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*Research article*

# Extinction and uniform persistence in a microbial food web with mycoloop: limiting behavior of a population model with parasitic fungi

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**Abstract:** It is recently known that parasites provide a better picture of an ecosystem, gaining attention in theoretical ecology. Parasitic fungi belong to a food chain between zooplankton and inedible phytoplankton, called *mycoloop*. We consider a chemostat model that incorporates a single mycoloop, and analyze the limiting behavior of solutions, adding to previous work on steady-state analysis. By way of persistence theory, we establish that a given species survives depending on the food web configuration and the nutrient level. Moreover, we conclude that the model predicts coexistence under bounded nutrient levels.

**Keywords:** uniform persistence; local and global stability; chemostat; mycoloop; phytoplankton; zooplankton; parasitic fungi

## 1. Introduction

It is important to determine survivors, which ultimately shape an ecosystem. However, answering this fundamental question depends on what we consider in a food web. There are studies on ecosystems that incorporate a different concept, like epidemics [10, 11] and allelopathy [8].

Our work considers a microbial food web in the presence of parasitic fungi (e.g., chytrids). The importance of parasites in food webs has been emphasized in the literature; see [5–7]. According to a review paper [15] by Sommer et al., researchers have only recently considered parasites as one of the main drivers for phytoplankton succession. This review highlights the theory of *mycoloop*, a food chain conceived by Kagami and her team to explain the transfer of energy from large phytoplankton (*Asterionella*) to zooplankton (*Daphnia*) via parasitic fungi [1–4].

In this paper, we consider the following chemostat model based on Figure 1, where $' = d/dt$.

$$\begin{cases} N'(t) = [I - qN(t)] - [a_S P_S(t) + a_L P_L(t)]\, N, & N(0) > 0, \\ P_S'(t) = [a_S N(t) - bZ(t) - q]\, P_S(t), & P_S(0) \geq 0, \\ P_L'(t) = [a_L N(t) - \beta F(t) - q]\, P_L(t), & P_L(0) \geq 0, \\ F'(t) = [f_F \beta P_L(t) - \gamma Z(t) - q]\, F(t), & F(0) \geq 0, \\ Z'(t) = [e_P b P_S(t) + e_F \gamma F(t) - (q + m_Z)]\, Z(t), & Z(0) \geq 0. \end{cases} \tag{1.1}$$

The parameters of this model are described in Table 1.

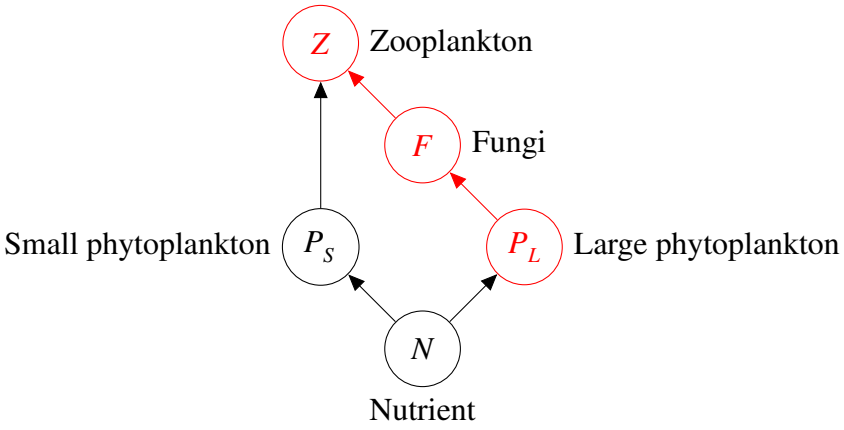


**Figure 1.** Food web of a microbial ecosystem with a mycoloop (red).

**Table 1.** Model parameters.

| Parameter | Description |
|---|---|
| $I$ | Input amount of phosphorus (nutrient level) |
| $N^{(0)}$ | Input concentration of nutrient |
| $q$ | Washout rate |
| $q + m_Z$ | Zooplankton mortality rate, $m_Z$ is the additional death rate besides washout rate $q$ |
| $a_J$ | Nutrient affinity of phytoplankton $P_J$ $(J = S, L)$ |
| $\beta$ | Infectivity constant of fungi |
| $b$ | Zooplankton clearance rate for small phytoplankton |
| $\gamma$ | Zooplankton clearance rate for fungi |
| $e_F$ | Gross growth efficiency (GGE) of zooplankton from fungi |
| $e_P$ | GGE of zooplankton from small phytoplankton |
| $f_F$ | GGE of fungi from its host $P_L$ |

Miki, Takimoto and Kagami formulated system (1.1) in their paper [9] and performed a local (steady-state) analysis to investigate the roles of parasitic fungi. We assume $I = qN^{(0)}$.

We focus on global dynamics and the limiting behavior of the solution

$$\varphi(t) = (N(t), P_S(t), P_L(t), F(t), Z(t))$$

as $t$ goes to infinity. In particular, we determine initial and parameter conditions for the solution to describe the survival and extinction of species $P_S$, $P_L$, $F$, and $Z$.

Let

$$X := \{x = (N, P_S, P_L, F, Z) : N > 0, P_S \geq 0, P_L \geq 0, F \geq 0, Z \geq 0\}.$$

It is easy to show the state space $X$ and its interior $int(X)$ are positively invariant.

The rest of this paper is organized as follows. In Section 2, we establish that our model is dissipative, from which the nutrient uniformly persists regardless of the input $I$. In Section 3, we study the boundary dynamics. Notably, we construct a Lyapunov function to determine the basin of attraction. An investigation on the local and global stability of boundary equilibrium points is presented in Section 4. In Section 5, we apply the uniform persistence theory [12, 13, 16] to prove the coexistence of species $P_S$, $P_L$, $F$, $Z$ with $F - Z$ link, i.e., $\gamma > 0$. Section 6 deals with the dynamics of system (1.1) with the presence of parasitic fungi, but no $F - Z$ link, i.e., $\gamma = 0$. We conclude the paper with a discussion in Section 7.

## 2. Dissipativity and nutrient persistence

First we show that our model system (1.1) is dissipative, as stated in the following theorem.

**Theorem 2.1.** *Each solution of system (1.1) in X satisfies the following inequality:*

$$\limsup_{t\to\infty} \left[ N(t) + P_S(t) + P_L(t) + \frac{F(t)}{f_F} + \frac{Z(t)}{\max\{e_P, \frac{f_F}{e_F}\}} \right] \leq N^{(0)}. \tag{2.1}$$

*Proof.* Let $c = \dfrac{1}{\max\{e_P, \frac{f_F}{e_F}\}}$. We introduce the variable

$$u = N + P_S + P_L + \frac{F}{f_F} + cZ.$$

It follows that $u' \leq q\left[N^{(0)} - u\right]$. Moreover,

$$u(t) \leq N^{(0)} + \left[u(0) - N^{(0)}\right] \exp(-qt) \tag{2.2}$$

for all $t \geq 0$. Passing the limit supremum to inequality (2.2) as $t \to \infty$, we get $\limsup_{t\to\infty} u(t) \leq N^{(0)}$, which is inequality (2.1). □

**Theorem 2.2.** *The nutrient N uniformly persists in X.*

*Proof.* Observe that

$$N' \geq I - qN - \max(a_S, a_L)(P_S + P_L)N$$

$$\geq I - qN - \max(a_S, a_L)\left(N^{(0)} + \epsilon\right)N$$
$$\geq I - \left(q + \max(a_S, a_L)\left(N^{(0)} + \epsilon\right)\right)N, \quad t \geq T_\epsilon.$$

Hence $N(t) \geq \delta > 0$ for $t \geq T_\epsilon$, where $\delta = \dfrac{I}{q + \max(a_S, a_L)\left(N^{(0)} + \epsilon\right)}$. This proves the uniform persistence of $N$ in $X$. □

## 3. Boundary Dynamics

The ecologically relevant equilibrium points lie in the state space $X$. For our analysis, we focus on *boundary equilibrium points*, which have at least one zero coordinate. To this end, we let

$$\lambda_S = \frac{q}{a_S}, \quad \lambda_L = \frac{q}{a_L}.$$

From [14], our basic assumption is

$$(H)\ \ 0 < \lambda_S < \lambda_L < \frac{I}{q}.$$

That is, we assume phytoplankton species of small size, $P_S$, is a strong competitor than that of large size, $P_L$.

