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Research article

Global dynamics for a staged progression epidemiological model with age-in-class structure for the post-infection classes

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Abstract: We study a compartment model for transmission of an infectious disease, with age-in-class structure combined with staged progression through an arbitrary number of compartments. Each post-infection compartment is assigned coefficient functions for the rate of progression to the next stage and for the mass action transmissibility. We provide the basic reproduction number $\mathcal{R}_0$, and show that the model exhibits the classic threshold behavior for global stability. If $\mathcal{R}_0 < 1$, then solutions tend to the disease-free equilibrium; if $\mathcal{R}_0 > 1$, then solutions tend to the endemic equilibrium (assuming that the disease is initially present). Furthermore, we characterize the attractor of bounded sets. Some key steps in the analysis are based on Volterra integral equations and Lyapunov's Direct Method.

Keywords: age-in-class structure; global stability; Lyapunov; epidemiology

1. Introduction

For some diseases, an individual's level of infectiousness and their instantaneous likelihood of progressing from one epidemiological stage to another can vary greatly in time, depending on how long since they were initially infected (age-of-infection) or since they entered their current stage (age-in-class).

For example, in the absence of treatment, an HIV infection can often take eight to ten years before the clinical syndrome (AIDS) occurs. The progression goes through several distinct stages, marked by very different $CD4^+$ T-cell counts and viral RNA levels. HIV-infected individuals are highly infectious in the first few weeks after infection, then remain in an asymptotic stage of low infectiousness for several years before gradually becoming more infectious as their immune system becomes compromised, and they progress to AIDS. The World Health Organization categorizes HIV/AIDS as having four clinical stages (asymptomatic and mildly, moderately, and severely symp-

tomatic) [1]. A discussion of age-in-class structure applied to HIV, with progression through three infectious classes, can be found in [2], where the authors focused on optimal intervention strategies.

For another example, it is well-established [3] that tuberculosis can remain dormant within a host's body for years at a time before being activated, whereby the individual may become symptomatic, infectious, or both. This long period of dormancy suggests that a compartmental model based on ordinary differential equations (ODEs) is unlikely to adequately fit the survival distributions (or equivalently, the waiting time distributions) before key epidemiological transitions occur. In [4], the authors studied an age-in-class model of tuberculosis with fast and slow progression to infectiousness while also including vaccination.

For HIV/AIDS and tuberculosis (and likely many other diseases), age-in-class models provide a more nuanced approximation of clinical behavior witnessed in the real world compared with other models.

In [5], a susceptible–infectious (SI) model with age-in-class structure for the infected population was considered. The global stability was resolved with a Lyapunov functional after uniform persistence was studied using nondensely defined Cauchy problems and integrated semi-groups. The same model was considered again in [6, Chapter 9], using a Volterra integral equation approach; this is the approach that we use here.

The author of [7] and [8] investigated susceptible–exposed–infectious (SEI) models with age-in-class structure for latently infected individuals and for infectious individuals, following the approach of [6].

In each of [9–12], the authors studied ODE models that included progression through an arbitrary number of infectious stages. The current work combines the staged progression feature of those models with the age-in-class structure of [5,7] to obtain a staged progression model with age-in-class structure. Infected individuals progress monotonely through a sequence of infected stages $x_1, \ldots, x_n$. The age-in-class structure allows the level of infectiousness, the progression rate from one stage to the next, and the mortality rate to depend on the age-in-class. The combination of staged progression with an age-in-class structure allows for considering discrete epidemiological stages, represented by multiple post-infection classes, while allowing stage-related parameters to depend on the time since entering the particular stage.

This combination results in calculations that are significantly more complex than for corresponding staged-progression ODE models or for models with fewer age-in-class stages, such as the aforementioned SEI models. Furthermore, allowing each post-infection class to be infectious provides much more generality than the SEI models.

In this work, we do not explore the individual applications; rather, we study the global attractor for this versatile and general model.

The model and state space are given in Sections 2 and 3, respectively. Some useful notation is introduced in Section 4. Section 5 provides a discussion of the equilibria and the basic reproduction number $\mathcal{R}_0$. Boundedness and asymptotic smoothness are discussed in Sections 6 and 7. An attractor $\mathcal{A}$ of bounded sets is shown to exist in Section 8. In Section 9, we show that $\mathcal{A}$ consists of only the disease-free equilibrium when $\mathcal{R}_0 < 1$. In Section 10, we establish that the system is uniformly persistent when $\mathcal{R}_0 > 1$, setting the stage for Section 11, where the resulting global dynamics are resolved. A brief discussion of the results appears in Section 12.

2. Model equations

The number of susceptibles at time t is denoted by $S(t)$. Infected individuals may pass through a sequence of compartments $x_1, \ldots, x_n$. For each of these infected groups, the duration (or age-in-class) for which an individual has been in that specific compartment is given by a so that the density of individuals in x_j at time t that have been there for duration a is $x_j(t, a)$ for $j = 1, \ldots, n$.

This allows parameters associated with x_j to be functions of the age-in-class. We assume homogeneous mixing, so we use mass action incidence to describe the rate at which new infections occur. Individuals who have been in class x_j for duration a infect the susceptibles with mass action coefficient $\beta_j(a)$, progress to x_{j+1} at per capita rate $\gamma_j(a)$, and are removed from the population at per capita rate $\mu_j(a)$. In order to simplify many statements throughout the paper, including the second line of Eq (2.1) below, we use the parameter γ_j with $j = n$, even though there is no progression out of x_n, but we take $\gamma_n \equiv 0$. Upon infection, newly infected individuals move into class x_1.

All recruitment into the population is into the susceptible class and occurs with constant flux Λ. Susceptibles are removed from the population at per capita rate μ_S. Parameter functions appear in Table 1, and scalar parameters appear in Table 2.

Table 1. Biological interpretations of parameter functions.

Notation	Description	Dimensions
$\mu_j(a)$	The age-in-class specific per-capita death rate for post-infection stage j, including deaths induced by the disease and by other causes.	Time^{-1}
$\beta_j(a)$	The age-in-class specific disease mass action coefficient for post-infection stage j.	$\text{Person}^{-1}\ \text{Time}^{-1}$
$\gamma_j(a)$	The age-in-class specific per-capita progression rate from post-infection stage j to stage $j+1$.	Time^{-1}
$\Omega_j(a)$	The probability that an individual entering post-infection stage j remains in stage j for duration of at least a.	Dimensionless

We obtain the following system of differential equations:

$$\begin{aligned} \frac{\mathrm{d}S(t)}{\mathrm{d}t} &= \Lambda - \mu_S S(t) - S(t)\sum_{j=1}^{n}\int_0^\infty \beta_j(a)x_j(t,a)\mathrm{d}a \\ \frac{\partial x_j(t,a)}{\partial t} + \frac{\partial x_j(t,a)}{\partial a} &= -(\gamma_j(a)+\mu_j(a))x_j(t,a) \qquad \text{for } j = 1,\ldots,n \end{aligned} \tag{2.1}$$

for $t, a > 0$, with boundary conditions

$$x_1(t,0) = S(t)\sum_{j=1}^{n}\int_0^\infty \beta_j(a)x_j(t,a)\mathrm{d}a$$
$$x_j(t,0) = \int_0^\infty \gamma_{j-1}(a)x_{j-1}(t,a)\mathrm{d}a, \quad 2 \le j \le n \tag{2.2}$$

for all $t > 0$.

Table 2. Biological interpretations of scalar parameters.

Notation	Description	Dimensions
Λ	Rate of recruitment of new individuals into the population via birth and immigration.	Person Time^{-1}
μ_S	The per-capita death rate for the susceptible class.	Time^{-1}
$A_j = \int_0^\infty \gamma_j(a)\Omega_j(a)da$	The probability that an individual entering post-infection stage j will survive to progress to stage $j+1$.	Dimensionless
$B_j = \int_0^\infty \beta_j(a)\Omega_j(a)da$	The expected number of secondary infections generated by an individual during their time in post-infection stage j.	Person^{-1}

We make the following hypotheses about the system parameters, where $\mathbb{L}^\infty_{\ge 0}$ denotes the space of non-negative, bounded, measurable functions defined on $[0, \infty)$.

(H1) $\Lambda, \mu_S > 0$.

(H2) $\beta_j, \gamma_j, \mu_j \in \mathbb{L}^\infty_{\ge 0}$ with respective upper bounds $\bar{\beta}, \bar{\gamma}, \bar{\mu}$ for all $j = 1, \ldots, n$.

(H3) There exists $\mu_0 \in (0, \mu_S]$ such that $\mu_j(a) \ge \mu_0$ for all $a > 0$ and all $j = 1, \ldots, n$.

(H4) β_j and γ_j are Lipschitz on $\mathbb{R}_{\ge 0}$ for all $j = 1, \ldots, n$, with Lipschitz coefficient M_{Lip}.

(H5) For $j = 1, \ldots, n$ and $i = 1, \ldots, n-1$, given any $a > 0$, there exists $a_{\beta_j}, a_{\gamma_i} > a$ such that β_j is positive in some neighborhood of a_{β_j}, and γ_i is positive in some neighborhood of a_{γ_i}.

By **(H4)**, the functions β_j and γ_j are Lipschitz, so another way to formulate **(H5)** would be to say that the support of the functions is unbounded. By the Lipschitz property, each point at which one of these functions is positive is contained in a neighborhood on which the function is positive.

Remark 1: The constant recruitment of Λ is reasonable in the case that the population size does not change substantially. If the population size does not vary excessively, then a proportional birth rate also gives a roughly constant supply of new individuals, so the two options for recruitment would not be substantially different. In such modeling scenarios, a value for Λ can be chosen in conjunction with the per capita death rate μ_S to help set the population size.

Remark 2: The Lipschitz requirement in **(H4)** allows jump discontinuities in the true parameter functions to be approximated to an arbitrary level of accuracy. It also seems that a finite number of

jump discontinuities could be accounted for by including additional post-infection groups so that **(H4)** is not overly restrictive.

3. State space

Following [13], the phase space for the system is

$$\mathcal{Y} = \mathbb{R}_{\geq 0} \times \prod_{j=1}^{n} \mathbb{L}^1_{\geq 0},$$

where $\mathbb{L}^1_{\geq 0}$ is the space of non-negative functions defined on $[0, \infty)$ that are Lebesgue integrable. The norm $\|\cdot\|_{\mathcal{Y}}$ on $\mathcal{Y}$ is defined by

$$\|(y, \varphi_1, \varphi_2, \ldots, \varphi_n)\|_{\mathcal{Y}} \;=\; |y| + \sum_{j=1}^{n} \int_0^\infty \left|\varphi_j(a)\right| \mathrm{d}a \;=\; y + \sum_{j=1}^{n} \int_0^\infty \varphi_j(a) \mathrm{d}a \tag{3.1}$$

and gives the total population size.

