Meta food webs

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Master stability functions reveal diffusion-driven pattern formation in networks

Brechtel et al. (2018)

alternatively: stability of the homogeneous state of meta food webs

2.Food webs

- generalized-model approach
- no explicit functional form of involved processes
- investigation of stability still possible

2.Food webs

For populations $X_1, \ldots, X_N$

$$\dot{X}_n = S_n(X_n) + \eta_n F_n(X_1, \ldots, X_N) - M_n(X_n) - \sum_{m=1}^{N} L_{m,n}(X_1, \ldots, X_N) \quad (1)$$

- $S_n(X_n)$: gain due to primary production
- $F_n(X_1, \ldots, X_N)$: gain due to predation
- η_n : biomass conversion efficiency
- $M_n(X_n)$: loss due to mortality
- $\sum_{m=1}^{N} L_{m,n}(X_1, \ldots, X_N)$: loss due to predation

2.Food webs

$L_{m,n}(X_1,\ldots,X_N)$ is related to $F_m(X_1,\ldots,X_N)$ via auxiliary variables

$$L_{m,n}(X_1,\ldots,X_N) = \underbrace{\frac{C_{m,n}(X_n)}{T_m(X_1,\ldots,X_N)}}_{\in[0,1]} F_m(T_m, X_m) \tag{2}$$

- $C_{m,n}(X_n)$: amount of species n that is available as prey to species m
- $T_m = \sum_{n=1}^{N} C_{m,n}(X_n)$: total amount of prey available to species m

Normalization of variables and functions to the steady state

$$x_n := \frac{X_n}{X_n^*} \Leftrightarrow X_n = X_n^* x_n$$

$$t_m := \frac{T_m(X_1^* x_1, \ldots, X_N^* x_N)}{T_m^*}$$

$$c_{m,n} := \frac{C_{m,n}(X_n^* x_n)}{C_{m,n}^*}$$

$$s_n(x_n) := \frac{S_n(X_n^* x_n)}{S_n^*}, \quad m_n(x_n) := \frac{M_n(X_n^* x_n)}{M_n^*}$$

$$f_n(x_1, \ldots, x_N) := \frac{F_n(X_1^* x_1, \ldots, X_N^* x_N)}{F_n^*}$$

$$l_{m,n}(x_1, \ldots, x_N) := \frac{L_{m,n}(X_1^* x_1, \ldots, X_N^* x_N)}{L_{m,n}^*}$$

insert in eq. (1)

$$\dot{x}_n = \frac{S_n^*}{X_n^*} s_n(x_n) + \eta_n \frac{F_n^*}{X_n^*} f_n(x_1, \ldots, x_N) - \frac{M_n^*}{X_n^*} m_n(x_n) - \sum_{m=1}^{N} \frac{L_{m,n}^*}{X_n^*} l_{m,n}(x_1, \ldots, x_N)$$

in the steady state $\dot{x}_n = 0$, $x_n = 1$, $s_n(1) = 1$, etc.

$$0 = \frac{S_n^*}{X_n^*} + \eta_n \frac{F_n^*}{X_n^*} - \frac{M_n^*}{X_n^*} - \sum_{m=1}^{N} \frac{L_{m,n}^*}{X_n^*}$$

2.Food webs

$$\Leftrightarrow \frac{S_n^*}{X_n^*} + \eta_n \frac{F_n^*}{X_n^*} = \frac{M_n^*}{X_n^*} + \sum_{m=1}^{N} \frac{L_{m,n}^*}{X_n^*} =: \alpha_n$$

- α_n: biomass flow rate in the steady state

Introducing further parameters describing the relative contributions

$$\rho_n := \frac{1}{\alpha_n} \eta_n \frac{F_n^*}{X_n^*}, \quad \tilde{\rho}_n := 1 - \rho_n = \frac{1}{\alpha_n} \frac{S_n^*}{X_n^*}$$

$$\sigma_n := \frac{1}{\alpha_n} \sum_{m=1}^{N} \frac{L_{m,n}^*}{X_n^*}, \quad \tilde{\sigma}_n := 1 - \sigma_n = \frac{1}{\alpha_n} \frac{M_n^*}{X_n^*}$$

$$\beta_{m,n} := \frac{1}{\alpha_n \sigma_n} \frac{L_{m,n}^*}{X_n^*} = \frac{\frac{L_{m,n}^*}{X_n^*}}{\sum_{m=1}^{N} \frac{L_{m,n}^*}{X_n^*}}$$

