

Population biology models with time-delay in a noisy environment

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Abstract: - This article initiates the ecological modeling process in population biology and is centered on the well-known Lotka-Volterra multispecies system. In these models populations interact, fight or cooperate, in real life conditions: such as with constant time-delays in a noisy environment. The illustrative systems are the epidemic models and the predator-prey model with possibly overcrowding. The Euler-Maruyama approximation method is used to solve nonlinear stochastic delay differential equations. The probability density function of the solutions is estimated via the Fokker-Planck equation. Appendices with examples and references are proposed to the users. The computations have been carried out with help of two mathematical software: MATLAB® 7.12 R2011a and Wolfram *MATHEMATICA*® 8.

Key-Words: - Diffusion model, Predator-prey model, Overcrowding, Stochastic delay differential equation, Euler-Maruyama method, Forward Kolmogorov equation, Fokker-Planck equation, Stratonovich calculus, Itô formulation.

1 Introduction

This introductory paper is dedicated to population growth dynamics in a noisy constrained environment [39, 40]. The time-delay systems [15, 42, 76] in population dynamics seek to explain the variation in size and composition of biological populations, such as humans, animals, plants and microorganisms or cells.¹ The computations use MATLAB® 7.12 R2011a with specialized toolboxes [6, 56, 57] and Wolfram *MATHEMATICA*® 5.1 to 8 [43, 44, 73].

Consider two interacting populations that may be of the same species or of different species. Populations of the same species may differ by status as in the epidemic models consisting of susceptible and infected sub-populations. Populations of different interacting species may be predators and prey [3]. Following the modeling procedure by [3], a general model of two interacting populations is first presented. Thereafter, the deterministic and the

stochastic forms of two major biology applications are deduced for a single species epidemic model and for the two species predator-prey model.

1.1 Population biology modeling

Consider two populations which sizes are denoted by the states $x_1(t)$ and $x_2(t)$ at time t . The interactions between the two populations are shown in Fig.1.

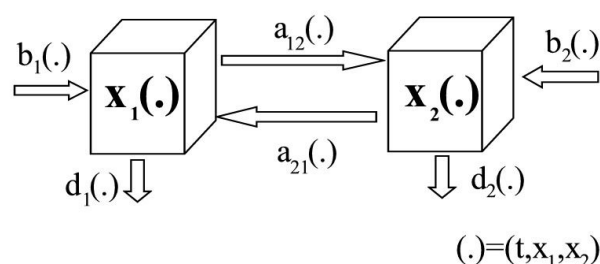


Figure 1: Diagram of the interactions between two populations at time t .

¹ A history on population dynamics is presented by [8, 34]. This review introduces to the different models in discrete and continuous time. The interactions among species are considered by [58] in application to the management of multispecies fisheries. Time lags in biological systems have been already analyzed by [26, 47, 52]. DDEs with applications in population dynamics are used.

six parameters depend on the states $x_1(t), x_2(t)$ and on time t . We have for coefficients

$$b_i = b_i(\cdot), d_i = d_i(\cdot), a_{ij} = a_{ij}(\cdot), i, j \in \{1, 2\},$$

where $(\cdot) \equiv (t, x_1, x_2)$.

Now, consider the events that may occur independently within a small time interval Δt , while neglecting the possibility of multiple events of order $(\Delta t)^2$. The possible changes in the two populations concern births, deaths and transformations for an individual. These changes are produced in Table 1, together with their corresponding probability.

Table 1: Possible changes in the population model with corresponding probabilities in Δt .

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

As in [3: p.146], the vector $\Delta \mathbf{x}^{(1)} = (1, 0)^T$ represents a birth in population x_1 with probability $p_1 = b_1 x_1 \Delta t$, proportional to the state x_1 with coefficient b_1 in Δt . The vector $\Delta \mathbf{x}^{(5)} = (-1, 1)^T$ represents the change of one individual from population x_1 into x_2 during Δt , with a probability that is proportional to x_1 .

Using Table 1, the expected change and covariance matrix are determined for $\Delta \mathbf{x} = (\Delta x_1, \Delta x_2)^T$. We obtain

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

and

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

where $\delta = a_{12} x_1 + a_{21} x_2$. The expectation vector $\boldsymbol{\mu}(t, x_1, x_2) = E[\Delta \mathbf{x}] / \Delta t$ express the drift coefficient of a stochastic process. The diffusion coefficient of this process is the square root of the covariance matrix $\mathbf{V}(t, x_1, x_2) = E[\Delta \mathbf{x} \cdot \Delta \mathbf{x}^T] / \Delta t$. We have [2]²

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

where $w = \sqrt{ac - b^2}$ and $d = \sqrt{a+c+2w}$ with $a = b_1 x_1 + d_1 x_1 + a_{12} x_1 + a_{21} x_2$, $b = -a_{12} x_1 - a_{21} x_2$ and $c = b_2 x_2 + d_2 x_2 + a_{12} x_1 + a_{21} x_2$. We deduce (see [3]) that the dynamics of the two interacting populations is an Itô stochastic differential equation (SDE) of the form

$$d\mathbf{x}(t) = \boldsymbol{\mu}(t, x_1, x_2) dt + \mathbf{B}(t, x_1, x_2) d\mathbf{W}(t),$$

with $\mathbf{x}(0) = \mathbf{x}_0$, where $\mathbf{W}(t) = (W_1(t), W_2(t))^T$ is a two-dimensional Wiener process.

² In the canonical form $\mathbf{V} = \mathbf{P}^T \mathbf{D} \mathbf{P}$ with $\mathbf{P}^T \mathbf{P} = \mathbf{I}$ and $d_{ii} > 0, i = 1, \dots, n$, we readily have $\mathbf{V}^{1/2} = \mathbf{P}^T \mathbf{D}^{1/2} \mathbf{P}$. For an $n \times n$ matrix, $\mathbf{V}^{1/2}$ must generally be calculated numerically.

1.2 Epidemic models

Two simple examples of epidemic models are considered: the SIS (Susceptible-Infected-Susceptible) model and the SIR (Susceptible-Infected-Recovered) model.

1.2.1 SIS epidemic model

SIS epidemic models for a single species [3: p.147-150, 7, 65] consists of susceptible and infected subpopulations. The susceptible individuals become infected, recover and susceptible again. This model is derived from the previous model of interacting species. The deterministic form of the SIS model is the system of ODEs (ordinary differential equations)

$$\begin{cases} \frac{dx_1(t)}{dt} = \gamma x_2(t) - \beta \frac{x_2(t)}{N} x_1(t) \\ \frac{dx_2(t)}{dt} = -\gamma x_2(t) + \beta \frac{x_1(t)}{N} x_2(t), \end{cases}$$

where the total population N is constant

$x_1(0) + x_2(0) = x_1(t) + x_2(t) = N$. In this model, x_1 denotes the susceptible population size, and x_2 the infected population size. The parameters are β the contact rate for transmitting the infection and γ the probability that an infected individual is removed from the infection process³. We suppose that the birth rates b_1, b_2 and the death rates d_1, d_2 are zero. The SIS model may be represented by the interacting scheme in Fig.1, with $a_{12} \equiv \frac{\beta x_2}{N}$ and $a_{21} \equiv \gamma$. The stochastic version of the SIS model may take the SDE Itô form

$$d\mathbf{x}(t) = \boldsymbol{\mu}(t, x_1, x_2) dt + \mathbf{B}(t, x_1, x_2) d\mathbf{W}(t),$$

where $\mathbf{x} = (x_1, x_2)^T$, $\mathbf{W} = (W_1, W_2)^T$. From the general model, we deduce

³ The ratio $\beta x_1 / N$ is the proportion of contacts by one infected individual and $(\beta x_1 / N) x_2$ the number of contacts by the infected population. The ratio $1 / \gamma$ denotes the average length of the infection period.

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

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

and

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

Omitting the time argument, the SDE in matrix form is

$$\begin{pmatrix} dx_1 \\ dx_2 \end{pmatrix} = \begin{pmatrix} -\beta \frac{x_1 x_2}{N} + \gamma x_2 \\ \beta \frac{x_1 x_2}{N} - \gamma x_2 \end{pmatrix} dt + \sqrt{\left(\beta \frac{x_1 x_2}{N} + \gamma x_2 \right)} / \sqrt{2} \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} dW_1 \\ dW_2 \end{pmatrix}.$$

The numerical values by [3:pp.148-149] are $\beta = 0.04$, $\gamma = 0.01$ with initial conditions $x_1(0) = 950$ and $x_2(0) = 50$. The time period is $[0, 100]$. The MATLAB code⁴ by [3: pp.129-130] allows 10,000 sample paths. Fig.2 displays the expected population sizes and one sample path for each subpopulation.

⁴ The MATLAB code solves the stochastic system by using a Euler's method.

