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AN AGE-STRUCTURED TWO-STRAIN EPIDEMIC MODEL WITH SUPER-INFECTION

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Dedicated to Horst R. Thieme on Occasion of his 60th Birthday

Abstract. This article focuses on the study of an age-structured two-strain model with super-infection. The explicit expression of basic reproduction numbers and the invasion reproduction numbers corresponding to strain one and strain two are obtained. It is shown that the infection-free steady state is globally stable if the basic reproductive number R_0 is below one. Existence of strain one and strain two exclusive equilibria is established. Conditions for local stability or instability of the exclusive equilibria of the strain one and strain two are established. Existence of coexistence equilibrium is also obtained under the condition that both invasion reproduction numbers are larger than one.

1. Introduction.

Understanding pathogens' ability to respond to selective pressures and change their genetic make-up is the key to combating numerous infectious diseases. Mathematical modeling can aid that process by providing insight into the mechanisms that sustain microorganisms' genetic diversity. Mechanisms allowing a strain that would normally be excluded to coexist with a competitively dominant strain are called trade-off mechanisms. Trade-off mechanisms have been widely investigated in the literature, particularly through ordinary differential equation models. Super-infection (one of the strains takes over immediately a host infected with another strain) [23, 20], co-infection (a host can be infected with two strains for prolonged period of time) [21], cross-immunity (infection with one strain in part protects against infection with another, after recovery from the first) [8, 9], mutation (one of the strains mutates into the other) [4], host density-dependent mortality [3] have all been identified to support coexistence of pathogen variants. More recently Dhirasakdanon and Thieme establish that a vertically transmitted strain may coexist with a more virulent horizontally transmitted strain either in a coexistence equilibrium or in an oscillatory regime [10, 11]. Because of their paramount importance in biology and public health, multi-strain models attract

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significant attention. Results of these research efforts have been summarized in three topical reviews [15, 19, 26].

Biological theory postulates that multiple competitors cannot coexist on a single resourse unless that resourse is heterogenous in some respect. Horst Thieme, whose profound contributions to theory and modeling in biology we celebrate on occasion of his 60th birthday, has been intrumental in the early justification of this principle in mathematical epidemiology. The main result on competitive exclusion of pathogen strains, established by Bremmerman and Thieme [5], shows that in the simplest epidemiological ordinary differential equation model with multiple strains, the strain with the largest reproduction number will persist and eliminate the remaining strains. Heterogeneity of the resourse may allow multiple competitors to coexist, if they can partition the resourse and persist in different niches. Consequently, heterogeneity of the host in age or space can be expected to allow for the coexistence of multiple pathogen variants. This hypothesis has been justified in the case of age heterogeneity of the host [18].

One of the important problems in development of infectious disease theory is the impact of host and pathogen heterogeneity on the dynamics of the disease. There is extensive research on the development and analysis of age-structured epidemic models in the study of the dynamics of the deseases in humans [2, 12, 31, 14]. The main question addressed through age-structured epidemic models is whether host age-structure, chronological or disease-induced, may lead to loss of stability of the endemic equilibrium and sustained oscillations. The question stems from the observation that the incidence of some childhood diseases follow seasonal pattern (see Fig. 6.3 in [2]). Several articles, all of which authored or co-authored by Horst Thieme, contribute significantly to the study of this question, particularly in the one-strain case. The first key result establishes (using the tools of semigroup theory) that in the most basic S-I-S age-structured single-strain epidemic model the unique endemic equilibrium is globally stable and sustained oscillations do not occur [6]. Thus, host age-structure by itself is not sufficient for sustained oscillations. However, Horst Thieme showed that in a simple age-structured S-I-R model sustained oscillations may occur [25]. Furthermore, Thieme and Castillo-Chavez [29, 30] showed that age-since-infection structure may also destabilize the endemic equilibrium and lead to oscillations in an HIV/AIDS epidemic model. Their results were numerically confirmed by Milner and Pugliese [22].

To acknowledge and celabrate Horst Thieme's contributions to mathematical biology, in this paper we introduce a two-strain version of the model discussed by Busenberg, Iannelli and Thieme in [6]. We include super-infection, as the most straight-forward extention of the single-strain S-I-S model in [6] is a model, nested in the one considered in this article. Our two-strain age-structured S-I-S model with super-infection is introduced in Section 2. As in [6] the total population size is modeled by a linear age-structured McKendrick-von Foerster model whose growth rate is assumed to be zero. Section 2 also contains rescaling and recasting of the original model. Section 3 introduces the disease-free equilibrium, and establishes its local and global stability. Section 4 determines the local stability of the single strain equilibria. Section 5 establishes rigorously the presence of a coexistence equilibrium. The mathematical tools, necessary for this task are somewhat different than the ones previously used in the age-since-infection structured multi-strain models. Section 6 summarizes our results and outlines our goals for future work on the present model.

2. The model formulation.

In this section, we introduce an age-structured two-strain model with super-infection. The total population $P(a,t)$ is divided into three classes: susceptible $S(a,t)$, infected with strain one $I(a,t)$, and infected with strain two $J(a,t)$. Susceptible individuals can become infected by strain one and move to the class $I(a,t)$, or infected by strain two and move to the class $J(a,t)$. We assume that those infected with strain two can come into a contact with infectious individuals with strain one and become super-infected with the first strain. This process is referred to as *super-infection.* We take the transmission rate $\lambda_1(a,t)$ in the separable intercohort constitutive form for the force of infection generated by $I(a,t)$:

$$\lambda_1(a,t) = k(a)\int_0^\infty h_1(a)I(a,t)da,$$

where $h_1(a)$ is the age-specific infectiousness for strain one, and $k(a)$, the age-specific susceptibility of susceptible individuals. We note that in essence what we have assumed is that the age-specific contact rate of individuals age a with individuals age b is separable: $c(a,b) = c_1(a)c_2(b)$. The assumption for separability of the contact rates is important part of our results. Without it different techniques may be necessary to treat the problem. The term $c_1(a)$ can be absorbed in the coefficient $k(a)$, while the term $c_2(b)$ is absorbed into the function $h_1(a)$. Similarly, we take $\lambda_2(a,t)$ in the separable intercohort constitutive form for the force of infection generated by $J(a,t)$:

$$\lambda_2(a,t) = k(a)\int_0^\infty h_2(a)J(a,t)da,$$

where $h_2(a)$ is the age-specific infectiousness for strain two. In this article we assume that the susceptibilities for the two strains are the same and given by $k(a)$ but our results can be easily and trivially extended to the case when they are different, that is $k_1(a) \neq k_2(a)$. The functions $h_i(a), k(a)$ have compact support and satisfy:

$$\begin{aligned} k(a), h_i(a) \in L^1(0,\infty), \quad & k(a), h_i(a) \geq 0 \quad \text{on} \quad [0,A] \\ \text{and} \quad k(a), h_i(a) = 0 \qquad & \text{for} \quad a > A \qquad \text{where} \quad i = 1,2. \end{aligned}$$

Furthermore, we assume that these functions are bounded with:

$$\bar{k} = \sup_{a\in[0,\infty)} k(a), \qquad \bar{h}_i = \sup_{a\in[0,\infty)} h_i(a), \qquad \text{for} \quad i = 1,2.$$

The transmission coefficient in the case of super-infection is $\delta\lambda_1(a,t)$, where δ is the coefficient of reduction or enhancement of infection at super-infection. In particular, if $\delta > 1$ then super-infection is more likely than the regular infection while if $0 < \delta < 1$ then super-infection is less likely than the regular infection. If $\delta = 0$ there is no super-infection. We assume that all newborns are susceptible and that an individual may become infected only through contact with an infectious individual. We also assume that the disease-induced death rate can be neglected. With these assumptions and $\delta = 0$ our model is a straight-forward two-strain extension of the model in [6], while with $\delta > 0$ our model is a two-strain extension with super-infection. The joint dynamics of the age-structured epidemiological SIS model are governed by the following partial differential equation problem:

$$\begin{cases} \dfrac{\partial S(a,t)}{\partial a} + \dfrac{\partial S(a,t)}{\partial t} = -\mu(a)S(a,t) - \lambda_1(a,t)S(a,t) - \lambda_2(a,t)S(a,t) \\ \qquad\qquad\qquad\qquad +\gamma_1(a)I(a,t) + \gamma_2(a)J(a,t), \\ \dfrac{\partial I(a,t)}{\partial a} + \dfrac{\partial I(a,t)}{\partial t} = -(\mu(a)+\gamma_1(a))I(a,t) + \lambda_1(a,t)S(a,t) + \delta\lambda_1(a,t)J(a,t), \\ \dfrac{\partial J(a,t)}{\partial a} + \dfrac{\partial J(a,t)}{\partial t} = -(\mu(a)+\gamma_2(a))J(a,t) + \lambda_2(a,t)S(a,t) - \delta\lambda_1(a,t)J(a,t), \\ S(0,t) = \displaystyle\int_0^\infty b(a)P(a,t)da, \quad I(0,t) = J(0,t) = 0, \\ S(a,0) = S_0(a), \quad I(a,0) = I_0(a), \quad J(a,0) = J_0(a), \end{cases} \tag{1}$$

where $b(a)$ is the age-specific per capita birth rate and $\gamma_i(a)$ is the age-specific recovery rate from strain i. Summing these equations we obtain the following problem for the total population density $P(a,t) = S(a,t) + I(a,t) + J(a,t)$:

$$\begin{cases} \dfrac{\partial P(a,t)}{\partial a} + \dfrac{\partial P(a,t)}{\partial t} = -\mu(a)P(a,t), \\ P(0,t) = \displaystyle\int_0^\infty b(a)P(a,t)da, \\ P(a,0) = P_0(a). \end{cases}$$

