Mathematical Analysis of Intraguild Interactions among Hosts, Parasitoids and Predators

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Abstract. In this work, we consider a mathematical model of an omnivorous ecosystem in which intermediate predators are infected by parasites. We first establish the boundeness and positivity of solution with conditions. Then the existence and local stability of all equilibria are clarified in $\mathbb{R}^4$. Finally, some global dynamics will be analyzed.

1 Introduction

An intraguild predation (IGP) model occurs when the top predator predates on the intermediate predator who shares a common resource with the top predator. Actually, this is a general part of the marine or terrestrial food web ecosystems. The intraguild predation has received considerable attention from empirical and theoretical research in the past three decades [4, 6, 7, 8].

Since the 1990's, there have been some interesting and impressive results on investigating the dynamics of prey-predator systems with prey infected with parasites [9, 10, 11, 13, 14, 15, 16, 17]. In particular, Chattopadhyay and Arino [9] found persistence and extinction conditions for the population and also determined conditions for Hopf bifurcation to periodic solutions. Han, Ma and Hethcote [11] analyzed a four species predator–prey model including a parasitic infection. They identified thresholds and proved global stability results. By modifying a standard susceptible-infected model, Spencer, Duffy and Cáceres [17] showed how productivity can modulate complex behavior induced by saturating and selective foraging behavior of predators in an otherwise stable host-parasite system.

Nakazawa and Yamamura [3] presented an interesting model framework. They developed an intraguild predation model for host-parasite-predation interactions in which the adult parasitoid density was explicitly expressedand the parasitization rate depends on parasitoid density. From a biological perspective, compared with traditional models, it is rather a different situation. In

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addition, they researched the strengths of interactions , and examined the relationship between interaction strength and community structure.

Modifying a prey–predator model with prey infection, we will propose a model of intraguild interactions among host, parasitoid, and predator, as response in [3], in which the density of the parasitized host is considered with a general form rather than a linear functional response. Because of the change in the expression of the parasitized host and the incorporation of these variables, our model is necessarily more complex and general than previous models. In this work, motivated by [1, 3], we consider the following model

$$\begin{cases} \dfrac{dS}{ds} = rS(1 - \dfrac{S}{K}) - a_{12}SI - a_{13}SQ, \\ \dfrac{dI}{ds} = a_{21}SP - G(I) - a_{23}IQ, \\ \dfrac{dP}{ds} = \eta G(I) - d_P P, \\ \dfrac{dQ}{ds} = \delta Q[a_{13}S + a_{23}I] - d_Q Q, \end{cases} \tag{1.1}$$

where S, I, P, and Q are the densities of the unparasitized host, the parasitized host, the parasitoid, and the predator, respectively, and r and K are the intrinsic growth rate and carrying capacity, respectively, of the host. We assume that the host is killed by parasitization, but that the parasitized host exists until a predator consumes it or the parasitoid emerges. Thus, the parasitized host does not affect intra-species competition or contribute to reproduction. This type of parasitoid is called an idiobiont. Parameters a_{12}, a_{13}, and a_{23} represent the efficiencies of parasitization, predation on the unparasitized host, and predation on the parasitized host, respectively. Parameter h is the emergence rate of the parasitoid, and the inverse $1/h$ indicates the average latent period during which the parasitoid remains within the host until emergence. Parameter η is the number of parasitoids that emerge from an individual host, and δ is the conversion rate for predator reproduction. Here, we set the conversion rates to be the same whether the predator consumes the unparasitized or parasitized host. Finally, d_P and d_Q are the mortality rates of the parasitoid and predator, respectively.

In this system, the parasitoid lays eggs in the host, the predator consumes both unparasitized and parasitized hosts, and the parasitoid emerges from parasitized hosts that survive predation. This interaction constitutes intraguild predation because the predator preys on the parasitoid by consuming parasitized hosts. System (1.1) can cause complex population dynamics depending on the expression of adult parasites and the general form $G(I)$. In fact, system (1.1) can be regarded as the traditional model [4], when we change the assumption to indicate the process of infection, as put forward in [4], replace $a_{12}SI = a_{21}SP$ and omit P. In this work, we consider the existence, locally stability and globally asymptotic stability of boundary and positive equilibria. Moreover, the corresponding biological interpretations are also analyzed.
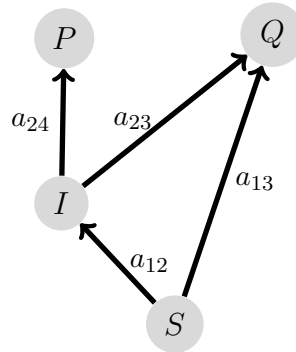
The remainder of this article is organized as follows. In Section 2, we first show a preliminary result which indicates solutions of system (2.1) are non-negative for all non-negative initial values and bounded with conditions. In Subsection 2.1, we first discuss the existence and the local stability of boundary equilibria in $\mathbb{R}^4$. Then the existence of a positive equilibrium will be shown by taking some constraints and local stability of coexistence is investigated by the Routh-Hurwitz criterion in Subsection 2.2. In Section 3, we discuss the global stability of equilibria by applying the Markus Theorem [2].

