FOOD WEBS FROM RNA STRUCTURES: THE EMERGENCE AND ANALYSIS OF COMPLEX ECOLOGICAL NETWORKS

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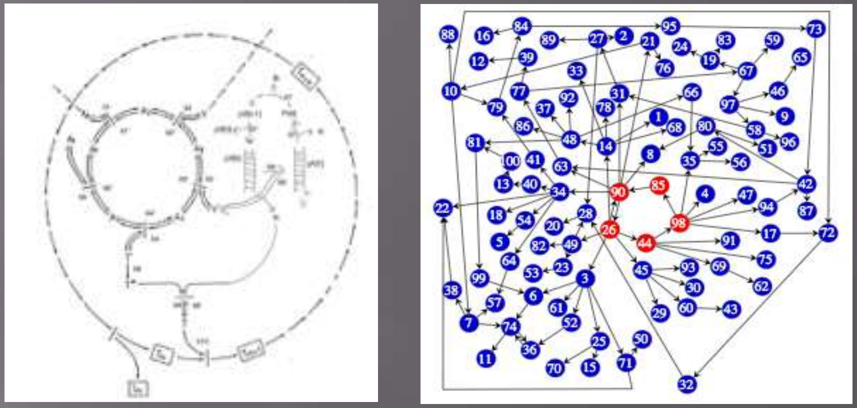
Abstract

- **Food Webs From RNA Structures: The Emergence and Analysis of Complex Ecological Networks**

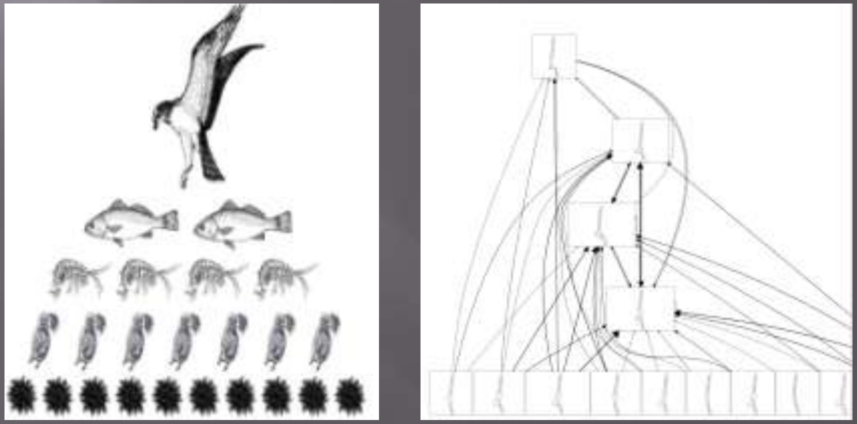
- *Abstract:* Understanding ecosystems is one of the most important challenges for theoretical biology and Artificial Life. We offer a bottom-up, fully individual-based model where phenotype-to-phenotype interactions of organisms define ecological networks and we study how simple conditions give rise to complex food webs if we allow for the evolution of phenotypes and hence phenotype interactions. A key element of the model is the notion of "rich phenotype" realized as a set of nonlinear tradeoffs in a multi-trait system. To approach this, we have chosen one of the best understood phenotypes, RNA structures, and assigned ecological functions to their features. In a series of experiments we show the emergence of complex food webs with generic properties, which indicates that minimalist assumptions such as having rich phenotype interactions might be sufficient to generate complex ecosytems and to explain some puzzling ecological features.

RNA

NOT:
Catalytic RNA



BUT:
Food webs built
from „RNA”-s



Europe

Central Europe

ELTE Campus, Budapest

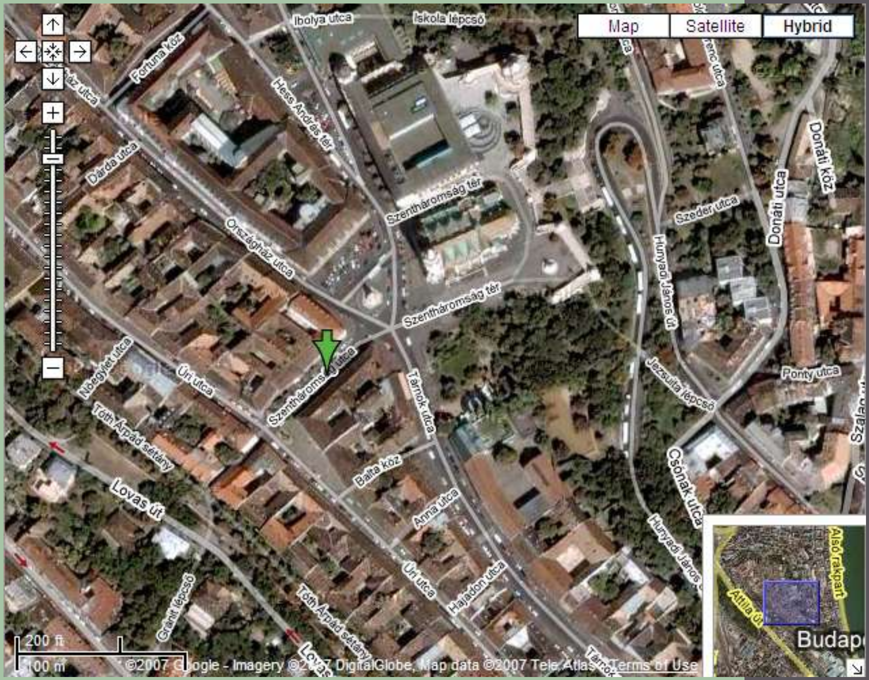
Collegium Budapest…

Welcome to

ollegium Budapest

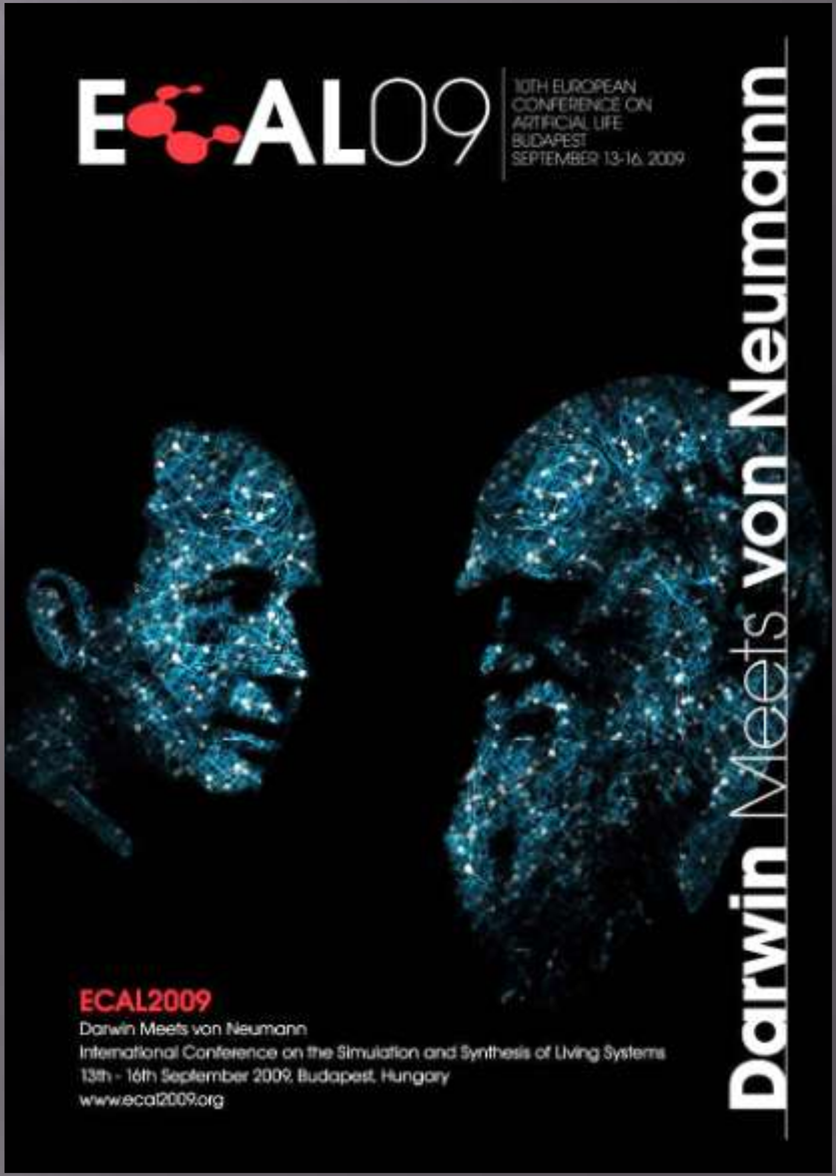
Institute for Advanced Study

Overview



Some personal background…

- Electric engineering 1981 -> theor.biol, evolutionary modeling 1983
- But lived in the Ethology dept (then Lab. of Behavior Genetics)
- Worked on methodology/relevance criteria for models
- Philosophy of science dept since 1994
  - Phil.Sci and Cogsci (e.g. BSCS programme, TSC2007)
  - But again, modeling (e.g. phenotype based evolution in ecosystems)
  - IT/methodology projects (EC, FP6/7, ESF)



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The Plan

- ALife, theor.biol, theor.ecol, network theory
- Motivation (prehistory)
- Background/history
- The closer problem: IBM of the emergence of complex ecosystems
  - The hard way
  - The easy way
- The Model
- Results
  - The dynamics
  - Qualitative analyis
  - Quantitative analysis
- Conclusions

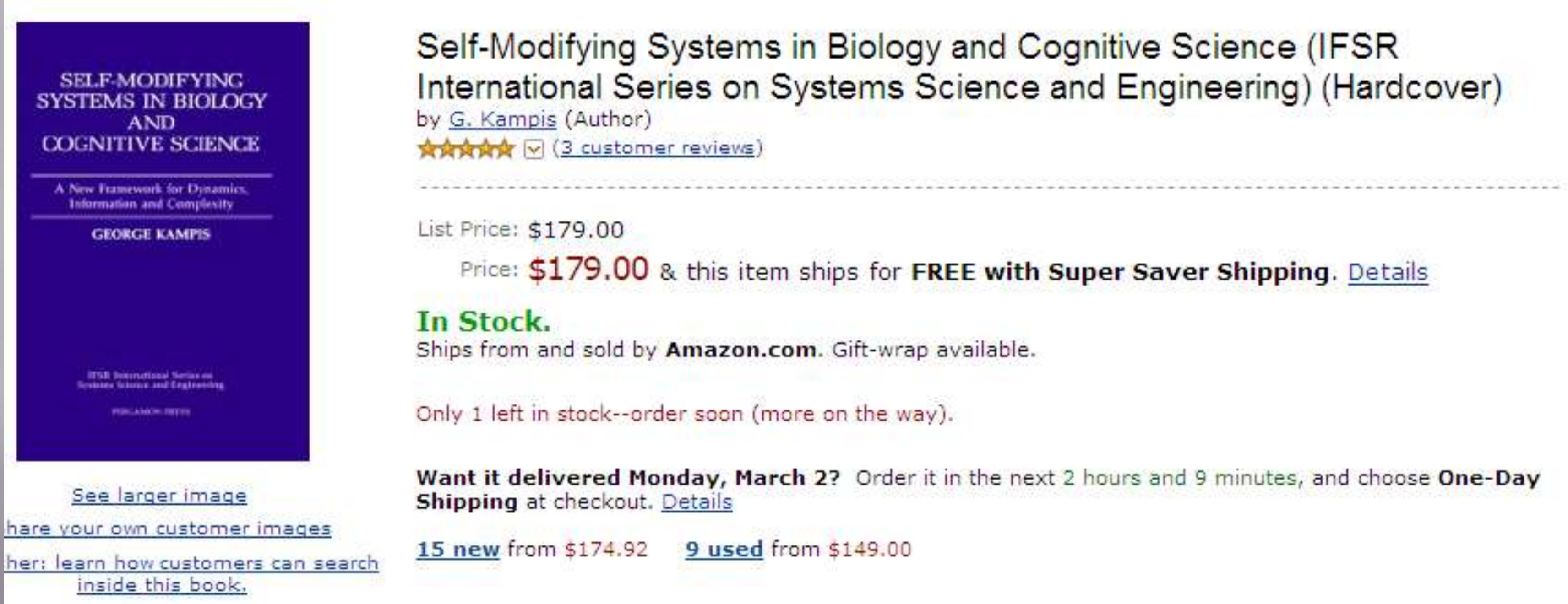
ALife, theoretical biology, theoretical ecology, network theory

- The constructivist stance: what we cannot build, we do not understand
- Recapitulates old questions in new forms
- Methods are continuous
- Aims slightly different, model-for vs model-of
- Agent based modeling and generative modeling increasingly important for network science also (dynamics on and of networks)
- Sufficient vs necessary conditions

Motivation (prehistory)

- Personal
- General

Personal: SMS



Self-Modifying Systems in Biology and Cognitive Science (IFSR International Series on Systems Science and Engineering) (Hardcover)
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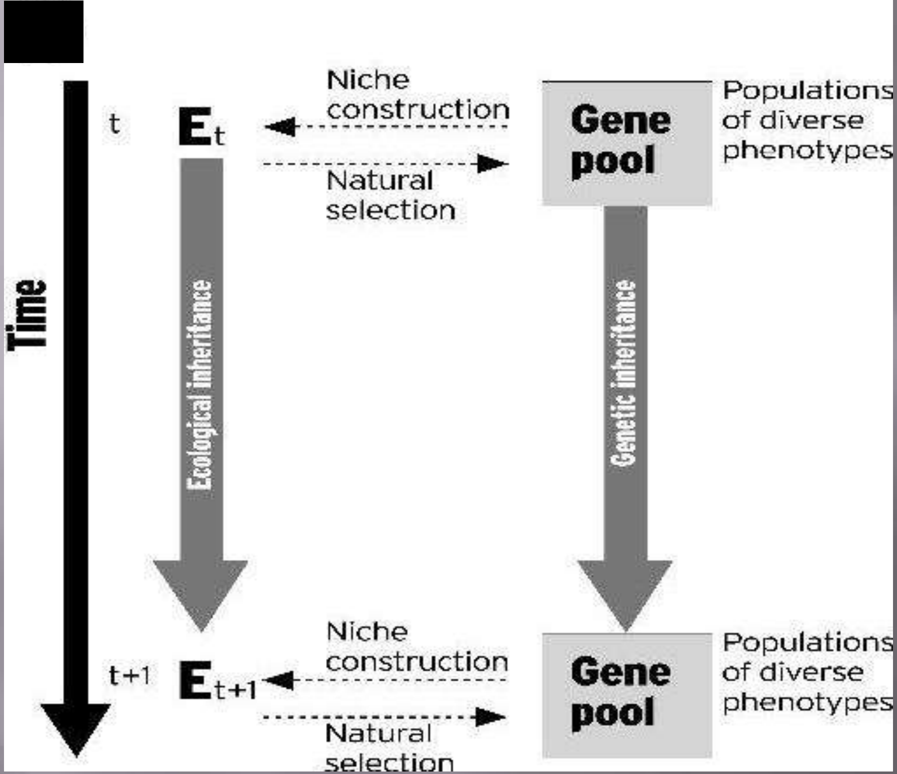
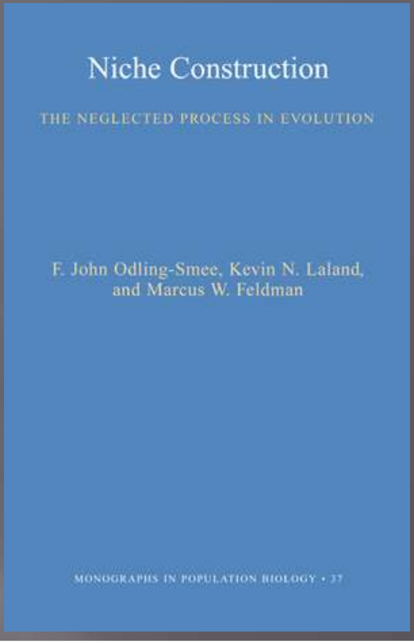
- „Matter matters" – how the overt complexity of systems can arise from the implicit complexity of objects
- Properties that change over time, in particular due to interaction (cf. social systems)
- Emergence via relational properties
- Especially in domains such as evolution

General: Niche construction



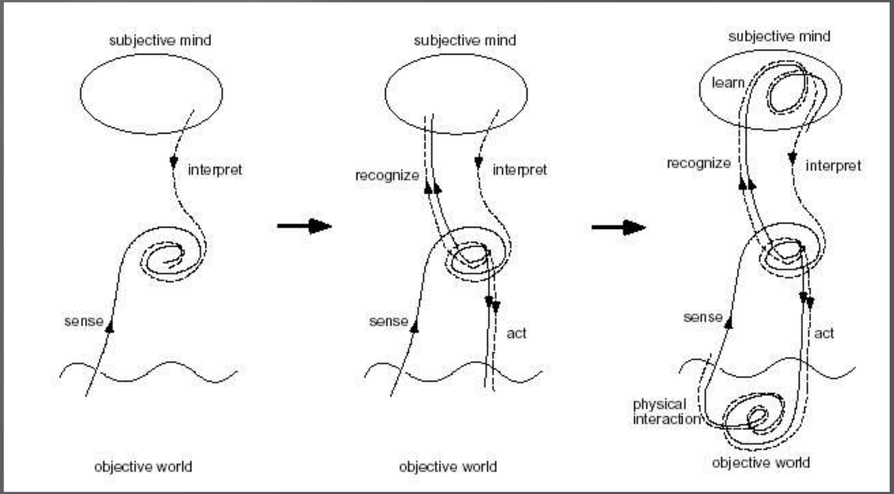
Lewontin R.C. (1983) The organism as the subject and object of evolution. Scientia 118:65–82.


