A simple model for competition, mutation, and major transitions

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Web-Page for further information:

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

Peter Schuster. Some mechanistic requirements for major transitions. *Phil. Trans. R. Soc.B* 371:e20150439, 2016

Peter Schuster. Increase in complexity and information through molecular evolution. *Entropy*, in press, 2016

1. A general and simple model for evolution
2. Mutation and quasispecies
3. Cooperation and major transitions
4. Can mutations counteract extinction ?
5. Some conclusions

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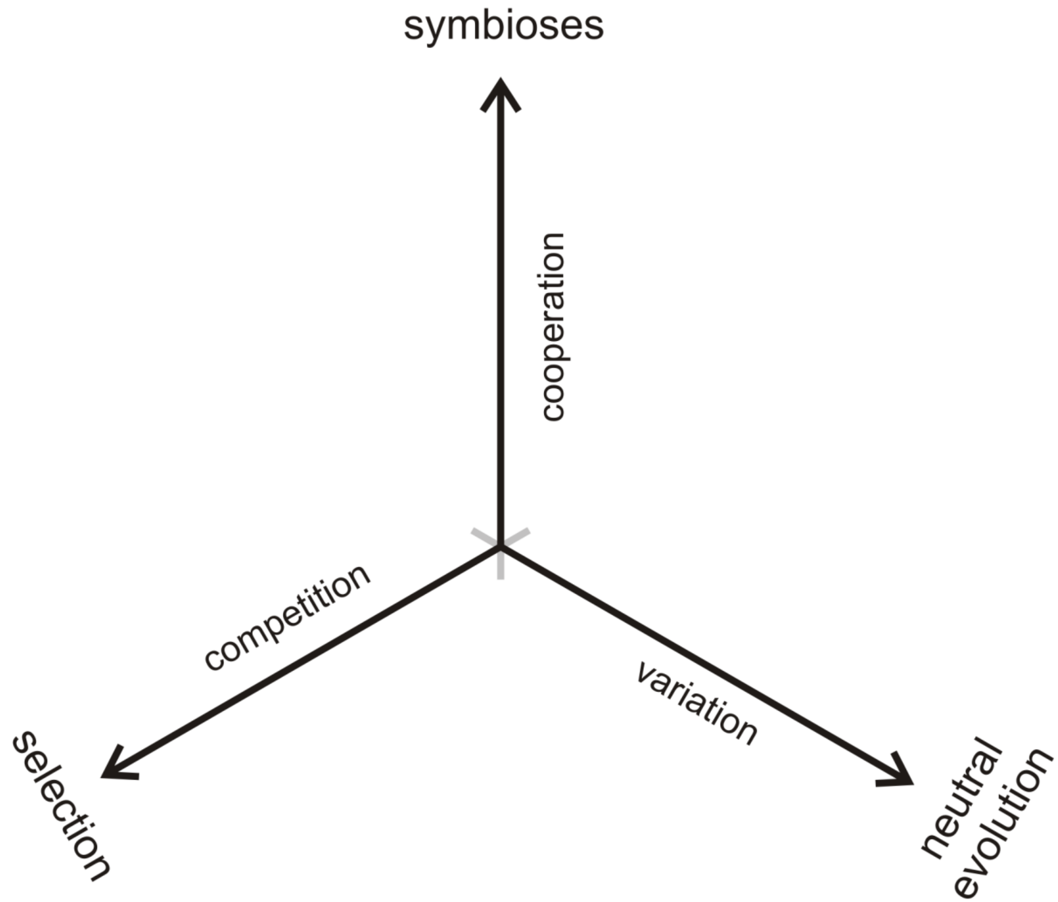
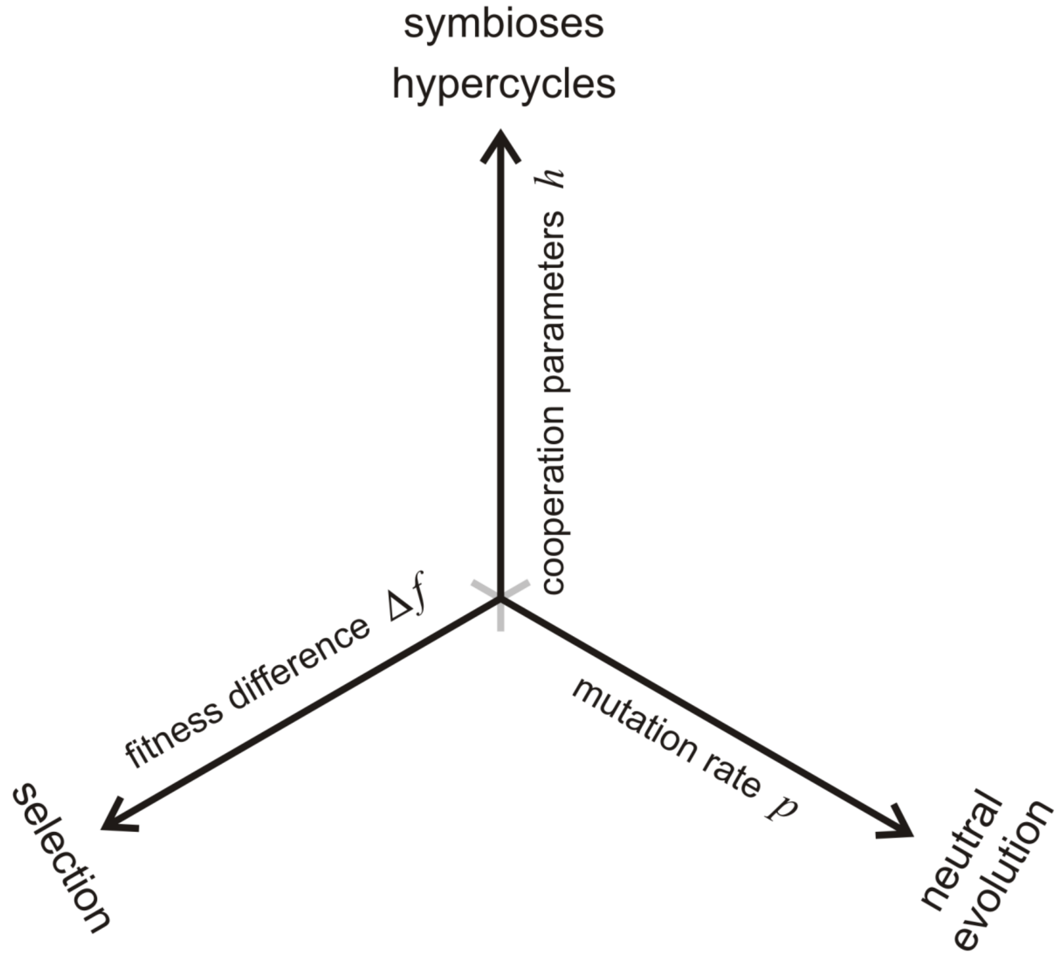
Motto: Occam‘s razor in the twentieth century

Everything should be made as simple as possible, but not simpler.

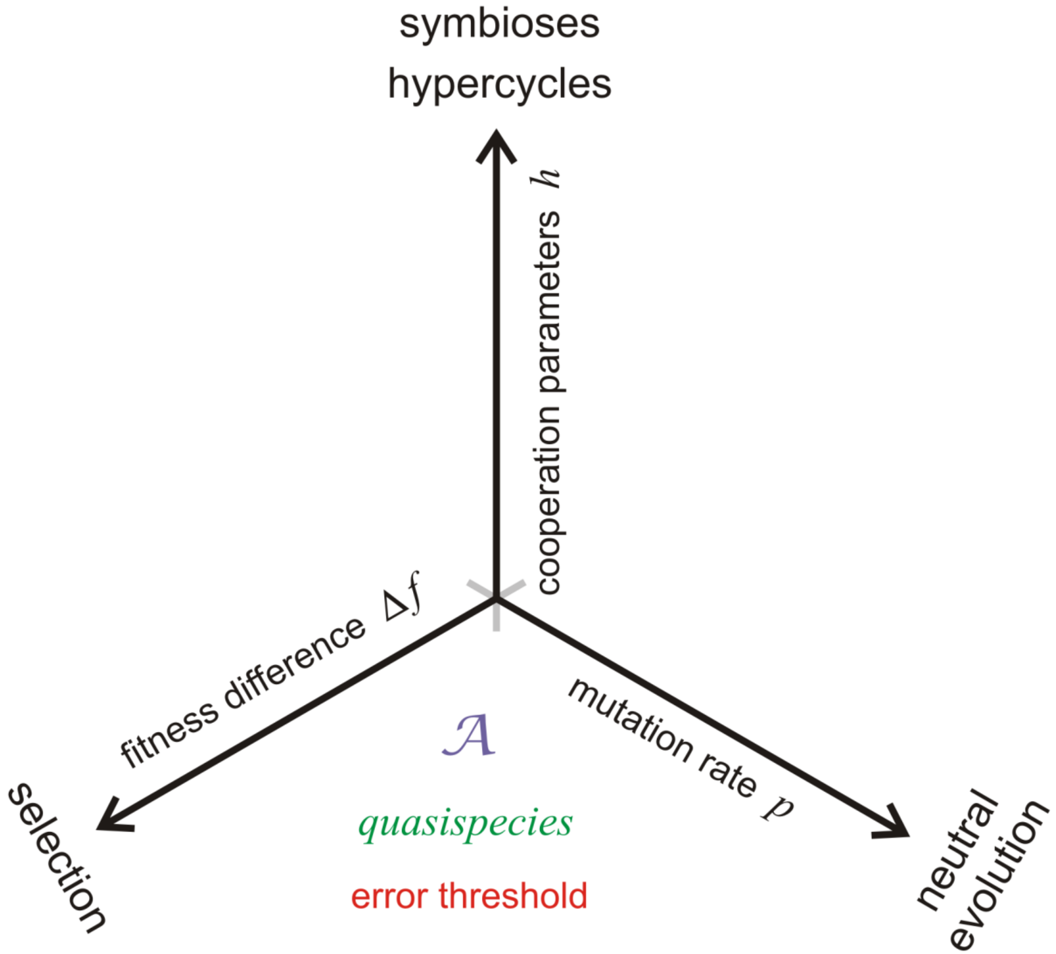
Attributed to Albert Einstein



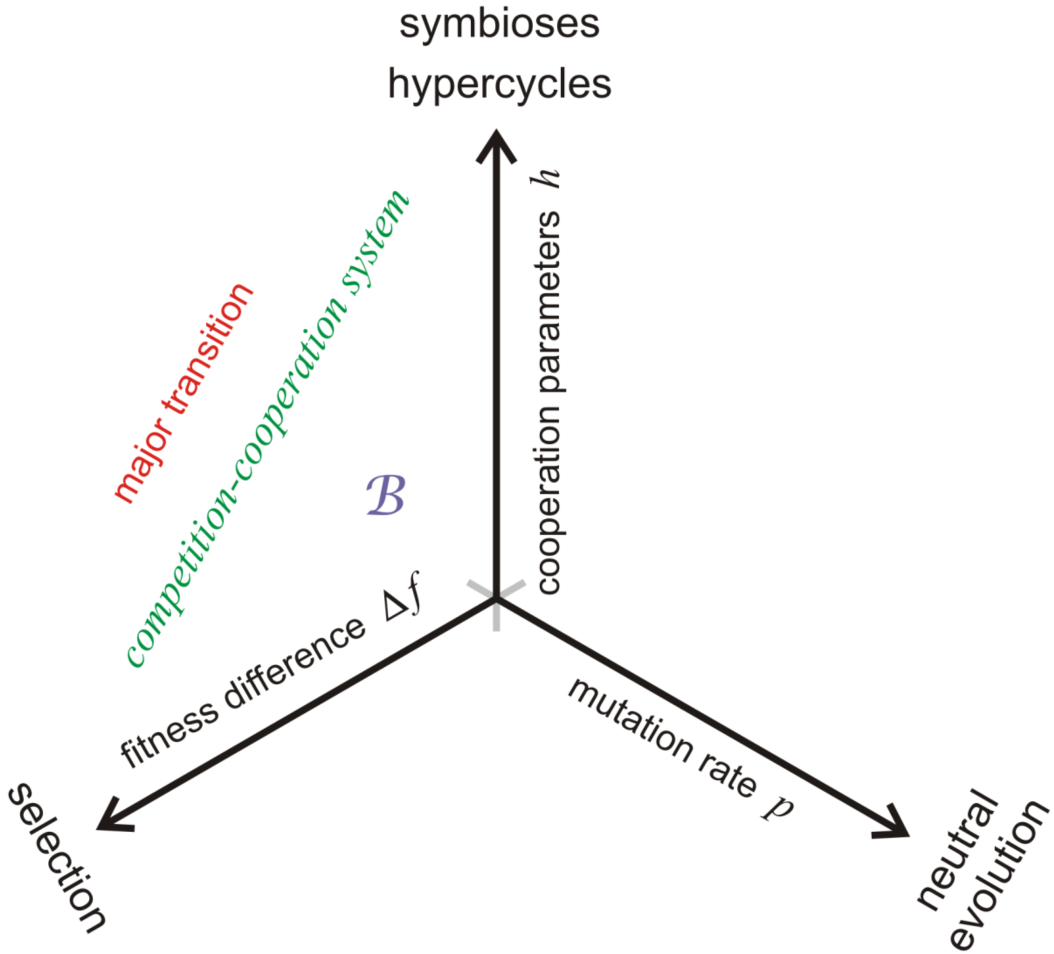
The three major processes driving evolution



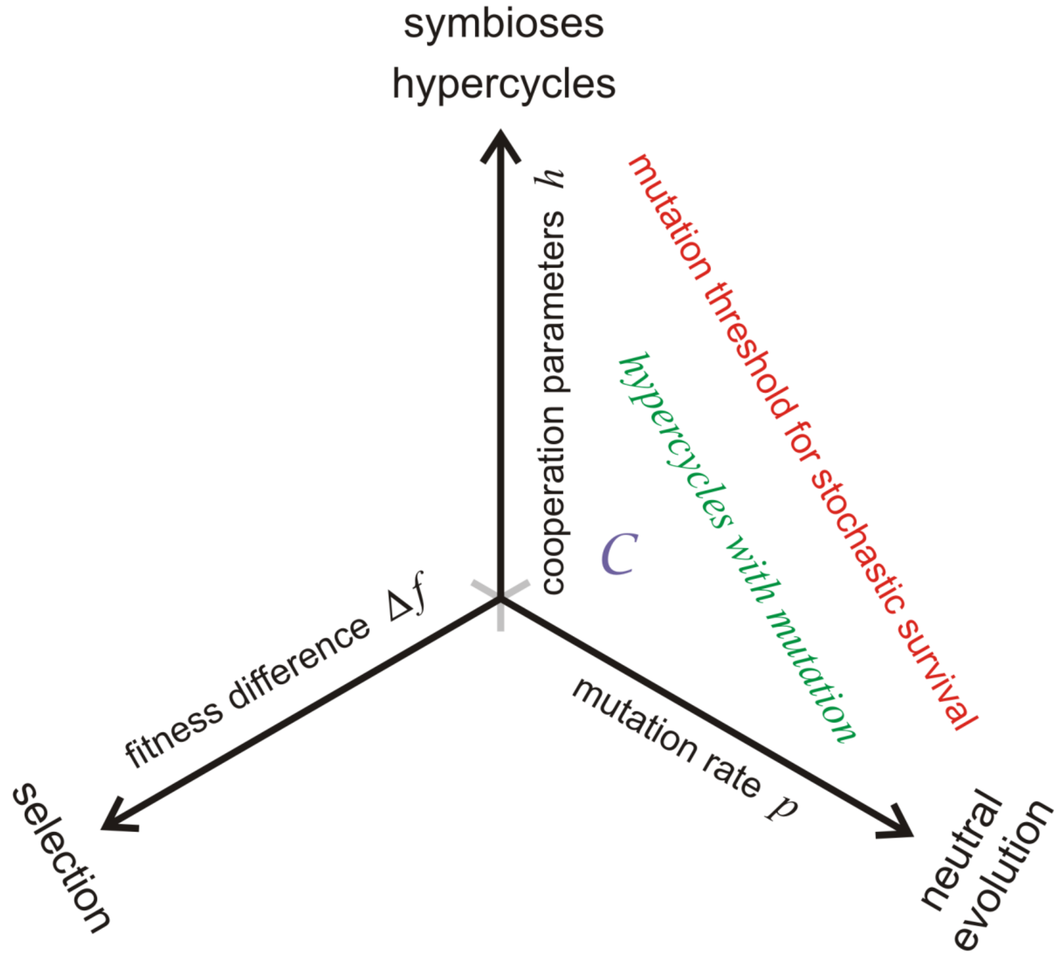
Three internal parameters driving evolution



