A two-strain reaction–diffusion malaria model with seasonality and vector-bias

Huijie Chu and Zhengu Bai

Abstract. To investigate the combined effects of drug resistance, seasonality and vector-bias, we formulate a periodic two-strain reaction–diffusion model. It is a competitive system for sensitive and resistant strains, but the single-strain subsystem is cooperative. We derive the basic reproduction number $R_i$ and the invasion reproduction number $\hat{R}_i$ for strain $i = 1, 2$, and establish the transmission dynamics in terms of these four quantities. More precisely, (i) if $R_1 \leq 1$ and $R_2 \leq 1$, then the disease is extinct; (ii) if $R_1 > 1 \geq R_2 \geq R_1$, then the sensitive (resistant) strains are persistent, while the resistant (sensitive) strains die out; (iii) if $R_1 > 1$ and $R_2 > 1$, then two strains are coexistent and periodic oscillation phenomenon is observed. We also study the asymptotic behavior of the basic reproduction number $R_0 = \max\{R_1, R_2\}$ for our model regarding small and large diffusion coefficients. Numerically, we demonstrate the outcome of competition for two strains in different cases.

Mathematics Subject Classification. 35K57, 37N25, 34K13.

Keywords. Malaria model, Two-strain, Seasonality, Reproduction number, Persistence and extinction.

1. Introduction

Malaria, caused by the Plasmodium parasite, is a mosquito-borne infectious disease. It is transmitted between humans through the effective bites of adult female Anopheles mosquitoes [1,2]. The most common symptoms are fever, headaches, shivering, vomiting and body aches. Although many measures have been taken in the prevention and control of malaria, it is still endemic in over 100 countries worldwide. It causes serious public health problems and a significant economic burden [3]. Therefore, it is necessary to gain a deeper understanding of malaria transmission dynamics.

Mathematical modeling plays an important role in malaria research. The earliest model dates back to the groundbreaking work of Ronald Ross [4] and was later reformulated by Macdonald in the early 1950s [5]. Ross’ model only consists of two equations, but it captures the essential feature of disease transmission between the mosquito vector and the human host. Since then, the modeling framework has formed the central core of malaria models, considering various aspects related to malaria epidemics, such as spatial heterogeneity [6–9], superinfection [10], and the effect of climate change [11,12]. However, few studies take into account the following biological factors for malaria transmission simultaneously.

Vector-bias effect The vector-bias describes that mosquitoes prefer biting infectious humans to susceptible ones. Kingsolver [13] first introduced a vector-bias model for the dynamics of malarial transmission. Following Kingsolver’s work, Hosack et al. [14] included the incubation time in mosquitoes to study the dynamics of the disease concerning the reproduction number. Further, Chamchod and Britton [15] extended the model from previous authors by defining attractiveness in a different way. Motivated by these works, Wang and Zhao incorporated seasonality into a vector-bias model with an incubation period [16].

This research was supported by the National Natural Science Foundation of China (No. 11971369) and the Fundamental Research Funds for the Central Universities (No. JB210711).
Bai et al. formulated a time-delayed periodic reaction–diffusion model with vector-bias effect [17] and found that ignorance of the vector-bias effect will underestimate the infection risk. These results suggest that the vector-bias has a vital role in the epidemiology of malaria.

**Drug-resistance** Currently, due to the lack of effective and safe vaccines, the primary strategy for controlling malaria is drugs. However, using anti-malarial drugs such as chloroquine, malarame, nivaquine, aralen and fansidar results in the appearance and spread of resistance in the parasite population [18,19]. This poses a significant challenge to the global control of malaria transmission or eradication of the disease. Therefore, it is essential to investigate the resistance in malaria transmission.

**Seasonality** It is generally believed that climatic factors such as temperature, rainfall, humidity, wind and duration of daylight greatly influence the transmission and distribution of vector-borne diseases [20–22]. For example, rising temperatures will reduce the number of days required for breeding, and thereby increase mosquito development rates [23]. There have been some mathematical models and field observations suggesting that the strength and mechanisms of seasonality can change the pattern of infectious diseases; see [23–25] and references therein. These results are beneficial for forecasting mosquito abundance and effectively controlling the disease.

Besides these considerations above, human and vector populations have also contributed to the spread of vector-borne diseases [6–9]. Therefore, this paper aims to investigate a periodic two-strain malaria model with diffusion, which is an extension of the autonomous limiting system in [26]. Because of the intrinsic mathematical structure of the model, we choose a time-varying region to carry out the dynamical analysis. This idea has also been used in [27]. In particular, we prove that any forward orbit in $M_0$ converges to one of the isolated invariant sets $\{M_0, M_1, M_2\}$. Since there are three invariant sets in $\partial C_0$, it is a non-trivial task to verify this fact (see Theorem 4.3).

The rest of this paper is organized as follows. In the next section, we formulate the model and study its well-posedness. In Sect. 3, we define the basic reproduction number $R_i$ and the invasion reproduction number $\mathcal{R}_i$ ($i = 1, 2$) for the sensitive and resistant strains, respectively. In Sect. 4, we investigate uniform persistence and extinction in terms of reproduction numbers. In Sect. 5, we analyze the asymptotic behavior of the basic reproduction number $R_0 = \max\{R_1, R_2\}$ for our model concerning small and large diffusion coefficients, and present the relation between $R_0$ and the vector-bias. In Sect. 6, we conduct a numerical study for our model. And the paper ends with a brief discussion.

### 2. Model formulation

Motivated by [17,26], we consider the model for malaria epidemics with no immunity. That is, individuals who recovered from malaria cannot resist reinfection of the disease and become susceptible directly. Assume that a susceptible human and mosquito can be infected by only one virus strain. The total human population is divided into three groups: susceptibles $S_h(t, x)$, infectious individuals with drug-sensitive strain $I_1(t, x)$ and infectious individuals with drug-resistant strain $I_2(t, x)$, where $t$ is time and $x$ stands for location. For the vector population, since adult male and immature mosquitoes do not take blood and thus they cannot contract the virus, we only consider adult female mosquitoes in our model. The mosquito population has three epidemiological classes: susceptible vectors $S_v(t, x)$, infectious with sensitive parasites $I_{v,1}(t, x)$ and infectious with resistant parasites $I_{v,2}(t, x)$.

Assume that all populations remain confined to a bounded domain $\Omega \subset \mathbb{R}^m (m \geq 1)$ with smooth boundary $\partial \Omega$. Following the line in [17], we suppose that the density of total human population $N(t, x) = S_h(t, x) + I_1(t, x) + I_2(t, x)$ satisfies the following reaction–diffusion equation:

\[
\begin{align*}
&\frac{\partial N(t, x)}{\partial t} = D_h \Delta N(t, x) + B(x, N)N(t, x) - dN(t, x), & t > 0, \ x \in \Omega, \\
&\frac{\partial N(t, x)}{\partial \nu} = 0, & t > 0, \ x \in \partial \Omega,
\end{align*}
\]  

(2.1)
with

\[
B(x, u) = \begin{cases} 
    b \left[1 - \frac{u}{K(x)}\right], & 0 \leq u < K(x), \ x \in \Omega, \\
    0, & u \geq K(x), \ x \in \Omega,
\end{cases}
\]

where \(\Delta\) is the usual Laplacian operator, \(\nu\) is the outward unit normal vector on \(\partial\Omega\) and \(\frac{\partial}{\partial \nu}\) means the normal derivative along \(\nu\) on \(\partial\Omega\). \(D_h > 0\) is the diffusion coefficient of humans, \(b\) and \(d\) \((0 < d < b)\) are, respectively, the maximal birth and natural death rates of humans, and \(K(x)\) denotes the local carrying capacity, which is supposed to be a positive continuous function of location \(x\). By employing [28, Theorems 3.1.5 and 3.1.6], we arrive at that system (2.1) admits a globally attractive positive steady state \(N^*(x)\) in \(C(\Omega, \mathbb{R}_+) \setminus \{0\}\).

We also assume that the equation of the total mosquito population \(M(t, x) = S_v(t, x) + I_{v1}(t, x) + I_{v2}(t, x)\) is of the form

\[
\begin{align*}
\frac{\partial M(t, x)}{\partial t} &= D_v \Delta M(t, x) + \Lambda(t, x) - \eta(t, x)M(t, x), & t > 0, \ x \in \Omega, \\
\frac{\partial M(t, x)}{\partial \nu} &= 0, & t > 0, \ x \in \partial \Omega,
\end{align*}
\]

where \(D_v > 0\) is the diffusion coefficient of mosquitoes, \(\Lambda(t, x)\) is the recruitment rate at which adult female mosquitoes emerge from larval at time \(t\) and location \(x\), and \(\eta(t, x)\) is the natural death rate of mosquitoes at time \(t\) and location \(x\). Functions \(\Lambda(t, x)\) and \(\eta(t, x)\) are Hölder continuous and nonnegative nontrivial on \(\mathbb{R} \times \bar{\Omega}\), and \(\omega\)-periodic in \(t\) for some \(\omega > 0\). It easily follows that system (2.2) admits a globally attractive positive \(\omega\)-periodic solution \(M^*(t, x)\) in \(C(\Omega, \mathbb{R}_+)\) (see, e.g., [29, Lemma 2.1]). Biologically, we may suppose that the total human and mosquito density at time \(t\) and location \(x\), respectively, stabilize at \(N^*(x)\) and \(M^*(t, x)\), that is, \(N(t, x) \equiv N^*(x)\) and \(M(t, x) \equiv M^*(t, x)\) for all \(t \geq 0\) and \(x \in \bar{\Omega}\).

For model parameters, since the impact of climate change on mosquitoes activities is much more than that on humans, the parameters corresponding to mosquitoes are assumed to be time-dependent. To incorporate a vector-bias term into the model, we use the parameters \(p\) and \(l\) to describe the probabilities that a mosquito arrives at a human at random and picks the human if he is infectious and susceptible, respectively [15,16]. Since infectious humans are more attractive to mosquitoes, we assume \(p \geq l > 0\). Let \(\beta(t, x)\) be the biting rate of mosquitoes at time \(t\) and location \(x\); \(c_1(\alpha_1)\) be the transmission probability per bite from infectious mosquitoes (humans) with sensitive strain to susceptible humans (mosquitoes), and \(c_2(\alpha_2)\) be the transmission probability per bite from infectious mosquitoes (humans) with resistant strain to susceptible humans (mosquitoes). According to the induction in [26], we obtain

\[
\begin{align*}
J_1(t, x, I_1(t, x), I_2(t, x)) &= \frac{c_1 \beta(t, x)l(N^*(x) - I_1(t, x) - I_2(t, x))}{p(I_1(t, x) + I_2(t, x)) + l(N^*(x) - I_1(t, x) - I_2(t, x))}, \\
J_2(t, x, I_1(t, x), I_2(t, x)) &= \frac{\alpha_1 \beta(t, x) p I_1(t, x)}{p(I_1(t, x) + I_2(t, x)) + l(N^*(x) - I_1(t, x) - I_2(t, x))}, \\
J_3(t, x, I_1(t, x), I_2(t, x)) &= \frac{c_2 \beta(t, x)l(N^*(x) - I_1(t, x) - I_2(t, x))}{p(I_1(t, x) + I_2(t, x)) + l(N^*(x) - I_1(t, x) - I_2(t, x))}, \\
J_4(t, x, I_1(t, x), I_2(t, x)) &= \frac{\alpha_2 \beta(t, x) p I_2(t, x)}{p(I_1(t, x) + I_2(t, x)) + l(N^*(x) - I_1(t, x) - I_2(t, x))},
\end{align*}
\]

where \(J_1(J_3)\) represents the density of newly infectious humans with sensitive (resistant) strain caused by an infected mosquito with sensitive (resistant) strain; and \(J_2(J_4)\) means the force of infection on mosquitoes due to the contact with infectious humans with sensitive (resistant) strain.
Taking into account all of these assumptions, we obtain the following periodic reaction–diffusion model:

\[
\begin{align*}
\frac{\partial I_1(t,x)}{\partial t} &= D_h \Delta I_1(t,x) - (d + \gamma_1) I_1(t,x) + J_1(t,x, I_1(t,x), I_2(t,x)) I_{v1}(t,x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{v1}(t,x)}{\partial t} &= D_v \Delta I_{v1}(t,x) - \eta(t,x) I_{v1}(t,x) + J_2(t,x, I_1(t,x), I_2(t,x))(M^*(t,x) - I_{v1}(t,x) - I_{v2}(t,x)), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_2(t,x)}{\partial t} &= D_h \Delta I_2(t,x) - (d + \gamma_2) I_2(t,x) + J_3(t,x, I_1(t,x), I_2(t,x)) I_{v2}(t,x), \quad t > 0, \ x \in \Omega,
\end{align*}
\]

(2.3)

Here, the positive constants $\gamma_1$ and $\gamma_2$ denote the recovery rates of the sensitive and resistant strains for humans, respectively. The function $\beta(t,x)$ is Hölder continuous and nonnegative but not zero identically on $\mathbb{R} \times \Omega$, and $\omega$-periodic in $t$. Other parameters are the same as above.

