THE DYNAMICS OF A TWO HOST-TWO VIRUS SYSTEM IN A CHEMOSTAT ENVIRONMENT

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Abstract. The coevolution or coexistence of multiple viruses with multiple hosts has been an important issue in viral ecology. This paper is to study the mathematical properties of the solutions of a chemostat model for two host species and two virus species. By virtue of the global dynamics of its submodels and the theories of uniform persistence and Hopf bifurcation, we derive sufficient conditions for the coexistence of two hosts with two viruses and coexistence of two hosts with one virus, as well as occurrence of Hopf bifurcation.

1. Introduction. Since the earlier works by Campbell [2], Levin et al [14] and Chao et al [3], mathematical models have been extensively studied to discover the effects of viruses on microbial communities and the coexistence of viruses and their hosts in complex ecosystems in chemostats. While Campbell’s model only involves the predator-prey relation between the virus and the bacteria, the models in Levin et al and Chao et al’s works explicitly include the relationship between virus growth and the resources. The latter models are the origin of the so-called resource-virus-host models that have been used and generalized widely. In fact, if the resource dynamics are much faster than both virus and bacteria dynamics, then a simple virus-host model, which carries a similar predator-prey relation as in Campbell’s model, can be derived from a resource-virus-host system (see e.g., Appendix B.3 in [21]).

To well understand the interactions between viruses and bacteria, it is critical to investigate the mathematical properties of the related models. For resource-virus-host models or simplified virus-host models involving one virus species and one bacteria species, based on experimental and theoretical results, according to conditions or constraints on model parameters, three potential long-term behaviors may occur: both virus and bacteria are extinct or washed out, only virus is washed out, both virus and bacteria coexist; see e.g., [1, 14, 3, 21, 13, 16].

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In a real situation of a chemostat or other environments, it is usually rare to have only one virus with one host, besides resources. Viruses may infect multiple hosts and hosts may be infected by more than one virus. In this case, different virus or host species may simply be mutant types of one virus or host species. While one can reasonably expect and experiments have also shown that coevolutionary or coexistence dynamics in such systems are deeply affected by a trade-off between infectivity-associated life history traits and other life history traits (see e.g., [21]), theoretical analyses of related models are generally difficult due to the complexity of the models. Thingstad [19] studied the coexistence dynamics of a Lotka-Volterra model in a monogamous infection network, where each virus specializes on a single host, and found that coexistence of competing bacterial species can be ensured by the presence of viruses that kill the winning bacterial strain. As a special type of infection structure that has been found in experiments (see e.g., [18]), nested virus-bacteria cross-infection networks have been considered in recent studies; see e.g., [9, 11, 10, 12]. In such networks, the specialist virus can infect the most permissive host, the next most specialized virus infects the most permissive host and the second most permissive host, and so on [9]. Jover et al [9] obtained coexistence of a Lotka-Volterra model in nested infection networks under the condition that bacteria that are superior competitors for nutrient devote the least effort to defence against infection and the virus that are the most efficient at infecting host have the smallest host range. Korytowski et al [11] then proved permanence dynamics for a chemostat-based nutrient-bacteria-virus model in nested infection networks under the same conditions as in [9] and their permanence result is also valid in a monogamous infection network as considered in [19]. In [7], the dependence of coexistence on diversity of phage and bacteria was quantitatively studied in monogamous infection networks and nested infection networks. In [12], permanence and stability (of a positive equilibrium ) dynamics of a “Kill the Winner” type bacteria-virus-zooplankton model was obtained in these two types of networks, where the “Kill the Winner” model is based on the assumptions that (1) all microbes compete for a common resource, (2) all microbes, except for one population, are susceptible to virus infection, (3) all microbes are subjected to zooplankton grazing, (4) viruses infect only a single type of bacteria (see also e.g., [19, 20, 21]). For a two host-two virus model in which one virus specializes on infecting one host, it has been proved that if a unique positive equilibrium exists, then it is stable; see [10]. In the most general case when there is no such restriction, the coexistence dynamics of the hosts and viruses in a two host-two virus model have not been fully discovered although there have been some examples showing coexistence; see e.g., [21, 6]. In this paper, we will consider a general two host-two virus model in a chemostat environment, i.e., equation (5.15) in [21], where host species share the same carrying capacity. Our goal is to understand better the coexistence or persistence dynamics of the chemostat system where both two viruses can infect two hosts. By virtue of the global dynamics of its submodels and the theories of uniform persistence and Hopf bifurcation, we are able to derive sufficient conditions for the coexistence of two hosts with two viruses and coexistence of two hosts with one virus, as well as occurrence of Hopf bifurcation.

The paper is organized as follows. In Section 2, we will introduce the two host-two virus model (1) that was proposed in [21]. In Section 3, we will present analyses of global dynamics for submodels of (1), a one host-one virus model, a two host model,
2. The model. In this paper, we will study the dynamics of a two host-two virus model in a chemostat environment (see equation (5.15) in [21]; see also [6]):

\[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + N_2}{K}\right) - \phi_{11} N_1 V_1 - \phi_{12} N_1 V_2 - \omega N_1, \\
\frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_1 + N_2}{K}\right) - \phi_{21} N_2 V_1 - \phi_{22} N_2 V_2 - \omega N_2, \\
\frac{dV_1}{dt} &= \beta_{11} \phi_{11} N_1 V_1 + \beta_{21} \phi_{21} N_2 V_1 - m_1 V_1 - \omega V_1, \\
\frac{dV_2}{dt} &= \beta_{12} \phi_{12} N_1 V_2 + \beta_{22} \phi_{22} N_2 V_2 - m_2 V_2 - \omega V_2.
\end{align*}
\]

Here \(N_i\) is the density of host \(i = 1, 2\), \(V_j\) is the density of virus \(j = 1, 2\), \(r_i\) is the intrinsic growth rate of host \(i\), \(K\) is the carrying capacity for the hosts, \(\phi_{ij} > 0\) is the adsorption rate for virus \(j\) attached to host \(i\), \(m_j\) is the natural decay rate of virus \(j\), \(\omega\) is the dilution/flow rate, and \(\beta_{ij}\) represents the burst size. When virus attach to host, both virus and host are lost. Thus, \(\beta_{ij}\)'s may be the true burst-size minus one. We assume that each virus is able to infect both hosts and both sets of hosts and viruses have distinct life history traits. In particular, we assume that the two hosts have different growth rates, i.e., \(r_1 \neq r_2\), and that there is always a flow in the environment, i.e., \(\omega > 0\).

3. Dynamics of submodels of (1). In order to understand the dynamics of (1), we first study the dynamics of some submodels of (1) in this section.

3.1. Dynamics of the one host-one virus model. When there is only one host with one virus in a chemostat environment, we have the following one host-one virus model:

\[
\begin{align*}
\frac{dN}{dt} &= r N \left(1 - \frac{N}{K}\right) - \phi N V - \omega N, \\
\frac{dV}{dt} &= \beta \phi N V - m V - \omega V,
\end{align*}
\]

where variables and parameters carry the same meanings as those in (1). Simple calculations quickly show that (2) admits three possible nonnegative equilibria: \(E_0^{nv} = (0, 0)\), \(E_1^{nv} = (\tilde{N}, 0)\), and \(E_2^{nv} = (N^*, V^*)\), with \(\tilde{N} = \frac{r - \omega}{\phi K}, N^* = \frac{m + \omega}{\beta \phi}\), \(V^* = (r - \omega - \frac{m + \omega}{\beta \phi}) \frac{1}{\phi} = \frac{r}{\beta K}(\tilde{N} - N^*)\).

The local dynamics of (2) are similar to those of a predator-prey model (see also e.g., Appendix B 2.2 in [21]). We present its global dynamics here.

**Lemma 3.1.** The following statements are valid for (2).

(i) If \(r < \omega\), \(E_0^{nv}\) is globally asymptotically stable for all nonnegative initial conditions.

(ii) If \(r > \omega\) and \(\frac{r - \omega}{\beta K} < \frac{m + \omega}{\beta \phi}\) (i.e., \(\tilde{N} < N^*\)), then \(E_0^{nv}\) is a saddle and \(E_1^{nv}\) is globally asymptotically stable for all positive initial conditions.

(iii) If \(r > \omega\) and \(\frac{r - \omega}{\beta K} > \frac{m + \omega}{\beta \phi}\) (i.e., \(\tilde{N} > N^*\)), then \(E_0^{nv}\) and \(E_1^{nv}\) are both saddles and \(E_2^{nv}\) is globally asymptotically stable for all positive initial conditions.
Proof. The eigenvalues of the Jacobian matrix at $E_0^{nw}$ are $r - \omega$ and $-m - \omega$; the
eigenvalues of the Jacobian matrix at $E_1^{nw}$ are $\omega - r$ and $K\beta\phi^2 V^*/r$; the trace
and the determinant of the Jacobian matrix at $E_3^{nw}$ are $-rN^*/K$ and $\beta\phi^2 N^*V^*$,
respectively. Therefore, $E_0^{nw}$ is locally asymptotically stable if and only if $r < \omega$
a and is a saddle if $r > \omega$; $E_1^{nw}$ is locally asymptotically stable if and only if $r > \omega$
and $\beta\phi(\tilde{N} - N^*) < 0$ and is a saddle if one of these conditions is not true; $E_3^{nw}$ is
stable whenever it is positive, that is, when $\tilde{N} > N^*$.

For any nonnegative solution $(N(t), V(t))$, we have $dN/dt \leq r(1 - N/K)$, which
implies that $0 \leq N(t) \leq K + 1$ when $t$ is sufficiently large. This also leads to $d(\beta N + \nu^*)/dt \leq r\beta(K + 1) - \omega(\beta N + V^*)$ for sufficiently large $t$. Thus, by comparison, we
know that every nonnegative solution of (2) eventually enters the region \{$(N, V) \in \mathbb{R}^+_2 : 0 \leq N \leq K + 1, 0 \leq V \leq r\beta(K + 1)/\omega + 1$\}.

Since the $N$ axis and the $V$ axis are invariant, respectively, there are no limit
cycles enclosing $E_0^{nw}$ or $E_1^{nw}$. Therefore, by Poincaré-Bendixson theorem, if $E_0^{nw}$ or
$E_1^{nw}$ is locally asymptotically stable in $\mathbb{R}^2_+$, then it is globally asymptotically stable,
in $\mathbb{R}^2_+$ for $E_0^{nw}$ or in $\mathbb{R}^2_+ \setminus V$-axis for $E_1^{nw}$. (i) and (ii) are proved.

When $E_3^{nw}$ is a positive equilibrium, choose the Lyapunov function
\[
\mathcal{V}(N, V) = \int_{N^*}^{N} \frac{s - N^*}{s} ds + \frac{1}{\beta} \int_{V^*}^{V} \frac{s - V^*}{s} ds.
\]
Then $\dot{\mathcal{V}} = -r(N - N^*)^2/K \leq 0$. By the LaSalle’s invariance principle, $(N(t), V(t))$
$\to E_0^{nw} = (N^*, V^*)$ as $t \to \infty$ for all solutions with positive initial conditions.
Hence, if $E_3^{nw}$ is positive, it is globally asymptotically stable for all positive initial
conditions. (iii) is proved.

3.2. Dynamics of the two host model. When there are only two host species
living in the chemostat without viruses, (1) becomes
\[
\begin{aligned}
\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + N_2}{K}\right) - \omega N_1, \\
\frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_1 + N_2}{K}\right) - \omega N_2.
\end{aligned}
\]

There are three equilibria of (3): $E_0^{mn} = (0, 0)$, $E_1^{mn} = (\tilde{N}_1, 0)$, and $E_2^{mn} = (0, \tilde{N}_2)$,
with $\tilde{N}_1 = \frac{r_1}{r_1 - \omega} K$ and $\tilde{N}_2 = \frac{r_2}{r_2 - \omega} K$. The eigenvalues of the Jacobian matrix at
$E_0^{mn}$ are $r_1 - \omega$ and $r_2 - \omega$; the eigenvalues of the Jacobian matrix at $E_1^{mn}$ are $\omega - r_1$
and $-\omega(r_1 - r_2)/r_1$; the eigenvalues of the Jacobian matrix at $E_2^{mn}$ are $\omega - r_2$ and
$\omega(r_1 - r_2)/r_2$. Note that the solutions of (3) are positively invariant in $\mathbb{R}^+_2$ and
nonnegative solutions are eventually bounded. This implies that there are no limit
cycles enclosing any of the equilibria. By using the Poincaré-Bendixson theorem, we
can obtain the following results.

**Lemma 3.2.** The following statements are valid for (3).

(i) If $r_1 < \omega$ and $r_2 < \omega$, $E_0^{mn}$ is globally asymptotically stable for all nonnegative
initial conditions.

(ii) If $r_1 > \omega$ and $r_1 > r_2$, then $E_0^{mn}$ is unstable (node if $r_2 > \omega$ or saddle if
$r_2 < \omega$), $E_1^{mn}$ is globally asymptotically stable for all positive initial conditions,
and $E_2^{mn}$ is a saddle if it is nonnegative.

(iii) If $r_2 > \omega$ and $r_1 < r_2$, then $E_0^{mn}$ is unstable (node if $r_1 > \omega$ or saddle if $r_1 < \omega$),
$E_1^{mn}$ is a saddle if it is nonnegative, and $E_2^{mn}$ is globally asymptotically stable for all positive initial conditions.
3.3. Dynamics of the two host-one virus model. When there are two host species living in the chemostat with one virus species, (1) becomes

\[
\begin{align*}
\frac{dN_1}{dt} &= r_1N_1 \left(1 - \frac{N_1 + N_2}{K}\right) - \phi_1N_1V - \omega N_1, \\
\frac{dN_2}{dt} &= r_2N_2 \left(1 - \frac{N_1 + N_2}{K}\right) - \phi_2N_2V - \omega N_2, \\
\frac{dV}{dt} &= \beta_1\phi_1N_1V + \beta_2\phi_2N_2V - mV - \omega V,
\end{align*}
\]  

(4)

where variables and parameters carry the same meanings as those in (1).

