nu > 0$, let $(Y_t)_{t \geq 0}$ be the continuous-time birth-and-death process with constant birth rate λ and death per individual rate ν (write $Y_t \sim \text{BD}(\lambda, \nu)$). In other words, Y_t is a Markov process on $\mathbb{Z}^+ = \{0, 1, 2, \dots\}$ such that its jumps from each state $k \geq 0$ to state $k + 1$ have rate λ , and jumps from state $k > 0$ to state $k - 1$ have rate $k\nu$. Assume that $Y_0 = 0$, and let $\tilde{\tau}$ be the time and let $\tilde{\kappa}$ be the number of jumps until this Markov chain first returns to the origin. For $z \geq 0$ and $s \in \mathbb{R}$, consider the function

$$\bar{\psi}(z, s) = \mathbf{E}_0[z^{\tilde{\kappa}} e^{s\tilde{\tau}}],$$

where $\mathbf{E}_m[\cdot]$ denotes the expectation corresponding to the initial state $m \geq 0$. Then the results in [5, App. A] imply the following claim

Lemma A.1. *There exist constants $\bar{z} > 1$, $\bar{s} > 0$ and $\bar{\gamma} > 0$ such that*

$$s \leq \bar{s}, 0 \leq z \leq \bar{z} \implies \bar{\psi}(z, s) \leq e^{\bar{\gamma}} < \infty. \quad (\text{A.1})$$

Remark A.1. Since $\bar{\psi}(\cdot, \cdot)$ is an analytic function of its arguments, it is not difficult to see that the smallest $\bar{\gamma}$ in (A.1) satisfies $\bar{\gamma} \searrow 0$ as both $\bar{z} \searrow 1$ and $\bar{s} \searrow 0$.

Since the process $(Y_t)_{t \geq 0}$ is a positive-recurrent Markov chain (whose stationary distribution is given by $\text{Poi}(\lambda/\nu)$), its trajectories can be split into i.i.d. parts — excursions — between the consecutive visits to the origin. According to Lemma A.1, both the time duration $\bar{\tau}$ and the number of jumps $\bar{\kappa}$ of an individual excursion have finite exponential moments in a neighbourhood of the origin.

Consider now a population consisting of two types of individuals, say of type A and of type B, each of which independently evolves as a birth-and-death process; namely, the dynamics of type A population coincides with that of $(Y_t)_{t \geq 0} \sim \text{BD}(\lambda, \nu)$, whereas the dynamics of type B population coincides with that of $\text{BD}(\delta, \nu)$ with some $\delta > 0$. Of course, the joint process $(Y_t^\delta)_{t \geq 0}$ is just $\text{BD}(\lambda + \delta, \nu)$ and can be considered as a perturbation of the original process $(Y_t)_{t \geq 0}$ describing the dynamics of type A population. Our aim here is to verify the following result, which provides a key estimate for our (cluster) expansion arguments in Section 3.2 above; this claim can be viewed as a continuous-time version of the classical cluster expansions for discrete structures (see, e.g., [9]).

Proposition A.1. *Let τ_δ be the time duration and let κ_δ be the total number of jumps of a single excursion of the process $(Y_t^\delta)_{t \geq 0}$. With $\#$ denoting the number of births of type B individuals during the excursion, let D be the event $\{\# \geq 2\}$. Then there exist $\beta > 0$ and $C > 0$ such that for all $\delta > 0$ small enough*

$$\mathbb{E}[\exp\{\beta\tau_\delta + \beta\kappa_\delta\}\mathbb{1}\{\text{D}\}] \leq C\delta^2. \quad (\text{A.2})$$

As a result, with some positive constants C_τ and C_κ , and $\delta > 0$ as above,

$$\mathbb{E}[\tau_\delta \mathbb{1}\{\text{D}\}] \leq C_\tau \delta^2 \quad \text{and} \quad \mathbb{E}[\kappa_\delta \mathbb{1}\{\text{D}\}] \leq C_\kappa \delta^2. \quad (\text{A.3})$$

