VERTICUM-TYPE SYSTEMS APPLIED TO ECOLOGICAL MONITORING

M. Gámez[a,*], I. López[a], I. Szabó[b] and Z. Varga[c]

[a] *Departament of Statistics and Applied Mathematics, University of Almería, La Cañada de San Urbano, 04120 Almería, Spain (mgamez@ual.es, milopez@ual.es)*

[b] *Institute of Mechanics and Machinery* (Szabo.Istvan@gek.szie.hu)

[c] *Institute of Mathematics and Informatics* (*Varga.Zoltan@gek.szie.hu*)

[b, c] *Szent István University, Páter K. u. 1., H-2103 Godollo, Hungary.*

Abstract. In the paper ecological interaction chains of the type *resource – producer – primary user – secondary consumer* are considered. The dynamic behaviour of these four-level chains is modelled by a system of differential equations, the linearization of which is a verticum-type systems introduced for the study of industrial verticums. Applying the technique of such systems, for the monitoring of the considered ecological system, an observer system is constructed, which makes it possible to recover the whole state process from the partial observation of the ecological interaction chain.

Keywords: ecological chain, stable coexistence, monitoring of an ecosystem, verticum-type system, observer design

1. Introduction

Monitoring of ecosystems and management of renewable natural resources are key issues of sustainable human activity. Methodologically both problems can be naturally related to basic concepts of mathematical systems theory such as observability and controllability. The basic theory concerning these concepts was developed in [1] for *linear* systems (a more recent reference is [2]), however, even the simplest ecosystem models incorporating interacting populations are *nonlinear*. The corresponding concepts and theorems have been extended with local character to nonlinear systems in [3], but found applications to population systems only recently, see e.g. [4]-[10]. These papers either deal with the theoretical problem of observability or, if also observers are constructed, the results concern only *Lotka-Volterra-type* population systems.

* Corresponding author. Fax: +34-950015167; Phone: +34-950015667
E-mail address: mgamez@ual.es (M. Gámez)

In the present paper, observer design for *non Lotka-Volterra-type* ecosystems will be presented. The ecological model considered in this paper differs from the classical Lotka-Volterra system because of the presence of the dynamics for the resource (or nutrient).

Until now in [5], only observability results have been obtained for a trophic chain of *resource – producer – primary consumer* type. (For a general stability study of multi-level trophic chains see e.g. [11]). In our paper, on the one hand, we extend and modify this model, to deal with a four-level ecological *interaction chain* of type *resource – producer – primary user – secondary consumer*. Here the term *primary user* refers to the fact that an animal species is in commensalism with the plant, rather than consuming it. On the other hand, we not only find sufficient conditions for observability, but by the construction of an observer system, we also estimate the state process. From methodological aspect, it will be seen, that the linearization of this four-level ecological interaction chain is a verticum-type system. Systems-theoretical study of such systems was carried out in Molnár [12]-[19], Molnár and Szigeti [20].

The present paper is organized as follows. In Section 2 the dynamic model of the considered four-level ecological chain is set up and its positive equilibrium is calculated. In Section 3 a sufficient condition for the stable coexistence of the ecosystem is proved. Section 4 is devoted to the problem of observability and observer design for the considered ecosystem. The method is also illustrated with a numerical example. In Section 5 a discussion of the results is given. Finally, in the Appendix some basic concepts and results concerning verticum-type systems are shortly recalled.

2. Description of the model and existence of an equilibrium

As a modification of the well-known three-level *trophic chain* consisting of *resource – producer – primary consumer* considered in [5], we consider the following four-level *ecological interaction chain*:

level 0: a *resource*;

level 1: the *producer* is a plant, supposed to die out without the resource, and the positive effect of the latter is proportional to the quantity of the resource present in the system;

level 2: the *primary user* (instead of consumer), i.e. a commensalist animal, making use of the plant as part of its habitat without harming it (e.g. an insect species hosted by the plant), displaying a logistic dynamics in absence of the plant and the secondary consumer;

level 3: the *secondary consumer* is a monophagous predator of the *primary user* (e.g. an insectivorous singing bird species), with intraspecific competition.

