Laboratoire de Physique Théorique et Modèles Statistiques

Ecological networks, complex systems, stability

Université Gustave Eiffel — October 2024

Valentina Ros @ LPTMS Orsay

The multiple equilibria of many-species ecosystems: how many, how stable, how relevant?

joint work with F. Roy, G. Biroli, G. Bunin, A. Turner

Physical Review Letters 130, 257401 (2023)
J. Phys. A: Math. Theor. 56 305003J (2023)

université PARIS-SACLAY GRADUATE SCHOOL Physique | PhOM Physique des Ondes et de la Matière

The setting

Review Article | Published: 11 October 2001

Catastrophic shifts in ecosystems

Marten Scheffer, Steve Carpenter, Jonathan A. Foley, Carl Folke & Brian Walker

Nature **413**, 591–596 (2001) | Cite this article

All ecosystems are exposed to gradual changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. Nature is usually assumed to respond to gradual change in a smooth way. However, studies on lakes, coral reefs, oceans, forests and arid lands have shown that smooth change can be interrupted by sudden drastic switches to a contrasting state. Although diverse

Article | Published: 27 June 2022

Chaos is not rare in natural ecosystems

Tanya L. Rogers, Bethany J. Johnson & Stephan B. Munch

Nature Ecology & Evolution **6**, 1105–1111 (2022) | Cite this article

Chaotic turnover of rare and abundant species in a strongly interacting model community

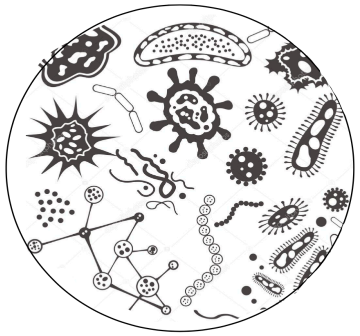
Emil Mallmin, Arne Traulsen, and Silvia De Monte Authors Info & Affiliations

Edited by Alan Hastings, University of California, Davis, CA; received July 28, 2023; accepted February 2, 2024

March 4, 2024 | 121 (11) e2312822121 | https://doi.org/10.1073/pnas.2312822121

This talk: a counting problem

Model of **high-dimensional** (many species) ecosystem dynamics with **random interactions**



$$\frac{dn_i(t)}{dt} = F_i(\mathbf{n}(t), \hat{a})$$

$n_i(t)$=species abundance

$\hat{a}$ = randomness

$i = 1,\cdots, D \gg 1$

Counting problem: how many equilibria $\mathbf{n}^*$ such that $F_i(\mathbf{n}^*, \hat{a}) = 0$ for all $i = 1,\cdots, D$

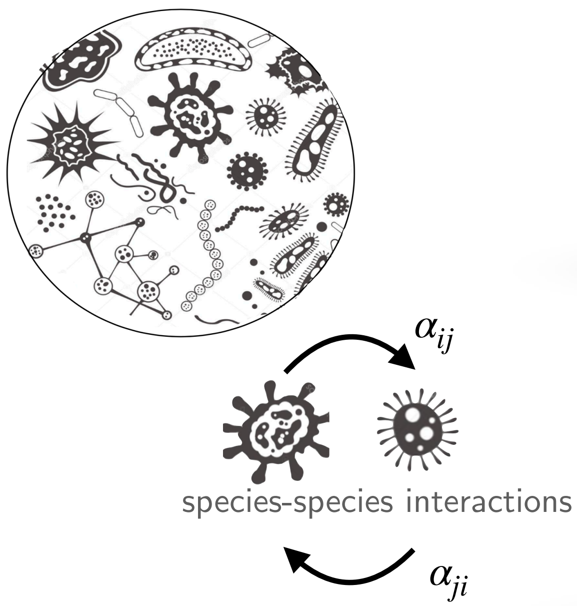
How many, ***typically:*** with highest probability ($\mathbb{P} \to 1$ when $D \to \infty$)

High-dimensional system of non-linear random equations: can have many solutions.

If many: how diverse, how stable, how relevant for dynamics?

Model for ecosystems dynamics: rGLVE

rGLVE - random Generalized Lotka-Volterra equations for *many* interacting species



$$\frac{dn_i(t)}{dt} = n_i(t)\left(1 - n_i(t) - \sum_{j=1}^{D} \alpha_{ij} n_j(t)\right)$$

$n_i(t) =$ (rescaled) abundance of species i

$i = 1, \cdots, D \gg 1$

Random pairwise interactions. α_{ij} Gaussian, correlated only with α_{ji}

$$\langle \alpha_{ij} \rangle = \frac{\mu}{D} \qquad \langle \alpha_{ij} \alpha_{kl} \rangle_c = \frac{\sigma^2}{D}\left(\delta_{ik}\delta_{jl} + \gamma\, \delta_{il}\delta_{jk}\right)$$

Reciprocal interactions: $\gamma = 1$

Three parameters: average interaction strength μ, variability of interactions σ, asymmetry γ

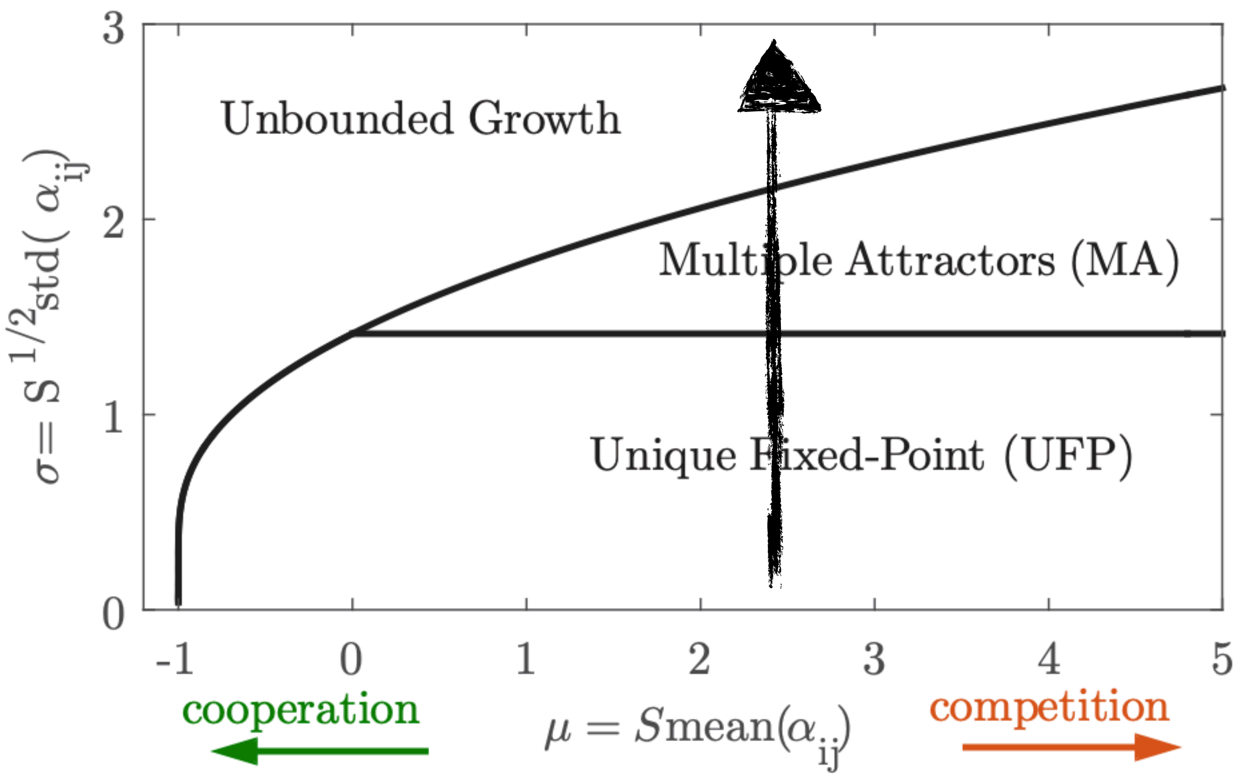
Several talks on this model, already! In this talk:

- A large-D scaling: all terms in equation are $\mathcal{O}(1)$ when $D \to \infty$. *vs S. Allesina*
- No sparsity: all-to-all interactions. No spatial eterogeneities. *vs W. Hachem, F. de Laender*
- Gaussian interactions. No time dependent couplings (“quenched randomness”). *vs S. Azaele*

