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Modelling Silicosis: Dynamics of a Model with Piecewise Constant Rate Coefficients

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Abstract
We study the dynamics about equilibria of an infinite dimensional system of ordinary differential equations of coagulation–fragmentation–death type that was introduced recently by da Costa et al. (Eur J Appl Math 31(6):950–967, 2020) as a model for the silicosis disease mechanism. For a class of piecewise constant rate coefficients an appropriate change of variables allows for the appearance of a closed finite dimensional subsystem of the infinite-dimensional system and the analysis of the eigenvalues of the linearizations of this finite dimensional subsystem about the equilibria is then used to obtain the results on the stability of the equilibria in the original infinite dimensional model.

Keywords Coagulation–fragmentation–death equations · Model of silicosis · Local stability of equilibria

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1 Introduction

Silicosis is an incurable, long-term lung disease, caused by breathing in dust that contains crystalline silica, which is commonly found in sand, rock, and mineral ores like quartz. Artificial stone containing high levels of silica can also become dangerous for workers manipulating it; see [10] for a recent review.

We give a brief description of the processes involved in the lungs immune system's response to the invasion by harmful silica dust particles.

When silica dust particles reach the lungs they trigger a response from the alveolar macrophages, either through chemotaxis or by chance encounters. The next step is the engulfment and removal of the pathogens and cell debris by the alveolar macrophages, this process is known as phagocytosis. In the lungs, three different populations of macrophages exist, including airway, alveolar, and interstitial macrophages. Alveolar macrophages are situated on the inner surface of the lung, and they account for 55% of the lung immune cells.

There is a diverse set of pathologies associated with silica exposure, so it seems unlikely that there is a single common mechanism responsible for all of the possible diseases. The exact sequence of events (from silica inhalation to disease) is unknown, but it is generally accepted that the alveolar macrophage plays a relevant role. Upon contact, the alveolar macrophage will bind to the silica and begin to engulf the particle. If the alveolar macrophage survives the silica encounter, it will likely migrate out of the lungs to either the proximal lymph nodes or through the mucosal-ciliary escalator and eventually out of the respiratory tract. If the alveolar macrophage stays in the lung it will migrate to the interstitial space and become an activated interstitial macrophage that could contribute directly to worsen the disease [9]. Although the reasons for the underlying mechanism are not clear, silica particles are toxic to the macrophages [8] and can lead to their death. If this happens while the macrophages are still in the lungs, the silica particles are released back into the respiratory system.

The probability for a given macrophage already containing i particles of silica to engulf an additional particle typically decreases with i and in the model in [11] a maximum load capacity of $n_{\max} < \infty$ is assumed *a priori*. In [3] this restriction was not explicitly considered, being the existence of an effective upper bound of the silica particles' load of the macrophages left as a consequence of the assumptions upon the rate coefficients. Because of the toxicity of silica particles to the macrophages referred to above, macrophages with a higher load of silica particles will die at a higher rate. Moreover, the ability of the macrophages to migrate through the mucociliary escalator is impaired by an increase in their load of silica particles. It is the balance of these processes that leads to the mathematical model in [11] and that we also consider here (and was already considered in [4]) with the changes introduced in [3].

Let $M_i = M_i(t)$ be the concentration of macrophages which contain i silica particles (we will refer to it as the i-th cohort) at time t, $x = x(t)$ be the concentration of silica particles, and r the rate of supply of new (with no silica particles) macrophages. Following the model considered in [11], we obtain the equations for the mechanism described above:

$$\frac{dM_0}{dt} = r - k_0 x M_0 - (p_0 + q_0)M_0, \tag{1}$$

$$\frac{dM_i}{dt} = k_{i-1} x M_{i-1} - k_i x M_i - (p_i + q_i)M_i, \quad i \geq 1, \tag{2}$$

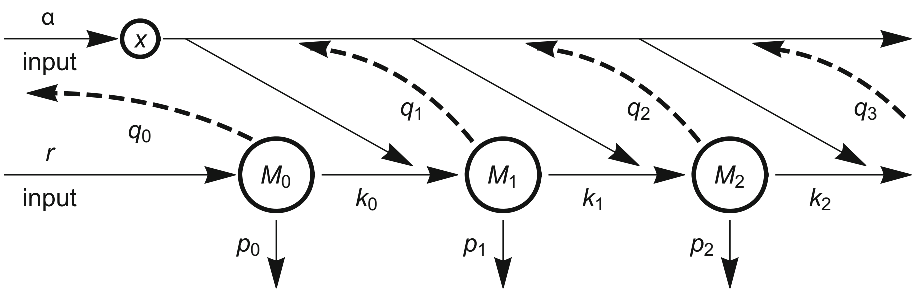

Fig. 1 Reaction scheme of the model considered in this paper [4]. The input rates of silica and of macrophages with no silica particles are α and r, respectively. The concentration of free silica particles and of macrophages containing j silica particles are represented by x and M_j, respectively. Macrophages M_j can be destroyed, releasing j silica particles (dashed lines), or they can be removed by rising in the mucociliary escalator (vertical downward lines), or they can ingest an additional silica particle becoming an M_{j+1} macrophage (horizontal rightward arrows)

where k_i is the rate of phagocytosis of a silica particle by a macrophage already containing i particles, p_i, is the transfer rate of macrophages in the i-th cohort to the mucociliary escalator, i.e., the rate of their removal from the pulmonary alveoli together with their quartz load, and q_i is the rate of death of the macrophages in the i-th cohort which results in the release of the quartz burden back into the lungs. As stated above the model in [3], unlike the one in [11], does not impose an upper limit on the number i of quartz particles a macrophage can contain, the existence of such a load capacity will be a consequence of the assumptions on the rate coefficients k_i and q_i.

The following governing equation for the evolution of the concentration of silica particles in the system was considered in [3], under the assumption of an inhalation rate α, valid under the same assumption about the validity of the mass action law used to obtain the equations for the M_i:

$$\frac{dx}{dt} = \alpha - x\sum_{i=0}^{\infty} k_i M_i + \sum_{i=0}^{\infty} q_i i M_i. \tag{3}$$

The second term in the right-hand side models the decrease in the concentration of free silica particles due to their ingestion by macrophages, and the third term represents their increase due to them being released into the lungs when macrophages die. A kinetic scheme of the processes modelled by the rate Eqs. (1)–(3) is presented in Fig. 1, [4].

For the functional setting in which to study (1)–(3) we consider the set of elements $y = (y_n) = (x, M_0, M_1, \ldots)$ of $\mathbb{R}^{\mathbb{N}}$ defined by

$$X = \{y = (y_n) : \|y\| < \infty\}$$

where

$$\|y\| := |x| + \sum_{i=0}^{\infty}(i+1)|M_i| = |x| + |((i+1)M_i)_{i=0,1,\ldots}|_{\ell^1}.$$

It is clear that $(X, \|\cdot\|)$ is a Banach space (and a subspace of ℓ^1). We say that $y \geq 0$ if and only if $y \in (\mathbb{R}_0^+)^{\mathbb{N}}$ and we denote the nonnegative cone of X by $X_+ := \{y \in X : y \geq 0\}$.

From a biological point of view we are only interested in nonnegative solutions of (1)–(3), $y(t) \geq 0$ for all $t \geq 0$. If $y(t) \in X_+$ then the quantity $\|y(t)\|$ represents the total amount of particles (macrophages cells and silica particles inside and outside the macrophages) per unit volume at time t, and so working in X_+ corresponds to consider solutions of (1)–(3) with finite amount of particles per unit volume.

Existence, uniqueness, continuous dependence and semigroup property of solutions to the Cauchy problem for the infinite dimensional system of ordinary differential Eqs. (1)–(3) were studied in [4]. Aspects of the structure of equilibria were analyzed in [3]. In this paper we consider aspects of the long time behaviour of solutions for the system with the following class of piecewise constant coefficients introduced and studied in [3, Section 3.1]:

$$k_i \equiv k, \quad p_i = \begin{cases} 1 & \text{if} \quad i \leq N, \\ 0 & \text{if} \quad i \geq N+1, \end{cases} \quad \text{and} \quad q_i = \begin{cases} 0 & \text{if} \quad i \leq N, \\ 1 & \text{if} \quad i \geq N+1, \end{cases} \tag{4}$$

for some fixed positive integer N.

This N can be biologically interpreted as a measure of the letal load of quartz particles in a macrophage: if $i \leq N$ macrophages do not die ($q_i = 0$) and the mucociliary clearance mechanism is effective in expelling the macrophages out of the system at a constant rate ($p_i = 1$), whereas for quartz loads $i > N$ the toxicity of the quartz leads to the death of the macrophages containing them at a certain rate ($q_i = 1$) and their heavy load of quartz impairs the workings of the mucociliary mechanism ($p_i = 0$). The assumption of constant k corresponds to saying that the capture of a quartz particle by a macrophage is independent of the already existing load of quartz in the macrophage; this is probably reasonable for small quartz loads but a more realistic assumption for large loads will turn the rigorous mathematical analysis excessively difficult, if not impossible, so we consider $k_i = k$ throughout the paper.

With these coefficients system (1)–(3) becomes

$$\begin{aligned} \frac{dM_0}{dt} &= r - kxM_0 - M_0, \\ \frac{dM_i}{dt} &= kxM_{i-1} - kxM_i - M_i, \quad i \geq 1, \\ \frac{dx}{dt} &= \alpha - kx \sum_{i=0}^{\infty} M_i + \sum_{i=N+1}^{\infty} iM_i, \end{aligned} \tag{5}$$

and the structure of its equilibria is completely understood and was proved in Propositions 1 and 2 of [3]:

Proposition 1 *For all $N \in \mathbb{N}$ and $k > 0$, there exists a unique $\mu^* > 0$ such that (5) has:*

1. *No equilibria if $\alpha/r > \mu^*$,*
2. *Exactly one equilibrium if $\alpha/r = \mu^*$,*
3. *Exactly two equilibria if $\alpha/r \in (0, \mu^*)$.*

As was proved in [3] and will be recalled below, each equilibrium solution of (5), $(x^{\text{eq}}, M_0^{\text{eq}}, M_1^{\text{eq}}, M_2^{\text{eq}}, \ldots)$, can be identified by its x component, and Proposition 1 can be graphically depicted by the bifurcation diagram presented in Fig. 2. In the same figure it is denoted by the letters "s" (for "locally exponentially stable") and "u" (for "unstable") the stability of the equilibria for the dynamics of (5) in the strong topology of the phase space X, as proved later in Theorems 4 and 5.

