3e Colloque National
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Vers une science et ingénierie des systèmes complexes

Imperial College London

Emergence of complex structure through co-evolution:

The Tangled Nature model of evolutionary ecology

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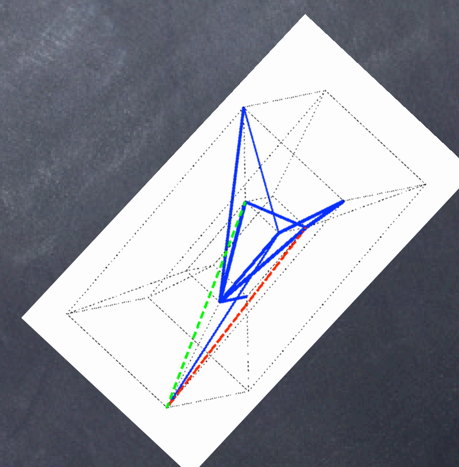


Collaborators:
Paul Anderson, Kim Christensen, Simone A di Collobiano, Matt Hall,
Domininc Jones, Simon Laird, Daniel Lawson, Paolo Sibani

What are we after ?

>> Connecting micro to macro

Micro level:

- stochastic individual based dynamics always running at clock speed one

Collective adaptation

Macro level:

- intermittent dynamics
- networks, structure

List of content:

- Motivation:
- The Tangled Nature Model
- Co-evolution and the evolved networks

Phenomenology:
- ❄ intermittency
- ❄ emergent networks
- ❄ connectance
- ❄ evolving correlations

Explanation

Simple mean field

Fokker-Planck equation

Motivation:

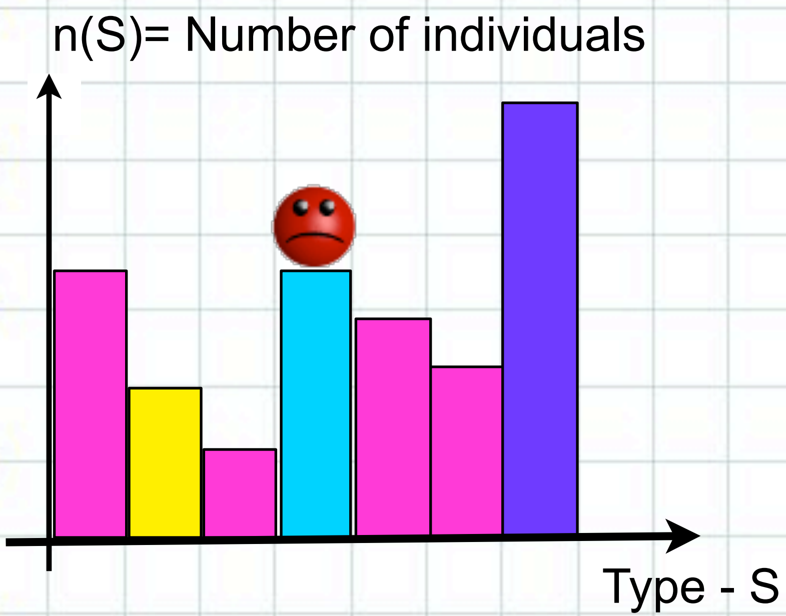
- How far can a minimal model go?
- Input: mutation prone reproduction at level of interacting individuals.
- Output: Species formation, macro dynamics, decreasing extinction rate + SAD, SAR, etc.
- Check: Trend in broad range of data.

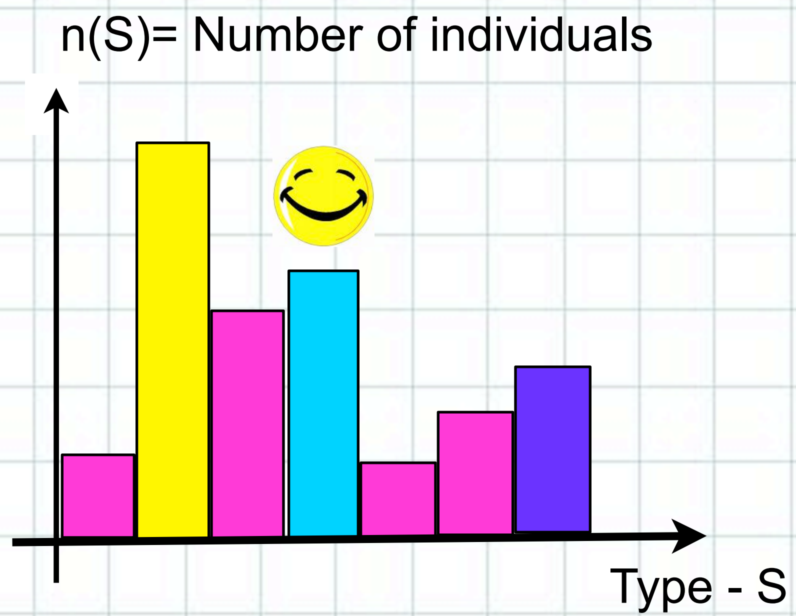

Phenomenology

Interaction and co-evolution

The Tangled Nature model

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

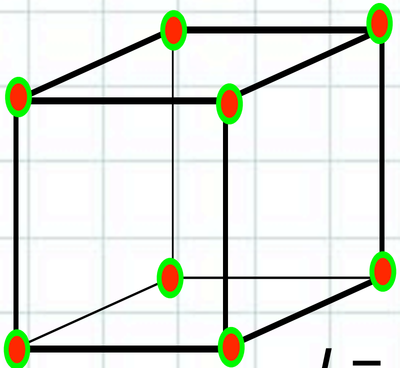




Definition

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

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



$L = 3$

Dynamics – a time step

Annihilation

Choose indiv. at random, remove with probability

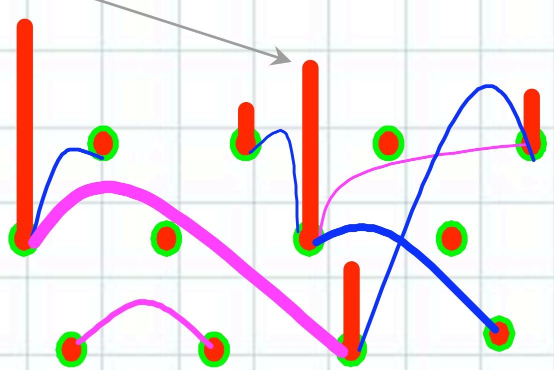
$$p_{kill} = const$$

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 $\mathbf{S}$

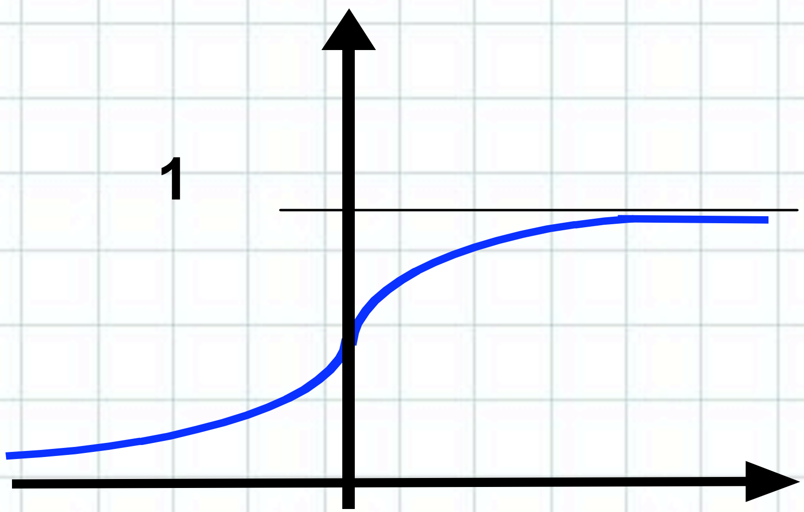


The coupling matrix $J(S, S')$

- Either consider $J(S, S')$ to be uncorrelated
- or to vary smoothly through type space.

