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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, and a two host-one virus model. In Section 4, we will derive the local dynamics analysis, Hopf Bifurcation, and persistence theory for (1). A short discussion completes the paper.

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]):

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1+N_2}{K}\right) - \phi_{11}N_1V_1 - \phi_{12}N_1V_2 - \omega N_1, \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{N_1+N_2}{K}\right) - \phi_{21}N_2V_1 - \phi_{22}N_2V_2 - \omega N_2, \\ \dfrac{dV_1}{dt} = \beta_{11}\phi_{11}N_1V_1 + \beta_{21}\phi_{21}N_2V_1 - m_1V_1 - \omega V_1, \\ \dfrac{dV_2}{dt} = \beta_{12}\phi_{12}N_1V_2 + \beta_{22}\phi_{22}N_2V_2 - m_2V_2 - \omega V_2. \end{cases} \tag{1}$$

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, ω is the dilution/flow rate, and β_{ij} represents the burst size. When virus attach to host, both virus and host are lost. Thus, β_{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:

$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) - \phi NV - \omega N, \\ \dfrac{dV}{dt} = \beta\phi NV - mV - \omega V, \end{cases} \tag{2}$$

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 $E_3^{nv} = (N^*, V^*)$, with $\tilde{N} = \frac{r-\omega}{r}K$, $N^* = \frac{m+\omega}{\beta\phi}$, $V^* = (r - \omega - r\frac{m+\omega}{\beta\phi K})\frac{1}{\phi} = \frac{r}{\phi K}(\tilde{N} - N^*)$.

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 $\frac{r-\omega}{r}K < \frac{m+\omega}{\beta\phi}$ (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 $\frac{r-\omega}{r}K > \frac{m+\omega}{\beta\phi}$ (i.e., $\tilde{N} > N^*$), then E_0^{nv} and E_1^{nv} are both saddles and E_3^{nv} is globally asymptotically stable for all positive initial conditions.

Proof. The eigenvalues of the Jacobian matrix at E_0^{nv} are $r-\omega$ and $-m-\omega$; the eigenvalues of the Jacobian matrix at E_1^{nv} are $\omega - r$ and $K\beta\phi^2V^*/r$; the trace and the determinant of the Jacobian matrix at E_3^{nv} are $-rN^*/K$ and $\beta\phi^2N^*V^*$, respectively. Therefore, E_0^{nv} is locally asymptotically stable if and only if $r<\omega$ and is a saddle if $r>\omega$; E_1^{nv} 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^{nv} is stable whenever it is positive, that is, when $\tilde{N}>N^*$.

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

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

When E_3^{nv} 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 $\dot{\mathcal{V}}=-r(N-N^*)^2/K\le 0$. By the LaSalle's invariance principle, $(N(t),V(t))\to E_3^{nv}=(N^*,V^*)$ as $t\to\infty$ for all solutions with positive initial conditions. Hence, if E_3^{nv} 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

$$\begin{cases}\dfrac{dN_1}{dt}=r_1N_1\left(1-\dfrac{N_1+N_2}{K}\right)-\omega N_1,\\ \dfrac{dN_2}{dt}=r_2N_2\left(1-\dfrac{N_1+N_2}{K}\right)-\omega N_2.\end{cases}\tag{3}$$

There are three equilibria of (3): $E_0^{nn}=(0,0)$, $E_1^{nn}=(\tilde{N}_1,0)$, and $E_2^{nn}=(0,\tilde{N}_2)$, with $\tilde{N}_1=\frac{r_1-\omega}{r_1}K$ and $\tilde{N}_2=\frac{r_2-\omega}{r_2}K$. The eigenvalues of the Jacobian matrix at E_0^{nn} are $r_1-\omega$ and $r_2-\omega$; the eigenvalues of the Jacobian matrix at E_1^{nn} are $\omega-r_1$ and $-\omega(r_1-r_2)/r_1$; the eigenvalues of the Jacobian matrix at E_2^{nn} 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^{nn} is globally asymptotically stable for all nonnegative initial conditions.

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

(iii) If $r_2>\omega$ and $r_1<r_2$, then E_0^{nn} is unstable (node if $r_1>\omega$ or saddle if $r_1<\omega$), E_1^{nn} is a saddle if it is nonnegative, and E_2^{nn} 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

$$\begin{cases} \dfrac{dN_1}{dt} = r_1N_1\left(1-\dfrac{N_1+N_2}{K}\right) - \phi_1N_1V - \omega N_1, \\ \dfrac{dN_2}{dt} = r_2N_2\left(1-\dfrac{N_1+N_2}{K}\right) - \phi_2N_2V - \omega N_2, \\ \dfrac{dV}{dt} = \beta_1\phi_1N_1V + \beta_2\phi_2N_2V - mV - \omega V, \end{cases} \tag{4}$$

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:

$$\begin{array}{lll} E_0^{nnv} = (0,0,0), & E_1^{nnv} = (\tilde{N}_1,0,0), & E_2^{nnv} = (0,\tilde{N}_2,0), \\ E_3^{nnv} = (N_1^*,0,\tilde{V}^*), & E_4^{nnv} = (0,N_2^*,V^*), & E_5^{nnv} = (N_1^c,N_2^c,V^c) \end{array} \tag{5}$$

with

$$\begin{aligned} &\tilde{N}_1 = \frac{r_1-\omega}{r_1}K, \quad \tilde{N}_2 = \frac{r_2-\omega}{r_2}K, \\ &N_1^* = \frac{m+\omega}{\beta_1\phi_1}, \quad \tilde{V}^* = \left(r_1-\omega-r_1\frac{m+\omega}{\beta_1\phi_1K}\right)\frac{1}{\phi_1} = \frac{r_1}{\phi_1K}(\tilde{N}_1-N_1^*), \\ &N_2^* = \frac{m+\omega}{\beta_2\phi_2}, \quad V^* = \left(r_2-\omega-r_2\frac{m+\omega}{\beta_2\phi_2K}\right)\frac{1}{\phi_2} = \frac{r_2}{\phi_2K}(\tilde{N}_2-N_2^*), \\ &N_1^c = \frac{K\beta_2\phi_2(\omega\phi_1-\omega\phi_2-\phi_1r_2+\phi_2r_1)+(\phi_1r_2-\phi_2r_1)(m+\omega)}{(\phi_1r_2-\phi_2r_1)(\beta_1\phi_1-\beta_2\phi_2)} = \frac{\beta_2\phi_2(N_2^*-\eta)}{\beta_1\phi_1-\beta_2\phi_2}, \\ &N_2^c = -\frac{K\beta_1\phi_1(\omega\phi_1-\omega\phi_2-\phi_1r_2+\phi_2r_1)+(\phi_1r_2-\phi_2r_1)(m+\omega)}{(\phi_1r_2-\phi_2r_1)(\beta_1\phi_1-\beta_2\phi_2)} = -\frac{\beta_1\phi_1(N_1^*-\eta)}{\beta_1\phi_1-\beta_2\phi_2}, \\ &V^c = \frac{(r_1-r_2)\omega}{\phi_1r_2-\phi_2r_1} = \frac{(\tilde{N}_1-\eta)r_1}{K\phi_1} = \frac{(\tilde{N}_2-\eta)r_2}{K\phi_2}, \\ &\eta = \frac{-(\omega\phi_1-\omega\phi_2-\phi_1r_2+\phi_2r_1)K}{\phi_1r_2-\phi_2r_1} = \frac{(r_1-\omega)\phi_2-(r_2-\omega)\phi_1}{r_1\phi_2-r_2\phi_1}K. \end{aligned} \tag{6}$$

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* $(\phi_1r_2-\phi_2r_1)(N_1^*-\eta) > 0$*. It is unstable if* $(\phi_1r_2-\phi_2r_1)(N_1^*-\eta) < 0$.

(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* $(\phi_1r_2-\phi_2r_1)(N_2^*-\eta) < 0$*. It is unstable if* $(\phi_1r_2-\phi_2r_1)(N_2^*-\eta) > 0$.

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

$$\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2} > 1,\ \frac{\phi_1}{\phi_2} > \frac{\beta_2}{\beta_1},\ N_1^* < \eta < N_2^*,$$

or

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

(b) E_5^{nnv} *is positive and unstable if*

$$\frac{\beta_2}{\beta_1} < \frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} < 1,\ N_1^* < \eta < N_2^*,$$

or

$$\frac{\beta_2}{\beta_1} > \frac{\phi_1}{\phi_2} > \frac{r_1}{r_2} > 1,\ N_1^* > \eta > N_2^*.$$

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

$$J(E_3^{nnv}) = \begin{bmatrix} -\frac{r_1 N_1^*}{K} & -\frac{r_1 N_1^*}{K} & -\phi_1 N_1^* \\ 0 & r_2(1 - \frac{N_1^*}{K}) - \phi_2 \tilde{V}^* - \omega & 0 \\ \beta_1\phi_1\tilde{V}^* & \beta_2\phi_2\tilde{V}^* & 0 \end{bmatrix}.$$

One eigenvalue of $J(E_3^{nnv})$ is

$$\lambda_{E_3^{nnv}} = r_2\left(1 - \frac{N_1^*}{K}\right) - \phi_2\tilde{V}^* - \omega = -\frac{(\phi_1 r_2 - \phi_2 r_1)}{K\phi_1}(N_1^* - \eta)$$

with $\lambda_{E_3^{nnv}} < 0$ if $(\phi_1 r_2 - \phi_2 r_1)(N_1^* - \eta) > 0$. The other two eigenvalues have negative real parts if $\tilde{V}^* > 0$.

(v). The Jacobian matrix at E_4^{nnv} is

$$J(E_4^{nnv}) = \begin{bmatrix} r_1(1 - \frac{N_2^*}{K}) - \phi_1 V^* - \omega & 0 & 0 \\ -\frac{r_2 N_2^*}{K} & -\frac{r_2 N_2^*}{K} & -\phi_2 N_2^* \\ \beta_1\phi_1 V^* & \beta_2\phi_2 V^* & 0 \end{bmatrix}.$$

One eigenvalue is

$$\lambda_{E_4^{nnv}} = r_1\left(1 - \frac{N_2^*}{K}\right) - \phi_1 V^* - \omega = \frac{(\phi_1 r_2 - \phi_2 r_1)}{(K\phi_2)}(N_2^* - \eta)$$

with $\lambda_{E_4^{nnv}} < 0$ if $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) < 0$. The other two eigenvalues have negative real parts if $V^* > 0$.

