

Structural instabilities of ecosystem dynamics and climate change

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Empirical food web

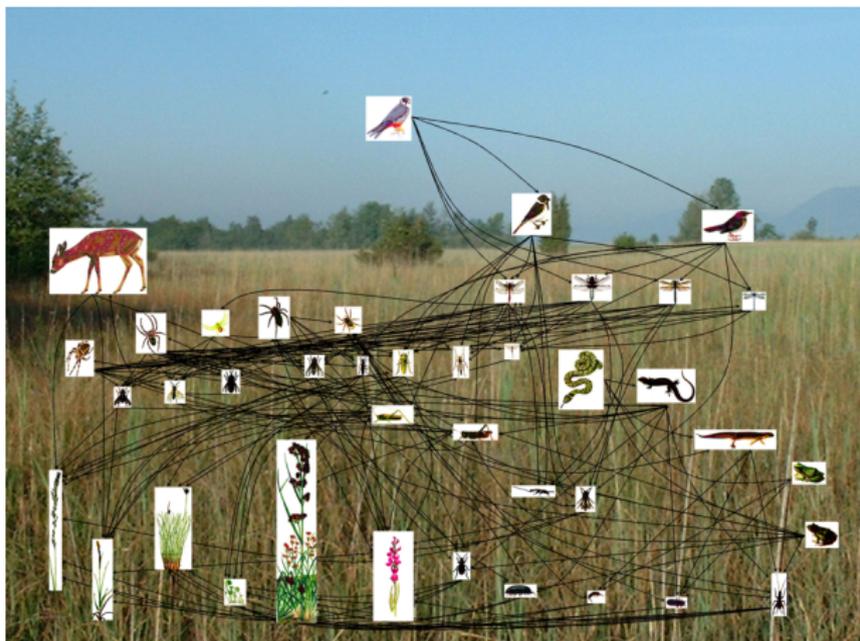
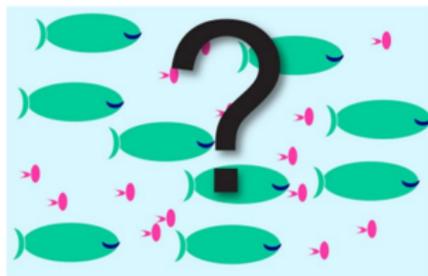


Figure: La Grande Caricaie, Switzerland, from L-F Bersier

Ecosystem modelling: a toy model

Simple ecosystem: what happens to the Shark and Tuna populations?



From Garfinkel et al. Bull. Math. Biol. (2022)

Figure: Predator prey system

Ecosystem modelling: a toy model

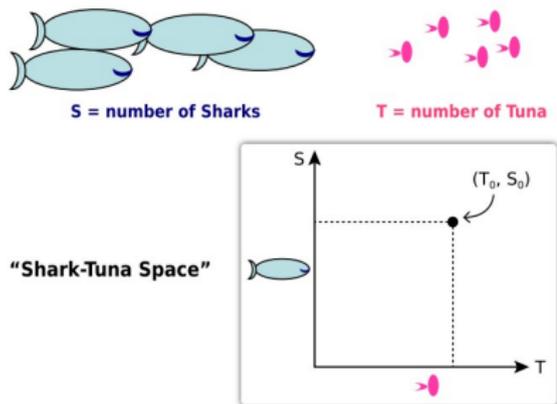
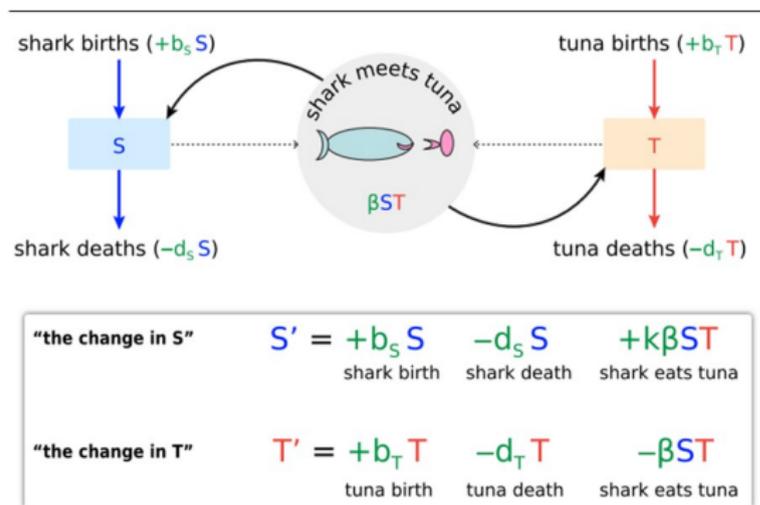


Fig. 2 Geometry of "Shark-Tuna space." Students learn in the first week that a point (T_0, S_0) represents the state of the system at a time

From Garfinkel et al. *Bull. Math. Biol.* (2022)

