Imperial College
London

The Tangled Nature Model of Evolutionary Ecology:

(Is the approach of Statistical Mechanics relevant to the New Ecology Systems Perspective project.)

Henrik Jeldtoft Jensen
Institute for Mathematical Sciences and Dept of Mathematics
Imperial College London
United Kingdom

Collaborators:
Daniel Lawson, Simon Laird, Paul Anderson, Kim Christensen, Matt Hall, Simone A di Collobiano,

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 characteristics: SAD, SAR, Connectance,...

Interaction and co-evolution

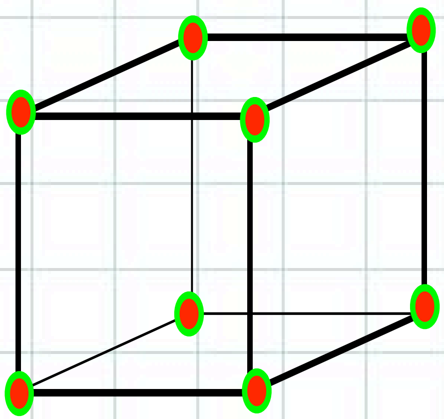
The Tangled Nature model

- Individuals reproducing in type space
- Different types influence the livelihood of each other

Definition

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

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



$L = 3$

Dynamics – a time step

Annihilation

Choose indiv. at random, remove with probability

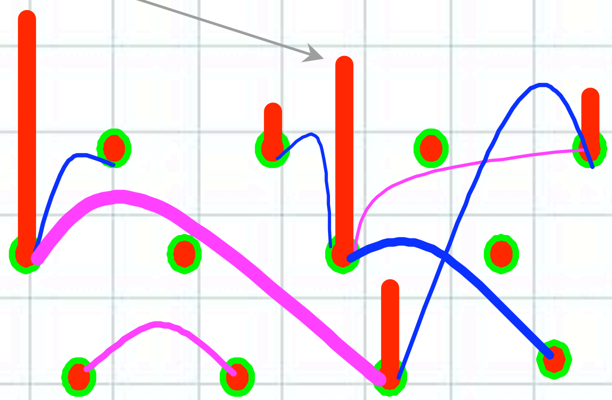
$$p_{kill} = const$$

Reproduction:

- Choose indiv. at random
- Determine

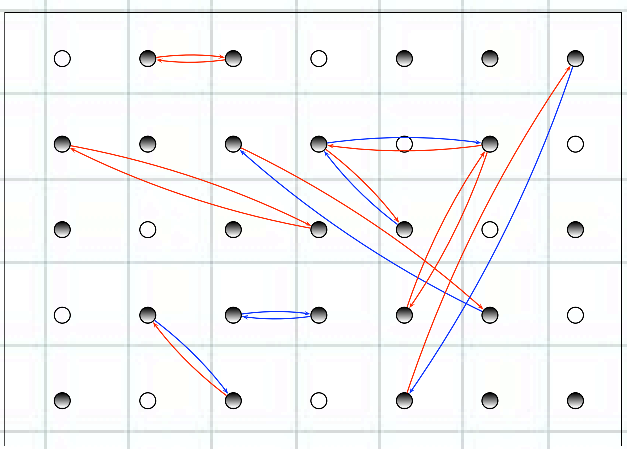
$$H(\mathbf{S}^\alpha, t) = \frac{k}{N(t)} \sum_{\mathbf{S}} J(\mathbf{S}^\alpha, \mathbf{S}) n(\mathbf{S}, t) - \mu N(t)$$

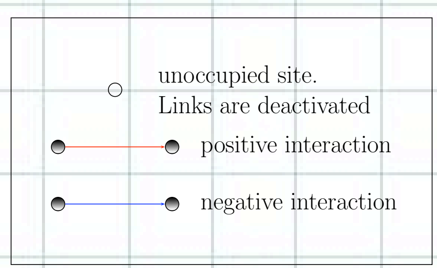
$n(\mathbf{S}, t) =$ occupancy at the location $\mathbf{S}$

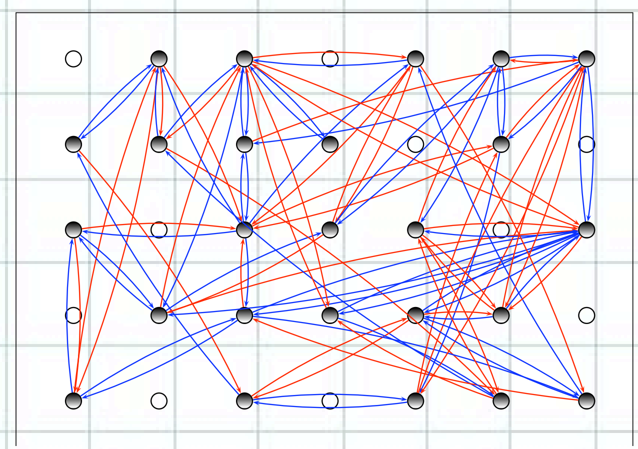


The coupling matrix J(S,*S'*)

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

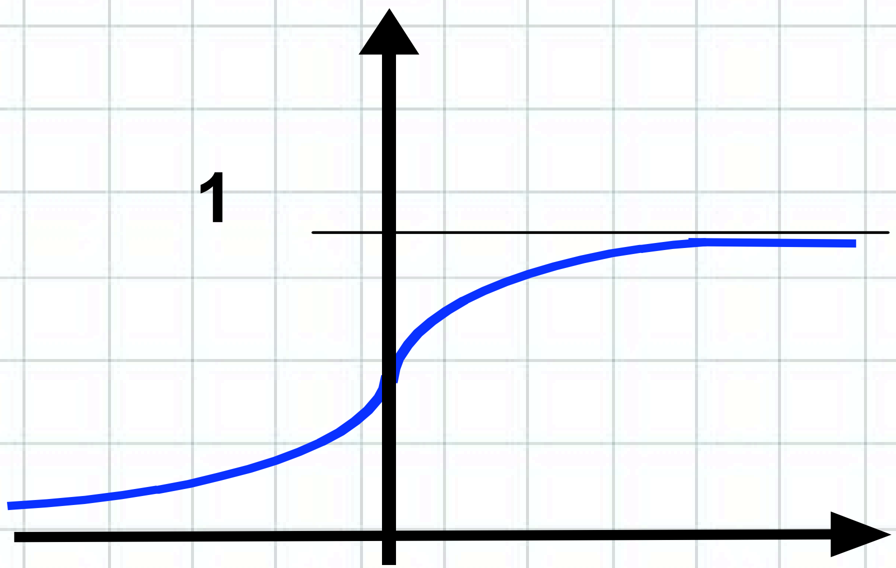






from $H(\mathbf{S}^{\alpha},t)$ reproduction probability

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



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

Asexual reproduction:

Replace $\mathbf{S}^{\alpha}$ **by two copies** $\mathbf{S}_1^{\alpha}$, $\mathbf{S}_2^{\alpha}$

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

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

Mutations

- Mutations occur with probability

p_{mut} , i.e.

$$S_i^\gamma \mapsto -S_i^\gamma$$

See also work on similar models by Rikvold et al.

