

Séminaire des dynamiques économiques complexes  
Université de Lille 1: EQUIPPE-Labo PAINLEVE- CLERSE  
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# Systemes différentiels à retards en avenir incertain: le modèle d'évolution stochastique de Lotka-Volterra

par André Keller  
CLERSE

# contenu

- 1. La modélisation stochastique des phénomènes de population

(La dynamique générale des interactions entre deux espèces; le cas particulier du système de Lotka-Volterra (LV); les étapes de la modélisation stochastique d'évènements; le modèle différentiel stochastique );

- 2. Le système stochastique sans retard de Lotka-Volterra

( Le système différentiel stochastique (SDS) du modèle sans surpeuplement des espèces ; les trajectoires bruitées du système par MatLab; le SDS du modèle avec surpeuplement des espèces; les conséquences du bruit sur la trajectoire en cas de surpeuplement des proies par MatLab);

- 3. Le système stochastique à retards de Lotka-Volterra

(Le système LV à retards généralisé à plus de deux espèces; le modèle LV à paramètres stochastiques; la probabilisation généralisée à tous les paramètres; la stabilité globale asymptotique en probabilité un).

# 1.A Formulation for 2 and more species

$$\begin{cases} \frac{dx_1}{dt} = x_1 \left( \overset{\text{natural growth}}{a_1} + \underset{\text{overcrowding coefficient}}{b_{11}x_1} + \overset{\text{interacting coefficient}}{b_{12}x_2} \right) & \dots \text{ biomass 1} \\ \frac{dx_2}{dt} = x_2 \left( a_2 + b_{21}x_1 + b_{22}x_2 \right) & \dots \text{ biomass 2} \end{cases}$$

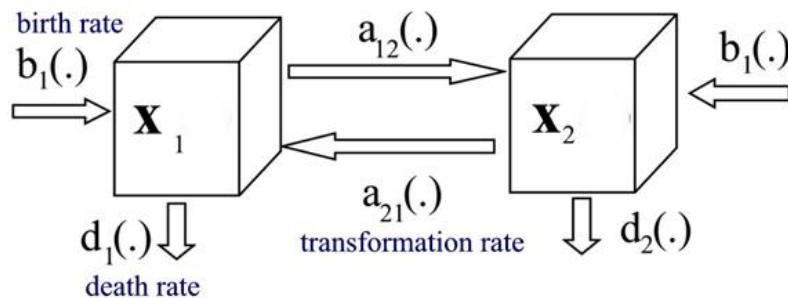
generalisation to n species

$$\frac{dx_i}{dt} = x_i \left( \underset{\text{intrinsic growth rates}}{a_i} + \overset{\text{interaction rates}}{\sum_{j=1}^n b_{ij}x_j} \right), \quad i = 1, \dots, n$$

or

$$\frac{d\mathbf{x}}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B}\mathbf{x}(t)), \quad \mathbf{x}, \mathbf{a} \in \mathbb{R}^n, \mathbf{B} \in \mathbb{R}^{n \times n}$$

# 1.B General population system



$$\begin{cases} \frac{dx_1}{dt} = x_1 (b_1(t, x_1, x_2) - d_1(t, x_1, x_2)) \\ \frac{dx_2}{dt} = x_2 (b_2(t, x_1, x_2) - d_2(t, x_1, x_2)) \end{cases}$$

$$\begin{cases} \frac{dx_1}{dt} = x_1 (b_1 - c_1 x_2) \\ \frac{dx_2}{dt} = x_2 (c_2 x_1 - d_2) \end{cases}$$

Nonzero steady state equilibrium at :

$$\left( \frac{d_2}{c_2}, \frac{b_1}{c_1} \right)$$

Integral solutions are closed curves in the  $(x_1 - x_2)$  plane to the steady state equilibrium.

