Stochastic Persistence

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  $\Rightarrow$ *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)).

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$\rightsquigarrow$ *based on previous works in collaboration with* Hofbauer (Wien), Sandholm (Madison), Schreiber (UC Davis)

Outline

I : Some motivating examples

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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*
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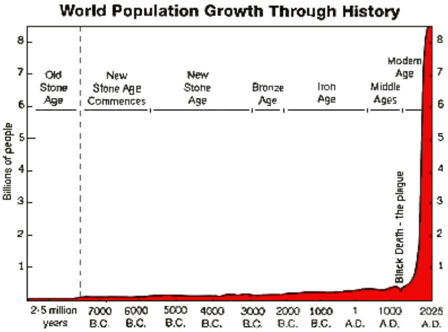

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Verhulst (or logistic) dynamics

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

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

$a =$ intrinsic *growth rate*,

$b \geq 0$

Verhulst dynamics

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

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

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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

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Environmental variability

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

Environmental variability

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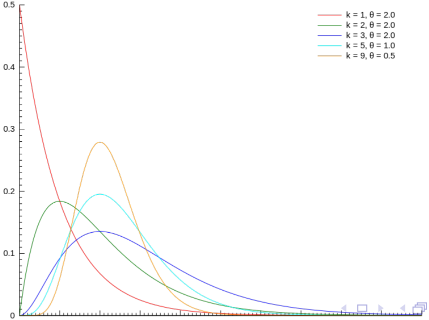

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Looks like a sensible definition of Stochastic Extinction/Persistence

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

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2. Prey-Predator model (Rosenzweig Mac-Arthur)

Prey-Predator

x = preys (or resources) abundance
y = predators abundance

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

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$$\frac{dx}{dt} = x(1 - \frac{x}{\gamma}) - xyh(x, y)$$

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$xh(x, y)$ = Per predator kill rate = predator reproduction rate

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- $h(x, y) = c$ Lotka-Volterra
- $h(x, y) = 1/(1 + x)$ Rosenzweig Mac-Arthur
- $h(x, y) = h(y/x)$ 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)

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

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Ok, but what if α or/and γ fluctuate (randomly) ?

Rosenzweig Mac-Arthur in fluctuating environment

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

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One day is fine, the next is Black

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

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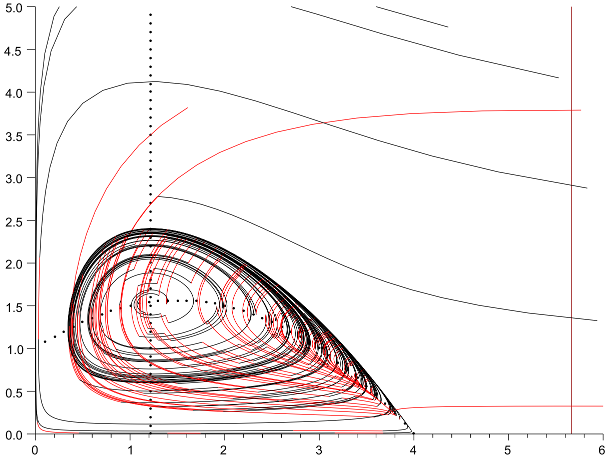
$$\alpha_t \text{ Markov process} \in \{\alpha_1, \ldots, \alpha_m\}$$


5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6

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

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

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

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

.

- Environment $\mathcal{E}$ is said *favorable to species* $\mathbf{x}$ if

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

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Theorem ("competitive exclusion")

If $\mathcal{E} \in \mathrm{Env}_{\mathbf{x}}$ 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 $t \to \infty$.

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i.e $\mathcal{E} \in \mathrm{Env}_{\mathbf{x}} \Rightarrow$ Extinction of $\mathbf{y}$ and Persistence of $\mathbf{x}$.

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Proof is classical (see e.g J. Hofbauer and K. Sigmund's book (1998))

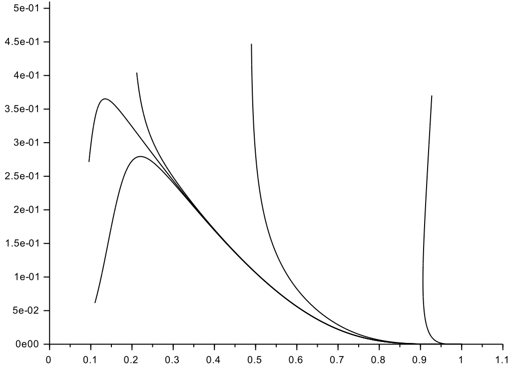

Figure: Phase portrait of $F_{\mathcal{E}}$ with $\mathcal{E} \in \mathrm{Env}_{\mathbf{x}}$.

