

An Open-System approach to ecological networks

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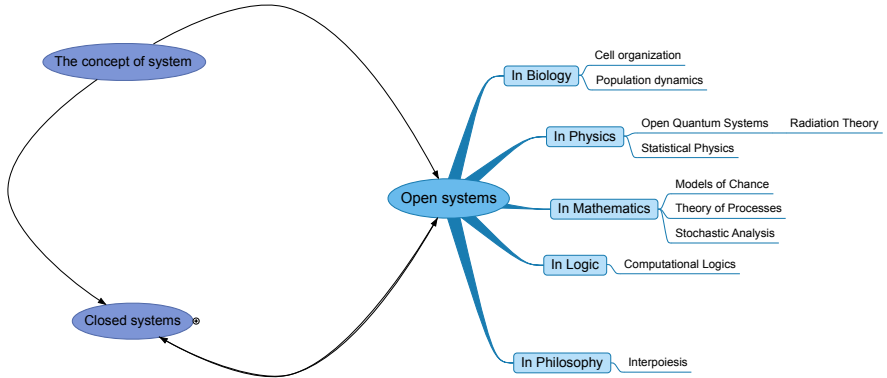
Examples based on joint work with S. Navarrete, S. Kéfi, S. Rojas and P. Marquet

1 Introduction: A view on Open Systems

- The dawn of open systems
- Stochastic methods are founded on the open system view on science

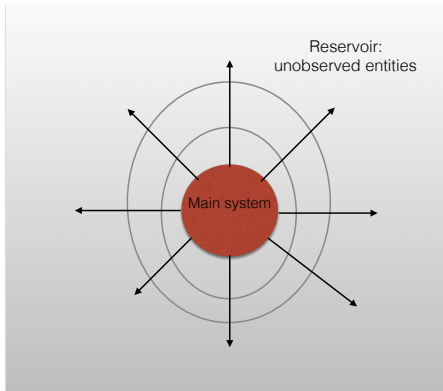
2 Applications to Complex Ecological Networks

- A general model
- Examples





The evolution of knowledge



Some basic questions

- What are the observables and the states?

Some basic questions

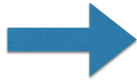
- What are the observables and the states?
- Time and space scales?

Some basic questions

- What are the observables and the states?
- Time and space scales?
- Noises?

Some basic questions

- What are the observables and the states?
- Time and space scales?
- Noises?



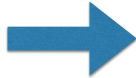
State (of Nature)



State (of Nature)



Flow (of life)



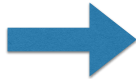
State (of Nature)



Flow (of life)

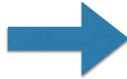


Observables
and
observations



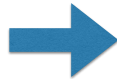
State (of Nature)

$\mathbb{E}$



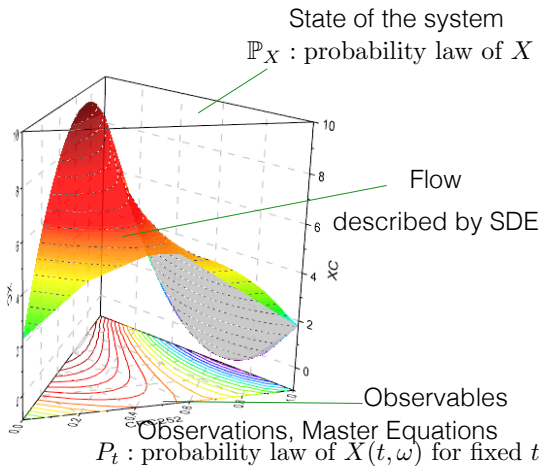
Flow (of life)

$X(t, \omega)$



Observables
and
observations

$f, f(X(t, \omega)), \mathbb{E}(f(X(t)))$



How do we obtain the state of the system?

