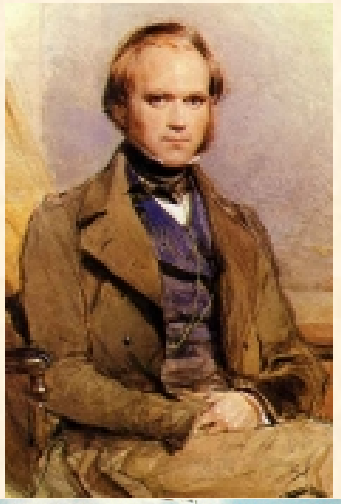
Happy 200th Birthday, Mr. Darwin!

February 12, 1809 – February 12, 2009



Macro-biophysics:
Statistical Physicists Look at Evolution and Ecology

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Why would a physicist be interested in biological evolution?

- Biological evolution involves
  - * Multiple interacting entities
  - * Nonlinear interactions
  - * Far-from-equilibrium conditions
- Some questions in biological evolution are
  - * Well suited for methods from
    statistical mechanics and
    computational physics

Modes of Evolution

- Does evolution proceed uniformly or in fits and starts?
- Scarcity of intermediate forms ("missing links") in the fossil record may suggest fits and starts.
- Fit-and-start evolution termed *punctuated equilibria* by Eldredge and Gould.
- Punctuated equilibria dynamics resemble *nucleation and growth in phase transformations* and *stick-slip motion in friction and earthquakes*.

Models of Coevolution

- In recent years, several models of evolution have been introduced and studied by physicists.
- Among physicists, the best-known coevolution model is probably the *Bak-Sneppen* model.
- The BS model acts directly on interacting species, which mutate into other species.
- But: in nature selection and mutation act directly on *individuals*.

Individual-based Coevolution Model

with R.K.P. Zia (Virginia Tech) and V. Sevim (FSU Ph.D.)

- Binary, haploid genome of length L gives 2^L different potential genotypes. **01100…101**
- Considering this genome as *coarse-grained*, we consider each different bit string a "species."
- Asexual reproduction in discrete, nonoverlapping generations.
- Simplified version of "tangled-nature" model introduced by Hall, Christensen, et al.,

  Phys. Rev. E **66**, 011904 (2002);

  J. Theor. Biol. **216**, 73 (2002).

Population Dynamics gives selection

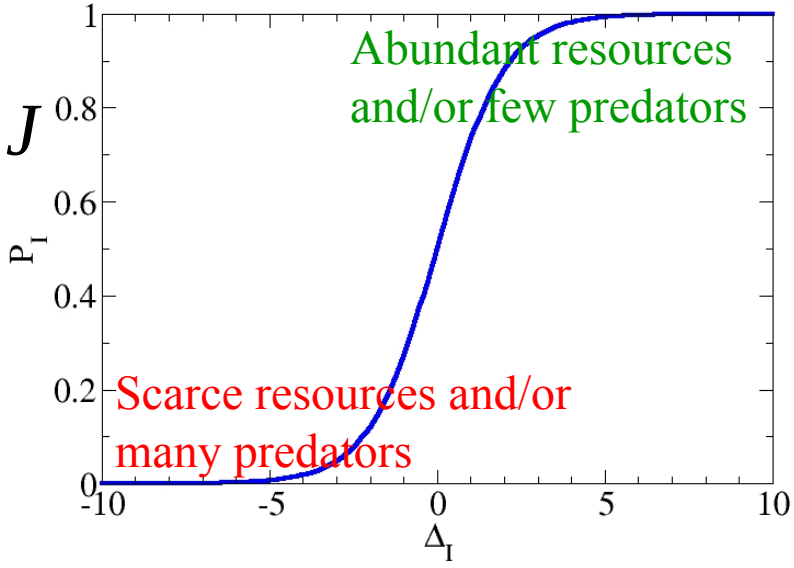
Probability that an individual of genotype I has F offspring in generation t before dying is $P_I(\{n_J(t)\})$.

Probability of dying without offspring is $(1-P_I)$.

$$P_I(\{n_J(t)\}) = \frac{1}{1+\exp\left[-\Delta_I\left(R,\{n_J(t)\}\right)\right]}$$

$n_J(t)$: Population size of genotype J

R: External resource



Evolution introduced through **Mutations!!**

Each individual *offspring* undergoes mutation to a different genotype with probability μ per individual.

General model

$$\Delta_I\left(\{n_J(t)\}\right) = -b_I + R\eta_I / N_{\text{tot}}(t) + \sum_J M_{IJ} n_J(t) / N_{\text{tot}}(t) - N_{\text{tot}}(t) / N_0$$

- b_I : Birth cost
- η_I :Coupling to external resource R
- $N_{\text{tot}} = \Sigma_J\, n_J(t)$: Total population
- N_0 : Carrying capacity (Verhulst factor)
- M_{IJ} : Effect of genotype J on birth probability of I.

  M_{IJ} and M_{JI} both positive: symbiosis or mutualism.

  M_{IJ} and M_{JI} both negative: competition.

  M_{IJ} and M_{JI} opposite sign: predator/prey relationship.

- Model A:

$$\Delta_I^{\mathrm{A}}\left(\{n_J(t)\}\right) = \sum_J M_{IJ} n_J(t) / N_{\mathrm{tot}}(t) - N_{\mathrm{tot}}(t) / N_0$$

M_{IJ} quenched, random $\in [-1,+1]$, except $M_{II} = 0$

No coupling to external resource. No birth cost. $F = 4$

- Model B:

$$\Delta_I^{\mathrm{B}}\left(\{n_J(t)\}\right) = -b_I + R\eta_I / N_{\mathrm{tot}}(t) + \sum_J M_{IJ} n_J(t) / N_{\mathrm{tot}}(t)$$

M_{IJ} antisymmetric => **predator/prey model**

M_{IJ} *connectance* = 10%

5% of potential species **producers** ($\eta_I \in (0,+1]$ random)

95% of potential species **consumers** ($\eta_I = 0$)

Random $b_I \in (0,+1]$ and $M_{II} \in [-1,0)$ limit population

No Verhulst effect ($N_0 = \infty$). $F = 2$

Deterministic approximation exactly solvable!

$$n_I(t+1) = n_I(t) FP_I(\{n_J(t)\})[1-\mu] + (\mu/L)\sum_{K(I)} n_{K(I)}(t) P_{K(I)}(\{n_J(t)\}) + O(\mu^2)$$

Stationary solution for N_{tot} in limit $M = 0$:

$$R\mathcal{E} + \Theta N^*_{\text{tot}} - {N^*_{\text{tot}}}^2/N_0 = 0$$

Here,

$$\Theta = \frac{1 - \langle 1|\hat{\mathbf{M}}^{-1}|\tilde{b}\rangle}{\langle 1|\hat{\mathbf{M}}^{-1}|1\rangle} \quad \text{and} \quad \mathcal{E} = \frac{\langle 1|\hat{\mathbf{M}}^{-1}|\eta\rangle}{\langle 1|\hat{\mathbf{M}}^{-1}|1\rangle}$$

