

# Stability, complexity and diversity in random replicator models of ecology and evolutionary game theory

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# Game theory

- **1944:** von Neumann and Morgenstern  
'Theory of games and economic behaviour'
- **1950s:** John Nash, equilibrium concepts
- Nash equilibria seen as only viable outcomes of careful reasoning of rational players
- **1982:** John Maynard Smith: 'Evolution and the theory of games', dynamics of a population of irrational players
- Nobel prizes:
  - 1994:** J.C. Harsanyi, John Nash and R. Selten
  - 2005:** R. Aumann, Th. Schelling

# A game

- is played by a (finite) number of players  $x, y, z, \dots$
- each of them has a set of strategies  $X, Y, Z, \dots$
- and each is paid a payoff depending on his choice of strategy and on the choice of the other players
- different players might have different strategy sets

symmetric versus asymmetric games

# Matrix games

E.g. prisoners dilemma

payoff for player 1	2 co-operates	2 defects
1 co-operates	4	0
1 defects	5	3

payoff for player 2	2 co-operates	2 defects
1 co-operates	4	5
1 defects	0	3

# Matrix games

Another example: rock-scissors-paper game

rock > scissors, scissors > paper but paper > rock

$$A = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$$

# Matrix games

- these were all so-called **symmetric** games: only one type of player
- now an **asymmetric game**

## Battle of the sexes:

- strategies for male: run or stay
- strategies for female: coy or fast
- successful raising of offspring: payoff  $G$  for each
- parental investment  $-C$  shared if male stays, otherwise borne entirely by female
- long engagement: cost  $-E$  for both

# Battle of the sexes

- successful raising of offspring: payoff  $G$  for each
- parental investment  $-C$  shared if male stays, otherwise borne entirely by female
- long engagement: cost  $-E$  for both

payoff for male	female coy	female fast
male runs	0	$G$
male stays	$G - \frac{C}{2} - E$	$G - \frac{C}{2}$

payoff for female	male runs	male stays
female coy	0	$G - \frac{C}{2} - E$
female fast	$G - C$	$G - \frac{C}{2}$

## Pure strategies

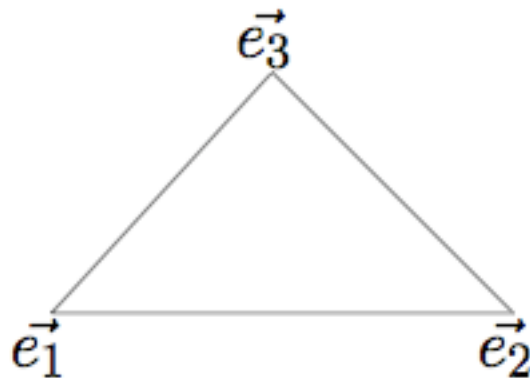
Assume player  $X$  has the choice between  $N$  **pure** strategies, labelled by

$$\vec{e}_i^x, i = 1, \dots, N$$

Then a **mixed** strategy corresponds to a vector

$$\vec{x} = (x_1, \dots, x_N), \quad \sum_i x_i = 1$$

$x_i$  is the probability to play pure strategy  $\vec{e}_i^x$ .





## Mixed strategies

- in general will have payoff matrices  $a_{ij}$  and  $b_{ij}$
- if player  $X$  plays mixed strategy  $\vec{x}$  and  $Y$  plays  $\vec{y}$  then

$$v^x(\vec{x}, \vec{y}) = \sum_{ij} x_i a_{ij} y_j$$

$$v^y(\vec{x}, \vec{y}) = \sum_{ij} x_i b_{ij} y_j$$

# Nash Equilibria

A Nash equilibrium is a point  $(\vec{x}^*, \vec{y}^*)$  such that no player has an incentive to change strategies unilaterally given the other player's choice of strategy:

- $\vec{x}^*$  is the best choice for  $X$  given  $Y$  plays  $\vec{y}^*$
- $\vec{y}^*$  is the best choice for  $Y$  given  $X$  plays  $\vec{x}^*$

$$v^x(\vec{x}^*, \vec{y}^*) = \max_{\vec{x}} v^x(\vec{x}, \vec{y}^*)$$

$$v^y(\vec{x}^*, \vec{y}^*) = \max_{\vec{y}} v^y(\vec{x}^*, \vec{y})$$

# Replicator dynamics

replicator equations

$$\frac{d}{dt}x_i(t) = x_i(t)[f_i[x(t)] - f(t)]$$

- ▶ evolutionary game theory
- ▶ learning dynamics, e.g. acquisition of grammar
- ▶ chemical reactions
- ▶ interacting species, eco-systems

## Replicator dynamics

- differential equations on a simplex  $S$
- population divided into  $N$  types  $i = 1, \dots, N$  with proportions  $x_i$
- fitness of  $i$ :  $f_i(t) = f_i[x_1(t), \dots, x_N(t)]$

The associated replicator equation reads

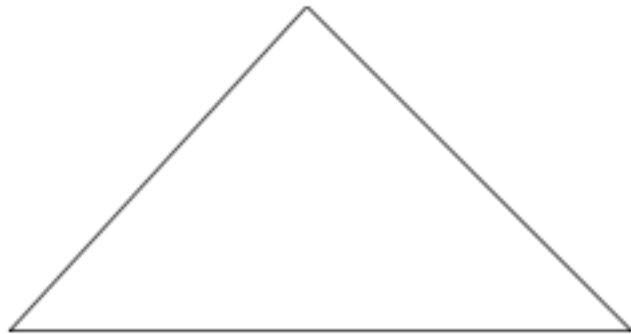
$$\frac{\dot{x}_i(t)}{x_i(t)} = f_i(t) - \bar{f}(t)$$

with  $\bar{f}(t) = \sum_i x_i(t) f_i(t)$  the mean fitness

# Replicator dynamics

$$\dot{x}_i(t) = x_i(t) (f_i(t) - \bar{f}(t))$$

- species fitter than the average prosper
- species less fit than the average decrease in concentration
- $\sum_i x_i = 1$  conserved in time



# One population models

- only one type of players  $X$
- e.g in the prisoner's dilemma or rock-scissors-paper game
- symmetric games

$$\dot{x}_i(t) = x_i(t) (f_i[x_1(t), \dots, x_N(t)] - \bar{f}(t))$$

# Multi-population models

- multiple types of players  $X, Y, Z, \dots$  taking different positions in the game
- e.g. male-female in battle of sexes, buyers-sellers in an economy
- asymmetric games

$$\begin{aligned}\dot{x}_i(t) &= x_i(t) \left( f_i^x [y_1(t), \dots, y_N(t)] - \overline{f^x}(t) \right) \\ \dot{y}_j(t) &= y_j(t) \left( f_j^y [x_1(t), \dots, x_M(t)] - \overline{f^y}(t) \right)\end{aligned}$$