Niche Construction

THE NEGLECTED PROCESS IN EVOLUTION

F. John Odling-Smee, Kevin N. Laland, and Marcus W. Feldman

MONOGRAPHS IN POPULATION BIOLOGY • 37



A link: rich phenotypes

- Fat phenotypes… implicit phenotypes etc.

The biological notion that reflects the complexity of the interacting body is that of the phenotype.

The concept (**see box**) is ambiguous, in that it speaks both about the ‘totality’ of physical constitution and the narrov definition of certain traits – often, phenotypes are understood via the latter.

We are interested in the interplay and how it can do work in evolution.

Definition: Phenotype

The phenotype of an individual organism is either its total physical appearance and constitution or a specific manifestation of a trait, such as size or eye color, that varies between individuals.

From:
http://en.wikipedia.org/wiki/Phenotype

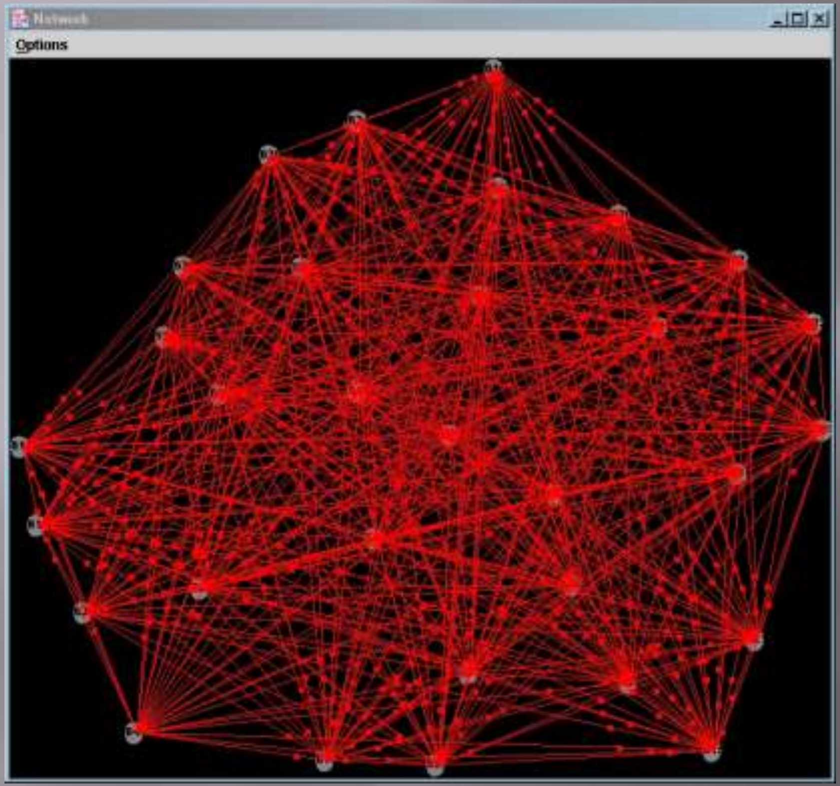
Background/history

- The EvoTech project and the FATINT system (2004-)
- Agent:
  - Phenotype vector in a multidimensional space.
  - Changing dimensionality

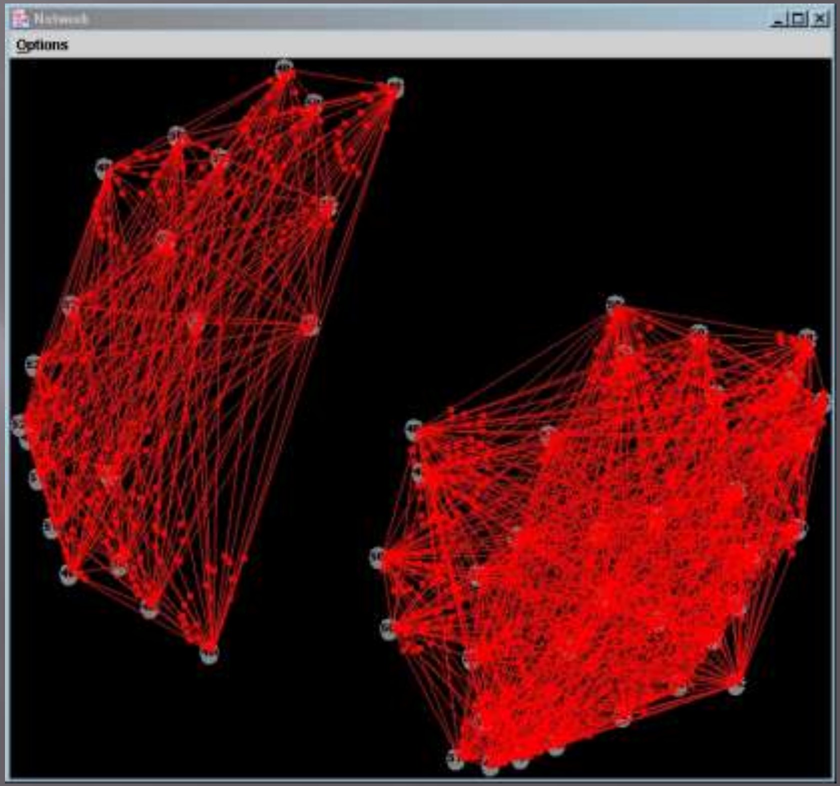
10 9 15 24 3 23 4 55 64 23 12 54 67 89 25 39 19 51 43 4	32

  - Type-independent, and
  - Type-based methods.
- NC or SMS element: selection force (sexual selection) from properties, change together
- Dynamic feedback to and from environment
- Via (similarity based) sexual reproduction and selection

Producing *Species*

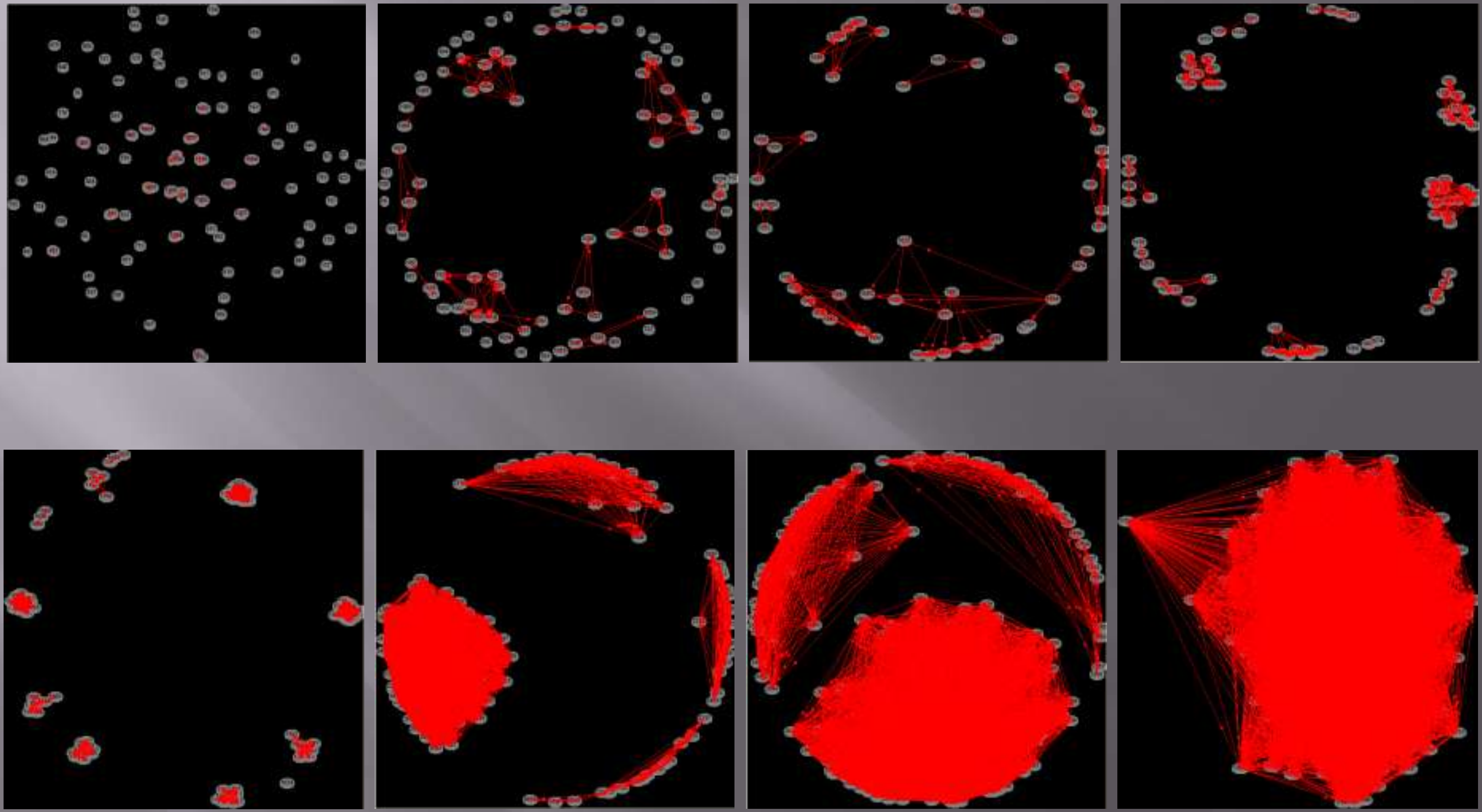


- A species is a set of interbreeding individuals.

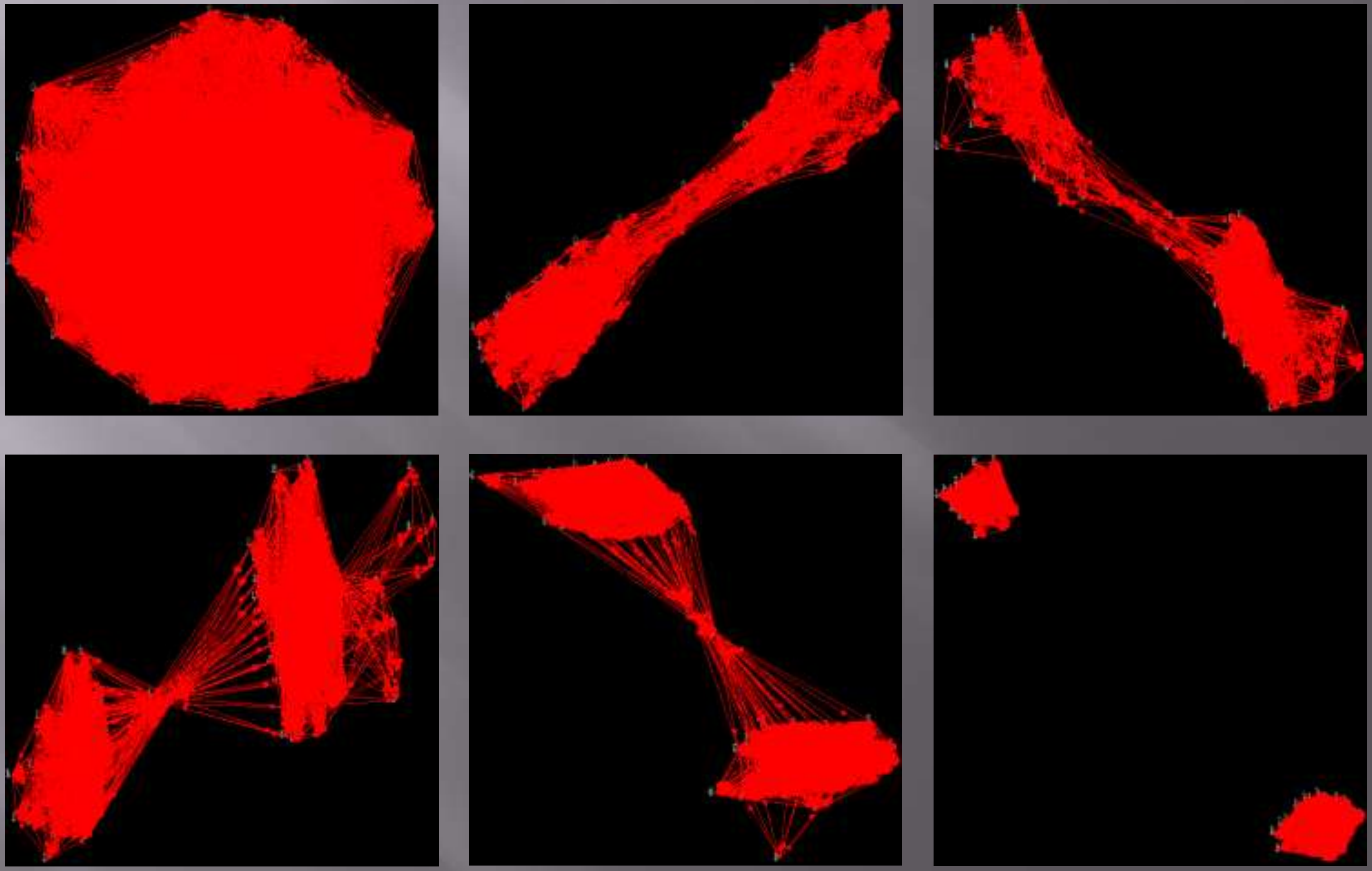


- Reproductively isolated from others
- Responding to different selection forces

Self-organization, static phenotypes



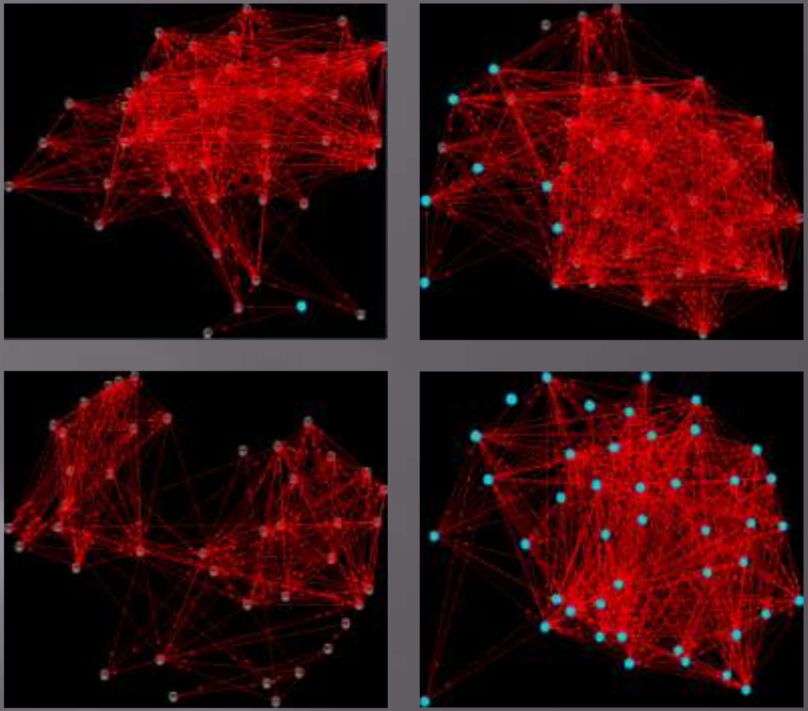
Self-organization, dynamic phenotype (recursive)



Limitations

- Only one function, sexual reproduction/selection
- Limited number of species (implicit competition)
- Also use of sexual selection was criticized
- Highly artificial handling of properties:
  - Lamarckian inheritance in the individual
  - Or epigenetic change in the whole species

What we want:



Form	**Cause**	**Type**
Point mutation	endog.	local
Phenocopies	exog.	partly global
Epigenetic change	both	partly global
Horizontal adapt.	both	global
Behavior change	social	global

Changing phenotypes

in natural and in model populations

The closer problem

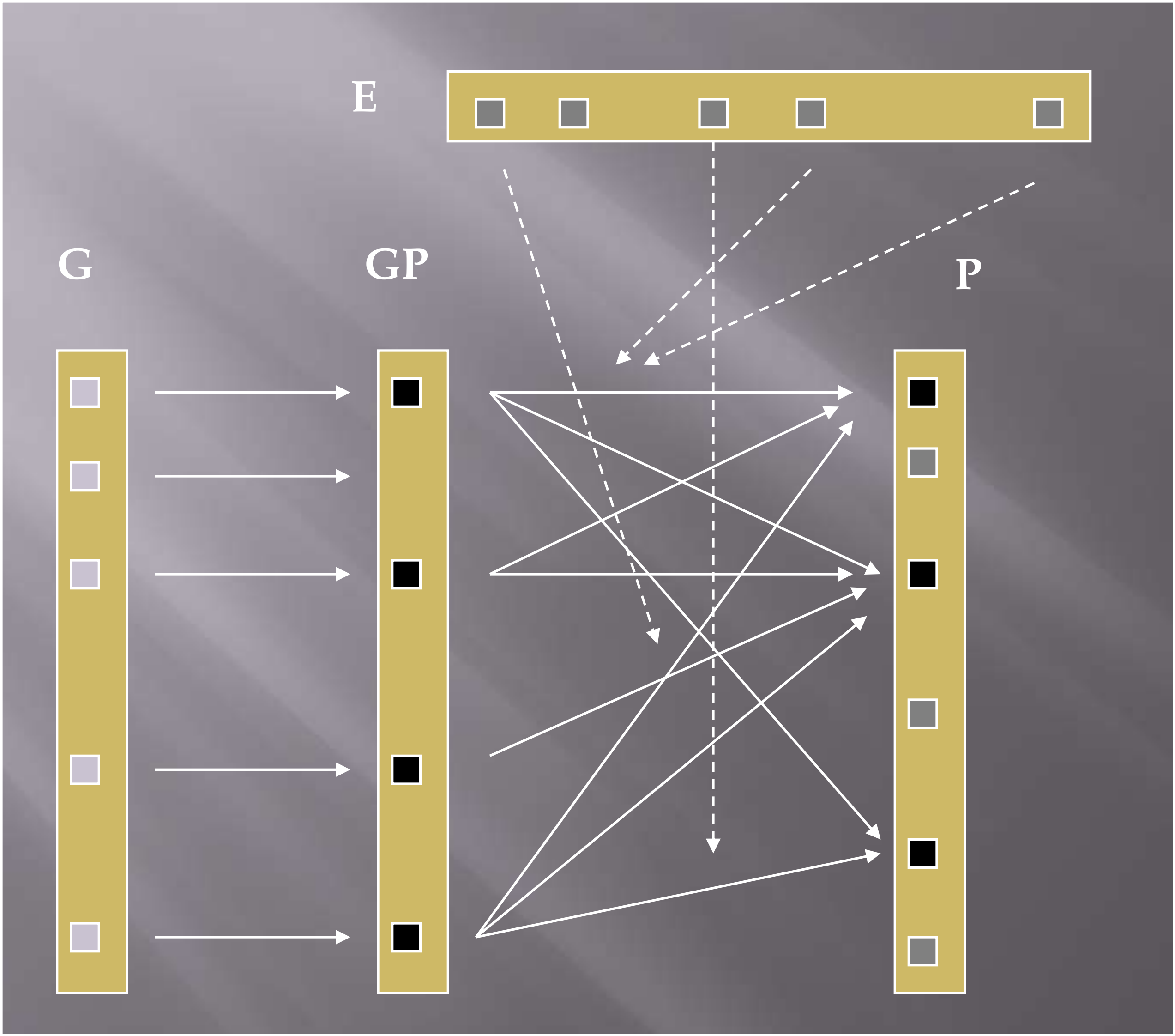
- Breed ecosystems, with:
  - Functional differentiation into emergent niches
  - Development of a complex food web structure
  - From a fully individual based perspective
- Can we do that?
- (What are the required properties of such systems? etc.)
- Constructivist stance…
- Cf. McKane and Drossel 2006

A. J. McKane and B. Drossel, *Models of food web evolution*, in *Ecological Networks*, M. Pascual and J. A. Dunne (eds) (Oxford University Press, Oxford, 2006), pp 223-243.