In this paper we study the local stability of the equilibria of the silicosis system (5). The paper is organized as follows:

In Sect. 2 we recall some results obtained in [3] about the time independent solutions of the silicosis system. In particular we present a bifurcation Eq. (9), whose solutions give (the

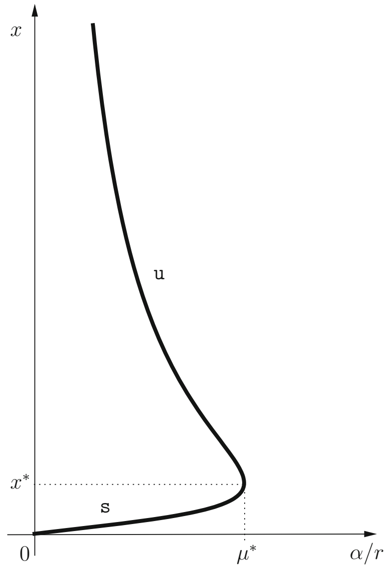

Fig. 2 Bifurcation diagram of the equilibria of (5) as inferred from Proposition 1, [3]. The stability information, "s" (for "locally exponentially stable") and "u" (for "unstable"), arises from Theorem 2 in Sect. 3 and theorems 4 and 5 in Sect. 4

component x of) the equilibria of (5) and point out properties of the bifurcation function that will be crucially important in the remaining of the paper.

Informally, the result about the number of equilibria (already presented above in Proposition 1 and Fig. 2) states that if the balance between the input rates of silica, α, and of macrophages, r, is such that, in some sense, the silica input does not dominate, then (5) will have two equilibria and, from an heuristic viewpoint, we expect the equilibria with a smaller load of silica dust x to be stable while the other is expected to be unstable. It is the goal of this paper to make this argument rigorous and to prove this intuition.

In Sect. 3 we show, in Sect. 3.1, that by introducing three bulk variables u, v and w defined by (13) system (5) is transformed into an infinite dimensional system (17) for the variables $(x, u, v, w, M_0, \ldots)$ for which the equations for the variables $(x, u, \ldots, M_N)$ consist of a closed $(N+5)$-dimension system of ordinary differential equations. It is this decoupling that allows the study of the stability of the equilibria of (5) to be done by first obtaining appropriate results about the spectra of the linearizations around the equilibria of this finite dimensional system, which is done in Sect. 3.2. Finally, in Sect. 3.3 we present examples of the numerically computed spectra of jacobian matrices corresponding to the linearization of the $(N+5)$-dimensional system about its equilibria. These numerical experiments illustrate the results rigorously proved in Sect. 3.2 and support the conjecture stated in that section about the dimension of the unstable manifold of the unstable equilibrium of the $(N+5)$-dimensional system. Additionally, it also suggest that, besides those properties proved in Sect. 3.2 which are relevant to our goal in this paper, the spectra has some other features that could be interesting to explore in the future.

In Sect. 4 we study the local dynamics about the equilibria of the full silicosis system (5) using the results about the stability properties of the equilibria of the reduced $(N+5)$-dimensional system obtained in the previous section. In particular we prove that our intuition was correct: the equilibrium of (5) with a lower load of silica dust x^{eq} is locally exponentially asymptotically stable in the strong topology of X, whereas the equilibrium with a higher silica load x^{eq} is unstable.

In Sect. 5 we discuss the possible biological interpretation of the results proved in this paper and point out some further mathematical work on this model that, in our judgement, is interesting to explore.

2 Preliminaries: The Equilibria

In this section we recall some of the results obtained in [3] for the time independent solutions of the silicosis system (5). In that article the authors solve Eqs. (1)–(2) with all the time derivatives equal to zero, thus obtaining the following expressions for the M_i^{eq} variables corresponding to the equilibrium solutions, for general coefficients, $k_i > 0$, $p_i \geq 0$, $q_i \geq 0$, in terms of the variable x^{eq}:

$$M_i^{\text{eq}} = \frac{r(x^{\text{eq}})^i}{k_i \prod_{j=0}^{i}(x^{\text{eq}} + d_j)}, \quad i \geq 0, \tag{6}$$

where $d_j = (p_j + q_j)/k_j$. For our particular choice of the coefficients, that is, for system (5), $d_j = 1/k$, and from (6) they are easily obtained,

$$\sum_{i=0}^{\infty} k_i M_i^{\text{eq}} = k \sum_{i=0}^{\infty} M_i^{\text{eq}} = rk, \tag{7}$$

$$\sum_{i=0}^{\infty} i q_i M_i^{\text{eq}} = \sum_{i=N+1}^{\infty} i M_i^{\text{eq}} = r\big(kx + (N+1)\big)\left(\frac{x^{\text{eq}}}{x^{\text{eq}} + 1/k}\right)^{N+1}. \tag{8}$$

Plugging (7) and (8) into the time independent version of the equation for the quartz concentration x in system (5), they obtain the bifurcation equation,

$$\frac{\alpha}{r} - \mathcal{F}_{N,k}(x^{\text{eq}}) = 0, \tag{9}$$

where, for all positive x,

$$\mathcal{F}_{N,k}(x) := kx\left(1 - \left(\frac{x}{x + 1/k}\right)^{N+1}\right) - (N+1)\left(\frac{x}{x + 1/k}\right)^{N+1}.$$

Proposition 1 in the previous section follows from the analysis of Eq. (9) that we briefly recall now: introducing the variable $y = \frac{x^{\text{eq}}}{x^{\text{eq}}+1/k}$, and defining the function $\widetilde{\mathcal{F}}_N$ by

$$\widetilde{\mathcal{F}}_N(y) := \frac{y}{1-y}\left(1 - (N+1)y^N + Ny^{N+1}\right),$$

Equation (9) can be written as,

$$\frac{\alpha}{r} - \widetilde{\mathcal{F}}_N(y) = 0. \tag{10}$$

Observe the independence of this bifurcation equation relatively to k: this coefficient only dictates how the variables x^{eq} and y are interrelated. Of relevance to our work are the arguments used in the proof of Proposition 2 in [3] based on the study of the derivative,

$$\widetilde{\mathcal{F}}_N'(y) = \frac{p_N(y)}{(1-y)^2}, \tag{11}$$

where,

$$p_N(y) := 1 - (N+1)^2 y^N + N(2N+3)y^{N+1} - N(N+1)y^{N+2}. \tag{12}$$

The authors prove that p_N is strictly decreasing in $\left(0, \frac{N+1}{N+2}\right)$ and strictly increasing in $\left(\frac{N+1}{N+2}, 1\right)$. Since $p_N(1) = 0$, then $p_N\left(\frac{N+1}{N+2}\right) < 0$ and, by the fact that $p_N(0) > 0$, it can be concluded that there is one and only one critical point y^* of $\widetilde{\mathcal{F}}_N$ in $(0, 1)$, and furthermore it satisfies, $y^* < \frac{N+1}{N+2}$. This corresponds to the critical point x^* of $\mathcal{F}_{k,N}$ that, together with (9), gives the bifurcation point (μ^*, x^*), displayed in the bifurcation diagram of Fig. 2.

3 A Finite Dimensional Reduced System

We start by showing that system (5) can be transformed into an infinite dimensional system whose study can be decoupled into a finite dimensional ODE system, followed by an infinite dimensional system that can be analysed recursively. The characterization of the stability properties of our silicosis system will then be based on the study of this finite dimensional ODE.

3.1 The Reduced System

Let us introduce the following three new variables:

$$u := \sum_{i=0}^{\infty} M_i, \quad v := \sum_{i=N+1}^{\infty} iM_i, \quad w := \sum_{i=N}^{\infty} M_i. \tag{13}$$

By [4, Corollary 5.3] the series in (13) are uniformly convergent. For any positive integer m, we get, from (5),

$$\begin{aligned}\sum_{i=0}^{m} \dot{M}_i &= r - kxM_0 - M_0 + kx\sum_{i=1}^{m}(M_{i-1} - M_i) - \sum_{i=1}^{m} M_i \\ &= r - mM_m - \sum_{i=0}^{m} M_i\end{aligned}$$

and, if $m > N$,

$$\begin{aligned}\sum_{i=N+1}^{m} i\dot{M}_i &= kx\sum_{i=N+1}^{m} i(M_{i-1} - M_i) - \sum_{i=N+1}^{m} iM_i \\ &= kx(NM_N - mM_m) + kx\sum_{i=N}^{m-1} M_i - \sum_{i=N+1}^{m} iM_i.\end{aligned}$$

Hence, by the uniform convergence as $m \to \infty$ of the right-hand sides of these equalities we conclude the left-hand sides are also uniformly convergent and since [4, Proposition 6.1] ensures that $M_i \in C^1([0, \infty))$, we conclude that u, v and w in (13) are C^1 functions and their derivative can be computed differentiating the series term-by-term:

$$\dot{u} = \sum_{i=0}^{\infty} \dot{M}_i = r - kxM_0 - M_0 + kx\sum_{i=1}^{\infty}(M_{i-1} - M_i) - \sum_{i=1}^{\infty} M_i$$

$$= r - u. \tag{14}$$

$$\dot{v} = \sum_{i=N+1}^{\infty} i\dot{M}_i = kx \sum_{i=N+1}^{\infty} (iM_{i-1} - iM_i) - \sum_{i=N+1}^{\infty} iM_i$$
$$= kx\left(\sum_{i=N+1}^{\infty} \big((i-1)M_{i-1} - iM_i\big) + \sum_{i=N+1}^{\infty} M_{i-1}\right) - \sum_{i=N+1}^{\infty} iM_i$$
$$= kxNM_N + kxw - v. \tag{15}$$

$$\dot{w} = \sum_{i=N}^{\infty} \dot{M}_i = kx \sum_{i=N}^{\infty} (M_{i-1} - M_i) - \sum_{i=N}^{\infty} M_i$$
$$= kxM_{N-1} - w. \tag{16}$$

Using our new variables in the x equation of (5), we can write that system augmented with (14), (15) and (16) as

$$\begin{cases} \dot{x} = \alpha - kxu + v \\ \dot{u} = r - u \\ \dot{v} = -v + kxw + kNxM_N \\ \dot{w} = -w + kxM_{N-1} \\ \dot{M}_0 = r - M_0 - kxM_0 \\ \dot{M}_i = -M_i - kxM_i + kxM_{i-1}, \quad i \geq 1. \end{cases} \tag{17}$$

