Stochastic Turing Patterns of Trichomes in *Arabidopsis* Leaves

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Young researchers @DMI

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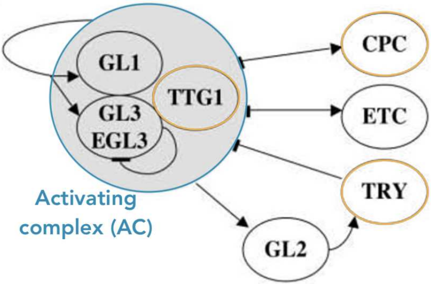
DIPARTIMENTO
DI MATEMATICA E INFORMATICA

Patterns in *Arabidopsis* leaves



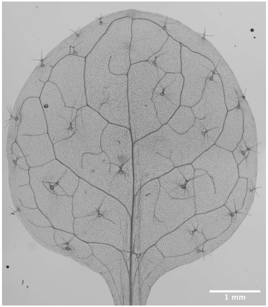
- *A. thaliana* is a popular model organism in plant biology and genetics.
- Trichomes are epidermal hairs in the aerial parts of plants that
  - provide a physical/chemical barrier against insect herbivores and UV light
  - reduce transpiration
  - increase tolerance to freezing

Commitment to trichome correlates with the accumulation of AC

Experimental data set

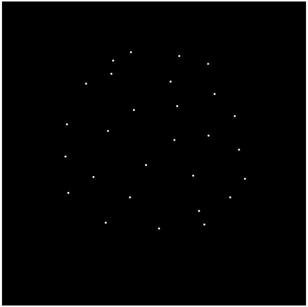
- 14-day old wild-type plant leaf
- 6 biological replicate – 250 leaves

Transmission light

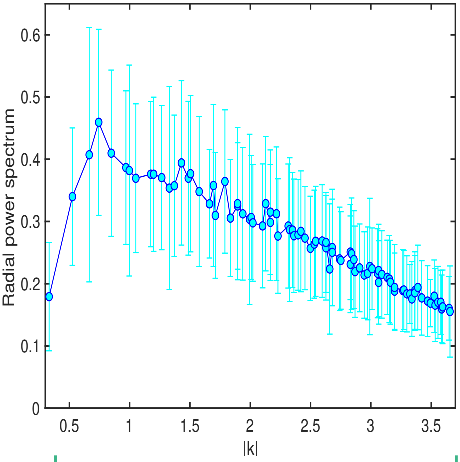


Cross polarizers

Positions of trichomes



Experimental power spectrum



$|\boldsymbol{k}| \simeq 0.3$
21 cells

$|\boldsymbol{k}| \simeq 3.5$
cell radius

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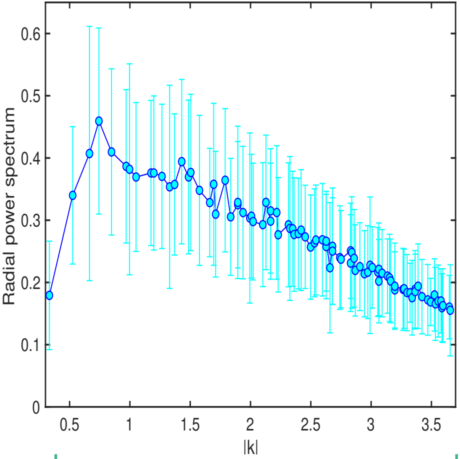

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How do patterns originate?

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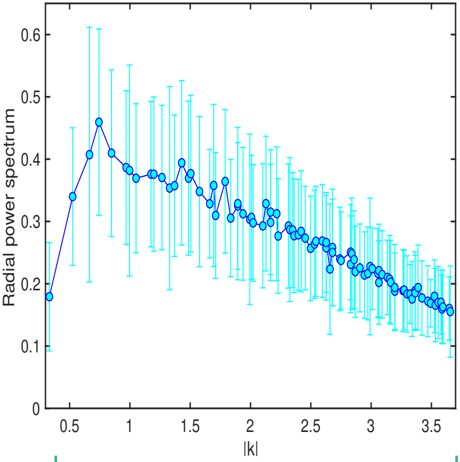

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How do patterns originate?