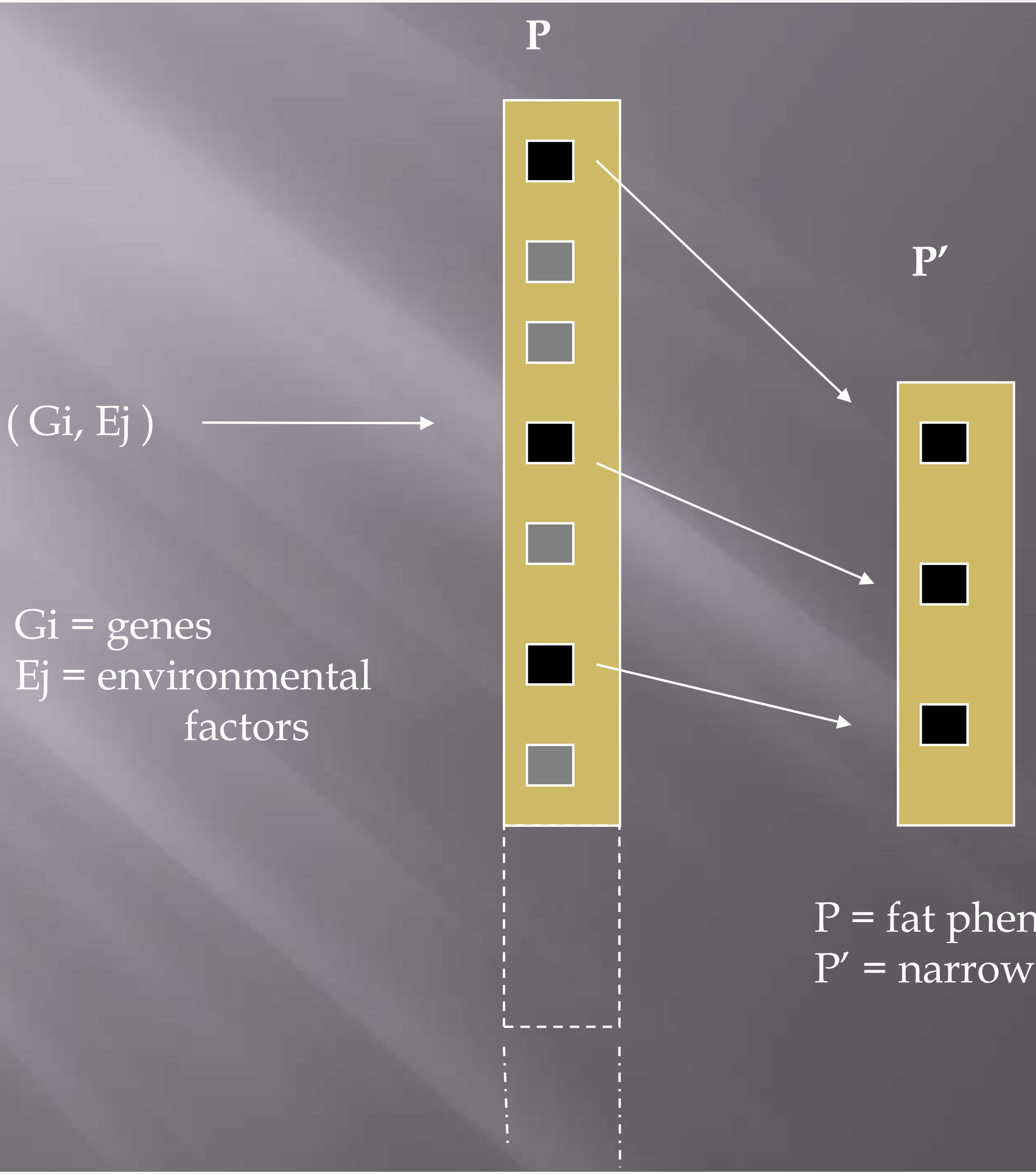
- Cf. DOVE

The introduction of new species/ individuals can be by immigration from another geographical region or by speciation of existing species in the community. Extinction would naturally occur when the number of individuals fell to zero. A model incorporating all of these aspects of web dynamics has not yet been constructed. It would presumably be an individual based model (IBM)

The Key: Genotype-phenotype map



G = genes
GP = gene products
E = environment
P = Phenotype



Gi = genes
Ej = environmental factors

P = fat phenotype
P′ = narrow phenotype

The hard way: development

- To realize various genotype-phenotype maps

- **Candidate approaches:**
  - GRN with environmental handles
  - Phenotype plasticity models
  - Epigenetic models

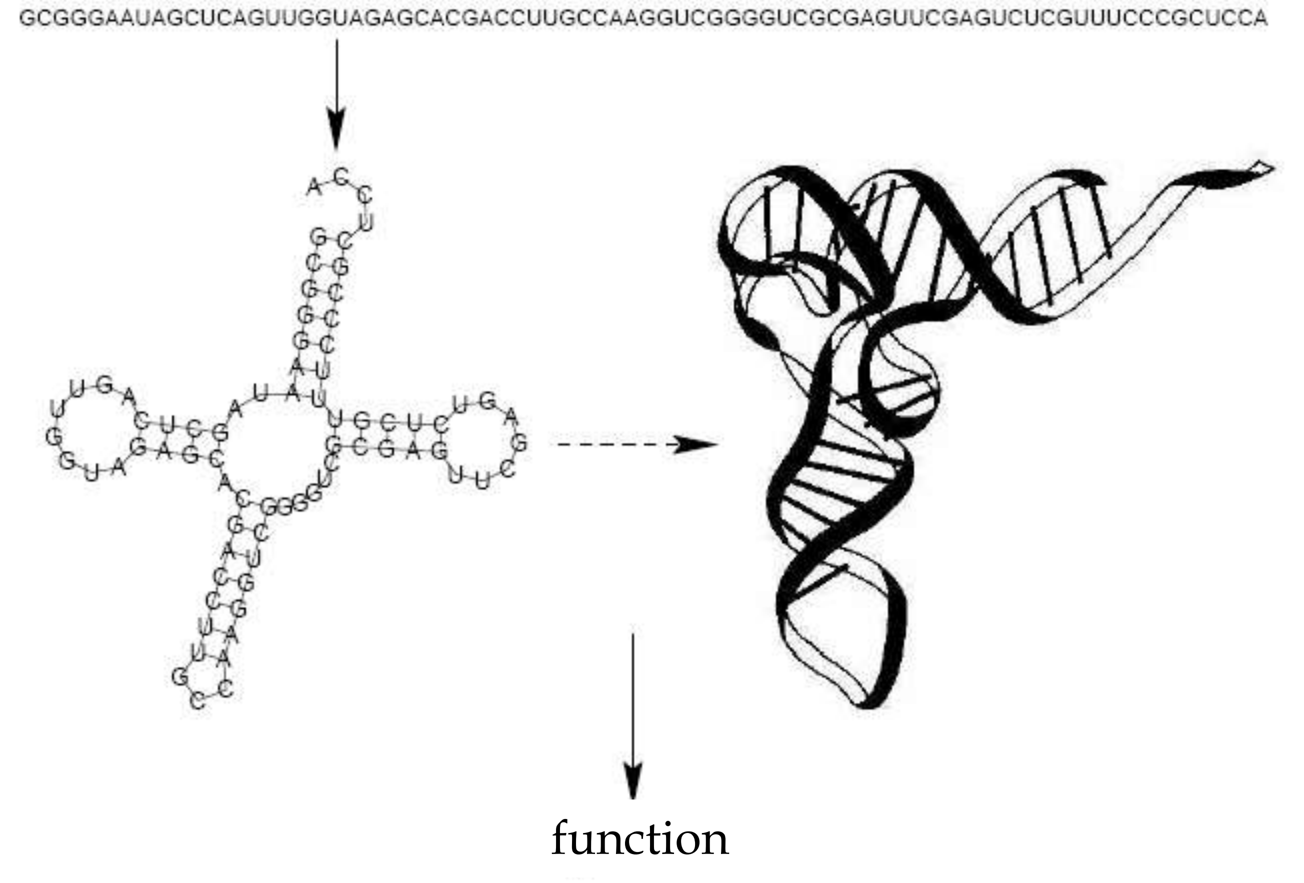
- Altenberg, Avida, etc..

The easy way: GPMs w/o tears

- Realistic, well tested/understood
- Yet without development (as in actual organisms)
- Having „good properties” …

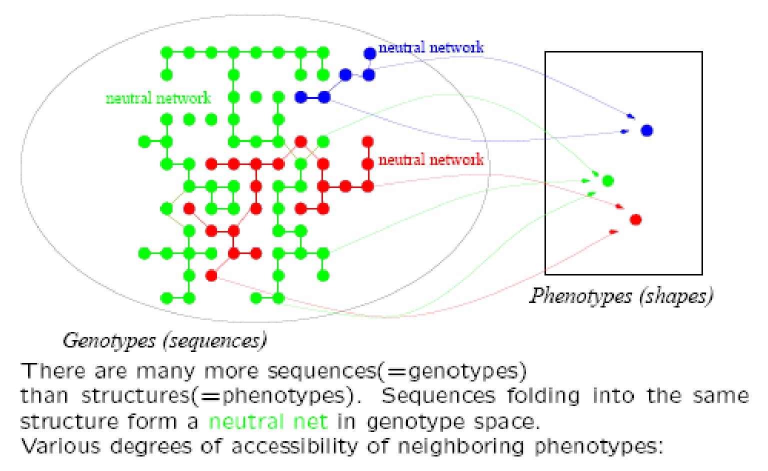
- … **the RNA!**
- G= sequence
- P= secondary structure, completely understood

RNA genotype-phenotype maps

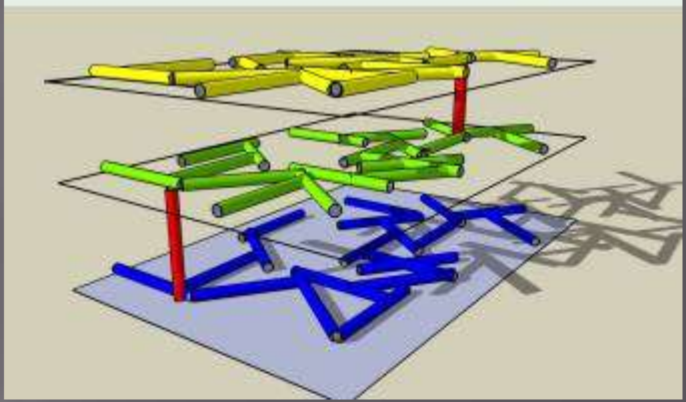


RNA evolutionary properties

- Catalytic RNA:
  - Neutral networks

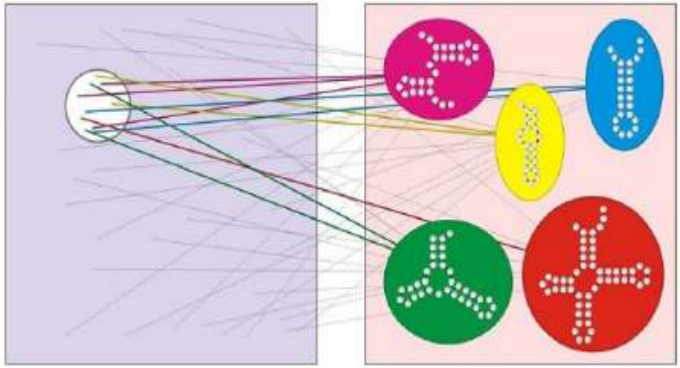


There are many more sequences(=genotypes) than structures(=phenotypes). Sequences folding into the same structure form a neutral net in genotype space.
Various degrees of accessibility of neighboring phenotypes:



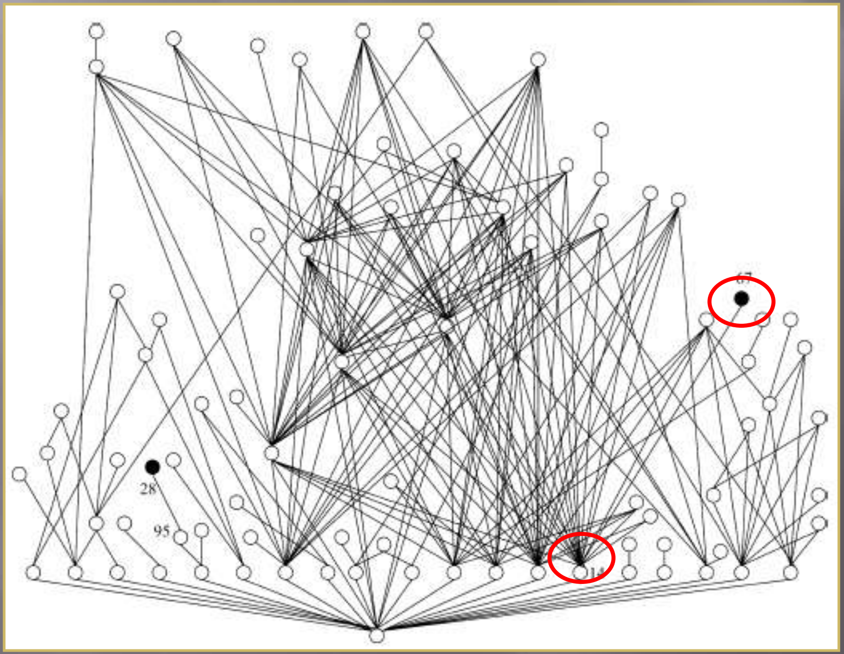
http://www.scholarpedia.org/article/Image:NN_FL.jpg

  - Mixing

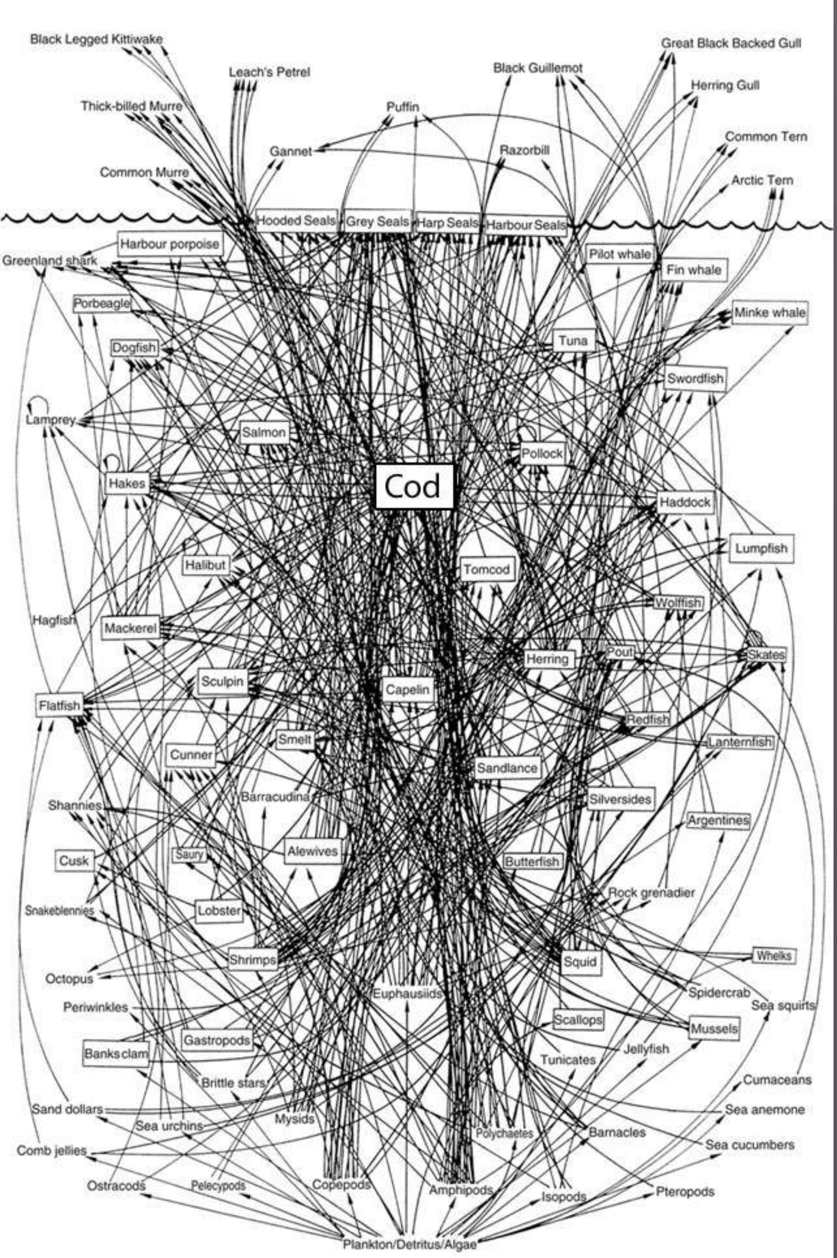


Food webs

- Representation of ecological communities
- Who eats whom relations
- Relates structure to stability
- Important for ecological conservation
- E.g topological keystone species



