Dynamic on ecological networks

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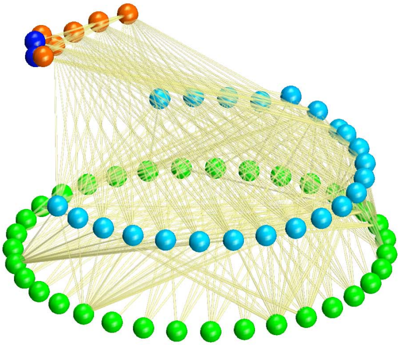
18-20 January 2015 - Mathematical and Computational Modelling in Life Sciences

Introduction

Ecological network



Nodes = species
Links = interactions

Adjacency matrix:

$$Y = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

Introduction

Types of interaction

Interaction strength matrix:

$$\boldsymbol{\beta} = \begin{bmatrix} \beta_{11} & \beta_{12} & \cdots & \beta_{1S} \\ \beta_{21} & \beta_{22} & & \vdots \\ \vdots & & \ddots & \vdots \\ \beta_{S1} & \cdots & \cdots & \beta_{1S} \end{bmatrix}$$

β_{ij} is the effect of species j on species i

if $Y_{ij} = 1$ then $\beta_{ij} \neq 0$ and/or $\beta_{ji} \neq 0$

(β_{ij}, β_{ji})	
(-,-)	competition
(+,+)	mutualism
(+,-) or (-,+)	antagonism
(+,0) or (0,+)	commensalism
(-,0) or (0,-)	amensalism

Introduction

Generalized Lotka-Volterra model

$$\frac{dN_i}{dt} = \alpha_i N_i + \sum_{j=1}^{S} \beta_{ij} N_j N_i = N_i \underbrace{\left(\alpha_i + \sum_{j=1}^{S} \beta_{ij} N_j\right)}_{\text{per capita growth of species } i}$$

N_i is the biomass/abundance of species i
α_i is the intrinsic per capita growth rate of species i
β_{ij} is the effect of species j on species i

In a matrix notation:

$$\frac{d\vec{N}}{dt} = diag(\vec{N})\left(\vec{\alpha} + \boldsymbol{\beta}\vec{N}\right)$$

Remark: if $\vec{N}(t = 0) > 0$, then $\vec{N}(T) \geq 0$ for all $T > 0$

Introduction

Example: one species

$$\frac{dN}{dt} = N(\alpha + \beta N)$$

4 cases:

1. $\alpha > 0$, $\beta > 0$
2. $\alpha < 0$, $\beta > 0$
3. $\alpha > 0$, $\beta < 0$
4. $\alpha < 0$, $\beta < 0$

Introduction

Example: one species

Case $\alpha > 0$ and $\beta < 0$

$$\frac{dN}{dt} = \underbrace{N(\alpha + \beta N)}_{:=f(N)}$$

Feasibility: solve the equation $\alpha + \beta N$ under the constraint $N > 0$

$\Rightarrow N^* = -\frac{\alpha}{\beta} > 0$

Stability (local): linearise the ODE around N^*. Set $n = N - N^*$,

$$\frac{dn}{dt} \approx f(N^*) + \frac{df}{dN}|_{N \to N^*} \cdot n = \underbrace{N^* \beta}_{<0} \cdot n$$

Introduction

Example: two competing species

$$\frac{dN_1}{dt} = N_1 \left(\alpha_1 + \beta_{11} N_1 + \beta_{12} N_2\right)$$
$$\frac{dN_2}{dt} = N_2 \left(\alpha_2 + \beta_{21} N_1 + \beta_{22} N_2\right)$$

with $\alpha_1, \alpha_2 > 0$ and $\beta_{11}, \beta_{12}, \beta_{21}, \beta_{22} < 0$

Feasibility: solve the following linear equations

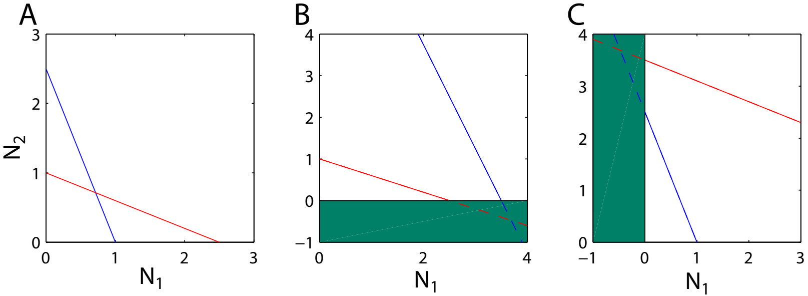
$$\alpha_1 = -\beta_{11} N_1 - \beta_{12} N_2$$
$$\alpha_2 = -\beta_{21} N_1 - \beta_{22} N_2$$

under the constraints $N_1 > 0$ and $N_2 > 0$.
(in matrix notation $\vec{\alpha} = -\boldsymbol{\beta} \vec{N}$)

