Stochastic delay Lotka-Volterra system to interacting population dynamics

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***Abstract*—**This article introduces to the modeling process and reviews the essential features of the well-known Lotka-Volterra multispecies system in ecological modelling. The interacting population dynamics may be competitive or cooperative in the noisy environment of real world situations. In this stochastic context, the conditions for positive non exploding solutions are given. The computations have been carried out by using the software *Wolfram Mathematica* ® 8

***Keywords*—**Lotka-Volterra system, stochastic delay L-V system, Ito's formula, Stratonovich integral, population dynamics.

I. INTRODUCTION

THIS introductive paper is dedicated to population growth dynamics in a noisy constrained environment. The time delay systems [20] 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]

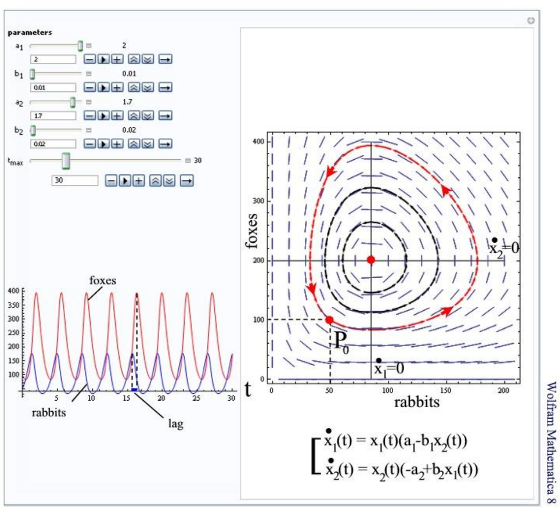

Figure 1. Lotka-Volterra system without internal competition.

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[1] A history on population dynamics is presented by Bacaër (2011)[2],. Hillion (1980)[16] introduces to the different models in discrete and continuous time. The interactions among species are considered by May *et al.* (1979)[29] in application to the management of multispecies fisheries. Time lags in biological systems have been already analyzed by MacDonald (1978)[26]. Gopalsamy (1992)[12] and Kuang (1993)[23] are using DDEs with applications in 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 predator and the other a prey, 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 I. The two-species system is

$$\begin{cases} \dot{x}_1(t) = x_1(t)\left(a_1 + b_{11}x_1(t) + b_{12}x_2(t)\right), \\ \dot{x}_2(t) = x_2(t)\left(a_2 + b_{21}x_1(t) + b_{22}x_2(t)\right). \end{cases} \tag{1}$$

Figure 1 illustrates[2] the deterministic Lotka-Volterra (L-V) system [24][32] for which one population x_1 is 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 $b_{11} = b_{22} = 0$, that the solution trajectory in the phase plane is

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

where k_1 is the constant of integration (See Gandolfo (1980)[9], pp. 428-454 and Shone (2002)[31], p.607).

TABLE I. POPULATION DYNAMICS

	$b_{12} \times b_{21} < 0$	$b_{12} \times b_{21} > 0$		$b_{12}, b_{21} = 0$
		$b_{12}, b_{21} < 0$	$b_{12}, b_{21} > 0$	
$b_{11}, b_{22} < 0$	Predator-prey with overcrowding	Full competition within & between	Over crowding & cooperate	Over crowding. & independence
$b_{11}, b_{22} = 0$	**Lotka-Volterra**	Competitive system	No over Crowding & cooperate	No over Crowding & 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

$$\dot{x}_i(t) = x_i(t)\left(a_i + \sum_{j=1}^{n} b_{ij}x_j(t)\right),\ i = 1, \ldots, n$$

[2] The *Mathematica* primitive Manipulate[…] creates an interactive object (as in **Figures 1** and **2**) containing controls (sliders) for different parameters of the system. These interactive applications let explore different ranges of values for the coefficients, the delays and the initial conditions. The consequences on the results of such modifications are observed immediately.

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

$$\dot{\mathbf{x}}(t) = \mathrm{diag}\left(\mathbf{x}(t)\right)\left(\mathbf{a} + \mathbf{B}\mathbf{x}(t)\right), \qquad (2)$$

where $\mathbf{x}, \mathbf{a} \in \mathbb{R}^n$, $\mathbf{B} \in \mathbb{R}^{n \times n}$. The existence of an equilibrium solution $\overline{\mathbf{x}}$ requires $\mathbf{a} + \mathbf{B}\overline{\mathbf{x}} = \mathbf{0}$. Gard [10] shows that $\overline{\mathbf{x}}$ is globally stable in $\mathbb{R}_+^n$ if there is $\mathbf{C} = \mathrm{diag}\left(c_1, \dots, c_n\right)$ with $c_i > 0,\ i = 1, \dots, n$ such that

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

is negative definite.