(vi). The Jacobian matrix at E_5^{nnv} is

$$J(E_5^{nnv}) = \begin{bmatrix} -\frac{r_1 N_1^c}{K} & -\frac{r_1 N_1^c}{K} & -\phi_1 N_1^c \\ -\frac{r_2 N_2^c}{K} & -\frac{r_2 N_2^c}{K} & -\phi_2 N_2^c \\ \beta_1\phi_1 V^c & \beta_2\phi_2 V^c & 0 \end{bmatrix}.$$

The characteristic equation of $J(E_5^{nnv})$ is

$$\lambda^3+\frac{N_1^c r_1+N_2^c r_2}{K}\lambda^2+V^c(N_1^c\beta_1\phi_1^2+N_2^c\beta_2\phi_2^2)\lambda+\frac{V^cN_1^cN_2^c(\phi_1 r_2-\phi_2 r_1)(\beta_1\phi_1-\beta_2\phi_2)}{K}=0.$$

It follows from the Routh-Hurwitz criteria that all eigenvalues of $J(E_5^{nnv})$ have negative real parts if and only if

$$\begin{cases}\dfrac{N_1^c r_1+N_2^c r_2}{K}>0,\\ \dfrac{V^cN_1^cN_2^c(\phi_1 r_2-\phi_2 r_1)(\beta_1\phi_1-\beta_2\phi_2)}{K}>0,\\ \dfrac{N_1^c r_1+N_2^c r_2}{K}(V^c(N_1^c\beta_1\phi_1^2+N_2^c\beta_2\phi_2^2))-\dfrac{V^cN_1^cN_2^c(\phi_1 r_2-\phi_2 r_1)(\beta_1\phi_1-\beta_2\phi_2)}{K}\\ =\dfrac{V^c(N_1^c\phi_1+N_2^c\phi_2)(N_1^c\beta_1\phi_1 r_1+N_2^c\beta_2\phi_2 r_2)}{K}>0.\end{cases}$$

Hence, E_5^{nnv} is locally asymptotically stable if and only if $(\phi_1 r_2-\phi_2 r_1)(\beta_1\phi_1-\beta_2\phi_2)>0$. $\square$

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

Equilibrium	Existence condition	Stability condition
$E_0^{nnv}=(0,0,0)$		$r_1<\omega$, $r_2<\omega$
$E_1^{nnv}=(\tilde{N}_1,0,0)$	$r_1>\omega$	$r_1>r_2$, $N_1^*>\tilde{N}_1$
$E_2^{nnv}=(0,\tilde{N}_2,0)$	$r_2>\omega$	$r_1<r_2$, $N_2^*>\tilde{N}_2$
$E_3^{nnv}=(N_1^*,0,\tilde{V}^*)$	$N_1^*<\tilde{N}_1$ ($r_1>\omega$ required)	$\left(\frac{\phi_1}{\phi_2}-\frac{r_1}{r_2}\right)(N_1^*-\eta)>0$
$E_4^{nnv}=(0,N_2^*,V^*)$	$N_2^*<\tilde{N}_2$ ($r_2>\omega$ required)	$\left(\frac{\phi_1}{\phi_2}-\frac{r_1}{r_2}\right)(N_2^*-\eta)<0$
$E_5^{nnv}=(N_1^c,N_2^c,V^c)$	$\left(\frac{\phi_1}{\phi_2}-\frac{r_1}{r_2}\right)(r_1-r_2)>0$ $(N_1^*-\eta)\left(\frac{\phi_1}{\phi_2}-\frac{\beta_2}{\beta_1}\right)<0$ $(N_2^*-\eta)\left(\frac{\phi_1}{\phi_2}-\frac{\beta_2}{\beta_1}\right)>0$	$\left(\frac{\phi_1}{\phi_2}-\frac{r_1}{r_2}\right)\left(\frac{\phi_1}{\phi_2}-\frac{\beta_2}{\beta_1}\right)>0$

TABLE 1. The conditions for existence and local stability of equilibria of (4). Here, an equilibrium exists means it is nonnegative for E_1^{nnv}-E_4^{nnv} and positive for E_5^{nnv}.

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 $E_0^{nnv}=(0,0,0)$ is globally asymptotically stable for (4) for all nonnegative initial conditions.*

Proof. When $r_1<\omega$ and $r_2<\omega$, $E_0^{nnv}=(0,0,0)$ is locally asymptotically stable. It follows from (4) that $\frac{dN_1}{dt}\le(r_1-\omega)N_1$ and $\frac{dN_2}{dt}\le(r_2-\omega)N_2$. 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. $\square$

Theorem 3.5. *(i) If $r_1>\omega$ and $r_2<\omega$, then E_1^{nnv} is globally asymptotically stable for (4) for all positive initial conditions when $N_1^*>\tilde{N}_1$ and E_3^{nnv} is globally asymptotically stable for (4) for all positive initial conditions when $N_1^*<\tilde{N}_1$.*

(ii) If $r_1 < \omega$ and $r_2 > \omega$, then E_2^{nnv} is globally asymptotically stable for (4) for all positive initial conditions when $N_2^* > \tilde{N}_2$ and E_4^{nnv} is globally asymptotically stable for (4) for all positive initial conditions when $N_2^* < \tilde{N}_2$.

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 $\frac{dN_2}{dt} \le (r_2 - \omega)N_2$, which implies $N_2(t) \to 0$ as $t \to \infty$. When $N_2(t) = 0$, the limiting system is

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1}{K}\right) - \phi_1 N_1 V - \omega N_1, \\ \dfrac{dV}{dt} = \beta_1 \phi_1 N_1 V - mV - \omega V. \end{cases} \tag{7}$$

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 $N_1^* > \tilde{N}_1$ and that $N_1(t) \to N_1^*$ and $V(t) \to \tilde{V}^*$ as $t \to \infty$ when $N_1^* < \tilde{N}_1$. Hence, for any positive initial condition of (4), we have $(N_1(t), N_2(t), V(t)) \to E_1^{nnv}$ as $t \to \infty$ when $N_1^* > \tilde{N}_1$ and $(N_1(t), N_2(t), V(t)) \to E_3^{nnv}$ as $t \to \infty$ when $N_1^* < \tilde{N}_1$. (i) is proved. □

Theorem 3.6. *If both E_3^{nnv} and E_4^{nnv} are nonnegative, E_3^{nnv} is stable and E_4^{nnv} is unstable (that is, when $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2}$, $N_1^* < \eta$, $N_2^* < \eta$ or when $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$ and $N_1^* > \eta$, $N_2^* > \eta$), then E_3^{nnv} is globally asymptotically stable for (4) for all positive initial conditions.*

Proof. Note that under the conditions of the theorem, E_0^{nnv}, E_1^{nnv}, and E_2^{nnv} are all unstable, and E_5^{nnv} 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 $w^0 = (N_1(0), N_2(0), V(0))$. Since $\frac{dN_1}{dt} \le r_1 N_1 \left(1 - \frac{N_1}{K}\right)$, 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, $\frac{d(\beta_1 N_1 + \beta_2 N_2 + V)}{dt} < -\omega(\beta_1 N_1 + \beta_2 N_2 + V) + (\beta_1 r_1 + \beta_2 r_2)(K+1)$ for $t > \max\{t_0, t_1\}$. This implies that $V(t)$ is bounded for $t \ge 0$. 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 $\xi_1, \xi_2 \in \mathbb{R}$,

$$\begin{aligned} &\xi_1 \tfrac{1}{N_2} \tfrac{dN_2}{dt} - \xi_2 \tfrac{1}{(m+\omega)V} \tfrac{dV}{dt} - \tfrac{1}{N_1} \tfrac{dN_1}{dt} \\ &= (\xi_1(r_2 - \omega) + \xi_2 - (r_1 - \omega)) + N_1(\tfrac{r_1}{K} - \xi_1 \tfrac{r_2}{K} - \tfrac{\xi_2}{N_1^*}) + N_2(\tfrac{r_1}{K} - \xi_1 \tfrac{r_2}{K} - \tfrac{\xi_2}{N_2^*}) \\ &+V(\phi_1 - \xi_1 \phi_2). \end{aligned}$$

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

$$\begin{aligned} &\xi_1 \tfrac{1}{N_2} \tfrac{dN_2}{dt} - \tfrac{\xi_2}{m+\omega} \tfrac{1}{V} \tfrac{dV}{dt} - \tfrac{1}{N_1} \tfrac{dN_1}{dt} \\ &= N_1(\tfrac{r_1}{K} - \tfrac{\phi_1}{\phi_2} \tfrac{r_2}{K} - \tfrac{\xi_2}{N_1^*}) + N_2(\tfrac{r_1}{K} - \tfrac{\phi_1}{\phi_2} \tfrac{r_2}{K} - \tfrac{\xi_2}{N_2^*}) \\ &= N_1(\tfrac{\xi_2}{\eta} - \tfrac{\xi_2}{N_1^*}) + N_2(\tfrac{\xi_2}{\eta} - \tfrac{\xi_2}{N_2^*}) \\ &= \xi_2(N_1(\tfrac{1}{\eta} - \tfrac{1}{N_1^*}) + N_2(\tfrac{1}{\eta} - \tfrac{1}{N_2^*})) \\ &< 0 \end{aligned}$$

since $N_1^* < \eta$ and $N_2^* < \eta$. This implies that

$$\left(\frac{N_2(t)}{N_2(0)}\right)^{\xi_1} < \left(\frac{V(t)}{V(0)}\right)^{\frac{\xi_2}{m+\omega}} \left(\frac{N_1(t)}{N_1(0)}\right) e^{\xi_2 \left(\frac{1}{\eta} - \frac{1}{N_2^*}\right) \int_0^t N_2(s) ds}.$$