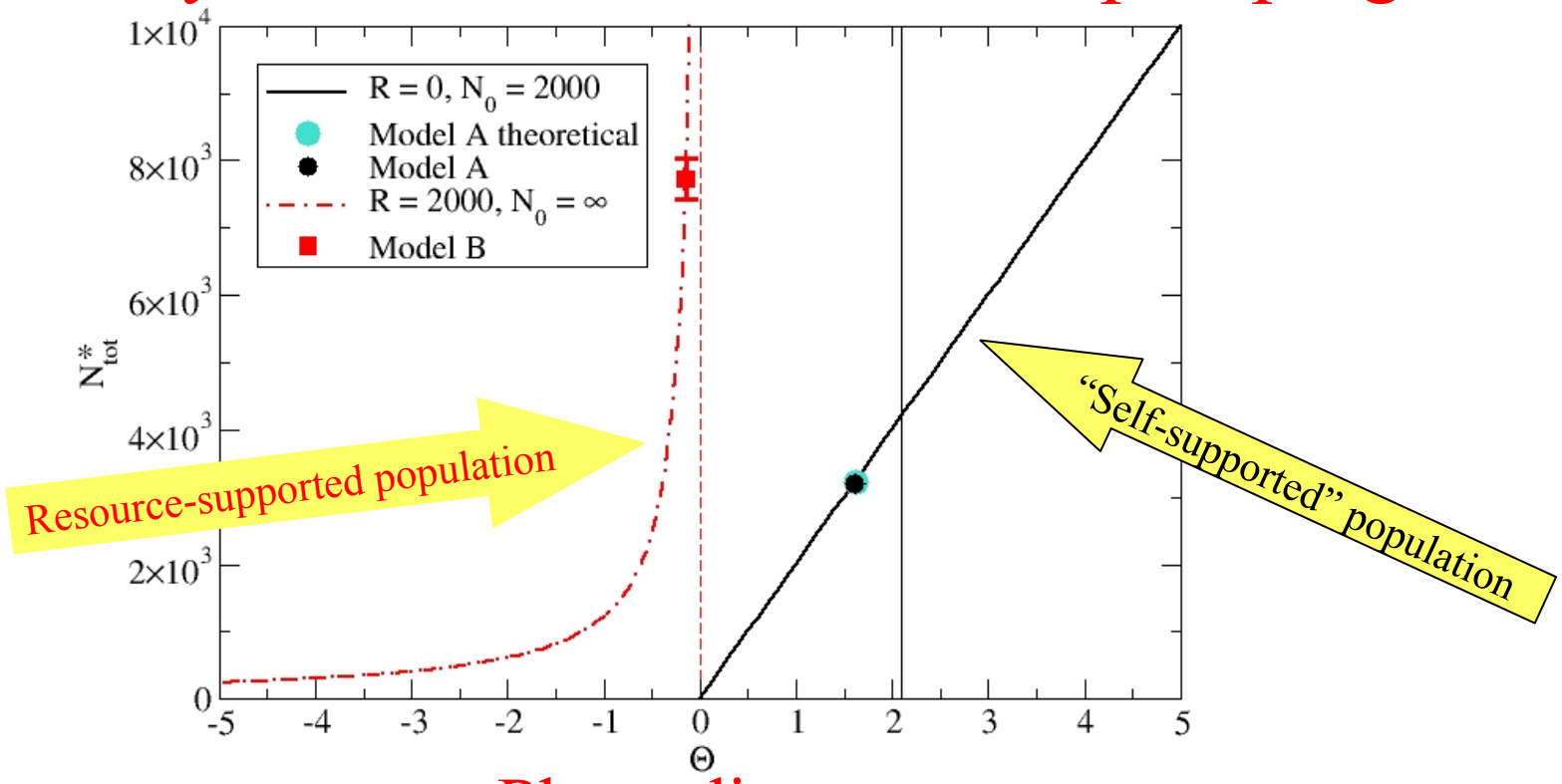
"Average" interaction

"Average" coupling to R

Solutions for individual n_I^* also available

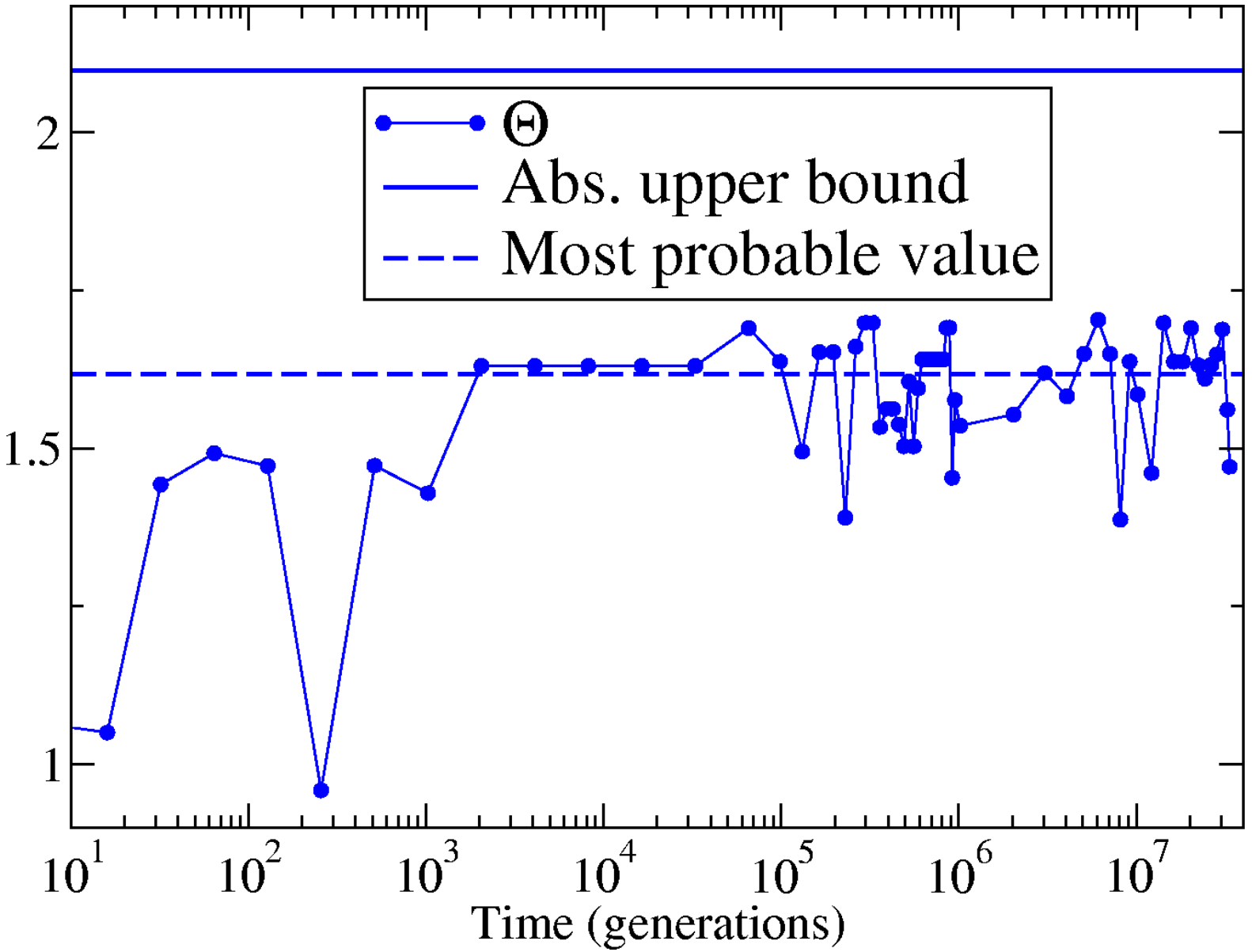
In the equation $R\mathcal{E} + \Theta N^*_{\rm tot} - {N^*_{\rm tot}}^2/N_0 = 0$, the resource *R* plays the role of an external field, and Θ a "pumping strength" as in a laser.

But this system can **evolve** its own "pumping"!



Phase diagram

Time evolution of Θ



Stability of fixed points

The ***internal*** stability of the fixed point is determined by the eigenvalues of the *community matrix*

$$\tilde{\Lambda}_{IJ} = \left.\frac{\partial n_I(t+1)}{\partial n_J(t)}\right|_{\{n_I^*\}} - \delta_{IJ} = \left(1-\frac{1}{F}\right)\frac{n_I^*}{N_{\text{tot}}^*}\left[M_{IJ} - \frac{R\eta_I + \left(\hat{\mathbf{M}}\middle| n^*\right\rangle_I}{N_{\text{tot}}^*} - \frac{N_{\text{tot}}^*}{N_0}\right]$$

The stability ***against an invading mutant*** *i* is given by the invader's *invasion fitness*:

$$\ln\left(\frac{n_i(t+1)}{n_i(t)}\right) = \ln\left[\frac{F}{1+\exp[-\Delta_i(R,\{n_J^*\})]}\right]$$

Monte Carlo algorithm:
3 layers of nested loops

1. Loop over generations t
2. Loop over genotypes I with $n_I > 0$ in t

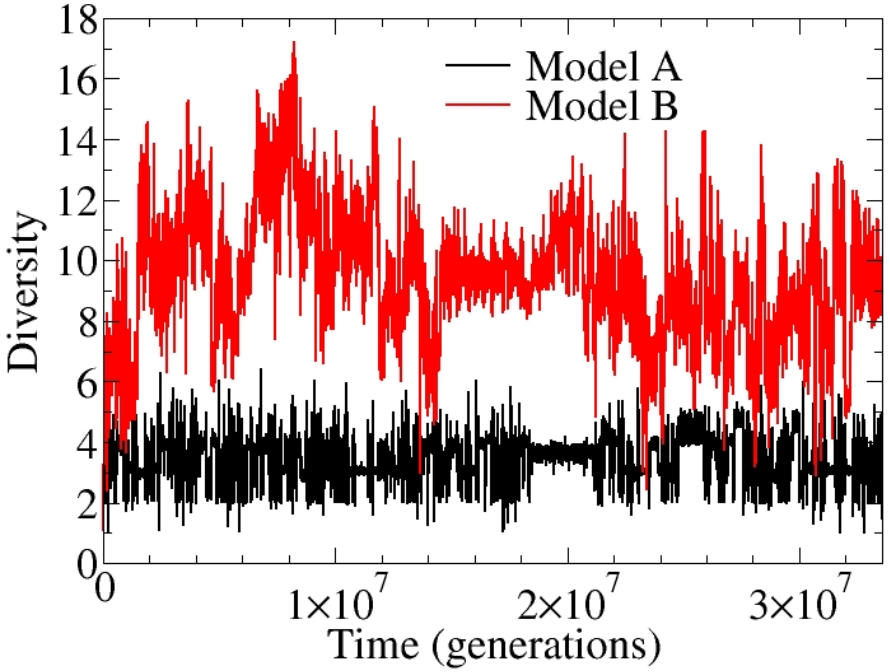
3a. Loop over individuals in I, producing F offspring with probability $P_I(\{n_J(t)\})$, or killing individual with probability $1-P_I$

3b. Loop over offspring to mutate with probability μ

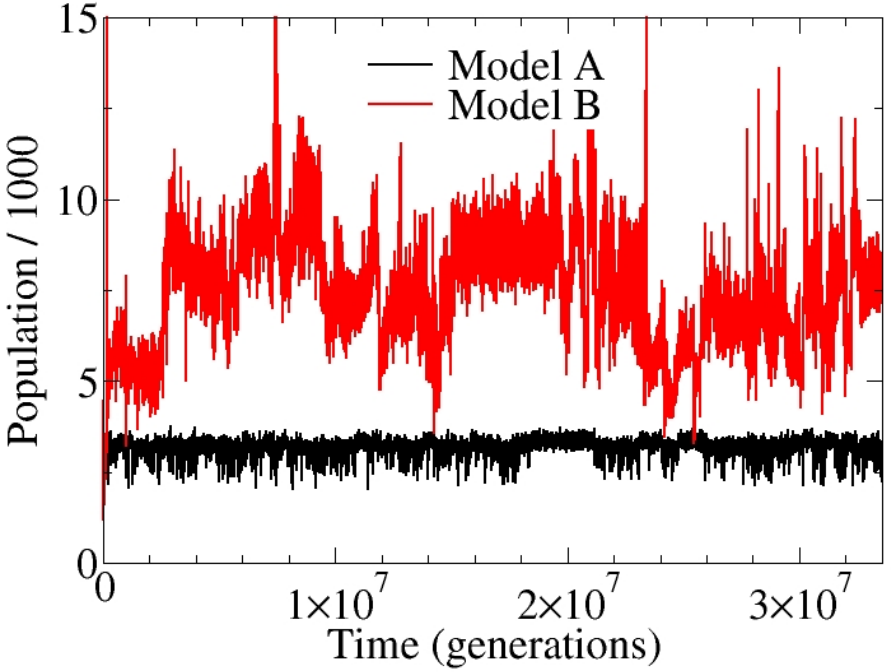
Monte Carlo time series

Periods of relative quiet (quasi-steady states, QSS), separated by periods of rapid evolution

Number of significant species



Total population size

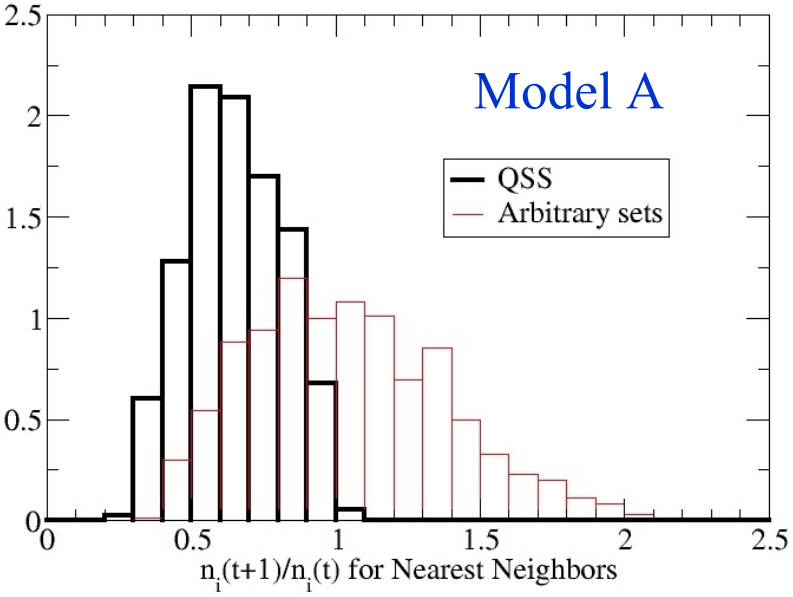


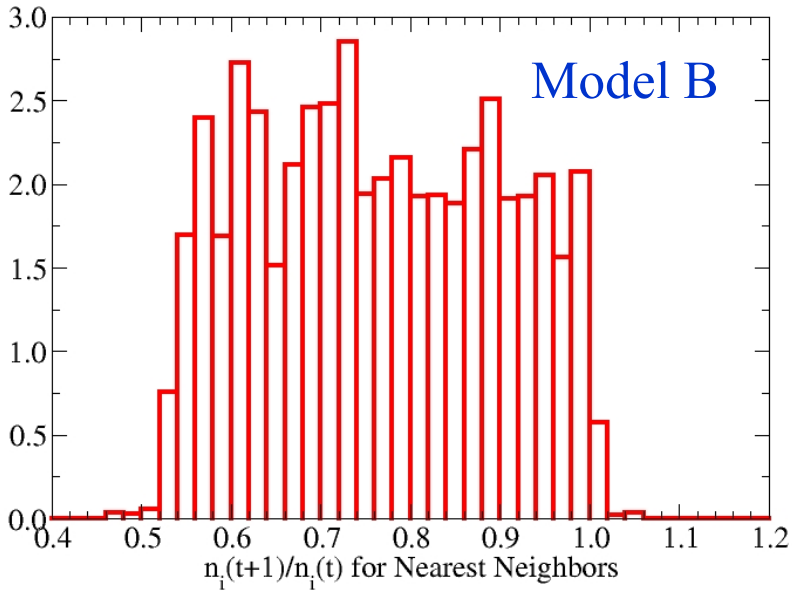
$L = 13$. Model A: $N_0 = 2000$. Model B: $R = 2000$.

