Sensitivity analysis of time varying ecological networks

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Our Team

We have been collaborating for many years with

- Rodrigo Ramos–Jiliberto, GEMA Center for Genomics, Ecology & Environment, Universidad Mayor, Santiago (Chile).
- Daniel Sepúlveda. Biomathematics Unit, Universidad Tecnológica Metropolitana, Santiago (Chile).


Our focus is to study the population dynamics described by nonautonomous differential equations.

Our team (some history of this result)

In 2010, Rodrigo proposed us to explain the following articles to PhD students in Ecology:

- E. Bender, T. Case and M.E. Gilpin, *Perturbation experiments in community ecology*. Ecology, 1984, 65:1–13).
- M. Higashi, and H. Nakajima, *Indirect effects in ecological interaction networks I. The chain rule approach*, Math. Biosci. 130 (1995), pp. 99–128.

We decided to generalize these results to the ω–periodic case, obtaining (2012) an *ergodic* version of the sensitivity matrix but a generalization turned to be impossible

In January 2020 we receive the visit of C. Pötzsche (Klagenfurt, Austria) whose work on nonautonomous dynamical systems provide us ideas to revisit our problem.

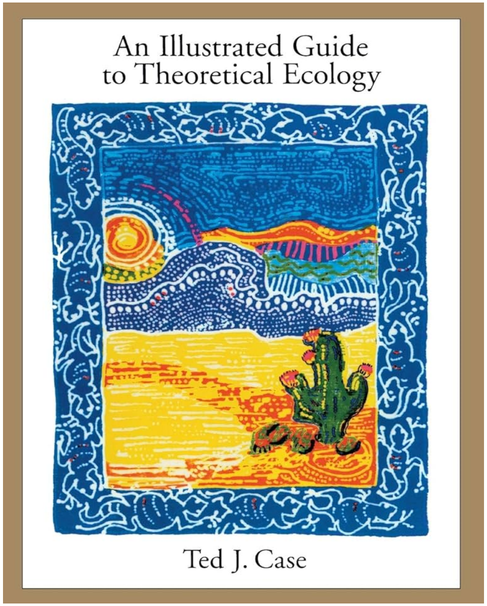
Our Team (Context)

- The Mathematics Department (U. de Chile) gathers a team working on nonautonomous differential equations.
- We realized that these tools allow to address several problems in theoretical ecology and improve models.
- Currently we are working on metapopulation and bioprocess models.

Agenda

a) *A short review of the state of art (autonomous case).*
b) *New results for the nonautonomous framework.*
c) *An iconic example: generalized Lotka–Volterra system.*

Part I: A short review of the state of art (autonomous)



We will revisit a classical topic of theoretical ecology: the sensitivity analysis to press perturbations in ecological networks.

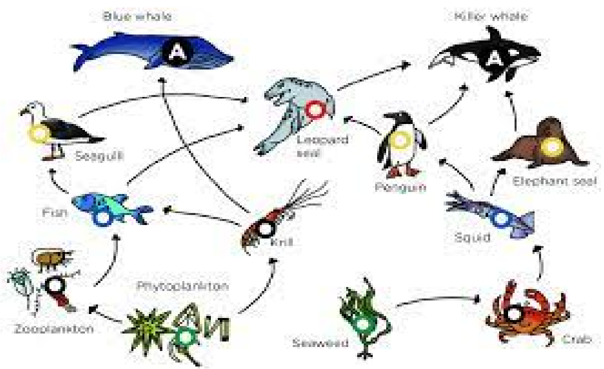


Figure 1: Theoretical ecological Network

- We consider a network of n species interacting with each other.
- How to measure the effect of the i–th species on the j–th species in the above network?
- We have in mind *total effects*, *direct effects* and *indirect effects*.

Ecological network: direct and indirect effects

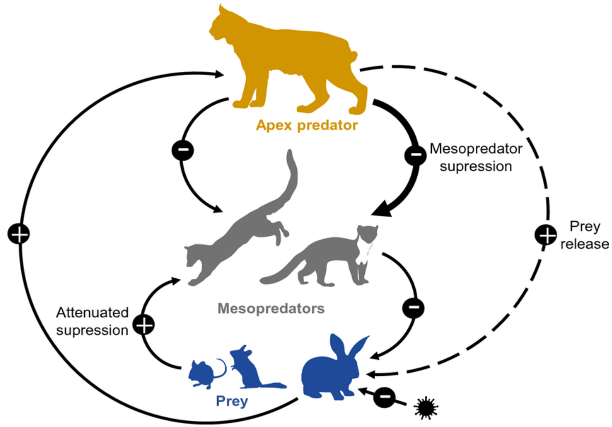


Figure 2: Simultaneously, a predator can have negative direct effects and positive indirect effects over a prey

- By one hand, predation has obviously a negative direct effect on the preys
- By the other hand, predation also has a positive indirect effect on the prey, which is less obvious and more subtle.

Ecological network: direct and indirect effects

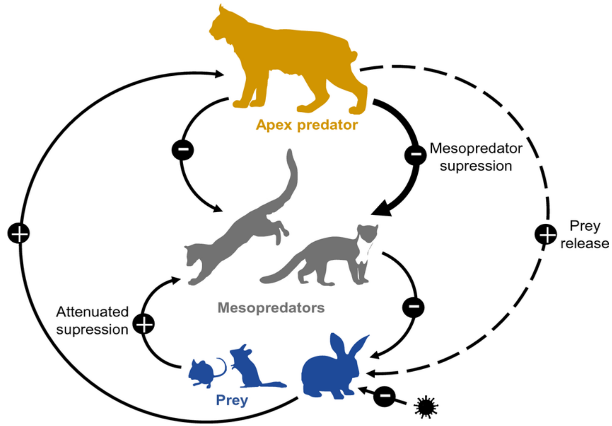


Figure 3: Simultaneously, a predator can have negative direct effects and positive indirect effects over a prey

- To neglect the indirect effect and exclusively focusing on mitigate consequences of the negative direct ones is the cause of several ecologic catastrophes.
- It is important to measure the total and the indirect effects in an ecological network.

