

Permanent Coexistence for a Nonlinear Response Omnivory Model

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Abstract: We use the growing body of mathematical theory known as permanence theory in order to study the long-term survival of species in an ecological community. The ecological community of interest involves a unique mixture of competition and predation known as omnivory—feeding on more than one trophic level. We approximate the natural system with a differential equation model in which the functional and numerical responses are nonlinear. The nonlinearity adds complexity to the model that is handled with the use of an Average Lyapunov function. Our analysis shows that three restrictions must be placed on the model parameters in order to ensure permanent coexistence. The restrictions are that the solutions of our model must be uniformly bounded, the Ω -limit of every orbit on the boundary consists of equilibrium points only, and no boundary equilibrium can be saturated.

Key-Words: Permanent Coexistence, Permanence, Omnivory, Intraguild Predation, Nonlinear Response

1 Introduction

Since human survival depends upon biodiversity and the understanding of natural systems, the long-term survival of species in an omnivory system is of great importance. The ubiquity of omnivory in natural systems is evident [6], [14], [13]. An omnivory model with linear functional and numerical responses was analyzed by Vance [15] using permanence theory. Permanence theory is based on the idea that species densities should be allowed to vary in any way (i.e. equilibria, chaos, etc.), as long as the densities do not remain too close to the boundary of the state space. The boundary is where species densities are zero and extinction occurs. We show the existence of an Average Lyapunov function which acts as a positive increasing (from the boundary) surface upon which state variables are projected. Most of the available theory on permanence requires that the boundary of the state space is invariant. We include a lemma and a theorem that show the invariance of the state space and global existence of solutions for our model.

2 Omnivory Model

The complexity of ecological interactions involving omnivory is well known (see [14], [12]). The search for robust mechanisms that can explain permanence of tightly linked omnivory systems remains an important challenge [11]. Intraguild predation (IGP), the simplest example, involves two species—a predator and

a consumer—that compete for a resource in a similar way, but also engage in direct predator-prey interactions [14], [13] (also see Figure 1a).

We focus our attention on the asymmetric classification of IGP as given by Polis et al. [14] as opposed to the symmetric classification (see Figure 1b) of IGP. Asymmetric omnivory involves a predator feeding on a consumer and a basal resource. The consumer feeds solely on the basal resource. We use nonlinear Type II functional and numerical responses in our model similar to Křivan and Diehl [11]. Type II responses assume that predator consumption increases to a maximum rate of victim consumption per predator. That is, the rate of consumption becomes saturated as victim densities increase. Our non-linear response omnivory model is given by the system of differential equations

$$\begin{aligned} \frac{dP}{dt} &= P \left[\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \right] \\ \frac{dC}{dt} &= C \left[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - m_C \right] \\ &\quad - C \left[\frac{\lambda_{CP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \\ \frac{dR}{dt} &= R \left[r \left(1 - \frac{R}{K} \right) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} \right] \\ &\quad - R \left[\frac{\lambda_{RP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \end{aligned} \quad (1)$$

with initial conditions

$$P(0) = c_1 > 0, \quad C(0) = c_2 > 0, \quad R(0) = c_3 > 0.$$

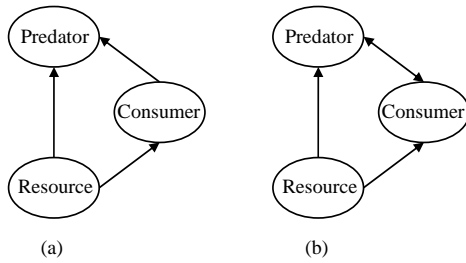


Figure 1: Two forms of ecological interactions. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) Asymmetrical intraguild predation. (b) Symmetrical intraguild predation

This forms an initial value problem

$$\frac{df}{dt} = f(x), \quad f(0) = c \quad (2)$$

on $D = \mathbb{R}_+ \times \mathbb{R}_+^3$ with the understood definitions for f, x , and c .

Parameter λ_{ij} is the search rate of species j for species i , e_{ij} is the efficiency with which species i is converted to new offspring of species j , and h_{ij} is the time spent by species j handling species i . K is the resource carrying capacity and r is the intrinsic rate of increase of the resource. The natural mortality rates of the predator and consumer are m_P and m_C , respectively.

