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SENSITIVITY MATRIX OF AN ECOLOGICAL NETWORK WITH PERIODIC DYNAMICS

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We study an ecological network composed by a set of interacting populations whose dynamics are governed by a non–autonomous ω–periodic ODE system, which has a unique solution ω–periodic and globally attractive. By following the chain rule approach combined with the Implicit Function Theorem, we deduce some identities between the community and the sensitivity matrix. The result generalizes the one obtained by Bender *et.al.* [1] and Nakajima [12],[15] for autonomous ODE systems having a unique stable equilibrium point. Our findings constitute a first step towards predicting the response of cyclic populations to sustained external perturbations.

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1. Introduction

1.1. *Preliminaries*

The purpose of this note is to study the sensitivity matrix (an explicit definition will be given later) of a periodic ecological network composed of n species and described by the following system of ordinary differential equations:

$$\begin{cases} \dot{x}_1 = g_1(t, x_1, \ldots, x_n), \\ \vdots \\ \dot{x}_n = g_n(t, x_1, \ldots, x_n), \end{cases} \tag{1}$$

or equivalently:

$$\dot{x} = g(t, x), \tag{2}$$

with n species, whose densities are defined by $x = (x_1, \ldots, x_n)^T$ and their dynamic behavior is described by $g(t,x) = \big(g_1(t,x), \ldots, g_n(t,x)\big)^T$. The function $g(\cdot,\cdot)$ is assumed to be continuously differentiable with respect to x and continuous ω–periodic with respect to t, *i.e.*,

$$g(t+\omega, x) = g(t,x) \quad \text{for any} \quad x \in \mathbb{R}^n \quad \text{and} \quad t \in \mathbb{R}. \tag{3}$$

Several ecological networks with periodic coefficients and periodic solutions have been considered in the mathematical literature, for example: predator–prey systems and trophic chains have been studied by several authors as Cui [4], Cushing [5], Eilbeck *et.al.* [6], Gopalsamy [8,9], Ortega [16], Takimoto *et.al.*, [19], Anh [20], Scheffer *et.al* [18], Zhongua *et.al.* [27]. Chemostats have been studied by Wolkowicz [21] and Yang [25], between others.

There exist two types of effects propagated from the i–th species to the j–th species in the network (1):

- **Indirect effects:** which are propagated along either a third k-th species (*i.e.*, $i \to k \to j$) or a chain of member species (*i.e.*, $i \to k_1 \to k_2 \to \ldots \to k_p \to j$ such that $k_\ell \neq i, j$ for any $\ell \in \{1, \ldots, p\}$).
- **Direct effects:** which are propagated by the direct interactions between the i–th and j–th species (*i.e.*, $i \to j$).

The distinction between direct and indirect effects is important. It is recognized nowadays that the responses of ecological communities to environmental changes can not be predicted based only on the structure of direct effects among species. Instead, it is the interplay between direct and indirect effects which finally dictates how community responds to perturbations [22]. Furthermore, indirect effects could be even more important than direct effects as drivers of shifts in community structure triggered by environmental stimuli [14,23].

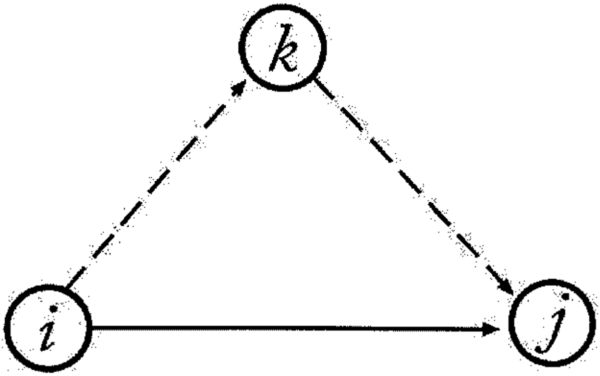

Figure 1. The direct effect propagated from the i–th species i to the j–th species is represented by the solid line. The indirect effect propagated through the k–th species is represented by the path composed by the dashed lines.

There exists an extensive theoretical literature devoted to the study of indirect effects and their relation with direct ones, see *e.g.*, Bender *et.al*, [1], Higashi *et.al.*, [10,11,12] and Nakajima [15]. The concept of sensitivity matrix (total effects matrix) plays a key role in this scenario.