Figure: Predator prey system state space

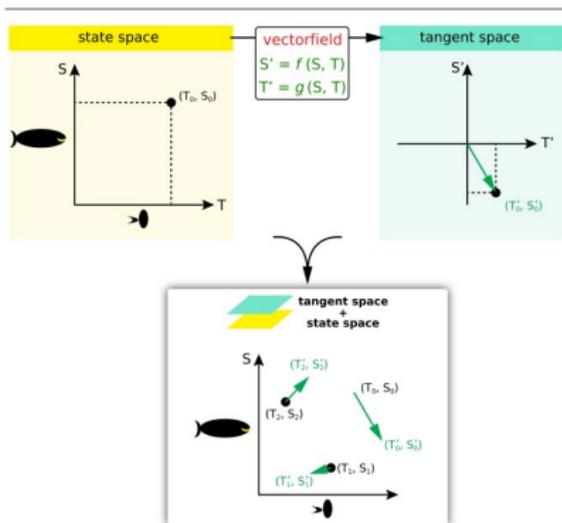
Ecosystem modelling: a toy model



From Garfinkel et al. *Bull. Math. Biol.* (2022)

Figure: Predator prey system: Lotka-Volterra (LV) differential equation

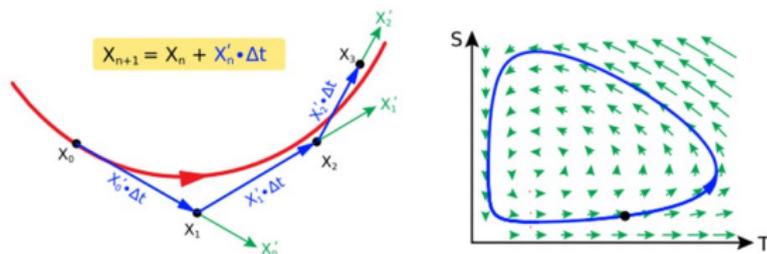
Ecosystem modelling: a toy model



From Garfinkel et al. Bull. Math. Biol. (2022)

Figure: Predator prey system: Vector Field

Ecosystem modelling: a toy model



From Garfinkel et al. *Bull. Math. Biol.* (2022)

Figure: The vector field (green) and a trajectory

Vector fields and ordinary differential equations (o.d.e.)

$$\begin{aligned}\frac{dx_1}{dt} &= F_1(x_1, x_2) \\ \frac{dx_2}{dt} &= F_2(x_1, x_2).\end{aligned}$$

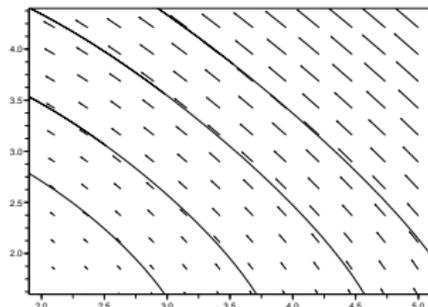


Figure: Vector field $F = (F_1, F_2)$ leads to o.d.e. The orbits are tangent to the vector field

Feasible equilibria $x^* > 0$ with $F(x^*) = 0$

One looks for

- special states x^* such that $F(x^*) = 0$, which are the so-called equilibria of the o.d.e., which give **constant solutions**,
- and more importantly, at **feasible equilibria with $x^* > 0$ and $F(x^*) = 0$ for which all species persist.**

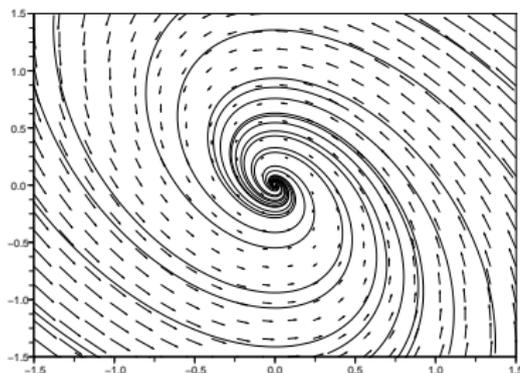


Figure: Equilibrium x^* with $F(x^*) = 0$

Stable equilibria

Such equilibria can be stable

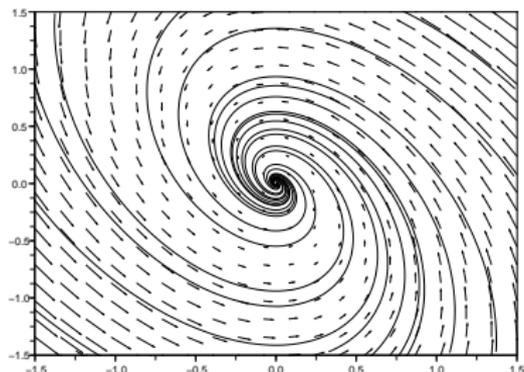


Figure: Stable equilibrium x^* : orbits starting near x^* will converge toward x^*

Unstable equilibria

or unstable

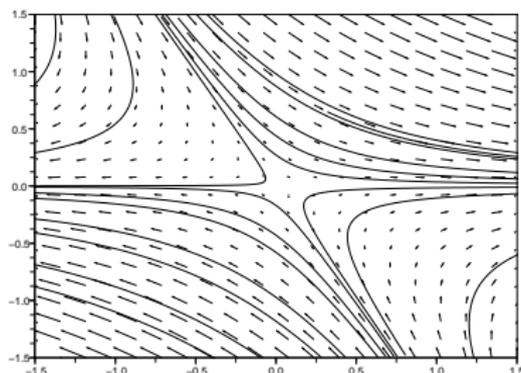
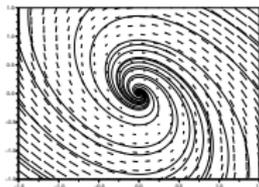


Figure: In this case, the equilibrium is unstable: the orbits avoid the equilibrium

Jacobian matrix at x^* and stability of x^*



Let x^* be an equilibrium with $F(x^*) = 0$. Let $J(x^*) = DF(x^*)$ be the Jacobian matrix of F at x^* , with

$$J(x^*) = \begin{pmatrix} \frac{\partial F_1}{\partial x_1}(x^*) & \frac{\partial F_1}{\partial x_2}(x^*) \\ \frac{\partial F_2}{\partial x_1}(x^*) & \frac{\partial F_2}{\partial x_2}(x^*) \end{pmatrix}$$

x^* is stable when all of the real parts of the eigenvalue of $J(x^*)$ are negative.