# Replicator dynamics

Fixed points:

$$0 = x_i (f_i - \bar{f})$$

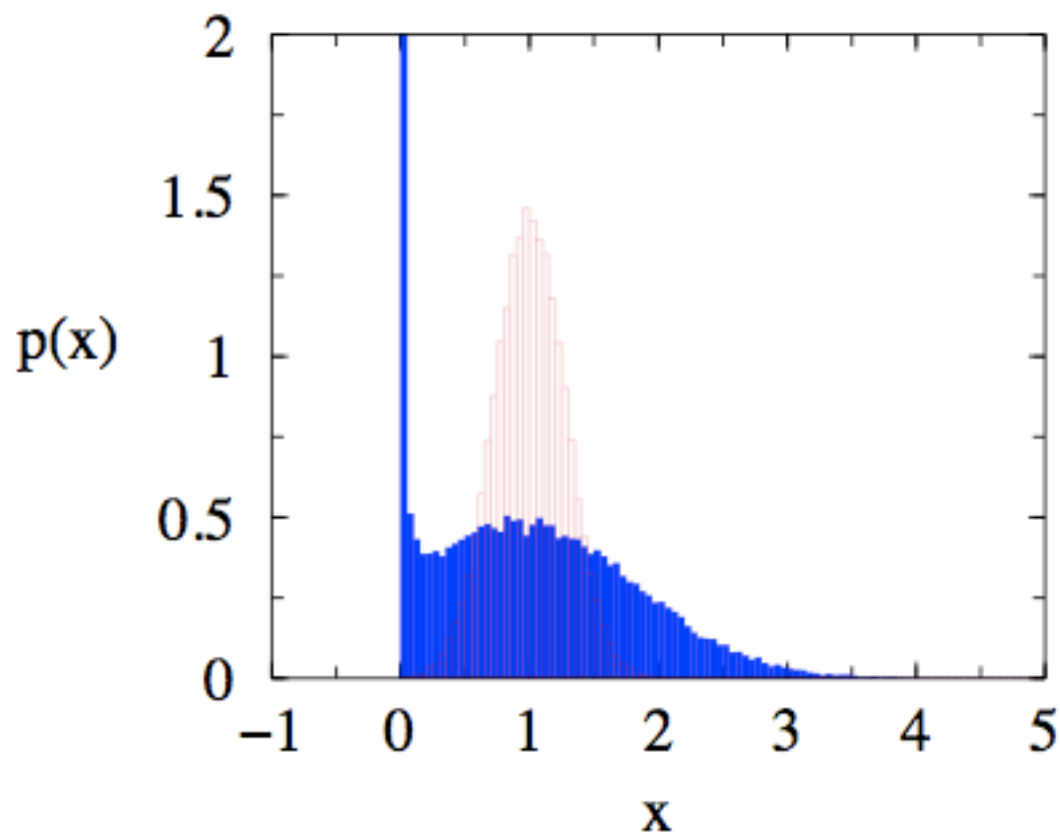
It turns out

- stable fixed points are Nash equilibria
- but Nash equilibria are not necessarily stable FP



# Fixed point distribution

- fraction  $\phi$  of surviving species,  $x_i > 0$
- distribution  $\sim$  truncated Gaussian +  $(1 - \phi)\delta(x)$



# Replicator dynamics

$$\dot{x}_i(t) = x_i(t) (f_i[x_1(t), \dots, x_N(t)] - \bar{f}(t))$$

- games between two players

$$f_i[x_1, \dots, x_N] = \sum_j J_{ij} x_j$$

- games between  $p$ -players

$$f_i[x_1, \dots, x_N] = \sum_{i_1, \dots, i_{p-1}} J_{i_1, i_2, \dots, i_{p-1}}^i x_{i_1} x_{i_2} \cdots x_{i_{p-1}}$$

# Replicator dynamics

study “all” matrix games → random payoff matrices

$$\dot{x}_i(t) = x_i(t) \left( \sum_j J_{ij} x_j(t) - \bar{f}(t) \right)$$

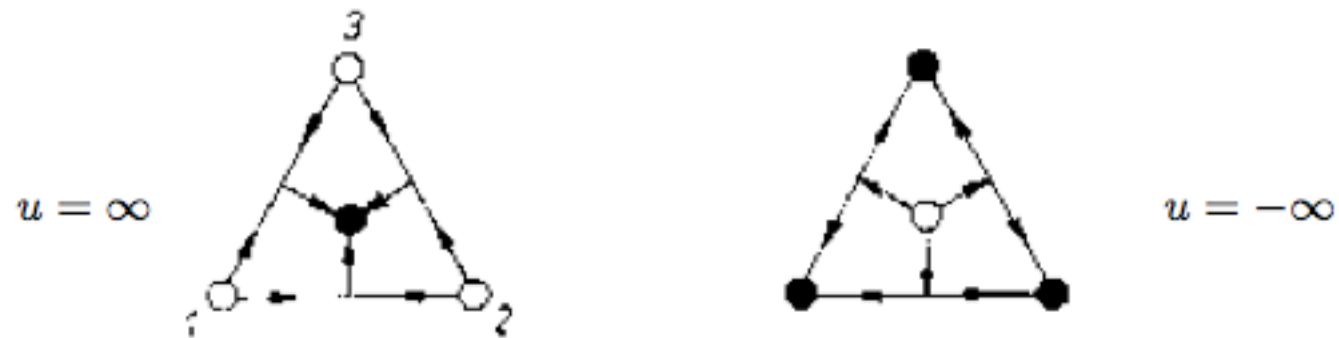
with

- $J_{ij}$  Gaussian couplings,  $\overline{J_{ij}^2} = 1/N$
- symmetry of couplings  $\overline{J_{ij} J_{ji}} = \Gamma/N$
- diagonal elements  $J_{ii} = -2u$
- $u$  denotes 'co-operation pressure', drives the system into the simplex

$$\sum_i x_i(t) = N \quad \forall t$$

# Co-operation pressure

[Peschel, Mende, The Prey-Predator model, Springer, 1985]



**Fig. 89** The influence of  $\hat{\lambda}$  upon source and sink behaviour

# Literature

- statistical mechanics of large one-population systems with random couplings
  - Opper/Diederich PRA '89, PRL '92
  - Fontanari, De Oliveira PRL '00, PRE '01, PRL '02, EPJB '03, PRE '04 (all replica)
  - Biscari/Parisi J.Phys. A '95 (1RSB)
- bi-matrix games
  - Berg/Engel PRL '99
  - Berg/Weigt Europhys. Lett '99
  - Berg PRE '00

## Random replicator equations

$$\dot{x}_i(t) = x_i(t) \left( \sum_j J_{ij} x_j(t) - \bar{f}(t) \right)$$

with random Gaussian couplings

- ★ can be solved with techniques from spin glass physics in the thermodynamic limit  $N \rightarrow \infty$
- ★ path-integrals, dynamical generating functionals
- ★ result: stochastic process for a representative strategy/species
- ★ fixed point ansatz gives closed equations for persistent OP

# Generating functional analysis

Study this with generating functionals.

- advantage over replica:
  - no Lyapunov function required
  - so that GFA can be used also for asymmetric couplings
  - replica theory only for symmetric couplings
- closed laws for dynamical order parameters:
  - correlation function  $C(t, t') = N^{-1} \sum_i \overline{\langle x_i(t) x_i(t') \rangle}$
  - response function  $G(t, t') = N^{-1} \sum_i \overline{\left\langle \frac{\partial x_i(t)}{\partial h(t')} \right\rangle}$
  - Lagrange multiplier  $\bar{f}(t)$

# Generating functional analysis

- effective species process

$$\dot{x}(t) = x(t) \left( -2ux(t) - \Gamma \frac{p(p-1)}{2} \int_{t_0}^t dt' G(t, t') C(t, t')^{p-2} x(t') + \eta(t) - \bar{f}(t) + h(t) \right)$$

- self-consistent problem

$$C(t, t') = \langle x(t)x(t') \rangle_{\star}, \quad G(t, t') = \left\langle \frac{\partial x(t)}{\partial h(t')} \right\rangle_{\star}, \quad \langle x(t) \rangle_{\star} = 1$$