Stability of Quasi-steady States (QSS)

Multiplication rate of small-population mutant *i* in presence of fixed point of $\mathcal{N}$ resident species, *J*, *K*:

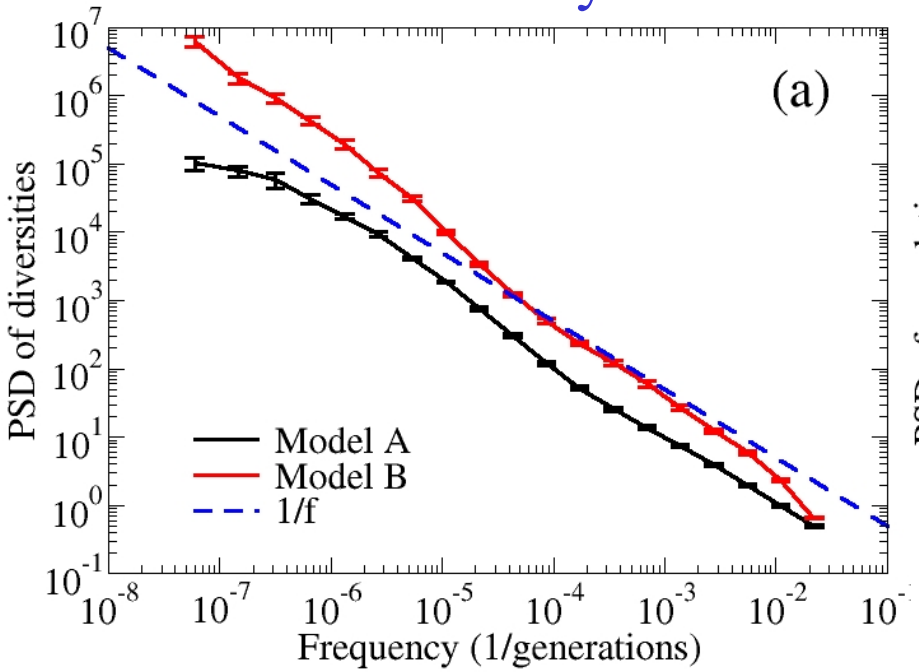
$$\ln\left(\frac{n_i(t+1)}{n_i(t)}\right) = \ln\left[\frac{F}{1+\exp[-\Delta_i(R,\{n_J^*\})]}\right]$$



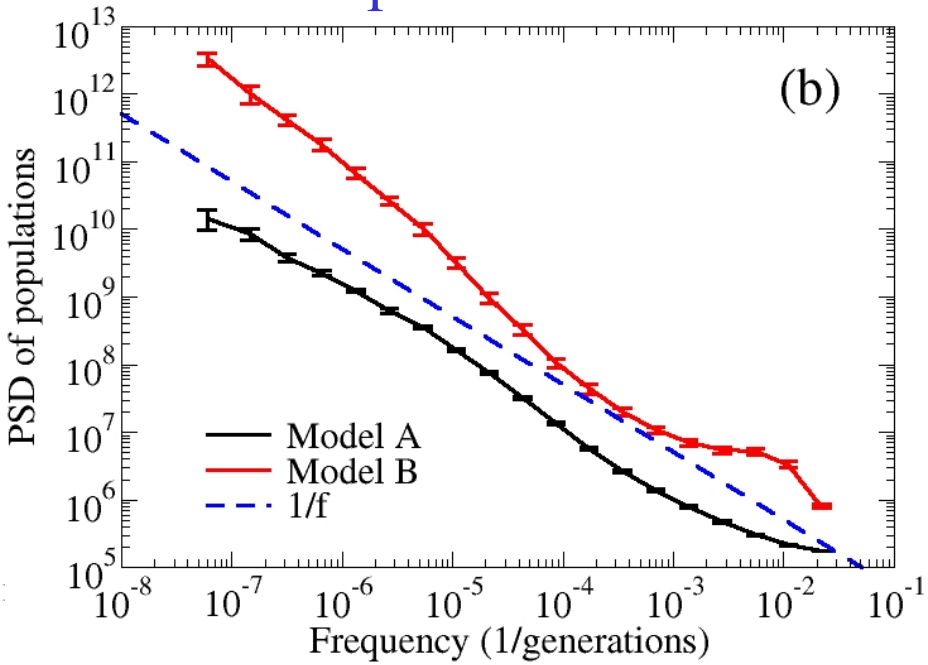


Power Spectral Densities (PSD)

Diversity



Population size

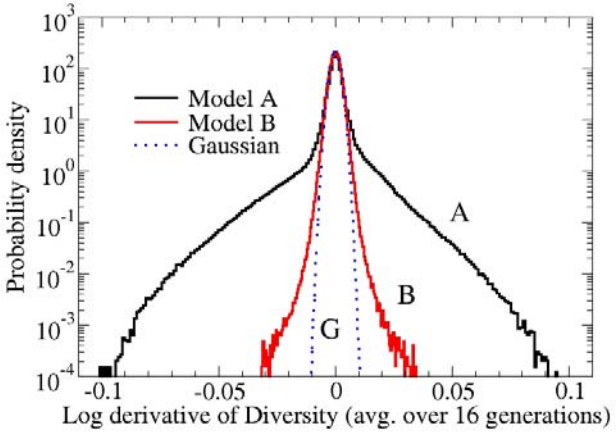


Both diversity and population size show approximate

$1/f$ behavior.

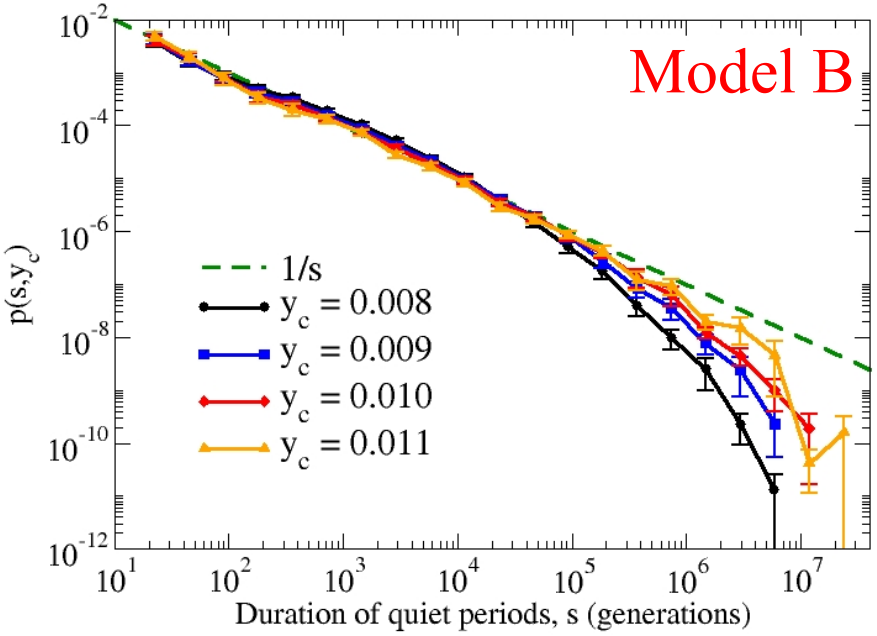
Population sizes contain additional high-frequency noise.

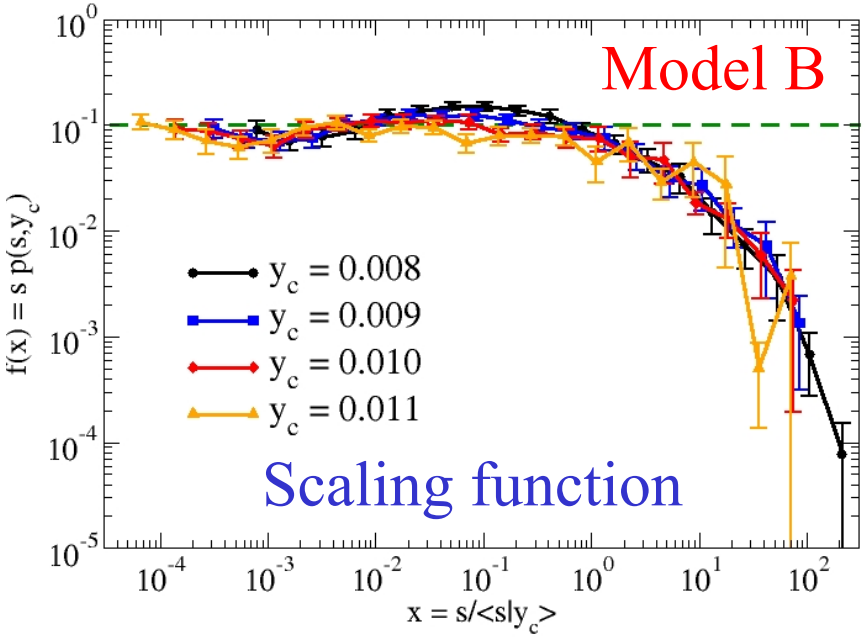
QSS statistics



$$p(s, y_c) = s^{-\tau} f(s / g(y_c))$$

Use
$\tau = 1$ and $g(y_c) = \langle s | y_c \rangle$



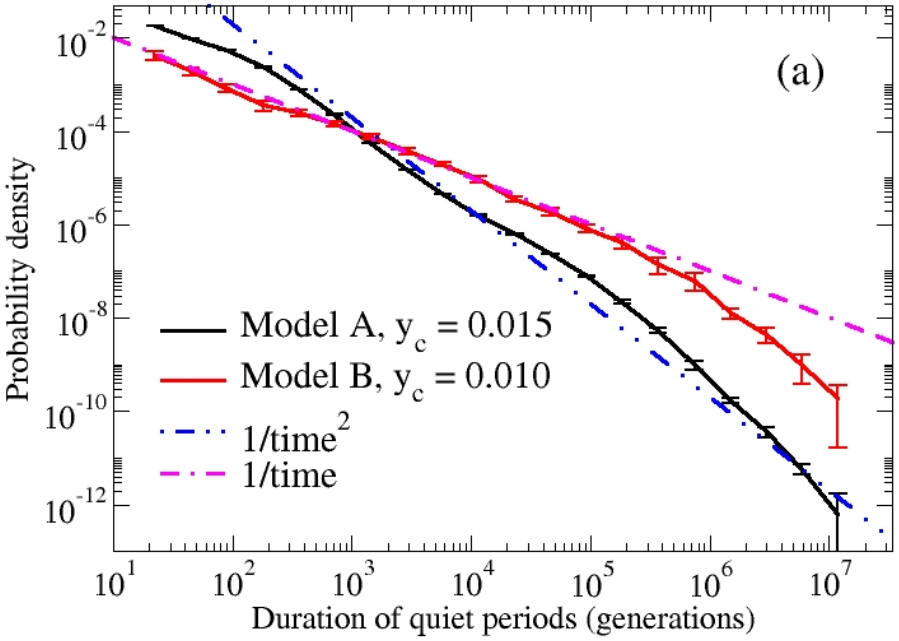


Characteristic times

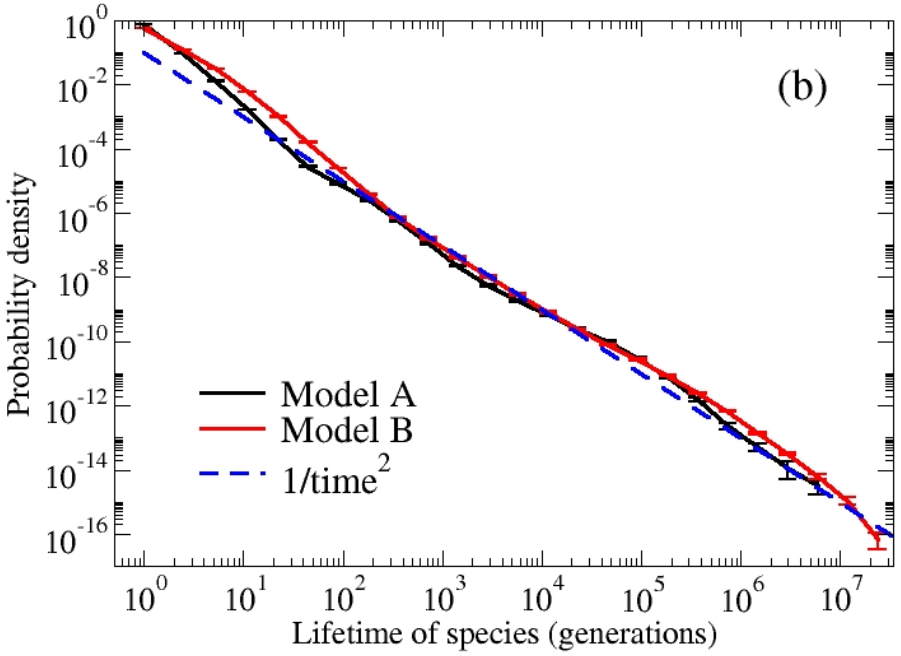
Approximate power laws over many decades

