Global Dynamics of A Reaction and Diffusion Model for Lyme Disease

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Introduction

Lyme disease is one of the most common vector-borne diseases of humans in the world. The disease is named after the town of Lyme, Connecticut, USA, where a number of cases were identified in 1975.

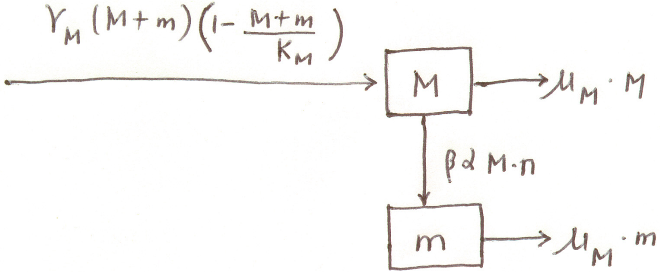
Ecological interactions underlying the epidemic of Lyme disease involve a spirochete, a tick with larval, nymph and adult stages, and two or more vertebrate hosts. Juvenile ticks ordinarily feed on mice and adult ticks feed on deer. Mice acquire the spirochete from infected nymphs and then pass the infection to larvae of the next tick generation.

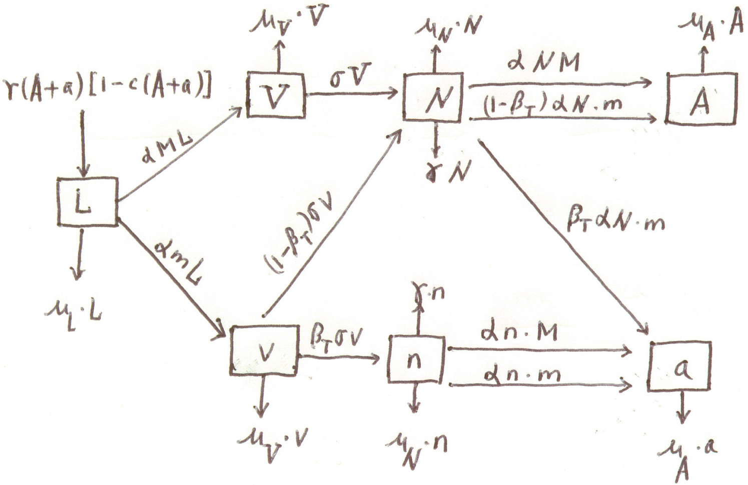
The two-year life cycle of the vector, a tick, scales similarly with the lifespan of its mammalian hosts. Larval ticks acquire the infection at the first blood meal, progress to the nymph stage, and then may infect a host at the second meal.

In order to study the effects of the vector's stage structure on the spatial expansion of infection, Caraco et al. (*The American Naturalist*, 2002) proposed a reaction and diffusion model for the Lyme disease in the northeast United States.

This model treats population densities at locations $x = (x_1, x_2)$ in a continuous two-dimensional domain Ω. Let $M(t, x)$ and $m(t, x)$ be densities of susceptible and pathogen-infected mice; $L(t, x)$ be the density of questing larvae; $V(t, x)$ and $v(t, x)$ be densities of larvae infesting susceptible and pathogen-infected mice; $N(t, x)$ and $n(t, x)$ be the densities of susceptible and infectious questing nymphs; $A(t, x)$ and $a(t, x)$ be the densities of uninfected and pathogen-infected adult ticks, respectively.

r_M: Maximal individual birth rate in mice;
K_M: Carrying capacity for mice;
μ_M: Mortality rate per mouse;
D_M: Diffusion coefficient for mice;
D_H: Diffusion coefficient for deer;
r: Maximal individual birth rate in ticks;
c: Crowding coefficient in ticks;
μ_L: Mortality rate per questing tick larva;
μ_V: Mortality rate per feeding tick larva;
μ_N: Mortality rate per tick nymph;
μ_A: Mortality rate per adult tick;
α: Attack rate, juvenile ticks on mice;
γ: Attack rate, tick nymphs on humans;
β: Susceptibility to infection in mice;
β_T: Susceptibility to infection in ticks;
σ: Rate at which larvae complete first blood meal.
Note that $\beta \in (0,1)$, $\beta_T \in (0,1)$, and $r_M > \mu_M$.