- $\{\eta(t)\}$  is coloured noise with correlator

$$\langle \eta(t)\eta(t') \rangle_{\star} = \frac{p}{2} C(t, t')^{p-1}$$

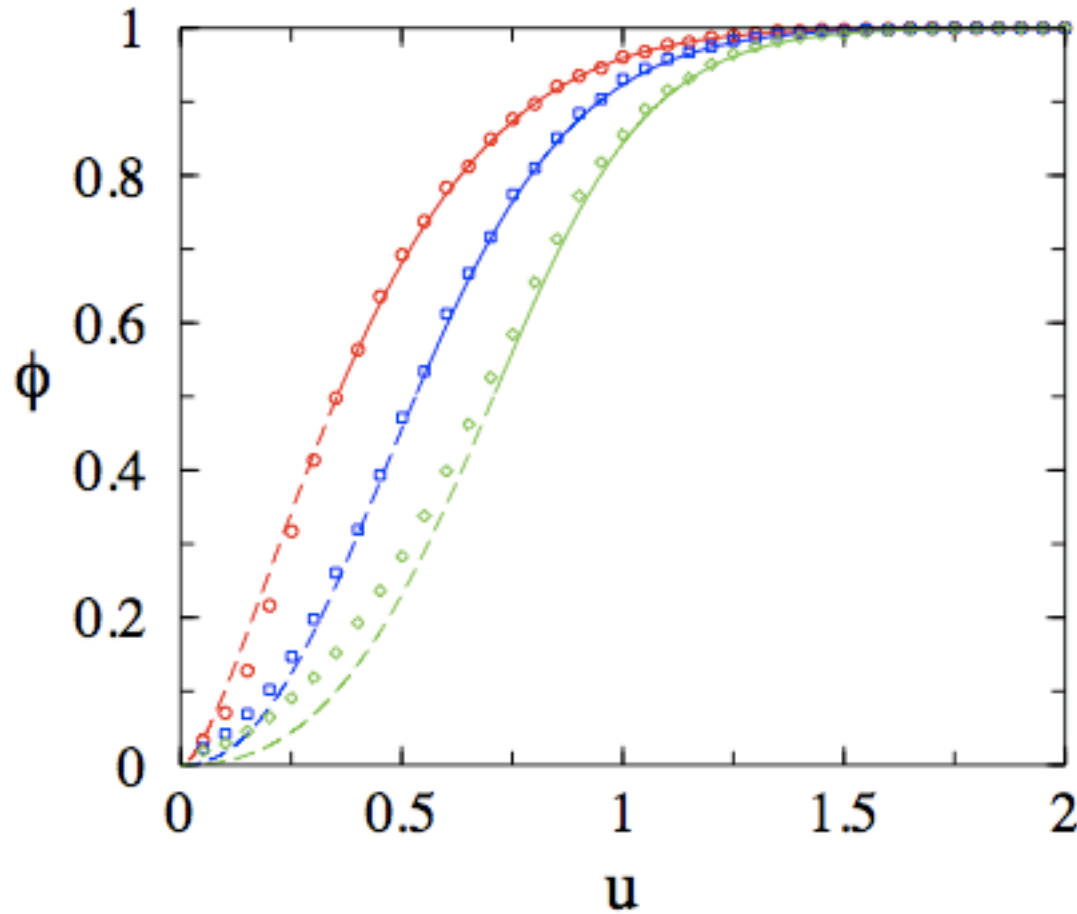
- retarded interaction  $\int_{t_0}^t dt' G(t, t') C^{p-2}(t, t') x(t')$