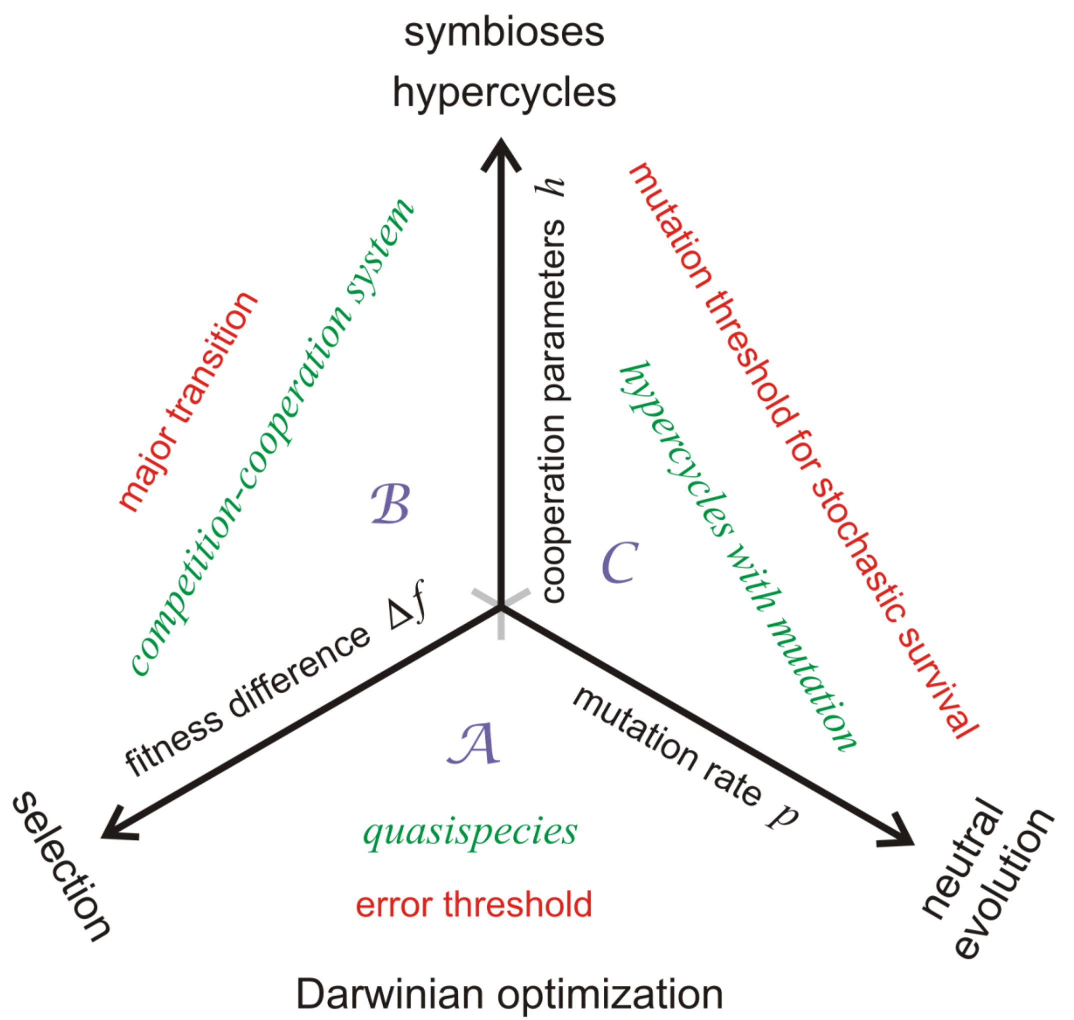
Competition and variation: error threshold



Competition and cooperation: major transition

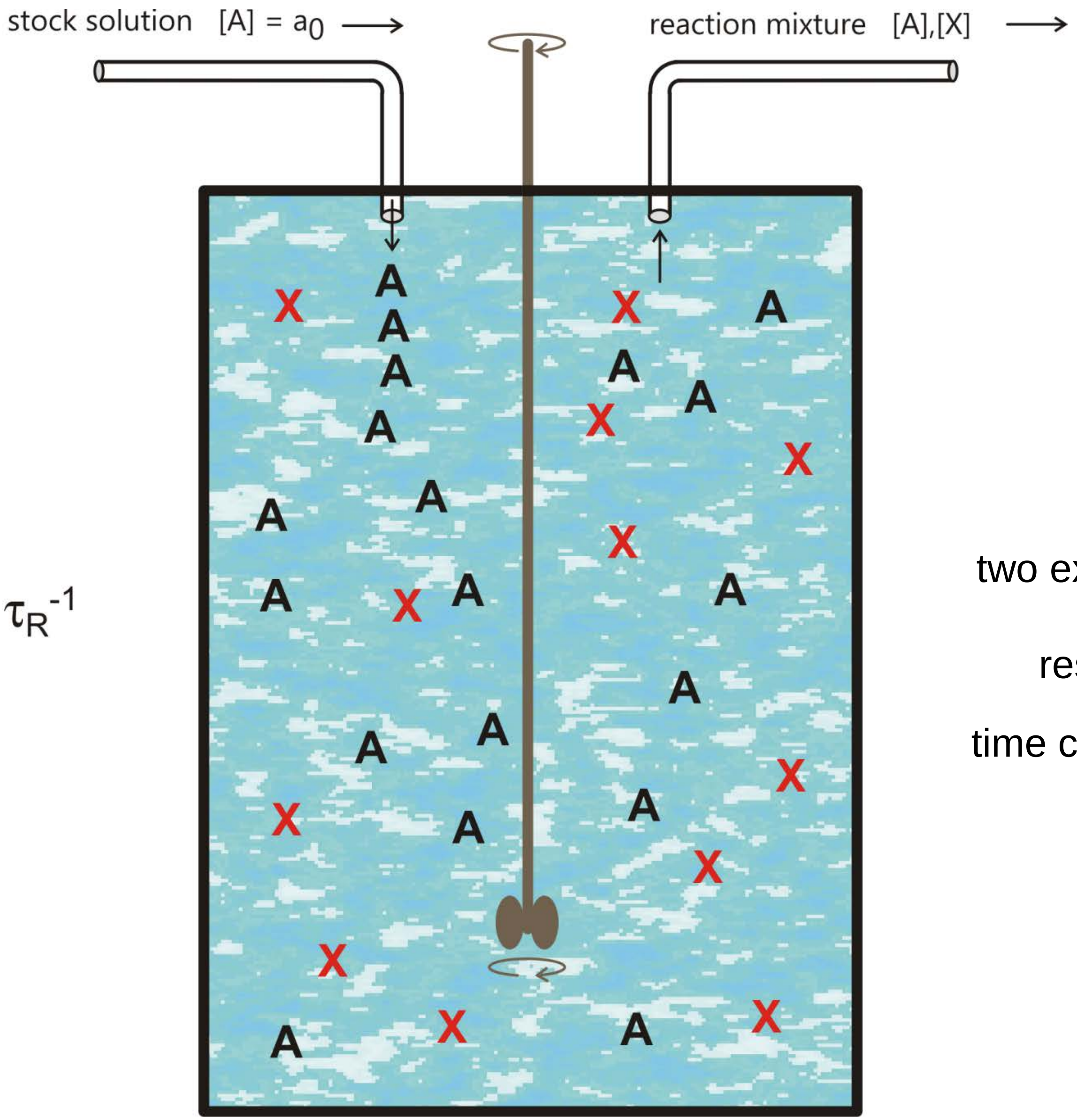


Cooperation and variation: survival threshold



The minimal model of evolution

flow rate $r = \tau_R^{-1}$



two external parameters:

resources **A** … a_0

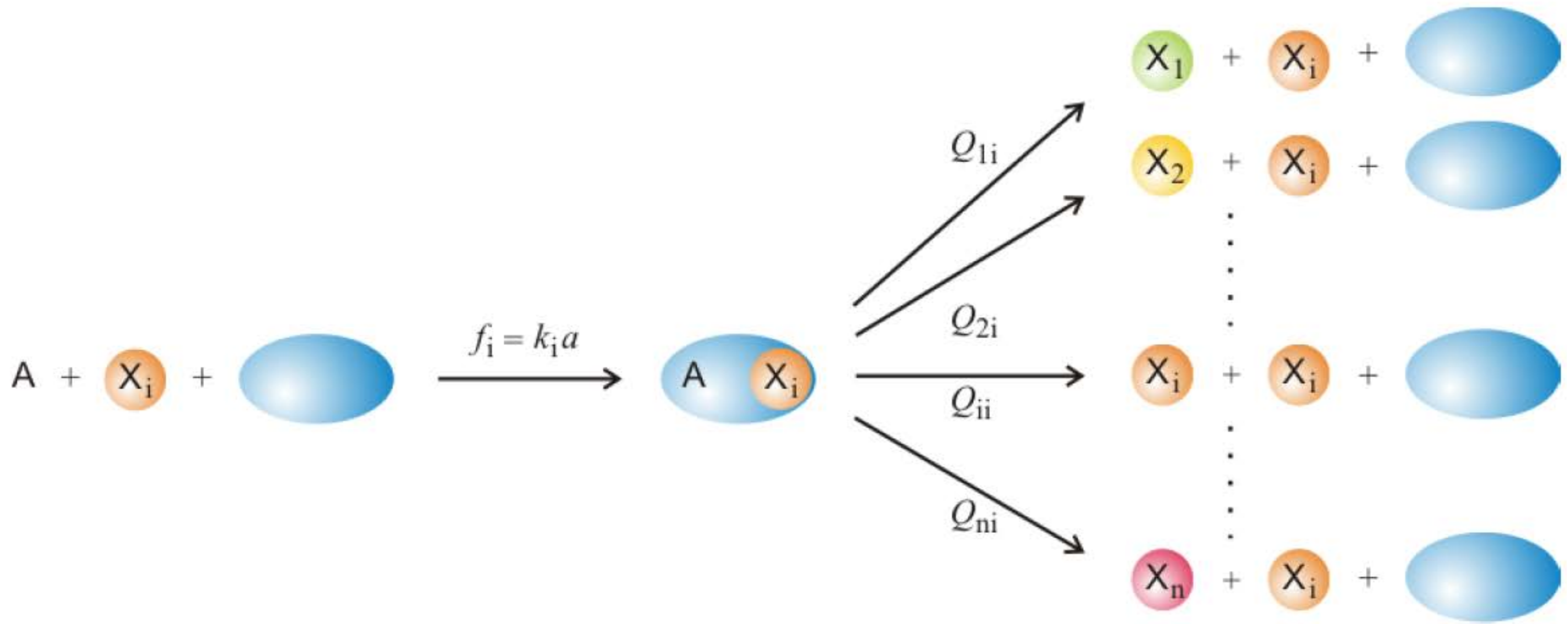
time constraint … $\tau_R = r^{-1}$

The continuously fed stirred tank reactor (CFSTR)

$$
\begin{aligned}
* \quad &\xrightarrow{\;a_0\, r\;} \quad \mathbf{A}\ , \\
\mathbf{A} + \mathbf{X}_i \quad &\xrightarrow{\;k_i\, Q_{ji}\;} \quad \mathbf{X}_i + \mathbf{X}_j\ ; \quad i,j = 1,\ldots,n\ , \\
\mathbf{A} + \mathbf{X}_i + \mathbf{X}_{i+1} \quad &\xrightarrow{\;l_i\, Q_{ji}\;} \quad \mathbf{X}_i + \mathbf{X}_j + \mathbf{X}_{i+1}\ ; \ i,j = 1,\ldots,n;\ i \bmod n\ , \\
\mathbf{A} \quad &\xrightarrow{\;r\;} \quad \varnothing\ , \quad \text{and} \\
\mathbf{X}_i \quad &\xrightarrow{\;r\;} \quad \varnothing\ ; \ i = 1,\ldots,n\ .
\end{aligned}
$$

chemical reaction equations: k_i, l_i … reaction rate parameters

Q_{ji} … elements of the mutation matrix



A molecular mechanism for mutation

$$\frac{\mathrm{d}a}{\mathrm{dt}} = -a \sum_{j=1}^{n} x_j \big(k_j + l_j x_{j+1}\big) + r\,(a_0 - a) \;\text{ and}$$

$$\frac{\mathrm{d}x_i}{\mathrm{dt}} = a\Big(\sum_{j=1}^{n} Q_{ij}(k_j + l_j x_{j+1})x_j\Big) - r x_i;\; i,j = 1\ldots,n;\; j \bmod n$$

$$Q_{ij}(p) = Q\,\varepsilon^{d_{\mathrm{H}}(X_i,X_j)} \;\text{ with }\; Q = (1-p)^{\nu} = Q_{ii}\,\forall\, i = 1,\ldots,n \;\text{ and }\; \varepsilon = \frac{p}{1-p}\,.$$

uniform error rate model

kinetic differential equations

$$
\begin{aligned}
\frac{\mathrm{d}P_{\mathbf{m}}}{\mathrm{d}t} = {} & a_0\, r P_{(\mathbf{m};m-1)} + r\Big((m+1)P_{(\mathbf{m};m+1)} + \sum_{j=1}^{n}(s_j+1)P_{(\mathbf{m};s_j+1)}\Big) + \\
& + (m+1)\sum_{j=1}^{n}\Big((k_j + l_j\, s_{j+1})(s_j-1)P_{(\mathbf{m};m+1,s_j-1)}\Big) - \\
& - \Big(r\Big(a_0 + m + \sum_{j=1}^{n} s_j\Big) + m\Big(\sum_{j=1}^{n}(k_j + l_j\, s_{j+1})\, s_j\Big)\Big)P_{\mathbf{m}} \,.
\end{aligned}
$$

$\mathbf{m} = (m, s_1, \ldots, s_n)$ and $(\mathbf{m}; m-1) = (m-1, s_1, \ldots, s_n)$, etc.

