INHOMOGENEOUS RANDOM SYSTEMS
Institut Henri Poincaré, Paris
29 January 2014

Time delays in stochastic systems

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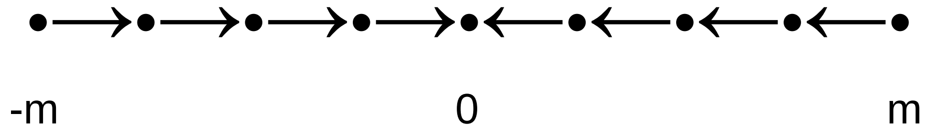
Why time delays may cause oscillations?

Example

$$x(t) \in \{-m, -m+1, ..., 0, ...m-1, m\}$$ t=0,1,…

arrow dynamics



let us introduce a time delay $0 < \tau < m$

initial conditions

$$x(t+1) = \begin{cases} x(t)+1 & if \;\; x(t-\tau) < 0, \\ x(t)-1 & if \;\; x(t-\tau) > 0, \\ x(t) & if \;\; x(t-\tau) = 0. \end{cases}$$

$x(0), x(-1), ..., x(-\tau)$ =1

there appears an asymptotically stable cycle of amplitude τ

and period $4\tau + 2$

Let us introduce stochastic perturbations

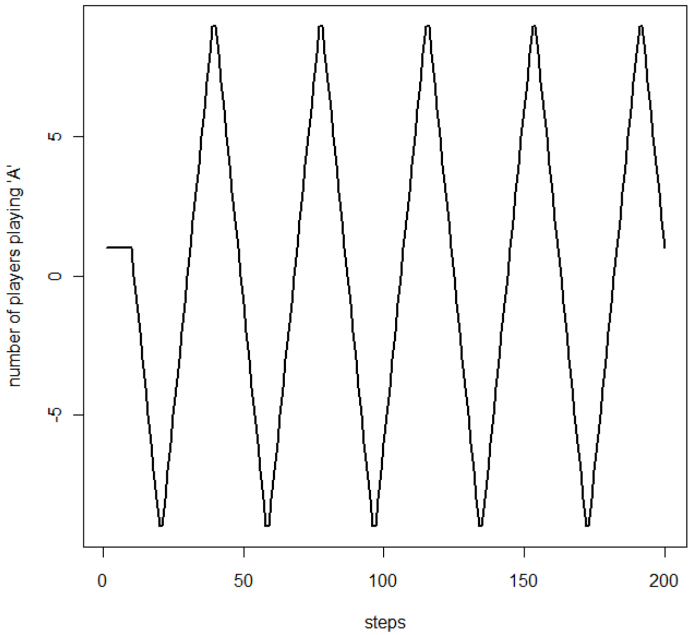
$$x(t+1) = \begin{cases} x(t)+1 & if \;\; x(t-\tau) < 0, \\ x(t)-1 & if \;\; x(t-\tau) > 0, \\ x(t) & if \;\; x(t-\tau) = 0. \end{cases}$$