We now observe that if we discard the equations for $\dot{M}_i$, with $i \geq N+1$, we obtain a closed system in the $N+5$ variables $x, u, v, w, M_0, \ldots, M_N$. If we solve this ODE, then, by using the computed x and M_N, all the remaining variables M_i can be recursively computed. Therefore, by defining,

$$U_1 := x, \quad U_2 := u, \quad U_3 := v, \quad U_4 := w, \quad U_i := M_{i-5}, \quad 5 \leq i \leq N+5,$$

we can write that finite dimensional system in the form

$$\dot{U} = F(U) \tag{18}$$

with $F : \mathbb{R}^{N+5} \to \mathbb{R}^{N+5}$ defined by

$$F(U) := \begin{bmatrix} \alpha + U_3 - kU_1U_2 \\ r - U_2 \\ -U_3 + kU_1U_4 + NkU_1U_{N+5} \\ -U_4 + kU_1U_{N+4} \\ r - U_5 - kU_1U_5 \\ -U_6 + kU_1U_5 - kU_1U_6 \\ \vdots \\ -U_{N+5} + kU_1U_{N+4} - kU_1U_{N+5} \end{bmatrix}. \tag{19}$$

Let $U^{\text{eq}} := (x^{\text{eq}}, u^{\text{eq}}, v^{\text{eq}}, w^{\text{eq}}, M_0^{\text{eq}}, \ldots, M_N^{\text{eq}})$ be U corresponding to one of the equilibrium solutions mentioned in the previous sections. Following [3] (see previous section), we introduce the variable

$$y := \frac{x^{\text{eq}}}{x^{\text{eq}} + 1/k},$$

and for the sake of simplifying notation (and since in the following we will only be referring to the equilibrium quantities) we drop the 'eq' superscript for the computations in the remaining of this section. Hence, for each one of the equilibrium solutions, using the results of the previous section, we have:

$$\begin{aligned} U_1 &:= x = \frac{1}{k}\frac{y}{1-y}, \\ U_2 &:= u = r, \\ U_3 &:= v = r\frac{y^{N+1}}{1-y}\big((N+1) - Ny\big), \\ U_4 &:= w = ry^N, \\ U_{5+i} &:= M_i = r(1-y)y^i, \quad 0 \le i \le N. \end{aligned}$$

3.2 Spectral Properties of the Equilibria of the Reduced System

To study the linear stability of the equilibria U of the ordinary differential Eq. (18) we have to compute the characteristic polynomial of the $(N+5) \times (N+5)$ jacobian matrix $A := DF(U)$, which is the goal of the next lemma.

Let us introduce the variable

$$\varDelta := 1 + \lambda(1-y). \tag{20}$$

Lemma 1 *The characteristic polynomial of the jacobian matrix A of* (18) *about an equilibrium is given by*

$$\begin{aligned} &\det(A - \lambda I_{N+5}) \\ &\quad = (-1)^N kr(1+\lambda)^2(1-y)^{-N-1}\Bigg\{(1+\lambda)\left(1+\frac{\lambda}{kr}\right)\varDelta^{N+1} \\ &\quad -y^N\Big[\varDelta^{N+1} + (1-y)\Big(\big(N(1-y)(1+\lambda)+1\big)(1+\cdots+\varDelta^N) - 1\Big)\Big]\Bigg\}. \end{aligned} \tag{21}$$

Proof Observing that

$$-1 - kU_1 = -\frac{1}{1-y}, \quad \text{and} \quad U_{i+4} - U_{i+5} = r(1-y^2)y^{i-1},$$

we can write the $(N+5)\times(N+5)$ linearization matrix $A = DF(U)$ in the form $A = \left[\begin{array}{c|c} B & C \\ \hline D & E \end{array}\right]$, where B is the 4×4 matrix

$$B = \begin{bmatrix} -kr & -\dfrac{y}{1-y} & 1 & 0 \\ 0 & -1 & 0 & 0 \\ kry^N\big(1+N(1-y)\big) & 0 & -1 & \dfrac{y}{1-y} \\ kry^{N-1}(1-y) & 0 & 0 & -1 \end{bmatrix},$$

C and D are, respectively, the $4 \times (N+1)$ and $(N+1) \times 4$ matrices

$$C = \begin{bmatrix} 0 \cdots & 0 & 0 \\ 0 \cdots & 0 & 0 \\ 0 \cdots & 0 & \dfrac{Ny}{1-y} \\ 0 \cdots & \dfrac{y}{1-y} & 0 \end{bmatrix}, \quad D = \begin{bmatrix} -kr(1-y) & 0\ 0\ 0 \\ kr(1-y)^2 & \vdots\ \vdots\ \vdots \\ kr(1-y)^2 y & \vdots\ \vdots\ \vdots \\ \vdots & \vdots\ \vdots\ \vdots \\ kr(1-y)^2 y^{N-1} & 0\ 0\ 0 \end{bmatrix},$$

and E is the $(N+1) \times (N+1)$ matrix

$$E = \begin{bmatrix} [1.8] - \frac{1}{1-y} & 0 & \cdots & \cdots & 0 \\ \frac{y}{1-y} & -\frac{1}{1-y} & & & \vdots \\ 0 & \ddots & \ddots & & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \dots & 0 & \frac{y}{1-y} & -\frac{1}{1-y} \end{bmatrix}.$$

To compute the determinant of $A - \lambda I_{N+5}$ we will take advantage of the particular structure of the matrix A pointed out above and start by writing

$$\det(A - \lambda I_{N+5}) = \det \left[\begin{array}{c|c} B - \lambda I_4 & C \\ \hline D & E - \lambda I_{N+1} \end{array} \right].$$

Then, we successively perform the following operations in $A - \lambda I_{N+5}$ to achieve a final matrix with equal determinant:

1. Factor out $\frac{1}{1-y}$ from the last $N+1$ columns;
2. Factor out $\frac{1}{1-y}$ from the third row;
3. Factor out $kr(1-y)$ from the first column;
4. Apply Laplace determinant expansion relative to the second row.

In the end we obtain,

$$\det(A - \lambda I_{N+5}) = -kr(1+\lambda)(1-y)^{-N-1} \det(\widetilde{A}_\lambda), \tag{22}$$

with $\widetilde{A}_\lambda = \left[\begin{array}{c|c} \widetilde{B}_\lambda & \widetilde{C} \\ \hline \widetilde{D} & \widetilde{E}_\lambda \end{array} \right]$, where, $\widetilde{B}_\lambda$ is the 3×3 matrix

$$\widetilde{B}_\lambda = \begin{bmatrix} -(1+\lambda/kr)(1-y)^{-1} & 1 & 0 \\ y^N\big(1+N(1-y)\big) & -(1+\lambda)(1-y) & y \\ y^{N-1} & 0 & -(1+\lambda) \end{bmatrix},$$

$\widetilde{C}$ and $\widetilde{D}$ are, respectively, the $3 \times (N+1)$ and $(N+1) \times 3$ matrices

$$\widetilde{C} = \begin{bmatrix} 0 \cdots 0 & 0 \\ 0 \cdots 0 & Ny(1-y) \\ 0 \cdots y & 0 \end{bmatrix}, \quad \widetilde{D} = \begin{bmatrix} -1 & 0\ 0 \\ 1-y & \vdots\ \vdots \\ (1-y)y & \vdots\ \vdots \\ \vdots & \vdots\ \vdots \\ (1-y)y^{N-1} & 0\ 0 \end{bmatrix},$$

and $\widetilde{E}_\lambda$ is the $(N+1)\times(N+1)$ matrix,

$$\widetilde{E}_\lambda = \begin{bmatrix} -\Delta & 0 & \cdots\cdots & 0 \\ y & -\Delta & & \vdots \\ 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots\ \ddots & 0 \\ 0 & \dots & 0 \quad y & -\Delta \end{bmatrix}.$$

The main idea here is to left multiply $\tilde{A}_\lambda$ by a square matrix of determinant 1, in such a way that the resulting matrix has a more easily computable determinant. For the following we consider that $\Delta \neq 0$. Consider the $(N+1)\times(N+1)$ matrix

$$\Lambda = \begin{bmatrix} 1 & 0 & \cdots\cdots & 0 \\ \frac{y}{\Delta} & 1 & & \vdots \\ \frac{y^2}{\Delta^2} & \frac{y}{\Delta} & 1 & \vdots \\ \vdots & \ddots & \ddots\ \ddots & 0 \\ \frac{y^N}{\Delta^N} & \frac{y^{N-1}}{\Delta^{N-1}} & \cdots\ \frac{y}{\Delta} & 1 \end{bmatrix},$$

and observe that $\Lambda \widetilde{E}_\lambda = -\Delta I_{N+1}$. Therefore,

$$\det(\widetilde{A}_\lambda) = \det\left(\left[\begin{array}{c|c} I_3 & 0 \\ \hline 0 & \Lambda \end{array}\right] \widetilde{A}_\lambda\right) = \det\left[\begin{array}{c|c} \widetilde{B}_\lambda & \widetilde{C} \\ \hline \Lambda\widetilde{D} & -\Delta I_{N+1} \end{array}\right]. \tag{23}$$

The second and third columns of $\Lambda\widetilde{D}$ are $N+1$ dimension nul columns, while the first column of $\Lambda\widetilde{D} = \begin{bmatrix} -1 & \alpha_0 & \alpha_1 & \cdots & \alpha_{N-1} \end{bmatrix}^\top$, where, for $0 \le i \le N-1$, these entries are given by,

$$\alpha_i := \begin{bmatrix} \frac{y^{i+1}}{\Delta^{i+1}} & \frac{y^i}{\Delta^i} & \cdots & 1 & 0 & \cdots & 0 \end{bmatrix} \begin{bmatrix} -1 \\ 1-y \\ (1-y)y \\ \vdots \\ (1-y)y^{N-1} \end{bmatrix}.$$

In particular we will need explicit expressions for the last two entries:

$$\begin{aligned} \alpha_{N-2} &= -\frac{y^{N-1}}{\Delta^{N-1}} + (1-y)\frac{y^{N-2}}{\Delta^{N-2}}(1+\Delta+\cdots+\Delta^{N-2}), \\ \alpha_{N-1} &= -\frac{y^N}{\Delta^N} + (1-y)\frac{y^{N-1}}{\Delta^{N-1}}(1+\Delta+\cdots+\Delta^{N-1}). \end{aligned} \tag{24}$$

