



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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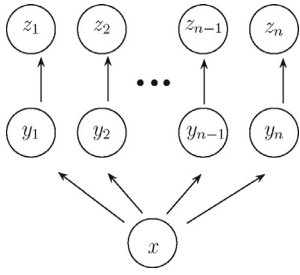


Fig. 1. Food web with n tri-trophic chains sharing a common resource.

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, λ_i (Λ_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 ω -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 ω -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 ω -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)

$$\begin{aligned}
 \frac{dx}{dt} &= rx\left(1 - \frac{x}{K}\right) - \lambda_1 y_1 x - \lambda_2 y_2 x \\
 \frac{dy_1}{dt} &= y_1(e_1 \lambda_1 x - m_1 - \Lambda_1 z_1) \\
 \frac{dy_2}{dt} &= y_2(e_2 \lambda_2 x - m_2 - \Lambda_2 z_2) \\
 \frac{dz_1}{dt} &= z_1(E_1 \Lambda_1 y_1 - M_1) \\
 \frac{dz_2}{dt} &= z_2(E_2 \Lambda_2 y_2 - M_2).
 \end{aligned}
 \tag{9}$$

All parameters in (9) are assumed to be positive and conditions (3) and (4) imply that the interior equilibrium (2) exists.

Theorem 1. *The interior equilibrium (2) (with $n = 2$) of (9) is globally asymptotically stable.*

Proof. We prove that the only ω -limit solution $(x^\omega(t), y_1^\omega(t), y_2^\omega(t), z_1^\omega(t), z_2^\omega(t))$ of trajectories starting from an interior point of $\mathbb{R}_+^5 = \{(x_1, \dots, x_5) | x_1 > 0, \dots, x_5 > 0\}$ is the interior equilibrium. The ω -limit solution must satisfy (6),

$$\lambda_1 y_1^\omega(t) + \lambda_2 y_2^\omega(t) = c := r\left(1 - \frac{x^*}{K}\right) \quad \text{for all } t \in \mathbb{R}. \tag{10}$$

Differentiating this equality and substituting, we get

$$\begin{aligned}
 \lambda_1 y_1^\omega(t)(e_1 \lambda_1 x^* - m_1 - \Lambda_1 z_1^\omega(t)) \\
 + \lambda_2 y_2^\omega(t)(e_2 \lambda_2 x^* - m_2 - \Lambda_2 z_2^\omega(t)) = 0.
 \end{aligned}
 \tag{11}$$

Due to (7) we also know that the limit solution is periodic. Let $\{t_n\}_{n=1}^\infty$ be a sequence of times such that $z_2^\omega(t_n) = z_2^*$. Then (11) implies that $z_1^\omega(t_n) = z_1^*$. We remark that $y_i^\omega(t_n) \neq y_i^*$, $i = 1, 2$.

For t 's close to but different from t_n , $z_2^\omega(t) \neq z_2^*$. In what follows we will show that $y_1^\omega(t_n)$ is independent of t_n , i.e., constant and equal to the equilibrium point. From (11) we get

$$\frac{\lambda_2 y_2^\omega(t)}{\lambda_1 y_1^\omega(t)} = -\frac{e_1 \lambda_1 x^* - m_1 - \Lambda_1 z_1^\omega(t)}{e_2 \lambda_2 x^* - m_2 - \Lambda_2 z_2^\omega(t)}$$

for t 's close to but different from t_n for all n . Using L'Hospital's rule we get

$$\frac{\lambda_2 y_2^\omega(t_n)}{\lambda_1 y_1^\omega(t_n)} = -\lim_{t \rightarrow t_n} \frac{e_1 \lambda_1 x^* - m_1 - \Lambda_1 z_1^\omega(t)}{e_2 \lambda_2 x^* - m_2 - \Lambda_2 z_2^\omega(t)} = \frac{\Lambda_1 (z_1^\omega)'(t_n)}{\Lambda_2 (z_2^\omega)'(t_n)}.$$

Substituting derivatives of z_i^ω from (7) gives

$$\frac{\lambda_2 y_2^\omega(t_n)}{\lambda_1 y_1^\omega(t_n)} = -\frac{\Lambda_1 z_1^\omega(t_n)(E_1 \Lambda_1 y_1^\omega(t_n) - M_1)}{\Lambda_2 z_2^\omega(t_n)(E_2 \Lambda_2 y_2^\omega(t_n) - M_2)}.$$