1.2. *Sensitivity matrix: an overview*

As pointed out by Borrett *et.al.* [2], most part of theoretical studies of indirect effects have considered stationary networks, *i.e.*, time invariant systems of differential equations of type:

$$\begin{cases} \dot{x}_1 = g_1(x_1, \ldots, x_n), \\ \vdots \\ \dot{x}_n = g_n(x_1, \ldots, x_n) \end{cases} \tag{4}$$

where x_i and $g_i(\cdot)$ are the abundance and the rate of change, respectively, of the species $i \in \{1, \ldots, n\}$.

For simplicity, we consider a shorter notation:

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

where $x = \mathrm{col}(x_1, \ldots, x_n)$ and $g(x) = \big(g_1(x), \ldots, g_n(x)\big)^T$. Moreover, the function $g\colon \mathbb{R}^n \mapsto \mathbb{R}^n$ is sufficiently smooth such that (4) satisfies the following properties:

(C1) The network (4) has a unique componentwise positive equilibrium point $x^* = (x_1^*, \ldots, x_n^*) \in \mathrm{Int}(\mathbb{R}_+^n)$. Moreover, all the eigenvalues of the matrix:

$$A = \{a_{ij}\} \quad \text{with} \quad a_{ij} = \frac{\partial g_i}{\partial x_j}(x^*), \quad \text{and} \quad i,j = 1, \ldots, n; \tag{6}$$

have negative real parts.

(C2) The perturbed system

$$\dot{x} = g(x) + z, \quad \text{with some} \quad z = (z_1, \ldots, z_n)^T \in \mathbb{R}^n, \tag{7}$$

has a unique componentwise positive equilibrium $\hat{x}(z) = (\hat{x}_1(z), \ldots, \hat{x}_n(z)) \in \mathrm{Int}(\mathbb{R}_+^n)$, which is dependendent on the perturbation z as follows:

i) In absence of perturbation, we have that $\hat{x}(0) = x^*$.
ii) The derivative $\partial \hat{x}_i(z)/\partial z_j$ exists when the perturbation z is small in some sense.

Remark 1.1. Property **(C1)** states that the equilibrium x^* is locally asymptotically stable, *i.e.*, there exists $\varepsilon > 0$ such that for any solution $x(t)$ of (4) satisfying $||x(0) - x^*|| < \varepsilon$ (here, $||\cdot||$ denotes a norm in $\mathbb{R}^n$). It follows that $\lim\limits_{t \to +\infty} x(t) = x^*$. In addition, the matrix A displays the *direct effects* between species in the network.

Remark 1.2. By following the seminal work of Bender *et.al.* and [1] Yodzis [26], the system (7) describes a *press perturbation* of (5), where the perturbation z_i represents a permanent artificial flow (either positive or negative) introduced to control the abundance of the species x_i $(i = 1, \ldots, n)$.

Remark 1.3. The property **(C2)** is a direct consequence of the Implicit Function Theorem [13]. Observe that **(C1)**–**(C2)** are satisfied for any Lotka–Volterra system having a positive stable equlibrium.

Given a disturbance (press perturbation) z_i on the i–th species, the properties **(C1)**–**(C2)** allow to study its total effect (direct plus indirect) on the j–th species [15] by means of the sensitivity matrix S, whose coefficients s_{ij} represent the sensitivity of the abundance x_i to changes in the perturbation z_j, more specifically:

$$S = \{s_{ij}\} \quad \text{with} \quad s_{ij} = \lim_{z \to 0} \frac{\partial \hat{x}_i}{\partial z_j}(z) \quad \text{and} \quad i, j = 1, \ldots, n. \tag{8}$$

Finally, by using the chain rule (see, *e.g.*, [15]), it can be deduced that the matrices A and S, satisfy the following property:

$$S = -A^{-1}, \tag{9}$$

which says that the total effects between species can be computed from the set of direct effects. The invertibility of A is a consequence of **(C1)**.

Remark 1.4. The identity (9) is a useful tool for studying the indirect effects and its impact in ecologic networks [12]. Indeed, the identity says that: i) the study of the matrix A can describe the changes in population arising from a press perturbation. ii) An empirical estimation of the coefficients of the matrix A can be obtained by carrying out a press pertubation to the network (4).

