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Complexity Science

Co-evolving individuals and the emergence of adaptive structures: group selection versus the individual.

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Collaboration also with

P. Anderson, E. Arcaute, K. Brinck, A. Cairoli, K. Christensen,
S.A. di Collobiano, J. Grujic, M. Hall, R. Hanel, D. Jones, S. Laird,
D.J. Lawson, D. Piovani, R.D. Robliano, P. Sibani and P. Vazquez.

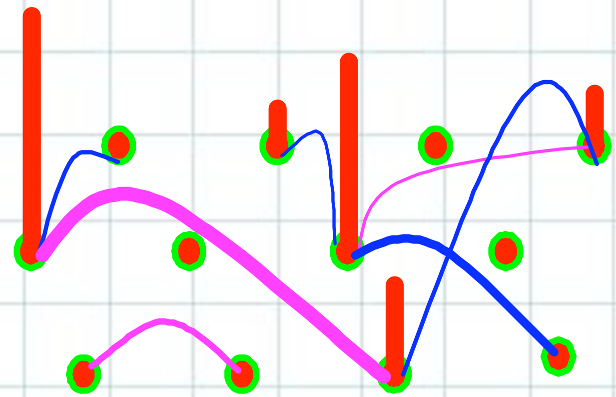
Complexity
Science

Outline

- Ideas behind the Tangled Nature (TaNa) framework
- Model definiton
- The emergence of correlations
- Multi-level selection/adaptation & Information flow
- Finish

Network perspective

dynamics of and on
nodes and links



Recent Review

H.J. Jensen,
Tangled Nature: A model of emergent structure and temporal mode among co-evolving agents.
European Journal of Physics **40**, 014005 (2018)

Why Tangled Nature ?

Last paragraph to the Origin of Species

It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.

Evolutionary ecology:

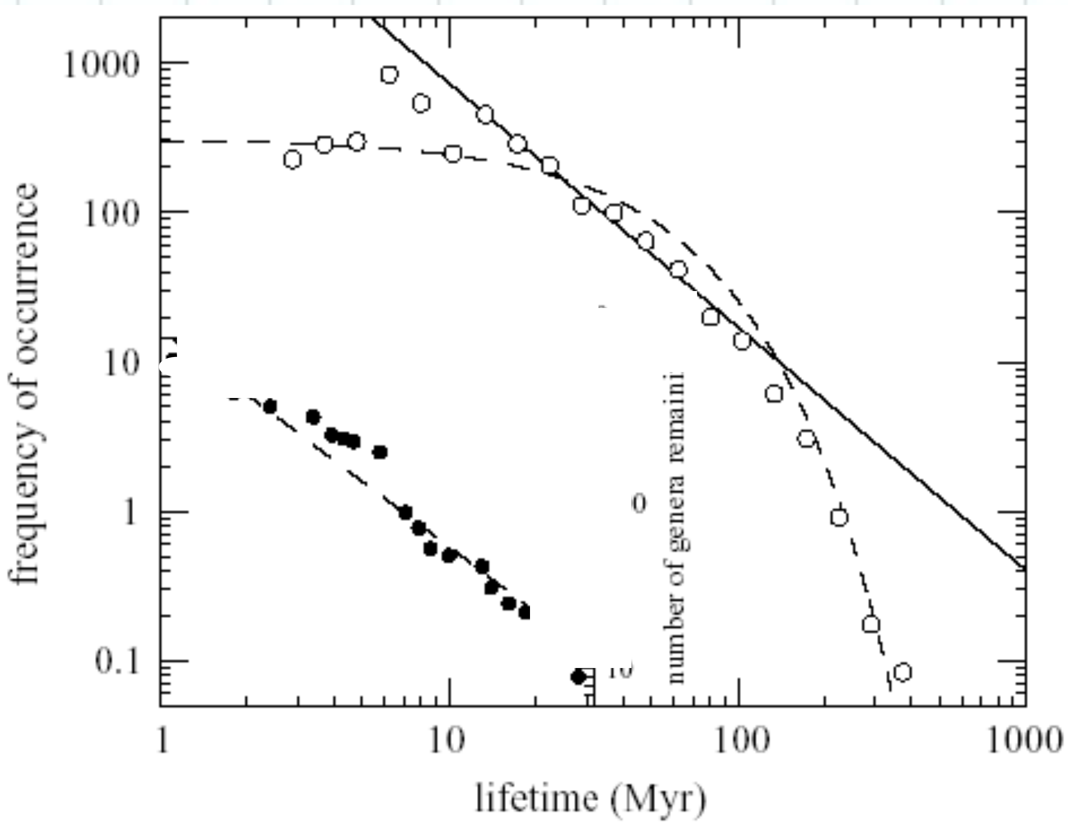
- Interacting organisms + Evolution → Evolving bio-net
- Each type will see an ever changing environment

Focus on system level properties

- ✓ stability
- ✓ mode of evolution
- ✓ nature of the adaptation
- ✓ ecological networks: SAD, SAR, Connectance,...

Motivation - Lifetimes

- Lifetime of taxa



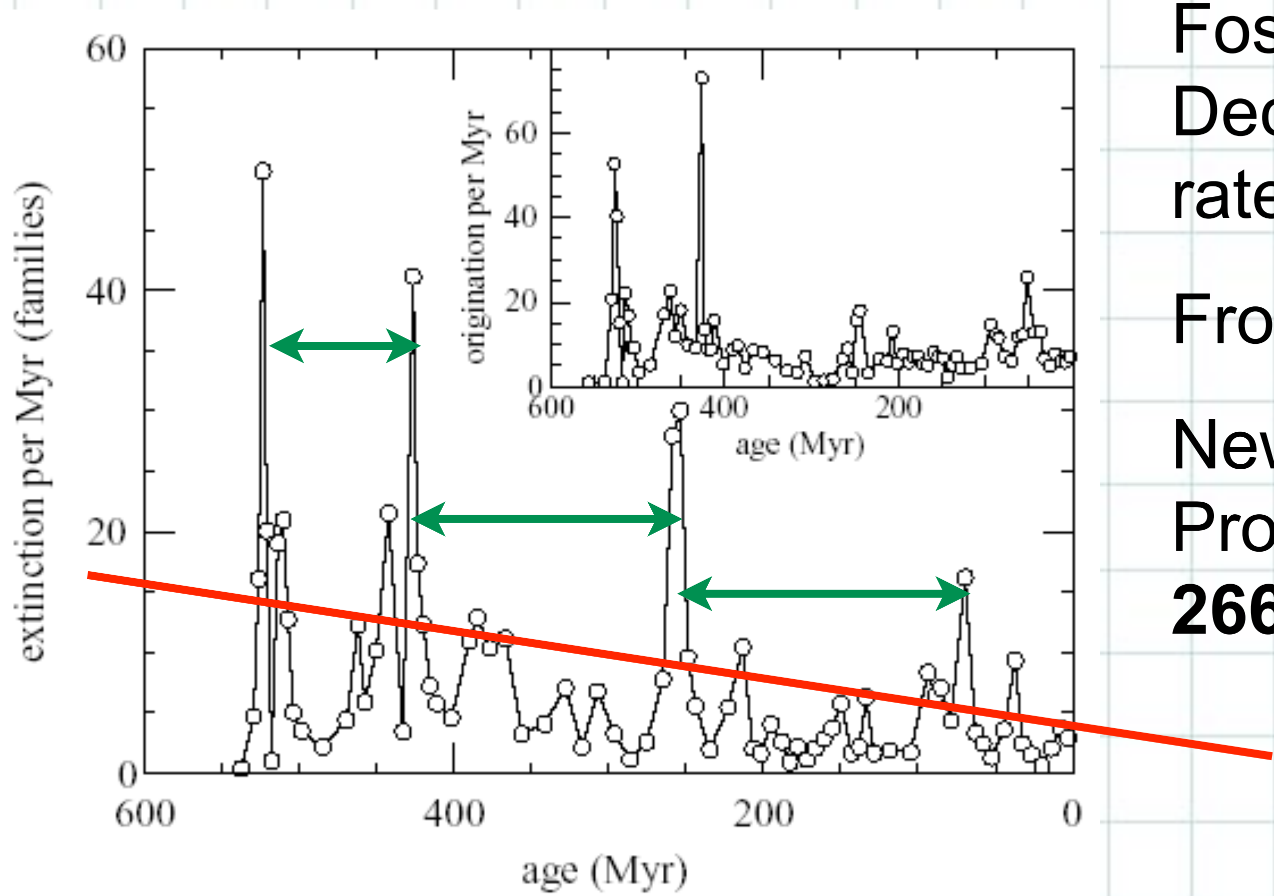
Fossil record: Frequency distribution of lifetimes of marine genus.

From:

Newman and Sibani, Proc. Roy. Soc. B. **266**, 1593 (1999)

Motivation - Tempo and mode

- Time dependent extinction rate



Fossil record: Decreasing extinction rate.

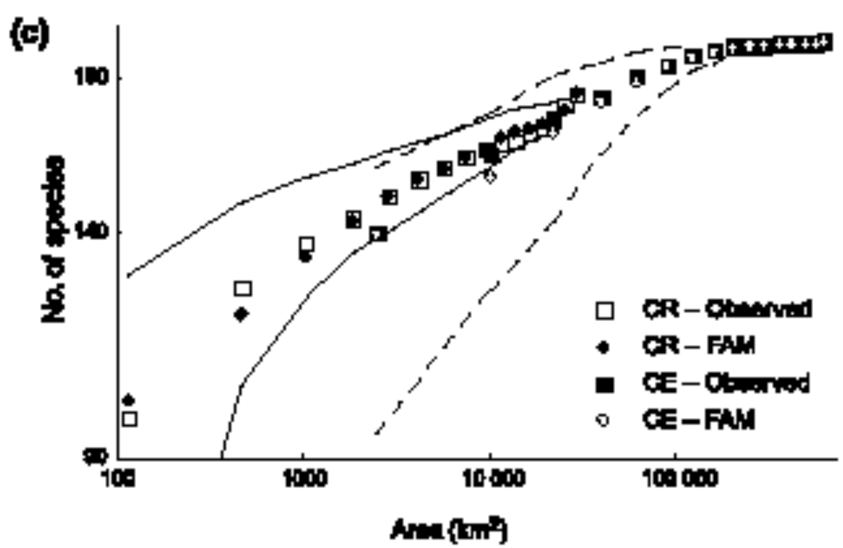
From:

Newman and Sibani, Proc. Roy. Soc. B. **266**, 1593 (1999)

Motivation - Ecology

- Species area relation

$$\# S \propto A^{z}$$



Bird species versus area; Czech Republic.

From:

A Stizling and D Storch

Ecol. Lett. **7**, 60 (2004)

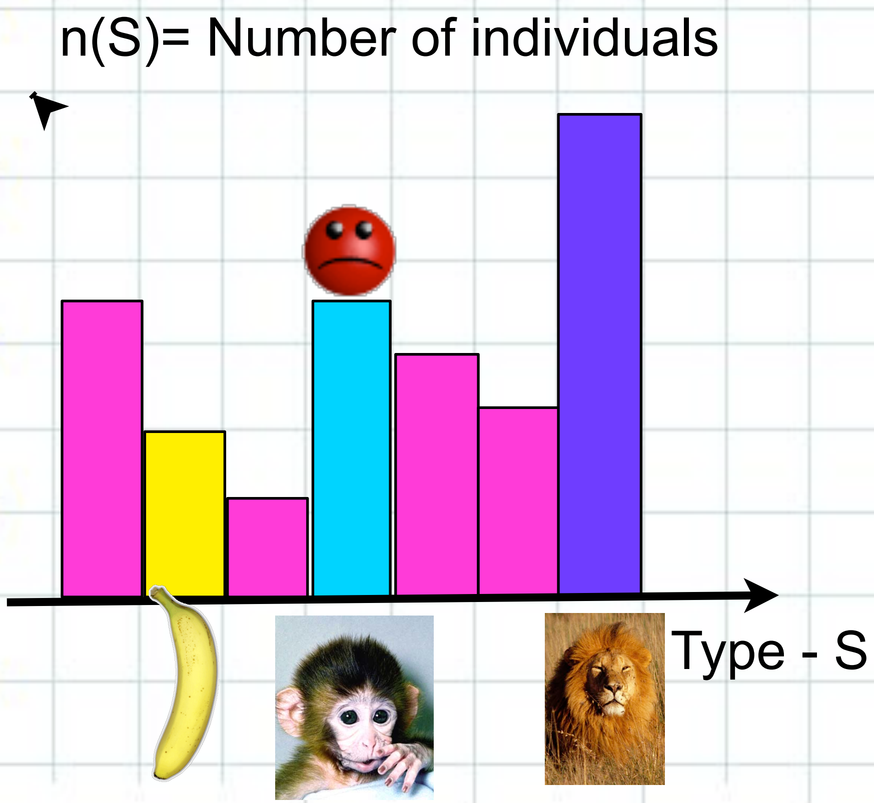
Model

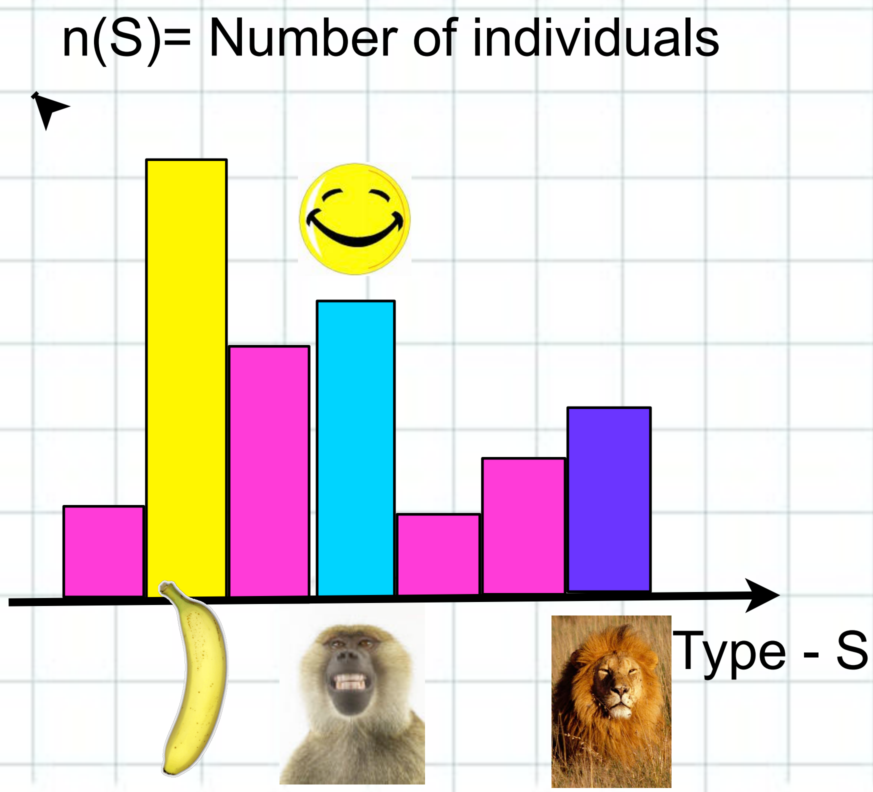
The prototype version

Interaction and co-evolution

The Tangled Nature model

- Individuals reproducing in type space
- Your success depends on who you are amongst

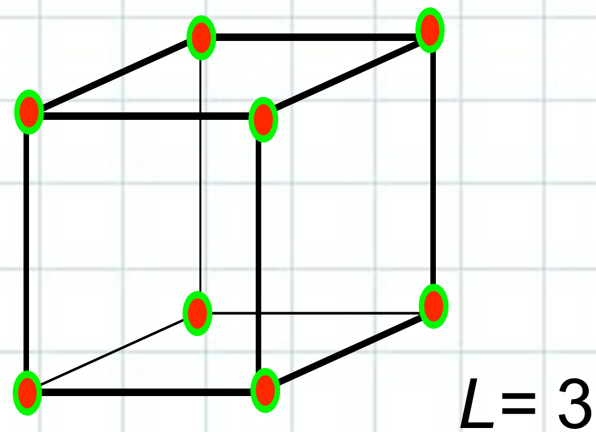




Definition

Individuals $\mathbf{S}^\alpha = (S_1^\alpha, S_2^\alpha, \ldots, S_L^\alpha)$, where $S_i^\alpha = \pm 1$

and $\alpha = 1,2,\ldots, N(t)$



Dynamics – a time step

Annihilation

Choose indiv. at random, remove with probability

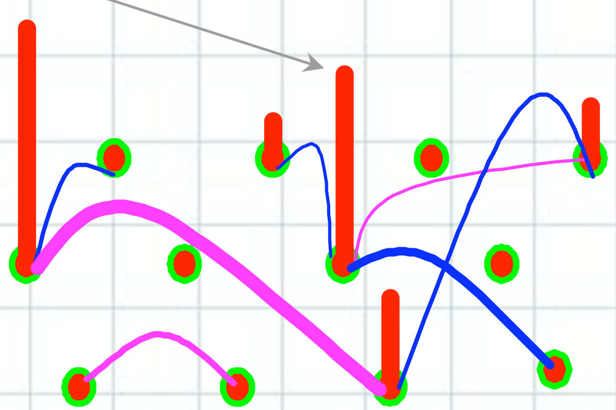
$$p_{kill} = const$$

Reproduction:

- Choose indiv. at random
- Determine

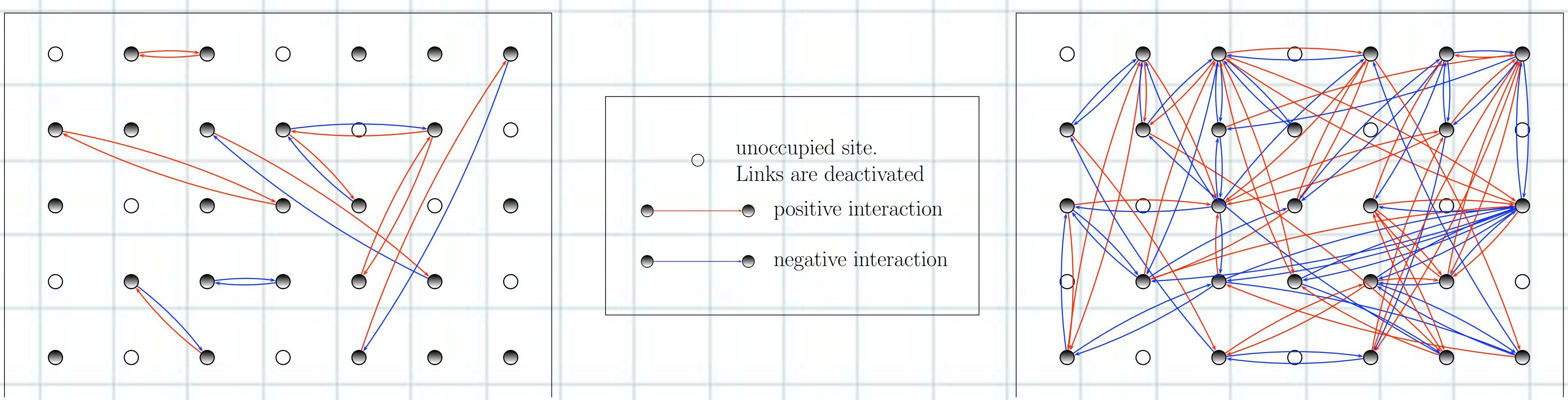
$$H(\mathbf{S}^{\alpha},t) = \frac{k}{N(t)} \sum_{\mathbf{S}} J(\mathbf{S}^{\alpha},\mathbf{S})\, n(\mathbf{S},t) - \mu N(t)$$

$n(\mathbf{S},t) =$ occupancy at the location $\mathbf{S}$



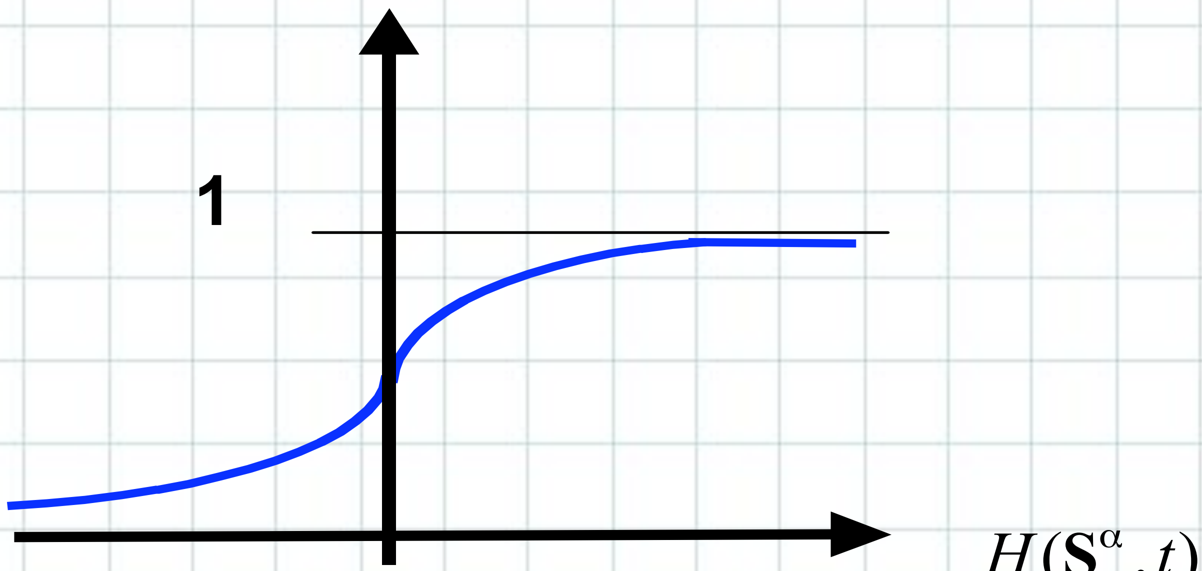
The coupling matrix J(S,*S'*)

- Either consider J(S,*S'*) to be uncorrelated
- or to vary smoothly through type space
- and sparse or dense



from $H(\mathbf{S}^{\alpha},t)$ reproduction probability

$$p_{off}(\mathbf{S}^{\alpha},t) = \frac{\exp[H(\mathbf{S}^{\alpha},t)]}{1+\exp[H(\mathbf{S}^{\alpha},t)]} \in [0,1]$$



Asexual reproduction:

Replace

$$\mathbf{S}^{\alpha} \rightarrow \mathbf{S}_1^{\alpha}, \quad \mathbf{S}^{\alpha} \rightarrow \mathbf{S}_2^{\alpha}$$

by two copies

with probability $p_{off}(\mathbf{S}^{\alpha}, t)$

Mutations

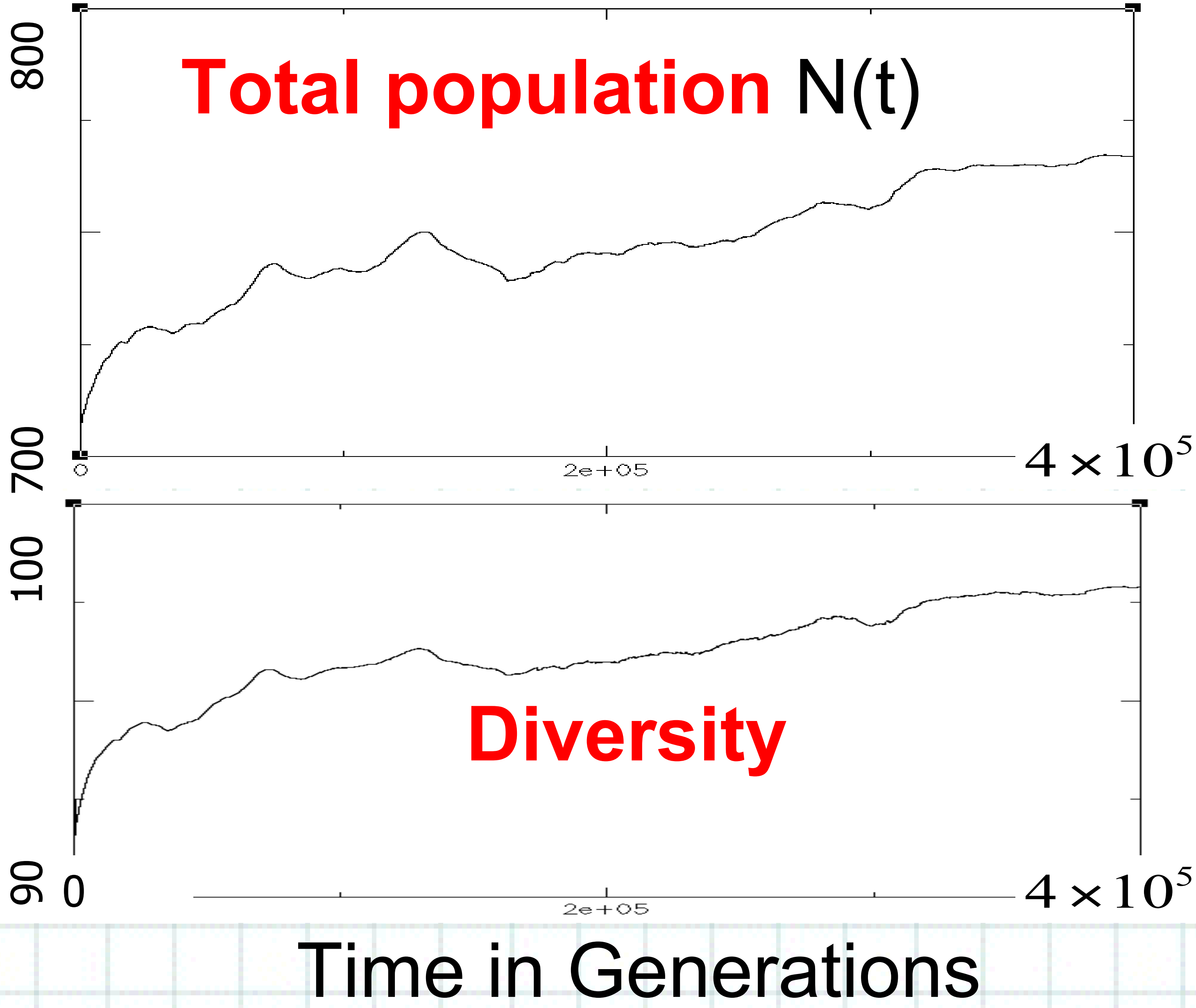
- Mutations occur with probability

p_{mut} , i.e.

$$S_i^{\gamma} \mapsto -S_i^{\gamma}$$

RESULTS

Time dependence (Average behaviour)



Origin of drift? Effect of mutation

Let $H = \tilde{J} - \mu N$, then the effect of a mutation is

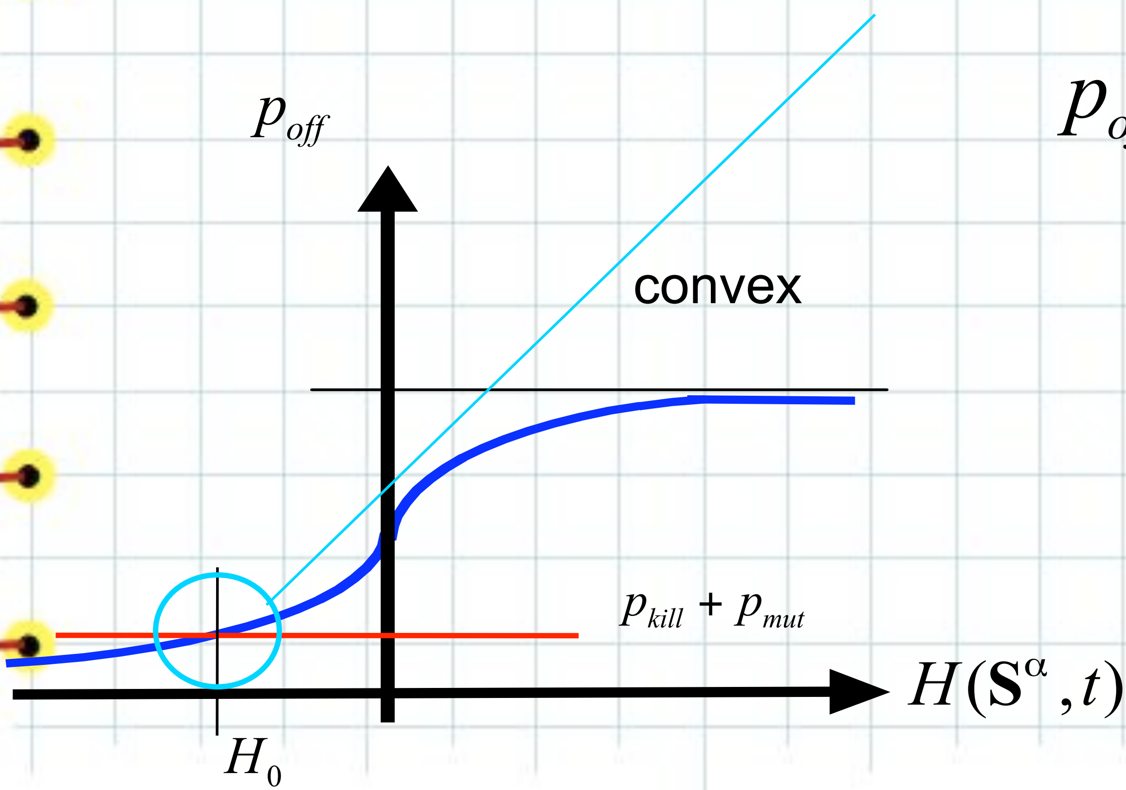
$$H \mapsto H + \delta \tilde{J}.$$

➡ Symmetric fluctuations $prob(\delta \tilde{J}) = prob(-\delta \tilde{J})$

leads to asymmetri

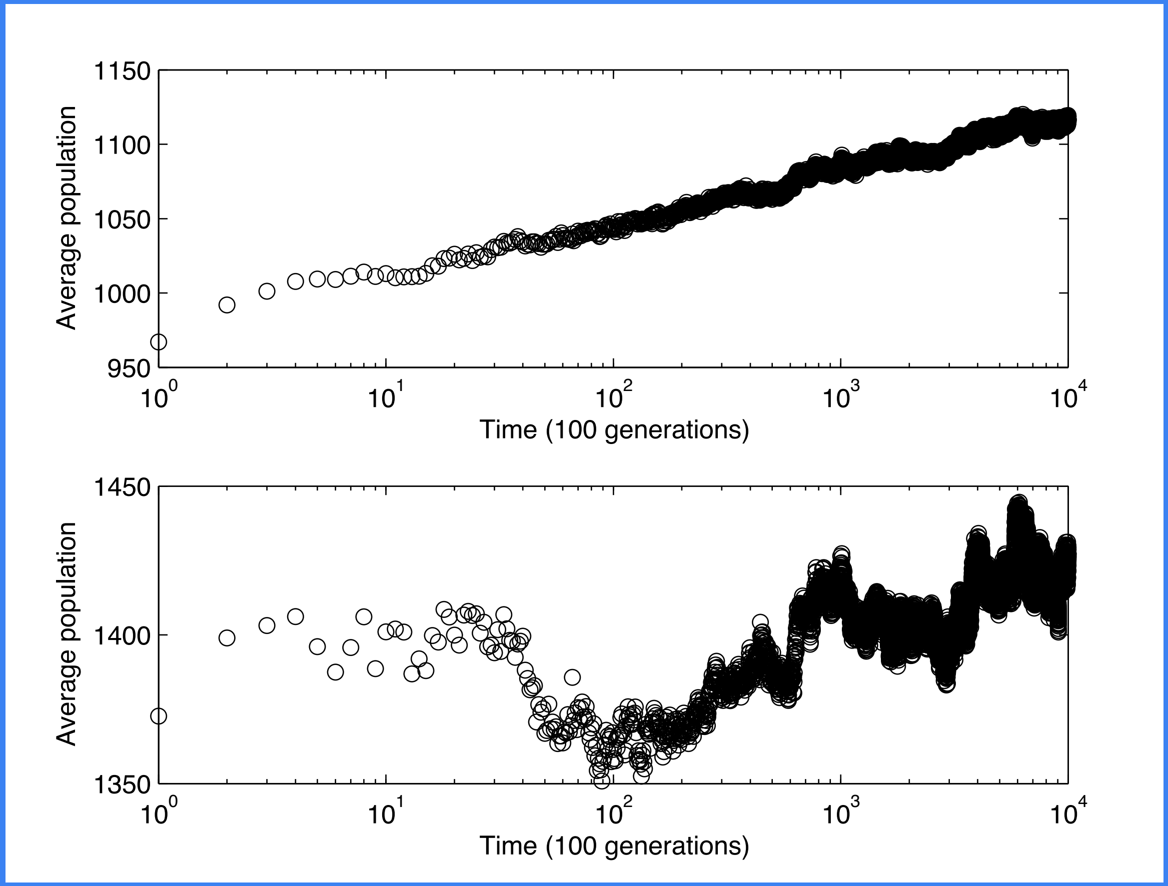
$$p_{off}(H_0 + \delta \tilde{J}) - p_{kill} >$$