RESULTS

Segregation in genotype space

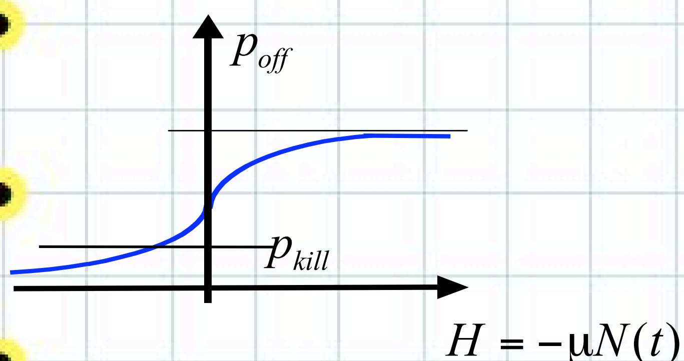
Initiation

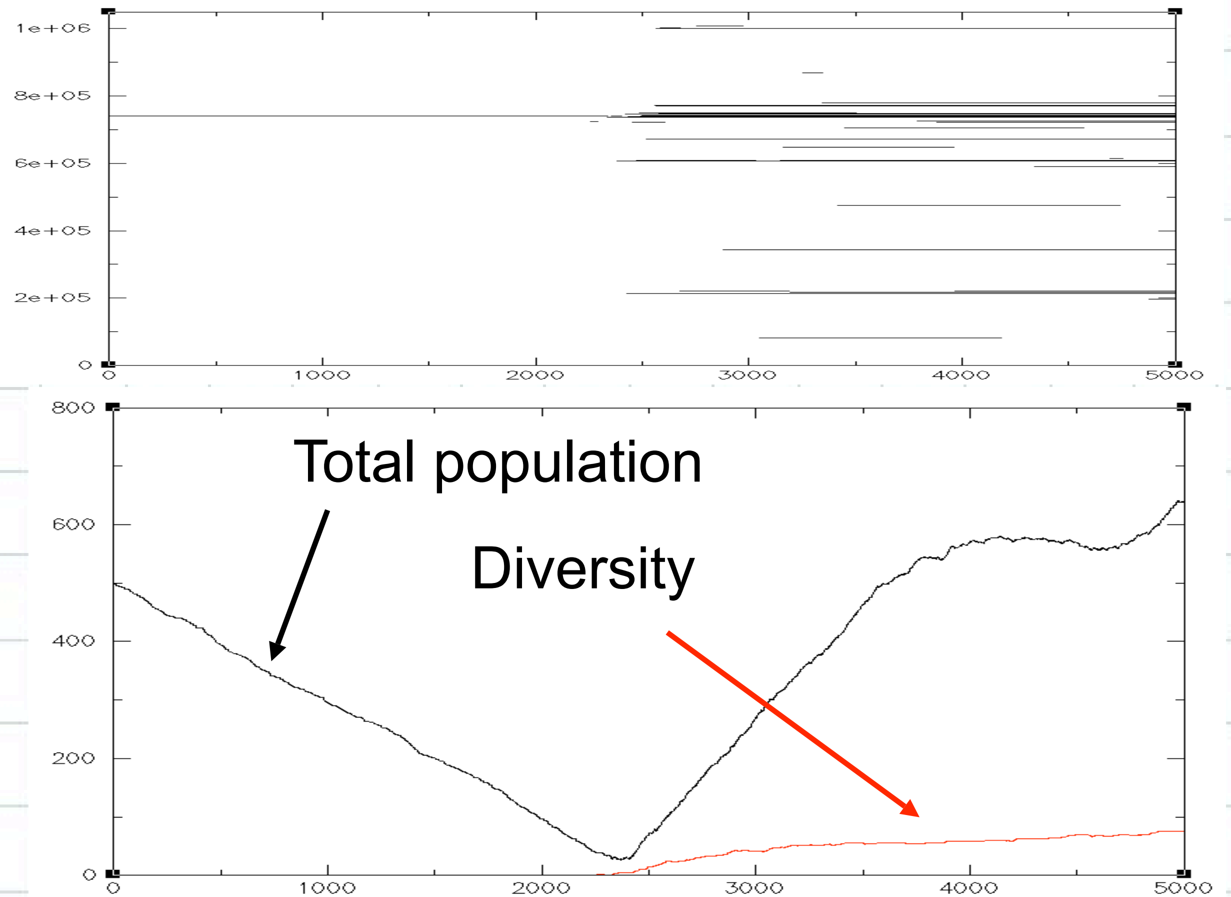
Only one genotype

Jn term = 0

$$H = \frac{k}{N(t)} \sum_{s} Jn - \mu N(t)$$

N(t) adjusts



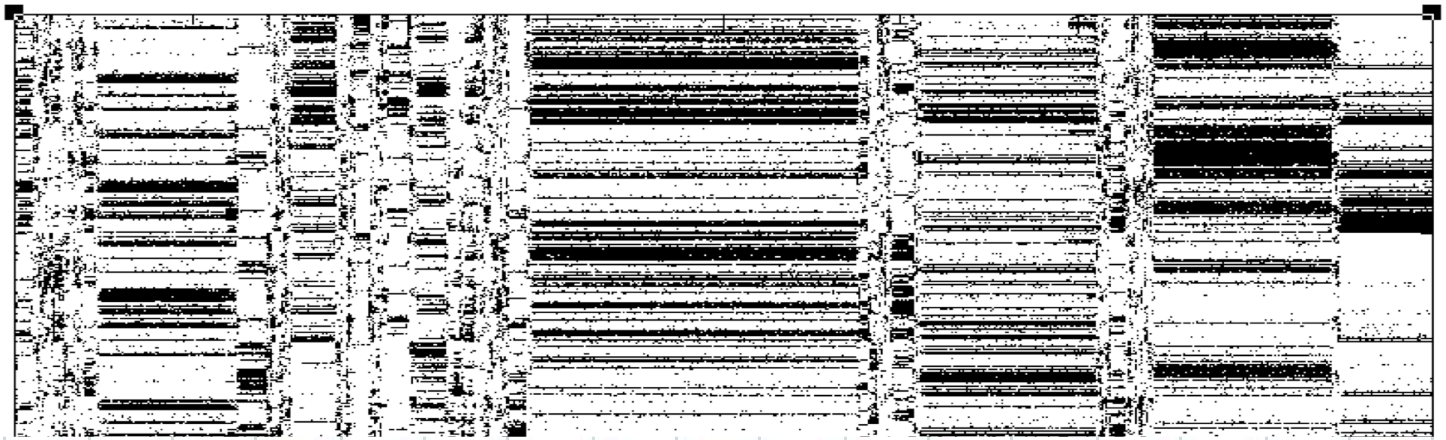


Time steps

Macro dynamics:

Non correlated

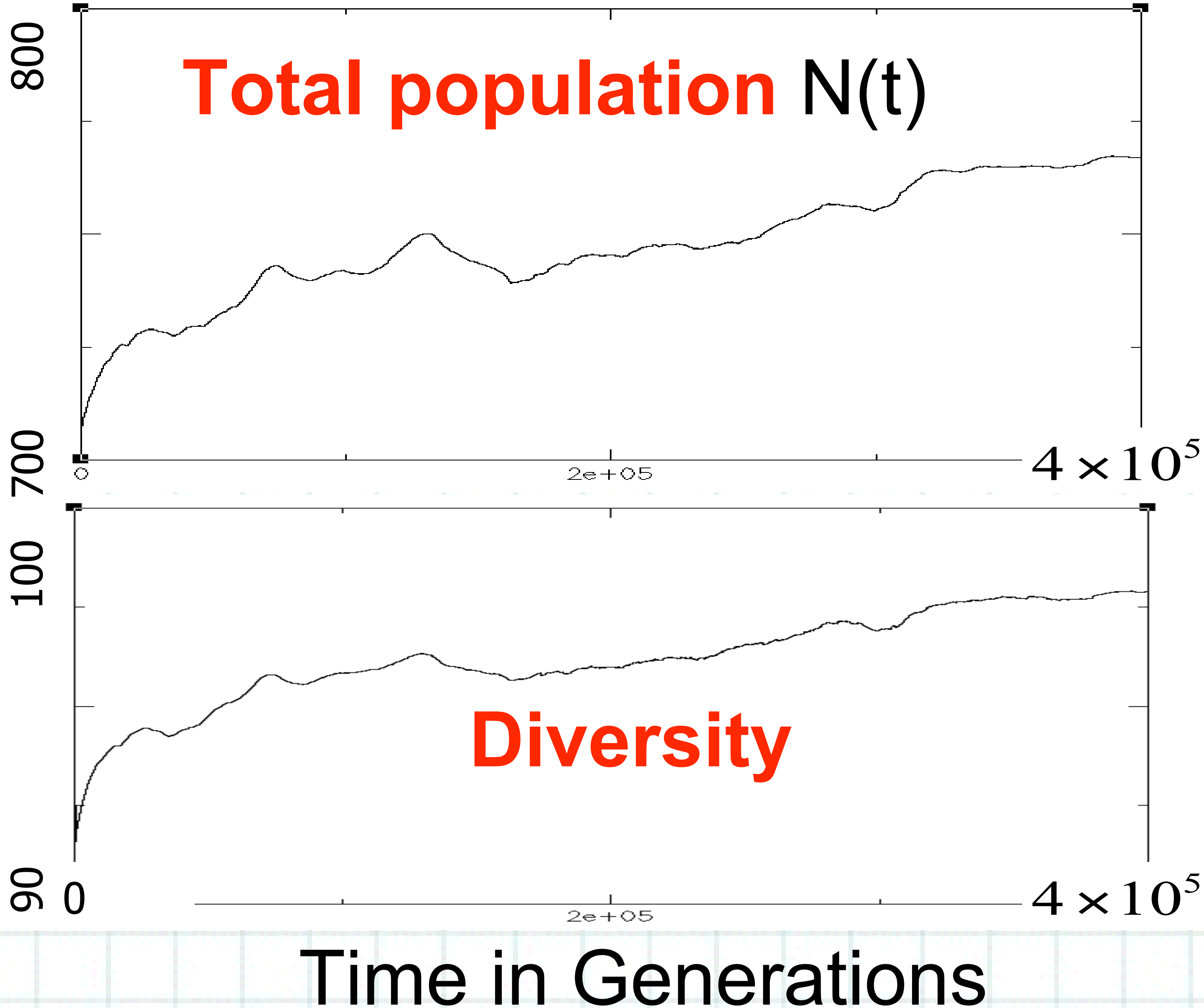
Graph courtesy to
Matt Hall



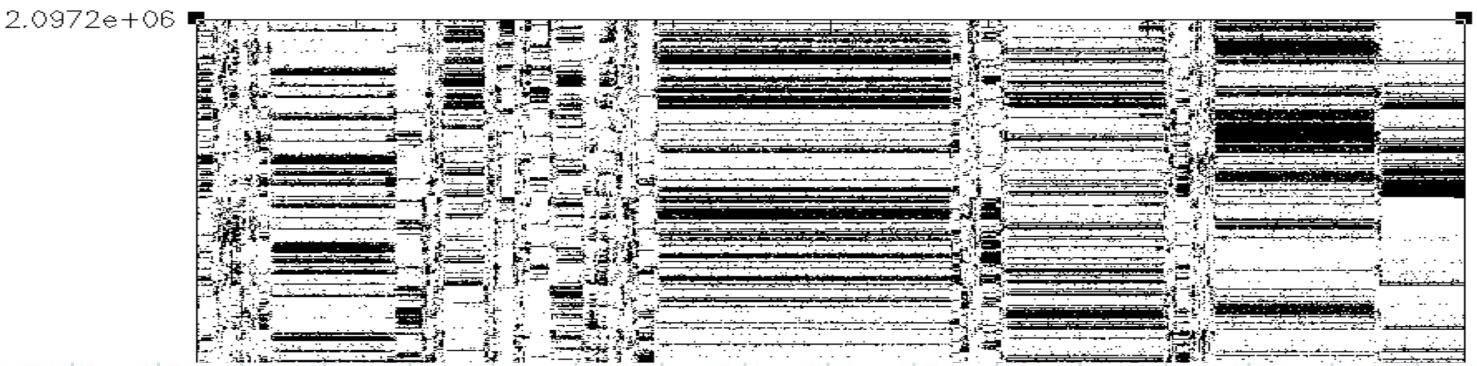
generations

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

Time dependence (Average behaviour)

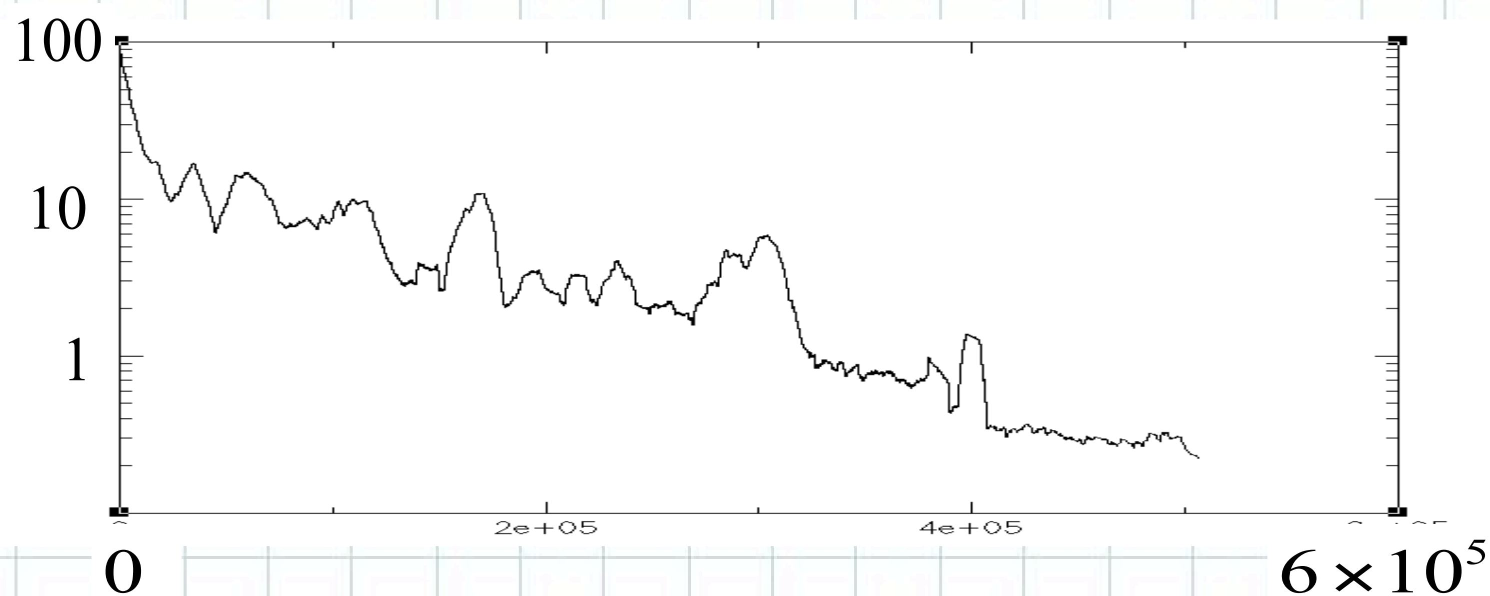


Intermittency:



# of transitions in window

Matt Hall



1 generation

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

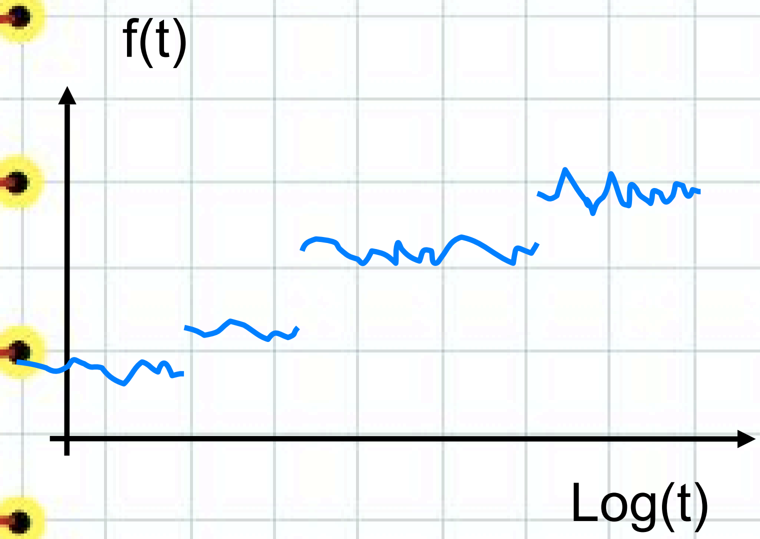
Complex dynamics:

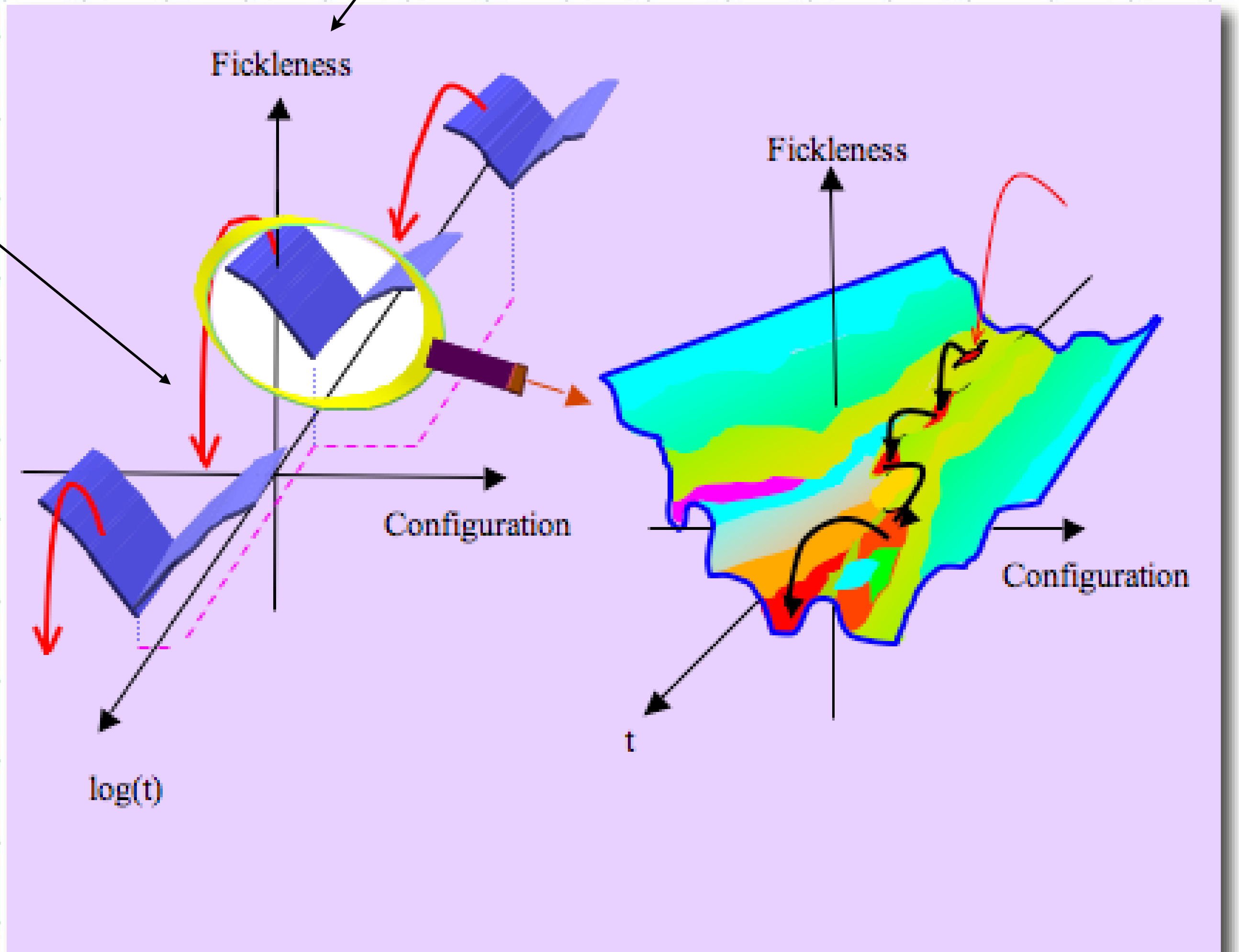
Exergy ? ?

Intermittent, non-stationary

Jumping through collective adaptation space: quake driven

Transitions



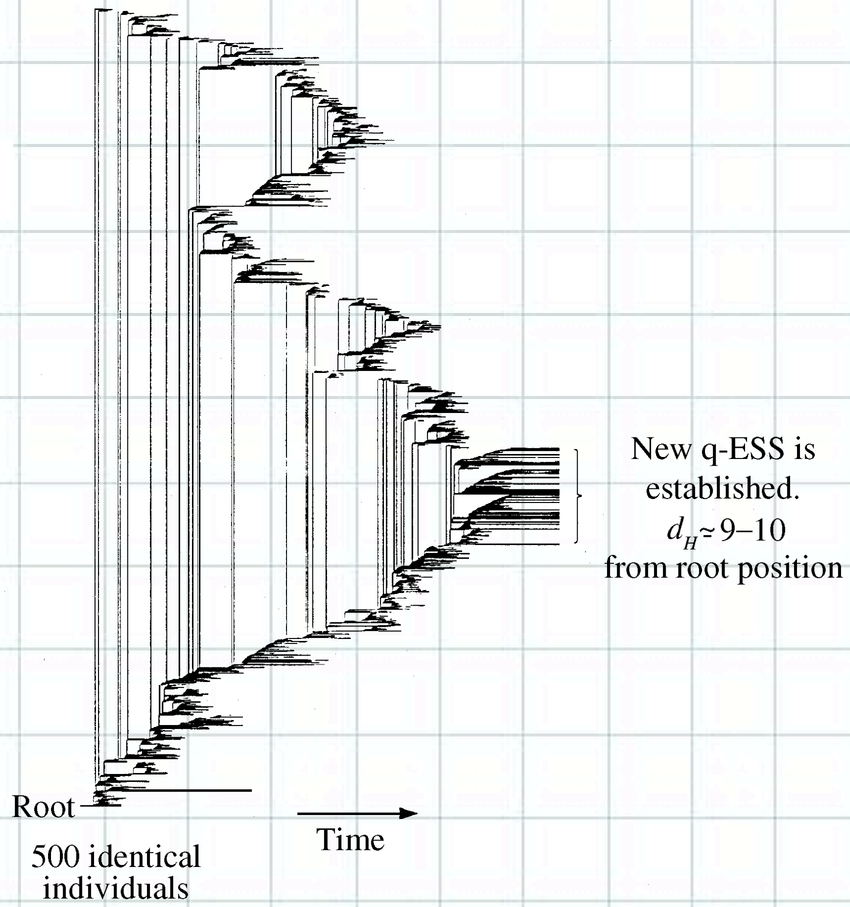


Henrik Jeldtoft Jensen

Macro dynamics - the transitions

Non correlated

Graph courtesy to
Matt Hall



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 $S' \neq S$

Macro dynamics:

Correlated

Simon Laird

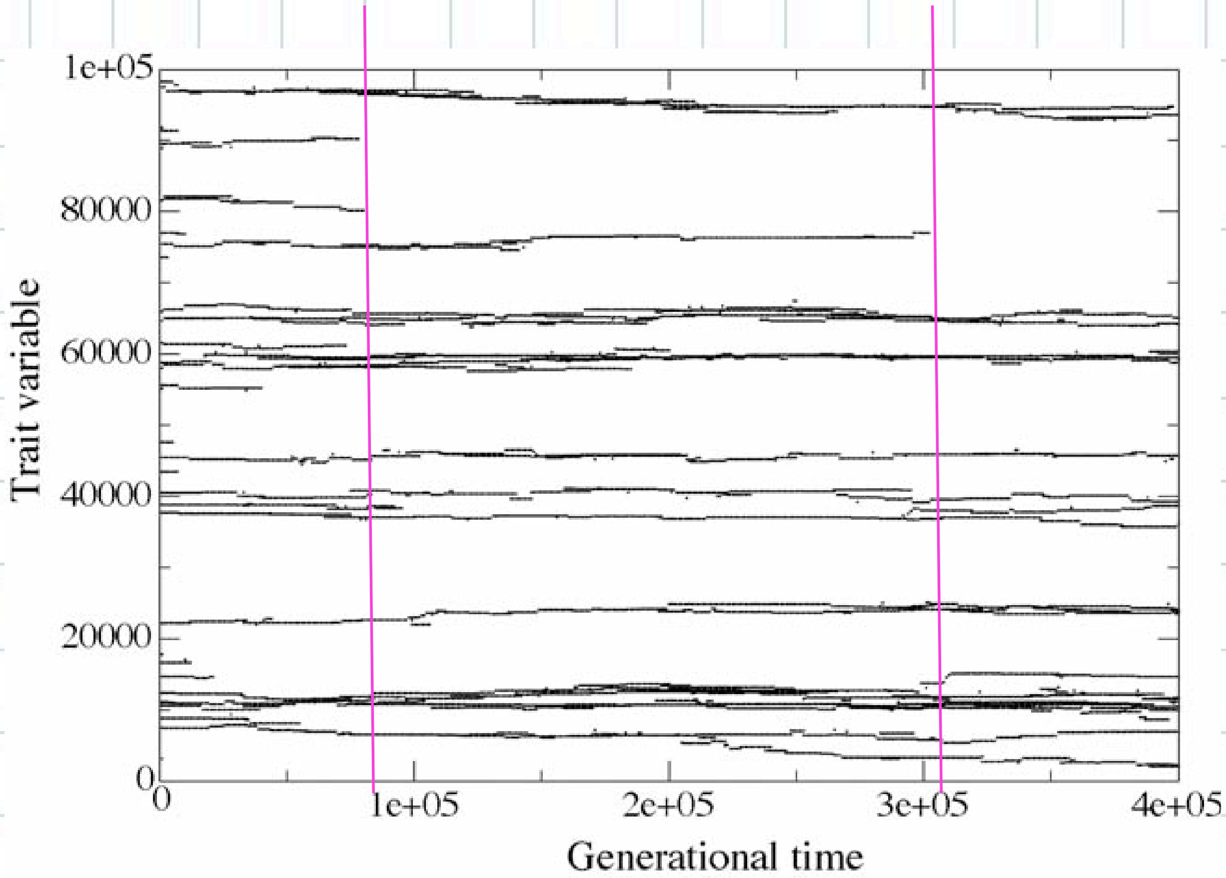


Fig. 1 – An occupation plot of a single run for a system with *R* = 10,000. For each timeslice a point appears where a phenotype is in existence but as the full space is in 16 dimensions a projection onto a single trait is used.