The initial condition is

$$X_0 \;=\; (S(0), x_1(0,\cdot), x_2(0,\cdot), \cdots, x_n(0,\cdot)) \;=\; (S_0, \varphi_1(\cdot), \varphi_2(\cdot), \cdots, \varphi_n(\cdot)) \;\in\; \mathcal{Y}$$

(with $S_0 \in \mathbb{R}_{\geq 0}$ and $\varphi_1, \ldots, \varphi_n \in \mathbb{L}^1_{\geq 0}$). Standard existence, uniqueness, continuability, and non-negativity results [13] hold, so the system defines a continuous semi-flow $\Phi : \mathbb{R}_{\geq 0} \times \mathcal{Y} \to \mathcal{Y}$, and the corresponding family of maps $\Phi_t : \mathcal{Y} \to \mathcal{Y}$ given by

$$\Phi(t, X_0) \;=\; \Phi_t(X_0) \;=\; (S(t), x_1(t,\cdot), x_2(t,\cdot), \cdots, x_n(t,\cdot)) \;\in\; \mathcal{Y} \;\text{ for }\; t \geq 0.$$

Remark 3: In this work, the main role of **(H5)** is to demonstrate that whenever the disease is initially present (i.e., whenever at least one of φ_j is positive on a set of positive measure), there will be infections at some future time (via β_j), and there will be further progression into later infection stages (due to γ_j). An alternative approach is to make weaker positivity requirements, perhaps only requiring that at least one of the β_j have positive support, for example, and then discussing which initial conditions would lead to further infections.

Starting in Section 8, we discuss attractors of bounded sets. For that, we need the notion of distance between sets $B, C \subseteq \mathcal{Y}$. The distance from a point $Y_1 \in B$ to C is

$$d(Y_1, C) = \inf_{Y_2 \in C} \|Y_1 - Y_2\|_{\mathcal{Y}},$$

and the distance between B and C is

$$\begin{aligned} d(B, C) &= \sup_{Y_1 \in B} d(Y_1, C) \\ &= \sup_{Y_1 \in B} \inf_{Y_2 \in C} \|Y_1 - Y_2\|_{\mathcal{Y}}. \end{aligned}$$

We note that the distance between sets is typically asymmetric.

4. Notation

We now introduce some notation in anticipation of upcoming calculations. Given an initial condition $X_0 \in \mathcal{Y}$, let $X(t)$ be the solution to Eq (2.1) that passes through X_0 at time 0. Then

$$X(t) \;=\; \Phi_t(X_0) \;=\; (S(t), x_1(t,\cdot), x_2(t,.), \cdots, x_n(t,\cdot)) \;\in\; \mathcal{Y}.$$

It follows from (3.1) that

$$\|X(t)\|_{\mathcal{Y}} \;=\; \|\Phi_t(X_0)\|_{\mathcal{Y}} \;=\; S(t) + \sum_{j=1}^{n} \int_0^\infty x_j(t,a)\mathrm{d}a.$$

For any $a \geq 0$ and for each $j \in \{1, 2, \ldots, n\}$, let

$$\Omega_j(a) = \mathrm{e}^{-\int_0^a \left(\gamma_j(\sigma)+\mu_j(\sigma)\right)\mathrm{d}\sigma}. \tag{4.1}$$

It follows from (**H2**) and (**H3**) that

$$0 < \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})a} \leq \Omega_j(a) \leq \mathrm{e}^{-\mu_0 a} \leq 1 \tag{4.2}$$

for any $a \geq 0$. Because $\gamma_j, \mu_j \in \mathbb{L}^\infty_{\geq 0}$, it also follows from the definition of Ω_j that

$$\Omega_j'(a) = -\Big(\gamma_j(a) + \mu_j(a)\Big)\,\Omega_j(a) \leq 0$$

for almost all $a \geq 0$.

Next, for each $j \in \{1, 2, \ldots, n\}$, let

$$B_j = \int_0^\infty \beta_j(a)\Omega_j(a)\mathrm{d}a \quad \text{and} \quad J_j(t) = \int_0^\infty \beta_j(a)x_j(t,a)\mathrm{d}a, \tag{4.3}$$

and let

$$J(t) = \sum_{j=1}^{n} J_j(t). \tag{4.4}$$

Finally, for each $j \in \{1, 2, \ldots, n-1\}$, let

$$A_j = \int_0^\infty \gamma_j(a)\Omega_j(a)\mathrm{d}a, \quad \text{and} \quad L_j(t) = \int_0^\infty \gamma_j(a)x_j(t,a)\mathrm{d}a. \tag{4.5}$$

It follows from **(H5)** and Eq (4.2) that B_j is positive for each $j \in \{1, 2, \ldots, n\}$. Similarly, A_j is positive for each $j \in \{1, 2, \ldots, n-1\}$.

Using the above notation, we can then rewrite the boundary conditions (2.2) as

$$x_1(t,0) = S(t)J(t) \qquad \text{and} \qquad x_j(t,0) = L_{j-1}(t) \tag{4.6}$$

for $j = 2, \ldots, n$ for all $t > 0$.

Solving the partial differential equation part of Eq (2.1) by the method of characteristics [14], we obtain

$$x_1(t,a) = \begin{cases} S(t-a)J(t-a)\Omega_1(a) & \text{for } 0 \leq a < t \\ \varphi_1(a-t)\dfrac{\Omega_1(a)}{\Omega_1(a-t)} & \text{for } t \leq a \end{cases} \tag{4.7}$$

and

$$x_j(t,a) = \begin{cases} L_{j-1}(t-a)\Omega_j(a) & \text{for } 0 \le a < t \\ \varphi_j(a-t)\dfrac{\Omega_j(a)}{\Omega_j(a-t)} & \text{for } t \le a \end{cases}$$

for $j \in \{2,\dots,n\}$. For later use, we note that

$$x_j(t,a) = x_j(t-a,0)\Omega_j(a) \qquad \text{for } 0 \le a < t \tag{4.8}$$

for each $j \in \{1,\dots,n\}$.

5. Equilibria and the basic reproduction number

A general equilibrium

$$\tilde{E} = \left(\tilde{S}, \tilde{x}_1(\cdot), \dots, \tilde{x}_n(\cdot)\right) \in \mathcal{Y}$$

satisfies

$$\frac{\mathrm{d}\tilde{x}_j(a)}{\mathrm{d}a} = -\left(\mu_j(a) + \gamma_j(a)\right)\tilde{x}_j(a),$$

so

$$\tilde{x}_j(a) = \Omega_j(a)\tilde{x}_j(0) \tag{5.1}$$

for $j = 1,\dots,n$. Evaluating the boundary conditions (2.2) at $\tilde{E}$ and using (5.1) gives

$$\begin{aligned} \tilde{x}_1(0) &= \tilde{S}\left(\sum_{j=1}^{n}\int_0^\infty \beta_j(a)\tilde{x}_j(a)\mathrm{d}a\right) \\ &= \tilde{S}\left(\sum_{j=1}^{n}\int_0^\infty \beta_j(a)\Omega_j(a)\tilde{x}_j(0)\mathrm{d}a\right) \\ &= \tilde{S}\sum_{j=1}^{n} B_j\tilde{x}_j(0) \end{aligned} \tag{5.2}$$

and, for $j = 2,\dots,n$,

$$\begin{aligned} \tilde{x}_j(0) &= \int_0^\infty \gamma_{j-1}(a)\tilde{x}_{j-1}(a)\mathrm{d}a \\ &= \int_0^\infty \gamma_{j-1}(a)\Omega_{j-1}(a)\tilde{x}_{j-1}(0)\mathrm{d}a \\ &= A_{j-1}\tilde{x}_{j-1}(0). \end{aligned}$$

It follows that

$$\tilde{x}_j(0) = \tilde{x}_1(0)\prod_{k=1}^{j-1} A_k \tag{5.3}$$

for $j = 2,\dots,n$. Filling into (5.2) gives

$$\tilde{x}_1(0) = \tilde{S}\,\tilde{x}_1(0)\sum_{j=1}^{n} B_j\prod_{k=1}^{j-1} A_k$$

(where the product is taken to be 1 if $j = 1$). Thus, either

$$\tilde{x}_1(0) = 0 \quad \text{or} \quad \tilde{S} = \frac{1}{\sum_{j=1}^{n} B_j \prod_{k=1}^{j-1} A_k}. \tag{5.4}$$

The first option leads to the disease-free equilibrium

$$\hat{E} = \left(\frac{\Lambda}{\mu_S}, \mathbf{0}, \ldots, \mathbf{0}\right),$$

and the second option leads to the endemic equilibrium $E^* = \left(S^*, x_1^*(\cdot), \ldots, x_n^*(\cdot)\right)$, with $S^* = \tilde{S}$ as given in (5.4) and the x_j^* to be determined below.

It is now useful to write the basic reproduction number, as calculated* using the next-generation operator [15]. We start by calculating the probability p_j that a newly infected individual survives to enter class x_j. Because all new infections enter class x_1, we have $p_1 = 1$. The probability that an individual who arrives in x_{j-1} will progress to x_j is A_{j-1} (see Table 2). Thus, $p_j = \prod_{k=1}^{j-1} A_k$. While in class x_j, the expected number of new infections caused by an individual is B_j. Thus, the total force of infection $\mathcal{F}$ upon susceptibles brought about by each newly infected individual is $\mathcal{F} = \sum_{j=1}^{n} p_j B_j = \sum_{j=1}^{n} \left[B_j \prod_{k=1}^{j-1} A_k\right]$. Multiplying this by the size of the susceptible population at the disease-free equilibrium (i.e., by $\frac{\Lambda}{\mu_S}$), we find

$$\begin{aligned} \mathcal{R}_0 &= \frac{\Lambda}{\mu_S} \sum_{j=1}^{n} \left[B_j \prod_{k=1}^{j-1} A_k \right] \\ &= \frac{\Lambda}{\mu_S} \sum_{j=1}^{n} \left[\int_0^\infty \beta_j(a)\Omega_j(a)\mathrm{d}a \prod_{k=1}^{j-1} \int_0^\infty \gamma_k(a)\Omega_k(a)\mathrm{d}a \right]. \end{aligned} \tag{5.5}$$

We note that $\mathcal{R}_0 = \frac{\Lambda}{\mu_S S^*}$.

Combining the boundary condition for x_1 given in (2.2) evaluated at E^* with the expression for $\frac{\mathrm{d}S}{\mathrm{d}t}$, also evaluated at E^*, we find

$$x_1^*(0) \;=\; S^* \sum_{j=1}^{n} \int_0^\infty \beta_j(a) x_j^*(a)\mathrm{d}a \;=\; \Lambda - \mu_S S^* \;=\; \mu_S S^* \left(\frac{\Lambda}{\mu_S S^*} - 1\right) \;=\; \mu_S S^* \left(\mathcal{R}_0 - 1\right).$$

Using (5.3), we see that E^* is given by

$$S^* = \frac{\Lambda}{\mu_S}\frac{1}{\mathcal{R}_0}, \quad x_1^*(a) = \Omega_1(a)\mu_S S^* \left(\mathcal{R}_0 - 1\right), \quad \text{and} \quad x_j^*(a) = A_1 \cdots A_{j-1}\Omega_j(a) x_1^*(0)$$

for $j = 2, \ldots, n$. Noting that E^* is only in $\mathcal{Y}$ if $\mathcal{R}_0 \geq 1$ and coincides with $\hat{E}$ if $\mathcal{R}_0 = 1$ gives the following result.

