

GLOBAL DYNAMICS OF A DELAY DIFFERENTIAL
SYSTEM OF A TWO-PATCH SIS-MODEL WITH
TRANSPORT-RELATED INFECTIONS

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Abstract. We describe the global dynamics of a disease transmission model between two regions which are connected via bidirectional or unidirectional transportation, where infection occurs during the travel as well as within the regions. We define the regional reproduction numbers and the basic reproduction number by constructing a next generation matrix. If the two regions are connected via bidirectional transportation, the basic reproduction number R_0 characterizes the existence of equilibria as well as the global dynamics. The disease free equilibrium always exists and is globally asymptotically stable if $R_0 < 1$, while for $R_0 > 1$ an endemic equilibrium occurs which is globally asymptotically stable. If the two regions are connected via unidirectional transportation, the disease free equilibrium always exists, but for $R_0 > 1$ two endemic equilibria can appear. In this case, the regional reproduction numbers determine which one of the two is globally asymptotically stable. We describe how the time delay influences the dynamics of the system.

Keywords: SIS model; asymptotically autonomous system; global asymptotic stability; Lyapunov functional; transport-related infection

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1. INTRODUCTION

In a recent paper, Liu et al. [6] proposed a delay differential model of SIS type to describe the spread of an infectious disease between two regions. Previous models of disease spread by population dispersal implicitly assumed that the transportation between regions occurs instantaneously, so they introduced a delay to express the time to complete a one-way travel. Further, they took into account the disease transmission dynamics during transportation as well. The main results of [6] are the global asymptotic stability of the disease free equilibrium if the basic reproduction number R_0 is less than one, and the uniform persistence of the disease if $R_0 > 1$. In the latter case there exists a unique endemic equilibrium which is locally asymptotically stable. In a subsequent paper, Nakata [8] proved the global asymptotic stability of this endemic equilibrium by constructing a Lyapunov functional. Both [6] and [8] assumed that the regions are identical sharing the same parameter values. In reality, diseases frequently spread between regions which have very different characteristics (for example, from countries with high population density to countries with lower density, from rural areas to cities or vice versa).

In order to model this phenomenon, here we consider arbitrary parameters (different population sizes; different dispersal, transmission, recovery, and mortality rates) for each region. This generalization of the previous model ([6], [8]) is more suitable for studying the impact of transport-related infections on the disease dynamics in distinct regions connected by human transportation ([5]). The model has been further generalized recently in [9] for n patches, where stronger results were obtained for the global dynamics. Here we offer alternative proofs for global asymptotic stability on two patches, which are more direct and do not rely on the heavily technical tools used in [9], and also provide further insights into the behavior on two patches, which were not obtained in [9]. We prove that in the case of bidirectional transportation on two different patches, the system has threshold dynamics: the disease free equilibrium is globally asymptotically stable if $R_0 < 1$, while for $R_0 > 1$ a unique endemic equilibrium exists which is globally asymptotically stable. The situation is different for unidirectional transportation, when partially endemic equilibrium can exist as well. Further, we discuss the role of the time delay on the disease dynamics.

2. MODEL FORMULATION

Consider two distinct regions. For $j \in \{1, 2\}$, denote by $S_j(t)$ and $I_j(t)$ the numbers of susceptible and infected individuals at time t in region j , respectively. Let A_j be the recruitment rate, d_j the natural death rate and δ_j the recovery rate of the infected individuals in region j . We use standard incidence $\beta_j S_j I_j / (S_j + I_j)$,

where β_j is the disease transmission coefficient in region j . Then we obtain the following basic SIS epidemic model:

$$\begin{aligned}\frac{dS_j(t)}{dt} &= A_j - d_j S_j(t) - \frac{\beta_j S_j(t) I_j(t)}{S_j(t) + I_j(t)} + \delta_j I_j(t), \\ \frac{dI_j(t)}{dt} &= \frac{\beta_j S_j(t) I_j(t)}{S_j(t) + I_j(t)} - (d_j + \delta_j) I_j(t)\end{aligned}$$

for $j \in \{1, 2\}$. We assume that, for $j \in \{1, 2\}$, A_j , β_j and d_j are positive and δ_j is nonnegative. Following [6], we incorporate transportation, assuming that individuals do not die or recover during travel. We denote by $s_{kj}(\theta, t)$ and $i_{kj}(\theta, t)$ the density of susceptible and infective individuals who left region k at time t and spent $\theta \leq \tau$ time in transportation to region j , where $\tau \in (0, \infty)$ is the time required to complete a one-way travel. Let $n_{kj}(\theta, t) = s_{kj}(\theta, t) + i_{kj}(\theta, t)$. Thus, $\int_{\theta_2}^{\theta_1} n_{kj}(\theta, t - \theta) d\theta$ is the number of individuals who left region k in the time interval $[t - \theta_1, t - \theta_2]$, where $\tau \geq \theta_1 \geq \theta_2 \geq 0$. In particular, for $\theta_1 = \tau$ and $\theta_2 = 0$, this gives the total number of individuals who are being in travel from region k to j at time t . Assume that susceptible and infected individuals leave region k to region j at a per capita rate $\alpha_{kj} \in [0, \infty)$. Considering the rates susceptible and infected individuals leave region k to j at time t_s , we obtain that

$$(2.1) \quad s_{kj}(0, t_s) = \alpha_{kj} S_k(t_s) \quad \text{and} \quad i_{kj}(0, t_s) = \alpha_{kj} I_k(t_s).$$

Then the disease dynamics in the transportation from region k to region j is governed by

$$(2.2a) \quad \frac{\partial}{\partial \theta} s_{kj}(\theta, t_s) = -\gamma_{kj} \frac{i_{kj}(\theta, t_s)}{i_{kj}(\theta, t_s) + s_{kj}(\theta, t_s)} s_{kj}(\theta, t_s),$$

$$(2.2b) \quad \frac{\partial}{\partial \theta} i_{kj}(\theta, t_s) = \gamma_{kj} \frac{i_{kj}(\theta, t_s)}{i_{kj}(\theta, t_s) + s_{kj}(\theta, t_s)} s_{kj}(\theta, t_s),$$

where $\gamma_{kj} \in (0, \infty)$ is the transmission rate during travel. Let us define $N_j(t) := S_j(t) + I_j(t)$ for $j \in \{1, 2\}$. Then

$$n_{kj}(\theta, t_s) = s_{kj}(\theta, t_s) + i_{kj}(\theta, t_s) = \alpha_{kj} (S_k(t_s) + I_k(t_s)) = \alpha_{kj} N_k(t_s) \text{ for any } \theta \geq 0.$$

