From Darwin‘s Natural Selection to Reproducing Molecular Networks

Peter Schuster

Institut für Theoretische Chemie, Universität Wien, Austria
and
The Santa Fe Institute, Santa Fe, New Mexico, USA

Heidelberg Initiative for the Origin of Life

Heidelberg, 01.06.2016

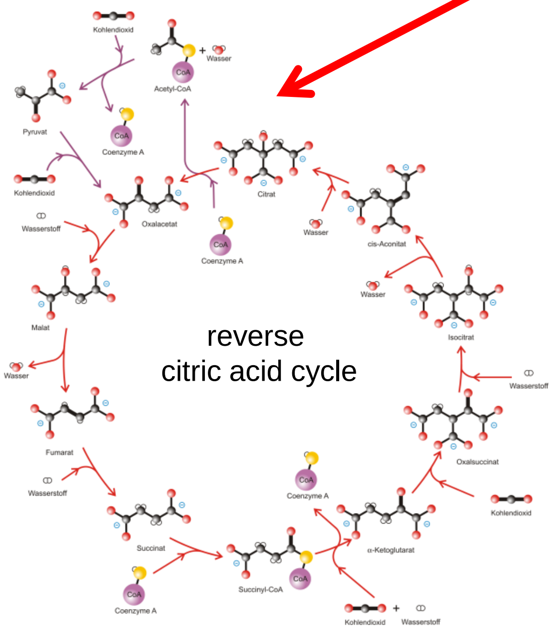
Web-Page for further information:

http://www.tbi.univie.ac.at/~pks

Prologue

small molecules

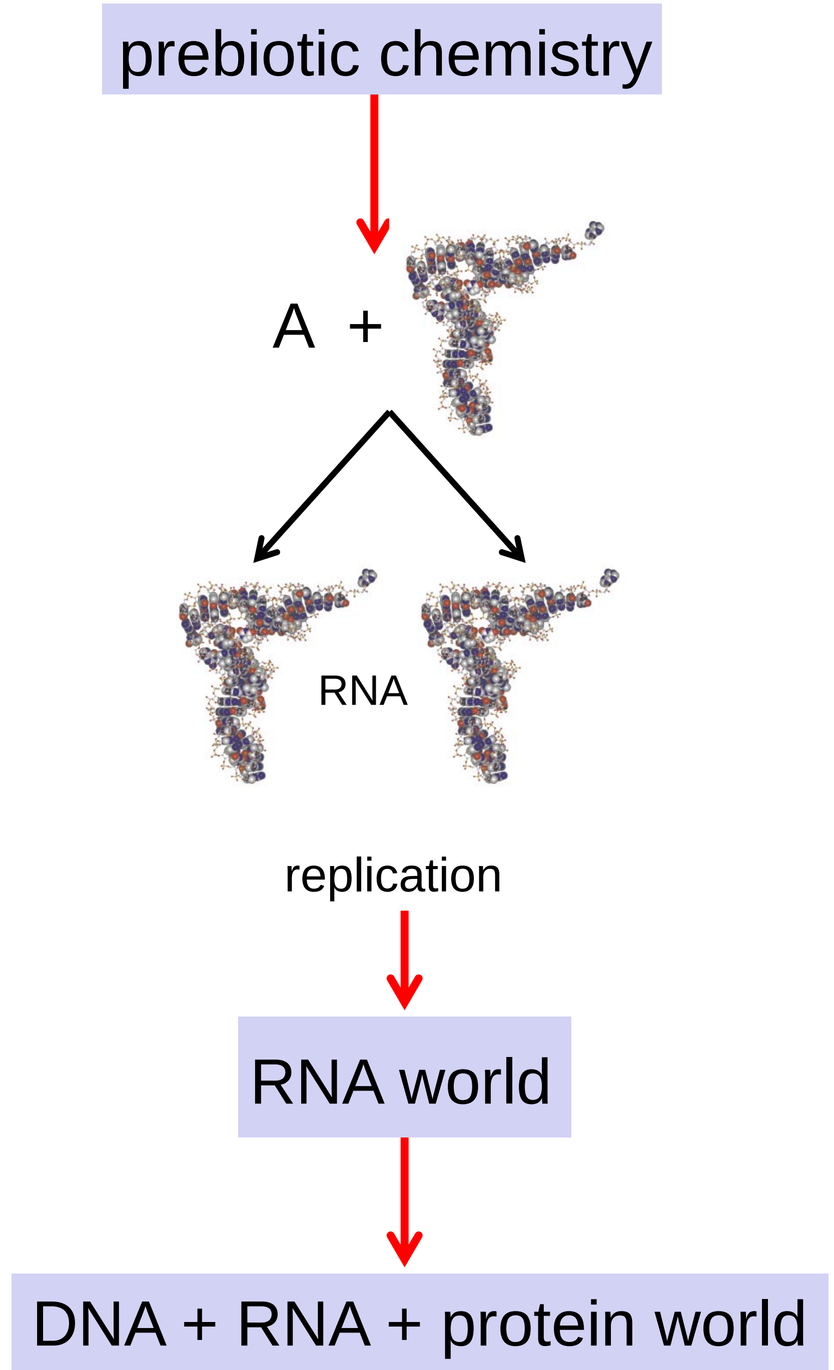
prebiotic chemistry



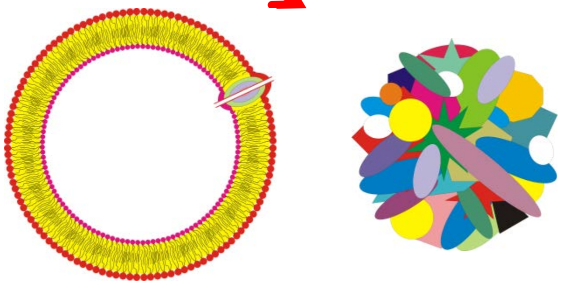
metabolism

RNA world

DNA + RNA + protein world


prebiotic chemistry
A +
RNA
replication
RNA world
DNA + RNA + protein world

prebiotic chemistry

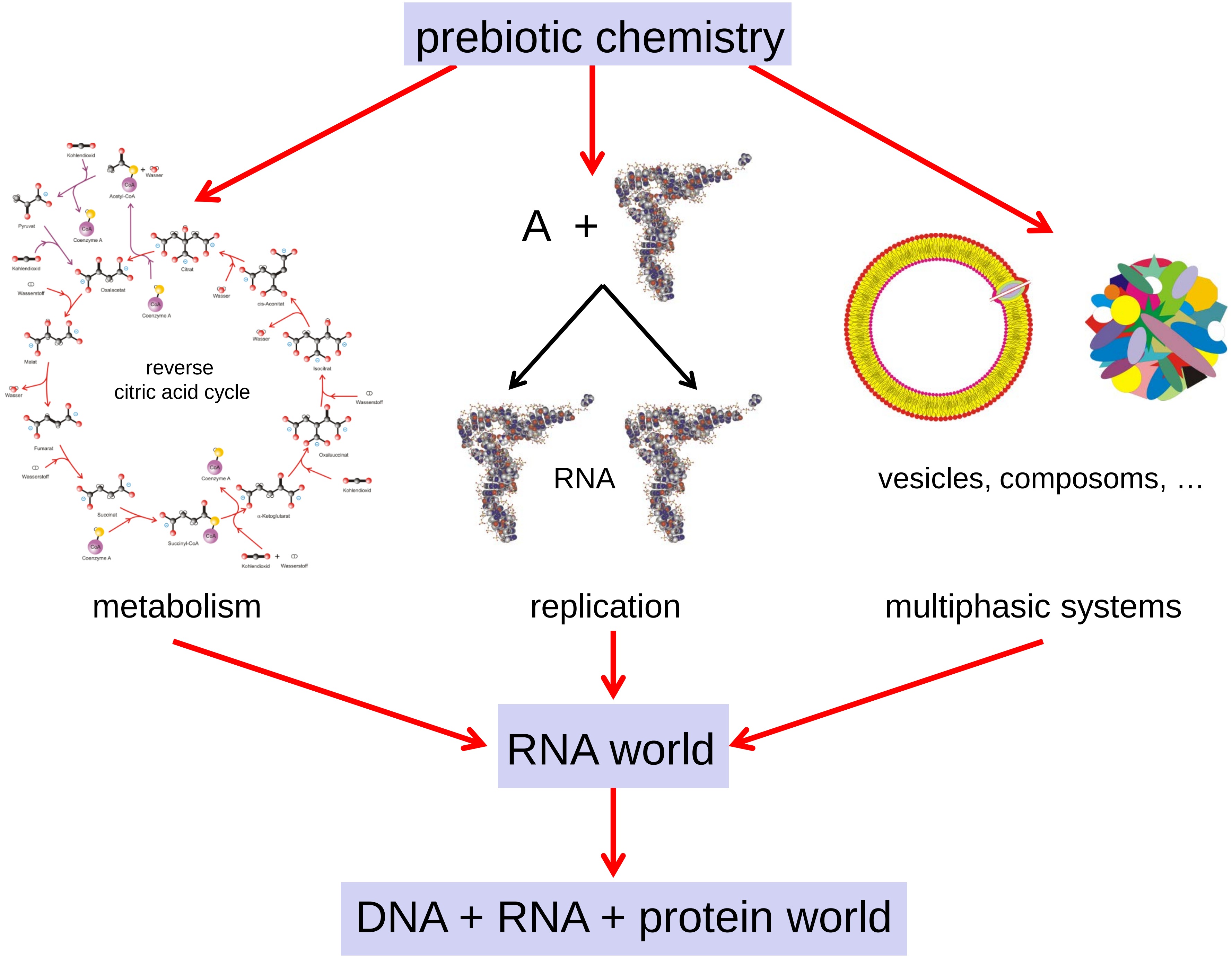


vesicles, composoms, …

multiphase systems

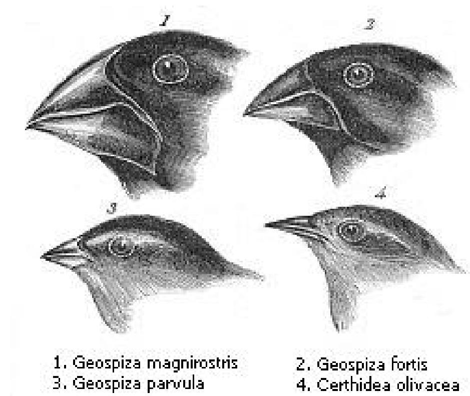
RNA world

DNA + RNA + protein world


prebiotic chemistry
reverse
citric acid cycle
Kohlendioxid
Acetyl-CoA
Wasser
Pyruvat
Coenzyme A
Citrat
Oxalacetat
Wasserstoff
cis-Aconitat
Malat
Isocitrat
Fumarat
Oxalsuccinat
Succinat
Succinyl-CoA
α-Ketoglutarat
A +
RNA
vesicles, composoms, …
metabolism
replication
multiphasic systems
RNA world
DNA + RNA + protein world

Charles Darwin, 1809 - 1882

Voyage on HMS Beagle, 1831 - 1836



Finches from Galapagos Archipelago

David Lack. Darwin’s Finches. Cambridge University Press, Cambridge (UK) 1947

Genotype, Genome

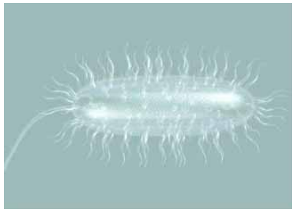
GCGGATTTAGCTCAGTTGGGAGAGCGCCAGACTGAAGATCTGGAGGTCCTGTGTTCGATCCACAGAATTCGCACCA

Biochemistry
Structural Biology
Molecular Biology
Molecular Evolution
Molecular Genetics
Systems Biology
Bioinfomatics

Genetics
Epigenetics
Environment

Development

Cell Biology
Developmental Biology
Neurobiology
Microbiology
Botany and Zoology
Anthropology
Ecology



Phenotype

Three necessary conditions for Darwinian evolution are:

1. **Multiplication,**
2. **Variation**, and
3. **Selection**.

Variation through mutation and recombination operates on the **genotype** whereas the **phenotype** is the target of **selection**.

One important property of the Darwinian scenario is that **variations** in the form of mutations or recombination events occur **uncorrelated** with their **effects on the selection process**.

Charles Darwin, 1809-1882

Three necessary conditions for Darwinian evolution are:

1. **Multiplication**,
1. **Variation**, and
1. **Selection**.

All three conditions are fulfilled not only by cellular organisms but also by **nucleic acid molecules** – **DNA** or **RNA** – **in** suitable **cell-free experimental assays**:

Darwinian evolution in the test tube

Darwin's mechanism explains optimization and adaptation.

natural selection *in vivo* and in evolution experiments

Darwin's mechanism cannot explain increases in complexity.

complexity of bacteria < protists < plants, animals, fungi

increasing complexity $\propto$ increasing genetic information

increasing genetic information $\propto$ increasing DNA lengths

termites

humans

replicating molecules	⇒	populations in compartments
independent replicators	⇒	chromosomes
RNA	⇒	DNA
prokaryotes	⇒	eukaryotes
asexual clones	⇒	sexual clones
protists	⇒	animals, plants, fungi
solitary individuals	⇒	colonies
primate societies	⇒	human societies

Eörs Szathmáry, John Maynard Smith. The major evolutionary transitions. Nature 374:227-232, 1995

John Maynard Smith, Eörs Szathmáry. The major transitions in evolution. Oxford University Press, New York 1995

Biological evolution of higher organisms is an exceedingly complex process not because the mechanism of selection is complex but because cellular metabolism and control of organismic functions is highly sophisticated.

The Darwinian mechanism of selection does neither require organisms nor cells for its operation.

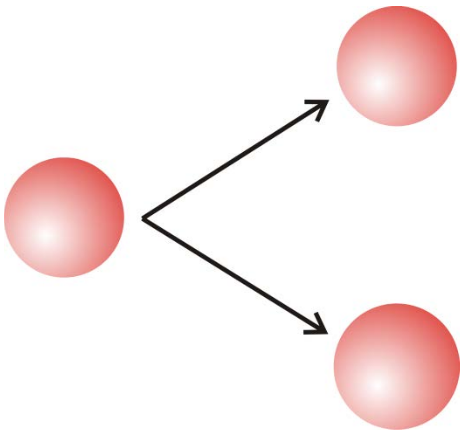
Make things as simple as possible,
but not simpler.

Albert Einstein, 1950 (?)

Occam's razor: Sir William Hamilton, 1852

1. Darwin's natural selection
2. Mutation and selection
3. A model for transitions
4. Cooperation tames competition
5. Effects of stochasticity
6. Scarcity is **not** the mother of invention!

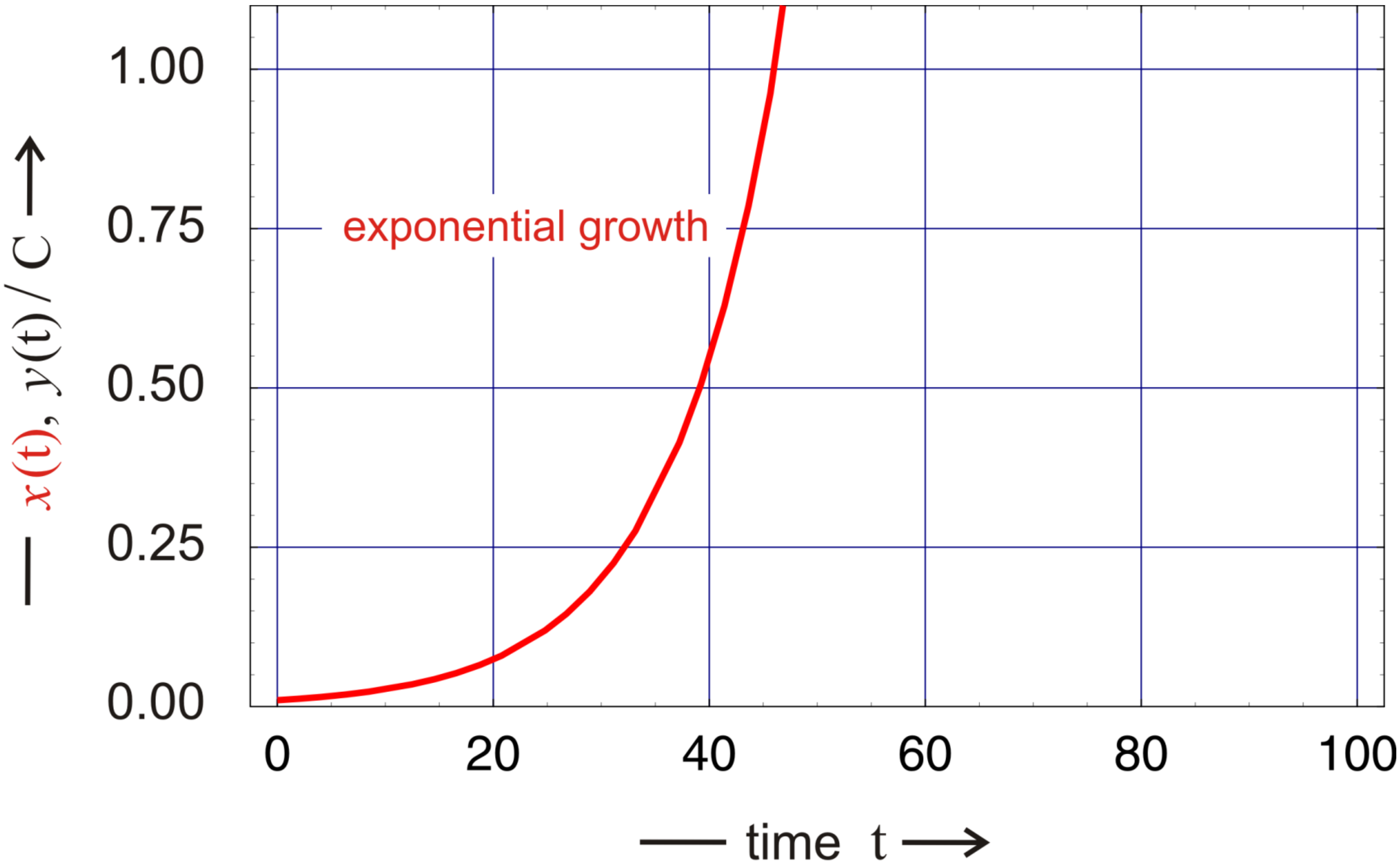
1. **Darwin's natural selection**
2. Mutation and selection
3. A model for transitions
4. Cooperation tames competition
5. Effects of stochasticity
6. Scarcity is **not** the mother of invention!



