

# Evolutionary dynamics

—

Tarmo Nurmi

CS-E5770 Topics in Complex Systems

14.5.2020



Aalto-yliopisto  
Aalto-universitetet  
Aalto University

# Contents

1. Intro - features of evolution
2. Replicator equation (simple)
3. Jain-Krishna model (linear)
4. CCC model (nonlinear), briefly
5. Summary

# Evolution

**“Nothing in biology makes sense except in the light of evolution”**

**Theodosius Dobzhansky, 1973**

**Darwinian description:**

**Individual elements in a given population produce offspring, similar but with variation. Some variations do well, reproduce more, and become more common (**fitness**). Some do badly and disappear. Different environments can favor different variations.**

# Algorithm

- 1. A new entity is created and placed in a specific environment.**
- 2. The new entity interacts with its environment. These interactions determine if the entity survives (proliferates) or dies out.**
- 3. If it survives, it becomes part of the environment and may introduce or change interactions in it. This can lead to cascading creation or extinction events.**

**Combinatorial evolution: new entities can be generated by consequence of already existing entities, Entity 1 + Entity 2 → Entity 3**

**Co-evolutionary dynamics: states and interactions (environment) update each other**

**Open-endedness: no goal, any number of species can be generated, equilibria don't last forever**

**Seems to be difficult to predict the specific course of the future; instead, model and predict statistical properties of evolution**

