

Marginal stability of the generalized random Lotka-Volterra model: logistic growth case and beyond

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Based on:

A. Altieri, S. Franz, Rapid Comm. Phys. Rev. E **99** (1) (2019)

A. Altieri, F. Roy, C. Cammarota, G. Biroli, Phys. Rev. Lett. **126**, 258301 (2021)

A. Altieri, G. Biroli, SciPost Physics **12**, 013 (2022)

G. Garcia Lorenzana, A. Altieri, Phys. Rev. E **105** (2022)

EverEvol - Population dynamics: from rare events to evolution

Grenoble - December 1st, 2022



Open questions in theoretical ecology

Understanding the mechanisms that shape the diversity, stability and functioning in ecological & biological systems is a **timely** and **challenging** problem.



- How does **diversity** affect the evolution of the other species? What is the diversity precisely?
- How does an ecosystem respond to external (pulse or probe) **perturbations**?
- Is a **multiple equilibria regime** possible for the same ecosystem?
- Can a population undergo **chaotic dynamics** and **avalanches** (extinction cascades)?
- How to describe cooperative **pattern formation** in complex communities?

C. Chen, S. Liu, X. Shi, *et al.*, *Nature* 542 (2017)

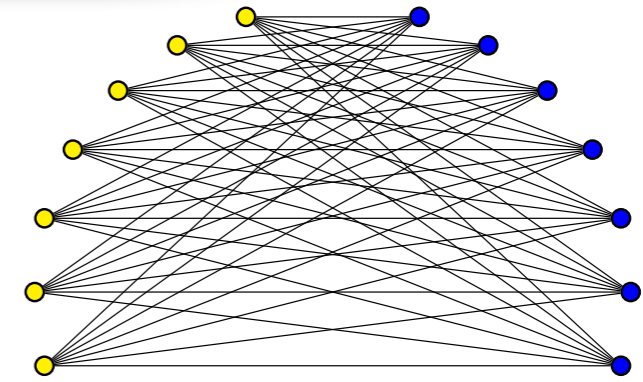
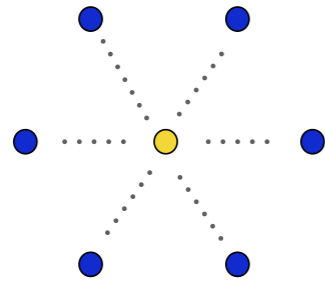
R.J. Schmitt, S.J. Holbrook *et al.*, *PNAS* 116 (10) 4372 (2019)

J. Sirota, B. Baiser, N.J. Gotelli, A.M. Ellison, *PNAS* 110, 7742 (2013)

E. Beninca, J. Huisman *et al.*, *Nature* 451: 822 (2008)

E. Beninca, K.D. Johnk *et al.*, *Ecol Lett* 12: 1367 (2009).

From a few to many interacting components



STATISTICAL MECHANICS

Emergent mechanisms and collective behaviour



PHASE TRANSITIONS

R.V. Solé, D. Alonso, A. McKane, *Phil. Trans. Roy. Soc. B* 357 (2002)

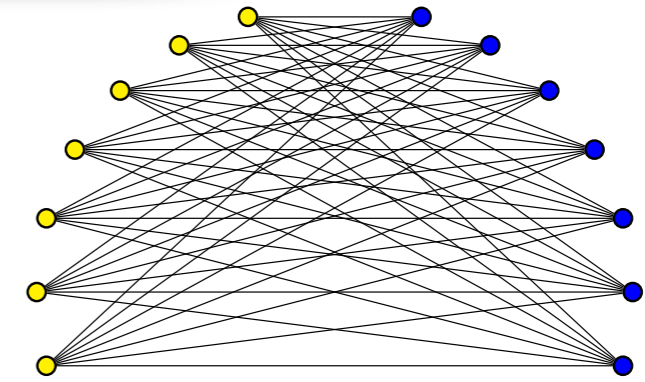
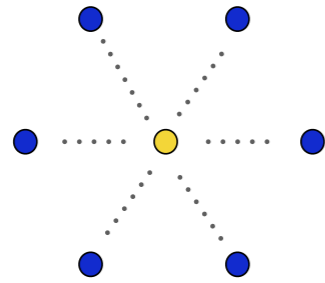
D. A. Kessler, N. M. Shnerb, *Phys. Rev. E* 91 (2015)

G. Bunin, *Phys. Rev. E* 95 (2017)

G. Biroli, G. Bunin, C. Cammarota, *New Journal of Physics* 20 (2018)

M. Tikhonov, R. Monasson, *Phys. Rev. Lett.* 118 (2017)

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Need for a general framework bridging the gap between models and experiments

MacArthur's model
(purely competitive)

Lotka-Volterra model
(competitive or cooperative)

• A. Altieri, S. Franz, *Phys. Rev. E* **99** (1) (2019)

- A. Altieri, F. Roy *et al.*, *Phys. Rev. Lett.* **126** (2021)
- A. Altieri, G. Biroli, *SciPost Physics* **12** (2022)
- G. Garcia Lorenzana, A. Altieri, *Phys. Rev. E* **105** (2022)

The random Lotka-Volterra model for species rich ecosystems

Dynamical equations for the relative species abundances $N_i \geq 0$, with $i = 1, \dots, S$

$$\frac{dN_i}{dt} = -N_i \left[\nabla_{N_i} V_i(N_i) + \sum_{j(j \neq i)} \alpha_{ij} N_j \right] + \underbrace{\sqrt{N_i} \eta_i(t)}_{\text{noise}} + \lambda_i \quad \text{immigration rate}$$

$$V_i(N_i) = -\rho_i \left(K_i N_i - \frac{N_i^2}{2} \right) \quad \text{with } \rho_i = r_i / K_i \text{ (growth rate/carrying capacity).}$$

Main assumptions:

- Well-mixed community (no space dependence)
- Demographic fluctuations modelled by Gaussian white noise with $\langle \eta_i(t) \rangle = 0$ and $\langle \eta_i(t) \eta_j(t') \rangle = 2T \delta_{ij} \delta(t - t')$ (within Ito's prescription).
- Complex behaviour described by random interactions α_{ij} with $\langle \alpha_{ij} \rangle = \mu / S$, $\langle \alpha_{ij}^2 \rangle_c = \sigma^2 / S$, $\langle \alpha_{ij} \alpha_{ji} \rangle_c = \gamma \langle \alpha_{ij}^2 \rangle_c$

R. May, *Stability and Complexity in Model Ecosystem*, Princeton University Press (1973)

Fisher, Mehta PNAS 111 (2014)

M. Barbier, J.F. Arnoldi, G. Bunin, M. Loreau, PNAS 115 (2018)

G. Bunin, Phys. Rev. E 95 (2017)

L. Sidhom, T. Galla, Phys. Rev. E 101(3) (2020).

The random Lotka-Volterra model with symmetric interactions

The dynamical equation admits an invariant probability distribution with:

$$P(\{N_i\}) = \exp\left(-\frac{H(\{N_i\})}{T}\right)$$

$$H = -\sum_{i=1}^S \left(N_i - \frac{N_i^2}{2}\right) + \sum_{i<j=1}^S \alpha_{ij} N_i N_j + \sum_{i=1}^S [T \ln N_i - \ln \theta(N_i - \lambda)]$$

Demographic noise Reflective wall

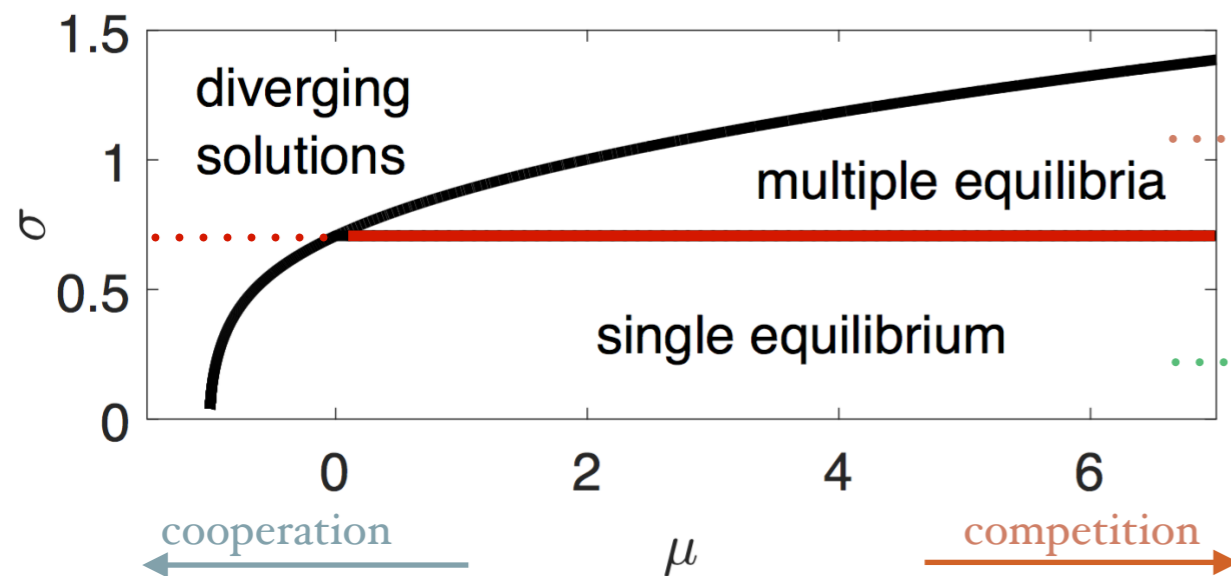
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Phase diagram at T=0



- What are the typical features of these equilibria?
- How many equilibria?
- Stability decreases upon increasing heterogeneity (May's conjecture through RMT)

G. Bunin, Phys. Rev. E **95** (2017); G. Biroli, G. Bunin, C. Cammarota, New Journal of Physics **20** (2018).

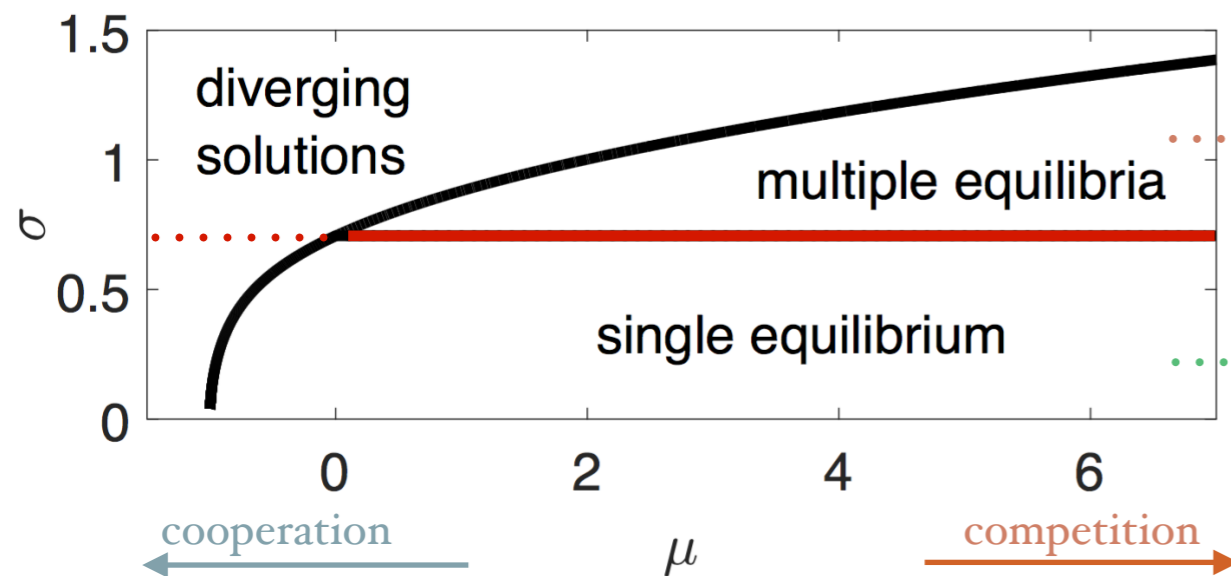
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What is the **effect of the demographic noise**?

Interplay between **stochasticity and immigration**?