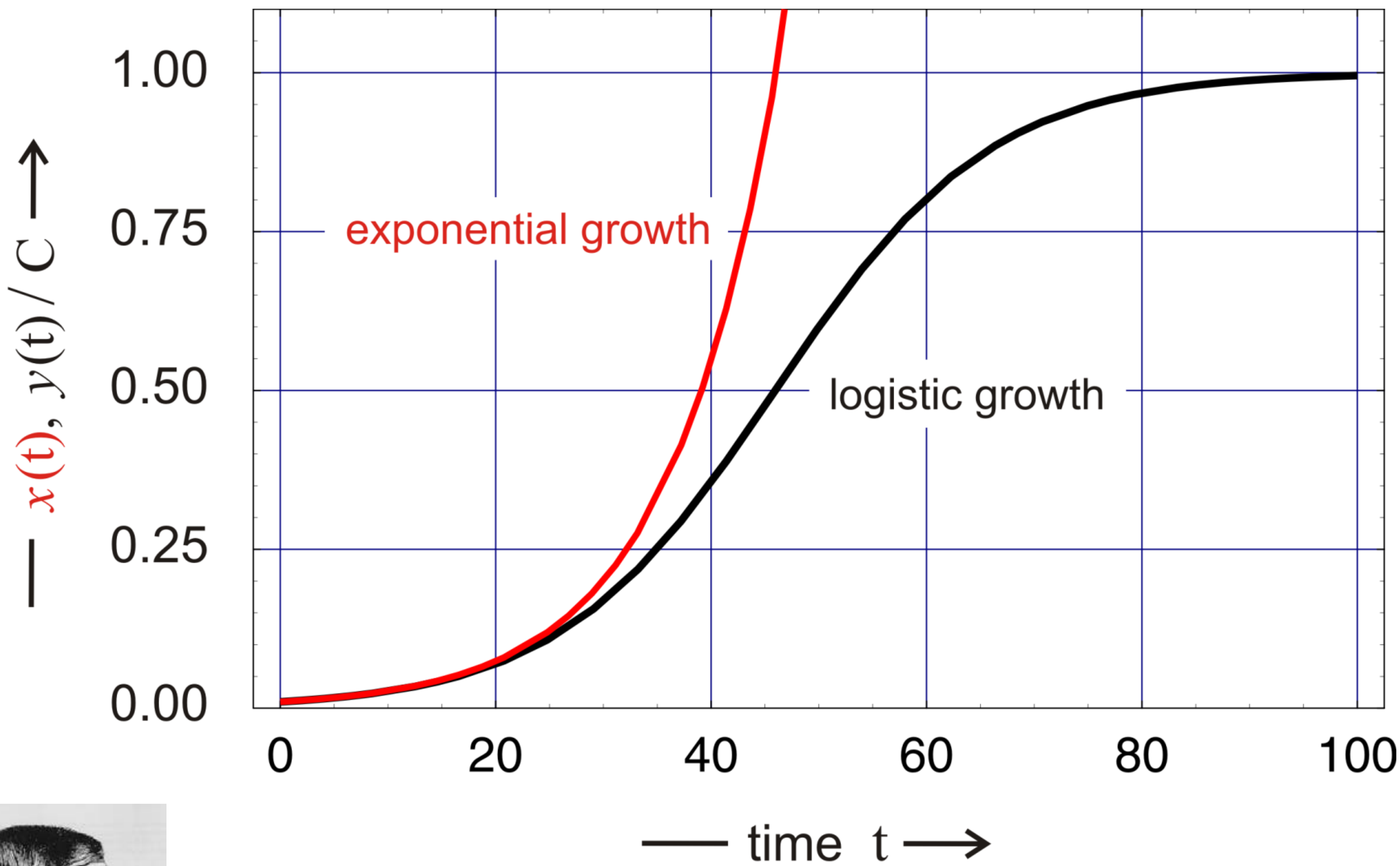
(A) + X = 2 X

$$\frac{dx}{dt} = f\,x \quad \Rightarrow \quad x(t) = x(0)\,e^{f\,t}$$

exponential growth



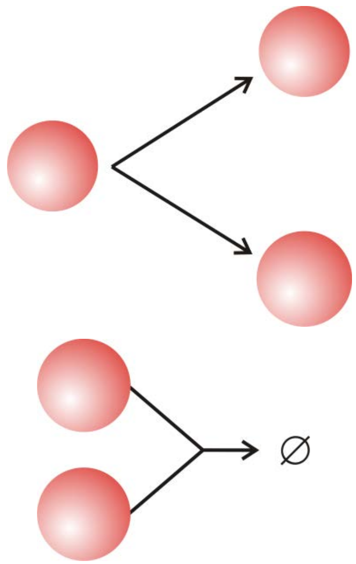
(A) + X $\rightarrow$ 2 X



Pierre-François
Verhulst,
1804-1849

$$(A) + X \rightarrow 2X$$
$$2X \rightarrow \varnothing$$

Was known 30 years
before the
'Origin of Species'



$$(A) + X \rightarrow 2X$$

$$2X \rightarrow \varnothing$$

$$\frac{dx}{dt} = f\,x - h x^2$$

$$x(t) = \frac{f\;x(0)}{h\,x(0) + \big(f - h\,x(0)\big)e^{-f\,t}} = \frac{x(0)\,C}{x(0) + \big(C - x(0)\big)e^{-f\,t}}$$

$$C = \frac{f}{h} \quad \ldots \quad \text{carrying capacity of the ecosystem}$$

logistic growth

$$\frac{\mathrm{d}x}{\mathrm{dt}} = f\ x\left(1 - \frac{x}{C}\right) \quad \Rightarrow \quad \frac{\mathrm{d}x}{\mathrm{dt}} = f\ x - \frac{x}{C}\ f\ x$$

$$f\ x \equiv \Phi(\mathrm{t}),\ C = 1: \quad \frac{\mathrm{d}x}{\mathrm{dt}} = x\left(f\ - \Phi\right)$$

Generalization of the logistic equation to *n* variables yields selection

$$(\mathrm{A}) + \mathrm{X}_i \rightarrow 2\,\mathrm{X}_i\,; \quad i = 1, 2, \ldots, \mathrm{n}$$

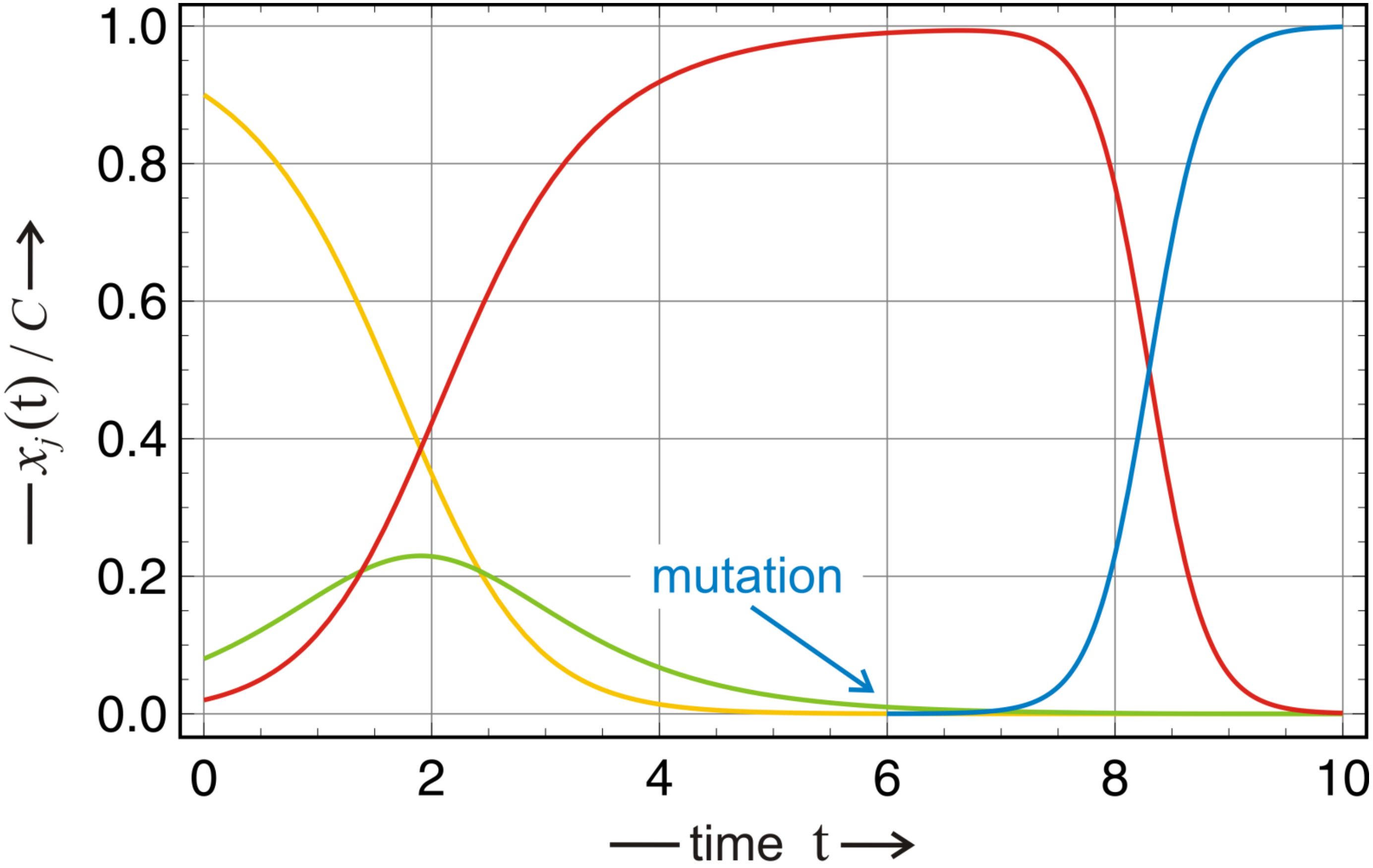
$$\mathrm{X}_1, \mathrm{X}_2, \ldots, \mathrm{X}_n : \quad [\mathrm{X}_i] = x_i\,; \quad \sum_{i=1}^{n} x_i = C = 1; \quad f_i = f(\mathrm{X}_i)$$

$$\boxed{\frac{\mathrm{d}x_j}{\mathrm{dt}} = x_j \left(f_j - \sum_{i=1}^{n} f_i\, x_i \right) = x_j \left(f_j - \Phi \right)} \;; \quad \Phi = \sum_{i=1}^{n} f_i\, x_i$$

Darwin

$$\boxed{\frac{\mathrm{d}\Phi}{\mathrm{dt}} = \,< f^2 > - < \bar{f} >^2 = \mathrm{var}\{f\} \geq 0}$$

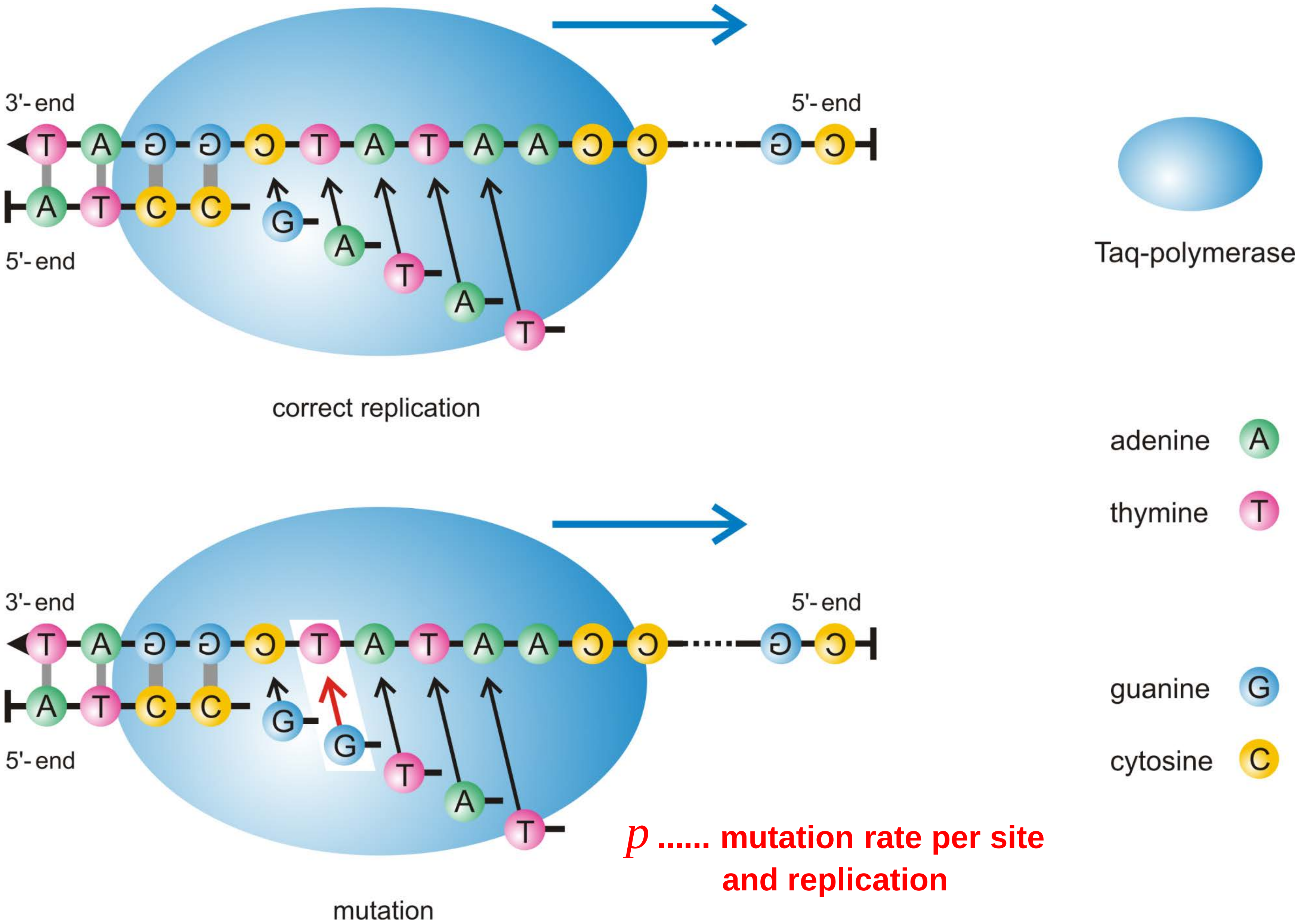
generalization of the logistic equation to *n* variables yields selection



$f_1 = 1\,,\ f_2 = 2\,,\ f_3 = 3\,,\ f_4 = 7$

before the development of molecular biology mutation was treated as a "deus ex machina"

1. Darwin's natural selection
2. **Mutation and selection**
3. A model for transitions
4. Cooperation tames competition
5. Effects of stochasticity
6. Scarcity is **not** the mother of invention!



DNA replication and mutation

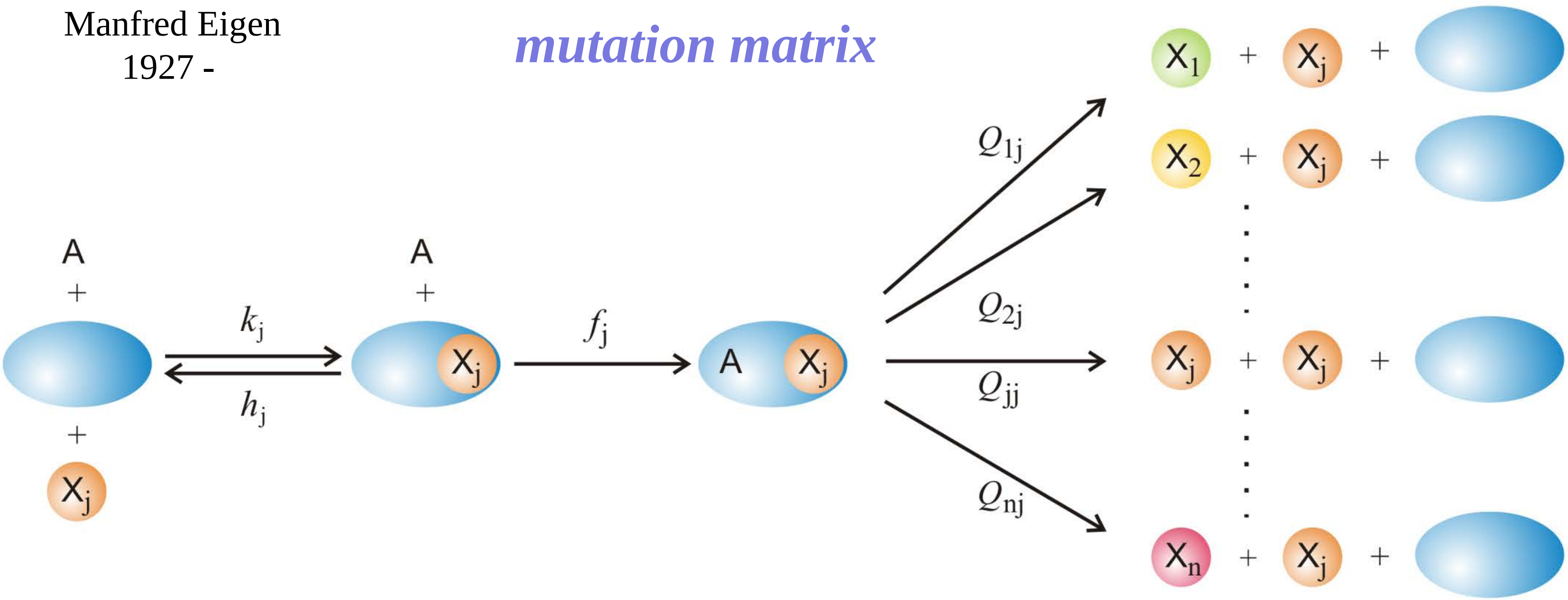
$$\frac{dx_j}{dt} = \sum_{i=1}^{n} W_{ji}\, x_i - x_j\, \Phi\,; \quad j = 1, 2, \dots, n$$

$$W_{ji} = Q_{ji} \cdot f_i\,, \quad \sum_{i=1}^{n} x_i = 1, \quad \Phi = \sum_{i=1}^{n} f_i\, x_i$$

fitness landscape

mutation matrix

Manfred Eigen
1927 -



Mutation and (correct) replication as parallel chemical reactions

M. Eigen. 1971. *Naturwissenschaften* 58:465,
M. Eigen & P. Schuster.1977-78. *Naturwissenschaften* 64:541, 65:7 und 65:341

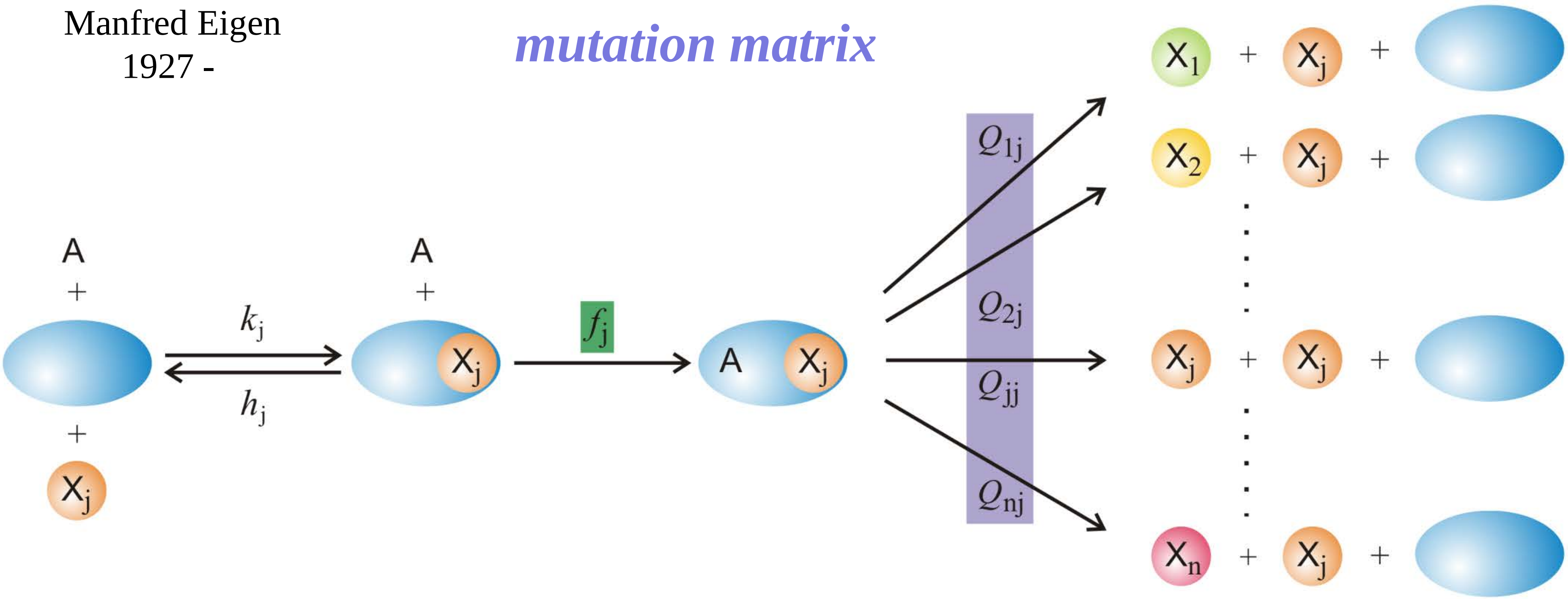
Manfred Eigen
1927 -

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = \sum_{i=1}^{n} W_{ji}\, x_i - x_j\, \Phi\,; \quad j = 1, 2, \ldots, n$$

$$W_{ji} = Q_{ji} \cdot f_i\,, \quad \sum_{i=1}^{n} x_i = 1, \quad \Phi = \sum_{i=1}^{n} f_i\, x_i$$