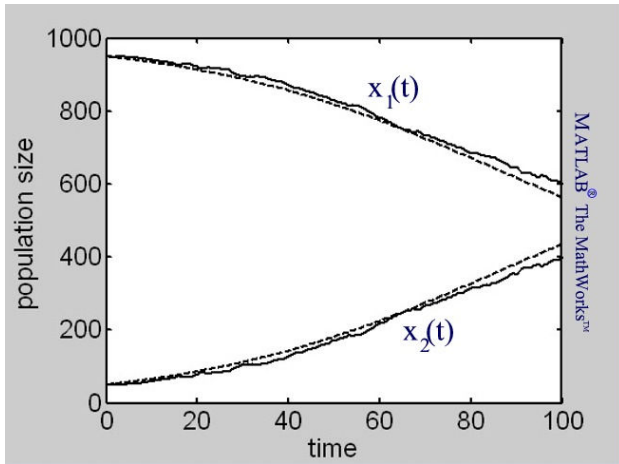


Figure 2: Sample path and expected population size for susceptible and infected individuals in a stochastic SIS model with a total population of 1,000.

1.2.2 SIR epidemic model

In the SIR epidemic model [4: pp.271-276, 5: pp.427-429], the population is divided into three categories of individuals: x_1 the susceptible individuals, x_2 the infected individuals and x_3 the recovered and immune individuals. The parameters of the model are denoted by β the contact rate, γ the probability of recovery. There is no birth. The deterministic model is a system of ODEs

$$\begin{cases} \frac{dx_1(t)}{dt} = -\frac{\beta x_2(t)}{N} x_1(t) \\ \frac{dx_2(t)}{dt} = \frac{\beta x_1(t)}{N} x_2(t) - \gamma x_2(t) \\ \frac{dx_3(t)}{dt} = \gamma x_2(t), \end{cases}$$

where $N = x_1(t) + x_2(t) + x_3(t)$.

In the stochastic model, $\mathbf{X} = (x_1, x_2)^T$ is composed of continuous random variables. The changes that append and their corresponding probabilities are shown in Table 2.

Table 2: Changes and corresponding probabilities in the SIR model.

Change	Probability	Event
$\Delta X^{(1)} = (-1, 1)^T$	$p_1 = \beta \frac{x_1 x_2}{N} \Delta t$	x_2 infected
$\Delta X^{(2)} = (0, -1)^T$	$p_2 = \gamma x_2 \Delta t$	x_2 recovered

The expectation vector $\boldsymbol{\mu}$ and the variance-covariance matrix \mathbf{V} are

$$\boldsymbol{\mu} = E[\Delta X] = \begin{pmatrix} -\beta \frac{x_1 x_2}{N} \\ \beta \frac{x_1 x_2}{N} - \gamma x_2 \end{pmatrix} \Delta t$$

and

$$\mathbf{V} = \frac{\beta x_1 x_2}{N} \begin{pmatrix} 1 & -1 \\ -1 & 1 + \frac{\gamma N}{\beta x_1} \end{pmatrix}.$$

For this problem, the root squared matrix $\mathbf{B} = \mathbf{V}^{1/2}$ can be found by using the Allen's formula⁵[2]. We have

$$\mathbf{B} = \frac{\sqrt{\beta x_1 x_2 / N}}{\sqrt{2 + \frac{\gamma N}{\beta x_1} + 2\sqrt{\frac{\gamma N}{\beta x_1}}}} \begin{pmatrix} 1 + \sqrt{\frac{\gamma N}{\beta x_1}} & -1 \\ -1 & 1 + \frac{\gamma N}{\beta x_1} + \sqrt{\frac{\gamma N}{\beta x_1}} \end{pmatrix}.$$

Omitting the time argument, the SDE of the stochastic SIR model is

⁵ Let $\mathbf{V} = \begin{pmatrix} V_{11} & V_{12} \\ V_{21} & V_{22} \end{pmatrix}$, the Allen's formula yields

$$V^{1/2} = \frac{1}{d} \begin{pmatrix} V_{11} + \delta & V_{12} \\ V_{21} & V_{22} + \delta \end{pmatrix}, \quad \text{where}$$

$$d = \sqrt{\text{tr}(\mathbf{V}) + 2\delta} \text{ and } \delta = \sqrt{\det(\mathbf{V})}.$$

$$\begin{pmatrix} dx_1 \\ dx_2 \end{pmatrix} = \begin{pmatrix} -\beta \frac{x_1 x_2}{N} \\ \beta \frac{x_1 x_2}{N} - \gamma x_2 \end{pmatrix} dt + \frac{\sqrt{\beta x_1 x_2 / N}}{\sqrt{2 + \frac{\gamma N}{\beta x_1} + 2\sqrt{\frac{\gamma N}{\beta x_1}}}} \begin{pmatrix} 1 + \frac{\gamma N}{\beta x_1} & -1 \\ -1 & 1 + \frac{\gamma N}{\beta x_1} + \sqrt{\frac{\gamma N}{\beta x_1}} \end{pmatrix} \begin{pmatrix} dW_1 \\ dW_2 \end{pmatrix}$$

In Fig.3, the stochastic sample path for each subpopulation is compared to the deterministic evolution (dashed lines).

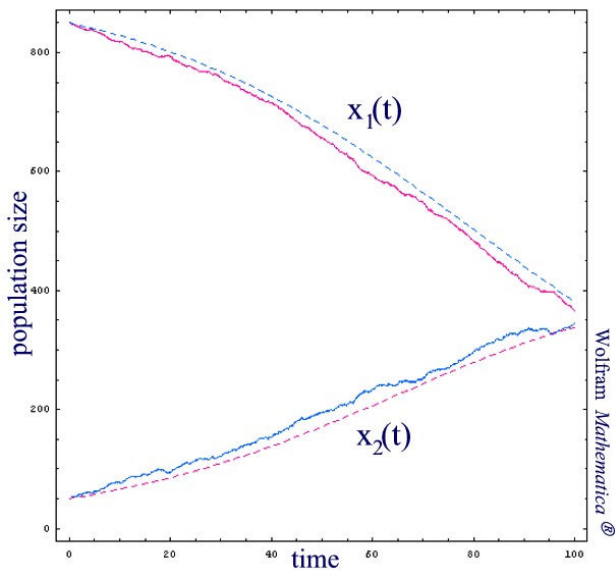


Figure 3: Sample path and deterministic evolution in a stochastic SIR model.

1.3 Competition models

In the competition models, multiple species interact in a closed area (habitat) without migrations [66: pp. 416-458]. Two situations for two species are presented: the standard predator-prey model (PP model) for few populations and a PP model with overcrowding, when prey and predators are competing with themselves for limited foods.

1.3.1 Standard predator-prey model

The two species PP model is also derived from the general model for interacting species. The deterministic model takes the form

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

where x_1 and x_2 are the population size of the prey and predator, respectively. 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

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

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

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

In the numerical application, the parameter values (from [66: pp. 433-436]) are $b_1 = d_2 = 2$, $c_1 = 0.01$ and $c_2 = 0.02$. Fig.4 shows the deterministic and the stochastic version of the standard PP model. The system has a cyclical pattern around the nonzero equilibrium point $E(100, 200)$. The trajectory is perturbed when a white noise is introduced.

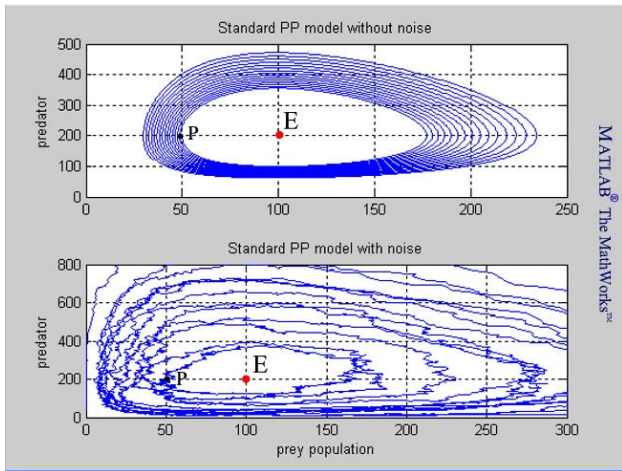


Figure 4: Trajectory of the deterministic and stochastic standard PP model around the equilibrium point $E(100,200)$.

1.3.2 Predator-prey model with overcrowding

In the PP model with overcrowding, we suppose that the numerous prey and predators come into competition with themselves for a limited food. The overcrowding factors $-\beta x_1$ and $-\delta x_2$ are introduced into the equations for prey and predators, respectively. We have the deterministic system

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

Taking the parameter values from [66: pp. 441-443], we have $b_1 = d_2 = 2$, $c_1 = 0.01$, $c_2 = 0.02$ and $\beta = 0.0133$. The stochastic version of the model introduces a multiplicative noise and takes the form (omitting the time argument)

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

where σ scales the amplitude of the noise (with $\sigma = 0.1$).

Fig.5 illustrates an asymptotically convergence towards the equilibrium point $E(112.5,50)$. In the random case, the perturbed trajectory also converges to the nonzero equilibrium point.