$r_M (M+m)\left(1-\frac{M+m}{K_M}\right)$
M
$\mu_M \cdot M$
$\beta\alpha M \cdot n$
m
$\mu_M \cdot m$


$\mu_V \cdot V$
$\mu_N \cdot N$
$\mu_A \cdot A$
αNM
$r(A+a)[1-c(A+a)]$
V
σV
N
$(1-\beta_T)\alpha N \cdot m$
A
αML
γN
L
$(1-\beta_T)\sigma v$
$\beta_T \alpha N \cdot m$
αmL
$\mu_L \cdot L$
$\gamma \cdot n$
$\beta_T \sigma v$
$\alpha n \cdot M$
v
n
$\alpha n \cdot m$
a
$\mu_V \cdot v$
$\mu_N \cdot n$
$\mu_A \cdot a$

$$
\begin{aligned}
\frac{\partial M}{\partial t} &= D_M \Delta M + r_M(M+m)\left(1-\frac{M+m}{K_M}\right) - \mu_M M - \alpha\beta M n,\\
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha\beta M n - \mu_M m,\\
\frac{\partial L}{\partial t} &= r(A+a)[1-c(A+a)] - \mu_L L - \alpha L(M+m),\\
\frac{\partial V}{\partial t} &= D_M \Delta V + \alpha M L - V(\sigma+\mu_V),\\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha m L - v(\sigma+\mu_V),\\
\frac{\partial N}{\partial t} &= \sigma[V+(1-\beta_T)v] - N[\gamma+\alpha(M+m)+\mu_N],\\
\frac{\partial n}{\partial t} &= \beta_T\sigma v - n[\gamma+\alpha(M+m)+\mu_N],\\
\frac{\partial A}{\partial t} &= D_H \Delta A + \alpha N[M+(1-\beta_T)m] - \mu_A A,\\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha[(M+m)n+\beta_T m N] - \mu_A a.
\end{aligned}
\tag{1.1}
$$

Caraco et al. defined the basic reproduction number, and investigated the existence and local stability of demographic equilibria and infection equilibria for the spatially homogeneous reaction system associated with model (1.1).

They further studied the spatial velocity of infection by the linear approximation method and made a conjecture on the existence of traveling waves for the reaction-diffusion system (1.1).

Our purpose is to study the global dynamics of nonlinear system (1.1) in the case of a bounded spatial domain, and the existence of spreading speed of the disease and traveling wave fronts for (1.1) in the case of a unbounded domain. In particular, we will show that the spreading speed is linearly determinate and coincides with the minimal wave speed for traveling wave fronts.

Let $\Omega \subset \mathbb{R}^2$ be a spatial habitat with smooth boundary $\partial\Omega$. We assume that all populations remain confined to the domain Ω for all time. Thus, the model system (1.1) is subject to the Neumann boundary conditions:

$$\frac{\partial M}{\partial \nu} = \frac{\partial n}{\partial \nu} = \frac{\partial L}{\partial \nu} = \frac{\partial V}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial N}{\partial \nu} = \frac{\partial n}{\partial \nu} = \frac{\partial A}{\partial \nu} = \frac{\partial a}{\partial \nu} = 0, \tag{1.2}$$

where $\frac{\partial}{\partial \nu}$ denotes the differentiation along the outward normal ν to $\partial\Omega$.

Let $\mathcal{M} = M + m$, $\mathcal{V} = V + v$, $\mathcal{N} = N + n$, $\mathcal{A} = A + a$. In view of system (1.1), we then obtain the following reaction-diffusion system:

$$
\begin{aligned}
\frac{\partial \mathcal{M}}{\partial t} &= D_M \Delta \mathcal{M} - \mu_M \mathcal{M} + r_M \mathcal{M}\left(1 - \frac{\mathcal{M}}{K_M}\right), \\
\frac{\partial L}{\partial t} &= r\mathcal{A}(1 - c\mathcal{A}) - \mu_L L - \alpha L \mathcal{M}, \\
\frac{\partial \mathcal{V}}{\partial t} &= D_M \Delta \mathcal{V} + \alpha \mathcal{M} L - (\sigma + \mu_V)\mathcal{V}, \\
\frac{\partial \mathcal{N}}{\partial t} &= \sigma \mathcal{V} - (\gamma + \alpha \mathcal{M} + \mu_N)\mathcal{N}, \\
\frac{\partial \mathcal{A}}{\partial t} &= D_H \Delta \mathcal{A} - \mu_A \mathcal{A} + \alpha \mathcal{M}\mathcal{N}.
\end{aligned}
\tag{1.3}
$$