reactions $\mathbf{m} \to \mathbf{m}'$:

$$
\begin{aligned}
\mathbf{m}' &= (\mathbf{m}' = m \pm 1, s_1, \ldots, s_n) \equiv (\mathbf{m}; m \pm 1) \\
\mathbf{m}' &= (\mathbf{m}' = m, s_1, \ldots, s_k - 1, \ldots, s_n) \equiv (\mathbf{m}; s_k - 1) \\
\mathbf{m}' &= (\mathbf{m}' = m - 1, s_1, \ldots, s_k' = s_k + 1, \ldots, s_n) \equiv (\mathbf{m}; m-1, s_k + 1)
\end{aligned}
$$

master equation of the evolution model

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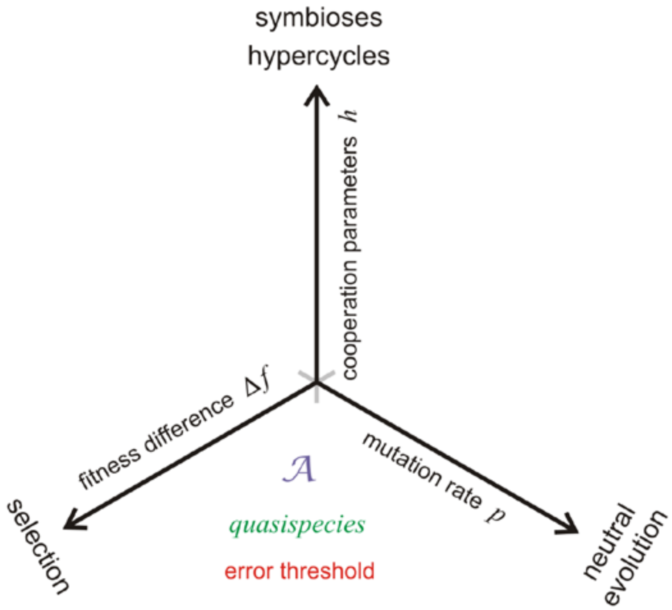
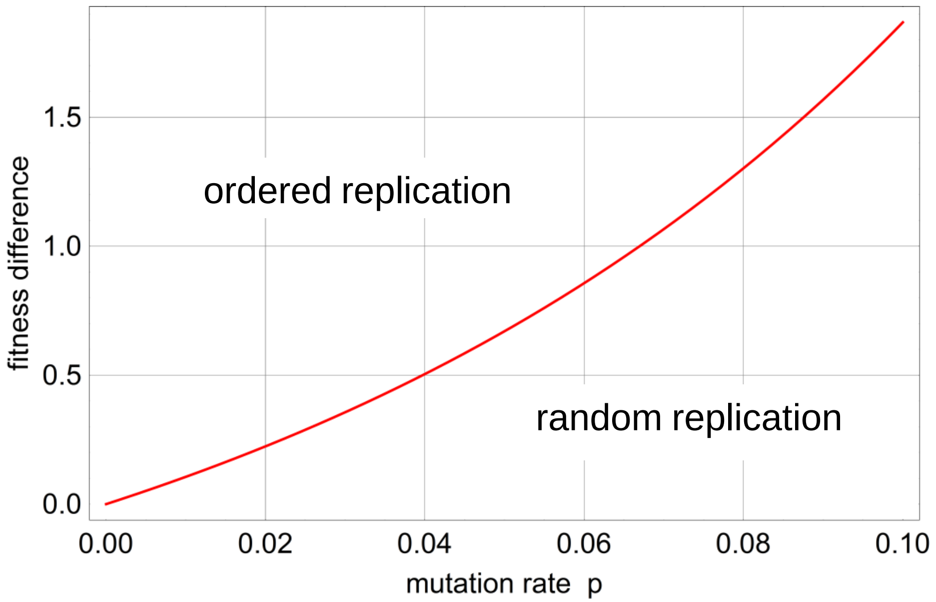
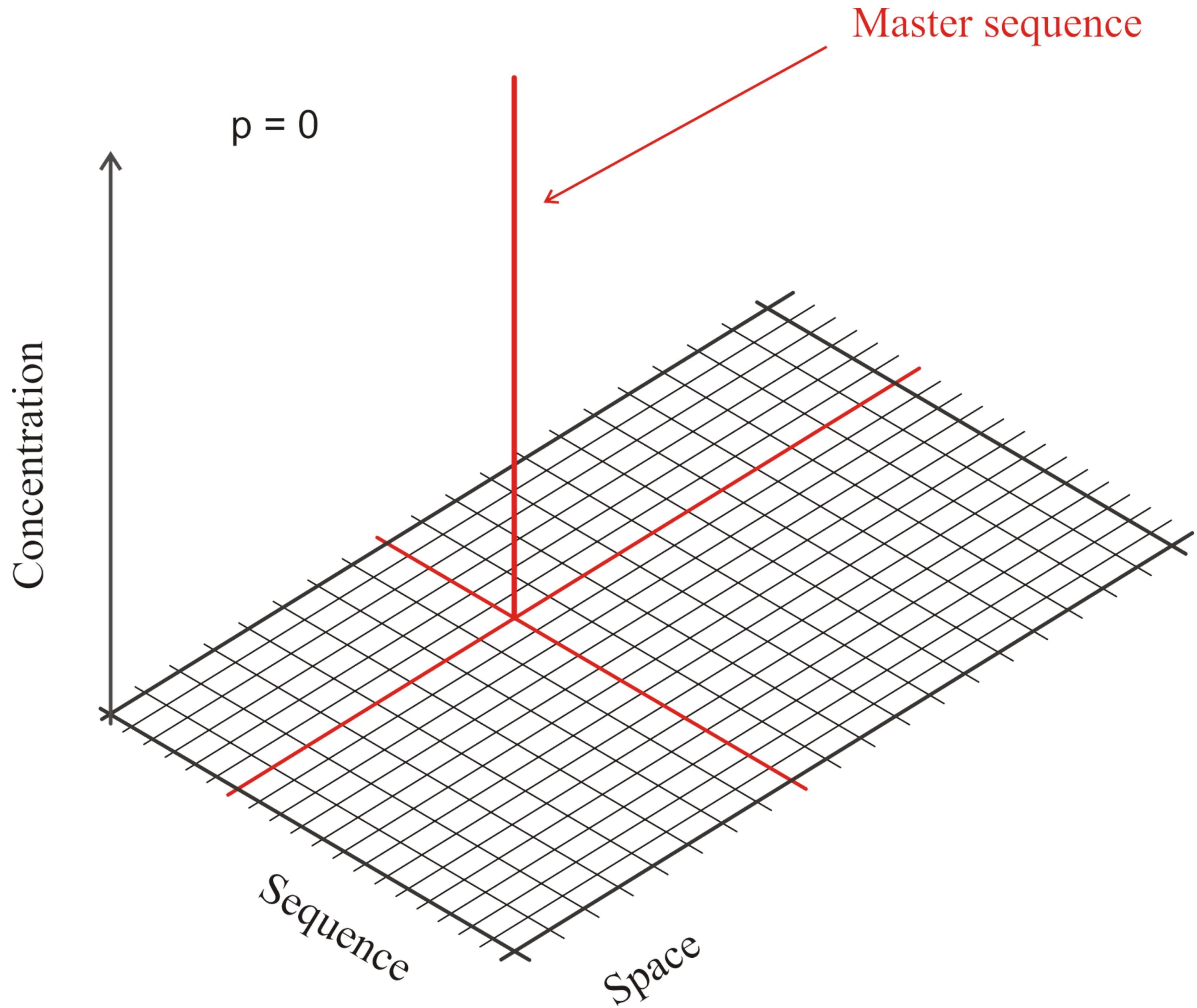


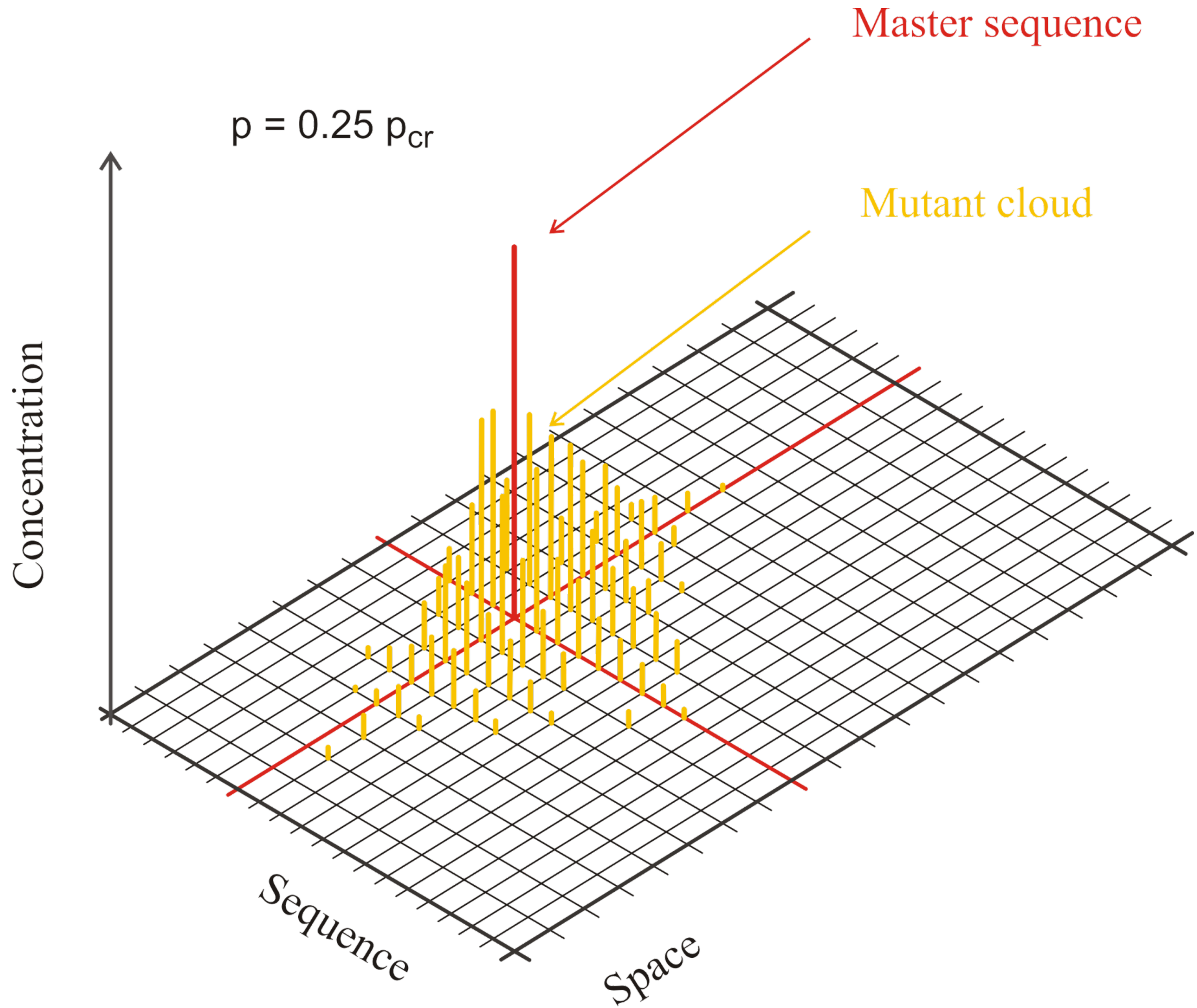


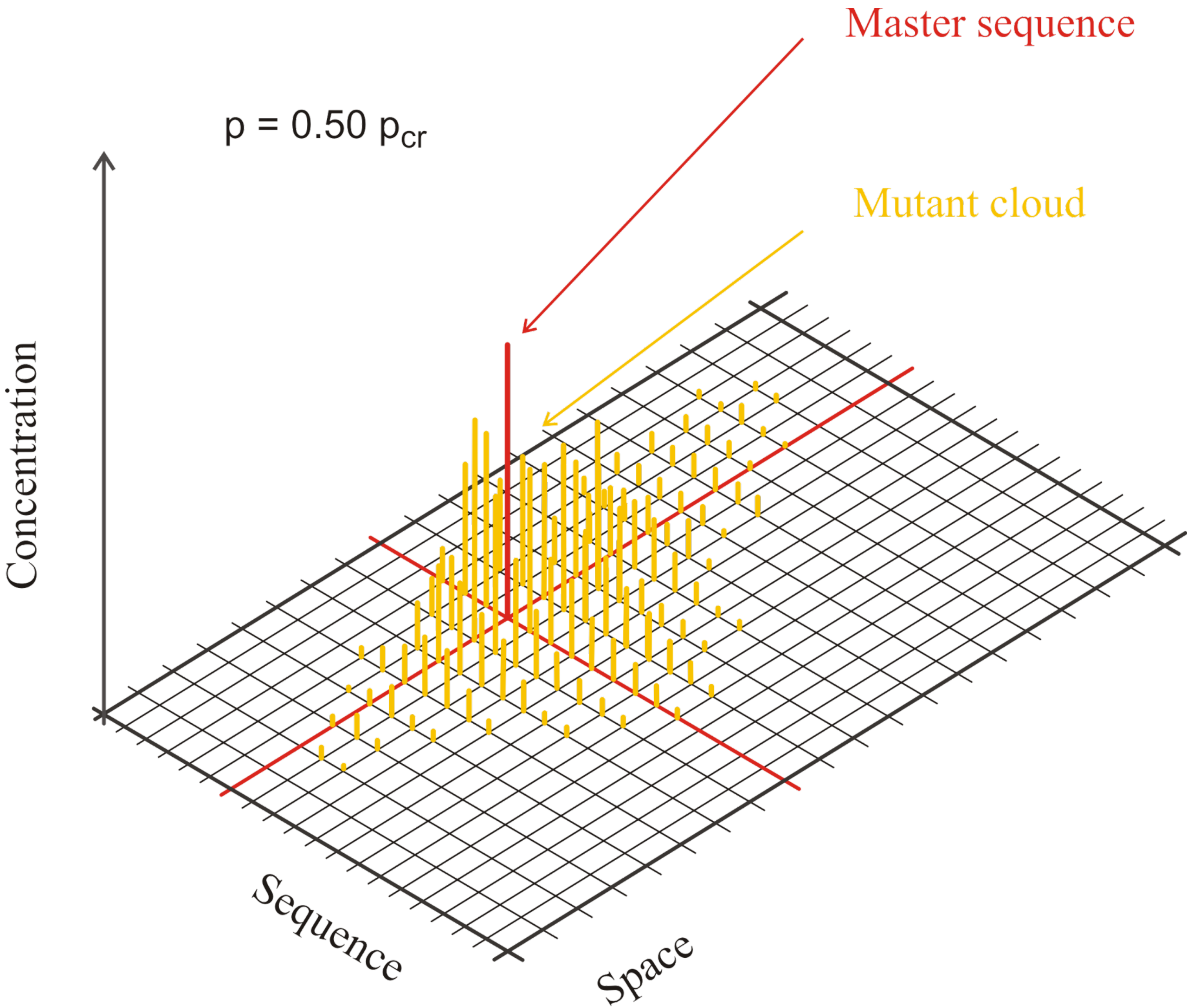
$$p_{cr} = 1 - \sigma^{-1/l}$$

$$\sigma - 1 = \frac{\Delta f}{f} = (1 - p)^{-l} - 1$$

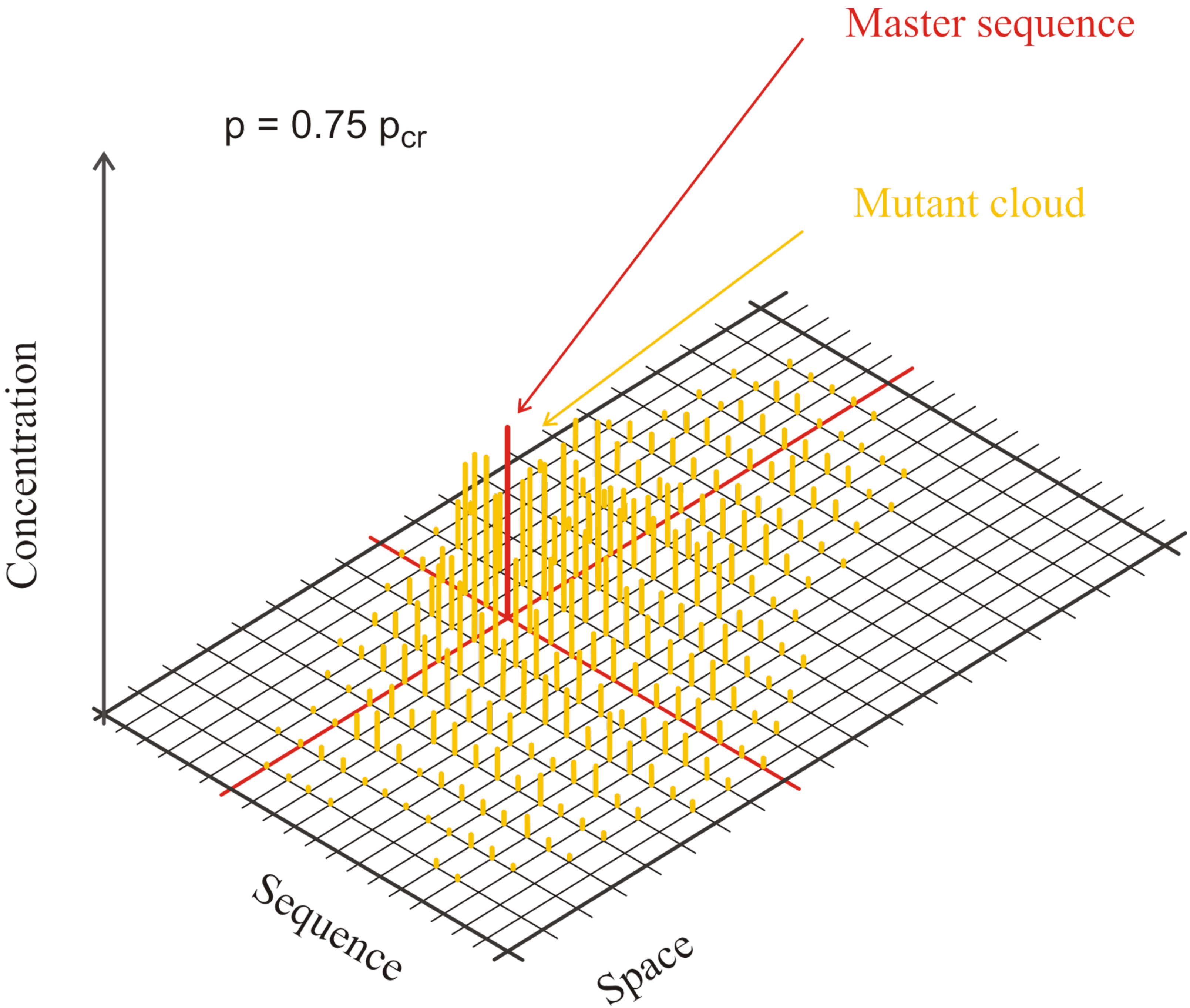
Competition and variation: error threshold


