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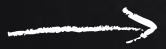
# Statistical Physics of Resource Competition in a Highly Diverse Ecosystem

March 8, 2021

# Resource Competition Model

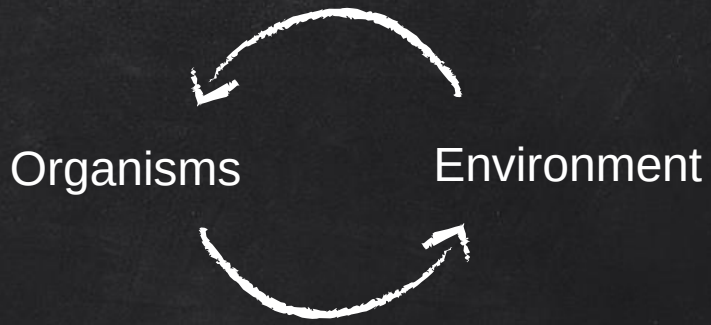
- ✗ Introduction
- ✗ Theory of the model
- ✗ Results and new observations
- ✗ Conclusions



“Collective Phase in Resource Competition in a Highly Diverse Ecosystem”, Tikhonov and Monasson

# INTRODUCTION

# The focus



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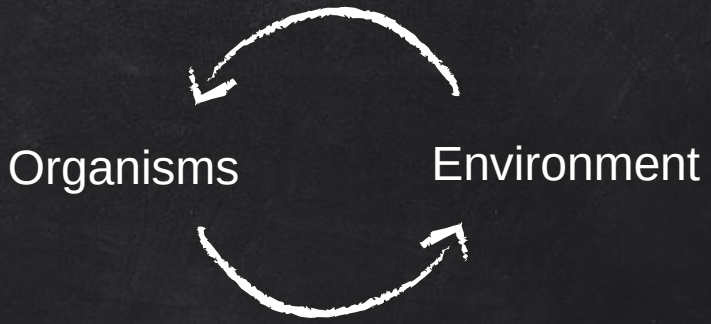
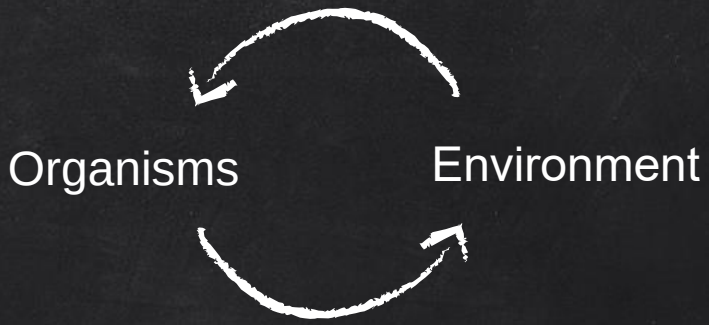



**Ecoevolutionary** dynamics for a large number of interacting species

# The focus




**Ecoevolutionary** dynamics for a large number of interacting species

- It is possible to set the *external condition* faced by the community
- The *immediate environment* for each individuals depends from all other organism

# History

1969 → Mac Arthur proposed an ecogical model of resource competition in a well-mixed community at equilibrium

1983 → Tilman gives a geometrical description of the model for a low number of resources ($N = 1,2$)

2016 → Tikhonov proposed a simulation-based study for a modestly large number of resources exhibiting *community cohesion* as a consequence of environmental feedback

# The aim

Tikhonov and Monasson proposed the *analytical solution* of the classic model of resource competition *in the limit of large* $N$

We wanto to model the feedback of organisms onto environment

# Theory of the model

## The basis

# Basic quantities

- ✗ Multispecies community in a well-mixed habitat
- ✗ Single *limiting element* X in $N$ forms $\longrightarrow$ $i \in \{1, \ldots, N\}$ substrates
- ✗ Total supply of resource $R_i$, $\forall i$

# Basic quantities

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- $\overrightarrow{\sigma_\mu} = \{\sigma_{\mu i}\}_{i=1,\dots,N}$ $\forall \mu$, *metabolic strategies:* species are defined by the their pathways

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- $h_i$ *resource avaiability,* $\forall i$, in the immediate environment
- Resource *surplus* $\Delta_\mu = \sum_i \sigma_{\mu i}\, h_i - \mathrm{X}_\mu$ $\longrightarrow$ determines the population growth

# What we want

For a specific $\{h_i\}$ the population growth rate of the species $\mu$ is determined by $\Delta_\mu$

$$\frac{dn_\mu}{dt} \sim n_\mu \Delta_\mu$$

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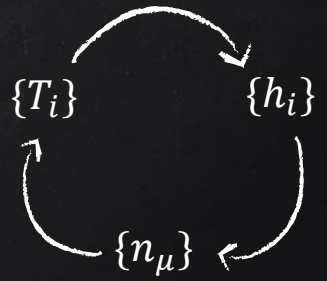
For a specific $\{h_i\}$ the population growth rate of the species $\mu$ is determined by $\Delta_\mu$

$$\frac{dn_\mu}{dt} \sim n_\mu \Delta_\mu = 0$$

We are interested in the **feedback loop** at *equilibrium*:



# From outside to inside

$$\mathrm{h}_i = H_i(T_i)$$

**Resource depletion rule** in general is an arbitrary decreasing function, different for each resource

**Simple model**: Organisms could share the fixed total influx of resource → $\mathrm{h}_i = \frac{R_i}{T_i}$

**Mac Arthur model**: dinamical resources with *renewal rate* $r_i$ and maximal availability $K_i$ → $\mathrm{h}_i = K_i(1 - \frac{T_i}{r_i})$

# Theory of the model

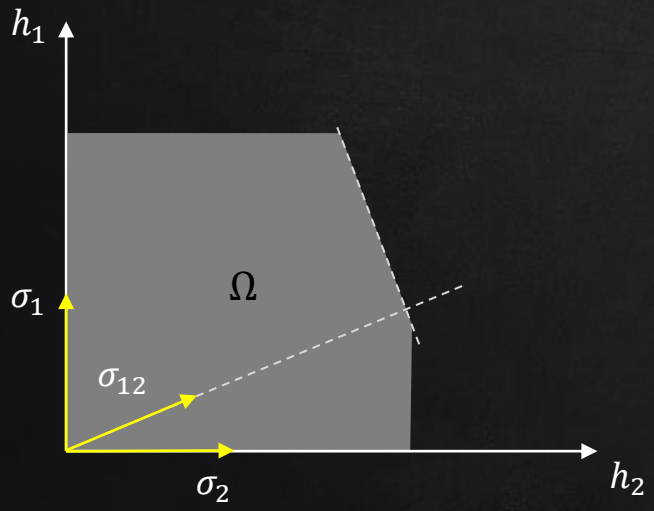
## The geometrical description

# The geometrical description

Consider:
- $\overrightarrow{\sigma_\mu}$ ⟶ $P$ vectors in the $N$-dimensional space of **resouces availability**
- $\vec{h} \cdot \vec{\sigma}_\mu = \mathrm{X}_\mu$ ⟶ hyperplane, $\forall \mu$

We can define the *Unsustainable Region:*

$$\Omega = \bigcap_{\mu=1}^{P} \left\{ \vec{h} \mid \vec{h} \cdot \overrightarrow{\sigma_\mu} < \mathrm{X}_\mu \right\}$$




$$\begin{cases} \vec{h} \text{ inside } \Omega \rightarrow \dfrac{dn_\mu}{dt} < 0, \forall \mu \\ \vec{h} \text{ outside } \Omega \rightarrow \dfrac{dn_\mu}{dt} > 0, \quad \text{at least for one } \mu \\ \vec{h} \text{ on the surface } \partial\Omega \rightarrow \dfrac{dn_\mu}{dt} = 0 \end{cases}$$

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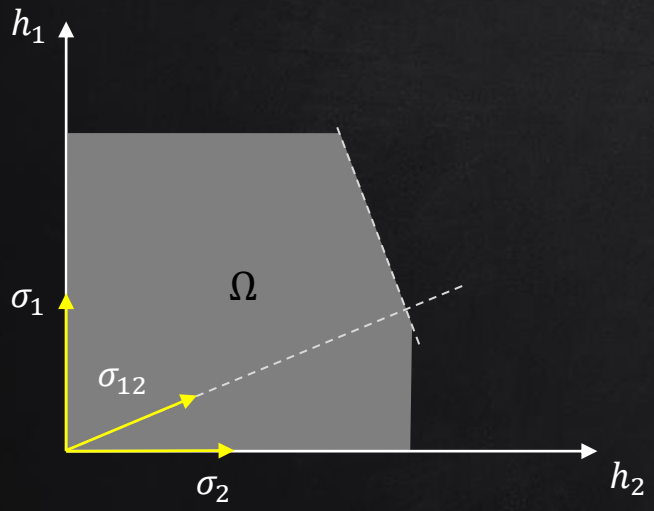


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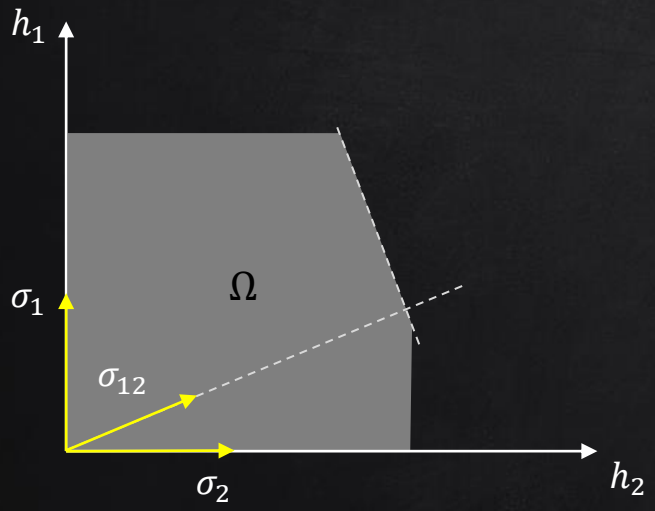



At equilibrium: $\begin{cases} n_\mu = 0,\ \Delta_\mu < 0, extinct \\ n_\mu > 0,\ \Delta_\mu = 0, survivals \end{cases}$

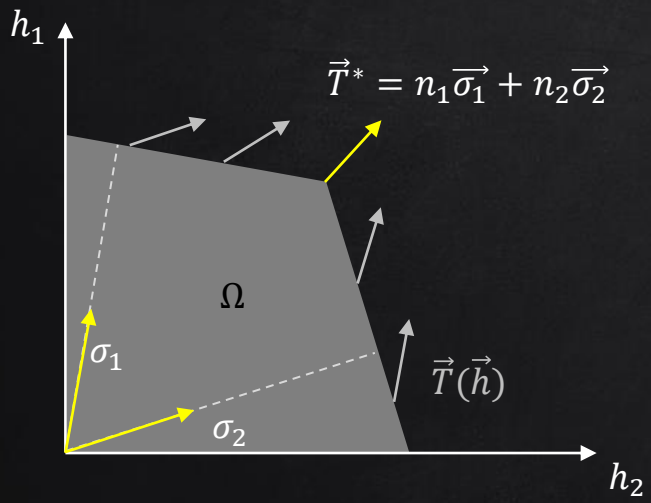
# The geometrical description

? How to find the *equilibrium point* $\vec{h}^* \in \partial\Omega$?