(For more details on the role of *commensalism* in ecological communities, we supposed between the producer and the primary user, see [21]).

For a dynamical model let x_0 be the time-dependent quantity, with a constant supply Q of the resource present in the system, x_1, x_2 and x_3 the time-varying population size (biomass or density) of the producer, the primary user and the secondary consumer, respectively. Assume that a unit of biomass of the plant consumes the resource at velocity $\alpha_0 x_0$; however, it increases the biomass of the plant at rate k_1. The relative rate of increase in biomass of the primary user, due to the presence of the plant is $k_2 x_1$. While the plant population is supposed to die out exponentially in the absence of the resource, with Malthus parameter m_1, the primary user displays a logistic growth with Malthus parameter m_2 and is limited by a carrying capacity $\frac{m_2}{\eta_2}$. Furthermore, the secondary consumer would die out at rate m_1, without the presence of the primary user, and there is an intraspecific competition among predators with rate η_3. We will consider a *partially closed system*, where the dead plants may be recycled into nutrient resource with rate β_1. Then with parameters

$$Q, \alpha_0, \alpha_1, \alpha_2, m_1, m_2, m_3, \eta_2, \eta_3 > 0; \quad k_1, k_2, k_3 \in]0,1[; \quad \beta_1 \in [0,1[,$$

we have the following dynamic model for the considered interaction chain:

$$\dot{x}_0 = Q - \alpha_0 x_0 x_1 + \beta_1 m_1 x_1 \quad (2.1)$$
$$\dot{x}_1 = x_1(-m_1 + k_1 \alpha_0 x_0) \quad (2.2)$$
$$\dot{x}_2 = x_2(m_2 + k_2 x_1 - \eta_2 x_2 - \alpha_2 x_3) \quad (2.3)$$
$$\dot{x}_3 = x_3(-m_3 + k_3 \alpha_2 x_2 - \eta_3 x_3) \quad (2.4)$$

Our purpose now is to find sufficient conditions for the existence of an ecological equilibrium of dynamic system (2.1)-(2.4), where all components are present. The right-hand side of the system is given by the following function:

$$f : R^4 \to R^4,\ f(x) = f(x_0, x_1, x_2, x_3) := \begin{bmatrix} Q - \alpha_0 x_0 x_1 + \beta_1 m_1 x_1 \\ x_1(-m_1 + k_1 \alpha_0 x_0) \\ x_2(m_2 + k_2 x_1 - \eta_2 x_2 - \alpha_2 x_3) \\ x_3(-m_3 + k_3 \alpha_2 x_2 - \eta_3 x_3) \end{bmatrix}. \quad (2.5)$$

Then a vector $x^* \in R^4, x^* > 0$ is an equilibrium for the dynamical system (2.1)-(2.4) if and only if, $f(x^*) = 0.$ From (2.2) we obviously get

$$x_0^* = \frac{m_1}{k_1 \alpha_0} > 0.$$

Since $k_1 \in]0,1[$ and $\beta_1 \in [0,1[$, from (2.1) we obtain

$$x_1^* = \frac{Q}{\alpha_0 \dfrac{m_1}{k_1 \alpha_0} - \beta_1 m_1} = \frac{Q k_1}{m_1(1 - \beta_1 k_1)} > 0\,.$$

From (2.3) and (2.4), we have

$$x_3^* = \frac{k_3 \alpha_2 \left(m_2 + k_2 \dfrac{Q k_1}{m_1(1 - \beta_1 k_1)} \right) - \eta_2 m_3}{k_3 \alpha_2^{\ 2} + \eta_2 \eta_3} > 0 \ \Leftrightarrow \ k_3 \alpha_2 \left(m_2 + k_2 \frac{Q k_1}{m_1(1 - \beta_1 k_1)} \right) - \eta_2 m_3 > 0.$$