Remark A.2. As the expectation in (A.2) is an analytic function of β in a neighbourhood of the origin, its β -derivative at the origin, $\mathbb{E}[(\tau_\delta + \kappa_\delta)\mathbb{1}\{\text{D}\}]$, satisfies a similar inequality; i.e., the estimates (A.3) hold. It is thus enough to check (A.2). Our argument is based on stochastic domination and semi-martingale inequalities, and provides a continuous-time analogue of the cluster expansion estimates, which are well known for discrete structures and discrete time processes, see, e.g., [9].

Proof. The process $(Y_t^\delta)_{t \geq 0}$ is just the L^1 -norm (i.e., the sum of components) of the process $(\mathcal{Y}_t^\delta)_{t \geq 0}$ on $(\mathbb{Z}^+)^2$ with the following rates:

$$\begin{aligned}
 (x, y) &\xrightarrow{\text{rate } \lambda} (x + 1, y) && x \geq 0, y \geq 0, \\
 (x, y) &\xrightarrow{\text{rate } \delta} (x, y + 1) && x \geq 0, y \geq 0, \\
 (x, y) &\xrightarrow{\text{rate } x\nu} (x - 1, y) && x > 0, y \geq 0, \\
 (x, y) &\xrightarrow{\text{rate } y\nu} (x, y - 1) && x \geq 0, y > 0.
 \end{aligned} \tag{A.4}$$

Here the x -component counts the number of type A individuals and the y -component counts the number of type B individuals, each species evolving independently. Of course, the dynamics of the process Y_t coincides with that of the x -component above (equivalently, this amounts to putting $\delta = 0$), and the rates in (A.4) can be used to construct a monotone coupling between Y_t and Y_t^δ in which $Y_t \leq Y_t^\delta$ for all $t \geq 0$.

As the joint process \mathcal{Y}_t^δ is positive recurrent, its trajectories can be decomposed into excursions between consecutive visits to the origin, and the claim of the proposition is that, on average, the time duration τ_δ and the number of jumps κ_δ of a single excursion having at least two arrivals of type B individuals (upward jumps along the y -direction) is of order δ^2 for small $\delta > 0$.

It is convenient to consider a modification $(\overline{\mathcal{Y}}_t^\delta)_{t \geq 0}$ of the joint process $(\mathcal{Y}_t^\delta)_{t \geq 0}$ in which all departures of type B individuals are suppressed as long as the system contains type A individuals, and at the moment when the last type A individual leaves the system, one existing type B individual instantaneously converts into a type A individual. In other words, jumps in $\overline{\mathcal{Y}}_t^\delta$ are as in (A.4) with the last line there replaced with the following line:

$$(0, y) \xrightarrow{\text{rate } \infty} (1, y - 1) \quad y > 0.$$

Clearly, the L^1 -norm \overline{Y}_t^δ of the process $\overline{\mathcal{Y}}_t^\delta$ provides an upper bound for Y_t^δ , in particular, both the time duration $\overline{\tau}_\delta$ and the number of jumps $\overline{\kappa}_\delta$ of a single excursion in $\overline{\mathcal{Y}}_t^\delta$ satisfy

$$\tau_\delta \leq \overline{\tau}_\delta \quad \text{and} \quad \kappa_\delta \leq \overline{\kappa}_\delta. \tag{A.5}$$

It is thus sufficient to verify estimates (A.2)–(A.3) for $\overline{\tau}_\delta$ and $\overline{\kappa}_\delta$ respectively.