$\exists \tilde{F}$, defined in the harvest space, such that:

$$\frac{\partial \tilde{F}}{\partial h_i} = T_i \quad \Leftrightarrow \quad H_i(h_i) = T_i, \qquad \forall i$$

The equilibrium community state corresponds to the maximum of $\tilde{F}$ over the unsustainable region $\Omega$




**Aim**: study the properties of a community at equilibrium, given by the mapping the external resources $\vec{R}$ into the environment *at equilibrium* $\vec{h}^*$**,** for a *typical community*

# The geometrical description

We consider:

$$H_i(T_i) = \frac{R_i}{T_i}$$

The general function is:

$$\tilde{F}(\{h_i\}) = [\vec{h} \cdot \vec{T} - \sum_i \widehat{H}_i(T_i)] \text{ with } \widehat{H}_i(T_i) = \int H_i(T_i) dT_i$$

In our case we get:

$$\widehat{H}_i(T_i) = R_i \log T_i \text{ and } T_i^* = \frac{R_i}{h_i^*}$$

The function that we need to maximize is:

$$\tilde{F}(\{h_i\}) = \sum_i R_i log h_i + const$$

# Theory of the model

For a large number of interacting species

# The Statistical Physics approach

We need to model the pool of competitors $P = \alpha N$, for $\alpha = cost$ and $N \to \infty$

↳ $\forall \mu$ we get:

- $\overrightarrow{\sigma_\mu}$ random binary vector with $\sigma_{\mu i} = \begin{cases} 1 \text{ with probability } p \\ 0 \text{ with probability } 1-p \end{cases}$
- Random cost $\mathrm{X}_\mu = \sum_i \sigma_{\mu i} + \epsilon x_\mu$, where $x_\mu \sim N(0,1)$

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THE ASSUMPTION: The costs $\mathrm{X}_\mu$ and the metabolic strategies $\{\sigma_{\mu i}\}$ are *uncorrelated*,
→ we can describe the compering strategies set with three parameters:

- $p$ sparsity
- $\epsilon$ width of the cost distribution
- $\alpha$ that determines the effective number of species in the pool

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Setting $h_i = 1$ the resource balance of all species is satisfied: neither specialists nor generalists are favourited

↳ We can characterize the fluctuations of the resource availability:

$$m = \sum_i (1 - h_i) \qquad q = \sum_i (1 - h_i)^2$$

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Our partition function in the harvest space is

$$Z = \int_0^\infty \prod_i dh_i \, e^{\beta \tilde{F}} \prod_\mu^P \theta\left(\mathrm{X}_\mu - \vec{h} \cdot \vec{\sigma}_\mu\right)$$

# TYPICAL REALIZATION

We are interested in the behavior of *the typical realization* of the system, thus we want to compute the mean of $Z$

**Replica trick**

$$\langle logZ \rangle = \lim_{n \to 0} \frac{\langle Z^n \rangle - 1}{n}$$

- Starting point
- Consider $Z^n$
- Compute the average over the disorder
- Decouple indices of resource availability $i$ and species $\mu$
- Decoupling replicas
- Compute the limit $n \to 0$
- Final expression

# The solution

$$\langle logZ \rangle = \beta \; extr \left\{ \frac{\bar{\gamma} - x}{2x\bar{\gamma}} q + \frac{\overline{\delta\tau^2}}{2} x - \frac{\lambda\tau\psi(q)}{p} - \frac{\alpha\psi^2(q)}{2xp(1-p)} I(\lambda) \right\}$$

with $I(\lambda) = \int_{\lambda}^{\infty} (y-\lambda)^2 e^{-\frac{y^2}{2}} \frac{dy}{\sqrt{2\pi}}$

- The extremum is over $x$, $q$ and $\lambda$
- $\bar{\tau}, \overline{\delta\tau^2}, \bar{\gamma}$ characterize the resource supply ⟶ In our case $\bar{\tau} = \bar{R} = 1, \bar{\gamma} = 1$and $\overline{\delta\tau^2} = \overline{\delta R^2}$
- $p, \alpha$ and $\epsilon$ characterize the pool of competitors

# The solution

$$\langle logZ \rangle = \beta \; extr \underbrace{\left\{ \frac{\bar{\gamma} - x}{2x\bar{\gamma}} q + \frac{\overline{\delta\tau^2}}{2} x - \frac{\lambda\tau\psi(q)}{p} - \frac{\alpha\psi^2(q)}{2xp(1-p)} I(\lambda) \right\}}_{= A}$$

Using the extremum condition we get:

$$\begin{cases} \dfrac{\partial A}{\partial x} = 0 \\ \dfrac{\partial A}{\partial q} = 0 \\ \dfrac{\partial A}{\partial \lambda} = 0 \end{cases} \longrightarrow \begin{cases} \dfrac{x}{\bar{\gamma}} = 1 - \alpha E(\lambda) \text{ with } E(\lambda) = \int_{\lambda}^{\infty} e^{-\frac{y^2}{2}} \dfrac{dy}{\sqrt{2\pi}} \\ \dfrac{1 - \alpha I(\lambda)}{1 - \alpha E(\lambda)} = 1 + \dfrac{\lambda}{\psi} \\ \psi^2[1 - \alpha I(\lambda)] = \epsilon^2 + \big(1 - \alpha E(\lambda)\big)^2 \bar{\gamma}^2 p(1-p)\overline{\delta\tau^2} \end{cases}$$

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Studing the system for $H_i = \frac{R_i}{T_i}$ with $\bar{R} = 1, \overline{\delta\tau^2} = \overline{\delta R^2}$, $\bar{\gamma} = 1$:

$$\begin{cases} \dfrac{1 - \alpha I(\lambda)}{1 - \alpha E(\lambda)} = 1 + (1-p)\dfrac{\lambda}{\psi} \\ \\ \psi^2[1 - \alpha I(\lambda)] = \epsilon^2 + p(1-p)\big(1 - \alpha E(\lambda)\big)^2 \overline{\delta R^2} \end{cases}$$

# The order parameter

$$\psi(q) = \sqrt{p(1-p)q + \epsilon^2}$$

It describes the spread of resource surplus

We are interested in the limit $\epsilon \to 0$, in this case we get:

- The scatter of intrinsic organisms cost is negligible
- It is possible to focus on the interaction-dependent factors

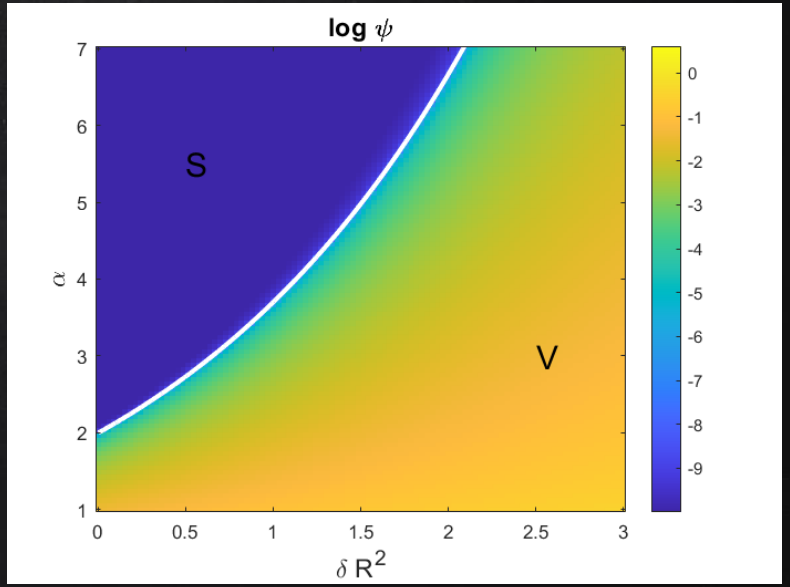
# The Phase Transition

For $\epsilon \to 0$:

We have the separation of the parameter space in **two phases**:

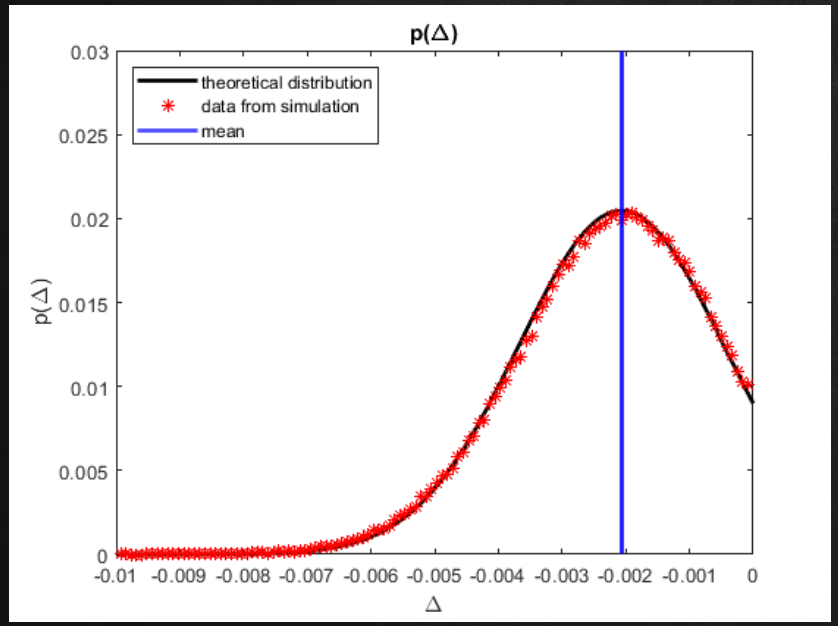
- *S phase*: environment **shielded** from external conditions, $\psi = 0$
- *V phase*: environment **vulnerable** to the external conditions, $\psi \neq 0$

→ the critical line is $\overline{\delta R_*^2} = \frac{1-p}{p} \frac{\lambda^2}{1-\alpha_* I(\lambda)}$



# The number of species that survive

We can compute the distribution of the *resource surplus* of all the species $P = \alpha N$ *at equilibrium*




$$p(\Delta) = \frac{1}{\sqrt{2\pi\psi^2}} e^{-\left[\frac{(\Delta+\lambda\psi)^2}{2\psi^2}\right]} \theta(-\Delta) + E(\lambda)\delta(\Delta)$$

$$\langle \Delta_\mu \rangle = \langle \sum_i h_i \sigma_{\mu i} - \mathrm{X}_{mu} \rangle = -pm, \;\; m = \sum_i (1 - h_i)$$

The number of survivors is given by the fraction of species whose resource demand is met, $\Delta_\mu = 0$

# RESULTS

# The Method

We generate the pool of competitors, $\forall \mu$ we get:

$$\overrightarrow{\sigma_\mu} = \{\sigma_{\mu i}\}_{i=1,\dots,N} \quad \text{and} \quad \mathrm{X}_\mu = \sum_i \sigma_{\mu i} + \epsilon x_\mu, \text{ with } \mathrm{x}_\mu \sim N(0,1)$$

Given the resource depletion rule $H_i(T_i) = \frac{R_i}{T_i}$ and considering the resource supply $R_i = \bar{R} \pm \frac{\delta R_i}{\sqrt{N}} = 1 \pm \frac{1}{\sqrt{50}}$

we want to find the equilibrium point $\overrightarrow{h^*}$ computing the maximum of:

$$\tilde{F}(\{h_i\}) = \sum_i R_i log h_i + const$$

- The resource surplus distribution
- The number of surviving species at equilibrium, given by $\Delta_\mu = 0$
- The equilibrium availability of resources
- The phase transition for different values of $\epsilon$

