ANALYZING PLASMID SEGREGATION: EXISTENCE AND STABILITY OF THE EIGENSOLUTION IN A NON-COMPACT CASE

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Abstract. We study the distribution of autonomously replicating genetic elements, so-called plasmids, in a bacterial population. When a bacterium divides, the plasmids are segregated between the two daughter cells. We analyze a model for a bacterial population structured by their plasmid content. The model contains reproduction of both plasmids and bacteria, death of bacteria, and the distribution of plasmids at cell division. The model equation is a growth-fragmentation-death equation with an integral term containing a singular kernel. As we are interested in the long-term distribution of the plasmids, we consider the associated eigenproblem. Due to the singularity of the integral kernel, we do not have compactness. Thus, standard approaches to show the existence of an eigensolution like the Theorem of Krein-Rutman cannot be applied. We show the existence of an eigensolution using a fixed point theorem and the Laplace transform. The long-term dynamics of the model is analyzed using the Generalized Relative Entropy method.

1. Introduction

Plasmids are mobile genetic elements in bacteria. They replicate autonomously, and are heritable [10]. A dividing bacterium segregates its plasmids between the two daughter cells.

Plasmids have been studied intensively due to, e.g., their role in the spread of antibiotic resistance genes in bacterial populations [10, 3] and their importance in biotechnology where they are used as vectors [11]. The genetic code of a protein that is to be produced can be inserted into a plasmid which is taken up by bacteria. These bacteria then produce the recombinant protein. There are two issues to deal with when using plasmids as vectors: the loss and the accumulation of plasmids. Sometimes, bacteria lose plasmids which results in a plasmid-free subpopulation and decreases the recombinant protein yield. In order to increase the yield, one often uses so-called high-copy plasmids, i.e., plasmids that can have several hundred copies in a single bacterium [10, 11]. However, these plasmids can accumulate in some bacteria, i.e., these bacteria contain a very high number of plasmids. As a consequence, the high metabolic burden renders these bacteria inactive which again decreases the yield [5]. In order to find ways to

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avoid both the loss and the accumulation of high-copy plasmids, it is of interest to study the mechanisms that lead to plasmid loss or accumulation.

We focus on high-copy plasmids as they are commonly used in biotechnology. This type of plasmids replicates independently of the cell division cycle, i.e., independent of the chromosomes and throughout the cell division cycle [30, 35, 21]. The segregation mechanism of high-copy plasmids remains unclear. In the past, it was typically assumed that they are randomly segregated between the two daughter cells. However, this assumption has been challenged [33, 10, 26].

There are various mathematical models for structured populations [22, 7, 23, 12], structured cellular population dynamics [32, 14, 1], and plasmids in bacterial populations [37, 17, 28, 36]. Some models distinguish between plasmid-free and plasmid-bearing cells [37] while others consider a bacterial population structured by the number of plasmids [17, 28]. In order to study the spread of a specific plasmid, like a resistance or virulence plasmid, it may suffice to distinguish plasmid-free and plasmid-bearing cells, but for biotechnological use, the plasmid content should be considered to include also the possibility of plasmid accumulation. To study the dynamics of a high-copy plasmid, the use of a continuous variable representing the plasmid content is appropriate. This variable can be interpreted, e.g., as the relative plasmid number or the level of fluorescence (plasmids can be marked with fluorescing proteins [29]). Models of a cellular population structured by a continuous variable often assume the form of aggregation-fragmentation or growth-fragmentation equations and have been studied extensively [8, 27]. These equations are typically analyzed using the theory of semigroups [38, 31], the Laplace transform [20], or theory of positive operators together with compactness [20, 14].

In the present paper, we consider the model for plasmid segregation of high-copy plasmids in a bacterial population developed in [28, 36]. The aim is to show the existence and stability of positive solutions of the corresponding eigenvalues.

The model contains reproduction and death of bacteria, reproduction of plasmids within the bacteria and independent of the cell division cycle, and the segregation of plasmids to the two daughter cells at cell division. It is a growth-fragmentation-death model and a hyperbolic partial differential equation with an integral term. The integral term contains a plasmid segregation kernel that models how a bacterium distributes the plasmids to its two daughter cells at cell division. The consistency conditions for this segregation kernel (see, e.g., [32]) imply that the kernel is singular. Moreover, we assume that the plasmid reproduction rate depends on the plasmid content of the cell and vanishes for plasmid-free cells and for cells that have reached the maximal plasmid number per cell. This behavior is modeled, e.g., by a logistic plasmid reproduction rate.

Usually, the existence of eigensolutions for growth-fragmentation problems is shown using compactness and the Krein-Rutman Theorem [9, 14, 36]. However, due to the singularity in the plasmid segregation kernel and the strictly positive cell division rate, we do not have compactness. Hence, we use a different approach to show the existence of an eigensolution using rescalings of the eigenfunction, fixed point arguments, and the Laplace transform. In order to show the stability of the eigensolution, we use the Generalized Relative Entropy method [32, 25] and adapt it to the case of a bounded plasmid number and a plasmid reproduction rate that vanishes for plasmid-free bacteria and bacteria with the maximal plasmid content. This method uses a Lyapunov functional to obtain stability results and does not require compactness.

This paper is structured as follows: firstly, we study the eigenproblem associated with the model equation. We show the existence of an eigensolution in Section 2. Secondly, we study the stability of the eigensolution using the Generalized Relative Entropy method in Section 3. Finally, we discuss our findings in Section 4. Appendix A contains the proof of Theorem 2.9 which is central in the proof of the existence of an eigensolution.

2. Existence of an eigensolution

We study the following model for a bacterial population structured by its plasmid content which was derived in [28, 36]:

$$\begin{cases} \partial_t u(z,t) + \partial_z\big(b(z)\,u(z,t)\big) = -\big(\beta+\mu\big)\,u(z,t) + \beta \displaystyle\int_z^{z_0} k(z,z')\,u(z',t)\,dz', \\ b(0)\,u(0,t) = 0 \text{ for all } t \geq 0, \qquad u(z,0) = u_0(z) \text{ for all } z \in [0,z_0]. \end{cases} \tag{2.1}$$

Here, $u(z,t)$ denotes the density of bacteria structured by their plasmid content z at time t. There is a maximal plasmid content z_0 such that $z \in [0, z_0]$. For example, z can represent the relative plasmid number or the level of fluorescence in bacteria where plasmids are marked with fluorescing proteins [29]. The plasmid reproduction rate is denoted by $b(z)$, the cell division rate by β, and the cell death rate by μ. At cell division, a mother cell with plasmid content z' divides its plasmids to the two daughter cells according to the plasmid segregation kernel $k(z,z')$. For the derivation of the model, see [28, 36].

In this section, we consider the specific example of logistic plasmid reproduction rate, constant cell division and death rate, and a special type of segregation kernel. Therefore, we make the following assumptions on the parameters of the model which we assume to hold throughout this section:

(A1) Plasmid reproduction is logistic, i.e., $b(z) = \frac{b_0}{z_0} z(z_0 - z)$ for $z_0 > 0$, $b_0 > 0$.
(A2) The cell division rate β is constant with $0 < \beta < \infty$.
(A3) The cell death rate μ is constant with $0 \leq \mu < \infty$.
(A4) There is a function $\Phi : [0,1] \to \mathbb{R}_{\geq 0}$ such that the plasmid segregation kernel k satisfies

$$k(z,z') = \frac{2}{z'}\,\Phi\Big(\frac{z}{z'}\Big)\,\chi_\Omega(z,z'),$$

for all $z' \in (0, z_0]$, where χ denotes the characteristic function and $\Omega := \{z, z' \in [0, z_0] : z \leq z'\}$. We assume that $\Phi \in L^\infty([0,1])$.
Furthermore, Φ satisfies the following consistency conditions:

$$\int_0^1 \Phi(\xi)\,d\xi = 1 \quad \text{ and } \quad \Phi(\xi) = \Phi(1-\xi) \text{ for all } \xi \in [0,1].$$

We call a plasmid segregation kernel k that satisfies Assumption **(A4)** *scalable* [28]. The consistency conditions on Φ imply that for all $z' \in (0, z_0]$ and $z \in [0, z_0]$

$$\int_0^{z'} k(z,z')\,dz = 2 \quad \text{and} \quad k(z,z') = k(z'-z, z').$$

The first condition is a consequence of the fact that a cell always divides into two daughter cells (see, e.g., [15, 24]) and the second conditions models that the second daughter receives all plasmids the first daughter did not receive, i.e., plasmids are conserved at cell division. Moreover, the two consistency conditions on Φ also imply that

$$\int_0^1 \xi\,\Phi(\xi)\,d\xi = \frac{1}{2},$$

meaning that k satisfies

$$\int_0^{z'} z\, k(z,z')\, dz = z' \text{ for all } z' \in (0, z_0].$$

This condition again models that plasmids are conserved at cell division as all daughter cells together have as many plasmids as the mother cell had. These three conditions on k, respectively on Φ, ensure consistency of the modeling (see, e.g., [32]).

Note that assumption **(A4)** implies that the plasmid segregation kernel k has a pole at 0. Due to the consistency condition $\int_0^{z'} k(z,z')\, dz = 2$ for all $z' > 0$, the kernel k has a pole at 0 regardless of whether it is scalable or not. However, the assumption that k is scalable has the advantage that one can assume the function Φ to be $L^\infty([0,1])$. In this way, it is possible to separate the plasmid segregation modeled by Φ and the pole in the kernel k from one another and simplify computations.

As we are interested in the long-time distribution of plasmids and our model equation (2.1) is linear, we expect to find a solution growing (or decreasing) exponentially in time. Thus, we consider the associated eigenproblem. Under Assumptions **(A1)** to **(A4)**, the eigenproblem associated with (2.1) is given by:

$$\begin{cases} \big(b(z)\,\mathcal{U}(z)\big)_z = -\,(\beta+\mu+\lambda)\,\mathcal{U}(z) + 2\beta \displaystyle\int_z^{z_0} \frac{1}{z'}\,\Phi\Big(\frac{z}{z'}\Big)\,\mathcal{U}(z')\, dz', \\[2ex] \displaystyle\lim_{z\to 0^+} b(z)\,\mathcal{U}(z) = 0, \quad \mathcal{U}(z) \geq 0 \text{ for all } z \in (0,z_0), \quad \int_0^{z_0} \mathcal{U}(z)\, dz = 1. \end{cases} \tag{2.2}$$

In the special case of constant cell division and death rate, we can give the eigenvalue explicitly (see [28, Corollary 3.3]).

Lemma 2.1. *There is an integrable solution to* (2.2) *only if* $\lambda = \beta - \mu$.

Remark 2.2. For constant β and μ we know λ but for non-constant β and μ depending on the plasmid content z we do not know λ. In general, i.e., for non-constant β and μ, it is non-trivial to determine λ. Furthermore, we do not (yet) know if there is a solution $\mathcal{U}$ to the eigenproblem (2.2). We aim to show existence of an eigenfunction and ideally would like our approach to be extendable to the case of non-constant β and μ. Therefore, we do not use the fact that we already know λ in the following. Moreover, we hope to gain a better understanding of the model in this way.

Remark 2.3. An eigenproblem similar to (2.2) was considered in [9, 14, 36]. In these cases, compactness and the Krein-Rutman Theorem could be used to show existence of an eigensolution. However, we do not have compactness due to the singularity of the plasmid segregation kernel and the assumption that $\beta > 0$. In particular, with a scalable plasmid segregation kernel we see that there is a pole at $z' = 0$. It is useful in the following to separate the plasmid segregation (modeled by Φ) and the pole of the kernel ($\frac{1}{z'}$). Due to lack of compactness, we cannot use the standard approach but we use a different approach to show existence of an eigensolution.

As a first step to establishing existence of an eigensolution $(\lambda, \mathcal{U})$, we rescale the eigenfunction.

Lemma 2.4. *There is a solution $(\lambda, \mathcal{U})$ with $\mathcal{U} \in \mathcal{C}^1((0, z_0))$ to the eigenproblem (2.2) if and only if there is a solution (λ, v) with $v \in \mathcal{C}^1((0, z_0))$ to*

$$\begin{cases} v'(z) + \dfrac{\lambda+\beta+\mu}{b_0}\, z_0\, \dfrac{v(z)}{z(z_0-z)} = \dfrac{2\beta z_0}{b_0} \displaystyle\int_z^{z_0} \dfrac{\Phi\left(\frac{z}{z'}\right) v(z')}{(z')^2\,(z_0-z')}\, dz', \\ \lim\limits_{z\to 0^+} v(z) = 0, \quad v(z) \geq 0 \text{ for all } z \in (0, z_0), \quad \displaystyle\int_0^{z_0} \dfrac{v(z)}{b(z)}\, dz = 1. \end{cases} \tag{2.3}$$

Proof. If $(\lambda, \mathcal{U})$ with $\mathcal{U} \in \mathcal{C}^1((0, z_0))$ is a solution to (2.2), then (λ, v) with $v(z) := b(z)\mathcal{U}(z) \in \mathcal{C}^1((0, z_0))$ is a solution to (2.3).

Likewise, if (λ, v) is a solution to (2.3), then define $\mathcal{U}(z) := \frac{v(z)}{b(z)}$. $\mathcal{U}$ is well-defined for $z \in (0, z_0)$ as $b(z) \neq 0$ for $z \in (0, z_0)$, $\mathcal{U} \in \mathcal{C}^1((0, z_0))$, and $(\lambda, \mathcal{U})$ is a solution to (2.2). □

For the sake of brevity, we define

$$\alpha = \alpha(\lambda) := \frac{\lambda+\beta+\mu}{b_0} \quad \text{and} \quad \alpha_0 := \frac{2\beta}{b_0}.$$

Note that if $\lambda = \beta - \mu$, then $\alpha = \alpha_0$.

There is a special case, where we have an explicit solution $\mathcal{U}$ to the eigenproblem (2.2).

Example 2.5. In the case $\Phi(\xi) = 1$ for all $\xi \in [0, 1]$, i.e., plasmids are segregated uniformly, $\mathcal{U}(z) = Cz^{-\alpha}(z_0-z)^{\alpha-1}$ with $C > 0$, $\lambda = \beta-\mu$, and $\alpha = \alpha_0$ is a solution to (2.2) [28]. Therefore, by Lemma 2.4, $v(z) = b(z)\mathcal{U}(z) = C\,\frac{b_0}{z_0}\, z^{1-\alpha}\,(z_0-z)^{\alpha}$ is a solution to (2.3).

This example motivates another rescaling of the solution v to (2.3).

Lemma 2.6. *If there is a solution (α, g) with $g \in \mathcal{C}^0((0, z_0]) \cap \mathcal{C}^1((0, z_0))$ to*

$$\begin{cases} g'(z) + \dfrac{\alpha}{z}\, g(z) = \dfrac{\alpha_0\, z_0}{(z_0-z)^{\alpha}} \displaystyle\int_z^{z_0} \Phi\left(\dfrac{z}{z'}\right) (z')^{-2}\,(z_0-z')^{\alpha-1}\, g(z')\, dz', \\ g(z_0) = 1,\ \lim\limits_{z\to 0^+} g(z) = 0,\ g(z) \geq 0 \text{ for } z \in (0, z_0),\ \displaystyle\int_0^{z_0} \dfrac{(z_0-z)^{\alpha} g(z)}{b(z)} dz < \infty, \end{cases} \tag{2.4}$$

then (λ, v) with $\lambda := \alpha\, b_0 - \beta - \mu$ and $v(z) := C\,(z_0-z)^{\alpha}\, g(z)$ for some $C > 0$ is a solution to (2.3) with $v \in \mathcal{C}^1((0, z_0))$.

Remark 2.7. In Lemma 2.6 we do not have equivalence as there can only be a function g with $v(z) = C\,(z_0-z)^{\alpha}\, g(z)$ and $g(z_0) = 1$ if $\lim\limits_{z\to z_0^-} \frac{v(z)}{(z_0-z)^{\alpha}} = C \in (0, \infty)$. This means that v behaves like $(z_0-z)^{\alpha}$ at z_0 which we write as $v(z) \sim (z_0-z)^{\alpha}$ at z_0. If v does not behave like $(z_0-z)^{\alpha}$ at z_0, then it holds that either $g(z_0) = 0$ or $\lim\limits_{z\to z_0^-} g(z) = \infty$ and thus the condition $g(z_0) = 1$ cannot be satisfied.

In Lemma 2.4, we had equivalence because we can simply rescale the solution $\mathcal{U}$ to (2.2) to obtain a solution v to (2.3) and vice versa. However, in Lemma 2.6, we do not just rescale but we assume that the solution v satisfies $v(z) \sim (z_0-z)^{\alpha}$ at z_0, i.e., v behaves like $(z_0-z)^{\alpha}$ near z_0, and then obtain a solution g to (2.4). If the function v does not satisfy this assumption, then it is not possible to find a solution g to (2.4) that satisfies $g(z_0) = 1$ and therefore we do not have equivalence.

By Example 2.5 we know that at least for $\Phi \equiv 1$, $v(z) \sim (z_0 - z)^\alpha$ at z_0.