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

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

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, ...

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Our Goal here will be to investigate the behavior of

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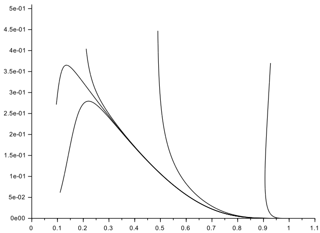
$$\mathbf{P}(u(t+s) = 1 | u(t) = 0, (u(r), r \leq t)) = \lambda_0 s + o(s),$$
$$\mathbf{P}(u(t+s) = 0 | u(t) = 1, ((u(r), r \leq t)) = \lambda_1 s + o(s),$$



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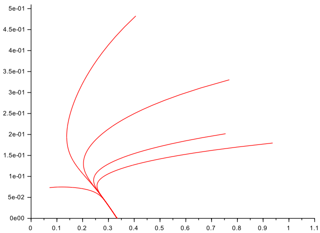
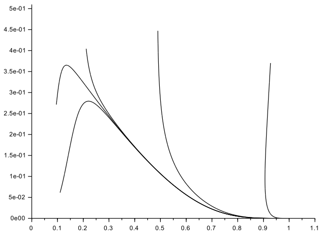


Figure: Phase portraits of $F_{\mathcal{E}_0}$ and $F_{\mathcal{E}_1}$



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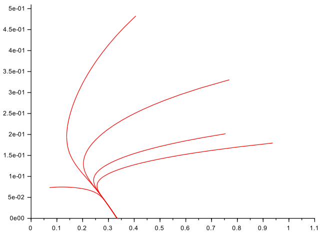

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Different values of λ_0, λ_1 can lead to **various behaviors...**

Simulations

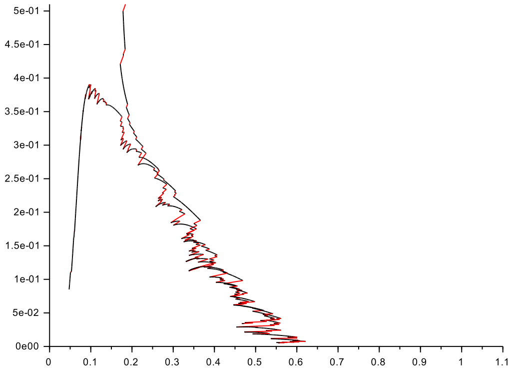


Figure: extinction of 2

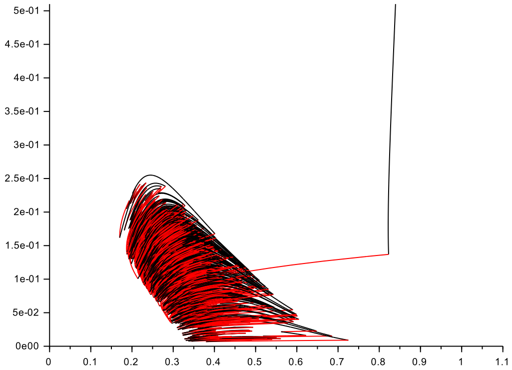
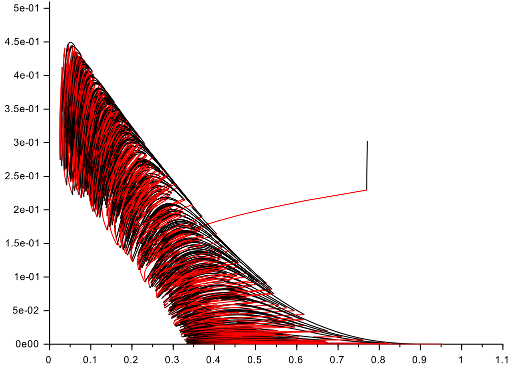