**Many couplings between species, genes, etc. are drawn randomly in models**

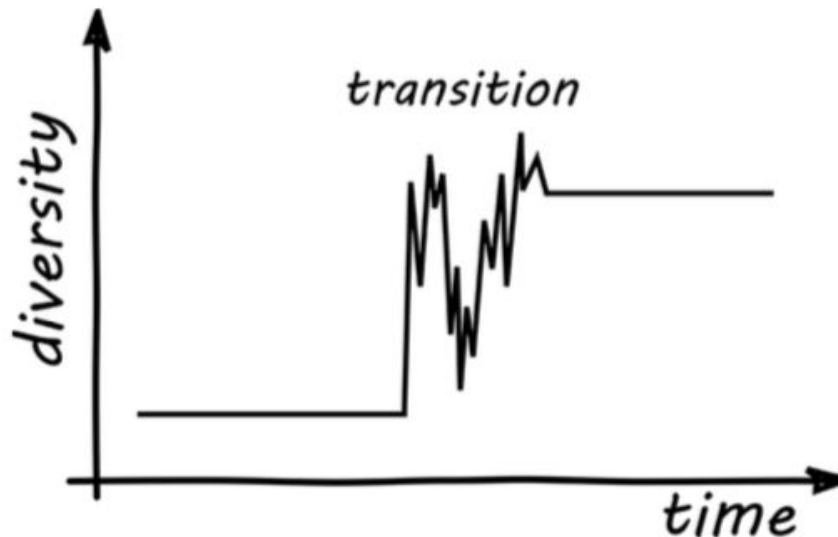
# Punctuated equilibrium

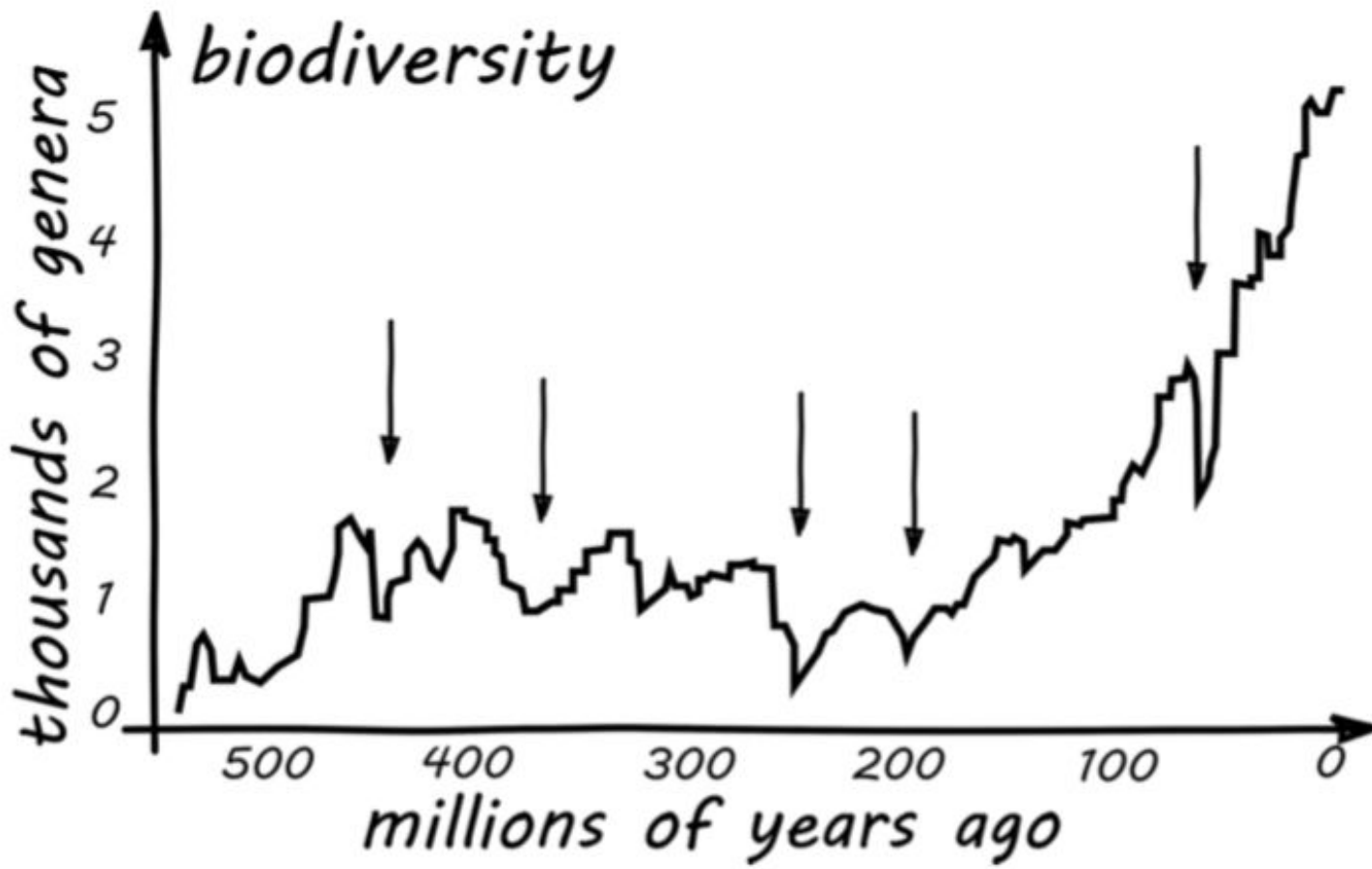
Creation and extinction events often occur in bursts

Most of the time, the system is in a temporary equilibrium

Transitions to other equilibria cause large diversity changes

Punctuated equilibria are associated with fat-tailed distributions in e.g. the size of diversity changes, creation or extinction rates, or lifetimes of entities





# Replicator equation

$$\frac{d}{dt} x_i = x_i [f_i(\mathbf{x}) - \phi(\mathbf{x})]$$

$$\phi(\mathbf{x}) = \sum_{j=1}^N x_j f_j(\mathbf{x})$$

$x_i$  = relative abundance of species  $i$ ,  $\mathbf{x} = (x_1, x_2, \dots, x_N)$