Deterministic patterns

- reaction-diffusion PDE
- Turing patterns: non-homogeneous perturbations of a stable steady state
- Turing patterns affected by random external noise

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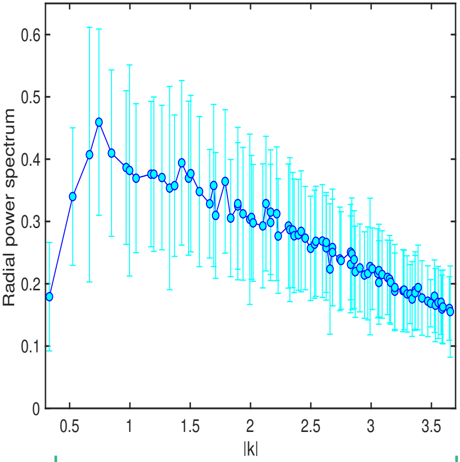

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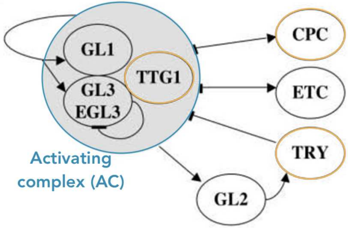
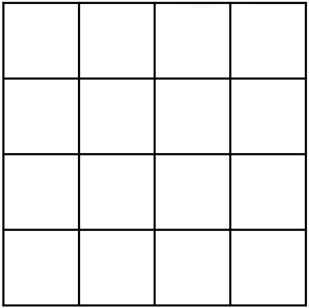
Stochastic Turing patterns

- Patterns induced by intrinsic noise

Deterministic model





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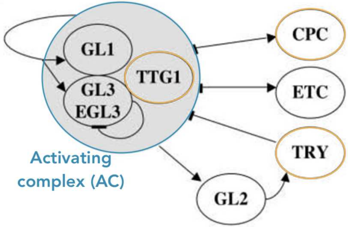
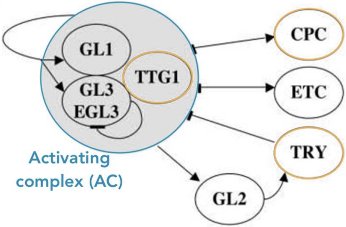
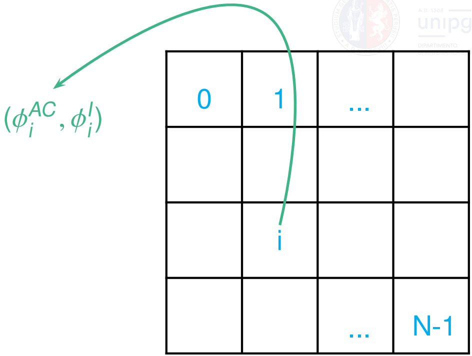


0	1	...	
		...	N-1

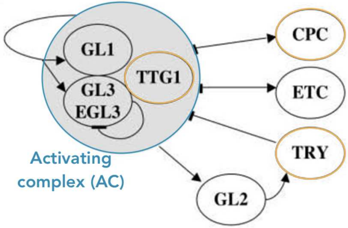
Deterministic model

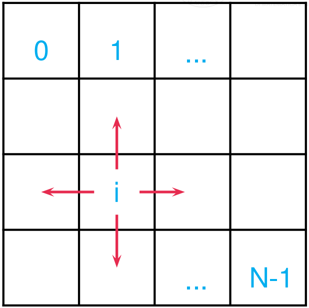




$$
\begin{cases}
\dfrac{d}{d\tau}\phi_i^{AC} = \alpha_{AC} + \beta_{AC}\dfrac{(\phi_i^{AC})^2}{\kappa + (\phi_i^{AC})^2} - \gamma\,\phi_i^{AC}\,\phi_i^{I} - \delta\,\phi_i^{AC} \\[2em]
\dfrac{d}{d\tau}\phi_i^{I} = \alpha_{I} + \beta_{I}\dfrac{(\phi_i^{AC})^2}{\kappa + (\phi_i^{AC})^2} - \gamma\,\phi_i^{AC}\,\phi_i^{I} - \delta\,\phi_i^{I}
\end{cases}
$$