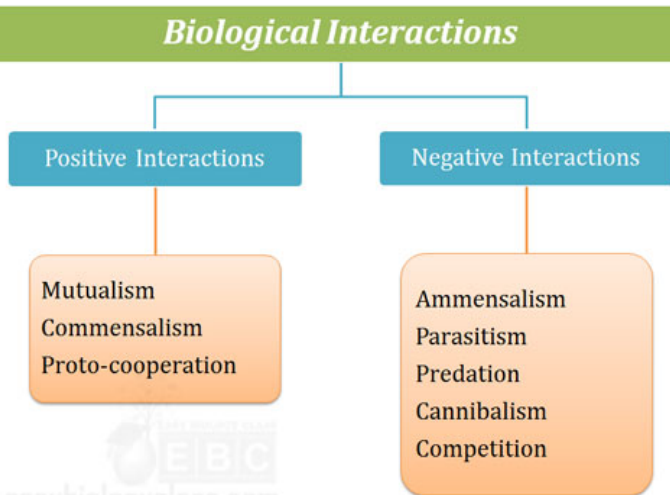
- Master equations only work under the Markov assumption
- In general, one has better information via the equations of the flow (where memory effects can be included)
- And one can try to approach the flow by a Markov one, (e.g. diffusion processes, Lévy Processes)

Open system approach—stochastic methods

Mathematical contributions from Stochastic Analysis

- Modeling via stochastic processes, stochastic differential equations, semigroup theory, partial differential equations
- Martingale methods
 - ▶ Martingale Problems, CLT, Diffusion Approximation
 - ▶ Law of Large Numbers and Ergodic Theory
 - ▶ Statistics of censored data
- Qualitative (geometric) analysis of Stochastic Dynamical Systems:: steady states, entropy functionals, production of entropy, equilibrium
- Stochastic Particles approach, stochastic numerics
- Algebraic (non commutative) Stochastic Analysis. In particular, Quantum Markov Semigroups
 - ▶ Model construction
 - ▶ Qualitative Analysis

Applications to Complex Ecological Networks



Mutualism



commensalism



Protocooperation



Ammensalism



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Parasitism



Predation



Cannibalism



Competition



Mathematical model of a complex biological network?

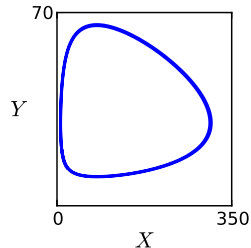
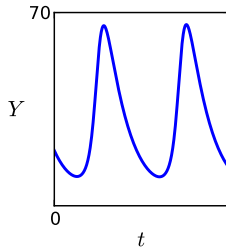
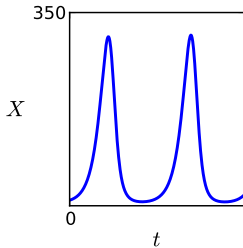
Traditionally, ecologists have been using systems of ordinary differential equations to model interactions (eg. Lotka-Volterra equations). However, these equations are adapted to closed-system descriptions.

The typical Lotka-Volterra equation, written in differential notation, is

$$dX(t) = [X(t)(r - \mu Y(t))]dt \quad (1)$$

$$dY(t) = [Y(t)(c\mu X(t) - d)]dt \quad (2)$$

The solutions to this system of equations are continuous -deterministic-functions. Typically, they looks like in the following pictures



In the above figures, $K_X = 350$, $K_Y = 30$, $r = 0.3$, $\mu = 0.01$, $c = 0.1$, $d = 0.08$.

According to this, an observation on the first species at time t say, is a function $f(X(t))$. The abundance of the species X at time t is the probability law of $X(t)$, which is a trivial probability -the Dirac measure $\delta_{X(t)}$ - which assigns the value 1 to any set containing $X(t)$ or 0 otherwise.

The equations (1), (2) describe a *closed dynamical system*, since no interaction with the environment is considered in its statement.