Thermodynamic analysis: replica computation

To evaluate the (disordered) free energy, an average over random couplings must be performed.

$$-\beta n F = \lim_{n \rightarrow 0} \ln \overline{Z^n} = \lim_{n \rightarrow 0} \ln \int \prod_{i,(ij)} dN_i^a d\alpha_{ij} \exp \left[- \sum_{(ij)} \frac{\alpha_{ij} - \mu/S}{2\sigma^2/S} - \beta H(\{N_i^a\}) \right]$$

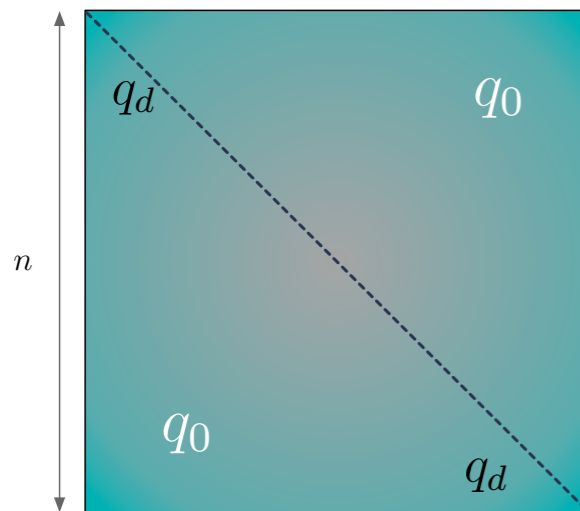
- $Q_{ab} = \frac{1}{S} \sum_{i=1}^S N_i^a N_i^b$



$$-\beta n F = \lim_{n \rightarrow 0} \ln \overline{Z^n} = \lim_{n \rightarrow 0} \ln \left[\int \prod_{ab} dQ_{ab} dQ_{aa} dH_a e^{S \mathcal{A}(Q_{ab}, Q_{aa}, H_a)} \right]$$

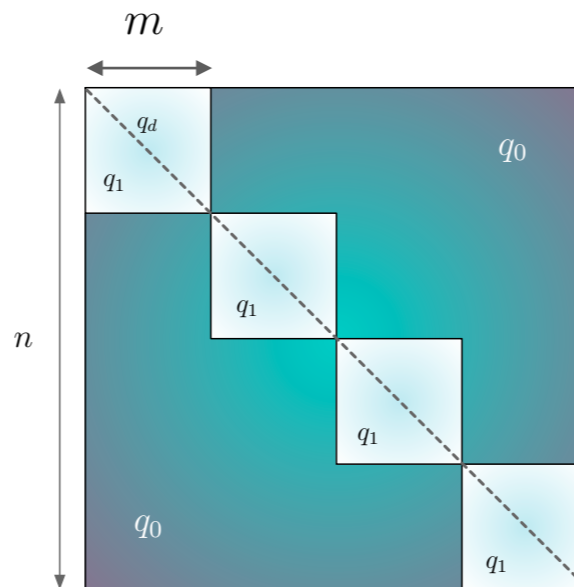
- $H_a = \frac{1}{S} \sum_{i=1}^S N_i^a$

RS Ansatz



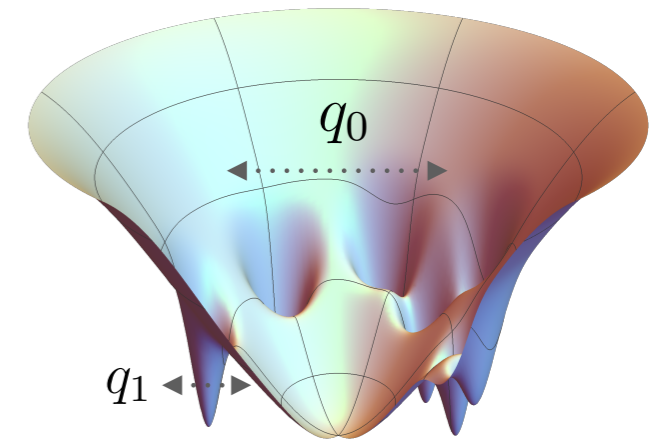
$$\begin{aligned} Q_{aa} &= q_d & \text{if } a &= b \\ Q_{ab} &= q_0 & \text{if } a &\neq b \\ H_a &= h & \forall a \end{aligned}$$

rRSB Ansatz



- $q_0 = \frac{1}{S} \sum_i \langle N_i \rangle_\alpha \langle N_i \rangle_\beta$
- $q_1 = \frac{1}{S} \sum_i \langle N_i \rangle_\alpha^2$

Landscape structure

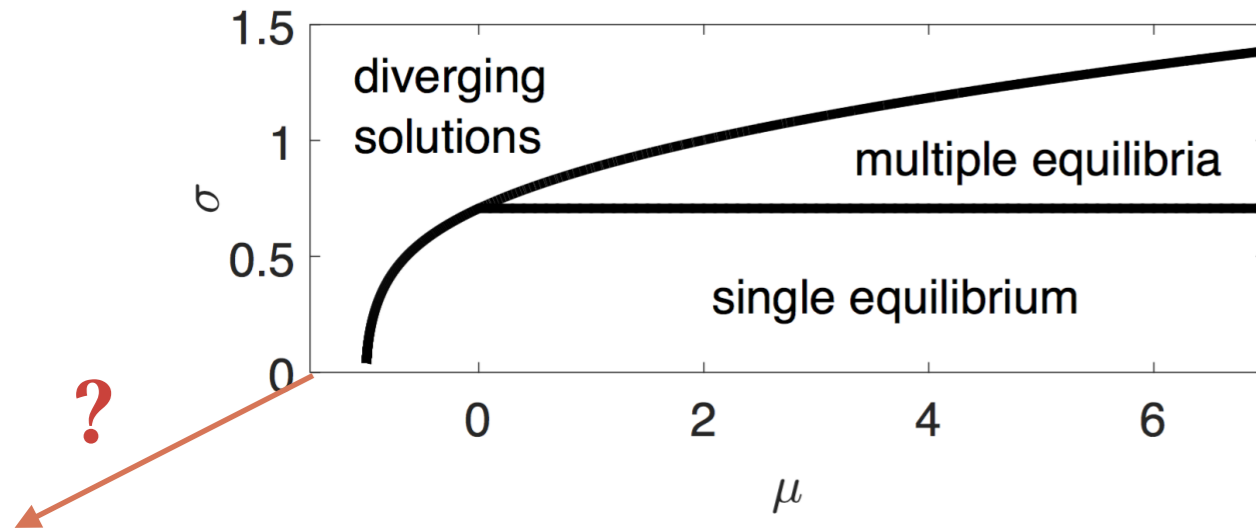


size of the largest basin

size of the innermost basin

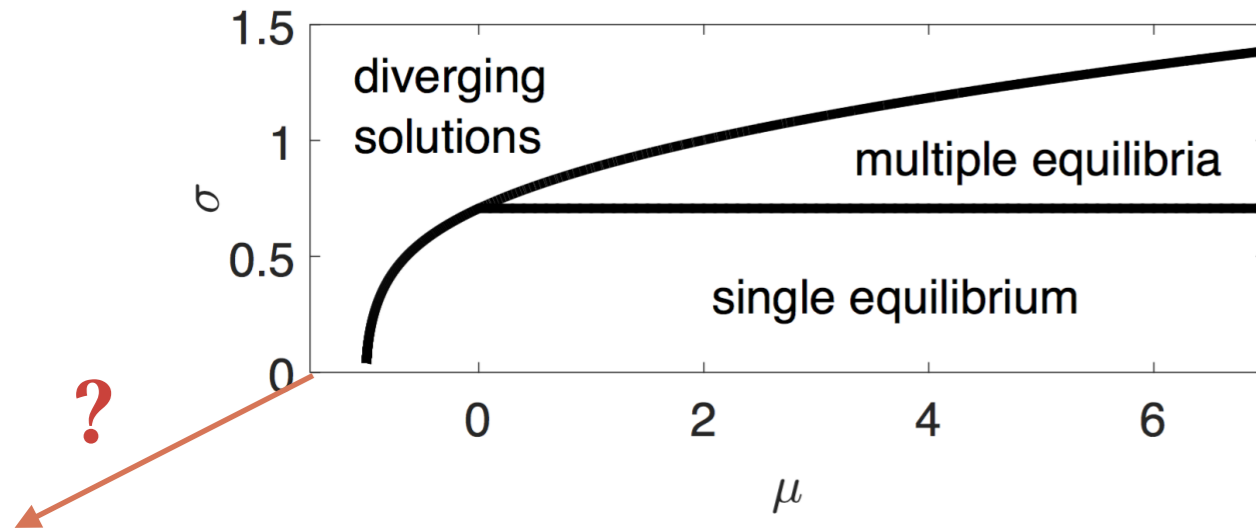
Phase diagram of the random LV with demographic fluctuations

Goal: characterizing emergent collective behaviours in terms of disordered glass-like phases.



Phase diagram of the random LV with demographic fluctuations

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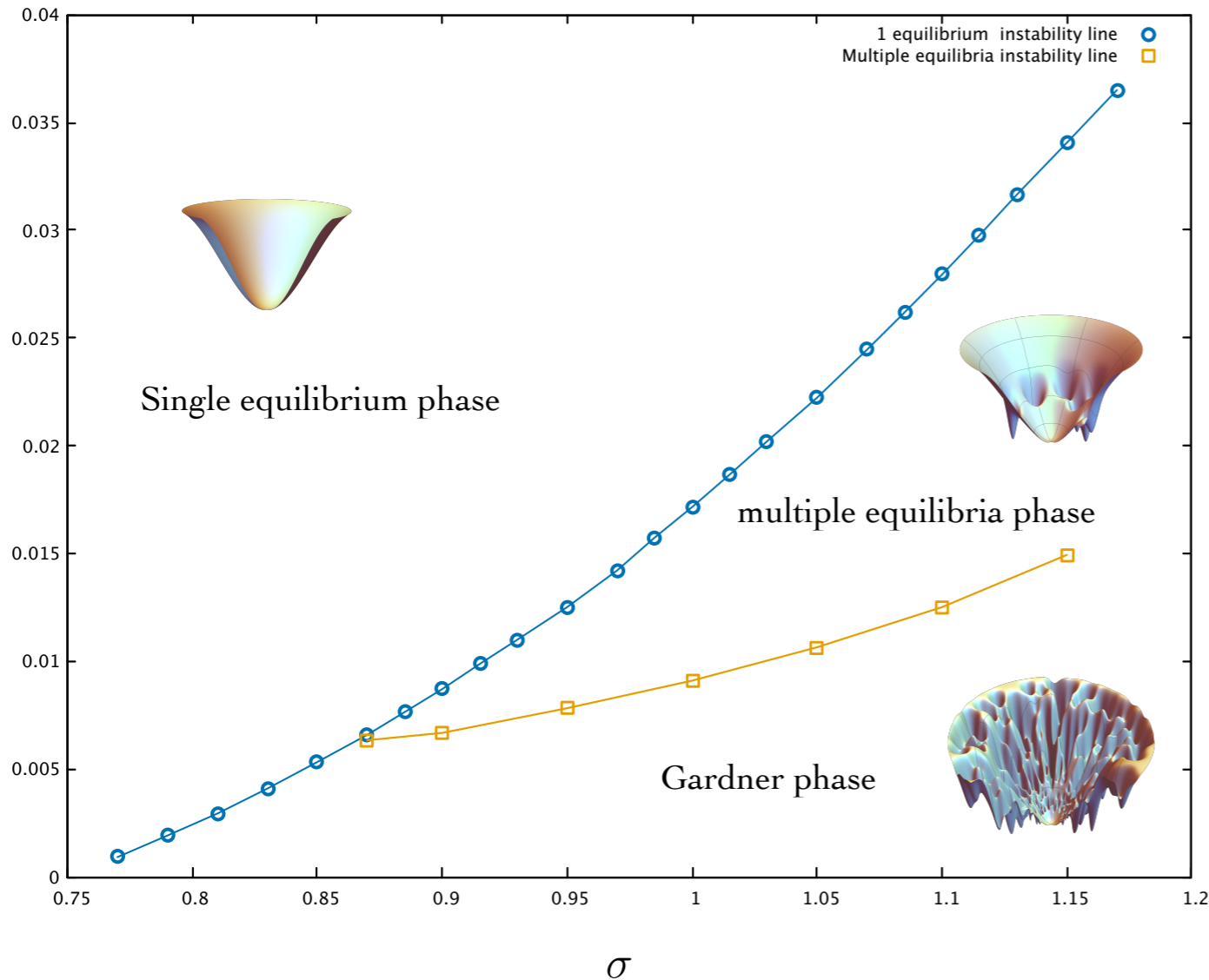
Analysis of the harmonic fluctuations of the free energy:

$$\mathcal{M}_{abcd} = -\frac{\partial^2 \mathcal{A}}{\partial Q_{ab} \partial Q_{cd}} = \beta^2 \rho^2 \sigma^2 \left[\delta_{(ab),(cd)} - (\beta^2 \rho^2 \sigma^2) \overline{\langle N^a N^b, N^c N^d \rangle}_c \right]$$

Whose smallest eigenvalue in the replica formalism reads: $\lambda_R = (\beta \rho \sigma)^2 \left[1 - (\beta \rho \sigma)^2 (\overline{\langle N^2 \rangle} - \langle N \rangle^2)^2 \right]$

Phase diagram of the random LV with demographic fluctuations

Goal: characterizing emergent collective behaviours in terms of disordered glass-like phases.