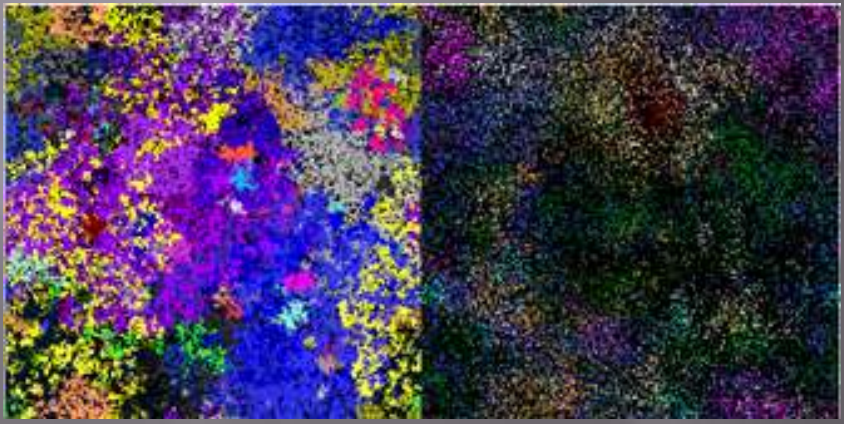
A most often shown (and highly complex) food web: the North Atlantic Food Web



A simplified food web for the Northwest Atlantic. © IMMA

The Model

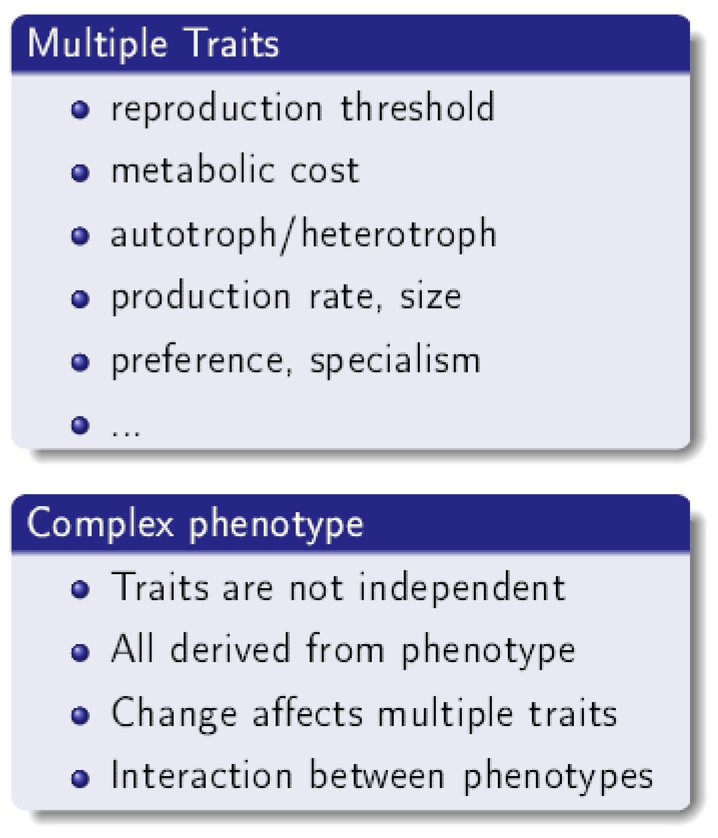
- Individual based (asexual) model, p2p interactions
- Individuals are fixed length (l=60) RNA-s
- In a 2-layer stochastic cellular automaton
- Evolve individual traits by mutations
- Study the emergence of food webs



Producers: sessile (constant energy flow)
Consumers: mobile (ident. speed)

Reproduction: occupy neighbor if empty

The individuals

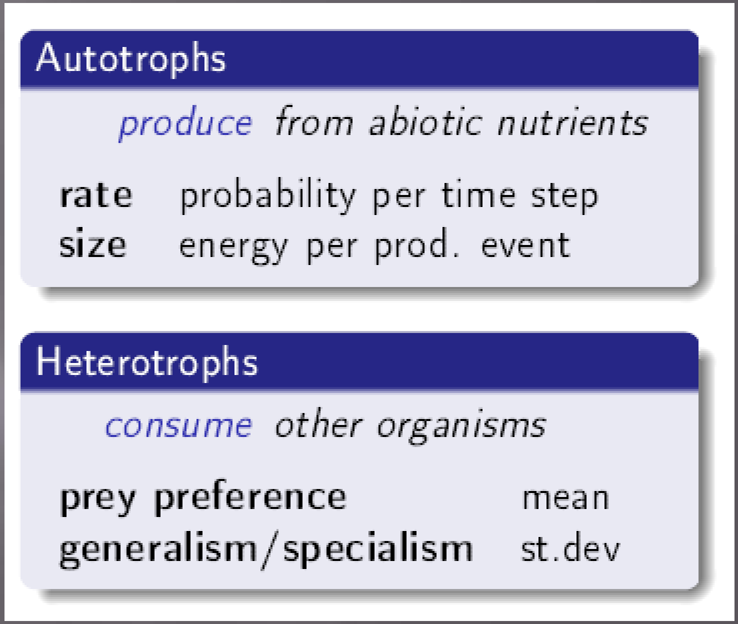


Multiple Traits

- reproduction threshold
- metabolic cost
- autotroph/heterotroph
- production rate, size
- preference, specialism
- ...

Complex phenotype

- Traits are not independent
- All derived from phenotype
- Change affects multiple traits
- Interaction between phenotypes



Autotrophs

produce from abiotic nutrients

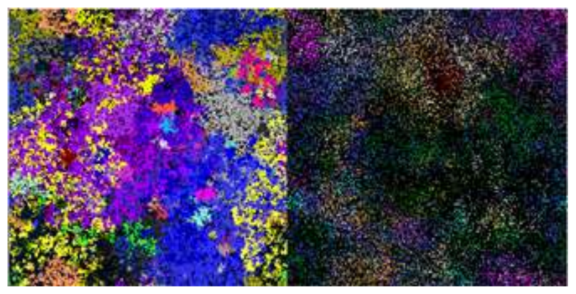
rate	probability per time step
size	energy per prod. event

Heterotrophs

consume other organisms

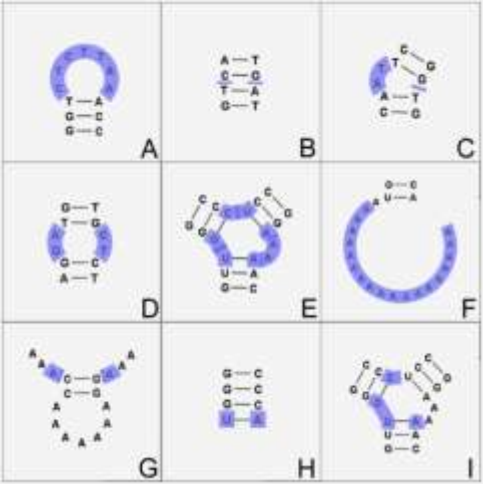
prey preference	mean
generalism/specialism	st.dev

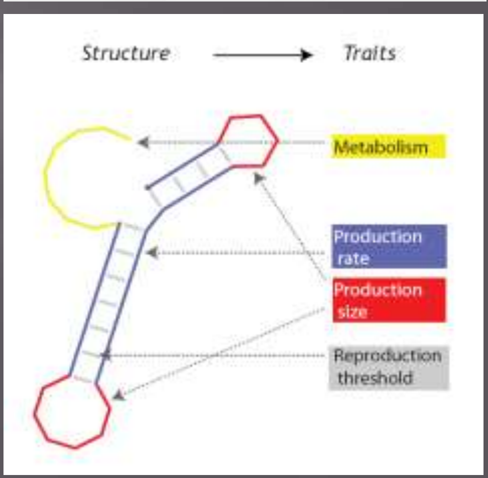
„energy" conservation!



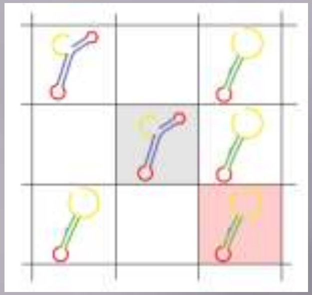
Phenotype to function

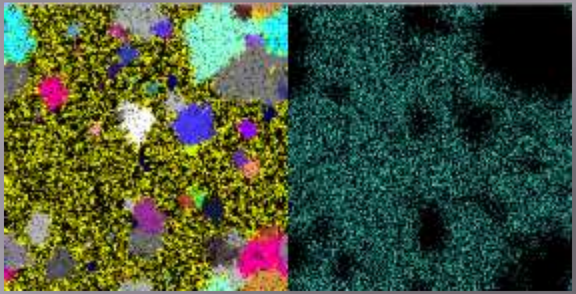
- Multiloop = consumer
- SET ECOLOGICAL PROPERTIES TO STRUCTURAL FEATURES
- 0 ‘A' (hairpin loop)
- 1 ‘D’ (interior loop)
- 2 ‘C' (bulge)
- 3 ‘E' (multi-loop)
- 4 ‘B' (stack)
- 5 ‘F' (external elements)
- Replication threshold -> # of base pairs („cost”)
- Producer:
  - Rate -> 1
  - Size ->2
  - Metabolism -> 5
- Consumer:
  - Generalism -> 3
  - Preference -> 3+1+0
  - Metabolism -> 5

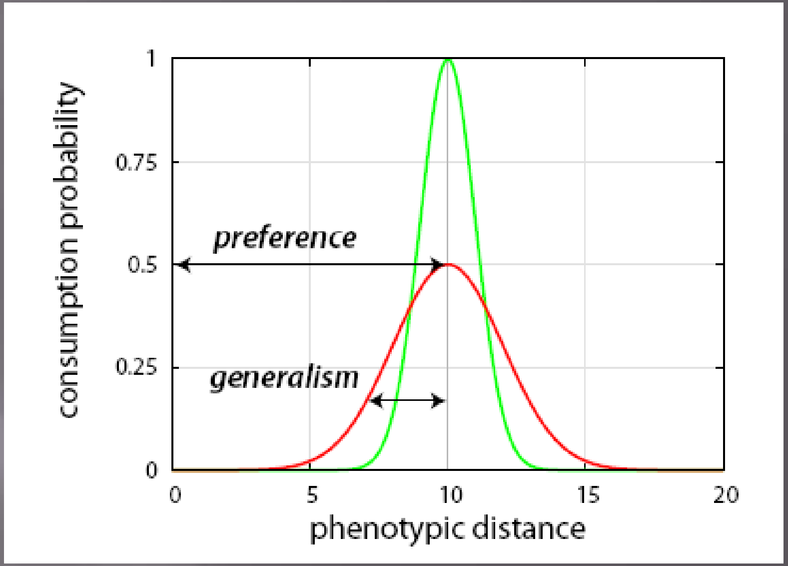




Interaction (consumption)





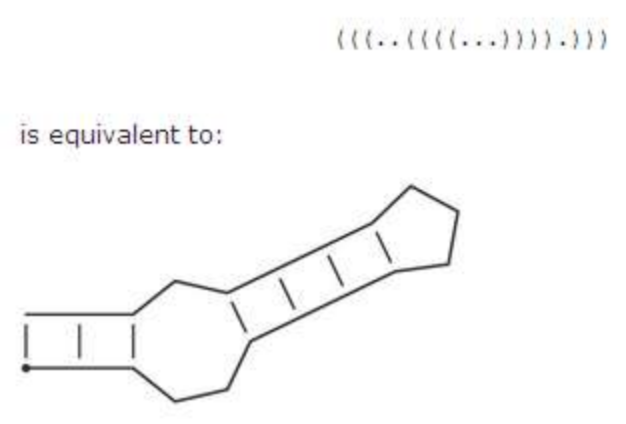


- Space stabilizes:
  - Population structure
  - Consumption saturation
  - Consumer interference
- On encounter:
  - Structural (tree) distance between both phenotypes
  - Consume with probability P(d)

Encapsulation (RNA is the vehicle)

- Static phenotype (in the lifetime of the organism)
- But properties are „encapsulated”: act together, heavily interdependent
- Nonlinear tradeoffs
- Adaptation in one property necessarily changes other properties in complex, non-transparent ways
- Making use of the material unity of phenotype (i.e. not just the traits themselves)

Two versions of the model

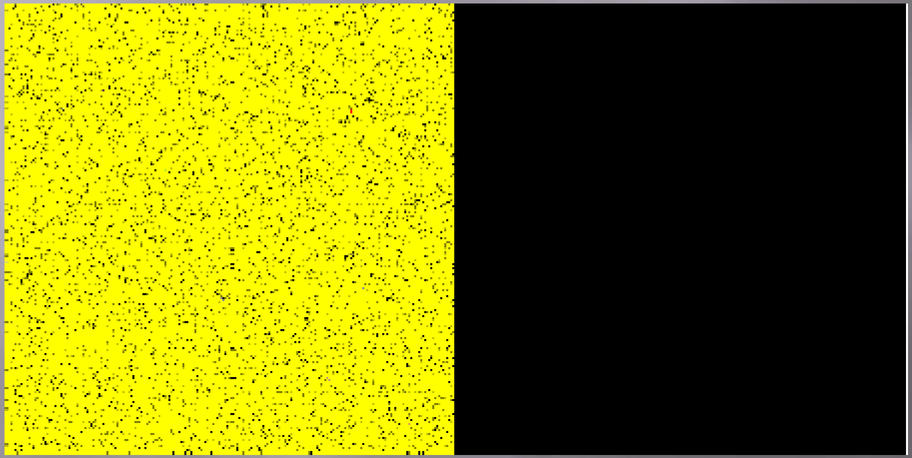


- Full GPM
  - G -> P -> F (sequence, folding, function)
  - Mutation acts on sequence
  - Event is allele subsitutions
  - New folding
- Phenotype mutations
  - P -> F (folded form, function)
  - Mutation acts on folded form
  - Event is dot <->bracket substitution
  - Bracket balancing

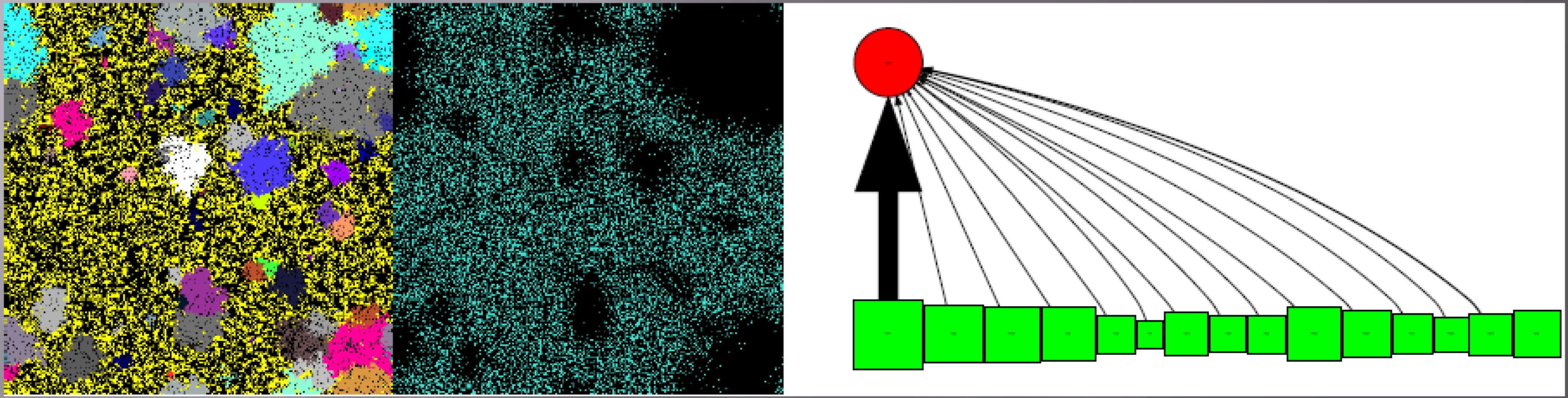
- W. de Back, S. Branciamore, G. Kampis :**Phenotype-based Evolution of Complex Foodwebs,** In: *Proceedings of the 11th Conference on Artificial Life, Winchester, UK, 2008.*
- W. de Back, G. Kampis: **Emergence and Analysis of Complex Food Webs in an Individual-based Artificial Ecology**, 2nd IEEE Conference on Artificial Life, Nashville, TN 2009.