Including interactions

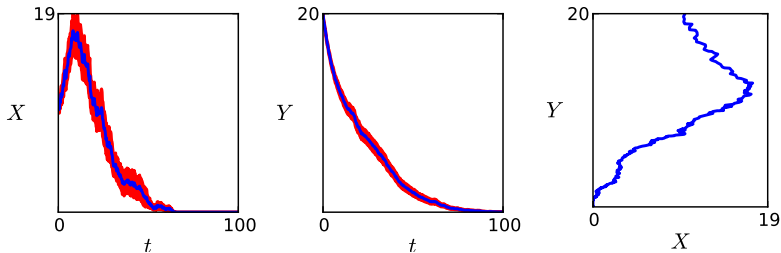
To include interactions in the form of very fast and frequent fluctuations, we add *noises* to the previous system of equations in the form

$$dX(t) = [X(t)(r - \mu Y(t))]dt + \sqrt{(K_X - X_t)^+ X_t} dW(t) \quad (3)$$

$$dY(t) = [Y(t)(c\mu X(t) - d)]dt + \sqrt{(K_Y - Y_t)^+ Y_t} dW(t), \quad (4)$$

where $W(t)$ is a Wiener or Brownian Motion stochastic process.

That is, this time, X and Y become stochastic processes $X(\omega, t)$, $Y(\omega, t)$, where ω is an element of a probability space. For each ω , we have one trajectory $t \mapsto X(\omega, t)$ of the process X . Here below we show 100 trajectories of the processes X , Y that solve (3) and (4). These are the pictures of the biomass flow.



An open system approach

We consider a main system of d -species -also called the *focal system*- defining a graph or network G . Each node i of the graph labels a species. Let us denote $x_i \in [0, 1]$ the proportion of biomass with respect to the carrying capacity of the species i . So that a vector

$$x = \begin{pmatrix} x_1 \\ \vdots \\ x_d \end{pmatrix} \in E = [0, 1]^d$$

represents the collection of species biomass proportions in the focal system.

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The transfer functions $\alpha_{i,j}$ between species are given in the form:

$$\alpha_{i,j}(x) = a_{i,j}(x)x_i, \quad (x \in E). \quad (5)$$

$$\begin{aligned}
dX_i(t) = & \left(\sum_{j=1, j \neq i}^d \alpha_{j,i}(X(t))X_i(t) - \sum_{j=1}^d \alpha_{i,j}(X(t))X_j(t) \right) dt \\
& + \sigma_i(X(t))dW(t) \\
& + \eta_i(X(t-))dZ_i(t), \quad (i = 1, \dots, d),
\end{aligned} \tag{6}$$

- W is a Brownian motion
- Z is an independent compound Poisson process:
 - ▶ N a canonical Poisson process
 - ▶ $(\xi_{i,n})_{i,n}$, $(1 \leq i \leq d; n \in \mathbb{N})$ i.i.d. Bernoulli random variables with values ± 1 , $p_i = \mathbb{P}(\xi_{i,n} = 1)$.

$$Z_i(t) = \sum_{k=1}^{N(t)} \xi_{i,k}, \quad Z(t) = \begin{pmatrix} Z_1(t) \\ \vdots \\ Z_d(t) \end{pmatrix}. \tag{7}$$

$$\begin{aligned}
 dX(t) &= X(t) \bullet \left([A_0^T(X(t)) - A(X(t))]X(t) \right) dt \\
 &+ \sigma(X(t))dW(t) \\
 &+ \eta(X(t-)) \bullet dZ(t).
 \end{aligned} \tag{8}$$

Equivalently, in integral form,

$$\begin{aligned}
 X(t) &= X(0) + \int_0^t X(s) \bullet \left([A_0^T(X(s)) - A(X(s))]X(s) \right) ds \\
 &+ \int_0^t \sigma(X(s))dW(s) \\
 &+ \int_0^t \eta(X(s-)) \bullet dZ(s).
 \end{aligned} \tag{9}$$

Theorem

There exists a probability space $(\Omega, \mathcal{F}, \mathbb{P})$ and a Markov process $(X(\omega, t))_{t \geq 0}$ defined therein, with positive components, which is a unique solution in distribution of the stochastic differential equation (8), given $X(0) \in E$.