Proof of Lemma 2.6. Define $v(z) := (z_0 - z)^\alpha g(z)$. As g is a solution to (2.4),

$$\begin{aligned} v'(z) &= g'(z)\,(z_0 - z)^\alpha + g(z)\,\alpha\,(z_0 - z)^{\alpha-1}\,(-1) \\ &= (z_0 - z)^\alpha \left(-\frac{\alpha}{z}\,g(z) + \frac{\alpha_0\, z_0}{(z_0 - z)^\alpha} \int_z^{z_0} \Phi\Big(\frac{z}{z'}\Big)\,(z')^{-2}\,(z_0 - z')^{\alpha-1}\,g(z')\,dz' \right) \\ &\quad - \frac{\alpha}{z_0 - z}\,v(z) \\ &= -\frac{\alpha\, z_0}{z\,(z_0 - z)} v(z) + \alpha_0\, z_0 \int_z^{z_0} \frac{\Phi\big(\frac{z}{z'}\big)\,v(z')}{(z')^2\,(z_0 - z')}\,dz'. \end{aligned}$$

Therefore, v is a solution to the PDE in (2.3). It is straightforward to check that v satisfies all conditions in (2.3), therefore (λ, v) with $\lambda = \alpha b_0 - \beta - \mu$ is a solution to (2.3). ☐

Before we consider the full equation (2.4), we focus on the integro-differential equation for g in (2.4) together with $g(z_0) = 1$, i.e., we omit (for now) the conditions $\lim_{z \to 0^+} g(z) = 0$, $g(z) \geq 0$ for all $z \in (0, z_0)$, and the integral condition:

$$\begin{cases} g'(z) + \dfrac{\alpha}{z}\,g(z) = \dfrac{\alpha_0\, z_0}{(z_0 - z)^\alpha} \displaystyle\int_z^{z_0} \Phi\Big(\frac{z}{z'}\Big)\,(z')^{-2}\,(z_0 - z')^{\alpha-1}\,g(z')\,dz', \\ g(z_0) = 1. \end{cases} \tag{2.5}$$

In the following lemma we show existence of a solution g to (2.5). We will use this lemma later in the proof of existence of a solution to the eigenproblem (2.2).

Lemma 2.8. *For every $\alpha > 0$ there exists a unique solution $g \in \mathcal{C}^0((0, z_0]) \cap \mathcal{C}^1((0, z_0))$ to (2.5).*

Proof. The proof uses a fixed point argument and is analogous to the proof of [36, Lemma 10]. ☐

The proof of Lemma 2.8 gives a method to iteratively construct a solution to (2.5). This solution can then be rescaled to obtain a solution for the eigenproblem (2.2) (see Figure 1 and [36]).

Note that Lemma 2.8 gives existence of a solution for every $\alpha > 0$, i.e., for $\lambda > -(\beta + \mu)$. We expect that there is a unique $\lambda > -(\beta + \mu)$ and therefore a unique $\alpha > 0$ for which the function $g(z)$ satisfies the previously omitted conditions $\lim_{z \to 0^+} g(z) = 0$ and $g(z) \geq 0$.

If $\alpha \leq 0$, then $\lambda \leq -(\beta + \mu) < 0$ and the bacterial population goes extinct. We are interested in finding a non-trivial asymptotic solution, therefore we consider in the following only the case $\alpha > 0$.

Now, we add again the conditions to equation (2.5) that we have omitted in the previous lemma and give necessary and sufficient conditions on the parameters of the model for existence and uniqueness of a solution to (2.4).

Theorem 2.9. *There is a unique solution $g \in \mathcal{C}^0((0,z_0]) \cap \mathcal{C}^1((0,z_0))$ to (2.4) with $g(z) > 0$ for $z \in (0, z_0]$ if and only if*

$$\alpha = \alpha_0, \;\; \textit{and } \alpha_0 < -\frac{1}{\tilde{\Phi}'(0)},$$

where $\tilde{\Phi}(s) := \int\limits_0^1 u^s\, \Phi(u)\, du$.

The proof of Theorem 2.9 can be found in Appendix A. So far, we have shown existence and uniqueness of a solution g to (2.4) but we are interested in a solution to the eigenproblem (2.2). Therefore, we rescale the solution g to obtain an eigensolution $\mathcal{U}$ and the following result.

Theorem 2.10. *If $\alpha = \alpha_0$ and $\alpha_0 < -\left(\tilde{\Phi}'(0)\right)^{-1}$ or equivalently if*

$$\lambda = \beta - \mu \quad \textit{and} \quad \frac{2\beta}{b_0} < -\frac{1}{\tilde{\Phi}'(0)},$$

then there exists a solution $\mathcal{U} \in \mathcal{C}^1((0,z_0))$ to (2.2) with $\mathcal{U}(z) > 0$ for all $z \in (0, z_0)$. Moreover, $\mathcal{U}$ is the unique solution to (2.2) with $\mathcal{U}(z) \sim (z_0 - z)^{\alpha-1}$ at z_0.

Proof. Theorem 2.10 follows directly from Theorem 2.9 using Remark 2.7 and Lemmas 2.4 and 2.6. □

We have shown existence of a solution $\mathcal{U}$ to (2.2) and that $\mathcal{U}(z) \sim (z_0 - z)^{\alpha-1}$ at z_0. Thus, we know the behavior of the eigensolution at z_0 (if it exists) and we obtain the following corollary that agrees with the known behavior of eigensolutions at z_0 (see [28, Corollary 4.19]).

Corollary 2.11. *Let the assumptions of Theorem 2.10 hold and $\tilde{\Phi}(s) = \int_0^1 u^s\, \Phi(u)\, du$ as in Theorem 2.9, then the eigensolution $\mathcal{U}$ to (2.2) satisfies:*

(a) If $\tilde{\Phi}'(0) \le -1$, then $\alpha < 1$, i.e., $2\beta < b_0$, and $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = \infty$.

(b) If $\tilde{\Phi}'(0) > -1$ and $\alpha = 1$, i.e., $2\beta = b_0$, then there exists a constant $C \in (0,\infty)$ such that $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = C$.

(c) If $\tilde{\Phi}'(0) > -1$ and $1 < \alpha < -\left(\tilde{\Phi}'(0)\right)^{-1}$, i.e., in particular $2\beta > b_0$, then $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = 0$.

Example 2.12. The condition $\alpha < -\left(\tilde{\Phi}'(0)\right)^{-1}$ in Theorem 2.9, Theorem 2.10, and Corollary 2.11 gives for different Φ the following conditions on α:

(a) For $\Phi(\xi) = 1$ for all $\xi \in [0,1]$, $\tilde{\Phi}'(0) = -1$, hence $\alpha < 1$.
Note that in this case we know that the explicit solution is given by $\mathcal{U}(z) = C\, z^{-\alpha}\,(z_0 - z)^{\alpha-1}$ (see Example 2.5). This solution is integrable over $[0, z_0]$ if and only if $\alpha \in (0,1)$ which agrees with the assumption that $\alpha > 0$ and the condition that $\alpha < -\left(\tilde{\Phi}'(0)\right)^{-1} = 1$.

(b) For $\Phi(\xi) = 6\,\xi\,(1-\xi)$, $\tilde{\Phi}'(0) = -\frac{5}{6}$, hence $\alpha < \frac{6}{5}$.
Therefore, depending on the parameters β and b_0, the eigensolution can satisfy either $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = 0$, $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = C \in (0,\infty)$, or $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = \infty$ (see Figure 1).

(c) For $\Phi(\xi) = 120\,\xi\left(\frac{1}{2}-\xi\right)^2(1-\xi)$, $\tilde{\Phi}'(0) = -\frac{31}{30}$, hence $\alpha < \frac{30}{31}$. Thus, $\lim\limits_{z\to z_0^-} \mathcal{U}(z) = \infty$.

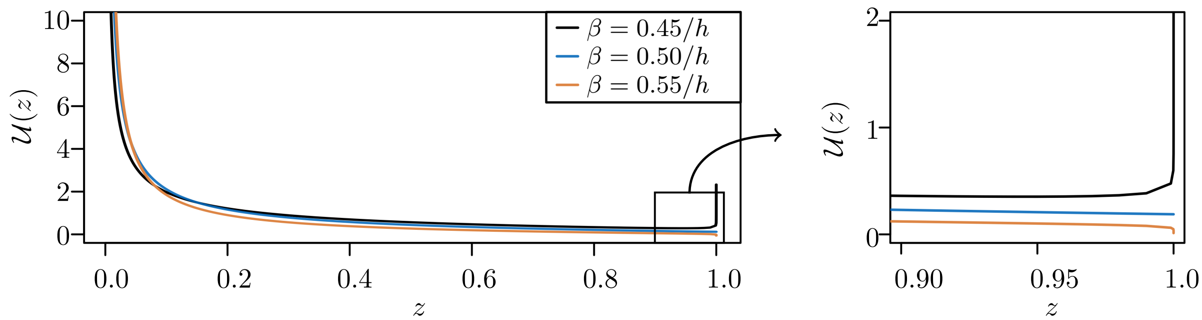

Figure 1. Numerically constructed eigenfunctions for $\Phi(\xi) = 6\,\xi\,(1-\xi)$, $\mu = 0.1/h$, $b(z) = z(1-z)/h$, and different β, viz. $\beta = 0.45/h$ (black), $0.5/h$ (blue), and $0.55/h$ (orange). The different cell division rates lead to different behavior of the eigenfunction $\mathcal{U}(z)$ at the maximal plasmid number $z_0 = 1$. The eigenfunction was numerically constructed using the software R [34] as described in [36, Section 5].

We have shown that if $\lambda = \beta - \mu$ and $\frac{2\beta}{b_0} < -\left(\tilde{\Phi}'(0)\right)^{-1}$, then a solution to the eigenproblem (2.2) exits and given examples for the second condition for different plasmid segregation kernels. We now try to interpret the second condition.

The reproduction of bacteria (modeled by the constant cell division rate β) may not be too fast compared to the reproduction of plasmids (modeled by $b(z) = \frac{b_0}{z_0}\,z\,(z_0 - z)$) as we expect otherwise that bacteria lose the plasmid in the long-run. If the plasmid is lost, then the density $u(z,t)$ converges to a delta distribution at $z = 0$ and we cannot find a continuously differentiable eigenfunction. Thus, $\frac{2\beta}{b_0}$ should be bounded.

For the interpretation of the second part of the condition, note that by the definition of $\tilde{\Phi}$ it holds that

$$-\frac{1}{\tilde{\Phi}'(0)} = \left(\int_0^1 (-\log(x))\,\Phi(x)\,dx\right)^{-1},$$

i.e., it is the inverse of the weighted average. The weight integrates to one and attaches a greater weight to plasmid segregation kernels where one daughter cell is plasmid-free or receives only a very small fraction of the mother's plasmids. Due to symmetry of the plasmid segregation kernel Φ, this means that a plasmid distribution where one daughter cell receives much more plasmids than the other, i.e., an unequal plasmid distribution, is weighted higher than an "equal" distribution of plasmids where both daughters receive approximately the same fraction of plasmids. Therefore, $-\left(\tilde{\Phi}'(0)\right)^{-1}$ can be interpreted as a measure of how equally the plasmids are distributed to the daughter cells. For uniform plasmid segregation we obtain the value 1, for an unimodal distribution, i.e., a distribution where daughters are more likely to receive about half of the mother's plasmids, we obtain a value larger than 1, and for a bimodal distribution, i.e., an unequal plasmid distribution, we obtain a value smaller than 1 (see Example 2.12).

It still remains to interpret the connection between the cell reproduction compared to the plasmid reproduction and the plasmid distribution. If the plasmid distribution is unequal, then there are more daughter cells with only few plasmids and plasmid reproduction needs to be large compared to cell reproduction in order for the plasmid not to be lost. In other words, we need $\frac{2\beta}{b_0}$ to be small. If, however, plasmid distribution is equal, then there are fewer daughters with few plasmids (compared to an unequal plasmid distribution). In this case, the condition on the connection between cell reproduction and plasmid reproduction can be relaxed a bit.

This is one possible interpretation of the condition on the parameters. We note that with this interpretation we have not accounted for the possibility of plasmid accumulation. If plasmids reproduce much faster than bacteria, then we would expect that the density $u(z,t)$ converges to a delta distribution at $z = z_0$ and we cannot find an eigenfunction $\mathcal{U} \in \mathcal{C}^1((0, z_0))$. However, we have no condition saying that $\frac{2\beta}{b_0}$ needs to be bounded below for an eigensolution to exist.

In a sense, this suggests that in our model plasmids will not accumulate in the population and there is no convergence to a delta distribution at z_0. This may be due to the fact that we show existence of an eigensolution $\mathcal{U}(z) \sim (z_0 - z)^{\alpha-1}$ at z_0, i.e., an eigensolution with a prescribed behavior at z_0. It may also be due to the assumptions of the model. By Assumptions **(A1)** to **(A4)**, the plasmid reproduction rate is small in a neighborhood of z_0 regardless of whether b_0 is small or large, but the cell division and death rates are the same for all bacteria. If a plasmid-free bacterium divides, then its daughters are also plasmid-free but if a bacterium with z_0 plasmids divides, then at most one of its daughters also contains z_0 plasmids. For this reason we expect that in our model plasmid-free bacteria grow faster than bacteria with z_0 plasmids, i.e., if plasmid-free bacteria do not outgrow plasmid-carrying bacteria, then also bacteria with z_0 plasmids do not outgrow plasmid-bearing bacteria with fewer than z_0 plasmids. Thus, under these assumptions, we expect that it suffices to control the behavior of the bacteria at $z = 0$.

3. Stability of the eigensolution with the Generalized Relative Entropy method

We now aim to show the stability of the eigensolution to (2.2) using the Generalized Relative Entropy (GRE) method [25, 32]. That is to say, we construct a Lyapunov functional for solutions in order to determine the long-time asymptotics.

In this section, we consider a more general version of the model equation (2.1) with a general plasmid reproduction rate $b(z)$ that is not necessarily logistic, both cell division and cell death rate may depend on the plasmid content of the bacterium, and a general plasmid segregation kernel k that does not need to be scalable in the sense of **(A4)**. The model equation is then given by:

$$\begin{cases} \partial_t u(z,t) + \partial_z\big(b(z)\, u(z,t)\big) = -\big(\beta(z) + \mu(z)\big)\, u(z,t) + \displaystyle\int_z^{z_0} \beta(z')\, k(z,z')\, u(z',t)\, dz', \\ b(0)\, u(0,t) = 0 \text{ for all } t \geq 0, \qquad u(z,0) = u_0(z) \text{ for all } z \in [0, z_0]. \end{cases} \tag{3.1}$$

We assume that the parameters of the model satisfy:

(A5) There is a $z_0 > 0$ such that $b(0) = b(z_0) = 0$, $b(z) > 0$ for all $z \in (0, z_0)$, and $b \in \mathcal{C}^1([0, z_0])$.
(A6) $\beta \in \mathcal{C}^0([0, z_0])$ and $0 < \underline{\beta} \leq \beta(z) \leq \overline{\beta}$ for all $z \in [, z_0]$.
(A7) $\mu \in \mathcal{C}^0([0, z_0])$ and $0 \leq \underline{\mu} \leq \mu(z) \leq \overline{\mu}$ for all $z \in [, z_0]$.

(A8) k is measurable, $\operatorname{supp}(k) \subseteq \Omega := \{z, z' \in [0, z_0] : z \leq z'\}$, $k \geq 0$, k is symmetric in the sense that $k(z, z') = k(z' - z, z')$ for all $(z, z') \in \Omega$, $\int_0^{z'} k(z, z')\, dz = 2$ for all $z' \in (0, z_0]$, and $\int_0^{z'} z\, k(z, z')\, dz = z'$ for all $z' \in (0, z_0]$.

These conditions are regularity and positivity respectively non-negativity conditions on b, β, μ, and k. Furthermore, we have consistency conditions on the plasmid segregation kernel k (see, e.g., [32]). These conditions model that a cell always divides into two daughter cells (first integral condition on k) and that plasmids are not lost at cell division, i.e., the second daughter receives all plasmids the first daughter has not received (symmetry condition) and the daughters have as many plasmids as the mother (second integral condition on k).

We consider eigensolutions $(\lambda, \mathcal{U}, \Psi)$, where $(\lambda, \mathcal{U})$ is a solution to the eigenproblem associated with (3.1),

$$\begin{cases} \dfrac{d}{dz}\big(b(z)\mathcal{U}(z)\big) = -\big(\beta(z) + \mu(z) + \lambda\big)\mathcal{U}(z) + \displaystyle\int_z^{z_0} \beta(z')\, k(z, z')\mathcal{U}(z')\, dz', \\ \lim\limits_{z \to 0^+} b(z)\mathcal{U}(z) = 0, \quad \mathcal{U}(z) > 0 \text{ for all } z \in (0, z_0), \quad \displaystyle\int_0^{z_0} \mathcal{U}(z)\, dz = 1 \end{cases} \tag{3.2}$$

and (λ, Ψ) is a solution to the dual eigenproblem

$$\begin{cases} -\, b(z)\, \dfrac{d}{dz}\Psi(z) = -\big(\beta(z) + \mu(z) + \lambda\big)\, \Psi(z) + \beta(z) \displaystyle\int_0^{z} k(z', z)\, \Psi(z')\, dz', \\ \Psi(z) \geq 0 \text{ for all } z \in (0, z_0), \quad \displaystyle\int_0^{z_0} \Psi(z)\mathcal{U}(z)\, dz = 1. \end{cases} \tag{3.3}$$

So far, we know that there is an eigensolution $(\lambda, \mathcal{U})$ to (3.2) with $\lambda = \beta - \mu$ and $\mathcal{U}(z) > 0$ for all $z \in (0, z_0)$ in the case that β and μ are constant, b is logistic, and k is scalable (see Section 2). For the eigensolution (λ, Ψ) to the dual eigenproblem (3.3) we have the following existence result.