3.3.1. Equilibria of (4) and their local stability. System (4) admits 6 possible nonnegative equilibria:

\[
E_0^{nnv} = (0, 0, 0), \quad E_1^{nnv} = (\tilde{N}_1, 0, 0), \quad E_2^{nnv} = (\tilde{N}_2, 0, 0), \quad E_3^{nnv} = (N_1^*, 0, V^*), \quad E_4^{nnv} = (0, N_2^*, V^*), \quad E_5^{nnv} = (N_1^*, N_2^*, V^*)
\]  

(5)

with

\[
\begin{align*}
\tilde{N}_1 &= \frac{r_1 - \omega}{r_1}K, \quad \tilde{N}_2 = \frac{r_2 - \omega}{r_2}K, \\
N_1^* &= \frac{m + \omega}{\beta_1\phi_1}, \quad \tilde{V}^* = \left(\frac{r_1 - \omega - r_1 m + \omega}{\beta_1\phi_1 K}\right) \frac{1}{\phi_1} \tilde{N}_1 (\tilde{N}_1 - N_1^*), \\
N_2^* &= \frac{m + \omega}{\beta_2\phi_2}, \quad V^* = \left(\frac{r_2 - \omega - r_2 m + \omega}{\beta_2\phi_2 K}\right) \frac{1}{\phi_2} \tilde{N}_2 (\tilde{N}_2 - N_2^*), \\
N_1^* &= \frac{K\beta_2\phi_2(\omega \phi_1 - \phi_1 r_2 + \phi_2 r_1) + (\phi_1 r_2 - \phi_2 r_1)(m + \omega)}{\beta_1\phi_1 - \beta_2\phi_2}, \\
N_2^* &= \frac{-K\beta_1\phi_1(\omega \phi_1 - \phi_1 r_2 + \phi_2 r_1) + (\phi_1 r_2 - \phi_2 r_1)(m + \omega)}{\beta_1\phi_1 - \beta_2\phi_2}, \\
V^* &= \left(\frac{r_1 - r_2}\phi_1\right) \frac{r_1 - \omega}{\phi_1 r_2 - \phi_2 r_1} K \phi_1, \\
N_1^* &= \frac{K\beta_2\phi_2(\omega \phi_1 - \phi_1 r_2 + \phi_2 r_1)K}{\phi_1 r_2 - \phi_2 r_1} = \frac{r_1 - \omega}{\phi_1 r_2 - \phi_2 r_1} K.
\end{align*}
\]  

(6)

We provide the local stability analysis of all nonnegative equilibria of (4).

Lemma 3.3. The following statements are valid for (4).

(i) $E_0^{nnv}$ is locally asymptotically stable if $r_1 < \omega$ and $r_2 < \omega$; it is unstable if $r_1 > \omega$ or $r_2 > \omega$.

(ii) $E_1^{nnv}$ is nonnegative if $r_1 > \omega$ and is locally asymptotically stable if $r_1 > r_2$ and $\frac{m + \omega}{\beta_1\phi_1} > \frac{(r_1 - \omega)K}{r_1}$ (or $N_1^* > \tilde{N}_1$). It is unstable if $r_1 < r_2$ or $N_1^* < \tilde{N}_1$.

(iii) $E_2^{nnv}$ is nonnegative if $r_2 > \omega$ and is locally asymptotically stable if $r_1 < r_2$ and $\frac{m + \omega}{\beta_2\phi_2} > \frac{(r_2 - \omega)K}{r_2}$ (or $N_2^* > \tilde{N}_2$). It is unstable if $r_1 > r_2$ or $N_2^* < \tilde{N}_2$.

(iv) $E_3^{nnv}$ is nonnegative if $\frac{m + \omega}{\beta_1\phi_1} < \frac{(r_1 - \omega)K}{r_1}$ (or $N_1^* < \tilde{N}_1$). It is locally asymptotically stable if $(\phi_1 r_2 - \phi_2 r_1)(N_1^* - \eta) > 0$. It is unstable if $(\phi_1 r_2 - \phi_2 r_1)(N_1^* - \eta) < 0$.

(v) $E_4^{nnv}$ is nonnegative if $\frac{m + \omega}{\beta_2\phi_2} < \frac{(r_2 - \omega)K}{r_2}$ (or $N_2^* < \tilde{N}_2$). It is locally asymptotically stable if $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) < 0$. It is unstable if $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) > 0$.

(vi) (a) $E_5^{nnv}$ is positive and locally asymptotically stable if

\[
\frac{\phi_1}{\phi_2} > r_1 > 1, \quad \frac{\phi_1}{\beta_1} > \frac{\beta_2}{\phi_2} N_1^* < \eta < N_2^*,
\]
or
\[
\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} < 1, \quad \frac{\phi_1}{\phi_2} < \frac{\beta_2}{\beta_1}, \quad N_1^* > \eta > N_2^*.
\]

(b) \(E_5^{nnv}\) is positive and unstable if
\[
\frac{\beta_2}{\beta_1} < \frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} < 1, \quad N_1^* < \eta < N_2^*.
\]

or
\[
\frac{\beta_2}{\beta_1} > \frac{\phi_1}{\phi_2} > \frac{r_1}{r_2} > 1, \quad N_1^* > \eta > N_2^*.
\]

Proof. The conditions for the equilibria to be nonnegative can be derived directly from the formulas of the equilibria. Local stability of the equilibria can be determined by the eigenvalues of the Jacobian matrix at each corresponding equilibrium. In the following, we only need to list the information about the eigenvalues of the Jacobian matrices.

(i). The eigenvalues of the Jacobian matrix at \(E_0^{nnv}\) are \(r_1 - \omega, r_2 - \omega, \) and \(-m - \omega\).

(ii). The eigenvalues of the Jacobian matrix \(J(E_1^{nnv})\) are \(\omega - r_1, -\omega(r_1 - r_2)/r_1,\) and \((r_1 - \omega)K\beta_1\phi_1/r_1 - m - \omega\).

(iii). The eigenvalues of the Jacobian matrix \(J(E_2^{nnv})\) are \(\omega - r_2, \omega(r_1 - r_2)/r_2,\) and \((r_2 - \omega)K\beta_2\phi_2/r_2 - m - \omega\).

(iv). The Jacobian matrix at \(E_3^{nnv}\) is
\[
J(E_3^{nnv}) = \begin{bmatrix}
-\frac{r_1N_1^*}{K} & 0 & -\phi_1N_1^* \\
0 & r_2(1 - \frac{N_1^*}{r_2}) - \phi_2V^* - \omega & 0 \\
\beta_1\phi_1V^* & \beta_2\phi_2V^* & 0
\end{bmatrix}.
\]

One eigenvalue of \(J(E_3^{nnv})\) is
\[
\lambda_{E_3^{nnv}} = r_2 \left(1 - \frac{N_1^*}{K}\right) - \phi_2V^* - \omega = -\frac{(\phi_1r_2 - \phi_2r_1)}{K\phi_1}(N_1^* - \eta)
\]

with \(\lambda_{E_3^{nnv}} < 0\) if \((\phi_1r_2 - \phi_2r_1)(N_1^* - \eta) > 0\). The other two eigenvalues have negative real parts if \(V^* > 0\).

(v). The Jacobian matrix at \(E_4^{nnv}\) is
\[
J(E_4^{nnv}) = \begin{bmatrix}
r_1(1 - \frac{N_2^*}{K}) - \phi_1V^* - \omega & 0 & 0 \\
-\frac{r_2N_2^*}{K} & \beta_1\phi_1V^* & -\phi_2N_2^*
\end{bmatrix}.
\]

One eigenvalue is
\[
\lambda_{E_4^{nnv}} = r_1 \left(1 - \frac{N_2^*}{K}\right) - \phi_1V^* - \omega = \frac{(\phi_1r_2 - \phi_2r_1)}{K\phi_1}(N_2^* - \eta)
\]

with \(\lambda_{E_4^{nnv}} < 0\) if \((\phi_1r_2 - \phi_2r_1)(N_2^* - \eta) < 0\). The other two eigenvalues have negative real parts if \(V^* > 0\).

(vi). The Jacobian matrix at \(E_5^{nnv}\) is
\[
J(E_5^{nnv}) = \begin{bmatrix}
-\frac{r_1N_1^*}{K} & -\frac{r_1N_1^*}{K} & -\phi_1N_1^* \\
-\frac{r_2N_2^*}{K} & -\frac{r_2N_2^*}{K} & -\phi_2N_2^*
\end{bmatrix}.
\]
Existence condition

When stable for (4) for all nonnegative initial conditions.

Theorem 3.4. It follows from the Routh-Hurwitz criteria that all eigenvalues of $J(E_{0}^{nv})$ have negative real parts if and only if

$$
\begin{align*}
N_1^c r_1 + N_2^c r_2 &> 0, \\
\frac{N_1^c r_1 + N_2^c r_2}{V_c N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2)} &> 0, \\
\frac{N_1^c r_1 + N_2^c r_2}{V_c (N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2)) - V_c N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2)} &> 0, \\
\frac{V_c (N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2)) - V_c N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2)}{V_c (N_1^c N_2^c (\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2))} &> 0.
\end{align*}
$$

Hence, $E_{0}^{nv}$ is locally asymptotically stable if and only if $(\phi_1 r_2 - \phi_2 r_1)(\beta_1 \phi_1 - \beta_2 \phi_2) > 0$.

For simplicity, we list the results in Lemma 3.3 in Table 1.

| Equilibrium  | Existence condition | Stability condition |
|--------------|---------------------|---------------------|
| $E_{0}^{nv}$ | $(0, 0, 0)$          | $r_1 < \omega$, $r_2 < \omega$ |
| $E_{1}^{nv}$ | $(\hat{N}_1, 0, 0)$ | $r_1 > \omega$       |
| $E_{2}^{nv}$ | $(0, N_2, 0)$       | $r_2 > \omega$       |
| $E_{3}^{nv}$ | $(N_1^*, 0, V^*)$   | $(\frac{\phi_1}{\phi_2} - \frac{\beta_1}{\beta_2})(N_1^* - \eta) > 0$ |
| $E_{4}^{nv}$ | $(0, N_2^*, V^*)$   | $(\frac{\phi_1}{\phi_2} - \frac{\beta_1}{\beta_2})(N_2^* - \eta) < 0$ |
| $E_{5}^{nv}$ | $(N_1^*, N_2^*, V^c)$ | $(\frac{\phi_1}{\phi_2} - \frac{\beta_1}{\beta_2})(N_1^* - \eta), (\frac{\phi_1}{\phi_2} - \frac{\beta_1}{\beta_2})(N_2^* - \eta) > 0$ |

Table 1. The conditions for existence and local stability of equilibria of (4). Here, an equilibrium exists means it is nonnegative for $E_{1}^{nv}$-$E_{4}^{nv}$ and positive for $E_{5}^{nv}$.

3.3.2. Global dynamics of (4). We first consider the global dynamics of (4) when there is no positive equilibrium.

Theorem 3.4. If $r_1 < \omega$ and $r_2 < \omega$, then $E_{0}^{nv} = (0, 0, 0)$ is globally asymptotically stable for (4) for all nonnegative initial conditions.

Proof. When $r_1 < \omega$ and $r_2 < \omega$, $E_{0}^{nv} = (0, 0, 0)$ is locally asymptotically stable. It follows from (4) that $\frac{dN_1}{dt} \leq (r_1 - \omega)N_1$ and $\frac{dN_2}{dt} \leq (r_2 - \omega)N_2$. Since $N_1$ and $N_2$ are nonnegative, this implies that $N_1(t) \to 0$ and $N_2(t) \to 0$ as $t \to \infty$. When $N_1(t) = N_2(t) = 0$, we have the limiting equation $\frac{dV}{dt} = -mV - \omega V$, which implies that $V(t) \to 0$ as $t \to \infty$ for nonnegative $V(0)$. Hence, $(N_1(t), N_2(t), V(t)) \to (0, 0, 0)$ as $t \to \infty$ for all nonnegative initial conditions.

Theorem 3.5. (i) If $r_1 > \omega$ and $r_2 < \omega$, then $E_{1}^{nv}$ is globally asymptotically stable for (4) for all positive initial conditions when $N_1^* > \hat{N}_1$ and $E_{3}^{nv}$ is globally asymptotically stable for (4) for all positive initial conditions when $N_1^* < \hat{N}_1$. 

(ii) If \( r_1 < \omega \) and \( r_2 > \omega \), then \( E^{nnv}_2 \) is globally asymptotically stable for (4) for all positive initial conditions when \( N^*_2 > N_2^* \) and \( E^{nnv}_4 \) is globally asymptotically stable for (4) for all positive initial conditions when \( N^*_2 < N_2^* \).

Proof. We only need to prove (i). (ii) can be proved similarly. Assume \( r_1 > \omega \) and \( r_2 < \omega \). By the second equation of (4), we have \( \frac{dN_2}{dt} \leq (r_2 - \omega)N_2 \), which implies \( N_2(t) \to 0 \) as \( t \to \infty \). When \( N_2(0) = 0 \), the limiting system is

\[
\begin{aligned}
\frac{dN_1}{dt} &= r_1N_1 \left( 1 - \frac{N_1}{K} \right) - \phi_1N_1V - \omega N_1, \\
\frac{dV}{dt} &= \beta_1\phi_1N_1V - mV - \omega V.
\end{aligned}
\]

(7)

It follows from Lemma 3.1 that for any positive initial conditions of (7), \( N_1(t) \to \tilde{N}_1 \) and \( V(t) \to 0 \) as \( t \to \infty \) when \( N^*_1 < \tilde{N}_1 \). Hence, for any positive initial condition of (4), we have \( (N_1(t), N_2(t), V(t)) \to E^{nnv}_1 \) as \( t \to \infty \) when \( N^*_1 > \tilde{N}_1 \) and \( (N_1(t), N_2(t), V(t)) \to E^{nnv}_3 \) as \( t \to \infty \) when \( N^*_1 < \tilde{N}_1 \). (i) is proved.

\[ \square \]

Theorem 3.6. If both \( E^{nnv}_4 \) and \( E^{nnv}_4 \) are nonnegative, \( E^{nnv}_4 \) is stable and \( E^{nnv}_4 \) is unstable (that is, when \( \phi_1 > \frac{r_1}{r_2} \), \( N^*_1 < \eta \), \( N^*_2 < \eta \) or when \( \phi_1 < \frac{r_1}{r_2} \) and \( N^*_1 > \eta \), \( N^*_2 > \eta \)), then \( E^{nnv}_4 \) is globally asymptotically stable for (4) for all positive initial conditions.

Proof. Note that under the conditions of the theorem, \( E^{nnv}_0 \), \( E^{nnv}_1 \), and \( E^{nnv}_2 \) are all unstable, and \( E^{nnv}_5 \) is not positive.

It is easy to see that the \( N_1N_2 \) plane, the \( N_1V \) plane, and the \( N_2V \) plane are invariant, respectively. This implies that for any nonnegative initial value, the solution \( (N_1(t), N_2(t), V(t)) \) of (4) is nonnegative. Let \( (N_1(t), N_2(t), V(t)) \) be a solution of (4) with positive initial condition \( u^0 = (N_1(0), N_2(0), V(0)) \). Since \( \frac{dN_1}{dt} \leq r_1N_1 \left( 1 - \frac{N_1}{K} \right) \), we obtain that \( N_1(t) < K + 1 \) for \( t > t_0 \) for some positive \( t_0 \).

Similarly, \( N_2(t) < K + 1 \) for \( t > t_1 \) for some positive \( t_1 \). Moreover, \( \frac{d}{dt} \left[ \beta_1N_1 + \beta_2N_2 + V \right] < -\omega(\beta_1N_1 + \beta_2N_2 + V) + (\beta_1r_1 + \beta_2r_2)(K + 1) \) for \( t > t_{max} \{t_0, t_1\} \). This implies that \( V(t) \) is bounded for \( t \geq 0 \). In the following we prove the result in three cases.