It is easy to see that the latter inequality holds, whenever for the model parameters we have

$$Q > \frac{m_1 m_3 \eta_2}{k_1 k_2 k_3 \alpha_2}\,. \quad (2.6)$$

Indeed, by $k_1 \in]0,1[$ and $\beta_1 \in [0,1[$, from (2.6) we get

$$\eta_2 m_3 < \frac{k_1 k_2 k_3 \alpha_2 Q}{m_1} < \frac{k_1 k_2 k_3 \alpha_2 Q}{m_1(1-\beta_1 k_1)} < k_3 \alpha_2 \left(m_2 + k_2 \frac{Q k_1}{m_1(1-\beta_1 k_1)} \right).$$

Finally, under condition (2.6), the positivity of x_3^* implies

$$x_2^* = \frac{m_3 + \eta_3 x_3^*}{k_3 \alpha_2} > 0 .$$

Therefore, we can state that if (2.6) holds then system (2.1)-(2.4) has a positive equilibrium.

3. Asymptotic stability of the equilibrium

For the analysis of stability for the above calculated ecological equilibrium x^*, let us linearize system (2.1)-(2.4) near x^*, obtaining

$$A := f'(x^*) = \begin{pmatrix} -\alpha_0 x_1^* & -\alpha_0 x_0^* + \beta_1 m_1 & 0 & 0 \\ k_1 \alpha_0 x_1^* & 0 & 0 & 0 \\ 0 & k_2 x_2^* & -\eta_2 x_2^* & -\alpha_2 x_2^* \\ 0 & 0 & k_3 \alpha_2 x_3^* & -\eta_3 x_3^* \end{pmatrix}. \tag{3.1}$$

Let us calculate the characteristic polynomial of this matrix:

$$p(\lambda) := \det \begin{pmatrix} -\alpha_0 x_1^* - \lambda & -\alpha_0 x_0^* + \beta_1 m_1 & 0 & 0 \\ k_1 \alpha_0 x_1^* & -\lambda & 0 & 0 \\ 0 & k_2 x_2^* & -\eta_2 x_2^* - \lambda & -\alpha_2 x_2^* \\ 0 & 0 & k_3 \alpha_2 x_3^* & -\eta_3 x_3^* - \lambda \end{pmatrix}$$
$$= a_0 + a_1 \lambda + a_2 \lambda^2 + a_3 \lambda^3 + a_4 \lambda^4,$$

where

$$\begin{aligned} a_4 &= 1 \\ a_3 &= \alpha_0 x_1^* + \eta_2 x_2^* + \eta_3 x_3^* \\ a_2 &= (\eta_2 \eta_3 + \alpha_2{}^2 k_3) x_2^* x_3^* + \alpha_0 x_1^* (\alpha_0 k_1 x_0^* - \beta_1 k_1 m_1 + \eta_2 x_2^* + \eta_3 x_3^*) \\ a_1 &= \alpha_0 x_1^* \left[(\eta_2 \eta_3 + \alpha_2{}^2 k_3) x_2^* x_3^* + k_1 (\eta_2 x_2^* + \eta_3 x_3^*)(\alpha_0 x_0^* - \beta_1 m_1) \right] \\ a_0 &= \alpha_0 k_1 (\eta_2 \eta_3 + \alpha_2{}^2 k_3)(\alpha_0 x_0^* - \beta_1 m_1) x_1^* x_2^* x_3^* . \end{aligned}$$

Now the well-known Routh-Hurwitz criterion (see e.g. [2]) can be applied: all roots of the polynomial $p(\lambda) = a_0 + a_1\lambda + a_2\lambda^2 + a_3\lambda^3 + a_4\lambda^4$ have negative real parts if and only if

$$a_i > 0 \quad i = 0,1,...,4 \quad ; \quad a_3 a_2 > a_1 a_4 \text{ and } a_1(a_3 a_2 - a_1 a_4) > a_0 {a_3}^2 . \qquad (3.2)$$