Lemma 3.1. *Let β and μ be constant and $(\lambda, \mathcal{U})$ be a solution to (3.2), then $\Psi \equiv 1$ is a solution to the dual eigenproblem (3.3).*

Proof. The proof is a straightforward computation using $\lambda = \beta - \mu$ and the consistency condition $\int_0^{z'} k(z, z')\, dz = 2$. $\square$

Since we aim to show the stability of the eigensolution $\mathcal{U}$, we assume that there exists an eigensolution $(\lambda, \mathcal{U}, \Psi)$ throughout this section:

(A9) There is an eigensolution $(\lambda, \mathcal{U}, \Psi)$ such that $(\lambda, \mathcal{U})$ is a solution to (3.2) with $\lambda \in \mathbb{R}$ and $\mathcal{U}(z) > 0$ for all $z \in (0, z_0)$ and (λ, Ψ) is a solution to (3.3).

In the case of logistic plasmid reproduction b, constant β and μ, and scalable plasmid segregation kernel k, we know Assumption **(A9)** holds. In the general setting, i.e., under Assumptions **(A5)** to **(A8)**, we do not know that it holds. Nonetheless, we consider the general case here.

We scale the solution to (3.1) by defining $\tilde{u}(z,t) := e^{-\lambda t}\, u(z,t)$. Then, the function $\tilde{u}$ is a solution to

$$\begin{cases} \partial_t \tilde{u}(z,t) + \partial_z\big(b(z)\tilde{u}(z,t)\big) = -\big(\beta(z)+\mu(z)+\lambda\big)\tilde{u}(z,t) + \displaystyle\int_z^{z_0} \beta(z')k(z,z')\tilde{u}(z',t)dz', \\ b(0)\,\tilde{u}(0,t) = 0 \text{ for all } t \geq 0, \qquad \tilde{u}(z,0) = u_0(z) \text{ for all } z \in [0,z_0]. \end{cases} \tag{3.4}$$

The idea behind the GRE method is to obtain a Lyapunov functional for solutions to (3.4) in order to determine the long-time asymptotics. The following theorem is the first step towards a Lyapunov functional.

Theorem 3.2. *Let $\tilde{u}(z,t)$ be a solution to (3.4) and $(\lambda, \mathcal{U}, \Psi)$ be an eigensolution as in* ***(A9)****. For every absolutely continuous function $H : \mathbb{R} \to \mathbb{R}$, it holds that*

$$\begin{aligned} &\partial_t \left[\Psi(z)\mathcal{U}(z)\, H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\right] + \partial_z \left[b(z)\,\Psi(z)\mathcal{U}(z)\, H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\right] \\ &+ \int_0^{z_0} \beta(z)\, k(z',z)\, \Psi(z')\mathcal{U}(z)\, H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right) - \beta(z')\, k(z,z')\, \Psi(z)\mathcal{U}(z')\, H\!\left(\frac{\tilde{u}(z',t)}{\mathcal{U}(z')}\right)\, dz' \\ &\quad = \int_0^{z_0} \beta(z')\, k(z,z')\, \Psi(z)\mathcal{U}(z') \left[H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right) - H\!\left(\frac{\tilde{u}(z',t)}{\mathcal{U}(z')}\right)\right. \\ &\qquad\quad \left. + H'\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\left[\frac{\tilde{u}(z',t)}{\mathcal{U}(z')} - \frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right]\right]\, dz'. \end{aligned}$$

The proof of Theorem 3.2 consists of lengthy but straightforward computations, it can be found in Appendix B.

Theorem 3.2 is the central theorem of this section, the following lemmas are basically consequences of the equation in Theorem 3.2. If we choose the function H in Theorem 3.2 to be convex, then the next lemma shows that we have a Lyapunov functional for a solution $\tilde{u}$ to (3.4).

Lemma 3.3. *Let $H : \mathbb{R} \to \mathbb{R}_{\geq 0}$ be a convex and absolutely continuous function, $\tilde{u}(z,t)$ a solution to (3.4), $(\lambda, \mathcal{U}, \Psi)$ an eigensolution as in* ***(A9)****, and let there be a $C > 0$ such that $|u_0(z)| \leq C\,\mathcal{U}(z)$ for all $z \in [0,z_0]$. Then, the map defined by*

$$t \mapsto \mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) := \int_0^{z_0} \Psi(z)\mathcal{U}(z)\, H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\, dz$$

satisfies

$$\begin{aligned} \frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) = \int_0^{z_0}\!\!\int_0^{z_0} &\beta(z')\, k(z,z')\, \Psi(z)\mathcal{U}(z') \left[H\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right) - H\!\left(\frac{\tilde{u}(z',t)}{\mathcal{U}(z')}\right)\right. \\ &\left. + H'\!\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\left[\frac{\tilde{u}(z',t)}{\mathcal{U}(z')} - \frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right]\right]\, dz'dz =: -\mathcal{D}_\Psi(\tilde{u}|\mathcal{U}) \leq 0. \end{aligned}$$

The proof of Lemma 3.3 can be found in Appendix B. We can use Lemma 3.3 to obtain a priori estimates for solutions to (3.4).

Lemma 3.4. *Under the assumptions of Lemma 3.3, we have* *(i)* Conservation of mass*:* $\int\limits_0^{z_0} \tilde{u}(z,t)\,\Psi(z)\,dz = \int\limits_0^{z_0} \tilde{u}(z,0)\,\Psi(z)\,dz =: m$ *for all* $t \geq 0$*.*

(ii) Contraction principle*:* $\int\limits_0^{z_0} |\tilde{u}(z,t)|\;\Psi(z)\,dz \leq \int\limits_0^{z_0} |\tilde{u}(z,0)|\;\Psi(z)\,dz$ *for all* $t \geq 0$*.*

Proof. The proof uses the formula for $\frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U})$ in Lemma 3.3.

(i) We choose $H(h) = h_+$, where $(\cdot)_+$ denotes the positive part, then

$$\begin{aligned}\frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) &= \int\limits_0^{z_0}\int\limits_0^{z_0} \beta(z')k(z,z')\Psi(z)\mathcal{U}(z')\left[\frac{\tilde{u}(z,t)}{\mathcal{U}(z)} - \frac{\tilde{u}(z',t)}{\mathcal{U}(z')} + \left[\frac{\tilde{u}(z',t)}{\mathcal{U}(z')} - \frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right]\right]dzdz' \\ &= 0.\end{aligned}$$

Therefore, $\mathcal{H}_\Psi(\tilde{u}|\mathcal{U})$ is constant in time and $\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) = \int_0^{z_0} \Psi(z)\,\tilde{u}(z,t)\,dz$.

(ii) With $H(h) = |h|$, we obtain from Lemma 3.3 that

$$\frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) = \frac{d}{dt}\int\limits_0^{z_0} |\tilde{u}(z,t)|\;\Psi(z)\,dz \leq 0.$$

Thus, the contraction principle follows.

□

In the next lemma, we show further a priori estimates for solutions to (3.4).

Lemma 3.5. *Under the conditions of Lemma 3.3,* $\Psi > 0$*, and the following conditions on the eigenfunction* $\mathcal{U}$ *and the initial condition* u_0 *of a solution* $\tilde{u}$ *to* (3.4)*:*

$$\frac{d}{dz}\big(b(z)\mathcal{U}(z)\big) \in L^1\big((0,z_0),\Psi(z)\,dz\big) \quad \textit{and} \quad \frac{d}{dz}\big((b(z)\,u_0(z)\big) \in L^1\big((0,z_0),\Psi(z)\,dz\big),$$

it holds that

(i) $|\tilde{u}(z,t)| \leq C\mathcal{U}(z)$ *for a.e.* $z \in [0,z_0]$ *and for all* $t \geq 0$*,*

(ii) $\int\limits_0^{z_0} |\partial_t\tilde{u}(z,t)|\,\Psi(z)\,dz \leq C_1(u_0)$ *for all* $t \geq 0$*, where* $C_1(u_0)$ *is a constant depending on* u_0*, and*

(iii) $\int\limits_0^{z_0} \big|\partial_z\big(b(z)\,\tilde{u}(z,t)\big)\big|\;\Psi(z)\,dz \leq C_2(u_0)$ *for all* $t \geq 0$*.*

Proof. This proof follows that of [32, Theorem 4.5].

(i) We choose $H(h) = \big(|h| - C\big)_+$, where $(\cdot)_+$ denotes the positive part. Therefore, by Lemma 3.3,

$$\begin{aligned}\frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) &= \frac{d}{dt}\int\limits_0^{z_0} \Psi(z)\mathcal{U}(z)\left(\frac{|\tilde{u}(z,t)|}{\mathcal{U}(z)} - C\right)_+ dz \\ &= \frac{d}{dt}\int\limits_0^{z_0} \Psi(z)\,\big(|\tilde{u}(z,t)| - C\,\mathcal{U}(z)\big)_+\,dz \leq 0.\end{aligned}$$

Hence,

$$0 \le \int_0^{z_0} \Psi(z)\left(|\tilde{u}(z,t)| - C\mathcal{U}(z)\right)_+ dz \le \int_0^{z_0} \Psi(z)\left(|\tilde{u}(z,0)| - C\mathcal{U}(z)\right)_+ dz = 0$$

and because $\Psi > 0$ a.e., we have $\left(|\tilde{u}(z,t)| - C\mathcal{U}(z)\right)_+ = 0$ for a.e. z. Therefore, $|\tilde{u}(z,t)| \le C\mathcal{U}(z)$ for a.e. $z \in [0, z_0]$ and for every $t \ge 0$.

(ii) Recall that $\tilde{u}$ is a solution to

$$\partial_t \tilde{u}(z,t) + \partial_z\big(b(z)\,\tilde{u}(z,t)\big) = -\big(\beta(z) + \mu(z) + \lambda\big)\,\tilde{u}(z,t) + \int_z^{z_0} \beta(z')\,k(z,z')\,\tilde{u}(z',t)\,dz'.$$

By differentiation in time t, we obtain that $q(z,t) := \partial_t \tilde{u}(z,t)$ also satisfies this equation. Therefore, we can apply the contraction principle from Lemma 3.4 to the solution q to conclude

$$\int_0^{z_0} |q(z,t)|\,\Psi(z)\,dz \le \int_0^{z_0} |q(z,0)|\,\Psi(z)\,dz.$$

By the definition of q we have

$$\begin{aligned} q(z,0) &= \partial_t \tilde{u}(z,0) \\ &= -\partial_z\big(b(z)u_0(z)\big) - \big(\beta(z) + \mu(z) + \lambda\big)u_0(z) + \int_z^{z_0} \beta(z')k(z,z')u_0(z')\,dz. \end{aligned}$$

Next, we use the assumption on u_0 to estimate the right hand side and the fact that $\mathcal{U}$ is a solution to (3.2) to obtain

$$\begin{aligned} |q(z,0)| &\le \left|\frac{d}{dz}\big(b(z)\,u_0(z)\big)\right| + |\beta(z) + \mu(z) + \lambda|\,C\,\mathcal{U}(z) + \int_z^{z_0} \beta(z')\,k(z,z')\,C\,\mathcal{U}(z')\,dz \\ &\le \left|\frac{d}{dz}\big(b(z)\,u_0(z)\big)\right| + 2\,|\beta(z) + \mu(z) + \lambda|\,C\,\mathcal{U}(z) + C\left|\frac{d}{dz}\big(b(z)\,\mathcal{U}(z)\big)\right|. \end{aligned}$$

Therefore,

$$\begin{aligned} \int_0^{z_0} |q(z,0)|\,\Psi(z)\,dz \le& \int_0^{z_0} \left[\left|\frac{d}{dz}\big(b(z)\,u_0(z)\big)\right| + C\left|\frac{d}{dz}\big(b(z)\,\mathcal{U}(z)\big)\right|\right]\Psi(z)\,dz \\ &+ 2C\big(\overline{\beta} + \overline{\mu} + |\lambda|\big) \le C_1(u_0) < \infty, \end{aligned}$$

where $C_1(u_0) > 0$ is some constant depending on the initial condition u_0. In the last step we have used that by assumption it holds that $\frac{d}{dz}(b(z)u_0(z))$ and $\frac{d}{dz}(b(z)\mathcal{U}(z)) \in L^1((0,z_0), \Psi(z)\,dz)$. Overall, we have

$$\int_0^{z_0} |\partial_t \tilde{u}(z,t)|\,\Psi(z)\,dz = \int_0^{z_0} |q(z,t)|\,\Psi(z)\,dz \le \int_0^{z_0} |q(z,0)|\,\Psi(z)\,dz \le C_1(u_0).$$

(iii) Since $\tilde{u}$ is a solution to (3.4), we have that

$$\partial_z\big(b(z)\,\tilde{u}(z,t)\big) = -\partial_t\tilde{u}(z,t) - \big(\beta(z)+\mu(z)+\lambda\big)\,\tilde{u}(z,t) + \int_0^{z_0} \beta(z')\,k(z,z')\,\tilde{u}(z',t)\,dz'.$$

We take the absolute value, multiply with Ψ, and integrate over z from 0 to z_0 and obtain with (i) and (ii) similar to the above calculation

$$\begin{aligned}\int_0^{z_0} \left|\frac{d}{dz}\big(b(z)\,\tilde{u}(z,t)\big)\right| \Psi(z)\,dz &\le \int_0^{z_0} |\partial_t\tilde{u}(z,t)|\,\Psi(z)\,dz + 2C\big(\overline{\beta}+\overline{\mu}+|\lambda|\,\big)\\ &\quad + C\int_0^{z_0}\left|\frac{d}{dz}\big(b(z)\mathcal{U}(z)\big)\right|\Psi(z)\,dz\\ &\le C_2(u_0).\end{aligned}$$

This finishes the proof. $\square$

Finally, we can now show the main theorem of this section on convergence of the solution to the eigensolution $\mathcal{U}$.

Theorem 3.6. *If the conditions of Lemma 3.5 hold and there exists a continuously differentiable function $\Gamma : [0,z_0] \to [0,\infty)$ such that $\Gamma(I) = [0,z_0]$ for some interval $I = [0,a] \subseteq [0,z_0]$,*

$$\{(z,\Gamma(z)),\ z\in I\} \subseteq \operatorname*{supp}_{[0,z_0]\times[0,z_0]} k(z,z'), \quad \text{and} \quad b(z)\,\Gamma'(z) \ne b(\Gamma(z)) \text{ for a.e. } z\in I \tag{3.5}$$

hold, then solutions to (3.1) tend to a steady state as with $m := \int_0^{z_0} u_0(z)\,\Psi(z)\,dz$ it holds that

$$\lim_{t\to\infty}\int_0^{z_0}\left|u(z,t)\,e^{-\lambda t} - m\,\mathcal{U}(z)\right| b(z)\,\Psi(z)\,dz = 0.$$

Remark 3.7. Condition (3.5) in Theorem 3.6 is a non-degeneracy condition on the support of the plasmid segregation kernel k. It holds, for example, for logistic plasmid reproduction and a scalable kernel, where $\Phi : [0,1] \to \mathbb{R}_{\ge 0}$ satisfies:

there are constants $0 < \delta_1 < \delta_2 < 1$ and $c > 0$ such that $\Phi(x) \ge c$ for all $x \in [\delta_1,\delta_2]$

(see [25, Remark 4.4]) because then there is some $a > 1$ such that $\Gamma(z) = az$ satisfies $\Gamma([0,\frac{z_0}{a}]) = [0,z_0]$, the graph of $\Gamma(z)$ for $z \in I = [0,\frac{z_0}{a}]$ is a subset of the support of k, and $\Gamma'(z) = a > \frac{a(z_0-az)}{z_0-z} = \frac{b(\Gamma(z))}{b(z)}$ for all $z \in I$.

Proof. This proof is based on the proofs of [32, Theorem 4.7] and [25, Theorems 3.2, 4.3] that we extend to the case of logistic plasmid reproduction $b(z)$, i.e., a logistic drift velocity. The proof consists of four steps. In the first and second step, we show convergence results. In Step 3, we show that the limit obtained in Step 2 can be written as $m\,b(z)\,\mathcal{U}(z)$. Finally, we combine Steps 1 to 3 to finish the proof.

Step 1: Convergence of $b(z)\,\tilde{u}_n(z,t)$

If $u(z,t)$ is a solution to (3.1), then $\tilde{u}(z,t) := u(z,t)\,e^{-\lambda t}$ is a solution to (3.4). We introduce the sequence $\tilde{u}_n(z,t) := \tilde{u}(z,t+t_n)$ where $(t_n)_{n\in\mathbb{N}}$ is a sequence with $t_n \ge 0$ and $t_n \xrightarrow{n\to\infty} \infty$.