Introduction

Two competing species: feasibility

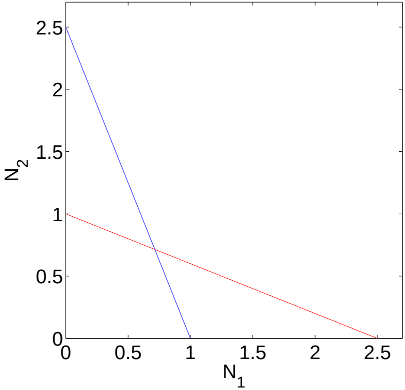
$$\alpha_1 = -\beta_{11} N_1 - \beta_{12} N_2 \text{ and } \alpha_2 = -\beta_{21} N_1 - \beta_{22} N_2$$



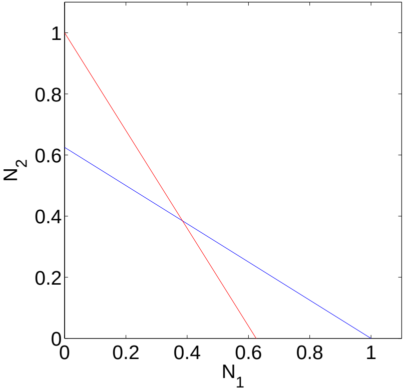
$$N_1^* = \frac{-\beta_{22}\alpha_1 + \beta_{12}\alpha_2}{\beta_{11}\beta_{22} - \beta_{12}\beta_{21}} \text{ and } N_2^* = \frac{-\beta_{11}\alpha_2 + \beta_{21}\alpha_1}{\beta_{11}\beta_{22} - \beta_{12}\beta_{21}}$$

Introduction

Two competing species: local stability



$$\vec{\alpha} = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \boldsymbol{\beta} = \begin{bmatrix} -1 & -0.4 \\ -0.4 & -1 \end{bmatrix}$$



$$\vec{\alpha} = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \boldsymbol{\beta} = \begin{bmatrix} -1 & -1.6 \\ -1.6 & -1 \end{bmatrix}$$

Introduction

Two competing species: local stability

$$\frac{dN_1}{dt} = \underbrace{N_1\left(\alpha_1 + \beta_{11}N_1 + \beta_{12}N_2\right)}_{=f_1(N_1,N_2)}$$

$$\frac{dN_2}{dt} = \underbrace{N_2\left(\alpha_2 + \beta_{21}N_1 + \beta_{22}N_2\right)}_{=f_1(N_1,N_2)}$$

Let's assume a feasible equilibrium ($N_1^* > 0, N_2^* > 0$), and let's linearise around it ($n_1 = N_1 - N_1^*, n_2 = N_2 - N_2^*$).

$$\frac{dn_1}{dt} \approx f_1(N_1^*, N_2^*) + \frac{\partial f_1}{\partial N_1}|_{(N_1,N_2)\to(N_1^*,N_2^*)} n_1 + \frac{\partial f_1}{\partial N_2}|_{(N_1,N_2)\to(N_1^*,N_2^*)} n_2$$

$$\frac{dn_2}{dt} \approx f_2(N_1^*, N_2^*) + \frac{\partial f_2}{\partial N_1}|_{(N_1,N_2)\to(N_1^*,N_2^*)} n_1 + \frac{\partial f_2}{\partial N_2}|_{(N_1,N_2)\to(N_1^*,N_2^*)} n_2$$

$$\frac{dn_1}{dt} \approx N_1^* \beta_{11} n_1 + N_1^* \beta_{12} n_2$$
$$\frac{dn_2}{dt} \approx N_2^* \beta_{21} n_1 + N_2^* \beta_{22} n_2$$