Master sequence
p = 0
Concentration
Sequence
Space

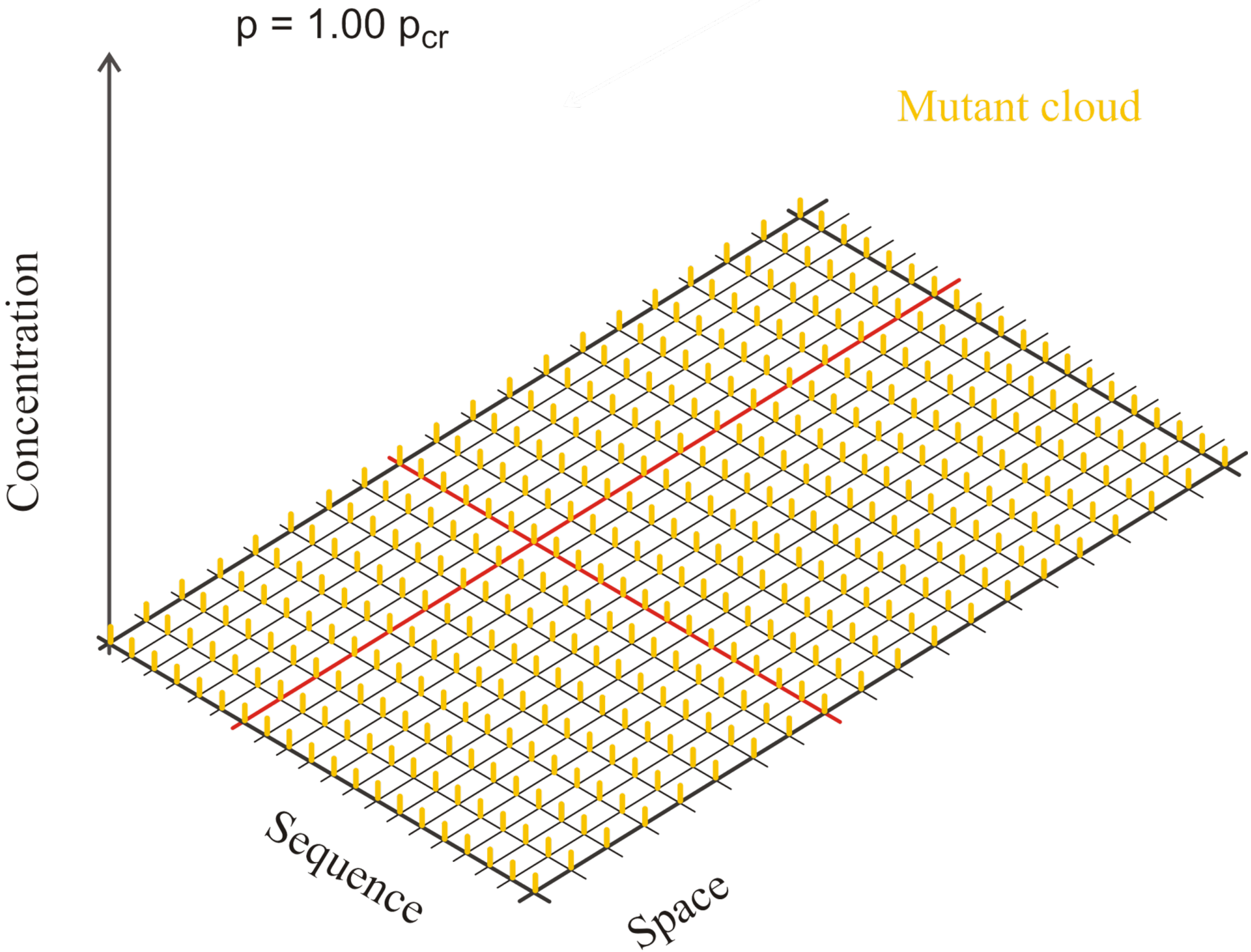

Master sequence
$p = 0.25\ p_{cr}$
Mutant cloud
Concentration
Sequence
Space



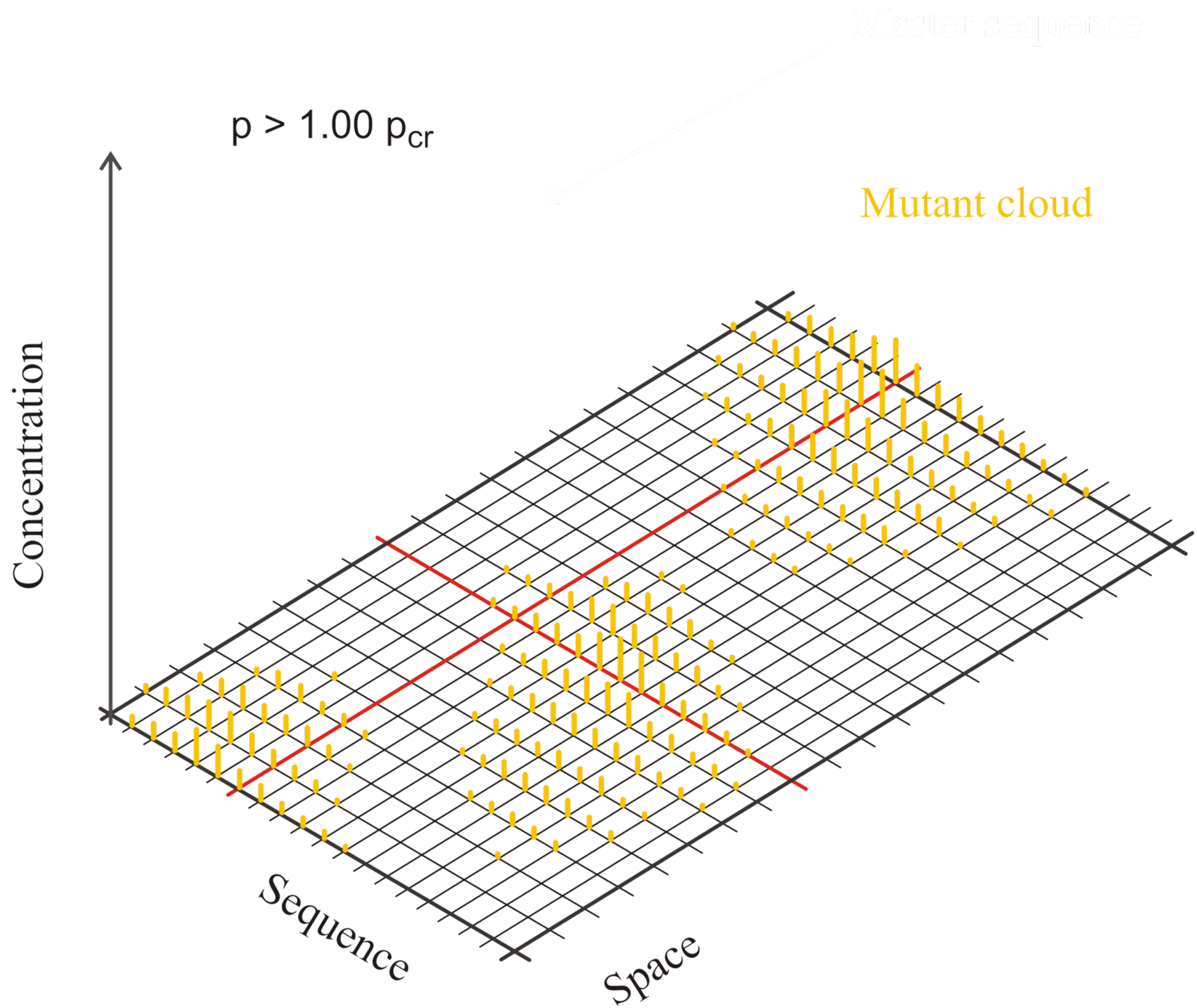
Master sequence
Mutant cloud
p = 0.50 p$_{cr}$
Concentration
Sequence
Space

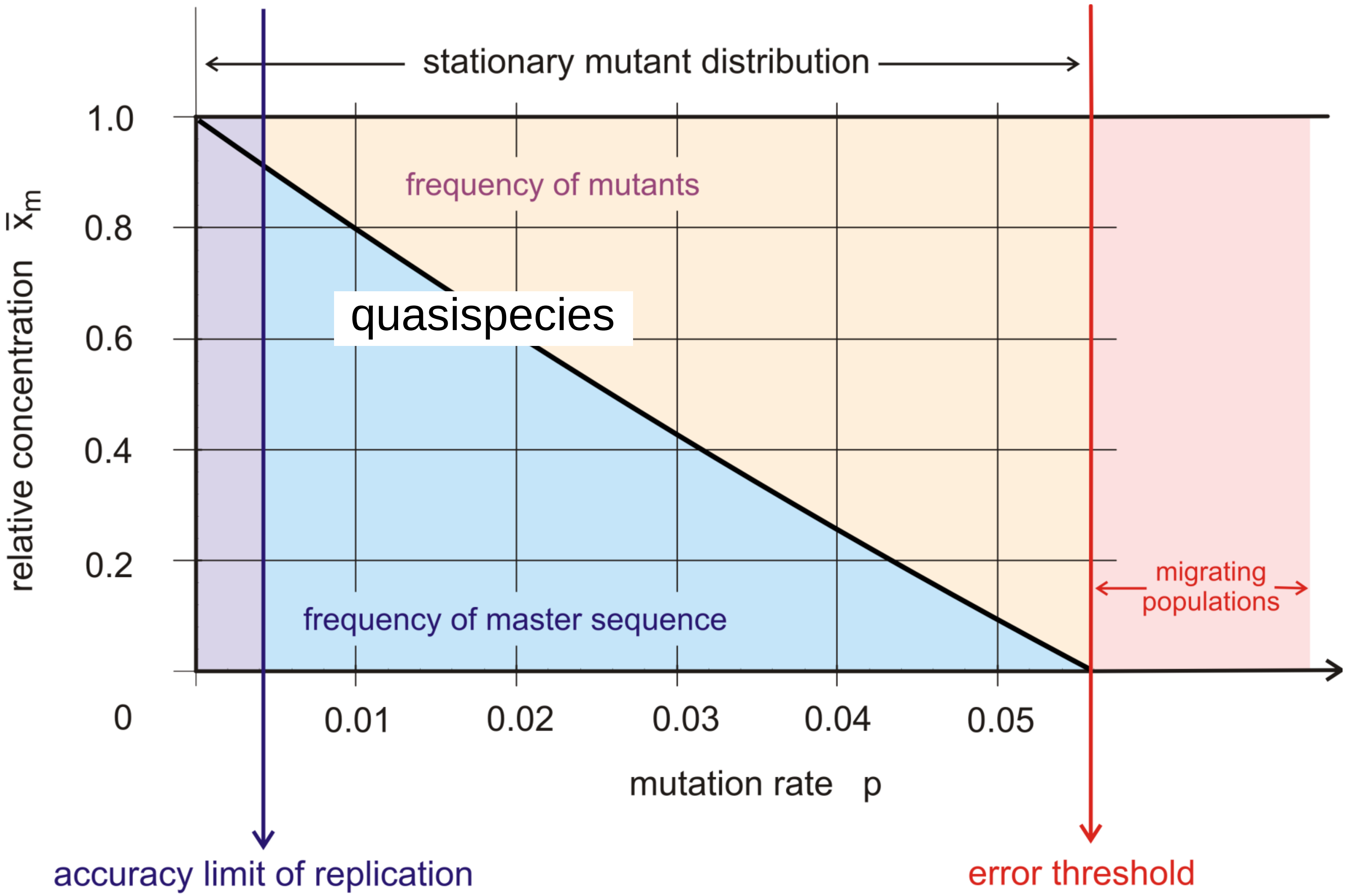


Master sequence
Mutant cloud
p = 0.75 p_cr
Concentration
Sequence
Space



$p = 1.00\ p_{cr}$
Mutant cloud
Concentration
Sequence
Space


Master sequence
p > 1.00 p_cr
Mutant cloud
Concentration
Sequence
Space



The error threshold in replication and mutation

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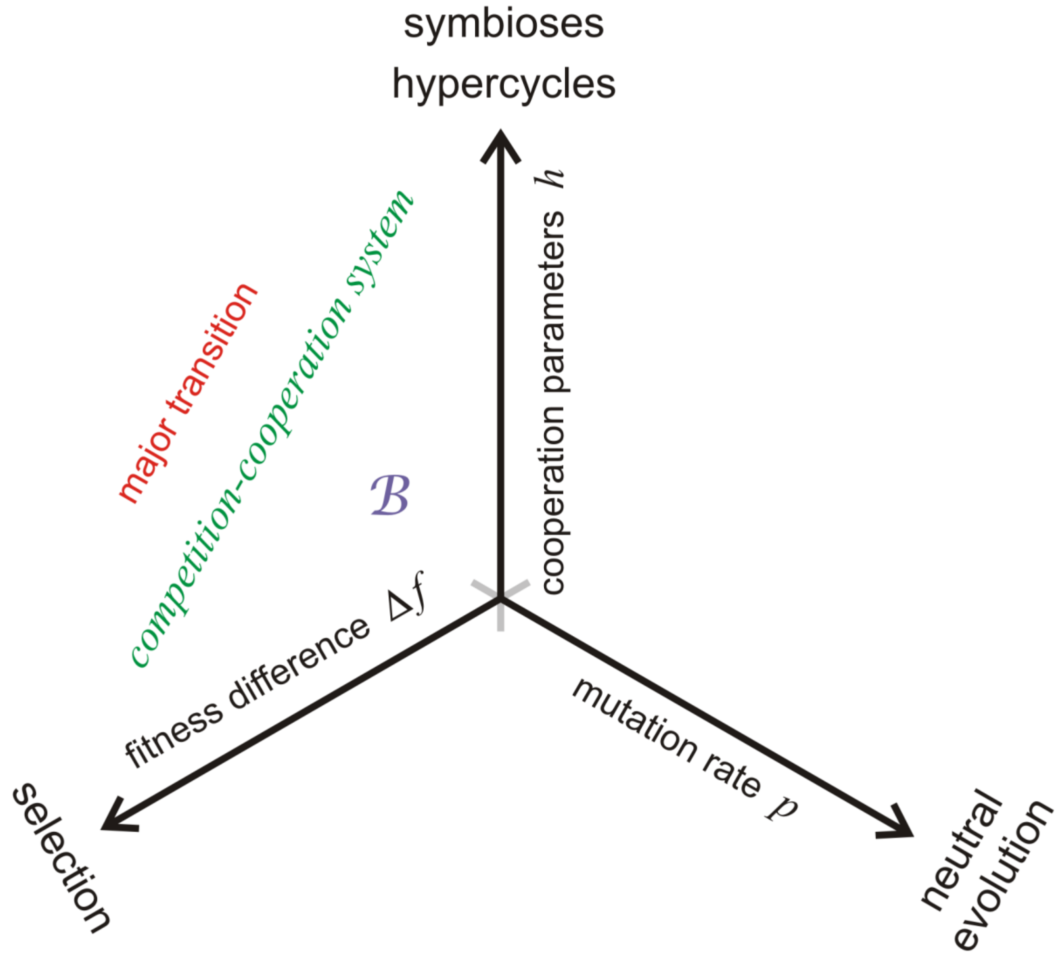
3. **Cooperation and major transitions**