Figure: Persistence



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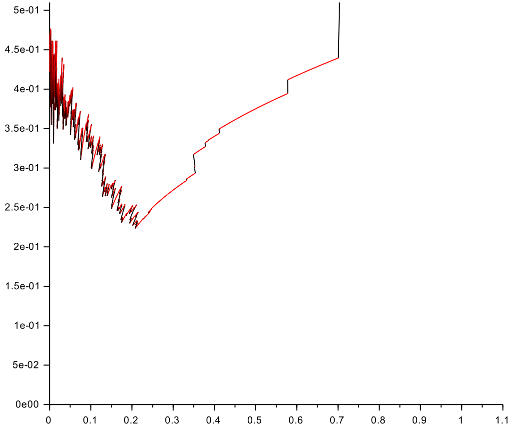

Figure: Extinction of 1

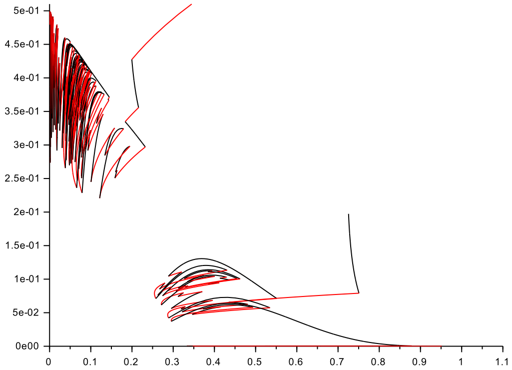

Figure: Extinction of 1 or 2

II : Some Math

Abstract Framework

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

$$M = M_+ \cup M_0$$

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$$M = M_+ \cup M_0$$

- 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

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

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e.g $I = \{1\}, I = \{1, \dots, n\}$

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- *State space* $M = \mathbb{R}_+^n$
- *Extinction set* $M_0 = \{x \in M \ : \prod_{i \in I} x_i = 0\}$

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e.g $I = \{1\}, I = \{1, \dots, n\}$

- *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

$$\frac{dx_i}{dt} = x_i(t)F_i(x(t), u(t)),\ i = 1 \dots n$$

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

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Stochastic Persistence

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

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

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

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• This definition goes back to Chesson (1978) "stochastic boundedness criterion"

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• If not, one need to assume that there is a "good" Lyapunov function which control the behavior at ∞

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- $\mathcal{L}$ 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:

- $V(x) \to \infty \Leftrightarrow x \to M_0$
- 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
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Definition ($H-$ Exponents)

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Definition ($H-$ persistence)

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

$$\Lambda^-(H) > 0$$

Examples

Example (Ecological SDE)

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

Invasion rate of species i

$$\lambda_i(x) = F_i(x) - \frac{1}{2}\sum_k (\sigma_i^k(x))^2$$

$\bullet M_0 = \{x \prod_{i \in I} x_i = 0\}$.

Proposition

The following are equivalent and imply H-persistence

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

$$\mu(\sum_{i \in I} p_i \lambda_i) > 0.$$

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

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$$\lambda_i(x, u) = F_i(x, u)$$

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Persistence Theorem

Theorem

H-Persistence $\Rightarrow$ *Stochastic Persistence*

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

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* $x \in M_+$

$$\Pi_t \to \Pi$$

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Theorem

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

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

for all $x \in M_+$.

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

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Weaker conditions = (Hormander type conditions + controllability)

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

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

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$$Q(x, dy) \geq \nu_0(dy)$$

where

$$Q(x, dy) = \int_0^{\infty} e^{-t} P_t(x, dy) dt.$$

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Extinction Theorem

Theorem

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

Extinction Theorem

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 $\mu \in \mathcal{P}_{erg}(M_0)$

$$\mu(\sum_{i \in I} p_i \lambda_i) < 0$$

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III : Back to examples

Example: Rosenzweig Mac-Arthur with environmental stochasticity

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

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

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One day is fine, the next is Black

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α_t Markov process $\in \{\alpha_1, \ldots, \alpha_m\}$

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- Ergodic measures supported by $M_0 =$

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

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

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Persistence condition

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

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$$\Leftrightarrow$$

$$\boxed{\sum_i \alpha_i \nu_{\alpha_i} = \langle \alpha, \nu \rangle < \frac{\gamma}{1+\gamma}}$$

Example: Rosenzweig Mac-Arthur with environmental stochasticity

- Furthermore, for some α_i the corresponding RMA model has an attracting periodic or equilibrium Γ_i. Γ_i is **accessible and the strong Bracket condition holds at Γ_i**

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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_+.