2   Preliminaries

To simplify (1.1), we use the following scaling :

$$x = S/K, \qquad y = I, \qquad p = P, \qquad z = Q,$$
$$\alpha_1 = a_{12}/r, \qquad \beta_1 = a_{13}/r, \qquad \alpha_2 = Ka_{21}/r, \qquad \gamma_1 = a_{23}/r,$$
$$d_p = d_P/r \qquad \beta_2 = K\delta a_{13}/r, \qquad \gamma_2 = \delta a_{23}/r, \qquad d_z = d_Q/r$$
$$rs = t,$$

then we have

$$\dot{x} = x(1 - x) - \alpha_1 xy - \beta_1 xz, \tag{2.1a}$$
$$\dot{y} = \alpha_2 xp - g(y) - \gamma_1 yz, \tag{2.1b}$$
$$\dot{p} = \eta g(y) - d_p p, \tag{2.1c}$$
$$\dot{z} = \beta_2 xz + \gamma_2 yz - d_z z, \tag{2.1d}$$

where "." means that d/dt and $g(y) = G(y)/r$.

First of all, we show that system (2.1) is well behavior. We can easily see that the solutions of (2.1) with non-negative/positive initial conditions are non-negative/positive. Moreover, the following results on the boundedness of solutions of systems (2.1) can be verified easily.

Assumption (A) on function $g(y)$: $g(0) = 0$, and $g(y) \geq \varepsilon y$ for $y \geq 0$ where ε is a positive number.(super-linearity)

Lemma 2.1. *The solutions of* (2.1) *are non-negative for all non-negative initial values. Moreover, they are also bounded if* $d_p > \alpha_2 \eta$.

Proof. Firstly, we observe that $x(t)$ cannot be vanished, since it is the basal resource of the whole system (2.1). Otherwise if $x(t) = 0$ for some time t, then system (2.1) will be crashed eventually. Mathematically, it can be verified that if $x(0) = 0$ then $\lim_{t\to\infty} y(t) = 0$. Consequently, $\lim_{t\to\infty} p(t) = \lim_{t\to\infty} z(t) = 0$.

Next, we would like to show that solutions with positive x initial conditions are non-negative. It is sufficient to show that solutions starting from the boundary of non-negative cone of $\mathbb{R}^4$ are still non-negative. Let $\big(x(t), y(t), p(t), z(t)\big)$ be a solution of (2.1) with $\big(x(0), y(0), p(0), z(0)\big) \in W_1 = \{x > 0, y = 0, p > 0, z > 0\}, W_2 = \{x > 0, y > 0, p = 0, z > 0\}$ or $W_3 = \{x > 0, y > 0, p > 0, z = 0\}$, then $\big(x(t), y(t), p(t), z(t)\big)$ stay on the boundary of non-negative cone of $\mathbb{R}^4$. Hence, one can easily show that solutions with positive x initial conditions are non-negative.

Finally, we let $W(t) = a_1 x(t) + (\eta + \delta)y(t) + p(t) + a_2 z(t)$ where δ is a small positive real number such that $d_p > (\eta + \delta)\alpha_2$ and $a_1 = \frac{(\eta+\delta)\gamma_1\beta_2}{\gamma_2\beta_1}, a_2 = \frac{(\eta+\delta)\gamma_1}{\gamma_2}$. Then

$$\frac{d}{dt}W(t) \leq a_1 x(1 - x) + (\eta + \delta)\alpha_2 p - d_p p - \delta g(y) - a_2 d_z z$$

$$\leq a_1 - a_1 x - \delta\varepsilon y - (d_p - (\eta + \delta)\alpha_2)p - a_2 d_z z$$

$$\leq a_1 - DW,$$

where $D = \min\{1, \frac{\delta\varepsilon}{\eta+\delta}, d_p - (\eta + \delta)\alpha_2, d_z\}$. Hence by comparison principle, we have $W(t)$ is bounded which implies solutions of (2.1) are bounded. $\square$

Remark 1. The inequality $d_p > \alpha_2\eta$ in Lemma 2.1 is a sufficient condition. Through a large number of numerical simulations, we assume that when the model (2.1) has a non-negative initial point, its solution will be bounded.

2.1 Local Stability of Boundary Equilibria in $\mathbb{R}^4$

In this subsection we start to discuss the dynamics of (2.1) in $\mathbb{R}^4$. The existence of boundary equilibria will be showed by taking some constraints and local stability of these points are investigated by the Routh-Hurwitz criterion.

It is easy to see that system (2.1) has the unstable trivial equilibrium $E_0 = (0, 0, 0, 0)$ by evaluating the Jacobian matrix

$$J(x, y, p, z) = \begin{bmatrix} 1 - 2x - \alpha_1 y - \beta_1 z & -\alpha_1 x & 0 & -\beta_1 x \\ \alpha_2 p & -g'(y) - \gamma_1 z & \alpha_2 x & -\gamma_1 y \\ 0 & \eta g'(y) & -d_p & 0 \\ \beta_2 z & \gamma_2 z & 0 & \beta_2 x + \gamma_2 y - d_z \end{bmatrix} \quad (2.2)$$

at E_0.