This is the standard age-structured Mckendrick-Von Forester equation [12]. Thus, the disease does not affect the population dynamics. The following hypotheses are typical for this problem:

$$b(a) \in L^\infty[0,\infty), \quad b(a) \geq 0 \text{ in } [0,\infty), \qquad \bar{b} = \sup_{a\in[0,\infty)} b(a).$$

$$\mu(a) \in L^1_{loc}[0,\infty), \quad \mu(a) \geq 0 \text{ in } [0,\infty),$$
$$\int_0^\infty \mu(a)da = \infty,$$

and $b(a)$ is assumed to be zero beyond some maximum age. Since the standard age-structured Mckendrick-Von Forester equation is linear, a steady state (time independent solution) exists only if the population growth rate is zero. Therefore, we assume that the net reproductive rate of the population is equal to unity and that the total population is at an equilibrium. This means that:

$$\int_0^\infty b(a)e^{-\int_0^a \mu(\tau)d\tau}da = 1.$$

Therefore,

$$P(a,t) = P_\infty(a) = b_0 e^{-\int_0^a \mu(\tau)d\tau} \qquad \text{for all } t.$$

This condition also implies that, in order to deal with model (1), we have to take the initial data so that:

$$S_0(a) \geq 0, I_0(a) \geq 0, J_0(a) \geq 0,$$
$$S_0(a) + I_0(a) + J_0(a) = P_\infty(a),$$

which forces the relation:

$$b_0 = \frac{\int_0^\infty P_\infty(a)da}{\int_0^\infty e^{-\int_0^a \mu(\tau)d\tau}da}.$$

Instead of system (1) throughout this article we will work with the normalized system. We introduce the following fractions:

$$s(a,t) = \frac{S(a,t)}{P_\infty(a)}, \quad i(a,t) = \frac{I(a,t)}{P_\infty(a)}, \quad j(a,t) = \frac{J(a,t)}{P_\infty(a)}.$$

We note that the proportions do not exceed one for any value of a and t. We can rewrite system (1) as follows:

$$\begin{cases} \dfrac{\partial s(a,t)}{\partial a} + \dfrac{\partial s(a,t)}{\partial t} = -\lambda_1(a,t)s(a,t) - \lambda_2(a,t)s(a,t) + \gamma_1(a)i(a,t) + \gamma_2(a)j(a,t), \\ \dfrac{\partial i(a,t)}{\partial a} + \dfrac{\partial i(a,t)}{\partial t} = -\gamma_1(a)i(a,t) + \lambda_1(a,t)s(a,t) + \delta\lambda_1(a,t)j(a,t), \\ \dfrac{\partial j(a,t)}{\partial a} + \dfrac{\partial j(a,t)}{\partial t} = -\gamma_2(a)j(a,t) + \lambda_2(a,t)s(a,t) - \delta\lambda_1(a,t)j(a,t), \\ s(0,t) = 1, \quad i(0,t) = j(0,t) = 0, \\ s(a,0) = s_0(a), \quad i(a,0) = i_0(a), \quad j(a,0) = j_0(a), \\ \lambda_1(a,t) = k(a)\displaystyle\int_0^{+\infty} h_1(a)P_\infty(a)i(a,t)da, \\ \lambda_2(a,t) = k(a)\displaystyle\int_0^{+\infty} h_2(a)P_\infty(a)j(a,t)da, \\ s(a,t) + i(a,t) + j(a,t) = 1. \end{cases}$$

Furthermore, we eliminate s from the second and third equation above, and obtain a system in i and j only. Thus, since $s(a,t) = 1 - i(a,t) - j(a,t)$, we obtain the final form of the system that we will consider in this article:

$$\begin{cases} \dfrac{\partial i(a,t)}{\partial a} + \dfrac{\partial i(a,t)}{\partial t} = -\gamma_1(a)i(a,t) + \lambda_1(a,t)(1 - i(a,t) - j(a,t)) \\ \qquad\qquad\qquad\qquad +\delta\lambda_1(a,t)j(a,t), \\ \dfrac{\partial j(a,t)}{\partial a} + \dfrac{\partial j(a,t)}{\partial t} = -\gamma_2(a)j(a,t) + \lambda_2(a,t)(1 - i(a,t) - j(a,t)) \\ \qquad\qquad\qquad\qquad -\delta\lambda_1(a,t)j(a,t), \\ i(0,t) = j(0,t) = 0, \\ i(a,0) = i_0(a), \quad j(a,0) = j_0(a), \\ \lambda_1(a,t) = k(a)\displaystyle\int_0^{+\infty} h_1(a)P_\infty(a)i(a,t)da, \\ \lambda_2(a,t) = k(a)\displaystyle\int_0^{+\infty} h_2(a)P_\infty(a)j(a,t)da. \end{cases} \tag{2}$$

In the next section, we discuss the stability of the disease-free equilibrium and derive an explicit expression for R_0, the basic reproduction number of the infection.

3. **Stability of the disease-free equilibrium.** The system (2) clearly has an infection-free steady state: $\mathcal{E}_0 = (0,0)$. In this case $s(a) = 1$. To study the local stability of this steady state we linearize the equations of system (2) about $\mathcal{E}_0 = (0,0)$ and consider exponential solutions of the form:

$$i(a,t) = \bar{i}(a)e^{\lambda t}, \quad j(a,t) = \bar{j}(a)e^{\lambda t}$$

where λ is a real or a complex number. Then the linear part of the first equation of system (2) is of the form:

$$\lambda \bar{i}(a) + \frac{d}{da}\bar{i}(a) = -\gamma_1(a)\bar{i}(a) + k(a)V_0^1, \qquad \bar{i}(0) = 0, \tag{3}$$

where

$$V_0^1 = \int_0^\infty h_1(a)P_\infty(a)\bar{i}(a)da. \tag{4}$$

Solving problem (3) we obtain:

$$\bar{i}(a) = \int_0^a k(\xi)V_0^1 e^{-\int_\xi^a [\lambda+\gamma_1(\tau)]d\tau} d\xi. \tag{5}$$

Substituting (5) into (4) we get:

$$\begin{aligned} V_0^1 &= \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)V_0^1 e^{-\int_\xi^a [\lambda+\gamma_1(\tau)]d\tau} d\xi da, \\ &= V_0^1 \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi) e^{-\int_\xi^a [\lambda+\gamma_1(\tau)]d\tau} d\xi da. \end{aligned}$$

Dividing both sides by V_0^1 (since $V_0^1 \neq 0$) we get the first characteristic equation, corresponding to strain one:

$$1 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi) e^{-\int_\xi^a [\lambda+\gamma_1(\tau)]d\tau} d\xi da = G(\lambda). \tag{6}$$

Similarly as for $\bar{i}(a)$ we have for $\bar{j}(a)$:

$$\lambda \bar{j}(a) + \frac{d}{da}\bar{j}(a) = -\gamma_2(a)\bar{j}(a) + k(a)V_0^2, \qquad \bar{j}(0) = 0, \tag{7}$$

where

$$V_0^2 = \int_0^\infty h_2(a)P_\infty(a)\bar{j}(a)da. \tag{8}$$

Solving (7) we obtain:

$$\bar{j}(a) = \int_0^a k(\xi)V_0^2 e^{-\int_\xi^a [\lambda+\gamma_2(\tau)]d\tau} d\xi. \tag{9}$$

Substituting (9) into (8) we get:

$$\begin{aligned} V_0^2 &= \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)V_0^2 e^{-\int_\xi^a [\lambda+\gamma_2(\tau)]d\tau} d\xi da, \\ &= V_0^2 \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi) e^{-\int_\xi^a [\lambda+\gamma_2(\tau)]d\tau} d\xi da. \end{aligned}$$

Dividing both sides by V_0^2 (since $V_0^2 \neq 0$) we get the second characteristic equation, corresponding to strain two:

$$1 = \int_0^\infty h_2(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a [\lambda + \gamma_2(\tau)] d\tau} d\xi da = H(\lambda). \tag{10}$$

We define the reproduction number of strain one as $R_0^1 = G(0)$, and the reproduction number of strain two as $R_0^2 = H(0)$. Therefore,

$$\begin{aligned} R_0^1 &= \int_0^\infty h_1(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a \gamma_1(\tau) d\tau} d\xi da, \\ R_0^2 &= \int_0^\infty h_2(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a \gamma_2(\tau) d\tau} d\xi da. \end{aligned}$$

One can also define a reproduction number of the infection as $R_0 = \max\{R_0^1, R_0^2\}$. With these notations the following result holds:

Theorem 3.1. *The disease-free equilibrium* $\mathcal{E}_0 = (0, 0)$ *is locally asymptotically stable if* $R_0 < 1$ *and unstable if* $R_0 > 1$.