We define $\tilde{v}_n(z,t) := b(z)\,\tilde{u}_n(z,t)$ for every $n \in \mathbb{N}$. Then, $\tilde{v}_n(z,t)$ is a solution to

$$\begin{cases} \partial_t \tilde{v}(z,t) + b(z)\partial_z \tilde{v}(z,t) = -\big(\beta(z)+\mu(z)+\lambda\big)\tilde{v}(z,t) \\ \qquad\qquad\qquad\qquad + b(z)\displaystyle\int_z^{z_0} \beta(z')\,k(z,z')\,\frac{\tilde{v}(z',t)}{b(z')}\,dz', \\ \tilde{v}(0,t) = 0 \text{ for all } t \geq 0, \qquad \tilde{v}(z,0) = b(z)\,\tilde{u}(z,0) \text{ for all } z \in (0,z_0), \end{cases} \tag{3.6}$$

where the initial condition is replaced by $\tilde{v}_n(z,0) = b(z)\,\tilde{u}_n(z,0)$. By Lemma 3.5, it holds that

$$|\tilde{v}_n(z,t)| = |b(z)\,\tilde{u}_n(z,t)| \leq \|b\|_\infty\,|\tilde{u}(z,t+t_n)| \leq \|b\|_\infty\,C\,\mathcal{U}(z)$$

for all $t \geq 0$ and all $n \in \mathbb{N}$,

$$\begin{aligned} \int_0^{z_0} |\partial_t \tilde{v}_n(z,t)|\,\Psi(z)\,dz &= \int_0^{z_0} \big|\partial_t\big(b(z)\,\tilde{u}_n(z,t)\big)\big|\,\Psi(z)\,dz \leq \|b\|_\infty \int_0^{z_0} |\partial_t \tilde{u}_n(z,t)|\,\Psi(z)\,dz \\ &= \|b\|_\infty \int_0^{z_0} |\partial_t \tilde{u}(z,t+t_n)|\,\Psi(z)\,dz \leq \|b\|_\infty\,C_1(u_0) < \infty, \end{aligned}$$

and

$$\begin{aligned} \int_0^{z_0} |\partial_z \tilde{v}_n(z,t)|\,\Psi(z)\,dz &= \int_0^{z_0} \big|\partial_z\big(b(z)\,\tilde{u}_n(z,t)\big)\big|\,\Psi(z)\,dz \\ &= \int_0^{z_0} \big|\partial_z\big(b(z)\,\tilde{u}(z,t+t_n)\big)\big|\,\Psi(z)\,dz \leq C_2(u_0) < \infty. \end{aligned}$$

This means that we have bounded variation regularity of the solution $\tilde{v}_n$ to (3.6) which gives local strong compactness of families of solutions to (3.6) (see [32, p. 91]). Therefore, there is a subsequence that we still denote by $\tilde{v}_n$ such that for all $T > 0$

$$\tilde{v}_n(z,t) \xrightarrow{n\to\infty} h(z,t) \quad \text{strongly in } L^1\big((0,z_0)\times[0,T]\big).$$

Then, $h(z,t)$ is a solution to the integro-differential equation in (3.6), and it holds that $|h(z,t)| \leq C\,\mathcal{U}(z)$ for some $C > 0$ due to $|\tilde{v}_n(z,t)| \leq \|b\|_\infty\,C\,\mathcal{U}(z)$ for all $t \geq 0$ and $n \in \mathbb{N}$.

Step 2: Convergence of $\mathcal{H}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)$ and $\tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)$

With $v(z,t) = b(z)\,u(z,t)$, $\mathcal{V}(z) = b(z)\,\mathcal{U}(z)$, $\tilde{\Psi}(z) = \frac{\Psi(z)}{b(z)}$, and $\tilde{v}(z,t) = b(z)\,\tilde{u}(z,t)$ we can show exactly as before (see Theorem 3.2 and Lemma 3.3) that

$$\frac{d}{dt}\mathcal{H}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t) = \frac{d}{dt}\int_0^{z_0} \tilde{\Psi}(z)\,\mathcal{V}(z)\,H\!\left(\frac{\tilde{v}(z,t)}{\mathcal{V}(z)}\right)\,dz = -\tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t) \leq 0,$$

where

$$\tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t) := \int_0^{z_0}\int_0^{z_0} \frac{b(z)}{b(z')}\,\beta(z')\,k(z,z')\,\tilde{\Psi}(z)\,\mathcal{V}(z')\left[H\left(\frac{\tilde{v}(z',t)}{\mathcal{V}(z')}\right) - H\left(\frac{\tilde{v}(z,t)}{\mathcal{V}(z)}\right)\right.$$
$$\left. + H'\left(\frac{\tilde{v}(z,t)}{\mathcal{V}(z)}\right)\left[\frac{\tilde{v}(z,t)}{\mathcal{V}(z)} - \frac{\tilde{v}(z',t)}{\mathcal{V}(z')}\right]\right] dz'\,dz.$$

Thus, for every solution g to (3.6) and every non-negative, convex, and a.e. differentiable function H, the function $\mathcal{H}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)$ is non-increasing and bounded below by 0 (as $\tilde{\Psi}$, $\mathcal{V}$, and H are non-negative). Therefore, $\mathcal{H}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)$ converges to some $L \geq 0$ for $t \to \infty$ and $\tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t) = -\frac{d}{dt}\mathcal{H}_{\tilde{\Psi}}(g|\,\mathcal{V})(t) \xrightarrow{t\to\infty} 0$.

Step 3: Solutions g to (3.6) with $\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)\,dt = 0$ satisfy $g(z,t) = mb(z)\mathcal{U}(z)$

Next, we characterize solutions g to the integro-differential equation in (3.6) that also satisfy the following equation: $\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)\,dt = 0$. With the choice $H(s) = s^2$ (for the remainder of this proof we always make this choice for H) and the definition of $\tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)$, we obtain that

$$0 = \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)\,dt$$
$$= \int_0^\infty\int_0^{z_0}\int_0^{z_0} \frac{b(z)}{b(z')}\,\beta(z')\,k(z,z')\,\tilde{\Psi}(z)\,\mathcal{V}(z')\left[\frac{g(z,t)}{\mathcal{V}(z)} - \frac{g(z',t)}{\mathcal{V}(z')}\right]^2 dz'dzdt.$$

Recall that $\underline{\beta} > 0$, $\Psi > 0$, $\mathcal{U} > 0$, $b(z) > 0$ for all $z \in (0,z_0)$, thus $\mathcal{V} > 0$ and $\tilde{\Psi} > 0$ in $(0,z_0)$, and for all z, $z' \in (0,z_0)$ it holds that $\frac{b(z)}{b(z')} > 0$. Therefore, for a.e. $t > 0$ and $(z,z') \in \mathrm{supp}(k)$ it holds that

$$\frac{g(z,t)}{\mathcal{V}(z)} = \frac{g(z',t)}{\mathcal{V}(z')}. \tag{3.7}$$

If we define $\psi(z,t) := \frac{g(z,t)}{\mathcal{V}(z)}$, then for a.e. $t > 0$, $z \in I \subseteq [0,z_0]$

$$\psi(z,t) = \psi(\Gamma(z),t).$$

As in the proof of Theorem 3.2, it is straightforward to show that for a.e. $t > 0$ and $z \in (0,z_0)$

$$\partial_t\psi(z,t) + b(z)\,\partial_z\psi(z,t) = 0, \tag{3.8}$$

where we use (3.7) and the same rescaling as before.

We aim to show that $\psi(z,t)$ is constant and therefore use that

$$\left(\partial_t\psi\right)(z,t) = \left(\partial_t\psi\right)(\Gamma(z),t) \quad \text{and} \quad \left(\partial_z\psi\right)(z,t) = \Gamma'(z)\left(\partial_z\psi\right)(\Gamma(z),t).$$

Hence, for a.e. $t > 0$ and $z \in I$

$$(\partial_t\psi)(\Gamma(z),t) + b(z)\,\Gamma'(z)\;(\partial_z\psi)(\Gamma(z),t) = 0$$

and

$$(\partial_t\psi)(\Gamma(z),t) + b(\Gamma(z))\,(\partial_z\psi)(\Gamma(z),t) = 0.$$

Overall, it holds that

$$\big(\Gamma'(z)\,b(z) - b(\Gamma(z))\big)\,(\partial_z\psi)(\Gamma(z),t) = 0.$$

As by assumption $b(z)\,\Gamma'(z) \neq b(\Gamma(z))$ for a.e. $z \in I$, it holds for a.e. $t > 0$ and $z \in I$ that

$$(\partial_z \psi)(\Gamma(z), t) = 0.$$

Since Γ is a continuously differentiable function it has the Luzin N-property which means that it maps sets of measure zero to sets of measure zero (see, e.g., [6, Definition 3.6.8]). Therefore, $(\partial_z \psi)(z,t) = 0$ for a.e. $z \in (0, z_0)$ and ψ is constant for a.e. $z \in (0, z_0)$. Equation (3.8) implies that ψ is also constant for a.e. $t > 0$.

By definition of ψ it follows that there is some constant $c > 0$ such that a solution g to (3.6) with $\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)\,dt = 0$ satisfies $g(z,t) = c\,\mathcal{V}(z) = c\,b(z)\,\mathcal{U}(z)$ for a.e. $t > 0$ and $z \in (0, z_0)$. Multiplying $g(z,t) = c\,\mathcal{V}(z)$ with $\tilde{\Psi}(z)$, integrating over z, and once again rescaling yields

$$\begin{aligned} c = c\int_0^{z_0} \mathcal{U}(z)\,\Psi(z)\,dz &= c\int_0^{z_0} \frac{\mathcal{V}(z)}{b(z)}\,b(z)\,\tilde{\Psi}(z)\,dz = \int_0^{z_0} c\,\mathcal{V}(z)\,\tilde{\Psi}(z)\,dz = \int_0^{z_0} g(z,t)\,\tilde{\Psi}(z)\,dz \\ &= \int_0^{z_0} b(z)\,\tilde{u}(z,t)\,\frac{\Psi(z)}{b(z)}\,dz = \int_0^{z_0} \tilde{u}(z,t)\,\Psi(z)\,dz = m. \end{aligned}$$

Therefore, every solution g to (3.6) with $\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(g|\,\mathcal{V})(t)\,dt = 0$ satisfies $g(z,t) = m\,\mathcal{V}(z) = m\,b(z)\mathcal{U}(z)$ for a.e. $t > 0$ and $z \in (0, z_0)$.

Step 4: Conclusion

Finally, we combine Steps 1, 2, and 3. Consider the sequence $\tilde{v}_n(z,t)$ from Step 1 and define the function $f : \mathbb{N} \times \mathbb{R}_{>0} \to \mathbb{R}$,

$$f(n,T) := \int_0^T \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt.$$

By Step 1, it holds for every $T > 0$ that $\lim_{n\to\infty} f(n,T) = \int_0^T \tilde{\mathcal{D}}_{\tilde{\Psi}}(h|\,\mathcal{V})(t)\,dt < \infty$ and for every $n \in \mathbb{N}$ it holds that $\lim_{T\to\infty} f(n,T) = \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt =: \tilde{g}(n) < \infty$, since with $\frac{d}{dt}\mathcal{H}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t) = -\tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)$,

$$\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt = \mathcal{H}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(0) - \lim_{t\to\infty} \mathcal{H}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t) = \mathcal{H}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(0) - L < \infty,$$

for every solution $\tilde{v}_n$ to (3.6) by Step 2. Furthermore, it holds that

$$\lim_{T\to\infty}\sup_{n\in\mathbb{N}}|f(n,T)-\tilde{g}(n)| = \lim_{T\to\infty}\sup_{n\in\mathbb{N}}\left|\int_0^T \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt - \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt\right|$$
$$= \lim_{T\to\infty}\sup_{n\in\mathbb{N}}\left|\int_0^T \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t+t_n)\,dt - \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t+t_n)\,dt\right|$$
$$= \lim_{T\to\infty}\sup_{n\in\mathbb{N}}\left|\int_{t_n}^{T+t_n} \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t)\,dt - \int_{t_n}^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t)\,dt\right|$$
$$= \lim_{T\to\infty}\sup_{n\in\mathbb{N}}\left|\int_{T+t_n}^{\infty} \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t)\,dt\right| = \lim_{T\to\infty}\int_{T+\inf\limits_{n\in\mathbb{N}} t_n}^{\infty} \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t)\,dt = 0.$$

Therefore, $f(n,T) \xrightarrow{T\to\infty} \tilde{g}(n)$ uniformly on $\mathbb{N}$ and by the Moore-Osgood Theorem (see, e.g., [18, p. 100]) it holds that $\lim\limits_{n\to\infty}\lim\limits_{T\to\infty} f(n,T) = \lim\limits_{T\to\infty}\lim\limits_{n\to\infty} f(n,T)$, i.e.,

$$\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt \xrightarrow{n\to\infty} \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(h|\,\mathcal{V})(t)\,dt.$$

On the other hand, it also holds that

$$\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}_n|\,\mathcal{V})(t)\,dt = \int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t+t_n)\,dt = \int_{t_n}^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(\tilde{v}|\,\mathcal{V})(t)\,dt \xrightarrow{n\to\infty} 0.$$

Since the limit is unique, we have that h is a solution to the integro-differential equation in (3.6) and it satisfies $\int_0^\infty \tilde{\mathcal{D}}_{\tilde{\Psi}}(h|\,\mathcal{V})(t)\,dt = 0$. Then, due to Step 3, it follows that $h(z,t) = m\,b(z)\mathcal{U}(z)$ a.e. and therefore

$$b(z)\,\tilde{u}(z,t) = \tilde{v}(z,t) \xrightarrow{t\to\infty} m\,b(z)\mathcal{U}(z) \quad \text{in } L^1((0,z_0),\,\Psi(z)\,dz)$$

or equivalently

$$\tilde{u}(z,t) \xrightarrow{t\to\infty} m\,\mathcal{U}(z) \quad \text{in } L^1((0,z_0),\,b(z)\,\Psi(z)\,dz).$$

This finishes the proof. □

Overall, we have shown that the eigensolution $\mathcal{U}$ is asymptotically stable if there is a solution to the eigenproblem (3.2) and the dual eigenproblem (3.3) satisfying Assumption **(A9)** and the assumptions in Theorem 3.6 on the initial condition u_0, the eigenfunction $\mathcal{U}$, the dual eigenfunction Ψ, and the support of k are satisfied. In particular, we have thus shown that the corresponding eigenvalue is a simple eigenvalue and the eigensolution is the unique solution to the eigenproblem.

Corollary 3.8. *Assume that Assumptions* ***(A1)*** *to* ***(A4)*** *hold,* $\lambda = \beta - \mu$, *and* $\frac{2\beta}{b_0} < -\left(\tilde{\Phi}'(0)\right)^{-1}$. *Let k satisfy the non-degeneracy condition in Theorem 3.6, and let the initial* *condition u_0 satisfy for some $C > 0$*

$$\frac{d}{dz}\big(b(z)\, u_0(z)\big) \in L^1((0, z_0)) \quad \textit{and} \quad |u_0(z)| \le C\,\mathcal{U}(z) \ \textit{ for all } z \in [0, z_0].$$

Then, there exists a positive and asymptotically stable eigensolution $\mathcal{U}$ for the eigenproblem (3.2).

Proof. By Theorem 2.10, there is an eigenfunction $\mathcal{U} > 0$ and by Lemma 3.1 there is a dual eigenfunction $\Psi \equiv 1$. It holds that $\Psi > 0$ and since $\mathcal{U} \in L^1((0, z_0))$ and $\mathcal{U}$ is a solution to (3.2),

$$\frac{d}{dz}\big(b(z)\mathcal{U}(z)\big) \in L^1((0, z_0)) = L^1((0, z_0),\ \Psi(z)\, dz).$$

Hence, the corollary is a direct consequence of Theorems 2.10 and 3.6. ☐

Thus, we have stability for our special case and also in a more general case as long as there is an eigensolution in the sense of **(A9)** and the conditions in Theorem 3.6 are satisfied.

4. Conclusion

In this paper, we considered the eigenproblem associated with a model for plasmid segregation of high-copy plasmids in a bacterial population. First, we have shown existence of an eigensolution. Due to lack of compactness standard approaches such the Krein-Rutman Theorem were not applicable. Instead, we used rescalings, a fixed point argument, and the Laplace transform to show existence of an eigensolution.

The conditions on the parameters for existence of an eigensolution coincide with a known Threshold Theorem for the long-term distribution of plasmids (see [28, Corollary 4.19]). Moreover, we gave a possible biological interpretation of the conditions on the parameters: the bacteria may not reproduce too fast compared to the plasmids, i.e., the quotient of the reproduction rate of bacteria and plasmids is bounded. The bound is given by a measure of how "equally" plasmids are distributed to the two daughter cells. If bacteria distribute their plasmids equally to both daughter cells, then this bound is higher than if plasmids are distributed unequally meaning if one daughter cell receives a larger fraction of plasmids than the other.

In order to investigate the stability of the eigensolution, we used the Generalized Relative Entropy method which does not require compactness. We adapted the method to the case of vanishing transport term at zero and the maximal plasmid content z_0. Thereby, we obtained the stability of the eigensolution under general assumptions on the parameters of the model and if an appropriate eigensolution exists.

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Appendix A. Proof of Theorem 2.9

In this section, we show the existence of a solution g to (2.4), i.e., we show Theorem 2.9.

In the proof of Theorem 2.9 we use the following notation (see for example [2]).