$f_i(\mathbf{x})$  = fitness function of  $i$

$\phi(\mathbf{x})$  = weighted population average fitness



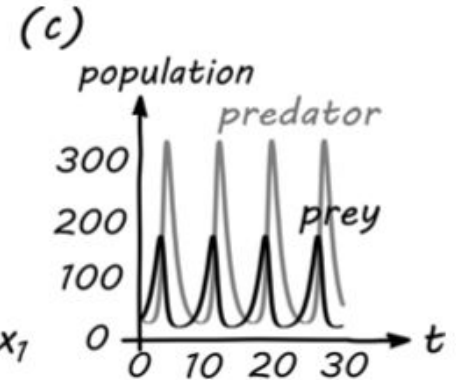
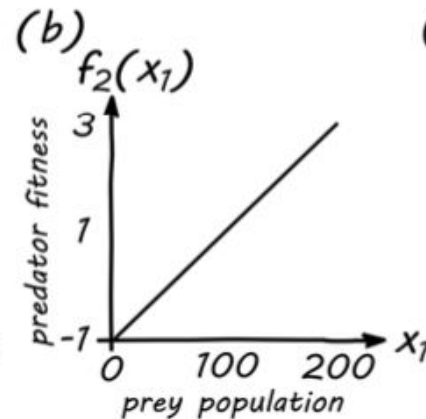
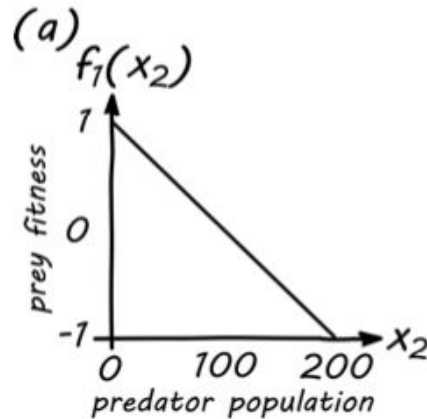
# Simple example: Lotka-Volterra system

Unnormalized

$$\frac{d}{dt}x_1 = x_1(p_{12}x_2 + f_1)$$

$$\frac{d}{dt}x_2 = x_2(p_{21}x_1 + f_2)$$

Static fitness landscape: limit cycle attractor



$$f_1 = 1, f_2 = -1, p_{12} = -0.01, p_{21} = 0.02$$

# Issues

**Set of species is fixed (not open-ended)**

**Does not have punctuated equilibrium dynamics (interaction rules not updated on long timescales)**

**Small variations in initial conditions lead to completely different trajectories (chaos) for high-dimensional systems**

# Jain-Krishna model

**Short timescale** (ecological dynamics):

$$\frac{d}{dt} x_i = \sum_{j=1}^N M_{ij} x_j - \phi x_i$$

$x_i$  = relative abundance of species  $i$

$M_{ij}$  = adjacency matrix of directed Erdős-Rényi network:

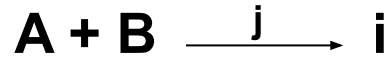
$M_{ij} = 1$  with probability  $p$  ( $i \neq j$ ), otherwise 0;  $M_{ii} = 0$

i.e. interaction is always constructive and with the same intensity

$\phi$  = dilution flux

# What does $M_{ij}$ represent?

$M_{ij}$  encodes the rate at which species  $i$  is produced by a “reaction” that is catalyzed by species  $j$ :



There are many catalyzed reactions and  $i$  itself may be a catalyst for another reaction

“A” and “B” are buffered, i.e. there is plenty of material for reaction

For example, a biological species may help another species proliferate

# Solution

Linear differential equation set solution:

$$\mathbf{x}(t) = e^{Mt} \mathbf{x}(0)$$

$$e^{Mt} = \sum_{k=0}^{\infty} \frac{1}{k!} (Mt)^k = I + Mt + \frac{1}{2}M^2t^2 + \dots$$

