

PERMANENT COEXISTENCE FOR A LINEAR RESPONSE OMNIVORY MODEL

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ABSTRACT

In mathematical ecology, the question of long-term survival for each species in a set of populations is very important. This paper focuses on populations that interact in a mixture of competition and predation known as omnivory. Omnivory is defined as the consumption of resources from more than one trophic level. Simple mathematical models have been developed for systems with omnivory. However, equilibrium analysis on these models shows that species extinction is likely. In this work, we investigate a differential equation model with linear responses and show under certain parameter restrictions that the model is permanent or permanently coexistent.

KEY WORDS

Permanent Coexistence, Permanence, Omnivory, Intraguild Predation

1 Introduction

The community interactions of predation and competition have a rich history of research and analysis. However, the unique combination of predation and competition known as omnivory has a relatively recent history of mathematical and biological study. Holt et al. [1] when discussing intraguild predation (IGP), a subset of omnivory, state that “there is growing evidence for the importance of IGP in many natural communities, yet little formal ecological theory addresses this particular blend of interactions”. We use a growing body of mathematical theory known as permanence theory which is concerned with the dynamics of the model near the boundary where densities are zero and hence, species go extinct. Our analysis is based upon the notion of an Average Lyapunov function. Our differential equation model depends upon model parameters that are estimated from ecological systems. Our results based on permanence theory place restrictions on the parameters.

2 Omnivory Model

Ecological interactions involving omnivory can be very complicated (see [2]). The simplest example of om-

nivory is intraguild predation. IGP 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 [3], [2] (also see Figure 1a). The search for robust mechanisms that can explain permanence of tightly linked omnivory systems remains an important challenge [4].

We focus our attention on the asymmetric classification of omnivory (IGP) as given by Polis et al. [2] as opposed to the symmetric classification (see Figure 1b) of omnivory.

Asymmetric omnivory is a community interaction that involves a predator feeding on a consumer (intermediate predator, [1]) and a basal resource. The consumer feeds solely on the basal resource. Holt et al. [1] developed a conceptual framework to analyze the population and community level implications of asymmetric IGP under Lotka-Volterra dynamics. The model,

$$\begin{aligned}\frac{dP}{dt} &= P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P] \\ \frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C] \\ \frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P],\end{aligned}\tag{1}$$

is a standard Lotka-Volterra model for a food chain with IGP added (see [1]). The parameters e_{RP} and e_{RC} are the efficiency rates at which resources are converted to new offspring of the predator and consumer respectively. e_{CP} is the efficiency rate at which consumers are converted to new offspring of the predator. α_{RP} and α_{RC} are the capture rates of the resource by the predator and consumer respectively. α_{CP} is the capture rate of the consumer by the predator. m_P and m_C are the respective mortality rates of the predator and consumer species.

Notice that the functional and numerical responses are linear. Thus, the system is classified as a linear response omnivory model.

3 Permanent Coexistence

The idea behind permanent coexistence or permanence for dynamical systems, specifically differential equations, is to allow arbitrary asymptotic behavior of orbits as

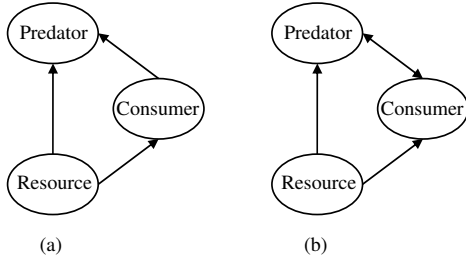


Figure 1. Two forms of ecological interactions. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) Asymmetrical intraguild predation. (b) Symmetrical intraguild predation

long as the orbits do not remain too close to the boundary. To meet this requirement, several mathematical concepts have been introduced in the literature.

Consider an ensemble of n population densities at time t given by

$$\mathbf{x}(t) = \{x_i(t)\}_{i=1}^n. \quad (2)$$

Let $D = \{\mathbf{x} : x_1, \dots, x_n \geq 0\}$, and let $\text{int}(D)$, ∂D denote the interior and boundary of D respectively. The curve $\gamma^+ = \{\mathbf{x}(t) : t \geq 0\}$ is known as an orbit.

