Lecture 3 – Impact of noise: the emergence of quasi cycles.

February 20, 2020

Outline

1. Stochastic driven oscillations in ecology.
2. Predator-prey stochastic cycles.
3. Other examples and applications.

The pioneering work by Bartlett, 50s

MONTE CARLO STUDIES IN ECOLOGY AND EPIDEMIOLOGY

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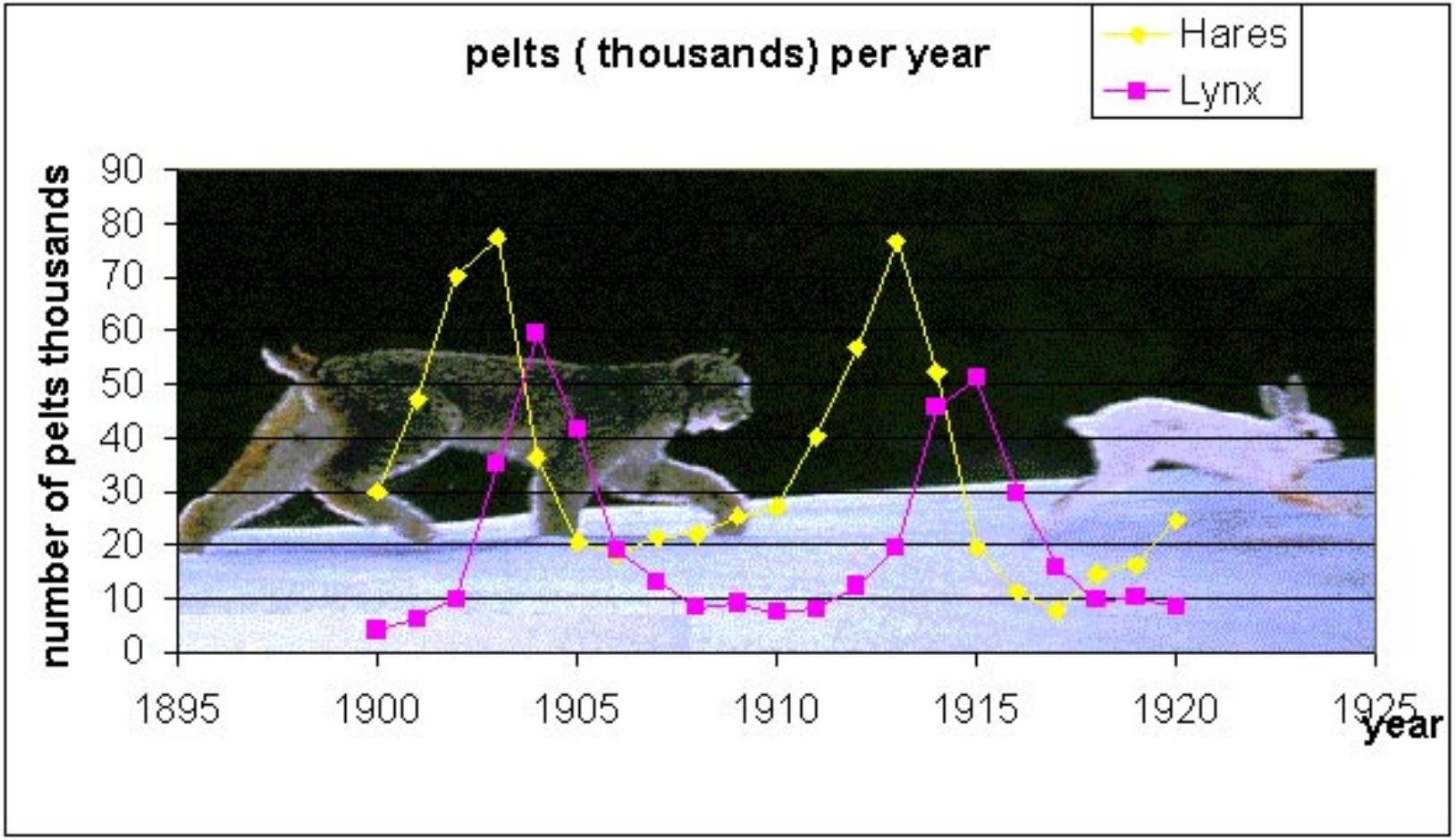
1. Introduction

"Monte Carlo" investigations, that is (at least in the present context), the simulation of real phenomena, or idealized models of them, involving a random or probabilistic element in their structure, by the deliberate use of "random" (or pseudorandom) numbers, have already played an important role in many applications of stochastic models and processes, both by way of background material in understanding qualitatively some of the properties of such models, and more quantitatively, in the study of particular problems that are not amenable to complete mathematical solution. The advent of electronic computers has

Predator-prey cycles in ecology



Simulations by Bartlett.

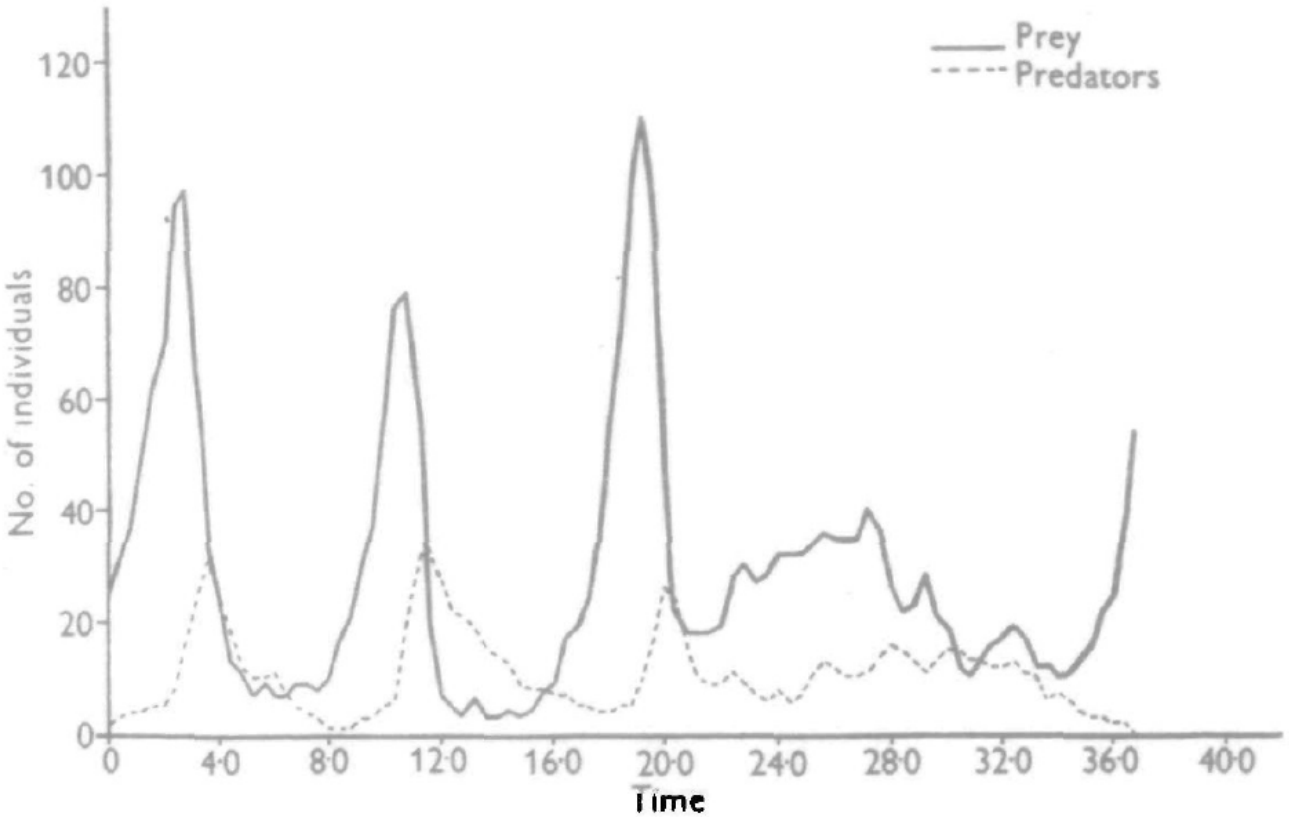


Fig. 1. An artificial realization of a stochastic model for the prey-predator relation.

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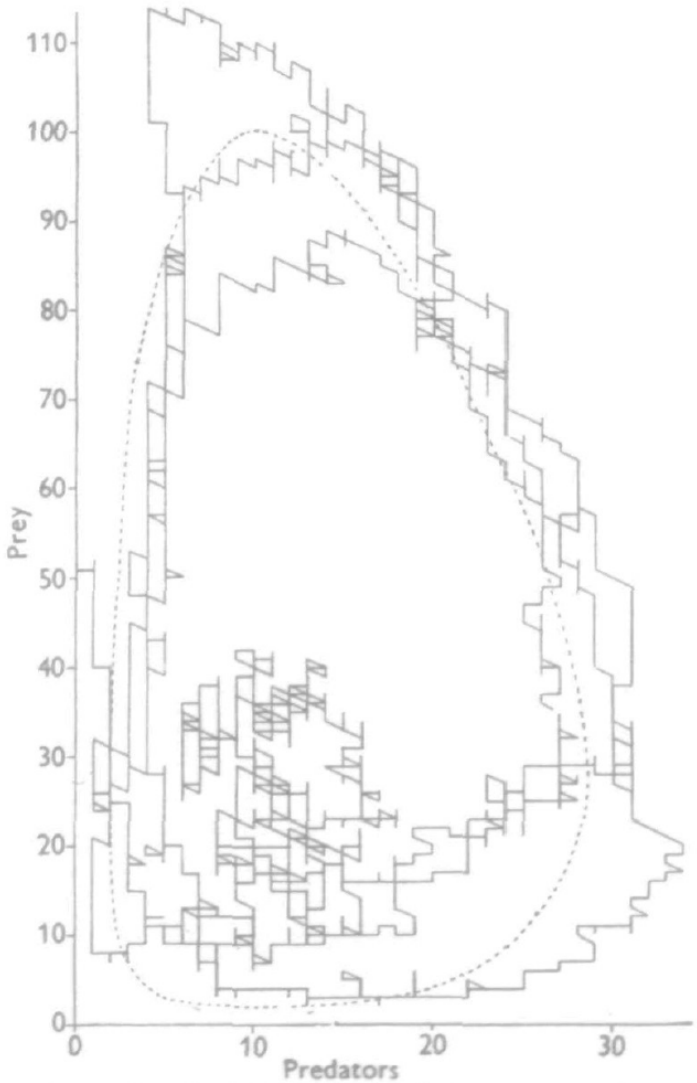

Fig. 2. Prey-predator 'cycles' for the artificial stochastic series. The closed deterministic cycle is also shown (the dotted curve) for comparison.

The theory of stochastic quasi-cycles, Mckane and Newman 2004

PRL **94,** 218102 (2005) PHYSICAL REVIEW LETTERS week ending 3 JUNE 2005

Predator-Prey Cycles from Resonant Amplification of Demographic Stochasticity

A. J. McKane[1] and T. J. Newman[2,3]

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[2]*Department of Physics and Astronomy, Arizona State University, Tempe, Arizona 85287, USA*
[3]*School of Life Sciences, Arizona State University, Tempe, Arizona 85287, USA*
(Received 18 December 2004; published 2 June 2005)

We present the simplest individual level model of predator-prey dynamics and show, via direct calculation, that it exhibits cycling behavior. The deterministic analogue of our model, recovered when the number of individuals is infinitely large, is the Volterra system (with density-dependent prey reproduction) which is well known to fail to predict cycles. This difference in behavior can be traced to a resonant amplification of demographic fluctuations which disappears only when the number of individuals is strictly infinite. Our results indicate that additional biological mechanisms, such as predator satiation, may not be necessary to explain observed predator-prey cycles in real (finite) populations.

DOI: 10.1103/PhysRevLett.94.218102 PACS numbers: 87.23.Cc, 02.50.Ey, 05.40.-a

A. The theory of stochastic quasi-cycles, Mckane and Newman 2004

The model

$$
\begin{aligned}
B + E &\xrightarrow{b} B + B \\
A &\xrightarrow{d_1} E \\
B &\xrightarrow{d_2} E \\
A + B &\xrightarrow{p_1} A + A \\
A + B &\xrightarrow{p_2} A + E
\end{aligned}
$$

- E stands for the vacancies or empty spaces.
- A is the predator and B the prey.
- n (resp. m) is the number of predators (resp. prey).

The stochastic model 1

Transition rates

$$
\begin{aligned}
T(n-1,m|n,m) &= d_1 \frac{n}{N} \\
T(n,m+1|n,m) &= 2b \frac{m}{N} \frac{(N-n-m)}{N} \\
T(n,m-1|n,m) &= 2p_2 \frac{n}{N} \frac{m}{N} + d_2 \frac{m}{N} \\
T(n+1,m-1|n,m) &= 2p_1 \frac{n}{N} \frac{m}{N}
\end{aligned}
$$

The stochastic model 2

Master equation

$$\frac{dP(n,m,t)}{dt} = \sum_{n',m'} \Big(T(n,m|n',m')P(n',m',t) - T(n',m'|n,m)P(n,m,t) \Big)$$

$$\begin{aligned}
& \frac{dP(n,m,t)}{dt} = \\
- \quad & T(n-1,m|n,m)P(n,m,t) + T(n,m|n+1,m)P(n+1,m,t) + \\
- \quad & T(n,m+1|n,m)P(n,m,t) + T(n,m|n,m-1)P(n,m-1,t) + \\
- \quad & T(n,m-1|n,m)P(n,m,t) + T(n,m|n,m+1)P(n,m+1,t) + \\
- \quad & T(n+1,m-1|n,m)P(n,m,t) \\
+ \quad & T(n,m|n-1,m+1)P(n-1,m+1,t).
\end{aligned}$$

The mean-field (deterministic) limit

Introduce the average population amount:

$$\begin{aligned}\langle n\rangle &= \sum_{n,m} nP(n,m,t)\\ \langle m\rangle &= \sum_{n,m} mP(n,m,t)\end{aligned}$$

The left-hand-side of the ME can be manipulated as follows ($\tau = t/N$):

$$\sum_{n,m} n\frac{dP(n,m,t)}{dt} = \frac{d}{dt}\sum_{n,m} nP(n,m,t) = \frac{d}{dt}\langle n\rangle = \frac{d}{d\tau}\frac{\langle n\rangle}{N}$$

The first two terms on the right-hand-side of the master equation can be re-written as (after replacing $n+1 \to n' \to n$, in the second):

$$\begin{aligned}\sum_{n,m} \quad & - \quad nT(n-1,m|n,m)P(n,m,t) \\ & + \quad (n-1)T(n-1,m|n,m)P(n,m,t) = -\langle T(n-1,m|n,m)\rangle\end{aligned}$$

Manipulating the other pairs in a similar fashion and organizing the obtained terms yield:

$$\frac{d}{d\tau}\frac{\langle n\rangle}{N} = -d_1\frac{\langle n\rangle}{N} + 2p_1\frac{\langle nm\rangle}{N^2}$$

A similar procedure can be implemented to yield the following equation for $\langle m \rangle$:

$$\frac{d}{d\tau}\frac{\langle m \rangle}{N} = (2b - d_2)\frac{\langle m \rangle}{N} - 2b\frac{\langle m^2 \rangle}{N^2} - 2(p_1 + p_2 + b)\frac{\langle mn \rangle}{N^2}$$

Introduce the mean field concentrations as:

$$\begin{aligned} \phi &= \lim_{N\to\infty} \frac{\langle n \rangle}{N} \\ \psi &= \lim_{N\to\infty} \frac{\langle m \rangle}{N} \end{aligned}$$

By performing the limit for $N \to \infty$ in the above equation one gets:

$$
\begin{aligned}
\dot{\phi} &= (2p_1\psi - d_1)\,\phi \\
\dot{\psi} &= \left[(2b - d_2)\left(1 - \frac{2b}{2b - d_2}\psi\right) - 2\,(p_1 + p_2 + b)\,\phi\right]\psi
\end{aligned}
$$

where use has been made of the following (exact in the $N \to \infty$ limit) condition:

$$
\begin{aligned}
\langle m^2 \rangle &\to \langle m \rangle^2 \\
\langle mn \rangle &\to \langle m \rangle \langle n \rangle
\end{aligned}
$$

The fixed points are:

$$(\phi^*, \psi^*) = \left(\frac{2bp_1 - bd_1 - p_1 d_2}{2p_1 (p_1 + p_2 + b)}, \frac{d_1}{2p_1} \right)$$

and the associated Jacobian matrix:

$$J = \begin{pmatrix} p_1 \psi - d_1 & p_1 \phi \\ -(p_1 + p_2)\psi & (b - d_2) - (p_1 + p_2)\phi \end{pmatrix}$$

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and thus:

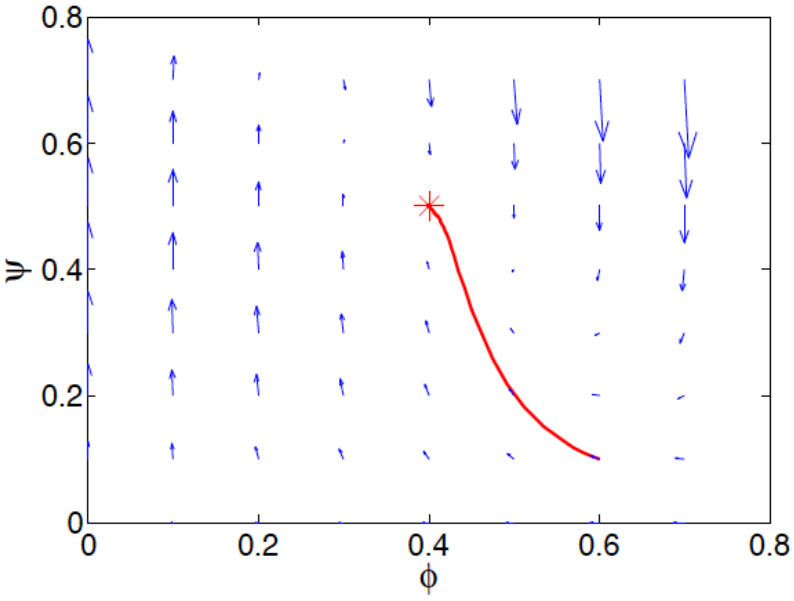
$$J_{(\phi^*, \psi^*)} = \begin{pmatrix} 0 & 2p_1 \phi^* \\ -2 (p_1 + p_2 + b) \psi^* & -2b\psi^* \end{pmatrix}$$

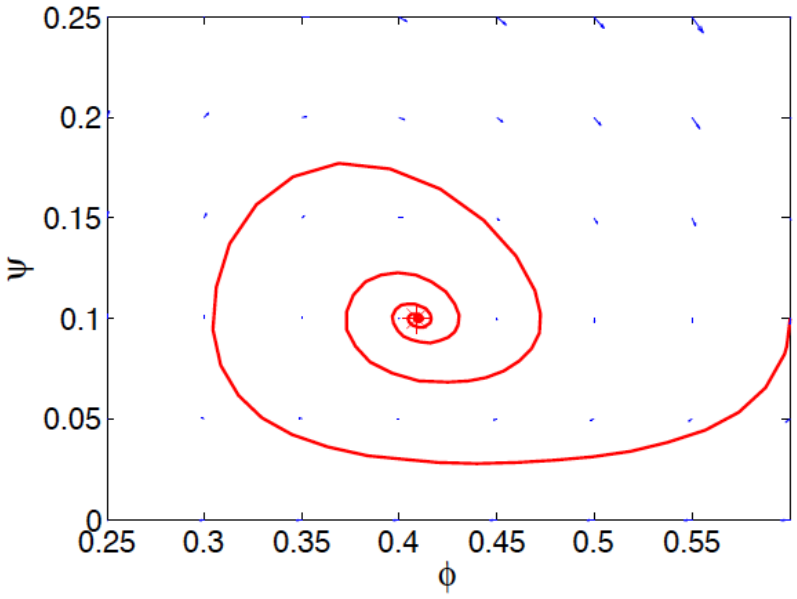
The associated eigenvalues are:

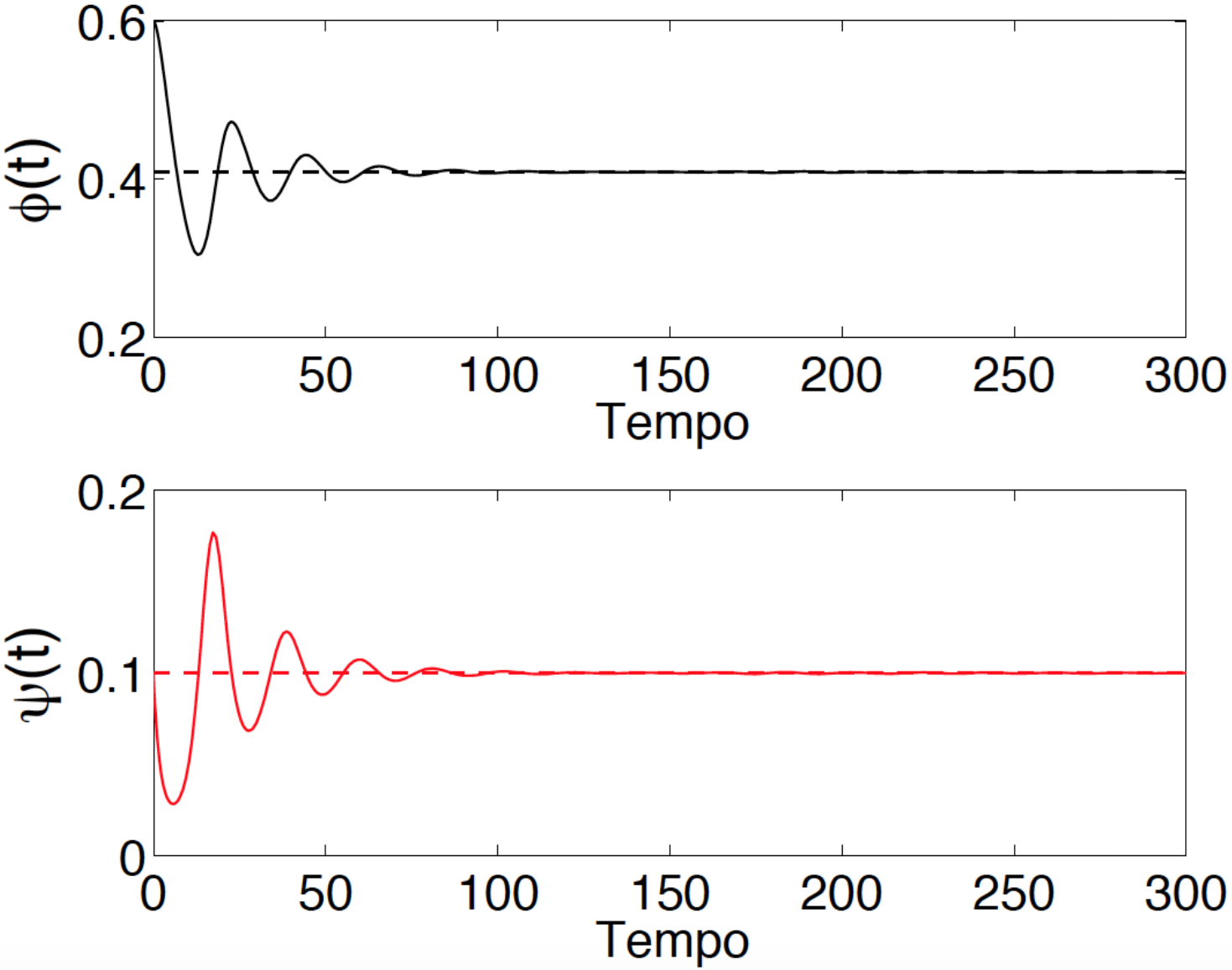
$$\lambda_{1,2} = \frac{-2b\psi^* \pm \sqrt{\Delta}}{2}$$

$$\Delta = (2b\psi^*)^2 - 16p_1 (p_1 + p_2 + b) \phi^* \psi^*$$

The real part is always negative (implying stability), while the complex part is present if $\Delta < 0$.






0.6
0.4
0.2
φ(t)
0
50
100
150
200
250
300
Tempo
0.2
0.1
0
ψ(t)
0
50
100
150
200
250
300
Tempo

Setting the stage for the system size expansion

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$$\begin{aligned} \varepsilon_n^{\pm} f(n,m) &= f(n \pm 1, m) \\ \varepsilon_m^{\pm} f(n,m) &= f(n, m \pm 1) \end{aligned}$$

$$\frac{dP(n,m,t)}{dt} = [\,(\varepsilon_n^{+} - 1)\, T(n-1,m|n,m) + (\varepsilon_m^{-} - 1)\, T(n,m+1|n,m) + (\varepsilon_m^{+} - 1)\, T(n,m-1|n,m) + (\varepsilon_n^{-}\varepsilon_m^{+} - 1)\, T(n+1,m-1|n,m)]P(n,m,t)$$

The ansatz

$$\frac{n}{N} = \phi(t) + \frac{\xi}{\sqrt{N}}$$
$$\frac{m}{N} = \psi(t) + \frac{\eta}{\sqrt{N}}$$

1. Introduce the distribution of fluctuations $\Pi(\xi, \eta, t)$
2. Plug in the master equation the van Kampen ansatz and expand in series of $1/\sqrt{N}$.
3. Isolate the contributions at leading order $(1/\sqrt{N})$.
4. Compute the next-to-leading terms $(1/N)$.

At the next to leading order....

The Fokker-Planck eq.

$$\frac{\partial}{\partial \tau}\Pi(z,\tau) = -\sum_{i=1}^{2}\frac{\partial}{\partial z_i}A_i(z)\Pi(z,\tau) + \frac{1}{2}\sum_{i,j=1}^{2}\frac{\partial^2}{\partial z_i \partial z_j}B_{ij}\Pi(z,\tau)$$

where $z \equiv (z_1, z_2) = (\xi, \eta)$ and $A_i(z)$ is the i-th component of the vector $A(z) = Mz$ where:

$$M = \begin{pmatrix} 0 & 2p_1\phi^* \\ -2\left(p_1 + p_2 + b\right)\psi^* & -2b\psi^* \end{pmatrix} = J_{(\phi^*,\psi^*)}$$

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where $z \equiv (z_1, z_2) = (\xi, \eta)$ and $A_i(z)$ is the i-th component of the vector $A(z) = Mz$. Moreover:

$$B = \begin{pmatrix} 2d_1\phi^* & -d_1\phi^* \\ -d_1\phi^* & -2d_1\left(1+\frac{p_2}{p_1}\right)\phi^* + 2d_2\psi^* \end{pmatrix}$$

The Langevin equations

$$\begin{aligned} \dot{\xi} &= M_{11}\xi + M_{12}\eta + \lambda_1 \\ \dot{\eta} &= M_{21}\xi + M_{22}\eta + \lambda_2 \end{aligned}$$

where M_{ij} stands for the entries of matrix M and:

The Fokker-Planck eq.

$$\begin{aligned} \langle \lambda_i(\tau) \rangle &= 0 \qquad i,j = 1,2 \\ \langle \lambda_i(\tau)_j(\tau') \rangle &= B_{ij}\delta(\tau - \tau') \end{aligned}$$

and $\delta(\cdot)$ is the Dirac delta.

Going to Fourier space...

$$
\begin{aligned}
-i\omega\hat{\xi} &= M_{11}\hat{\xi} + M_{12}\hat{\eta} + \hat{\lambda}_1 \\
-i\omega\hat{\eta} &= M_{21}\hat{\xi} + M_{22}\hat{\eta} + \hat{\lambda}_2
\end{aligned}
$$

Combining the two above equation yields:

$$
\hat{\xi}\left[(i\omega + M_{11}) - \frac{M_{12}M_{21}}{i\omega + M_{22}}\right] = \frac{M_{12}}{i\omega + M_{22}}\hat{\lambda}_2 - \hat{\lambda}_1
$$

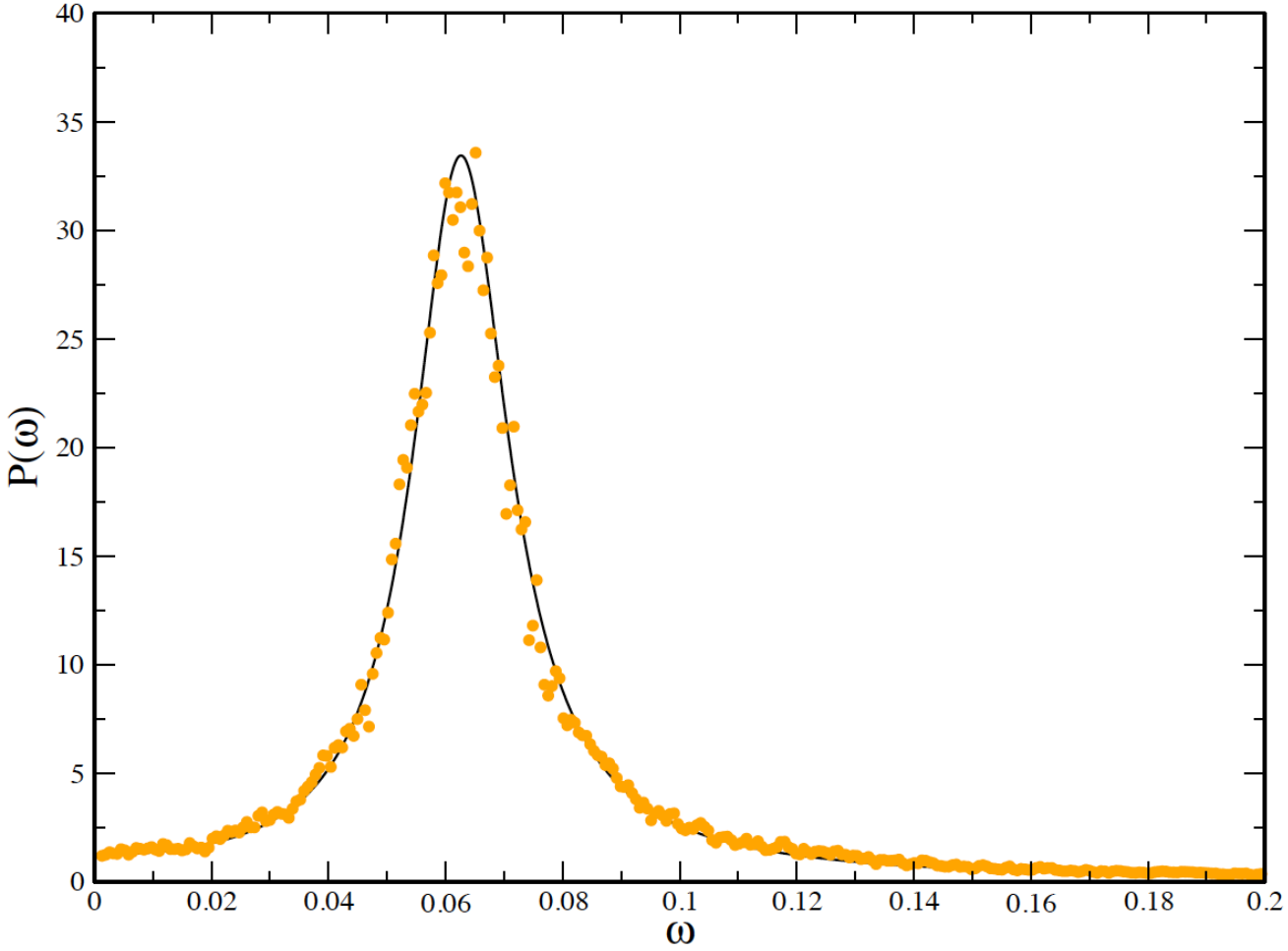
A straightforward manipulation yields:

$$P(\omega) \equiv \langle |\hat{\xi}|^2 \rangle = \frac{\alpha + \beta\omega^2}{\left[\left(\omega^2 - \Omega^2\right)^2 + \Gamma^2\omega^2 \right]}$$

with:

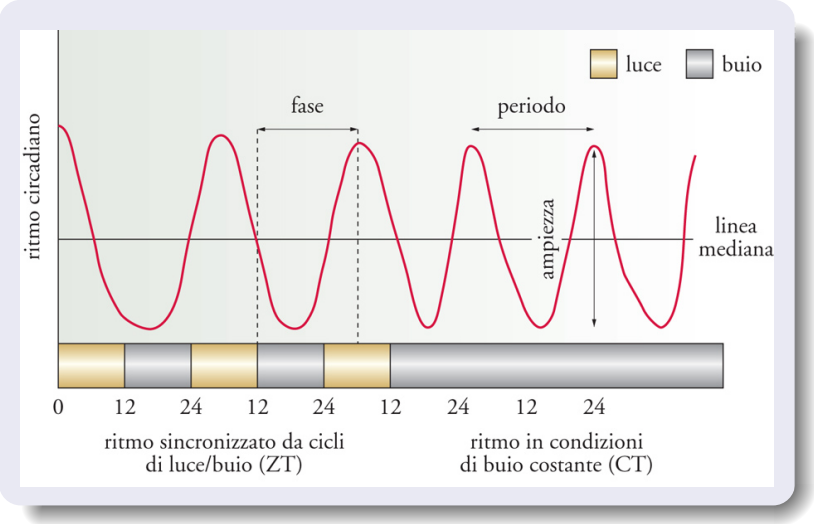
- $\alpha = B_{11}M_{22}^2 + 2B_{12}M_{12}|M_{22}| + B_{22}M_{12}^2$
- $\beta = B_{11}$
- $\Omega^2 = M_{12}|M_{21}|$
- $\Gamma = |M_{22}|$

Comparing theory and simulations.



B. Circadian clocks (from the inaugural lecture).

A circadian clock is a biochemical oscillator which makes it possible for the organism to adjust to the day-night cycle.