From (2.2b) we obtain that

$$(2.3) \quad \frac{\partial}{\partial \theta} i_{kj}(\theta, t_s) = \gamma_{kj} i_{kj}(\theta, t_s) \left(1 - \frac{i_{kj}(\theta, t_s)}{\alpha_{kj} N_k(t_s)} \right),$$

which is a logistic equation. Using (2.1) as an initial condition, we solve (2.3) explicitly to obtain

$$(2.4) \quad i_{kj}(\tau, t_s) = \frac{\alpha_{kj} I_k(t_s)}{e^{-\gamma_{kj}\tau} S_k(t_s) + I_k(t_s)} N_k(t_s),$$

$$s_{kj}(\tau, t_s) = \alpha_{kj} N_k(t_s) - i_{kj}(\tau, t_s) = \frac{\alpha_{kj} e^{-\gamma_{kj}\tau} S_k(t_s)}{e^{-\gamma_{kj}\tau} S_k(t_s) + I_k(t_s)} N_k(t_s),$$

where $s_{kj}(\tau, t_s)$ and $i_{kj}(\tau, t_s)$ are the population densities of susceptible and infective individuals arriving to region j from k at time $t_s + \tau$. Therefore, the respective population densities at time t become $s_{kj}(\tau, t - \tau)$ and $i_{kj}(\tau, t - \tau)$. Consequently, we obtain the following model:

$$(2.5a) \quad \frac{dS_j(t)}{dt} = A_j - (d_j + \alpha_{jk})S_j(t) - \frac{\beta_j S_j(t) I_j(t)}{S_j(t) + I_j(t)} + \delta_j I_j(t) + s_{kj}(\tau, t - \tau),$$

$$(2.5b) \quad \frac{dI_j(t)}{dt} = \frac{\beta_j S_j(t) I_j(t)}{S_j(t) + I_j(t)} - (d_j + \delta_j + \alpha_{jk})I_j(t) + i_{kj}(\tau, t - \tau)$$

for $j, k \in \{1, 2\}$ and $j \neq k$. One can see that the transport-related infection model formulated in Liu et al. [6] is a special case of the system (2.5).

2.1. Asymptotically autonomous system. To analyse the dynamics of (2.5) it is convenient to consider a system which is described in terms of N and I instead of S and I . As an equivalent system to (2.5) one can obtain

$$(2.6a) \quad \frac{dN_j(t)}{dt} = A_j - (d_j + \alpha_{jk})N_j(t) + \alpha_{kj}N_k(t - \tau),$$

$$(2.6b) \quad \frac{dI_j(t)}{dt} = I_j(t) \left\{ \beta_j - (d_j + \delta_j + \alpha_{jk}) - \frac{\beta_j}{N_j(t)} I_j(t) \right\} + i_{kj}(\tau, t - \tau)$$

for $j, k \in \{1, 2\}$ and $j \neq k$, where now

$$(2.7) \quad i_{kj}(\tau, t - \tau) = \frac{\alpha_{kj} e^{\gamma_{kj}\tau} I_k(t - \tau)}{1 + \frac{e^{\gamma_{kj}\tau} - 1}{N_k(t - \tau)} I_k(t - \tau)}.$$

We denote by $C = C([- \tau, 0], \mathbb{R}^2)$ the Banach space of continuous functions mapping the interval $[- \tau, 0]$ into \mathbb{R}^2 equipped with the sup-norm. The standard existence and uniqueness results hold [3], [4]. The nonnegative cone of C is defined as $C_+ = C([- \tau, 0], \mathbb{R}_+^2)$. We define a set, which only contains strictly positive functions, as

$$G := \{ \varphi \in C_+ : \varphi_1(\theta) > 0, \varphi_2(\theta) > 0 \text{ for } s \in [- \tau, 0] \}.$$

Due to the biological interpretation, we consider initial conditions for (2.6a) as

$$(N_1(\theta), N_2(\theta)) = \psi(\theta)$$

for $\theta \in [-\tau, 0]$, where $\psi \in G$. We use the notation $x_t(\theta) := x(t + \theta)$ for $\theta \in [-\tau, 0]$ as usual in the theory of functional differential equations, see e.g. [3]. One can obtain that $(N_{1,t}, N_{2,t}) \in G$ for $t > 0$ and thus both components of the solution of (2.6a) are strictly positive for $t > 0$.

Remark 2.1. For any nonnegative initial function system (2.6a) generates a strictly positive solution. However, we restrict the initial function of (2.6a) to the function in G to define (2.7) for $t \in (0, \tau]$. We prove the following result for (2.6a).

Lemma 2.1. *There exists a unique positive equilibrium (N_1, N_2) of (2.6a), where*

$$(2.8) \quad \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} := \begin{pmatrix} d_1 + \alpha_{12} & -\alpha_{21} \\ -\alpha_{12} & d_2 + \alpha_{21} \end{pmatrix}^{-1} \begin{pmatrix} A_1 \\ A_2 \end{pmatrix}.$$

The positive equilibrium is asymptotically stable.

Proof. We define $x_j(t) := N_j(t) - N_j$ for $j \in \{1, 2\}$. We obtain

$$(2.9a) \quad \frac{d}{dt}x_1(t) = -(d_1 + \alpha_{12})x_1(t) + \alpha_{21}x_2(t - \tau),$$

$$(2.9b) \quad \frac{d}{dt}x_2(t) = -(d_2 + \alpha_{21})x_2(t) + \alpha_{12}x_1(t - \tau).$$

Since d_1 and d_2 are positive and $(d_1 + \alpha_{12})(d_2 + \alpha_{21}) > \alpha_{12}\alpha_{21}$, condition (16) in Suzuki and Matsunaga [12], Example 2, page 1384, holds. Thus the zero solution of (2.9) is asymptotically stable. \square

We can view (2.6b) as a system of non-autonomous delay differential equations with non-autonomous terms $N_j(t)$ for $j \in \{1, 2\}$, which are governed by system (2.6a). In the following, using Lemma 2.1, we derive a limiting system of (2.6b). For $j, k \in \{1, 2\}$ and $j \neq k$ we define a positive function

$$f_{kj}(I) := \frac{\alpha_{kj}e^{\gamma_{kj}\tau}I}{1 + \frac{e^{\gamma_{kj}\tau} - 1}{N_k}I} \quad \text{for } I \in [0, \infty),$$

where N_k is the positive equilibrium of (2.6a) given as in (2.8). By Lemma 2.1 one can obtain

$$\lim_{t \rightarrow \infty} (i_{kj}(\tau, t - \tau) - f_{kj}(I_{kj}(t - \tau))) = 0.$$

Then we find that system (2.6b) is asymptotically autonomous with the limiting system of delay differential equations

$$(2.10) \quad \frac{dI_j(t)}{dt} = I_j(t) \left\{ \beta_j - (d_j + \delta_j + \alpha_{jk}) - \frac{\beta_j}{N_j} I_j(t) \right\} + f_{kj}(I_k(t - \tau))$$

for $j, k \in \{1, 2\}$ and $j \neq k$. To obtain information on the long-term behavior of solutions of (2.6b) we analyse global stability of system (2.10) and apply the theory of asymptotically autonomous systems [1], [7], [13] in Sections 4 and 5.

3. THE BASIC REPRODUCTION NUMBER

We define and give an explicit formula for a basic reproduction number R_0 for (2.6). In absence of the inflow into a region due to the transportation, we define regional reproduction numbers as

$$(3.1) \quad R_j := \frac{\beta_j}{d_j + \delta_j + \alpha_{jk}}$$

for $j \in \{1, 2\}$, $k \neq j$. If we introduce a single infective into a fully susceptible region j , it will generate R_j new infectives in this region in the expected sojourn time. Let us consider the expected number of infective individuals appearing in region k due to the transportation by a typical infective individual introduced into region j : the probability of moving out from I_j by means of travel is $\alpha_{jk}/(d_j + \delta_j + \alpha_{jk})$, and the expected number of infected individuals who arrive at region j if the travel was started with a single infective is $e^{\gamma_{jk}\tau}$ (this follows from the linear part of (2.3)). Taking the product of these two numbers, for $j, k \in \{1, 2\}$ and $j \neq k$ we define

$$r_{jk} := \frac{\alpha_{jk} e^{\gamma_{jk}\tau}}{d_j + \delta_j + \alpha_{jk}}.$$

We construct a next generation matrix for (2.6) as

$$(3.2) \quad M := \begin{pmatrix} R_1 & r_{21} \\ r_{12} & R_2 \end{pmatrix},$$

define the basic reproduction number as the spectral radius of M and denote it by R_0 . Then one finds the explicit expression

$$(3.3) \quad R_0 = \frac{1}{2} \left\{ (R_1 + R_2) + \sqrt{(R_1 - R_2)^2 + 4r_{12}r_{21}} \right\}.$$

If $\alpha_{12} = 0$ or $\alpha_{21} = 0$, then $R_0 = \max\{R_1, R_2\}$.