Possibly consistent with fossil record

QSS duration



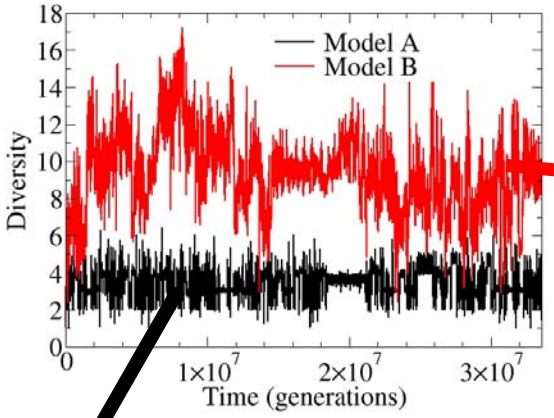
Species lifetimes



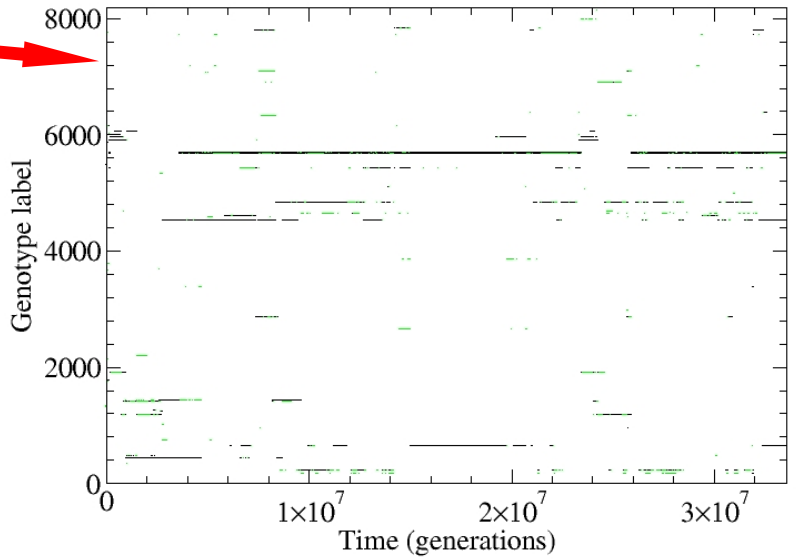
Different powers
for the two models

Same power
for both models

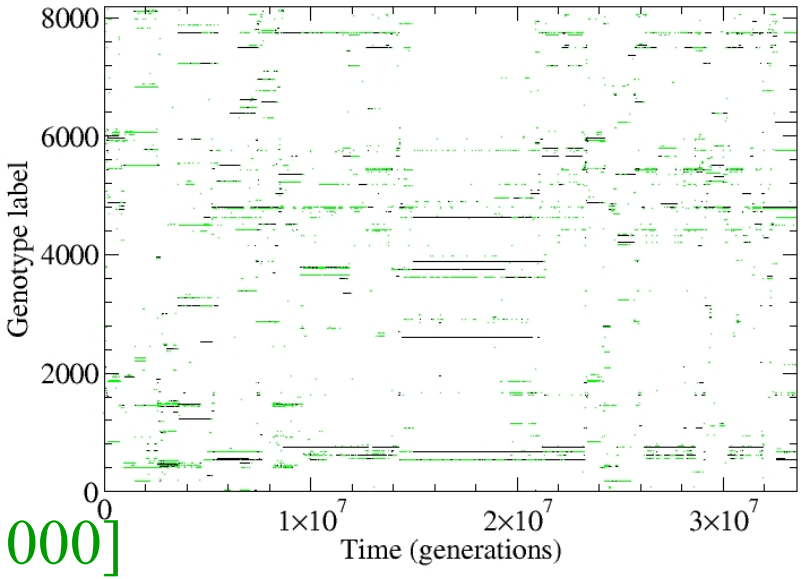
WHY?



Model B

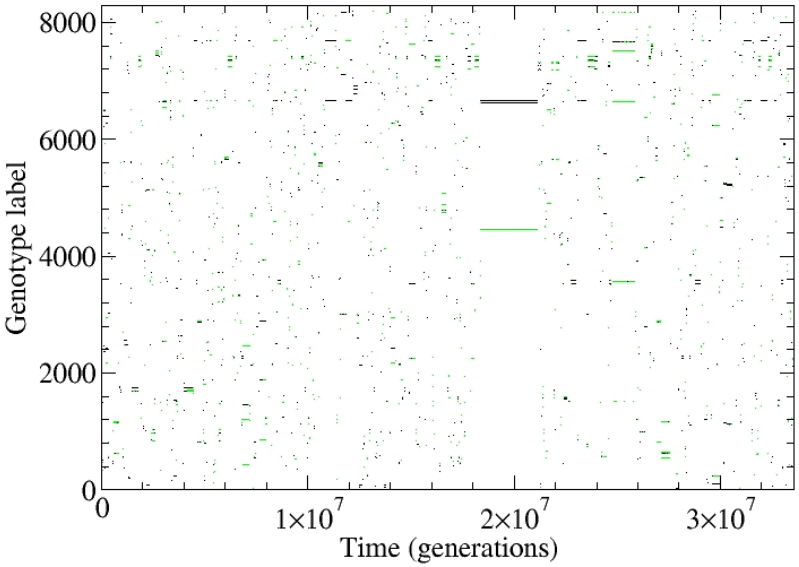


Producers



Consumers

Model A



Synchronized!

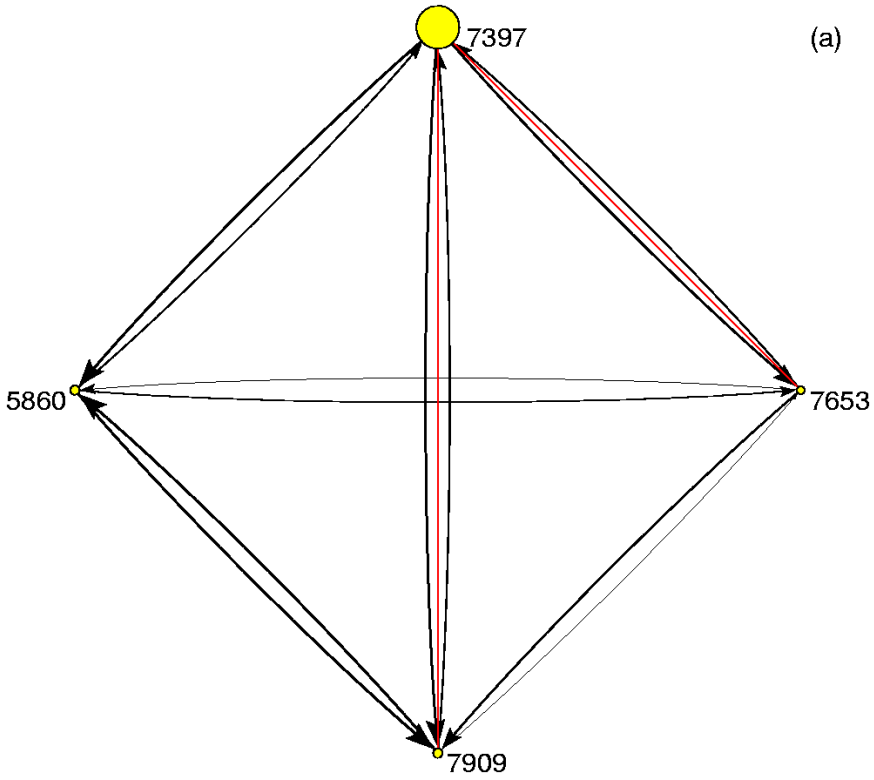
Green: $n_{I,2} \in [101,1000]$

Black: $n_I > 1000$

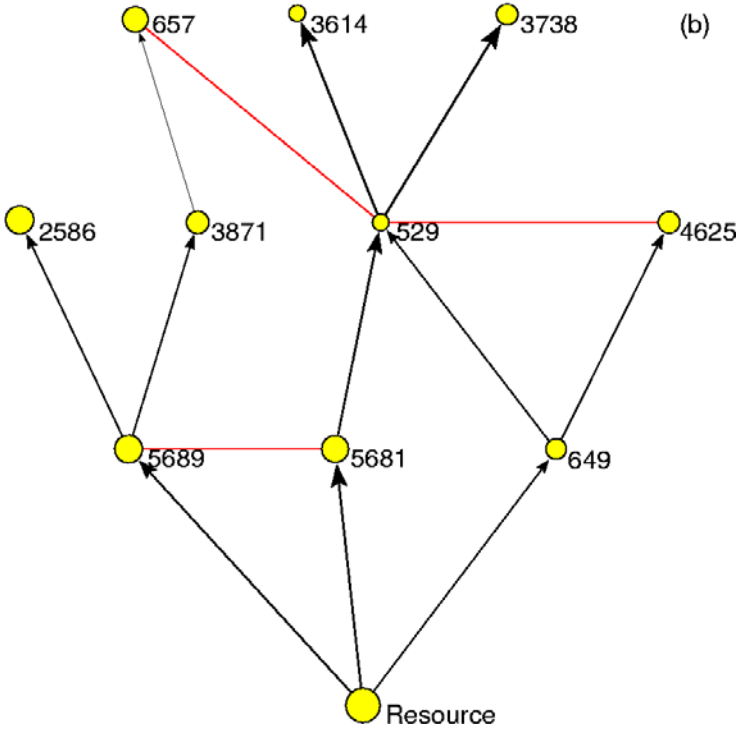
Not synchronized!