Since this system is of Kolmogorov type, the boundary is invariant [15]. Hence, $P(t), C(t), R(t) \geq 0$ for all $t \geq 0$. This allows for more mathematically tractable analysis and satisfactory results.

3 Solution to System

First, we must show that a unique solution exists for all $t \geq 0$ in order to investigate long-term species survival. Since f and its partial derivatives are all continuous with respect to P, C , and R for all positive t, P, C , and R by an existence and uniqueness theorem [16] our initial value problem 2 has exactly one solution in D .

In order to show that a unique solution exists for all nonnegative time, we need a lemma on differential inequalities similar to the one used by Birkhoff [1].

Lemma 1 Let S be a differentiable function on $[a, b]$. Part A: If S satisfies the differential inequality

$$\dot{S}(t) \leq \lambda S(t), \quad a \leq t \leq b \quad (3)$$

where $\lambda > 0$ is a constant, then

$$S(t) \leq S(a)e^{\lambda(t-a)} \quad \text{for } a \leq t \leq b.$$

Part B: If S satisfies the differential inequality

$$\dot{S}(t) + \lambda S(t) \leq M_1, \quad a \leq t \leq b \quad (4)$$

where $M_1 > 0$ and $\lambda > 0$ are constants, then

$$S(t) \leq \frac{M_1}{\lambda} + \left(S(a) - \frac{M_1}{\lambda} \right) e^{\lambda(a-t)} \quad \text{for } a \leq t \leq b.$$

Part C: If S satisfies the differential inequality

$$\dot{S}(t) \leq (M_1 + M_2 e^{\lambda t}) S(t), \quad a \leq t \leq b \quad (5)$$

where $M_1 > 0, M_2 > 0$, and $\lambda > 0$ are constants, then

$$S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})} \quad \text{for } a \leq t \leq b.$$

Proof. The first and second results are proved similar to the third result except for multiplying both sides of (3) by $e^{-\lambda t}$ and (4) by $e^{\lambda t}$, respectively. For Part C, multiply both sides of (5) by

$$e^{-\left(M_1 t + \frac{M_2}{\lambda} e^{\lambda t}\right)}$$

to get

$$\begin{aligned} 0 &\geq e^{-\left(M_1 t + \frac{M_2}{\lambda} e^{\lambda t}\right)} \left[\dot{S} - \left(M_1 + M_2 e^{\lambda t} \right) S(t) \right] \\ &= \frac{d}{dt} \left\{ e^{-\left(M_1 t + \frac{M_2}{\lambda} e^{\lambda t}\right)} S(t) \right\}. \end{aligned}$$

Thus, the function $e^{-\left(M_1 t + \frac{M_2}{\lambda} e^{\lambda t}\right)} S(t)$ has a non-positive derivative and so is non-increasing for $a \leq t \leq b$. Therefore,

$$e^{-\left(M_1 t + \frac{M_2}{\lambda} e^{\lambda t}\right)} S(t) \leq e^{-\left(M_1 a + \frac{M_2}{\lambda} e^{\lambda a}\right)} S(a)$$

and rearranging yields

$$S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})}.$$

□

Theorem 1 The initial value problem 2 has a unique solution in \mathbb{R}_+^3 for all $t \geq 0$.

Proof: We have the differential inequality

$$\frac{dR(t)}{dt} \leq R(t)r(1 - R(t)/K). \quad (6)$$

However, the initial value problem

$$\frac{du(t)}{dt} = u(t)r(1 - u(t)/K), \quad u(0) = u_0 \quad (7)$$

has the unique solution

$$u(t) = \frac{K}{1 + \left(\frac{K}{u_0} - 1\right) e^{-rt}}. \quad (8)$$

Then applying a theorem on differential inequalities [3], we have that $R(t) \leq u(t)$ for $0 \leq t \leq \infty$. If in addition, we let $K_{max} = \max(u_0, K)$, then $u(t) \leq K_{max}$ and we have

$$R(t) \leq K_{max} \text{ for } 0 \leq t \leq \infty. \quad (9)$$

Also,

$$\begin{aligned} \frac{dC(t)}{dt} &\leq \frac{e_{RC}\lambda_{RC}R(t)}{1 + h_{RC}\lambda_{RC}R(t)}C(t) \\ &\leq e_{RC}\lambda_{RC}R(t)C(t). \end{aligned}$$

Since $R(t) \leq K_{max}$, we have that

$$\frac{dC(t)}{dt} \leq e_{RC}\lambda_{RC}K_{max}C(t) \text{ for } 0 \leq t \leq \infty.$$

If we define

$$\Gamma = e_{RC}\lambda_{RC}K_{max}$$

then by Lemma 1 Part A

$$C(t) \leq c_2 e^{\Gamma t}. \quad (10)$$

This exponential function does not reach infinity in finite time.