Example: Food-web with two producers and one consumer

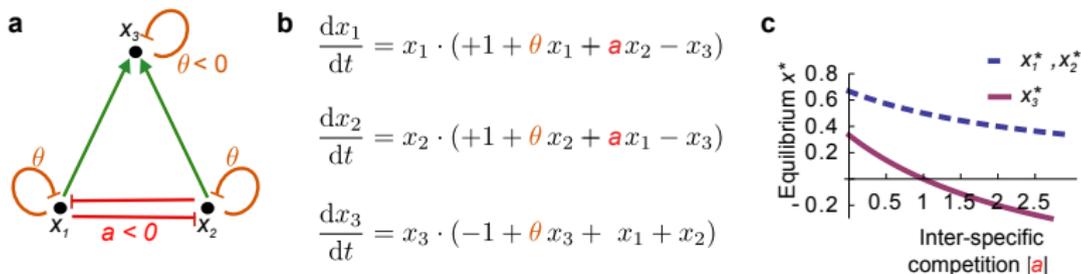


Figure: The o.d.e. associated to a consumer-resource web. The solutions are such that $x_i(t) > 0$ when $x_i(0) > 0$.

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

Food-web with two producers and one consumer

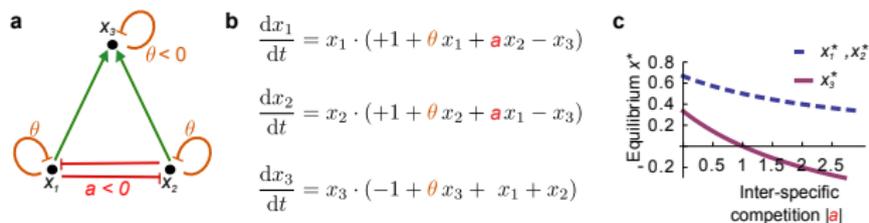


Figure: The o.d.e. associated to a consumer-resource web

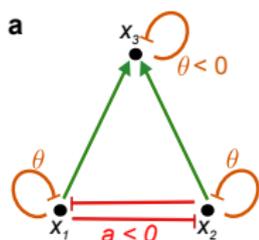
The related vector field $F = (F_1, F_2, F_2)$ is

$$F_1(x) = x_1(1 + \theta x_1 + a x_2 - x_3),$$

$$F_2(x) = x_2(1 + \theta x_2 + a x_1 - x_3),$$

$$F_3(x) = x_3(-1 + \theta x_3 + x_1 + x_2).$$

Equilibria and parameter changes

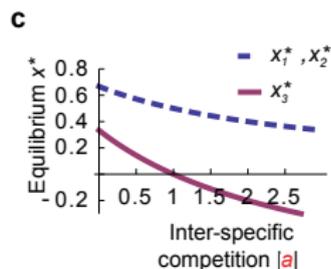


b

$$\frac{dx_1}{dt} = x_1 \cdot (+1 + \theta x_1 + a x_2 - x_3)$$

$$\frac{dx_2}{dt} = x_2 \cdot (+1 + \theta x_2 + a x_1 - x_3)$$

$$\frac{dx_3}{dt} = x_3 \cdot (-1 + \theta x_3 + x_1 + x_2)$$



Set $\theta = -1$. When $|a| > 1$, the consumer's non-zero critical value $x_3^* \neq 0$ becomes negative: no feasible equilibrium

- When $|a| < 1$, the non-zero equilibrium has positive components so that all species persist. The non-zero equilibrium x^* with $F(x^*) = 0$ is stable and feasible.
- When $|a| > 1$, the consumer becomes extinct $x_3^* = 0$ while the two consumers attain positive equilibria $x_1^* = x_2^* > 0$.

Lotka-Volterra dynamical systems on complex networks

$$\frac{dx_i}{dt} = x_i \left(r_i + \theta x_i + \sum_j a_{ij} x_j \right), \quad i = 1, \dots, S,$$

where

- S is the number of species of the ecosystem,
- a_{ij} : per capita effect of species j on species i
- r_i : intrinsic growth rate of species i
- $\theta < 0$: coefficient reflecting intraspecific competition

Lotka-Volterra model

$$\frac{dx_i}{dt} = x_i \left(r_i + \theta x_i + \sum_j a_{ij} x_j \right).$$

For food webs that describe **who eats whom**, species j preys on species i when

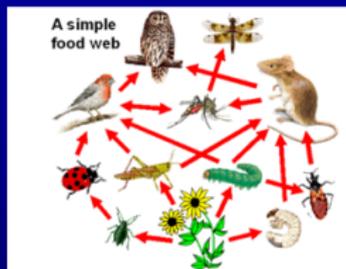
$$a_{ij} < 0 \text{ and } a_{ji} > 0.$$

One can then consider a directed graph where the arrow ($i \rightarrow j$) means that j consumes i .