Results

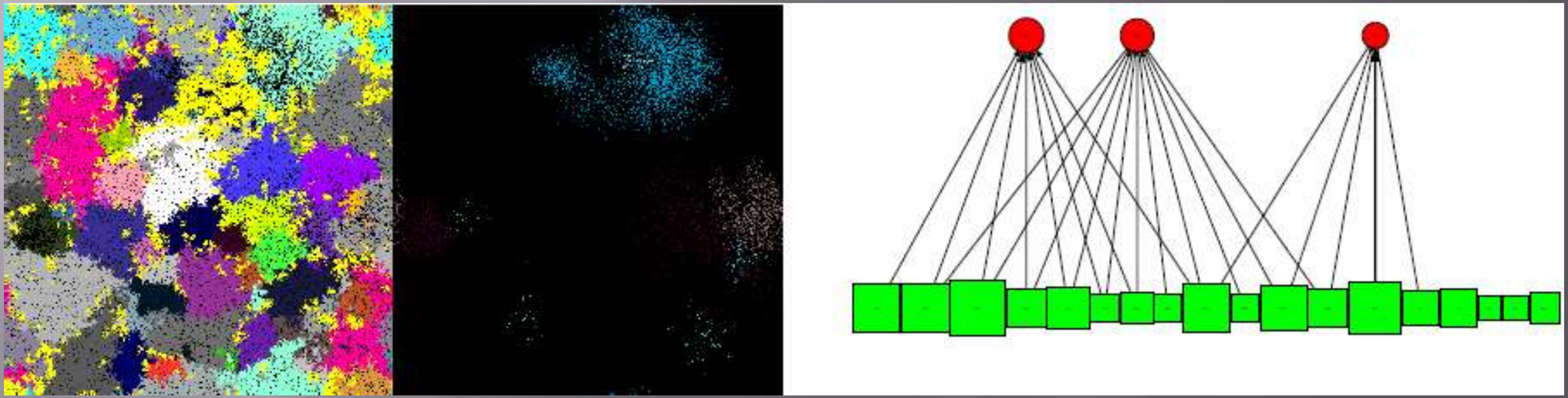
The dynamics



The dynamics



The dynamics



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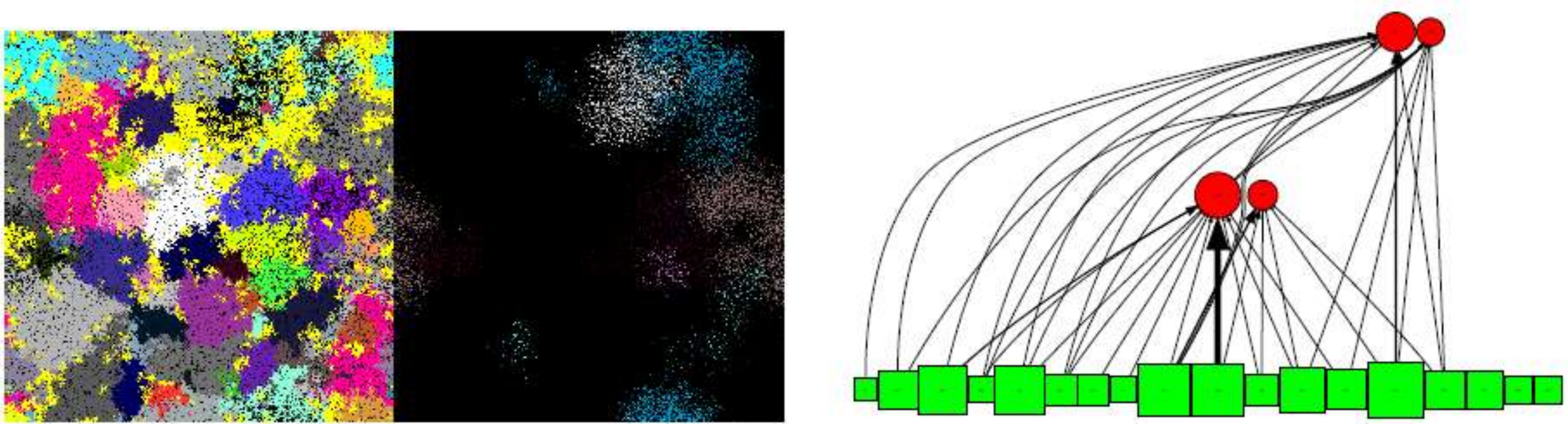

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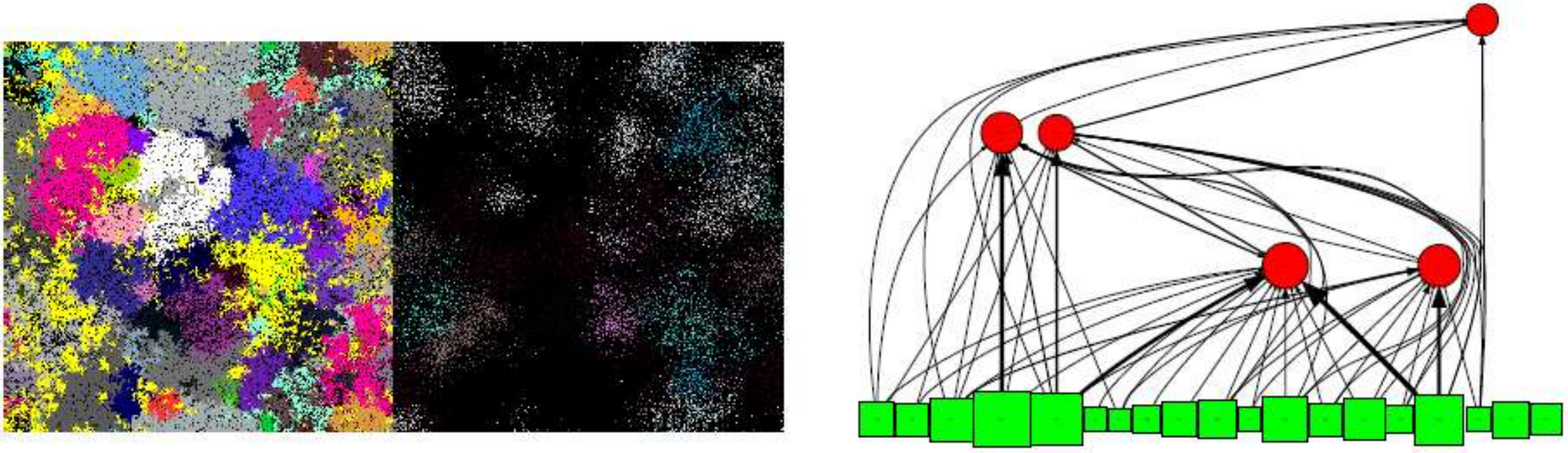
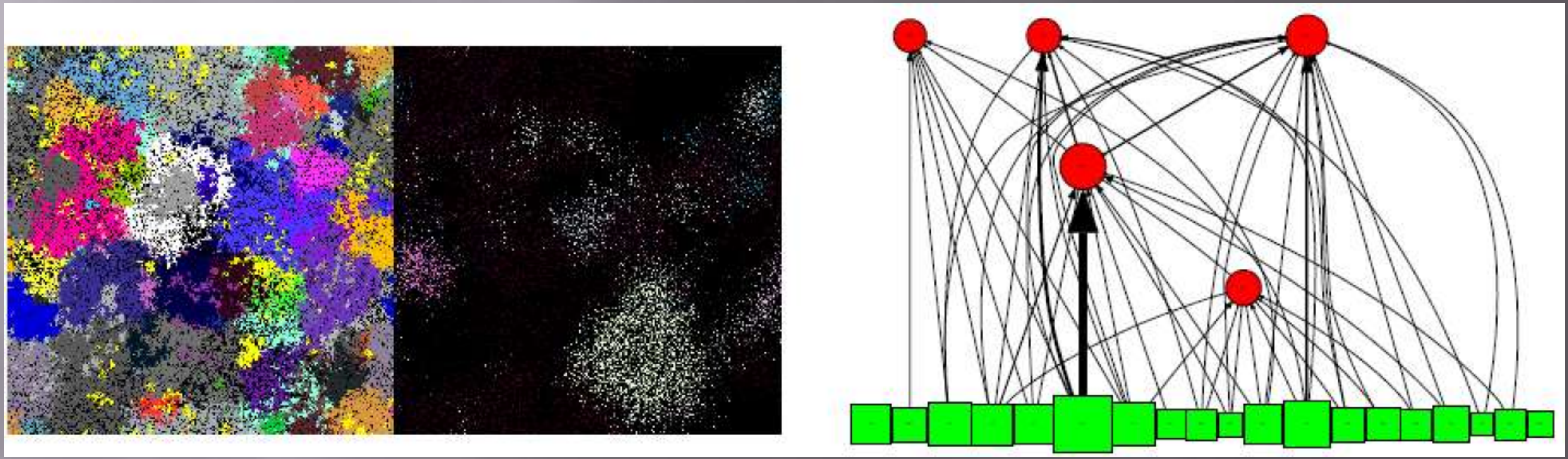
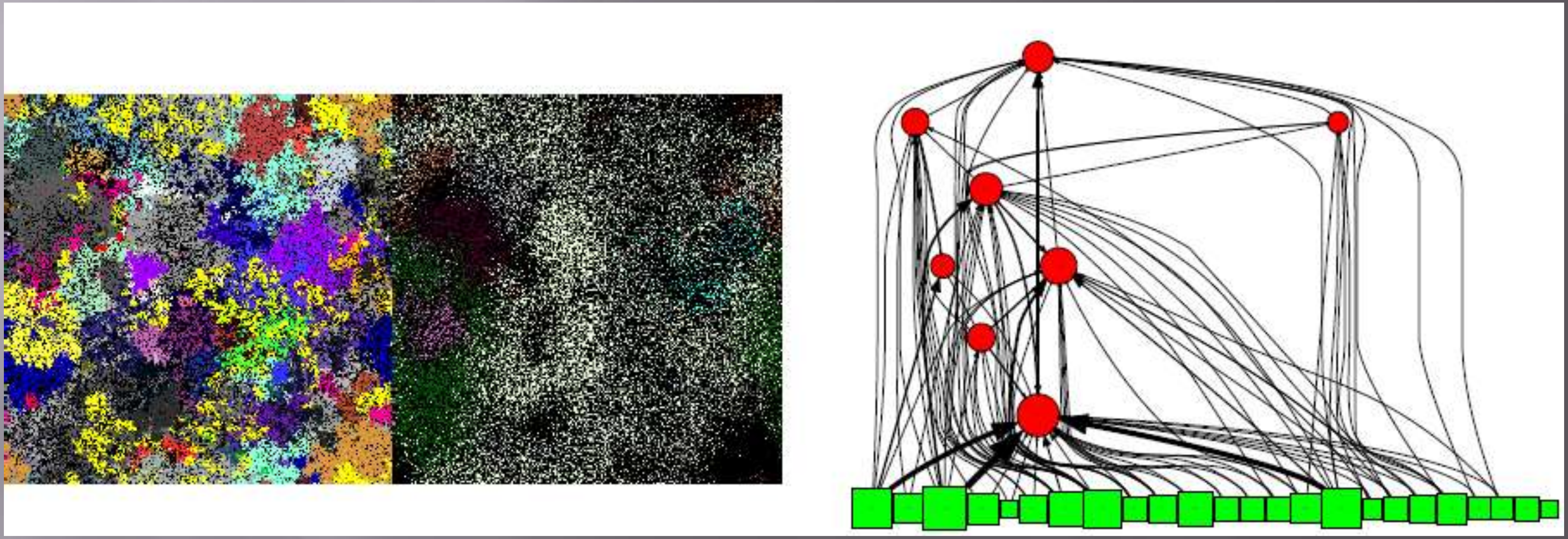


