The dynamics of a two host-two virus system in a chemostat environment

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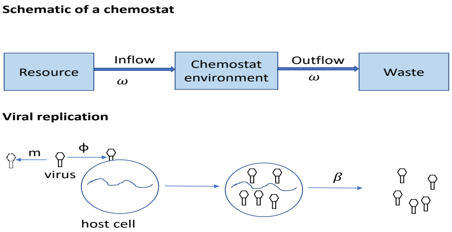
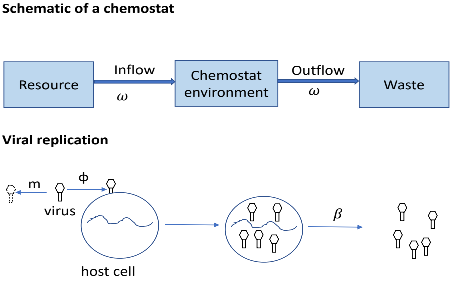
The host-virus model in a chemostat environment



The nutrient-bacteria-virus model in a chemostat environment:

$$\begin{cases} \dfrac{dR}{dt} = \omega J_0 - f(R)N - \omega R, \\ \dfrac{dN}{dt} = \epsilon f(R)N - \phi NV - \omega N, \\ \dfrac{dV}{dt} = \beta\phi NV - mV - \omega V. \end{cases}$$

R :	concentration of nutrient	J_0 :	Inflow nutrient concentration
N :	density of host	ω :	dilution/flow rate
V :	density of virus	m :	natural decay rate of virus
f :	consumption rate	β :	burst size
ϵ :	conversion rate	ϕ :	adsorption rate for virus attached to host



The bacteria-virus model in a chemostat environment:

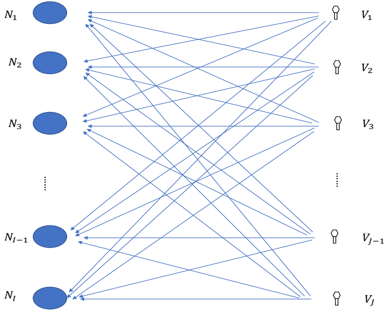
$$\begin{cases} \dfrac{dN}{dt} = f(N) - \phi NV - \omega N, \\ \dfrac{dV}{dt} = \beta\phi NV - mV - \omega V. \end{cases}$$

N :	density of host	ϕ :	adsorption rate for virus attached to host
V :	density of virus	m :	natural decay rate of virus
f :	growth rate of host	β :	burst size
ω :	dilution/flow rate		

The I-host J-virus model in a chemostat environment

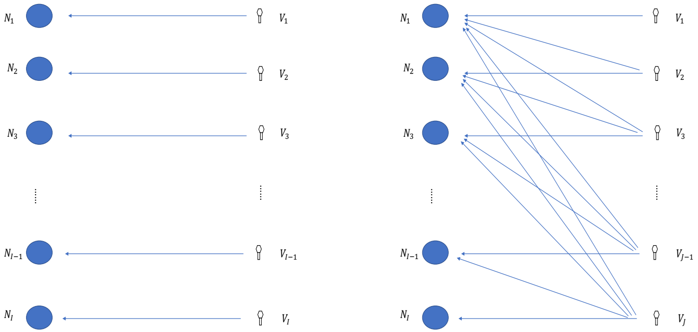
$$\begin{cases} \dfrac{dN_i}{dt} = r_i N_i \left(1 - \dfrac{\sum_{k=1}^{I} N_k}{K}\right) - \displaystyle\sum_{j=1}^{J} \phi_{ij} N_i V_j - \omega N_i, \quad i = 1, 2, \cdots, I, \\ \dfrac{dV_j}{dt} = \displaystyle\sum_{i=1}^{I} \beta_{ij} \phi_{ij} N_i V_j - m_j V_j - \omega V_j, \quad j = 1, 2, \cdots, J. \end{cases}$$

N_i :	density of host	ϕ_{ij} :	adsorption rate for virus attached to host
V_j :	density of virus	β_{ij} :	burst size
r_i :	intrinsic growth rate of host	m_j :	natural decay rate of virus
K:	carrying capacity of hosts	ω :	dilution/flow rate



The multi-host-virus model in a chemostat environment

1. In monogamous infection networks, when one virus specializes on infecting one host (e.g., $v_1 \to N_1$, $v_2 \to N_2$), if a unique positive equilibrium exists, then it is stable [Korytowski 2016].
2. In nested infection networks (e.g., $v_1 \to N_1$, $v_2 \to N_1 \& N_2$), permanence dynamics can be obtained under certain conditions [Jover et al 2013, Korytowski et al 2014].