Eq. (1) with new parameters

$$\begin{aligned}\dot{x}_n =& \alpha_n \Bigg[\tilde{\rho}_n s_n(x_n) + \rho_n f_n(t_n, x_n) - \tilde{\sigma}_n m_n(x_n) \\ & - \sigma_n \sum_{m=1}^{N} \beta_{m,n} l_{m,n}(x_1, \dots, x_N) \Bigg]\end{aligned}$$

with

$$\begin{aligned} l_{m,n} =& \frac{c_{m,n}}{t_m} f_m(t_m, x_n) \\ t_m =& \sum_{n=1}^{N} \underbrace{\frac{C^*_{m,n}}{T^*_m}}_{=:\chi_{m,n}} c_{m,n} \end{aligned}$$

- so far: normalization and new parameters
- easy interpretation of parameters
- easy to choose based on experimental data
- example: $\alpha_1 = 1/80$, $\tilde{\rho}_1 = 1$, $\rho_1 = 0$, $\tilde{\sigma}_1 = 0.25$, $\sigma_1 = 0.75$ and $\beta_{2,1} = 0.5$
- normalized functions still there $\rightarrow$ new parameters

2.Food webs

exponent parameters/elasticities defined through derivatives in the Jacobian

$$\phi_n := \frac{\partial}{\partial x_n} s_n(x_n)\Big|_1$$

$$\mu_n := \frac{\partial}{\partial x_n} m_n(x_n)\Big|_1$$

$$\lambda_{m,n} := \frac{\partial}{\partial x_n} c_{m,n}(x_n)\Big|_1$$

$$\gamma_n := \frac{\partial}{\partial t_n} f_n(t_n, x_n)\Big|_1$$

$$\psi_n := \frac{\partial}{\partial x_n} f_n(t_n^*, x_n)\Big|_1$$

also easy interpretation

$$\phi_n := \frac{\partial}{\partial x_n} s_n(x_n)\bigg|_1 = \frac{\partial}{\partial \log X_n} \log S_n(X_n)\bigg|_{X^*} \tag{3}$$

- $S(X_n) = X_n^2 \rightarrow \phi_n = 2$
- in general measures the nonlinearity
- examples: $\phi_1 = 1$, $\phi_1 = 0$

$\rightarrow$ all functional relations are eliminated
$\rightarrow$ Jacobian/stability only depends on parameters

3.Diffusion-driven instabilities

- occur in diffusion-reaction systems
- Turing bifurcation destroys the homogeneous state → pattern formation
- continuum: periodic pattern, networks: differentiation of nodes

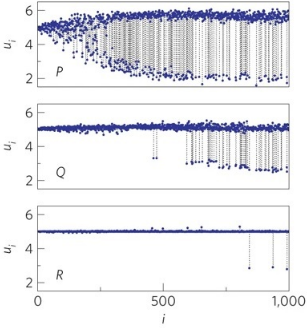


Figure: Turing patterns, Nakao & Mikhailov (2010)

3.Diffusion-driven instabilities

general diffusion-reaction system with N agents and M nodes

$$\dot{X}_{i,a} = R_a(\mathbf{X_i}) - \sum_j C_a L_{i,j} X_{j,a} \tag{4}$$

- $X_{i,a}$: concentration of agent a at node i
- $R_a(\mathbf{X_i})$: reactions occurring at the node, non-spatial network
- C_a : diffusion constant of a
- L_{ij} : Laplacian