II. DELAY LOTKA-VOLTERRA SYSTEM

B 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 species[3] on another is introduced by means of lagged interaction terms [4], such as

$$\dot{\mathbf{x}}(t) = \mathrm{diag}\left(\mathbf{x}(t)\right)\left(\mathbf{a} + \mathbf{B}\,\mathbf{x}(t-\tau)\right), \qquad (4)$$

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 delays, as in Lu & Chen (2007)[25]

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

where $i = 1, \dots, n$. All the coefficients are real constants[5]. 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 [11]

$$\dot{x}_i(t) = x_i(t)\left(b_i - \sum_{j=1}^{n} a_{ij} x_j\left(t - \tau_{jj}\right)\right). \qquad (5)$$

THEOREM 2.1 (Gopalsamy, 1991) [11] *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* $\overline{\mathbf{x}}$ *such that*

$$\sum_{j=1}^{n} a_{ij} x_j = b_i,\ \ i = 1, \dots, n$$

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

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

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

Proof. See Gopalsamy (1991)[11], pp.442-447.□

[3] The delay is generally justified by resources that have been already accumulated.

[4] The predator-prey system with aftereffect has been introduced by Volterra (1931)[32]. 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 [22].

[5] 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 $a_{ii} > 0, a_{ij} < 0, b_{ij} < 0, i, j = 1, \dots, n, i \ne j$.

B Instability Effects of Delays

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

$$\begin{cases} \dot{x}_1(t) = x_1(t)\left(-1 + x_2(t - \tau_2)\right), \\ \dot{x}_2(t) = x_2(t)\left(2 - x_1(t - \tau_1)\right), \end{cases}$$

where $x_1(t)$ and $x_2(t)$ denote the biomasses 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

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

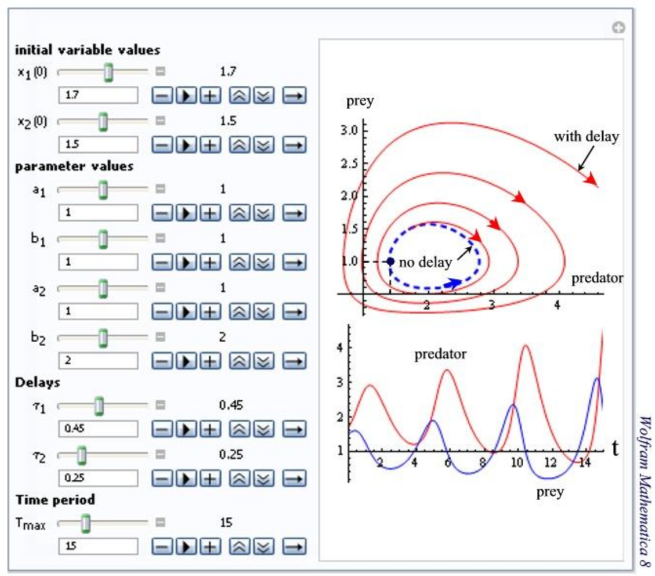

Figure 2. Effect of delays on the periodic orbit of the L-V system.

The presence of delays in biological systems is a potent source of nonstationary problems (periodic oscillations and instabilities): the loss of stability intervenes at a certain threshold. Figure 2 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 delays can stabilize unstable dynamical systems [4].

B Delay Lotka-Volterra Food Chain

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

$$\dot{\mathbf{x}}(t) = \mathrm{diag}\left(\mathbf{x}(t)\right)\left(\mathbf{b} + \mathbf{A}\,\mathbf{x}(t) + \mathbf{B}\,\mathbf{x}(t - \tau)\right),\ \ \mathbf{x} \in \mathbb{R}^3 \qquad (6)$$

where

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

where x_1, x_2 and x_3 are respectively the population densities for a prey, an intermediate predator and a top predator. Gard [10], p.174 shows[6] that an equilibrium $\bar{\mathbf{x}}=(\bar{x}_1,\bar{x}_2,\bar{x}_3)^T$ exists in the positive cone $\mathbb{R}^3_+$, if

$$b_1-\frac{a_{11}}{a_{21}}b_2-\frac{a_{11}a_{22}+a_{12}a_{21}}{a_{21}a_{32}}b_3>0 \tag{7}$$

The equilibrium is globally asymptotically stable as long as the condition (3) is satisfied[7].