Let $X := C(\bar{\Omega}, \mathbb{R}^4)$ be the Banach space with the maximum norm $\| \cdot \|$ and $X^+ := C(\bar{\Omega}, \mathbb{R}^4_+)$. For each $t \geq 0$, we define

\[X(t) := \{ \varphi = (\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in X^+ : 0 \leq \varphi_1(x) + \varphi_3(x) \leq N^*(x), \]

\[0 \leq \varphi_2(x) + \varphi_4(x) \leq M^*(t,x), \ \forall x \in \bar{\Omega} \}.
\]

Let $Y := C(\bar{\Omega}, \mathbb{R})$ and $Y^+ := C(\bar{\Omega}, \mathbb{R}^+).$ Let $T_1(t,s), T_2(t,s), T_v(t,s) : Y \to Y$, $t \geq s$, be the linear evolution operators associated with

\[
\begin{align*}
\frac{\partial v_1(t,x)}{\partial t} &= D_h \Delta v_1(t,x) - (d + \gamma_1) v_1(t,x) := A_1 v_1(t,x), \\
\frac{\partial v_2(t,x)}{\partial t} &= D_h \Delta v_2(t,x) - (d + \gamma_2) v_2(t,x) := A_2 v_2(t,x), \\
\frac{\partial v(t,x)}{\partial t} &= D_v \Delta v(t,x) - \eta(t,x) v(t,x) := A(t) v(t,x),
\end{align*}
\]

subject to the Neumann boundary condition, respectively. Clearly, $T_j(t + \omega, s + \omega) = T_j(t, s)$ for $(t, s) \in \mathbb{R}^2$ with $t \geq s, j = 1, 2$. Since $\eta(t,x)$ is $\omega$-periodic in $t$, \[30, \text{ Lemma 6.1} \] implies that $T_v(t + \omega, s + \omega) = T_v(t, s)$ for $(t, s) \in \mathbb{R}^2$ with $t \geq s$. Moreover, for $(t, s) \in \mathbb{R}^2$ with $t > s$, $T_1(t, s), T_2(t, s)$ and $T_v(t, s)$ are compact and strongly positive. Set $T(t,s) = \text{diag}(T_1(t,s), T_2(t,s), T_v(t,s))$ and $A(t) = \text{diag}(A_1, A(t), A_2, A(t))$. Define $F = (F_1, F_2, F_3, F_4) : [0, \infty) \times X^+ \to X$ by

\[
\begin{align*}
F_1(t, \varphi) &= \frac{c_{1\beta}(t, \cdot) l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot))}{p(\varphi_1(\cdot) + \varphi_3(\cdot)) + l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot)) \varphi_2(\cdot)}, \\
F_2(t, \varphi) &= \frac{a_{1\beta}(t, \cdot) p \varphi_1(\cdot)}{p(\varphi_1(\cdot) + \varphi_3(\cdot)) + l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot)) (M^*(t, \cdot) - \varphi_2(\cdot) - \varphi_4(\cdot)),} \\
F_3(t, \varphi) &= \frac{c_2 \beta(t, \cdot) l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot))}{p(\varphi_1(\cdot) + \varphi_3(\cdot)) + l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot)) \varphi_4(\cdot)}, \\
F_4(t, \varphi) &= \frac{a_2 \beta(t, \cdot) p \varphi_3(\cdot)}{p(\varphi_1(\cdot) + \varphi_3(\cdot)) + l(N^*(\cdot) - \varphi_1(\cdot) - \varphi_3(\cdot)) (M^*(t, \cdot) - \varphi_2(\cdot) - \varphi_4(\cdot)).}
\end{align*}
\]
Then, system (2.3) becomes
\[
\begin{align*}
\frac{du}{dt} &= A(t)u + F(t,u), & t > 0, \\
u(0) &= \varphi \in X^+,
\end{align*}
\]
which can be written as an integral equation
\[
u(t, \varphi) = T(t, 0)\varphi + \int_0^t T(t, s)F(s, u)\,ds, \quad \forall t \geq 0, \quad \varphi \in X^+,
\]
where
\[
u(t, x) = (u_1(t, x), u_2(t, x), u_3(t, x), u_4(t, x)) = (I_1(t, x), I_{c1}(t, x), I_2(t, x), I_{c2}(t, x)).
\]
As usual, solutions of (2.4) are called mild solutions to system (2.3).

**Lemma 2.1.** For any \( \varphi \in X(0) \), system (2.3) has a unique solution \( \nu(t, \cdot, \varphi) \) with \( \nu(0, \cdot, \varphi) = \varphi \) such that \( \nu(t, \cdot, \varphi) \in X(t) \) for all \( t \in [0, \infty) \). Moreover, system (2.3) generates an \( \omega \)-periodic semiflow \( Q(t) : X(0) \to X(t) \) defined by \( Q(t)\varphi = \nu(t, \cdot, \varphi), \forall t \geq 0 \). In addition, \( Q := Q(\omega) \) admits a strong global attractor in \( X(0) \).

**Proof.** From the expression of \( F \), we see that \( F \) is locally Lipschitz continuous. For any \( (t, \psi) \in \mathbb{R}_+ \times X^+ \) and \( h > 0 \), in view of \( p \geq l > 0 \), we have
\[
\psi(x) + hF(t, \psi)(x) = \begin{pmatrix}
\psi_1(x) + h \frac{c_1\beta(t, x)(N^*(x) - \psi_1(x) - \psi_3(x))}{p(\psi_1(x) + \psi_3(x)) + l(N^*(x) - \psi_1(x) - \psi_3(x))} \psi_2(x) \\
\psi_2(x) + h \frac{\alpha_1\beta(t, x)p\psi_1(x)(M^*(t, x) - \psi_2(x) - \psi_4(x))}{p(\psi_1(x) + \psi_3(x)) + l(N^*(x) - \psi_1(x) - \psi_3(x))} \\
\psi_3(x) + h \frac{c_2\beta(t, x)(N^*(x) - \psi_1(x) - \psi_3(x))}{p(\psi_1(x) + \psi_3(x)) + l(N^*(x) - \psi_1(x) - \psi_3(x))} \psi_4(x) \\
\psi_4(x) + h \frac{\alpha_2\beta(t, x)p\psi_3(x)(M^*(t, x) - \psi_2(x) - \psi_4(x))}{p(\psi_1(x) + \psi_3(x)) + l(N^*(x) - \psi_1(x) - \psi_3(x))}
\end{pmatrix}
\]
This implies that
\[
\lim_{h \to 0^+} \frac{1}{h} \text{dist}(\psi + hF(t, \psi), X^+) = 0, \quad \forall (t, \psi) \in \mathbb{R}_+ \times X^+.
\]
In addition, \( T(t, s)X^+ \subseteq X^+, \forall t \geq s \geq 0 \). Therefore, by [31, Corollary 4] with \( K = X^+ \) and \( S(t, s) = T(t, s) \), system (2.3) admits a unique non-continuable mild solution \( \nu(t, \cdot, \psi) \) on its maximal existence interval \( [0, t_\psi) \) with \( \nu(0, \cdot, \psi) = \psi \), and \( \nu(t, \cdot, \psi) \geq 0 \) for all \( t \in [0, t_\psi) \), where \( t_\psi \leq \infty \).
Based on the above analysis, we obtain that for any \( \varphi \in X(0) \subset \mathbb{X}^+ \), system (2.3) has a unique solution \( u(t, \cdot, \varphi) \in \mathbb{X}^+ \) on \([0, t_\varphi)\) with \( u(0, \cdot, \varphi) = \varphi \), where \( t_\varphi \leq \infty \). Next we want to show that \( u(t, x, \varphi) \) is bounded for all \( t \in [0, t_\varphi) \), which then implies \( t_\varphi = \infty \). To this end, we set

\[
I_h(t, x) = I_1(t, x) + I_2(t, x), \quad I_v(t, x) = I_v1(t, x) + I_v2(t, x).
\]

It turns out that \( N^*(x) \) and \( M^*(t, x) \) are, respectively, the upper solutions of the following two equations:

\[
\begin{align*}
\frac{\partial I_h(t, x)}{\partial t} &= D_h \Delta I_h(t, x) - dI_h(t, x) - \gamma_1 I_1(t, x) - \gamma_2 I_2(t, x) \\
&\quad + J_1(t, x, I_1(t, x), I_2(t, x)) I_v1(t, x) + J_3(t, x, I_1(t, x), I_2(t, x)) I_v2(t, x), \quad t \in (0, t_\varphi), \ x \in \Omega, \\
\frac{\partial I_h(t, x)}{\partial t} &= 0, \quad t \in (0, t_\varphi), \ x \in \partial \Omega,
\end{align*}
\]

and

\[
\begin{align*}
\frac{\partial I_v(t, x)}{\partial t} &= D_v \Delta I_v(t, x) - \eta(t, x) I_v(t, x) + J_2(t, x, I_1(t, x), I_2(t, x))(M^*(t, x) - I_v(t, x)) \\
&\quad + J_4(t, x, I_1(t, x), I_2(t, x))(M^*(t, x) - I_v(t, x)), \quad t \in (0, t_\varphi), \ x \in \Omega, \\
\frac{\partial I_v(t, x)}{\partial t} &= 0, \quad t \in (0, t_\varphi), \ x \in \partial \Omega.
\end{align*}
\]

Thus, the comparison principle implies that solutions of (2.3) are bounded on \([0, t_\varphi)\), and thus, \( t_\varphi = \infty \). In addition, we also have that \( u(t, \cdot, \varphi) \in X(t) \) for all \( t \geq 0 \), and it is a classical solution for \( t > 0 \).

Define a family of operators \( \{Q(t)\}_{t \geq 0} \) from \( X(0) \) to \( X(t) \) by

\[
Q(t) \varphi = u(t, \cdot, \varphi), \quad \forall \varphi \in X(0).
\]

By the proof of [29, Lemma 2.1], we can show that \( \{Q(t)\}_{t \geq 0} \) is an \( \omega \)-periodic semiflow, and thus \( Q := Q(\omega) : X(0) \to X(\omega) = X(0) \) is the Poincaré map associated with system (2.3). The fact that \( u(t, \cdot, \varphi) \in X(t) \) for all \( t \geq 0 \) also indicates that solutions of (2.3) are ultimately bounded. Hence, by [32, Theorem 2.9], \( Q \) has a strong global attractor in \( X(0) \).