Substituting $y_2^\omega(t) = (c - \lambda_1 y_1^\omega(t))/\lambda_2$, $c = \frac{\lambda_1 M_1}{E_1 \Lambda_1} + \frac{\lambda_2 M_2}{E_2 \Lambda_2}$ and solving the resulting quadratic equation for unknown $y_1^\omega(t_n)$ we obtain two solutions: $y_1^\omega(t_n) = y_1^*$ and

$$y_1^\omega(t_n) = \frac{\Lambda_2 z_2^*(E_1 M_2 \Lambda_1 \lambda_2 + E_2 M_1 \Lambda_2 \lambda_1)}{E_1 \Lambda_1 (E_1 \Lambda_1^2 \lambda_2 z_1^* + E_2 \lambda_1 \Lambda_2^2 z_2^*)}. \tag{12}$$

Solution $y_1^\omega(t_n) = y_1^*$ corresponds to the equilibrium point (y_1^*, z_1^*) . Equality (10) implies that $y_2^\omega(t_n) = y_2^*$ for all t_n . Thus, the corresponding ω -limit solution is the equilibrium.

There is no ω -limit solution corresponding to the other solution (12). Indeed, any non-constant periodic solution must attain two different values $y_1^\omega(t_n)$ and $y_1^\omega(t_{n+1})$ (one which is larger and one which is smaller than y_1^*). However, we obtained only one such solution (12). \square

2.2. The case of several competing food chains.

In this section we prove local asymptotic stability of equilibrium (2) for any number of food chains. We use the following lemmas.

Lemma 1. *There exists a constant $\mathcal{K} > 0$ such that*

$$\max_{i=1, \dots, n} \{y_i^\omega(t), z_i^\omega(t)\} \leq \mathcal{K}, \quad t \in \mathbb{R}$$

for every ω -limit solution $(y^\omega, z^\omega) \in \mathbb{R}^{2n}$ of (1).

Proof. Every ω -limit solution $(y^\omega(t), z^\omega(t)) \in \mathbb{R}^{2n}$ of (1) is periodic and satisfies equality (6). As we consider only non-negative solutions, it follows from (6) that y -coordinates of the solution are bounded, i.e., $y_i^\omega(t) < \mathcal{K}_1$ for all $i = 1, \dots, n$ and all $t \in \mathbb{R}$. Now we prove that z -coordinates are bounded too.

For every food chain ($i = 1, \dots, n$) there exists a sequence of times $t_{i,k} \rightarrow \infty$ such that $z_i^\omega(t_{i,k}) = z_i^*$. Thus, from (8) it follows that for all $t_{i,k}$

$$V_i(t_{i,k}) = \frac{1}{e_i} \left(y_i^\omega(t_{i,k}) - y_i^* - y_i^* \ln \frac{y_i^\omega(t_{i,k})}{y_i^*} \right), \quad i = 1, \dots, n. \tag{13}$$

As we already know that $y_i^\omega(t)$ are bounded and $V_i \geq 0$ is constant along $(y_i^\omega(t), z_i^\omega(t))$ we get that $z_i^\omega(t)$, $i = 1, \dots, n$ are bounded too. This concludes the proof. \square

The next result follows from the existence of the Lyapunov function V_i defined by (8).

Lemma 2. *There exists a function $\eta(\epsilon)$ defined for $\epsilon > 0$, $\lim_{\epsilon \rightarrow 0} \eta(\epsilon) = 0$, $\lim_{\epsilon \rightarrow \infty} \eta(\epsilon) = \infty$ such that if ω -limit solution $(y_i^\omega(t), z_i^\omega(t))$ satisfies*

$$\max_{i=1, \dots, n} \sqrt{(y_i(t_0) - y_i^*)^2 + (z_i(t_0) - z_i^*)^2} < \epsilon$$

for some $t_0 \in \mathbb{R}$ then

$$\sup_{t \in \mathbb{R}} \max_{i=1, \dots, n} \sqrt{(y_i^\omega(t) - y_i^*)^2 + (z_i^\omega(t) - z_i^*)^2} < \eta(\epsilon).$$

The next lemma is a crucial part of the proof of local asymptotic stability of (2). We prove that in a small neighborhood of the equilibrium the only ω -limit solution of model (1) is the equilibrium solution. The proof is by induction with respect to the number of food chains. In what follows we set

$$a_i = e_i \lambda_i x^* - m_i, \quad b_i = \Lambda_i, \quad c_i = E_i \Lambda_i, \quad d_i = M_i, \quad \omega_i = \sqrt{a_i d_i}. \tag{14}$$

We remark that $2\pi/\omega_i$ is the approximate period of small oscillations in the Lotka–Volterra predator–prey model at the equilibrium [16].