4. Can mutations counteract extinction ?

5. Some conclusions



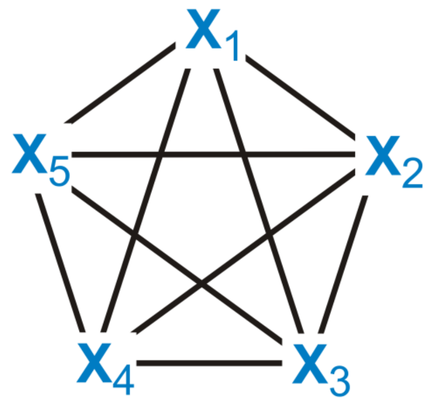
Competition and cooperation: major transition

$$
\begin{aligned}
* &\xrightarrow{a_0\, r} \mathbf{A}\ , \\
\mathbf{A} + \mathbf{X}_j &\xrightarrow{k_j} 2\,\mathbf{X}_j\ ; \quad j = 1, \ldots, n\ , \\
\mathbf{A} + \mathbf{X}_j + \mathbf{X}_i &\xrightarrow{l_{ji}} 2\,\mathbf{X}_j + \mathbf{X}_i\ ; \ i, j = 1, \ldots, n \\
\mathbf{A} &\xrightarrow{r} \varnothing\ , \quad \text{and} \\
\mathbf{X}_j &\xrightarrow{r} \varnothing\ ; \ j = 1, \ldots, n\ .
\end{aligned}
$$

A simple model for the analysis of competition and cooperation

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

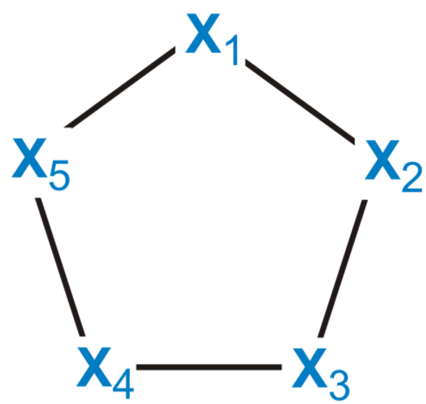
n^2 catalytic terms



A simple model for the analysis of competition and cooperation

$$\mathbf{A} + \mathbf{X}_i + \mathbf{X}_{i+1} \xrightarrow{\;\; l_i \;\;} 2\,\mathbf{X}_i + \mathbf{X}_{i+1}\,;\;\; i,j = 1,\ldots,n$$

n catalytic terms



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

A still simpler model for the analysis of competition and cooperation

$$
\begin{aligned}
* \quad &\xrightarrow{a_0\, r} \quad \mathbf{A}\ , \\
\mathbf{A} + \mathbf{X}_i \quad &\xrightarrow{k_i} \quad 2\,\mathbf{X}_i\ ; \quad i = 1, \ldots, n\ , \\
\mathbf{A} + \mathbf{X}_i + \mathbf{X}_{i+1} \quad &\xrightarrow{l_i} \quad 2\,\mathbf{X}_i + \mathbf{X}_{i+1}\ ;\ i, j = 1, \ldots, n \\
\mathbf{A} \quad &\xrightarrow{r} \quad \varnothing\ , \quad \text{and} \\
\mathbf{X}_i \quad &\xrightarrow{r} \quad \varnothing\ ;\ i = 1, \ldots, n\ .
\end{aligned}
$$

A still simpler model for the analysis of competition and cooperation

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

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

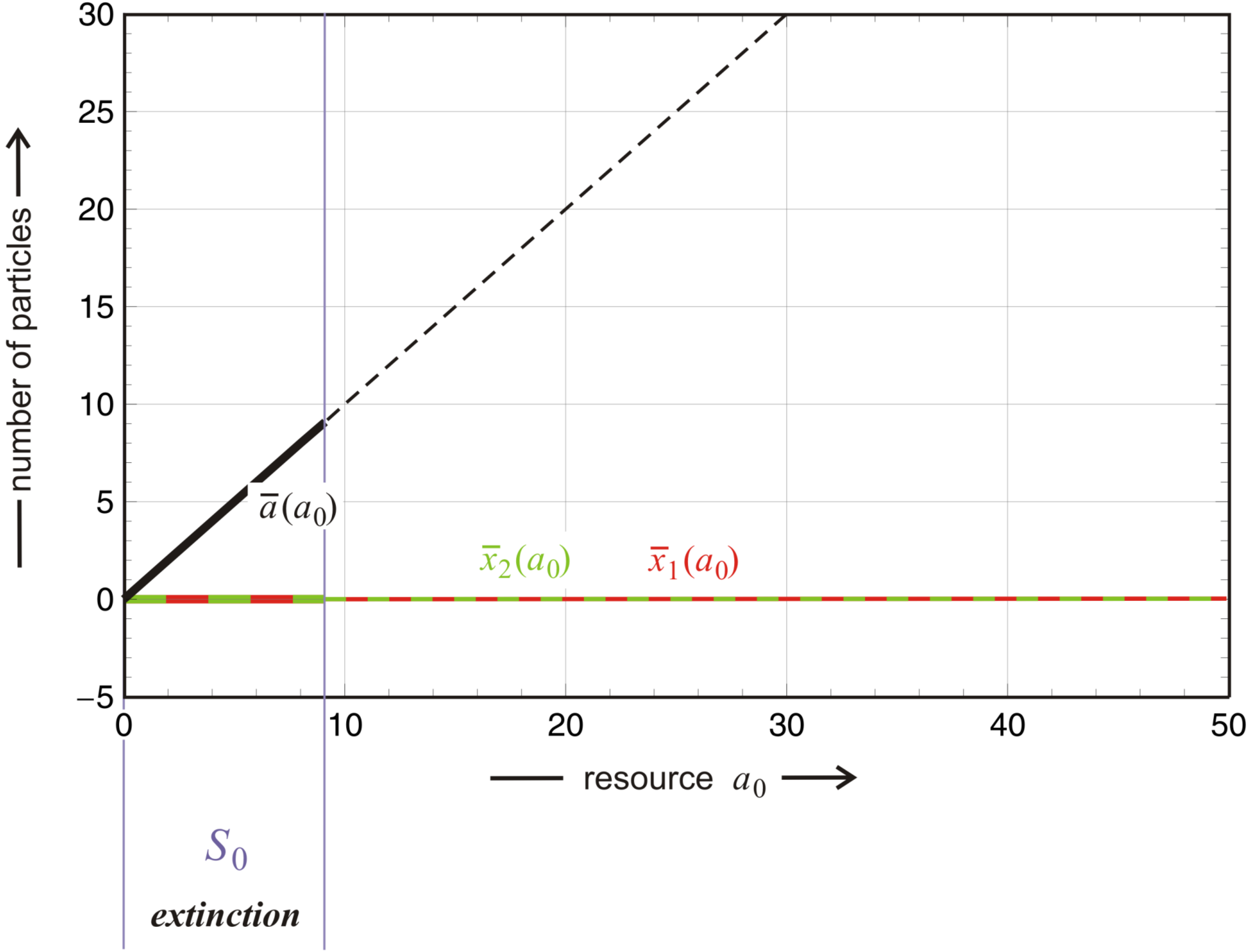
$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = x_j\Big(\big(k_j + l_j x_{j+1}\big)\,a - r\Big)\,;\ j = 1, \ldots, n\,;\ j \mod n$$

quasi-stationary solutions: (i) $\bar{x}_j = 0\,;\ j = 1, \ldots, n$

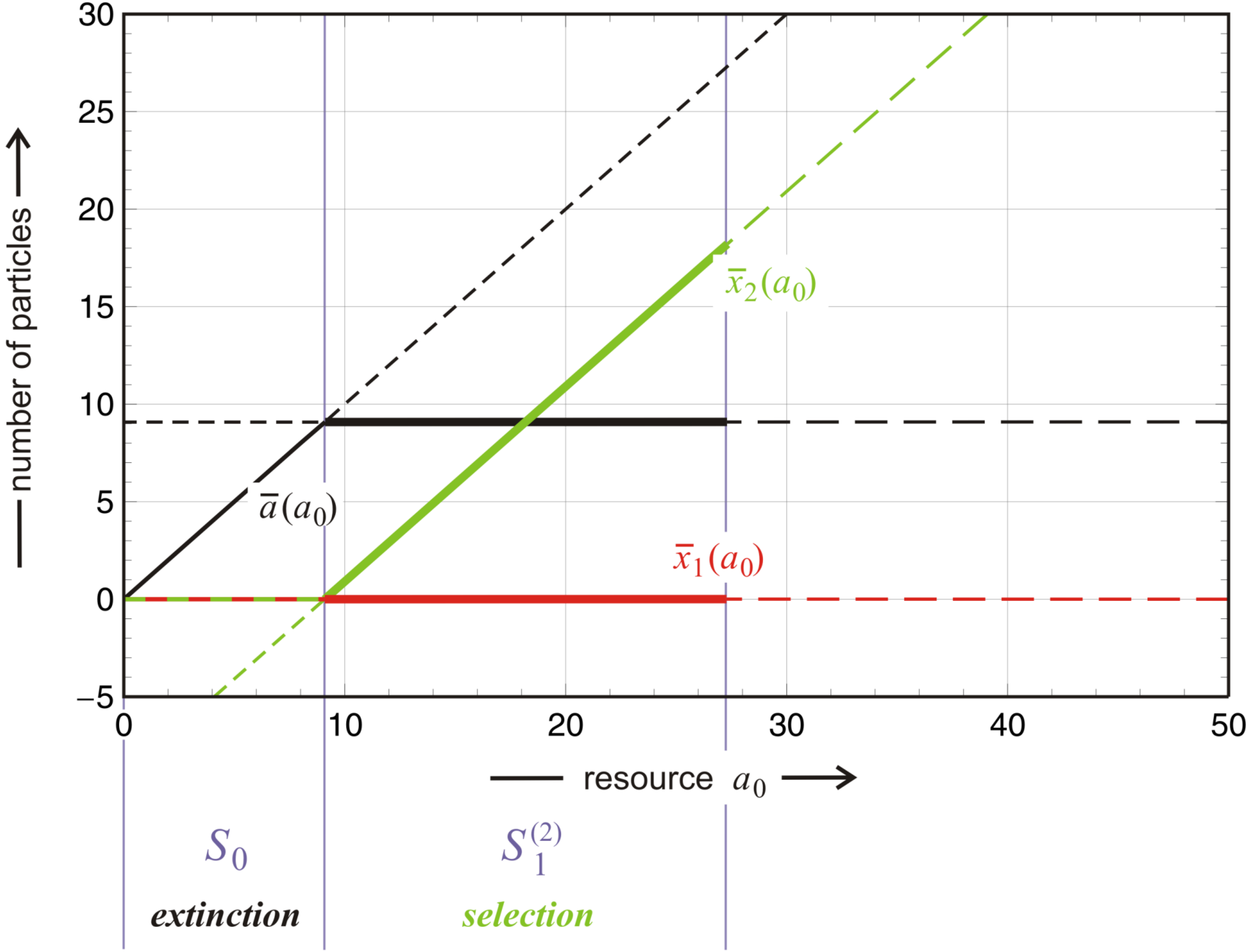
(ii) $\big(k_j + l_j \bar{x}_{j+1}\big)\,\bar{a} - r = 0\,;\ j \mod n$

In case of compatibility and linearity the number of stationary solutions is 2^n.

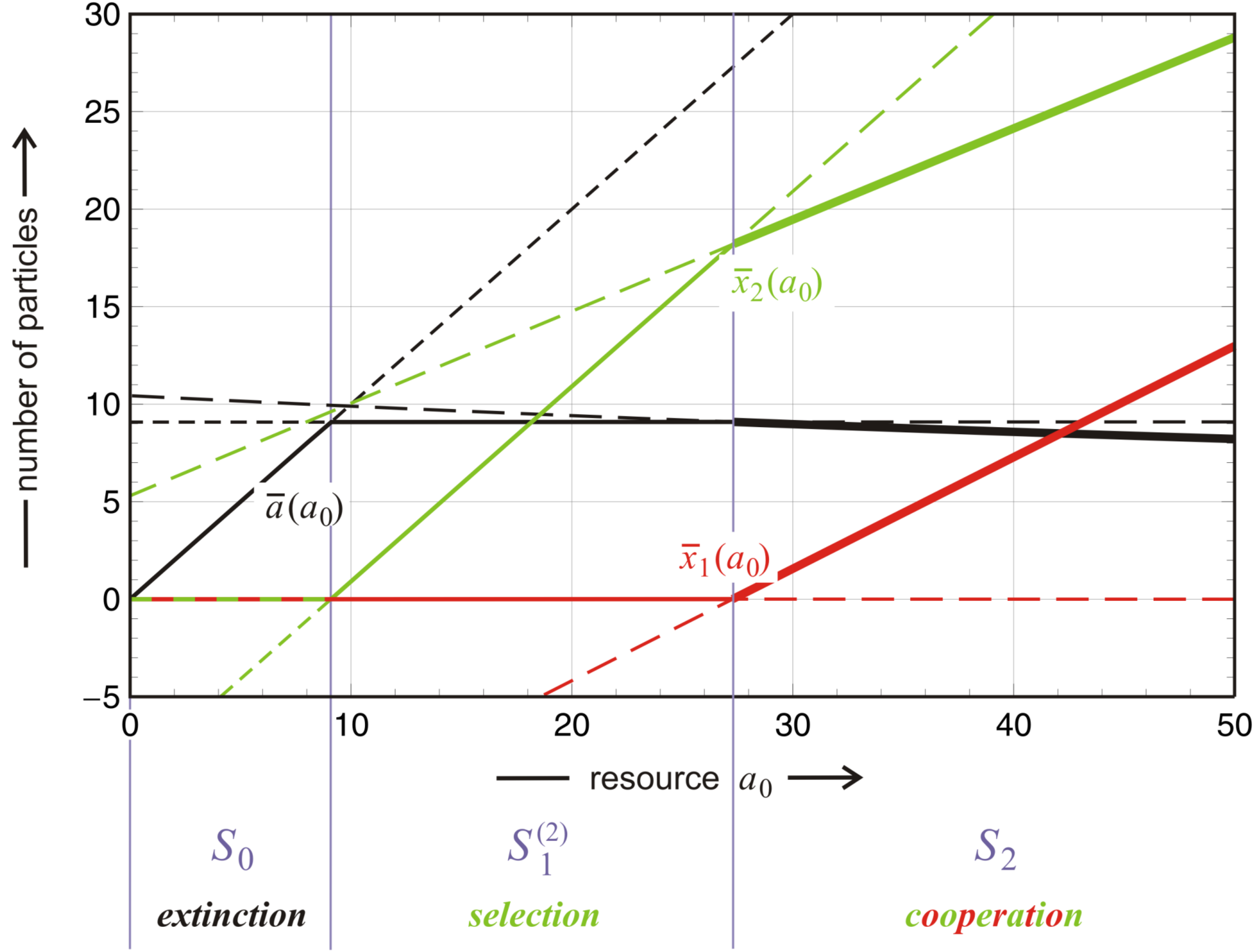
Kinetic differential equations and stationary solutions



number of particles
resource a_0
$\bar{a}(a_0)$
$\bar{x}_2(a_0)$
$\bar{x}_1(a_0)$
S_0
extinction