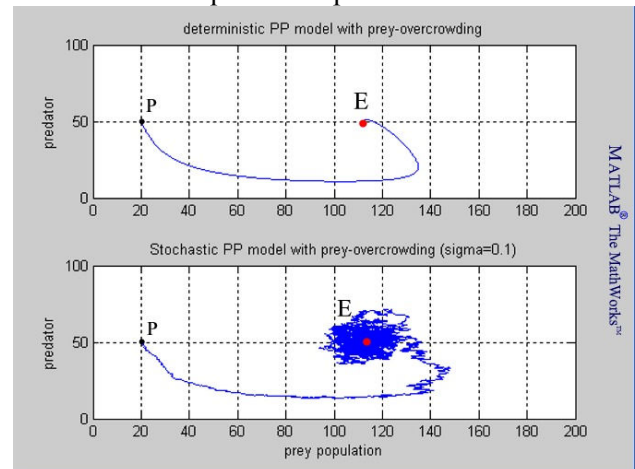


Figure 5: Trajectory of the deterministic and stochastic PP model with prey-overcrowding around the equilibrium point $E(112.5,50)$.

1.3.3 General population dynamics

Suppose a closed system (no migration) with two species. The possible interactions may correspond to one of the following four situations: 1) a competition between and/or within the two populations, 2) a conflict between them, one being a prey and the other a predator, 3) a mutual benefit of both populations or 4) completely independent species. Such situations are depending on the sign of the parameters as indicated in Table 3. The two-species system is

$$\begin{cases} \frac{dx_1(t)}{dt} = x_1(t)(a_1 + b_{11}x_1(t) + b_{12}x_2(t)) \\ \frac{dx_2(t)}{dt} = x_2(t)(a_2 + b_{21}x_1(t) + b_{22}x_2(t)). \end{cases} \quad (1)$$

Fig.6 illustrates⁶ the deterministic Lotka-Volterra (L-V) system [50,70] for which one population x_1 is

⁶ The Mathematica primitive Manipulate[...] creates an interactive object (as in Fig.6 and 7) containing controls (sliders) for different parameters of the system. These interactive applications let explore different ranges of values for the coefficients, the time-delays and the initial conditions. The consequences on the results of such modifications are observed immediately.

the prey (e.g. rabbits, plants) and the other x_2 the predator (e.g. foxes, herbivores). As shown, the trajectories turn around the nonzero steady state counterclockwise. Using the 2-species system (1), without internal competition $b_{11} = b_{22} = 0$. We find that the solution trajectory in the phase plane is

$$H(x_1(t), x_2(t)) \equiv b_{21}x_1(t) + a_2 \ln x_1(t) - b_{12}x_2(t) - a_1 \ln x_2(t) = k_1,$$

where k_1 is the constant of integration (See [22: pp. 428-454] and [67: p.607].

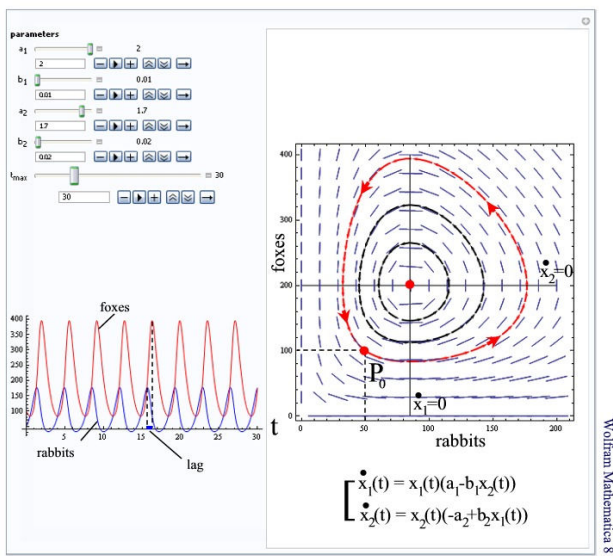


Figure 6: Lotka-Volterra system without internal competition.

Table 3. Population dynamics.

	$b_{12}, b_{21} < 0$	$b_{12}, b_{21} > 0$		$b_{12}, b_{21} = 0$
		$b_{12}, b_{21} < 0$	$b_{12}, b_{21} > 0$	
$b_{11}, b_{22} < 0$	Predator-prey with overcrowding	Full competition within & between	Overcrowding & cooperation	Overcrowding & independence
$b_{11}, b_{22} = 0$	Lotka-Volterra	Competitive system	No overcrowding & cooperation	No overcrowding & independence
$b_{11}, b_{22} > 0$	Expansion	Expansion & competition	Mutual benefit	Expansion & independence

The generalization to n interacting species is the n -dimensional Lotka-Volterra system

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

where the a_i 's are the intrinsic growth rates, and the b_{ij} 's the interaction rates, whose signs reflect the type of population dynamics. In matrix form, we also have

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B}\mathbf{x}(t)), \quad (2)$$

where $\mathbf{x}, \mathbf{a} \in \mathbb{R}^n$, $\mathbf{B} \in \mathbb{R}^{n \times n}$. The existence of an equilibrium solution $\bar{\mathbf{x}}$ requires $\mathbf{a} + \mathbf{B}\bar{\mathbf{x}} = \mathbf{0}$. [23] shows that $\bar{\mathbf{x}}$ is globally stable in \mathbb{R}_+^n if there is $\mathbf{C} = \text{diag}(c_1, \dots, c_n)$ with $c_i > 0, i = 1, \dots, n$ such that

$$\mathbf{C}\mathbf{B} + \mathbf{B}^T\mathbf{C} \quad (3)$$

is negative definite.

2 Delay Lotka-Volterra System⁷

2.1 Multispecies delay systems

To model the population dynamics of n interacting species in a common habitat, an n -dimensional system of DDEs may be introduced. A delayed effect of one species⁸ on another is introduced by means of lagged interaction terms⁹, such as

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B} \mathbf{x}(t - \tau)), \quad (4)$$

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, as in [51]

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

$$i = 1, \dots, n$$

where $i = 1, \dots, n$. All the coefficients are real constants¹⁰. The permanence of all the populations supposes that the linear system

$$b_i - \sum_{j=1}^n a_{ij} x_j - \sum_{j=1}^n b_{ij} x_j = 0$$

has a positive solution.

Let a simplified L-V system of the form [25]

⁷ Bocharov *et al.* [14] analyse the qualitative and quantitative effects of time-delays in population dynamics, epidemiology, physiology, immunology, neural networks and cell kinetics.

⁸ The delay is generally justified by resources that have been already accumulated.

⁹ The predator-prey system with aftereffect has been introduced by Volterra (1931)[70]. The growth rate of a species is also influenced by the past history of the population. Thus, the loss of prey may affect the growth rate of predators in future [46].

¹⁰ The b_i 's are birth rates ($b_i > 0$) or death rates

($b_i < 0$). The L-V system is competitive with time delays, if $a_{ij}, b_{ij} > 0$, $i, j = 1, \dots, n$.

On the contrary, the L-V system is cooperative with time delays, if $a_{ii} > 0, a_{ij} < 0, b_{ij} < 0, i, j = 1, \dots, n, i \neq j$.

$$\frac{dx_i}{dt} = x_i(t) \left(b_i - \sum_{j=1}^n a_{ij} x_j(t - \tau_{jj}) \right). \quad (5)$$

Theorem 1. (Gopalsamy, 1991) [25] *Suppose that the L-V system (5) satisfies the conditions*

(i) *the coefficients b_i, a_{ij} ($i, j = 1, \dots, n$) are real constants such that $a_{ii} > 0, i = 1, \dots, n$ and the system (5) has a positive steady-state equilibrium*

$$\bar{x} \text{ such that } \sum_{j=1}^n a_{ij} x_j = b_i, \quad i = 1, \dots, n$$

(ii) *$q \tau e > 1$, where*

$$q = \min_{1 \leq i \leq n} \left\{ \bar{x}_i \left(a_{ii} - \sum_{j=1, j \neq i}^n |a_{ji}| \right) \right\} \text{ and } \tilde{\tau} = \min_{1 \leq i \leq n} \{ \tau_{ii} \}.$$

Then every nonconstant solution of (5) on $[-\tau, \infty)$ is oscillatory about the steady-state.

Proof. See [25: pp.442-447]. $\square \square$

2.2 Instability effects of delays

Let the two species L-V system be the numerical system

$$\begin{cases} \frac{dx_1(t)}{dt} = x_1(t)(-1 + x_2(t - \tau_2)) \\ \frac{dx_2(t)}{dt} = x_2(t)(2 - x_1(t - \tau_1)), \end{cases}$$

where $x_1(t)$ and $x_2(t)$ denote the biomass of the predator (or parasite) and of the prey (or host), respectively. Without delays ($\tau_1 = \tau_2 = 0$), there is a stable periodic solution which expression is

$$H(t) \equiv 2 \ln x_1(t) + x_1(t) + \ln x_2(t) - x_2(t) = k_1.$$

The presence of time-delays in biological systems is a potential source of non-stationary problems (periodic oscillations and instabilities): the loss of stability intervenes at a certain threshold. Fig.7 depicts the dynamic instabilities due to the two lags $\tau_1 = 0.45$ and $\tau_2 = 0.25$. However, time-delays can also enhance stability, and short time-delays can stabilize unstable dynamical systems [10].