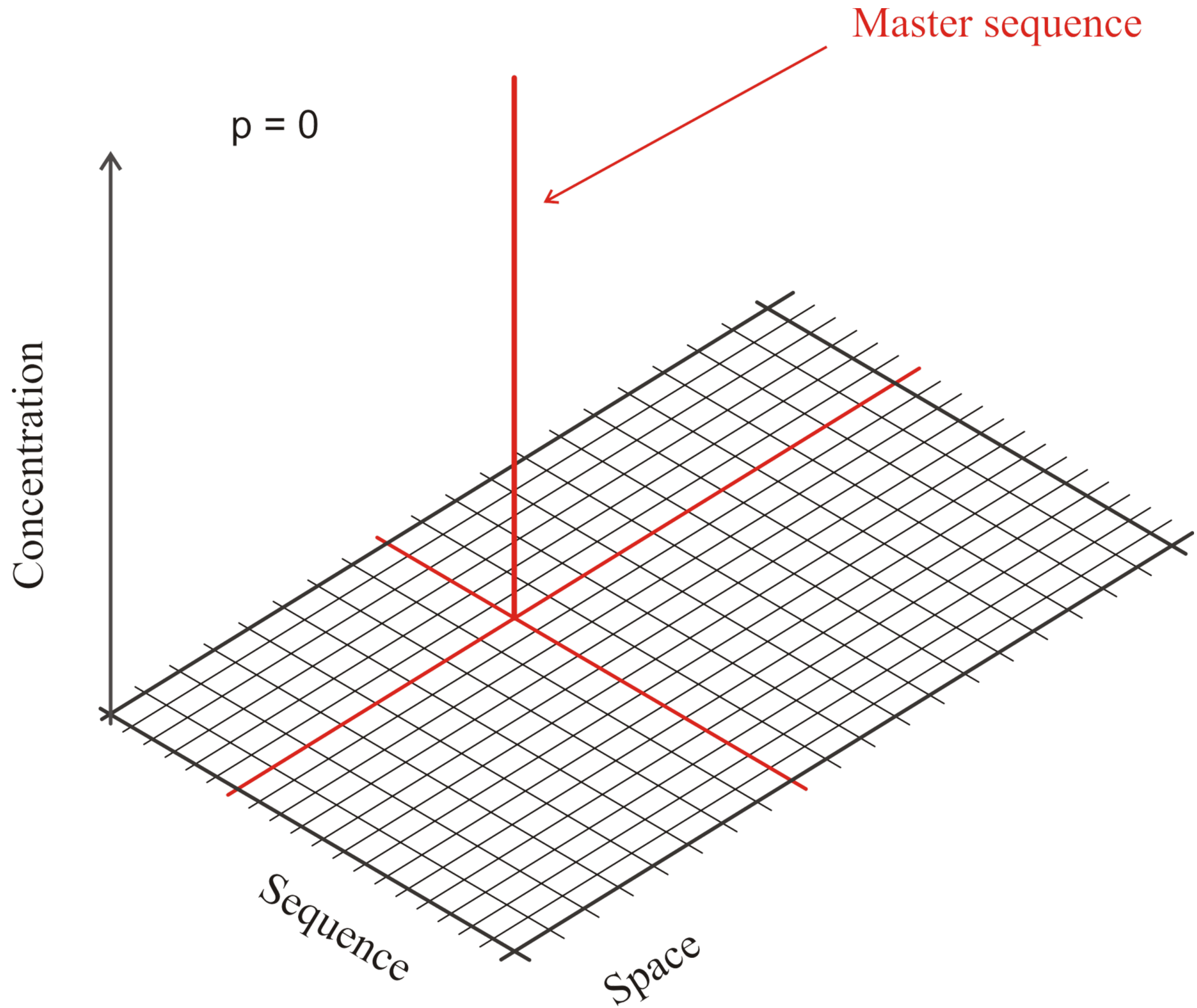
fitness landscape

mutation matrix

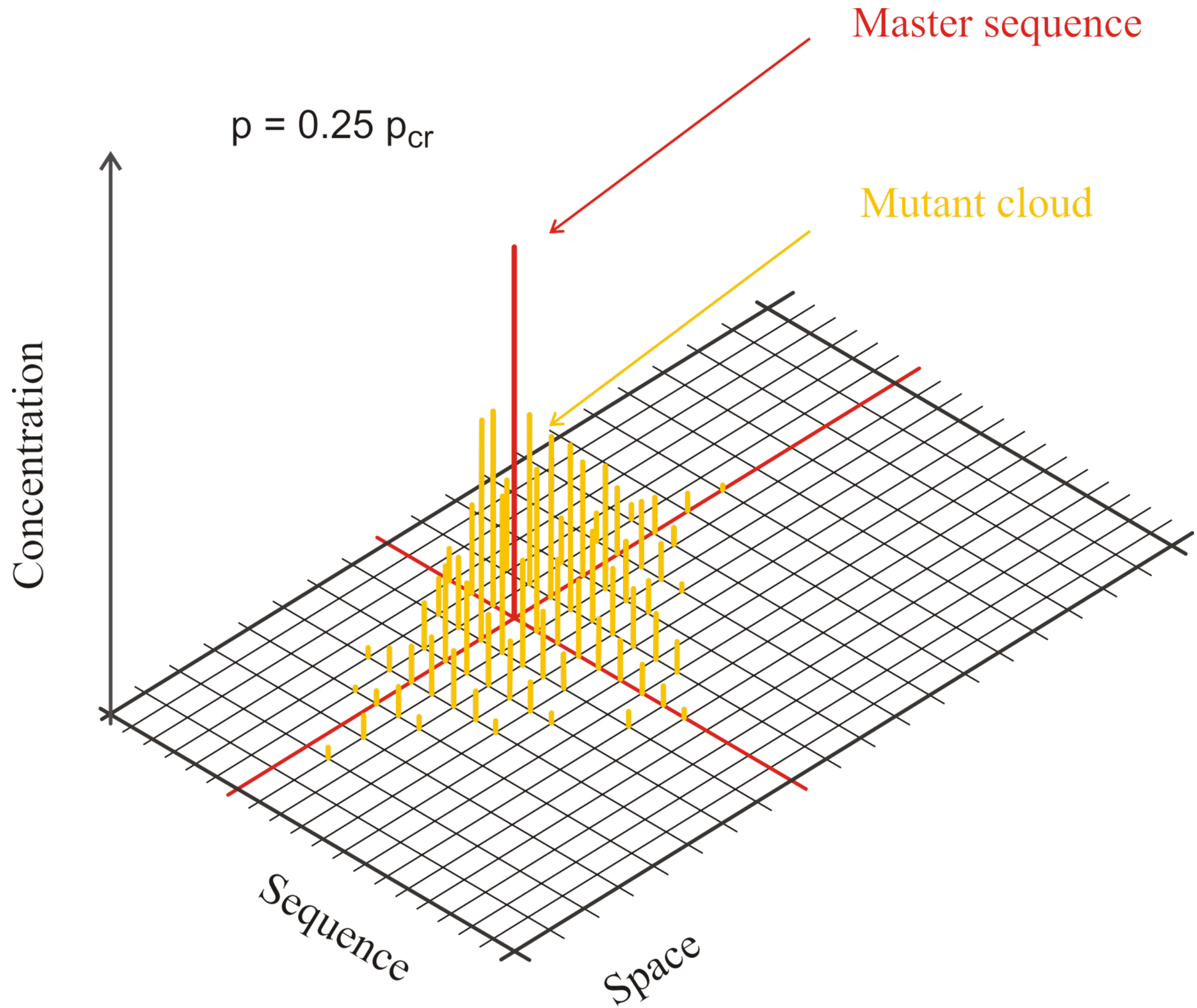


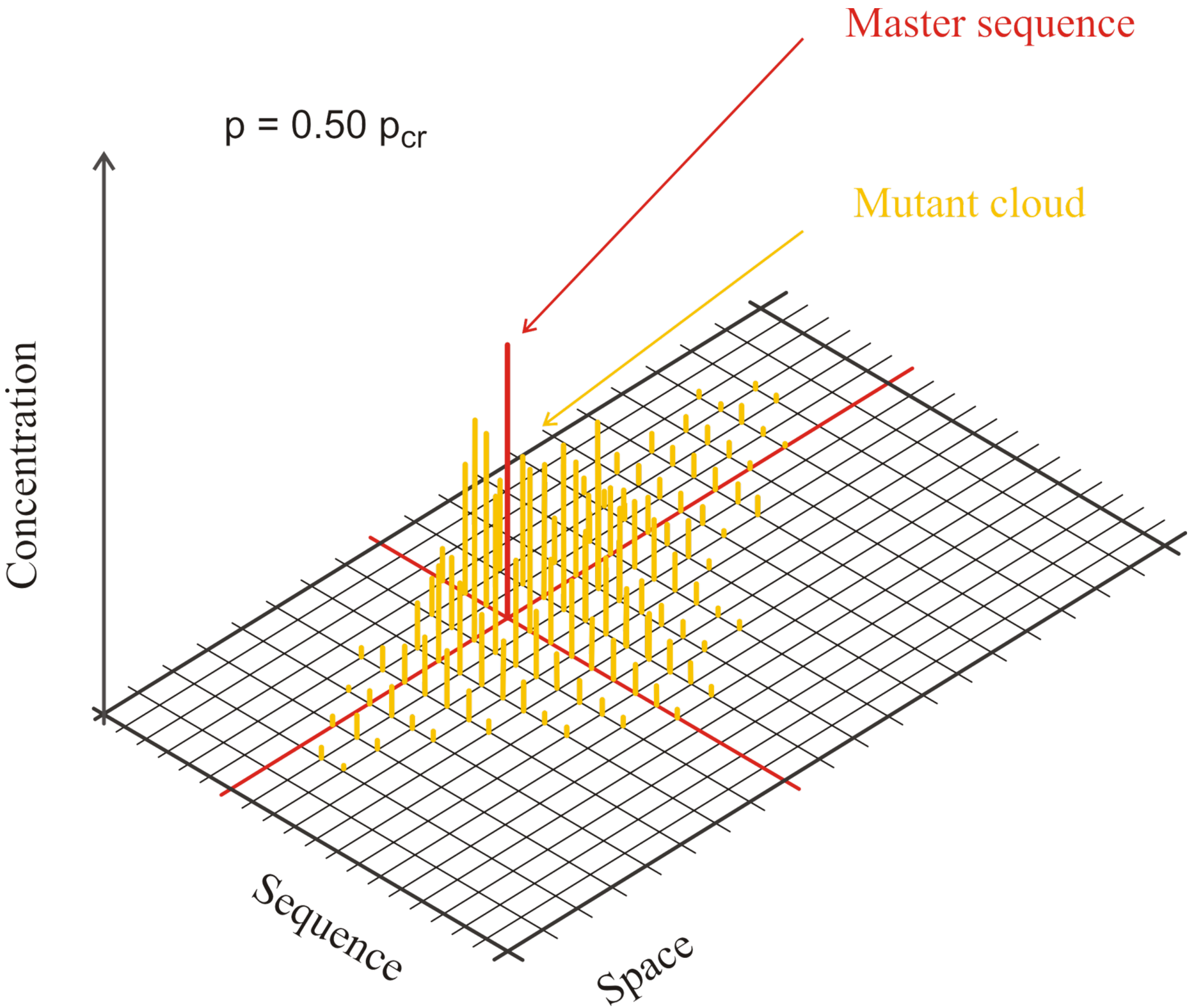
Mutation and (correct) replication as parallel chemical reactions

M. Eigen. 1971. *Naturwissenschaften* 58:465,
M. Eigen & P. Schuster.1977-78. *Naturwissenschaften* 64:541, 65:7 und 65:341

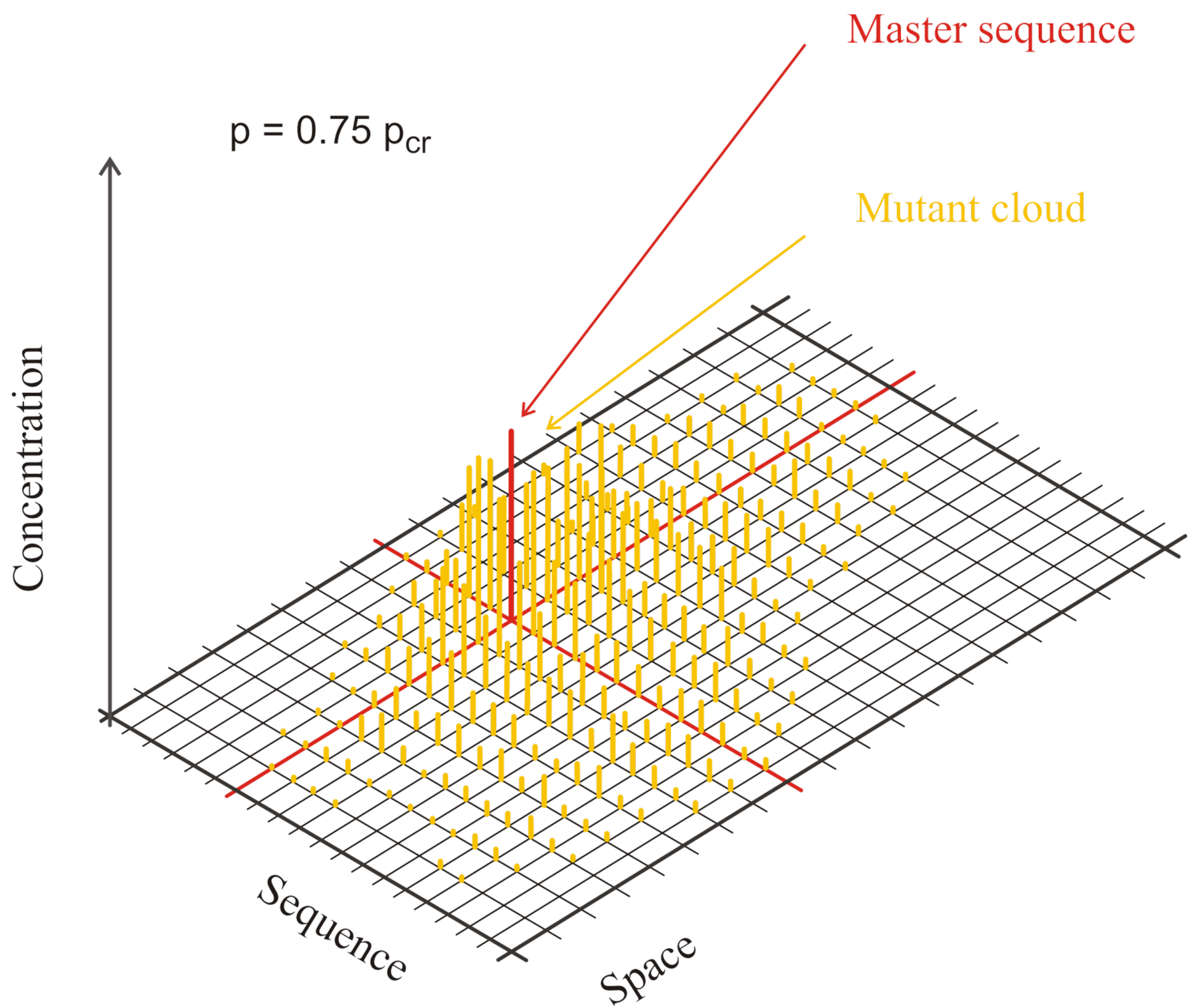


Master sequence
p = 0
Concentration
Sequence
Space

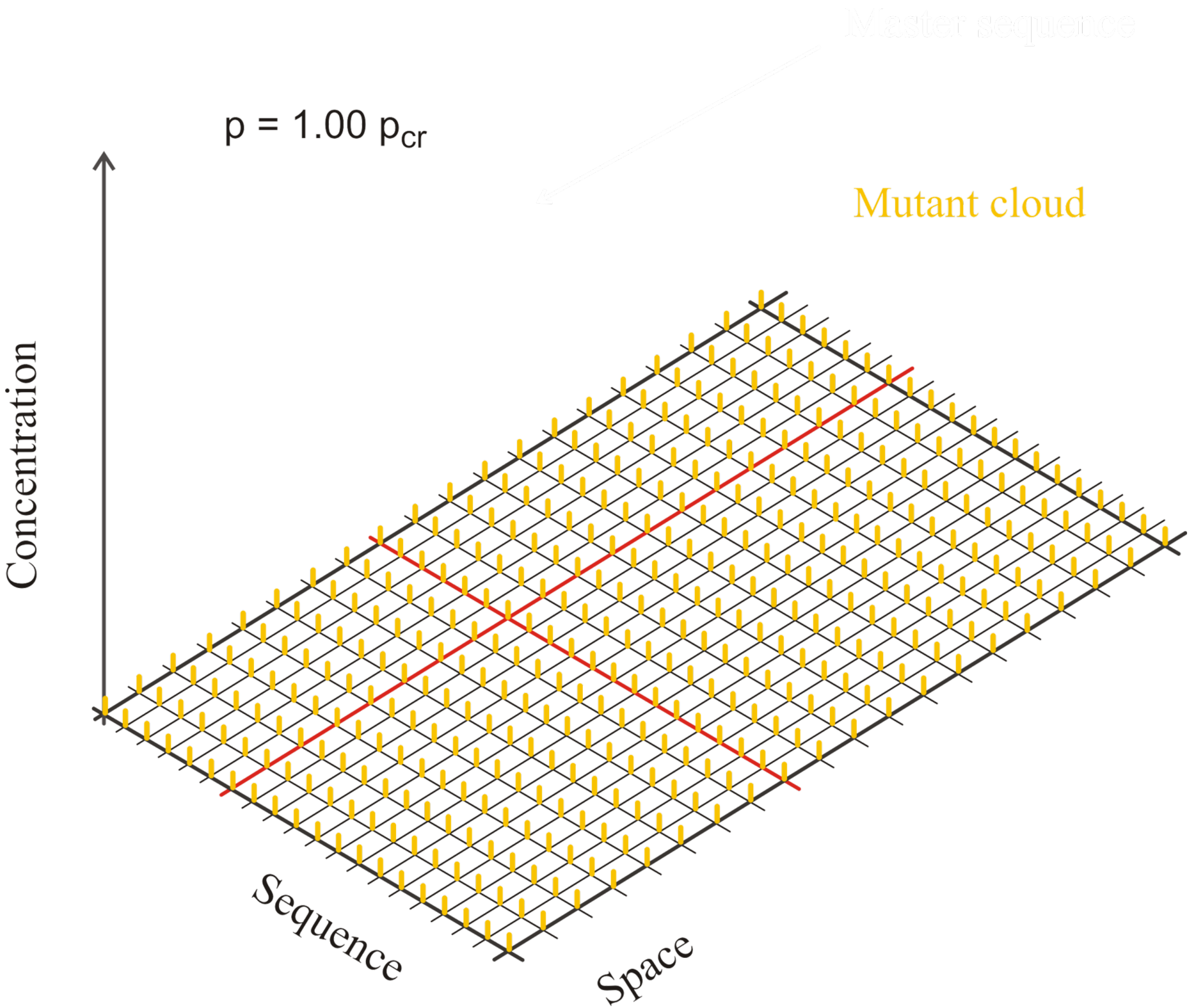

Master sequence
p = 0.25 p_{cr}
Mutant cloud
Concentration
Sequence
Space



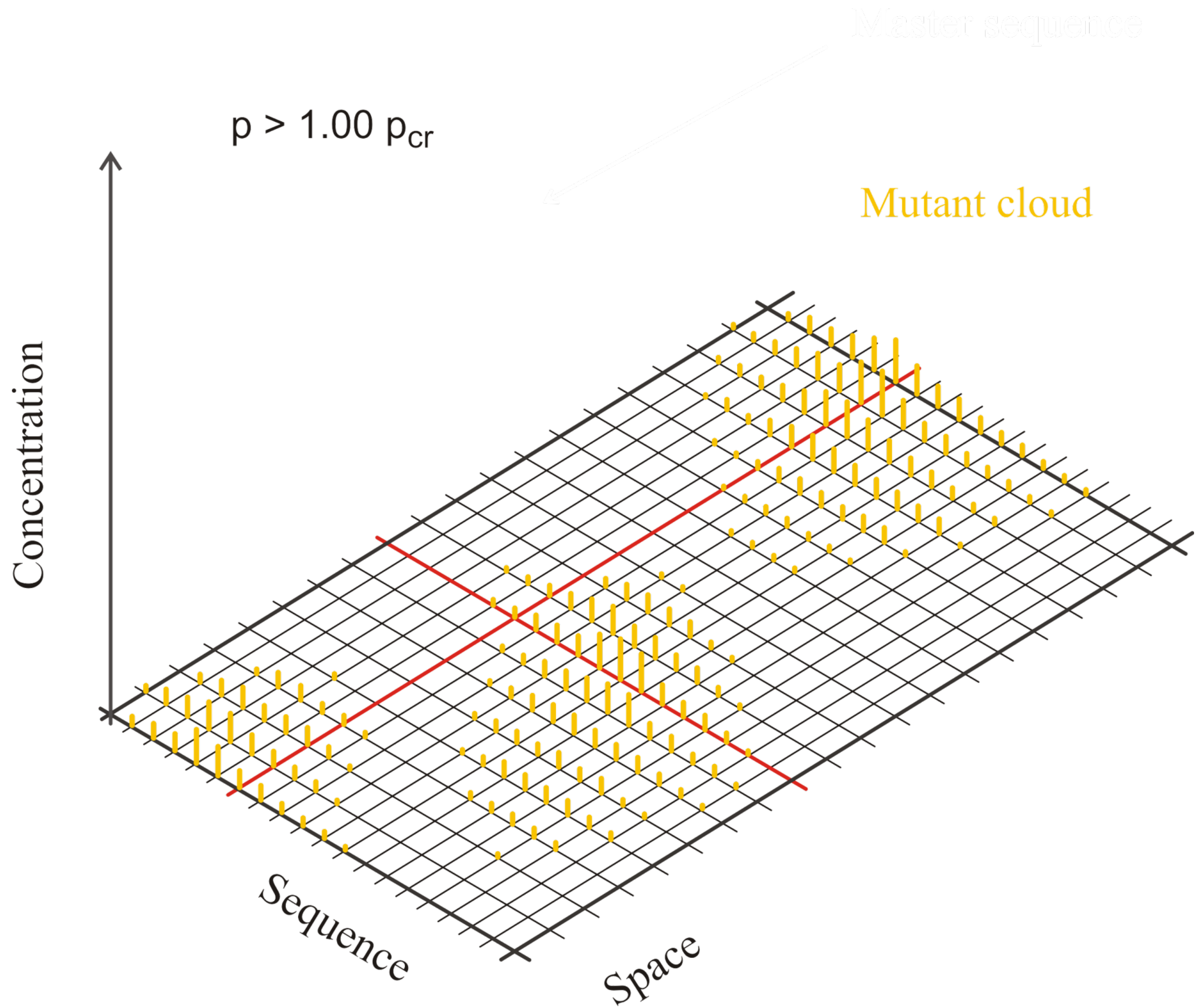
Master sequence
$p = 0.50\ p_{cr}$
Mutant cloud
Concentration
Sequence
Space