Now, we eliminate the nonzero entries of $\widetilde{C}$. By multiplying the last row of the last matrix in (23) by $\frac{Ny(1-y)}{\Delta}$ and adding to the second row, we eliminate the last entry of this row. Then, by multiplying the penultimate row by $\frac{y}{\Delta}$ and adding to the third row, we eliminate the penultimate entry of this row. Therefore, from (23)

$$\det(\widetilde{A}_\lambda) = \det\left[\begin{array}{c|c} \widetilde{B}^*_\lambda & 0 \\ \hline \Lambda\widetilde{D} & -\Delta I_{N+1} \end{array}\right] = (-1)^{N+1}\Delta^{N+1}\det\widetilde{B}^*_\lambda, \tag{25}$$

where,

$$\widetilde{B}_\lambda^* = \begin{bmatrix} -(1+\lambda/kr)(1-y)^{-1} & 1 & 0 \\ y^N\big(1+N(1-y)\big)+\alpha_{N-1}\frac{Ny(1-y)}{\Delta} & -(1+\lambda)(1-y) & y \\ y^{N-1}+\alpha_{N-2}\frac{y}{\Delta} & 0 & -(1+\lambda) \end{bmatrix},$$

and therefore,

$$\begin{aligned} \det \widetilde{B}_\lambda^* =& -(1+\lambda)^2\left(1+\frac{\lambda}{kr}\right) \\ &+\left(y^N\big(1+N(1-y)\big)+\alpha_{N-1}\frac{Ny(1-y)}{\Delta}\right)(1+\lambda) \\ &+y^N+\alpha_{N-2}\frac{y^2}{\Delta}. \end{aligned} \tag{26}$$

Using the explicit expressions for α_{N-1} and α_{N-2} given by (24) we get

$$\begin{aligned} &y^N\big(1+N(1-y)\big)+\alpha_{N-1}\frac{Ny(1-y)}{\Delta} \\ &= y^N\left[1+N(1-y)\left(1+\frac{y^{1-N}}{\Delta}\alpha_{N-1}\right)\right] \\ &= y^N\left[1+\frac{N(1-y)}{\Delta^{N+1}}(\Delta-y)(1+\cdots+\Delta^N)\right], \end{aligned}$$

and

$$\begin{aligned} y^N+\alpha_{N-2}\frac{y^2}{\Delta} &= y^N\left[1+\frac{1}{\Delta^N}\left(-y+(1-y)(\Delta+\cdots+\Delta^{N-1})\right)\right] \\ &= \frac{y^N}{\Delta^N}(\Delta-y)(1+\cdots+\Delta^{N-1}) \\ &= \frac{y^N}{\Delta^{N+1}}\left[(\Delta-y)(1+\cdots+\Delta^N)-(\Delta-y)\right]. \end{aligned}$$

By plugging this last expression in (26) we have,

$$\begin{aligned} \det \widetilde{B}_\lambda^* =& -(1+\lambda)^2\left(1+\frac{\lambda}{kr}\right) \\ &+y^N\Big\{1+\lambda+\frac{N(1-y)(1+\lambda)}{\Delta^{N+1}}(\Delta-y)(1+\cdots+\Delta^N) \\ &+\frac{1}{\Delta^{N+1}}\left[(\Delta-y)(1+\cdots+\Delta^N)-(\Delta-y)\right]\Big\} \\ =& -(1+\lambda)^2\left(1+\frac{\lambda}{kr}\right) \\ &+y^N(1+\lambda)\left\{1+\frac{(1-y)}{\Delta^{N+1}}\left[\left(N(1-y)(1+\lambda)+1\right)(1+\cdots+\Delta^N)-1\right]\right\}, \end{aligned}$$

where we have used the fact that $\Delta - y = (1+\lambda)(1-y)$. By using (22), (25) and the last equation, we obtain (21). □

The determinant of the matrix A is obtained from (21) by making $\lambda = 0$, in which case, also $\Delta = 1$ and we obtain:

$$\det A = (-1)^N kr(1-y)^{-N-1}P_N(y). \tag{27}$$

Therefore, if we compare this with (12) we see that the bifurcation condition $p_N(y) = 0$ is equivalent to $\det A = 0$, as it should be. Let $y^* = y^*(N)$ be the unique solution of this bifurcation equation to which corresponds $\alpha/r = \mu^* = \mathcal{F}_N(y^*)$. Our next step is to show that $\lambda = 0$ is a simple eigenvalue of A, when $y = y^*$.

Lemma 2 *For $y = y^*$, $\lambda = 0$ is a simple eigenvalue of A.*

Proof First, for a generic equilibrium, and therefore for a generic $y \in (0, 1)$, we compute a_1 (depending on N, kr, y) such that, as $\lambda \to 0$,

$$\det(A - \lambda I_{N+5}) = \det A + a_1\lambda + O(|\lambda|^2), \tag{28}$$

with fixed N, kr, y.

It is convenient to introduce

$$g(\Delta) := \sum_{i=0}^{N} \Delta^i.$$

Therefore, since $g(1) = N + 1$, and $g'(1) = \frac{N(N+1)}{2}$, we obtain, as $\lambda \to 0$,

$$g(\Delta) = g_0 + g_1\lambda + O(|\lambda|^2),$$

for $g_0 = N + 1$ and $g_1 = \frac{1}{2}N(N + 1)(1 - y)$. Hence, in (21), we will have

$$\begin{aligned}
&\big(N(1-y)(1+\lambda)+1\big)g(\Delta)\\
&\quad= \big[N(1-y)+1+N(1-y)\lambda\big]\big(g_0+g_1\lambda\big)+O\left(|\lambda|^2\right)\\
&\quad= \big[N(1-y)+1\big]g_0+\big[\big(N(1-y)+1\big)g_1+N(1-y)g_0\big]\lambda+O\left(|\lambda|^2\right)\\
&\quad= b_0+b_1\lambda+O\left(|\lambda|^2\right),
\end{aligned}$$

where,

$$\begin{aligned}
b_0 &:= (N+1)\big(N(1-y)+1\big)\\
b_1 &:= \frac{1}{2}N(N+1)(1-y)\big(N(1-y)+3\big).
\end{aligned}$$

Taking in account that,

$$\Delta^{N+1} = 1 + (N+1)(1-y)\lambda + O\left(|\lambda|^2\right),$$

so that

$$\left[(1+\lambda)\left(1+\frac{\lambda}{kr}\right)-y^N\right]\Delta^{N+1} = c_0 + c_1\lambda + O\left(|\lambda|^2\right),$$

where,

$$\begin{aligned}
c_0 &= 1 - y^N\\
c_1 &= 1 + \frac{1}{kr} + (N+1)(1-y)(1-y^N),
\end{aligned}$$

we have in (21),

$$\begin{aligned}
&(1+\lambda)\left(1+\frac{\lambda}{kr}\right)\Delta^{N+1}\\
&\qquad - y^N\Big[\Delta^{N+1}+(1-y)\Big(\big(N(1-y)(1+\lambda)+1\big)(g(\Delta)-1\big)\Big)\Big]
\end{aligned}$$

$$= d_0 + d_1\lambda + O\left(|\lambda|^2\right),$$

where,

$$d_0 = 1 - y^N\Big[1 + (1-y)\Big(\big(N(1-y)+1\big)(N+1) - 1\Big)\Big] \tag{29}$$

$$d_1 = 1 + \frac{1}{kr} + (N+1)(1-y)\left\{1 - y^N\left[1 + \frac{N(1-y)}{2}\big(N(1-y)+3\big)\right]\right\}. \tag{30}$$

Therefore, by (21)

$$\det(A - \lambda I_{N+5}) = (-1)^N kr(1-y)^{-N-1}\big(d_0 + (2d_0 + d_1)\lambda\big) + O\left(|\lambda|^2\right).$$

Now, by comparing (29) and (12), we observe that $d_0 = p_N(y)$, so that,

$$\det(A - \lambda I_{N+5}) = \det A + \left[2\det A + (-1)^N kr(1-y)^{-N-1} d_1\right]\lambda + O\left(|\lambda|^2\right).$$

Therefore, we obtain (28) with

$$a_1 = 2\det A + (-1)^N kr(1-y)^{-N-1} d_1.$$

Now, when we are considering the equilibrium corresponding to $(\alpha/r, y) = (\mu^*, y^*)$ we know that $\det A = 0$, so that, as $\lambda \to 0$,

$$\det(A - \lambda I_{N+5}) = (-1)^N kr(1-y^*)^{-N-1} d_1\lambda + O\left(|\lambda|^2\right).$$

Hence, $\lambda = 0$ will be a simple eigenvalue of A if and only if $d_1 \neq 0$ for $y = y^*$, what we are going to show that indeed it is here the case. Let us define in (30),

$$\begin{aligned} q_N(y) &:= 1 - y^N\left[1 + \frac{N(1-y)}{2}\big(N(1-y)+3\big)\right] \\ &= 1 - y^N\left[1 + \frac{3}{2}N(1-y) + \frac{1}{2}N^2(1-y)^2\right]. \end{aligned}$$

Rewriting $p_N(y)$ in the form

$$p_N(y) = 1 - y^N\Big[1 + N(1-y) + N(N+1)(1-y)^2\Big],$$

we easily obtain

$$q_N(y) - p_N(y) = \frac{1}{2}y^N(1-y)N\Big[(N+2)(1-y) - 1\Big].$$

Now, consider the case $y = y^*$. Since by definition, $p_N(y^*) = 0$, we get,

$$q_N(y^*) = \frac{1}{2}(y^*)^N(1-y)N\Big[(N+2)(1-y^*) - 1\Big].$$

But according to [3] (see previous section), we know that $0 < y^* < \frac{N+1}{N+2}$, so that,

$$(N+2)(1-y^*) - 1 > (N+2)\left(1 - \frac{N+1}{N+2}\right) - 1 = 0,$$

which proves that, for $y = y^*$, $q_N(y^*) > 0$, and therefore, $d_1 > 0$. This completes the proof that, for $y = y^*$, $\lambda = 0$ is a simple eigenvalue of A. □

The next lemma will be crucial for the stability result in Theorem 2

Lemma 3 *For every $0 < y \leq y^*$, the matrix A does not have pure imaginary eigenvalues.*