Definition A.1. The *convolution* of two L^1-functions $f,\, g : [0, \infty) \to \mathbb{R}$ is defined by

$$(f * g)\,(t) := \int_0^t f(\tau)\, g(t - \tau)\, d\tau.$$

For $n \in \mathbb{N}$, we define the *n-fold convolution of f with g* by

$$\left(f^{*n} * g\right)(t) := \left(f * \left(f^{*(n-1)} * g\right)\right)(t), \quad \text{where } \left(f^{*0} * g\right)(t) := g(t).$$

We prove Theorem 2.9 in steps. Firstly, we derive the conditions on the parameters given existence of the solution g to (2.4). By rescaling the solution g, we obtain a function q that satisfies an equation containing n-fold convolutions. This equation can be simplified with the Laplace transform as the Laplace transform of a convolution is the product of the Laplace transforms. Then, the boundedness of the Laplace transform yields a first condition on the parameters. The remaining conditions follow from positivity and boundedness of the Laplace transform.

Secondly, we show that the conditions on the parameters imply the existence of the unique solution g to (2.4). By Lemma 2.8, we know that there is a unique solution g to the integro-differential equation in (2.4). It thus remains to show that g satisfies the integrability condition in (2.4) and is a positive function. To this end, we use the assumptions on the parameters, the same rescaling as in the first part of the proof, and the Laplace transform to obtain an iteration formula for the Laplace transform of q. This iteration formula can be used to extend the Laplace transform. Finally, we show that the integral condition on g holds using the uniqueness (a.e.) of the inverse Laplace transform. The positivity condition on g follows via a proof by contradiction.

We now start by assuming that there is a solution g to (2.4) and showing that the rescaled solution q satisfies an equation containing n-fold convolutions.

Proposition A.2. *If there is a solution $g \in \mathcal{C}^0\left((0, z_0]\right) \cap \mathcal{C}^1\left((0, z_0)\right)$ to (2.4), then the function $q : \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ defined by*

$$q(t) := \left(1 - e^{-t}\right)^{\alpha} g(z_0\, e^{-t})$$

satisfies $q(0) = 0$, $\lim_{t\to\infty} q(t) = 0$, $q(t) \geq 0$ for all $t \geq 0$, and $q \in \mathcal{C}^0([0,\infty)) \cap \mathcal{C}^1((0,\infty))$. Moreover, there exist $M > 0$ and $a > 0$ such that $q(t) \leq M e^{-at}\left(1 - e^{-t}\right)^{\alpha}$ for all $t \geq 0$, and with $\check{\Phi}(t) := \Phi(e^{-t})\, e^{-t}$ the following equation holds for every $n \in \mathbb{N}$:

$$\begin{aligned} \alpha\, q(t) = {} & \left(1 - e^{-t}\right) \sum_{k=0}^{n} \left(\frac{\alpha_0}{\alpha}\right)^{k} \left(\check{\Phi}^{*k} * \left(q'(s)\right)\right)(t) \\ & + \left(1 - e^{-t}\right) \left(\frac{\alpha_0}{\alpha}\right)^{n+1} \left(\check{\Phi}^{*(n+1)} * \left(\frac{\alpha\, q(s)}{1 - e^{-s}}\right)\right)(t). \end{aligned} \tag{A.1}$$

Proof. We rescale g to derive the equation for q.

Assume there is a solution g to (2.4) and let $g\big(z_0\, e^{-t}\big) = e^{\alpha t}\, h(t)$ or equivalently $g(z) = \left(\frac{z_0}{z}\right)^{\alpha} h\big(-\log(\frac{z}{z_0})\big)$. Then h satisfies

$$h(0) = 1, \quad \lim_{t\to\infty} e^{\alpha t}\, h(t) = 0, \quad h(t) \geq 0 \text{ for all } t \geq 0, \quad h \in \mathcal{C}^0([0,\infty)) \cap \mathcal{C}^1((0,\infty)),$$

$$\int_0^{z_0} \frac{(z_0 - z)^{\alpha}\, z^{-\alpha}\, h(-\log(z/z_0))}{b(z)}\, dz < \infty.$$

The integrability condition on g in (2.4) is

$$\int_0^{z_0} \frac{(z_0 - z)^{\alpha}\, g(z)}{z\,(z_0 - z)}\, dz = \int_0^{z_0} (z_0 - z)^{\alpha - 1}\, z^{-1}\, g(z)\, dz < \infty.$$

The integrand is integrable in a neighborhood of zero if and only if[1] there exist $\varepsilon > 0$, $C > 0$, and $a > 0$ such that for all $0 < z < \varepsilon$ it holds that

$$g(z) \le C\, z^a.$$

Therefore, with the transformation to h and since $h \in \mathcal{C}^0([0,\infty))$ it holds for h that

$$\text{there exist } M > 0,\ a > 0 \text{ such that } h(t) \le M e^{-(a+\alpha)t} \text{ for all } t \ge 0.$$

With $\check{\Phi}(t) := \Phi(e^{-t})\, e^{-t}$ and the transform $\sigma = -\log(z'/z_0)$, we obtain

$$\begin{aligned}
h'(t) &= \left(e^{-\alpha t} g(z_0 e^{-t})\right)' = -\alpha e^{-\alpha t} g(z_0 e^{-t}) + e^{-\alpha t} g'(z_0 e^{-t})\,(-z_0 e^{-t}) \\
&= -\alpha e^{-\alpha t} g(z_0 e^{-t}) - z_0 e^{-(\alpha+1)t} \Bigg[-\frac{\alpha}{z_0 e^{-t}} g(z_0 e^{-t}) \\
&\qquad + \frac{\alpha_0 z_0}{(z_0 - z_0 e^{-t})^\alpha} \int_{z_0 e^{-t}}^{z_0} \Phi\left(\frac{z_0 e^{-t}}{z'}\right) (z')^{-2} (z_0 - z')^{\alpha-1} g(z')\, dz' \Bigg] \\
&= -\frac{\alpha_0}{(e^t - 1)^\alpha} \int_0^t \check{\Phi}(t-\sigma)\, h(\sigma)\, e^{\alpha\sigma}\, (1 - e^{-\sigma})^{\alpha-1}\, d\sigma \\
&= -\frac{\alpha_0}{\alpha (e^t - 1)^\alpha} \int_0^t \check{\Phi}(t-\sigma)\, h(\sigma)\, \frac{d}{d\sigma} (e^\sigma - 1)^\alpha\, d\sigma.
\end{aligned}$$

Therefore,

$$\left(e^t - 1\right)^\alpha h'(t) = -\frac{\alpha_0}{\alpha} \int_0^t \check{\Phi}(t-\sigma)\, h(\sigma)\, \frac{d}{d\sigma}\, (e^\sigma - 1)^\alpha\ d\sigma.$$

We now use n-fold convolutions and the notation from Definition A.1 to rewrite the equation for h as

$$\left(e^t - 1\right)^\alpha h'(t) = -\frac{\alpha_0}{\alpha} \left(\check{\Phi}^{*1} * \left(h(s)\, \frac{d}{ds}\, (e^s - 1)^\alpha \right) \right)(t).$$

[1] It holds that $\int_0^\varepsilon \frac{1}{z} g(z)\, dz < \infty$ for all $\varepsilon \in (0, z_0)$. Let $\varepsilon \in (0, \min\{z_0, 1\})$, $C > 0$, and assume that for all $a > 0$ it holds that $g(z) > Cz^a$ on $(0,\varepsilon)$, then $g(z) \ge \lim_{a \to 0^+} Cz^a = C\,\mathrm{sgn}(z)$, where sgn denotes the sign function, i.e., $\mathrm{sgn}(z) = 1$ for $z > 0$, $\mathrm{sgn}(0) = 0$, and $\mathrm{sgn}(z) = -1$ for $z < 0$. Therefore, $\int_0^\varepsilon \frac{1}{z} g(z)\, dz \ge C \int_0^\varepsilon \frac{1}{z}\, dz = \infty$ which is a contradiction to the integrability of $\frac{1}{z} g(z)$. Hence, there exist $a > 0$ and $C > 0$ such that $g(z) \le C\, z^a$ for all $z \in (0, \varepsilon)$.

Thus, we obtain

$$
\begin{aligned}
h(t)\,\frac{d}{dt}\big(e^t-1\big)^{\alpha} &= \frac{d}{dt}\Big[\big(e^t-1\big)^{\alpha}\,h(t)\Big] - \big(e^t-1\big)^{\alpha}\,\frac{d}{dt}h(t)\\
&= \frac{d}{dt}\Big[\big(e^t-1\big)^{\alpha}\,h(t)\Big] + \frac{\alpha_0}{\alpha}\left(\check{\Phi}^{*1} * \left(h(s)\,\frac{d}{ds}(e^s-1)^{\alpha}\right)\right)(t)\\
&= \left(\frac{\alpha_0}{\alpha}\right)^{0}\left(\check{\Phi}^{*0} * \left(\frac{d}{ds}\big[(e^s-1)^{\alpha}\,h(s)\big]\right)\right)(t) + \frac{\alpha_0}{\alpha}\left(\check{\Phi}^{*1} * \left(\frac{d}{ds}\big[(e^s-1)^{\alpha}\,h(s)\big]\right)\right)(t)\\
&\quad - \frac{\alpha_0}{\alpha}\left(\check{\Phi}^{*1} * \left((e^s-1)^{\alpha}\,\frac{d}{ds}h(s)\right)\right)(t)\\
&= \left(\frac{\alpha_0}{\alpha}\right)^{0}\left(\check{\Phi}^{*0} * \left(\frac{d}{ds}\big[(e^s-1)^{\alpha}\,h(s)\big]\right)\right)(t) + \frac{\alpha_0}{\alpha}\left(\check{\Phi}^{*1} * \left(\frac{d}{ds}\big[(e^s-1)^{\alpha}\,h(s)\big]\right)\right)(t)\\
&\quad + \left(\frac{\alpha_0}{\alpha}\right)^{2}\left(\check{\Phi}^{*2} * \left(h(s)\,\frac{d}{ds}(e^s-1)^{\alpha}\right)\right)(t).
\end{aligned}
$$

Proceeding recursively, we obtain for every $n \in \mathbb{N}$

$$
\begin{aligned}
h(t)\,\frac{d}{dt}\big(e^t-1\big)^{\alpha} = \sum_{k=0}^{n}\left(\frac{\alpha_0}{\alpha}\right)^{k}\left(\check{\Phi}^{*k} * \left(\frac{d}{ds}\big[\,(e^s-1)^{\alpha}\,h(s)\big]\right)\right)(t)&\\
+ \left(\frac{\alpha_0}{\alpha}\right)^{n+1}\left(\check{\Phi}^{*(n+1)} * \left(h(s)\,\frac{d}{ds}(e^s-1)^{\alpha}\right)\right)(t).&
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
\alpha\, h(t)\,\big(e^t-1\big)^{\alpha} = \big(1-e^{-t}\big)\sum_{k=0}^{n}\left(\frac{\alpha_0}{\alpha}\right)^{k}\left(\check{\Phi}^{*k} * \left(\frac{d}{ds}\left[(e^s-1)^{\alpha}\,h(s)\right]\right)\right)(t)&\\
+ \big(1-e^{-t}\big)\left(\frac{\alpha_0}{\alpha}\right)^{n+1}\left(\check{\Phi}^{*(n+1)} * \left(h(s)\,\frac{d}{ds}\,(e^s-1)^{\alpha}\right)\right)(t).&
\end{aligned}
\tag{A.2}
$$

Now let $q(t) := h(t)\,\big(e^t-1\big)^{\alpha}$, then $q(t) = (1-e^{-t})^{\alpha}\, g(z_0\, e^{-t})$ and q satisfies

$$
\begin{gathered}
q(0) = 0, \quad \lim_{t\to\infty} q(t) = 0, \quad q(t) \geq 0 \text{ for all } t \geq 0, \quad q \in \mathcal{C}^0([0,\infty)) \cap \mathcal{C}^1((0,\infty)),\\
\text{there exist } M > 0 \text{ and } a > 0 \text{ such that } q(t) \leq M e^{-at}\left(1-e^{-t}\right)^{\alpha} \text{ for all } t \geq 0.
\end{gathered}
$$

By (A.2), q satisfies

$$
\begin{aligned}
\alpha\, q(t) = \big(1-e^{-t}\big)\sum_{k=0}^{n}\left(\frac{\alpha_0}{\alpha}\right)^{k}\left(\check{\Phi}^{*k} * \big(q'(s)\big)\right)(t)&\\
+ \big(1-e^{-t}\big)\left(\frac{\alpha_0}{\alpha}\right)^{n+1}\left(\check{\Phi}^{*(n+1)} * \left(\frac{\alpha\, q(s)}{1-e^{-s}}\right)\right)(t).&
\end{aligned}
$$

This finishes the proof. $\square$

The function q satisfies equation (A.1) which contains n-fold convolutions. As a convolution is transformed into a multiplication under the Laplace transform, we next simplify (A.1) by taking the Laplace transform.

Proposition A.3. *Assume there is a solution $g \in \mathcal{C}^0((0,z_0]) \cap \mathcal{C}^1((0,z_0))$ to (2.4), define the function q as in Proposition A.2, and denote its Laplace transform by $\hat{q}$. Then, $\hat{q} : \mathbb{R} \to \mathbb{R}$ satisfies*

$$\hat{q}(s) > 0 \text{ for all } s \geq 0, \quad \hat{q} \in \mathcal{C}^\infty([0,\infty)),$$

and for every $n \in \mathbb{N}$ and $s > 0$,

$$\hat{q}(s+n) = \hat{q}(s)\, \frac{\alpha - \alpha_0\, \tilde{\Phi}(s+n)}{\alpha - \alpha_0\, \tilde{\Phi}(s)} \prod_{k=1}^{n} \frac{(s+k-1) - \alpha + \alpha_0\, \tilde{\Phi}(s+k-1)}{s+k}, \tag{A.3}$$

where $\tilde{\Phi}(s) := \int_0^1 u^s\, \Phi(u)\, du$.

Furthermore, it holds that $\alpha_0 \leq \alpha$.

Proof. The Laplace transforms $\mathcal{L}\{q(t)\}(s)$ and $\mathcal{L}\Big\{\frac{\alpha\, q(t)}{1-e^{-t}}\Big\}(s)$ exist for $\Re(s) \geq 0$ as there are $M > 0$ and $a > 0$ such that $q(t) \leq M\, e^{-at}\,(1-e^{-t})^\alpha$ for all $t \geq 0$ by Proposition A.2.

We ultimately aim to prove Theorem 2.9. To do so it suffices to consider the Laplace transforms only on the real axis. Therefore, for the remainder of this proof we let $s \in \mathbb{R}$.

Denote by $\hat{q}(s)$ the Laplace transform of $q(t)$ and

$$\tilde{\Phi}(s) := \mathcal{L}\big\{\check{\Phi}(t)\big\}(s) = \int_0^\infty e^{-st}\, \Phi\big(e^{-t}\big)\, e^{-t}\, dt = \int_0^1 u^s\, \Phi(u)\, du,$$

$$\mathcal{L}\big\{q'(t)\big\}(s) = s\hat{q}(s) - \lim_{x\to 0^+} q(x) = s\hat{q}(s),$$

for $s > 0$. Note that $\tilde{\Phi}$ has the following properties

$$\tilde{\Phi}(0) = 1, \quad \tilde{\Phi}(1) = \frac{1}{2}, \quad \tilde{\Phi}'(s) < 0 \ \forall s \geq 0, \quad \lim_{s\to\infty} \tilde{\Phi}(s) = 0, \quad \tilde{\Phi}(s) \in (0,1) \ \forall s \in (0,\infty).$$

These properties are a direct consequence of the properties of Φ. Taking the Laplace transform of equation (A.1) yields for $s > 0$,

$$\begin{aligned}
\alpha\, \hat{q}(s) &= \sum_{k=0}^{n} \left(\frac{\alpha_0}{\alpha}\right)^k \tilde{\Phi}^k(s)\, s\, \hat{q}(s) - \sum_{k=0}^{n} \left(\frac{\alpha_0}{\alpha}\right)^k \tilde{\Phi}^k(s+1)\,(s+1)\,\hat{q}(s+1) \\
&\quad + \left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s)\right)^{n+1} \mathcal{L}\left\{\frac{\alpha\, q(t)}{1-e^{-t}}\right\}(s) - \left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s+1)\right)^{n+1} \mathcal{L}\left\{\frac{\alpha q(t)}{1-e^{-t}}\right\}(s+1) \\
&= \frac{\left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s)\right)^{n+1} - 1}{\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s) - 1}\, s\, \hat{q}(s) - \frac{\left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s+1)\right)^{n+1} - 1}{\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s+1) - 1}\,(s+1)\,\hat{q}(s+1) \\
&\quad + \left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s)\right)^{n+1} \mathcal{L}\left\{\frac{\alpha\, q(t)}{1-e^{-t}}\right\}(s) - \left(\frac{\alpha_0}{\alpha}\,\tilde{\Phi}(s+1)\right)^{n+1} \mathcal{L}\left\{\frac{\alpha\, q(t)}{1-e^{-t}}\right\}(s+1).
\end{aligned} \tag{A.4}$$

As the functions q and $\frac{\alpha\, q(t)}{1-e^{-t}}$ are integrable (for $\alpha > 0$) and non-negative, their Laplace transforms $\hat{q}(s)$ and $\mathcal{L}\Big\{\frac{\alpha\, q(t)}{1-e^{-t}}\Big\}(s)$ are bounded and positive for $s \geq 0$. Moreover, $\tilde{\Phi}(0) = 1$ and $\tilde{\Phi}(s) < 1$ for $s > 0$ and therefore the inequality $\alpha_0 \leq \alpha$ follows by contradiction:
Assume $\alpha_0 > \alpha$, then there are $0 < \underline{s} < \overline{s}$ such that $\frac{\alpha_0}{\alpha}\tilde{\Phi}(s) > 1$ and $\frac{\alpha_0}{\alpha}\tilde{\Phi}(s+1) < 1$ for all $s \in [\underline{s}, \overline{s}]$. Hence, for $s \in [\underline{s}, \overline{s}]$ the first and third summand in (A.4) are increasing in $n \in \mathbb{N}$ and tending to infinity for $n \to \infty$, while the second and fourth summand remain bounded for all

$n \in \mathbb{N}$. This is a contradiction to the boundedness of $\hat{q}(s)$ for all $s \geq 0$ and all $n \in \mathbb{N}$ (which follows directly from g being a solution to (2.4) and the definitions of q and $\hat{q}$ respectively), therefore, $\alpha_0 \leq \alpha$.

