

HOST EXTINCTION DYNAMICS IN A SIMPLE PARASITE-HOST INTERACTION MODEL

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ABSTRACT. This short article carefully formulate a simple SI model for a parasite-host interaction through the basic birth and death processes analysis. This model reveals and corrects an error in similar models studied recently by various authors. Complete mathematical investigation of this simple model shows that the host extinction dynamics can happen and the outcomes may depend on the initial conditions. We also present biological implications of our findings.

1. Introduction. The phenomenon that parasites can dramatically reduce host density and even drive host population to extinction has been shown by numerous experimental studies (Ebert et al. 2000). Specifically, it is widely regarded as the culprit of a number of high profile extinctions on various islands (McCallum and Dobson 1995). In an effort to understand such parasite induced host population reduction and extinction, Ebert et al. (2000) formulated the following epidemiological microparasite model with horizontal transmission:

$$\begin{cases} x'(t) &= a(x + \theta y)[1 - c(x + y)] - dx - bxy, \\ y'(t) &= -(d + \alpha)y + bxy, \\ x(0) &= x_0 > 0, y(0) = y_0 > 0, \end{cases} \quad (1.1)$$

where $x(t), y(t)$ represent the densities of uninfected (susceptible) and infected (infective) hosts at time t respectively. According to Ebert et al. (2000), a is the maximum per capita birth rate of uninfected hosts; θ is the relative fecundity of an infected host; c measures the per capita density-dependent reduction in birth rate; d is the parasite-independent host background mortality; b is the infection rate constant and α is the parasite-induced excess death rate. Notice that the disease transmission is assumed to be horizontal. This SI deterministic model predicts the existence of a positive steady state and no periodic orbits in the region $\Delta = \{(x, y) \in \mathbb{R}_+^2 \mid c(x + y) < 1\}$. (A proof can be easily obtained by the application of the Dulac criterion with the standard auxiliary function $1/xy$). Such simple

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dynamics fails to explain the observed rich outcomes dependent on parameter values and initial population levels (Ebert et al. 2000).

After a routine modification of the infection rate b (in view of the fact that the total host and infected populations may not be constant) in the above ad hoc deterministic model, we (Hwang and Kuang 2003) considered the following SI deterministic model:

$$\begin{cases} x'(t) &= a(x + \theta y)[1 - c(x + y)] - dx - b\frac{xy}{x + y}, \\ y'(t) &= -(d + \alpha)y + b\frac{xy}{x + y}, \\ x(0) &= x_0 > 0, y(0) = y_0 > 0. \end{cases} \quad (1.2)$$

In (1.2), b is the maximum number of infections an infective host can cause in a unit of time. Notice that when the total population is constant, the infection term bxy maybe justified (since $b/(x+y)$ is now a constant). Through a blow-up change of variable $((x, y) \rightarrow (u, y), u = x/y)$, we (Hwang and Kuang 2003) transformed (1.2) into a well studied Gause-type predator-prey system and obtained an almost complete understanding of the asymptotic behavior of the solutions for (1.2). For later comparisons, we summarize our main results in (Hwang and Kuang 2003) in Table 1. The most important finding here is that the origin can be an attractor (global) for model (1.2), which may explain the often-observed deterministic extinctions of hosts. This host extinction dynamics has resulted from the degeneracy of the origin due to the ratio-dependent infection term. Such extinction dynamics in the context of predator-prey interaction has been studied recently by many researchers (see the references cited in Kuang and Beretta 1998 and Hsu et al. 2001). There is an unusual feature for model (1.2): even if the basic reproduction number (Hethcote 2000) for the disease $R_0 = b/(d + \alpha)$ is greater than 1 (equivalent to $s > r + \delta$), the disease may not persist. Instead, it may simply drive the host to extinction (when $b > \alpha + a\frac{d + \alpha - d\theta}{d + \alpha - a\theta}$ or equivalent to $s\mu_0/(1 + \mu_0) < r + \delta$ in model (1.2)).

TABLE 1. Main results in Hwang and Kuang (2003). Here GS stands for globally stable, $s = \frac{b}{a}$, $\delta = d/a$, $r = \alpha/a$, $\mu_0 = \theta/(s - r - 1)$.