A dynamical transition

$$\frac{dn_i(t)}{dt} = n_i(t)\left(1 - n_i(t) - \frac{\mu}{D}\sum_{j=1}^{D} n_j(t) + \frac{\sigma}{\sqrt{D}}\sum_{j=1}^{D} a_{ij}n_j(t)\right) \qquad \langle a_{ij}a_{kl}\rangle = \delta_{ik}\delta_{jl} + \gamma\,\delta_{il}\delta_{jk}$$

For D large: two different dynamical phases separated by a transition



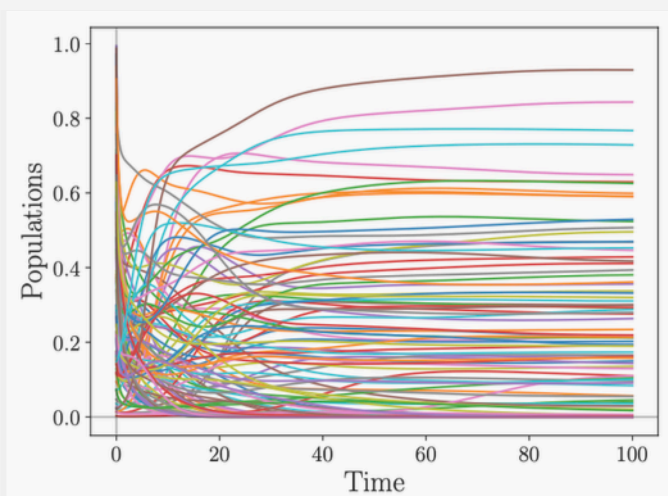
Phase diagram from Bunin 2017

A dynamical transition

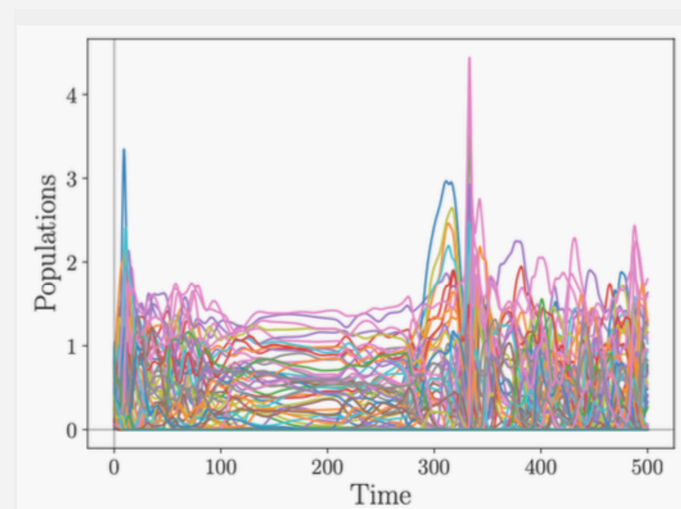
$$\frac{dn_i(t)}{dt} = n_i(t)\left(1 - n_i(t) - \frac{\mu}{D}\sum_{j=1}^{D} n_j(t) + \frac{\sigma}{\sqrt{D}}\sum_{j=1}^{D} a_{ij}n_j(t)\right) \qquad \langle a_{ij}a_{kl}\rangle = \delta_{ik}\delta_{jl} + \gamma\,\delta_{il}\delta_{jk}$$

For D large: two different dynamical phases separated by a transition

stationary, unique equilibrium — **non-stationary dynamics**



$$\sigma_c = \frac{\sqrt{2}}{1+\gamma}$$



σ - variability

Simulation of dynamics from: Roy, Biroli, Cammarota 2019

Similar transitions in many large-D models of agents with random interactions & non-linearity

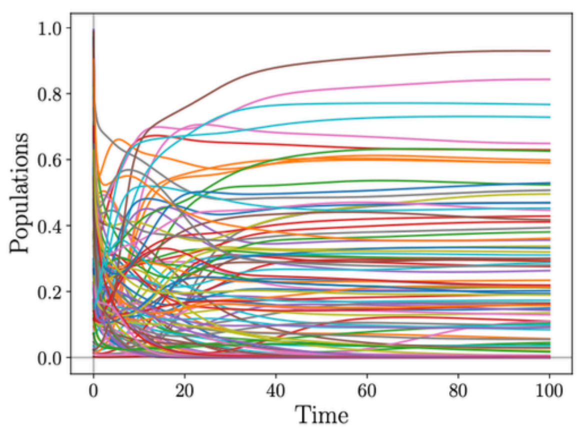
Neural networks: Sompolinsky, Crisanti, Sommers 1988

Ecosystems: Rieger 1989 Opper, Diederich 1991 Opper, Diederich 1999

Game theory: Berg, Weigt 1999 Galla, Farmer 2013 Garnier-Brun, Benzaquen, Ciliberti, Bouchaud 2021

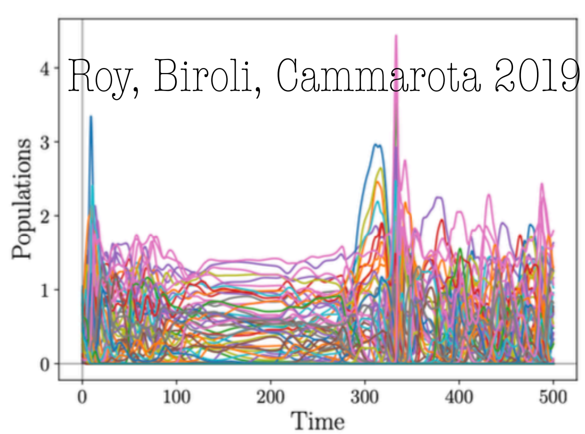
Some questions & some tools

stationary, unique equilibrium



transition σ_c

non-stationary dynamics



variability σ

Stationary regime: properties of the equilibrium?

self-consistent large-D arguments: cavity, AMP
review: Barbier, Arnoldi 2017

talk W. Hachem

Loss of stability of equilibrium?

(non)-linear response & its breakdown

Loss of uniqueness: emergence of multiple, competing equilibria, i.e. glassiness? Which properties?

Methods from glasses [replica method]
& random matrix theory [Kac-Rice methods]

Species turnover
Rescuing, intermittency

Chaotic dynamics?
Slow dynamics with aging?
Fundamental mechanisms?

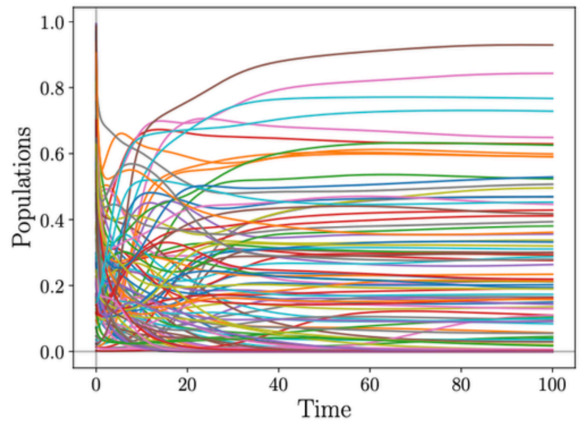
Simulations dynamics

Effective single-particle dynamical processes: DMFT
review: Cugliandolo 2023
Galla 2023

talk S. Azaele

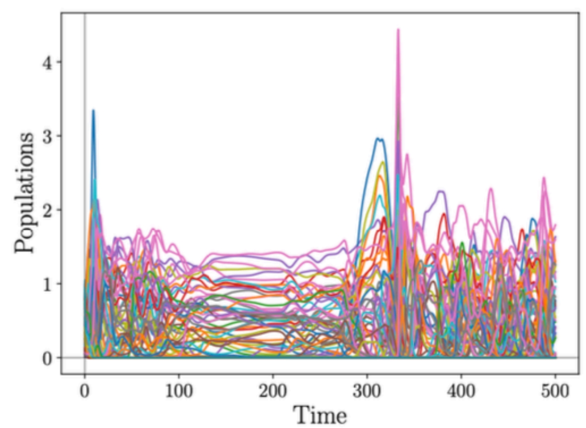
Some questions & some tools

stationary, unique equilibrium



transition σ_c

non-stationary dynamics



variability σ

Stationary regime:
properties of the equilibrium?

Loss of stability of equilibrium?

This talk

Loss of uniqueness: emergence of multiple, competing equilibria, i.e. glassiness? Which properties?