Lemma 3. *Let $\omega_i \neq \omega_j$ for $i \neq j$, $i, j = 1, \dots, n$. Then there exists $\epsilon > 0$ so that the only ω -limit solution of model (1) satisfying*

$$\min_{i=1, \dots, n} \inf_{t \in \mathbb{R}} \sqrt{(y_i^\omega(t) - y_i^*)^2 + (z_i^\omega(t) - z_i^*)^2} < \epsilon$$

is the equilibrium solution $(x^*, y^*, z^*) \in \mathbb{R}^{2n+1}$ given by (2).

Proof. The proof is by induction with respect to the number of food chains n .

For $n = 1$ it follows from (6) that any ω -limit solution $y_1(t)$ must be constant so the condition is met.

Let us assume that Lemma 3 holds for any system consisting of $n - 1$ food chains and it does not hold for a system consisting of n food chains. This means that there exists a sequence of ω -limit solutions $\{y^k(t), z^k(t)\} \in \mathbb{R}^{2n}$ of (7) and a non-empty set of indexes $\mathcal{I} = \{i_1, \dots, i_s\}$, $1 \leq s \leq n$ such that

$$\inf_{t \in \mathbb{R}} \sqrt{(y_{j_1}^k(t) - y_{j_1}^*)^2 + (z_{j_1}^k(t) - z_{j_1}^*)^2} < 1/k, \quad j \in \mathcal{I}.$$

For all other indexes $\mathcal{J} = \{1, \dots, n\} \setminus \mathcal{I}$ we have

$$\min_{j \in \mathcal{J}} \inf_{t \in \mathbb{R}} \sqrt{(y_{j_1}^k(t) - y_{j_1}^*)^2 + (z_{j_1}^k(t) - z_{j_1}^*)^2} > \delta$$

for some $\delta > 0$. Lemma 2 implies that for every $j \in \mathcal{J}$, $(y_j^k(t), y_j^k(t))$ are bounded and we can choose an uniformly converging subsequence whose limit is again a component of an ω -solution different from the equilibrium solution.

There are two possibilities. First, not all components of the ω -limit solution converge to the components of the equilibrium, i.e., $s < n$. In this case some components of the ω -limit solution converge to the equilibrium point which contradicts the induction assumption that for $n - 1$ food chains there are no ω -limit solutions in the neighborhood of the equilibrium that are different from the equilibrium.

Second, all components ($s = n$) of the ω -limit solutions converge to the equilibrium point, i.e., for all $k \in \mathbb{N}$

$$\min_{i=1, \dots, n} \inf_{t \in \mathbb{R}} \sqrt{(y_i^k(t) - y_i^*)^2 + (z_i^k(t) - z_i^*)^2} < 1/k. \tag{15}$$

Using (14) we write system (7) in the form

$$\begin{aligned} y_i' &= y_i(a_i - b_i z_i), \quad i = 1, \dots, n \\ z_i' &= z_i(c_i y_i - d_i), \quad i = 1, \dots, n. \end{aligned} \tag{16}$$

Let $\varepsilon^k = \sqrt{\sum_{i=1}^n (y_{0i}^k - y_i^*)^2 + (z_{0i}^k - z_i^*)^2}$ where $(y_{0i}, z_{0i}) \in \mathbb{R}^{2n}$ are initial conditions for (16) and

$$u_i^k(t) = \frac{y_i^k(t) - y_i^*}{\varepsilon^k},$$

$$v_i^k(t) = \frac{z_i^k(t) - z_i^*}{\varepsilon^k}$$

where $u_i^* = y_i^* = d_i/c_i$ and $v_i^* = z_i^* = a_i/b_i$. The transformed variables satisfy

$$\begin{aligned} (u_i^k)'(t) &= -b_i v_i^k(t) (\varepsilon^k u_i^k(t) + u_i^*), \quad i = 1, \dots, n \\ (v_i^k)'(t) &= c_i u_i^k(t) (\varepsilon^k v_i^k(t) + v_i^*), \quad i = 1, \dots, n. \end{aligned}$$

As k tends to infinity, ε^k tends to 0. Moreover since

$$u_{0i}^k = \frac{y_i^k(0) - y_i^*}{\varepsilon^k},$$

$$v_{0i}^k = \frac{z_i^k(0) - z_i^*}{\varepsilon^k},$$

$\sum_{i=1}^n (u_{0i}^k)^2 + (v_{0i}^k)^2 = 1$, and we can choose a convergent subsequence of initial conditions that converges to $(\tilde{v}_{0i}, \tilde{v}_{0i})$. The corresponding ω -limit solutions converge to the solution of the linear system

$$\begin{aligned} (u_i^k)'(t) &= -b_i v_i^k(t) u_i^*, \quad i = 1, \dots, n \\ (v_i^k)'(t) &= c_i u_i^k(t) v_i^*, \quad i = 1, \dots, n. \end{aligned}$$