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

Case 2. $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$, $N_1^* > \eta$, $N_2^* > \eta$, 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 $\xi \in \mathbb{R}$,

$$\begin{aligned}&\xi \tfrac{1}{N_2}\tfrac{dN_2}{dt} - \tfrac{1}{N_1}\tfrac{dN_1}{dt}\\ &= \xi(r_2(1-\tfrac{N_1+N_2}{K}) - \phi_2 V - \omega) - (r_1(1-\tfrac{N_1+N_2}{K}) - \phi_1 V - \omega)\\ &= (\xi(r_2-\omega) - (r_1-\omega)) + (N_1+N_2)(\tfrac{r_1}{K} - \xi\tfrac{r_2}{K}) + V(\phi_1 - \xi\phi_2).\end{aligned}$$

Choose $\xi > 0$ such that $\xi < \frac{r_1-\omega}{r_2-\omega}, \xi > \frac{r_1}{r_2}$, and $\xi > \frac{\phi_1}{\phi_2}$. Then $\xi(r_2-\omega)-(r_1-\omega) < 0$, $\frac{r_1}{K} - \xi\frac{r_2}{K} < 0$, $\phi_1 - \xi\phi_2 < 0$, and

$$\xi \frac{1}{N_2}\frac{dN_2}{dt} - \frac{1}{N_1}\frac{dN_1}{dt} < (\xi(r_2-\omega) - (r_1-\omega)) < 0.$$

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

$$\left(\frac{N_2(t)}{N_2(0)}\right)^{\xi} < \left(\frac{N_1(t)}{N_1(0)}\right) e^{((\xi(r_2-\omega)-(r_1-\omega)))t} < Me^{((\xi(r_2-\omega)-(r_1-\omega)))t},$$

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

$$\xi_1 \tfrac{1}{N_2}\tfrac{dN_2}{dt} - \tfrac{\xi_2}{m+\omega}\tfrac{1}{V}\tfrac{dV}{dt} - \tfrac{1}{N_1}\tfrac{dN_1}{dt} < 0$$

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 $(N_2(t))^{\xi_1}(V(t))^{-\frac{\xi_2}{m+\omega}} \to 0$ 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 $N_2(t_n) \to \hat{N}_2 > 0$ for some $\hat{N}_2 > 0$. Similarly, there is a subsequence of $\{t_n\}$, which we still write as $\{t_n\}$, such that $N_1(t_n) \to \hat{N}_1$ as $t \to \infty$ for some $\hat{N}_1 \geq 0$. If $\hat{N}_1 = 0$, then $(0, \hat{N}_2, 0) \in \omega(w^0)$, where $\omega(w^0)$ is the ω-limit set of w^0. By invariance of ω-limit set, $E_2^{nnv} = (0, (r_2-\omega)K/r_2, 0) \in \omega(w^0)$. 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_4^{nnv}. We assume that $E_2^{nnv} \neq \omega(w^0)$. In the N_1N_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]), $(0,0,0) \in \omega(w^0)$ (as $(0,0,0)$ is the α-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_2V plane and there is a trajectory connecting from E_2^{nnv} to E_4^{nnv}, again by Butler-Mcgehee Lemma, $E_4^{nnv} \in \omega(w^0)$. Thus, there is a subsequence $\bar{t}_n$ such that $(N_1(\bar{t}_n), N_2(\bar{t}_n), V(\bar{t}_n)) \to E_4^{nnv}$ as $n \to \infty$, which is a contradiction to $N_2(t)V(t) \to 0$ as $t \to \infty$. If $\hat{N}_1 > 0$, then $(\hat{N}_1, \hat{N}_2, 0) \in \omega(w^0)$. Since $(\hat{N}_1, \hat{N}_2, 0)$ is not an equilibrium of the model, the whole solution through $(\hat{N}_1, \hat{N}_2, 0)$ is in $\omega(w^0)$.

Since the ω-limit set of $(\hat{N}_1, \hat{N}_2, 0)$ 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 $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2}$, $N_1^* > \eta$, $N_2^* > \eta$ or when $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$ 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 $r_1 > r_2$, $N_1^* > \tilde{N}_1$, and $N_2^* < \tilde{N}_2$, then E_0^{nnv}, E_2^{nnv}, and E_4^{nnv} are unstable, and E_1^{nnv} is globally asymptotically stable.

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

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

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

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

(vi) If $r_1 < r_2$, $N_1^* > \tilde{N}_1$, and $N_2^* > \tilde{N}_2$, 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 $r_1 > r_2$, $N_1^* > \tilde{N}_1$, and $N_2^* < \tilde{N}_2$. 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_4^{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 $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2}$ and $\frac{\phi_2}{\phi_1} > \frac{r_2}{r_1}$. Since $r_1 > r_2$, we have $\frac{r_1-\omega}{r_2-\omega} > \frac{r_1}{r_2}$ and $\frac{r_2-\omega}{r_1-\omega} < \frac{r_2}{r_1}$. Then we have $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} < \frac{r_1-\omega}{r_2-\omega}$ and $\frac{\phi_2}{\phi_1} > \frac{r_2}{r_1} > \frac{r_2-\omega}{r_1-\omega}$, which implies $\eta > \tilde{N}_1$ and $\eta > \tilde{N}_2 > N_2^*$. 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 $\frac{\phi_2}{\phi_1} \geq \frac{r_2-\omega}{r_1-\omega}$, then $\eta \leq 0$ and hence, $N_1^* > \eta$. If $\frac{\phi_2}{\phi_1} < \frac{r_2-\omega}{r_1-\omega} < \frac{r_2}{r_1}$, then we still have $N_1^* > \eta$. Therefore, $N_1^* > \eta$ is always true. If $\beta_1\phi_1 - \beta_2\phi_2 \geq 0$, then $\eta < N_1^* \leq N_2^*$, which implies that E_4^{nnv} is unstable. If $\beta_1\phi_1 - \beta_2\phi_2 < 0$, then for one component of E_5^{nnv} to be negative, we must have $N_2^* > \eta$, which again implies that E_4^{nnv}

is unstable. Therefore, we always have E_4^{nnv} 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^{nnv} is negative.

Now we prove the global stability of E_1^{nnv}. In Case (1) as above, we have $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2} < \frac{r_1-\omega}{r_2-\omega}$. Similarly as we do in Case 2 in the proof of Theorem 3.6, we can obtain $N_2(t) \to 0$ as $t \to \infty$. Then Lemma 3.1 (ii) implies that E_1^{nnv} is globally asymptotically stable. In Case (2) as above, similarly as we do in Cases 2 and 3 in the proof of Theorem 3.6, we again have $N_2(t) \to 0$ as $t \to \infty$, and hence, E_1^{nnv} is globally asymptotically stable. $\square$

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^{nnv} is positive.

Theorem 3.9. *In the case where $r_1 > \omega$, $r_2 > \omega$, and E_5^{nnv} 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^{nnv}, E_1^{nnv}, E_2^{nnv}, and E_5^{nnv} are unstable, but E_3^{nnv} and E_4^{nnv} 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^{nnv}, E_1^{nnv}, E_2^{nnv}, E_3^{nnv} and E_4^{nnv} are unstable, and E_5^{nnv} 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^{nnv}, E_2^{nnv}, and E_5^{nnv} are unstable, E_1^{nnv} and E_4^{nnv} 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^{nnv}, E_1^{nnv}, and E_5^{nnv} are unstable, E_2^{nnv} and E_3^{nnv} 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^{nnv}, E_1^{nnv}, E_2^{nnv}, E_3^{nnv} are unstable, and E_5^{nnv} is locally asymptotically stable.*
6. *If $r_1 < r_2$, $\phi_1 r_2 < \phi_2 r_1$, $N_1^* > \tilde{N}_1$, $\tilde{N}_2 > \tilde{N}_1 > \eta > N_2^*$, then E_0^{nnv}, E_1^{nnv}, E_2^{nnv}, E_4^{nnv} are unstable, E_5^{nnv} 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^{nnv} is positive and locally asymptotically stable. Let $X = \mathbb{R}_3^+$ with $||x|| = \max_{i=1,2,3} |x_i|$ for $x = (x_1, x_2, x_3) \in X$, $X_0 = \{(x_1, x_2, x_3) \in X : x_1 > 0, x_2 > 0, x_3 > 0\}$, $\partial X_0 = X \setminus X_0 = \{(x_1, x_2, x_3) \in X : x_1 = 0 \text{ or } x_2 = 0 \text{ or } x_3 = 0\}$.

Theorem 3.10. *If all the nonnegative equilibria are unstable except that the positive equilibrium E_5^{nnv} is stable (that is, in cases (o), (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 (o), (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^{nnv}-E_4^{nnv} being unstable and the positive equilibrium E_5^{nnv} being stable.

By the equations in (4), we see that X_0 and ∂X_0 are both positively invariant. By the proof of Theorem 3.6, we know that there exist $u_{N_1} > 0$, $u_{N_2} > 0$, $u_V > 0$,