Taking the limit $n \to \infty$ in (A.4) yields, because of $\alpha_0 \leq \alpha$ and $\tilde{\Phi}(s) < 1$ for $s > 0$,

$$\alpha\, \hat{q}(s) = \frac{s\, \hat{q}(s)}{1 - \alpha_0\, \tilde{\Phi}(s)/\alpha} - \frac{(s+1)\, \hat{q}(s+1)}{1 - \alpha_0\, \tilde{\Phi}(s+1)/\alpha}. \tag{A.5}$$

We rearrange the terms in equation (A.5) to obtain

$$\begin{aligned}\hat{q}(s+1) &= \hat{q}(s)\, \frac{1 - \alpha_0\, \tilde{\Phi}(s+1)/\alpha}{s+1} \left(\frac{s}{1 - \alpha_0\, \tilde{\Phi}(s)/\alpha} - \alpha \right) \\ &= \hat{q}(s)\, \frac{\left(1 - \alpha_0\, \tilde{\Phi}(s+1)/\alpha\right)\left(s - \alpha + \alpha_0\, \tilde{\Phi}(s)\right)}{(s+1)\left(1 - \alpha_0\, \tilde{\Phi}(s)/\alpha\right)} \\ &= \hat{q}(s)\, \frac{\left(\alpha - \alpha_0\, \tilde{\Phi}(s+1)\right)\left(s - \alpha + \alpha_0\, \tilde{\Phi}(s)\right)}{(s+1)\left(\alpha - \alpha_0\, \tilde{\Phi}(s)\right)}.\end{aligned}$$

By iteration, we obtain equation (A.3), i.e., for $n \in \mathbb{N}$, $s > 0$, and $\alpha_0 \leq \alpha$,

$$\hat{q}(s+n) = \hat{q}(s)\, \frac{\alpha - \alpha_0\, \tilde{\Phi}(s+n)}{\alpha - \alpha_0\, \tilde{\Phi}(s)} \prod_{k=1}^{n} \frac{(s+k-1) - \alpha + \alpha_0\, \tilde{\Phi}(s+k-1)}{s+k}.$$

As $q \geq 0$, $\hat{q}(s) > 0$ for all $s \geq 0$ and $\hat{q} \in \mathcal{C}^\infty([0,\infty))$ as q is of bounded exponential growth, meaning there are constants $c \in \mathbb{R}$, $a > 0$, and $M > 0$ such that $|q(t)| \leq M\, e^{ct}$ for all $t > a$. $\square$

In the last two propositions we have rescaled the solution g to (2.4), we have shown that the Laplace transform $\hat{q}$ of the rescaled solution satisfies (A.3), and using the boundedness of $\hat{q}$ we have obtained $\alpha_0 \leq \alpha$. We can now finish the first part of the proof of Theorem 2.9 by deriving the remaining conditions on α, α_0, and the plasmid segregation kernel Φ in the following proposition.

Proposition A.4. *If $\alpha_0 \leq \alpha$ and there is a positive function $\hat{q} \in \mathcal{C}^\infty([0,\infty))$ which satisfies (A.3), then*

$$\alpha = \alpha_0 \text{ and } \alpha_0 < -\frac{1}{\tilde{\Phi}'(0)}.$$

Proof. The function $\hat{q}$ is determined by $\hat{q}|_{(0,1]}$ and (A.3) with $s \in (0,1]$ and $n \in \mathbb{N}$.

By positivity of $\hat{q}$, $\hat{q}|_{(0,1]} > 0$ and all factors on the right-hand side of (A.3) are positive. As $\alpha_0 \leq \alpha$ and $\tilde{\Phi}(s) < 1$ for $s > 0$, we obtain for the second factor on the right-hand side of (A.3) and for $s > 0$

$$0 < \frac{\alpha - \alpha_0 \tilde{\Phi}(s+n)}{\alpha - \alpha_0 \tilde{\Phi}(s)} < \infty \quad \text{for all } s \in (0,1] \text{ and } n \in \mathbb{N}.$$

By positivity of the denominator of the third term on the right-hand side of (A.3), we obtain the following condition for the numerator: for all $k \in \mathbb{N}$ and $s \in (0,1]$

$$\begin{aligned}&(s+k-1) - \alpha + \alpha_0\, \tilde{\Phi}(s+k-1) > 0 \\ \Leftrightarrow\ &\alpha < s + k - 1 + \alpha_0 \tilde{\Phi}(s+k-1) =: f(s+k-1).\end{aligned}$$

This inequality can only hold if $f(x) > f(0) = \alpha_0$ for all $x > 0$, because otherwise it would contradict $\alpha \geq \alpha_0$. Therefore, we require $f'(0) \geq 0$. Furthermore, from the definition of f,

$$f'(x) = 1 + \alpha_0 \tilde{\Phi}'(x) \qquad \text{and} \qquad f''(x) = \alpha_0 \tilde{\Phi}''(x),$$

where

$$\tilde{\Phi}'(x) = \int_0^1 \log(u)\, u^x\, \Phi(u)\, du < 0 \qquad \text{and} \qquad \tilde{\Phi}''(x) = \int_0^1 (\log(u))^2\, u^x\, \Phi(u)\, du > 0.$$

If $f'(0) \geq 0$, then it follows because of $f''(x) > 0$ for all $x \geq 0$ that $f'(x) > 0$ for all $x > 0$. By the definition of f, it holds that

$$f'(0) \geq 0 \quad \text{if and only if} \quad \alpha_0 \leq -\frac{1}{\tilde{\Phi}'(0)}.$$

Therefore, $-\alpha + \alpha_0 \tilde{\Phi}(s + k - 1) + s + k - 1 > 0$ holds for all $k \in \mathbb{N}$ and $s \in (0, 1]$ if $\alpha \leq \alpha_0 \leq -\left(\tilde{\Phi}'(0)\right)^{-1}$ since $\alpha < f(x)$ for all $x > 0$ and, in particular, due to continuity of f we have that $\alpha \leq f(0) = \alpha_0$. Together with the condition $\alpha_0 \leq \alpha$, we have the following necessary conditions for positivity:

$$\alpha = \alpha_0 \quad \text{and} \quad \alpha_0 \leq -\left(\tilde{\Phi}'(0)\right)^{-1}.$$

It only remains show that $\alpha_0 < -\left(\tilde{\Phi}'(0)\right)^{-1}$.

In the following we use $\alpha = \alpha_0$. The function $\hat{q}$ is continuous. In particular, $\hat{q}|_{[0,1]}$ is continuous and $\hat{q}(n)$ is continuous at $n \in \mathbb{N}$, i.e.,

$$\hat{q}(n) = \lim_{s \to 0^+} \hat{q}(n + s) \qquad \text{for all } n \in \mathbb{N}.$$

Using (A.3) and continuity of $\tilde{\Phi}$, yields for $n = 1$,

$$\begin{aligned}
\lim_{s \to 0^+} \hat{q}(s + 1) &= \lim_{s \to 0^+} \hat{q}(s) \frac{1 - \tilde{\Phi}(s + 1)}{1 - \tilde{\Phi}(s)} \, \frac{-\alpha_0 + \alpha_0 \tilde{\Phi}(s) + s}{s + 1} \\
&= \hat{q}(0) \left(1 - \tilde{\Phi}(1)\right) \lim_{s \to 0^+} \frac{-\alpha_0 + \alpha_0 \tilde{\Phi}(s) + s}{1 - \tilde{\Phi}(s)}.
\end{aligned}$$

With L'Hôpital's rule,

$$\lim_{s \to 0^+} \frac{-\alpha_0 + \alpha_0 \tilde{\Phi}(s) + s}{1 - \tilde{\Phi}(s)} = \lim_{s \to 0^+} (-\alpha_0) \frac{1 - \tilde{\Phi}(s)}{1 - \tilde{\Phi}(s)} + \frac{s}{1 - \tilde{\Phi}(s)} = -\alpha_0 + \frac{1}{-\tilde{\Phi}'(0)}.$$

Therefore,

$$\hat{q}(1) = \hat{q}(0)\, \frac{1}{2} \left(-\alpha_0 - \frac{1}{\tilde{\Phi}'(0)}\right),$$

i.e., $\hat{q}(1)$ is positive if and only if

$$\alpha_0 < -\frac{1}{\tilde{\Phi}'(0)}.$$

This finishes the proof. $\square$

We have now established the first part of Theorem 2.9, i.e., we have shown that if there is a unique positive solution $g \in \mathcal{C}^0((0,z_0]) \cap \mathcal{C}^1((0,z_0))$ to (2.4), then $\alpha = \alpha_0$ and $\alpha_0 < -\big(\tilde{\Phi}'(0)\big)^{-1}$. We proceed to the second part, i.e., we show that the conditions on the parameters imply existence and uniqueness of a positive solution g to (2.4). To this end, we use the same rescalings and transformations as in the previous propositions.

Proposition A.5. *Let $\alpha = \alpha_0$ and $\alpha_0 < -\left(\tilde{\Phi}'(0)\right)^{-1}$. Then, there exists a unique solution $g \in \mathcal{C}^0((0,z_0]) \cap \mathcal{C}^1((0,z_0))$ to (2.5). There is a $C > 0$ such that the function $\hat{q}$ defined as in Propositions A.2 and A.3 is holomorphic for $s \in \mathbb{C}$ with $\Re(s) > C$ and satisfies for all $n \in \mathbb{N}$ and $s \in \mathbb{C}$ with $\Re(s) > C$,*

$$\hat{q}(s+n) = \hat{q}(s)\, \frac{1-\tilde{\Phi}(s+n)}{1-\tilde{\Phi}(s)} \prod_{k=1}^{n} \frac{(s+k-1) - \alpha + \alpha\, \tilde{\Phi}(s+k-1)}{s+k}. \tag{A.6}$$

Furthermore, for all $s \in \mathbb{C}$ with $\Re(s) > C$ and all $n \in \mathbb{N}$ it holds that $\hat{q}(s) \neq 0$, $1-\tilde{\Phi}(s+n) \neq 0$, and $f(s) := s - \alpha + \alpha\, \tilde{\Phi}(s) \neq 0$.

Proof. Let $\alpha = \alpha_0$ and $\alpha_0 < -\left(\tilde{\Phi}'(0)\right)^{-1}$. By Lemma 2.8, we know that there is a unique solution $g \in \mathcal{C}^0((0,z_0]) \cap \mathcal{C}^1((0,z_0))$ to (2.5). Using the same rescaling as in the proof of Proposition A.2, i.e., $g(z) = \left(\frac{z_0}{z}\right)^{\alpha} h\left(-\log(\frac{z}{z_0})\right)$ or equivalently $h(t) = e^{-\alpha t}\, g(z_0\, e^{-t})$, we obtain a solution $h \in \mathcal{C}^0([0,\infty)) \cap \mathcal{C}^1((0,\infty))$ to

$$h'(t) = -\int_0^t \check{\Phi}(t-\sigma)\, h(\sigma)\, \frac{\frac{d}{d\sigma}(e^{\sigma}-1)^{\alpha}}{(e^{t}-1)^{\alpha}}\, d\sigma \quad \text{and} \quad h(0) = 1, \tag{A.7}$$

where $\check{\Phi}(t) := \Phi(e^{-t})\, e^{-t}$. We aim to apply the Laplace transform to the function q that again defined as in the proof of Proposition A.2 by $q(t) := h(t)\, \left(e^{t}-1\right)^{\alpha}$. Therefore, we show that the Laplace transforms of $q(t)$ and $\frac{\alpha\, q(t)}{1-e^{-t}}$ exist by applying the Grönwall-Bellman inequality [4, p. 266] to the function $|h|$.

Renaming t to τ and integrating (A.7) over τ from 0 to t yields

$$h(t) - h(0) = -\int_0^t \int_0^{\tau} \check{\Phi}(\tau-\sigma)\, h(\sigma)\, \frac{\frac{d}{d\sigma}(e^{\sigma}-1)^{\alpha}}{(e^{\tau}-1)^{\alpha}}\, d\sigma d\tau,$$

$$h(t) = 1 - \int_0^t \int_0^{\tau} \check{\Phi}(\tau-\sigma)\, h(\sigma)\, \frac{\frac{d}{d\sigma}(e^{\sigma}-1)^{\alpha}}{(e^{\tau}-1)^{\alpha}}\, d\sigma d\tau.$$

We take the absolute value and interchange the order of the integration,

$$|h(t)| \leq 1 + \int_0^t \int_0^{\tau} \check{\Phi}(\tau-\sigma)\; |h(\sigma)|\; \frac{\frac{d}{d\sigma}(e^{\sigma}-1)^{\alpha}}{(e^{\tau}-1)^{\alpha}}\, d\sigma d\tau,$$

$$|h(t)| \leq 1 + \int_0^t \int_{\sigma}^{t} \check{\Phi}(\tau-\sigma)\; (e^{\tau}-1)^{-\alpha}\; d\tau\, \frac{d}{d\sigma}(e^{\sigma}-1)^{\alpha}\; |h(\sigma)|\; d\sigma.$$

Define $B(\sigma,t) := \int_\sigma^t \check{\Phi}(\tau-\sigma)\,(e^\tau-1)^{-\alpha}\,d\tau\,\frac{d}{d\sigma}(e^\sigma-1)^\alpha$. In order to apply the Grönwall-Bellman inequality, B must not depend on t. As B is increasing in t, we estimate

$$
\begin{aligned}
B(\sigma,t) &\le \int_\sigma^\infty \check{\Phi}(\tau-\sigma)\,(e^\tau-1)^{-\alpha}\;d\tau\,\frac{d}{d\sigma}(e^\sigma-1)^\alpha \\
&\le \|\Phi\|_{L^\infty([0,1])}\int_\sigma^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau\;e^\sigma\,\alpha\,e^\sigma\,(e^\sigma-1)^{\alpha-1}\,.
\end{aligned}
$$

We develop an upper bound for the integral on the right-hand side as otherwise the Grönwall-Bellman inequality gives the estimate $|h(t)| \le \infty$, i.e., we require the following integral to be finite

$$
\begin{aligned}
\int_0^t\int_\sigma^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau\,\alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\;d\sigma = &\int_0^t\int_0^\tau \alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\;d\sigma\,\frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau \\
&+\int_t^\infty\int_0^t \alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\;d\sigma\,\frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau.
\end{aligned}
\tag{A.8}
$$

Using that with the transformation $x = e^\sigma$ yields

$$
\begin{aligned}
\int_0^t \alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\;d\sigma &= \int_1^{e^t}\alpha\,x\,(x-1)^{\alpha-1}\,dx = \left[\frac{(x-1)^\alpha\,(\alpha\,x+1)}{\alpha+1}\right]_{x=1}^{x=e^t} \\
&= \frac{1}{\alpha+1}\left(e^t-1\right)^\alpha\left(\alpha e^t+1\right).
\end{aligned}
$$

Thus, we obtain for (A.8),

$$
\begin{aligned}
&\int_0^t\int_\sigma^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau\,\alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\;d\sigma \\
&= \frac{1}{\alpha+1}\int_0^t \alpha+e^{-\tau}\,d\tau + \frac{1}{\alpha+1}\left(e^t-1\right)^\alpha\left(\alpha\,e^t+1\right)\int_t^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau \\
&\le \frac{\alpha\,t}{\alpha+1} + \frac{1}{\alpha+1}\left[-e^{-\tau}\right]_{\tau=0}^{\tau=t} + \frac{1}{\alpha+1}\left(e^t+1\right)^\alpha\left(\alpha\,e^t+1\right)\left(e^t-1\right)^{-\alpha}\int_t^\infty e^{-\tau}\,d\tau \\
&= \frac{\alpha\,t+1-e^{-t}}{\alpha+1} + \frac{\alpha+e^{-t}}{\alpha+1} = \frac{\alpha t+\alpha+1}{\alpha+1}.
\end{aligned}
$$

We estimate

$$
|h(t)| \le 1 + \int_0^t \|\Phi\|_{L^\infty([0,1])}\int_\sigma^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau\,\alpha\,e^{2\sigma}\,(e^\sigma-1)^{\alpha-1}\,|h(\sigma)|\;d\sigma
$$

and therefore the Grönwall-Bellman inequality yields for $t \ge 0$

$$
|h(t)| \le e^{\int_0^t \|\Phi\|_{L^\infty([0,1])}\int_\sigma^\infty \frac{e^{-\tau}}{(e^\tau-1)^\alpha}\,d\tau\,\alpha\,e^{2\sigma}(e^\sigma-1)^{\alpha-1}\,d\sigma} \le e^{\|\Phi\|_{L^\infty([0,1])}\,\frac{\alpha t+\alpha+1}{\alpha+1}} = Ce^{s_0\,t},
$$

where $C := e^{\|\Phi\|_{L^\infty([0,1])}} > 0$ and $s_0 := \alpha \, \|\Phi\|_{L^\infty([0,1])} / (\alpha + 1) > 0$.