# The External Supply

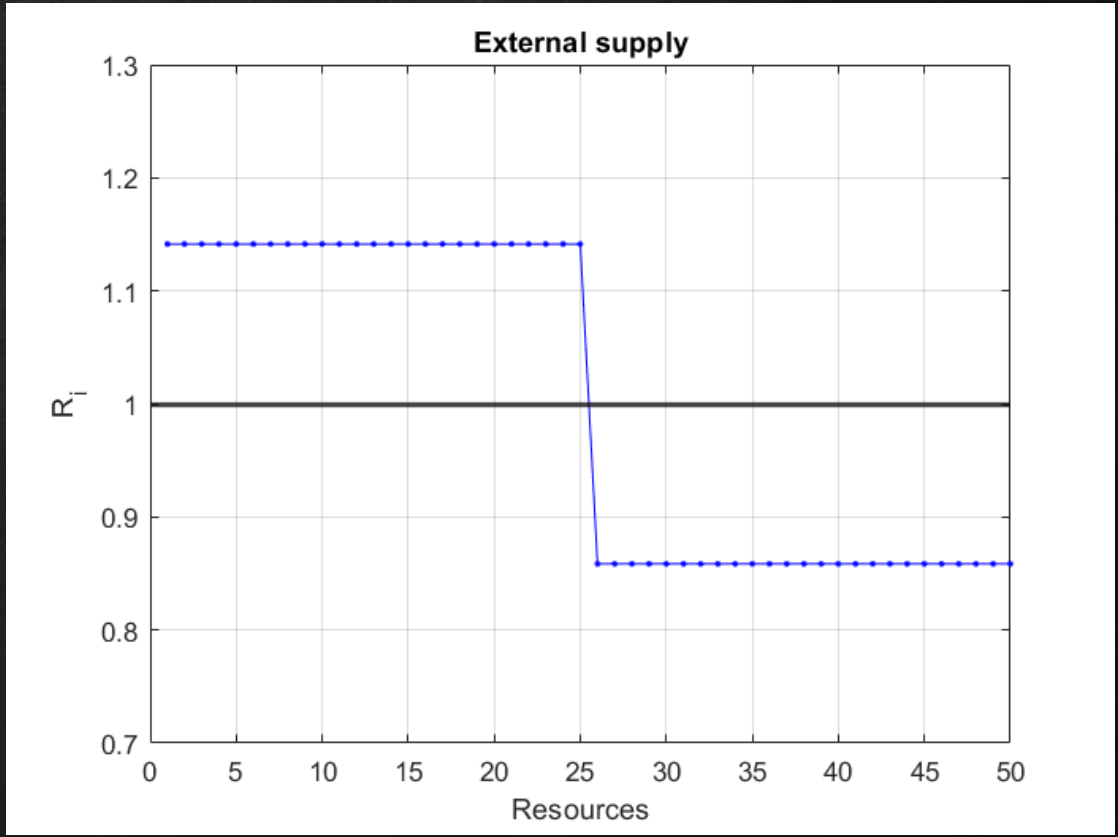
$$H_i(T_i) = \frac{R_i}{T_i}$$

$N = 50$

$\bar{R} = 1$

$\overline{\delta R^2} = 1$

$$R_i = \bar{R} \pm \frac{\delta R_i}{\sqrt{N}} = 1 \pm \frac{1}{\sqrt{50}}$$



# The resource surplus distribution

$\#realizations = 500$

$N = 50$

$p = 0.5$

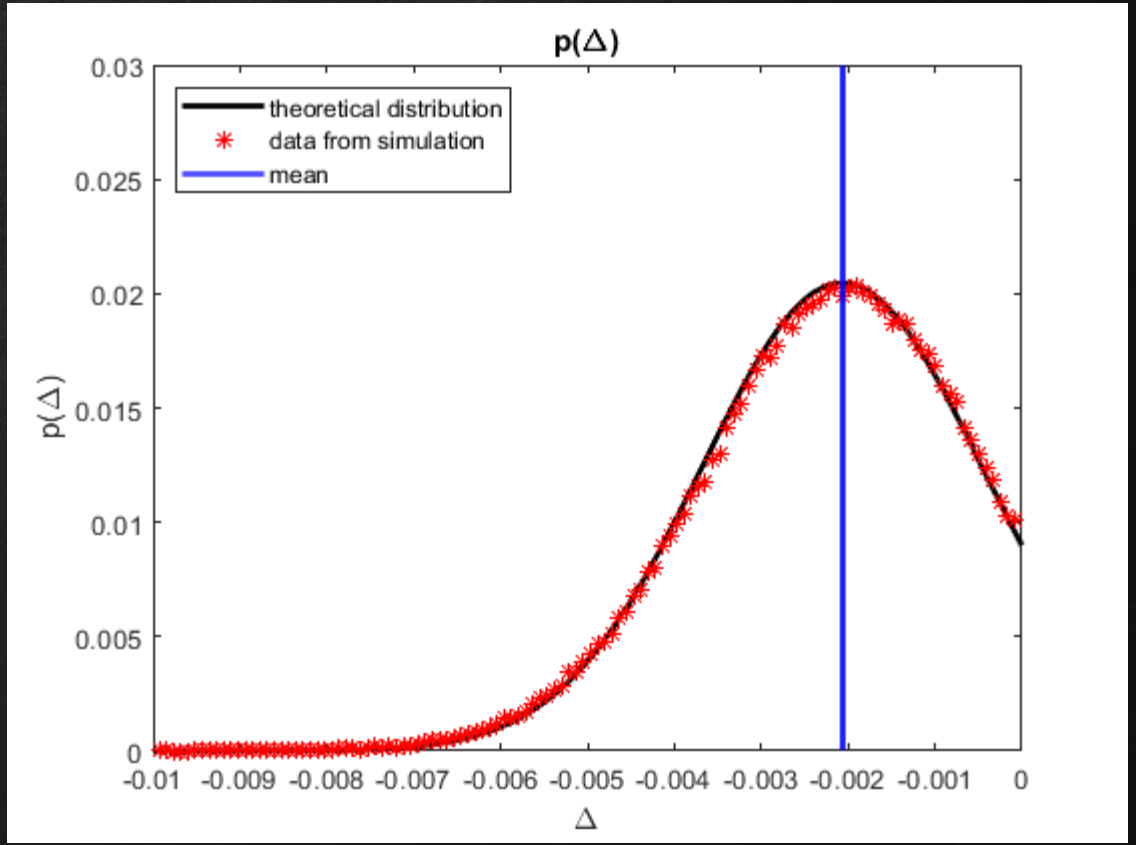
$\overline{\delta R^2} = 1$

$\bar{R} = 1$

$\epsilon = 10^{-3}$

$\alpha_S = 10$

$$p(\Delta) = \frac{1}{\sqrt{2\pi\psi^2}} e^{-\left[\frac{(\Delta+\lambda\psi)^2}{2\psi^2}\right]} \theta(-\Delta)$$



# The number of surviving species at equilibrium

$\#realizations = 500$

$N = 50$

$p = 0.5$

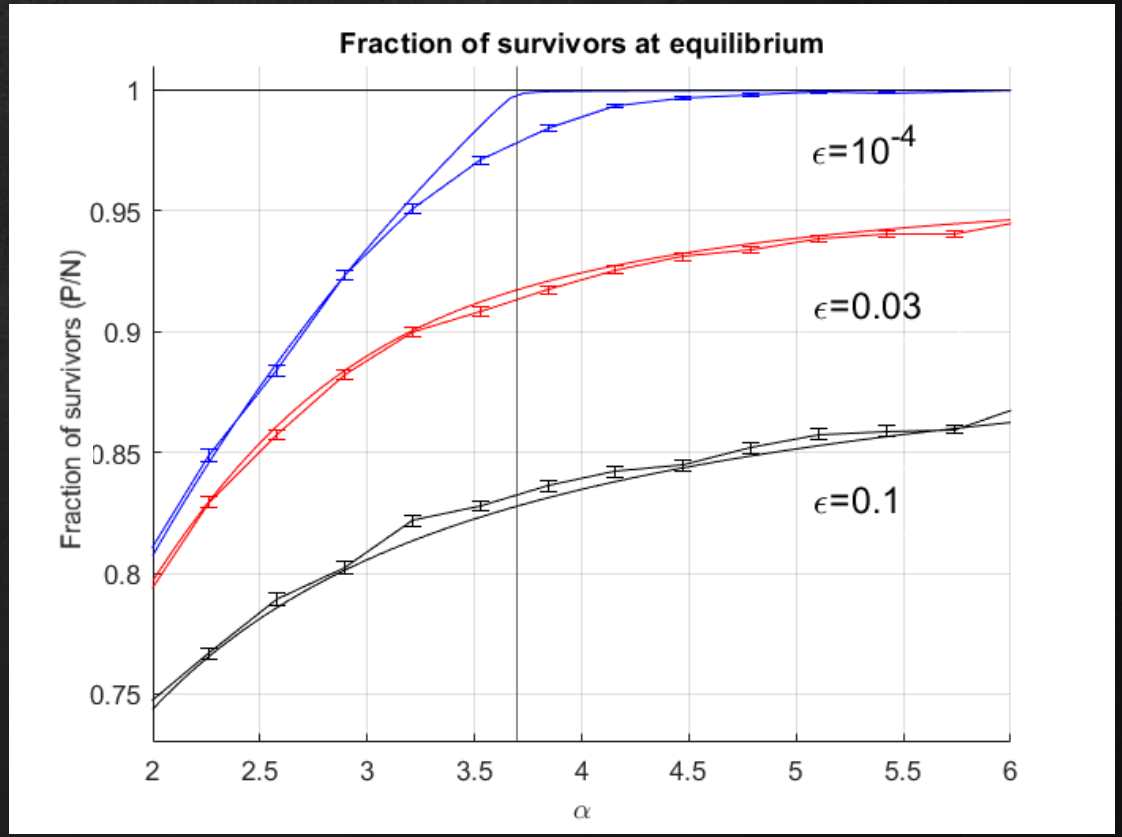
$\overline{\delta R^2} = 1$

$\bar{R} = 1$

$\epsilon = [10^{-4}, 0.03, 0.1]$

The number of survival species is given by the number of species with

$$\Delta_\mu = \left( \sum_i \frac{\sigma_{\mu i}}{\sum_i \sigma_{\mu i}} \cdot h_i \right) - \frac{X_\mu}{\sum_i \sigma_{\mu i}} = 0$$