Deterministic model





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\dfrac{d}{d\tau}\phi_i^{I} = \alpha_I + \beta_I \dfrac{(\phi_i^{AC})^2}{\kappa + (\phi_i^{AC})^2} - \gamma\, \phi_i^{AC}\, \phi_i^{I} - \delta\, \phi_i^{I} + \mu_I \sum_{j=0}^{N-1} \Delta_{ij}\phi_j^{I}
\end{cases}
$$

where $\Delta_{ij} = A_{ij} - k_i\delta_{ij}$ is the Laplacian matrix, A_{ij} the adjacency matrix.

Homogeneous stable equilibrium point

$$(\phi^*_{AC}, \phi^*_I)$$

Rescaling

$$\tilde{\phi}^{AC}_i = \frac{\phi^{AC}_i}{\phi^*_{AC}} \qquad \tilde{\phi}^I_i = \frac{\phi^I_i}{\phi^*_I} \qquad \tilde{\alpha}_{AC} = \frac{\alpha_{AC}}{\phi^*_{AC}\cdot\delta} \qquad \tilde{\alpha}_I = \frac{\alpha_I}{\phi^*_I\cdot\delta} \qquad \tilde{\mu}_{AC} = \frac{\mu_{AC}}{\delta} \qquad \tilde{\mu}_I = \frac{\mu_I}{\delta}$$

$$\tilde{\beta}_{AC} = \frac{\beta_{AC}}{\phi^*_{AC}\cdot\delta} \qquad \tilde{\beta}_I = \frac{\beta_I}{\phi^*_I\cdot\delta} \qquad \tilde{\gamma}_{AC} = \frac{\gamma\phi^*_I}{\delta} \qquad \tilde{\gamma}_I = \frac{\gamma\phi^*_{AC}}{\delta} \qquad \tilde{\kappa} = \frac{\kappa}{(\phi^*_{AC})^2} \qquad \tilde{\tau} = \tau\,\delta$$

$$\begin{cases} \dfrac{d}{d\tilde{\tau}}\tilde{\phi}^{AC}_i = & \tilde{\alpha}_{AC} + \tilde{\beta}_{AC}\dfrac{(\tilde{\phi}^{AC}_i)^2}{\tilde{\kappa} + (\tilde{\phi}^{AC}_i)^2} - \tilde{\gamma}_{AC}\,\tilde{\phi}^{AC}_i\,\tilde{\phi}^I_i - \tilde{\phi}^{AC}_i + \tilde{\mu}_{AC}\displaystyle\sum_{j=0}^{N-1}\Delta_{ij}\tilde{\phi}^{AC}_j \\ \dfrac{d}{d\tilde{\tau}}\tilde{\phi}^I_i = & \tilde{\alpha}_I + \tilde{\beta}_I\dfrac{(\tilde{\phi}^{AC}_i)^2}{\tilde{\kappa} + (\tilde{\phi}^{AC}_i)^2} - \tilde{\gamma}_I\,\tilde{\phi}^{AC}_i\,\tilde{\phi}^I_i - \tilde{\phi}^I_i + \tilde{\mu}_I\displaystyle\sum_{j=0}^{N-1}\Delta_{ij}\tilde{\phi}^I_j \end{cases}$$

Linear stability analysis (Turing 1952)

- Introduce small inhomogeneous perturbations $\delta\tilde{\phi}_i^{AC}$ and $\delta\tilde{\phi}_i^{I}$, to the uniform steady state as

$$(\tilde{\phi}_i^{AC}, \tilde{\phi}_i^{I}) = (\tilde{\phi}_{AC}^{*}, \tilde{\phi}_I^{*}) + (\delta\tilde{\phi}_i^{AC}, \delta\tilde{\phi}_i^{I})$$

- Perform a Taylor expansion of the system
- Expand the non–homogeneous perturbations $\delta\tilde{\phi}_i^{AC}$ and $\delta\tilde{\phi}_i^{I}$ as

$$\delta\tilde{\phi}_i^{AC} = \sum_{\alpha=0}^{N-1} a_\alpha e^{\lambda^{(\alpha)} t} v_i^{(\alpha)} \quad \delta\tilde{\phi}_i^{I} = \sum_{\alpha=0}^{N-1} b_\alpha e^{\lambda^{(\alpha)} t} v_i^{(\alpha)}$$

where a_α and b_α can be self-consistently calculated, while $\mathbf{\Delta v}^{(\alpha)} = \Lambda^{(\alpha)} \mathbf{v}^{(\alpha)}$ for $\alpha = 0, \ldots, N-1$.