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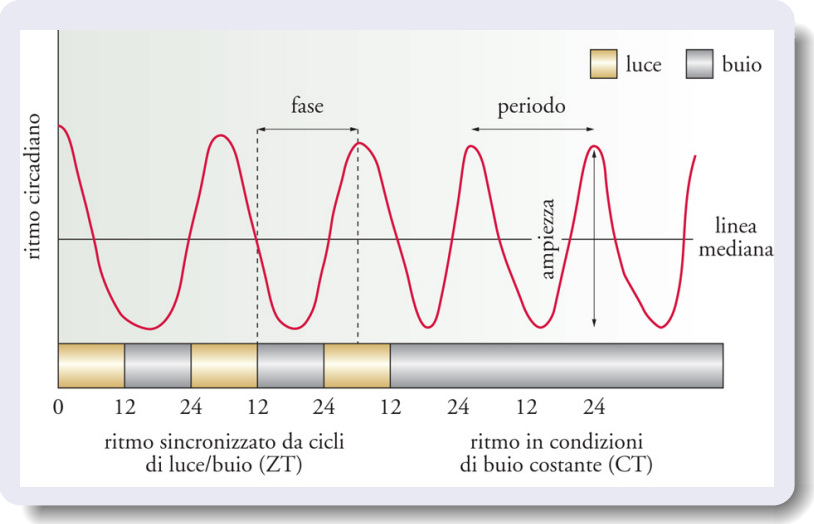

Key properties:

- Endogenous rhythmicity when stimuli are lacking.
- Susceptibility to external stimuli which prompt synchronization.
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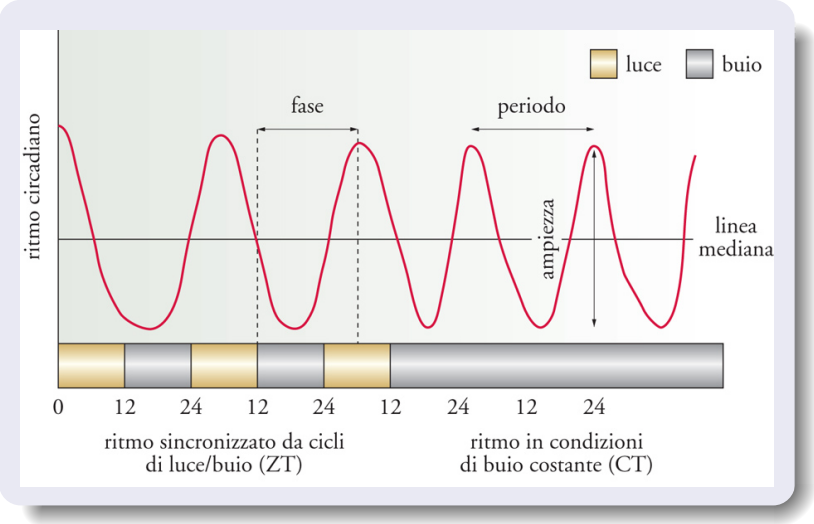

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Cianobacteria are among the simplest organisms to possess a biological cyrcadian clock.

Cyrcadian clocks in cianobacteria

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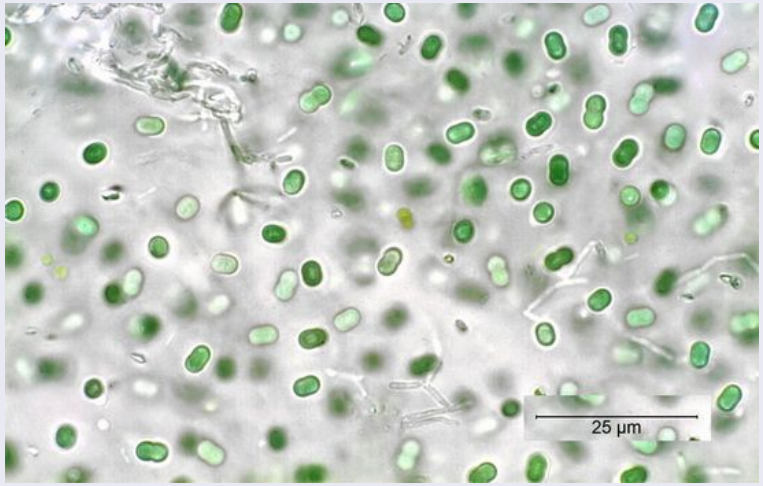

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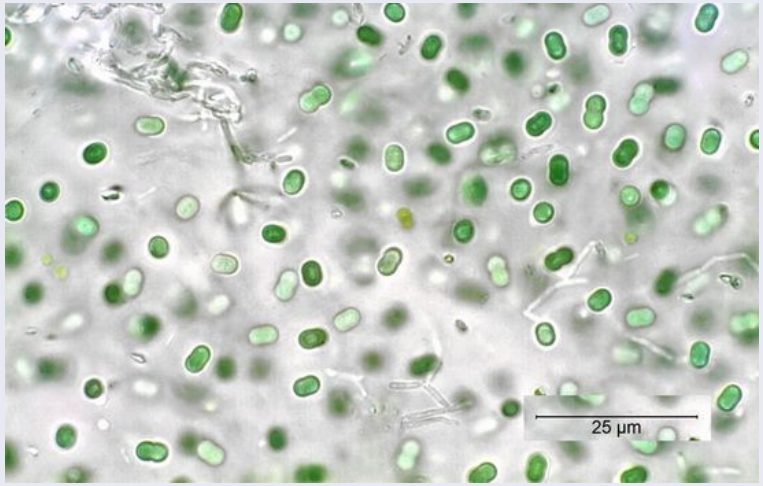

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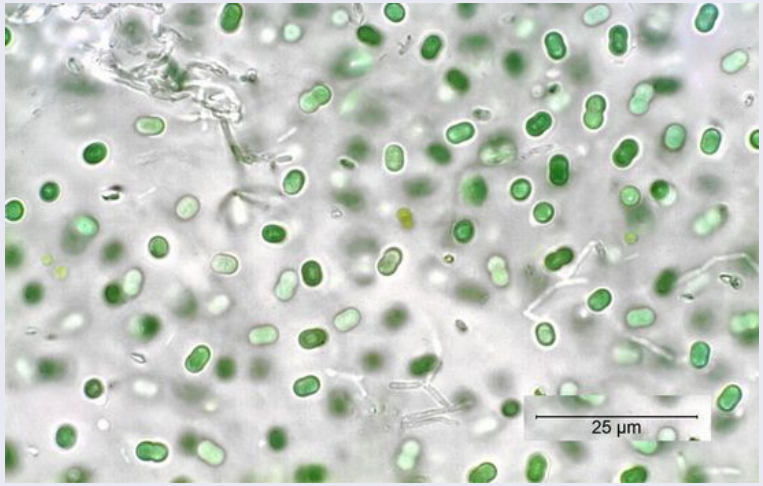

Anabaena sp.

The core of the circadian clock in cyanobacteria is composed by three proteins: KaiA, KaiB e KaiC.

Modeling the dynamics – 1

- **KaiC** phosphorylates on sites T and S. Phosphorylation modifies the structure of the protein with the inclusion of a phosphate group PO_4^{3-}.

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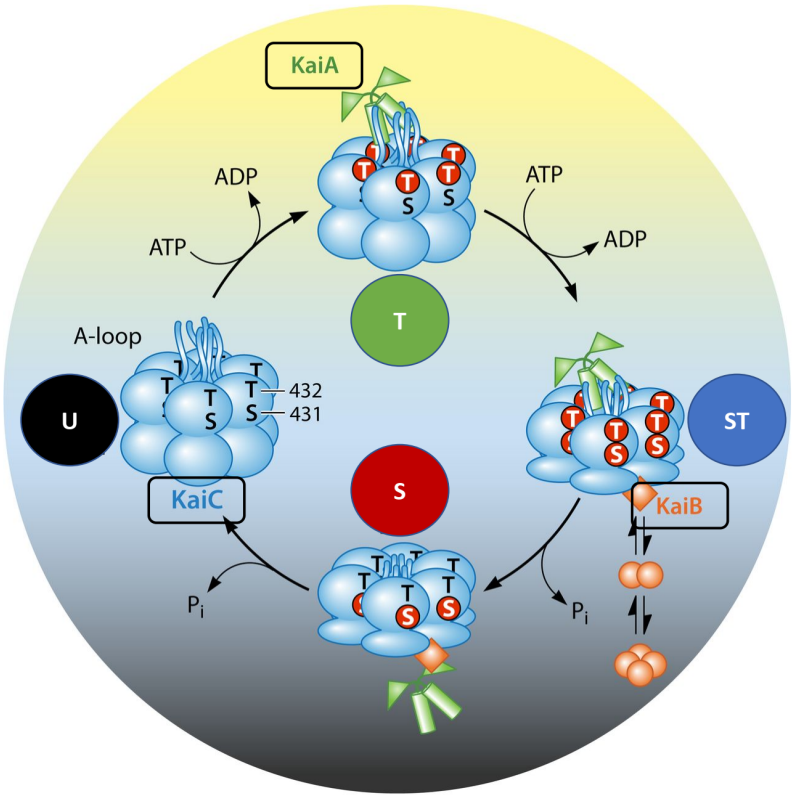

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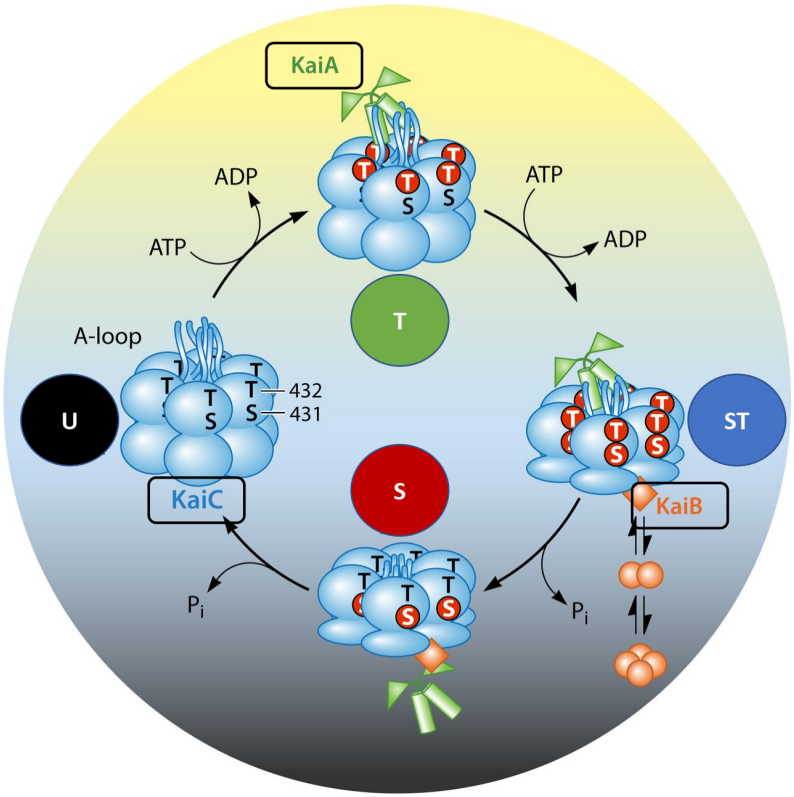

- ***KaiA*** and ***KaiB*** interact with ***KaiC*** following a ordered scheme which drives regular oscillations in th concentration amount delle fosfoforme
- **T**= T-KaiC, **D**= ST-KaiC, **S**= S-KaiC

Modeling the dynamics – 2

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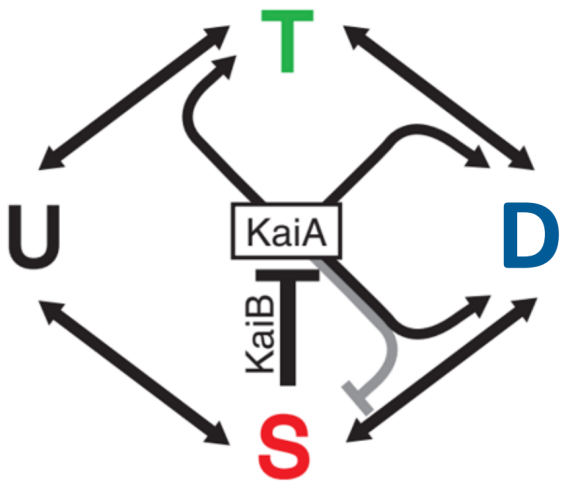

[Rust *et al.*, *Science*, 2007]

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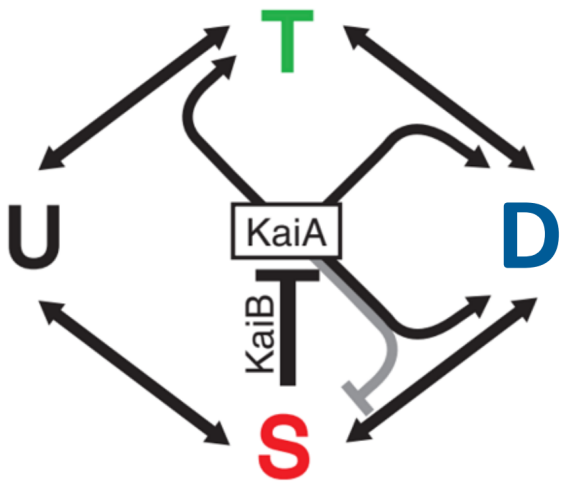

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$$\begin{cases} \dot{\phi}_T = \phi_U k_{UT} + \phi_D k_{DT} - \phi_T k_{TU} - \phi_T k_{TD} \\ \dot{\phi}_D = \phi_T k_{TD} + \phi_S k_{SD} - \phi_D k_{DT} - \phi_D k_{DS} \\ \dot{\phi}_S = \phi_U k_{US} + \phi_D k_{DS} - \phi_S k_{SU} - \phi_S k_{SD} \end{cases}$$

$$\phi_U = [\text{KaiC}] - \phi_T - \phi_D - \phi_S$$

Modeling the dynamics – 2

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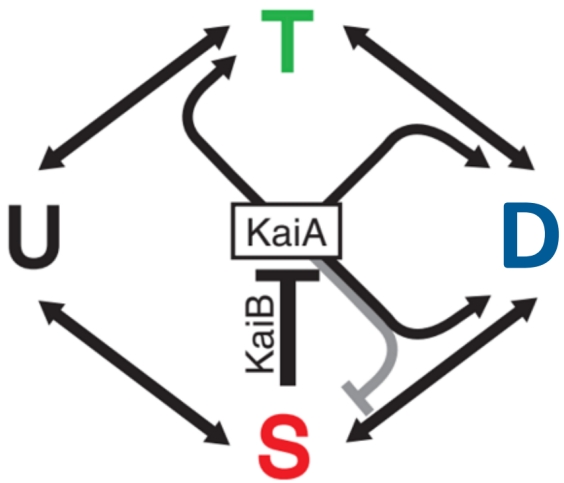
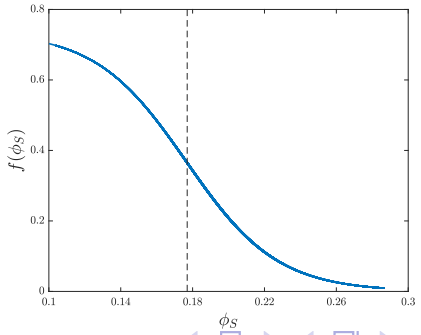


$$\begin{cases} \dot{\phi}_T = \phi_U k_{UT} + \phi_D k_{DT} - \phi_T k_{TU} - \phi_T k_{TD} \\ \dot{\phi}_D = \phi_T k_{TD} + \phi_S k_{SD} - \phi_D k_{DT} - \phi_D k_{DS} \\ \dot{\phi}_S = \phi_U k_{US} + \phi_D k_{DS} - \phi_S k_{SU} - \phi_S k_{SD} \end{cases}$$

$$\boxed{k_{XY}(\phi_S) = k^0_{XY} + k^A_{XY} f(\phi_S)}$$



The idealized continuum limit

A linear stability analysis around the fixed point solution $\left(\phi_T^*, \phi_D^*, \phi_S^*\right)$ yields the following scenario

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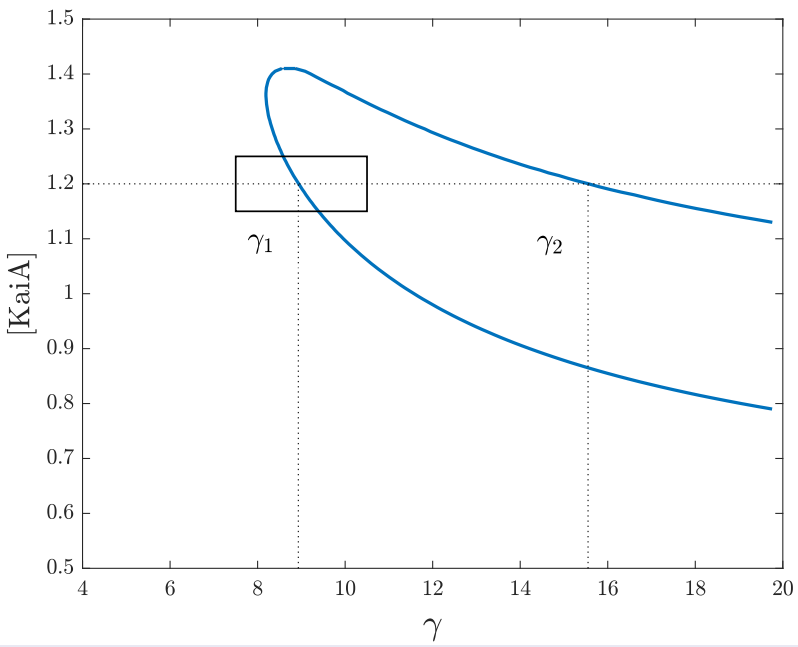
Parameter plane (γ, [KaiA])