Consider now a single excursion $(\overline{\mathcal{Y}}_t^\delta)_{0 \leq t \leq \overline{\tau}_\delta}$. It is convenient to decompose it into sub-excursions separated by the consecutive visits by the process $\overline{\mathcal{Y}}_t^\delta$ to states $(0, y)$ without type A individuals. If $m = m_\delta \geq 1$ is the number of such sub-excursions, denote their individual durations and numbers of jumps by

$$\theta_1, \theta_2, \dots, \theta_m \quad \text{and} \quad \ell_1, \ell_2, \dots, \ell_m$$

respectively. Of course, (θ_j, ℓ_j) are i.i.d. random vectors whose distribution is closely related to that of the pair $(\tilde{\tau}, \tilde{\kappa})$, describing individual excursions of the process $(Y_t)_{t \geq 0}$. In particular, by Lemma A.1, the pair $(\tilde{\tau}, \tilde{\kappa})$, and therefore (θ, ℓ) has finite exponential moments in a neighbourhood of the origin; namely, there exist $\alpha > 0$ and $\beta > 0$ so that

$$\mathbb{E} \exp \{5\beta(\tilde{\tau} + \tilde{\kappa})\} < e^\alpha; \tag{A.6}$$

as a result,

$$\begin{aligned} \mathbb{E} \exp\{\beta(\theta + \ell)\} &= \mathbb{E}[\exp\{\beta(\tilde{\tau} + \tilde{\kappa})\} \mathbb{E}[\exp\{\beta(\ell - \tilde{\kappa})\} \mid \tilde{\tau}, \tilde{\kappa}]] \\ &= \mathbb{E} \exp \{(\beta + (e^\beta - 1)\delta)\tilde{\tau} + \beta\tilde{\kappa}\} < e^\alpha \end{aligned}$$

if only $\delta > 0$ is small enough. In the computation above we used the fact that during time $\theta \sim \tilde{\tau}$ the number ξ of upward jumps of the y -component has distribution $\text{Poi}(\delta\theta)$; notice that this implies that the vertical shift of an individual sub-excursion is $\xi - 1$, i.e., belongs to $\{-1, 0, 1, \dots\}$.

Let $0 = \bar{\tau}_0 < \bar{\tau}_1 < \bar{\tau}_2 < \bar{\tau}_3 < \dots$ be the consecutive moments when the process \bar{Y}_t^δ visits a state without type A individuals, and let $\bar{\kappa}_j$ be the number of jumps the process \bar{Y}_t^δ makes up to time $\bar{\tau}_j$, i.e., $\bar{\tau}_j = \sum_{i=1}^j \theta_i$ and $\bar{\kappa}_j = \sum_{i=1}^j \ell_i$. Then the increments of the induced process $\bar{Y}_n = (\bar{Y}_{\bar{\tau}_n}^\delta)_{n \geq 0}$ satisfy

$$\mathbb{E}(\bar{Y}_{n+1} - \bar{Y}_n \mid \bar{Y}_n > 0, \bar{\tau}_{n+1} - \bar{\tau}_n = \theta) = \delta\theta - 1,$$

and thus $\mathbb{E}(\bar{Y}_{n+1} - \bar{Y}_n) < 0$ if $\delta\mathbb{E}\theta < 1$. By a simple semi-martingale argument, the expectation of the first return to the origin time $\bar{\tau}_\delta$ is finite,

$$\mathbb{E}\bar{\tau}_\delta < \infty,$$

provided δ is small enough. As we will see below, $\bar{\tau}_\delta$ has even finite exponential moments in a neighbourhood of the origin.

With $\alpha > 0$ and $\beta > 0$ fixed as in (A.6), Remark A.1 implies existence of $\gamma > 0$, $\delta > 0$ and $\eta > 0$ so that

$$\delta\mathbb{E}\tilde{\tau} < 1 \quad \text{and} \quad \mathbb{E} \exp \{2\zeta\tilde{\tau} + 2\beta\tilde{\kappa}\} < e^{\alpha-\gamma}, \tag{A.7}$$

where

$$\zeta = (e^\alpha - 1)\delta + \beta + \eta \in (0, 2\beta). \tag{A.8}$$

Then the process

$$M_n = \exp \{ \alpha \bar{Y}_{\bar{\tau}_n}^\delta + \beta \bar{\tau}_n + \beta \bar{\kappa}_n + \gamma n \}$$