Ecological network: a fundamental question

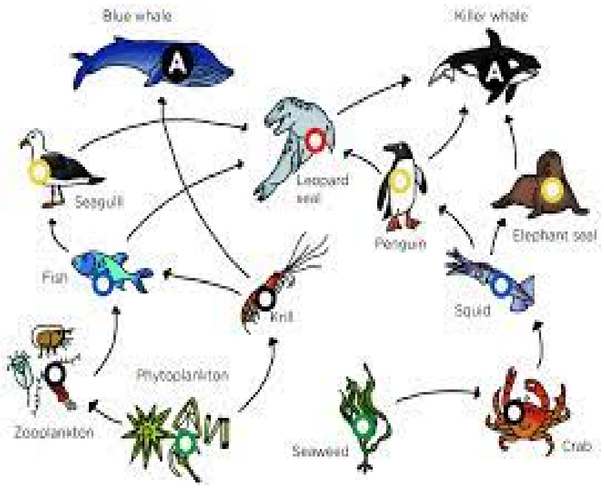


Figure 4: Each species have effect on the other ones

How to measure the total effects in an ecological network?

Modelling Ecological networks (1)

Let us consider an ecological network of n species whose interactions are described by a system of differential equations:

$$\begin{cases} \dot{x}_1 &= x_1 f_1(x_1,\ldots,x_n) \\ \dot{x}_2 &= x_2 f_2(x_1,\ldots,x_n) \\ \quad\vdots & \quad\vdots \\ \dot{x}_n &= x_n f_n(x_1,\ldots,x_n) \end{cases} \quad \text{or} \quad \dot{x} = G(x) \tag{1}$$

- x_i describes the abundance of the i–th species.
- $x := (x_1,\ldots,x_n)$.
- We assume the existence of a positive equilibrium $\overline{x} = (\overline{x}_1,\ldots,\overline{x}_n)$:

$$f_i(\overline{x}_1,\ldots,\overline{x}_n) = 0 \quad \text{for any } i = 1,\ldots,n.$$

- The above equilibrium will be assumed to be hyperbolic.

Modelling Ecological Networks (2)

Given the previous system

$$\begin{cases} \dot{x}_1 &= x_1 f_1(x_1, \ldots, x_n) \\ \dot{x}_2 &= x_2 f_2(x_1, \ldots, x_n) \\ \vdots & \vdots \\ \dot{x}_n &= x_n f_n(x_1, \ldots, x_n) \end{cases} \quad \text{or} \quad \dot{x} = G(x)$$

- The Jacobian matrix evaluated at the hyperbolic equilibrium $\overline{x} = (\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n)$ is:

$$DG(\bar{x}) = \begin{bmatrix} \bar{x}_1 \frac{\partial f_1}{\partial x_1}(\bar{x}) & \bar{x}_1 \frac{\partial f_1}{\partial x_2}(\bar{x}) & \ldots & \bar{x}_1 \frac{\partial f_1}{\partial x_n}(\bar{x}) \\ \bar{x}_2 \frac{\partial f_2}{\partial x_1}(\bar{x}) & \bar{x}_2 \frac{\partial f_2}{\partial x_2}(\bar{x}) & \ldots & \bar{x}_2 \frac{\partial f_2}{\partial x_n}(\bar{x}) \\ \vdots & \vdots & \ddots & \vdots \\ \bar{x}_n \frac{\partial f_n}{\partial x_1}(\bar{x}) & \bar{x}_n \frac{\partial f_n}{\partial x_2}(\bar{x}) & \ldots & \bar{x}_n \frac{\partial f_n}{\partial x_n}(\bar{x}) \end{bmatrix}$$

Modelling Ecological Networks (3)

Given the previous system

$$\left\{\begin{array}{lcl} \dot{x}_1 & = & x_1 f_1(x_1, \ldots, x_n) \\ \dot{x}_2 & = & x_2 f_2(x_1, \ldots, x_n) \\ \quad\vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(x_1, \ldots, x_n) \end{array}\right. \qquad \text{or} \quad \dot{x} = G(x)$$

- The corresponding Jacobian matrix evaluated at the hyperbolic equilibrium $\overline{x} = (\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n)$ is:

$$DG(\bar{x}) = \mathrm{Diag}\{\bar{x}_1, \ldots, \bar{x}_n\} \begin{bmatrix} \frac{\partial f_1}{\partial x_1}(\bar{x}) & \frac{\partial f_1}{\partial x_2}(\bar{x}) & \ldots & \frac{\partial f_1}{\partial x_n}(\bar{x}) \\ \frac{\partial f_2}{\partial x_1}(\bar{x}) & \frac{\partial f_2}{\partial x_2}(\bar{x}) & \ldots & \frac{\partial f_2}{\partial x_n}(\bar{x}) \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1}(\bar{x}) & \frac{\partial f_n}{\partial x_2}(\bar{x}) & \ldots & \frac{\partial f_n}{\partial x_n}(\bar{x}) \end{bmatrix}$$

Modelling Ecological Networks (4)

Given the previous system

$$\begin{cases} \dot{x}_1 & = & x_1 f_1(x_1,\ldots,x_n) \\ \dot{x}_2 & = & x_2 f_2(x_1,\ldots,x_n) \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(x_1,\ldots,x_n) \end{cases} \qquad \text{or} \quad \dot{x} = G(x)$$

- The Jacobian matrix evaluated at the equilibrium $\bar{x}$ is:

$$DG(\bar{x}) := A = \underbrace{\mathrm{Diag}\{\bar{x}_1,\ldots,\bar{x}_n\}}_{:=B} C \quad \text{with } C_{ij} = \frac{\partial f_i}{\partial x_j}(\vec{x}).$$

- We linearize around the hyperbolic equilibrium $\bar{x}$. By HGT, the solutions are topologically conjugated to $\dot{u} = DG(\bar{x})u$ in $B_\delta(0)$.

$$\dot{u}_i = \bar{x}_1 C_{i1} u_1 + \ldots + \bar{x}_j C_{ij} u_j + \ldots + \bar{x}_n C_{in} u_n \quad \text{where } u_i = x_i - \bar{x}_i$$

Modelling Ecological Networks (5)

Given the previous system

$$\begin{cases} \dot{x}_1 & = & x_1 f_1(x_1, \ldots, x_n) \\ \dot{x}_2 & = & x_2 f_2(x_1, \ldots, x_n) \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(x_1, \ldots, x_n) \end{cases} \quad \text{or} \quad \dot{x} = G(x)$$

- The jacobian matrix evaluated at the equilibrium $\bar{x}$ is:

$$DG(\bar{x}) := A = \mathrm{Diag}\{\bar{x}_1, \ldots, \bar{x}_n\}C \quad \text{with } C_{ij} = \frac{\partial f_i}{\partial x_j}(\vec{x}).$$

- We linearize around the hyperbolic equilibrium $\bar{x}$. By HGT, the solutions are topologically conjugated to $\dot{u} = DG(\bar{x})u$ in $B_\delta(0)$.

$$\dot{u}_i = \bar{x}_1 C_{i1} u_1 + \ldots + \bar{x}_j C_{ij} u_j + \ldots + \bar{x}_n C_{in} u_n \quad \text{where } u_i = x_i - \bar{x}_i$$

- C_{ij} describes the direct effect of the j–species on the i–th species.