Proof. First, notice that if λ is real we have:

$$\begin{aligned} & G'(\lambda) < 0, \;\; H'(\lambda) < 0, \\ & G(0) = R_0^1, \;\; H(0) = R_0^2, \\ & \lim_{\lambda \to \infty} G(\lambda) = 0, \\ & \lim_{\lambda \to \infty} H(\lambda) = 0. \end{aligned}$$

Thus, if $R_0 > 1$, the characteristic equation (6) or (10) has a unique positive real solution. Therefore, the disease-free equilibrium $\mathcal{E}_0 = (0, 0)$ is unstable. If $R_0 < 1$, both characteristic equations (6) and (10) have a unique negative real solution $\lambda_1^* < 0, \; \lambda_2^* < 0$. We will show that λ_1^* is the dominant root of $G(\lambda) = 1$, that is, all other roots have real part smaller than λ_1^*. Similarly, λ_2^* is the dominant real root of $H(\lambda) = 1$. To show that λ_1^* is the dominant root of $G(\lambda) = 1$, let $\lambda = x + iy$ be an arbitrary complex solution to the characteristic equation $G(\lambda) = 1$. Note that:

$$\begin{aligned} G(\lambda_1^*) = 1 \quad &= G(\lambda) \\ &= G(x + iy) \\ &= \int_0^\infty h_1(a) P_\infty(a) \int_0^a k(\xi) e^{\lambda(\xi - a)} e^{-\int_\xi^a \gamma_1(\tau) d\tau} d\xi da \\ &= \int_0^\infty h_1(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a \gamma_1(\tau) d\tau} e^{x(\xi - a)} [\cos y(\xi - a) \\ &\qquad\qquad + i \sin y(\xi - a)] d\xi da \\ &= \int_0^\infty h_1(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a \gamma_1(\tau) d\tau} e^{x(\xi - a)} \cos y(\xi - a) d\xi da \\ &\leq \int_0^\infty h_1(a) P_\infty(a) \int_0^a k(\xi) e^{-\int_\xi^a [\gamma_1(\tau) + x] d\tau} d\xi da \\ &= G(x) = G(\Re\lambda). \end{aligned}$$

Since $G(\lambda)$ is a decreasing function of λ, the inequality $G(\lambda_1^*) \leq G(\Re\lambda)$ implies that $\Re\lambda \leq \lambda_1^*$. Similarly, we can prove that λ_2^* is dominant real root of $H(\lambda)$. It follows that the infection-free steady state is locally asymptotically stable if $R_0 < 1$ and unstable if $R_0 > 1$. This completes the proof. □

Theorem 3.2. *Assume* $0 \leq \delta \leq 1$. *Then, the disease-free equilibrium is globally asymptotically stable if* $R_0 < 1$.

Proof. To see the global stability we let:

$$\begin{aligned} L(a,t) &= k(a)V_1(t)[(1-i(a,t)-j(a,t))+\delta j(a,t)] \\ &\leq k(a)V_1(t), \end{aligned} \tag{11}$$

where

$$V_1(t) = \int_0^\infty h_1(a)P_\infty(a)i(a,t)da. \tag{12}$$

Here we have used the fact that $(1-i(a,t)-j(a,t))+\delta j(a,t) \leq 1$, and the assumption $0 \leq \delta \leq 1$. Integrating the first equation of system (2) along the characteristic lines we get:

$$i(a,t) = \int_0^a e^{-\int_\xi^a \gamma_1(\tau)d\tau} L(\xi, t-a+\xi)d\xi, \ \ a < t. \tag{13}$$

Hence, by (11), (12) and (13) we obtain the inequality:

$$\begin{aligned} L(a,t) &\leq k(a)V_1(t) \\ &= k(a)\int_0^\infty h_1(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_1(\tau)d\tau} L(\xi, t-a+\xi)d\xi da. \end{aligned} \tag{14}$$

Let

$$W(a) = \limsup_{t\to\infty} L(a,t) \leq k(a)\int_0^\infty h_1(a)P_\infty(a)da.$$

The last inequality implies that $W(a)$ is integrable. Taking the lim sup when $t \to \infty$ of both sides of inequality (14) and using Fatou's Lemma we get:

$$W(a) \leq k(a)\int_0^\infty h_1(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_1(\tau)d\tau} W(\xi)d\xi da. \tag{15}$$

Let C denote the constant:

$$C = \int_0^\infty h_1(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_1(\tau)d\tau} W(\xi)d\xi da. \tag{16}$$

Since the function $W(a)$ is integrable, the constant C is finite. Then inequality (15) can be written as:

$$W(a) \leq Ck(a),$$

and equation (16) yields:

$$\begin{aligned} C &\leq C\int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)e^{-\int_\xi^a \gamma_1(\tau)d\tau} d\xi da \\ &= CR_0^1. \end{aligned} \tag{17}$$

From (17) it follows that $C = 0$ if $R_0 < 1$ (since $R_0^1 < 1$). This implies that $W(a) = 0$ a.e. and therefore

$$\limsup_{t\to\infty} L(a,t) = 0.$$

From equation (13) we see that

$$\lim_{t\to\infty} i(a,t) = 0.$$

Since the model is not completely symmetric, we also consider the case of strain two. In a similar way we set

$$\begin{aligned} M(a,t) &= \lambda_2(a,t)[1-i(a,t)] \\ &\le \lambda_2(a,t) = k(a)V_2(t) \\ &\le k(a)\int_0^\infty h_2(a)P_\infty(a)da, \end{aligned}$$

where

$$V_2(t) = \int_0^\infty h_2(a)P_\infty(a)j(a,t)da.$$

The second equation of system (2) can be written as:

$$\frac{\partial j(a,t)}{\partial a} + \frac{\partial j(a,t)}{\partial t} = -[\gamma_2(a) + \delta\lambda_1(a,t) + \lambda_2(a,t)]j(a,t) + \lambda_2(a,t)[1-i(a,t)].$$

We integrate this equation along the characteristic lines to get:

$$j(a,t) = \int_0^a e^{-\int_\xi^a [\gamma_2(\tau)+\delta\lambda_1(\tau,t)+\lambda_2(\tau,t)]d\tau} M(\xi, t-a+\xi)d\xi, \ \ a < t.$$

Hence, we obtain the inequality

$$\begin{aligned} M(a,t) &\le k(a)V_2(t) \\ &= k(a)\int_0^\infty h_2(a)P_\infty(a)\int_0^a e^{-\int_\xi^a [\gamma_2(\tau)+\delta\lambda_1(\tau,t)+\lambda_2(\tau,t)]d\tau} \\ &\qquad M(\xi,t-a+\xi)d\xi da \\ &\le k(a)\int_0^\infty h_2(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_2(\tau)d\tau} M(\xi,t-a+\xi)d\xi da. \end{aligned}$$

Let

$$N(a) = \limsup_{t\to\infty} M(a,t).$$

As before, the function $N(a)$ is integrable. Taking the lim sup when $t \to \infty$ on both sides of the inequality for $M(a,t)$, and using Fatou's Lemma we get

$$N(a) \le k(a)\int_0^\infty h_2(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_2(\tau)d\tau} N(\xi)d\xi da. \tag{18}$$

Let D denote the constant

$$D = \int_0^\infty h_2(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_2(\tau)d\tau} N(\xi)d\xi da. \tag{19}$$

Since $N(a)$ is integrable, the constant D is finite. Then (18) can be rewritten as

$$N(a) \le Dk(a).$$

It follows from (19) that

$$\begin{aligned} D &\le D\int_0^\infty h_2(a)P_\infty(a)\int_0^a e^{-\int_\xi^a \gamma_2(\tau)d\tau} k(\xi)d\xi da \\ &= DR_0^2. \end{aligned}$$

From this we get that $D = 0$ if $R_0 < 1$ (that is $R_0^2 < 1$). Which implies that $N(a) = 0$ a.e., that is,

$$\limsup_{t\to\infty} M(a,t) = 0.$$

Therefore,

$$\lim_{t\to\infty} j(a,t) = 0.$$

Since $s(a,t) = 1 - i(a,t) - j(a,t)$, taking the limit when $t \to \infty$ on both sides we get:

$$\lim_{t\to\infty} s(a,t) = 1.$$

This completes the proof. □

4. **Exclusive equilibria and their stabilities.** The system (2) has, besides $\mathcal{E}_0$, the following strain exclusive equilibria which are feasible under some conditions on R_0^1 and R_0^2. Namely, we have

Theorem 4.1. *(1) There exists a unique strain one exclusive equilibrium* $\mathcal{E}_1 = (i_1^*, 0)$ *if and only if* $R_0^1 > 1$*;*

(2) There exists a unique strain two exclusive equilibrium $\mathcal{E}_2 = (0, j_2^*)$ *if and only of* $R_0^2 > 1$.

Proof. The method commonly used to find a steady state for age-structured models consists of obtaining explicit expressions for a time independent solution of system (2). To find the strain one exclusive equilibrium $\mathcal{E}_1 = (i_1^*, 0)$ we solve the system:

$$\begin{cases} \dfrac{di_1^*(a)}{da} = \lambda_1^*(a)(1 - i_1^*(a)) - \gamma_1(a) i_1^*(a) \\ i_1^*(0) = 0 \end{cases} \tag{20}$$

where

$$\begin{aligned} \lambda_1^*(a) &= k(a)\int_0^\infty h_1(a)P_\infty(a) i_1^*(a)da = k(a)V_1^*, \\ V_1^* &= \int_0^\infty h_1(a)P_\infty(a)i_1^*(a)da. \end{aligned} \tag{21}$$

Solving the first equation in (20) we have that

$$i_1^*(a) = V_1^* \int_0^a k(\xi) e^{-\int_\xi^a \gamma_1(\tau)d\tau} e^{-V_1^*\int_\xi^a k(\tau)d\tau} d\xi. \tag{22}$$

Substituting in the expression for V_1^* we get:

$$V_1^* = V_1^* \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)e^{-\int_\xi^a \gamma_1(\tau)d\tau} e^{-V_1^*\int_\xi^a k(\tau)d\tau} d\xi da.$$

Since we are looking for a non-zero solution, $V_1^* \neq 0$. Canceling V_1^* from both sides of the equation above, we obtain an equation for V_1^*:

$$1 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)e^{-\int_\xi^a \gamma_1(\tau)d\tau} e^{-V_1^*\int_\xi^a k(\tau)d\tau} d\xi da = Q(V_1^*). \tag{23}$$

The function $Q(V_1^*)$ is a decreasing function of V_1^*, approaching zero as V_1^* get large. Since $Q(0) = R_0^1$, the equation $Q(V_1^*) = 1$ has a positive solution V_1^* if and only if $R_0^1 > 1$. This solution is unique. Once we have determined V_1^* from (23), we can obtain $i_1^*(a)$ from (22). This completes the proof of (1).