Case 1. \( \frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} \) and \( N^*_1 < \eta \), \( N^*_2 < \eta \). We have \( \eta > 0 \) and hence \( \frac{r_1 - \omega}{r_2 - \omega} > \frac{\phi_1}{\phi_2} \). For constants \( \xi_1, \xi_2 \in \mathbb{R} \),

\[
\begin{aligned}
\xi_1 \frac{1}{N_2^*} \frac{dN_2}{dt} - \xi_2 \frac{V}{N_2^*} \frac{dV}{dt} - \frac{1}{N_2^*} \frac{dN_1}{dt} \\
= (\xi_1(r_2 - \omega) + \xi_2(r_1 - \omega)) + N_1\left( \frac{r_1}{K} - \xi_1 \frac{r_2}{K} - \xi_2 \frac{r_1}{K} \right) + N_2\left( \frac{r_2}{K} - \xi_1 \frac{r_2}{K} - \frac{\phi_1}{\phi_2} \frac{r_2}{K} \right) \\
+ V(\phi_1 - \xi_1 \phi_2).
\end{aligned}
\]

Let \( \xi_1 = \frac{\phi_1}{\phi_2} \), \( \xi_2 = r_1 - \omega - (r_2 - \omega) \frac{\phi_1}{\phi_2} \). Note that \( \xi_2 > 0 \). We then have

\[
\begin{aligned}
\xi_1 \frac{1}{N_2^*} \frac{dN_2}{dt} - \frac{\xi_2}{r_2 - \omega} \frac{V}{N_2^*} \frac{dV}{dt} - \frac{1}{N_2^*} \frac{dN_1}{dt} \\
= N_1\left( \frac{r_1}{K} - \frac{\phi_1}{\phi_2} \frac{r_2}{K} - \xi_2 \frac{r_2}{K} \right) + N_2\left( \xi_2 \frac{r_2}{K} - \frac{\phi_1}{\phi_2} \frac{r_2}{K} \right) \\
= N_1\left( \frac{\xi_2}{\eta} - \frac{\xi_2}{N_2^*} \right) + N_2\left( \frac{\xi_2}{\eta} - \frac{\xi_2}{N_2^*} \right) \\
= \xi_2(N_1\left( \frac{\xi_2}{\eta} - \frac{\xi_2}{N_2^*} \right) + N_2\left( \frac{\xi_2}{\eta} - \frac{\xi_2}{N_2^*} \right)) \\
< 0
\end{aligned}
\]

since \( N^*_1 < \eta \) and \( N^*_2 < \eta \). This implies that

\[
\left( \frac{N_2(t)}{N_2(0)} \right)^{\xi_1} < \left( \frac{V(t)}{V(0)} \right)^{\xi_2} \left( \frac{N_1(t)}{N_1(0)} \right)e^{\xi_2\left( \frac{1}{\eta} - \frac{1}{N_2^*} \right) \int_0^t N_2(s)ds}.
\]
Since \( N_1(t) \) and \( V(t) \) are bounded for large \( t > 0 \), it follows from the fact that \( N_2^* < \eta \) that \( \lim_{t \to \infty} N_2(t) = 0 \). Then by Lemma 3.1, \( \lim_{t \to \infty} N_1(t) = N_1^* \) and \( \lim_{t \to \infty} V(t) = V^* \).

That is, \( \lim_{t \to \infty} (N_1(t), N_2(t), V(t)) = E_3^{nnv} \).

**Case 2.** \( \frac{\alpha_1}{\phi_2} > \frac{r_1}{r_2} \), \( N_1^* > \eta \), \( N_2^* > \eta \), and \( \eta < 0 \). We have \( \frac{r_1 - \omega}{r_2 - \omega} > \frac{\phi_1}{\phi_2} > \frac{r_1}{r_2} \). For a constant \( \xi \in \mathbb{R} \),

\[
\frac{N_2(t)}{N_1(t)} = \frac{\xi}{\xi_2} \frac{dN_2}{dt} - 1 - \frac{N_1}{\xi_1} \frac{dN_1}{dt} = \xi (r_2 (1 - \frac{N_1}{N_2^*}) - \phi_2 V - \omega) - (1 - \frac{N_1}{N_2^*} - \phi_1 V - \omega) + (N_1 + N_2)(\frac{1}{\xi_1} - 1) + (\phi_1 - \phi_2).
\]

Choose \( \xi > 0 \) such that \( \xi < \frac{\phi_1}{\phi_2}, \xi > \frac{r_1}{r_2} \). Then \( \xi (r_2 - \omega) - (r_1 - \omega) < 0 \), \( \frac{r_1}{r_2} - \xi \frac{\phi_2}{\phi_1} < 0 \), and \( \xi \frac{1}{\xi_1} \frac{dN_2}{dt} - 1 - \frac{N_1}{\xi_1} \frac{dN_1}{dt} < (\xi (r_2 - \omega) - (r_1 - \omega)) < 0 \).

Integrating this inequality from 0 to \( t \) (with \( t > t_0 \)) and taking exponentials on both sides yield

\[
\left( \frac{N_2(t)}{N_1(0)} \right) \leq \left( \frac{N_2(0)}{N_1(t)} \right)^{e^{\xi t}} = M e^{\xi (r_2 - \omega) - (r_1 - \omega) t},
\]

where \( M = (K + 1)/N_1(0) \). This implies that \( N_2(t) \to 0 \) as \( t \to \infty \), and hence, as in Case 1, we have \( \lim_{t \to \infty} (N_1(t), N_2(t), V(t)) = E_3^{nnv} \).

**Case 3.** \( \frac{\alpha_1}{\phi_2} > \frac{r_1}{r_2} \), \( N_1^* > \eta \), \( N_2^* > \eta \), and \( \eta > 0 \). We have \( \frac{r_1}{r_2} < \frac{\phi_1}{\phi_2} \), \( \frac{r_2 - \omega}{r_1 - \omega} < \frac{\phi_1}{\phi_2} \). Then

\[
\xi \frac{1}{\xi_1} \frac{dN_2}{dt} - 1 - \frac{N_1}{\xi_1} \frac{dN_1}{dt} < 0
\]

for \( \xi_1 = \frac{\phi_1}{\phi_2}, \xi_2 = r_1 - \omega - (r_2 - \omega) \frac{\phi_1}{\phi_2} < 0 \). This, similarly as in Case 1, implies that

\[
(N_2(t))^{\xi_1 (V(t)) - \frac{\phi_1}{\phi_2}} \to 0 \text{ as } t \to \infty,
\]

and hence \( N_2(t) V(t) \to 0 \) as \( t \to \infty \).

Now we prove that \( N_2(t) \to 0 \) as \( t \to \infty \). If this is not true, then there exists \( \epsilon_0 > 0 \) and a sequence \( \{t_n\} \) with \( t_n \to \infty \), such that \( N_2(t_n) \geq \epsilon_0 \). Since \( N_2(t) V(t) \to 0 \) as \( t \to \infty \), we have \( V(t_n) \to 0 \) as \( t \to \infty \). Since \( \{N_2(t_n)\} \) is bounded, there is a subsequence of \( \{t_n\} \), which without loss of generality we still write as \( \{t_n\} \), such that \( N_2(t_n) \to \tilde{N}_2 > 0 \) for some \( \tilde{N}_2 > 0 \). Similarly, there is a subsequence of \( \{t_n\} \), which we still write as \( \{t_n\} \), such that \( N_1(t_n) \to \tilde{N}_1 \) as \( t \to \infty \) for some \( \tilde{N}_1 \geq 0 \). If \( \tilde{N}_1 = 0 \), then \( (0, \tilde{N}_2, 0) \in \omega(u) \), where \( \omega(u) \) is the \( \omega \)-limit set of \( u \). By invariance of \( \omega \)-limit set, \( E_3^{nnv} = (0, (r_2 - \omega)K/r_2, 0) \in \omega(u) \). Note that this theorem is to prove the global stability of \( E_3^{nnv} \) for initial conditions not on the stable manifold of \( E_0^{nnv}, E_1^{nnv}, E_2^{nnv} \), and \( E_3^{nnv} \). We assume that \( E_2^{nnv} \neq \omega(u) \). In the \( N_1 N_2 \) plane, there are two possibilities: (i) \( E_1^{nnv} \) is stable but \( E_2^{nnv} \) is a saddle or (ii) \( E_1^{nnv} \) is a saddle but \( E_2^{nnv} \) is stable. Note that \( (N_1(t), N_2(t), V(t)) \) is bounded. In case (i), from Butler-Mcgehee Lemma (see e.g., Lemma 1.2.7 in [22]), \( (0, 0, 0) \in \omega(u) \) as \( (0, 0, 0) \) is the \( \alpha \)-limit set of a bounded orbit on the stable manifold of \( E_2^{nnv} \), which is a contradiction since \( (0, 0, 0) \) is a repeller. In case (ii), since \( E_2^{nnv} \) is a saddle in the \( N_2 V \) plane and there is a trajectory connecting from \( E_2^{nnv} \) to \( E_3^{nnv} \), again by Butler-Mcgehee Lemma, \( E_4^{nnv} \in \omega(u) \). Thus, there is a subsequence \( t_n \) such that \( (N_2(t_n), N_3(t_n), V(t_n)) \to E_4^{nnv} \) as \( n \to \infty \), which is a contradiction to \( N_2(t) V(t) \to 0 \) as \( t \to \infty \). If \( \tilde{N}_1 > 0 \), then \( (\tilde{N}_1, \tilde{N}_2, 0) \in \omega(u) \). Since \( (\tilde{N}_1, \tilde{N}_2, 0) \) is not an equilibrium of the model, the whole solution through \( (\tilde{N}_1, \tilde{N}_2, 0) \) is in \( \omega(u) \).
Since the $\omega$-limit set of $(N_1, N_2, 0)$ is either $E_1^{nnv}$ or $E_2^{nnv}$, we then have either $E_1^{nnv} \in \omega(w^0)$ or $E_2^{nnv} \in \omega(w^0)$. If $E_2^{nnv} \in \omega(w^0)$, then the above arguments yield contradictions. If $E_1^{nnv} \in \omega(w^0)$ in case (ii), Butler-Mcgehee Lemma implies that $E_0^{nnv} = (0, 0, 0) \in \omega(w^0)$, which is a contradiction. If $E_1^{nnv} \in \omega(w^0)$ in case (i), then Butler-Mcgehee Lemma implies that $E_3^{nnv} \in \omega(w^0)$. Since $E_3^{nnv}$ is an attractor and $\omega(w^0)$ is a compact internally chain transitive set, it follows from Theorem 1.2.1 in [22] that $\omega(w^0) = E_3^{nnv}$, which is exactly what we want to prove in this theorem. Thus, we have proved that either $N_2(t) \to 0$ as $t \to \infty$ or $\omega(w^0) = E_3^{nnv}$ in case 3, either of which leads to the result that $\lim_{t \to \infty} (N_1(t), N_2(t), V(t)) = E_3^{nnv}$. □

Similarly we can prove the following result.

**Theorem 3.7.** If both $E_3^{nnv}$ and $E_4^{nnv}$ are nonnegative, $E_3^{nnv}$ is unstable but $E_4^{nnv}$ is stable (that is, when $\frac{\phi_1}{\phi_2} < \frac{r_2}{r_1}$, $N_1^* > \eta$, $N_2^* > \eta$ or when $\frac{\phi_1}{\phi_2} > \frac{r_2}{r_1}$ and $N_1^* < \eta$, $N_2^* < \eta$), then $E_4^{nnv}$ is globally asymptotically stable for (4) for all positive initial conditions.

In the other cases when $r_1 > \omega$, $r_2 > \omega$, and $E_5^{nnv}$ is not positive, we can also prove that one of the nonnegative equilibria is globally asymptotically stable while the others are unstable, by using similar arguments as in Theorems 3.6 and 3.7.

**Theorem 3.8.** In the case where $r_1 > \omega$, $r_2 > \omega$, and one component of $E_5^{nnv}$ is negative, the following statements are valid for system (4).

(i) If $r_1 > r_2$, $N_1^* > \bar{N}_1$, and $N_2^* < \bar{N}_2$, then $E_0^{nnv}$, $E_2^{nnv}$, and $E_4^{nnv}$ are unstable, and $E_1^{nnv}$ is globally asymptotically stable.

(ii) If $r_1 < r_2$, $N_1^* < \bar{N}_1$, and $N_2^* > \bar{N}_2$, then $E_3^{nnv}$, $E_1^{nnv}$, and $E_3^{nnv}$ are unstable, and $E_2^{nnv}$ is globally asymptotically stable.

(iii) If $r_1 > r_2$, $N_1^* < \bar{N}_1$, and $N_2^* > \bar{N}_2$, then $E_0^{nnv}$, $E_1^{nnv}$, and $E_2^{nnv}$ are unstable, and $E_3^{nnv}$ is globally asymptotically stable.

(iv) If $r_1 < r_2$, $N_1^* > \bar{N}_1$, and $N_2^* < \bar{N}_2$, then $E_0^{nnv}$, $E_1^{nnv}$, and $E_2^{nnv}$ are unstable, and $E_4^{nnv}$ is globally asymptotically stable.

(v) If $r_1 > r_2$, $N_1^* > \bar{N}_1$, and $N_2^* > \bar{N}_2$, then $E_0^{nnv}$ and $E_2^{nnv}$ are unstable, and $E_4^{nnv}$ is globally asymptotically stable.

(vi) If $r_1 < r_2$, $N_1^* > \bar{N}_1$, and $N_2^* > \bar{N}_2$, then $E_0^{nnv}$ and $E_1^{nnv}$ are unstable, and $E_2^{nnv}$ is globally asymptotically stable.

**Proof.** We only prove (i). (ii)-(vi) can be similarly proved.

Assume $r_1 > r_2$, $N_1^* > \bar{N}_1$, and $N_2^* < \bar{N}_2$. By Lemma 3.3, $E_0^{nnv}$ and $E_2^{nnv}$ are unstable, $E_1^{nnv}$ is locally asymptotically stable, $E_3^{nnv}$ is negative, and $E_4^{nnv}$ is nonnegative.

We now prove that $E_2^{nnv}$ is unstable. Note that we are considering the case where at least one component of $E_5^{nnv}$ is negative. Case (1). $\phi_1 r_2 - \phi_2 r_1 < 0$. This implies $\frac{\phi_2}{\phi_1} < \frac{r_2}{r_1}$ and $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$. Since $r_1 > r_2$, we have $\frac{r_2 - \omega}{r_2 - \omega} > \frac{r_1}{r_2}$ and $\frac{r_2 - \omega}{r_1 - \omega} < \frac{r_2}{r_1}$. Then we have $\frac{\phi_2}{\phi_1} < \frac{r_2}{r_1}$ and $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$, which implies $\eta > \bar{N}_1$ and $\eta > \bar{N}_2$. Hence, $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) > 0$, which indicates that $E_4^{nnv}$ is unstable. Case (2). $\phi_1 r_2 - \phi_2 r_1 > 0$. Then $\frac{\phi_2}{\phi_1} > \frac{r_2}{r_1}$. Moreover, $\frac{r_2 - \omega}{r_1 - \omega} < \frac{r_2}{r_1}$. If $\frac{\phi_2}{\phi_1} > \frac{r_2 - \omega}{r_1 - \omega}$, then $\eta > 0$ and hence, $N_1^* > \eta$. If $\frac{\phi_2}{\phi_1} < \frac{r_2 - \omega}{r_1 - \omega}$, then we still have $N_1^* > \eta$. Therefore, $N_1^* > \eta$ is always true. If $\phi_1 \phi_2 - \phi_2^2 \phi_2 > 0$, then $\eta < N_1^* < N_2^*$, which implies that $E_4^{nnv}$ is unstable. If $\phi_1 \phi_2 - \phi_2^2 \phi_2 < 0$, then for one component of $E_5^{nnv}$ to be negative, we must have $\bar{N}_2 > \eta$, which again implies that $E_4^{nnv}$
is unstable. Therefore, we always have $E_{5}^{nu}$ is unstable if $r_1 > r_2$, $N_1^* > \tilde{N}_1$, $N_2^* < \tilde{N}_2$, and at least one component of $E_5^{nu}$ is negative.