### *3.1. Boundary dynamics in the absence of parasitic fungi*

When $F \equiv 0$, system (1.1) becomes

$$\begin{cases} \dfrac{dN}{dt} = I - qN - a_S P_S N - a_L P_L N, \\ \dfrac{dP_S}{dt} = a_S P_S N - bZP_S - qP_S, \\ \dfrac{dP_L}{dt} = a_L N P_L - qP_L, \\ \dfrac{dZ}{dt} = e_P b P_S Z - (q + m_Z)Z \end{cases} \tag{3.1}$$

and its food web is shown in Figure 2.

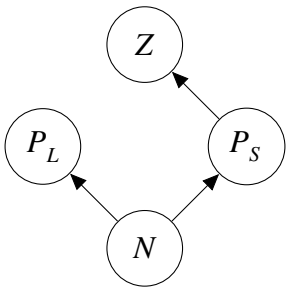


**Figure 2.** The food web in the absence of parasitic fungi.

The conditions for the global stability of the equilibrium points of system (3.1) are stated in the next theorem.

**Theorem 3.1.** *Let* $(H)$ *hold and*

$$N^\star = \frac{I}{q + a_S P_S^\star}, \quad P_S^\star = \frac{q + m_Z}{e_P b}.$$

*For system (3.1), the following statements hold:*

*(i) If* $N^\star < \lambda_S$, *then* $E_S^F = \left(\lambda_S, N^{(0)} - \lambda_S, 0, 0\right)$ *is globally asymptotically stable (G.A.S.).*

*(ii) If* $\lambda_S < N^\star < \lambda_L$, *then* $E_{SZ}^F = \left(N^\star, P_S^\star, 0, Z^\star\right)$ *is G.A.S., where* $Z^\star = \dfrac{a_S N^\star - q}{b}$.

*(iii) If* $\lambda_S < \lambda_L < N^\star < \frac{I}{q}$, *then* $E_{SLZ}^F = \left(\lambda_L, P_S^\star, \widetilde{P_L}, \widetilde{Z}\right)$ *exists and is G.A.S., where* $\widetilde{Z} = \dfrac{1}{b}\left(a_S \lambda_L - q\right)$ *and* $\widetilde{P_L} = \dfrac{I}{q} - \lambda_L - \dfrac{a_S}{a_L} P_S^\star$.

*Proof.* The statements are established as follows:

(i) We introduce the Lyapunov function given by

$$V = \int_{\lambda_S}^{N} \frac{\xi - \lambda_S}{\xi} d\xi + c_1 \int_{\widehat{P_S}}^{P_S} \frac{\xi - \widehat{P_S}}{\xi} d\xi + c_2 P_L + c_3 Z,$$

where $\widehat{P_S} = N^{(0)} - \lambda_S$, and $c_1, c_2, c_3 > 0$ are to be determined. Then

$$\begin{aligned}
\dot{V} =& (N - \lambda_S)\left(\frac{I}{N} - q - a_S P_S - a_L P_L\right) \\
&+ c_1\left(P_S - \widehat{P_S}\right)\left(a_S N - bZ - q\right) \\
&+ c_2 P_L\left(a_L N - q\right) + c_3 Z\left(e_P b P_S - (q + m_Z)\right) \\
=& (N - \lambda_S)\left(\frac{I}{N} - \frac{I}{\lambda_S} - a_S\left(P_S - \widehat{P_S}\right) - a_L P_L\right) \\
&+ c_1\left(P_S - \widehat{P_S}\right)\left(a_S\left(N - \lambda_S\right) - bZ\right) \\
&+ c_2 P_L\left(a_L\left(N - \lambda_S\right) - a_L\left(\lambda_L - \lambda_S\right)\right) \\
&+ c_3 Z\left(e_P b\left(P_S - \widehat{P_S}\right) - \left((q + m_Z) - e_P b \widehat{P_S}\right)\right).
\end{aligned}$$

Choose $c_1 = 1, c_2 = 1, c_3 = \frac{1}{e_P}$. Since

$$\frac{q + m_Z}{e_P b} = P_S^\star > \widehat{P_S} = \frac{I - q\lambda_S}{a_S \lambda_S} \Leftrightarrow I - q\lambda_S < a_S \lambda_S P_S^\star \Leftrightarrow N^\star < \lambda_S,$$

it follows that

$$\dot{V} = \frac{-I\left(N - \lambda_S\right)^2}{N\lambda_S} - P_L a_L\left(\lambda_L - \lambda_S\right) - \frac{1}{e_P}\left((q + m_Z) - e_P b \widehat{P_S}\right) Z \le 0.$$

Therefore, LaSalle's invariance principle implies that $E_S^F = \left(\lambda_S, \widehat{P_S}, 0, 0\right)$ is G.A.S.

(ii) Note that $N^\star > \lambda_S$ implies that $Z^\star > 0$ . Define the Lyapunov function

$$V = \int_{N^\star}^{N} \frac{\xi - N^\star}{\xi} d\xi + \int_{P_S^\star}^{P_S} \frac{\xi - P_S^\star}{\xi} d\xi + P_L + \frac{1}{e_P} \int_{Z^\star}^{Z} \frac{\xi - Z^\star}{\xi} d\xi.$$

We obtain

$$\begin{aligned}
\dot{V} &= (N - N^\star)\left[\frac{I}{N} - \frac{I}{N^\star} - a_S\left(P_S - P_S^\star\right) - a_L P_L\right] \\
&\quad + \left(P_S - P_S^\star\right)\left[a_S\left(N - N^\star\right) - b\left(Z - Z^\star\right)\right] \\
&\quad + P_L\left(a_L\left(N - N^\star\right) - \left(q - a_L N^\star\right)\right) \\
&\quad + \frac{1}{e_P}\left(Z - Z^\star\right)\left(e_P b\left(P_S - P_S^\star\right)\right) \\
&= \frac{-I\left(N - N^\star\right)^2}{NN^\star} - P_L\left(q - a_L N^\star\right) \\
&\leq 0,
\end{aligned}$$

by using the equivalent expression

$$\lambda_L > N^\star \Leftrightarrow q - a_L N^\star > 0.$$

Hence, by LaSalle's invariance principle, $E_{SZ}^F = \left(N^\star, P_S^\star, 0, Z^\star\right)$ is G.A.S.

(iii) We construct the following Lyapunov function:

$$V = \int_{N_C}^{N} \frac{\xi - N_C}{\xi} d\xi + \int_{P_S^C}^{P_S} \frac{\xi - P_S^C}{\xi} d\xi + \int_{P_L^C}^{P_L} \frac{\xi - P_L^C}{\xi} d\xi + \frac{1}{e_P} \int_{Z_C}^{Z} \frac{\xi - Z_C}{\xi} d\xi,$$

where

$$\begin{aligned}
N_C &= \lambda_L, \quad P_S^C = \frac{q + m_Z}{e_P b} = P_S^\star \\
P_L^C &= \frac{1}{a_L}\left(\frac{I}{N_C} - q - a_S P_S^\star\right) \\
Z_C &= \frac{1}{b}\left(a_S N_C - q\right).
\end{aligned}$$

From the assumptions that $N_C = \lambda_L > \lambda_S = \frac{q}{a_S}$ and $N^\star > \lambda_L$, we see that $P_L^C > 0$ and $Z_C > 0$. Thus

$$\begin{aligned}
\dot{V} &= \left(N - N_C\right)\left[\frac{I}{N} - \frac{I}{N_C} - a_S\left(P_S - P_S^C\right) - a_L\left(P_L - P_L^C\right)\right] \\
&\quad + \left(P_S - P_S^C\right)\left[a_S\left(N - N_C\right) - b\left(Z - Z_C\right)\right] \\
&\quad + \left(P_L - P_L^C\right)\left(a_L\left(N - N_C\right)\right) \\
&\quad + \frac{1}{e_P}\left(Z - Z_C\right)\left(e_P b\left(P_S - P_S^C\right)\right) \\
&= \frac{-I\left(N - N_C\right)^2}{NN_C} \\
&\leq 0.
\end{aligned}$$

We conclude from the invariance principle that $E^F_{SLZ}$ is G.A.S. □

As a consequence of the above theorem, we obtain the following equivalent expressions:

$$\begin{aligned} N^\star < \lambda_S &\Leftrightarrow I < \lambda_S\left(q + a_S P_S^\star\right) = q\left(\lambda_S + P_S^\star\right) \\ \lambda_S < N^\star < \lambda_L &\Leftrightarrow \lambda_S\left(q + a_S P_S^\star\right) < I < \lambda_L\left(q + a_S P_S^\star\right) \\ &\Leftrightarrow q\left(\lambda_S + P_S^\star\right) < I < q\left(\lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star\right) \\ \lambda_L < N^\star < \frac{I}{q} &\Leftrightarrow \lambda_L\left(q + a_S P_S^\star\right) < I \\ &\Leftrightarrow q(\lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star) < I \end{aligned}$$

Letting $I_1^F = q\left(\lambda_S + P_S^\star\right)$ and $I_2^F = q\left(\lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star\right)$ with $I_1^F < I_2^F$, we conclude that

(i) if $0 < I < I_1^F$, then $E_S^F = \left(\lambda_S, \widehat{P_S}, 0, 0\right)$ is G.A.S.