- No sensitive dependence on the average interaction parameter.

- Exponential number of locally stable states

$$\Sigma(f) \equiv \lim_{S \rightarrow \infty} \frac{1}{S} \overline{\log \mathcal{N}(f)} \quad \dots \rightarrow \quad \mathcal{N}_{\text{eq}} \sim \exp S$$

* Stability landscape:

Beisner et al., Front Ecol. Environ. (2003);
Scheffer and Carpenter, Trends in Ecology and Evolution (2003)

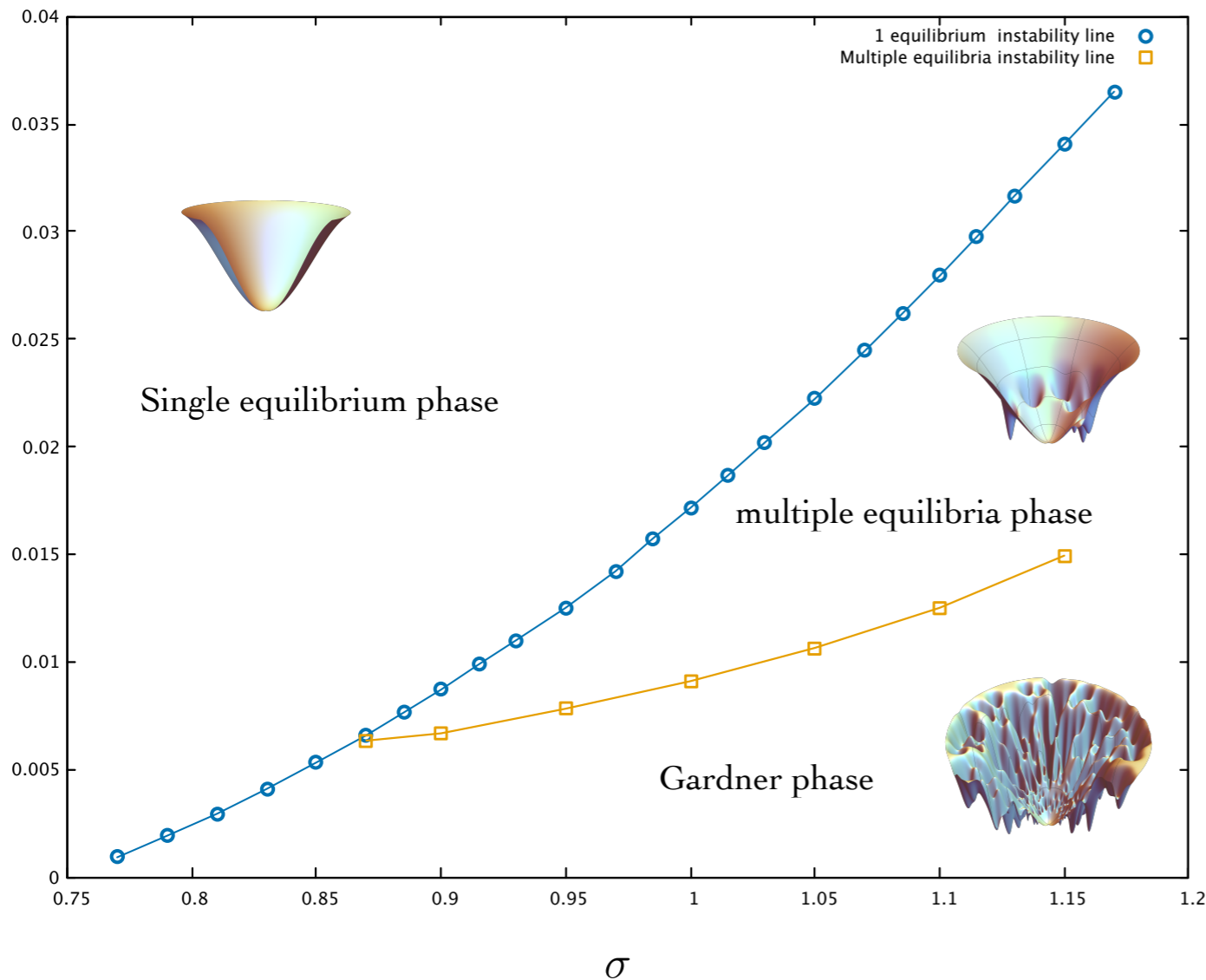
* Ecological Resilience:

Botton et al., Critical reviews in microbiology 32.2 (2006)

- **Recent works by J. Gore's group** (2021);

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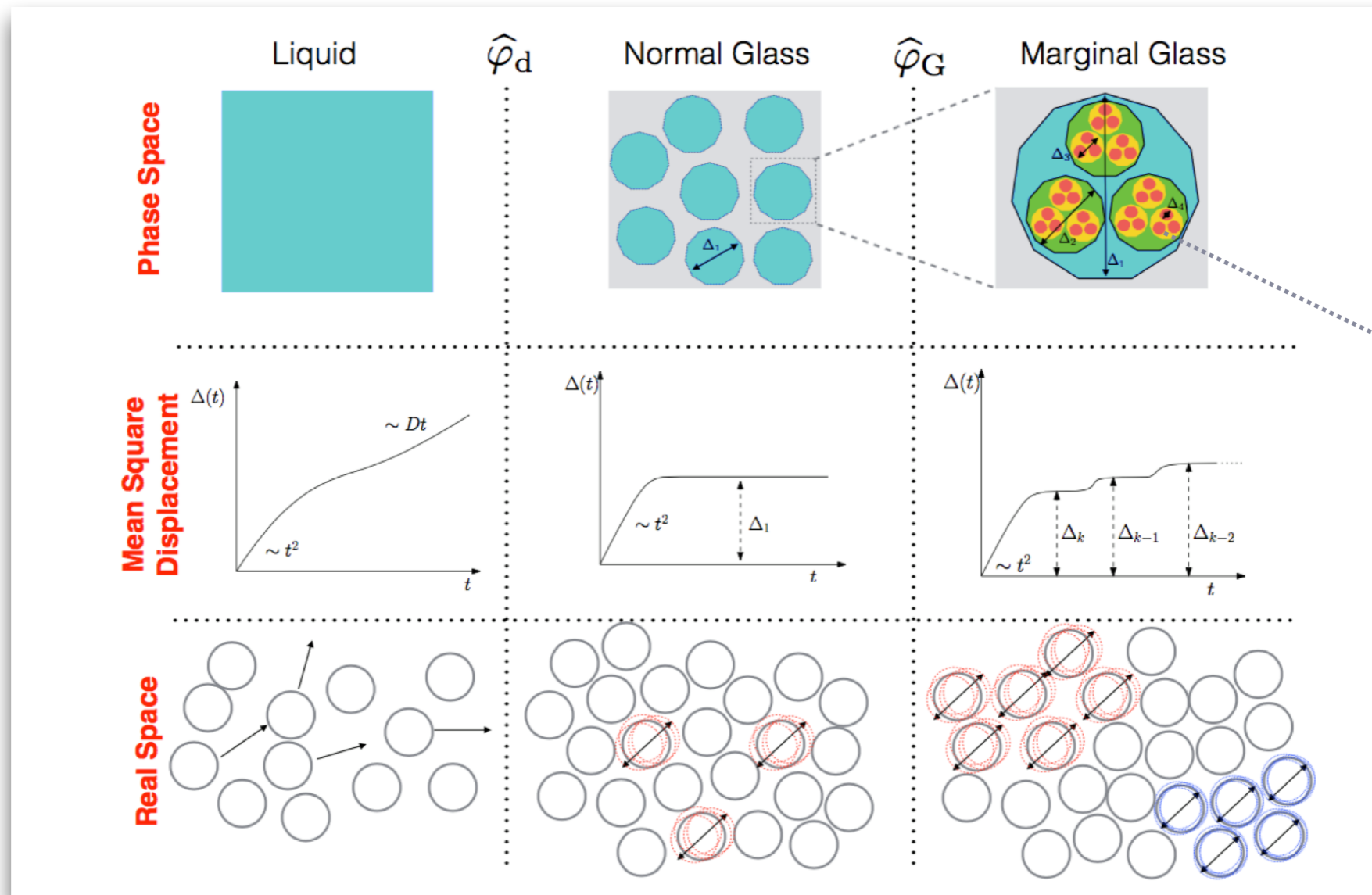
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- **Recent works by J. Gore's group** (2021);

- At very low demographic noise a **marginally stable amorphous phase**

First evidence of a **Gardner phase** akin to low-temperature glassy system phenomenology.

Analogies with glassy systems in the low-temperature phase



P. Charbonneau, J. Kurchan, G. Parisi, P. Urbani, F. Zamponi, *Annu. Rev. Condens. Matter Phys.* **8** (2017)

Liquid phase: single smooth basin, reflecting the unbroken symmetry (ergodic phase);

Stable glass phase: many smooth and distinct basins characterizing the landscape

Marginal glass: infinitely broken phase \rightarrow each basin breaks up into many sub-basins (hierarchically organised).



Dynamical mean-field theory (DMFT)

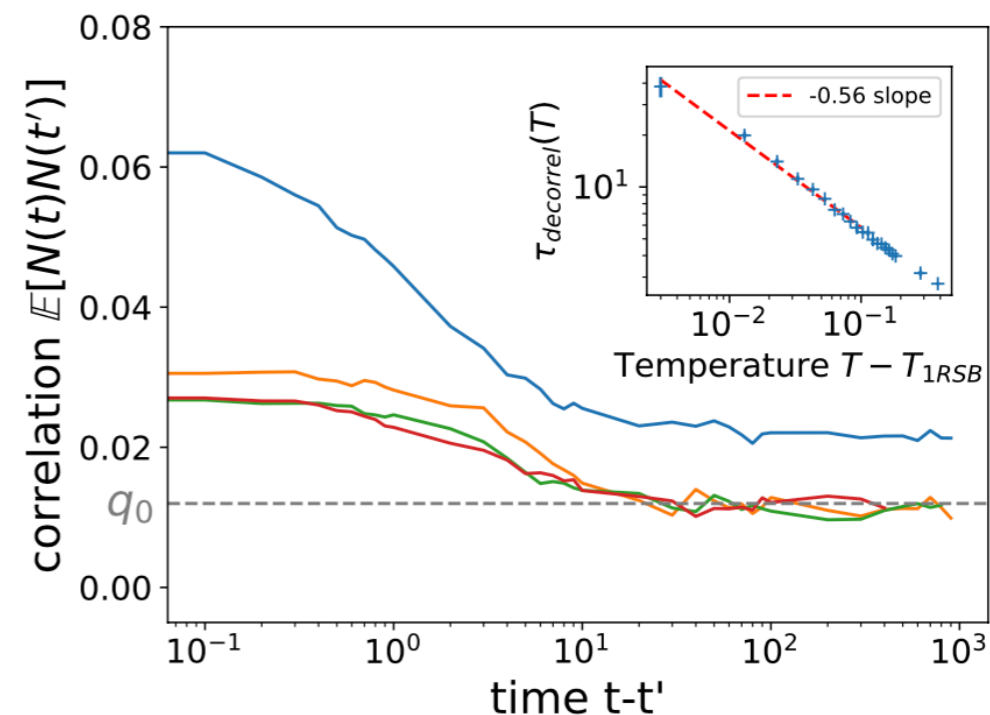
Dynamical correlation functions

Single equilibrium phase

$$\mathbb{E}[N(t)N(t')] = \frac{1}{SN_{sample}} \sum_{i=1}^S \sum_{r=1}^{N_{sample}} N_i^r(t)N_i^r(t')$$

$$\forall t \geq t' > t_{wait} \quad \mathbb{E}[N(t)N(t')] = C(t, t') \simeq C(t - t')$$

Time translationally invariant (TTI) regime



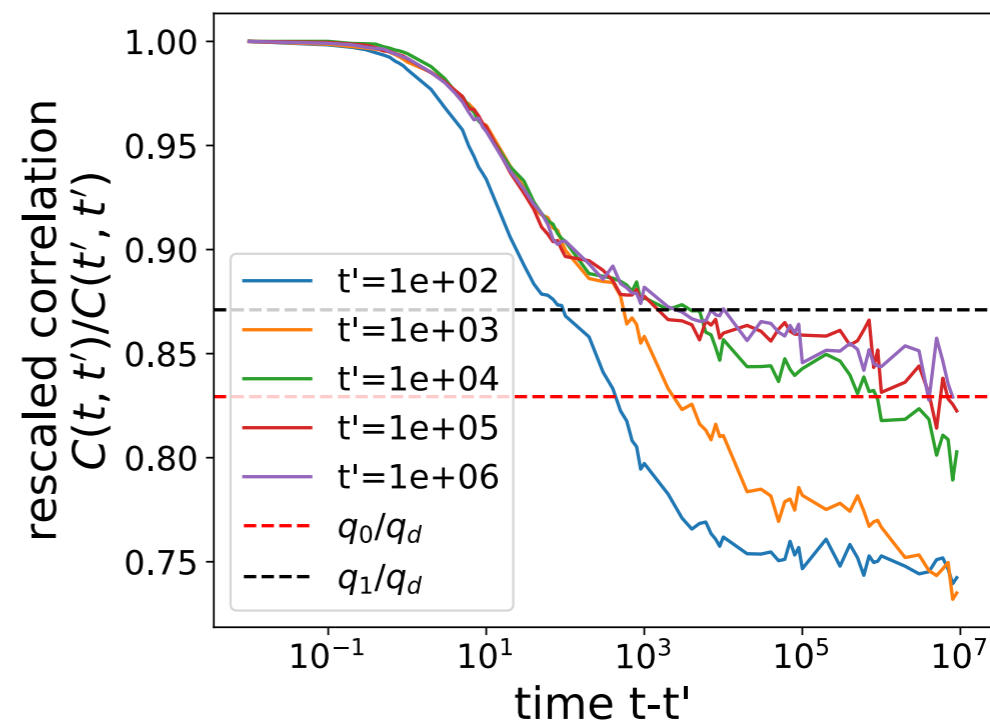
Multiple equilibria phase

Aging dynamics as in mean-field spin-glasses

L. Cugliandolo, J. Kurchan, PRL (1993)

Dramatic slowing down of the dynamics:

It never sits down in any of these equilibria wandering across the most numerous and marginally stable directions.