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

$$\mathbf{S}_1^{\alpha} \qquad \mathbf{S}_2^{\alpha}$$

with probability

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

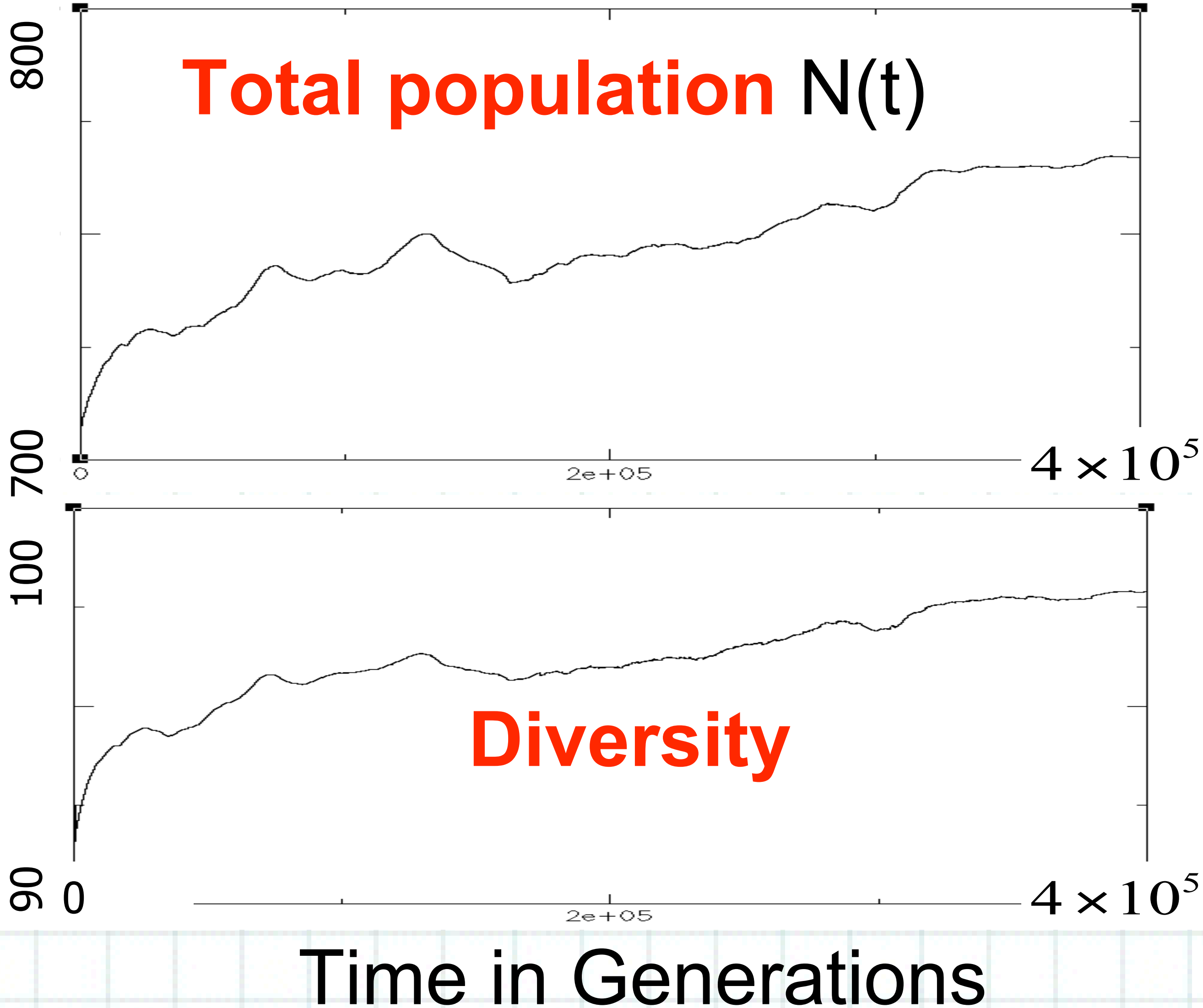
Mutations

- Mutations occur with probability

p_{mut} , i.e.

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

Time dependence (Average behaviour)



Origin of drift? Effect of mutation

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

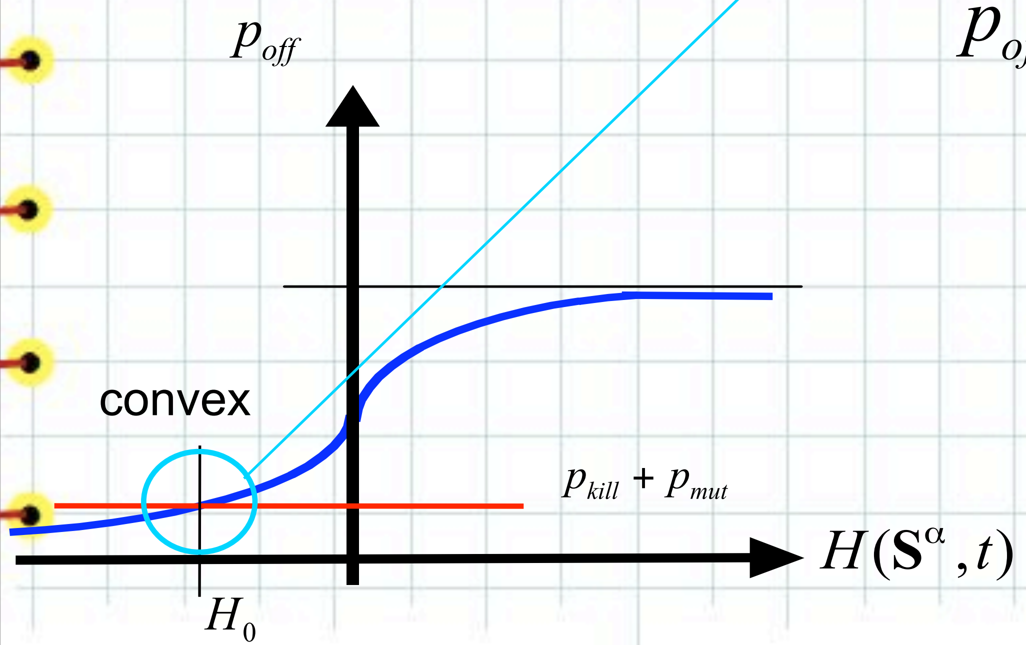
$H \mapsto H + \delta \tilde{J}$.

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

leads to asymmetri

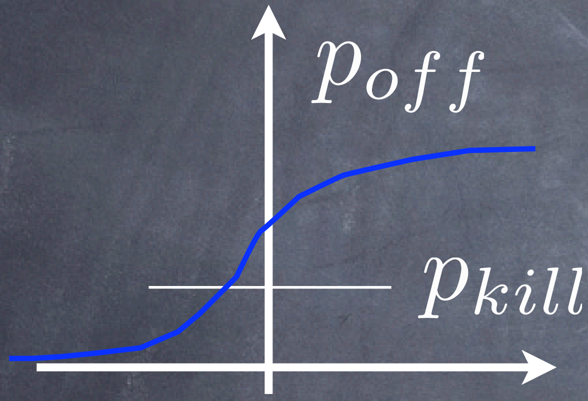
$p_{off}(H_0 + \delta \tilde{J}) - p_{kill} >$

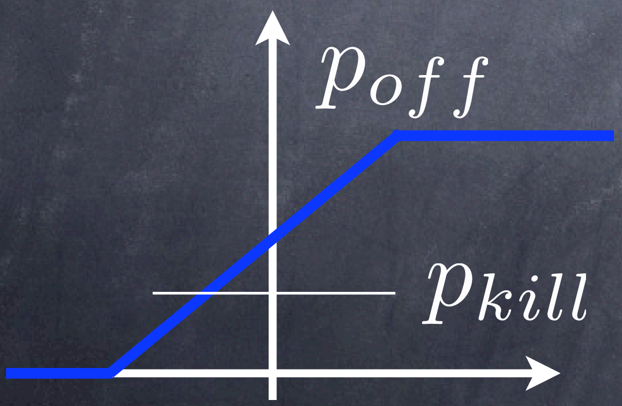
$p_{kill} - p_{off}(H_0 - \delta \tilde{J})$

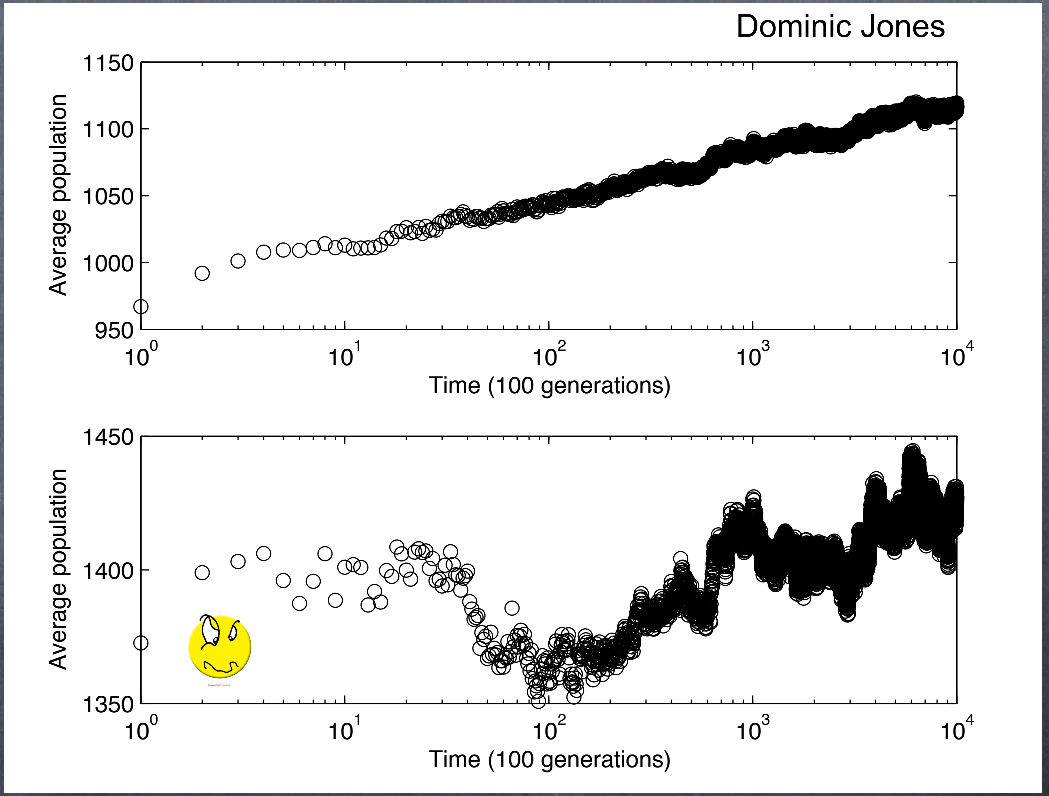


Dynamics:

The functional form of reproduction probability

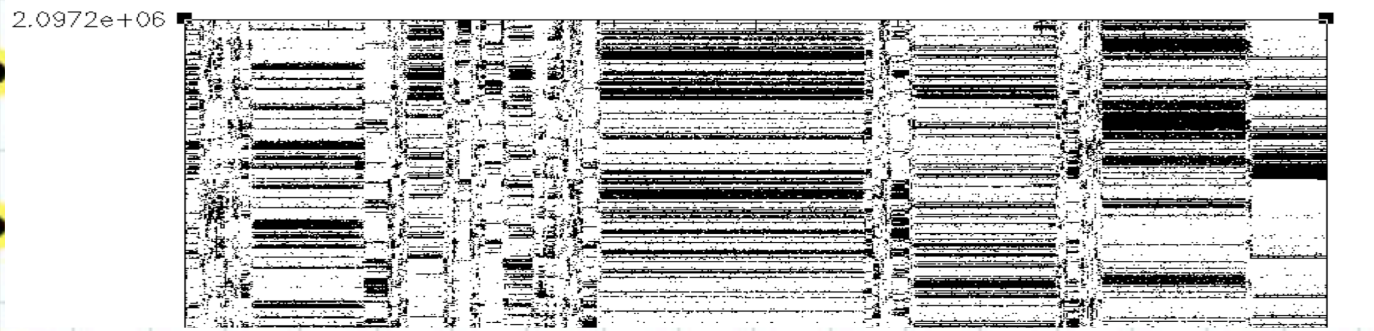






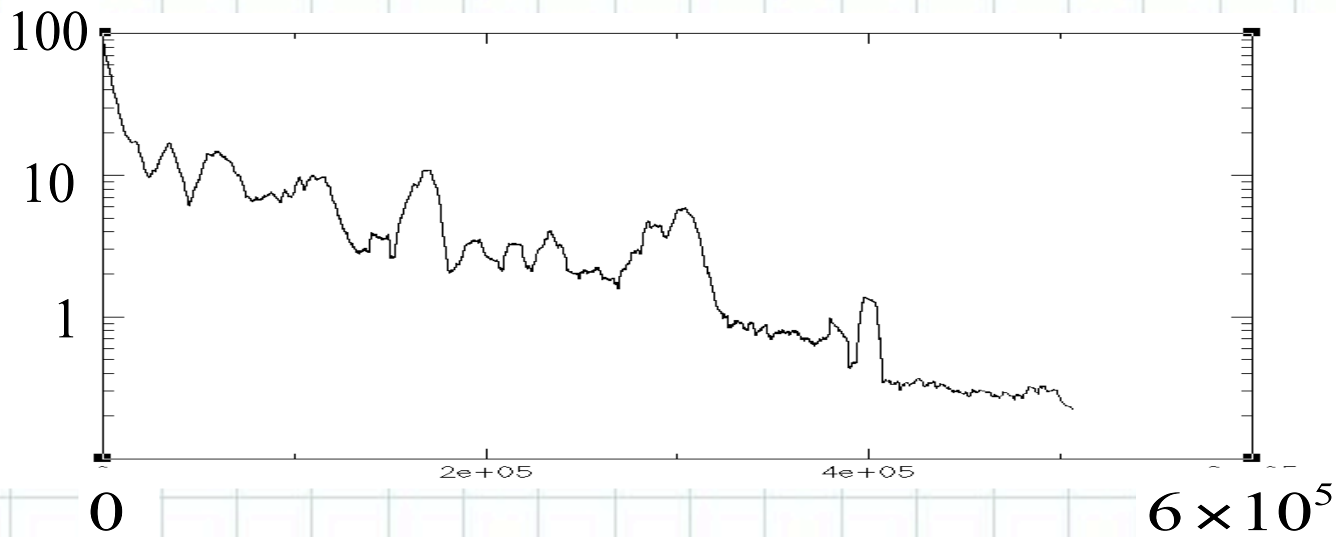
Intermittency:

Non Correlated



# of transitions in window

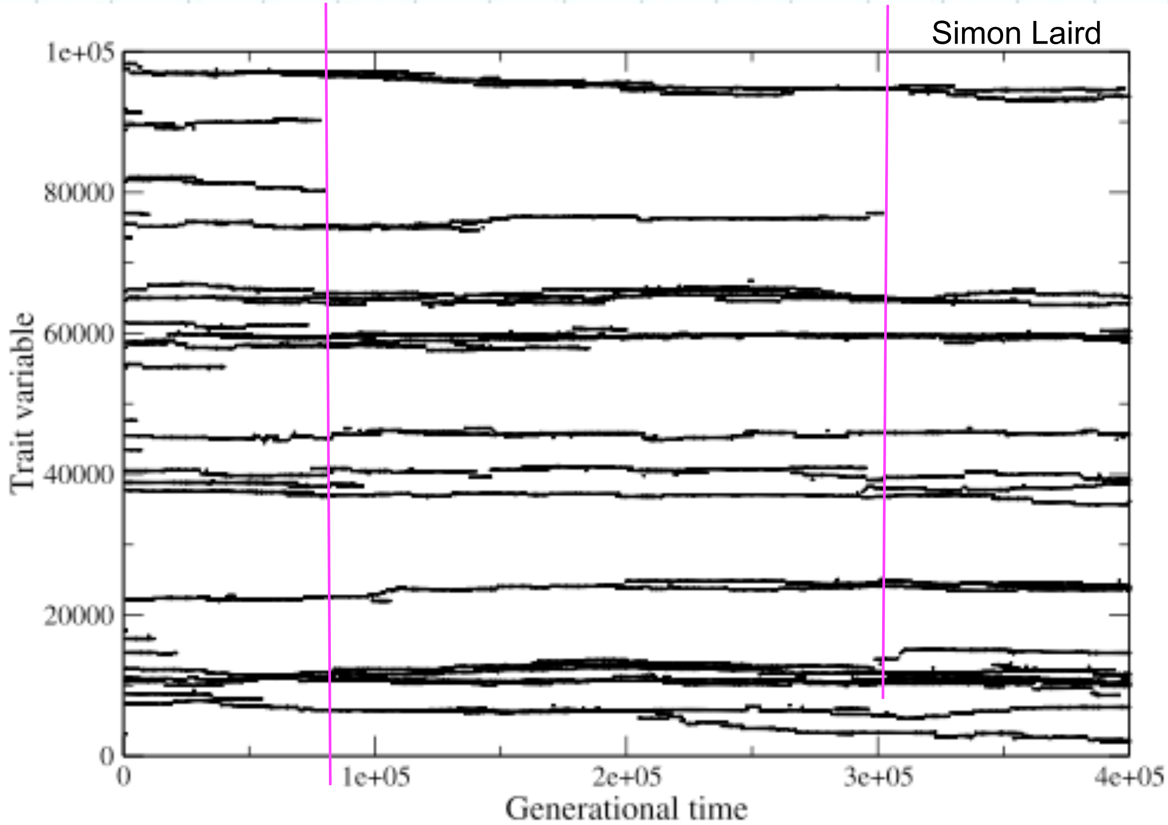
Matt Hall



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

Intermittency at systems level:

Correlated

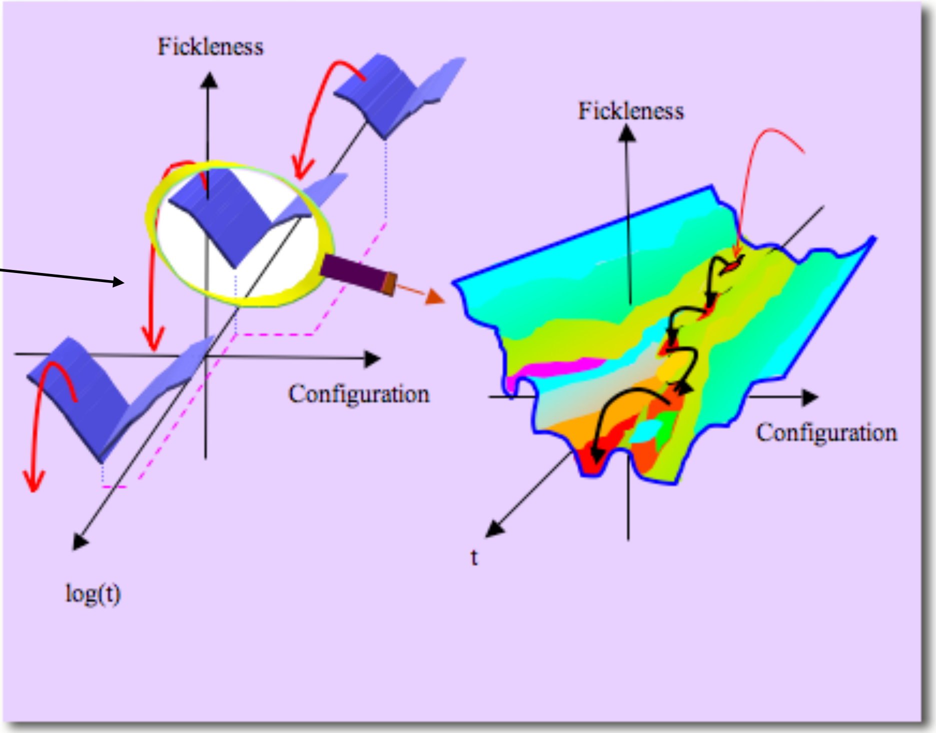


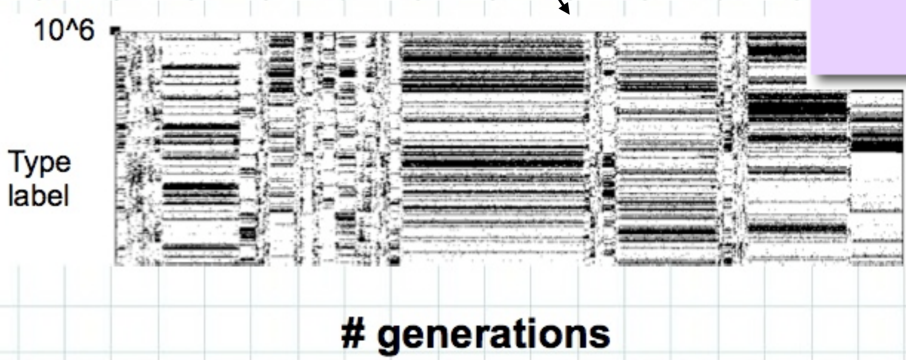
Complex dynamics:

Intermittent, non-stationary

Jumping through collective adaptation space

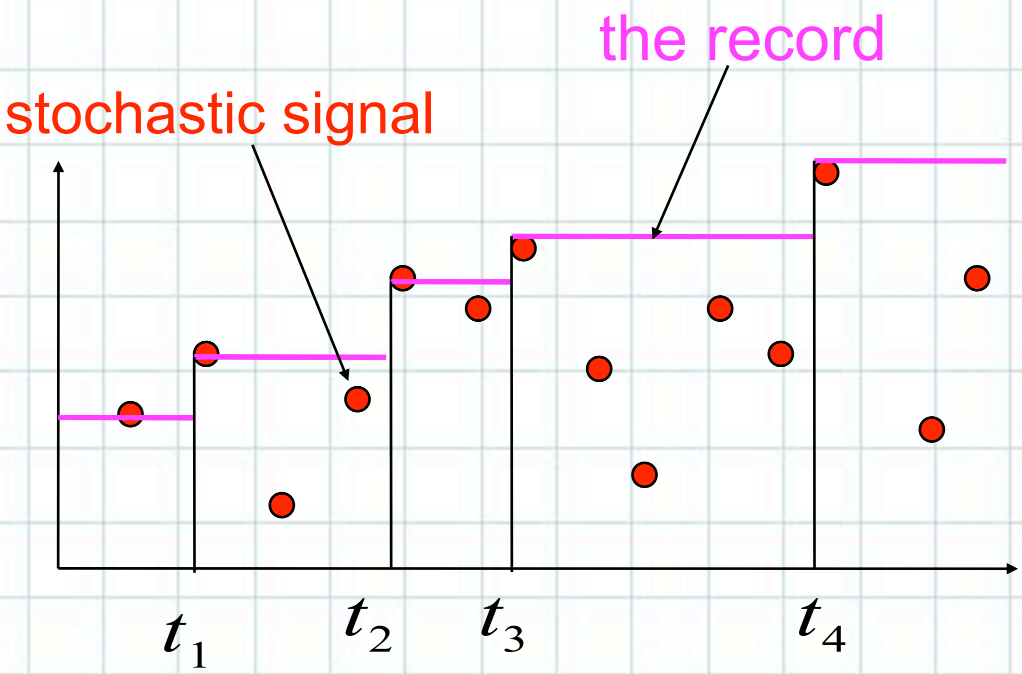
Transitions





Record dynamics

Record dynamics:



Paolo Sibani and Peter Littlewood:

$$\tau = \ln(t_k) - \ln(t_{k-1}) = \ln(\frac{t_k}{t_{k-1}})$$ exponentially distributed

Record dynamics:

$$\tau = \ln(t_k) - \ln(t_{k-1}) = \ln\left(\frac{t_k}{t_{k-1}}\right)$$ exponentially distributed

- Poisson process in logarithmic time
- Mean and variance

$$\langle Q \rangle \propto \ln(t) \quad \text{and} \quad \left\langle (Q - \langle Q \rangle)^2 \right\rangle \propto \ln(t)$$

- Rate of records constant as function of ln(t)
- Rate decreases

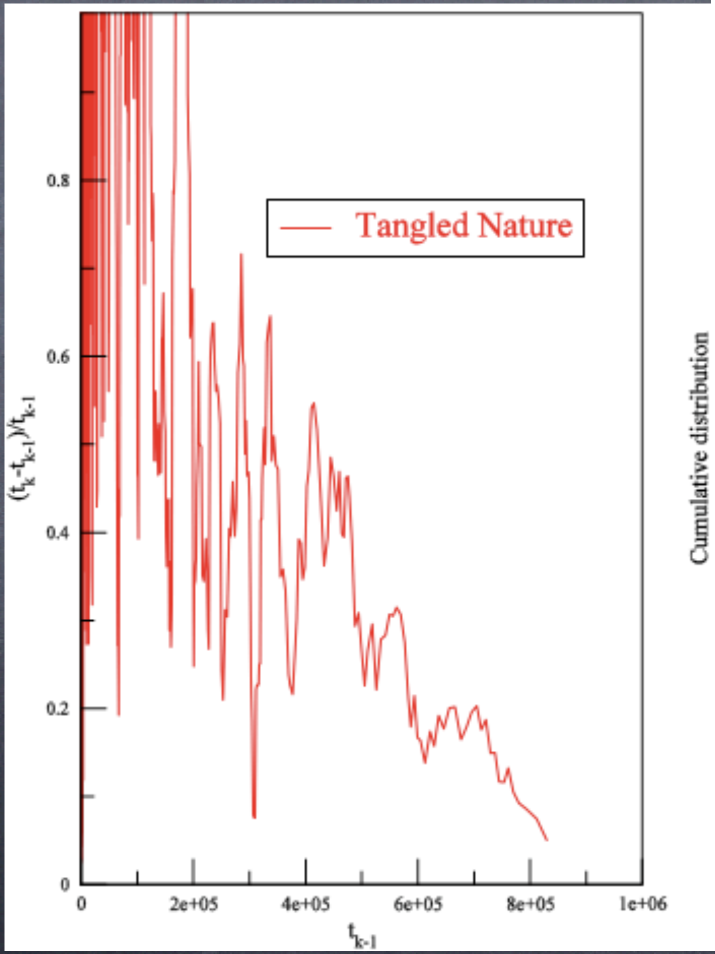
$$\propto 1/t$$

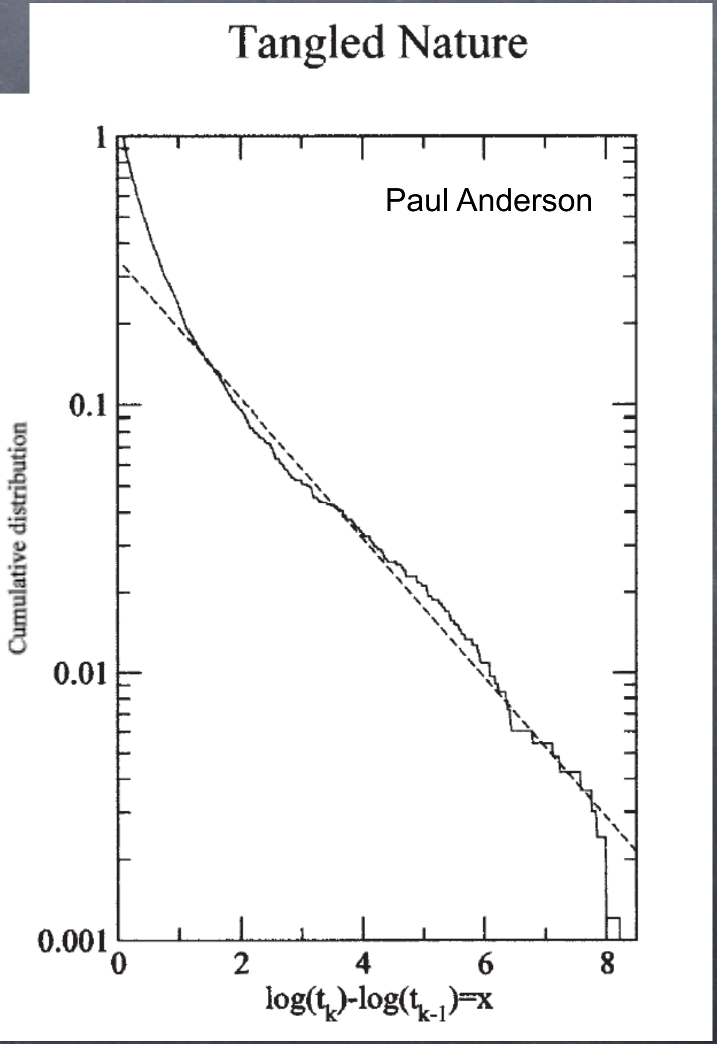
Record dynamics:

Ratio $(t_k - t_{k-1})/t_{k-1}$

remains non-zero

Cumulative Distribution



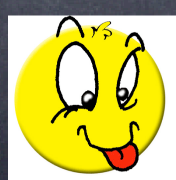


Consequences of record dynamics.

Statistics of transition times independent of underlying "noise mechanism".

Evolution:

same intermittent dynamics in micro- as in macro-evolution.



Decreasing extinction rate.

Other systems

- Ants:

  exit times

- Earthquakes:

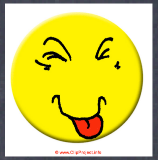
  After shocks - Omori law (?)