By a standard result on logistic type reaction-diffusion equations, it follows that for any continuous and nonnegative initial data $\mathcal{M}(0, \cdot) \in C(\overline{\Omega}, \mathbb{R}^2_+) \setminus \{0\}$, we have

$$\lim_{t\to\infty} \mathcal{M}(t,x) = K_M\left(1-\frac{\mu_M}{r_M}\right) := Q$$

uniformly for $x=(x_1,x_2)\in\overline{\Omega}$. This gives rise to the following limiting system:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= r\mathcal{A}(1-c\mathcal{A}) - (\mu_L+\alpha Q)L,\\
\frac{\partial \mathcal{V}}{\partial t} &= D_M\Delta\mathcal{V} + \alpha QL - (\sigma+\mu_V)\mathcal{V},\\
\frac{\partial \mathcal{N}}{\partial t} &= \sigma\mathcal{V} - (\gamma+\alpha Q+\mu_N)\mathcal{N},\\
\frac{\partial \mathcal{A}}{\partial t} &= D_H\Delta\mathcal{A} - \mu_A\mathcal{A} + \alpha Q\mathcal{N}.
\end{aligned} \tag{1.4}$$

Under appropriate conditions, we are able to show that every positive solution of system (1.4) converges, as $t\to\infty$, to the unique positive equilibrium $(L^*,\mathcal{V}^*,\mathcal{N}^*,\mathcal{A}^*)$ uniformly for $x\in\overline{\Omega}$.

By the theory of asymptotically autonomous semiflows or the theory of chain transitive sets, it follows that every positive solution of system (1.3) satisfies

$$\lim_{t\to\infty}(\mathcal{M}(t,x), L(t,x), \mathcal{V}(t,x), \mathcal{N}(t,x), \mathcal{A}(t,x)) = (Q, L^*, \mathcal{V}^*, \mathcal{N}^*, \mathcal{A}^*)$$

uniformly for $x \in \overline{\Omega}$. To obtain the global dynamics of (1.1), it then suffices to study the following limiting system:

$$\begin{aligned} \frac{\partial m}{\partial t} &= D_M \Delta m - \mu_M m + \alpha\beta(Q-m)n, \\ \frac{\partial v}{\partial t} &= D_M \Delta v - (\sigma + \mu_v)v + \alpha L^* m, \\ \frac{\partial n}{\partial t} &= -(\gamma + \alpha Q + \mu_N)n + \beta_T \sigma v, \\ \frac{\partial a}{\partial t} &= D_H \Delta a - \mu_A a + \alpha Q n + \alpha\beta_T m(\mathcal{N}^* - n). \end{aligned} \tag{1.5}$$

Global dynamics

Clearly, $(0,0,0,0)$ is an equilibrium of (1.4). A simple computation shows that system (1.4) has a spatially homogeneous equilibrium $(L^*, \mathcal{V}^*, \mathcal{N}^*, \mathcal{A}^*)$, which is defined by

$$
\begin{aligned}
\mathcal{A}^* &= \frac{1}{c} - \frac{(\alpha Q + \mu_L)(\sigma + \mu_V)(\gamma + \alpha Q + \mu_N)\mu_A}{rc\sigma(\alpha Q)^2},\\
L^* &= \frac{(\sigma + \mu_V)(\gamma + \alpha Q + \mu_N)\mu_A}{\sigma(\alpha Q)^2}\mathcal{A}^*,\\
\mathcal{V}^* &= \frac{(\gamma + \alpha Q + \mu_N)\mu_A}{\sigma \alpha Q}\mathcal{A}^*,\\
\mathcal{N}^* &= \frac{\mu_A}{\alpha Q}\mathcal{A}^*.
\end{aligned}
\tag{2.1}
$$