Lotka-Volterra model without noise: connection with Random Replicants

Replicator equations of great interest in: population genetics, analysis of Nash equilibria, evolutionary game theory, and complex economic systems.

J. Hofbauer, J. Nonlinear Anal. 5, 1003 (1981)

S. Diederich, M. Opper, Phys. Rev. A 39 (1989)

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G. W.A. Constable, A. J. McKane, Phys. Rev. E 96 (2017)

$$H = \sum_i V_i(N_i) + \sum_{ij} \alpha_{ij} N_i N_j$$
$$\mathcal{H}_R = \sum_{i<j=1}^S J_{ij} x_i x_j - a \sum_{i=1}^S x_i^2$$
$$\sum_i x_i = S$$

Additional constraint

P. Biscari, G. Parisi, J. Phys. A 28 (1995)

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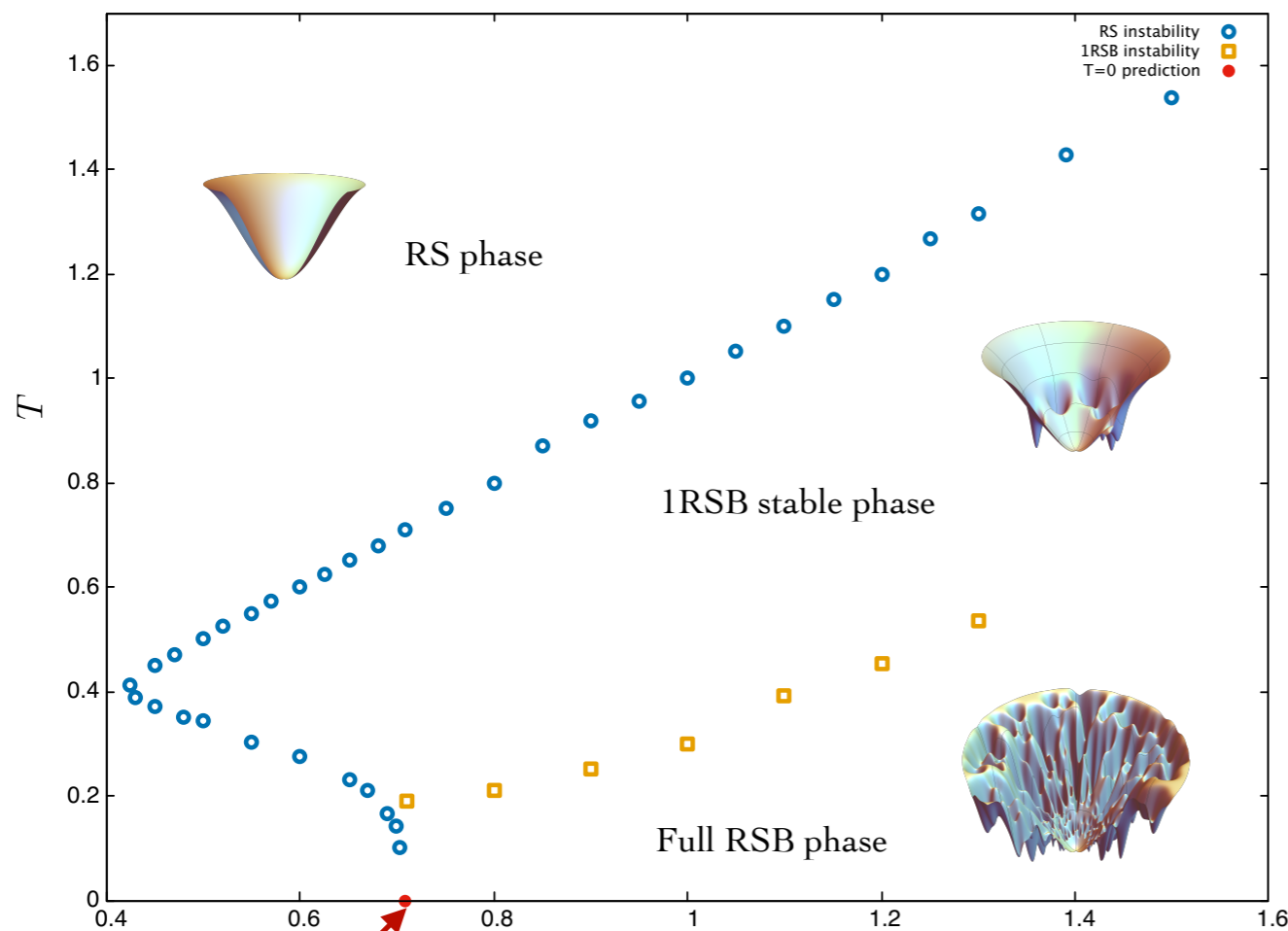
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Zero-demographic noise critical point.

We established an exact mapping between the two:

$$[\rho - \rho^2 \sigma^2 \beta (q_d - q_0)] \iff -\beta J (a/J - q)$$

$$(\rho \mu h - z \rho \sigma \sqrt{q_0} - \rho) \iff -2z \sqrt{\tilde{t}} - \tilde{\gamma}$$

? Effect of introducing **non-symmetric interactions/non-conservative forces**?

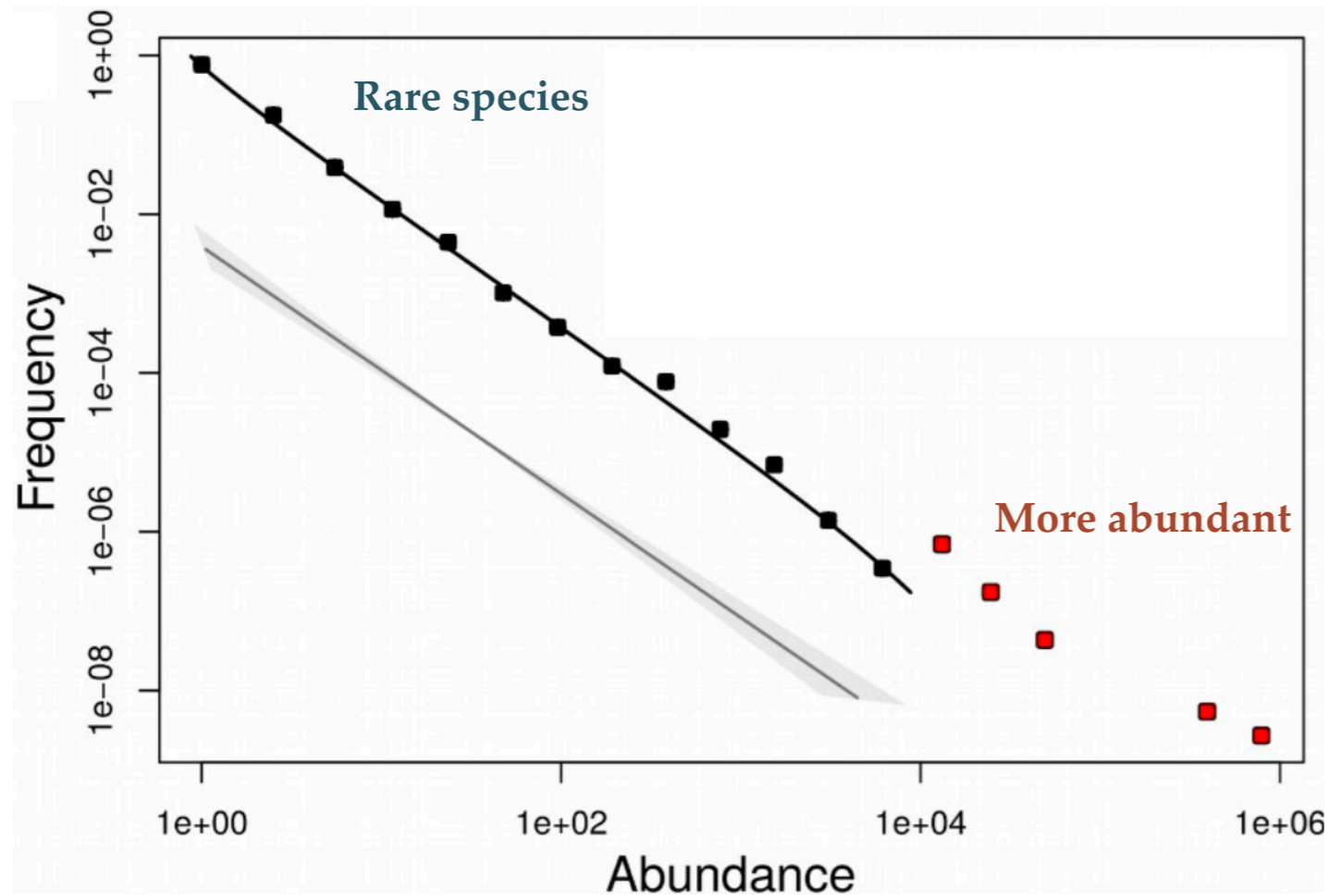


Strongly competitive interactions

Empirical motivation

Other scalings can suitably be considered in the field, e.g. $\alpha_{ij} \sim O(1)$

Chaotic phases and intermittent dynamics can appear: sudden turnovers between very low abundance periods and high abundance periods. D. A. Kessler, N. M. Shnerb, Phys. Rev. E 91 (2015)



Strong competition regime

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We specifically consider here $\mu \propto S$, $\sigma \propto \sqrt{S}$

- 1) Solve the equations at finite demographic noise.
- 2) Then in the zero-noise regime, leading to



$$h = \overline{N^*(z)} = \frac{\sqrt{q_0}\sigma}{1 - \sigma^2\Delta q} \omega_1(\Delta)$$

$$q_0 = \overline{N^*(z)^2} = \frac{q_0\sigma^2}{(1 - \sigma^2\Delta q)^2} \omega_2(\Delta)$$

$$\Delta q = \frac{\overline{\theta(N^*(z))}}{H''_{RS}(N^*(z))} = \frac{1}{1 - \sigma^2\Delta q} \omega_0(\Delta)$$