Time evolution of

Distribution of active coupling strengths

Non correlated

Low connectivity

High connectivity

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

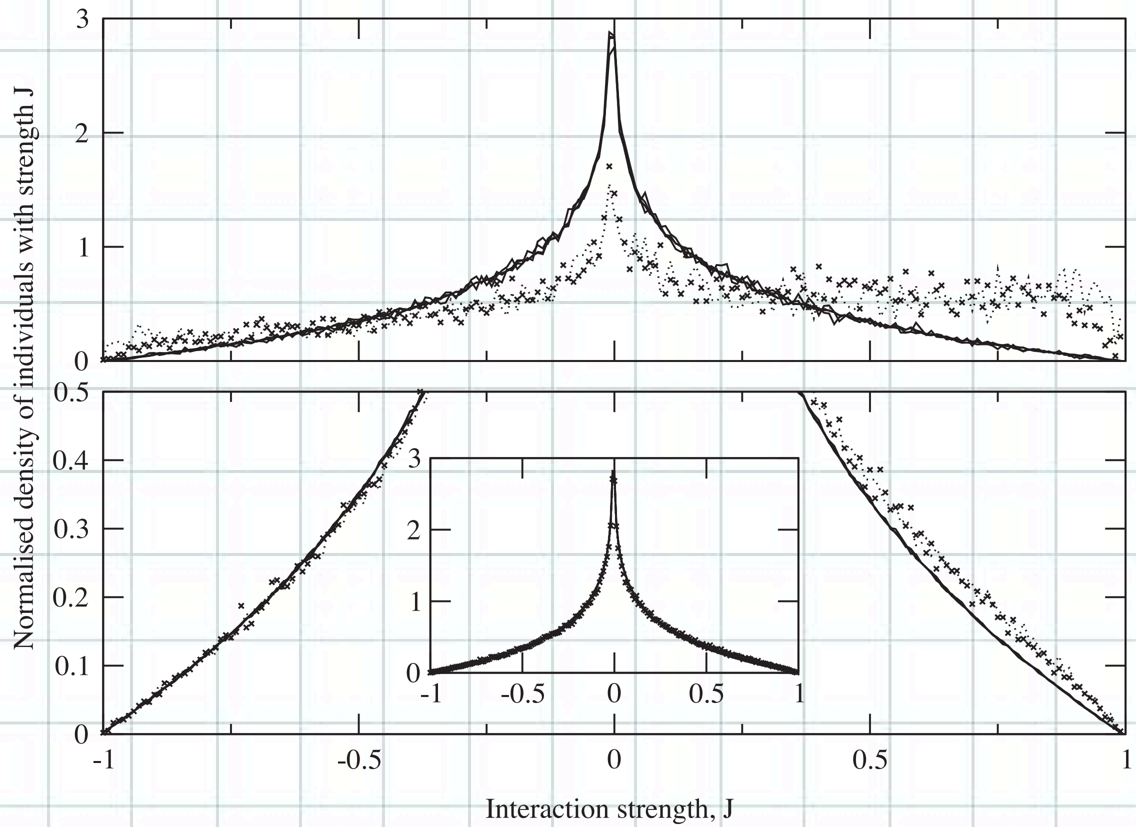


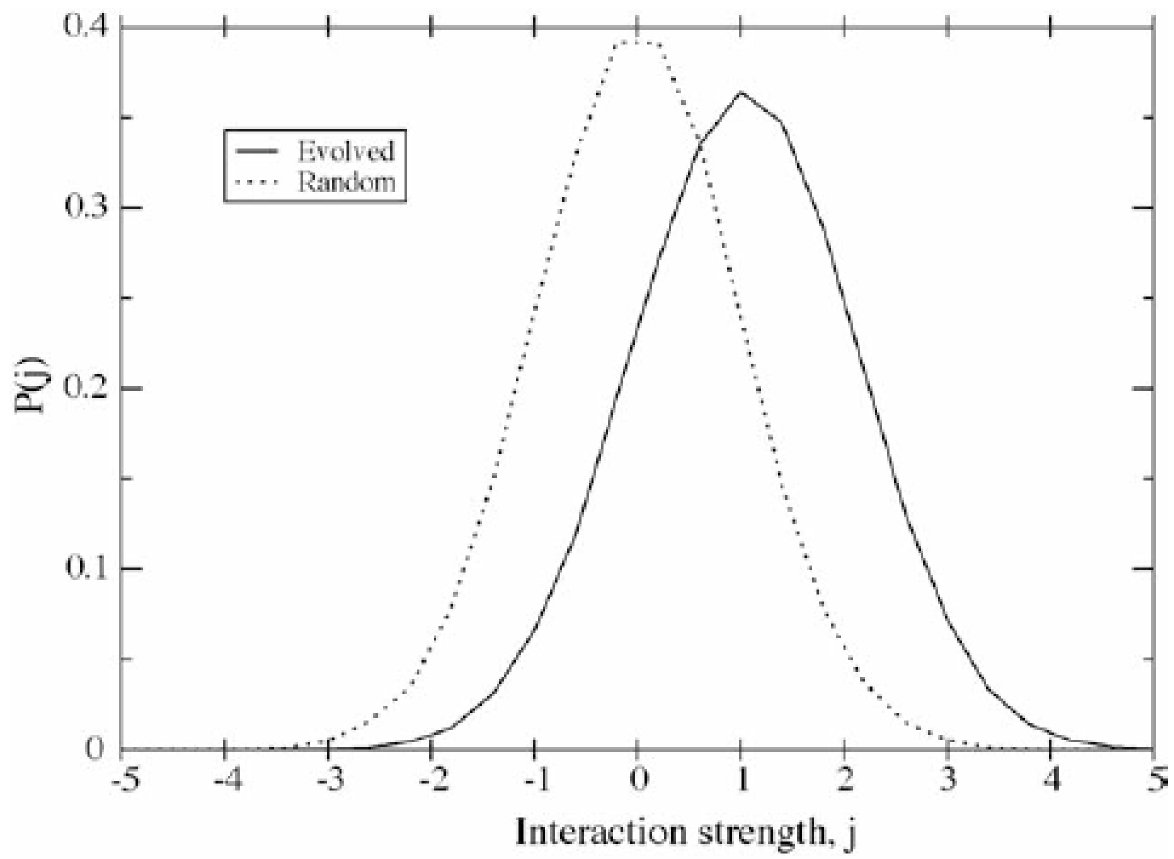
Fig. 3. Interaction distributions. Top: Distribution of interaction strengths between individuals for $\theta = 0.005$. Bottom: $\theta = 0.25$. Inset: Entire distribution. Solid lines, random; crosses, simulation at $t = 500$; dotted lines, simulation at $t = 500,000$. All plots are normalized so that 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

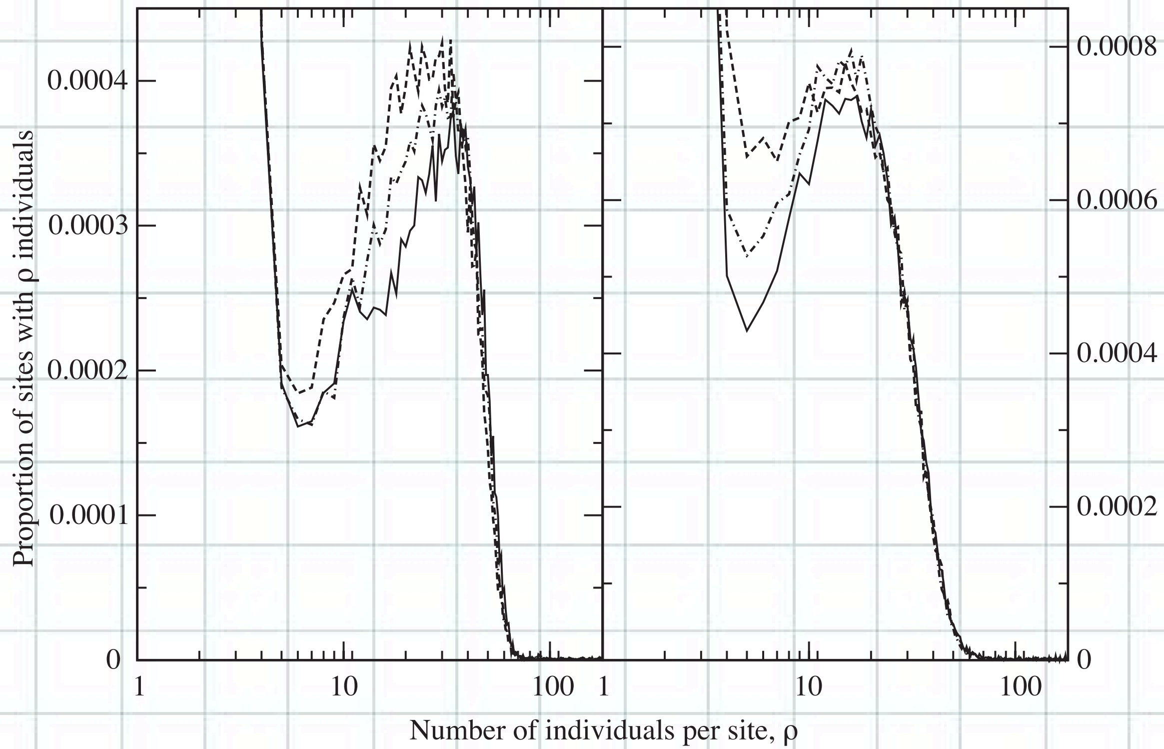


Fig. 5. Species abundance distributions. Species abundance distributions for the simulations only. Dashed line, $t = 500$; dashed–dotted line, $t = 5000$; solid line, $t = 500,000$. Low θ on the left, high θ on the right. The ecologically realistic log-normal form is only seen for high θ.

Low connectivity High connectivity

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

Time evolution of

Degree distribution

Non Correlated

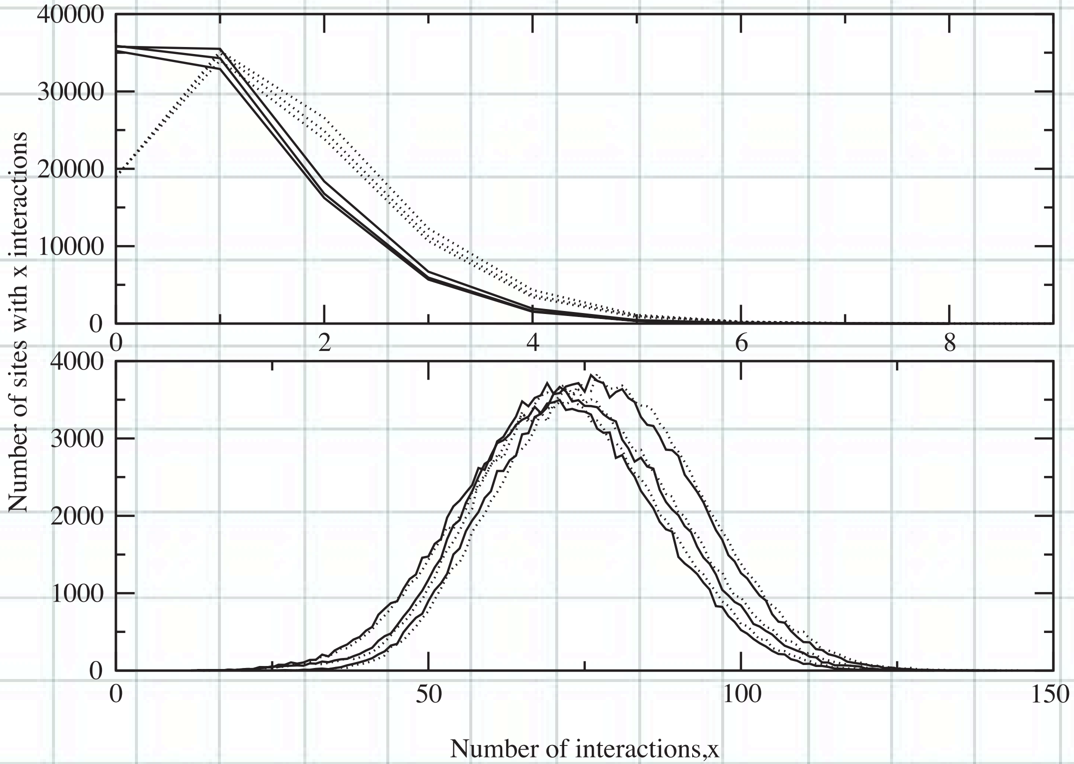


Fig. 2. Degree histograms. Top: Degree histogram for $\theta = 0.005$. Bottom: $\theta = 0.25$. Solid lines, random; dotted lines, simulation. From the left, the pairs of curves are for $t = 500$, 5000 and 500,000. At later times, the number of active links increases for both the simulation and random data.

