Stochastic Persistence

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• An important issue in ecology is to find out *under which conditions a group of interacting species - plants, animals, viral particles - can coexist.*

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⇒ Mathematical theory of Deterministic Persistence
• An important issue in ecology is to find out *under which conditions a group of interacting species - plants, animals, viral particles* - can coexist.

• Classical approach to these questions has been the development of **Deterministic Models of Interaction** ODEs, PDEs, Difference equations, etc.

⇒ *Mathematical theory of Deterministic Persistence*

• The theory began in the late 1970s and developed rapidly with the help of the available tools from dynamical system theory (see e.g the book by Smith and Thieme (2011)).
• To take into account environmental fluctuations one need to consider **Stochastic Models of Interaction**
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⇒ *Mathematical theory of stochastic Persistence*

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⇒ *Mathematical theory of stochastic Persistence*

The theory began to emerge with the work of Chesson, Ellner, and others in the 80s but, from a "math perspective", is still in its infancy

• *Purpose of this mini-course: present some recent results on the subject* : (B, 2014), (B & Lobry, 2016), (B & Strickler, 2017) (Hening & Nguyen, 2017)
• To take into account environmental fluctuations one need to consider **Stochastic Models of Interaction**

\[ \Rightarrow \text{Mathematical theory of stochastic Persistence} \]

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• *Purpose of this mini-course*: present some recent results on the subject:(B, 2014), (B & Lobry, 2016), (B & Strickler, 2017) (Hening & Nguyen, 2017)

\[ \sim \Rightarrow \text{based on previous works in collaboration with Hofbauer (Wien), Sandholm (Madison), Schreiber (UC Davis)} \]
Outline

1. Examples
2. Maths
3. Back to examples
1: Some motivating examples
I: Some motivating examples

1. A simple historical model: The Verhulst (or logistic) dynamics
Verhulst Model (1840)

Malthus T.R. 1798. An Essay on the Principle of Population.

"Yet in all societies, even those that are most vicious, the tendency to a virtuous attachment is so strong that there is a constant effort towards an increase of population."
Verhulst Model (1840)

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"Yet in all societies, even those that are most vicious, the tendency to a virtuous attachment is so strong that there is a constant effort towards an increase of population."
Verhulst. P.-F. 1838. Notice sur la loi que la population suit dans son accroissement

*On sait que le célèbre Malthus a établi comme principe que la population humaine tend à croître en progression géométrique, (...) Cette proposition est incontestable, si l’on fait abstraction de la difficulté toujours croissante de se procurer des subsistances lorsque la population a acquis un certain degré d’agglomération. (...)*
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Verhulst (or logistic) dynamics

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

\(x \geq 0\), abundance of the population,

\(a = \text{intrinsic growth rate},\)

\(b \geq 0\)
Verhulst dynamics

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

- \( a < 0 \) \( \Rightarrow \) \( x(t) \rightarrow 0 \) : Extinction

- \( a > 0 \) \( \Rightarrow \) \( x(t) \rightarrow \gamma := \frac{a}{b} \) : Persistence
Verhulst dynamics

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

• $a < 0 \Rightarrow x(t) \to 0$: Extinction

• $a > 0 \Rightarrow x(t) \to \gamma := \frac{a}{b}$: Persistence

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

Variability of ecological processes may have different natures:

- **Demographic Stochasticity**

- **Environmental Stochasticity**
Variability of ecological processes may have different natures:

- **Demographic Stochasticity**

  Even if all individuals in a population are identical, the birth/death of each individual is a random event

- **Environmental Stochasticity**
Stochastic Variability

Variability of ecological processes may have different natures:

- **Demographic Stochasticity**

  Even if all individuals in a population are identical, the birth/death of each individual is a random event.

- **Environmental Stochasticity**

  Light, precipitation, temperature, nutrient availability,
Stochastic Variability

Variability of ecological processes may have different natures:

- **Demographic Stochasticity**

  Even if all individuals in a population are identical, the birth/death of each individual is a random event
  → Fascinating questions (*mean-field approximations, branching, time to extinction, quasi-invariant measures,* ) but not the subject of this course

- **Environmental Stochasticity**

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Stochastic Variability

Variability of ecological processes may have different natures:

- **Demographic Stochasticity**

  Even if all individuals in a population are identical, the birth/death of each individual is a random event
  → Fascinating questions (*mean-field approximations, branching, time to extinction, quasi-invariant measures,* ) but not the subject of this course see the works of N. Champagnat, S. Méléard, D. Villemonais, ...

- **Environmental Stochasticity**

  Light, precipitation, temperature, nutrient availability, *Subject of the course*
Environmental variability

\[ \frac{dx}{dt} = x(a - bx) \]
• Assume Gaussian fluctuations of the intrinsic growth rate

\[ a \leftarrow a + \text{noise} \]

\[ \frac{dx}{dt} = x(a - bx) \]
Environmental variability

- Assume Gaussian fluctuations of the intrinsic growth rate

\[ a \leftarrow a + \text{noise} \]

\[ dx = x(a - bx)dt + x\sigma dB_t \]
Environmental variability

- Assume Gaussian fluctuations of the intrinsic growth rate

\[ a \leftarrow a + \text{noise} \]

\[ dx = x(a - bx)dt + x\sigma dB_t \ (\text{not } \sqrt{x}\sigma dB_t) \]
Environmental variability