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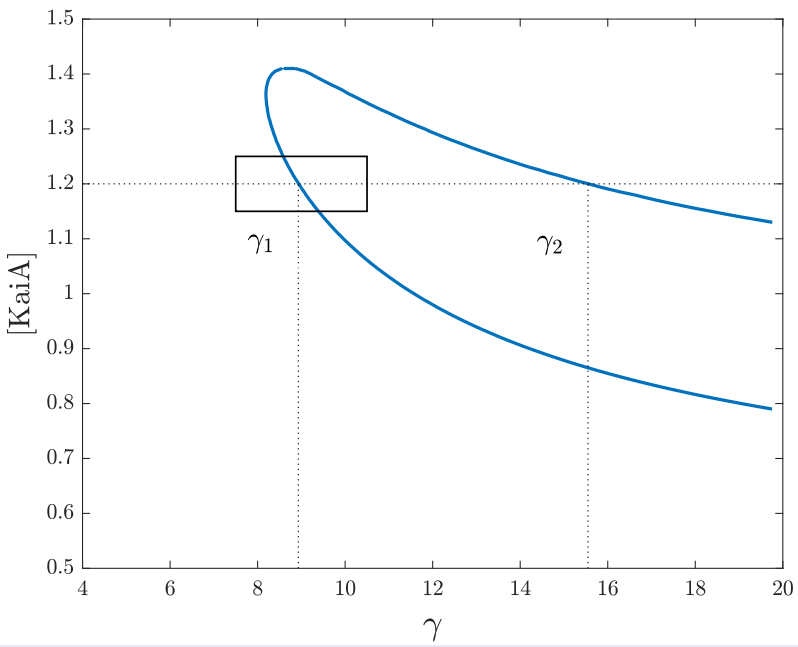
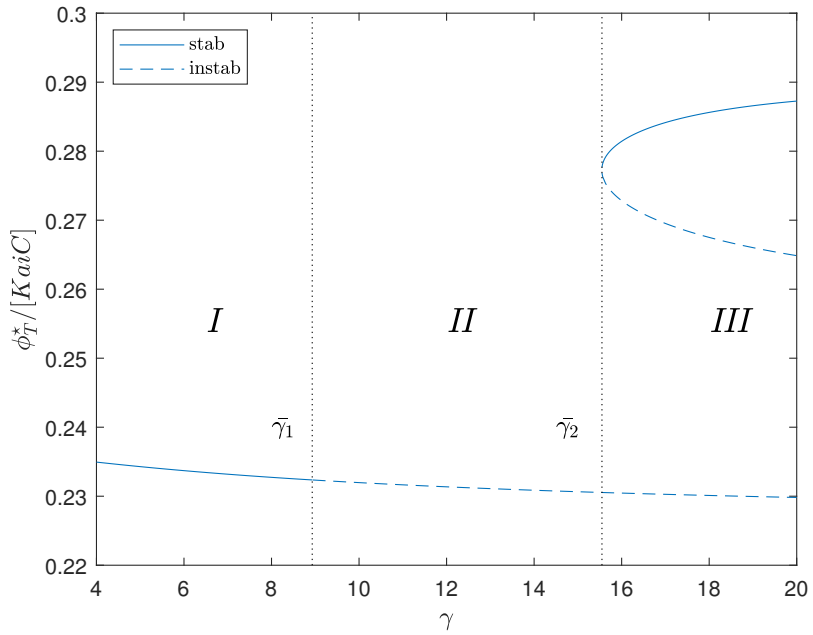
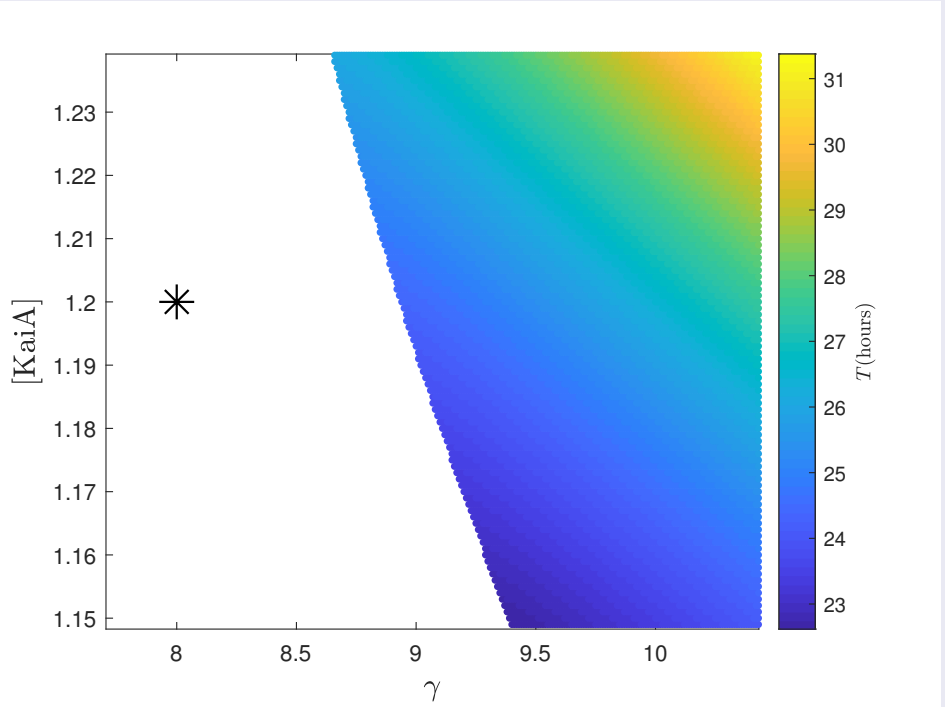


Bifurcation diagram, ϕ_T.



Exploring different dynamical regimes



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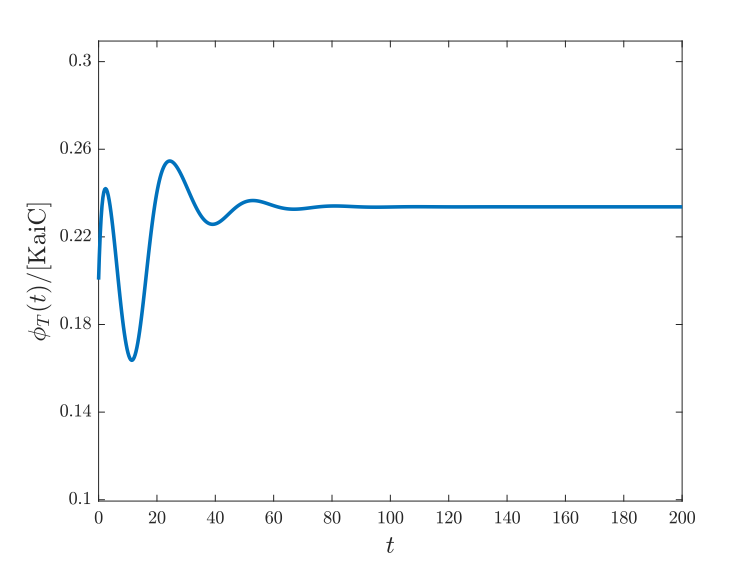

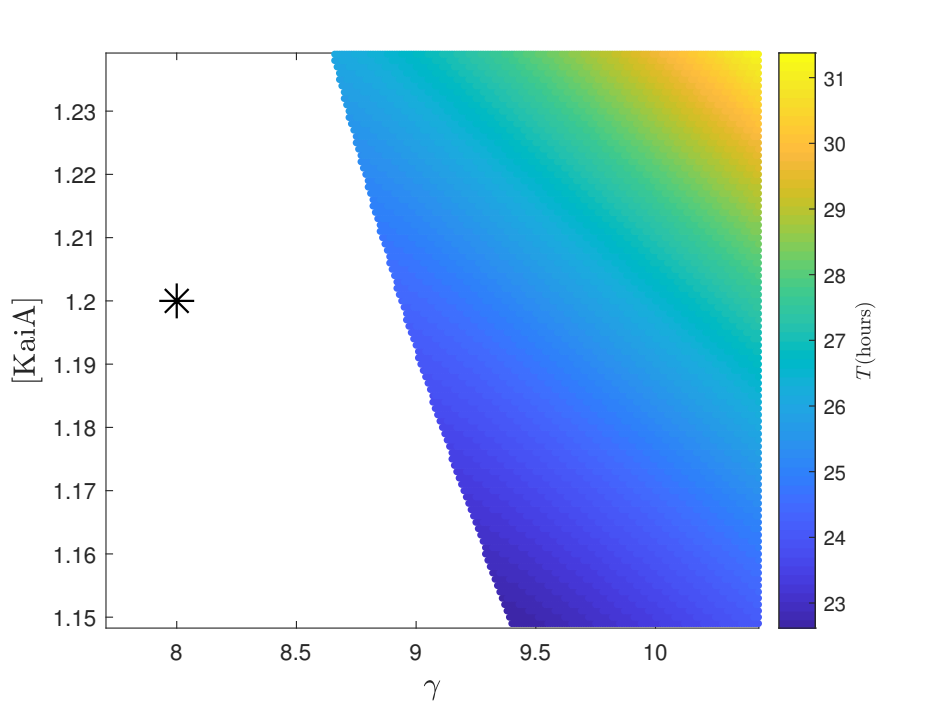

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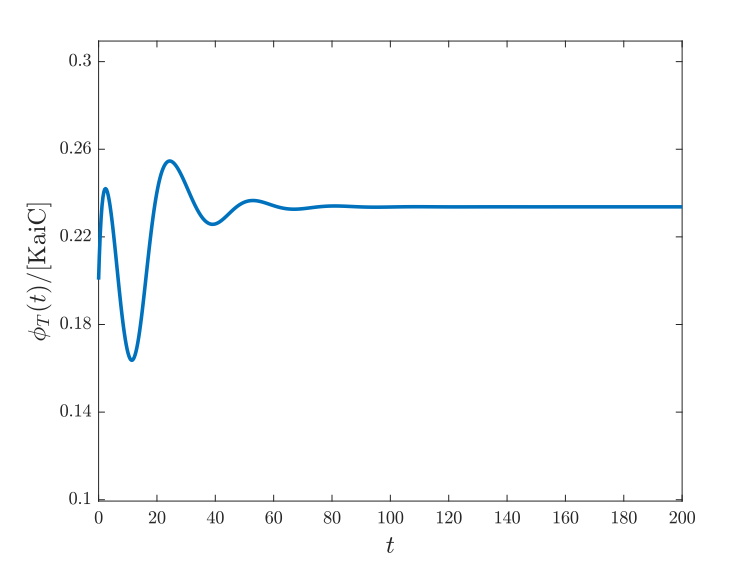
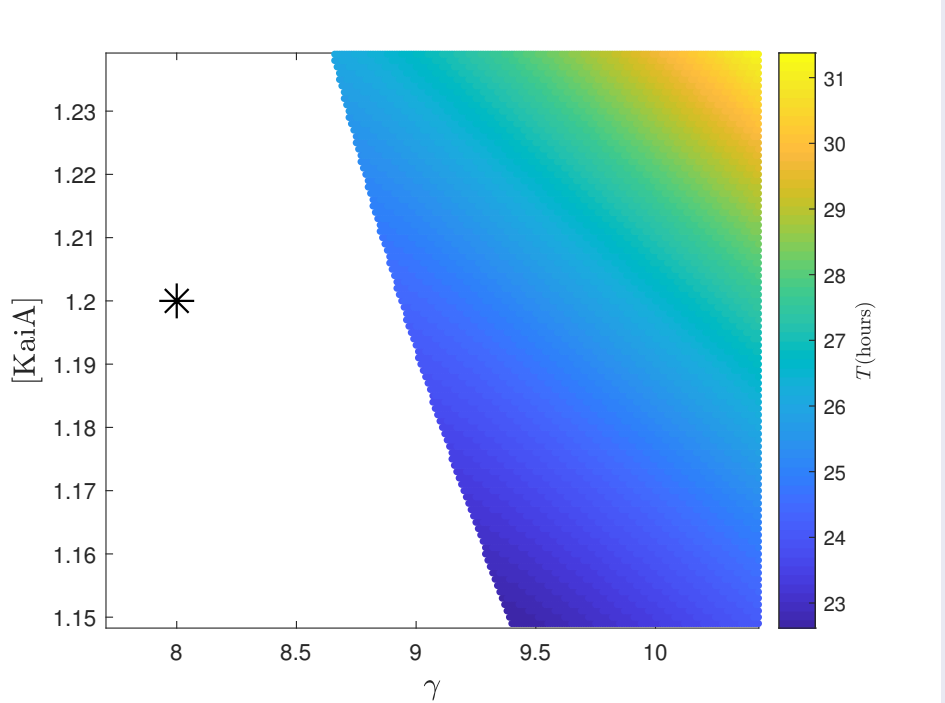
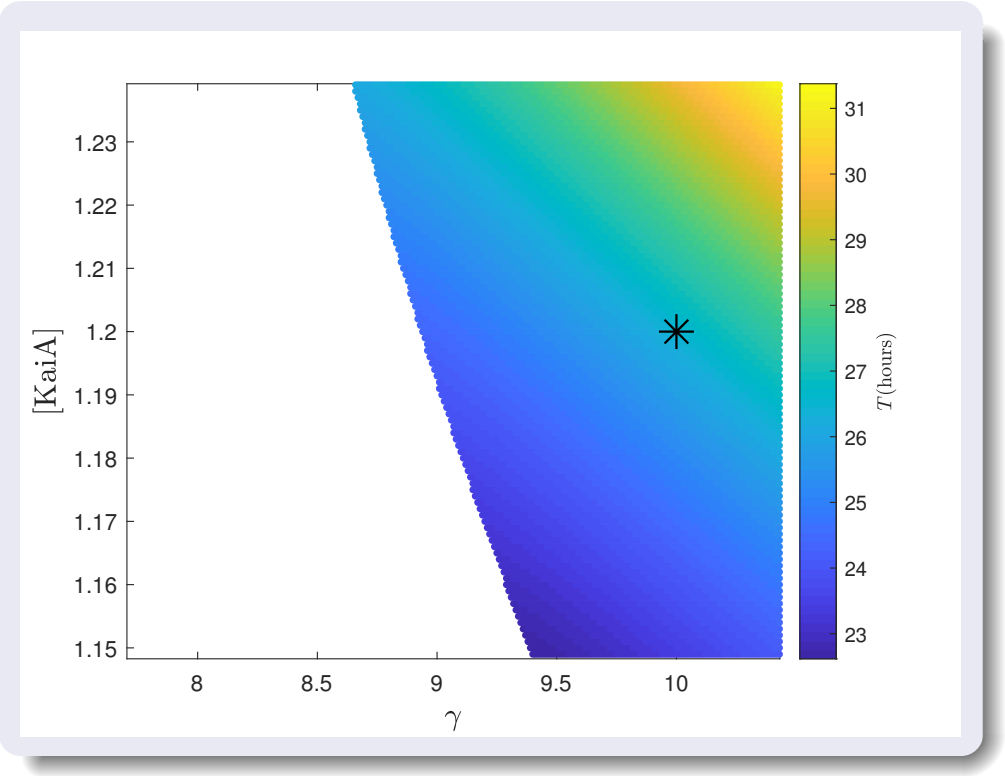




In region I the concentration of the phosphoforms of KaiC converges to a fixed point (absence of circadian cycles).