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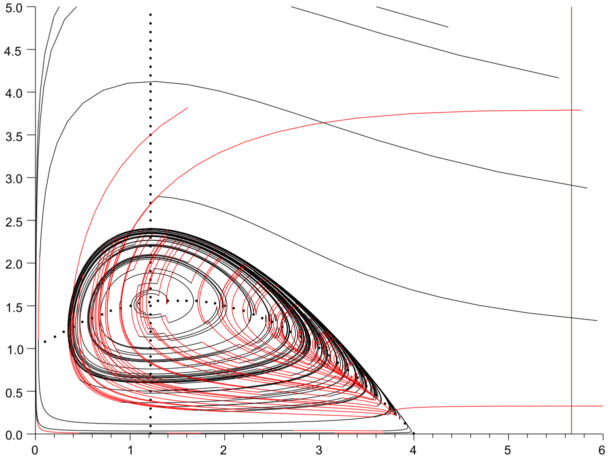
If $\langle \alpha, \nu \rangle > \frac{\gamma}{1+\gamma}$ $X_t \to M_0$


5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6

Example: Predator-Prey with Brownian perturbations

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

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Example: Predator-Prey with Brownian perturbations

General prey growth rate

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

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

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Allee effect promotes extinction

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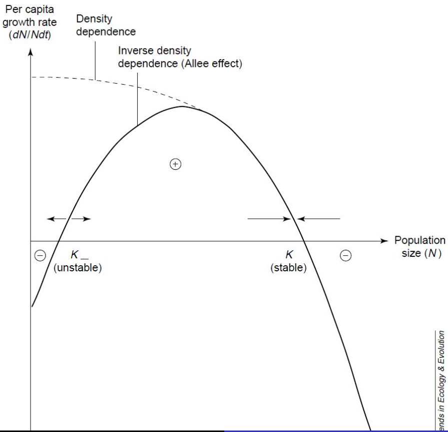

$\bullet f(0) > 0 \Rightarrow$ Ergodic measures on $M_0 = \{\delta_{0,0}, \mu_\sigma\}$,

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

with (Laplace principle)

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persistence condition $\Leftrightarrow \boxed{\frac{x^*}{1+x^*} > \alpha}$

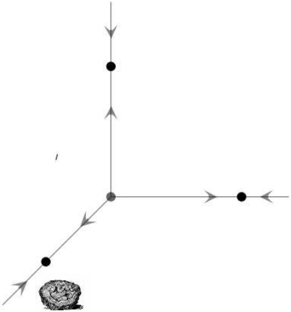
Another example : May Leonard (1975)

- 3 species A, B, C

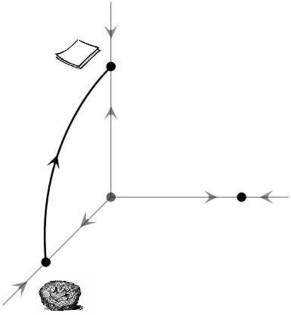
$$\begin{cases} \dot{x} = x(1 - x - \alpha y - \beta z) \\ \dot{y} = y(1 - \beta x - y - \alpha z) \\ \dot{z} = z(1 - \alpha x - \beta y - z) \end{cases}$$

$0 < \beta < 1 < \alpha.$

May Leonard (1975)

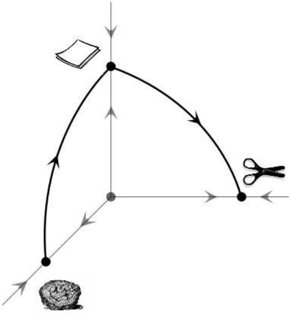


May Leonard (1975)



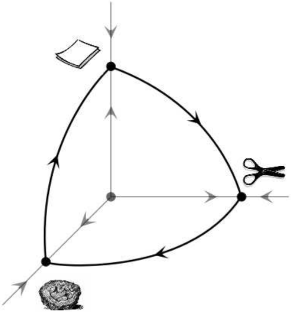
C beats B

May Leonard (1975)



A beats B

May Leonard (1975)