We define

$$\tilde{u}_i(t) = \lim_{k \rightarrow \infty} u_i^k(t) = \tilde{u}_{0i} \cos(t\omega_i) - \tilde{v}_{0i} \frac{b_i}{c_i} \sqrt{\frac{d_i}{a_i}} \sin(t\omega_i) \tag{17}$$

and

$$\tilde{v}_i(t) = \lim_{k \rightarrow \infty} v_i^k(t) = \tilde{v}_{0i} \cos(t\omega_i) + \tilde{u}_{0i} \frac{c_i}{b_i} \sqrt{\frac{a_i}{d_i}} \sin(t\omega_i). \tag{18}$$

From (6) we get

$$\sum_{i=1}^n \lambda_i u_i^k(t) = 0$$

and

$$\sum_{i=1}^n \lambda_i \tilde{u}_i(t) = 0. \tag{19}$$

The last equality can be written as

$$\sum_{i=1}^n (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0$$

where α_i and β_i depend on the initial conditions. By double differentiation we obtain

$$-\sum_{i=1}^n \omega_i^2 (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0.$$

We add this equation with equation

$$\omega_1^2 \sum_{i=1}^n (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0$$

to get

$$\sum_{i=2}^n (\omega_1^2 - \omega_i^2) (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0.$$

Again, by double differentiation we obtain

$$-\sum_{i=2}^n \omega_i^2 (\omega_1^2 - \omega_i^2) (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0.$$

We add this equation with equation

$$\omega_2^2 \sum_{i=2}^n (\omega_1^2 - \omega_i^2) (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0,$$

to get

$$\sum_{i=3}^n (\omega_1^2 - \omega_i^2) (\omega_2^2 - \omega_i^2) (\alpha_i \cos(\omega_i t) + \beta_i \sin(\omega_i t)) = 0.$$

Repeating double derivation and summation n times we finally get

$$\prod_{i=1}^{n-1} (\omega_i^2 - \omega_n^2) (\alpha_n \cos(\omega_n t) + \beta_n \sin(\omega_n t)) = 0.$$

As the last term cannot be equal to 0 ($\omega_n = \sqrt{a_n d_n} > 0$ and considered solutions are non-trivial), we obtain a contradiction with the assumption that $\omega_i \neq \omega_j$ for $i \neq j$. It follows that the lemma holds for n too. \square

Theorem 2. Let $\omega_i \neq \omega_j$ for $i \neq j, i, j = 1, \dots, n$. Then the interior equilibrium $(x^*, y^*, z^*) \in \mathbb{R}_+^{2n+1}$ of model (1) is locally asymptotically stable.

Proof. Because (x^*, y^*, z^*) is a stable equilibrium of (1), solutions that start close to this point stay in a vicinity of this point. If there was a solution of (1) such that for some $i \in \{1, \dots, n\}$, $y_i(t), z_i(t)$ did not converge to the equilibrium point, there would exist an ω -solution in a neighborhood of the equilibrium different from the equilibrium. This contradicts Lemma 3. \square

3. Discussion

In this article we proved that species in a food web consisting of several tri-trophic food chains with a shared resource can coexist in a locally asymptotically stable interior equilibrium. In particular, when there are only two such food chains, the interior equilibrium is globally asymptotically stable. These results extend the work of Harrison [14] who proved that the interior equilibrium of a single tri-trophic food chain is globally asymptotically stable whenever it exists.

The food web with n -food chains that share a common resource was considered in [11]. It was suggested there that population dynamics converge to the interior equilibrium whenever this equilibrium exists. The problem is that numerical simulations document such convergence clearly for low dimensional systems (i.e., one, two, or three food chains) but for many food chains convergence is not that