Exploring different dynamical regimes



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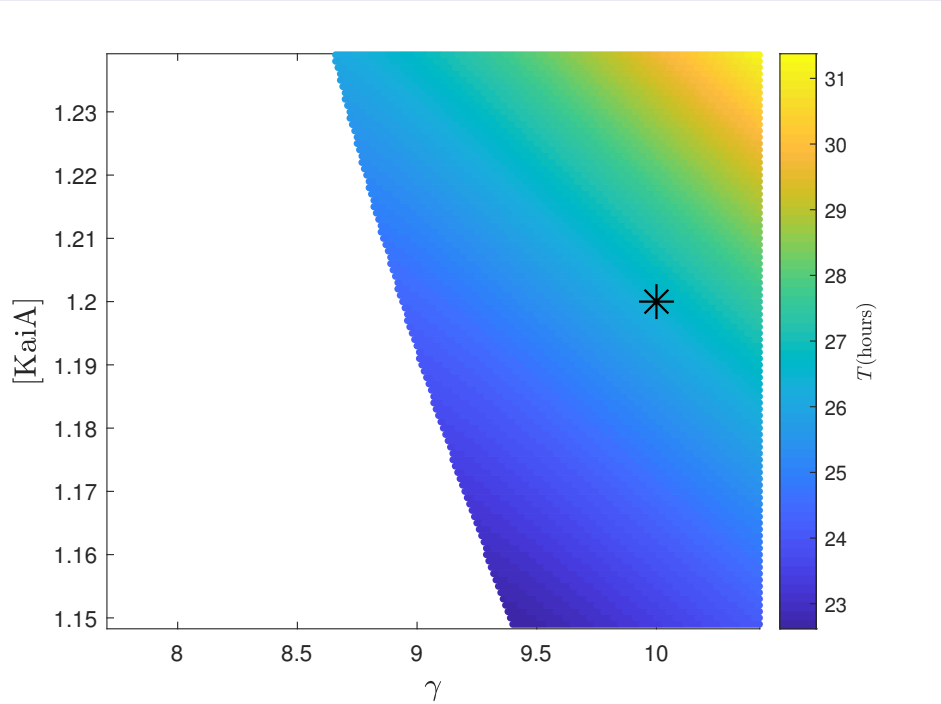

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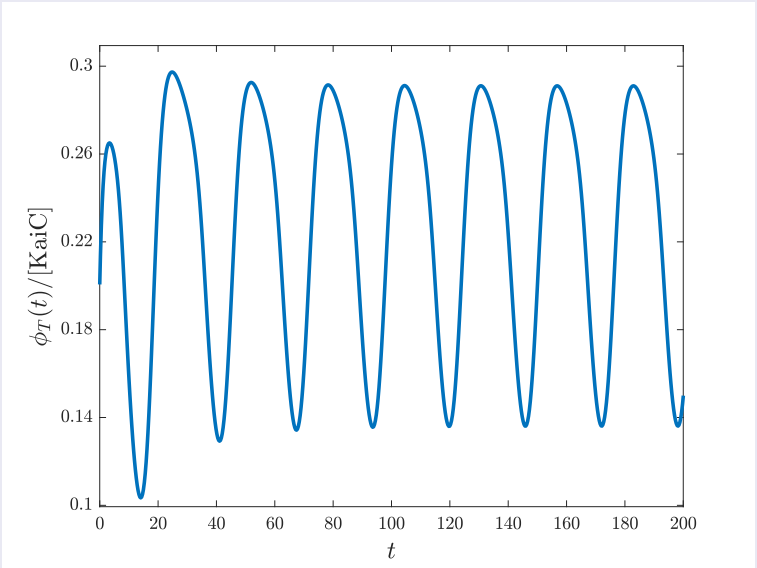

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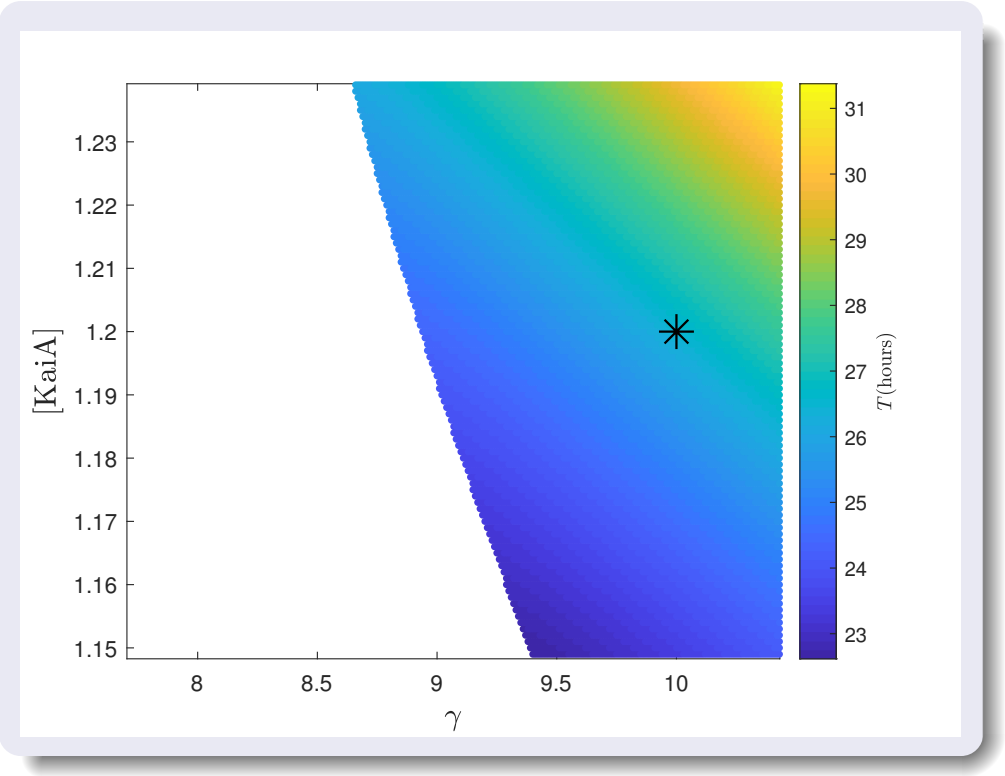

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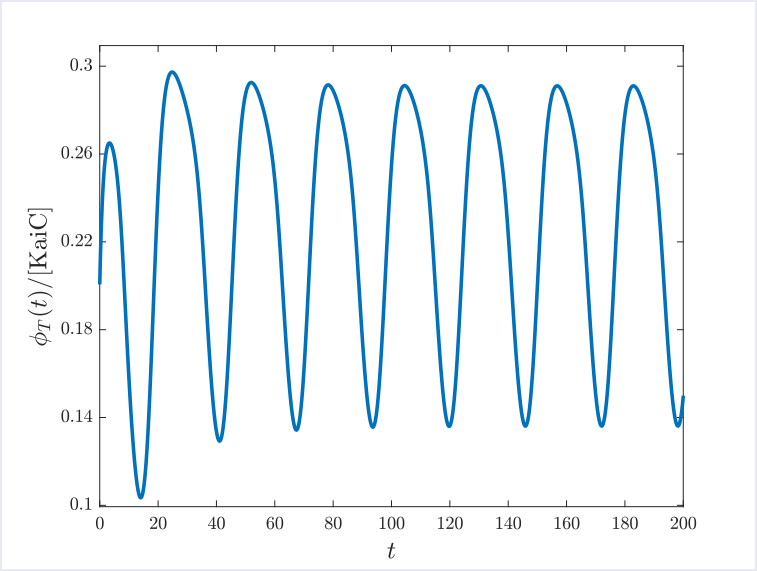

In region II the concentration of the phosphoforms of KaiC displays regular oscillations (with cyrcadian period).

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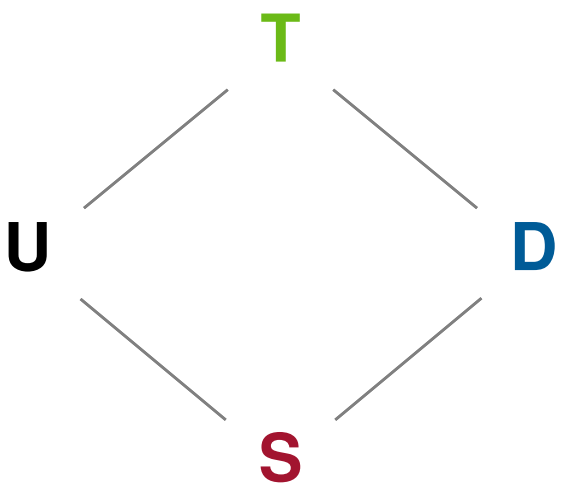

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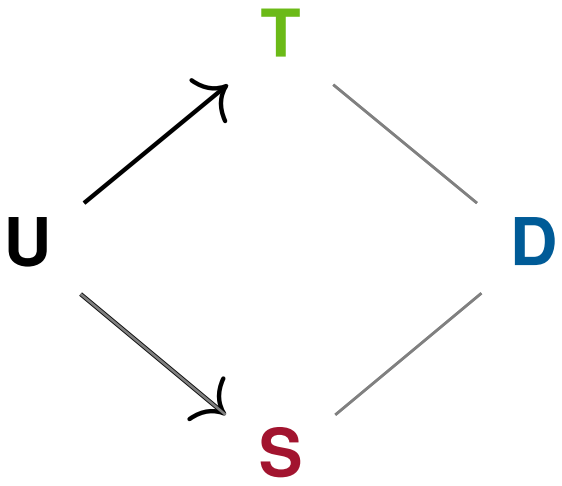

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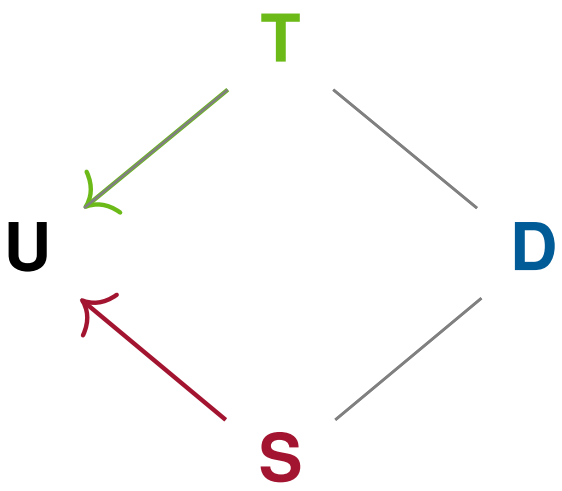

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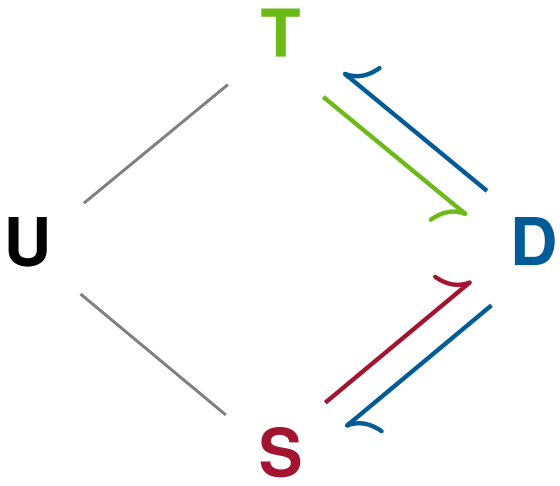

phosphorylation	$U \xrightarrow{k_{UT}} T,$	$U \xrightarrow{k_{US}} S$
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inter-conversion	$T \xrightarrow{k_{TD}} D,$	$S \xrightarrow{k_{SD}} D$
	$D \xrightarrow{k_{DT}} T,$	$D \xrightarrow{k_{DS}} S$

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Master equation in its full complexity.

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\begin{aligned}
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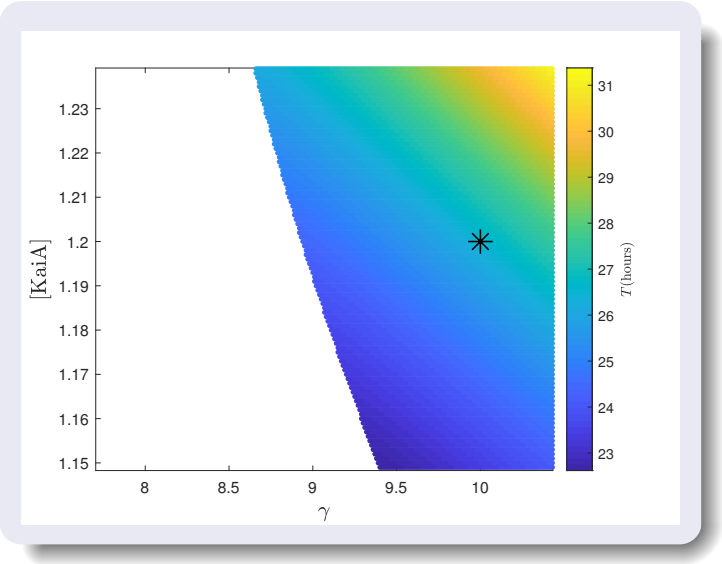

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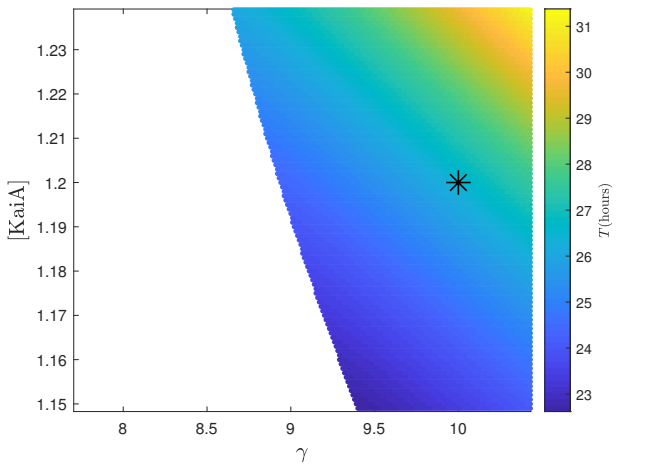

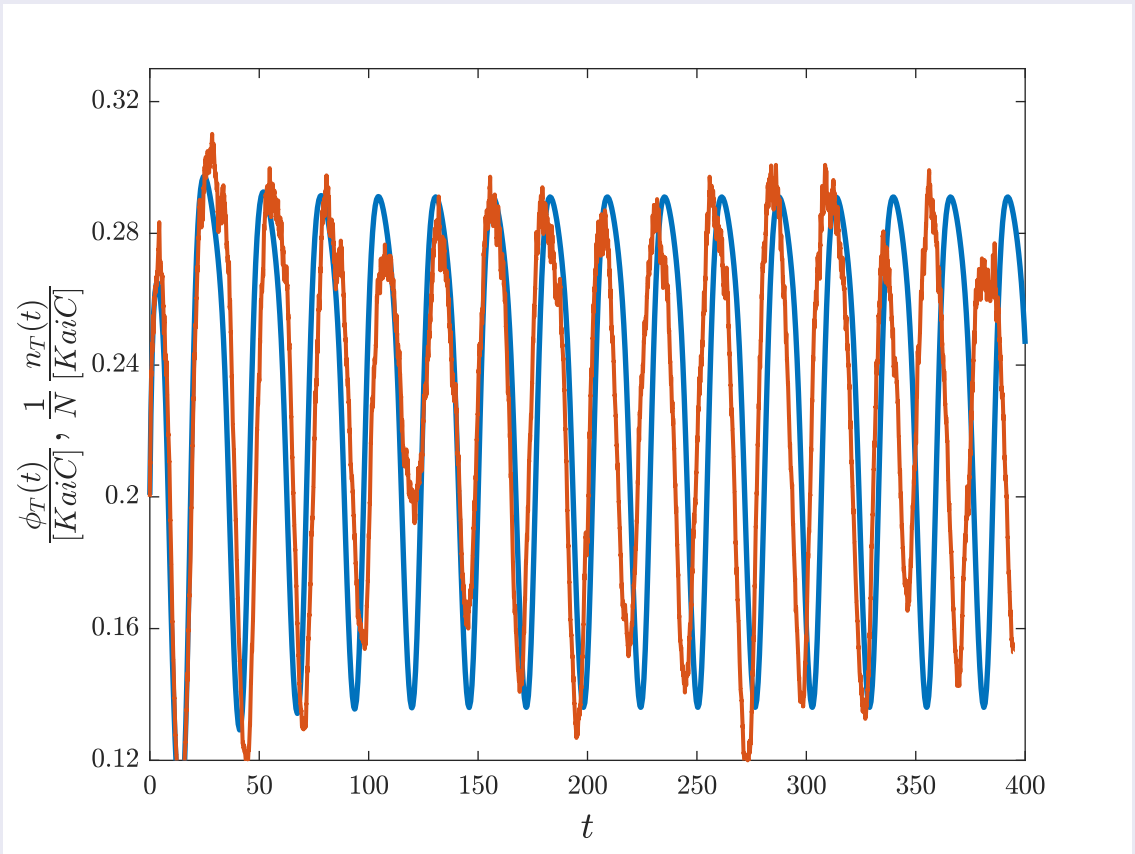

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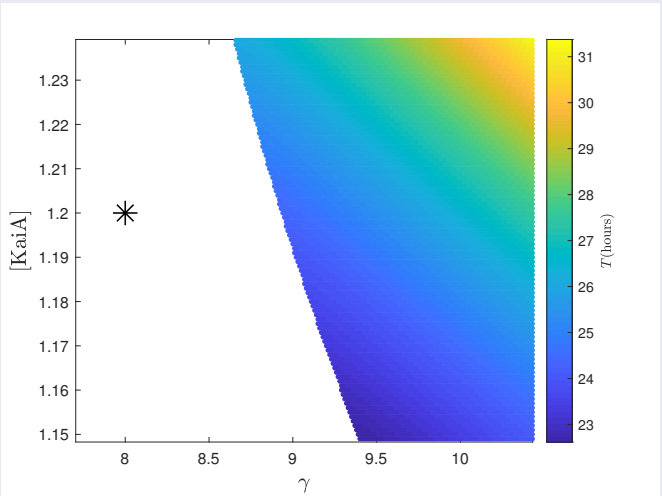

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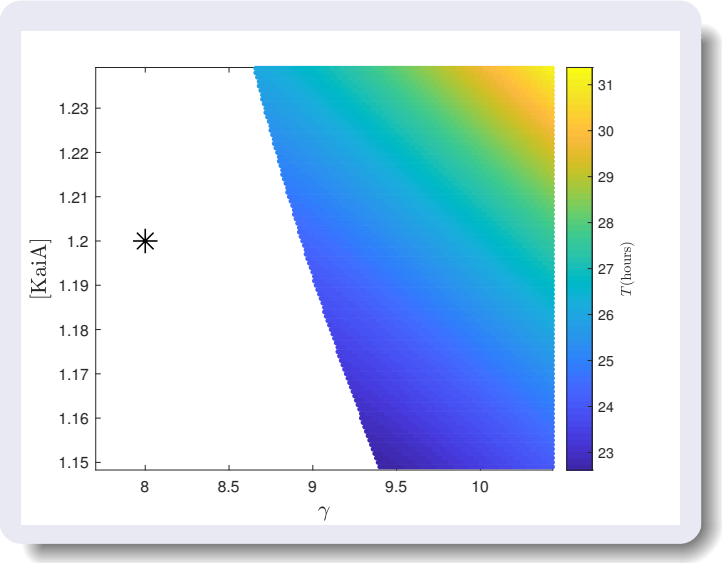