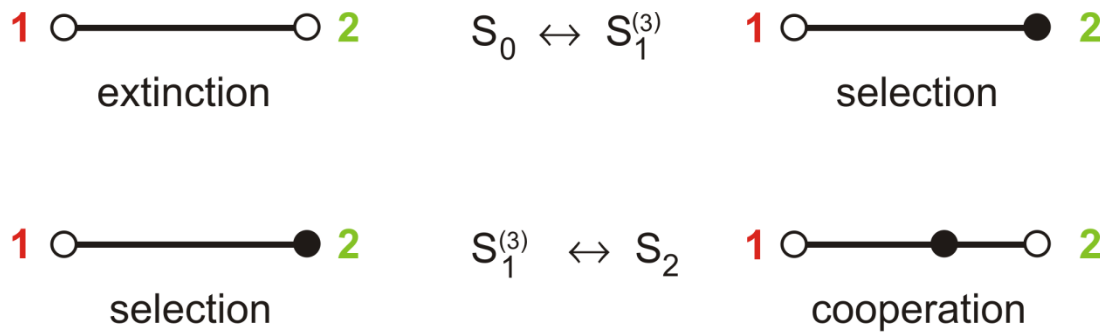
number of particles
30
25
20
15
10
5
0
−5
0
10
20
30
40
50
resource a_0
$\bar{a}(a_0)$
$\bar{x}_2(a_0)$
$\bar{x}_1(a_0)$
S_0
$S_1^{(2)}$
extinction
selection



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

increasing a_0-values

$k_1 < k_2$ and $l_1 > l_2$



Name	Symbol	Stationary Values			Stability Range
		$\overline{a}$	$\overline{x}_1$	$\overline{x}_2$	
extinction	S_0	a_0	0	0	$0 \leq a_0 \leq \frac{r}{k_2}$
selection	$S_1^{(2)}$	$\frac{r}{k_2}$	0	$a_0 - \frac{r}{k_2}$	$\frac{r}{k_2} \leq a_0 \leq \frac{r}{k_2} + \frac{k_2 - k_1}{l_1}$
cooperation	S_2	α	$\frac{r - k_2 \alpha}{l_2 \alpha}$	$\frac{r - k_1 \alpha}{l_1 \alpha}$	$\frac{r}{k_2} + \frac{k_2 - k_1}{l_1} \leq a_0$

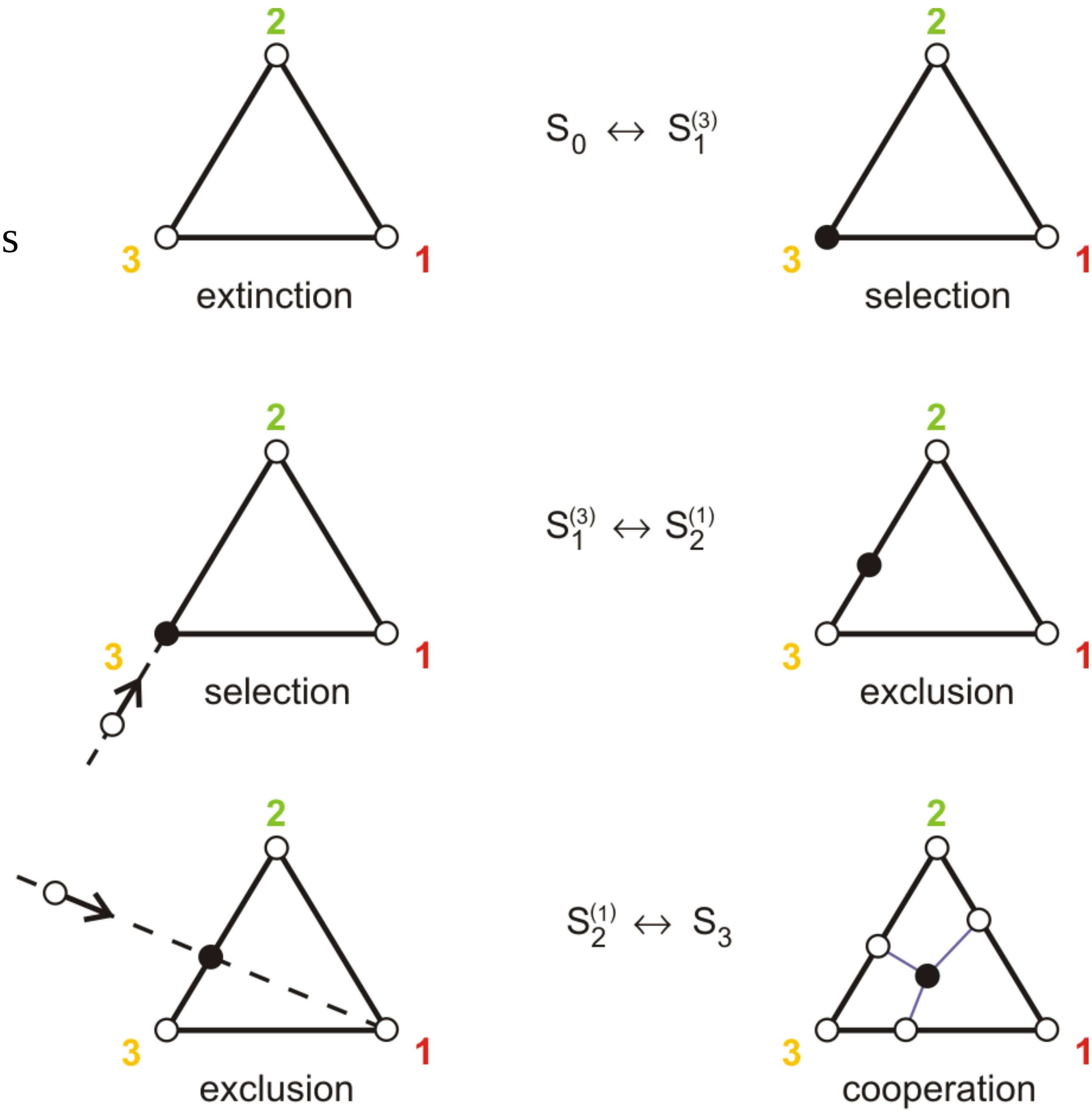
$$\overline{a}_{S_2} = \alpha = \frac{1}{2}\left(a_0 + \psi - \sqrt{(a_0 + \psi)^2 - 4r\phi}\right) \text{ with } \psi = \sum_{i=1}^{n} \frac{k_i}{l_i}, \ \phi = \sum_{i=1}^{n} \frac{1}{l_i}$$

$$r \leq \frac{1}{4\phi}(a_0 + \psi)^2$$

$k_1 < k_2 < k_3$

$l_1 > l_2 > l_3$

increasing a_0-values



$$k_1 < k_2 < k_3 \text{ and } l_1 > l_2 > l_3$$

increasing a_0-values

Name	Symbol	Stationary Values				Stability Range
		$\overline{a}$	$\overline{x}_1$	$\overline{x}_2$	$\overline{x}_3$	
extinction	S_0	a_0	0	0	0	$0 \leq a_0 \leq \frac{r}{k_3}$
selection	$S_1^{(3)}$	$\frac{r}{k_3}$	0	0	$a_0 - \frac{r}{k_3}$	$\frac{r}{k_3} \leq a_0 \leq \frac{r}{k_3} + \frac{k_3-k_2}{l_2}$
exclusion	$S_2^{(1)}$	$\frac{r}{k_3}$	0	$a_0 - \frac{r}{k_3} - \frac{k_3-k_2}{l_2}$	$\frac{k_3-k_2}{l_2}$	$\frac{r}{k_3} + \frac{k_3-k_2}{l_2} \leq a_0 \leq \frac{r}{k_3} + \frac{k_3-k_2}{l_2} + \frac{k_3-k_1}{l_1}$
cooperation	S_3	α	$\frac{r-k_3\alpha}{l_3\alpha}$	$\frac{r-k_1\alpha}{l_1\alpha}$	$\frac{r-k_2\alpha}{l_2\alpha}$	$\frac{r}{k_3} + \frac{k_3-k_2}{l_2} + \frac{k_3-k_1}{l_1} \leq a_0$

$$\overline{a}_{S_2} = \alpha = \frac{1}{2}\left(a_0 + \psi - \sqrt{(a_0+\psi)^2 - 4r\phi}\right) \text{ with } \psi = \sum_{i=1}^{n} \frac{k_i}{l_i}\,,\ \phi = \sum_{i=1}^{n} \frac{1}{l_i}$$

$$r \leq \frac{1}{4\phi}(a_0+\psi)^2$$

$$
\begin{aligned}
* \quad &\xrightarrow{a_0\, r} \quad \mathbf{A}\ , \\
\mathbf{A} + \mathbf{X}_j + \mathbf{X}_{j+1} \quad &\xrightarrow{l_i} \quad 2\,\mathbf{X}_j + \mathbf{X}_{j+1}\,;\ \ j = 1,\ldots,n;\ j \bmod n\ , \\
\mathbf{A} \quad &\xrightarrow{r} \quad \varnothing\ , \quad \text{and} \\
\mathbf{X}_j \quad &\xrightarrow{r} \quad \varnothing\,;\ \ j = 1,\ldots,n\ .
\end{aligned}
$$

Hypercycle dynamics in the flow reactor

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

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

change of coordinates: $\xi_{j+1} = l_j\, x_{j+1}$ leads to

$$\frac{\mathrm{d}\xi_j}{\mathrm{dt}} = \xi_j(a\,\xi_{k+1} - r);\; j = 1,\ldots,n;\; j, j+1 \bmod n$$

$$\bar{\boldsymbol{\xi}} = (\bar{\xi}_1,\ldots,\bar{\xi}_n) = \left(\frac{r}{\bar{a}},\ldots,\frac{r}{\bar{a}}\right),\; \bar{\xi}_j = \bar{\xi} = r\,/\,\bar{a}$$

$$\bar{\xi} = \frac{1}{2\phi}\left(a_0 + \sqrt{a_0^2 - 4r\phi}\right)$$

eigenvalues of the Jacobian: $\omega_k;\; k = 0, 1, \ldots, n-1$

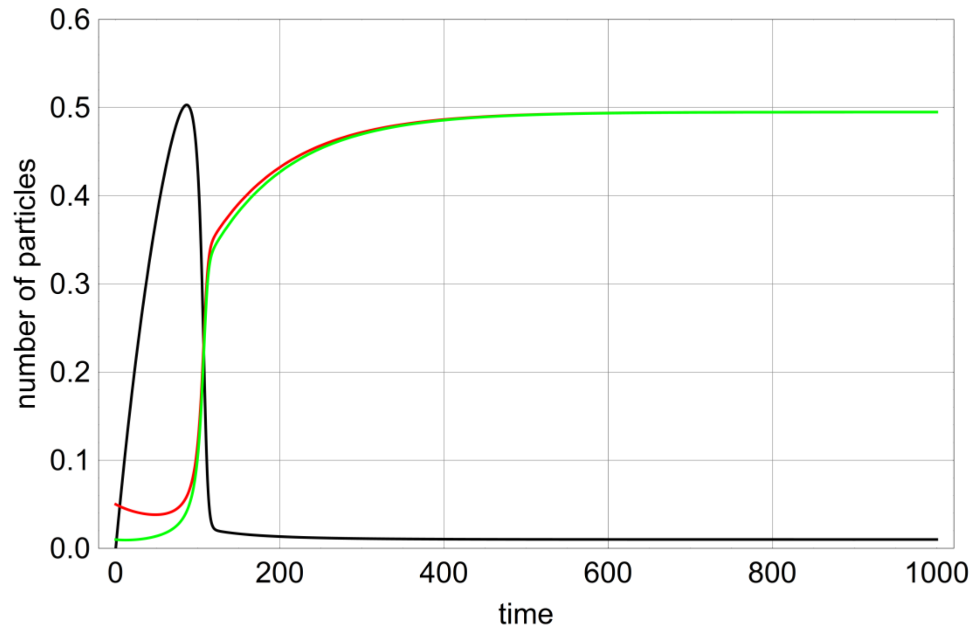
$$\omega_0 = \bar{\xi}\left(a_0 - 2\bar{\xi}\phi\right) < 0 \;\text{ and }\; \omega_k = r\exp\left(\frac{2\pi\, \imath}{n}\, k\right)$$

barycentric transformation

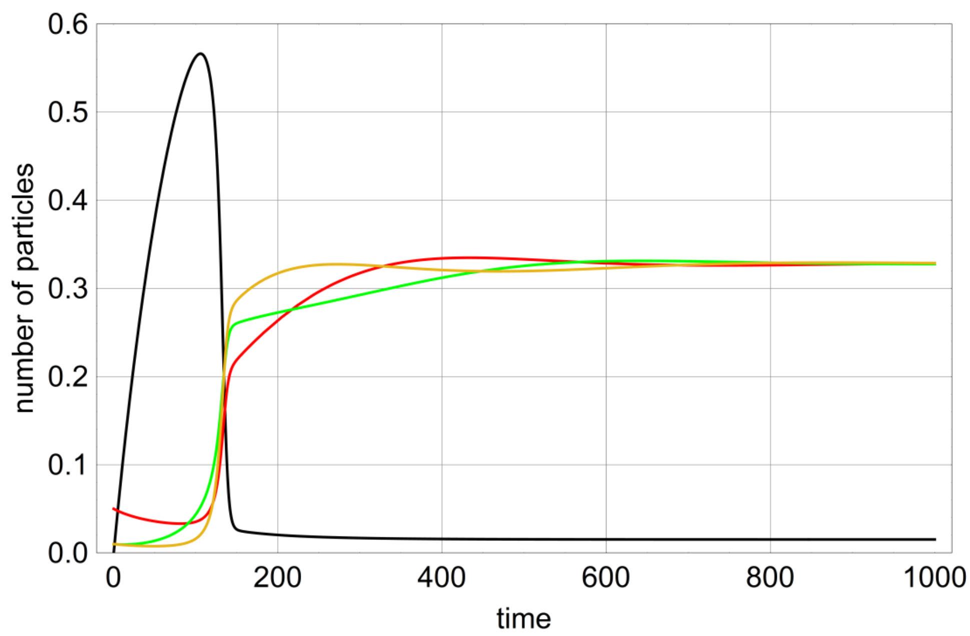
Long-time behavior of hypercycles in the flow reactor

P. Schuster, K. Sigmund. Dynamics of evolutionary optimization. *Ber.Bunsenges.Phys.Chem.* **89**:668-682, 1985.

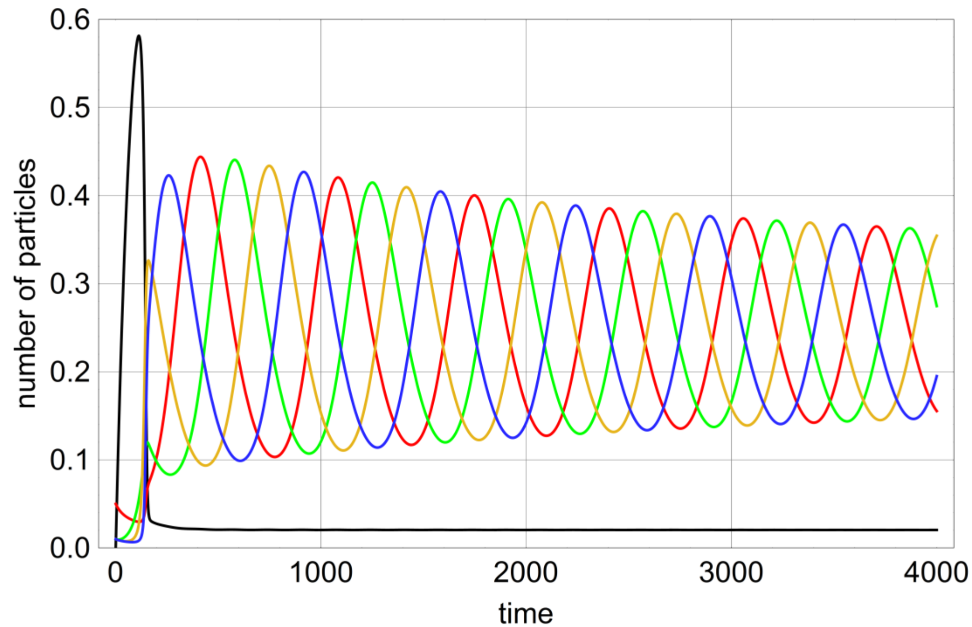
$n = 2$
$l_1 = l_2 = 2$, $r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.05$, $x_2(0) = 0.01$



