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Research article

Dynamics of a coevolving host-virus system with resistance-growth trade-off

Xiaoshuang Li[1,2] **and Danfeng Pang**[3,*]

[1] College of Education, Xizang Minzu University, Xianyang 712082, China
[2] School of Mathematics and Statistics, Shaanxi Normal University, Xi'an 710119, China
[3] School of Mathematics and Data Science, Shaanxi University of Science and Technology, Xi'an 710021, China

* **Correspondence:** Email: pdf0803@163.com.

Abstract: This study investigated biodiversity changes in host-virus coevolution, focusing on a system incorporating a resistance-growth trade-off. We derived the basic reproduction number for the host system and identified conditions for host-virus coexistence. Numerical simulations revealed that the resistance-growth trade-off may influence diversity patterns, leading to both monotonic and unimodal dynamics. Additionally, the resistance-growth trade-off may drive transitions between stable equilibria and periodic solutions under specific mutation rates, cause shifts in dominant species in both algal and viral communities, and trigger a hydra effect under specific dilution rates. Our results offer insights into the mechanisms driving biodiversity fluctuations in host-virus coevolutionary dynamics.

Keywords: host-virus system; resistance-growth trade-off; basic reproduction number; hydra effect; biodiversity

1. Introduction

Evolutionary and ecological processes often operate on similar time scales, jointly shaping the dynamics of ecological communities [1, 2]. A well-known example of eco-evolutionary dynamics is the introduction of the myxoma virus into Australia and parts of Europe to control the European rabbit *Oryctolagus cuniculus* [3, 4]. Given that biodiversity is influenced by multiple factors such as evolutionary processes [5, 6], biological interactions [7–9], and environmental changes [10, 11], it is crucial to understand how evolutionary processes interact with population dynamics to alter key aspects of community dynamics.

Mathematical modeling has been essential in advancing our understanding of host-parasite coevolution. Pimentel [12] pioneered the integration of population dynamics into coevolutionary models, suggesting that prey evolution in a plant-herbivore system could drive either stabilizing or oscillatory predator dynamics. Building on this framework, Pimentel and colleagues [13, 14] provided empirical evidence for eco-evolutionary dynamics. Moreover, the incorporation of coevolutionary dynamics extended these foundational studies. Levin and Udovic [15] developed a general framework for two-species coevolutionary dynamics, while Schaffer and Rosenzweig [16] introduced an innovative approach to track the evolution of ecologically relevant parameters, which could be integrated into the ecological Rosenzweig-MacArthur model. These works laid the groundwork for eco-evolutionary analysis. Recent studies have further emphasized the role of eco-evolutionary feedback mechanisms in host-parasite coevolution [17], and explicitly examined the impact of incorporating or excluding this feedback in models, revealing significant shifts in evolutionary outcomes [18–21].

Coevolutionary models often incorporate pleiotropy through trade-offs between life-history traits, reflecting empirical observations that enhanced host resistance may come at the cost of reduced growth or reproduction [22–25]. The shape and strength of these trade-offs are critical determinants of evolutionary dynamics [26, 27]. For example, variations in adaptation costs can drive transitions between stable equilibria and fluctuating selection in host-parasite coevolution models [28, 29]. A key contribution by Forde et al. [5] developed a bacteria-phage coevolution framework that integrates two major trade-offs: (a) increasing host resistance to phages reduces host growth rates [22, 23], and (b) enhancing the number of hosts a phage can infect requires a balance between adsorption efficiency and burst size [23]. Their model successfully replicated experimental results, showing that resource input modulates biomass and diversity, consistent with natural populations [30–33]. Notably, this study specifically focused on systems where the adsorption matrix of the bacteria-phage model is square, meaning the number of host types exactly matches the number of phage types.

To systematically explore the resistance-growth trade-off, Frickel et al. [6] recently developed a novel experimental eukaryotic host-virus system, incorporating a modified gene-for-gene infection mechanism [5]. The key distinction lies in the rectangular structure of the adsorption matrix (N host types $\times$ $N-1$ viral types), governed by a hierarchical infection rule: viral type P_j can infect host type B_i only if $j \geq i$. Their findings showed that polymorphic equilibria, where two or more strains coexist, depend crucially on the strength of the trade-off, as predicted by coevolutionary theory [28, 29]. However, the model's sensitivity to variations in other parameters, which typically link to biological traits or environmental factors, remains unexplored. To address this gap and advance theoretical development, we propose a systematic investigation of the qualitative dynamics in host-virus coevolution models across different parametric configurations. The primary goal of this study is to analyze the combined effects of the resistance-growth trade-off and biological factors on evolutionary outcomes. Our main contributions include deriving the basic reproduction number for the host system and establishing the conditions for host-virus coexistence. A key challenge is that the virus-free equilibrium in the host-virus system is not necessarily unique. We show that varying the strength of the resistance-growth trade-off may lead to distinct patterns of species diversity, including both monotonic and unimodal configurations, depending on biological factors. Notably, we identify dilution rate-induced hydra effects in both algal and viral populations, and demonstrate how the resistance-growth trade-off may drive transitions between stable equilibria and periodic solutions in the host-virus system.

The remainder of this paper is organized as follows. Section 2 introduces a coevolving host-virus system that includes a resistance-growth trade-off. In Section 3, we derive the basic reproduction number for the host system, analyze the conditions for host-virus coexistence, and explore the uniform persistence of the host-virus system. Section 4 presents numerical simulations to examine the effects of ecological factors on eco-evolutionary dynamics. The final section summarizes the key findings and outlines directions for future research.

2. Model description

We revisit a coevolving host-virus system that was originally formulated by Frickel et al. [6]:

$$
\begin{cases}
\frac{dS}{dt} = D(S_0 - S) - \gamma[g_1(S)B_1 + g_2(S)B_2 + g_3(S)B_3 + g_4(S)B_4], \\
\frac{dB_1}{dt} = (1-\varepsilon)g_1(S)B_1 + \frac{\varepsilon}{2}g_2(S)B_2 - \alpha B_1(P_1 + P_2 + P_3) - DB_1, \\
\frac{dB_2}{dt} = \varepsilon g_1(S)B_1 + (1-\varepsilon)g_2(S)B_2 + \frac{\varepsilon}{2}g_3(S)B_3 - \alpha B_2(P_2 + P_3) - DB_2, \\
\frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(S)B_2 + (1-\varepsilon)g_3(S)B_3 + \varepsilon g_4(S)B_4 - \alpha B_3 P_3 - DB_3, \\
\frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(S)B_3 + (1-\varepsilon)g_4(S)B_4 - DB_4, \\
\frac{dP_1}{dt} = \alpha\beta[(1-\varepsilon)B_1P_1 + \frac{\varepsilon}{2}(B_1 + B_2)P_2] - \alpha B_1 P_1 - DP_1, \\
\frac{dP_2}{dt} = \alpha\beta[\varepsilon B_1 P_1 + (1-\varepsilon)(B_1 + B_2)P_2 + \varepsilon(B_1 + B_2 + B_3)P_3] - \alpha(B_1 + B_2)P_2 - DP_2, \\
\frac{dP_3}{dt} = \alpha\beta[\frac{\varepsilon}{2}(B_1 + B_2)P_2 + (1-\varepsilon)(B_1 + B_2 + B_3)P_3] - \alpha(B_1 + B_2 + B_3)P_3 - DP_3, \\
S(0) \geq 0,\ B_i(0) \geq 0,\ P_j(0) \geq 0,\ i = 1,2,3,4,\ j = 1,2,3,
\end{cases}
\tag{2.1}
$$

where S_0 is the concentration of abiotic resources in the input vessel supplying the chemostat, and S denotes the concentration of that limiting resource within the chemostat. The densities of four algal types and three viral types are represented by B_i (for $i = 1,2,3,4$) and P_j (for $j = 1,2,3$), respectively. The virus adsorption rate is denoted by α, and β represents the virus burst size. The first equation of system (2.1) describes the rate of change of resource concentration S in the chemostat, which is governed by the dilution rate D. Resource consumption is modeled through the resource conversion rate γ and the algal growth rate $g_i(S)$, given by the Monod function:

$$
g_i(S) = \frac{a_i S}{H + S},\ i = 1,2,3,4,
$$

where a_i represents the maximum growth rate, and H is the half-saturation constant for the resource. Algae and virus evolve through mutation at a rate ε, which alters both resistance range and host range. We assume that all algal types share the same half-saturation constant for resources. A resistance-growth trade-off is included, where the host growth rate decreases as resistance increases [22,23]. This relationship is expressed as [6]

$$
a_i = \frac{a_N - a_1}{N - 1}(i - 1) + a_1,\ i = 1,2,3,4,\ N = \max\{i\}.
$$

As a result, B_1 is the least resistant type but has the highest growth rate, while B_4 is the most resistant type with the lowest growth rate, i.e., $0 < a_4 \leq a_3 \leq a_2 \leq a_1 < 1$. We also assume that viral type P_j can infect algal type B_i if and only if $j \geq i$, implying that algal type B_4 is generally resistant. Additionally, P_1 has the smallest host range, whereas P_3 has the widest host range. The biological meanings of the parameters are listed in Table 1 and the values of the parameters follow from Frickel et al. [6].

Table 1. List of parameters in model (2.1).

Parameter	Biological meaning	Value [6]
S_0	Inflow resource concentration	$30\ (\mu g\ mL^{-1})$
D	Chemostat dilution rate	$0.1\ (d^{-1})$
γ	Resource conversion rate	2.3×10^{-5}
H	Half-saturation constant	$1\ (\mu g\ mL^{-1})$
a_1	Maximum growth rate of algal type B_1	$0.25\ (d^{-1})$
α	Adsorption rate of virus	$7.5\times10^{-8}\ (d^{-1})$
β	Burst size of virus	100
ε	Mutation rate	10^{-3}

We assume that all parameters are positive constants, with $\beta > 1$ and $0 < \varepsilon \le 1$ throughout this paper. Let

$$W(t) = S(t) + \gamma[B_1(t) + B_2(t) + B_3(t) + B_4(t)] + \frac{\gamma}{\beta-1}[P_1(t) + P_2(t) + P_3(t)], \tag{2.2}$$

and then we have

$$\frac{dW}{dt} = D(S_0 - W). \tag{2.3}$$

Noting that

$$\lim_{t\to\infty} W(t) = S_0, \tag{2.4}$$

we obtain the following limiting system:

$$\begin{cases} \frac{dB_1}{dt} = (1-\varepsilon)g_1(\tilde{S}_0)B_1 + \frac{\varepsilon}{2}g_2(\tilde{S}_0)B_2 - \alpha B_1(P_1+P_2+P_3) - DB_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\tilde{S}_0)B_1 + (1-\varepsilon)g_2(\tilde{S}_0)B_2 + \frac{\varepsilon}{2}g_3(\tilde{S}_0)B_3 - \alpha B_2(P_2+P_3) - DB_2, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\tilde{S}_0)B_2 + (1-\varepsilon)g_3(\tilde{S}_0)B_3 + \varepsilon g_4(\tilde{S}_0)B_4 - \alpha B_3P_3 - DB_3, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\tilde{S}_0)B_3 + (1-\varepsilon)g_4(\tilde{S}_0)B_4 - DB_4, \\ \frac{dP_1}{dt} = \alpha\beta[(1-\varepsilon)B_1P_1 + \frac{\varepsilon}{2}(B_1+B_2)P_2] - \alpha B_1P_1 - DP_1, \\ \frac{dP_2}{dt} = \alpha\beta[\varepsilon B_1P_1 + (1-\varepsilon)(B_1+B_2)P_2 + \varepsilon(B_1+B_2+B_3)P_3] - \alpha(B_1+B_2)P_2 - DP_2, \\ \frac{dP_3}{dt} = \alpha\beta[\frac{\varepsilon}{2}(B_1+B_2)P_2 + (1-\varepsilon)(B_1+B_2+B_3)P_3] - \alpha(B_1+B_2+B_3)P_3 - DP_3, \\ B_i(0) \ge 0,\ P_j(0) \ge 0,\ i = 1,2,3,4,\ j = 1,2,3, \end{cases} \tag{2.5}$$

where

$$\tilde{S}_0 = S_0 - \gamma[B_1 + B_2 + B_3 + B_4] - \frac{\gamma}{\beta-1}[P_1 + P_2 + P_3]. \tag{2.6}$$

3. Results

This section focuses on analyzing the dynamics of the host-virus system and presents the main results, with proofs provided in the Appendix.

Let

$$\mathbb{Y} = \{\phi = (\phi_1,\phi_2,\phi_3,\phi_4,\phi_5,\phi_6,\phi_7) \in \mathbb{R}^7_+ :\ \phi_1 + \phi_2 + \phi_3 + \phi_4 + \frac{1}{\beta-1}[\phi_5 + \phi_6 + \phi_7] \le S_0/\gamma\}.$$

Then the following results hold for the limiting system (2.5).