	Condition	E_0^{nnv}	E_1^{nnv}	E_2^{nnv}	E_3^{nnv}	E_4^{nnv}	E_5^{nnv}
(a)	$r_1 < \omega,\, r_2 < \omega$	GAS	-	-	-	-	-
(b)	$r_2 < \omega < r_1,\, N_1^* > \tilde{N}_1$	U	GAS	-	-	-	-
(c)	$r_2 < \omega < r_1,\, N_1^* < \tilde{N}_1$	U	U	-	GAS	-	-
(d)	$r_1 < \omega < r_2,\, N_2^* > \tilde{N}_2$	U	-	GAS	-	-	-
(e)	$r_1 < \omega < r_2,\, N_2^* < \tilde{N}_2$	U	-	U	-	GAS	-
(f)	$r_1, r_2 > \omega, N_1^* < \tilde{N}_1, N_2^* < \tilde{N}_2$ $(\phi_1 r_2 - \phi_2 r_1)(N_1^* - \eta) < 0$ $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) < 0$	U	U	U	U	GAS	-
(g)	$r_1, r_2 > \omega, , N_1^* < \tilde{N}_1, N_2^* < \tilde{N}_2$ $(\phi_1 r_2 - \phi_2 r_1)(N_1^* - \eta) > 0$ $(\phi_1 r_2 - \phi_2 r_1)(N_2^* - \eta) > 0$	U	U	U	GAS	U	-
(h)	$r_1 > r_2 > \omega,\, N_1^* > \tilde{N}_1,\, N_2^* < \tilde{N}_2$	U	GAS	U	-	U	-
(i)	$\omega < r_1 < r_2,\, N_1^* < \tilde{N}_1,\, N_2^* > \tilde{N}_2$	U	U	GAS	U	-	-
(j)	$r_1 > r_2 > \omega,\, N_1^* < \tilde{N}_1,\, N_2^* > \tilde{N}_2$	U	U	U	GAS	-	-
(k)	$\omega < r_1 < r_2,\, N_1^* > \tilde{N}_1,\, N_2^* < \tilde{N}_2$	U	U	U	-	GAS	-
(l)	$r_1 > r_2 > \omega,\, N_1^* > \tilde{N}_1,\, N_2^* > \tilde{N}_2$	U	GAS	U	-	-	-
(m)	$\omega < r_1 < r_2,\, N_1^* > \tilde{N}_1,\, N_2^* > \tilde{N}_2$	U	U	GAS	-	-	-
(n)	(a) $r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1,$ $\tilde{N}_1 > N_1^* > \eta > N_2^*, \tilde{N}_2 > N_2^*;$ or (b) $\omega < r_1 < r_2, \phi_1 r_2 < \phi_2 r_1,$ $N_1^* < \eta < N_2^* < \tilde{N}_2, N_1^* < \tilde{N}_1$	U	U	U	S	S	U
(o)	(a) $r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1,$ $N_1^* < \eta < N_2^* < \tilde{N}_2 < \tilde{N}_1;$ or (b) $\omega < r_1 < r_2, \phi_1 r_2 < \phi_2 r_1,$ $\tilde{N}_2 > \tilde{N}_1 > N_1^* > \eta > N_2^*$	U	U	U	U	U	S
(p)	$r_1 > r_2 > \omega,\, \phi_1 r_2 > \phi_2 r_1,$ $N_1^* > \tilde{N}_1 > \tilde{N}_2 > \eta > N_2^*$	U	S	U	-	S	U
(q)	$\omega < r_1 < r_2, \phi_1 r_2 < \phi_2 r_1,$ $N_1^* < \eta < \tilde{N}_1 < \tilde{N}_2 < N_2^*$	U	U	S	S	-	U
(r)	$r_1 > r_2 > \omega, \phi_1 r_2 > \phi_2 r_1,$ $N_1^* < \eta < \tilde{N}_2 < \tilde{N}_1, \tilde{N}_2 < N_2^*$	U	U	U	U	-	S
(s)	$\omega < r_1 < r_2, \phi_1 r_2 < \phi_2 r_1,$ $N_1^* > \tilde{N}_1, \tilde{N}_2 > \tilde{N}_1 > \eta > N_2^*$	U	U	U	-	U	S

TABLE 2. Global or local dynamics of (4). E_0^{nnv}-E_5^{nnv} are defined in (5). Conditions for E_5^{nnv} 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".

such that when t is sufficiently large, $0 \le N_1(t) < u_{N_1}$, $0 \le N_2(t) < u_{N_2}$, and $0 \le V(t) < u_V$ 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 $Q(t, w^0)$ ($t \ge 0$).

Claim 1. $\cup_{w^0 \in \partial X_0} \omega(w^0) \subseteq \cup_{i=0}^{4} \{E_i^{nnv}\}$.

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} ($i = 0, \cdots, 4$) is a uniform weak repeller for X_0 in the sense that there exists $\rho > 0$ such that*

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

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

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

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 $N_1^* < \tilde{N}_1$. Let $\epsilon > 0$ be sufficiently small such that $\tilde{N}_1 - \epsilon - N_1^* > 0$. 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 $t > t_0$, $\tilde{N}_1 - \epsilon < N_1(t)$, $N_2(t) < \epsilon$, $V(t) < \epsilon$, 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 $N_2^* < \tilde{N}_2$. 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 $\lambda_{E_3^{nnv}} = r_2(1 - \frac{N_1^*}{K}) - \phi_2 \tilde{V}^* - \omega > 0$. Let $\epsilon > 0$ be sufficiently small such that $r_2(1 - \frac{N_1^*}{K}) - \phi_2 \tilde{V}^* - \omega - \epsilon(\frac{2r_2}{K} + \phi_2) > 0$. 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 $t > t_0$, $N_1^* - \epsilon < N_1(t) < N_1^* + \epsilon$, $N_2(t) < \epsilon$, $\tilde{V}^* - \epsilon < N_1(t) < \tilde{V}^* + \epsilon$, and

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

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 ∂X_0 converges to $\cup_{i=0}^4 \{E_i^{nnv}\}$, each of these equilibria is isolated in X, and $W^s(E_i^{nnv}) \cap X_0 = \varnothing$ for $i = 0, \cdots, 4$, where $W^s(E_i^{nnv})$ is the stable set of E_i^{nnv}. Moreover, by the positive invariance of ∂X_0 and Lemmas 3.1 and 3.2, we obtain that all possible connections among E_i^{nnv}'s 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 $E_2^{nnv} \to E_1^{nnv}$ if $r_1 > r_2$ or $E_1^{nnv} \to E_2^{nnv}$ if $r_1 < r_2$, and hence, there is no cycle in ∂X_0 from $\cup_{i=0}^4 \{E_i^{nnv}\}$ to themselves.

Define a continuous function $p : X \to [0, \infty)$ by $p(w^0) = \min\{N_1^0, N_2^0, V^0\}$ for $w^0 = (N_1^0, N_2^0, V^0) \in X$. 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,

$\liminf_{t\to\infty} N_1(t) > \xi$, $\liminf_{t\to\infty} N_2(t) > \xi$, $\liminf_{t\to\infty} V(t) > \xi$ for any initial condition $w^0 \in X_0$. Then by Theorem 1.3.6 in [22], (4) admits a global attractor in X_0. $\square$

Remark 3.11. The results in Table 2 and Theorem 3.10 show the following:
(i) when the equilibrium E_5^{nnv} is not positive, if one nonnegative equilibrium is locally asymptotically stable, then it is globally asymptotically stable;
(ii) when E_5^{nnv} is positive but unstable, then bistability appears;
(iii) when E_5^{nnv} 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^{nnv} 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^{nnv} 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^{nnv} is positive, then it is locally asymptotically stable.

Let

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

Then for positive c_1 and c_2, $\mathcal{V} > 0$ for all $N_1 > 0$, $N_2 > 0$ and $V > 0$ and $\mathcal{V}$ is radially unbounded. Moreover,

$$\begin{aligned}
\frac{d\mathcal{V}}{dt} = \ & (N_1 - N_1^c)\left(-\frac{r_1}{K}(N_1 + N_2 - (N_1^c + N_2^c)) - \phi_1(V - V^c)\right) \\
& + c_1(N_2 - N_2^c)\left(-\frac{r_2}{K}(N_1 + N_2 - (N_1^c + N_2^c)) - \phi_2(V - V^c)\right) \\
& + c_2(V - V^c)(\beta_1\phi_1(N_1 - N_1^c) + \beta_2\phi_2(N_2 - N_2^c)) \\
= \ & -\frac{r_1}{K}\left(N_1 - N_1^c + \frac{r_1 + c_1 r_2}{2r_1}(N_2 - N_2^c)\right)^2 + \frac{(r_1 - c_1 r_2)^2}{4r_1 K}(N_2 - N_2^c)^2 \\
& + (c_2\beta_1 - 1)\phi_1(N_1 - N_1^c)(V - V^c) + (c_2\beta_2 - c_1)\phi_2(N_2 - N_2^c)(V - V^c)
\end{aligned}$$

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

$$\frac{d\mathcal{V}}{dt} = -\frac{r_1}{K}(N_1 - N_1^c + N_2 - N_2^c)^2 \leq 0.$$

By LaSalle's invariance principle, the set of accumulation points of any solution is contained in $\mathcal{I}$, which is the union of complete trajectories contained entirely in the set $\{\mathbf{x} : d\mathcal{V}(\mathbf{x})/dt = 0\}$. Since E_5^{nnv} 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 $V^0 > 0$. $\square$

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):

$E_0 = (0, 0, 0, 0)$, $\quad E_1 = (\tilde{N}_1, 0, 0, 0)$, $\quad E_2 = (0, \tilde{N}_2, 0, 0)$,
$E_3 = (N_{1,1}^*, 0, \frac{r_1(\tilde{N}_1 - N_{1,1}^*)}{K\phi_{11}}, 0)$, $\quad E_4 = (N_{1,2}^*, 0, 0, \frac{r_1(\tilde{N}_1 - N_{1,2}^*)}{K\phi_{12}})$,
$E_5 = (0, N_{2,1}^*, \frac{r_2(\tilde{N}_2 - N_{2,1}^*)}{K\phi_{21}}, 0)$, $\quad E_6 = (0, N_{2,2}^*, 0, \frac{r_2(\tilde{N}_2 - N_{2,2}^*)}{K\phi_{22}})$,
$E_7 = (N_1^c, N_2^c, V_1^c, 0)$, $\quad E_8 = (\hat{N}_1^c, \hat{N}_2^c, 0, \hat{V}_2^c)$, $\quad E_9 = (N_1^p, N_2^p, V_1^p, V_2^p)$,