Modelling Ecological Networks (6)

Given the previous system

$$\begin{cases} \dot{x}_1 & = & x_1 f_1(x_1, \ldots, x_n) \\ \dot{x}_2 & = & x_2 f_2(x_1, \ldots, x_n) \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(x_1, \ldots, x_n) \end{cases} \quad \text{or} \quad \dot{x} = G(x).$$

- The corresponding Jacobian matrix evaluated at the hyperbolic equilibrium $\overline{x}$ is:

$$DG(\overline{x}) := A = \mathrm{Diag}\{\bar{x}_1, \ldots, \bar{x}_n\}C,$$

  and the matrix A is usually called the community matrix.
- C_{ij} describes the direct effect of the j–species on the i–th species.
- How to determine the total effects? Idea: Press perturbations.

Ecological Networks with press perturbations (1)

Imagine the previous system at the equilibrium $\overline{x} = (\bar{x}_1, \ldots, \bar{x}_n)$.

The per capita growth rate of the i–th species is perturbed by a small enough quantity p_i. The systems becomes:

$$\begin{cases} \dot{x}_1 &=& x_1 f_1(x_1, \ldots, x_n) \\ \dot{x}_2 &=& x_2 f_2(x_1, \ldots, x_n) \\ &\vdots& \\ \dot{x}_i &=& x_i\{f_i(x_1, \ldots, x_n) + p_i\} \\ &\vdots& \\ \dot{x}_n &=& x_n f_n(x_1, \ldots, x_n) \end{cases}$$

- If p_i is small enough, there will be a new equilibrium (close to $\overline{x}$) since the unperturbed species will readjust numerically[1].
- This perturbation of the i–th species will be useful to measure the total effects.

[1] This is a description of the **Implicit Function Theorem**.

Ecological Networks with press perturbations (2)

The per capita growth rate of all species is perturbed by a small enough vector $p = (p_1, \ldots, p_n)$*. The systems becomes:*

$$\begin{cases} \dot{x}_1 &= x_1\{f_1(x_1, \ldots, x_n) + p_1\} \\ \dot{x}_2 &= x_2\{f_2(x_1, \ldots, x_n) + p_2\} \\ \vdots & \vdots \\ \dot{x}_n &= x_n\{f_n(x_1, \ldots, x_n) + p_n\} \end{cases} \tag{2}$$

- The above system can be written in the abbreviated form

$$\dot{x} = F(x, p) \tag{3}$$

- It can be proved that

$$F(x, 0) = G(x) \quad \text{and} \quad \frac{\partial F_i}{\partial p_j}(x, p) = x_i\,\delta_{ij}$$

and it follows that $D_pF(x, p) = \text{Diag}\{x_1, \ldots, x_n\}$.

Ecological Networks with press perturbations (3)

The per capita growth rate of all species is perturbed by a small enough vector $p = (p_1, \ldots, p_n)$. *The systems becomes:*

$$\begin{cases} \dot{x}_1 & = & x_1\{f_1(x_1, \ldots, x_n) + p_1\} \\ \dot{x}_2 & = & x_2\{f_2(x_1, \ldots, x_n) + p_2\} \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n\{f_n(x_1, \ldots, x_n) + p_n\} \end{cases} \tag{4}$$

- The above system can be written in the abbreviated form

$$\dot{x} = F(x, p) \tag{5}$$

- By hypothesis, we know that $F(\overline{x}, 0) = G(\overline{x}) = 0$.
- The IFT implies existence of $\delta > 0$ and $p \mapsto x^*(p) \in \mathbb{R}^n$ such that:

$$x^*(0) = \overline{x} \quad \text{and} \quad F(x^*(p), p) = 0 \quad \text{for any } p \in B_\delta(0)$$

Ecological Networks with press perturbations (4)

The per capita growth rate of the species is perturbed by a small enough vector $p = (p_1, \ldots, p_n)$. The system becomes:

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and

$$D_x F(x^*(p), p) \frac{\partial x^*}{\partial p}(x^*(p), p) = -D_p F(x^*(p), p)$$

Ecological Networks with press perturbations (5)

The per capita growth rate of the i–th species is perturbed by a small enough quantity p_i. The system becomes:

$$\begin{cases} \dot{x}_1 & = & x_1\{f_1(x_1,\ldots,x_n)+p_1\} \\ \dot{x}_2 & = & x_2\{f_2(x_1,\ldots,x_n)+p_2\} \\ \quad\vdots & & \vdots \\ \dot{x}_n & = & x_n\{f_n(x_1,\ldots,x_n)+p_n\} \end{cases}$$

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$$x^*(0) = \overline{x} \quad \text{and} \quad F(x^*(p),p) = 0 \quad \text{for any } p \in B_\delta(0)$$

and

$$\frac{\partial x^*}{\partial p}(x^*(p),p) = -\left[D_x F(x^*(p),p)\right]^{-1} D_p F(x^*(p),p)$$

Sensitivity Matrix

- The sensitivity matrix is defined by

$$S := \frac{\partial x^*}{\partial p}(x^*(p), p)\Big|_{p=0} = -\left[D_x F(\overline{x}, 0)\right]^{-1} D_p F(\overline{x}, 0),$$

- It can be proved that

$$\underbrace{D_x F(\overline{x}, 0)}_{:=A} = \underbrace{\mathrm{Diag}\{\overline{x}_1, \ldots, \overline{x}_n\}C}_{:=BC} \quad \text{and} \quad D_p F(\overline{x}, 0) : \underbrace{\mathrm{Diag}\{\overline{x}_1, \ldots, \overline{x}_n\}}_{:=B}$$

- Then we have that

$$S := -A^{-1}B = -C^{-1}$$

- The community matrix $A = BC$ describes the direct effects between the species: C_{ij} describes the effect of the j–th species on the i–th one.