Theorem 3.1. *For any initial value* $\phi \in \mathbb{Y}$*, system* (2.5) *has a unique non-negative solution on* $[0,\infty)$*, and solutions are ultimately bounded.*

Theorem 3.2. *Let* $(B_1(t),B_2(t),B_3(t),B_4(t),P_1(t),P_2(t),P_3(t))$ *be the solution of system* (2.5) *with initial data in* $\mathbb{Y}$*. If there exists a* $t^0 \geq 0$ *such that* $B_{i_0}(t^0) > 0$ *for some* $i_0 \in \{1,2,3,4\}$*, then* $B_i(t) > 0$ *for all* $t > t^0$ *and* $i = 1,2,3,4$*. Furthermore, if* $P_{j_0}(t^0) > 0$ *for some* $j_0 \in \{1,2,3\}$*, then* $P_j(t) > 0$ *for all* $t > t^0$ *and* $j = 1,2,3$*.*

3.1. The host system

In this subsection, we investigate the dynamical behavior of the host system. Let $P_1 = P_2 = P_3 = 0$ in system (2.1), and then we obtain the following host system:

$$\begin{cases} \frac{dS}{dt} = D(S_0 - S) - \gamma[g_1(S)B_1 + g_2(S)B_2 + g_3(S)B_3 + g_4(S)B_4], \\ \frac{dB_1}{dt} = (1-\varepsilon)g_1(S)B_1 + \frac{\varepsilon}{2}g_2(S)B_2 - DB_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(S)B_1 + (1-\varepsilon)g_2(S)B_2 + \frac{\varepsilon}{2}g_3(S)B_3 - DB_2, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(S)B_2 + (1-\varepsilon)g_3(S)B_3 + \varepsilon g_4(S)B_4 - DB_3, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(S)B_3 + (1-\varepsilon)g_4(S)B_4 - DB_4, \\ S(0) \geq 0,\ B_i(0) \geq 0,\ i = 1,2,3,4. \end{cases} \tag{3.1}$$

Let $W = S + \gamma[B_1 + B_2 + B_3 + B_4]$. Then we have $\frac{dW}{dt} = D(S_0 - W)$, which leads to $\lim_{t\to\infty} W(t) = S_0$. Thus, the following limiting system is obtained:

$$\begin{cases} \frac{dB_1}{dt} = (1-\varepsilon)g_1(\bar{S}_0)B_1 + \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 - DB_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\bar{S}_0)B_1 + (1-\varepsilon)g_2(\bar{S}_0)B_2 + \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 - DB_2, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 + (1-\varepsilon)g_3(\bar{S}_0)B_3 + \varepsilon g_4(\bar{S}_0)B_4 - DB_3, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 + (1-\varepsilon)g_4(\bar{S}_0)B_4 - DB_4, \\ B_i(0) \geq 0,\ i = 1,2,3,4, \end{cases} \tag{3.2}$$

where $\bar{S}_0 = S_0 - \gamma[B_1 + B_2 + B_3 + B_4]$. Obviously, system (3.2) has a trivial equilibrium $E_0 := (0,0,0,0)$. Linearizing system (3.2) at E_0, we obtain the following system:

$$\begin{cases} \frac{dB_1}{dt} = (1-\varepsilon)g_1(S_0)B_1 + \frac{\varepsilon}{2}g_2(S_0)B_2 - DB_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(S_0)B_1 + (1-\varepsilon)g_2(S_0)B_2 + \frac{\varepsilon}{2}g_3(S_0)B_3 - DB_2, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(S_0)B_2 + (1-\varepsilon)g_3(S_0)B_3 + \varepsilon g_4(S_0)B_4 - DB_3, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(S_0)B_3 + (1-\varepsilon)g_4(S_0)B_4 - DB_4, \\ B_i(0) \geq 0,\ i = 1,2,3,4. \end{cases}$$

Denote $s(J^0)$ as the stability modulus of the following matrix J^0:

$$J^0 = \begin{pmatrix} (1-\varepsilon)g_1(S_0) - D & \frac{\varepsilon}{2}g_2(S_0) & 0 & 0 \\ \varepsilon g_1(S_0) & (1-\varepsilon)g_2(S_0) - D & \frac{\varepsilon}{2}g_3(S_0) & 0 \\ 0 & \frac{\varepsilon}{2}g_2(S_0) & (1-\varepsilon)g_3(S_0) - D & \varepsilon g_4(S_0) \\ 0 & 0 & \frac{\varepsilon}{2}g_3(S_0) & (1-\varepsilon)g_4(S_0) - D \end{pmatrix}.$$

Recall that the stability modulus of an $n \times n$ matrix M is defined by

$$s(M) := \max\{\mathrm{Re}\lambda : \lambda \text{ is an eigenvalue of } M\}.$$

Since $0 < \varepsilon \leq 1$, it is easy to see that J^0 is irreducible and has non-negative off-diagonal elements. Consequently, $s(J^0)$ is a simple eigenvalue of J^0 with a positive eigenvector in light of Theorem A.5 of [34].

We now use the approach of the next generation matrix [35] to compute R_0^h, the host basic reproduction number, which is defined as the average number of secondary host reproductions. We introduce the following matrices:

$$F = \begin{pmatrix} (1-\varepsilon)g_1(S_0) & 0 & 0 & 0 \\ 0 & (1-\varepsilon)g_2(S_0) & 0 & 0 \\ 0 & 0 & (1-\varepsilon)g_3(S_0) & 0 \\ 0 & 0 & 0 & (1-\varepsilon)g_4(S_0) \end{pmatrix}, \tag{3.3}$$

and

$$V = \begin{pmatrix} D & -\frac{\varepsilon}{2}g_2(S_0) & 0 & 0 \\ -\varepsilon g_1(S_0) & D & -\frac{\varepsilon}{2}g_3(S_0) & 0 \\ 0 & -\frac{\varepsilon}{2}g_2(S_0) & D & -\varepsilon g_4(S_0) \\ 0 & 0 & -\frac{\varepsilon}{2}g_3(S_0) & D \end{pmatrix}. \tag{3.4}$$

By direct calculation, we have

$$FV^{-1} = \frac{1}{\det(V)} \begin{pmatrix} G_{11} & G_{12} & G_{13} & G_{14} \\ G_{21} & G_{22} & G_{23} & G_{24} \\ G_{31} & G_{32} & G_{33} & G_{34} \\ G_{41} & G_{42} & G_{43} & G_{44} \end{pmatrix}, \tag{3.5}$$

where

$$\begin{aligned}
G_{11} &= D(D^2 - \tfrac{\varepsilon^2}{4}g_2(S_0)g_3(S_0) - \tfrac{\varepsilon^2}{2}g_3(S_0)g_4(S_0))(1-\varepsilon)g_1(S_0),\\
G_{12} &= \tfrac{\varepsilon}{2}g_2(S_0)(D^2 - \tfrac{\varepsilon^2}{2}g_3(S_0)g_4(S_0))(1-\varepsilon)g_1(S_0),\\
G_{13} &= \tfrac{\varepsilon^2}{4}Dg_2(S_0)g_3(S_0)(1-\varepsilon)g_1(S_0),\\
G_{14} &= \tfrac{\varepsilon^3}{4}g_2(S_0)g_3(S_0)g_4(S_0)(1-\varepsilon)g_1(S_0),\\
G_{21} &= \varepsilon g_1(S_0)(D^2 - \tfrac{\varepsilon^2}{2}g_3(S_0)g_4(S_0))(1-\varepsilon)g_2(S_0),\\
G_{22} &= D(D^2 - \tfrac{\varepsilon^2}{2}g_3(S_0)g_4(S_0))(1-\varepsilon)g_2(S_0),\\
G_{23} &= \tfrac{\varepsilon}{2}D^2g_3(S_0)(1-\varepsilon)g_2(S_0),\\
G_{24} &= \tfrac{\varepsilon^2}{2}Dg_3(S_0)g_4(S_0)(1-\varepsilon)g_2(S_0),\\
G_{31} &= \tfrac{\varepsilon^2}{2}Dg_1(S_0)g_2(S_0)(1-\varepsilon)g_3(S_0),\\
G_{32} &= \tfrac{\varepsilon}{2}D^2g_2(S_0)(1-\varepsilon)g_3(S_0),\\
G_{33} &= D(D^2 - \tfrac{\varepsilon^2}{2}g_1(S_0)g_2(S_0))(1-\varepsilon)g_3(S_0),\\
G_{34} &= \varepsilon g_4(S_0)(D^2 - \tfrac{\varepsilon^2}{2}g_1(S_0)g_2(S_0))(1-\varepsilon)g_3(S_0),\\
G_{41} &= \tfrac{\varepsilon^3}{4}g_1(S_0)g_2(S_0)g_3(S_0)(1-\varepsilon)g_4(S_0),\\
G_{42} &= \tfrac{\varepsilon^2}{4}Dg_2(S_0)g_3(S_0)(1-\varepsilon)g_4(S_0),\\
G_{43} &= \tfrac{\varepsilon}{2}g_3(S_0)(D^2 - \tfrac{\varepsilon^2}{2}g_1(S_0)g_2(S_0))(1-\varepsilon)g_4(S_0),\\
G_{44} &= D(D^2 - \tfrac{\varepsilon^2}{2}g_1(S_0)g_2(S_0) - \tfrac{\varepsilon^2}{4}g_2(S_0)g_3(S_0))(1-\varepsilon)g_4(S_0),
\end{aligned}$$

and

$$\det(V) = D^2(D^2 - \frac{\varepsilon^2}{4}g_2(S_0)g_3(S_0) - \frac{\varepsilon^2}{2}g_3(S_0)g_4(S_0)) - \frac{\varepsilon^2}{2}g_1(S_0)g_2(S_0)(D^2 - \frac{\varepsilon^2}{2}g_3(S_0)g_4(S_0)).$$

It then follows from [35] that the host basic reproduction number R_0^h corresponds to the spectral radius of FV^{-1}:

$$R_0^h = \rho(FV^{-1}). \tag{3.6}$$

In view of the structure of Eqs (3.3)–(3.6), we know that R_0^h is related to evolution-related parameter ε and resource-related factors S_0 and D. Moreover, we have the following local stability of the trivial equilibrium $E_0 = (0,0,0,0)$.

Lemma 3.3. *[36] The following statements hold:*

- (i) $R_0^h = 1$ *if and only if* $s(J^0) = 0$*;*
- (ii) $R_0^h > 1$ *if and only if* $s(J^0) > 0$*;*
- (iii) $R_0^h < 1$ *if and only if* $s(J^0) < 0$.

Thus, the trivial equilibrium E_0 *is locally asymptotically stable if* $R_0^h < 1$*, and unstable if* $R_0^h > 1$.

Next, we establish the threshold dynamics of the limiting system (3.2) in terms of R_0^h. Let

$$\Omega := \{(\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in \mathbb{R}_+^4 | \ \varphi_1 + \varphi_2 + \varphi_3 + \varphi_4 \leq S_0/\gamma\},$$

and define $\Omega_0 := \{(\varphi_1, \varphi_2, \varphi_3, \varphi_4) \in \Omega | \ (\varphi_1, \varphi_2, \varphi_3, \varphi_4) \not\equiv \mathbf{0}\}$, $\partial\Omega_0 := \Omega \backslash \Omega_0$. We can prove, similarly to Theorem 3.1, that system (3.2) has a unique non-negative solution on Ω, and the solution is ultimately bounded. Next, we define the solution semiflow $Q(t) : \Omega \to \Omega$ of system (3.2) as

$$Q(t)\varphi = (B_1(t,\varphi), B_2(t,\varphi), B_3(t,\varphi), B_4(t,\varphi)) \text{ for any } \varphi \in \Omega,$$

where $(B_1(t,\varphi), B_2(t,\varphi), B_3(t,\varphi), B_4(t,\varphi))$ is the solution of system (3.2) with initial condition $\varphi \in \Omega$. Then the following result holds for the limiting system (3.2).

Lemma 3.4. *Let* $0 < \varepsilon \leq 1$. *Assume that* $(B_1(t), B_2(t), B_3(t), B_4(t))$ *is the solution of system* (3.2) *with the initial value in* Ω. *Then the following statements are valid:*

- (i) *If* $R_0^h < 1$ *(i.e.,* $s(J^0) < 0$*), then the trivial equilibrium* $E_0 = (0,0,0,0)$ *is globally attractive in* Ω *for system* (3.2) *in the sense that*

$$\lim_{t\to\infty}(B_1(t), B_2(t), B_3(t), B_4(t)) = (0,0,0,0);$$

- (ii) *If* $R_0^h > 1$ *(i.e.,* $s(J^0) > 0$*), then there exists a constant* $\bar{\sigma} > 0$ *such that any solution of system* (3.2) *with an initial value in* Ω_0 *satisfies*

$$\liminf_{t\to\infty} B_i(t) \geq \bar{\sigma}, \ i = 1,2,3,4.$$

Furthermore, system (3.2) *admits at least one positive equilibrium* $E^* = (B_1^*, B_2^*, B_3^*, B_4^*)$.

Remark 3.1. *From Lemma 3.4(ii), we see that* $Q(t) : \Omega \to \Omega$ *is uniformly persistent with respect to* $(\Omega_0, \partial\Omega_0)$ *provided that* $R_0^h > 1$ *(i.e.,* $s(J^0) > 0$*). It follows from Theorem 1.3.7 of [37] that* $Q(t) : \Omega_0 \to \Omega_0$ *has a global attractor* A_0*. Since* $A_0 \subset \Omega_0$ *and* $A_0 = Q(t)(A_0)$*, we further have* $A_0 \subset Int(\mathbb{R}_+^4)$*.*

Let

$$\bar{\Omega}_0 := \{(\varphi_1, \varphi_2, \varphi_3, \varphi_4, \varphi_5) \in \mathbb{R}_+^5 | \ (\varphi_2, \varphi_3, \varphi_4, \varphi_5) \not\equiv \mathbf{0}\}.$$

In view of Lemma 3.4, we can easily lift the dynamics of the limiting system (3.2) to system (3.1) by the theory of chain transitive sets [37].

