Feasibility of equilibria in large ecosystems

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Empirical food web

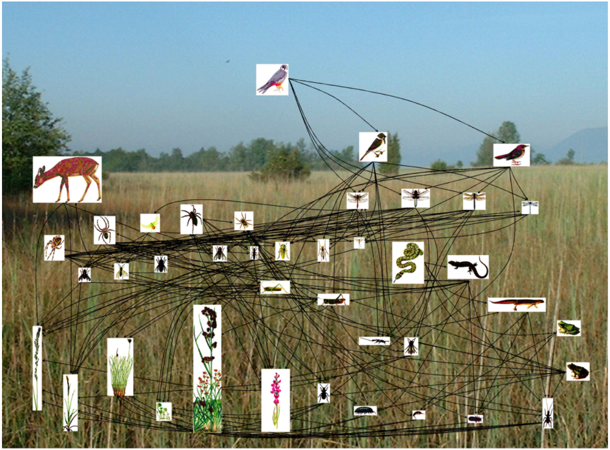

Figure: La Grande Caricaie, Switzerland

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Feasibility in two-level food web

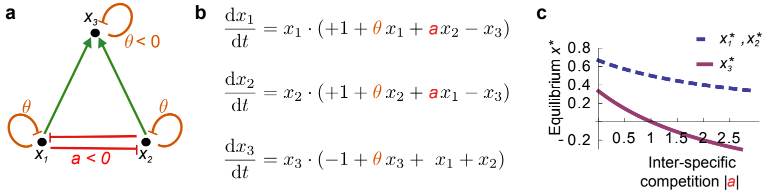
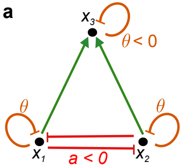


Figure: Equilibrium abundances for a two-level food web. Two producers and one consumer. **The network is feasible if all species equilibrium values are positive**.

- Interspecific competition coefficient $a < 0$.
- Intraspecific competition coefficient $\theta < 0$.

Feasibility in two-level food web

a



b

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = x_1 \cdot (+1 + \theta\, x_1 + a\, x_2 - x_3)$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = x_2 \cdot (+1 + \theta\, x_2 + a\, x_1 - x_3)$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = x_3 \cdot (-1 + \theta\, x_3 + \; x_1 + x_2)$$

c

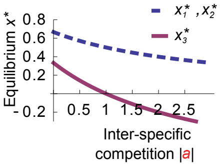


Figure: Equilibrium abundances for a two-level food web. Two producers and one consumer.

When the inter-specific competition coefficient is too large, the consumer's equilibrium solution to the associated Lotka-Volterra differential equation becomes negative: **the equilibrium is unfeasible.**

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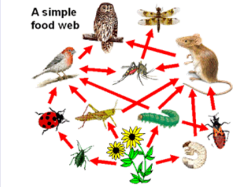
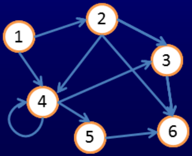
Food web and adjacency matrix

Food web networks



A Food Web is a biological network that describes who eats whom in an ecosystem

- Nodes = species
- Edges = trophic interactions (flow of energy)
- Predation matrix = adjacency matrix of the network



Predation matrix

species as prey \ species as predators	1	2	3	4	5	6
1	0	1	0	1	0	0
2	0	0	1	1	0	1
3	0	0	0	0	0	1
4	0	0	1	1	1	0
5	0	0	0	0	0	1
6	0	0	0	0	0	0

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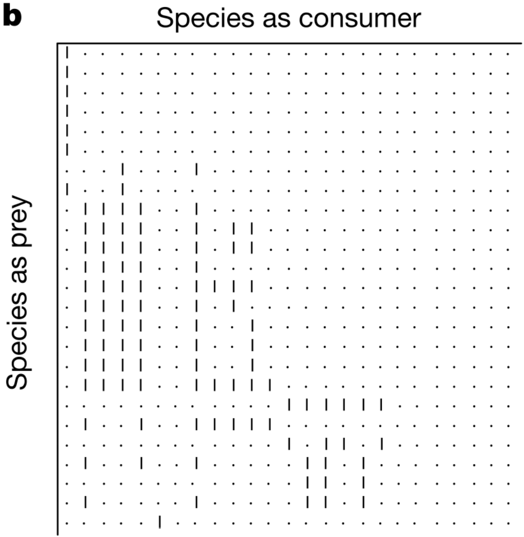
The Bridge Brook Lake matrix



Web topology and interaction strengths

What are the roles of web topologies and interaction strengths on feasibility and stability.