- Magnetic relaxation:

  temperature independent creep rate

- Spin glass:

  exponential tails

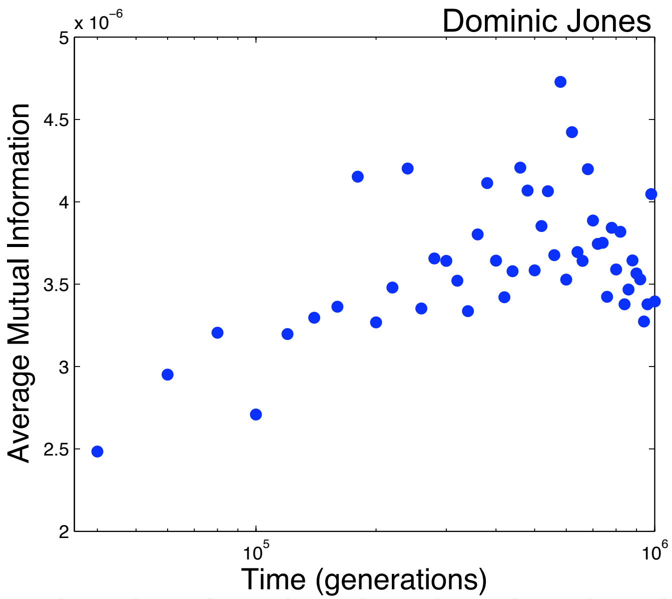


Dynamics - correlations:

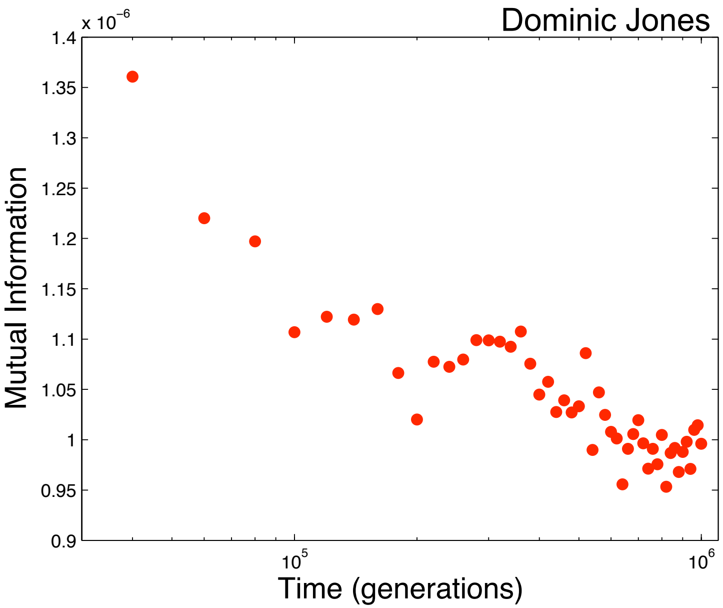
Dynamics - correlations:

The evolution of the correlations

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



Mutual information of core



Mutual information of all

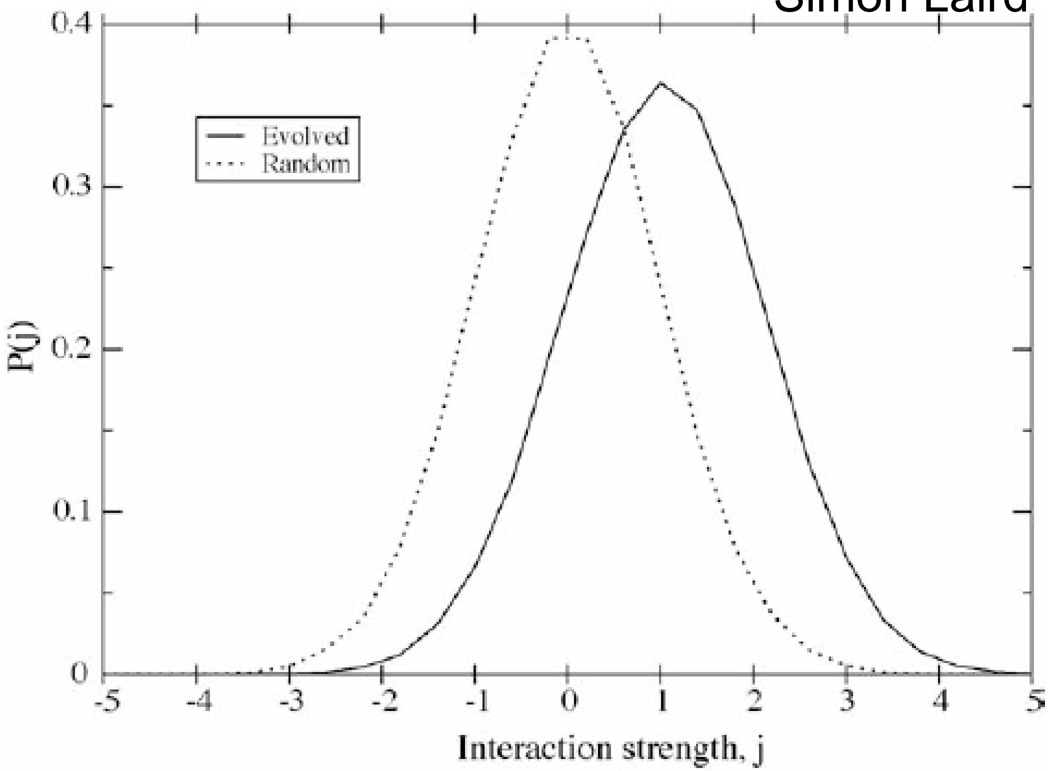
Networks emerge

Time evolution of

Distribution of active coupling strengths

Correlated

Simon Laird



The evolved degree distribution

Correlated

Simon Laird

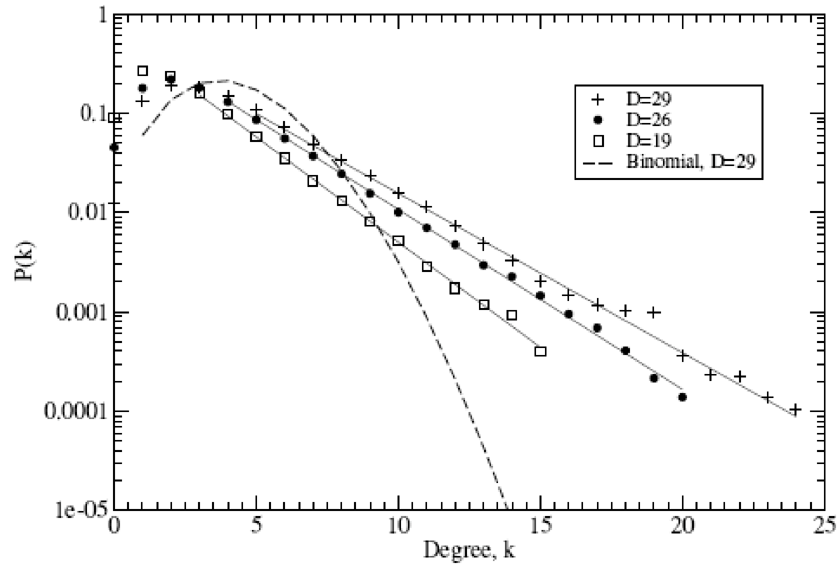
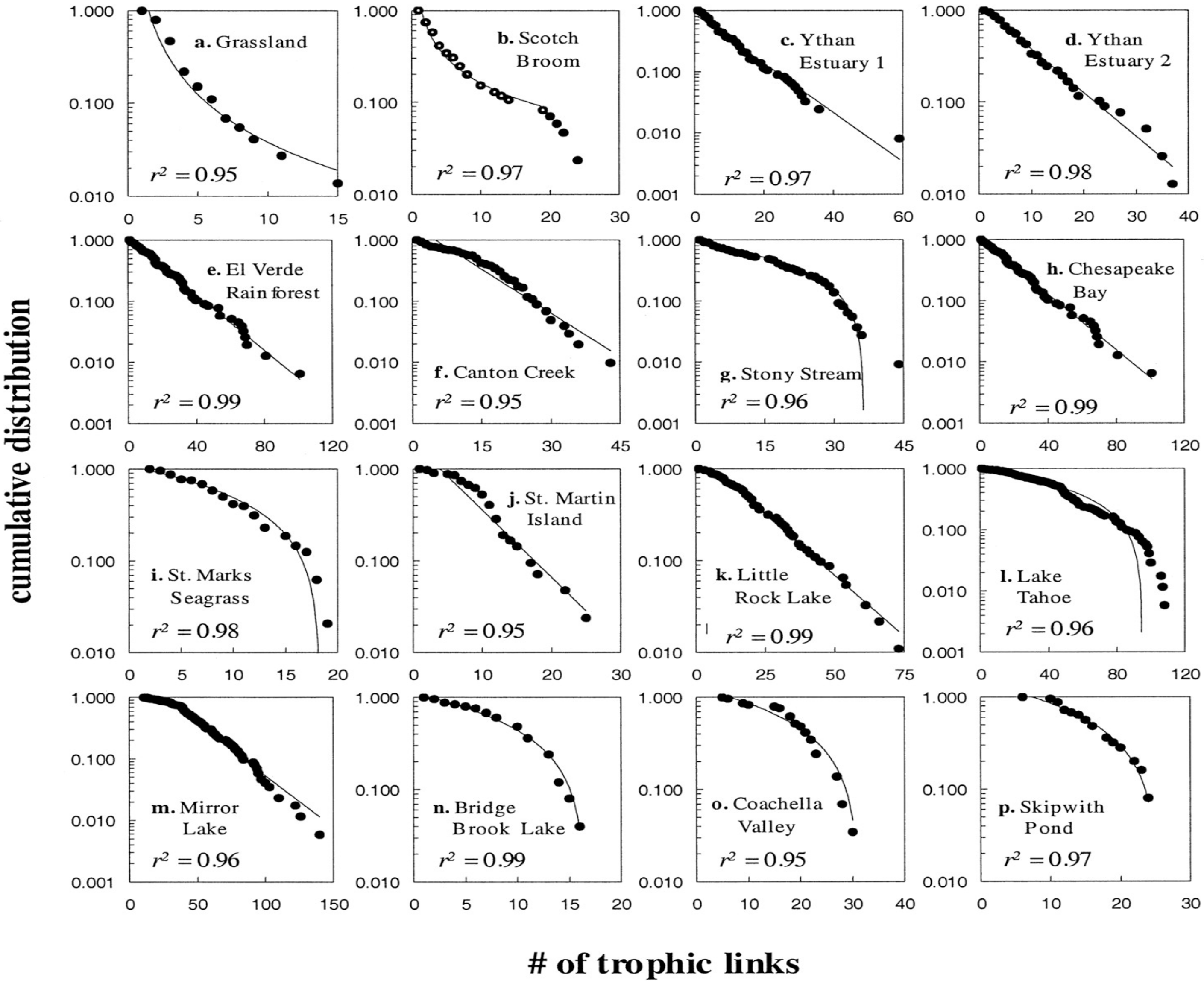