To find other equilibria with positive x, we should solve the following system of nonlinear equations,

$$0 = 1 - x - \alpha_1 y - \beta_1 z \quad (2.3a)$$
$$0 = \alpha_2 xp - g(y) - \gamma_1 yz \quad (2.3b)$$
$$0 = \eta g(y) - d_p p, \quad (2.3c)$$
$$0 = z(\beta_2 x + \gamma_2 y - d_z). \quad (2.3d)$$

By (2.3) and assumption of function g, three observations should be mentioned. The first one is that solution of (2.3) has the constrains, $0 < x \leq 1$, $0 \leq y < 1/\alpha_1$, and $0 \leq z < 1/\beta_1$ by (2.3a); the second one is that $y = 0$ if and only if $p = 0$ by (2.3c); and the final one is that the solvability and positivity of y implies the solvability and positivity of p.

Two sub-cases, $z = 0$ and $z > 0$, are considered. If $z = 0$, then system (2.3) can be simplified as the form,

$$\begin{cases} 0 = 1 - x - \alpha_1 y, \\ 0 = \alpha_2 xp - g(y), \\ 0 = \eta g(y) - d_p p. \end{cases} \quad (2.4)$$

By previous observations, we can obtain two semi-trivial equilibria, $E_1 = (1, 0, 0, 0)$ and $E_2 = (x_2^*, y_2^*, p_2^*, 0)$, where

$$x_2^* = \frac{d_p}{\alpha_2 \eta}, \qquad y_2^* = \frac{1 - x_2^*}{\alpha_1}, \text{ and } \quad p_2^* = \frac{\eta g(y_2^*)}{d_p}.$$

with constrain $\frac{d_p}{\alpha_2 \eta} < 1$ which means that the resources provided by the ecosystem for species y and species p can offset the mortality of species p. The local stability of E_1 and E_2 can be obtained easily by evaluating Jacobian matrix (2.2) and calculating eigen-values.

Lemma 2.2.   (i) *Equilibrium E_1 is stable if $d_p > \alpha_2 \eta$ and $d_z > \beta_2$.*

(ii) *Equilibrium E_2 exists if $d_p < \alpha_2\eta$. Moreover, it is stable if*

$$\frac{d_p}{\alpha_2\eta}(\gamma_2 - \alpha_1\beta_2) > \gamma_2 - \alpha_1 d_z. \tag{2.5}$$

Proof. By evaluating Jacobian matrix (2.2) at E_1, it is easy to see that

$$J(E_1) = \begin{bmatrix} -1 & -\alpha_1 & 0 & -\beta_1 \\ 0 & -g'(0) & \alpha_2 & 0 \\ 0 & \eta g'(0) & -d_p & 0 \\ 0 & 0 & 0 & \beta_2 - d_z \end{bmatrix}.$$

Hence part (i) can be established by calculating eigenvalues of the above matrix.

Similarly, by evaluating Jacobian matrix at E_2, we obtain

$$J(E_2) = \begin{bmatrix} -x_2^* & -\alpha_1 x_2^* & 0 & -\beta_1 x_2^* \\ \alpha_2 p_2^* & -g'(y_2^*) & \alpha_2 x_2^* & -\gamma_1 y_2^* \\ 0 & \eta g'(y_2^*) & -d_p & 0 \\ 0 & 0 & 0 & \beta_2 x_2^* + \gamma_2 y_2^* - d_z \end{bmatrix}.$$

Hence E_2 is stable if $\beta_2 x_2^* + \gamma_2 y_2^* - d_z < 0$ and three eigenvalues of upper-left 3×3 block matrix of $J(E_2)$ are negative. By straightforward computations, the corresponding eigen-polynomial is

$$\lambda^3 + \lambda^2\big(d_p + g'(y_2^*) + x_2^*\big) +$$
$$\lambda\big(\alpha_1\alpha_2 p_2^* x_2^* + d_p x_2^* + g'(y_2^*)x_2^*\big) + \alpha_1\alpha_2 d_p p_2^* x_2^*.$$

It is easy to check that these three eigenvalues are all negative by the Routh criterion. Therefore, E_2 is stable if $\beta_2 x_2^* + \gamma_2 y_2^* - d_z < 0$, or equivalently, $\frac{d_p}{\alpha_2\eta}(\gamma_2 - \alpha_1\beta_2) > \gamma_2 - \alpha_1 d_z$. We complete the proof. $\qquad\square$

Let us consider another sub-case, $z > 0$. If $z > 0$ and $y = 0$ (which implies $p = 0$), then (2.3) can be simplified as the form,

$$\begin{cases} 0 = 1 - x - \beta_1 z, \\ 0 = \beta_2 x - d_z, \end{cases}$$

and the third semi-trivial equilibrium $E_3 = (x_3^*, 0, 0, z_3^*)$ can be obtained where

$$x_3^* = \frac{d_z}{\beta_2} \qquad \text{and} \qquad z_3^* = \frac{1 - x_3^*}{\beta_1}.$$

which constrain $\frac{d_z}{\beta_2} < 1$. It means that species z can maintain the survival of the race through predation of species x.