4. DISEASE TRANSMISSION DYNAMICS: BIDIRECTIONAL TRANSPORTATION

In this section we consider a situation in which two regions are connected to each other via bidirectional transportation. Thus we assume that

$$(4.1) \quad \alpha_{jk} \in (0, \infty) \quad \text{for } j, k \in \{1, 2\} \text{ and } j \neq k.$$

We prove that (2.6) admits a unique endemic equilibrium if and only if $R_0 > 1$ while there always exists a disease free equilibrium. Performing global stability analysis we show that R_0 works as a threshold quantity to determine which equilibrium is globally asymptotically stable.

4.1. Existence of equilibria. In order to prove the existence of the endemic equilibrium, we introduce a relation between the basic reproduction number and regional reproduction numbers.

Proposition 4.1. (A) For

$$(4.2) \quad r_{12}r_{21} \in (0, 1),$$

the following statements hold:

(A1) $R_0 < 1$ if and only if

$$(4.3) \quad r_{12}r_{21} < (1 - R_1)(1 - R_2) \quad \text{for } \max\{R_1, R_2\} \in (0, 1).$$

(A2) $R_0 = 1$ if and only if

$$(4.4) \quad r_{12}r_{21} = (1 - R_1)(1 - R_2) \quad \text{for } \max\{R_1, R_2\} \in (0, 1).$$

(A3) $R_0 > 1$ if and only if either

$$(4.5) \quad r_{12}r_{21} > (1 - R_1)(1 - R_2) \quad \text{for } \max\{R_1, R_2\} \in (0, 1).$$

or

$$(4.6) \quad \max\{R_1, R_2\} \geq 1.$$

(B) If

$$(4.7) \quad r_{12}r_{21} \geq 1,$$

then $R_0 > 1$ for any $(R_1, R_2) \in (0, \infty) \times (0, \infty)$.

Proof. (A) We only prove statement (A3), statements (A1) and (A2) can be shown in a similar way. Assume (4.2). If we suppose (4.6), then

$$R_0 > \frac{1}{2} \left\{ (R_1 + R_2) + \sqrt{(R_1 - R_2)^2} \right\} = \max\{R_1, R_2\} \geq 1.$$

From (3.3), $R_0 > 1$ if and only if

$$(4.8) \quad \sqrt{(R_1 - R_2)^2 + 4r_{12}r_{21}} > 2 - (R_1 + R_2).$$

If $\max\{R_1, R_2\} < 1$, we can square both sides to obtain the equivalent inequality $r_{12}r_{21} > (1 - R_1)(1 - R_2)$, as in (4.5). Therefore, both (4.5) and (4.6) imply $R_0 > 1$. For the other direction, suppose $R_0 > 1$. Then either (4.6) or $\max\{R_1, R_2\} < 1$ holds. In the latter case, we obtain $r_{12}r_{21} > (1 - R_1)(1 - R_2)$ from (4.8) and thus (4.5) holds.

(B) Assume that (4.7) holds. Then from (3.3) we get $R_0 > 1$. The proof is complete. \square

Next we consider the existence of equilibria of (2.6). We define

$$g_j(z) := z \left\{ \beta_j - (d_j + \delta_j + \alpha_{jk}) - \frac{\beta_j}{N_j} z \right\} \quad \text{for } z \in [0, \infty)$$

for $j, k \in \{1, 2\}$ and $j \neq k$ and

$$h_1(x, y) := g_1(x) + f_{21}(y), \quad h_2(x, y) := g_2(y) + f_{12}(x).$$

In the following we study the solution of

$$(4.9) \quad 0 = h_1(x, y) = h_2(x, y) \quad \text{for } (x, y) \in [0, \infty) \times [0, \infty).$$

Proposition 4.2. *For (4.9) there always exists a trivial solution $(0, 0)$. There exists a unique solution, with both components strictly positive, if and only if $R_0 > 1$.*

Proof. Clearly $(0, 0)$ is always a solution of (4.9). For the existence of the positive solution, we show that (4.9) defines two curves having a unique intersection in the first quadrant if and only if $R_0 > 1$. We define $y^\infty := \lim_{y \rightarrow \infty} f_{21}(y)$. One easily proves that $y^\infty < \infty$ and that $f_{21}(y)$ is monotone increasing on $[0, \infty)$ with range $[0, y^\infty)$. Therefore, it is a bijection and thus invertible on this domain: there exists an inverse function of f_{21} such that $f_{21}^{-1}: [0, y^\infty) \rightarrow [0, \infty)$. We define

$$x_*(R_1) := \max \left\{ 0, N_1 \left(1 - \frac{1}{R_1} \right) \right\}.$$

We see that $g_1(x_*(R_1)) = 0$, $\lim_{x \rightarrow \infty} g_1(x) = -\infty$ and $g_1(x)$ is monotone decreasing for $x \in [x_*(R_1), \infty)$. We can find a unique x such that $-g_1(x) = y^\infty$ and denote it by x^* . Then we define a function $G_1: [x_*(R_1), x^*) \rightarrow [0, \infty)$ as

$$G_1(x) := f_{21}^{-1}(-g_1(x)),$$

which is a continuous and monotone increasing function such that

$$(4.10) \quad G_1(x_*(R_1)) = 0 \quad \text{and} \quad \lim_{x \rightarrow x^*} G_1(x) = \infty.$$

The graph of G_1 is the zero level set of h_1 , i.e.,

$$(4.11) \quad h_1(x, G_1(x)) = 0.$$

Similarly, we see that $f_{12}(0) = 0$, $\lim_{x \rightarrow \infty} f_{12}(x) < \infty$ and $f_{12}(x)$ is monotone increasing for $x \in [0, \infty)$. We define

$$y_*(R_2) := \max \left\{ 0, N_2 \left(1 - \frac{1}{R_2} \right) \right\}.$$

One can prove that $g_2(y)$ is monotone decreasing on $[y_*(R_2), \infty)$ with range $(-\infty, 0]$. Therefore, it is a bijection and thus invertible on this domain: there exists an inverse function of g_2 such that $g_2^{-1}: (-\infty, 0] \rightarrow [y_*(R_2), \infty)$. We define $y^* := g_2^{-1}(-\lim_{x \rightarrow \infty} f_{12}(x)) < \infty$. Then we define a function $G_2: [0, \infty) \rightarrow [y_*(R_2), y^*)$ as

$$G_2(x) := g_2^{-1}(-f_{12}(x)),$$

which is a continuous and monotone increasing function such that

$$(4.12) \quad G_2(0) = y_*(R_2) \quad \text{and} \quad \lim_{x \rightarrow \infty} G_2(x) = y^*.$$

The graph of G_2 is the zero level set of h_2 , i.e.,

$$(4.13) \quad h_2(x, G_2(x)) = 0.$$

Consequently, intersections of the curves are given as a solution of the equation $G_1(x) = G_2(x)$. For proving the existence of the solution we divide the proof into two cases.