Let  $\mathbf{v}_i$  and  $\lambda_i$  be eigenvectors and eigenvalues of  $M$

Write  $\mathbf{x}(0)$  as a linear combination of eigenvectors:

$$\mathbf{x}(0) = \sum_{m=1}^N \alpha_m \mathbf{v}_m$$

Apply to  $\mathbf{x}(t)$ :

$$\mathbf{x}(t) = \sum_{m=1}^N \alpha_m e^{Mt} \mathbf{v}_m = \sum_{m=1}^N \alpha_m e^{\lambda_m t} \mathbf{v}_m$$

$$X\mathbf{u} = a\mathbf{u} \Rightarrow e^X \mathbf{u} = e^a \mathbf{u} \Rightarrow e^{Mt} \mathbf{v}_m = e^{\lambda_m t} \mathbf{v}_m$$

**Perron-Frobenius theorem** (can be applied because  $M$  is positive semidefinite):

**Largest eigenvalue  $\lambda_1$  is real and entries in  $\mathbf{v}_1$  are real and  $\geq 0$**

**When  $t$  goes to infinity, the largest term (with  $\lambda_1$ ) dominates:**

$$\mathbf{x}^* = \lim_{t \rightarrow \infty} \mathbf{x}(t) = \mathbf{v}_1$$

The Perron-Frobenius eigenvector (**the vector of eigenvector centralities of the network represented by  $M$** ) is the end-state of the model in the short timescale (ecological balance)

In order to have punctuated equilibria, there needs to be environment change events in the longer time scale: we assume that between such events, the ecological balance state is reached

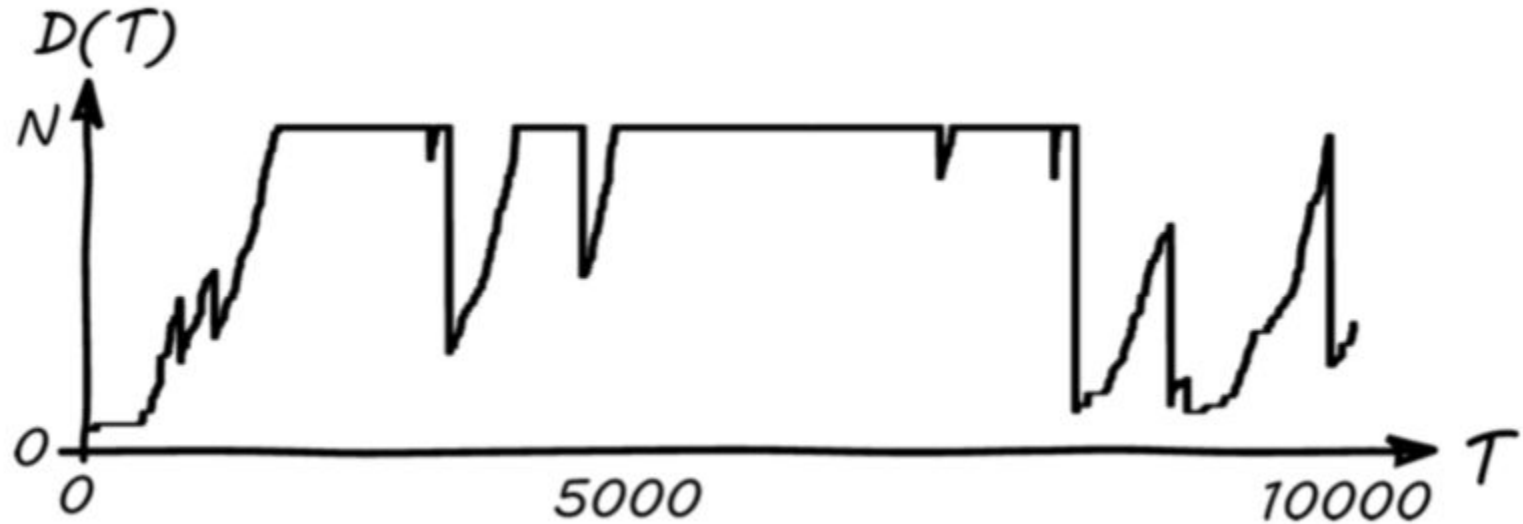
## Long timescale (evolutionary dynamics):