Theorem 5.1. *If $\mathcal{R}_0 \leq 1$, then the only equilibrium is $\hat{E}$. If $\mathcal{R}_0 > 1$, then there are two equilibria, $\hat{E}$ and E^*.*

*In the language of [15], there is no heterogeneity, so the h-state variable is scalar. Hence, the expected infectivity operator $A(\tau, \xi, \eta)$ reduces to the scalar function $A(\tau)$, where τ represents the time since infection. Integrating over all $\tau \geq 0$ according to their Eq (3.1) gives the scalar force of infection that we denote by $\mathcal{F}$. Multiplying by the size of the susceptible population at the disease-free equilibrium according to their Eq (3.3) gives $\mathcal{R}_0$.

6. Boundedness

Let

$$\mathcal{Y}_\Delta = \left\{ Y \in \mathcal{Y} : 0 \le \|Y\|_{\mathcal{Y}} \le \frac{\Lambda}{\mu_0} \right\}.$$

The results of this section are similar to the propositions in [7, Section 4], and our proof follows a similar path.

Proposition 6.1. *Let X_0 in $\mathcal{Y}$. Then*

1) $\frac{\mathrm{d}}{\mathrm{d}t} \|\Phi_t(X_0)\|_{\mathcal{Y}} \le \Lambda - \mu_0 \|\Phi_t(X_0)\|_{\mathcal{Y}}$ *for all* $t \ge 0$*;*

2) $\|\Phi_t(X_0)\|_{\mathcal{Y}} \le \max\left\{\frac{\Lambda}{\mu_0}, \frac{\Lambda}{\mu_0} + \mathrm{e}^{-\mu_0 t}\left(\|X_0\|_{\mathcal{Y}} - \frac{\Lambda}{\mu_0}\right)\right\} \le \max\left\{\frac{\Lambda}{\mu_0}, \|X_0\|_{\mathcal{Y}}\right\}$ *for all* $t \ge 0$*;*

3) $\limsup_{t\to\infty} \|\Phi_t(X_0)\|_{\mathcal{Y}} \le \frac{\Lambda}{\mu_0}$*;*

4) Φ *is point dissipative;*

5) the bounded set $\mathcal{Y}_\Delta$ *attracts all points in* $\mathcal{Y}$*;*

6) $\mathcal{Y}_\Delta$ *is positively invariant.*

Proof. We first note that

$$\frac{\mathrm{d}}{\mathrm{d}t} \|\Phi_t(X_0)\|_{\mathcal{Y}} = \frac{\mathrm{d}S}{\mathrm{d}t} + \sum_{j=1}^{n} \frac{\mathrm{d}}{\mathrm{d}t} \int_0^\infty x_j(t,a)\mathrm{d}a. \tag{6.1}$$

By Eq (4.7), we have

$$\int_0^\infty x_1(t,a)\mathrm{d}a = \int_0^t S(t-a)J(t-a)\Omega_1(a)\mathrm{d}a + \int_t^\infty \varphi_1(a-t)\frac{\Omega_1(a)}{\Omega_1(a-t)}\mathrm{d}a.$$

We make the substitution $a = t - \sigma$ in the first integral and $a = t + \tau$ in the second integral, and differentiating by t, we get

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\int_0^\infty x_1(t,a)\mathrm{d}a &= \frac{\mathrm{d}}{\mathrm{d}t}\int_0^t S(\sigma)J(\sigma)\Omega_1(t-\sigma)\mathrm{d}\sigma + \frac{\mathrm{d}}{\mathrm{d}t}\int_0^\infty \varphi_1(\tau)\frac{\Omega_1(t+\tau)}{\Omega_1(\tau)}\mathrm{d}\tau \\ &= S(t)J(t)\Omega_1(0) + \int_0^t S(\sigma)J(\sigma)\Omega_1'(t-\sigma)\mathrm{d}\sigma + \int_0^\infty \varphi_1(\tau)\frac{\Omega_1'(t+\tau)}{\Omega_1(\tau)}\mathrm{d}\tau.\end{aligned}$$

Converting back to integrals in terms of a, noting that $\Omega_1'(a) = -(\gamma_1(a) + \mu_1(a))\,\Omega_1(a)$ almost everywhere and that $\Omega_1(0) = 1$, and combining the two integrals into a single integral, we find

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\int_0^\infty x_1(t,a)\mathrm{d}a &= S(t)J(t) - \int_0^\infty (\gamma_1(a) + \mu_1(a))\, x_1(t,a)\mathrm{d}a \\ &= S(t)\sum_{j=1}^{n}\int_0^\infty \beta_j(a)x_j(t,a)\mathrm{d}a - \int_0^\infty (\gamma_1(a) + \mu_1(a))\, x_1(t,a)\mathrm{d}a.\end{aligned} \tag{6.2}$$

Similarly, for $j = 2, \ldots, n$, we obtain

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^\infty x_j(t,a)\mathrm{d}a = \int_0^\infty \gamma_{j-1}(a)x_{j-1}(t,a)\mathrm{d}a - \int_0^\infty \Big(\gamma_j(a)+\mu_j(a)\Big)x_j(t,a)\mathrm{d}a. \tag{6.3}$$

Combining Eqs (6.2) and (6.3) with the expression for $\frac{\mathrm{d}S}{\mathrm{d}t}$ given in (2.1) (and recalling that $\gamma_n \equiv 0$), we see that Eq (6.1) becomes

$$\frac{\mathrm{d}}{\mathrm{d}t}\left\|\Phi_t(X_0)\right\|_{\mathcal{Y}} = \Lambda - \mu_S S(t) - \sum_{j=1}^{n}\int_0^\infty \mu_j(a)x_j(t,a)\mathrm{d}a.$$

Then by (**H3**), we have

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\left\|\Phi_t(X_0)\right\|_{\mathcal{Y}} &\le \Lambda - \mu_0 S(t) - \mu_0\sum_{j=1}^{n}\int_0^\infty x_j(t,a)\mathrm{d}a\\ &= \Lambda - \mu_0\left\|\Phi_t(X_0)\right\|_{\mathcal{Y}},\end{aligned}$$

which proves the first statement in the proposition.

Using standard theory for differential inequalities [16, Theorem I.6.1], the second statement of the proposition follows from the first. Taking the limsup of the second statement as t tends to infinity gives the third statement. The third statement implies the fourth statement (based on the definition of point dissipativity) and also implies the fifth statement. The sixth statement follows from the second statement by considering initial conditions $X_0 \in \mathcal{Y}_\Delta$. □

The following results are direct consequences of Proposition 6.1.

Corollary 6.2. *Let $X_0 \in \mathcal{Y}$ and let $K \ge \max\left\{\frac{\Lambda}{\mu_0}, \|X_0\|_{\mathcal{Y}}\right\}$. Then the following hold for all $t \ge 0$.*

1) $S(t), \int_0^\infty x_j(t,a)\mathrm{d}a \le K$ for all $j = 1, \ldots, n$;

2) $J(t) \le \bar{\beta}K$;

3) $x_1(t,0) = S(t)J(t) \le \bar{\beta}K^2$ and $x_j(t,0) \le \bar{\gamma}K$ for $j = 2, \ldots, n$.

Corollary 6.3. *Let $B \subseteq \mathcal{Y}$ be bounded. Then*

1) $\Phi(\mathbb{R}_{\ge 0}, B)$ is bounded;

2) Φ is eventually bounded on B;

3) given $K > \frac{\Lambda}{\mu_0}$, there exists T such that $\|\Phi_t(X_0)\|_{\mathcal{Y}} \le K$ for all $X_0 \in B$ and $t \ge T$;

4) if B is bounded by $K > \frac{\Lambda}{\mu_0}$, then $\Phi(\mathbb{R}_{\ge 0}, B)$ is also bounded by K.

Additionally, the differential inequality $\frac{\mathrm{d}S(t)}{\mathrm{d}t} \le \Lambda - \mu_S S(t)$ yields the following result.

Proposition 6.4. *Let X_0 in $\mathcal{Y}$. Then* $\limsup_{t\to\infty} S(t) \le \frac{\Lambda}{\mu_S}$.

7. Asymptotic smoothness

A semi-flow is called asymptotically smooth if each forward-invariant bounded closed set is attracted by a nonempty compact set. A key step in showing that Φ is asymptotically smooth is to show that the boundary conditions given in Eq (2.2) are Lipschitz continuous. We frame this in terms of the functions J_j and L_j, as defined in Eqs (4.3) and (4.5). We follow the approach used in the proof of [7, Proposition 5].

Proposition 7.1. *Let $K \geq \max\left\{\frac{\Lambda}{\mu_0}, \|X_0\|_{\mathcal{Y}}\right\}$. There exists M^*_{Lip} such that the functions $J_1, \ldots, J_n$ and $L_1, \ldots, L_{n-1}$ and J are Lipschitz on $\mathbb{R}_{\geq 0}$, with Lipschitz coefficient M^*_{Lip}. Furthermore, M^*_{Lip} can be chosen as a function of K and the system parameters.*

Proof. We prove here that J_1 is Lipschitz. Let $K \geq \max\left\{\frac{\Lambda}{\mu_0}, \|X_0\|_{\mathcal{Y}}\right\}$. Then, by Proposition 6.1, $\|X(t)\|_{\mathcal{Y}} \leq K$ for all $t \geq 0$.

Let $t \geq 0$ and let $h > 0$. Then

$$\begin{aligned} J_1(t+h) - J_1(t) &= \int_0^\infty \beta_1(a)x_1(t+h,a)\mathrm{d}a - \int_0^\infty \beta_1(a)x_1(t,a)\mathrm{d}a \\ &= \int_0^h \beta_1(a)x_1(t+h,a)\mathrm{d}a + \int_h^\infty \beta_1(a)x_1(t+h,a)\mathrm{d}a - \int_0^\infty \beta_1(a)x_1(t,a)\mathrm{d}a \\ &= \int_0^h \beta_1(a)x_1(t+h-a,0)\Omega_1(a)\mathrm{d}a + \int_h^\infty \beta_1(a)x_1(t+h,a)\mathrm{d}a - \int_0^\infty \beta_1(a)x_1(t,a)\mathrm{d}a. \end{aligned}$$

For the first integral, **(H2)** gives the bound $\beta_1(a) \leq \bar{\beta}$, the Part (3) of Corollary 6.2 gives $x_1(t + h - a, 0) \leq \bar{\beta}K^2$, and Eq (4.2) gives $\Omega_1(a) \leq 1$; for the second integral, we make the substitution $\sigma = a - h$, obtaining

$$J_1(t+h) - J_1(t) \leq \bar{\beta}^2K^2h + \int_0^\infty \beta_1(\sigma+h)x_1(t+h,\sigma+h)\mathrm{d}\sigma - \int_0^\infty \beta_1(a)x_1(t,a)\mathrm{d}a.$$

From Eq (4.8), we note that $x_1(t + h, \sigma + h) = x_1(t, \sigma)\frac{\Omega_1(\sigma+h)}{\Omega_1(\sigma)}$. This helps the two integrals to be combined, giving

$$\begin{aligned} J_1(t+h) - J_1(t) &\leq \bar{\beta}^2K^2h + \int_0^\infty \left(\beta_1(a+h)\frac{\Omega_1(a+h)}{\Omega_1(a)} - \beta_1(a)\right)x_1(t,a)\mathrm{d}a \\ &= \bar{\beta}^2K^2h + \int_0^\infty \left(\beta_1(a+h)\mathrm{e}^{-\int_a^{a+h}(\gamma_1(\tau)+\mu_1(\tau))\mathrm{d}\tau} - \beta_1(a)\right)x_1(t,a)\mathrm{d}a \\ &= \bar{\beta}^2K^2h + \int_0^\infty \beta_1(a+h)\left(\mathrm{e}^{-\int_a^{a+h}(\gamma_1(\tau)+\mu_1(\tau))\mathrm{d}\tau} - 1\right)x_1(t,a)\mathrm{d}a \\ &\qquad + \int_0^\infty \left(\beta_1(a+h) - \beta_1(a)\right)x_1(t,a)\mathrm{d}a. \end{aligned} \tag{7.1}$$