For this polynomial we clearly have that $a_i > 0 \quad i = 0,1,...,4$ since $k_1 \in]0,1[$ and $\beta_1 \in [0,1[$, moreover, $a_3 a_2 - a_1 a_4$ can be written as

$$\begin{aligned} a_3 a_2 - a_1 a_4 &= {\alpha_0}^3 k_1 x_0^* (x_1^*)^2 + (\eta_2\eta_3 + {\alpha_2}^2 k_3) x_2^* x_3^* (\eta_2 x_2^* + \eta_3 x_3^*) + \\ &\quad + \alpha_0 x_1^* (\eta_2 x_2^* + \eta_3 x_3^*)^2 + (\alpha_0 x_1^*)^2 (-\beta_1 m_1 k_1 + \eta_2 x_2^* + \eta_3 x_3^*) = \\ &= (\alpha_0 x_1^*)^2 (\alpha_0 k_1 x_0^* - \beta_1 m_1 k_1 + \eta_2 x_2^* + \eta_3 x_3^*) + \\ &\quad + (\eta_2\eta_3 + {\alpha_2}^2 k_3) x_2^* x_3^* (\eta_2 x_2^* + \eta_3 x_3^*) + \alpha_0 x_1^* (\eta_2 x_2^* + \eta_3 x_3^*)^2 , \end{aligned}$$

where again by $\beta_1, k_1 \in [0,1[$ we have that $a_3 a_2 - a_1 a_4 > 0$. Finally, under condition $Qk_1\alpha_0 > 2m_1^2$ we have $a_1(a_3 a_2 - a_1 a_4) - a_0 {a_3}^2 > 0$, therefore all inequalities in (3.2) hold.

Now, the above reasoning can be summarized in the following result.

Theorem 3.1. Let us suppose that for given biological parameters, the resource supply is high enough,

$$Q > \frac{m_1 m_3 \eta_2}{k_1 k_2 k_3 \alpha_2}, \qquad Q > \frac{2m_1^2}{k_1 \alpha_0} . \qquad (3.3)$$

Then, both the *open* ($\beta_1 = 0$) and the *partially closed* ($\beta_1 > 0$) ecological chains stably coexist in the sense there exists a positive equilibrium x^* of system calculated in Section 2, which is asymptotically stable.

Remark 3.1. The conditions of Theorem 3.1 can also be formulated conversely: Given a resource supply *Q*, biological parameters satisfying conditions (3.3) imply the stable coexistence of the considered ecological chain.

4. Observability and observer design

In this section, in order to address the monitoring problem of the considered ecosystem, first we find sufficient conditions for the observability of the system, reducing the problem, by linearization to the observability of a verticum-type system. Then observer design is used for the asymptotic estimation of the unknown state process, on the basis of a partial observation of the ecosystem.

4.1 Observability of the ecological chain

Let us consider now the following two auxiliary 2-dimension systems

$$\begin{aligned} \dot{x}_0 &= Q - \alpha_0 x_0 x_1 + \beta_1 m_1 x_1 \\ \dot{x}_1 &= x_1(-m_1 + k_1 \alpha_0 x_0) \end{aligned} \tag{4.1}$$

and

$$\begin{aligned} \dot{x}_2 &= x_2(m_2 + k_2 x_1^* - \eta_2 x_2 - \alpha_2 x_3) \\ \dot{x}_3 &= x_3(-m_3 + k_3 \alpha_2 x_2 - \eta_3 x_3) \end{aligned} \tag{4.2}$$

In ecological terms (4.1) is a subsystem of the original chain (2.1)-(2.4), while in (4.2) the positive effect of the plant on the animal species 2 appears with the equilibrium value x_1^* of the plant. We note that by setting $k_2 := 0$ (i.e. considering the original system without commensalisms), the original ecological chain is split up into two components without interaction.

Remark 4.1. The biological interpretation of system (4.2) is the following: Suppose that system (2.1)-(2.4) is in equilibrium, and the two animal species, by an external disturbance, deviate from their equilibrium densities. Then the *resource-primary consumer* subsystem can maintain its equilibrium, and the *predator-prey* subsystem will be governed by system (4.2).