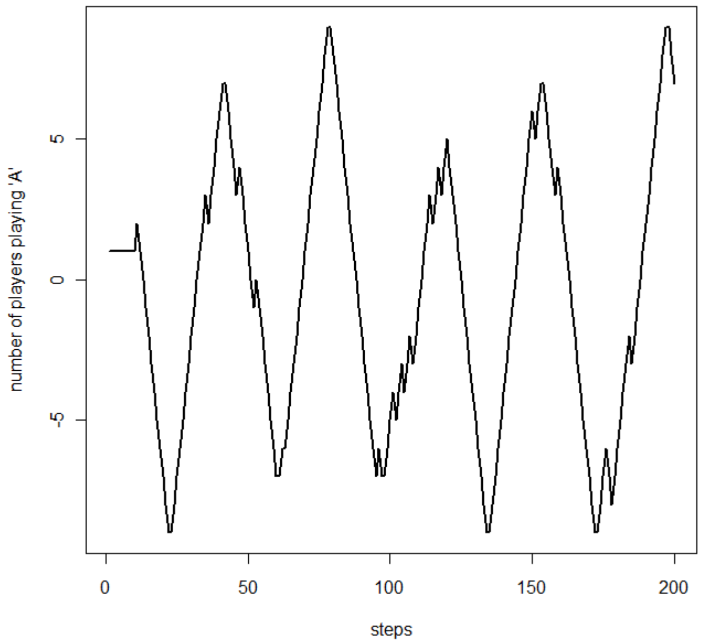
with probability 1 - ε

$$x(t+1) = x(t)$$

with probability ε

we obtained a simple stochastic model with a time delay


number of players playing 'A'
-5
0
5
0
50
100
150
200
steps


number of players playing 'A'
-5
0
5
0
50
100
150
200
steps

m = 20 τ = 9

ε = 0.1

The state of our system is now the history of states

$$(x(t), x(t-1), x(t-2), x(t-\tau))$$

we get an ergodic Markov Chain

with the stationary state μ_ε and the space state Ω

Definition

$x \in \Omega$ is stochastically stable if $\lim_{\varepsilon \to 0} \mu_\varepsilon (x) > 0$ (=1)

Theorem (JM and Sergiusz Wesołowski, Dyn Games and Appl, 2011)

$$\lim_{\varepsilon \to 0} \mu_\varepsilon (\text{cycle}) = 1$$

Random walk on Z with time delays

(0hira, Milton, Yamane, Phys. Rev. 1995, 2000)

$X(t) \in \mathbf{Z}$ P(t) – probability of the walker to go to the right

$$P(t) = \begin{cases} p & if \;\; X(t-\tau) > 0, \\ 0.5 & if \;\; X(t-\tau) = 0, \\ 1-p & if \;\; X(t-\tau) < 0. \end{cases}$$

$p < 0.5$

$$\sigma(\tau) \sim (0.59 - 1.18p)\tau + \frac{1}{\sqrt{2}(1-2p)}$$

Probability of moves towards the origin depend on the position of the walker

$$\frac{\mathrm{d}x}{\mathrm{d}t} = -\beta x(t-\tau) + \xi_t$$ Langevin equation

$$\mathrm{d}x = -\beta x(t-\tau)\mathrm{d}t + \mathrm{d}W$$ Ito equation

$$\mathrm{Var}(x) = \frac{1+\sin\beta\tau}{2\beta\cos\beta\tau}$$ (Kuchler, Mensch, Stoch. Rep, 1992)