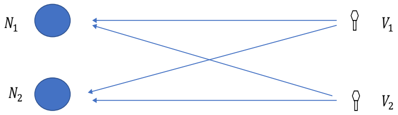


Left: a monogamous infection network; right: a nested infection network.

A two host-two virus model in a chemostat environment (see (5.15) in [Weitz 2016])

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_{11} N_1 V_1 - \phi_{12} N_1 V_2 - \omega N_1, \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_{21} N_2 V_1 - \phi_{22} N_2 V_2 - \omega N_2, \\ \dfrac{dV_1}{dt} = \beta_{11}\phi_{11} N_1 V_1 + \beta_{21}\phi_{21} N_2 V_1 - m_1 V_1 - \omega V_1, \\ \dfrac{dV_2}{dt} = \beta_{12}\phi_{12} N_1 V_2 + \beta_{22}\phi_{22} N_2 V_2 - m_2 V_2 - \omega V_2. \end{cases} \tag{1}$$

N_i	the density of host $i = 1, 2$
V_j	the density of virus $j = 1, 2$
r_i	the intrinsic growth rate of host i ($r_1 \neq r_2$)
K	the carrying capacity for the hosts
ϕ_{ij}	the adsorption rate for virus j attached to host i
m_j	the natural decay rate of virus j
ω	the dilution/flow rate
β_{ij}	the burst size



Dynamics of the one host-one virus model

The one host-one virus model:

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

Three possible nonnegative equilibria:

$$E_0^{nv} = (0,0), \quad E_1^{nv} = (\tilde{N}, 0), \quad E_3^{nv} = (N^*, V^*),$$

with

$$\tilde{N} = \frac{r-\omega}{r}K, \quad N^* = \frac{m+\omega}{\beta\phi}, \qquad V^* = \left(r - \omega - r\frac{m+\omega}{\beta\phi K}\right)\frac{1}{\phi} = \frac{r}{\phi K}(\tilde{N} - N^*).$$

Global dynamics of (2):

		E_0^{nv}	E_1^{nv}	E_3^{nv}
(i)	$r < \omega$	g.a.s.		
(ii)	$r > \omega$ $\frac{r-\omega}{r}K < \frac{m+\omega}{\beta\phi}$ (i.e., $\tilde{N} < N^*$)	saddle	g.a.s.	
(iii)	$r > \omega$ $\frac{r-\omega}{r}K > \frac{m+\omega}{\beta\phi}$ (i.e., $\tilde{N} > N^*$)	saddle	saddle	g.a.s.

The two host model in the chemostat:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \omega N_1, \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \omega N_2. \end{cases} \tag{3}$$

Three equilibria of (3):

$$E_0^{nn} = (0, 0), \quad E_1^{nn} = (\tilde{N}_1, 0), \quad E_2^{nn} = (0, \tilde{N}_2),$$

with

$$\tilde{N}_1 = \frac{r_1 - \omega}{r_1} K, \quad \tilde{N}_2 = \frac{r_2 - \omega}{r_2} K.$$

Global dynamics of (3):

		E_0^{nn}	E_1^{nn}	E_2^{nn}
(i)	$r_1 < \omega$ $r_2 < \omega$	g.a.s.		
(ii)	$r_1 > \omega$ $r_1 > r_2$	unstable	g.a.s.	saddle
(iii)	$r_2 > \omega$ $r_1 < r_2$	unstable	saddle	g.a.s.