Conditions	Results
1. $\delta > 1$, or $s - r \leq \delta$ plus $\delta \geq 1$	$(0, 0)$ is GS
2. $s - r \leq \delta$, $\delta < 1$	$(1 - \delta, 0)$ is GS
3. $1 \geq s - r > \delta$	(x^*, y^*) is GS
4. $s - r > 1$, $s\mu_0/(1 + \mu_0) \leq r + \delta$	$(0, 0)$ is GS
5. $s - r > 1$, $s\mu_0/(1 + \mu_0) > r + \delta$	(x^*, y^*) is GS

Recently, a more general system was considered by Berezhovsky et al. (2004):

$$\begin{cases} x'(t) &= a(x + \theta y)[1 - c(x + y)] - (d + m)x - b\frac{xy}{x + y}, \\ y'(t) &= -(d + \alpha)y + b\frac{xy}{x + y}, \\ x(0) &= x_0 > 0, y(0) = y_0 > 0, \end{cases} \quad (1.3)$$

where $m \geq 0$ is the per-capita emigration rate of susceptible individuals. Clearly, if $m = 0$ then (1.3) reduces to (1.2). By applying two blow-up transformations, Berezovsky et al. (2004) showed that system (1.3) can be completely studied. Let $\mathcal{R}_0 = \frac{b}{d + \alpha}$, $\mathcal{R}_d = \frac{a}{d + m}$, $\nu = \frac{d + m}{d + \alpha}$. Then their results can be summarized in Table 2.

TABLE 2. Main results in Berezovsky et al. (2004)

Conditions	Results
1. $0 < \mathcal{R}_0, \mathcal{R}_d < 1$	$(0, 0)$ is GS
2. $0 < \mathcal{R}_0 < 1 < \mathcal{R}_d$	GS
3. $1 < \mathcal{R}_0, \frac{\nu + \mathcal{R}_0 - 1}{\nu(\theta(\mathcal{R}_0 + 1) + 1)} < \mathcal{R}_d$	(x_θ^*, y_θ^*) is GS
4. $1 < \mathcal{R}_0, 1 < \mathcal{R}_d < \frac{\nu + \mathcal{R}_0 - 1}{\nu(\theta(\mathcal{R}_0 + 1) + 1)}, \nu\theta < 1$	$(0, 0)$ is GS (elliptic sector)
5. $\mathcal{R}_d < 1 < \mathcal{R}_0, \nu\theta < 1$	$(0, 0)$ is GS
6. $1 < \mathcal{R}_0, \mathcal{R}_d < \frac{\nu + \mathcal{R}_0 - 1}{\nu(\theta(\mathcal{R}_0 + 1) + 1)}, \nu\theta > 1$	$(0, 0)$ is GS

Notice that the region $\bar{\Delta}$ is positively invariant and that $x'(0) = a\theta y(0)(1 - cy(0)) < 0$ if $x(0) = 0, y(0) > 1/c$.

Recall that in the logistic model $x'(t) = ax(1 - x/K)$, a is to be viewed as the growth rate, which is usually the difference of birth and death rates. However, in all the above models, the linear death term dx is added to the x equation. The crowding effect term described by $c(x + y)$ is also very ad hoc and in need of justification. Moreover, the placement of θy is also questionable. In an attempt to set these sensitive modeling issues, we formulate below a parasite-host model using the standard birth and death processes (or gain and loss mechanisms) approach (Turchin (2001) and Thieme 2003). According to the biological assumption of model (1.1) on the birth process, we see that the birth function of x takes the form of $ax + a\theta y = a(x + y) - a(1 - \theta)y$. The loss terms of x include those due to death and immigration $(d + m)x$, crowding effect $cx(x + y)$ and infection $bxy/(x + y)$. The birth term of y is simply $bxy/(x + y)$, and the loss terms include those from $(d + \alpha)y$ death and crowding effect $cy(x + y)$. With these intuitive but important modifications, we arrive at the following simple SI model:

$$\begin{cases} x'(t) &= a(x + y) - a(1 - \theta)y - cx(x + y) - (d + m)x - b\frac{xy}{x + y}, \\ y'(t) &= -(d + \alpha)y - cy(x + y) + b\frac{xy}{x + y}, \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0 \end{cases} \tag{1.4}$$

where $a, c, d, b, \alpha > 0$ and $\theta \in [0, 1]$.