- Assume Gaussian fluctuations of the intrinsic growth rate

\[ a \leftarrow a + \text{noise} \]

\[ dx = x(a - bx)dt + x\sigma dB_t \]
Elementary one dimensional SDEs theory \( \Rightarrow \)

\[
a - \frac{\sigma^2}{2} < 0 \Rightarrow x(t) \to 0
\]
• Elementary one dimensional SDEs theory

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

2. $a - \frac{\sigma^2}{2} > 0 \Rightarrow \text{Law}\ (x(t)) \to \Gamma(1 - \frac{\sigma^2}{2a}, \frac{\sigma^2}{2b})$
• Elementary one dimensional SDEs theory $\sim$

1

\[ a - \frac{\sigma^2}{2} < 0 \Rightarrow x(t) \to 0 \]

2

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

Looks like a sensible definition of Stochastic Extinction/Persistence
• Elementary one dimensional SDEs theory \[ \Rightarrow \]

1. \[ a - \frac{\sigma^2}{2} < 0 \Rightarrow x(t) \to 0 \]

2. \[ a - \frac{\sigma^2}{2} > 0 \Rightarrow \text{Law} \ (x(t)) \to \Gamma(\frac{\sigma^2}{2a} - 1, \frac{\sigma^2}{2b}) \]

Looks like a sensible definition of Stochastic Extinction/Persistence

Ok, BUT what if the model is more complicated or the noise non gaussian?
1: Some motivating examples

1. A simple historical model: The Verhulst (or logistic) dynamics
I: Some motivating examples

1. A simple historical model: The Verhulst (or logistic) dynamics
2. Prey-Predator model (Rosenzweig Mac-Arthur)
Prey-Predator

\[ x = \text{preys (or resources) abundance} \]
\[ y = \text{predators abundance} \]

\[
\frac{dx}{dt} = x(1 - \frac{x}{\gamma})
\]

\[
\frac{dy}{dt} = -\alpha y
\]
Prey-Predator

\[ x = \text{preys (or resources) abundance} \]
\[ y = \text{predators abundance} \]

\[ \frac{dx}{dt} = x\left(1 - \frac{x}{\gamma}\right) - xyh(x, y) \]

\[ \frac{dy}{dt} = -\alpha y + xyh(x, y) \]

\[ xh(x, y) = \text{Per predator kill rate} = \text{predator reproduction rate} \]
Prey-Predator

\[ x = \text{preys (or resources) abundance} \]
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\[ \frac{dx}{dt} = x(1 - \frac{x}{\gamma}) - xyh(x, y) \]

\[ \frac{dy}{dt} = -\alpha y + xyh(x, y) \]

\[ xh(x, y) = \text{Per predator kill rate} = \text{predator reproduction rate} \]

- \[ h(x, y) = c \text{ Lotka-Volterra} \]
- \[ h(x, y) = 1/(1 + x) \text{ Rosenzweig Mac-Arthur} \]
- \[ h(x, y) = h(y/x) \text{ Arditi Ginzburg, ...} \]
Rosenzweig Mac-Arthur (1963)

\[
\frac{dx}{dt} = x(1 - \frac{x}{\gamma} - \frac{y}{1+x})
\]

\[
\frac{dy}{dt} = y(-\alpha + \frac{x}{1+x})
\]

"http://experiences.math.cnrs.fr/simulations/matheco-RosenzweigMcArthur"

"http://www.espace-turing.fr/Sur-les-modeles-proie-predateur-en.html?artpage=5-6"
Rosenzweig Mac-Arthur (1963)

- $\alpha > \frac{\gamma}{1+\gamma} \Rightarrow \text{Extinction}$
- $\alpha < \frac{\gamma}{1+\gamma} \Rightarrow \text{Persistence}$
Rosenzweig Mac-Arthur (1963)

- $\alpha > \frac{\gamma}{1+\gamma} \Rightarrow \text{Extinction}$
- $\alpha < \frac{\gamma}{1+\gamma} \Rightarrow \text{Persistence}$

Ok, but what if $\alpha$ or/and $\gamma$ fluctuate (randomly)?
Rosenzweig Mac-Arthur in fluctuating environment

\[ \frac{dx}{dt} = x \left( 1 - \frac{x}{\gamma} - \frac{y}{1 + x} \right) \]

\[ \frac{dy}{dt} = y \left( -\alpha + \frac{x}{1 + x} \right) \]
Rosenzweig Mac-Arthur in fluctuating environment

One day is fine, the next is Black

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - \frac{x}{\gamma} - \frac{y}{1 + x}) \\
\frac{dy}{dt} &= y(-\alpha t + \frac{x}{1 + x})
\end{align*}
\]
Rosenzweig Mac-Arthur in fluctuating environment

*One day is fine, the next is Black*

\[
\frac{dx}{dt} = x \left( 1 - \frac{x}{\gamma} - \frac{y}{1 + x} \right)
\]

\[
\frac{dy}{dt} = y \left( -\alpha_t + \frac{x}{1 + x} \right)
\]

\(\alpha_t\) Markov process \(\in \{\alpha_1, \ldots, \alpha_m\}\)
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1: Some motivating examples

1. A simple historical model: The Verhulst (or logistic) dynamics
2. Prey-Predator model (Rosenzweig Mac-Arthur)
3. Lotka-Volterra
Lotka-Volterra (based on B & Lobry 2016)

- 2 species $x$ and $y$ characterized by their abundances $x, y \geq 0$. 
Lotka-Volterra (based on B & Lobry 2016)

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

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

$$ F_\mathcal{E}(x, y) = \begin{cases} 
\alpha x (1 - ax - by) \\
\beta y (1 - cx - dy) 
\end{cases} $$
Lotka-Volterra (based on B & Lobry 2016)

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

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

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

$$\alpha, a, b, \beta, c, d > 0$$
• Environment $\mathcal{E}$ is said *favorable to species* $x$ if

$$a < c \text{ and } b < d.$$ 

• $\text{Env}_x = \text{set of environments favorable to } x.$
• Environment $\mathcal{E}$ is said \textit{favorable to species} $x$ if

$$a < c \text{ and } b < d.$$  

• $\text{Env}_x = \text{set of environments favorable to } x$.