Now we prove the global stability of $E_1^{nu}$. In Case (1) as above, we have $\frac{\phi_1}{\phi_2} < \frac{\omega}{N_1^*} < \frac{\omega}{r}$. Similarly as we do in Case 2 in the proof of Theorem 3.6, we can obtain $\tilde{N}_2(t) \to 0$ as $t \to \infty$. Then Lemma 3.1 (ii) implies that $E_1^{nu}$ is globally asymptotically stable.

Based on the existence and stability conditions for all equilibria in Table 1 and similar arguments as in Theorem 3.8, we can obtain all possible local dynamics of (4) when $r_1 > \omega$, $r_2 > \omega$, and $E_5^{nu}$ is positive.

**Theorem 3.9.** In the case where $r_1 > \omega$, $r_2 > \omega$, and $E_5^{nu}$ is positive, the following statements are valid for system (4).

1. If (a) $r_1 > r_2$, $\phi_1 r_2 > \phi_2 r_1$, $\tilde{N}_1 > N_1^* > \eta > N_2^*$, $\tilde{N}_2 > N_2^*$ or (b) $r_1 < r_2$, $\phi_1 r_2 < \phi_2 r_1$, $N_1^* < \eta < N_2^* < \tilde{N}_2$, $N_1^* < \tilde{N}_1$, then $E_0^{nu}$, $E_1^{nu}$, $E_2^{nu}$, and $E_5^{nu}$ are unstable, but $E_3^{nu}$ and $E_4^{nu}$ are locally asymptotically stable.

2. If (a) $r_1 > r_2$, $\phi_1 r_2 > \phi_2 r_1$, $N_1^* < \eta < N_2^* < \tilde{N}_2 < \tilde{N}_1$ or, (b) $r_1 < r_2$, $\phi_1 r_2 < \phi_2 r_1$, $\tilde{N}_2 > \tilde{N}_1 > N_1^* > \eta > N_2^*$, then $E_0^{nu}$, $E_1^{nu}$, $E_2^{nu}$, $E_3^{nu}$ and $E_4^{nu}$ are unstable, and $E_5^{nu}$ is locally asymptotically stable.

3. If $r_1 > r_2$, $\phi_1 r_2 > \phi_2 r_1$, $N_1^* > \tilde{N}_1 > \tilde{N}_2 > \eta > N_2^*$, then $E_0^{nu}$, $E_2^{nu}$, and $E_5^{nu}$ are unstable, $E_1^{nu}$ and $E_4^{nu}$ are locally asymptotically stable.

4. If $r_1 < r_2$, $\phi_1 r_2 < \phi_2 r_1$, $N_1^* < \eta < \tilde{N}_1 < \tilde{N}_2 < N_2^*$, then $E_0^{nu}$, $E_1^{nu}$, and $E_5^{nu}$ are unstable, $E_2^{nu}$ and $E_3^{nu}$ are locally asymptotically stable.

5. If $r_1 > r_2$, $\phi_1 r_2 > \phi_2 r_1$, $N_1^* < \eta < \tilde{N}_2 < \tilde{N}_1$, $\tilde{N}_2 > N_2^*$, then $E_0^{nu}$, $E_4^{nu}$, $E_3^{nu}$ and $E_5^{nu}$ are unstable, and $E_4^{nu}$ is locally asymptotically stable.

6. If $r_1 < r_2$, $\phi_1 r_2 < \phi_2 r_1$, $\tilde{N}_1 > \tilde{N}_2 > \tilde{N}_1 > N_1^*$, then $E_0^{nu}$, $E_4^{nu}$, $E_2^{nu}$, $E_5^{nu}$ are unstable, and $E_4^{nu}$ is locally asymptotically stable.

The results in Theorems 3.4-3.9 are listed in Table 2.

In the following, we study the persistence dynamics of (4) when $E_5^{nu}$ is positive and locally asymptotically stable. Let $X = X_2^{\phi_1}$ with $||x|| = \max_{i=1,2,3} |x_i|$ for $x = (x_1, x_2, x_3) \in X$, $X_0 = \{(x_1, x_2, x_3) : x_1 > 0, x_2 > 0, x_3 > 0\}$. Then $X_0 = X \setminus \{ (x_1, x_2, x_3) \in X : x_1 = 0 \text{ or } x_2 = 0 \text{ or } x_3 = 0 \}$.

**Theorem 3.10.** If all the nonnegative equilibria are unstable except that the positive equilibrium $E_5^{nu}$ is stable (that is, in cases (a), (r), or (s) in Table 2), then system (4) is uniformly persistent in the sense that there exists $\xi > 0$ such that

$$\liminf_{t \to \infty} N_1(t) > \xi, \liminf_{t \to \infty} N_2(t) > \xi, \liminf_{t \to \infty} V(t) > \xi,$$

for any solution $(N_1(t), N_2(t), V(t))$ of (4) with positive initial conditions. Moreover, (4) admits a global attractor in $X_0$.

**Proof.** The assumptions cover the cases (a), (r), and (s) in Table 2. We will only prove the result in case (o). The proof is similar in the other two cases. Therefore, we assume that all equilibria of (4) are nonnegative with $E_0^{nu}$- $E_4^{nu}$ being unstable and the positive equilibrium $E_5^{nu}$ being stable.

By the equations in (4), we see that $X_0$ and $\partial X_0$ are both positively invariant. By the proof of Theorem 3.6, we know that there exist $u_{N_1} > 0$, $u_{N_2} > 0$, $u_V > 0$, $u_{E_1} > 0$, $u_{E_2} > 0$, $u_{E_3} > 0$, $u_{E_4} > 0$, and $u_{E_5} > 0$.
such that when $t$ is sufficiently large, $0 \leq N_1(t) < u_{N_1}$, $0 \leq N_2(t) < u_{N_2}$, and $0 \leq V(t) < u_V$ for any solution $(N_1(t), N_2(t), V(t))$ of (4) with initial conditions in $X$. This implies that (4) admits a global attractor in $X$.

For any initial condition $w^0 \in X$, let $Q(t, w^0) = (N_1(t), N_2(t), V(t))$ be the solution of model (4) with initial condition $w^0 = (N_1^0, N_2^0, V^0) \in X$ and $\omega(w^0)$ be the omega limit set of the orbit $Q(t, w^0)$ ($t \geq 0$).

**Claim 1.** $U_{w^0 \in \partial X} \omega(w^0) \subseteq \bigcup_{i=0}^{T_l} \{E_i^{\text{inv}}\}$. 

| Condition | $E_0^{\text{inv}}$ | $E_1^{\text{inv}}$ | $E_2^{\text{inv}}$ | $E_3^{\text{inv}}$ | $E_4^{\text{inv}}$ | $E_5^{\text{inv}}$ |
|-----------|------------------|------------------|------------------|------------------|------------------|------------------|
| (a) $r_1 < \omega, r_2 < \omega$ | GAS | - | - | - | - | - |
| (b) $r_2 < \omega < r_1, N_1^* > N_1$ | U | GAS | - | - | - | - |
| (c) $r_2 < \omega < r_1, N_1^* < N_1$ | U | U | - | GAS | - | - |
| (d) $r_1 < \omega < r_2, N_2^* > N_2$ | U | - | GAS | - | - | - |
| (e) $r_1 < \omega < r_2, N_2^* < N_2$ | U | - | U | - | GAS | - |
| (f) $r_1, r_2 > \omega, N_1^* < N_1, N_2^* < N_2$ | U | U | U | U | GAS | - |
| (g) $(\phi_2 r_2 - \phi_2 r_1)(N_2^* - \eta) < 0$ | U | U | U | GAS | U | - |
| (h) $r_1 > r_2 > \omega, N_1^* > N_1, N_2^* < N_2$ | U | GAS | U | - | U | - |
| (i) $\omega < r_1 < r_2, N_1^* < N_1, N_2^* > N_2$ | U | U | GAS | U | - | - |
| (j) $r_1 > r_2 > \omega, N_1^* < N_1, N_2^* > N_2$ | U | U | U | GAS | - | - |
| (k) $\omega < r_1 < r_2, N_1^* > N_1, N_2^* < N_2$ | U | U | - | GAS | - | - |
| (l) $r_1 > r_2 > \omega, N_1^* > N_1, N_2^* > N_2$ | U | GAS | U | - | - | - |
| (m) $\omega < r_1 < r_2, N_1^* > N_1, N_2^* > N_2$ | U | U | GAS | - | - | - |
| (n) $(a) r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1$ | U | U | S | S | S | U |
| (o) $(a) r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1$ | U | U | U | U | S | |
| (p) $r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1$ | U | S | U | - | S | U |
| (q) $r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1$ | U | U | S | S | S | - |
| (r) $r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1$ | U | U | U | - | S | - |
| (s) $\omega < r_1 < r_2, \phi_1 r_2 > \phi_2 r_1$ | U | U | U | - | S | - |

**Table 2.** Global or local dynamics of (4). $E_0^{\text{inv}}$-$E_5^{\text{inv}}$ are defined in (5). Conditions for $E_0^{\text{inv}}$ to be positive or not may not be all listed. “-” represents that some compartments of the equilibrium are negative. “U” represents “unstable”; “GAS” represents “globally asymptotically stable”, “S” represents “locally asymptotically stable”.
Given \( w^0 \in \partial X_0 \), we have \( Q(t,w^0) \in \partial X_0 \) for all \( t \geq 0 \). Hence, \( N_1(t) \equiv 0 \) or \( N_2(t) \equiv 0 \) or \( V(t) \equiv 0 \) for all \( t \geq 0 \). By Lemmas 3.1 and 3.2, we know that if \( N_1(t) \equiv 0 \), then \( \omega(w^0) \in E_0^{nnv} \cup E_2^{nnv} \cup E_4^{nnv} \), that if \( N_2(t) \equiv 0 \), then \( \omega(w^0) \in E_0^{nnv} \cup E_1^{nnv} \cup E_3^{nnv} \), and that if \( V(t) \equiv 0 \), then \( \omega(w^0) \in E_0^{nnv} \cup E_1^{nnv} \cup E_2^{nnv} \). Claim 1 is proved.

**Claim 2.** each \( E_i^{nnv} (i = 0, \ldots, 4) \) is a uniform weak repeller for \( X_0 \) in the sense that there exists \( \rho > 0 \) such that

\[
\limsup_{t \to \infty} \|Q(t,w^0) - E_i^{nnv}\| \geq \rho, \text{ for all } w^0 \in X_0. \quad (8)
\]

Assume that (8) is not true for \( E_0^{nnv} \). Since \( r_1 > \omega \), there exists \( \epsilon > 0 \) such that \( r_1 - \omega - \left(\frac{2r_1}{K} + \phi_1\right) \epsilon > 0 \). Assume that \( \limsup_{t \to \infty} \|Q(t,w^0)\| < \epsilon \) for some \( w^0 \in X_0 \). Then there exists \( t_0 > 0 \) such that for \( t > t_0 \), \( N_1(t) < \epsilon, N_2(t) < \epsilon \), and \( V(t) < \epsilon \), and

\[
\frac{dN_1}{dt} = r_1N_1 \left(1 - \frac{N_1 + N_2}{K}\right) - \phi_1N_1V - \omega N_1 > \left(r_1 - \omega - \left(\frac{2r_1}{K} + \phi_1\right) \epsilon\right) N_1,
\]

which implies \( N_1(t) \to \infty \) as \( t \to \infty \). A contradiction. Hence, (8) is true for \( E_0^{nnv} \). Assume that (8) is not true for \( E_1^{nnv} \). Note that the conditions in this theorem imply \( N_1^* < N_1 \). Let \( \epsilon > 0 \) be sufficiently small such that \( N_1 - \epsilon < N_1^* > 0 \). Assume that \( \limsup_{t \to \infty} \|Q(t,w^0) - E_1^{nnv}\| < \epsilon \) for some \( w^0 \in X_0 \). Then there exists \( t_0 > 0 \) such that for \( t > t_0 \), \( N_1 - \epsilon < N_1(t), N_2(t) < \epsilon, V(t) < \epsilon \), and

\[
\frac{dV}{dt} = \beta_1 \phi_1 N_1 V + \beta_2 \phi_2 N_2 V - mV - \omega V > \beta_1 \phi_1 (\tilde{N}_1 - \epsilon - N_1^*) V,
\]

which implies \( V(t) \to \infty \) as \( t \to \infty \). A contradiction. Hence, (8) is true for \( E_1^{nnv} \). Similarly, we can prove that (8) is true for \( E_2^{nnv} \) by applying the fact \( N_2^* < N_2 \). Assume that (8) is not true for \( E_3^{nnv} \). Since \( E_3^{nnv} \) is unstable, the eigenvalue \( \lambda_{E_3^{nnv}} \) of \( J(E_3^{nnv}) \) satisfies \( \lambda_{E_3^{nnv}} = r_2(1 - \frac{N_1^*}{K}) - \phi_2 \hat{V}^* - \omega > 0 \). Let \( \epsilon > 0 \) be sufficiently small such that \( r_2(1 - \frac{N_1^*}{K}) - \phi_2 \hat{V}^* - \omega - \epsilon(\frac{2r_2}{K} + \phi_2) > 0 \). Assume that \( \limsup_{t \to \infty} \|Q(t,w^0) - E_3^{nnv}\| < \epsilon \) for some \( w^0 \in X_0 \). Then there exists \( t_0 > 0 \) such that for \( t > t_0 \), \( N_1^* - \epsilon < N_1(t), \epsilon \), \( N_2(t) < \epsilon, V^* - \epsilon < N_1(t) < V^* + \epsilon \), and

\[
\frac{dN_2}{dt} > \left(r_2(1 - \frac{N_1^*}{K}) - \phi_2 \hat{V}^* - \omega - \epsilon(\frac{2r_2}{K} + \phi_2)\right) N_2,
\]

which implies \( N_2(t) \to \infty \) as \( t \to \infty \). A contradiction. Hence, (8) is true for \( E_3^{nnv} \). Similarly, we can prove that (8) is true for \( E_4^{nnv} \) by applying the fact the eigenvalue \( \lambda_{E_4^{nnv}} \) of \( J(E_4^{nnv}) \) is positive. The proof of Claim 2 is completed.

By the above arguments, we know that any forward orbit of (4) in \( \partial X_0 \) converges to \( \bigcup_{i=0}^{4} \{E_i^{nnv}\} \), each of these equilibria is isolated in \( X \), and \( W^s(E_i^{nnv}) \cap X_0 = \emptyset \) for \( i = 0, \ldots, 4 \), where \( W^s(E_i^{nnv}) \) is the stable set of \( E_i^{nnv} \). Moreover, by the positive invariance of \( \partial X_0 \) and Lemmas 3.1 and 3.2, we obtain that all possible connections among \( E_i^{nnv} \) are \( E_0^{nnv} \to E_1^{nnv}, E_0^{nnv} \to E_2^{nnv}, E_1^{nnv} \to E_3^{nnv}, \) and \( E_2^{nnv} \to E_4^{nnv} \), as well as \( E_2^{nnv} \to E_3^{nnv} \) if \( r_1 > r_2 \) or \( E_3^{nnv} \to E_4^{nnv} \) if \( r_1 < r_2 \), and hence, there is no cycle in \( \partial X_0 \) from \( \bigcup_{i=0}^{4} \{E_i^{nnv}\} \) to themselves.