Finally,

$$\begin{aligned} \frac{dP(t)}{dt} &\leq \frac{e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t)}{1 + \lambda_{RP}h_{RP}R(t) + \lambda_{CP}h_{CP}C(t)}P(t) \\ &\leq (e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t))P(t). \end{aligned}$$

Since $R(t) \leq K_{max}$ and $C(t) \leq c_2 e^{\Gamma t}$, we have that

$$\frac{dP(t)}{dt} \leq (\Gamma + e_{CP}\lambda_{CP}c_2 e^{\Gamma t})P(t) \text{ for } 0 \leq t \leq \infty.$$

If we define

$$\Phi = e_{CP}\lambda_{CP}c_2$$

and

$$\Lambda = \frac{\Phi}{\Gamma}$$

then by Lemma 1 Part C

$$P(t) \leq c_1 e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \quad (11)$$

This exponential function does not reach infinity in finite time. So, by a global existence and uniqueness lemma [7] and inequalities (6), (10), and (11) a unique solution for the initial value problem 2 exists for all $t \geq 0$. \square

4 Permanent Coexistence

In this section we show that our nonlinear response omnivory model is permanently coexistent under certain parameter restrictions. Consider a system of three equations of Kolmogorov type:

$$\frac{dx_i}{dt} = x_i f_i(x), \quad 1 \leq i \leq 3, \quad (12)$$

where the $f_i : \mathbb{R}_+^3 \rightarrow \mathbb{R}$ are C^1 .

Definition 1 We say that an orbit of (12) is ultimately in $M \subset \mathbb{R}_+^3$ if and only if there exists $T(\mathbf{x}) < \infty$ such that $\mathbf{x}(t) \in M$ for $t \geq T(\mathbf{x})$. Also, we use the notation $A - B$ to denote set difference for two sets A and B .

Definition 2 An equilibrium point $\bar{\mathbf{x}}$ is saturated if

$$f_i(\bar{\mathbf{x}}) \leq 0 \text{ for all } i \text{ with } \bar{x}_i = 0. \quad (13)$$

Note that every equilibrium point in the interior of the state space is saturated. For an equilibrium point on the boundary, saturated means that the dynamics do not “call for” the missing species [5].

Definition 3 The system (12) is permanently coexistent if and only if there exists a compact set $M \subset \mathbb{R}_+^3$ such that orbits are ultimately in M for all $\mathbf{x} \in \mathbb{R}_+^3$.

Our proof on permanent coexistence will be based on the following theorem from Hutson et al. [9] which is an extension of a result by Hofbauer [4].

Theorem 2 Let $B \subseteq \mathbb{R}_+^3$ be compact and S a compact subset of B . Assume that S and $B - S$ are invariant. Suppose that there is a C^1 function $P : B \rightarrow \mathbb{R}_+$ which is such that $P(\mathbf{x}) = 0$ if and only if $\mathbf{x} \in S$. Take $\Psi(\mathbf{x}) = \dot{P}(\mathbf{x})/P(\mathbf{x})$ and assume that Ψ is bounded below on $B - S$. Define its (lower semicontinuous) extension to S , still denoted by Ψ , by setting

$$\Psi(\mathbf{x}) = \liminf_{\mathbf{y} \rightarrow \mathbf{x}, \mathbf{y} \in B - S} \Psi(\mathbf{y}) \quad (\mathbf{x} \in S) \quad (14)$$

and assume that for

$$\mathbf{x} \in \overline{\Omega(S)}, \quad \sup_{t \geq 0} \int_0^t \Psi(\mathbf{x}(t)) dt > 0. \quad (15)$$

Then there is a compact invariant set M with $d(M, S) > 0$ which is such that every orbit generated by (12) with $\mathbf{x} \in \mathbb{R}_+^3$ is ultimately in M . That is the system (12) is permanently coexistent.