restricted to the set $\bar{Y}_n = \bar{Y}_{\bar{\tau}_n}^\delta > 0$ is a supermartingale with respect to its natural filtration. Indeed,

$$\mathbb{E} \left[\frac{M_{n+1}}{M_n} \mid \theta_{n+1}, \ell_{n+1}, \bar{Y}_n > 0 \right] = \exp \{ \gamma - \alpha + ((e^\alpha - 1)\delta + \beta)\theta_{n+1} + \beta\ell_{n+1} \},$$

so that by (A.7)–(A.8) the expectation of the expression on the right does not exceed one. A similar argument shows that the number of jumps of the induced process $(\bar{Y}_n)_{n \geq 0}$ between consecutive returns to the origin (equivalently, the number m_δ of sub-excursions up to time $\bar{\tau}_\delta$) has finite exponential moments in a neighbourhood of the origin. By the optional stopping theorem, this implies that $\mathbb{E} \exp\{\beta(\bar{\tau}_\delta + \bar{\kappa}_\delta)\} < \infty$ for some $\beta > 0$ small enough.

With m_δ defined as above, we have $\bar{Y}_{m_\delta} = 0$, $\bar{\tau}_{m_\delta} = \bar{\tau}_\delta$, and $\bar{\kappa}_{m_\delta} = \bar{\kappa}_\delta$. Our aim is to show that

$$\mathbb{E}(M_{m_\delta} \mathbf{1}\{D\}) = O(\delta^2) \quad \text{as } \delta \rightarrow 0. \quad (\text{A.9})$$

In view of (A.5), the target estimates (A.3) then follow by differentiation. To this end we (disjointly) decompose

$$D = D_1 \cup D_2, \quad D_1 = \{\bar{Y}_1 = 1, \bar{Y}_2 \geq 1\}, \quad D_2 = \{\bar{Y}_1 \geq 2\},$$

so that it is enough to show that

$$\mathbb{E}(M_{m_\delta} \mathbf{1}\{D_1\}) = O(\delta^2) \quad \text{and} \quad \mathbb{E}(M_{m_\delta} \mathbf{1}\{D_2\}) = O(\delta^2) \quad \text{as } \delta \rightarrow 0.$$

In our computations below, we will use the following elementary inequalities: for every integer $k \geq 1$, real $z \geq 0$ and $\eta > 0$,

$$\sum_{j \geq k} \frac{z^j}{j!} \leq \frac{z^k}{k!} e^z, \quad \frac{z^k}{k!} \leq \frac{k^k}{(\eta e)^k k!} e^{\eta z}. \quad (\text{A.10})$$

The first of these inequalities is immediate from the term-wise comparison of the two series, whereas the second one follows from the fact that the maximum of the function $z^k \exp\{-\eta z\}$ for $z > 0$ occurs when $\eta z = k$.

We start by observing that, by the supermartingale property,

$$\mathbb{E}[M_{m_\delta} \mid \bar{Y}_1, \theta_1, \ell_1] \leq M_1 = \exp\{\alpha \bar{Y}_1 + \beta \theta_1 + \beta \ell_1 + \gamma\}.$$

At the same time, using inequalities (A.10),

$$\begin{aligned} \mathbb{E}[M_1 \mathbf{1}\{D_2\} \mid \bar{\tau}_1, \bar{\kappa}_1] &= \exp\{\beta(\bar{\tau}_1 + \bar{\kappa}_1) + \gamma - \alpha\} \sum_{j \geq 2} \frac{(\delta \bar{\tau}_1 e^\alpha)^j}{j!} \exp\{-\delta \bar{\tau}_1\} \\ &\leq \exp\{\beta(\bar{\tau}_1 + \bar{\kappa}_1) + \gamma - \alpha\} \frac{(\delta \bar{\tau}_1 e^\alpha)^2}{2} \exp\{(e^\alpha - 1)\delta \bar{\tau}_1\} \\ &\leq \frac{2\delta^2 e^{\alpha + \gamma}}{(\eta e)^2} \exp\{\zeta \bar{\tau}_1 + \beta \bar{\kappa}_1\}, \end{aligned}$$