In matrix format

$$\frac{d\vec{n}}{dt} \approx \underbrace{diag(\vec{N}^*)\boldsymbol{\beta}}_{\boldsymbol{J} \text{ (Jacobian)}} \vec{n}$$

$\vec{N}^*$ is locally stable if the real parts of all the eigenvalues of $\boldsymbol{J}$ are negative.
Here, this is equivalent to $\det(\boldsymbol{\beta}) = \beta_{11}\beta_{22} - \beta_{12}\beta_{21} > 0$

Introduction

Two competing species

$$\frac{dN_1}{dt} = N_1\left(\alpha_1 + \beta_{11}N_1 + \beta_{12}N_2\right)$$
$$\frac{dN_2}{dt} = N_2\left(\alpha_2 + \beta_{21}N_1 + \beta_{22}N_2\right)$$

Local stability (assuming feasibility):

$$\det(\boldsymbol{\beta}) = \beta_{11}\beta_{22} - \beta_{12}\beta_{21} > 0$$

Note that this condition is independent of α_1 and α_2.

Feasibility:

$$N_1^* = \frac{-\beta_{22}\alpha_1+\beta_{12}\alpha_2}{\beta_{11}\beta_{22}-\beta_{12}\beta_{21}} \text{ and } N_2^* = \frac{-\beta_{11}\alpha_2+\beta_{21}\alpha_1}{\beta_{11}\beta_{22}-\beta_{12}\beta_{21}}$$

Introduction

Generalized Lotka-Volterra model

$$\frac{d\vec{N}}{dt} = diag(\vec{N}) \quad \underbrace{\left(\vec{\alpha} + \boldsymbol{\beta}\vec{N}\right)}_{\text{per capita growth rates}}$$

$\vec{\alpha}$ is the vector of intrinsic growth rates
$\boldsymbol{\beta}$ is the matrix of interaction strength

Question: under which conditions on $\vec{\alpha}$ and $\boldsymbol{\beta}$ their exist a feasible and stable equilibrium point $\vec{N}^*$.

Note that a feasible equilibrium is the solution of the linear equation $\vec{\alpha} = -\boldsymbol{\beta}\vec{N}^*$.

Stability

Jacobian of the Lotka-Volterra model

$$\frac{dN_i}{dt} = \underbrace{N_i \left(\alpha_i + \sum_{j=1}^{S} \beta_{ij} N_j \right)}_{f_i(\vec{N})}$$

Elements of the Jacobian matrix: $J_{ij} = \frac{\partial f_i}{\partial N_j}$ We obtain:

$$J_{ii} = \alpha_i + \sum_{j=1}^{S} \beta_{ij} N_j + N_i \beta_{ii}$$

and

$$J_{ij} = N_i \beta_{ij}$$

Stability

Jacobian of the Lotka-Volterra model

$$J = \begin{bmatrix} \alpha_1 + \sum_{j=1}^{S} \beta_{1j} N_j + N_1 \beta_{11} & N_1 \beta_{12} & \cdots \\ N_2 \beta_{21} & \alpha_2 + \sum_{j=1}^{S} \beta_{2j} N_j + N_2 \beta_{22} & \cdots \\ \vdots & \vdots & \ddots \end{bmatrix}$$

Evaluated at a feasible equilibrium $\vec{N}^* > 0$:

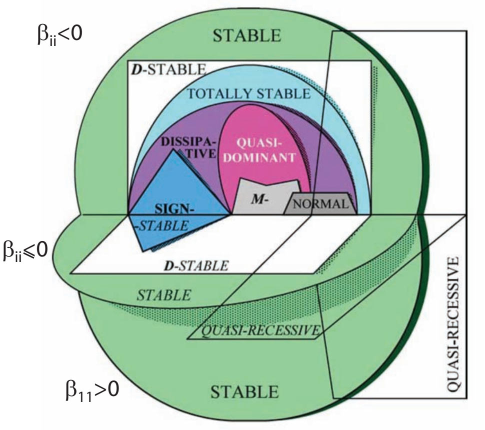
$$J = \begin{bmatrix} N_1^* \beta_{11} & N_1^* \beta_{12} & \cdots \\ N_2^* \beta_{21} & N_2^* \beta_{22} & \cdots \\ \vdots & \vdots & \ddots \end{bmatrix}$$

In matrix notation

$$J = diag(\vec{N}^*) \beta$$

Stability

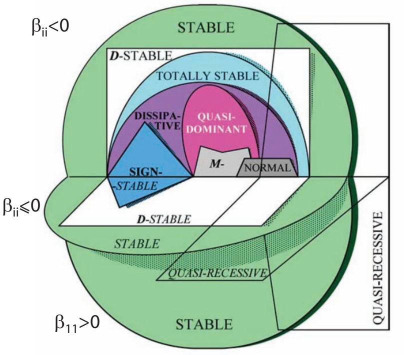
Class of matrix stability



Dimitrii O. Logofet (2005), *Stronger-than-Lyapunov notions of matrix stability, or how "flowers" help solve problems in mathematical ecology*, Linear Algebra and its Applications, 398:75-100.