Theorem 3.5. *Let* $0 < \varepsilon \leq 1$*. Assume that* $(S(t), B_1(t), B_2(t), B_3(t), B_4(t))$ *is the solution of system* (3.1) *with the initial value in* $\mathbb{R}_+^5$*. Then the following statements are valid:*

(i) *If* $R_0^h < 1$ *(i.e.,* $s(J^0) < 0$*), then the resource-only equilibrium* $(S_0, 0, 0, 0, 0)$ *is globally attractive in* $\mathbb{R}_+^5$ *for system* (3.1) *in the sense that*

$$\lim_{t\to\infty}(S(t), B_1(t), B_2(t), B_3(t), B_4(t)) = (S_0, 0, 0, 0, 0);$$

(ii) *If* $R_0^h > 1$ *(i.e.,* $s(J^0) > 0$*), then there exists a constant* $\sigma > 0$ *such that any solution of system* (3.1) *with the initial value in* $\bar{\Omega}_0$ *satisfies*

$$\liminf_{t\to\infty} B_i(t) \geq \sigma, \ i = 1, 2, 3, 4.$$

Furthermore, system (3.1) *admits at least one positive equilibrium* $(S^*, B_1^*, B_2^*, B_3^*, B_4^*)$*, where* $S^* = S_0 - \gamma(B_1^* + B_2^* + B_3^* + B_4^*)$*.*

3.2. Coexistence of the host-virus system

In this subsection, we further study the dynamical behavior of the host-virus system (2.1). We know that system (2.1) has two types of equilibria: (a) the resource-only equilibrium, denoted by $\mathscr{E}_0$, given by

$$\mathscr{E}_0 = (S, B_1, B_2, B_3, B_4, P_1, P_2, P_3) = (S_0, 0, 0, 0, 0, 0, 0, 0),$$

which represents the absence of both host and virus; (b) the virus-free equilibrium, denoted by $\mathscr{E}_B$, given by

$$\mathscr{E}_B = (S, B_1, B_2, B_3, B_4, P_1, P_2, P_3) = (S^*, B_1^*, B_2^*, B_3^*, B_4^*, 0, 0, 0),$$

which corresponds to the presence of host and the absence of virus, and the positive equilibrium $(S^*, B_1^*, B_2^*, B_3^*, B_4^*)$ may not be unique (see Theorem 3.5(ii) and Remark 3.1). Biologically, the interesting question is whether both the host and virus can coexist in the system. Mathematically, we aim to establish the existence of positive (coexistence) solutions to system (2.1) under suitable conditions. Our research method is motivated by Lemma 4.2 of [38], which also considered the non-unique zooplankton-extinct steady-state solution.

Let

$$\mathbb{Y}_0 = \{(\phi_1, \phi_2, \phi_3, \phi_4, \phi_5, \phi_6, \phi_7) \in \mathbb{Y} | \ (\phi_1, \phi_2, \phi_3, \phi_4) \not\equiv \mathbf{0} \text{ and } (\phi_5, \phi_6, \phi_7) \not\equiv \mathbf{0}\},$$

and $\partial\mathbb{Y}_0 = \mathbb{Y} \backslash \mathbb{Y}_0$. It follows that system (2.5) generates a semiflow $\Sigma(t) : \mathbb{Y} \to \mathbb{Y}$. Moreover, we let $M_0 = \{(0, 0, 0, 0, 0, 0, 0)\}$ and $M_1 = A_0 \times \{(0, 0, 0)\}$, where $A_0 \subset \text{Int}(\mathbb{R}_+^4)$ is a global attractor of the semiflow generated by system (3.2) (see Remark 3.1).

Define $G : A_0 \to \mathbb{R}^{3\times 3}$ by

$$G(\phi) = \begin{pmatrix} \alpha[\beta(1-\varepsilon)-1]\phi_1 - D & \frac{\varepsilon}{2}\alpha\beta(\phi_1+\phi_2) & 0 \\ \alpha\beta\varepsilon\phi_1 & \alpha[\beta(1-\varepsilon)-1](\phi_1+\phi_2)-D & \alpha\beta\varepsilon(\phi_1+\phi_2+\phi_3) \\ 0 & \frac{\varepsilon}{2}\alpha\beta(\phi_1+\phi_2) & \alpha[\beta(1-\varepsilon)-1](\phi_1+\phi_2+\phi_3)-D \end{pmatrix}$$

for all $\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in A_0$. For any $\phi,\ \tilde{\phi} \in A_0$, we define $G(\phi) \geq G(\tilde{\phi})$ if each element of $G(\phi) - G(\tilde{\phi})$ is non-negative. Let

$$\underline{s}(G) = \min_{\phi \in A_0} s(G(\phi)),$$

where $s(G(\phi))$ is the stability modulus of $G(\phi)$ for any $\phi \in A_0$. Then the following results hold for the limiting system (2.5).

Lemma 3.6. *Let* $0 < \varepsilon < 1$ *and* $\beta(1-\varepsilon) - 1 > 0$*. If* $R_0^h > 1$ *and* $\underline{s}(G) > 0$*, then* M_1 *is a uniform weak repeller in the sense that there exists* $\delta_0 > 0$ *such that*

$$\limsup_{t\to\infty} dist(\Sigma(t)\mathbf{v}^0 - M_1) \geq \delta_0, \ \textit{for all}\ \mathbf{v}^0 := (\mathbf{B}^0, \mathbf{P}^0) \in \mathbb{Y}_0. \tag{3.7}$$

Lemma 3.7. *Let* $0 < \varepsilon \leq 1$*. Assume* $R_0^h > 1$*, and then* M_0 *is a uniform weak repeller in the sense that there exists* $\delta_1 > 0$ *such that*

$$\limsup_{t\to\infty} \|\Sigma(t)\mathbf{v}^0 - M_0\| \geq \delta_1, \ \textit{for all}\ \mathbf{v}^0 := (\mathbf{B}^0, \mathbf{P}^0) \in \mathbb{Y}_0. \tag{3.8}$$

Lemma 3.8. *Assume that* $(B_1(t), B_2(t), B_3(t), B_4(t), P_1(t), P_2(t), P_3(t))$ *is the solution of system* (2.5) *with initial values in* $\mathbb{Y}$*. Let* $0 < \varepsilon < 1$ *and* $\beta(1-\varepsilon) - 1 > 0$*. If* $R_0^h > 1$ *and* $\underline{s}(G) > 0$*, then there exists a constant* $\zeta > 0$ *such that any solution of system* (2.5) *with initial values in* $\mathbb{Y}_0$ *satisfies*

$$\liminf_{t\to\infty} B_i(t) \geq \zeta, \ \liminf_{t\to\infty} P_j(t) \geq \zeta, \ i = 1,2,3,4, \ j = 1,2,3.$$

Furthermore, system (2.5) *admits at least one (componentwise) positive solution.*

Let

$$\mathbb{X}_0 = \left\{ (\phi_1, \phi_2, \phi_3, \phi_4, \phi_5, \phi_6, \phi_7, \phi_8) \in \mathbb{R}_+^8 |\ (\phi_2, \phi_3, \phi_4, \phi_5) \not\equiv \mathbf{0} \text{ and } (\phi_6, \phi_7, \phi_8) \not\equiv \mathbf{0} \right\}.$$

In light of Lemma 3.8, we now obtain the dynamical behavior of system (2.1) by the theory of chain transitive sets [37].

Theorem 3.9. *Assume that* $(S(t), B_1(t), B_2(t), B_3(t), B_4(t), P_1(t), P_2(t), P_3(t))$ *is the solution of system* (2.1) *with initial values in* $\mathbb{R}_+^8$*. Let* $0 < \varepsilon < 1$ *and* $\beta(1-\varepsilon) - 1 > 0$*. If* $R_0^h > 1$ *and* $\underline{s}(G) > 0$*, then there exists a constant* $\zeta > 0$ *such that any solution of system* (2.1) *with initial values in* $\mathbb{X}_0$ *satisfies*

$$\liminf_{t\to\infty} B_i(t) \geq \zeta, \ \liminf_{t\to\infty} P_j(t) \geq \zeta, i = 1,2,3,4, j = 1,2,3.$$

Furthermore, system (2.1) *admits at least one (componentwise) positive solution.*

From simple calculations, we can obtain the following properties of R_0^h and $\underline{s}(G)$.

Proposition 1. *The following conclusions hold:*

(i) $R_0^h \to 0$ *as* $D \to \infty$;
(ii) $R_0^h \to g_1(S_0)/D$ *as* $\varepsilon \to 0$;
(iii) $\underline{s}(G) \to -D$ *as* $\alpha \to 0$;
(iv) $\underline{s}(G) \to \min_{\phi=(\phi_1,\phi_2,\phi_3,\phi_4)\in A_0}\{-\alpha\phi_1 - D\}$ *as* $\beta \to 0$;
(v) $\underline{s}(G) \to \min_{\phi=(\phi_1,\phi_2,\phi_3,\phi_4)\in A_0}\{\alpha(\beta-1)(\phi_1+\phi_2+\phi_3) - D\}$ *as* $\varepsilon \to 0$.

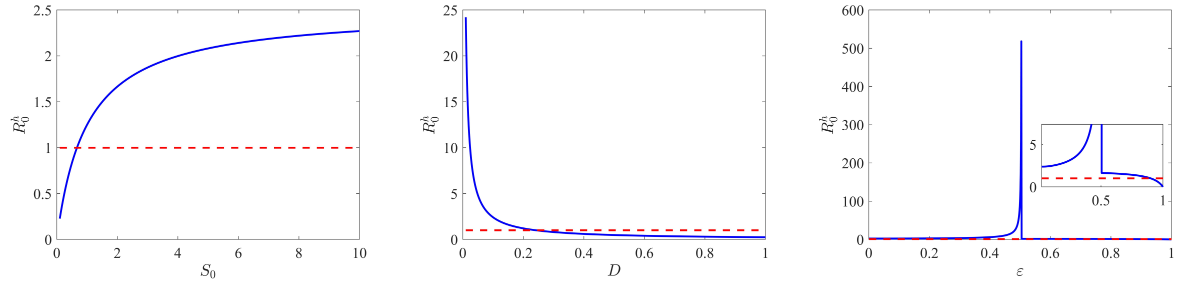
Remark 3.2. *The above proposition shows the asymptotic behavior of* R_0^h *and* $\underline{s}(G)$*, while the monotonicity of* R_0^h *and* $\underline{s}(G)$ *with respect to the model parameters remains unclear. We will use numerical simulation to obtain some intuitive results (see Figures 1 and 2).*

4. Numerical simulation and discussion

In this section, we investigate the effects of ecological factors on eco-evolutionary dynamics through numerical simulation under three different strengths of resistance-growth trade-off, including without trade-off ($a_N = 0.25$), weak trade-off ($a_N = 0.15$), and strong trade-off ($a_N = 0.05$) [6]. Letting $\widetilde{t} = Dt, \widetilde{S} = \frac{S}{S_0}, \widetilde{B}_i = \frac{\gamma B_i}{S_0}, \widetilde{P}_j = \frac{\gamma P_j}{S_0}$ in system (2.1), then the dimensionless system is numerically integrated by employing the ode45 solver with a relative error tolerance of 1×10^{-5}, an absolute error tolerance of 1×10^{-8}, a maximum step size of 0.1, and a total integration time of 300,000 seconds. Unless otherwise stated, the initial value is $(0.9, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1)$. The parameter values are derived from Table 1.

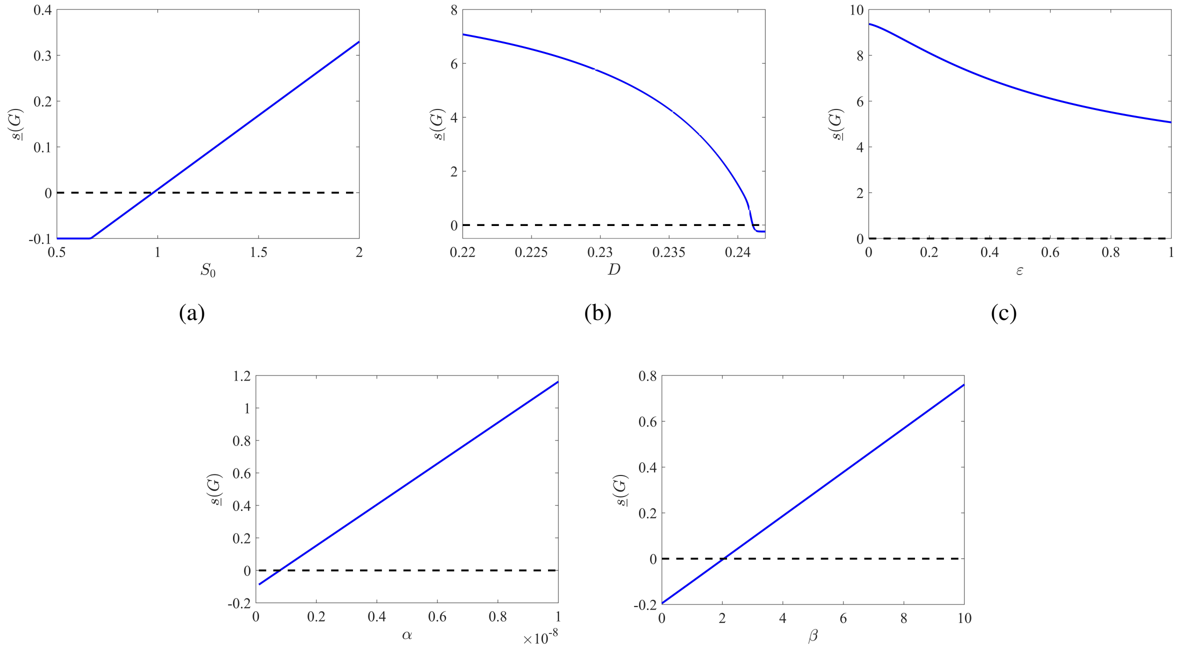
4.1. Threshold dynamics

In light of the complexity of R_0^h and $\underline{s}(G)$, their trends with respect to the ecological parameters are obtained through numerical simulation. Here $a_N = 0.15$ (experimentally observed weak trade-off [6]) and the remaining parameter values are derived from Table 1. It can be seen from Figure 1 that low S_0 is unfavorable for algal growth, while low D is conducive to algal growth (Theorem 3.5). Additionally, Figure 2 reveals that high S_0, α, and β or low D facilitate viral propagation (Theorem 3.9), that is, high resource input, adsorption rate, and burst size are beneficial for viral propagation while low dilute rate favors host-virus coexistence.