Typical community structures

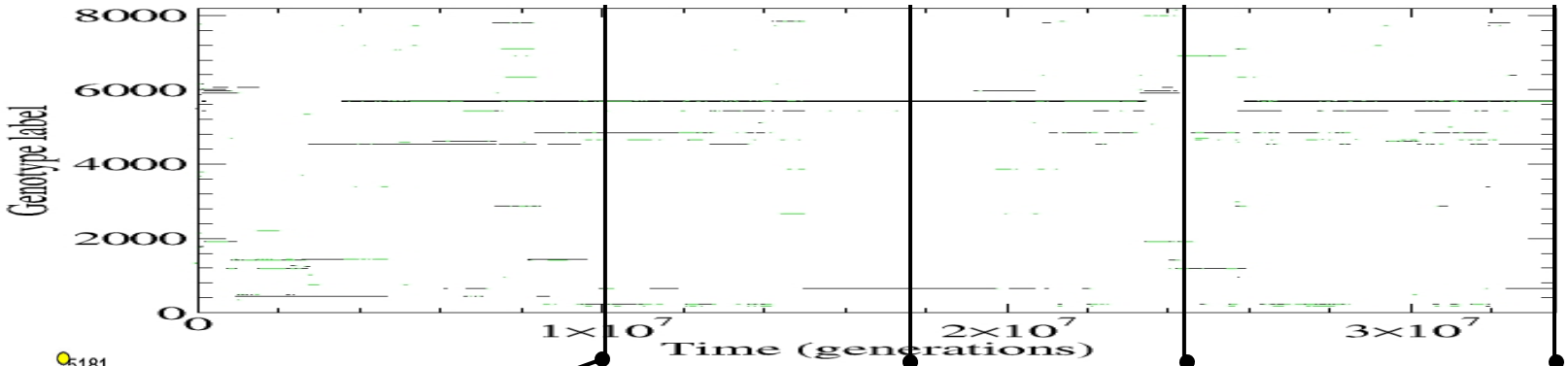
Model A



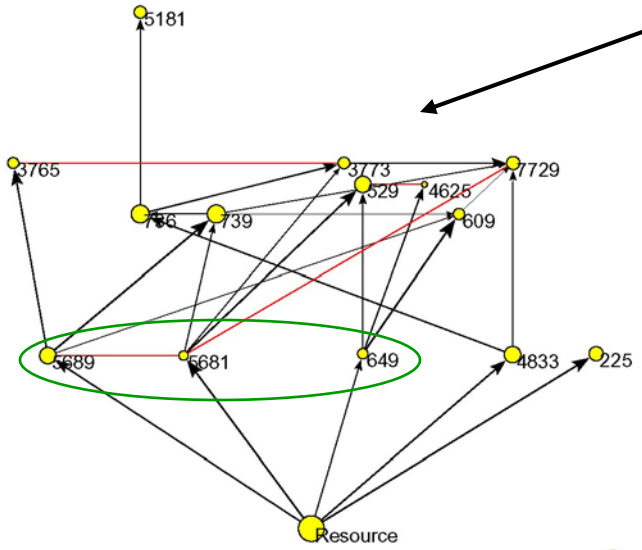
Model B

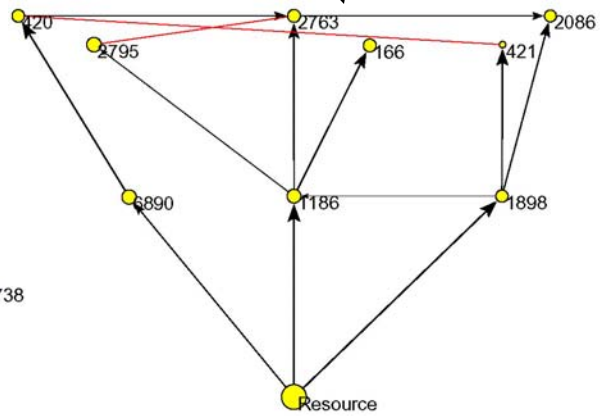


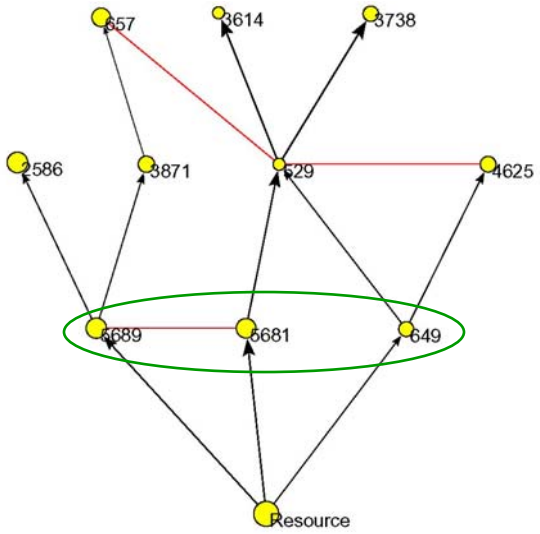
Communities in Model B

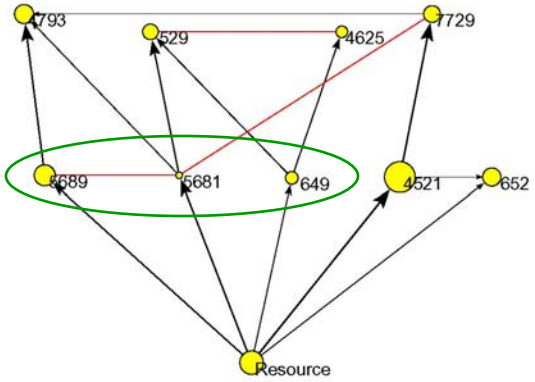


Producers









Moment of "truth"

Fossil data

Power spectrum

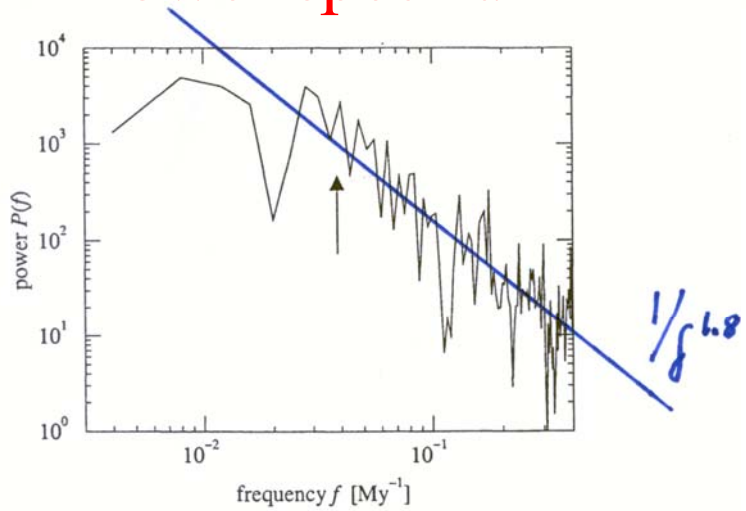


FIGURE 1.7 The power spectrum of familial extinction for marine animals over the last 250 My, calculated using data from the database compiled by Sepkoski (1992). The arrow marks the frequency corresponding to the conjectured 26 My periodicity of extinctions. Note that the scales on both axes are logarithmic.

Genus lifetime pdf

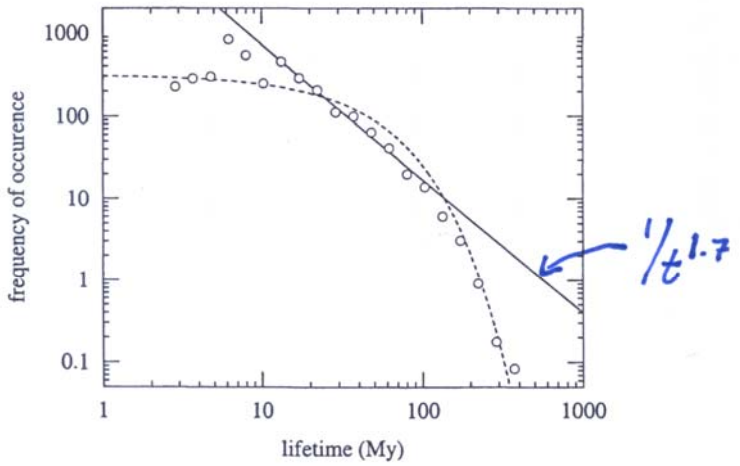
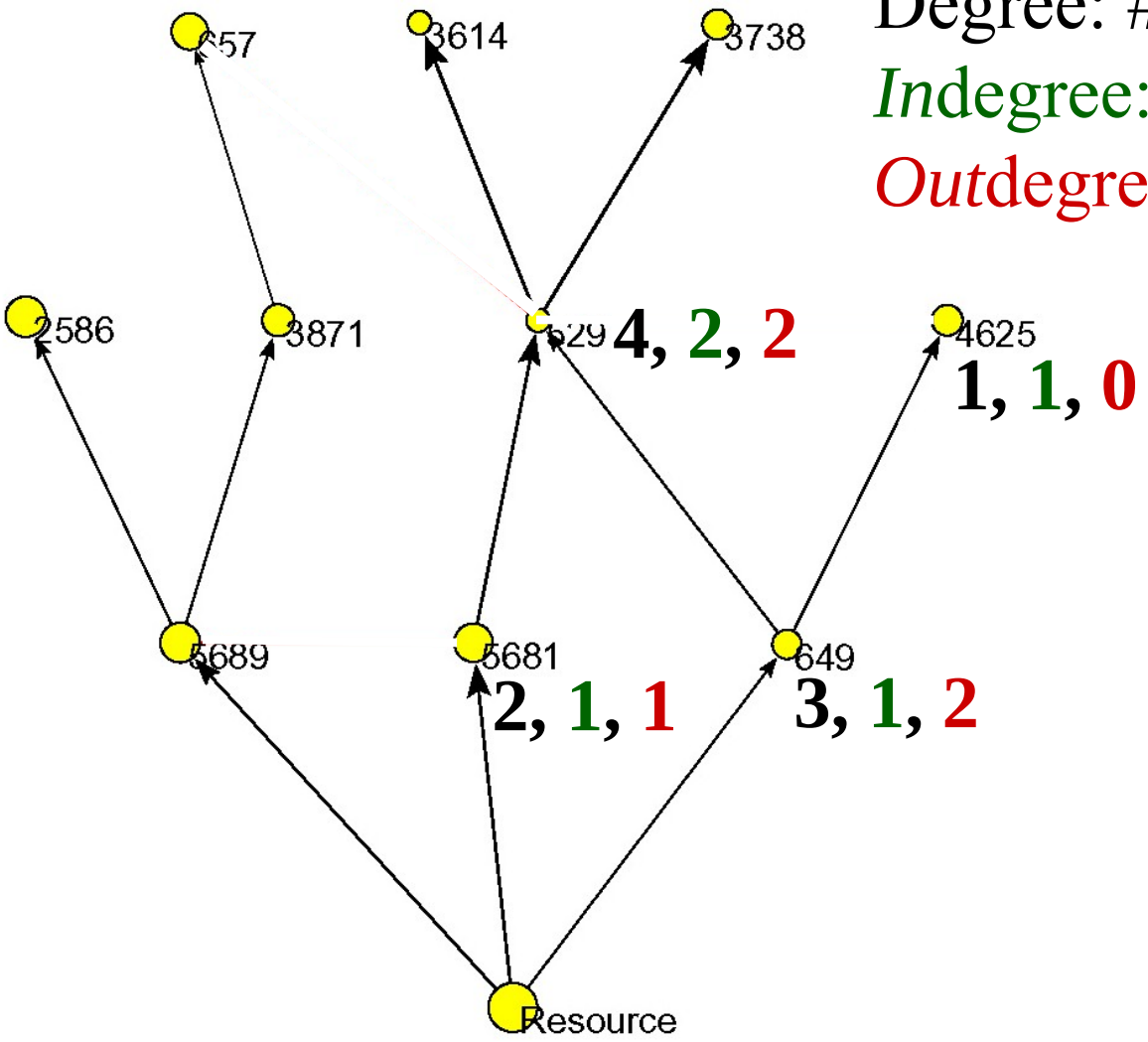


FIGURE 1.10 Frequency distribution of marine genus lifetimes in the fossil record. The solid line is the best power-law fit to the data between 10 and 100 My, while the dotted line is the best exponential fit to all the data. After Newman and Sibani (1999).

Figures from M.E.J. Newman and R.G. Palmer, *Modeling Extinction* (Oxford Univ. Press, 2003).