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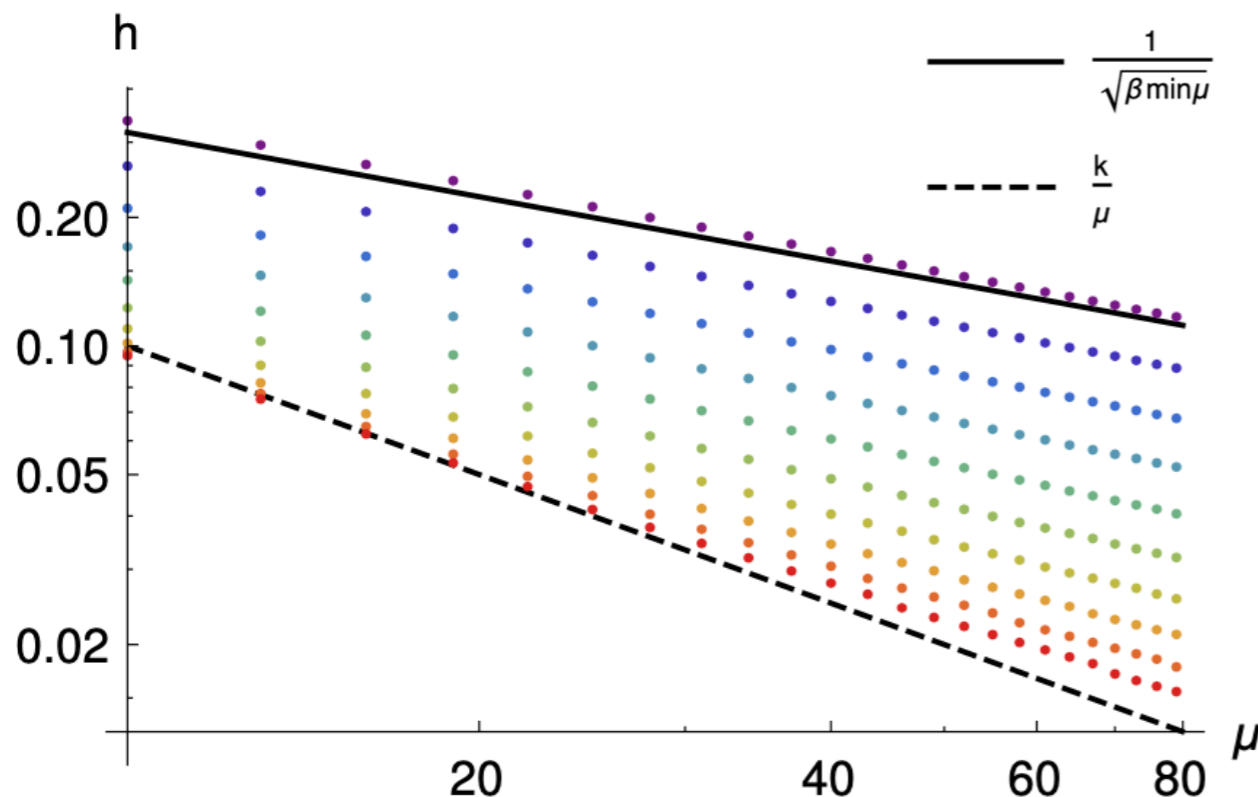
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$$\omega_i(\Delta) = \int_{-\Delta}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-\frac{z^2}{2}} (z + \Delta)^i \quad \Delta = \frac{k - \mu h}{\sqrt{q_0}\sigma}$$



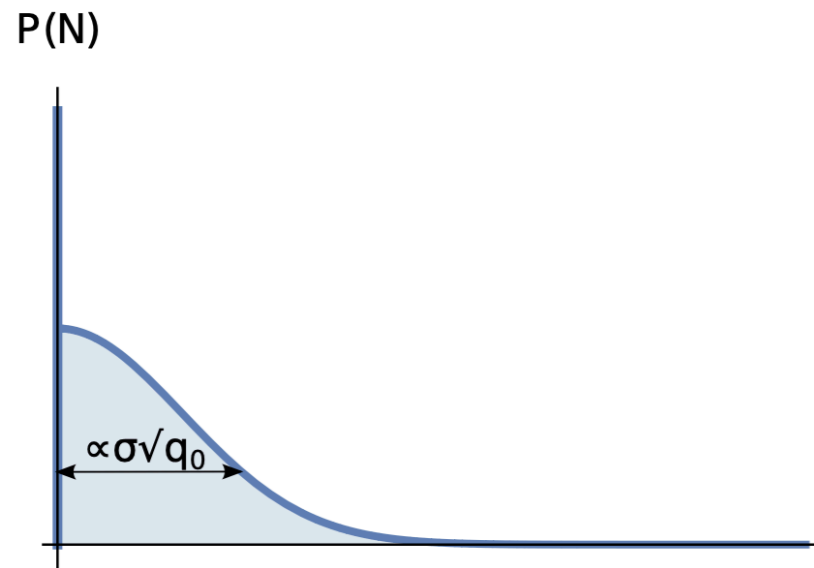
- Thermal fluctuations strongly suppress the diversity

$$\phi = \int_{-\Delta}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-\frac{z^2}{2}}$$

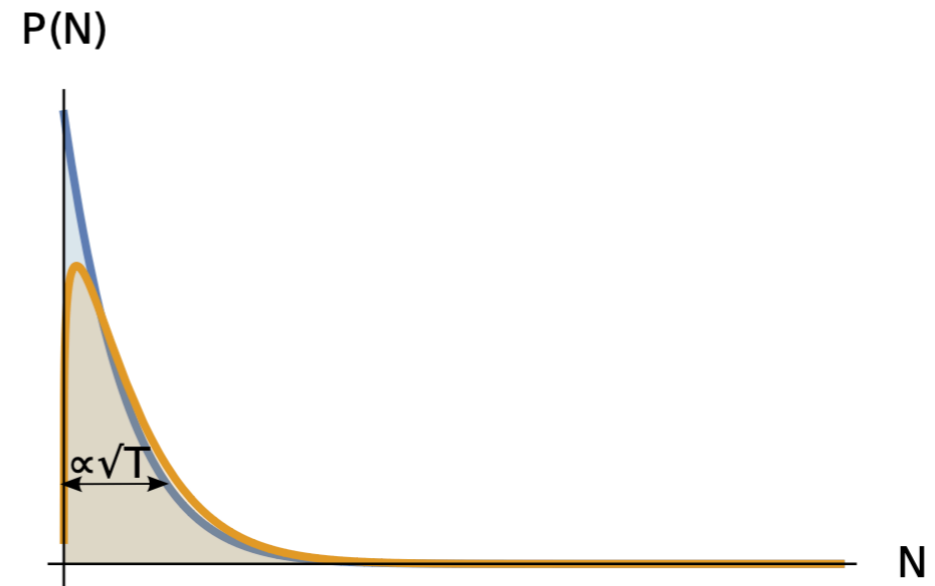
- Diversity bound saturated (T=0)

Species abundance distribution in the RS phase

In both cases, we find out truncated Gaussian distributions.



(a) $T = 0$



(b) $T > 0$

- The finite width of the distribution is due to **disorder**.
- Truncated Gaussian + δ -function.
- **The disorder is negligible.**
- Variability in the abundances is only due to thermal fluctuations.
- Still the tail of a Gaussian distribution.
- Similar distributions found in disordered systems in presence of hard constraints.
- How to go further and obtain **power-law scalings**?



Next step: modelling intra-specific cooperative effects

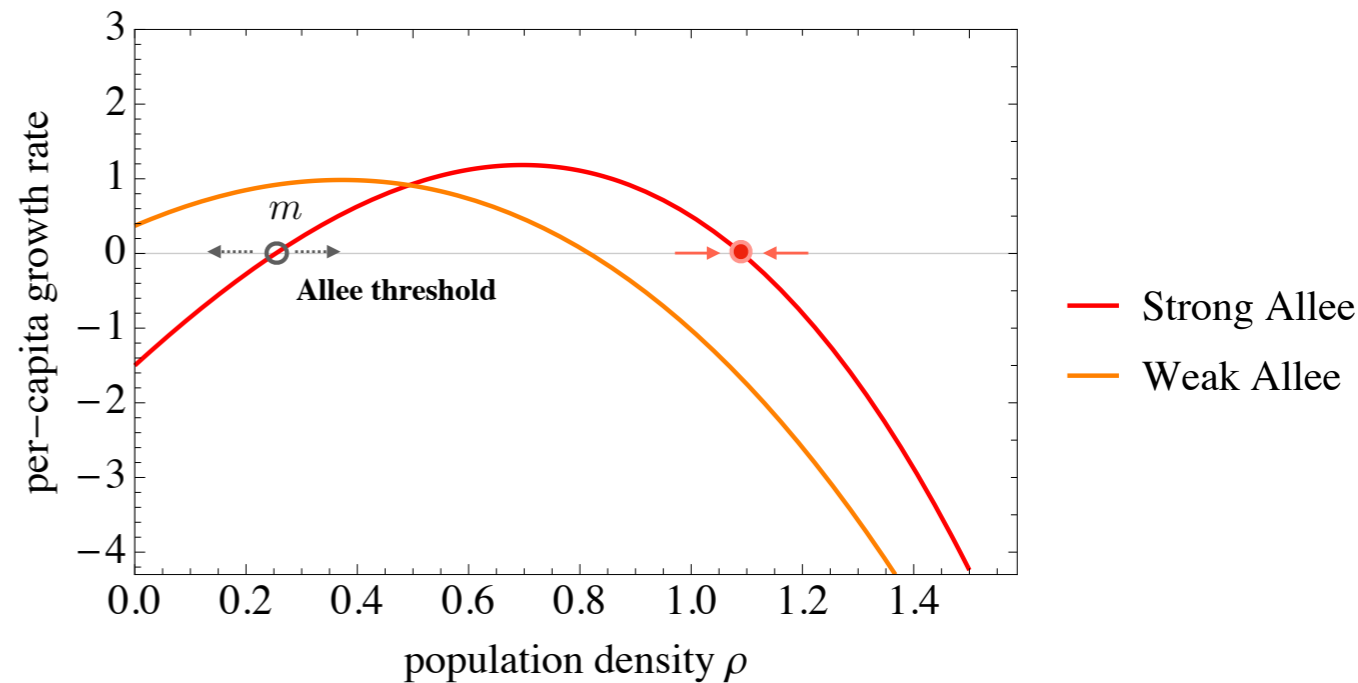
Beyond the purely logistic growth: Allee effect

$$\frac{dN_i}{dt} = -N_i \left[\nabla_{N_i} V_i(N_i) + \sum_{j(j \neq i)} \alpha_{ij} N_j \right] + \sqrt{N_i} \eta_i(t) + \lambda_i$$

$$\langle \eta_i(t) \eta_j(t') \rangle = 2T \delta_{ij} \delta(t - t')$$

Consider a higher-order potential with finite threshold

$$V_i(N_i) = -r_i \left(1 - \frac{N_i}{K_i} \right) (N_i - \underline{m}) N_i$$



Modelization of the so-called **Allee effect** = positive correlation between population density and mean individual fitness.

In many species **undercrowding** - not only competition - contributes to limiting population growth.

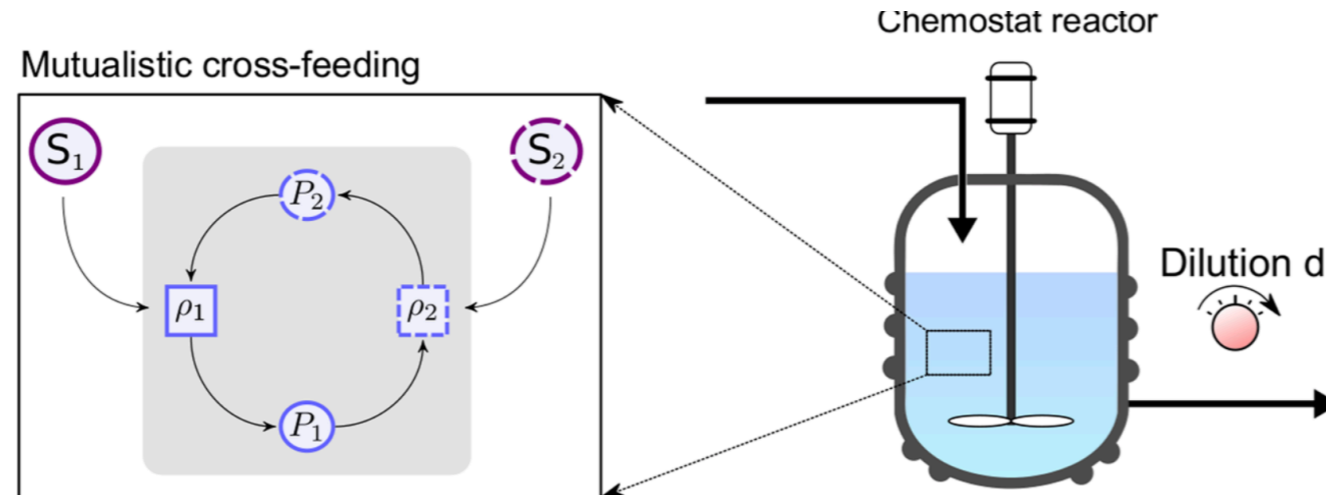
Empirical evidences in marine populations, reptiles and mammals.