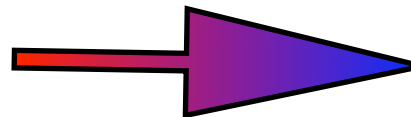
# Some results

$$(\Gamma = 0, \frac{1}{2}, 1)$$

fraction  
of  
survivors

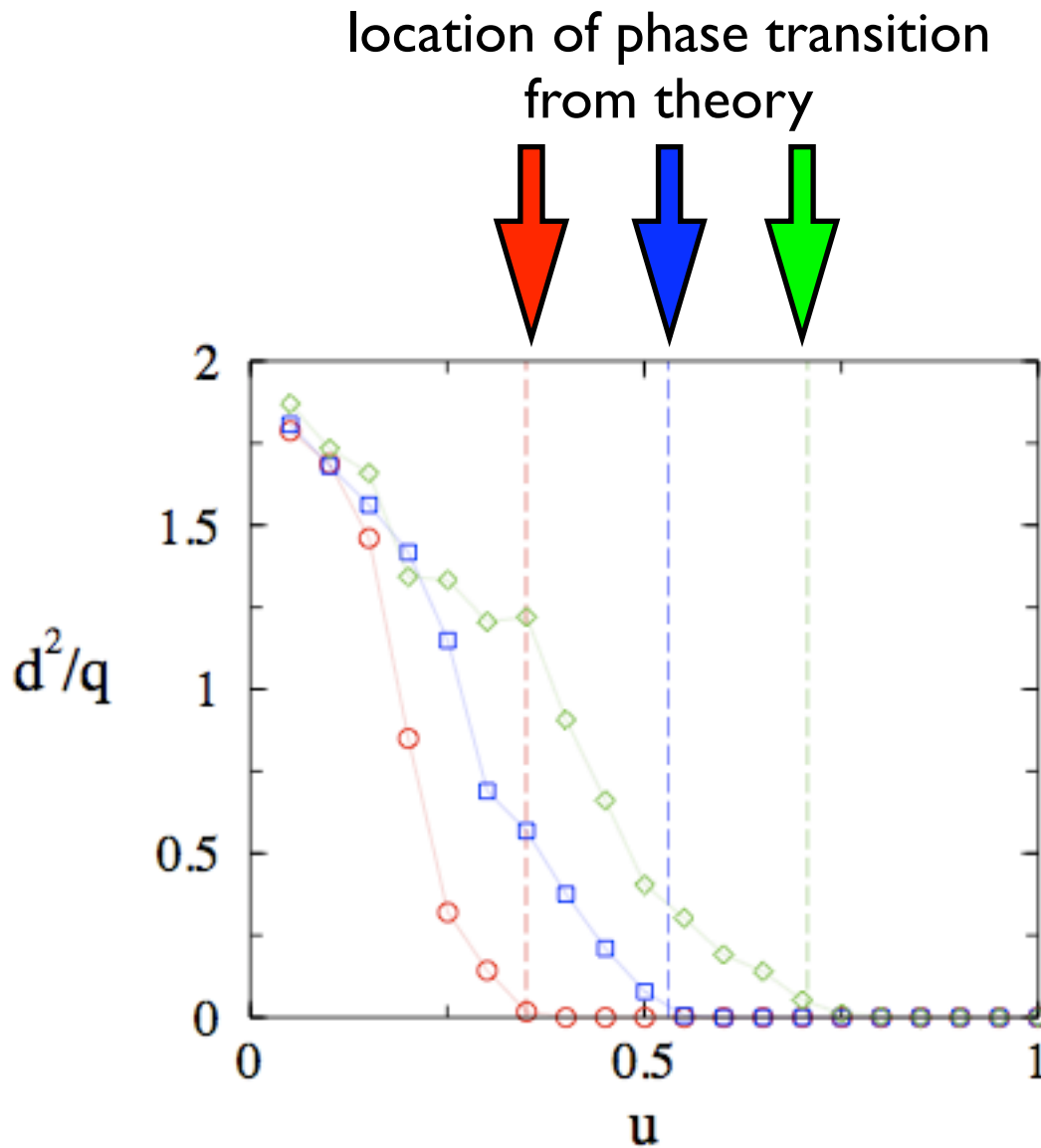


weak co-operation  
pressure

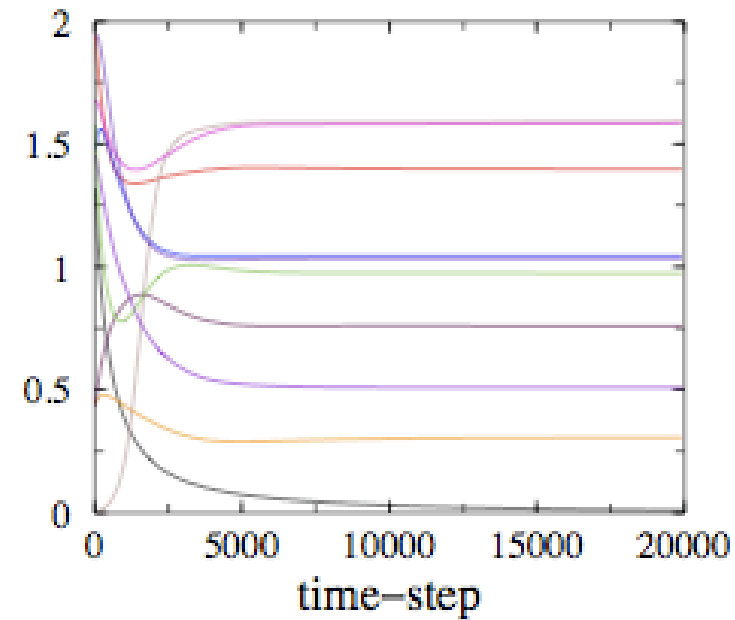
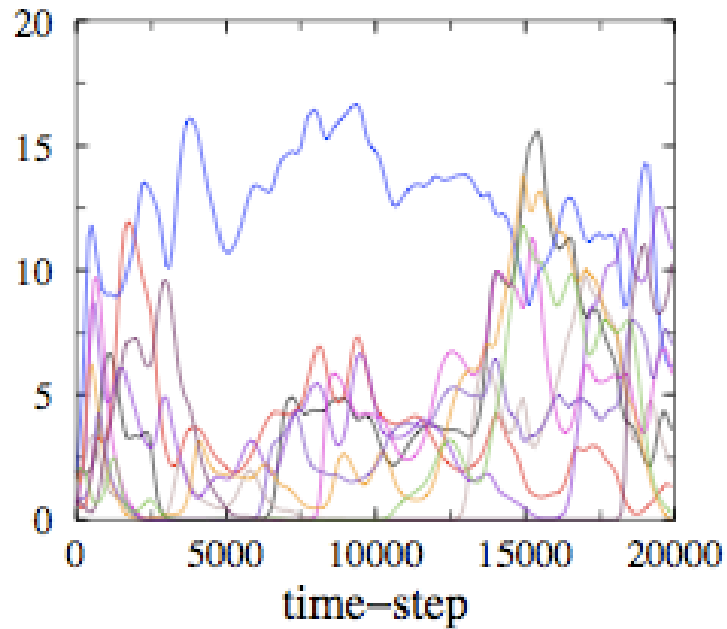