With the transformation $q(t) = h(t) \left(e^t - 1\right)^{\alpha}$, we obtain for all $t \geq 0$ that

$$|q(t)| \left(e^t - 1\right)^{-\alpha} \leq C e^{s_0 t}.$$

Therefore,

$$|q(t)| \leq C e^{s_0 t} \left(e^t - 1\right)^{\alpha} = C e^{(s_0+\alpha)t} \left(1 - e^{-t}\right)^{\alpha} \leq C e^{(s_0+\alpha)t}$$

and it follows that both the Laplace transform $\hat{q}(s)$ of $q(t)$ and the Laplace transform of $\frac{\alpha \, q(t)}{1-e^{-t}}$ exist for $\Re(s) > s_0 + \alpha$. Furthermore, q satisfies equation (A.1).

Now, we can take the Laplace transform of equation (A.1) and obtain for all $s \in \mathbb{C}$ with $\Re(s) > s_0 + \alpha$,

$$\begin{aligned} \alpha \, \hat{q}(s) = {} & \frac{1 - \tilde{\Phi}^{n+1}(s)}{1 - \tilde{\Phi}(s)} \, s \, \hat{q}(s) - \frac{1 - \tilde{\Phi}^{n+1}(s+1)}{1 - \tilde{\Phi}(s+1)} \, (s+1) \, \hat{q}(s+1) \\ & + \tilde{\Phi}^{n+1}(s) \, \mathcal{L}\left\{\frac{\alpha \, q(t)}{1 - e^{-t}}\right\}(s) - \tilde{\Phi}^{n+1}(s+1) \, \mathcal{L}\left\{\frac{\alpha q(t)}{1 - e^{-t}}\right\}(s+1). \end{aligned}$$

As in the proof of Proposition A.3, we can now take the limit $n \to \infty$ because we know that $\left|\tilde{\Phi}(s)\right| \leq \tilde{\Phi}(\Re(s)) < 1$ for $\Re(s) > s_0 + \alpha > 0$. Recursively, we obtain (A.6), i.e., for all $n \in \mathbb{N}$ and $s \in \mathbb{C}$ with $\Re(s) > s_0 + \alpha$,

$$\hat{q}(s+n) = \hat{q}(s) \, \frac{1 - \tilde{\Phi}(s+n)}{1 - \tilde{\Phi}(s)} \prod_{k=1}^{n} \frac{(s+k-1) - \alpha + \alpha \, \tilde{\Phi}(s+k-1)}{s+k}.$$

The Laplace transform $\hat{q}$ of q is analytic, i.e., holomorphic, on $\Re(s) > s_0 + \alpha$. We know by Lemma 2.8 that $g(z_0) = 1$ and $g \in \mathcal{C}^0((0, z_0]) \cap \mathcal{C}^1((0, z_0))$. Therefore, there is a set of positive measure where q is strictly positive.

If there is a $s \in \mathbb{C}$ with $\Re(s) > s_0 + \alpha$ and $\hat{q}(s) = 0$, then $\hat{q}(s+n) = 0$ for all $n \in \mathbb{N}$ by (A.6). Hence, $\hat{q}$ vanishes on a sequence of equidistant points along a line parallel to the real axis, therefore $q = 0$ a.e. by [13, Theorem 5.3]. This is a contradiction to $q > 0$ on a set of positive measure. Therefore, $\hat{q}(s) \neq 0$ for $s \in \mathbb{C}$ with $\Re(s) > s_0 + \alpha$.

In particular, due to (A.6) it also follows that for all $s \in \mathbb{C}$ with $\Re(s) > s_0 + \alpha$ and for all $n \in \mathbb{N}$ that $1 - \tilde{\Phi}(s+n) \neq 0$, and $f(s) := s - \alpha + \alpha\tilde{\Phi}(s) \neq 0$. ☐

We have shown that the function $\hat{q}(s)$ is defined in a right half-plane ($\Re(s) > C > 0$) and satisfies the iteration formula (A.6). Next, we use now the iteration formula (A.6) to extend the function $\hat{q}$ to a function $\hat{q}^*$ defined on the right half-plane given by $\Re(s) > -\varepsilon$ for some $\varepsilon > 0$.

Proposition A.6. *If $\alpha = \alpha_0$ and $\alpha_0 < -\left(\tilde{\Phi}'(0)\right)^{-1}$, then there exists an $\varepsilon > 0$ such that the function $\hat{q}$ defined in Propositions A.2 and A.3 can be extended to a holomorphic function $\hat{q}^*$ on the half-plane $\Re(s) \geq -\varepsilon$.*

Proof. By Proposition A.5, there is a $C > 0$ such that for all $s \in \mathbb{C}$ with $\Re(s) > C$ the function $\hat{q}(s)$ is holomorphic, $\hat{q}$ satisfies (A.6) for all $n \in \mathbb{N}$, $\hat{q}(s) \neq 0$, $1 - \tilde{\Phi}(s+n) \neq 0$ for all $n \in \mathbb{N}$, and $f(s) := s - \alpha + \alpha \, \tilde{\Phi}(s) \neq 0$.

As $\hat{q}(s) \neq 0$ for $s \in \mathbb{C}$ with $\Re(s) > C$, we can write equivalently to (A.6) for $\Re(s) > C$

$$\hat{q}(s) = \hat{q}(s+n) \, \frac{1 - \tilde{\Phi}(s)}{1 - \tilde{\Phi}(s+n)} \prod_{k=1}^{n} \frac{s+k}{(s+k-1) - \alpha + \alpha \, \tilde{\Phi}(s+k-1)}. \tag{A.9}$$

We use (A.9) to construct an extension of $\hat{q}$ to $s \in \mathbb{C}$ with $\Re(s) > -\varepsilon$ for some $\varepsilon > 0$.

Let $m \geq \lceil C + 2 \rceil$, where $\lceil x \rceil$ denotes the ceiling function that maps x to the least integer greater than or equal to x. First, we show that the right-hand side of (A.9) is well-defined, i.e., that $1 - \tilde{\Phi}(s+n) \neq 0$ and $f(s+k-1) := (s+k-1) - \alpha + \alpha\, \tilde{\Phi}(s+k-1) \neq 0$ for all $s \in \mathbb{C}$ with $\Re(s) > -\varepsilon$, $k \in \mathbb{N}$, for some $\varepsilon > 0$, and for $n = m$.

By the choice of m we already know that $1 - \tilde{\Phi}(s+m) \neq 0$ for all $s \in \mathbb{C}$ with $\Re(s) > -1$. It remains to show that $f(z) \neq 0$ for $\Re(z) > -\varepsilon$. With $z = a + ib$ for $a > -1$ and $b \in \mathbb{R}$,

$$
\begin{aligned}
f(z) = z - \alpha + \alpha\tilde{\Phi}(z) &= a + ib - \alpha + \alpha \int_0^1 u^{a+ib} \Phi(u)\, du \\
&= a - \alpha + ib + \alpha \int_0^1 u^a (\cos(b\log(u)) + i \sin(b \log(u)))\Phi(u)\, du \\
&= a - \alpha + \alpha \int_0^1 u^a \cos(b\log(u))\Phi(u)\, du + i \left(b + \alpha \int_0^1 u^a \sin(b\log(u))\Phi(u)\, du \right).
\end{aligned}
$$

As $f(z) = 0$ if and only if $\Re(f(z)) = 0$ and $\Im(f(z)) = 0$, we are searching for a, $b \in \mathbb{R}$ satisfying both

$$
\begin{aligned}
f_1(a,b) &:= \int_0^1 u^a \cos(b\log(u))\Phi(u)\, du + \frac{a}{\alpha} \overset{!}{=} 1 \quad \text{and} \\
f_2(a,b) &:= \int_0^1 u^a \sin(b\log(u))\Phi(u)\, du + \frac{b}{\alpha} \overset{!}{=} 0.
\end{aligned}
$$

We see that (a, b) is a solution to $f_1(a, b) = 1$ and $f_2(a, b) = 0$ if and only if $(a, -b)$ is a solution. Therefore, it suffices to consider $b \geq 0$.

For $b = 0$, it holds that $f_2(a, 0) = 0$ for all $a \in \mathbb{R}$. The partial derivative of f_2 w.r.t. b is

$$
\begin{aligned}
\partial_b f_2(a,b) &= \int_0^1 u^a \cos(b\log(u))\, \log(u)\, \Phi(u)\, du + \frac{1}{\alpha}, \\
\partial_b f_2(a,0) &= \int_0^1 u^a \log(u)\, \Phi(u)\, du + \frac{1}{\alpha} = \tilde{\Phi}'(a) + \frac{1}{\alpha}.
\end{aligned}
$$

The function $\tilde{\Phi}'$ is negative and strictly increasing (this follows directly from the properties of Φ, see proofs of Propositions A.3 and A.4). As $0 < \alpha < -1/\tilde{\Phi}'(0)$ there is an $l < 0$ such that $\alpha = -1/\tilde{\Phi}'(l)$ by continuity of $\tilde{\Phi}'$. Hence,

$$
\partial_b f_2(a,0) = \tilde{\Phi}'(a) - \tilde{\Phi}'(l) > 0
$$

if and only if $a > l$. For $b > 0$,

$$\partial_b f_2(a,b) = \int_0^1 u^a \cos(b\log(u))\, \log(u)\, \Phi(u)\, du - \tilde{\Phi}'(l)$$
$$= \int_0^1 \log(u)\, \Phi(u) \left(u^a \cos(b\log(u)) - u^l\right)\, du.$$

For $u \in (0,1)$, $\log(u) < 0$, $\Phi(u) \geq 0$, and

$$u^a \cos(b\log(u)) - u^l \leq u^a - u^l \leq 0$$

if $a > l$. Therefore, for $a > l$, $\partial_b f_2(a,b) \geq 0$ for all $b > 0$ and $\partial_b f_2(a,0) > 0$, i.e., there cannot be a solution to $f_2(a,b) = 0$ other than $b = 0$. If $b = 0$, then we are looking for a real solution to $f(s) = s - \alpha + \alpha\,\tilde{\Phi}(s) = 0$. In this case we know that $s = 0$ is a solution. Moreover, $f'(s) > 0$ for $s \geq 0$, $f'(s) = 1 + \alpha\,\tilde{\Phi}'(s) = 0$ if and only if $s = l$ by definition of l, and $f''(s) > 0$ for all $s \in \mathbb{R}$. Therefore, $f(s) < 0$ for $s \in (l, 0)$ and the only solution to $f(s) = 0$ in (l, ∞) is $s = 0$.

Define $\varepsilon := \min\{-l, 1\}/2$, then $f(z) = 0$ only for $z = 0$ and $f(z) \neq 0$ for all $z \in \mathbb{C}$ with $z \neq 0$ and $\Re(z) \geq -\varepsilon$.

We rewrite (A.9) with $n = m$, where $m \geq \lceil C + 2 \rceil$,

$$\hat{q}(s) = \frac{\hat{q}(s+m)\,(s+1)}{1 - \tilde{\Phi}(s+m)}\, \frac{1 - \tilde{\Phi}(s)}{s - \alpha + \alpha\,\tilde{\Phi}(s)} \prod_{k=2}^{m} \frac{s+k}{(s+k-1) - \alpha + \alpha\,\tilde{\Phi}(s+k-1)}. \tag{A.10}$$

For $s \in \mathbb{C} \setminus \{0\}$ with $\Re(s) \geq -\varepsilon$ the expression on the right-hand side is holomorphic as it is the product of holomorphic functions. The function $\hat{q}$ is holomorphic as it is the Laplace transform of q and the fact that $\tilde{\Phi}$ is holomorphic is easily checked using the definition of $\tilde{\Phi}$. With L'Hôpital's rule for analytic functions of a complex variable (see, e.g., [39, Theorem 3.3]),

$$\lim_{z\to 0} \frac{1 - \tilde{\Phi}(z)}{z - \alpha + \alpha\,\tilde{\Phi}(z)} = \lim_{z\to 0} \frac{-\tilde{\Phi}'(z)}{1 + \alpha\,\tilde{\Phi}'(z)} = \frac{-\tilde{\Phi}'(0)}{1 + \alpha\,\tilde{\Phi}'(0)},$$

which is finite by the assumption $\alpha > -1/\tilde{\Phi}'(0)$. Therefore, the right-hand side of (A.10) is holomorphically extendable to $z = 0$ by the Riemann removable singularities theorem (see, e.g., [19, Theorem 4.1.1]) and the following extension of $\hat{q}$ is holomorphic, for $s \in \mathbb{C}$ with $\Re(s) \geq -\varepsilon$,

$$\hat{q}^*(s) = \begin{cases} \frac{\hat{q}(s+m)(s+1)}{1-\tilde{\Phi}(s+m)} \frac{1-\tilde{\Phi}(s)}{s-\alpha+\alpha\tilde{\Phi}(s)} \prod_{k=2}^{m} \frac{s+k}{(s+k-1)-\alpha+\alpha\tilde{\Phi}(s+k-1)}, & \text{if } \Re(s) \in [-\varepsilon, m],\ s \neq 0, \\ \frac{\hat{q}(m)}{1-\tilde{\Phi}(m)} \frac{-\tilde{\Phi}'(0)}{1+\alpha\tilde{\Phi}'(0)} \prod_{k=2}^{m} \frac{k}{(k-1)-\alpha+\alpha\tilde{\Phi}(k-1)}, & \text{if } s = 0, \\ \hat{q}(s), & \text{if } \Re(s) > m. \end{cases}$$

The function $\hat{q}^*(s)$ is holomorphic as for $\Re(s) > m$ it agrees with the holomorphic function $\hat{q}(s)$, for $\Re(s) \in (-\varepsilon, m)$ and $s \neq 0$ it is a product and quotient of holomorphic functions, and for $s = 0$ we defined $\hat{q}^*$ such that it is holomorphic by the Riemann removable singularities theorem. It thus only remains to argue that $\hat{q}^*$ is holomorphic at $\Re(s) = m$. By definition of $\hat{q}^*$ and since $\hat{q}$ is holomorphic and satisfies equation (A.9) for all $\Re(s) > C > 0$ where $m \geq C + 2$, it follows that $\hat{q}^*(s) = \hat{q}(s)$ for all $\Re(s) \in (m - \varepsilon, m + \varepsilon)$. Thus, $\hat{q}^*$ is holomorphic at $\Re(s) = m$ because $\hat{q}$ is holomorphic. □

We are now ready to gather the results of Propositions A.2 to A.6 and finish the proof of Theorem 2.9.

Proof of Theorem 2.9.

Step 1: From the solution g to the conditions on the parameters.
Assume there is a solution $g \in \mathcal{C}^0((0, z_0]) \cap \mathcal{C}^1((0, z_0))$ for (2.4), then Propositions A.2 to A.4 directly give the conditions on α and α_0.

Step 2: From the conditions on the parameters to the unique solution g.
Lemma 2.8 gives existence of a unique solution $g \in \mathcal{C}^0((0, z_0]) \cap \mathcal{C}^1((0, z_0))$ to (2.5). It remains show that the solution g to (2.5) is also a solution to (2.4), i.e., that g satisfies

$$\lim_{z\to 0^+} g(z) = 0, \quad g(z) \geq 0 \text{ for all } z \in (0, z_0), \quad \text{and} \int\limits_0^{z_0} \frac{(z_0 - z)^\alpha g(z)}{b(z)}\, dz < \infty.$$

In the following, we use Propositions A.5 and A.6, take the inverse Laplace transform of $\hat{q}^*$, $\mathcal{L}^{-1}\{\hat{q}^*(s)\}(t) =: q^*(t)$, and show that $q(t) = q^*(t)$ for a.e. $t \geq 0$.