Lemma 2.3. *Equilibrium E_3 exists if $\beta_2 > d_z$. Moreover, it is stable if*

$$d_p\gamma_1(\beta_2 - d_z) + g'(0)\beta_1(d_p\beta_2 - \alpha_2\eta d_z) > 0. \tag{2.6}$$

Proof. By evaluating Jacobian matrix (2.2) at E_3, it is easy to see that

$$J(E_3) = \begin{bmatrix} -x_3^* & -\alpha_1 x_3^* & 0 & -\beta_1 x_3^* \\ 0 & -g'(0) - \gamma_1 z_3^* & \alpha_2 x_3^* & 0 \\ 0 & \eta g'(0) & -d_p & 0 \\ \beta_2 z_3^* & \gamma_2 z_3^* & 0 & 0 \end{bmatrix}$$

with eigen-polynomial,

$$(\lambda^2 + x_3^*\lambda + \beta_1\beta_2 x_3^* z_3^*)(\lambda^2 + [d_p + \gamma_1 z_3^* + g'(0)]\lambda - \alpha_2\eta g'(0)x_3^* + d_p\gamma_1 z_3^* + d_p g'(0)).$$

The real part of two eigenvalues of first quadratic factor in the eigen-polynomial are negative. So E_3 is stable if $d_p\gamma_1 z_3^* + d_p g'(0) > \alpha_2\eta g'(0)x_3^*$, that is, $d_p\gamma_1(\beta_2 - d_z) + g'(0)\beta_1(d_p\beta_2 - \alpha_2\eta d_z) > 0$. The proof is complete.

$\square$

Remark 2. We summarize these results and divide them into four categories,

(a) $d_z > \beta_2$ and $d_p > \alpha_2\eta$:E_1 is stable, E_2 and E_3 are non-existent.

(b) $d_z > \beta_2$ and $d_p < \alpha_2\eta$:E_1 is unstable, E_2 is existent, E_3 is non-existent.

(c) $d_z < \beta_2$ and $d_p > \alpha_2\eta$:E_1 is unstable, E_2 is non-existent, E_3 is existent.

(d) $d_z < \beta_2$ and $d_p < \alpha_2\eta$:E_1 is unstable, E_2 and E_3 are existent.

Then, we can classify the local dynamics for all semi-trivial equilibria in Table 1.

2.2 Existence of Coexistence State and its Local Stability

In this subsection, we consider the existence of coexistence state by taking some constrains. Then the local stability of positive equilibrium is investigated by the Routh-Hurwitz criterion.

If $z > 0$ and $y > 0$ (which implies $p > 0$), then it is a coexistence state, $E_* = (x_*, y_*, p_*, z_*)$. To find E_*, we should solve positive solution of the following system,

$$0 = 1 - x - \alpha_1 y - \beta_1 z \tag{2.7a}$$

$$0 = \alpha_2 xp - g(y) - \gamma_1 yz \tag{2.7b}$$

$$0 = \eta g(y) - d_p p, \tag{2.7c}$$

Table 1: Classification of local dynamics for all semi-trivial equilibria.

	$d_z > \beta_2$	$d_z < \beta_2$
	E_1: stable	E_1:unstable
$d_p > \alpha_2\eta$	E_2:non-existent	E_2:non-existent
	E_3:non-existent	E_3:existent
	E_* :?	E_* :?
	E_1:unstable	E_1:unstable
$d_p < \alpha_2\eta$	E_2:existent	E_2:existent
	E_3:non-existent	E_3:existent
	E_* :?	E_* :?

$$0 = \beta_2 x + \gamma_2 y - d_z. \tag{2.7d}$$

System (2.7) can be simplified as an equivalent system,

$$0 = 1 - x - \alpha_1 y - \beta_1 z \tag{2.8a}$$

$$0 = \frac{\alpha_2\eta}{d_p} x g(y) - g(y) - \gamma_1 y z \tag{2.8b}$$

$$0 = \beta_2 x + \gamma_2 y - d_z, \tag{2.8c}$$

for $0 < x < \min\{1, d_z/\beta_2\}$, $0 < y < \min\{1/\alpha_1, d_z/\gamma_2\}$, and $0 < z < 1/\beta_1$. By (2.8a) and (2.8c), we have

$$\frac{1}{\alpha_1} - \frac{x}{\alpha_1} - \frac{\beta_1 z}{\alpha_1} = y = \frac{d_z}{\gamma_2} - \frac{\beta_2 x}{\gamma_2}.$$

Hence for each fixed $y \in (0, \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}\})$, there are two lines on the first quadrant of x-z plane,

$$L_1 : \beta_2 x = d_z - \gamma_2 y,$$
$$L_2 : x + \beta_1 z = 1 - \alpha_1 y.$$

Please refer Figure 1.

Therefore, the inequality,

$$\frac{d_z}{\beta_2} - \frac{\gamma_2}{\beta_2} y < 1 - \alpha_1 y, \tag{2.9}$$

can guarantee the existence of intersection for lines L_1 and L_2 with coordinates, x and z, which can be represented as a linear function of y,