strong co-operation  
pressure

# Ergodicity breaking - sensitivity to initial conditions

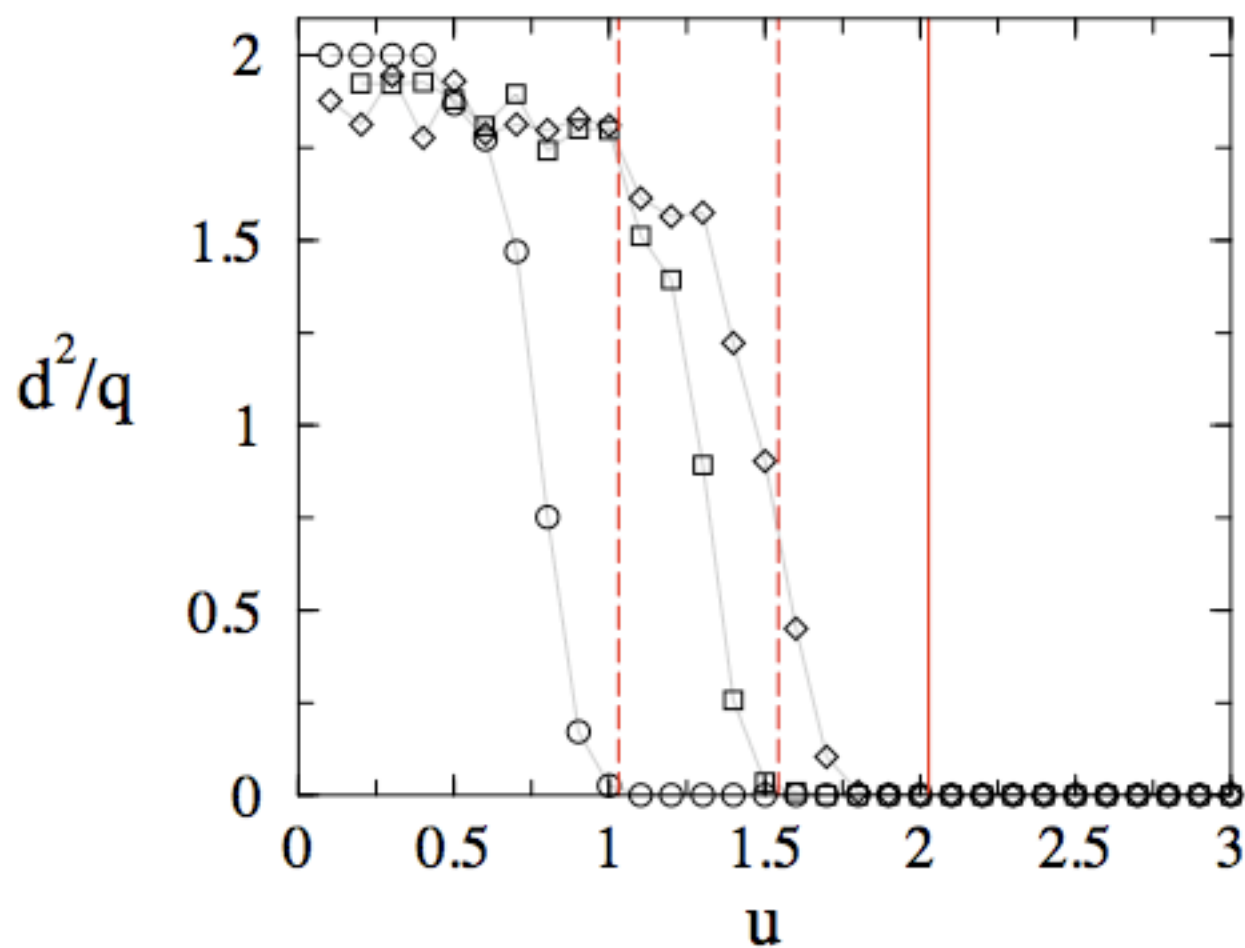


# Typical trajectories



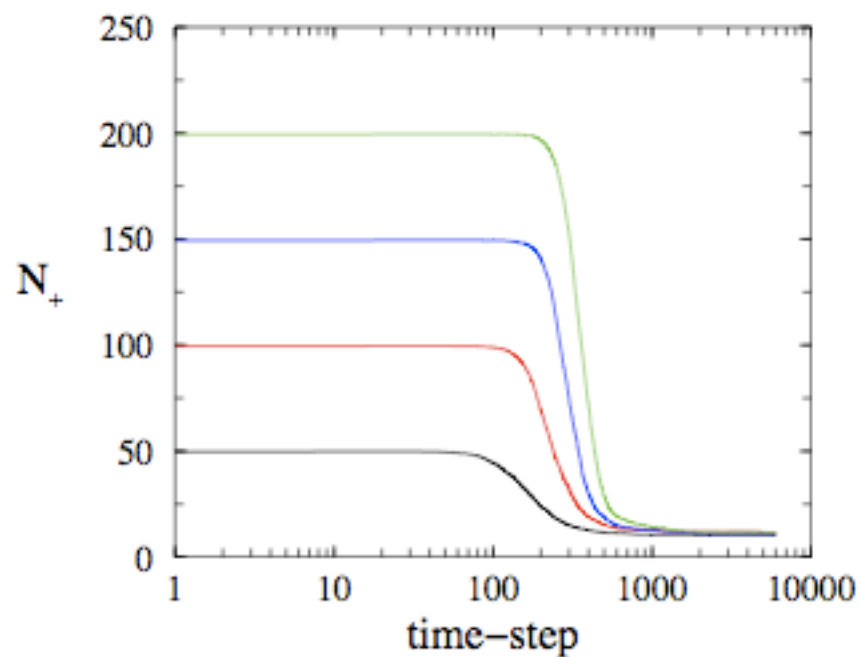
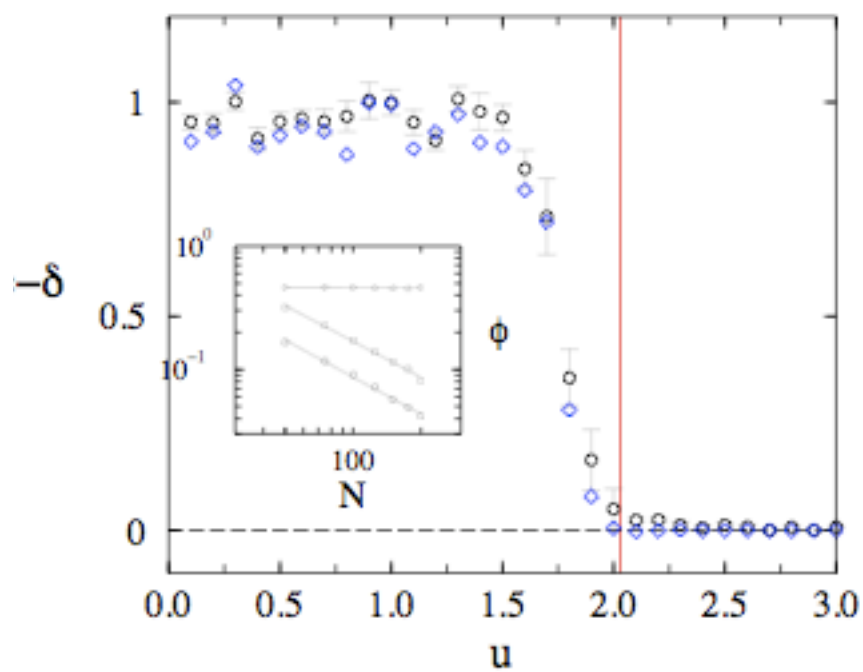
$$p = 3$$

Find ergodicity breaking also for  $p = 3$ :



But if  $p = 3$  but quadratic self-interaction find collapse of extensivity

$$\phi \sim N^\delta$$



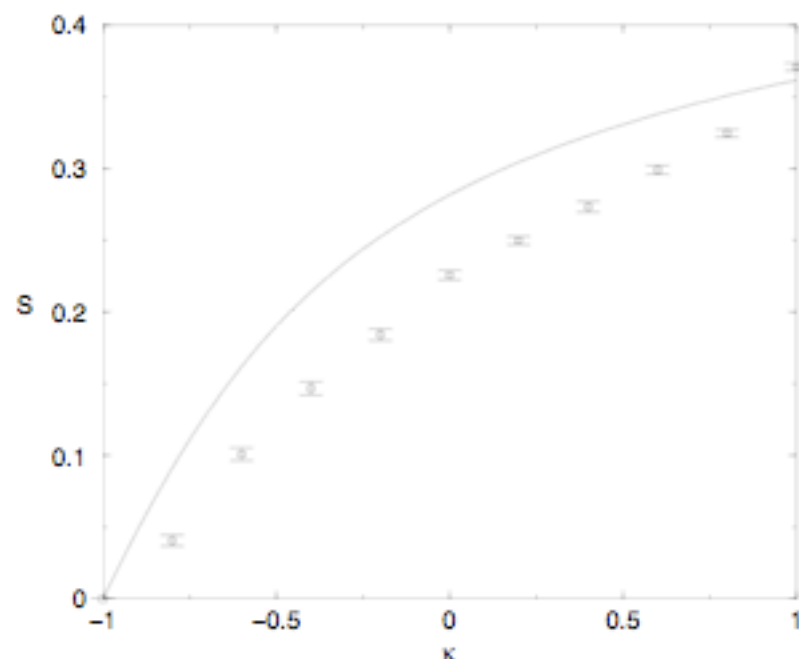
# Bi-matrix games

Payoff matrices  $a_{ij}, b_{ij}$  with

$$\overline{a_{ij}^2} = \overline{b_{ij}^2} = 1/N, \quad \overline{a_{ij}b_{ji}} = \Gamma/N$$

Berg/Weigt [Europhys. Lett. 48 129 (1999)]:

$$S = \frac{1}{N} \ln \langle \#Nash \rangle$$



# Bi-matrix games:

two-population random replicators

$$\begin{aligned}\dot{x}_i &= x_i(t) \left( -2ux_i + \sum_j a_{ij}y_j - \nu^x \right) \\ \dot{y}_j &= y_j(t) \left( -2uy_j + \sum_i b_{ij}x_i - \nu^y \right)\end{aligned}$$