If

$$\lim_{s\to\infty} \hat{q}^*(s) = 0 \quad \text{and} \quad \lim_{s\to\infty} s\, \hat{q}^*(s) < \infty,$$

then the inverse Laplace transform q^* of $\hat{q}^*$ exists [16, p. 135]. We know that

$$0 = \lim_{t\to 0^+} q(t) = \lim_{s\to\infty} s\, \hat{q}(s),$$

by the Initial Value Theorem (see, e.g., [13, Theorem 33.5]), and for $s \in \mathbb{C}$ with $\Re(s) \geq -\varepsilon$ and $|s| > \delta > 0$ and for $m := \lceil C + 2 \rceil$,

$$\hat{q}^*(s) = \hat{q}(s+m)\, \frac{1 - \tilde{\Phi}(s)}{1 - \tilde{\Phi}(s+m)} \prod_{k=1}^{m} \frac{s+k}{(s+k-1) - \alpha + \alpha\, \tilde{\Phi}(s+k-1)}.$$

Since

$$\left|\tilde{\Phi}(s)\right| \leq \tilde{\Phi}(\Re(s)) \leq \tilde{\Phi}(-\varepsilon) < \infty$$

and for all $k \in \mathbb{N}$, $k \leq m$, and all $|s| > \delta > 0$

$$\frac{s+k}{s+k-1-\alpha+\alpha\, \tilde{\Phi}(s+k-1)} = \frac{1 + \frac{k}{s}}{1 + \frac{k-1-\alpha}{s} + \frac{\alpha\, \tilde{\Phi}(s+k-1)}{s}} < \infty,$$

it holds that $\hat{q}^*(s) = h(s)\, \hat{q}(s+m)$ for some function h that is bounded for all $s \in \mathbb{C}$ with $\Re(s) \geq -\varepsilon$ and $|s| > \delta > 0$. Therefore,

$$\lim_{s\to\infty} s\, \hat{q}^*(s) = 0$$

and the inverse Laplace transformation q^* of $\hat{q}^*$ exists.

Due to uniqueness of the inverse Laplace transform (see, e.g., [13, Theorem 5.4]), q^* and q are a.e. equal. In particular, with $q(t) = g(z_0 e^{-t}) \left(1 - e^{-t}\right)^\alpha$ and the change of variables $z = z_0 e^{-t}$,

$$\hat{q}^*(0) = \int\limits_0^\infty q^*(t)\, dt = \int\limits_0^\infty q(t)\, dt = \int\limits_0^{z_0} g(z) \left(1 - \frac{z}{z_0}\right)^\alpha \frac{1}{z}\, dz$$

$$= z_0^{-\alpha} \int\limits_0^{z_0} \frac{g(z)\, (z_0 - z)^\alpha}{z}\, dz < \infty.$$

Therefore, $g(z)/z$ is integrable at $z=0$. As $g \in \mathcal{C}^0\big((0,z_0]\big)$ with $g(z_0)=1$ there are $\delta>0$ and a $c>0$ such that

$$\frac{g(z)\,(z_0-z)^\alpha}{z\,(z_0-z)} \le c\,\frac{(z_0-z)^\alpha}{z_0-z} \quad \text{for all } z\in[z_0-\delta,z_0],$$

it holds that $\frac{g(z)\,(z_0-z)^\alpha}{z\,(z_0-z)}$ is integrable at $z=z_0$. Hence,

$$\lim_{z\to 0^+} g(z)=0 \quad \text{and} \quad \int_0^{z_0} \frac{g(z)(z_0-z)^\alpha}{b(z)}\,dz<\infty.$$

Step 3: Positivity of the solution g.
The function $v(z):=C(z_0-z)^\alpha g(z)$ for some $C>0$ is a solution to (2.3) by Lemma 2.6 and $v\ge 0$ if and only if $g\ge 0$ on $(0,z_0)$. We know that $\lim\limits_{z\to 0^+} v(z)=0$, $v(z_0)=0$, and v is positive in a neighborhood of z_0 as $g(z_0)=1$ and g is continuous in $(0,z_0]$. With $\alpha=\alpha_0$, integrating (2.3) from z to z_0 yields

$$v(z_0)-v(z)=-\alpha\,z_0\int_z^{z_0}\frac{v(z')}{z'(z_0-z')}\,dz'+\alpha\,z_0\int_z^{z_0}\int_y^{z_0}\frac{\Phi\left(\frac{y}{z'}\right)v(z')}{(z')^2(z_0-z')}\,dz'dy.$$

By change of variables $\xi=\frac{y}{z'}$, we obtain

$$\begin{aligned} v(z)&=\alpha\,z_0\left(\int_z^{z_0}\frac{v(z')}{z'(z_0-z')}\,dz'-\int_z^{z_0}\int_{z/z'}^{1}\Phi(\xi)\,d\xi\,\frac{v(z')}{z'(z_0-z')}\,dz'\right)\\ &=\alpha\,z_0\int_z^{z_0}\int_0^{z/z'}\Phi(\xi)\,d\xi\,\frac{v(z')}{z'(z_0-z')}\,dz'. \end{aligned}$$

Due to continuity of v, v can only be negative if there is a $z\in(0,z_0)$ such that $v(z)=0$. Let $z^*\in(0,z_0)$ be the largest $z\in(0,z_0)$ such that $v(z)=0$, i.e., $v(z)>0$ for all $z\in(z^*,z_0)$. Therefore,

$$v(z^*)=\alpha\,z_0\int_{z^*}^{z_0}\int_0^{z^*/z'}\Phi(\xi)\,d\xi\,\frac{v(z')}{z'(z_0-z')}\,dz'.$$

By definition of z^*, it holds that

$$\frac{v(z')}{z'(z_0-z')}>0 \quad \text{for all } z\in(z^*,z_0).$$

Moreover, there is an $\varepsilon>0$ such that for all $z'\in(z^*,z^*+\varepsilon)$

$$\int_0^{z^*/z'}\Phi(\xi)\,d\xi>0.$$

Therefore, $v(z^*)>0$, which is a contradiction to the definition of z^*, $v(z^*)=0$. This means that there is no z^* with $v(z^*)$ and thereby $v(z)>0$ for all $z\in(0,z_0)$. Hence, $g\ge 0$ and $g(z)>0$ for all $z\in(0,z_0]$.

Overall, we have shown that the unique solution $g \in \mathcal{C}^0\big((0,z_0]\big) \cap \mathcal{C}^1\big((0,z_0)\big)$ to (2.5) is also a solution to (2.4) in Step 2. Since every solution to (2.4) is also a solution to (2.5) the function g is the unique solution to (2.4). Moreover, because of $v(z) > 0$ for $z \in (0,z_0)$, $v(z) = C\,(z_0 - z)^\alpha g(z)$ with $C > 0$, and $g(z_0) = 1$ it follows that $g(z) > 0$ for $z \in (0, z_0]$. $\square$

Appendix B. Other proofs

Proof of Theorem 3.2. The proof is lengthy but consists of straightforward computations.

We define $U(z,t) := e^{\lambda t}\,\mathcal{U}(z)$. Then, $U(z) > 0$ for all $z \in (0,z_0)$ and U is a solution to (3.1). Furthermore, we define $\psi(z,t) := e^{-\lambda t}\Psi(z)$. Then ψ is a solution to the dual equation of (3.1), i.e., it is a solution to

$$\begin{cases} -\,\partial_t \psi(z,t) - b(z)\partial_z \psi(z,t) = -\left(\beta(z) + \mu(z)\right)\psi(z,t) + \beta(z) \displaystyle\int_0^z k(z',z)\psi(z',t)\,dz', \\ \psi(z,t) \geq 0 \text{ for all } z \in (0,z_0) \text{ and } t \geq 0, \quad \displaystyle\int_0^{z_0} \psi(z,t)\,U(z,t)\,dz = 1. \end{cases} \tag{B.1}$$

With these definitions, we obtain

$$\begin{aligned} \Psi(z)\,\mathcal{U}(z)\,H\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right) &= \Psi(z)\,e^{-\lambda t}\,e^{\lambda t}\,\mathcal{U}(z)\,H\left(\frac{\tilde{u}(z,t)\,e^{\lambda t}}{\mathcal{U}(z)\,e^{\lambda t}}\right) \\ &= \psi(z,t)\,U(z,t)\,H\left(\frac{u(z,t)}{U(z,t)}\right). \end{aligned}$$

Recall that as H is absolutely continuous, it is differentiable a.e. and the derivative H' is Lebesgue-integrable. For the sake of brevity, we omit the arguments of ψ, U, and u everywhere except in the integrals. It holds that

$$\begin{aligned} &\partial_t \left[\psi\,U\,H\Big(\frac{u}{U}\Big)\right] + \partial_z \left[b(z)\,\psi\,U\,H\Big(\frac{u}{U}\Big)\right] \\ &\quad = (\partial_t \psi)\;U\;H\Big(\frac{u}{U}\Big) + \psi\;(\partial_t U)\;H\Big(\frac{u}{U}\Big) + \psi\,U\,H'\left(\frac{u}{U}\right)\,\partial_t\left(\frac{u}{U}\right) \\ &\qquad + (\partial_z \psi)\;b(z)\,U\,H\Big(\frac{u}{U}\Big) + \psi\,\partial_z(b(z)\,U)\,H\Big(\frac{u}{U}\Big) + \psi\,b(z)\,U\,H'\left(\frac{u}{U}\right)\,\partial_z\left(\frac{u}{U}\right) \\ &\quad = U\,H\Big(\frac{u}{U}\Big)\left[\partial_t\psi + b(z)\,\partial_z\psi\right] + \psi\,H\Big(\frac{u}{U}\Big)\left[\partial_t U + \partial_z(b(z)\,U)\right] \\ &\qquad + \psi\,U\,H'\Big(\frac{u}{U}\Big)\left[\partial_t\Big(\frac{u}{U}\Big) + b(z)\,\partial_z\Big(\frac{u}{U}\Big)\right]. \end{aligned}$$

Now, we use the fact that ψ is a solution to (B.1) and U is a solution to (3.1):

$$
\begin{aligned}
&\partial_t \left[\psi U H\Big(\frac{u}{U}\Big)\right] + \partial_z \left[b(z)\psi U H\Big(\frac{u}{U}\Big)\right] \\
&\quad = U H\Big(\frac{u}{U}\Big) \left[(\beta(z)+\mu(z))\,\psi - \beta(z)\int_0^z k(z',z)\psi(z',t)\,dz'\right] \\
&\qquad + \psi\, H\Big(\frac{u}{U}\Big) \left[-\left(\beta(z)+\mu(z)\right) U + \int_z^{z_0} \beta(z')\,k(z,z')\,U(z',t)\,dz'\right] \\
&\qquad + \psi\, U\, H'\Big(\frac{u}{U}\Big) \left[\partial_t\left(\frac{u}{U}\right) + b(z)\,\partial_z\left(\frac{u}{U}\right)\right] \\
&\quad = -\int_0^{z_0} \beta(z)\,k(z',z)\,\psi(z',t)\,U(z,t)\,H\bigg(\frac{u(z,t)}{U(z,t)}\bigg)\,dz' \\
&\qquad + \int_0^{z_0} \beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,H\bigg(\frac{u(z,t)}{U(z,t)}\bigg)\,dz' \\
&\qquad + \psi\, U\, H'\Big(\frac{u}{U}\Big) \left[\partial_t\Big(\frac{u}{U}\Big) + b(z)\,\partial_z\Big(\frac{u}{U}\Big)\right].
\end{aligned}
$$

We compute that

$$
\begin{aligned}
\partial_t\Big(\frac{u}{U}\Big) + b(z)\,\partial_z\Big(\frac{u}{U}\Big) &= \frac{\partial_t u}{U} - \frac{u\,\partial_t U}{U^2} + b(z)\left(\frac{\partial_z u}{U} - \frac{u\,\partial_z U}{U^2}\right) \\
&= \frac{1}{U}\left[-\partial_z(b(z)u) - (\beta(z)+\mu(z))\,u + \int_z^{z_0} \beta(z')\,k(z,z')\,u(z',t)\,dz' + b(z)\,\partial_z u\right] \\
&\quad - \frac{u}{U^2}\left[-\partial_z(b(z)U) - (\beta(z)+\mu(z))\,U + \int_z^{z_0} \beta(z')\,k(z,z')\,U(z',t)\,dz' + b(z)\,\partial_z U\right] \\
&= \int_0^{z_0} \beta(z')\,k(z,z')\left(\frac{u(z',t)}{U(z,t)} - \frac{U(z',t)\,u(z,t)}{U^2(z,t)}\right)\,dz' \\
&\quad + \frac{1}{U}\left[-\partial_z(b(z)u) + b(z)\,\partial_z u - \frac{u}{U}\left(-\partial_z(b(z)U) + b(z)\,\partial_z U\right)\right] \\
&= \int_0^{z_0} \beta(z')k(z,z')\frac{U(z',t)}{U(z,t)}\left(\frac{u(z',t)}{U(z',t)} - \frac{u(z,t)}{U(z,t)}\right)dz' + \frac{1}{U}\left[-b'(z)\,u - \frac{u}{U}\big(-b'(z)\,U\big)\right],
\end{aligned}
$$

then the last summand is zero. Therefore, we obtain

$$\partial_t\Big[\psi\, U\, H\Big(\frac{u}{U}\Big)\Big] + \partial_z\Big[b(z)\,\psi\, U\, H\Big(\frac{u}{U}\Big)\Big] = -\int_0^{z_0}\Big\{\beta(z)k(z',z)\psi(z',t)U(z,t)H\Big(\frac{u(z,t)}{U(z,t)}\Big)$$

$$-\,\beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,H\Big(\frac{u(z',t)}{U(z',t)}\Big)\Big\}\,dz'$$

$$+\int_0^{z_0}\beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,\Big[H\Big(\frac{u(z,t)}{U(z,t)}\Big) - H\Big(\frac{u(z',t)}{U(z',t)}\Big)\Big]\,dz'$$

$$+\,\psi\, U\, H'\Big(\frac{u}{U}\Big)\int_0^{z_0}\beta(z')\,k(z,z')\,\frac{U(z',t)}{U(z,t)}\,\Big(\frac{u(z',t)}{U(z',t)} - \frac{u(z,t)}{U(z,t)}\Big)\,dz'$$

$$= -\int_0^{z_0}\Big\{\beta(z)\,k(z',z)\,\psi(z',t)\,U(z,t)\,H\Big(\frac{u(z,t)}{U(z,t)}\Big)$$

$$-\,\beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,H\Big(\frac{u(z',t)}{U(z',t)}\Big)\Big\}\,dz'$$

$$+\int_0^{z_0}\beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,\Big[H\Big(\frac{u(z,t)}{U(z,t)}\Big) - H\Big(\frac{u(z',t)}{U(z',t)}\Big)\Big]\,dz'$$

$$+\int_0^{z_0}\beta(z')\,k(z,z')\,\psi(z,t)\,U(z',t)\,H'\Big(\frac{u(z,t)}{U(z,t)}\Big)\,\Big(\frac{u(z',t)}{U(z',t)} - \frac{u(z,t)}{U(z,t)}\Big)\,dz'.$$

Together with

$$\psi(z,t)\,U(z,t) = \Psi(z)\,\mathcal{U}(z) \quad\text{and}\quad \frac{u(z,t)}{U(z,t)} = \frac{\tilde u(z,t)}{\mathcal{U}(z)}$$

this finishes the proof. □

Proof of Lemma 3.3. Following [25], we start with the formula in Theorem 3.2 and integrate it w.r.t. z from 0 to z_0. Then, the second summand on the left-hand side is

$$b(z)\,\Psi(z)\,\mathcal{U}(z)\,H\Big(\frac{\tilde u(z,t)}{\mathcal{U}(z)}\Big)\Big|_{z=0}^{z=z_0} = 0,$$

as $\int_0^{z_0}\Psi(z)\,\mathcal{U}(z)\,dz = 1$, by Assumption **(A5)**, $U > 0$, and since $\tilde u$ is bounded for every $t \geq 0$. The third summand on the left-hand side is

$$\int_0^{z_0}\int_0^{z_0}\beta(z)\,k(z,z')\,\Psi(z')\,\mathcal{U}(z)\,H\Big(\frac{\tilde u(z,t)}{\mathcal{U}(z)}\Big)\,dz'dz$$

$$-\int_0^{z_0}\int_0^{z_0}\beta(z')\,k(z,z')\,\Psi(z)\,\mathcal{U}(z')\,H\Big(\frac{\tilde u(z',t)}{\mathcal{U}(z')}\Big)\,dzdz' = 0.$$

Therefore,

$$\frac{d}{dt}\int_0^{z_0} \Psi(z)\,\mathcal{U}(z)\,H\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\,dz = \int_0^{z_0}\int_0^{z_0} \beta(z')\,k(z,z')\,\Psi(z)\,\mathcal{U}(z')\left[H\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\right.$$

$$\left. -H\left(\frac{\tilde{u}(z',t)}{\mathcal{U}(z')}\right) + H'\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\left[\frac{\tilde{u}(z',t)}{\mathcal{U}(z')} - \frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right]\right]\,dz'dz,$$

which shows the second part of the lemma.

Since H is convex and a.e. differentiable it holds for almost all $x,\ y \in \mathbb{R}$ that $H(x) \geq H(y) + H'(y)(x-y)$ or equivalently $H'(y)(x-y) \leq H(x) - H(y)$. Hence,

$$H\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right) - H\left(\frac{\tilde{u}(z',t)}{\mathcal{U}(z')}\right) + H'\left(\frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right)\left[\frac{\tilde{u}(z',t)}{\mathcal{U}(z')} - \frac{\tilde{u}(z,t)}{\mathcal{U}(z)}\right] \leq 0$$

and

$$\frac{d}{dt}\mathcal{H}_\Psi(\tilde{u}|\mathcal{U}) \leq 0,$$

i.e., the map $t \mapsto \mathcal{H}_\Psi(\tilde{u}|\mathcal{U})$ is non-increasing. □

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