The function P is known as an Average Lyapunov function [9]. Note that (15) holds if $\Psi > 0$ on $\overline{\Omega(S)}$. Also, the function $P(x)$ should not be confused with the state variable $P(t)$.

We begin our analysis by showing that our non-linear system (1) has uniformly bounded orbits and enters a compact region of \mathbb{R}_+^3 .

Theorem 3 *Provided that $e_{RP} < e_{CPE_{RC}}$, all solutions of the system (1) that initiate in \mathbb{R}_+^3 are uniformly bounded and enter a certain region B defined by*

$$B = \{(P, C, R) \in \mathbb{R}_+^3 : 0 \leq P+C+R \leq M\} \quad (16)$$

where

$$M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CPE_{RC}}\lambda} \right\},$$

$$M_1 = \frac{Ke_{CPE_{RC}}(r + \lambda)^2}{4r},$$

and

$$0 < \lambda < \min(m_C, m_P).$$

Proof: Recall that we have already stated that the components of all solutions of the system that initiate in \mathbb{R}_+^3 are bounded below by zero. Now, define

$$S(t) = e_{CPE_{RC}}R + e_{CPC} + P.$$

Taking the time derivative along a solution of the system we have the following inequality fulfilled for each $\lambda > 0$:

$$\begin{aligned} \dot{S}(t) + \lambda S(t) &\leq (e_{CPE_{RC}}r + e_{CPE_{RC}}\lambda)R - (e_{CPE_{RC}}/K)R^2. \end{aligned}$$

since $e_{RP} < e_{CPE_{RC}}$ and we choose $\lambda < \min(m_C, m_P)$. Because the right hand side is a parabola that opens downward, it is bounded for all $(P, C, R) \in \mathbb{R}_+^3$. Specifically, the right hand side is bounded by $M_1 = \frac{Ke_{CPE_{RC}}(r+\lambda)^2}{4r}$. Thus, we find an $M_1 > 0$ with

$$\dot{S} + \lambda S \leq M_1.$$

Applying Lemma 1 Part B, we obtain

$$\begin{aligned} 0 &\leq S(P, C, R) \\ &\leq \frac{M_1}{\lambda} + \left(S(P(0), C(0), R(0)) - \frac{M_1}{\lambda} \right) e^{-\lambda t} \end{aligned}$$

and as $t \rightarrow \infty, 0 \leq e_{CPE_{RC}}R + e_{CPC} + P \leq M_1/\lambda$.

Now let $M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CPE_{RC}}\lambda} \right\}$, then

$$0 \leq P + C + R \leq M.$$

Thus, there is a compact neighborhood $B \subseteq \mathbb{R}_+^3$ such that for sufficiently large $T = T(c_1, c_2, c_3), (P(t), C(t), R(t)) \in B$ for all $t \geq T$, where $(P(t), C(t), R(t))$ is a solution to (1) that initiates in \mathbb{R}_+^3 . \square

Since we have global existence and uniqueness of a solution, \mathbb{R}_+^3 and the compact set B from Theorem 3 are invariant. Now define the set $S = B \cap \partial\mathbb{R}_+^3$.

Lemma 2 *The sets S and $B - S$ are invariant.*

Proof: Assume that $x_0 \in S$ and $x(t)$ is a solution of the system (1) with $x(t_0) = x_0$. Since B and $\partial\mathbb{R}_+^3$ are invariant, then $x(t) \in B$ and $x(t) \in \mathbb{R}_+^3$ for all $t > t_0$. Thus, $S = B \cap \partial\mathbb{R}_+^3$ is invariant. Now assume that $x_0 \in B - S$ and $x(t)$ is a solution of the system (1) with $x(t_0) = x_0$. Since S and B are invariant we have global existence and uniqueness of solutions, then $x(t) \in B$ and $x(t) \notin S$ for all $t > t_0$. Hence, $B - S$ is invariant. \square

Now, we show that the Ω -limit set of every orbit in $\partial\mathbb{R}_+^3$ is an equilibrium point. The zero equilibrium is unstable due to the fact that r and K are positive. Also, it is well known that solutions to the logistic equation quickly reach the fixed carrying capacity K [2]. However, for the predator-prey subsystems, there may be periodic orbits.