$$
\begin{aligned}
x(y) &= \frac{d_z}{\beta_2} - \frac{\gamma_2}{\beta_2} y, \\
z(y) &= \frac{\beta_2 - d_z}{\beta_1\beta_2} + \frac{\gamma_2 - \alpha_1\beta_2}{\beta_1\beta_2} y.
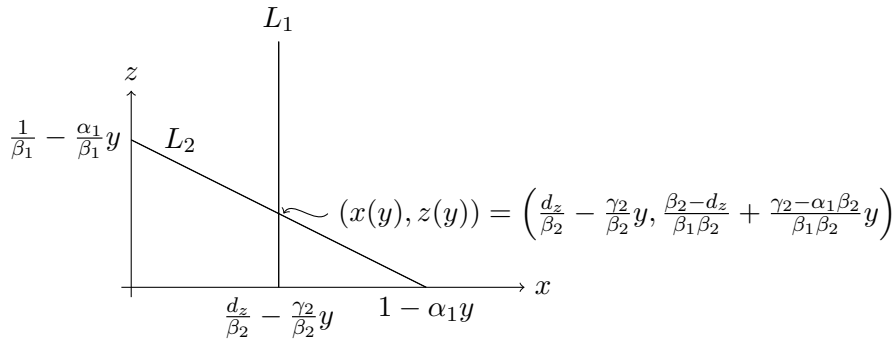\end{aligned}
\tag{2.10}
$$

Figure 1: The intersection of the two straight lines L_1, L_2 of subsystem (2.8)

for each fixed $y \in (0, \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}\})$. Inequality (2.9), which is equivalent to

$$\beta_2 - d_z > (\alpha_1\beta_2 - \gamma_2)y,$$

should be required for positivity of $z(y)$.

Throughout following work, we always assume that

Assumption (B) $\beta_2 > d_z$.

Assumption (B) is actually a biological restriction, which means that when species y and p die out, species z can maintain the survival of the population by preying on species x. The above inequality is always true if $\gamma_2 > \alpha_1\beta_2$. However, if $\gamma_2 < \alpha_1\beta_2$, we need an extra condition

$$y < \frac{\beta_2 - d_z}{\alpha_1\beta_2 - \gamma_2}.$$

Hence, in this case, we need to find a positive $y < \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}, \frac{\beta_2-d_z}{\alpha_1\beta_2-\gamma_2}\}$. Finally, with (2.10), we solve (2.8b) by defining a function,

$$f(y) \equiv \frac{\alpha_2\eta}{d_p}x(y)g(y) - g(y) - \gamma_1 y z(y).$$

The existence of positive root in $(0, \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}, \frac{\beta_2-d_z}{\alpha_1\beta_2-\gamma_2}\})$ or $(0, \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}\})$ of function $f(y)$ is equivalent to the existence of positive equilibrium of (2.7).

By the above arguments, generically, we discuss two categories, $\gamma_2 > \alpha_1\beta_2$ and $\gamma_2 < \alpha_1\beta_2$, to investigate the existence of positive solution.

(1) $\gamma_2 > \alpha_1\beta_2$: In this category, we have $z(y)$ is positive by (2.10) and $\min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}\} = \frac{d_z}{\gamma_2}$, since , with assumption (**B**), $\gamma_2 > \alpha_1\beta_2$ if and only if

$$\frac{1}{\alpha_1} > \frac{\beta_2}{\gamma_2} > \frac{d_z}{\gamma_2}.$$

By direct computations, we have

$$x\left(\frac{d_z}{\gamma_2}\right) = 0,\ z\left(\frac{d_z}{\gamma_2}\right) = \frac{\gamma_2 - \alpha_1 d_z}{\beta_1 \gamma_2} > 0 \text{ and } f\left(\frac{d_z}{\gamma_2}\right) = -g\left(\frac{d_z}{\gamma_2}\right) - \gamma_1 \frac{d_z}{\gamma_2} z\left(\frac{d_z}{\gamma_2}\right) < 0.$$

Moreover, it is easy to see that $f(0) = 0$, and

$$\begin{aligned}
\frac{df}{dy}\Big|_{y=0} &= \frac{\alpha_2 \eta}{d_p} x(0) g'(0) - g'(0) - \gamma_1 z(0) \\
&= \frac{\alpha_2 \eta}{d_p} \frac{d_z}{\beta_2} g'(0) - g'(0) - \gamma_1 \frac{\beta_2 - d_z}{\beta_1 \beta_2} \\
&= \frac{1}{d_p \beta_1 \beta_2} \big(\beta_1 g'(0)(\alpha_2 \eta d_z - d_p \beta_2) - d_p \gamma_1 (\beta_2 - d_z)\big).
\end{aligned}$$

The only possibility that there is positive root of $f(y)$ in $(0, \frac{d_z}{\gamma_2})$ is $\frac{df}{dy}\big|_{y=0} > 0$, that is,

$$\beta_1 g'(0)(\alpha_2 \eta d_z - d_p \beta_2) - d_p \gamma_1 (\beta_2 - d_z) > 0$$

which implies boundary equilibrium E_3 is unstable by Lemma 2.3.