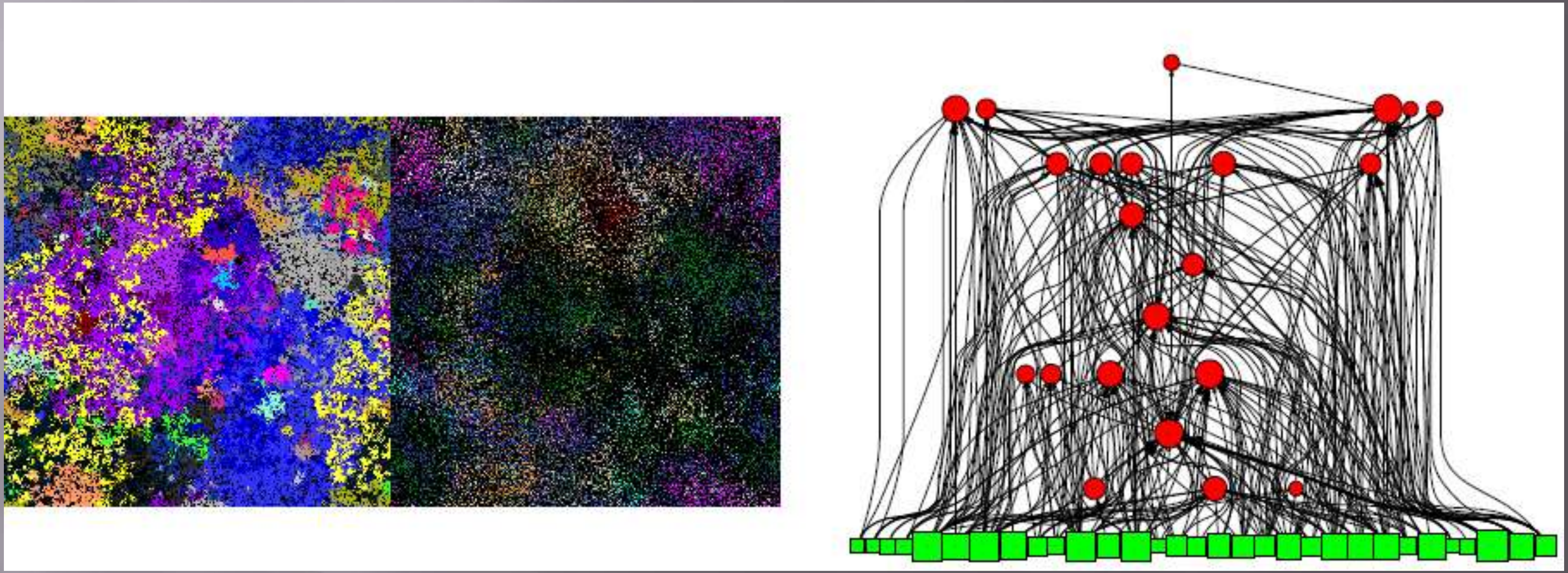
The dynamics



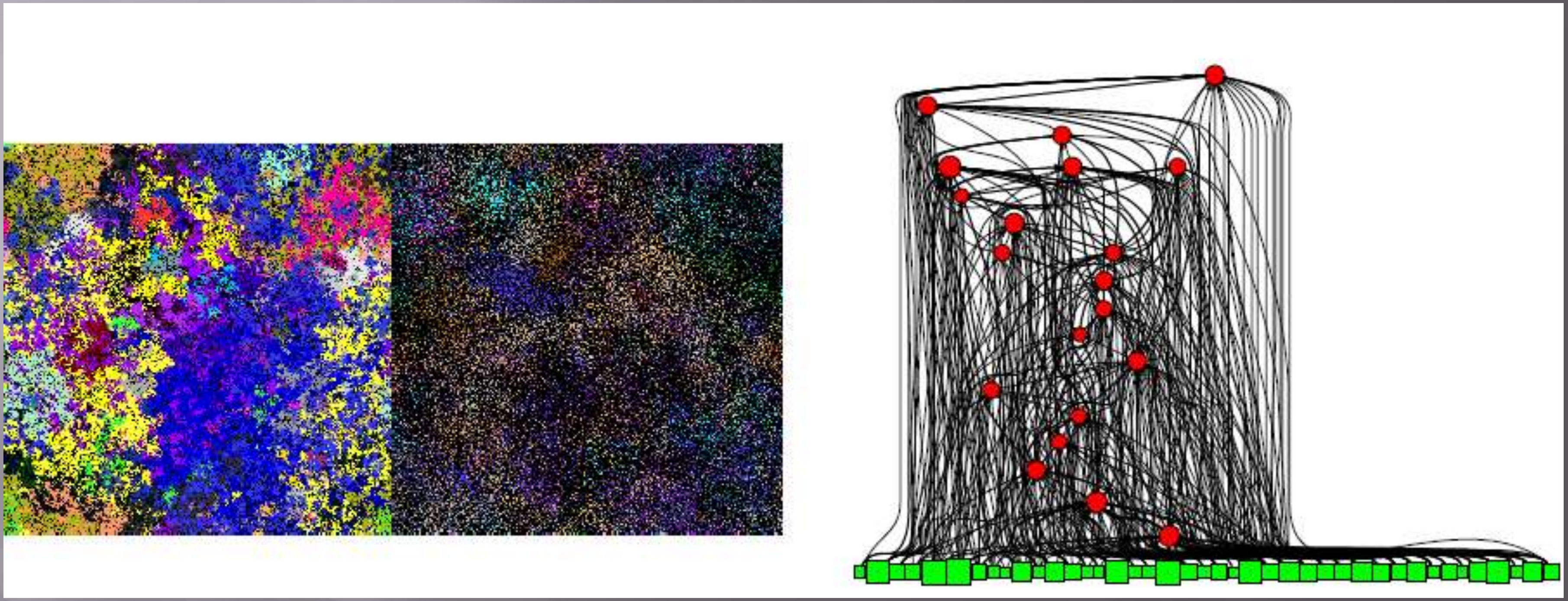
The dynamics



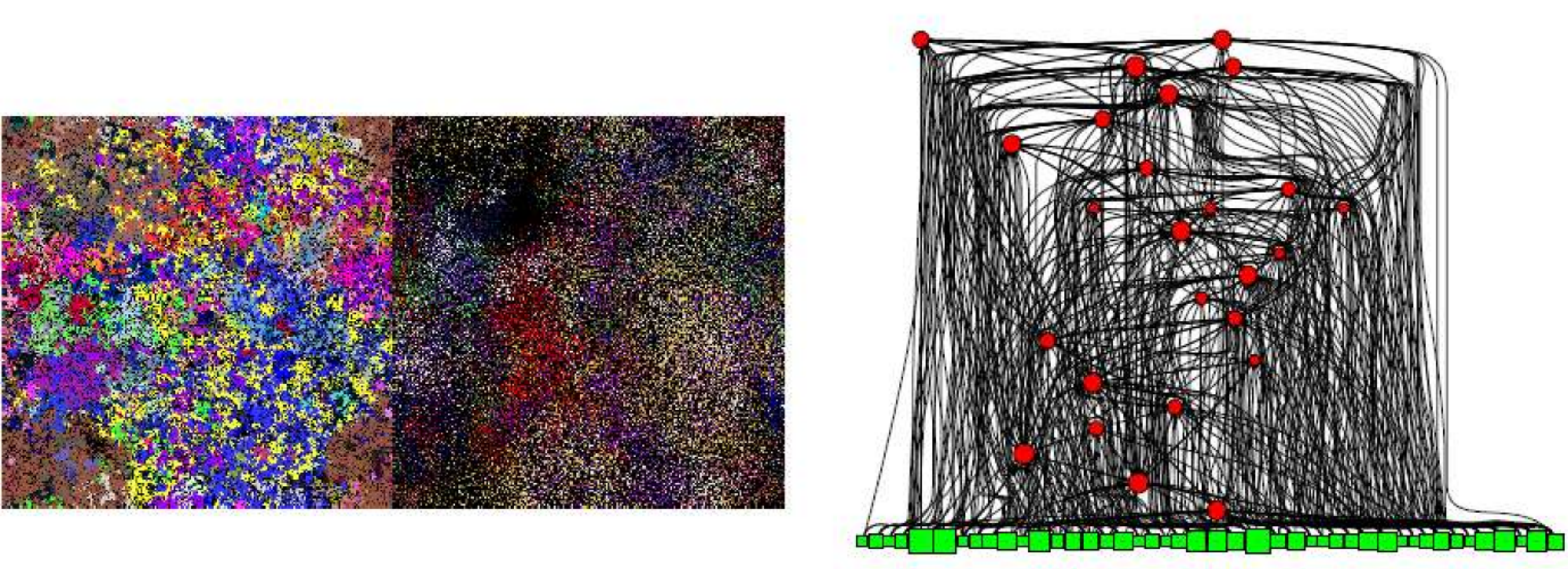
The dynamics



The dynamics

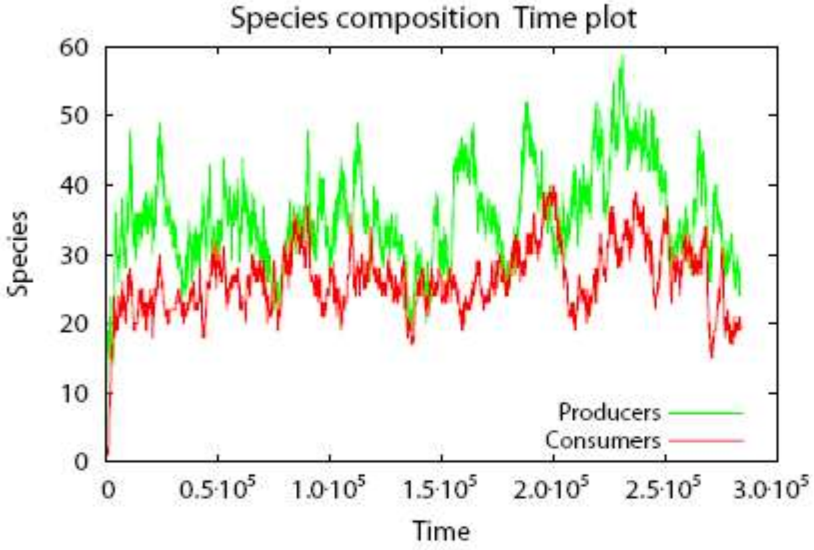


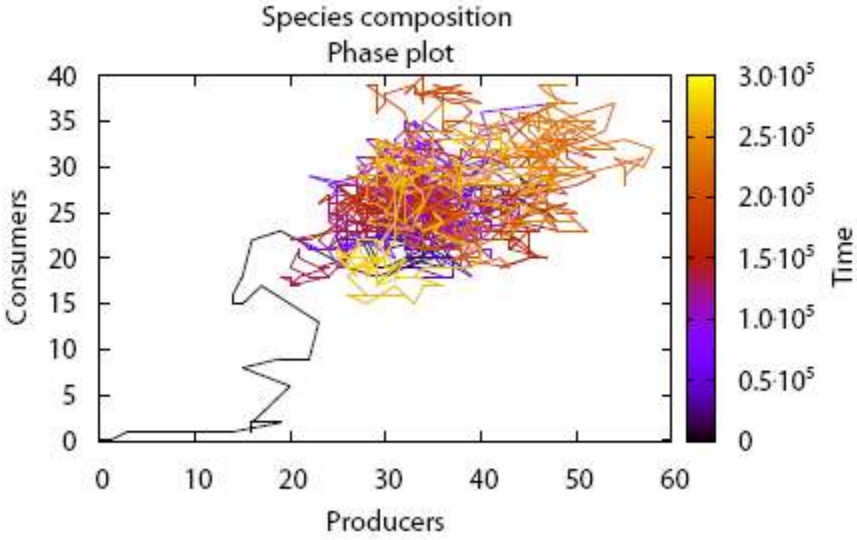
The dynamics



- …and so on.

Species composition



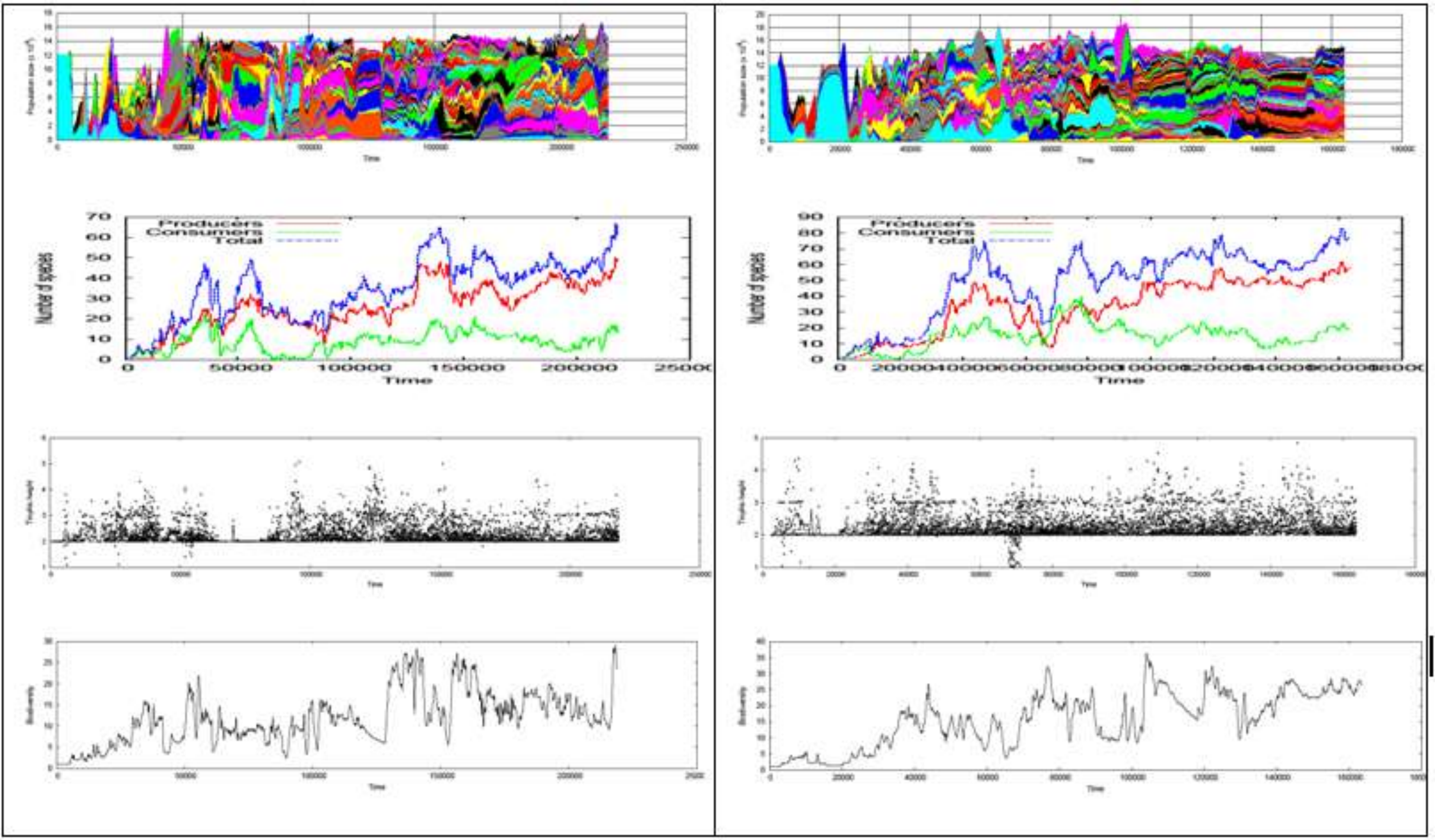


Qualitative analysis

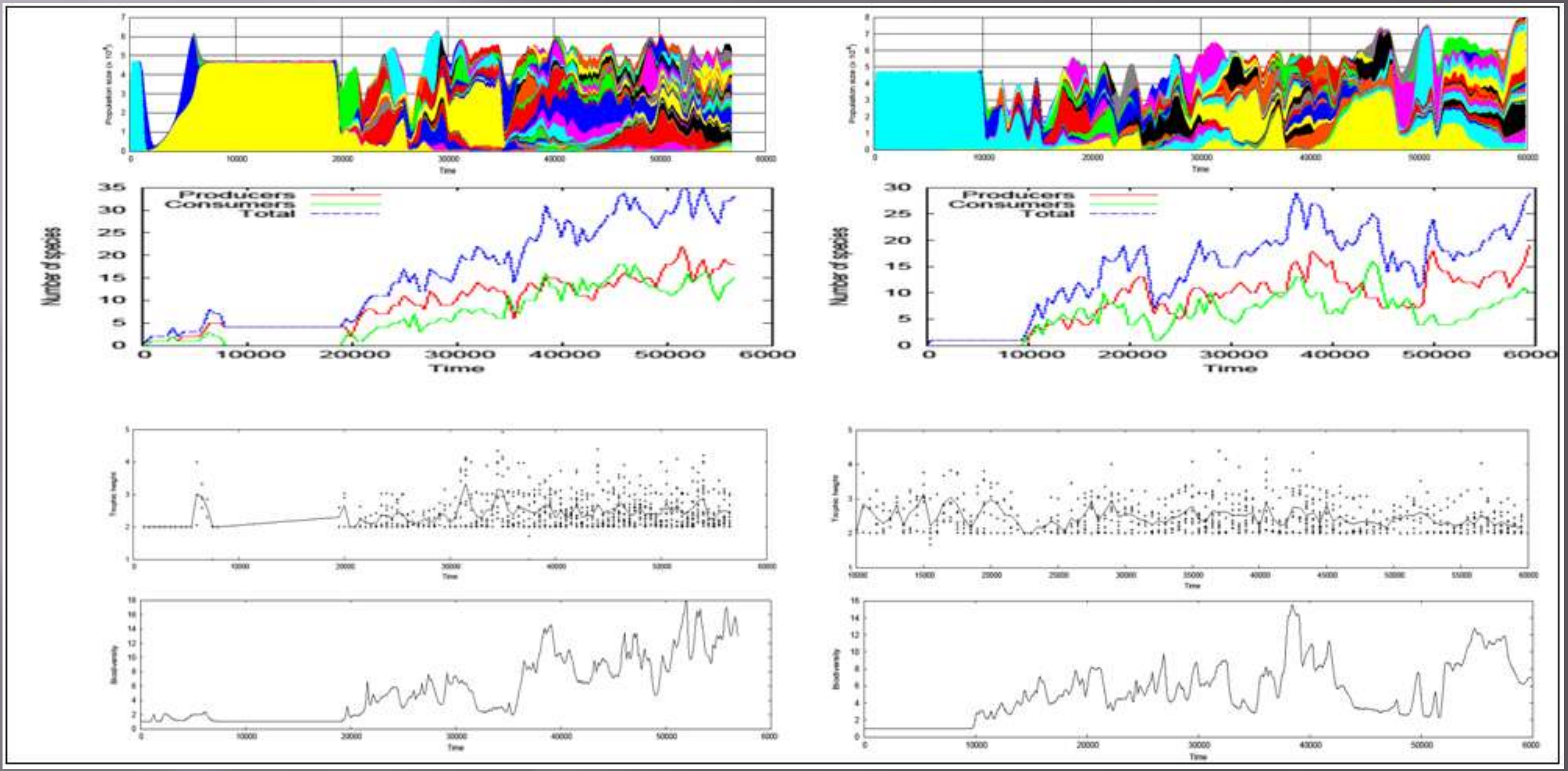
- So…. We can grow complex food webs from individuals from nothing but individual interactions!

- But how well do they behave?
  - Dynamic behavior
  - Other parameters
    - Trophic height
    - Ecological stability
    - Search properties in form space (”mixing”)

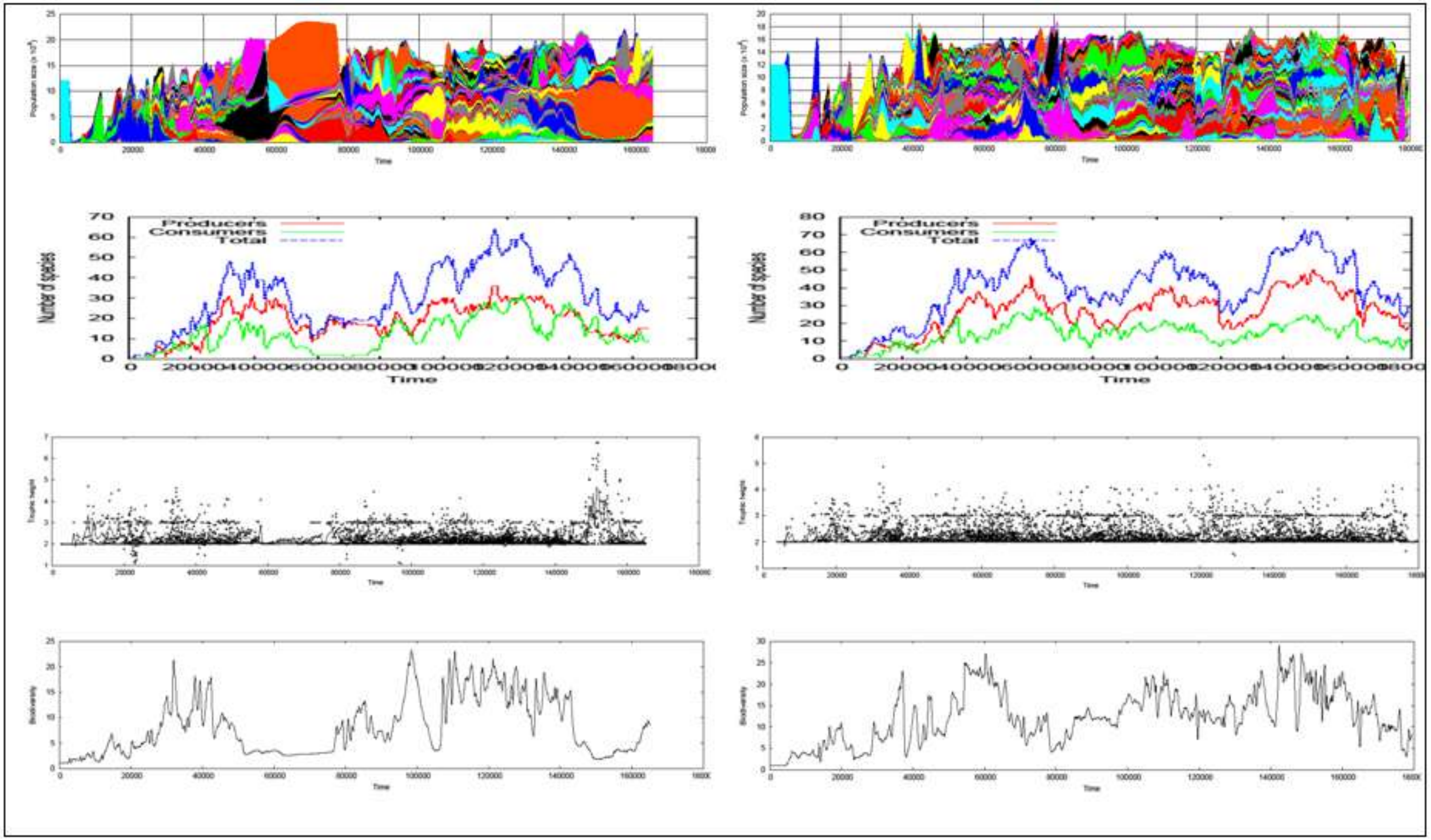
Best behavior



Adaptive radiation (t<50,000)