for small time delays

$$\mathrm{Var}(x) = \frac{1}{2\beta}(1+\beta\tau)$$

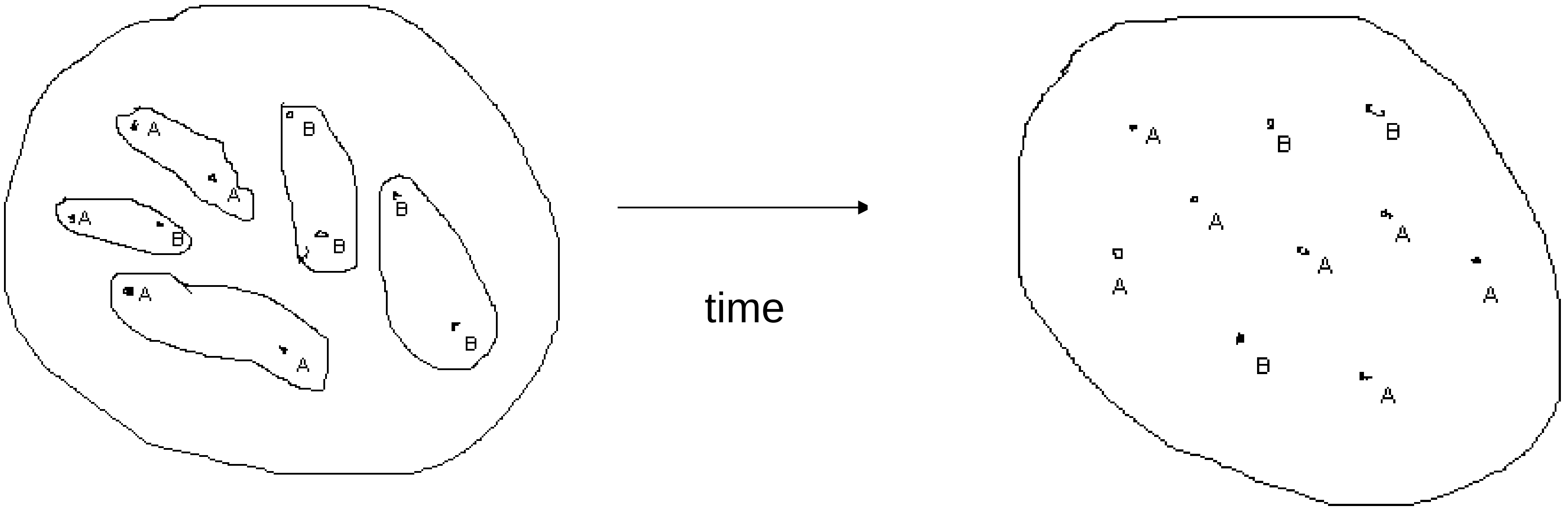
Non-markovian systems

Master, Fokker-Planck, Langevin/Ito equations with time delays

see for example Guillouzic, L'Heurex, Longtin, Phys. Rev. E, 1999

How to model time delays

Example: Population dynamics of evolutionary games



A and B are two possible behaviors, fenotypes or strategies of each individual

Deterministic replicator dynamics

		A	B
U =	A	a	b
	B	c	d

$p_A(t)$ – number of individuals playing A at a time t
$p_B(t)$ – number of individuals playing B at a time t

$$x(t) = \frac{p_A(t)}{p_A(t) + p_B(t)}$$

$U_A = ax + b(1-x)$

$U_B = cx + d(1-x)$

$U_{av} = xU_A + (1-x)U_B$

Now we propose

$$p_A(t+\varepsilon)=(1-\varepsilon)p_A(t) + \varepsilon p_A(t)U_A(t)$$

$p_A(t+\varepsilon) = (1-\varepsilon)p_A(t) + \varepsilon p_A(t)U_A(t)$
$p_B(t+\varepsilon) = (1-\varepsilon)p_B(t) + \varepsilon p_B(t)U_B(t)$

$p(t+\varepsilon) = (1-\varepsilon)p(t) + \varepsilon p(t)U_{av}(t)$

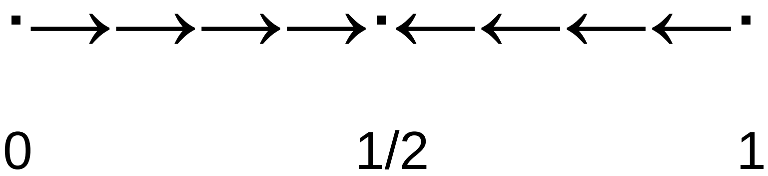
$$x(t+\epsilon) - x(t) = \epsilon \frac{x(t)[U_A(t) - U_{av}(t)]}{1-\epsilon+\epsilon U_{av}(t)}$$

$$\frac{dx}{dt} = x(U_A - U_{av}) = x(1-x)(U_A - U_B)$$

$$dx/dt = x(1-x)(U_A - U_B)$$

Hawk-Dove

	H	D
H	-1	2
D	0	1



mixed Nash equilibrium is asymptotically stable

Time delay

$\rightarrow\rightarrow\rightarrow\rightarrow x^* \leftarrow\leftarrow\leftarrow\leftarrow$

social-type delay

We assume that individuals at time t replicate due to average payoffs obtain by their strategies at time t-τ for some delay τ>0.

We propose

$$p_i(t+\epsilon) = (1-\epsilon)p_i(t) + \epsilon p_i(t)U_i(t-\tau); \quad i = A, B$$

$$p(t+\epsilon) = (1-\epsilon)p(t) + \epsilon p(t)U'_{av}(t-\tau)$$

$$U'_{av}(t-\tau) = x(t)U_A(t-\tau) + (1-x(t))U_B(t-\tau)$$

$$x(t+\epsilon) - x(t) = \epsilon \frac{x(t)[U_A(t-\tau) - U'_{av}(t-\tau)]}{1-\epsilon+\epsilon U'_{av}(t-\tau)}$$

$$x(t+\epsilon) - x(t) = -\epsilon x(t)(1-x(t))[x(t-\tau) - x^*]\frac{\delta}{1-\epsilon+\epsilon U'_{av}(t-\tau)}$$

$$\delta = c - a + b - d$$

The corresponding replicator dynamics in the continuous time reads

$$\frac{dx(t)}{dt} = x(t)[U_A(t-\tau) - U'_{av}(t-\tau)]$$

and can be also written as

$$\frac{dx(t)}{dt} = x(t)(1-x(t))[U_A(t-\tau) - U_B(t-\tau)] = -\delta x(t)(1-x(t))(x(t-\tau) - x^*)$$