The Markov semigroup associated to the process X has an infinitesimal generator given by:

$$\begin{aligned}
 Lf(x) = & \frac{1}{2} \sum_{i=1}^d \gamma_i x_i (1 - x_i) \frac{\partial^2}{\partial x_i^2} f(x) \\
 & + \sum_{i=1}^d \left(\sum_{j=1}^d (a_{j,i}(x) - a_{i,j}(x)) x_j - a_{i,i}(x) x_i \right) x_i \frac{\partial}{\partial x_i} f(x) \\
 & + \sum_{i=1}^d p_i (f(x + m_i x_i) - f(x)) \\
 & + \sum_{i=1}^d q_i (f(x - m_i x_i) - f(x)), \tag{10}
 \end{aligned}$$

for all C^2 -function $f : \mathbb{R}^d \rightarrow \mathbb{R}$ with bounded partial derivatives.

The abundance $\rho_t(x)$ satisfies the corresponding Fokker-Planck equation:

$$\begin{aligned}
 \frac{\partial}{\partial t} \rho_t(x) = & \frac{1}{2} \sum_{i=1}^d \gamma_i \frac{\partial^2}{\partial x_i^2} [x_i(1 - x_i) \rho_t(x)] \\
 & - \sum_{i=1}^d \frac{\partial}{\partial x^i} \left(\sum_{j=1}^d (a_{j,i}(x) - a_{i,j}(x)) x_j - a_{i,i}(x) x_i \right) x_i \rho_t(x) \\
 & + \sum_{i=1}^d p_i (\rho_t(x - m_i x_i) - \rho_t(x)) \\
 & + \sum_{i=1}^d q_i (\rho_t(x + m_i x_i) - \rho_t(x)).
 \end{aligned} \tag{11}$$

Corollary

Under the probability $\mathbf{P}_x$, the process X has right-continuous trajectories with left-hand limits almost surely and moreover, it is a Lévy process, for all $x \in E$.

Extinction of species

Let be given a vector $\lambda \in E$, such that, $\lambda_i > 0$, $i = 1, \dots, d$ and $\sum_{i=1}^d \lambda_i = 1$. Define $V(x) = \langle \lambda, x \rangle$, ($x \in E$). Furthermore, we add an important hypothesis to our model:

$$\left\{ \begin{array}{l} \text{For any } x \in E, \text{ and all } i = 1, \dots, d, \text{ the following inequality holds:} \\ \sum_{j=1}^d (a_{j,i}^0(x) - a_{i,j}(x))x_j + (p_i - q_i)m_i \leq 0. \end{array} \right. \quad (\text{H})$$

To analyze the recurrence in 0 of the biomass flow, we consider the stopping times

$$D_r(\omega) := \inf \{t \geq 0 : |X(t, \omega)| \leq r\}, \quad (0 < r < 1), \quad (12)$$

and

$$\tau(\omega) = \inf \{t \geq 0 : X(t, \omega) = 0\}. \quad (13)$$

Theorem

Under the hypothesis (H), it holds

$$\mathbb{P}_x(D_r < \infty) = 1, \quad (14)$$

for all $x \in E$, all $0 < r < 1$. As a result, $\mathbb{P}_x(\tau < \infty) = 1$ and 0 is an absorption point for the Markov process $(X(t))_{t \geq 0}$.

Model descriptions

Model	Matrix $A(x)$
Tri-trophic Food Web (TFW)	$\begin{pmatrix} -D_1/x_1 & g_2(x_1) & 0 \\ 0 & D_2/x_2 & g_3(x_2) \\ 0 & 0 & D_3/x_3 \end{pmatrix}$
Tri-trophic Interaction web with a Non-Trophic Interaction (NTI)	$\begin{pmatrix} -D_1/x_1 & g_2(x_1) & 0 \\ 0 & D_2/x_2 & n_3(x_1, x_2) \\ 0 & 0 & D_3/x_3 \end{pmatrix}$

$$g_i(x_j) = \frac{A_i}{1 + B_i x_j}, \quad n_3(x_1, x_2) = \exp(-\varepsilon x_1) g_3(x_2)$$

Example 1

Table: Attack coefficients, handling times, death rates, initial conditions

A_i	B_i	D_i	$X_i(0)$
		$D_1 = -0.08$	$X_1(0) = 0.5$
$A_2 = 0.6$	$B_2 = 0.01$	$D_2 = 0.01$	$X_2(0) = 0.2$
$A_3 = 0.5$	$B_3 = 0.8$	$D_3 = 0.08$	$X_3(0) = 0.2$