Dispersion relation

$$\det\left(\mathbf{J} + \mathbf{D}\Lambda^{(\alpha)} - \lambda_\alpha \mathbb{I}_2\right) = 0$$

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- $\mathbf{J}$ is the Jacobian matrix
- $D = \begin{pmatrix} \tilde{\mu}_{AC} & 0 \\ 0 & \tilde{\mu}_I \end{pmatrix}$
- $\Lambda^{(\alpha)} \longleftrightarrow -|\mathbf{k}|^2$

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Imposed perturbations get magnified if $Re(\lambda) > 0$

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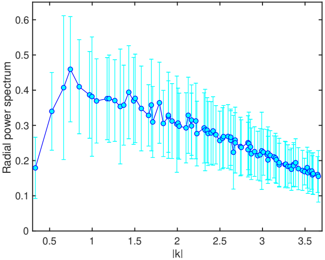
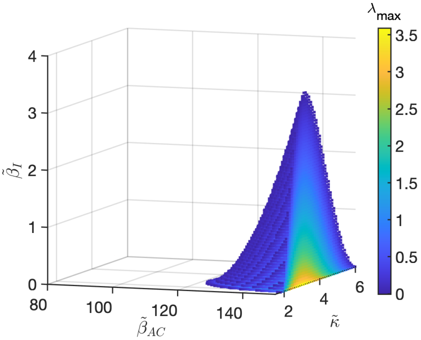
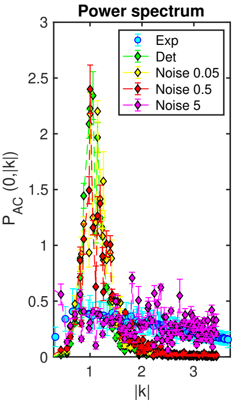
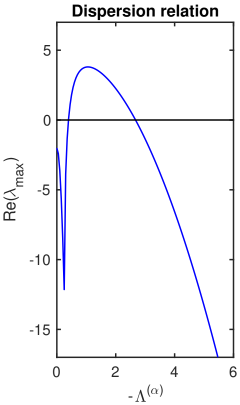
Deterministic Turing instability region









Stochastic model

V is the volume of individual cells

Reaction rules

$$\emptyset \xrightarrow{\tilde{\alpha}_{AC}+\tilde{\beta}_{AC}\frac{(n_i^{AC}/V)^2}{\tilde{\kappa}+(n_i^{AC}/V)^2}} AC_i$$

$$\emptyset \xrightarrow{\tilde{\alpha}_{I}+\tilde{\beta}_{I}\frac{(n_i^{AC}/V)^2}{\tilde{\kappa}+(n_i^{AC}/V)^2}} I_i$$

$$AC_i \xrightarrow{1+\tilde{\gamma}_{AC}\frac{n_i^I}{V}} \emptyset$$

$$I_i \xrightarrow{1+\tilde{\gamma}_{I}\frac{n_i^{AC}}{V}} \emptyset$$

Diffusion rules

$$AC_i \xrightarrow{\tilde{\mu}_{AC}} AC_j$$

$$I_i \xrightarrow{\tilde{\mu}_{I}} I_j$$

Transition rates

$$\mathbb{T}_1(n_i^{AC}+1|n_i^{AC}) = \tilde{\alpha}_{AC}+\tilde{\beta}_{AC}\frac{(n_i^{AC}/V)^2}{\tilde{\kappa}+(n_i^{AC}/V)^2}$$