Let $X = C(\overline{\Omega}, \mathbb{R}^4)$, $X^+ = C(\overline{\Omega}, \mathbb{R}^4_+)$, By the theory of abstract semilinear integral equations, it follows that for any $\phi \in X^+$, system (1.4) has a unique nonnegative and non-continuable solution

$$u(t,x,\phi) := (L(t,x,\phi), \mathcal{V}(t,x,\phi), \mathcal{N}(t,x,\phi), \mathcal{A}(t,x,\phi))$$

on $[0, \sigma_\phi)$ with $u(0,\cdot,\phi) = \phi$.

Note that the function $g(u) := ru(1-cu)$ has a maximum value $b := g(\frac{1}{2c}) = \frac{r}{4c}$ on $[0,\infty)$. Thus, the nonlinear system (1.4) is dominated by the following linear cooperative system

$$\begin{aligned}
\frac{\partial L}{\partial t} &= b - (\mu_L + \alpha Q)L, \\
\frac{\partial \mathcal{V}}{\partial t} &= D_M \Delta \mathcal{V} + \alpha Q L - (\sigma + \mu_V)\mathcal{V}, \\
\frac{\partial \mathcal{N}}{\partial t} &= \sigma \mathcal{V} - (\gamma + \alpha Q + \mu_N)\mathcal{N}, \\
\frac{\partial \mathcal{A}}{\partial t} &= D_H \Delta \mathcal{A} - \mu_A \mathcal{A} + \alpha Q \mathcal{N}.
\end{aligned} \tag{2.2}$$

By a simple comparison argument, it then follows that solutions $u(t,\cdot,\phi)$ of (1.4) are uniformly bounded in X^+, and hence, $\sigma_\phi = \infty$ for any $\phi \in X^+$. Further, solutions of (1.4) are ultimately bounded in X^+, that is,

$$\begin{aligned}
&\lim_{t\to\infty} \sup_{x\in\overline{\Omega}} L(t,x,\phi) \le \frac{b}{\mu_L + \alpha Q},\\
&\lim_{t\to\infty} \sup_{x\in\overline{\Omega}} \mathcal{V}(t,x,\phi) \le \frac{\alpha Q b}{(\sigma+\mu_V)(\mu_L+\alpha Q)},\\
&\lim_{t\to\infty} \sup_{x\in\overline{\Omega}} \mathcal{N}(t,x,\phi) \le \frac{\sigma\alpha Q b}{(\gamma+\alpha Q+\mu_N)(\sigma+\mu_V)(\mu_L+\alpha Q)},\\
&\lim_{t\to\infty} \sup_{x\in\overline{\Omega}} \mathcal{A}(t,x,\phi) \le \frac{\sigma(\alpha Q)^2 b}{(\gamma+\alpha Q+\mu_N)(\sigma+\mu_V)(\mu_L+\alpha Q)\mu_A}.
\end{aligned} \tag{2.3}$$

Let $\Phi(t) : X^+ \to X^+, t \geq 0$, be the solution semiflow associated with (1.4), that is, $\Phi(t)\phi = u(t, \cdot, \phi)$, $\forall \phi \in X^+$. By a decomposition technique for the solution maps, it easily follows that $\Phi(t)$ is an α-contraction on X^+ for each $t > 0$. Thus, $\Phi(t)$ has a global compact attractor on X^+.

For the sake of convenience, we set

$$W := \frac{(\alpha Q + \mu_L)(\sigma + \mu_V)(\gamma + \alpha Q + \mu_N)\mu_A}{\sigma(\alpha Q)^2}.$$

To get the existence and global attractivity of the positive spatially homogeneous equilibrium of (1.4), we need the following assumption:

(H1) $W < r \leq 3W$.

Theorem 2.1 Let (H1) hold. Then (1.4) has a unique positive constant equilibrium $u^* := (L^*, \mathcal{V}^*, \mathcal{N}^*, \mathcal{A}^*)$ such that $\lim_{t\to\infty} u(t,\cdot,\phi) = u^*$ in X for any $\phi \in X^+ \setminus \{0\}$.