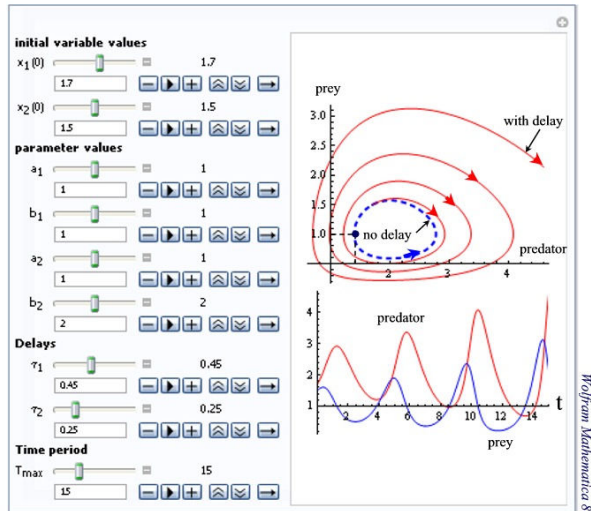


Figure 7: Effect of time-delays on the periodic orbit of the L-V system.

2.3 Delay Lotka-Volterra food chain

Let the LV system of food chain with time-delayed interactions, for three species

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{b} + \mathbf{A} \mathbf{x}(t) + \mathbf{B} \mathbf{x}(t - \tau)), \quad (6)$$

where

$$\mathbf{x} \in \mathbb{R}^3, \quad \mathbf{b} = \begin{pmatrix} b_1 \\ -b_2 \\ -b_3 \end{pmatrix}, \quad \mathbf{A} = \begin{pmatrix} -a_{11} & 0 & 0 \\ 0 & -a_{22} & 0 \\ 0 & 0 & -a_{33} \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} 0 & -a_{12} & 0 \\ a_{21} & 0 & -a_{23} \\ 0 & a_{32} & 0 \end{pmatrix}.$$

The states x_1, x_2 and x_3 are respectively the population densities for a prey, an intermediate predator and a top predator. Gard [23: p.174] shows¹¹ that a stationary equilibrium

$\bar{\mathbf{x}} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)^T$ exists in the positive cone \mathbb{R}_+^3 , if

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

The equilibrium is globally asymptotically stable as long as the condition (3) is satisfied¹².

¹¹ The notations have been adapted to this study.

¹² Indeed, we have

$$\mathbf{C}(\mathbf{A} + \mathbf{B}) + (\mathbf{A} + \mathbf{B})^T \mathbf{C} = -2 \begin{pmatrix} c_1 a_{11} & 0 & 0 \\ 0 & c_2 a_{22} & 0 \\ 0 & 0 & c_3 a_{33} \end{pmatrix}.$$

3 Stochastic Delay Lotka-Volterra System

3.1 Stochastic Lotka-Volterra system

Let the nondelay multispecies L-V system be (2), and suppose that all the parameters b_{ij} 's are stochastically perturbed [54] with $b_{ij} \rightarrow b_{ij} + \sigma_{ij} dW(t)/dt$, where $dW(t)/dt$ is a white noise. The SDEs corresponding to that system is¹³

$$d\mathbf{x}(t) = \text{diag}(\mathbf{x}(t))\{\mathbf{a} + \mathbf{B}\mathbf{x}(t)\}dt + \boldsymbol{\sigma}\mathbf{x}(t)d\mathbf{W}(t), \quad (7)$$

where $\mathbf{a} \in \mathbb{R}^n$, $\mathbf{B} \in \mathbb{R}^{n \times n}$ and where the noise intensity matrix $\boldsymbol{\sigma} = (\sigma_{ij})_{n \times n}$ supposes that (H1): $\sigma_{ii} > 0$ if $1 \leq i \leq n$, while $\sigma_{ij} \geq 0$ if $i \neq j$. The nonnegative solution¹⁴ may explode in a finite time, since the coefficients do not satisfy the linear growth sufficient condition, though they are locally Lipschitz continuous: the Lipschitz condition ensures the existence and uniqueness of the solution, whereas the linear growth condition ensures the boundedness of the solution. Mao *et al.* (2002)[54] prove that the environmental Brownian noise suppresses a deterministic explosion.

Theorem 2. (Mao, Marion, & Renshaw 2002) [54] *Under assumption H1, for any coefficients \mathbf{a}, \mathbf{B} and any initial value $\mathbf{x}_0 \in \mathbb{R}_+^n$, there is a unique global solution $\mathbf{x}(t)$ to (7) on $t \geq 0$. Moreover, the solution will remain in the cone \mathbb{R}_+^n with probability one.*

Proof. See [54: pp. 99-102]. \square

3.2 Stochastic delay Lotka-Volterra system

The following delay LV system generalizes the deterministic n -dimensional system (4). We have, as in (6)[9, 11, 16, 55]

¹³ All the coefficients may be stochastically perturbed with $\mathbf{b} \rightarrow \mathbf{b} + \boldsymbol{\beta} d\mathbf{W}_1(t)/dt$ and $\mathbf{A} \rightarrow \mathbf{A} + \boldsymbol{\sigma} d\mathbf{W}_2(t)/dt$, where $\mathbf{W}_1(t)$ and $\mathbf{W}_2(t)$ are independent Brownian motions, as in [54].

¹⁴ The size x_i of the i th species should be nonnegative.

$$\frac{d\mathbf{x}(t)}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{b} + \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{x}(t-\tau)), \mathbf{x} \in \mathbb{R}^n \quad (8)$$

Suppose a noisy environment, where the intrinsic growth rates b_i 's are replaced by $b_i + \sigma_{ii} \left(x_j - \bar{x}_j \right) dW(t) / dt$, where \bar{x}_j is an equilibrium state component, σ_{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 Lotka-Volterra SDDE, corresponding to (8) is

$$d\mathbf{x}(t) = \text{diag}(\mathbf{x}(t)) \left\{ (\mathbf{A}\mathbf{x}(t) - \bar{\mathbf{x}}) + \mathbf{B}(\mathbf{x}(t-\tau) - \bar{\mathbf{x}}) \right\} dt + \boldsymbol{\sigma}(\mathbf{x}(t) - \bar{\mathbf{x}}) d\mathbf{W} \quad (9)$$

Theorem 3 (Mao, Yuan, & Zou, 2005)[55] *Under assumption (H1), for any coefficients \mathbf{A} , \mathbf{B} and any initial data $\{\mathbf{x}(t) : t \in [-\tau, 0]\} \in C([- \tau, 0]; \mathbb{R}_+^n)$, there is a unique global solution $\mathbf{x}(t)$ to (9) on $t \geq -\tau$. Moreover, the solution will remain in the cone \mathbb{R}_+^n with probability one.*¹⁵

Proof. See [55: pp. 303-305]. \square

3.3 Stochastic delay Lotka-Volterra food chain¹⁶

The stochastic version of (6), around the equilibrium state $\bar{\mathbf{x}}$ is

¹⁵ The uniqueness of a positive solution under some conditions and the fact that the solution will not explode in a finite time with probability one has been also proved by [77] for a generalized stochastic delay L-V system of the form

$$d\mathbf{x}(t) = \text{diag}(\mathbf{x}(t)) \left\{ (\mathbf{f}(\mathbf{x}(t)) + \mathbf{g}(\mathbf{x}(t-\tau))) dt + \mathbf{h}(\mathbf{x}(t)) d\mathbf{W}(t) \right\},$$

where $\mathbf{f}, \mathbf{g} : \mathbb{R}^n \mapsto \mathbb{R}^n$, $\mathbf{h} : \mathbb{R}^n \mapsto \mathbb{R}^{n \times m}$ are continuous functions and $\mathbf{W}(t) = (W_1(t), \dots, W_m(t))^T$ an m -dimensional Brownian motion.

¹⁶ This stochastic L-V system with constant time-delay has been extended to a variable time-delay in [75].

$$d\mathbf{x}(t) = \text{diag}(\mathbf{x}(t)) \left\{ (\mathbf{A}(\mathbf{x}(t) - \bar{\mathbf{x}}) + \mathbf{B}(\mathbf{x}(t-\tau) - \bar{\mathbf{x}})) dt + \boldsymbol{\sigma}(\mathbf{x}(t-\tau) - \bar{\mathbf{x}}) d\mathbf{W}(t) \right\}, \mathbf{x} \in \mathbb{R}^3 \quad (10)$$

where $\boldsymbol{\sigma} = \text{diag}(\sigma_{11}, \sigma_{22}, \sigma_{33})$. Mao *et al* [Mao05] conclude that the equilibrium $\bar{\mathbf{x}}$ 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

$$\hat{c} \left\{ (a_{12}^2 + a_{32}^2) \vee (a_{21}^2 + a_{23}^2) \right\} \leq 1 \quad (11)$$

and

$$\sigma_{ii}^2 \leq \frac{a_{ii}}{x_i} \left\{ 1 - \hat{c} \left((a_{12}^2 + a_{32}^2) \vee (a_{21}^2 + a_{23}^2) \right) \right\}, \quad 1 \leq i \leq n \quad (12)$$

The condition (11) guarantees [55] that the steady state equilibrium $\bar{\mathbf{x}}$ of the deterministic system (6) is globally asymptotically stable. The condition (12) gives [55] the upper bound for the noise, so that the equilibrium of the SDDE (10) is still globally asymptotically stable with probability one.