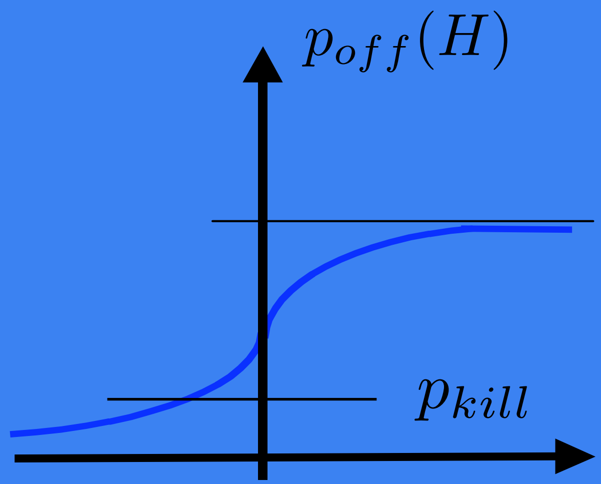
$$p_{kill} - p_{off}(H_0 - \delta \tilde{J})$$

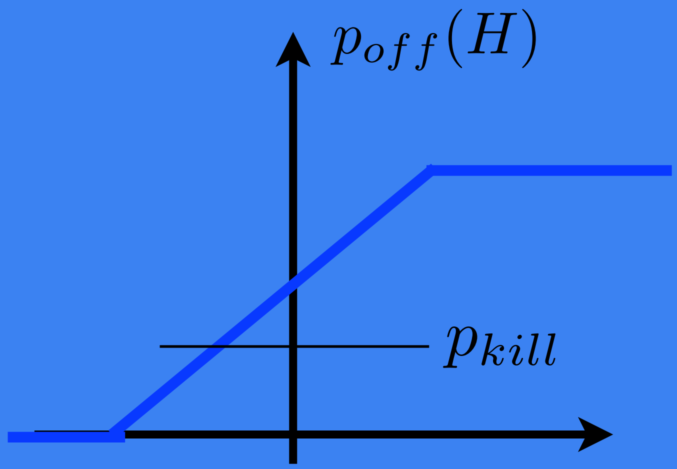


Dynamics:

The functional form of

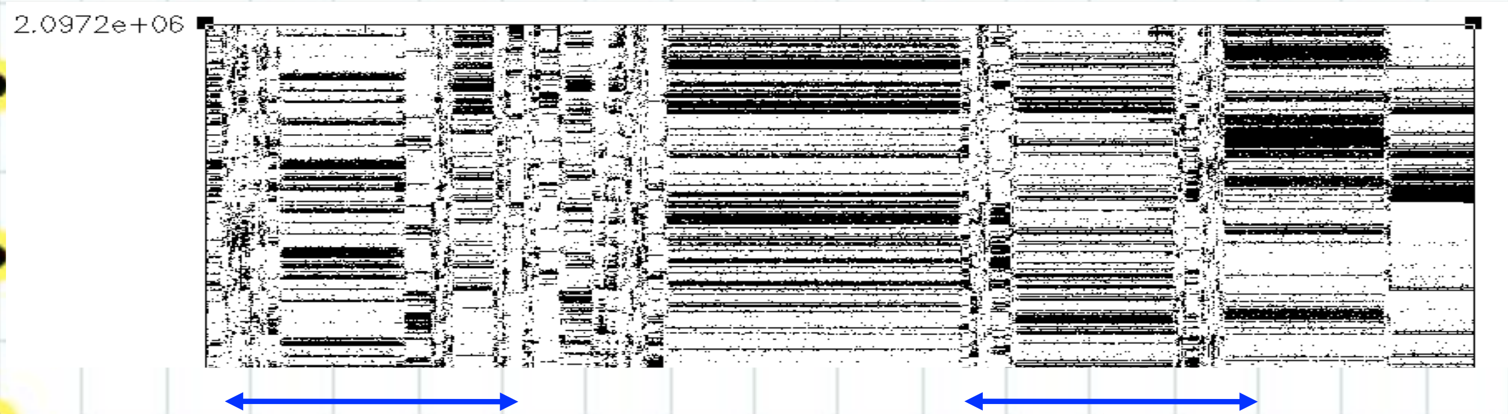






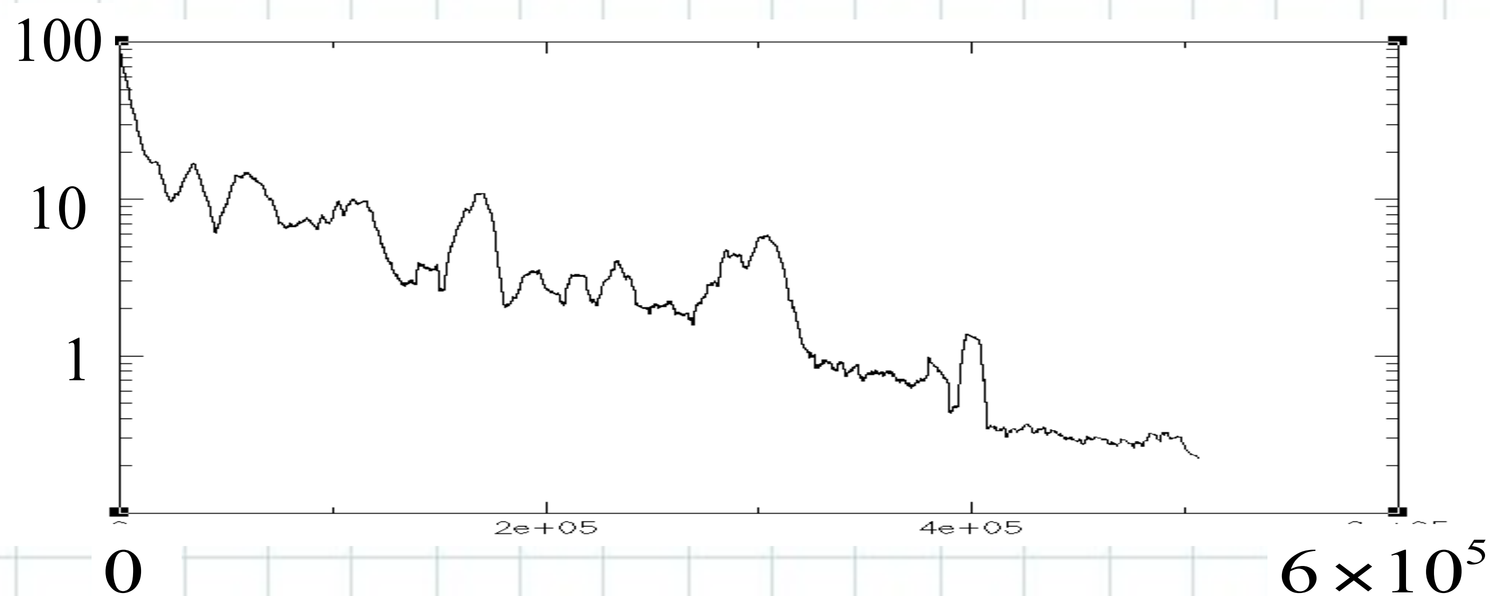
Dominic Jones

Intermittency:



# of transitions in window

Matt Hall



1 generation

= $N(t)/p_{kill}$

Stability of the q-ESS:

Consider simple adiabatic approximation.

Stability of genotype S assuming: $n(S',t)$ independent of t for $S' \neq S$

Consider $$\frac{\partial n(S,t)}{\partial t} = [p_{off}(n(S,t),t) - p_{kill} - p_{mut}]\frac{n(S,t)}{N(t)}$$

Stationary solution $n_0(S)$ corresponds to $p_{off}(n_0(S)) - p_{kill} - p_{mut} = 0$

Fluctuation $\delta = n(S,t) - n_0(S)$

Fulfil $$\dot{\delta} = A\frac{n_0}{N_0}\delta$$

$$\text{with } A = -(1 - p_{mut})(p_{off})^2 e^{-H_0}(\frac{J}{N_0^{\,2}} + \mu) < 0$$

i.e. stability

Transitions between q-ESS caused by co-evolutionary collective fluctuations

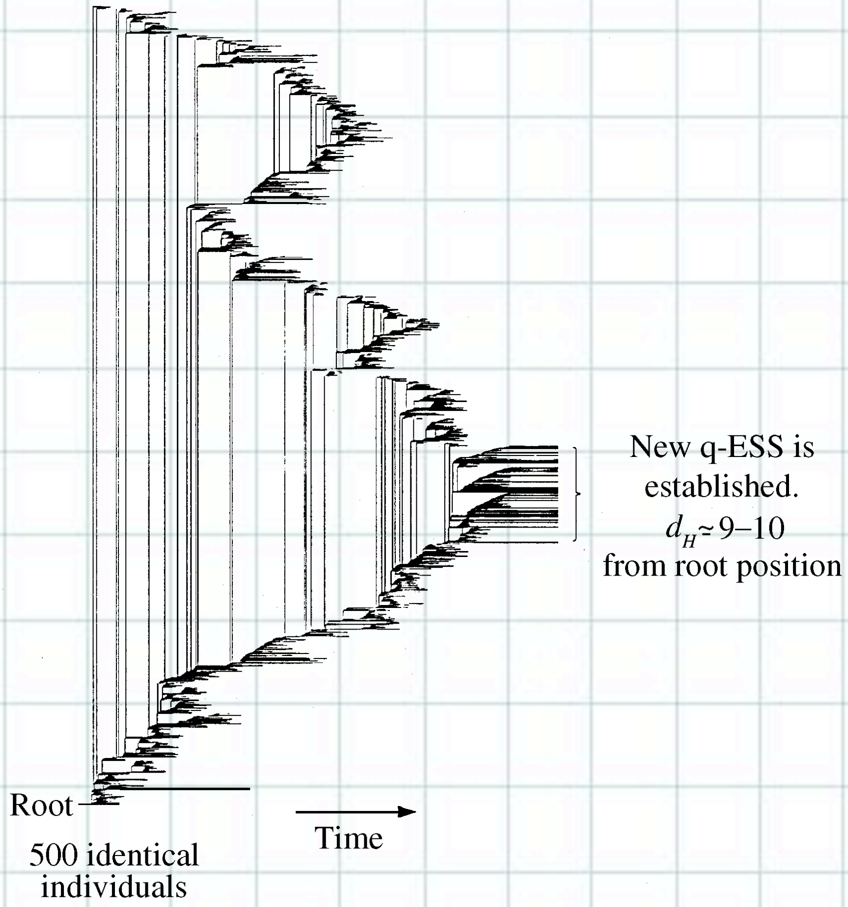
$n(S',t)$ needs to be considered

dependent of t for $S' \neq S$

Complexity Science

Monitoring and Forecasting the transition

From:
http://insite.artinstitutes.edu/designers-rely-on-trend-forecasting-to-color-their-worlds-14877.aspx



Duccio Piovani, Andrea Cairoli

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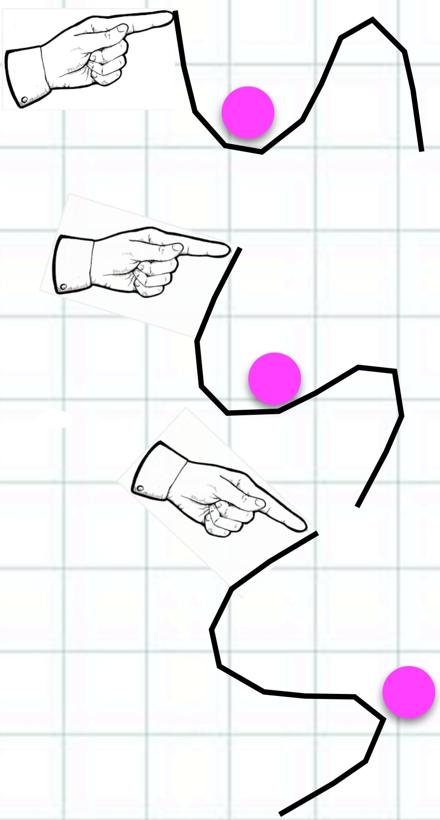
The Scheffer approach

Complexity Science

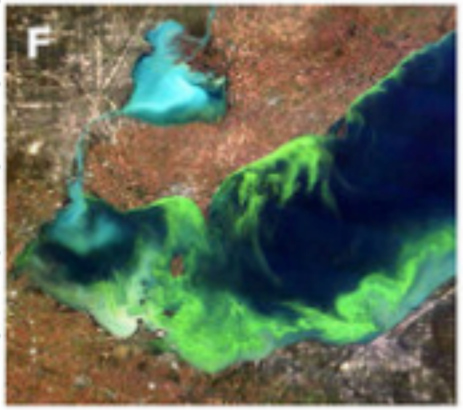
Cause of the transition:

External



Example: Lake Erie - algae bloom

1st June 2011



9 October 2011

This sequence of satellite photos of Lake Erie's western basin shows the progress of the 2011 algae bloom. A: June 1, soon after a surge of fertilizer-loaded storm runoff from the Maumee River has flowed into the lake basin; B: July 19, as the bloom begins to grow; C: July 31, about two weeks after the bloom's start; D: August 11, as the bloom spreads east toward the central basin; E: Sept. 3, as the bloom reaches the central basin and a second phase forms on the basin's north shore; F: Oct. 9, as the bloom begins to decline in the western basin.

Courtesy of University of Wisconsin-Madison Space Science and Engineering Center

http://www.cleveland.com/science/index.ssf/2013/04/record-sized_lake_erie_algae_b.html

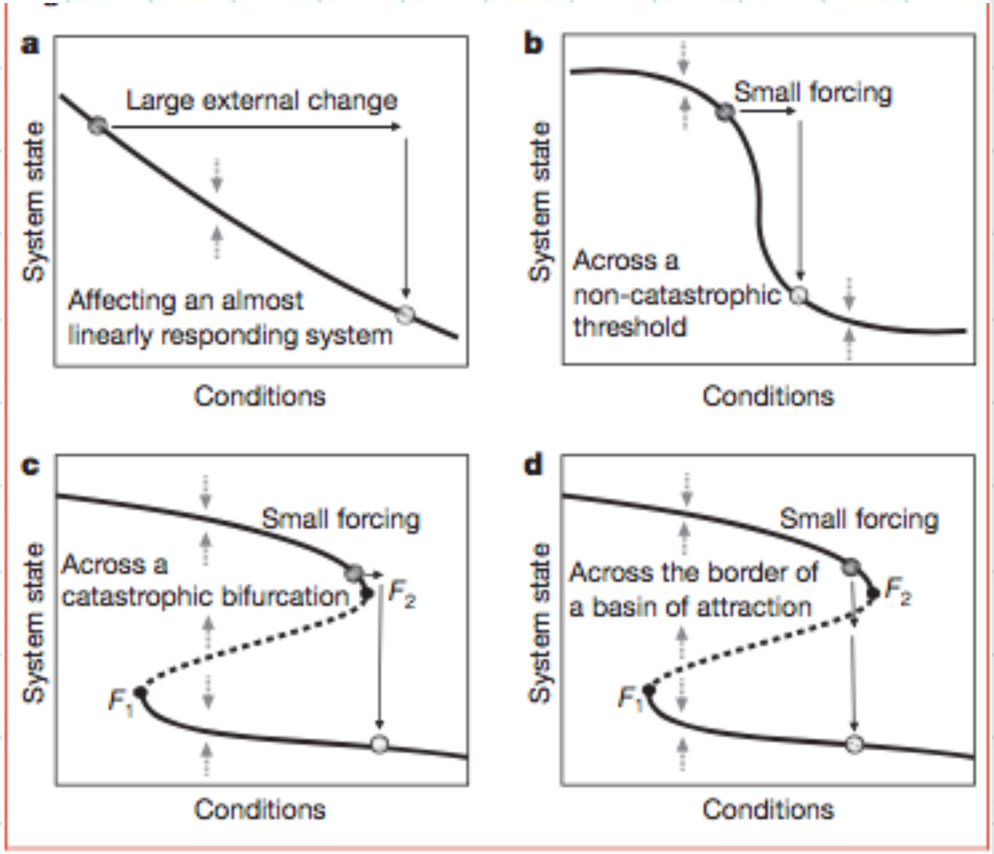
Complexity Science

Bifurcation approach: Critical fluctuations and slowing down.

This approach is promoted by Scheffer and collaborators (see. e.g. Nature 461, 53 (2003)

External forcing drives the system through a bifurcation

Degrees of freedom well established



Scheffer et al. Nature 461, 53 (2003)

Complexity Science

Bifurcation approach: Critical fluctuations and slowing down.