Freedman and Waltman [5] introduced the idea of (weak) persistence, that is

$$\limsup_{t \rightarrow \infty} x_i(t) > 0 \quad (3)$$

for all i , whenever $x_i(t_0) > 0$ for some t_0 . Gard et al. [6] constructed a Lyapunov-like function to obtain weak persistence criteria for food chain models of Lotka-Volterra type. However, although weakly persistent, May and Leonard's system [7] spirals out toward the boundary in a heteroclinic cycle [8]. Weak persistence "guarantees only that extinction is not certain" [9].

Freedman and Waltman [10] formulated the notion that each orbit should be asymptotically at a non-zero distance from the boundary in order for the system to be (strongly) persistent:

$$\liminf_{t \rightarrow \infty} x_i(t) > 0 \quad (4)$$

for all i , whenever $x_i(t_0) > 0$ for some t_0 . In this case, the distance depends on the particular orbit and so is not a global criterion.

A stronger condition of permanence that avoids this difficulty is known as uniform persistence. Uniform persistence of the system means that for any positive initial condition $\mathbf{x}(t_0) = \mathbf{x}_0$ there exists a positive constant m such that

$$\liminf_{t \rightarrow \infty} x_i(t) \geq m \quad (5)$$

for all i . A dynamical system describing the evolution of $\mathbf{x}(t)$ is said to be dissipative if trajectories are uniformly

bounded in positive t . That is, there exists a constant M such that

$$\limsup_{t \rightarrow \infty} \|\mathbf{x}(t)\| \leq M. \quad (6)$$

If (5) and (6) hold, then there are numbers m, M with $0 < m \leq M < \infty$ such that given any initial condition in D there is a $T = T(\mathbf{x})$ such that

$$m \leq x_i(t) \leq M \quad (t > T, i = 1, \dots, n). \quad (7)$$

If this condition holds, then the system is known as permanently coexistent or permanent. Hutson et al. [8] use the term permanently coexistent, but Hofbauer and Sigmund [11] use the term permanent.

We say that a real-valued function $P \in C^1(D)$ is a Lyapunov function if it satisfies the relations

$$\begin{aligned} P(\mathbf{x}) &= 0 \quad \text{for } \mathbf{x} \in \partial D, \\ P(\mathbf{x}) &> 0 \quad \text{for } \mathbf{x} \in \text{int}(D), \\ \text{and } \dot{P}(\mathbf{x}) &> 0 \quad \text{for } \mathbf{x} \in D. \end{aligned}$$

Here $\dot{P}(\mathbf{x})$ is defined as $\dot{P}(\mathbf{x}) := P(\mathbf{x})\Psi(\mathbf{x})$ where Ψ is a continuous function on D . $\dot{P}(\mathbf{x})$ is called the derivative of P along trajectories.

Since we want the boundary to repel orbits, it is enough to require that $\dot{P}(\mathbf{x}) > 0$ close to the boundary. Notice that for $\dot{P}(\mathbf{x}) = P(\mathbf{x})\Psi(\mathbf{x}) > 0$ near the boundary, it is enough to show that $\Psi > 0$ at all points on the boundary since Ψ is a continuous function. However, it may be difficult to check all points in the boundary to see if they satisfy $\Psi > 0$. A weaker version in which the time average behaves as a Lyapunov function can be used in some circumstance to overcome this drawback.

We say that a real-valued function $P \in C^1(D)$ is an Average Lyapunov function [11] if it satisfies the following properties:

1) We have

$$\begin{aligned} P(\mathbf{x}) &= 0 \quad \text{for } \mathbf{x} \in \partial D \\ \text{and } P(\mathbf{x}) &> 0 \quad \text{for } \mathbf{x} \in \text{int}(D) \end{aligned}$$

and

2) there exists a continuous function Ψ on D such that the following two conditions hold:

i) We have

$$\Psi(\mathbf{x}) = \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} \quad \text{for } \mathbf{x} \in \text{int}(D) \quad (8)$$

and

ii) for $\mathbf{x} \in \partial D$,

$$\int_0^T \Psi(\mathbf{x}(t)) dt > 0 \quad \text{for some } T > 0. \quad (9)$$

3.1 Kolmogorov Type Models

Our omnivory model falls under the category of a model of Kolmogorov type. The general n -species Kolmogorov type model has the form

$$\frac{dx_i}{dt} = x_i f_i(x), \quad 1 \leq i \leq n, \quad (10)$$

where $\mathbf{x} = \{x_i\}$. We assume the per capita net growth rates f_i , $i = 1, \dots, n$ are such that they guarantee a unique solution. We define the non-negative cone in \mathbb{R}^n as

$$\mathbb{R}_+^n = \{\mathbf{x} \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}. \quad (11)$$

We define each bounding hypersurface as

$$H_i = \{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0\} \quad 1 \leq i \leq n. \quad (12)$$

A region R is invariant for (10) if $\mathbf{x}_0 \in R$ and $\mathbf{x}(t)$ is the solution of (10) with $\mathbf{x}(t_0) = \mathbf{x}_0$, then $\mathbf{x}(t) \in R$ for all $t > t_0$.