Theorem (Jan Alboszta and JM, J. Theor. Biol. 231: 175-179, 2004)

x^* is asymptotically stable if τ is sufficiently small
x^* is unstable for large τ

biological-type time delay

We assume that individuals are born τ units of time after their parents played and received payoffs.

We propose

$$p_i(t+\epsilon) = (1-\epsilon)p_i(t) + \epsilon p_i(t-\tau)U_i(t-\tau); \quad i = A, B$$

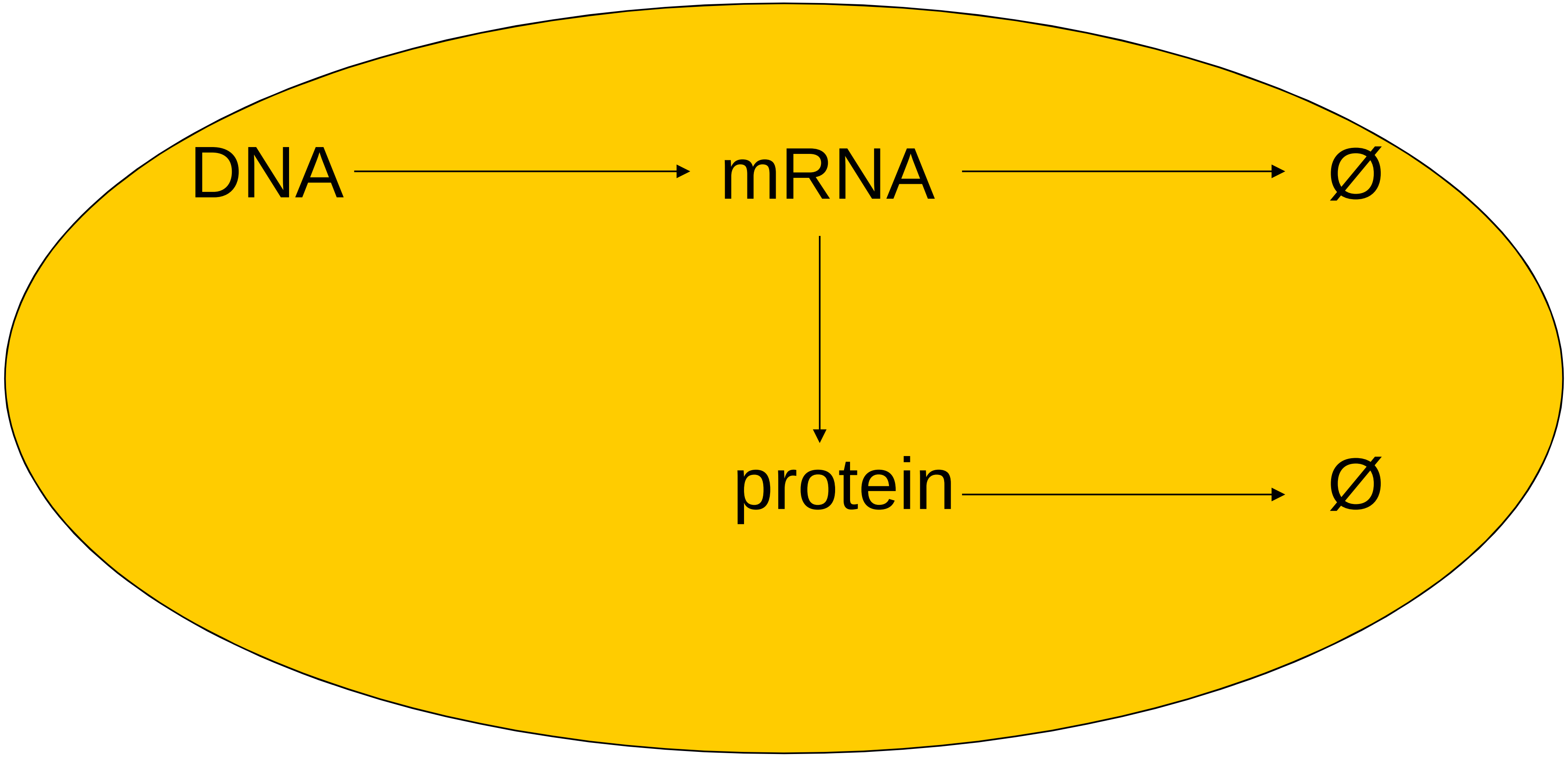
$$p(t+\epsilon) = (1-\epsilon)p(t) + \epsilon p(t)\left[\frac{x(t)p_A(t-\tau)}{p_A(t)}U_A(t-\tau) + \frac{(1-x(t))p_B(t-\tau)}{p_B(t)}U_B(t-\tau)\right]$$