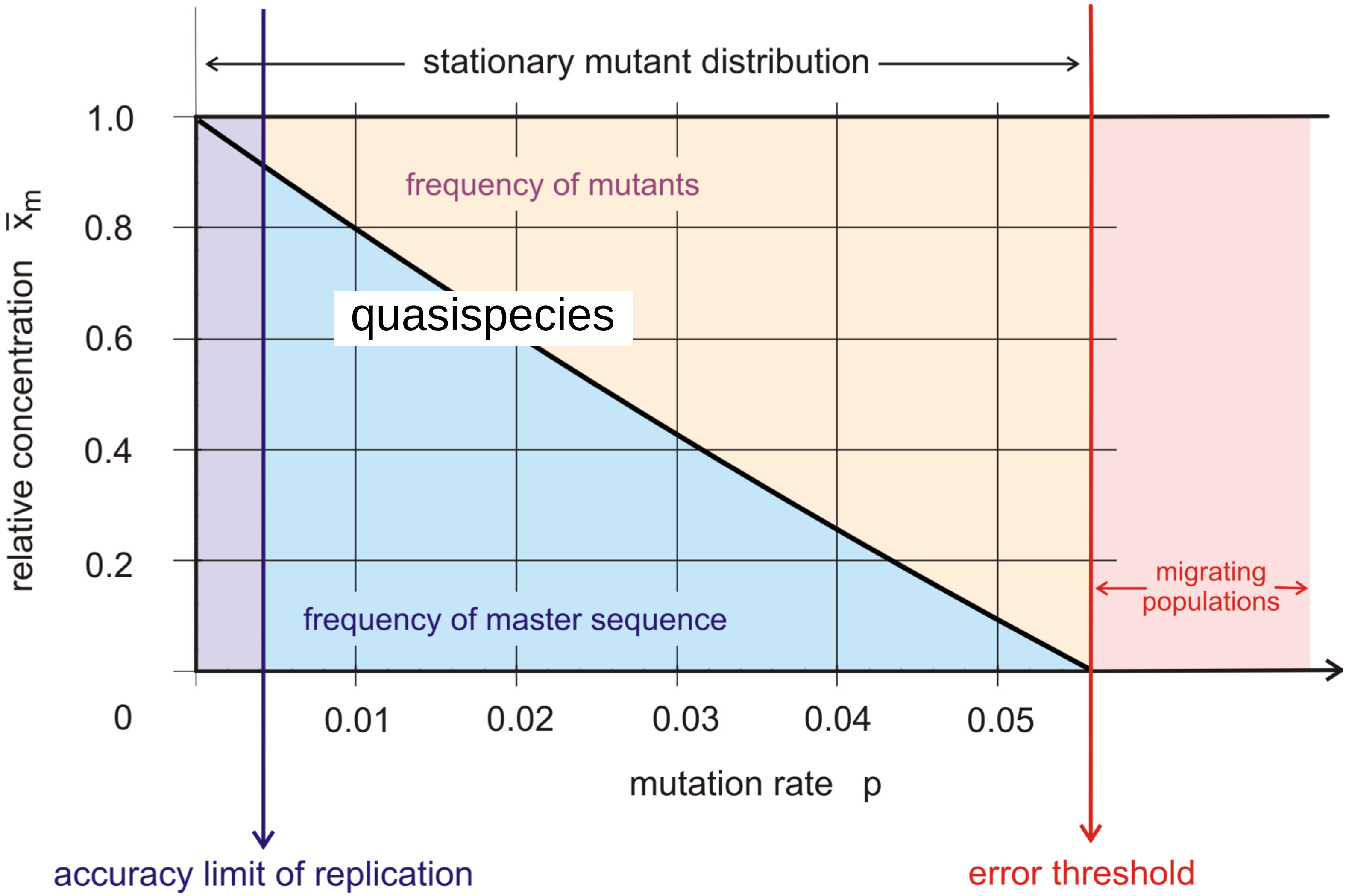
Master sequence
Mutant cloud
$p = 0.75\ p_{cr}$
Concentration
Sequence
Space



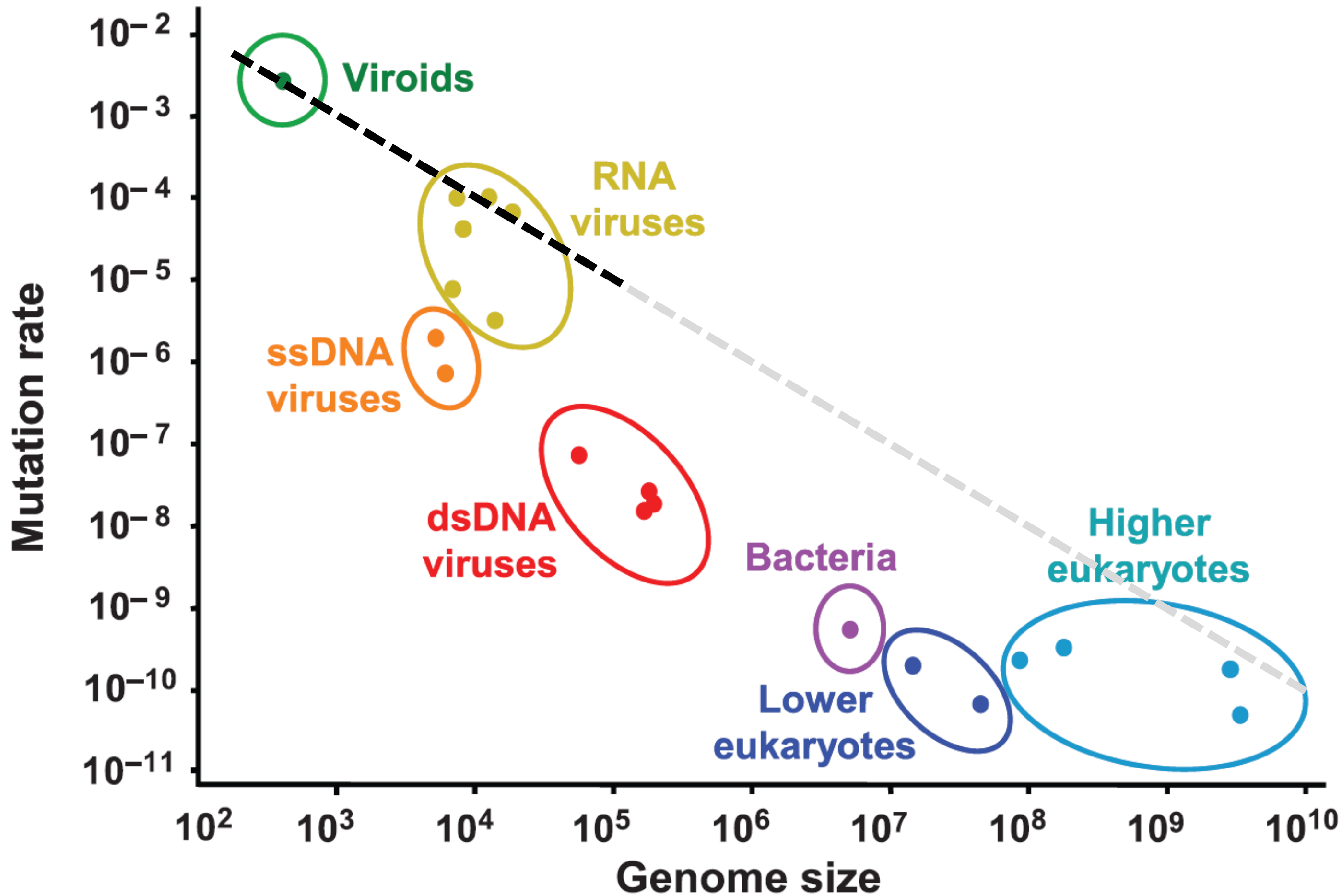
Master sequence
p = 1.00 p_{cr}
Mutant cloud
Concentration
Sequence
Space



Master sequence
p > 1.00 p_cr
Mutant cloud
Concentration
Sequence
Space



The error threshold in replication and mutation



Selma Gago, Santiago F. Elena, Ricardo Flores, Rafael Sanjuán. 2009. Extremely high mutation rate of a hammerhead viroid. Science 323:1308.

Mutation rate and genome size

replicating molecules	⇒	populations in compartments
independent replicators	⇒	chromosomes
RNA	⇒	DNA
prokaryotes	⇒	eukaryotes
asexual clones	⇒	sexual clones
protists	⇒	animals, plants, fungi
solitary individuals	⇒	colonies
primate societies	⇒	human societies

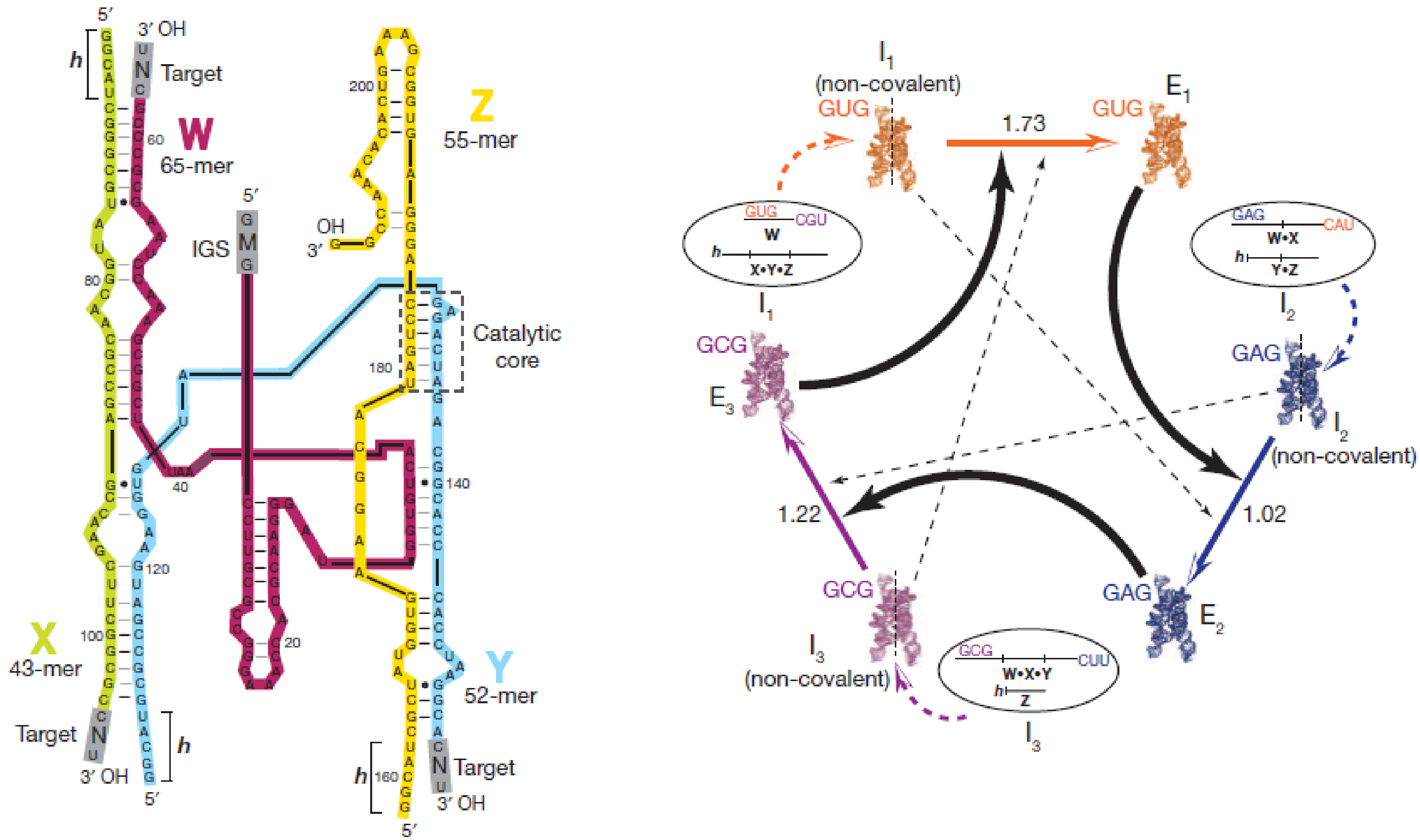
Eörs Szathmáry, John Maynard Smith. The major evolutionary transitions. Nature 374:227-232, 1995

John Maynard Smith, Eörs Szathmáry. The major transitions in evolution. Oxford University Press, New York 1995

Consequences of the error threshold phenomenon

Replicase ribozymes are not accurate enough for faithful replication of RNA molecules of its own lengths.

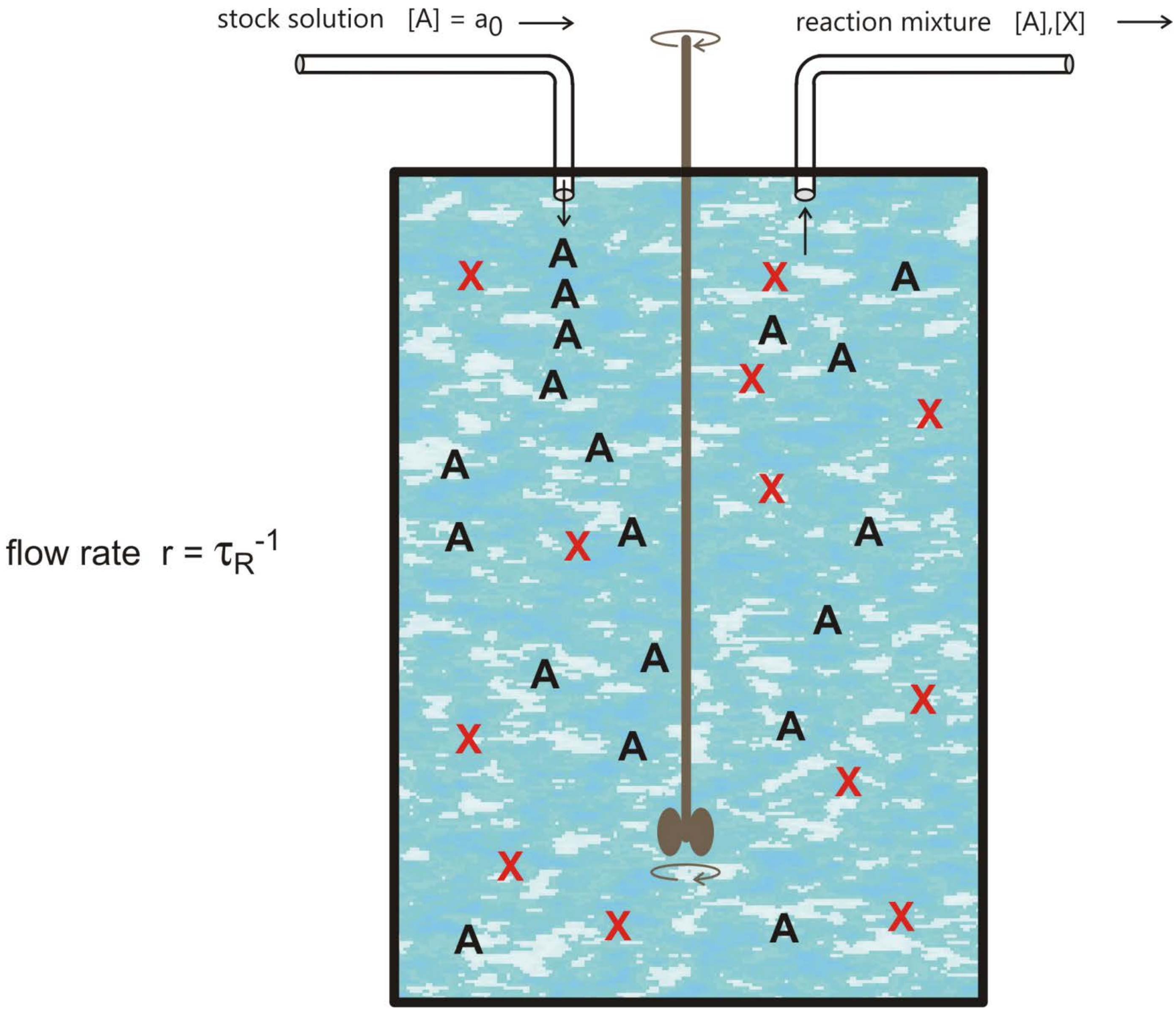
Cooperation of two or more RNA molecules is required



Nilesh Vaidya, Michael L. Manapar, Irene A. Chen, Ramon Xulvi_Brunet, Eric J. Hayden and Niles Lehman. Spontaneous network formation among cooperative RNA replicators. Nature 491:73-77, 2012

Cooperative RNA replicators

1. Darwin's natural selection
2. Mutation and selection
3. **A model for transitions**
4. Cooperation tames competition
5. Effects of stochasticity
6. Scarcity is **not** the mother of invention!



The continuously fed stirred tank reactor (CFSTR)

$$\star \xrightarrow{a_0 \cdot r} \mathbf{A}$$

$$\mathbf{A} + \mathbf{X}_j \xrightarrow{f_j} 2\,\mathbf{X}_j\,, \;\; j = 1, \ldots, n$$

$$\mathbf{A} + \mathbf{X}_j + \mathbf{X}_i \xrightarrow{k_{ji}} 2\,\mathbf{X}_j + \mathbf{X}_i\,; \;\; i, j = 1, \ldots, n$$

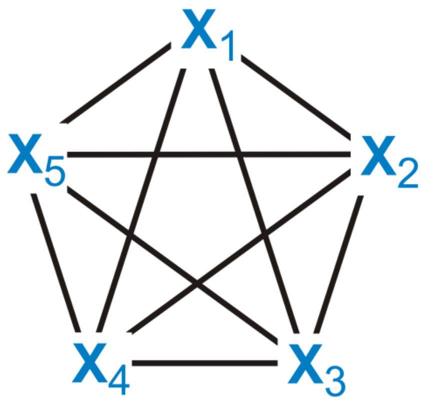
$$\mathbf{A} \xrightarrow{r} \varnothing$$

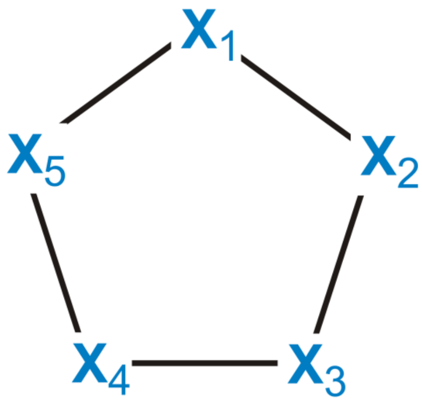
$$\mathbf{X}_j \xrightarrow{r} \varnothing\,, \;\; j = 1, \ldots, n$$

Toy model for the analysis of competition and cooperation

$$\mathbf{A} + \mathbf{X}_j + \mathbf{X}_i \xrightarrow{k_{ji}} 2\,\mathbf{X}_j + \mathbf{X}_i\,;\ i,j = 1,\ldots,n$$

n^2 catalytic terms





$$\mathbf{X}_n \Leftarrow \mathbf{X}_1 \Leftarrow \mathbf{X}_2 \Leftarrow \cdots \Leftarrow \mathbf{X}_{n-1} \Leftarrow \mathbf{X}_n$$

$$\mathbf{A} + \mathbf{X}_j + \mathbf{X}_{j+1} \xrightarrow{k_j} 2\,\mathbf{X}_j + \mathbf{X}_{j+1}\,;\; j = 1, \ldots, n\,,\; j \bmod n$$

n catalytic terms

$$\begin{aligned}
\star \quad &\xrightarrow{a_0 \cdot r} \quad \mathbf{A} \\
\mathbf{A} + \mathbf{X}_j \quad &\xrightarrow{f_j} \quad 2\,\mathbf{X}_j\,,\ j = 1, \ldots, n \\
\mathbf{A} + \mathbf{X}_j + \mathbf{X}_{j+1} \quad &\xrightarrow{k_j} \quad 2\,\mathbf{X}_j + \mathbf{X}_{j+1}\,;\ j = 1, \ldots, n\,,\ j \bmod n \\
\mathbf{A} \quad &\xrightarrow{r} \quad \varnothing \\
\mathbf{X}_j \quad &\xrightarrow{r} \quad \varnothing\,,\ j = 1, \ldots, n
\end{aligned}$$

Toy model for the analysis of competition and cooperation

$$[\mathbf{A}] = a \quad \text{and} \quad [\mathbf{X}_j] = x_j\,;\ j = 1,\ldots,n$$

$$\frac{\mathrm{d}a}{\mathrm{d}t} = -a\left(\sum_{j=1}^{n}(f_j + k_j x_{j+1})x_j + r\right) + a_0\, r$$

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = x_j\left((f_j + k_j x_{j+1})a - r\right),\ j = 1,\ldots,n\,,\ j \bmod n$$

stationary solutions: $\bar{x}_j = 0 \quad \text{or} \quad (f_j + k_j \bar{x}_{j+1})\bar{a} - r = 0$

In case of compatibility and linear equations we obtain 2^n solution.

