Modelling Ecosystem Evolution

A Complexity Science Approach

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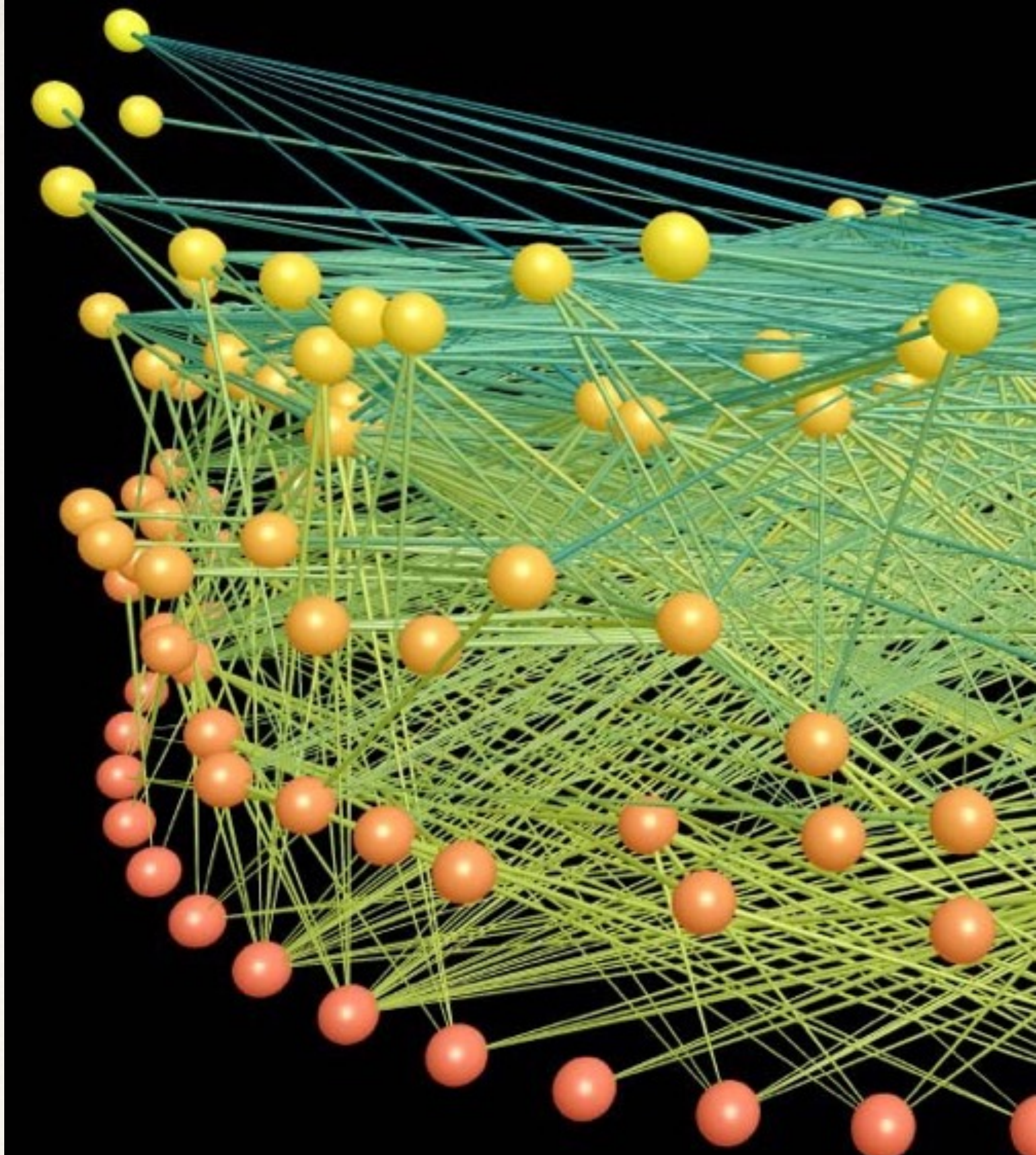


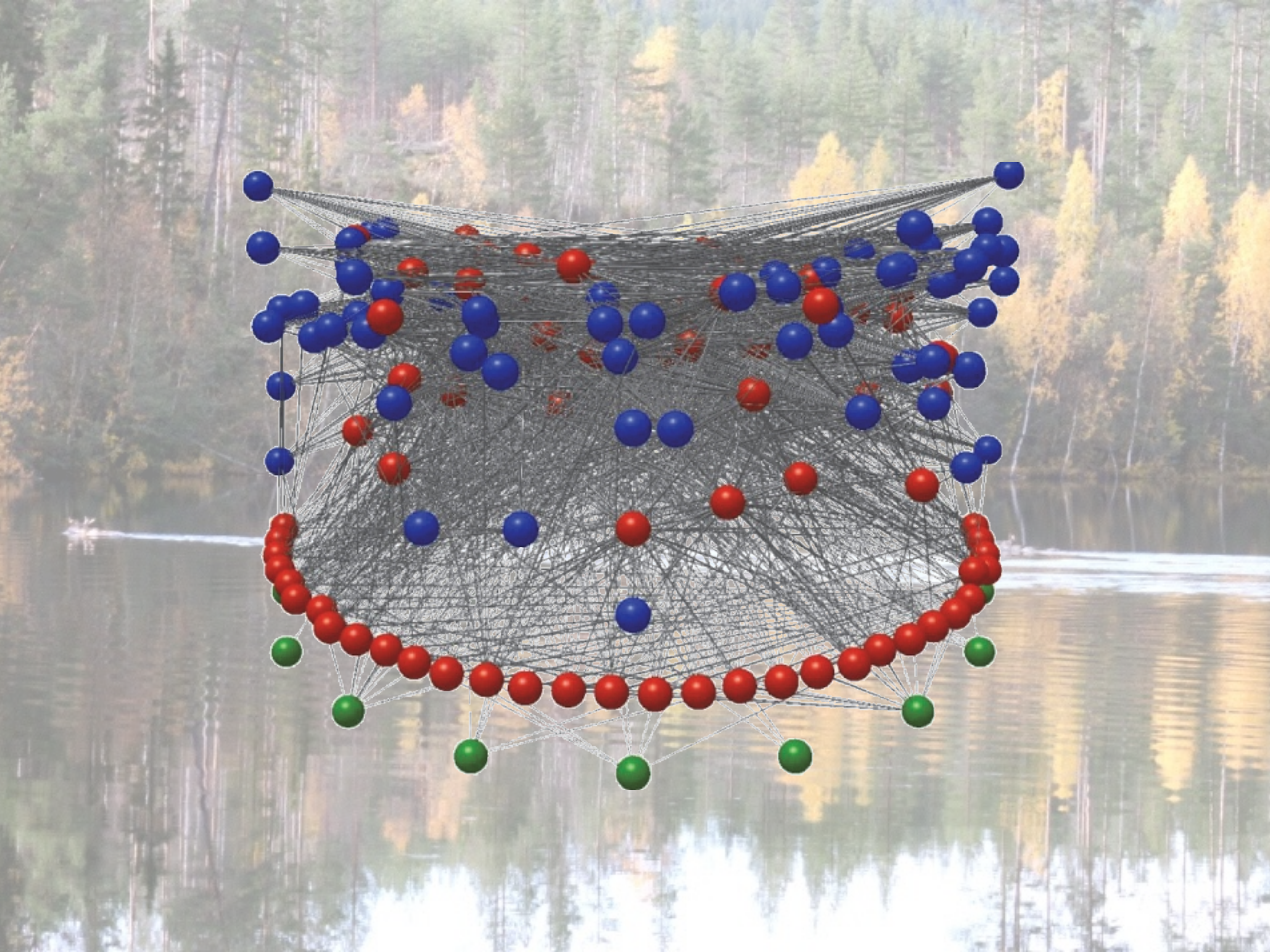
„In anything at all, perfection is finally attained not when there is no longer anything to add, but when there is no longer anything to take away.“

[Antoine de Saint-Exupéry, Wind, Sand and Stars, 1939]

Agenda

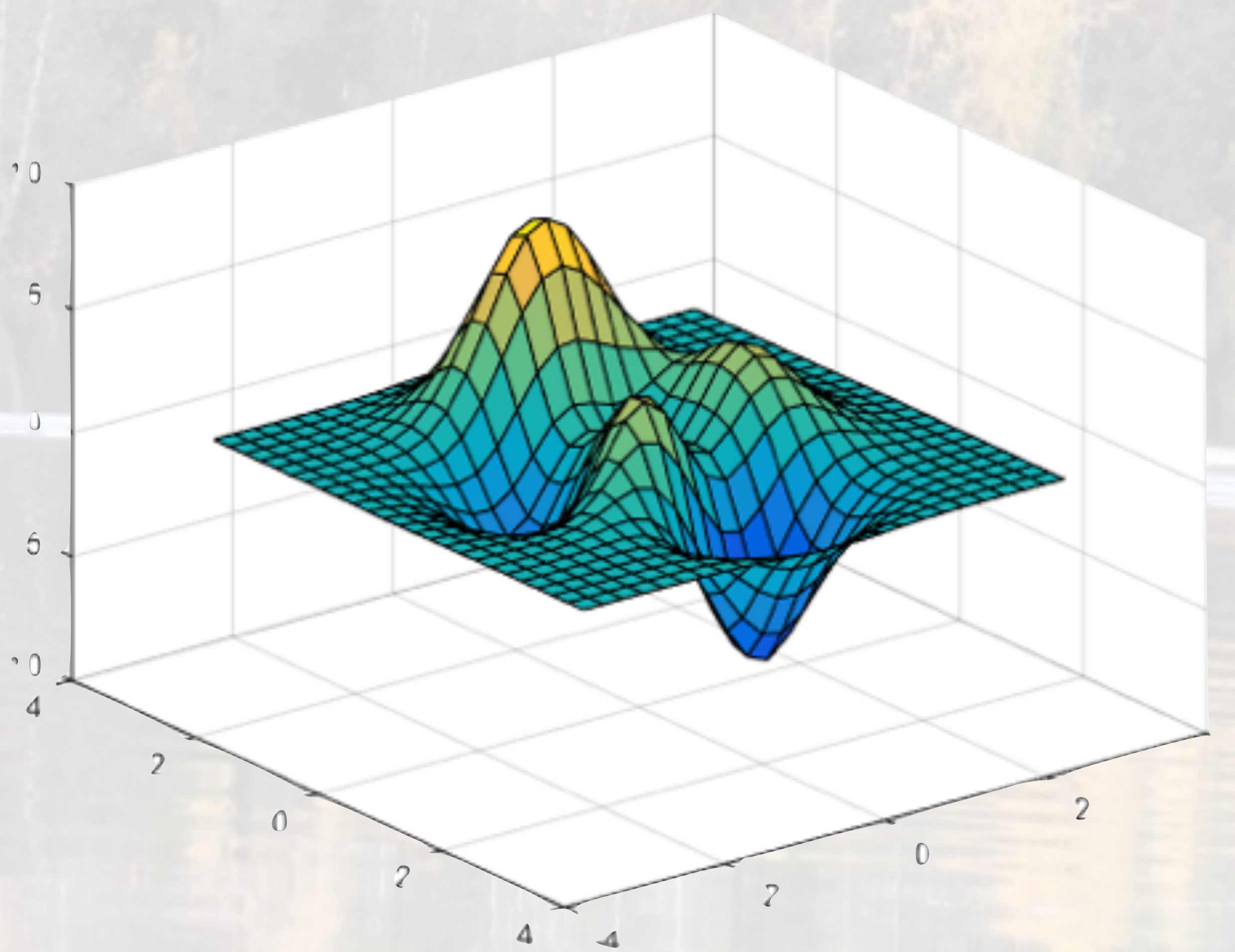
- Why complexity science and ecology? What is complexity science?
- Modelling complex ecosystem evolution: the Tangled Nature Model of Evolutionary Ecology
- Capturing macroscopic patterns: the Maximum Entropy Theory of Ecology


Why complexity science
and ecology?