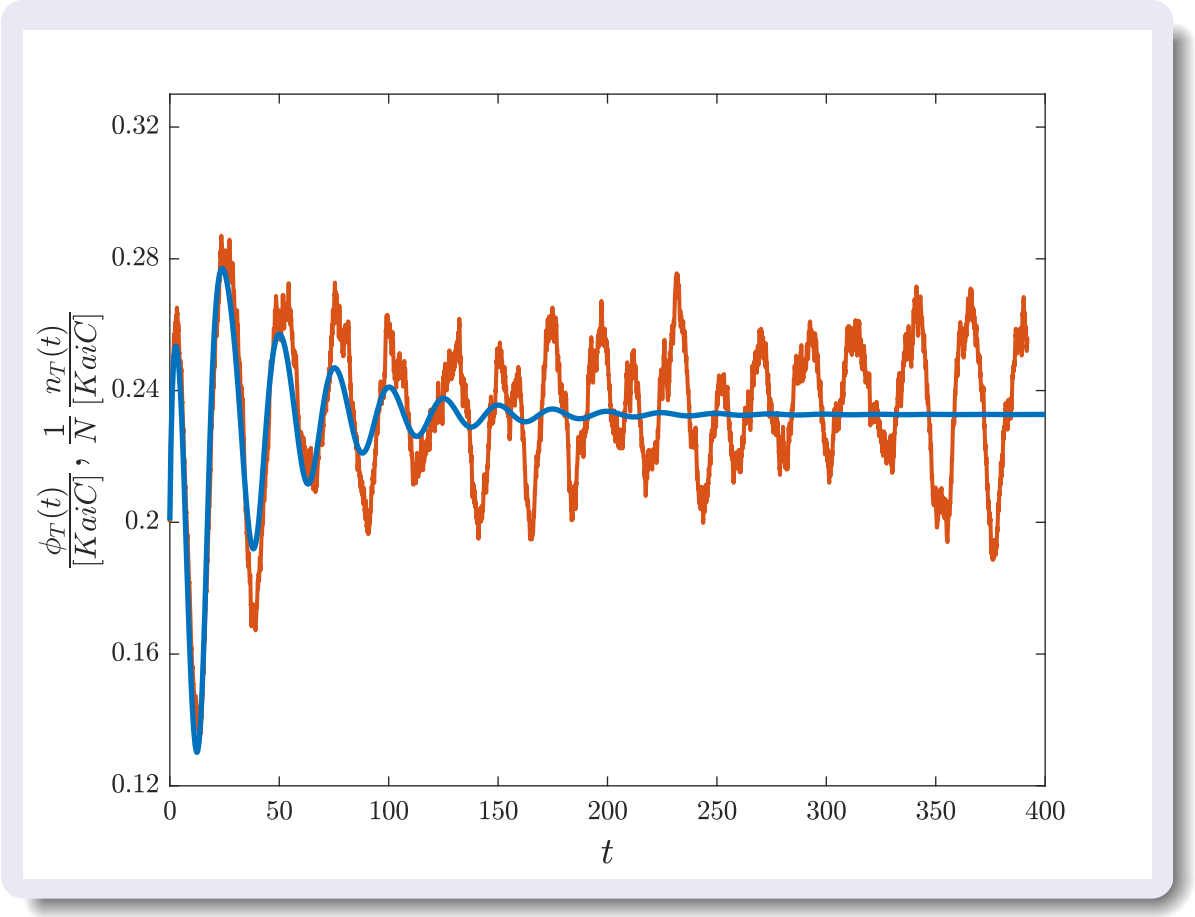

R. Arbel-Goren et al., (2020)

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- Perturbative expansion in the small parameter $\frac{1}{\sqrt{N}}$, where N is the size of the system.

van Kampen expansion

- At the leading order of the expansion $\longrightarrow$ one recovers the mean field equations

$$\boxed{\begin{cases} \dot{\phi}_T = \phi_U k_{UT} + \phi_D k_{DT} - \phi_T k_{TU} - \phi_T k_{TD} \\ \dot{\phi}_D = \phi_T k_{TD} + \phi_S k_{SD} - \phi_D k_{DT} - \phi_D k_{DS} \\ \dot{\phi}_S = \phi_U k_{US} + \phi_D k_{DS} - \phi_S k_{SU} - \phi_S k_{SD} \end{cases}}$$

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$$\boxed{\frac{\partial \Pi(\boldsymbol{\xi}, t)}{\partial \tau} = -\sum_{i=1}^{3} \frac{\partial}{\partial \xi_i}\Big[A_i(\boldsymbol{\xi})\Pi(\boldsymbol{\xi}, \tau)\Big] + \frac{1}{2}\sum_{i,j=1}^{3} \frac{\partial^2}{\partial \xi_i \partial \xi_j}\Big[B_{ij}\Pi(\boldsymbol{\xi}, \tau)\Big]}$$

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Going to Fourier space and computing the power spectrum of fluctuations for the i-species yields:

$$\boxed{P_{ii}(\omega) = \langle \left|\tilde{\xi}_i(\omega)\right|^2 \rangle = \left(\Phi^{-1} B (\Phi^{\dagger})^{-1}\right)_{ii}} \qquad \Phi = -i\omega 1 - J$$

Comparing with the experiments - Synechococcus el.

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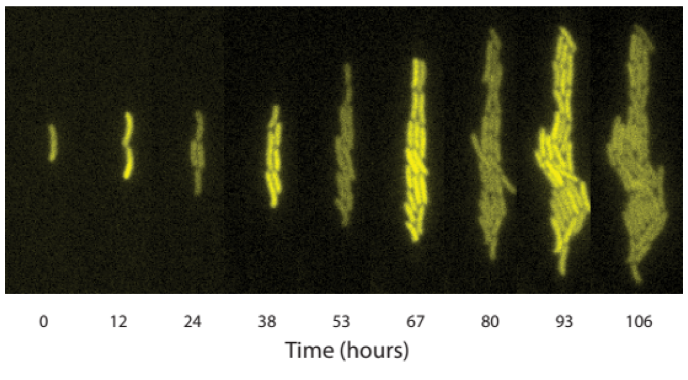
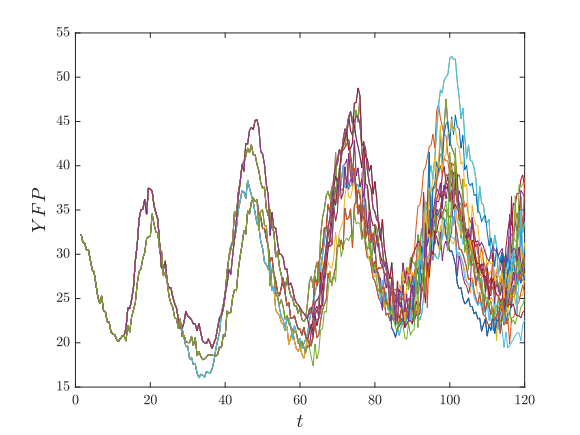
Fluorescence activity in *Synechococcus el.*





[In collaboration with J. Stavans group @Weizmann]

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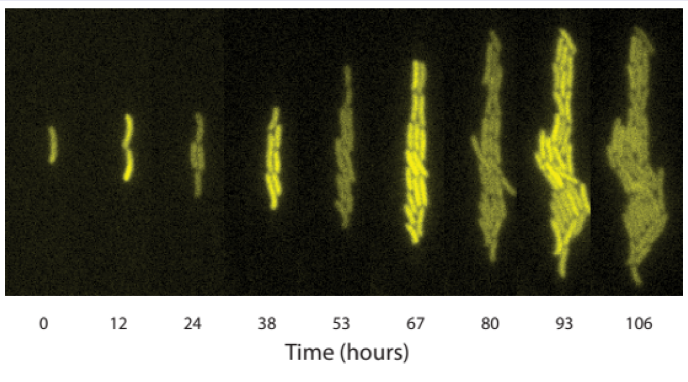

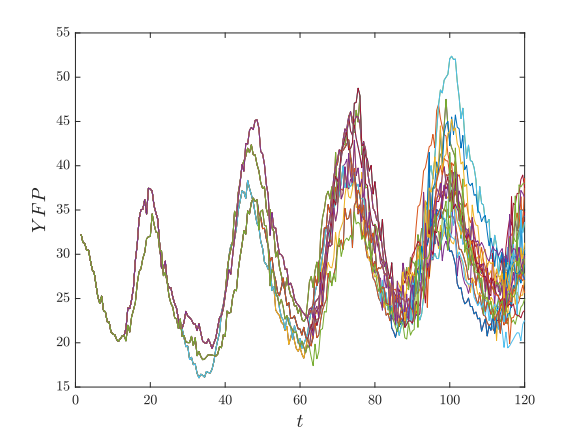

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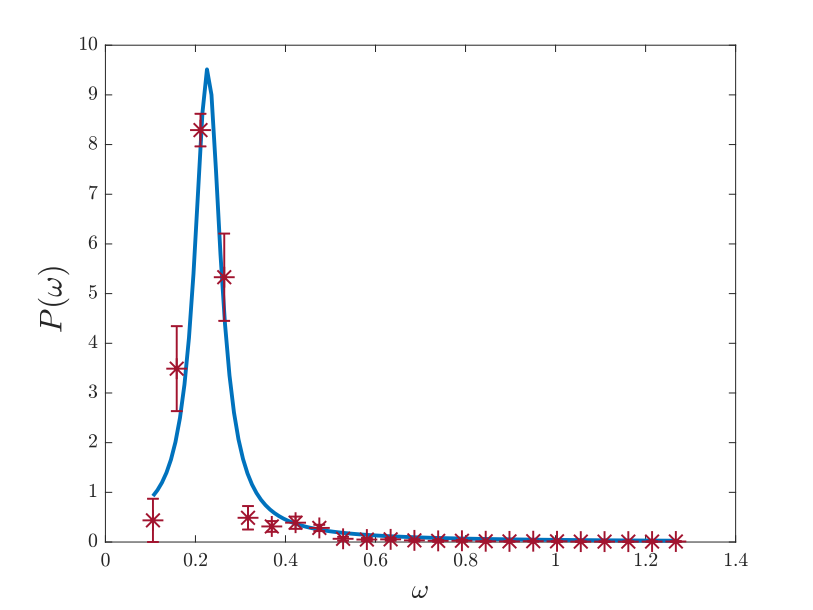
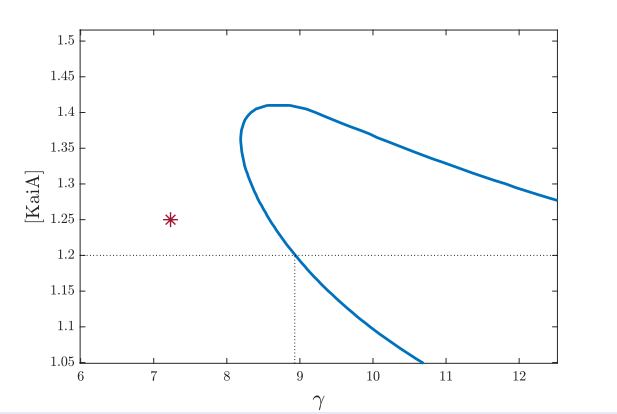
Power spectrum

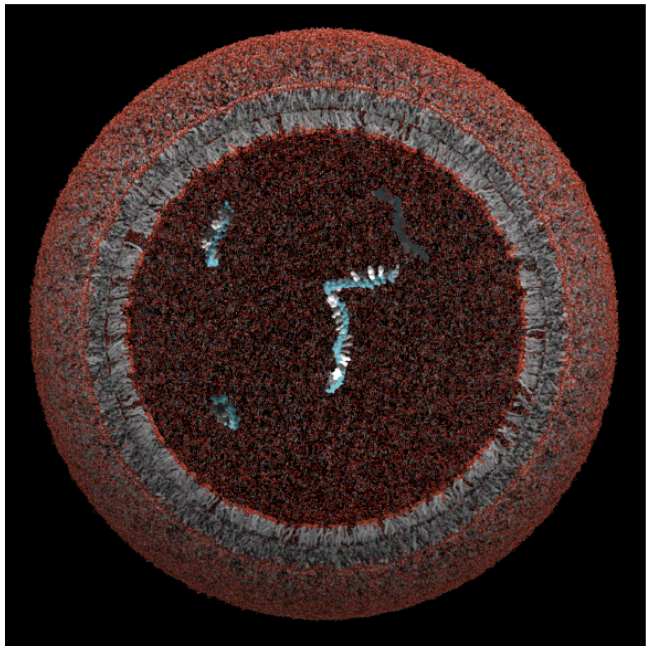




C. Autocatalytic oscillations.

Protocells

Protocells are hypothetical lifelike entities, capable of growing and dividing, thus giving rise to offspring that are similar to their parents but, due to the noise inherent in the process, not identical to them.



Protocells therefore possess all the ingredients necessary for Darwinian evolution, and it is possible to imagine that a population of initially very simple protocells change in time, acquiring more sophisticated properties.

R. Serra (2010)

Mimimal living entities must embodie three operational functionalities:

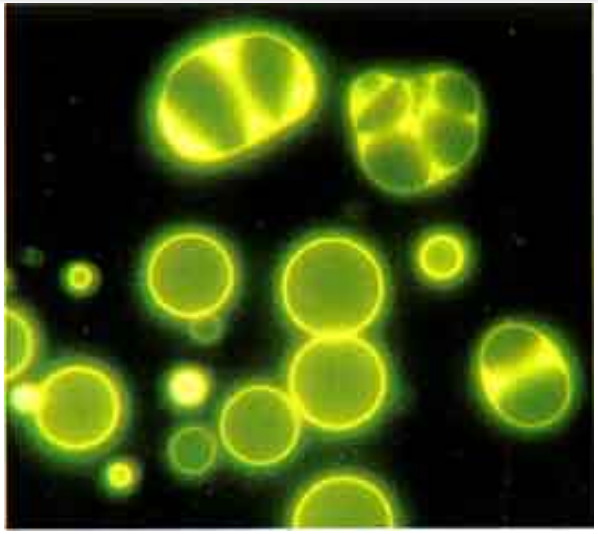
- A metabolism that extracts usable energy form the environment (open system)
- Genes that chemically realize informational control of living functionalities
- Container that keeps them all together.

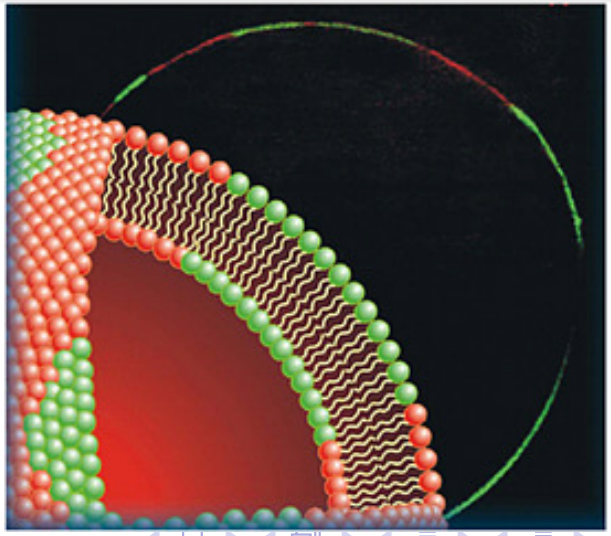
The container

Vesicles

Vesicles are small cell-like structure in which the membrane separating the inner constituent and outer environment takes the form of a lipid bilayer.

Living cells are essentially very complicated vesicles with the membrane containing a mixture of different lipids, a cytoskeleton and complex surface structures.





Simple vesicles without any additional structure display many fascinating properties when observed in the lab: their growth, their shape and the fact that they divide...

This self-replication ability is especially interesting in the context of models of protocells, the primordial life bricks.