The proof of (2) is the same as the proof of (1). This completes the proof of the Theorem. □

To study the local stability of the strain one dominant equilibrium, we linearize system (2) about $\mathcal{E}_1 = (i_1^*(a), 0)$ and consider exponential solutions of the form:

$$i(a,t) = i_1^*(a) + \overline{i}(a)e^{\lambda t}, \quad j(a,t) = \overline{j}(a)e^{\lambda t}.$$

Then the linear part of the second equation of system (2) takes the form:

$$\lambda \overline{j}(a) + \frac{d}{da}\overline{j}(a) = -\gamma_2(a)\overline{j}(a) + k(a)V_2^1(1 - i_1^*(a)) - \delta k(a)V_1^*\overline{j}(a), \tag{24}$$

where

$$V_1^* = \int_0^\infty h_1(a)P_\infty(a)i_1^*(a)da,$$
$$V_2^1 = \int_0^\infty h_2(a)P_\infty(a)\overline{j}(a)da.$$

Solving (24) we obtain

$$\overline{j}(a) = \int_0^a k(\xi)V_2^1(1 - i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau}d\xi. \tag{25}$$

Substituting (25) into V_2^1 we obtain

$$\begin{aligned} V_2^1 &= \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)V_2^1(1 - i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau}d\xi da, \\ &= V_2^1 \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1 - i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau}d\xi da. \end{aligned} \tag{26}$$

Dividing both sides of (26) by V_2^1 (since $V_2^1 \neq 0$) we get the first characteristic equation of the strain one exclusive equilibrium $\mathcal{E}_1$:

$$1 = \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1 - i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau}d\xi da = E(\lambda). \tag{27}$$

We define the invasion reproduction number of strain two at the equilibrium of strain one as $R_2^1 = E(0)$, that is as:

$$R_2^1 = \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1 - i_1^*(\xi))e^{-\int_\xi^a[\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau}d\xi da.$$

We are now ready to establish the following theorem:

Theorem 4.2. *Let $R_0^1 > 1$. Then the strain one exclusive equilibrium $\mathcal{E}_1 = (i_1^*, 0)$ is locally asymptotically stable if $R_2^1 < 1$, and unstable if $R_2^1 > 1$.*

Proof. If we consider $E(\lambda)$ as function of the real variable λ, we can note that:

$$E'(\lambda) < 0, \ E(0) = R_2^1, \ \lim_{\lambda\to\infty} E(\lambda) = 0.$$

Then, if $R_2^1 > 1$, the characteristic equation (27) has a unique positive real solution $\lambda^* > 0$. Thus, the strain one exclusive equilibrium $\mathcal{E}_1 = (i_1^*, 0)$ is unstable. If $R_2^1 < 1$, characteristic equation (27) has a unique negative real solution $\lambda^* < 0$. Moreover, we can prove that λ^* is the dominant real root of $E(\lambda) = 1$, that is all other roots of the characteristic equation $E(\lambda) = 1$ are complex with real part smaller than λ^*.

To see that, let $\lambda = x + iy$ be an arbitrary complex solution to the characteristic equation $E(\lambda) = 1$. We have that:

$$\begin{aligned} E(\lambda^*) &= 1 = E(\lambda) = E(x+iy) \\ &= \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1-i_1^*(\xi)) \\ &\qquad e^{-\int_\xi^a[\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau} e^{x(\xi-a)}[\cos y(\xi-a) + i\sin y(\xi-a)]d\xi da \\ &= \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1-i_1^*(\xi))e^{-\int_\xi^a[\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau} e^{x(\xi-a)} \\ &\qquad \cos y(\xi-a)d\xi da \\ &\le \int_0^\infty h_2(a)P_\infty(a)\int_0^a k(\xi)(1-i_1^*(\xi))e^{-\int_\xi^a[\gamma_2(\tau)+\delta V_1^* k(\tau)]d\tau} e^{x(\xi-a)}dad\xi \\ &= E(x) = E(\Re\lambda). \end{aligned}$$

Since $E(\lambda)$ is a decreasing function of it argument, the inequality $E(\lambda^*) \le E(\Re\lambda)$ indicates that $\Re\lambda \le \lambda^*$. In the case when $R_2^1 < 1$, to see that the strain one exclusive equilibrium is locally asymptotically stable, we consider the linearization of the first equation in system (2) around $\mathcal{E}_1 = (i_1^*, 0)$. Similarly to (24) we have:

$$\lambda\bar{i}(a) + \frac{d}{da}\bar{i}(a) = -\gamma_1(a)\bar{i}(a) + k(a)V_1^1(1-i_1^*(a)) - k(a)V_1^*(\bar{i}(a)+\bar{j}(a)) + \delta k(a)V_1^*\bar{j}(a), \tag{28}$$

where

$$V_1^* = \int_0^\infty h_1(a)P_\infty(a)i_1^*(a)da,$$
$$V_1^1 = \int_0^\infty h_1(a)P_\infty(a)\bar{i}(a)da.$$

For values of λ that solve the equation $E(\lambda) = 1$, we find a non-zero $\bar{j}(a)$ from (25), and a corresponding value of $\bar{i}(a)$ from (28). However, equation (28) may have non-trivial solutions even if $\bar{j}(a) = 0$. To find those we look for non-zero solutions of

$$\lambda\bar{i}(a) + \frac{d}{da}\bar{i}(a) = -\gamma_1(a)\bar{i}(a) + k(a)V_1^1(1-i_1^*(a)) - k(a)V_1^*\bar{i}(a). \tag{29}$$

Solving (29) we obtain

$$\bar{i}(a) = \int_0^a k(\xi)V_1^1(1-i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_1(\tau)+V_1^* k(\tau)]d\tau}d\xi. \tag{30}$$

Substituting (30) into V_1^1 we obtain

$$\begin{aligned} V_1^1 &= \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)V_1^1(1-i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_1(\tau)+V_1^* k(\tau)]d\tau}d\xi da, \\ &= V_1^1\int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)(1-i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_1(\tau)+V_1^* k(\tau)]d\tau}d\xi da. \end{aligned} \tag{31}$$

Dividing both sides of (31) by V_1^1 (since $V_1^1 \ne 0$) we get the second characteristic equation of the strain one exclusive equilibrium $\mathcal{E}_1$:

$$1 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)(1-i_1^*(\xi))e^{-\int_\xi^a[\lambda+\gamma_1(\tau)+V_1^* k(\tau)]d\tau}d\xi da = D(\lambda). \tag{32}$$

As before, $D(\lambda)$ is a decreasing function of the real variable λ satisfying:

$$D'(\lambda) < 0, \ \lim_{\lambda\to\infty} D(\lambda) = 0.$$

From (23) it follows that $D(0) < 1$. Therefore, the unique real solution to the equation $D(\lambda) = 1$ is negative: $\lambda^* < 0$. One can show, as we showed before, that all other solutions of that equation are complex with real part smaller than λ^*. Thus, if $R_2^1 < 1$ all characteristic values are negative or have negative real part. We conclude that the strain one exclusive equilibrium is locally asymptotically stable if $R_2^1 < 1$ and unstable if $R_2^1 > 1$. This completes the proof. □

To study the local stability of the strain two exclusive equilibrium, we linearize system (2) about the strain two exclusive equilibrium $\mathcal{E}_2 = (0, j_2^*(a))$. As before, we consider exponential solutions of the form:

$$i(a,t) = \bar{i}(a)e^{\lambda t}, \ \ j(a,t) = j_2^*(a) + \bar{j}(a)e^{\lambda t}.$$

Then the linear part of the first equation of system (2) is of the form:

$$\lambda\bar{i}(a) + \frac{d}{da}\bar{i}(a) = -\gamma_1(a)\bar{i}(a) + k(a)V_1^2(1 - j_2^*(a)) + \delta k(a)V_1^2 j_2^*(a), \tag{33}$$

where

$$V_1^2 = \int_0^\infty h_1(a)P_\infty(a)\bar{i}(a)da.$$

Solving (33) we obtain:

$$\bar{i}(a) = \int_0^a k(\xi)V_1^2[(1 - j_2^*(\xi)) + \delta j_2^*(\xi)]e^{-\int_\xi^a[\lambda+\gamma_1(\tau)]d\tau}d\xi \tag{34}$$

Substituting (34) into V_1^2 we obtain:

$$\begin{aligned} V_1^2 \ &= \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)V_1^2[(1 - j_2^*(\xi)) + \delta j_2^*(\xi)]e^{-\int_\xi^a[\lambda+\gamma_1(\tau)]d\tau}d\xi da \\ &= V_1^2\int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)[(1 - j_2^*(\xi)) + \delta j_2^*(\xi)]e^{-\int_\xi^a[\lambda+\gamma_1(\tau)]d\tau}d\xi da. \end{aligned} \tag{35}$$

Dividing both sides by V_1^2 (since $V_1^2 \neq 0$) in (35) we get the first characteristic equation of the strain two exclusive equilibrium $\mathcal{E}_2$:

$$1 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)[(1 - j_2^*(\xi)) + \delta j_2^*(\xi)]e^{-\int_\xi^a[\lambda+\gamma_1(\tau)]d\tau}d\xi da = F(\lambda). \tag{36}$$

Now we are ready to define the invasion reproduction number of strain one at the equilibrium of strain two as $R_1^2 = F(0)$, that is,

$$R_1^2 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(\xi)[(1 - j_2^*(\xi)) + \delta j_2^*(\xi)]e^{-\int_\xi^a \gamma_1(\tau)d\tau}d\xi da.$$

The following theorem holds:

Theorem 4.3. *Let $R_0^2 > 1$. Then strain two exclusive equilibrium $\mathcal{E}_2(0, j_2^*)$ is locally asymptotically stable if $R_1^2 < 1$ and unstable if $R_1^2 > 1$.*

Proof. Proof of Theorem 4.3 is similar to proof of Theorem 4.2 and is ommitted. □