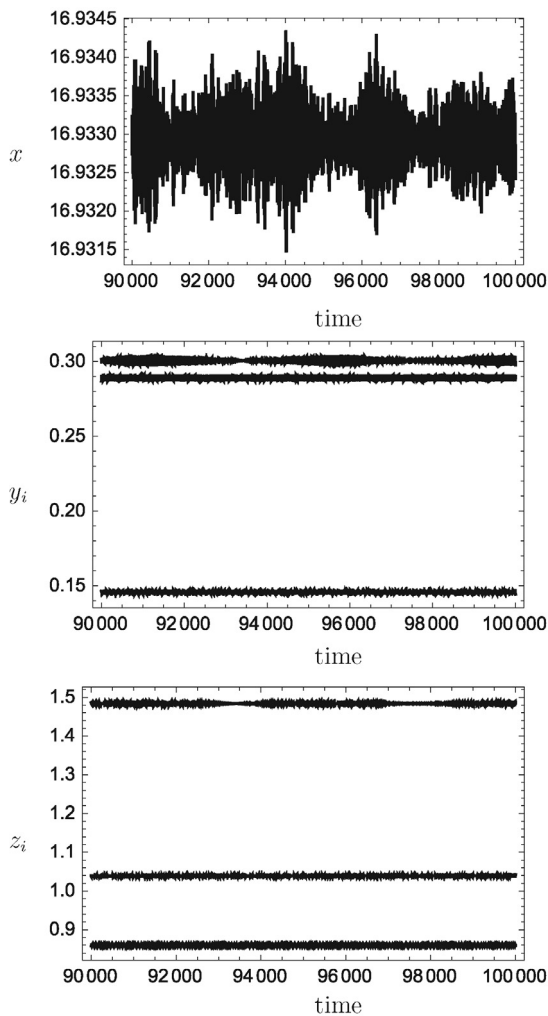


Fig. 2. This plot shows simulations of model (1) with 50 consumer and predator species ($n = 50$ in model (1)). For clarity only three trajectories for consumers and predators are shown. Simulations were done in Mathematica 10 using `NDSolve` function. Parameters of model (1) were generated at random from the normal distribution $N(\nu, \sigma)$ with mean ν and standard deviation σ : $r = N(2, 0.4)$, $\lambda = N(0.1, 0.02)$, $\Lambda = N(1, 0.2)$, $m = N(0.2, 0.04)$, $M = N(0.1, 0.02)$, $e = N(0.5, 0.1)$, $E = N(0.5, 0.1)$, $K = N(50, 10)$.

clear. For example, numerical simulations in Mathematica 10 as those in Fig. 2 show small persistent fluctuations of trajectories around the equilibrium for a food web consisting of 50 food chains. From the ecological point of view the reason is that stability of the interior equilibrium is driven by negatively density dependent resource growth (i.e., the per capita population growth rate decreases as the population density increases) modeled by the logistic equation. As the number of food chains increases, this negative density dependence “dilutes” which is manifested by increasing values of the real part of the leading eigenvalue associated with consumer and predator species (Fig. 3). Albeit these largest real parts are still negative, they are very small in absolute value for large number of food chains. Thus, the bottom up regulation of the food web gets weaker with the number of food chains and the consumer and resources are more prone to oscillations after a disturbance. This shows that ecological resilience [17], defined as the rate with which a system returns to its equilibrium after a perturbation, decreases with the number of food chains in the food web. The resilience is measured as the absolute value of the real part of the dominant eigenvalue and the inverse of resilience is often termed the return time. Our results show that the return time

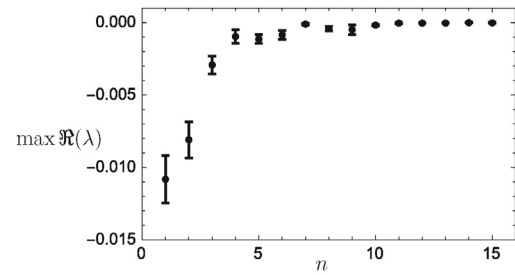


Fig. 3. Dependence of the largest real part eigenvalue of model (1) on the number of food chains n in the food web. Dots show averages of 30 simulations and bars are ± 1 standard error. Parameters of model (1) were generated at random from the normal distribution $N(\nu, \sigma)$ with mean ν and standard deviation σ same as in those used in Fig. 2.

increases with the number of food chains supported by a single resource. This shows that although mathematically stable, the real food webs consisting of several food chains sharing a common resource will be oscillating around the equilibrium.

We proved that the global asymptotic convergence to equilibrium holds for any parameter values for which the interior population equilibrium for two food chains exists. For the case of more than 2 food chains we were unable to extend this proof and we used a slightly different approach based on linearization of the original system at the interior equilibrium. This linearization led to the requirement that the parameters of the model are such that the periods of the oscillations of the linearized model are pairwise different (i.e., $\omega_i \neq \omega_j$ in Theorem 2). It is likely that the result holds even without this additional assumption and the stability is global.

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