Stability

Class of matrix stability



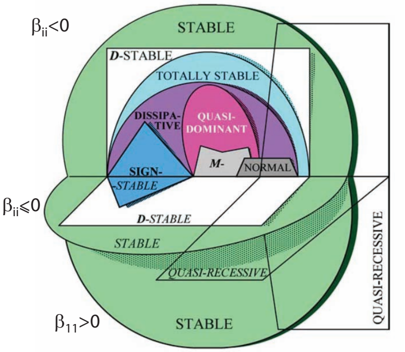
Class of stable matrix

A matrix is called stable if the real parts of all its eigenvalues are negative $(\mathrm{Re}(\lambda_i) < 0)$

$\Rightarrow$ If an interaction matrix $\boldsymbol{\beta}$ is stable, we have local stability of a feasible equilibrium such that: $N_1^* = N_2^* = \cdots = N_S^*$.

Stability

Class of matrix stability



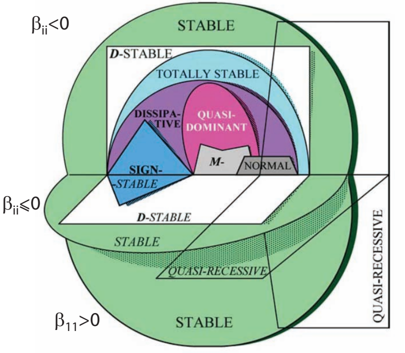
Class of D-stable matrix

A matrix $\boldsymbol{A}$ is called D-Stable if the matrix $\boldsymbol{DA}$ is stable for any positive diagonal matrix $\boldsymbol{D}$.

$\Rightarrow$ If an interaction matrix $\boldsymbol{\beta}$ is D-stable, we have local stability of any feasible equilibrium (recall that $\boldsymbol{J} = diag(\vec{N}^*)\boldsymbol{\beta}$)

Stability

Class of matrix stability



Class of dissipative matrix

A matrix $\boldsymbol{A}$ is called dissipative if their exist a positive diagonal matrix $\boldsymbol{D}$ such that $\boldsymbol{D}\boldsymbol{A} + \boldsymbol{A}^T\boldsymbol{D}$ is stable.

$\Rightarrow$ If an interaction matrix $\boldsymbol{\beta}$ is dissipative, we have global stability of any feasible equilibrium

Stability

Dissipative matrix and Lyapunov function

Let's assume the existence of a feasible equilibrium $\vec{N}^*$. Then if the interaction matrix $\boldsymbol{\beta}$ is dissipative, $\vec{N}^*$ is globally stable.
The proofs is based on the following Lyapunov function:

$$V(\vec{N}) = \sum_{i=1}^{S} d_i (N_i - N_i^* - N_i^* \log \frac{N_i}{N_i^*}),$$

where $diag(\vec{d})\boldsymbol{\beta} + \boldsymbol{\beta}^T diag(\vec{d})$ is stable.
We obtain

$$\frac{dV}{dt} = \sum_{i,j=1}^{S} (N_i - N_i^*) d_i \beta_{ij} (N_j - N_j^*) < 0$$

Stability

Two competing species

Let $\boldsymbol{D} = \begin{bmatrix} -1/\beta_{12} & 0 \\ 0 & -1/\beta_{21} \end{bmatrix}$ be a positive diagonal matrix. We obtain

$$\boldsymbol{D\beta} = \begin{bmatrix} -1/\beta_{12} & 0 \\ 0 & -1/\beta_{21} \end{bmatrix} \begin{bmatrix} \beta_{11} & \beta_{12} \\ \beta_{21} & \beta_{22} \end{bmatrix} = \begin{bmatrix} -\beta_{11}/\beta_{12} & -1 \\ -1 & -\beta_{22}/\beta_{21} \end{bmatrix}.$$

Therefore $\det(\boldsymbol{D\beta} + \boldsymbol{\beta}^T\boldsymbol{D}) > 0$ if and only if $\det(\boldsymbol{\beta}) > 0$. Moreover, $\mathit{Trace}(\boldsymbol{D\beta}) < 0$. Then local stability implies global stability.