Define a continuous function \( p : X \to [0, \infty) \) by \( p(w^0) = \min\{N_1^0, N_2^0, V_0^0\} \) for \( w^0 = (N_1^0, N_2^0, V_0^0) \in X \). It follows that \( p^{-1}(0, \infty) \subseteq X_0 \) and \( p \) has the property that if \( p(w^0) > 0 \) then \( p(Q(t,w^0)) > 0 \) for all \( t > 0 \). So, \( p \) is a generalized distance function for the solution map of (4). By [17, Theorem 3], it follows that there exists a \( \xi > 0 \) such that for any \( w^0 \in X_0 \), \( \liminf_{t \to \infty} p(Q(t,w^0)) > \xi \). Hence,
lim \inf_{t \to \infty} N_1(t) > \xi, \liminf_{t \to \infty} N_2(t) > \xi, \liminf_{t \to \infty} V(t) > \xi \text{ for any initial condition } w^0 \in X_0. \text{ Then by Theorem 1.3.6 in [22], (4) admits a global attractor in } X_0.

Remark 3.11. The results in Table 2 and Theorem 3.10 show the following:

(i) when the equilibrium \( E_{5}^{nu} \) is not positive, if one nonnegative equilibrium is locally asymptotically stable, then it is globally asymptotically stable;
(ii) when \( E_{5}^{nu} \) is positive but unstable, then bistability appears;
(iii) when \( E_{5}^{nu} \) is positive and locally asymptotically stable, then the two host-one virus model (4) is uniformly persistent.

In the following, we give some sufficient condition for \( E_{5}^{nu} \) to be globally asymptotically stable when it is positive.

Theorem 3.12. If \( \frac{r_1}{r_2} = \frac{\beta_2}{\beta_1} \) and \( E_{5}^{nu} \) is positive, then it is globally asymptotically stable.

Proof. Note that when \( \frac{r_1}{r_2} = \frac{\beta_2}{\beta_1} \), if \( E_{5}^{nu} \) is positive, then it is locally asymptotically stable.

Let

\[ V = N_1 - N_1^c - N_2^c \ln \frac{N_1}{N_1^c} + c_1 \left( N_2 - N_2^c - N_2^c \ln \frac{N_2}{N_2^c} \right) + c_2 \left( V - V^c - V^c \ln \frac{V}{V^c} \right). \]

Then for positive \( c_1 \) and \( c_2 \), \( V > 0 \) for all \( N_1 > 0, N_2 > 0 \) and \( V > 0 \) and \( V \) is radially unbounded. Moreover,

\[
\frac{dV}{dt} = \left( N_1 - N_1^c \right) \left( -\frac{r_1}{K} (N_1 + N_2 - (N_1^c + N_2^c)) - \phi_1(V - V^c) \right) \\
+ c_1 \left( N_2 - N_2^c \right) \left( -\frac{r_2}{K} (N_1 + N_2 - (N_1^c + N_2^c)) - \phi_2(V - V^c) \right) \\
+ c_2 (V - V^c) (\beta_1 \phi_1(N_1 - N_1^c) + \beta_2 \phi_2(N_2 - N_2^c)) \\
= -\frac{r_1}{K} \left( N_1 - N_1^c + \frac{r_1 + c_1 r_2}{2 r_1} (N_2 - N_2^c) \right)^2 + \frac{(r_1 - c_1 r_2)^2}{4 r_1 K} (N_2 - N_2^c)^2 \\
+ (c_2 \beta_1 - 1) \phi_1(N_1 - N_1^c)(V - V^c) + (c_2 \beta_2 - c_1) \phi_2(N_2 - N_2^c)(V - V^c)
\]

Choose \( c_2 = \frac{1}{\beta_1}, c_1 = \frac{\beta_2}{\beta_1} \). If \( r_1 = c_1 r_2 = \frac{\beta_2}{\beta_1} r_2 \), then

\[
\frac{dV}{dt} = -\frac{r_1}{K} (N_1 - N_1^c + N_2 - N_2^c)^2 \leq 0.
\]

By LaSalle’s invariance principle, the set of accumulation points of any solution is contained in \( Z \), which is the union of complete trajectories contained entirely in the set \( \{ x : dV(x)/dt = 0 \} \). Since \( E_{5}^{nu} \) is the only complete solution in this set, it is globally asymptotically stable with respect to initial conditions \( N_1^0 > 0, N_2^0 > 0, \) and \( V^0 > 0 \).

4. Dynamics of the two host-two virus model (1). In this section, we study the local dynamics and persistence of the two host-two virus model (1).

4.1. Equilibria and their local stability. There are potentially 10 nonnegative equilibria of (1):

\[
E_0 = (0, 0, 0, 0), \quad E_1 = (\hat{N}_1, 0, 0, 0), \quad E_2 = (0, \hat{N}_2, 0, 0),
\]

\[
E_3 = (N_1^*, 1, 0, \frac{r_1 (N_1^* - N_1^*)}{K + r_1 N_1^*}), \quad E_4 = (N_1^*, 0, 0, \frac{r_1 (N_1^* - N_1^*)}{K + r_1 N_1^*}),
\]

\[
E_5 = (0, N_2^*, 0, \frac{r_2 (N_2^* - N_2^*)}{K + r_2 N_2^*}), \quad E_6 = (0, N_2^*, 0, \frac{r_2 (N_2^* - N_2^*)}{K + r_2 N_2^*}),
\]

\[
E_7 = (N_1^*, N_2^*, \hat{V}_1^*, 0), \quad E_8 = (N_1^*, \hat{N}_2^*, 0, \hat{V}_2^*), \quad E_9 = (N_1^*, N_2^*, \hat{V}_1^*, \hat{V}_2^*),
\]

Here \( \hat{N}_1, \hat{N}_2, \hat{V}_1, \hat{V}_2 \) are positive constants.
where

\[
\begin{align*}
\dot{N}_1 &= (r_1 - \omega)K, \quad \dot{N}_2 = (r_2 - \omega)K, \\
N_{1,1} &= \frac{m_1 + \omega}{\beta_1 \phi_{11}}, \quad N_{2,1} = \frac{m_2 + \omega}{\beta_2 \phi_{21}}, \quad \dot{N}_{1,2} = \frac{m_2 + \omega}{\beta_{12} \phi_{12}}, \quad \dot{N}_{2,2} = \frac{m_2 + \omega}{\beta_{22} \phi_{22}}, \\
\eta_1 &= (\phi_{11}(r_2 - \omega) - \phi_{21}(r_1 - \omega))K, \quad \eta_2 = (\phi_{12}(r_2 - \omega) - \phi_{22}(r_1 - \omega))K, \\
N_1 &= \frac{\beta_1 \phi_{11}(N_{1,1} - \eta_1) - \beta_1 \phi_{12}(N_{1,2} - \eta_2)}{\beta_1 \phi_{12} - \beta_2 \phi_{22}}, \quad N_2 = \frac{\beta_1 \phi_{21}(N_{2,1} - \eta_1) - \beta_2 \phi_{22}(N_{2,2} - \eta_2)}{\beta_1 \phi_{12} - \beta_2 \phi_{22}}, \\
\dot{N}_1 &= \frac{\beta_1 \phi_{11}(N_{1,1} - \eta_1)}{\beta_1 \phi_{12} - \beta_2 \phi_{22}}, \quad \dot{N}_2 = \frac{\beta_1 \phi_{21}(N_{2,1} - \eta_1)}{\beta_1 \phi_{12} - \beta_2 \phi_{22}}, \\
V_1 &= \frac{(\beta_1 \phi_{11}(m_2 + \omega) - \beta_2 \phi_{21}(m_1 + \omega))K}{(\beta_1 \phi_{12} - \beta_2 \phi_{22})(m_1 + \omega)}, \quad V_2 = \frac{(\beta_1 \phi_{11}(m_2 + \omega) - \beta_2 \phi_{21}(m_1 + \omega))K}{(\beta_1 \phi_{12} - \beta_2 \phi_{22})(m_1 + \omega)}, \\
B\Phi &= \beta_1 \beta_2 \phi_{11}(m_2 + \omega) - \beta_2 \phi_{12}(m_1 + \omega), \quad B\Phi_1 = \beta_1 \phi_{11}(m_2 + \omega) + \beta_2 \phi_{22}(m_1 + \omega), \\
NN &= (N_{1,1} + N_{2,1} - 1),
\end{align*}
\]

(9)

For simplicity, we denote

\begin{align*}
B\Phi &= \beta_1 \beta_2 \phi_{11}(m_2 + \omega) - \beta_2 \phi_{12}(m_1 + \omega), \quad B\Phi_1 = \beta_1 \phi_{11}(m_2 + \omega) + \beta_2 \phi_{22}(m_1 + \omega), \\
B\Phi &= \beta_1 \phi_{11}(m_2 + \omega) - \beta_2 \phi_{12}(m_1 + \omega), \quad B\Phi_1 = \beta_1 \phi_{11}(m_2 + \omega) + \beta_2 \phi_{22}(m_1 + \omega), \\
N &N &= (N_{1,1} + N_{2,1} - 1).
\end{align*}

(10)

**Lemma 4.1.** The following statements are valid for (1).

(i) \(E_0\) is locally asymptotically stable if \(r_1 < \omega\) and \(r_2 < \omega\); it is unstable if \(r_1 > \omega\) or \(r_2 > \omega\).

(ii) \(E_1\) is nonnegative if \(r_1 > \omega\) and is locally asymptotically stable if \(r_1 > r_2\), \(N_1 < N_{1,1}\), and \(N_1 < N_{1,2}\).

(iii) \(E_2\) is nonnegative if \(r_2 > \omega\) and is locally asymptotically stable if \(r_1 < r_2\), \(N_2 < N_{2,1}\) and \(N_2 < N_{2,2}\).

(iv) \(E_3\) is nonnegative if \(N_1 > N_{1,1}\) and is locally asymptotically stable if \(\beta_1 \phi_{11}(m_2 + \omega) > \beta_2 \phi_{12}(m_1 + \omega)\), and \((\phi_{11}r_2 - \phi_{21}r_1)(N_{1,1} - \eta_1) > 0\).

(v) \(E_4\) is nonnegative if \(N_1 > N_{1,2}\) and is locally asymptotically stable if \(\beta_1 \phi_{11}(m_2 + \omega) < \beta_2 \phi_{12}(m_1 + \omega)\), and \((\phi_{11}r_2 - \phi_{21}r_1)(N_{1,2} - \eta_2) > 0\).

(vi) \(E_5\) is nonnegative if \(N_2 > N_{2,1}\) and is locally asymptotically stable if \(\beta_2 \phi_{21}(m_2 + \omega) > \beta_2 \phi_{22}(m_1 + \omega)\) and \((\phi_{11}r_2 - \phi_{21}r_1)(N_{2,1} - \eta_1) < 0\).

(vii) \(E_6\) is nonnegative if \(N_2 > N_{2,2}\) and is locally asymptotically stable if \(\beta_2 \phi_{21}(m_2 + \omega) < \beta_2 \phi_{22}(m_1 + \omega)\), and \((\phi_{11}r_2 - \phi_{21}r_1)(N_{2,2} - \eta_2) < 0\).

(viii) \(E_7\) is nonnegative if \(\beta_1 \phi_{11} - \beta_2 \phi_{21}(N_{2,1} - \eta_1) > 0, (\beta_1 \phi_{11} - \beta_2 \phi_{21})(N_{2,1} - \eta_1) < 0, \) and \((\phi_{11}r_2 - \phi_{21}r_1)(r_1 - r_2) > 0\). It is locally asymptotically stable if \(\frac{N_{1,1}}{N_{1,2}} + \frac{N_{1,2}}{N_{2,2}} < 1\) and \((\phi_{11}r_2 - \phi_{21}r_1)(\beta_1 \phi_{11} - \beta_2 \phi_{21}) > 0\).
(ix) \(E_8\) is nonnegative if \((\beta_{12}\phi_{12} - \beta_{22}\phi_{22})(N_{2,1}^* - \eta_2) > 0, (\beta_{12}\phi_{12} - \beta_{22}\phi_{22})(\eta_2 - N_{2,2}^*) < 0, (\phi_{21}r_1 - \phi_{22}r_2)(r_1 - r_2) > 0\). It is locally asymptotically stable if 
\[
\frac{\tilde{N}_1}{\tilde{N}_{1,1}} + \frac{\tilde{N}_2}{\tilde{N}_{2,1}} - 1 < 0 \text{ and } (\phi_{12}r_2 - \phi_{22}r_1)(\beta_{12}\phi_{12} - \beta_{22}\phi_{22}) > 0.
\]

(x) \(E_9\) is positive if \(N_{1}^p > 0, N_{2}^p > 0, V_{1}^p > 0\) and \(V_{2}^p > 0\). \(E_9\) is locally asymptotically stable if \(\Phi \Phi \cdot B\Phi > 0\) and (14) are true.

**Proof.** The conditions for the equilibria to be nonnegative can be derived directly from the formulas of the equilibria. Local stability of the equilibria can be determined by the eigenvalues of the Jacobian matrix at each corresponding equilibrium. In the following, we only need to list the information about the eigenvalues of the Jacobian matrix at each equilibrium.

(i). At \(E_0\), the eigenvalues of the Jacobian matrix are \(r_1 - \omega, r_2 - \omega, -m_1 - \omega, -m_2 - \omega\).

(ii). At \(E_1\), the eigenvalues of the Jacobian matrix are \(\omega - r_1, -\omega(r_1 - r_2)/r_1, \beta_{12}\phi_{12}(\tilde{N}_1 - N_{1,2}^*), \beta_{11}\phi_{11}(\tilde{N}_1 - N_{1,1}^*)\).

(iii). At \(E_2\), the eigenvalues of the Jacobian matrix are \(\omega - r_2, \omega(r_1 - r_2)/r_2, \beta_{22}\phi_{22}(\tilde{N}_2 - N_{2,2}^*), \beta_{21}\phi_{21}(\tilde{N}_2 - N_{2,1}^*)\).