Example: We conclude this section with a specific example. Consider the following specific choices for the parameters:

$$\begin{aligned} h_1(a) &= h_1 a e^{-\alpha_1 a}, \qquad & h_2(a) &= h_2 a e^{-\alpha_2 a}, \\ k(a) &= k, \qquad & \mu(a) &= \mu, \\ \gamma_1(a) &= \gamma_1, \qquad & \gamma_2(a) &= \gamma_2, \end{aligned}$$

where h_1, h_2, k, μ, γ_1 and γ_2 are given constants. The reproduction numbers of the two strains $i = 1, 2$ in this case are given by:

$$R_0^i = \frac{k b_0 h_i(\gamma_i + 2\alpha_i + 2\mu)}{(\alpha_i + \mu)^2(\alpha_i + \mu + \gamma_i)^2}.$$

The system has the disease-free equilibrium $\mathcal{E}_0 = (0, 0)$. According to Theorem 4.1 if $R_0^1 > 1$ there also exist strain one exclusive equilibrium $\mathcal{E}_1 = (i_1^*, 0)$, where

$$i_1^*(a) = \frac{V_1^* k}{\gamma_1 + V_1^* k}\left(1 - e^{-(\gamma_1 + V_1^* k)a}\right).$$

In the expression above V_1^* is the unique positive solution of equation (23) which takes the form

$$\frac{h_1 k b_0(2\alpha_1 + 2\mu + \gamma_1 + V_1^* k)}{(\alpha_1 + \mu)^2(\alpha_1 + \mu + \gamma_1 + V_1^* k)^2} = 1.$$

Strain two exclusive equilibrium $\mathcal{E}_2 = (0, j_2^*)$ exists if $R_0^2 > 1$ where j_2^* is given by the same expression. By Theorem 4.2 the strain one exclusive equilibrium is stable if $R_2^1 < 1$ where

$$\begin{aligned} R_2^1 = &\frac{h_2 k b_0 \gamma_1(2\alpha_2 + 2\mu + \gamma_2 + \delta V_1^* k)}{(\gamma_1 + V_1^* k)(\alpha_2 + \mu)^2(\alpha_2 + \mu + \gamma_2 + \delta V_1^* k)^2} \\ &+ \frac{h_2 b_0 V_1^* k^2(2\alpha_2 + 2\mu + \gamma_1 + V_1^* k + \gamma_2 + \delta V_1^* k)}{(\gamma_1 + V_1^* k)(\alpha_2 + \mu + \gamma_2 + \delta V_1^* k)^2(\alpha_2 + \mu + \gamma_1 + V_1^* k)^2}. \end{aligned}$$

Specific values of the parameters may tell us whether strain one equilibrium is locally asymptotically stable or not. Similar results can be established for the strain two exclusive equilibrium.

The next section we discuss the existence of a coexistence equilibrium.

5. Coexistence equilibria.

In this section we will establish the existence of a coexistence equilibrium, that is an equilibrium in which both strains are present. The method commonly used to find endemic steady states for age-structured models consists in assuming that the force of infection at equilibrium (a quantity similar to V_1^*) is given and obtaining explicit expressions for a time independent solution. Similar approach works for age-since-infection multi-strain models [13, 16, 17], and even for the somewhat simplified chronological age-structured model considered in [18].

In our case a coexistence equilibrium $\mathcal{E}^* = (i^*(a), j^*(a))$ is a time independent solution of equations (2) that satisfies:

$$\begin{cases} \dfrac{d}{da} i^*(a) = \lambda_1^*(a; i^*)(1 - i^*(a) - j^*(a)) + \delta\lambda_1^*(a; i^*) j^*(a) - \gamma_1(a) i^*(a), \\ \dfrac{d}{da} j^*(a) = \lambda_2^*(a; j^*)(1 - i^*(a) - j^*(a)) - \delta\lambda_1^*(a; i^*) j^*(a) - \gamma_2(a) j^*(a), \\ i^*(0) = 0, j^*(0) = 0, \end{cases} \tag{44}$$

where

$$\lambda_1^*(a;i^*) = k(a)\int_0^{+\infty} P_\infty(a)h_1(a)i^*(a)da = k(a)V_3^*,$$

$$\lambda_2^*(a;j^*) = k(a)\int_0^{+\infty} P_\infty(a)h_2(a)j^*(a)da = k(a)V_4^*,$$

For models where individuals only move forward it is possible to solve the steady state equations recurrently. We cannot follow this approach here because system (44) is a full system in $i^*(a)$ and $j^*(a)$, and consequently, we are unable to obtain an explicit expression for $i^*(a)$ and $j^*(a)$ in terms of V_3^* and V_4^*. We need a somewhat more indirect approach. We adapt the setting and methods employed in [6] where a one-strain version of our model is considered. This approach only works in the case $0 \le \delta \le 1$, so in this section we will assume δ satisfies these inequalities. As before, we can find the corresponding equilibrial value of $s^*(a)$ from the equality: $s^*(a) = 1 - i^*(a) - j^*(a)$.

We will use the following abstract setting. Consider the Banach space $X = L^1(0,\infty) \times L^1(0,\infty)$, and the positive cone in it $X_+ = L^1_+(0,\infty) \times L^1_+(0,\infty)$. Elements of X are denoted by $u = (i,j)^T$. We introduce the bounded closed convex subset of the positive cone of X:

$$\mathcal{C} = \{u \in X_+ : i(a) + j(a) \le 1 \qquad \text{a.e.}\}.$$

Furthermore, we define the non-linear operator $F[u] = (F_1[u], F_2[u])$ such that $F : \mathcal{C} \longrightarrow X$ and is defined as follows:

$$F[u](a) = \begin{cases} F_1[u](a) = \lambda_1^*(a;i)(1 - i(a) - j(a)) + \delta\lambda_1^*(a;i)j(a); \\ F_2[u](a) = \lambda_2^*(a;j)(1 - i(a) - j(a)) - \delta\lambda_1^*(a;i)j(a). \end{cases} \tag{45}$$

Since F acts on the bounded closed set $\mathcal{C}$, then it is not hard to see that F is Lipschitz continuous. Let $\alpha > 0$ be an arbitrary number to be chosen later. We rewrite the differential equation model (44) as an integral equation model

$$\begin{cases} i(a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_1(\sigma)\,d\sigma}\{i(s) + \alpha F_1[u](s)\}\,ds, \\ j(a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_2(\sigma)\,d\sigma}\{j(s) + \alpha F_2[u](s)\}\,ds, \end{cases} \tag{46}$$

where we have omitted the stars. We define a non-linear operator $\mathcal{T} : \mathcal{C} \longrightarrow X$ as follows:

$$\mathcal{T}[u](a) = \begin{cases} \mathcal{T}_1[u](a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_1(\sigma)\,d\sigma}\{i(s) + \alpha F_1[u](s)\}\,ds, \\ \mathcal{T}_2[u](a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_2(\sigma)\,d\sigma}\{j(s) + \alpha F_2[u](s)\}\,ds. \end{cases} \tag{47}$$

The non-linear operator $\mathcal{T}$ has a number of important properties. Before we discuss them, we introduce a new cone in X. Let

$$K = L^1_+(0,\infty) \times (-L^1_+(0,\infty)).$$

Clearly, K is a cone in X. For $u, v \in X$ we write $u \le v$ if $v - u \in X_+$, and $u \le_K v$, if $v - u \in K$. Component-wise, if $v = (\bar{i}, \bar{j})^T$, then $u \le v$ means that $i \le \bar{i}$ and $j \le \bar{j}$, while $u \le_K v$ means that $i \le \bar{i}$ and $j \ge \bar{j}$.

Theorem 5.1. *There exists $\alpha > 0$ such that the non-linear operator $\mathcal{T}$ is Lipschitz continuous, and maps the set $\mathcal{C}$ into itself: $\mathcal{T} : \mathcal{C} \longrightarrow \mathcal{C}$. In addition, the non-linear operator $\mathcal{T}$ is a monotone operator in the ordering introduced by the cone K. In other words,*

$$u \leq_K v \qquad\qquad \textit{implies} \qquad\qquad \mathcal{T}[u] \leq_K \mathcal{T}[v].$$

Theorem 5.1. follows from the proposition below which establishes the above results for the non-linear operator $I + \alpha F$.

Proposition 5.2. *There exists $\alpha > 0$ such that the non-linear operator $I + \alpha F$ is Lipschitz continuous, and maps the set $\mathcal{C}$ into itself: $I + \alpha F : \mathcal{C} \longrightarrow \mathcal{C}$. In addition, the non-linear operator $I + \alpha F$ is a monotone operator in the ordering introduced by the cone K. In other words,*

$$u \leq_K v \qquad\qquad \textit{implies} \qquad\qquad u + \alpha F[u] \leq_K v + \alpha F[v].$$

Proof. (Proposition 5.2) First we prove the monotonicity of the operator $I + \alpha F$. Let $u = (i, j)^T$ and $v = (\bar{i}, \bar{j})^T$ with $u \leq_K v$. That is, we have $i \leq \bar{i}$ and $j \geq \bar{j}$. Then, the first component of the operator $I + \alpha F$ satisfies:

$$\begin{aligned}
(i + \alpha \quad & F_1[u])(a) \\
&= i(a) + \alpha\lambda_1^*(a; i)(1 - i(a) - (1 - \delta)j(a)) \\
&\leq i(a) + \alpha\lambda_1^*(a; \bar{i})(1 - i(a) - (1 - \delta)\bar{j}(a)) \\
&= i(a)(1 - \alpha\lambda_1^*(a; \bar{i})) + \alpha\lambda_1^*(a; \bar{i})(1 - (1 - \delta)\bar{j}) \\
&\leq \bar{i}(a)(1 - \alpha\lambda_1^*(a; \bar{i})) + \alpha\lambda_1^*(a; \bar{i})(1 - (1 - \delta)\bar{j}) \\
&= \bar{i}(a) + \alpha\lambda_1^*(a; \bar{i})(1 - \bar{i}(a) - (1 - \delta)\bar{j}(a)) \\
&= (\bar{i} + \alpha F_1[v])(a).
\end{aligned}$$