(2) $\gamma_2 < \alpha_1 \beta_2$: In this category, y should be taken in the interval $(0, \min\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}, \frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\})$. It is easy to see that

$$\frac{1}{\alpha_1} > \frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2} \quad \text{if and only if} \quad \frac{1}{\alpha_1} < \frac{d_z}{\gamma_2},$$

and vice versa. Hence we have

$$\min\left\{\frac{1}{\alpha_1}, \frac{d_z}{\gamma_2}, \frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right\} = \frac{d_z}{\gamma_2} \text{ or } \frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}.$$

If this minimal is taken d_z/γ_2, then arguments are similar in the case (i). Let us discuss the case that the minimal is taken the second one, $(\beta_2 - d_z)/(\alpha_1 \beta_2 - \gamma_2)$, that is, the inequalities

$$\frac{d_z}{\gamma_2} > \frac{1}{\alpha_1} > \frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}$$

hold. By direct computations, we obtain

$$\begin{aligned}
x\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) &= \frac{\alpha_1 d_z - \gamma_2}{\alpha_1 \beta_2 - \gamma_2} > 0, \\
z\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) &= 0, \text{ and} \\
f\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) &= g\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) \frac{\alpha_1(\alpha_2 \eta d_z - d_p \beta_2) - \gamma_2(\alpha_2 \eta - d_p)}{d_p(\alpha_1 \beta_1 - \gamma_2)}.
\end{aligned}$$

Note that $f\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) > 0$ also implies boundary equilibrium E_2 is stable. So in this case, $\gamma_2 < \alpha_1 \beta_2$, there are two possibilities to ensure the existence of positive equilibrium,

(i) $\frac{df}{dy}(0) > 0$ and $f\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) < 0$;

(ii) $\frac{df}{dy}(0) < 0$ and $f\left(\frac{\beta_2 - d_z}{\alpha_1 \beta_2 - \gamma_2}\right) > 0$.

In particular, if $g(y) = hy$, system (2.7) an be simplified as a linear system,

$$0 = 1 - x - \alpha_1 y - \beta_1 z, \tag{2.11a}$$

$$0 = \alpha_2 x \eta h / d_p - h - \gamma_1 z, \tag{2.11b}$$

$$0 = \beta_2 x + \gamma_2 y - d_z. \tag{2.11c}$$

By (2.11c), we can obtain, with substitution $y = \frac{d_z - \beta_2 x}{\gamma_2}$, an x-z linear subsystem,

$$L_1 : (1 - \frac{\alpha_1 \beta_2}{\gamma_2})x + \beta_1 z = 1 - \frac{\alpha_1 d_z}{\gamma_2}, \tag{2.12a}$$

$$L_2 : \frac{\alpha_2 \eta h}{d_p} x - \gamma_1 z = h. \tag{2.12b}$$

We can obtain the linear equation

$$\gamma_1 (1 - \frac{\alpha_1 \beta_2}{\gamma_2})x + \beta_1 \frac{\alpha_2 \eta h}{d_p}x = \gamma_1 (1 - \frac{\alpha_1 d_z}{\gamma_2}) + \beta_1 h \tag{2.13}$$

which is transformed from the subsystem (2.12). Then we can easily get

$$x_* = \frac{d_p \gamma_1 (\gamma_2 - \alpha_1 d_z) + \beta_1 d_p \gamma_2 h}{d_p \gamma_1 (\gamma_2 - \alpha_1 \beta_2) + \alpha_2 \beta_1 \eta \gamma_2 h}. \tag{2.14}$$

Finally, with the preceding x_* and by solving the second equation of (2.12), we obtain

$$z_* = \frac{\alpha_2 \eta h}{d_p \gamma_1} x_* - \frac{h}{\gamma_1}. \tag{2.15}$$

where z_* is positive if and only if

$$\frac{d_p}{\alpha_2 \eta} < x_*, \tag{2.16}$$

which implies $x_* > 0$. And this inequality (2.16) is equivalent to

$$\frac{\frac{d_p}{\alpha_2 \eta}(\gamma_2 - \alpha_1 \beta_2) - (\gamma_2 - \alpha_1 d_z)}{\frac{d_p}{\alpha_2 \eta}(\gamma_2 - \alpha_1 \beta_2) + \frac{\beta_1 \gamma_2 h}{\gamma_1}} < 0$$

Hence, (2.16) can be divided into the following cases,

(i) $-\frac{\beta_1 \gamma_2 h}{\gamma_1} < \frac{d_p}{\alpha_2 \eta}(\gamma_2 - \alpha_1 \beta_2) < \gamma_2 - \alpha_1 d_z,$

(ii) $\gamma_2 - \alpha_1 d_z < \frac{d_p}{\alpha_2 \eta}(\gamma_2 - \alpha_1 \beta_2) < -\frac{\beta_1 \gamma_2 h}{\gamma_1}$.

Moreover, if $x < d_z/\beta_2$, then $y = \frac{d_z - \beta_2 x}{\gamma_2} > 0$ which implies $p > 0$. We summmarize above existence conditions in the following theorem.

Proposition 2.1. *If $g(y) = hy$ and $\frac{d_p}{\alpha_2 \eta} < x < \min\left\{1, \frac{d_z}{\beta_2}\right\}$, then the positive equilibrium of (2.7) exists uniquely.*