(iv). At \(E_3\), the eigenvalues of the Jacobian matrix are 
\[
\frac{(\phi_{11}r_1 - \phi_{21}r_1)(N_{1,1}^* - \eta_1)}{(\beta_{11}\phi_{11})(\beta_{21}\phi_{21})}, \text{ and other two with negative real parts when } E_3 \text{ is nonnegative.}
\]

(v). At \(E_4\), the eigenvalues of the Jacobian matrix are 
\[
\frac{(\phi_{11}r_1 - \phi_{21}r_1)(N_{1,2}^* - \eta_2)}{(\beta_{11}\phi_{11})(\beta_{21}\phi_{21})}, \text{ and other two with negative real parts when } E_4 \text{ is nonnegative.}
\]

(vi). At \(E_5\), the eigenvalues of the Jacobian matrix are 
\[
\frac{(\phi_{11}r_1 - \phi_{21}r_1)(N_{2,1}^* - \eta_1)}{(\beta_{11}\phi_{11})(\beta_{21}\phi_{21})}, \text{ and other two with negative real parts when } E_5 \text{ is nonnegative.}
\]

(vii). At \(E_6\), the eigenvalues of the Jacobian matrix are 
\[
\frac{(\phi_{11}r_1 - \phi_{21}r_1)(N_{2,2}^* - \eta_2)}{(\beta_{11}\phi_{11})(\beta_{21}\phi_{21})}, \text{ and other two with negative real parts when } E_6 \text{ is nonnegative.}
\]

(viii). At \(E_7\), one eigenvalue of the Jacobian matrix is \(\lambda_{E_7} = (m_2 + \omega)(\frac{N_{1}^p}{N_{1,2}^*} + \frac{N_{2}^p}{N_{2,2}^*} - 1)\); all other eigenvalues have negative real parts if and only if \((\phi_{11}r_2 - \phi_{21}r_1)(\beta_{11}\phi_{11} - \beta_{21}\phi_{21}) > 0\) if \(E_7\) is nonnegative.

(ix). At \(E_8\), one eigenvalue of the Jacobian matrix is \(\lambda_{E_8} = (m_1 + \omega)(\frac{N_{1}^p}{N_{1,1}^*} + \frac{N_{2}^p}{N_{2,1}^*} - 1)\); all other eigenvalues have negative real parts if and only if \((\phi_{12}r_2 - \phi_{22}r_1)(\beta_{12}\phi_{12} - \beta_{22}\phi_{22}) > 0\) if \(E_8\) is nonnegative.

(x). When \(E_9\) is positive, the Jacobian matrix at \(E_9\) is
\[
J(E_9) = \begin{bmatrix}
-\frac{r_1 N_{1}^p}{K_1} & -\frac{r_1 N_{2}^p}{K_1} & -\phi_{11} N_{1}^p & -\phi_{12} N_{2}^p \\
-\frac{r_2 N_{1}^p}{K_1} & -\frac{r_2 N_{2}^p}{K_1} & -\phi_{21} N_{1}^p & -\phi_{22} N_{2}^p \\
\beta_{11}\phi_{11} V_{1}^p & \beta_{21}\phi_{21} V_{1}^p & 0 & 0 \\
\beta_{12}\phi_{12} V_{2}^p & \beta_{22}\phi_{22} V_{2}^p & 0 & 0
\end{bmatrix}.
\]

The characteristic equation of \(J(E_9)\) is
\[
\lambda^4 + b_1 \lambda^3 + b_2 \lambda^2 + b_3 \lambda + b_4 = 0,
\]

(11)
where
\[ b_1 = \frac{N_1^p r_1 + N_2^p r_2}{K}, \]
\[ b_2 = N_1^p V_1^p \beta_{11} \phi_{11} + N_1^p V_2^p \beta_{12} \phi_{12} + N_2^p V_1^p \beta_{21} \phi_{21} + N_2^p V_2^p \beta_{22} \phi_{22}, \]
\[ b_3 = N_1^p N_2^p (V_1^p (\phi_{11} r_2 - \phi_{21} r_1)/(\beta_{11} \phi_{11} - \beta_{21} \phi_{21}) + V_2^p (\phi_{12} r_2 - \phi_{22} r_1)/(\beta_{12} \phi_{12} - \beta_{22} \phi_{22})), \]
\[ b_4 = N_1^p N_2^p V_1^p V_2^p (\phi_{11} \phi_{22} - \phi_{12} \phi_{21})/(\beta_{11} \beta_{22} \phi_{11} \phi_{22} - \beta_{12} \beta_{21} \phi_{12} \phi_{21}). \]

Let
\[ \Delta_1 = b_1, \]
\[ \Delta_2 = b_1 b_2 - b_3 \]
\[ = \frac{N_1^p N_2^p (V_1^p (\beta_{11} \phi_{11} \phi_{21} r_1 + \beta_{21} \phi_{11} \phi_{21} r_2) + V_2^p (\beta_{12} \phi_{12} \phi_{22} r_1 + \beta_{22} \phi_{12} \phi_{22} r_2))}{K} \]
\[ + (N_1^p)^2 (V_1^p \beta_{11} \phi_{11} r_1 + V_1^p \beta_{12} \phi_{12} r_1) + (N_2^p)^2 (V_2^p \beta_{21} \phi_{21} r_2 + V_2^p \beta_{22} \phi_{22} r_2), \]
\[ \Delta_3 = -b_4 b_1^2 + b_3 \Delta_2 \]
\[ = \frac{N_1^p N_2^p}{K^2} \cdot (B \Phi_1 (N_1^p \phi_{11} + N_2^p \phi_{21})V_1^p + B \Phi_2 (N_1^p \phi_{12} + N_2^p \phi_{22})V_2^p) \]
\[ \cdot (\Phi R_1 (N_1^p \beta_{11} \phi_{11} r_1 + N_2^p \beta_{21} \phi_{21} r_2)V_1^p + \Phi R_2 (N_1^p \beta_{12} \phi_{12} r_1 + N_2^p \beta_{22} \phi_{22} r_2)V_2^p). \]

By using Routh-Hurwitz theorem, we know that all eigenvalues of the Jacobian matrix have negative real parts if and only if \( \Delta_i > 0 \) for \( i = 1, 2, 3 \) and \( b_4 > 0 \), which is equivalent to that the following two conditions are true:
\[ \Phi \Phi \cdot B \Phi > 0 \]
\[ (B \Phi_1 (N_1^p \phi_{11} + N_2^p \phi_{21})V_1^p + B \Phi_2 (N_1^p \phi_{12} + N_2^p \phi_{22})V_2^p) \]
\[ \cdot (\Phi R_1 (N_1^p \beta_{11} \phi_{11} r_1 + N_2^p \beta_{21} \phi_{21} r_2)V_1^p + \Phi R_2 (N_1^p \beta_{12} \phi_{12} r_1 + N_2^p \beta_{22} \phi_{22} r_2)V_2^p) > 0. \]

The results in Lemma 4.1 are concluded in Table 3.

4.2. Hopf bifurcation. In the following, we study the Hopf bifurcation for (1) when there exists a positive equilibrium \( E_0 \).

By (11), if \( \lambda = ki \) \((k \neq 0)\) is an eigenvalue of \( J(E_0) \), then
\[ k^4 - b_1 k^3 i + b_2 k^2 i^2 + b_3 k i + b_4 = 0, \]
which implies
\[ k^4 - b_2 k^2 + b_4 = 0 \] and \( -b_1 k^3 + b_3 k = 0 \). Then \( k^2 = \frac{b_2 \pm \sqrt{b_2^2 - 4b_4}}{2b_1} = \frac{b_2}{b_1}. \)
Hence, \( b_3 > 0 \) and \( \Delta_3 = -b_4 b_1^2 + b_1 b_2 b_3 - b_3^2 = 0 \). Moreover, there can be at most one simple pair of pure imaginary eigenvalues \( \pm \sqrt{\frac{b_2}{b_1}} i \). Note that 0 is an eigenvalue if \( b_4 = 0 \). Therefore, if \( b_3 > 0, b_4 \neq 0, \) and \( \Delta_3 = 0, \) then \( J(E_0) \), admits a simple pair of pure imaginary eigenvalues and no other eigenvalues have zero real parts.

Take a parameter \( \mu \) of (1) \((\text{e.g., } \mu = \beta_{11})\) for the bifurcation parameter and let \( \lambda(\mu) = \lambda_1(\mu) + i \lambda_2(\mu) \) be an eigenvalue of \( J(E_0) \). Assume that at \( \mu = \mu_0, J(E_0) \), admits a simple pair of pure imaginary eigenvalues \( \lambda(\mu_0) = \pm ki \) and no other eigenvalues with zero real parts. Then \( b_3(\mu_0) > 0, b_4(\mu_0) \neq 0, \) and \( \Delta_3(\mu_0) = 0. \) 
\( \lambda(\mu) \) satisfies the characteristic equation
\[ (\lambda_1(\mu) + i \lambda_2(\mu))^3 + b_1(\lambda_1(\mu) + i \lambda_2(\mu))^3 + b_2(\lambda_1(\mu) + i \lambda_2(\mu))^2 + b_3(\lambda_1(\mu) + i \lambda_2(\mu)) + b_4 = 0, \]
(15)
whose real part and imaginary part both being zero implies

$$\lambda_1^2(\mu) - 6\lambda_2^2(\mu)\lambda_3^2(\mu) - 3\lambda_1(\mu)\lambda_3^2(\mu)b_1 - \lambda_2^2(\mu)b_2 + \lambda_1^2(\mu)$$

$$+ \lambda_1^2(\mu)b_1 + \lambda_2^2(\mu)b_2 + \lambda_1(\mu)b_3 + b_4 = 0,$$

$$\lambda_2(\mu)(4\lambda_2^2(\mu) - 3\lambda_1(\mu)\lambda_3^2(\mu) - \lambda_2^2(\mu)b_1 + 2\lambda_1(\mu)b_2 + b_3) = 0.$$  

Differentiating these equations with respect to $\mu$ and then taking function values at $\mu = \mu_0$ yield

$$\frac{d\lambda_1}{d\mu} \bigg|_{\mu = \mu_0} = \frac{-4b'_1b_4k^6 + 2b'_2b_4k^5 - 3b'_3b_4k^4 + 4b'_4b_4k^3 + 6b'_5b_4k^2 - 2b'_6b_4k^2 + 3b'_7b_4k^2 - b'_8b_4}{-4b'_1b_4k^6 + 2b'_2b_4k^5 - 3b'_3b_4k^4 + 4b'_4b_4k^3 + 6b'_5b_4k^2 - 2b'_6b_4k^2 + 3b'_7b_4k^2 - b'_8b_4} \bigg|_{\mu = \mu_0}$$

$$= \frac{2(2b_1b_4 - b_2b_3)(b'_1b_3 - b'_2b_4) + 2b'_3b_3k^2 - \frac{3}{2}b'_4b_4}{4b'_1b_4k^6 + 2b'_2b_4k^5 - 3b'_3b_4k^4 + 4b'_4b_4k^3 + 6b'_5b_4k^2 - 2b'_6b_4k^2 + 3b'_7b_4k^2 - b'_8b_4} \bigg|_{\mu = \mu_0},$$

where $b'_i = \frac{db_i}{d\mu}$, $i = 1, \cdots, 4$, $\lambda_1(\mu_0) = 0$, $\lambda_2(\mu_0) = k$. The denominator of $\frac{d\lambda_1}{d\mu} \bigg|_{\mu = \mu_0}$ is positive, so the sign of $\frac{d\lambda_1}{d\mu} \bigg|_{\mu = \mu_0}$ is determined by its numerator

$$d_1(\mu_0) = [(2b_1b_4 - b_2b_3)(b'_1b_3 - b'_2b_4) + b'_3b_3k^2 - \frac{3}{2}b'_4b_4] \bigg|_{\mu = \mu_0}. \quad (16)$$

Therefore, by the Hopf Theorem (see e.g., [4]), we have the following result.

**Theorem 4.2.** Let $\mu$ be one of the parameters of model (1). Assume that (1) admits a positive equilibrium $E_0$ when $\mu = \mu_0$. Let $b'_i$’s, $\Delta_i$’s, and $d_1$ be defined in (12), (13), and (16), respectively. If $b_3(\mu_0) > 0$, $b_4(\mu_0) \neq 0$, $\Delta_3(\mu_0) = 0$, and $d_1(\mu_0) \neq 0$, then model (1) may admit a Hopf bifurcation at $\mu_0$. 

| Equilibrium | Existence condition | Stability condition |
|-------------|---------------------|---------------------|
| $E_0 = (0, 0, 0, 0)$ | $r_1 > \omega$ | $r_2 < \omega$, $r_3 < \omega$ |
| $E_1 = (N_1, 0, 0, 0)$ | $r_1 > r_2$, $\eta_1^*, N_1 > N_1^*$, $N_1^* > N_1$ | |
| $E_2 = (0, N_2, 0, 0)$ | $r_2 > \omega$ | $r_1 < r_2$, $N_2^* > N_2$, $N_2^* > N_2$ |
| $E_3 = (N_1^*, 0, 0, 0)$ | $N_1^* < N_1$ | $\Phi R_1 \cdot (\eta_1^* - \eta_1) > 0$ |
| $E_4 = (N_1^*, 0, 0, 0)$ | $N_1^* < N_1$ | $\Phi R_2 \cdot (\eta_1^* - \eta_2) > 0$ |
| $E_5 = (N_2^*, 0, 0, 0)$ | $N_2^* < N_2$ | $\Phi R_1 \cdot (\eta_2^* - \eta_1) > 0$ |
| $E_6 = (N_2^*, 0, 0, 0)$ | $N_2^* < N_2$ | $\Phi R_2 \cdot (\eta_2^* - \eta_2) < 0$ |
| $E_7 = (N_1^*, N_1^*, 0, V_1^*, 0)$ | $(N_1^* - \eta_1) \cdot B\Phi_1 > 0$ | $\Phi R_1 \cdot B\Phi_1 > 0$ |
| $E_8 = (N_1^*, N_1^*, 0, V_1^*, 0)$ | $(N_1^* - \eta_1) \cdot B\Phi_1 < 0$ | $\Phi R_1 \cdot B\Phi_1 < 0$ |
| $E_9 = (N_2^*, N_2^*, 0, V_2^*, 0)$ | $(N_2^* - \eta_2) \cdot B\Phi_2 > 0$ | $\Phi R_2 \cdot B\Phi_2 > 0$ |
| $E_{10} = (N_2^*, N_2^*, 0, V_2^*, 0)$ | $(N_2^* - \eta_2) \cdot B\Phi_2 < 0$ | $\Phi R_2 \cdot B\Phi_2 < 0$ |
| $E_{11} = (N_1^*, N_1^*, V_1^*, V_2^*, 0)$ | $\Phi R_1 \cdot B\Phi_1 \cdot N_2^* - B\Phi_1 \cdot B\Phi_2 > 0$ | $\Phi R_2 \cdot B\Phi_2 \cdot N_2^* - B\Phi_1 \cdot B\Phi_2 > 0$ |

*Table 3.* The conditions for existence and stability of equilibria of model (1). Here, an equilibrium exists means it is nonnegative for $E_1-E_8$ and positive for $E_9$. The notations are defined in (9) and (10)
Example. We revisit the example in Section 5.3.1 in [21]. Let $r_1 = 1.28$, $r_2 = 2.6$, $K = 10^7$, $\phi_{11} = 2.3 \cdot 10^{-9}$, $\phi_{12} = 6.35 \cdot 10^{-9}$, $\phi_{21} = 9.75 \cdot 10^{-9}$, $\phi_{22} = 1.04 \cdot 10^{-8}$, $m_1 = 0.64$, $m_2 = 0.9$, $\omega = 0.01$, $\beta_{11} = \beta_{12} = \beta_{21} = \beta_{22} = \beta$. Assume $\beta$ is the bifurcation parameter. When $\beta = \beta_9 = 12.24183257$, we have $E_9 = (4.54205522 \cdot 10^9, 4.37434856 \cdot 10^6, 1.018711763 \cdot 10^5, 1.65779440 \cdot 10^5)$, $b_3 = 0.00677619686 > 0$, $b_4 = 0.0007258324845 \neq 0$, $\Delta_3 = 0$, $d_1 = 0.0000223499860 > 0$. A unique stable limit cycle bifurcates from $E_9$ as $\beta$ increases from $\beta_9$. In particular, when $\beta = 11.5 < \beta_0$, (1) admits a stable positive equilibrium $E_9 = (4.835050396 \cdot 10^9, 4.656525458 \cdot 10^6, 5.345635691 \cdot 10^6, 6.73753279 \cdot 10^6)$, while when $\beta = 20 > \beta_0$, (1) admits an unstable positive equilibrium $E_9 = (2.780159378 \cdot 10^6, 2.677502138 \cdot 10^6, 3.930095605 \cdot 10^6, 7.575241231 \cdot 10^6)$ and a stable limit cycle. Figure 1 shows the projection of the phase diagram of (1) onto the $N_1N_2$ plane in these two cases ($\beta = 11.5$ and $\beta = 20$); Figure 2 shows the time series of some solutions of (1) in these cases. Our result consists with the phenomenon shown in the example in Section 5.3.1 in [21] that a cycle can be found when $\beta = 20$.