**Lemma 2.2.** For any \( \varphi \in X(0) \), let \( u(t, x, \varphi) \) be the solution of system (2.3). If there exists some \( t_0 \geq 0 \) such that \( u_i(t_0, \cdot, \varphi) \neq 0 \) for some \( i \in \{1, 2, 3, 4\} \), then

\[
u_i(t, x, \varphi) > 0, \quad \forall t > t_0, \ x \in \bar{\Omega}.
\]

**Proof.** For any given \( \varphi \in X(0) \), one easily sees

\[
\begin{align*}
\frac{\partial u_1(t, x)}{\partial t} &\geq D_h \Delta u_1(t, x) - (d + \gamma_1)u_1(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial u_2(t, x)}{\partial t} &\geq D_v \Delta u_2(t, x) - \bar{\eta} u_2(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial u_3(t, x)}{\partial t} &\geq D_h \Delta u_3(t, x) - (d + \gamma_2)u_3(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial u_4(t, x)}{\partial t} &\geq D_v \Delta u_4(t, x) - \bar{\eta} u_4(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial u_1(t, x)}{\partial \nu} = \frac{\partial u_2(t, x)}{\partial \nu} = \frac{\partial u_3(t, x)}{\partial \nu} = \frac{\partial u_4(t, x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega,
\end{align*}
\]

where \( \bar{\eta} = \max_{(t, x) \in [0, \omega] \times \Omega} \eta(t, x) \). If there exists \( t_0 \geq 0 \) such that \( u_i(t_0, \cdot, \varphi) \neq 0 \) for some \( i \in \{1, 2, 3, 4\} \), it then follows from the maximum principle [33, Proposition 13.1] that \( u_i(t, x, \varphi) > 0 \) for all \( t > t_0 \) and \( x \in \bar{\Omega} \).

\( \square \)
3. Reproduction numbers

In this section, we first define the basic reproduction number \( R_0 \) of (2.3), and then introduce the invasion reproduction number \( \bar{R}_i \) for strain \( i \) (\( i = 1, 2 \)).

3.1. Basic reproduction number

In order to derive the basic reproduction number of (2.3), we consider two subsystems: one involves sensitive strains alone and the other involves resistant strains alone. Fix \( i \in \{1, 2\} \) and let \( I_j(t, x) \equiv 0 \), \( I_{vj}(t, x) \equiv 0 \), \( \forall t \geq 0 \), \( x \in \Omega \), \( j \in \{1, 2\} \) and \( j \neq i \). Then, system (2.3) reduces to the following single-strain model:

\[
\begin{align*}
\frac{\partial I_i(t, x)}{\partial t} &= D_h \Delta I_i(t, x) - (d + \gamma_i)I_i(t, x) \\
&\quad + \frac{c_i \beta(t, x)l(N^*(x) - I_i(t, x))}{pI_i(t, x) + l(N^*(x) - I_i(t, x))} I_{vi}(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{vi}(t, x)}{\partial t} &= D_v \Delta I_{vi}(t, x) - \eta(t, x)I_{vi}(t, x) \\
&\quad + \frac{\alpha_i \beta(t, x)pI_i(t, x)}{pI_i(t, x) + l(N^*(x) - I_i(t, x))} (M^*(t, x) - I_{vi}(t, x)), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_i(t, x)}{\partial \nu} &= 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]  

(3.1)

Let \( E := C(\Omega, \mathbb{R}^2) \) and \( E^+ := C(\bar{\Omega}, \mathbb{R}^2_+) \). Linearizing system (3.1) at \((0,0)\) yields

\[
\begin{align*}
\frac{\partial I_i(t, x)}{\partial t} &= D_h \Delta I_i(t, x) - (d + \gamma_i)I_i(t, x) + c_i \beta(t, x)I_{vi}(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{vi}(t, x)}{\partial t} &= D_v \Delta I_{vi}(t, x) - \eta(t, x)I_{vi}(t, x) + \frac{\alpha_i \beta(t, x)pI_i(t, x)}{lN^*(x)} I_i(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_i(t, x)}{\partial \nu} &= \frac{\partial I_{vi}(t, x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]  

(3.2)

Define the operator \( F_i(t) : E \rightarrow E \) by

\[
F_i(t) \left( \begin{array}{c} \psi_1 \\ \psi_2 \end{array} \right) = \left( \begin{array}{c} c_i \beta(t, \cdot)\psi_2(\cdot) \\ \alpha_i \beta(t, \cdot)pM^*(\cdot)lN^*(\cdot) \psi_1(\cdot) \end{array} \right), \quad \forall t \in \mathbb{R}, \ \psi = (\psi_1, \psi_2) \in E.
\]

Let \( \Psi_i(t, s) = \text{diag}(T_i(t, s), T_v(t, s)) \), \( t \geq s \), be the evolution operator associated with the following system:

\[
\begin{align*}
\frac{\partial v_1}{\partial t} &= D_h \Delta v_1 - (d + \gamma_i)v_1, \quad t > 0, \ x \in \Omega, \\
\frac{\partial v_2}{\partial t} &= D_v \Delta v_2 - \eta(t, x)v_2, \quad t > 0, \ x \in \Omega, \\
\frac{\partial v_1}{\partial \nu} &= \frac{\partial v_2}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]

The exponential growth bound of \( \Psi_i(t, s) \) is defined as

\[
\hat{\omega}(\Psi_i) = \inf \{ \tilde{\omega}_i : \exists M \geq 1 \text{ such that } \| \Psi_i(t + s, s) \|_E \leq Me^{\tilde{\omega}_i t}, \ \forall s \in \mathbb{R}, \ t \geq 0 \}.
\]

By the Krein–Rutman theorem and [33, Lemma 14.2], we have

\[
0 < r(\Psi_i(\omega, 0)) = \max \{ r(T_i(\omega, 0)), r(T_v(\omega, 0)) \} < 1,
\]

where \( \omega = 0 \).
where \( r(\Psi_1(\omega,0)) \) is the spectral radius of \( \Psi_1(\omega,0) \). It then follows from [34, Proposition 5.5] with \( s = 0 \) that \( \omega(\Psi_i) < 0 \). Moreover, it is easy to see that \( \mathcal{F}_i(t) \) and \( \Psi_i(t,s) \) satisfy

**H1** For each \( t \geq 0 \), \( \mathcal{F}_i(t) \) is a positive operator on \( E \);

**H2** For any \( t \geq s \), \( \Psi_i(t,s) \) is a positive operator on \( E \), and \( \omega(\Psi_i) < 0 \).

Let \( C_\omega(\mathbb{R},E) \) (or \( C_\omega(\mathbb{R},X) \)) be the Banach space of all \( \omega \)-periodic and continuous functions from \( \mathbb{R} \) to \( E \) (or \( X \)) equipped with the maximum norm. Following the theory developed in [35,36], we define two linear operators on \( C_\omega(\mathbb{R},E) \) by

\[
[L_i v](t) := \int_0^\infty \Psi_i(t,t-s)\mathcal{F}_i(t-s)v(t-s)ds, \quad \forall t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R},E), \ i = 1, 2.
\]

Motivated by the concept of next-generation operators [34–37], we define the basic reproduction number as \( \mathcal{R}_i := r(L_i) \) for system (3.1), where \( r(L_i) \) is the spectral radius of \( L_i \).

The disease-free state of (2.3) is \((0,0,0,0)\) and the corresponding linearized system is

\[
\begin{aligned}
\frac{\partial I_1(t,x)}{\partial t} &= D_h \Delta I_1(t,x) - (d + \gamma_1)I_1(t,x) + c_1\beta(t,x)I_1(t,x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{v1}(t,x)}{\partial t} &= D_v \Delta I_{v1}(t,x) - \eta(t,x)I_{v1}(t,x) + \frac{c_1\beta(t,x)pM^*(t,x)}{lN^*(x)}I_1(t,x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_2(t,x)}{\partial t} &= D_h \Delta I_2(t,x) - (d + \gamma_2)I_2(t,x) + c_2\beta(t,x)I_{v2}(t,x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{v2}(t,x)}{\partial t} &= D_v \Delta I_{v2}(t,x) - \eta(t,x)I_{v2}(t,x) + \frac{c_2\beta(t,x)pM^*(t,x)}{lN^*(x)}I_2(t,x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_1(t,x)}{\partial \nu} &= \frac{\partial I_{v1}(t,x)}{\partial \nu} = \frac{\partial I_2(t,x)}{\partial \nu} = \frac{\partial I_{v2}(t,x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\end{aligned}
\]  

Define the operator \( \mathcal{F}(t) : X \rightarrow X \) by

\[
\mathcal{F}(t) \begin{pmatrix} \psi_1 \\ \psi_2 \\ \psi_3 \\ \psi_4 \end{pmatrix} = \begin{pmatrix} c_1\beta(t,\cdot)\psi_2(\cdot) \\ \frac{c_1\beta(t,\cdot)pM^*(t,\cdot)}{lN^*(\cdot)}\psi_1(\cdot) \\ c_2\beta(t,\cdot)\psi_4(\cdot) \\ \frac{c_2\beta(t,\cdot)pM^*(t,\cdot)}{lN^*(\cdot)}\psi_3(\cdot) \end{pmatrix}, \quad \forall t \in \mathbb{R}, \ \psi = (\psi_1, \psi_2, \psi_3, \psi_4) \in X,
\]

and \( \Psi(t,s) = T(t,s), \ \forall t \geq s \). Denote a linear operator \( \mathcal{L} : C_\omega(\mathbb{R},X) \rightarrow C_\omega(\mathbb{R},X) \) by

\[
[L v](t) := \int_0^\infty \Psi(t,t-s)\mathcal{F}(t-s)v(t-s)ds, \quad \forall t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R},X).
\]

Then, the basic reproduction number of system (2.3) is \( \mathcal{R}_0 = r(\mathcal{L}) \). Moreover, we have the following nice characterization.

**Lemma 3.1.** \( \mathcal{R}_0 = \max\{\mathcal{R}_1, \mathcal{R}_2\} \).

**Proof.** Let \( v = (v_1, v_2, v_3, v_4) \in C_\omega(\mathbb{R},X) \). From the definition of \( \mathcal{L} \) and \( \mathcal{L}_i, i = 1, 2 \), we find

\[
[L v](t) = ([L_1 \bar{v}](t), [L_2 \bar{v}](t)), \quad \bar{v} = (v_1, v_2), \quad \bar{v} = (v_3, v_4).
\]

Since \( \mathcal{L} \) is a compact operator, the spectrum \( \sigma(\mathcal{L}) \setminus \{0\} \) consists of eigenvalues only. Compact operators \( \mathcal{L}_1 \) and \( \mathcal{L}_2 \) also have the same property. Moreover, it is easy to prove that \( \sigma(\mathcal{L}) = \sigma(\mathcal{L}_1) \cup \sigma(\mathcal{L}_2) \), and hence, \( r(\mathcal{L}) = \max\{r(\mathcal{L}_1), r(\mathcal{L}_2)\} \). This establishes the desired assertion. \( \square \)
For any given \( t \geq 0 \), let \( P_i(t) \) be the solution map of (3.2) on \( \mathbb{E} \). Then, \( P_i := P_i(\omega) \) is the corresponding Poincaré map. Let \( r(P_i) \) be the spectral radius of \( P_i \). Similarly as in Lemma 3.1, we can show that \( r(P) = \max\{r(P_1), r(P_2)\} \), where \( r(P) \) is the spectral radius of the Poincaré map \( P \) associated with (3.3). By [36, Theorem 3.7] with \( \tau = 0 \), we have the following observation.

**Lemma 3.2.** \( R_i - 1 \) has the same sign as \( r(P_i) - 1 \), \( i = 1, 2 \), and thus \( R_0 - 1 \) has the same sign as \( r(P) - 1 \).

### 3.2. Invasion reproduction number

In this subsection, we define the invasion reproduction number for each strain. The invasion reproduction number of strain \( i \), denoted \( R_i \), measures the ability of strain \( i \) to invade, while strain \( j \) (\( j \neq i \)) is already at an endemic state [38].

For each \( t \geq 0 \), let \( E(t) \) be subset in \( \mathbb{E} \) defined by

\[
E(t) := \{ \psi = (\psi_1, \psi_2) \in \mathbb{E}^+ : 0 \leq \psi_1(x) \leq N^*(x), \ 0 \leq \psi_2(x) \leq M^*(t, x), \ \forall x \in \Omega \}.
\]

After a similar process in [27, Lemma 3], we obtain that for any \( \psi \in E(0) \), system (3.1) has a unique solution \( v_i(t, \cdot, \psi) = (I_i(t, x), I_{vi}(t, x)) \) with \( v_i(0, \cdot, \psi) = \psi \) such that \( v_i(t, \cdot, \psi) \in E(t) \) for all \( t \geq 0 \). The following result is concerned with the global dynamics of (3.1).