For simplicity, we nondimensionalizes the system (1.4) with the following scaling:

$$\bar{t} = at, \quad \bar{x} = cx/a, \quad \bar{y} = cy/a.$$

Dropping the overlines on the variables, system (1.4) takes the form

$$\begin{cases} x'(t) &= x + y - (1 - \theta)y - x(x + y) - \delta x - s\frac{xy}{x + y} \equiv F(x, y), \\ y'(t) &= -(\delta + r)y - y(x + y) + s\frac{xy}{x + y} \equiv G(x, y), \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0, \end{cases} \tag{1.5}$$

where

$$s = \frac{b}{a}, \quad \delta = \frac{d+m}{a}, \quad r = \frac{\alpha}{a}. \quad (1.6)$$

Observe that $\lim_{(x,y) \rightarrow (0,0)} F(x,y) = \lim_{(x,y) \rightarrow (0,0)} G(x,y) = 0$. We thus define that $F(0,0) = G(0,0) = 0$. Clearly, with this assumption, both F and G are continuous on the closure of \mathbf{R}_+^2 and C^1 smooth in \mathbf{R}_+^2 where $\mathbf{R}_+^2 = \{(x,y) \mid x > 0, y > 0\}$. So, by applying standard arguments, we see that the solutions of system (1.5) are positive, bounded and defined on $[0, \infty)$. It is straightforward to see that $0 < x(t) + y(t) < 1$ for all $t > 0$ provided that $0 < x_0 + y_0 < 1$. Furthermore, if there exists a solution such that $x(t) + y(t) \geq 1$ for all $t \geq 0$, then $(x+y)'(t) < -\delta(x+y)(t)$ and hence $\lim_{t \rightarrow \infty} (x(t) + y(t)) = 0 < 1$. This contradiction implies that all positive solutions of (1.5) eventually enter and stay in the triangular positive invariant region $\Omega = \{(x,y) \in \mathbf{R}_+^2 \mid x + y < 1\}$. Specifically, we have the following proposition:

PROPOSITION 1.1. *Let $(x(t), y(t))$ be the solution of (1.5), starting at $(x_0, y_0) \in \mathbf{R}_+^2$. Then there is a $t_0 > 0$ such that for $t > t_0$, we have $(x(t), y(t)) \in \Omega$.*

For convenience, in the rest of this paper, we assume that

(A1): $x_0 > 0, y_0 > 0$, and $x_0 + y_0 < 1$.

Observe that if birth rate a is not greater than the sum of death rate d and per capita emigration rate m , then $\delta \geq 1$. We have $(x+y)' < -(\delta-1)(x+y) - (x+y)^2$, which implies that $\lim_{t \rightarrow \infty} (x(t), y(t)) = (0, 0)$. This is the trivial and intuitive outcome of the extinction of the host. So, in the rest of this paper, we assume further that

(A2): $\delta < 1$.

Our goal is to gain a thorough understanding of the global dynamics of model (1.5) or equivalently (1.4).

The rest of this paper is organized as follows. In section 2, we find that the ratio $u = x/y$ function satisfies a linear differential equation which can be solved easily. Taking advantage of this, we obtain a complete understanding of the asymptotic behavior of the solutions of system (1.5). Section 3 presents direct biological implications and limitations of our mathematical results in terms of the original parameters in system (1.4).

2. Mathematical analysis and results. To remove the nonsmoothness at the origin, we carry out the blow-up transformation $(x, y) \rightarrow (u, y)$ where $u = x/y$ in system (1.5). This transforms it into the following system:

$$\begin{aligned} u'(t) &= (1+r-s)u + \theta, \\ y'(t) &= \varphi(u)y - \rho(u)y^2, \\ u(0) &= u_0 = x_0/y_0 > 0, \quad y(0) = y_0 > 0, \end{aligned} \quad (2.1)$$

where

$$\begin{aligned} \varphi(u) &= s - r - \delta - \frac{s}{u+1}, \\ \rho(u) &= u + 1. \end{aligned} \quad (2.2)$$

Obviously, from the first equation in system (2.1), we have

$$u(t) = \begin{cases} \theta t + u_0 & \text{if } s - r = 1, \\ (u_0 - u^*)e^{(1+r-s)t} + u^* & \text{if } s - r \neq 1, \end{cases} \tag{2.3}$$

where $u^* = \frac{\theta}{s-r-1}$. Consequently, $u = u_0$ if $\theta = s - r - 1 = 0$, and u tends to u^* exponentially if $s - r > 1$ and $\theta \in [0, 1]$. If either $s - r < 1$ and $\theta \in [0, 1]$, or $s - r = 1$ and $\theta \in (0, 1]$ hold then $\lim_{t \rightarrow \infty} u(t) = \infty$. Hence, the system (2.1) or equivalently, the system (1.5) has no periodic orbits.