Lemma 1 For $n = 3$, the bounding hypersurfaces H_i , $1 \leq i \leq 3$ are invariant for (10).

3.2 Solution to System

In order to investigate the long-term survival of the resource, consumer, and predator species we need to ensure that in fact a unique solution to our differential equation model exists for all non-negative time.

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

3.3 Lotka-Volterra Dynamics

To make our analysis simpler, we redefine the third vector component, $R(t)$, in the following way:

$$\bar{R}(t) = \frac{R(t)}{K}. \quad (13)$$

Then, we take

$$(x_1(t), x_2(t), x_3(t))^T = (P(t), C(t), \bar{R}(t))^T$$

to form the classical Lotka-Volterra equations for three populations,

$$\dot{x}_i(t) = x_i(t) f_i(\mathbf{x}(t)) = x_i(t) \left(r_i + \sum_{j=1}^3 a_{ij} x_j(t) \right)$$

for $i = 1, 2, 3$ where $r_1 = -m_P$, $r_2 = -m_C$, and $r_3 = r$. We define the interaction matrix to be

$$A = (a_{ij}) = \begin{pmatrix} 0 & e_{CP}\alpha_{CP} & e_{RP}\alpha_{RP} \\ -\alpha_{CP} & 0 & e_{RC}\alpha_{RC} \\ -\alpha_{RP} & -\alpha_{RC} & -1 \end{pmatrix}. \quad (14)$$

In order to use available theory from Hofbauer et al. [11], we need the following definitions. We define the replicator equation as

$$\dot{x}_i = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x})$$

defined on the simplex

$$S_n = \{\mathbf{x} = (x_1, \dots, x_n)^T \in \mathbb{R}^n : x_i \geq 0 \text{ and } \sum_{i=1}^n x_i = 1\}$$

where

$$(A\mathbf{x})_i = \sum_{j=1}^n a_{ij} x_j. \quad (15)$$

We say that an equilibrium point $\bar{\mathbf{x}}$ is saturated if

$$f_i(\bar{\mathbf{x}}) \leq 0 \text{ for all } i \text{ with } \bar{x}_i = 0. \quad (16)$$

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 [11].

We use the following theorem from Hofbauer et al. [11] to show that the replicator equation in n variables is equivalent to the Lotka-Volterra equation in $n-1$ variables.

Theorem 2 There exists a differentiable, invertible map from $\hat{S}_n = \{\mathbf{x} \in S_n : x_n > 0\}$ onto \mathbb{R}_+^{n-1} mapping the orbits of the replicator equation

$$\dot{x}_i = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x}) \quad (17)$$

onto the orbits of the Lotka-Volterra equation

$$\dot{y}_i(t) = y_i(t) \left(r_i + \sum_{j=1}^3 a'_{ij} y_j(t) \right) \quad i = 1, \dots, n-1 \quad (18)$$

where $r_i = a_{in} - a_{nn}$ and $a'_{ij} = a_{ij} - a_{nj}$.

Then, we use the following two theorems on Average Lyapunov functions also from Hofbauer et al. [11] to show that a dynamical system on S_n is permanent.

Theorem 3 Consider a dynamical system on S_n that leaves the boundary invariant. Let $P : S_n \rightarrow \mathbb{R}$ be a differentiable function vanishing on ∂S_n and strictly positive in $\text{int}(S_n)$. If there exists a continuous function Ψ on S_n such that the following two conditions hold:

$$\text{for } \mathbf{x} \in \text{int}(S_n), \quad \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} = \Psi(\mathbf{x}) \quad (19)$$

and

$$\text{for } \mathbf{x} \in \partial(S_n), \quad \int_0^T \Psi(\mathbf{x}(t)) dt > 0 \text{ for some } T > 0, \quad (20)$$

then the dynamical system is permanent.