There is no clear answer at present time. All observed empirical webs exhibit similar topological properties. Usually biologists think that web topologies play a fundamental role, while other state that the topology only plays a marginal role...

Concerning the role of interaction strengths for complex webs, weak interaction strengths seem to enforce stability and feasibility. But no clear view point on this question

At present time, analytical results have been only obtained for random unstructured webs with random interaction weights.

Complex random predator-prey networks

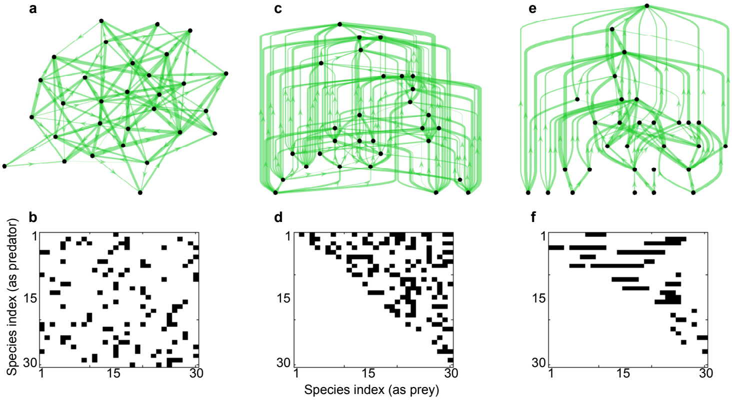
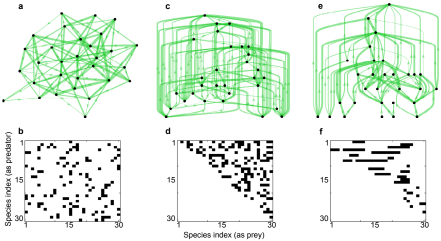


Figure: Three network mathematical model for predation. (a-b) Unstructured networks. (c-d) Cascade model. (e-f) Niche model, which have designed to mimic the topologies of empirical webs

Web topologies



- **Random unstructured webs:** Random graphs of Erdös-Renyi type where the probability that any edge is present is given by $C = L/S(S-1)$, where L is the total number of edges.
- **Structured networks:** Random webs obtained from the cascade, niche, nested-hierarchy models and from empirical data.

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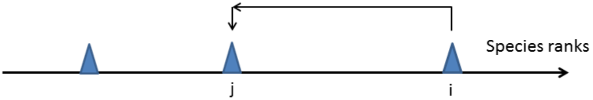
The cascade model (Cohen, 1985)

The cascade model



Species i can feed only on species j having strictly lower ranks

No loop

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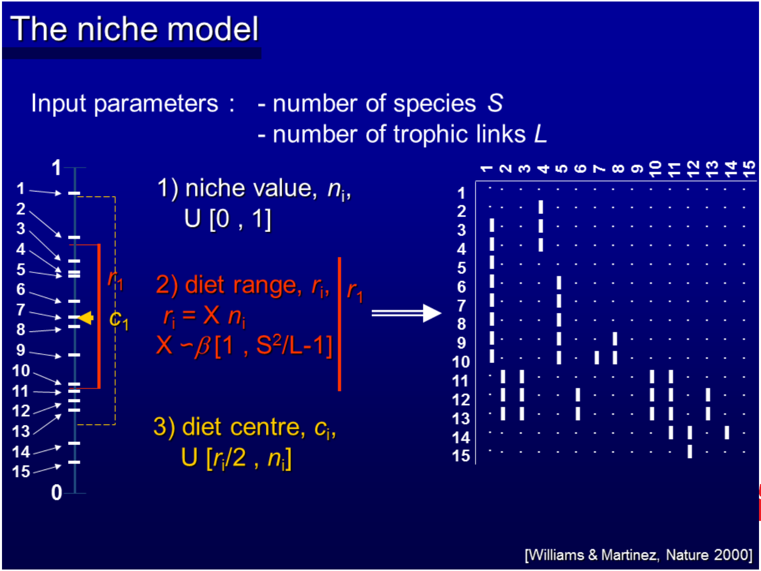
The cascade model