Assume that the positive equilibrium $E_* = (x_*, y_*, z_*)$ of (2.1) exists, we are on the position to investigate local stability of E_*. By direct computations, the variational matrix evaluated at E_* is

$$J(E_*) = \begin{bmatrix} -x_* & -\alpha_1 x_* & 0 & -\beta_1 x_* \\ \alpha_2 p_* & -g'(y_*) - \gamma_1 z_* & \alpha_2 x_* & -\gamma_1 y_* \\ 0 & \eta g'(y_*) & -d_p & 0 \\ \beta_2 z_* & \gamma_2 z_* & 0 & 0 \end{bmatrix}$$

and the characteristic equation is

$$P(s) = \lambda^4 + a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0 = 0,$$

where

$a_3 = d_p + \gamma_1 z_* + g'(y_*) + x_*,$

$a_2 = \alpha_1 \alpha_2 p_* x_* + (d_p - \alpha_2 \eta x_*)g'(y_*) + \beta_1 \beta_2 x_* z_* + d_p \gamma_1 z_* + d_p x_* + \gamma_1 \gamma_2 y_* z_* + \gamma_1 x_* z_* + g'(y_*)x_*,$

$a_1 = \alpha_1 \alpha_2 d_p p_* x_* - \alpha_1 \beta_2 \gamma_1 x_* y_* z_* + \alpha_2 \beta_1 \gamma_2 p_* x_* z_* - \alpha_2 \eta g'(y_*)x_*^2 + \beta_1 \beta_2 d_p x_* z_* + \beta_1 \beta_2 \gamma_1 x_* z_*^2 +$
    $\beta_1 \beta_2 g'(y_*)x_* z_* + d_p \gamma_1 \gamma_2 y_* z_* + d_p \gamma_1 x_* z_* + d_p g'(y_*)x_* + \gamma_1 \gamma_2 x_* y_* z_*,$

$a_0 = -\alpha_1 \beta_2 d_p \gamma_1 x_* y_* z_* - \alpha_2 \beta_1 \beta_2 \eta g'(y_*)x_*^2 z_* + \alpha_2 \beta_1 d_p \gamma_2 p_* x_* z_* + \beta_1 \beta_2 d_p \gamma_1 x_* z_*^2 +$
    $\beta_1 \beta_2 d_p g'(y_*)x_* z_* + d_p \gamma_1 \gamma_2 x_* y_* z_*.$

By the Routh-Hurwitz criterion the positive equilibrium E_* is asymptotically stable if and only if

$$a_n > 0, n = 0, 1, 2, 3 \tag{2.17a}$$

$$a_3 a_2 > a_1 \tag{2.17b}$$

$$a_3 a_2 a_1 > a_1^2 + a_3^2 a_0 \tag{2.17c}$$

Actually, we can find that (2.17b) need not be verified as a result of (2.17c) implies $a_3 a_2 a_1 > a_1^2$ with (2.17a). But it is tedious and complex to find some sufficient conditions to guarantee the Routh-Hurwitz criterion (2.17).

Theorem 2.1. *Let us assume that the positive equilibrium E_* of (2.1) exists. If conditons (2.17) hold, then the positive equilibrium of (2.1) is asymptotically stable.*

3 The Global Dynamics of Equilibria in $\mathbb{R}^4$

In this subsection, we investigate some global dynamics of boundary equilibria. We give sufficient conditions to show that E_1 and E_2 are actually globally asymptotically stable. We also find sufficient conditions to guarantee the extinction of species z.

Proposition 3.1.   (i) *If $d_p > \alpha_2\eta$ and $d_z > \beta_2$, then solutions of* (2.1) *with positive initial conditions will tend to E_1 eventually, that is, E_1 is globally asymptotically stable.*

(ii) *Similarly, if $d_p > \alpha_2\eta$ and $d_z < \beta_2$, then E_3 is globally asymptotically stable.*

Proof. First, we show part (i). It is easy to see that $x(t) \leq 1$ by (2.1a) for t large enough. Using straight forward computations and (2.1b)-(2.1c), we obtain

$$
\begin{aligned}
\frac{d}{dt}\big(\eta y(t) + p(t)\big) &= \eta \dot{y}(t) + \dot{p}(t) \\
&= \alpha_2\eta xp - \eta\gamma_1 yz - d_p p \\
&\leq \alpha_2\eta p - d_p p = (\alpha_2\eta - d_p)p < 0.
\end{aligned}
$$

This inequality implies that

$$
\frac{\frac{d}{dt}\big(\eta y(t) + p(t)\big)}{\eta y(t) + p(t)} < \frac{\frac{d}{dt}\big(\eta y(t) + p(t)\big)}{p(t)} < \alpha_2\eta - d_p < 0,
$$

which implies that $\lim_{t\to\infty}\big(\eta y(t) + p(t)\big) = 0$. This is sufficient to show that

$$
\lim_{t\to\infty} y(t) = 0 \quad \text{and} \quad \lim_{t\to\infty} p(t) = 0,
$$

since $y(t)$ and $p(t)$ are positive for all time t.

Consequently, we can conclude that the dynamics of (2.1) is asymptotically to the following limiting system,

$$
A_\infty : \begin{cases} \dot{x} = x(1-x) - \beta_1 xz, \\ \dot{y} = 0, \\ \dot{p} = 0, \\ \dot{z} = \beta_2 xz - d_z z, \end{cases}
$$
$$
x(0) > 0, y(0) = 0, p(0) = 0, z(0) > 0,
$$

by Markus Theorem [2].