(a) (b) (c)

Figure 1. Dependence of R_0^h on some model parameters. Here $a_N = 0.15$ and the remaining parameter values are derived from Table 1. (a) R_0^h vs. S_0; (b) R_0^h vs. D; (c) R_0^h vs. ε. The red dashed line represents $R_0^h = 1$.



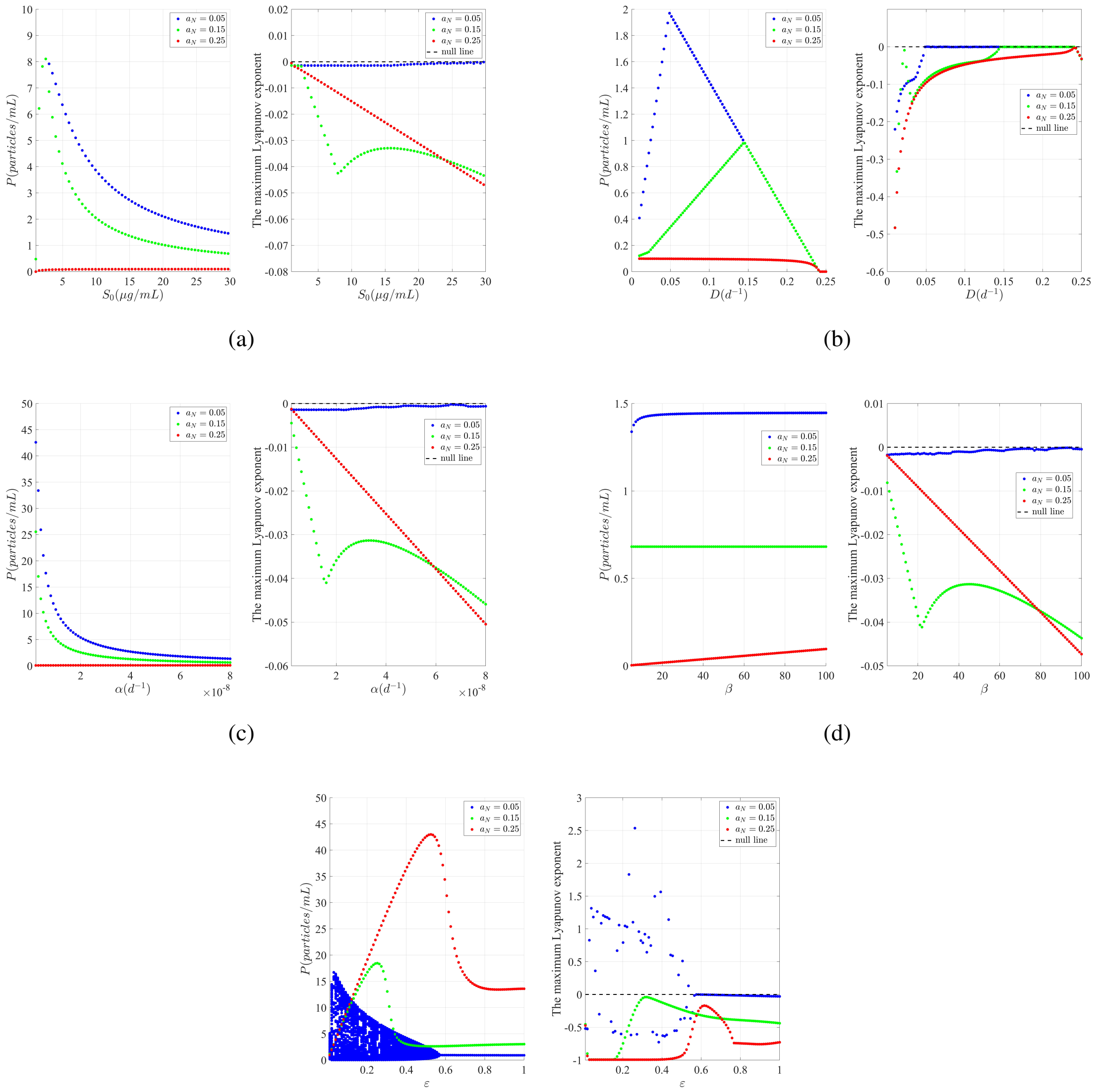
(a) (b) (c)

(d) (e)

Figure 2. Dependence of $\underline{s}(G)$ on some model parameters. Here $a_N = 0.15$ and the remaining parameter values are derived from Table 1. (a) S_0; (b) D; (c) ε; (d) α; (e) β. The black dashed line represents $\underline{s}(G) = 0$.

4.2. *Resistance-growth trade-off driven periodic oscillation*

Based on Theorem 3.9, a further investigation is conducted on the existence of periodic solutions in system (2.1). Figure 3 displays the bifurcation diagrams and corresponding maximum Lyapunov exponents for varying parameters within the parameter space where positive solutions exist. As shown in Figure 3(a–d), periodic solutions may not be induced by changes in resource input, dilution rate, adsorption rate, and burst size of virus. However, Figure 3(e) reveals that a strong trade-off may trigger periodic dynamics when the viral mutation rate changes. Take $\varepsilon = 0.2727$, where the solution of system (2.1) converges to a stable positive equilibrium for $a_N = 0.15$ (weak trade-off) (Figure 4(a)), while algal and viral populations oscillate periodically for $a_N = 0.05$ (strong trade-off) (Figure 4(b)). It indicates that strong resistance-growth trade-off may promote the emergence of periodic oscillation in a coevolving host-virus system. Although the positive periodic solution represents a crucial dynamical behavior, the theoretical proof of the existence of a Hopf bifurcation and positive periodic solution remains challenging due to the fact that the expression of a positive equilibrium of a high-dimensional host-virus system remains unclear.



(a) (b)

(c) (d)

(e)

Figure 3. Bifurcation diagrams and corresponding maximum Lyapunov exponents for varying parameters under three different strengths of resistance-growth trade-off. (a) S_0; (b) D; (c) α; (d) β; (e) ε. The three viral types are P_1, P_2, and P_3, and $P = P_1 + P_2 + P_3$.

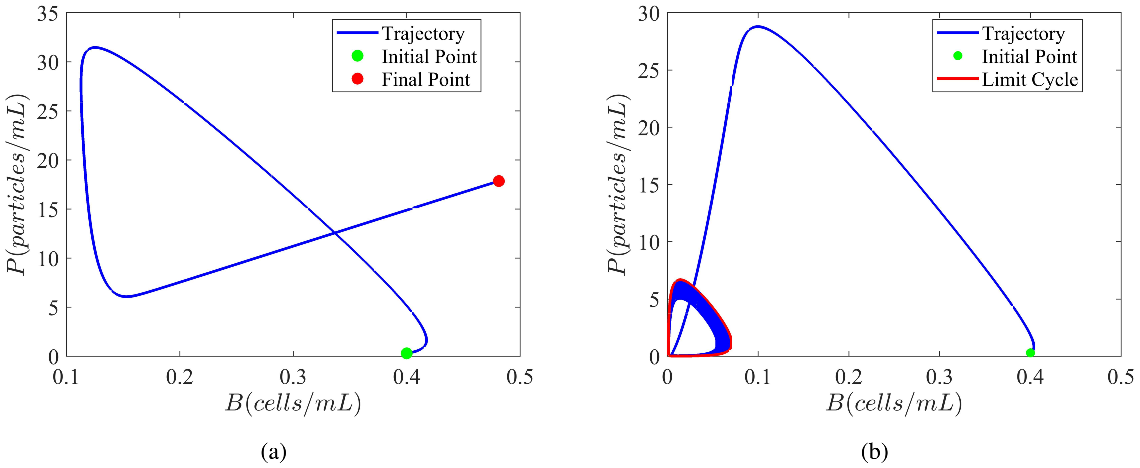


Figure 4. Phase diagram of total algal and viral biomass under weak/strong trade-off for $\varepsilon = 0.2727$. (a) $a_N = 0.15$; (b) $a_N = 0.05$. The four algal types are B_1, B_2, B_3, and B_4. The three viral types are P_1, P_2, and P_3. Moreover, $B = B_1 + B_2 + B_3 + B_4$ and $P = P_1 + P_2 + P_3$.

4.3. *Effects of ecological factors under distinct resistance-growth trade-offs*

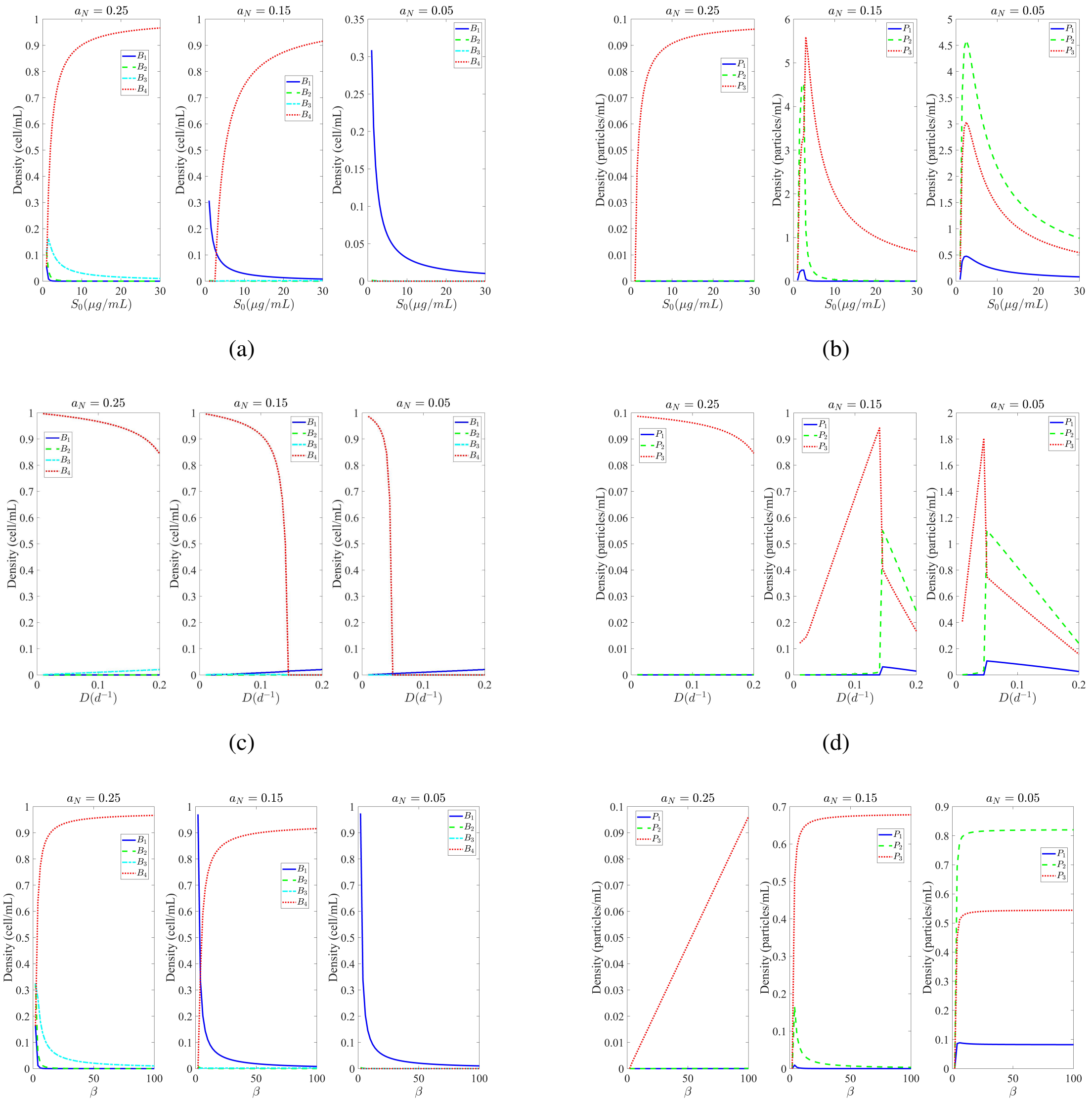
In this subsection, we mainly focus on the impacts of ecological factors on population density and species diversity under distinct resistance-growth trade-offs. In order to ensure the host-virus coexistence for system (2.1), the range of ecological factors satisfies the conditions of Theorem 3.9. We measure species diversity using Hill–Simpson diversity [39, 40], which is equivalent to the inverse of the traditional Simpson index [41]:

$$H(B) = 1/\sum_{i=1}^{4}\left(\frac{B_i}{B}\right)^2, \quad H(P) = 1/\sum_{j=1}^{3}\left(\frac{P_j}{P}\right)^2,$$

where $H(B)$ and $H(P)$ represent the diversity index of algal and viral species, respectively, B_i and P_j are the biomass of algal type i and viral type j, respectively, B and P are the total algal and viral biomass, respectively, with $B = B_1 + B_2 + B_3 + B_4$ and $P = P_1 + P_2 + P_3$. Moreover, when the biomass of algal or viral type varies during a cycle, the average within a single cycle is taken as the average biomass of that algal or viral type.

