

Stochastic Persistence

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Introduction

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*under which conditions a group of interacting species -
plants, animals, viral particles - can coexist.*

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- The theory began in the late 1970s and developed rapidly with
the help of the available tools from dynamical system theory.

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↪ *and recent works with*
Claude Lobry (Nice), Edouard Strickler (Neuchatel)

Outline

- 1 Examples
- 2 A glimpse of the Maths

I : Some motivating examples

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① Verhulst

Verhulst model (1840)

$$\frac{dx}{dt} = x(a - bx)$$

$x \geq 0$, *abundance* of the population,

a = intrinsic *growth rate*,

$b \geq 0$

Verhulst model (1840)

$$\frac{dx}{dt} = x(a - bx)$$

- $a < 0 \Rightarrow x(t) \rightarrow 0$: **Extinction**
- $a > 0 \Rightarrow x(t) \rightarrow \gamma := \frac{a}{b}$ **Persistence**

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Ok but what does it mean if there is (stochastic) variability ?

Environmental variability

$$\frac{dx}{dt} = x(a - bx)$$

Environmental variability

- Assume Gaussian fluctuations of the intrinsic growth rate

$$a \leftarrow a + \text{noise}$$

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- Elementary one dimensional SDEs theory \rightsquigarrow

1

$$a - \frac{\sigma^2}{2} < 0 \Rightarrow x(t) \rightarrow 0$$

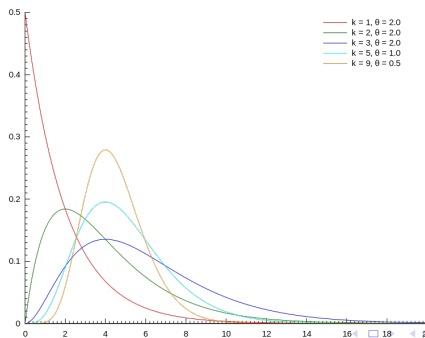
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$$a - \frac{\sigma^2}{2} < 0 \Rightarrow x(t) \rightarrow 0$$

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$$a - \frac{\sigma^2}{2} > 0 \Rightarrow \text{Law}(x(t)) \rightarrow \Gamma(1 - \sigma^2/2a, \sigma^2/2b)$$



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Looks like a sensible definition of Stochastic Extinction/Persistence

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Ok, BUT what if the model is more complicated or the noise non gaussian ?

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1 Verhulst

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- 2 Lotka-Volterra

Lotka Volterra (based on B & Lobry, Annals of Applied Prob 2016)

- 2 species x and y characterized by their **abundances** $x, y \geq 0$.

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- Lotka Volterra ODE

$$(\dot{x}, \dot{y}) = F_{\varepsilon}(x, y)$$

$$F_{\varepsilon}(x, y) = \begin{cases} \alpha x(1 - ax - by) \\ \beta y(1 - cx - dy) \end{cases}$$

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$$F_{\mathcal{E}}(x, y) = \begin{cases} \alpha x(1 - ax - by) \\ \beta y(1 - cx - dy) \end{cases}$$

- $\mathcal{E} = (\alpha, a, b, \beta, c, d)$ is the *environment*:

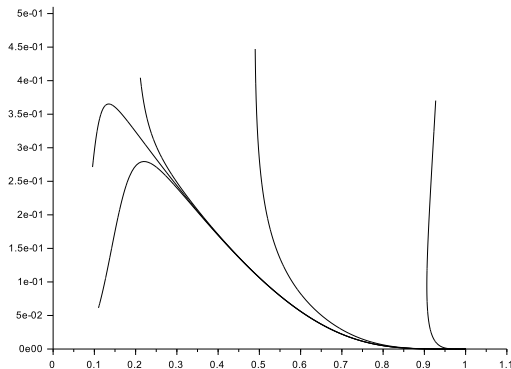
$$\alpha, a, b, \beta, c, d > 0$$

- Environment \mathcal{E} is said *favorable to species* x if
$$a < c \text{ and } b < d.$$

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⇒ *Extinction* of y and *Persistence* of x .



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i.e

$$(\dot{X}, \dot{Y}) = F_{\mathcal{E}_{u(t)}}(X, Y)$$

where

- $\mathcal{E}_0, \mathcal{E}_1$ are two **favorable** environments

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$0 \rightarrow 1$ at rate λ_0

$1 \rightarrow 0$ at rate λ_1 .