In general we have

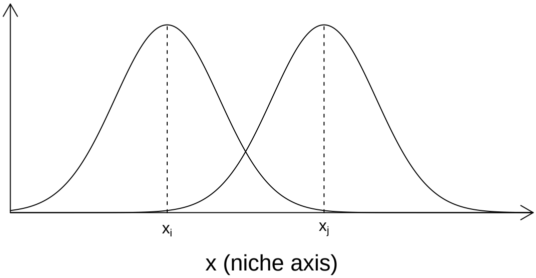
$$\boxed{\text{Dissipative}} \Rightarrow \boxed{\text{D-stable}} \Rightarrow \boxed{\text{Stable}}$$

For some class of matrices we have $\boxed{\text{Stable}} \Rightarrow \boxed{\text{Dissipative}}$.

1. Symmetric matrices.
2. Matrices of the form: $\boldsymbol{A} = \begin{bmatrix} a_{11} & a_{12} & \cdots \\ a_{21} & a_{22} & \cdots \\ \vdots & \vdots & \ddots \end{bmatrix}$, with $a_{ii} < 0$ and $a_{ij} \geq 0$.

Stability

Examples of dissipative matrix: niche overlap



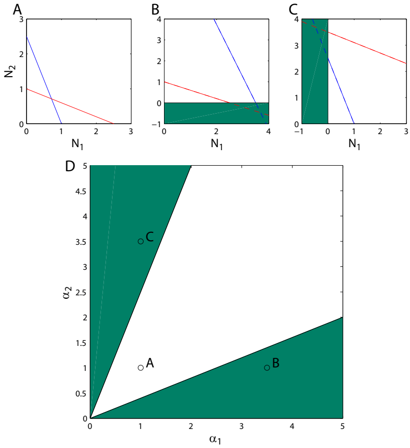
$$f_i(x) = e^{-(x_i - x)^2/\sigma^2}$$

Niche overlap:

$$\beta_{ij} = -\int_{-\infty}^{\infty} f_i(x) f_j(x) dx = -\sqrt{\pi} e^{-(x_i - x_j)^2/2\sigma^2}$$

Feasibility

Two competing species



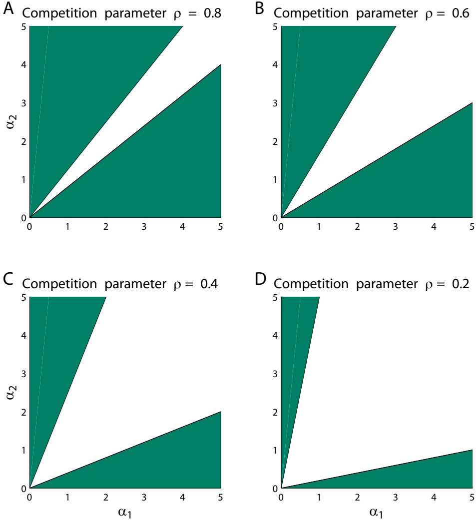
$$\boldsymbol{\beta} = \begin{bmatrix} -1 & -0.4 \\ -0.4 & -1 \end{bmatrix}$$

The feasible equilibrium is given by
$N_1^* = (\alpha_1 - 0.4\alpha_2)/0.84$
$N_2^* = (\alpha_2 - 0.4\alpha_1)/0.84$

Let's compute the set of α_1 and α_2 compatible with feasibility:
$\alpha_1 = N_1 + 0.4N_2$
$\alpha_2 = 0.4N_2 + N_1$
with $N_1 > 0$ and $N_2 > 0$

Feasibility

Two competing species



$$\beta = \begin{bmatrix} -1 & -\rho \\ -\rho & -1 \end{bmatrix}$$

Let's compute the set of α_1 and α_2 compatible with feasibility:

$\alpha_1 = N_1 + \rho N_2$

$\alpha_2 = \rho N_2 + N_1$

with $N_1 > 0$ and $N_2 > 0$

Feasibility

Generalized Lotka-Volterra model

$$\frac{d\vec{N}}{dt} = diag(\vec{N})(\vec{\alpha} + \boldsymbol{\beta}\vec{N})$$