$$\mathbb{T}_2(n_i^{I}+1|n_i^{I}) = \tilde{\alpha}_{I}+\tilde{\beta}_{I}\frac{(n_i^{AC}/V)^2}{\tilde{\kappa}+(n_i^{AC}/V)^2}$$

$$\mathbb{T}_3(n_i^{AC}-1|n_i^{AC}) = \left(1+\tilde{\gamma}_{AC}\frac{n_i^I}{V}\right)\frac{n_i^{AC}}{V}$$

$$\mathbb{T}_4(n_i^{I}-1|n_i^{I}) = \left(1+\tilde{\gamma}_{I}\frac{n_i^{AC}}{V}\right)\frac{n_i^{I}}{V}$$

$$\mathbb{T}_5(n_i^{AC}-1, n_j^{AC}+1|n_i^{AC}, n_j^{AC}) = \tilde{\mu}_{AC}\frac{n_i^{AC}}{V}$$

$$\mathbb{T}_6(n_i^{I}-1, n_j^{I}+1|n_i^{I}, n_j^{I}) = \tilde{\mu}_{I}\frac{n_i^{I}}{V}$$

Master equation

State of the system

$$(\mathbf{n}^{AC}, \mathbf{n}^{I}) \qquad \text{with} \qquad \begin{array}{l} \mathbf{n}^{AC} = (n_0^{AC}, \ldots, n_{N-1}^{AC}) \\ \mathbf{n}^{I} = (n_0^{I}, \ldots, I_{N-1}) \end{array}$$

$$\begin{aligned} \frac{d}{dt} P(\mathbf{n}^{AC}, \mathbf{n}^{I}; t) = \sum_{i=0}^{N-1} \Big\{ & \left(\epsilon_{AC,i}^{-} - 1\right) \mathbb{T}_1(n_i^{AC} + 1 | n_i^{AC}) + \left(\epsilon_{I,i}^{-} - 1\right) \mathbb{T}_2(n_i^{I} + 1 | n_i^{I}) \\ & + \left(\epsilon_{AC,i}^{+} - 1\right) \mathbb{T}_3(n_i^{AC} - 1 | n_i^{AC}) + \left(\epsilon_{I,i}^{+} - 1\right) \mathbb{T}_4(n_i^{I} - 1 | n_i^{I}) \\ & + \sum_{j=0}^{N-1} A_{ij} \Big[\left(\epsilon_{AC,i}^{+} \epsilon_{AC,j}^{+} - 1\right) \mathbb{T}_5(n_i^{AC} - 1, n_j^{AC} + 1 | n_i^{AC}, n_j^{AC}) \\ & + \left(\epsilon_{I,i}^{+} \epsilon_{I,j}^{+} - 1\right) \mathbb{T}_6(n_i^{I} - 1, n_j^{I} + 1 | n_i^{I}, n_j^{I}) \Big] \Big\} P(\mathbf{n}^{AC}, \mathbf{n}^{I}; t) \end{aligned}$$

Step operators

$$\begin{aligned} \epsilon_{AC,i}^{\pm} f(\mathbf{n}^{AC}, \mathbf{n}^{I}) &= f(\ldots, n_i^{AC} \pm 1, \ldots, \mathbf{n}^{I}) \\ \epsilon_{I,i}^{\pm} f(\mathbf{n}^{AC}, \mathbf{n}^{I}) &= f(\mathbf{n}^{AC}, \ldots, n_i^{I} \pm 1, \ldots) \quad . \end{aligned}$$

The van Kampen expansion

New variables

$$
\begin{aligned}
\frac{n_i^{AC}}{V} &= \tilde{\phi}_i^{AC} + \frac{1}{\sqrt{V}}\,\xi_{AC,i} \\
\frac{n_i^{I}}{V} &= \tilde{\phi}_i^{I} + \frac{1}{\sqrt{V}}\,\xi_{I,i}
\end{aligned}
$$

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Deterministic variables $\phi_i = \lim_{V\to\infty} \frac{\langle n_i \rangle}{V}$

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Stochastic variables (fluctuations)

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Stochastic variables (fluctuations)

New probability

$$P(\mathbf{n}^{AC}, \mathbf{n}^{I}; t) \to \Pi(\xi_{AC}, \xi_{I}; t)$$

The van Kampen expansion

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System–size expansion w.r.t. $1/\sqrt{V}$