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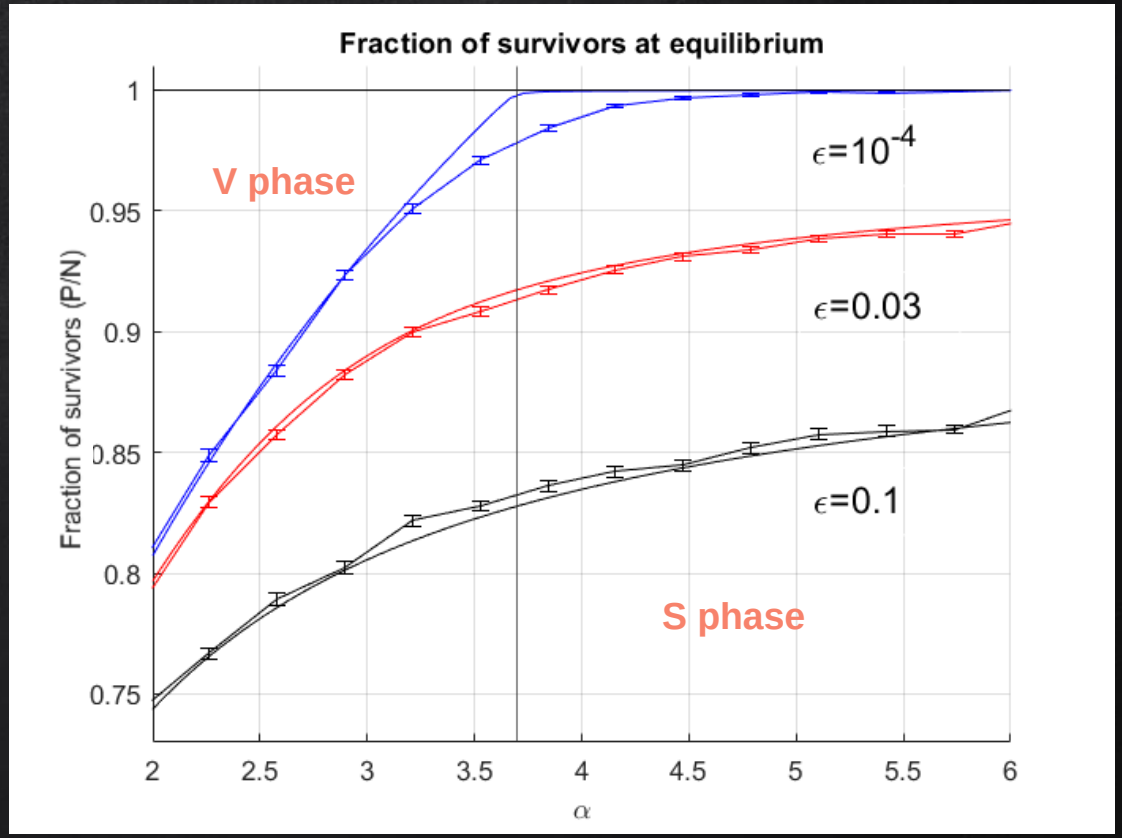


# The equilibrium availability of resources

$\#realizations = 500$

$N = 50$

$p = 0.5$

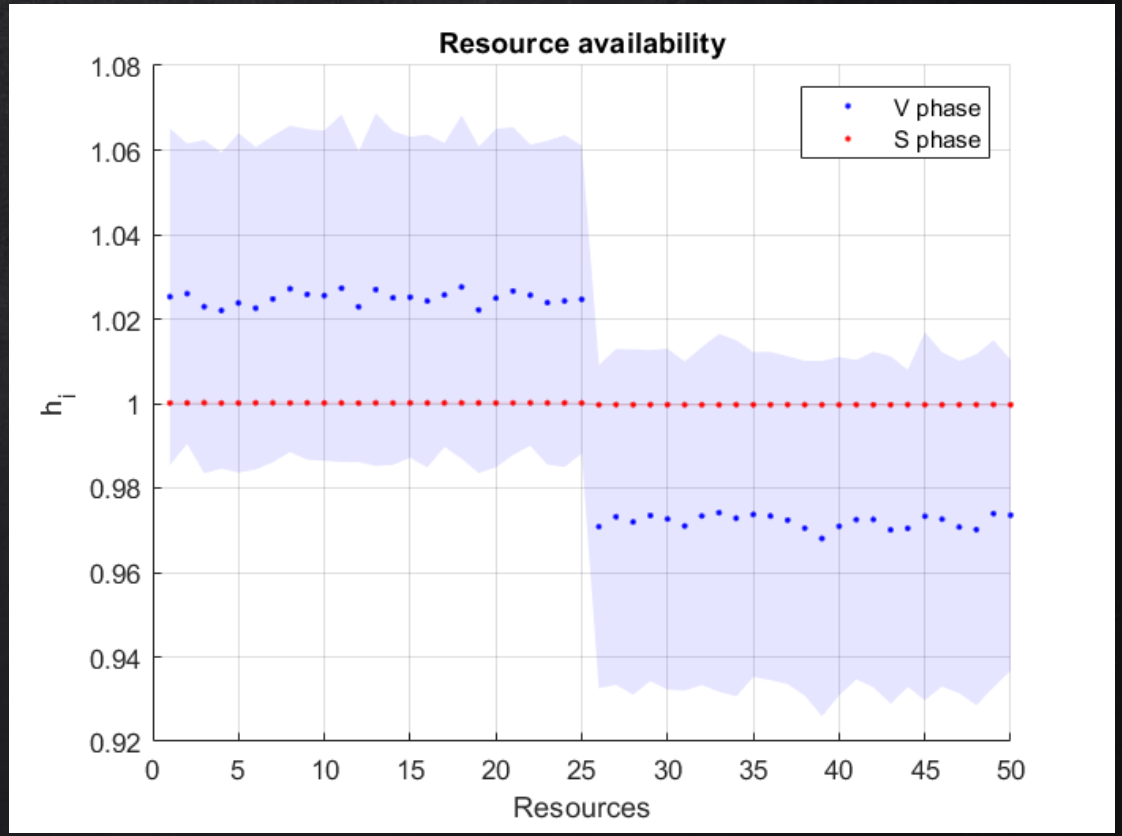
$\overline{\delta R^2} = 1$

$\bar{R} = 1$

$\epsilon = 10^{-3}$

$\alpha_V = 2, \alpha_S = 10$

NOTE: $h_i = 1 \; \forall i$ satisfies the resource balance of all species: neither specialists or generalists have an advantage