Theorem 4 It is sufficient to verify (20) for all $\mathbf{x} \in \Omega(\partial S_n)$, the Ω -limit set of orbits on the boundary of S_n .

From the preceding three theorems, we can now state a theorem on Average Lyapunov functions for a Lotka-Volterra equation on \mathbb{R}_+^n . An extended version for autonomous differential equations is given by Hutson [12].

Theorem 5 Consider a Lotka-Volterra equation with uniformly bounded orbits on \mathbb{R}_+^n that leaves the boundary invariant. Let $P : \mathbb{R}_+^n \rightarrow \mathbb{R}$ be a differentiable function vanishing on $\partial\mathbb{R}_+^n$ and strictly positive in $\text{int}(\mathbb{R}_+^n)$. If there

exists a continuous function Ψ on \mathbb{R}_+^n such that the following two conditions hold:

$$\text{for } \mathbf{x} \in \text{int}(\mathbb{R}_+^n), \quad \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} = \Psi(\mathbf{x}) \quad (21)$$

and

$$\text{for } \mathbf{x} \in \Omega(\partial\mathbb{R}_+^n), \quad \int_0^T \Psi(\mathbf{x}(t)) dt > 0 \text{ for some } T > 0, \quad (22)$$

then the Lotka-Volterra equation is permanent.

We now present a theorem that provides a sufficient condition for permanence for Lotka-Volterra systems that is a very useful strengthening of Theorem 5 on Average Lyapunov functions. A similar result for a replicator equation is given by Hofbauer et al. [11].

Theorem 6 *If there exists a $\mathbf{p} \in \text{int}(\mathbb{R}_+^n)$ such that*

$$\mathbf{p} \cdot (\mathbf{r} + A\mathbf{x}) > 0 \quad (23)$$

for all equilibrium points $\mathbf{x} \in \partial\mathbb{R}_+^n$, then the Lotka-Volterra equation with uniformly bounded orbits on \mathbb{R}_+^n that leaves the boundary invariant is permanent.

Notice that only equilibrium points on the boundary of \mathbb{R}_+^n are involved. Since the Ω -limit set on the boundary may be considerably more complicated, this is a very helpful result.

Proof. We will use Theorem 5 on Average Lyapunov functions with the function

$$P(\mathbf{x}) = \prod_{i=1}^n x_i^{p_i} \quad (24)$$

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

$$\begin{aligned} \dot{P}(\mathbf{x}) &= p_1 x_1^{p_1-1} \dot{x}_1 \left(\prod_{i=2}^n x_i^{p_i} \right) \\ &+ x_1^{p_1} \left(p_2 x_2^{p_2-1} \dot{x}_2 \left(\prod_{i=3}^n x_i^{p_i} \right) + \dots \right) \\ &= \left(\prod_{i=1}^n x_i^{p_i} \right) p_1 \left(\frac{\dot{x}_1}{x_1} \right) + \dots \\ &= P(\mathbf{x}) \cdot (\mathbf{p} \cdot (\mathbf{r} + A\mathbf{x})) = P(\mathbf{x})\Psi(\mathbf{x}) \end{aligned}$$

where

$$\Psi(\mathbf{x}) = \mathbf{p} \cdot (\mathbf{r} + A\mathbf{x}). \quad (25)$$

Next, we must show that for every $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$ there is a $T > 0$ such that

$$\int_0^T \Psi(\mathbf{y}(t)) dt > 0. \quad (26)$$

We use proof by math induction on the number k of positive components of \mathbf{y} . For $k = 1$, \mathbf{y} has only one positive component and thus, lies on one of the positive axes of

\mathbb{R}_+^n . Since each axis is invariant, the form of the equations requires that the Ω -limit set of orbits on each axis contains only the equilibrium points on that axis. Then, (26) is an immediate consequence of our assumption (23).

We proceed with math induction by assuming that (26) is valid for $k = 2, \dots, m-1$. Define the index set

$$I = \{i : 1 \leq i \leq n \text{ and } y_i > 0\} \quad (27)$$

with cardinality m . Notice that I is a proper subset of $\{1, \dots, n\}$. Also, define

$$H(I) = \{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0 \text{ for all } i \notin I\} \quad (28)$$

a subset of \mathbb{R}_+^n .

Now we must distinguish two cases:

- 1) $\mathbf{y}(t)$ converges to the boundary of the hypersurface $H(I)$ or
- 2) $\mathbf{y}(t)$ does not converge to the boundary of the hypersurface $H(I)$.