- $\frac{d}{dt} P(\mathbf{n}^{AC}, \mathbf{n}^{I}; t) = \sum_{i=0}^{N-1} \left(\frac{\partial \Pi}{\partial t} - \frac{\partial \Pi}{\partial \xi_{AC,i}} \sqrt{V} \dot{\tilde{\phi}}_i^{AC} - \frac{\partial \Pi}{\partial \xi_{I,i}} \sqrt{V} \dot{\tilde{\phi}}_i^{I} \right)$
- $\epsilon_{X,i}^{\pm} \simeq 1 \pm \frac{1}{\sqrt{V}} \frac{\partial}{\partial_{\xi_{X,i}}} + \frac{1}{2V} \frac{\partial^2}{\partial_{\xi_{X,i}^2}}$ for $X = AC, I$

The leading order Order

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

Deterministic mean–field equations ($\lim V \to \infty$)

$$\begin{cases} \dfrac{d}{d\tilde{\tau}}\tilde{\phi}_i^{AC} & = \tilde{\alpha}_{AC} + \tilde{\beta}_{AC}\dfrac{(\tilde{\phi}_i^{AC})^2}{\tilde{\kappa} + (\tilde{\phi}_i^{AC})^2} - \tilde{\gamma}_{AC}\,\tilde{\phi}_i^{AC}\,\tilde{\phi}_i^{I} - \tilde{\phi}_i^{AC} + \tilde{\mu}_{AC}\displaystyle\sum_{j=0}^{N-1}\Delta_{ij}\tilde{\phi}_j^{AC} \\ \dfrac{d}{d\tilde{\tau}}\tilde{\phi}_i^{I} & = \tilde{\alpha}_{I} + \tilde{\beta}_{I}\dfrac{(\tilde{\phi}_i^{AC})^2}{\tilde{\kappa} + (\tilde{\phi}_i^{AC})^2} - \tilde{\gamma}_{I}\,\tilde{\phi}_i^{AC}\,\tilde{\phi}_i^{I} - \tilde{\phi}_i^{I} + \tilde{\mu}_{I}\displaystyle\sum_{j=0}^{N-1}\Delta_{ij}\tilde{\phi}_j^{I} \end{cases}$$

Next-to-leading order

Fokker-Planck equation

$$\frac{\partial}{\partial \tau}\Pi = \sum_{i=0}^{N-1}\Big(-\sum_{q=1}^{2} \frac{\partial}{\partial \xi_{q,i}}(A_{q,i}\Pi) + \frac{1}{2}\sum_{q,l=1}^{2}\sum_{j=0}^{N-1}(B_{ql,ij}\Pi)\Big)$$

with

$$A_{q,i} = \sum_{l=1}^{2}\sum_{j=0}^{N-1} M_{rl,ij}\xi_{s,j}$$

where the $2N \times 2N$ matrices **M** and **B** are given by

$$\begin{aligned} M_{ql,ij} &= M_{ql}^{(NS)}\delta_{ij} + M_{ql}^{(SP)}\Delta_{ij} \\ B_{ql,ij} &= B_{ql}^{(NS)}\delta_{ij} + B_{ql}^{(SP)}\Delta_{ij} \end{aligned}$$

and

$$\begin{aligned} q = 1 &\equiv AC \\ q = 2 &\equiv I \end{aligned}$$

$$\mathbf{M}^{(NS)} = \begin{pmatrix} \frac{2\tilde{\beta}_{AC}\tilde{\kappa}}{(\tilde{\kappa}+1)^2} - \tilde{\gamma}_{AC} - 1 & -\tilde{\gamma}_{AC} \\ \frac{2\tilde{\beta}_{I}\tilde{\kappa}}{(\tilde{\kappa}+1)^2} - \tilde{\gamma}_{I} & -\tilde{\gamma}_{I} - 1 \end{pmatrix} \qquad \mathbf{M}^{(SP)} = \begin{pmatrix} \tilde{\mu}_{AC} & 0 \\ 0 & \tilde{\mu}_{I} \end{pmatrix}$$