The equilibrium is called feasible if the solution $\vec{N}^*$ of

$$\vec{\alpha} = -\boldsymbol{\beta}\vec{N}^*$$

is positive. Let's change our point of view, and let's compute the set of $\vec{\alpha}$ compatible with a positive solution $\vec{N}^*$.

$$\boldsymbol{\beta} = \begin{bmatrix} \beta_{11} & \beta_{12} & \cdots & \beta_{1S} \\ \beta_{21} & \beta_{22} & & \beta_{2S} \\ \vdots & & \ddots & \vdots \\ \beta_{S1} & \beta_{S2} & \cdots & \beta_{1S} \end{bmatrix} = \begin{bmatrix} \vdots & \vdots & & \vdots \\ -\vec{v}_1 & -\vec{v}_2 & \cdots & -\vec{v}_S \\ \vdots & \vdots & & \vdots \end{bmatrix}$$

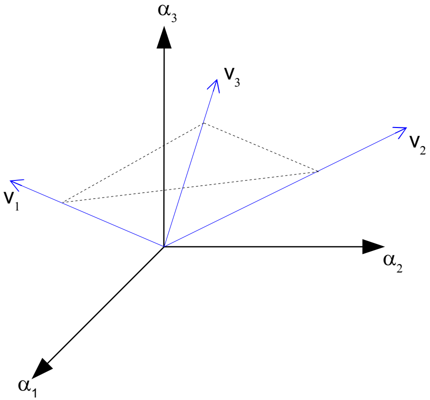
Then

$$\vec{\alpha} = N_1\vec{v}_1 + N_2\vec{v}_2 + \cdots + N_S\vec{v}_S$$

with $N_1, N_2, \cdots, N_S > 0$.

Feasibility

Generalized Lotka-Volterra model



$$\boldsymbol{\beta} = \begin{bmatrix} \beta_{11} & \beta_{12} & \cdots & \beta_{1S} \\ \beta_{21} & \beta_{22} & & \beta_{2S} \\ \vdots & & \ddots & \vdots \\ \beta_{S1} & \beta_{S2} & \cdots & \beta_{1S} \end{bmatrix}$$

$$= \begin{bmatrix} \vdots & \vdots & & \vdots \\ -\vec{v}_1 & -\vec{v}_2 & \cdots & -\vec{v}_S \\ \vdots & \vdots & & \vdots \end{bmatrix}$$

Remark: we can always chose the $\vec{\alpha}$, such that $\vec{N}^{*} = -\beta^{-1}\vec{\alpha}$ is feasible.

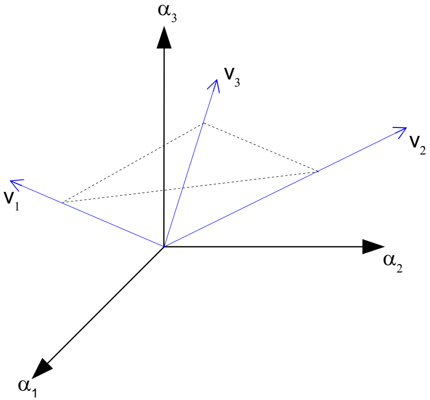
Conclusion: the relevant question is how easy it is to have a feasible solution, i.e., how width is the cone of feasibility?

In mathematics this is called structural stability: how the behaviour of a dynamical system is function of its parameters, and how large is the domain in the parameter space compatible with a given behaviour.

In ecology, an important behaviour is: the stable coexistence of all species.

Feasibility

Competition system



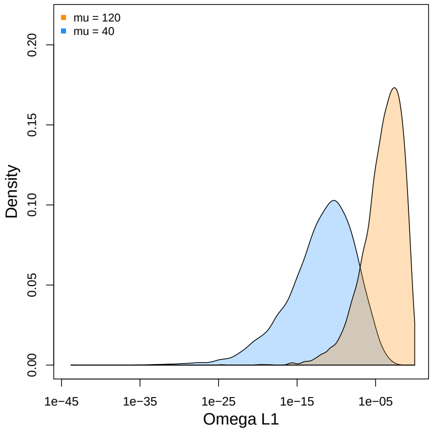
For a competition system ($\beta_{ij} \leq 0$) we have an analytic formula. Solid angle:

$$\Omega_{L_1} = \frac{|\det(\beta)|}{\prod_j \sum_i |\beta_{ij}|}$$

Yuri M. Svirezhev and Dimitrii O. Logofet (1982), *Stability of Biological Communities*, Mir Publishers, Moscow, Russia.