4.3.1. Switching of dominant species of algae and viruses

Generally, resistance-growth trade-off may reshape the dominant species of algae and viruses. Specifically, as the strength of resistance-growth trade-off increases, the dominant algal species shifts from B_4-type to B_1-type (Figure 5(a),(c),(e)), while the dominant viral species shifts from P_3-type to P_2-type (Figure 5(b),(d),(f)). This implies that strong resistance-growth trade-off ($a_N = 0.05$) may reduce the growth rates of algal types B_2-B_4, allowing B_1-type algae to dominate, which subsequently drives viral type P_2 to gain advantage. Additionally, under both weak and strong trade-off conditions, the dilution rate also alters the dominance patterns of algae and viruses (Figure 5(c),(d)). Specifically, the dominant algal species shifts from B_4-type to B_1-type with increasing dilution rate (Figure 5(c)), as B_1-type algae exhibits growth advantages under weak and strong resistance-growth trade-offs. Meanwhile, the dominant viral species shifts from P_3-type to P_2-type with increasing dilution rate (Figure 5(d)). Consequently, the synergistic effects of resistance-growth trade-off and ecological factors may drive the switching of dominant species in both algal and viral communities.



(a) (b)

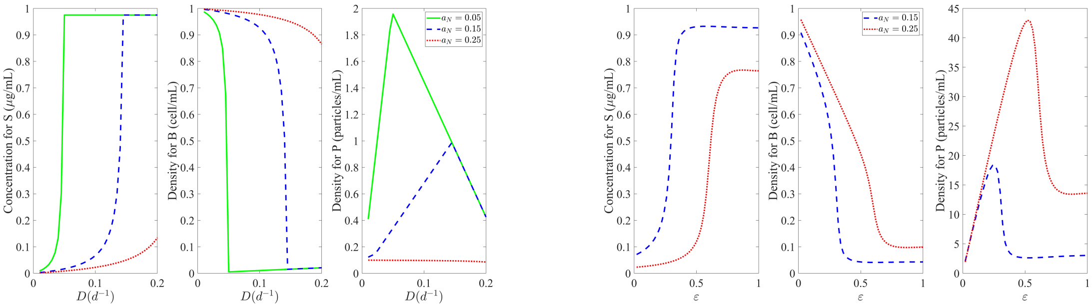
(c) (d)

(e) (f)

Figure 5. The relationship between the densities of four algal types and three viral types and ecological factors under distinct resistance-growth trade-offs ($a_N = 0.25$, $a_N = 0.15$, and $a_N = 0.05$). (a),(b) S_0; (c),(d) D; (e),(f) β. In each pair, the left column represents algal density while the right column shows viral density.

4.3.2. Changes in the total biomass of algae and viruses

We discover that resistance-growth trade-off and ecological factors may collectively drive changes in the total biomass of algae and viruses. Specifically, increasing resistance-growth trade-off reduces the total biomass of algae while increasing the total biomass of viruses (Figure 6(a)). This implies that strong resistance-growth trade-off ($a_N = 0.05$) may suppress algal growth by reducing their growth rates, thereby indirectly stimulating viral proliferation. Furthermore, under both weak and strong trade-offs, a specific range of dilution rates may trigger a hydra effect [42,43] of viruses (Figure 6(a)), where their total biomass increases with a rising dilution rate [44–46]. Additionally, a unimodal pattern is observed in the viral biomass while a monotonic pattern is seen in the algal biomass as a function of the mutation rate (Figure 6(b)), indicating that a high mutation rate may inhibit the growth of both algae and viruses, but a low mutation rate may counterintuitively promote viral proliferation.



(a)

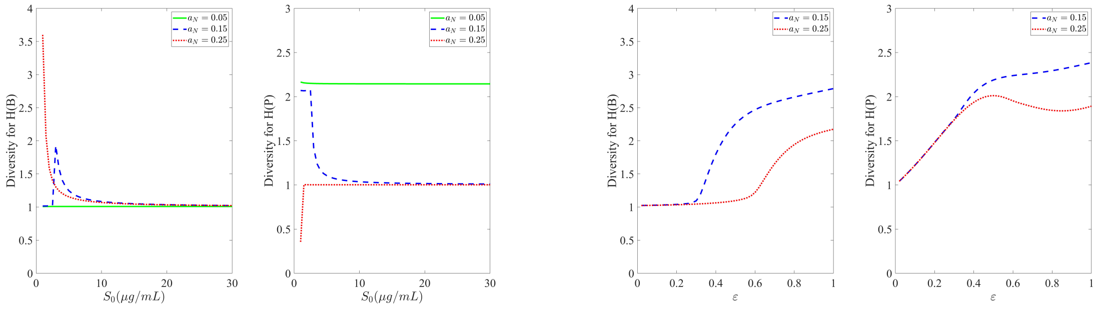
(b)

Figure 6. The relationship between the total biomass of algae and viruses and ecological factors under distinct resistance-growth trade-offs. (a) D; (b) ε. S is the resource concentration, B and P are the total biomass of algae and viruses, respectively, where $B = B_1 + B_2 + B_3 + B_4$ and $P = P_1 + P_2 + P_3$. The green solid, blue dashed, and red dotted curves represent $a_N = 0.05$ (strong trade-off), $a_N = 0.15$ (weak trade-off), and $a_N = 0.25$ (without trade-off), respectively.

4.3.3. Changes in species diversity of algae and viruses

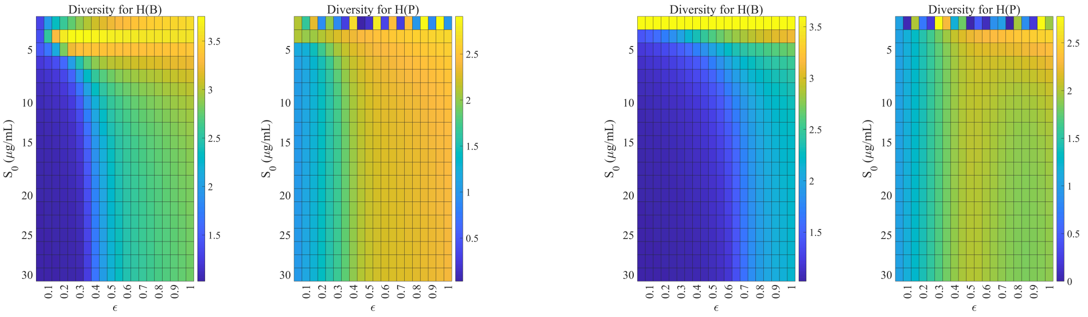
We detect that resistance-growth trade-off and ecological factors may jointly drive changes in species diversity of algae and viruses. Specifically, under relationships where species diversity depends on resource input, increasing resistance-growth trade-off reduces algal diversity while enhancing viral diversity (Figure 7(a)). This implies that strong resistance-growth trade-off ($a_N = 0.05$) may diminish algal species' richness by lowering their growth rates, thereby indirectly increasing viral species' richness. However, enhanced resistance-growth trade-off leads to increases in both algal and viral diversity under a high mutation rate (Figure 7(b)), suggesting that the combination of resistance-growth trade-off and a high mutation rate may promote species richness of both algae and viruses. Additionally, resistance-growth trade-off may alter diversity patterns depending on ecological factors, including monotonic and unimodal patterns [5]. For example, in terms of resource input, algal diversity exhibits a monotonic decline without trade-off ($a_N = 0.25$), whereas it first rapidly increases and then sharply decreases under weak resistance-growth trade-off

($a_N = 0.15$) (Figure 7(a)). In light of the mutation rate, viral diversity follows a unimodal pattern (initial increase followed by decrease) without trade-off but shifts to a monotonic increase under weak resistance-growth trade-offs (Figure 7(b)). Moreover, Figure 8 illustrates algal and viral diversities in the $\varepsilon - S_0$ plane under weak and without trade-offs. A notable feature is that weak resistance-growth trade-off ($a_N = 0.15$) significantly elevates algal and viral diversity relative to the without-trade-off group ($a_N = 0.25$) (Figure 8(a) vs. Figure 8(b)). These findings collectively underscore that both mutation-driven adaptation and trait allocation trade-offs may synergistically regulate biodiversity in antagonistic coevolution.



(a) (b)

Figure 7. The relationship between the diversities of algae and viruses and ecological factors under distinct resistance-growth trade-offs. (a) S_0; (b) ε. $H(B)$ and $H(P)$ represent algal and viral diversities, respectively. The green solid, blue dashed, and red dotted curves represent $a_N = 0.05$ (strong trade-off), $a_N = 0.15$ (weak trade-off), and $a_N = 0.25$ (without trade-off), respectively.



(a) (b)

Figure 8. Algal and viral diversities in the $\varepsilon - S_0$ plane under weak and without trade-off. (a) weak trade-off $a_N = 0.15$; (b) without trade-off $a_N = 0.25$. $H(B)$ and $H(P)$ represent algal and viral diversities, respectively.

5. Conclusions

This paper investigates the effects of ecological factors on the dynamics of a coevolving host-virus system formulated by Frickel et al. [6]. Although they demonstrated how arms race dynamics (ARDs) switch to trade-off driven dynamics (TDDs) and how the costly resistance of the host stabilized host-virus dynamics, the effects of ecological factors on eco-evolutionary dynamics are unexplored beyond resistance-growth trade-off. The main objective of this paper is to fill this gap and highlight the role of ecological factors. Compared with the existing result of Frickel et al. [6], there are two novel points. The first is to provide the basic reproduction number for the host system and the sufficient conditions for the coexistence of host and virus (Theorem 3.9). The second is to elucidate the joint influences of resistance-growth trade-off and ecological factors on species diversity through numerical simulation.

Based on theoretical and numerical analysis, we explored the relationship between species diversity and ecological factors, including viral infection-related parameter α, evolution-related parameter ε, and resource-related factors S_0 and D. Our findings indicate that the synergistic effects of resistance-growth trade-off and ecological factors may drive the switching of dominant species and the changes of total biomass and diversity in both algal and viral communities. Specially, resistance-growth trade-off may alter diversity patterns depending on ecological factors, including monotonic and unimodal patterns, which is consistent with the findings in [5].

Our other significant contribution lies in the discovery of the hydra effect, where viruses may exhibit this phenomenon within specific ranges of the dilution rate (Figure 6(a)). However, establishing theoretical conditions for the occurrence of the hydra effect in high-dimensional ordinary differential equation (ODE) systems remains challenging. Although strong resistance-growth trade-off may drive transitions between stable equilibria and the periodic solution when the viral mutation rate changes (Figure 3(e) and Figure 4(b)), the existence and stability of a periodic solution in this coevolving host-virus system present intriguing and scientifically meaningful questions. While the current model incorporates only a single resistance-growth trade-off, it is imperative to simultaneously consider the impacts of two well-established trade-offs proposed by Forde et al. [5]. This constitutes a critical direction for our subsequent research efforts.

Appendix

Appendix A: Proofs of Theorems 3.1 and 3.2

Proof of Theorem 3.1. For any initial value $\phi \in \mathbb{Y}$, we can easily verify that the nonlinear term in system (2.5) satisfies local Lipschitz continuity. By applying Theorems 2.2.1 and 2.2.3 from [47], it follows that there exists a constant $t_\phi > 0$ such that system (2.5) has a unique solution on the maximal interval of existence $[0, t_\phi)$. Furthermore, it is easy to show that $\mathbb{Y}$ is positively invariant for system (2.5). In view of (2.2)–(2.6) and the positivity of solutions, it is easy to show that the solutions of system (2.5) are ultimately bounded. This completes the proof.

Proof of Theorem 3.2. According to Theorem 3.1, we know that $B_i(t) \geq 0$, $P_j(t) \geq 0$ for all $i \in \{1,2,3,4,\}$, $j \in \{1,2,3\}$ on $[0,\infty)$. If there is a $t^0 \geq 0$ such that $B_1(t^0) > 0$, then it follows from Theorem 3.1 and the first equation of system (2.5) that

$$\begin{aligned}
\frac{dB_1}{dt} &= (1-\varepsilon)g_1(\tilde{S}_0)B_1 + \frac{\varepsilon}{2}g_2(\tilde{S}_0)B_2 - \alpha B_1(P_1+P_2+P_3) - DB_1 \\
&\geq (1-\varepsilon)g_1(\tilde{S}_0)B_1 - \alpha B_1(P_1+P_2+P_3) - DB_1 \\
&= B_1[(1-\varepsilon)g_1(\tilde{S}_0) - \alpha(P_1+P_2+P_3) - D].
\end{aligned}$$

Thus, for $t > t^0$, we have

$$B_1(t) \geq B_1(t^0)\exp\left[\int_{t^0}^{t} \big((1-\varepsilon)g_1(\tilde{S}_0(s)) - \alpha(P_1(s)+P_2(s)+P_3(s)) - D\big)\,ds\right] > 0.$$

From the second equation of system (2.5), we have

$$\begin{aligned}\frac{dB_2}{dt} &= \varepsilon g_1(\tilde{S}_0)B_1 + (1-\varepsilon)g_2(\tilde{S}_0)B_2 + \frac{\varepsilon}{2}g_3(\tilde{S}_0)B_3 - \alpha B_2(P_2+P_3) - DB_2 \\ &\geq \varepsilon g_1(\tilde{S}_0)B_1 - [\alpha(P_2+P_3)+D]B_2.\end{aligned}$$

Let $z = S_0/\gamma - [\phi_1+\phi_2+\phi_3+\phi_4] - \frac{1}{\beta-1}[\phi_5+\phi_6+\phi_7]$, and then we have

$$\frac{dz}{dt} = S_0/\gamma - z - [g_1(\gamma z)\phi_1 + g_2(\gamma z)\phi_2 + g_3(\gamma z)\phi_3 + g_4(\gamma z)\phi_4]. \tag{A.1}$$

From (A.1), we have

$$\begin{aligned}\frac{dz}{dt} &\geq S_0/\gamma - z - [a_1\phi_1 + a_2\phi_2 + a_3\phi_3 + a_4\phi_4] \\ &\geq S_0/\gamma - z - a_1[\phi_1+\phi_2+\phi_3+\phi_4] \\ &\geq (1-a_1)S_0/\gamma - z,\end{aligned}$$

and then we obtain

$$z(t) \geq z(t^0)e^{-(t-t^0)} + (1-e^{-(t-t^0)})(1-a_1)S_0/\gamma > 0,\ \forall t > t^0.$$

Thus, $\tilde{S}_0 = \gamma z(t) > 0$ for all $t > t^0$. Hence, for $t > t^0$,

$$\begin{aligned}B_2(t) \geq{}& B_2(t^0)\exp\left(-\int_{t^0}^{t}(\alpha(P_2(\tau)+P_3(\tau))+D)\,d\tau\right) \\ &+ \left[\int_{t^0}^{t}\varepsilon g_1(\tilde{S}_0(s))B_1(s)\exp\left(\int_{t}^{s}(\alpha(P_2(\tau)+P_3(\tau))+D)\,d\tau\right)ds\right] > 0.\end{aligned}$$

By using similar arguments, we have $B_3(t) > 0$ and $B_4(t) > 0$ for $t > t^0$. Then $B_i(t) > 0$ for all $t > t^0$ and $i = 1,2,3,4$. Other cases can be proved similarly.