# 1. La modélisation stochastique des phénomènes de population

## 1C. Steps of the stochastic modeling process :

step 1: population events and probabilities

- independent events (births, deaths and transformations): one event in each infinitesimal time intervals (i.e. multiple events are neglected)
- line 1: +1 birth in the population 1; the corresponding probability  $p_1$  is proportional to the density  $x_1$ .
- line 5: one member of the population 1 changes his characteristic (the original population 1 changes by -1) into that of the destination population 2 (population 2 changes by +1); the corresponding probability is proportional to the density of the original population.

Change	Probability	Event
$\Delta \mathbf{x}^{(1)} = (1, 0)^T$	$p_1 = b_1 x_1 \Delta t$	birth in $x_1$
$\Delta \mathbf{x}^{(2)} = (0, 1)^T$	$p_2 = b_2 x_2 \Delta t$	birth in $x_2$
$\Delta \mathbf{x}^{(3)} = (-1, 0)^T$	$p_3 = d_1 x_1 \Delta t$	death in $x_1$
$\Delta \mathbf{x}^{(4)} = (0, -1)^T$	$p_4 = d_2 x_2 \Delta t$	death in $x_2$
$\Delta \mathbf{x}^{(5)} = (-1, 1)^T$	$p_5 = a_{12} x_1 \Delta t$	$x_1$ into $x_2$
$\Delta \mathbf{x}^{(6)} = (1, -1)^T$	$p_6 = a_{21} x_2 \Delta t$	$x_2$ into $x_1$
$\Delta \mathbf{x}^{(7)} = (0, 0)^T$	$p_7 = 1 - \sum_{i=1}^6 p_i$	no change

## 1C. Steps of the stochastic modeling process :

step 2: expectation vector of and covariance matrix

- find the mean change expectation and the covariance matrix  $V$  of the population changes for an infinitesimal time interval.
- the 2x2 symmetric matrix  $V$ , which is positive definite, has a positive square root  $B$  (involved by the modeling procedure)

### Expectation vector of the population changes

$$E[\Delta \mathbf{x}] = \sum_{i=1}^7 p_i \Delta \mathbf{x}^{(i)} = \begin{pmatrix} b_1 x_1 - d_1 x_1 - a_{12} x_1 + a_{21} x_2 \\ b_2 x_2 - d_2 x_2 + a_{12} x_1 - a_{21} x_2 \end{pmatrix} \Delta t$$

### Covariance matrix of the population changes

$$E[\Delta \mathbf{x} \cdot \Delta \mathbf{x}^T] = \sum_{i=1}^7 p_i \Delta \mathbf{x}^{(i)} \cdot \Delta \mathbf{x}^{(i)T}, = \begin{pmatrix} b_1 x_1 + d_1 x_1 + \delta & -\delta \\ -\delta & b_2 x_2 + d_2 x_2 + \delta \end{pmatrix} \Delta t,$$

# 1C. Steps of the stochastic modeling process :

## step 3: stochastic differential system

- several methods for the square root matrix determination: 1) Allen's formula for a 2x2 matrix V; 2) diagonalization of the nxn symmetric matrix V; 3) direct numerical procedure by Lalic & Petkovic (1998)

### Determination of the squared root matrix B calculation

For  $V = \begin{pmatrix} a & b \\ b & c \end{pmatrix}$ , we obtain  $B = V^{1/2} = \frac{1}{d} \begin{pmatrix} a+w & b \\ b & c+w \end{pmatrix}$

where  $w = \sqrt{ac - b^2}$  and  $d = \sqrt{a+c+2w}$  with  $a = b_1x_1 + d_1x_1 + a_{12}x_1 + a_{21}x_2$ ,  $b = -a_{12}x_1 - a_{21}x_2$  and  $c = b_2x_2 + d_2x_2 + a_{12}x_1 + a_{21}x_2$ .