Nevertheless, a key assumption is that the species are in a locally stable equilibrium x^*, potentially achievable in an homogeneous environment in time (*i.e.,* described by autonomous differential equations). A question of particular interest is to extend the previous results to ecological networks of fluctuating environments and more complex types of equilibria.

In particular, the novelty of this note is to study the sensitivity matrix of an ω–periodic network with an ω–periodic equilibrium.

2. Assumptions

The following assumption about of network (1) will play a fundamental role:

- **(P1)** The network (1) has a unique ω–periodic solution denoted by $p(t)$, which is asymptotically stable, *i.e.*, there exists $\varepsilon > 0$ such that for any solution $x(t)$ of (1) with initial conditions satisfying $||x(0) - p(0)|| < \varepsilon$, it follows that $\lim_{t \to +\infty} (p(t) - x(t)) = 0$.

Let us define $u(\cdot) = x(\cdot) - p(\cdot)$ and observe that the linearization of (1)–(2) along the ω–periodic curve solution $(t, p(t))$ (with, $-\infty < t < +\infty$) leads to the linear system

$$\dot{u} = A(t)u, \tag{10}$$

where the matrix $A(t)$ is defined as follows

$$A(t) = \{a_{ij}(t)\} \quad \text{with} \quad a_{ij}(t) = \frac{\partial g_i}{\partial x_j}(t, p(t)). \tag{11}$$

Let $\Phi(t)$ be the fundamental matrix of (10), *i.e.*, $\dot{\Phi}(t) = A(t)\Phi(t)$. By using Floquet's theory [24], it follows that there exists a nonsingular ω–periodic matrix $P(t)$ and a constant complex matrix Q such that

$$\Phi(t) = P(t)e^{Qt},$$

and a consequence of **(P1)** is that all the eigenvalues of Q have negative real parts. In addition, the change of variables $u = P(t)z$ transforms (10) into:

$$\dot{z} = Qz. \tag{12}$$

2.1. *Averaging techniques*

Let $f\colon \mathbb{R} \mapsto \mathbb{R}$ be a continuous ω–periodic function. The mean value of f and its variance, namely $\mathcal{M}\{f\}$ and $\text{var}\{f\}$ are defined respectively, in analogy to statistical measures as follows (see *e.g.*, Puccia *et.al.*[17]):

$$\mathcal{M}\{f\} = \frac{1}{\omega}\int_0^{\omega} f(s)\,ds \quad \text{and} \quad \text{var}\{f\} = \frac{1}{\omega}\int_0^{\omega} [f(s) - \mathcal{M}\{f\}]^2\,ds. \tag{13}$$

When f and g are continuous ω–periodic functions, the covariance between f and g, is defined by

$$\text{cov}(f,g) = \frac{1}{\omega}\int_0^{\omega} [f(s) - \mathcal{M}\{f\}][g(s) - \mathcal{M}\{g\}]\,ds. \tag{14}$$

Similar definitions can be given for ω–periodic matrices $A(t)$, where each entry $a_{ij}(t)$ is a continuous ω–periodic function. Indeed

$$\mathcal{M}\{A\} = \begin{bmatrix} \mathcal{M}\{a_{11}\} & \mathcal{M}\{a_{12}\} & \cdots & \mathcal{M}\{a_{1n}\} \\ \mathcal{M}\{a_{21}\} & \mathcal{M}\{a_{22}\} & \cdots & \mathcal{M}\{a_{2n}\} \\ \vdots & \vdots & \ddots & \vdots \\ \mathcal{M}\{a_{n1}\} & \mathcal{M}\{a_{n2}\} & \cdots & \mathcal{M}\{a_{nn}\} \end{bmatrix}.$$

3. Extending the theory to the periodic case (some results)

In general, the modeling of ecological networks by autonomous system (4) is a consequence of considering several parameters as constants. Nevertheless, some of them can experiment seasonal or cyclic variations (birth rates, death rates, migration rates, inputs of resources, etc.). In consequence, the exclusive use of (4) can limit in some cases the study of direct/indirect effects described in the previous section. By this reason, we consider the more general case described by (1).