The last inequality is valid since the functions $\lambda_1^*(a; \bar{i})$ is bounded, say by Λ_1. Choosing α so that $1 - \alpha\Lambda_1 > 0$, the expression in the parenthesis is positive for all a. Thus, we can replace i with $\bar{i}$. Next, we consider the second component of $I + \alpha F$. We have

$$\begin{aligned}
(j + \alpha \quad & F_2[u])(a) \\
&= j(a) + \alpha\lambda_2^*(a; j)(1 - i(a) - j(j)) - \alpha\delta\lambda_1^*(a; i)j(a) \\
&\geq j(a) + \alpha\lambda_2^*(a; \bar{j})(1 - \bar{i}(a) - j(j)) - \alpha\delta\lambda_1^*(a; \bar{i})j(a) \\
&= j(a)(1 - \alpha\lambda_2^*(a; \bar{j}) - \alpha\delta\lambda_1^*(a; \bar{i})) + \alpha\lambda_2^*(a; \bar{j})(1 - \bar{i}(a)) \\
&\geq \bar{j}(a)(1 - \alpha\lambda_2^*(a; \bar{j}) - \alpha\delta\lambda_1^*(a; \bar{i})) + \alpha\lambda_2^*(a; \bar{j})(1 - \bar{i}(a)) \\
&= (\bar{j} + \alpha F_2[v])(a).
\end{aligned}$$

As before, the last inequality follows from the boundedness of $\lambda_2^*(a; \bar{j})$ by Λ_2 and of $\lambda_1^*(a; \bar{i})$ by Λ_1. We can choose $\alpha > 0$ but small enough so that $1 - \alpha\Lambda_2 - \alpha\delta\Lambda_1 > 0$, as well as $1 - \alpha\Lambda_1 > 0$. This establishes the monotonicity of $I + \alpha F$ in the ordering, introduced by the cone K.

Next, we have to show that $I + \alpha F$ maps the set $\mathcal{C}$ into itself. First, we notice that the set $\mathcal{C}$ has largest and smallest element in the ordering introduced by the cone K. The smallest element will be denoted by $\underline{u}$ while the largest element will be denoted by $\bar{u}$. These elements are given as follows:

$$\underline{u} = (0, 1)^T \qquad\qquad \text{and} \qquad\qquad \bar{u} = (1, 0)^T.$$

Clearly, any element $u \in \mathcal{C}$ satisfies $\underline{u} \leq_K u \leq_K \bar{u}$. The operator $I + \alpha F$ acts on these two boundary elements as follows:

$$(\underline{u} + \alpha F[\underline{u}])(a) = \begin{cases} 0 \\ 1 \end{cases}$$

$$(\bar{u} + \alpha F[\bar{u}])(a) = \begin{cases} 1 \\ 0. \end{cases}$$

Since for any element $u \in \mathcal{C}$ we have $\underline{u} \leq_K u \leq_K \bar{u}$, we may apply the operator $I + \alpha F$ to this inequality, to get:

$$\underline{u} \leq_K \underline{u} + \alpha F[\underline{u}] \leq_K u + \alpha F[u] \leq_K \bar{u} + \alpha F[\bar{u}] \leq_K \bar{u}.$$

The above inequalities imply that for any $u \in \mathcal{C}$, the output $u + \alpha F[u]$ has components that are between zero and one. In order to show that $u + \alpha F[u] \in \mathcal{C}$, it remains to be shown that

$$i + \alpha F_1[u] + j + \alpha F_2[u] \leq 1.$$

To see that let

$$h(a) = \max\{h_1(a), h_2(a)\}.$$

Denote by $\lambda^*(a; i+j) = k(a) \int_0^\infty P_\infty(a) h(a)(i(a) + j(a))\, da$. As before $\lambda(a; i+j)$ is bounded by a constant, say Λ, and we assume that α is such that $1 - \alpha\Lambda > 0$. Then,

$$\begin{aligned} i + {} & \alpha F_1[u] + j + \alpha F_2[u] \\ & = i + j + \alpha(\lambda_1^*(a;i) + \lambda_2^*(a;j))(1 - i - j) + \alpha\delta\lambda_1^*(a;i)j - \alpha\delta\lambda_1^*(a;i)j \\ & = i + j + \alpha(\lambda_1^*(a;i) + \lambda_2^*(a;j))(1 - i - j) \\ & \leq i + j + \alpha\lambda^*(a; i+j)(1 - i - j) \\ & \leq i + j + \alpha\lambda^*(a;1)(1 - i - j) \\ & \leq (i+j)(1 - \alpha\lambda^*(a;1)) + \alpha\lambda^*(a;1) \\ & \leq 1 - \alpha\lambda^*(a;1) + \alpha\lambda^*(a;1) \\ & = 1. \end{aligned}$$

This completes the proof. □

In the previous section we established that if $R_2^1 > 1$ the exclusive equilibrium $\mathcal{E}_1 = (i_1^*, 0)$ is unstable. In addition, if $R_1^2 > 1$ the the exclusive equilibrium $\mathcal{E}_2 = (0, j_2^*)$ is unstable. Thus, if $R_2^1 > 1$ and $R_1^2 > 1$ then both exclusive equilibria are unstable. In this section we will show that in this case there exists a coexistence equilibrium.

To see that, we consider the exclusive equilibria as $\mathcal{E}_1 = (i_1^*, 0)$ and $\mathcal{E}_2 = (0, j_2^*)$. We have to connect the non-linear operator $\mathcal{T}$ with its linearizations around each of the exclusive equilibria. Thus, for any element $u = (i,j)^T \in X$ one can see that

$$\mathcal{T}[\mathcal{E}_j + u] = \mathcal{T}[\mathcal{E}_j] + D\mathcal{T}(\mathcal{E}_j)u + \mathcal{N}(u), \qquad \textit{for} \quad j = 1, 2. \tag{48}$$

We note that $\mathcal{E}_j$ is a fixed point of the operator $\mathcal{T}$. Thus, the first term gives $\mathcal{T}[\mathcal{E}_j] = \mathcal{E}_j$ for $j = 1, 2$. Furthermore, $D\mathcal{T}(\mathcal{E}_j)u$ is the linearization of the non-linear operator $\mathcal{T}$ around the exclusive equilibrium $\mathcal{E}_j$ for $j = 1, 2$. The linearizations of the operator F around the equilibria $\mathcal{E}_1$ and $\mathcal{E}_2$ are given by $L(\mathcal{E}_j)$:

$$(L(\mathcal{E}_1)u)(a) = \begin{cases} -\lambda_1^*(a; i_1^*)(i + j) + \lambda_1^*(a; i)(1 - i_1^*) + \delta\lambda_1^*(a; i_1^*)j \\ \lambda_2^*(a; j)(1 - i_1^*) - \delta\lambda_1^*(a; i_1^*)j \end{cases}$$

and

$$(L(\mathcal{E}_2)u)(a) = \begin{cases} \lambda_1^*(a; i)(1 - j_2^*) + \delta\lambda_1^*(a; i)j_2^* \\ -\lambda_2^*(a; j_2^*)(i + j) + \lambda_2^*(a; j)(1 - j_2^*) - \delta\lambda_1^*(a; i)j_2^*. \end{cases}$$

Thus, the linearization of the operator $\mathcal{T}$ around the exclusive equilibrium $\mathcal{E}_j$ is given by:

$$(D\mathcal{T}(\mathcal{E}_j)u)(a) = \begin{cases} D\mathcal{T}_1(\mathcal{E}_j)u(a) = \\ \qquad \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_1(\sigma)\,d\sigma}\{i(s) + \alpha L_1(\mathcal{E}_j)u(s)\}\,ds, \\ D\mathcal{T}_2(\mathcal{E}_j)u(a) = \\ \qquad \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_2(\sigma)\,d\sigma}\{j(s) + \alpha L_2(\mathcal{E}_j)u(s)\}\,ds. \end{cases} \tag{49}$$

Finally, the nonlinear operator $\mathcal{N}(u)$ in (48) is given by

$$\mathcal{N}(u)(a) = \begin{cases} \mathcal{N}_1(u)(a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_1(\sigma)\,d\sigma}\{-\alpha\lambda_1^*(s; i)(i(s) + j(s)) \\ \qquad\qquad + \alpha\delta\lambda_1^*(s; i)j(s)\}\,ds, \\ \mathcal{N}_2(u)(a) = \dfrac{1}{\alpha}\displaystyle\int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_2(\sigma)\,d\sigma}\{-\alpha\lambda_2^*(s; j)(i(s) + j(s)) \\ \qquad\qquad - \alpha\delta\lambda_1^*(s; i)j(s)\}\,ds. \end{cases} \tag{50}$$

We denote by ρ_1 the spectral radius of the linear operator $D\mathcal{T}(\mathcal{E}_1)$ and by ρ_2 the spectral radius of the linear operator $D\mathcal{T}(\mathcal{E}_2)$. We want to apply the Krein-Ruthman Theorem to conclude that ρ_1 and ρ_2 are eigenvalues. First, it is easy to see that the cone K is reproducing (that is, every element of X can be represented as a difference of two elements in K). Next, we need to show that the two linear operators $D\mathcal{T}(\mathcal{E}_1)$ and $D\mathcal{T}(\mathcal{E}_2)$ are positive, that is, each of them maps the cone K into itself. We show that for $D\mathcal{T}(\mathcal{E}_1)$. Let $u \in K$. Then if $u = (i, j)^T$ we have $i \geq 0$ while $j \leq 0$. The sign of the first component of $D\mathcal{T}(\mathcal{E}_1)u$ is given by the sign of $i(a) + \alpha L_1(\mathcal{E}_1)u(a)$. Consequently,

$$\begin{aligned} i(a) \quad & + \alpha L_1(\mathcal{E}_1)u(a) \\ & = i(a) - \alpha\lambda_1^*(a; i_1^*)(i + j) + \alpha\lambda_1^*(a; i)(1 - i_1^*) + \alpha\delta\lambda_1^*(a; i_1^*)j \\ & = i(a)(1 - \alpha\lambda_1^*(a; i_1^*)) - \alpha(1 - \delta)\lambda_1^*(a; i_1^*)j + \alpha\lambda_1^*(a; i)(1 - i_1^*). \end{aligned}$$