Now we are in a position to prove the following main theorem.

THEOREM 2.1. *For system (1.5), the following statements are true:*

- (a) *The equilibrium $(1 - \delta, 0)$ is globally attractive if either $s - r < 1$ and $\theta \in [0, 1]$, or $s - r = 1$ and $\theta \in (0, 1]$ hold.*
- (b) *The equilibrium $(0, 0)$ is globally attractive if $0 \leq \theta \leq 1 < s - r$ and $\varphi(u^*) \leq 0$.*
- (c) *The equilibrium (x^*, y^*) is globally attractive if $0 \leq \theta \leq 1 < s - r$ and $\varphi(u^*) > 0$ where $y^* = \varphi(u^*)/\rho(u^*)$, $x^* = u^*y^*$.*
- (d) *Let $D_1 = \{(x, y) \in \Delta | \varphi(x/y) \leq 0\}$, $D_2 = \{(x, y) \in \Delta | \varphi(x/y) > 0\}$. Assume $\theta = s - r - 1 = 0$. Then $\lim_{t \rightarrow \infty} (x(t), y(t)) = (0, 0)$ if $(x_0, y_0) \in D_1$ and $\lim_{t \rightarrow \infty} (x(t), y(t)) = (\hat{x}, \hat{y})$ if $(x_0, y_0) \in D_2$ where $\hat{y} = \varphi(u_0)/\rho(u_0)$, $\hat{x} = u_0\hat{y}$.*

Proof. For part (a), observe that $y = x/u \leq 1/u$, thus, from (2.3), we have $\lim_{t \rightarrow \infty} y(t) = 0$ for all solutions $(x(t), y(t))$ of system (1.5). Hence, for any given $\varepsilon > 0$, there exists a sufficiently large T_ε such that $y(t) \leq \varepsilon x(t)$ for all $t \geq T_\varepsilon$. Then one can see that $-x(t)y(t) \geq -\varepsilon x^2(t)$ for all $t \geq T_\varepsilon$. Now from (1.5), we have

$$\begin{aligned} x'(t) &= x(1 - \delta - x) - xy + \theta y - sxy/(x + y) \\ &\geq x(1 - \delta - x) - \varepsilon x^2 - s\varepsilon x/(1 + \varepsilon) \\ &= x(1 - \delta - s\varepsilon/(1 + \varepsilon)) - (1 + \varepsilon)x \end{aligned}$$

for all $t \geq T_\varepsilon$. If we choose ε small enough such that $1 - \delta - s\varepsilon/(1 + \varepsilon) > 0$ then, by a standard comparison theorem, one obtains $\liminf_{t \rightarrow \infty} x(t) = l > 0$. Let $\limsup_{t \rightarrow \infty} x(t) = L$. We claim that $L = l$. Otherwise, we have $L > l$, and there are two sequences $\{t_n\}, \{s_n\}$ such that $x'(t_n) = x'(s_n) = 0$ for all $n \geq 1$ and $\lim_{n \rightarrow \infty} x(s_n) = l, \lim_{n \rightarrow \infty} x(t_n) = L$. Thus

$$L(1 - \delta - L) = l(1 - \delta - l) = 0,$$

a contradiction. Now we have $\lim_{t \rightarrow \infty} x(t) = L$. From (1.5), we see that x'' is bounded on $[0, \infty)$. Hence $\lim_{t \rightarrow \infty} x'(t) = 0$. Therefore,

$$0 = \lim_{t \rightarrow \infty} x'(t) = F(L, 0) = L(1 - \delta - L).$$

This implies $\lim_{t \rightarrow \infty} x(t) = 1 - \delta$, and the first assertion follows.