The cascade model is stochastic: species can only consume prey of lower rank with some probability which is the same for all species. The related adjacency matrices are upper triangular, with no cannibalistic loop and no circuits. Cohen discovered an excess of non-triangulated webs compared to observed food-webs.

The cascade model poorly reproduces the structure of highly resolved food-webs.

The niche model (Martinez, 2000)



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Stochastic niche models and beyond

- Based on the assumption of a single trophic niche dimension
- Produce contiguous diets for all species and interval food-webs
- Able to reproduce closely many empirical patterns
- Major improvement of the cascade model but
- Contiguous diets are never observed in observed food-webs.

Besides the cascade and the niche models, the *nested-hierachy model* (Cattin, 2004) and and a model of Rossberg (2005) **take evolutionary of food-webs into account** and relaxes the intervality of the diets of the niche model. We will also use observed food-webs.

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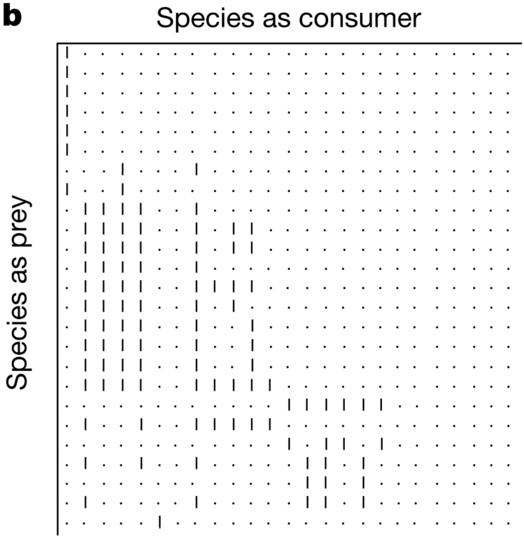
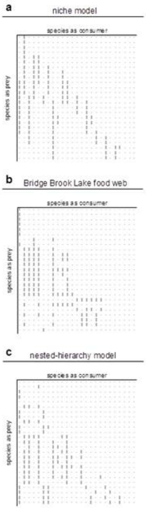
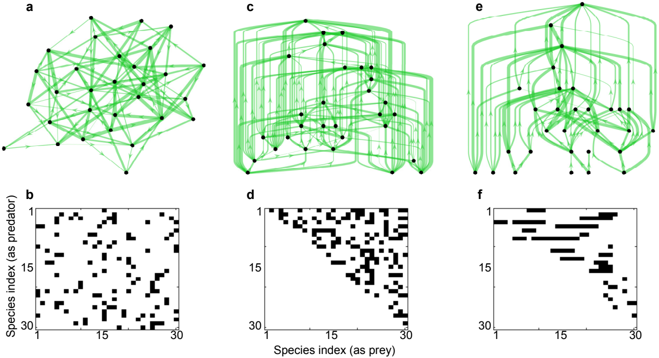
The Bridge Brook Lake matrix



Bridge Brook Lake matrix fitting



Lotka-Volterra dynamical systems on complex networks



For each realization of the random network, consider the following system of differential equations

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i\left(r_i + \theta x_i + \frac{1}{(CS)^\delta}\sum_j a_{ij}x_j\right).$$

Lotka-Volterra dynamical systems on complex networks

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i\left(r_i + \theta x_i + \frac{1}{(CS)^\delta}\sum_j a_{ij}x_j\right),$$

where

- a_{ij}: per capita effect of species j on species i
- r_i: intrinsic growth rate of species i
- θ: coefficient reflecting intraspecific competition
- C: connectance= number of observed links divided by the number of possible links
- δ: scaling factor modelling interaction strength

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Interaction weights

In most empirical network, **both the growth rate vector r and the interaction matrix A are unknown**

A possible method for overcoming this problem, which is of common use in statistical mechanics, consists in assuming that both r and the matrix A are random.