**Theorem 3.1.** The following statements are valid:

(i) If \( R_i \leq 1 \), then \((0, 0) \) is globally asymptotically stable for (3.1) in \( E(0) \).

(ii) If \( R_i > 1 \), then system (3.1) admits a unique positive \( \omega \)-periodic solution \((I_i^*(t, x), I_{vi}^*(t, x)) \), and it is globally asymptotically stable for (3.1) in \( E(0) \setminus \{(0, 0)\} \). Moreover, \( I_i^*(t, x) < N^*(x) \) and \( I_{vi}^*(t, x) < M^+(t, x) \) for all \( t \in [0, \infty) \), \( x \in \Omega \) and \( i = 1, 2 \).

**Proof.** The statement (i) and the former part of (ii) are directly from [27, Theorem 1]. We now prove the latter part. Let \( U_i(t, x) = N^*(x) - I_i^*(t, x) \) and \( V_i(t, x) = M^+(t, x) - I_{vi}^*(t, x) \) for \( i = 1, 2 \). Then, \( U_i(t, x) \) and \( V_i(t, x) \) satisfy

\[
\begin{align*}
\frac{\partial U_i(t, x)}{\partial t} &= D_u \Delta U_i(t, x) - d U_i(t, x) + B(x, N^*(x)) N^*(x) + \gamma_i I_i^*(t, x) - c_i(\beta(t, x) I_i(t, x) + \eta(t, x) V_i(t, x)), \\
\frac{\partial U_i(t, x)}{\partial v} &= 0, \quad t > 0, \ x \in \partial \Omega,
\end{align*}
\]

and

\[
\begin{align*}
\frac{\partial V_i(t, x)}{\partial t} &= D_v \Delta V_i(t, x) + \Lambda(t, x) - \eta(t, x) V_i(t, x) - \frac{c_i(\beta(t, x) I_i(t, x) + \eta(t, x) V_i(t, x))}{p I_i(t, x) + l(N^*(x) - I_i^*(t, x))} V_i(t, x), \\
\frac{\partial V_i(t, x)}{\partial v} &= 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]

We claim that there is a \( \bar{t} \in [0, \infty) \) such that \( U_i(\bar{t}, \cdot) > 0 \). Otherwise, we have \( U_i(\cdot, \cdot) \equiv 0 \) for any \( t \geq 0 \), and thus

\[
B(x, N^*(x)) N^*(x) + \gamma_i I_i^*(t, x) = 0, \ \forall t \in [0, \infty), \ x \in \Omega,
\]

which is a contradiction. By the maximum principle and the periodicity of \( U_i(t, x) \) in \( t \), we obtain \( U_i(t, x) > 0 \) for all \( t \geq 0 \) and \( x \in \Omega \). The positivity of \( V_i(t, x) \) can be proved similarly.

For ease of presentation, we introduce the following notations:

- \( E_0 = (0, 0, 0, 0) \): the disease-free state of (2.3).
• $E_1(t, x) = (I_1^*(t, x), I_{v1}^*(t, x), 0, 0)$: the sensitive strain $\omega$-periodic solution of (2.3).
• $E_2(t, x) = (0, 0, I_2^*(t, x), I_{v2}^*(t, x))$: the resistant strain $\omega$-periodic solution of (2.3).

According to Theorem 3.1, we see that when $\mathcal{R}_i > 1$ ($i = 1, 2$), system (2.3) admits a unique semitrivial boundary $\omega$-periodic solution $E_i(t, x)$. Linearizing (2.3) at the $E_j(t, x)$, $j \neq i$, $i, j = 1, 2$, and considering only the equations for $I_i(t, x)$ and $I_{vi}(t, x)$, we get

$$
\begin{aligned}
\frac{\partial I_i(t, x)}{\partial t} &= D_h \Delta I_i(t, x) - (d + \gamma_i) I_i(t, x) \\
&\quad + \frac{c_i \beta(t, x) l(N^*(x) - I_j^*(t, x))}{p I_j^*(t, x) + l(N^*(x) - I_j^*(t, x))} I_{vi}(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{vi}(t, x)}{\partial t} &= D_v \Delta I_{vi}(t, x) - \eta(t, x) I_{vi}(t, x) \\
&\quad + \frac{\alpha_i \beta(t, x) p(M^*(t, x) - I_{v1}^*(t, x))}{p I_j^*(t, x) + l(N^*(x) - I_j^*(t, x))} I_i(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_i(t, x)}{\partial \nu} &= \frac{\partial I_{vi}(t, x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\end{aligned}
$$

(3.4)

Analogously, we define two linear operators on $C_\omega(\mathbb{R}, \mathbb{E})$ by

$$
[\hat{L}_i v](t) := \int_0^\infty \Psi_i(t, t - s) \hat{F}_i(t - s) v(t - s) ds, \ \forall t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{E}), \ i = 1, 2,
$$

where $\hat{F}_i(t): \mathbb{E} \to \mathbb{E}$ is given by

$$
\hat{F}_i(t) \begin{pmatrix}
\psi_1 \\
\psi_2
\end{pmatrix} = \begin{pmatrix}
\frac{c_i \beta(t, \cdot) l(N^*(\cdot) - I_j^*(t, \cdot))}{p I_j^*(t, \cdot) + l(N^*(\cdot) - I_j^*(t, \cdot))} \psi_2(\cdot) \\
\frac{\alpha_i \beta(t, \cdot) p(M^*(t, \cdot) - I_{v1}^*(t, \cdot))}{p I_j^*(t, \cdot) + l(N^*(\cdot) - I_j^*(t, \cdot))} \psi_1(\cdot)
\end{pmatrix}, \ \forall t \in \mathbb{R}, \ \psi = (\psi_1, \psi_2) \in \mathbb{E}.
$$

Hence, we define $\hat{\mathcal{R}}_i := r(\hat{L}_i)$. Let $\hat{P}_i$ be the Poincaré map associated with (3.4). Again using [36, Theorem 3.7] with $\tau = 0$, we see that $\hat{\mathcal{R}}_i - 1$ has the same sign as $r(\hat{P}_i) - 1$. Note that for each $t \in \mathbb{R}$, $\hat{F}_i(t) \leq F_i(t)$.

By [39, Theorem 1.1], we obtain the following relation between $\hat{\mathcal{R}}_i$ and $\mathcal{R}_i$.

**Lemma 3.3.** If $\hat{\mathcal{R}}_i > 1$, then $\mathcal{R}_i > 1$ for $i = 1, 2$.

4. Disease extinction and uniform persistence

In this section, we establish the dynamics of (2.3) in terms of $\mathcal{R}_i$ and $\hat{\mathcal{R}}_i$, $i = 1, 2$.

4.1. Global extinction

**Theorem 4.1.** If $\mathcal{R}_1 \leq 1$ and $\mathcal{R}_2 \leq 1$, then $E_0$ is globally attractive for (2.3) in $X(0)$. 
Proof. Let \((I_1(t,x), I_{v1}(t,x), I_2(t,x), I_{v2}(t,x))\) be the solution of (2.3) with initial data \(\varphi \in X(0)\). It is easily seen that

\[
\frac{\partial I_1(t,x)}{\partial t} \leq D_h \Delta I_1(t,x) - (d + \gamma_1)I_1(t,x) + \frac{c_1 \beta(t,x) l(N^*(x) - I_1(t,x))}{p I_1(t,x) + l(N^*(x) - I_1(t,x))} I_{v1}(t,x), \quad t > 0, \ x \in \Omega,
\]

\[
\frac{\partial I_{v1}(t,x)}{\partial t} \leq D_v \Delta I_{v1}(t,x) - \eta(t,x) I_{v1}(t,x) + \frac{\alpha_1 \beta(t,x) p I_1(t,x)}{p I_1(t,x) + l(N^*(x) - I_1(t,x))} (M^*(t,x) - I_{v1}(t,x)), \quad t > 0, \ x \in \Omega,
\]

\[
\frac{\partial I_2(t,x)}{\partial t} \leq D_h \Delta I_2(t,x) - (d + \gamma_2)I_2(t,x) + \frac{c_2 \beta(t,x) l(N^*(x) - I_2(t,x))}{p I_2(t,x) + l(N^*(x) - I_2(t,x))} I_{v2}(t,x), \quad t > 0, \ x \in \Omega,
\]

\[
\frac{\partial I_{v2}(t,x)}{\partial t} \leq D_v \Delta I_{v2}(t,x) - \eta(t,x) I_{v2}(t,x) + \frac{\alpha_2 \beta(t,x) p I_2(t,x)}{p I_2(t,x) + l(N^*(x) - I_2(t,x))} (M^*(t,x) - I_{v2}(t,x)), \quad t > 0, \ x \in \Omega,
\]

\[
\frac{\partial I_1(t,x)}{\partial \nu} = \frac{\partial I_{v1}(t,x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega,
\]

and

\[
\frac{\partial I_2(t,x)}{\partial \nu} = \frac{\partial I_{v2}(t,x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\]

When \(\mathcal{R}_1 \leq 1\), Theorem 3.1(i) implies that \((0,0)\) is globally stable for (3.1). Hence, the comparison principle applies to (4.1) and ensures that

\[
\lim_{t \to \infty} (I_1(t,x), I_{v1}(t,x)) = (0,0) \text{ uniformly for } x \in \bar{\Omega}.
\]

In the case where \(\mathcal{R}_2 \leq 1\), by using the similar procedure as above to (4.2), one has

\[
\lim_{t \to \infty} (I_2(t,x), I_{v2}(t,x)) = (0,0) \text{ uniformly for } x \in \bar{\Omega}.
\]

Therefore, the desired result is established. \(\square\)

4.2. Competitive exclusion and coexistence

**Theorem 4.2.** Let \((I_1(t,\cdot,\varphi), I_{v1}(t,\cdot,\varphi), I_2(t,\cdot,\varphi), I_{v2}(t,\cdot,\varphi))\) be the solution of (2.3) through \(\varphi \in X(0)\). Then, the following assertions hold true:

1. If \(\mathcal{R}_1 > 1 \geq \mathcal{R}_2\) and \(\varphi_1, \varphi_2 \neq 0\), then

\[
\lim_{t \to \infty} ((I_1(t,x,\varphi), I_{v1}(t,x,\varphi), I_2(t,x,\varphi), I_{v2}(t,x,\varphi)) - E_1(t,x)) = (0,0,0,0)
\]

uniformly for \(x \in \bar{\Omega}\).

2. If \(\mathcal{R}_2 > 1 \geq \mathcal{R}_1\) and \(\varphi_3, \varphi_4 \neq 0\), then

\[
\lim_{t \to \infty} ((I_1(t,x,\varphi), I_{v1}(t,x,\varphi), I_2(t,x,\varphi), I_{v2}(t,x,\varphi)) - E_2(t,x)) = (0,0,0,0)
\]

uniformly for \(x \in \bar{\Omega}\).
Proof. We only prove statement (1), since statement (2) can be treated similarly. In the case where \( R_2 \leq 1 \), one immediately has that \( \lim_{t \to -\infty} (I_2(t, \cdot, \varphi), I_{v2}(t, \cdot, \varphi)) = (0, 0) \). Then, the limiting system of (2.3) is the system (3.1) with \( i = 1 \). Moreover, by appealing to the theory of internally chain transitive sets (see, e.g., [28]), we conclude that

\[
\lim_{t \to -\infty} \left( (I_1(t, x, \varphi), I_{v1}(t, x, \varphi)) - (I_0^1(t, x), I_{v0}^1(t, x)) \right) = (0, 0)
\]

uniformly for \( x \in \Omega \). \qed

Let \( C = X(0), C_0 := \{ \varphi = (\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in C : \varphi_i(\cdot) \neq 0, \forall i = 1, 2, 3, 4 \} \), and

\[
\partial C_0 := C \setminus C_0 = \{ \varphi = (\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in C : \varphi_i(\cdot) \equiv 0 \text{ at least for one } i \}.
\]

In order to study the coexistence of two strains, we first give the following lemma.