1. At time  $T$ , solve the ecological balance  $x^* = v_1$
2. Find the least-abundant (least-fit) species  $s$
3. Remove  $s$  by setting  $M_{is} = M_{si} = 0$  for all  $i$
4. Introduce a new species with random interactions:  $M_{is} = 1$  and  $M_{sj} = 1$  (separately) with probability  $p$  ( $i, j \neq s$ ).
5. Set time  $T = T + 1$  and go back to 1

The model is co-evolutionary, since the interactions  $M$  change with the species abundance  $x$

**Fitness** is an emergent property of the interaction network





$D(T)$  = number of species with non-zero entries in  $x^*$

<https://csh.ac.at/vis/Jain-Krishna/>

(NB! at  $\lambda_1 = 0$  the eigenvector does not tell the diversity)

# Diversity and autocatalytic sets

Directed cycle in  $M$  = autocatalytic cycle

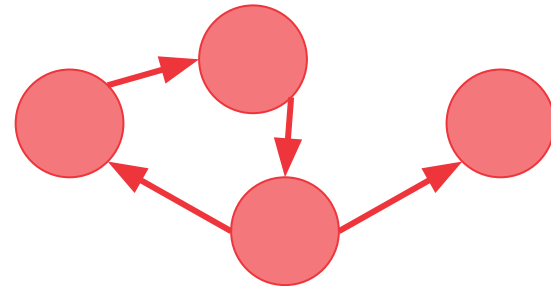
Species in a strongly connected component are in one or more autocatalytic cycles

Autocatalytic set = species in a strongly connected component + species in an out-component

Each member in an autocatalytic set is the product of another catalyst in the set

No autocatalytic cycle  $\rightarrow \lambda_1 = 0$

At least one cycle  $\rightarrow \lambda_1 \geq 1$



**No cycles: species concentrations flow to the furthest leaf nodes**

→ **diversity equal to the number of furthest leaf nodes**

**At least one cycle: only species that are part of (the dominant) autocatalytic set survive**

→ **diversity equal to the size of the dominant autocatalytic set**

**Emergence of diversity:**

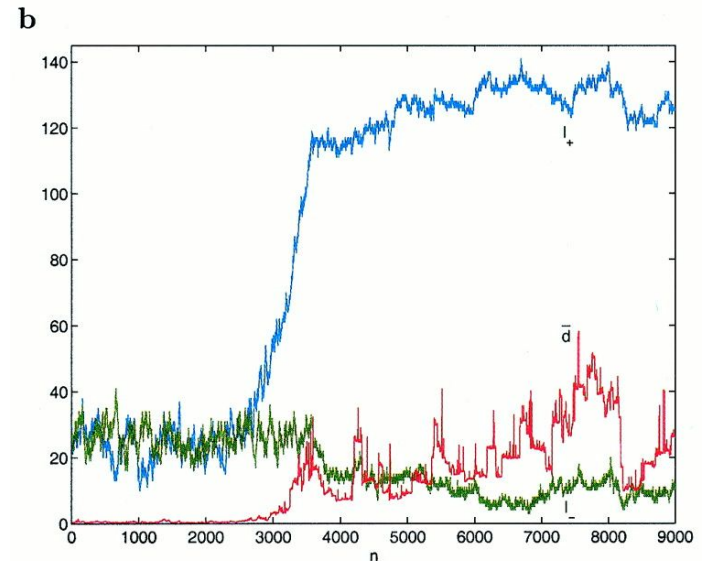
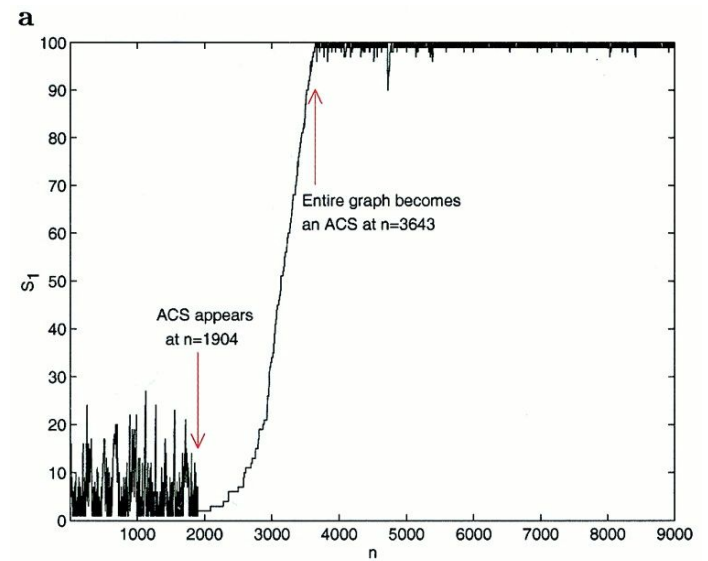
**First, the network has no cycles (sparse). When the first cycle appears, its autocatalytic set dominates. Then, more and more species join that set. When *all* species are in the set, one of them is removed, and the cycle might break, causing a collapse. Another autocatalytic set might also take over as the dominant and decrease diversity (diversity doesn't have to be nondecreasing as  $t$  increases).**