Step 1. Robust persistence: see [Smith and Zhao, *Nonlinear Analysis,TMA*, 2001]. Let $X_0 := \{\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in X^+ : \phi_4 \not\equiv 0\}$ and $\partial X_0 := X^+ \setminus X_0$. Then prove that $\liminf_{t\to\infty} \min_{x\in\overline{\Omega}} \mathcal{A}(t,x,\phi)) \geq \delta, \quad \forall \phi \in X_0$.

Step 2. Fluctuation method: see [Thieme and Zhao, *Nonlinear Analysis, RWA*,2001]. For any given $\phi \in X_0$, let

$$u(t,x,\phi) = (L(t,x), \mathcal{V}(t,x), \mathcal{N}(t,x), \mathcal{A}(t,x)),$$

and $L^\infty(x) := \limsup_{t\to\infty} L(t,x), \quad L_\infty(x) := \liminf_{t\to\infty} L(t,x)$. We can define $\mathcal{V}^\infty(x)$, $\mathcal{V}_\infty(x)$, $\mathcal{N}^\infty(x)$, $\mathcal{N}_\infty(x)$, $\mathcal{A}^\infty(x)$, and $\mathcal{A}_\infty(x)$ in a similar way.

Let

$$L^\infty := \sup_{x \in \overline{\Omega}} L^\infty(x), \quad L_\infty := \inf_{x \in \overline{\Omega}} L_\infty(x),$$

and define $\mathcal{V}^\infty$, $\mathcal{V}_\infty$, $\mathcal{N}^\infty$, $\mathcal{N}_\infty$, $\mathcal{A}^\infty$, and $\mathcal{A}_\infty$ in a similar way. Then prove that $\mathcal{A}_\infty = \mathcal{A}^\infty = \mathcal{A}^*$, $L^\infty = L_\infty$, $\mathcal{V}^\infty = \mathcal{V}_\infty$, and $\mathcal{N}^\infty = \mathcal{N}_\infty$. It then follows that $(L^\infty, \mathcal{V}^\infty, \mathcal{N}^\infty, \mathcal{A}^*)$ is a nonnegative and nonzero constant equilibrium of system (1.4), and hence, $(L^\infty, \mathcal{V}^\infty, \mathcal{N}^\infty, \mathcal{A}^*) = (L^*, \mathcal{V}^*, \mathcal{N}^*, \mathcal{A}^*)$. Consequently, we have

$$\lim_{t \to \infty} u(t, x, \phi) = (L^*, \mathcal{V}^*, \mathcal{N}^*, \mathcal{A}^*), \quad \forall x \in \overline{\Omega}.$$

Step 3. Using the omega limit set to show that $\lim_{t \to \infty} u(t, \cdot, \phi) = u^*$ in X.

Next, we consider the global dynamics of system (1.5). Let $Y = C(\overline{\Omega}, [0, Q]) \times C(\overline{\Omega}, \mathbb{R}^3_+)$. By the similar arguments to those for system (1.4), it follows that for any $\phi \in Y$, system (1.5) admits a unique solution

$$w(t, x, \phi) := (m(t, x, \phi), v(t, x, \phi), n(t, x, \phi), a(t, x, \phi))$$

on $[0, \infty)$ with $w(0, \cdot, \phi) = \phi$. Further, $w(t, \cdot, \phi) \in Y$, $\forall t \geq 0$, and solutions of system (1.5) are uniformly bounded and ultimately bounded in Y.