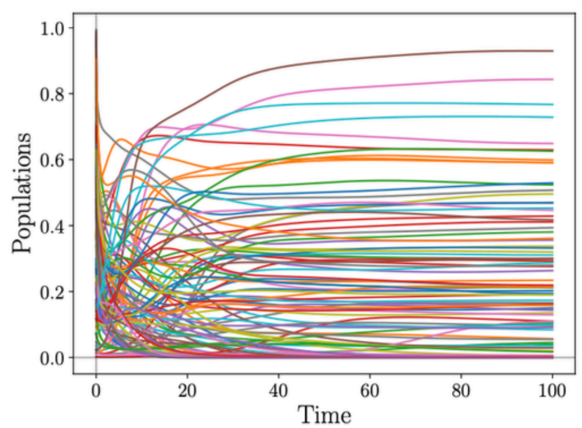
Methods from glasses
[replica method]
& random matrix theory
[Kac-Rice methods]

Species turnover
Rescuing, intermittency

Chaotic dynamics?
Slow dynamics with aging?
Fundamental mechanisms?

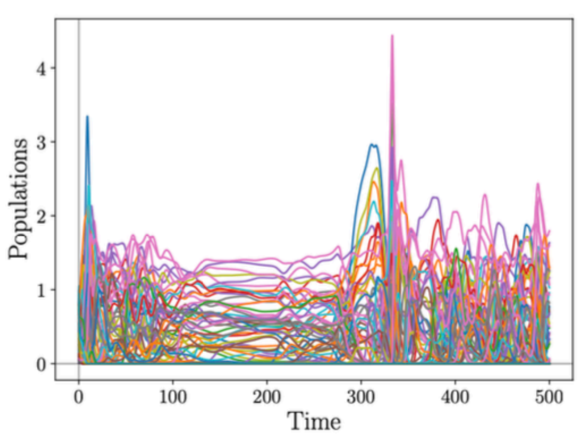
...

stationary, unique equilibrium



transition σ_c

non-stationary dynamics



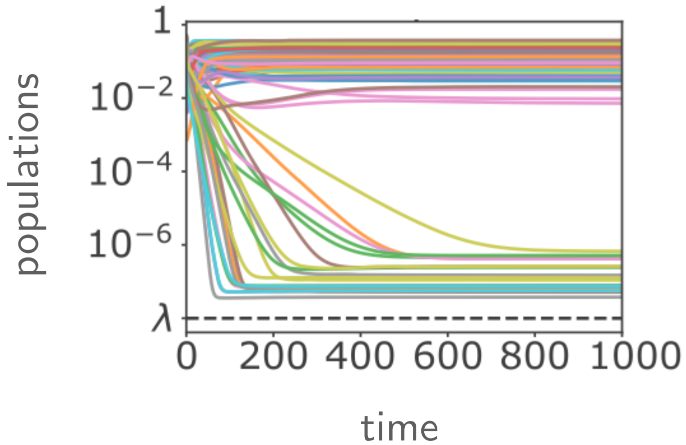
variability σ

Plan of the rest of the talk

- When the equilibrium is unique: self-consistency, diversity, stability
- Beyond the transition I: the high-D math tools
- Beyond the transition II: equilibria for uncorrelated interactions $(\gamma = 0)$
- Beyond the transition III: tuning the non-reciprocity
- Work in progress & summary

When the equilibrium is unique.

Properties of an equilibrium



Arnoulx de Pirey, Bunin 2024

Equilibrium: vector $\mathbf{n}^* = (n_1, \cdots, n_D)$ such that for all $i = 1, \cdots, D$

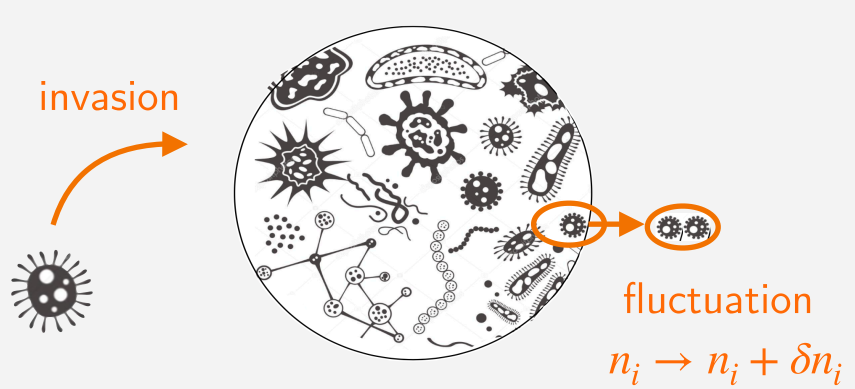
$$\frac{dn_i(t)}{dt} = n_i \left(1 - n_i - \frac{\mu}{D}\sum_{j=1}^{D} n_j + \frac{\sigma}{\sqrt{D}}\sum_{j=1}^{D} a_{ij} n_j + \epsilon_i \right)\Bigg|_{\mathbf{n}^*, \epsilon=0} = n_i\, f_i(\mathbf{n}, \hat{a})\Big|_{\mathbf{n}^*, \epsilon=0} = 0$$

effective growth rates/forces

Two notions of stability of the equilibrium.

"saturation"

- Un-invadibility $\quad f_i(\mathbf{n}^*, \hat{a}) < 0 \quad$ for $\quad n_i^* = 0$
- Linear stability matrix $\quad M_{ij} = \dfrac{\partial f_i(\mathbf{n}^*, \hat{a})}{\partial n_j}$
  negative definite for $n_i^*, n_j^* > 0$



Equlibrium is a random vector. For large D, has properties that are **typical** ($\rightarrow$ concentrating):

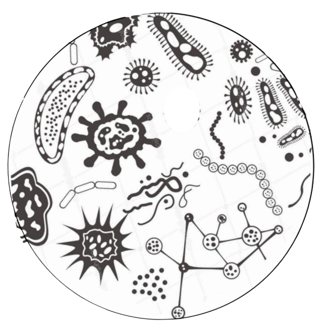
- Diversity $\quad \phi = \dfrac{1}{D}\sum_{i=1}^{D} 1_{n_i^*>0}$ - coexisting species
- Abundance $\quad m = \dfrac{1}{D}\sum_{i=1}^{D} n_i^*$
- Self-similarity $\quad q = \dfrac{1}{D}\sum_{i=1}^{D} [n_i^*]^2$
- Suceptibility $\quad \chi = \dfrac{1}{D}\sum_{i=1}^{D} \dfrac{dn_i^*}{d\epsilon_i}\Big|_{\epsilon=0}$

Unique equilibrium: self-consistent “cavity” analysis

(i) **assume unique, un-invadable stable equilibrium** $\mathbf{n} = (n_1, \cdots, n_D)$ with D species and given q, m, χ, ϕ .

(ii) add one species: $0 \to n_0$. When D large, small perturbation that should modify weakly the equilibrium

> Assume other species **react linearly**: $n_i = n_{i/0} + \delta n_i$
>
> Derive an equation for n_0 at new equilibrium as a function of parameters of old equilibrium

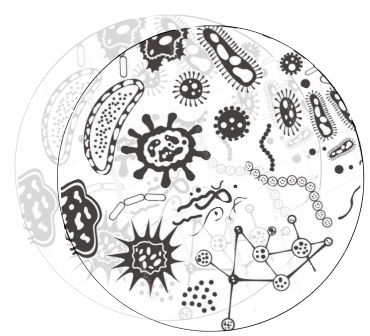


equilibrium

+

new species

=



new equilibrium

$$n_0 = \max \left\{ 0, \frac{1 - \mu m + m\sigma\sqrt{q}\, Z_G}{(1 - \gamma\chi)m} \right\}$$

Z_G = standard Gaussian

(iii) impose **self-consistency**: new species behaves statistically like all others → closed equations for m, ϕ, χ, q.

Lotka-Volterra/replicator: Diederich, Opper 1989 Bunin 2017 Barbier Arnoldi 2017

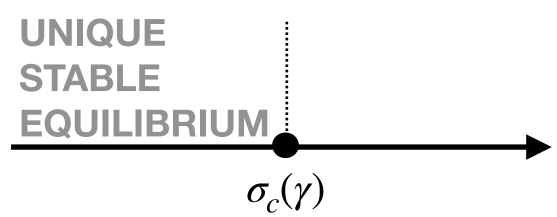
MacArthur: Advani, Bunin, Mehta 2017 Blumenthal, Rocks, Mehta 2024

Dynamical version (DMFT): Opper, Diederich 1991 Galla 2006 Galla 2018 Roy, Biroli, Cammarota 2019

Transition: instability and marginality

Consistency of the cavity derivation can be checked: breaks down at $\sigma_c = \sqrt{2}(1+\gamma)^{-1}$.