Furthermore, if $P_1(t^0) > 0$, according to Theorem 3.1 and the fifth equation of system (2.5), we have

$$\begin{aligned}\frac{dP_1}{dt} &= \alpha\beta[(1-\varepsilon)B_1P_1 + \frac{\varepsilon}{2}(B_1+B_2)P_2] - \alpha B_1P_1 - DP_1 \\ &\geq \alpha\beta(1-\varepsilon)B_1P_1 - \alpha B_1P_1 - DP_1 \\ &= P_1[\alpha[\beta(1-\varepsilon)-1]B_1 - D].\end{aligned}$$

Then we obtain

$$P_1(t) \geq P_1(t^0)\exp\left[\int_{t^0}^{t}(\alpha[\beta(1-\varepsilon)-1]B_1(s) - D)\,ds\right] > 0 \text{ for } t > t^0.$$

By using similar arguments, we have $P_2(t) > 0$ and $P_3(t) > 0$ for $t > t^0$. Then $P_j(t) > 0$ for all $t > t^0$ and $j = 1,2,3$. Other cases can be proved similarly. This completes the proof.

Appendix B: Proofs of Lemma 3.4 and Theorem 3.5

Proof of Lemma 3.4. (i) In the case where $R_0^h < 1$, we have

$$\begin{aligned}\frac{dB_1}{dt} &= (1-\varepsilon)g_1(\bar{S}_0)B_1 + \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 - DB_1\\ &\le [(1-\varepsilon)g_1(S_0) - D]B_1 + \frac{\varepsilon}{2}g_2(S_0)B_2,\\ \frac{dB_2}{dt} &= \varepsilon g_1(\bar{S}_0)B_1 + (1-\varepsilon)g_2(\bar{S}_0)B_2 + \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 - DB_2\\ &\le \varepsilon g_1(S_0)B_1 + [(1-\varepsilon)g_2(S_0) - D]B_2 + \frac{\varepsilon}{2}g_3(S_0)B_3,\\ \frac{dB_3}{dt} &= \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 + (1-\varepsilon)g_3(\bar{S}_0)B_3 + \varepsilon g_4(\bar{S}_0)B_4 - DB_3\\ &\le \frac{\varepsilon}{2}g_2(S_0)B_2 + [(1-\varepsilon)g_3(S_0) - D]B_3 + \varepsilon g_4(S_0)B_4,\\ \frac{dB_4}{dt} &= \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 + (1-\varepsilon)g_4(\bar{S}_0)B_4 - DB_4\\ &\le \frac{\varepsilon}{2}g_3(S_0)B_3 + [(1-\varepsilon)g_4(S_0) - D]B_4.\end{aligned}$$

Note that the following system

$$\begin{cases}\frac{dB_1}{dt} = (1-\varepsilon)g_1(S_0)B_1 + \frac{\varepsilon}{2}g_2(S_0)B_2 - DB_1,\\ \frac{dB_2}{dt} = \varepsilon g_1(S_0)B_1 + (1-\varepsilon)g_2(S_0)B_2 + \frac{\varepsilon}{2}g_3(S_0)B_3 - DB_2,\\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(S_0)B_2 + (1-\varepsilon)g_3(S_0)B_3 + \varepsilon g_4(S_0)B_4 - DB_3,\\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(S_0)B_3 + (1-\varepsilon)g_4(S_0)B_4 - DB_4\end{cases}$$

has a solution $\theta_0 e^{s(J^0)t}\varphi^0$, where φ^0 is a positive eigenvector of $s(J^0)$ and θ_0 is a positive constant. We choose θ_0 such that θ_0 satisfies $(B_1(0), B_2(0), B_3(0), B_4(0))^\top \le \theta_0\varphi^0$, where $\top$ represents the transpose of a vector. It then follows from the comparison principle that

$$(B_1(t), B_2(t), B_3(t), B_4(t))^\top \le \theta_0 e^{s(J^0)t}\varphi^0,\ t \ge 0.$$

Hence, $\lim\limits_{t\to\infty}(B_1(t), B_2(t), B_3(t), B_4(t)) = (0,0,0,0)$ based on $s(J^0) < 0$.

(ii) In the case where $R_0^h > 1$, we can prove that the solution semiflow $Q(t)$ of system (3.2) admits a global attractor in Ω by Theorem 2.9 in [48]. Next, we prove that $Q(t)$ is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$. To this end, we first prove the following claim.

Claim. E_0 is a uniform weak repeller for Ω_0 in the sense that there exists $\delta > 0$ such that $\limsup_{t\to\infty}\|Q(t)\varphi - E_0\| \ge \delta$ for any $\varphi \in \Omega_0$.

Suppose, by contradiction, that $\limsup_{t\to\infty}\|Q(t)\varphi - E_0\| < \delta$ for some $\varphi \in \Omega_0$. Then there exists a sufficiently large $T_1 > 0$ such that for all $t \ge T_1$, we have

$$B_i(t) < \delta\ (i = 1,2,3,4).$$

Furthermore, we choose a $\delta > 0$ such that

$$\bar{S}_0 = S_0 - \gamma[B_1 + B_2 + B_3 + B_4] > S_0 - 4\gamma\delta > 0.$$

Let $\check{S} := S_0 - 4\gamma\delta$, and then we obtain

$$\begin{cases} \frac{dB_1}{dt} = (1-\varepsilon)g_1(\bar{S}_0)B_1 + \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 - DB_1 \\ \qquad \geq [(1-\varepsilon)g_1(\check{S}) - D]B_1 + \frac{\varepsilon}{2}g_2(\check{S})B_2,\ t \geq T_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\bar{S}_0)B_1 + (1-\varepsilon)g_2(\bar{S}_0)B_2 + \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 - DB_2 \\ \qquad \geq \varepsilon g_1(\check{S})B_1 + [(1-\varepsilon)g_2(\check{S}) - D]B_2 + \frac{\varepsilon}{2}g_3(\check{S})B_3,\ t \geq T_1, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\bar{S}_0)B_2 + (1-\varepsilon)g_3(\bar{S}_0)B_3 + \varepsilon g_4(\bar{S}_0)B_4 - DB_3 \\ \qquad \geq \frac{\varepsilon}{2}g_2(\check{S})B_2 + [(1-\varepsilon)g_3(\check{S}) - D]B_3 + \varepsilon g_4(\check{S})B_4,\ t \geq T_1, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\bar{S}_0)B_3 + (1-\varepsilon)g_4(\bar{S}_0)B_4 - DB_4 \\ \qquad \geq \frac{\varepsilon}{2}g_3(\check{S})B_3 + [(1-\varepsilon)g_4(\check{S}) - D]B_4,\ t \geq T_1. \end{cases}$$

Let

$$\check{J} = \begin{pmatrix} (1-\varepsilon)g_1(\check{S}) - D & \frac{\varepsilon}{2}g_2(\check{S}) & 0 & 0 \\ \varepsilon g_1(\check{S}) & (1-\varepsilon)g_2(\check{S}) - D & \frac{\varepsilon}{2}g_3(\check{S}) & 0 \\ 0 & \frac{\varepsilon}{2}g_2(\check{S}) & (1-\varepsilon)g_3(\check{S}) - D & \varepsilon g_4(\check{S}) \\ 0 & 0 & \frac{\varepsilon}{2}g_3(\check{S}) & (1-\varepsilon)g_4(\check{S}) - D \end{pmatrix}.$$

It is easy to see that $\check{J}$ is irreducible and has non-negative off-diagonal elements when $0 < \varepsilon \leq 1$, and it follows from Theorem A.5 of [34] that $s(\check{J})$ is a simple eigenvalue of $\check{J}$ with a positive eigenvector $\check{\varphi}$. Consequently, the following system

$$\begin{cases} \frac{dB_1}{dt} = [(1-\varepsilon)g_1(\check{S}) - D]B_1 + \frac{\varepsilon}{2}g_2(\check{S})B_2,\ t \geq T_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\check{S})B_1 + [(1-\varepsilon)g_2(\check{S}) - D]B_2 + \frac{\varepsilon}{2}g_3(\check{S})B_3,\ t \geq T_1, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\check{S})B_2 + [(1-\varepsilon)g_3(\check{S}) - D]B_3 + \varepsilon g_4(\check{S})B_4,\ t \geq T_1, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\check{S})B_3 + [(1-\varepsilon)g_4(\check{S}) - D]B_4,\ t \geq T_1 \end{cases}$$

admits a solution $\theta_1 e^{s(\check{J})(t-T_1)}\check{\varphi}$ for all $t \geq T_1$, where θ_1 is a positive constant. We choose θ_1 such that θ_1 satisfies

$$(B_1(T_1), B_2(T_1), B_3(T_1), B_4(T_1))^\top \geq \theta_1\check{\varphi}.$$

By the comparison principle, we know that

$$(B_1(t), B_2(t), B_3(t), B_4(t))^\top \geq \theta_1 e^{s(\check{J})(t-T_1)}\check{\varphi},\ t \geq T_1.$$

If $R_0^h > 1$ (i.e., $s(J^0) > 0$), then $s(\check{J}) > 0$ for sufficiently small $\delta > 0$. As a result, we have

$$\lim_{t\to\infty} B_i(t) = \infty,\ i = 1,2,3,4,$$

which contradicts the boundedness of the solution of system (3.2).

The above claim implies that E_0 is an isolated invariant set for $Q(t)$ in Ω and $W^S(E_0) \cap \Omega_0 = \emptyset$, where $W^S(E_0)$ is the stable set of E_0 for $Q(t)$. Moreover, by the same arguments in Theorem 3.2, we can easily prove that $B_i(t,\varphi) > 0$, $i = 1,2,3,4$, for any $t > 0$ and $\varphi \in \Omega_0$, which implies that $Q(t)\Omega_0 \subseteq \Omega_0$ for all $t \geq 0$. Let $\tilde{M}_\partial := \{\varphi \in \partial\Omega_0 |\ Q(t)\varphi \in \partial\Omega_0,\ \forall t \geq 0\}$ and $\omega(\varphi)$ be the omega limit set of the forward orbit of $Q(t)$. For any $\psi \in \tilde{M}_\partial$, $Q(t)\psi \in \partial\Omega_0$. Thus, $B_1(t,\psi) = B_2(t,\psi) = B_3(t,\psi) = B_4(t,\psi) = 0$, $\forall t \geq 0$. Then we have $\lim_{t\to\infty}(B_1(t,\psi), B_2(t,\psi), B_3(t,\psi), B_4(t,\psi)) = (0,0,0,0)$, $\forall t \geq 0$. Consequently, $Q(t)\psi \to E_0$ as $t \to \infty$ for any $\psi \in \tilde{M}_\partial$. Thus, $\bigcup_{\psi\in\tilde{M}_\partial} \omega(\psi) = E_0$ and E_0 cannot form a cycle for $Q(t)$ in $\partial\Omega_0$. By the theory of uniform persistence (see Theorem 1.3.1 and Remark 1.3.1 of [37]), we have that $Q(t) : \Omega \to \Omega$ is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$.

Define a continuous function $p : \Omega \to \mathbb{R}_+$ by $p(\varphi) = \min_{i=1,2,3,4}\{\varphi_i\}$, $\forall \varphi \in \Omega$. It then follows from Theorem 1.3.2 in [37] that there exists a positive constant $\bar{\sigma}$ such that $\min\{p(\psi) : \psi \in \omega(\varphi)\} > \bar{\sigma}$, $\forall \varphi \in \Omega_0$. Hence,

$$\liminf_{t\to\infty} B_i(t) \geq \bar{\sigma},\ i = 1,2,3,4.$$

Furthermore, Theorem 1.3.6 and Remark 1.3.4 in [37] imply that $Q(t) : \Omega_0 \to \Omega_0$ has a global attractor. Therefore, it follows from Theorem 1.3.11 of [37] that system (3.2) has an equilibrium $E^* = (B_1^*, B_2^*, B_3^*, B_4^*) \in \Omega_0$.