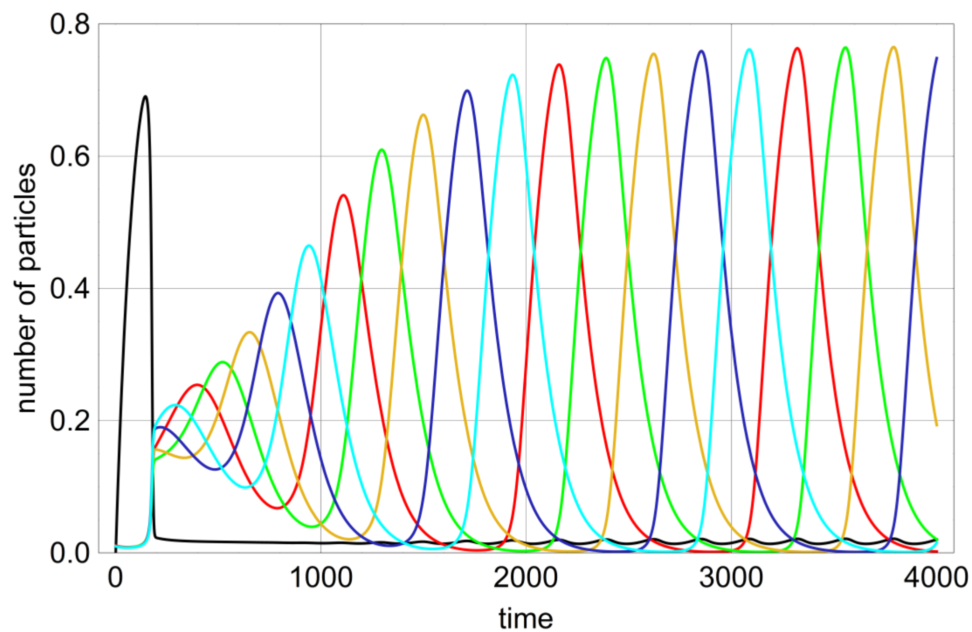
$n = 3$
$l_1 = l_2 = l_3 = 2$, $r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.05$,
$x_2(0) = x_3(0) = 0.01$



$n = 4$
$l_1 = l_2 = l_3 = l_4 = 2$, $r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.05$,
$x_2(0) = x_3(0) = x_4(0) = 0.01$



$n = 5$
$l_1 = l_2 = l_3 = l_4 = l_5 = 3$,
$r = 0.01$, $a_0 = 1$
$a(0) = 0$, $x_1(0) = 0.011$,
$x_2(0) = x_3(0) = x_4(0) = x_5(0) = 0.01$



$$[\mathbf{A}] = \mathrm{m}\,, \ [\mathbf{X}_j] = \mathrm{s}_j\,; \ j = 1, \ldots, n$$

$$\mathbf{X} = (\mathrm{m}, \mathrm{s}_j; j = 1, \ldots, n)$$

$$(\mathbf{X}; \mathrm{s}'_k) = (\mathrm{m}, \mathrm{s}_1, \ldots, \mathrm{s}_k = k', \ldots, n) = (\mathrm{s}'_k)$$

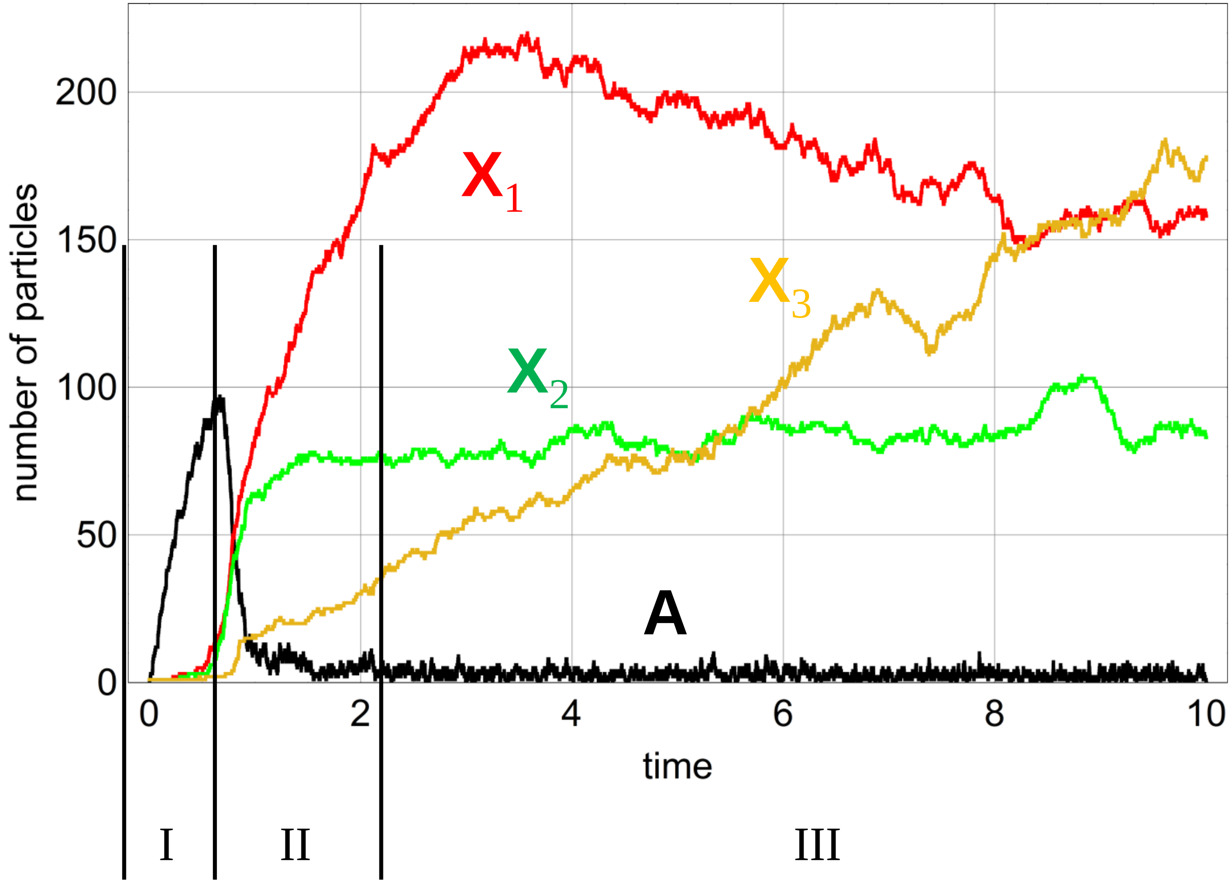
$$P_{\mathbf{X}}(t) = \mathrm{Prob}\Big([\mathbf{A}(t)] = \mathrm{m}, [\mathbf{X}_j(t)] = \mathrm{s}_j\,; \ j = 1, \ldots, n\Big)$$

$$\frac{\mathrm{d}P_{\mathbf{X}}}{\mathrm{dt}} = a_0\, r\, P_{(\mathrm{m}-1)} + r\Big((\mathrm{m}+1) P_{(\mathrm{m}+1)} + \sum_{j=1}^{n} (\mathrm{s}_j + 1) P_{(\mathrm{s}+1)}\Big) +$$

$$+ (\mathrm{m}+1) \sum_{j=1}^{n} \Big((k_j + l_j\, \mathrm{s}_{j+1})(\mathrm{s}_j - 1) P_{(\mathrm{m}+1, \mathrm{s}_j - 1)}\Big) -$$

$$- \Bigg(r\Big(a_0 + \mathrm{m} + \sum_{j=1}^{n} \mathrm{s}_j\Big) + \mathrm{m}\Big(\sum_{j=1}^{n} (f_j + k_j\, \mathrm{s}_{j+1})\, \mathrm{s}_j\Big)\Bigg) P_{\mathbf{X}}$$

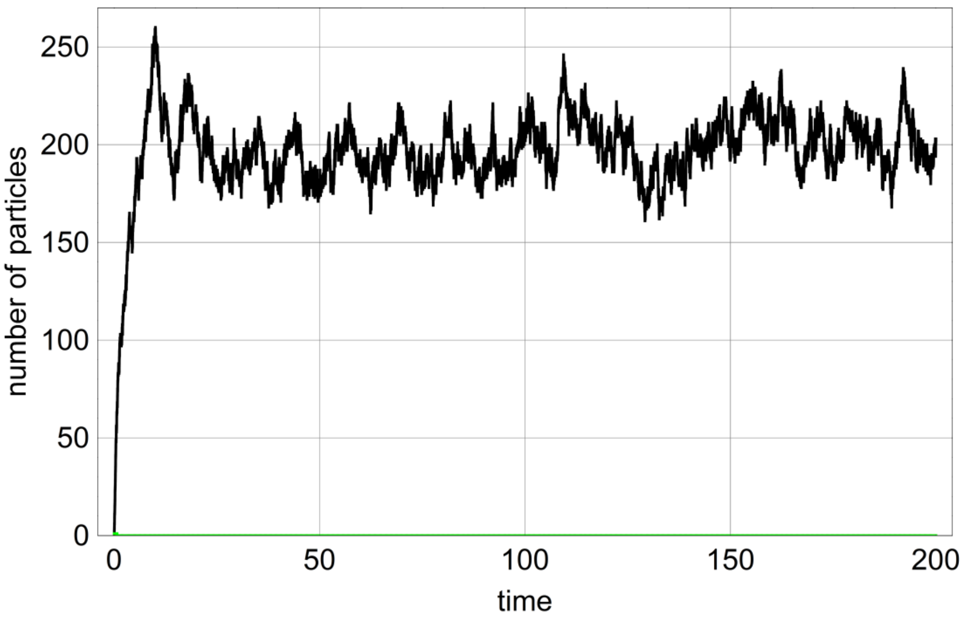
The master equation for competition and cooperation



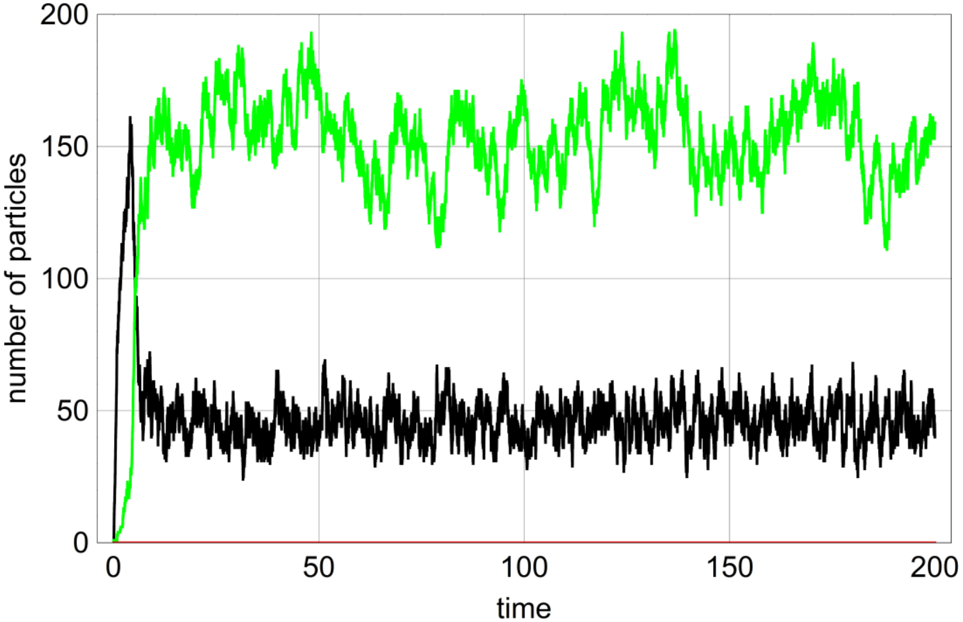
phase I: raise of [**A**] ; phase II: random choice of quasistationary state ;

phase III: convergence to quasistationary state

Gillespie simulation: D.T. Gillespie, Annu.Rev.Phys.Chem. 58:35-55, 2007



extinction and selection

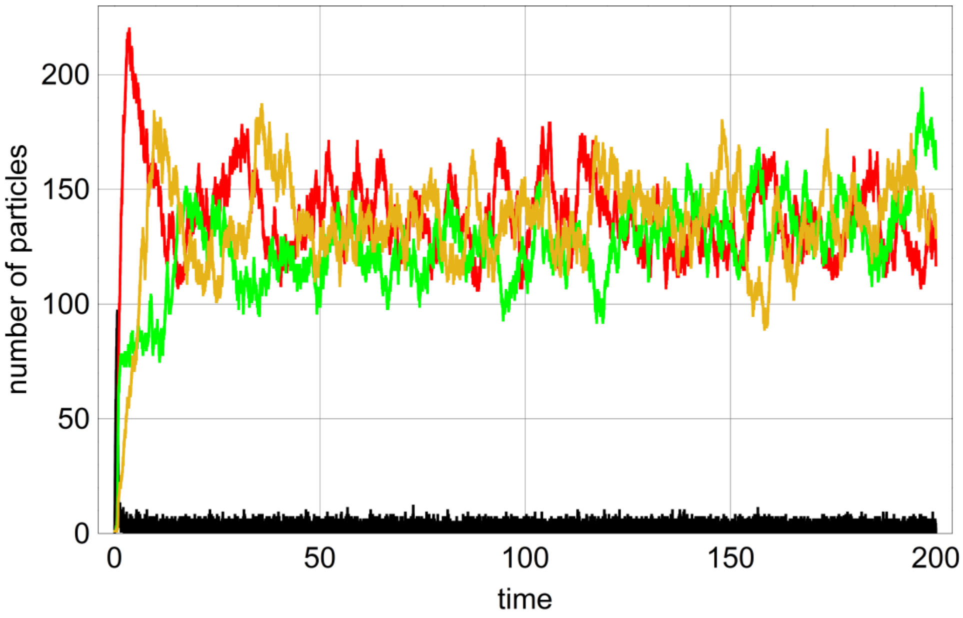


Initial values		Final states		
$X_1(0)$	$X_2(0)$	N_{S_0}	$N_{S_1^{(1)}}$	$N_{S_1^{(2)}}$
1	1	263.1 ± 10.32	503.2 ± 15.99	233.6 ± 13.07
2	2	71.5 ± 8.16	741.5 ± 8.89	187.0 ± 7.33
3	3	20.0 ± 3.94	873.8 ± 9.54	106.1 ± 11.15
4	4	5.9 ± 2.81	933.1 ± 11.01	60.5 ± 9.37

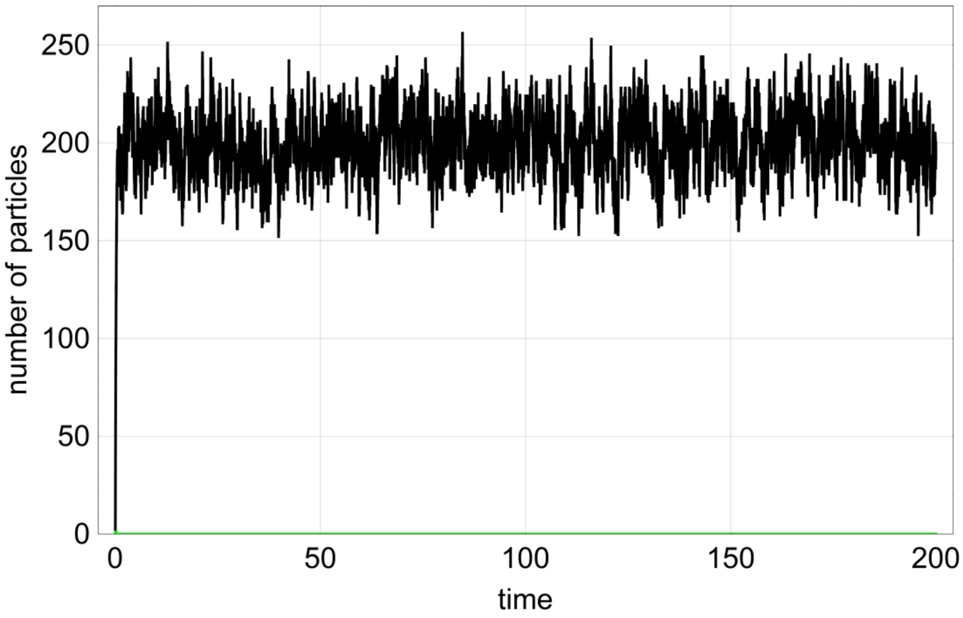
Choice of parameters: $k_1 = 0.11$ [$M^{-1}t^{-1}$]; $k_2 = 0.09$ [$M^{-1}t^{-1}$]; $a_0 = 200$; $r = 0.5$ [Vt^{-1}]