\textbf{Theorem ("competitive exclusion")}

\textit{If $\mathcal{E} \in \text{Env}_x$ every solution to $(\dot{x}, \dot{y}) = F_\mathcal{E}(x, y)$ with initial condition $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+$ converges to } \left( \frac{1}{a}, 0 \right) \text{ as } t \to \infty.
• Environment $\mathcal{E}$ is said *favorable to species* $x$ if

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• $\text{Env}_x = \text{set of environments favorable to } x$.

**Theorem ("competitive exclusion")**

*If $\mathcal{E} \in \text{Env}_x$ every solution to $(\dot{x}, \dot{y}) = F_\mathcal{E}(x, y)$ with initial condition $(x, y) \in \mathbb{R}^*_+ \times \mathbb{R}_+$ converges to $(\frac{1}{a}, 0)$ as $t \to \infty$.***

i.e $\mathcal{E} \in \text{Env}_x \Rightarrow \text{Extinction of } y \text{ and Persistence of } x$. 
• Environment $\mathcal{E}$ is said \textit{favorable to species} $x$ if

$$a < c \text{ and } b < d.$$  

• $Env_x = \text{set of environments favorable to } x$.

\begin{tcolorbox}[amsfonts]
\textbf{Theorem ("competitive exclusion")}

If $\mathcal{E} \in Env_x$ every solution to $(\dot{x}, \dot{y}) = F_\mathcal{E}(x, y)$ with initial condition $(x, y) \in \mathbb{R}_+^* \times \mathbb{R}_+$ converges to $(\frac{1}{a}, 0)$ as $t \to \infty$.

\end{tcolorbox}

i.e $\mathcal{E} \in Env_x \Rightarrow \text{Extinction of } y \text{ and } \text{Persistence of } x$.

Proof is classical (see e.g J. Hofbauer and K. Sigmund’s book (1998))
Figure: Phase portrait of $F_\xi$ with $\xi \in \text{Env}_x$. 
Lotka Volterra in fluctuating environment

Ok but what if the environment fluctuates?
Lotka Volterra in fluctuating environment

Ok but what if the environment fluctuates?

i.e

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

where \(\{\mathcal{E}_{u(t)}\}\) is a time-dependent environment
Old works by Koch (74), Cushing (80, 86) de Mottoni and Schiaffino (81) + recent work by T. Sari, show that

when \( t \mapsto E_u(t) \) is periodic around \( E \in \text{Env}_x \) the system may have periodic persistent orbits \( x(t) > 0, y(t) > 0 \).
Old works by Koch (74), Cushing (80, 86) de Mottoni and Schiaffino (81) + recent work by T. Sari, show that

when $t \mapsto \mathcal{E}_{u(t)}$ is periodic around $\mathcal{E} \in \text{Env}_x$ the system may have periodic persistent orbits $x(t) > 0, y(t) > 0$.

This provides "some math interpretation" of a well known fact in ecology:
• Old works by Koch (74), Cushing (80, 86) de Mottoni and Schiaffino (81) + recent work by T. Sari, show that

when \( t \mapsto \mathcal{E}_{u(t)} \) is periodic around \( \mathcal{E} \in \text{Env}_x \) the system may have periodic persistent orbits \( x(t) > 0, y(t) > 0 \).

• This provides "some math interpretation" of a well known fact in ecology:

\[ \text{temporal fluctuations of the environment can reverse the trend of competitive exclusion} \]

Hutchinson’s paradox (61), Work of Chesson and co-authors in the 80s, ...
Our Goal here will be to investigate the behavior of

$$(\dot{X}, \dot{Y}) = F_{\varepsilon_{u(t)}}(X, Y)$$
Our Goal here will be to investigate the behavior of

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

- $\mathcal{E}_0, \mathcal{E}_1$ are two favorable environments
Our Goal here will be to investigate the behavior of

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

- \(\mathcal{E}_0, \mathcal{E}_1\) are two favorable environments
- \(u(t) \in \{0, 1\}\) is a jump process
Our Goal here will be to investigate the behavior of

\[
(\dot{X}, \dot{Y}) = F_{E_{u(t)}}(X, Y)
\]

- $E_0, E_1$ are two favorable environments
- $u(t) \in \{0, 1\}$ is a jump process

\[
\begin{align*}
P(u(t + s) = 1|u(t) = 0, (u(r), r \leq t)) &= \lambda_0 s + o(s), \\
P(u(t + s) = 0|u(t) = 1, ((u(r), r \leq t)) &= \lambda_1 s + o(s),
\end{align*}
\]
Figure: Phase portraits of $F_{E_0}$ and $F_{E_1}$
Figure: Phase portraits of $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$

Different values of $\lambda_0, \lambda_1$ can lead to various behaviors...
Figure: extinction of 2
Figure: Persistence
Figure: Persistence
Figure: Extinction of 1
Figure: Extinction of 1 or 2
II : Some Math
Abstract Framework