Recently, increasing interest **in engineered biology, cancer cell evolution and epidemiology.**

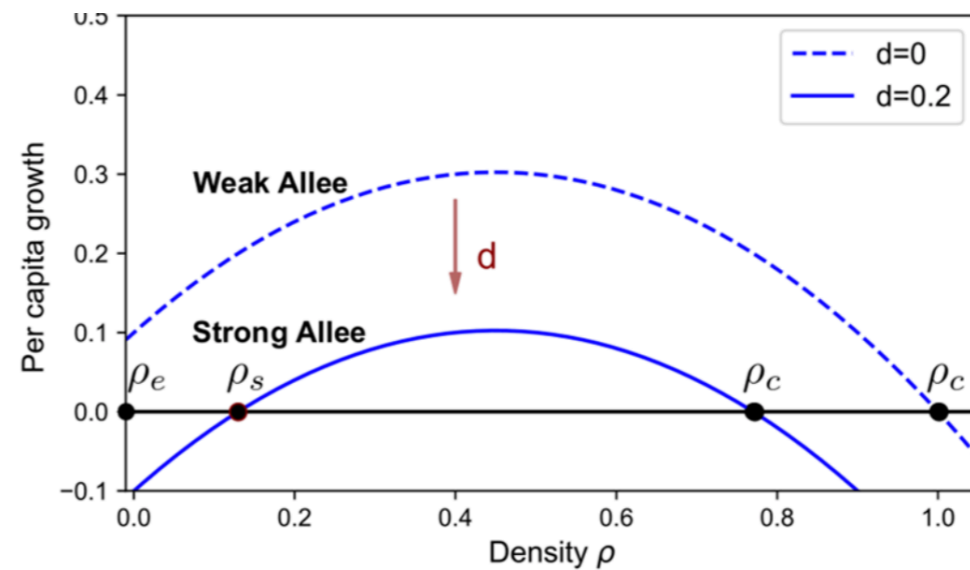
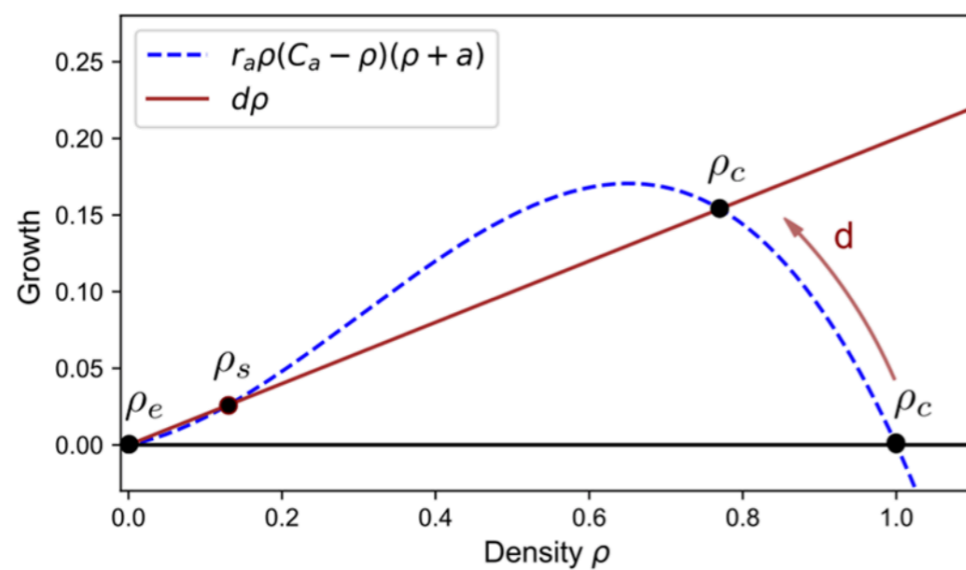
Empirical evidence: mutualistic cross-feeding

Another noteworthy example is given by microbial ecosystems.

Mutualism, as a result of metabolic cross-feeding, is responsible for a weak Allee effect.

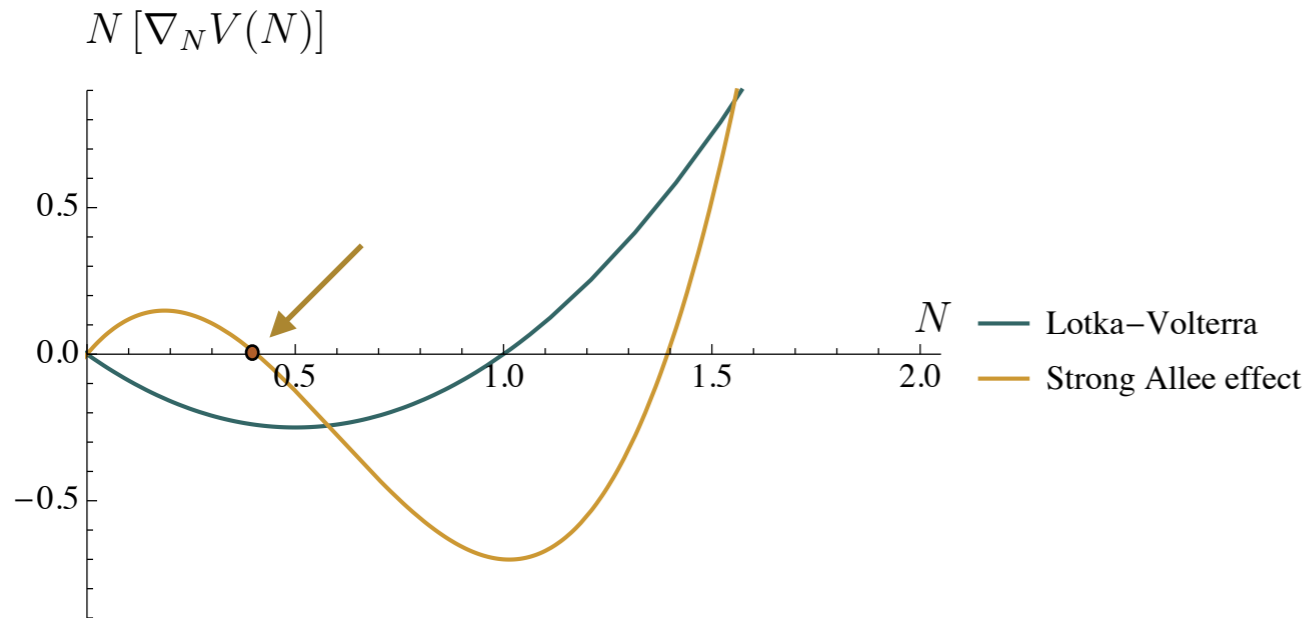


Dilution is a crucial condition for bistability.



Qualitative and quantitative differences with the logistic growth LV model

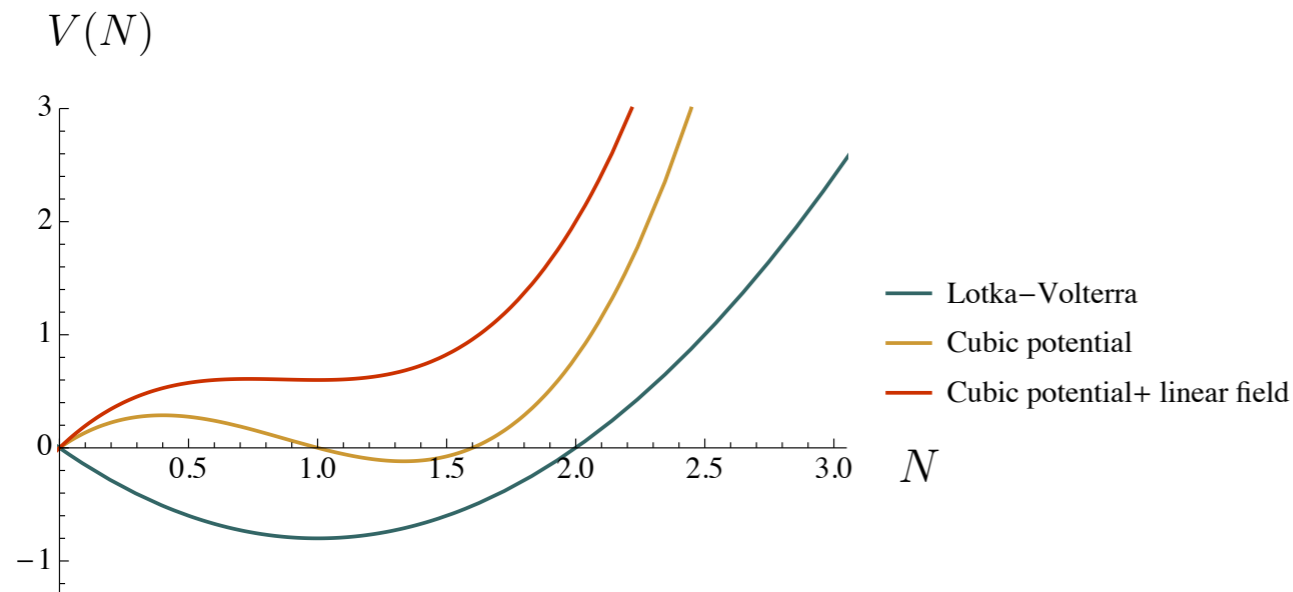
The introduction of a cubic potential complicates the analysis and leads to *a priori* unsolved competition.



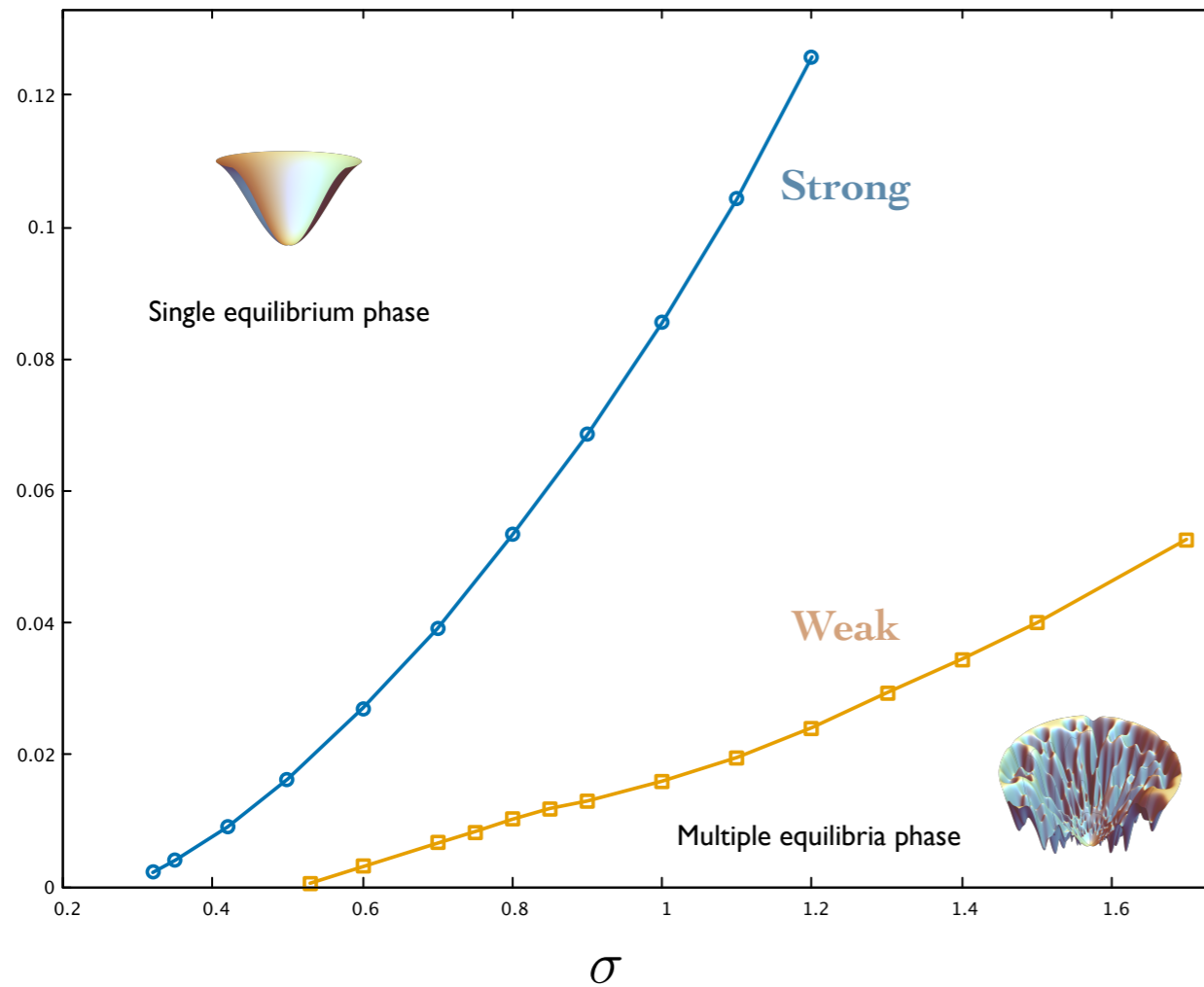
- The globally asymptotic unstable fixed point changes to a **neutral stable fixed point**;

- A strong Allee effect (positive threshold) is associated with a double-well potential;

- A weak effect (negative or zero threshold) is framed by a single-well potential.