Let us consider a press perturbation to the network (1)

$$\begin{cases} \dot{x}_1 = g_1(t, x_1, \dots, x_n) + z_1, \\ \vdots \\ \dot{x}_n = g_n(t, x_1, \dots, x_n) + z_n. \end{cases} \tag{15}$$

The implicit function theorem allows us to prove the following result [3]:

Proposition 3.1. *If* **(P1)** *is satisfied and the perturbations z satisfy the inequality*

$$\sqrt{z_1^2 + z_2^2 + \ldots + z_n^2} < \delta \tag{16}$$

for some $\delta > 0$ sufficiently small, then the system (15) *has a unique solution*

$$q(t, z) = \operatorname{col}\big(q_1(t, z_1, \dots, z_n), \dots, q_n(t, z_1, \dots, z_n)\big), \tag{17}$$

which is continous and ω-periodic in t and differentiable in z satisfying (16). *In addition, $q(t, 0) = p(t)$.*

Proposition 3.1 allow us to define a generalized sensitivity matrix as follows:

$$S(t) = \{s_{ij}(t)\} \quad \text{with} \quad s_{ij}(t) = \frac{\partial q_i}{\partial z_j}(t, 0), \tag{18}$$

with $q_i(t, z)$ given by (17).

Lemma 3.1. *The sensitivity matrix* (18) *is ω-periodic.*

Proof. Let $e_j = (\delta_{1j}, \delta_{2j}, \dots, \delta_{nj})$, where $\delta_{ij} = 0$ when $i = j$ and 0 otherwise. Observe that:

$$\frac{\partial q_i}{\partial z_j}(t + \omega, z) = \lim_{\Delta \to 0} \frac{q_i(t + \omega, z + \Delta e_j) - q_i(t + \omega, z)}{\Delta}$$

$$= \lim_{\Delta \to 0} \frac{q_i(t, z + \Delta e_j) - q_i(t, z)}{\Delta},$$

where the last identity follows from ω-periodicity of $q(\cdot, z)$, ensured by Proposition 3.1. In consequence, we have that

$$\frac{\partial q_i}{\partial z_j}(t + \omega, z) = \frac{\partial q_i}{\partial z_j}(t, z)$$

and the Lemma follows by letting $z \to 0$. □

Theorem 3.1. *The sensitivity matrix satisfy the identity:*

$$\frac{1}{\omega}\int_0^\omega A(t)S(t)\,dt = -I. \tag{19}$$

Given an ω–periodic function $B(\cdot)$, we can define its A–weighted average as follows:

$$\mathcal{M}_A\{B\} = \frac{1}{\omega}\int_0^\omega A(t)B(t)\,dt.$$

On the other hand, we can define an equivalence relation in the set ω–periodic matrices:

$$S_1(\cdot) \sim S_2(\cdot) \iff \mathcal{M}_A\{S_1 - S_2\} = 0.$$

In consequence, the sensitivity matrix has to be in the same equivalence class of $-A(\cdot)^{-1}$, which means that $S(\cdot)$ and $-A^{-1}(\cdot)$ differs only in a function with null A–weighted average.

By using the covariance definition (14) for the matrices $A(t)$ and $S(t)$, we obtain the following identity:

Corollary 3.1. *The sensitivity matrix satisfy the identity:*

$$\mathcal{M}\{S\} = -\mathcal{M}\{A\}^{-1}\Big\{I + \mathrm{cov}(A,S)\Big\}. \tag{20}$$

Proof. Observe that

$$\begin{aligned}
\mathrm{cov}(A,S) &= \frac{1}{\omega}\int_0^\omega [A(r) - \mathcal{M}\{A\}][S(r) - \mathcal{M}\{S\}]\,dr,\\
&= \frac{1}{\omega}\int_0^\omega A(r)S(r)\,dr - \frac{1}{\omega}\int_0^\omega A(r)\,dr\mathcal{M}\{S\}\\
&\quad -\mathcal{M}\{A\}\frac{1}{\omega}\int_0^\omega S(r)\,dr + \mathcal{M}\{A\}\mathcal{M}\{S\},\\
&= -I - \mathcal{M}\{A\}\mathcal{M}\{S\},
\end{aligned}$$

where the last identity is ensured by (19). □

Observe that (4) is a particular case of (1). In this context, **(C1)**–**(C2)** is a particular case of **(P1)**. By using (13), it follows that when A and S are constants, then $\mathrm{cov}(A,S) = 0$ and (20) reduces to (9).