Recall that the basic reproduction number R_0 is defined to be

$$R_0 = \frac{\beta_T \sigma \alpha L^*}{(\sigma + \mu_V)\mu_M} \cdot \frac{\beta \alpha Q}{\gamma + \alpha Q + \mu_N} = \frac{\beta \beta_T \mu_A \mathcal{A}^*}{\mu_M Q}.$$

In the case where $R_0 > 1$, a straightforward computation shows that system (1.5) has a unique positive constant equilibrium $w^* = (m^*, v^*, n^*, a^*)$, which is defined as

$$
\begin{aligned}
m^* &= Q\frac{\beta\beta_T\mu_A\mathcal{A}^* - \mu_M Q}{\beta\beta_T\mu_A\mathcal{A}^*},\\
v^* &= \frac{(\gamma+\alpha Q+\mu_N)(\beta\beta_T\mu_A\mathcal{A}^* - \mu_M Q)}{\sigma\alpha Q\beta\beta_T},\\
n^* &= \frac{\beta\beta_T\mu_A\mathcal{A}^* - \mu_M Q}{\beta\alpha Q},\\
a^* &= \frac{\alpha Q n^* + \alpha\beta_T m^* N^*}{\mu_A},
\end{aligned}
\tag{2.4}
$$

where $N^* := \mathcal{N}^* - n^* = \frac{\mu_A(1-\beta_T)\mathcal{A}^*}{\alpha Q} + \frac{\mu_M}{\alpha\beta}$.

Theorem 2.2 Let $r > W$. Then the following statements are valid:

(i) If $R_0 \leq 1$, then $(0,0,0,0)$ is globally attractive for all nonnegative solutions of system (1.5) in Y.

(ii) If $R_0 > 1$, then system (1.5) has a unique positive constant equilibrium $w^* = (m^*, v^*, n^*, a^*)$ such that w^* is globally attractive for all positive solutions of system (1.5) in Y.

Step 1. It suffices to prove that the above threshold dynamics holds for the following reaction-diffusion system:

$$
\begin{aligned}
\frac{\partial m}{\partial t} &= D_M \Delta m - \mu_M m + \alpha\beta(Q - m)n, \\
\frac{\partial v}{\partial t} &= D_M \Delta v - (\sigma + \mu_v)v + \alpha L^* m, \\
\frac{\partial n}{\partial t} &= -(\gamma + \alpha Q + \mu_N)n + \beta_T \sigma v.
\end{aligned}
\tag{2.5}
$$

Let $Z = C(\overline{\Omega}, [0, Q]) \times C(\overline{\Omega}, \mathbb{R}^2_+)$. It follows that for any $\phi \in Z$, system (2.5) admits a unique solution

$$z(t, x, \phi) := (m(t, x, \phi), v(t, x, \phi), n(t, x, \phi))$$

on $[0, \infty)$ with $z(0, \cdot, \phi) = \phi$. Let $Q(t)$ be the solution semiflow associated with system (2.5), that is, $Q(t)\phi = z(t, \cdot, \phi)$, $\forall \phi \in Z$.

Step 2. Using the theory of monotone and subhomogeneous systems, see [Zhao, *Dynamical Systems in Population Biology*, Springer-Verlag, New York, 2003].

By the theory of chain transitive sets, see [Hirsch, Smith and Zhao, *JDDE*, 2001], we can lift the threshold dynamics for (1.5) to the full model system (1.1).

Theorem 2.3 Let (H1) hold. Then the following statements are valid:

(i) If $R_0 \leq 1$, then the disease-free equilibrium $(Q, 0, L^*, \mathcal{V}^*, 0, \mathcal{N}^*, 0, \mathcal{A}^*, 0)$ is globally attractive for all nonnegative and nonzero solutions of system (1.1) in $C(\overline{\Omega}, \mathbb{R}^9_+)$.

(ii) If $R_0 > 1$, then system (1.1) has a unique (positive) endemic equilibrium $E^* = (M^*, m^*, L^*, V^*, v^*, N^*, n^*, A^*, a^*)$ such that E^* is globally attractive for all positive solutions of (1.1) in $C(\overline{\Omega}, \mathbb{R}^9_+)$, where M^*, V^*, N^* and A^* are defined by $M^* + m^* = Q$, $V^* + v^* = \mathcal{V}^*$, $N^* + n^* = \mathcal{N}^*$ and $A^* + a^* = \mathcal{A}^*$, respectively.

Spreading speeds and traveling waves

Let R_0 be the basic reproduction number defined as in section 2. In order to get the spreading speed of the disease, we assume that $R_0 > 1$ throughout this section.