• \((X_t)\) a "good" (Feller, cad-lag, good behavior at \(\infty\), etc.)
Markov process on some "good" (Polish, locally compact) space

\[ M = M_+ \cup M_0 \]
Abstract Framework

- \((X_t)\) a "good" \((Feller, \text{cad-lag}, \text{good behavior at } \infty, \text{etc.})\)
- Markov process on some "good" \((Polish, \text{locally compact})\) space

\[ M = M_+ \cup M_0 \]

- \(M_0\) is a closed set = extinction set
Abstract Framework

- $(X_t)$ a "good" (Feller, cad-lag, good behavior at $\infty$, etc.) Markov process on some "good" (Polish, locally compact) space

$$M = M_+ \cup M_0$$

- $M_0$ is a closed set = extinction set
- $M_+ = M \setminus M_0$ = coexistence set
Abstract Framework

- \((X_t)\) a "good" (Feller, cad-lag, good behavior at \(\infty\), etc.) Markov process on some "good" (Polish, locally compact) space

\[ M = M_+ \cup M_0 \]

- \(M_0\) is a closed set = extinction set
- \(M_+ = M \setminus M_0\) = coexistence set
- Both \(M_0\) and \(M_+ = M \setminus M_0\) are invariant:
  \[ x \in M_0 \Rightarrow X_t^x \in M_0, \]
  \[ x \in M_+ \Rightarrow X_t^x \in M_+ \]
Two (canonical) Models
Model I. Ecological SDEs

\[ dx_i = x_i[F_i(x)dt + \sum_{j=1}^{m} \sigma_i^j(x) dB_t^j], \quad i = 1 \ldots n \]
Model I. Ecological SDEs

\[ dx_i = x_i [F_i(x) dt + \sum_{j=1}^{m} \sigma_{ij}(x) dB_t^j], \quad i = 1 \ldots n \]

- \( x_i \geq 0 \) = abundance of species \( i \).
Introduction

Examples

Maths

Back to examples

Framework

Canonical models

Stochastic Persistence

H-persistence

Model I. Ecological SDEs

\[ dx_i = x_i[F_i(x)dt + \sum_{j=1}^{m} \sigma^j_i(x)dB^j_t], \quad i = 1 \ldots n \]

- \( x_i \geq 0 \) = abundance of species \( i \).
- \( I \subset \{1, \ldots, n\} \) a given subset of species,
  e.g. \( I = \{1\}, I = \{1, \ldots, n\} \)
Model I. Ecological SDEs

\[ dx_i = x_i[F_i(x)dt + \sum_{j=1}^{m} \sigma^j_i(x)dB^j_t], \quad i = 1 \ldots n \]

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- \( I \subset \{1, \ldots, n\} \) a given subset of species,
  e.g. \( I = \{1\}, I = \{1, \ldots, n\} \)
- \textit{State space} \( M = \mathbb{R}^n_+ \)
- \textit{Extinction set} \( M_0 = \{ x \in M : \prod_{i \in I} x_i = 0 \} \)
**Model I. Ecological SDEs**

\[ dx_i = x_i[F_i(x)dt + \sum_{j=1}^{m} \sigma_i^j(x)dB_t^j], \ i = 1 \ldots n \]

- \( x_i \geq 0 \) = abundance of species \( i \).
- \( I \subset \{1, \ldots, n\} \) a given subset of species, e.g. \( I = \{1\} \), \( I = \{1, \ldots, n\} \)
- **State space** \( M = \mathbb{R}^n_+ \)
- **Extinction set** \( M_0 = \{x \in M : \prod_{i \in I} x_i = 0\} \)

The dynamics on \( M_0 \) is an ecological SDE
Model II. Ecological random ODEs

\[
\frac{dx_i}{dt} = x_i(t)F_i(x(t), u(t)), \ i = 1 \ldots n
\]

\[u(t) \in \{1, \ldots, m\}\] is a Markov process controlled by \(x\)
Model II. Ecological random ODEs

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\frac{dx_i}{dt} = x_i(t)F_i(x(t), u(t)), \quad i = 1 \ldots n
\]

\(u(t) \in \{1, \ldots, m\}\) is a Markov process controlled by \(x\)

\[
P(u(t + s) = v | u(s), s \leq t, u(t) = u) = \lambda_{uv}(x(t))s + o(s)
\]

for all \(u \neq v\)
Model II. Ecological random ODEs

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P(u(t + s) = v | u(s), s \leq t, u(t) = u) = \lambda_{uv}(x(t))s + o(s)
\]

for all \(u \neq v\)

- **State space** \(M = \mathbb{R}_+^n \times \{1, \ldots m\}\)

- **Extinction set** \(M_0 = \{(x, u) \in M : \prod_{i \in I} x_i = 0\}\)
Model II. Ecological random ODEs

\[ \frac{dx_i}{dt} = x_i(t)F_i(x(t), u(t)), \ i = 1 \ldots n \]

\( u(t) \in \{1, \ldots, m\} \) is a Markov process controlled by \( x \)

\[ \mathbb{P}(u(t+s) = v|u(s), s \leq t, u(t) = u) = \lambda_{uv}(x(t))s + o(s) \]

for all \( u \neq v \)

- **State space** \( M = \mathbb{R}^n_+ \times \{1, \ldots m\} \)
- **Extinction set** \( M_0 = \{(x, u) \in M : \prod_{i \in I} x_i = 0\} \)