(ii) if $I_1^F < I < I_2^F$, then $E_{SZ}^F = \left(N^\star, P_S^\star, 0, Z^\star\right)$ is G.A.S.

(iii) if $I_2^F < I$, then $E_{SLZ}^F\left(\lambda_L, P_S^\star, \widetilde{P_L}, \widetilde{Z}\right)$ is G.A.S.

The global stability of equilibrium points of system (3.1) is depicted in Figure 3.

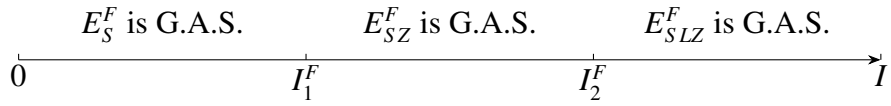


**Figure 3.** Operation diagram of system (3.1).

### *3.2. Boundary dynamics in the absence of zooplankton*

We consider the case that $Z \equiv 0$. Then system (1.1) becomes

$$\begin{cases} N' = I - qN - a_S P_S N - a_L P_L N, \\ P_S' = \left[a_S N - q\right] P_S, \\ P_L' = \left(a_L N - \beta F - q\right) P_L, \\ F' = \left(f_F \beta P_L - q\right) F, \\ N(0) > 0, P_S(0) > 0, P_L(0) > 0, F(0) > 0 \end{cases} \tag{3.2}$$

and its food web is presented in Figure 4.

From hypothesis $(H)$, we see that $P_S$ is a better competitor for nutrient than $P_L$. Obviously from the fact that parasitic fungi $F$ only consume $P_L$, it follows that $E_S^Z = \left(\lambda_S, \widehat{P_S}, 0, 0\right)$ with $\widehat{P_S} = N^{(0)} - \lambda_S$ is G.A.S. Below we state the result without proof.

**Theorem 3.2.** *Under assumption $(H)$, $E_S^Z = \left(\lambda_S, \widehat{P_S}, 0, 0\right)$ is G.A.S. for system (3.2).*

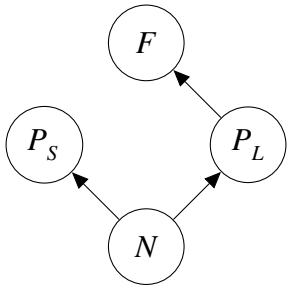


**Figure 4.** The food web in the absence of zooplankton.

### *3.3. Boundary dynamics in the absence of phytoplankton species*

For the case when $P_S \equiv 0$, system (1.1) becomes

$$\begin{cases} \dfrac{dN}{dt} = I - qN - a_L P_L N, \\ \dfrac{dP_L}{dt} = a_L N P_L - \beta F P_L - q P_L, \\ \dfrac{dF}{dt} = f_F \beta P_L F - \gamma Z F - qF, \\ \dfrac{dZ}{dt} = e_F \gamma F Z - (q + m_Z) F, \\ N(0) > 0, P_L(0) > 0, F(0) > 0, Z(0) > 0 \end{cases} \tag{3.3}$$

with the corresponding food web provided in Figure 5.

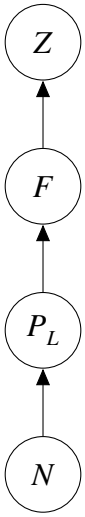


**Figure 5.** The food web in the absence of phytoplankton species.

Using the same Lyapunov functions $V$ as defined in Theorem 3.1, we can prove Theorem 3.3 stated below. We thus omit the proof.

**Theorem 3.3.** *Let hypothesis* $(H): 0 < \lambda_S < \lambda_L < \frac{I}{q}$ *hold. Then the solution of system (3.3) satisfies the following statements:*

*(i) If* $0 < I < \lambda_L q\left(1 + \frac{a_L}{f_F\beta}\right)$, *then* $E_L^{P_S} = \left(\lambda_L, N^{(0)} - \lambda_L, 0, 0\right)$ *is G.A.S.*

*(ii) If* $\lambda_L q\left(1 + \frac{a_L}{f_F\beta}\right) < I < \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right)\left(q + \frac{\beta}{e_P\gamma}(q + m_Z)\right)$, *then* $E_{LF}^{P_S} = \left(\overline{N}, \overline{P_L}, \overline{F}, 0\right)$ *is G.A.S. Here* $\overline{P_L} = \frac{q}{f_F\beta}$, $\overline{N} = \frac{I}{q + a_L\overline{P_L}}$, $\overline{F} = \frac{a_L\overline{N} - q}{\beta} > 0$.

*(iii) If* $I > \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right)\left(q + \frac{\beta}{e_F\gamma}(q + m_Z)\right)$, *then the positive equilibrium* $E_{LFZ}^{P_S} = \left(\widehat{N}, \widehat{P_L}, \widehat{F}, \widehat{Z}\right)$ *exists and is G.A.S. Here* $\widehat{F} = \frac{q + m_Z}{\gamma e_F}$, $\widehat{N} = \frac{\beta\widehat{F} + q}{a_L}$, $\widehat{Z} = \frac{f_F\beta\widehat{P_L} - q}{\gamma} > 0$, $\widehat{P_L} = \frac{I - q\widehat{N}}{a_L\widehat{N}} > 0$.

Taking $I_1^{P_S} = \lambda_L q\left(1 + \frac{a_L}{f_F\beta}\right)$ and $I_2^{P_S} = \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right)\left(q + \frac{\beta}{e_F\gamma}(q + m_Z)\right)$, the global stability of equilibrium points of system (3.3) is provided in Figure 6.

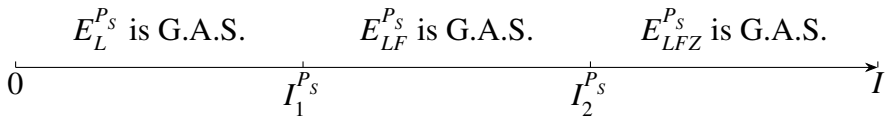


**Figure 6.** Operation diagram of system (3.3).

## 4. Boundary equilibrium points of system (1.1) and their stability

From Section 3, there are seven distinct boundary equilibrium points of system (1.1) listed below :

$$\begin{aligned}
E_0 &= \left(N^{(0)}, 0, 0, 0, 0\right),\\
E_S &= \left(\lambda_S, N^{(0)} - \lambda_S, 0, 0, 0\right), N^{(0)} > \lambda_S,\\
E_{SZ} &= \left(N^\star, P_S^\star, 0, 0, Z^\star\right), N^{(0)} > \lambda_S + P_S^\star,\\
E_{SLZ} &= \left(\lambda_L, P_S^\star, \widetilde{P_L}, 0, \widetilde{Z}\right), N^{(0)} > \lambda_L + \frac{\lambda_L}{\lambda_S}P_S^\star,\\
E_L &= \left(\lambda_L, 0, N^{(0)} - \lambda_L, 0, 0\right), N^{(0)} > \lambda_L,\\
E_{LF} &= \left(\overline{N}, 0, \overline{P_L}, \overline{F}, 0\right), N^{(0)} > \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right),\\
E_{LFZ} &= \left(\widehat{N}, 0, \widehat{P_L}, \widehat{F}, \widehat{Z}\right), N^{(0)} > \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right)\left(1 + \frac{\beta}{e_F\gamma}\left(1 + \frac{m_Z}{q}\right)\right),
\end{aligned} \tag{4.1}$$

where

$$\begin{aligned}
&N^\star = \frac{I}{q + a_S P_S^\star},\ P_S^\star = \frac{q + m_Z}{e_P b},\ Z^\star = \frac{a_S N^\star - q}{b} > 0,\\
&\widetilde{P_L} = \frac{I}{q} - \lambda_L - \frac{a_S}{a_L} P_S^\star > 0,\ \widetilde{Z} = \frac{1}{b}\left(a_S \lambda_L - q\right) > 0,\\
&\overline{N} = \frac{I}{q + a_L \overline{P_L}},\ \overline{P_L} = \frac{q}{f_F \beta},\ \overline{F} = \frac{a_L \overline{N} - q}{\beta} > 0,\\
&\widehat{F} = \frac{q + m_Z}{\gamma e_F},\ \widehat{N} = \frac{\beta \widehat{F} + q}{a_L},\ \widehat{Z} = \frac{f_F \beta \widehat{P_L} - q}{\gamma} > 0,\ \widehat{P_L} = \frac{I - q\widehat{N}}{a_L \widehat{N}} > 0.
\end{aligned} \tag{4.2}$$

Next we discuss the local asymptotic stability of the boundary equilibrium points in (4.1) with respect to system (1.1). Obviously $E_0$ is unstable under hypothesis $(H)$.