→ **Diversification events, balance periods, and extinction events**

Works also with  $M_{ij} \in [-1,1], i \neq j$ ,  
and  $M_{ii} \in [-1,0]$

→ Emergence of  
cooperation/mutualism as  
positive links have selection bias,  
diversity explosion sees also  
increase in number of positive  
links

blue: positive links  
green: negative links  
red: “interdependency”



# Issues

**Not open-ended: no emergence of new species from combinatory events**

# Co-evolving combinatorial critical model (CCC), briefly

$\sigma_i(t) \in \{0,1\}$  is the state of entity  $i$  at time  $t$

At time  $t$  do:

1. Pick entity  $i$  at random
2. Compute fitness of  $i$ ,  $f_i(t)$
3. Set the next state of  $i$  accordingly
4. With probability  $p$ , switch that state
5. Continue until all existing entities have been updated once, then go to the next time step  $t = t + 1$

$$f_i(t) = \sum_{j,k=1}^N (M_{ijk}^+ - M_{ijk}^-) \sigma_j(t) \sigma_k(t)$$

$$f_i(t) > 0 \rightarrow \sigma_i(t + 1) = 1$$

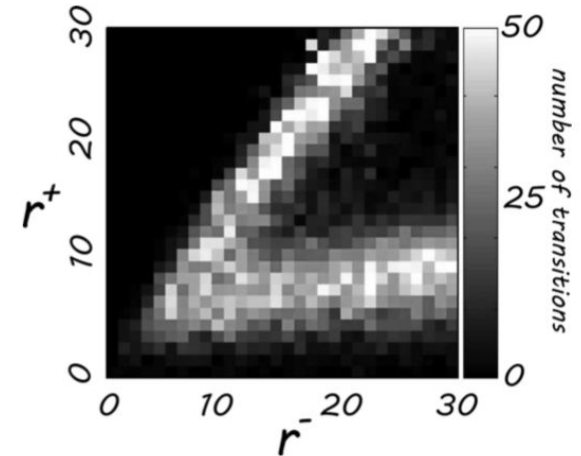
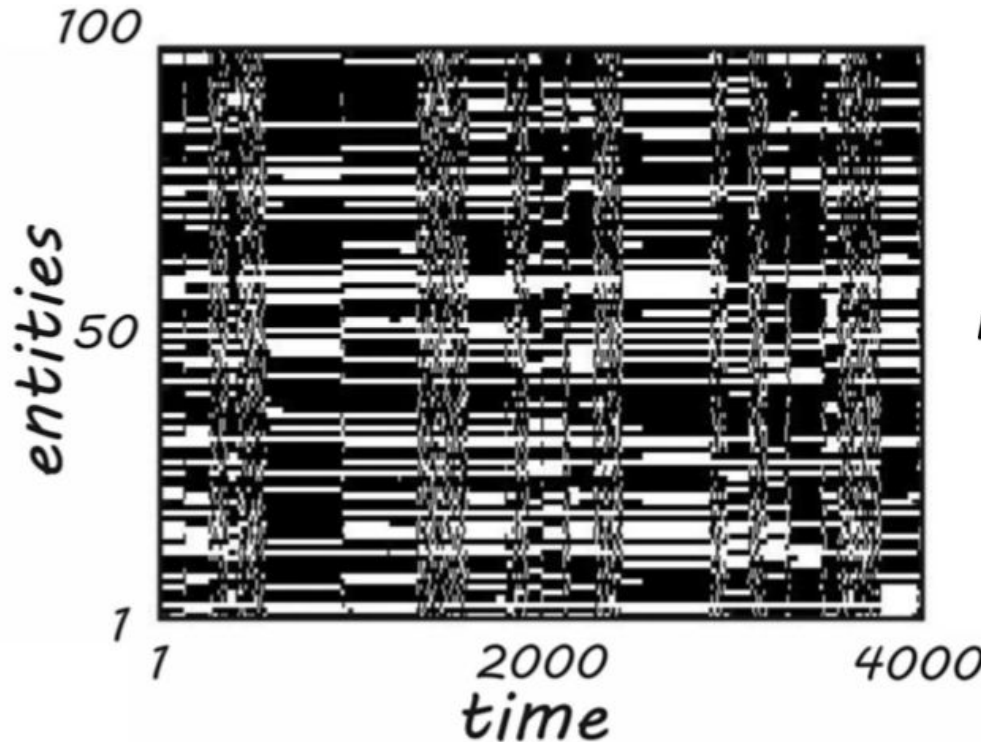
$$f_i(t) < 0 \rightarrow \sigma_i(t + 1) = 0$$

$$f_i(t) = 0 \rightarrow \sigma_i(t + 1) = \sigma_i(t)$$

Tensors  $M^+$  and  $M^-$  are called production and destruction tables, and describe rules of combinatorial interactions

For example, random tensors with average number of productive/destructive sets per entity given by  $r^+/r^-$ , respectively

$r^+ = 10$   
 $r^- = 15$   
 $p = 0.002$   
 $N = 100$