**Lemma 4.1.** Let \((I_1(t, \cdot, \varphi), I_{v1}(t, \cdot, \varphi), I_2(t, \cdot, \varphi), I_{v2}(t, \cdot, \varphi))\) be the solution of (2.3) with the initial value \( \varphi \in C_0 \). If \( R_1 > 1 \) and \( R_2 > 1 \), then there exists \( \delta > 0 \) such that

\[
\limsup_{t \to -\infty} \|(I_1(t, \cdot, \varphi), I_{v1}(t, \cdot, \varphi), I_2(t, \cdot, \varphi), I_{v2}(t, \cdot, \varphi)) - E_0\| \geq \delta.
\]

**Proof.** Suppose, by contradiction, that there exists some \( \psi \in C_0 \) such that

\[
\limsup_{t \to -\infty} \|(I_1(t, \cdot, \psi), I_{v1}(t, \cdot, \psi), I_2(t, \cdot, \psi), I_{v2}(t, \cdot, \psi)) - E_0\| < \delta.
\]

Then, there exists \( t_1 > 0 \) such that

\[
0 < I_i(t, x, \psi) < \delta, \quad 0 < I_{v1}(t, x, \psi) < \delta, \quad i = 1, 2
\]

for all \( t \geq t_1 \) and \( x \in \Omega \). Accordingly, \( I_1(t, x, \psi) \) and \( I_{v1}(t, x, \psi) \) satisfy

\[
\begin{align*}
\frac{\partial I_1(t, x)}{\partial t} & \geq D_h \Delta I_1(t, x) - (d + \gamma_1)I_1(t, x) \\
& \quad + \frac{c_1 \beta(t, x) l(N^*(x) - 2\delta)}{2p\delta + lN^*(x)} I_{v1}(t, x), \quad t \geq t_1, \ x \in \Omega, \\
\frac{\partial I_{v1}(t, x)}{\partial t} & \geq D_v \Delta I_{v1}(t, x) - \eta(t, x)I_{v1}(t, x) \\
& \quad + \frac{\alpha_1 \beta(t, x)p(M^*(x) - 2\delta)}{2p\delta + lN^*(x)} I_1(t, x), \quad t \geq t_1, \ x \in \Omega, \\
\frac{\partial I_1(t, x)}{\partial \nu} & = \frac{\partial I_{v1}(t, x)}{\partial \nu} = 0, \quad t \geq t_1, \ x \in \partial \Omega.
\end{align*}
\]

Let \( P^\delta_1 : E \to \mathbb{E} \) be the Poincaré map associated with the following system:

\[
\begin{align*}
\frac{\partial I_1(t, x)}{\partial t} &= D_h \Delta I_1(t, x) - (d + \gamma_1)I_1(t, x) \\
& \quad + \frac{c_1 \beta(t, x) l(N^*(x) - 2\delta)}{2p\delta + lN^*(x)} I_{v1}(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{v1}(t, x)}{\partial t} &= D_v \Delta I_{v1}(t, x) - \eta(t, x)I_{v1}(t, x) \\
& \quad + \frac{\alpha_1 \beta(t, x)p(M^*(x) - 2\delta)}{2p\delta + lN^*(x)} I_1(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_1(t, x)}{\partial \nu} &= \frac{\partial I_{v1}(t, x)}{\partial \nu} = 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]
In view of Lemma 3.2, we have that \( R_1 > 1 \) is equivalent to \( r(P_1) > 1 \). Then, \( \lim_{\delta \to 0} r(P_1^\delta) = r(P_1) > 1 \). Fix a sufficiently small number \( \delta > 0 \) such that

\[
0 < \delta < \min \left\{ \frac{\min_{(t,x) \in [0,\omega] \times \Omega} M^*(t,x)}{2}, \frac{\min_{x \in \Omega} N^*(x)}{2} \right\}
\]

and \( r(P_1^\delta) > 1 \).

Since \( P_1^\delta \) is compact and strongly positive, the celebrated Krein–Rutman theorem implies that \( r(P_1^\delta) \) is a simple eigenvalue of \( P_1^\delta \) having a strongly positive eigenvector. By the arguments similar to those in [40, Theorem 2.16 and Remark 2.20], there is a positive \( \omega \)-periodic function \( \hat{\vartheta}(t,x) \) such that \( e^{\mu t} \hat{\vartheta}(t,x) \) is a positive solution of (4.3), where \( \mu^\delta = \frac{\ln r(P_1^\delta)}{\omega} > 0 \). From Lemma 2.2, we know that

\[
I_1(t,x,\psi) > 0 \quad \text{and} \quad I_{v1}(t,x,\psi) > 0, \quad \forall t > 0, \quad x \in \bar{\Omega}.
\]

Thus, we may choose a \( c > 0 \) such that

\[
(I_1(t_1,x,\psi), I_{v1}(t_1,x,\psi)) \geq ce^{\mu^\delta t_1} \hat{\vartheta}(t_1,x), \quad \forall x \in \bar{\Omega}.
\]

A simple comparison leads to

\[
(I_1(t,x,\psi), I_{v1}(t,x,\psi)) \geq ce^{\mu^\delta t} \hat{\vartheta}(t,x), \quad \forall t \geq t_1, \quad x \in \bar{\Omega}.
\]

Since \( \mu^\delta > 0 \), it follows that

\[
\lim_{t \to \infty} I_1(t,x,\psi) = \infty, \quad \lim_{t \to \infty} I_{v1}(t,x,\psi) = \infty \quad \text{uniformly for } x \in \bar{\Omega}.
\]

By performing a similar analysis on \((I_2(t,x,\psi), I_{v2}(t,x,\psi))\), when \( R_2 > 1 \),

\[
\lim_{t \to \infty} I_2(t,x,\psi) = \infty, \quad \lim_{t \to \infty} I_{v2}(t,x,\psi) = \infty \quad \text{uniformly for } x \in \bar{\Omega}.
\]

This contradicts the boundedness of \( I_i \) and \( I_{v_i} \), \( i = 1, 2 \). \qed

**Theorem 4.3.** Suppose that \( R_1 > 1 \) and \( R_2 > 1 \), then system (2.3) admits at least one positive \( \omega \)-periodic solution, and there exists a constant \( \delta^* > 0 \) such that for any \( \varphi \in \mathcal{C}_0 \), we have

\[
\liminf_{t \to \infty} \min_{x \in \bar{\Omega}} I_i(t,x,\varphi) \geq \delta^*, \quad \liminf_{t \to \infty} \min_{x \in \bar{\Omega}} I_{v1}(t,x,\varphi) \geq \delta^*, \quad i = 1, 2.
\]

**Proof.** For any \( \varphi \in \mathcal{C}_0 \), by Lemma 2.2,

\[
I_i(t,x,\varphi) > 0, \quad I_{v1}(t,x,\varphi) > 0, \quad i = 1, 2, \quad \forall t > 0, \quad x \in \bar{\Omega}.
\]

Thus, \( Q^n(\mathcal{C}_0) \subset \mathcal{C}_0, \quad \forall n \in \mathbb{N} \). Furthermore, \( Q \) admits a global attractor on \( \mathcal{C} \).

Next, we prove that \( Q \) is uniformly persistent with respect to \((\mathcal{C}_0, \partial \mathcal{C}_0)\). Recalling the definitions of \( E_0, E_1(t,x) \) and \( E_2(t,x) \) in Sect. 3.2, we let

\[
M_0 = E_0, \quad M_1 = E_1(0,\cdot), \quad M_2 = E_2(0,\cdot).
\]

Then, we have the following claims.

**Claim 1.** There is a \( \delta_1 > 0 \) such that

\[
\limsup_{n \to \infty} \|Q^n(\varphi) - M_0\| \geq \delta_1, \quad \forall \varphi \in \mathcal{C}_0.
\]

This claim directly follows from Lemmas 3.3 and 4.1.
Consider an auxiliary system with parameter \( \varepsilon \):

\[
\begin{align*}
\frac{\partial I_2(t, x)}{\partial t} &= D_h \Delta I_2(t, x) - (d + \gamma_2)I_2(t, x) \\
&\quad + \frac{c_2 \beta(t, x)l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}{p(I_1^*(t, x) + 2\varepsilon) + l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}I_2(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_{v2}(t, x)}{\partial t} &= D_v \Delta I_{v2}(t, x) - \eta(t, x)I_{v2}(t, x) \\
&\quad + \frac{\alpha_2 \beta(t, x)p(M^*(t, x) - I_{v1}^*(t, x) - 2\varepsilon)}{p(I_1^*(t, x) + 2\varepsilon) + l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}I_2(t, x), \quad t > 0, \ x \in \Omega, \\
\frac{\partial I_2(t, x)}{\partial \nu} &= 0, \quad t > 0, \ x \in \partial \Omega.
\end{align*}
\]

(4.4)

Let \( \tilde{P}_2^\varepsilon : \mathbb{E} \rightarrow \mathbb{E} \) be the Poincaré map of (4.4). In the case where \( \tilde{R}_2 > 1 \), we have \( r(\tilde{P}_2^\varepsilon) > 1 \). Since \( \lim_{\varepsilon \rightarrow 0} r(\tilde{P}_2^\varepsilon) = r(\tilde{P}_2) \), we can fix a small number \( \varepsilon > 0 \) such that \( r(\tilde{P}_2^\varepsilon) > 1 \) and \( 0 < \varepsilon < \min \left\{ \frac{\min_{(t, x) \in [0, \omega] \times \bar{\Omega}} M^*(t, x) - I_{v1}^*(t, x)}{2}, \frac{\min_{x \in \bar{\Omega}} N^*(x) - I_1^*(t, x)}{2} \right\} \).

As discussed in Lemma 4.1, there exists a positive \( \omega \)-periodic function \( \varphi^\varepsilon(t, x) \) such that \( e^{\mu^\varepsilon t} \varphi^\varepsilon(t, x) \) is a positive solution of (4.4), where \( \mu^\varepsilon = \max_{\varphi \in \mathbb{C}} \frac{\ln r(\tilde{P}_2^\varepsilon)}{\varepsilon} > 0 \). For the above \( \varepsilon > 0 \), by the continuous dependence of solutions on the initial value, there exists \( \delta_2 = \delta_2(\varepsilon) > 0 \) such that for all \( \varphi \in \mathbb{C}_0 \) with \( \|\varphi - M_1\| \leq \delta_2 \), we have \( \|Q(t)\varphi - Q(t)M_1\| < \varepsilon \), \( \forall t \in [0, \omega] \).

Claim 2. \( \limsup_{n \rightarrow \infty} \|Q^n(\varphi) - M_1\| \geq \delta_2, \forall \varphi \in \mathbb{C}_0 \).