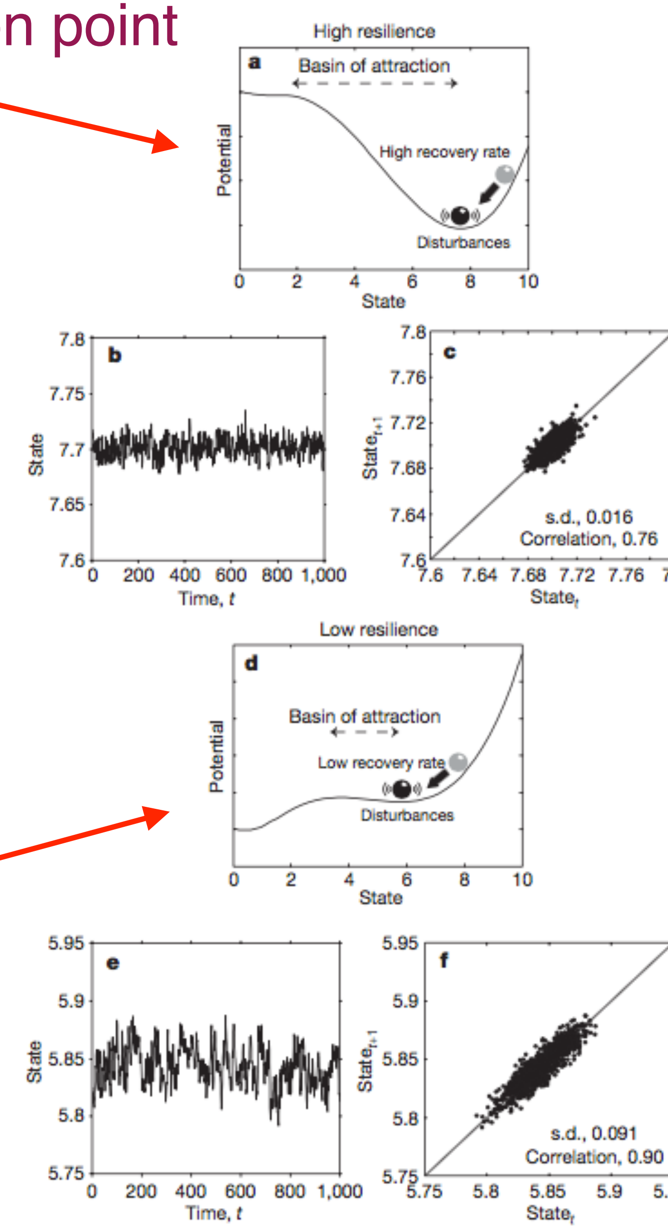
Approach promoted e.g. by Scheffer et al. [Nature 461, 53 (2003)]

Indicators

- Increase in fluctuations
- Slower recovery rate

Far from bifurcation point

Close to bifurcation point

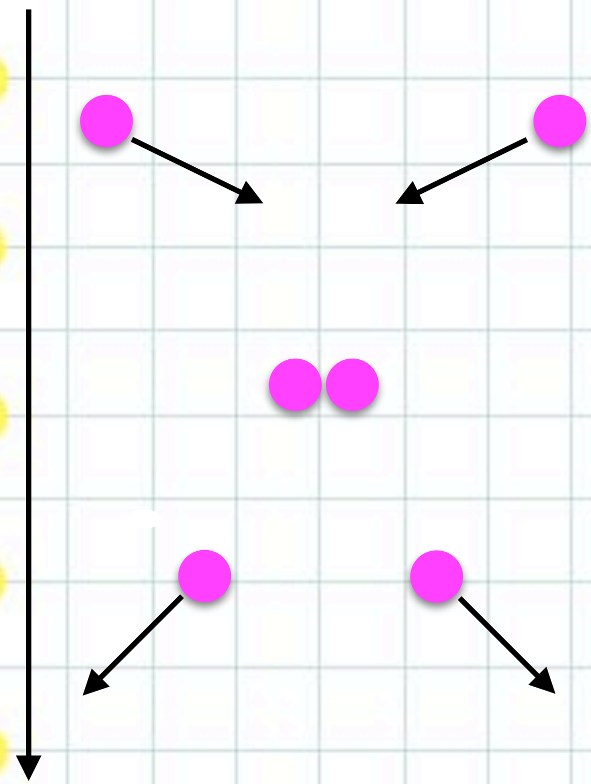


Scheffer et al. Nature 461, 53 (2003)

Complexity & Networks

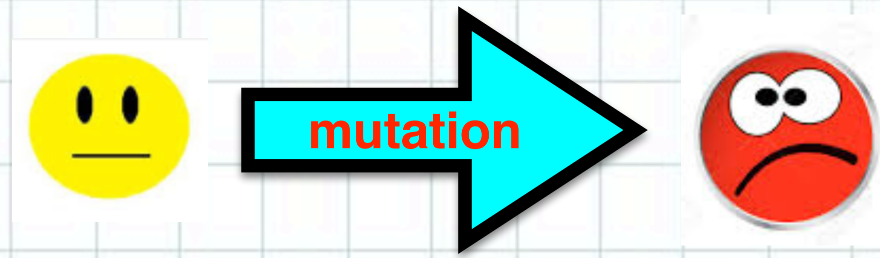
Cause of the transition:

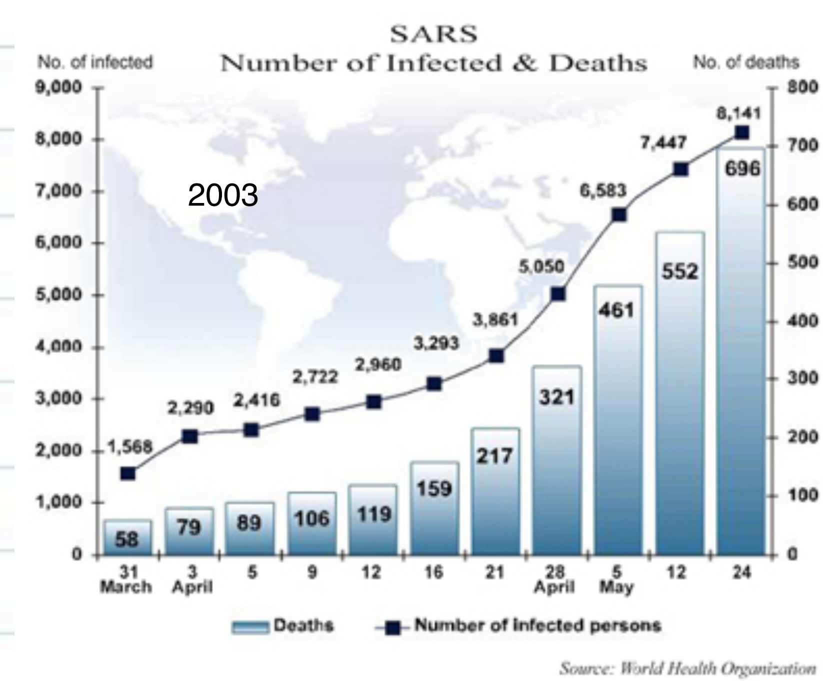
Internal



Time

Example: SARS virus

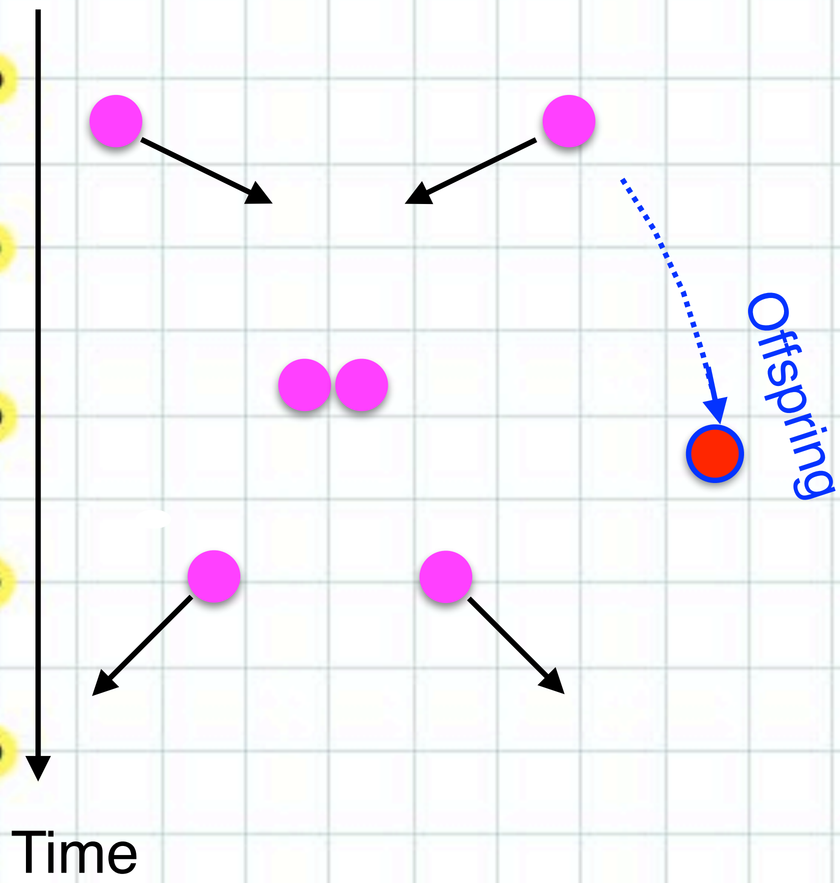




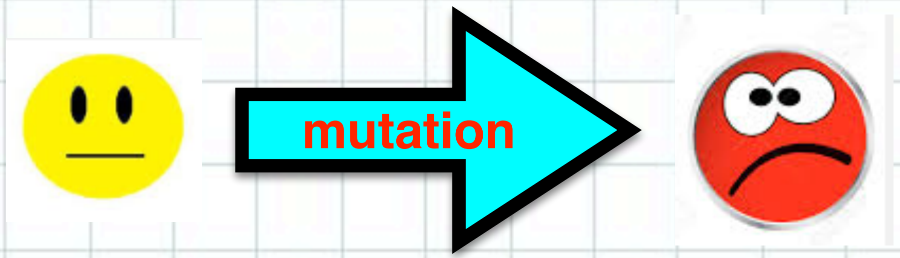
Complexity & Networks

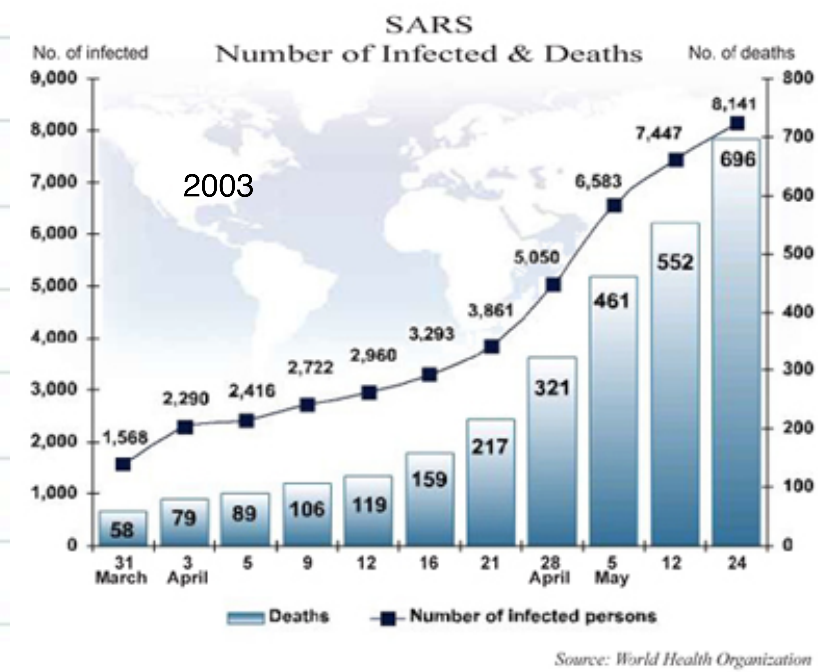
Cause of the transition:

Internal



Example: SARS virus





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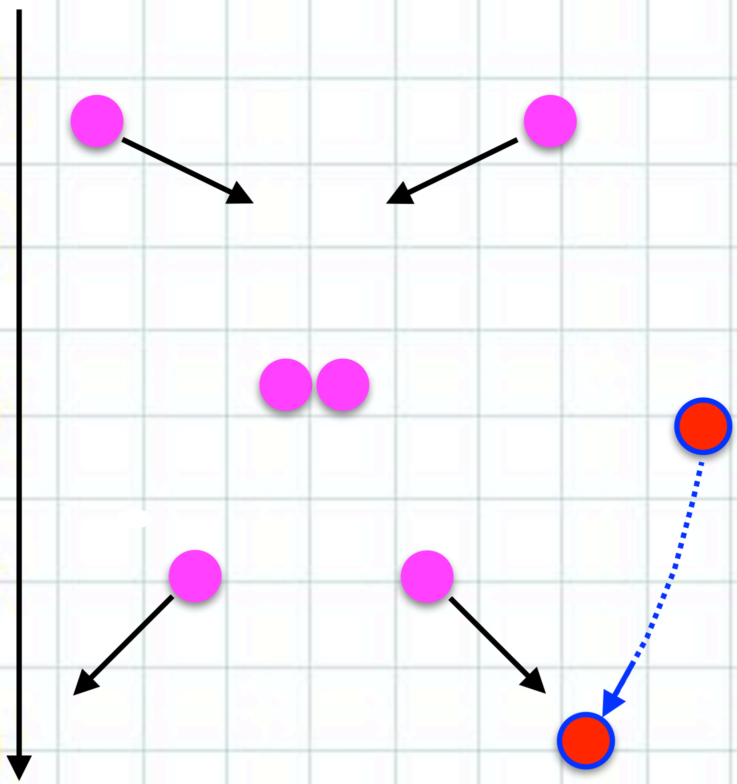
Complexity & Networks

Cause of the transition:

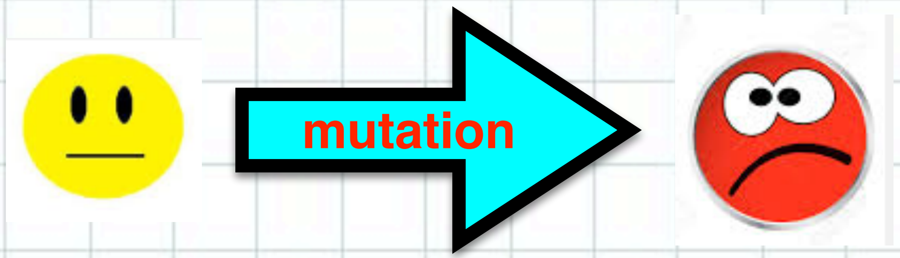
Internal



Time

Kauffman's phrase
The adjacent possible

Example: SARS virus



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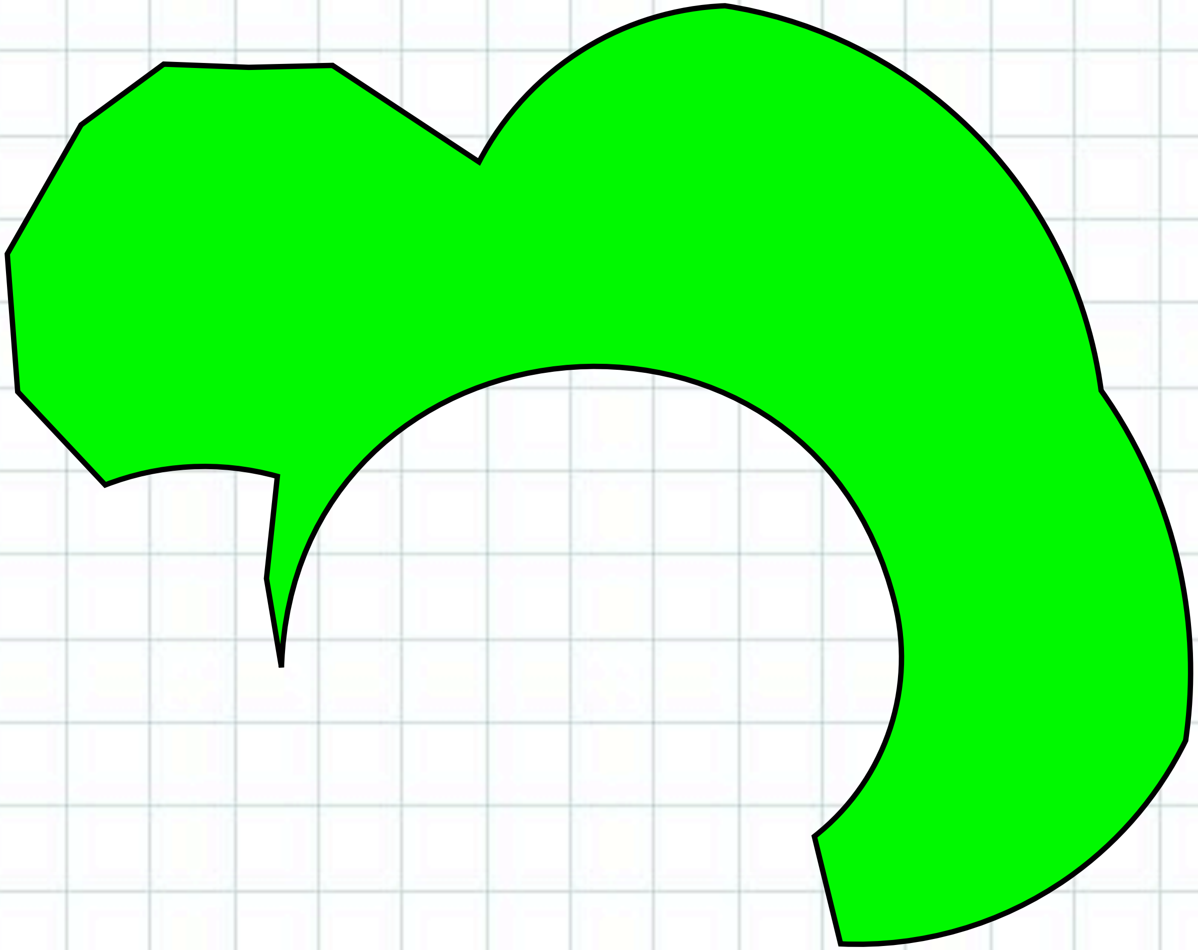
Phase space of the system