Figure 1: Degree distributions for the Tangled Nature model simulations. Shown are ensemble averaged data taken from all networks with diversity, $D = \{19, 26, 29\}$ over 50 simulation runs of 10^6 generations each. The exponential forms are highlighted by comparison with a binomial distribution of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



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

The evolved connectance

$$\frac{\#edges}{D(D-1)}$$

Correlated

Simon Laird

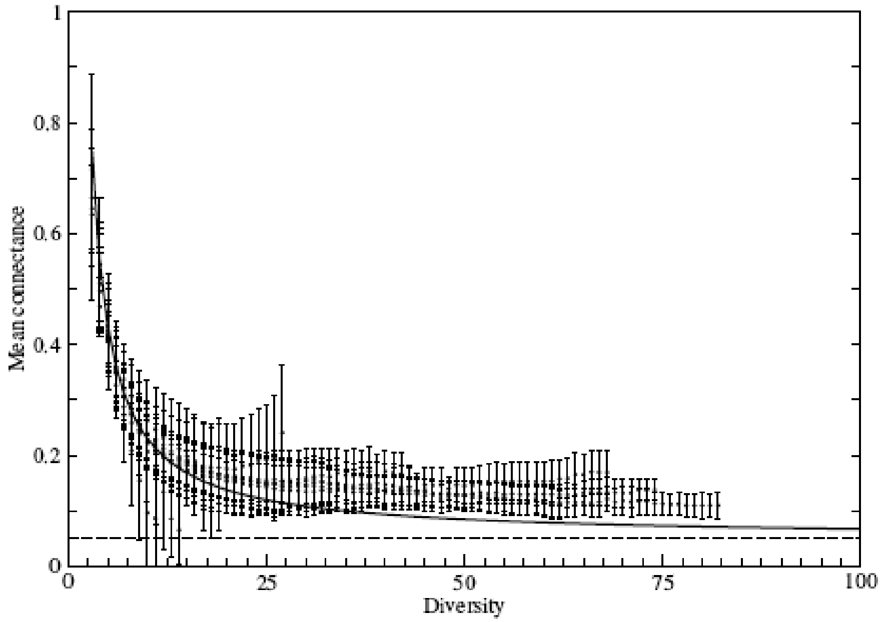
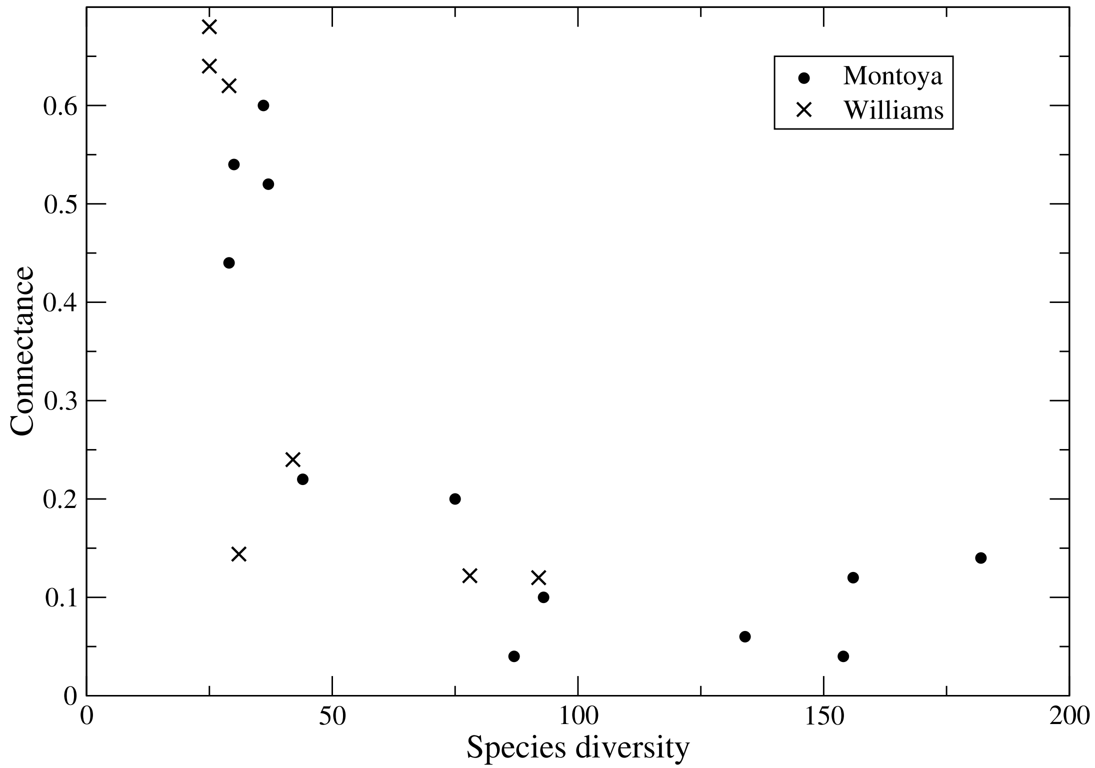


Figure 4: Plot of ensemble-averaged mean connectances, $< C >$ against species diversity. Error bars represent the standard error. The lower dotted line marks the null system connectance, $C_J = 0.05$, which the evolved systems clearly surpass. The overlaid functional form is that given by Eq.(8) using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

Connectance



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

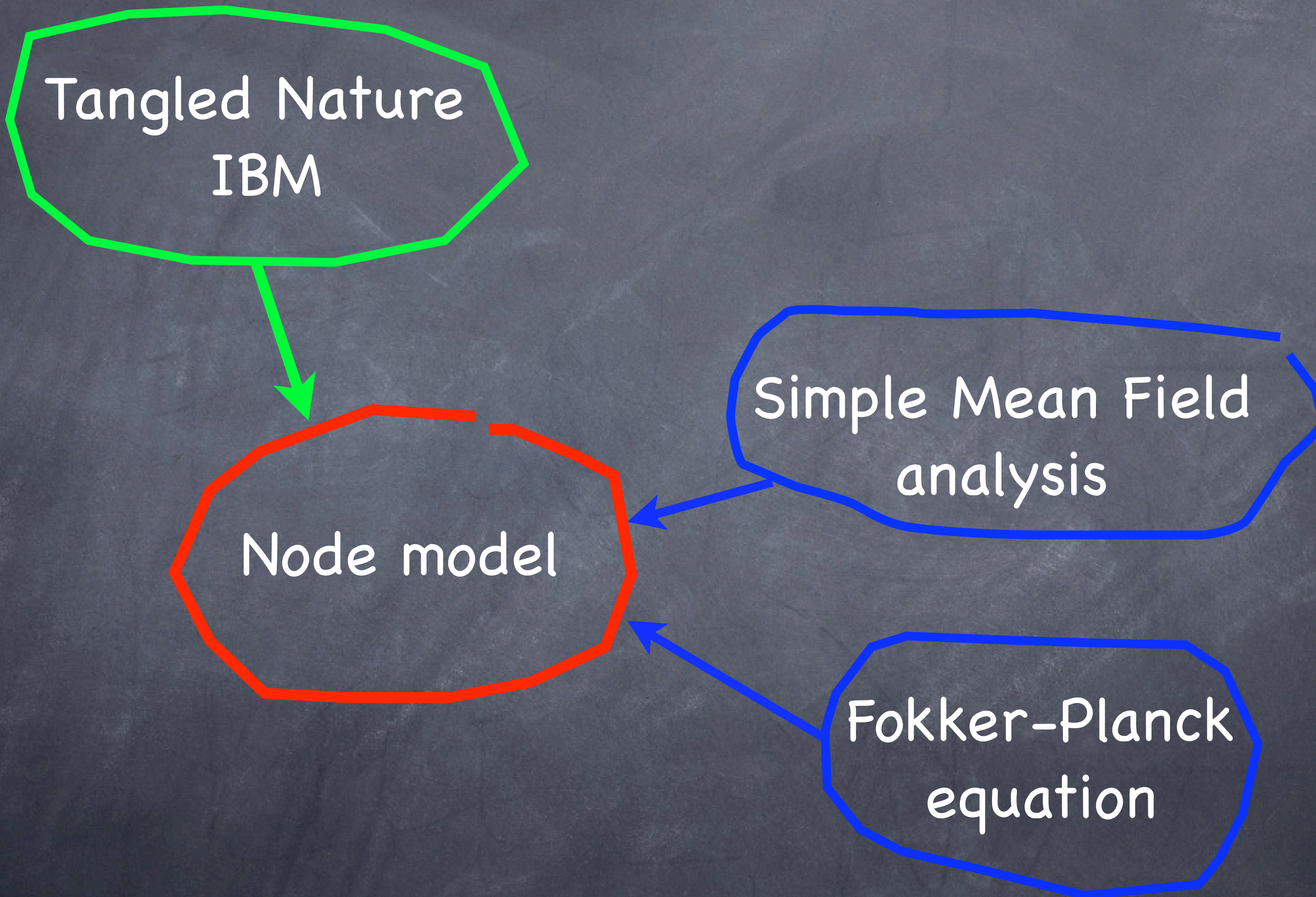
Williams RJ, Berlow EL, Dunne JA, Barabasi AL, Martinez ND *Two degrees of separation in complex food webs*, PNAS **99**, 12913-12916 (2002)