By **(H2)**, $0 \geq -\int_a^{a+h}(\gamma_1(\tau) + \mu_1(\tau))\,\mathrm{d}\tau \geq -(\bar{\gamma} + \bar{\mu})\,h$. Therefore,

$$1 \geq \mathrm{e}^{-\int_a^{a+h}(\gamma_1(\tau)+\mu_1(\tau))\mathrm{d}\tau} \geq \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})h} \geq 1 - (\bar{\gamma} + \bar{\mu})\,h,$$

where the final inequality comes from the fact that e^x lies above its tangent at zero. Therefore, $0 \le \beta_1(a+h)\left|e^{-\int_a^{a+h}(\gamma_1(\tau)+\mu_1(\tau))d\tau} - 1\right| \le \bar{\beta}(\bar{\gamma}+\bar{\mu})h$. Recalling, that $\int_0^\infty x_1(t,a)da \le \|X(t)\|_{\mathcal{Y}} \le K$, we see that Eq (7.1) implies

$$|J_1(t+h) - J_1(t)| \le \bar{\beta}^2 K^2 h + \bar{\beta}(\bar{\gamma}+\bar{\mu})Kh + \int_0^\infty |\beta_1(a+h) - \beta_1(a)|\, x_1(t,a)da. \tag{7.2}$$

Next, we show that the remaining integral in Eq (7.2) is of order h. Using **(H4)**, we find

$$\int_0^\infty |\beta_1(a+h) - \beta_1(a)|\, x_1(t,a)da \le \int_0^\infty M_{\text{Lip}} h\, x_1(t,a)da \le M_{\text{Lip}} hK.$$

Combining with Eq (7.2), we see that J_1 is Lipschitz with coefficient $\left(\bar{\beta}^2 K + \bar{\beta}(\bar{\gamma}+\bar{\mu}) + M_{\text{Lip}}\right)K$.

The proofs for the other J_k and the L_k are essentially the same. The Lipschitz coefficient for J can be chosen to be the sum of the coefficients for the J_k. Choose M^*_{Lip} to be the maximum of each the individual coefficients. □

The semi-flow Φ can be shown to be asymptotically smooth in the same manner that was used for the semi-flow studied in [7], which was based on [6, Theorem 2.46] and [6, Theorem B.2].

Theorem 7.2. *The semi-flow $\Phi : \mathbb{R}_{\ge 0} \times \mathcal{Y} \to \mathcal{Y}$ is asymptotically smooth if there are maps $\Theta, \Psi : \mathbb{R}_{\ge 0} \times \mathcal{Y} \to \mathcal{Y}$ such that $\Phi(t,X) = \Theta(t,X) + \Psi(t,X)$, and the following hold for any bounded closed set C that is forward-invariant under Φ:*

1) $\lim_{t\to\infty} \operatorname{diam} \Theta(t,C) = 0$*;*

2) there exists $t_C \ge 0$ such that $\Psi(t,C)$ has compact closure for each $t \ge t_C$.

We now give Theorem B.2. from [6], as it applies to $L^1_+(\mathbb{R}_{\ge 0})$.

Theorem 7.3. *A set $C \subseteq L^1_+(\mathbb{R}_{\ge 0})$ has compact closure if and only if the following conditions hold:*

1) $\sup_{f\in C} \int_0^\infty f(a)da < \infty$*;*

2) $\lim_{r\to\infty} \int_r^\infty f(a)da \to 0$ *uniformly in $f \in C$;*

3) $\lim_{h\to 0^+} \int_0^\infty |f(a+h) - f(a)|\, da \to 0$ *uniformly in $f \in C$;*

4) $\lim_{h\to 0^+} \int_0^h f(a)da \to 0$ *uniformly in $f \in C$.*

Theorem 7.4. *The flow Φ is asymptotically smooth.*

Proof. Let $C \subset \mathcal{Y}$ be bounded. Let $K > \frac{\Lambda}{\mu_0}$ be a bound for C. Let $X_0 \in C$. We consider the solution $X(t) = \Phi(t, X_0) = (S(t), x_1(t,\cdot), \dots, x_n(t,\cdot))$.

For $t \ge 0$, let $\Psi(t, X_0) = (S(t), \tilde{x}_1(t,\cdot), \dots, \tilde{x}_n(t,\cdot))$ and $\Theta(t, X_0) = (0, \tilde{\varphi}_1(t,\cdot), \dots, \tilde{\varphi}_n(t,\cdot))$, where

$$\tilde{x}_1(t,a) = \left\{ \begin{array}{ll} x_1(t,a) & \text{for } 0 \le a \le t \\ 0 & \text{for } t < a \end{array} \right\} = \left\{ \begin{array}{ll} S(t-a)J(t-a)\Omega_1(a) & \text{for } 0 \le a \le t \\ 0 & \text{for } t < a, \end{array} \right.$$

$$\tilde{x}_j(t,a) = \left\{ \begin{array}{ll} x_j(t,a) & \text{for } 0 \le a \le t \\ 0 & \text{for } t < a \end{array} \right\} = \left\{ \begin{array}{ll} L_{j-1}(t-a)\Omega_j(a) & \text{for } 0 \le a \le t \\ 0 & \text{for } t < a, \end{array} \right.$$

and

$$\tilde{\varphi}_j = x_j - \tilde{x}_j.$$

Then $\Phi = \Theta + \Psi$.

For $t \geq 0$, we have

$$\tilde{\varphi}_j(t,a) = \left\{ \begin{array}{ll} 0 & \text{for } 0 \leq a \leq t \\ x_j(t,a) & \text{for } t < a \end{array} \right\} = \left\{ \begin{array}{ll} 0 & \text{for } 0 \leq a \leq t \\ \varphi_j(a-t)\frac{\Omega_j(a)}{\Omega_j(a-t)} & \text{for } t < a. \end{array} \right.$$

Let the standard norm on L^1 be denoted by $\|\cdot\|_1$. For each $j = 1, \ldots, n$,

$$\left\|\tilde{\varphi}_j(t,\cdot)\right\|_1 \;=\; \int_0^\infty \left|\tilde{\varphi}_j(t,a)\right| \mathrm{d}a \;=\; \int_t^\infty \varphi_j(a-t)\frac{\Omega_j(a)}{\Omega_j(a-t)}\mathrm{d}a \;=\; \int_0^\infty \varphi_j(\sigma)\frac{\Omega_j(\sigma+t)}{\Omega_j(\sigma)}\mathrm{d}\sigma.$$

Using Eq (4.1) to replace Ω_j and then using **(H3)**, we find

$$\left\|\tilde{\varphi}_j(t,\cdot)\right\|_1 \;=\; \int_0^\infty \varphi_j(\sigma)\mathrm{e}^{-\int_\sigma^{\sigma+t}(\gamma(\tau)+\mu(\tau))\mathrm{d}\tau}\mathrm{d}\sigma \;\leq\; \mathrm{e}^{-\mu_0 t}\int_0^\infty \varphi_j(\sigma)\mathrm{d}\sigma \;\leq\; K\mathrm{e}^{-\mu_0 t},$$

which tends to zero as t goes to ∞. It follows that $\Theta(t, X_0)$ approaches $\mathbf{0} \in \mathcal{Y}$ with uniform exponential speed, and therefore $\lim_{t\to\infty} \operatorname{diam} \Theta(t, C) = 0$, as required by Theorem 7.2.

Next, we show that there exists $t_C \geq 0$ such that $\Psi(t, C) \subseteq \mathcal{Y}$ has compact closure for each $t \geq t_C$. Pick any $t_C > 0$, and suppose $t \geq t_C$.

By Part (4) of Corollary 6.3, we know that $S(t)$ remains in the compact set $[0, K]$. Next, we show that $\tilde{x}_1$ remains in a pre-compact subset of L^1_+ that is independent of X_0. This is done by verifying Conditions (1–4) of Theorem 7.3.

By Corollary 6.2 and Eq (4.2), we have

$$0 \leq \tilde{x}_1(t,a) = \left\{ \begin{array}{ll} S(t-a)J(t-a)\Omega_j(a) & \text{for } 0 \leq a \leq t \\ 0 & \text{for } t < a \end{array} \right\} \leq \bar{\beta}K^2,$$

from which Conditions (1, 2, 4) of Theorem 7.3 follow directly. Now, we demonstrate that Condition (3) holds. Because we are interested in the limit as h tends to 0^+, we consider $h \in (0, t)$. (Such an h

exists because $t \geq t_C > 0$.) Then

$$\begin{aligned}
&\int_0^\infty |\tilde{x}_1(t,a+h) - \tilde{x}_1(t,a)|\mathrm{d}a \\
&\quad = \int_0^{t-h} |S(t-a-h)J(t-a-h)\Omega_1(a+h) - S(t-a)J(t-a)\Omega_1(a)|\,\mathrm{d}a \\
&\qquad\qquad + \int_{t-h}^{t} |0 - S(t-a)J(t-a)\Omega_1(a)|\,\mathrm{d}a \\
&\quad \leq \bar{\beta}K^2 h + \int_0^{t-h} |S(t-a-h)J(t-a-h)\Omega_1(a+h) - S(t-a)J(t-a)\Omega_1(a)|\,\mathrm{d}a \\
&\quad \leq \bar{\beta}K^2 h + \int_0^{t-h} S(t-a-h)J(t-a-h)\,|\Omega_1(a+h) - \Omega_1(a)|\,\mathrm{d}a \\
&\qquad\qquad + \int_0^{t-h} |S(t-a-h)J(t-a-h) - S(t-a)J(t-a)|\,\Omega_1(a)\mathrm{d}a \\
&\quad \leq \bar{\beta}K^2 h + \bar{\beta}K^2 \int_0^{t-h} |\Omega_1(a+h) - \Omega_1(a)|\,\mathrm{d}a \\
&\qquad\qquad + \int_0^{t-h} |S(t-a-h)J(t-a-h) - S(t-a)J(t-a)|\,\Omega_1(a)\mathrm{d}a.
\end{aligned} \tag{7.3}$$

Recalling Eqs (4.1) and (4.2), we note that Ω_1 is a decreasing function, which takes values in the unit interval. Thus,

$$\int_0^{t-h} |\Omega_1(a+h) - \Omega_1(a)|\,\mathrm{d}a \;=\; \int_0^{t-h} (\Omega_1(a) - \Omega_1(a+h))\,\mathrm{d}a \;=\; \int_0^{h} \Omega_1(a)\mathrm{d}a - \int_{t-h}^{t} \Omega_1(a)\mathrm{d}a \;\leq\; h.$$

Combining this with Eq (7.3), we find

$$\begin{aligned}
&\int_0^\infty |\tilde{x}_1(t,a+h) - \tilde{x}_1(t,a)|\mathrm{d}a \\
&\qquad\qquad \leq 2\bar{\beta}K^2 h + \int_0^{t-h} |S(t-a-h)J(t-a-h) - S(t-a)J(t-a)|\,\Omega_1(a)\mathrm{d}a.
\end{aligned} \tag{7.4}$$

Next, we show that the remaining integral on the right-hand side is also of order h. Combining Corollary 6.2 with the expression for $\frac{\mathrm{d}S}{\mathrm{d}t}$ given in Eq (2.1), we see that $\left|\frac{\mathrm{d}S}{\mathrm{d}t}\right|$ is bounded by $M_S = \Lambda + \mu_S K + \bar{\beta}K^2$, and therefore $S(\cdot)$ is Lipschitz on $[0,\infty)$, with coefficient M_S. By Proposition 7.1, J is also Lipschitz, with coefficient M^*_{Lip}.