For part (b), since $s - r - 1 > 0$, it is clear from (2.3) that $\lim_{t \rightarrow \infty} u(t) = u^*$. Since $\rho(u) > 1$ and it is assumed that $\varphi(u^*) \leq 0$, we see that for any given $\varepsilon < \ll 1$, there is a $T_\varepsilon > 0$ such that for $t > T_\varepsilon, \varphi(u(t)) < \varepsilon$. Hence for $t > T_\varepsilon$,

$$y'(t) = \varphi(u)y - \rho(u)y^2 < y(\varepsilon - y),$$

which implies that

$$\limsup_{t \rightarrow \infty} y(t) \leq \varepsilon.$$

Letting ε tends to zero, we see that $\lim_{t \rightarrow \infty} y(t) = 0$. Hence, $\lim_{t \rightarrow \infty} x(t) = 0$.

We now consider part (c). Notice that $\lim_{t \rightarrow \infty} u(t) = u^*$ for all solutions $(u(t), y(t))$ of system (2.1) and $\varphi(u)$ is a continuous function. We have, for any given $\epsilon > 0$, there exists a $\delta_\epsilon > 0$ a sufficiently large T_ϵ such that $u^* - \delta_\epsilon < u(t) < u^* + \delta_\epsilon$ and $\varphi(u(t)) > \varphi(u^*) - \epsilon$ for all $t \geq T_\epsilon$. Now from (2.1), we have

$$y'(t) = \varphi(u)y - \rho(u)y^2 \geq y(\varphi(u^*) - \epsilon - (1 + u^* + \epsilon)y)$$

for all $t \geq T_\epsilon$. If we choose ϵ small enough such that $\varphi(u^*) - \epsilon > 0$ then, by a standard comparison argument, one obtains $\liminf_{t \rightarrow \infty} y(t) = l > 0$. Let $\limsup_{t \rightarrow \infty} y(t) = L$. We claim that $L = l$. For otherwise, we have $L > l$ and there are two sequences $\{t_n\}, \{s_n\}$ such that $y'(t_n) = y'(s_n) = 0$ for all $n \geq 1$ and $\lim_{n \rightarrow \infty} y(s_n) = l, \lim_{n \rightarrow \infty} y(t_n) = L$. Thus

$$L(\varphi(u^*) - \rho(u^*)L) = l(\varphi(u^*) - \rho(u^*)l) = 0,$$

a contradiction. Now we have $\lim_{t \rightarrow \infty} y(t) = L$. From (2.1), we see that y'' is bounded on $[0, \infty)$. Hence $\lim_{t \rightarrow \infty} y'(t) = 0$. Therefore,

$$0 = \lim_{t \rightarrow \infty} y'(t) = L(\varphi(u^*) - \rho(u^*)L).$$

This implies $\lim_{t \rightarrow \infty} y(t) = \varphi(u^*)/\rho(u^*)$ and $\lim_{t \rightarrow \infty} x(t) = u^*y^*$. Hence, assertion (c) follows.

For part (d), since $u(t) = u_0$, the function y satisfies the logistic equation:

$$y'(t) = y(\varphi(u_0) - \rho(u_0)y).$$

Assertion (d) follows easily. ■

Observe that the second equation of (2.1) is a Bernoulli equation. We can actually solve $y(t)$ (and hence $x(t)$). This gives

$$\begin{aligned} y(t) &= e^{\int_0^t \varphi(u(\xi))d\xi} / (y_0 + \int_0^t \rho(u(\tau))e^{\int_0^\tau \varphi(u(\xi))d\xi} d\tau), \\ x(t) &= u(t)e^{\int_0^t \varphi(u(\xi))d\xi} / (y_0 + \int_0^t \rho(u(\tau))e^{\int_0^\tau \varphi(u(\xi))d\xi} d\tau). \end{aligned} \tag{2.4}$$

While it is nice to have an explicit expression for the solution, the solution's asymptotical behavior is far from clear. For this purpose, we provide below an approximation of this analytical expression in the following corollary for the special case of $0 \leq \theta \leq 1 < s - r, \varphi(u^*) > 0$ and $y_0 < \varphi(u^*)/\rho(u^*)$.