In more general webs, **competition** (or mutualism) between species i and j is modelled by imposing $a_{ij} < 0$ and $a_{ji} < 0$ (or $a_{ij} > 0$ and $a_{ji} > 0$).

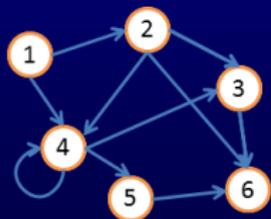
Food web and adjacency matrix

Food web networks



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

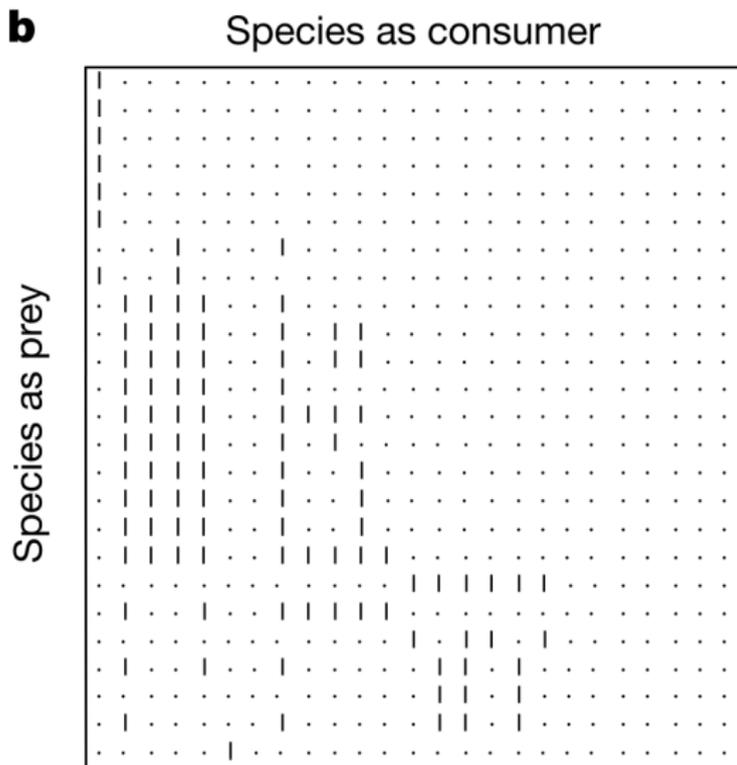
- Nodes = species
- Edges = trophic interactions (flow of energy)
- Predation matrix = adjacency matrix of the network



Predation matrix

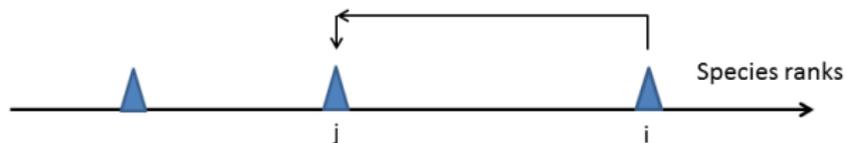
1	$\begin{bmatrix} 0 & 1 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$
6	
	1 2 3 4 5 6
	species as predators

The Bridge Brook Lake matrix



The cascade model (Cohen, 1985)

The cascade model



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

No loop

The cascade model

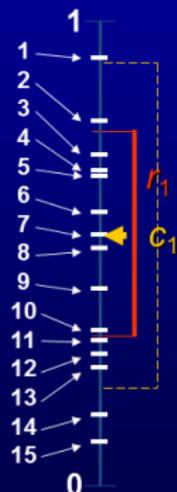
The cascade model is stochastic: species can only consume prey of lower rank with some probability which is the same for all species. The related adjacency matrices are upper triangular, with no cannibalistic loop and no circuits. Cohen discovered an excess of non-triangulated webs compared to observed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

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

The niche model (Martinez, 2000)

The niche model

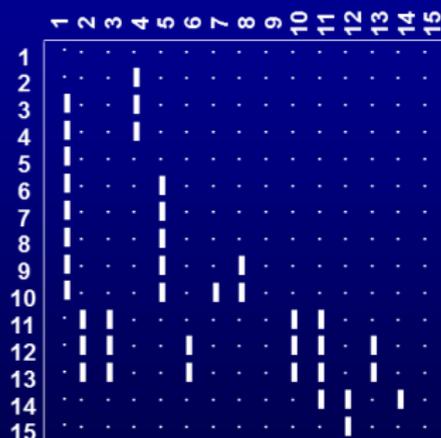
Input parameters : - number of species S
 - number of trophic links L



1) niche value, n_i ,
 $U [0, 1]$

2) diet range, r_i , r_1
 $r_i = X n_i$
 $X \sim \beta [1, S^2/L-1]$

3) diet centre, c_i ,
 $U [r_i/2, n_i]$



[Williams & Martinez, Nature 2000]

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-hierarchy model* (Cattin, 2004) 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.