Allee effect: phase diagram and marginal stability condition



- For the Allee case, only two phases take place. **No** evidence of an **amorphous Gardner**-like phase.

- **The functional response**, at variance with the LV model, **depends** on the species abundance.

The smallest eigenvalue of the stability matrix:

$$\lambda_R = (\beta\rho\sigma)^2 \left[1 - \frac{\rho^2\sigma^2}{(-\Delta q\rho^2\sigma^2 + V''(N^*))^2} \right]$$

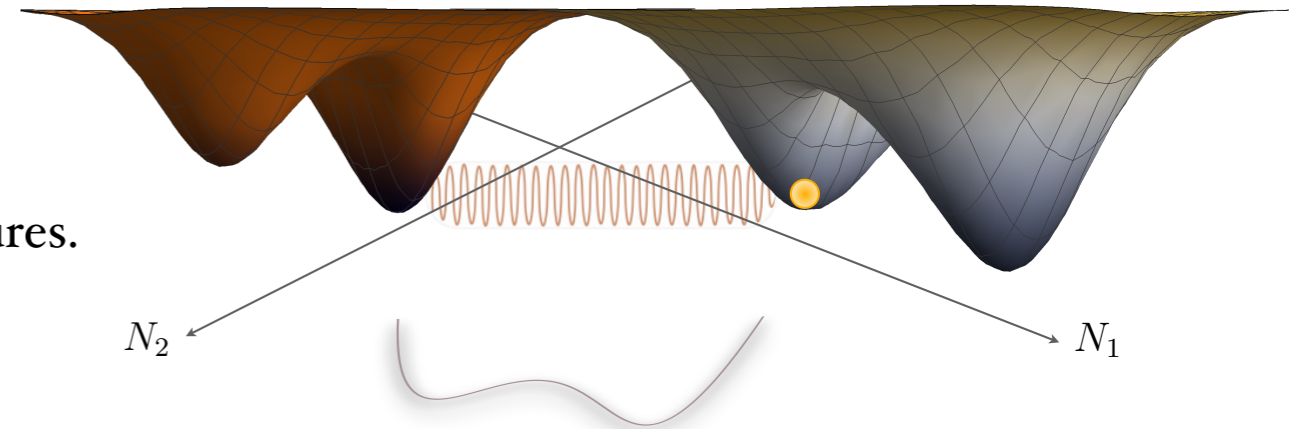
↓
Heterogeneity
↖
Effective potential

This last condition can be rephrased in terms of the probability distribution of the local curvatures of the potential:

$$\text{Condition for stability (or marginal stability): } 1 - (\rho\sigma)^2 \int \frac{dV''_{\text{eff}} P(V''_{\text{eff}}(N^*))}{(V''_{\text{eff}}(N^*))^2} \geq 0$$

In the models of ecosystems we are considering, a peculiar marginality condition appears.

It leads to a constraint on the fluctuations of the local curvatures.



Dynamical cavity argument

$$\dot{N}_i(t) = N_i \left[-V'(N_i) - \sum_{j \neq i} \alpha_{ij} N_j + \xi_i \right]$$

External perturbation

$$N_i = N_{i \setminus k} - \frac{\partial N_i}{\partial \xi_i} \alpha_{ik} N_k$$

Cavity field

↓

Diagonal susceptibility

Model of Gaussian coupled potential

$$\mathcal{E}_{ij} = \frac{1}{2} N_i^2 V''_{\text{eff}}(N_i^*) + \frac{1}{2} N_j^{*2} V''_{\text{eff}}(N_j) + \alpha_{ij} N_i N_j$$

$$\mathbf{A} = \begin{pmatrix} V''_{\text{eff}}(N_i^*) & \alpha_{ij} \\ \alpha_{ij} & V''_{\text{eff}}(N_j^*) \end{pmatrix}$$

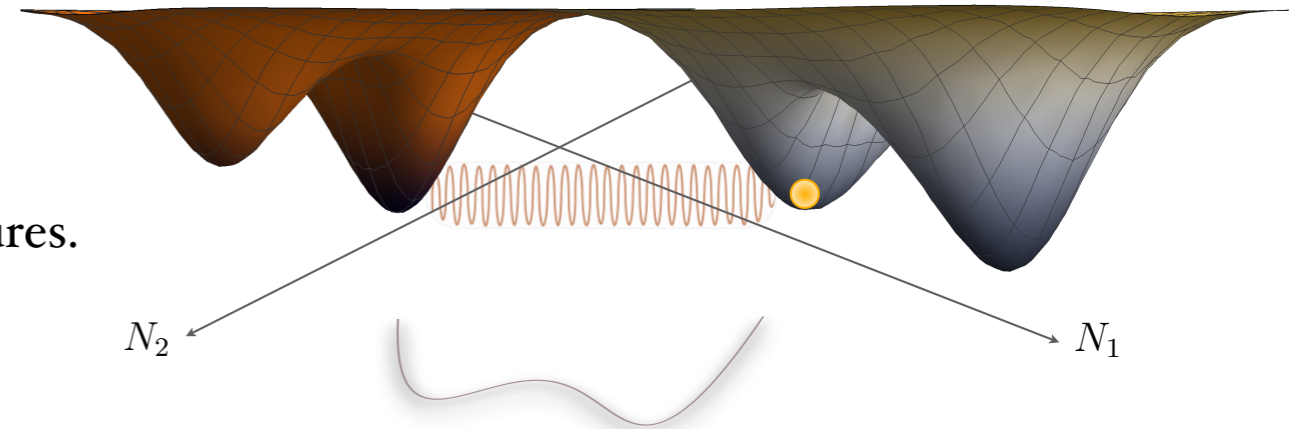
Energy variation due to an infinitesimal field:

$$\delta \mathcal{E} = \frac{1}{2} \sum_i \delta N_i^2 V''_{\text{eff}}(N_i^*)$$

Functional response of the single species in the limit of zero stochasticity

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Energy variation due to an infinitesimal field:

$$\delta \mathcal{E} = \frac{1}{2} \sum_i \delta N_i^2 V''_{\text{eff}}(N_i^*)$$

In both cases, when looking at minimal local curvatures $V''_{\text{eff}}(N^*) \sim V''_{\text{min}}$

we can deduce that if $P(V''_{\text{eff}}) \sim |V''_{\text{eff}}|^\alpha \Rightarrow |V''_{\text{eff}}| \sim \frac{1}{N^{\frac{1}{1+\alpha}}}$ with $\alpha \geq 1$

Conclusions and Perspectives

Generalized Lotka-Volterra model:

- low demographic noise and highly heterogenous interactions:
multiple equilibria phase (locally stable) + **amorphous Gardner-like phase** (full RSB - marginal);
- One-to-one mapping with the Random Replicant Model;
- Modelization of positive feedback loop and **intra-specific cooperative effects** (different universality class).

Conclusions and Perspectives

Generalized Lotka-Volterra model:

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Work in progress... 

- Introduction of a notion of **space**: model of metacommunities coupled by migration (directed-percolation coupled processes + disorder).
Hastings, Journal of Math. Biology (1978);
Mobilia, Täuber, J. Stat. Phys. (2007);
Denk, Hallatschek. PNAS (2022).
- Dynamical Mean-Field Theory with **asymmetric interactions** for:
 - Mixed MacArthur model along with the analysis of slow timescales;
 - Robust theoretical framework to capture boom-and-bust population dynamics and power laws (Tara expedition data);
 - Analysis of the volume distribution of the attractors.

Thank you for your kind attention!



Back-up slides

One-step replica symmetry breaking: multiple equilibria phase

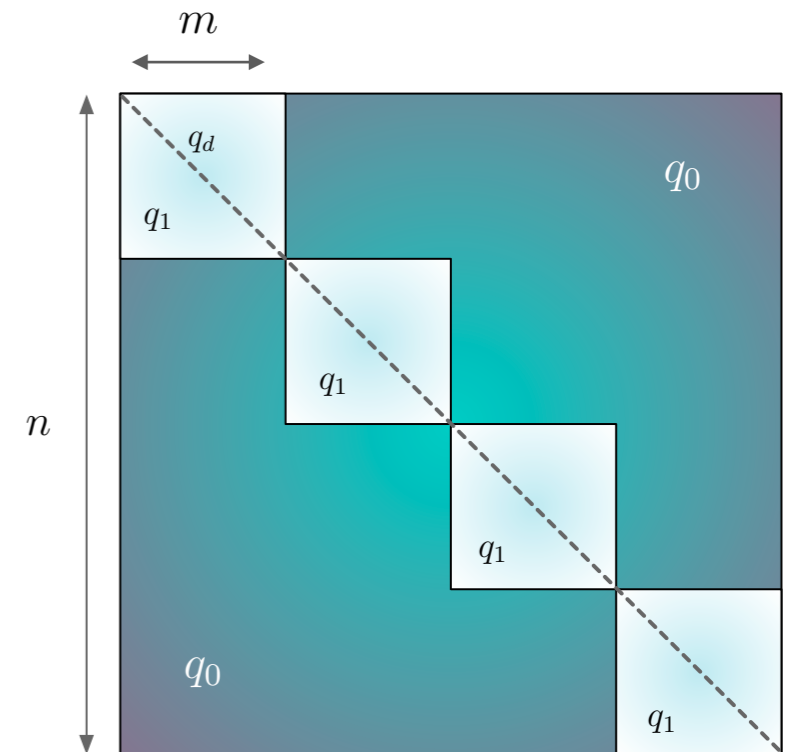
The overlap matrix $Q_{ab} = \frac{1}{S} \sum_i \overline{\langle N_i^a N_i^b \rangle}_R$

must be then parametrised according to a different replica Ansatz (r-step replica symmetry breaking).

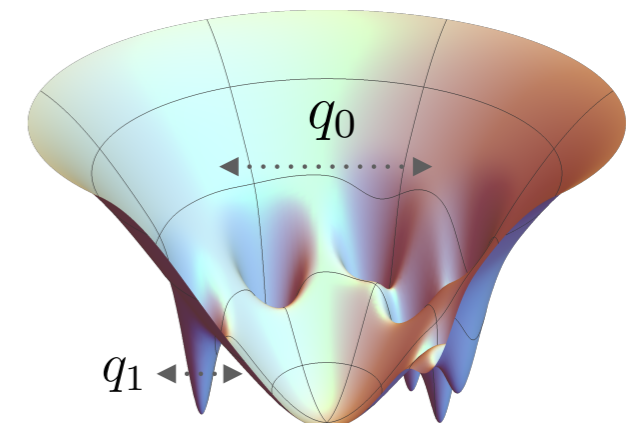
A double Gaussian integration comes into play now leading to two different averages:

$$\langle \cdot \rangle_{1r} = \frac{\int_{N_c}^{\infty} dN \exp[-\beta H_{1RSB}(N, z, t_{aB})]}{\int_{N_c}^{\infty} dN \exp[-\beta H_{1RSB}(N, z, t_{aB})]},$$

$$\langle \cdot \rangle_{m-r} = \frac{\int \frac{dt_{aB}}{\sqrt{2\pi}} e^{-\frac{t_{aB}^2}{2}} \left(\int_{N_c}^{\infty} dN \exp[-\beta H_{1RSB}(N, z, t_{aB})] \right)^m}{\int \frac{dt_{aB}}{\sqrt{2\pi}} e^{-\frac{t_{aB}^2}{2}} \left(\int_{N_c}^{\infty} dN \exp[-\beta H_{1RSB}(N, z, t_{aB})] \right)^m}.$$



- $q_0 = \frac{1}{S} \sum_i \langle N_i \rangle_{\alpha} \langle N_i \rangle_{\beta}$



- $q_1 = \frac{1}{S} \sum_i \langle N_i \rangle_{\alpha}^2$

$$h = \int \mathcal{D}z \frac{\int_{N_c}^{\infty} e^{-\beta H_{RS}(q_0, q_d, h, z)} N}{\int_{N_c}^{\infty} dN e^{-\beta H_{RS}(q_0, q_d, h, z)}} = \overline{\langle N \rangle}$$

Immigration

$$q_d = \int \mathcal{D}z \left(\frac{\int_{N_c}^{\infty} dN e^{-\beta H_{RS}(q_0, q_d, h, z)} N^2}{\int_{N_c}^{\infty} dN e^{-\beta H_{RS}(q_0, q_d, h, z)}} \right) = \overline{\langle N^2 \rangle},$$