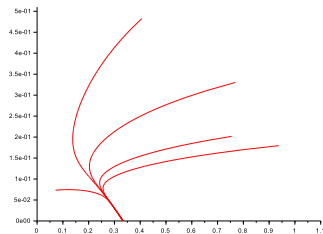
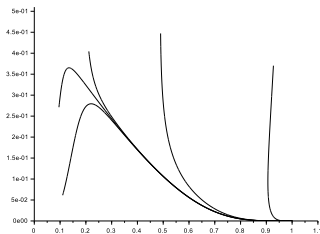


Figure: Phase portraits of F_{ε_0} and F_{ε_1}

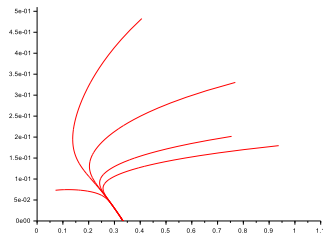
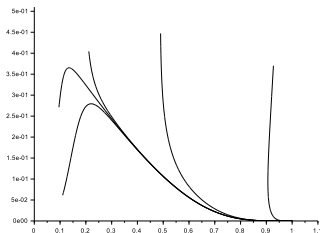


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Different values of λ_0, λ_1 can lead to **various behaviors...**

Simulations

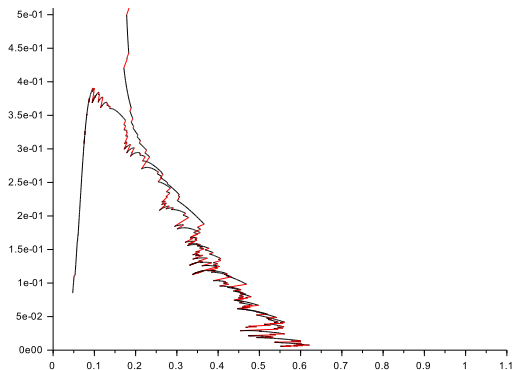


Figure: extinction of 2

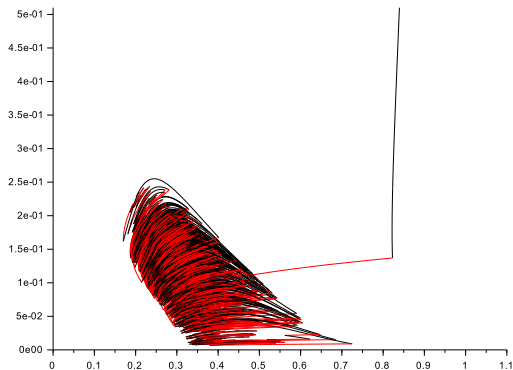


Figure: Persistence

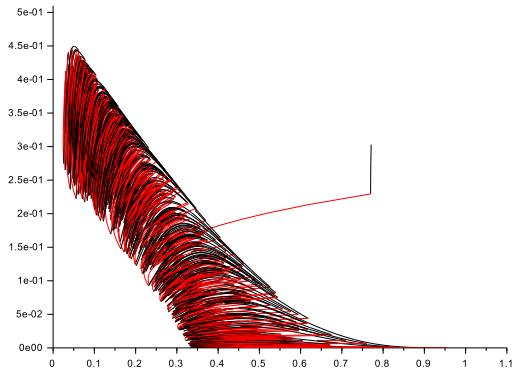


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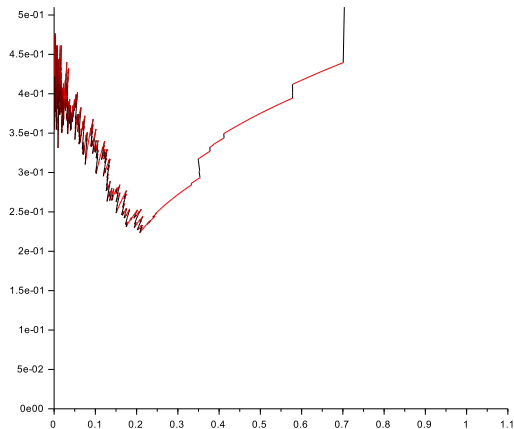


Figure: Extinction of 1

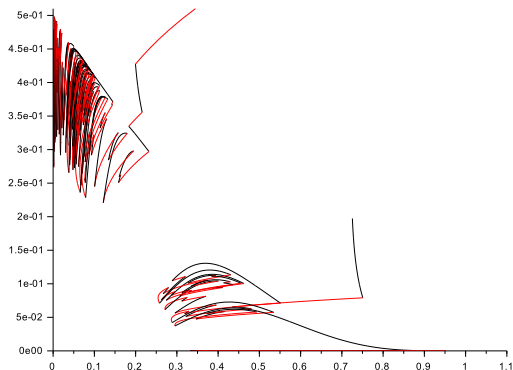


Figure: Extinction of 1 or 2

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- 3 Lajmanovich and Yorke

Lajmanovich and Yorke (based on B & Strickler Annals of Applied Prob 2019)

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- In each group each individual can be infected
- $0 \leq x_i \leq 1$ = proportion of infected individuals in group i .