Proof We intend to prove that, if $0 < y \leq y^*$, then, the equation $\det(A - \lambda I_{N+5}) = 0$ does not have pure imaginary solutions. Using (21), this equation, for $kr \neq 0$ and $\lambda \neq -1$, is equivalent to

$$(1+\beta\lambda)y^{-N} = \Big[1 + (1-y)\Big(\big(N(1-y)(1+\lambda)+1\big)g(\Delta) - 1\Big)\Delta^{-N-1}\Big](1+\lambda)^{-1},$$

recalling that, $g(\Delta) := \sum_{i=0}^{N} \Delta^i$, and defining $\beta := \frac{1}{kr}$. By writing,

$$F_N(\lambda, \beta, y) := (1+\beta\lambda)y^{-N},$$
$$G_N(\lambda, y) := \Big[1 + (1-y)\Big(\big(N(1-y)(1+\lambda)+1\big)g(\Delta) - 1\Big)\Delta^{-N-1}\Big](1+\lambda)^{-1},$$

the above equation can be written as

$$F_N(\lambda, \beta, y) = G_N(\lambda, y). \tag{31}$$

Now, take $\lambda = i\omega$, with real $\omega \neq 0$. Then, since $\beta > 0$,

$$|F_N(i\omega, \beta, y)| = y^{-N}\sqrt{1+\beta^2\omega^2} > y^{-N}.$$

On the other hand, defining

$$\hat{g}(\Delta) := \sum_{i=1}^{N} \Delta^{-i},$$

we can write,

$$G_N(\lambda, y) = \big(1 + (1-y)\Delta^{-1}\hat{g}(\Delta)\big)(1+\lambda)^{-1} + N(1-y)^2(\hat{g}(\Delta)+1)\Delta^{-1}.$$

By observing that, for $\lambda = i\omega$, with real $\omega \neq 0$, we have $|(1+\lambda)^{-1}| < 1$, but also $|\Delta^{-1}| < 1$, which in turn implies, $|\hat{g}(\Delta)| < N$, we conclude that,

$$|G_N(i\omega, y)| < 1 + N(1-y) + N(N+1)(1-y)^2,$$

so that,

$$|F_N(i\omega, \beta, y)| - |G_N(i\omega, y)| > y^{-N} - \Big[1 + N(1-y) + N(N+1)(1-y)^2\Big] = y^{-N}p(y).$$

But recalling the results summarized in Sect. 2., we know that, for $0 < y \leq y^*$, $p_N(y) \geq 0$, and therefore,

$$|F_N(i\omega, \beta, y)| - |G_N(i\omega, y)| > 0$$

which makes it impossible for Eq. (31) to be satisfied for any $\lambda = i\omega$, with $\omega \neq 0$. □

We can now state the main result of this section:

Theorem 2 *Let μ^* be as in Proposition 1, and let x^* be the value of the U_1 component of the unique equilibrium of (18) when $\alpha/r = \mu^*$ (see Fig. 2). Then, for every $\alpha/r \in (0, \mu^*)$ and all $kr > 0$, the equilibrium solution U^{1*}, with $U_1^{1*} < x^*$, is locally exponentially asymptotically stable, and the equilibrium solution U^{2*}, with $U_1^{2*} > x^*$, is unstable.*

Proof Let us rewrite (21) as follows:

$$\det(A-\lambda I_{N+5}) = (-1)^N(1-y)^{-N-1}(1+\lambda)^3\lambda\Delta^{N+1} - kr(-1)^N(1-y)^{-N-1}(1+\lambda)^2 \times \Big\{(1+\lambda)\lambda\Delta^{N+1} - y^N\Big[\Delta^{N+1} + (1-y)\Big(\big(N(1-y)(1+\lambda)+1\big)(1+\cdots+\Delta^N)-1\Big)\Big]\Big\}. \tag{32}$$

Observe that, if $kr = 0$, then $\det(A-\lambda I_{N+5}) = (-1)^N(1-y)^{-N-1}(1+\lambda)^3\lambda\Delta^{N+1}$, and the eigenvalues of A are $\lambda = 0$ (simple), $\lambda = -1$ (with algebraic multiplicity 3,) and $\lambda = -\frac{1}{1-y}$ (with algebraic multiplicity $N+1$.) Let $y = y^*$. Then, from Lemmas 2 and 3, for every $kr > 0$ the linearization of (18) around the equilibrium U^* with $y = y^*$ has $N+4$ nonzero eigenvalues with negative real parts and the remaining eigenvalue $\lambda = 0$ is simple.

For $0 < \alpha/r < \mu^*$ let $y^{1*} < y^* < y^{2*}$ be the only two values of y that solve the bifurcation Eq. (10). To these values of y corresponds two equilibria of (18): U^{1*} (corresponding to y^{1*}) and U^{2*} (corresponding to y^{2*}.) By what was done previously, in particular from (11), (12), (27), (28), (29), and (30), the jacobian matrix of the linearization of (18) around U^{j*} has eigenvalues given by the solutions λ of

$$p_N(y^{j*}) + (2p_N(y^{j*}) + d_1)\lambda + O(|\lambda|^2) = 0 \quad \text{as } \lambda \to 0, \tag{33}$$

with $d_1 = d_1(y^{j*})$ given by (30). From the study of equilibria in [3], recalled in Sect. 2, we know that $p_N(y^{1*}) > 0$ for all $y^{1*} < y^*$, and $p_N(y^{2*}) < 0$ for all $y^{2*} > y^*$. From the proof above we have $d_1(y^*) > 0$ and hence, by continuity, for y^{1*} and y^{2*} sufficiently close to y^* it still holds that $2p_N(y^{j*}) + d_1(y^{j*}) > 0$. This implies that, for sufficiently small $kr > 0$, Eq. (33) has a negative solution when $j = 1$ and a positive solution when $j = 2$.

Thus, from the argument above, the zero eigenvalue of the jacobian matrix at the bifurcation point y^* is perturbed to a negative eigenvalue for the linearization about the equilibrium U^{1*} when y^{1*} is close to y^*. By Lemma 3 all the other eigenvalues of the Jacobian at U^{1*} have negative real parts, and since $\lambda = 0$ is not an eigenvalue if y is not equal to y^*, we conclude that for all equilibria U^{1*} (not necessarily close to U^*) the real negative eigenvalue originated from $\lambda = 0$ at the bifurcation point cannot become nonnegative. Hence, for all values of the parameters $\alpha/r \in (0, \mu^*)$, $kr > 0$, the equilibrium U^{1*} of (18) is locally exponentially asymptotically stable.

As in the case of U^{1*} above, when U^{2*} is a sufficiently small perturbation of U^*, the zero eigenvalue of the corresponding jacobian is perturbed to a positive real eigenvalue, and, by continuity, all other eigenvalues have negative real parts if the perturbation is sufficiently small. Also, this positive eigenvalue cannot become nonpositive if y remains larger than y^*. This implies that, for all values of the parameters $\alpha/r \in (0, \mu^*)$, $kr > 0$, the equilibrium U^{2*} of (18) is unstable.

This completes the proof of the theorem. □

Remark 1 In the instability part of the previous proof we establish that the eigenvalue of the jacobian matrix at U^{2*} that becomes positive when U^{2*} is a small perturbation of U^* cannot become nonpositive for larger perturbations (i.e., for larger positive values of $y - y^*$). However, note that for these equilibria with $y > y^*$ we could not prove a result analogous to Lemma 3 and so we cannot guarantee that, by changing the system's parameters, one or more pairs of complex conjugated eigenvalues will not cross the imaginary axis from left to right thus increasing the dimension of the unstable manifold of the equilibrium solution.

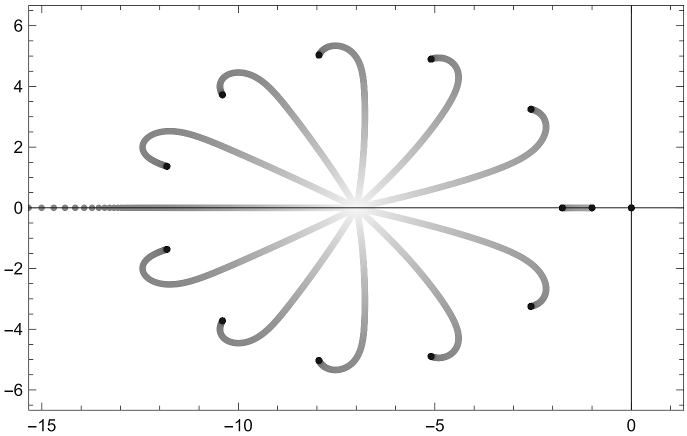

Fig. 3 Plot of the eigenvalues of the jacobians $DF(U^*)$ with $N = 10$, kr from 0 (light gray) to 10^5 (black). The real eigenvalue with largest absolute value gets out of the chosen window for kr large enough. As follows from (32) and Lemmas 2 and 3, the behaviour illustrated herein holds true for all values of N, k and r, with $\alpha/r = \mu^*$

Numerical evidence, some presented next in Sect. 3.3, lead us to conjecture that this is not the case.

Conjecture 3 *With the assumptions and notation of Theorem* 2 *we have that for all* $\alpha/r \in (0, \mu^*)$ *and all* $kr > 0$, *the unstable manifold of all equilibria* U^{2*} *has dimension one.*

3.3 Numerical Illustrations and Explorations of the Spectra of the Reduced System

In this subsection we start, in Figs. 3, 4 and 5, by presenting, for several values of the parameters α/r and kr, and for some dimensions $N + 5$ of the system, numerical evidence illustrating the results about the eigenvalues of the jacobian matrices DF computed at the equilibria of Eq. (18) that were proved in lemmas 2, 3, and Theorem 2. Then in Fig. 6 we present a situation providing support for Conjecture 3. Finally, in Fig. 7, we illustrate the behaviour of the eigenvalue of the jacobians $DF(U^{j*})$ with smaller absolute value, which allows for a better understanding of the spectra close to the bifurcation value μ^*.

The first evidence to be presented corresponds to cases with $\alpha/r = \mu^*$. In these cases there is a single equilibrium U^*, which is the saddle-node bifurcation point of the system. We present the plots of the numerical computed eigenvalues of the Jacobian $DF(U^*)$ of Eq. (18) at U^*. Figure 3 shows the spectra of this matrix for the reduced system with $N = 10$ (hence with dimension $N + 5 = 15$) for several values of kr from 0 to 10^5. The eigenvalues corresponding to small values of kr are ploted in light gray and cases with larger values of kr become progressively darker. The eigenvalues in the case of $kr = 10^5$ is represented by the black dots. Note the existence of a (black) point at the origin: this corresponds to the zero eigenvalue, whose existence and simplicity, for all $kr \geq 0$, was established in Lemma 2.