The two host-one virus model:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_1 N_1 V - \omega N_1, \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_2 N_2 V - \omega N_2, \\ \dfrac{dV}{dt} = \beta_1 \phi_1 N_1 V + \beta_2 \phi_2 N_2 V - mV - \omega V. \end{cases} \tag{4}$$

System (4) admits 6 possible nonnegative equilibria:

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

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

Local dynamics of the two host-one virus model

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: 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}.

Global dynamics of (4)

Theorem

If $r_1 < \omega$ and $r_2 < \omega$, then $E_0^{nnv} = (0, 0, 0)$ is g.a.s. for (4) for all nonnegative initial conditions.

Theorem

(i) *If $r_1 > \omega$ and $r_2 < \omega$, then*
$E_1^{nnv} = (\tilde{N}_1, 0, 0)$ is g.a.s. for (4) for all positive initial conditions when $N_1^* > \tilde{N}_1$;
$E_3^{nnv} = (N_1^*, 0, \tilde{V}^*)$ is g.a.s. for (4) for all positive initial conditions when $N_1^* < \tilde{N}_1$.

(ii) *If $r_1 < \omega$ and $r_2 > \omega$, then*
$E_2^{nnv} = (0, \tilde{N}_2, 0)$ is g.a.s. for (4) for all positive initial conditions when $N_2^* > \tilde{N}_2$;
$E_4^{nnv} = (0, N_2^*, V^*)$ is g.a.s. for (4) for all positive initial conditions when $N_2^* < \tilde{N}_2$.

Theorem

If both $E_3^{nnv} = (N_1^*, 0, \tilde{V}^*)$ and $E_4^{nnv} = (0, N_2^*, V^*)$ 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 g.a.s. for (4) for all positive initial conditions.

Proof Note that E_0^{nnv}, E_1^{nnv}, and E_2^{nnv} are all unstable, E_5^{nnv} is not positive.

Case 1: $\frac{\phi_1}{\phi_2} < \frac{r_1}{r_2}$ and $N_1^* < \eta$, $N_2^* < \eta$. Let $\xi_1 = \frac{\phi_1}{\phi_2}$, $\xi_2 = r_1 - \omega - (r_2 - \omega)\frac{\phi_1}{\phi_2} > 0$.

$$\xi_1 \frac{1}{N_2}\frac{dN_2}{dt} - \frac{\xi_2}{m+\omega}\frac{1}{V}\frac{dV}{dt} - \frac{1}{N_1}\frac{dN_1}{dt} = \xi_2\left(N_1\left(\frac{1}{\eta} - \frac{1}{N_1^*}\right) + N_2\left(\frac{1}{\eta} - \frac{1}{N_2^*}\right)\right) < 0.$$

Integrating this inequality from 0 to t and taking exponentials on both sides yield

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

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 $\lim_{t\to\infty} N_1(t) = N_1^*$ and $\lim_{t\to\infty} V(t) = \tilde{V}^*$.

Case 2: $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$, $N_1^* > \eta$, $N_2^* > \eta$, and $\eta < 0$.

Case 3: $\frac{\phi_1}{\phi_2} > \frac{r_1}{r_2}$, $N_1^* > \eta$, $N_2^* > \eta$, and $\eta > 0$.

Theorem

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 g.a.s. for (4) for all positive initial conditions.

Theorem

If $\frac{r_1}{r_2} = \frac{\beta_2}{\beta_1}$ and E_5^{nnv} is positive, then it is g.a.s. .

Proof When $\frac{r_1}{r_2} = \frac{\beta_2}{\beta_1}$, if E_5^{nnv} is positive, it is l.a.s. .
Let

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

with $c_1 = \frac{\beta_2}{\beta_1}$, $c_2 = \frac{1}{\beta_1}$. Then $\mathcal{V} > 0$ for all $N_1 > 0$, $N_2 > 0$ and $V > 0$ and $\mathcal{V}$ is radially unbounded,

$$\begin{aligned} \frac{d\mathcal{V}}{dt} &= -\frac{r_1}{K} \left(N_1 - N_1^c + \frac{r_1 + c_1 r_2}{2r_1}(N_2 - N_2^c) \right)^2 + \frac{(r_1 - c_1 r_2)^2}{4 r_1 K}(N_2 - N_2^c)^2 \\ &\quad + (c_2\beta_1 - 1)\phi_1(N_1 - N_1^c)(V - V^c) + (c_2\beta_2 - c_1)\phi_2(N_2 - N_2^c)(V - V^c) \\ &= -\frac{r_1}{K}(N_1 - N_1^c + N_2 - N_2^c)^2 \\ &\leq 0. \end{aligned}$$

By LaSalle's invariance principle, E_5^{nnv} is g.a.s. with respect to initial conditions $N_1^0 > 0$, $N_2^0 > 0$, and $V^0 > 0$.