# And for finite ε?

$\#realizations = 10$

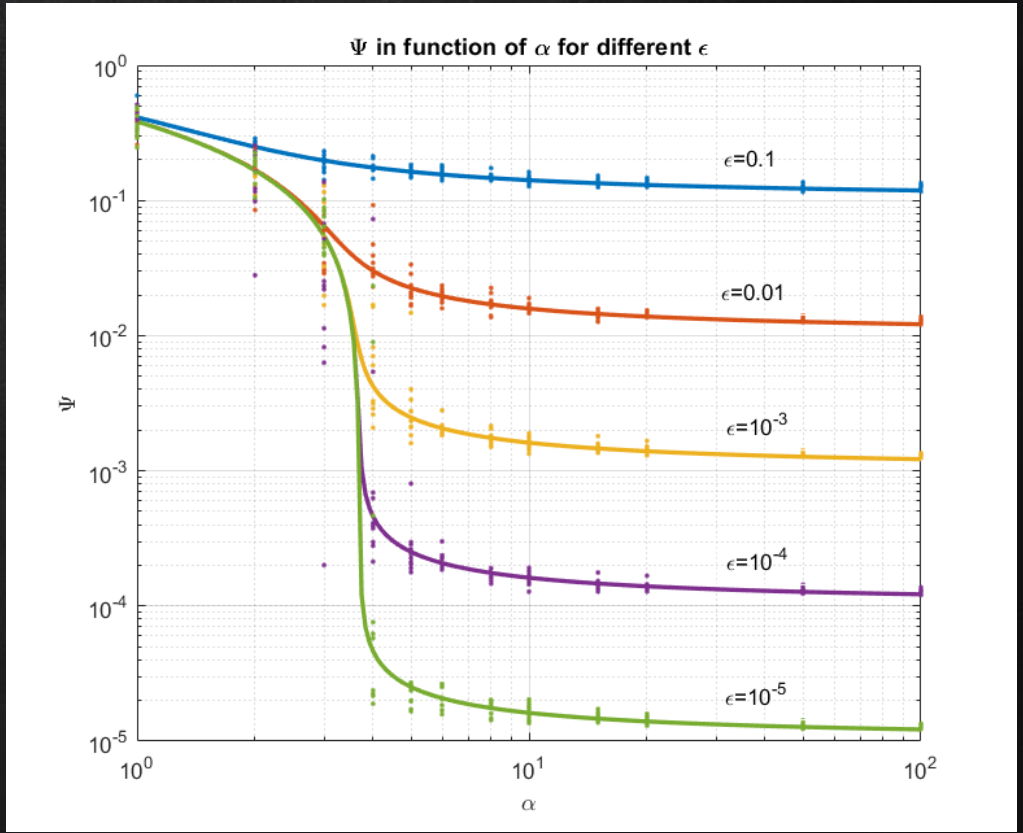
$N = 50$

$p = 0.5$

$\overline{\delta R^2} = 1$

$\bar{R} = 1$

$\epsilon = [10^{-5}, 10^{-4}, 10^{-3}, 0.01, 0.1]$



# Changing the parameters

Modify $\overline{\delta R^2}$

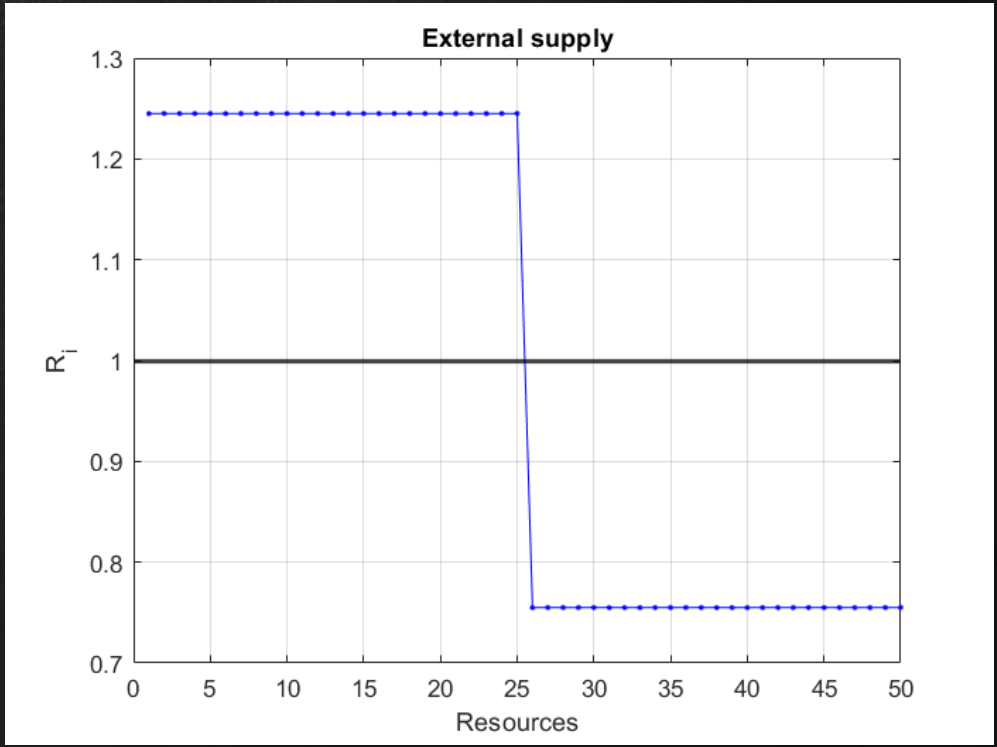
# Modify $\overline{\delta R^2}$

$N = 50$

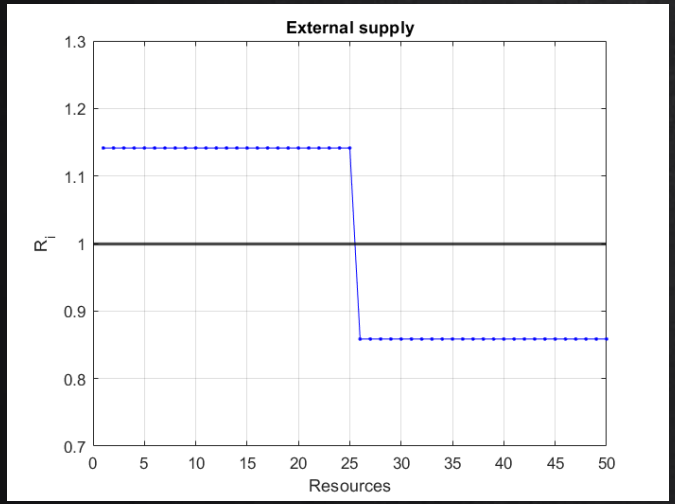
$\bar{R} = 1$

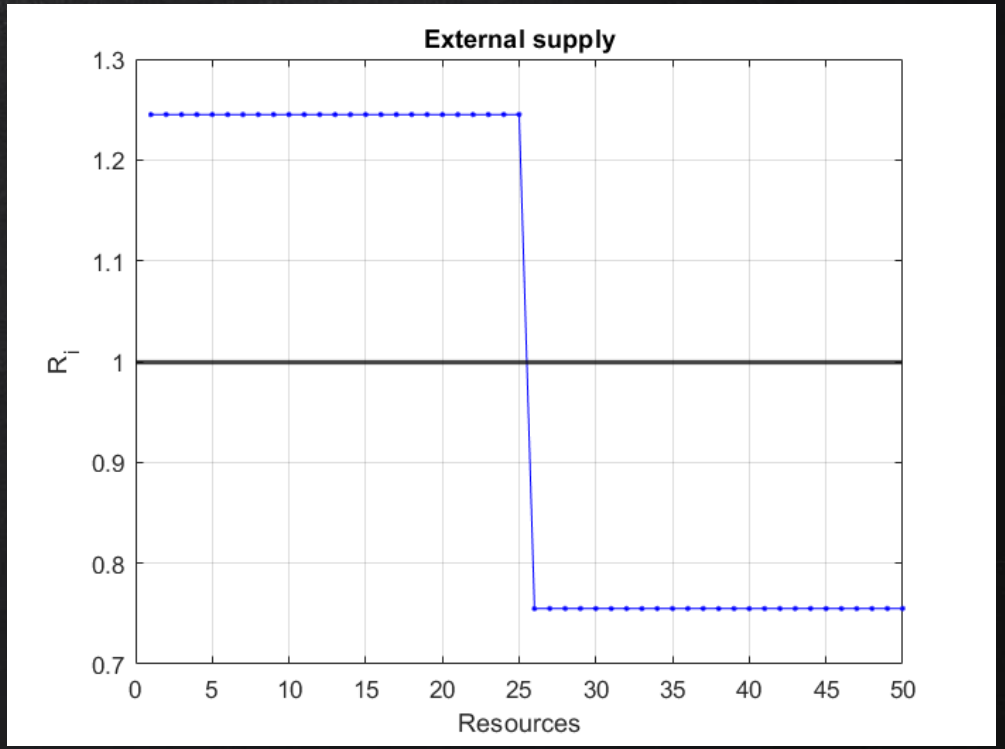
$\overline{\delta R^2} = 3$

$$R_i = \bar{R} \pm \frac{\delta R_i}{\sqrt{N}} = 1 \pm \frac{\sqrt{3}}{\sqrt{50}}$$