so that

$$\mathbb{E}[M_{m_\delta} \mathbf{1}\{D_2\}] \leq \frac{2\delta^2 e^{\alpha + \gamma}}{(\eta e)^2} \mathbb{E} \exp\{\zeta \bar{\tau}_1 + \beta \bar{\kappa}_1\}. \quad (\text{A.11})$$

A similar argument shows that

$$\mathbb{E}[M_2 \mathbb{1}\{\bar{Y}_2 \geq 1\} \mid \bar{Y}_1, \theta_1, \theta_2, \ell_1, \ell_2] \leq M_1 \frac{\delta e^\gamma}{\eta e} \exp\{\zeta \theta_2 + \beta \ell_2\}$$

and

$$\mathbb{E}[M_1 \mathbb{1}\{\bar{Y}_1 = 1\} \mid \theta_1, \ell_1] \leq \frac{\delta e^{\alpha+\gamma}}{\eta e} \exp\{\zeta \theta_1 + \beta \ell_1\}.$$

Combining the last two estimates with the supermartingale inequality, we get

$$\mathbb{E}[M_{m_\delta} \mathbb{1}\{D_1\}] \leq \frac{\delta^2 e^{\alpha+2\gamma}}{(\eta e)^2} \mathbb{E} \exp\{\zeta \bar{\tau}_2 + \beta \bar{\kappa}_2\}, \quad (\text{A.12})$$

which together with (A.11) gives

$$\mathbb{E}[M_{m_\delta} \mathbb{1}\{D\}] \leq \frac{3\delta^2 e^{\alpha+2\gamma}}{(\eta e)^2} \mathbb{E} \exp\{\zeta \bar{\tau}_2 + \beta \bar{\kappa}_2\}.$$

By independence of the individual sub-excursions,

$$\mathbb{E} \exp\{\zeta \bar{\tau}_2 + \beta \bar{\kappa}_2\} \equiv \mathbb{E} \exp\{2\zeta \bar{\tau} + 2\beta \bar{\kappa}\} < \exp\{\alpha - \gamma\},$$

so that

$$\mathbb{E}[M_{m_\delta} \mathbb{1}\{D\}] \leq \frac{3\delta^2 e^{2\alpha+\gamma}}{(\eta e)^2}.$$

As the expectation on the left is an analytic function of the variables α , β and γ in a neighbourhood of the origin, its β -derivative at the origin, $\mathbb{E}[(\bar{\tau}_\delta + \bar{\kappa}_\delta) \mathbb{1}\{D\}]$, is bounded above by $C\delta^2$ with some finite constant C . This implies the target inequalities (A.3). \square

Let $0 = \tau_0^\delta < \tau_1^\delta < \tau_2^\delta < \dots$ be the consecutive moments when the process Y_t^δ visits the origin. In agreement with Proposition A.1, let D_j be the event that the excursion $[\tau_{j-1}^\delta, \tau_j^\delta)$ is of type D, i.e., contains at least two births of type B individuals. Denote

$$\ell = \ell_t^\delta = \max \{j \geq 0 : \tau_j^\delta \leq t\},$$

write κ_t^δ for the total number of jumps of the process Y_t^δ up to time t , and let

$$\kappa_t^D = \sum_{j=1}^{\ell_t^\delta} (\kappa_{\tau_j^\delta}^\delta - \kappa_{\tau_{j-1}^\delta}^\delta) \mathbb{1}\{D_j\} + (\kappa_t^\delta - \kappa_{\tau_{\ell_t^\delta}^\delta}^\delta) \quad (\text{A.13})$$

be the total number of jumps by time t during excursions of type D plus the time of the last unfinished excursion, if any. Our next step is to verify the following claim.