Complex random predator-prey network models

Mathematical models have been designed to mimic properties of experimental webs:

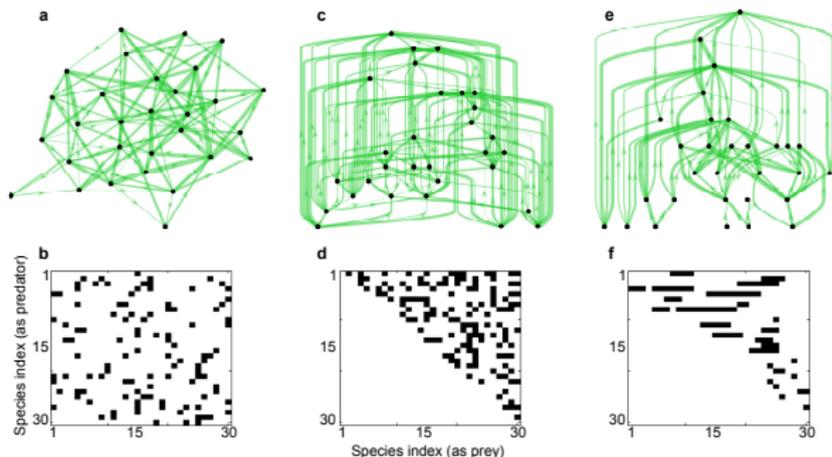
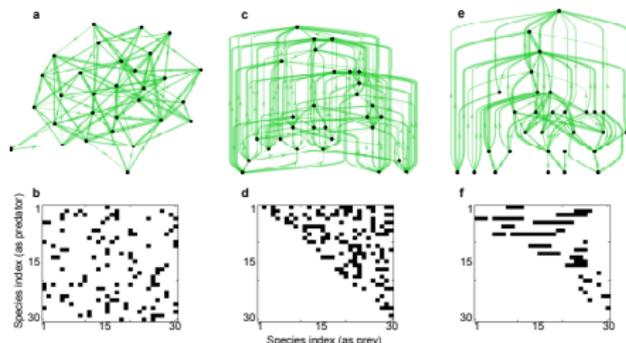


Figure: Three network mathematical model for predation. (a-b) Unstructured networks. (c-d) Cascade model. (e-f) Niche model, which have designed to mimic the topologies of empirical webs

Random webs



- **Random unstructured webs:** Random graphs of Erdős-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 and nested hierarchy models and empirical webs

Random 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 consists in assuming that r is random. The interaction matrix $A = (a_{ij})$ is chosen at random with, e.g. gaussian entries, of variance σ^2 .

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

$$\frac{dx}{dt} = x \circ \left(r + (\theta \text{id} + \frac{1}{(CS)^\delta} A) x \right).$$

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 interaction regime with $\delta = 1/2$ ensures that the total effect of interactions on species is controlled for species rich systems and is $O(1)$ of $O(1)$ variance as a function of S .

Web topology, interaction strengths and stability

Let x^* be such that $F(x^*) = 0$ where F is the vector field associated to a LV dynamics. x^* is feasible when $x^* > 0$.

What are the roles of web topologies and interaction strengths on feasibility and stability of x^* ?

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

Climate change and LV models

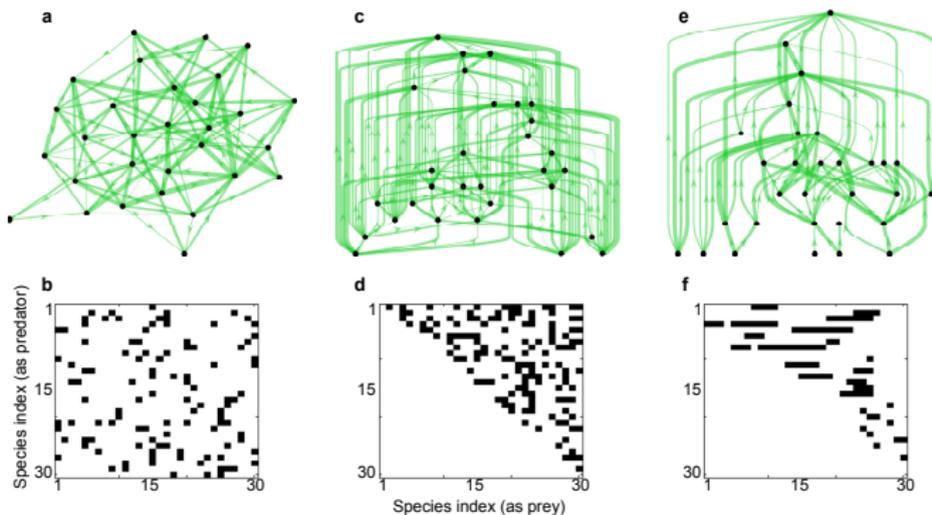
We will present some results on **structural instabilities** associated to such models, where **small changes in parameters like interaction coefficients for LV dynamics can change drastically the nature of the equilibria**, like e.g. stable equilibria that change into unstable equilibria.

We will then consider such consumer-resource models where the interaction parameters depend on temperature and where consumers interact in a direct way with interaction coefficients γ_{ij}

$$\frac{dN_i}{dt} = d_i \left(\mathcal{K}_i - \sum_{j=1}^n \alpha_{ij} N_j - \sum_{j=1}^n \gamma_{ij} N_j \right), \quad (1)$$

and present the effect of high temperature amplitudes on ecosystems.

Lotka-Volterra dynamical systems on random networks



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

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

Lotka-Volterra dynamical systems on complex networks

$$\frac{dx_i}{dt} = x_i \left(r_i + \theta x_i + \frac{1}{S\delta} \sum_j a_{ij} x_j \right),$$

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,
- $C = 1$.
- δ : scaling factor modelling interaction strength.

Lotka-Volterra dynamical systems on complex networks

$$\frac{dx}{dt} = x \circ \left(r + (\theta \text{id} + \frac{1}{S^\delta} A)x \right).$$

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

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

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

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

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

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

has eigenvalues of negative real parts. It can be shown that stability can be studied by looking solely at $\theta \text{id} + \frac{1}{S\delta} A$.