- The sensitivity matrix S describes the sensitivity of the species with respect to the press perturbation parameters: S_{ij} describes the effect of the j–th species on the i–th species.

Brief summary

• Given a trophic network with equilibrium at $\bar{x}$:

$$\dot{x} = G(x) \quad \text{with} \quad G(\bar{x}) = 0,$$

we study

$$\dot{u} = Au \quad \text{where } DG(\bar{x}) = A = BC$$

• The matrices A and C are called community matrices and describe the direct effects in a trophic network.

• The eigenvalues of A have non – zero real part (the equilibrium $\bar{x}$ is hyperbolic).

• The deduction of the total effect matrix $S = -A^{-1}B = -C^{-1}$ in terms of the community matrix A is a classical topic in Th. Ecology.

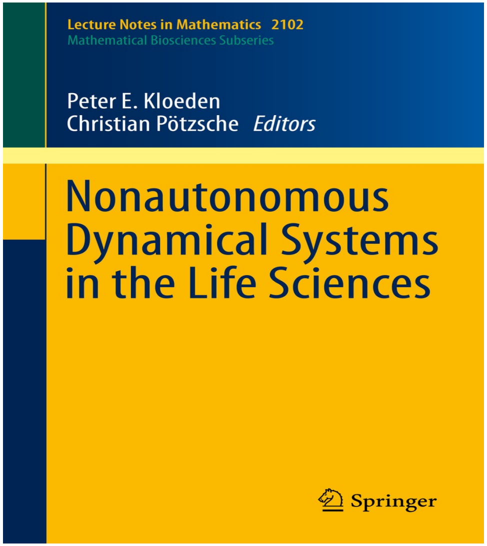
Agenda

a) *A short review of the state of art (autonomous case).*

b) *New results for the nonautonomous framework*

c) *An iconic example: generalized Lotka–Volterra system.*

Part II: New results for time varying networks



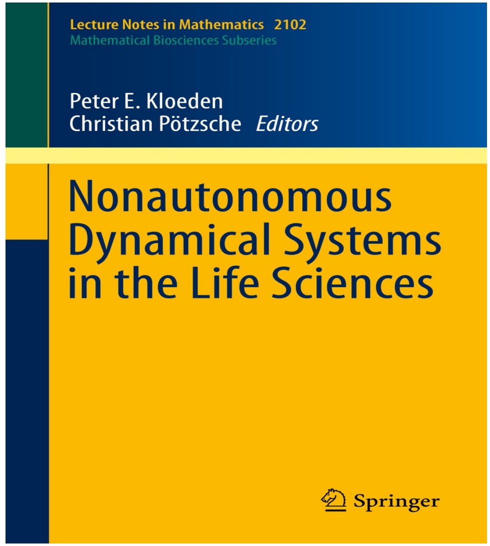
Some bad news

The previous results cannot be easily generalized for time varying networks :(

There are no univocal definition of hyperbolicity :(

The stability cannot be studied by eigenvalues :(

Part II: New results for time varying networks



Some good news :)

There exists a classical way to study the sensitivity of any solution with respect to the parameters.

Instead of using equilibria as before, we will study the sensitivity of bounded solutions with respect to the parameters.

Exponential dichotomy emulates basic features of hyperbolicity.

The time varying case (1)

We will generalize the previous methods for ecological networks described by time varying ODE systems $x' = F(t,x)$

$$\left\{\begin{array}{rcl} \dot{x}_1 & = & x_1 f_1(x_1,\ldots,x_n) \\ \dot{x}_2 & = & x_2 f_2(x_1,\ldots,x_n) \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(x_1,\ldots,x_n) \end{array}\right. \Rightarrow \left\{\begin{array}{rcl} \dot{x}_1 & = & x_1 f_1(t,x_1,\ldots,x_n) \\ \dot{x}_2 & = & x_2 f_2(t,x_1,\ldots,x_n) \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n f_n(t,x_1,\ldots,x_n) \end{array}\right. \tag{6}$$

- Equilibria $\overline{x} \Rightarrow$ *Nonautonomous Equilibrium* $t \mapsto \overline{x}(t)$
- Hyperbolicity Condition $\Rightarrow$ *Exponential Dichotomy* property
- We say that $t \mapsto \overline{x}(t)$ is a Nonautonomous Equilibrium of (6) if[2]:

  a) $t \mapsto \overline{x}(t)$ is solution of (6) for any $t \in \mathbb{R}$.

  b) $t \mapsto \overline{x}(t)$ is bounded for any $t \in \mathbb{R}$.
- Exponential Dichotomy is a property of $u' = DF(t,\overline{x}(t))u$.

[2] Note that any equilibrium is a Nonautonomous Equilibrium

The time varying case (2)

Given the time varying system

$$\begin{cases} \dot{x}_1 &= & x_1 f_1(t, x_1, \ldots, x_n) \\ \dot{x}_2 &= & x_2 f_2(t, x_1, \ldots, x_n) \\ \vdots & & \vdots \\ \dot{x}_n &= & x_n f_n(t, x_1, \ldots, x_n), \end{cases}$$

we will assume that

(A1) The system has a Nonautonomous equilibrium $t \mapsto \overline{x}(t) \in \Omega$, where $\Omega \subset \mathbb{R}^n$ is an open subset of $\mathbb{R}_0^+$.

The time varying case (3)

Now, we will consider press perturbations

$$\begin{cases} \dot{x}_1 & = & x_1\{f_1(t, x_1, \ldots, x_n) + p_1\} \\ \dot{x}_2 & = & x_2\{f_2(t, x_1, \ldots, x_n) + p_2\} \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n\{f_n(t, x_1, \ldots, x_n) + p_n\} \end{cases} \tag{7}$$

- It will be useful to write the above system with the abbreviated form:

$$\dot{x} = F(t, x, p),$$

where $x = (x_1, \ldots, x_n)$ and $p = (p_1, \ldots, p_n)$.

- We have to impose technical assumptions on this system.