$f_2 > f_1$ and $k_2 < k_1$

increasing a_0-values

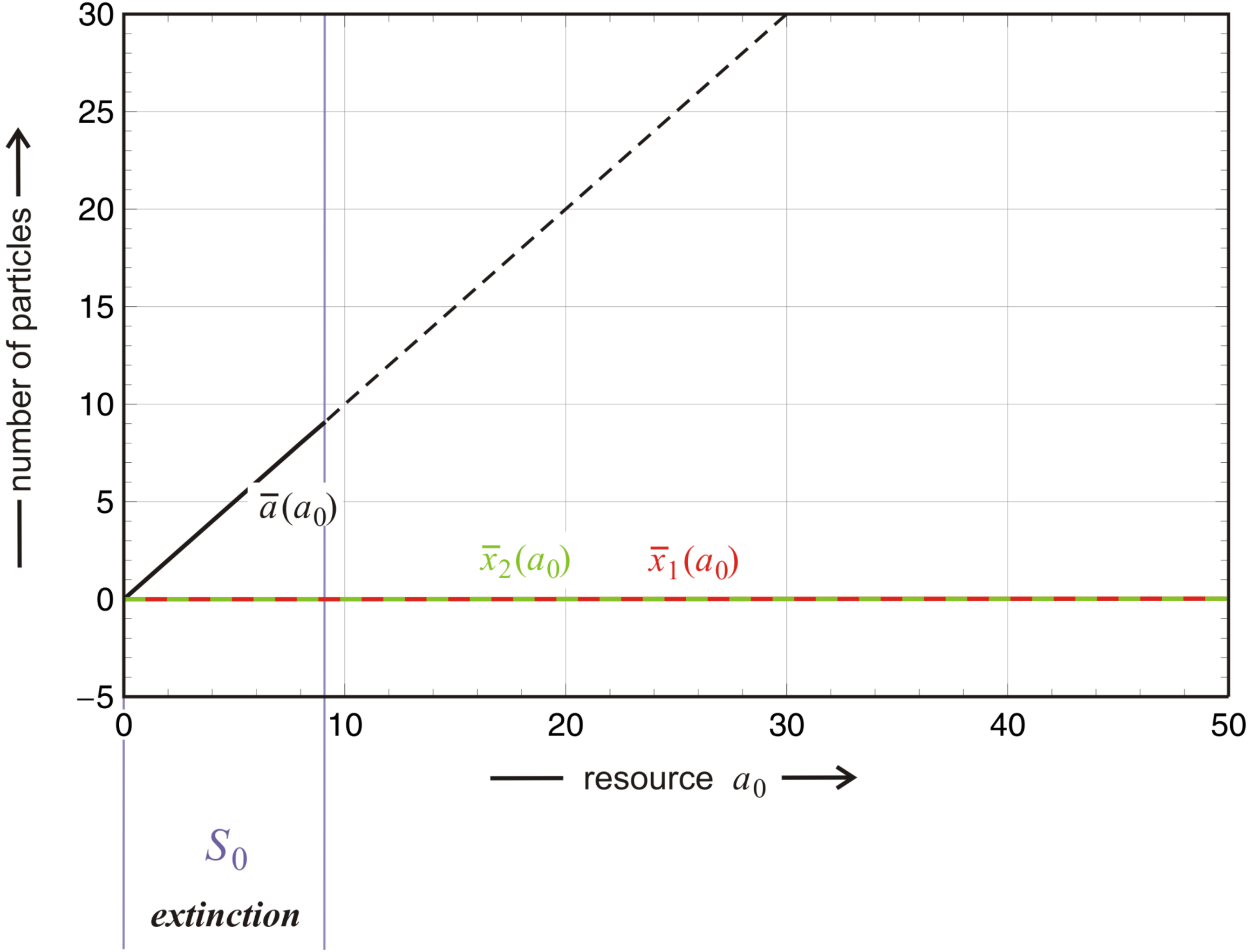
$S_0 \leftrightarrow S_1^{(3)}$

$S_1^{(3)} \leftrightarrow S_2$

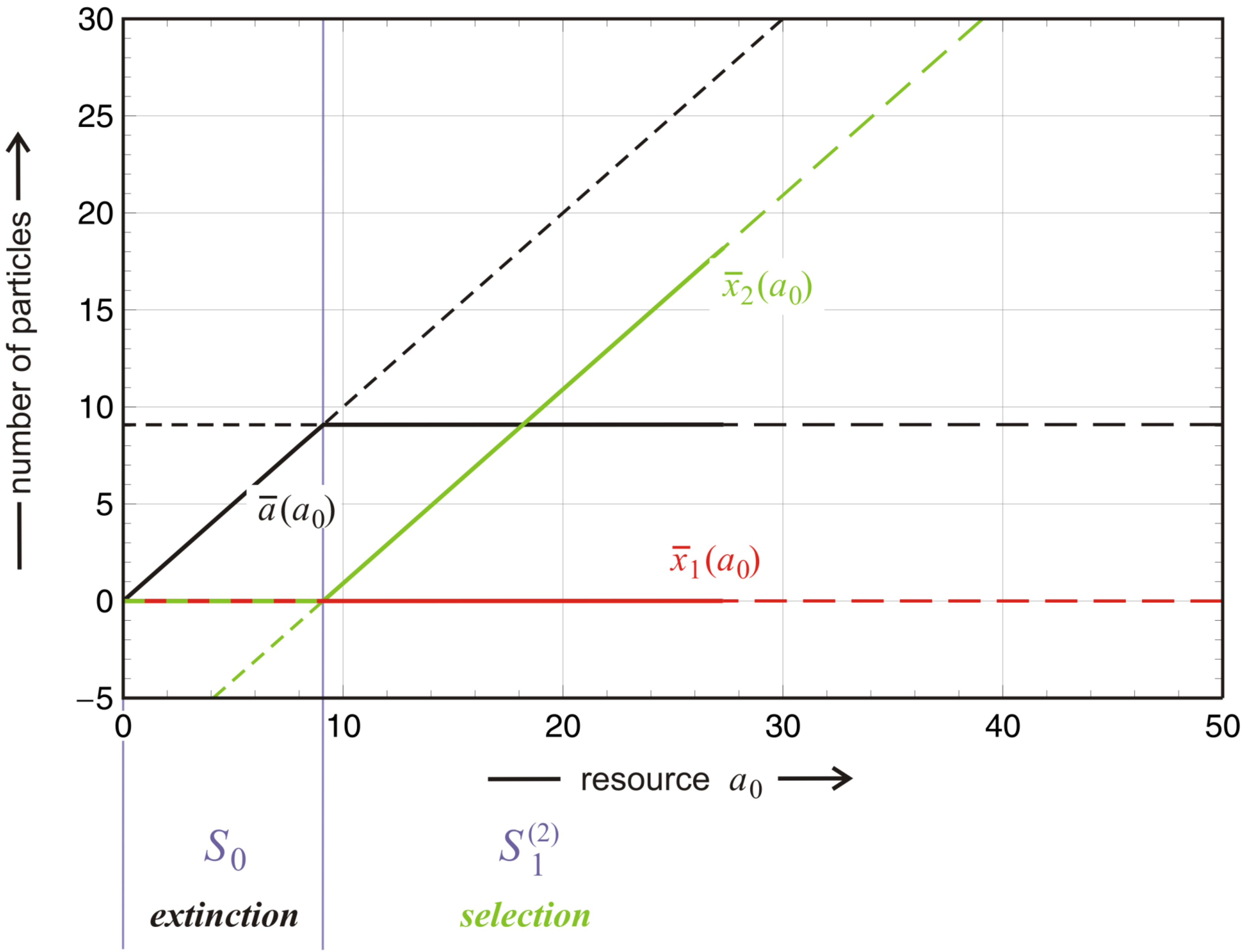
name	**symbol**	**stationary values** $\overline{a}$	$\overline{x}_1$	$\overline{x}_2$	**stability range**
extinction	S_0	a_0	0	0	$0 \leq a_0 \leq \frac{r}{f_2}$
selection	$S_1^{(2)}$	$\frac{r}{f_2}$	0	$a_0 - \frac{r}{f_2}$	$\frac{r}{f_2} \leq a_0 \leq \frac{r}{f_2} + \frac{f_2 - f_1}{k_1}$
cooperation	S_2	α	$\frac{r - f_2\alpha}{k_2\alpha}$	$\frac{r - f_1\alpha}{k_1\alpha}$	$\frac{r}{f_2} + \frac{f_2 - f_1}{k_1} \leq a_0$

$$\overline{a} = \alpha = \frac{1}{2}\left(a_0 + \psi - \sqrt{(a_0 + \psi)^2 - 4\,r\phi}\right) \qquad r \leq (a_0 + \psi)^2 \,/\, 4\phi$$

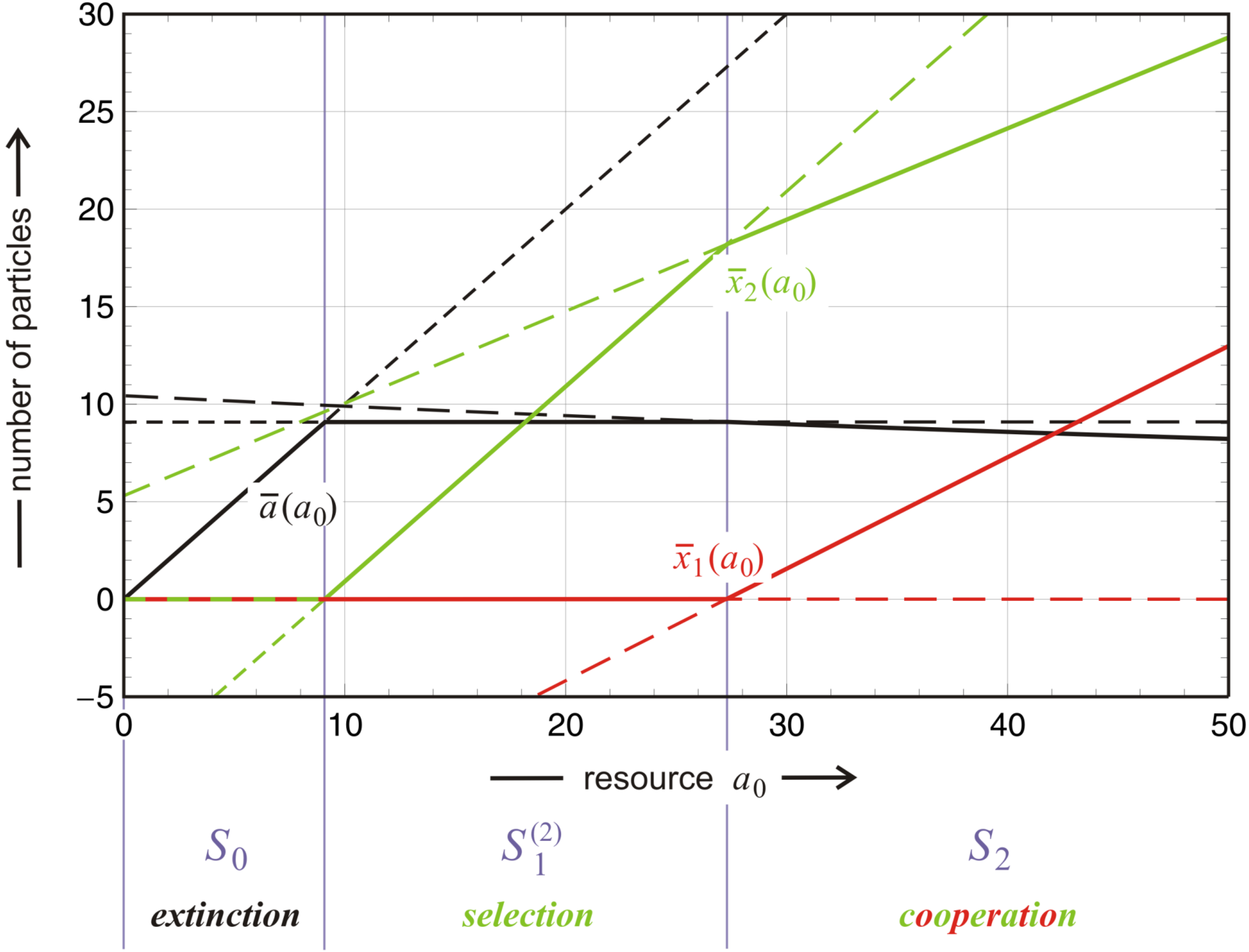
$$\psi = \sum_{i=1}^{n} \frac{f_i}{k_i} \quad \text{and} \quad \phi = \sum_{i=1}^{n} \frac{1}{k_i}$$



30
25
20
15
10
5
0
−5
0
10
20
30
40
50
number of particles
resource a_0
$\bar{a}(a_0)$
$\bar{x}_2(a_0)$
$\bar{x}_1(a_0)$
S_0
extinction



30
25
20
15
10
5
0
–5
0
10
20
30
40
50
number of particles
resource a_0
$\bar{x}_2(a_0)$
$\bar{a}(a_0)$
$\bar{x}_1(a_0)$
S_0
$S_1^{(2)}$
extinction
selection



30
25
20
15
10
5
0
−5
0
10
20
30
40
50
number of particles
resource a_0
$\bar{x}_2(a_0)$
$\bar{a}(a_0)$
$\bar{x}_1(a_0)$
S_0
$S_1^{(2)}$
S_2
extinction
selection
cooperation

$$f_3 > f_2 > f_1 \quad \text{and} \quad k_3 < k_2 < k_1$$

increasing a_0-values

name	symbol	stationary values				stability range
		$\bar{a}$	$\bar{x}_1$	$\bar{x}_2$	$\bar{x}_3$	
extinction	S_0	a_0	0	0	0	$0 \le a_0 \le \frac{r}{f_3}$
selection	$S_1^{(3)}$	$\frac{r}{f_3}$	0	0	$a_0 - \frac{r}{f_3}$	$\frac{r}{f_3} \le a_0 \le \frac{r}{f_3} + \frac{f_3 - f_2}{k_2}$
exclusion	$S_2^{(1)}$	$\frac{r}{f_3}$	0	$a_0 - \frac{r}{f_3} - \frac{f_3 - f_2}{k_2}$	$\frac{f_3 - f_2}{k_2}$	$\frac{r}{f_3} + \frac{f_3 - f_2}{k_2} \le a_0 \le \frac{r}{f_3} + \frac{f_3 - f_2}{k_2} + \frac{f_3 - f_1}{k_1}$
cooperation	S_3	α	$\frac{r - f_3\alpha}{k_3\alpha}$	$\frac{r - f_1\alpha}{k_1\alpha}$	$\frac{r - f_2\alpha}{k_2\alpha}$	$\frac{r}{f_3} + \frac{f_3 - f_2}{k_2} + \frac{f_3 - f_1}{k_1} \le a_0$

$$\bar{a} = \alpha = \frac{1}{2}\left(a_0 + \psi - \sqrt{(a_0 + \psi)^2 - 4\,r\phi}\right) \qquad r \le (a_0 + \psi)^2 \,/\, 4\phi$$

$$\psi = \sum_{i=1}^{n} \frac{f_i}{k_i} \quad \text{and} \quad \phi = \sum_{i=1}^{n} \frac{1}{k_i}$$

1. Darwin's natural selection

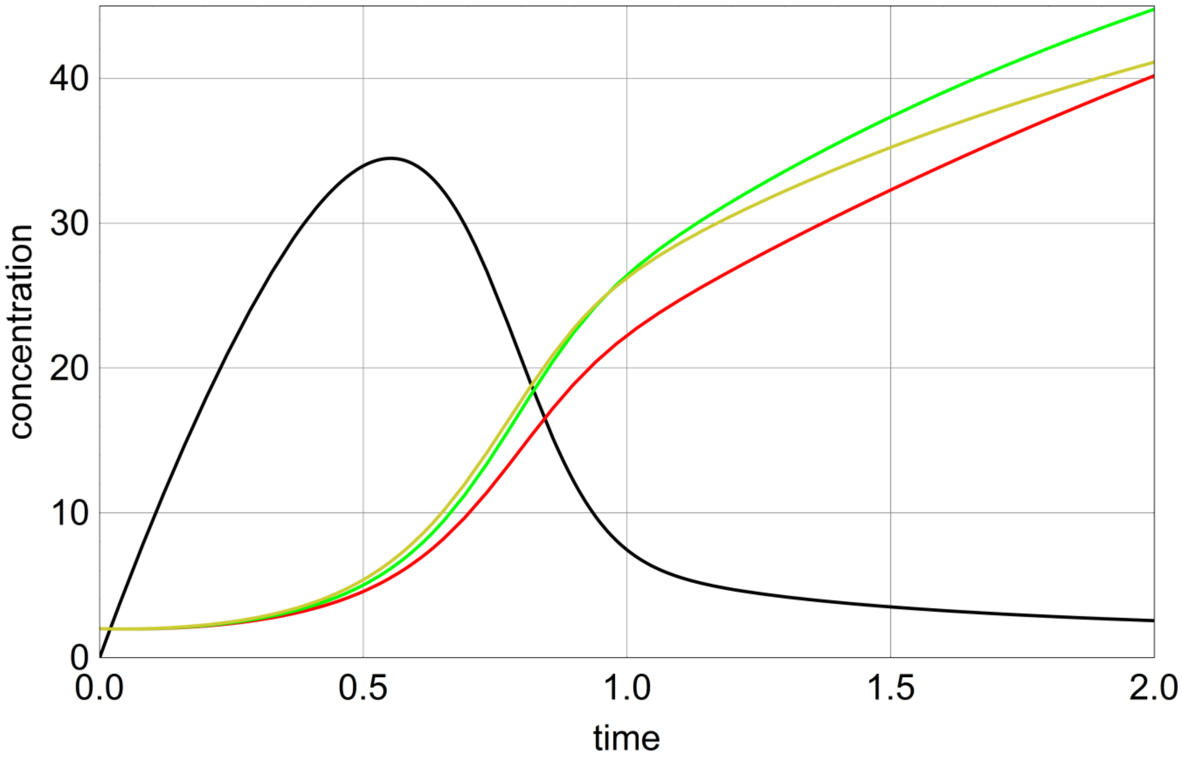
2. Mutation and selection

3. A model for transitions

4. **Cooperation tames competition**

5. Effects of stochasticity

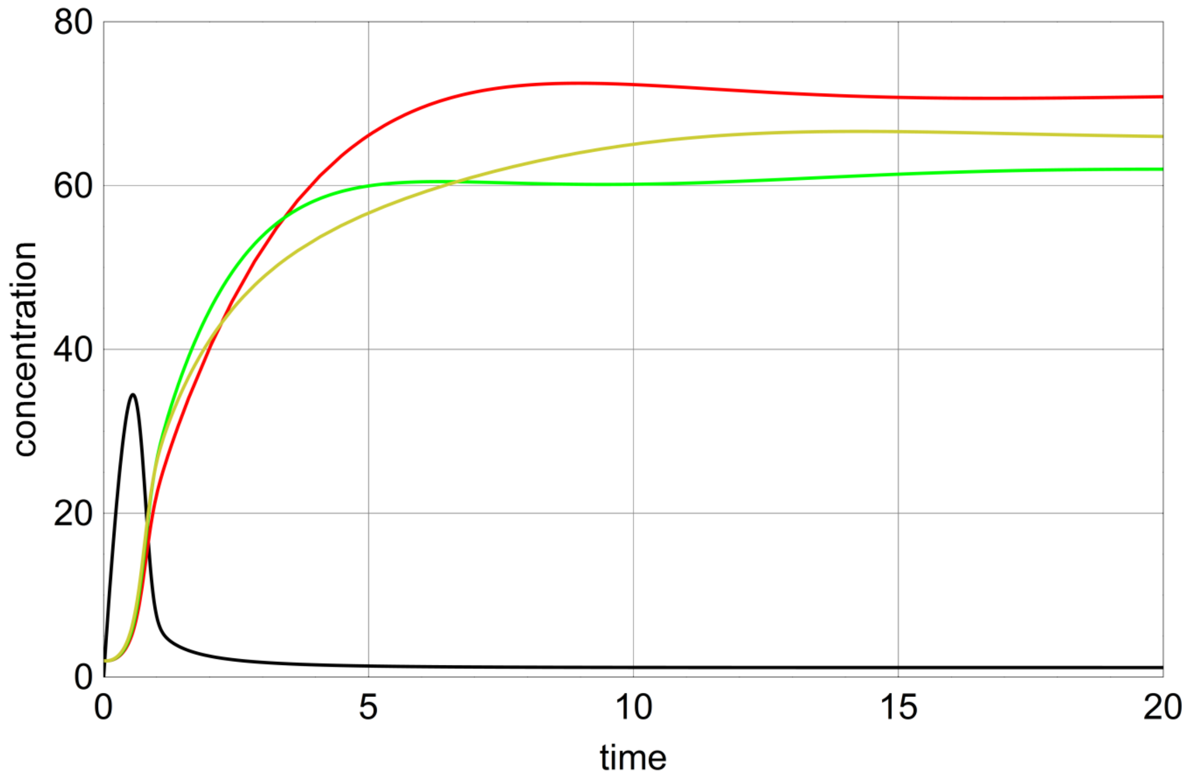
6. Scarcity is **not** the mother of invention!