4 Conclusion

Two questions deserve to be addressed for conclude: the main features, goals and limitations of this study and the further developments and applications in this domain. This introductory research has been concentrated on real life modeling of populations, by using both diffusion and competition standard models with time-delays in a noisy environment: simple epidemic models and predator-prey models with possibly overcrowding. The two mathematical software MATLAB[®]/MathWorks and Wolfram/MATHEMATICA[®] have been used to compute and graph examples. The modeling process consists in three main steps, as it is shown with simple examples: firstly, the definition of events and their respective probability, secondly the determination of the mean vector and of the covariance matrix, and thirdly the elaboration and resolution of an Itô matrix SDE. This presentation is restricted to a maximum of two species. Constant time-delays and white noise are considered. The stochastic models are supposed to incorporate only small time-delays. The resolution of such equations may require approximation techniques and use the Euler-Maruyama approach. Forward Kolmogorov equations (Fokker-Planck equations) are used to find the probability density

function of solutions. Appendices allow to specify some technical aspects of the modeling process: the basic environmental noise modeling, the Ornstein-Uhlenbeck process, the delay stochastic process and the logistic case modeling with constant (small) delays.

Further developments and applications may extend this introductory presentation [3, 53]. The models can be generalized to multiple species. Other specifications may be chosen as an alternative to the Verhulst approach, such as with Gompertz or Richards [64]. Other domains of the population biology may be treated. Larger and variable time-delays may be considered. The resolution may use another approximation techniques like the Milstein method [18, 71]. Periodic oscillations may be applied to the parameters. Turing instability is analysed by [32] in a discrete competitive L-V model. SDDEs are used in the modeling of the genetic regulation due to biochemical reactions [69]. Volterra-Fredholm integral equations are used by [61]. Backward Kolmogorov equations may be used to estimate the mean persistence-time of the system, i.e. the expected time it takes to have a zero size of either population [3]. Other aspects of the domain may introduce more realism: different habitat for prey and shared resources, distributed delays, ratio-dependent models [20, 36] and age-structure. Other domains are infection in marine bacteria populations [12, 13, 17, 28, 49], cotton fiber breakage [68]

Appendix A. Environmental Noise Modeling¹⁷

Consider one species population dynamics in a varying environment [3:pp.153-156]. The simple deterministic model is

$$\frac{dx(t)}{dt} = b(t)x(t) - d(t)x(t),$$

where $x(t)$ denotes the time-continuous population size, and $b(t), d(t)$ the time-continuous per capita birth and death rates, respectively. The environment is supposed to produce random effects on the birth

and death rates. The changes in Δt for $\Delta x, \Delta b, \Delta d$ are presented in Table 4 with their corresponding probabilities.

Table 4: Possible changes in a noisy environment with corresponding probabilities in Δt .

Change	Probability
$\Delta x^{(1)} = -1$	$p_1 = d x \Delta t$
$\Delta x^{(2)} = 1$	$p_2 = b x \Delta t$
$\Delta x^{(3)} = 0$	$p_3 = 1 - (p_1 + p_2)$
$\Delta b^{(1)} = -\alpha_b$	$p_4 = (q_b - \beta_b(\bar{b} - b)) \Delta t$
$\Delta b^{(2)} = \alpha_b$	$p_5 = (q_b + \beta_b(\bar{b} - b)) \Delta t$
$\Delta b^{(3)} = 0$	$p_6 = 1 - (p_4 + p_5)$
$\Delta d^{(1)} = -\alpha_d$	$p_7 = (q_d - \beta_d(\bar{d} - d)) \Delta t$
$\Delta d^{(2)} = \alpha_d$	$p_8 = (q_d + \beta_d(\bar{d} - d)) \Delta t$
$\Delta d^{(3)} = 0$	$p_9 = 1 - (p_7 + p_8)$

In the expressions of the probabilities p_4, p_5 , the terms $\pm \beta_b(\bar{b} - b)$ correspond to the drift, while $q_b \Delta t$ is with the diffusion process. The probability of moving closer to the average \bar{b} is greater than the probability of moving away from it [3]. The system of Itô SDEs is deduced from the mean vector-valued μ and from the square root of the matrix-valued covariance. We have

¹⁷ SDELab [24] is a package for solving SDEs within MATLAB including Milstein's method. Picchini [62] also developed a SDE toolbox for the simulation and estimation of SDEs with MATLAB. Higham [33] introduces to the numerical simulation of SDEs in MATLAB with codes. MATLAB codes for SDDEs are in [59].

$$\begin{pmatrix} dx \\ db \\ dd \end{pmatrix} = \begin{pmatrix} bx - dx \\ 2\alpha_b\beta_b(\bar{b} - b) \\ 2\alpha_d\beta_d(\bar{d} - d) \end{pmatrix} dt + \begin{pmatrix} \sqrt{bx - dx} & 0 & 0 \\ 0 & \alpha_b\sqrt{2q_b} & 0 \\ 0 & 0 & \alpha_d\sqrt{2q_d} \end{pmatrix} \begin{pmatrix} dW_1 \\ dW_2 \\ dW_3 \end{pmatrix}.$$

The numerical values in the application are (as in [3]) $T = 1$, $2\alpha_b\beta_b = 2\alpha_d\beta_d = 1$, $\alpha_b\sqrt{2q_b} = \alpha_d\sqrt{2q_d} = 0.5$, $\bar{b} = 1$, $\bar{d} = 1.4$, $x_0 = 30$, $b(0) = \bar{b} = 1$ and $d(0) = \bar{d} = 1.4$. Fig.8 plots the effect of the environmental noise on the states $x(t), b(t), d(t)$. The absence of environmental noise supposes $2\alpha_b\beta_b = 2\alpha_d\beta_d = 0$ and $\alpha_b\sqrt{2q_b} = \alpha_d\sqrt{2q_d} = 0$.

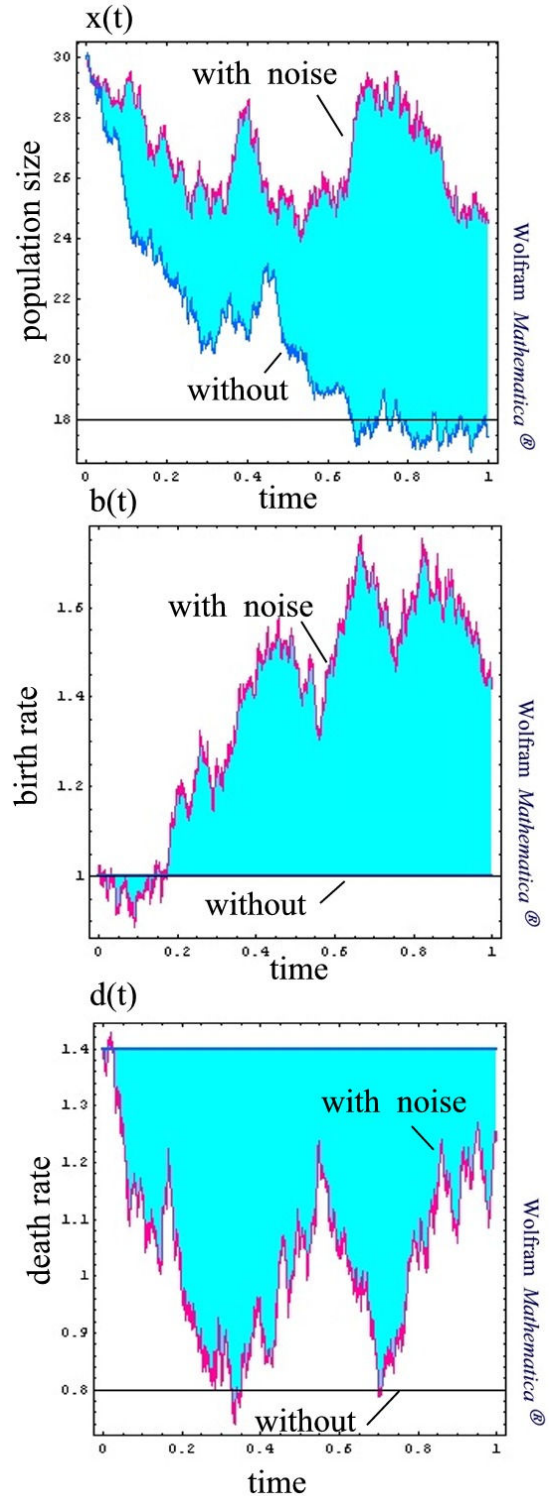


Figure 6: Effect of the environmental noise on the population size, on birth and death rates.