The time varying case (4)

Now, as before, we will introduce press perturbations

$$\begin{cases} \dot{x}_1 & = & x_1\{f_1(t, x_1, \ldots, x_n) + p_1\} \\ \dot{x}_2 & = & x_2\{f_2(t, x_1, \ldots, x_n) + p_2\} \\ \vdots & & \vdots \\ \dot{x}_n & = & x_n\{f_n(t, x_1, \ldots, x_n) + p_n\} \end{cases} \tag{8}$$

- It will be useful to write the above system with the abbreviated form:

$$\dot{x} = F(t, x, p),$$

(A2) The map F is continuous in (t, x, p) and has continuous first partial derivatives with respect to x and p.

The time varying case (5)

Summarizing, we have the assumption with respect to

$$\dot{x} = F(t, x, 0) \tag{9}$$

(A1) The system (9) has a NE $t \mapsto \overline{x}(t) \in \Omega$.

We also have the assumptions with respect to the perturbed system

$$\dot{x} = F(t, x, p) \tag{10}$$

(A2) The map F is continuous in (t, x, p) and has continuous first partial derivatives with respect to x and p.

Can we ensure the existence of a NE $t \mapsto x^*(t, p)$ for small values of p?
In the autonomous case, it was a consequence of the hyperbolicity of the equilibrium combined with the IFT.

Linearization around the nonaut. equilibrium $t \mapsto \overline{x}(t)$

- Let $t \mapsto \overline{x}(t)$ be a nonautonomous equilibrium of

$$\dot{x} = F(t, x, 0)$$

- The linearization of the above system around $t \mapsto \overline{x}(t)$ is defined by

$$\dot{u} = A(t)u \qquad \text{where } A(t) := D_x F(t, \overline{x}(t), 0). \tag{11}$$

- This linear system play a key role in the statement of the next results.
- Its fundamental matrix will be denoted by $U(t)$.
- Its transition matrix will be denoted by $U(t, s) = U(t)U^{-1}(s)$.

Existence of NE for $x' = F(t, x, p)$

Lemma (C. Pötzsche (2011))

If the linear system

$$\dot{u} = A(t)u \qquad \text{where } A(t) := D_x F(t, \overline{x}(t), 0).$$

has an exponential dichotomy on $\mathbb{R}$, then it follows that

- *For any $p \in B_\delta(0)$, the system $\dot{x} = F(t, x, p)$ has a unique NE such that $t \mapsto x^*(t, p) \in \Omega$ for any $t \in \mathbb{R}$ and $x^*(t, 0) = \overline{x}(t)$.*
- *The map $p \mapsto x^*(t, p)$ is continuously differentiable.*

Existence of NE for $\dot{x} = F(t,x,p)$

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- *For any $p \in B_\delta(0)$, the system $\dot{x} = F(t,x,p)$ has a unique NE such that $t \mapsto x^*(t,p) \in \Omega$ for any $t \in \mathbb{R}$ and $x^*(t,0) = \overline{x}(t)$.*
- *The map $p \mapsto x^*(t,p)$ is continuously differentiable.*

We recall that the property of exponential dichotomy means that there exists a projector P and a pair of positive constants (K, α) such that:

$$P(t)U(t,s) = U(t,s)P(s) \quad \text{for any } t,s \in \mathbb{R},$$

$$\begin{cases} ||U(t,s)P(s)|| & \leq & Ke^{-\alpha(t-s)} & \text{for } t \geq s \text{ with } t,s \in \mathbb{R}, \\ ||U(t,s)[I-P(s)]|| & \leq & Ke^{-\alpha(s-t)} & \text{for } t < s \text{ with } t,s \in \mathbb{R}. \end{cases}$$

Existence of NE for $\dot{x} = F(t, x, p)$

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has an exponential dichotomy on $\mathbb{R}$, *then*

- *For any* $p \in B_\delta(0)$, *the system* $\dot{x} = F(t, x, p)$ *has a unique NE such that* $t \mapsto x^*(t, p) \in \Omega$ *for any* $t \in \mathbb{R}$ *and* $x^*(t, 0) = \overline{x}(t)$.
- *The map* $p \mapsto x^*(t, p)$ *is continuously differentiable.*

The property of exponential dichotomy emulates the hyperbolicity condition for the equilibria in the autonomous case. This is due to the fact that any solution $t \mapsto u(t)$ of the linear system can be splitted as

$$u(t) = U(t, t_0)u(t_0) = \underbrace{U(t, t_0)P(t_0)u(t_0)}_{\text{Contraction}} + \underbrace{U(t, t_0)[I - P(t_0)]u(t_0)}_{\text{Expansion}}$$

Existence of NE for $\dot{x} = F(t,x,p)$

Lemma (C. Pötzsche (2011))

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$$\dot{u} = A(t)u \qquad \text{where } A(t) := D_x F(t, \overline{x}(t), 0).$$

has an exponential dichotomy on $\mathbb{R}$, then

- *For any $p \in B_\delta(0)$, the system (8) has a unique NE such that $t \mapsto x^*(t,p) \in \Omega$ for any $t \in \mathbb{R}$ and verifies $x^*(t,0) = \overline{x}(t)$.*
- *The map $p \mapsto x^*(t,p)$ is continuously differentiable.*

A particular (but important) case of exponential dichotomy is the uniform exponential stability: there exists positive constants (K, α) such that the transition matrix $U(t,s)$ satisfies

$$||U(t,s)|| \quad \leq \quad K e^{-\alpha(t-s)} \quad \text{for } t \geq s \text{ with } t, s \in \mathbb{R}$$

Lemma

If a time–varying ecological network described by the system

$$\dot{x} = F(t,x,p) \quad \text{with } A(t) = D_x F(t,\overline{x}(t),0)$$

verifies **(A1)–(A2)** *and* $\dot{u} = A(t)u$ *has an exponential dichotomy on* $\mathbb{R}$*, then the network has a sensitivity function* $t \mapsto S(t) = \frac{\partial x^*}{\partial p}(t,p)\,|_{p=0}$ *which is solution of the MDE:*

$$S'(t) = A(t)S(t) + B(t) \;\; \text{with} \;\; B(t) = D_p F(t,\overline{x}(t),0)$$

Sketch of proof:

- If $p \in B_\delta(0)$, by Pötzsche's Lemma there exists a unique NE:

$$x^*(t,p) = x^*(t_0,p) + \int_{t_0}^{t} F(s,x^*(s,p),p)\,ds.$$

- Taking partial derivatives with respect to p gives

$$\frac{\partial x^*}{\partial p}(t,p) = \frac{\partial x^*}{\partial p}(t_0,p) + \int_{t_0}^{t}\Big[D_x F(s,x^*(s,p),p)\frac{\partial x^*}{\partial p}(s,p) + D_p F(s,x^*(s,p),p)\Big]$$