Simon Laird

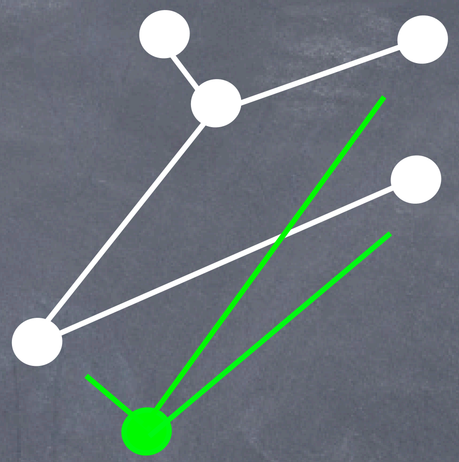
Coarse Grained Description

Node and Edge Model

Analysis approach:



Focus only on whether a type is occupied or not



Dynamical Rules

Removal: with probability $1/D$

Duplication:

place edge between parent and child P_p

copy existing edge with probability P_e

introduce new edge with probability P_n

Self-consistent Mean Field Degree Dynamics

Resulting evolution equation for degree distribution

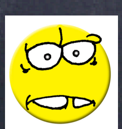
$$
\begin{aligned}
n_k(t+1) &= n_k(t) - \frac{n_k(t)}{D} \\
&+ \langle k \rangle \frac{n_{k+1} - n_k}{D} \\
&+ [P_e \langle k \rangle + P_n (D - 1 - \langle k \rangle)] \frac{n_{k-1} - n_k}{D} \\
&+ P_p \frac{n_{k-1}}{D} + (1 - P_p) \frac{n_k}{D}
\end{aligned}
$$

Removed node

Adjacent node looses an edge

Adjacent gains an edge

Daughter node

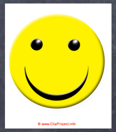


Mean field Degree Dynamics

Stationary solution $$n(k) = n(0)\exp[-k/k_0]$$

with $k_0 \rightarrow \infty \text{ as } P_n \rightarrow 0$

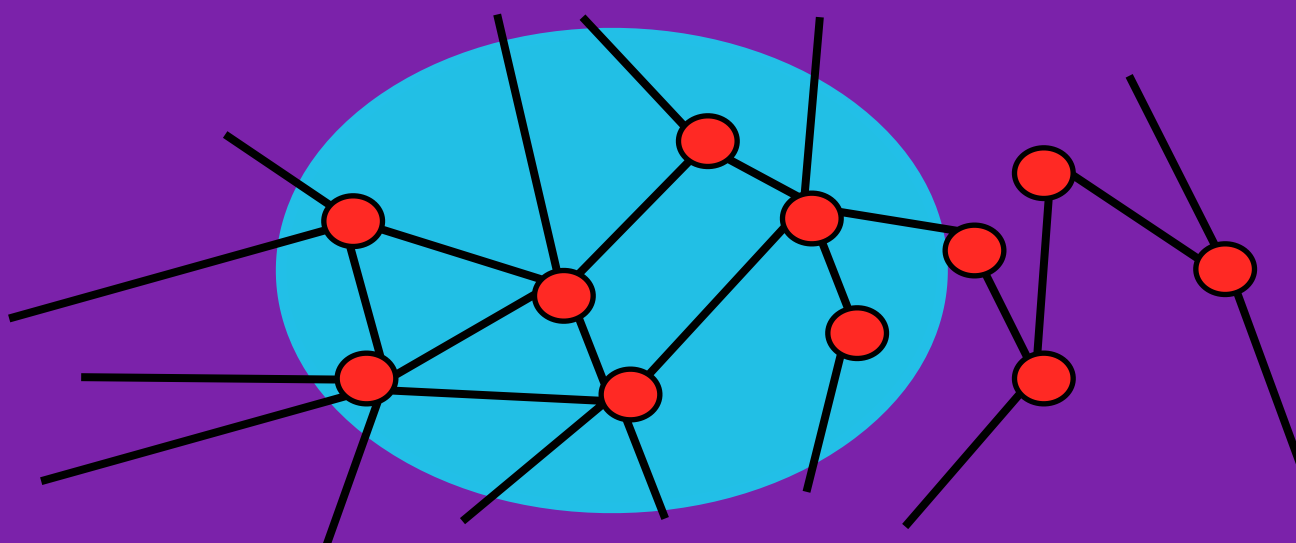
Qualitative agreement with simulations of Node Model (and TaNa)



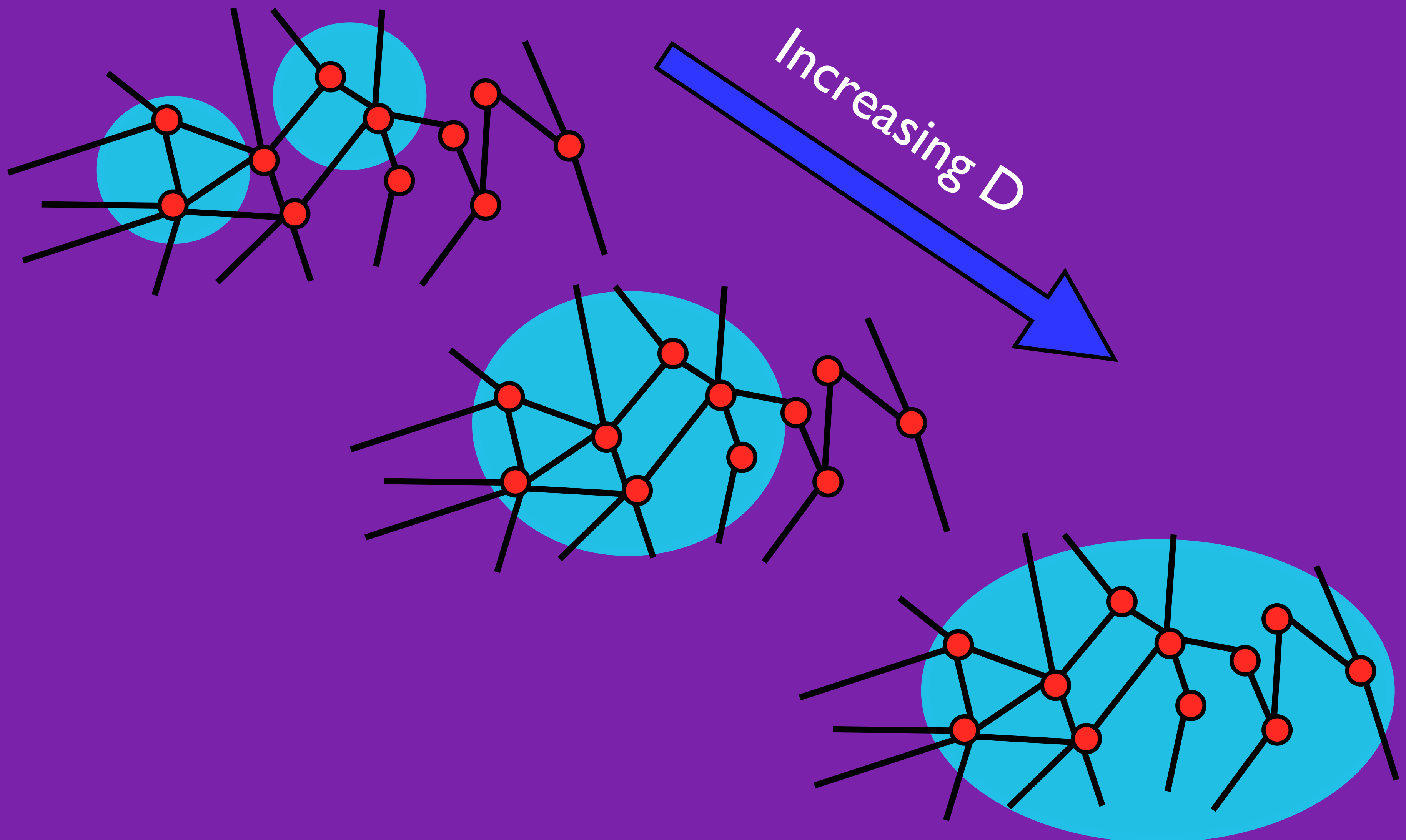
Effect of adaptation on connectance

Underlying type space is a binomial net - place a sub-net of size D

Some regions of this space will, due to fluctuations, locally have an above average conenctance. It is beneficial for the evolved configurations to enter into these regions



With increasing size, D, of the adapted sub-net; it becomes increasingly difficult to confine the sub-net to within the above average regions



Effect of selection on connectance

Consider a binomial net of size D and connectance C (= edge probability).