In Fig. 4 the same plot is presented for the case $N = 25$ and kr from 0 to 10. The reduced range of values for kr is only due to the fact that bigger N implies a much larger computational effort in the computation of the spectra and is not relevant as the goal of these pictures is only to illustrate the behaviour of the spectra whose main characteristic of staying in the left

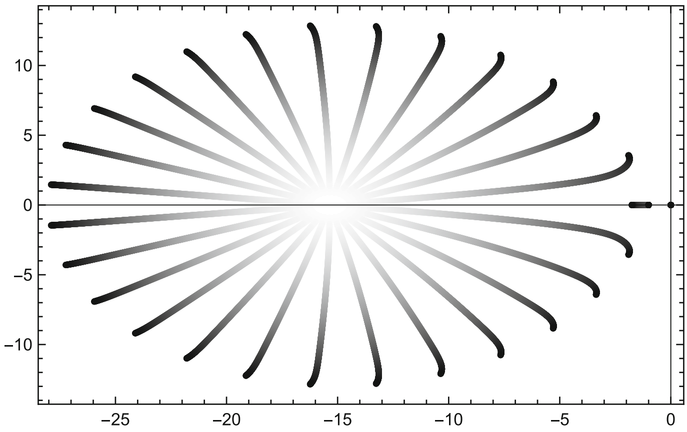

Fig. 4 Plot of the eigenvalues of the jacobians $DF(U^*)$ with $N = 25$, kr from 0 (light gray) to 10 (black). As in Fig. 3, the behaviour illustrated therein was proved to hold for all values of the parameters by (32) and lemmas 2 and 3

half plane for all values of the parameters was already rigorously proved above in Sect. 3.2 for the full range $kr \geq 0$.

In both cases of Figs. 3 and 4 it is clear that except for the zero eigenvalue, all other eigenvalues have negative real parts and seem to remain bounded away from the imaginary axis when kr increases. Other experiments, for other values of N, exhibit the same behaviour.

If $\alpha/r < \mu^*$ the corresponding numerical experiments for the spectra of the jacobian matrices $DF(U^{j*})$ about the two equilibria U^{j*}, with $j = 1, 2$ (using the notation of Theorem 2), show a similar behaviour, except for the eigenvalue which was zero in the previous case (when $\alpha/r = \mu^*$) and is now negative for $j = 1$ and positive for $j = 2$. This is illustrated in Figs. 5 and 6, respectively. In both cases all other eigenvalues stay with negative real parts for all values of the parameters, in accordance with Theorem 2 and, in the case of Fig. 6, also lending support to Conjecture 3. Observe that in Fig. 6 the eigenvalue that is zero when $kr = 0$ becomes real positive when $kr > 0$ but hardly moves at all. This behaviour is shown more clearly in the insert in the right side of Figs. 6 and 7.

The final plot, in Fig. 7, shows, in a window with y^{j*} between 0.75 and 0.98, the values of the eigenvalue of $DF(U^{j*})$ that is zero at the bifurcation point (μ^*, y^*) when $kr \in [0, 100]$. Superimposed to the graph we plot lines highlighting those eigenvalues for values of y at the equilibria U^{1*} and U^{2*} when α/r equals 2.746 (dotted line) and 2.436 (dashed lines). The full line is the zero eigenvalue of the critical equilibrium U^* (with $y = y^*$), which corresponds to $\alpha/r = \mu^* \approx 2.881$. Observe that the eigenvalues change very steeply from the zero eigenvalue when kr is very close to 0 but then they remain essentially independent of kr and never stray very far from the origin, as has already been observed in Figs. 5 and 6.

4 Local Dynamics of the Infinite Dimension Silicosis System (5)

We shall now use the results about the stability properties of equilibria of the finite dimensional reduced system (18) obtained in Sect. 3.3 to draw conclusions about the stability properties of the infinite dimensional system (5) in the phase space X. This is done in the next two theorems.

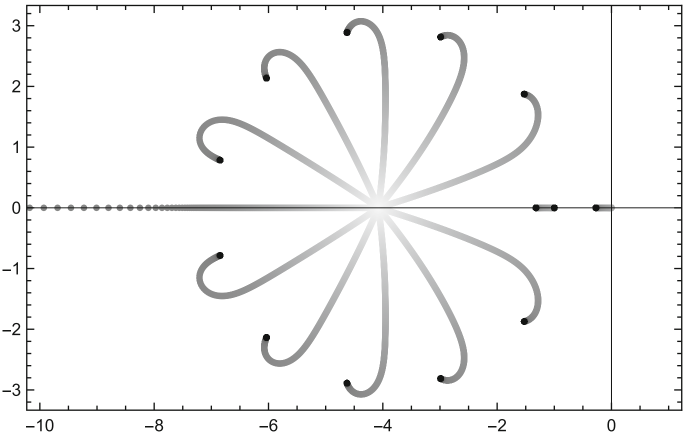

Fig. 5 Plot of the eigenvalues of the jacobians $DF(U^{1*})$ with $N = 10$, $\alpha/r = 2.44$, kr from 0 (light gray) to 10^5 (black). Observe the eigenvalue close to the origin starts at the origin when $kr = 0$ and moves slowly to the left half plane as kr increases. The real negative eigenvalue of largest absolute value gets out of the chosen window for kr large enough

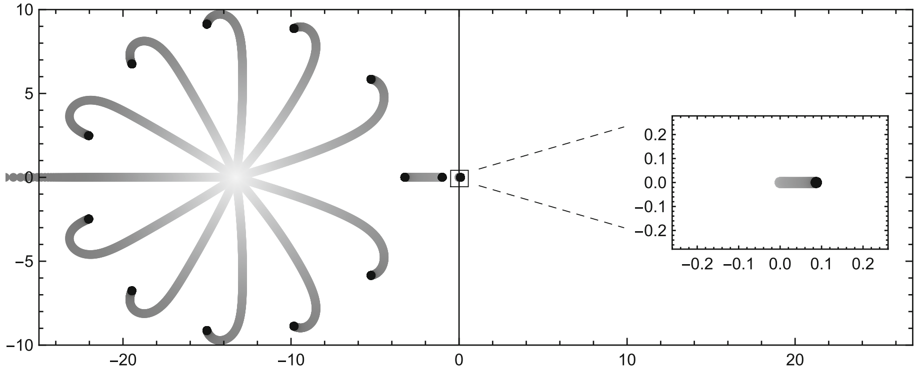

Fig. 6 Plot of the eigenvalues of the jacobians $DF(U^{2*})$ with $N = 10$, $\alpha/r = 2.44$, kr from 0 (light gray) to 10^5 (black). Observe that the eigenvalue close to the origin starts at the origin when $kr = 0$ and moves very slowly to the right half plane as kr increases as is clearly visible in the zoomed in insert in the right of the figure. The real negative eigenvalue of largest absolute value gets out of the chosen window for kr large enough

Theorem 4 *Let $\alpha/r < \mu^*$ and let $\widetilde{U}^{eq} = (x^{eq}, M_0^{eq}, M_1^{eq}, \ldots)$ be an equilibrium solution of (5) such that the corresponding equilibrium of the $(N+5)$-dimensional system (18), $U^{eq} = (U_1^{eq}, \ldots, U_{N+5}^{eq})$, is locally exponentially asymptotically stable. Then, $\widetilde{U}^{eq}$ is a locally asymptotically stable solution of (5) in the strong topology of X.*

Proof Remember that the silicosis system (5) is equivalent to the infinite system (17) with restrictions (13). To every point $\widetilde{U} = (x, M_0, M_1, \ldots) \in X_+$ there corresponds a unique $U = (x, u, v, w, M_0, \ldots, M_N) \in \mathbb{R}_+^{N+5}$. By what was done in Sect. 2 we know that there exists an open set $\Omega \subset \mathbb{R}^{N+5}$ containing U^{eq} such that for every initial condition in Ω the corresponding solution of the $(N+5)$-dimensional system (18) converges to U^{eq} when $t \to +\infty$. In particular, for those initial conditions, we have that $x(t) \to x^{\mathrm{eq}}$ and $M_i(t) \to M_i^{\mathrm{eq}}$ as $t \to +\infty$ for all $i = 0, \ldots, N$. Using this in the equations in (5) for M_i with $i > N$ we

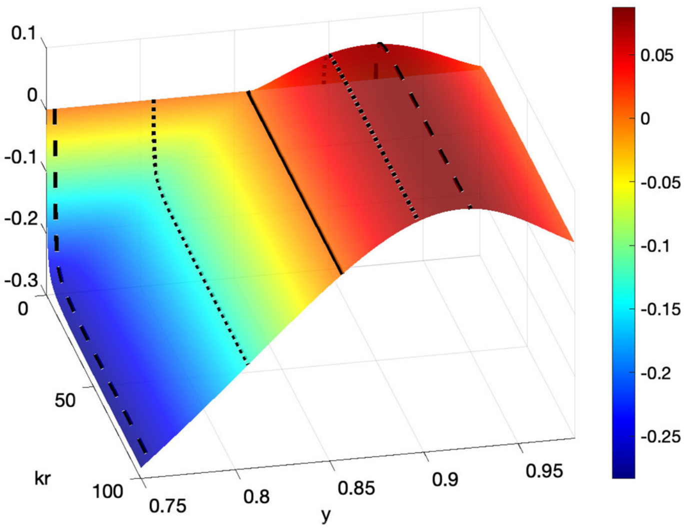

Fig. 7 Plot of the eigenvalue of the jacobians $DF(U^{j*})$ with smaller absolute value, when $N = 10$, $kr \in [0, 100]$, and y in $[0.75, 0.98]$. Superimposed to the graph we plot lines showing the values of y at the equilibria U^{1*} and U^{2*} for values of α/r equal to 2.746 (dotted line) and 2.436 (dashed lines). The full line is the value of y^* of the critical equilibrium U^*, which corresponds to $\alpha/r = \mu^* \approx 2.881$. For any given value of $\alpha/r < \mu^*$ the line corresponding to U^{1*} is always to the left of that of U^{2*}

conclude that all components of the solution $\widetilde{U} = (x, M_0, M_1, \ldots)$ converge exponentially to the corresponding components of $\widetilde{U}^{\text{eq}} = (x^{\text{eq}}, M_0^{\text{eq}}, M_1^{\text{eq}}, \ldots)$ when $t \to +\infty$.