This method has been used in practical situations for example to predict the effect of introducing a new species to an ecosystem (which can be very risky), see, e.g. Baker et al., Conservation Biol. 2016.

Interaction strength

The **interaction strength coefficient** $0 < \delta \leq 1$ defines three regimes:

- **Strong interaction strength:** $\delta < 1/2$.
- **Moderate interaction strength:** $\delta = 1/2$.
- **Weak interaction strength:** $\delta > 1/2$.

The moderate regime $\delta = 1/2$ corresponds to the classical random matrix model of Wigner.

Lotka-Volterra dynamical systems on complex networks

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x \circ \left(r + (\theta \mathrm{id} + \frac{1}{(CS)^{\delta}} A) x \right).$$

One first looks at the equilibria x^* which solve the system

$$0 = x^* \circ \left(r + (\theta \mathrm{id} + \frac{1}{(CS)^{\delta}} A) x^* \right),$$

and then looks for its feasibility and its stability properties as a function of both r and A.

Feasibility and stability of equilibria

An equilibrium solving the equation

$$r + (\theta \mathrm{id} + \frac{1}{(CS)^{\delta}} A) x^* = 0,$$

is **feasible** when $x_i^* > 0, \forall i$. It is **linearly stable when the Jacobian matrix (the community matrix)**

$$J(x^*) = \mathrm{diag}(x^*)(\theta \mathrm{id} + \frac{1}{(CS)^{\delta}} A),$$

has eigenvalues of negative real parts.

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May's stability criterion

The consensus that complexity (e.g. large values of S) begets stability (McArthur, 1955) was challenged by Levins, Ashby, Gardner and May in the seventies. May focused on random unstructured random webs with random weights a_{ij} such that $a_{ii} \equiv 0$, and used results from random matrix theory when $\delta = 1/2$ to study the spectrum of the random matrix

$$\tilde{J} = \theta \mathrm{id} + \frac{1}{(CS)^\delta} A.$$

The associated eigenvalues have negative real parts when

$$\frac{\sigma}{(CS)^\delta} \sqrt{CS} < |\theta|,$$

which is the well known **May's stability condition**.

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Feasibility

Let

$$B := (\theta \mathrm{id} + \frac{1}{(CS)^{\delta}} A), \text{ so that } x^* = -B^{-1} r.$$

The probability of feasibility is defined by

$$P_S = P_{A,r}(x^* = -B^{-1} r > 0),$$

when A and r are chosen at random. When A is fixed and r is random, we denote it by

$$P_r(B^{-1} r < 0).$$

Feasibility

Then

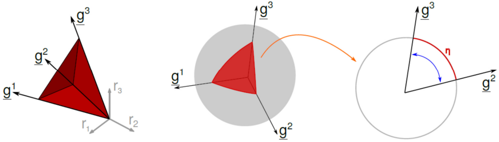
$$P_S = \int \prod_i \Theta(-(B^{-1}r)_i) f(B) g(r) \mathrm{d}B \mathrm{d}r = \mathbb{E}_B(P_r(B^{-1}r < 0)),$$

where f (resp. g) is the density of the random matrix B (resp. of the random growth rate vector r). $\Theta(x) = 1$ when $x > 0$ is zero otherwise.

Solid feasibility angle

Rohr et al. (2014) and Grilli et al. (2017) focused on the solid angle associated to the feasibility cone (figure from Grilli (2017))

$$K(B) = \{r \in \mathbb{R}^S;\ B^{-1}r < 0\},$$



Solid feasibility angle

The solid angle is defined by

$$\Xi(B) = 2^S \frac{\mathrm{Vol}_{S-1}(K(B) \cap \mathbb{S}^{S-1})}{\mathrm{Vol}_{S-1}(\mathbb{S}^{S-1})},$$

where the factor 2^S is introduced to ensure that $\Xi = 1$ when species do not interact. They studied analytically the mean field case where all the coefficients a_{ij}, $i \neq j$ are constant and equal to some E_1. They then performed simulations and showed that the mean field case provides a nice approximation to the random case (when B is random and is associated to a Erdös-Renyi random graph with random i.i.d. interaction weights.

