



# Asymptotic stability of tri-trophic food chains sharing a common resource



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## ABSTRACT

One of the key results of the food web theory states that the interior equilibrium of a tri-trophic food chain described by the Lotka–Volterra type dynamics is globally asymptotically stable whenever it exists. This article extends this result to food webs consisting of several food chains sharing a common resource. A Lyapunov function for such food webs is constructed and asymptotic stability of the interior equilibrium is proved. Numerical simulations show that as the number of food chains increases, the real part of the leading eigenvalue, while still negative, approaches zero. Thus the resilience of such food webs decreases with the number of food chains in the web.

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## 1. Introduction

Competition is one of the main driving forces reducing biodiversity in complex food webs. The “competitive exclusion principle” formulated by Gause [1] excludes coexistence of two species that compete for a single resource. Levin [2] proved that  $n$  competing species cannot coexist at a population equilibrium if they are limited by less than  $n$  limiting factors. As species are often limited by a few nutrients (e.g., phosphorus and/or nitrogen in lakes) how is it then possible that many species do survive [3]? Several mechanisms explaining species coexistence were proposed. These include, but are not limited to non-equilibrium dynamics due to environmental [3] or internal [4] fluctuations in population dynamics, relative nonlinearity in species responses to competition [5,6], predation on competing species [7,8], or adaptive foraging [9,10]. These mechanisms fit into two broad categories [5]: (i) stabilizing mechanisms that tend to increase negative intraspecific interactions relative to interspecific interactions (density dependent mechanisms, e.g., the logistic population growth) and (ii) equalizing mechanisms that tend to decrease average fitness differences between species. These latter mechanisms are often expressed through changes in evolutionary/behavioral traits.

The interplay of these two mechanisms on stability and persistence in di- and tri-trophic food webs were studied in [11]. That study was motivated by “the paradox of phytoplankton” where in lakes a large number of phytoplankton species survives on just one or two common resources (e.g., phosphorus) [3]. One of the food web modules considered assumed that each of the phytoplankton species was regulated by a specialized predator (e.g., a zooplankton species) (Fig. 1). Thus the  $n$  consumer species were competing for a single resource, but as each of them was consumed by a specialized predator, there were  $n + 1$  limiting factors so that the exclusion principle did not apply. Indeed, numerical simulations confirmed that all species could coexist. Such a food web is a generalization of a single tri-trophic food chain studied intensively in ecology [12,13]. Using a Lyapunov function, Harrison [14] proved that the interior equilibrium of the tri-trophic food chain is globally asymptotically stable whenever it exists. However, numerical simulations show that as the number of food chains sharing a common resource increases the stabilizing effect of the negative resource density dependence (modeled by the logistic resource growth) dilutes and numerical simulations are inconclusive with respect to the asymptotic stability of the interior equilibrium (more details are given in Section 3).

In this article we extend the result on the asymptotic equilibrium stability for a single tri-trophic food chain to many food chains sharing a common resource. Using a Lotka–Volterra type Lyapunov function we show that the resource density converges to an equilibrium and on the attractor each food chain dynamics are described by a Lotka–Volterra predator–prey model. However, these Lotka–Volterra

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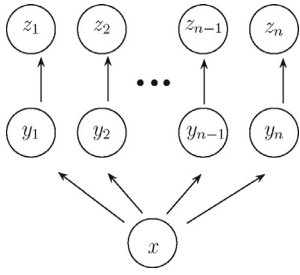


Fig. 1. Food web with  $n$  tri-trophic chains sharing a common resource.

predator-prey models are not independent as their trajectories satisfy a constraint. Using this information we prove in Section 2.1 that for two food chains sharing a common resource the population equilibrium is globally asymptotically stable. We extend this result in Section 2.2 where we prove that the population equilibrium is locally asymptotically stable for any number of food chains.

2. Model

We consider a tri-trophic food-web consisting of a common resource  $(x)$ ,  $n$  consumers  $(y_1, \dots, y_n)$  and top specialist predators  $(z_1, \dots, z_n)$  illustrated in Fig. 1. Such a food web topology can describe e.g., a single plant species with several aphid species each of them parasitized by a specialized parasitoid [15]. The Lotka–Volterra conceptualization of population dynamics in such a food web is