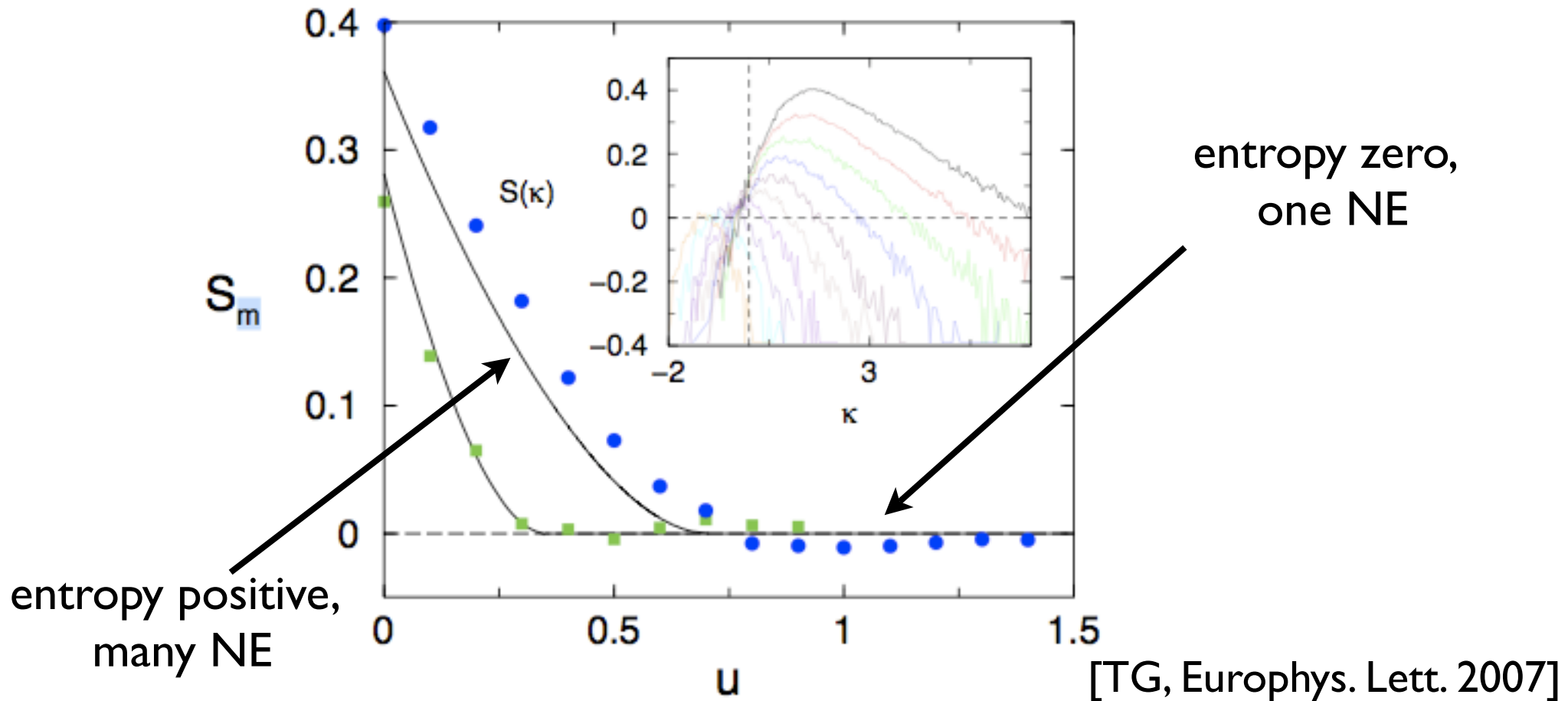
generating functionals lead to two coupled effective processes

$$\begin{aligned}\dot{x} &= x(t) \left( -2ux + \Gamma \int dt' G_y(t, t') x(t') - \nu^x - \eta^x(t) \right) \\ \dot{y} &= y(t) \left( -2uy + \Gamma \int dt' G_x(t, t') y(t') - \nu^y - \eta^y(t) \right)\end{aligned}$$

with

$$\langle \eta^x(t) \eta^x(t') \rangle = \langle y(t) y(t') \rangle \quad \langle \eta^y(t) \eta^y(t') \rangle = \langle x(t) x(t') \rangle$$

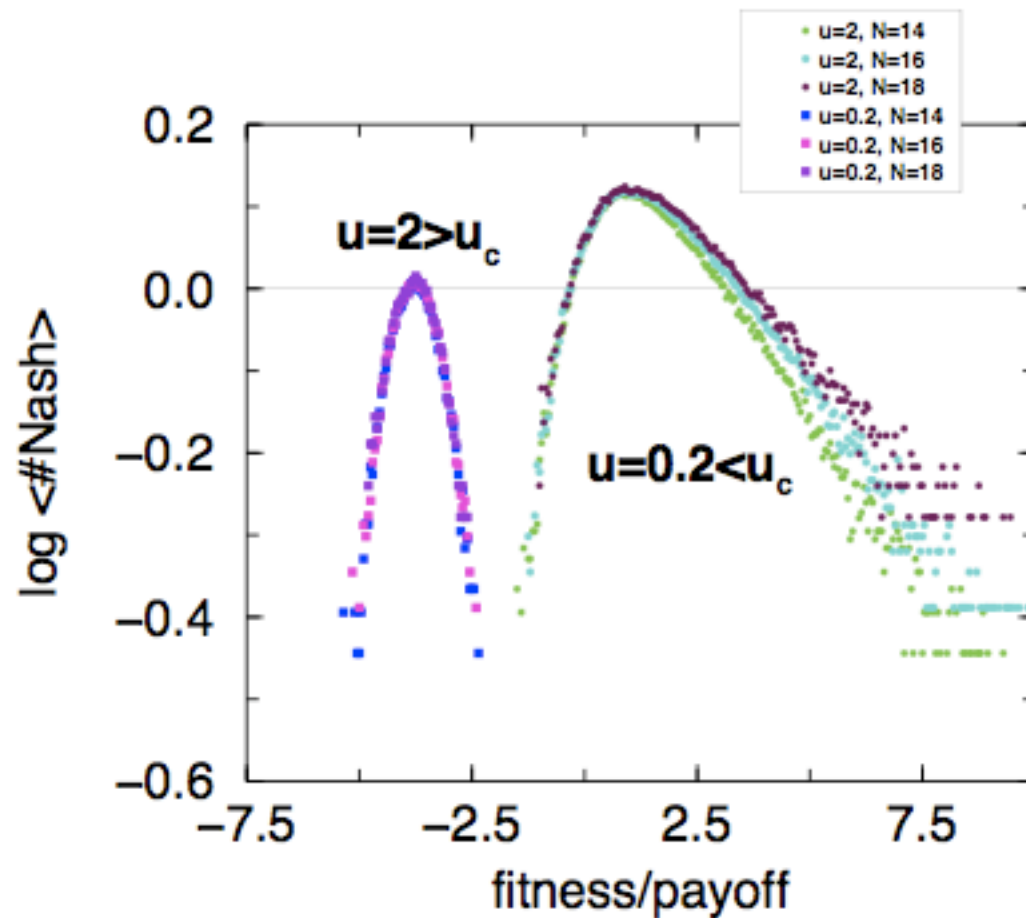
# Dynamic instability and number of Nash equilibria



dynamic instability coincides with onset of  
exponential number of NE



# Counting the Nash Equilibria



Statistical mechanics  
of simple model eco-systems

work with

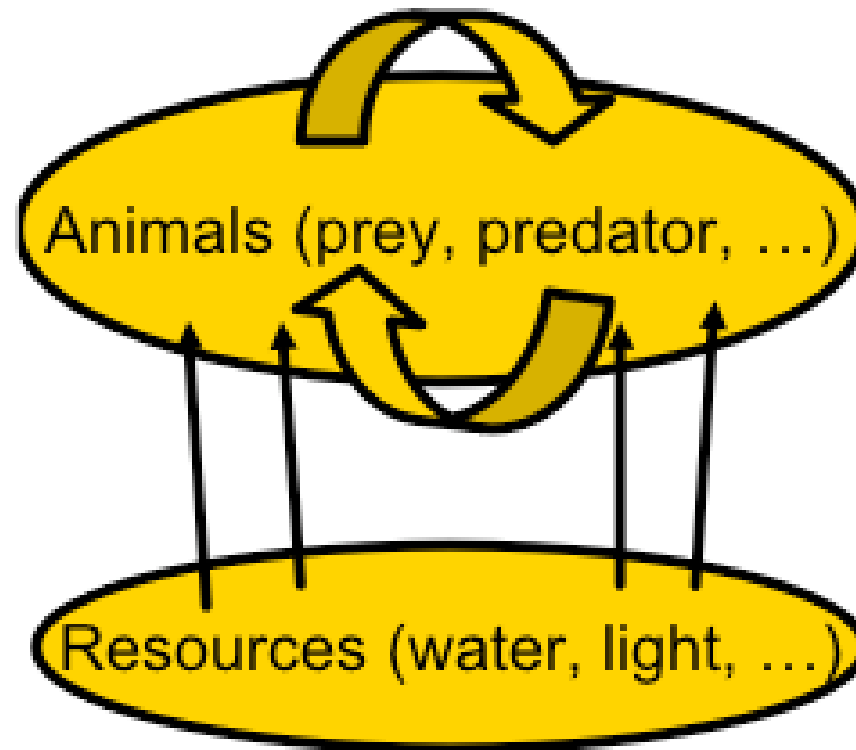
Yoshimi Yoshino and Kei Tokita (Osaka)