Persistence dynamics of (4)

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

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.

	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".

Global stability of the positive equilibrium

Remark The results in Table 2 and Theorem 6 show the following:

(i) when the equilibrium E_5^{nnv} is not positive, if one nonnegative equilibrium is l.a.s. , then it is g.a.s. ;

(ii) when E_5^{nnv} is positive but unstable, then bistability appears;

(iii) when E_5^{nnv} is positive and l.a.s. , then the two host-one virus model (4) is uniformly persistent.

E_5^{nnv} is positive and l.a.s. 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

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

Dynamics of the two host-two virus model (7)

$$
\begin{cases}
\dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_{11} N_1 V_1 - \phi_{12} N_1 V_2 - \omega N_1, \\
\dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{N_1 + N_2}{K}\right) - \phi_{21} N_2 V_1 - \phi_{22} N_2 V_2 - \omega N_2, \\
\dfrac{dV_1}{dt} = \beta_{11}\phi_{11} N_1 V_1 + \beta_{21}\phi_{21} N_2 V_1 - m_1 V_1 - \omega V_1, \\
\dfrac{dV_2}{dt} = \beta_{12}\phi_{12} N_1 V_2 + \beta_{22}\phi_{22} N_2 V_2 - m_2 V_2 - \omega V_2.
\end{cases}
\tag{7}
$$

Nonnegative equilibria of (7)

$$
\begin{aligned}
E_0 &= (0, 0, 0, 0), & E_1 &= (\tilde{N}_1, 0, 0, 0), & E_2 &= (0, \tilde{N}_2, 0, 0),\\
E_3 &= (N^*_{1,1}, 0, \frac{r_1(\tilde{N}_1 - N^*_{1,1})}{K\phi_{11}}, 0), & E_4 &= (N^*_{1,2}, 0, 0, \frac{r_1(\tilde{N}_1 - N^*_{1,2})}{K\phi_{12}}), & &\\
E_5 &= (0, N^*_{2,1}, \frac{r_2(\tilde{N}_2 - N^*_{2,1})}{K\phi_{21}}, 0), & E_6 &= (0, N^*_{2,2}, 0, \frac{r_2(\tilde{N}_2 - N^*_{2,2})}{K\phi_{22}}), & &\\
E_7 &= (N^c_1, N^c_2, V^c_1, 0), & E_8 &= (\hat{N}^c_1, \hat{N}^c_2, 0, \hat{V}^c_2), & E_9 &= (N^p_1, N^p_2, V^p_1, V^p_2),
\end{aligned}
$$

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}}, \quad N^*_{2,1} = \frac{m_1 + \omega}{\beta_{21}\phi_{21}}, \quad 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}, \quad \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{8}
$$

Local dynamics of (7)