Case 1: $\max\{R_1, R_2\} > 1$ holds. From (4.10), (4.12) and monotonicity of G_2 , it follows that

$$G_1(x_*(R_1)) = 0 \leq y_*(R_2) = G_2(0) \leq G_2(x_*(R_1)).$$

We have that either $x_*(R_1) > 0$ or $y_*(R_2) > 0$. Therefore, we obtain that $G_1(x_*(R_1)) < G_2(x_*(R_1))$. On the other hand, there exists $x_0 \in (x_*, x^*)$ such that $G_1(x_0) > G_2(x_0)$, since $\lim_{x \rightarrow \infty} G_2(x) = y^*$ and $\lim_{x \rightarrow x^*} G_1(x) = \infty$ due to (4.10) and (4.12). By the continuity, there must be an $\bar{x} \in (x_*(R_1), x^*)$ such that $G_1(\bar{x}) = G_2(\bar{x})$ (see Figure 1 (a), (b) and (c)).

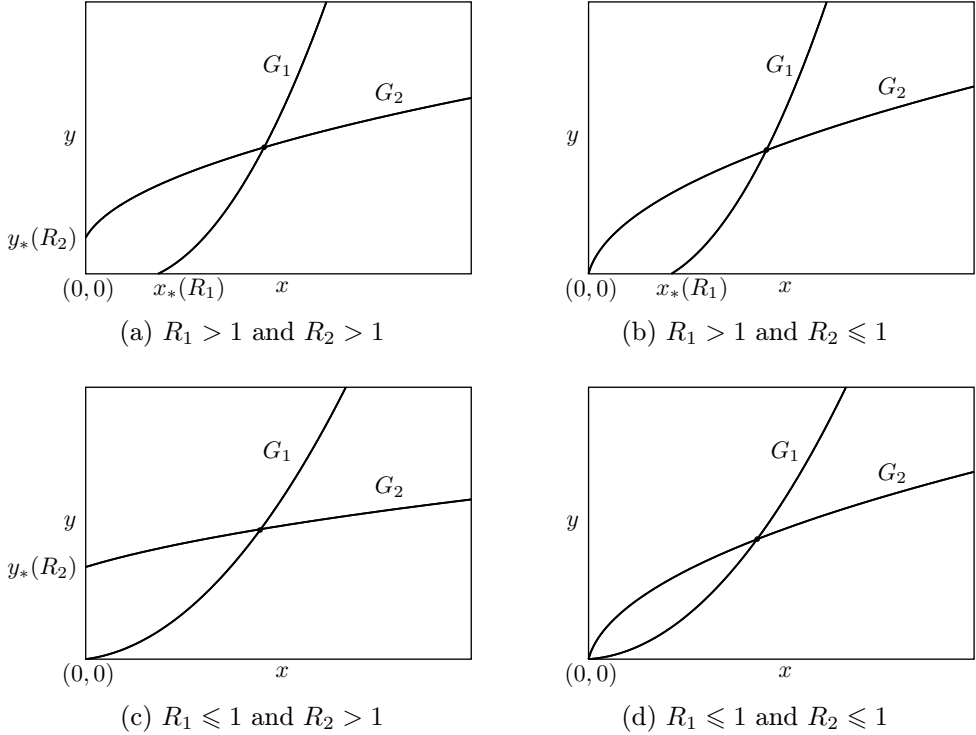


Figure 1. Graph of G_1 and G_2 for $R_0 > 1$. The unique intersection of G_1 and G_2 denotes the unique endemic equilibrium.

Case 2: $\max\{R_1, R_2\} \leq 1$ holds. In this case, by (4.5) we have that $x_*(R_1) = 0$ and that $y_*(R_2) = 0$. Then $G_1(0) = G_2(0) = 0$. We compute the slopes of G_1 and G_2 at zero to determine the existence of the intersection. By differentiation of (4.11) and evaluating at zero we obtain

$$(4.14) \quad G_1'(0) = -\frac{g_1'(0)}{f_{21}'(0)} = \frac{1 - R_1}{r_{21}}.$$

Similarly, from (4.13), we get that

$$(4.15) \quad G_2'(0) = \frac{r_{12}}{1 - R_2} \quad (\text{whenever } R_2 < 1),$$

and in the case $R_2 = 1$ the graph of G_2 is tangential to the y -axis at 0. If $\max\{R_1, R_2\} \leq 1$ but $R_0 > 1$, then from Proposition 4.1, either (4.7) holds or (4.2) and (4.6) hold. In any case we get $G_1'(0) < G_2'(0)$ (where $G_2'(0) = \infty$ when $R_2 = 1$). Hence there is some $x_1 > 0$ such that $G_1(x_1) < G_2(x_1)$. Since we have that $\lim_{x \rightarrow \infty} G_2(x) = y^* < \infty$ and $\lim_{x \rightarrow x^*} G_1(x) = \infty$ from (4.10) and (4.12), there exists x_0 such that $G_1(x_0) > G_2(x_0)$. By the continuity, there must be an $\bar{x} \in (x_*, x^*)$ such that $G_1(\bar{x}) = G_2(\bar{x})$ (see Figure 1 (d)).

For the uniqueness of \bar{x} we examine the convexity properties of G_1 and G_2 . Applying implicit differentiation of $h_1(x, y) = 0$ and using that

$$\frac{\partial^2 h_1(x, y)}{\partial y \partial x} = \frac{\partial^2 h_1(x, y)}{\partial x \partial y} = 0,$$

we obtain

$$0 = \frac{\partial^2 h_1(x, y)}{\partial x^2} + \frac{\partial^2 h_1(x, y)}{\partial y^2} G_1'(x)^2 + \frac{\partial h_1(x, y)}{\partial y} G_1''(x).$$

Simple calculations show that

$$\frac{\partial^2 h_1(x, y)}{\partial x^2} < 0, \quad \frac{\partial^2 h_1(x, y)}{\partial y^2} < 0 \quad \text{and} \quad \frac{\partial h_1(x, y)}{\partial y} > 0.$$

Hence, it follows that

$$G_1''(x) = - \frac{\frac{\partial^2 h_1(x, y)}{\partial x^2} + \frac{\partial^2 h_1(x, y)}{\partial y^2} G_1'(x)^2}{\frac{\partial h_1(x, y)}{\partial y}} > 0.$$

On the other hand, analogous calculations give $G_2''(x) < 0$. By these convexity properties we deduce that there is a unique positive solution \bar{x} of $G_1(x) = G_2(x)$. Therefore, there exists a unique endemic equilibrium if $R_0 > 1$.

Finally, we assume that $R_0 \leq 1$ holds. Then either (4.3) or (4.4) in Proposition 4.1 holds, which gives $G_1'(0) \geq G_2'(0)$ from (4.14) and (4.15). The convexity properties of G_1 and G_2 show that there is no positive solution of $G_1(x) = G_2(x)$. Therefore, there exists no endemic equilibrium if $R_0 \leq 1$. The proof is complete. \square

For $R_0 > 1$ we denote by (I_{1+}, I_{2+}) the unique positive solution of (4.9). We obtain the following result on the existence of equilibria of (2.6).

Theorem 4.1. For (2.6) there always exists a disease free equilibrium given as

$$(N_1, N_2, 0, 0).$$

A unique endemic equilibrium, given as

$$(N_1, N_2, I_{1+}, I_{2+}),$$

exists if and only if $R_0 > 1$.