Continuing the study of systems (4.1) and (4.2), we can easily check that they have respective equilibria $w_0^* := (x_0^*, x_1^*)$ and $w_1^* := (x_2^*, x_3^*)$. For system (4.1) with notation $w_0 := (x_0, x_1)$, let us consider observation function

$$h_0(w_0) = h_0(x_0, x_1) := x_0 - x_0^*. \tag{4.3}$$

This means that the deviation of the resource from its equilibrium value is observed. In order to check local controllability, we calculate the linearization of system (4.1) at equilibrium w_0^*:

$$A_{00} := \begin{pmatrix} -\alpha_0 x_1^* & -\alpha_0 x_0^* + \beta_1 m_1 \\ k_1 \alpha_0 x_1^* & 0 \end{pmatrix} \quad ; \quad C_0 := h_0'(w_0^*) = (1 \quad 0) \; . \tag{4.4}$$

Hence we easily calculate

$$\mathrm{rank}\begin{pmatrix} C_0 \\ C_0 A_{00} \end{pmatrix} = 2 \, ,$$

provided $\beta_1 > 0$. From the classical sufficient condition for the local observability of nonlinear systems, [3], we obtain the local observability of system (4.1) near the equilibrium, with observation (4.3).

Similarly, suppose that in system (4.2) the deviation of the density of the prey from its equilibrium value is observed, i.e., with notation $w_1 := (x_2, x_3)$ we consider the observation function

$$h_1(w_1) := x_2 - x_2^* \, . \tag{4.5}$$

The linearization of system (4.2) at equilibrium w_1^* is

$$A_{11} := \begin{pmatrix} -\eta_2 x_2^* & -\alpha_2 x_2^* \\ k_3 \alpha_2 x_3^* & -\eta_3 x_3^* \end{pmatrix} \quad ; \quad C_1 := h_1'(w_1^*) = (1 \quad 0) \, .$$

Checking again the rank condition, by $\alpha_2 > 0$ we get

$$\mathrm{rank}\begin{pmatrix} C_1 \\ C_1 A_{11} \end{pmatrix} = 2 \, , \tag{4.8}$$

implying local observability of system (4.2), (4.5) near w_1^*.

Now, let us observe that with definition

$$A_{10} := \begin{pmatrix} 0 & k_2 x_2^* \\ 0 & 0 \end{pmatrix},$$

system matrix

$$A := \begin{pmatrix} A_{00} & 0 \\ A_{10} & A_{11} \end{pmatrix},$$

together with observation matrix

$$C := \begin{pmatrix} C_0 & 0 \\ 0 & C_1 \end{pmatrix}$$

define a verticum-type linear observation system in the sense defined in the Appendix. Applying Theorem A.1 of the Appendix, we obtain that the linear observation system

$$\dot{w} = Aw \tag{4.7}$$

$$y = Cw \tag{4.8}$$

is observable. Since A is just the Jacobian of the righ-hand side of system (2.1)-(2.4) calculated in (3.1), therefore (4.7) is just the linearization system (2.1)-(2.4). Furthermore (4.8) is the linearization of observation function

$$h(x) := col(x_0 - x_0^*\,,\, x_2 - x_2^*) \tag{4.9}$$

which can be associated with system (2.1)-(2.4). Finally, applying again the classical rank condition of [3], we can summarize the reasoning of this subsection in the following theorem.

Theorem 4.1. Let us suppose that ecological chain (2.1)-(2.4) is partially closed (β_1>0).Then with observation function (4.9), system (2.1)-(2.4) is locally observable near equilibrium x^* calculated in Section 2.

4.2. Construction of an observer system

Following the procedure of Sundarapandian [22], let us first determine conditions for the construction of observers for systems (4.1) and (4.2), with respective observation functions (4.3) and (4.5).

For matrices A_{00} and C_0, figuring in (4.4), we have to find a matrix $H_0 := col(h_{00}\,,\, h_{01})$ such that

$$A_{00} - H_0 C_0 = \begin{pmatrix} -\alpha_0 x_1^* - h_{00} & -\alpha_0 x_0^* + \beta_1 m_1 \\ k_1 \alpha_0 x_1^* - h_{01} & 0 \end{pmatrix}$$

is a Hurwitz matrix, i.e. all roots of the characteristic polynomial p_0 of matrix $A_{00} - H_0 C_0$ have real negative parts. It is easy to check that the latter condition is satisfied if and only if the following inequalities hold:

$$h_{00} > -\alpha_0 x_1^* \tag{4.10}$$

$$h_{01} < k_1\alpha_0 x_1^* . \tag{4.11}$$

Simple sufficient conditions for (4.10) and (4.11) are $h_{00} > 0$ and $h_{01} < 0$, respectively. By the Theorem of Sundarapandian [22], the observer for system (4.1) with observation function (4.3) can be determined.