Proof of Theorem 3.5. We consider the following equivalent system of (3.1):

$$\begin{cases} \frac{dW}{dt} = D(S_0 - W), \\ \frac{dB_1}{dt} = (1-\varepsilon)g_1(\bar{S})B_1 + \frac{\varepsilon}{2}g_2(\bar{S})B_2 - DB_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\bar{S})B_1 + (1-\varepsilon)g_2(\bar{S})B_2 + \frac{\varepsilon}{2}g_3(\bar{S})B_3 - DB_2, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\bar{S})B_2 + (1-\varepsilon)g_3(\bar{S})B_3 + \varepsilon g_4(\bar{S})B_4 - DB_3, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\bar{S})B_3 + (1-\varepsilon)g_4(\bar{S})B_4 - DB_4, \end{cases} \tag{B.1}$$

where $\bar{S} = W - \gamma[B_1 + B_2 + B_3 + B_4]$. Then we can similarly prove that system (B.1) has a unique non-negative solution and the solution is ultimately bounded as those in Theorem 3.1. Hence, system (B.1) generates a solution semiflow $\Phi(t)$ on $\Omega_* := \{(W, B_1, B_2, B_3, B_4) \in \mathbb{R}_+^5 : W \geq \gamma(B_1 + B_2 + B_3 + B_4)\}$. Let $\omega = \omega(W(0), B_1(0), B_2(0), B_3(0), B_4(0))$ be the omega limit set of the orbit $(W(t), B_1(t), B_2(t), B_3(t), B_4(t))$ through $(W(0), B_1(0), B_2(0), B_3(0), B_4(0))$ for the solution semiflow $\Phi(t)$ of system (B.1), that is,

$$\omega := \{(W, B_1, B_2, B_3, B_4) \in \Omega_* : \lim_{n\to\infty}(W(t_n), B_1(t_n), B_2(t_n), B_3(t_n), B_4(t_n)) = (W, B_1, B_2, B_3, B_4)\}.$$

Since $(W(t), B_1(t), B_2(t), B_3(t), B_4(t)) \in \Omega_*, \forall t \geq 0$, we have $W(t) \geq \gamma[B_1(t) + B_2(t) + B_3(t) + B_4(t)] \geq 0$, and hence, $\omega = \{S_0\} \times \omega_1$ with $\omega_1 \in \Omega$. Since $\Phi(t)(\omega) = \omega$ for all $t \geq 0$, we see that

$$\Phi(t)(S_0, \bar{B}_1, \bar{B}_2, \bar{B}_3, \bar{B}_4) = (S_0, Q(t)(\bar{B}_1, \bar{B}_2, \bar{B}_3, \bar{B}_4)),\ \forall (S_0, \bar{B}_1, \bar{B}_2, \bar{B}_3, \bar{B}_4) \in \omega,\ t \geq 0,$$

where $Q(t)$ is the solution semiflow of the limiting system (3.2) on Ω. It then follows that $Q(t)(\omega_1) = \omega_1$, $\forall t \geq 0$, and ω_1 is an internally chain transitive set for $Q(t)$ on Ω.

In the case where $R_0^h < 1$ (i.e., $s(J^0) < 0$), we see from Lemma 3.4 (i) that $W^S((0,0,0,0)) = \Omega$, and thus, $\omega_1 \cap W^S((0,0,0,0)) \neq \emptyset$. By Hirsch et al. ([49, Theorem 3.1 and Remak 4.6]), it follows that $\omega_1 = \{(0,0,0,0)\}$. Hence, we have $\omega = \{(S_0,0,0,0,0)\}$, and this implies

$$\lim_{t\to\infty}(W(t), B_1(t), B_2(t), B_3(t), B_4(t)) = (S_0,0,0,0,0).$$

Hence,

$$\lim_{t\to\infty} S(t) = (W(t) - \gamma[B_1(t)+B_2(t)+B_3(t)+B_4(t)]) = S_0.$$

In the case where $R_0^h > 1$ (i.e., $s(J^0) > 0$), we see from Lemma 3.4 (ii) and Remark 3.1 that $W^S(A_0) = \Omega_0$. Now we show that $\omega_1 \cap W^S(A_0) \neq \emptyset$. Assume, by contradiction, that $\omega_1 \cap W^S(A_0) = \emptyset$. Then $\omega_1 = \{(0,0,0,0)\}$, and hence, $\omega = \{S_0,0,0,0,0\}$. Thus we have

$$\lim_{t\to\infty}(W(t),B_1(t),B_2(t),B_3(t),B_4(t)) = (S_0,0,0,0,0).$$

Then there is a sufficiently large $T > 0$ and a small $\eta_0 > 0$ such that $W(t) > S_0 - \eta_0$ and $B_i(t) < \eta_0$ for all $t \geq T$ and $i = 1,2,3,4$, and hence, we have

$$\begin{cases} \frac{dB_1}{dt} \geq (1-\varepsilon)g_1(S_{\eta_0})B_1 + \frac{\varepsilon}{2}g_2(S_{\eta_0})B_2 - DB_1, \\ \frac{dB_2}{dt} \geq \varepsilon g_1(S_{\eta_0})B_1 + (1-\varepsilon)g_2(S_{\eta_0})B_2 + \frac{\varepsilon}{2}g_3(S_{\eta_0})B_3 - DB_2, \\ \frac{dB_3}{dt} \geq \frac{\varepsilon}{2}g_2(S_{\eta_0})B_2 + (1-\varepsilon)g_3(S_{\eta_0})B_3 + \varepsilon g_4(S_{\eta_0})B_4 - DB_3, \\ \frac{dB_4}{dt} \geq \frac{\varepsilon}{2}g_3(S_{\eta_0})B_3 + (1-\varepsilon)g_4(S_{\eta_0})B_4 - DB_4 \end{cases}$$

for all $t \geq T$, where $S_{\eta_0} = S_0 - \eta_0 - 4\gamma\eta_0$. Let the matrix

$$J^\eta = \begin{pmatrix} (1-\varepsilon)g_1(S_\eta) - D & \frac{\varepsilon}{2}g_2(S_\eta) & 0 & 0 \\ \varepsilon g_1(S_\eta) & (1-\varepsilon)g_2(S_\eta) - D & \frac{\varepsilon}{2}g_3(S_\eta) & 0 \\ 0 & \frac{\varepsilon}{2}g_2(S_\eta) & (1-\varepsilon)g_3(S_\eta) - D & \varepsilon g_4(S_\eta) \\ 0 & 0 & \frac{\varepsilon}{2}g_3(S_\eta) & (1-\varepsilon)g_4(S_\eta) - D \end{pmatrix}$$

for all $\eta > 0$, where $S_\eta = S_0 - \eta - 4\gamma\eta$. It then follows that $\lim_{\eta\to 0^+} s(J^\eta) = s(J^0) > 0$. Thus, we can fix such small $\eta_0 > 0$ such that $s(J^{\eta_0}) > 0$. By [34, Theorem 5.5.1 and Corollary 5.5.2], we know that the following system

$$\begin{cases} \frac{du_1}{dt} = (1-\varepsilon)g_1(S_{\eta_0})u_1 + \frac{\varepsilon}{2}g_2(S_{\eta_0})u_2 - Du_1, \\ \frac{du_2}{dt} = \varepsilon g_1(S_{\eta_0})u_1 + (1-\varepsilon)g_2(S_{\eta_0})u_2 + \frac{\varepsilon}{2}g_3(S_{\eta_0})u_3 - Du_2, \\ \frac{du_3}{dt} = \frac{\varepsilon}{2}g_2(S_{\eta_0})u_2 + (1-\varepsilon)g_3(S_{\eta_0})u_3 + \varepsilon g_4(S_{\eta_0})u_4 - Du_3, \\ \frac{du_4}{dt} = \frac{\varepsilon}{2}g_3(S_{\eta_0})u_3 + (1-\varepsilon)g_4(S_{\eta_0})u_4 - Du_4 \end{cases}$$

has a solution $u(t) = e^{s(J^{\eta_0})t}u_0$ for $u_0 \gg 0$. Thus, by the comparison principle, we obtain

$$\lim_{t\to\infty}(B_1(t),B_2(t),B_3(t),B_4(t)) = (+\infty,+\infty,+\infty,+\infty),$$

which is a contradiction. Thus, $\omega_1 \cap W^S(A_0) \neq \emptyset$. By Hirsch et al. ([49, Theorem 3.1 and Remak 4.6]), we then obtain that $\omega_1 = \{A_0\}$. Hence, $\omega = (S_0, A_0)$, and this implies system (B.1) has at least one positive equilibrium $(S_0, B_1^*, B_2^*, B_3^*, B_4^*)$, where $(B_1^*, B_2^*, B_3^*, B_4^*) \in A_0$, and thus,

$$\lim_{t\to\infty} S(t) = (W(t) - \gamma[B_1(t)+B_2(t)+B_3(t)+B_4(t)]) = S_0 - \gamma(B_1^* + B_2^* + B_3^* + B_4^*).$$

This completes the proof.

Appendix C: Proofs of Lemmas 3.6–3.8

Proof of Lemma 3.6. Our argument is motivated by Lemma 4.2 of [38]. Since $\underline{s}(G) > 0$, we choose a sufficiently small constant $\varepsilon_1 > 0$ such that $\underline{s}(G^{\varepsilon_1}) > 0$, where $G^{\varepsilon_1} := G(\phi) - \varepsilon_1 H$ for any $\phi \in A_0$, and

$$H = \begin{pmatrix} 1 & 1 & 0 \\ 1 & 1 & 1 \\ 0 & 1 & 1 \end{pmatrix}.$$

Suppose that (3.7) is not true. Then there exists $\mathbf{v}^0 = (\mathbf{B}^0, \mathbf{P}^0) \in \mathbb{Y}_0$ such that

$$\limsup_{t\to\infty} \operatorname{dist}(\Sigma(t)\mathbf{v}^0 - M_1) < \delta_0.$$

This implies that

$$\limsup_{t\to\infty} \operatorname{dist}((B_1(t), B_2(t), B_3(t), B_4(t)), A_0) < \delta_0, \tag{C.1}$$

and

$$\limsup_{t\to\infty} |P_j(t)| < \delta_0, \ j = 1,2,3. \tag{C.2}$$

From (C.1), we can choose a sufficiently large $t_0 > 0$ such that

$$\operatorname{dist}((B_1(t), B_2(t), B_3(t), B_4(t)), A_0) < \delta_0, \ \ t \geq t_0,$$

and then there exists $\phi^* \in A_0$ such that

$$-\varepsilon_1 H \leq G((B_1(t), B_2(t), B_3(t), B_4(t)) - G(\phi^*) \leq \varepsilon_1 H, \ \ t \geq t_0.$$

Hence,

$$G((B_1(t), B_2(t), B_3(t), B_4(t)) \geq G(\phi^*) - \varepsilon_1 H, \ \ t \geq t_0.$$

In view of $0 < \varepsilon < 1$ and $\beta(1-\varepsilon) - 1 > 0$, it then follows from the fifth, sixth, and seventh equations of (2.5) that

$$\frac{dP}{dt} = G((B_1(t), B_2(t), B_3(t), B_4(t))P \geq (G(\phi^*) - \varepsilon_1 H)P, \ \ t \geq t_0,$$

where $P = (P_1, P_2, P_3)^\top$. It is easy to see that $G(\phi^*) - \varepsilon_1 H$ is irreducible and has non-negative off-diagonal elements for sufficiently small $\varepsilon_1 > 0$. It follows from Theorem A.5 of [34] that $s(G(\phi^*) - \varepsilon_1 H)$ is a simple eigenvalue of $G(\phi^*) - \varepsilon_1 H$ with a positive eigenvector ψ^{ε_1}. Hence, the following system

$$\frac{dP}{dt} = (G(\phi^*) - \varepsilon_1 H)P, \ \ t \geq t_0$$

has a solution $k_0 e^{s(G(\phi^*) - \varepsilon_1 H)(t-t_0)} \psi^{\varepsilon_1}$, where k_0 is a positive constant. We choose k_0 such that k_0 satisfies

$$(P_1(t_0), P_2(t_0), P_3(t_0))^\top \geq k_0 \psi^{\varepsilon_1}.$$

By the comparison principle, we have

$$(P_1(t), P_2(t), P_3(t))^\top \geq k_0 e^{s(G(\phi^*) - \varepsilon_1 H)(t-t_0)} \psi^{\varepsilon_1}, \ t \geq t_0.$$

Moreover, we know $s(G(\phi^*)-\varepsilon_1 H)\geq \underline{s}(G^{\varepsilon_1})>0$. As a result,

$$(P_1(t),P_2(t),P_3(t))^\top \geq k_0 e^{\underline{s}(G^{\varepsilon_1})(t-t_0)}\psi^{\varepsilon_1},\ \ t\geq t_0.$$

Therefore, we get $P_j(t)\to\infty$ as $t\to\infty$ for $j=1,2,3$, which contradicts (C.2). This completes the proof.