The dynamics on \( M_0 \) is an ecological random ODE
Stochastic Persistence

- \( \Pi_t(.) = \frac{1}{t} \int_0^t \delta_{\chi_s} ds = \) empirical occupation measure

\[ \Pi_t(A) = \text{proportion of time spent in } A \text{ up to } t \]
Stochastic Persistence

\[ \Pi_t(.):= \frac{1}{t} \int_0^t \delta_x ds = \text{empirical occupation measure} \]

\[ \Pi_t(A) = \text{proportion of time spent in } A \text{ up to } t \]

**Definition**

We call the process *stochastically persistent* if for all \( \epsilon > 0 \) there exists a compact \( K \subset M_+ \) such that

\[ \liminf_{t \to \infty} \Pi_t(K) \geq 1 - \epsilon \]

whenever \( x = x(0) \in M_+ \).
Stochastic Persistence

**Definition**

We call the process *persistent in probability* if for all $\epsilon > 0$ there exists a compact $K \subset M_+$ such that

$$\liminf_{t \to \infty} P_x(X_t \in K) \geq 1 - \epsilon$$

whenever $x = x(0) \in M_+$.
Stochastic Persistence

Definition

We call the process *persistent in probability* if for all $\epsilon > 0$ there exists a compact $K \subset M_+$ such that

$$\liminf_{t \to \infty} P_x(X_t \in K) \geq 1 - \epsilon$$

whenever $x = x(0) \in M_+$

- This definition goes back to Chesson (1978) "stochastic boundedness criterion"
How can we prove / disprove stochastic persistence?
How can we prove / disprove stochastic persistence?

- For simplicity I will now assume that $M$ is compact!
How can we prove / disprove stochastic persistence?

- For simplicity I will now assume that $M$ is compact!
- If not, one need to assume that there is a "good" Lyapunov function which control the behavior at $\infty$
H-persistence

- $\mathcal{P}_{inv}(M) =$ the set of invariant probabilities for $(X_t)$
- $\mathcal{P}_{erg}(M) =$ the subset of ergodic probabilities
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• $\mathcal{P}_{inv}(M_0), \mathcal{P}_{erg}(M_0)$ idem but on $M_0$
H-persistence

- \( \mathcal{P}_{inv}(M) = \) the set of invariant probabilities for \( (X_t) \)
- \( \mathcal{P}_{erg}(M) = \) the subset of ergodic probabilities
- \( \mathcal{P}_{inv}(M_0), \mathcal{P}_{erg}(M_0) \) idem but on \( M_0 \)
- \( \mathcal{L} \) generator of \( (P_t) \) with domain \( \mathcal{D} \subset C(M) \)
- \( \mathcal{D}^2 = \{ f \in \mathcal{D}, f^2 \in \mathcal{D} \} \).
- \( \Gamma : \mathcal{D}^2 \mapsto \mathbb{R}_+, \Gamma(f) = \mathcal{L}(f^2) - 2f \mathcal{L}(f) \)
Suppose there exist $V : M_+ \mapsto \mathbb{R}_+, H : M \mapsto \mathbb{R}$ with the following properties:

- $V(x) \to \infty \iff x \to M_0$

- For all compact set $K \subset M_+$, $\exists V_K \in \mathcal{D}^2$ such that
  
  (a) $V = V_K$ and $\mathcal{L}V_K = H$ on $K$
  
  (b) $\sup \{ P_t(\Gamma(V_K))(x) : K \text{ compact} \cdot t \geq 0 \} < \infty$. 

\[ \Lambda^-(H) = -\sup \{ \mu_H : \mu_H \in \text{Perg}(M_0) \}, \]

\[ \Lambda^+(H) = -\inf \{ \mu_H : \mu_H \in \text{Perg}(M_0) \}. \]
Suppose there exist $V : M_+ \to \mathbb{R}_+$, $H : M \to \mathbb{R}$ with the following properties:

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**Definition ($H-$ Exponents)**

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

\[
\Lambda^{+}(H) = -\inf\{\mu H : \mu \in \mathcal{P}_{\text{erg}}(M_0)\}.
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Suppose there exist \( V : M_+ \mapsto \mathbb{R}_+ \), \( H : M \mapsto \mathbb{R} \) with the following properties:

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**Definition (\( H^- \) Exponents)**

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

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

**Definition (\( H^- \) persistence)**

The process is said \( H \)-persistent if there exist \( (V, H) \) as above such that

\[
\Lambda^- (H) > 0
\]
Example (Ecological SDE)

\[ dx_i = x_i [F_i(x)dt + \sum_{j=1}^{m} \sigma_i^j(x)dB_t^j], \ i = 1 \ldots n \]

*Invasion rate of species* \(i\)

\[ \lambda_i(x) = F_i(x) - \frac{1}{2} \sum_k (\sigma_i^k(x))^2 \]
• $M_0 = \{ x \prod_{i \in I} x_i = 0 \}$.