We use a lemma from Hsu [8] which is based on an application of the Poincaré-Bendixson Theorem and the Dulac Criterion [10] to show that a positive stable equilibrium of a predator-prey system is globally stable. Consider the predator-prey model

$$\begin{aligned} \frac{dy}{dt} &= y[e_{xy}p(x) - m_y] \\ \frac{dx}{dt} &= xg(x) - yp(x) \end{aligned}$$

where y represents the predator density and x represents the prey density and

$$\begin{aligned} g(x) &= r \left(1 - \frac{x}{K} \right) \\ p(x) &= \frac{\lambda_{xy}x}{1+x}. \end{aligned}$$

To investigate global stability, we compute the variational matrix evaluated at the positive equilibrium (y^*, x^*) ,

$$H(x^*) = x^* g'(x^*) + g(x^*) - \frac{x^* g(x^*) p'(x^*)}{p(x^*)}.$$

Then the equilibrium is (locally) asymptotically stable if $H(x^*) \leq 0$ [8].

We prove the following lemma on the Ω -limit set of every orbit in $\partial\mathbb{R}_+^3$ using a lemma from Hsu [8] that gives conditions under which local stability of (y^*, x^*) implies global stability of (y^*, x^*) .

Lemma 3 Assume that (\bar{C}, \bar{R}) and (\bar{P}, \bar{R}) of the appropriate subsystems of (1) are stable and

$$H(\bar{R}) = \frac{rm_C(\lambda_{RC}(K-1)\xi_1 - 2m_C)}{\lambda_{RC}K\xi_1(m_C + \lambda_{RC}\xi_1)} \leq 0 \quad (17)$$

$$\frac{d^2}{dx^2} \left(\frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RC}K} < 0 \quad (18)$$

and

$$H(\bar{R}) = \frac{rm_P(\lambda_{RP}(K-1)\xi_2 - 2m_P)}{\lambda_{RP}K\xi_2(m_P + \lambda_{RP}\xi_2)} \leq 0 \quad (19)$$

$$\frac{d^2}{dx^2} \left(\frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RP}K} < 0 \quad (20)$$

where

$$\xi_1 = e_{RC} - m_C h_{RC} \quad (21)$$

$$\xi_2 = e_{RP} - m_P h_{RP}. \quad (22)$$

Then for the system (1), the Ω -limit set of every orbit in $\partial\mathbb{R}_+^3$ is an equilibrium point.

Proof: From the above comments, we see that the Ω -limit set of every orbit on each axis is an equilibrium point. Since the above conditions hold, each stable equilibrium in the bounding hyperplanes is globally stable. That is, the Ω -limit set of every orbit in each bounding hyperplane is an equilibrium point. \square

Notice that conditions on the curvature are trivially satisfied for our system because we assume $r, K, \lambda_{RC}, \lambda_{RP} > 0$.

Finally, we use Theorem 2 to determine conditions that guarantee permanence of the system (1).

Theorem 4 Assume that the following conditions hold:

(H1) The solutions of (1) in \mathbb{R}_+^3 are uniformly bounded.

(H2) The Ω -limit set of every orbit on $\partial\mathbb{R}_+^3$ consists of equilibrium points.

(H3) No boundary equilibrium is saturated.

Then the system (1) is permanent.

We use the following conditions and assignments for the proof:

$$\frac{e_{RP}\lambda_{RP}K}{1+\lambda_{RP}h_{RP}K} - m_P > 0, \quad (23)$$

$$\frac{e_{RC}\lambda_{RC}K}{1+\lambda_{RC}h_{RC}K} - m_C > 0, \quad (24)$$

and

$$\bar{C} = \frac{re_{RC}[K\lambda_{RC}(e_{RC} - m_C h_{RC}) - m_C]}{K(\lambda_{RC})^2(e_{RC} - m_C h_{RC})^2}$$

$$\bar{P} = \frac{re_{RP}[K\lambda_{RP}(e_{RP} - m_P h_{RP}) - m_P]}{K(\lambda_{RP})^2(e_{RP} - m_P h_{RP})^2}$$

$$\bar{R}_1 = \frac{m_C}{\lambda_{RC}(e_{RC} - m_C h_{RC})}$$

$$\bar{R}_2 = \frac{m_P}{\lambda_{RP}(e_{RP} - m_P h_{RP})}.$$

Proof: We break the proof up into two parts. In Part I, we find the equilibria of the system (1). For Part II, we use Theorem 2 to show permanence.