Assume that adapted sub-net is located in a region of the master-network in which the total number of edges E is larger than the global average.

Estimate this increase as

Fraction

Fluctuations in E

$$
\begin{aligned}
E &= \langle E(D,C) \rangle + s\sigma(D,C) \\
&= E_m C + s[E_m C(1-C)]^{\frac{1}{2}}
\end{aligned}
$$

Max,i.e., Em=D(D-1)

Effect of selection on connectance

The resulting estimate for the connectance, E/Em, of the adapted sub-net

$$
\begin{aligned}
C_{Adap} &= C + s\left[\frac{C(1-C)}{E_m}\right]^{\frac{1}{2}} \\
&= C + s\left[\frac{2C(1-C)}{D(D-1)}\right]^{\frac{1}{2}}.
\end{aligned}
$$

Qualitative agreement with simulations of Tangled Nature model

The evolved connectance

$$\frac{\#edges}{D(D-1)}$$

Correlated

Simon Laird

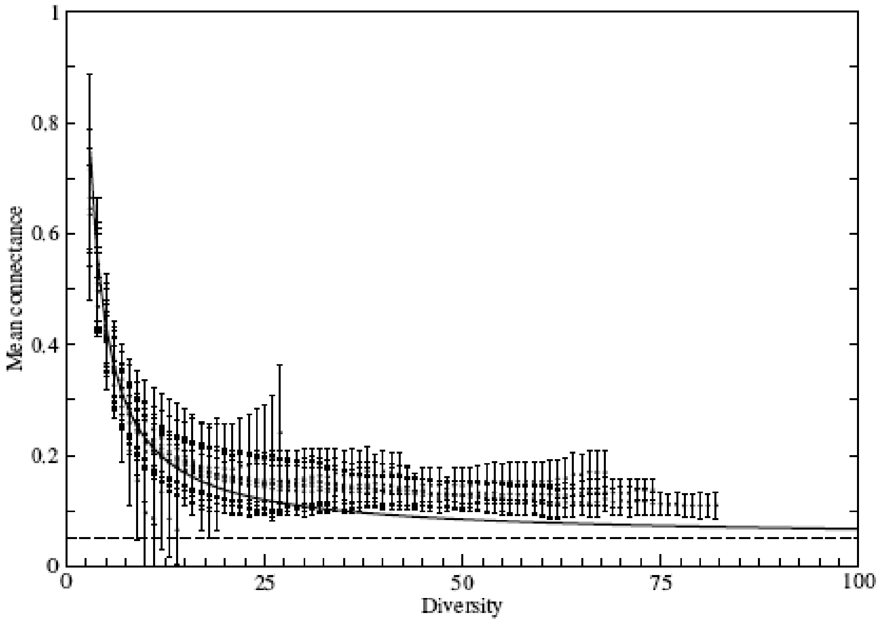


Figure 4: Plot of ensemble-averaged mean connectances, $< C >$ against species diversity. Error bars represent the standard error. The lower dotted line marks the null system connectance, $C_J = 0.05$, which the evolved systems clearly surpass. The overlaid functional form is that given by Eq.(8) using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

Fokker-Planck equation

Analytical result

$$n_k(t+1) = n_k(t) + \Gamma_R(D,k,t) + \Gamma_{Du}(D-1,k,t).$$

$$\Gamma_R(D,k,t) = \Gamma_R^d(k) + \Gamma_R^N(k+1) - \Gamma_R^N(k).$$

$$\begin{aligned}\Gamma_{Du}(D-1,k,t) \quad &= \quad \Gamma_{Du}^P(k-1) - \Gamma_{Du}^P(k) + \Gamma_{Du}^C(k) \\ &\quad + \Gamma_{Du}^N(k-1) - \Gamma_{Du}^N(k).\end{aligned}$$

Fokker-Planck eq. iterated

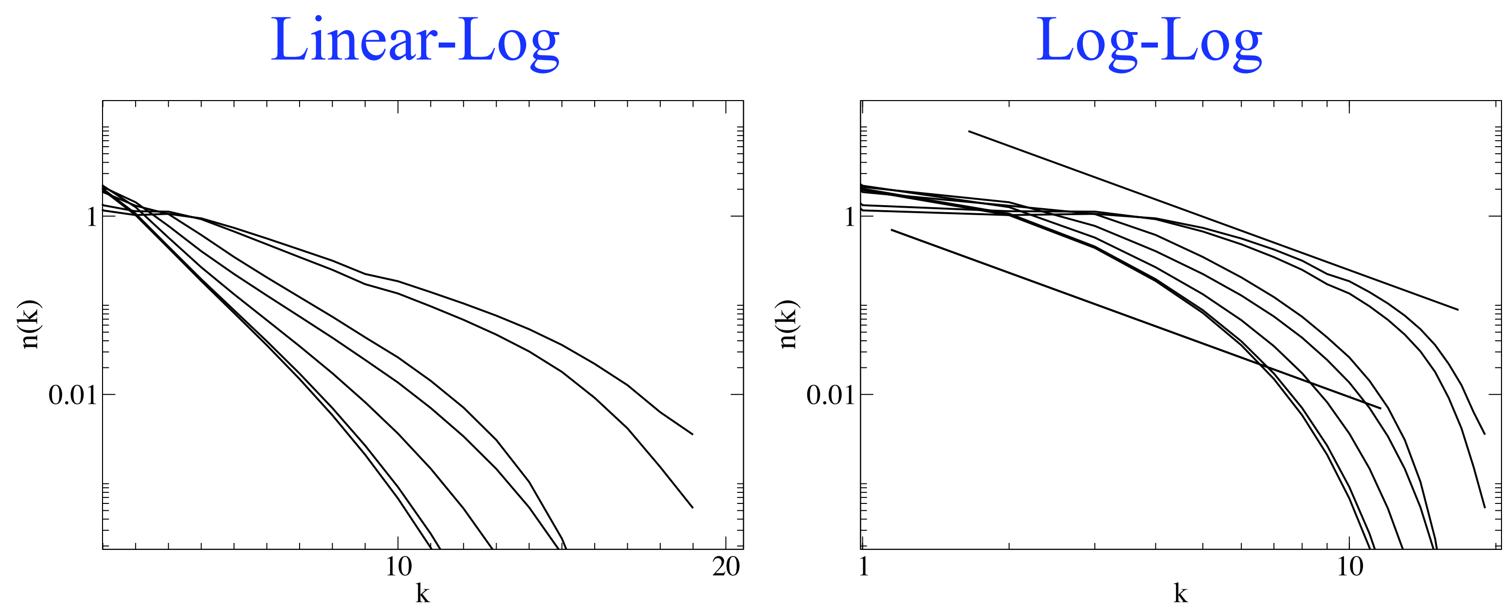


Figure 2: The degree distribution obtained by iteration of the Fokker-Planck equation (9). The exponential form is visible for a broad range of parameter values in the linear-log plot to the left. The approach towards a $1/k$ dependence in the limit of $P_e \to 1$ can be seen in the log-log plot to the right. The two straight lines have slope -1. The parameters are $D = 20$, $P_e = 0.01, 0.1, 0.3, 0.5, 0.7, 0.9, 0.95$ and $P_p = 0.01$. P_n was chosen to be $P_n = P_p(1 - P_e)/(1 - P_p)$)

HJ Jensen, PRS A 2008

Limiting behaviour

In limit mutations $\longrightarrow$ 0

Implies $P_e = 1 \text{ and } P_n \rightarrow 0$

Fokker-Planck eq. reduces to

$$
\begin{aligned}
n_k(t+1) \quad = \quad & n_k(t) + n_k\left(\frac{1}{D-1} - \frac{1}{D}\right) + \frac{2P_p}{D-1}(n_{k-1} - n_k) \\
& + \sum_{k_1=1}^{D-2} \sum_{q=1}^{k_1} q n_{k1}\left[\frac{1}{D} P_{Ed}(k_1, k+1, q) - \frac{1}{D-1} P_{Ed}(k_1, k, q)\right. \\
& \left. - \frac{1}{D} P_{Ed}(k_1, k, q) + \frac{1}{D-1} P_{Ed}(k_1, k-1, q)\right]
\end{aligned}
$$

Limiting behaviour

Include only leading terms from $k_1 = 1$ and $q = 1$

$$n_k(t+1) = n_k + \frac{n_k}{D(D-1)} + \frac{2P_p}{D-1}[n_{k-1} - n_k] + \frac{n_1}{M}[\frac{1}{D}\{(k+1)n_{k+1} - kn_k\} - \frac{1}{D-1}\{kn_k - (k-1)n_{k-1}\}].$$

Stationary solution $n_k \propto 1/k$

Summary

Summary and conclusion

From minimal micro-dynamics

- Collective evolution and adaptation
- Intermittent dynamics >> record dynamics.
- Nature of the evolved networks - compares well
- Dynamics (degree of overlap with parent) determines degree distribution
- Adaptation/selection influences connectance

Thank you for the chance to speak

Papers from

www.ma.ic.ac.uk/~hjjens

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