where

$$
\begin{aligned}
&\tilde{N}_1 = \frac{(r_1-\omega)K}{r_1}, \quad \tilde{N}_2 = \frac{(r_2-\omega)K}{r_2},\\
&N^*_{1,1} = \frac{m_1+\omega}{\beta_{11}\phi_{11}}, \qquad N^*_{2,1} = \frac{m_1+\omega}{\beta_{21}\phi_{21}}, \qquad N^*_{1,2} = \frac{m_2+\omega}{\beta_{12}\phi_{12}}, \quad N^*_{2,2} = \frac{m_2+\omega}{\beta_{22}\phi_{22}},\\
&\eta_1 = \frac{(\phi_{11}(r_2-\omega)-\phi_{21}(r_1-\omega))K}{\phi_{11}r_2-\phi_{21}r_1}, \qquad \eta_2 = \frac{(\phi_{12}(r_2-\omega)-\phi_{22}(r_1-\omega))K}{\phi_{12}r_2-\phi_{22}r_1},\\
&N^c_1 = \frac{\beta_{21}\phi_{21}(N^*_{2,1}-\eta_1)}{\beta_{11}\phi_{11}-\beta_{21}\phi_{21}}, \quad N^c_2 = -\frac{\beta_{11}\phi_{11}(N^*_{1,1}-\eta_1)}{\beta_{11}\phi_{11}-\beta_{21}\phi_{21}}, \quad V^c_1 = \frac{(r_1-r_2)\omega}{\phi_{11}r_2-\phi_{21}r_1},\\
&\hat{N}^c_1 = \frac{\beta_{22}\phi_{22}(N^*_{2,2}-\eta_2)}{\beta_{12}\phi_{12}-\beta_{22}\phi_{22}}, \quad \hat{N}^c_2 = -\frac{\beta_{12}\phi_{12}(N^*_{1,2}-\eta_2)}{\beta_{12}\phi_{12}-\beta_{22}\phi_{22}}, \quad \hat{V}^c_2 = \frac{(r_1-r_2)\omega}{\phi_{12}r_2-\phi_{22}r_1},\\
&N^p_1 = -\frac{\beta_{21}\phi_{21}(m_2+\omega)-\beta_{22}\phi_{22}(m_1+\omega)}{\beta_{11}\beta_{22}\phi_{11}\phi_{22}-\beta_{12}\beta_{21}\phi_{12}\phi_{21}},\\
&N^p_2 = \frac{\beta_{11}\phi_{11}(m_2+\omega)-\beta_{12}\phi_{12}(m_1+\omega)}{\beta_{11}\beta_{22}\phi_{11}\phi_{22}-\beta_{12}\beta_{21}\phi_{12}\phi_{21}},\\
&V^p_1 = \frac{(\phi_{12}r_2-\phi_{22}r_1)(\beta_{12}\phi_{12}-\beta_{22}\phi_{22})(m_1+\omega)(\frac{\hat{N}^c_1}{N^*_{1,1}}+\frac{\hat{N}^c_2}{N^*_{2,1}}-1)}{(\beta_{11}\beta_{22}\phi_{11}\phi_{22}-\beta_{12}\beta_{21}\phi_{12}\phi_{21})(\phi_{11}\phi_{22}-\phi_{12}\phi_{21})K},\\
&V^p_2 = \frac{(\phi_{11}r_2-\phi_{21}r_1)(\beta_{11}\phi_{11}-\beta_{21}\phi_{21})(m_2+\omega)(\frac{N^c_1}{N^*_{1,2}}+\frac{N^c_2}{N^*_{2,2}}-1)}{(\beta_{11}\beta_{22}\phi_{11}\phi_{22}-\beta_{12}\beta_{21}\phi_{12}\phi_{21})(\phi_{11}\phi_{22}-\phi_{12}\phi_{21})K}.
\end{aligned}
\tag{9}
$$

For simplicity, we denote

$$
\begin{aligned}
&B\Phi = \beta_{11}\beta_{22}\phi_{11}\phi_{22}-\beta_{12}\beta_{21}\phi_{12}\phi_{21}, && \Phi\Phi = (\phi_{11}\phi_{22}-\phi_{12}\phi_{21}),\\
&\Phi R_1 = (\phi_{11}r_2-\phi_{21}r_1), && \Phi R_2 = (\phi_{12}r_2-\phi_{22}r_1),\\
&B\Phi_1 = (\beta_{11}\phi_{11}-\beta_{21}\phi_{21}), && B\Phi_2 = (\beta_{12}\phi_{12}-\beta_{22}\phi_{22}),\\
&B\Phi_3 = \beta_{11}\phi_{11}(m_2+\omega)-\beta_{12}\phi_{12}(m_1+\omega), && B\Phi_4 = \beta_{21}\phi_{21}(m_2+\omega)-\beta_{22}\phi_{22}(m_1+\omega),\\
&NN_h = (\tfrac{\hat{N}^c_1}{N^*_{1,1}}+\tfrac{\hat{N}^c_2}{N^*_{2,1}}-1), && NN = (\tfrac{N^c_1}{N^*_{1,2}}+\tfrac{N^c_2}{N^*_{2,2}}-1).
\end{aligned}
\tag{10}
$$

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* $r_1 > r_2$, $\tilde{N}_1 < N^*_{1,1}$*, and* $\tilde{N}_1 < N^*_{1,2}$.

(iii) E_2 *is nonnegative if* $r_2 > \omega$ *and is locally asymptotically stable if* $r_1 < r_2$, $\tilde{N}_2 < N^*_{2,1}$, $\tilde{N}_2 < N^*_{2,2}$.

(iv) E_3 *is nonnegative if* $\tilde{N}_1 > N^*_{1,1}$ *and is locally asymptotically stable if* $\beta_{11}\phi_{11}(m_2+\omega) > \beta_{12}\phi_{12}(m_1+\omega)$*, and* $(\phi_{11}r_2-\phi_{21}r_1)(N^*_{1,1}-\eta_1) > 0$.

(v) E_4 *is nonnegative if* $\tilde{N}_1 > N^*_{1,2}$ *and is locally asymptotically stable if* $\beta_{11}\phi_{11}(m_2+\omega) < \beta_{12}\phi_{12}(m_1+\omega)$*, and* $(\phi_{12}r_2-\phi_{22}r_1)(N^*_{1,2}-\eta_2) > 0$.

(vi) E_5 *is nonnegative if* $\tilde{N}_2 > N^*_{2,1}$ *and is locally asymptotically stable if* $\beta_{21}\phi_{21}(m_2+\omega) > \beta_{22}\phi_{22}(m_1+\omega)$ *and* $(\phi_{11}r_2-\phi_{21}r_1)(N^*_{2,1}-\eta_1) < 0$.

(vii) E_6 *is nonnegative if* $\tilde{N}_2 > N^*_{2,2}$ *and is locally asymptotically stable if* $\beta_{21}\phi_{21}(m_2+\omega) < \beta_{22}\phi_{22}(m_1+\omega)$*, and* $(\phi_{12}r_2-\phi_{22}r_1)(N^*_{2,2}-\eta_2) < 0$.

(viii) E_7 *is nonnegative if* $(\beta_{11}\phi_{11}-\beta_{21}\phi_{21})(N^*_{2,1}-\eta_1) > 0$, $(\beta_{11}\phi_{11}-\beta_{21}\phi_{21})(N^*_{1,1}-\eta_1) < 0$*, and* $(\phi_{11}r_2-\phi_{21}r_1)(r_1-r_2) > 0$*. It is locally asymptotically stable if* $\frac{N^c_1}{N^*_{1,2}}+\frac{N^c_2}{N^*_{2,2}}-1 < 0$ *and* $(\phi_{11}r_2-\phi_{21}r_1)(\beta_{11}\phi_{11}-\beta_{21}\phi_{21}) > 0$.

(ix) *E_8 is nonnegative if $(\beta_{12}\phi_{12}-\beta_{22}\phi_{22})(N^*_{2,2}-\eta_2)>0$, $(\beta_{12}\phi_{12}-\beta_{22}\phi_{22})(N^*_{1,2}-\eta_2)<0$, $(\phi_{12}r_2-\phi_{22}r_1)(r_1-r_2)>0$. It is locally asymptotically stable if $\frac{\hat{N}_1^c}{N^*_{1,1}}+\frac{\hat{N}_2^c}{N^*_{2,1}}-1<0$ 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 $-\frac{\beta_{11}\phi_{11}(m_2+\omega)-\beta_{12}\phi_{12}(m_1+\omega)}{(\beta_{11}\phi_{11})}$, $-\frac{(\phi_{11}r_2-\phi_{21}r_1)(N^*_{1,1}-\eta_1)}{(K\phi_{11})}$, and other two with negative real parts when E_3 is nonnegative.

(v). At E_4, the eigenvalues of the Jacobian matrix are $\frac{\beta_{11}\phi 11(m_2+\omega)-\phi_{12}\beta_{12}(m_1+\omega)}{\beta_{12}\phi_{12}}$, $-\frac{(\phi_{12}r_2-\phi_{22}r_1)(N^*_{1,2}-\eta_2)}{(K\phi_{12})}$, and other two with negative real parts when E_4 is nonnegative.

(vi). At E_5, the eigenvalues of the Jacobian matrix are $-\frac{\beta_{21}\phi_{21}(m_2+\omega)-\beta_{22}\phi_{22}(m_1+\omega)}{(\beta_{21}\phi_{21})}$, $\frac{(\phi_{11}r_2-\phi_{21}r_1)(N^*_{2,1}-\eta_1)}{(K\phi_{21})}$, and other two with negative real parts when E_5 is nonnegative.

(vii). At E_6, the eigenvalues of the Jacobian matrix are $\frac{\beta_{21}\phi_{21}(m_2+\omega)-\beta_{22}\phi_{22}(m_1+\omega)}{\beta_{22}\phi_{22}}$, $\frac{(\phi_{12}r_2-\phi_{22}r_1)(N^*_{2,2}-\eta_2)}{(K\phi_{22})}$, and other two with negative real parts when E_6 is nonnegative.