Ecosystems are complex

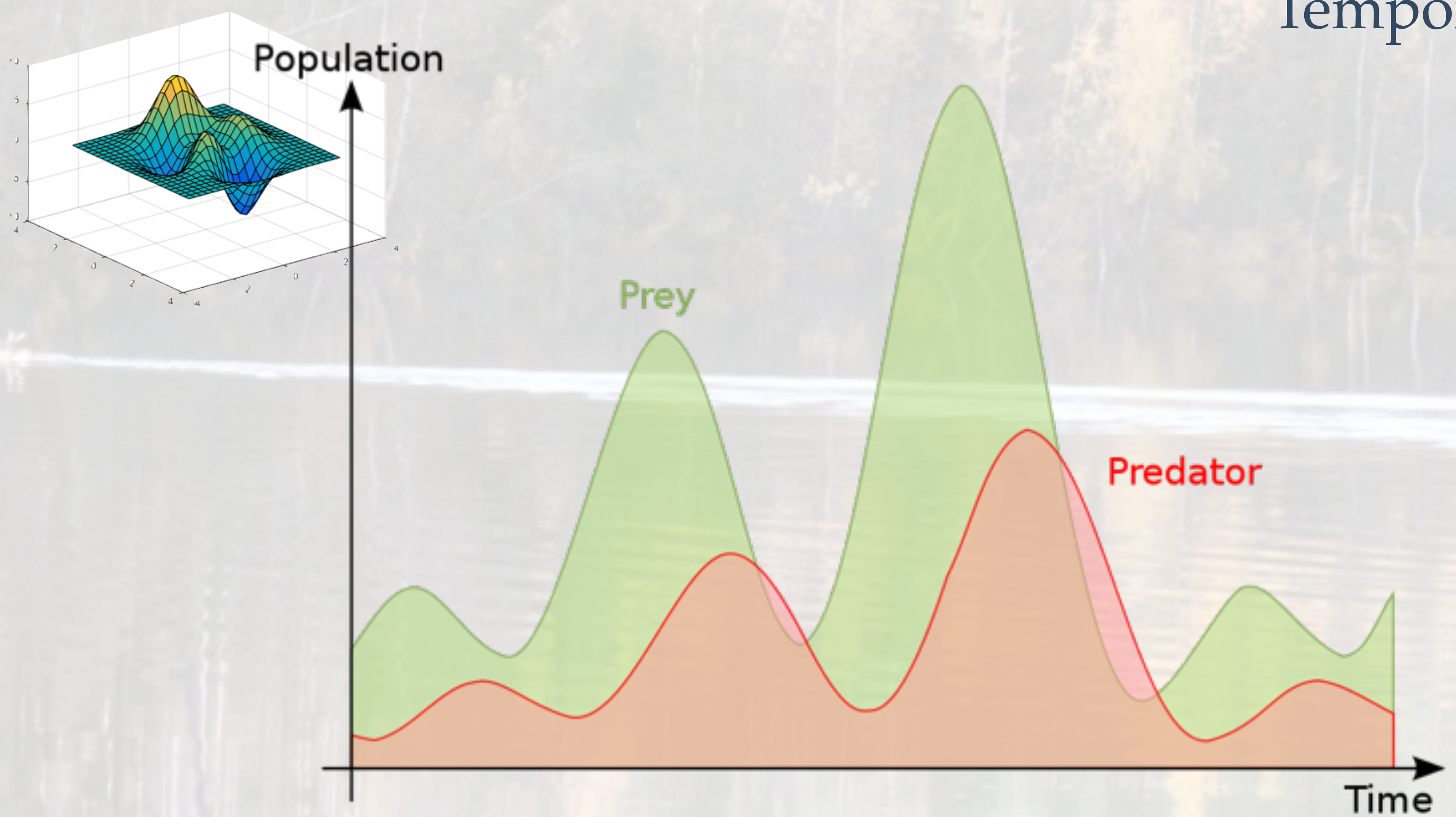
Spatial Complexity



Lohle 2004

Ecosystems are complex

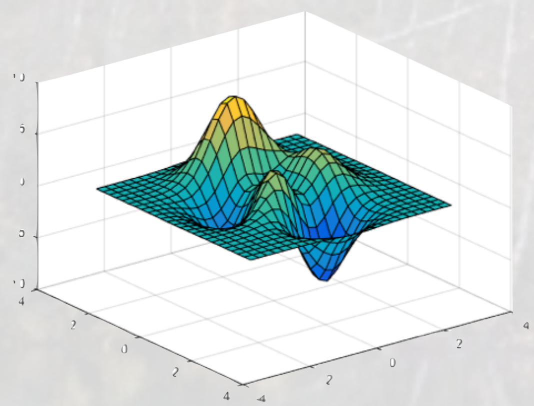
Temporal Complexity

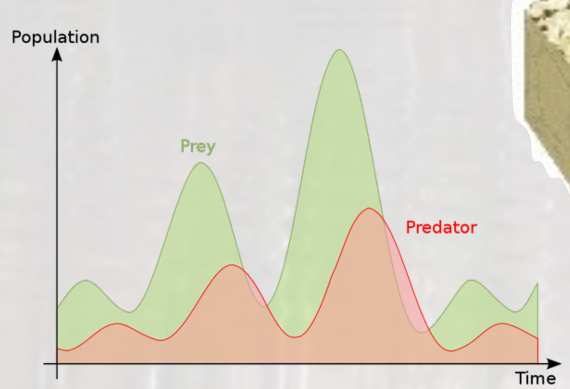


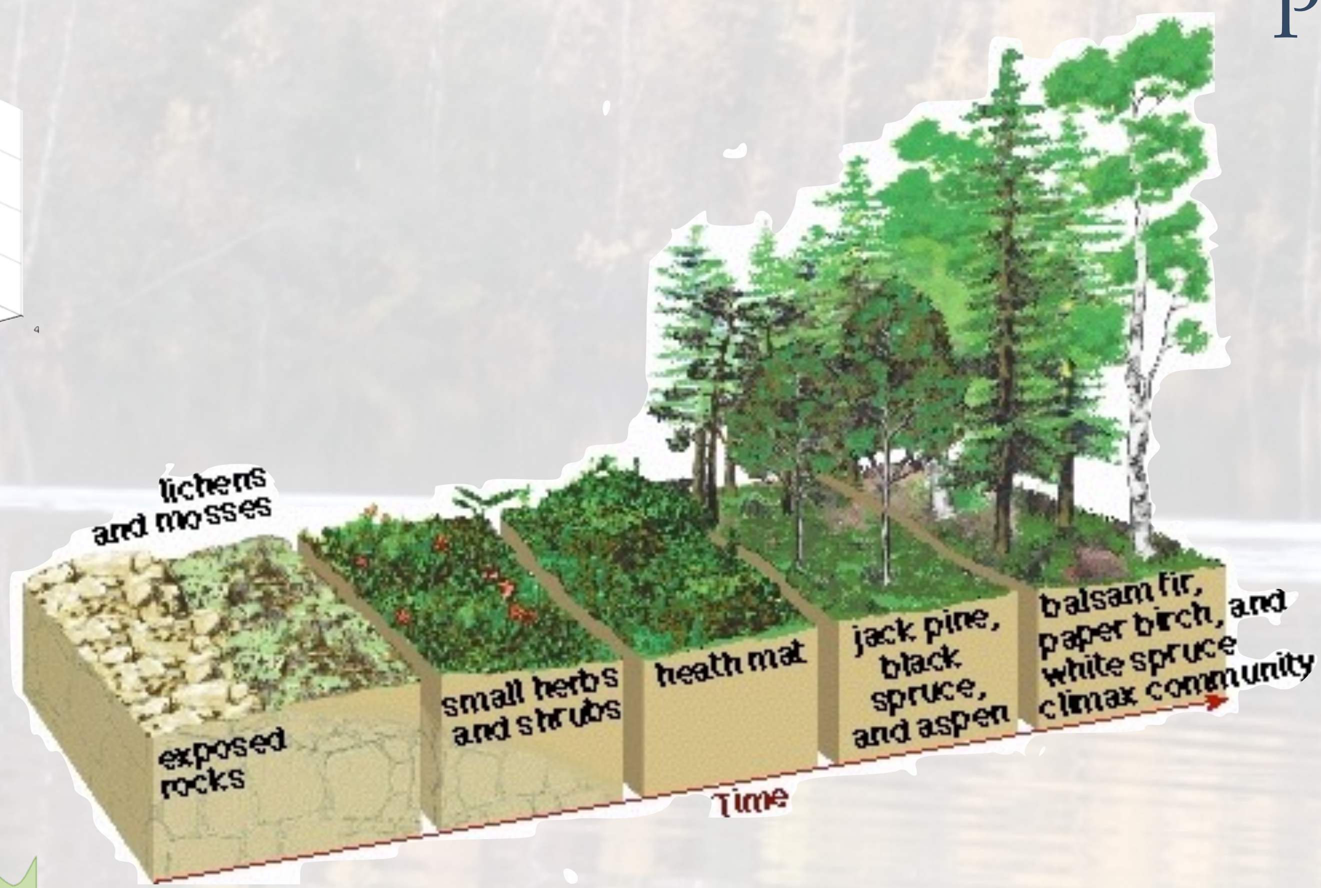
Lohle 2004

Ecosystems are complex

Process Complexity



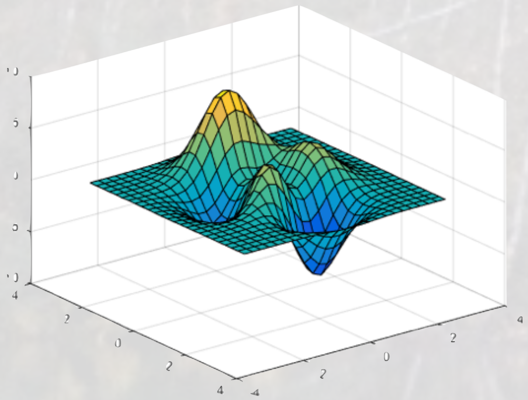


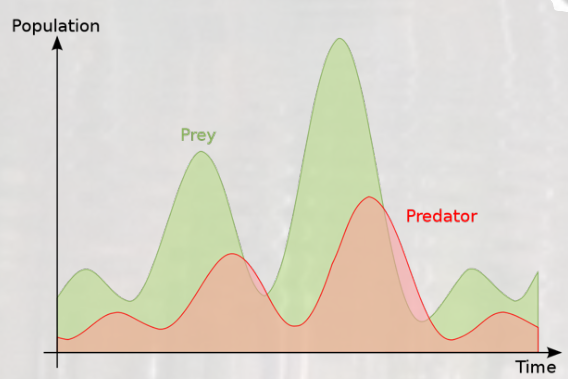


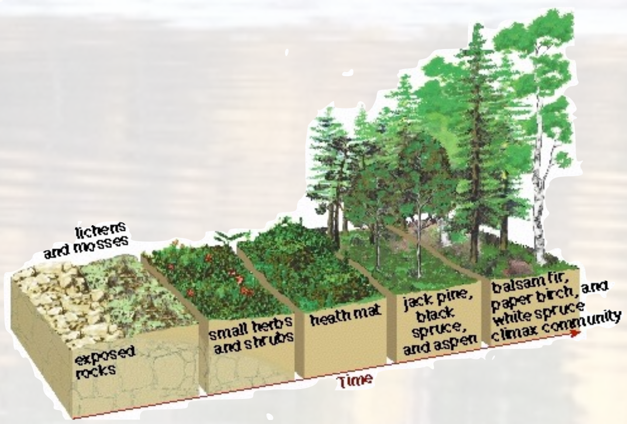
Lohle 2004

Ecosystems are complex

Behavioural Complexity



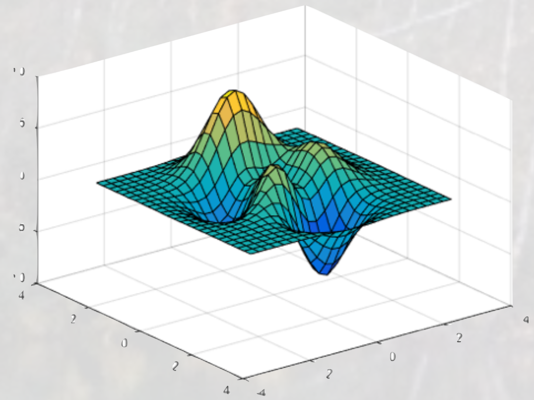


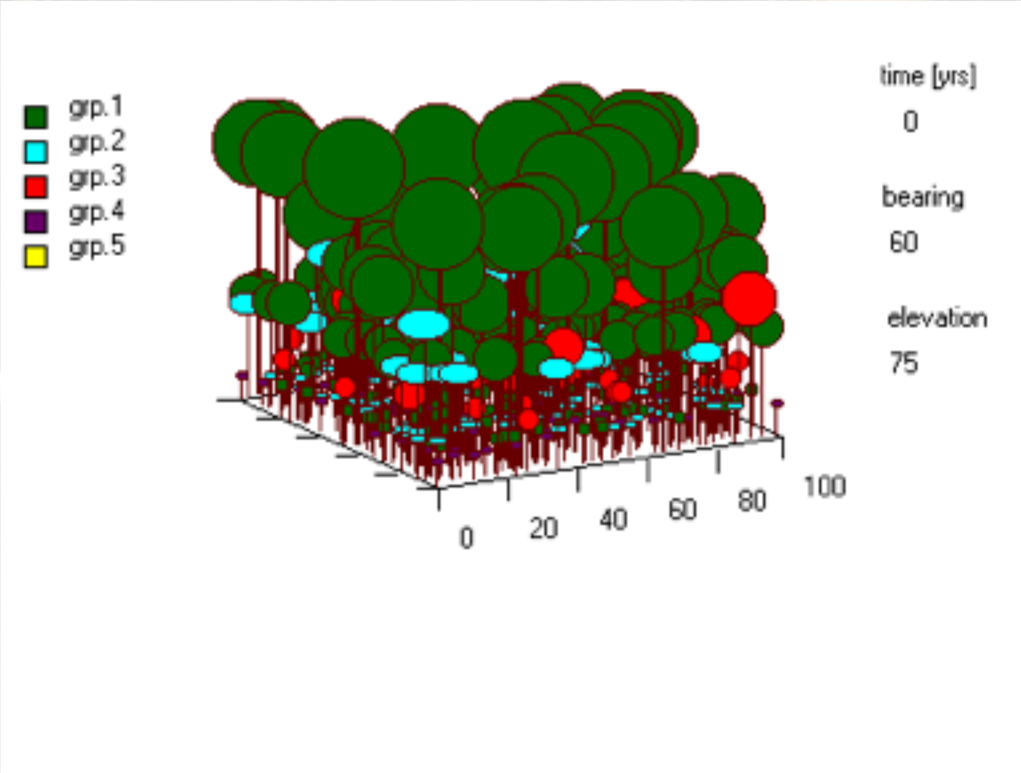


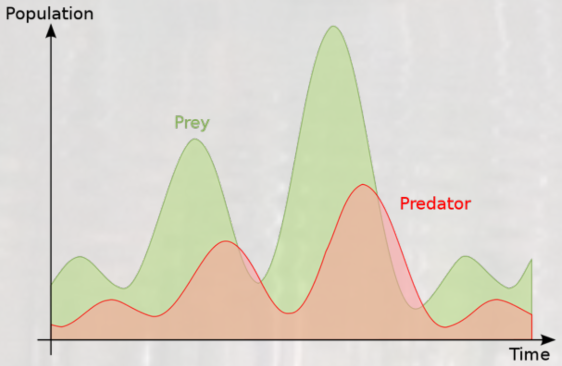
Lohle 2004

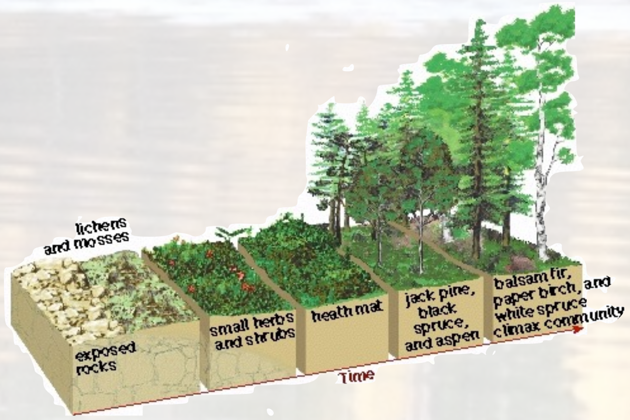
Ecosystems are complex

Geometric Complexity





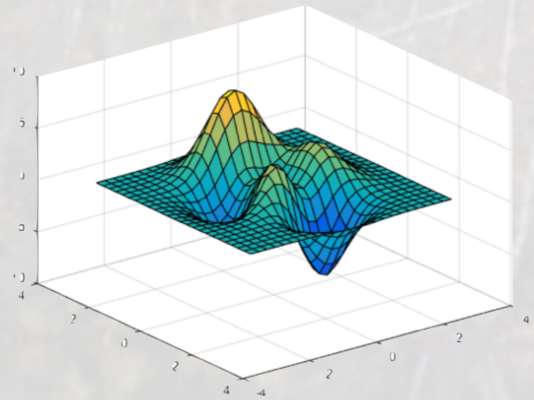


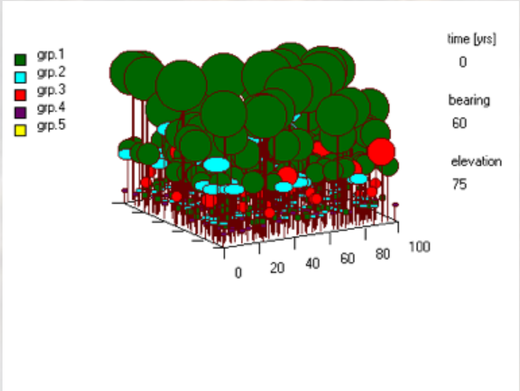


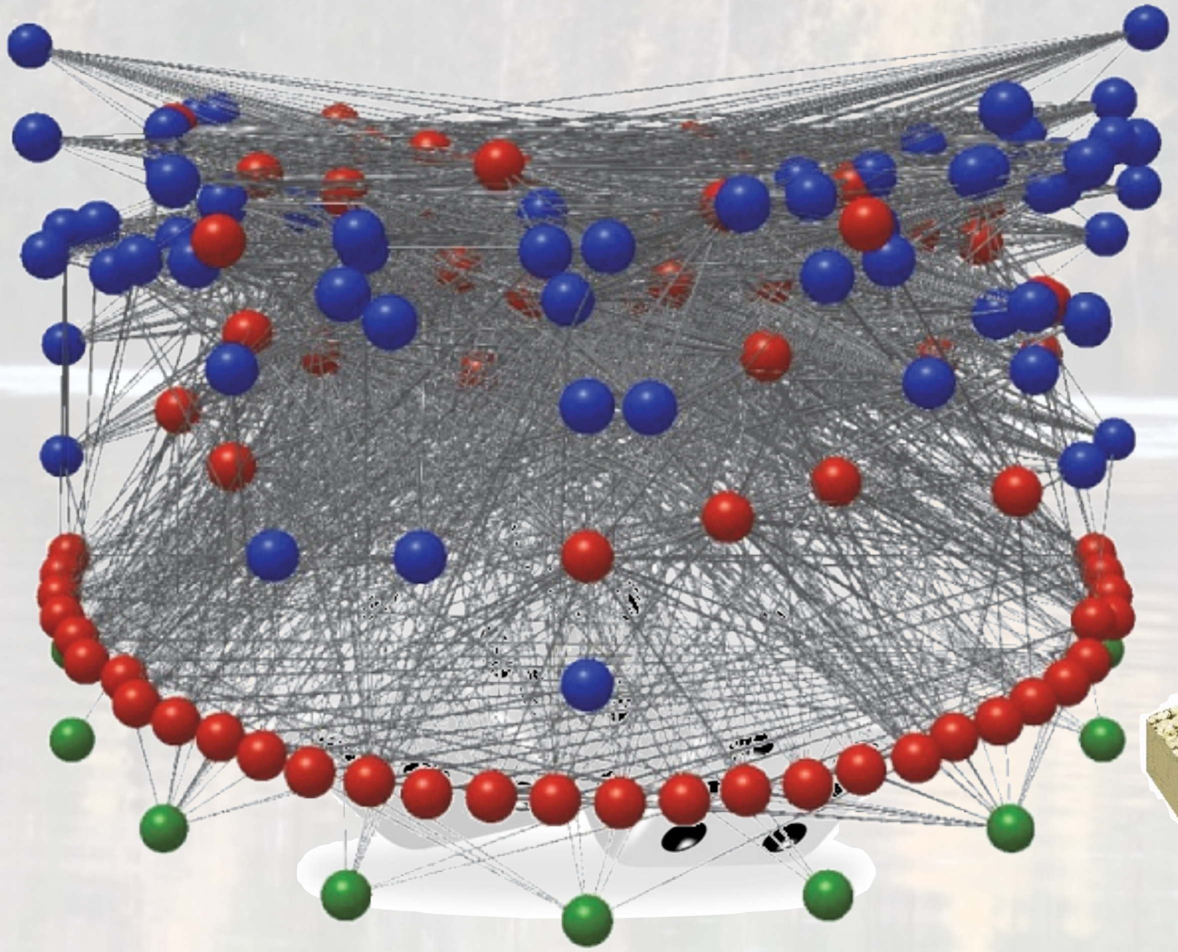
Lohle 2004

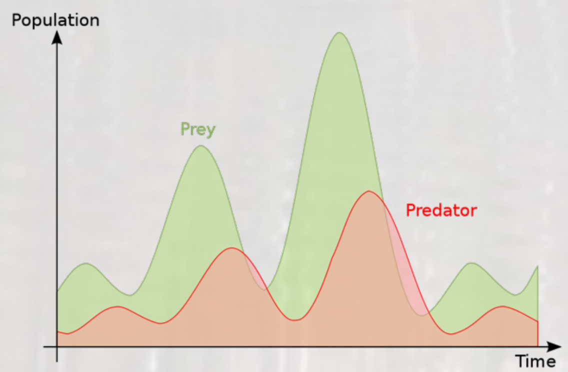
Ecosystems are complex

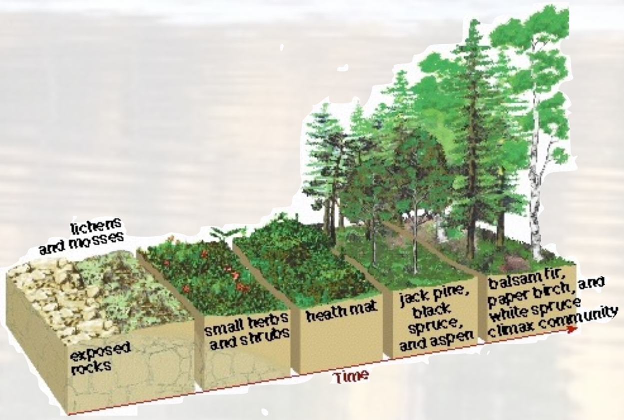
Structural Complexity











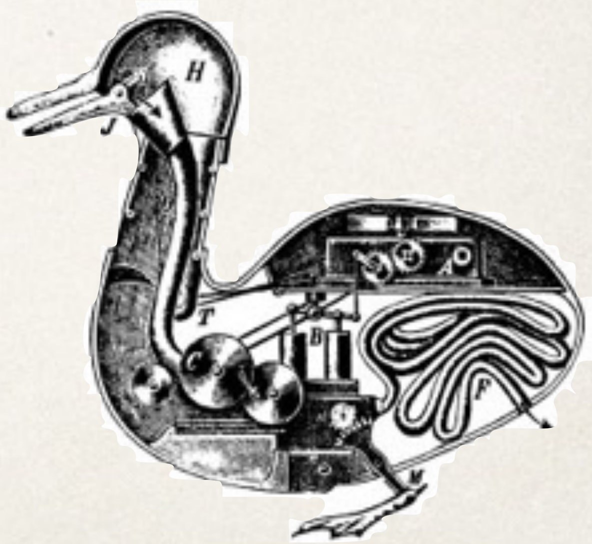
Lohle 2004

Philosophy

Reductionism

„A complex system is nothing more but the sum of its parts.“

- „The unity of science“ (Oppenheim & Putnam)
- Materialism, Physicalism, Supervenience (Neurath & Carnap)
- Theory Reduction (Nagel)



Science: Cause and Effect

Philosophy

Holism

„The whole is greater than the sum of its parts“ [Aristotle ~350 BC]

„More is different“ [Anderson 1972]

„Reinventing Physics from the Bottom Down“ [Laughlin 2005]

- System’s Perspective
- Emergence
- Chaos and Complexity

Biological Hierarchy

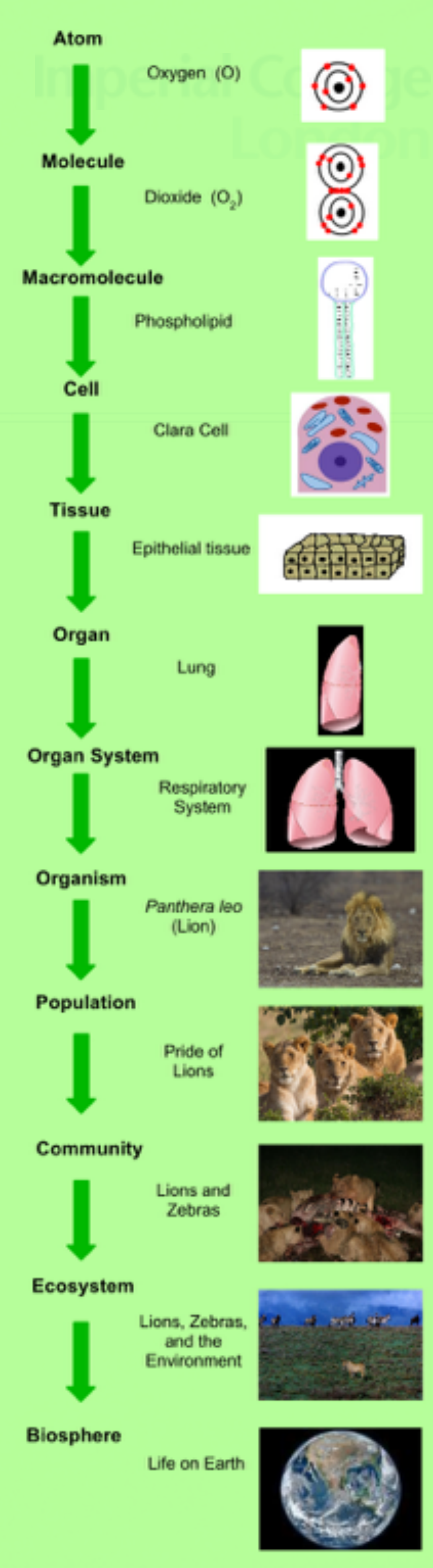
- re-cellular level
- Sub-ce r level
- Cellu evel
- Super llular level
- Orga
- Orga ms
- Popu ns
- Communities
- Ecosystems

Reductionsm

Holism

Macro y

Keep it simple



What is a complex system?

„Complex Systems consist of a large number of interacting components. The interactions give rise to emergent hierarchical structures.

Complexity is concerned with the emergent properties at systems level originating from the underlying multitude of microscopic interactions.“ *www.complexity.org.uk*

What is Emergence?

„When people say something is an emergent property, it just means they don't understand the phenomena."

Lord Robert May

Interactions of individual components on a micro-scale
-> Collective coherent behaviour on the macro-scale

Complexity Science

Statistical Mechanics

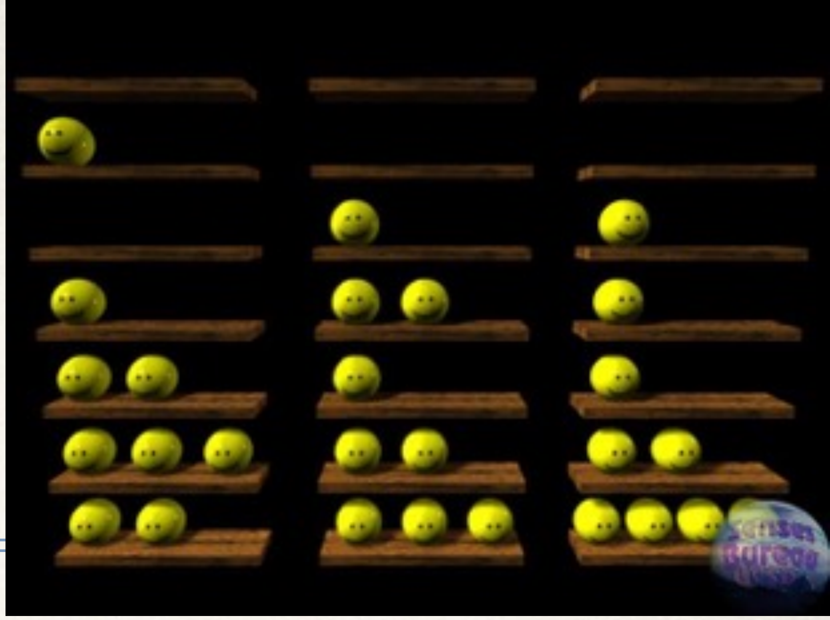
Understanding the macroscopic properties of chemical systems (eg. gases) from the behaviour of the microscopic constituents (eg. molecules)

Measurable and perceivable: macroscopic properties: Volume, pressure, temperature

Actual agents: interacting particles

System's behaviour: average over individuals' behaviour

Statistical Mechanics



System of particles, each of which can be in a certain state s_i

State of the system: $s = (s_1, s_2, s_3, ..., s_n)$

Hypothesis: **Microcanonical Ensemble**
For a closed system it is assumed that all micro-states, consistent with the macroscopic constraints, occur with equal probability.

$$\Rightarrow p(s) = \frac{1}{\Omega(s)}$$

Entering the macroscopic constraints:

$$p(s) = \frac{e^{-\frac{E_s}{k_b T}}}{Z}$$

Jensen 2009a

Statistical Mechanics

Motion of the ball describable by…

…trajectories of individual molecules
…trajectory of the centre of mass, as molecules move together in a coordinated way

Averaging means…

…loss of information
…gain of describability, practicability, insight

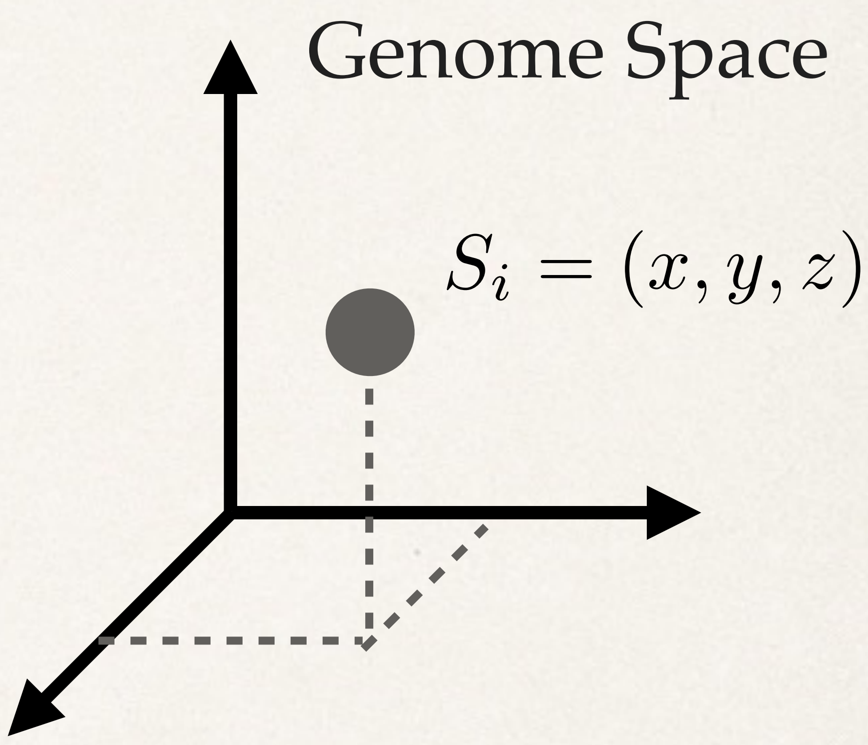
Jensen 2009a

The Tangled Nature Model of Evolutionary Ecology

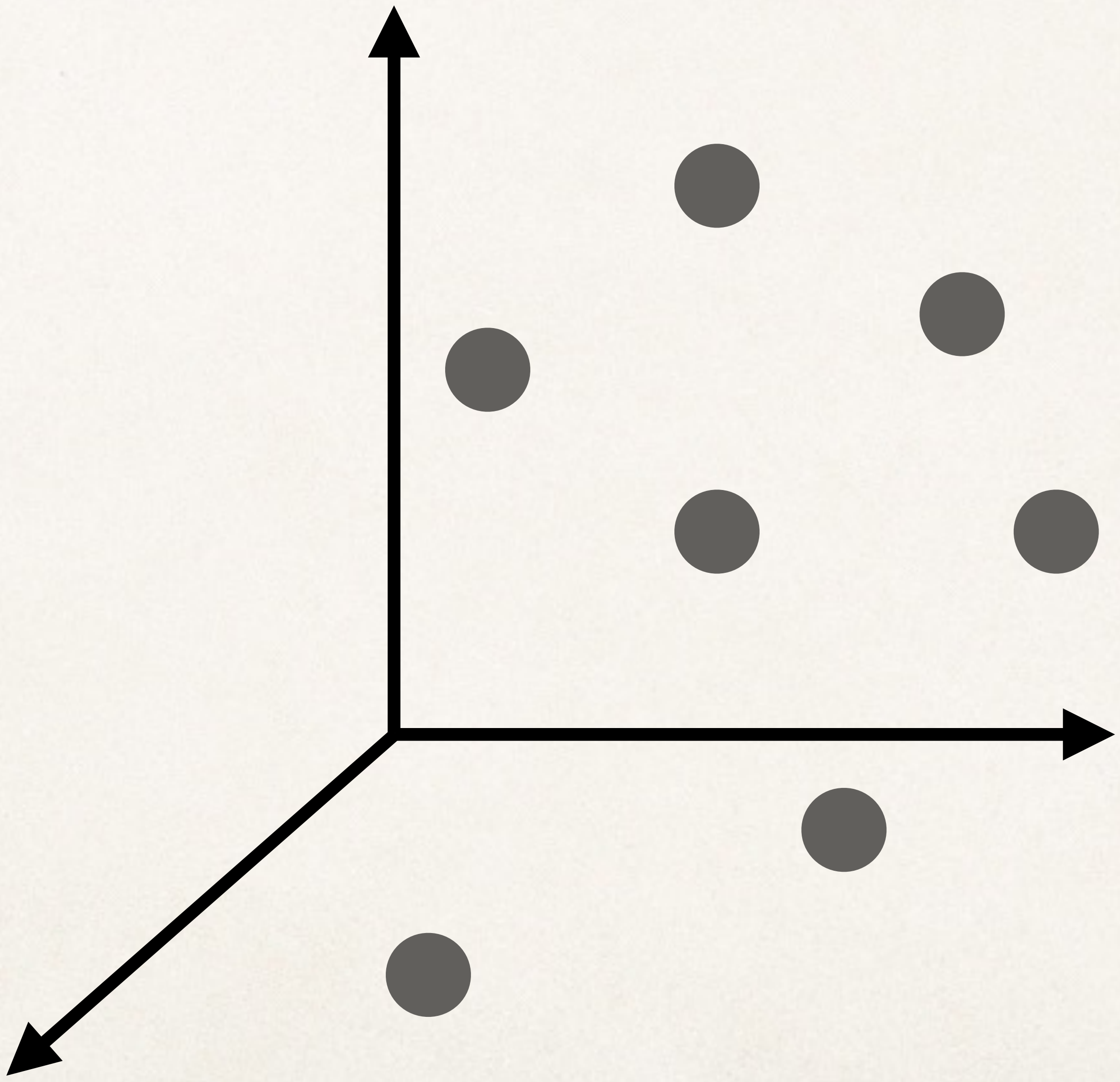
Henrik Jeldtoft Jensen
Imperial College

The Tangled Nature Model

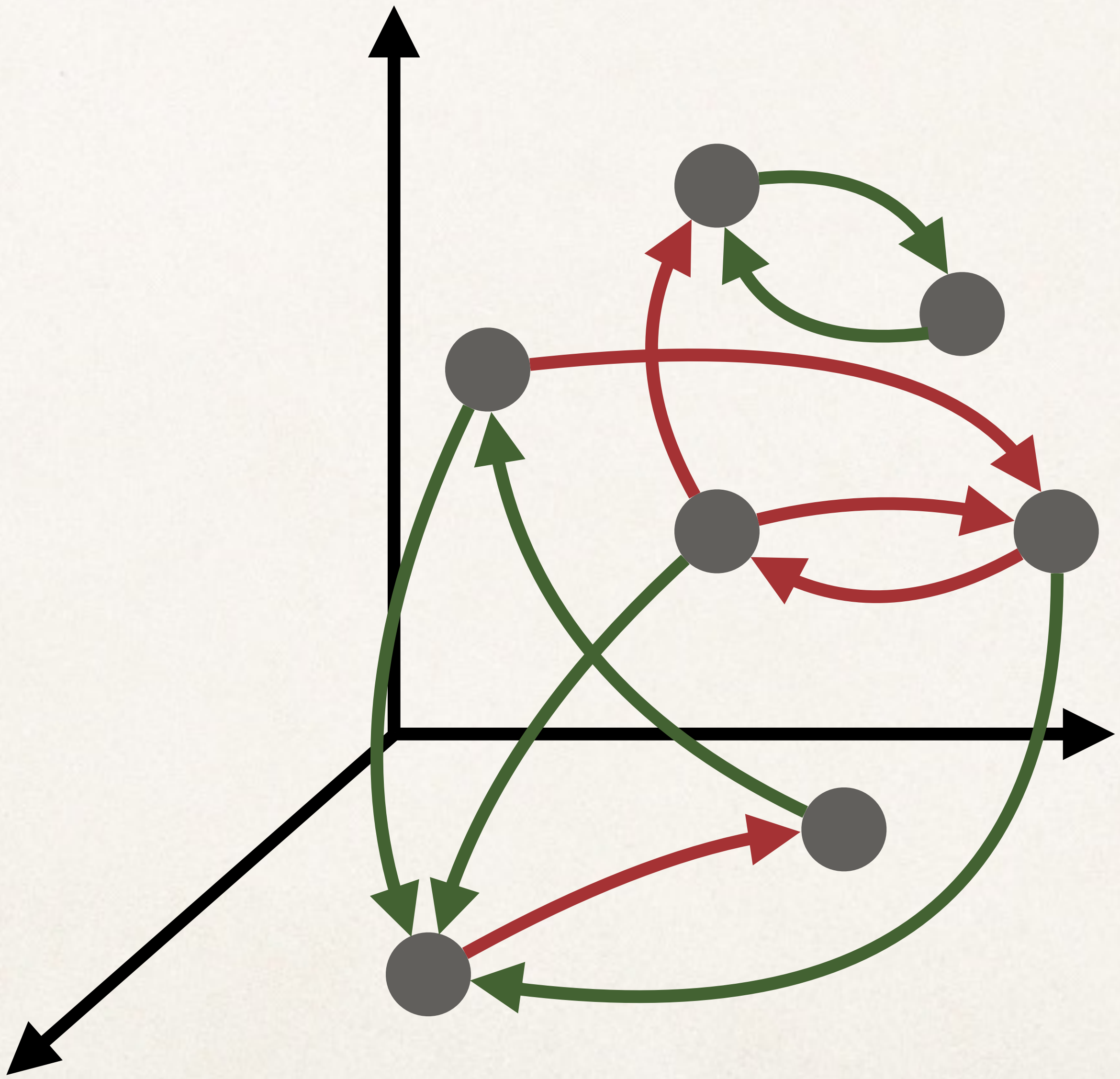
- Individual based model
- Fitness dependent on interaction with present community
- Predefined interaction network
- Evolving biological network/ community