Equilibrium	Existence condition	Stability condition
$E_0 = (0, 0, 0, 0)$		$r_1 < \omega$, $r_2 < \omega$
$E_1 = (\tilde{N}_1, 0, 0, 0)$	$r_1 > \omega$	$r_1 > r_2$, $N^*_{1,1} > \tilde{N}_1$, $N^*_{1,2} > \tilde{N}_1$
$E_2 = (0, \tilde{N}_2, 0, 0)$	$r_2 > \omega$	$r_1 < r_2$, $N^*_{2,1} > \tilde{N}_2$, $N^*_{2,2} > \tilde{N}_2$
$E_3 = (N^*_{1,1}, 0, \frac{r_1(\tilde{N}_1 - N^*_{1,1})}{K\phi_{11}}, 0)$	$N^*_{1,1} < \tilde{N}_1$	$B\Phi_3 > 0$ $\Phi R_1 \cdot (N^*_{1,1} - \eta_1) > 0$
$E_4 = (N^*_{1,2}, 0, 0, \frac{r_1(\tilde{N}_1 - N^*_{1,2})}{K\phi_{12}})$	$N^*_{1,2} < \tilde{N}_1$	$B\Phi_3 < 0$ $\Phi R_2 \cdot (N^*_{1,2} - \eta_2) > 0$
$E_5 = (0, N^*_{2,1}, \frac{r_2(\tilde{N}_2 - N^*_{2,1})}{K\phi_{21}}, 0)$	$N^*_{2,1} < \tilde{N}_2$	$B\Phi_4 > 0$ $\Phi R_1 \cdot (N^*_{2,1} - \eta_1) < 0$
$E_6 = (0, N^*_{2,2}, 0, \frac{r_2(\tilde{N}_2 - N^*_{2,2})}{K\phi_{22}})$	$N^*_{2,2} < \tilde{N}_2$	$B\Phi_4 < 0$ $\Phi R_2 \cdot (N^*_{2,2} - \eta_2) < 0$
$E_7 = (N^c_1, N^c_2, V^c_1, 0)$	$(N^*_{2,1} - \eta_1) \cdot B\Phi_1 > 0$ $(N^*_{1,1} - \eta_1) \cdot B\Phi_1 < 0$ $(r_1 - r_2)\Phi R_1 > 0$	$NN < 0$ $\Phi R_1 \cdot B\Phi_1 > 0$
$E_8 = (\hat{N}^c_1, \hat{N}^c_2, 0, \hat{V}^c_2)$	$(N^*_{2,2} - \eta_2) \cdot B\Phi_2 > 0$ $(N^*_{1,2} - \eta_2) \cdot B\Phi_2 < 0$ $(r_1 - r_2)\Phi R_2 > 0$	$NN_h < 0$ $\Phi R_2 \cdot B\Phi_2 > 0$
$E_9 = (N^p_1, N^p_2, V^p_1, V^p_2)$	$B\Phi \cdot B\Phi_3 < 0$ $B\Phi \cdot B\Phi_4 > 0$ $\Phi R_1 \cdot B\Phi_1 \cdot NN \cdot B\Phi \cdot \Phi\Phi > 0$ $\Phi R_2 \cdot B\Phi_2 \cdot NN_h \cdot B\Phi \cdot \Phi\Phi > 0$	$B\Phi \cdot \Phi\Phi > 0$ (9)

$B\Phi = \beta_{11}\beta_{22}\phi_{11}\phi_{22} - \beta_{12}\beta_{21}\phi_{12}\phi_{21}$, $\quad \Phi\Phi = (\phi_{11}\phi_{22} - \phi_{12}\phi_{21})$,

$\Phi R_1 = (\phi_{11}r_2 - \phi_{21}r_1)$, $\quad \Phi R_2 = (\phi_{12}r_2 - \phi_{22}r_1)$,

$B\Phi_1 = (\beta_{11}\phi_{11} - \beta_{21}\phi_{21})$, $\quad B\Phi_2 = (\beta_{12}\phi_{12} - \beta_{22}\phi_{22})$,

$B\Phi_3 = \beta_{11}\phi_{11}(m_2 + \omega) - \beta_{12}\phi_{12}(m_1 + \omega)$, $\quad B\Phi_4 = \beta_{21}\phi_{21}(m_2 + \omega) - \beta_{22}\phi_{22}(m_1 + \omega)$,

$NN_h = (\frac{\hat{N}^c_1}{N^*_{1,1}} + \frac{\hat{N}^c_2}{N^*_{2,1}} - 1)$, $\quad NN = (\frac{N^c_1}{N^*_{1,2}} + \frac{N^c_2}{N^*_{2,2}} - 1)$.

$$(B\Phi_1(N^p_1\phi_{11} + N^p_2\phi_{21})V^p_1 + B\Phi_2(N^p_1\phi_{12} + N^p_2\phi_{22})V^p_2) \cdot (\Phi R_1(N^p_1\beta_{11}\phi_{11}r_1 + N^p_2\beta_{21}\phi_{21}r_2)V^p_1 + \Phi R_2(N^p_1\beta_{12}\phi_{12}r_1 + N^p_2\beta_{22}\phi_{22}r_2)V^p_2) > 0. \tag{9}$$

If $E_7 = (N_1^c, N_2^c, V_1^c, 0)$ and $E_8 = (\hat{N}_1^c, \hat{N}_2^c, 0, \hat{V}_2^c)$ 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 (7) is uniformly persistent.