**Exhibits punctuated equilibrium, self-organized criticality, autocatalytic production cycles**

**Interaction rules can be thought of as underlying rules of nature which are fixed, but the system moves through the possibilities offered by them**

**Even if the initial set of species is finite, the rule tables can be infinite and thus the model is open-ended**

**In the calculation of fitness, only the currently existing species are summed over, but they can produce any number of new species defined by the rule tables**



# Summary

**Punctuated equilibrium, open-endedness through combinatorial interactions, and co-evolution of species and the fitness landscape are important features of evolutionary systems**

**The Jain-Krishna model creates and explains punctuated equilibrium through the formation and destruction of autocatalytic sets via co-evolution of species and interactions, and describes fitness as an emergent interaction network property**

**The CCC model also adds open-endedness through infinitely large production and destruction tables, through which the finite set of species moves in time**

# Sources and further reading

**Introduction to the Theory of Complex Systems, chapter 5. Thurner, S., Hanel, R., & Klimek, P. Oxford University Press, 2018.**

**Jain, S., & Krishna, S. (1998). Autocatalytic sets and the growth of complexity in an evolutionary model. *Physical Review Letters*, 81(25), 5684.**

**Jain, S., & Krishna, S. (2001). A model for the emergence of cooperation, interdependence, and structure in evolving networks. *Proceedings of the National Academy of Sciences*, 98(2), 543-547.**