$A(t)$, $X_1(t)$, $X_2(t)$, $X_3(t)$

phase of competition and selection

Competition and cooperation with $n = 3$

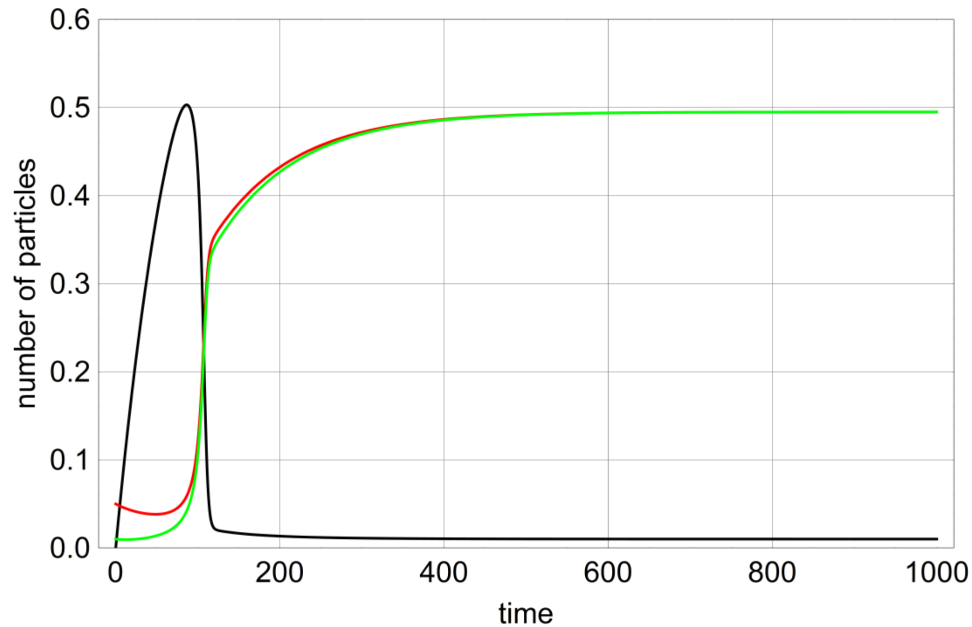


$A(t)$, $X_1(t)$, $X_2(t)$, $X_3(t)$

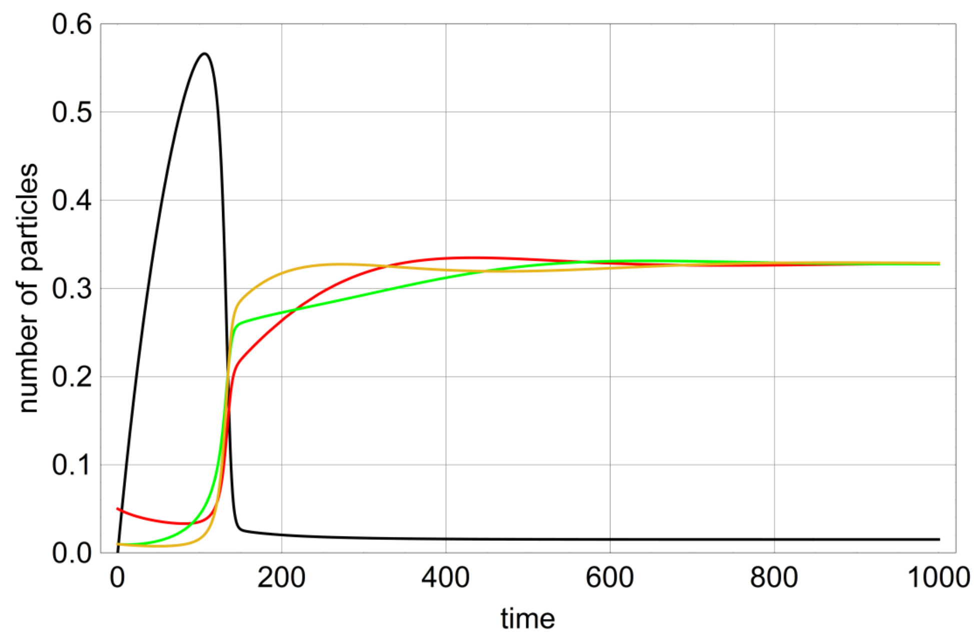
phase of cooperation

Competition and cooperation with $n = 3$

$n = 2$
$k_1 = k_2 = 2$, $r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.05$, $x_2(0) = 0.01$



$n = 3$
$k_1 = k_2 = k_3 = 2$, $r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.05$,
$x_2(0) = x_3(0) = 0.01$

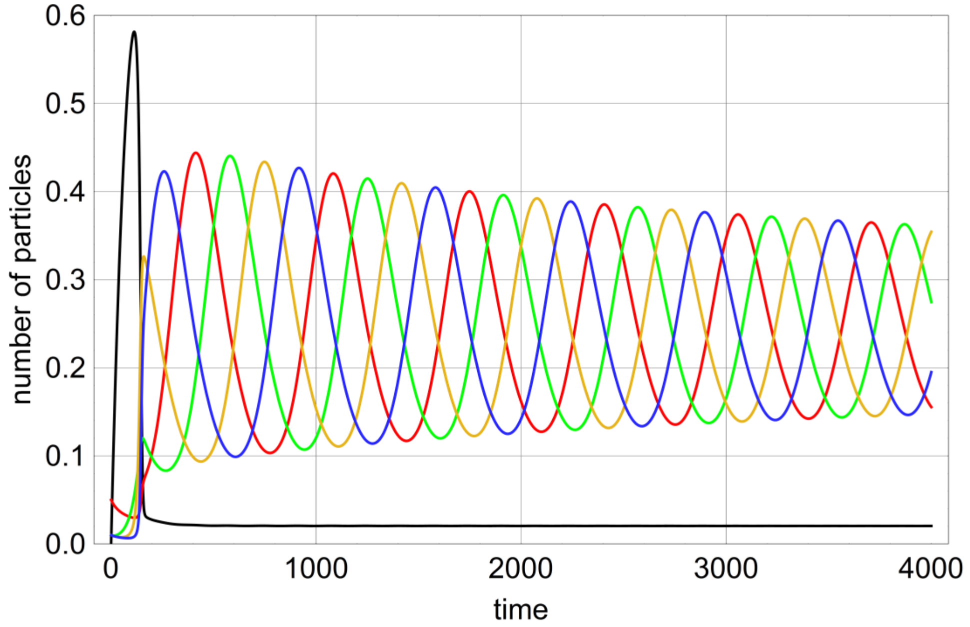


$n = 4$

$k_1 = k_2 = k_3 = k_4 = 2$, $r = 0.01$, $a_0 = 1$

$a(0) = 0$, $x_1(0) = 0.05$,

$x_2(0) = x_3(0) = x_4(0) = 0.01$



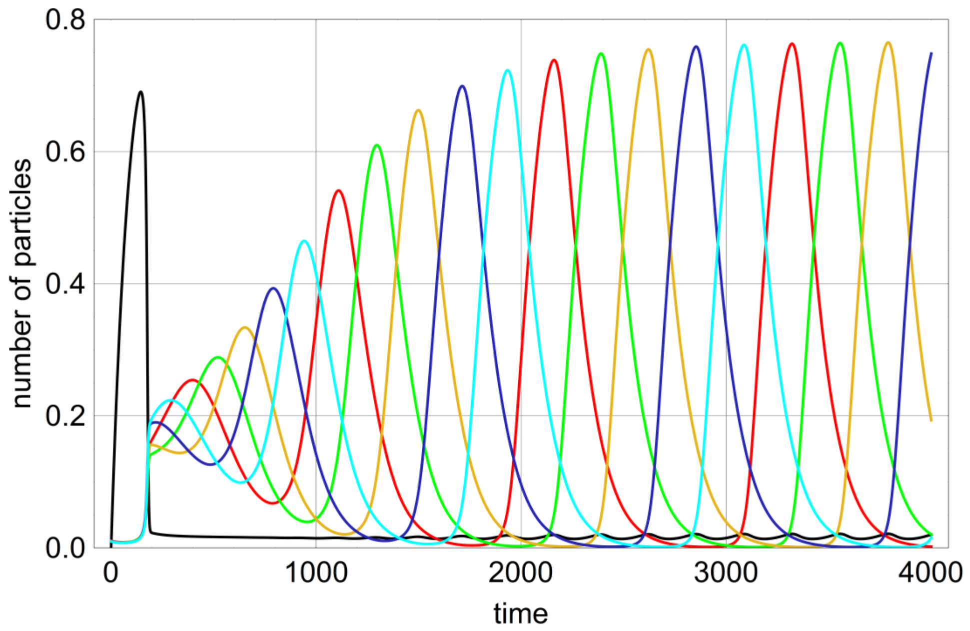
$n = 5$

$k_1 = k_2 = k_3 = k_4 = k_5 = 3$,

$r = 0.01$, $a_0 = 1$

$a(0) = 0$, $x_1(0) = 0.011$,

$x_2(0) = x_3(0) = x_4(0) = x_5(0) = 0.01$



1. Darwin's natural selection

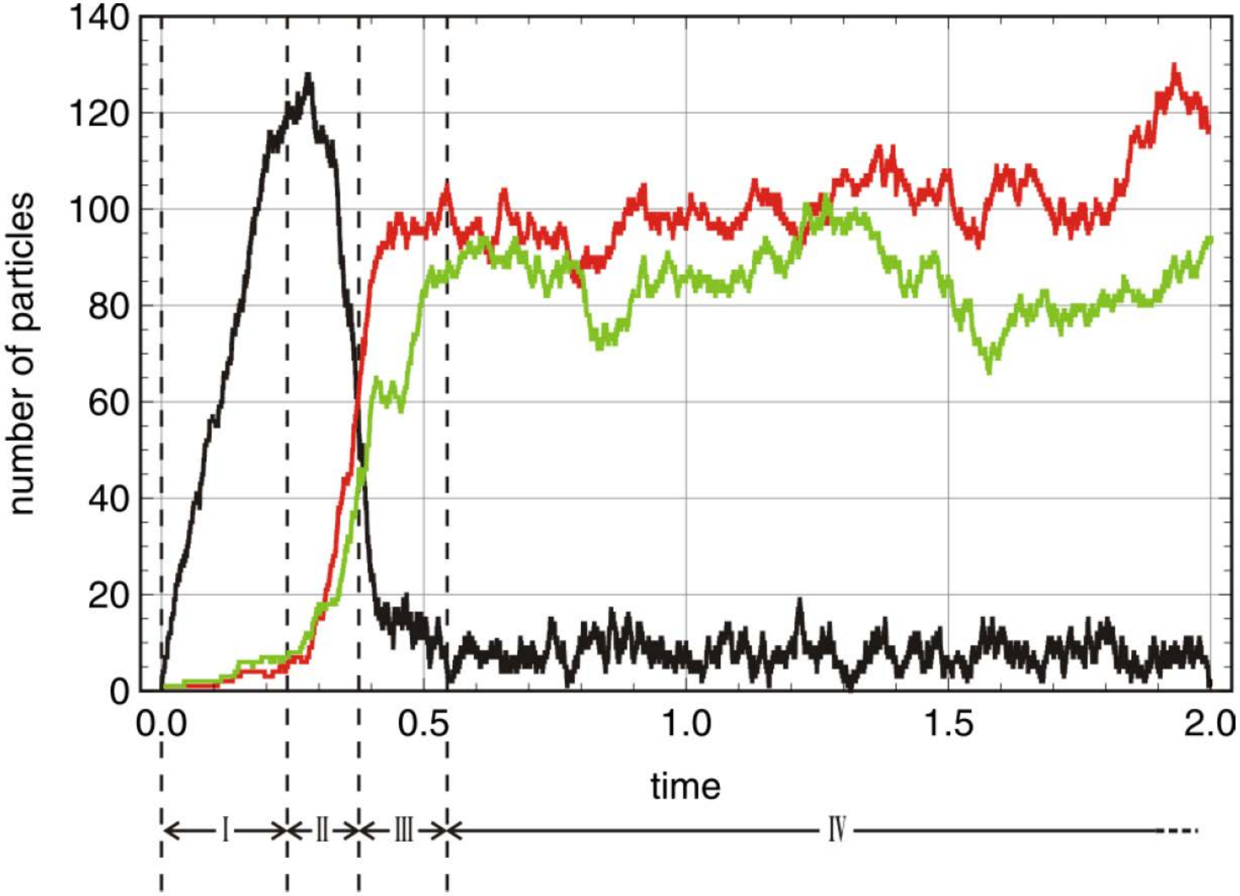
2. Mutation and selection

3. A model for transitions

4. Cooperation tames competition

5. **Effects of stochasticity**

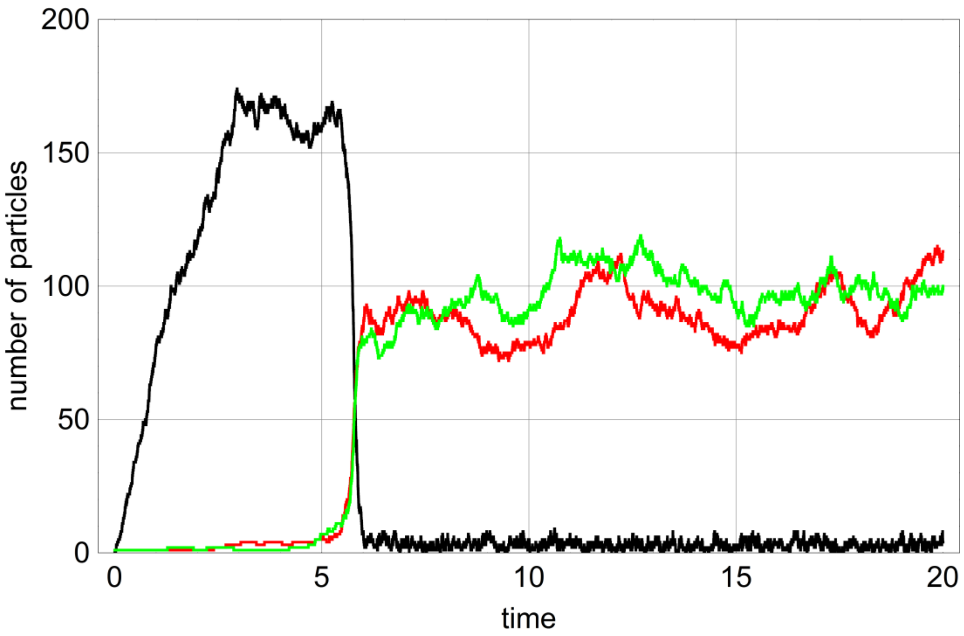
6. Scarcity is **not** the mother of invention!



phases of stochastic cooperation with n = 2

Initial values		Probability of extinction
$X_1(0)$	$X_2(0)$	$P(S_0)$
1	1	0.71741 ± 0.00402
2	2	0.29879 ± 0.00461
3	3	0.08599 ± 0.00272
4	4	0.01951 ± 0.00129
5	5	0.00360 ± 0.00038

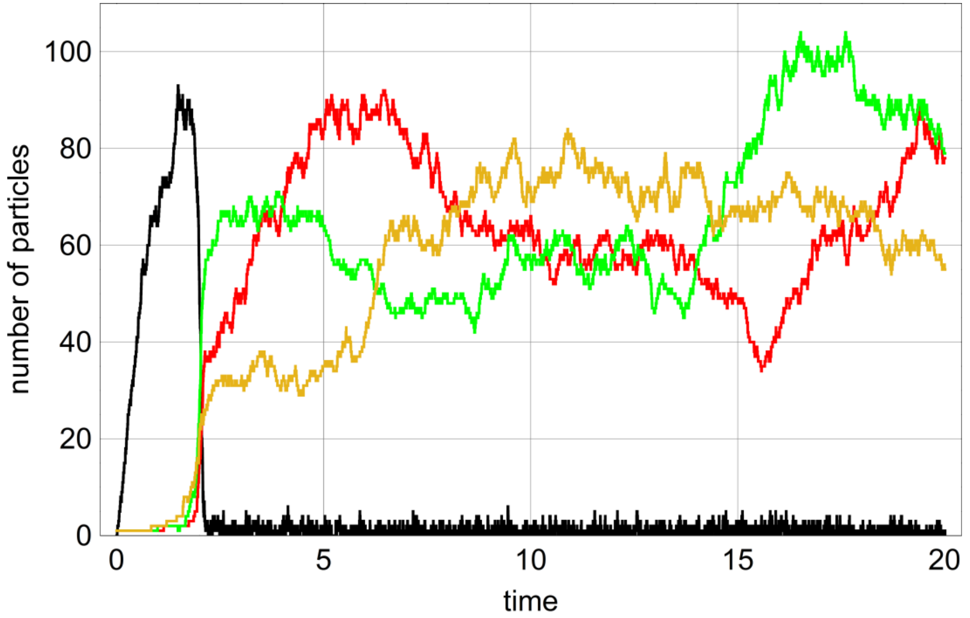
$k_1 = k_2 = 0.01$ [$M^{-1}t^{-1}$]



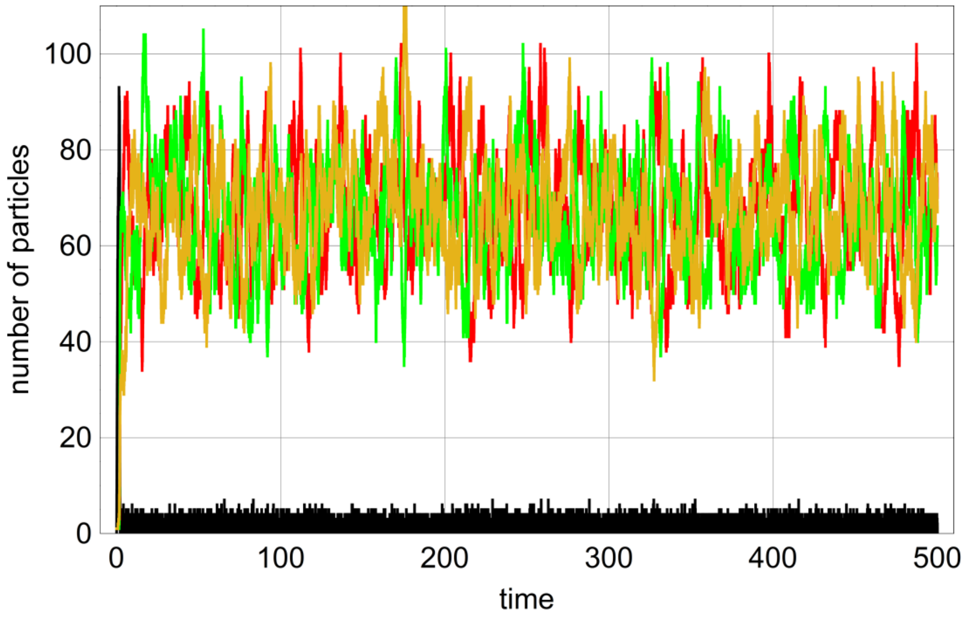
$k_1 = k_2 = 0.002$ [$M^{-1}t^{-1}$]

Choice of other parameters: $a_0 = 200$; $r = 0.5$ [Vt^{-1}]