Degree of a network node

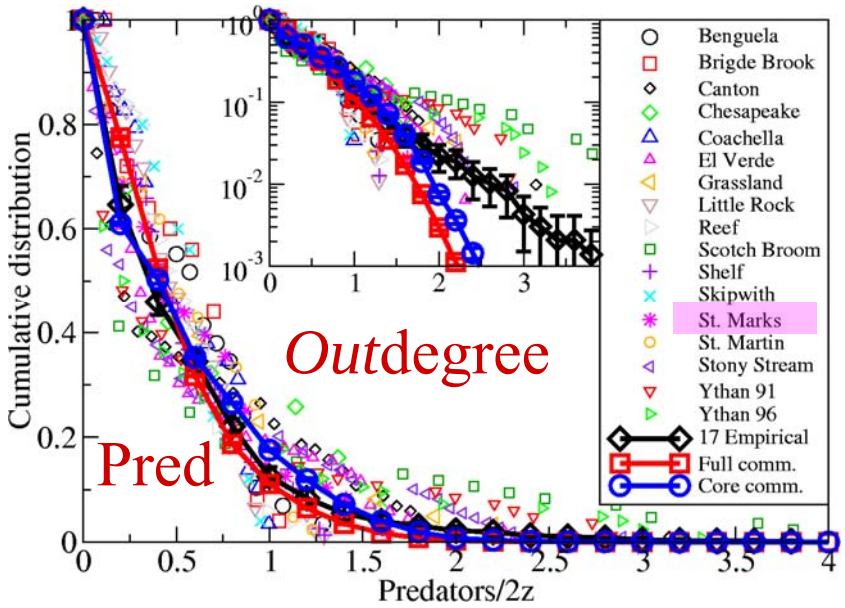


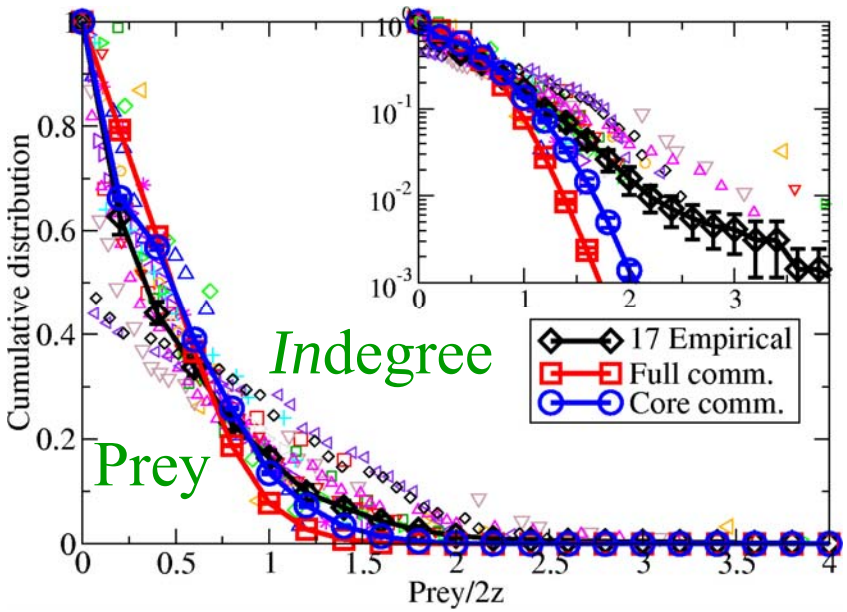
Degree: # of links

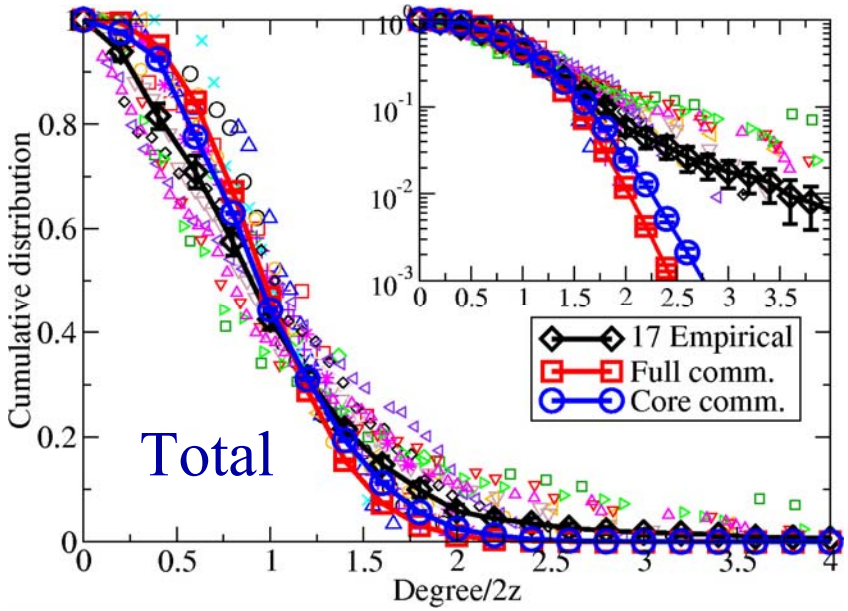
*In*degree: # of *in*links

*Out*degree: # of *out*links

Scaled, cumulative degree distributions







Model B

Mutation vs Invasion

work with

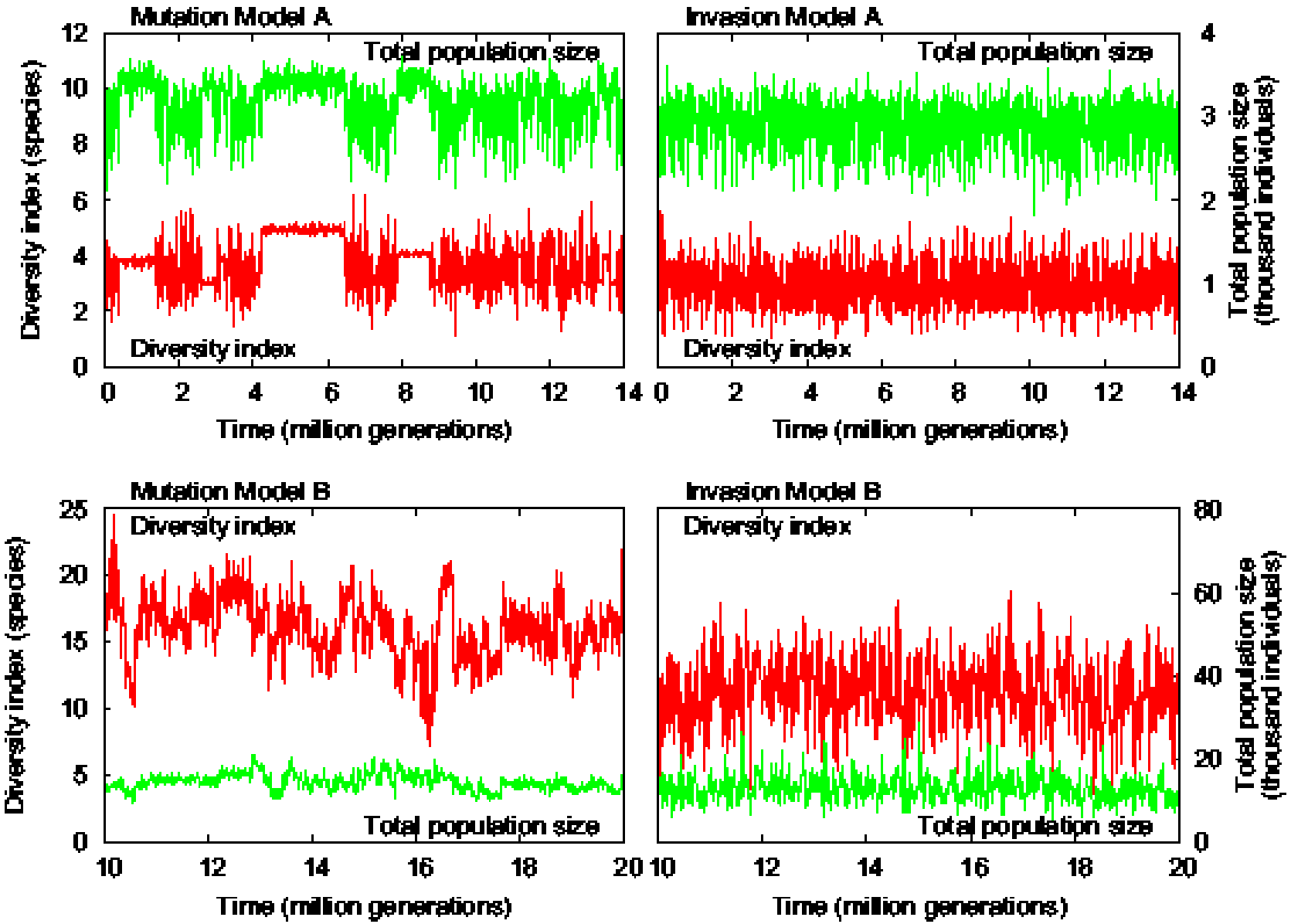
Y. Murase, T. Shimada, and N. Ito,

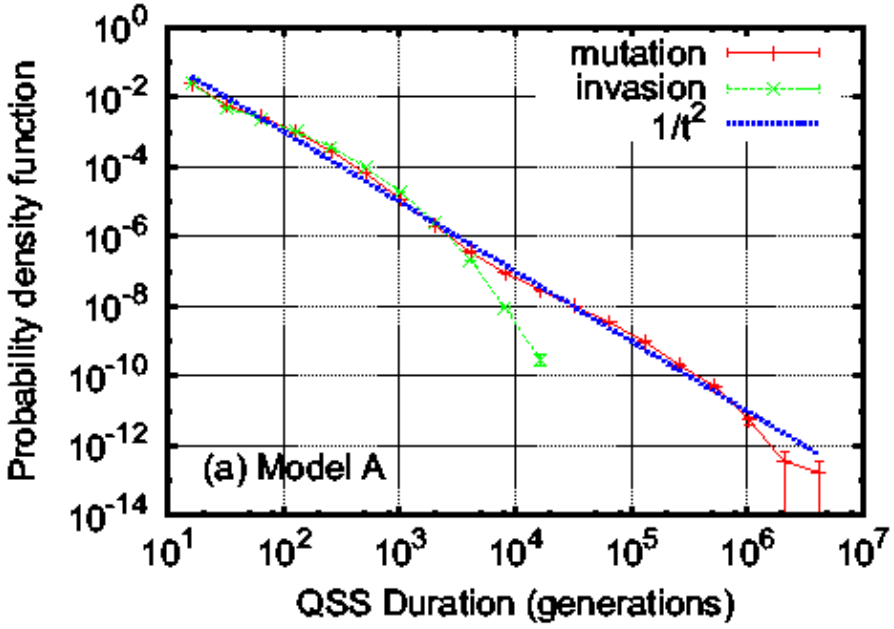
University of Tokyo

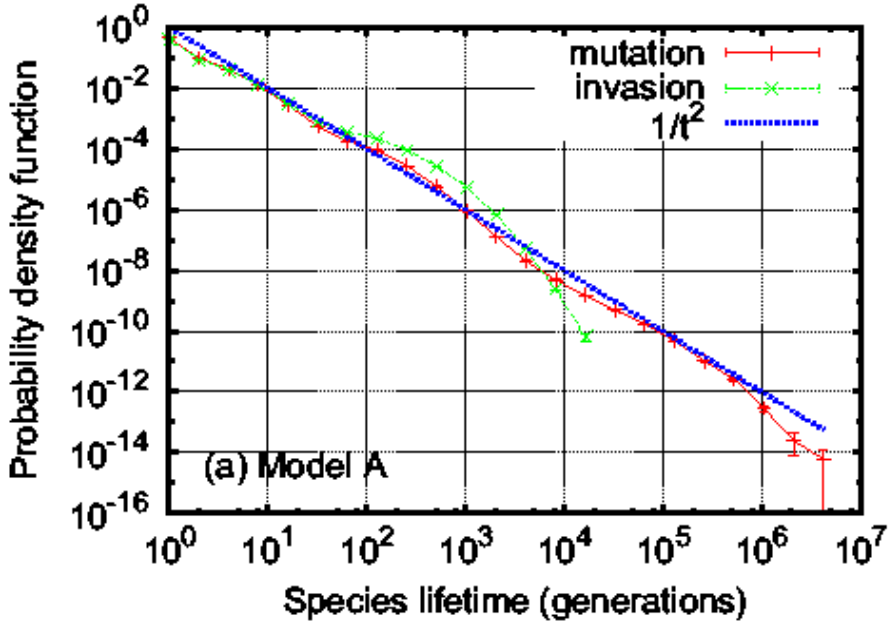
- Mutation: Number of different mutants accessible to a given community

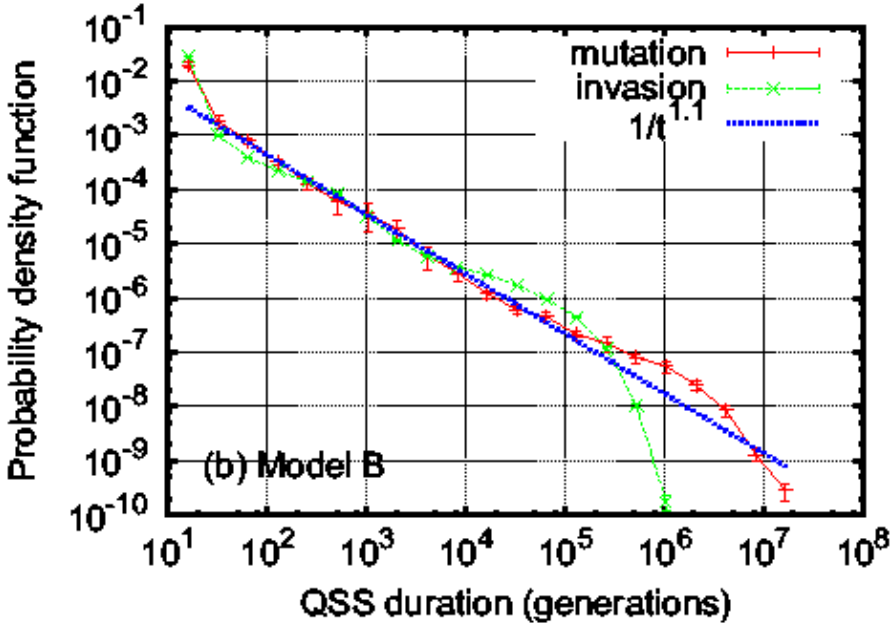
  limited to genetic neighbors.