Proposition A.2. *Let κ_t^{D} be as defined in (A.13). There exist positive constants K , A , and a such that for all $\delta > 0$ small enough and all t large enough,*

$$\mathbb{P}(\kappa_t^{\text{D}} > K\delta^2 t) \leq Ae^{-at}. \quad (\text{A.14})$$

Moreover, for some constant $K_1 > 0$, we have, with probability one,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \kappa_t^{\text{D}} \leq K_1 \delta^2. \quad (\text{A.15})$$

Proof. We start by noticing that the last term in (A.13) is stochastically dominated by κ_δ , the total number of jumps in a single excursion of the process Y_t^δ . Since κ_δ has finite exponential moments in a neighbourhood of the origin, the standard large deviation estimate [2] implies that for all $K\delta^2 > 0$ there exist $A_1 > 0$ and $a_1 > 0$ so that the inequality

$$\mathbb{P}\left(\kappa_t^\delta - \kappa_{\tau_{\ell_t^\delta}^\delta}^\delta > \frac{1}{2}K\delta^2 t\right) \leq A_1 \exp\{-a_1 t\} \quad (\text{A.16})$$

holds for all t large enough. To get (A.14) it thus remains to show that for some $K > 0$, $A_2 > 0$ and $a_2 > 0$ the random variable

$$\kappa_m^{\text{D}} \equiv \sum_{j=1}^m (\kappa_{\tau_j^\delta}^\delta - \kappa_{\tau_{j-1}^\delta}^\delta) \mathbb{1}\{D_j\}, \quad m \geq 1, \quad (\text{A.17})$$

satisfies the inequality

$$\mathbb{P}\left(\kappa_{\ell_t^\delta}^{\text{D}} > \frac{1}{2}K\delta^2 t\right) \leq A_2 \exp\{-a_2 t\} \quad (\text{A.18})$$

with t large enough.

To this end, we start by observing that the process Y_t^δ stochastically dominates the process $Y_t^0 \equiv Y_t$ without type B individuals. Consequently, for all $\delta \geq 0$, the number of excursions ℓ_t^δ is stochastically dominated by ℓ_t^0 , the number of excursions by time t for the process Y_t . Using Lemma A.1 we deduce the following large deviation bound: for every $\zeta > 0$ there exist positive B and b so that

$$\mathbb{P}\left(\left|\ell_t^0 - \frac{t}{\mathbb{E}\tau_1^0}\right| > \zeta t\right) < Be^{-bt}$$

for all t large enough, where τ_1^0 denotes the duration of a single excursion for the process Y_t . As a result, there exist $B_1 > 0$ and $b_1 > 0$ such that

$$\mathbb{P}\left(\ell_t^\delta \geq \frac{2t}{\mathbb{E}\tau_1^0}\right) \leq \mathbb{P}\left(\ell_t^0 \geq \frac{2t}{\mathbb{E}\tau_1^0}\right) \leq B_1 \exp\{-b_1 t\}, \quad (\text{A.19})$$

if only t is large enough.

Next, the terms in (A.17) are independent and identically distributed, with finite exponential moments in a neighbourhood of the origin and the expectation

$$\mathbb{E}[(\kappa_{\tau_j^\delta}^\delta - \kappa_{\tau_{j-1}^\delta}^\delta) \mathbb{1}\{D_j\}] \leq \mathbb{E}[\kappa_\delta \mathbb{1}\{D\}] \leq C_\kappa \delta^2.$$