Notice: cavity equations can still be solved beyond this boundary: meaning?

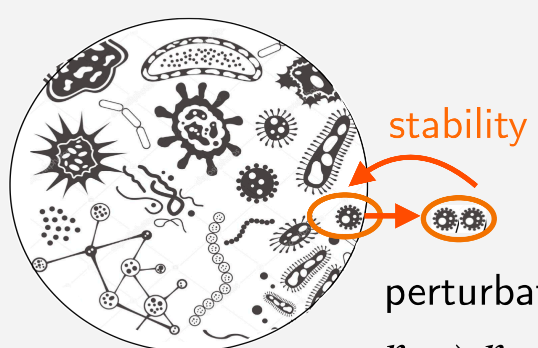


Perturb infinitesimally all coexisting species: $n_i \to n_i + \epsilon \Delta n_i$, Δn_i random

Boundary of stability: $\langle \left(\frac{\delta n_0}{\delta \epsilon} \right)^2 \rangle \to \infty$ $\quad \sigma_c(\gamma) = \sqrt{2}(1+\gamma)^{-1}$

What happens to the equilibrium?

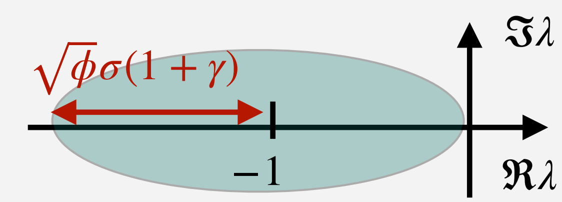
Becomes marginally stable at $\sigma_c(\gamma)$



perturbation
$n_i \to n_i + \delta n_i$

Linear stability matrix $M_{ij} = \dfrac{\partial f_i(\mathbf{n}^*, \hat{a})}{\partial n_j}$ has a spectrum touching zero

$\text{supp}[\rho(\lambda)]$ — evalue density of $M/\sqrt{D}$



$$\text{Cov}\left(\alpha_{ij}\alpha_{kl}\right) = \frac{\sigma^2}{D}\left(\delta_{ik}\delta_{jl} + \gamma\, \delta_{il}\delta_{jk}\right)$$

Diversity and stability are related by **May stability bound:** lineraly stable equilibria for $\phi < \phi_{\text{May}} = \dfrac{1}{\sigma^2(1+\gamma)^2}$

Bound saturated at transition. R. May 1972

Beyond the transition I

The high-D math tools.

What we compute: the complexity

$$n_i \left(1 - n_i - \frac{\mu}{D}\sum_{j=1}^{D} n_j + \frac{\sigma}{\sqrt{D}}\sum_{j=1}^{D} a_{ij} n_j\right) = n_i\, f_i(\mathbf{n}) = 0$$

Equilibria: $\mathbf{n}^\alpha = (n_1^\alpha, \cdots, n_D^\alpha)$

Effective growth rates: $\mathbf{f}^\alpha = (f_1(\mathbf{n}^\alpha), \cdots, f_D(\mathbf{n}^\alpha))$

Un-invadibility: $f_i(\mathbf{n}^\alpha) < 0 \quad \text{if} \quad n_i^\alpha = 0$

Typical properties are now distributed over equilibria

- Diversity $\phi^\alpha = \frac{1}{D}\sum_{i=1}^{D} 1_{n_i^\alpha > 0}$
- Abundance $m^\alpha = D^{-1}\sum_{i=1}^{D} n_i^\alpha$
- Similarity $q^{\alpha\beta} = D^{-1}\sum_{i=1}^{D} n_i^\alpha n_i^\beta$
- More .....

$\sigma > \sigma_c$, number of equilibria $\mathcal{N}$ scales as $\mathcal{N} \sim O(e^D)$

Concentration of the log:

$$\lim_{D\to\infty} \frac{\log \mathcal{N}}{D} = \lim_{D\to\infty} \frac{\mathbb{E}[\log \mathcal{N}]}{D} \equiv \Sigma$$

"(quenched) complexity"

Computer Physics Communications 121–122 (1999) 141–144

Replicator dynamics

Manfred Opper [a,1], Sigurd Diederich [b]

It is possible to calculate the average of the number $\mathcal{N}$ of locally stable fixed point solutions. We can show that

here $u \to \sigma^{-1}$ and $\eta \to \gamma$

$$\lim_{N\to\infty} \frac{1}{N} \ln\langle \mathcal{N}\rangle = \begin{cases} = 0 & \text{for } u > u_c \text{ and all } \eta, \\ > 0 & \text{for } u < u_c \text{ at } \eta = 1, \\ < 0 & \text{for } u < u_c \text{ at } \eta = 0. \end{cases} \qquad (4)$$

the log makes a difference!

talk H. Benisty

The Kac-Rice formula & replicas

Number $\mathcal{N}(\phi)$ of equilibria $\mathbf{n}^*$ such that $\mathbf{f}(\mathbf{n}^*) = 0$ and $\Phi(\mathbf{n}^*) = \phi$ (arbitrary constraints) is a random variable with scaling: $\mathcal{N}(\phi) \sim e^{D\,\Sigma(\phi)+o(D)}$.

The **"Kac-Rice formula"** gives a recipe to compute the first moment of $\mathcal{N}(\phi)$

$$\mathbb{E}[\mathcal{N}(\phi)] = \int_{\mathcal{M}_D} d\mathbf{n}\, \mathcal{P}_{\mathbf{n}}\left(\mathbf{f} = \mathbf{0}\right) \mathbb{E}_{\mathbf{n}}\left[\left|\det\left(\frac{\partial f_i(\mathbf{n})}{\partial n_j}\right)\right| \chi_{\Phi(\mathbf{n})=\phi} \,\middle\|\, \mathbf{f} = \mathbf{0}\right]$$

Extracting the large-D limit of this, we obtain the **"annealed complexity"**

$$\Sigma^A(\phi) = \lim_{D\to\infty} \frac{\log \mathbb{E}[\mathcal{N}(\phi)]}{D}$$

Exponentially-large quantities: asymptotics of the average is not asymptotics of the typical value!

To characterize typical values, rather compute the **"quenched complexity"**

$$\Sigma^Q = \lim_{D\to\infty} \frac{\mathbb{E}[\log \mathcal{N}]}{D} = \lim_{D\to\infty} \lim_{m\to 0} \frac{\mathbb{E}[\mathcal{N}^m] - 1}{Dm} \qquad \textbf{Replica Trick!}$$

A high-D variational problem

The Kac-Rice formulas for higher moments:

$$\mathbb{E}[\mathcal{N}^m(\phi)] = \int_{\mathcal{M}_D^{\otimes m}} \prod_{k=1}^{m} d\mathbf{n}^{(k)} \, \mathcal{P}_{\{\mathbf{n}^{(k)}\}}\left(\left\{\mathbf{f}^{(k)}=\mathbf{0}\right\}\right) \mathbb{E}_{\{\mathbf{n}^{(k)}\}}\left[\prod_{k=1}^{m}\left|\det\left(\frac{\partial f_i(\mathbf{n}^{(k)})}{\partial n_j^{(k)}}\right)\right| \chi_{\Phi(\mathbf{n}^{(k)})=\phi} \, \Big\| \left\{\mathbf{f}^{(k)}=\mathbf{0}\right\}\right]$$