Dynamics

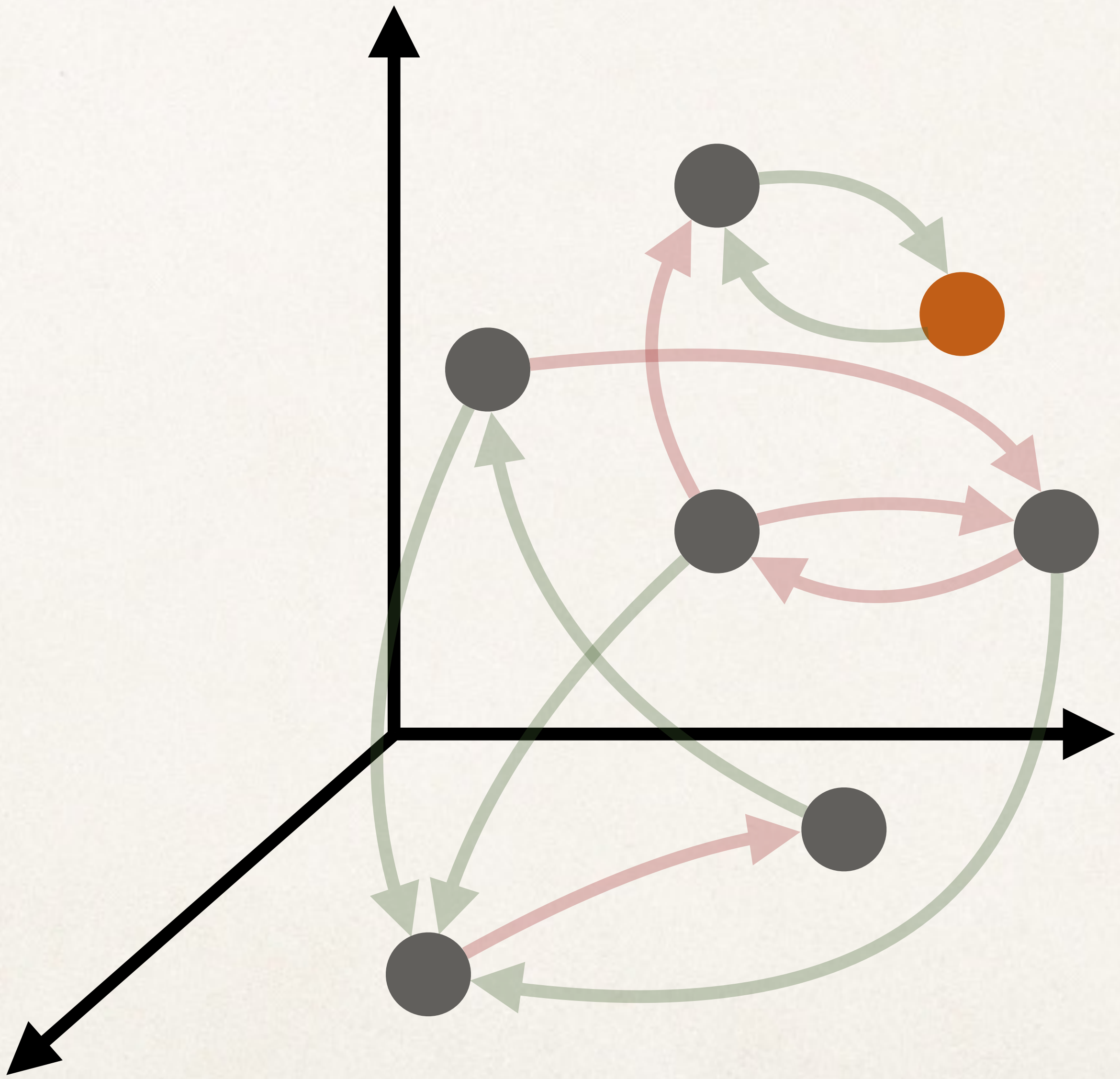


Dynamics



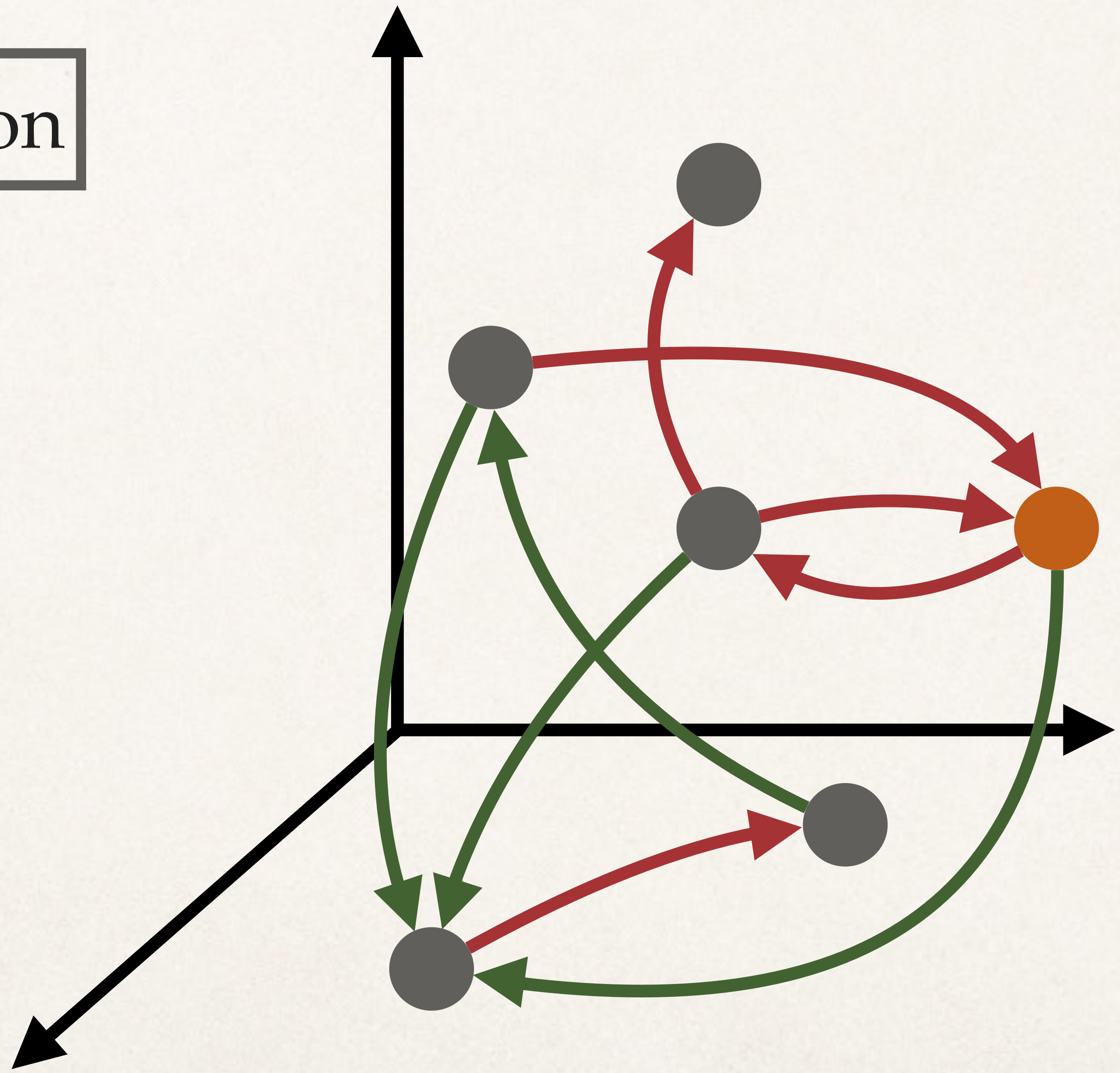
Dynamics

Death



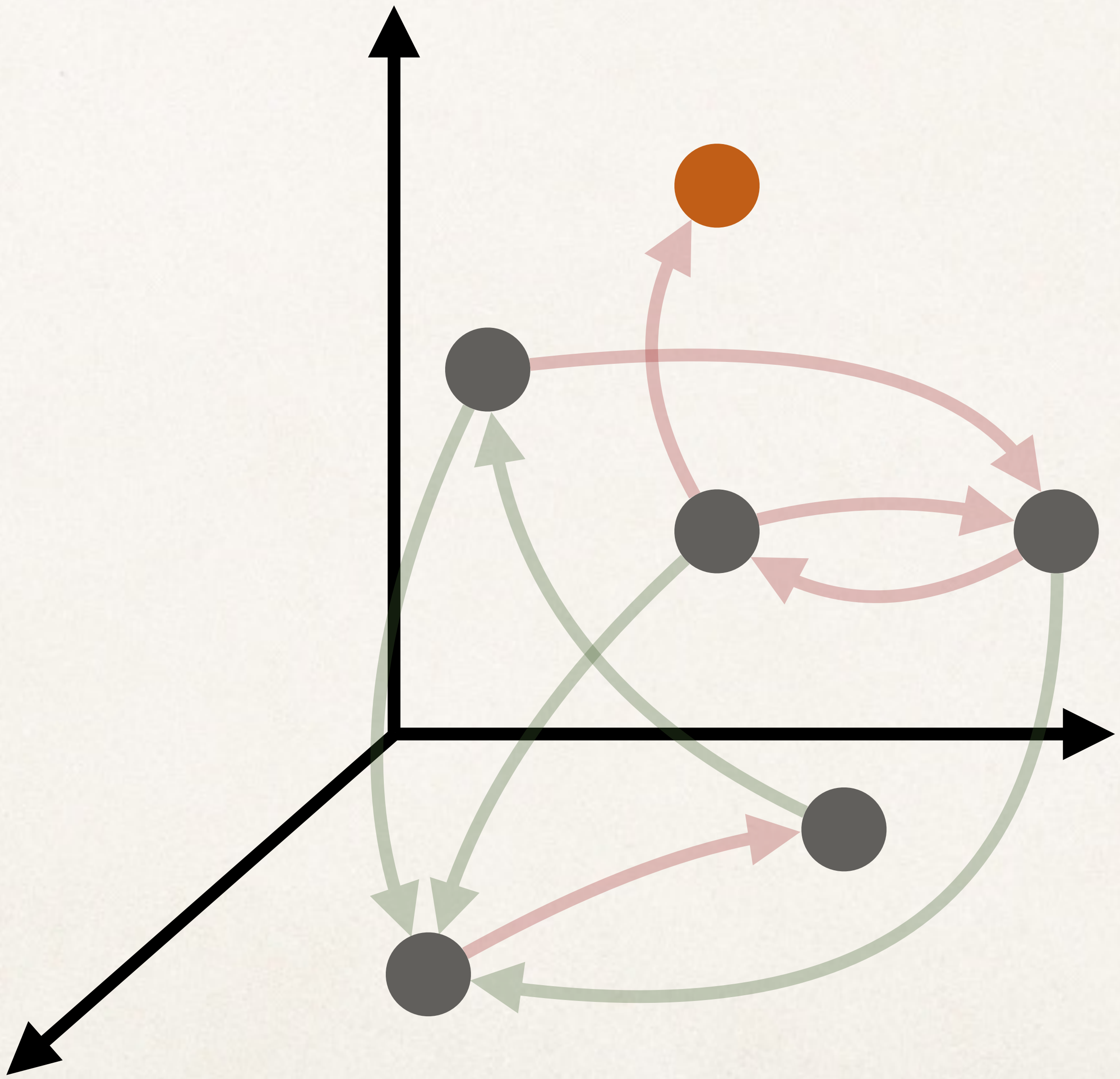
Dynamics

Reproduction



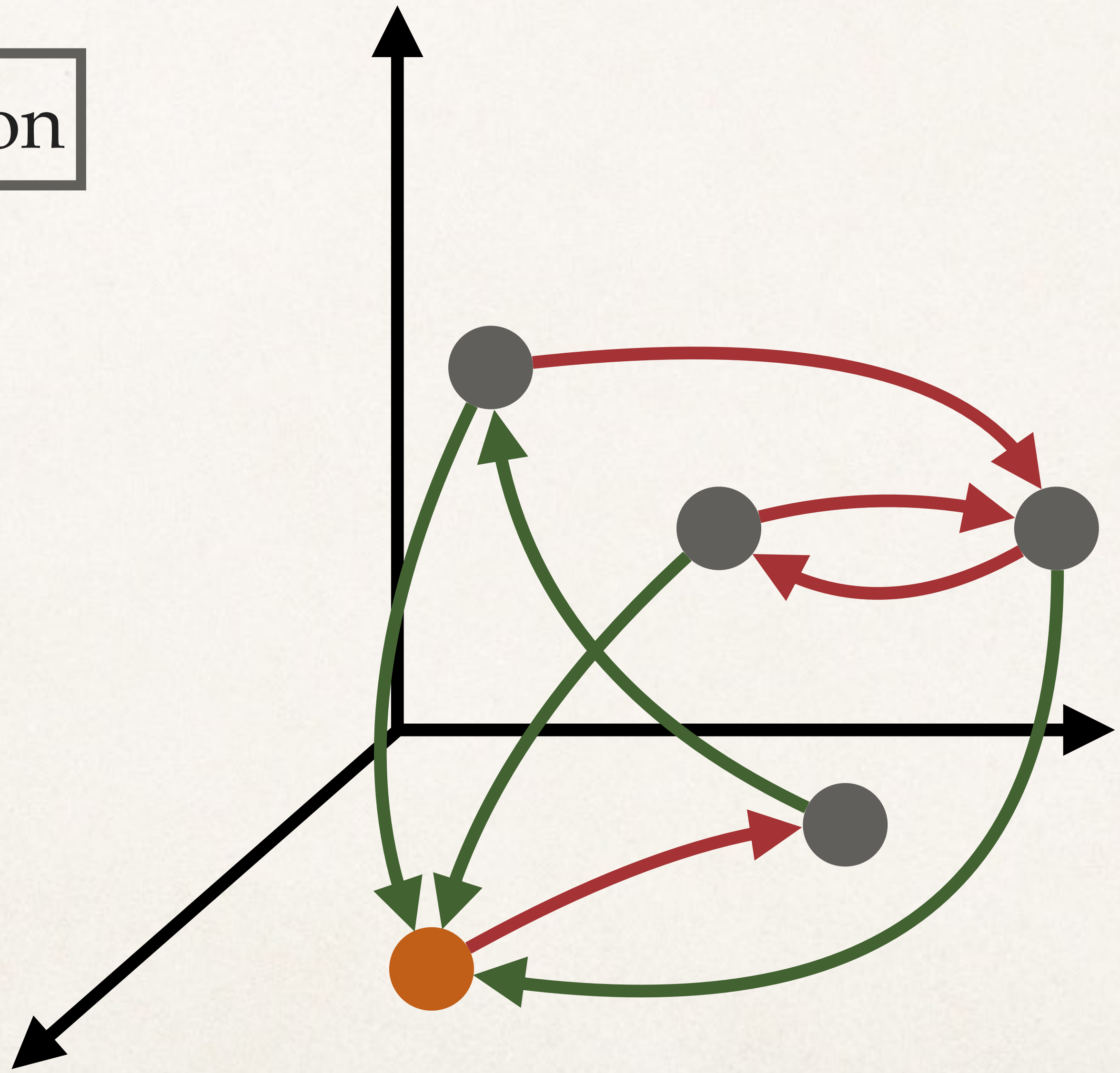
Dynamics

Death



Dynamics

Reproduction



Dynamics

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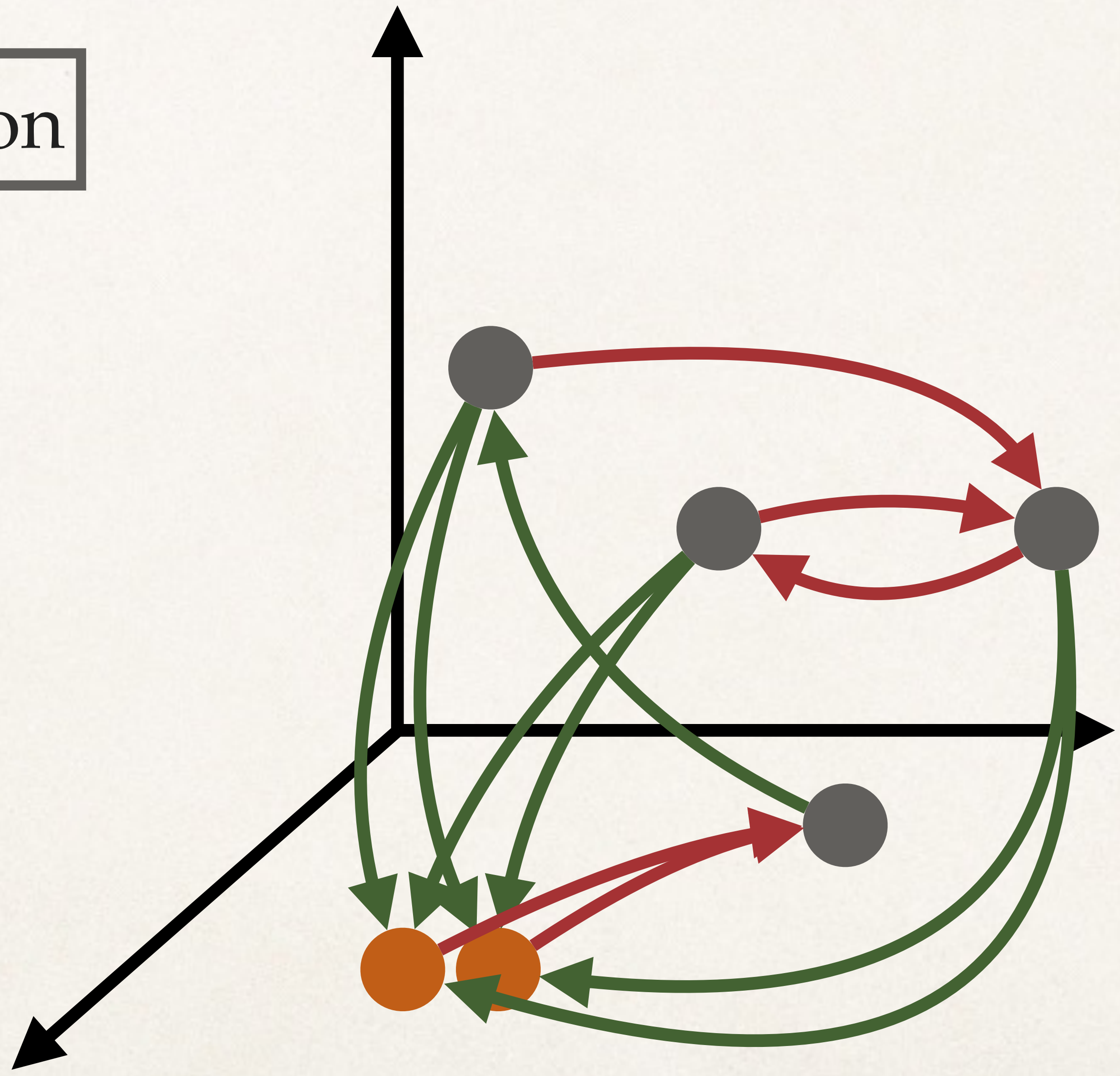

Dynamics

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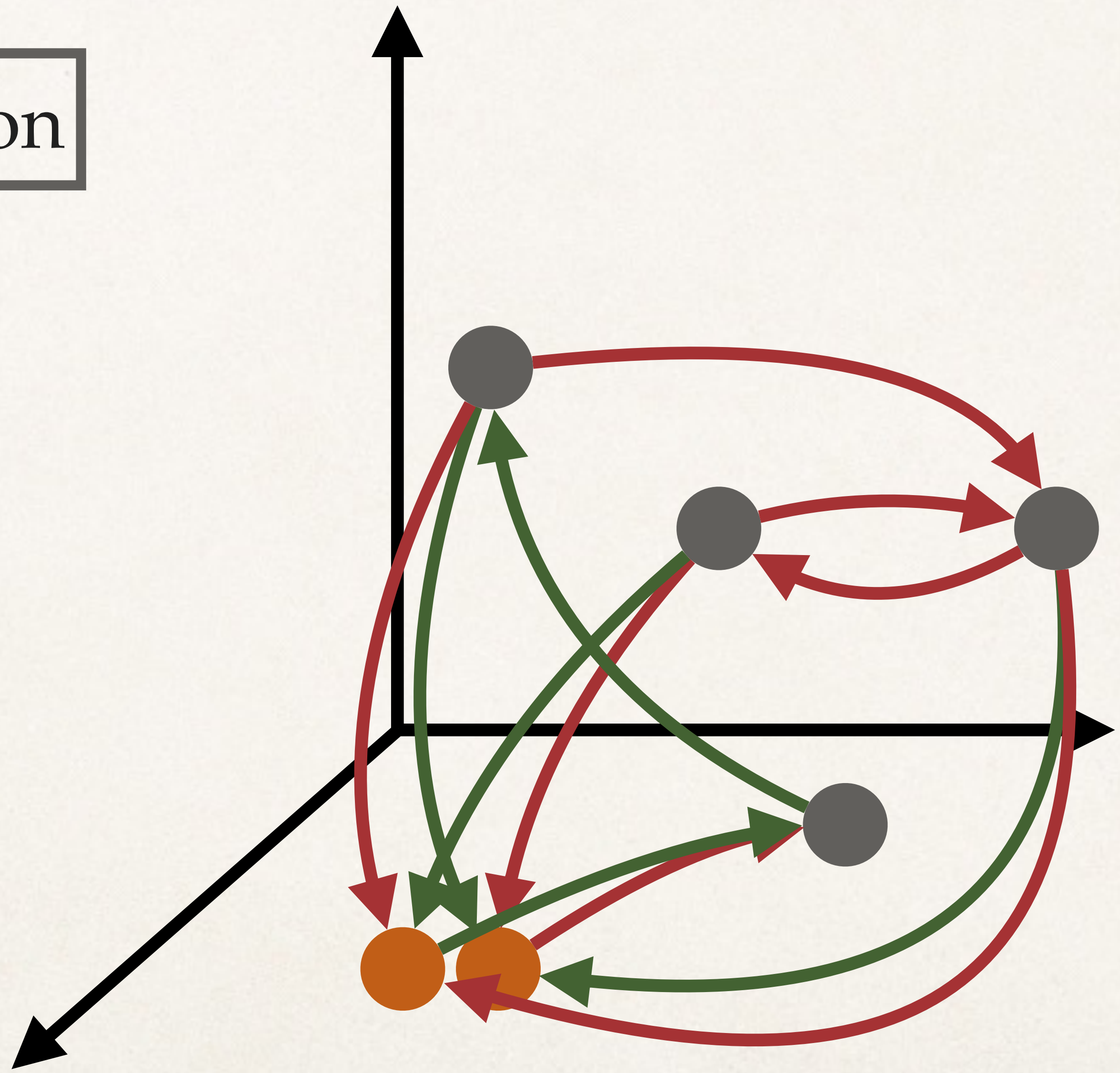
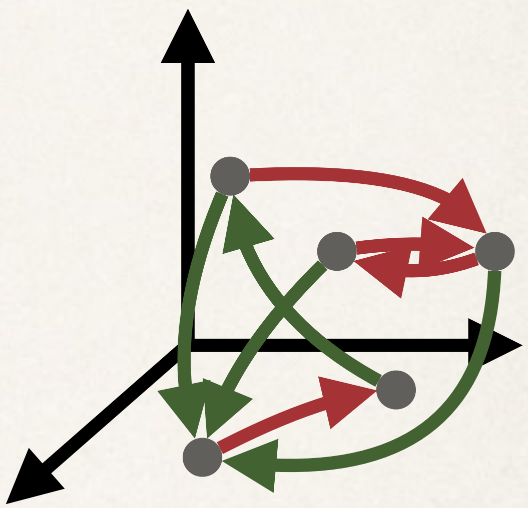


Dynamics

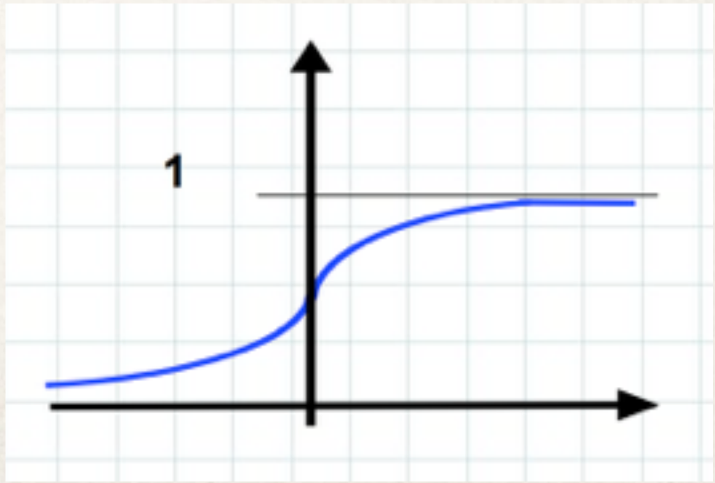
$$S_i = (gene_1, gene_2, ..., gene_L)$$



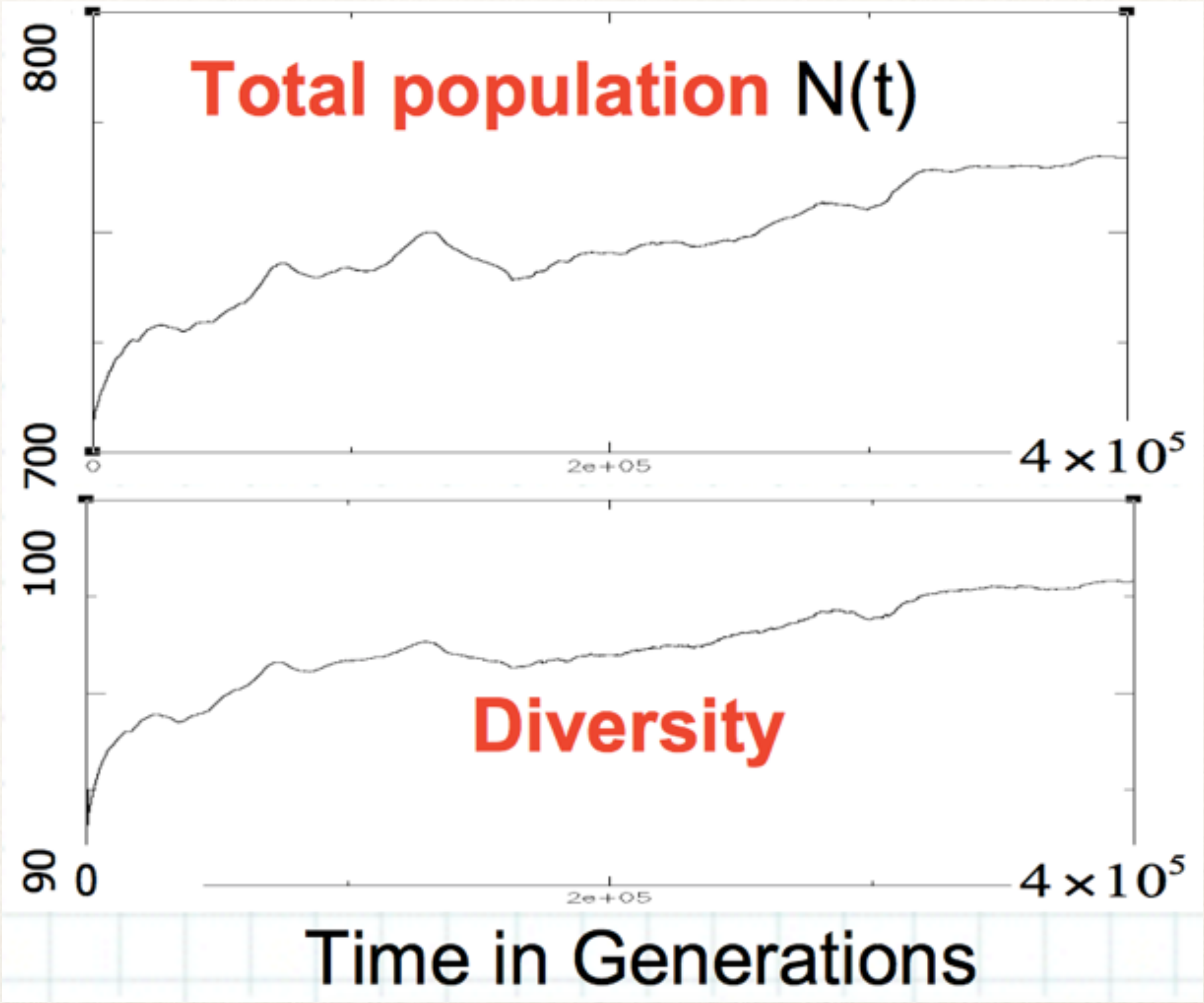
$$p_{kill} = const. \qquad p_{mut} = const.$$

$$H(S_i, t) = \frac{1}{cN(t)} \sum_j J(S_i, S_j) n(S_j, t) - \mu N(t)$$

$$p_{off}(S_i, t) = \frac{e^{H(S_i,t)}}{1 + e^{H(S_i,t)}} \in [0, 1]$$

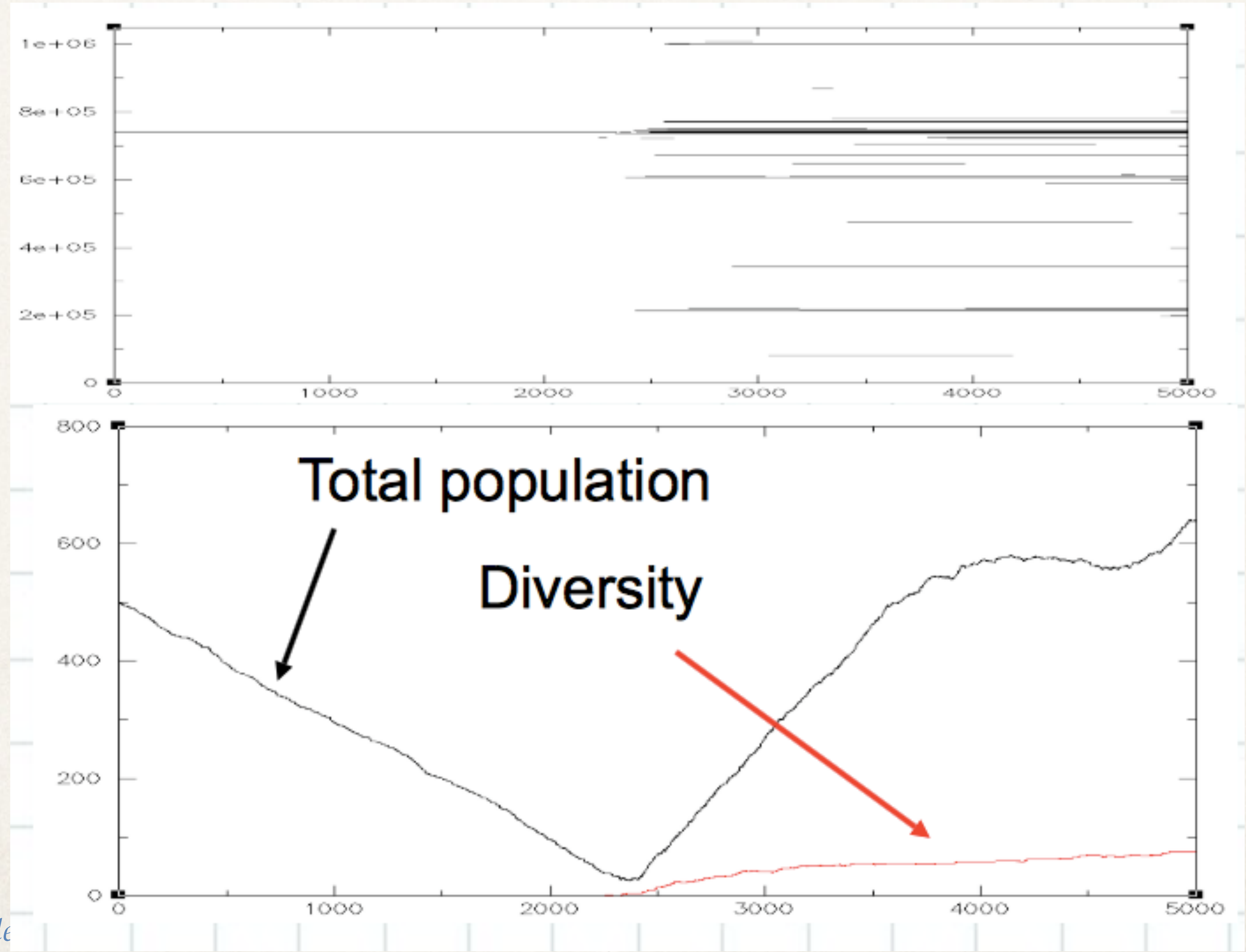


Drift



Jensen 2009b

Segregation in Genotype Space

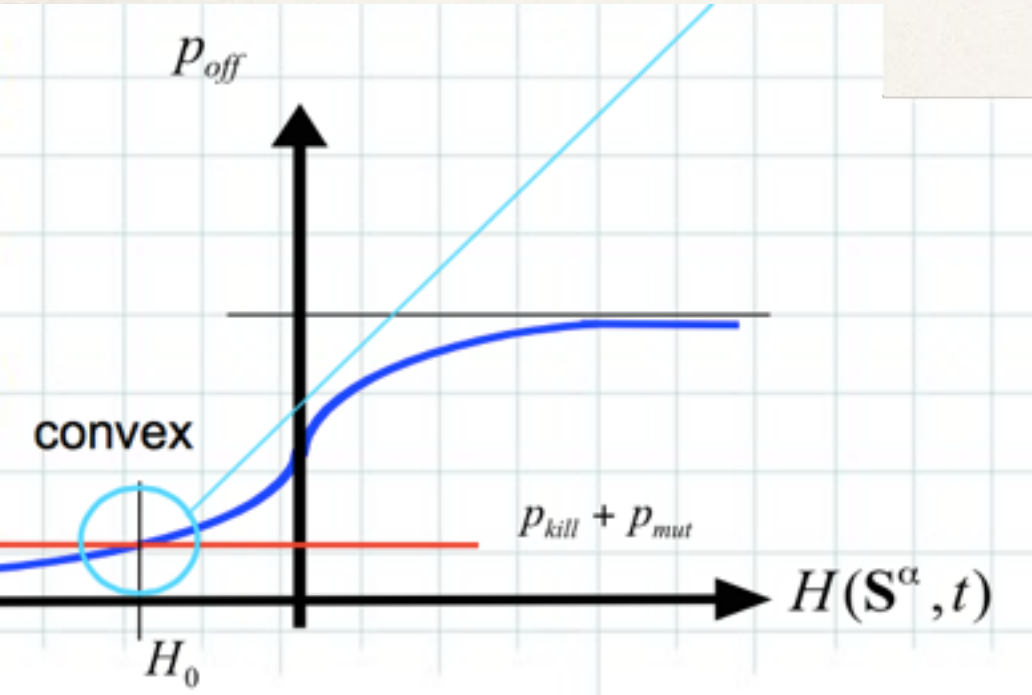


Symmetry Breaking

$$H = J^* - \mu N$$

Effect of a mutation: $H \to H + \delta J^*$

=> Symmetric fluctuations $P(\delta J^*) = P(-\delta J^*)$

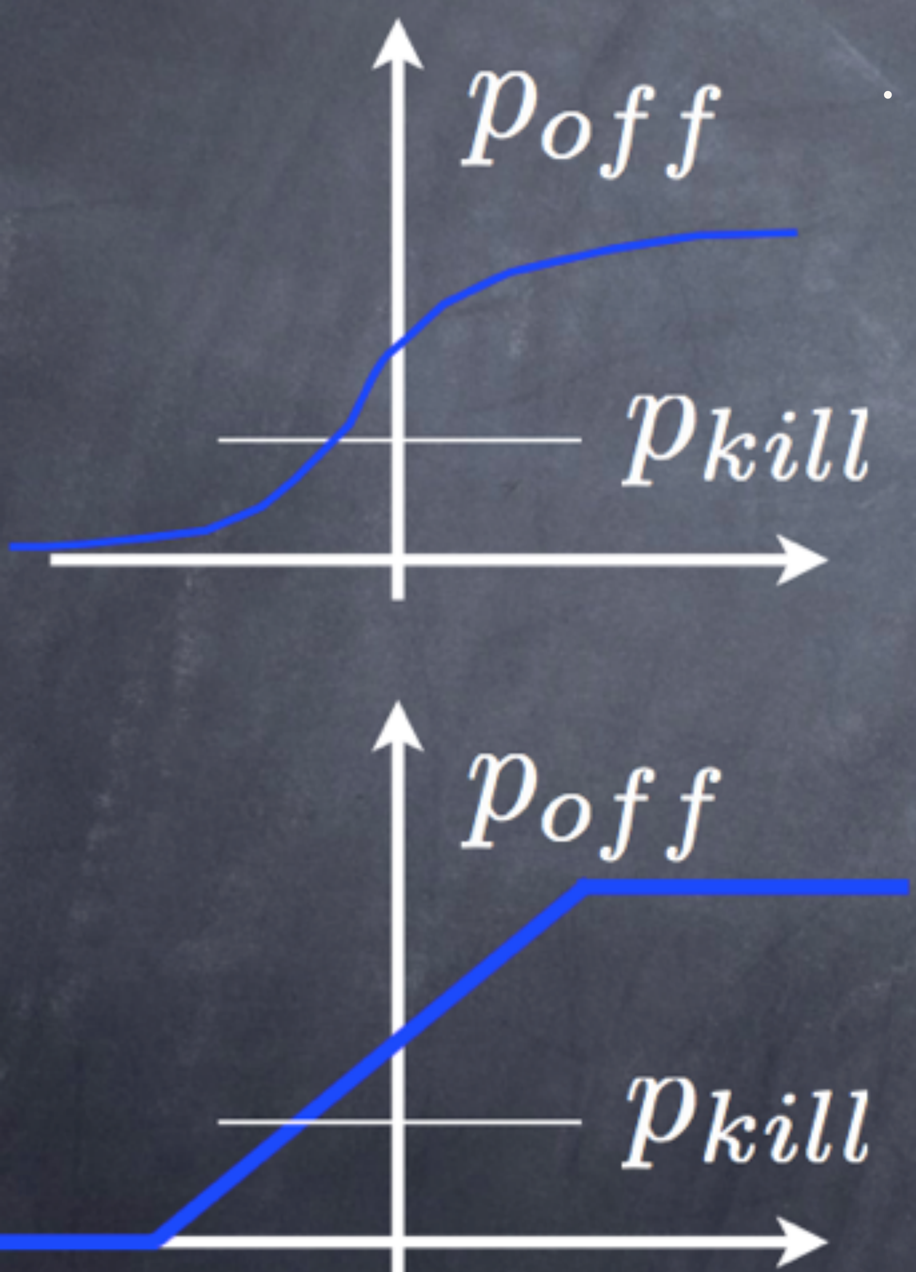


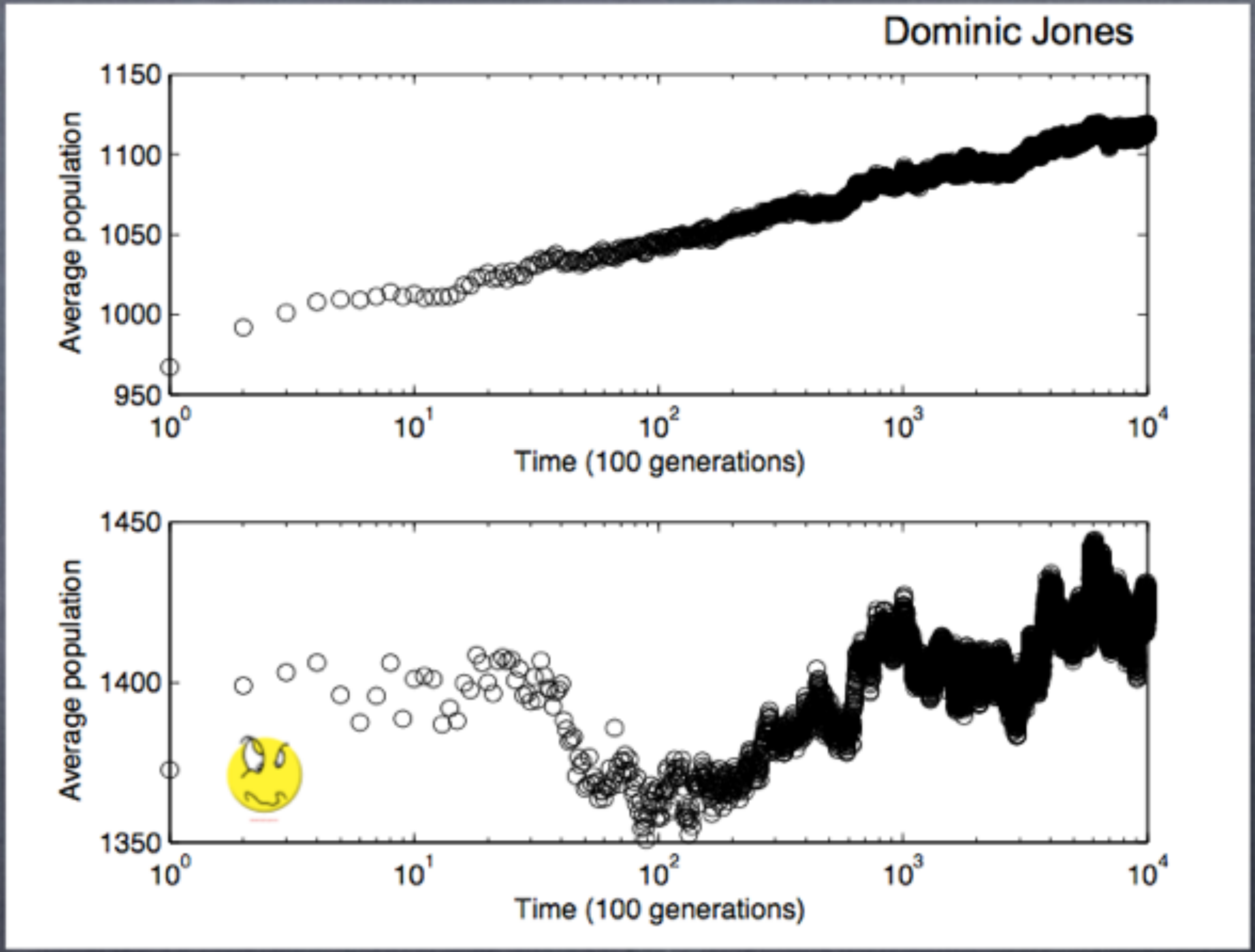
lead to asymmetry:

$$P_{off}(H + \delta J^*) - P_{kill} > P_{kill} - P(H - \delta J^*)$$

Jensen 2009b

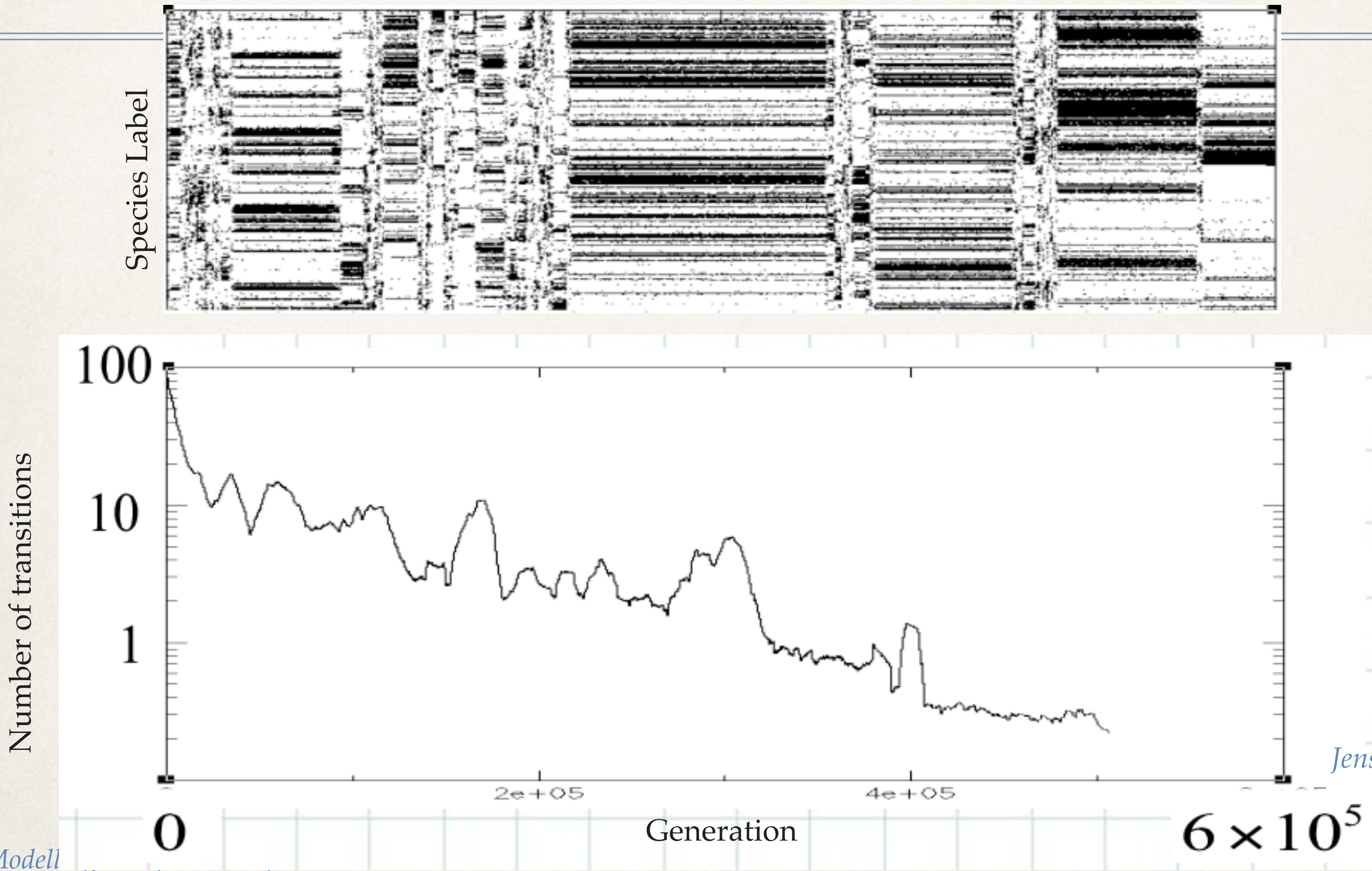
Symmetry Breaking





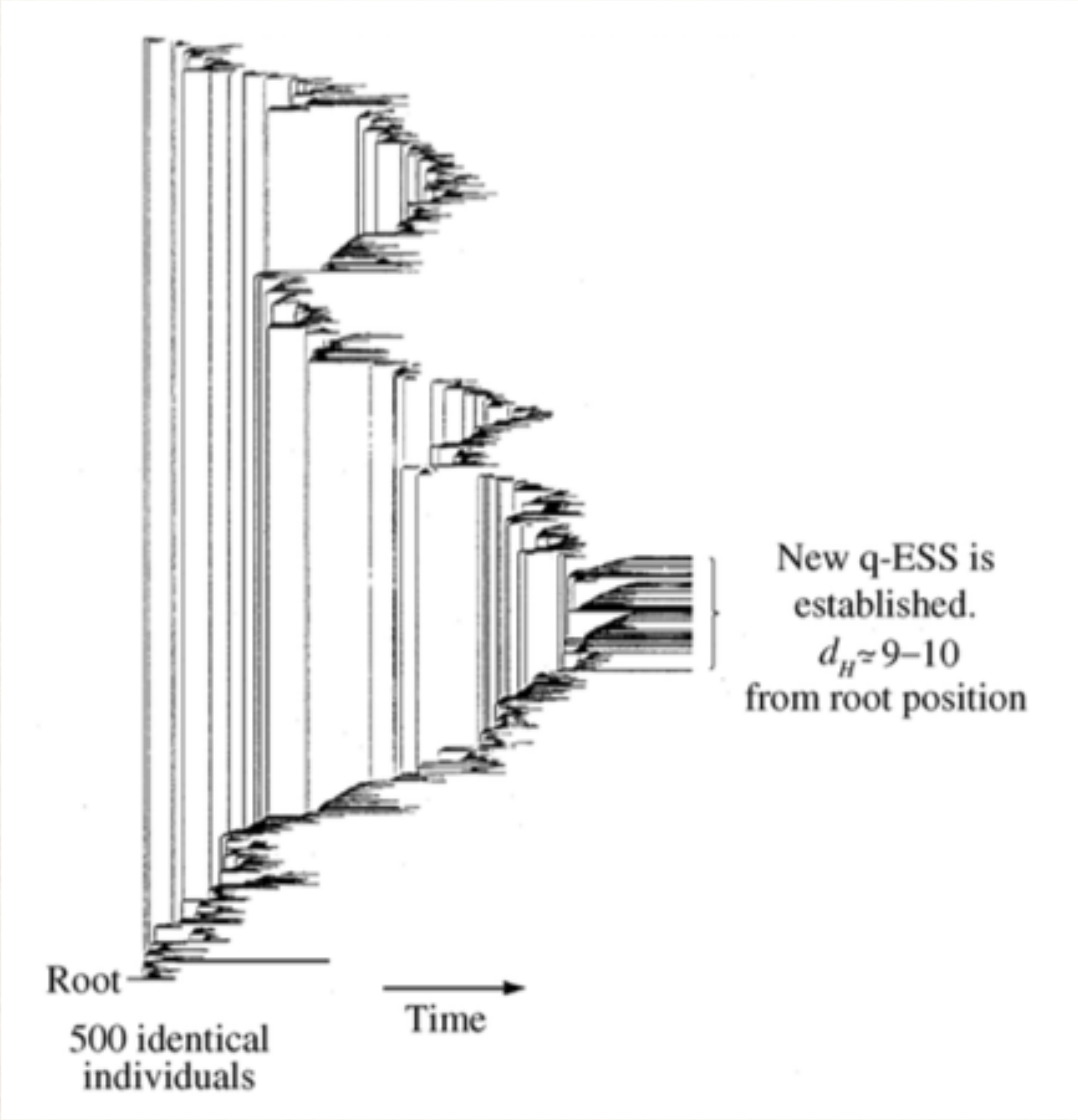
Jensen 2009b

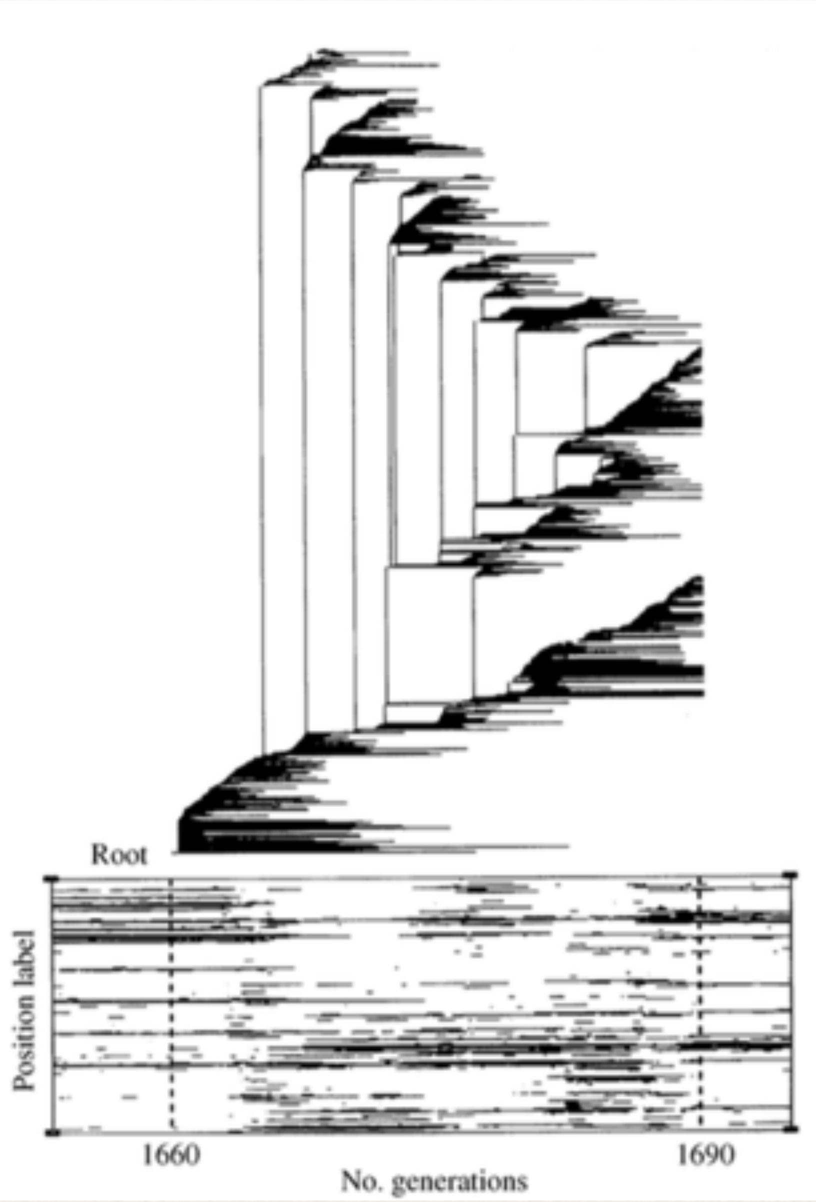
Intermittency



Jensen 2009b

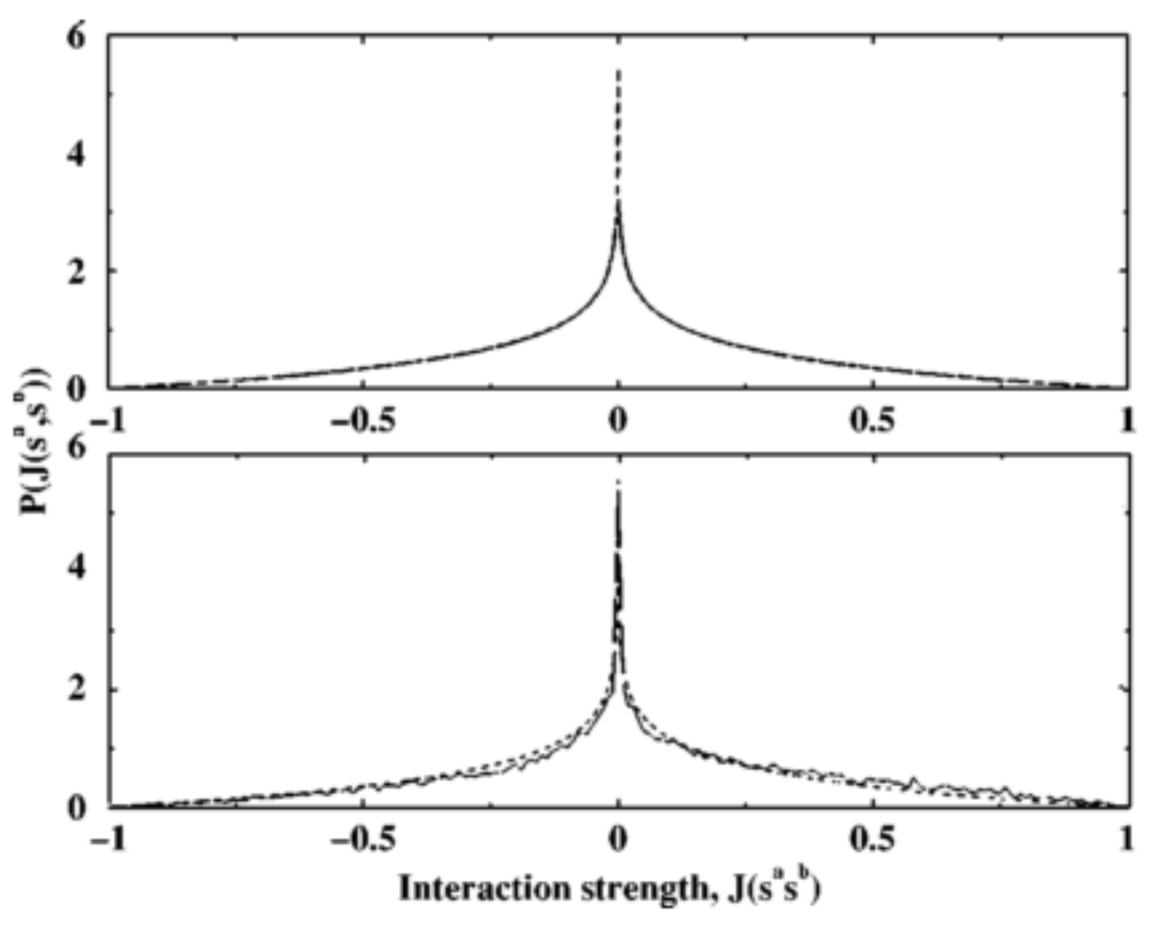
Intermittency

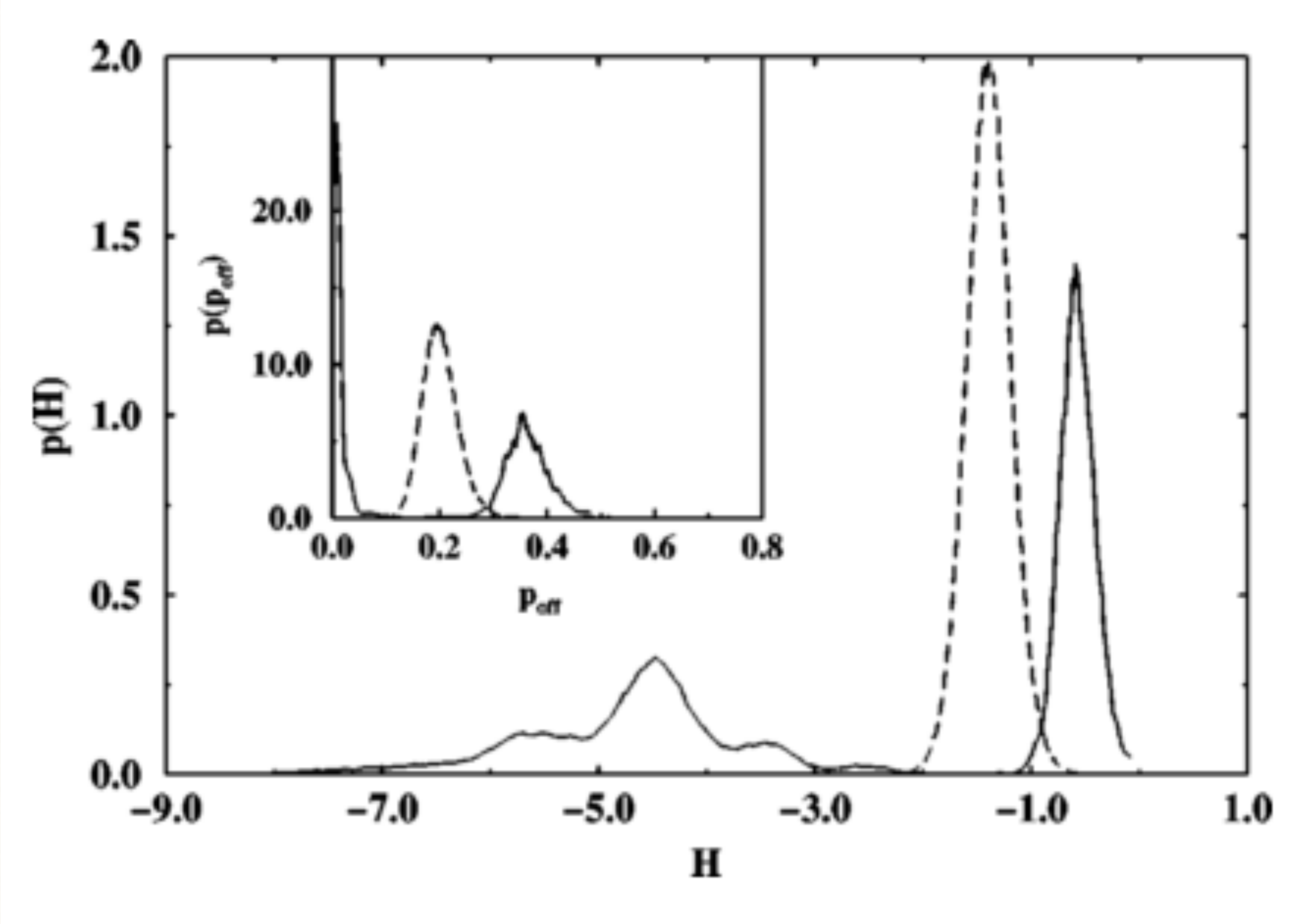




Christensen et al. 2002

Interaction Strength

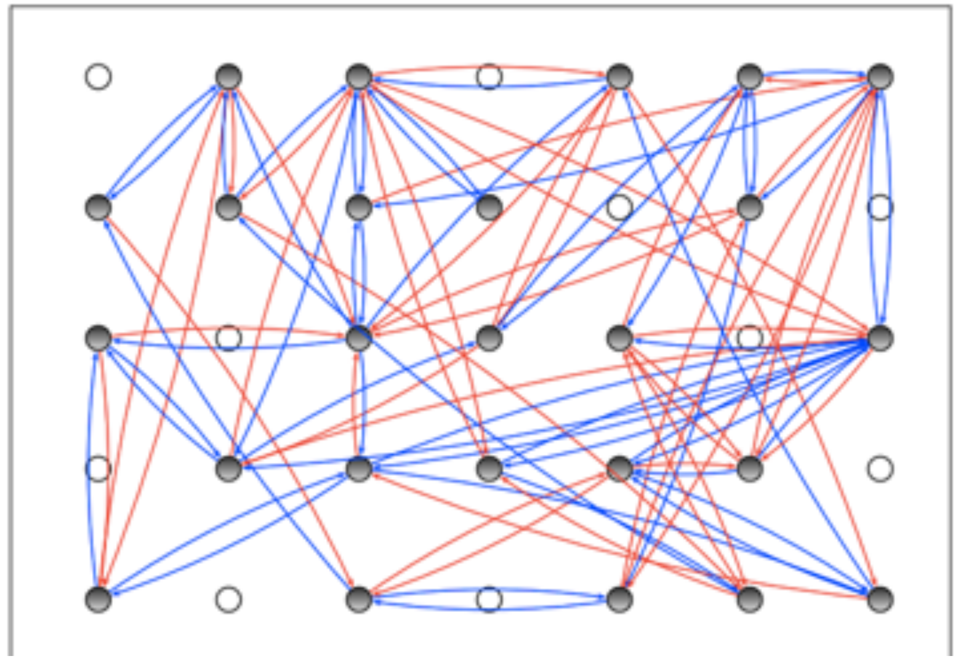


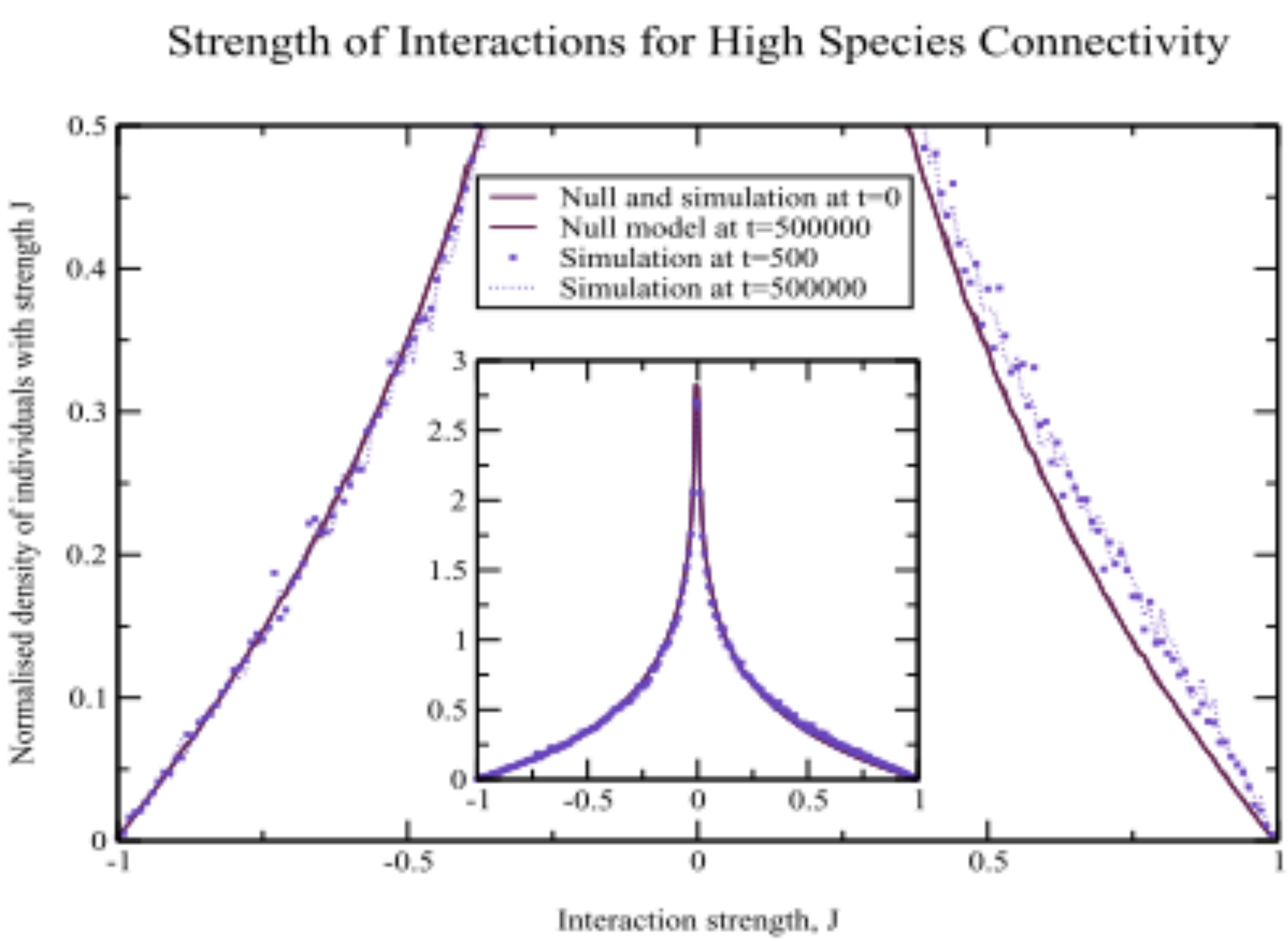


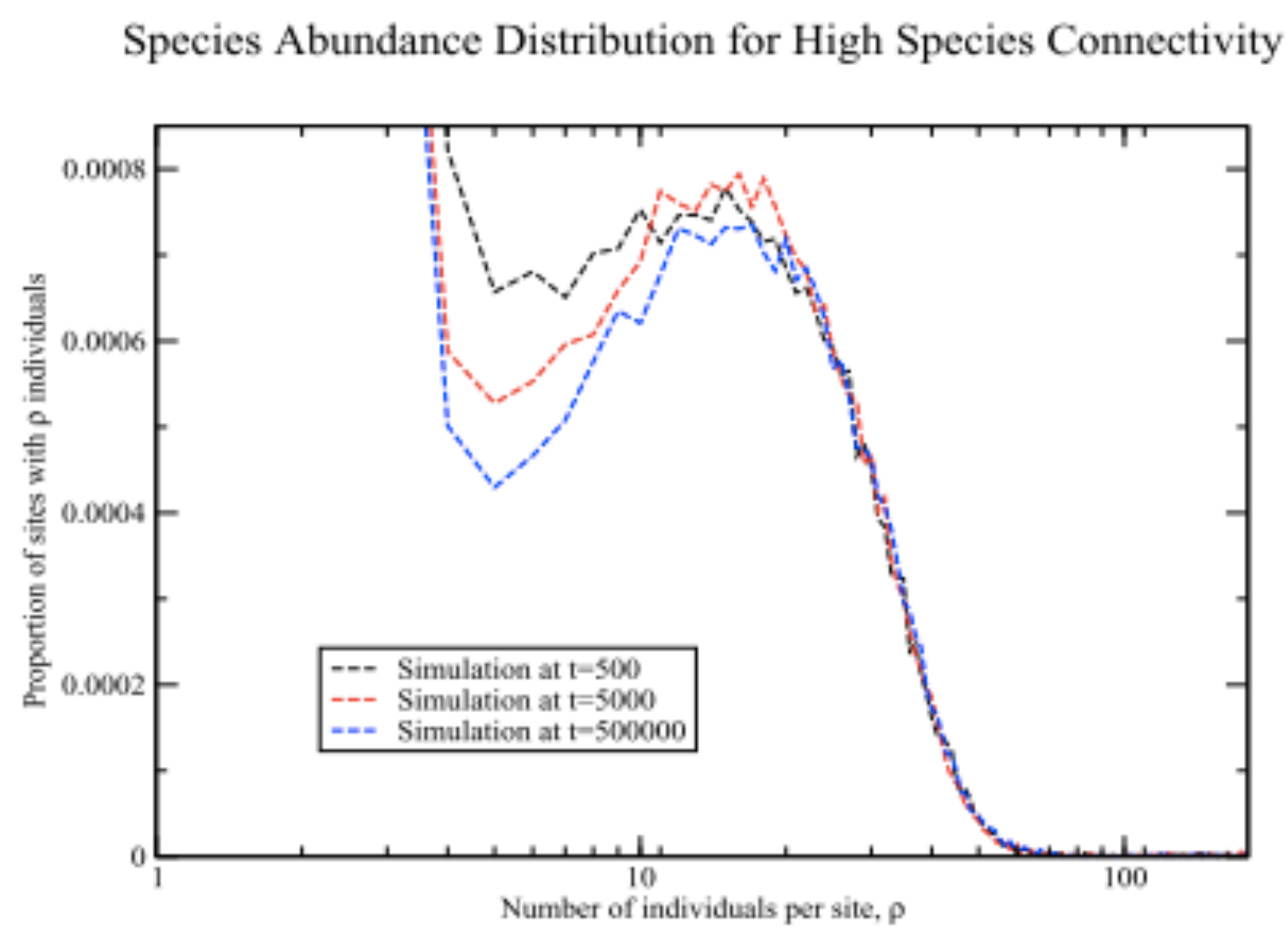
Hall et al. 2002

Species Abundance Distribution

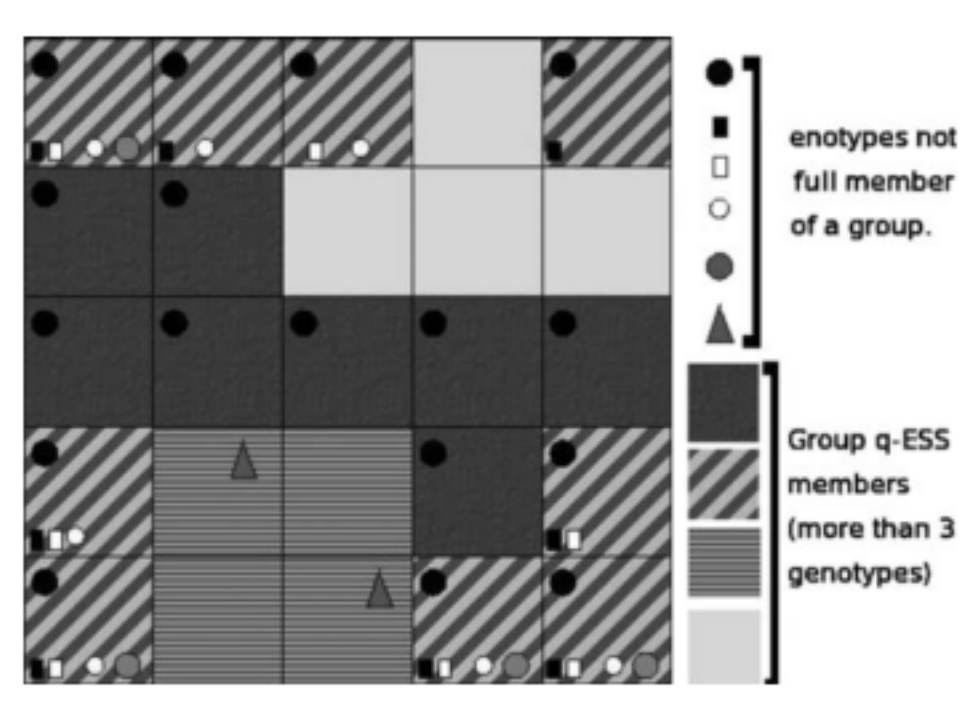
Anderson & Jensen 2005