Appendix B. Ornstein-Uhlenbeck Process

The Ornstein-Uhlenbeck process [60: p.75] is the unique solution X_t of the following Langevin equation [63]

$$dX_t = -aX_t + \sigma dW_t, X_0 \text{ given.}$$

The explicit solution is¹⁸

$$X_t = X_0 e^{-at} + \sigma \int_0^t e^{a(s-t)} dW_s$$

The mean and variance are

$$E[X_t] = X_0 e^{-at}, \quad \text{Var}[X_t] = \sigma^2 \frac{1 - e^{-2at}}{2a}.$$

Proof.

$$E[X_t] = X_0 e^{-at} + \sigma e^{-at} E\left[\int_0^t e^{as} dW_s\right] = X_0 e^{-at},$$

since $E\left[\int_0^t (e^{as})^2 ds\right] < +\infty$ and $\int_0^t e^{as} dW_s$ is a zero martingale at time $t = 0$ QED.

$$\begin{aligned} \text{Var}[X_t] &= E\left[(X_t - E[X_t])^2\right], \\ &= \sigma^2 E\left[e^{-2at} \left(\int_0^t e^{as} dW_s\right)^2\right] = \sigma^2 e^{-2at} E\left[\int_0^t e^{2as} dW_s\right], \\ &= \sigma^2 \frac{1 - e^{-2at}}{2a}. \text{ QED } \square \end{aligned}$$

Let the SDE

$$dX_t = f(t, X_t) dt + g(t, X_t) dW_t \quad (13)$$

The probability density function (pdf) of (13) satisfies the forward Kolmogorov equation

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial x}(p \times f(t, x)) + \frac{1}{2} \frac{\partial^2}{\partial x^2}(p \times g(t, x)^2),$$

¹⁸ To find the explicit solution, we may take the integrating factor e^{at} , multiply both sides of the SDE, compare with $d(e^{at} X_t)$, and integrate (see also [48, 79]).

where $p \equiv p(t, x)$ is the pdf. For the Langevin SDE

$$dX_t = -X_t dt + \sigma dW_t, X_0 = 0,$$

Fig.9 graphs a numerical example for $\sigma = 10$, of the pdf over time, of the probability distribution at the final time and the second moment of $X(t)$ over time.¹⁹

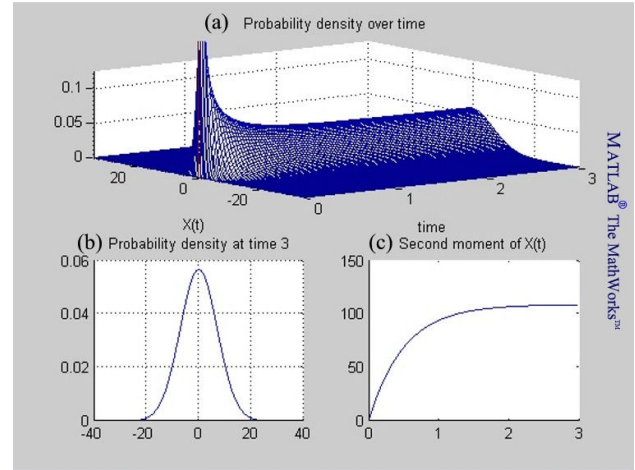


Figure 9: Probability density function over time satisfying the forward Kolmogorov equation with $\sigma = 10$: (a) pdf over time, (b) pdf at the final time and (c) second moment of $X(t)$ over time.

Remark: the mean-reverting Ornstein-Uhlenbeck process is the solution X_t of the following SDE

$$dX_t = (\bar{X} - X_t) dt + \sigma dW_t,$$

where \bar{X} is a constant and for X_0 given. The solution is

$$X_t = \bar{X} + (X_0 - \bar{X}) e^{-t} + \sigma \int_0^t e^{s-t} dW_s$$

The mean and the variance are

$$E[X_t] = \bar{X} + (X_0 - \bar{X}) e^{-t}$$

¹⁹ The original MATLAB codes for the forward and backward Kolmogorov equations are available on line at http://www_math.bgsu.edu/~zirbel/sde.

and

$$\text{Var}[X_t] = \frac{\sigma^2}{2}(1 - e^{-2t}).$$

Fig.10 plots a path for both process, with the following data $T = 10, a = 0.5, \sigma = 0.1$ and $X_0 = 1, \bar{X} = 0.5$.

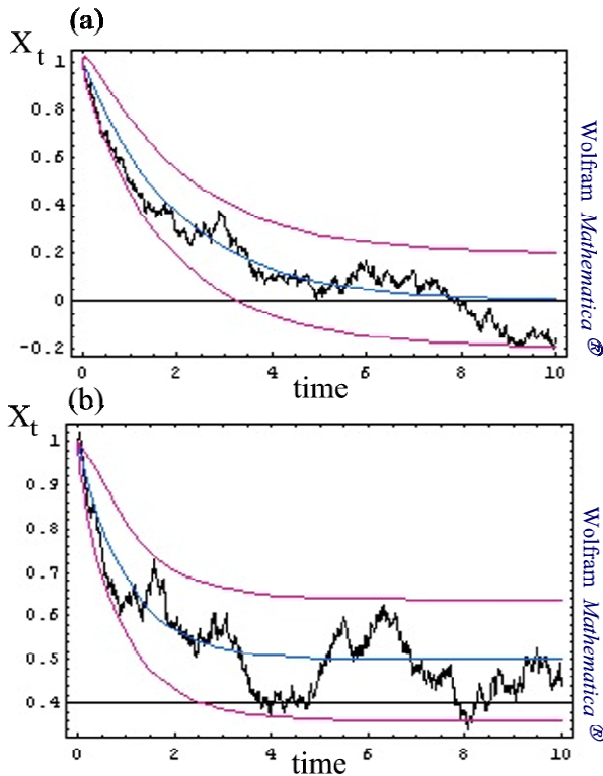


Figure 10: Orstein-Uhlenbeck process (a) and mean-reverting version (b) with mean and 95% confidence bands.

Appendix C. Delay Stochastic Process

C.1 Itô formula [3, 21, 45,60]

Definition 1. (Wiener process). *A continuous-time stochastic process $z(t), t \geq 0$ is a Wiener process (or Brownian motion), if it satisfies the three properties*

(i) initial value $z(0) = 0$,

(ii) stationary independent increments $z(t_k) - z(t_{k-1})$ for $k = 1, \dots, n$

(iii) Normal distribution with

$$\mathbf{E}[z(t) - z(s)] = (t - s)\mu \text{ and}$$

$$\mathbf{E}[(z(t) - z(s))^2] = (t - s)\sigma^2, \text{ where } \mu \text{ denotes the drift and } \sigma \text{ the diffusion rate}^{20}.$$

Theorem 4. (Itô's formula) (Oksendal, 2003[60]) *Let $x(t)$ be an Itô process given by $dX_t = u dt + b dB_t$. Let $g(\cdot)$ a twice continuously differentiable function. Then $Y_t = g(t, X_t)$ is again an Itô process, and*

$$dY_t = \frac{\partial g}{\partial t}(t, X_t)dt + \frac{\partial g}{\partial x}(t, X_t)dX_t + \frac{1}{2} \frac{\partial^2 g}{\partial x^2}(t, X_t)(dX_t)^2,$$

where $(dX_t)^2 = (dX_t)(dX_t)$ is calculated according to the multiplication rules

$$dt \cdot dt = dt \cdot dB_t = dB_t \cdot dt = 0, dB_t \cdot dB_t = dt.$$

Proof. See Oksendal (2003)[60: p.46]. \square

C.2 Stochastic Delay Differential Equation [41, 60, 72].

Let a stochastic nondelay differential equation (SDE) be

$$\frac{dX_t}{dt} = b(t, X_t) + \sigma(t, X_t)W_t, \quad (14)$$

where $b(\cdot)$ and $\sigma(\cdot)$ are given functions and W_t is the white noise process²¹. According to (14), X_t is the solution of the integral equation

²⁰ The probability function is given by

$$f(z) = \left(\sqrt{2\pi\sigma^2 t}\right)^{-1} e^{-\frac{1}{2}\left(\frac{z-\mu}{\sigma\sqrt{t}}\right)^2}.$$

²¹ We can replace $w_k \Delta t_k$ by $\Delta B_k = B_{t_k} - B_{t_{k-1}}$, where the process $\{B_t\}_{t \geq 0}$ is the Brownian motion [60: p.22].

$$X_t = X_0 + \int_0^t b(s, X_s) ds + \int_0^t \sigma(s, X_s) dW_s, \quad (15)$$

for an appropriate Itô or an Stratonovich interpretation ²²of the second integral in (15).