Using the product rule [7, Proposition 6], we see that $S(\cdot)J(\cdot)$ is Lipschitz on $[0,\infty)$, with coefficient $M_{SJ} = KM^*_{\mathrm{Lip}} + M_S\bar{\beta}K$. Therefore, for $a \in [0, t-h)$,

$$|S(t-a-h)J(t-a-h) - S(t-a)J(t-a)|\,\Omega_1(a) \;\leq\; M_{SJ}h\Omega_1(a) \;\leq\; M_{SJ}h\mathrm{e}^{-\mu_0 a}.$$

Thus, Eq (7.4) leads to

$$\begin{aligned}\int_0^\infty |\tilde{x}_1(t,a+h)-\tilde{x}_1(t,a)|\mathrm{d}a &\le 2\bar{\beta}K^2h + M_{SJ}h\int_0^{t-h}\mathrm{e}^{-\mu_0 a}\mathrm{d}a\\ &\le 2\bar{\beta}K^2h + \frac{M_{SJ}}{\mu_0}h\\ &= \left(2\bar{\beta}K^2 + \frac{M_{SJ}}{\mu_0}\right)h.\end{aligned}$$

We note that M_{SJ} depends on K, which depends on the set C, but not on X_0. Therefore, this inequality holds for any $X_0 \in C$, so Condition (3) of Theorem 7.3 is satisfied. Thus, $\tilde{x}_1$ remains in a pre-compact subset $C_{K,1}$ of L^1_+. Similarly, $\tilde{x}_j$ remains in a pre-compact subset $C_{K,j}$ of L^1_+. Thus, $\Psi(t,C) \subseteq [0,K]\times C_{K,1}\times\cdots\times C_{K,n}$, which has compact closure in $\mathcal{Y}$. It follows that $\Psi(t,C)$ has compact closure for each $t \ge t_C$. Thus, the second condition of Theorem 7.2 is satisfied, and therefore Φ is asymptotically smooth. □

8. The attractor of bounded sets

A total trajectory of Φ is a function $X : \mathbb{R} \to \mathcal{Y}$ such that $\Phi_s(X(t)) = X(t+s)$ for all $t \in \mathbb{R}$ and all $s \ge 0$. For a total trajectory,

$$x_j(t,a) = x_j(t-a,0)\Omega_j(a) \tag{8.1}$$

for all $t \in \mathbb{R}$ and all $a \ge 0$ [6]. We now extend the definitions of $J_j(t)$, $J(t)$, and $L_j(t)$, given in Eqs (4.3)–(4.5), to all $t \in \mathbb{R}$ when $X(t)$ is a total trajectory. Total trajectories often have nice properties [6]. For example:

Proposition 8.1. *If $Y : \mathbb{R} \to \mathcal{Y}$ is a total trajectory, then the corresponding functions $J(t)$ and $L_j(t)$ are Lipschitz on $[t_\square, \infty)$ for any $t_\square$ in $\mathbb{R}$ and for any $j \in \{1,\dots,n-1\}$.*

Proof. Given $t_\square \in \mathbb{R}$, let $X_0 = Y(t_\square)$. Then the result follows from Proposition 7.1. □

A nonempty set $\tilde{A}$ is an attractor of bounded sets if $\tilde{A}$ is invariant under Φ and if $d(\Phi_t(B), \tilde{A})$ tends to zero for each bounded set $B \subset \mathcal{Y}$; that is, given any $\epsilon > 0$, there exists $T > 0$ such that for each $X_0 \in B$, there exists $Y_0 \in \tilde{A}$ such that

$$\|\Phi_T(X_0) - Y_0\|_{\mathcal{Y}} < \epsilon.$$

Such an attractor consists of total trajectories; that is, for each Y_0 in $\tilde{A}$, there exists a total trajectory Y such that $Y(0) = Y_0$ and $Y(t) \in \tilde{A}$ for all $t \in \mathbb{R}$.

Theorem 8.2. *There exists a compact set $\mathcal{A} \subseteq \mathcal{Y}_\Delta$, which is the attractor of bounded sets.*

Proof. Proposition 6.1, Corollary 6.3, and Theorem 7.4 show that Φ is point dissipative, eventually bounded on bounded sets, and asymptotically smooth. Thus, the existence of an attractor $\mathcal{A}$ of bounded sets follows from Theorem 2.33 of [6]. The fact that $\mathcal{A}$ is a subset of $\mathcal{Y}_\Delta$ follows from Part (5) of Proposition 6.1. □

The following corollary follows from Propositions 6.1 and 6.4.

Corollary 8.3. *If $X_0 = (S_0, \varphi_1, \dots, \varphi_n)$ in $\mathcal{A}$, then $\|X_0\|_{\mathcal{Y}} \le \frac{\Lambda}{\mu_0}$ and $0 \le S_0 \le \frac{\Lambda}{\mu_S}$.*

9. Behavior for $\mathcal{R}_0 < 1$

Suppose $X_0 \in \mathcal{A}$ and $X(t)$ is a total trajectory in $\mathcal{A}$ satisfying $X(0) = X_0$. Let

$$\bar{J} = \sup_{t\in\mathbb{R}} J(t) \qquad \text{and} \qquad \bar{L}_j = \sup_{t\in\mathbb{R}} L_j(t) \tag{9.1}$$

for $j = 1, \ldots, n-1$.

Using, in sequence, the second part of (4.5), (8.1), (4.6), and (9.1) and then the first part of (4.5), it follows, for all $t \in \mathbb{R}$ and for $j = 2, \ldots, n-1$, that

$$\begin{aligned} L_j(t) &= \int_0^\infty \gamma_j(a)x_j(t,a)\mathrm{d}a \\ &= \int_0^\infty \gamma_j(a)\Omega_j(a)x_j(t-a,0)\mathrm{d}a \\ &= \int_0^\infty \gamma_j(a)\Omega_j(a)L_{j-1}(t-a)\mathrm{d}a \\ &\le \int_0^\infty \gamma_j(a)\Omega_j(a)\bar{L}_{j-1}\mathrm{d}a \\ &\le A_j\bar{L}_{j-1}. \end{aligned}$$

Taking the supremum on the left-hand side, we obtain

$$\bar{L}_j \le A_j\bar{L}_{j-1} \qquad \text{for } j = 2, \ldots, n. \tag{9.2}$$

Using similar steps, along with Corollary 8.3 to bound S, we obtain

$$\bar{L}_1 \le \frac{\Lambda}{\mu_S}A_1\bar{J}. \tag{9.3}$$

Combining (9.2) and (9.3), we have

$$\bar{L}_j \le \frac{\Lambda}{\mu_S}\left(\prod_{i=1}^{j} A_i\right)\bar{J} \qquad \text{for } j = 1, \ldots, n. \tag{9.4}$$

By a similar process, using (4.3) in place of (4.5), we obtain

$$\bar{J} \le \frac{\Lambda}{\mu_S}B_1\bar{J} + \sum_{k=1}^{n-1} B_{k+1}\bar{L}_k. \tag{9.5}$$

Combining (9.4) with (9.5) and then with (5.5), we obtain

$$\begin{aligned} \bar{J} &\le \frac{\Lambda}{\mu_S}\left(B_1 + B_2A_1 + \cdots + B_n\prod_{i=1}^{n-1} A_i\right)\bar{J} \\ &= \mathcal{R}_0\bar{J}. \end{aligned}$$

If $\mathcal{R}_0 < 1$, then the only non-negative solution to this is $\bar{J} = 0$. By **(H5)**, the support of each β_j is unbounded. If x_j is not identically zero, then at some later time, J_j would be positive, and hence, $\bar{J}$ would be positive. Thus, $\bar{J}$ being zero means that each x_j is identically zero for the solution $X(t)$ in the attractor, from which it follows that $S(t)$ is identically equal to the value of S at the disease-free equilibrium. Because this is true for each solution in the attractor, we have the following result.

Theorem 9.1. *If $\mathcal{R}_0 < 1$, then the attractor of bounded sets is $\mathcal{A} = \{\hat{E}\}$.*

By reducing our focus to the attractor for individual solutions, we get the following result.

Theorem 9.2. *If $\mathcal{R}_0 < 1$, then*

$$\lim_{t\to\infty} X(t) = \hat{E}.$$

10. Uniform persistence for $\mathcal{R}_0 > 1$

We begin by showing that the system is uniformly weakly ρ-persistent with persistence function $\rho(X(t)) = J(t)$, by using a Laplace transform approach. We then show that the system is uniformly (strongly) ρ-persistent, following the approach in [6, Chapter 9].

Recall that φ_j, the initial condition for x_j, is an element of $\mathbb{L}^1_{\geq 0}$. Note that if φ_j is the zero function for each j, then the disease is initially absent; in that case, the disease would remain absent for all $t > 0$. The more interesting situation involves initial conditions for which the disease is initially present.

Proposition 10.1. *Either $\varphi_j = \mathbf{0}$ for all j, and therefore $x_j(t, .) = \mathbf{0}$ for all j and $t > 0$, or $J(t)$ takes on positive values for arbitrarily large values of t.*

Proof. Choose any $T > 0$. We want to show that there exists $t \geq T$ such that $J(t)$ is positive.

For any $t \geq 0$,

$$\begin{aligned} J(t) &= \sum_{j=1}^{n} \int_0^\infty \beta_j(a) x_j(t,a) \mathrm{d}a \\ &= \sum_{j=1}^{n} \int_0^t \beta_j(a) x_j(t-a,0) \Omega_j(a) \mathrm{d}a + \sum_{j=1}^{n} \int_t^\infty \beta_j(a) \varphi_j(a-t) \frac{\Omega_j(a)}{\Omega_j(a-t)} \mathrm{d}a \\ &\geq \sum_{j=1}^{n} \int_t^\infty \beta_j(a) \varphi_j(a-t) \frac{\Omega_j(a)}{\Omega_j(a-t)} \mathrm{d}a. \end{aligned}$$

It follows from the definition of Ω_j in (4.1) combined with **(H2)** that $\frac{\Omega_j(a)}{\Omega_j(a-t)} \geq \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t}$. Thus,

$$J(t) \geq \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t} \sum_{j=1}^{n} \int_t^\infty \beta_j(a) \varphi_j(a-t) \mathrm{d}a.$$

Assume that $\varphi_{j_0} \not\equiv \mathbf{0}$ for some $j_0 \in \{1, \ldots, n\}$. Then there exists a set $C \subseteq \mathbb{R}_{\geq 0}$ of positive measure such that $\varphi_{j_0} > 0$ on C. Let σ be the essential infimum of C; then an integral of φ_{j_0} on any interval beginning at σ will always be positive.