III. STOCHASTIC DELAY LOTKA-VOLTERRA SYSTEM

B 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 [27] with $b_{ij}\to b_{ij}+\sigma_{ij}\dot{w}(t)$. The SDEs corresponding to that system is[8]

$$d\mathbf{x}(t)=\operatorname{diag}(\mathbf{x}(t))\{(\mathbf{a}+\mathbf{B}\mathbf{x}(t))\,dt+\boldsymbol{\sigma}\mathbf{x}(t)d\mathbf{w}(t)\}, \tag{8}$$

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 $1\le i\le n$, while $\sigma_{ij}\ge 0$ if $i\ne j$. The nonnegative solution [9] 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)[27] prove that the environmental Brownian noise suppresses a deterministic explosion.

THEOREM 3.1 (Mao, Marion, & Renshaw 2002) [27] *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 (8) on* $t\ge 0$. *Moreover, the solution will remain in the cone* $\mathbb{R}^n_+$ *with probablity one.*

Proof. See Mao, Marion, & Renshaw (2002)[27], pp. 99-102.

[6] The notations have been adapted to this study.

[7] Here, we have

$$\mathbf{C}(\mathbf{A}+\mathbf{B})+(\mathbf{A}+\mathbf{B})^T\mathbf{C}=-2\begin{pmatrix} c_1a_{11} & 0 & 0\\ 0 & c_2a_{22} & 0\\ 0 & 0 & c_3a_{33}\end{pmatrix}.$$

[8] All the coefficients may be stochastically perturbed with $\mathbf{b}\to\mathbf{b}+\boldsymbol{\beta}\,\dot{\mathbf{w}}_1(t)$ and $\mathbf{A}\to\mathbf{A}+\boldsymbol{\sigma}\,\dot{\mathbf{w}}_2(t)$, where $\mathbf{w}_1(t)$ and $\mathbf{w}_2(t)$ are independent Brownian motions , as in Mao *et al.*(2002)[27].

[9] The size x_i of the *i*th species should be nonnegative.

B Stochastic Delay Lotka-Volterra System

The following delay LV system generalizes the deterministic n-dimensional system (4). We have [3][5][6][28]

$$\dot{\mathbf{x}}(t)=\operatorname{diag}(\mathbf{x}(t))(\mathbf{b}+\mathbf{A}\mathbf{x}(t)+\mathbf{B}\mathbf{x}(t-\tau)),\ \mathbf{x}\in\mathbb{R}^n \tag{9}$$

Suppose a noisy environment, where the intrinsic growth rates b_i's are replaced by $b_i+\sigma_{ii}(x_j-\bar{x}_j)\dot{w}(t)$, where $\bar{x}_j$ is an equilibrium state component, σ_{ii}'s positive constants, $w(t)$ a Brownian motion on a completely probability space $(\Omega,\mathcal{F},\{\mathcal{F}_t\}_{t\ge 0},\mathbb{P})$ and $\dot{w}(t)$ a white noise. The Lotka-Volterra SDDE, corresponding to (9) is

$$\begin{aligned} d\mathbf{x}(t)=\operatorname{diag}(\mathbf{x}(t))\{&(\mathbf{A}(\mathbf{x}(t)-\bar{\mathbf{x}})+\mathbf{B}(\mathbf{x}(t-\tau)-\bar{\mathbf{x}}))\,dt\\ &+\boldsymbol{\sigma}(\mathbf{x}(t)-\bar{\mathbf{x}})\,d\mathbf{w}(t)\}\end{aligned} \tag{10}$$

THEOREM 3.2 (Mao, Yuan, & Zou, 2005)[28] *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 (10) on* $t\ge-\tau$. *Moreover , the solution will remain in the cone* $\mathbb{R}^n_+$ *with probability one.*[10]

Proof. See Mao, Yuan, & Zou (2005)[28], pp. 303-305.