The observed degrees of freedom or, say, agents



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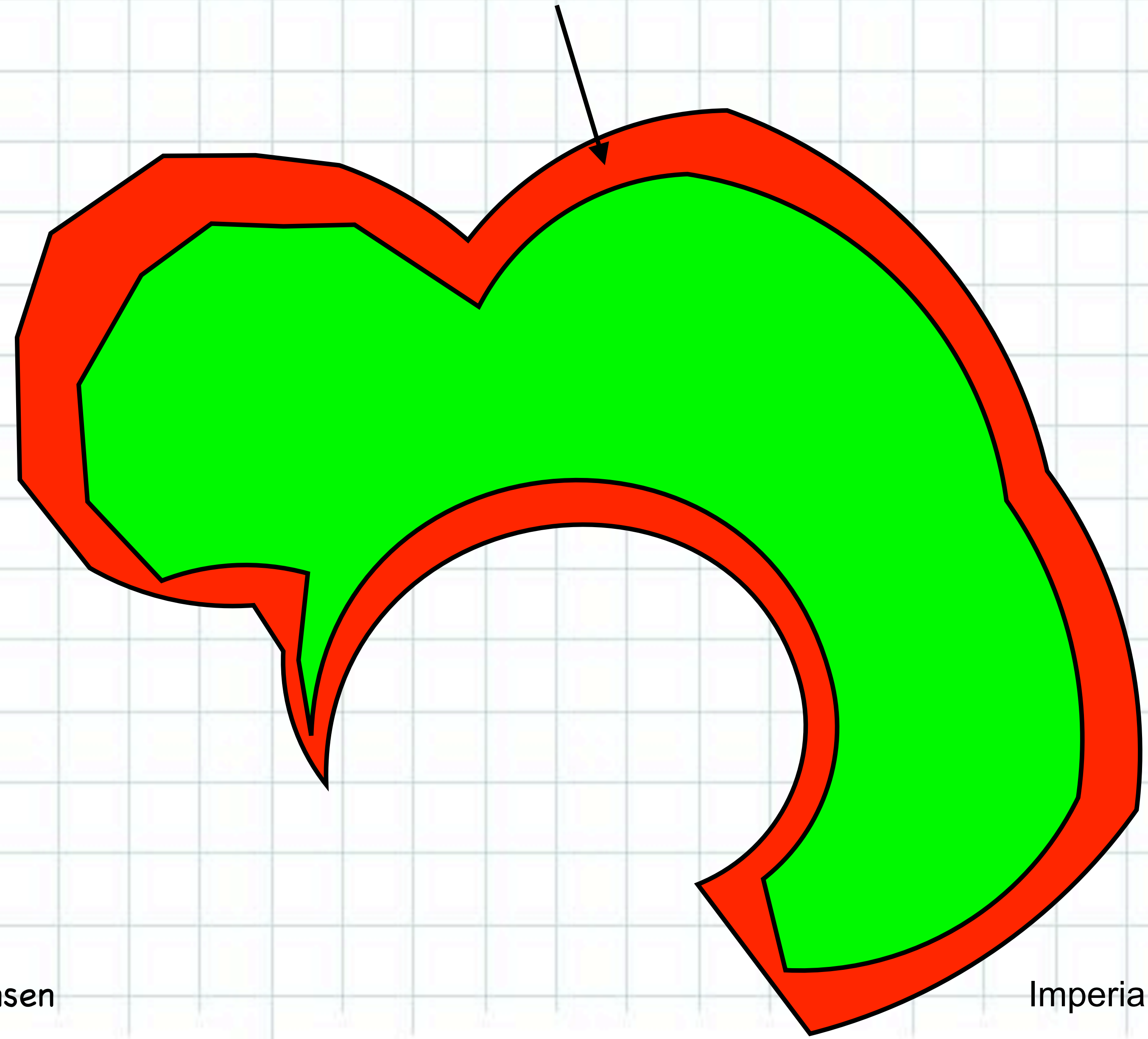
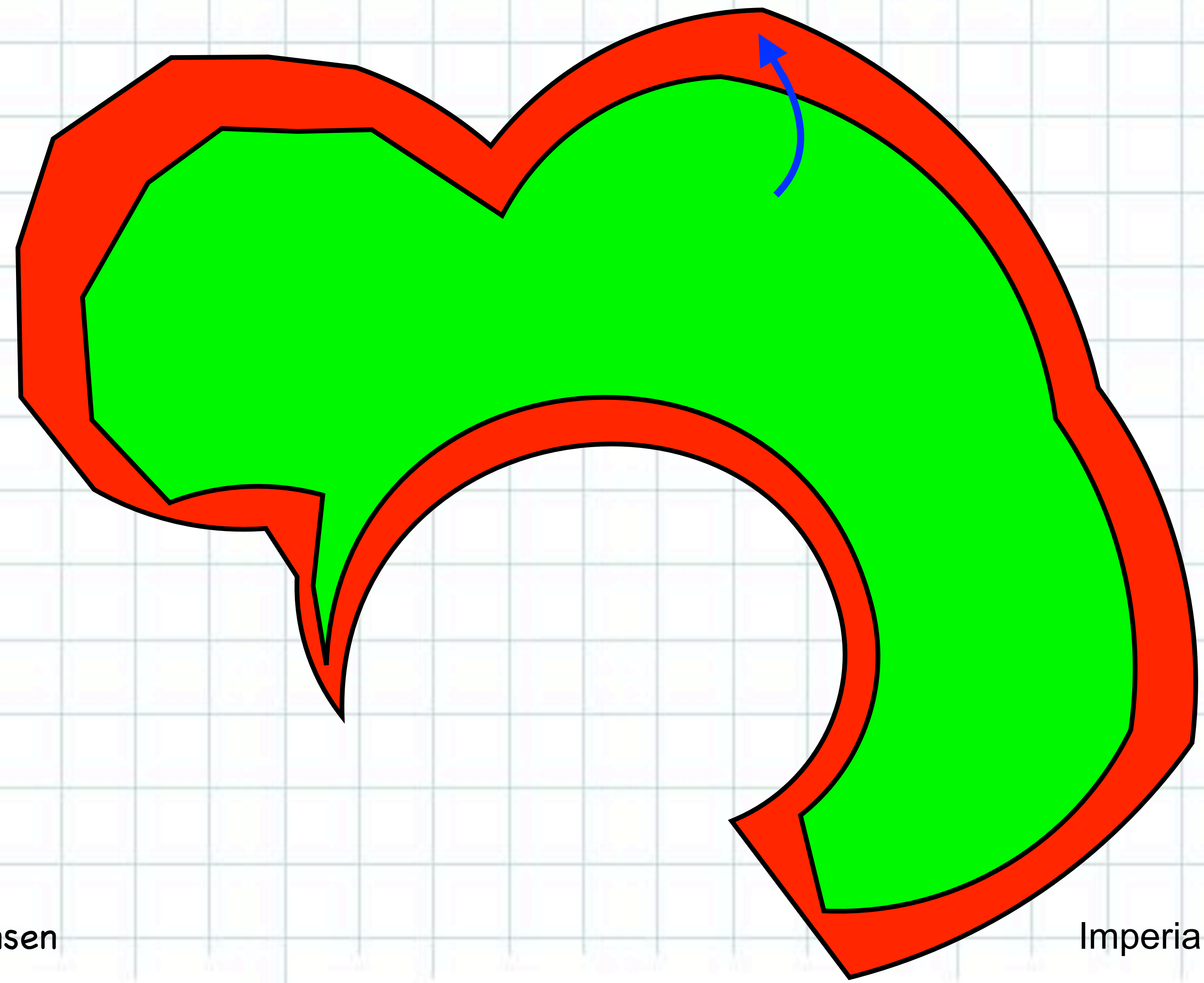
Essential to include the adjacent possible



Essential to include the adjacent possible



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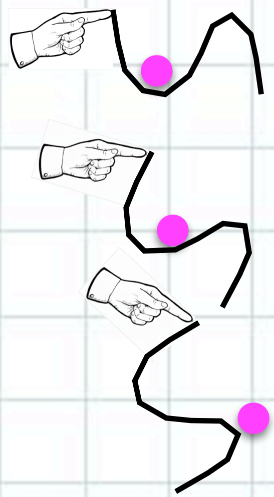
When do we expect which type to be relevant

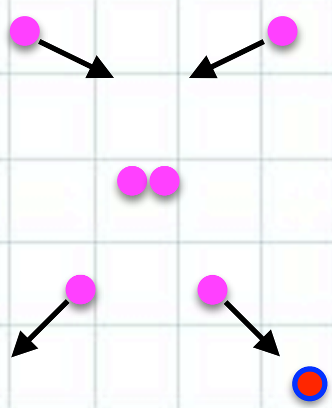
External



- A “robust” macro-variable must exist
- Clear distinction between internal and external

  Say change of nutrition in an ecosystem
  over shortish period of time

Internal



- Macro-variables subject to essential fluctuations.
- Internal and external not clearly separable
  (often the case for complex systems)

  New mutants, new agents

Complexity Science

Forecasting the transition

beyond the single macroscopic variable

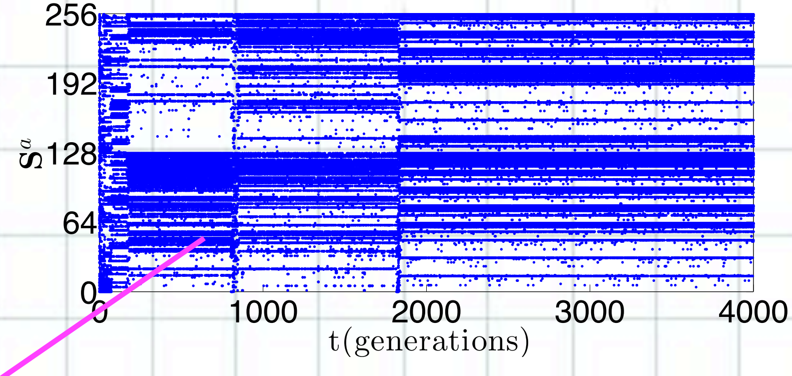
- Mean field analysis

state vector $$\mathbf{n}(t) = [n(\mathbf{S}^1, t), n(\mathbf{S}^2, t), ..., n(\mathbf{S}^{2^L}, t)]$$

time evolution $$\boxed{\mathbf{n}(t+1) - \mathbf{n}(t) = \frac{1}{N(t)} \mathbb{T}[\mathbf{n}(t)]\mathbf{n}(t)}$$

where

$$\{\mathbb{T}[\mathbf{n}(t)]\}_{ab} = \left(p^b_{off}(\mathbf{n}(t))(2p_0 - 1) - p_{kill}\right)\delta_{ab} + 2\,p^b_{off}(\mathbf{n}(t))(p_{mut})^{Ld_{ab}}(1 - p_{mut})^{L(1-d_{ab})}(1 - \delta_{ab})$$



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Linear stability analysis

Stationary state $\mathbf{n}^*(t)$:

- the q-ESS configurations

$$\frac{d\mathbf{n}}{dt} = 0$$

$$0 = (p_{off}^a(\mathbf{n}^*)(2p_0 - 1) - p_{kill})\, n_a^* + 2 \sum_{\substack{b=1 \\ b\neq a}}^{2^L} p_{off}^b(\mathbf{n}^*)(p_{mut})^{Ld_{ab}}(1 - p_{mut})^{L(1-d_{ab})} n_b^*$$

Consider fluctuations about $\mathbf{n}^*(t)$

$$\mathbf{n}(t) = \delta\mathbf{n}(t) + \mathbf{n}^*$$

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Time evolution of the deviation from $\mathbf{n}^*(t)$

$$\frac{\partial}{\partial t}\delta\mathbf{n}(t) = \mathbb{M}[\mathbf{n}^*]\,\delta\mathbf{n}(t)$$

$$\boxed{\delta n_i(t) = \sum_{i,j=1}^{n} c_{ij} e^{\lambda_j (t-t_0)} \delta n_{i,0}}$$

where the configuration vector is expanded on the (normalised) eigenvectors

$$\mathbb{M}\mathbf{e}_i = \lambda_i \mathbf{e}_i$$

So $\delta n_i(t)$ is the component of $\delta\mathbf{n}(t)$ along $\mathbf{e}_i$

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Importance of unstable direction

A measure of instability

$$Q(t) = \max_{\lambda \in Sp^{+}(\mathbb{M}[\bar{\mathbf{n}}_{stoc}])} \left| e^{\lambda} \langle (\mathbf{n}(t) - \bar{\mathbf{n}}_{stoc}), \mathbf{e}_{\lambda} \rangle \right|$$

A measure of response

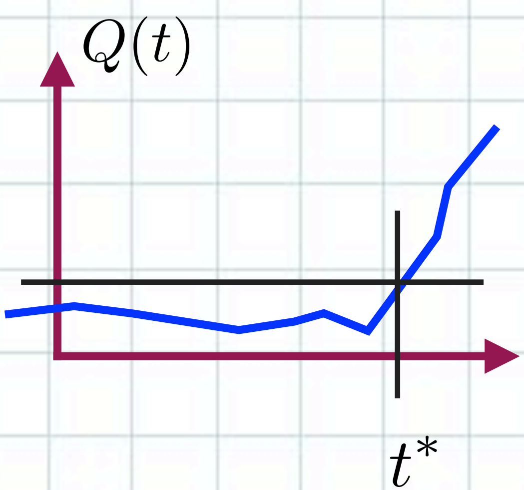
$$\|\delta \mathbf{n}(t)\| = \|\mathbf{n}(t) - \bar{\mathbf{n}}_{stoc}\|$$

namely Q(t) estimate the change of the deviation

$$\mathbf{n}(t) - \bar{\mathbf{n}}_{stoc} \quad \text{to} \quad \mathbf{n}(t+1) - \bar{\mathbf{n}}_{stoc}$$

We define t^* as the time at which $Q(t)$ increases above a certain threshold q

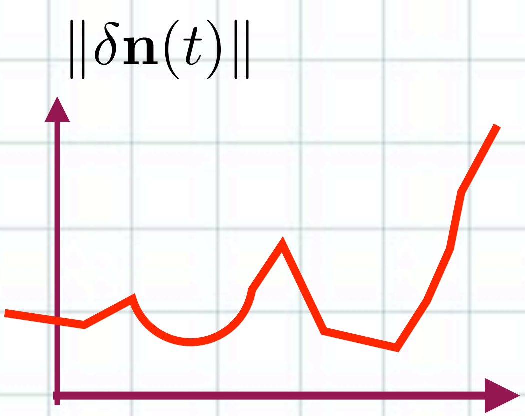
$$Q(t) = \max_{\lambda \in Sp^+(\mathbb{M}[\bar{\mathbf{n}}_{stoc}])} \left| e^{\lambda} \langle (\mathbf{n}(t) - \bar{\mathbf{n}}_{stoc}), \mathbf{e}_{\lambda} \rangle \right|$$



And monitor how

$$\|\delta \mathbf{n}(t)\| = \|\mathbf{n}(t) - \bar{\mathbf{n}}_{stoc}\|$$

evolves.