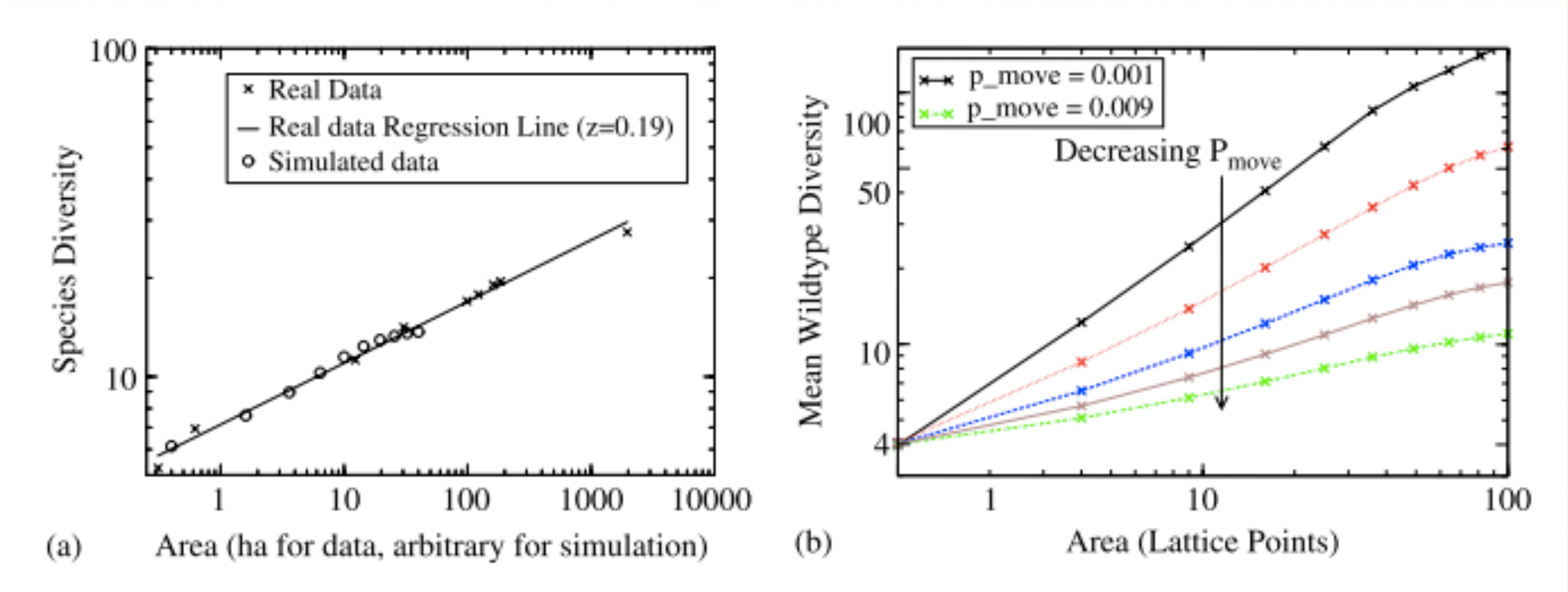






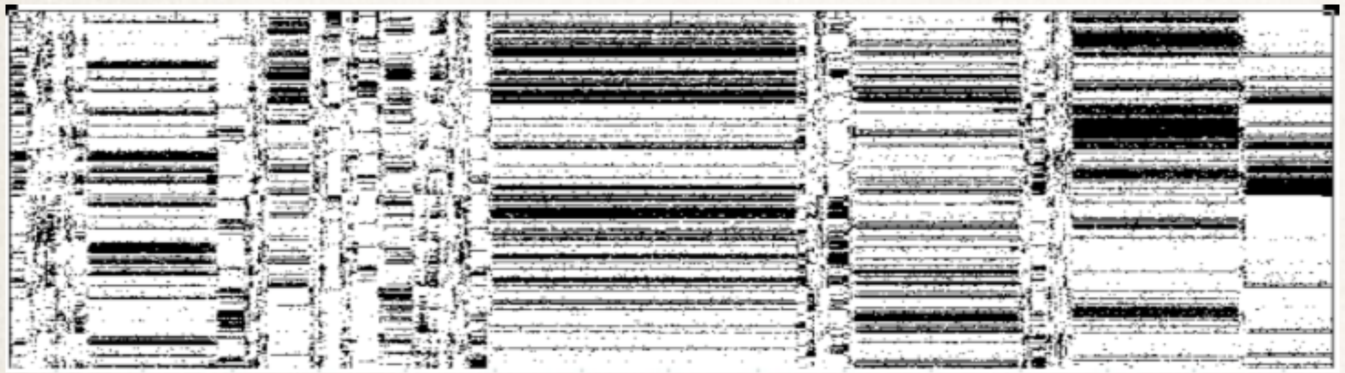
Spatial Version



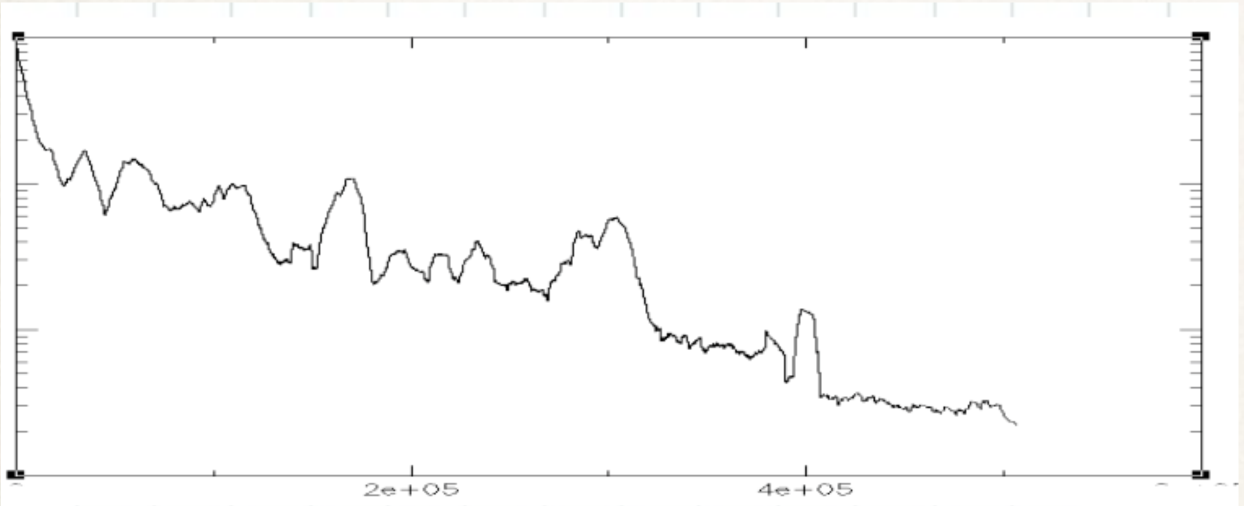


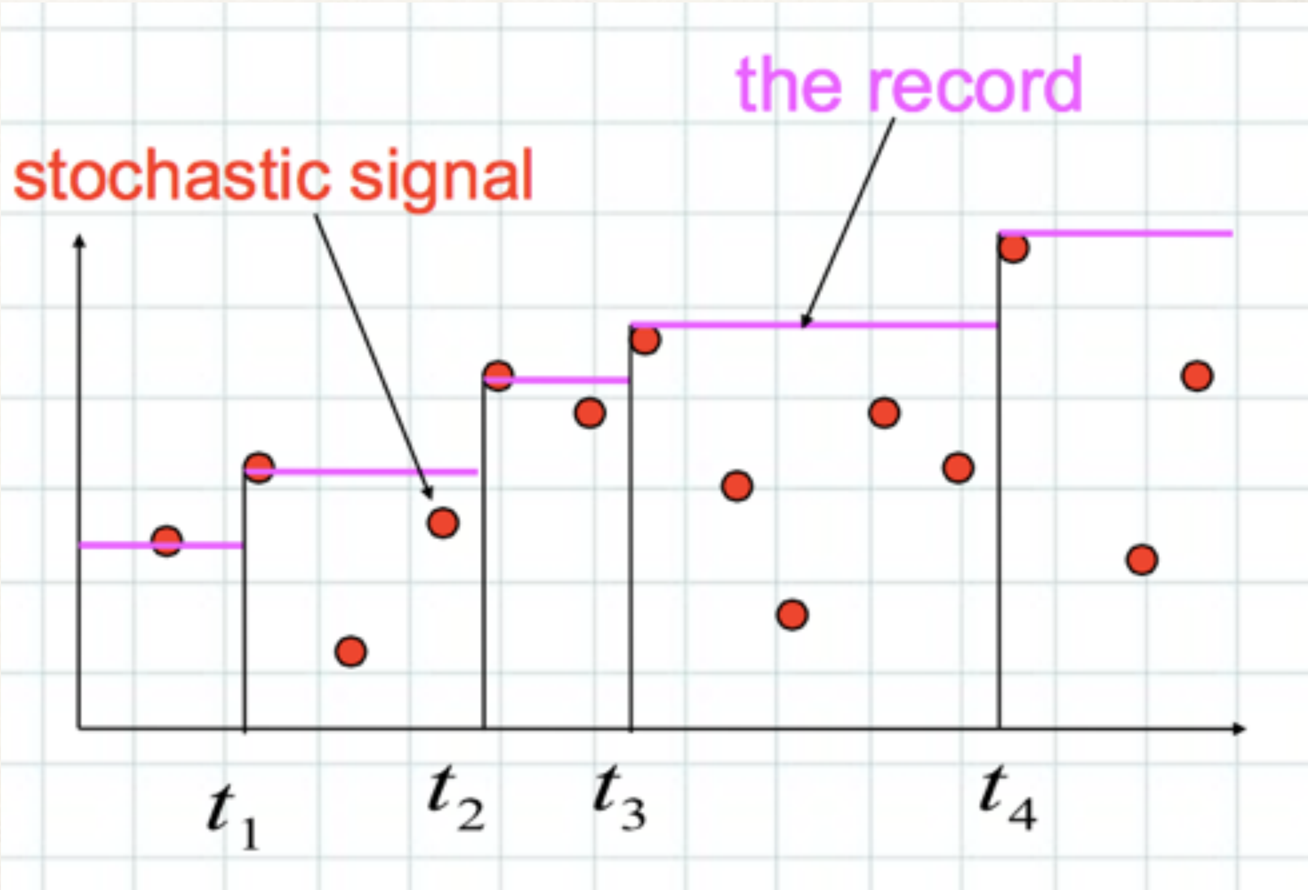
Lawson & Jensen 2006

Record Dynamics

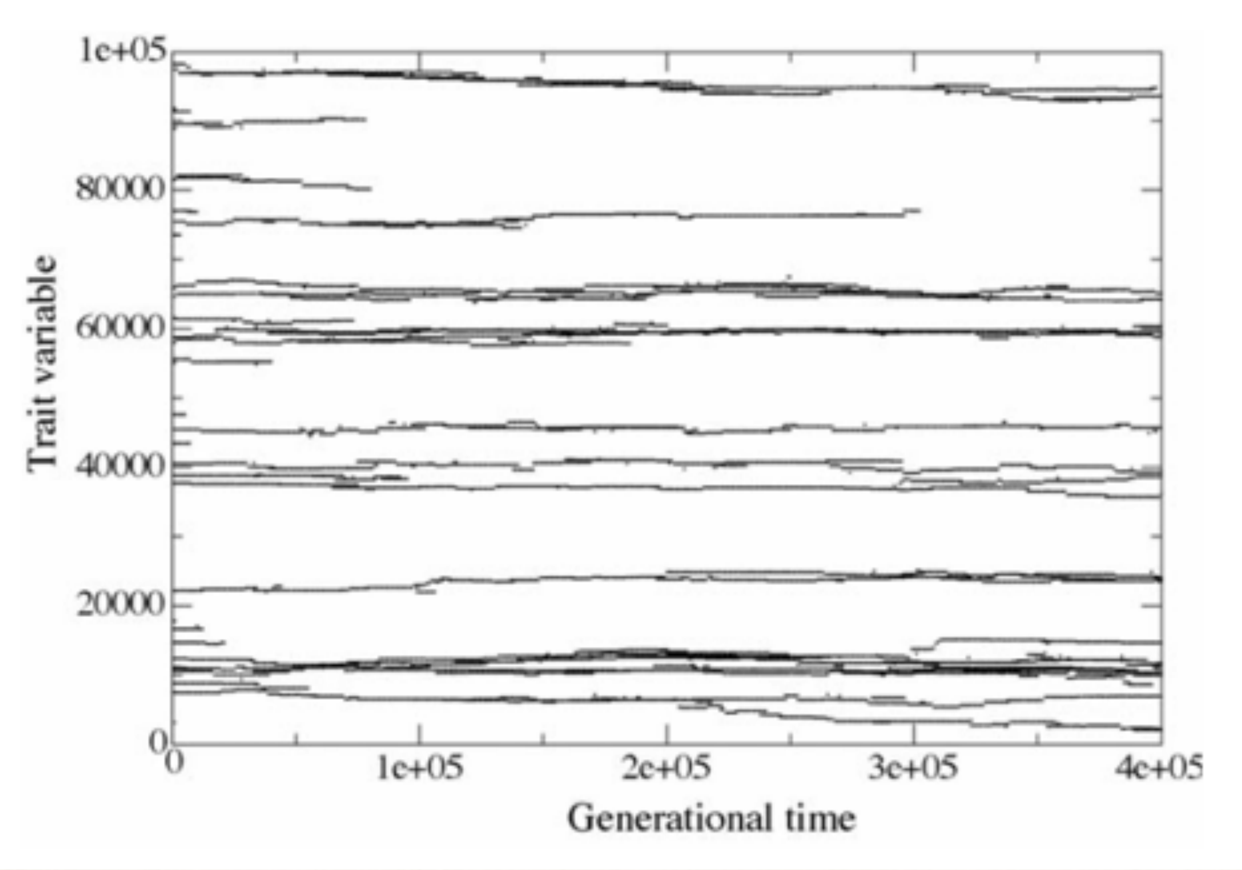


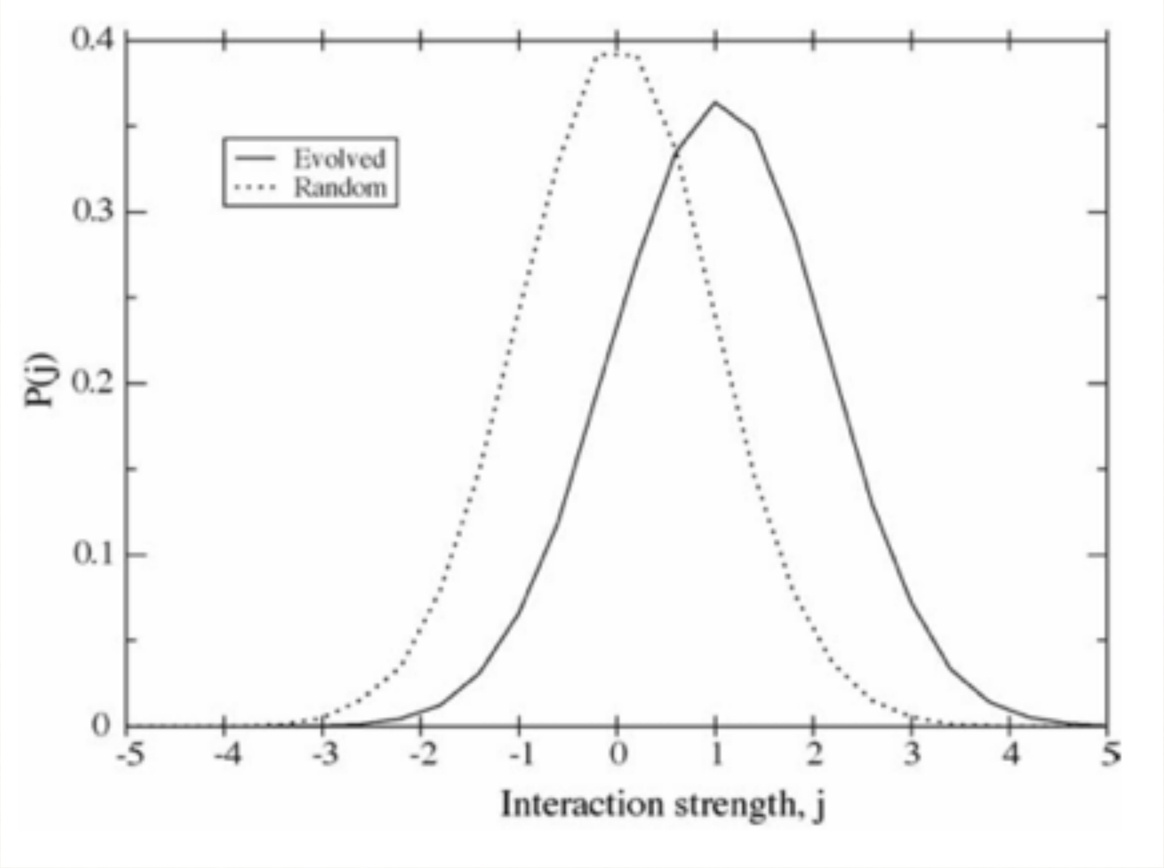
Number of transitions





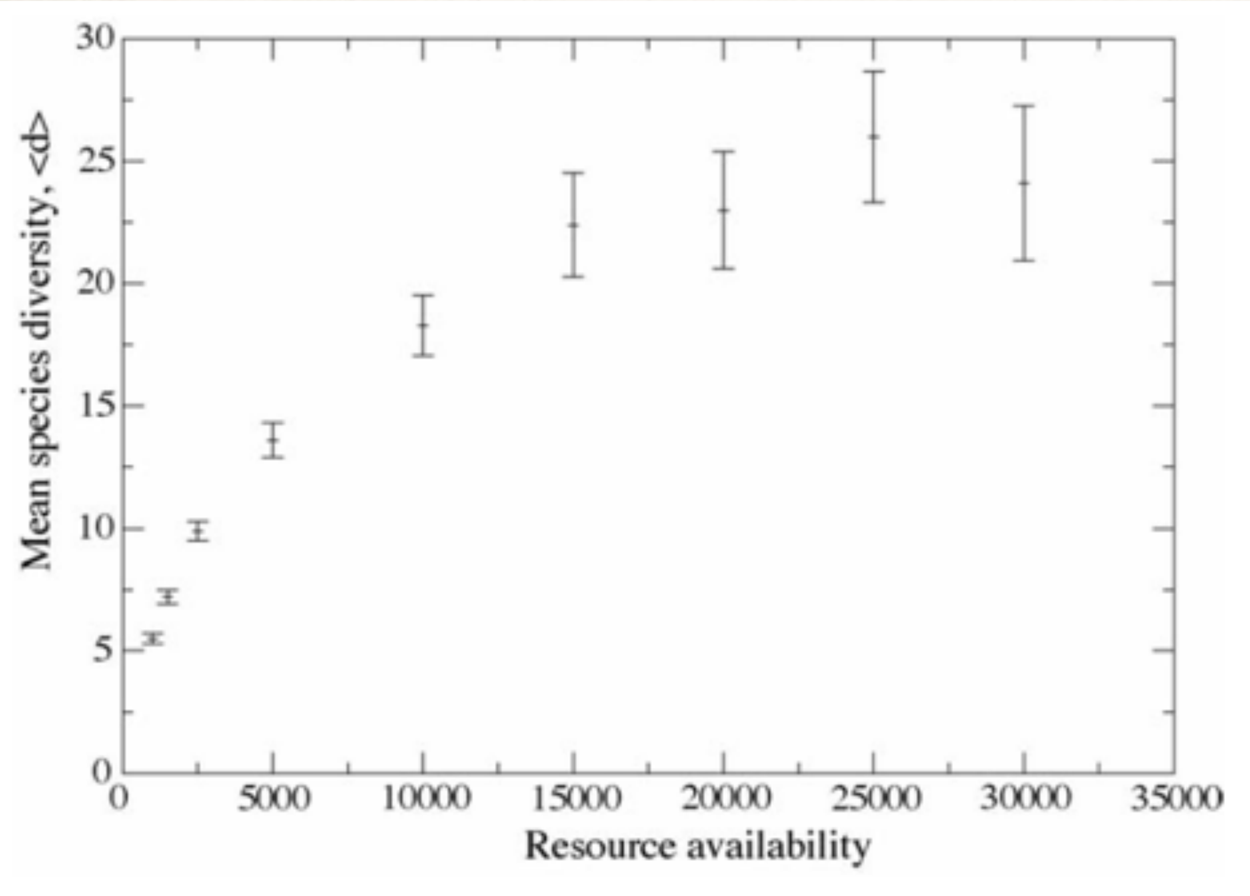
Correlated Genome-Space

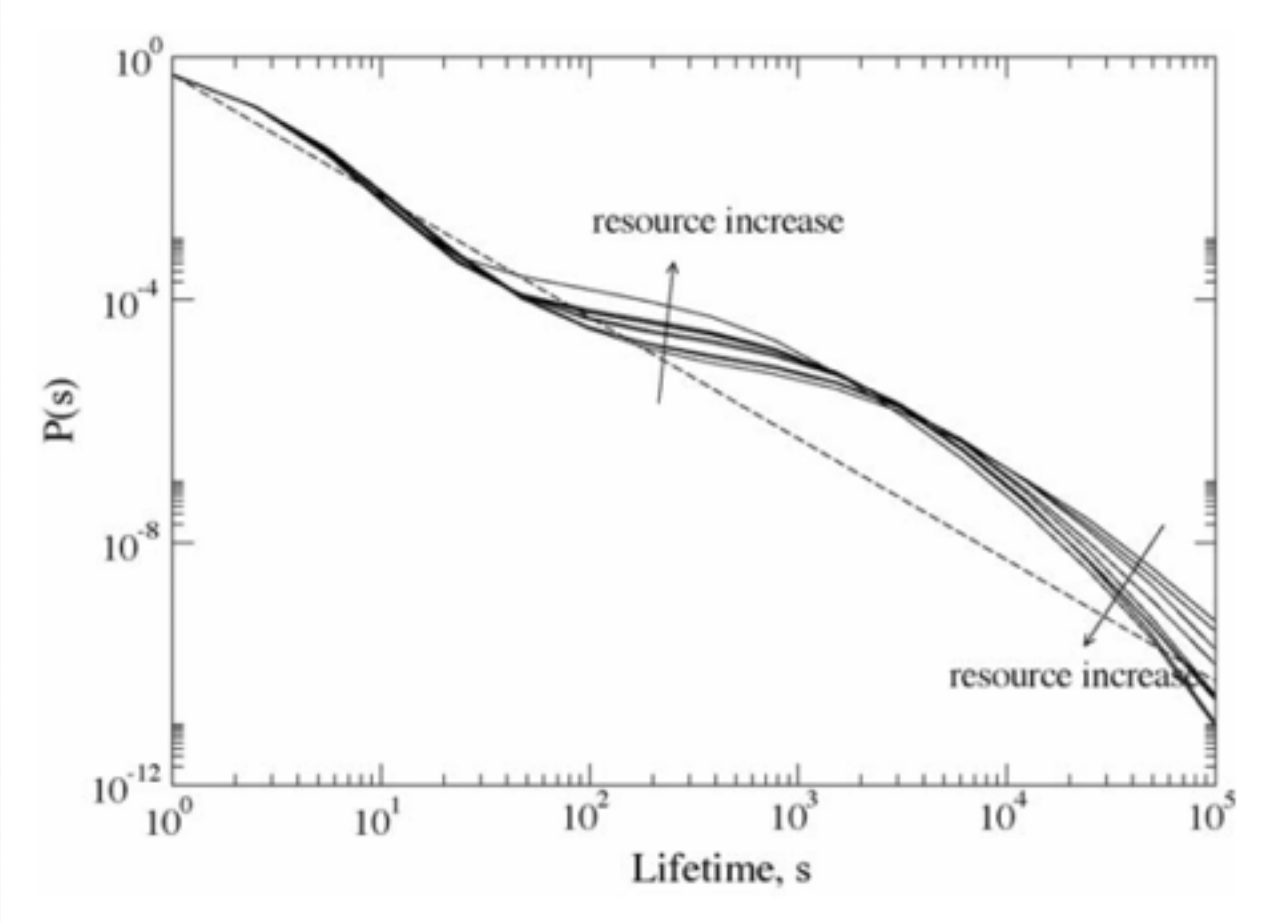




Laird et al. 2006

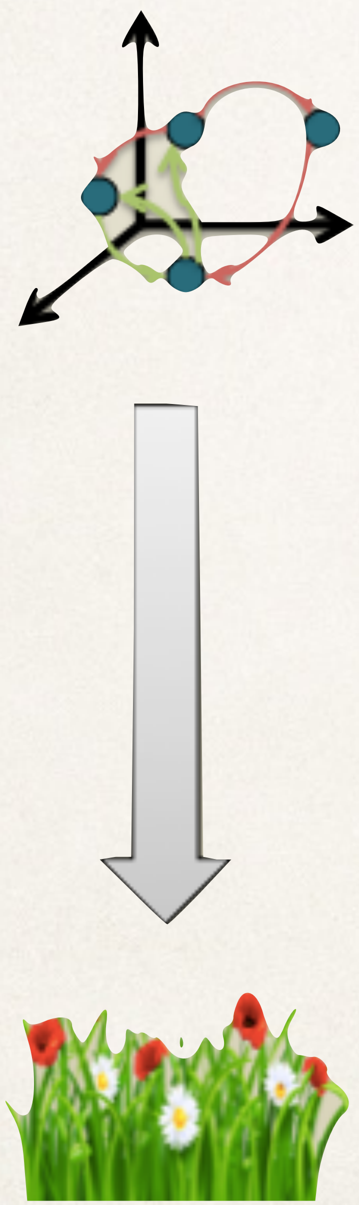
Ressource Constraint

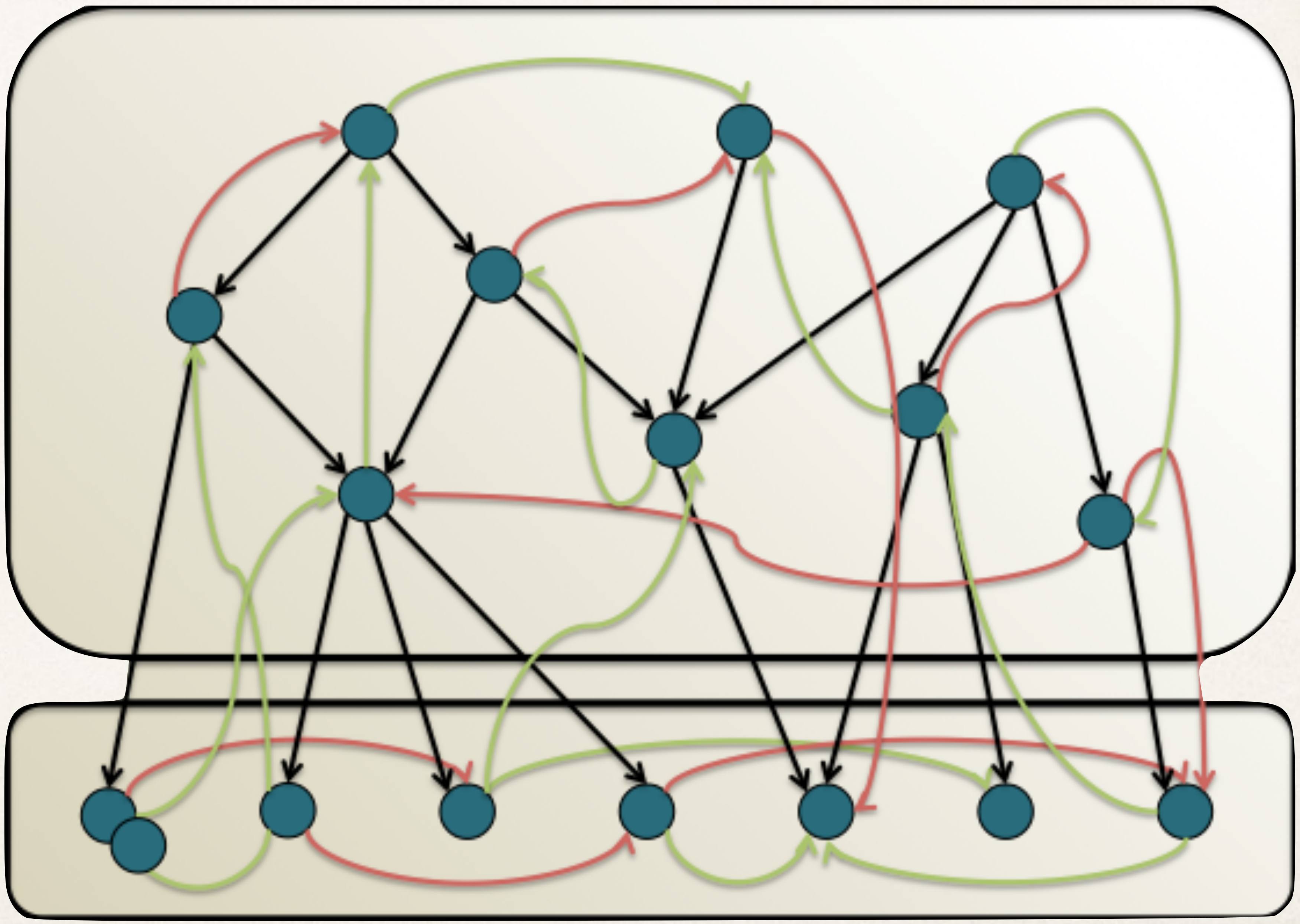




Laird et al. 2006

Tangled Food Webs






Why complexity science
and ecology?