### Itô stochastic differential equation

$$dx(t) = \mu(t, x_1, x_2) dt + B(t, x_1, x_2) dW(t),$$

with  $x(0) = x_0$ , where  $W(t) = (W_1(t), W_2(t))^T$  is a two-dimensional Wiener process. From the general model, we deduce

$$\mu = (-a_{12}x_1 + a_{21}x_2, a_{12}x_1 - a_{21}x_2)^T,$$

$$V = \begin{pmatrix} a_{12}x_1 + a_{21}x_2 & -a_{12}x_1 - a_{21}x_2 \\ -a_{12}x_1 - a_{21}x_2 & a_{12}x_1 + a_{21}x_2 \end{pmatrix},$$

and

$$B = V^{1/2} = \sqrt{\frac{a_{12}x_1 + a_{21}x_2}{2}} \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix}_1$$



## 2. Le système stochastique sans retard de Lotka-Volterra

## 2.A Stochastic Lotka-Volterra system without delays : variant 1: the PP system without overcrowding

- a competition system between two species without internal competition (no overcrowding for low densities of the populations);
- the mean vector is the drift of the SDE, and square root matrix B is the diffusion of the process

### Stochastic LV system without overcrowding

The standard PP model is obtained for  $b_1(\cdot) = b_1$ ,  $d_1(\cdot) = c_1 x_2$ ,  $b_2(\cdot) = c_2 x_1$  and  $d_2(\cdot) = d_2$ . In the stochastic version of the model, since we have  $a_{12} = a_{21} = 0$ , the mean vector is

$$\boldsymbol{\mu} = \begin{pmatrix} (b_1 - c_1 x_2) x_1 \\ (c_2 x_1 - d_2) x_2 \end{pmatrix}$$

and the diffusion matrix is

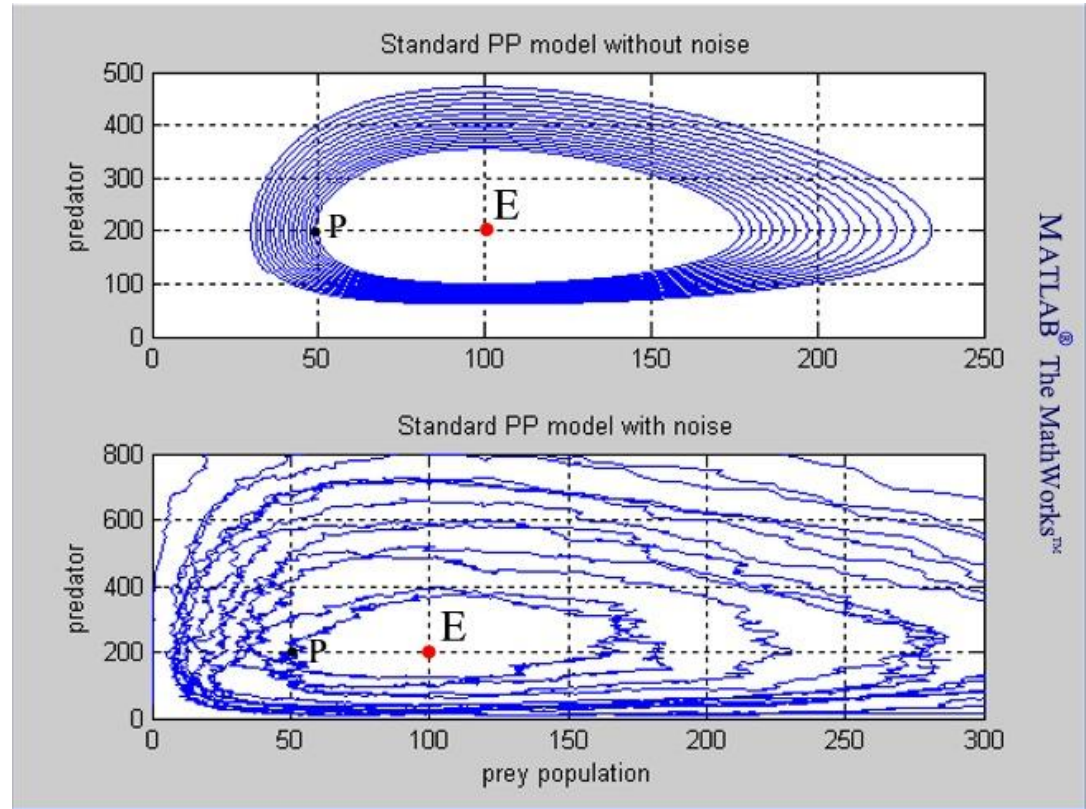
$$\mathbf{B} = \mathbf{V}^{1/2} = \begin{pmatrix} \sqrt{(b_1 + c_1 x_2) x_1} & 0 \\ 0 & \sqrt{(c_2 x_1 + d_2) x_2} \end{pmatrix}$$