Similarly, for matrices A_{11} and C_1, figuring in (4.6), we need to find a matrix $H_1 := col(h_{12}, h_{13})$ such that all roots of the characteristic polynomial p_1 of matrix

$$A_{11} - H_1 C_1 = \begin{pmatrix} -\eta_2 x_2^* - h_{12} & -\alpha_2 x_2^* \\ k_3\alpha_2 x_3^* - h_{13} & -\eta_3 x_3^* \end{pmatrix}$$

have real negative parts.

Now a straightforward checking shows that the latter condition is satisfied if and only if h_{12} and h_{13} satisfy the following inequalities:

$$h_{12} > -\eta_2 x_2^* - \eta_3 x_3^*, \tag{4.12}$$

$$h_{13} < \frac{(\eta_2 x_2^* + h_{21})\eta_3 x_3^* + k_3 \alpha_2{}^2 x_2^* x_3^*}{\alpha_2 x_2^*}. \tag{4.13}$$

Similarly to the previous case, in order to satisfy conditions (4.12) and (4.13), it is sufficient to set $h_{12} > 0$ and $h_{13} < 0$, and again by the Theorem of Sundarapandian [22], the observer for system (4.2) with observation function (4.5) can be determined.

Finally, based on the above reasoning, it will be easy to prove the following result:

Theorem 4.2. Given

$$H = \begin{pmatrix} h_{00} & 0 \\ h_{01} & 0 \\ 0 & h_{12} \\ 0 & h_{13} \end{pmatrix},$$

with h_{00}, $h_{12} > 0$ and h_{01}, $h_{13} < 0$, and function f defined in (2.5) system

$$\dot{z} = f(z) + H(y - h(z))$$

is a local exponential observer for system (2.1)-(2.4) with observation equation $y = h(x)$, where h is defined in (4.9).

Proof. Let p be the characteristic polynomial of matrix *A-HC* with

$$C := h'(x^*) = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}.$$

Then, it is easy to see that $p = p_1 \cdot p_2$ and therefore, from conditions (4.10)-(4.13) we can conclude that *A-HC* is a Hurwitz matrix and by the Theorem of Sundarapandian [22] the proof is complete.

Example 4.1. We consider the following system

$$\begin{aligned} \dot{x}_0 &= 2.1 - 0.2x_0x_1 + 0.2 \cdot 0.4x_1 \\ \dot{x}_1 &= x_1(-0.4 + 0.84 \cdot 0.2x_0) \\ \dot{x}_2 &= x_2(0.25 + 0.7x_1 - 0.1x_2 - 0.4x_3) \\ \dot{x}_3 &= x_3(-0.1 + 0.9 \cdot 0.4x_2 - 0.5x_3). \end{aligned} \tag{4.14}$$

System (4.14) has a positive equilibrium $x^* = (2.38\ ,5.3,\ 10.41,\ 7.3)$, which is asymptotically stable, because conditions of Theorem 3.1 are satisfied. In Fig. 1 it can be seen how, e.g. from initial condition $x(0) := (1, 6, 9, 5)$ near the equilibrium, the solution x of system (4.14) tends to this positive equilibrium, see Fig. 1.