### Proposition

The following are equivalent and imply H-persistence

(i) There exist weights $p_1, \ldots, p_n \geq 0$ such that for every $\mu \in \mathcal{P}_{\text{erg}}(M_0)$

\[
\mu \left( \sum_{i \in I} p_i \lambda_i \right) > 0.
\]

(ii) For every $\mu \in \mathcal{P}_{\text{inv}}(M_0)$ $\exists i \in I$ such that $\mu \lambda_i > 0$. 
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**Proposition**

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Hence (ii) means that in environment \( \mu \) at least one species can "invade"
**Example (Random Ecological ODE)**

\[
\frac{dx_i}{dt} = x_i(t)F_i(x(t), u(t)), \quad i = 1 \ldots n
\]

\[
P(u(t + s) = v \mid u(s), \quad s \leq t, u(t) = u) = \lambda_{uv}(x(t))s + o(s)
\]

*Invasion rate of species i*

\[
\lambda_i(x, u) = F_i(x, u)
\]
\[ M_0 = \{ (x, u) \prod_{i \in I} x_i = 0 \}. \]

**Proposition**

The following are equivalent and imply H-persistence

(i) There exist weights \( p_1, \ldots, p_n \geq 0 \) such that for every \( \mu \in \mathcal{P}_{\text{erg}}(M_0) \)

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**Proposition**

The following are equivalent and imply $H$-persistence

(i) There exist weights $p_1, \ldots, p_n \geq 0$ such that for every $\mu \in \mathcal{P}_{\text{erg}}(M_0)$

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Hence (ii) means that in environment $\mu$ at least one species can "invade"
Persistence Theorem

**Theorem**

\[ H\text{-Persistence} \Rightarrow Stochastic\ Persistence \]
Persistence Theorem

Theorem

\( H\text{-Persistence} \implies \text{Stochastic Persistence} \)

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

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

$$\Pi_t \to \Pi$$
**Persistence Theorem**

**Corollary**

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

\[
\Pi_t \rightarrow \Pi
\]

**Theorem**

If furthermore, the process is **strongly irreducible** then \( \exists \lambda, \theta > 0 \)

\[
\|P(X_t \in . | X_0 = x) - \Pi(.)\| \leq Cste \frac{e^{-\lambda t}}{1 + e^{\theta V(x)}}
\]

for all \( x \in M_+ \).
**Persistence Theorem**

**Corollary**

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

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**Theorem**

If furthermore, the process is **strongly irreducible** then $\exists \lambda, \theta > 0$

$$\|P(X_t \in . | X_0 = x) - \Pi(.)\| \leq \text{Cste} \frac{e^{-\lambda t}}{1 + e^{\theta V(x)}}$$

for all $x \in M_+$.

"Irreducible" and "strongly irreducible" need to be defined!
Persistence Theorem

- For the Ecological SDE model, a sufficient condition for strong irreducibility is given by the non degeneracy of the diffusion matrix

\[ \sigma(x)\sigma(x)^* \]
For the **Ecological SDE model**, a sufficient condition for strong irreducibility is given by the non degeneracy of the diffusion matrix

\[ \sigma(x)\sigma(x)^* \]

Weaker conditions = (Hormander type conditions + controllability)
Persistence Theorem

For the **Ecological Random ODE model**, a sufficient condition for *irreducibility* is given by:

1. **Accessibility** There exists an *accessible* point \( x_0 \in M_+ \):
Persistence Theorem

For the Ecological Random ODE model, a sufficient condition for irreducibility is given by:

1. **Accessibility** There exists an accessible point \( x_0 \in M_+ \):

   One can go from every \( x \in M^+ \) to every neighborhood of \( x_0 \) by integrating the fields \( F(\cdot, u), \ u = 1, \ldots, m \)
Persistence Theorem

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2. **Weak Bracket** The Lie algebra generated by \( \{F(\cdot, u), u = 1, \ldots, m\} \) has full rank at \( x_0 \)

\[ \text{Michel Benaim Neuchâtel University} \]

**Stochastic Persistence**
Persistence Theorem

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Follows from recent results by (Bakthin, Hurth, 2012); (Benaim, Leborgne, Malrieu, Zitt, 2012, 2015)
Persistence Theorem

For the **Ecological Random ODE model**, a sufficient condition for **strong irreducibility** is given by:

1. **Accessibility** There exists an accessible point \( x_0 \in M_+ \):
   
   \[
   \text{One can go from every } x \in M^+ \text{ to every neighborhood of } x_0 \text{ by integrating the fields } F(\cdot, u), \ u = 1, \ldots, m
   \]

2. **Strong Bracket** \( G_0 = \{ F(\cdot, u) - F(\cdot, v) : u, v = 1, \ldots n \} \)
   
   \[ G_{k+1} = G_k \cup \{ [F(\cdot, u), V] : V \in G_k \} \text{ has full rank at } x_0 \text{ for some } k. \]

Follows from recent results by (Bakthin, Hurth, 2012); (Benaim, Leborgne, Malrieu, Zitt, 2012, 2015)
Persistence Theorem

For the **Ecological Random ODE model**, a sufficient condition for **strong irreducibility** is given by:

1. **Accessibility** There exists an accessible point $x_0 \in M_+$:
   
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Follows from recent results by (Bakthin, Hurth, 2012); (Benaim, Leborgne, Malrieu, Zitt, 2012, 2015)

for other results on "PDMP" see also (Cloez, Hairer 2013); (Lawley, Mattingly Reed 2013), (Bakthin, Hurth, Mattingly, 2014); (BLMZ 2014)
Persistence Theorem

For the general model, a sufficient condition for irreducibility is given by:

1. **Accessibility** There exists a point $x_0 \in M_+$ accessible from $M_+$: For every neighborhood $U$ of $x_0$ and $x \in M_+$ $\exists t > 0$ such that $P_t(x, U) > 0$. 
Persistence Theorem

For the general model, a sufficient condition for irreducibility is given by:

1. **Accessibility** There exists a point \( x_0 \in M_+ \) accessible from \( M_+ \): For every neighborhood \( U \) of \( x_0 \) and \( x \in M_+ \) \( \exists t > 0 \) such that \( P_t(x, U) > 0 \).