If the claim is false, then \( \limsup_{n \rightarrow \infty} \|Q^n(\psi) - M_1\| < \delta_2 \) for some \( \psi \in \mathbb{C}_0 \). Therefore, there exists an integer \( N_1 \geq 1 \) such that \( \|Q^n(\psi) - M_1\| < \delta_2 \) for \( n \geq N_1 \). For any \( t \geq N_1 \omega \), letting \( t = n\omega + \bar{t} \) with \( n = [t/\omega] \) and \( \bar{t} \in [0, \omega] \), we have

\[
\|Q(t)\psi - Q(t)M_1\| = \|Q(\bar{t})(Q^n(\psi)) - Q(\bar{t})M_1\| < \varepsilon.
\]

According to the above inequality and Lemma 2.2, we deduce that

\[
0 < I_1(t, x, \psi) < I_1^*(t, x, \psi) + \varepsilon, \quad 0 < I_{v1}(t, x, \psi) < I_{v1}^*(t, x, \psi) + \varepsilon, \quad 0 < I_2(t, x, \psi) < \varepsilon, \quad 0 < I_{v2}(t, x, \psi) < \varepsilon, \quad \forall t \geq N_1 \omega, \ x \in \bar{\Omega}.
\]

As a result, \( I_2(t, x, \psi) \) and \( I_{v2}(t, x, \psi) \) satisfy

\[
\begin{align*}
\frac{\partial I_2(t, x)}{\partial t} &\geq D_h \Delta I_2(t, x) - (d + \gamma_2)I_2(t, x) \\
&\quad + \frac{c_2 \beta(t, x)l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}{p(I_1^*(t, x) + 2\varepsilon) + l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}I_2(t, x), \quad t > N_1 \omega, \ x \in \Omega, \\
\frac{\partial I_{v2}(t, x)}{\partial t} &\geq D_v \Delta I_{v2}(t, x) - \eta(t, x)I_{v2}(t, x) \\
&\quad + \frac{\alpha_2 \beta(t, x)p(M^*(t, x) - I_{v1}^*(t, x) - 2\varepsilon)}{p(I_1^*(t, x) + 2\varepsilon) + l(N^*(x) - I_1^*(t, x) - 2\varepsilon)}I_2(t, x), \quad t > N_1 \omega, \ x \in \Omega, \\
\frac{\partial I_2(t, x)}{\partial \nu} &= \frac{\partial I_{v2}(t, x)}{\partial \nu} = 0, \quad t > N_1 \omega, \ x \in \partial \Omega.
\end{align*}
\]

(4.5)

Note that \( I_2(t, x, \psi) > 0 \) and \( I_{v2}(t, x, \psi) > 0 \) for all \( t > 0 \) and \( x \in \bar{\Omega} \). Then, there exists \( k > 0 \) such that

\[
(I_2(N_1 \omega, x, \psi), I_{v2}(N_1 \omega, x, \psi)) \geq ke^{\mu^\varepsilon N_1 \omega} \varphi^\varepsilon(N_1 \omega, x), \quad \forall x \in \bar{\Omega}.
\]

An application of the comparison theorem to (4.5) yields

\[
(I_2(t, x, \psi), I_{v2}(t, x, \psi)) \geq ke^{\mu^\varepsilon t} \varphi^\varepsilon(t, x), \quad \forall t \geq N_1 \omega, \ x \in \bar{\Omega}.
\]
In view of $\mu^e > 0$, it follows that $I_2(t, \cdot, \psi) \rightarrow \infty$ and $I_{\nu_2}(t, \cdot, \psi) \rightarrow \infty$ as $t \rightarrow \infty$. This gives rise to a contradiction, and thereby, the above claim is true.

In a similar way, we can prove the following claim.

**Claim 3.** There exists $\delta_3 > 0$ such that

$$
\limsup_{n \rightarrow \infty} \|Q^n(\varphi) - M_2\| \geq \delta_3, \forall \varphi \in C_0.
$$

With the above three claims, we see that $M_0, M_1$ and $M_2$ are isolated invariant sets for $Q$ in $C$ and $W^s(M_i) \cap C_0 = \emptyset$, $i = 0, 1, 2$, where $W^s(M_i)$ is the stable set of $M_i$ for $Q$. Set

$$
M_0 := \{ \varphi \in \partial C_0 : Q^n(\varphi) \in \partial C_0, \forall n \in \mathbb{N} \}.
$$

We now show that $M_0 = M_0$, where

$$
M_0 := \{ \varphi \in C : \varphi_1(\cdot) + \varphi_2(\cdot) \equiv 0 \text{ or } \varphi_3(\cdot) + \varphi_4(\cdot) \equiv 0 \}.
$$

Obviously, it suffices to prove $M_0 \subset M_0$. For any given $\varphi \in M_0$, we see that $Q^n(\varphi) \in \partial C_0, \forall n \in \mathbb{N}$. Thus, for each $n \in \mathbb{N}$, it follows that $I_1(nw, \cdot, \varphi) \equiv 0$ or $I_{\nu_1}(nw, \cdot, \varphi) \equiv 0$ or $I_2(nw, \cdot, \varphi) \equiv 0$ or $I_{\nu_2}(nw, \cdot, \varphi) \equiv 0$.

Based on Lemma 2.2, we further derive that for each $\tau \geq 1$, $I_1(t, \cdot, \varphi) \equiv 0$ or $I_{\nu_1}(t, \cdot, \varphi) \equiv 0$ or $I_2(t, \cdot, \varphi) \equiv 0$ or $I_{\nu_2}(t, \cdot, \varphi) \equiv 0$. Suppose, by contradiction, that $\varphi \notin M_0$. Then, there are eight possibilities as below:

(i) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) \equiv 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) > 0$.

(ii) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) \equiv 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) \equiv 0$.

(iii) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) \equiv 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) > 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) > 0$.

(iv) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) > 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) \equiv 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) \equiv 0$.

(v) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) > 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) \equiv 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) \equiv 0$.

(vi) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) > 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) > 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) > 0$.

(vii) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) \equiv 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) \equiv 0$.

(viii) $\varphi_1(\cdot) = I_1(0, \cdot, \varphi) > 0$, $\varphi_2(\cdot) = I_{\nu_1}(0, \cdot, \varphi) > 0$, $\varphi_3(\cdot) = I_2(0, \cdot, \varphi) \equiv 0$, $\varphi_4(\cdot) = I_{\nu_2}(0, \cdot, \varphi) \equiv 0$.

By Lemma 2.2, in case (i), we obtain that $I_{\nu_1}(t, x, \varphi) > 0$ and $I_{\nu_2}(t, x, \varphi) > 0$ for all $t > 0$ and $x \in \Omega$. Further, using the first and third equation of (2.3), one can deduce that $I_1(t, x, \varphi) > 0$ and $I_2(t, x, \varphi) > 0, \forall t > \omega, x \in \Omega$, which contradicts with the fact $\varphi \notin M_0$. By performing a similar analysis, we can further show that (ii)–(viii) are impossible. Hence, $\varphi \in M_0$, which means $M_0 \subset M_0$.

Let $\omega(\varphi)$ be the omega limit set of the forward orbit $\gamma^+(\varphi) := \{Q^n(\varphi) : \forall n \in \mathbb{N} \}$. We further make the following claims.

**Claim 4.** $\omega(\varphi) \subset \{ M_0, M_1, M_2 \}$.

Obviously, there are three possibilities for $\varphi = (\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in M_0 = M_0$:

- **Case (a):** $\varphi_1(\cdot) + \varphi_2(\cdot) \equiv 0$, $\varphi_3(\cdot) + \varphi_4(\cdot) \equiv 0$;
- **Case (b):** $\varphi_1(\cdot) + \varphi_2(\cdot) \equiv 0$, $\varphi_3(\cdot) + \varphi_4(\cdot) \equiv 0$;
- **Case (c):** $\varphi_1(\cdot) \equiv 0$, $\forall i = 1, 2, 3, 4$.

In what follows, we aim to show that Claim 4 holds for each of the above three cases.

If **Case (a)** happens, then $I_1(t, x, \varphi) = I_{\nu_1}(t, x, \varphi) \equiv 0$ for all $t \geq 0$ and $x \in \Omega$. In view of system (2.3), $I_2(t, x, \varphi), I_{\nu_2}(t, x, \varphi)$ satisfy system (3.1) with $i = 2$. Under the condition $\mathcal{R}_2 > 1$, we have $\mathcal{R}_2 > 1$ due to Lemma 3.3. It then follows from Theorem 3.1(ii) that

$$
\lim_{t \rightarrow \infty} (I_2(t, x, \varphi) - I_{\nu_2}^*(t, x)) = 0, \quad \lim_{t \rightarrow \infty} (I_{\nu_2}(t, x, \varphi) - I_{\nu_2}^*(t, x)) = 0
$$

uniformly for $x \in \Omega$. Hence, $\omega(\varphi) = M_2$. For **Case (b)**, by repeating arguments similar to **Case (a)**, we can show that $\omega(\varphi) = M_1$. For **Case (c)**, one immediately finds that

$$
(I_1(t, x, \varphi), I_{\nu_1}(t, x, \varphi), I_2(t, x, \varphi), I_{\nu_2}(t, x, \varphi)) = (0, 0, 0, 0), \forall t \geq 0, x \in \Omega.
$$

This implies that $\omega(\varphi) = M_0$. Summarizing these three cases, Claim 4 is established.
Let $M_0 = M_0^1 \cup M_0^2$, where
\[ M_0^1 := \{ \varphi \in \mathbb{C} : \varphi_1(\cdot) + \varphi_2(\cdot) \equiv 0 \}, \quad M_0^2 := \{ \varphi \in \mathbb{C} : \varphi_3(\cdot) + \varphi_4(\cdot) \equiv 0 \}. \]

Claim 5. $M_i$ is globally stable for $Q$ in $M_0^i \setminus \{ M_0 \}$, where $i, j = 1, 2$ and $i \neq j$, and $M_0$ is unstable in $M_0^j$.

If $\varphi \in M_0^j$, then system (2.3) restricted on $M_0^j$ becomes system (3.1). Note that $\hat{R}_i > 1$ implies $\mathcal{R}_i > 1$. It then follows from Theorem 3.1(ii) that $M_i$ is globally stable for $Q$ in $M_0^i \setminus \{ M_0 \}$, and $M_0$ is unstable in $M_0^j$.

Based on Claim 5, we see that no subset of $\{ M_0, M_1, M_2 \}$ forms a cycle in $\partial \mathcal{C}_0$. Consequently, the acyclicity theorem on uniform persistence for maps (see [28, Theorem 1.3.1 and Remark 1.3.1]) asserts that $Q : \mathbb{C} \to \mathbb{C}$ is uniformly persistent with respect to $(\mathcal{C}_0, \partial \mathcal{C}_0)$ in the sense that there exists $\delta > 0$ such that
\[
\liminf_{n \to \infty} d(Q^n(\varphi), \partial \mathcal{C}_0) \geq \delta, \quad \forall \varphi \in \mathbb{C},
\]
where $d$ is the norm-induced distance in $\mathbb{X}$. By [32, Theorem 4.5] with $\rho(\phi) = d(\phi, \partial \mathcal{C}_0)$, $Q$ admits a global attractor $A_0$ in $\mathcal{C}_0$, and $Q$ has a fixed point in $\varphi \in A_0$. Hence, $u(t, \cdot, \varphi)$ is an $\omega$-periodic solution of (2.3), and it is strictly positive due to Lemma 2.2.

Finally, we show the practical uniform persistence. Since $A_0 = Q(A_0)$, we have $\varphi \equiv 0$ for all $\varphi \in A_0$. Let $B_0 := \cup_{t \in [0, \omega]} Q(t)A_0$. Then, $\psi \equiv 0$ for all $\psi \in B_0$, and [28, Theorem 3.1.1] implies that $\lim_{t \to \infty} d(Q(t)\varphi, B_0) = 0$ for all $\varphi \in \mathcal{C}_0$. Define a continuous function $g : \mathbb{C} \to \mathbb{R}_+$ by
\[
g(\psi) := \min_{x \in \Omega} \{ \min_{x \in \Omega} \psi_1(x), \min_{x \in \Omega} \psi_2(x), \min_{x \in \Omega} \psi_3(x), \min_{x \in \Omega} \psi_4(x) \}, \quad \forall \psi \in \mathbb{C}.
\]
Since $B_0$ is a compact set, it follows that $\inf_{\psi \in B_0} g(\psi) > 0$. By virtue of the attractivity of $B_0$, we conclude that there exists a $\delta^* > 0$ such that for any $\varphi \in \mathcal{C}_0$,
\[
\liminf_{t \to \infty} \min_{x \in \Omega} I_i(t, x, \varphi) \geq \delta^*, \quad \liminf_{t \to \infty} \min_{x \in \Omega} I_{vi}(t, x, \varphi) \geq \delta^*, \quad i = 1, 2.
\]
The proof is completed. 

5. Effects of diffusion and vector-bias on $\mathcal{R}_0$

In this section, we first use the recent theory developed in [41] to study the asymptotic behavior of $\mathcal{R}_0$ regarding the diffusion coefficients. To stress the dependence on diffusion coefficients, in what follows we write $N^*(x)$, $M^*(t, x)$ and $\mathcal{R}_0$ as $N^*_h(x)$, $M^*_v(t, x)$ and $\mathcal{R}_0(D_h, D_v) = \max\{ \mathcal{R}_1(D_h, D_v), \mathcal{R}_2(D_h, D_v) \}$, respectively.