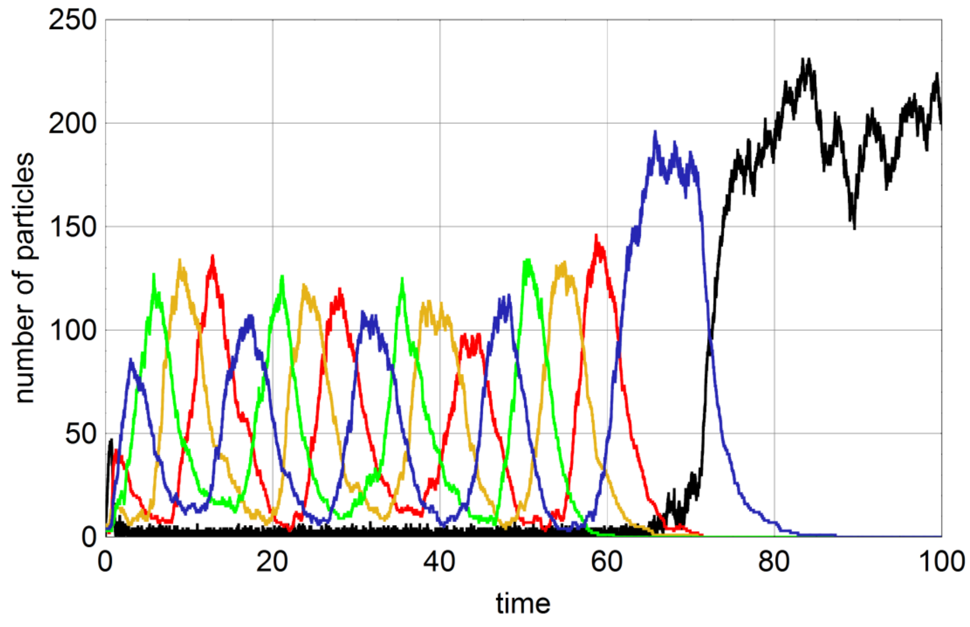
stochastic cooperation with $n = 2$



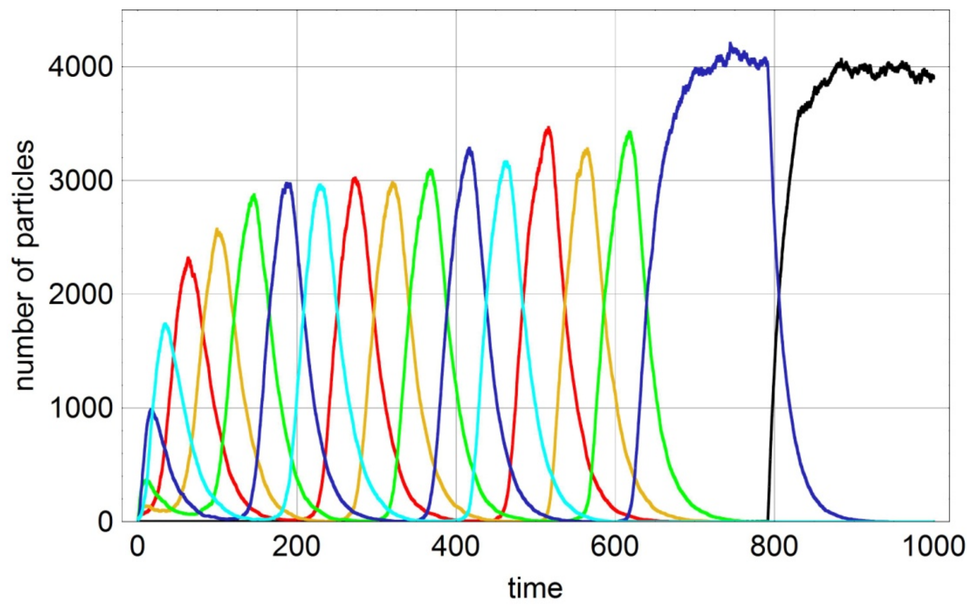
stochastic hypercycles with $n = 3$

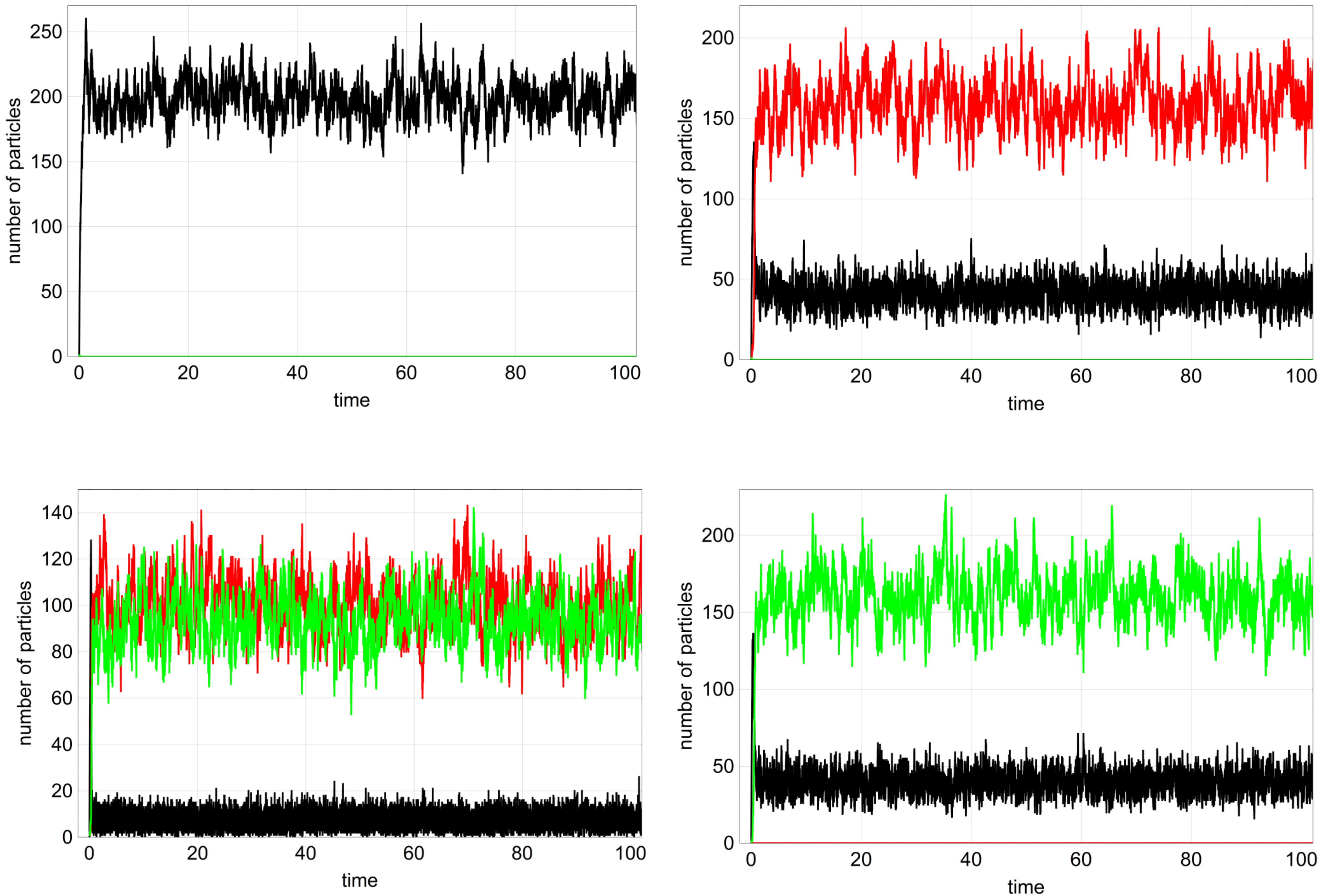


stochastic hypercycles with $n = 4$

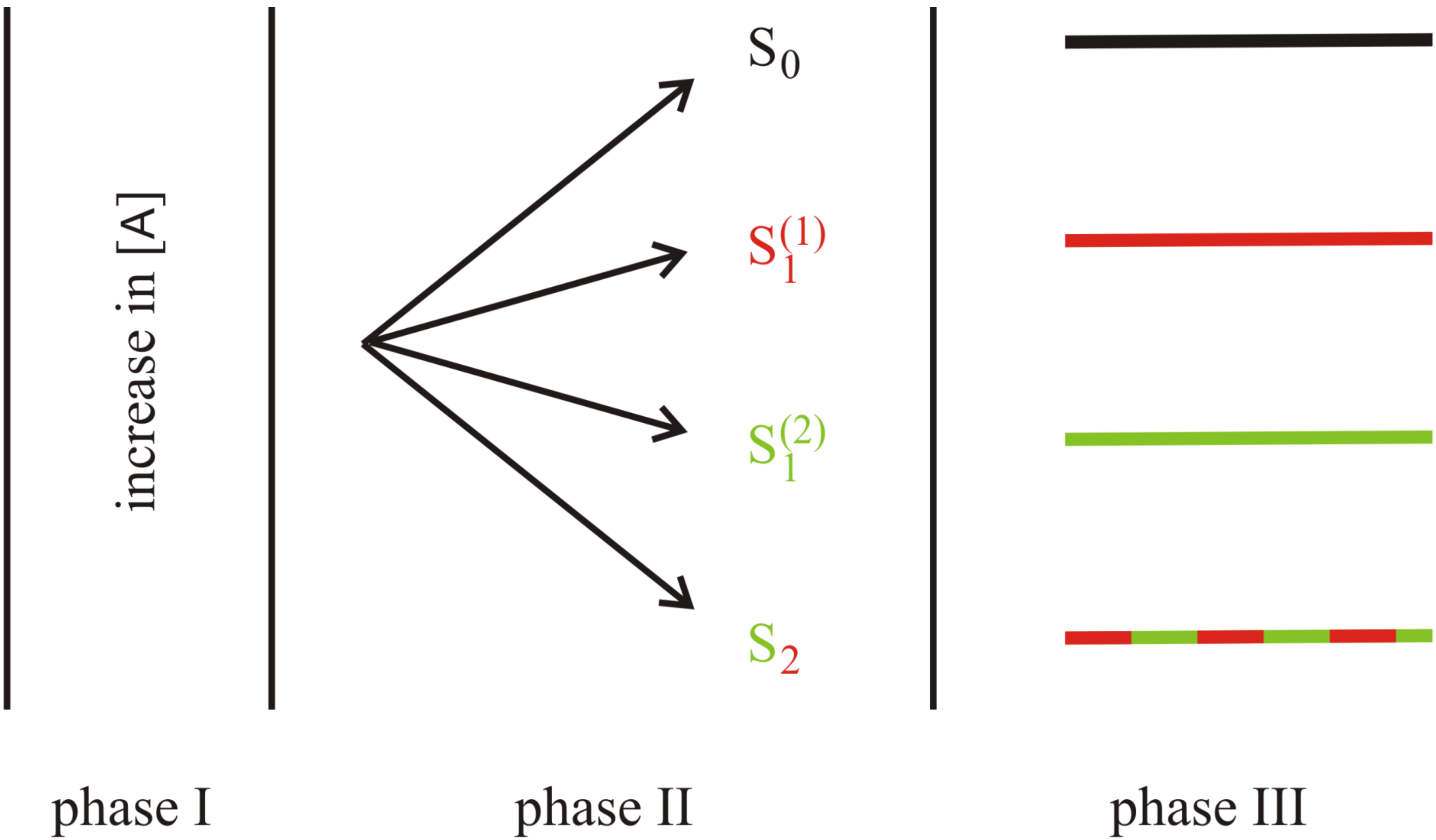


stochastic hypercycles with $n = 5$





competition and cooperation with $n = 2$



Random decision in the stochastic process

Initial values		Counted states of final outcomes			
$X_1(0)$	$X_2(0)$	N_{S_0}	$N_{S_1^{(1)}}$	$N_{S_1^{(2)}}$	N_{S_2}
1	1	385.1 ± 23.6	1481.0 ± 36.8	1719.6 ± 37.8	6414.3 ± 53.8
2	1	77.4 ± 9.1	1822.6 ± 41.6	367.6 ± 17.0	7733.3 ± 38.3
1	2	71.6 ± 8.5	280.6 ± 20.0	2075.8 ± 28.9	7572.0 ± 39.2
3	1	15.0 ± 2.9	1900.4 ± 30.9	74.6 ± 10.0	8009.0 ± 35.3
1	3	14.0 ± 3.7	53.1 ± 4.8	2180.5 ± 48.4	7752.3 ± 53.8
2	2	14.9 ± 2.6	303.7 ± 16.0	354.5 ± 23.8	9326.8 ± 44.9
3	3	0	70.2 ± 10.0	106.2 ± 10.9	9823.4 ± 15.7
4	4	0	12.1 ± 2.6	28.0 ± 5.0	9959.9 ± 6.4
5	5	0	2.5 ± 1.1	6.3 ± 2.6	9991.2 ± 3.0

Choice of parameters: f_1 = 0.011 [$M^{-1}t^{-1}$]; f_2 = 0.009 [$M^{-1}t^{-1}$];

k_1 = 0.0050 [$M^{-2}t^{-1}$]; k_2 = 0.0045 [$M^{-2}t^{-1}$];

a_0 = 200; r = 0.5 [Vt^{-1}]; $a(0)$ = 0

Competition and cooperation with $n = 2$

Initial values		Counted states of final outcomes			
$X_1(0)$	$X_2(0)$	N_{S_0}	$N_{S_1^{(1)}}$	$N_{S_1^{(2)}}$	N_{S_2}
1	1	385.1 ± 23.6	1481.0 ± 36.8	1719.6 ± 37.8	6414.3 ± 53.8
2	1	77.4 ± 9.1	1822.6 ± 41.6	367.6 ± 17.0	7733.3 ± 38.3
1	2	71.6 ± 8.5	280.6 ± 20.0	2075.8 ± 28.9	7572.0 ± 39.2
3	1	15.0 ± 2.9	1900.4 ± 30.9	74.6 ± 10.0	8009.0 ± 35.3
1	3	14.0 ± 3.7	53.1 ± 4.8	2180.5 ± 48.4	7752.3 ± 53.8
2	2	14.9 ± 2.6	303.7 ± 16.0	354.5 ± 23.8	9326.8 ± 44.9
3	3	0	70.2 ± 10.0	106.2 ± 10.9	9823.4 ± 15.7
4	4	0	12.1 ± 2.6	28.0 ± 5.0	9959.9 ± 6.4
5	5	0	2.5 ± 1.1	6.3 ± 2.6	9991.2 ± 3.0

Choice of parameters: $f_1 = 0.011$ [M^{-1}t^{-1}]; $f_2 = 0.009$ [M^{-1}t^{-1}];

$k_1 = 0.0050$ [M^{-2}t^{-1}]; $k_2 = 0.0045$ [M^{-2}t^{-1}];

$a_0 = 200$; $r = 0.5$ [Vt^{-1}]; $a(0) = 0$

Competition and cooperation with $n = 2$

Initial values		Counted states of final outcomes			
$X_1(0)$	$X_2(0)$	N_{S_0}	$N_{S_1^{(1)}}$	$N_{S_1^{(2)}}$	N_{S_2}
1	1	385.1 ± 23.6	1481.0 ± 36.8	1719.6 ± 37.8	6414.3 ± 53.8
2	1	77.4 ± 9.1	1822.6 ± 41.6	367.6 ± 17.0	7733.3 ± 38.3
1	2	71.6 ± 8.5	280.6 ± 20.0	2075.8 ± 28.9	7572.0 ± 39.2
3	1	15.0 ± 2.9	1900.4 ± 30.9	74.6 ± 10.0	8009.0 ± 35.3
1	3	14.0 ± 3.7	53.1 ± 4.8	2180.5 ± 48.4	7752.3 ± 53.8
2	2	14.9 ± 2.6	303.7 ± 16.0	354.5 ± 23.8	9326.8 ± 44.9
3	3	0	70.2 ± 10.0	106.2 ± 10.9	9823.4 ± 15.7
4	4	0	12.1 ± 2.6	28.0 ± 5.0	9959.9 ± 6.4
5	5	0	2.5 ± 1.1	6.3 ± 2.6	9991.2 ± 3.0

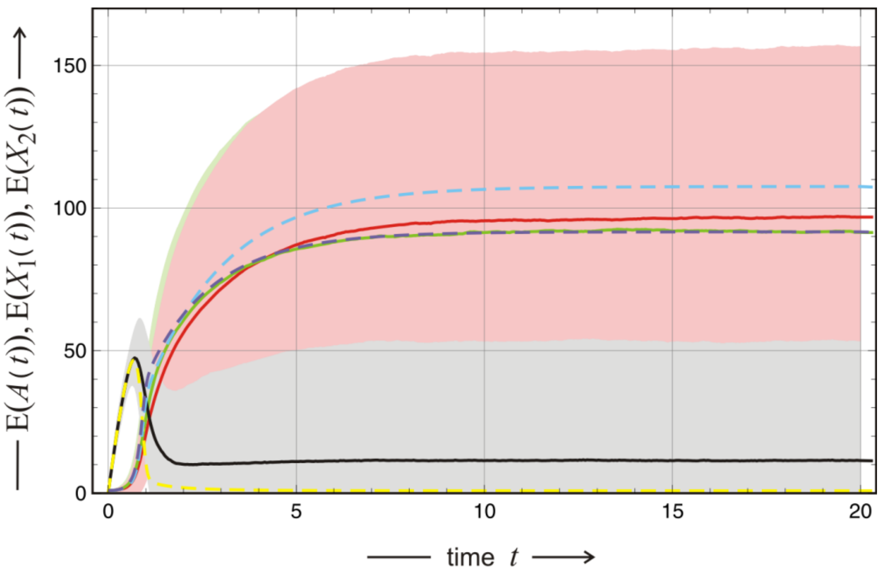
Choice of parameters: $f_1 = 0.011$ [$M^{-1}t^{-1}$]; $f_2 = 0.009$ [$M^{-1}t^{-1}$];

$k_1 = 0.0050$ [$M^{-2}t^{-1}$]; $k_2 = 0.0045$ [$M^{-2}t^{-1}$];

$a_0 = 200$; $r = 0.5$ [Vt^{-1}]; $a(0) = 0$

Competition and cooperation with $n = 2$

$a(0) = 0,\ x_1(0) = x_2(0) = 1$



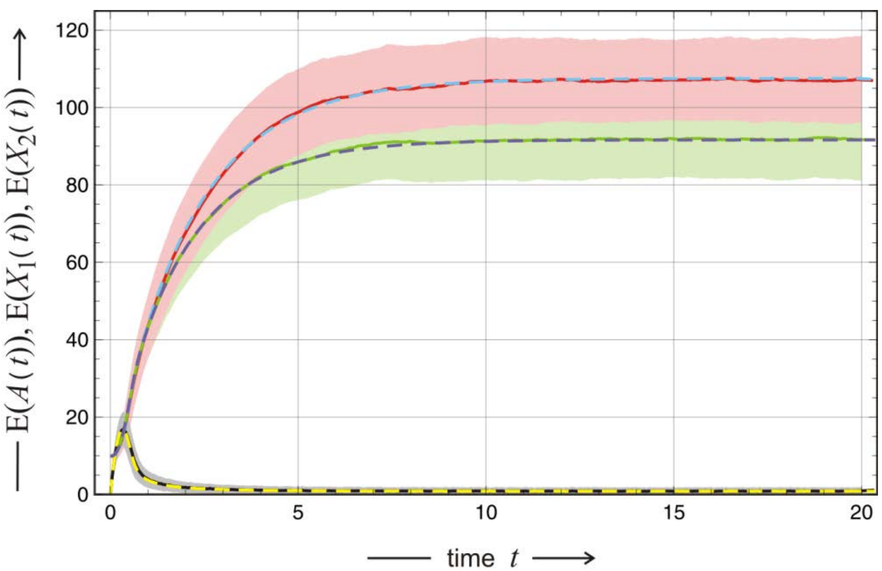
expectation values and 1σ-bands

choice of parameters: $a_0 = 200$, $r = 0.5$ [Vt^{-1}]

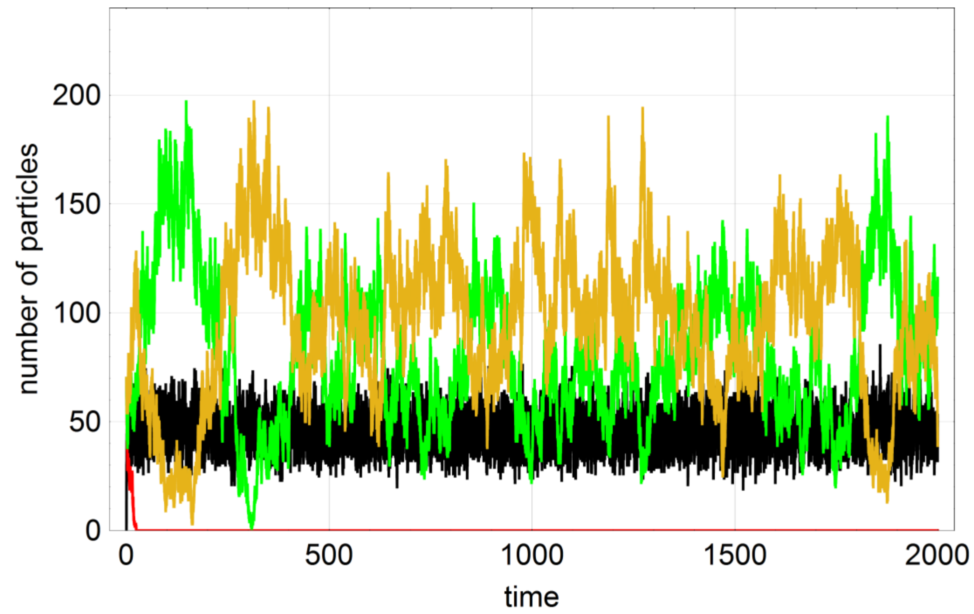
$f_1 = 0.09$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$], $f_2 = 0.11$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$],

$k_1 = 0.0050$ [$\mathrm{M}^{-2}\mathrm{t}^{-1}$], $k_2 = 0.0045$ [$\mathrm{M}^{-2}\mathrm{t}^{-1}$]