2. **Weak Doeblin** There exists a neighborhood \( U_0 \) of \( x_0 \) and a nonzero measure \( \nu \) such that for all \( x \in U_0 \)

\[
Q(x, dy) \geq \nu_0(dy)
\]

where

\[
Q(x, dy) = \int_0^\infty e^{-t} P_t(x, dy) dt.
\]
For the general model, a **sufficient condition** for strong irreducibility is given by:

1. **Accessibility** There exists a point \( x_0 \in \mathcal{M}_+ \) **accessible** from \( \mathcal{M}_+ \) : For every neighborhood \( U \) of \( x_0 \) and \( x \in \mathcal{M}_+ \) \( \exists \ t > 0 \) such that \( P_t(x, U) > 0 \).
For the general model, a **sufficient condition** for strong irreducibility is given by:

1. **Accessibility** There exists a point $x_0 \in M_+$ accessible from $M_+$: For every neighborhood $U$ of $x_0$ and $x \in M_+ \exists \ t > 0$ such that $P_t(x, U) > 0$.

2. **Strong Doeblin** There exists a neighborhood $U_0$ of $x_0$, a nonzero measure $\nu_0$, and a interval $0 \leq t_0 < t_1$ such that for all $x \in U$ and $t_0 \leq t \leq t_1$

$$P_t(x, dy) \geq \nu_0(dy)$$
Extinction Theorem

Theorem

\[ \Lambda^-(H) > 0 \Rightarrow \text{Stochastic Persistence} \]
Theorem (Extinction)

Suppose that

\[ \Lambda^+(H) < 0 \]

and that \( M_0 \) is accessible. Then \( X_t \to M_0 \) almost surely.
Extinction Theorem

For the ecological SDE or random ODE model

**Theorem (Extinction)**

*Suppose that there exists weights \( p_i \geq 0 \) such that for each \( \mu \in \mathcal{P}_{erg}(M_0) \)

\[
\mu\left(\sum_{i \in I} p_i \lambda_i\right) < 0
\]

*and that \( M_0 \) is accessible.* Then \( X_t \to M_0 \) almost surely
III : Back to examples
Example: Rosenzweig Mac-Arthur with environmental stochasticity

\[ \frac{dx}{dt} = x(1 - \frac{x}{\gamma} - \frac{y}{1 + x}) \]

\[ \frac{dy}{dt} = y(-\alpha + \frac{x}{1 + x}) \]
Example: Rosenzweig Mac-Arthur with environmental stochasticity

One day is fine, the next is Black

\[
\frac{dx}{dt} = x\left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right)
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\(\alpha_t\) Markov process \(\in \{\alpha_1, \ldots, \alpha_m\}\)
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Ergodic measures supported by $M_0 = \mu_1 = \delta_{0,0} \otimes \nu$ $\mu_2 = \delta_{\gamma,0} \otimes \nu$

$\nu = \text{invariant probability of } \{\alpha_t\}.$
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Ergodic measures supported by $M_0 =$

\[ \mu^1 = \delta_{0,0} \otimes \nu \quad \mu^2 = \delta_{\gamma,0} \otimes \nu \]

$\nu = \text{invariant probability of } \{\alpha_t\}.$

**Persistence condition**

\[ \exists p_1, p_2 > 0 \ (p_1, p_2) \begin{pmatrix} \lambda_1(\mu_1) & \lambda_1(\mu_2) \\ \lambda_2(\mu_1) & \lambda_2(\mu_2) \end{pmatrix} > 0 \]
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Ergodic measures supported by $M_0 =$

$$\mu^1 = \delta_{0,0} \otimes \nu \quad \mu^2 = \delta_{\gamma,0} \otimes \nu$$

$\nu =$ invariant probability of $\{\alpha_t\}$.

**Persistence condition**

$$\exists p_1, p_2 > 0 \ (p_1, p_2) \begin{pmatrix} \lambda_1(\mu_1) & \lambda_1(\mu_2) \\ \lambda_2(\mu_1) & \lambda_2(\mu_2) \end{pmatrix} > 0$$

$$\iff$$

$$\sum_i \alpha_i \nu_{\alpha_i} = \langle \alpha, \nu \rangle < \frac{\gamma}{1+\gamma}$$
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Furthermore, for some $\alpha_i$ the corresponding RMA model has an attracting periodic or equilibrium $\Gamma_i$. $\Gamma_i$ is accessible and the strong Bracket condition holds at $\Gamma_i$. 

$$\Downarrow$$
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Furthermore, for some $\alpha_i$ the corresponding RMA model has an attracting periodic or equilibrium $\Gamma_i$. $\Gamma_i$ is accessible and the strong Bracket condition holds at $\Gamma_i$.

\[ \Downarrow \]

**Corollary (Persistence)**

*If $\langle \alpha, \nu \rangle < \frac{\gamma}{1+\gamma}$ both the empirical occupation measure and the law of $X_t$ converge, as $t \to \infty$ to $\Pi(x)dx$ supported by $M_+$.***
Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Furthermore, for some $\alpha_i$ the corresponding RMA model has an attracting periodic or equilibrium $\Gamma_i$. $\Gamma_i$ is accessible and the strong Bracket condition holds at $\Gamma_i$

\[ \downarrow \]

**Corollary (Persistence)**

If $\langle \alpha, \nu \rangle < \frac{\gamma}{1+\gamma}$ both the empirical occupation measure and the law of $X_t$ converge, as $t \to \infty$ to $\Pi(x)dx$ supported by $M_+$. 