→ problems of **coupled random matrices**

The essence of the procedure: map into a variational problem in large-D:

$$\mathbb{E}[\mathcal{N}^m(\phi)] = \int \prod_{a<b<=1}^{m} dq_{ab}\, dm_a\, dp_a e^{Dm\mathcal{A}[q_{ab},m_a,p_a]+\cdots} \sim e^{Dm\mathcal{A}[q^*_{ab},m^*_a,p^*_a]}$$

mean-field dimensionality reduction

values optimizing the action

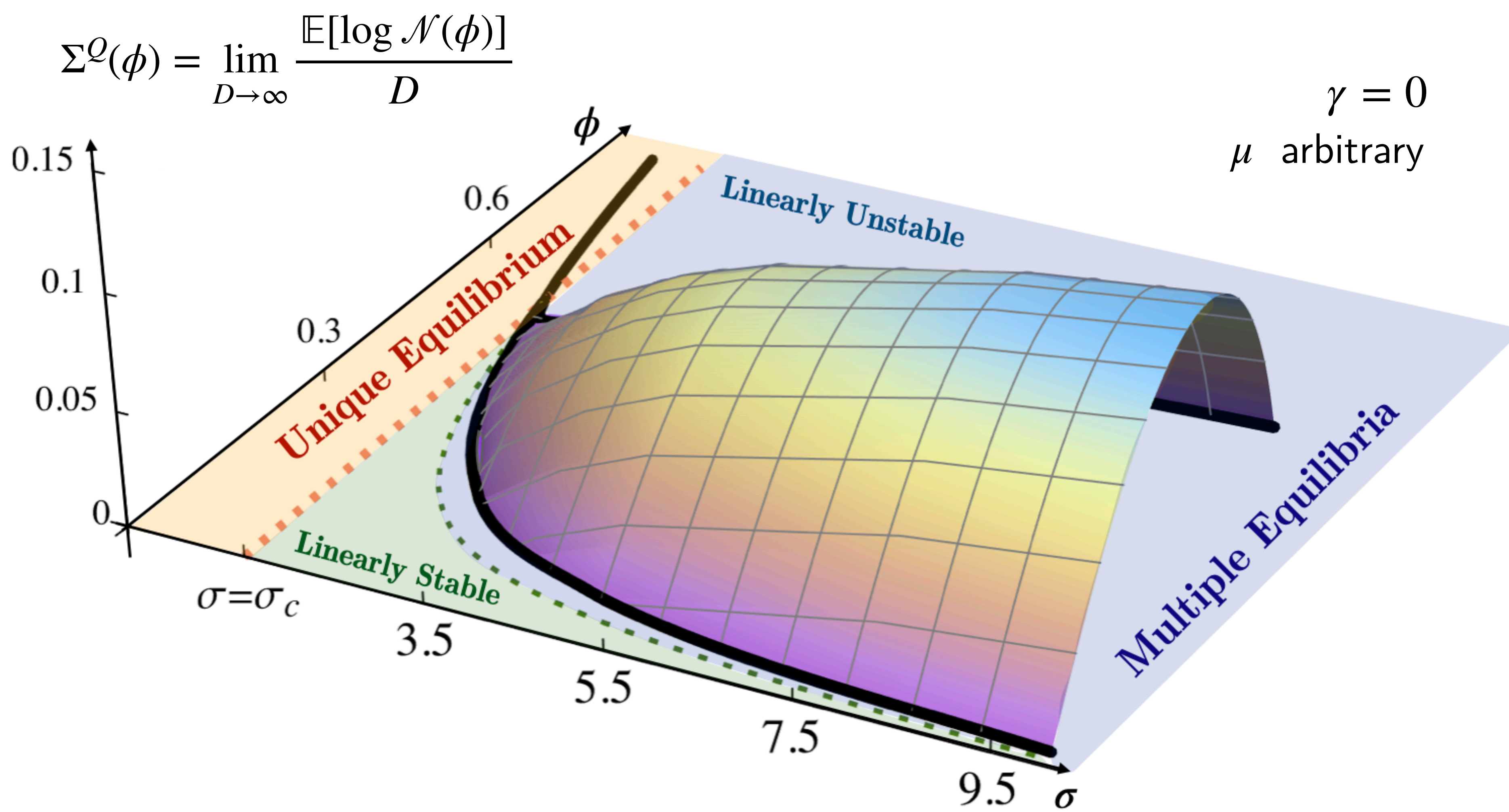
Result: coupled, self-consistent equations for parameters describing equilibria (abundance, similarity, effective growth rates)

"Replicated Kac-Rice" for quenched complexities: VR, Ben Arous, Biroli, Cammarota 2019

Beyond the transition II

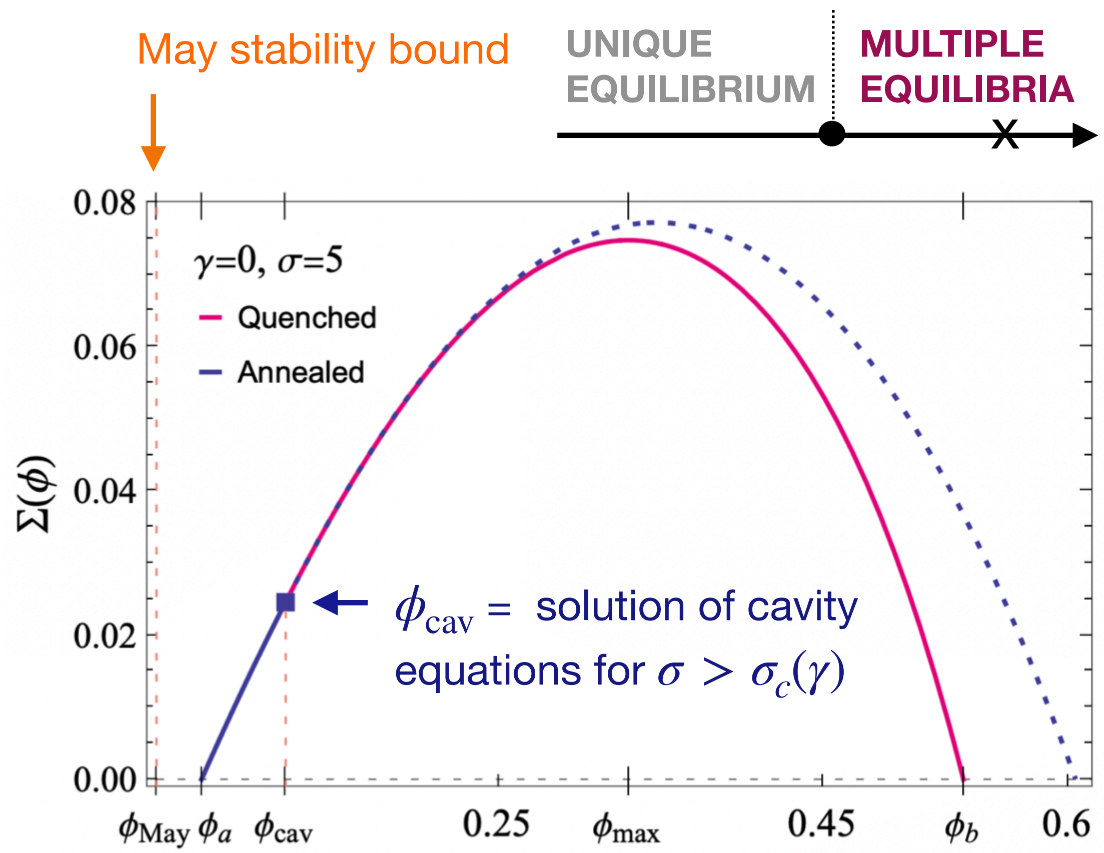
Equilibria for uncorrelated interactions

The complexity of equilibria: the results



- Complexity independent of μ. Parameters describing equilibria like abundance m, similarity q_{ab} depend on μ
- It vanishes in unique equilibrium phase at a single ϕ: same value predicted by cavity calculation
- For $\sigma > \sigma_c$, **exponentially-many un-invadable equilibria** with a continuous **distribution of diversity:** we know the maximal and minimal diversity one can expect
- For $\sigma > \sigma_c$, all uninvadable equilibria are **linearly unstable: $\phi > \phi_{\text{May}}$**