Proof. We obtain the first and second components of the equilibria from Lemma 2.1. Since the third and fourth components of the equilibria of (2.6) are determined by (4.9), from Proposition 4.2 we obtain the conclusion. \square

From Theorem 4.1, one can easily obtain the existence of equilibria of (2.10).

Theorem 4.2. For (2.10) there always exists the trivial equilibrium $(0, 0)$. A unique positive equilibrium given as (I_{1+}, I_{2+}) exists if and only if $R_0 > 1$.

4.2. Global dynamics analysis. For (2.6b) and (2.10) we consider the same initial conditions

$$(4.16) \quad (I_1(\theta), I_2(\theta)) = \varphi(\theta)$$

for $\theta \in [-\tau, 0]$, where $\varphi \in C_+$. We denote by $\hat{0}$ the function which is identically zero, i.e., $\varphi(\theta) = 0$ for $\theta \in [-\tau, 0]$. In the following we assume

$$(4.17) \quad \varphi \in C_+ \setminus \{\hat{0}, \hat{0}\}.$$

The proof of the following lemma is straightforward thus omitted.

Lemma 4.1. Both (2.6b) and (2.10) have unique nonnegative solutions $(I_1(t), I_2(t))$, defined for all $t > 0$, which are bounded. We have $I_j(t) > 0$, $j = \{1, 2\}$ for $t > \tau$, thus $(I_{1,t}, I_{2,t}) \in G$ for $t > 2\tau$.

Remark 4.1. For (2.6b) and (2.10) if $\varphi = (\hat{0}, \hat{0})$ then it follows that $(I_1(t), I_2(t)) = (0, 0)$ for $t > 0$, thus $(I_{1,t}, I_{2,t}) = (\hat{0}, \hat{0})$ for $t > 0$. We analyse the global stability of the trivial equilibrium of (2.10).

Theorem 4.3. The trivial equilibrium of (2.10) is globally asymptotically stable for $R_0 < 1$ while it is unstable for $R_0 > 1$.

P r o o f. We define

$$l_j := \beta_j - (d_j + \delta_j + \alpha_{jk}) \quad \text{for } j, k \in \{1, 2\} \text{ and } j \neq k.$$

By linearizing (2.10) at the trivial equilibrium we obtain that

$$(4.18) \quad \frac{d}{dt}y(t) = B_1y(t) + B_2y(t - \tau),$$

where $y(t) \in \mathbb{R}^2$ and

$$B_1 := \begin{pmatrix} l_1 & 0 \\ 0 & l_2 \end{pmatrix}, \quad B_2 := \begin{pmatrix} 0 & \alpha_{21}e^{\gamma_{21}\tau} \\ \alpha_{12}e^{\gamma_{12}\tau} & 0 \end{pmatrix}.$$

Since (4.18) is a cooperative and irreducible system, according to Smith [11], Chapter 5, Corollary 5.2, the stability of the trivial equilibrium is equivalent to that for

$$(4.19) \quad \frac{d}{dt}y(t) = (B_1 + B_2)y(t).$$

One can show by a straightforward calculation that the trivial equilibrium of (4.19) is asymptotically stable if $R_0 < 1$ while it is unstable if $R_0 > 1$. Hence we obtain the conclusion on the stability of the trivial equilibrium of (2.10). Next we prove the global attractivity. From (2.10) we obtain that

$$\frac{d}{dt} \begin{pmatrix} I_1(t) \\ I_2(t) \end{pmatrix} \leq B_1 \begin{pmatrix} I_1(t) \\ I_2(t) \end{pmatrix} + B_2 \begin{pmatrix} I_1(t - \tau) \\ I_2(t - \tau) \end{pmatrix}.$$

Since for $R_0 < 1$ we have that $\lim_{t \rightarrow \infty} y(t) = (0, 0)$ for (4.18), using the standard comparison argument as in Smith [11], Chapter 5, Corollary 2.4, we conclude that $\lim_{t \rightarrow \infty} I_j(t) = 0$ for $j \in \{1, 2\}$. Thus the trivial equilibrium is globally attractive. \square

Next we analyse the global stability of the positive equilibrium of (2.10). For the proof we employ Lyapunov's direct method. For the construction of the Lyapunov functional we let

$$g(z) := z - 1 - \ln z \quad \text{for } z \in (0, \infty).$$

One can see that $g(z)$ has the global minimum at $z = 1$ with $g(1) = 0$. The following elementary Lemma is taken from Nakata [8], Lemma 2.4. We use it to prove the global asymptotic stability.

Lemma 4.2. For any $x, y \in (0, \infty)$ we have

$$(4.20) \quad \left(\frac{x}{y} - \frac{f_{kj}(x)}{f_{kj}(y)}\right) \left(\frac{f_{kj}(x)}{f_{kj}(y)} - 1\right) \geq 0$$

and

$$(4.21) \quad g\left(\frac{x}{y}\right) - g\left(\frac{f_{kj}(x)}{f_{kj}(y)}\right) \geq 0$$

for $j, k \in \{1, 2\}$ and $j \neq k$.

Theorem 4.4. The positive equilibrium of (2.10) is globally asymptotically stable for $R_0 > 1$.

Proof. The equilibrium condition of (2.10) yields

$$\beta_j - (d_j + \delta_j + \alpha_{jk}) = \frac{\beta_j I_{j+}}{N_j} - \frac{f_{kj}(I_{k+})}{I_{k+}}.$$

Then from (2.10) we obtain that

$$(4.22) \quad \frac{dI_j(t)}{dt} = \frac{\beta_j}{N_j} I_j(t) (I_{j+} - I_j(t)) + f_{kj}(I_k(t - \tau)) - f_{kj}(I_{k+}) \frac{I_j(t)}{I_{j+}}$$

for $j, k \in \{1, 2\}$ and $j \neq k$. For $(\varphi_1, \varphi_2) \in G$ we consider the following functional defined as

$$(4.23) \quad U(\varphi_1, \varphi_2) := \sum_{j, k \in \{1, 2\}, j \neq k} \left(\frac{I_{j+}}{f_{kj}(I_{k+})} g\left(\frac{\varphi_j(0)}{I_{j+}}\right) + \int_{-\tau}^0 g\left(\frac{f_{kj}(\varphi_k(s))}{f_{kj}(I_{k+})}\right) ds \right).$$

By Lemma 4.1 there exists t_0 such that $(I_{1,t}, I_{2,t}) \in G$ for $t \geq t_0 > 2\tau$. We differentiate U with respect to t along the solution of (4.22). For the convenience we drop '+' in index from the notation. Hence

$$(4.24) \quad \begin{aligned} \frac{d}{dt} \left[g\left(\frac{I_j(t)}{I_j}\right) \right] &= \frac{1}{I_j} \left(1 - \frac{I_j}{I_j(t)}\right) \left\{ \frac{\beta_j I_j(t)}{N_j} I_j \left(1 - \frac{I_j(t)}{I_j}\right) \right. \\ &\quad \left. + f_{kj}(I_k) \left(\frac{f_{kj}(I_k(t - \tau))}{f_{kj}(I_k)} - \frac{I_j(t)}{I_j}\right) \right\} \\ &= -\frac{\beta_j I_j}{N_j} \left(1 - \frac{I_j(t)}{I_j}\right)^2 \\ &\quad + \frac{f_{kj}(I_k)}{I_j} \left(1 - \frac{I_j}{I_j(t)}\right) \left(\frac{f_{kj}(I_k(t - \tau))}{f_{kj}(I_k)} - \frac{I_j(t)}{I_j}\right). \end{aligned}$$