By the large deviation principle, there exist $B_2 > 0$ and $b_2 > 0$ so that

$$\mathbb{P}(\kappa_m^D \geq 2C_\kappa \delta^2 m) \leq \mathbb{P}(\kappa_m^D \geq (\mathbb{E}[\kappa_\delta \mathbb{1}\{D\}] + C_\kappa \delta^2) m) \leq B_2 \exp\{-b_2 m\} \quad (\text{A.20})$$

for all $m \geq 1$. Combining (A.19) with (A.20), and using $K = 8C_\kappa/\mathbb{E}\tau_1^0 > 0$ in (A.18), we get the inequality

$$\mathbb{P}\left(\kappa_{\ell_t^\delta}^D > \frac{4C_\kappa}{\mathbb{E}\tau_1^0} \delta^2 t\right) \leq \mathbb{P}\left(\ell_t^\delta \geq \frac{2t}{\mathbb{E}\tau_1^0}\right) + \mathbb{P}\left(\kappa_{\ell_t^\delta}^D \geq 2C_\kappa \delta^2 \ell_t^\delta\right) \leq B_3 \exp\{-b_3 t\}$$

for t large enough, where $B_3 = B_1 + B_2$ and $b_3 = \min(b_1, b_2)$. Together with (A.16) this implies the target bound (A.14) for the chosen value of K .

The upper bound (A.15) follows along the lines of the standard proof of the Ergodic theorem for positive recurrent Markov chains, see e.g., [10]. First, by the strong law of large numbers, the convergence

$$\lim_{m \rightarrow \infty} \frac{1}{m} \kappa_m^D = \mathbb{E}[\kappa_\delta \mathbb{1}\{D\}] \quad \text{and} \quad \lim_{t \rightarrow \infty} \frac{1}{t} \ell_t^\delta = \frac{1}{\mathbb{E}\tau_1^\delta}$$

holds with probability one. It is an easy exercise to check that there exist positive constants $a_1(\bar{\lambda}, \mu)$ and $a_2(\bar{\lambda}, \mu)$ so that, uniformly in $\max(\lambda^+ + \delta, \lambda^-) \leq \bar{\lambda}$, we have

$$a_1(\bar{\lambda}, \mu) < \mathbb{E}\tau_1^\delta < a_2(\bar{\lambda}, \mu),$$

and thus that, with probability one, $\ell_t^\delta \rightarrow \infty$ as $t \rightarrow \infty$. From (A.3) we deduce that

$$\lim_{t \rightarrow \infty} \frac{1}{t} \kappa_{\ell_t^\delta}^D = \frac{\mathbb{E}[\kappa_\delta \mathbb{1}\{D\}]}{\mathbb{E}\tau_1^\delta} < \frac{C_\kappa \delta^2}{a_1(\bar{\lambda}, \mu)} \leq \frac{1}{2} K_1 \delta^2,$$

with probability one. On the other hand, the variable

$$\kappa_t^D - \kappa_{\ell_t^\delta}^D \equiv (\kappa_t^\delta - \kappa_{\tau_{\ell_t^\delta}^\delta}^\delta) \mathbb{1}\{D_t\}$$

is stochastically dominated by κ_δ . Since $\mathbb{E}\kappa_\delta < \infty$, the Borel–Cantelli lemma together with Proposition A.1 and the estimate (A.16) imply that

$$\limsup_{t \rightarrow \infty} \frac{1}{t} (\kappa_t^D - \kappa_{\ell_t^\delta}^D) = 0,$$

with probability one (alternatively, use [3, Proposition 6.1.1]). The target estimate (A.15) now follows from the last two displays. \square

Let τ_t^D be the total time spent in excursions of type D up to time t , plus the time of the last unfinished excursion if any (cf. (A.13)),

$$\tau_t^D = \sum_{j=1}^{\ell_t^\delta} (\tau_j^\delta - \tau_{j-1}^\delta) \mathbb{1}\{D_j\} + (t - \tau_{\ell_t^\delta}^\delta).$$

Corollary A.1. For τ_t^D defined as above, there exists $K_\tau > 0$ such that, with probability one,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \tau_t^D \leq K_\tau \delta^2.$$

The proof of this claim is similar to that of Proposition A.2, and is omitted.

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