Define the spatial averages of $\theta(t, x)$, where $\theta = \Lambda, \eta, \beta$, and $K(x)$ as
\[
\tilde{\theta}(t) = |\Omega|^{-1} \int_{\Omega} \theta(t, x)dx, \quad \tilde{K} = |\Omega|^{-1} \int_{\Omega} K(x)dx.
\]
It is easy to see that for each $x \in \Omega$, the equation
\[
\frac{dN(t)}{dt} = B(x, N(t))N(t) - dN(t), \quad t > 0,
\]
admits a unique equilibrium $N_0(x) = \frac{(b-d)K(x)}{b}$, which is globally asymptotically stable in $\mathbb{R}_+$. Set
\[
\tilde{B}(u) = \begin{cases} 
    b \left[ 1 - \frac{u}{\tilde{K}} \right], & 0 \leq u < \tilde{K}, \\
    0, & u \geq \tilde{K}.
\end{cases}
\]
It follows that the following equation
\[
\frac{dN(t)}{dt} = \tilde{B}(N(t))N(t) - dN(t), \quad t > 0,
\]
has a globally stable equilibrium \(N_\infty = \frac{(b-d)\bar{K}}{b}\) in \(\mathbb{R}_+.\)

On the other hand, for each \(x \in \Omega\), the equation
\[
\frac{dM(t)}{dt} = \Lambda(t, x) - \eta(t, x)M(t), \quad t > 0,
\]
admits a unique positive \(\omega\)-periodic solution
\[
M_0(t, x) = \left[ \int_0^t \Lambda(s, x) e^0 \int_0^s \eta(\xi, x) d\xi ds + \int_0^\omega \frac{\int_0^s \eta(\xi, x) d\xi ds}{e^0 \int_0^s \eta(s, x) ds - 1} \right] \left[ e^{-t \int_0^\infty \eta(s, x) ds} \right],
\]
which is globally asymptotically stable, and it is continuous on \(\mathbb{R} \times \bar{\Omega}\). And the linear periodic equation
\[
\frac{dM(t)}{dt} = \tilde{\Lambda}(t) - \tilde{\eta}(t)M(t), \quad t > 0,
\]
has a globally stable positive \(\omega\)-periodic solution \(M_\infty(t)\), expressed by
\[
M_\infty(t) = \left[ \int_0^t \tilde{\Lambda}(s) e^0 \int_0^s \tilde{\eta}(\xi) d\xi ds + \int_0^\omega \frac{\int_0^s \tilde{\eta}(\xi) d\xi ds}{e^0 \int_0^s \tilde{\eta}(s) ds - 1} \right] \left[ e^{-t \int_0^\infty \tilde{\eta}(s) ds} \right].
\]

It can be verified that assumptions (H1)–(H5) in [41] are satisfied. An direct application of [41, Theorems 5.2 and 5.5] yields that
\[
\lim_{D_h \to 0} \|N^*_{D_h}(\cdot) - N_0(\cdot)\|_Y = 0, \quad \lim_{D_h \to 0} \|N^*_{D_h}(\cdot) - N_\infty\|_Y = 0,
\]
and
\[
\lim_{D_v \to 0} \|M^*_{D_v}(t, \cdot) - M_0(t, \cdot)\|_Y = 0, \quad \lim_{D_v \to \infty} \|M^*_{D_v}(t, \cdot) - M_\infty(t)\|_Y = 0 \text{ uniformly for } t \in \mathbb{R}.
\]
For each \(x \in \bar{\Omega}\), let \(\{\Gamma^i_{x,0}(t, s) : t \geq s\} (i = 1, 2)\) be the evolution family on \(\mathbb{R}^2\) associated with the following ODE system
\[
\begin{aligned}
\frac{dI_i(t)}{dt} &= -(d + \gamma_i)I_i(t), \quad t \geq s, \\
\frac{dI_{vi}(t)}{dt} &= -\eta(t, x)I_{vi}(t), \quad t \geq s.
\end{aligned}
\]
Define
\[
F^i_0(t, x) \begin{pmatrix} \psi_1 \\ \psi_2 \end{pmatrix} = \begin{pmatrix} c_i \beta(t, x) \psi_2 \\ \alpha_i \beta(t, x) p N_0(x) \psi_1 \end{pmatrix}, \quad \forall t \in \mathbb{R}, \ x \in \bar{\Omega}, \ \psi = (\psi_1, \ \psi_2) \in \mathbb{R}^2.
\]
Let \(\{\Gamma^i_{\infty}(t, s) : t \geq s\} (i = 1, 2)\) be the evolution family on \(\mathbb{R}^2\) of the following system
\[
\begin{aligned}
\frac{dI_i(t)}{dt} &= -(d + \gamma_i)I_i(t), \quad t \geq s, \\
\frac{dI_{vi}(t)}{dt} &= -\tilde{\eta}(t)I_{vi}(t), \quad t \geq s,
\end{aligned}
\]
and define
\[ F^i(t) \begin{pmatrix} \psi_1 \\ \psi_2 \end{pmatrix} = \begin{pmatrix} c_i \beta(t) \psi_2 \\ \frac{\alpha_i \beta(t) \rho M_{\infty}(t)}{\ell_{\infty}^2} \psi_1 \end{pmatrix}, \quad \forall t \in \mathbb{R}, \; \psi = (\psi_1, \psi_2) \in \mathbb{R}^2. \]

Let \( C_\omega(\mathbb{R}, \mathbb{R}^2) \) be the Banach space of all continuous and \( \omega \)-periodic functions from \( \mathbb{R} \) to \( \mathbb{R}^2 \), which is endowed with the maximum norm. For each \( x \in \Omega \), we define the bounded linear positive operator \( L_{x,0}^i \) on \( C_\omega(\mathbb{R}, \mathbb{R}^2) \) by
\[ [L^i_{x,0} v](t) := \int_0^\infty \Gamma_{x,0}^i(t,t-s)F^i_0(t-s,x)v(t-s)ds, \quad i = 1, 2, \quad \forall t \in \mathbb{R}, \quad v \in C_\omega(\mathbb{R}, \mathbb{R}^2), \]
and introduce the operator \( L^i_\infty \) with the form of
\[ [L^i_\infty v](t) := \int_0^\infty \Gamma_{\infty}^i(t-s)F^i_\infty(t-s)v(t-s)ds, \quad i = 1, 2, \quad \forall t \in \mathbb{R}, \quad v \in C_\omega(\mathbb{R}, \mathbb{R}^2). \]

Now, we define \( R_i(x,0) := r(L^i_{x,0}), \quad \forall x \in \Omega \), and \( R_i(\infty) := r(L^i_\infty), \quad i = 1, 2. \) By [41, Theorem 4.3] with \( \kappa = \text{diag}(D_h, D_v), \quad \chi = (D_h, D_v), \quad \chi_0 = (0, 0), \) and \( \kappa = \text{diag}(D_h, D_v), \quad \chi = \left( \frac{1}{D_h}, \frac{1}{D_v} \right), \quad \chi_0 = (0, 0), \) respectively, one deduces that
\[ \lim_{\max(D_h, D_v) \to 0} R_i(D_h, D_v) = \max_{x \in \Omega} R_i(x,0) \quad \text{and} \quad \lim_{\min(D_h, D_v) \to \infty} R_i(D_h, D_v) = R_i(\infty), \quad i = 1, 2. \]
Therefore,
\[ \lim_{\max(D_h, D_v) \to 0} R_0(D_h, D_v) = \max\{\max R_1(x,0), \max R_2(x,0)\}, \]
\[ \lim_{\min(D_h, D_v) \to \infty} R_0(D_h, D_v) = \max\{R_1(\infty), R_2(\infty)\}. \]

Next, we investigate the effect of vector-bias on \( R_0 \). We use \( q := l/p \) to measure the relative attractivity of susceptible host versus infection one. Recalling the definition of \( \Psi_i(t,s) \) and \( F_i(t) \) in Sect. 3, let \( A^i \) and \( B^i \) \( i = 1, 2 \) be two bounded linear operators on \( C_\omega(\mathbb{R}, \mathbb{E}) \) given by
\[ [A^i v](t) := \int_0^\infty \Psi_i(t,t-s)v(t-s)ds, \quad [B^i v](t) := F_i(t)v(t), \quad \forall t \in \mathbb{R}, \quad v \in C_\omega(\mathbb{R}, \mathbb{E}). \]

Inspired by [36, Section 4.2], we write
\[ A^i v = (A^i_1 v_1, A^i_2 v_2) \quad \text{and} \quad B^i v = (B^i_1 v_2, B^i_2 v_1), \quad \forall v = (v_1, v_2) \in C_\omega(\mathbb{R}, \mathbb{E}), \]
where
\[ [A^i_1 v_1](t) = \int_0^\infty T_i(t,t-s)v_1(t-s)ds, \quad [A^i_2 v_2](t) = \int_0^\infty T_i(t,t-s)v_2(t-s)ds, \]
\[ [B^i_1 v_2](t) = c_i b(t, \cdot) v_2(t), \quad [B^i_2 v_1](t) = \frac{\alpha_i \beta(t, \cdot) M^*(t, \cdot)}{q N^*(\cdot)} v_1(t), \quad i = 1, 2. \]

According to Sect. 3.1, \( \mathcal{L}_i(q)v = A^i B^i v = (A^i_1 B^i_1 v_1, A^i_2 B^i_2 v_1) \), it then follows that
\[ \mathcal{L}_i^2(q)v = (A^i_1 B^i_1 A^i_1 B^i_1 v_1, A^i_2 B^i_2 A^i_1 B^i_1 v_2) = \frac{1}{q} \mathcal{L}_i^2(1)v, \quad i = 1, 2, \]
and hence, \( \mathcal{L}_i^2(q) = \frac{1}{q} \mathcal{L}_i^2(1) \). In view of \( r^2(\mathcal{L}_i(q)) = r(\mathcal{L}_i^2(q)) \), we obtain
\[ \mathcal{R}_i(q) := r(\mathcal{L}_i(q)) = \frac{1}{\sqrt{q}} r(\mathcal{L}_i(1)) = \frac{1}{\sqrt{q}} \mathcal{R}_i(1), \quad i = 1, 2. \]
Table 1. Parameter values in simulation

| Parameter | Value (range) | Dimension | Resource |
|-----------|---------------|-----------|----------|
| $d$       | $1/(70 \times 12)$ | Month$^{-1}$ | [17]     |
| $\eta(t, x)$ | 0.8 | Month$^{-1}$ | [26]     |
| $D_h$    | 0.4 | km$^2 \cdot$ month$^{-1}$ | [17]     |
| $D_v$    | 0.02 | km$^2 \cdot$ month$^{-1}$ | [17]     |
| $p$      | 0.8 (0–1) | Dimensionless | [15]     |
| $l$      | 0.2 (0–1) | Dimensionless | [15]     |

Therefore, $R_0(q) = \max\{R_1(q), R_2(q)\} = \frac{1}{\sqrt{q}} \max\{R_1(1), R_2(1)\}$. This shows that the ignorance of the vector-bias effect will underestimate the value of $R_0$.

6. Numerical simulations

In this section, we perform illustrative numerical investigations on the dynamics of model (2.3). We choose the period of our model to be $\omega = 12$ months and concentrate on one dimensional domain $\Omega = (0, \pi)$. For the sake of convenience, we assume that the density of total population $N^*(x) = 242 \, p \cdot km^{-1}$, where $p$ stands for a person, and the biting rate $\beta(t, x) = 4(1 + \cos(2x))$ month$^{-1}$. Biologically, the birth peak of mosquitoes is usually from June to September, and hence, we let $\Lambda(t, x) = 780 \times (1 + 0.6 \sin(\frac{\pi t}{6} + \frac{4\pi}{3})) \, m \cdot$ month$^{-1}$, where $m$ denotes a mosquito.

Unless stated otherwise, other baseline parameters are seen in Table 1. We use the numerical scheme proposed in [36, Lemma 2.5 and Remark 3.2] to compute the reproduction numbers of each strain. In order to demonstrate the outcome of competitive exclusion and coexistence, we consider the following three cases.