By **(H4)** and **(H5)**, there exist $\delta, \nu > 0$ and $\tilde{a} > T + \sigma$ such that $\beta_{j_0}(a) > \nu$ for $a \in [\tilde{a}, \tilde{a} + \delta]$ and such that, based on how σ was chosen, $\int_\sigma^{\sigma+\delta} \varphi_{j_0}(a) \mathrm{d}a$ is positive.

Let $t = \tilde{a} - \sigma$. Then $t > T$ and

$$\begin{aligned} J(t) &\geq \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t} \int_t^\infty \beta_{j_0}(a)\varphi_{j_0}(a-t)\mathrm{d}a \\ &= \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t} \int_0^\infty \beta_{j_0}(u+t)\varphi_{j_0}(u)\mathrm{d}u \\ &\geq \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t} \int_\sigma^{\sigma+\delta} \beta_{j_0}(u+t)\varphi_{j_0}(u)\mathrm{d}u. \end{aligned}$$

Noting that $\beta_{j_0}(u+t) > \nu$ for $u \in (\sigma, \sigma+\delta)$, we have

$$\begin{aligned} J(t) &\geq \nu \mathrm{e}^{-(\bar{\gamma}+\bar{\mu})t} \int_\sigma^{\sigma+\delta} \varphi_{j_0}(u)\mathrm{d}u \\ &> 0, \end{aligned}$$

as desired. □

For the remainder of this section, we assume that the disease is initially present; that is, the support of at least one of φ_j has a positive measure, and therefore $J(t)$ takes positive values for arbitrarily large values of t (see Proposition 10.1). Recalling that $J(t)$ is Lipschitz (see Proposition 7.1), it follows that J is positive on a set of positive measure.

We now obtain an inequality involving long-term behavior of $J(t)$, which assists in the proof of Theorem 10.2 below. In particular, we will demonstrate that the limit superior of $J(t)$ is positive.

From the definition of $J_1(t)$ (see (4.3)), we can observe that

$$\begin{aligned} J_1(t) &\geq \int_0^t \beta_1(a)x_1(t,a)\mathrm{d}a \\ &= \int_0^t \beta_1(a)\Omega_1(a)x_1(t-a,0)\mathrm{d}a \\ &= \int_0^t \beta_1(a)\Omega_1(a)S(t-a)J(t-a)\mathrm{d}a. \end{aligned}$$

For $j = 1, \ldots, n$, let $\omega_j(a) = \beta_j(a)\Omega_j(a)$ and let $f_j(a) = \gamma_j(a)\Omega_j(a)$. Then

$$J_1(t) \geq \int_0^t \omega_1(a)S(t-a)J(t-a)\mathrm{d}a. \tag{10.1}$$

Using the same process as above, for $j = 2, \ldots, n$, we find

$$J_j(t) \geq \int_0^t \int_0^{t-a_j} \cdots \int_0^{t-a_j-\cdots-a_2} \Big[Q_j\Big]\mathrm{d}a_1 \ldots \mathrm{d}a_{j-1}\,\mathrm{d}a_j, \tag{10.2}$$

where

$$Q_j = \omega_j\left(a_j\right) f_{j-1}\left(a_{j-1}\right) f_{j-2}\left(a_{j-2}\right) \ldots f_1\left(a_1\right) S\left(t-a_j-\cdots-a_1\right) J\left(t-a_j-\cdots-a_1\right).$$

Because $J(t) = \sum_{j=1}^n J_j(t)$, Eqs (10.1) and (10.2) yield

$$J(t) \geq \int_0^t \omega_1(a)S(t-a)J(t-a)\mathrm{d}a + \sum_{j=2}^n \int_0^t \int_0^{t-a_j} \cdots \int_0^{t-a_j-\cdots-a_2} \Big[Q_j\Big]\mathrm{d}a_1 \ldots \mathrm{d}a_{j-1}\,\mathrm{d}a_j. \tag{10.3}$$

Let

$$J^\infty = \limsup J(t) \qquad \text{and} \qquad S_\infty = \liminf S(t).$$

Let $\epsilon > 0$. Then there exist $T_1 \geq 0$ such that $J(t) \leq J^\infty + \frac{\epsilon}{2}$ for all $t \geq T_1$. Then it follows from the expression for $\frac{\mathrm{d}S(t)}{\mathrm{d}t}$ that $S_\infty \geq \frac{\Lambda}{\mu_S + J^\infty + \frac{\epsilon}{2}}$. Thus, there exist $T_2 \geq T_1$ such that

$$S(t) \geq \frac{\Lambda}{\mu_S + J^\infty + \epsilon} \tag{10.4}$$

for all $t \geq T_2$. We now perform a time-shift of T_2 on the solution being studied; that is, we replace the initial condition X_0 by $X_1 = \Phi_{T_2}(X_0)$. The solution passing through X_1 at time $t = 0$ satisfies (10.3) for all $t \geq 0$. Furthermore, the bound (10.4) is valid for the new solution for all $t \geq 0$. Thus, Eq (10.3) leads to

$$\begin{aligned} J(t) \geq \frac{\Lambda}{\mu_S + J^\infty + \epsilon}\Bigg(& \int_0^t \omega_1(a) J(t-a)\mathrm{d}a \\ & + \sum_{j=2}^{n} \int_0^t \int_0^{t-a_j} \cdots \int_0^{t-a_j-\cdots-a_2} \Big[\omega_j\left(a_j\right) f_{j-1}\left(a_{j-1}\right) f_{j-2}\left(a_{j-2}\right) \ldots f_1\left(a_1\right) \\ & \qquad J\Big(t - a_j - \cdots - a_1\Big)\Big]\mathrm{d}a_1 \ldots \mathrm{d}a_{j-1}\, \mathrm{d}a_j\Bigg). \end{aligned}$$

Using the definition of convolution, this can be rewritten as

$$J(t) \geq \frac{\Lambda}{\mu_S + J^\infty + \epsilon}\left[(\omega_1 * J) + \sum_{j=2}^{n}\Big(\omega_j * f_{j-1} * \ldots * f_1 * J\Big)\right](t).$$

Taking the Laplace transform of both sides converts the sum of convolutions to a sum of products, giving

$$\hat{J}(\lambda) \geq \frac{\Lambda}{\mu_S + J^\infty + \epsilon}\left[\hat{\omega}_1(\lambda) + \sum_{j=2}^{n} \hat{\omega}_j(\lambda)\hat{f}_{j-1}(\lambda)\ldots\hat{f}_1(\lambda)\right]\hat{J}(\lambda). \tag{10.5}$$

J is positive on a set of positive measure, and therefore $\hat{J}(\lambda)$ is strictly positive; hence, both sides of (10.5) can be divided by $\hat{J}(\lambda)$. Taking the limit as ϵ tends to zero, we obtain

$$1 \geq \frac{\Lambda}{\mu_S + J^\infty}\left[\hat{\omega}_1(\lambda) + \sum_{j=2}^{n} \hat{\omega}_j(\lambda)\hat{f}_{j-1}(\lambda)\ldots\hat{f}_1(\lambda)\right]. \tag{10.6}$$

Recall the Laplace transform definition, giving $\hat{\omega}_1(\lambda) = \int_0^\infty \mathrm{e}^{-\lambda a}\omega_1(a)\mathrm{d}a$. It follows that $\lim_{\lambda\to 0}\hat{\omega}_1(\lambda) = \int_0^\infty \omega_1(a)\mathrm{d}a$, with similar limits applying to the other Laplace transforms. Thus, in the limit as λ tends to zero, (10.6) yields

$$\begin{aligned} 1 &\geq \frac{\Lambda}{\mu_S + J^\infty}\left[\int_0^\infty \beta_1(a)\Omega_1(a)\mathrm{d}a + \sum_{j=2}^{n}\int_0^\infty \beta_j(a)\Omega_j(a)\mathrm{d}a \prod_{k=1}^{j-1}\int_0^\infty \gamma_k(a)\Omega_k(a)\mathrm{d}a\right] \\ &= \frac{\Lambda}{\mu_S + J^\infty}\sum_{j=1}^{n}\left(B_j\prod_{k=1}^{j-1}A_k\right) \\ &= \frac{\mu_S}{\mu_S + J^\infty}\mathcal{R}_0. \end{aligned}$$

Rearranging leads to

$$J^\infty \geq \mu_S \left(\mathcal{R}_0 - 1\right),$$

which is clearly positive for $\mathcal{R}_0 > 1$.

Now, define $\rho : \mathcal{Y} \to \mathbb{R}_{\geq 0}$ by

$$\rho\left(x_1, \varphi_1, \ldots, \varphi_n\right) = \sum_{j=1}^{n} \int_0^\infty \beta_j(a)\varphi_j(a)\mathrm{d}a. \tag{10.7}$$

The *disease-free space* is

$$\mathcal{Y}_{\mathrm{DF}} = \{Y_0 \in \mathcal{Y} : \rho\left(\Phi_t(Y_0)\right) = 0 \text{ for all } t \in \mathbb{R}_{\geq 0}\}.$$

For $t \geq 0$,

$$\rho(\Phi_t(X_0)) \;=\; \sum_{j=1}^{n} \int_0^\infty \beta_j(a)x_j(t,a)\mathrm{d}a \;=\; J(t).$$

Consequently, if the disease is initially present, then $\limsup \rho(\Phi_t(X_0)) = J^\infty \geq \mu_S\left(\mathcal{R}_0 - 1\right)$. We have proved the following.

Theorem 10.2. *If $\mathcal{R}_0 > 1$, then the semi-flow is uniformly weakly ρ-persistent.*

In order to move from uniform weak persistence to uniform persistence, we follow the approach in [6, Lemma 9.12]. To this end, we state without proof the following proposition, whose proof is similar to [7, Proposition 9].

Proposition 10.3. *For a total trajectory $X(\cdot)$ in $\mathcal{Y}$, $S(t)$ is strictly positive, and either J is identically zero or J is strictly positive.*

Theorem 10.4. *If $\mathcal{R}_0 > 1$, then the semi-flow is uniformly ρ-persistent.*

Proof. The result follows from Proposition 7.1 (which implies that J is continuous), Theorem 8.2, Theorem 10.2, Proposition 10.3, and [6, Theorem 5.2]. □

The following result follows from Proposition 7.1, Theorem 10.2, Proposition 10.3, and [6, Theorem 5.7]. It describes the *disease-free attractor* $\mathcal{A}_{\mathrm{DF}}$ (the attractor for subsets of the disease-free space) and the *persistence attractor* $\mathcal{A}_{\mathrm{P}}$ (the attractor for subsets that remain bounded away from the disease-free space), along with the set C of saddle connectors between them (i.e., solutions that approach $\mathcal{A}_{\mathrm{DF}}$ as t tends to negative infinity and approach $\mathcal{A}_{\mathrm{P}}$ as t tends to infinity)).