May stability condition

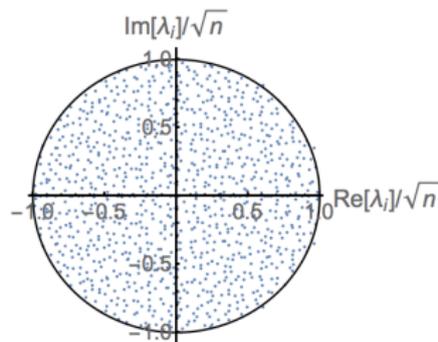
McArthur (1955) argued that **complexity**, as e.g., measured using the number of edges in experimental webs or as a function of species richness, **begets stability**.

This consensus was challenged by Levins, Ashby, Gardner and May in the seventies.

May used tools from random matrix theory.

The circular law

When the interaction coefficients a_{ij} are i.i.d. centered random variables of unit variance, the eigenvalues of A are asymptotically located inside the disc of radius \sqrt{S}



The circular law

For centered entries a_{ij} of variance σ^2 , the eigenvalues λ_i are located in the disc of radius $\sigma\sqrt{S}$. The real parts of the eigenvalues $\tilde{\lambda}_i$ of $\theta \text{id} + \frac{1}{S^\delta} A$ are such that

$$\text{Re}(\tilde{\lambda}_i) \leq \theta + \frac{\sqrt{S}}{S^\delta} \sigma,$$

so that the stability of x^* is ensured when

$$\frac{\sqrt{S}}{S^\delta} \sigma < |\theta|.$$

- May's original argument for the case $\delta = 0$: As the web becomes more complex with $S \gg 1$, the equilibrium is unstable.
- When $\delta = 1/2$, stability occurs when $\sigma < |\theta|$.

Feasibility

Let

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

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.

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 Erdős-Renyi type.

Suppose that

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

Then the equilibrium x^* is composed of asymptotically independent gaussian random variables

Feasibility for random unstructured webs

The random equilibrium $x^* = (x_i^*)$ is such that the random variable are asymptotically independent with the same normal distribution of mean μ and variance $\hat{\sigma}^2$ given by

$$\mu = -\frac{\mathbb{E}(r_1)}{\theta} > 0, \quad \hat{\sigma}^2 = \frac{\text{Var}(r_1)}{\theta^2} + \frac{\mathbb{E}(r_1^2)\sigma^2}{\theta^2(\theta^2 - \sigma^2)}.$$

Hence,

$$P_S = P(x_i^* > 0, i = 1, \dots, S) \sim \prod_{i=1}^S P(x_i^* > 0) = P(x_1^* > 0)^S,$$

with

$$P(x_1^* > 0) \sim \Phi\left(\frac{\mathbb{E}(r_1)}{\hat{\sigma}}\right) \text{ where } \Phi(t) = \int_{-\infty}^t \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{u^2}{2}\right) du.$$

Probability of feasibility for large random unstructured webs

Therefore,

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

where Φ is the standard gaussian cumulative distribution function.

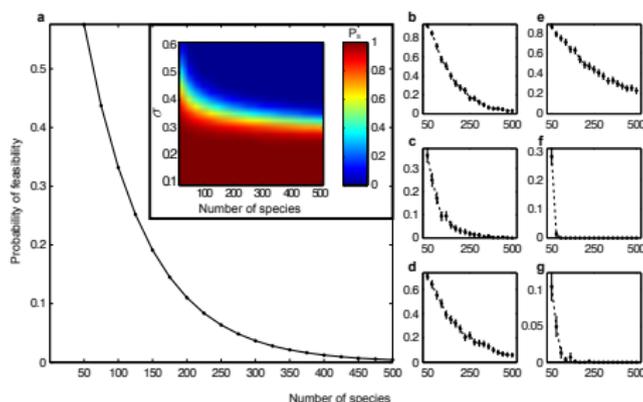


Figure: Plot of P_S for increasing species numbers S . Predictions for random mutualistic networks, random competitive networks, random predator-prey networks, the cascade model, the niche model, and the nested-hierarchy model.

Feasible steady states are stable

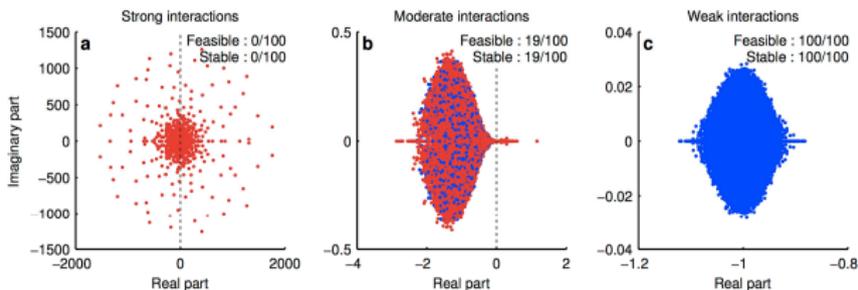


Figure: b) moderate interactions: eigenvalues of the Jacobian $J(x^*)$ for 100 realizations of May's model when $S = 150$, $\theta = -1$ and $\sigma = 0.4$. Eigenvalues of feasible systems are in blue