Observe that, from the definition of the variables u and v in (13), we conclude that, if $\widetilde{U} = (x, M_0, M_1, \ldots)$ is a nonnegative solution of (5) in $[0, +\infty)$, then, for all $t \geq 0$, the norm of $\widetilde{U}(t)$ can be written in the form

$$\|\widetilde{U}(t)\| = x(t) + u(t) + v(t) + \sum_{i=0}^{N} i M_i(t). \tag{34}$$

Let $B_\varepsilon \subset X_+$ be an open ball of radius ε centered at the equilibrium $\widetilde{U}^{\text{eq}}$. Take an initial condition $\widetilde{U}(0) \in B_\varepsilon$. Then, since

$$\Big| \|\widetilde{U}(0)\| - \|\widetilde{U}^{\text{eq}}\| \Big| \leq \|\widetilde{U}(0) - \widetilde{U}^{\text{eq}}\| < \varepsilon,$$

the equality (34) with $t = 0$ implies that, if we choose ε small enough, the corresponding initial condition $U(0)$ for the $(N+5)$-dimensional system (18) will be in Ω.

Hence, for small enough ε, to every initial condition $\widetilde{U}(0) \in B_\varepsilon \subset X_+$ corresponds a vector $U(0) \in \mathbb{R}_+^{N+5}$ in Ω, and so, the solution $\widetilde{U}(\cdot)$ of (5) satisfies $\|\widetilde{U}(t)\| \to \|\widetilde{U}^{\text{eq}}\|$ exponentially as $t \to +\infty$. This, together with the componentwise convergence of $\widetilde{U}$ to $\widetilde{U}^{\text{eq}}$, implies, by a standard result (see, e.g., [2, Lemma 3.3]), that $\widetilde{U}(t) \to \widetilde{U}^{\text{eq}}$ strongly in X as $t \to +\infty$. □

Theorem 5 *Under the assumptions of Theorem 4 the solutions of (5) that converge in the strong topology of X to the locally asymptotically stable solution* $\widetilde{U}^{eq}$ *do so at an exponential rate.*

Proof Let $\widetilde{U}(t) \to \widetilde{U}^{\text{eq}}$ in X, as $t \to +\infty$. We know that each component of $\widetilde{U}(t)$ converges exponentially to the corresponding component of $\widetilde{U}^{\text{eq}}$. To prove the theorem we need to show that $\|\widetilde{U}(t) - \widetilde{U}^{\text{eq}}\|$ converges exponentially fast to zero as $t \to +\infty$. First, we have to prove the same holds for the ℓ^1 norm.

From (5), we obtain

$$\frac{d}{dt}(M_0 - M_0^{\text{eq}}) = -(1 + kx^{\text{eq}})(M_i - M_i^{\text{eq}}) - kM_0(x - x^{\text{eq}}),$$

and, for each $i \geq 1$,

$$\frac{d}{dt}(M_i - M_i^{\text{eq}}) = -(1 + kx^{\text{eq}})(M_i - M_i^{\text{eq}}) \\ + kx^{\text{eq}}(M_{i-1} - M_{i-1}^{\text{eq}}) - k(M_i - M_{i-1})(x - x^{\text{eq}}).$$

For each $t > 0$ and integer $i \geq 0$ define

$$\delta_i(t) := M_i(t) - M_i^{\text{eq}}(t), \quad \varphi_i(t) := \left(x^{\text{eq}}\right)^{-1} M_i(t)\left(x(t) - x^{\text{eq}}\right).$$

Changing the time variable t(18), denoting by $(\cdot)'$ the derivarive $\frac{d}{d\tau}$, and defining $\beta := \frac{1}{kx^{\text{eq}}}$, the system above can be written as

$$\delta_0' = -(1 + \beta)\delta_0 - \varphi_0(\tau) \tag{35}$$

and

$$\delta_i' = -(1 + \beta)\delta_i + \delta_{i-1} - \varphi_i(\tau) + \varphi_{i-1}(\tau), \quad i = 1, 2, \ldots \tag{36}$$

Note that system (35)–(36) can be solved recursively, starting with the equation for δ_0 and then sequentially for δ_i for $i = 1, 2, \ldots$, since the equation for δ_i only depends on the components of the solutions with $j \leq i$. So, consider the $(n + 1)$-dimensional system for the vector of displacements $\boldsymbol{\delta}_n = (\delta_0, \delta_1, \ldots, \delta_n)^T$,

$$\boldsymbol{\delta}_n' = J_{n+1}\boldsymbol{\delta}_n + \boldsymbol{\Phi}_n(\tau), \tag{37}$$

where $\boldsymbol{\Phi}_n = (\Phi_i)_{i=0,\ldots,n}^T$ with $\Phi_0 = -\varphi_0$ and $\Phi_i = -\varphi_i + \varphi_{i-1}$ if $i \geq 1$, and J_{n+1} is the $(n + 1)$-dimensional Jordan matrix

$$J_{n+1} := \begin{bmatrix} -(1+\beta) & & & & \\ 1 & -(1+\beta) & & & \\ & 1 & -(1+\beta) & & \\ & & \ddots & \ddots & \\ & & & 1 & -(1+\beta) \end{bmatrix}. \tag{38}$$

The solution of (37) is given by the variation of constants formula

$$\boldsymbol{\delta}_n(\tau) = e^{J_{n+1}\tau}\boldsymbol{\delta}_n(0) + \int_0^\tau e^{J_{n+1}(\tau - s)}\boldsymbol{\Phi}_n(s)ds \tag{39}$$

and we now estimate each of the terms in the right-hand side of this expression separately.

For the first term in the right-hand side of (39) we have

$$e^{J_{n+1}\tau}\boldsymbol{\delta}_n(0) = e^{-(1+\beta)\tau}\begin{bmatrix} 1 & 0 & 0 & \cdots 0 \\ \tau & 1 & 0 & \cdots 0 \\ \frac{\tau^2}{2!} & \tau & 1 & \cdots 0 \\ \vdots & \vdots & \vdots & \ddots \vdots \\ \frac{\tau^n}{n!} & \frac{\tau^{n-1}}{(n-1)!} & \frac{\tau^{n-2}}{(n-2)!} & \ldots 1 \end{bmatrix}\begin{bmatrix}\delta_0(0)\\ \delta_1(0)\\ \delta_2(0)\\ \vdots \\ \delta_n(0)\end{bmatrix}$$
$$= e^{-(1+\beta)\tau}\begin{bmatrix} \delta_0(0) \\ \tau\delta_0(0)+\delta_1(0) \\ \frac{\tau^2}{2!}\delta_0(0)+\tau\delta_1(0)+\delta_2(0) \\ \vdots \\ \frac{\tau^n}{n!}\delta_0(0)+\frac{\tau^n}{n!}\delta_0(0)+\cdots+\tau\delta_{n-1}(0)+\delta_n(0)\end{bmatrix}$$

and hence

$$\begin{aligned}\left\| e^{J_{n+1}\tau}\boldsymbol{\delta}_n(0)\right\|_{\ell^1} &\leq e^{-(1+\beta)\tau}\sum_{j=0}^{n}\Big(\sum_{k=0}^{j}\frac{\tau^k}{k!}\left|\delta_{j-k}(0)\right|\Big) \\ &= e^{-(1+\beta)\tau}\sum_{k=0}^{n}\frac{\tau^k}{k!}\sum_{p=0}^{n-k}\left|\delta_p(0)\right| \\ &\leq e^{-(1+\beta)\tau}e^{\tau}\left\|\boldsymbol{\delta}(0)\right\|_{\ell^1} = e^{-\beta\tau}\left\|\boldsymbol{\delta}(0)\right\|_{\ell^1}, \end{aligned} \tag{40}$$

where $\boldsymbol{\delta}(0) := (\delta_0(0), \delta_1(0), \delta_2(0), \ldots)^T$.

For the second term in the right-hand side of (39) we can write

$$\begin{aligned}&\int_0^{\tau} e^{J_{n+1}(\tau-s)}\boldsymbol{\Phi}_n(s)ds \\ &= \int_0^{\tau} e^{-(1+\beta)(\tau-s)}\begin{bmatrix} 1 & 0 & 0 & \cdots 0 \\ (\tau-s) & 1 & 0 & \cdots 0 \\ \frac{(\tau-s)^2}{2!} & (\tau-s) & 1 & \cdots 0 \\ \vdots & \vdots & \vdots & \ddots \vdots \\ \frac{(\tau-s)^n}{n!} & \frac{(\tau-s)^{n-1}}{(n-1)!} & \frac{(\tau-s)^{n-2}}{(n-2)!} & \ldots 1\end{bmatrix}\begin{bmatrix}\Phi_0(s)\\ \Phi_1(s)\\ \Phi_2(s)\\ \vdots \\ \Phi_n(s))\end{bmatrix} ds \\ &= \int_0^{\tau} e^{-(1+\beta)(\tau-s)}\begin{bmatrix}\Phi_0(s) \\ (\tau-s)\Phi_0(s)+\Phi_1(s) \\ \frac{(\tau-s)^2}{2!}\Phi_0(s)+(\tau-s)\Phi_1(s)+\Phi_2(s) \\ \vdots \\ \frac{(\tau-s)u^n}{n!}\Phi_0(s)+\frac{(\tau-s)^n}{n!}\Phi_1(s)+\cdots+(\tau-s)\Phi_{n-1}(s)+\Phi_n(s)\end{bmatrix} ds, \end{aligned} \tag{41}$$

and hence

$$\left\|\int_0^{\tau} e^{J_{n+1}(\tau-s)}\boldsymbol{\Phi}_n(s)ds\right\|_{\ell^1} \leq \int_0^{\tau} e^{-(1+\beta)(\tau-s)}\sum_{j=0}^{n}\sum_{k=0}^{j}\frac{(\tau-s)^k}{k!}\left|\Phi_{j-k}(0)\right| ds$$