Furthermore,

$$(4.25) \quad \begin{aligned} \frac{d}{dt} \int_{t-\tau}^t g\left(\frac{f_{kj}(I_k(s))}{f_{kj}(I_k)}\right) ds &= g\left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)}\right) - g\left(\frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)}\right) \\ &= \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} - \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} - \ln \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} + \ln \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)}. \end{aligned}$$

We define

$$\begin{aligned} C_{jk}(t) &:= \left(1 - \frac{I_j}{I_j(t)}\right) \left(\frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} - \frac{I_j(t)}{I_j}\right) \\ &\quad + \left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} - \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} - \ln \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} + \ln \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)}\right) \end{aligned}$$

for $j, k \in \{1, 2\}$ and $j \neq k$. Then from (4.24) and (4.25) we obtain that

$$(4.26) \quad \frac{d}{dt} U(I_{1t}, I_{2t}) = \sum_{j=1}^2 \left\{ -\frac{\beta_j I_j^2}{N_j f_{kj}(I_k)} \left(1 - \frac{I_j(t)}{I_j}\right)^2 \right\} + \sum_{j,k \in \{1,2\}, j \neq k} C_{jk}(t).$$

Now we determine the sign of $C_{jk}(t)$:

$$\begin{aligned} C_{jk}(t) &= \left(\frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} - \frac{I_j(t)}{I_j} - \frac{I_j}{I_j(t)} \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} + 1\right) \\ &\quad + \left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} - \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} - \ln \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} + \ln \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)}\right) \\ &= \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} - \frac{I_j(t)}{I_j} - \frac{I_j}{I_j(t)} \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} \\ &\quad + 1 - \ln \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} + \ln \frac{f_{kj}(I_k(t-\tau))}{f_{kj}(I_k)} \\ &= \left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)} - 1 - \ln \frac{f_{kj}(I_k(t))}{f_{kj}(I_k)}\right) - \left(\frac{I_j(t)}{I_j} - 1 - \ln \frac{I_j(t)}{I_j}\right) \\ &\quad - \left(\frac{I_j f_{kj}(I_k(t-\tau))}{I_j(t) f_{kj}(I_k)} - 1 - \ln \frac{I_j f_{kj}(I_k(t-\tau))}{I_j(t) f_{kj}(I_k)}\right) \\ &= g\left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)}\right) - g\left(\frac{I_j(t)}{I_j}\right) - g\left(\frac{I_j f_{kj}(I_k(t-\tau))}{I_j(t) f_{kj}(I_k)}\right). \end{aligned}$$

Therefore, using (4.21) in Lemma 4.2, we obtain that

$$\begin{aligned} \sum_{j,k \in \{1,2\}, j \neq k} C_{jk}(t) &= \sum_{j,k \in \{1,2\}, j \neq k} \left\{ g\left(\frac{f_{kj}(I_k(t))}{f_{kj}(I_k)}\right) - g\left(\frac{I_k(t)}{I_k}\right) \right. \\ &\quad \left. - g\left(\frac{I_j f_{kj}(I_k(t-\tau))}{I_j(t) f_{kj}(I_k)}\right) \right\} \leq 0. \end{aligned}$$

Consequently, $(d/dt)U(I_{1,t}, I_{2,t}) \leq 0$ for $t \geq t_0$.

If (I_{1,t_0}, I_{2,t_0}) is the function identically equal to (I_1, I_2) , then it is obvious that it follows that $(I_{1,t}, I_{2,t}) = (I_1, I_2)$ for $t > t_0$. Thus we assume that (I_{1,t_0}, I_{2,t_0}) is not the function identically equal to (I_{1+}, I_{2+}) . Then there exists $c > 0$ such that $c = U(I_{1,t_0}, I_{2,t_0})$. We define

$$G_c := \{\varphi \in G; U(\varphi) \leq c\}.$$

We see that G_c is closed and positively invariant. Thus the closure of G_c is again G_c and G_c contains $(I_{1,t}, I_{2,t})$ for all $t \geq t_0$. Since U is continuous on G_c , U is a Lyapunov functional on G_c , see [3], Chapter 5.3. We define the set

$$\Sigma := \left\{ (\varphi_1, \varphi_2) \in G_c : \frac{d}{dt} U(\varphi_1, \varphi_2) = 0 \right\}.$$

We obtain

$$\Sigma = \{(\varphi_1, \varphi_2) : \varphi_j(0) = \varphi_j(-\tau) = I_j, j \in \{1, 2\}\}.$$

Let L be the largest subset in Σ that is invariant with respect to (2.10). From the invariance, L consists of only the function identically equal to (I_1, I_2) . Then, by LaSalle's invariance principle [3], Theorem 3.1, we conclude that the solution tends to the positive equilibrium of (2.10). Since for every solution we can choose c , the positive equilibrium is globally attractive. The stability of the equilibrium follows from [3], Section 5, Corollary 3.1, if we define $a(\cdot)$ as

$$a(\varphi_1(0), \varphi_2(0)) := \sum_{j,k \in \{1,2\}, j \neq k} \frac{I_j}{f_{kj}(I_k)} g\left(\frac{\varphi_j(0)}{I_j}\right).$$

Hence the positive equilibrium is globally asymptotically stable. \square

Finally, we extend the global stability results in Theorems 4.3 and 4.4 to the original system (2.6) by applying the theory of asymptotic autonomous systems [13], Theorem 4.1.

Theorem 4.5. *For (2.6) the following statements hold. The disease free equilibrium is globally asymptotically stable if $R_0 > 1$ and it is unstable if $R_0 < 1$. For $R_0 > 1$, the endemic equilibrium is globally asymptotically stable.*

Proof. We first show that the stability properties of (2.6) are the same as those of (2.10). Let

$$N(t) := (N_1(t), N_2(t)) \quad \text{and} \quad I(t) := (I_1(t), I_2(t)).$$

We define functions $F: (\mathbb{R}^2)^2 \rightarrow \mathbb{R}^2$ and $H: (\mathbb{R}^2)^4 \rightarrow \mathbb{R}^2$ as right hand sides of (2.6), i.e., (2.6) can be written as

$$\begin{aligned}\frac{d}{dt}N(t) &= F(N(t), N(t - \tau)), \\ \frac{d}{dt}I(t) &= H(N(t), N(t - \tau), I(t), I(t - \tau)).\end{aligned}$$

To analyse stability of (2.6) we apply the principle of linearized stability [2], Chapter VII, Theorem 6.8. For an equilibrium (N, I) of (2.6) we define

$$A := \begin{pmatrix} D_1F(N, N) & 0 \\ D_1H(N, N, I, I) & D_3H(N, N, I, I) \end{pmatrix}$$

and

$$B := \begin{pmatrix} D_2F(N, N) & 0 \\ D_2H(N, N, I, I) & D_4H(N, N, I, I) \end{pmatrix}.$$

We define

$$D(\lambda) := \det(\lambda E - A - Be^{-\lambda\tau}),$$

where E is the identity matrix. Then for an equilibrium (N, I) the characteristic equation is

$$(4.27) \quad D(\lambda) = 0.$$

We define

$$\begin{aligned}D_1(\lambda) &:= \det(\lambda E - D_1F(N, N) - D_2F(N, N)e^{-\lambda\tau}), \\ D_2(\lambda) &:= \det(\lambda E - D_3H(N, N, I, I) - D_4H(N, N, I, I)e^{-\lambda\tau}).\end{aligned}$$

Then it follows that

$$D(\lambda) = D_1(\lambda)D_2(\lambda).$$

From Lemma 2.1 we know that every root of $D_1(\lambda)$ has negative real part. Thus (4.27) has a root in the right complex half plane if and only if

$$(4.28) \quad D_2(\lambda) = 0$$

has a root in the right complex half plane. We can write

$$\frac{d}{dt}I(t) = H(N, N, I(t), I(t - \tau))$$

as (2.10). Then one can see that (4.28) is also the characteristic equation of (2.10). Therefore the stability of (2.10) is equivalent to that of (2.6). Finally, from Theorems 4.3 and 4.4, we obtain the statements on stability of both the disease free equilibrium and the endemic equilibrium of (2.6).