Remark 4.3. If we set $\beta_{11} = \beta_{12} = \beta_{21} = \beta_{22} = \beta$ and $m_1 = m_2$, and assume $\mu = \beta$ as the bifurcation parameter, then the bifurcation point $\mu_0$ in Theorem 4.2 can be found as

$$
\mu_0 = \beta_0 = -\frac{\Phi R_1 \cdot \Phi R_2 \cdot (\phi_{21} - \phi_{22}) (\phi_{11} - \phi_{12})(\phi_{11} - \phi_{12} - \phi_{21} + \phi_{22})(m + \omega)}{\Phi \Phi \cdot K \cdot d_2}
$$

and the value $d_1(\mu_0)$ is

$$
d_1(\mu_0) = \frac{(m + \omega)^2 K (r_1 - r_2)^2 (\phi_{11} \phi_{12} (\phi_{21} - \phi_{22}) - (\phi_{11} - \phi_{12}) \phi_{21} \phi_{22}) (\Phi R_1 - \Phi R_2)^2 \omega^2}{\Phi \Phi \cdot K \cdot d_2} \cdot d_2,
$$

where $d_2 = (\phi_{11} \phi_{12} (\phi_{21} - \phi_{22}) - (\phi_{11} - \phi_{12}) \phi_{21} \phi_{22}) (\Phi R_1 - \Phi R_2) \omega - \Phi R_1 \cdot \Phi R_2 \cdot (\phi_{21} - \phi_{22}) (\phi_{11} - \phi_{12})$. Hence, the sign of $d_1(u_0)$ is determined by

$$
d_3 = (\phi_{11} \phi_{12} (\phi_{21} - \phi_{22}) - (\phi_{11} - \phi_{12}) \phi_{21} \phi_{22}) \cdot \Phi \Phi \cdot \Phi R_2 \cdot \Phi R_1 \cdot d_2.
$$

4.3. Global stability of some equilibria. Due to the complexity of model (1), it is difficult to establish global stability for all of its equilibria, but we can still obtain some results about global stability of some equilibria under certain conditions.

By similar arguments as in Theorem 3.4, we can easily obtain the global stability of $E_0$.

Theorem 4.4. If $r_1 < \omega$ and $r_2 < \omega$, then $E_0 = (0, 0, 0, 0)$ is globally asymptotically stable for (1) for all nonnegative initial conditions.

Theorem 4.5. If $N^*_1 < N^*_1$ and $N^*_2 < N^*_2$, then $V_2(t) \to 0$ as $t \to \infty$.

Proof. Assume $N^*_1 < N^*_2$ and $N^*_2 < N^*_2$. For a constant $\xi \in \mathbb{R},$

$$
\frac{1}{V_2} \frac{dV_2}{dt} - \frac{1}{V_1} \frac{dV_1}{dt} = \xi (\phi_{11} \phi_{12} N_1 + \beta_{22} \phi_{22} N_2 - m_2 - \omega) - (\beta_{11} \phi_{11} N_1 + \beta_{21} \phi_{21} N_2 - m_1 - \omega)
$$

$$
= (\xi (m_2 + \omega) \left( \frac{N_1}{N^*_1} - \frac{N_2}{N^*_2} - 1 \right) - (m_1 + \omega) \left( \frac{N_1}{N^*_1} + \frac{N_2}{N^*_2} - 1 \right)
$$

$$
= N_1 \left( \frac{\xi (m_2 + \omega) + m_1 + \omega}{N^*_1} \right) + N_2 \left( \frac{\xi (m_2 + \omega) - m_1 + \omega}{N^*_2} \right) - \xi (m_2 + \omega) + m_1 + \omega.
$$
Choose $\xi > 0$ such that $\xi > \frac{m_1 + \omega}{m_2 + \omega}$, $\frac{\xi (m_2 + \omega)}{N_{1,2}} - \frac{m_1 + \omega}{N_{1,1}} < 0$, and $\frac{\xi (m_2 + \omega)}{N_{2,2}} - \frac{m_1 + \omega}{N_{2,1}} < 0$.

This is equivalent to $\frac{m_1 + \omega}{m_2 + \omega} < \xi < \min \left\{ \frac{N_{1,2}^{*}}{N_{1,1}}, \frac{N_{2,2}^{*}}{N_{2,1}} \right\}$. Then we have

$$\xi \frac{1}{V_2} \frac{dV_2}{dt} - \frac{1}{V_1} \frac{dV_1}{dt} < -\xi (m_2 + \omega) + m_1 + \omega < 0.$$ 

By using similar arguments as in the proof of Theorem 3.6 and the fact that the solutions of model (1) with nonnegative initial conditions are bounded, we can obtain that $V_2(t) \to 0$ as $t \to \infty$.

The following result can be similarly obtained.

**Theorem 4.6.** If $N_{1,2}^{*} < N_{1,1}^{*}$ and $N_{2,2}^{*} < N_{2,1}^{*}$, then $V_1(t) \to 0$ as $t \to \infty$. 

---

**Figure 1.** The projection of the phase diagram of model (1) onto the $N_1, N_2$ plane. Left: $\beta = 11.5$; right: $\beta = 20$. 
Figure 2. The time series of model (1). Left: $\beta = 11.5$; right: $\beta = 20$.

We can also prove that if there is only one host, then one virus will eventually be extinct.

**Theorem 4.7.** If $N_1(t) \equiv 0$ or $N_2(t) \equiv 0$, then $V_1(t) \to 0$ or $V_2(t) \to 0$ as $t \to \infty$.

**Proof.** We only prove the case when $N_1(t) \equiv 0$.

For $a, b \in \mathbb{R},$

$$
\frac{1}{V_2} \frac{dV_2}{dt} + b \frac{1}{V_1} \frac{dV_1}{dt} = a(\beta_{22}\phi_{22}N_2 - m_2 - \omega) + b(\beta_{21}\phi_{21}N_2 - m_1 - \omega) = (a\beta_{22}\phi_{22} + b\beta_{21}\phi_{21})N_2 - a(m_2 + \omega) - b(m_1 + \omega).
$$
If $N_{2,2}^* < N_{2,1}^*$, then let $a$ satisfy $-\frac{m_1+\omega}{m_2+\omega} < a < -\frac{m_1+\omega}{m_2+\omega}$, $\frac{N_{2,2}^*}{N_{2,1}^*} = -\frac{\beta_2\phi_{21}}{\beta_2\phi_{22}}$ and $b = 1$. We have
\[
\frac{1}{V_2} \frac{dV_2}{dt} + \frac{1}{V_1} \frac{dV_1}{dt} = (a\beta_{22}\phi_{22} + \beta_{21}\phi_{21})N_2 - a(m_2 + \omega) - m_1 - \omega < 0,
\]
which implies $V_1(t) \to 0$ as $t \to \infty$. If $N_{2,2}^* = N_{2,1}^*$, then let $a = -\frac{m_1+\omega}{m_2+\omega}$, $\frac{N_{2,2}^*}{N_{2,1}^*} = -\frac{\beta_1\phi_{21}}{\beta_2\phi_{22}}$ and $b = 2$. We have
\[
\frac{1}{V_2} \frac{dV_2}{dt} + \frac{1}{V_1} \frac{dV_1}{dt} = -m_1 - \omega < 0,
\]
which implies $V_1(t) \to 0$ as $t \to \infty$. If $N_{2,2}^* > N_{2,1}^*$, then let $a$ satisfy $-\frac{m_1+\omega}{m_2+\omega} < a < -\frac{m_1+\omega}{m_2+\omega}$, $\frac{N_{2,2}^*}{N_{2,1}^*} = -\frac{\beta_1\phi_{21}}{\beta_2\phi_{22}}$ and $b = -1$. We have
\[
\frac{1}{V_2} \frac{dV_2}{dt} - \frac{1}{V_1} \frac{dV_1}{dt} = (a\beta_{22}\phi_{22} - \beta_{21}\phi_{21})N_2 - a(m_2 + \omega) + m_1 + \omega < 0,
\]
which implies $V_2(t) \to 0$ as $t \to \infty$. Thus, the result is proved in the case when $N_1(t) = 0$. The result can be similarly proved when $N_2(t) = 0$.

The above theorems and Theorems 3.5-3.12 as well as Table 2 and Remark 3.11 imply the global or local stability of the equilibria of model (1) with $V_1 = 0$ or $V_2 = 0$. Hence, we have the following results.

**Theorem 4.8.** (i) Assume $N_{1,1}^* < N_{1,2}^*$ (i.e., $B\Phi_3 > 0$) and $N_{2,1}^* < N_{2,2}^*$ (i.e., $B\Phi_4 > 0$).

(a) If one of $E_0$, $E_1$, $E_2$, $E_3$, and $E_5$ is the only nonnegative equilibrium that is locally asymptotically stable, then it is globally asymptotically stable.

(b) If $E_7$ is nonnegative and unstable, then bistability appears. It is possible that $E_3$ and $E_5$, or $E_1$ and $E_5$, or $E_2$ and $E_3$ are stable at the same time.

(c) If $E_7$ is nonnegative and locally asymptotically stable, then $N_1$, $N_2$ and $V_1$ coexist.

(ii) Assume $N_{1,2}^* < N_{1,1}^*$ (i.e., $B\Phi_3 < 0$) and $N_{2,2}^* < N_{2,1}^*$ (i.e., $B\Phi_4 < 0$).

(a) If one of $E_0$, $E_1$, $E_2$, $E_4$, and $E_6$ is the only nonnegative equilibrium that is locally asymptotically stable, then it is globally asymptotically stable.

(b) If $E_8$ is nonnegative and unstable, then bistability appears. It is possible that $E_4$ and $E_6$, or $E_3$ and $E_6$, or $E_2$ and $E_4$ are stable at the same time.

(c) If $E_8$ is nonnegative and locally asymptotically stable, then $N_1$, $N_2$ and $V_2$ coexist.

4.4. **Uniform persistence.** If $E_7$ and $E_8$ are both nonnegative and unstable with conditions $NN > 0$ and $NNh > 0$, then equilibria $E_0$-$E_8$ are all unstable. We can prove that in this case system (1) is uniformly persistent.

**Theorem 4.9.** Assume that $E_7$ and $E_8$ are both nonnegative and unstable and that $NN > 0$ and $NNh > 0$ are valid. System (1) is uniformly persistent in the sense that there exists a $\xi > 0$ such that
\[
\liminf_{t \to \infty} N_i(t) > \xi, \quad \liminf_{t \to \infty} V_i(t) > \xi, \quad i = 1, 2,
\]
for any solution $(N_1(t), N_2(t), V_1(t), V_2(t))$ of (1) with positive initial condition.

**Proof.** It is easy to see that a solution $(N_1(t), N_2(t), V_1(t), V_2(t))$ of (1) with nonnegative initial value is nonnegative. Since $\frac{dN_1}{dt} \leq r_1 N_1 (1 - \frac{N_1}{K})$ and $\frac{dN_2}{dt} \leq$
Let $\Phi(t, w^0) = (N_1(t), N_2(t), V_1(t), V_2(t))$ be the solution of model (1) with initial condition $w^0 = (N_1^0, N_2^0, V_1^0, V_2^0) \in \mathbb{R}^4_+$ and

\[ W = \{ w^0 \in \mathbb{R}^4_+ : 0 \leq N_1^0 \leq K, 0 \leq N_2^0 \leq K, 0 \leq V_1^0, V_2^0 \leq \tilde{V} \}, \]

\[ W^0 = \{ w^0 \in Y : N_1^0 > 0, N_2^0 > 0, V_1^0 > 0, V_2^0 > 0 \}, \]

\[ \partial W^0 = Y \setminus W^0 = \{ w^0 \in Y : N_1^0 \equiv 0 \text{ or } N_2^0 \equiv 0 \text{ or } V_1^0 \equiv 0 \text{ or } V_2^0 \equiv 0 \}. \]

Then $W^0$ and $\partial W^0$ are positively invariant for model (1). Let $\omega(w^0)$ be the omega limit set of the orbit $\Phi(t, w^0)$ \((t \geq 0)\).

Let $A_1$ and $A_2$ be the global attractors in the positive cones of the $N_1 N_2 V_1$ space and the $N_1 N_2 V_2$ space, respectively (see Theorem 3.10).

**Claim 1.** \( \cup_{w^0 \in \partial W^0} \omega(w^0) \subseteq \cup_{i=0}^{4} \{ E_i \} \cup_{i=1}^{2} A_i. \)

Given $w^0 \in \partial W^0$, we have $\Phi(t, w^0) \in \partial W^0$ for all $t \geq 0$. Hence, $N_1(t) \equiv 0$ or $N_2(t) \equiv 0$ or $V_1(t) \equiv 0$ or $V_2(t) \equiv 0$, for all $t \geq 0$. By Theorems 3.4-3.12, we know that if $N_1(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_2 \cup E_3 \cup E_6$; if $N_2(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_4 \cup E_5 \cup E_6 \cup E_8$; if $V_1(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_2 \cup E_3 \cup E_6 \cup E_7 \cup A_1$; if $V_2(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_2 \cup E_3 \cup E_6 \cup E_7 \cup A_1$.

**Claim 2.** each $E_i$ \((i = 0, \ldots, 8)\) is a uniform weak repellor for $W^0$ in the sense that there exists $\rho > 0$ such that

\[ \lim_{t \to \infty} \sup_{x} \| \Phi(t, w^0) - E_i \| \geq \rho, \forall w^0 \in W^0, \] (17)

and each $A_i$ \((i = 1, 2)\) is a uniform weak repellor for $W^0$ in the sense that

\[ \lim_{t \to \infty} \sup_{x} \| \Phi(t, w^0) - A_i \| \geq \rho, \forall w^0 \in W^0, \] (18)

where $\| x \| = \max_{i=1, \ldots, 4} \{ x_i \}$ for $x = (x_1, x_2, x_3, x_4) \in \mathbb{R}^4_+$.