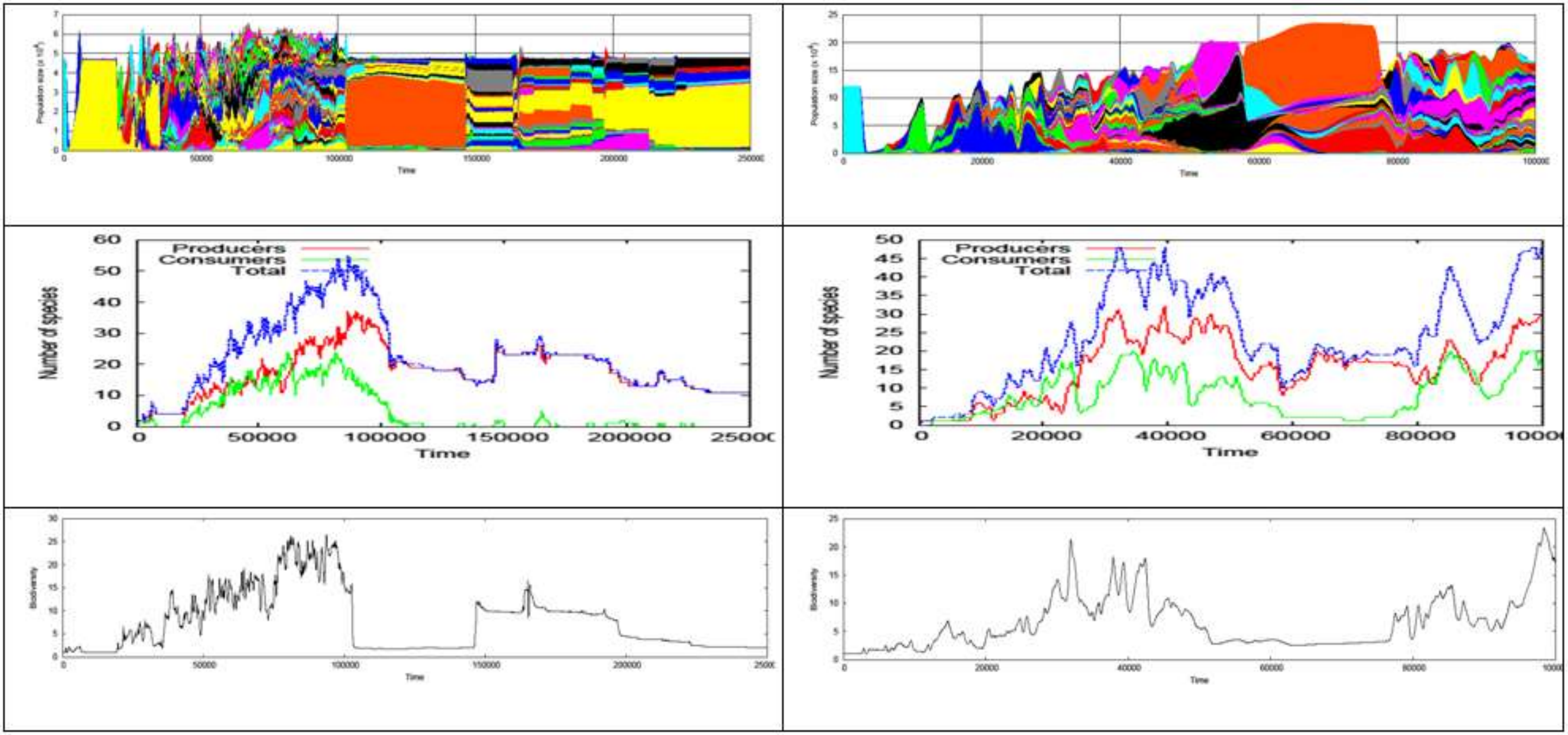


Epochs (the typical thing)

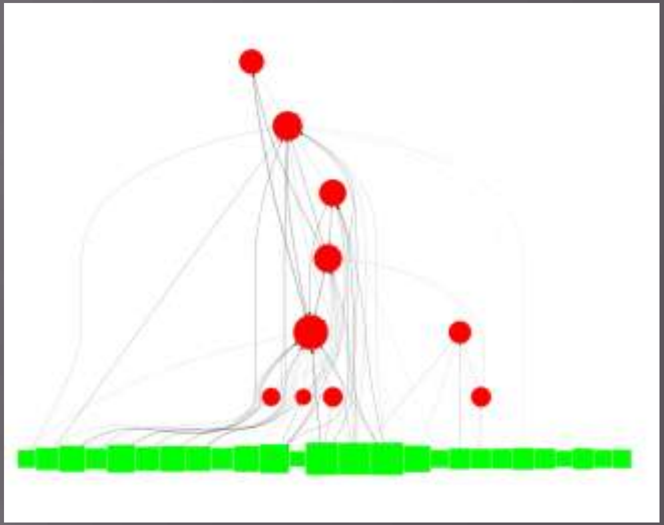


Typical length t= 50-80,000 steps (individual lifetime ca. 100-200 steps)

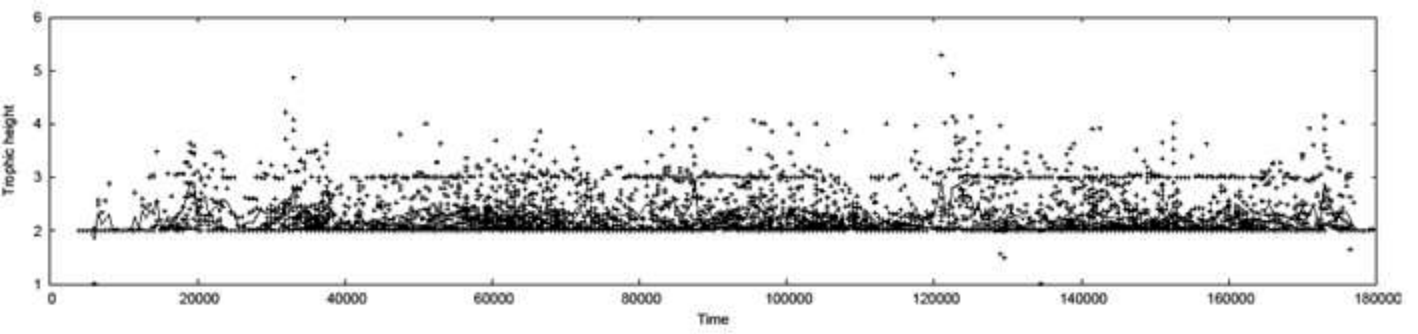
All is that shines is not gold



Trophic Height

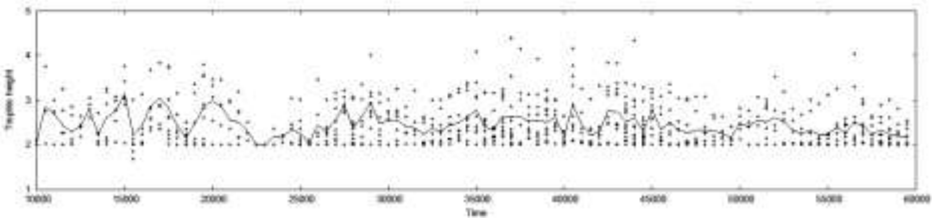


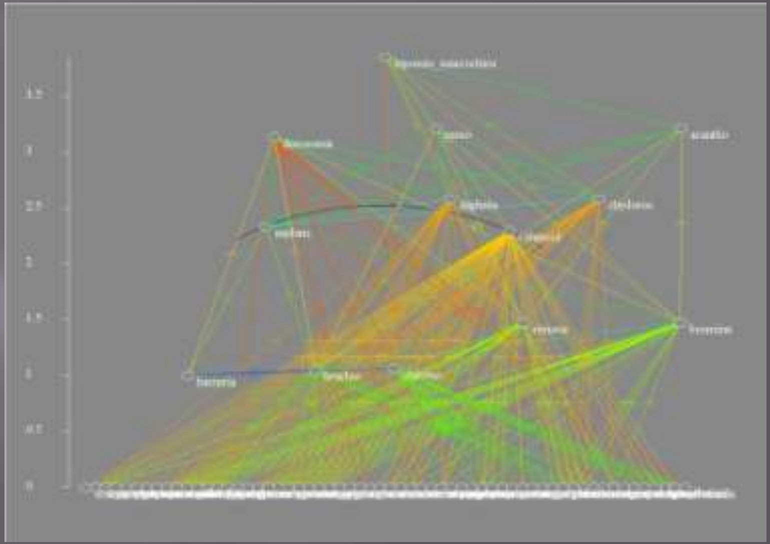
- TH= avg. of individual trophic heigts (ITH)
- ITH= 1.0 + avg. path lengths from a species to producers
- Use weighted path length (robust against truncating by removing weak links



Trophic height comparisons

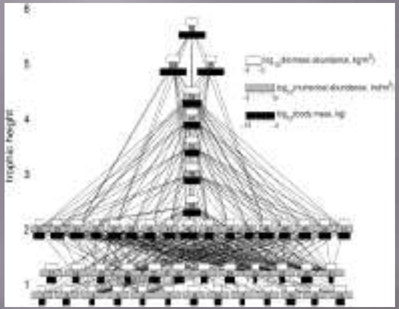
- In the model: average 2-3, max 6-7

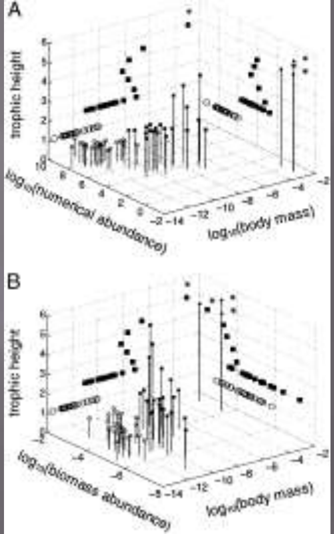




http://www.biologie.ens.fr/~legendre/

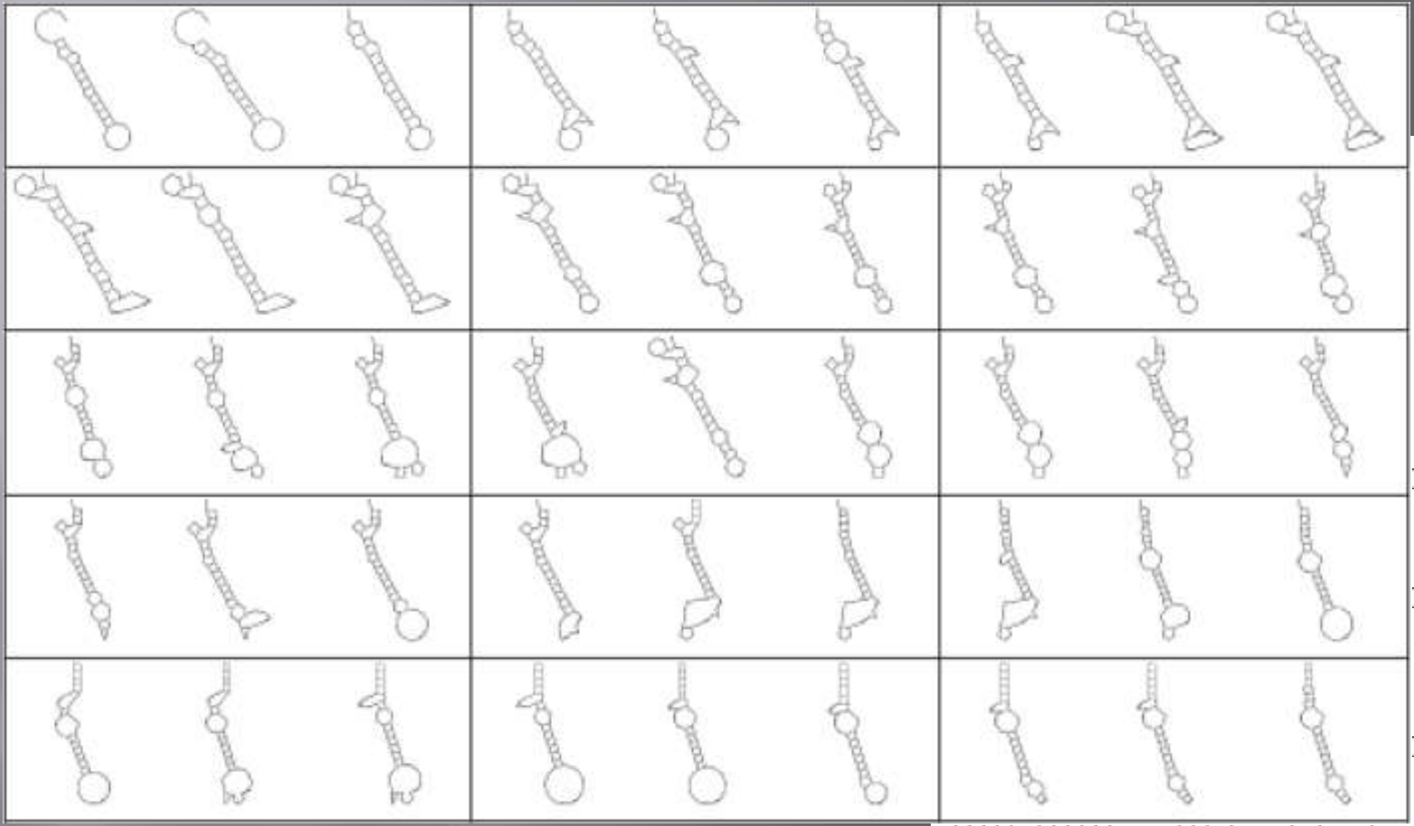
- In nature, same:





Cohen J. E. et.al. PNAS 2003;
100:1781-1786

Bestiary of phenotype mutants



45 consecutive mutants

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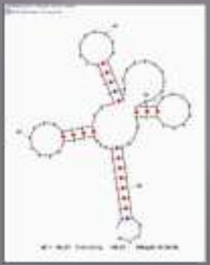
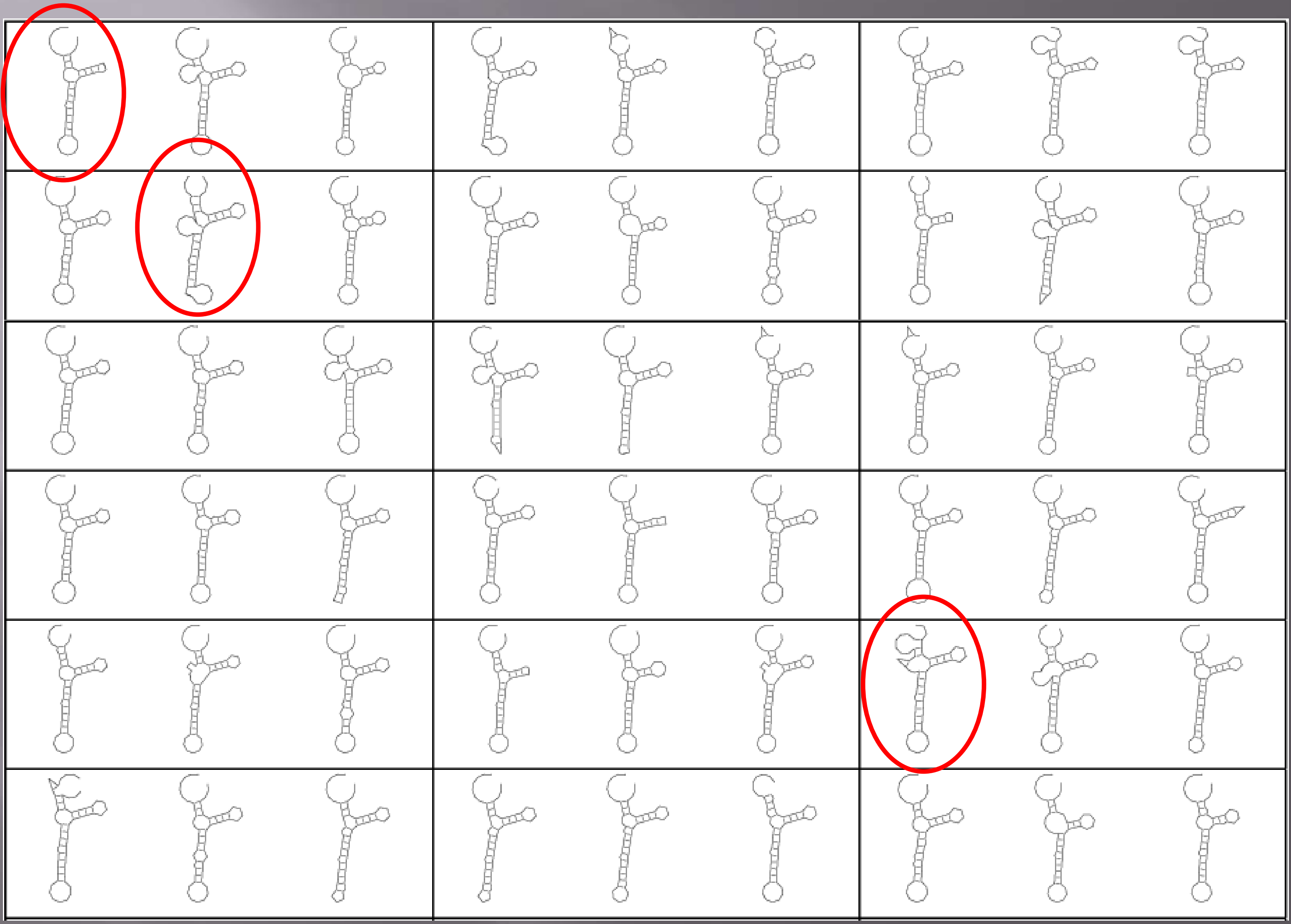


„predatory RNA”