Since the fourth equation in system (1.5) is decoupled from the first three equations, we focus on the following reaction and diffusion system:

$$\begin{aligned} \frac{\partial m}{\partial t} &= D_M \Delta m - \mu_M m + \alpha\beta(Q - m)n, \\ \frac{\partial v}{\partial t} &= D_M \Delta v - (\sigma + \mu_v)v + \alpha L^* m, \\ \frac{\partial n}{\partial t} &= -(\gamma + \alpha Q + \mu_N)n + \beta_T \sigma v. \end{aligned} \tag{3.1}$$

By Theorem 2.2, it then follows that the spatially homogeneous system

$$\begin{aligned} \frac{dm}{dt} &= -\mu_M m + \alpha\beta(Q-m)n, \\ \frac{dv}{dt} &= -(\sigma+\mu_v)v + \alpha L^* m, \\ \frac{dn}{dt} &= -(\gamma+\alpha Q+\mu_N)n + \beta_T \sigma v, \end{aligned} \tag{3.2}$$

admits a globally attractive positive equilibrium $z^* = (m^*, v^*, n^*)$ in $[0, Q] \times \mathbb{R}^2_+$.

Let $\{Q_t\}_{t\geq 0}$ be the solution semiflow associated with system (3.1) on $\mathcal{C}_{z^*}$, that is,

$$Q_t(\phi)(x) = u(t,x,\phi), \quad \forall \phi \in \mathcal{C}_{z^*},\ x \in \mathbb{R},\ t \geq 0. \tag{3.3}$$

According to the theory of spreading speeds for monotone semiflows, see [Weinberger, *SIMA*, 1982] and [Liang and Zhao, *CPAM*, 2007], the map $Q_1 : \mathcal{C}_{z^*} \to \mathcal{C}_{z^*}$ admits a spreading speed c^*.

In order to estimte c^*, we consider the linear ordinary differential system

$$\begin{aligned} \frac{d\bar{u}_1(t)}{dt} &= D_M \mu^2 \bar{u}_1(t) - \mu_M \bar{u}_1(t) + \alpha\beta Q \bar{u}_3(t), \\ \frac{d\bar{u}_2(t)}{dt} &= D_M \mu^2 \bar{u}_2(t) - (\sigma + \mu_v)\bar{u}_2(t) + \alpha L^* \bar{u}_1(t), \quad (3.4) \\ \frac{d\bar{u}_3(t)}{dt} &= -(\gamma + \alpha Q + \mu_N)\bar{u}_3(t) + \beta_T \sigma \bar{u}_2(t), \end{aligned}$$

where $\mu \geq 0$ is a parameter. Let $\bar{u}(t, \bar{u}_0)$ be the unique solution of (3.4) satisfying $\bar{u}(0, \bar{u}_0) = \bar{u}_0 \in \mathbb{R}^3$.

It is easy to see that $u(t,x) = e^{-\mu x}\bar{u}(t,\bar{u}_0)$ is a solution of the following linear reaction and diffusion system

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_M \Delta u_1 - \mu_M u_1 + \alpha\beta Q u_3, \\ \frac{\partial u_2}{\partial t} &= D_M \Delta u_2 - (\sigma + \mu_v) u_2 + \alpha L^* u_1, \\ \frac{\partial u_3}{\partial t} &= -(\gamma + \alpha Q + \mu_N) u_3 + \beta_T \sigma u_2. \end{aligned} \tag{3.5}$$

Let $\{M_t\}_{t\geq 0}$ be the solution semiflow associated with system (3.5). Note that the fundamental solution matrix of system (3.4) is $e^{A(\mu)t}$ with

$$A(\mu) := \begin{bmatrix} D\mu^2 - \mu_M & 0 & \alpha\beta Q \\ \alpha L^* & D\mu^2 - (\sigma + \mu_v) & 0 \\ 0 & \beta_T \sigma & -(\gamma + \alpha Q + \mu_N) \end{bmatrix}.$$

Define $B_\mu^t : \mathbb{R}^3 \to \mathbb{R}^3$ as

$$B_\mu^t(z) := M_t(ze^{-\mu x})(0) = \bar{u}(t,z) = e^{A(\mu)t}z, \quad \forall z \in \mathbb{R}^3.$$