Omitting the time argument, the standard stochastic PP model takes the form

$$\begin{pmatrix} dx_1 \\ dx_2 \end{pmatrix} = \begin{pmatrix} (b_1 - c_1 x_2) x_1 \\ (c_2 x_1 - d_2) x_2 \end{pmatrix} dt + \begin{pmatrix} \sqrt{(b_1 + c_1 x_2) x_1} & 0 \\ 0 & \sqrt{(c_2 x_1 + d_2) x_2} \end{pmatrix} \begin{pmatrix} dW_1 \\ dW_2 \end{pmatrix}$$

## 2.A Stochastic Lotka-Volterra system without delays : variant 1: the PP system without overcrowding (followed)

- the parameter values of the numerical application:  $b_1=d_2=2$ ,  $c_1=0.01, c_2=0.002$ .
- the figures picture the deterministic and stochastic trajectories.
- both figures have a cyclical pattern around the nonzero equilibrium  $E(100,200)$ .
- the noise perturbs the trajectories.



## 2.B Stochastic Lotka-Volterra system without delays : variant 2: the PP system with overcrowding

- Preys and predators come into competition with themselves, as a consequence of a population overcrowding phenomena (e.g.; Food limitations)
- This phenomena introduces new factors (beta times density) into the system
- The stochastic differential matrix equation introduce the new parameter sigma, which scales the noise.

### Stochastic LV system with overcrowding

We have the deterministic system

$$\begin{cases} \frac{dx_1(t)}{dt} = x_1(t)(b_1 - c_1x_2(t) - \beta x_1(t)) \\ \frac{dx_2(t)}{dt} = x_2(t)(-d_2 + c_2x_1(t) - \delta x_2(t)). \end{cases}$$

The stochastic version of the model introduces a multiplicative noise and takes the form (omitting the time argument)