Lemma

If a time–varying ecological network described by the system

$$\dot{x} = F(t,x,p) \quad \text{with } A(t) = D_xF(t,\overline{x}(t),0)$$

verifies **(A1)–(A2)** *and* $\dot{u} = A(t)u$ *has an exponential dichotomy on* $\mathbb{R}$*, then the network has a sensitivity function* $t \mapsto S(t) = \frac{\partial x^*}{\partial p}(t,p)\,|_{p=0}$ *which is solution of the MDE:*

$$S'(t) = A(t)S(t) + B(t) \;\; \text{with} \;\; B(t) = D_pF(t,\overline{x}(t),0)$$

- Taking partial derivatives with respect to p gives

$$\frac{\partial x^*}{\partial p}(t,p) = \frac{\partial x^*}{\partial p}(t_0,p) + \int_{t_0}^{t}\Big[D_xF(s,x^*(s,p),p)\frac{\partial x^*}{\partial p}(s,p) + D_pF(s,x^*(s,p),p$$

- We evaluate at $p = 0$:

$$S(t) = S(t_0) + \int_{t_0}^{t} \left[D_xF(s,\overline{x},0)S(s) + D_pF(s,\overline{x}(s),0)\right] ds.$$

Lemma

If a time–varying ecological network described by the system

$$\dot{x} = F(t,x,p) \quad \text{with } A(t) = D_x F(t,\overline{x}(t),0)$$

verifies **(A1)–(A2)** *and* $u' = A(t)u$ *has an exponential dichotomy on* $\mathbb{R}$*, then the network has a sensitivity function* $t \mapsto S(t) = \frac{\partial x^*}{\partial p}(t,p) \mid_{p=0}$ *which is solution of the MDE:*

$$S'(t) = A(t)S(t) + B(t) \;\; \text{with} \;\; B(t) = D_p F(t,\overline{x}(t),0)$$

- We evaluate at $p=0$:

$$\begin{aligned} S(t) &= S(t_0) + \int_{t_0}^{t} \left[D_x F(s,\overline{x},0)S(s) + D_p F(s,\overline{x}(s),0) \right] ds \\ &= S(t_0) + \int_{t_0}^{t} \left[A(s)S(s) + B(s) \right] ds \end{aligned}$$

- We recover the classical sensitivity matrix differential equation

$$S'(t) = A(t)S(t) + B(t)$$

and the result follows $\square$

Theorem (Ramos, R., Sepúlveda)

If a time–varying ecological network described by the previous system verifies the properties **(A1)–(A2)** *such that the linear system*

$$u' = A(t)u \quad (\text{where } A(t) = D_x F(t, \overline{x}(t), 0))$$

is uniformly exponentially stable (UES) then:

a) *There exists a unique sensitivity function* $S_\infty(t)$ *bounded on* $(-\infty, +\infty)$, *which is defined by*

$$S_\infty(t) := \int_{-\infty}^{t} U(t,\tau)B(\tau)\,d\tau. \tag{12}$$

b) *Any sensitivity matrix* $S(t)$ *such that* $S(0) \neq S_\infty(0)$ *verifies*

$$\lim_{t\to+\infty} ||S(t) - S_\infty(t)|| = 0. \tag{13}$$

- To prove the Theorem, let us recall that uniform exponential stability is a particular case of exponential dichotomy with $P = I$.
- The sensitivity matrix $S(t)$ verifies

$$\underbrace{S'(t) = A(t)S(t)}_{Exponential\ Dichotomy} + \underbrace{B(t)}_{Bounded\ Function}$$

- Admissibility results (Perron, Massera) allows to prove the existence of a <u>unique</u> bounded solution

$$S_{\infty}(t) = \int_{-\infty}^{t} U(t,s)P(s)B(s)\,ds - \int_{t}^{+\infty} U(t,s)[I - P(s)]B(s)\,ds$$

- As $P = I$ we have that

$$S_{\infty}(t) = \int_{-\infty}^{t} U(t,s)B(s)\,ds$$

- If $S(t)$ is other sensitivity matrix, then $V(t) = S_{\infty}(t) - S(t)$ verifies

$$V'(t) = A(t)V(t) \quad \text{which is UAS and } V(t) \to 0.$$

Corollary (Ramos, R., Sepúlveda)

If an ω–periodic ecological network verifies the properties **(A1)–(A2)** *such that the linear periodic system*

$$u' = A(t)u \quad (\text{where } A(t) = D_x F(t, \overline{x}(t), 0))$$

is uniformly exponentially stable (UES) then:

a) *There exists a unique sensitivity function $S_\infty(t)$ bounded on $(-\infty, +\infty)$, which is defined by*

$$S_\infty(t) := \int_{-\infty}^{t} U(t,\tau)B(\tau)\, d\tau \quad \textit{and} \quad S_\infty(t+\omega) = S_\infty(t). \tag{14}$$

b) *Any sensitivity matrix $S(t)$ such that $S(0) \neq S_\infty(0)$ verifies*

$$\lim_{t \to +\infty} ||S(t) - S_\infty(t)|| = 0. \tag{15}$$

Autonomous case: $S(t) = -A^{-1}B = -C^{-1}$

- Given the static equilibrium $\overline{x}$, we can verify that

$$DG(\bar{x}) := A = \mathrm{Diag}\{\overline{x}_1, \ldots, \overline{x}_n\}C \quad \text{and} \quad B = \mathrm{Diag}\{\overline{x}_1, \ldots, \overline{x}_n\}$$

- Let us assume that the linear system

$$\dot{u} = BC\,u \quad \text{that is } U(t,s) = e^{BC(t-s)}$$

is uniformly exponentially stable (that is BC is a Hurwitz matrix),

- Then, any sensitivity matrix is attracted to the bounded matrix

$$\begin{aligned}
S_\infty(t) &= \int_{-\infty}^t U(t,s)\underbrace{\mathrm{Diag}\{\overline{x}_1, \ldots, \overline{x}_n\}}_{=B}\,ds \\
&= \left(\int_{-\infty}^t e^{BC(t-s)}B\,ds\right) CC^{-1} \\
&= e^{BCt}\left(\int_{-\infty}^t e^{-BCs}BCds\right) C^{-1} = e^{BCt}\left(\int_{-\infty}^t -\frac{d}{ds}e^{-BCs}ds\right) A^{-1} \\
&= e^{-BCt}\left\{-e^{BCt}+0\right\} C^{-1} = -C^{-1} = -A^{-1}B.
\end{aligned}$$