Proof of Lemma 3.7. Suppose that (3.8) is not true. Then there exists $\mathbf{v}^0:=(\mathbf{B}^0,\mathbf{P}^0)\in\mathbb{Y}_0$ such that

$$\limsup_{t\to\infty}\|\Sigma(t)\mathbf{v}^0-M_0\|<\delta_1.$$

This implies that

$$\limsup_{t\to\infty}|B_i(t)|<\delta_1,\ i=1,2,3,4, \tag{C.3}$$

and

$$\limsup_{t\to\infty}|P_j(t)|<\delta_1,\ j=1,2,3.$$

As a result, there exists a sufficiently large $t_1>0$ such that for all $t\geq t_1$, we have

$$B_i(t)<\delta_1\ (i=1,2,3,4),\quad P_j(t)<\delta_1\ (j=1,2,3).$$

Moreover, for all $t\geq t_1$, we choose a $\delta_1>0$ such that

$$\tilde{S}_0=S_0-\gamma[B_1+B_2+B_3+B_4]-\frac{\gamma}{\beta-1}(P_1+P_2+P_3)>S_0-4\gamma\delta_1-\frac{3\gamma}{\beta-1}\delta_1>0.$$

Let $\hat{S}:=S_0-4\gamma\delta_1-\frac{3\gamma}{\beta-1}\delta_1$, and then we obtain

$$\begin{cases}\frac{dB_1}{dt}=(1-\varepsilon)g_1(\tilde{S}_0)B_1+\frac{\varepsilon}{2}g_2(\tilde{S}_0)B_2-\alpha B_1(P_1+P_2+P_3)-DB_1\\ \qquad\geq[(1-\varepsilon)g_1(\hat{S})-D-3\alpha\delta_1]B_1+\frac{\varepsilon}{2}g_2(\hat{S})B_2,\ t\geq t_1,\\ \frac{dB_2}{dt}=\varepsilon g_1(\tilde{S}_0)B_1+(1-\varepsilon)g_2(\tilde{S}_0)B_2+\frac{\varepsilon}{2}g_3(\tilde{S}_0)B_3-\alpha B_2(P_2+P_3)-DB_2\\ \qquad\geq\varepsilon g_1(\hat{S})B_1+[(1-\varepsilon)g_2(\hat{S})-D-2\alpha\delta_1]B_2+\frac{\varepsilon}{2}g_3(\hat{S})B_3,\ t\geq t_1,\\ \frac{dB_3}{dt}=\frac{\varepsilon}{2}g_2(\tilde{S}_0)B_2+(1-\varepsilon)g_3(\tilde{S}_0)B_3+\varepsilon g_4(\tilde{S}_0)B_4-\alpha B_3P_3-DB_3\\ \qquad\geq\frac{\varepsilon}{2}g_2(\hat{S})B_2+[(1-\varepsilon)g_3(\hat{S})-D-\alpha\delta_1]B_3+\varepsilon g_4(\hat{S})B_4,\ t\geq t_1,\\ \frac{dB_4}{dt}=\frac{\varepsilon}{2}g_3(\tilde{S}_0)B_3+(1-\varepsilon)g_4(\tilde{S}_0)B_4-DB_4\\ \qquad\geq\frac{\varepsilon}{2}g_3(\hat{S})B_3+[(1-\varepsilon)g_4(\hat{S})-D]B_4,\ t\geq t_1.\end{cases}$$

Let

$$\hat{J}=\begin{pmatrix}G_1-3\alpha\delta_1 & \frac{\varepsilon}{2}g_2(\hat{S}) & 0 & 0\\ \varepsilon g_1(\hat{S}) & G_2-2\alpha\delta_1 & \frac{\varepsilon}{2}g_3(\hat{S}) & 0\\ 0 & \frac{\varepsilon}{2}g_2(\hat{S}) & G_3-\alpha\delta_1 & \varepsilon g_4(\hat{S})\\ 0 & 0 & \frac{\varepsilon}{2}g_3(\hat{S}) & G_4\end{pmatrix},$$

where $G_i=:(1-\varepsilon)g_i(\hat{S})-D$ for $i=1,2,3,4$. Clearly, $\hat{J}$ is irreducible and has non-negative off-diagonal elements for $0<\varepsilon\leq 1$. It follows from Theorem A.5 of [34] that $s(\hat{J})$ is a simple eigenvalue of $\hat{J}$ with a positive eigenvector $\hat{\phi}$. We can easily verify that the following system

$$\begin{cases} \frac{dB_1}{dt} = [(1-\varepsilon)g_1(\hat{S}) - D - 3\alpha\delta_1]B_1 + \frac{\varepsilon}{2}g_2(\hat{S})B_2,\ t \geq t_1, \\ \frac{dB_2}{dt} = \varepsilon g_1(\hat{S})B_1 + [(1-\varepsilon)g_2(\hat{S}) - D - 2\alpha\delta_1]B_2 + \frac{\varepsilon}{2}g_3(\hat{S})B_3,\ t \geq t_1, \\ \frac{dB_3}{dt} = \frac{\varepsilon}{2}g_2(\hat{S})B_2 + [(1-\varepsilon)g_3(\hat{S}) - D - \alpha\delta_1]B_3 + \varepsilon g_4(\hat{S})B_4,\ t \geq t_1, \\ \frac{dB_4}{dt} = \frac{\varepsilon}{2}g_3(\hat{S})B_3 + [(1-\varepsilon)g_4(\hat{S}) - D]B_4,\ t \geq t_1 \end{cases}$$

admits a solution $k_1 e^{s(\hat{J})(t-t_1)}\hat{\phi}$ for all $t \geq t_1$, where k_1 is a positive constant. We choose k_1 such that k_1 satisfies $(B_1(t_1), B_2(t_1), B_3(t_1), B_4(t_1))^\top \geq k_1\hat{\phi}$. By the comparison principle, we know that the solution of system (2.5) satisfies

$$(B_1(t), B_2(t), B_3(t), B_4(t))^\top \geq k_1 e^{s(\hat{J})(t-t_1)}\hat{\phi},\ t \geq t_1.$$

If $R_0^h > 1$ (i.e., $s(J^0) > 0$), then $s(\hat{J}) > 0$ for sufficiently small $\delta_1 > 0$. Consequently, we have $\lim\limits_{t\to\infty} B_i(t) = \infty$, $i = 1,2,3,4$, which contradicts (C.3). This completes the proof.

Proof of Lemma 3.8. Following a similar proof to that in Theorem 3.2, we know that $\Sigma(t)\mathbb{Y}_0 \subseteq \mathbb{Y}_0$ for all $t \geq 0$. Let $M_\partial := \{\phi \in \partial\mathbb{Y}_0 |\ \Sigma(t)\phi \in \partial\mathbb{Y}_0,\ \forall t \geq 0\}$, and let $\omega(\phi)$ denote the omega limit set of the forward orbit of $\Sigma(t)$. We can prove that any forward orbit of $\Sigma(t)$ in M_∂ converges to either M_0 or M_1. Indeed, for any $\phi \in M_\partial$ and $t \geq 0$, we have $B_i(t,\phi) = 0$ for all $i = 1,2,3,4$ or $P_j(t,\phi) = 0$ for all $j = 1,2,3$.

In the case where $B_i(t,\phi) = 0$, $\forall t \geq 0$ for all $i = 1,2,3,4$, then we can easily prove that for any $t \geq 0$,

$$\lim_{t\to\infty}(B_1(t,\phi), B_2(t,\phi), B_3(t,\phi), B_4(t,\phi), P_1(t,\phi), P_2(t,\phi), P_3(t,\phi)) = (0,0,0,0,0,0,0).$$

Thus, $\lim_{t\to\infty}\Sigma(t)\phi = M_0$ for any $\phi \in M_\partial$.

In the case where $P_j(t,\phi) = 0$, $\forall t \geq 0$ for all $j = 1,2,3$, substituting it into system (2.5) allows the equations for (B_1, B_2, B_3, B_4) to satisfy system (3.2), and we will discuss the following two subcases:

(i) If $B_i(0) = 0$ for all $i = 1,2,3,4$, then we have $B_i(t,\phi) = 0$ for all $i = 1,2,3,4$. Thus, $\lim_{t\to\infty}\Sigma(t)\phi = M_0$.

(ii) If $B_i(0) > 0$ for some $i = 1,2,3,4$, then it follows from Theorem 3.2 that $B_i(t,\phi) > 0$ for all $i = 1,2,3,4$. Since $R_0^h > 1$, from Lemma 3.4 and Remark 3.1, we know that $(B_1(t,\phi), B_2(t,\phi), B_3(t,\phi), B_4(t,\phi))$ will eventually enter the global attractor $A_0 \subset \mathrm{Int}(\mathbb{R}_+^4)$. Thus, $\Sigma(t)\phi$ will eventually enter the global attractor M_1. Therefore, $\cup_{\phi\in M_\partial}\omega(\phi) = \{M_0, M_1\}$. By Lemmas 3.6 and 3.7, M_0 and M_1 are isolated in $\mathbb{Y}$ and $W^S(M_0) \cap \mathbb{Y}_0 = \emptyset$, $W^S(M_1) \cap \mathbb{Y}_0 = \emptyset$, where $W^S(M_0)$ and $W^S(M_1)$ are the stable sets of M_0 and M_1, respectively. Furthermore, M_0 and M_1 cannot form a cycle in $\partial\mathbb{Y}_0$.

Define a distance function $p : \mathbb{Y} \to \mathbb{R}_+$ by

$$p(\phi) = \min\{\phi_1(0), \phi_2(0), \phi_3(0), \phi_4(0), \phi_5(0), \phi_6(0), \phi_7(0)\},\ \forall \phi \in \mathbb{Y}.$$

It follows from Theorem 3.2 that $p^{-1}(0,\infty) \subseteq \mathbb{Y}_0$ and p has the property that if $p(\phi) > 0$ or $\phi \in \mathbb{Y}_0$ with $p(\phi) = 0$, then $p(\Sigma(t)\phi) > 0$, $\forall t > 0$. That is, p is a generalized distance function for the semiflow

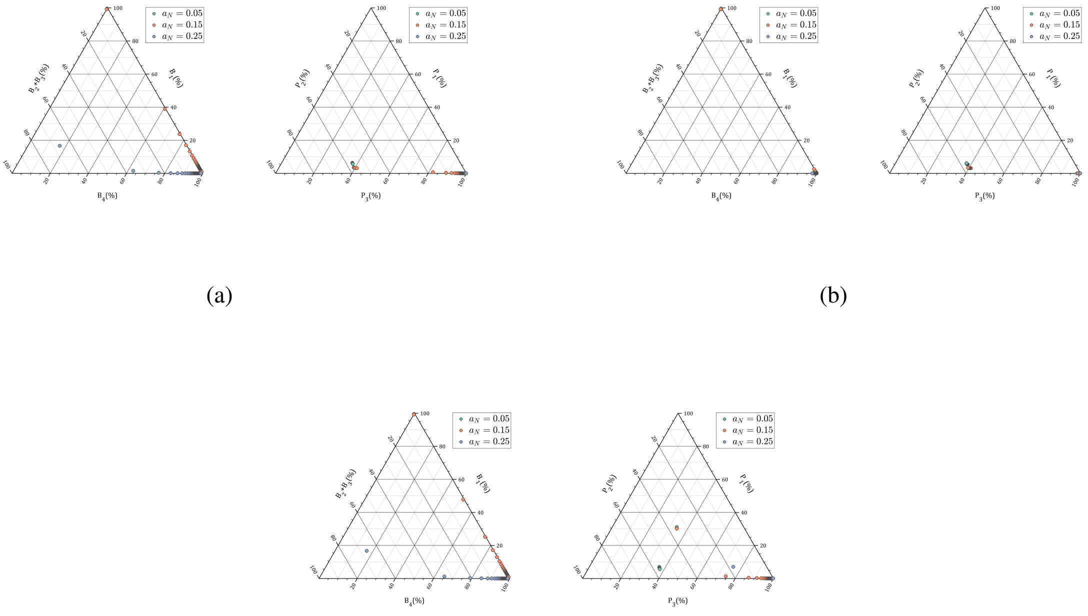
$\Sigma(t) : \mathbb{Y} \to \mathbb{Y}$. By Theorem 3.1, it is easy to see that $\Sigma(t) : \mathbb{Y} \to \mathbb{Y}$ has a global compact attractor in $\mathbb{Y}$, $\forall t \geq 0$. It then follows from Theorem 3 in [50] that there exists a positive constant ζ such that $\min\{p(\psi) : \psi \in \omega(\phi)\} > \zeta$ for any $\phi \in \mathbb{Y}_0$, which means

$$\liminf_{t\to\infty} B_i(t) \geq \zeta,\ \liminf_{t\to\infty} P_j(t) \geq \zeta,\ i = 1,2,3,4,\ j = 1,2,3,$$

which implies that the uniform persistence stated in our theorem is valid. In light of Theorem 3.7 and Remark 3.10 in [48], we know that $\Sigma(t) : \mathbb{Y}_0 \to \mathbb{Y}_0$ has a global attractor. It then follows from Theorem 4.7 in [48] that system (2.5) has a positive equilibrium. This completes the proof.

Appendix D: Ternary diagram

The ternary diagram corresponding to Figure 5 is shown below.



(a)

(b)

(c)

Figure D1. Ternary diagram for the densities of four algal types and three viral types under distinct resistance-growth trade-offs ($a_N = 0.25$, $a_N = 0.15$, and $a_N = 0.05$). (a) S_0; (b) D; (c) β. In each pair, the left column represents algal density while the right column shows viral density.

Appendix E: Effect of heterogeneous H

We assume that the half-saturation constant H for resources increases as resistance increases, and the relationship is expressed as

$$H_i = \frac{H_N - H_1}{N-1}(i-1) + H_1,\ i = 1,2,3,4,\ N = \max\{i\}.$$

As a result, B_1 is the least resistant type with the smallest half-saturation constant, while B_4 is the most resistant type with the largest half-saturation constant, i.e., $H_4 > H_3 > H_2 > H_1 = 1$. Figure E1 shows that heterogeneous H reduces the total biomass of algae while increasing the total biomass of viruses when the dilution rate is low. This indicates that biomass may be primarily driven by the heterogeneity in algal half-saturation constants under low dilution rates, but by external environmental conditions under high dilution rates.

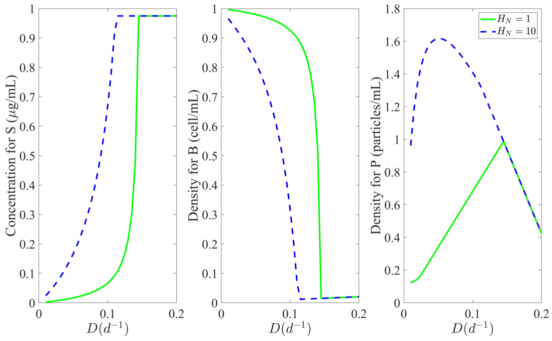


Figure E1. The relationship between the total biomass of algae and viruses and the dilution rate under $H_N = 1$ and $H_N = 10$. S is the resource concentration, B and P are the total biomass of algae and viruses, respectively, where $B = B_1 + B_2 + B_3 + B_4$ and $P = P_1 + P_2 + P_3$. The green solid and blue dashed curves represent $H_N = 1$ and $H_N = 10$, respectively.

Use of AI tools declaration

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

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Conflict of interest

The authors declare there are no conflicts of interest.

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