COROLLARY 2.1. *If $0 \leq \theta \leq 1 < s - r, \varphi(u^*) > 0$ and $y_0 < \varphi(u^*)/\rho(u^*)$ then*

$$\begin{aligned} y(t) &\simeq \frac{\varphi(u^*)}{2\rho(u^*)} \left(1 + \tanh \left(\frac{\varphi(u^*)}{2}t + \tau \right) \right); \\ y'(t) &\simeq \frac{\varphi^2(u^*)}{4\rho(u^*)} \operatorname{sech}^2 \left(\frac{\varphi(u^*)}{2}t + \tau \right) \end{aligned}$$

where $\tanh \tau = 2y_0 \frac{\rho(u^*)}{\varphi(u^*)} - 1$.

Proof. From Theorem 2.1, we have u tends to u^* exponentially. Hence, the second equation in (2.1) can be approximated by

$$y' \simeq y(\varphi(u^*) - \rho(u^*)y). \tag{2.5}$$

A straightforward computation yields $y(t) \simeq \frac{\varphi(u^*)}{2\rho(u^*)} \left(1 + \tanh \left(\frac{\varphi(u^*)}{2}t + \tau \right) \right)$, where $\tanh \tau = 2y_0 \frac{\rho(u^*)}{\varphi(u^*)} - 1$. Substituting this expression into (2.5), we obtain the desired expression for $y'(t)$. This completes the proof of the corollary. ■

3. Discussion. To facilitate our discussion, we first summarize our main results of system (1.5) in Table 3.

TABLE 3. Complete global results of system (1.5).

Conditions	Results
a. $\delta \geq 1$	$(0, 0)$ is GS.
b. $\delta < 1, s - r < 1$	$(1 - \delta, 0)$ is GS.
c. $\delta < 1, s - r = 1$ plus $0 < \theta \leq 1$	$(1 - \delta, 0)$ is GS.
d. $\delta < 1, s - r > 1, \varphi(u^*) \leq 0$	$(0, 0)$ is GS.
e. $\delta < 1, s - r > 1, \varphi(u^*) > 0$	(x^*, y^*) is GS.
f. $\delta < 1, s - r - 1 = \theta = 0$	$\lim_{t \rightarrow \infty} (x(t), y(t)) = (0, 0)$ (or (\hat{x}, \hat{y})) if $\varphi(u_0) \leq$ (or $>$) 0 .

Here $s = b/a, \delta = (d + m)/a, r = \alpha/a$ and $u_0 = x_0/y_0$.

Notice that the condition $\delta \geq 1$ is equivalent to $d + m \geq a$. That is, the birth rate is no greater than the sum of death rate d and per-capita emigration rate m . This means there is no growth in total host population. Thus, the whole population declines steadily and eventually dies out (even if there is no disease).

When $\delta < 1$ (or $d + m < a$), the net change rate of susceptibles is positive in the absence of infection. The survival of susceptibles may depend on the effects of the disease. Observe that $a(s - r - 1) = (b - (\alpha + d)) - (a - d)$; that is, the difference of net growth rates of infectives and susceptibles. So the scenario of (b) and (c) in Table 3 describes that except for the extreme case $s - r - 1 = \theta = 0$, the disease will die out and some individuals will escape the disease if the net growth rate of the infective group is no greater than the susceptible group. Figure 2 depicts some solutions in cases (e) and (d).

The conclusion (f) is the main difference between Tables 1 and 3. It describes the scenario that when the net growth rate of infectives and susceptibles are the same ($s - r = 1$) and the infection makes the infected group infertile ($\theta = 0$). In this unlikely case, the outcomes of system (1.5) depend on initial conditions. Recall that $\varphi(u_0) \leq 0$ is equivalent to $x_0 \leq \frac{r + \delta}{1 - \delta} y_0$. In terms of original parameters in (1.4), this condition is equivalent to

$$x_0 \leq \frac{b - (a - d - m)}{a - d - m} y_0.$$

This means that if the ratio of uninfected to infected hosts population is not large enough, then the system will collapse. Otherwise, the disease will persist.