For the stability of $E_S$, let $N^{(0)} < \lambda_S + \frac{q+m_Z}{e_P b}$. Then

$$\begin{aligned}
&\frac{1}{F} F'(t)\mid_{E_S} = f_F \beta P_L - \gamma Z - q = -q < 0,\\
&\frac{1}{Z} Z'(t)\mid_{E_S} = e_P b\left(N^{(0)} - \lambda_S\right) - (q + m_Z) < 0,\\
&\frac{1}{P_L} P_L'(t)\mid_{E_S} = a_L \lambda_S - q < 0
\end{aligned} \tag{4.3}$$

and all of the eigenvalues of the Jacobian matrix of system (1.1) at $E_S$ are negative. Hence $E_S$ is asymptotically stable if $N^{(0)} < \lambda_S + \frac{q+m_Z}{e_P b}$.

For the stability of $E_{SZ}$, if $N^{(0)} < \lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star$, then

$$\begin{aligned}
&\frac{1}{P_L} P_L'\mid_{E_{SZ}} = a_L N^\star - q < 0,\\
&\frac{1}{F} F'\mid_{E_{SZ}} = -\gamma Z^\star - q < 0.
\end{aligned} \tag{4.4}$$

Thus, if $N^{(0)} < \lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star$, then $E_{SZ}$ is asymptotically stable .

For the stability of $E_{SLZ}$, consider

$$\frac{1}{F} F'\mid_{E_{SLZ}} = f_{\overline{F}} \beta \widetilde{P_L} - \gamma \widetilde{Z} - q < 0. \tag{4.5}$$

Therefore, $E_{SLZ}$ is asymptotically stable if (4.5) holds.

For the stability of $E_L$, let $N^{(0)} < \lambda_L + \frac{q}{f_F \beta}$. Then

$$\begin{aligned}
&\frac{1}{P_S} P_S'\mid_{E_L} = a_S \lambda_L - q > 0,\\
&\frac{1}{F} F'\mid_{E_L} = f_F \beta\left(N^{(0)} - \lambda_L\right) - q < 0\\
&\frac{1}{Z} Z'\mid_{E_L} = -(q + m_Z) < 0.
\end{aligned} \tag{4.6}$$

**Table 2.** Conditions for existence and local asymptotic stability of boundary equilibrium points of system (1.1).

| | Existence | Locally asymptotically stable if |
|---|---|---|
| $E_0$ | always | $\star$ |
| $E_S$ | under $(H)$ | $N^{(0)} < \lambda_S + P_S^\star$ |
| $E_{SZ}$ | $\lambda_S + P_S^\star < N^{(0)}$ | $N^{(0)} < \lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star$ |
| $E_{SLZ}$ | $\lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star < N^{(0)}$ | $f_F \beta \widetilde{P_L} - \gamma \widetilde{Z} - q < 0$ |
| $E_L$ | under $(H)$ | $\star$ |
| $E_{LF}$ | $N^{(0)} > \lambda_L \left(1 + \frac{a_L}{f_F \beta}\right)$ | $\star$ |
| $E_{LFZ}$ | $N^{(0)} > \lambda_L \left(1 + \frac{a_L}{f_F \beta}\right)\left(1 + \frac{\beta}{e_F \gamma}\left(1 + \frac{m_Z}{q}\right)\right)$ | $a_S \widehat{N} - b\widehat{Z} - q < 0$ |

We conclude that $E_L$ is unstable in the $P_S$ direction and stable in $F$ and $Z$ directions.

For the stability of $E_{LF}$, the assumption and $\overline{F} > \frac{q+m_Z}{e_F \gamma}$ imply that

$$\frac{1}{P_S} P_S' \mid_{E_{LF}} = a_S \overline{N} - q > 0,$$
$$\frac{1}{Z} Z' \mid_{E_{LF}} = e_F \gamma \overline{F} - (q + m_Z) > 0$$

For the stability of $E_{LFZ}$, consider

$$\frac{1}{P_S} P_S' \mid_{E_{LFZ}} = a_S \widehat{N} - b\widehat{Z} - q. \tag{4.7}$$

Hence $E_{LFZ}$ is asymptotically stable if $a_S \widehat{N} - b\widehat{Z} - q < 0$.

A summary of the results on the asymptotic stability of boundary equilibrium points of system (1.1) is provided in Table 2.

Now we present some extinction results in the next theorem.

**Theorem 4.1.** *Suppose $f_F \le \frac{e_P}{e_F}$ holds. Then the following statements hold.*

*(i) If $N^{(0)} < \lambda_S + \frac{q+m_Z}{e_P b}$, then $E_S = \left(\lambda_S, N^{(0)} - \lambda_S, 0, 0, 0\right)$ attracts each point $\left(N, P_S, P_L, F, Z\right) \in \mathbb{R}^5_+$.*

*(ii) If $\lambda_S + P_S^\star < N^{(0)} < \lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star$, then $E_{SZ} = \left(N^\star, P_S^\star, 0, 0, Z^\star\right)$ attracts each point $\left(N, P_S, P_L, F, Z\right) \in \mathbb{R}^5_+$.*

*Proof.* (i) Introduce the Lyapunov function

$$V = \int_{\lambda_S}^{N} \frac{\xi - \lambda_S}{\xi} d\xi + c_1 \int_{N^{(0)} - \lambda_S}^{P_S} \frac{\xi - \left(N^{(0)} - \lambda_S\right)}{\xi} d\xi + c_2 P_L + c_3 F + c_4 Z.$$

Choose $c_1 = c_2 = 1$, $c_3 = \frac{e_F}{e_P}$, and $c_4 = \frac{1}{e_P}$. Then

$$\dot{V} = (N - \lambda_S)\left(\frac{I}{N} - \frac{I}{\lambda_S} - a_S\left(P_S - \left(N^{(0)} - \lambda_S\right)\right) - a_L P_L\right)$$

$$
\begin{aligned}
&+\left(P_S-\left(N^{(0)}-\lambda_S\right)\right)\left(a_S\left(N-\lambda_S\right)-bZ\right)\\
&+P_L\left(a_L\left(N-\lambda_S\right)-\beta F+\left(a_L\lambda_S-q\right)\right)\\
&+\frac{e_F}{e_P}F\left(f_P\beta P_L-\gamma Z-q\right)\\
&+\frac{1}{e_P}Z\left(e_Pb\left(P_S-\left(N^{(0)}-\lambda_S\right)\right)+e_F\gamma F+\left(e_Pb\left(N^{(0)}-\lambda_S\right)-\left(q+m_Z\right)\right)\right)\\
&=\left(N-\lambda_S\right)\left(\frac{I}{N}-\frac{I}{\lambda_S}\right)+P_L\left(a_L\lambda_S-q\right)-\frac{e_F}{e_P}qF\\
&+P_LF\left(-\beta+f_F\beta\frac{e_F}{e_P}\right)+Z\left(e_Pb\left(N^{(0)}-\lambda_S\right)-\left(q+m_Z\right)\right)\\
&\leq 0.
\end{aligned}
$$

It folows from the invariance principle that $E_S$ is a global attractor.