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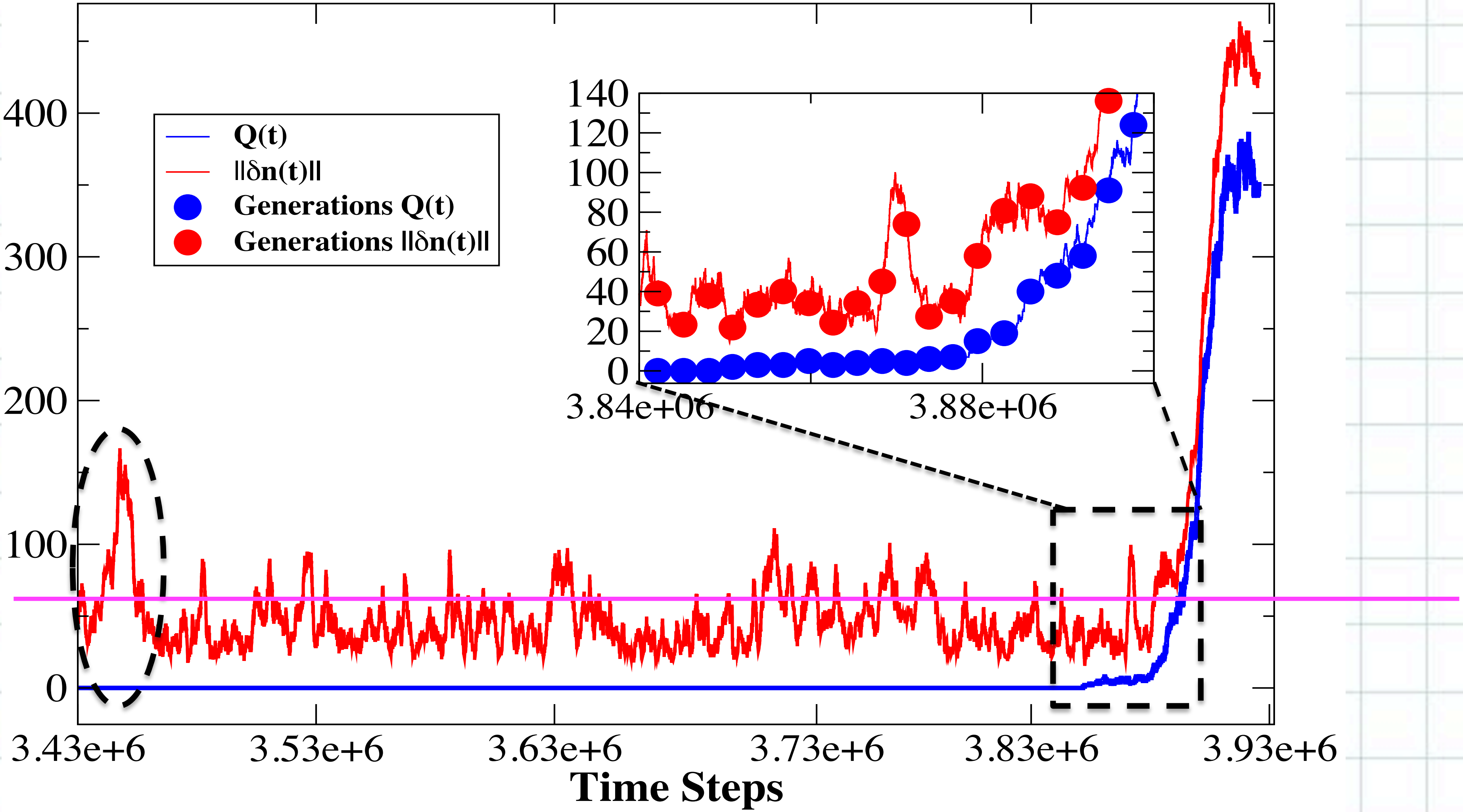
Duccio Piovani



About 80% accuracy

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Forecasting the transition — data driven

beyond the single macroscopic variable
— a suggestion

- Need time evolution $\boxed{\mathbf{n}(t+1)-\mathbf{n}(t)=\frac{1}{N(t)}\mathbb{T}[\mathbf{n}(t)]\mathbf{n}(t)}$

has a vector of time series $\mathbf{n}(t)$

compute information theoretic causal interdependence

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— a suggestion

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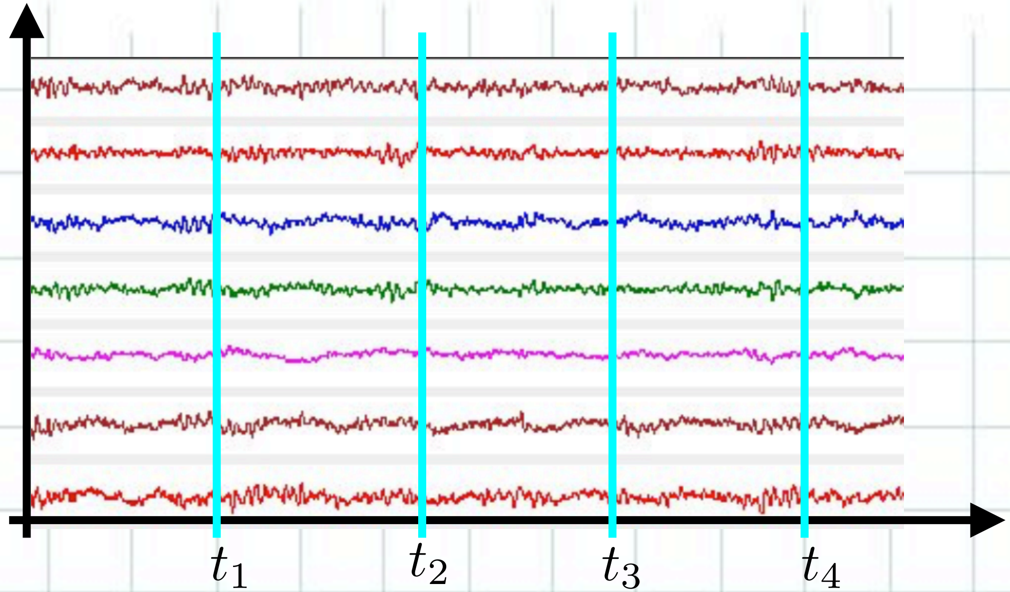


- Compute information theoretic causal interdependence $\mathbf{M}(t_k) = \{M_{ij}\}$
  - Time averaged correlations
  - Mutual information
  - MIME
  - PMIME
  - Etc.

- Assume $\mathbf{M}(t_k)$ contains the information of a dynamical matrix
- Do eigenvalue stability analysis on $\mathbf{M}(t_k)$

Temporal evolution of the ecosystems

Time evolution of

Distribution of active coupling strengths

Non correlated

Low connectivity

High connectivity

From Anderson & Jensen
J Theor Biol. **232**, 551 (2005)

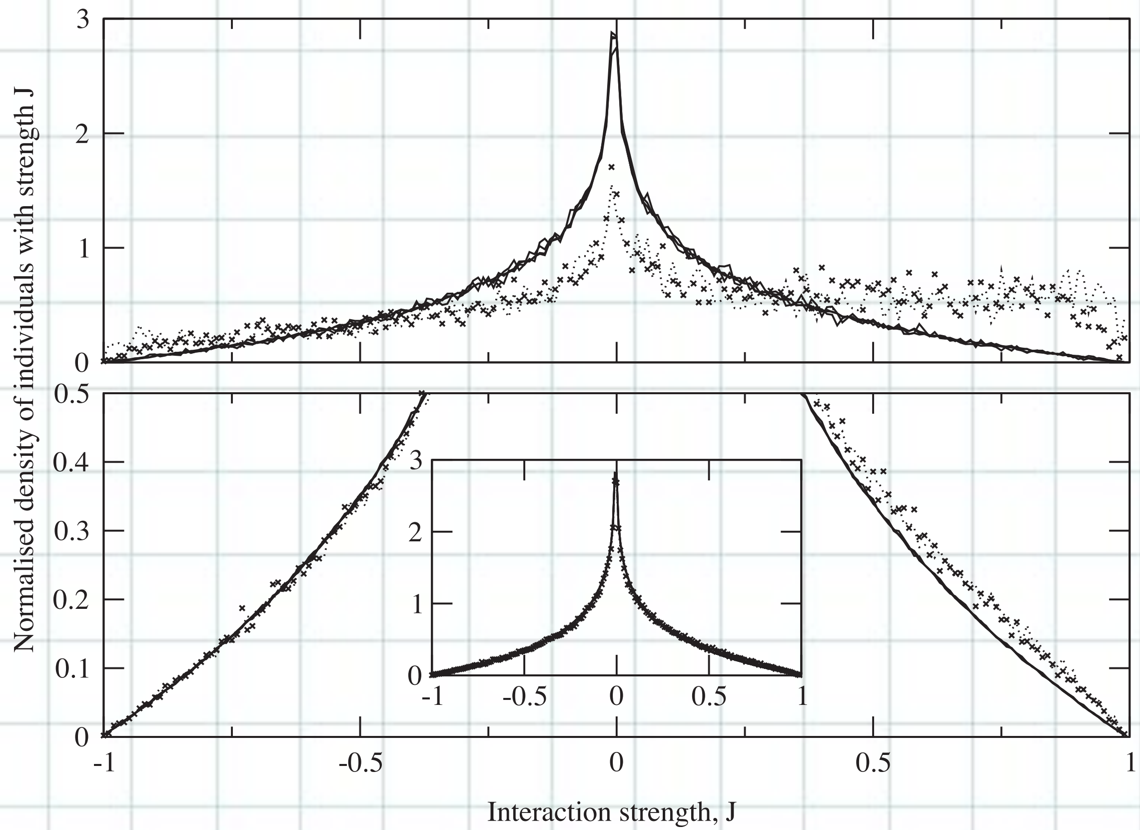


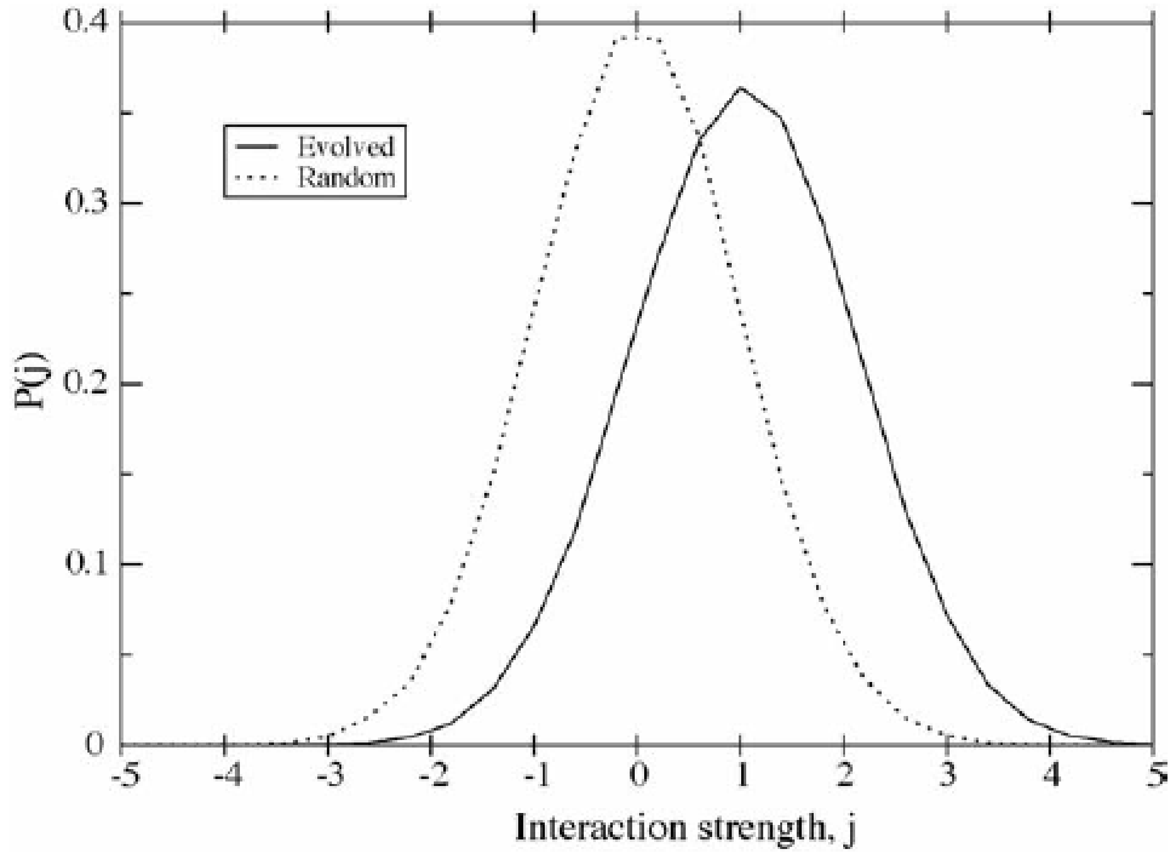
Fig. 3. Interaction distributions. Top: Distribution of interaction strengths between individuals for $\theta = 0.005$. Bottom: $\theta = 0.25$. Inset: Entire distribution. Solid lines, random; crosses, simulation at $t = 500$; dotted lines, simulation at $t = 500,000$. All plots are normalized so that their area is one. For high θ, a significant increase in positive interactions is seen. For low θ, a change is seen but for trivial reasons.

Time evolution of

Distribution of active coupling strengths

Correlated

High connectivity

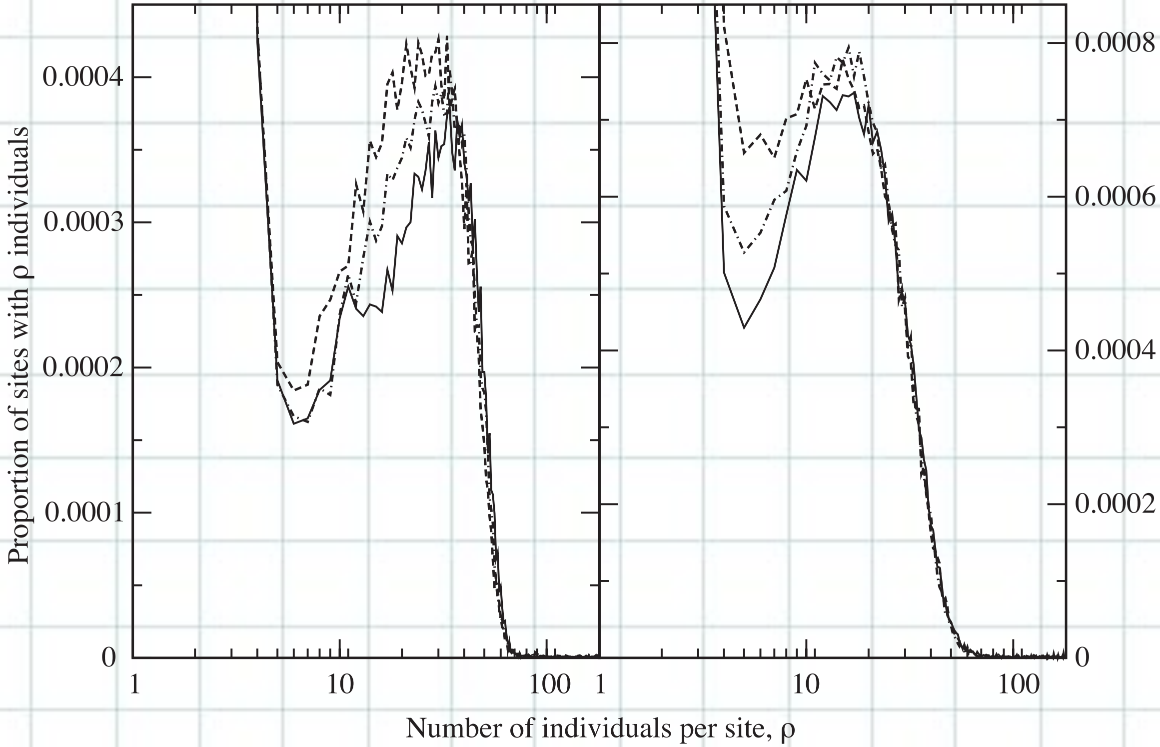


From Laird & Jensen, Ecol Compl. **3**, 253 (2006)

Time evolution of

Species abundance distribution

Non Correlated

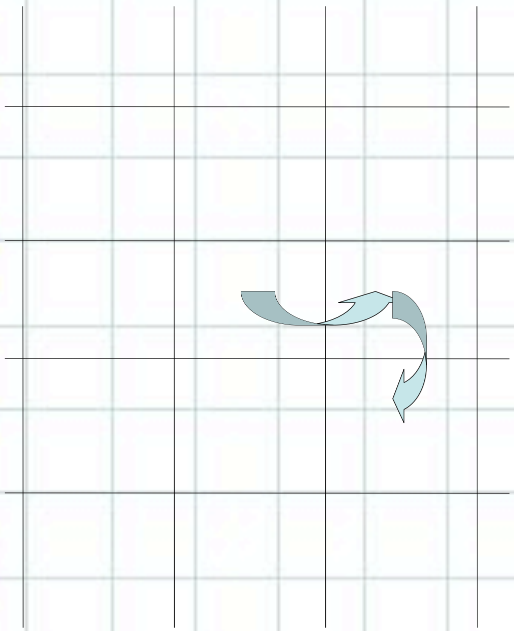


From Anderson & Jensen
J Theor Biol. **232**, 551 (2005)