Theorem 10.5. *If $\mathcal{R}_0 > 1$, then the attractor $\mathcal{A}$ is the disjoint union $\mathcal{A} = \mathcal{A}_{DF} \cup C \cup \mathcal{A}_{P}$, where the following hold:*

1) $\mathcal{A}_{DF}$ and $\mathcal{A}_{P}$ are compact and invariant;

2) $\mathcal{A}_{DF} = \mathcal{A} \cap \mathcal{Y}_{DF}$ is the compact attractor of all bounded sets in $\mathcal{Y}_{DF}$;

3) ρ is bounded away from 0 on $\mathcal{A}_{P}$;

4) $\mathcal{A}_{P}$ attracts all bounded sets in $\mathcal{Y} \setminus \mathcal{Y}_{DF}$ on which $\rho \circ \Phi$ is eventually uniformly positive;

5) $\mathcal{A}_P$ is stable;

6) $\mathcal{C}$ is invariant and consists of total trajectories with alpha limit sets in $\mathcal{A}_{DF}$ and omega limit sets in $\mathcal{A}_P$.

Corollary 10.6. *Suppose $\mathcal{R}_0 > 1$. Let $X(t) = (S(t), x_1(t,.), \ldots, x_n(t,.))$ be a total trajectory in $\mathcal{A}_P$. Then there exists $\epsilon > 0$ such that $S(t), x_1(t,0), \cdots, x_n(t,0) > \epsilon$ for all $t \in \mathbb{R}$.*

Proof. Because $X(t)$ is a total trajectory in the persistence attractor $\mathcal{A}_P$, the bound in Eq (10.4) must be valid for $S(t)$ for all $t \in \mathbb{R}$, so $S(t)$ is bounded away from zero. For $j = 1, \ldots, n$, let

$$\bar{\epsilon}_j = \inf_{t\in\mathbb{R}} x_j(t,0).$$

It follows from the first part of Eq (4.6) and Part (iii) of Theorem 10.5 that $\bar{\epsilon}_1 > 0$.

For $j = 1, \ldots, n-1$, it follows from the second part of (4.6) that

$$\begin{aligned} x_{j+1}(t,0) = L_j(t) &= \int_0^\infty \gamma_j(a)x_j(t,a)\mathrm{d}a = \int_0^\infty \gamma_j(a)x_j(t-a,0)\Omega_j(a)\mathrm{d}a \\ &\geq \bar{\epsilon}_j \int_0^\infty \gamma_j(a)\Omega_j(a)\mathrm{d}a \\ &= \bar{\epsilon}_j A_j. \end{aligned}$$

Taking the infimum over all t of the left-hand side, we have

$$\bar{\epsilon}_{j+1} \geq \bar{\epsilon}_j A_j.$$

Because each A_j is positive (see the paragraph following Eq (4.5)), it follows that each $\bar{\epsilon}_j$ is positive, from which the corollary follows. □

11. Behavior for $\mathcal{R}_0 > 1$.

Throughout this section, it will be useful to work with new variables that scale the original variables to the equilibrium value. This will allow lengthy expressions in the upcoming Lyapunov calculation to be written more concisely. Let

$$s = s(t) = \frac{S(t)}{S^*}, \qquad y_j = y_j(t,a) = \frac{x_j(t,a)}{x_j^*(a)}, \quad \text{and} \quad z_j = z_j(t) = \frac{x_j(t,0)}{x_j^*(0)}.$$

The following result is similar to [7, Section 9] and can be proved similarly.

Theorem 11.1. *If $X_0 \in \mathcal{Y}_{DF}$, then $X(t)$ tends to the disease-free equilibrium $\hat{E}$. Furthermore, $\mathcal{A}_{DF} = \{\hat{E}\}$.*

The following lemma will be useful during the Lyapunov calculation. It allows groups of terms to be added to the integrand of certain integrals without changing the value of the full expression. It will be used in the proof of Theorem 11.4 to move from (11.6) to (11.7).

Lemma 11.2. *Each solution of Eq (2.1) satisfies*

$$\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[sy_j(t,a)-z_1-\frac{sy_j(t,a)}{z_1}+1\right]\mathrm{d}a=0 \tag{11.1}$$

and satisfies

$$\int_0^\infty \gamma_j(a)x_j^*(a)\left[y_j(t,a)-z_{j+1}-\frac{y_j(t,a)}{z_{j+1}}+1\right]\mathrm{d}a=0 \tag{11.2}$$

for $j=1,\dots,n-1$.

Proof. Using the boundary condition given in Eq (2.2), we observe that

$$\begin{aligned}
0 &= x_1(t,0)-x_1^*(0)\frac{x_1(t,0)}{x_1^*(0)}\\
&= \sum_{j=1}^{n}\int_0^\infty \beta_j(a)S(t)x_j(t,a)\mathrm{d}a-\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\mathrm{d}a\frac{x_1(t,0)}{x_1^*(0)}\\
&= \sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[\frac{S(t)}{S^*}\frac{x_j(t,a)}{x_j^*(a)}-\frac{x_1(t,0)}{x_1^*(0)}\right]\mathrm{d}a\\
&= \sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\Big[sy_j(t,a)-z_1\Big]\mathrm{d}a.
\end{aligned}$$

Multiplying by $\left(1-\frac{1}{z_1}\right)$ gives (11.1). Similarly, for $j=1,\dots,n-1$, using the boundary condition for $x_{j+1}(t,0)$, and eventually multiplying by $\left(1-\frac{1}{z_{j+1}}\right)$ gives (11.2). □

The next result appears as Lemma 9.4 in [7], and will be a key part of the calculation that leads to the proof of Theorem 11.4, allowing the integral terms in the Lyapunov functional to be differentiated.

Lemma 11.3. *Let q be a non-negative, bounded Lebesgue measurable function. Let w_1 and w_2 be nonzero solutions of*

$$\frac{\partial w}{\partial t}+\frac{\partial w}{\partial a}=-q(a)\,w(t,a),$$

for $t\in\mathbb{R}$ and $a>0$, with $w_j(t,0)>0$ for all $t\in\mathbb{R}$, for $j=1,2$. Let

$$U(t)=\int_0^\infty \alpha(a)\,G\left(\frac{w_1(t,a)}{w_2(t,a)}\right)\mathrm{d}a,$$

where G is continuous and $\alpha(a)=\int_a^\infty \xi(\sigma)\mathrm{d}\sigma$, with $\xi,\alpha\in\mathbb{L}^1_{\geq 0}$. Then

$$\frac{\mathrm{d}U}{\mathrm{d}t}=\int_0^\infty \xi(a)\left[G\left(\frac{w_1(t,0)}{w_2(t,0)}\right)-G\left(\frac{w_1(t,a)}{w_2(t,a)}\right)\right]\mathrm{d}a.$$

We now state and prove a key result about Eqs (2.1) and (2.2). Loosely speaking, it states that the endemic equilibrium is globally attracting (amongst solutions for which disease is present) if the basic reproduction number is greater than one.

Theorem 11.4. *Suppose $\mathcal{R}_0 > 1$. Then $\mathcal{A}_P = \{E^*\}$. Furthermore, each solution for which the disease is initially present tends to the endemic equilibrium E^*.*

Proof. Define $g : (0, \infty) \to [0, \infty)$ by

$$g(u) = u - 1 - \ln u.$$

Then g is differentiable and non-negative and has a unique global minimum at 1, with $g(1) = 0$.

Let $X(t) = (S(t), x_1(t, \cdot), \cdots, x_n(t, \cdot))$ be a total trajectory in the persistence attractor $\mathcal{A}_P$, and recall that $\mathcal{A}_P$ is bounded.

Combining the results of Corollaries 6.2 and 10.6, there exist $K_1, K_2 > 0$ such that $K_1 \leq \frac{S(t)}{S^*}, \frac{x_j(t,0)}{x_j^*(0)} \leq K_2$ for $j = 1, \ldots, n$. Furthermore, because

$$\frac{x_j(t,a)}{x_j^*(a)} = \frac{x_j(t-a,0)\Omega_j(a)}{x_j^*(0)\Omega_j(a)} = \frac{x_j(t-a,0)}{x_j^*(0)},$$

the bounds K_1 and K_2 also apply to each $\frac{x_j(t,a)}{x_j^*(a)}$ for any $a \geq 0$. It follows that there exists $K_g > 0$, such that $g(u) \leq K_g$, where $u = \frac{S(t)}{S^*}, \frac{x_j(t,a)}{x_j^*(a)}, \frac{x_j(0,a)}{x_j^*(a)}$ for any $t \in \mathbb{R}$, $a \geq 0$, $j = 1, \ldots, n$, that is, for $u = s, y_j, z_j$.

For $j = 1, \ldots, n$, let

$$\alpha_j(a) = \int_a^\infty (\beta_j(\sigma)S^* + c_j\gamma_j(\sigma))x_j^*(\sigma)\mathrm{d}\sigma,$$

where $c_n = 0$ and $c_1, \ldots, c_{n-1} > 0$ will be determined below.

Recall that $\beta_j(a) \leq \bar{\beta}$ and $\gamma_j(a) \leq \bar{\gamma}$ for all $a \geq 0$. Let $c_{\max} = \max c_j$. Recall also that $x_j^*(a) = x_j^*(0)\Omega_j(a) \leq x_j^*(0)\mathrm{e}^{-\mu_S a}$. Thus,

$$\alpha_j(a) \leq \left(\bar{\beta}S^* + c_{\max}\bar{\gamma}\right)x_j^*(0)\int_a^\infty \mathrm{e}^{-\mu_S\sigma}\mathrm{d}\sigma = \frac{\left(\bar{\beta}S^* + c_{\max}\bar{\gamma}\right)x_j^*(0)}{\mu_S}\mathrm{e}^{-\mu_S a}, \tag{11.3}$$

and therefore $\alpha_j \in \mathbb{L}^1_{\geq 0}$ for $j = 1, \ldots, n$.

We now define a Lyapunov functional V. Let

$$V_S = S^* g\left(\frac{S(t)}{S^*}\right) \qquad \text{and} \qquad V_j = \int_0^\infty \alpha_j(a) g\left(\frac{x_j(t,a)}{x_j^*(a)}\right)\mathrm{d}a$$

for $j = 1, \ldots, n$, and let

$$V = V_S + \sum_{j=1}^n V_j.$$

From how g is used in the definition of V_j, it follows that $V_j \leq \int_0^\infty \alpha_j(a)K_g\mathrm{d}a$ and then from (11.3) that $V_j < \infty$. Additionally, $V_S \leq S^*K_g$. Thus, V is finite (and the required integrals are well-defined) for each $t \geq 0$.