Ergodic Results arising from $S'_\infty(t) = A(t)S_\infty(t) + B(t)$

If the sensitivity matrix $t \mapsto S_\infty(t)$ is ω–periodic, its average is well defined

$$\mathcal{M}\{S_\infty\} = \frac{1}{\omega}\int_0^\omega S_\infty(t)\,dt.$$

Corollary

If $\mathcal{M}\{A\}$ is invertible, it follows that

$$\mathcal{M}\{S_\infty\} = -\mathcal{M}\{A\}^{-1}\left\{\mathcal{M}\{B\} + \mathrm{Cov}(A, S_\infty)\right\}$$

where

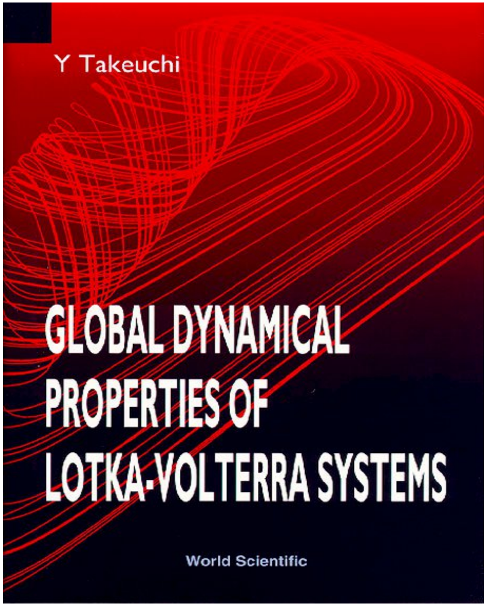
$$\mathrm{Cov}(A, S_\infty) := \frac{1}{\omega}\int_0^\omega [A(t) - \mathcal{M}\{A\}][S_\infty(t) - \mathcal{M}\{S_\infty\}]\,dt$$

The proof follows from $\mathcal{M}\{AS_\infty\} = \mathcal{M}\{A\}\mathcal{M}\{S_\infty\} + \mathrm{Cov}(A, S_\infty)$.

Agenda

a) *A short review of the state of art (autonomous case).*
b) *New results for the nonautonomous framework*
c) *An iconic example: generalized Lotka–Volterra system*.

Part III: An iconic example



We will apply our results to a generalized Lotka–Volterra system.

Periodic Lotka Volterra System (1)

- Let us consider the nonautonomous Lotka–Volterra system

$$\dot{x}_i = x_i \left\{ b_i(t) - \sum_{j=1}^{n} a_{ij}(t) x_j \right\}; \quad n \geq 1;\, i = 1, \ldots, n, \tag{16}$$

where the functions $b_i \colon \mathbb{R} \to \mathbb{R}$ and $a_{ij} \colon \mathbb{R} \to \mathbb{R}$ are strictly positive, continuous and ω–periodic. The system (16) can also be written as

$$\dot{x} = x \left\{ b(t) - C(t)x \right\}, \quad \text{with } C(t) = \{a_{ij}(t)\}_{i,j} \tag{17}$$

- We introduce the following notation:

$$b_i^\ell := \min_{t \in [0,\omega]} b_i(t), \quad b_i^u := \max_{t \in [0,\omega]} b_i(t), \quad a_{ij}^\ell := \min_{t \in [0,\omega]} a_{ij}(t), \quad a_{ij}^u := \max_{t \in [0,\omega]} a_{ij}(t)$$

Periodic Lotka–Volterra system (2)

- Moreover, we will assume that

$$b_i^\ell > \sum_{j=1, j\neq i}^{n} a_{ij}^u (b_j^u / a_{jj}^\ell) \quad \text{for any } i = 1, \ldots, n. \tag{18}$$

Theorem (Gopalsamy (1985))

If the inequality (18) is verified and there exist $\alpha > 0$ such that

$$\min_{t\in[0,\omega]} a_{jj}(t) > \left\{ \sum_{j=1, j\neq i}^{n} \max_{t\in[0,\omega]} a_{ij}(t) \right\} + \alpha \quad j = 1, \ldots, n. \tag{19}$$

Then the system has an ω–periodic and GAS solution $t \mapsto \overline{x}(t) \in \Omega$.

- Gopalsamy's Theorem implies that (A1) is satisfied.

Periodic Lotka–Volterra system with press perturbations

- Given the unique ω–periodic solution $t \mapsto \overline{x}(t)$, we can verify that

$$DF_x(t,\bar{x}(t)) = \mathrm{Diag}\{\overline{x}_1(t),\ldots,\overline{x}_n(t)\}C(t)+\mathrm{Diag}\{b_i(t)-\Sigma_{j=1}^{n} a_{ij}(t)\overline{x}_j(t)\}_i$$

- It can be proved[3] that the linear system

$$\dot{u} = D_x F(t,\bar{x}(t))u$$

is uniformly exponentially stable,

- Any sensitivity matrix is attracted to the bounded sensitiviy matrix

$$S_\infty(t) = \int_{-\infty}^{t} U(t,s)\,\mathrm{Diag}\{\overline{x}_1(s),\ldots,\overline{x}_n(s)\}\,ds \quad \text{with} \quad S_\infty(t+\omega) = S_\infty(t).$$

[3] We follow ideas from A.C. Lazer: "Characteristic exponents and diagonally dominant linear differential equations" J. Math. Anal. Appl., (35) 1971: 215–229.

Numerical example (1)

- Let us consider the Lotka–Volterra system with press perturbations:

$$\begin{cases} \dot{x}_1 &= x_1\left(4+\sin\left(\frac{t}{2\pi}\right)-0.9x_1-0.2x_2-0.2x_3+p_1\right) \\ \dot{x}_2 &= x_2\left(2.5+0.5\sin\left(\frac{t}{2\pi}\right)-0.2x_1-0.8x_2-0.2x_3+p_2\right) \\ \dot{x}_3 &= x_3\left(2.5+0.5\cos\left(\frac{t}{2\pi}\right)-0.2x_1-0.2x_2-0.7x_3+p_3\right). \end{cases} \tag{20}$$

- It is easy to verify that the system satisfies Gopalsamy's conditions.