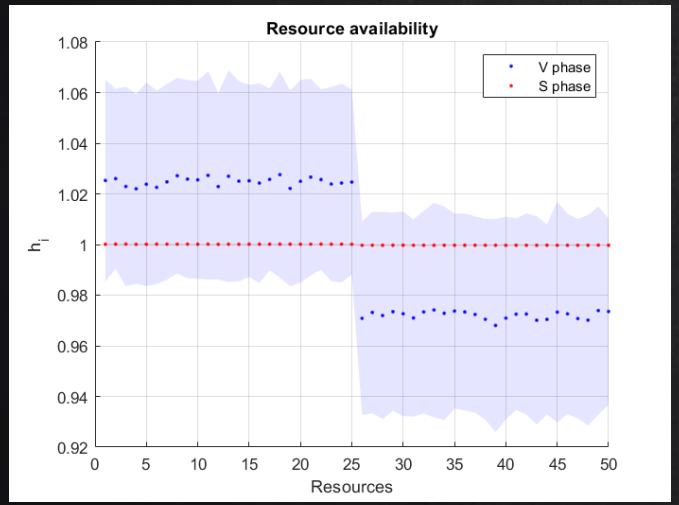


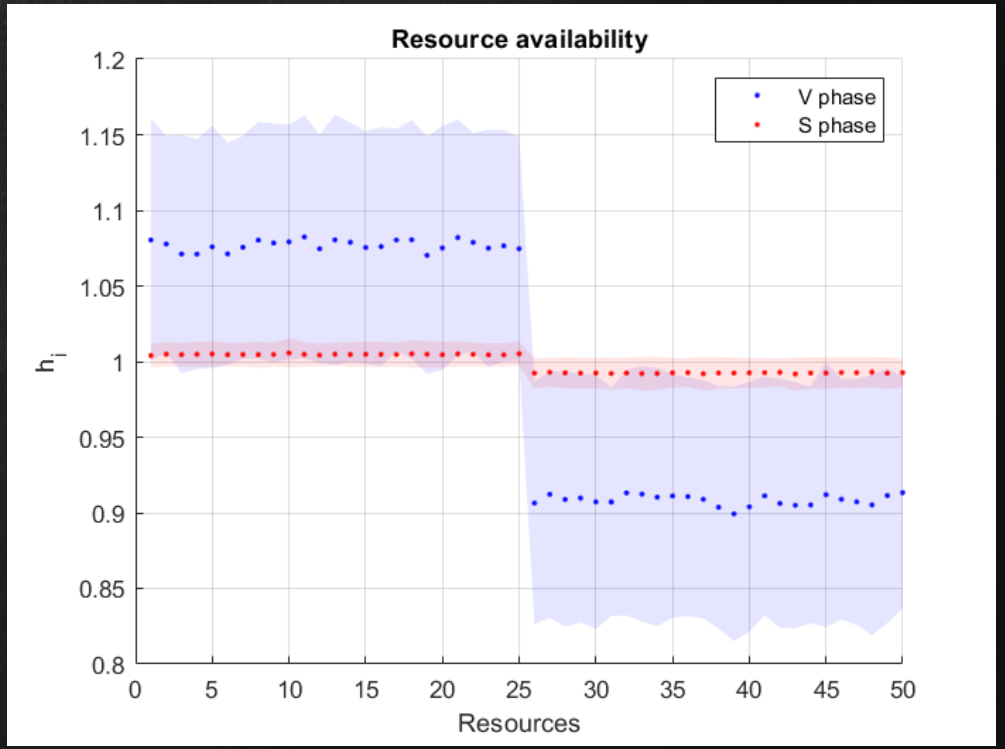
# Modify $\overline{\delta R^2}$



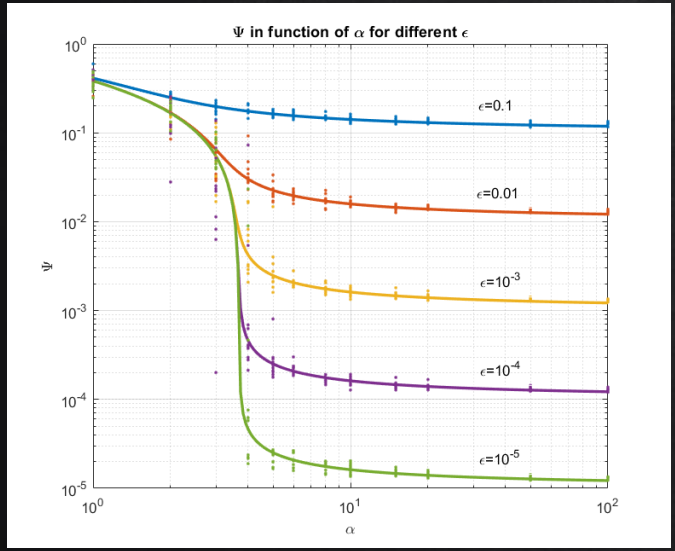



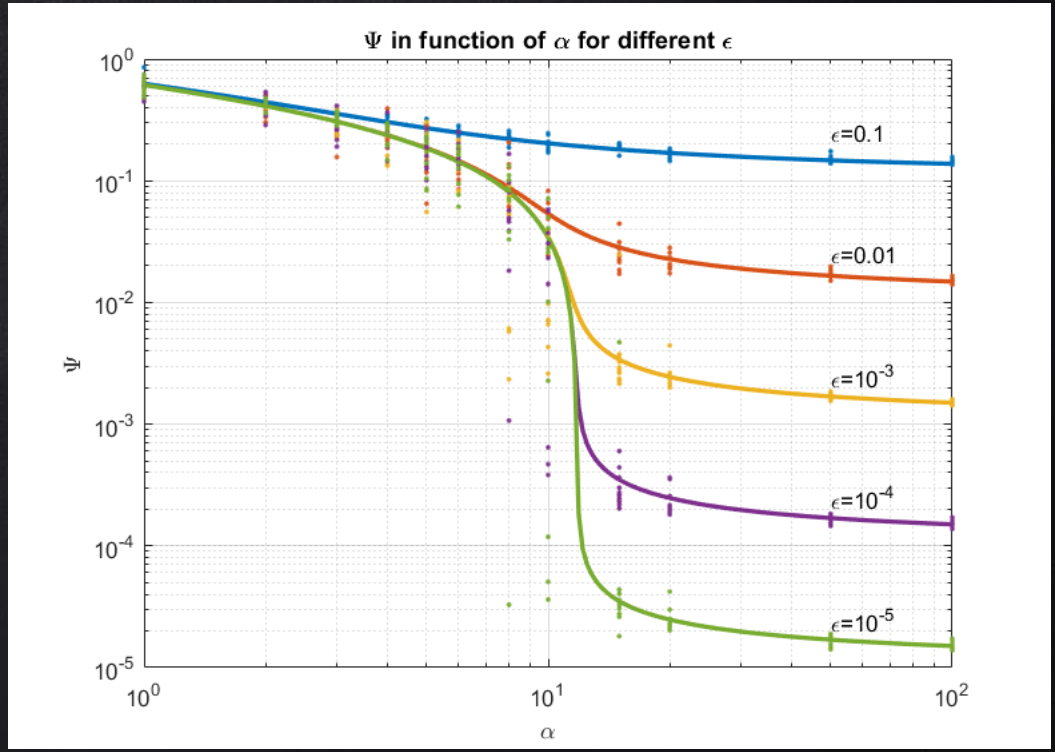
# Modify $\overline{\delta R^2}$



# Modify $\overline{\delta R^2}$

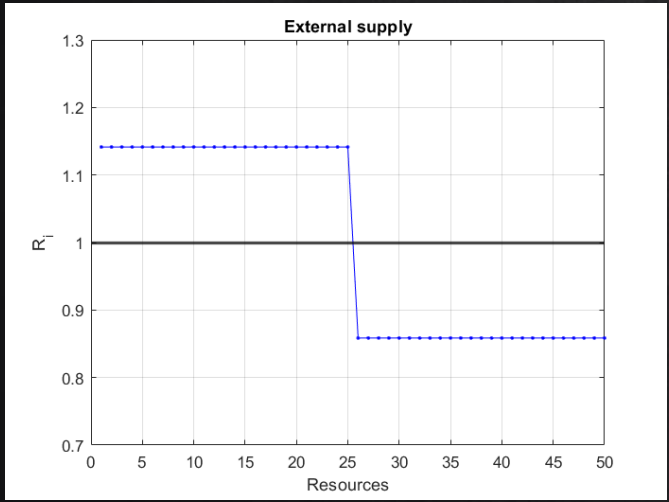


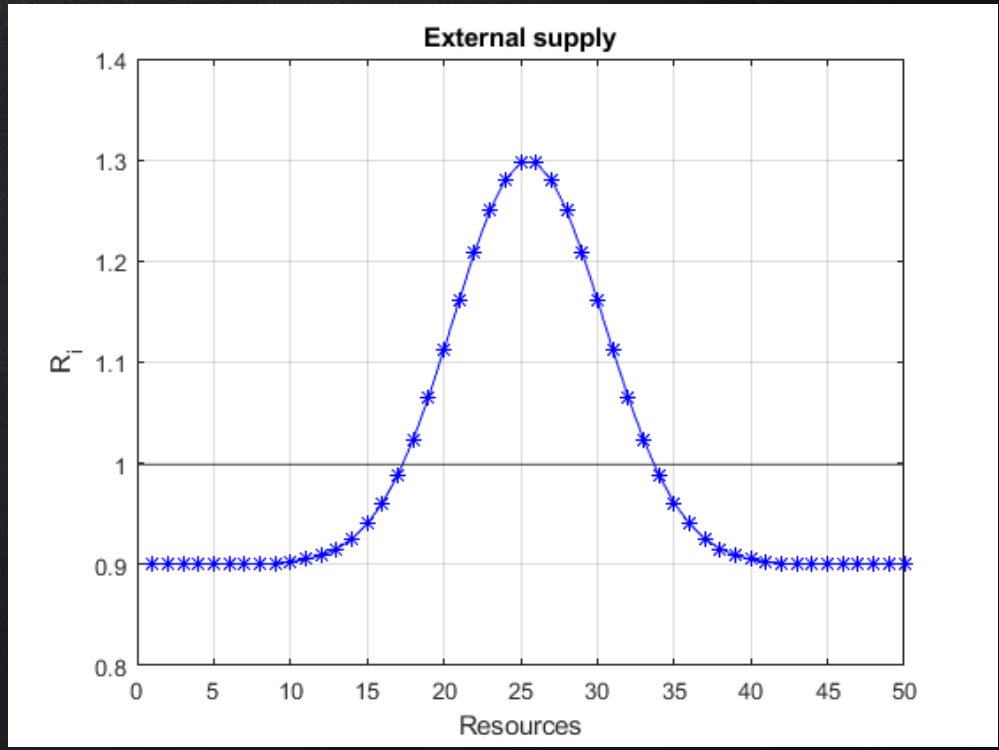



# Changing the parameters

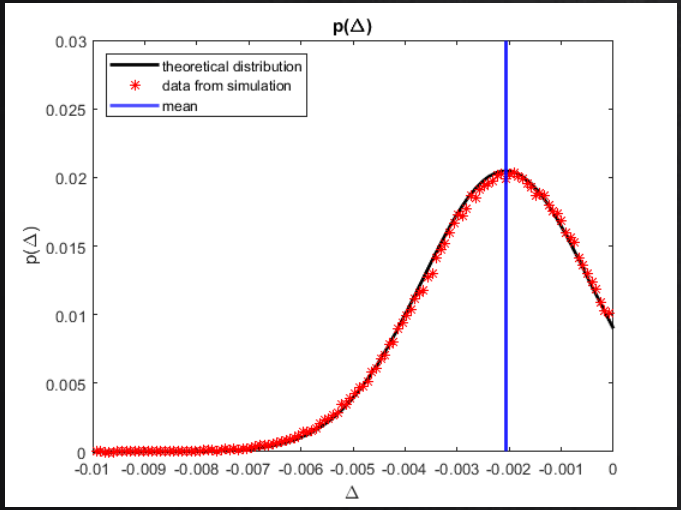
## Modify the external supply

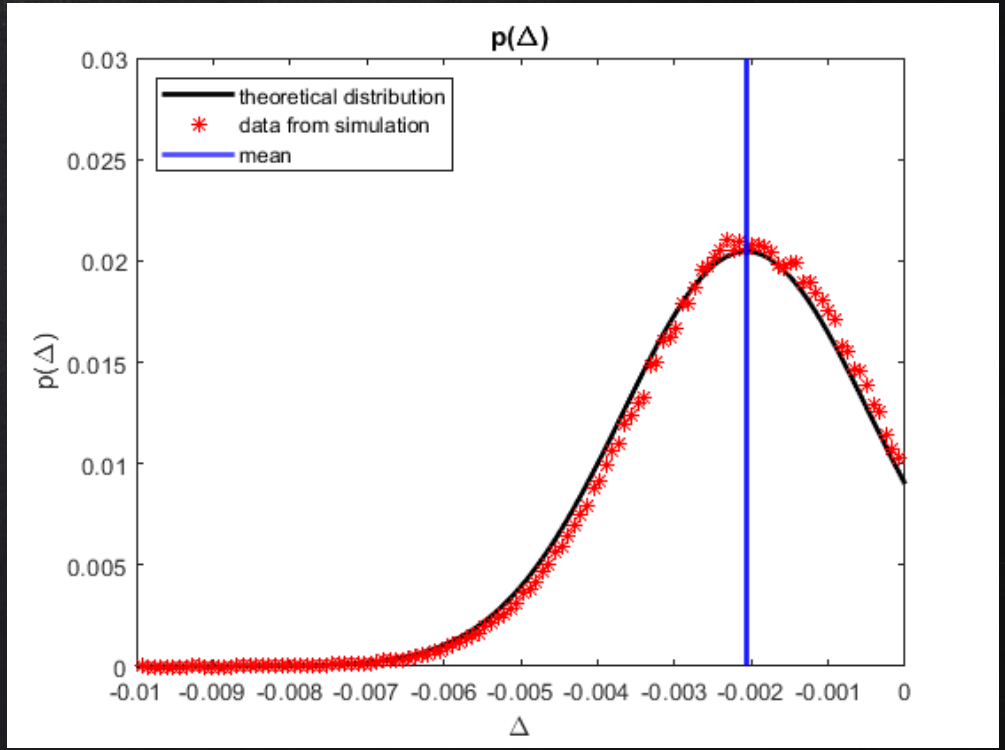
# Modify the external supply



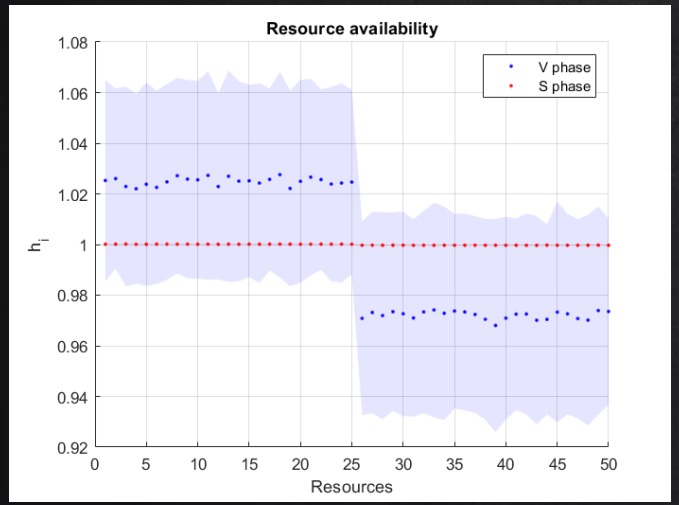



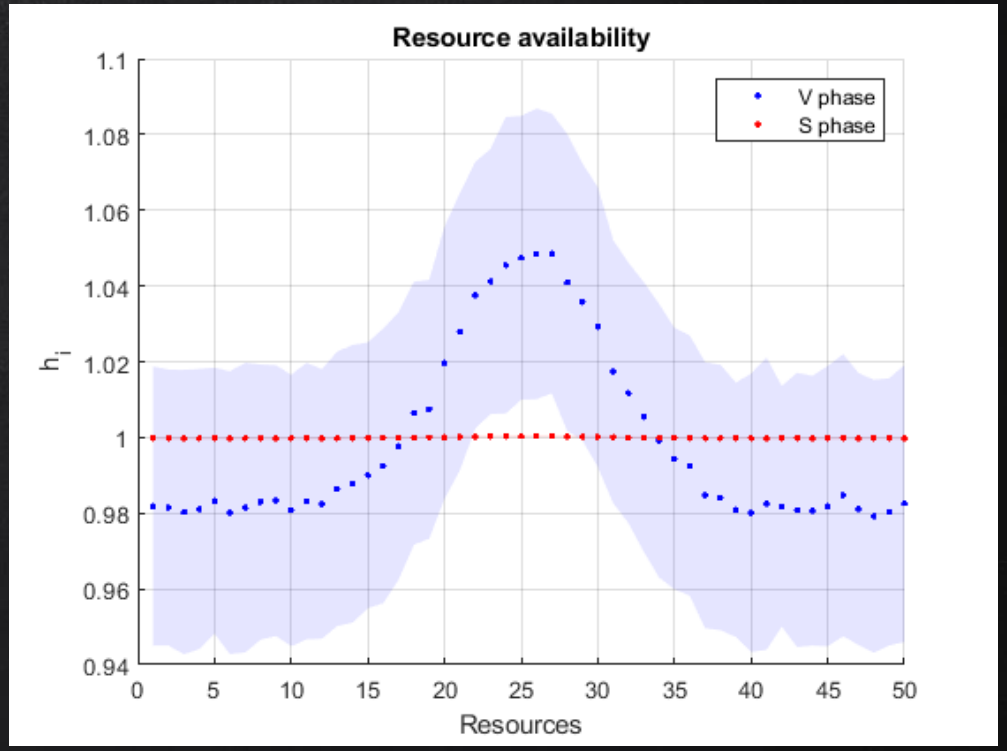
# Modify the external supply



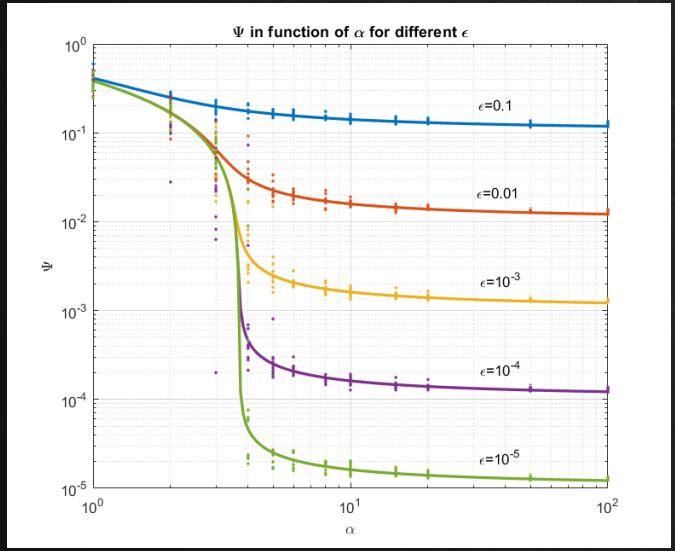