J. Stat. Mech. (2007) P09003

Phys. Rev. E (2008) to appear

# The model

two 'trophic levels':



# Model definitions

two 'trophic levels':

▶ N species

$$i = 1, \dots, N$$

▶ P resources

$$\mu = 1, \dots, P$$

$$\alpha = \frac{P}{N}$$

fitness of  
species  $i$

$$f_i = \sum_j J_{ij} x_j + \sum_{\mu} \xi_i^{\mu} A^{\mu}$$

direct interaction  
between species

use of resources

abundance of  
resource  $\mu$

$$A^{\mu}(t) = A_0^{\mu} - \sum_i \xi_i^{\mu} x_i(t)$$

# Model definitions

abundance of  
resource  $\mu$

$$A^\mu(t) = A_0^\mu - \sum_i \xi_i^\mu x_i(t)$$

abundance in absence  
of species

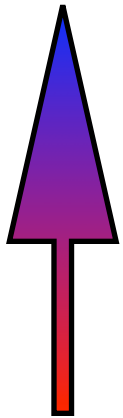
use of resources

$\xi_i^\mu$  random variable of variance 1

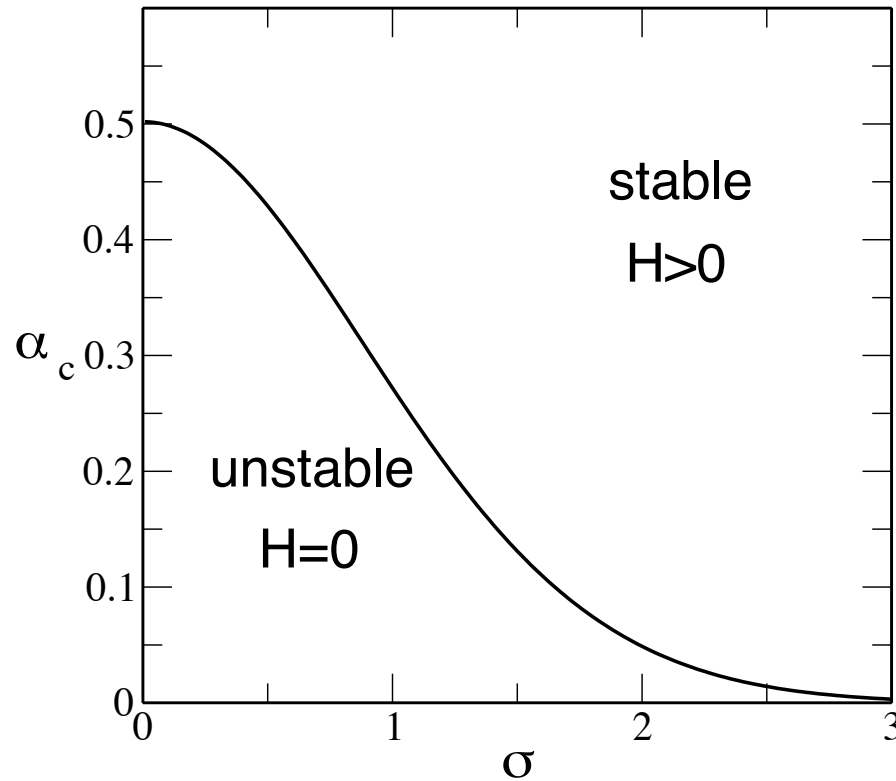
$A_0^\mu$  random variable of variance  $\sigma^2$