Assume that (17) is not true for $E_0$. Let $\epsilon > 0$ be sufficiently small such that $r_1 - \omega + \epsilon (2 \beta_{11} + \phi_{11} + \phi_{12}) > 0$. Assume that for $w^0 \in W^0$, there exists $t_0 > 0$, such that $\| \Phi(t, w^0) \| < \epsilon$ for $t > t_0$. This implies that for $t > t_0$, $0 < N_1(t) < \epsilon$, $0 < N_2(t) < \epsilon$, $0 < V_1(t) < \epsilon$, $0 < V_2(t) < \epsilon$, and hence $\frac{dN_1}{dt} > (r_1 - \omega - \epsilon (2 \beta_{11} + \phi_{11} + \phi_{12}) N_1)$ for $t > t_0$. Therefore, $N_1(t) \to \infty$ as $t \to \infty$. A contradiction. Hence, (17) is true for $E_0$. Assume that (17) is not true for $E_1$. For $\epsilon > 0$, there exists $w^0 \in W^0$, such that there exists $t_0 > 0$, such that $\| \Phi(t, w^0) - E_1 \| < \epsilon$ for $t > t_0$, that is, for $t > t_0$, $\bar{N}_1 < \epsilon < N_1(t) < \bar{N}_1 + \epsilon$, $0 < N_2(t) < \epsilon$, $0 < V_1(t) < \epsilon$, $0 < V_2(t) < \epsilon$. If $r_1 > r_2$, the conditions in this theorem gives $\bar{N}_1, 1 < \bar{N}_1$. Let $\epsilon > 0$ be sufficiently small such that $\bar{N}_1 < \epsilon < N_1^*$. Then $\frac{dN_1}{dt} > (m_1 + \omega)(\frac{N_{1^*}}{N_{1^*}} - 1)V_1$. Therefore, $V_1(t) \to \infty$ as $t \to \infty$. A contradiction. If $r_1 \leq r_2$, then $\bar{N}_1 < \bar{N}_2$. Let $\epsilon > 0$ be sufficiently small such that $\bar{N}_2 - \bar{N}_1 - \epsilon (2 \beta_{21} + \phi_{21} + \phi_{22}) > 0$. Then $\frac{dN_2}{dt} \geq N_2(r_2(1 - \epsilon - \frac{\bar{N}_1}{\bar{N}_2}) - \phi_{21} \epsilon - $
\( \phi_{22}(\epsilon - \omega) = \frac{\epsilon}{\kappa} N_2(\hat{N}_2 - \hat{N}_1 - \epsilon(2\frac{\epsilon}{\kappa} + \phi_{21} + \phi_{22})). \) Therefore, \( N_2(t) \to \infty \) as \( t \to \infty \). A contradiction. Hence, (17) is true for \( E_1 \). A similar proof works for \( E_2 \). Assume that (17) is not true for \( E_3 \). For \( \epsilon > 0 \), there exists \( w^0 \in W^0 \), such that there exists \( t_0 > 0 \), such that \( ||\Phi(t, w^0) - E_3|| < \epsilon \) for \( t > t_0 \). This implies that for \( t > t_0 \), \( N_{1,1}^* - \epsilon < N_1(t) < N_{1,1}^* + \epsilon, 0 < N_2(t) < \epsilon, \frac{r_1(N_1 - N_1^*)}{K_{S_{11}}} - \epsilon < V_1(t) < \frac{r_1(N_1 - N_1^*)}{K_{S_{11}}} + \epsilon, 0 < V_2(t) < \epsilon. \) If \( B \Phi_{13} = \beta_{11} \phi_{11}(m_2 + \omega) - \beta_{12} \phi_{12}(m_1 + \omega) < 0 \), then let \( \epsilon > 0 \) be sufficiently small such that \( \frac{\beta_{12} \phi_{12}(m_1 + \omega) - \beta_{11} \phi_{11}(m_2 + \omega) - \beta_{12} \phi_{12}}{K_{S_{11}}} > 0 \). We have \( \frac{dV_2}{dt} > V_2(\beta_{12} \phi_{12}(N_{1,1}^* - \epsilon) - m_2 - \omega) = (\beta_{12} \phi_{12}(m_1 + \omega) - \beta_{11} \phi_{11}(m_2 + \omega) - \beta_{12} \phi_{12}) \epsilon V_2(t) > 0 \). Therefore, \( V_2(t) \to \infty \) as \( t \to \infty \). A contradiction. If \( \Phi R_1 \cdot (N_{1,1}^* - \eta_1) < 0 \), then let \( \epsilon > 0 \) be sufficiently small such that \( \frac{\Phi R_1 \cdot (N_{1,1}^* - m_1)}{K_{S_{11}}} - \frac{\Phi R_1 \cdot (N_{1,1}^* - \eta_1)}{K_{S_{11}}} + \epsilon > 0. \) Then \( \frac{dN_2}{dt} > N_2(t) \left( 1 - \frac{r_1(N_1 - N_1^*)}{K_{S_{11}}} + \epsilon \right) \phi_{21}(N_{1,1}^* - \eta_1) - \phi_{22}(\epsilon - \omega) = N_2 \left( \frac{\phi R_1 \cdot (N_{1,1}^* - m_1)}{K_{S_{11}}} - \frac{\phi R_1 \cdot (N_{1,1}^* - \eta_1)}{K_{S_{11}}} + \epsilon \right) > 0. \) Therefore, \( N_2(t) \to \infty \) as \( t \to \infty \). A contradiction. Hence, (17) is true for \( E_3 \). Similar arguments work for \( E_4-E_6 \). Assume that (17) is not true for \( E_7 \). Let \( \epsilon > 0 \) be sufficiently small such that \( \frac{N_{1,1}^* - \epsilon}{N_{1,2}^*} + \frac{N_{1,1}^* - \epsilon}{N_{1,2}^*} > 1 > 0 \). Assume that for \( w^0 \in W^0 \), there exists \( t_0 > 0 \), such that \( ||\Phi(t, w^0) - E_7|| < \epsilon \) for \( t > t_0 \). This implies that for \( t > t_0 \), \( N_{1,1}^* - \epsilon < N_1(t) < N_{1,1}^* + \epsilon, N_{2,1}^* + \epsilon < N_2(t) < N_{2,1}^* + \epsilon, N_{1,2}^* - \epsilon < V_1(t) < N_{1,2}^* + \epsilon, 0 < V_2(t) < \epsilon, \) and hence \( \frac{dV_2}{dt} > V_2(m_2 + \omega)(\frac{N_{1,1}^* - \epsilon}{N_{1,2}^*} + \frac{N_{2,1}^* - \epsilon}{N_{1,2}^*} + 1). \) This implies that \( V_2(t) \to \infty as \( t \to \infty \). A contradiction. Hence, (17) is true for \( E_7 \). Similarly, we can obtain that (17) is true for \( E_8 \). If (1) admits a positive global attractor \( A_1 \) in the \( N_1 N_2 X \) space, then \( E_7 \subset A_1 \) and \( E_7 \) is locally asymptotically stable in the \( N_1 N_2 V \) space. Assume that (18) is not true for \( A_1 \). For \( \epsilon > 0 \), there exists \( w^0 \in W^0 \) such that for some \( t_0 > 0 \), \( ||\Phi(t, w^0) - A_1|| < \epsilon \) for \( t > t_0 \). This implies that for \( t > t_0 \), \( ||\Phi(t, w^0) - E_7|| < \epsilon. \) By the above arguments, this leads to \( V_2(t) \to \infty as \( t \to \infty \). A contradiction. Hence, (18) is true for \( A_1 \). Similarly we can prove that if (1) admits a positive global attractor \( A_2 \) in the \( N_1 N_2 V_2 \) space, then (18) is true for \( A_2 \). Claim 2 is proved.

Define a continuous function \( p : W \to [0, \infty) \) by \( p(w^0) = \min\{N_1^0, N_2^0, V_1^0, V_2^0\} \) for \( w^0 = (N_1^0, N_2^0, V_1^0, V_2^0) \in W \). It follows that \( p^{-1}(0, \infty) \subseteq W^0 \) and \( p \) has the property that if \( p(w^0) > 0 \) then \( p(\Phi(t, w^0)) > 0 \) for all \( t > 0 \). So, \( p \) is a generalized distance function for the solution map of (1).

By the above arguments, we know that any forward orbit of (1) in \( \partial W^0 \) converges to \( \bigcup_{i=0}^{\infty} E_i \bigcup_{i=1}^{\infty} A_i \), each of these invariant sets is isolated in \( W \), and \( W^*(E_i) \cap W^0 = \emptyset \) for \( i = 0, \cdots , 8, W^*(A_i) \cap W^0 = \emptyset \) for \( i = 1, 2 \), where \( W^*(E_i) \) and \( W^*(A_i) \) are the stable set of \( E_i \) and \( A_i \), respectively. All possible connections among \( E_i \)’s and \( A_i \)’s are \( E_0 \to E_1, E_0 \to E_2 \to E_1 \to E_2 \to E_3 \to E_5 \to E_7 \) and \( \{A_1\}, E_1 \to E_4 \to E_8 \) (or \( A_2 \), \( E_2 \to E_5 \to E_7 \) (or \( A_1 \), \( E_2 \to E_5 \to E_7 \) (or \( A_1 \), \( E_2 \to E_8 \to E_8 \) (or \( A_2 \) if \( r_1 > r_2 \), and hence, there is no cycle in \( \partial W^0 \) from \( \bigcup_{i=0}^{\infty} E_i \bigcup_{i=1}^{\infty} A_i \) to themselves in this case. Similarly, there is no cycle in \( \partial W^0 \) from \( \bigcup_{i=0}^{\infty} E_i \bigcup_{i=1}^{\infty} A_i \) if \( r_1 < r_2 \). By [17, Theorem 3], it follows that there exists an \( \xi > 0 \) such that \( \liminf_{t \to \infty} p(\Phi(t, w^0)) > \xi \), for any \( w^0 \in W^0 \). Hence, \( \liminf_{t \to \infty} N_1(t) > \xi, \liminf_{t \to \infty} N_2(t) > \xi, \liminf_{t \to \infty} V_1(t) > \xi, \liminf_{t \to \infty} V_2(t) > \xi \) for any initial condition \( w^0 \in W^0 \). \( \square \)

5. Discussion. It is generally difficult to fully understand the coexistence or persistence dynamics of a chemostat host-virus system that involves interactions among multiple hosts and multiple types of viruses, due to the mathematical complexity following from the complex interactions between hosts and viruses. In most of
the existing studies, coexistence results such as a globally stable positive equilibrium are usually obtained when the virus-host relations are restricted to specific structures such as nested virus-bacteria cross-infection networks or monogamous infection networks; see e.g., [9, 19, 7, 11, 10, 12, 21].

In this paper, we attempt to study the dynamics of a two host-two virus chemostat system (1) with a general structure in the sense that both viruses can infect both hosts and both sets of hosts and viruses have distinct life history traits. To fulfill this duty, we first establish the global dynamics of its submodels, a one host-one virus model (2), a two host model (3), and a two host-one virus model (4). Using these results and the theory of uniform persistence, we then develop sufficient conditions for the coexistence of two hosts with two viruses and coexistence of two hosts with one virus. We also derive conditions for a Hopf bifurcation, which consists with the existing finding in [6, 21] that a positive limit cycle may appear for the two host-two virus model.

An interesting phenomenon that we find from the analyses is the possibility of bistability of equilibria. In cases (n), (p) and (q) of Table 2, we see that when the positive equilibrium is unstable, two boundary equilibria of (4) may be stable at the same time, which leads to a result that each host may persist by itself or coexist with the virus in a two host-one virus chemostat system. This also results in possibility of bistability for the two host-two virus model (1). As we have verified the occurrence of a Hopf bifurcation, this implies that if the positive equilibrium is unstable, although coexistence cannot happen in the two host-one virus system, it might happen in the two host-two virus system.

While we are able to establish uniform persistence or coexistence for the two host-one virus model (4) and for the two host-two virus model (1), it seems difficult to fully obtain the global specific dynamics in these cases. For the two host-one virus model (4), the global dynamics has been well understood except in the case where the positive equilibrium $E_5^{nnv}$ is locally stable and is actually the only stable nonnegative equilibrium. In a special case when $r_1\beta_1 = r_2\beta_2$, we could use a Lyapunov function to prove the global stability of $E_5^{nnv}$, but it is hard to extend the result to all cases when $E_5^{nnv}$ is locally stable, that is, in cases of

\[(o)(a) \quad 1 < \frac{r_1}{r_2} < \frac{r_1 - \omega}{r_2 - \omega} < \frac{\phi_1}{\phi_2}, \quad \frac{1}{\beta_1 \phi_1} < \frac{1}{\beta_2 \phi_2} < \frac{(r_1 - \omega) \phi_2 -(r_2 - \omega) \phi_1}{r_1 \phi_2 - r_2 \phi_1} \frac{K}{m + \omega} < \frac{1}{\beta_1 \phi_1} < \frac{r_2 - \omega}{r_2} \frac{K}{m + \omega},
\]

\[(o)(b) \quad \frac{\phi_1}{\phi_2} < \frac{r_1 - \omega}{r_2 - \omega} < \frac{r_2}{r_2} < 1, \quad \frac{1}{\beta_2 \phi_2} < \frac{1}{\beta_1 \phi_1} < \frac{(r_1 - \omega) \phi_2 -(r_2 - \omega) \phi_1}{r_1 \phi_2 - r_2 \phi_1} \frac{K}{m + \omega} < \frac{1}{\beta_1 \phi_1} < \frac{r_2 - \omega}{r_2} \frac{K}{m + \omega},
\]

\[(r) \quad 1 < \frac{r_1}{r_2} < \frac{r_1 - \omega}{r_2 - \omega} < \frac{\phi_1}{\phi_2}, \quad \frac{1}{\beta_1 \phi_1} < \frac{1}{\beta_2 \phi_2} < \frac{(r_1 - \omega) \phi_2 -(r_2 - \omega) \phi_1}{r_1 \phi_2 - r_2 \phi_1} \frac{K}{m + \omega} < \frac{r_2 - \omega}{r_2} \frac{K}{m + \omega} < \frac{1}{\beta_2 \phi_2},
\]

\[(s) \quad \frac{\phi_1}{\phi_2} < \frac{r_1 - \omega}{r_2 - \omega} < \frac{r_2}{r_2} < 1, \quad \frac{1}{\beta_2 \phi_2} < \frac{1}{\beta_1 \phi_1} < \frac{(r_1 - \omega) \phi_2 -(r_2 - \omega) \phi_1}{r_1 \phi_2 - r_2 \phi_1} \frac{K}{m + \omega} < \frac{r_2 - \omega}{r_2} \frac{K}{m + \omega} < \frac{1}{\beta_1 \phi_1}.
\]

listed in Table 2 but rewritten in terms of parameters in model (4) (with $r_1, r_2 > \omega$). We suspect that $E_5^{nnv}$ is globally asymptotically stable whenever it is locally asymptotically stable, but it remains to be a future problem to prove it. On the other hand, few results about global dynamics of the two host-two virus model (1) have been achieved in this paper. We were only able to obtain some results for global stability of equilibria in which at least one host and one virus disappear; see Theorems 4.4 and 4.8. We have had no result about the global stability of the positive equilibrium $E_0$ or the equilibria where only one virus disappears, i.e., $E_7$ and $E_8$. We will leave all these for future work.
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