Part I: From the form of the equations in (1), we see that $\mathbf{F}_0 = (0, 0, 0)^T$ is a boundary equilibrium point in \mathbb{R}_+^3 . The only possible one species equilibrium is $\mathbf{F}_R = (0, 0, K)^T$. The two species equilibria involve the resource and consumer, F_{RC} , and the resource and predator, F_{RP} :

$$\mathbf{F}_{RC} = (0, \bar{C}, \bar{R}_1)^T, \quad \mathbf{F}_{RP} = (\bar{P}, 0, \bar{R}_2)^T. \quad (25)$$

The equilibrium with the resource absent is never positive and thus does not exist. Notice that boundary equilibrium \mathbf{F}_{RC} exists in \mathbb{R}_+^3 if and only if (24) holds. This is due to the fact that

$$\begin{aligned} & \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \\ & \Rightarrow e_{RC} > m_C \left(h_{RC} + \frac{1}{K\lambda_{RC}} \right) > m_C h_{RC}. \end{aligned}$$

Similarly, boundary equilibrium \mathbf{F}_{RP} exists in \mathbb{R}_+^3 if and only if (23) holds.

Part II: Let $\mathbf{x}(t) = (P(t), C(t), R(t))^T$ and

$$P(\mathbf{x}) = x_1^{p_1} x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\epsilon. \quad (26)$$

Clearly, $P(\mathbf{x}) = 0$ for $\mathbf{x} \in \partial\mathbb{R}_+^3$ and $P(\mathbf{x}) > 0$ for $\mathbf{x} \in \text{int}(\mathbb{R}_+^3)$. Also,

$$\begin{aligned} \dot{P}(\mathbf{x}) &= p_1 x_1^{p_1-1} \dot{x}_1 (x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\epsilon) \\ &+ x_1^{p_1} (p_2 x_2^{p_2-1} \dot{x}_2 x_3^{p_3} (x_1 + x_2)^\epsilon \\ &+ x_2^{p_2} (p_3 x_3^{p_3-1} \dot{x}_3 (x_1 + x_2)^\epsilon \\ &+ x_3^{p_3} \epsilon (x_1 + x_2)^{\epsilon-1} (\dot{x}_1 + \dot{x}_2)) \\ &= P(\mathbf{x})\Psi(\mathbf{x}) \end{aligned}$$

where

$$\Psi(\mathbf{x}) = \sum_{i=1}^3 p_i f_i(\mathbf{x}) + \epsilon(x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})) / (x_1 + x_2)$$

in $\text{int}(\mathbb{R}_+^3)$. However, the last term in Ψ does not admit a continuous extension to the x_3 -axis. To correct

this, we take the lower semicontinuous extension and the last term in (4) becomes

$$\Psi(0, 0, x_3) = \epsilon \min(f_1(0, 0, x_3), f_2(0, 0, x_3)).$$

By (H2), condition (15) reduces to

$$\Psi(\mathbf{x}) > 0 \tag{27}$$

for all equilibrium points in $\partial\mathbb{R}_+^3$, for a suitable choice of $\epsilon \geq 0, p_1, p_2, p_3 > 0$. For \mathbf{F}_{RC} and \mathbf{F}_{RP} , (27) becomes,

$$p_1 f_1(0, \bar{C}, \bar{R}_1) > 0 \tag{28}$$

$$p_2 f_2(\bar{P}, 0, \bar{R}_2) > 0 \tag{29}$$

respectively. But, we assumed that no boundary equilibria are saturated. Thus, we have that (28) and (29) hold for any $p_1, p_2 > 0$.