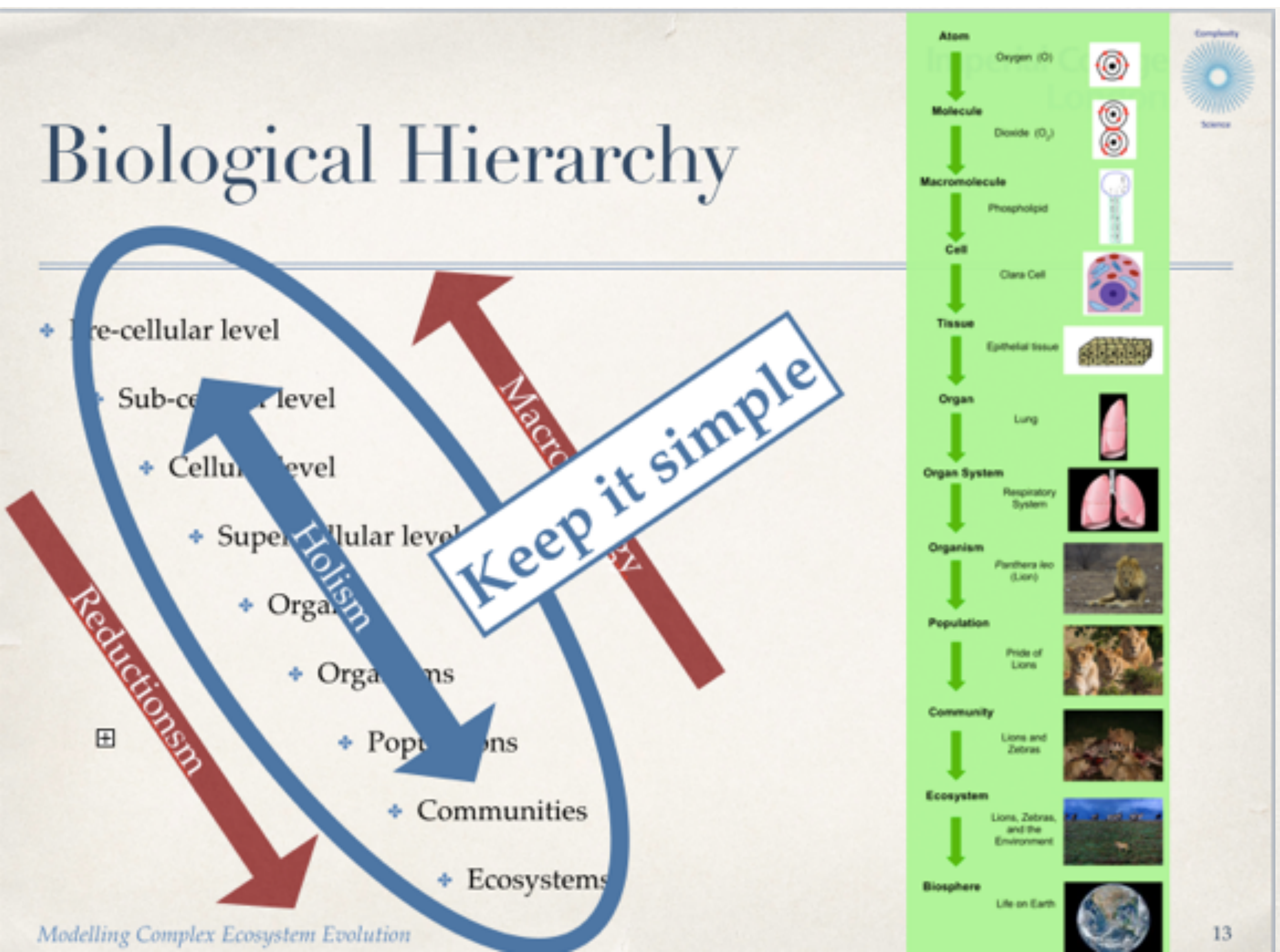
METE - The Maximum Entropy Theory of Ecology

John Harte, UC Berkeley

Articles

Macroecology: The Division of Food and Space Among Species on Continents

James H. Brown and Brian A. Maurer



Brown & Maurer 1989

Goal: Explanation of statistical patterns of abundance, distribution and diversity

From Description to Prediction - A Dilemma

- Numerous ecological mechanisms and processes…
  (predation, mutualism, competition, dispersal, speciation, birth, death, pollination, cannibalism, migration…)

- …coupled with numerous species traits & behaviours…
  (body size, phenology, food preferences, rooting depth, mating strategies, coloration, temperature tolerance, nutrient acquisition strategies…)

- …all operating within stochastic environments…

- influence patterns in…
  …abundance, distribution and energetics of species

Problem: Falsifiability

Motivation behind METE

How to predict patterns in distribution, abundance, energetics and network structure

- across individuals and species
- across spatial scales
- across temporal scales
- across habitat categories

without having to decide upon

- adjustable parameters
- combinations of mechanisms, traits and behaviors that operate in ecosystems?

The Maximum Entropy Theory of Ecology (METE)

Input Data

State variables

- Area A
- Number of Species S
- Number of Individuals N
- Total Metabolism E

MaxEnt

Predictions

Metrics of Ecology

- SAR, SAD
- Body Size Distributions
- Spatial aggregations patterns
- …

The Maximum Entropy Principle of Inference - General Rational

Edwin T. Jaynes (1922 – 1998)

- In science we generally **begin with prior knowledge** which we seek to expand.
- **Knowledge is not absolute but rather probabilistic** in nature, and thus the expanded knowledge we seek can be expressed mathematically in the form of probability distributions.
- Our **prior knowledge** can often be expressed in the **form of constraints** on those unknown distributions.
- We seek **expanded knowledge that is „least biased“**, in the sense that the expanded knowledge does not assume anything about the distributions other than the information contained in the prior knowledge.

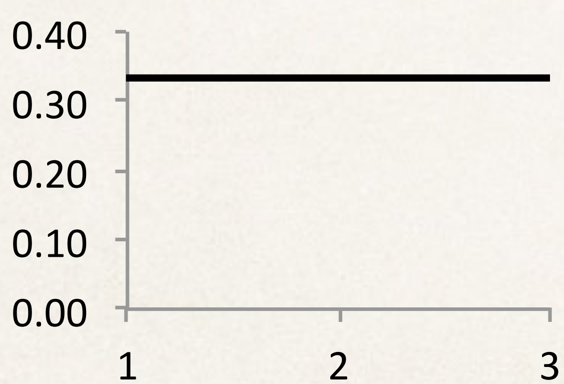
Jaynes 1957

The Maximum Entropy Principle of Inference - Concrete Idea

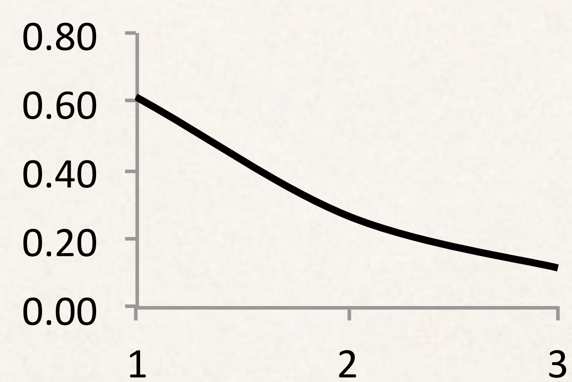
Edwin T. Jaynes (1922 – 1998)

- Goal: form of probability distribution P(n)
- Knowledge: prior information about P(n) in the form of constraints
- Inference: Least biased form of probability distribution

- Goal: P(n), n in {1,2,3}
- Constraint: $\langle n \rangle = 2$ $\qquad$ $\langle n \rangle = 1.5$



$$P(n) = \frac{1}{3}$$



$$P(n) \approx 1.42e^{-0.83n}$$

=> Measure to capture information content of a distribution

Jaynes 1957

Digression: Information Entropy

How much information does throwing a 5 contain?

$p_i = P(X = i) = \text{probability of throwing } i$

Demands on a measure of information:

$I(p_i) \geq 0$
$I(1) = 0$
$I(p_i p_j) = I(p_i) + I(p_j)$

MaxEnt: maximize H(X) given the constraints

Shannon: $I(p_i) = \log(\frac{1}{p_i})$

$$H(X) = E[I(p_i)] = -\sum_{i=1}^{n} p_i \log(p_i)$$

Shannon 1948

Digression: Khinchin Axioms

$H(X) = -\sum_{i=1}^{n} p_i \log(p_i)$

Where does the logarithm come from?

Khinchin Axioms:

$$H(X) = H(p_1, p_2, ...p_n)$$

$$H(1/n, ...1/n) \geq H(X)\ \forall X$$

$$H(p_1, p_2, ...p_n) = H(p_1, p_2, ...p_n, 0)$$

$$H(p_{ij}) = H(p_i) + \sum_{i=1}^{n} p_i H(P(j|i))$$

Khinchin 1957

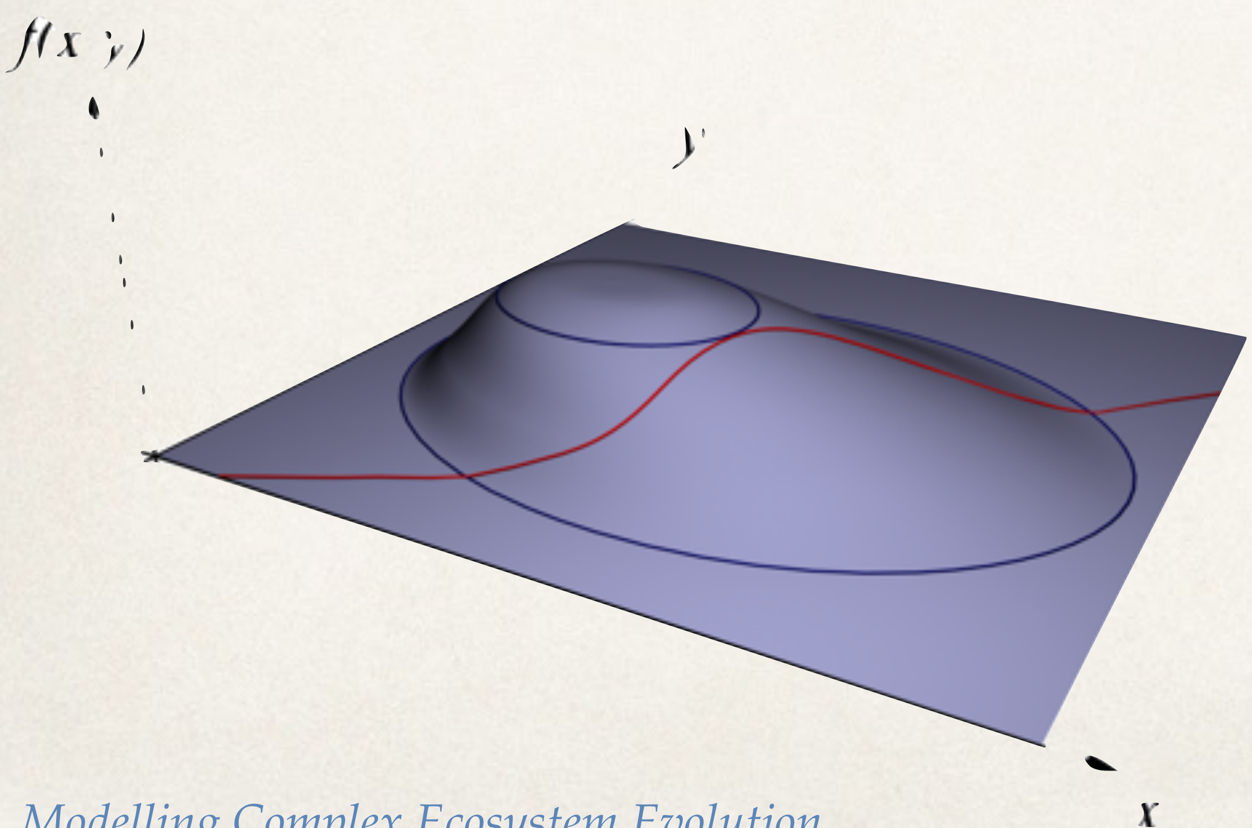
Digression: Constrained Optimisation

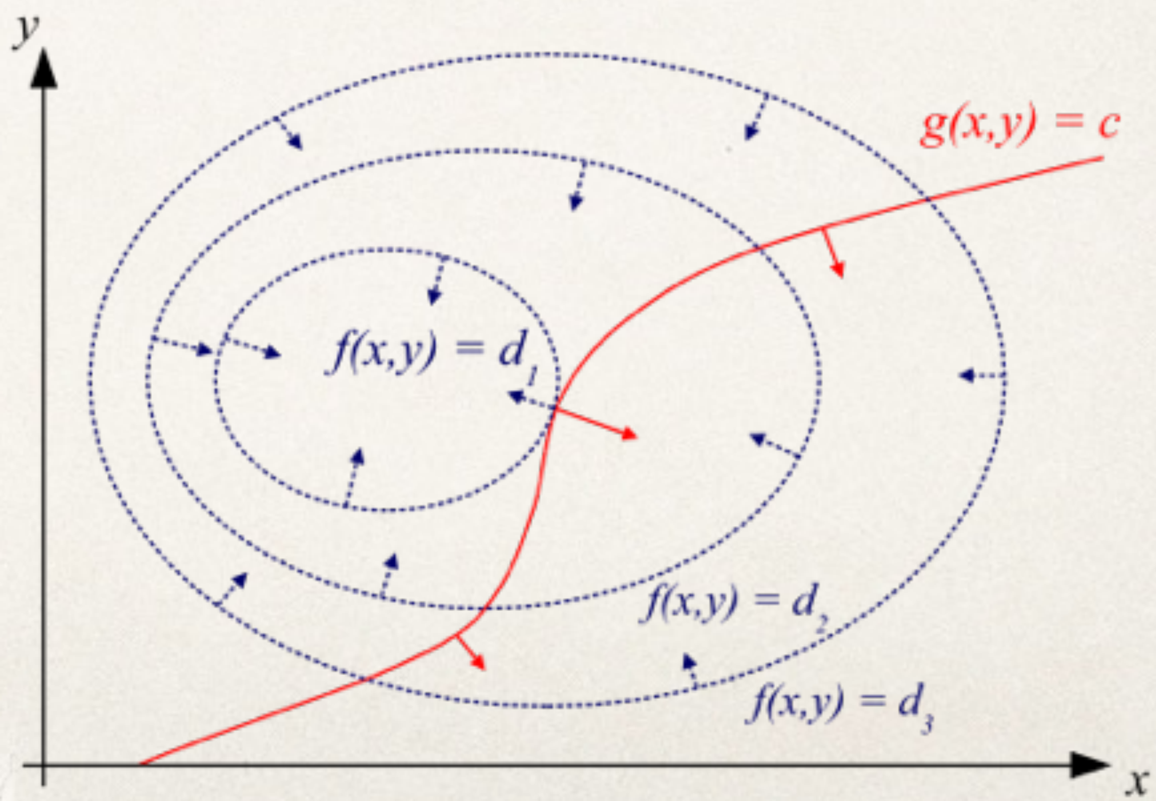
$$H(X) = -\sum_{i=1}^{n} p_i \log(p_i)$$

MaxEnt: maximize H(X) given the constraints

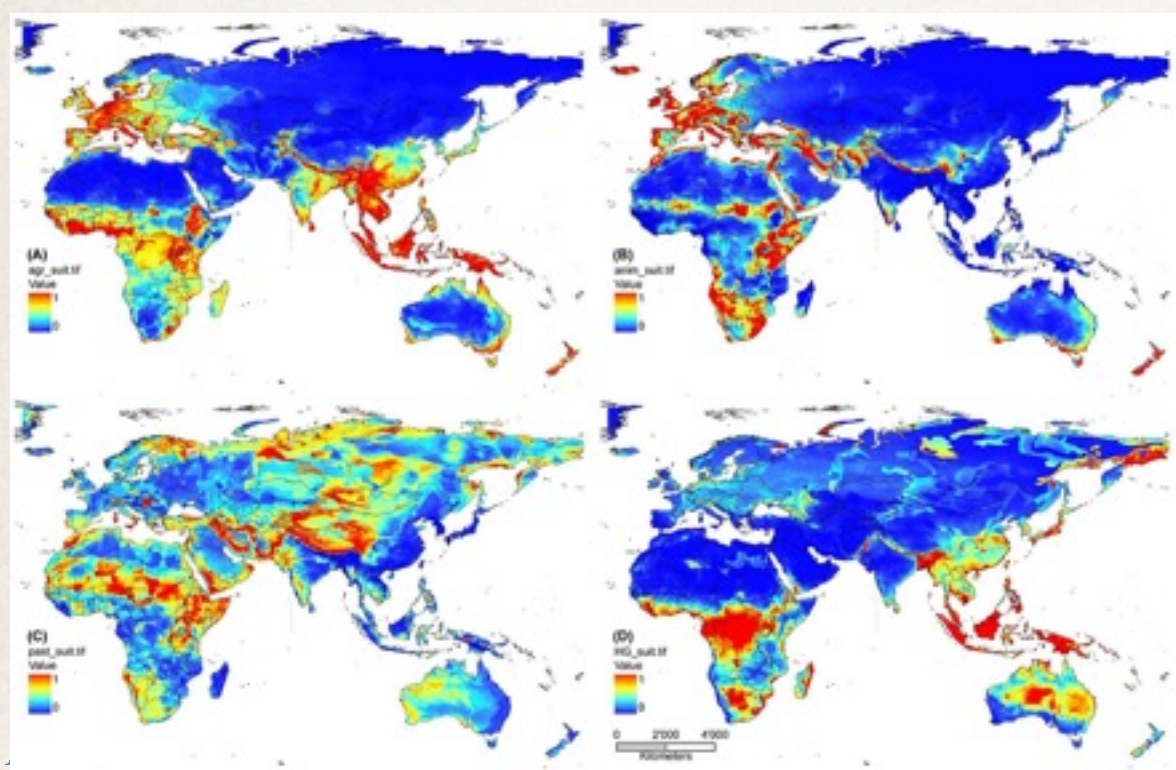
$$\sum_{i=1}^{n} p_i = 1 \qquad \sum_{i=1}^{n} f_k(i) p_i = \langle f_k \rangle$$

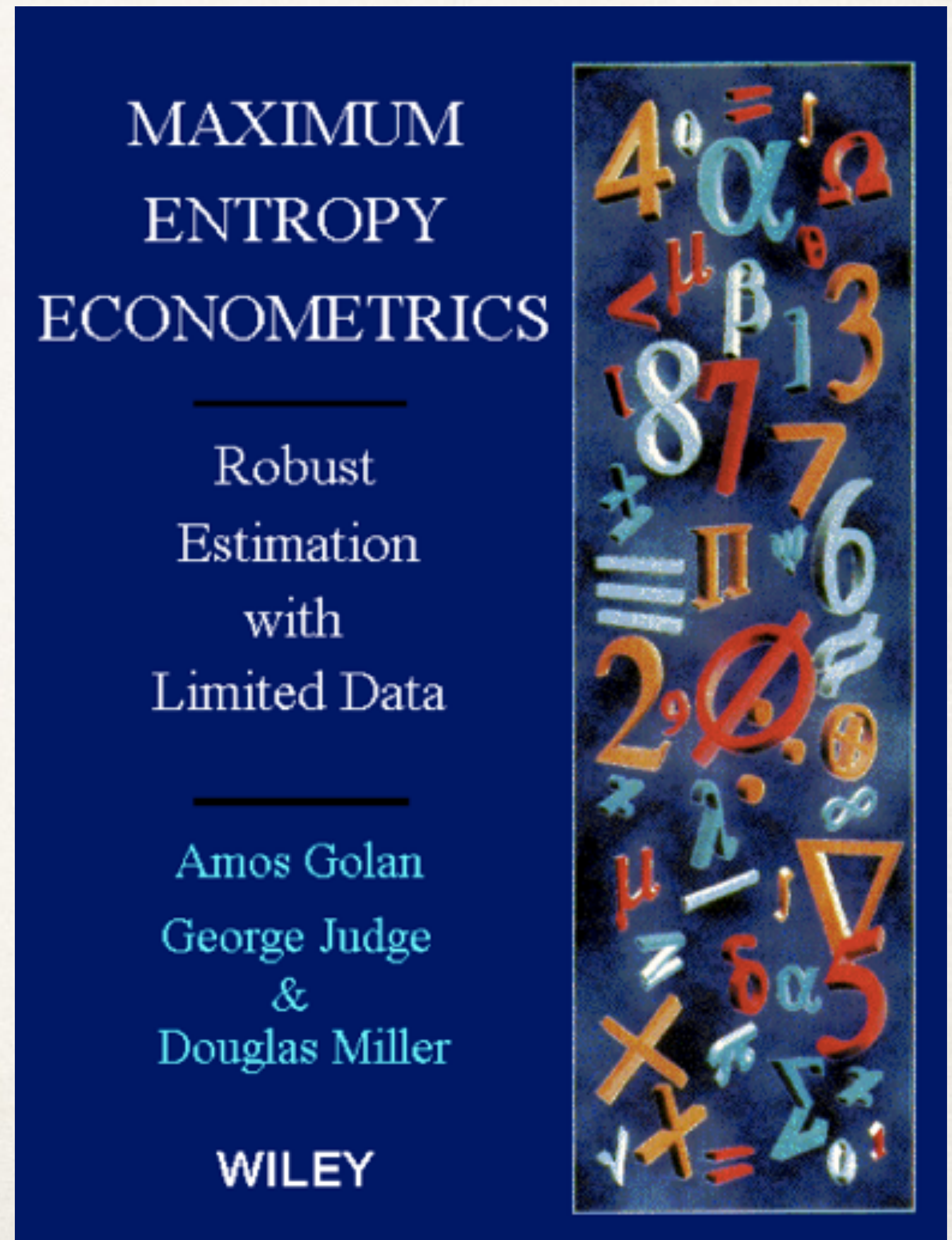
$$\nabla f = -\lambda \nabla g$$





Applications of MaxEnt





The Maximum Entropy Theory of Ecology (METE)

Ecosystem structure function $R(n,\epsilon|A_0,\ S_0,\ N_0,\ E_0)$

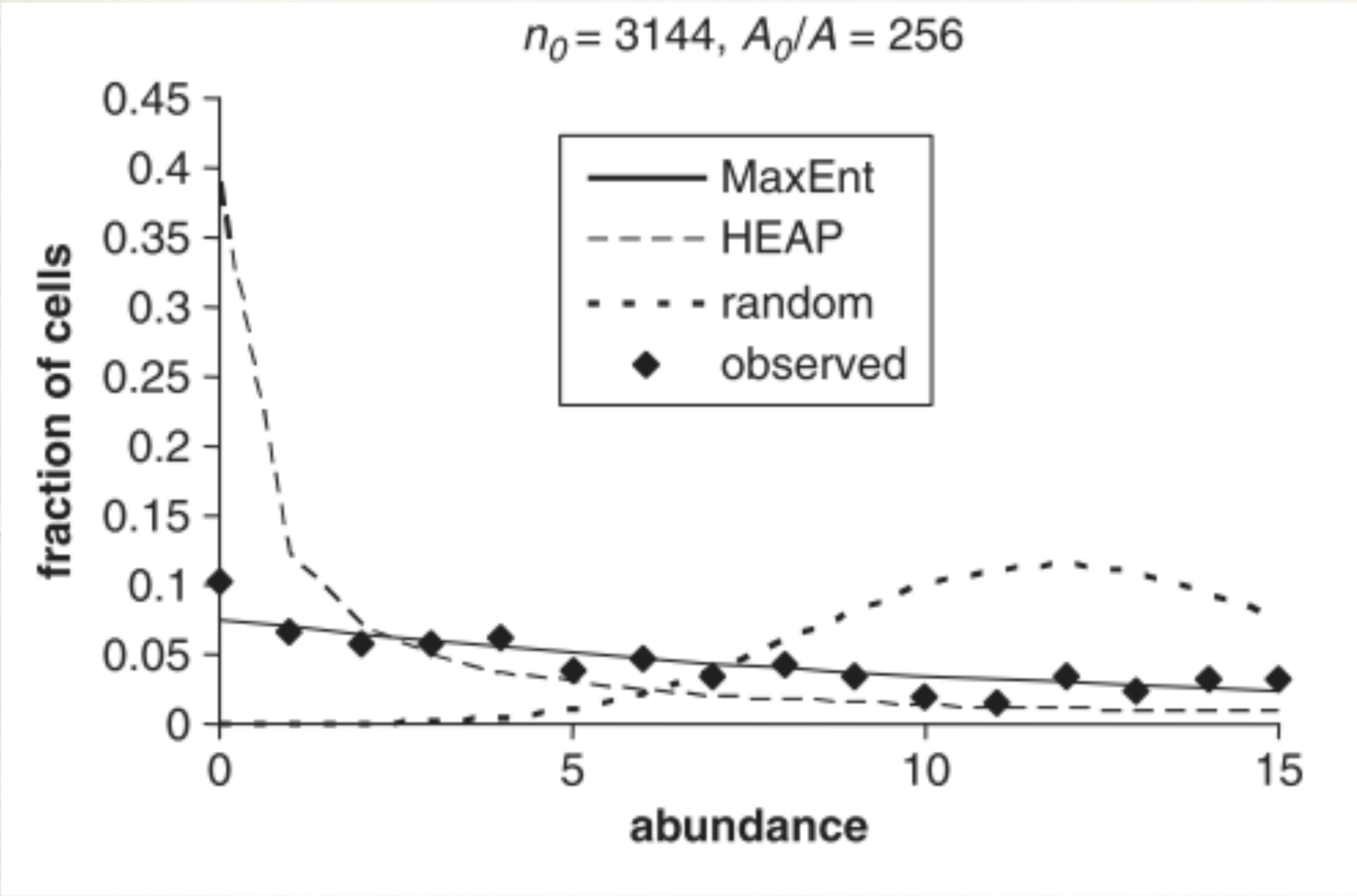
Constraints:
$$\sum_{n=1}^{N_0}\int_{\varepsilon=1}^{E_0} d\varepsilon\cdot R(n,\varepsilon|A_0,S_0,N_0,E_0)=1$$

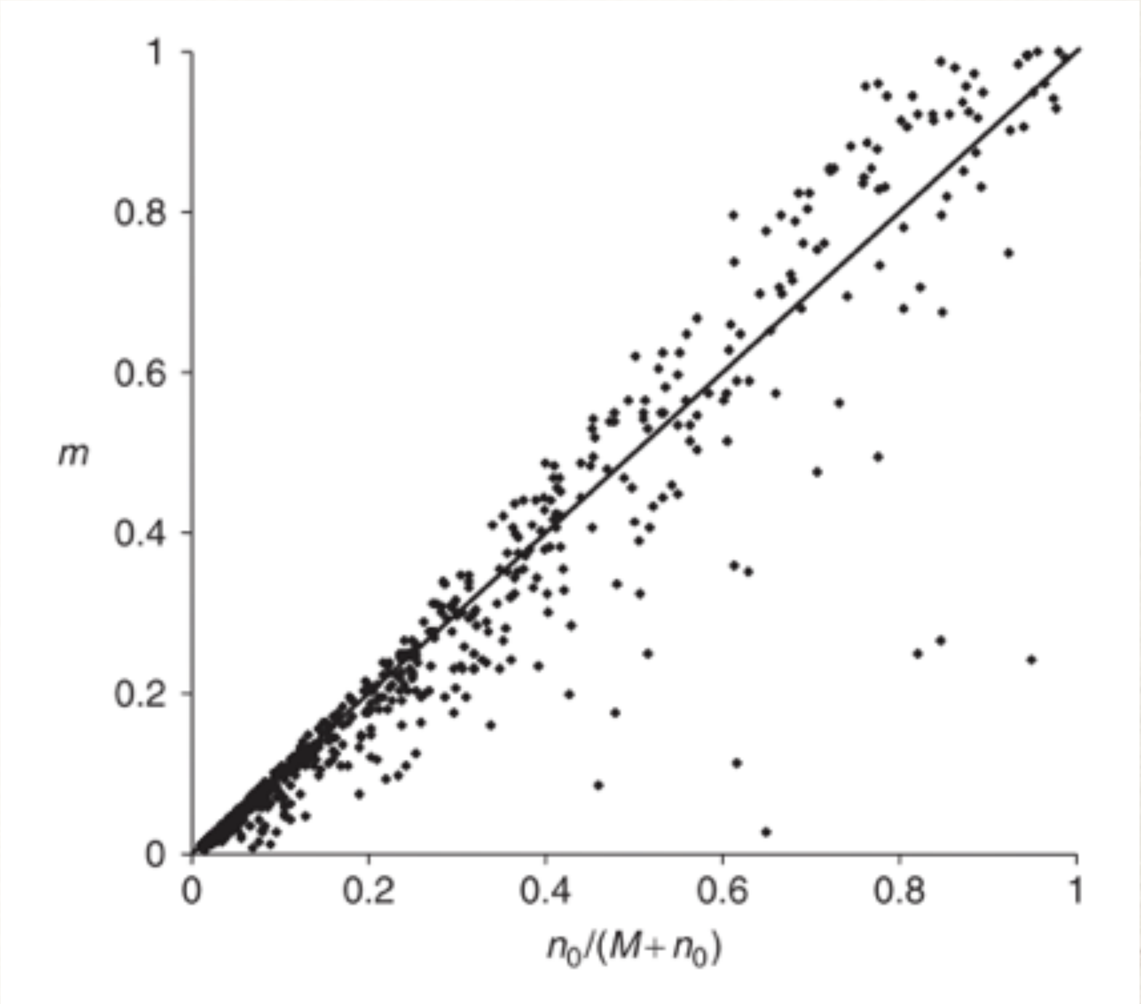
$$\sum_{n=1}^{N_0}\int_{\varepsilon=1}^{E_0} d\varepsilon\cdot n\cdot R(n,\varepsilon|A_0,S_0,N_0,E_0)=\frac{N_0}{S_0}$$

$$\sum_{n=1}^{N_0}\int_{\varepsilon=1}^{E_0} d\varepsilon\cdot n\cdot\varepsilon\cdot R(n,\varepsilon|A_0,S_0,N_0,E_0)=\frac{E_0}{S_0}$$