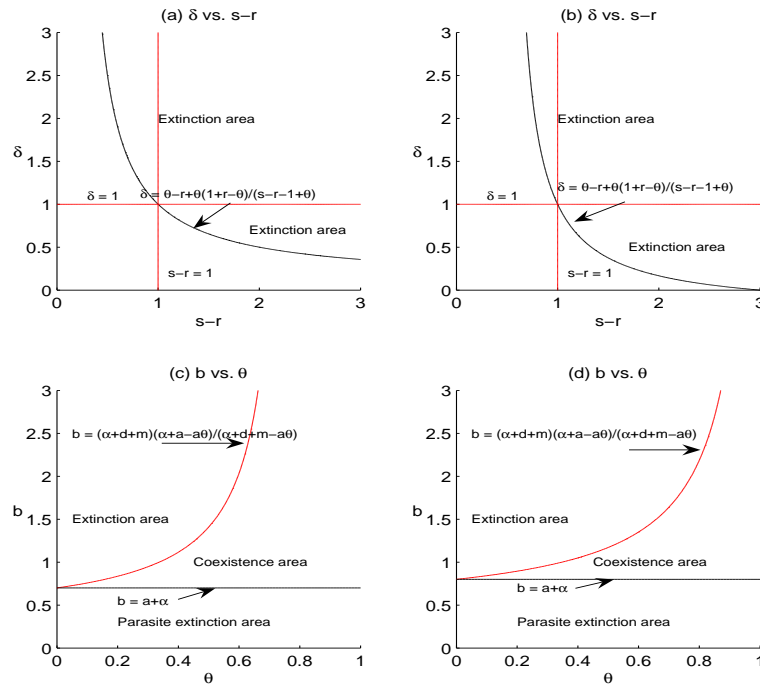


FIGURE 1. The extinction region, parasite extinction region and coexistence region for model (1.5) and (1.4) in θ, b and $\delta, s - r$ parameters space are depicted for $(r, \theta) = (0.7, 0.8), (0.75, 0.5)$ and $c = 1, a = 0.4, d = 0.01, m = 0$, and $\alpha = 0.3, 0.4$, respectively.

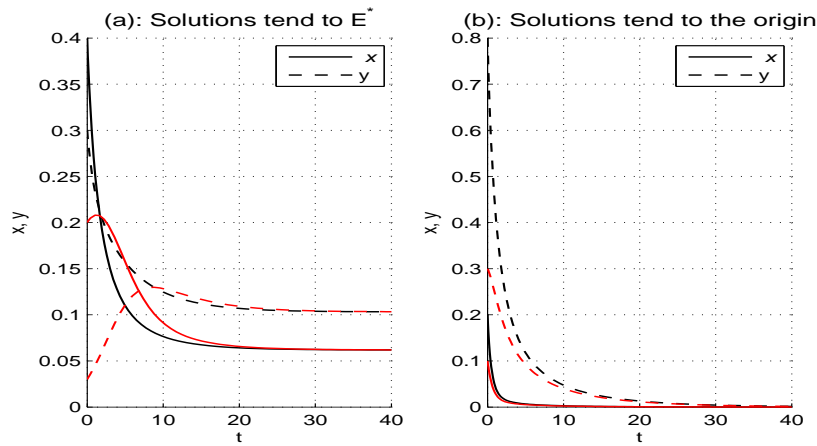


FIGURE 2. In (a), solutions tend to E^* monotonically after a brief transition period. Here $a = 0.4, d = 0.01, \alpha = 0.2, \theta = 0.6, b = 1, c = 1, m = 0$. In (b), solutions tend to the origin monotonically after a brief transition period. Here $a = 0.4, d = 0.01, \alpha = 0.2, \theta = 0.2, b = 2, c = 1, m = 0$.

The deterministic extinction effect on host is reproduced here as well. This occurs if $s - r > 1$ and $\varphi(u^*) < 0$. Recall that $\varphi(u^*) < 0$ is equivalent to $\theta \leq \frac{s-r-1}{s-r-\delta}(r+\delta)$. In terms of the original parameters in (1.4), this condition is equivalent to

$$b \geq (d+m+\alpha) \frac{\alpha+a-a\theta}{d+m+\alpha-a\theta}.$$

So the scenario describes a situation when infection rate is high ($s > r+1$) and the infection imposes a severe reduction in the birth rate of the infected group (small θ), or some significant yet subtle increases in the additional death rate (α) to the infected group (Figure 1).

We conclude this paper by repeating the limitation statements we mentioned in Hwang and Kuang (2003). *Although model (1.4) exhibits the desirable host deterministic extinction dynamics, we recognize that to reach extinction by a continuous-time model, a population must eventually become very small and the stochastic effects become noticeable and important.* A more plausible explanation of the often-observed host extinction phenomenon is that the deterministic infection dynamics brings the total host population to the brink of extinction and the demographic stochasticity actually drives the host population to extinction.

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