(viii). At E_7, one eigenvalue of the Jacobian matrix is $\lambda_{E_7}=(m_2+\omega)(\frac{N_1^c}{N^*_{1,2}}+\frac{N_2^c}{N^*_{2,2}}-1)$; 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 $\lambda_{E_8}=(m_1+\omega)(\frac{\hat{N}_1^c}{N^*_{1,1}}+\frac{\hat{N}_2^c}{N^*_{2,1}}-1)$; 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

$$J(E_9)=\begin{bmatrix} -\frac{r_1N_1^p}{K} & -\frac{r_1N_1^p}{K} & -\phi_{11}N_1^p & -\phi_{12}N_1^p \\ -\frac{r_2N_2^p}{K} & -\frac{r_2N_2^p}{K} & -\phi_{21}N_2^p & -\phi_{22}N_2^p \\ \beta_{11}\phi_{11}V_1^p & \beta_{21}\phi_{21}V_1^p & 0 & 0 \\ \beta_{12}\phi_{12}V_2^p & \beta_{22}\phi_{22}V_2^p & 0 & 0 \end{bmatrix}.$$

The characteristic equation of $J(E_9)$ is

$$\lambda^4+b_1\lambda^3+b_2\lambda^2+b_3\lambda+b_4=0, \tag{11}$$

where

$$\begin{aligned}
b_1 &= \frac{N_1^p r_1 + N_2^p r_2}{K},\\
b_2 &= N_1^p V_1^p \beta_{11}\phi_{11}^2 + N_1^p V_2^p \beta_{12}\phi_{12}^2 + N_2^p V_1^p \beta_{21}\phi_{21}^2 + N_2^p V_2^p \beta_{22}\phi_{22}^2,\\
b_3 &= \frac{N_1^p N_2^p (V_1^p(\phi_{11}r_2 - \phi_{21}r_1)(\beta_{11}\phi_{11} - \beta_{21}\phi_{21}) + V_2^p(\phi_{12}r_2 - \phi_{22}r_1)(\beta_{12}\phi_{12} - \beta_{22}\phi_{22}))}{K},\\
b_4 &= N_1^p N_2^p V_1^p V_2^p (\phi_{11}\phi_{22} - \phi_{12}\phi_{21})(\beta_{11}\beta_{22}\phi_{11}\phi_{22} - \beta_{12}\beta_{21}\phi_{12}\phi_{21}).
\end{aligned} \tag{12}$$

Let

$$\begin{aligned}
\Delta_1 =&\ b_1,\\
\Delta_2 =&\ b_1 b_2 - b_3\\
=&\ \frac{N_1^p N_2^p (V_1^p(\beta_{11}\phi_{11}\phi_{21}r_1 + \beta_{21}\phi_{11}\phi_{21}r_2) + V_2^p(\beta_{12}\phi_{12}\phi_{22}r_1 + \beta_{22}\phi_{12}\phi_{22}r_2))}{K}\\
&+ \frac{(N_1^p)^2(V_1^p\beta_{11}\phi_{11}^2 r_1 + V_2^p\beta_{12}\phi_{12}^2 r_1) + (N_2^p)^2(V_1^p\beta_{21}\phi_{21}^2 r_2 + V_2^p\beta_{22}\phi_{22}^2 r_2)}{K},\\
\Delta_3 =&\ -b_4 b_1^2 + b_3\Delta_2\\
=&\ \frac{N_1^p N_2^p}{K^2}\cdot (B\Phi_1(N_1^p\phi_{11} + N_2^p\phi_{21})V_1^p + B\Phi_2(N_1^p\phi_{12} + N_2^p\phi_{22})V_2^p)\\
&\cdot(\Phi R_1(N_1^p\beta_{11}\phi_{11}r_1 + N_2^p\beta_{21}\phi_{21}r_2)V_1^p + \Phi R_2(N_1^p\beta_{12}\phi_{12}r_1 + N_2^p\beta_{22}\phi_{22}r_2)V_2^p).
\end{aligned} \tag{13}$$

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:

$$\Phi\Phi \cdot B\Phi > 0 \text{ and}$$

$$\begin{aligned}
&(B\Phi_1(N_1^p\phi_{11} + N_2^p\phi_{21})V_1^p + B\Phi_2(N_1^p\phi_{12} + N_2^p\phi_{22})V_2^p)\\
&\cdot(\Phi R_1(N_1^p\beta_{11}\phi_{11}r_1 + N_2^p\beta_{21}\phi_{21}r_2)V_1^p + \Phi R_2(N_1^p\beta_{12}\phi_{12}r_1 + N_2^p\beta_{22}\phi_{22}r_2)V_2^p) > 0.
\end{aligned} \tag{14}$$

□

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_9.

By (11), if $\lambda = ki$ ($k \neq 0$) is an eigenvalue of $J(E_9)$, then

$$k^4 - b_1k^3 i - b_2k^2 + b_3ki + b_4 = 0,$$

which implies $k^4 - b_2k^2 + b_4 = 0$ and $-b_1k^3 + b_3k = 0$. Then $k^2 = \frac{b_2 \pm \sqrt{b_2^2 - 4b_4}}{2} = \frac{b_3}{b_1}$. Hence, $b_3 > 0$ and $\Delta_3 = -b_4b_1^2 + b_1b_2b_3 - b_3^2 = 0$. Moreover, there can be at most one simple pair of pure imaginary eigenvalues $\pm\sqrt{\frac{b_3}{b_1}}i$. Note that 0 is an eigenvalue if $b_4 = 0$. Therefore, if $b_3 > 0$, $b_4 \neq 0$, and $\Delta_3 = 0$, then $J(E_9)$, admits a simple pair of pure imaginary eigenvalues and no other eigenvalues have zero real parts.

Take a parameter μ of (1) (e.g., $\mu = \beta_{11}$) for the bifurcation parameter and let $\lambda(\mu) = \lambda_1(\mu) + i\lambda_2(\mu)$ be an eigenvalue of $J(E_9)$. Assume that at $\mu = \mu_0$, $J(E_9)$, 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

$$(\lambda_1(\mu) + i\lambda_2(\mu))^4 + b_1(\lambda_1(\mu) + i\lambda_2(\mu))^3 + b_2(\lambda_1(\mu) + i\lambda_2(\mu))^2 + b_3(\lambda_1(\mu) + i\lambda_2(\mu)) + b_4 = 0, \tag{15}$$

Equilibrium	Existence condition	Stability condition
$E_0 = (0,0,0,0)$		$r_1 < \omega$, $r_2 < \omega$
$E_1 = (\tilde{N}_1, 0, 0, 0)$	$r_1 > \omega$	$r_1 > r_2$, $N_{1,1}^* > \tilde{N}_1$, $N_{1,2}^* > \tilde{N}_1$
$E_2 = (0, \tilde{N}_2, 0, 0)$	$r_2 > \omega$	$r_1 < r_2$, $N_{2,1}^* > \tilde{N}_2$, $N_{2,2}^* > \tilde{N}_2$
$E_3 = (N_{1,1}^*, 0, \frac{r_1(\tilde{N}_1 - N_{1,1}^*)}{K\phi_{11}}, 0)$	$N_{1,1}^* < \tilde{N}_1$	$B\Phi_3 > 0$ $\Phi R_1 \cdot (N_{1,1}^* - \eta_1) > 0$
$E_4 = (N_{1,2}^*, 0, 0, \frac{r_1(\tilde{N}_1 - N_{1,2}^*)}{K\phi_{12}})$	$N_{1,2}^* < \tilde{N}_1$	$B\Phi_3 < 0$ $\Phi R_2 \cdot (N_{1,2}^* - \eta_2) > 0$
$E_5 = (0, N_{2,1}^*, \frac{r_2(\tilde{N}_2 - N_{2,1}^*)}{K\phi_{21}}, 0)$	$N_{2,1}^* < \tilde{N}_2$	$B\Phi_4 > 0$ $\Phi R_1 \cdot (N_{2,1}^* - \eta_1) < 0$
$E_6 = (0, N_{2,2}^*, 0, \frac{r_2(\tilde{N}_2 - N_{2,2}^*)}{K\phi_{22}})$	$N_{2,2}^* < \tilde{N}_2$	$B\Phi_4 < 0$ $\Phi R_2 \cdot (N_{2,2}^* - \eta_2) < 0$
$E_7 = (N_1^c, N_2^c, V_1^c, 0)$	$(N_{2,1}^* - \eta_1) \cdot B\Phi_1 > 0$ $(N_{1,1}^* - \eta_1) \cdot B\Phi_1 < 0$ $(r_1 - r_2)\Phi R_1 > 0$	$NN < 0$ $\Phi R_1 \cdot B\Phi_1 > 0$
$E_8 = (\hat{N}_1^c, \hat{N}_2^c, 0, \hat{V}_2^c)$	$(N_{2,2}^* - \eta_2) \cdot B\Phi_2 > 0$ $(N_{1,2}^* - \eta_2) \cdot B\Phi_2 < 0$ $(r_1 - r_2)\Phi R_2 > 0$	$NN_h < 0$ $\Phi R_2 \cdot B\Phi_2 > 0$
$E_9 = (N_1^p, N_2^p, V_1^p, V_2^p)$	$B\Phi \cdot B\Phi_3 < 0$ $B\Phi \cdot B\Phi_4 > 0$ $\Phi R_1 \cdot B\Phi_1 \cdot NN \cdot B\Phi \cdot \Phi\Phi > 0$ $\Phi R_2 \cdot B\Phi_2 \cdot NN_h \cdot B\Phi \cdot \Phi\Phi > 0$	$B\Phi \cdot \Phi\Phi > 0$ (14)

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)

whose real part and imaginary part both being zero implies

$$\begin{aligned}
&\lambda_2^4(\mu) - 6\lambda_1^2(\mu)\lambda_2^2(\mu) - 3\lambda_1(\mu)\lambda_2^2(\mu)b_1 - \lambda_2^2(\mu)b_2 + \lambda_1^4(\mu) \\
&+\lambda_1^3(\mu)b_1 + \lambda_1^2(\mu)b_2 + \lambda_1(\mu)b_3 + b_4 = 0, \\
&\lambda_2(\mu)(4\lambda_1^3(\mu) + 3\lambda_1^2(\mu)b_1 - 4\lambda_1(\mu)\lambda_2^2(\mu) - \lambda_2^2(\mu)b_1 + 2\lambda_1(\mu)b_2 + b_3) = 0.
\end{aligned}$$

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

$$\begin{aligned}
&\frac{d\lambda_1}{d\mu}|_{\mu=\mu_0} \\
&= \frac{-4b_1'k^6 + 2b_1'b_2k^4 - 3b_2'b_1k^4 + 4b_3'k^4 + b_2'b_3k^2 - 2b_3'b_2k^2 + 3b_4'b_1k^2 - b_4'b_3}{9b_1^2k^4 + 16k^6 - 16b_2k^4 - 6b_1b_3k^2 + 4b_2^2k^2 + b_3^2}|_{\mu=\mu_0} \\
&= \frac{\frac{2(2b_1b_4 - b_2b_3)(b_1'b_3 - b_3'b_1)}{b_1^2} + 2b_4'b_3 - 2\frac{b_2'b_3^2}{b_1}}{4\frac{b_3}{b_1}(b_1b_3 + b_2^2 - 4b_4)}|_{\mu=\mu_0} \\
&= \frac{(2b_1b_4 - b_2b_3)(b_1'b_3 - b_3'b_1) + b_4'b_3b_1^2 - b_2'b_3^2b_1}{2b_3b_1(b_1b_3 + b_2^2 - 4b_4)}|_{\mu=\mu_0},
\end{aligned}$$