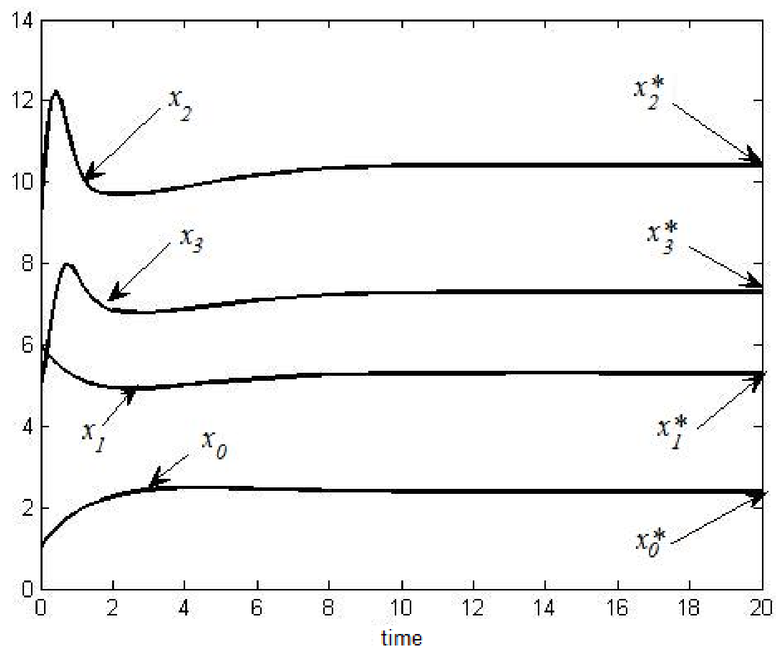

Fig. 1. Solution of system (4.14) with initial condition $x(0) = (1, 6, 9, 5)$

Consider now system (4.14) with observation

$$y = h(x) = (x_0 - x_0^*, x_2 - x_2^*).$$

Since matrix

$$H = \begin{pmatrix} 10 & 0 \\ -20 & 0 \\ 0 & 10 \\ 0 & -0.01 \end{pmatrix},$$

satisfies the conditions of Theorem 4.2, we can construct the following observer

$$\begin{aligned} \dot{z}_0 &= 2.1 - 0.2 z_0 z_1 + 0.2 \cdot 0.4 z_1 \\ \dot{z}_1 &= z_1(-0.4 + 0.84 \cdot 0.2 z_0) \\ \dot{z}_2 &= z_2(0.25 + 0.7 z_1 - 0.1 z_2 - 0.4 z_3) \\ \dot{z}_3 &= z_3(-0.1 + 0.9 \cdot 0.4 z_2 - 0.5 z_3) \end{aligned} + \begin{pmatrix} 10 & 0 \\ -20 & 0 \\ 0 & 10 \\ 0 & -0.01 \end{pmatrix} \cdot (y - h(z)) \quad (4.15)$$

Solving (4.15) with initial condition $z(0) = (2, 4, 7, 7)$ near to the equilibrium, we can check how this solution tends to recover the corresponding solution of system (4.14), see Fig. 2.

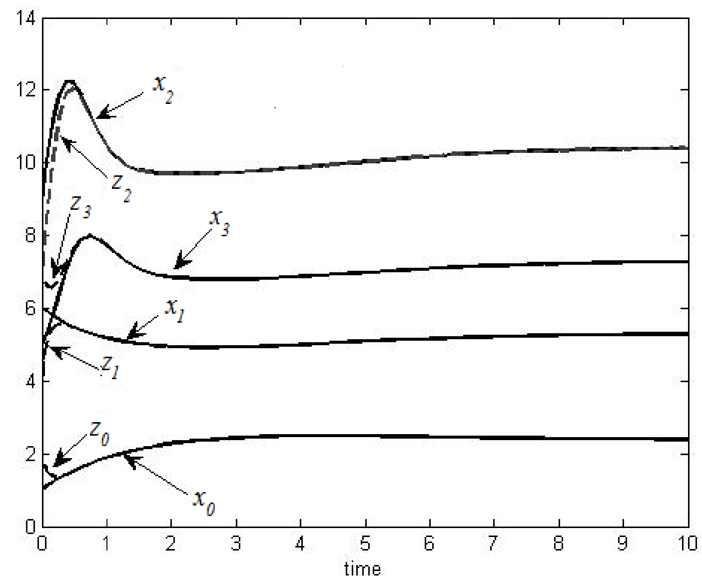

Fig. 2. Solutions of system (4.14) and (4.15) with the respective initial conditions $x(0) = (1, 6, 9, 5)$ and $z(0) = (2, 4, 7, 7)$

5. Discussion

From the ecological point of view, in comparison to the existing results, the novelty of the paper consists in extending the state estimation (monitoring) from three-level trophic chains to four-level ecological chains, where, a non-trophic interaction (namely commensalism) also takes place. From the methodological aspect, this the first time that by the linearization of the underlying nonlinear dynamic ecosystem model, the technique of verticum-type linear systems (developed for the investigation of industrial systems) is applied to the monitoring of specially structured (chain-type) ecosystems. Finally, we note that the proposed method can be extended to a longer, five-level ecological chain by adding a tertiary consumer (a top predator, e.g. a predator bird consuming the singing bird) to the model.