Solid feasibility angle and probability of feasibility

Let r be a spherically symmetric random vector. Then

$$P(r \in K(B)) = P(\frac{r}{||r||} \in K(B) \cap \mathbb{S}^{S-1}),$$

with $r/||r||$ uniform on the sphere $\mathbb{S}^{S-1}$. Hence,

$$P_r(B^{-1}r < 0) = P(r \in K(B)) = \frac{1}{2^S}\Xi(B).$$

Choosing r to be a standard multivariate gaussian random vector of density g, one obtains

$$\Xi(B)/2^S = \int_{\mathbb{R}^s} \prod_i \Theta(-(B^{-1}r)_i) g(r) \mathrm{d}r = P_r(B^{-1}r < 0),$$

Solid feasibility angle and probability of feasibility

$$\Xi(B)/2^S = \frac{\sqrt{|G|}}{\sqrt{2\pi}^S} \int_{\mathbb{R}^s} \prod_i \Theta(z_i) \exp(-\frac{1}{2} z^T G z) \mathrm{dz}, \quad G = B^T B.$$

For random B, the mean solid angle is a probability of feasibility P_S

$$P_S = P_{A,r}(B^{-1} r < 0) = \mathbb{E}_B(\Xi(B))/2^S.$$

The average value for random B of the solid feasibility angle is given by P_S for i.i.d. standard normal $N(0,1)$ random growth rates r_i.

A natural question consists in checking the concentration of the law of $\Xi(B)$ around its mean value P_S for random B. Similar problems have been studied for disordered systems like spin glasses.

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Computation of the feasibility probability: mathematical side

The probability of feasibility has been studied for the various (unstructured) models by several authors (e.g. by Stone (1988,2017), Bunin(2017), Dougoud(2018) and ...). Some authors use approximations to compute $B^{-1}r$, which are based on the first term of the Neumann expansion of $B^{-1}r$, or on the *cavity method* from statistical mechanics (spin glass theory). These methods have been validated numerically.

We used a fully rigorous method which is adapted from Geman(1982). The method uses the full Neumann series expansion of $B^{-1}r$ and the moment method from random matrix theory. Many related mathematical problems remain however open.

Feasibility for random unstructured webs

In Dougoud et al. (2018), we focus on the moderate interaction strength regime $\delta = 1/2$, and assume that the underlying random graph is of Erdös-Renyi type. Using previous results of Geman(1982) on solutions to systems of random linear equations, we have proven that if

- the random growth rates r_i are i.i.d., independent of A,
- the entries a_{ij} are i.i.d. centred,
- $\mathbb{E}(r^2)\mathbb{E}(a_{11}^2) < \theta^2/4$,

then the equilibrium x^* **is composed of asymptotically independent gaussian random variables of mean μ and variance** $\hat{\sigma}^2$ given by

$$\mu = -\frac{\mathbb{E}(r_1)}{\theta},$$

$$\hat{\sigma}^2 = \frac{\mathrm{Var}(r_1)}{\theta^2} + \frac{\mathbb{E}(r_1^2)\sigma^2}{\theta^2(\theta^2 - \sigma^2)}.$$

Sketch of proof

We follow Geman (1982) and suppose that $r = \mathbf{1} = (1, \cdots, 1)^T$, $\theta = -1$, $C = 1$ and assume that $\delta = 1/2$. The equilibrium equations becomes

$$x^* = \mathbf{1} + \frac{A}{\sqrt{S}} x^*,$$

so that

$$x^* = (\mathrm{Id} - \frac{A}{\sqrt{S}})^{-1} \mathbf{1}.$$

The idea is to consider the geometric series to arrive at the approximation

$$x^p = \mathbf{1} + \sum_{k=1}^{p-1} \Big(\frac{A}{\sqrt{S}} \Big)^k \mathbf{1},$$

and to control the difference $e^p = x^* - x^p$, as $p \to \infty$.