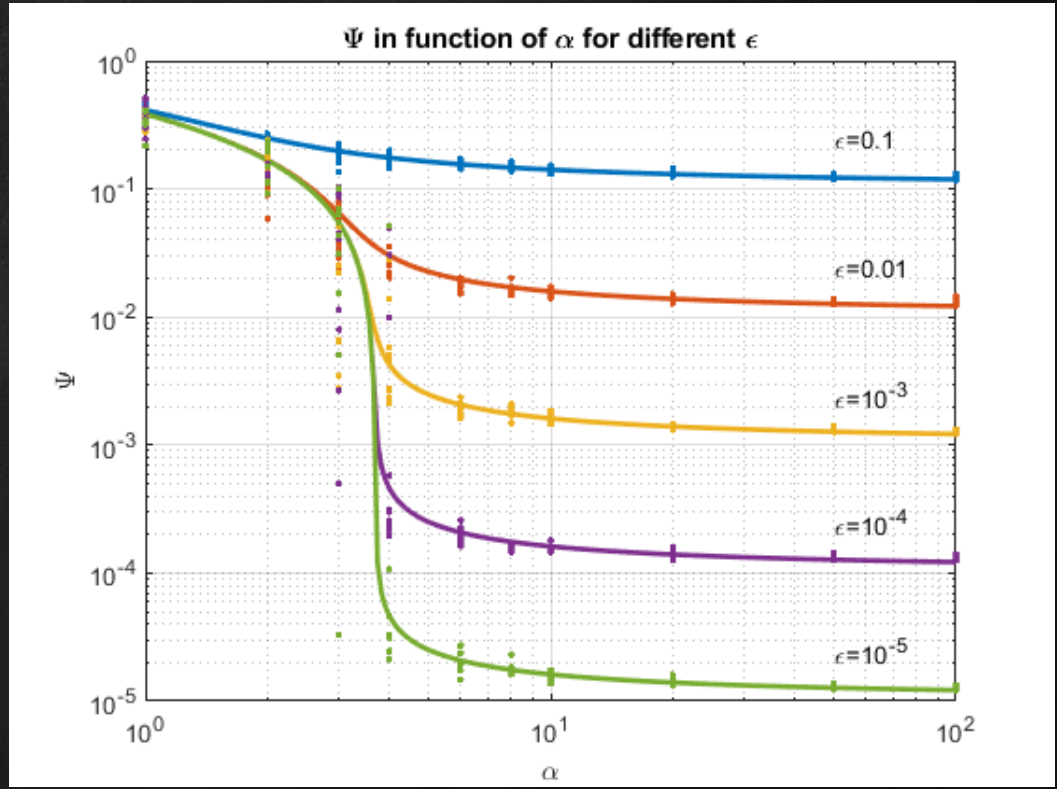
# Modify the external supply



# Modify the external supply



# Changing the parameters

## Studying the survival species

# Studying the surviving species

$N = 50$

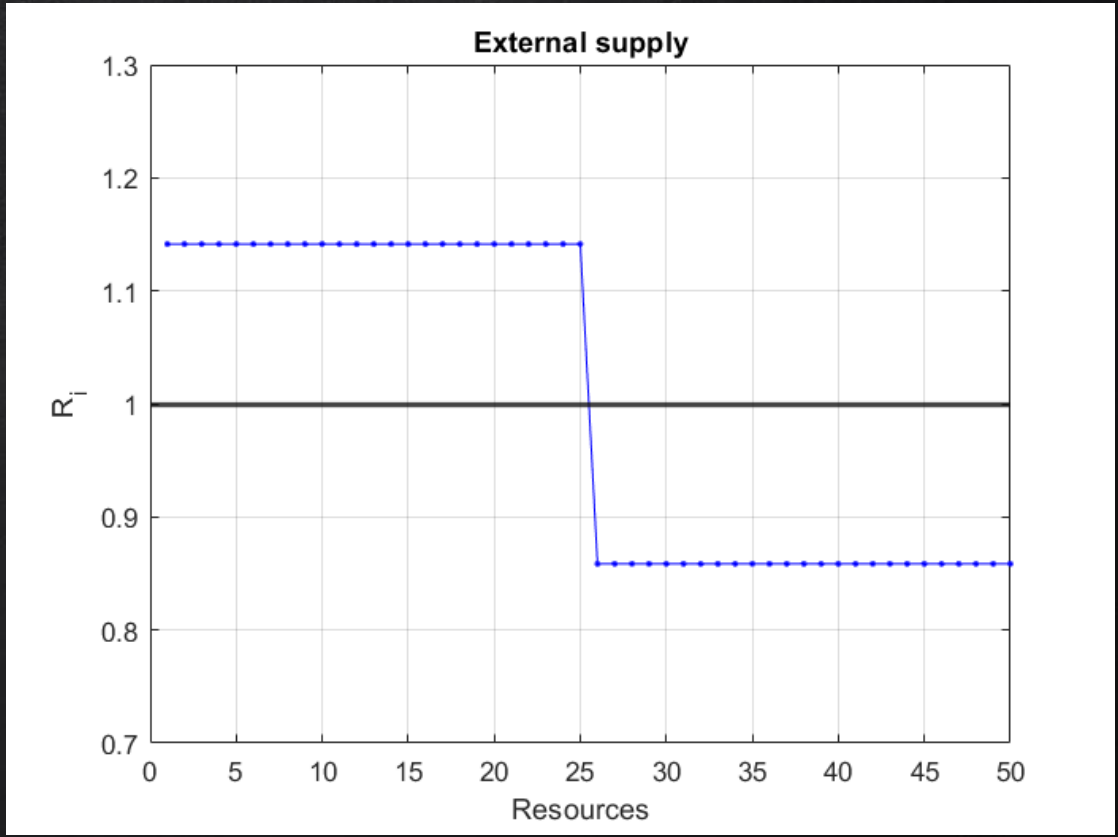
$\bar{R} = 1$

$\overline{\delta R^2} = 1$

$$R_i = \bar{R} \pm \frac{\delta R_i}{\sqrt{N}} = 1 \pm \frac{1}{\sqrt{50}}$$

We select a fixed cost $X_\mu$ imposing:

$$\epsilon = 0$$



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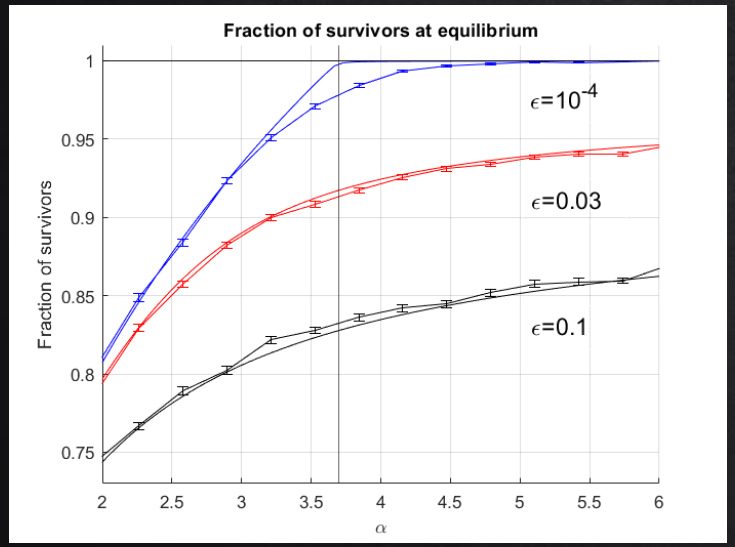
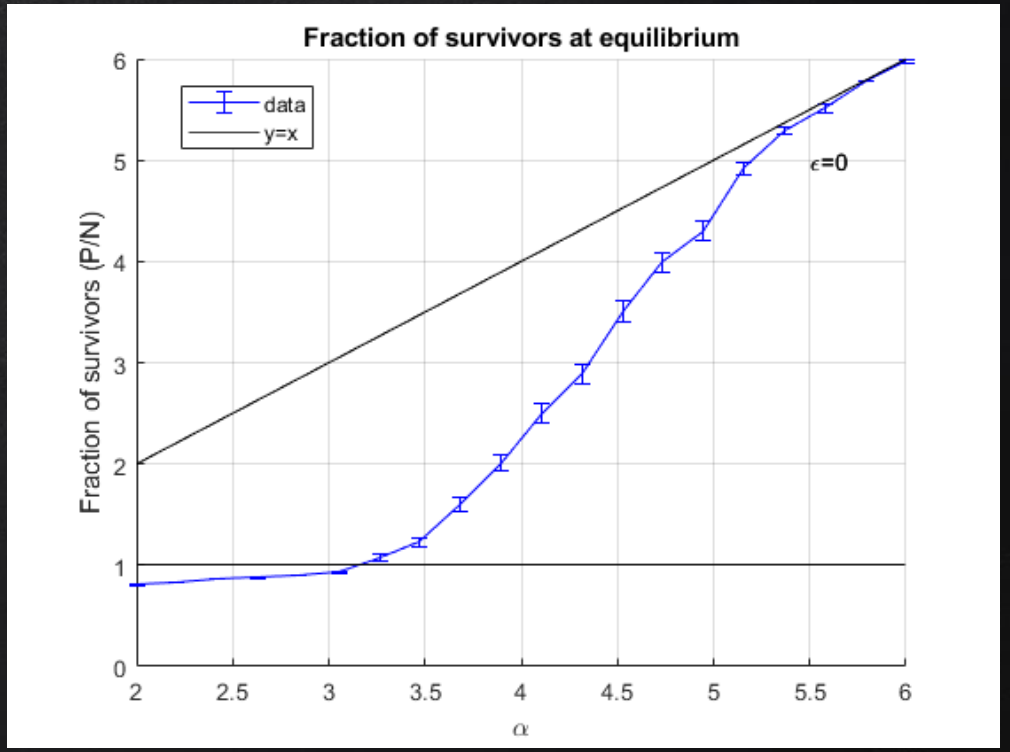
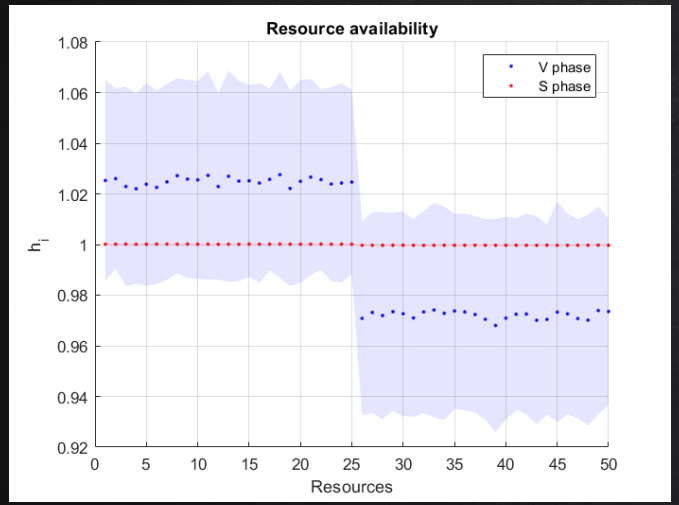
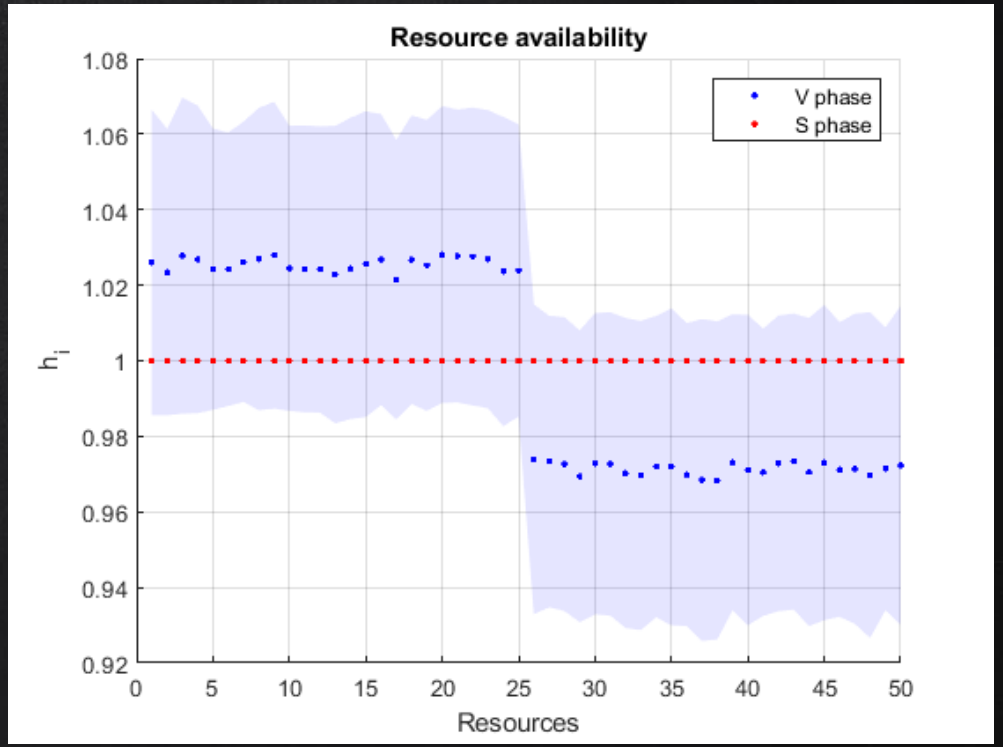