3.Diffusion-driven instabilities

restructure the variables

$$X_{i,a} \;\rightarrow\; \mathbf{Y} = (X_{1,1}, \dots, X_{1,N}, X_{2,1}, \dots) \tag{5}$$

then the $NM \times NM$ Jacobian $\mathbf{J}$ is given by

$$J_{l,m} = \frac{\partial}{\partial Y_m} \dot{Y}_l \bigg|_{Y^*} \tag{6}$$

3.Diffusion-driven instabilities

non-spatial term:

$$\frac{\partial}{\partial X_{j,b}} R_a(X_i) = 0 \quad \forall i \neq j \tag{7}$$

$$\frac{\partial}{\partial X_{i,b}} R_a(X_i)\Bigg|_{Y^*} = P_{a,b} \tag{8}$$

- $\mathbf{P}$: $N \times N$ Jacobian of the non-spatial system
- all derivatives taken together: $\mathbf{E}_M \otimes \mathbf{P}_N$

3.Diffusion-driven instabilities

diffusion term:

$$\frac{\partial}{\partial X_{j,b}} \sum_j C_a L_{i,k} X_{k,a} \Big|_{Y*} = C_a L_{i,j} \frac{\partial X_{j,a}}{\partial X_{j,b}} = (\mathbf{L}_M \otimes \mathbf{C}_N)_{ia,jb} \tag{9}$$

- $\mathbf{C}_N$: matrix of the diffusion constants of each agent
- diagonal for simple diffusion
- off-diagonal elements for cross diffusion

3.Diffusion-driven instabilities

total Jacobian

$$\mathbf{J} = \mathbf{E}_M \otimes \mathbf{P}_N - \mathbf{L}_M \otimes \mathbf{C}_N \tag{10}$$

for a given Laplacian eigenvector with eigenvalue κ_n

$$\mathrm{Ev}(\mathbf{J}) = \bigcup_{n=1}^{M} \mathrm{Ev}(\mathbf{P} - \kappa_n \mathbf{C}) \tag{11}$$

stable if

$$\lambda = \mathrm{Ev}(\mathbf{P} - \kappa_n \mathbf{C}) < 0 \quad \forall n \tag{12}$$

4.Meta food webs

- combine previous chapters
- nodes $\rightarrow$ patches (upper indices), species (lower indices)

$$\dot{X}_a^i = z_a(\mathbf{X}^i) + \sum_j \left[E_a^{i,j}(\mathbf{X}^i, \mathbf{X}^j) - E_a^{j,i}(\mathbf{X}^i, \mathbf{X}^j) \right] \tag{13}$$

- $z_a(\mathbf{X}^i)$: food web interactions
- $E_a^{i,j}(\mathbf{X}^i)$: emigration of species a from patch j to patch i
- generalized approach as previously
- new sources of gain and loss $\rightarrow$ new parameters
- relative loss and gain due to migration

stability:
again

$$\mathbf{J} = \mathbf{E}_M \otimes \mathbf{P}_N - \mathbf{L}_M \otimes \mathbf{C}_N \tag{14}$$

with $\mathbf{C}_N$ determined by

$$\left.\frac{\partial \log E_a^{i,j}}{\partial \log X_a^i}\right|_{X^*} = C_{a,b} A^{i,j}$$

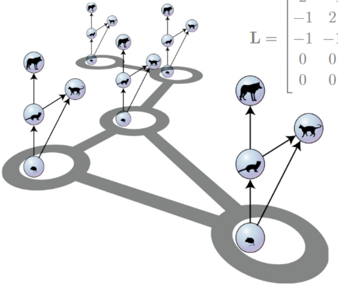
stable if

$$\underbrace{\mathrm{Re}(\lambda_{max}(\kappa_i))}_{=:S(\kappa)} < 0 \quad \forall i$$

$S(\kappa)$ is independent of the spatial network

5.Examples

simple example from Brechtel et al.