B beats A

Side-blotched lizards

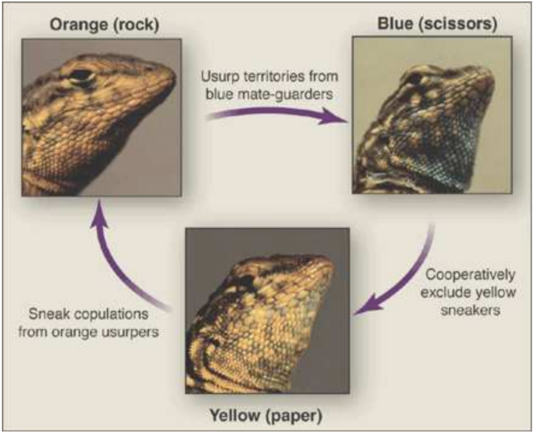
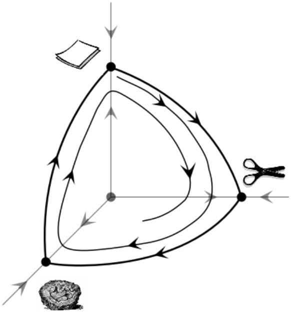


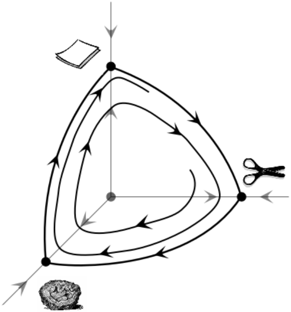
Figure: picture from Lisa C. Hazard (UC Santa Cruz) homepage

May Leonard (1975)



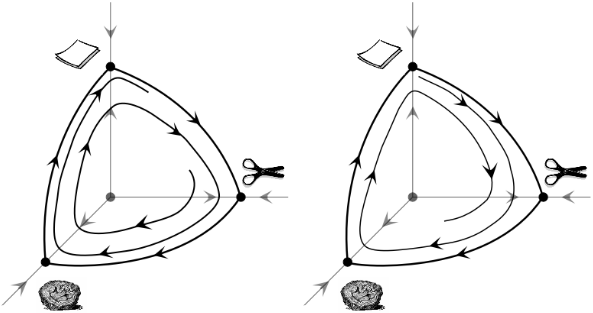
$\alpha + \beta < 2 \Rightarrow$ **Persistence**

May Leonard (1975)



$\alpha + \beta > 2 \Rightarrow$ **The boundary is an attractor** (weak form of extinction)

May Leonard (1975)



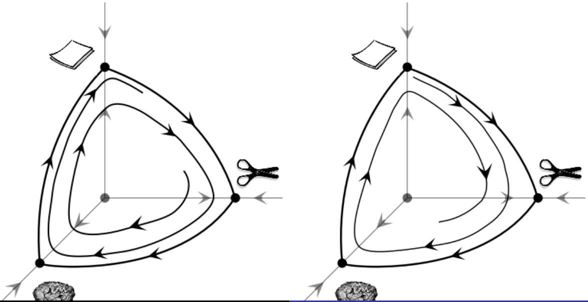
What if α and β fluctuate randomly ?

Example: May Leonard with environmental stochasticity

$$\begin{cases} \dot{x} = x(1 - x - \alpha_t y - \beta_t z) \\ \dot{y} = y(1 - \beta_t x - y - \alpha_t z) \\ \dot{z} = z(1 - \alpha_t x - \beta_t y - z) \end{cases}$$

(α_t, β_t) Markov process $\in \{(\alpha_1, \beta_1) \ldots, (\alpha_m, \beta_m)\}$

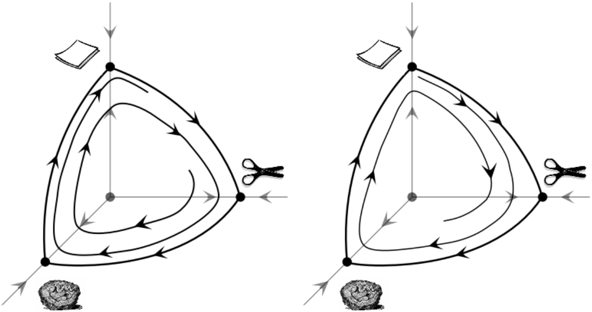
with invariant measure ν.



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 $\Leftrightarrow$

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

$$\Leftrightarrow$$

$$\boxed{\langle \alpha, \nu \rangle + \langle \beta, \nu \rangle < 2}$$