For given λ_i, $i = 1, \cdots, m$, Geman considered characteristic functions and showed that

$$\mathbb{E}(\exp(i\sum_{j=1}^{m}\lambda_j x_j^*)) \longrightarrow \exp(i\sum_{j=1}^{m}\lambda_j - \frac{\sigma^2}{1-\sigma^2}\sum_j \lambda_j^2).$$

The idea is to first show that $\sum_{j=1}^{m}\lambda_j x_j^p$ converges in law to a normal distribution using the method of moments, and to next prove that

$$\limsup_{p\to\infty}\limsup_{S\to\infty} P(|\sum_{j=1}^{m}\lambda_j e_j^p| > \varepsilon) = 0,$$

$\forall\varepsilon > 0$.

Probabiliy of feasibility for large random unstructured webs

We also obtained that, under the same hypotheses,

$$0 \leq P_S \sim \Phi\left(\frac{\mathbb{E}(r_1)}{\hat{\sigma}}\right)^S,$$

where Φ is the standard gaussian cumulative distribution function.

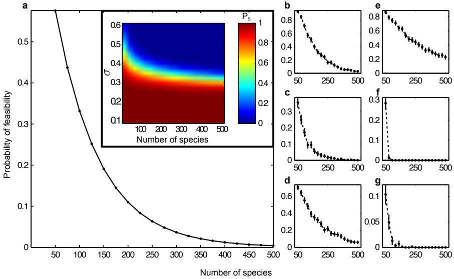

Figure: Plot of P_S for increasing species numbers S. Predictions for random mutualistic networks, random competitive networks, random predator-prey networks, the cascade model, the niche model, and the nested-hierarchy model.

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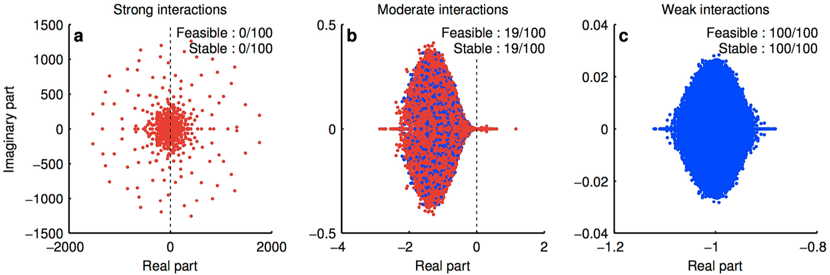
Stability and feasibility



A feasibility phase transition for moderate interaction strength and gaussian weights

In a recent work, Bizeul and Najim (2019) consider random LV linear systems of the form

$$1 - x_i + \frac{1}{\alpha_S S^{1/2}} \sum_j a_{ij} x_j \equiv 0,$$

where $\alpha_S \to \infty$ as $S \to \infty$. Let $\alpha_S^* = \sqrt{2\ln(n)}$. They proved the following phase transition phenomenon for centred standard gaussian weights a_{ij}:

- If there exists $\varepsilon > 0$ with $\alpha_S \leq (1-\varepsilon)\alpha_S^*$, then the solution of the above linear system is such that

  $$P(\min x_i > 0) \longrightarrow 0,$$

  $S \to \infty$.
- If there exists $\varepsilon > 0$ with $\alpha_S \geq (1+\varepsilon)\alpha_S^*$, then

  $$P(\min x_i > 0) \longrightarrow 1.$$

Weak interactions $\delta = 1$, unstructured webs

Following Dougoud et al. (2018), assume that

- $\delta = 1$,
- The entries a_{ij} are i.i.d. of mean $C\mu_A$ with $|\mu_A| < |\theta|$,
- the growth rates are bounded,

Assuming some moment condition, we have proven that, as $S \to \infty$, the limiting equilibrium x^* is deterministic with

$$x_i^* = \frac{r_i}{|\theta|} + \frac{\mu_A}{|\theta|(|\theta| - \mu_A)}\bar{r},$$

where $\bar{r}$ is the arithmetical mean of the r_i. If $r_i \geq \mu_A/(\mu_A + \theta)\bar{r}$, then x^* is feasible with probability one.