**Corollary (Extinction)**

If $\langle \alpha, \nu \rangle > \frac{\gamma}{1+\gamma}$ $X_t \to M_0$
Example: Predator-Prey with Brownian perturbations

\[
\frac{dx}{dt} = x \left(1 - \frac{x}{\gamma} - \frac{y}{1 + x}\right)
\]

\[
\frac{dy}{dt} = y \left(-\alpha + \frac{x}{1 + x}\right)
\]
Example: Predator-Prey with Brownian perturbations

General prey growth rate

$$\frac{dx}{dt} = x(f(x) - \frac{y}{1+x})$$

$$\frac{dy}{dt} = y(-\alpha + \frac{x}{1+x})$$
Example: Predator-Prey with Brownian perturbations

General prey growth rate + *Brownian perturbations*

\[ dx = x(f(x) - \frac{y}{1 + x})dt + x\sigma dB_t \]

\[ dy = y(-\alpha + \frac{x}{1 + x})dt + y\sigma dB_t \]

\[ \sigma << 1 \]
Example: Predator-Prey with Brownian perturbations

$f(0) < 0 \Rightarrow$ Ergodic measures on $M_0 = \{\delta_{0,0}\}$
Example: Predator-Prey with Brownian perturbations

$f(0) < 0 \Rightarrow$ Ergodic measures on $M_0 = \{\delta_{0,0}\} \Rightarrow Extinction$
Example: Predator-Prey with Brownian perturbations

- $f(0) < 0 \Rightarrow \text{Ergodic measures on } M_0 = \{\delta_{0,0}\} \Rightarrow \text{Extinction}$

*Allee effect promotes extinction*
Example: Predator-Prey with Brownian perturbations

- \( f(0) < 0 \Rightarrow \) Ergodic measures on \( M_0 = \{\delta_{0,0}\} \Rightarrow Extinction \)

*Allee effect promotes extinction*
\[ f(0) > 0 \implies \text{Ergodic measures on } M_0 = \{ \delta_{0,0}, \mu_\sigma \}, \]

\[ \mu_\sigma(dx dy) \sim \delta_{x^*}(dx)\delta_0(dy) \]

with (Laplace principle)

\[ x^* = \arg \max \int_{1}^{x} \frac{2f(u)}{u} du \]
• $f(0) > 0 \Rightarrow \text{Ergodic measures on } M_0 = \{\delta_{0,0}, \mu_\sigma\},$

$$\mu_\sigma(dx dy) \sim \delta_{x^*}(dx)\delta_0(dy)$$

with (Laplace principle)

$$x^* = \arg\max \int_1^x \frac{2f(u)}{u} du$$

persistence condition $\iff \frac{x^*}{1 + x^*} > \alpha$
Another example: May Leonard (1975)

- 3 species $A, B, C$

\[
\begin{align*}
\dot{x} &= x(1 - x - \alpha y - \beta z) \\
\dot{y} &= y(1 - \beta x - y - \alpha z) \\
\dot{z} &= z(1 - \alpha x - \beta y - z)
\end{align*}
\]

$0 < \beta < 1 < \alpha$. 
May Leonard (1975)
May Leonard (1975)

C beats B
May Leonard (1975)

A beats B
May Leonard (1975)

\[ B \text{ beats } A \]
Side-blotched lizards

**Figure:** picture from Lisa C. Hazard (UC Santa Cruz) homepage
May Leonard (1975)

\[ \alpha + \beta < 2 \Rightarrow \text{Persistence} \]
$\alpha + \beta > 2 \Rightarrow \text{The boundary is an attractor (weak form of extinction)}$
What if $\alpha$ and $\beta$ fluctuate randomly?
Example: May Leonard with environmental stochasticity

\[
\begin{align*}
\dot{x} &= x(1 - x - \alpha_t y - \beta_t z) \\
\dot{y} &= y(1 - \beta_t x - y - \alpha_t z) \\
\dot{z} &= z(1 - \alpha_t x - \beta_t y - z)
\end{align*}
\]

\((\alpha_t, \beta_t)\) Markov process \(\in\ \{(\alpha_1, \beta_1) \ldots, (\alpha_m, \beta_m)\}\)

with invariant measure \(\nu\).
Example: May Leonard with environmental stochasticity

Ergodic measures on $M_0$:

$$\mu^0 = \delta(0,0,0) \otimes \nu; \mu^i = \delta_{e_i} \otimes \nu, i = 1, \ldots 3$$
Example: May Leonard with environmental stochasticity

Persistence condition \iff

\[ \exists p_1, p_2, p_3 > 0 : (p_1, p_2, p_3) \begin{pmatrix} 0 & 1 - \langle \alpha, \nu \rangle & 1 - \langle \beta, \nu \rangle \\ 1 - \langle \beta, \nu \rangle & 0 & 1 - \langle \alpha, \nu \rangle \\ 1 - \langle \alpha, \nu \rangle & 1 - \langle \beta, \nu \rangle & 0 \end{pmatrix} > 0 \]

\iff

\[ \langle \alpha, \nu \rangle + \langle \beta, \nu \rangle < 2 \]