Case 1. $\hat{R}_1 > 1$ and $\hat{R}_2 > 1$. We choose $\gamma_1 = 0.23$ month$^{-1}$, $\gamma_2 = 0.196$ month$^{-1}$, $\alpha_1 = 0.56$, $\alpha_2 = 0.6$, $c_1 = 0.25$ and $c_2 = 0.2$. Then, we obtain $\hat{R}_1 = 2.9573$ and $\hat{R}_2 = 1.6311$. Figure 1 shows that the disease is uniformly persistent, and periodic oscillation phenomenon occurs, which is consistent with Theorem 4.3.
Case 2. \( R_2 > 1, \hat{R}_1 > 1 \) and \( \hat{R}_2 < 1 \). Taking \( \gamma_1 = 0.082 \text{ month}^{-1}, \gamma_2 = 0.06 \text{ month}^{-1}, \alpha_1 = 0.4, \alpha_2 = 0.15, c_1 = 0.1 \) and \( c_2 = 0.05 \), then \( R_2 = 2.6816, \hat{R}_1 = 3.8657 \) and \( \hat{R}_2 = 0.2861 \). Figure 2 shows that the sensitive strains survive, but the resistant strains die out.

Case 3. \( R_1 > 1, \hat{R}_2 > 1 \) and \( \hat{R}_1 < 1 \). Set \( \gamma_1 = 0.066 \text{ month}^{-1}, \gamma_2 = 0.082 \text{ month}^{-1}, \alpha_1 = 0.1, \alpha_2 = 0.35, c_1 = 0.05 \) and \( c_2 = 0.1 \). Then, we get \( R_1 = 2.1894, \hat{R}_2 = 3.3402 \) and \( \hat{R}_1 = 0.696 \). Figure 3 depicts that the resistant strains persist, but the sensitive strains go extinct.

It should be pointed out that in Figs. 1, 2, 3, we plot the graph of \( x \)-intersection with \( x = 0.7448 \). In addition, for the second and third case, the competitive exclusion phenomena are observed. It is a pity that we now cannot prove it, which is left for future consideration.

In order to explore the effect of seasonality, we set \( \Lambda(t, \cdot) = a_0(1 + b_0 \sin(\frac{\pi}{6}t + \frac{4\pi}{3})) \), where \( a_0 \) is the average recruitment rate, and \( b_0 \in [0, 1] \) is the strength of seasonal forcing. We use the same parameter values as in Case 1. Figure 4 describes the dependence of \( R_0 \) on \( a_0 \) and \( b_0 \). More specifically, Figure 4a shows that \( R_0 \) is an increasing function of \( a_0 \) for fixed \( b_0 = 0.6 \). Figure 4b compares the influences of...
the time-dependent recruitment rate and the time-averaged recruitment rate $[\Lambda] := \frac{1}{\omega} \int_0^\omega \Lambda(t, \cdot) dt$ on $R_0$, where $a_0 = 780$. As shown in Figure 4b, the use of the time-averaged recruitment rate may overestimate the value of $R_0$.

7. Discussion

In this paper, we have proposed a two-strain malaria model with seasonality and vector-bias. It is of interest to note that our model is a competitive system for sensitive and resistant strains, but the corresponding subsystem of each strain is cooperative. To characterize this mathematical structure, we define a time-dependent region $X(t)$. The introduction of this region brings out some mathematical difficulties. Fortunately, the solution map $Q(t) : X(0) \rightarrow X(t)$ can generate an $\omega$-periodic semiflow. This nice property allows us to use the persistence theory for periodic semiflows for our model analysis. The results show that the zero solution is global attractiveness if $R_0 = \max\{R_1, R_2\} \leq 1$ (see Theorem 4.1); sensitive (resistant) strains are uniformly persistent if $R_1 > 1 \geq R_2$ ($R_2 > 1 \geq R_1$) (see Theorem 4.2); and the model is uniformly persistent and admits a positive periodic solution if $\hat{R}_1 > 1$ and $\hat{R}_2 > 1$ (see Theorem 4.3). We also have analyzed the asymptotic behavior of the basic reproduction number in the case of small and large diffusion coefficients. Numerically, we have demonstrated the long-time behaviors of solutions, including competitive exclusion and coexistence, and revealed the influences of key parameters on the basic reproduction number. It is found that $R_0$ is a decreasing function of the strength of seasonal forcing.

Finally, we mention that in the phase space $X(0)$, system (2.3) is a monotone system with respect to the partial order $\leq_K$, which is induced by the cone $K = E^+ \times (-E^+)$. Hence, if we can prove the uniqueness of the positive periodic solution in Theorem 4.3, then the positive periodic solution is globally attractive in $C_0$ by the theory of monotone systems. This is a challenging problem and left for future study.
Acknowledgements

The authors are grateful to two anonymous referees for their valuable comments which led to improvements of our original manuscript.

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

References

[1] Chitnis, N., Hyman, J.M., Cushing, J.M.: Determining important parameters in the spread of malaria through the sensitivity analysis of a mathematical model. Bull. Math. Biol. 70, 1272–1296 (2008)
[2] Forouzannia, F., Gumel, A.B.: Mathematical analysis of an age-structured model for malaria transmission dynamics. Math. Biosci. 247, 80–94 (2014)
[3] Gutierrez, J.B., Galinski, M.R., Cantrell, S., et al.: From host dynamics to the epidemiology of infectious disease: scientific overview and challenges. Math. Biosci. 270, 143–155 (2015)
[4] Ross, R.: The Prevention of Malaria, 2nd edn. Murray, London (1911)
[5] Macdonald, G.: The Epidemiology and Control of Malaria. Oxford University Press, London (1957)
[6] Cosner, C., Beier, J.C., Cantrell, R.S., et al.: The effects of human movement on the persistence of vector-borne diseases. J. Theor. Biol. 258, 550–560 (2009)
[7] Lou, Y., Zhao, X.-Q.: A reaction–diffusion malaria model with incubation period in the vector population. J. Math. Biol. 62, 543–568 (2011)
[8] Xiao, Y., Zou, X.: Transmission dynamics for vector-borne diseases in a patchy environment. J. Math. Biol. 69, 113–146 (2014)
[9] Gao, D., van den Driessche, P., Cosner, C.: Habitat fragmentation promotes malaria persistence. J. Math. Biol. 79, 2255–2280 (2019)
[10] Alonso, D., Dobson, A., Pascual, M.: Critical transitions in malaria transmission models are consistently generated by superinfection. Philos. Trans. R. Soc. B 374, 20180275 (2019)
[11] Lou, Y., Zhao, X.-Q.: A climate-based malaria transmission model with structured vector population. SIAM J. Appl. Math. 70, 2023–2044 (2010)
[12] Wang, B.-G., Qiang, L., Wang, Z.-C.: An almost periodic Ross–Macdonald model with structured vector population in a patchy environment. J. Math. Biol. 80, 835–863 (2020)
[13] Kingsolver, J.G.: Mosquito host choice and the epidemiology of malaria. Am. Nat. 130, 811–827 (1987)
[14] Hosack, G.R., Rossignol, P.A., van den Driessche, P.: The control of vector-borne disease epidemics. J. Theor. Biol. 255, 16–25 (2008)
[15] Chamchod, F., Britton, N.F.: Analysis of a vector-bias model on malaria transmission. Bull. Math. Biol. 73, 639–657 (2011)
[16] Wang, X., Zhao, X.-Q.: A periodic vector-bias malaria model with incubation period. SIAM J. Appl. Math. 77, 181–201 (2017)
[17] Bai, Z., Peng, R., Zhao, X.-Q.: A reaction–diffusion malaria model with seasonality and incubation period. J. Math. Biol. 77, 201–228 (2018)
[18] Aneke, S.J.: Mathematical modelling of drug resistant malaria parasites and vector populations. Math. Methods Appl. Sci. 25, 335–346 (2002)
[19] Klein, E.Y.: Antimalarial drug resistance: a review of the biology and strategies to delay emergence and spread. Int. J. Antimicrob. Ag. 41, 311–317 (2013)
[20] Hoshen, M.B., Morse, A.P.: A weather-driven model of malaria transmission. Malar. J. 3, 32 (2004)
[21] Agusto, F.B., Gumel, A.B., Parham, P.E.: Qualitative assessment of the role of temperature variations on malaria transmission dynamics. J. Biol. Syst. 23, 1–34 (2015)
[22] Caillly, P., Tran, A., Balenghien, T., et al.: A climate-driven abundance model to assess mosquito control strategies. Ecol. Model. 227, 7–17 (2012)
[23] Ewing, D.A., Cobbold, C.A., Purse, B.V., et al.: Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes. J. Theor. Biol. 400, 65–79 (2016)
[24] Altizer, S., Dobson, A., Hosseini, P., et al.: Seasonality and the dynamics of infectious diseases. Ecol. Lett. 9, 467–484 (2006)
[25] Eikenberry, S.E., Gumel, A.B.: Mathematical modeling of climate change and malaria transmission dynamics: a historical review. J. Math. Biol. 77, 857–933 (2018)
[26] Shi, Y., Zhao, H.: Analysis of a two-strain malaria transmission model with spatial heterogeneity and vector-bias. J. Math. Biol. 82, 24 (2021)
[27] Li, F., Zhao, X.-Q.: Global dynamics of a reaction-diffusion model of Zika virus transmission with seasonality. Bull. Math. Biol. 83, 43 (2021)
[28] Zhao, X.-Q.: Dynamical Systems in Population Biology, 2nd edn. Springer, New York (2017)
[29] Zhang, L., Wang, Z.-C., Zhao, X.-Q.: Threshold dynamics of a time periodic reaction–diffusion epidemic model with latent period. J. Differ. Equ. 258, 3011–3036 (2015)
[30] Daners, D., Medina, P.K.: Abstract Evolution Equations, Periodic Problems and Applications, Pitman Research Notes in Mathematics Series, vol. 279. Longman Scientific and Technical, Harlow (1992)
[31] Martin, R.H., Smith, H.L.: Abstract functional differential equations and reaction–diffusion systems. Trans. Am. Math. Soc. 321, 1–44 (1990)
[32] Magal, P., Zhao, X.-Q.: Global attractors and steady states for uniformly persistent dynamical systems. SIAM J. Math. Anal. 37, 251–275 (2005)
[33] Hess, P.: Periodic-Parabolic Boundary Value Problems and Positivity, Pitman Research Notes in Mathematics Series, vol. 247. Longman Scientific and Technical, Harlow (1991)
[34] Thieme, H.R.: Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. SIAM J. Appl. Math. 70, 188–211 (2009)
[35] Zhao, X.-Q.: Basic reproduction ratios for periodic compartmental models with time delay. J. Dyn. Differ. Equ. 29, 67–82 (2017)
[36] Liang, X., Zhang, L., Zhao, X.-Q.: Basic reproduction ratios for periodic abstract functional differential equations (with application to a spatial model for Lyme disease). J. Dyn. Differ. Equ. 31, 1247–1278 (2019)
[37] Bacaër, N., Guernaoui, S.: The epidemic threshold of vector-borne diseases with seasonality. J. Math. Biol. 53, 421–436 (2006)
[38] Mitchell, C., Kribs, C.: Invasion reproductive numbers for periodic epidemic models. Infect. Dis. Model. 4, 124–141 (2019)
[39] Burlando, L.: Monotonicity of spectral radius for positive operators on ordered Banach spaces. Arch. Math. 56, 49–57 (1991)
[40] Liang, X., Zhang, L., Zhao, X.-Q.: The principal eigenvalue for degenerate periodic reaction–diffusion systems. SIAM J. Math. Anal. 49, 3603–3636 (2017)
[41] Zhang, L., Zhao, X.-Q.: Asymptotic behavior of the basic reproduction ratio for periodic reaction–diffusion systems. SIAM J. Math. Anal. 53, 6873–6909 (2021)

Huijie Chu and Zhenguo Bai
School of Mathematics and Statistics
Xi’an University
Xi’an 710126
China
e-mail: zgbai@xidian.edu.cn

(Received: February 1, 2022; revised: November 1, 2022; accepted: November 1, 2022)