A feasibility phase transition

In a recent work, Bizeul and Najim (2019) consider random LV linear equilibrium equations ($\theta = -1$, $r = \mathbf{1}_S$)

$$1 - x_i^* + \frac{1}{\alpha_S S^{1/2}} \sum_j a_{ij} x_j^* \equiv 0, \quad \mathbf{1}_S + Bx^* = 0,$$

where $\alpha_S \rightarrow \infty$ as $S \rightarrow \infty$. Let

$$\alpha_S^* = \sqrt{2 \ln(S)}.$$

They proved the following phase transition phenomenon

- If there exists $\varepsilon > 0$ with $\alpha_S \leq (1 - \varepsilon)\alpha_S^*$, then

$$P(\min x_i^* > 0) \rightarrow 0,$$

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

$$P(\min x_i^* > 0) \rightarrow 1.$$

Stability but no feasibility, loss of biodiversity

When σ is fixed, stable equilibria of LV dynamics with random coefficients are not feasible, so that **species extinctions occur generically in LV mathematical models of species rich ecosystems**, for both unstructured and structured models exhibiting competition, mutualism and predation.

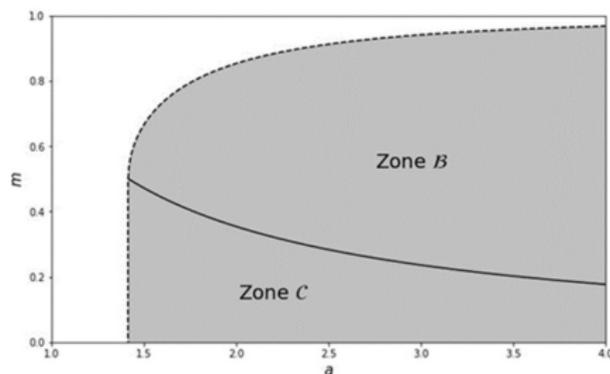
Adopting the LV modelling framework, one can try to check **what are the consequences of climate change on the LV dynamics**.

Globally asymptotically stable equilibria

Clenet et al. (2022), arXiv, considered LV systems with

$$B = -\text{id} + \frac{A}{\alpha\sqrt{S}} + \frac{\mu}{S}\mathbf{1}\mathbf{1}^T,$$

where $\mathbf{1} = (1, \dots, 1)^T$. The dashed grey domain ensures the existence of a unique (non-feasible) globally asymptotically stable equilibrium ($a = \alpha$ and $m = \mu$)



Consumer-resource web

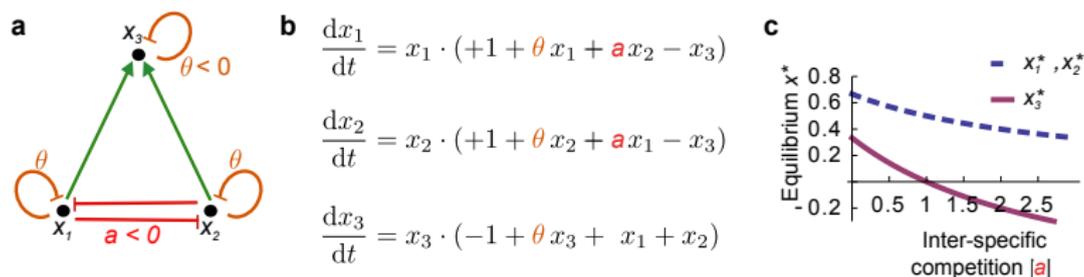


Figure: The o.d.e. associated to a consumer-resource web.

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

McArthur model for consumer-resource webs

MacArthur developed a seminal consumer resource model that describes the time evolution of the biomass N_i of consumer i and that of abundance of resource k :

$$\frac{dN_i}{dt} = d_i N_i \left(\sum_k c_{ik} w_k R_k - T_i \right), \quad (2)$$

where

- R_k denotes the abundance of resource k ,
- w_k is the weight of item of resource k in gram,
- c_{ik} is the probability that consumer i encounters and eats an item of resource k per unit of time,
- d_i is a constant of proportionality governing the biochemical conversion of grams of resource into grams of N_i .

McArthur model for consumer-resource webs

The resources have equations describing their own renewal

$$\frac{dR_k}{dt} = \left\{ \frac{r_k}{K_k} (K_k - R_k) \right\} - \sum_j c_{jk} N_j, \quad (3)$$

where the term in bracket is a logistics self-inhibition of resource by itself.

MacArthur assumed a quasi-equilibrium by setting $dR_k/dt = 0$, so that

$$R_k = K_k - \sum_j c_{jk} \frac{K_k}{r_k} N_j, \quad (4)$$

Consumer-resource dynamics at quasi-equilibrium

This quasi-equilibrium leads to the LV equation

$$\frac{dN_i}{N_i} = d_i \left(\mathcal{K}_i - \sum_{j=1}^n \alpha_{ij} N_j \right), \quad (5)$$

with indirect resource based interaction coefficient

$$\alpha_{ij} = \sum_k c_{ik} c_{jk} \frac{w_k K_k}{r_k} = \alpha_{ji}.$$

For a single resource, this becomes $\alpha_{ij} = c_i c_j$. Within this quasi-equilibrium where resources reach equilibrium much faster than consumers, [the competition matrix \$\alpha\$ is symmetric](#). MacArthur used this symmetry to get a Lyapunov function that shows that the orbit of the o.d.e. reach [the globally asymptotically stable equilibrium point](#).