Next we prove the global attractivity of the equilibria of (2.6b) by applying [13], Theorem 4.1. Since we have the boundedness of solutions from Lemma 4.1, we can show that forward orbits of (2.6b) are precompact, thus the ω -limit sets are not empty, see e.g. Smith [10], Chapter 5. Consider first the case $R_0 < 1$. From Theorem 4.3 and Remark 4.1 the basin of attraction of the trivial equilibrium of (2.10) is C_+ . Hence the ω -limit set of every forward orbit of (2.6b) intersects the basin of attraction. By [13], Theorem 4.1, we can conclude that every solution of (2.6b) converges to $(0, 0)$. Now suppose $R_0 > 1$. We prove the global attractivity of the endemic equilibrium of (2.6). To apply [13], Theorem 4.1, we exclude the possibility that the ω -limit set of a forward orbit of (2.6b) contains $(\hat{0}, \hat{0})$. Suppose the contrary, then there is a solution $(I_1(t), I_2(t))$ of (2.6b) such that

$$(4.29) \quad \lim_{t \rightarrow \infty} (I_1(t), I_2(t)) = (0, 0).$$

Since, from Lemma 2.1, it holds that $\lim_{t \rightarrow \infty} N_j(t) = N_j$ for $j \in \{1, 2\}$, for any $\varepsilon > 0$ and $j, k \in \{1, 2\}$, $j \neq k$ there exists a sufficiently large T such that

$$\frac{1}{1 + \frac{e^{\gamma_{kj}\tau} - 1}{N_k(t - \tau)} I_k(t - \tau)} > 1 - \varepsilon \quad \text{and} \quad R_j \frac{I_j(t)}{N_j(t)} < \varepsilon \quad \text{for } t > T.$$

For $t > T$, from (2.6b) we find the estimate

$$(4.30) \quad \frac{dI_j(t)}{dt} > I_j(t)(d_j + \delta_j + \alpha_{jk})(R_j - 1 - \varepsilon) + (1 - \varepsilon)\alpha_{kj}e^{\gamma_{kj}\tau} I_k(t - \tau)$$

for $j, k \in \{1, 2\}$, $j \neq k$. For $j \in \{1, 2\}$ if $R_j > 1$, then, choosing a sufficiently small ε , we see that $I_j(t)$ is nondecreasing, which contradicts (4.29). Hence we focus on the case when $\max\{R_1, R_2\} \leq 1$. We introduce the notation

$$a_j^\varepsilon := (d_j + \delta_j + \alpha_{jk})(R_j - 1 - \varepsilon) \quad \text{and} \quad b_j^\varepsilon := (1 - \varepsilon)\alpha_{kj}e^{\gamma_{kj}\tau}$$

for $j, k \in \{1, 2\}$, $j \neq k$. With this notation (4.30) can be written as

$$\frac{dI_j(t)}{dt} > a_j^\varepsilon I_j(t) + b_j^\varepsilon I_k(t - \tau).$$

Let

$$V(I_{1,t}, I_{2,t}): = -a_2^\varepsilon \left(I_1(t) + b_1^\varepsilon \int_{t-\tau}^t I_2(s) \, ds \right) + b_1^\varepsilon \left(I_2(t) + b_2^\varepsilon \int_{t-\tau}^t I_1(s) \, ds \right).$$

We note that $a_2^\varepsilon < 0$. Differentiating V , the delayed terms and the coefficients of $I_2(t)$ cancel out, and we obtain

$$\frac{d}{dt} V(I_{1,t}, I_{2,t}) = I_1(t)(b_1^\varepsilon b_2^\varepsilon - a_1^\varepsilon a_2^\varepsilon).$$

From Proposition 4.1 (A3), $R_0 > 1$ implies $b_1^0 b_2^0 - a_1^0 a_2^0 > 0$, therefore for a sufficiently small ε , $b_1^\varepsilon b_2^\varepsilon - a_1^\varepsilon a_2^\varepsilon > 0$ also holds. Thus V is nondecreasing; on the other hand, for positive solutions we have $V(I_{1,t}, I_{2,t}) > 0$. Since we assume (4.29), which leads to $\lim_{t \rightarrow \infty} V(I_{1,t}, I_{2,t}) = 0$, we obtain a contradiction. Thus the ω -limit set of any forward orbit of (2.6b) does not contain $(\hat{0}, \hat{0})$. Then by [13], Theorem 4.1, every solution of (2.6) converges to the endemic equilibrium. \square

5. DISEASE TRANSMISSION DYNAMICS: UNIDIRECTIONAL TRANSPORTATION

In this section we assume that two regions are connected via unidirectional transportation. Without loss of generality we assume that individuals move toward region 1 from region 2, but the opposite way is inhibited. Thus we assume that

$$(5.1) \quad \alpha_{12} = 0 \quad \text{and} \quad \alpha_{21} \in (0, \infty).$$

For the convenience of the notation, for $j \in \{1, 2\}$ we define

$$\bar{I}_j := \left(1 - \frac{1}{R_j}\right) N_j.$$

For $R_2 > 1$ we define a quadratic polynomial function for $I \in [0, \infty)$ as

$$(5.2) \quad \eta(I) := I(d_1 + \delta_1) \left(R_1 - 1 - \frac{R_1}{N_1} I \right) + f_{21}(\bar{I}_2).$$

Proposition 5.1. *If $R_2 > 1$ then*

$$(5.3) \quad I^* := \frac{R_1 - 1 + \sqrt{(R_1 - 1)^2 + 4 \frac{R_1 f_{21}(\bar{I}_2)}{N_1 d_1 + \delta_1}}}{2R_1} N_1$$

is a unique positive solution of $\eta(I) = 0$. Furthermore, one has

$$(5.4) \quad \eta(I) \begin{cases} > 0 & \text{for } I \in [0, I^*), \\ = 0 & \text{for } I = I^*, \\ < 0 & \text{for } I \in (I^*, \infty). \end{cases}$$

Proof. We see that the coefficient at I^2 of η is negative with $\eta(0) = f_{21}(\bar{I}_2) > 0$. Since η is a quadratic function, there exists a unique positive solution of $\eta(I) = 0$ and one can obtain (5.3) as a unique positive solution. Since we have $\eta(0) > 0$, it is easy to get (5.4). The proof is complete. \square

We now formulate results on the existence of equilibria in terms of regional reproduction numbers.