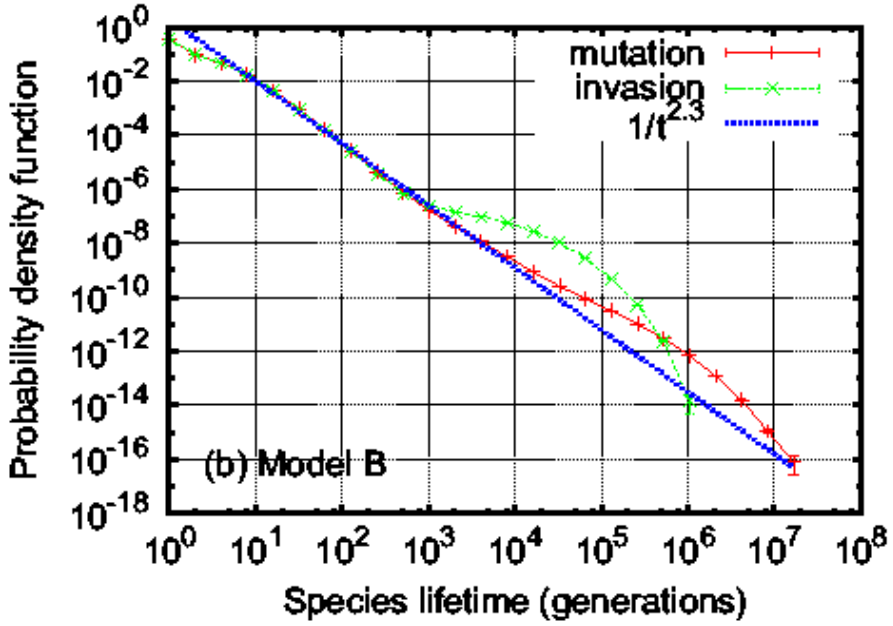
- Invasion: Number of possible invaders *unlimited*.


Mutation Model A
Total population size
Diversity index
Diversity index (species)
Time (million generations)
Invasion Model A
Total population size
Diversity index
Total population size (thousand individuals)
Time (million generations)
Mutation Model B
Diversity index
Total population size
Diversity index (species)
Time (million generations)
Invasion Model B
Diversity index
Total population size
Total population size (thousand individuals)
Time (million generations)

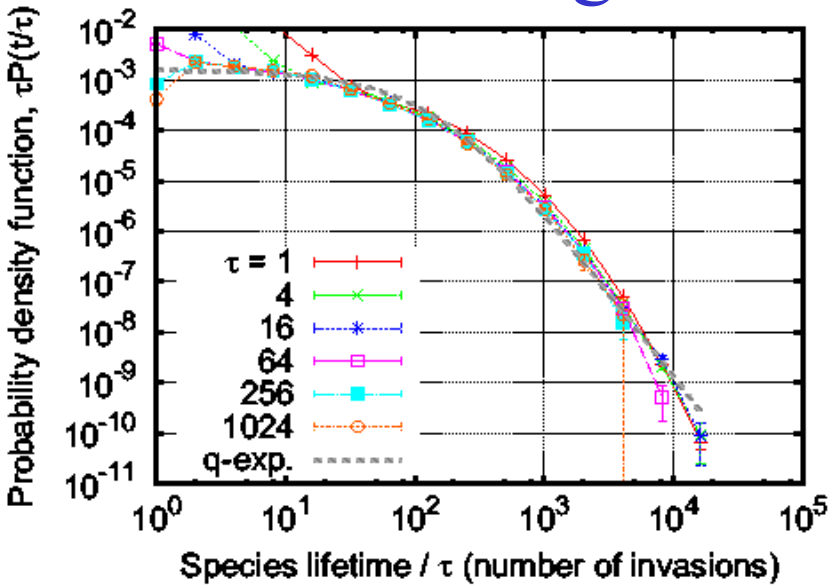

mutation
invasion
1/t^2
(a) Model A
Probability density function
QSS Duration (generations)

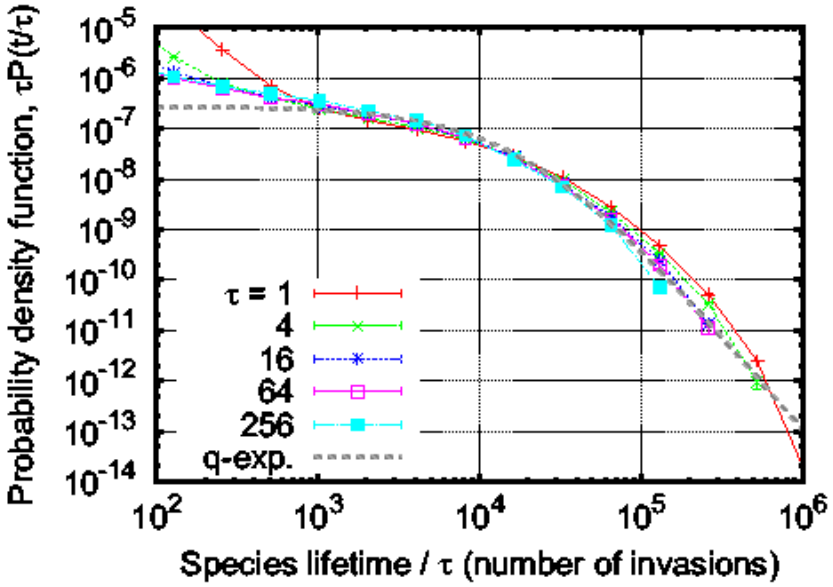

mutation
invasion
1/t^2
(a) Model A
Probability density function
Species lifetime (generations)


mutation
invasion
1/t^1.1
(b) Model B
Probability density function
QSS duration (generations)


mutation
invasion
1/t^2.3
(b) Model B
Probability density function
Species lifetime (generations)

Scaling for invasion model





Scaling function for lifetimes (and QSS durations) fitted with q-exponential,

$$[1-(1-q)\beta t]^{1/(1-q)}$$

with $\beta > 0$ and $q > 1$.

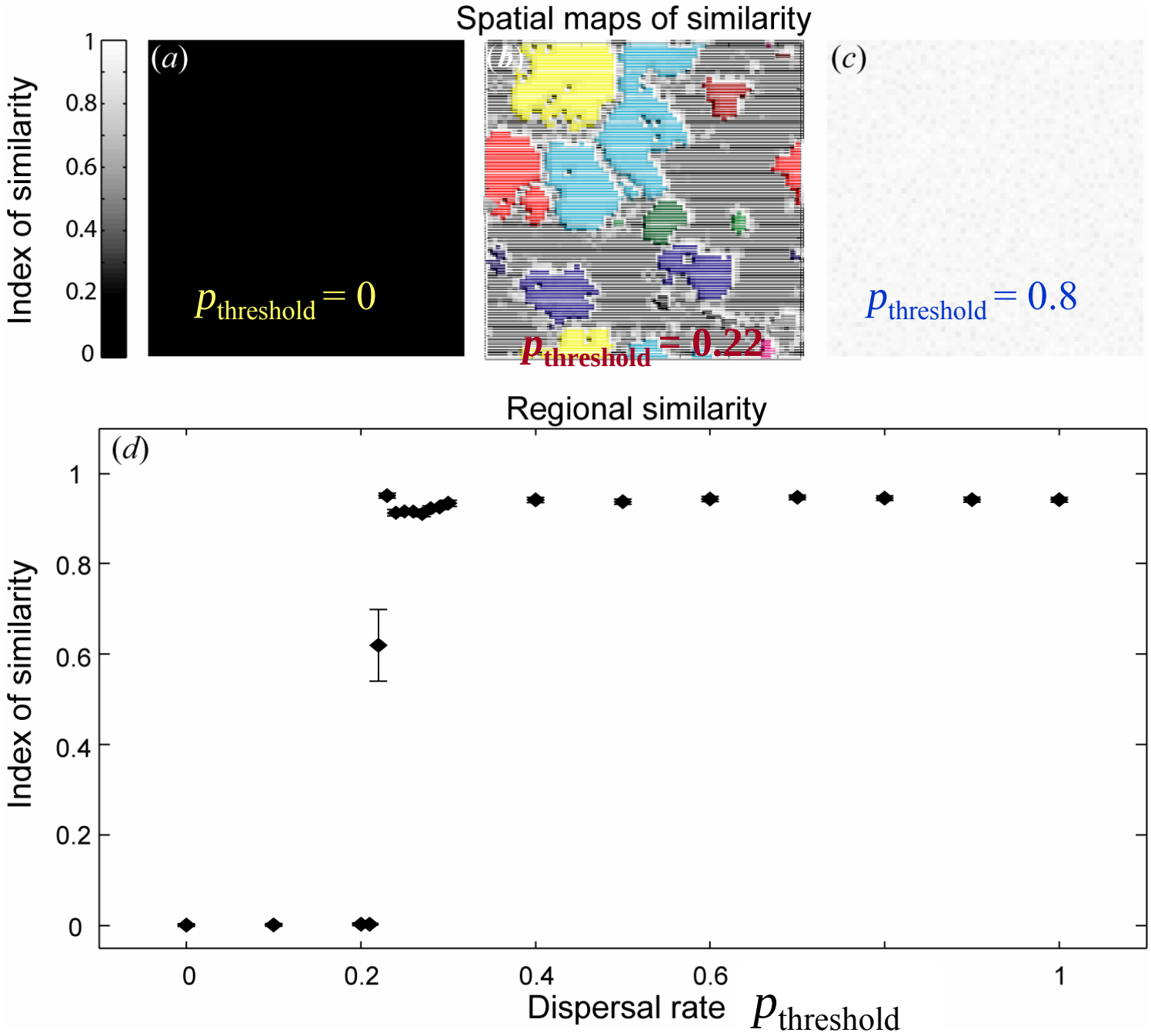
$\beta t >> 1$: power law

$q \to 1^{-}$: exponential

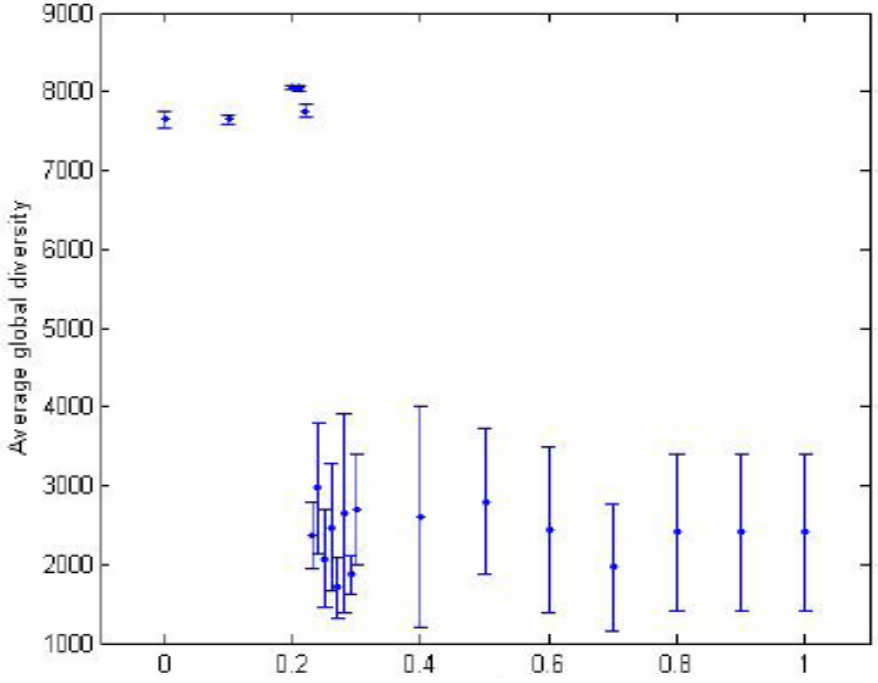
Spatially extended model

- Work with Elise Filotas and Lael Parrott (U. Montreal) and Martin Grant (McGill U.).
- Place **Model A** on 2D lattice.
- Include "community-dependent" dispersion: Individuals with $P_I < p_{\text{threshold}}$

  move randomly to neighboring site in the "hope" of improving their chances somewhere else.