B Stochastic Delay Lotka-Volterra Food Chain[11]

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

$$\begin{aligned} d\mathbf{x}(t)=\operatorname{diag}(\mathbf{x}(t))\{&(\mathbf{A}(\mathbf{x}(t)-\bar{\mathbf{x}})+\mathbf{B}(\mathbf{x}(t-\tau)-\bar{\mathbf{x}}))dt\\ &+\boldsymbol{\sigma}(\mathbf{x}(t-\tau)-\bar{\mathbf{x}})d\mathbf{B}(t)\},\ \mathbf{x}\in\mathbb{R}^3\end{aligned} \tag{11}$$

where $\boldsymbol{\sigma}=\operatorname{diag}(\sigma_{11},\sigma_{22},\sigma_{33})$. Mao *et al.* (2005)[28] 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

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

and

$$\sigma_{ii}^2\le\frac{a_{ii}}{\bar{x}_i}\left\{1-\hat{c}\left(\left(a_{12}^2+a_{32}^2\right)\vee\left(a_{21}^2+a_{23}^2\right)\right)\right\},1\le i\le n \tag{13}$$

The condition (12) guarantees [28] that the steady state equilibrium $\bar{\mathbf{x}}$ of the deterministic system (6) is globally asymptotically stable. The condition (13) gives [28] the upper bound for the noise, so that the equilibrium of the SDDE (11) is still globally asymptotically stable with probability one.

[10] 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 Yin *et al.*(2009)[36] *for a generalized stochastic delay L-V system of the form*

$$d\mathbf{x}(t)=\operatorname{diag}(\mathbf{x}(t))\{(\mathbf{f}(\mathbf{x}(t))+\mathbf{g}(\mathbf{x}(t-\tau)))dt+\mathbf{h}(\mathbf{x}(t))d\mathbf{B}(t)\},$$

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* $\mathbf{B}(t)=(B_1(t),\dots,B_m(t))^T$ *an* $m-$*dimensional Brownian motion.*

[11] This stochastic L-V system with constant delay has been extended to a variable delay in Xu *et al.* (2009)[35]

APPENDIX A : DELAY STOCHASTIC PROCESS

B Itô Formula [1][8]

DEFINITION A1 (Wiener process). *A continuous-time stochastic process* $z(t), t \geq 0$ *is a Wiener process (or Brownian motion) satisfying three the properties*

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

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

(iii) Normal distribution with $\mathbf{E}[z(t) - z(s)] = (t-s)\mu$ *and* $\mathbf{E}\left[(z(t) - z(s))^2\right] = (t-s)\sigma^2$, *where* μ *denotes the drift and* σ *the diffusion rate*[12].

THEOREM A1 (Itô's formula). (Oksendal, 2003[30]) *Let* $x(t)$ *be an Itô process given by* $dX_t = u\, dt + b\, dB_t$. *Let* $g(.)$ *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* $dt.dt = dt.dB_t = dB_t.dt = 0, dB_t.dB_t = dt$.

Proof. See Oksendal (2003)[30], p.46.

B Stochastic Delay Differential Equation [19][30][33]

Let a stochastic nondelay differential equation (SDE) be

$$\dot{X}(t) = b(t, X_t) + \sigma(t, X_t) W_t, \qquad (14)$$

where $b(.)$ and $\sigma(.)$ are given functions and W_t is the white noise process[13]. According to (14), X_t is the solution of the integral equation

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

for an appropriate Itô or an Stratonovich interpretation [14]of the second integral in (15).

Now, we consider the following SDDE [14]

$$dx(t) = f(x(t), x(t-\tau))\, dt + \sigma g(x(t))\, dW(t), \qquad (16)$$

where $f(.)$ and $g(.)$ are known functions, τ is the delay, σ scales the noise amplitude and $W(t)$ is a Wiener process for which $< W(t) >= 0$ and $< W^2(t) >= t$. If (16) is interpreted using Stratonovich calculus, the equivalent Itô formulation is

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

EXAMPLE A1. A stochastic delay logistic equation satisfies the following SDE

$$dx(t) = (a - bx(t-\tau))\, x(t) dt + \sigma x(t)\, dW(t). \qquad (17)$$

According to the Stratonovich interpretation of (17), we have the equivalent Itô SDDE

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

Proof. Using (16), we have the following equivalences $f(x(t), x(t-\tau)) \equiv (a - bx(t-\tau))\, x(t)$ and $g(x(t)) \equiv x(t)$ □

B Solution to Basic Stochastic Processes

EXAMPLE A2 (Geometric Brownian Motion (GBM). For a GBM taking the form

$$\frac{dx(t)}{x(t)} = a\, dt + b\, dW(t), \qquad (18)$$

the solution in term of $W(t)$ is[15]

$$x(t) = x(0) e^{\left(a - \frac{b^2}{2}\right)t + bW(t)}, \, t \geq 0 \qquad (19)$$