Low connectivity

High connectivity

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

The evolved degree distribution

Correlated

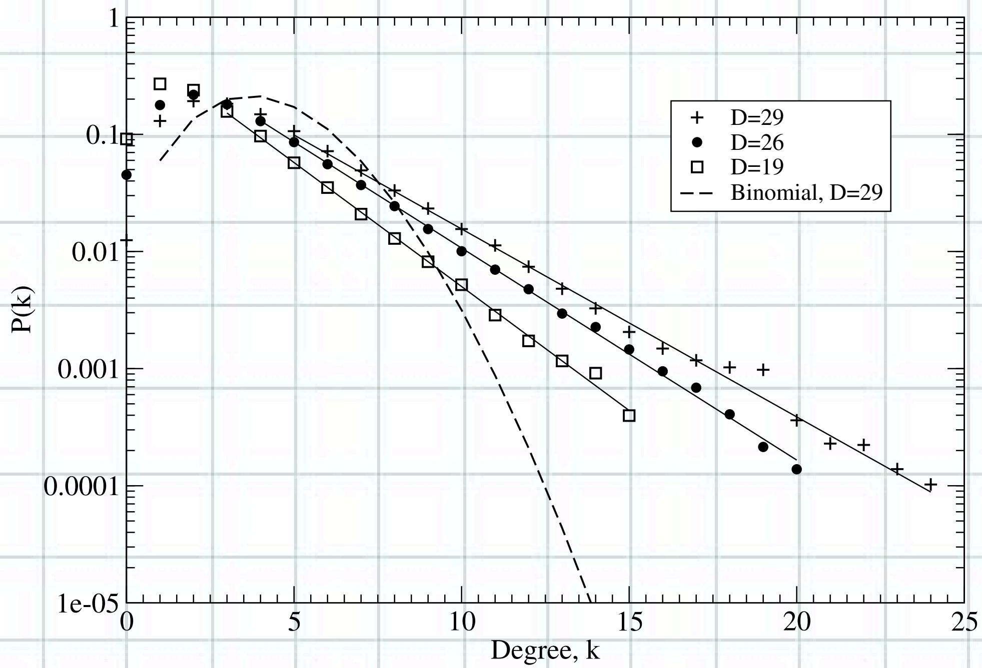


Figure 1: Degree distributions for the Tangled Nature model simulations. Shown are ensemble averaged data taken from all networks with diversity, $D = \{19, 26, 29\}$ over 50 simulation runs of 10^6 generations each. The exponential forms are highlighted by comparison with a binomial distribution of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

Diversity and interaction

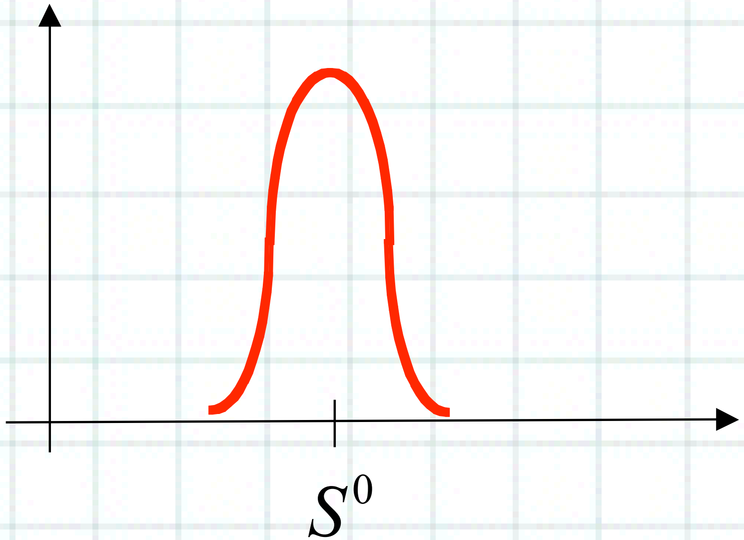
Weight function $$H_0(\mathbf{S}^\alpha,t) = \frac{k}{N(t)}\sum_{\mathbf{S}} J(\mathbf{S}^\alpha,\mathbf{S})n(\mathbf{S},t) - \mu N(t)$$

$$H(S^\alpha) = H_0 + \begin{cases} \varepsilon\, E(S^\alpha)\dfrac{n(S^\alpha,t)}{N(t)} \\ \varepsilon\, E(S^\alpha) \end{cases}$$

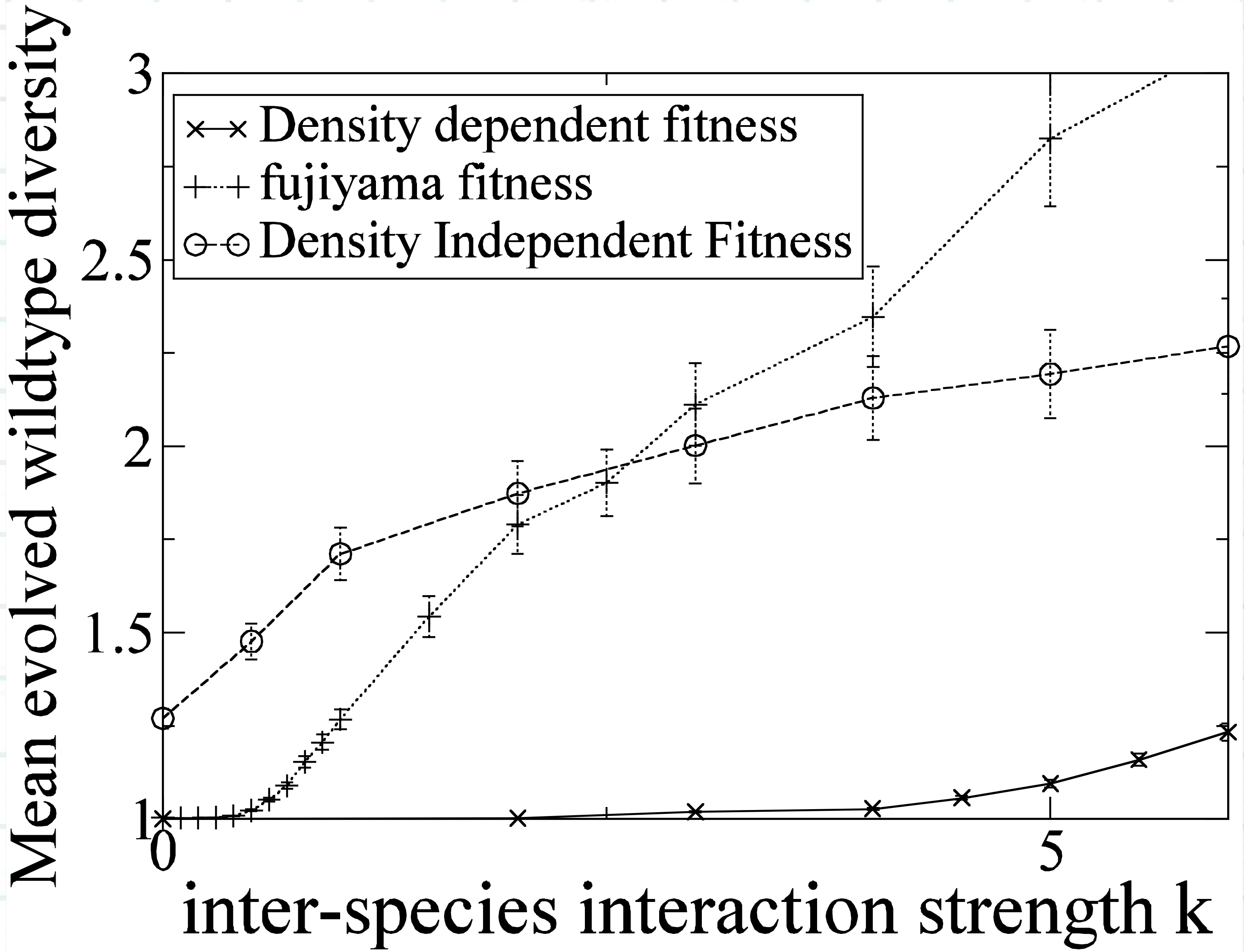
Density dependent

Density independent
Fujiyama lanscape

with $E \in [0,1]$ and ε a scale parameter



Diversity and interaction



From Lawson, Jensen & Kaneko, J Theo. Biol. **243**, 299 (2006)