For case 1), since $\mathbf{y}(t)$ converges to the boundary of the hypersurface $H(I)$, the $\Omega(\mathbf{y})$ is contained in a union of hypersurfaces of dimension $m-1$. Thus, by the inductive assumption, (26) holds for all $\mathbf{z} \in \Omega(\mathbf{y})$.

For case 2), since $\mathbf{y}(t)$ does not converge to the boundary of the hypersurface $H(I)$, there exists an $\epsilon > 0$ and a sequence $T_s \rightarrow +\infty$ such that

$$y_i(T_s) > \epsilon \text{ for all } i \in I \text{ and } s = 1, 2, \dots \quad (29)$$

Now, we define a sequence of T ,

$$\bar{y}_i(T) = \frac{1}{T} \int_0^T y_i(t) dt.$$

Since the orbits of our states are uniformly bounded, the sequence $\bar{y}_i(T_s)$ is bounded. So, we may obtain a subsequence, which we will again denote by T_s , such that $\bar{y}_i(T_s)$ converges. We will denote the limit by \bar{x}_i .

For $i \in I$, using (29), we have

$$\frac{d}{dt}(\log y_i(t)) = \frac{\dot{y}_i(t)}{y_i(t)} = r_i + (A\mathbf{y})_i.$$

Integrating from 0 to T_s and dividing by T_s , we obtain

$$\begin{aligned} \frac{1}{T_s} \int_0^{T_s} \frac{d}{dt}(\log y_i(t)) dt &= \frac{1}{T_s} \int_0^{T_s} r_i + (A\mathbf{y}(t))_i dt \\ &= \frac{1}{T_s} (r_i T_s - 0) \\ &+ \frac{1}{T_s} \int_0^{T_s} \sum_{j=1}^n a_{ij} y_j(t) dt \\ &= r_i + \sum_{j=1}^n a_{ij} \frac{1}{T_s} \int_0^{T_s} y_j(t) dt \\ &= r_i + \sum_{j=1}^n a_{ij} \bar{y}_j(T_s) \\ &= r_i + (A\bar{\mathbf{y}}(T_s))_i. \end{aligned}$$

Thus,

$$\frac{1}{T_s}((\log y_i(T_s) - \log y_i(0)) = r_i + (A\bar{y}(T_s))_i. \quad (30)$$

Since $\log y_i(T_s)$ is bounded, the left hand side converges to zero. Hence,

$$r_i + (A\bar{x}(T_s))_i = 0 \text{ for all } i \in I. \quad (31)$$

Note that $\bar{x}_i \geq 0$ for all i and $\bar{x}_i = 0$ for $i \notin I$, because the boundary is invariant. Hence, $r_i + (A\bar{x}(T_s))_i = 0$ for $i \in I$ and $\bar{x}_i = 0$ for $i \notin I$. Thus, \bar{x} is an equilibrium point in $S(I)$. Now,

$$\frac{1}{T_s} \int_0^{T_s} \Psi(\mathbf{y}(t)) dt = \sum_{i=1}^n p_i \frac{1}{T_s} \int_0^{T_s} [r_i + (A\mathbf{y})_i] dt$$

converges to

$$\sum_{i=1}^n p_i [r_i + (A\bar{x})_i] = \mathbf{p} \cdot (\mathbf{r} + A\mathbf{x})$$

which is positive by our assumption (23). Thus, we have proved (26) holds for all $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$ with m components strictly positive. So by math induction, (26) holds for all $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$. Hence our system is permanent, completing the proof.

In order to apply the above theorems, our system must have uniformly bounded orbits. Note that if the original system (1) has uniformly bounded orbits, then the Lotka-Volterra system (14) with $K = 1$, has uniformly bounded orbits. The condition for the system (1) to have uniformly bounded orbits is given in the following theorem.

Theorem 7 *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*

$$B = \{(P, C, R) \in \mathbb{R}_+^3 : 0 \leq P + C + R \leq M\} \quad (32)$$

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

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

That is, the system (1) is dissipative with the asymptotic bound M .

Proof. Define

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

For each $\lambda > 0$ the following inequality is fulfilled when taking the time derivative along a solution:

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

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 a comparison theorem [13], 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 $t \rightarrow \infty$, $0 \leq e_{CPE_{RC}}R + e_{CP}C + P \leq M_1/\lambda$.

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

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

Hence, system (1) is dissipative with the asymptotic bound M . This completes the proof.