$$\mathbf{B}^{(NS)} = \mathbf{S} \cdot \begin{pmatrix} \tilde{\alpha}_{AC} + \frac{\tilde{\beta}_{AC}}{\tilde{\kappa}+1} & 0 & 0 & 0 \\ 0 & \tilde{\alpha}_{I} + \frac{\tilde{\beta}_{I}}{\tilde{\kappa}+1} & 0 & 0 \\ 0 & 0 & 1 + \tilde{\gamma}_{AC} & 0 \\ 0 & 0 & 0 & 1 + \tilde{\gamma}_{I} \end{pmatrix} \mathbf{S}^t$$

$$\mathbf{B}^{(SP)} = \begin{pmatrix} -2\tilde{\mu}_{AC} & 0 \\ 0 & -2\tilde{\mu}_{I} \end{pmatrix} \quad .$$

The matrix **S** is the stoichiometric matrix that reflects the local reaction rules and takes the form

$$\mathbf{S} = \begin{pmatrix} 1 & 0 & -1 & 0 \\ 0 & 1 & 0 & -1 \end{pmatrix}$$

Langevin equation

$$\frac{d\xi_{q,i}}{d\tau} = \sum_{l=1}^{2}\sum_{j=0}^{N-1} M_{ql,ij}\xi_{l,j} + \eta_{q,i}$$

where $\eta_{q,i}$ is a Gaussian white noise, with zero mean and correlator

$$\langle \eta_{q,i}(\tau)\eta_{l,j}(\tau^{'})\rangle = B_{ql,ij}\delta(\tau - \tau^{'})$$

Temporal and spatially-discrete Fourier transform

$$\hat{f}_{\alpha}(\omega) = \int_{0}^{+\infty} d\tau \sum_{j=0}^{N-1} f_j(\tau) v_j^{(\alpha)} e^{i\omega\tau}$$

Power spectrum

The application of the Fourier transform to the Langevin equation gives

$$\hat{\xi}_{q,\alpha} = \sum_{l=1}^{2} \mathbf{F}_{ql}^{-1} \hat{\eta}_{l,\alpha}$$

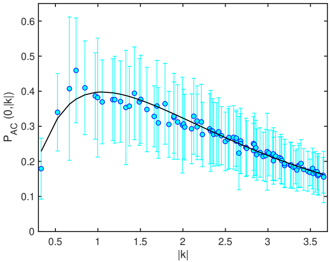
where $\mathbf{F} = (-i\omega\mathbb{I} - M^{(NS)} - M^{(SP)}\Lambda^{(\alpha)})$.

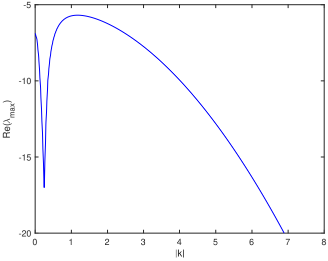
Power spectrum

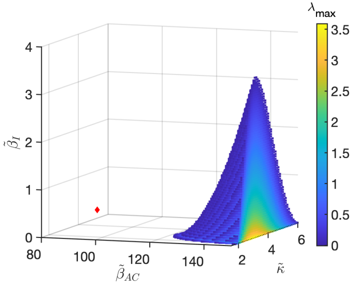
$$P_q(\omega, \Lambda^{(\alpha)}) = \langle|\hat{\xi}_{q,\alpha}(\omega)|^2\rangle = \sum_{l,m=1}^{2} \mathbf{F}_{ql}^{-1}(B_{lm}^{(NS)} + B_{lm}^{(SP)}\Lambda^{(\alpha)})(\mathbf{F}^{\dagger})_{mq}^{-1}$$

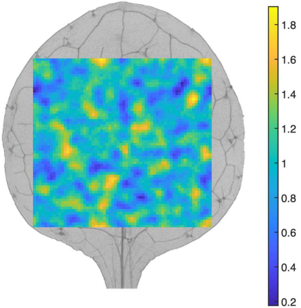
where the symbol $\dagger$ denotes the adjoint operator.

Experiment – theory – simulations









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Thanks for your attention!