The first term in the expression above is positive for appropriate choice of α. The second term is positive because j is negative. The last term is positive because i is non-negative. Similarly, the second component can be shown to have the sign of j, that is the second component is negative. Thus, the linear operators $D\mathcal{T}(\mathcal{E}_1)$ and $D\mathcal{T}(\mathcal{E}_2)$ map the cone K into itself, and therefore they are positive operators. Then Krein-Ruthman Theorem implies that ρ_1 is an eigenvalue of the operator $D\mathcal{T}(\mathcal{E}_1)$. The eigenvector that corresponds to that eigenvalue, say v, is an element of the cone K, that is,

$$D\mathcal{T}(\mathcal{E}_1)v = \rho_1 v.$$

Similarly, Krein-Ruthman Theorem implies that ρ_2 is an eigenvalue of the operator $D\mathcal{T}(\mathcal{E}_2)$. The eigenvector that corresponds to that eigenvalue, say w, is an element of the cone K, that is,

$$D\mathcal{T}(\mathcal{E}_2)w = \rho_2 w.$$

We would like to connect the spectral radii ρ_1 and ρ_2 to the invasion reproduction numbers $R^i_j > 1$ we computed in the previous section. This connection is established in the proposition below.

Proposition 5.3. *The spectral radius $\rho_i > 1$ if and only if $R^i_j > 1$ for $i, j = 1, 2$ and $i \neq j$.*

Proof. We show that in one of the cases, the other case is similar. By the Krein-Ruthman Theorem, we have

$$D\mathcal{T}(\mathcal{E}_2)w = \rho_2 w,$$

where w is the eigenvector corresponding to eigenvalue ρ_2. The eigenvector $w = (i, j)^T$ belongs to K. For the first component of the eigenvalue equation above we have

$$\frac{1}{\alpha}\int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_1(\sigma)\,d\sigma}[i(s) + \alpha L_1(\mathcal{E}_2)w(s)]\,ds = \rho_2 i(a).$$

We rewrite this expression in the form

$$\frac{1}{\alpha}\int_0^a e^{\frac{1}{\alpha}s} e^{\int_0^s \gamma_1(\sigma)\,d\sigma}[i(s) + \alpha L_1(\mathcal{E}_2)w(s)]\,ds = \rho_2 e^{\frac{1}{\alpha}a} e^{\int_0^a \gamma_1(\sigma)\,d\sigma} i(a).$$

Differentiating this equality with respect to a and simplifying:

$$\frac{1}{\alpha}[i(a) + \alpha L_1(\mathcal{E}_2)w(a)] = \rho_2[\frac{1}{\alpha}i(a) + \gamma_1(a)i(a) + i'(a)].$$

Solving this equation for $i(a)$ we have

$$i(a) = \frac{1}{\rho_2}\int_0^a e^{-\xi(a-s)} e^{-\int_s^a \gamma_1(\sigma)\,d\sigma} L_1(\mathcal{E}_2)w(s)\,ds,$$

where

$$\xi = \frac{1}{\alpha}\left(1 - \frac{1}{\rho_2}\right).$$

We note that $\xi = 0$ if and only if $\rho_2 = 1$. Furthermore, $\xi > 0$ if and only if $\rho_2 > 1$. Substituting $i(a)$ in the definition of V^2_1 (see equation (33)) we obtain an equation similar to (36):

$$\rho_2 = \int_0^\infty h_1(a)P_\infty(a)\int_0^a k(s)[1 - j^*_2(s) + \delta j^*_2(s)]e^{-\int_s^a[\xi+\gamma_1(\tau)]d\tau}dsda.$$

The right-hand side of the equation above is equal to R^2_1 if and only if $\xi = 0$, that is $\rho_2 = 1$. Therefore, if $\rho_2 > 1$ we have $\rho_2 \leq R^2_1$. Consequently $R^2_1 > 1$. If $\rho_2 < 1$ we have that $R^2_1 \leq \rho_2$, and therefore $R^2_1 < 1$. Conversely, assume $R^2_1 > 1$. Then we either have $\rho_2 \geq R^2_1$ in which case $\rho_2 > 1$ or we have $\rho_2 \leq R^2_1$ in which case the equation above implies $\rho_2 > 1$. Similar argument implies that if $R_1^2 < 1$ then $\rho_2 < 1$. This completes the proof of Proposition 5.3. $\square$

Before we give the Theorem that establishes the existence of at least one coexistence equilibrium, we consider the following auxiliary Lemma. Let

$$m(a) = \int_0^a k(\sigma) d\sigma.$$

Lemma 5.4. *There exist constants* K_1 *and* K_2*, with* $K_1 < K_2$ *such that the first component of* $\mathcal{E}_1$ *and the second component of* $\mathcal{E}_2$ *satisfy:*

$$\begin{gathered} K_1 m(a) \le i_1^*(a) \le K_2 m(a) \\ K_1 m(a) \le j_2^*(a) \le K_2 m(a). \end{gathered}$$

Similar inequalities are valid for the first components of the eigenvectors $v = (i_1, j_1)^T$ *and* $w = (i_2, j_2)^T$*, if they are non-zero. The second components, if non-zero, satisfy:*

$$\begin{gathered} K_1 m(a) \le -j_1(a) \le K_2 m(a) \\ K_1 m(a) \le -j_2(a) \le K_2 m(a). \end{gathered}$$

Proof. We first establish that for the first component of $\mathcal{E}_1$. The result for the second component of $\mathcal{E}_2$ and the first components of the eigenvectors is analogous. We will later establish the inequality for the second component of v. The first component of $\mathcal{E}_1$ has the form

$$i_1^*(a) = V_1^* \int_0^a k(s) e^{-\int_s^a \gamma_1(\sigma)\, d\sigma} e^{-V_1^* \int_s^a k(\sigma)\, d\sigma} ds.$$

Clearly,

$$i_1^*(a) \le V_1^* m(a).$$

Thus K_2 should be chosen larger than V_1^*. To see the lower bound, notice that

$$i_1^*(a) \ge V_1^* e^{-\int_0^A \gamma_1(\sigma)\, d\sigma} e^{-V_1^* \int_0^A k(\sigma)\, d\sigma} m(a) \ge K_1 m(a)$$

where we recall that A is the upper bound of the support of $k(a)$, and K_1 is an appropriately chosen constant which depends on V_1^*. We note that $V_1^* \ne 0$, since if it were zero, $i_1^*(a)$ would be identically zero. The second component of v satisfies:

$$\frac{1}{\alpha} \int_0^a e^{-\frac{1}{\alpha}(a-s)} e^{-\int_s^a \gamma_2(\sigma)\, d\sigma} \{j_2(s) + \alpha L_2(\mathcal{E}_1) v(s)\} ds = \rho_1 j_1(a).$$

Rearranging that expression and differentiating we obtain

$$j_1' + \gamma_2(a) j_1 + \frac{1}{\alpha} = \frac{1}{\alpha \rho_1} [j_1 + \alpha L_2(\mathcal{E}_1) v(a)].$$

Using the form of $L_2(\mathcal{E}_1)v(a)$ we obtain the following expression for $j_1(a)$:

$$[-j_1(a)] = (-V_2^1) \frac{1}{\rho_1} \int_0^a k(s) e^{-\bar{\xi}(a-s)} e^{-\delta V_1^* \int_s^a k(\tau) d\tau} e^{-\int_s^a \gamma_2(\tau) d\tau} (1 - i_1^*)\, ds,$$

where

$$\bar{\xi} = \frac{1}{\alpha} \left(1 - \frac{1}{\rho_1} \right)$$

and

$$V_2^1 = \int_0^\infty h_2(a) P_\infty(a) j_1(a) da.$$

If $j_1(a) \ne 0$ then $V_2^1 < 0$, and it is a given non-zero constant. We can proceed as in the case with $i_1^*(a)$ to establish the inequalities. Finally, we have chosen as K_1

the smallest of all lower bound constants, and as K_2 the largest of all upper bound constants. ☐

Theorem 5.5. *Assume* $R_1^2 > 1$ *and* $R_2^1 > 1$. *Then, there is at least one coexistence equilibrium* $\mathcal{E}^* = (i^*, j^*)$.