(ii) Define the Lyapunov function by

$$
V=\int_{N^\star}^{N}\frac{\xi-N^\star}{\xi}d\xi+c_1\int_{P_S^\star}^{P_S}\frac{\xi-P_S^\star}{\xi}d\xi+c_2P_L+c_3F+c_4\int_{Z^\star}^{Z}\frac{\xi-Z^\star}{\xi}d\xi.
$$

Let $c_1=1$, $c_2=1$, $c_3=\frac{e_F}{e_P}$, and $c_4=\frac{1}{e_P}$. Then

$$
\begin{aligned}
\dot{V}=&\left(N-N^\star\right)\left(\frac{I}{N}-\frac{I}{N^\star}-a_S\left(P_S-P_S^\star\right)-a_LP_L\right)\\
&+\left(P_S-P_S^\star\right)\left(a_S\left(N-N^\star\right)-b\left(Z-Z^\star\right)\right)\\
&+\left(a_L\left(N-N^\star\right)-\beta F+\left(a_LN^\star-q\right)\right)P_L\\
&+\frac{e_F}{e_P}\left(f_F\beta P_L-\gamma\left(Z-Z^\star\right)+\left(-\gamma Z^\star-q\right)\right)F\\
&+\frac{1}{e_P}\left(Z-Z^\star\right)\left(e_Pb\left(P_S-P_S^\star\right)+e_F\gamma F+e_PbP_S^\star-\left(q+m_Z\right)\right)\\
&=\left(N-N^\star\right)\left(\frac{I}{N}-\frac{I}{N^\star}\right)+FP_L\left(-\beta c_2+f_F\beta\frac{e_F}{e_P}\right)\\
&+\left(a_LN^\star-q\right)P_L+\frac{e_F}{e_P}\left(-\gamma Z^\star-q\right)F\\
&\leq 0.
\end{aligned}
$$

By invariance principle, $E_{SZ}$ is a global attractor. □

**Remark 4.2:** From our numerical simulation results,we conjecture that the equilibria $E_S$ and $E_{SZ}$ are G.A.S. even when $f_F>\frac{e_P}{e_F}$.

## 5. Uniform persistence of system (1.1) with both parasitic fungi and an $F$-$Z$ link, i.e., $\gamma>0$

In this section, we determine conditions for the species in system (1.1) to coexist by applying the theory of uniform persistence of Butler, Freedman and Waltman [12, 13, 16]. Since the boundary

dynamics for $F \equiv 0$, $Z \equiv 0$, and $P_S \equiv 0$ are discussed in Section 3 and the acyclic conditions are easy to verify, it remains only to verify that $W^S(\mathcal{M}_i) \cap \underline{\text{Int}}(\mathbb{R}^5_+) = \phi$ for each boundary equilibrium $\mathcal{M}_i$.

Consider the operation diagram in Figure 3 and the case that $I > I_2^F = \lambda_L\left(q + a_L P_S^\star\right)$. From the equation for $F$ in system (1.1), the invasion condition for the boundary equilibrium $E_{SLZ} = \left(\lambda_L, P_S^\star, \widetilde{P_L}, 0, \widetilde{Z}\right)$ is $\frac{F'}{F} > 0$. That is,

$$f_F\beta\widetilde{P_L} - \gamma\widetilde{Z} - q > 0, \tag{5.1}$$

where $\widetilde{P_L} = \frac{I}{q} - \lambda_L - \frac{a_S}{a_L}P_S^\star > 0$, $\widetilde{Z} = \frac{1}{b}(a_S\lambda_L - q) > 0$, and $P_S^\star = \frac{q+m_Z}{e_P b}$ (See (4.2)).

Lemma 5.1 below shows that inequality (5.1) is equivalent to

$$I > \lambda_L(q + a_L P_S^\star) + \frac{a_L}{f_F\beta}\lambda_L\left(\gamma\frac{a_S}{b}(\lambda_L - \lambda_S) + q\right) = I_2. \tag{5.2}$$

Next, we consider the operation diagram in Figure 6 and the case that

$$I > I_2^{P_S} = \lambda_L\left(1 + \frac{a_S}{f_F\beta}\right)\left(q + \frac{\beta}{e_P\gamma}(q + m_Z)\right).$$

Similarly, the equation for $P_S$ in system (1.1) provides the following invasion condition for the boundary equilibrium $E_{LFZ} = \left(\widehat{N}, 0, \widehat{P_L}, \widehat{F}, \widehat{Z}\right)$:

$$a_S\widehat{N} - b\widehat{Z} - q > 0, \tag{5.3}$$

where $\widehat{F} = \frac{q+m_Z}{\gamma e_F}$, $\widehat{P_L} = \frac{I - q\widehat{N}}{a_L\widehat{N}} > 0$, $\widehat{Z} = \frac{f_F\beta\widehat{P_L} - q}{\gamma}$, and $\widehat{N} = \frac{\beta\widehat{F} + q}{a_L}$ (See (4.2)).

In Lemma 5.1, we also prove that inequality (5.3) is equivalent to

$$I < I_3 = \lambda_L\left(q + \beta\widehat{F}\right)\left(1 + \frac{a_L}{f_F\beta}\right) + \left(\beta\widehat{F} + q\right)\frac{1}{f_F\beta}\left(\left(\frac{\lambda_L}{\lambda_S} - 1\right)q + \frac{\lambda_L}{\lambda_S}\beta\widehat{F}\right)\frac{\gamma}{b}. \tag{5.4}$$

We state the lemma below.

**Lemma 5.1.** *The three statements hold.*

*(i) Inequalities* (5.1) *and* (5.2) *are equivalent.*

*(ii) Inequalities* (5.3) *and* (5.4) *are equivalent.*

*(iii) If* $\frac{e_P}{e_F} > f_F$, *then* $I_3 > I_2$.

*Proof.* (i) Equivalence is established by substituting $\widetilde{P_L} = \frac{I}{q} - \lambda_L - \frac{a_S}{a_L}P_S^\star$ and $\widetilde{Z} = \frac{1}{b}(a_S\lambda_L - q)$ into inequality (5.1). We have

$$\begin{aligned} &\frac{1}{F}\frac{dF}{dt}\Big|_{E_{SLZ}} = f_F\beta\widetilde{P_L} - \gamma\widetilde{Z} - q > 0 \\ \Leftrightarrow\ &\widetilde{P_L} > \frac{\gamma}{f_F\beta}\widetilde{Z} + \frac{q}{f_F\beta} \end{aligned}$$

$$\Leftrightarrow \frac{1}{a_L}\left(\frac{I}{\lambda_L} - q - a_S P_S^\star\right) > \frac{\gamma}{f_F\beta}\widetilde{Z} + \frac{q}{f_F\beta}$$
$$\Leftrightarrow I > \lambda_L\left(q + a_S P_S^\star + a_L\left(\frac{\gamma}{f_F\beta}\widetilde{Z} + \frac{q}{f_F\beta}\right)\right)$$
$$\Leftrightarrow I > \lambda_L(q + a_S P_S^\star) + \frac{a_L}{f_F\beta}\lambda_L\left(\gamma\frac{a_S}{b}(\lambda_L - \lambda_S) + q\right) = I_2.$$

This proves (i).

(ii) First note that $\widehat{N} = \frac{\beta}{a_L}\widehat{F} + \lambda_L > \lambda_S$ implies $a_S\widehat{N} - q > 0$. We have

$$\frac{1}{P_S}\frac{dP_S}{dt}\,|_{E_{LFZ}} = a_S\widehat{N} - b\widehat{Z} - q > 0$$
$$\Leftrightarrow a_S\widehat{N} - q > b\widehat{Z} = b\frac{f_F\beta\widehat{P_L} - q}{\gamma}$$
$$\Leftrightarrow \frac{\gamma}{bf_F\beta}\left(a_S\widehat{N} - q + \frac{bq}{\gamma}\right) > \widehat{P_L} = \frac{I}{a_L\widehat{N}} - \lambda_L$$
$$\Leftrightarrow \lambda_L + \frac{\gamma}{bf_F\beta}\left(a_S\widehat{N} - q + \frac{bq}{\gamma}\right) > \frac{I}{a_L\widehat{N}}$$
$$\Leftrightarrow I < a_L\widehat{N}\left(\lambda_L + \frac{\gamma}{bf_F\beta}\left(a_S\widehat{N} - q + \frac{bq}{\gamma}\right)\right) = I_3.$$

Using the equalities

$$a_L\widehat{N} = \beta\widehat{F} + q \quad \text{and}$$
$$a_S\widehat{N} - q = a_S\left(\widehat{N} - \lambda_S\right) = a_S\left((\lambda_L - \lambda_S) + \frac{\beta\widehat{F}}{a_L}\right),$$

we express $I_3$ as

$$I_3 = \left(\beta\widehat{F} + q\right)\left(\lambda_L + \frac{\gamma}{bf_F\beta}\left(a_S(\lambda_L - \lambda_S) + \frac{a_S\beta\widehat{F}}{a_L} + \frac{bq}{\gamma}\right)\right).$$

Next, by the equivalence

$$q = \lambda_L a_L < \frac{\gamma}{b}\left(a_S(\lambda_L - \lambda_S) + \frac{a_S}{a_L}\beta\widehat{F} + \frac{bq}{\gamma}\right)$$
$$\Leftrightarrow 1 + \frac{a_L}{f_F\beta} < 1 + \frac{\gamma}{bf_F\beta}\left(a_S\left(1 - \frac{\lambda_S}{\lambda_L}\right) + \frac{a_S}{a_L}\frac{1}{\lambda_L}\beta\widehat{F} + \frac{bq}{\gamma}\frac{1}{\lambda_L}\right),$$

it follows that $I_2^{P_S} = \lambda_L\left(1 + \frac{a_L}{f_F\beta}\right)\left(q + \beta\widehat{F}\right) < I_3$. Hence (ii) is established.