Proof. By integrating both sides of (18), we get $\int \frac{dx(t)}{x(t)} = at + bW(t)$. To evaluate the integral on the LHS, the Itô formula is used for the function $f(t,x) = \ln x, x > 0$. We have $dg(t,x) = g'_t\, dt + g'_x\, dx + \frac{1}{2} g''_{xx} (dx)^2$. 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 $\int_0^t \frac{dx(t)}{x(t)} = \ln \frac{x(t)}{x(0)} + \frac{1}{2} b^2 t$ and get (19) .□

EXAMPLE A3 (Stochastic delay logistic equation). For a logistic SDDE taking the form

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

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

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

Proof. See Gard (1988)[10], p. 166.

[12] The probability function is given by

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

[13] We also replace $W_k \Delta t_k$ by $\triangle B_k = B_{t_k} - B_{t_k}$, where the process $\{B_t\}_{t \geq 0}$ is the Brownian motion [30], p.22.

[14] The Itô and the Stratonovich stochastic integrals generally differ [1]. For example, the Itô integral $\int_0^t W(s) dW(s) = \frac{1}{2}\left(W^2(t) - W^2(0)\right) - \frac{t^2}{2}$, Differs from the Stratonovich integral for this example

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

Proof. See Allen (1980)[1], pp. 80-81.

[15] Numerical applications may use the *Mathematica 5.1* packages Statistics`ContinuousDistributions, StochasticEquations `EulerSimulate and Itovns3[19]. 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.

APPENDIX B : DELAY LOGISTIC EQUATION

A. Logistic growth

A single species population growth $\dot{n}(t)$ not only with the population size $n(t)$. As it growths, 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

$$\dot{n}(t) = k\, n(t) - k_1 \frac{n(t)\left(n(t)-1\right)}{2}.$$

In a constant environment (r, K), we may also write as in Hofbauer & Sigmund (1988)[17], p. 33

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

where r is the Malthusian growth rate and K the carrying capacity of the environment [16] The global solution is

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

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

B Delay logistic equation

The population growth may be controlled by a feedback loop with reaction lag, as in the following Hutchinson logistic form [13][15][18]

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

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 [21][34]

$$\dot{y}(t) = -\alpha\left(1 + y(t)\right) y(t-\tau),\ y(t) > 0,\ t \ge \tau$$

where $\alpha = r\,\tau$. Qualitative studies show that the presence of delays is a potential source of nonstationarities such as with periodic oscillations and instabilities (TABLE II) [4]

TABLE II. PATTERNS OF THE SOLUTION

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

Changing the variable, we may write the equivalent form

[16] In a changing environment, the parameters r and K become time-dependent (periodic) functions. The solution is also a periodic solution (see Zhang & Gopalsamy, 1990)[37].

$$\dot{x}(t) = -\alpha f\left(x(t-\tau)\right) \quad (20)$$

Proof. The equivalent form (20) is obtained by letting $\ln\left(1 + y(t)\right) \equiv x(t)$ for $y(t) > -1$, and $f(x) = e^{x} - 1$ □

By reparameterizing the equation and by scaling the time [7], we also get

$$\dot{x}(t) = -\alpha\tau f\left(x(t-1)\right)$$

B Stochastic delay logistic equation

Given the single-species population dynamics

$$\dot{x}(t) = x(t)\left(a - bx(t-\tau)\right),\ a, b > 0 \quad (21)$$

where a is the Malthusian growth rate, b scales the environmental constraints and time-delay τ is the reaction time of the population to environment. The fixed points of (21) are $\bar{x}_1 = 0$ and $\bar{x}_2 = \frac{a}{b}$. Linearizing around $\bar{x}_2$ leads to the equivalent Langevin equation [14]

$$\dot{x}(t) = -ax(t-\tau),\ a > 0$$

Suppose that the parameter b in (21) is stochastically perturbed with $b \to b + \sigma\dot{w}(t)$, where σ scales the noise amplitude. The Wiener process $w(t)$ is characterized by the following averages over realizations $< w(t) > = 0$ and $< w(t)^2 > = t$. For the Itô interpretation, we retain the following SDDE

$$dx(t) = \left(a - bx(t-\tau)\right) x(t)\, dt + \sigma x(t)\, dw(t). \quad (22)$$

If (22) is interpreted using a Stratonovich calculus, the equivalent Itô SDDE is

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

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