Theorem 5.1. *For (2.6) the following statements hold.*

- (i) *There always exists a disease free equilibrium, which is given as $(N_1, N_2, 0, 0)$.*
- (ii) *There exists an endemic equilibrium only for region 1, which is given as $(N_1, N_2, \bar{I}_1, 0)$, if and only if $R_1 > 1$.*
- (iii) *There exists an endemic equilibrium for both regions, which is given as $(N_1, N_2, I^*, \bar{I}_2)$, if and only if $R_2 > 1$.*

Proof. By Lemma 2.1 we obtain the first and second components of equilibria. We omit the proofs of (i) and (ii), since they are straightforward. Assume $R_2 > 1$. Then we see that the positive equilibrium of the second component of (2.6b) is \bar{I}_2 . To find the equilibrium of the first component of (2.6b) we consider the equation $\eta(I) = 0$. Since from Proposition 5.1 $I = I^*$ is a unique positive solution of $\eta(I) = 0$, we obtain the equilibrium. \square

For (2.6b) and (2.10) we consider the initial conditions $I_1(0) = I_1^0 \in \mathbb{R}_+$ and $I_2(\theta) = \varphi_2(\theta)$ for $\theta \in [-\tau, 0]$, where $\varphi_2 \in C([-\tau, 0], \mathbb{R}_+)$. We assume that $\varphi_2(0) > 0$.

Lemma 5.1. *Both (2.6b) and (2.10) have unique nonnegative solutions $(I_1(t), I_2(t))$, defined for all $t > 0$, which are bounded. It holds that $I_1(t) > 0$ for $t > \tau$ and that $I_2(t) > 0$ for $t > 0$.*

Remark 5.1. If $\varphi_2(0) = 0$ then $I_2(t) = 0$ for $t > 0$. If $I_1^0 = 0$ and $\varphi_2 = \hat{0}$ then $I_j(t) = 0$ for $j \in \{1, 2\}$ and $t > 0$. To obtain the global stability results for (2.6), we first consider the limit equation (2.10) and then apply the theory of asymptotically autonomous semiflow, as in the proof of Theorem 4.5. We here omit the details of the proof, see also Section 5.2 in [9].

Theorem 5.2. *For (2.6) the following statements hold.*

- (i) *The disease free equilibrium is globally asymptotically stable if $\max\{R_1, R_2\} < 1$ and it is unstable if $\max\{R_1, R_2\} > 1$.*
- (ii) *The endemic equilibrium for only region 1 is globally asymptotically stable if $R_1 > 1 > R_2$ and it is unstable if $R_2 > 1$.*
- (iii) *The endemic equilibrium for both regions is globally asymptotically stable if $R_2 > 1$.*

6. THE ROLE OF THE TRAVEL DELAY

Theorem 6.1. *Assume $\alpha_{12} > 0$ and $\alpha_{21} > 0$. Then R_0 and all the components of the endemic equilibrium (in the case of $R_0 > 1$) are increasing functions of the travel delay τ .*

Proof. The monotonicity of R_0 with respect to τ is clear from (3.3) and the definition of r_{jk} . The components of the endemic equilibrium are given by the intersection of the curves G_1 and G_2 , see Figure 1. It is easy to check that f_{jk} are also increasing in τ , while g_i are independent of τ . Consider some τ with the corresponding G_i and f_{ji} functions and the endemic equilibrium (x_*, y_*) , and a $\tilde{\tau} > \tau$ with \tilde{G}_i , \tilde{f}_{ji} , and endemic equilibrium $(\tilde{x}_*, \tilde{y}_*)$ (which now we know that it exists). Then, for any x , $\tilde{f}_{ji}(x) > f_{ji}(x)$, hence $\tilde{f}_{ji}^{-1}(x) < f_{ji}^{-1}(x)$ and $\tilde{G}_1(x) = \tilde{f}_{21}^{-1}(-g_1(x)) < f_{21}^{-1}(-g_1(x)) = G_1(x)$. Since g_2^{-1} is decreasing, we also have $\tilde{G}_2(x) = g_2^{-1}(-\tilde{f}_{12}(x)) > g_2^{-1}(-f_{12}(x)) = G_2(x)$. We obtained that $\tilde{G}_1 < G_1$ and $\tilde{G}_2 > G_2$, which geometrically means that the graph of \tilde{G}_1 is shifted downwards, and the graph of \tilde{G}_2 is shifted upwards, compared to the graphs of G_1 and G_2 , whenever they are defined. Given the monotonicity and the geometric configuration of these curves, we find that $(\tilde{x}_*, \tilde{y}_*) > (x_*, y_*)$, see again Figure 1 for a clear picture. \square

To visualize the previous theorem, we plot the endemic equilibrium and the basic reproduction number as a function of τ in Figures 2 and 3, in two different situations. From Figure 2 we can conclude that ignoring the travel delay and the transport related infections, the severity of an epidemics can be easily underestimated. Figure 3 shows the possibility that due to infection during travel, somewhat paradoxically,

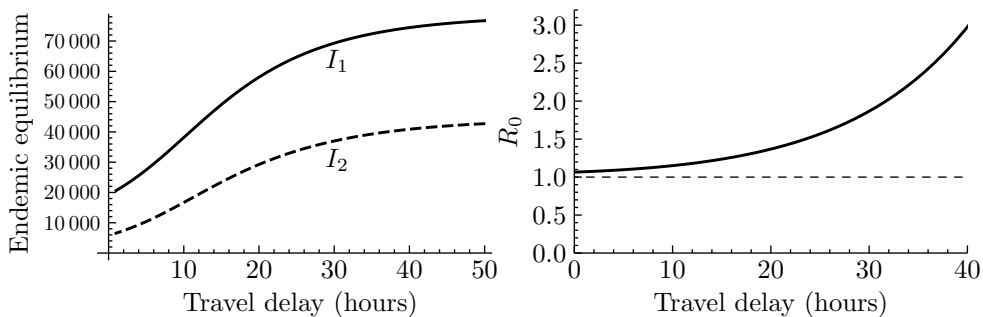


Figure 2. Plots of the components of the endemic equilibrium and R_0 as functions of the travel delay τ . Demographic parameters are chosen such that the total populations of the patches are 8×10^5 and 3×10^5 . Transmission parameters are chosen such that $R_0 > 1$ even in the absence of travel related infections.

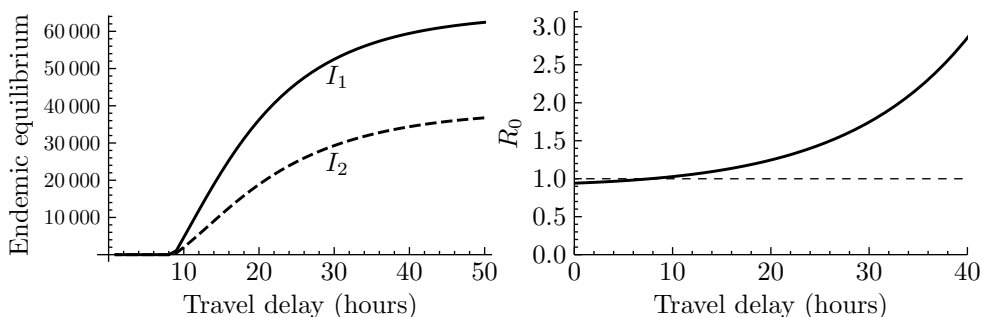


Figure 3. Plots of the components of the endemic equilibrium and R_0 as functions of the travel delay τ . Demographic parameters are chosen as in Figure 2, but transmission parameters are chosen such that $R_0 < 1$ in the absence of travel related infections ($\tau = 0$).

a disease can die out if the two regions are near (small τ), but remains endemic in both regions for larger travel delay, as R_0 becomes larger than one at $\tau = \tau_* \approx 7$. Thus the dynamics of the system suddenly changes as the delay is passing through the critical value τ_* .

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