(iii) Expanding $I_2$ and $I_3$, we have

$$I_2 = \lambda_L q + \lambda_L a_S\frac{q + m_Z}{e_P b}\frac{q}{f_F\beta}\gamma\frac{a_S}{b}(\lambda_L - \lambda_S) + \frac{q^2}{f_F\beta},$$

and

$$\begin{aligned} I_3 = &\beta\frac{q+m_Z}{\gamma e_F}\lambda_L + \beta\frac{q+m_Z}{\gamma e_F}\frac{\gamma}{bf_F\beta}a_S\left(\lambda_L-\lambda_S\right)\\ &+\beta\frac{q+m_Z}{\gamma e_F}\frac{\gamma}{bf_F\beta}\frac{a_s}{a_L}\beta\frac{q+m_Z}{\gamma e_F} + \beta\frac{q+m_Z}{\gamma e_F}\frac{q}{f_F\beta}\\ &+q\lambda_L + \frac{\gamma}{bf_F\beta}qa_S\left(\lambda_L-\lambda_S\right)\\ &+q\frac{a_S\beta}{a_L}\frac{q+m_Z}{\gamma e_F} + \frac{b}{\gamma}q^2\frac{\gamma}{bf_F\beta}. \end{aligned}$$

If $e_Ff_F < e_P$, then $\frac{a_S\lambda_L}{bf_Fe_F} > \frac{a_S\lambda_L}{e_Pb}$. Thus, it is easy to verify that $I_3 - I_2 > 0$.

□

We establish the coexistence of species in the next theorem wherein the proof follows directly from the above lemma.

**Theorem 5.2.** *The following statements hold:*

*(i) If $I_2 < I < I_3$, then system (1.1) is uniformly persistent and the positive equilibrium is globally asymptotically stable.*

*(ii) If $I > I_3$, then $P_S(t) \to 0$ as $t \to \infty$.*

Using the parameter values $q = 1$, $a_S = 0.8$, $a_L = 0.5$, $\lambda_s = 1.25$, $\lambda_L = 2$, $b = 1$, $e_P = 0.5$, $e_F = 0.4$, $\beta = 1$, $\gamma = 1$, $f_F = 0.6$, and $m_Z = 0.5$, we have $I_2 = 11.35$ and $I_3 = 66.92$. By setting $I = 20$, we obtain a numerical simulation of statement (i) as depicted in Figure 7. Letting $I = 80$, a numerical simulation for statement (ii) is shown in Figure 8.

## 6. Dynamics with parasitic fungi, but without an $F$-$Z$ link

When $\gamma \equiv 0$, system (1.1) becomes

$$\begin{cases} \dfrac{dN}{dt} = I - qN - a_SP_SN - a_LP_LN,\\ \dfrac{dP_S}{dt} = a_SNP_S - bZP_S - qP_S,\\ \dfrac{dP_L}{dt} = a_LNP_L - \beta FP_L - qP_L,\\ \dfrac{dF}{dt} = f_F\beta P_LF - qF,\\ \dfrac{dZ}{dt} = e_Pbp_SZ - (q+m_Z)Z \end{cases} \tag{6.1}$$

and its food web is shown in Figure 9.

**Theorem 6.1.** *Let $(H): 0 < \lambda_S < \lambda_L < \frac{I}{q}$ hold.*

*(i) If $P_S^\star > \widehat{P_S}$, then $\widetilde{E}_S = \left(\lambda_S, \widehat{P_S}, 0, 0, 0\right)$ is G.A.S., where $\widehat{P_S} = \frac{I-q\lambda_S}{a_S\lambda_S}$ and $P_S^\star = \frac{q+m_Z}{e_Pb}$.*

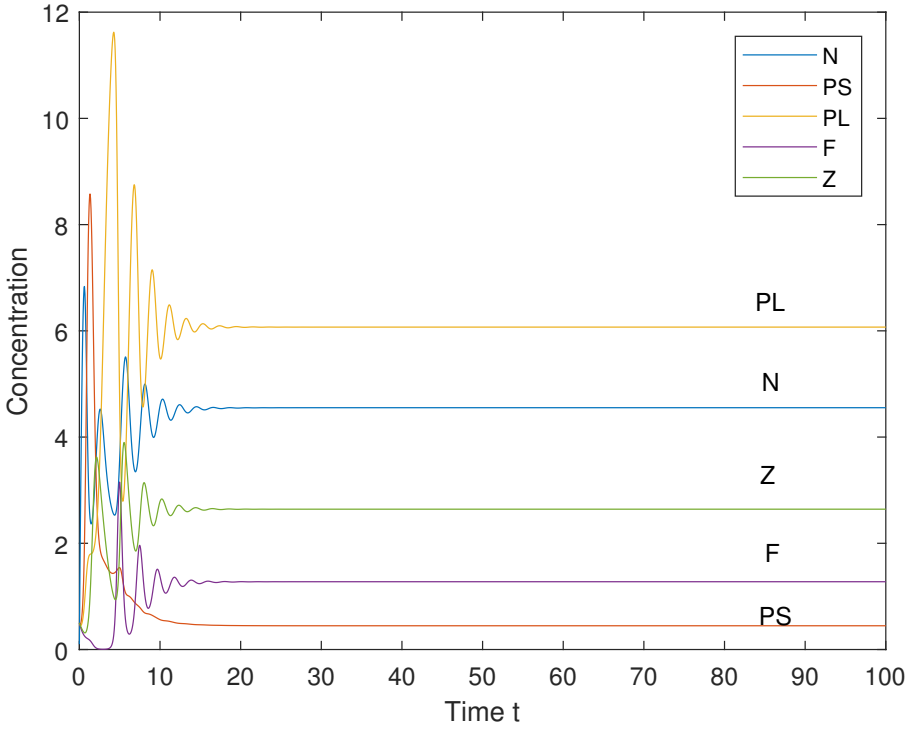


**Figure 7.** Numerical solution of Model (1.1) exhibiting uniform persistence with parameter values $q = 1$, $a_S = 0.8$, $a_L = 0.5$, $\lambda_s = 1.25$, $\lambda_L = 2$, $b = 1$, $e_P = 0.5$, $e_F = 0.4$, $\beta = 1$, $\gamma = 1$, $f_F = 0.6$, $m_Z = 0.5$, $I_2 = 11.35$, $I_3 = 66.92$, and $I = 20$.

*(ii)* *If* $P_S^\star < \widehat{P_S}$ *and* $\lambda_S < N^\star < \lambda_L$, *then* $\widetilde{E}_{SZ} = \left(N^\star, P_S^\star, 0, 0, Z^\star\right)$ *is G.A.S., where* $N^\star = \frac{I}{q+a_S P_S^\star}$ *and* $Z^\star = \frac{a_S N^\star - q}{b}$.

*(iii)* *If* $P_S^\star < \widehat{P_S}$ *and* $N_C < \lambda_L < N^\star$, *then* $\widetilde{E}_{SLZ} = \left(\lambda_L, P_S^\star, P_L^\star, 0, \widehat{Z}\right)$ *is G.A.S., where* $P_L^\star = \frac{I - q\lambda_L - a_S P_S^\star \lambda_L}{a_L \lambda_L}$.