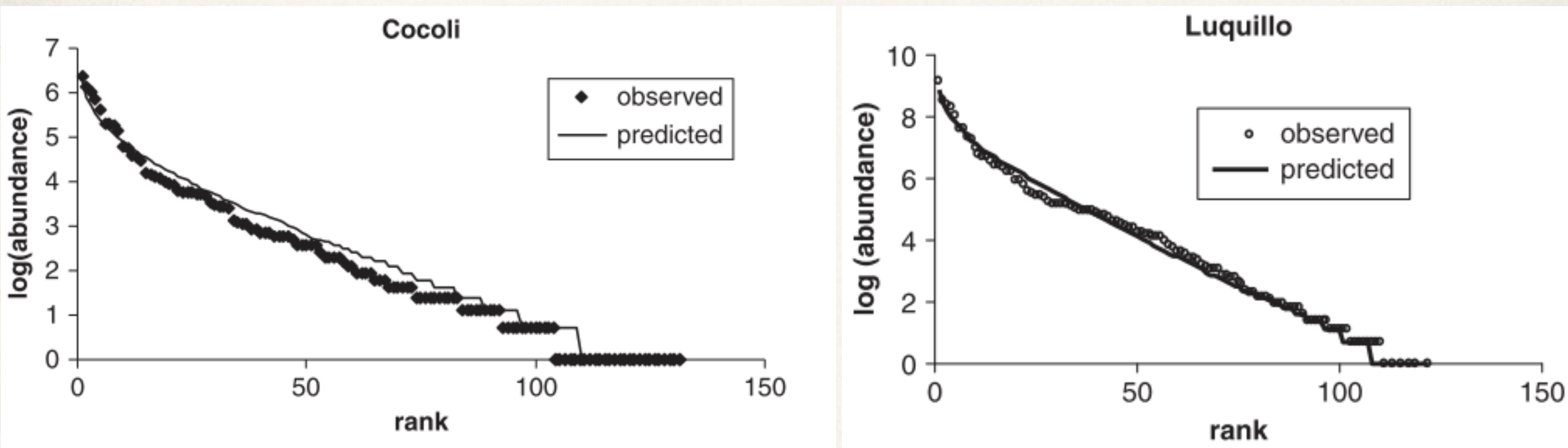
Information Entropy:
$$-\sum_{n=1}^{N_0}\int_{\varepsilon=1}^{E_0} d\varepsilon\cdot R(n,\varepsilon)\cdot\log(R(n,\varepsilon))$$

Species-Area-Relationship

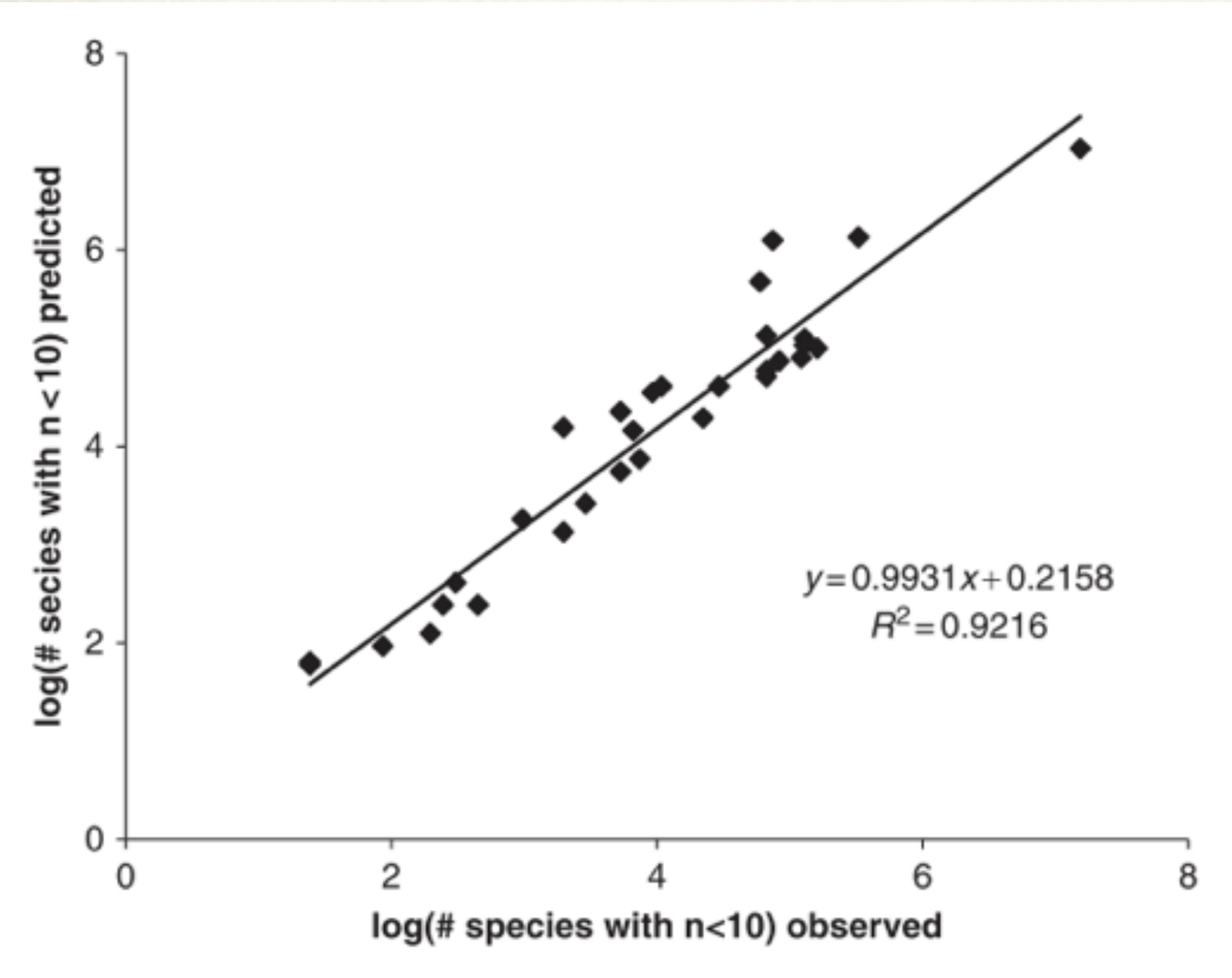


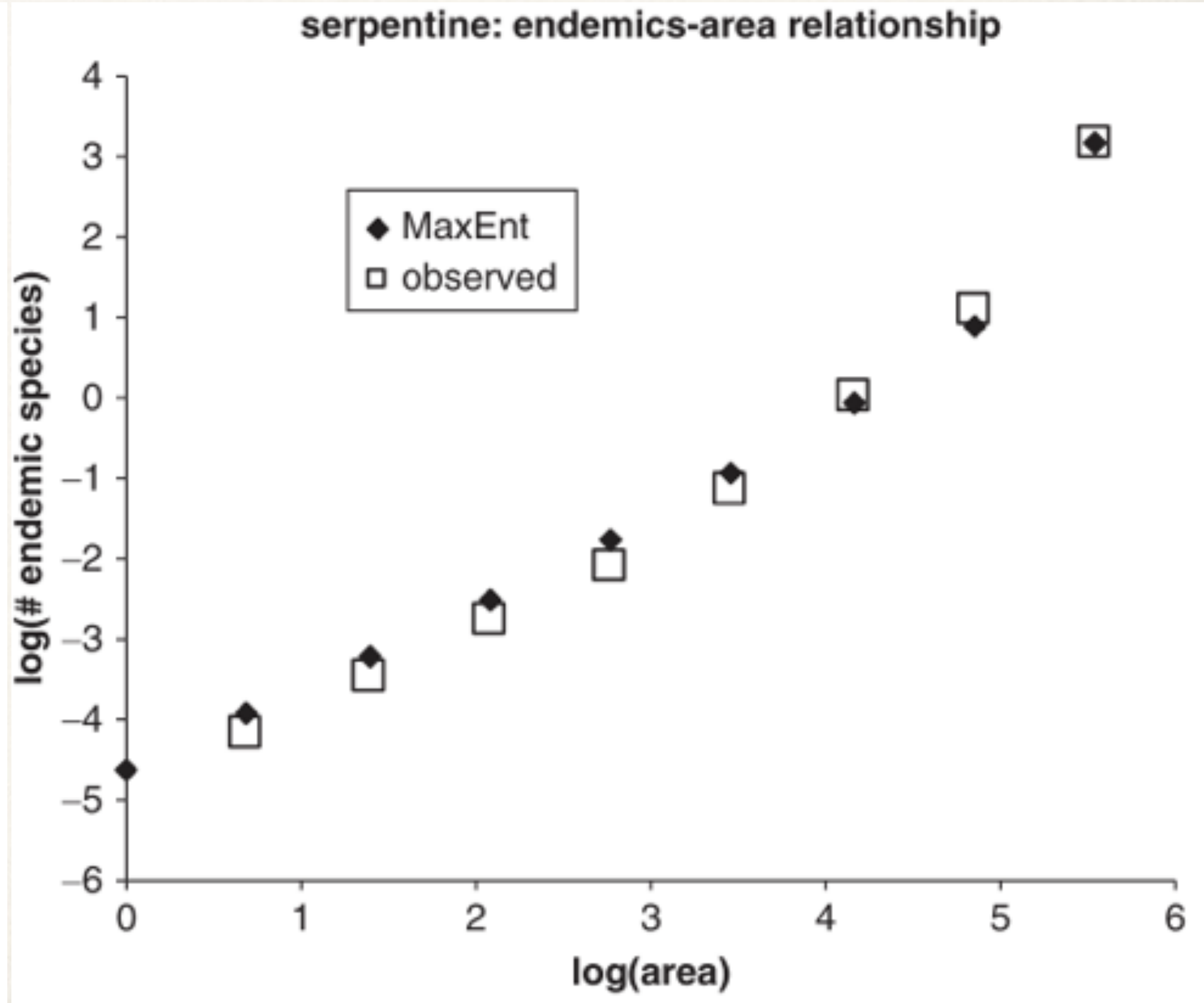


Species Abundance Distribution

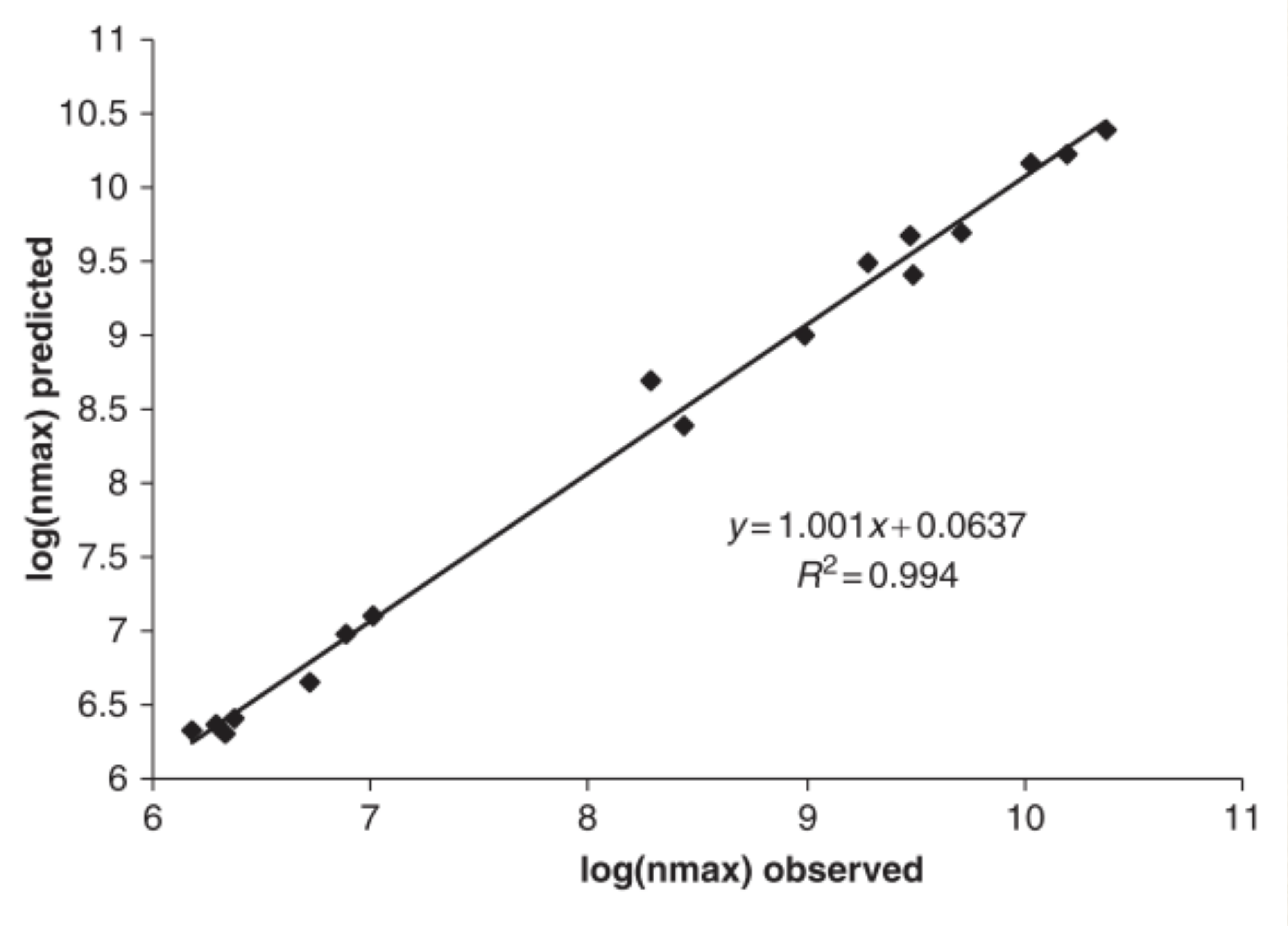


Endemic Species

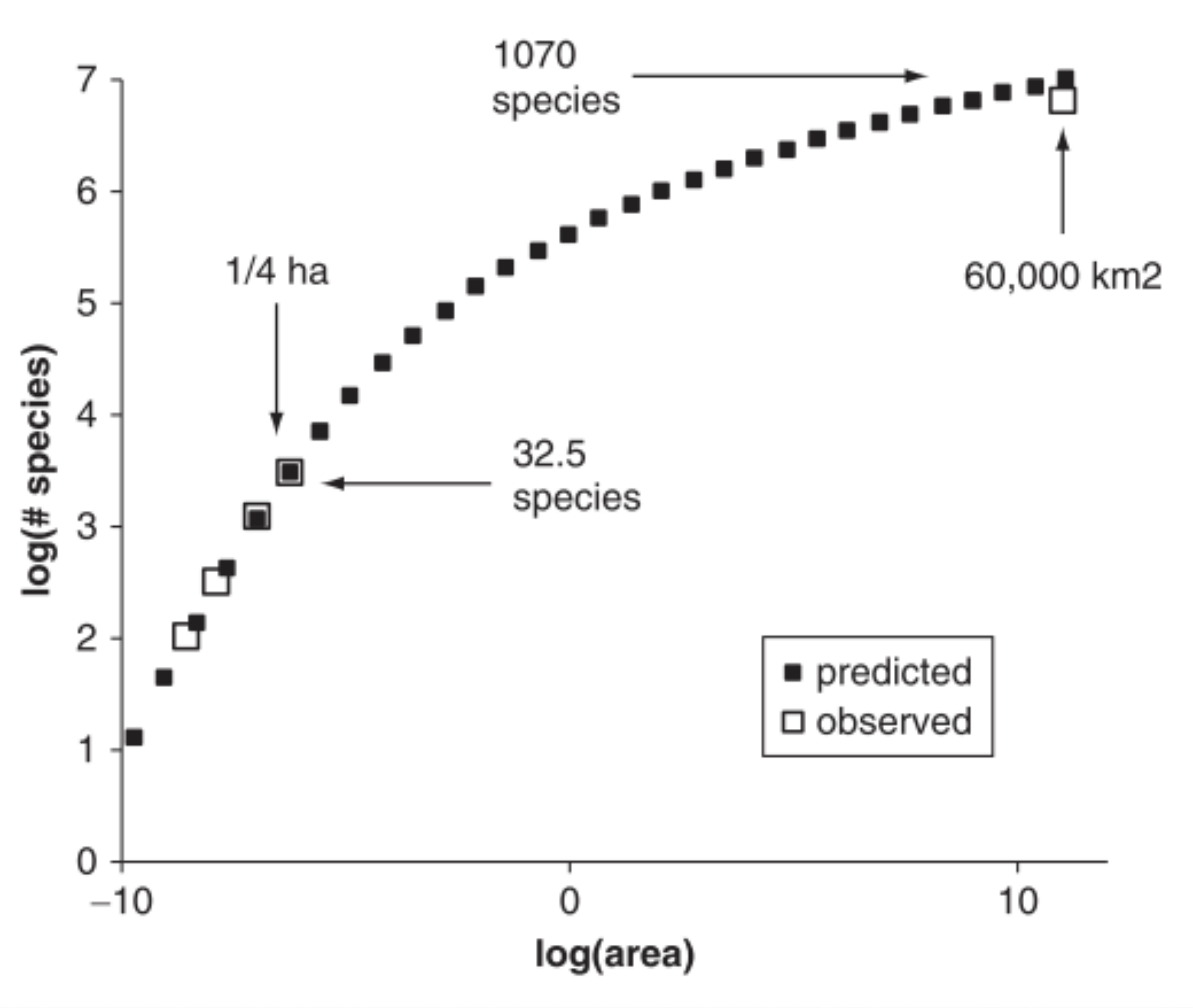




Most Abundant Species



Upscaling



1070
species
1/4 ha
60,000 km2
32.5
species
log(# species)
log(area)
predicted
observed
0
1
2
3
4
5
6
7
–10
0
10

What if MaxEnt fails?

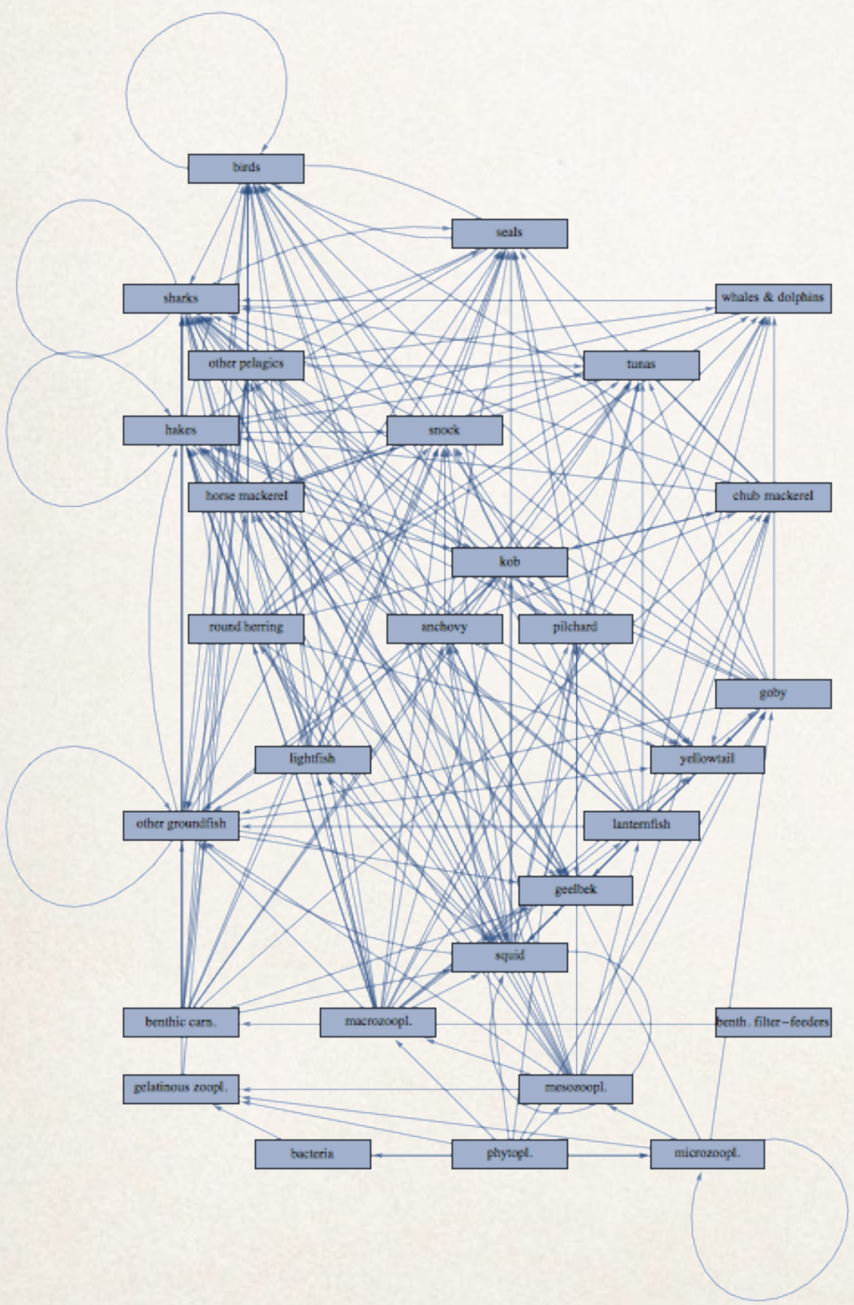
- Mathematical error
- Error in prior knowledge
- Constraints don't provide enough adequate information

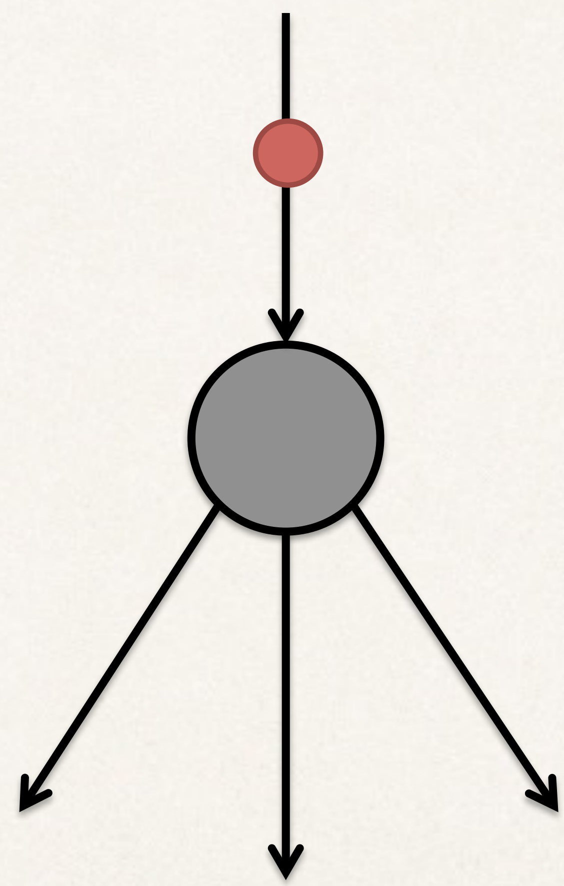
- ➡ MaxEnt neutral starting point
- ➡ Success does NOT imply mechanism but suggests that state variables incorporate crucial information
- ➡ Failure calls for additional mechanistic information

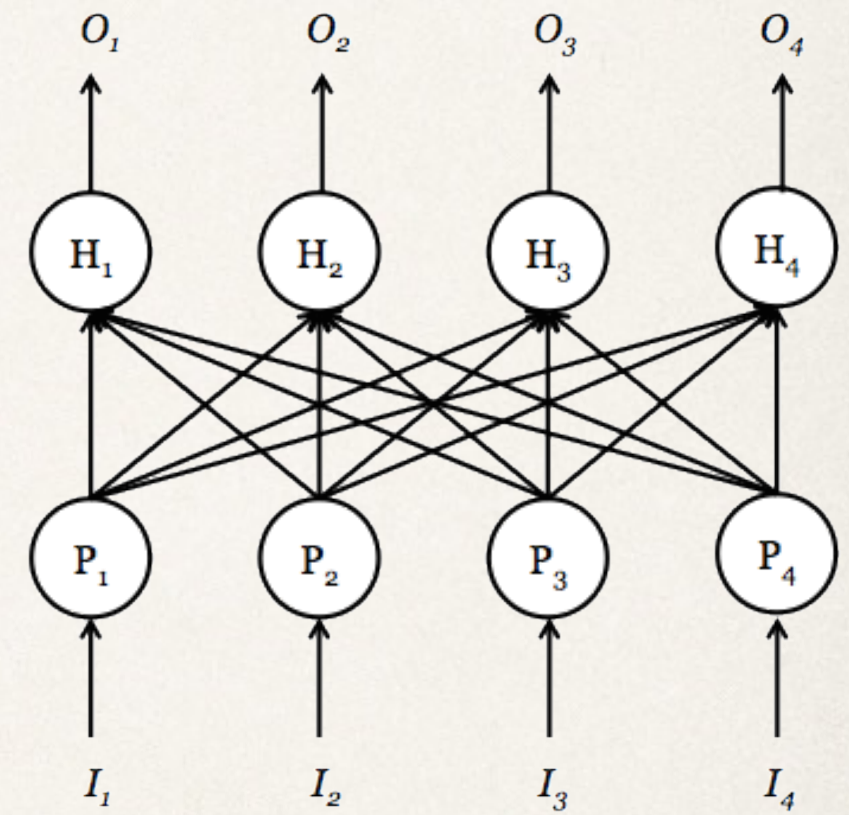

METE - Your Opinion?