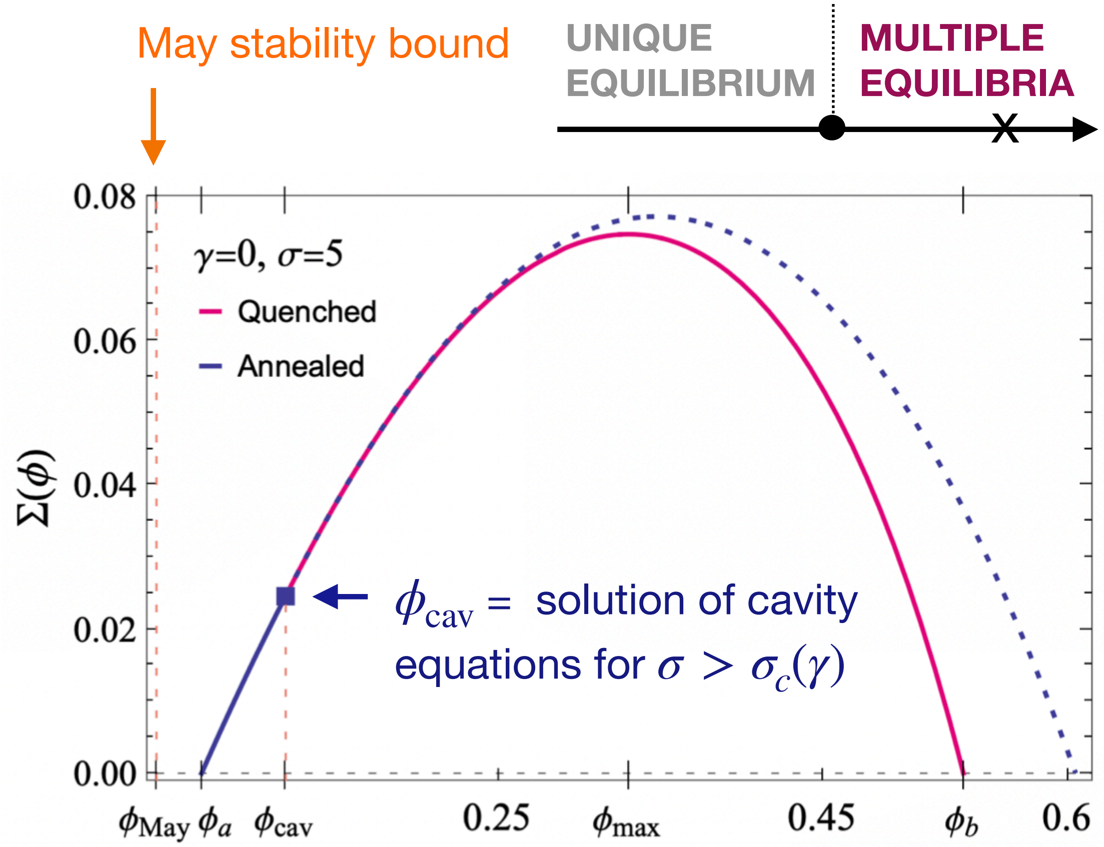
Quenched, Annealed, Cavity "matching point"



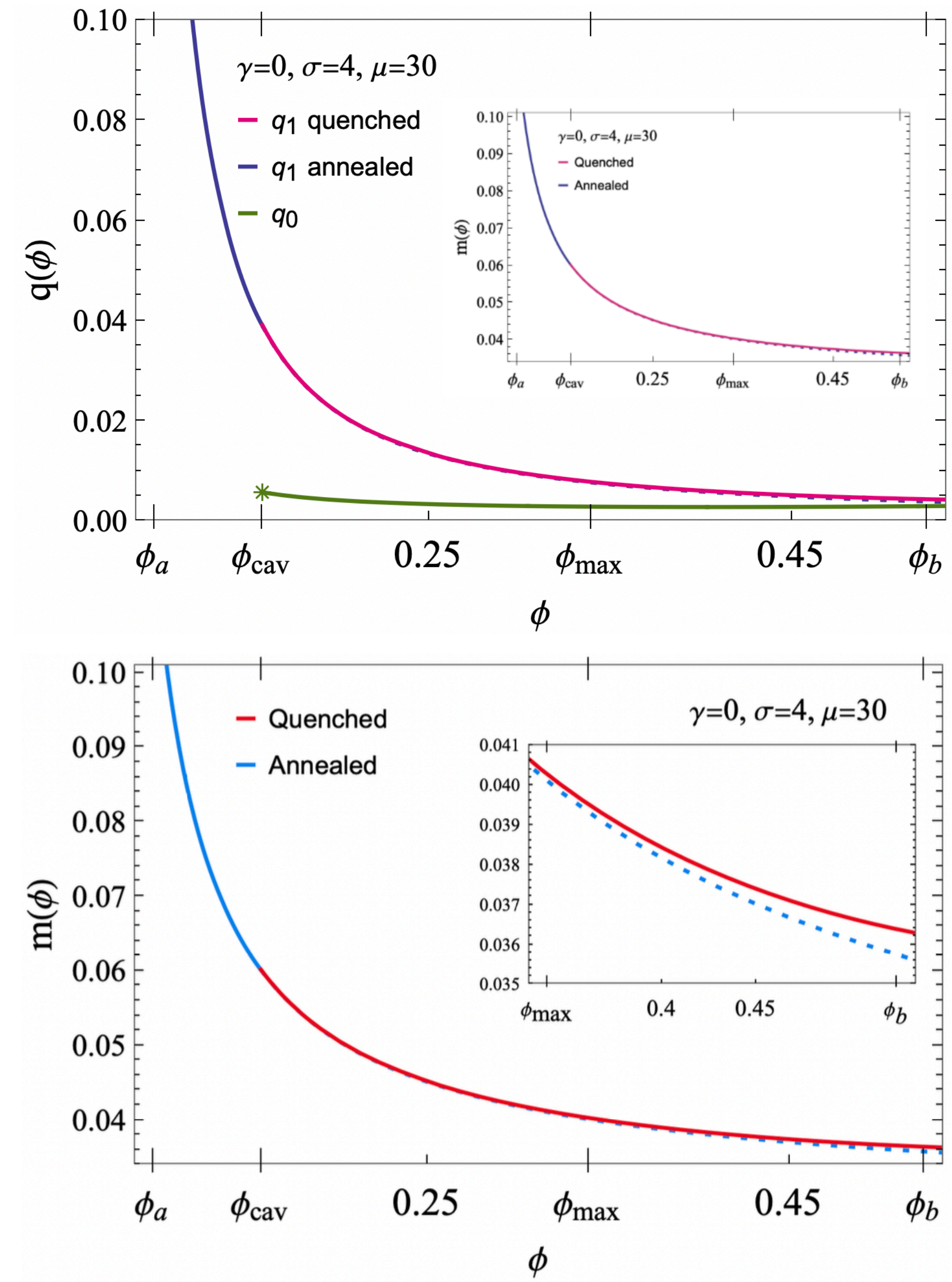
ϕ= diversity- fraction of non-extinct species

- Cavity calculation **still picks up equilibria**, but not the most numerous

Quenched, Annealed, Cavity “matching point”