At \mathbf{F}_0 and \mathbf{F}_R , (27) yields:

$$p_1 f_1(\mathbf{0}) + p_2 f_2(\mathbf{0}) + p_3 f_3(\mathbf{0}) + \epsilon \min(f_1(\mathbf{0}), f_2(\mathbf{0})) > 0 \tag{30}$$

$$p_1 f_1(0, 0, K) + p_2 f_2(0, 0, K) + \epsilon \min(f_1(0, 0, K), f_2(0, 0, K)) > 0. \tag{31}$$

Since $r > 0$ we have that \mathbf{F}_0 is not saturated. In order for \mathbf{F}_R not to be saturated, we need either

$$f_1(0, 0, K) = \frac{e_{RP} \lambda_{RP} K}{1 + \lambda_{RP} h_{RP} K} - m_P > 0$$

or

$$f_2(0, 0, K) = \frac{e_{RC} \lambda_{RC} K}{1 + \lambda_{RC} h_{RC} K} - m_C > 0$$

or both, since $\bar{P} = \bar{C} = 0$. So in either case, we can first choose $p_1 > 0, p_2 > 0$, and $\epsilon = 0$ such that (31) holds. Since $f_3(\mathbf{0}) > 0$, then for large p_3 , (30) holds too. Hence, by Theorem 2 the system 1 is permanent. \square

5 Conclusion

In this paper we have analyzed the conditions under which our nonlinear response omnivory model is permanent, or in a realistic biological sense, the coexistence of species is ensured. In summary, permanence requires that the solutions of (1) are uniformly bounded in \mathbb{R}_+^3 , the Ω -limit set of every orbit on $\partial\mathbb{R}_+^3$ consists of equilibrium points, and no boundary equilibrium can be saturated.

The permanence of models with migration dynamics, symmetrical interactions, and additional species is still an open question. One limiting factor is that most available theory assumes that the boundary of the state space is invariant. Therefore, it would be useful to investigate these more complicated models and provide the theory to analyze the permanence of these models.

References:

- [1] Birkhoff, G. and Rota, G.C., *Ordinary Differential Equations*, John Wiley & Sons, New York, 1989.
- [2] Gotelli, N.J., *A Primer of Ecology*, Sinauer Associates, Sunderland, MA., 2001.
- [3] Hale, J., *Ordinary Differential Equations*, Wiley-Interscience, New York, 1969.
- [4] Hofbauer, J., A General Cooperation Theorem for Hypercycles, *Monatshefte für Mathematik*, 91 (1981), pp. 233-240.
- [5] Hofbauer, J. and Sigmund, K., *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, 1998.
- [6] Holt, R.D. and G.A. Polis, A Theoretical Framework for Intraguild Predation, *The American Naturalist*, 149, 1997, pp. 745-764.
- [7] Hsieh, P. and Sibuya, Y., *Basic Theory of Ordinary Differential Equations*, Springer, New York, 1999.
- [8] Hsu, S.B., On Global Stability of a Predator-Prey System, *Mathematical Biosciences*, 39 (1978), pp. 1-10.
- [9] Hutson, V., A Theorem on Average Liapunov Functions, *Monatshefte für Mathematik*, 149, 1984, pp. 267-275.
- [10] Jordon, D.W. and Smith, P., *Nonlinear Ordinary Differential Equations*, Oxford Applied Mathematics and Computing Science Series, Clarendon Press, Oxford, 1987.
- [11] Křivan, V. and S. Diehl, Adaptive Omnivory and Species Coexistence in Tri-Trophic Food Webs, *Theoretical Population Biology*, 67, 2005, pp. 85-99.
- [12] Polis, G.A., Complex Trophic Interactions in Deserts: An Empirical Assessment of Food Web Theory, *The American Naturalist*, 138 (1989), pp. 123-155.
- [13] Polis, G.A. and R.D. Holt, Intraguild Predation: The Dynamics of Complex Trophic Interactions, *Trends in Ecology and Evolution*, 7, 1992, pp. 151-154.
- [14] Polis, G.A., C.A. Myers, and R.D. Holt, The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other, *Annual Review of Ecology and Systematics*, 20, 1989, pp. 297-330.
- [15] Vance, J.A., Permanent Coexistence for a Linear Response Omnivory Model, *Proceedings of the 18th IASTED International Conference on Modelling and Simulation*, 2007, pp. 642-647.
- [16] Walter, W., *Ordinary Differential Equations*, Springer-Verlag, New York, 1998.