MaxEnt and Food Webs

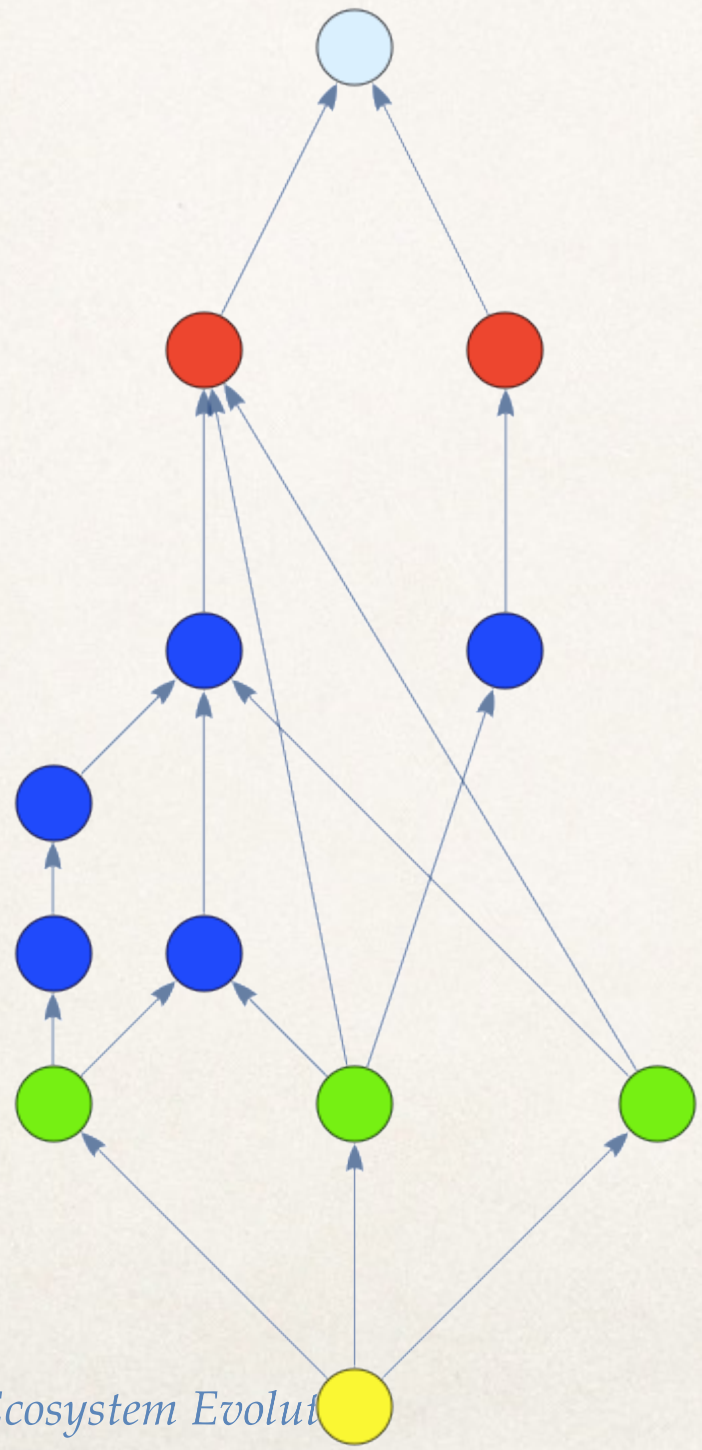
MaxEnt and Network Flow

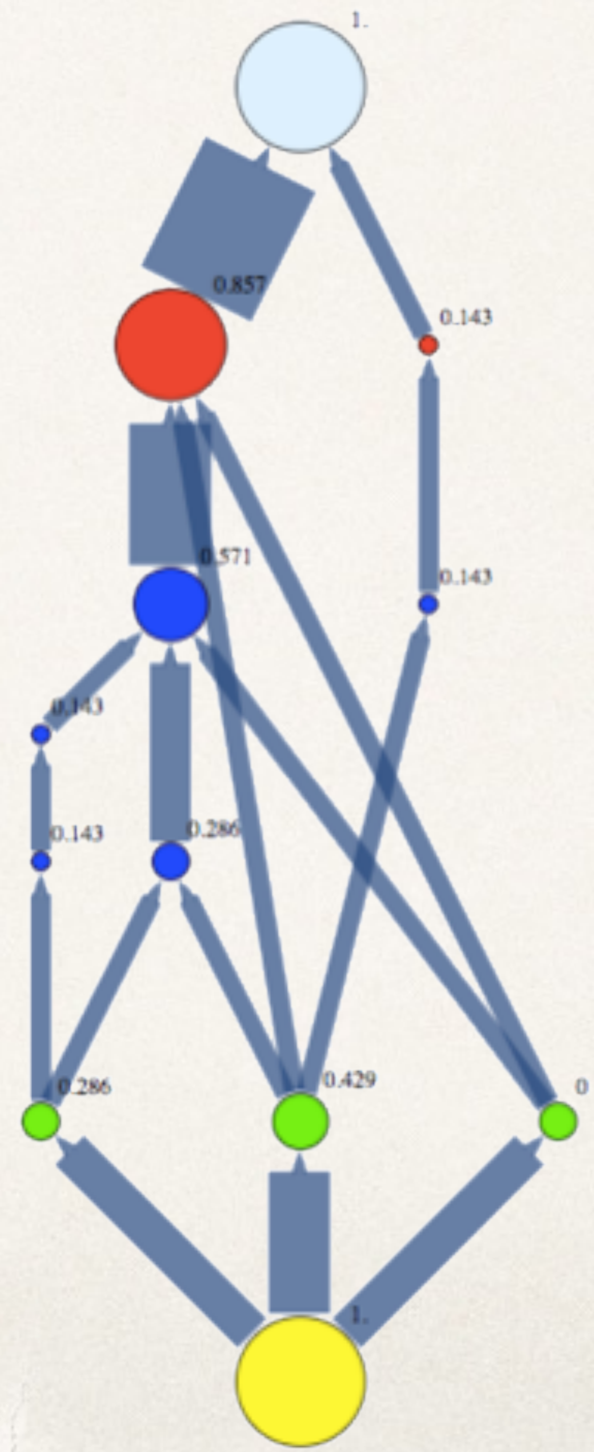






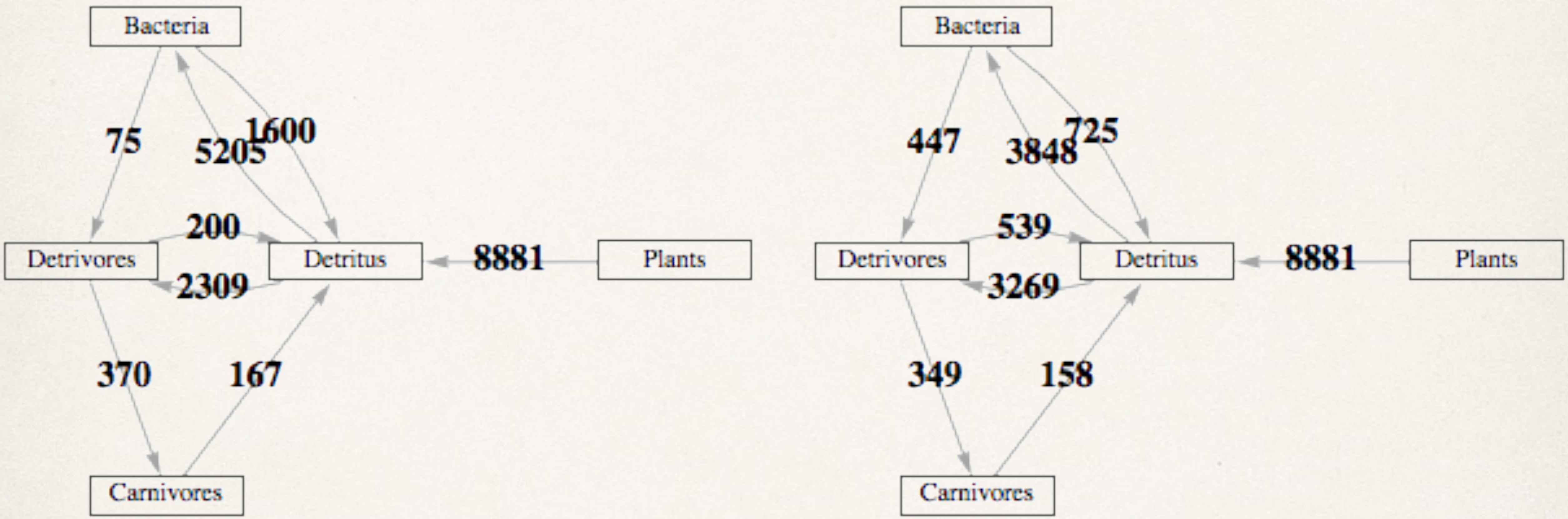
Flow from Topology





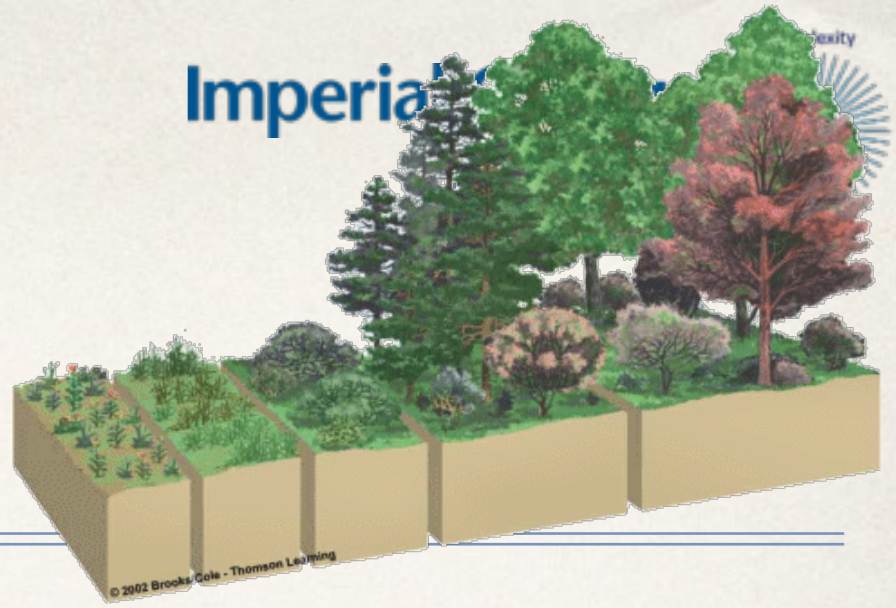
flow ~ number of pathes through a node

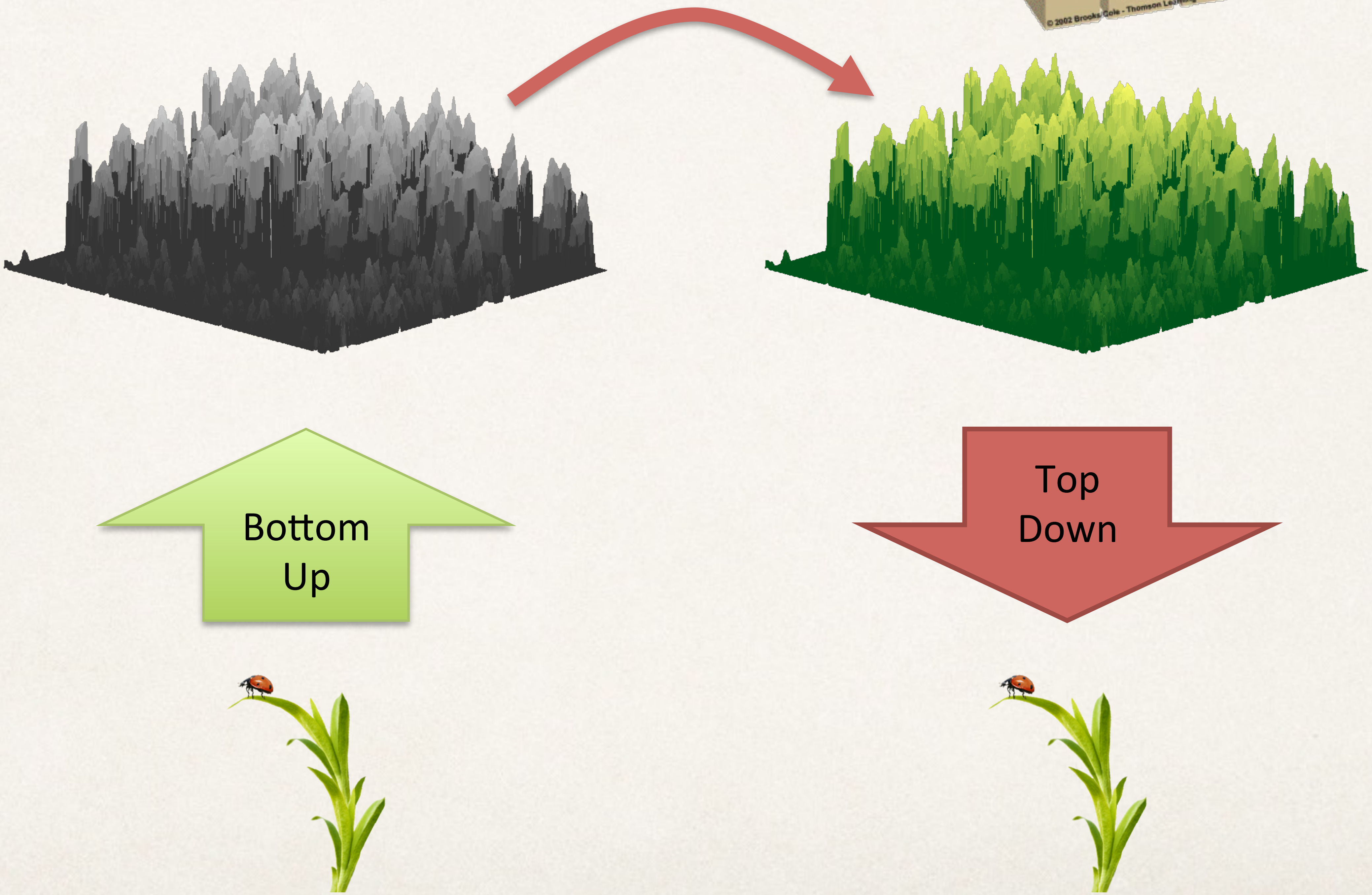
Comparison to Data



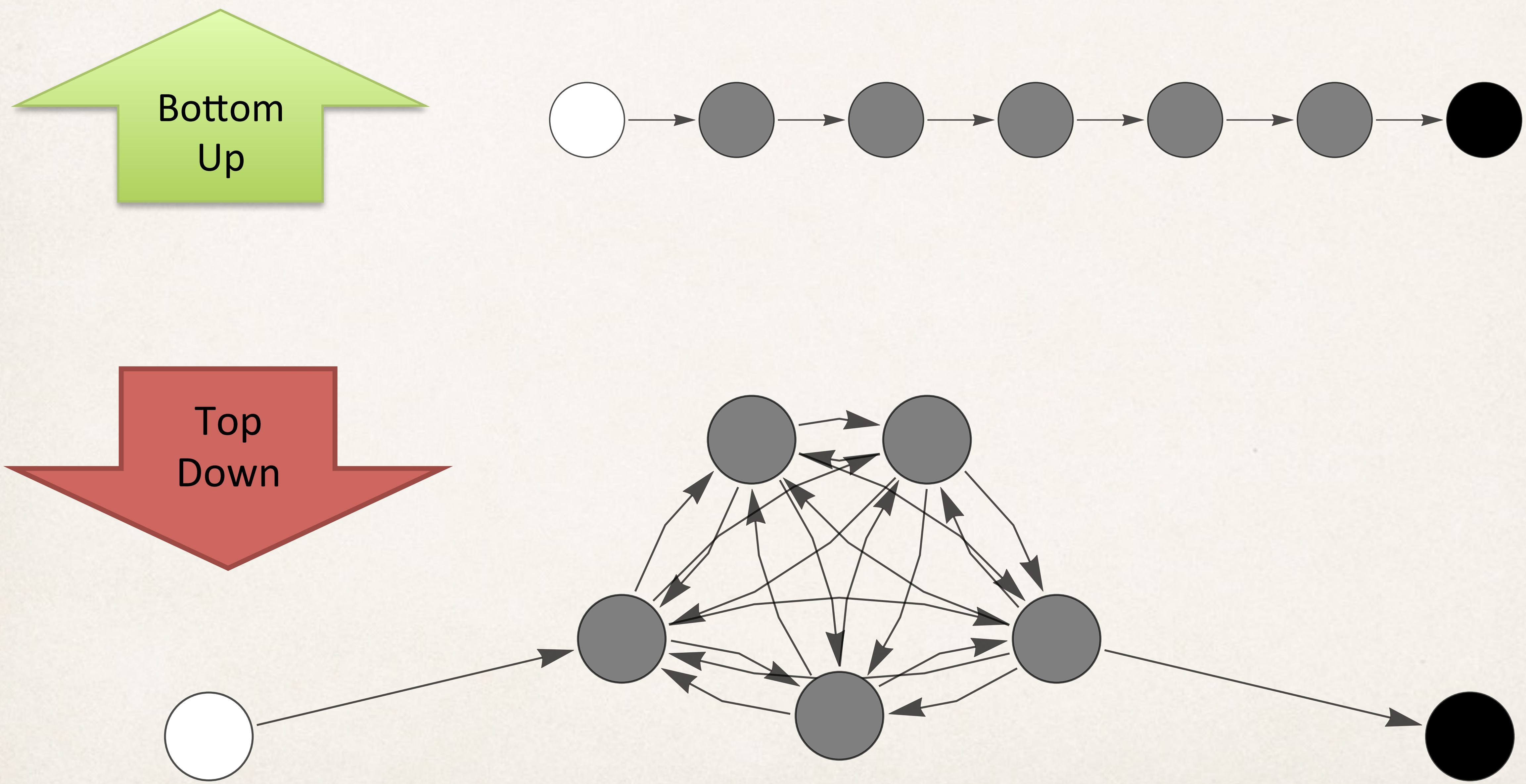
	S_o	L_o	Flow entropy data	Flow entropy MaxEnt-flow
Cone Spring	5	8	5311	6283
North Sea	10	13	515	580
Crystal River	17	69	995	6050

Ecosystem Evolution

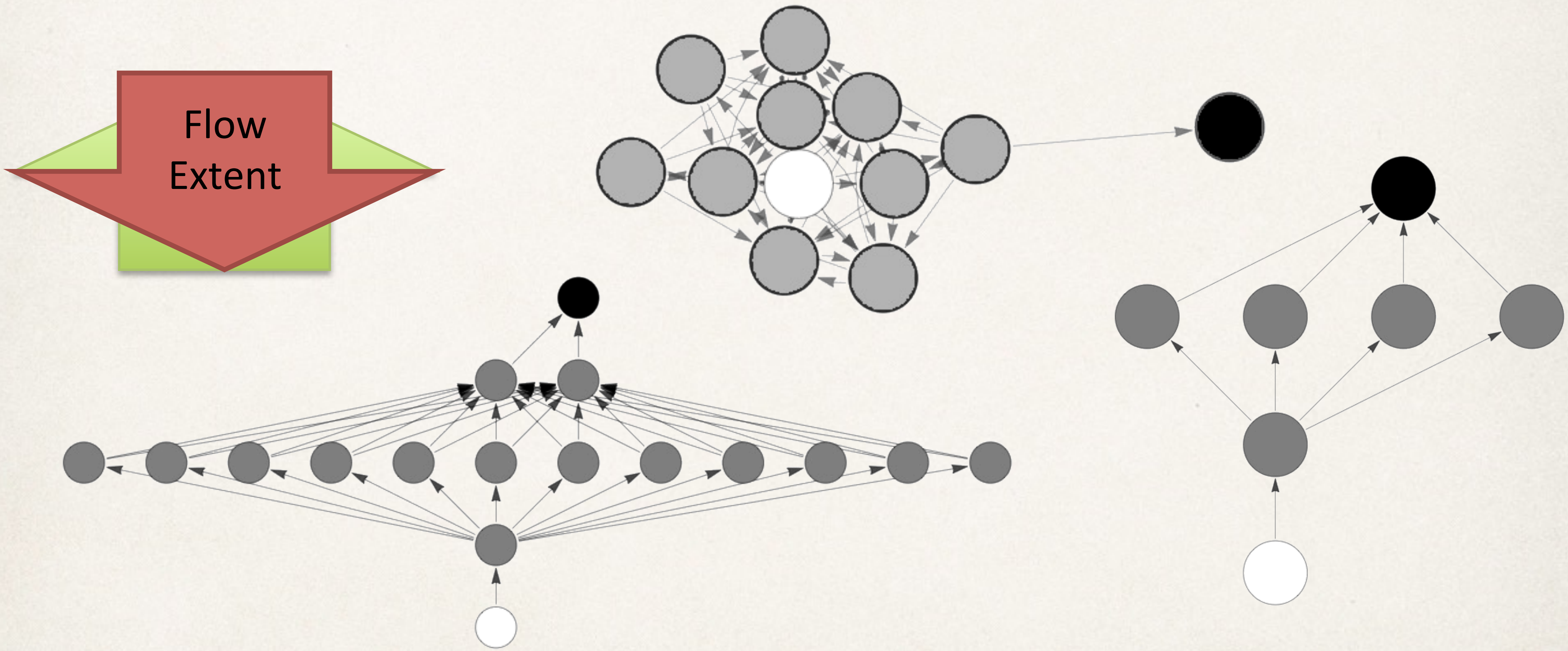




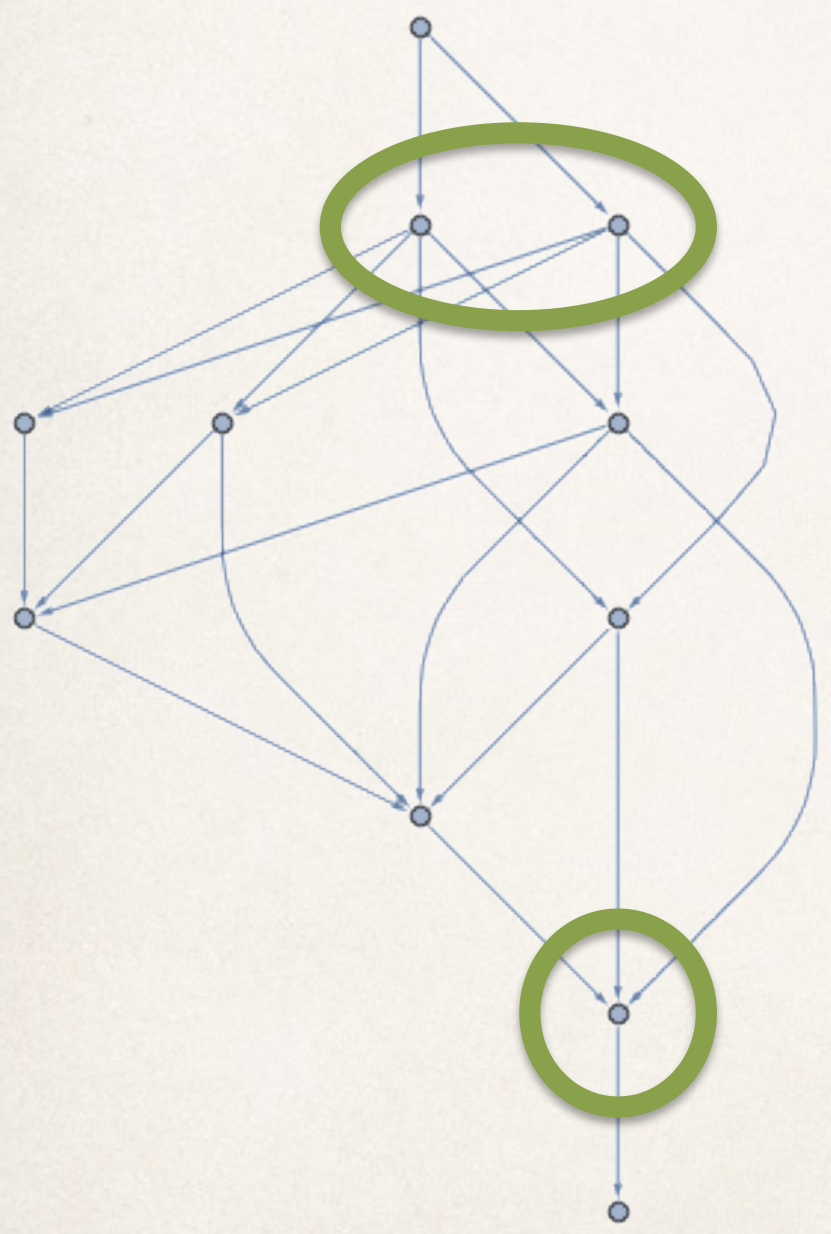
Ecosystem Structure Evolution



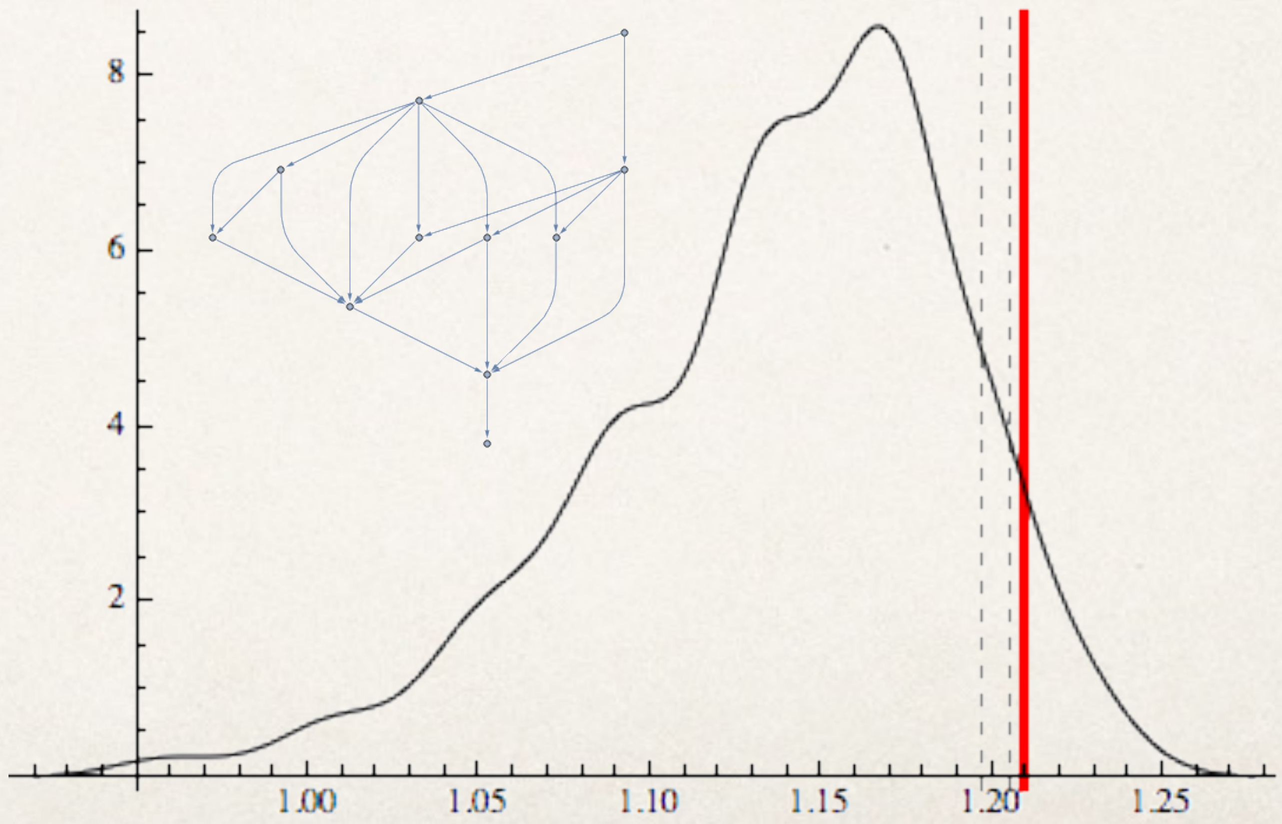
Ecosystem Structure Evolution



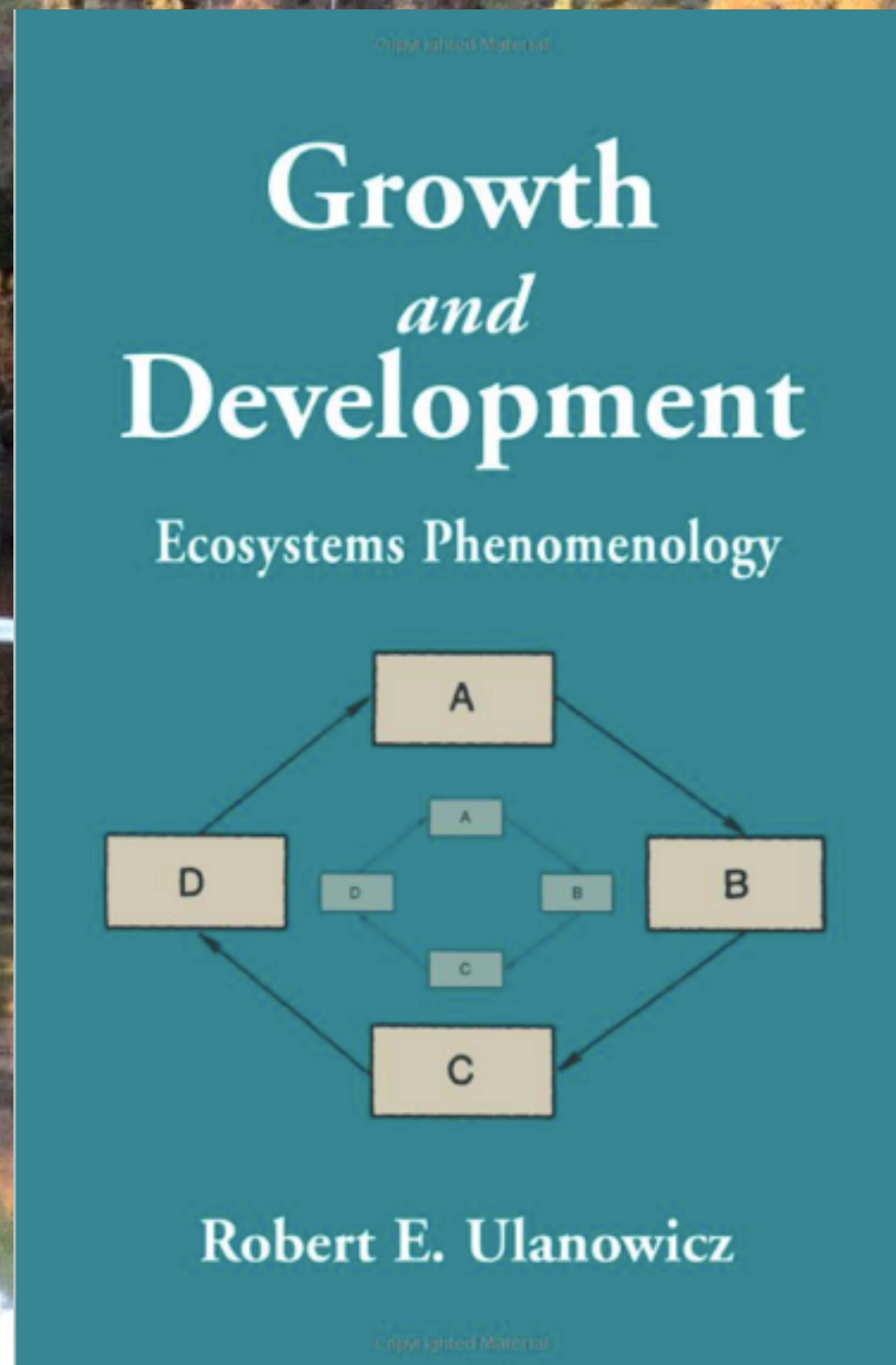
Flow Extent in Real World Ecosystems

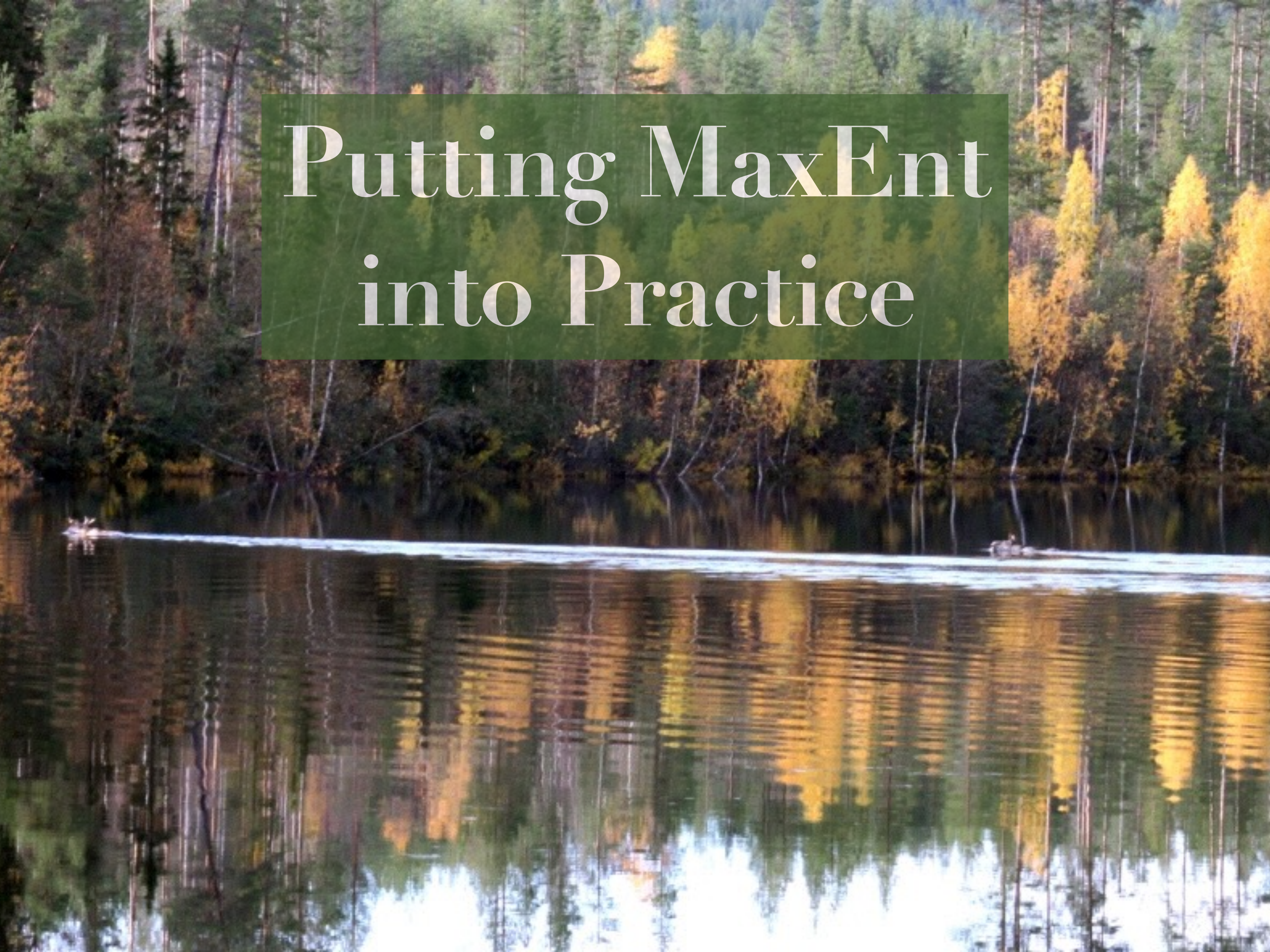


Prior knowledge:
- Number of species
- Number of primary producers
- Number of top consumers
- Number of interaction links



Ecosystem Ascendency




Putting MaxEnt
into Practice

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