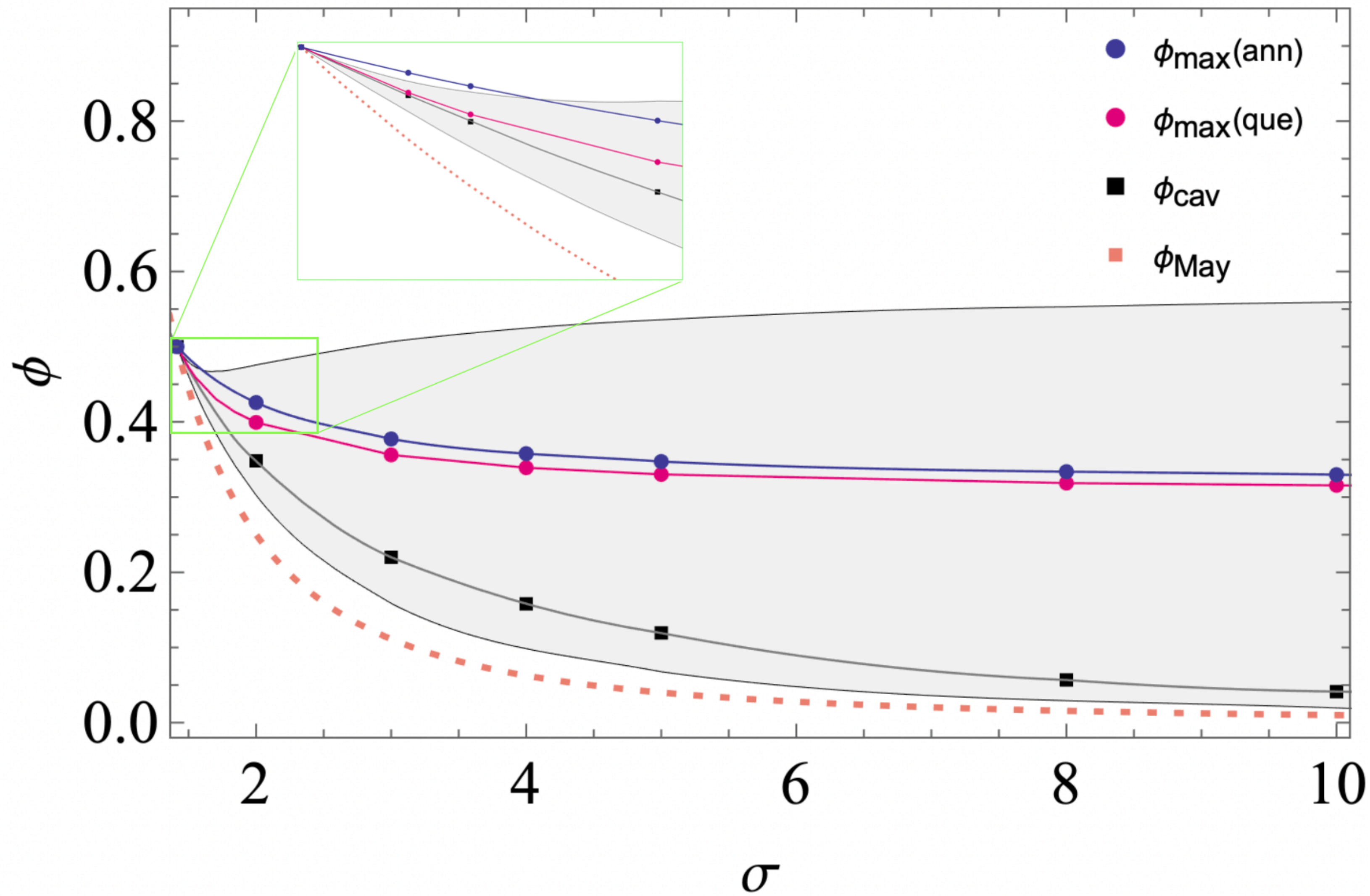


ϕ= diversity- fraction of non-extinct species



- Cavity calculation **still picks up equilibria**, but not the most numerous
- Equilibria with more coexisting species have **lower average abundance & are less similar to each others**
- Order parameters do **depend on μ**: as μ increases, m grows towards “unbounded” phase

Average vs typical



- Diversity of most numerous equilibria not captured by annealed approximation
- At $\sigma \sim \sigma_c$: annealed gives exponentially many equilibria at diversity were there is none!

  Similar phenomenology in econophysics models: Garnier-Brun, Benzaquen, Ciliberti, Bouchaud 2021

Beyond the transition III

Tuning non-reciprocity

A special limit: conservative dynamics ($\gamma = 1$)

Symmetric interactions ($\gamma = 1$) the model is conservative: like a spin-glass model with random energy $\mathcal{E}(\mathbf{n}, \hat{\alpha})$.

$$\frac{dn_i}{dt} = n_i f_i(\mathbf{n}, \hat{a}) + \kappa\xi_i(t) = -n_i\partial_{n_i}\mathcal{E}(\mathbf{n}, \hat{a}) + \kappa\xi_i(t)$$

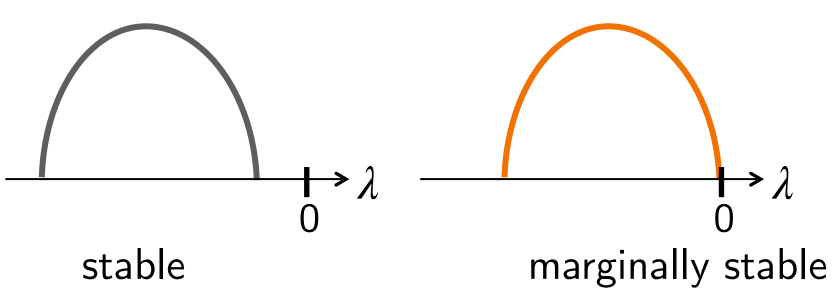
Stable equilibria are minima of $\mathcal{E}(\mathbf{n}, \hat{a})$: Can be characterized with **spin-glasses techniques for metastability**.

$$F_\beta(\hat{a}) = \log \mathcal{Z}_\beta(\hat{a}) = \log \int_{\mathcal{M}_D} d\mathbf{n}\, e^{-\beta\mathcal{E}(\mathbf{n},\hat{a})} \qquad \beta \to \infty$$

and "tilded" versions

$\sigma > \sigma_c$: many local minima. As in spin glasses, many **are *marginally stable:*** diversity saturates May bound, $\phi = \phi_{\text{May}}$.

spectra of stability matrix $\rho(\lambda)$



Without noise ($\kappa = 0$): Biroli, Bunin, Cammarota 2018

With noise ($\kappa > 0$): Altieri, Roy, Cammarota, Biroli 2021

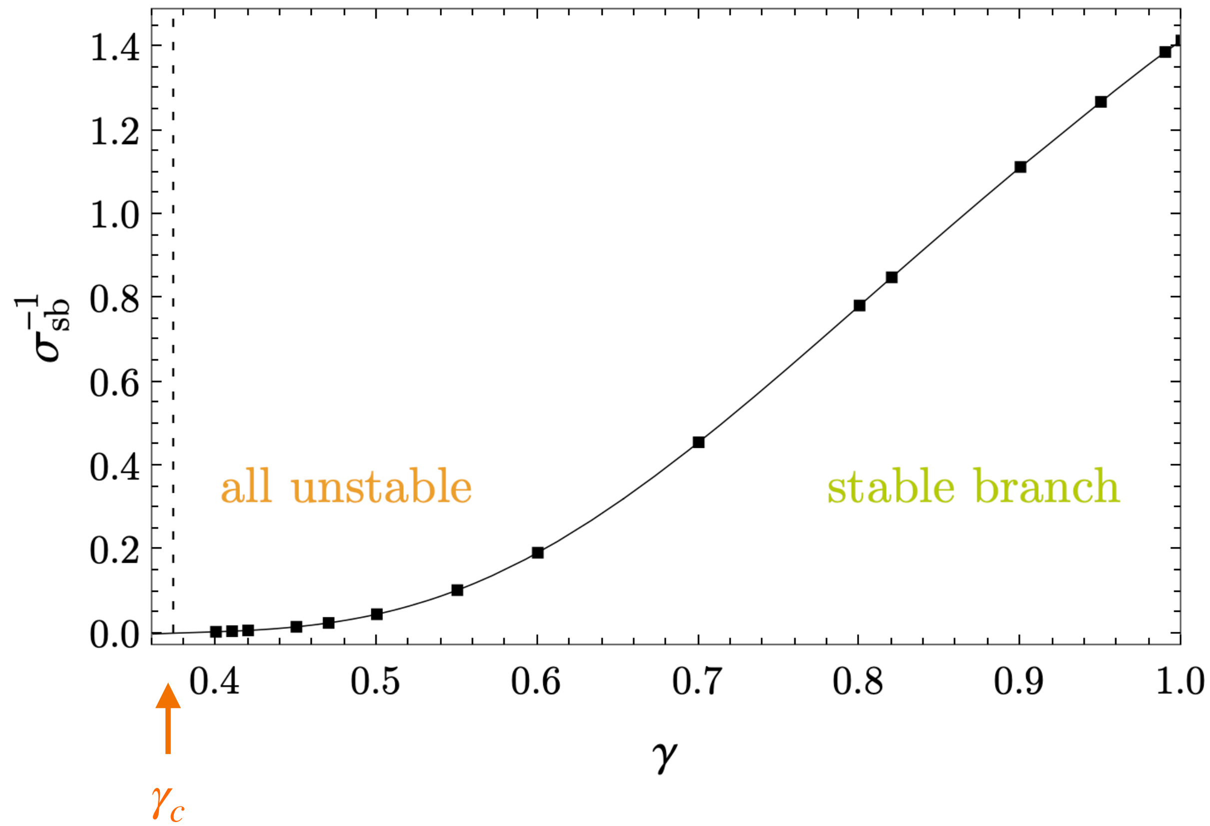
In spin-glass models: long-time dynamics converges to **marginally stable** minima; convergence slow, aging.