$$x(t+\epsilon) - x(t) = \epsilon \frac{x(t-\tau)U_A(t-\tau) - x(t)U_{av}(t-\tau)}{(1-\epsilon)\frac{p(t)}{p(t-\tau)} + \epsilon U_{av}(t-\tau)}$$

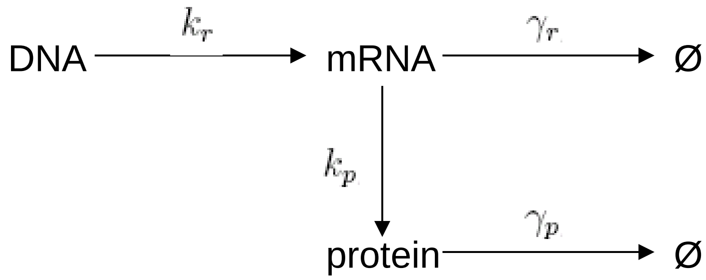
Theorem (JA and JM, JTB 2004)

x^* is asymptotically stable for any time delay τ

Mathematical cell



Macroscopic level, deterministic approach



$\rho_r \quad - \quad density\ of\ mRNA$

$\rho_p \quad - \quad density\ of\ protein$

$$\frac{d\rho_r}{dt} = k_r - \gamma_r \rho_r$$

$$\frac{d\rho_p}{dt} = k_p \rho_r - \gamma_p \rho_p$$

in the stationary state we have

$$\rho_r = \frac{k_r}{\gamma_r} \quad \rho_p = \frac{k_r k_p}{\gamma_r \gamma_p}$$

What is responsible for oscillations in biological systems ??

Time delays

Biochemical reactions take certain time to finish after initiation

Examples: average transcription speed - 20 nucleotides/s

average translation speed - 2 codons/s

the average length of human gene - 55 000 nucleotides, 2750 seconds to transcribe

the average length of the coding region - 2700 nucleotides, 450 seconds to translate

Delay-induced stochastic oscillations in gene regulation

Bratsun et al.   in PNAS 102: 14593 (2005)

delayed degradation

DNA ⟶ protein ⟶ Ø

$$\frac{d\rho_r}{dt} = k_r - \gamma \rho_r(t-\tau)$$

$$Let\ us\ note\ that\ if\ \tau > \frac{\pi}{2\gamma_r},\ then\ oscillations\ occur\ - Hopf\ bifurcation$$

It is assumed implicitly that a molecule which is on a path of a delayed degradation can take part in another delayed degradation.

A molecule can die many times

Problem: negative solutions

Delayed degradation does not cause osccilations

JM, J. Poleszczuk, M.Bodnar, U.Foryś, BMB 2011

consuming reactions

nonconsuming reactions

Let us assume that degradation is a consuming reaction

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

x – active molecules

$$\frac{dy}{dt} = k - \gamma x(t - \tau)$$

y – observed molecules

We can easily solve this system of differential equations and obtain

$$\lim_{t \to \infty} y(t) = \frac{k}{\gamma}(1 + \tau\gamma) = < x > (1 + \tau\gamma)$$

Stochastic model (x and y denote now number of molecules):

$$< y > = < x > (1 + \gamma\tau)$$

var (y) = <y>

Combined effects of time delays and stochasticity

Example: Three-player evolutionary games, (JM, Michał Matuszak, 2014)