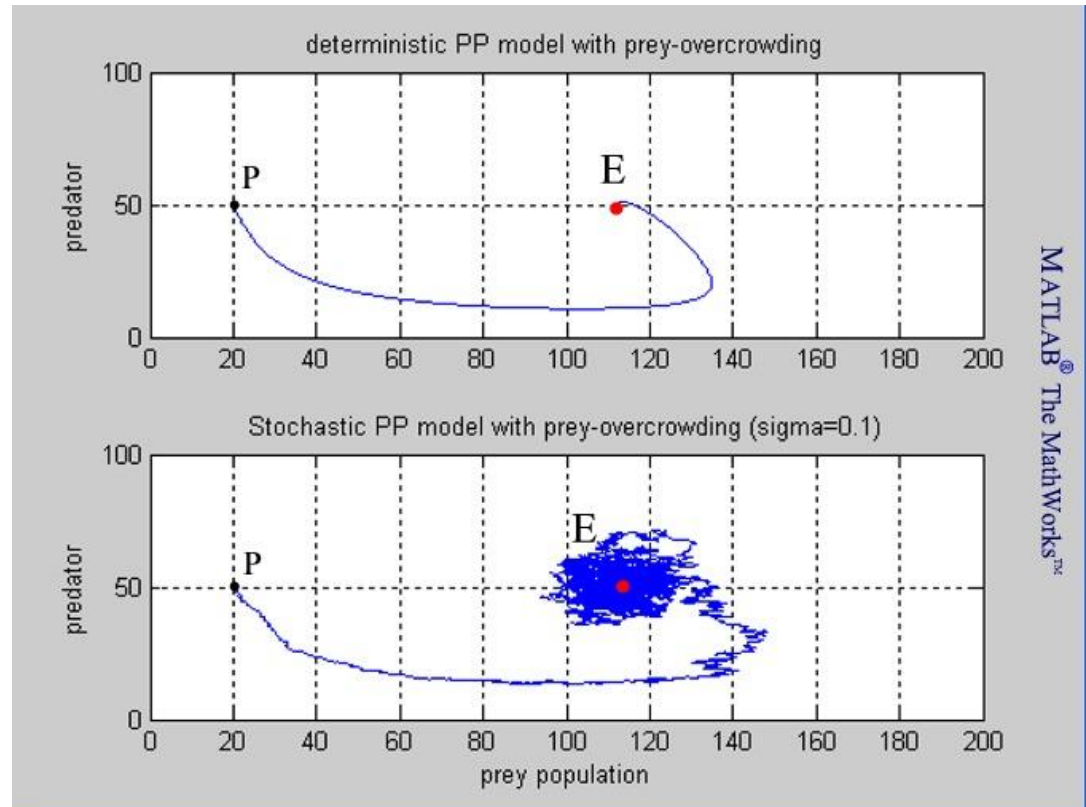
$$\begin{pmatrix} dx_1 \\ dx_2 \end{pmatrix} = \begin{pmatrix} (b_1 - c_1x_2 - \beta x_1)x_1 \\ (-d_2 + c_2x_1 - \delta x_2)x_2 \end{pmatrix} dt + \begin{pmatrix} \sigma x_1 & 0 \\ 0 & \sigma x_2 \end{pmatrix} \begin{pmatrix} dW_1 \\ dW_2 \end{pmatrix},$$

where  $\sigma$  scales the amplitude of the noise .

## 2.B Stochastic Lotka-Volterra system without delays :

variant 2: the PP system with overcrowding (followed)

- the PP model is prey-overcrowded
- the parameter values of the numerical application:  $b_1=d_2=2$ ,  $c_1=0.01$ ,  $c_2=0.002$ ,  $\beta=0.0133$
- the figures picture the globally asymptotically convergent deterministic and stochastic trajectory.
- both figures have a spiral pattern directed towards the nonzero equilibrium  $E(112.5,50)$ .
- the noise perturbs the trajectories.



### 3. Le système stochastique à retards de Lotka-Volterra

### 3A. Generalized stochastic system with delays : outline

- the LV differential system with delays is generalized to n species
- In a noisy environment , only the intrinsic growth rates are perturbed.
- a stochastic differential matrix equation is obtained

#### The LV differential system with delays

A delayed effect of one species<sup>1</sup> on another is introduced by means of lagged interaction terms, such as

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B}\mathbf{x}(t - \tau)),$$

where  $\mathbf{x}, \mathbf{a} \in \mathbb{R}^n$ ,  $\mathbf{B} \in \mathbb{R}^{n \times n}$ . The autonomous competitive or cooperative L-V system may have several time-delays,

$$\frac{dx_i(t)}{dt} = x_i(t) \left( b_i - \sum_{j=1}^n a_{ij} x_j(t) - \sum_{j=1}^n b_{ij} x_j(t - \tau_{ij}) \right), \quad i = 1, \dots, n$$

where  $i = 1, \dots, n$ . All the coefficients are real constants deterministic

#### The generalized LV differential system with delays

The following delay LV system generalizes the preceding deterministic  $n$ -dimensional system. We have

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{b} + \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{x}(t - \tau)), \quad \mathbf{x} \in \mathbb{R}^n$$

Suppose a noisy environment, where the intrinsic growth rates  $b_i$ 's are replaced by

$b_i + \sigma_{ii} (x_j - \bar{x}_j) dW(t) / dt$ , where  $\bar{x}_j$  is an equilibrium state component,  $\sigma_{ii}$ 's positive constants,