Therefore, B_μ^t is the solution map of the linear system (3.4) on $\mathbb{R}^3$, and its principal eigenvalue is $e^{\lambda(\mu)t}$, where $\lambda(\mu)$ is the principal eigenvalue of the matrix $A(\mu)$. Now we define the function

$$\Phi(\mu) := \frac{1}{\mu}\ln e^{\lambda(\mu)} = \frac{\lambda(\mu)}{\mu}, \quad \forall \mu > 0. \tag{3.6}$$

Since $\lim_{\mu\to 0}\Phi(\mu) = +\infty$ and $\lim_{\mu\to+\infty}\Phi(\mu) = +\infty$, $\Phi(\mu)$ assumes its minimum at some finite value μ^*. Moreover, we have the following result.

Theorem 3.1 Let c^* be the spreading speed of the map Q_1 on $\mathcal{C}_{z^*}$. Then $c^* = \inf_{\mu>0}\Phi(\mu)$, and hence, $c^* > 0$.

By using the theory of spreading speeds for monotone semiflows [Liang and Zhao, *CPAM*, 2007] (see also [Weinberger, Lewis and Li, *JMB*, 2002], which needs an additional condition on initial data), we have the following result.

Theorem 3.2 Assume that $R_0 > 1$, let $c^* = \inf_{\mu>0} \Phi(\mu)$, and let $u(t,x,\phi)$ be the solution of system (3.1) with $u(0,\cdot,\phi) = \phi \in \mathcal{C}_{z^*}$. Then the following statements are valid:

(i) For any $c > c^*$, if $\phi \in \mathcal{C}_{z^*}$ with $0 \leq \phi \ll z^*$, and $\phi(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\geq ct} u(t,x,\phi) = (0,0,0)$;

(ii) For any $c \in (0, c^*)$, if $\phi \in \mathcal{C}_{z^*}$ and $\phi \not\equiv 0$, then $\lim_{t\to\infty, |x|\leq ct} u(t,x,\phi) = z^*$.

By using the theory of traveling waves for monotone semiflows [Liang, Yi and Zhao, *JDE*, 2006] and [Liang and Zhao, *CPAM*, 2007], we have the following result. Note that one cannot use the result in [Li, Weinberger and Lewis, *Math. Biosci.*, 2005].

Theorem 3.3 Assume that $R_0 > 1$ and let $c^* = \inf_{\mu>0} \Phi(\mu)$. Then the following statements are valid:

(i) System (3.1) admits no traveling wave solution with wave speed $c \in (0, c^*)$;

(ii) For every $c \geq c^*$, system (3.1) has a traveling wave solution $U(x - ct)$ connecting u^* to 0 such that $U(s)$ is continuous and non-increasing in $s \in \mathbb{R}$.

Remark 3.1 For any given solution of system (1.5), we can regard $a(t,x)$ as a solution to the following linear hon-homogeneous equation

$$\frac{\partial a}{\partial t} = D_H \Delta a - \mu_A a + \alpha Q n(t,x) + \alpha \beta_T m(t,x)(\mathcal{N}^* - n(t,x)).$$

It then follows that the similar conclusions in Theorems 3.2 and 3.3 also hold for $a(t,x)$, and hence, the number c^* is the spreading speed and the minimal wave speed for system (1.5).

Future works

- The formula given in Theorem 3.1 can be used to compute the spreading speed numerically. Indeed, one may first get the expression of $\lambda(\mu)$, the unique eigenvalue of the 3×3 matrix $A(\mu)$ with a positive eigenvector, and then solve μ^* from the algebraic equation $\Phi'(\mu) = 0$ to obtain $c^* = \Phi(\mu^*)$.
- The model (1.1) ignores seasonal pattern in abundances and activities of different stages. A further research project may use the time-periodic version of model (1.5) to study the effect of the seasonality on the spread of disease by appealing to the theory developed in [Liang, Yi and Zhao, *JDE*, 2006] for periodic evolution systems.
- A more challenging problem is to consider the spreading speeds and traveling waves in the case where some parameters are spatially heterogeneous. For spatially periodic case, see [Liang and Zhao,*JFA*, 2010].

Thank you!