*(iv)* *If* $P_S^\star < \widehat{P_S}$, $N^\star > \lambda_L$, *and* $N_C > \lambda_L$, *then* $\widetilde{E}_C = \left(N_C, P_S^C, P_L^C, F_C, Z_C\right)$ *is G.A.S., where* $P_L^C = \frac{q}{f_F \beta}$, $P_S^C = \frac{q+m_Z}{e_P b} = P_S^\star$, $N_C = \frac{I}{q+a_S P_S^C + a_L P_L^C}$, $Z_C = \frac{a_S N_C - q}{b}$, *and* $F_C = \frac{a_L N_C - q}{\beta}$.

Let $\widetilde{I}_1 = q\lambda_S + a_S P_S^C \lambda_S$, $\widetilde{I}_2 = q\lambda_L + a_S P_S^C \lambda_L$ and $\widetilde{I}_3 = q\lambda_L + a_S P_S^C \lambda_L + a_L P_L^C \lambda_L$. Then $\widetilde{I}_1 < \widetilde{I}_2 < \widetilde{I}_3$. As a consequence of Theorem 6.1, the following statements hold.

(i) If $0 < I < \widetilde{I}_1$, then $\widetilde{E}_S$ is G.A.S.

(ii) If $\widetilde{I}_1 < I < \widetilde{I}_2$, then $\widetilde{E}_{SZ}$ is G.A.S.

(iii) If $\widetilde{I}_2 < I < \widetilde{I}_3$, then $\widetilde{E}_{SLZ}$ is G.A.S.

(iv) If $I > \widetilde{I}_3$, then $\widetilde{E}_C$ is G.A.S.

The global stability of system (6.1) is given in Figure 10.

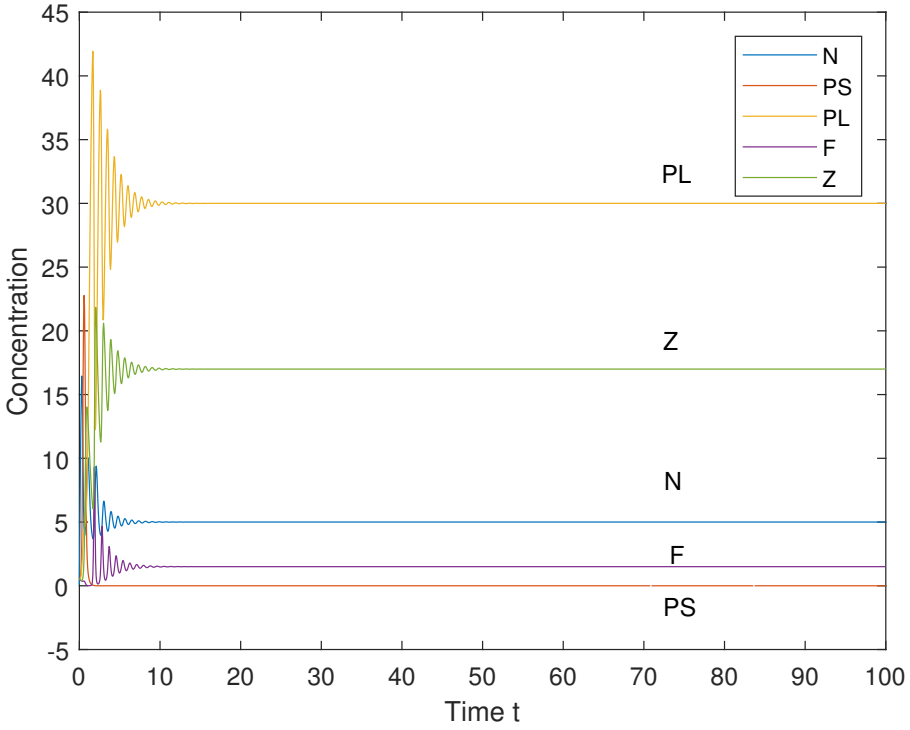


**Figure 8.** Numerical solution of system (1.1) exhibiting the extinction of $P_S(t)$ with parameter values $q = 1$, $a_S = 0.8$, $a_L = 0.5$, $\lambda_s = 1.25$, $\lambda_L = 2$, $b = 1$, $e_P = 0.5$, $e_F = 0.4$, $\beta = 1$, $\gamma = 1$ ,$f_F = 0.6$, $m_Z = 0.5$, $I_2 = 11.35$, $I_3 = 66.92$, and $I = 80$.

*Proof.* (i) Note that $\widehat{P_S} > P_S^\star \Leftrightarrow N^\star > \lambda_S \Leftrightarrow Z^\star > 0$. We introduce the Lyapunov function

$$V = \int_{\lambda_S}^{N} \frac{\xi - \lambda_S}{\xi} d\xi + \int_{P_S^\star}^{P_S} \frac{\xi - P_S^\star}{\xi} d\xi + P_L + \frac{1}{f_F} F + \frac{1}{e_P} Z.$$

Then

$$\begin{aligned}
\dot{V} &= (N - \lambda_S)\left[\frac{I}{N} - \frac{I}{\lambda_S} - a_S\left(P_S - P_S^\star\right) - a_L P_L\right] \\
&\quad + \left(P_S - P_S^\star\right)\left[a_S\left(N - \lambda_S\right) - bZ\right] \\
&\quad + P_L\left[a_L\left(N - \lambda_S\right) - \left(q - a_L\lambda_S\right) - \beta F\right] \\
&\quad + \frac{1}{f_F} F\left(f_F \beta P_L - q\right) \\
&\quad + \frac{1}{e_P} Z\left[e_P b\left(P_S - P_S^\star\right) - \left[\left(q + m_Z\right) - e_P b P_S^\star\right]\right] \\
&= \frac{-\left(N - \lambda_S\right)^2}{N\lambda_S} - \frac{q}{f_F} F - \left(\left(q + m_Z\right) - e_P b P_S^\star\right)\frac{1}{e_P} Z - \left(q - a_L\lambda_S\right) P_L \\
&\leq 0,
\end{aligned}$$

from the assumption $P_S^\star > \widehat{P_S}$. Thus $\widetilde{E_S}$ is G.A.S. by invariance principle.

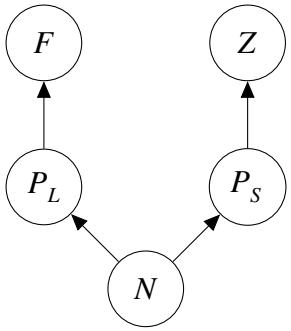


**Figure 9.** The food web of system (6.1).

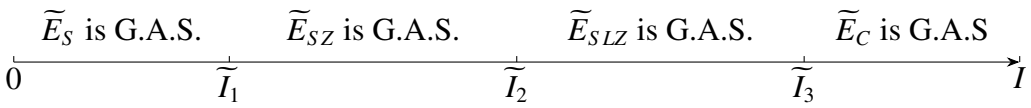


**Figure 10.** Operation diagram of system (6.1).

(ii) Note that $\widehat{P_S} > P_S^\star$ ensures that $Z^\star > 0$. Introduce the Lyapunov function

$$V = \int_{N^\star}^{N} \frac{\xi - N^\star}{\xi} d\xi + \int_{P_S^C}^{P_S} \frac{\xi - P_S^*}{\xi} d\xi + P_L + \frac{1}{f_P} F + \frac{1}{e_P} \int_{Z^\star}^{Z} \frac{\xi - Z^\star}{\xi} d\xi.$$

Then, by the assumptions $P_S^\star < \widehat{P_S}$ and $N^\star < \lambda_L$, we have

$$\begin{aligned}
\dot{V} =& (N - N^\star)\left[\frac{I}{N} - \frac{I}{N^\star} - a_S\left(P_S - P_S^\star\right) - a_L P_L\right] \\
&+ \left(P_S - P_S^\star\right)\left[a_S\left(N - N^\star\right) - b\left(Z - Z^\star\right)\right] \\
&+ P_L\left(a_L\left(N - N^\star\right) - \beta F - \left(q - a_L N^\star\right)\right) \\
&+ \frac{1}{f_F} F\left(f_F \beta P_L - q\right) \\
&+ \frac{1}{e_P}\left(Z - Z^\star\right)\left[e_P b\left(P_S - P_S^\star\right) - \left[\left(q + m_Z\right) - e_P b P_S^\star\right]\right] \\
=& \frac{-\left(N - N^\star\right)^2}{N N^\star} - \left(q - a_L N^\star\right) P_L - \frac{q}{f_F} F \\
\leq& 0.
\end{aligned}$$

Therefore $\widetilde{E}_{SZ}$ is G.A.S. by invariance principle.