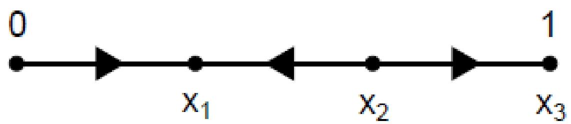
$$U = \begin{array}{c|cc|cc} & A & B & A & B \\ A & a & 0 & 0 & 0 \\ B & 0 & b & b & c \end{array}$$

$p_A(t)$ – number of individuals playing A at a time t
$p_B(t)$ – number of individuals playing B at a time t

$$x(t) = \frac{p_A(t)}{p_A(t) + p_B(t)}$$

$$f_A = ax^2, \quad f_B = 2bx(1-x) + c(1-x)^2,$$

$$\frac{dx}{dt} = x(1-x)(f_A - f_B).$$



Stochastic dynamics of finite unstructured populations

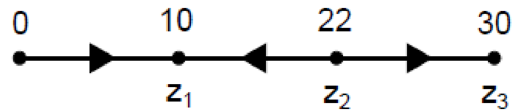
n - # of individuals

z_t - # of individuals playing A at time t

Ώ ={0,…,n} - state space

selection

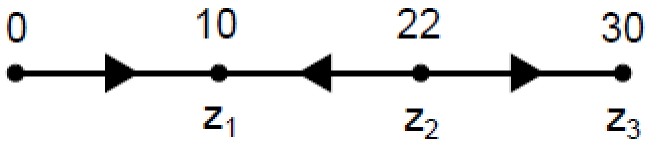
$$z_{t+1} = \begin{cases} z_t + 1 & if \;\; f_A(z_t) > f_B(z_t), \\ z_t - 1 & if \;\; f_A(z_t) < f_B(z_t), \\ z_t & if \;\; f_A(z_t) = f_B(z_t), \end{cases}$$



mutation

each individual may mutate and switch to the other strategy
with a probability ε

$$\lim_{\varepsilon \to 0} \mu_\varepsilon (z_1) = 1$$



1. **Deterministic model without time delays**

   Bassins of attraction

2. **Deterministic model with time delays**

   Cycles

$$z_{t+1} = \begin{cases} z_t + 1 & if \;\; f_A(z_{t-\tau}) > f_B(z_{t-\tau}), \\ z_t - 1 & if \;\; f_A(z_{t-\tau}) < f_B(z_{t-\tau}), \\ z_t & if \;\; f_A(z_{t-\tau}) = f_B(z_{t-\tau}), \end{cases}$$

3. **Stochastic model without time delays**

   Stochasic stability of the interior equilibrium z_1

4. **Stochastic model with a time delay**

   Stochasic stability of the boundary equilibrium z_3

Bibliography

Random walks, Ito, Fokker Planck, with time delays

U. Küchler, B. Mensch, Langevin stochastic differential equation
extended by a time-delayed term, Stoch Stoch Rep 40: 23–42 (1992).

T. Ohira, J. G. Milton, Delayed random walks,
Phys. Rev. E 52: 3277–80 (1995).

S. Guillouzic, I. L'Heureux, A. Longtin, Small delay approximation
of stochastic delay differential equations. Phys. Rev. E 59: 3970–82 (1999).

Evolutionary game theory with time delays

Y. Tao, Z. Wang, Effect of time delay and evolutionarily stable strategy,
J. Theor. Biol.187:111–6 (1997).

J. Alboszta, J. Miękisz, Stability of evolutionarily stable strategies
in discrete replicator dynamics with time delay,
J. Theor. Biol. 231: 175-179 (2004).

J. Miękisz, S. Wesołowski, Stochasticity and time delays in evolutionary games,
Dynamic Games and Applications 1: 440-448 (2011).

Gene expression with time delay

D. Bratsun, D. Volfson, L.S. Tsimring, J. Hasty,
Delay-induced stochastic oscillations in gene regulation.
Proc Natl Acad Sci USA 102:14593–8 (2005).

J. Miękisz, J. Poleszczuk, M. Bodnar, U. Foryś, Stochastic model of gene expression with delayed degradation, Bull. Math. Biol. 73: 2231-2247 (2011).

J. Miękisz, Stochasticity and time delays in gene expression and evolutionary game theory, Probabilistic Engineering Mechanics 26: 33–38 (2011).