Now, we use Theorem 6 to determine conditions that guarantee permanence of the system (1).

Theorem 8 *If the system (1) has uniformly bounded orbits ($e_{RP} < e_{CPE_{RC}}$) and no boundary equilibrium is saturated, then the system is permanent.*

Proof. We break the proof up into three parts. In Part I, we find the equilibria of the system (1). In this part of the proof, our results do not change for any $K > 0$. For Part II, we use Theorem 6 to show permanence for the Lotka-Volterra system (14) with $K = 1$. In Part III, we extend these results to include the case for any $K > 0$.

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, \mathbf{F}_{RC} , and the resource and predator, \mathbf{F}_{RP} :

$$\begin{aligned} \mathbf{F}_{RC} &= \left(0, \frac{r}{\alpha_{RC}} \left(1 - \frac{m_C}{e_{RC}\alpha_{RC}K} \right), \frac{m_C}{e_{RC}\alpha_{RC}} \right)^T \\ \mathbf{F}_{RP} &= \left(\frac{r}{\alpha_{RP}} \left(1 - \frac{m_P}{e_{RP}\alpha_{RP}K} \right), 0, \frac{m_P}{e_{RP}\alpha_{RP}} \right)^T. \end{aligned}$$

The equilibrium with the resource absent is never positive and thus does not exist.

Part II: Note that the equilibria for the Lotka-Volterra system are the same as for the system in Part I with $K = 1$. Now we apply Theorem 6 to the Lotka-Volterra system (14). We have to find $p_1, p_2, p_3 > 0$ such that

$$\sum_{i:\bar{x}_i=0} p_i \left(r_i + \sum_{j=1}^3 a_{ij}x_j \right) > 0 \quad (33)$$

at each boundary equilibria \bar{x} .

For \mathbf{F}_{RC} , (33) becomes,

$$p_1(r_1 + a_{12}\bar{x}_2 + a_{13}\bar{x}_3) > 0. \quad (34)$$

But, we assumed that \mathbf{F}_{RC} is not saturated. Since $\bar{x}_1 = 0$, this is the condition $r_1 + a_{12}\bar{x}_2 + a_{13}\bar{x}_3 > 0$. Thus, we have that (34) holds for any $p_1 > 0$.

Similarly, for \mathbf{F}_{RP} we need that

$$p_2(r_2 + a_{11}\bar{x}_1 + a_{13}\bar{x}_3) > 0. \quad (35)$$

Since \mathbf{F}_{RC} is not saturated we have that (35) holds for any $p_2 > 0$.

At \mathbf{F}_0 and \mathbf{F}_R , (33) yields:

$$p_1 r_1 + p_2 r_2 + p_3 r_3 > 0 \quad (36)$$

$$p_1(r_1 + a_{13}\bar{x}_3) + p_2(r_2 + a_{23}\bar{x}_3) > 0. \quad (37)$$

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

$$f_1(0, 0, 1) = e_{RP}\alpha_{RP} - m_P > 0 \quad (38)$$

or

$$f_2(0, 0, 1) = e_{RC}\alpha_{RC} - m_C > 0 \quad (39)$$

or both, since $\bar{x}_1 = \bar{x}_2 = 0$. But,

$$r_1 + a_{13}\bar{x}_3 = e_{RP}\alpha_{RP} - m_P \quad (40)$$

and

$$r_2 + a_{23}\bar{x}_3 = e_{RC}\alpha_{RC} - m_C. \quad (41)$$

In either case, we can first choose p_1 and p_2 such that (37) holds. Then for large p_3 , (36) holds as well. Thus, we have found a positive solution of (33). Hence, by Theorem 6 the system (14) is permanent.

Part III: In all of the above calculations, the presence of a $K > 0$ with $K \neq 1$, does not change the existence of a positive solution of (33) under the conditions set forth in the theorem. Hence, the system 1 is permanent. This completes the proof.

4 Conclusion

In this paper we have analyzed the conditions under which our linear response omnivory model is permanent, or in a realistic biological sense, the coexistence of species is ensured. Our analysis was based on a technique of developing an Average Lyapunov function which led to the following conclusions for permanence:

- The linear response omnivory model should have uniformly bounded orbits.
- The Ω limit set of the boundary of the state space should consist of equilibrium points only.
- The missing species should be able to invade the system when the other species are present and at equilibrium.

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.

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