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \sum_{i=1}^n \lambda_i y_i x \\ \frac{dy_i}{dt} &= y_i (e_i \lambda_i x - m_i - \Lambda_i z_i) \quad i = 1, \dots, n \\ \frac{dz_i}{dt} &= z_i (E_i \Lambda_i y_i - M_i) \quad i = 1, \dots, n, \end{aligned} \tag{1}$$

where  $r$  is the resource specific growth rate,  $K$  is the resource environmental capacity,  $\lambda_i$  ( $\Lambda_i$ ) is the consumer (predator) search rate for resource (consumer)  $i$ ,  $e_i$  ( $E_i$ ) is the efficiency rate with which the resources (consumers) are converted to new consumers (predators), and  $m_i$  ( $M_i$ ) is the consumer (predator) mortality rate [11]. In what follows we assume that all these parameters are positive and we consider only solutions of (1) that are non-negative (i.e., all initial conditions are positive). The interior equilibrium of (1) is

$$\begin{aligned} x^* &= K \left(1 - \frac{1}{r} \sum_{i=1}^n \frac{\lambda_i M_i}{E_i \Lambda_i}\right) \\ y_i^* &= \frac{M_i}{E_i \Lambda_i} \quad i = 1, \dots, n \\ z_i^* &= \frac{e_i \lambda_i x^* - m_i}{\Lambda_i} \quad i = 1, \dots, n. \end{aligned} \tag{2}$$

This equilibrium is positive provided the intrinsic per capita resource population growth rate is high enough so that

$$r > \sum_{i=1}^n \frac{\lambda_i M_i}{E_i \Lambda_i} \tag{3}$$

and the resource environmental carrying capacity satisfies

$$K \left(1 - \frac{1}{r} \sum_{i=1}^n \frac{\lambda_i M_i}{E_i \Lambda_i}\right) > \frac{m_i}{e_i \lambda_i}, \quad i = 1, \dots, n. \tag{4}$$

In what follows we will assume the above two inequalities hold and we study stability of equilibrium (2).

First we observe that the resource density  $x(t)$  converges to the equilibrium  $x^*$ .

**Proposition 1.** Positive solutions of (1) are bounded and component  $x(t)$  of every solution converges to the equilibrium  $x^*$ .

**Proof.** Let

$$\begin{aligned} V &= x - x^* - x^* \ln \frac{x}{x^*} + \sum_{i=1}^n \frac{1}{e_i} \left( y_i - y_i^* - y_i^* \ln \frac{y_i}{y_i^*} \right) \\ &\quad + \sum_{i=1}^n \frac{1}{e_i E_i} \left( z_i - z_i^* - z_i^* \ln \frac{z_i}{z_i^*} \right). \end{aligned}$$

Then  $V(x^*, y_1^*, \dots, y_n^*, z_1^*, \dots, z_n^*) = 0$ ,  $V$  is non-negative and

$$\frac{dV}{dt} = -\frac{r}{K} (x - x^*)^2 \tag{5}$$

along trajectories of model (1). Thus  $V$  is a Lyapunov function and all trajectories of model (1) are bounded.

Let us consider a non-trivial solution of (1) and let us assume that  $x(t)$  does not converge to  $x^*$ . There exists a sequence of times  $t_s \rightarrow \infty$  and  $\delta_1 > 0$  so that  $|x(t_s) - x^*| > \delta_1$ . Because the trajectory is bounded, its derivative is bounded as well and there exists  $\delta_2 > 0$  such that  $|x(t) - x^*| > \delta_1/2$  for  $t \in (t_s - \delta_2, t_s + \delta_2)$  and all  $t_s$ . Thus, (5) implies that  $V$  cannot be non-negative for all  $t$ 's, a contradiction with non-negativity of  $V$ .  $\square$

Second, let us consider an  $\omega$ -limit solution  $(x^\omega(t), y^\omega(t), z^\omega(t))$  of (1). It follows from Proposition 1 that  $x^\omega(t) = x^*$  for every  $t \in \mathbb{R}$  and therefore from (1)

$$\sum_{i=1}^n \lambda_i y_i^\omega(t) = r \left(1 - \frac{x^*}{K}\right). \tag{6}$$

Moreover, the  $\omega$ -limit solution satisfies the following Lotka–Volterra system of paired equations

$$\begin{aligned} \frac{dy_i^\omega}{dt} &= y_i^\omega (e_i \lambda_i x^* - m_i - \Lambda_i z_i^\omega) \quad i = 1, \dots, n \\ \frac{dz_i^\omega}{dt} &= z_i^\omega (E_i \Lambda_i y_i^\omega - M_i) \quad i = 1, \dots, n. \end{aligned} \tag{7}$$

These equations are pairs of the Lotka–Volterra predator-prey equations so that on the attractor we have the following Lyapunov functions

$$\begin{aligned} V_i &= \frac{1}{e_i} \left( y_i^\omega - y_i^* - y_i^* \ln \frac{y_i^\omega}{y_i^*} \right) \\ &\quad + \frac{1}{e_i E_i} \left( z_i^\omega - z_i^* - z_i^* \ln \frac{z_i^\omega}{z_i^*} \right), \quad i = 1, \dots, n. \end{aligned} \tag{8}$$

We want to prove that the only  $\omega$ -limit solution of system (7) that satisfies (6) is the constant solution coinciding with equilibrium (2). The case of a single food chain ( $n = 1$ ) was studied in [14] so we begin with the case  $n = 2$ .

2.1. The case of two competing food chains.

We start with a system consisting of two food chains with a common limiting resource  $(x)$

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