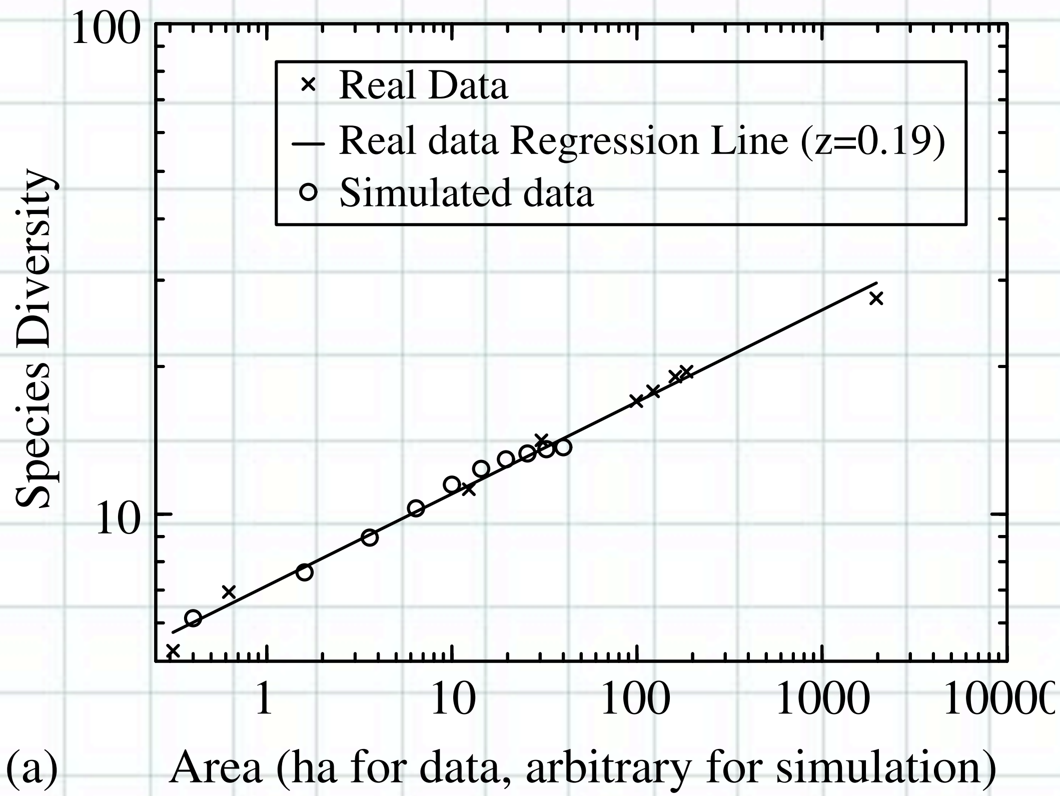
Fig. 5. Species abundance distributions. Species abundance distributions for the simulations only. Dashed line, $t = 500$; dashed–dotted line, $t = 5000$; solid line, $t = 500,000$. Low θ on the left, high θ on the right. The ecologically realistic log-normal form is only seen for high θ.

Low connectivity High connectivity

Species area relation: $\#S \propto A^z$



Dispersion by random walk



x plant data from Hertfordshire, see
ML Rosenzweig, Species Diversity in Space and Time, Cambridge University Press, 1995

From Lawson & Jensen, J Theo. Biol. **241**, 590 (2006)

The evolved degree distribution

Correlated

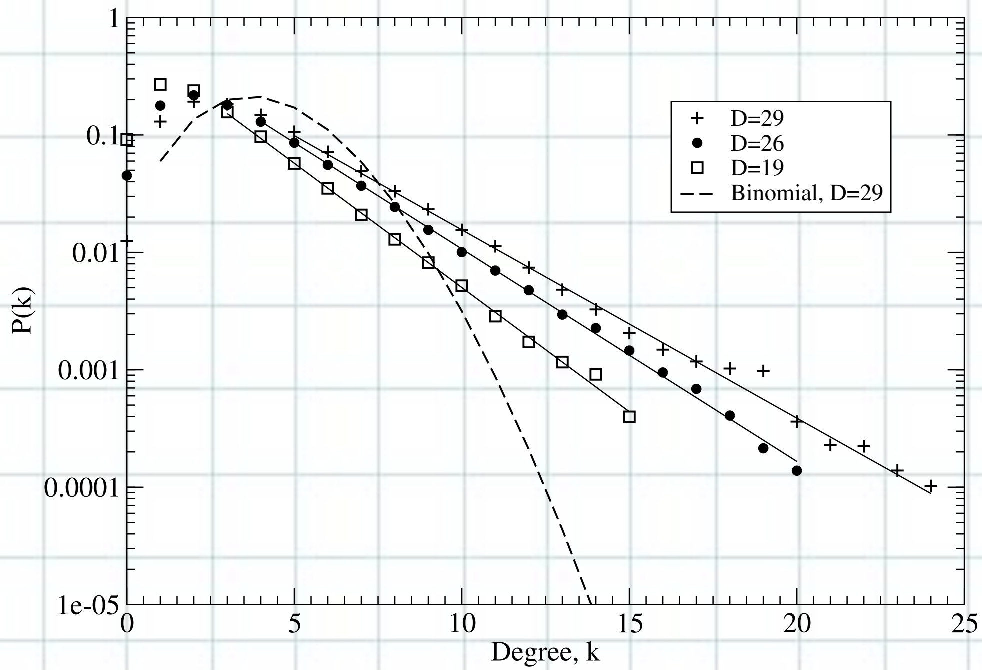
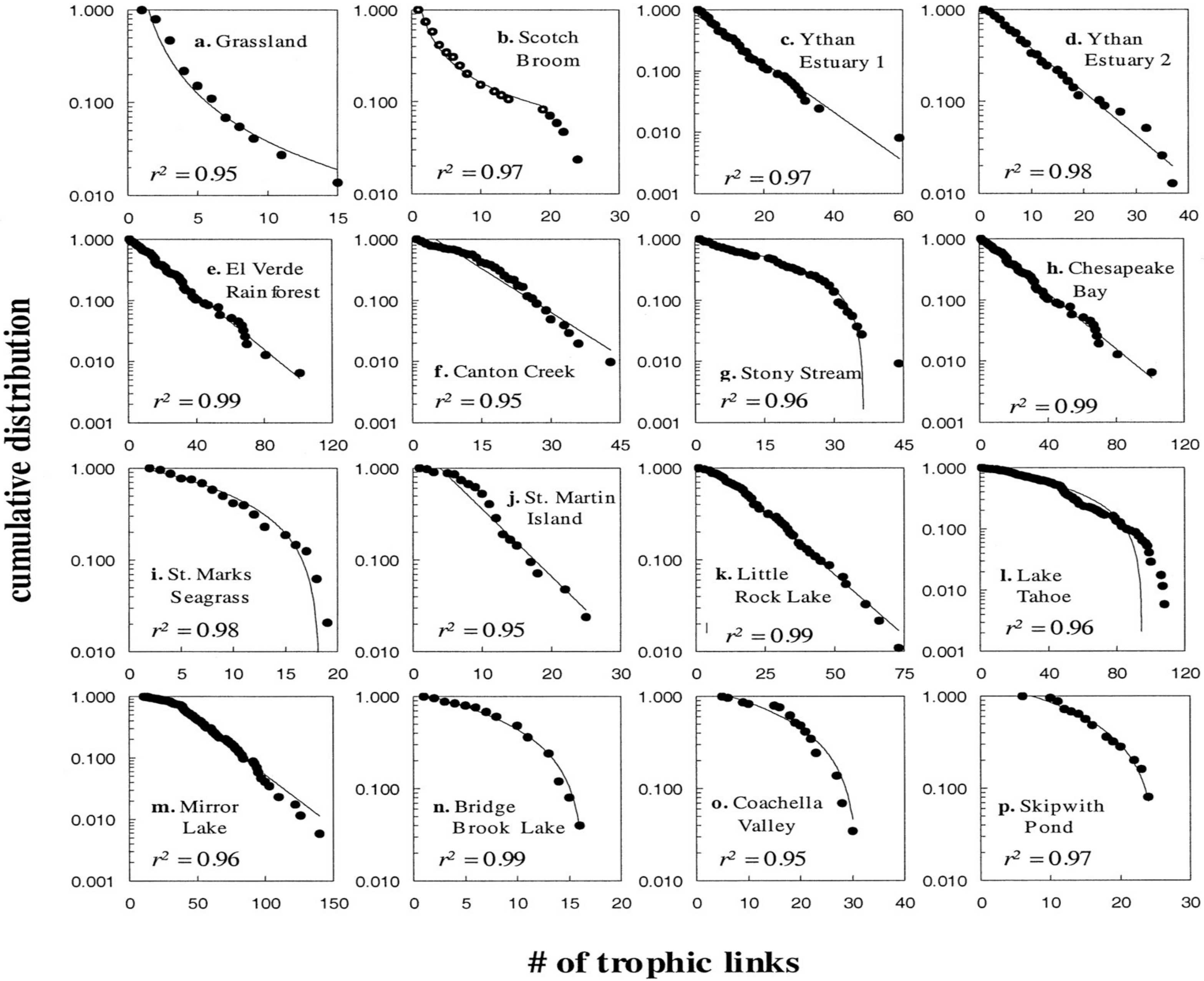


Figure 1: Degree distributions for the Tangled Nature model simulations. Shown are ensemble averaged data taken from all networks with diversity, $D = \{19, 26, 29\}$ over 50 simulation runs of 10^6 generations each. The exponential forms are highlighted by comparison with a binomial distribution of $D = 29$ and equivalent connectance, $C \simeq 0.145$ to the simulation data of the same diversity.

Exponential becomes 1/k in limit of vanishing mutation rate

From Laird & Jensen, Ecol. Model. In Press
See also Laird & Jensen, EPL, **76**, 710 (2006)



Dunne, Jennifer A. et al. (2002) Proc. Natl. Acad. Sci. USA 99, 12917-12922

The evolved connectance

Correlated

$$\langle C \rangle = \frac{\#\ \text{Edges}}{\#\ \text{Possible Edges}}$$

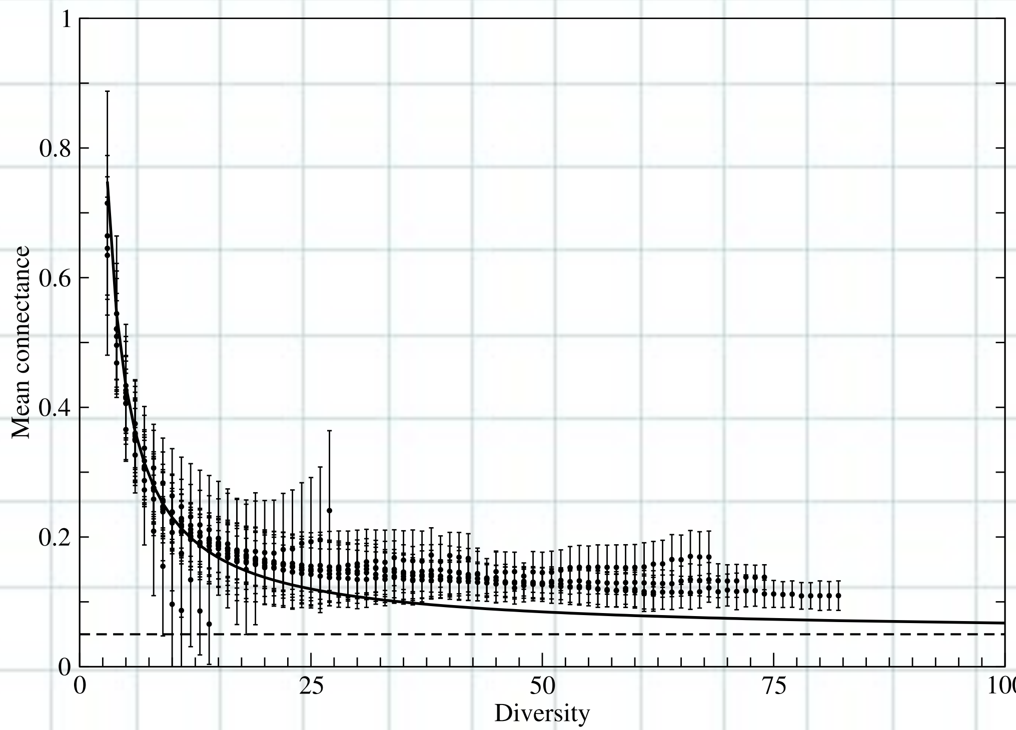
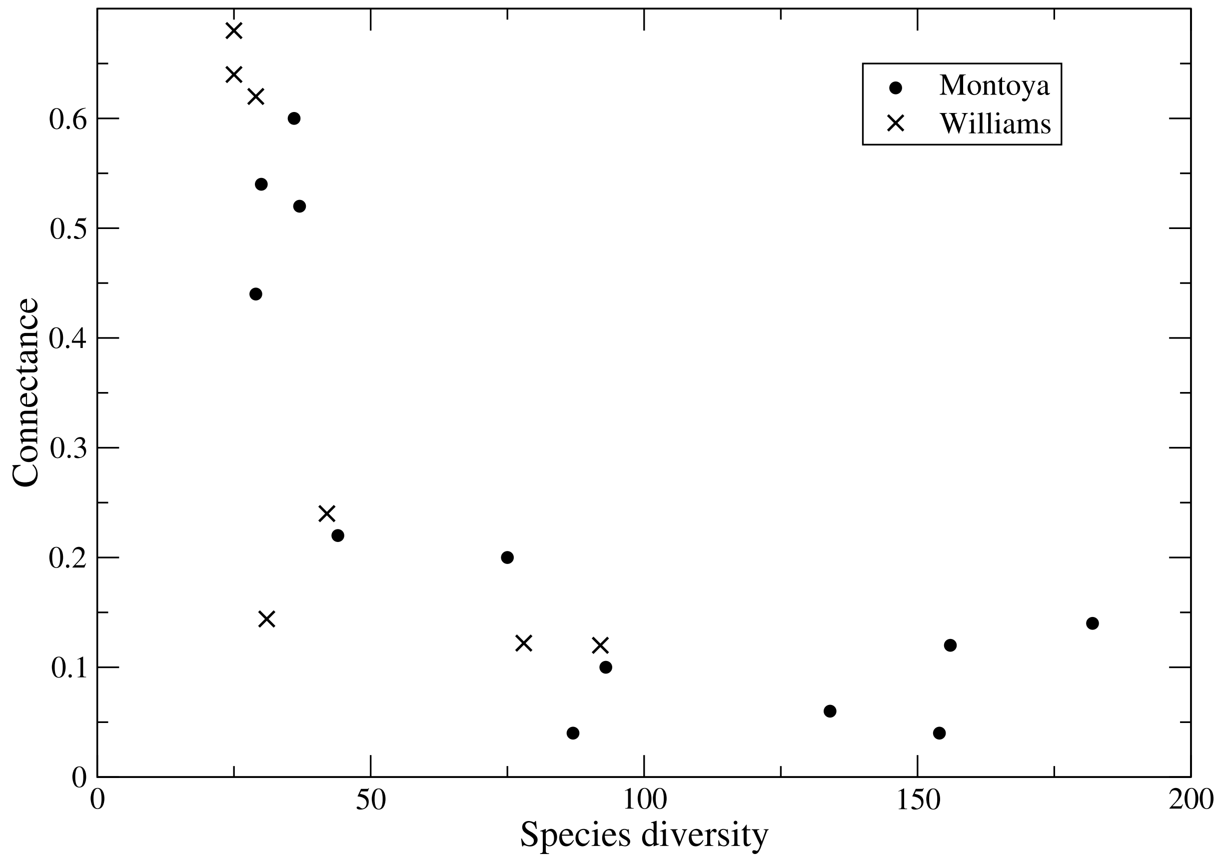


Figure 4: Plot of ensemble-averaged mean connectances, $< C >$ against species diversity. Error bars represent the standard error. The lower dotted line marks the null system connectance, $C_J = 0.05$, which the evolved systems clearly surpass. The overlaid functional form is that given by Eq.(8) using the correct background connectance, $C_J = 0.05$ and with a value of, $s = 5.5$ for the selection parameter.