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$$\frac{dx_i}{dt} = (1 - x_i) \left(\sum_j C_{ij} x_j \right) - D_i x_i$$

- C_{ij} = rate of infection from group i to group j .
- D_i cure rate in group i

Suppose C irreducible

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Theorem (Lajmanovich and Yorke 1976)

If $\lambda(A) \leq 0$, the disease free equilibrium 0 is a global attractor

If $\lambda(A) > 0$ there exists another equilibrium $x^ \gg 0$ and every non zero trajectory converges to x^**

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- Example:

$$C^1 = \begin{pmatrix} 1 & 4 \\ 0 & 1 \end{pmatrix}, D^1 = \begin{pmatrix} 2 \\ 2 \end{pmatrix},$$

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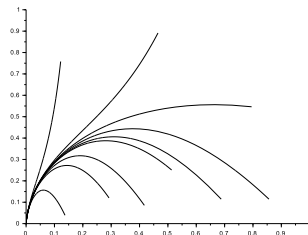
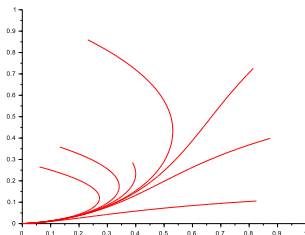
and

$$C^2 = \begin{pmatrix} 2 & 0 \\ 4 & 2 \end{pmatrix}, D^2 = \begin{pmatrix} 3 \\ 3 \end{pmatrix}.$$

$$\lambda(A^1) = \lambda(A^2) = -1 < 0$$

\Rightarrow

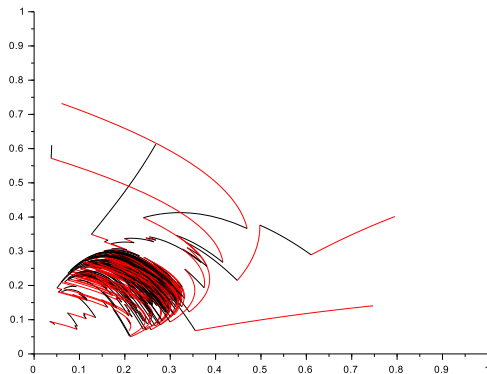
The disease free equilibrium is a global attractor in each environment



1

Figure: Phase portraits of F^1 and F^2

Still, Random Switching may reverse the trend !



,

- More surprising !

$$C^0 = 10 \begin{pmatrix} 1 & 0 & 0 \\ 1 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \quad C^1 = 10 \begin{pmatrix} 1 & 0 & 1 \\ 0 & 1 & 0 \\ 0 & 1 & 1 \end{pmatrix}.$$

$$D^0 = \begin{pmatrix} 11 \\ 11 \\ 20 \end{pmatrix}, \quad D^1 = \begin{pmatrix} 20 \\ 20 \\ 11 \end{pmatrix}$$

F^0, F^1 the associated vector fields on $[0, 1]^3$.

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Here, **for every** $0 \leq t \leq 1$ 0 is a global attractor of

$$F^t = (1 - t)F^1 + tF^0$$

- Fast switching \Rightarrow Extinction of the disease

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- Slow switching \Rightarrow Extinction of the disease
- However, switching at "intermediate rate" \Rightarrow persistence.

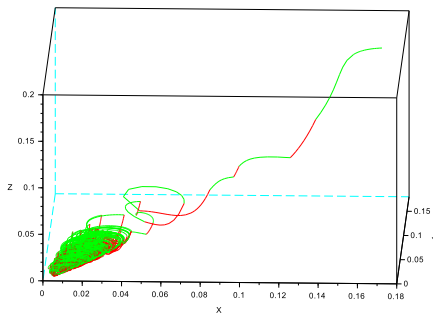


Figure: Switching at rate $\beta = 10$.

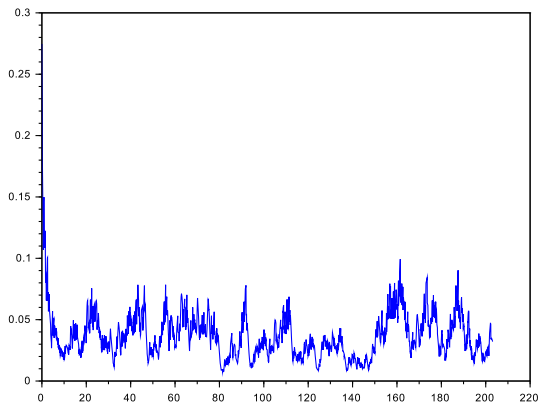


Figure: Simulation of $\|X_t\|$ for $\beta = 10$.