Origin of threshold in k:

A balance between inter-species and intra-species Interaction.

$$H = H_0 + \varepsilon\, E(S^\alpha, t)\frac{n(S^\alpha, t)}{N(t)},$$

where $E \in [0,1]$ and

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

Mean field sketch

Weight function for $D = 1$: $\mathrm{H}_1 = \varepsilon E - \mu N_1$

Weight function for $D = 2$: $H_2 = \frac{k}{N_2} J n_2 + \varepsilon E - \mu N_2$

Assume $n_2 = \frac{1}{2} N_2$ and $N_1 \approx N_2$ then

$$H_1 > H_2 \Rightarrow k > \frac{\varepsilon\, E}{J}$$

The evolved connectance

Correlated

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

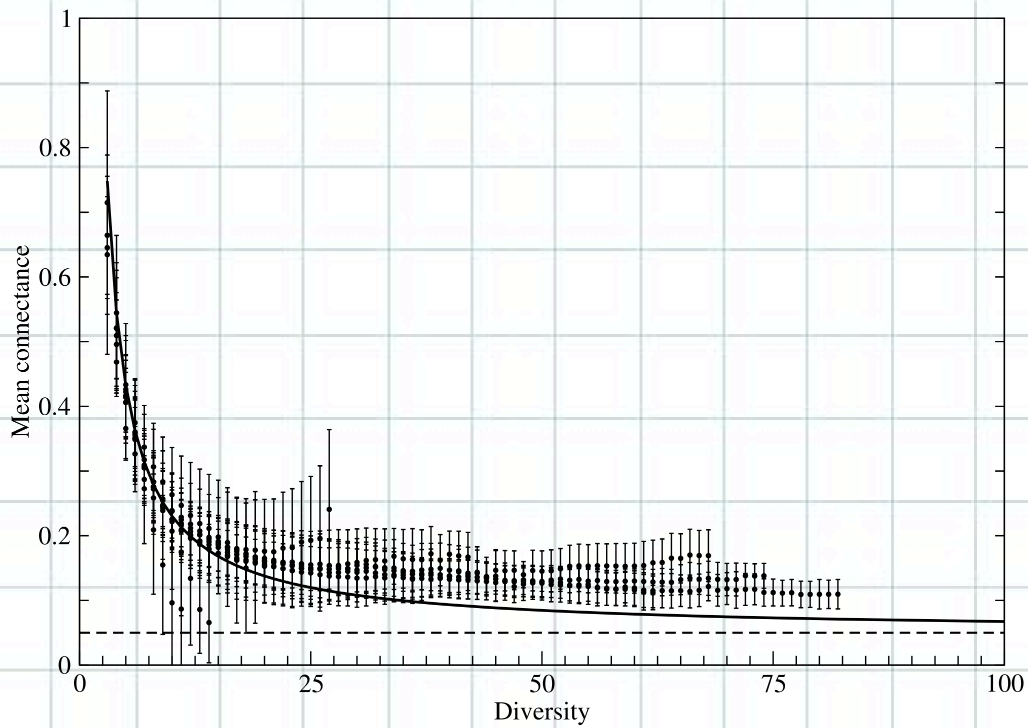
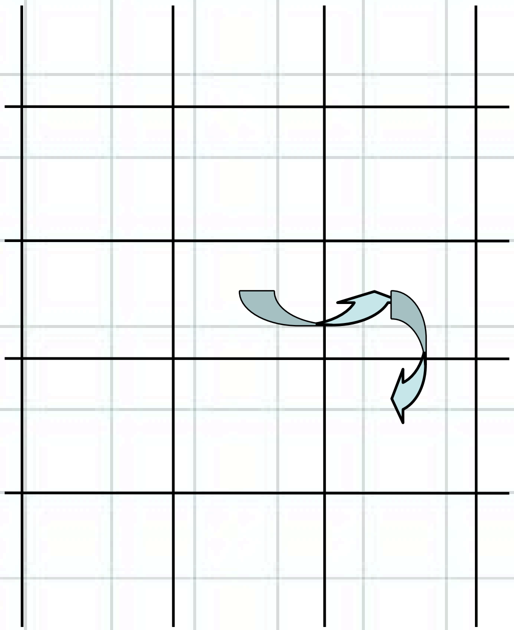


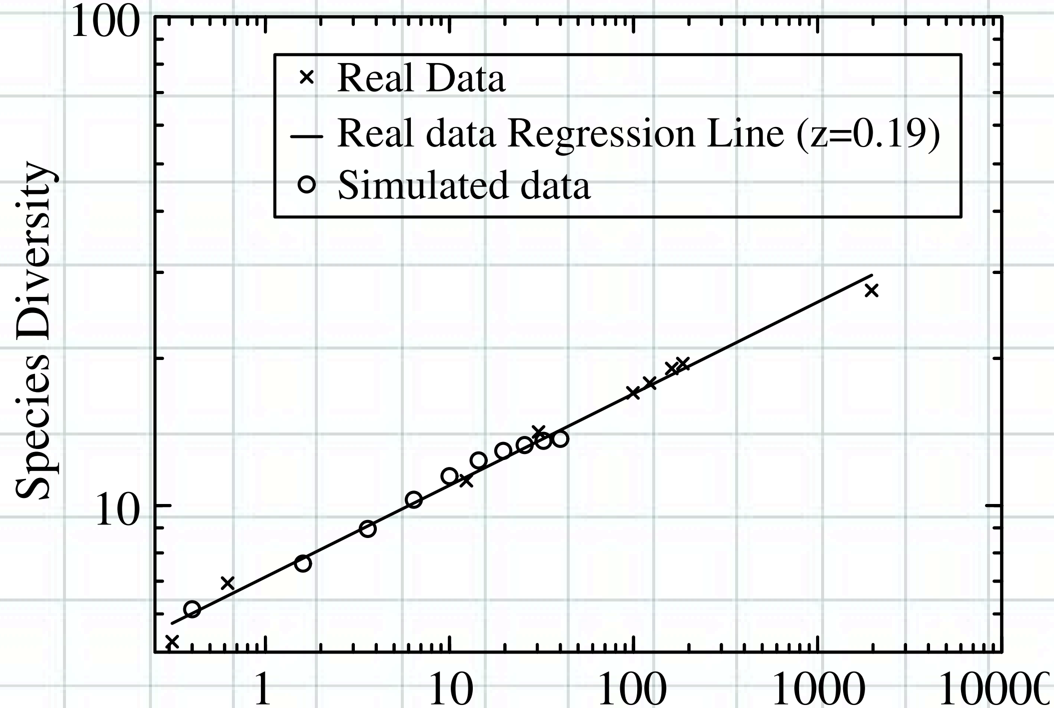
Figure 4: Plot of ensemble-averaged mean connectances, $< C >$ against species diversity. Error bars represent the standard error. The lower dotted line marks the null system connectance, $C_J = 0.05$, which the evolved systems clearly surpass. The overlaid functional form is that given by Eq.(8) using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

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



Dispersion by random walk



(a) Area (ha for data, arbitrary for simulation)

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 individual in ever evolving surroundings:

- Collective system level adaptation towards mutualistic biased webs of interactions
- Macro-Evolution through intermittent transitions

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