4. Conclusion and future directions

The study of time–varying ecological networks presents several difficulties in comparison with stationary ones. Indeed, from a mathematical point of view, the network (1) is a non–autonomous ODE system, whose qualitative theory is far more complex (and less complete) in comparison with the autonomous case. On the other hand, from an ecological point of view, Lemma 3.1 suggests that the total effects matrix has cyclical variations: these facts make interesting and at the same time difficult the study of direct/indirect effects in (1): to determinate which results obtained for autonomous models remain valid for time varying ones is an open question.

We have deduced some identities concerning the sensitivity matrix for an ω–periodic ecological network having a unique locally asymptotically stable periodic solution. The Theorem 3.1 and Corollary 3.1 can be seen as averaged versions of identity (9).

This note is a first stage to studying indirect effects in time varying ecological networks. Indeed, several problems remain to be solved. They are summarized as follows:

- In an ω–periodic context, we hope to use identities (19)–(20) in order to obtain similar results as those described in Remark 1.4. In particular, to quantify the relation between direct/indirect effects.
- To consider the network (1) as a perturbation of the averaged system:

  $$y' = f(y) = \frac{1}{\omega}\int_0^{\omega} g(t,y)\,dt.$$

  This autonomous system (in special, when has an stable equilibrium) is interesting since provides another way to consider "in average" the direct/indirect effects. In this case, it is easy to compute its sensitivity matrix. An open question is to study its relation with the sensitivity matrix (18).
- It would be of interest to extend this analysis to the case where the network (1) is Bohr almost periodic [7] with respect to t. This is reasonable since almost periodic motions have biological sense and its average properties generalizes the periodic ones.
- It is necessary to compare our approach with other works considering time variable ecological networks: the work of Takimoto *et.al.* [19] considers a system of one consumer, two resources and one subsidy, which has periodical inputs. The autors employ a method of time scale separation combined with press perturbations and dis-

covers that the time scale hierarchy helps to study indirect effects. In addition, the work of Borret *et.al.* [2] studies the relation between the length of paths $i \to k_1 \to k_2 \to \ldots \to k_p \to j$ and the speed of propagation of indirect effects by using the technique of network environment analysis.

Appendix: Proof of Theorem 3.1

By using the ω–periodicity of solution $q(t,z)$, it follows that

$$q_i(\omega,z) - q_i(0,z) = \int_0^\omega g_i(t, q_1(t,z), \ldots, q_n(t,z))\, dt + z_i\omega = 0.$$

for any $i = 1, \ldots, n$.

Differentiating respect to z_j and using Leibnitz's rule, we obtain.

$$\int_0^\omega \sum_{k=1}^n \frac{\partial g_i(t,q(t,z))}{\partial x_k} \frac{\partial q_k(t,z)}{\partial z_j}\, dt + \delta_{ij}\omega = 0,$$

which can be rewritten as:

$$\frac{1}{\omega}\int_0^\omega \sum_{k=1}^n \frac{\partial g_i(t,q(t,z))}{\partial x_k} \frac{\partial q_k(t,z)}{\partial z_j}\, dt = -\delta_{ij}, \tag{21}$$

where $\delta_{ij} = 1$ if $i = j$ and $\delta_{ij} = 0$ otherwise.

On the other hand, the continuity of the functions

$$\frac{\partial g_i(t,q(t,z))}{\partial z_k}, \quad \frac{\partial q_k(t,z)}{\partial z_j}, \quad \text{and} \quad q(t,z)$$

in a neighborhood of $z = 0$, implies that

$$\lim_{z\to 0} \frac{\partial g_i(t,q(t,z))}{\partial x_k} = \frac{\partial g_i}{\partial x_k}(t, p(t)) \tag{22}$$

and

$$\lim_{z\to 0} \frac{\partial q_k(t,z)}{\partial z_j} = \frac{\partial q_k}{\partial z_j}(t, 0). \tag{23}$$

By letting $z \to 0$ in (21) and using (22)–(23), it follows that:

$$\frac{1}{\omega}\int_0^\omega \sum_{k=1}^n \frac{\partial g_i(t,p(t))}{\partial x_k} \frac{\partial q_k(t,0)}{\partial z_j}\, dt = -\delta_{ij}.$$

By using (11) and (18), it follows that this last equality is equivalent to

$$\frac{1}{\omega}\int_0^\omega \sum_{k=1}^n a_{ik}(t) s_{kj}(t)\, dt = -\delta_{ij} \tag{24}$$

which is equivalent to (19) and the Theorem follows.

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