Next, we show that $\frac{\mathrm{d}V}{\mathrm{d}t}$ is nonpositive. We first find the derivatives of V_S and V_j individually, before combining. We begin with V_S and make the substitution $\Lambda = \mu_S S^* + \sum_{j=1}^n \int_0^\infty \beta_j(a)S^*x_j^*(a)\mathrm{d}a$.

$$\begin{aligned}\frac{\mathrm{d}V_S}{\mathrm{d}t} &= \left(1-\frac{S^*}{S}\right)\left[\Lambda-\mu_S S-\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S\,x_j(t,a)\mathrm{d}a\right]\\ &= \left(1-\frac{S^*}{S}\right)\left[\mu_S S^*\left(1-\frac{S}{S^*}\right)+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left(1-\frac{S}{S^*}\frac{x_j(t,a)}{x_j^*(a)}\right)\mathrm{d}a\right] \qquad (11.4)\\ &= \mu_S S^*\left(2-s-\frac{1}{s}\right)+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[1-\frac{1}{s}-sy_j(t,a)+y_j(t,a)\right]\mathrm{d}a.\end{aligned}$$

For $j=1,\dots,n$, Lemma 11.3 gives the derivative of V_j as

$$\begin{aligned}\frac{\mathrm{d}V_j}{\mathrm{d}t} &= \int_0^\infty \Big(\beta_j(a)S^*+c_j\gamma_j(a)\Big)x_j^*(a)\left[g\left(\frac{x_j(t,0)}{x_j^*(0)}\right)-g\left(\frac{x_j(t,a)}{x_j^*(a)}\right)\right]\mathrm{d}a\\ &= \int_0^\infty \Big(\beta_j(a)S^*+c_j\gamma_j(a)\Big)x_j^*(a)\Big[g\left(z_j\right)-g\left(y_j(t,a)\right)\Big]\mathrm{d}a \qquad (11.5)\\ &= \int_0^\infty \Big(\beta_j(a)S^*+c_j\gamma_j(a)\Big)x_j^*(a)\Big[z_j-y_j(t,a)+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\Big]\mathrm{d}a.\end{aligned}$$

Combining (11.4) and (11.5), we get

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2-s-\frac{1}{s}\right)+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[1-\frac{1}{s}-sy_j(t,a)+y_j(t,a)\right]\mathrm{d}a\\ &\quad+\sum_{j=1}^{n}\int_0^\infty \Big(\beta_j(a)S^*+c_j\gamma_j(a)\Big)x_j^*(a)\Big[z_j-y_j(t,a)+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\Big]\mathrm{d}a\\ &= \mu_S S^*\left(2-s-\frac{1}{s}\right) \qquad (11.6)\\ &\quad+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[1-\frac{1}{s}-sy_j(t,a)+z_j+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\right]\mathrm{d}a\\ &\quad+\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\Big[z_j-y_j(t,a)+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\Big]\mathrm{d}a.\end{aligned}$$

We use Lemma 11.2 to add terms into each of the integrals, obtaining

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2-s-\frac{1}{s}\right)\\ &\quad+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[2-\frac{1}{s}-z_1-\frac{sy_j(t,a)}{z_1}+z_j+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\right]\mathrm{d}a \qquad (11.7)\\ &\quad+\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\Big[z_j-z_{j+1}-\frac{y_j(t,a)}{z_{j+1}}+1+\ln\left(y_j(t,a)\right)-\ln\left(z_j\right)\Big]\mathrm{d}a.\end{aligned}$$

Next, we add and subtract certain logarithms to the integrands (and use properties of logarithms) with the intention (on the next step) of grouping some terms into copies of g. We have

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2-s-\frac{1}{s}\right)\\ &+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[2-\frac{1}{s}-\ln(s)-\frac{sy_j(t,a)}{z_1}+\ln\left(\frac{sy_j(t,a)}{z_1}\right)\right]\mathrm{d}a\\ &+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\Big[-z_1+\ln(z_1)+z_j-\ln\left(z_j\right)\Big]\mathrm{d}a\\ &+\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\left[1-\frac{y_j(t,a)}{z_{j+1}}+\ln\left(\frac{y_j(t,a)}{z_{j+1}}\right)\right]\mathrm{d}a\\ &+\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\Big[z_j-\ln\left(z_j\right)-z_{j+1}+\ln\left(z_{j+1}\right)\Big]\mathrm{d}a.\end{aligned}$$

Next, we group the terms on the second and fourth lines into copies of g. At the same time, inside the square brackets of the third and fifth rows, we add and subtract one, allowing two copies of g to manifest in each integrand, obtaining

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2-s-\frac{1}{s}\right)-\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[g\left(\frac{1}{s}\right)+g\left(\frac{sy_j(t,a)}{z_1}\right)\right]\mathrm{d}a\\ &+\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\Big[-g(z_1)+g\left(z_j\right)\Big]\mathrm{d}a\\ &-\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\,g\left(\frac{y_j(t,a)}{z_{j+1}}\right)\mathrm{d}a\\ &+\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\Big[g\left(z_j\right)-g\left(z_{j+1}\right)\Big]\mathrm{d}a.\end{aligned}\tag{11.8}$$

The terms in the square brackets on the second and fourth lines of (11.8) (involving z's) do not depend on a and can be taken outside of the integrals. At this point, it is useful to define the positive constants

$$\begin{aligned}a_j &= \int_0^\infty \beta_j(a)S^*x_j^*(a)\mathrm{d}a \qquad\qquad \text{for } j=1,\ldots,n,\\ b_j &= \int_0^\infty \gamma_j(a)x_j^*(a)\mathrm{d}a \qquad\qquad \text{for } j=1,\ldots,n-1.\end{aligned}$$

Then (11.8) can be written as

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2-s-\frac{1}{s}\right)-\sum_{j=1}^{n}\int_0^\infty \beta_j(a)S^*x_j^*(a)\left[g\left(\frac{1}{s}\right)+g\left(\frac{sy_j(t,a)}{z_1}\right)\right]\mathrm{d}a\\ &-\sum_{j=1}^{n-1}\int_0^\infty c_j\gamma_j(a)x_j^*(a)\,g\left(\frac{y_j(t,a)}{z_{j+1}}\right)\mathrm{d}a\;+\;\mathbf{Z},\end{aligned}\tag{11.9}$$

where

$$\mathbf{Z} = \sum_{j=2}^{n} a_j\Big[-g\left(z_1\right) + g\left(z_j\right)\Big] + \sum_{j=1}^{n-1} c_j b_j\Big[g\left(z_j\right) - g\left(z_{j+1}\right)\Big]. \tag{11.10}$$

The a_1 term in the first summation for $\mathbf{Z}$ has a coefficient of zero, so it has been omitted from the sum.

Note that except for $\mathbf{Z}$, the terms on the right-hand side of (11.9) are automatically nonpositive (because $2 - s - \frac{1}{s} \leq 0$ by the Arithmetic Mean Geometric Mean Inequality, and because $-g(u) \leq 0$ for all $u > 0$).

It now remains to choose the coefficients $c_1, \ldots, c_{n-1} > 0$ such that $\mathbf{Z}$ is identically zero. We do this by arranging for the coefficient of each $g\left(z_j\right)$ in $\mathbf{Z}$ to be zero. Regrouping the terms in (11.10), we have

$$\mathbf{Z} = g\left(z_1\right)\left[c_1 b_1 - \left(\sum_{j=2}^{n} a_j\right)\right] + \sum_{j=2}^{n-1} g\left(z_j\right)\left[a_j + c_j b_j - c_{j-1} b_{j-1}\right] + g\left(z_n\right)\left[a_n - c_{n-1} b_{n-1}\right]. \tag{11.11}$$

For $j = 1, \ldots, n-1$, let

$$c_j = \frac{1}{b_j} \sum_{i=j+1}^{n} a_i. \tag{11.12}$$

Then each c_j is positive, and substituting (11.12) into (11.11) makes $\mathbf{Z}$ identically zero. Thus,

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mu_S S^*\left(2 - s - \frac{1}{s}\right) - \sum_{j=1}^{n} \int_0^{\infty} \beta_j(a) S^* x_j^*(a)\left[g\left(\frac{1}{s}\right) + g\left(\frac{s y_j(t,a)}{z_1}\right)\right]\mathrm{d}a \\ &\quad - \sum_{j=1}^{n-1} \int_0^{\infty} c_j \gamma_j(a) x_j^*(a)\, g\left(\frac{y_j(t,a)}{z_{j+1}}\right)\mathrm{d}a \\ &\leq 0.\end{aligned}$$

It follows that V is nonincreasing. It must be the case that V is constant on the alpha limit set of $X(\cdot)$, and therefore that the alpha limit set must be contained in $\mathcal{M}$, the largest invariant subset of $\left\{\frac{\mathrm{d}V}{\mathrm{d}t} = 0\right\}$.

In order to have $\frac{\mathrm{d}V}{\mathrm{d}t} = 0$, it is necessary that $S = S^*$, and therefore it is necessary that $\frac{\mathrm{d}S}{\mathrm{d}t}$ is identically zero in $\mathcal{M}$. This implies that

$$0 = \Lambda - \mu_S S^* - S^* \sum_{j=1}^{n} \int_0^{\infty} \beta_j(a) x_j(t,a)\mathrm{d}a$$

for all t, which can only happen if

$$\sum_{j=1}^{n} \int_0^{\infty} \beta_j(a) x_j(t,a)\mathrm{d}a = \sum_{j=1}^{n} \int_0^{\infty} \beta_j(a) x_j^*(a)\mathrm{d}a$$

for all t.

Combining this with the boundary condition given in Eq (2.2), we see that $x_1(t,0) \equiv x_1^*(0)$, so $x_1(t,a) = x_1^*(a)$ for all t and a. Then, using Eq (2.2) for each $j = 2,\ldots,n$ in turn, it follows that $x_j(t,0) \equiv x_j^*(0)$, so $x_j(t,a) = x_j^*(a)$ for each j. Thus, we may conclude that $\mathcal{M} = \{E^*\}$.

Thus, the alpha limit set of $X(\cdot)$ consists of just the endemic equilibrium E^*. Once again using the fact that $V(X(t))$ is nonincreasing, it follows that

$$V(X(t)) \;\leq\; \lim_{t\to-\infty} V(X(t)) \;=\; V(E^*).$$

Noting that E^* is the point in $\mathcal{Y}$ that minimizes V, we have $X(t) \equiv E^*$. That is, $\mathcal{A}_{\mathrm{P}} = \{E^*\}$. The remaining statement of the theorem follows from the definition of $\mathcal{A}_{\mathrm{P}}$ as the persistence attractor. □

Corollary 11.5. *If $\mathcal{R}_0 > 1$, then the attractor of bounded sets consists of the disease-free equilibrium, which is unstable; the endemic equilibrium, which is stable; and heteroclinic connectors between the two equilibria.*

By reducing our focus to the attractor for individual solutions, we get the following result for solutions for which the disease is initially present.

Theorem 11.6. *If $\mathcal{R}_0 > 1$ and the disease is initially present, then*

$$\lim_{t\to\infty} X(t) = E^*.$$

12. Discussion

The results of our work are theoretical in nature. We focused on the attractor of bounded sets, so that by knowing that the initial state of the system is bounded (even with uncertainty in the exact initial distribution of infections), the long-term behavior of solutions can be reliably predicted. We have proved that the global dynamics of the given model have a rather succinct description.

If the basic reproduction number $\mathcal{R}_0$ is less than or equal to one, then the attractor of bounded sets consists of just the disease-free equilibrium $\hat{E}$, so the disease will die out without intervention.

On the other hand, if the basic reproduction number is greater than one, then the attractor of bounded sets consists of the disease-free equilibrium, the endemic equilibrium E^*, and the heteroclinic connectors connecting them. In particular, the persistence attractor consists of just the endemic equilibrium, so whenever the disease is initially present, the system will approach this positive steady state.

By considering individual points for initial conditions (rather than bounded sets), we have the common threshold behavior: if $\mathcal{R}_0 \leq 1$, then $\hat{E}$ is globally asymptotically stable; if $\mathcal{R}_0 > 1$, then E^* is globally asymptotically stable (amongst solutions for which the disease is initially present).

Further work in the direction of Lyapunov calculations include allowing for more complicated connections between the post-infection classes similar to [17], rather than strict stage progression. This would allow for treatment and quarantine for example. The addition of another pre-infection compartment to account for vaccination is also of interest, as is optimal control analysis related to disease reduction.

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors have no conflict of interest.

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