Feasibility

Competition system

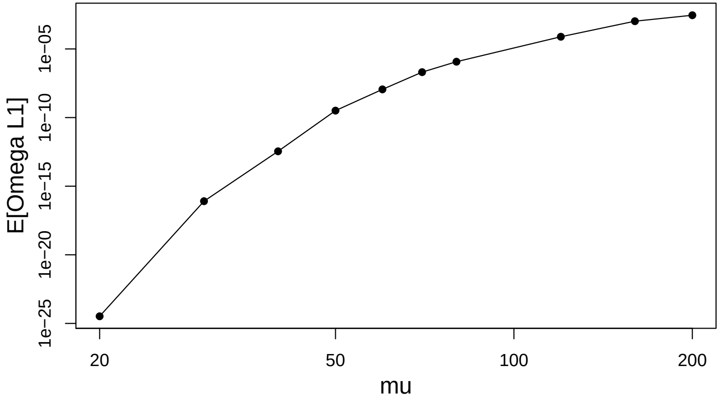


$$x_i \backsim Unif(0, \cdots, \mu)$$

$$\beta_{ij} = -e^{-(x_i - x_j)^2}$$

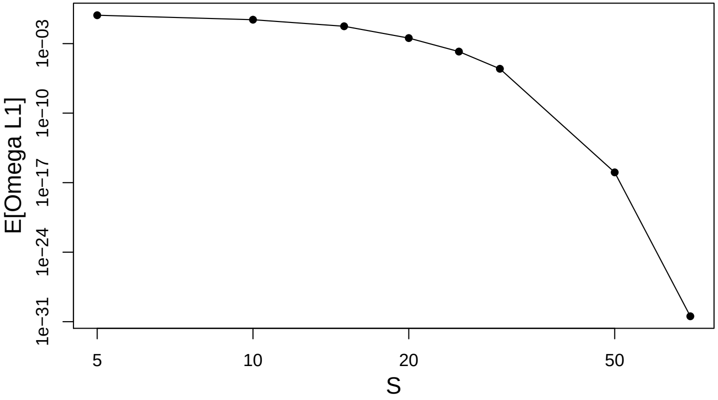
Feasibility

Competition system



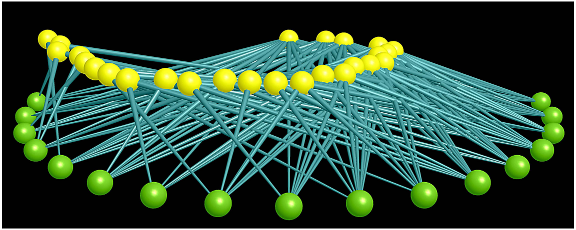
Feasibility

Competition system



Feasibility

Mutualism

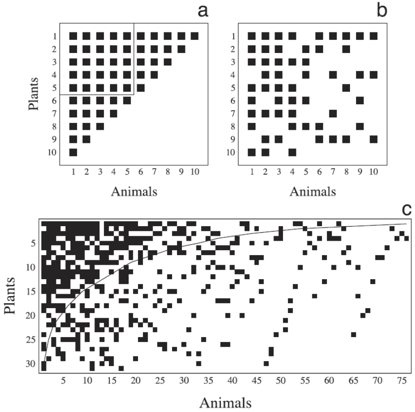


$$\frac{dP_i}{dt} = P_i\left(\alpha_i^{(P)} - \sum_j \beta_{ij}^{(P)} P_j + \frac{\sum_j \gamma_{ij}^{(P)} A_j}{1+h\sum_j \gamma_{ij}^{(P)} A_j}\right)$$

$$\frac{dA_i}{dt} = A_i\left(\alpha_i^{(A)} - \sum_j \beta_{ij}^{(A)} A_j + \frac{\sum_j \gamma_{ij}^{(A)} P_j}{1+h\sum_j \gamma_{ij}^{(A)} P_j}\right)$$

Feasibility

Mutualism: nestedness



Jordi Bascompte et *al.* (2012), *The nested assembly of plant-animal mutualistic networks*, PNAS, 100:9383-9387.