# E.g. phase diagram in dependence of number of resources and their variability

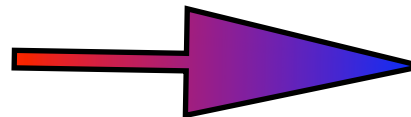
many resources



few resources



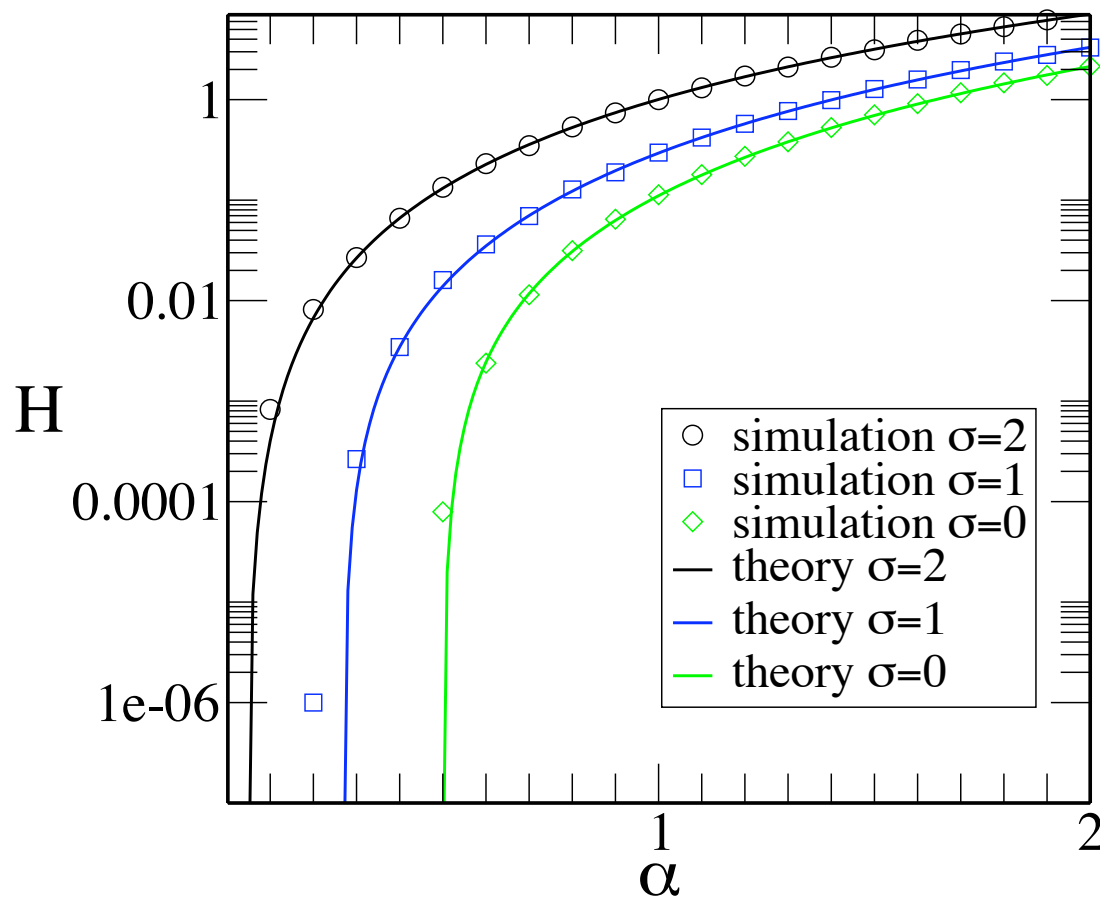
small variability



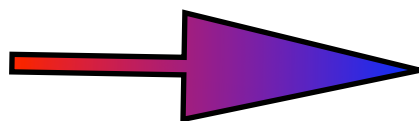
large variability

# Use of resources

$$H = \frac{1}{P} \sum_{\mu=1}^P \langle A^{\mu}(t) \rangle^2$$

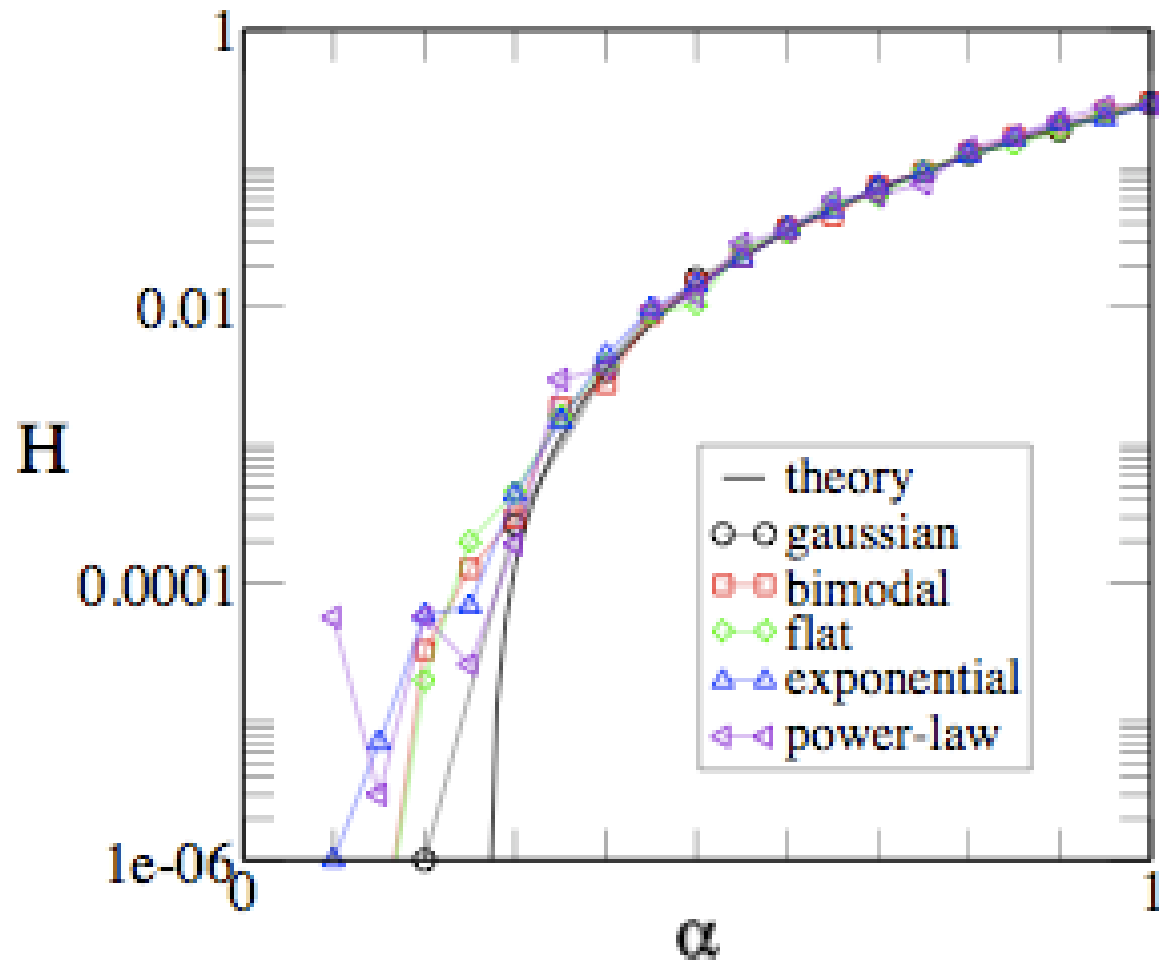


few resources



many resources

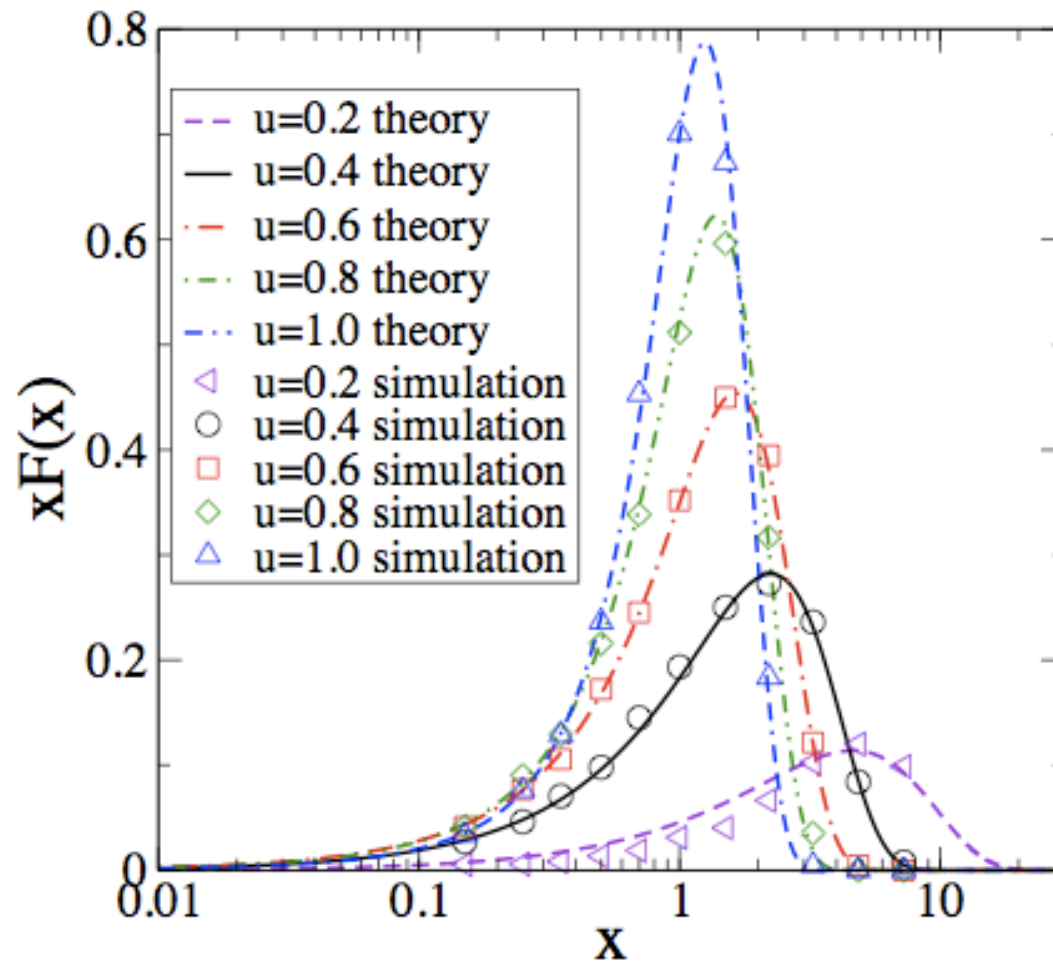
# Robustness of the model: distribution of species-resource couplings



□



# Species abundance distributions in replicator models



[Yoshino, Galla, Tokita, PRE (2008) to appear]

[Tokita, PRL 2004]

# Conclusions

- ▶ used techniques from statistical physics used to study replicator systems with random interaction matrices
- ▶ transition between ergodic-stable and non-ergodic-unstable phase
- ▶ order parameters computable in stable regime
- ▶ extension to simple model-eco system with two trophic levels
- ▶ phases with perfect exploitation of resources