Probability of feasibility: Summary

Table 1. Summary of the different results presented on PS for S → ∞.

Model		Moderate interactions ($\delta = \frac{1}{2}$)	Weak interactions ($\frac{1}{2} < \delta \leq 1$)
Unstr.	May's model	$P_S \to 0$	$P_S \to 0$ or 1
	Competition	$P_S \to 0$	$P_S \to 0$ or 1
	Mutualism	$P_S \to 0$	$P_S \to 0$ or 1
	Predation	$P_S \to 0$	$P_S \to 0$ or 1
Struct.	Cascade	$P_S \to 0$	$P_S \to 0$ or 1
	Niche	$P_S \to 0$	x^* not deterministic and $P_S \to 0$ or 1
	Nested hierarchy	$P_S \to 0$	x^* not deterministic and $P_S \to 0$ or 1

The probability P_S converges towards 0 as $S \to \infty$ for moderate interactions (and with the mean structural vector) in unstructured (unstr.) and structured (struct.) networks. For weak interactions, $P_S \to 0$ or $P_S \to 1$, depending on the parameters. The equilibrium x^* is deterministic in the unstructured case and for the cascade model. x^* has a non-trivial distribution and is feasible with positive probability for the niche and nested-hierarchy models.

https://doi.org/10.1371/journal.pcbi.1005988.t001

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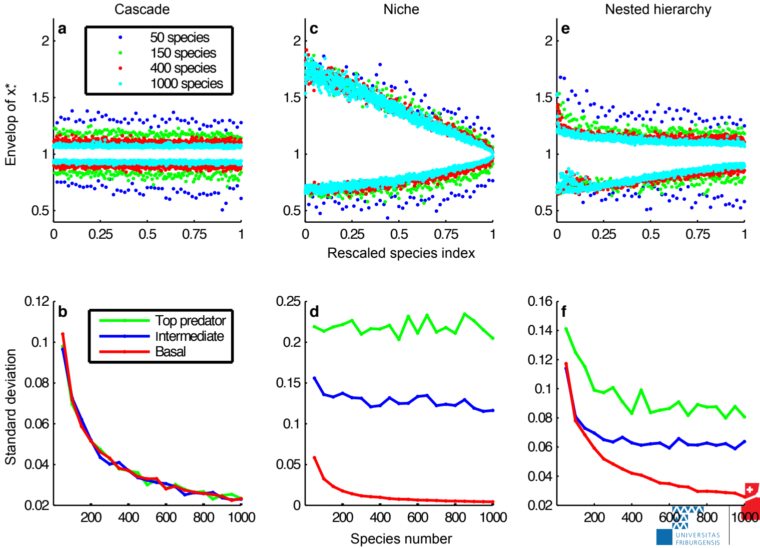
Dougoud M, Vinckenbosch L, Rohr RP, Bersier LF, Mazza C (2018) The feasibility of equilibria in large ecosystems: A primary but neglected concept in the complexity-stability debate. PLOS Computational Biology 14(2): e1005988.

Weak interactions, law of x^* for structured webs



Weak interactions, law of x_i^* and trophic level

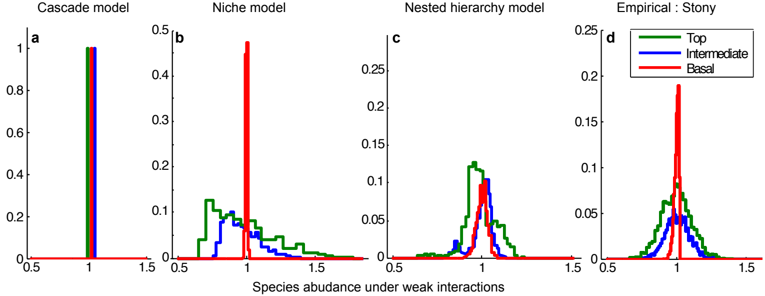


Figure: The equilibrium abundances are deterministic for the random unstructured webs and for the cascade model, while abundances are random for the niche and the nested-hierarchy random web models. The species abundance variance depends on trophic level, with high variances for top predators and low variances for basal species.