Theorem

Assume that E_7 and E_8 are both nonnegative and unstable and that $NN > 0$ and $NN_h > 0$ are valid. System (7) 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 (7) with positive initial condition.

Theorem

1. *If* $r_1 < \omega$ *and* $r_2 < \omega$, *then* $E_0 = (0,0,0,0)$ *is g.a.s. for (7) for all nonnegative initial conditions.*
2. *If* $\dfrac{m_1+\omega}{\beta_{11}\phi_{11}} < \dfrac{m_2+\omega}{\beta_{12}\phi_{12}}$ *and* $\dfrac{m_1+\omega}{\beta_{21}\phi_{21}} < \dfrac{m_2+\omega}{\beta_{22}\phi_{22}}$, *then* $V_2(t) \to 0$ *as* $t \to \infty$.
3. *If* $\dfrac{m_2+\omega}{\beta_{12}\phi_{12}} < \dfrac{m_1+\omega}{\beta_{11}\phi_{11}}$ *and* $\dfrac{m_2+\omega}{\beta_{22}\phi_{22}} < \dfrac{m_1+\omega}{\beta_{21}\phi_{21}}$, *then* $V_1(t) \to 0$ *as* $t \to \infty$.
4. *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* $t \to \infty$.

Global stability of equilibria

Theorem

(i). *Assume* $\frac{m_1+\omega}{\beta_{11}\phi_{11}} < \frac{m_2+\omega}{\beta_{12}\phi_{12}}$ *and* $\frac{m_1+\omega}{\beta_{21}\phi_{21}} < \frac{m_2+\omega}{\beta_{22}\phi_{22}}$.

1. *If one of* E_0, E_1, E_2, E_3, *and* E_5 *is the only nonnegative equilibrium that is l.a.s. , then it is g.a.s. .*
2. *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.*
3. *If* E_7 *is nonnegative and l.a.s. , then* N_1, N_2 *and* V_1 *coexist.*

(ii). *Assume* $\frac{m_2+\omega}{\beta_{12}\phi_{12}} < \frac{m_1+\omega}{\beta_{11}\phi_{11}}$ *and* $\frac{m_2+\omega}{\beta_{22}\phi_{22}} < \frac{m_1+\omega}{\beta_{21}\phi_{21}}$.

1. *If one of* E_0, E_1, E_2, E_4, *and* E_6 *is the only nonnegative equilibrium that is l.a.s. , then it is g.a.s. .*
2. *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.*
3. *If* E_8 *is nonnegative and l.a.s. , then* N_1, N_2 *and* V_2 *coexist.*

Theorem

*Let μ be one of the parameters of model (7). Assume that (7) admits a positive equilibrium E_9 when $\mu = \mu_0$. Let b_i's, Δ_i's, and d_1 be defined in (**??**), (**??**), and (**??**), 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 (7) admits a Hopf bifurcation at μ_0.*

Example We revisit the example in [Weitz 2016]. 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. A unique stable limit cycle bifurcates from E_9 as β increases from $\beta_0 = 12.24183257$.

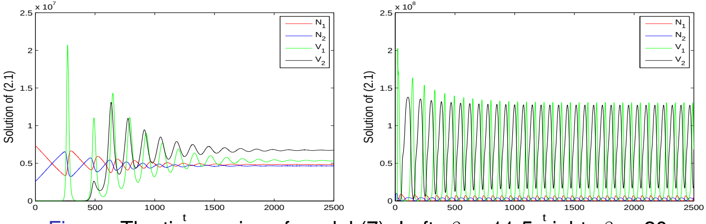


Figure: The time series of model (7). Left: $\beta = 11.5$; right: $\beta = 20$.

Thank you!