$W(t)$  a Brownian motion on a completely probability space  $(\Omega, \mathcal{F}, \{\mathcal{F}_t\}_{t \geq 0}, \mathbb{P})$ . The corresponding

Lotka-Volterra SDDE is

$$d\mathbf{x}(t) = \text{diag}(\mathbf{x}(t)) \left\{ (\mathbf{A}(\mathbf{x}(t) - \bar{\mathbf{x}}) + \mathbf{B}(\mathbf{x}(t - \tau) - \bar{\mathbf{x}})) dt + \sigma(\mathbf{x}(t) - \bar{\mathbf{x}}) d\mathbf{W} \right\}$$

# 3A. Generalized stochastic system with delays : properties

## Properties of the generalized stochastic LV system with delays

**Assumption.** The noise intensity matrix  $\sigma = (\sigma_{ij})_{n \times n}$  supposes that (H1):  $\sigma_{ii} > 0$  if  $1 \leq i \leq n$ , while  $\sigma_{ij} \geq 0$  if  $i \neq j$ .

**Theorem** (Mao, Yuan, & Zou, 2005) *Under assumption (H1), for any coefficients  $A$ ,  $B$  and any initial data  $\{x(t) : t \in [-\tau, 0]\} \in C([- \tau, 0]; \mathbb{R}_+^n)$ , there is a unique global solution  $x(t)$  to the system on  $t \geq -\tau$ . Moreover, the solution will remain in the cone  $\mathbb{R}_+^n$  with probability one.*



### 3B. Application : the food chain

- one prey population and two predator populations (one is intermediate and the other is superior)
- for this application, two conditions are to be satisfied to have a globally asymptotically stable equilibrium with the probability one.

The stochastic version of the PP model, around the equilibrium state  $\bar{x}$  is

$$dx(t) = \text{diag}(x(t)) \left\{ (A(x(t) - \bar{x}) + B(x(t - \tau) - \bar{x})) dt + \sigma(x(t - \tau) - \bar{x}) dW(t) \right\}$$

where  $x \in \mathbb{R}^3$  and  $\sigma = \text{diag}(\sigma_{11}, \sigma_{22}, \sigma_{33})$

and

$$b = \begin{pmatrix} b_1 \\ -b_2 \\ -b_3 \end{pmatrix}, A = \begin{pmatrix} -a_{11} & 0 & 0 \\ 0 & -a_{22} & 0 \\ 0 & 0 & -a_{33} \end{pmatrix}, B = \begin{pmatrix} 0 & -a_{12} & 0 \\ a_{21} & 0 & -a_{23} \\ 0 & a_{32} & 0 \end{pmatrix}.$$

The states  $x_1, x_2$  and  $x_3$  are respectively the population densities for a prey, an intermediate predator and a top predator. A stationary equilibrium  $\bar{x} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)^T$  exists in the positive cone  $\mathbb{R}_+^3$ , if

$$b_1 - \frac{a_{11}}{a_{21}} b_2 - \frac{a_{11} a_{22} + a_{12} a_{21}}{a_{21} a_{32}} b_3 > 0$$

Mao *et al* (2005) conclude that the equilibrium  $\bar{x}$  is globally asymptotically stable with probability one, if two conditions are satisfied. Letting  $\hat{c} = a_{11}^{-2} + a_{22}^{-2} + a_{33}^{-2}$ , we have the two conditions

$$\hat{c} \left( (a_{12}^2 + a_{32}^2) \vee (a_{21}^2 + a_{23}^2) \right) \leq 1$$

and

$$\alpha_{ii}^2 \leq \frac{\alpha_{ii}}{\bar{x}_i} \left( 1 - \hat{c} \left( (a_{12}^2 + a_{32}^2) \vee (a_{21}^2 + a_{23}^2) \right) \right), 1 \leq i \leq n$$

# Fin de la présentation

Merci pour votre présence