Similarly, considering system A_∞ with parameters $d_z > \beta_2$, we obtain

$$
\frac{\dot{z}}{z} = \beta_2 x - d_z \leq \beta_2 - d_z < 0,
$$

which implies $\lim_{t\to\infty} z(t) = 0$. By Markus results again, asymptotic dynamics of system (2.1) is further approaching to the following limiting system,

$$
\bar{A}_\infty : \begin{cases} \dot{x} = x(1-x), \\ \dot{y} = 0, \\ \dot{p} = 0, \\ \dot{z} = 0, \end{cases}
$$
$$
x(0) > 0, y(0) = 0, p(0) = 0, z(0) = 0,
$$

which implies $\lim_{t\to\infty} x(t) = 1$. Hence, we can get that E_1 is globally asymptotically stable.

For part (ii), the inequality, $d_p > \alpha_2\eta$, implies that $y(t)$ and $p(t)$ approach to zero as $t \to \infty$ and the dynamics of (2.1) is asymptotically to the limiting system A_∞ by similar arguments of part (i). Then consider the Lyapunov function for A_∞. If we can show E_3 is globally asymptotically stable in the $X - Z$ place, then we conclude that E_3 is globally asymptotically stable in the positive octant of R^4. Let $E_3^* = (x_3^*, z_3^*)$ the positive equilibrium, that is $x_3^* + \beta_1 z_3^* = 1$ and $d_z = \beta_2 x_3^*$. Consider the Lyapunov function

$$
L(x(t), z(t)) = \frac{1}{\beta_1} \int_{x(0)}^{x(t)} \frac{\eta - x_3^*}{\eta} \, d\eta + \frac{1}{\beta_2} \int_{z(0)}^{z(t)} \frac{\eta - z_3^*}{\eta} \, d\eta.
$$

Then

$$
\frac{d}{dt} L(x(t), z(t)) = -\frac{1}{\beta_1}(x - x_3^*)^2 \leq 0
$$

We can get that E_3^* is globally asymptotically stable in x-z plane.   □

Proposition 3.2. *If $d_p < \alpha_2\eta$ and*

$$
d_z > \beta_2 + \frac{\gamma_2}{\alpha_1}, \tag{3.1}
$$

then the species z will die out eventually with positive initial conditions.

Remark 3. One can see that inequality (3.1) is a sufficient condition of (2.5). Since (3.1) is equivalent to the inequality $\frac{\gamma_2}{\alpha_1}(\alpha_2\eta - d_p) < (d_z - \beta_2)(\alpha_2\eta - d_p)$ which implies

$$
\begin{aligned}
\frac{\gamma_2}{\alpha_1}(\alpha_2\eta - d_p) &< (d_z - \beta_2)(\alpha_2\eta - d_p) \\
&= (d_z - \beta_2)\alpha_2\eta - (d_z - \beta_2)d_p \\
&< d_z\alpha_2\eta - \beta_2\alpha_2\eta \\
&< d_z\alpha_2\eta - \beta_2 d_p.
\end{aligned}
$$

Proof of Proposition 3.2. Let $\phi(t) = \big(x(t), y(t), p(t), z(t)\big)$ be a solution of (2.1) with positive initial conditions. Consider

$$\frac{\gamma_2}{\alpha_1}\frac{\dot{x}}{x} + \frac{\dot{z}}{z} = (1-x)\frac{\gamma_2}{\alpha_1} - \gamma_2 y - \frac{\beta_1\gamma_2}{\alpha_1}z + \beta_2 x + \gamma_2 y - d_z \le \frac{\gamma_2}{\alpha_1} + \beta_2 - d_z < 0.$$

Hence by integrating both sides of the above inequality, we can obtain that

$$x(t)^{\frac{\gamma_2}{\alpha_1}} z(t) \to 0 \text{ as } t \to \infty,$$

which implies that there is a sequence of time $\{t_k\}$ such that $x(t_k) \to 0$ or $z(t_k) \to 0$. Suppose that the case, $z(t_k) \to 0$, happens. Then system (2.1) asymptotically approaches to the imiting system . Moreover, all solutions of (2.1) with positive initial conditions approach to $\bar{E}_2$ eventually by previous lemma. Hence, by Markus theorem, equilibrium E_2 is globally asymptotically stable.

On the other hand, if $x(t_k) \to 0$ as $k \to \infty$, there is $p_1 \in \omega(\phi)$ for some point $p_1 \in y\text{-}p\text{-}z$ subspace. Furthermore, the $y\text{-}p\text{-}z$ subspace is the stable manifold of the equilibrium E_0. By the invariance of omega limit set $\omega(\phi)$, we also have $E_0 \in \omega(\phi)$. It is clear that $\omega(\phi) \ne \{E_0\}$. Then by Bulter-McGehee lemma, there is a point q_1 in the unstable manifold of E_0 such that $q_1 \in \omega(\phi)$. Actually, q_1 is on the x-axis which is the unstable manifold of E_0. Similarly, the x-axis is the stable manifold of equilibrium E_1 and this also implies that $E_1 \in \omega(\phi)$. Again, $\omega(\phi) \ne \{E_1\}$ and by Bulter-McGehee lemma, we can a point p_2 on the stable manifold of E_1 such that $p_2 \in \omega(\phi)$. By observing the Jacobian matrix of E_1 carefully, the stable manifold of E_1 is the $x\text{-}y\text{-}p$ subspace. Hence p_2 is in the the $x\text{-}y\text{-}p$ subspace, that is, the species z dies out. So we complete the proof. $\square$

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