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 $\frac{d\lambda_1}{d\mu}|_{\mu=\mu_0}$ is positive, so the sign of $\frac{d\lambda_1}{d\mu}|_{\mu=\mu_0}$ is determined by its numerator

$$d_1(\mu_0) := [(2b_1b_4 - b_2b_3)(b_1'b_3 - b_3'b_1) + b_4'b_3b_1^2 - b_2'b_3^2b_1]|_{\mu=\mu_0}. \tag{16}$$

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

Theorem 4.2. *Let μ be one of the parameters of model (1). Assume that (1) admits a positive equilibrium E_9 when $\mu = \mu_0$. Let b_i's, Δ_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 μ_0.*

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 β is the bifurcation parameter. When $\beta = \beta_0 = 12.24183257$, we have $E_9 = (4.542055223 \cdot 10^6, 4.374348568 \cdot 10^6, 1.018711763 \cdot 10^7, 1.657794400 \cdot 10^7)$, $b_3 = 0.006776196866 > 0$, $b_4 = 0.0007258324845 \neq 0$, $\Delta_3 = 0$, $d_1 = 0.000002243989060 > 0$. A unique stable limit cycle bifurcates from E_9 as β increases from β_0. In particular, when $\beta = 11.5 < \beta_0$, (1) admits a stable positive equilibrium $E_9 = (4.835050396 \cdot 10^6, 4.656525458 \cdot 10^6, 5.345635091 \cdot 10^6, 6.737532279 \cdot 10^6)$, while when $\beta = 20 > \beta_0$, (1) admits an unstable positive equilibrium $E_9 = (2.780153978 \cdot 10^6, 2.677502138 \cdot 10^6, 3.930095605 \cdot 10^7, 7.575241231 \cdot 10^7)$ 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 μ_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

$$d_1(\mu_0) = \frac{(m+\omega)^2 K (r_1 - r_2)^2 (\phi_{11}\phi_{12}(\phi_{21} - \phi_{22}) - (\phi_{11} - \phi_{12})\phi_{21}\phi_{22})(\Phi R_1 - \Phi R_2)^2 \omega^2}{\Phi\Phi \cdot \Phi R_2^5 \cdot \Phi R_1^5 (\phi_{11} - \phi_{12} - \phi_{21} + \phi_{22})^4 (\phi_{21} - \phi_{22})^4 (\phi_{11} - \phi_{12})^4} \cdot d_2,$$

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 $N_{1,1}^* < N_{1,2}^*$ and $N_{2,1}^* < N_{2,2}^*$, then $V_2(t) \to 0$ as $t \to \infty$.*

Proof. Assume $N_{1,1}^* < N_{1,2}^*$ and $N_{2,1}^* < N_{2,2}^*$. For a constant $\xi \in \mathbb{R}$,

$$\begin{aligned}
&\xi \frac{1}{V_2}\frac{dV_2}{dt} - \frac{1}{V_1}\frac{dV_1}{dt} \\
&= \xi(\beta_{12}\phi_{12}N_1 + \beta_{22}\phi_{22}N_2 - m_2 - \omega) - (\beta_{11}\phi_{11}N_1 + \beta_{21}\phi_{21}N_2 - m_1 - \omega) \\
&= \xi(m_2 + \omega)\left(\frac{N_1}{N_{1,2}^*} + \frac{N_2}{N_{2,2}^*} - 1\right) - (m_1 + \omega)\left(\frac{N_1}{N_{1,1}^*} + \frac{N_2}{N_{2,1}^*} - 1\right) \\
&= N_1\left(\frac{\xi(m_2 + \omega)}{N_{1,2}^*} - \frac{m_1 + \omega}{N_{1,1}^*}\right) + N_2\left(\frac{\xi(m_2 + \omega)}{N_{2,2}^*} - \frac{m_1 + \omega}{N_{2,1}^*}\right) - \xi(m_2 + \omega) + m_1 + \omega.
\end{aligned}$$

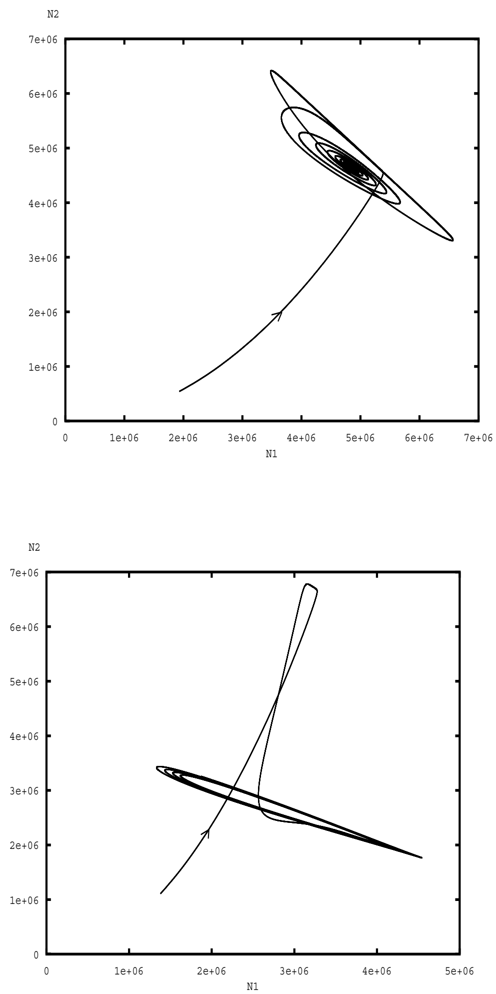

FIGURE 1. The projection of the phase diagram of model (1) onto the N_1N_2 plane. Left: $\beta = 11.5$; right: $\beta = 20$.

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 $\frac{m_1+\omega}{m_2+\omega} < \xi < \frac{m_1+\omega}{m_2+\omega} \cdot \min\left\{\frac{N^*_{1,2}}{N^*_{1,1}}, \frac{N^*_{2,2}}{N^*_{2,1}}\right\}$. 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 $t \to \infty$. $\square$

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 $t \to \infty$.*

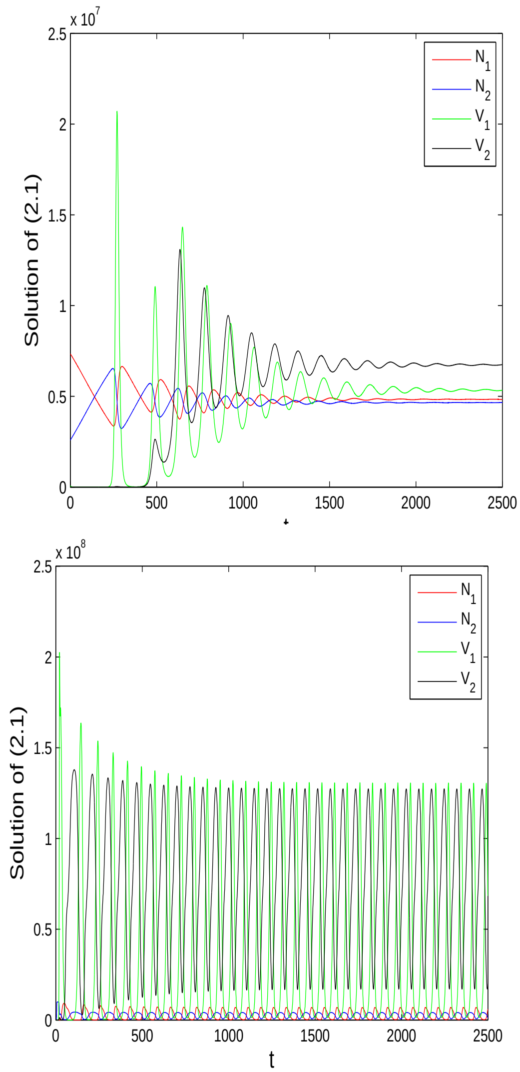

FIGURE 2. The time series of model (1). Left: $\beta = 11.5$; right: $\beta = 20$.

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

$$\begin{aligned} & a\frac{1}{V_2}\frac{dV_2}{dt} + b\frac{1}{V_1}\frac{dV_1}{dt} \\ = \;& a(\beta_{22}\phi_{22}N_2 - m_2 - \omega) + b(\beta_{21}\phi_{21}N_2 - m_1 - \omega) \\ = \;& (a\beta_{22}\phi_{22} + b\beta_{21}\phi_{21})N_2 - a(m_2 + \omega) - b(m_1 + \omega). \end{aligned}$$

If $N_{2,2}^* < N_{2,1}^*$, then let a satisfy $-\frac{m_1+\omega}{m_2+\omega} < a < -\frac{m_1+\omega}{m_2+\omega} \cdot \frac{N_{2,2}^*}{N_{2,1}^*} = -\frac{\beta_{21}\phi_{21}}{\beta_{22}\phi_{22}}$ and $b = 1$. We have

$$a\frac{1}{V_2}\frac{dV_2}{dt} + \frac{1}{V_1}\frac{dV_1}{dt} = (a\beta_{22}\phi_{22} + \beta_{21}\phi_{21})N_2 - a(m_2+\omega) - m_1 - \omega < 0,$$

which implies $V_1(t) \to 0$ as $t \to \infty$. If $N_{2,2}^* = N_{2,1}^*$, then let $a = -\frac{m_1+\omega}{m_2+\omega} = -\frac{m_1+\omega}{m_2+\omega} \cdot \frac{N_{2,2}^*}{N_{2,1}^*} = -\frac{\beta_{21}\phi_{21}}{\beta_{22}\phi_{22}}$ and $b = 2$. We have

$$a\frac{1}{V_2}\frac{dV_2}{dt} + \frac{1}{V_1}\frac{dV_1}{dt} = -m_1 - \omega < 0,$$

which implies $V_1(t) \to 0$ as $t \to \infty$. If $N_{2,2}^* > N_{2,1}^*$, then let a satisfy $\frac{m_1+\omega}{m_2+\omega} < a < \frac{m_1+\omega}{m_2+\omega} \cdot \frac{N_{2,2}^*}{N_{2,1}^*} = \frac{\beta_{21}\phi_{21}}{\beta_{22}\phi_{22}}$ and $b = -1$. We have

$$a\frac{1}{V_2}\frac{dV_2}{dt} - \frac{1}{V_1}\frac{dV_1}{dt} = (a\beta_{22}\phi_{22} - \beta_{21}\phi_{21})N_2 - a(m_2+\omega) + m_1 + \omega < 0,$$

which implies $V_2(t) \to 0$ as $t \to \infty$. Thus, the result is proved in the case when $N_1(t) \equiv 0$. The result can be similarly proved when $N_2(t) \equiv 0$. ☐