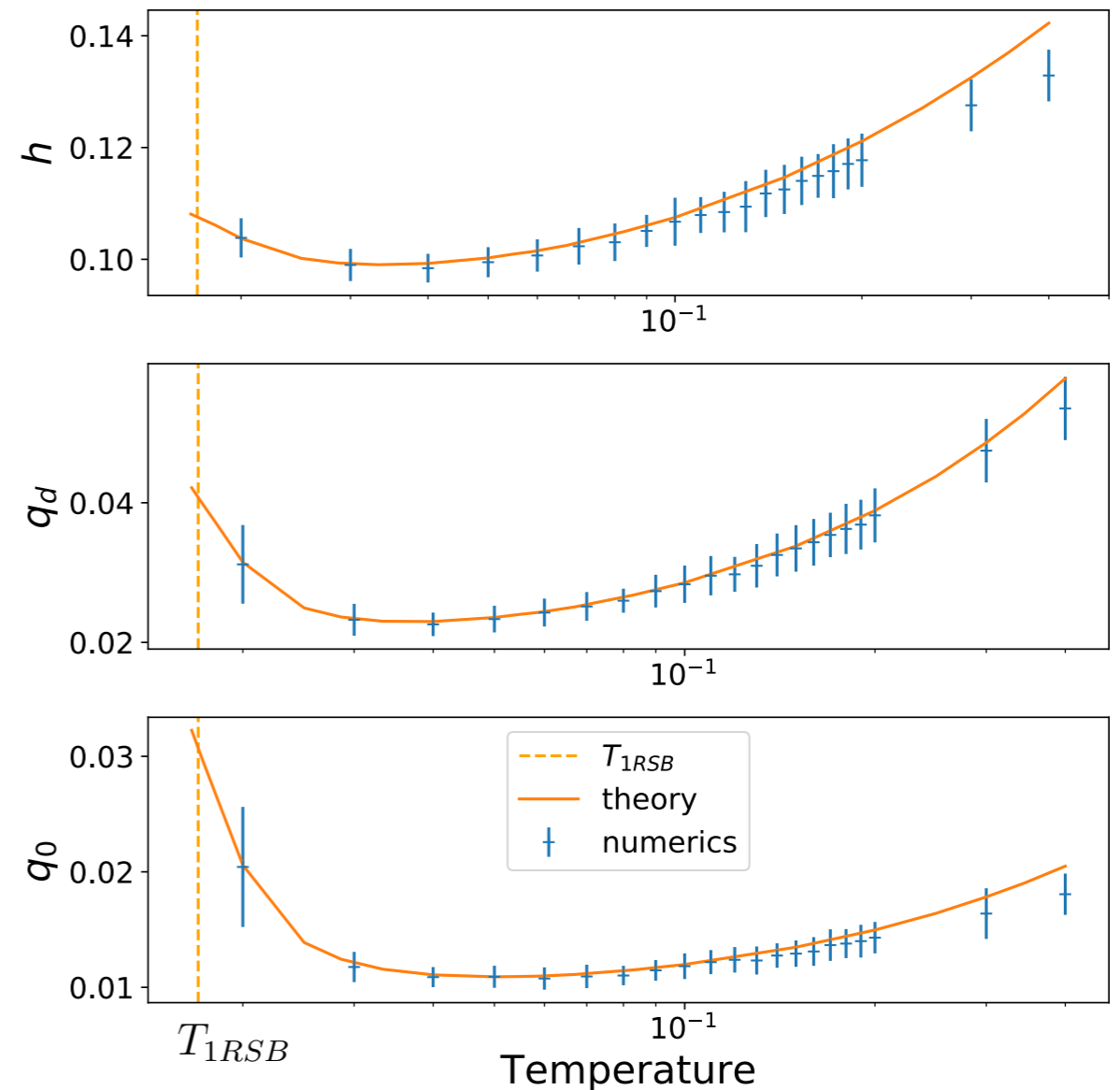
$$q_0 = \int \mathcal{D}z \left(\frac{\int_{N_c}^{\infty} dN e^{-\beta H_{RS}(q_0, q_d, h, z)} N}{\int_{N_c}^{\infty} dN e^{-\beta H_{RS}(q_0, q_d, h, z)}} \right)^2 = \overline{\langle N \rangle^2},$$



$$h = \mathbb{E}[N(t)]$$

$$q_d = C(0) = \mathbb{E}[N(t)^2]$$

$$q_0 = \lim_{\tau \rightarrow \infty} C(\tau) = \lim_{\tau \rightarrow \infty} \mathbb{E}[N(t)N(t+\tau)]$$



Ergodicity breaking effects start to appear.

Quenched complexity computation

Goal: determining the number of local minima of the free energy, averaged over quenched disorder.

$$\Sigma(f) \equiv \lim_{S \rightarrow \infty} \frac{1}{S} \overline{\log \mathcal{N}(f)} \quad \text{Log of the number of minima divided by the \# of species.}$$

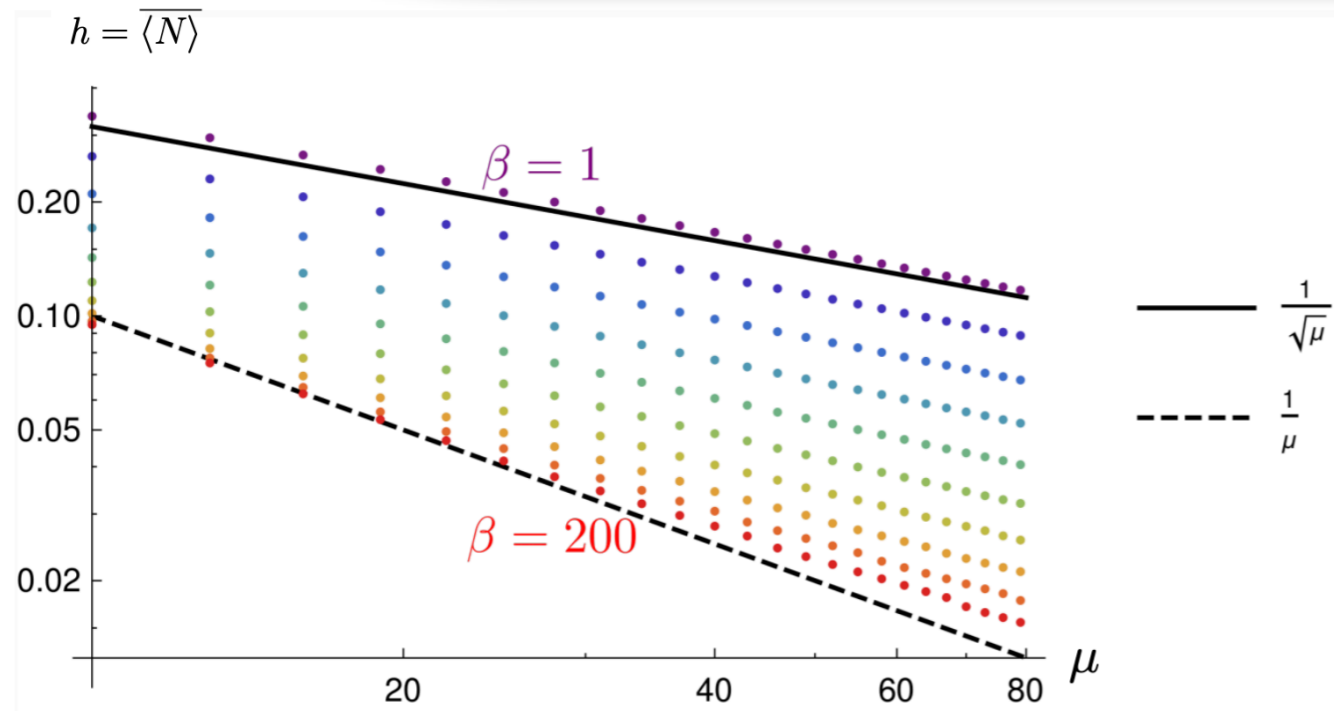


$$\Sigma = m^2 \frac{d}{dm} (\beta F^{1\text{RSB}}) = -m^2 \frac{d}{dm} \left(\frac{1}{n} \ln \int dq_d dq_1 dq_0 dh e^{S\mathcal{A}(q_d, q_1, q_0, h)} \right)$$

$$\Sigma = \frac{m^2 \rho^2 \sigma^2 \beta^2}{4} (q_1^2 - q_0^2) + \int \mathcal{D}z \ln \left[\int \frac{dt_{aB}}{\sqrt{2\pi}} e^{-\frac{t_{aB}}{2}} A(z, t_{aB})^m \right] - m \int \mathcal{D}z \frac{\int \frac{dt_{aB}}{\sqrt{2\pi}} e^{-\frac{t_{aB}}{2}} A(z, t_{aB})^m \ln A(z, t_{aB})}{\int \frac{dt_{aB}}{\sqrt{2\pi}} A(z, t_{aB})^m}$$

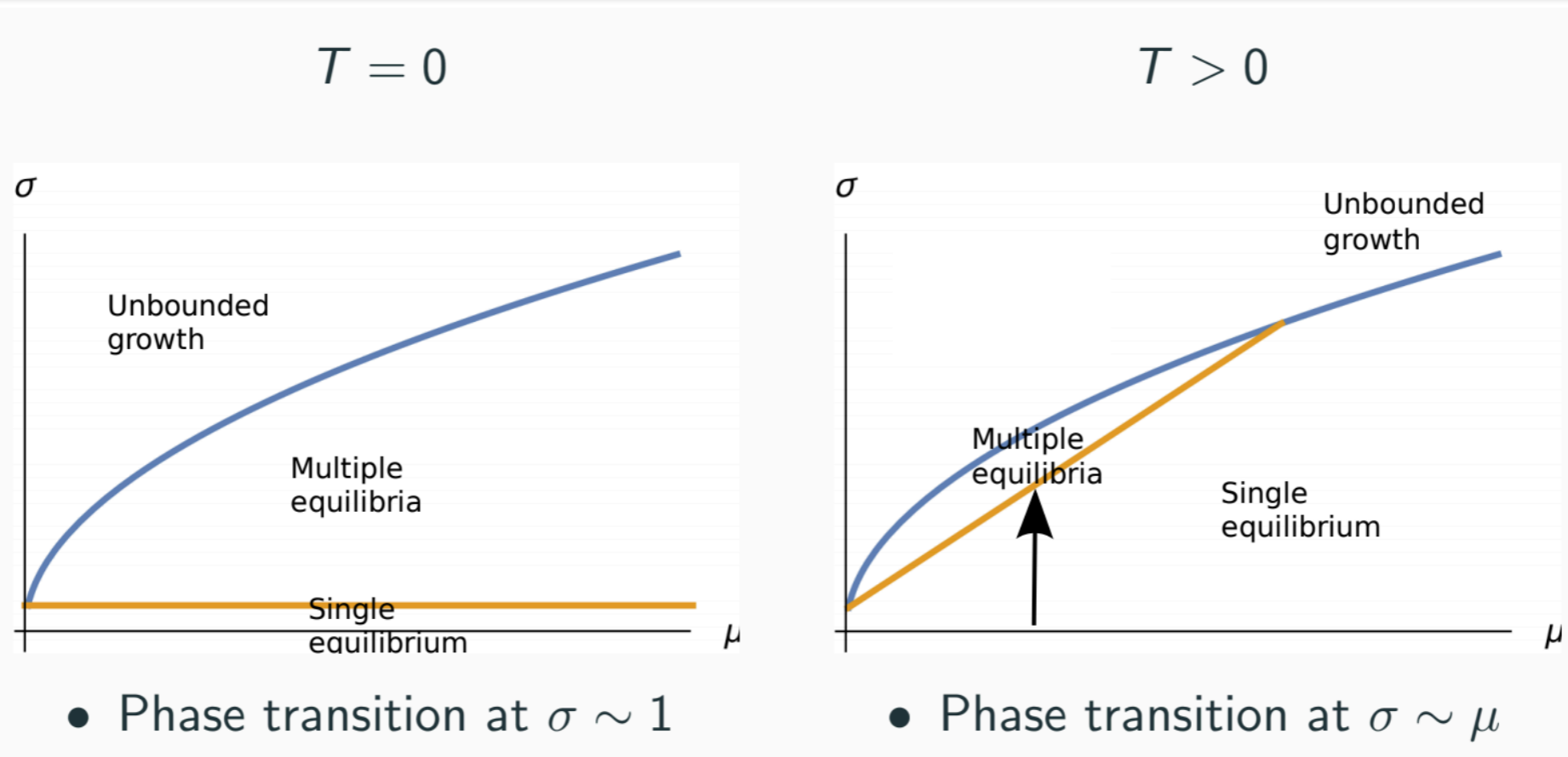
Strictly positive complexity at finite temperature (in the 1RSB phase),
and compatible with previous analysis at zero temperature.

Scaling and phase diagrams in the strongly competitive case



Two different scalings depending on finite or zero demographic noise regime. Continuous crossover between the two.

Phase diagrams in the two regimes: no difference w.r.t to the weak interaction case ($T=0$); dramatically affected in the $T>0$ case



● Phase transition at $\sigma \sim 1$

● Phase transition at $\sigma \sim \mu$