Proof. From Proposition 5.3. it follows that $R_1^2 > 1$ and $R_2^1 > 1$ imply that $\rho_1 > 1$ and $\rho_2 > 1$. We recall that v is an eigenvector corresponding to the eigenvalue ρ_1, and w is the eigenvector corresponding to eigenvalue ρ_2. Both v and w belong to the cone K. That means that if $v = (i_1, j_1)^T$ and $w = (i_2, j_2)^T$, then $i_1 \geq 0, i_2 \geq 0$ while $j_1 \leq 0$, $j_2 \leq 0$. Since $\mathcal{E}_2 \leq_K \mathcal{E}_1$, Lemma 5.4 implies that for $\epsilon > 0$ and $\eta > 0$ but small enough we still have

$$\mathcal{E}_2 + \eta w \leq_K \mathcal{E}_1 - \epsilon v. \tag{51}$$

We will apply the operator $\mathcal{T}$ to this inequality. Using equality (48) we have

$$\begin{aligned} \mathcal{T}[\mathcal{E}_2 + \eta w] \quad &= \\ &= \mathcal{T}[\mathcal{E}_2] + \eta D\mathcal{T}(\mathcal{E}_2)w + \eta^2\mathcal{N}(w) \\ &= \mathcal{E}_2 + \eta\rho_2 w + \eta^2\mathcal{N}(w) \\ &= \mathcal{E}_2 + \eta w + \eta(\rho_2 - 1)w + \eta^2\mathcal{N}(w) \\ &\geq_K \mathcal{E}_2 + \eta w. \end{aligned} \tag{52}$$

The last inequality above is valid since $\rho_2 > 1$, and for η small enough $(\rho_2 - 1)w + \eta\mathcal{N}(w) \geq_K 0$. To see that $(\rho_2 - 1)w + \eta\mathcal{N}(w) \geq_K 0$ we consider the first component only. The second component is established similarly. The first component of the above inequality is given by:

$$\begin{aligned} &= (\rho_2 - 1)i_2(a) + \eta\int_0^a e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_1(\tau)d\tau}\{-k(s)V_1^1(i_2(s) + j_2(a)) \\ &\qquad\qquad +\delta k(s)V_1^1 j_2(s)\}ds \\ &\geq (\rho_2 - 1)i_2(a) - \eta V_1^1\int_0^a k(s)e^{-\frac{1}{\alpha}(a-s)}e^{-\int_s^a \gamma_1(\tau)d\tau}i_2(s)ds \\ &\geq (\rho_2 - 1)K_1 m(a) - \eta V_1^1 m(a) \geq 0 \end{aligned}$$

where η has absorbed appropriate constants and is positive and small enough. In the above system of inequalities V_1^1 denotes

$$V_1^1 = \int_0^\infty h_1(a)P_\infty(a)i_2(a)da.$$

Similarly, for the right-hand side of (51) we would have

$$\begin{aligned} \mathcal{T}[\mathcal{E}_1 - \epsilon v] \quad &= \\ &= \mathcal{T}[\mathcal{E}_1] - \epsilon D\mathcal{T}(\mathcal{E}_1)v - \epsilon^2\mathcal{N}(v) \\ &= \mathcal{E}_1 - \epsilon\rho_1 v - \epsilon^2\mathcal{N}(v) \\ &= \mathcal{E}_1 - \epsilon v - \epsilon(\rho_1 - 1)v - \epsilon^2\mathcal{N}(v) \\ &\leq_K \mathcal{E}_1 - \epsilon v. \end{aligned} \tag{53}$$

As before, since $\rho_1 > 1$, for $\epsilon > 0$ and small enough we have $(\rho_1-1)v+\epsilon\mathcal{N}(v) \geq_K 0$. Therefore, $\mathcal{T}[\mathcal{E}_1 - \epsilon v] \leq_K \mathcal{E}_1 - \epsilon v$. Applying $\mathcal{T}$ again, and taking into account its monotonicity with respect to the order $\leq_K$, we have $\mathcal{T}^2[\mathcal{E}_1 - \epsilon v] \leq_K \mathcal{T}[\mathcal{E}_1 - \epsilon v]$. Iterating this step, we obtain

$$\mathcal{T}^n[\mathcal{E}_1 - \epsilon v] \leq_K \mathcal{T}^{n-1}[\mathcal{E}_1 - \epsilon v].$$

In other words, the sequence $\mathcal{T}^n[\mathcal{E}_1 - \epsilon v]$ is decreasing in the order generated by the cone K. On the other hand, applying $\mathcal{T}$ to inequality (51) and using (52) we have

$$\mathcal{E}_2 + \eta w \leq_K \mathcal{T}[\mathcal{E}_2 + \eta w] \leq_K \mathcal{T}[\mathcal{E}_1 - \epsilon v].$$

Applying $\mathcal{T}$ and using (52) iteratively, we have

$$\mathcal{E}_2 + \eta w \leq_K \mathcal{T}^n[\mathcal{E}_1 - \epsilon v].$$

Thus, the sequence $\mathcal{T}^n[\mathcal{E}_1 - \epsilon v]$ for $n = 1, 2, \ldots$ is a decreasing sequence of elements of $\mathcal{C}$. It is bounded from below from an element of $\mathcal{C}$ that is larger than $\mathcal{E}_2$. Thus, it converges to an element of $\mathcal{C}$ that does not have an identically equal to zero component, that is (i^*, j^*) with $i^* \neq 0$ and $j^* \neq 0$. On the other hand, this element of $\mathcal{C}$ is a fixed point for the operator $\mathcal{T}$, in other words, it a coexistence equilibrium, and a solution to (44). This completes the proof. $\square$

6. **Summary and future work.** This article introduces a two-strain extention with super-infection of the age-structured S-I-S epidemic model considered in [6]. We compute the reproduction numbers of the two strains as well as the reproduction number of the whole system R_0. We find that there is a unique disease-free equilibrium which always exists, and is locally stable if the reproduction number $R_0 < 1$ and unstable if $R_0 > 1$. Furthermore, the disease-free equilibrium is also globally stable in the case when super-infection is less likely than an original infection with strain one: $0 \leq \delta \leq 1$. We also establish that to each strain there corresponds a unique single-strain equilibrium, which exists whenever the corresponding reproduction number is larger than one. The single strain equilibrium of strain i is locally asymptotically stable if and only if the invasion reproduction number of strain j is smaller than one, that is, if and only if strain j cannot invade the equilibrium of strain i. Local stability of the single-strain equilibrium in our model is not surprizing as it agrees with the results of [6]. However, we establish local stability using different mathematical techniques. Finally, we show that if both invasion numbers are larger than one, there exists a coexistence equilibrium. This result follows from the monotonicity of the system with respect to the competitive cone. We rewrite the system of differential equations for the coexsitence equilibrium as a system of integral equations. The integral operator $\mathcal{T}$ has properties similar to the ones established in [6]. A novel critical component that we provide in this article is the connection between the invasion reroduction numbers and the spectral radii of the Fréchet derivatives of the integral operator $\mathcal{T}$.

Although system (1) is more complex than most of the structured two-strain models analyzed so far, we were able to derive in this article all results that are typically obtained for such systems. However, we believe that there are many interesting questions pertaining to system (1) which we have not addressed but could be addressed in the future.

- Persistence. There are multiple different types of persistence (see e.g. [1], p.221). We are most interested in uniform strong persistence. Horst Thieme's results on uniform strong persistence in single strain models will build the backbone of our approach [27, 28]. However, these techniques have never been applied to structured multi-strain models. We expect to establish the following result, currently stated as conjecture:

Conjecture 1. *Assume* $R_0^i > 1$ *and* $R_j^i > 1$*. Then, there exists* $\eta > 0$*, independent of the initial conditions, such that*

$$\liminf_{t} V_j(t) \geq \eta.$$

- Competitive exclusion. It is now known that in the simplest multi-strain ODE models competitive exclusion holds with the strain with the largest reproduction number dominating-a result to which Horst Thieme has contributed immensely [5]. Such a result has not been established for any structured epidemic model, although it is conceivable that the tools developed in [7] could be extended to yield it, at least in the case when no coexistence occurs. No global results on competitive exclusion seem to exist in an age or age-since-infection-structured epidemic model where coexistence is also possible.

  We believe that such a result holds for system (1) and can be derived from conditions on the reproduction numbers and invasion reproduction numbers only. We include our expected result in the form of a conjecture:

  Conjecture 2. *Assume* $R_0^1 > 1$*,* $R_0^2 > 1$*. Assume also* $R_1^2 > 1$ *and* $R_2^1 < 1$*. Then strain one persists, while strain two goes extinct, that is* $j(a,t) \to 0$ *as* $t \to \infty$ *for almost all* a*.*

  Symmetrical result holds where strain one becomes extinct which should also be possible to be established. Clearly, such results may not hold for *all* multi-strain epidemic models but they hold for model (1) and possibly for many other multi-strain epidemic models. Developing the mathematical techniques to derive global results for such classes of models is a task for the future.

  Since model (1) is a monotone model, one may like to use results on monotone dynamical systems – an area to which Horst Thieme has also contributed [24]. Unfortunetely, many of those results are not directly applicable to age-structured models, as one of the common assumptions in that theory is that the baseline space has a positive cone with non-empty interior, a requirement not satisfied by L^1.
- Additional open problems with system (1): Besides persistence and competitive exclusion, there is a number of open and interesting questions regarding system (1). Addressing those questions will further our understanding of age-structured multi-strain epidemic models and their ability to capture key issues in biology, such as genetic diversity, competition, and oscillations.
  1. We have established the global stability of the DFE in the case $0 \leq \delta \leq 1$. Global stability of the DFE typically fails when subthreshold equilibria exist. Does system (1) have subthreshold coexistence equilibria? The presence of subthreshold equilibria in an age-structured two-strain model has previously been established in [18].
  2. A related question is: Does system (1) have a unique coexistence equilibrium, or it may have multiple coexistence equilibria? What conditions on the parameters will guarantee uniqueness of the coexistence equilibrium?

3. Can the coexistence equilibrium become unstable? Are sustained oscillations possible? The answer to this question for the ODE version of model (1) is negative. On the other hand it is known that age-structure in the single-strain S-I-S model does not lead to oscillation [6]. So, if oscillations occur in the age-structured two-strain case, they are a result of the presence of age-structure *and* the interaction of the strains.
4. The presence of super-infection guarantees that coexistence of pathogens will occur even in the ODE version of model (1). However, if super-infection is "turned off", that is $\delta = 0$, then in the ODE version of model (1) coexistence would not occur. If $\delta = 0$ in model (1), would coexistence occur when age is present? We believe that the answer is "yes" and that answer can be established similarly as in [18].

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