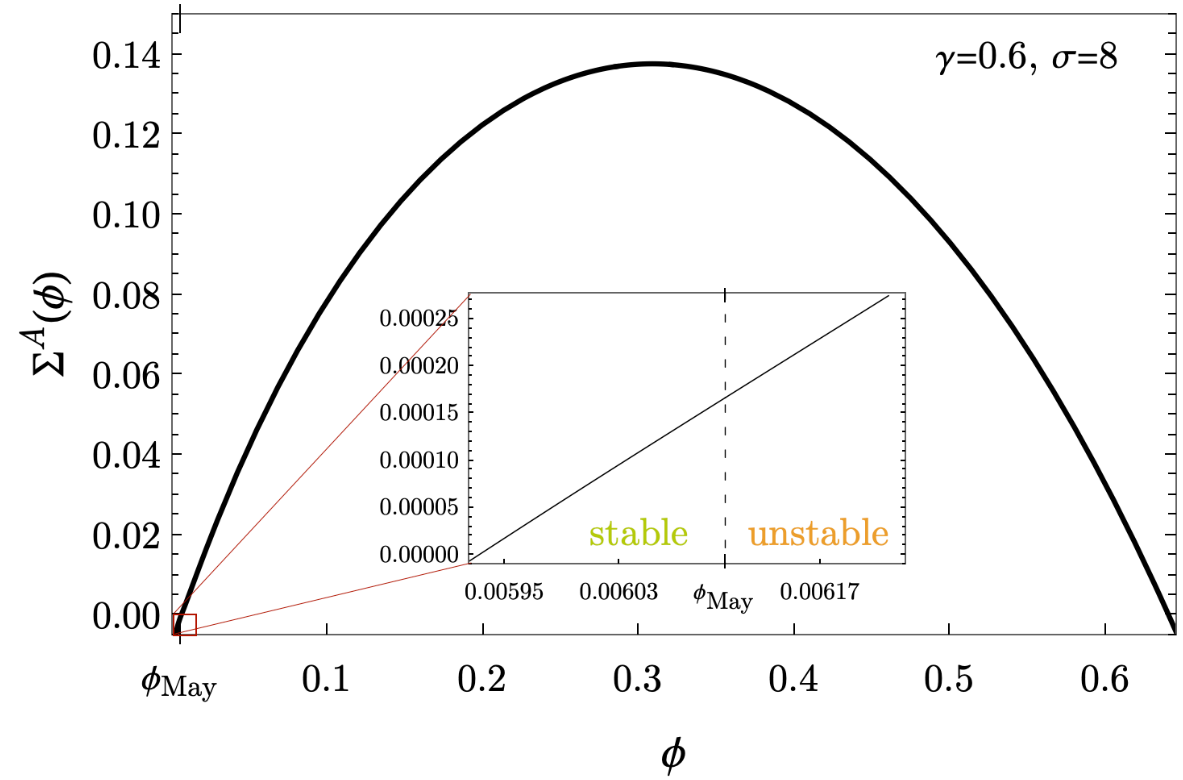
Cugliandolo, Kurchan 1995 **selection principle for equilibria!**

Symmetric rGLV: convergence to equilibria with $\phi = \phi_{\text{May}}$, with aging

Roy, Biroli, Bunin, Cammarota 2019

The case $\gamma \neq 0$: average number





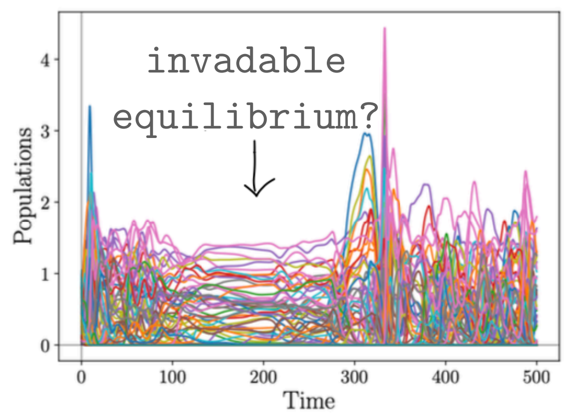
- Transition at $\gamma_c = 0.373$: for $\gamma < \gamma_c$, all equilibria are unstable
- For $\gamma > \gamma_c$, at $\sigma > \sigma_{\rm sb}$ some stable and marginally stable equilibria exist at small ϕ

The same "absolute instability transition" in the average number shown for other models:
Fyodorov 2016, Ben Arous, Fyodorov, Khoruzhenko 2021

What about typical number? $\rightarrow$ work in progress.

Summing up

Follow-ups and work in progress

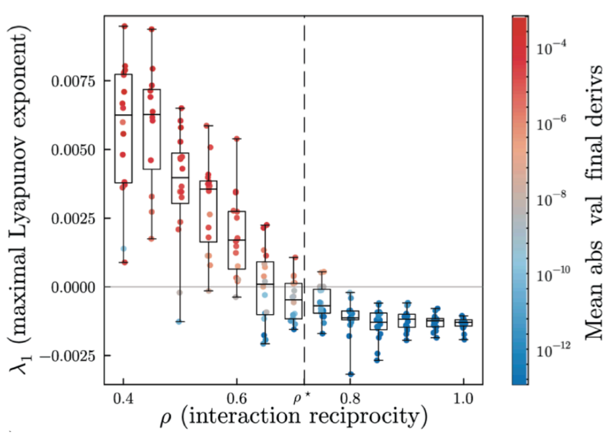


- Complexity of **invadable equilibria**, might be relevant for dynamics

  Arnoulx de Pirey, Bunin 2024

- Quenched complexity for general γ: **"absolute instability transition"** beyond the annealed approximation

  Ben Arous, Fyodorov, Khoruzhenko 2021



- Chaotic dynamics for non-reciprocal interactions observed in several models

  Roy, Biroli, Cammarota 2019

  Blumenthal, Rocks, Mehta PRL 132, 2024

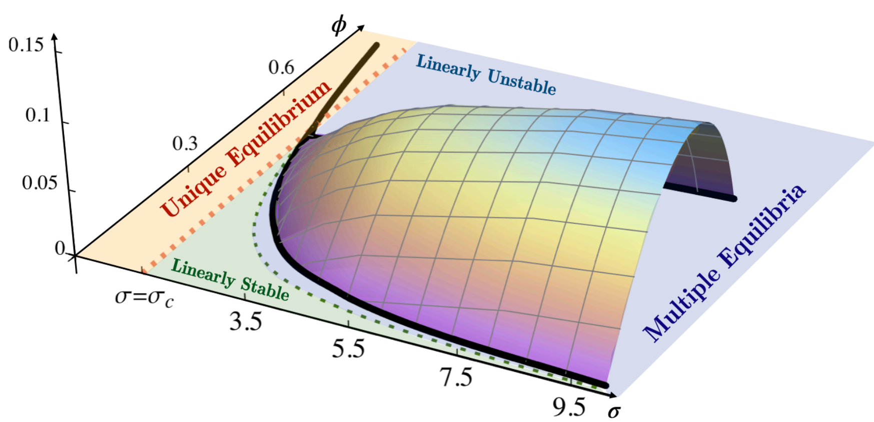
  Lyapunov exponent computed explicitly in neural-network models

  Sompolinsky, Crisanti, Sommers PRL 61, 1988

  Relations between complexity and Lyapunov

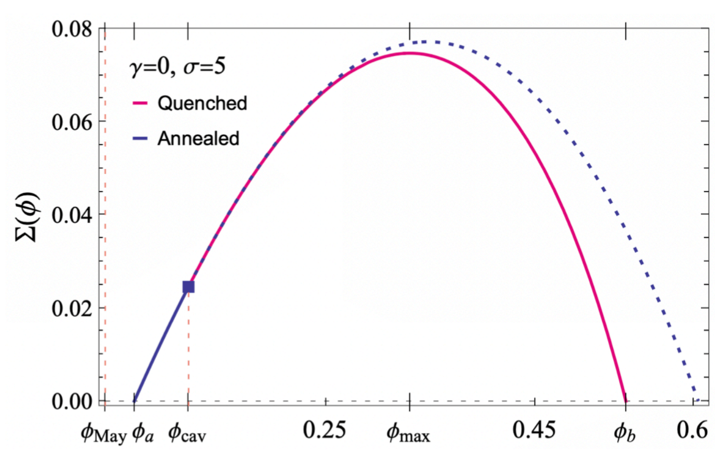
  Wainrib, Toboul, PRL 110, 2013

Summary results.



Equilibria of rGLVE with independent ($\gamma = 0$), non-reciprocal interactions

- Un-invadable, linearly stable equilibria **do not exist**
- Exponentially many **un-invadable, linearly unstable** equilibria
- Diversity **correlates negatively** with abundance & similarity
- We know the **range in diversity** and abundance



More technically

- Computation of quenched compexity of equillibria for non-conservative models with **non-reciprocal interactions**
- Quenched matter: the average can be a **very poor indicator**
- Cavity calculation makes sense **beyond its stability boundary**

References

V. Ros, F. Roy, G. Biroli, G. Bunin and A. Turner , Physical Review Letters 130, 257401 (2023)

V. Ros, F. Roy, G. Biroli, G. Bunin, J. Phys. A: Math. Theor. 56 305003J (2023)

Thank you.