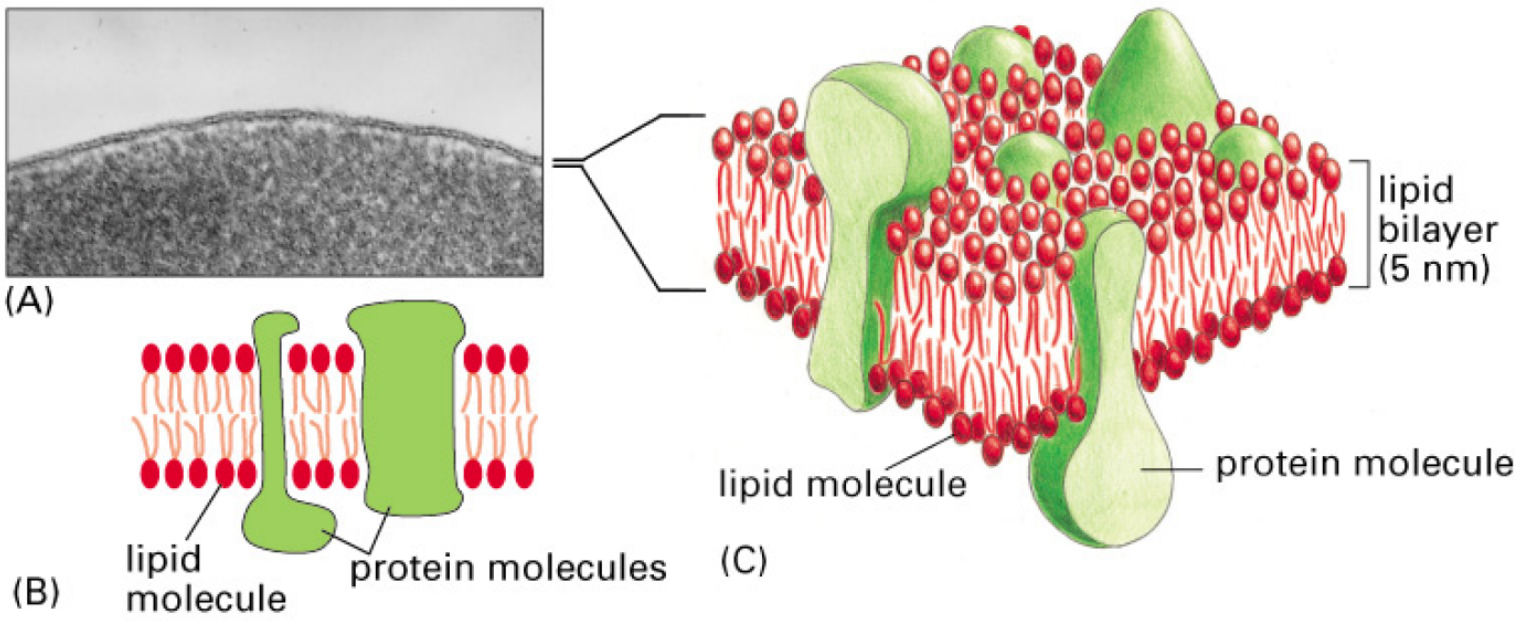
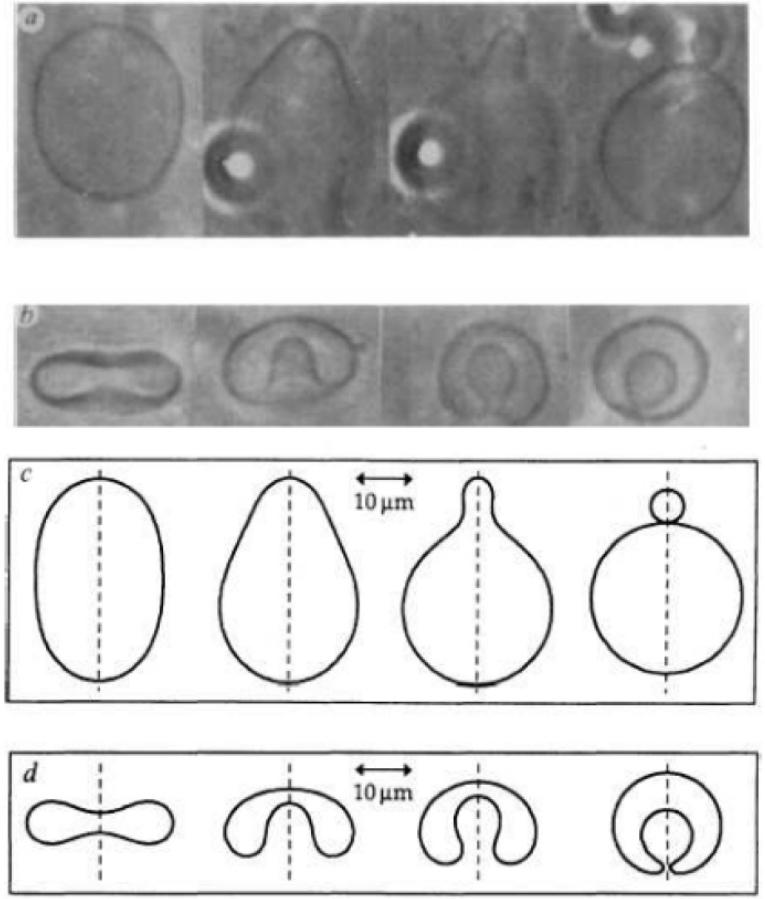


Figure 10–1. Molecular Biology of the Cell, 4th Edition.

The vesicles self-organize in a sealed compartment.

Different shapes with the lowest bending energy can be attained: prolate and oblate ellipsoids, dumb-bell, pear shapes



The interior

While vesicles can possibly define the scaffold of prototypical cell models, what to can one say about the internal constituents?

It is believed that autocatalytic reactions might have played a role in producing complex molecules required for the origin of life.

A chemical reaction is called autocatalytic if one of the reaction products is itself a catalyst for the chemical reaction. Clearly the reaction will speed up as more catalyst is produced.

Nested catalytic reactions yields more complex behavior, with some reactions producing catalysts for other reactions.

The interior of the protocell might have been occupied by interacting families of replicators, organized in autocatalytic cycles.

Autocatalytic reactions are robust and cooperative: they are a possible solution of the Eigen paradox, i.e. the evolutionary drive to self-destruction.

The model (Togashi and Kaneko)

Chemical equations

- Autocatalytic reaction

$$X_i + X_{i+1} \xrightarrow{r_{i+1}} 2X_{i+1}$$

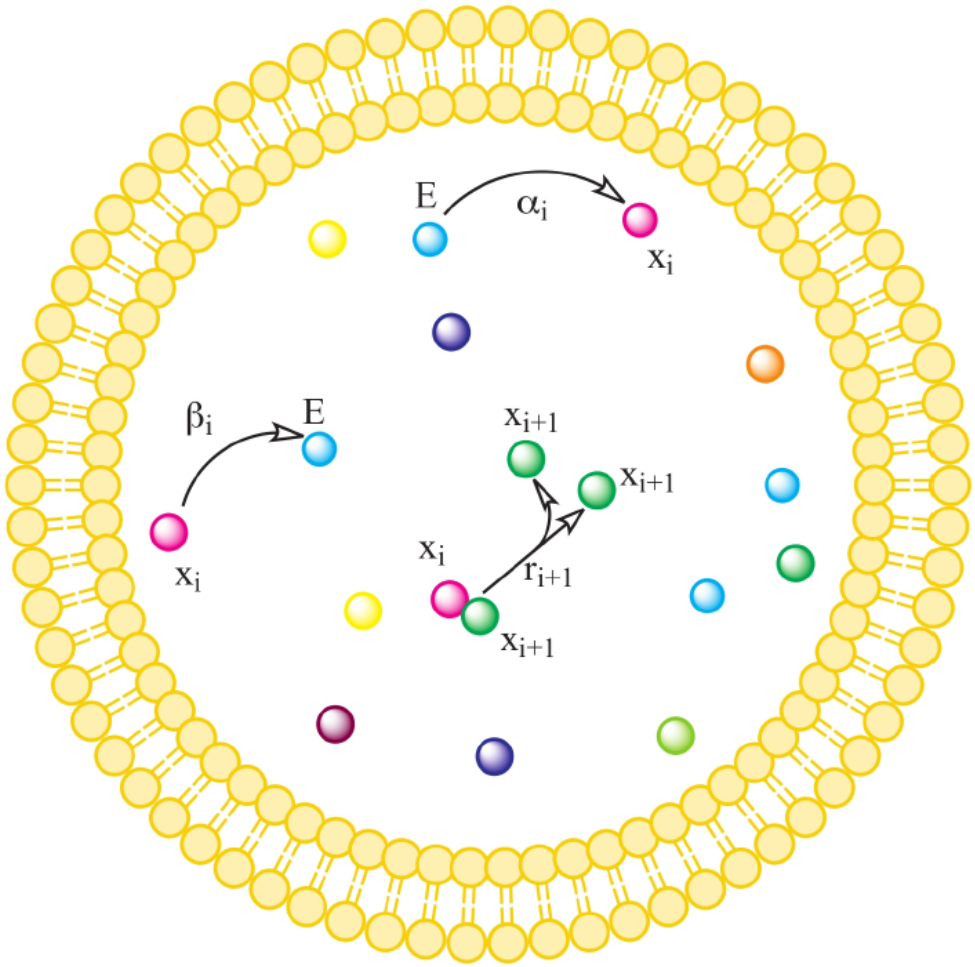
with $X_{k+1} \equiv X_1$

- Inward diffusion

$$E \xrightarrow{\alpha_i} X_i$$

- Outward diffusion

$$X_i \xrightarrow{\beta_i} E$$



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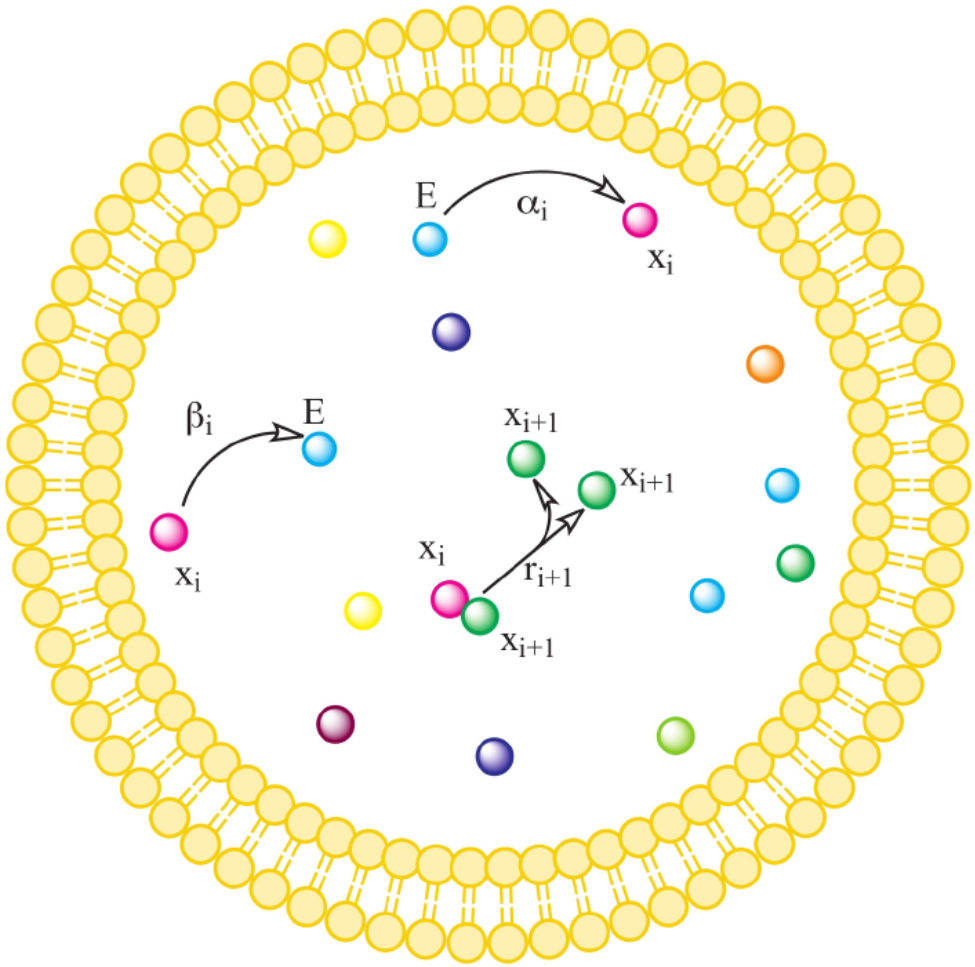

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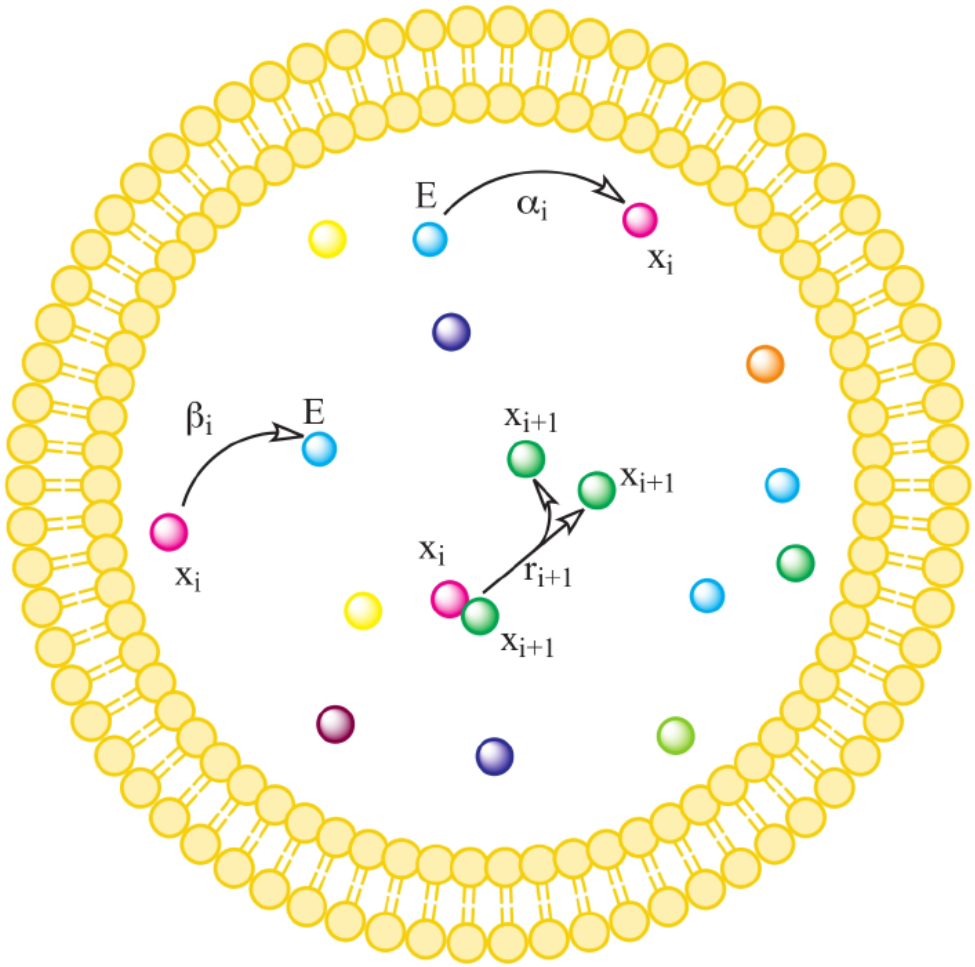

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n_i = number of molecules of type X_i

$$\sum_{i=1}^{k} n_i + n_E = N$$

$$n_E = N - \sum_{i=1}^{k} n_i$$

$$\boldsymbol{n} \equiv (n_1, \ldots, n_k)$$

The Master equation

Denote with $P(\mathbf{n}, t)$ the probability of seeing the system in state $\mathbf{n}$ at time t.

Under the Markov hypothesis the stochastic process obeys to the following balance equation:

$$\frac{dP(\mathbf{n}, t)}{dt} = -\sum_{\mathbf{n}' \neq \mathbf{n}} T(\mathbf{n}'|\mathbf{n}) P(\mathbf{n}, t) + \sum_{\mathbf{n}' \neq \mathbf{n}} T(\mathbf{n}|\mathbf{n}') P(\mathbf{n}', t)$$

where $T(\mathbf{n}'|\mathbf{n})$ stands for the transition rate from the initial state $\mathbf{n}$ to the final state $\mathbf{n}'$

Transition rates follow from the chemical equations

Consider the reaction:

$$X_i + X_{i+1} \xrightarrow{r_{i+1}} 2X_{i+1}$$

- The probability of extracting from the urn one individual of type X_i is n_i/N

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- Finally the probability for the reaction to occur reads

$$r_{i+1}\frac{n_i}{N}\frac{n_{i+1}}{N}.$$

Table of transition probabilities

- Reaction $X_i + X_{i+1} \xrightarrow{r_{i+1}} 2X_{i+1}$

$$T(n_1, \ldots, n_i - 1, n_{i+1} + 1, \ldots, n_k | \boldsymbol{n}) = r_{i+1} \frac{n_i}{N} \frac{n_{i+1}}{N}$$

- Reaction $E \xrightarrow{\alpha_i} X_i$

$$T(n_1, \ldots, n_i + 1, \ldots, n_k | \boldsymbol{n}) = \alpha_i \left(1 - \frac{\sum_{j=1}^{k} n_j}{N} \right)$$

- Reaction $X_i \xrightarrow{\beta_i} E$

$$T(n_1, \ldots, n_i - 1, \ldots, n_k | \boldsymbol{n}) = \beta_i \frac{n_i}{N}$$

Step–operators

$$E_i^{\pm 1} f(\boldsymbol{n}) = f(n_1, \ldots, n_i \pm 1, \ldots, n_k)$$

Master equation (ME)

$$\begin{aligned}
\frac{d}{dt} P(\boldsymbol{n}, t) \quad = \quad & \sum_{i=1}^{k} \left(E_i E_{i+1}^{-1} - 1 \right) \\
& \times \left[T(n_1, \ldots, n_i - 1, n_{i+1} + 1, \ldots, n_k | \boldsymbol{n}) P(\boldsymbol{n}, t) \right] \\
& + \sum_{i=1}^{k} \left(E_i^{-1} - 1 \right) \left[T(n_1, \ldots, n_i + 1, \ldots, n_k | \boldsymbol{n}) P(\boldsymbol{n}, t) \right] \\
& + \sum_{i=1}^{k} \left(E_i - 1 \right) \left[T(n_1, \ldots, n_i - 1, \ldots, n_k | \boldsymbol{n}) P(\boldsymbol{n}, t) \right]
\end{aligned}$$

The Master equation is difficult to handle analytically. Two strategies are possible:

- Perturbative theory: approximate the Master equation with dedicated machineries, e.g. the van Kampen system size expansion.
- Numerical simulations. Resort to stochastic simulations simulations that enables one to solve exactly the stochastic dynamics.