# Studying the surviving species



# CONCLUSION

# Limits & Further studies

- ✗ No spatial structure → Consider a different spatial structure
- ✗ Inspect just the equilibrium state → out-of-equilibrium statistical physics to study dynamical behavior
- ✗ Deterministic dynamics
- ✗ Purely competitive behaviour

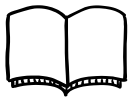
# CONCLUSIONS

Tikhonov and Monasson developed methods of statistical physics to analytically solve a classic ecological model of resource competition

- ✗ In high dimension the systems have a strongly collective regime
- ✗ The model allows to explore specifically the *feedback* loop between organisms and their environment
- ✗ We characterized the environment shaped by a community as condequence of the ecoevolutionary dynamics

# Thank you

Clelia Corridori

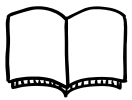


# Starting point

$$Z = \int_0^\infty \prod_i dh_i e^{\beta \tilde{F}} \prod_{\mu=1}^{P} \theta\left(\chi_\mu - \vec{h}\cdot\vec{\sigma}_\mu\right) \qquad \text{with} \qquad h_i \equiv 1 - \tfrac{g_i}{N}$$

$$Z = \int_{-\infty}^{N} \prod_i \frac{dg_i}{N} e^{\beta \tilde{F}(\{g_i\})} \prod_{\mu=1}^{P} \int d\Delta_\mu\, \theta(-\Delta_\mu)\, \delta\left(\Delta_\mu + \epsilon x_\mu + \frac{1}{N}\sum_i g_i \sigma_{\mu i}\right)$$

$$= \int_{-\infty}^{N} \prod_i \frac{dg_i}{N} e^{\beta \tilde{F}(\{g_i\})} \prod_{\mu=1}^{P} \int \frac{d\Delta_\mu\, d\hat{\Delta}_\mu}{2\pi}\, \theta(-\Delta_\mu) \exp\left[i \sum_\mu \hat{\Delta}_\mu \left(\Delta_\mu + \epsilon x_\mu + \frac{1}{N}\sum_i g_i \sigma_{\mu i}\right)\right]$$



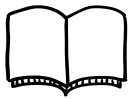
# Consider $Z^n$

$$Z^n = \int_{-\infty}^{N} \prod_{i,a} \frac{dg_i^a}{N} e^{\beta \sum_a \tilde{F}(\{g_i^a\})} \prod_{\mu,a} \int \frac{d\Delta_\mu^a \, d\hat{\Delta}_\mu^a}{2\pi} \theta(-\Delta_\mu^a) \exp\left[ i \sum_{\mu,a} \hat{\Delta}_\mu^a \left( \Delta_\mu^a + \epsilon x_\mu + \frac{1}{N} \sum_i g_i^a \sigma_{\mu i} \right) \right]$$

The metabolic strategies and the costs are uncorrelated

$$\langle Z^n \rangle_{x_\mu, \vec{\sigma}_\mu} = \int \prod_{i,a} \frac{dg_i^a}{N} e^{\beta \sum_a \tilde{F}(g_i^a)} \prod_{\mu,a} \frac{d\Delta_\mu^a \, d\hat{\Delta}_\mu^a}{2\pi} \theta(-\Delta_\mu^a) \, e^{i \sum_{\mu,a} \hat{\Delta}_\mu^a \Delta_\mu^a}$$

$$\times \prod_\mu \left\langle e^{i\epsilon \sum_a \hat{\Delta}_\mu^a x_\mu} \right\rangle_{x_\mu} \times \prod_{i,\mu} \left\langle e^{\frac{i}{N} \sum_a \hat{\Delta}_\mu^a g_i^a \sigma_{\mu i}} \right\rangle_{\sigma_{\mu i}}$$



# Averaging over the disorder

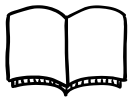
Considering

$$\prod_{\mu} \left\langle e^{i\epsilon \sum_a \hat{\Delta}_\mu^a x_\mu} \right\rangle_{x_\mu} = \exp\left[ -\frac{1}{2}\epsilon^2 \sum_\mu \left( \sum_a \hat{\Delta}_\mu^a \right)^2 \right]$$

$$\prod_{i,\mu} \left\langle e^{\frac{i}{N} \sum_a \hat{\Delta}_\mu^a g_i^a \sigma_{\mu i}} \right\rangle_{\sigma_{\mu i}} = \exp\left[ \frac{ip}{N} \sum_{i,\mu,a} \hat{\Delta}_\mu^a g_i^a - \frac{p(1-p)}{2N^2} \sum_{i,\mu} \left( \sum_a \hat{\Delta}_\mu^a g_i^a \right)^2 + o(1/N^2) \right]$$

$$\langle Z^n \rangle_{\text{disorder}} = \int \prod_{i,a} \frac{dg_i^a}{N} e^{\beta \sum_a \tilde{F}(\{g_i^a\})} \prod_{\mu,a} \frac{d\Delta_\mu^a \, d\hat{\Delta}_\mu^a}{2\pi} \theta(-\Delta_\mu^a)$$

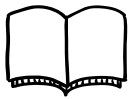
$$\times \exp\left\{ i \sum_{\mu,a} \hat{\Delta}_\mu^a \left( \Delta_\mu^a + \frac{p}{N} \sum_i g_i^a \right) - \frac{1}{2}\epsilon^2 \sum_\mu \left( \sum_a \hat{\Delta}_\mu^a \right)^2 - \frac{p(1-p)}{2N^2} \sum_{i,\mu} \left( \sum_a \hat{\Delta}_\mu^a g_i^a \right)^2 \right\}$$



# Decouple indices $i$ and $\mu$

$$m^a \equiv \frac{1}{N}\sum_i g_i^a \qquad\qquad q^{ab} \equiv \frac{1}{N^2}\sum_i g_i^a g_i^b$$

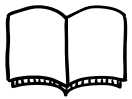
$$\begin{aligned}
\langle Z^n \rangle = &\int \prod_{a\le b} \frac{dq^{ab}\, d\hat{q}^{ab}}{2\pi} \int \prod_a \frac{dm^a\, d\hat{m}^a}{2\pi} \exp\left[ i\sum_{a\le b} q^{ab}\hat{q}^{ab} + i\sum_a \hat{m}^a m^a \right] \\
&\times \prod_i \left\{ \int_{-\infty}^{N} \prod_a \frac{dg_i^a}{N} \exp\left[ \sum_a \beta \tilde{F}_i(\{g_i^a\}) - \frac{i}{N}\sum_a \hat{m}^a g_i^a - \frac{i}{N^2}\sum_{a\le b} \hat{q}^{ab} g_i^a g_i^b \right] \right\} \\
&\times \prod_\mu \left\{ \int \prod_a \frac{d\Delta_\mu^a\, d\hat{\Delta}_\mu^a}{2\pi} \prod_a \theta(-\Delta_\mu^a) \exp\left[ i\sum_a \hat{\Delta}_\mu^a(\Delta_\mu^a + p m^a) - \frac{1}{2}\sum_{a,b} \left( p(1-p)q^{ab} + \epsilon^2 \right) \hat{\Delta}_\mu^a \hat{\Delta}_\mu^b \right] \right\}
\end{aligned}$$



# Decoupling replicas

**Replica symmetry ansatz**
The results must be symmetric under a permutation of replicas

$$\log\langle Z^n\rangle = \mathrm{extr}\left\{in\, q_D\hat{q}_D + i\frac{n(n-1)}{2}q_O\hat{q}_O + in\hat{m}^*m^* + \sum_i \log A_i + P\log B\right\}$$



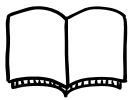
# Compute the limit $n \to 0$

Changing variables

$$\left.\begin{aligned} i\left(\hat{q}_D - \frac{1}{2}\hat{q}_O\right) &\equiv \beta a \\ \sqrt{-i\hat{q}_O} &\equiv \frac{\beta b}{\sqrt{N}} \\ i\hat{m}^* &\equiv \beta \hat{m} \end{aligned}\right\} \qquad \sum_i \lim_{n\to 0} \frac{\log A_i}{n} = \beta \frac{b^2 + \delta\hat{m}^2 + \overline{\delta\tau^2}}{4a + 2/\bar{\gamma}}$$

$$\left.\begin{aligned} q_D - q_O &\equiv \frac{Nx}{\beta} \\ q_D \approx q_O &\equiv q \\ \sqrt{p(1-p)q + \epsilon^2} &\equiv \psi \\ pm^*/\psi &\equiv \lambda \end{aligned}\right\} \qquad \lim_{n\to 0} \frac{\log B}{n} = -\frac{\beta\psi^2}{2Np(1-p)x} \int_{-\infty}^{-\lambda} \mathcal{D}w\,(w+\lambda)^2 = -\frac{\beta\psi^2}{2Np(1-p)x} I(\lambda)$$

with $$I(\lambda) \equiv \int_0^\infty e^{-\frac{(w-\lambda)^2}{2}} w^2 \frac{dw}{\sqrt{2\pi}} = -\frac{\lambda}{\sqrt{2\pi}} e^{-\frac{\lambda^2}{2}} + \frac{1+\lambda^2}{2} \operatorname{erfc}\left(\frac{\lambda}{\sqrt{2}}\right)$$



# Final expression

$$\langle \log Z \rangle = \lim_{n\to 0} \frac{\langle Z^n - 1 \rangle}{n} = \lim_{n\to 0} \frac{\log \langle Z^n \rangle}{n}$$
$$= \lim_{n\to 0} \operatorname{extr} \left\{ i \left( \hat{q}_D - \frac{1}{2}\hat{q}_O \right) q_D - \frac{q_D - q_O}{2}(-i\hat{q}_O) + i\hat{m}^* m^* + \frac{1}{n}\sum_i \log A_i + \frac{P}{n}\log B \right\}$$

Considering the following equations on $x, \lambda$ and $q$

$$\frac{\delta\hat{m}}{2a + 1/\bar{\gamma}} = \frac{1}{N}\frac{\psi\lambda}{p} \qquad a = \frac{\bar{\gamma} - x}{2x\gamma} \qquad b^2 = \frac{q}{x^2} - \overline{\delta\tau^2}$$

$$\langle \log Z \rangle = \beta \operatorname{extr} \left\{ \frac{\bar{\gamma} - x}{2x\bar{\gamma}} q + \frac{\overline{\delta\tau^2}}{2} x - \frac{\lambda\tau\psi(q)}{p} - \frac{\alpha\psi^2(q)}{2xp(1-p)} I(\lambda) \right\}$$