The considered model can be extended by adding a tertiary consumer (a top predator, e.g. a predator bird consuming the singing bird).

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Appendix

In this section, based on [18], we summarize some concepts, notation and a basic sufficient condition for observability of verticum-type systems, in a simplified form used in the present paper. Let $k, n_i, r_i \in \mathbf{N}$ $\left(i \in \overline{0,k}\right)$ and assume that

$$A_{00} \in R^{n_0 \times n_0}, C_0 \in R^{r_0 \times n_0}, \tag{A.1}$$

and for all $i \in \overline{0,k}$

$$A_{i,i-1} \in R^{n_i \times n_{i-1}}, A_{ii} \in R^{n_i \times n_i}, C_i \in R^{r_i \times n_i}. \tag{A.2}$$

Consider systems

$$(\mathrm{V}_0) \qquad \begin{aligned} \dot{x}_0 &= A_{00} x_0 \\ y_0 &= C_0 x_0, \end{aligned}$$

and for all $i \in \overline{1,k}$

$$(\mathrm{V}_\mathrm{i}) \qquad \begin{aligned} \dot{x}_i &= A_{ii} x_i + A_{ii-1} x_{i-1} \\ y &= C_i x_i \end{aligned} .$$

Denoting $n := \sum_{i=0}^{k} n_i,\ r := \sum_{i=0}^{k} r_i$, define the matrices $A \in R^{n\times n}, C \in R^{r\times n}$ as follows:

$$A = \begin{pmatrix} A_{00} & 0 & 0 & \dots & 0 & \dots & 0 \\ A_{10} & A_{11} & 0 & \dots & 0 & \dots & 0 \\ 0 & A_{21} & A_{22} & \dots & 0 & \dots & 0 \\ \cdot & \cdot & \cdot & \dots & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot & \dots & \cdot \\ 0 & 0 & 0 & \dots & \cdot & A_{k-1,k-1} & 0 \\ 0 & 0 & 0 & \dots & \cdot & A_{k,k-1} & A_{k,k} \end{pmatrix}$$

$$C = \begin{pmatrix} C_1 & & & & 0 \\ & C_2 & & & \\ & & \cdot & & \\ & & & \cdot & \\ 0 & & & & C_k \end{pmatrix}.$$

Definition A.1. System

$$(V) \qquad \begin{aligned} \dot{x} &= Ax \\ y &= Cx \end{aligned}$$

is said to be of *verticum type.*

Given the verticum-type system (V), using the above notation, let $i, j \in \overline{0,k}$ with $j \le j$, and define system

$$(V_{ij}) \qquad \begin{aligned} \dot{x}_i &= A_{ii}x_i \\ \dot{x}_l &= A_{ll-1}x_{i-1} + A_{ll}x_l \qquad (l \in i+1, j, \text{if } i < j), \end{aligned}$$

with observation matrix

$$C_{ij} := \begin{pmatrix} C_i & & & & 0 \\ & C_{i+1} & & & \\ & & \cdot & & \\ & & & \cdot & \\ 0 & & & & C_j \end{pmatrix}.$$

Remark A.1. Intuitively, a verticum-type system consists of a finite series of “subsystems” where each “subsystem” is connected only with the previous one.

Theorem A.1. For given $s \in \overline{1,k}$, let $i_p, j_p \in \overline{0,k}$ with $i_p \leq j_p \quad (p \in 1,s)$, and suppose that all systems $\mathrm{V}_{\mathrm{i_p j_p}}$ with observation matrix $C_{i_p j_p}$ are observable. Then the verticum-type system (V) is also observable.