Overlap matrix:

$$n_{ij}^{(P)} = \sum_k Y_{ik} Y_{jk}$$

Nestedness:

$$\eta^{(P)} = \frac{\sum_{i<j} n_{ij}^{(P)}}{\sum_{i<j} \min(d_i^{(P)}, d_j^{(P)})}$$

with $d_i^{(P)} = \sum_k Y_{ik}$

Numerical simulations

$\alpha_i \in [0.85, 0.11]$

$\beta_{ii} \in [0.99, 1.01]$

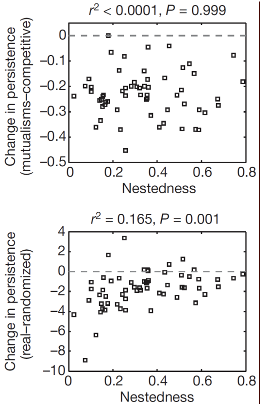
$\beta_{ij} \in [0.22, 0.24]\,(i \neq k)$

$\gamma_{ij} \in [0.19, 0.21]$

$h = 0.1$

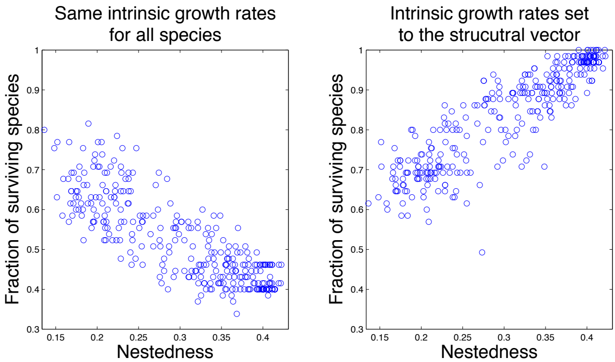
$$\frac{dP_i}{dt} = P_i\left(\alpha_i^{(P)} - \sum_j \beta_{ij}^{(P)} P_j + \frac{\sum_j \gamma_{ij}^{(P)} A_j}{1+h\sum_j \gamma_{ij}^{(P)} A_j}\right)$$

$$\frac{dA_i}{dt} = A_i\left(\alpha_i^{(A)} - \sum_j \beta_{ij}^{(A)} A_j + \frac{\sum_j \gamma_{ij}^{(A)} P_j}{1+h\sum_j \gamma_{ij}^{(A)} P_j}\right)$$



Alex James et *al.* (2012), *Disentangling nestedness from models of ecological complexity*, Nature, 487:227-230.

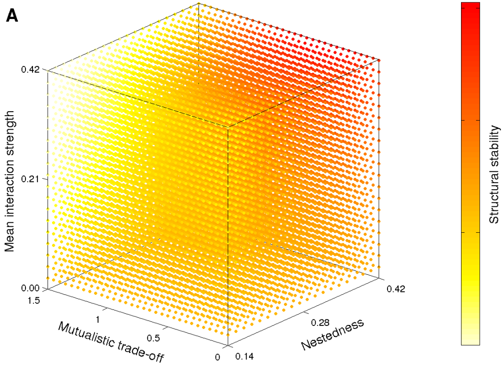
Numerical simulations



Conclusion: conclusions drawn from numerical simulations may strongly be dependent on the parameters choice, especially the $\vec{\alpha}$.

Feasibility

Mutualism



$\beta_{ij} = 0.2$

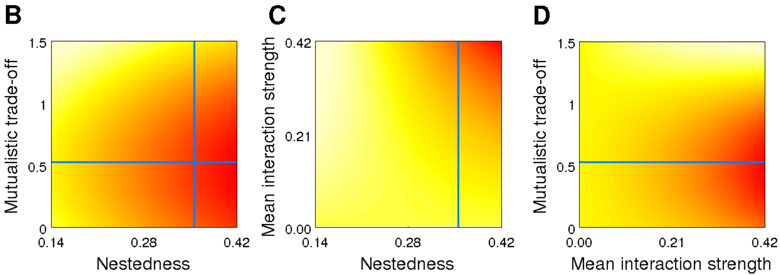
$\beta_{ii} = 1$

$h = 0.1$

$\gamma_{ij} = \frac{\gamma_0 Y_{ij}}{d_i^{\delta}}$
($\delta =$ mutualistic trade-off)

Feasibility

Mutualism



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