C.3 Solution to basic stochastic processes

Example 1. (Geometric Brownian Motion (GBM)). For a GBM taking the form

$$\frac{dx(t)}{x(t)} = a dt + b dW(t), \quad (16)$$

the solution in term of $W(t)$ is²³

$$x(t) = x(0)e^{\left(a - \frac{b^2}{2}\right)t + bW(t)}, \quad t \geq 0, \quad (17)$$

Proof. By integrating both sides of (16), we get

$$\int \frac{dx(t)}{x(t)} = at + bW(t). \text{ To evaluate the integral on the}$$

LHS, the Itô formula is used for the function $f(t, x) = \ln x, x > 0$. We have

$$dg(t, x) = g'_t dt + g'_x dx + \frac{1}{2} g''_{xx} (dx)^2. \text{ After some}$$

calculations, we deduce $d \ln x(t) = \frac{dx(t)}{x(t)} - \frac{1}{2} b^2 dt$,

then evaluate the integral as

$$\int_0^t \frac{dx(t)}{x(t)} = \ln \frac{x(t)}{x(0)} + \frac{1}{2} b^2 t \text{ and get (17). QED} \square \square$$

Example 2. (Stochastic delay logistic equation). For a logistic SDDE taking the form

²² The Itô and the Stratonovich stochastic integrals generally differ [3]. For example, the Itô integral

$$\int_0^t W(s) dW(s) = \frac{1}{2} (W^2(t) - W^2(0)) - \frac{t^2}{2},$$

differs from the Stratonovich integral for this example

$$\int_0^t W(s) \circ dW(s) = \frac{1}{2} (W^2(t) - W^2(0)).$$

Proof. See [3: pp. 80-81]. \square

²³ Numerical applications may use the *Mathematica 5.1* packages `Statistics`ContinuousDistributions``, `StochasticEquations`EulerSimulate`` and `Itovns3` [43, 44]. The primitive of `EulerSimulate` is `EulerSimulate[drift,diffusion,{x,x0},{duration,nsteps}]`. The primitive returns a list of simulated values for the corresponding Itô process.

$$dx(t) = ax(t) \left(1 - \frac{x(t)}{K}\right) dt + g(x(t)) dW(t),$$

the solution in term of $W(t)$ is

$$x(t) = \frac{x(0)e^{\left(a - \frac{b^2}{2}\right)t + bW(t)}}{1 + \frac{x(0)}{K} a \int_0^t e^{\left(a - \frac{b^2}{2}\right)s + bW(s)} ds}, \quad t \geq 0,$$

Proof. See Gard (1988)[23], p. 166. \square

C.4 Small delay stochastic process

Now, consider the following SDDE [29, 30]

$$dx(t) = f(x(t), x(t - \tau)) dt + \sigma g(x(t)) dW(t), \quad (18)$$

where $f(\cdot)$ and $g(\cdot)$ are known functions, τ is the time-delay, σ scales the noise amplitude and $W(t)$ is a Wiener process for which $\langle W(t) \rangle = 0$ and $\langle W^2(t) \rangle = t$. If (18) is interpreted using Stratonovich calculus, the equivalent Itô formulation is

$$dx(t) = \left[f(x_0, x(t - \tau)) + \frac{\sigma^2}{2} g(x_0) \frac{d}{dx_0} g(x_0) \right]_{x_0=x(t)} dt + \sigma g(x(t)) dW(t). \quad (19)$$

Example 3. A stochastic delay logistic equation satisfies the following SDE

$$dx(t) = x(t)(a - bx(t - \tau)) dt + \sigma x(t) dW(t). \quad (20)$$

According to the Stratonovich interpretation of (20), we have the equivalent Itô SDDE

$$dx(t) = x(t) \left(a + \frac{\sigma^2}{2} - bx(t - \tau) \right) dt + \sigma x(t) dW(t).$$

Proof. From (18), we use the following equivalences $f(x(t), x(t - \tau)) \equiv x(t)(a - bx(t - \tau))$

and $g(x(t)) \equiv x(t)$. \square

A $O(\tau^2)$ Taylor expansion on $f(x(t), x(t - \tau))$ around $\tau = 0$ yields

$$f(x(t), x(t-\tau))dt \approx f(x(t), x(t))dt - \tau \left[\frac{\partial}{\partial x_\tau} f(x(t), x_\tau) \right]_{x_\tau=x(t)} dx(t),$$

where x_τ is a dummy variable. According to (18), we get the following (Stratonovich) approximation

$$dx(t) = f_a(x(t))dt + \sigma g_a(x(t)) \circ dW(t), \quad (21)$$

where

$$f_a(x_0) \equiv f(x_0, x_0) \left[1 - \tau \frac{\partial}{\partial x_\tau} f(x_0, x_\tau) \right]_{x_\tau=x_0} \quad (22)$$

and

$$g_a(x_0) \equiv g(x_0) \left[1 - \tau \frac{\partial}{\partial x_\tau} f(x_0, x_\tau) \right]_{x_\tau=x_0}, \quad (23)$$

where x_0, x_τ are dummies.

Example 4. The Stratonovich SDE approximation of the SDDE (20) is

$$dx(t) = \left\{ x(t)(a - bx(t))(1 + \tau bx(t)) \right\} dt + \sigma x(t)(1 + \tau bx(t)) \circ dW(t),$$

Proof. In fact, we have the approximations

$$f_a(x_0) = x_0(a - bx_0)(1 + \tau bx_0)$$

and

$$g_a(x_0) = x_0(1 + \tau bx_0)$$

Then, we apply (21) to (23). \square

The equivalent Itô SDE approximation is deduced from (19), and we get

$$dx(t) = \left\{ x(t) \left(a + \frac{\sigma^2}{2} - b(1 - \tau\sigma^2) \right) \times (1 + \tau bx(t)) \right\} dt + \sigma x(t)(1 + \tau bx(t)) dW(t) \quad (24)$$

Appendix D. Stochastic Delay Logistic Equation

D.1 Logistic growth

A single species population growth $dn(t)/dt$ not only with the population size $n(t)$. As it grows, its members come into competition for food and other limited resources. Additional deaths are due to the $n(n-1)/2$ interactions. We then have

$$\frac{dn(t)}{dt} = k n(t) - k_1 \frac{n(t)(n(t)-1)}{2}.$$

In a constant environment (r, K) , we may also write as in [35: p. 33]

$$\frac{dx(t)}{dt} = r x(t) \left(1 - \frac{x(t)}{K} \right),$$

where r is the Malthusian growth rate and K the carrying capacity of the environment²⁴. The global solution is

$$x(t) = \frac{K x_0 e^{r t}}{K + x_0 (e^{r t} - 1)}, \quad t \geq 0$$

Proof. The solution can be obtained by separating the variables. Integrate the inverse $\frac{dt}{dx}$ yields $t(x)$

and invert. $\square \square$

D.2 Delay logistic equation

The population growth may be controlled by a feedback loop with reaction lag, as in the following Hutchinson logistic form [27, 31, 37]

$$\frac{dx(t)}{dt} = r x(t) \left(1 - \frac{x(t-\tau)}{K} \right), \quad r, K > 0$$

where τ denotes the required time-lag to reproduce a limited resource. Rescaling the variable with

$$x(t) = K \left(1 + y \left(\frac{t}{\tau} \right) \right),$$

we have the Wright's equation [43, 73]

$$\frac{dy(t)}{dt} = -\alpha (1 + y(t)) y(t-\tau), \quad y(t) > 0, \quad t \geq \tau$$

where $\alpha = r \tau$. Qualitative studies show that the presence of time-delays is a potential source of non-

²⁴ In a changing environment, the parameters r and K become time-dependent (periodic) functions. The solution is also a periodic solution (see [78]).

stationarities such as with periodic oscillations and instabilities (Table 5) [10]

Table 5: Pattern of the solution

α	Solution pattern
$(0, e^{-1})$	Monotonic convergence to K
$(e^{-1}, \frac{\pi}{2})$	Oscillatory convergence to K
$(\frac{\pi}{2}, \infty)$	Oscillations in a stable limit cycle

Changing the variable, we may write the equivalent form

$$\frac{dx(t)}{dt} = -\alpha f(x(t-\tau)) \quad (25)$$

Proof. The equivalent form (25) is obtained by letting $\ln(1+y(t)) \equiv x(t)$ for $y(t) > -1$, and $f(x) = e^x - 1$. \square

By reparameterizing the equation and by scaling the time [19], we also get

$$\frac{dx(t)}{dt} = -\alpha\tau f(x(t-1)).$$

D.3 Stochastic logistic growth

Some assumptions can be retained on the probabilities of birth and death rate changes [5]. Table 6 shows the possible changes and their corresponding probabilities²⁵.

Table 6: Changes in the logistic growth model with corresponding probabilities.