$a(0) = 0,\ x_1(0) = x_2(0) = 10$

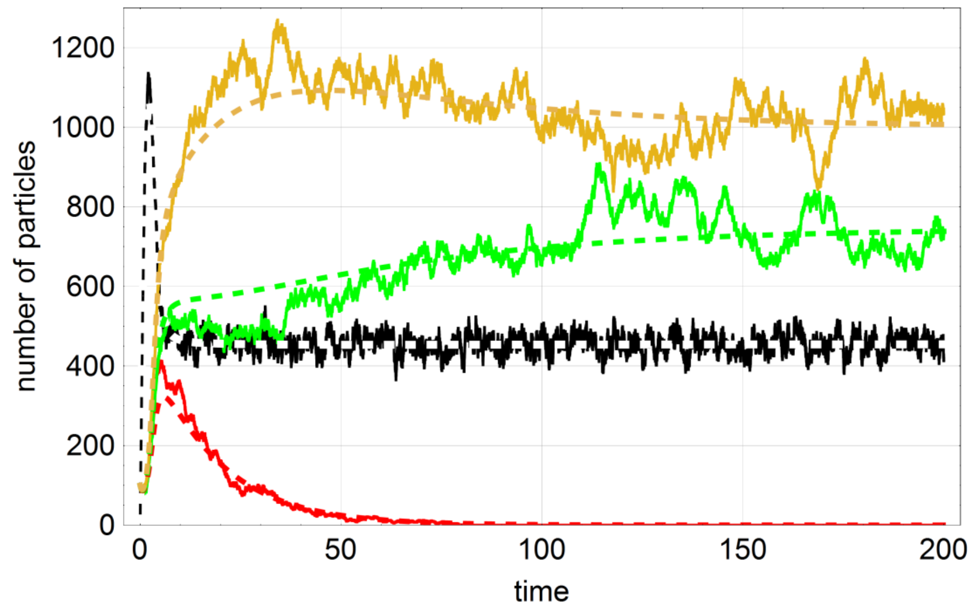


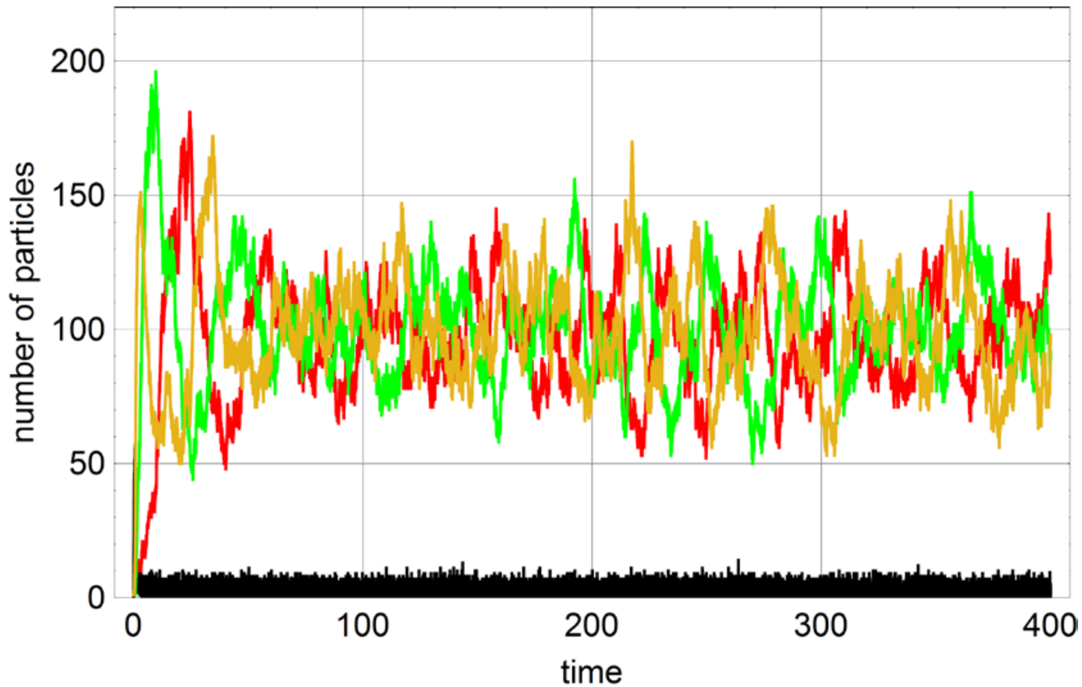
$a_0 = 220$



$n = 3$, state of exclusion $S_2^{(1)}$

$a_0 = 2200$





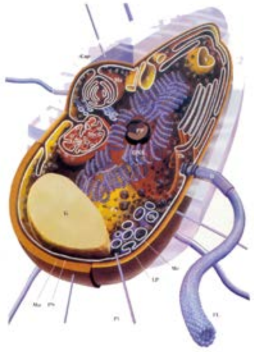
$n = 3$, state of cooperation S_3

1. Darwin's natural selection
2. Mutation and selection
3. A model for transitions
4. Cooperation tames competition
5. Effects of stochasticity
6. **Scarcity is not the mother of invention!**

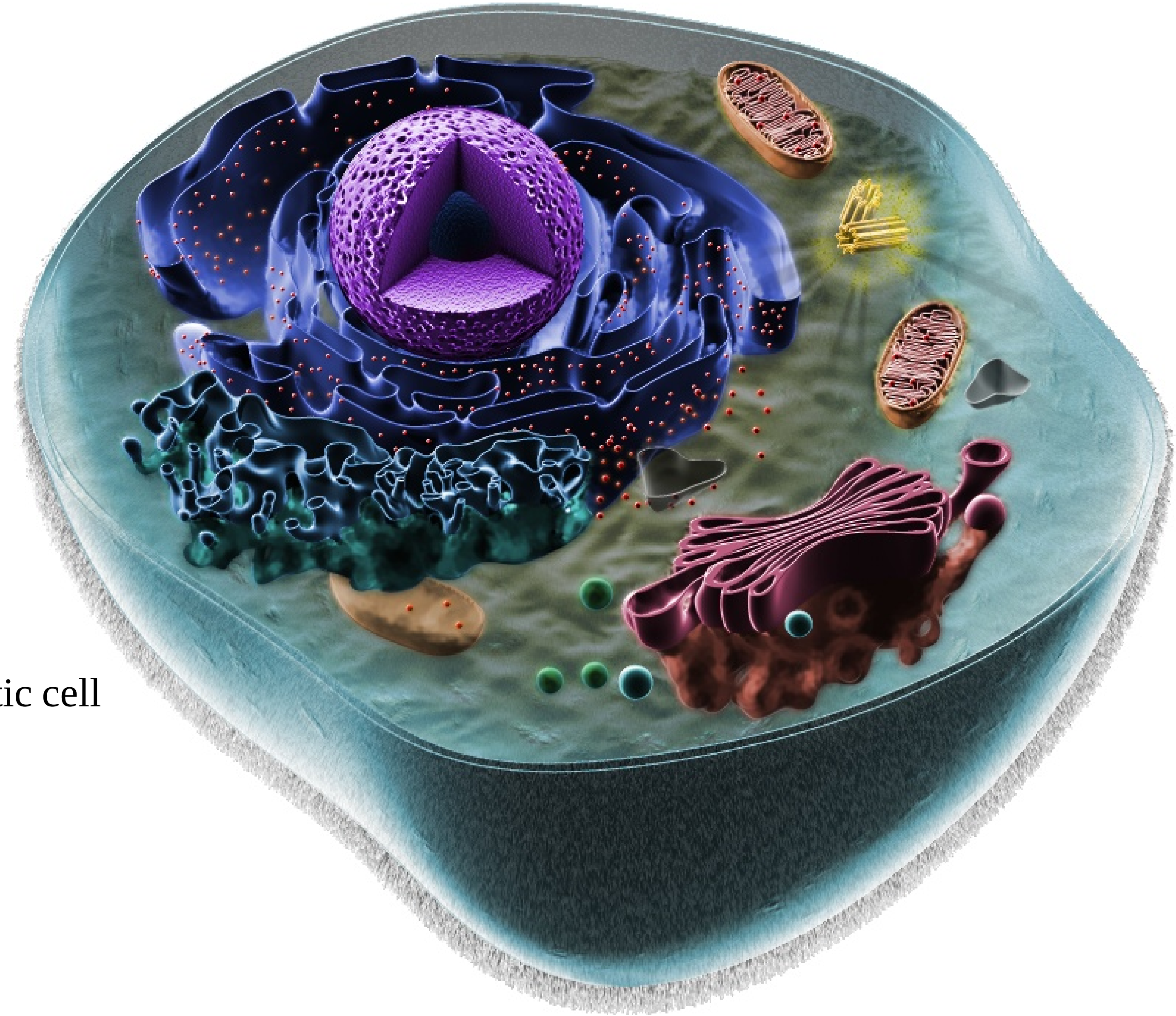
replicating molecules	⇒	populations in compartments
independent replicators	⇒	chromosomes
RNA	⇒	DNA
prokaryotes	⇒	eukaryotes
asexual clones	⇒	sexual clones
protists	⇒	animals, plants, fungi
solitary individuals	⇒	colonies
primate societies	⇒	human societies

Eörs Szathmáry, John Maynard Smith. The major evolutionary transitions. Nature 374:227-232, 1995

John Maynard Smith, Eörs Szathmáry. The major transitions in evolution. Oxford University Press, New York 1995

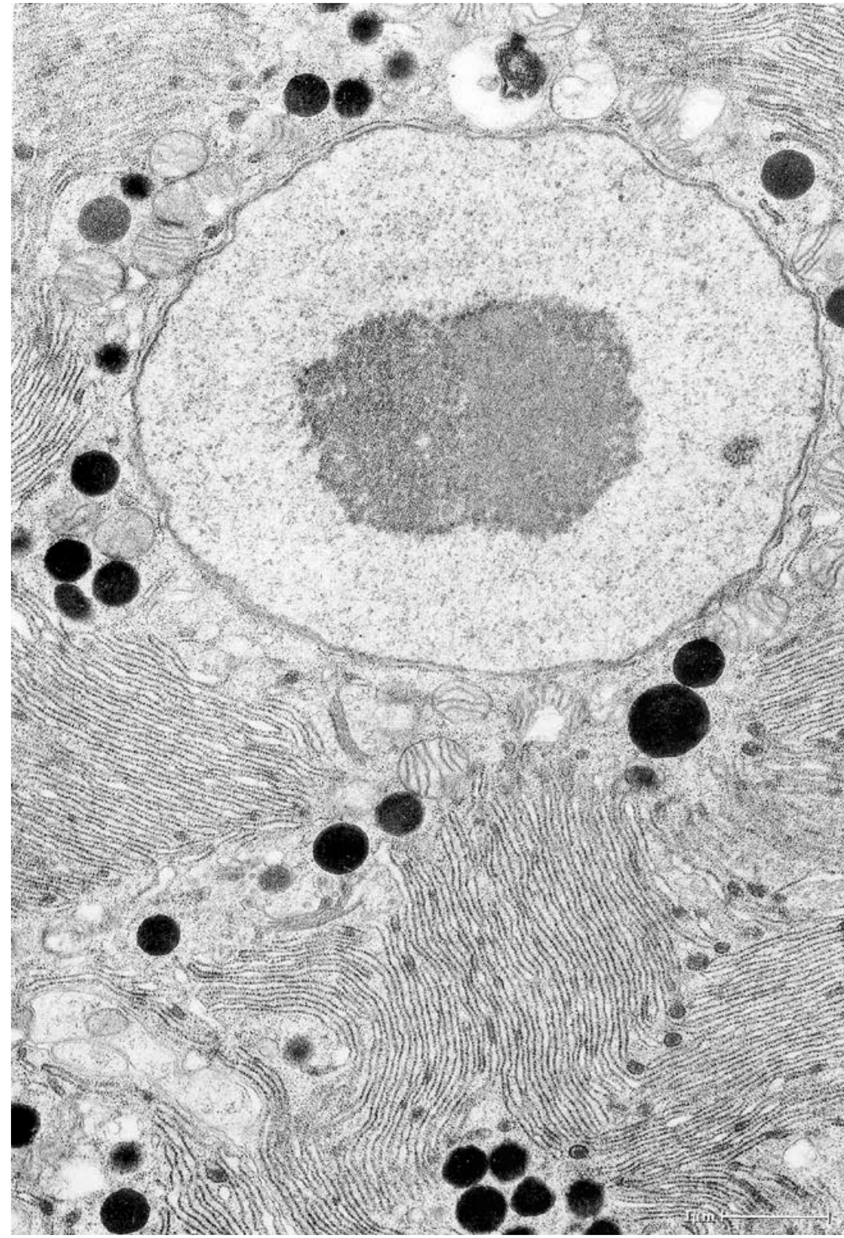


prokaryotic cell

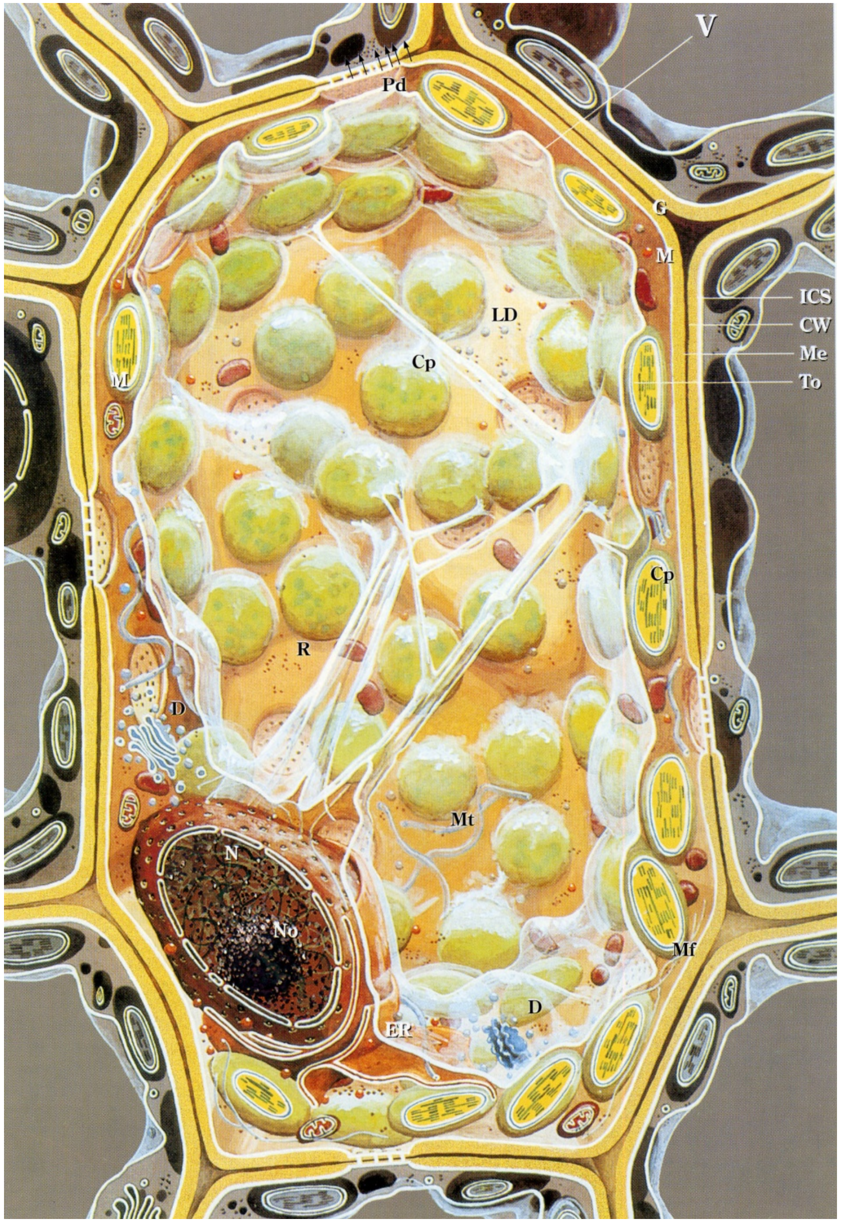


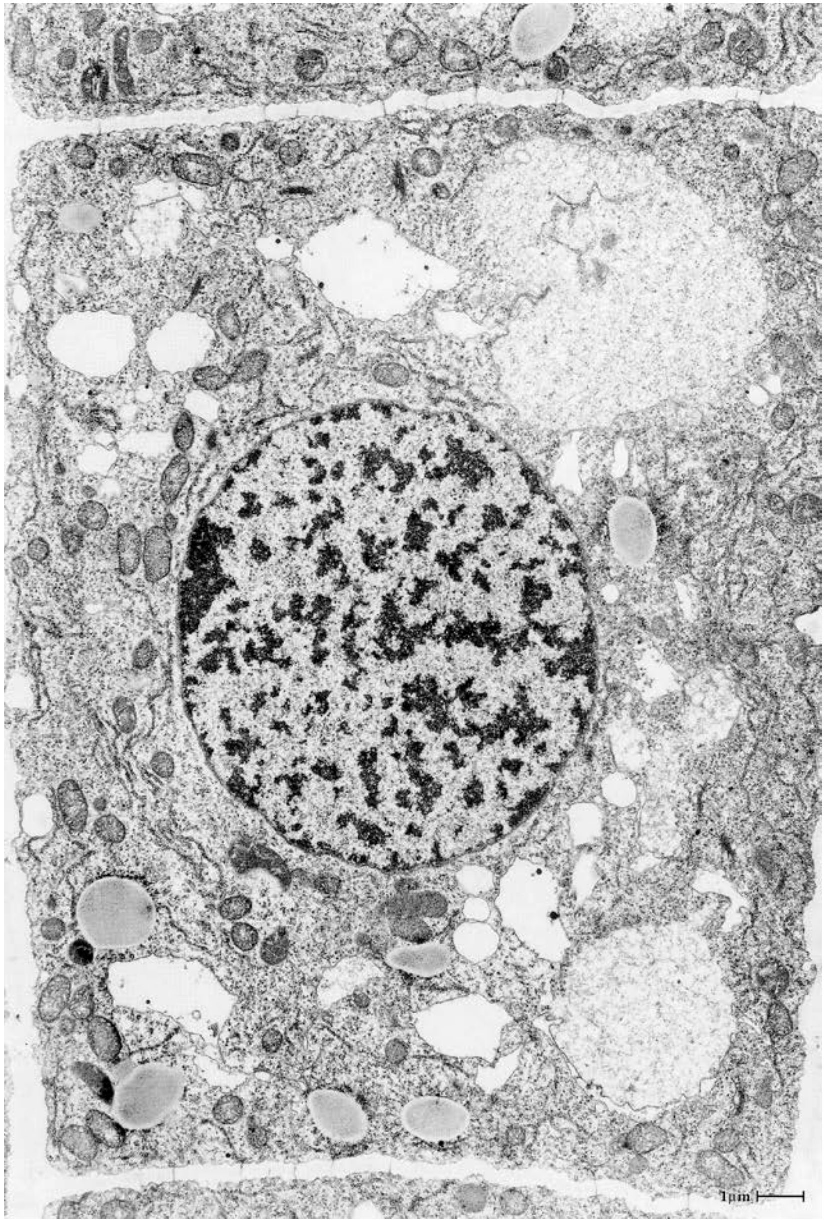
eukaryotic cell

Zaldua I., Equisoain J.J., Zabalza A., Gonzalez E.M., Marzo A., Public University of Navarre - Own work, https://commons.wikimedia.org/w/index.php?curid=46386894



an animal cell





a plant cell

How Does Complexity Arise in Evolution

Nature's recipe for mastering scarcity, abundance, and unpredictability

Three temporal characteristics of terrestrial environments were mentioned in the article's subtitle: *scarcity* and *abundance* of resources, as well as *unpredictability*. In summary, we have argued that nature uses optimization to deal with scarcity, she takes advantage of abundance to create innovation, and her recipe to master unpredictability is tinkering and modular design.

Peter Schuster. ***Complexity*** **2** (1): 22-30, 1996

Major Transitions in Evolution and in Technology

What They Have in Common and Where They Differ

The complexity of organisms has not increased gradually in biological evolution but stepwise. The steps are called *major transitions* and coincide with the origin of new hierarchical levels of organization. The first systematic survey and discussion of possible mechanisms for such transitions has been presented in 1995 in a monograph by Maynard Smith and Szathmáry [1]. Major transitions listed by Maynard Smith and Szathmáry lead, for example, from independent replicators of an RNA world to chromosomes, from RNA as gene and catalyst to DNA and protein, from prokaryotes to eukaryotes, from asexual clones to sexual populations, from unicellular protists to multicellular organisms with cell differentiation and development, from solitary individuals to insect colonies with cast systems, and finally from primate to human societies. Although the transitions involve very different molecular, metabolic, and organizational changes they share a common principle: Before the transition the individuals reproduced and evolved independently, and competed in populations according to the Darwinian mechanism of selection. After the transition we are dealing with a new unit in which the previous competitors are integrated and forced to cooperate. They have lost their independence although the degree of retained individuality is highly variable in the different transitions. There are several mechanisms suppressing natural selection, the simplest one is catalyzed reproduction as used, for example, in mathematical models of symbiosis or hypercycles [2,3].

PETER SCHUSTER

Peter Schuster is the Editor-in-Chief of Complexity at the Institut für Theoretische Chemie der Universität Wien, Währingerstraße 17, Wien 1090, Austria (e-mail: pks@tbi.univie.ac.at)

***Complexity* 21**(4): 7-13, 2016

Symbiosis

The presumably most common form is the endosymbiosis [12] in eukaryotic cells of animals and fungi where the cellular nucleus and the mitochondria reproduce autonomously but strong mutual dependence is caused by the majority of mitochondrial genes being stored in the nuclear genome and strong metabolic interaction since oxidative phosphorylation is performed only in mitochondria. The extension to three cooperating partners has happened in the cells of plants and algae where the chloroplasts represent a second class of endosymbionts [23]. Several other examples of three-way symbiosis are known, for example, the systematic studies on ants–fungi–bacteria systems [24]. Examples of four-way symbiosis seem to be rare [25].

Austerity versus abundance

In summary, the toy model for transitions has nicely demonstrated that small resources give rise to selection whereas abundant resources allow for the formation of cooperative systems and in this way initiate major transitions. The model was conceived for the formation of symbiontic units, which admittedly is based on an easy to understand and to formalize mode of cooperative interaction. Other cooperative interactions in biology and the complex interaction networks in technology based economics are much harder to model but it seems highly plausible that the result will be the same: Scarcity drives optimization but true innovation and major transitions require abundant resources

Complexity **21** (4): 13 (2016)

Thank you for your attention!

Coworkers

Peter Stadler, **Bärbel M. Stadler**, Universität Leipzig, GE

Paul E. Phillipson, University of Colorado at Boulder, CO

Walter Fontana, Harvard Medical School, MA

Martin Nowak, Harvard University, MA

Christian Reidys, Viginia Tech, Blacksburn, VA

Christian Forst, Los Alamos National Laboratory, NM

Ivo L.Hofacker, **Christoph Flamm**, Universität Wien, AT

Web-Page for further information:

http://www.tbi.univie.ac.at/~pks