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_1 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 $NN_h > 0$, 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 $NN_h > 0$ are valid. System (1) is uniformly persistent in the sense that there exists a $\xi > 0$ such that*

$$\liminf_{t\to\infty} N_i(t) > \xi, \ \liminf_{t\to\infty} V_i(t) > \xi, \ i = 1, 2,$$

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 $\frac{dN_1}{dt} \leq r_1 N_1 \left(1 - \frac{N_1}{K}\right)$ and $\frac{dN_2}{dt} \leq$

$r_2N_2\left(1-\frac{N_2}{K}\right)$, we obtain that for a solution with nonnegative initial condition, $N_1(t) < K+1$ and $N_2(t) < K+1$ for $t > t_0$ for some positive t_0. Moreover, $\frac{d(\beta_{11}N_1+\beta_{21}N_2+V_1)}{dt} < -\omega(\beta_{11}N_1+\beta_{21}N_2+V_1)+(\beta_{11}r_1+\beta_{21}r_2)(K+1)$ and $\frac{d(\beta_{12}N_1+\beta_{22}N_2+V_2)}{dt} < -\omega(\beta_{12}N_1+\beta_{22}N_2+V_2)+(\beta_{12}r_1+\beta_{22}r_2)(K+1)$ for $t > \max\{t_0, t_1\}$. This implies that there exists $\bar{V} > 0$ such that $V_1(t) < \bar{V}$ and $V_2(t) < \bar{V}$ for all $t \geq t_2$ for some $t_2 > \max\{t_0, t_1\}$. Therefore, for any initial condition $w^0 \in \mathbb{R}^4_+$, the solution of (1) is eventually bounded in $\mathbb{R}^4_+$. Then (1) admits a global attractor in $\mathbb{R}^4_+$.

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

$$W = \{w^0 \in \mathbb{R}^4_+ : 0 \leq N_1^0 \leq K+1, 0 \leq N_2^0 \leq K+1, 0 \leq V_1^0, V_2^0 \leq \bar{V}\},$$

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

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

Then W^0 and ∂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 $N_1N_2V_1$ space and the $N_1N_2V_2$ space, respectively (see Theorem 3.10).

Claim 1. $\cup_{w^0\in\partial W^0}\omega(w^0) \subseteq \cup_{i=0}^8\{E_i\} \cup_{i=1}^2 A_i$.

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 $\omega(w^0) \in E_0 \cup E_2 \cup E_5 \cup E_6$; if $N_2(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_3 \cup E_4$; if $V_1(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_2 \cup E_4 \cup E_6 \cup E_8 \cup A_2$; if $V_2(t) \equiv 0$, then $\omega(w^0) \in E_0 \cup E_1 \cup E_2 \cup E_3 \cup E_5 \cup E_7 \cup A_1$.

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

$$\limsup_{t\to\infty} ||\Phi(t, w^0) - E_i|| \geq \rho, \forall w^0 \in W^0, \tag{17}$$

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

$$\limsup_{t\to\infty} ||\Phi(t, w^0) - A_i|| \geq \rho, \forall w^0 \in W^0, \tag{18}$$

where $||x|| = \max_{i=1,\cdots,4}\{x_i\}$ 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 $r_1 - \omega - \epsilon(2\frac{r_1}{K} + \phi_{11} + \phi_{12}) > 0$. 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 $\frac{dN_1}{dt} > (r_1 - \omega - \epsilon(2\frac{r_1}{K} + \phi_{11} + \phi_{12}))N_1$ 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 $t > t_0$, $\tilde{N}_1 - \epsilon < N_1(t) < \tilde{N}_1 + \epsilon$, $0 < N_2(t) < \epsilon$, $0 < V_1(t) < \epsilon$, $0 < V_2(t) < \epsilon$. If $r_1 > r_2$, the conditions in this theorem gives $N^*_{1,1} < \tilde{N}_1$. Let $\epsilon > 0$ be sufficiently small such that $\tilde{N}_1 - \epsilon > N^*_{1,1}$. Then $\frac{dV_1}{dt} > (m_1 + \omega)(\frac{\tilde{N}_1 - \epsilon}{N^*_{1,1}} - 1)V_1$. Therefore, $V_1(t) \to \infty$ as $t \to \infty$. A contradiction. If $r_1 < r_2$, then $\tilde{N}_1 < \tilde{N}_2$. Let $\epsilon > 0$ be sufficiently small such that $\tilde{N}_2 - \tilde{N}_1 - \epsilon(\frac{2r_2}{K} + \phi_{21} + \phi_{22}) > 0$. Then $\frac{dN_2}{dt} \geq N_2(r_2(1 - \frac{\tilde{N}_1+\epsilon+\epsilon}{K}) - \phi_{21}\epsilon -$

$\phi_{22}\epsilon - \omega) = \frac{r_2}{K} N_2(\tilde{N}_2 - \tilde{N}_1 - \epsilon(\frac{2r_2}{K} + \phi_{21} + \phi_{22}))$. 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 $t > t_0$, $N_{1,1}^* - \epsilon < N_1(t) < N_{1,1}^* + \epsilon$, $0 < N_2(t) < \epsilon$, $\frac{r_1(\tilde{N}_1 - N_{1,1}^*)}{K\phi_{11}} - \epsilon < V_1(t) < \frac{r_1(\tilde{N}_1 - N_{1,1}^*)}{K\phi_{11}} + \epsilon$, $0 < V_2(t) < \epsilon$. If $B\Phi_3 = \beta_{11}\phi_{11}(m_2 + \omega) - \beta_{12}\phi_{12}(m_1 + \omega) < 0$, then let $\epsilon > 0$ be sufficiently small such that $\frac{\beta_{12}\phi_{12}(m_1+\omega) - \beta_{11}\phi_{11}(m_2+\omega)}{\beta_{11}\phi_{11}} - \beta_{12}\phi_{12}\epsilon > 0$. We have $\frac{dV_2}{dt} > V_2(\beta_{12}\phi_{12}(N_{1,1}^* - \epsilon) - m_2 - \omega) = (\frac{\beta_{12}\phi_{12}(m_1+\omega) - \beta_{11}\phi_{11}(m_2+\omega)}{\beta_{11}\phi_{11}} - \beta_{12}\phi_{12}\epsilon)V_2$ for $t > t_0$. 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 $\frac{-\Phi R_1 \cdot (N_{1,1}^* - \eta_1)}{K\phi_{11}} - (\frac{2r_2}{K} + \phi_{21} + \phi_{22})\epsilon > 0$. Then $\frac{dN_2}{dt} > N_2(r_2\left(1 - \frac{N_{1,1}^* + \epsilon + \epsilon}{K}\right) - \phi_{21}(\frac{r_1(\tilde{N}_1 - N_{1,1}^*)}{K\phi_{11}} + \epsilon) - \phi_{22}\epsilon - \omega) = N_2(\frac{-\Phi R_1 \cdot (N_{1,1}^* - \eta_1)}{K\phi_{11}} - (\frac{2r_2}{K} + \phi_{21} + \phi_{22})\epsilon)$. 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 $\frac{N_1^c - \epsilon}{N_{1,2}^*} + \frac{N_2^c - \epsilon}{N_{2,2}^*} - 1 > 0$. 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 $t > t_0$, $N_1^c - \epsilon < N_1(t) < N_1^c + \epsilon$, $N_2^c - \epsilon < N_2(t) < N_2^c + \epsilon$, $V_1^c - \epsilon < V_1(t) < V_1^c + \epsilon$, $0 < V_2(t) < \epsilon$, and hence $\frac{dV_2}{dt} > V_2(m_2 + \omega)(\frac{N_1^c - \epsilon}{N_{1,2}^*} + \frac{N_2^c - \epsilon}{N_{2,2}^*} - 1)$. 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 $N_1N_2V_1$ space, then $E_7 \in A_1$ and E_7 is locally asymptotically stable in the $N_1N_2V_1$ 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 $N_1N_2V_2$ space, then (18) is true for A_2. Claim 2 is proved.

Define a continuous function $p : W \to [0, \infty)$ by $p(v^0) = \min\{N_1^0, N_2^0, V_1^0, V_2^0\}$ for $v^0 = (N_1^0, N_2^0, V_1^0, V_2^0) \in W$. It follows that $p^{-1}(0, \infty) \subseteq W^0$ and p has the property that if $p(v^0) > 0$ 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 ∂W^0 converges to $\cup_{i=0}^8 \{E_i\} \cup_{i=1}^2 A_i$, each of these invariant sets is isolated in W, and $W^s(E_i) \cap W^0 = \varnothing$ for $i = 0, \cdots, 8$, $W^s(A_i) \cap W^0 = \varnothing$ for $i = 1, 2$, where $W^s(E_i)$ and $W^s(A_i)$ are the stable set of E_i and A_i, respectively. All possible connections among E_i's and A_i's are $E_0 \to E_1$, $E_0 \to E_2 \to E_1 \to E_3 \to E_7$ (or A_1), $E_1 \to E_4 \to E_8$ (or A_2), $E_2 \to E_5 \to E_7$ (or A_1), $E_2 \to E_6 \to E_8$ (or A_2) if $r_1 > r_2$, and hence, there is no cycle in ∂W^0 from $\cup_{i=0}^8 \{E_i\} \cup_{i=1}^2 \{A_i\}$ to themselves in this case. Similarly, there is no cycle in ∂W^0 from $\cup_{i=0}^8 \{E_i\} \cup_{i=1}^2 \{A_i\}$ 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 $w^0 \in W^0$. □

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

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

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

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

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_9 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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