Change	Probability
$\Delta X^{(1)} = 1$	$p_1 = (rX) \Delta t$
$\Delta X^{(2)} = -1$	$p_2 = (rX^2 / K) \Delta t$

The following SDE corresponds to the mean change and to the variance per time interval. We get

$$dX(t) = rX(t) \left(1 - \frac{X(t)}{K}\right) dt + \sqrt{rX(t) \left(1 + \frac{X(t)}{K}\right)} dW(t),$$

where $X \in [0, \infty)$. To approximate the solution numerically, a discretization of the time interval $[t_0, T]$ is such as $t_0 < t_1 < \dots < t_n < \dots < t_n = T$. According to the Euler-Maruyama method, we have the following iterative scheme

$$\tilde{X}_{n+1} = \tilde{X}_n + r\tilde{X}_n \left(1 - \frac{\tilde{X}_n}{K}\right) h_n + \sqrt{\tilde{X}_n + r\tilde{X}_n \left(1 + \frac{\tilde{X}_n}{K}\right)} \sqrt{h_n} \Delta W_n,$$

where $\tilde{X}_n \in [0, \infty)$ and $\tilde{X}_n = X(t_n)$ is the discretization of X_t at times $t_n = \sum_{k=0}^{n-1} \Delta_k$, $h_n = t_{n+1} - t_n = \int_{t_n}^{t_{n+1}} ds$ the discrete time interval, and $\Delta W_n = W(t_{n+1}) - W(t_n) = \int_{t_n}^{t_{n+1}} dW_s \sim N(0, h_n)$ the Wiener with normal distribution and $W(t_0) = 0$. Fig.11 plots three sample paths for this stochastic process, with the deterministic evolution with the following numerical values: $T = 250$, $r = 0.02$ and $K = 10$.

²⁵ One another set of assumptions is mentioned by [5]: $p_1 = rX(1 - X/(2K))\Delta t$ and $p_2 := rX^2/(2K)\Delta t$. These assumptions yield the following SDE: $dX(t) = rX(t)(1 - X(t)/K) dt + \sqrt{rX(t)} dW(t)$.

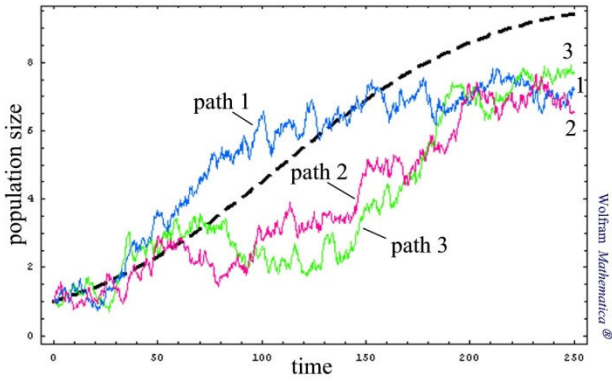


Figure 11: Three sample paths for the stochastic logistic model and deterministic evolution.

The forward Kolmogorov differential equation (Fokker-Planck equation) for the logistic SDE yields the probability distribution of the solution. The parabolic partial differential equation (PDE) for this process is²⁶

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial x} (f(x) \times p) + \frac{1}{2} \frac{\partial^2}{\partial x^2} (g(x)^2 \times p),$$

where $p \equiv p(t, x)$ is the pdf, and two functions are defined by $f(x) := rx \left(1 - \frac{x}{K}\right)$ and

$$g(x) := \sqrt{rx \left(1 + \frac{x}{K}\right)}.$$

The logistic SDE is useful to model fisheries management problems [38]. The SDE may also be developed from the deterministic model in three different ways. Let the deterministic logistic be the ODE

$$\frac{dX(t)}{dt} = rX(t) \left(1 - \frac{X(t)}{K}\right).$$

²⁶ For a Brownian motion, the pdf is the solution of the following PDE: $\frac{\partial}{\partial t} p(t, x) = \frac{K}{2} \frac{\partial^2}{\partial x^2} p, x \in (-\infty, \infty)$. The pdf has a normal distribution, with zero mean and variance Kt . We have

$$p(t, x) = \left(\sqrt{2\pi Kt}\right)^{-1} e^{-\frac{(x-x_0)^2}{2Kt}}.$$

In the first way for modeling, a stochastic term is just added to provide the SDE

$$dX(t) = rX(t) \left(1 - \frac{X(t)}{K}\right) dt + \sigma X(t) dW(t).$$

The second way is to replace the parameter r by $r + \sigma W(t)$, then obtaining the SDE

$$dX(t) = rX(t) \left(1 - \frac{X(t)}{K}\right) dt + \sigma X(t) \left(1 - \frac{X(t)}{K}\right) dW(t).$$

The third way consists in replacing the parameter $\frac{1}{K}$ by $\frac{1}{K} + \sigma W(t)$, thus obtaining the SDE

$$dX(t) = rX(t) \left(1 - \frac{X(t)}{K}\right) dt + \sigma rX(t)^2 dW(t).$$

Fig.12 illustrates one random path corresponding to each of these ways of modeling.

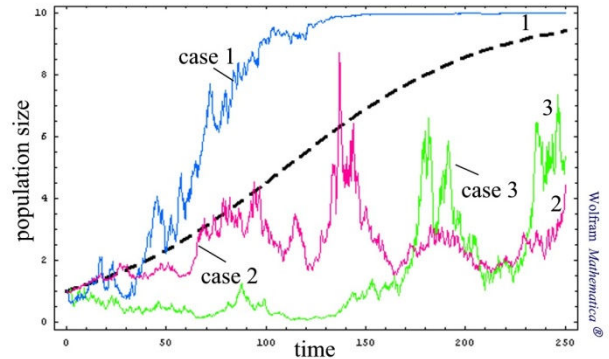


Figure 12: One random path for each modeling option with case 1 (add a term), case 2 (modify the intrinsic growth rate) and case (modify the carrying capacity of the environment).

D.4 Stochastic delay logistic equation

Given the single-species population dynamics

$$\frac{dx(t)}{dt} = rx(t) \left(1 - \frac{x(t-\tau)}{K}\right), \quad a, b > 0 \quad (26)$$

where r is the Malthusian growth rate, $\frac{r}{K}$ scales the

environmental constraints and time-delay τ is the reaction time of the population to environment. The fixed points of (26) are $\bar{x}_1 = 0$ and $\bar{x}_2 = K$. Linearizing around \bar{x}_2 leads to the equivalent Langevin equation [30]

$$\frac{dx(t)}{dt} = -rx(t-\tau), a > 0$$

Suppose that a multiplicative noise is added to (26), We have the SDE

$$dx(t) = rx(t) \left(1 - \frac{x(t-\tau)}{K}\right) dt + \sigma x(t) dW(t). \quad (27)$$

If (27) is interpreted using a Stratonovich calculus, the equivalent Itô SDDE is

$$dx(t) = \left\{ rx(t) \left(1 - \frac{x(t-\tau)}{K}\right) + \frac{\sigma^2}{2} x(t) \right\} dt + \sigma x(t) dW(t).$$

From the comparison between (20) and (26), we deduce the equivalences $a=r$ and $b=r/K$. Replacing a and b in the approximated Itô SDE (24), yields

$$dx(t) = \left\{ x(t) \left(1 - \frac{\tau r}{K} x(t)\right) \times \left(r + \frac{\sigma^2}{2} - \frac{r}{K} (1 - \tau \sigma^2) x(t) \right) \right\} dt + \sigma x(t) \left(1 - \frac{\tau r}{K} x(t)\right) dW(t).$$

Fig.13 illustrates the effect of the small delays for different values of the delay $\tau \in \{0.1, 0.3, 0.5, 0.7\}$.

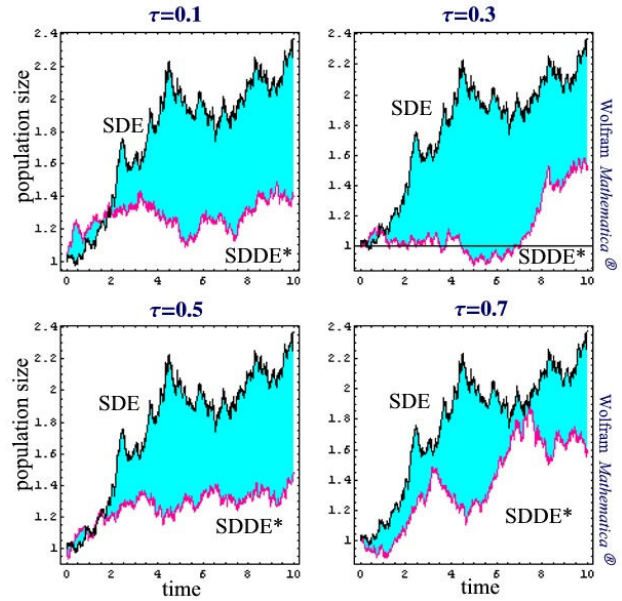


Figure 13: Effect of different small delays in SDDEs for $\tau \in \{0.1, 0.3, 0.5, 0.7\}$.

Acknowledgment I would like to thank The MathWorks France, for allowing me to use for trials, the MATLAB software and some specialized toolboxes.

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