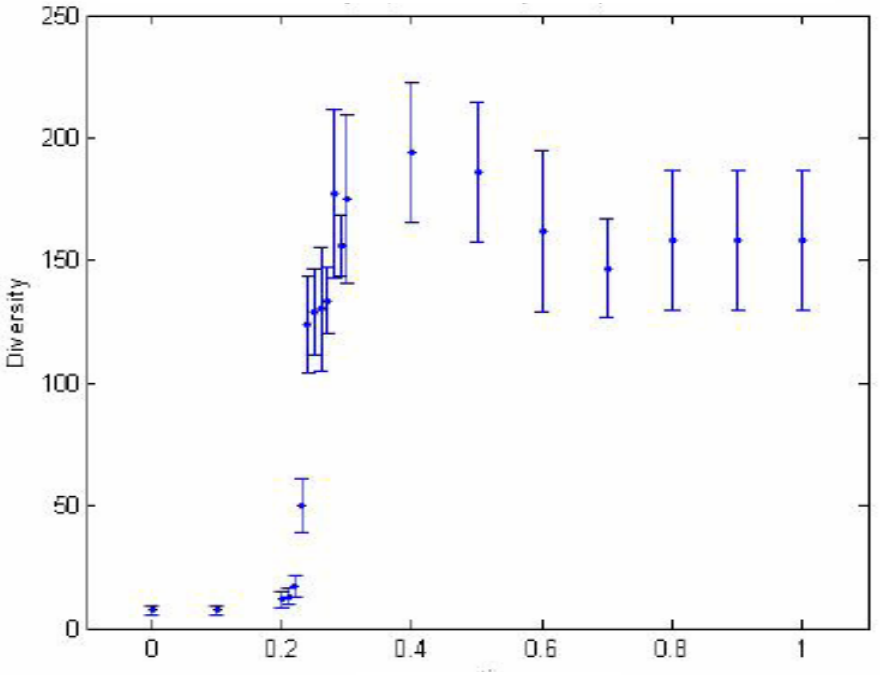

Spatial maps of similarity
Index of similarity
1
0.8
0.6
0.4
0.2
0
(a)
$p_{threshold} = 0$
(b)
$p_{threshold} = 0.22$
(c)
$p_{threshold} = 0.8$
Regional similarity
(d)
Index of similarity
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
1
Dispersal rate $p_{threshold}$

Average global (γ) diversity



$p_{\text{threshold}}$

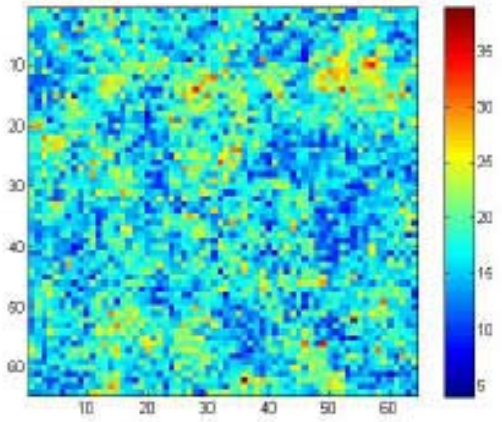
Average local (α) diversity



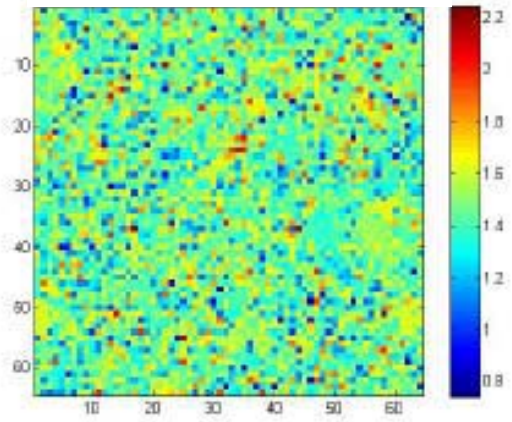
$p_{\text{threshold}}$

$p_{\text{threshold}} = 0.22$

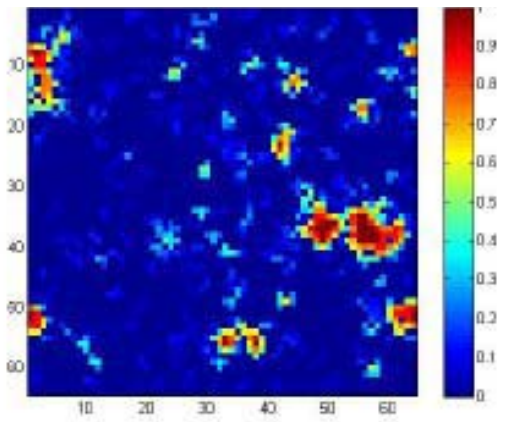
Diversity



Shannon diversity

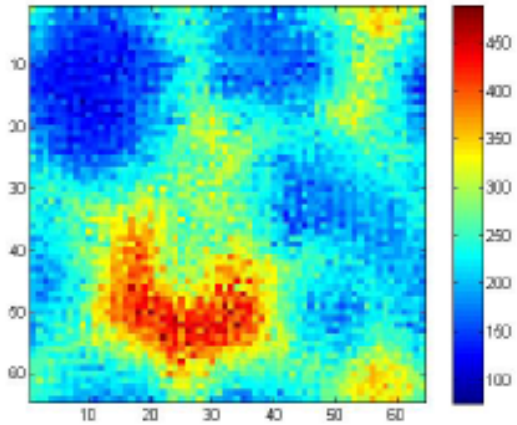


Neighborhood similarity

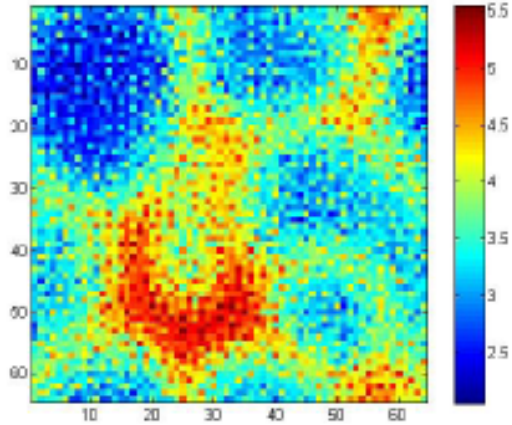


$p_{\text{threshold}} = 0.28$

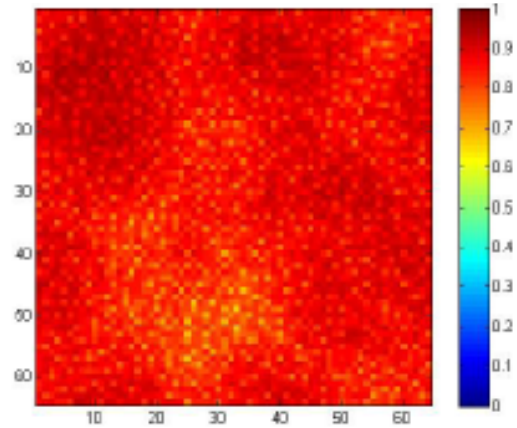
Diversity



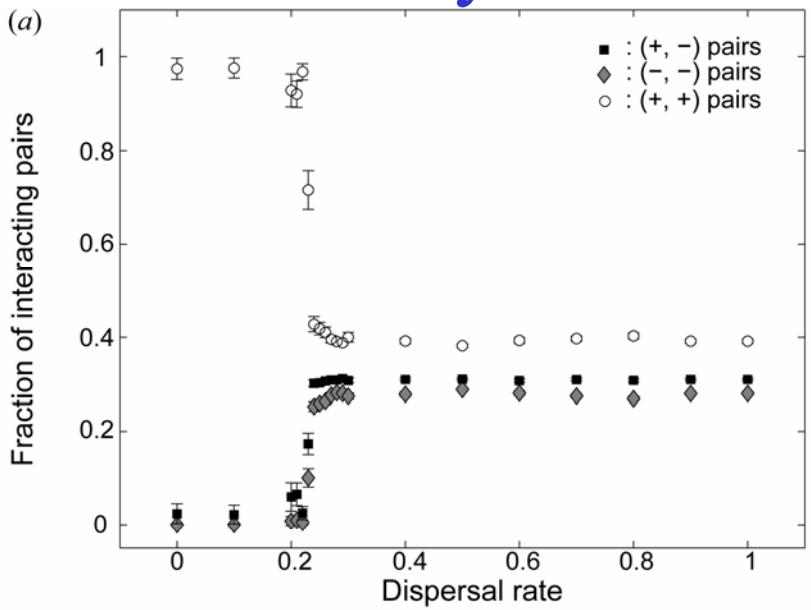
Shannon diversity

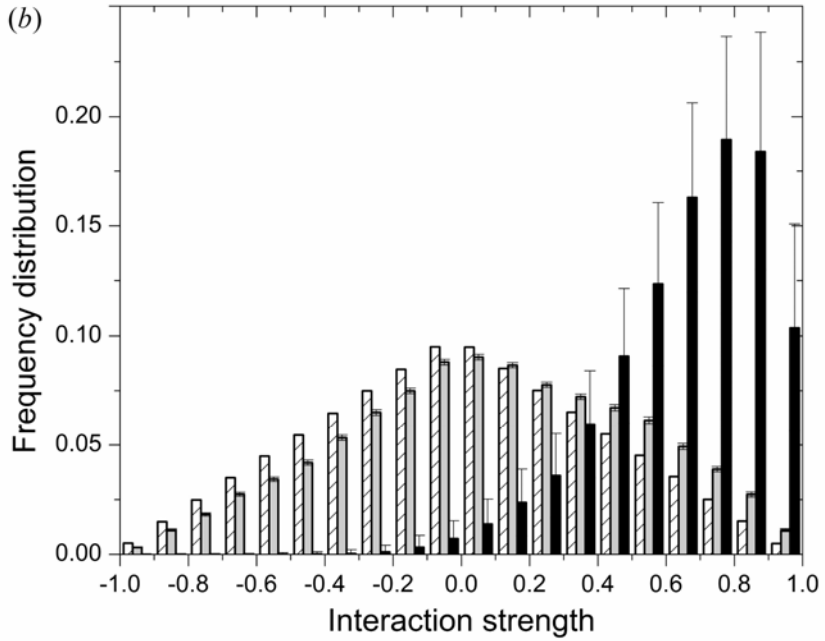


Neighborhood similarity



Community structure





$p_{\text{threshold}} = 0$

$p_{\text{threshold}} = 0.8$

unselected

Conclusions

- Biological evolution involves highly interactive, nonlinear problems well suited for statistical mechanics.
- Mapping onto ϕ^3 system with ***evolving*** "pump strength"
- Model A generates "spontaneous population",
  Model B generates "resource-supported population"
- Intermittent dynamics reminiscent of
  punctuated equilibria.
- Power-law distributions
  of species lifetimes and QSS durations
- Approximate $1/f$ noise
- Model B generates communities with
  multiple trophic levels.
- Invasion models do **not** have long-time correlations.
- Spatially extended **Model A** has phase transition with respect to dispersion threshold.

Publications

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- V. Sevim and P.A.R., J. Phys. A, **38**, 9475 (2005).
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- P.A.R., J. Math. Biol. **55**, 653-677 (2007).
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- E. Filotas, M. Grant, L. Parrott, and P.A.R, Ecol. Complex **5**, 238-251 (2008) and submitted to J. Theor. Biol.
- Y. Murase et al., submitted to J. Theor. Biol.