(iii) Define the Lyapunov function

$$V = \int_{\lambda_L}^{N} \frac{\xi - \lambda_L}{\xi} d\xi + \int_{P_S^\star}^{P_S} \frac{\xi - P_S^\star}{\xi} d\xi + \int_{P_L^\star}^{P_L} \frac{\xi - P_L^\star}{\xi} d\xi + \frac{1}{f_F} F + \frac{1}{e_P} \int_{\widehat{Z}}^{Z} \frac{\xi - \widehat{Z}}{\xi} d\xi.$$

Then

$$\begin{aligned}\dot{V} &= (N-\lambda_L)\left[\frac{I}{N}-\frac{I}{\lambda_L}-a_S\left(P_S-P_S^\star\right)-a_L\left(P_L-P_L^\star\right)\right]\\ &\quad+\left(P_S-P_S^\star\right)\left[a_S\left(N-\lambda_L\right)-b\left(Z-\widehat{Z}\right)\right]\\ &\quad+\left(P_L-P_L^\star\right)\left(a_L\left(N-\lambda_L\right)-\beta F\right)\\ &\quad+\frac{1}{f_F}F\left(f_F\beta\left(P_L-P_L^\star\right)-\left(q-f_F\beta P_L^\star\right)\right)\\ &\quad+\frac{1}{e_P}\left(Z-\widehat{Z}\right)\left(e_P b\left(P_S-P_S^\star\right)\right)\\ &= \frac{-I\left(N-\lambda_L\right)^2}{N\lambda_L}-\frac{1}{f_F}\left(q-f_F\beta P_L^\star\right).\end{aligned}$$

Using the assumptions $P_S^\star < \widehat{P_S}$ and $N_C < \lambda_L < N^\star$, and the equivalence below

$$\begin{aligned}q-f_F\beta P_L^\star>0 &\Leftrightarrow \frac{q}{f_F\beta}=P_L^C>P_L^\star\\ &\Leftrightarrow P_L^C>\frac{I-q\lambda_L-a_S P_S^\star\lambda_L}{a_L\lambda_L}\\ &\Leftrightarrow \left(q+a_S P_S^\star+a_L P_L^C\right)\lambda_L>I\\ &\Leftrightarrow \lambda_L>N_C=\frac{I}{q+a_S P_S^\star+a_L P_L^C},\end{aligned}$$

we have $\dot{V}\le 0$. Hence $\widetilde{E}_{SLS}$ is G.A.S. by invariance principle.

(iv) Observe that the assumptions $P_S^\star < \widehat{P_S}$, $N^\star > \lambda_L$, and $N_C > \lambda_L$ imply $\widehat{P_S} > 0$, $P_L^* > 0$, and $F_C > 0$, respectively. By introducing the Lyapunov function

$$\begin{aligned}V=&\int_{N_C}^{N}\frac{\xi-N_C}{\xi}d\xi+\int_{P_S^C}^{P_S}\frac{\xi-P_S^C}{\xi}d\xi+\int_{P_L^C}^{P_L}\frac{\xi-P_L^C}{\xi}d\xi\\ &+\frac{1}{f_F}\int_{F_C}^{F}\frac{\xi-F_C}{\xi}d\xi+\frac{1}{e_P}\int_{Z_C}^{Z}\frac{\xi-Z_C}{\xi}d\xi,\end{aligned}$$

we obtain

$$\begin{aligned}\dot{V} &= (N-N_C)\left[\frac{I}{N}-\frac{I}{N_C}-a_S\left(P_S-P_S^C\right)-a_L\left(P_L-P_L^C\right)\right]\\ &\quad+\left(P_S-P_S^C\right)\left[a_S\left(N-N_C\right)-b\left(Z-Z_C\right)\right]\\ &\quad+\left(P_L-P_L^C\right)\left(a_L\left(N-N_C\right)-\beta\left(F-F_C\right)\right)\\ &\quad+\frac{1}{f_F}\left(F-F_C\right)\left(f_F\beta\left(P_L-P_L^C\right)\right)\\ &\quad+\frac{1}{e_P}\left(Z-Z_C\right)\left(e_P b\left(P_S-P_S^C\right)\right)\end{aligned}$$

$$= \frac{-I\,(N - N_C)^2}{NN_C}$$
$$\leq 0.$$

Therefore it follows from invariance principle that $\widetilde{E}_C$ is G.A.S.

□

## 7. Discussion

In this paper, we study an aquatic ecosystem with five species : a single nutrient resource $N$ (Phosphorus), the small phytoplankton $P_S$, the large phytoplankton $P_L$, the zooplankton $Z$, and the parasitic fungi $F$. Both $P_S$ and $P_L$ consume $N$. In the food web (see Figure 1), the zooplankton $Z$ only consumes the small phytoplankton $P_S$ but the large phytoplankton $P_L$ is inedible to the zooplankton. In the absence of zooplankton, we assume that the small phytoplankton $P_S$ is a better competitor than the large $P_L$ in the exploitative competition for nutrient. With the presence of parasitic fungi $F$, we consider two cases : the food web with an $F - Z$ link and that without an $F - Z$ link. In Section 3, we first study the boundary dynamics of the food web, i.e., the population dynamics under the assumptions that $F \equiv 0$, $Z \equiv 0$ and $P_S \equiv 0$. We then employ Lyapunov functions to establish the results of global stability as the nutrient input I varies. Section 4 deals with the determination of conditions for the local stability of boundary equilibrium points of system (1.1) and the proofs of several partial results on the extinction of species. In Section 5, with the well understood information of boundary dynamics proven in Section 3, we establish the uniform persistence of the food web. Section 6 is devoted to determine conditions for the global stability of species in the system of food web without an $F - Z$ link.

Now we discuss the role played by parasitic fungi in the coexistence of species in the food web. Recall that, in the absence of parasitic fungi, from Figure 3, coexistence of species occurs when $I > I_2^F$. When parasitic fungi are present in the food web, we consider two cases: one with an $F - Z$ link and another without an $F - Z$ link. In the case without an $F - Z$ link, coexistence of species occurs when $I > \widetilde{I}_3$ (see Theorem 6.1), whereas in the case with an $F - Z$ link, coexistence of species occurs when $I_2 < I < I_3$ (see Theorem 5.2). A comparison of the three quantities $I_2^F$, $\widetilde{I}_3$, $I_2$ shows that

$$I_2^F < \widetilde{I}_3 < I_2 < I_3,$$

where

$$I_2^F = q\left(\lambda_L + \frac{\lambda_L}{\lambda_S} P_S^\star\right), \quad P_S^\star = \frac{q + m_Z}{e_P b}$$
$$\widetilde{I}_3 = \lambda_L q + a_S P_S^\star \lambda_L + a_L \frac{q}{f_F \beta} \lambda_L$$
$$= I_2^F + a_L \frac{q}{f_F \beta} \lambda_L$$
$$I_2 = \lambda_L (q + a_S P_S^\star) + \frac{a_L}{f_F \beta} \lambda_L \left(q + \gamma \frac{a_S}{b} (\lambda_L - \lambda_S)\right)$$
$$I_3 = \widetilde{I}_3 + \frac{a_L}{f_F \beta} \lambda_L \gamma \frac{a_S}{b} (\lambda_L - \lambda_S).$$

In view of the above, the best case for the coexistence of species of the food web is when $I > I_2^F$. That is, coexistence of species occurs if there is no parasitic fungus. In the case that parasitic fungus is present and there is no $F - Z$ link, coexistence of species occurs if $I > \widetilde{I_3}$. With the presence of parasitic fungi and an $F - Z$ link, we have coexistence in the parameter region $I_2 < I < I_3$. From our numerical simulation (see Figure 8), we observe that, if $I > I_3$, then the small phytoplankton $P_S$ goes to extinction.

Finally, we note that in [9] the authors discuss the role of parasitic fungi in zooplankton biomass at steady states. Their conclusion is that the presence of an $F - Z$ link can benefits large phytoplankton and strengthens competition between small and large phytoplankton reducing material transfer from smaller phytoplankton to zooplankton. While our analysis shows that without $F - Z$ link if $I_1^F < I < I_2^F$ then zooplankton, fungi, small phytoplankton coexist; if $I > I_2^F$, the zooplankton, fungi, small and large phytoplankton coexist (see Figure 3). However, with $F - Z$ link, the system (1.1) is uniformly persistent if $I_2 < I < I_3$ (Theorem 5.2). From the inequality $I_2^F < I_2 < I_3$, it is easier to obtain coexistence when there is no $F - Z$ link.

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## Conflict of interest

The authors declare there is no conflict of interest.

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