Table: diffusion coefficients, migration rates, immigration probability

γ	$b(x)$	p
$\gamma_1 = 0.01$	$m_1 = 0.03$	$p_1 = 0.5$
$\gamma_2 = 0.005$	$m_2 = 0.05$	$p_2 = 0.3$
$\gamma_3 = 0.005$	$m_3 = 0.04$	$p_3 = 0.3$

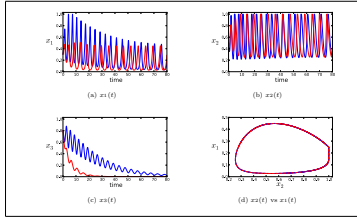


Fig. 2: (a)-(c) Bounded temporal dynamics of the biomass flow of each species in absence of noise for the TI (blue) and NTI (red) models. (d) x_2 vs x_1 plot of the closed unstable cycle obtained starting from a sufficiently large generational time in both models.

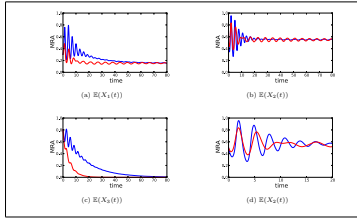


Fig. 3: (a)-(c) Mean temporal dynamics of the biomass flow of each species, when noise is considered to reflect interactions with the environment, for the TI (blue) and NTI (red) models. Plots obtained considering migration rates $m = (0.001, 0.001, 0.001)$, with probability $p = (0.5, 0.5, 0.5)$, and 10000 independent samples. (d) zoom of the mean temporal dynamic of the second species in the generational time interval [0, 20]. Time axis considers up to 80 generations of the predator species. $\text{cond} = [0.19, 0.3, 0.12]$.

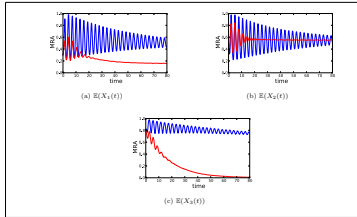


Fig. 4: (a)-(c) Mean temporal dynamics of the biomass flow of each species, for the TI (blue) and NTI (red) models. Plots obtained considering migration rates $m = (0.001, 0.001, 0.02)$, with probability $p = (0.5, 0.5, 0.98)$, and 10000 independent samples. Time axis considers up to 80 generations of the predator species. $\text{cond} = [0.19, 0.3, 0.1008]$.

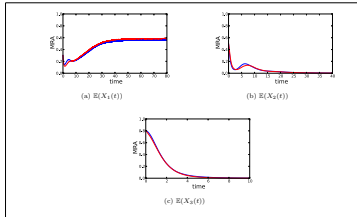


Fig. 5: Mean temporal dynamics of the biomass flow of each species in the system, for the TI (blue) and NTI (red) models. Plots obtained considering migration rates $m = (0.15, 0.001, 0.001)$, with probability $p = (0.02, 0.5, 0.5)$, and 10000 independent samples. In this case, autotroph biomass is exported from the system, leading to extinction of the herbivore and carnivore. Time axis considers up to 80 generations of the predator species. $\text{cond} = [0.046, 0.3, 0.145]$.

Example 2

The model has been applied to represent the intertidal food web of 104 species.

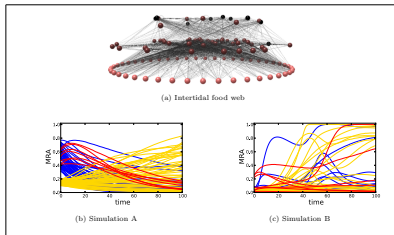


Fig. 6: (a) Representation of the Intertidal food web composed by 104 species with a total of 1346 trophic interactions (see [12] for details). (b) Mean temporal dynamics for a simulation considering set of parameters A in Table 3. (c) Mean temporal dynamics for simulation considering set of parameters B in Table 3. Yellow lines correspond to basal, blue to intermediate and red to top species, respectively.

However, the inference problem of describing interactions from abundance data still open

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