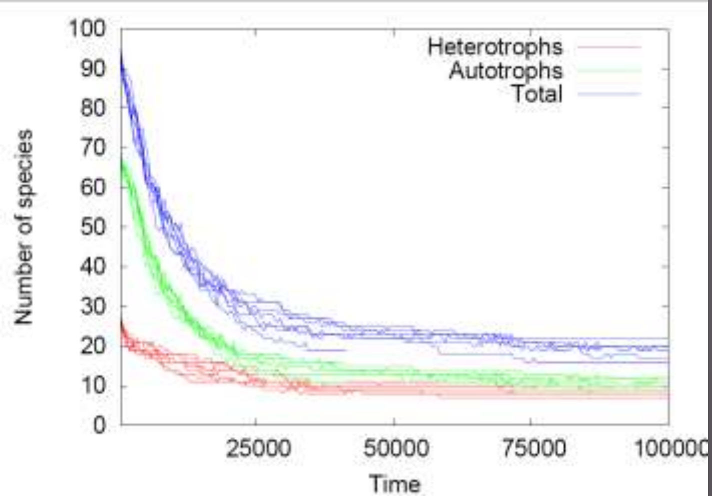
„wild type” RNA

Single-step phenotype mutants

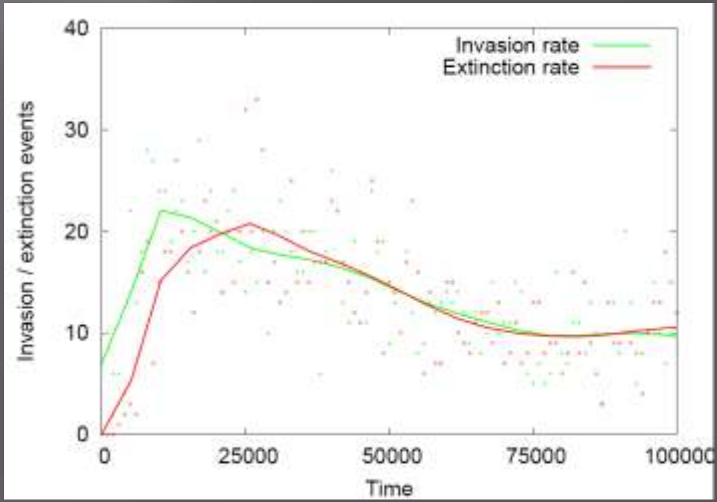


Ecological stability

- Mutation turned off
- Single napshot
  at t=200,000
  10 different runs



- Invasion and extinction rates
- Avg. plot of 10 runs

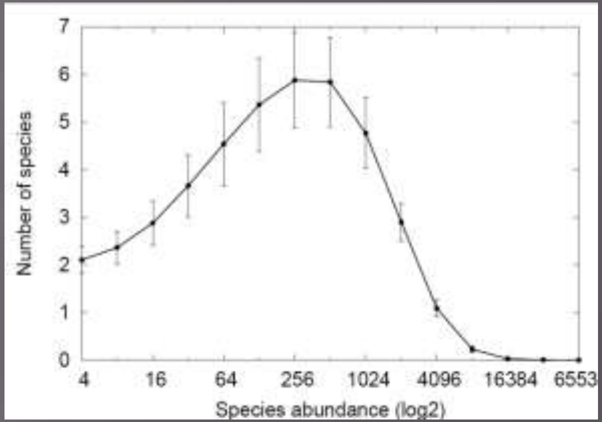


Quantitative analysis

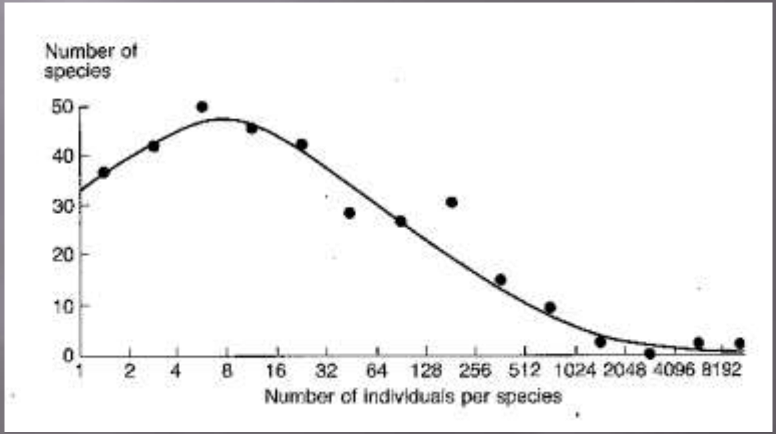
- Species abundance
- Species-area distribution
- Network complexity
  - Link-species relations
  - Degree distribution
  - Weak links

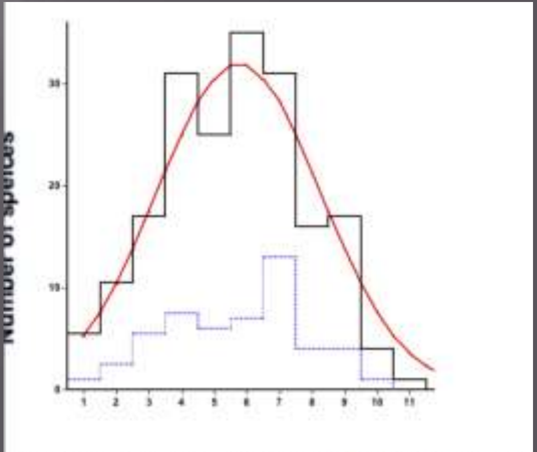
Species abundance

- Our data: lognormal, but more bias towards rare
- Due to occasional species



- *Kelly, C. K., M. G. Bowler, O. G. Pybus, and P. H. Harvey. (2008)* ***Phylogeny, niches and relative abundance in natural communities****. Ecology 89:962-970.*





Log-normal species abundance curve for the Chamela data set.

http://web2.uwindsor.ca/courses/biology/macisaac/55-437/lecture9/LOGNORM.JPG

Species–area distribution

- Species richness increases with habitat area
- Often found/assumed power law, $S=cA^z$

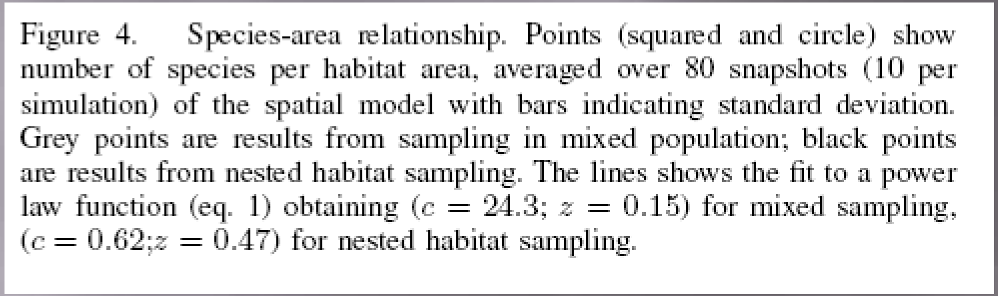
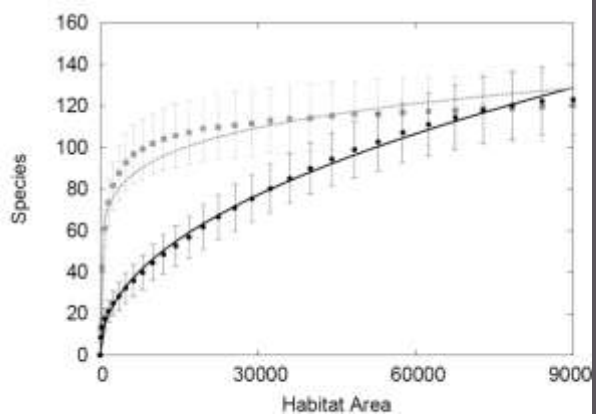
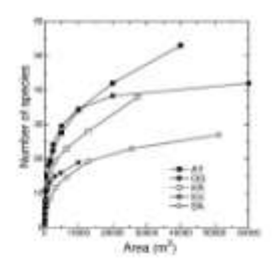
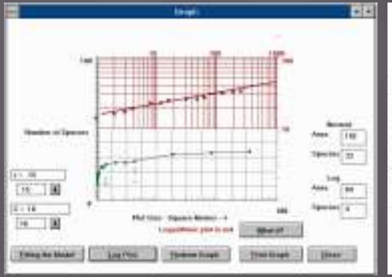


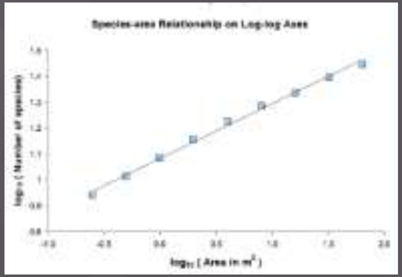
Figure 4. Species-area relationship. Points (squared and circle) show number of species per habitat area, averaged over 80 snapshots (10 per simulation) of the spatial model with bars indicating standard deviation. Grey points are results from sampling in mixed population; black points are results from nested habitat sampling. The lines shows the fit to a power law function (eq. 1) obtaining ($c = 24.3$; $z = 0.15$) for mixed sampling, ($c = 0.62$;$z = 0.47$) for nested habitat sampling.



- „common wisdom”, but caveat:







A. Clauset, C.R. Shalizi, and M.E.J. Newman, "Power-law distributions in empirical data" *SIAM Review*, to appear (2009).

Network complexity I. Link–species relations

- In the model:

- In nature:
  - General form $L= bS^u$
  - „Links-species scaling law”, $u=1$
  - „Constant connectance”, $u=2$

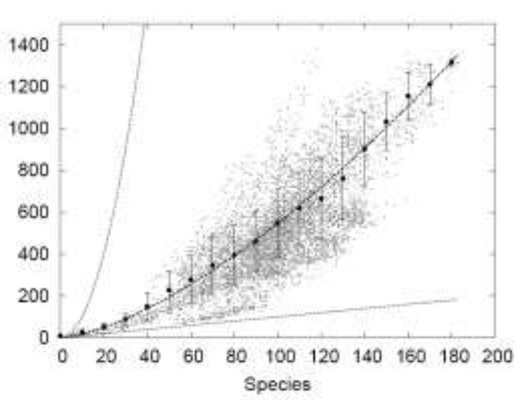
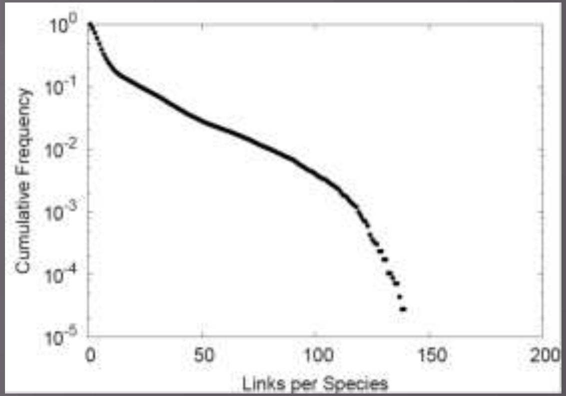


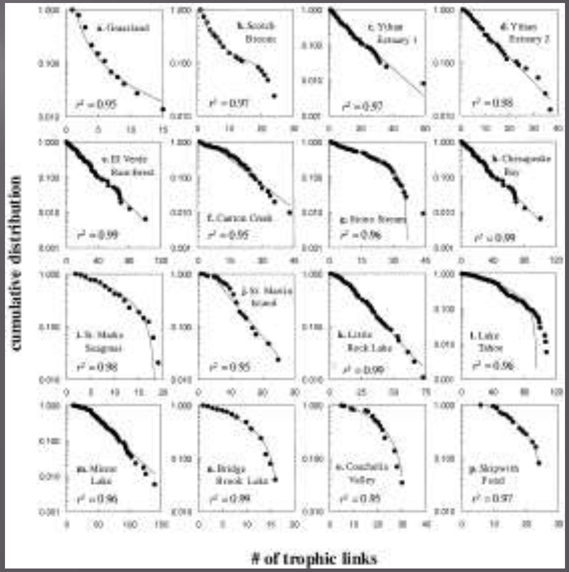
Figure 6. Links species scaling. Grey dots are the data points obtained from 8 independent simulations. Circles represent the mean of the data points, binned in species intervals of 10; bars show standard deviation. Dashed gray lines indicate the theoretical minimal ($L = S - 1$) and maximal ($L = S^2$) connectance. The black line show the fitted function (equation 2; with $u = 1.50$ and $b = 0.55$).

Brose, U., A. *Ostling*, K. Harison, and N. D. *Martinez*. *2004*. Unified spatial scaling of species and their trophic interactions. *Nature* 428:167-171

Network complexity II. Degree distribution

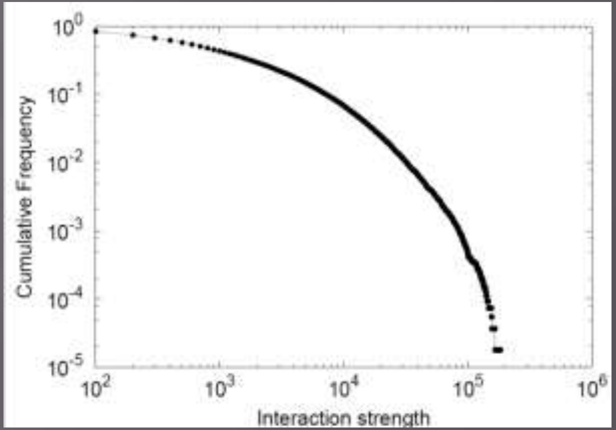
- In the model:
  - Strong exponential part
  - Uniform at higher end
  - Occasional species (mutats)
- In nature:
  - Exponential or uniform
  - A few „power law”





Dunne, J.A., R.J. Williams, and **N.D. Martinez**. 2002. Food-web structure and network theory: the role of connectance and size .Proceedings of the National Academy of Sciences 99:12917-12922.

Network complexity III.
Weak links



- In the model: exponential
- In nature:
  - Consensus on weak skew
  - Consensus on weak links ‘stabilizing role
  - Few data available (emerging business)
  - Exponential is one of the assumed forms

J. T. Wootton and M. Emmerson. Measurement of interaction strength in nature. <u>Annual Review of Ecology, Evolution and Systematics</u> 36:419-444.

M. Novak and J. T. Wootton. Estimating nonlinear interaction strengths: an observational method for species-rich food webs. <u>Ecology</u> 89:2083-2089.

Analysis summary

- Robust production of networks with „realistic” ecological properties
- This suggests that some of these properties might be inexorable (or highly probable) consequences (side effects) of simple factors and need no special explanation
- (cf. neutral theory, Hubbel 2001)

Question: universality?

- Questions of robustness of the model against:
    - Trait assigment
    - Choice of GPM
    - Details of interaction (e.g. Gaussian)
    - Etc.
- Stability: should it be better or is this okay?
    - Can we stabilize the models (invasion, dyn.collapse)
    - Can we stabilize ecosystems (invasion, dyn.collapse)?

Conclusions

- Presented an individual based model of food web assembly
- Based on rich phenotypes and encapsulation:
  - Multiple interdependent traits
  - Inherent trade-offs
- Shows robust emergent complexity, and „realistic” ecological properties („for free?”)
- Enables new approach to studying food webs:
  - Popul. dynamic analysis, network structure analysis
  - Relate structure to individual traits!

People

- Members of the team:
  - Walter de Back (RNA ecosystems)

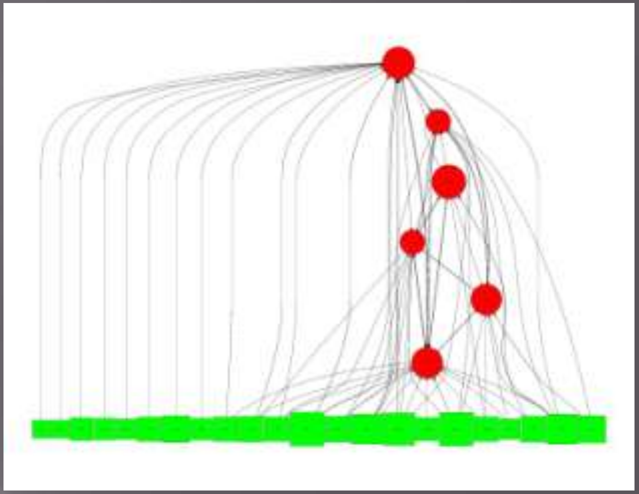
  - Laszlo Gulyas (FATINT)

- Special stanks to:
  - Sergio Branciamore (RNA folding)

- all: Collegium Budapest. (LG also ELTE)

Thank you!

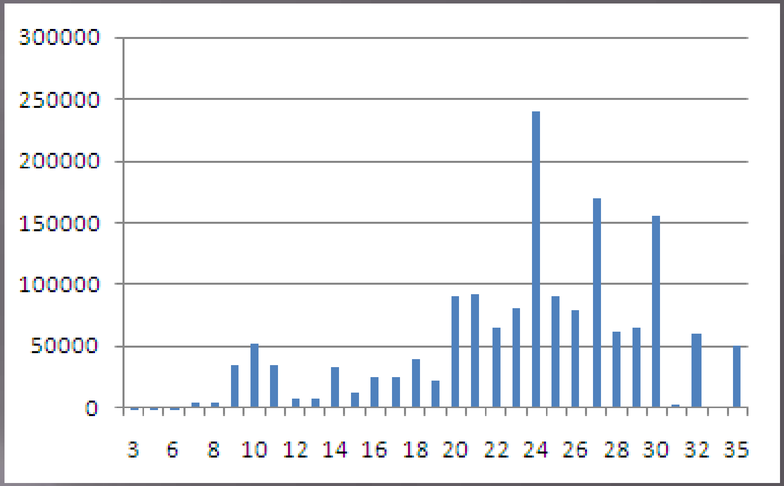
Low specificity



- Sometimes (usually) many (weak) links
- Which also tend to cross many trophic levels
- „Omnivorous” consumers
- A consequence of Gaussian (lack of strong specialization)
- But also of insufficient structural distance between species in RNA folds space?
- Phenotype mutations show less mixing.

Tree edit distances

- Histogram of a run



- One-step mutations (less neutrality than in full GPM)