Consumer-resource dynamics at quasi-equilibrium

We obtained the following LV system assuming quasi-equilibrium in the McArthur consumer-resource system

$$\frac{dN_i}{dt} = d_i N_i \left(\mathcal{K}_i - \sum_{j=1}^S \alpha_{ij} N_j \right), \quad (6)$$

with indirect resource based interaction coefficient

$$\alpha_{ij} = \sum_{k=1}^M c_{ik} c_{jk} = \alpha_{ji},$$

for M resources. This corresponds to a LV model with interaction matrix

$$B = -CC^T, \quad C = (c_{ik}) \in \mathbb{R}^{S \times M}.$$

In this case there is a unique globally asymptotically stable equilibrium

Structural instabilities for consumer-resource models

Dalmedigos and Bunin, PLOS Comput. Biol. 2020, considered perturbations of (6) of the form

$$\frac{dN_i}{dt} = d_i N_i \left(\mathcal{K}_i + \sum_{j=1}^S B_{ij} N_j \right) + \eta_i,$$

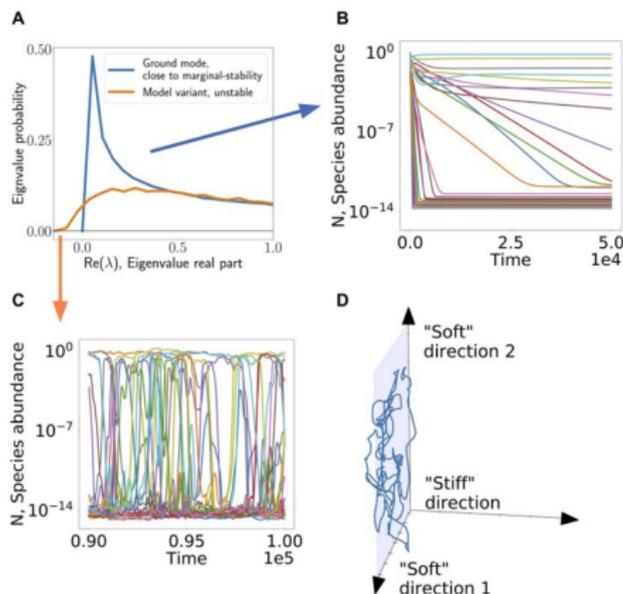
where the extra parameter η_i models immigration (which is assumed to be small). In this study, $S, M \rightarrow \infty$. The perturbed LV interaction matrix takes the form

$$-B = \omega \underbrace{\left(\frac{A}{\sqrt{S}} + \frac{\mu_d}{S} \mathbf{1}_S \mathbf{1}_S^T \right)}_{\text{non-symmetric perturbation}} + \underbrace{\frac{\sigma_c^2}{S} \left(a + \frac{\mu_c}{\sqrt{S} \sigma_c} \mathbf{1}_S \mathbf{1}_M^T \right) \left(a + \frac{\mu_c}{\sqrt{S} \sigma_c} \mathbf{1}_S \mathbf{1}_M^T \right)^T}_{\frac{C}{\sigma_c / \sqrt{S}} CC^T},$$

where ω is a parameter modelling the strength of the perturbation, which is adjusted to preserve a fixed amount of perturbation.

Structural instabilities for consumer-resource models

These plots illustrate perpetual oscillations for the previous model



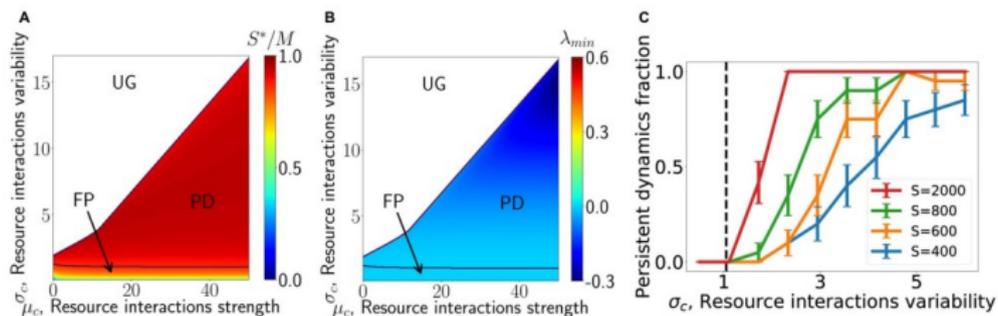


Fig 2. The model exhibits three phases, i.e. regions with qualitatively distinct behavior. In one, the system converges to a stable fixed point (FP), in another fixed points of the system are unstable yielding persistent dynamics (PD). In the third phase, unbounded growth (UG), species abundances grow without bound. ω is adjusted in order to maintain constant perturbation strength of 0.05. (A) Color map of the ratio S^*/M , indicating how close the system is to competitive exclusion $S^*/M = 1$, assuming an equilibrium reached. In the PD phase the calculation of S^*/M is no longer valid and $S^*/M > 1$ may be reached (see later sections). (B) The minimal real part of eigenvalues of the interaction matrix between coexisting species, λ_{min} . Fixed point stability is lost at $\lambda_{min} = 0$, where the solid line separates the FP and PD phases. The increase in S^*/M reduces the stability of the equilibria, triggering a transition to persistent dynamics. (C) Probability of reaching persistent dynamics along a vertical cross section of the diagrams in panels A and B, in simulations with different pool richness S . The transition between equilibrium and non-equilibrium outcomes becomes sharper as system size increases, and matches the theoretically predicted transition point between the phases (dashed line).

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Figure: FP: stable equilibrium. PD: persistent dynamics. UG: unbounded growth