$$
\begin{aligned}
&= \int_0^\tau e^{-(1+\beta)(\tau-s)} \sum_{k=0}^{n} \frac{(\tau-s)^k}{k!} \sum_{p=0}^{n-k} \left|\Phi_p(0)\right| ds \\
&\le \int_0^\tau e^{-(1+\beta)(\tau-s)} e^{\tau-s} \left\|\boldsymbol{\Phi}(s)\right\|_{\ell^1} ds \\
&= \int_0^\tau e^{-\beta(\tau-s)} \left\|\boldsymbol{\Phi}(s)\right\|_{\ell^1} ds, \qquad (42)
\end{aligned}
$$

where $\boldsymbol{\Phi} := (\Phi_i)^T_{i\in\mathbb{N}_0}$. To estimate $\|\boldsymbol{\Phi}(s)\|_{\ell^1}$ observe that, because we have, for each $t \ge 0$, $\widetilde{U} = (x, M_0, M_1, \ldots) \in X \subset \ell^1$, and each component converges exponentially to the corresponding component of the limit equilibrium $\widetilde{U}^{\text{eq}}$, and thus, in particular, $|x(\tau) - x^{\text{eq}}| \le C_1 e^{-\eta\tau}$ for some $C_1, \eta > 0$, and all $\tau > 0$, so that we get

$$
|\Phi_0(s)| = |-\varphi_0(s)| = \frac{1}{x^{\text{eq}}} |M_0(s)| \left|x(s) - x^{\text{eq}}\right| \le \frac{C_1}{x^{\text{eq}}} e^{-\eta s} |M_0(s)|, \qquad (43)
$$

and, for $i \ge 1$,

$$
\begin{aligned}
|\Phi_i(s)| &= |-\varphi_i(s) + \varphi_{i-1}| \le |\varphi_i(s)| + |\varphi_{i-1}| \\
&\le \frac{C_1}{x^{\text{eq}}} e^{-\eta s}\Big(|M_i(s)| + |M_{i-1}(s)|\Big). \qquad (44)
\end{aligned}
$$

Thus

$$
\|\boldsymbol{\Phi}(s)\|_{\ell^1} = \sum_{i=0}^{\infty} |\Phi_i(s)| \le \frac{2C_1}{x^{\text{eq}}} \left\|\widetilde{U}(s)\right\|_{\ell^1} e^{-\eta s} \le \frac{C_2}{x^{\text{eq}}} e^{-\eta s}, \qquad (45)
$$

where $C_2 \ge 2C_1 \max_{s\ge 0}\left\{\left\|\widetilde{U}(s)\right\|, \left\|\widetilde{U}^{\text{eq}}\right\|\right\}$, and the maximum exists by the result about convergence in Theorem 4. Hence, plugging (45) into (42), we conclude that

$$
\left\| \int_0^\tau e^{J_{n+1}(\tau-s)} \boldsymbol{\Phi}_n(s) ds \right\|_{\ell^1} \le \begin{cases} C_2 \tau e^{-\beta\tau}, & \text{if} \quad \eta = \beta \\ \frac{C_2}{|\beta-\eta|} e^{-\min\{\eta,\beta\}\tau}, & \text{if} \quad \eta \ne \beta, \end{cases} \qquad (46)
$$

which, together with (40), allow us to write, for all $\tau \ge 0$,

$$
\|\boldsymbol{\delta}(\tau)\|_{\ell^1} \le e^{-\beta\tau} \|\boldsymbol{\delta}(0)\|_{\ell^1} + \begin{cases} C_2 \tau e^{-\beta\tau}, & \text{if} \quad \eta = \beta \\ \frac{C_2}{|\beta-\eta|} e^{-\min\{\eta,\beta\}\tau}, & \text{if} \quad \eta \ne \beta. \end{cases} \qquad (47)
$$

Let us now consider convergence in the norm of X. Since

$$
\begin{aligned}
\|\boldsymbol{\delta}(\tau)\| &= \left|x(\tau) - x^{\text{eq}}\right| + \sum_{i=0}^{\infty} (i+1) |\delta_i(\tau)| \\
&= \left|x(\tau) - x^{\text{eq}}\right| + \|\boldsymbol{\delta}(\tau)\|_{\ell^1} + \|\boldsymbol{\xi}(\tau)\|_{\ell^1}, \qquad (48)
\end{aligned}
$$

where $\boldsymbol{\xi} = (\xi_i) := (i\delta_i)$. Multiplying (36) by i we get the system for ξ_i:

$$
\xi_i' = -(1+\beta)\xi_i + \xi_{i-1} + \Psi_i(\tau), \quad i = 1, 2, \ldots
$$

where $\Psi_i(\tau) := \delta_{i-1}(\tau) + i\Phi_i(\tau)$, for $i \ge 1$, and $\xi_0(\tau) \equiv 0$. Again, like (36) this system can be solved recursively for $i = 1, 2, \ldots$, because the equation for ξ_i only depends on information with $j \le i$, and so, similarly to what was done before, we can consider a finite n-dimensional system for the vector $\boldsymbol{\xi}_n = (\xi_1, \ldots, \xi_n)^T$,

$$
\boldsymbol{\xi}_n' = J_n \boldsymbol{\xi}_n + \boldsymbol{\Psi}_n(\tau),
$$

where $\boldsymbol{\Psi}_n = (\Psi_i)^T_{i=1,\ldots,n}$, and J_n is the n-dimensional Jordan matrix with the form (38). Now computations analogous to those done previously give the following decay estimate for $\|\boldsymbol{\xi}(\tau)\|_{\ell^1}$ for τ sufficiently large:

$$\|\boldsymbol{\xi}(\tau)\|_{\ell^1} \leq e^{-\beta\tau} \|\boldsymbol{\xi}(0)\|_{\ell^1} + \begin{cases} C_3\tau e^{-\beta\tau}, & \text{if} \quad \eta > \beta \\ C_4\tau^2 e^{-\beta\tau}, & \text{if} \quad \eta = \beta. \\ C_5 e^{-\eta\tau}, & \text{if} \quad \eta < \beta, \end{cases}$$

where the constants C_j are independent of τ. This, together with (47), the exponential decay bound for $|x(\tau) - x^{\text{eq}}|$, and (48), allow us to conclude that $\|\boldsymbol{\delta}(\tau)\|$ converge exponentially fast to zero when $\tau \to +\infty$ which, recalling that $\tau = kx^{\text{eq}}t$, proves the theorem. □

5 Conclusion and Discussion

In this paper we studied the local stability of equilibria of the model (5) for the silicosis disease, which is a particular case of a more general model (1)–(3) when the special class of piecewise constant parameters (4) is considered, which can be biologically interpreted as the existence of a uniform effectiveness of quartz ingestion by macrophages, independently of the macrophage's quartz load, and of a letal load of quartz particles per macrophage, as explained in the Introduction immediately after (4).

With these assumptions it was known from [3] that the balance between the input rates of silica and of new macrophages, α and r respectively, determine the existence (when α/r is below a certain threshold μ^*) or non-existence (when it is above) of equilibria of the infinite dimensional system (5), as presented in the bifurcation diagram in Fig. 2.

We proved that, for each α/r below the critical value μ^*, the equilibrium with smaller value of x is always a locally exponentially asymptotically stable solution of (5) in the strong topology of the space $X \subset \ell^1$ of sequences with finite number of particles per unit volume introduced in [4]. We prove also that the equilibrium solutions with larger values of x are unstable.

This stability result is proved by considering an appropriate change of variables (13) that allow us to write (5) in the form (17) in which a closed finite dimensional subsystem can be identified. The analysis of the eigenvalues of the linearizations of this finite dimensional system about the equilibria is done by writing the determinant of the jacobian as the sum of a term independent of the product kr with another which is zero when this product is zero. A careful study of each of these terms, together with a continuity argument from the case $kr = 0$ to $kr > 0$ allow us to complete the analysis of the finite dimensional system for all parameter values, which is the crucial step to prove the stability properties of the equilibria of the original infinite dimensional model. It is interesting to observe that although the case $kr = 0$ (i.e., $k = 0$, since α/r is assumed to take always real positive values) is not biologically reasonable, as it corresponds to the imune system being inactive (see Sect. 1, and in particular Figure 1 with $k_j \equiv k = 0$), the argument used is based in a careful perturbation argument for the jacobian polynomial when $kr = 0$.

One should realize that the immune system is exceedingly complex and mathematical models of parts of it, such as the one presented here, which, as pointed in the Introduction, was based on the model in [11], or even subparts of it such as the mucociliary escalator [12], are bound to be mere caricatures when, in many cases, even the basic Biology is still the subject of current research (see, e.g., [8, 9]). Thus, the discussion of the biological interpretation of the mathematical results proved in this paper have to be considered with the necessary circumspection.

To biologically interpret the stability result we observe that, having a constant input rate α of silica particles into the system, the only way the system can converge to a non-negative steady state (with a finite concentration x^{eq} of silica particles) is if the mechanism eliminating silica particles by transporting them inside the macrophages through the mucociliary escalator off the respiratory system is highly efficient. From the results in this paper, this can only occur in this model if both the following conditions hold: (i) the rate of input of macrophages r is sufficiently large compared with the input rate of silica α (so that α/r is below the threshold μ^*), and (ii) the initial load of silica in the system is sufficiently small, so that the initial condition is inside the basin of attraction of the asymptotically stable equilibrium. If at least one of these conditions fails to hold, then solutions to (5) do not converge to an equilibrium (which do not even exist if (i) fails). The rigorous study of what happens in those cases is still lacking. However, preliminary numerical studies (not presented in this paper) suggest that, in those cases, solutions are such that $x(t)$ increase without bound. This unbounded increase in the amount of silica dust in the respiratory system is the way this model expresses the fatal run off of the amount of crystalline quartz dust in the lungs leading to death.

It is an interesting mathematical open problem to study this run off regime and to investigate if it corresponds to some self-similar regime, as is the case in other types of coagulation equations with inputs [5–7].

Other mathematically interesting open problems arise by considering systems (1)–(3) with more general rate coefficients k_i, p_i and q_i, in particular those satisfying power laws in the variable i considered in [3]. The study of those systems will require a more precise enquiry into the exact number of equilibria than was achieved in [3] and, likely, a different way to attack the stability problem in the infinite dimensional system (1)–(3), as the trick of using a change of variables to decouple the system into a closed finite dimensional subsystem determining the dynamics is unlikely to be applicable in the general case. However, based on the results about the structure of equilibria proved in [3], we expect the results in this paper to extend to systems with more general coefficients satisfying power law assumptions.

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Declarations

Conflict of interest The authors declare no competing financial interests.

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