From Laird & Jensen, Ecol Compl. **3**, 253 (2006)

Connectance



Montoya JM, Sole RV *Topological properties of food webs: from real data to community assembly models*, OIKOS **102**, 614-622 (2003)

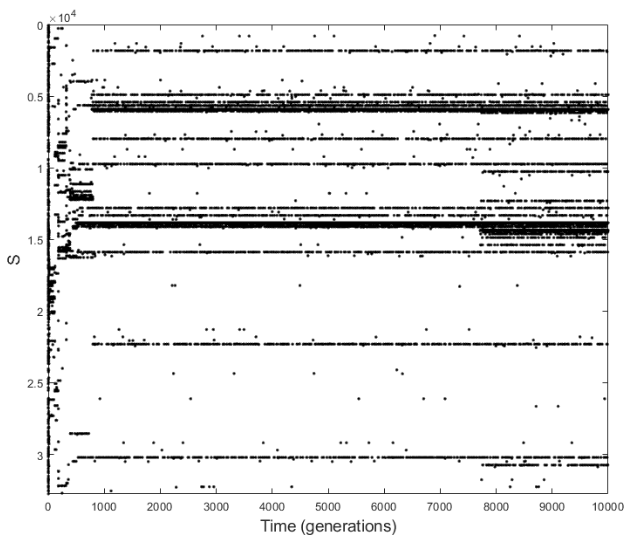
Williams RJ, Berlow EL, Dunne JA, Barabasi AL, Martinez ND *Two degrees of separation in complex food webs*, PNAS **99**, 12913-12916 (2002)

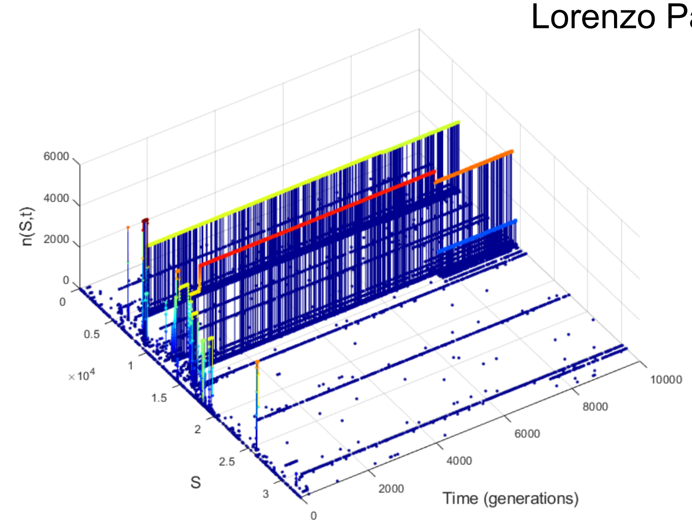
Simon Laird

Imperial College
London

The core and the cloud

Lorenzo Palmieri





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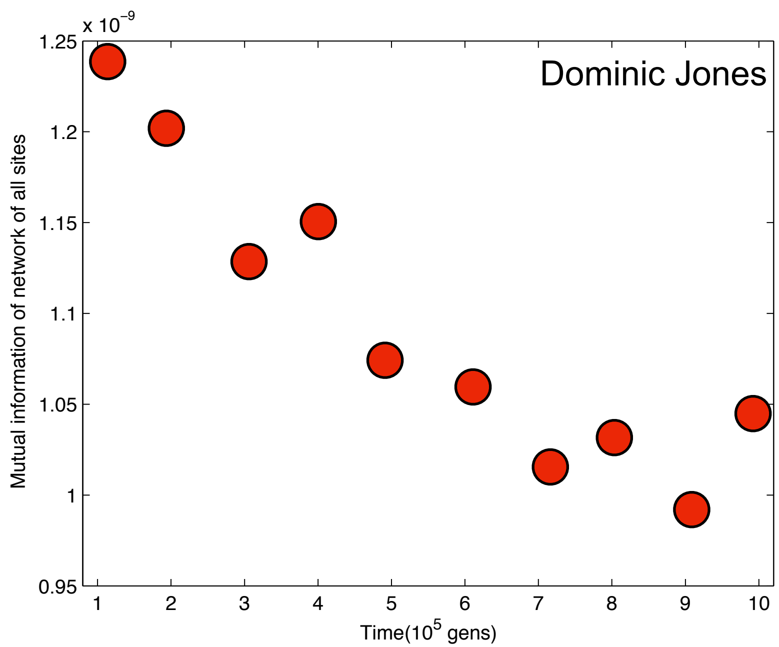
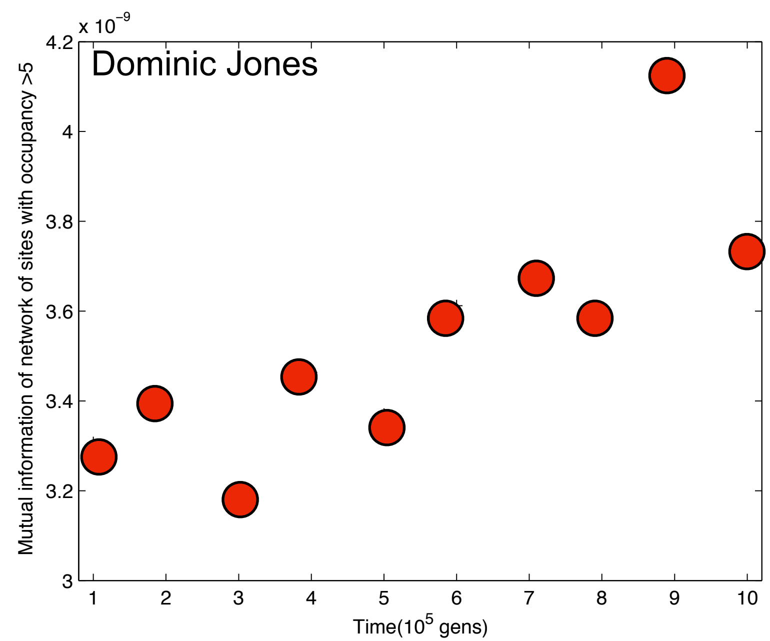
Dynamics - correlations:

The evolution of the correlations between couplings

$$I = \sum_{J_1, J_2} P(J_1, J_2) \log\left[\frac{P(J_1, J_2)}{P(J_1)P(J_2)}\right]$$



Mutual information of all



Mutual information of core

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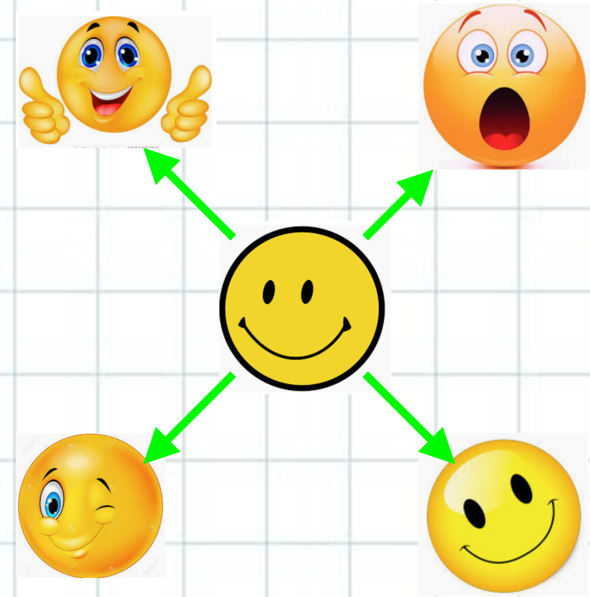
Multi-level selection
Top-down versus bottom-up



Inclusive fitness: Hamilton's inclusive fitness approach assigns to the focal individual the fitness effects of its behaviour on other related individuals,

and
Direct fitness: whereas the direct fitness approach assigns the fitness effects of other actors to the focal individual.

Group selection versus individual selection

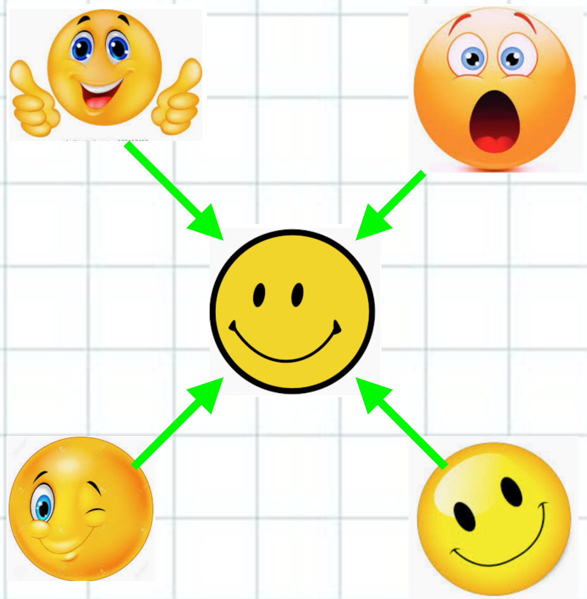
Is a species able to strive because of collective features
(collaboration between members, hunting asa a pack)

or is just that the individual members have some fortunate features (sharp teeth)

Multi-level selection

Top-down versus bottom-up

Inclusive fitness: Hamilton's inclusive fitness approach assigns to the focal individual the fitness effects of its behaviour on other related individuals,



and

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Group selection versus individual selection

Is a species able to strive because of collective features (collaboration between members, hunting asa a pack)

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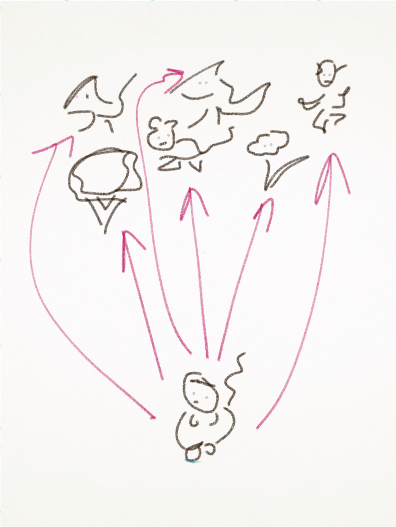
Complexity Science

The question:

At what level does selection act: individual versus group

Ecosystem

Situation 1



Situation 2

Situation 1: the selection success a linear sum of the “fitness” of the individuals

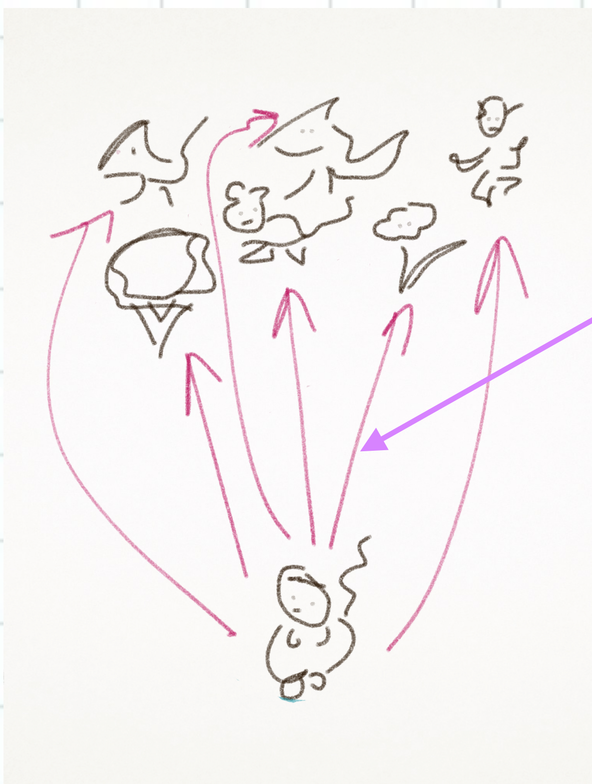
Situation 2: the the whole and the individual interwoven

Henrik Jeldtoft Jensen

Individual versus group

Situation 1
The selection success a
linear sum of the “fitness” of the individuals

Situation 2
The whole and the individual interwoven



Direction of information flow

Imperial College
London

Ref. Katharina Brinck & HJJ
arXiv:1807.00527

Complexity
Science

Top-down versus bottom-up

Time series X and Y:

X

Y

$$m_{S^\alpha}(t) = n(S^\alpha, t)$$

$$M_{S^\alpha}(t) = N(t) - n(S^\alpha, t)$$

Individual

Collective

Where $N(t) = \sum_\alpha n(S^\alpha, t)$

Now look at the information (causal) flow between the individual and the collective.

Complexity Science

Multi-level selection

Top-down versus bottom-up

Ref. Katharina Brinck & HJJ
arXiv:1807.00527

Information flow

- use Transfer Entropy

$$TE_{X\to Y} = \sum P(Y_{n+1}, Y_n, X_n) \ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)}$$

Time series X and Y:

Individual

$$m_{S^\alpha}(t) = n(S^\alpha, t)$$

$$M_{S^\alpha}(t) = N(t) - n(S^\alpha, t)$$

System

Complexity Science

Multi-level selection

Top-down versus bottom-up

Ref. Katharina Brinck & HJJ
arXiv:1807.00527

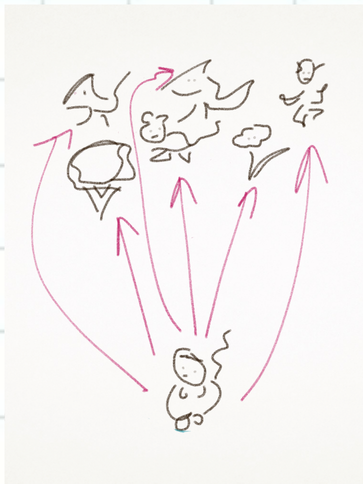
$$TE_{X\to Y} = \sum P(Y_{n+1}, Y_n, X_n) \ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)}$$

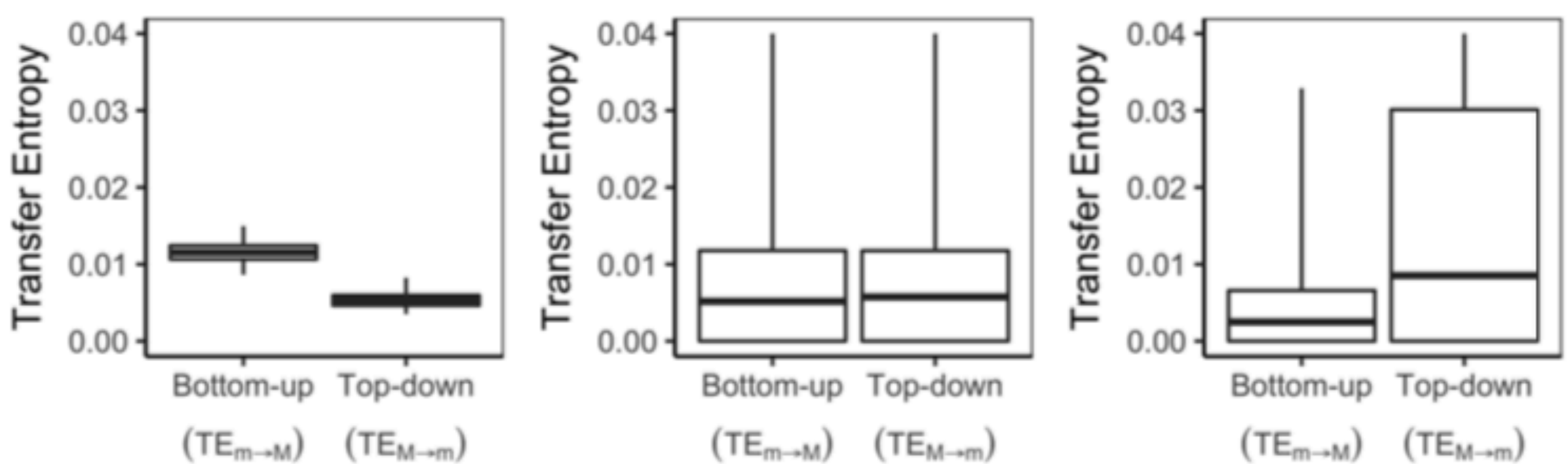
$$m_{S^\alpha}(t) = n(S^\alpha, t)$$
$$M_{S^\alpha}(t) = N(t) - n(S^\alpha, t)$$

Information flow

- From individual to system: m $\rightarrow$ M
- From system to individual: M $\rightarrow$ m

The behaviour of top-down versus bottom-up





(a) Early successional stage (b) Medium successional stage (c) Late successional stage

Summary & Conclusion

- TaNa model fully stochastic evolutionary dynamics
  - ability to reproduce determined through interactions
  - population moves around in type space
- Collective systemic adaptation
  - collective adaptation more important as the eco-system age.

Various version of the TaNa frame work has appeared over the years.

Some examples:

- Rikvold et al. parallel update → 1/f in the fossil record
- Rikvold et al. & Brinck: include trophic levels → food webs
- Sibani et al.: phenotypical aspects → organisation and cultural evolution
- Laird, Robliano, Sibani et al.: correlated interrelations →
- ecosystems, economy, sustainability
- Arthur: type specific carrying capacity → Gaia
- Schulman: horizontals gene-transfer → anti-biotic resistance

For a review see HJJ arXiv:1807.04228

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London

Complexity Science

Thank you

Collaboration also with

P. Anderson, E. Arcaute, K. Brinck,
A. Cairoli, K. Christensen, S.A. di Collobiano,
B. J. Grujic, M. Hall, D. Jones, S. Laird,
D.J. Lawson, D. Piovani, R.D. Robliano, P. Sibani
and P. Vazquez.

Recent Review

H.J. Jensen,
Tangled Nature: A model of emergent structure and temporal mode among co-evolving agents.
European Journal of Physics **40**, 014005 (2018)