The perturbative approach

The Van Kampen reads:

$$\frac{n_i}{N} = \phi_i(t) + \frac{1}{\sqrt{N}}\xi_i$$

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- $\phi_i(t)$ is the deterministic concentration
- ξ_i is a stochastic variable which accounts for finite size fluctuations

The scaling factor $1/\sqrt{N}$ controls the amplitude of stochastic fluctuations: for large, though finite system sizes it acts as a small perturbative parameter.

Expanding the left–hand side of the Master equation

New probability

$$P(\boldsymbol{n}, t) \to \Pi(\boldsymbol{\xi}, t)$$

$$\frac{d}{d\tau} P(\boldsymbol{n}, t) = \frac{\partial}{\partial \tau} \Pi(\boldsymbol{\xi}, t) - \frac{1}{\sqrt{N}} \sum_{i=1}^{k} \frac{\partial \Pi(\boldsymbol{\xi}, t)}{\partial \xi_i} \frac{d\phi_i}{d\tau}$$

$$E_i^{\pm 1} = 1 \pm \frac{1}{\sqrt{N}} \frac{\partial}{\partial \xi_i} + \frac{1}{2N} \frac{\partial^2}{\partial \xi_i^2} + \dots$$

Expanding the right–hand side of Master equation

Terms of order $N^{-1/2}$

$$\sum_{i=1}^{k}\left\{r_{i+1}\phi_i\phi_{i+1}\left[\frac{\partial}{\partial\xi_i}-\frac{\partial}{\partial\xi_{i+1}}\right]-\alpha_i\left(1-\sum_{j=1}^{k}\phi_j\right)\frac{\partial}{\partial\xi_i}+\beta_i\phi_i\frac{\partial}{\partial\xi_i}\right\}\Pi(\boldsymbol{\xi},t)$$

Terms of order N^{-1} and involving first order derivatives

$$\sum_{i=1}^{k}\left\{r_{i+1}\phi_i\frac{\partial}{\partial\xi_i}\xi_{i+1}+(r_{i+1}\phi_{i+1}+\beta_i)\frac{\partial}{\partial\xi_i}\xi_i-r_{i+1}\phi_i\frac{\partial}{\partial\xi_{i+1}}\xi_{i+1}-r_{i+1}\phi_{i+1}\frac{\partial}{\partial\xi_{i+1}}\xi_i+\alpha_i\sum_{j=1}^{k}\frac{\partial}{\partial\xi_i}\xi_j\right\}\Pi(\boldsymbol{\xi},t)$$

Terms of order N^{-1} and involving second order derivatives

$$\frac{1}{2}\sum_{i=1}^{k}\left\{r_{i+1}\phi_i\phi_{i+1}\left[\frac{\partial^2}{\partial\xi_i^2}-\frac{\partial^2}{\partial\xi_{i+1}^2}\right]^2+\alpha_i\left(1-\sum_{j=1}^{k}\phi_j\right)\frac{\partial^2}{\partial\xi_i^2}+\beta_i\phi_i\frac{\partial^2}{\partial\xi_i^2}\right\}\Pi(\boldsymbol{\xi},t)$$

The leading order

Collecting together terms involving $1/\sqrt{N}$ we get

Mean–field equations

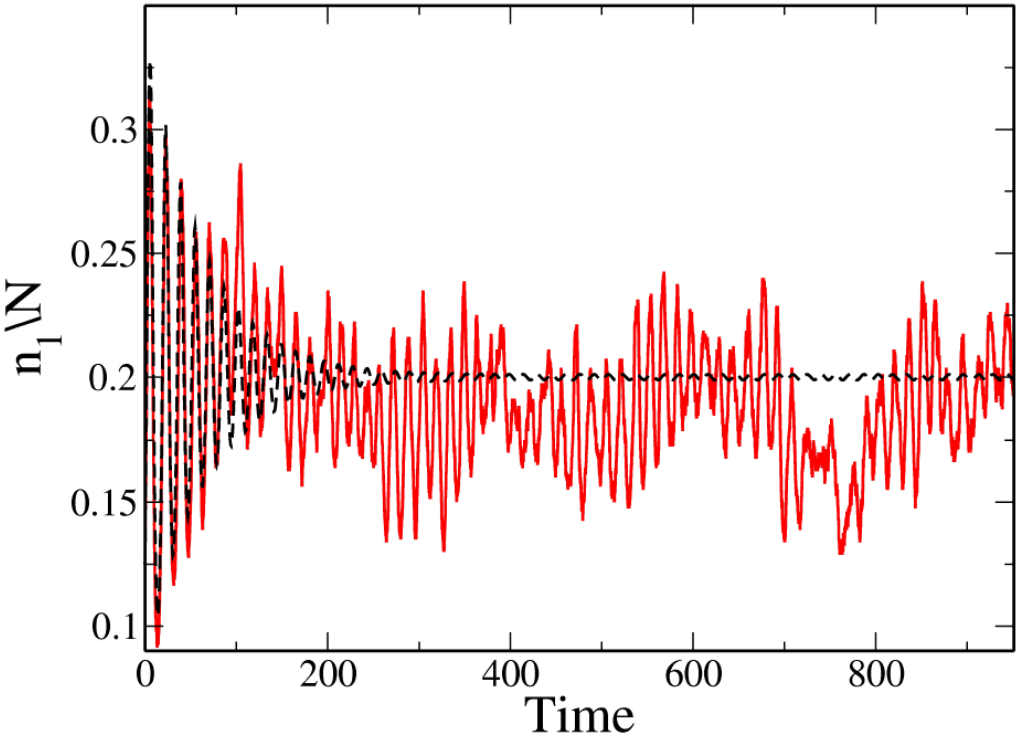
$$\frac{d\phi_i}{d\tau} = \left(r_i\phi_{i-1} - r_{i+1}\phi_{i+1}\right)\phi_i + \alpha_i\left(1 - \sum_{j=1}^{k}\phi_j\right) - \beta_i\phi_i$$

If $\alpha_i = \alpha$, $\beta_i = \beta$ and $r_i = r$ for all $i = 1, \ldots k$

Equilibrium point

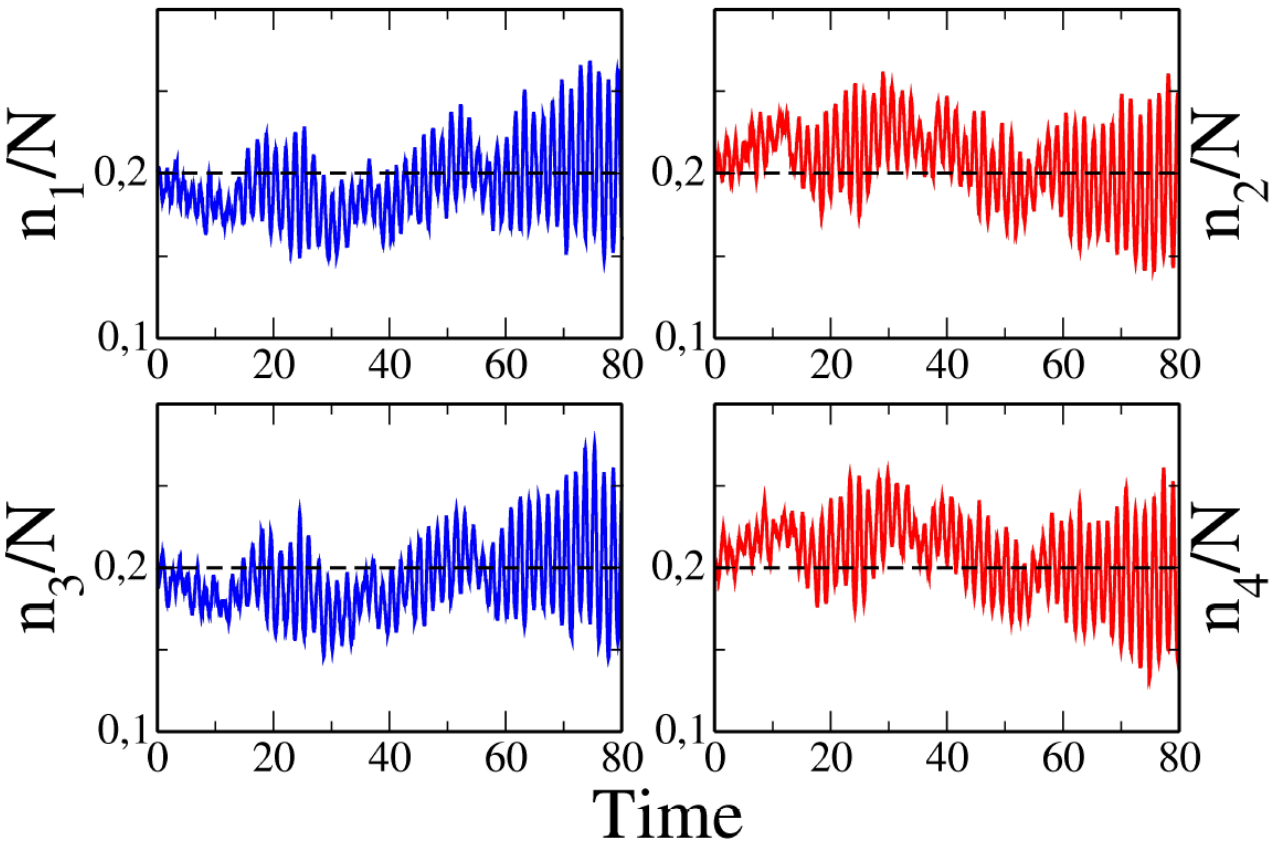
$$\phi^* = \frac{\alpha}{\beta + k\alpha}$$

Deterministic vs. stochastic simulations



The deterministic solution converges to a fixed point, while the stochastic solution displays self-sustained oscillations.

Deterministic vs. stochastic simulations



The next–to–leading order

Fokker Planck equation

$$\frac{\partial \Pi}{\partial \tau} = -\sum_i \frac{\partial}{\partial \xi_i}\left(A_i(\boldsymbol{\xi})\Pi\right) + \frac{1}{2}\sum_{ij} B_{ij}\frac{\partial^2 \Pi}{\partial \xi_i \partial \xi_j}$$

where

$$A_i(\boldsymbol{\xi}) = \sum_{j=1}^{k} M_{ij}\xi_j$$

and M and B are $k \times k$ matrices.

Equivalent formulation of the Fokker Planck equation

Langevin equations

$$\frac{d\xi_i}{d\tau} = \sum_{j=1}^{k} M_{ij}\xi_j(\tau) + \eta_i(\tau)$$

where η_i is a Gaussian white noise with zero mean and

$$\langle \eta_i(\tau)\eta_j(\tau')\rangle = B_{ij}\delta(\tau - \tau')$$

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Go to Fourier space

Power spectrum

$$\sum_{j=1}^{k} \left(-i\omega\delta_{ij} - M_{ij}\right) \tilde{\xi}_j(\omega) = \tilde{\eta}_i(\omega)$$

defining $\Phi_{ij}(\omega) = -i\omega\delta_{ij} - M_{ij}$

$$\tilde{\xi}_i(\omega) = \sum_{j=1}^{k} \Phi_{ij}^{-1}(\omega)\tilde{\eta}_j(\omega)$$

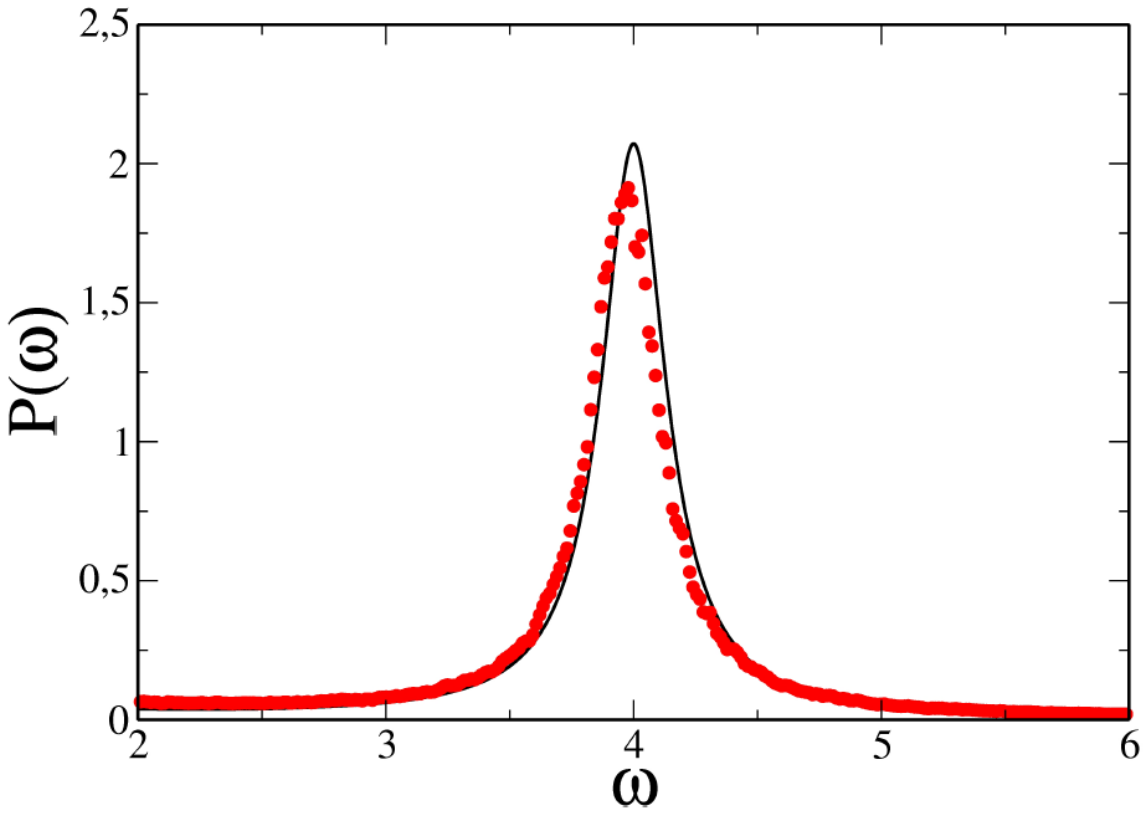
Power spectrum

$$P_i(\omega) = \sum_j \sum_k \Phi_{ij}^{-1}(\omega) B_{jk} (\Phi_{ij}^{\dagger})^{-1}(\omega)$$

Power spectrum for $k = 4$

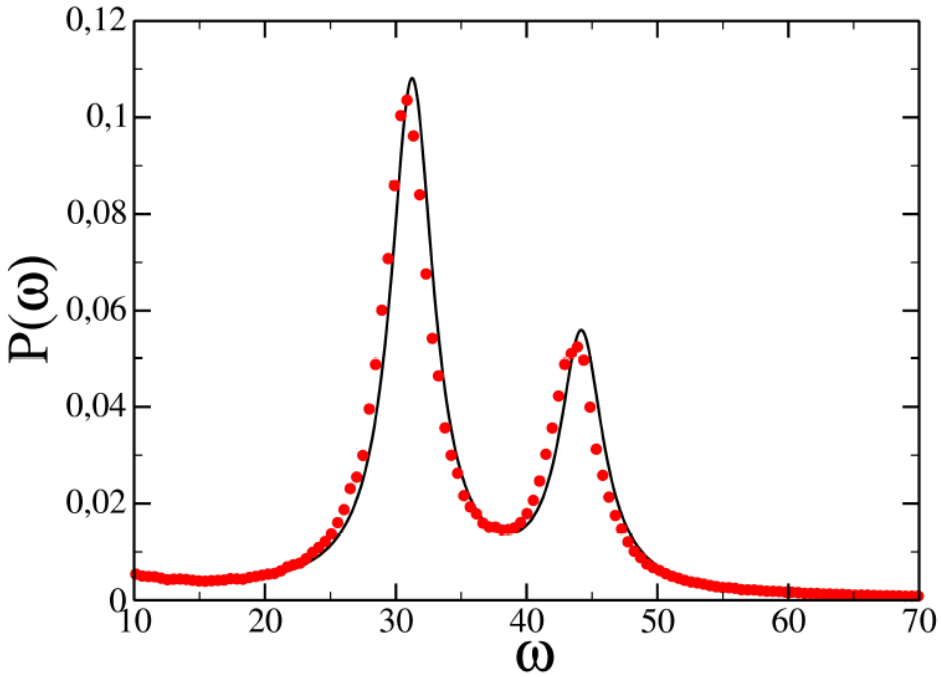
$$\lambda_0 = -\beta - 4\alpha \qquad \lambda_2 = -\beta$$
$$\lambda_1 = -\beta - 2ir\phi^* \qquad \lambda_3 = \lambda_1^*$$

$$\omega_c = \sqrt{4r^2\left(\phi^*\right)^2 - \beta^2} \simeq 4$$



Power spectrum for $k = 8$

$$\lambda_0 = -\beta - 8\alpha \qquad \lambda_4 = -\beta$$
$$\lambda_1 = -\beta - \sqrt{2} i r \phi^* \qquad \lambda_7 = \lambda_1^*$$
$$\lambda_2 = -\beta - 2 i r \phi^* \qquad \lambda_6 = \lambda_2^*$$
$$\lambda_3 = -\beta - \sqrt{2} i r \phi^* \qquad \lambda_5 = \lambda_3^*$$



$$\omega_{c1} = \sqrt{\frac{2r^2\alpha^2}{(\beta + 8\alpha)^2} - \beta^2} \simeq 31.2$$

$$\omega_{c2} = \sqrt{\frac{4r^2\alpha^2}{(\beta + 8\alpha)^2} - \beta^2} \simeq 44.1$$