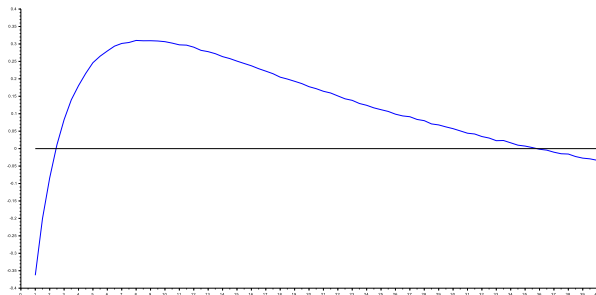


Figure: the critical curve $\beta \mapsto \Lambda(\beta)$.

$\Lambda(\beta) > 0 \Rightarrow$ persistence

$\Lambda(\beta) < 0 \Rightarrow$ extinction

II : A Glimpse of the Maths

Abstract Framework

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$$M = M_+ \cup M_0$$

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$$x \in M_0 \Leftrightarrow X_t^x \in M_0.$$

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(here $x = X_0^x$)

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(I) (**weak version**) $\forall x \in M^+$ limits points of

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- (II) (**strong version**) $\exists \Pi$ invariant probability **on** M^+ ; such that
 $\forall x \in M^+$

$$\lim_{t \rightarrow \infty} |\text{Law}(X_t^x) - \Pi| = 0.$$

How can we prove / disprove
stochastic persistence ?

Key idea Introduce a **stochastic** version of Hofbauer's **average** Lyapunov function:

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$V : M_+ \mapsto \mathbb{R}_+$, such that :

- $V(x) \rightarrow \infty \Leftrightarrow x \rightarrow M_0$

- LV extends continuously to $H : M \mapsto \mathbb{R}$,

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- LV extends continuously to $H : M \mapsto \mathbb{R}$,
Here L is the generator of (P_t)

Definition (H - Exponents)

$$\Lambda^-(H) = -\sup\{\mu H : \mu \in \mathcal{P}_{erg}(M_0)\},$$

$$\Lambda^+(H) = -\inf\{\mu H : \mu \in \mathcal{P}_{erg}(M_0)\}.$$

Here $\mathcal{P}_{erg}(M_0)$ = ergodic probabilities on M_0

- Toy example (Verlhust)

$$dx = x(a - bx)dt + x\sigma dB_t,$$

$$M = \mathbb{R}_+, M_0 = \{0\}, \mathcal{P}_{erg}(M_0) = \{\delta_0\}$$

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$$V(x) = -\log(x),$$

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$$V(x) = -\log(x), LV(x) = -(a - bx) + \frac{1}{2}\sigma^2 \text{ extends to } M_0, \text{ and}$$

$$\Lambda^-(H) = \Lambda^+(H) = a - \frac{1}{2}\sigma^2$$

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- For general population models a good choice for V is

$$V(x) = -\sum_i p_i \log(x_i)$$

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- **For general population models** a good choice for V is

$$V(x) = -\sum_i p_i \log(x_i)$$

- **For epidemic models** things are more complicated ... but V, H can be defined

- $\Lambda^+(H)$ = top Lyapounov exponent of the linearized system
- Often, $\Lambda^-(H) = \Lambda^+(H)$

Persistence Theorem

Theorem

$\Lambda^-(H) > 0 \Rightarrow \text{(weak) Stochastic Persistence}$

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Generalizes previous results in collaboration with Hofbauer & Sandholm 2008, Schreiber 2009, Atchade & Schreiber 2011

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Corollary

If furthermore, the process is *irreducible*, there exists a unique invariant probability $\Pi(dx) = \pi(x)dx$ on M_+ such that for all $x \in M_+$

$$\Pi_t \rightarrow \Pi$$

Persistence Theorem

Theorem

$\Lambda^-(H) > 0 \Rightarrow \text{Stochastic Persistence}$

Generalizes previous results in collaboration with Hofbauer & Sandholm 2008, Schreiber 2009, Atchade & Schreiber 2011

Corollary

If furthermore, the process is **strongly irreducible** there exists a unique invariant probability $\Pi(dx) = \pi(x)dx$ on M_+ such that for all $x \in M_+$

$$\|\mathbf{P}(X_t \in \cdot | X_0 = x) - \Pi(\cdot)\| \leq Ce^{-\lambda t} / (1 + e^{\theta V(x)})$$

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- 1 There exists an **accessible** point $x_0 \in M_+$;
- 2 A weak (strong) **Doebelin condition** holds at x_0 .

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 - Idem for Random Switching (with other Hormander conditions).

Follows from (Bakthin, Hurth, 2012); (Benaïm, Leborgne, Malrieu, Zitt, 2012, 2015)