Indeed, note that: $b_1^u=5$, $b_2^u=3$, $b_3^u=3$, and

$$3=b_1^\ell > c_{12}b_2^u/c_{22}^\ell + c_{13}b_3^u/c_{33} \approx 1.607,$$

$$2=b_2^\ell > c_{21}b_1^u/c_{11}^\ell + c_{23}b_3^u/c_{33} \approx 1.968,$$

$$2=b_3^\ell > c_{31}b_1^u/c_{11}^\ell + c_{32}b_2^u/c_{22} \approx 1.861.$$

- On the other hand diagonal dominance is satisfied since we have:

$$\begin{aligned} c_{11}=0.9 &> 0.2+0.2, \\ c_{22}=0.8 &> 0.2+0.2, \\ c_{33}=0.7 &> 0.2+0.2. \end{aligned}$$

Numerical example (1)

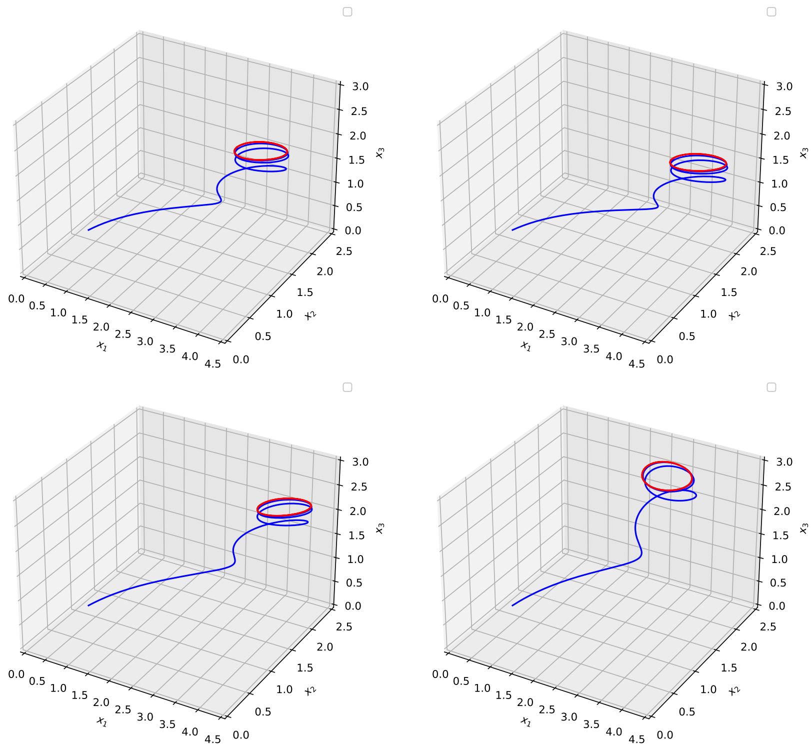


Figure 5: Periodic solution (red) and a convergent solution (blue).

Numerical example (2)

$$S_\star(t) =$$

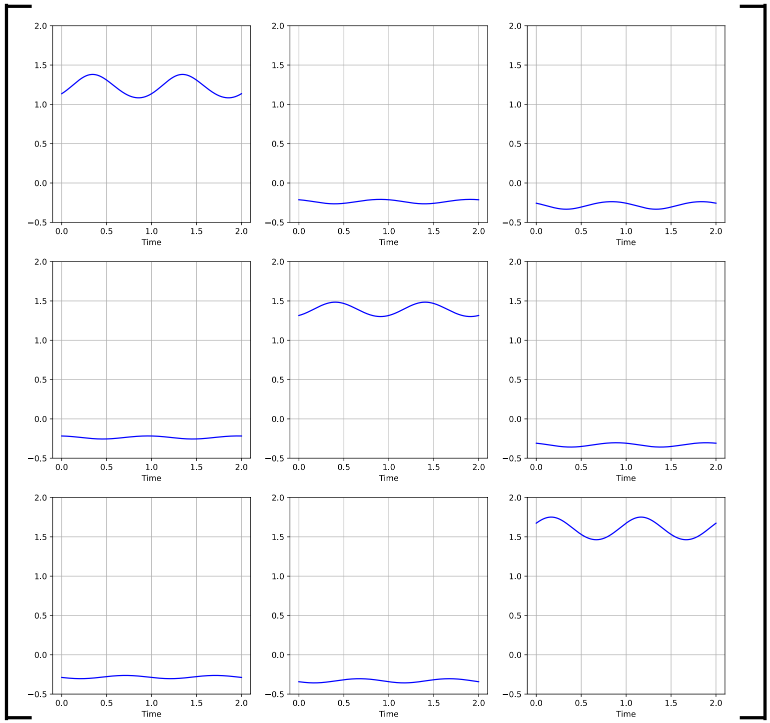


Figure 6: The time-varying sensitivity matrix . Each plot in the position i, j represents the change in the periodic trajectory of species i after a perturbation is exerted on species j.

Numerical example (2)

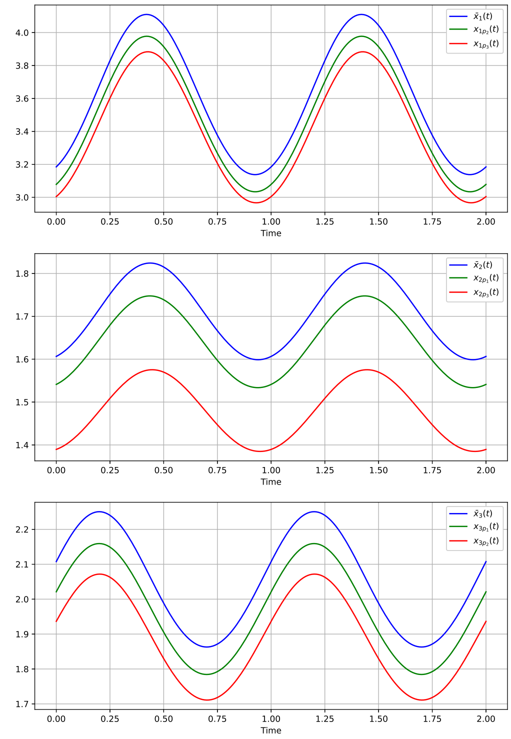


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Figure 8: ¡Muchas gracias por su cordial invitación!