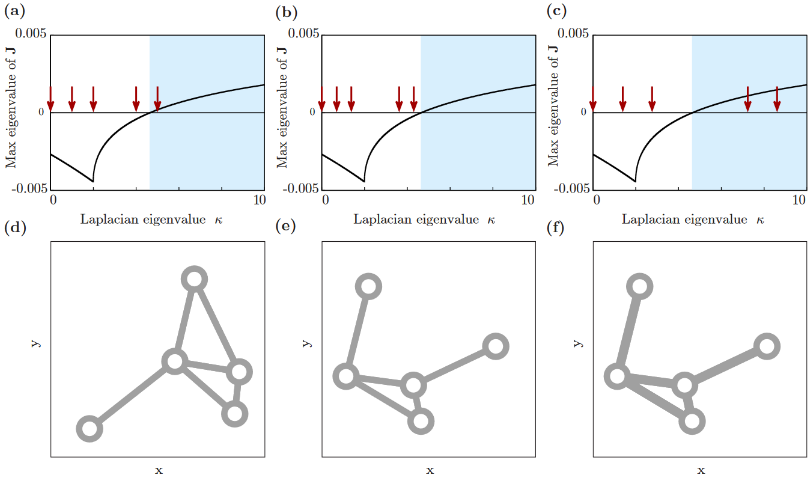


$$\mathbf{L} = \begin{bmatrix} 2 & -1 & -1 & 0 & 0 \\ -1 & 2 & -1 & 0 & 0 \\ -1 & -1 & 3 & -1 & 0 \\ 0 & 0 & -1 & 2 & -1 \\ 0 & 0 & 0 & -1 & 1 \end{bmatrix} \quad \mathbf{P} = \begin{bmatrix} P_{11} & P_{12} & P_{13} & 0 \\ P_{21} & P_{22} & P_{23} & P_{24} \\ P_{31} & P_{32} & P_{33} & 0 \\ 0 & P_{42} & 0 & P_{44} \end{bmatrix} \quad \mathbf{C} = \begin{bmatrix} C_{11} & 0 & 0 & 0 \\ 0 & C_{22} & 0 & 0 \\ 0 & 0 & C_{33} & 0 \\ 0 & 0 & 0 & C_{44} \end{bmatrix}$$

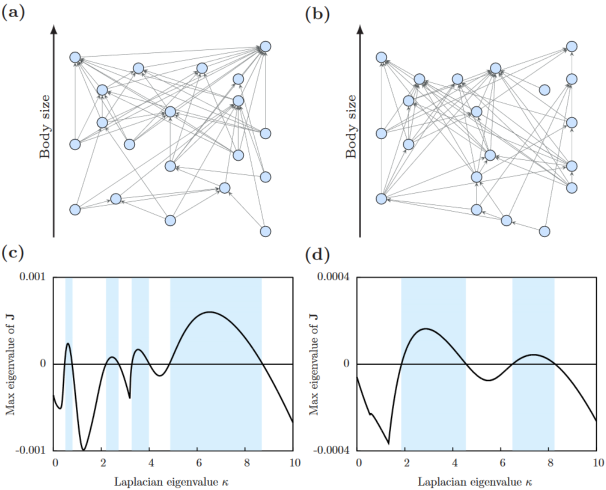
$$\mathbf{J} = \begin{bmatrix} \mathbf{P}-2\mathbf{C} & \mathbf{C} & \mathbf{C} & 0 & 0 \\ \mathbf{C} & \mathbf{P}-2\mathbf{C} & \mathbf{C} & 0 & 0 \\ \mathbf{C} & \mathbf{C} & \mathbf{P}-3\mathbf{C} & \mathbf{C} & 0 \\ 0 & 0 & \mathbf{C} & \mathbf{P}-2\mathbf{C} & \mathbf{C} \\ 0 & 0 & 0 & \mathbf{C} & \mathbf{P}-\mathbf{C} \end{bmatrix}$$

5.Examples

master stability function



complex 20-species food web



References and further reading

- Brechtel A, Gramlich P, Ritterskamp D, Drossel Barbara and Gross T, Master stability functions reveal diffusion-driven pattern formation in networks Phys. Rev. E **97** 032307 (2018)

Generalized model

- Gross T and Feudel U, Generalized models as a universal approach to the analysis of nonlinear dynamical systems Phys. Rev. E **73** 016205 (2006)

Turing patterns

- Nakao H and Mikhailov A, Turing patterns in network-organized activator-inhibitor systems Nature Phys **6** 544–550 (2010)