Counting of final states

quasistationary state of
cooperation

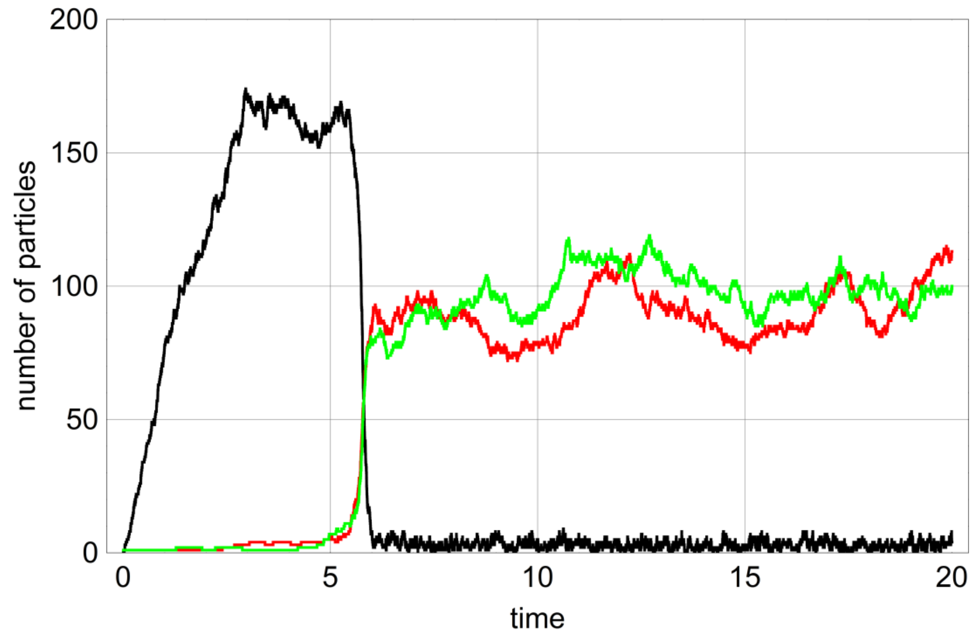


absorbing state of
extinction



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

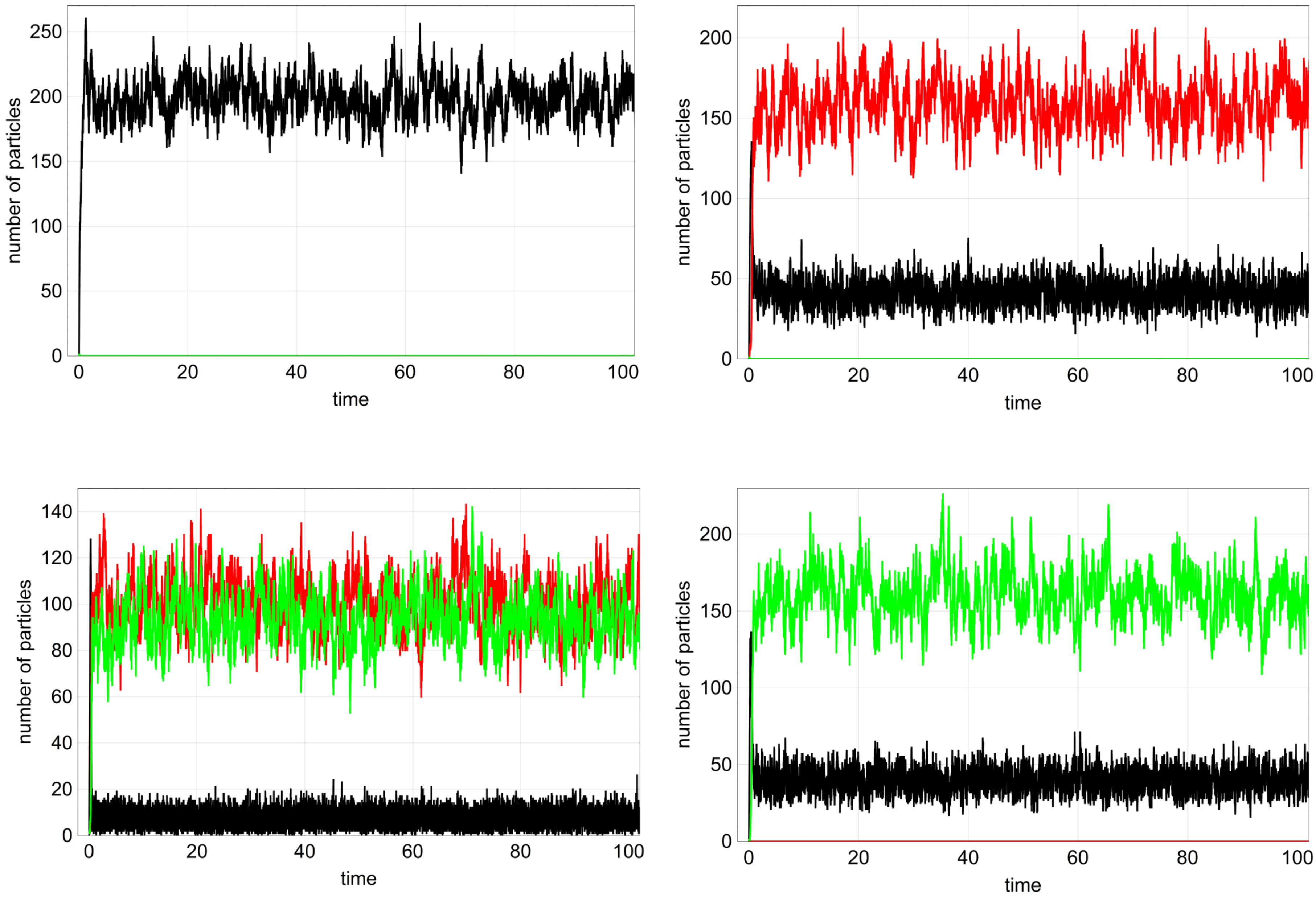
$l_1 = l_2 = 0.01$ [$M^{-1}t^{-1}$]



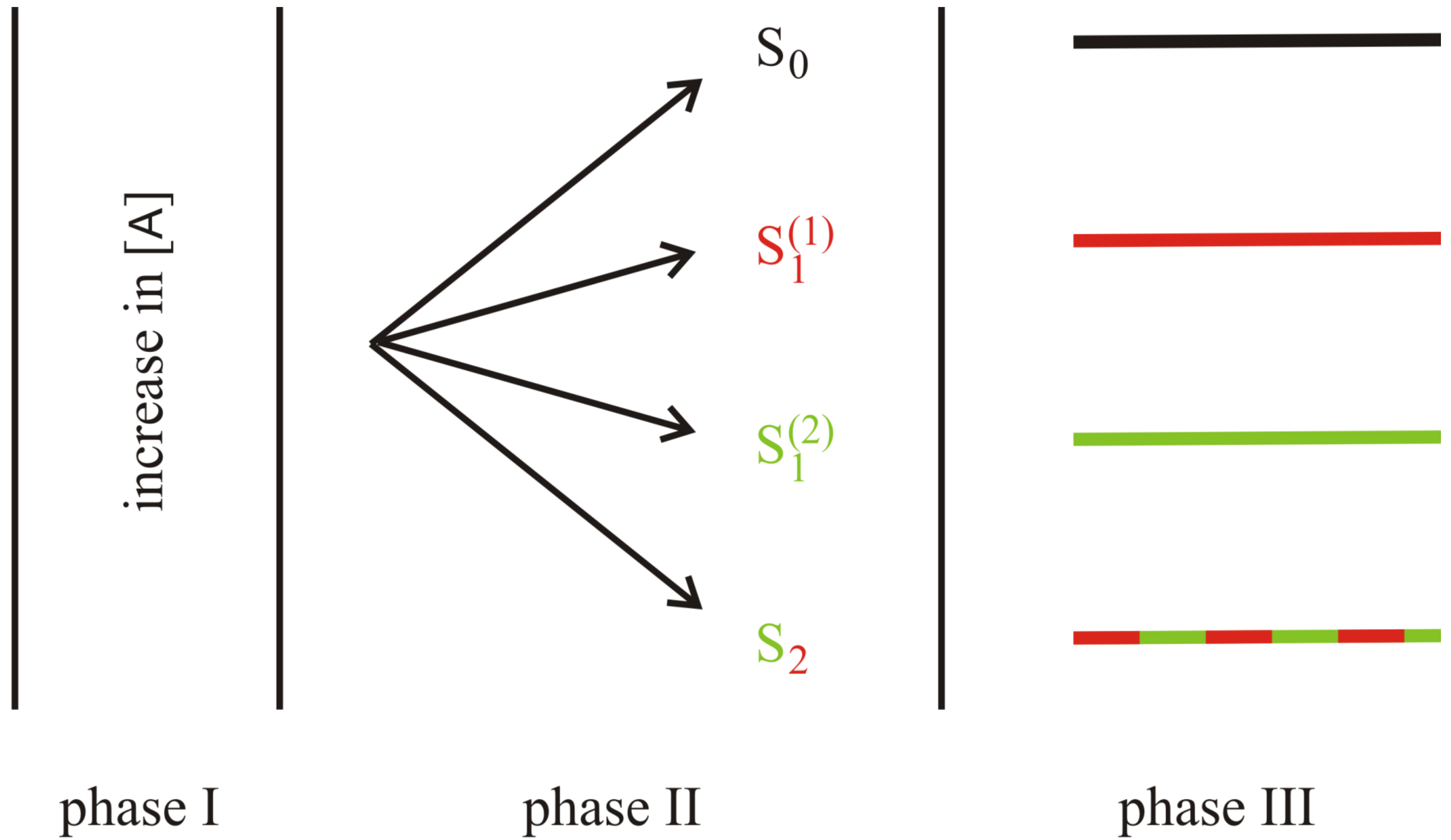
$l_1 = l_2 = 0.002$ [$M^{-1}t^{-1}$]

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

Stochastic cooperation with $n = 2$



Competition and cooperation with $n = 2$



Random decision in the stochastic process

Initial values		Final states			
$X_1(0)$	$X_2(0)$	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	2	14.9 ± 2.6	303.7 ± 16.0	354.5 ± 23.8	9326.8 ± 22.7
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

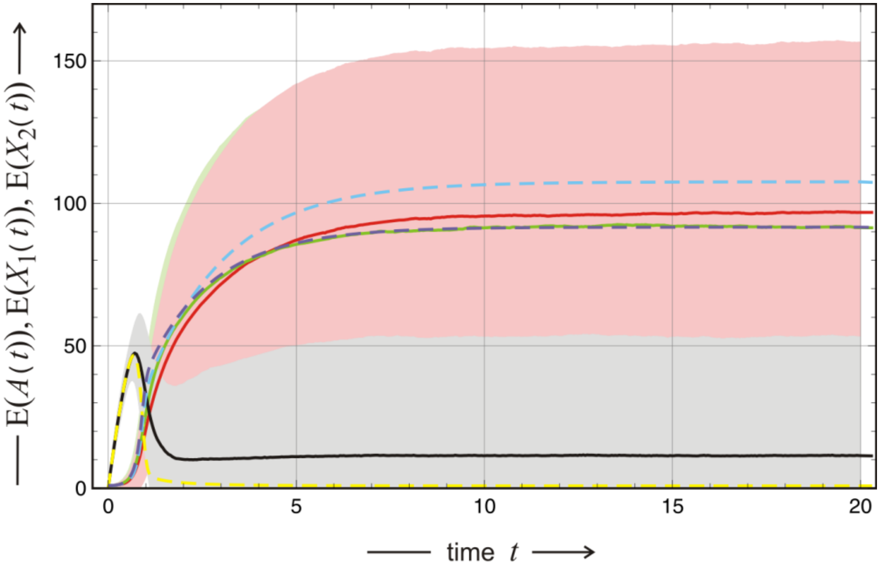
Choice of parameters: $k_1 = 0.011$ [$M^{-1}t^{-1}$]; $k_2 = 0.009$ [$M^{-1}t^{-1}$];

$l_1 = 0.0050$ [$M^{-2}t^{-1}$]; $l_2 = 0.0045$ [$M^{-2}t^{-1}$];

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

Competition and cooperation with $n = 2$

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

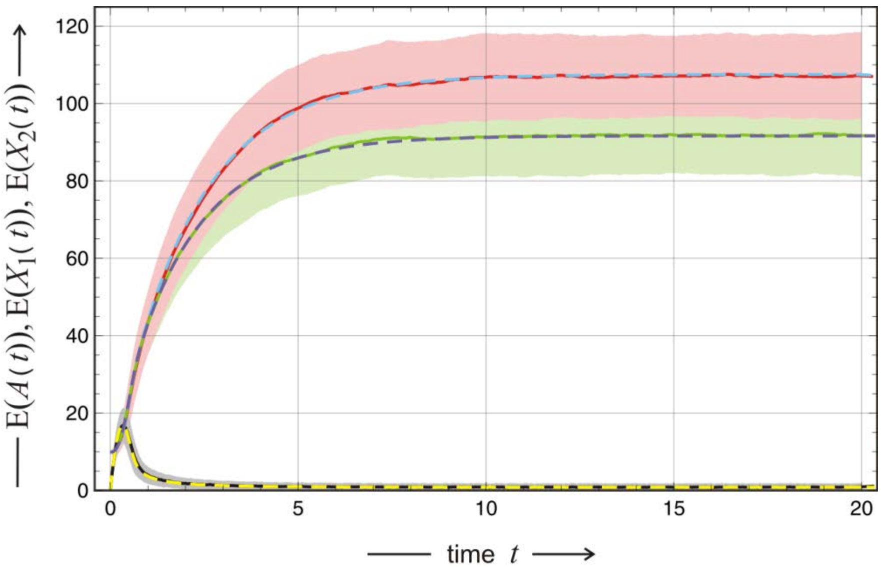


expectation values and 1σ-bands

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

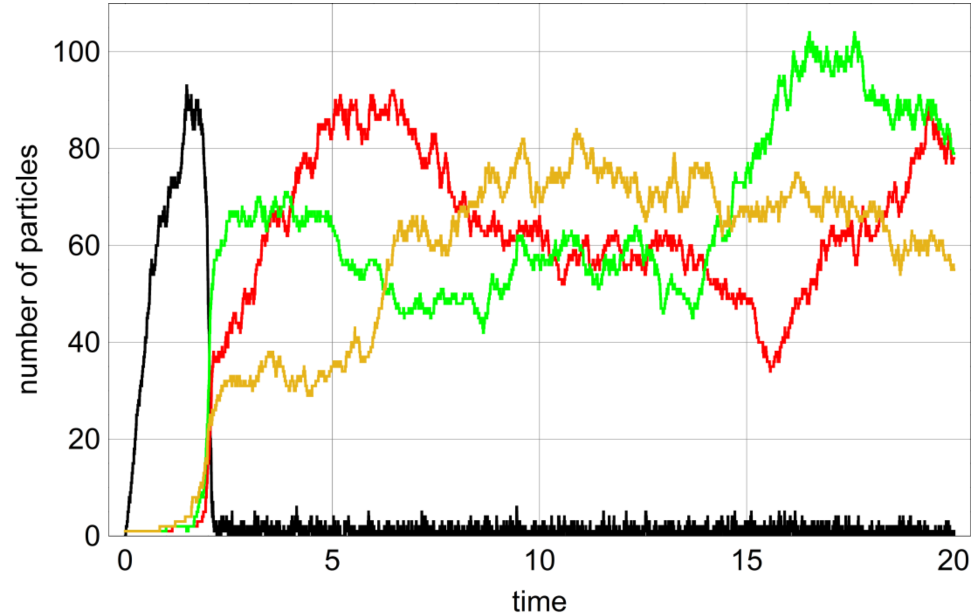
$k_1 = 0.09$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$], $k_2 = 0.11$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$],

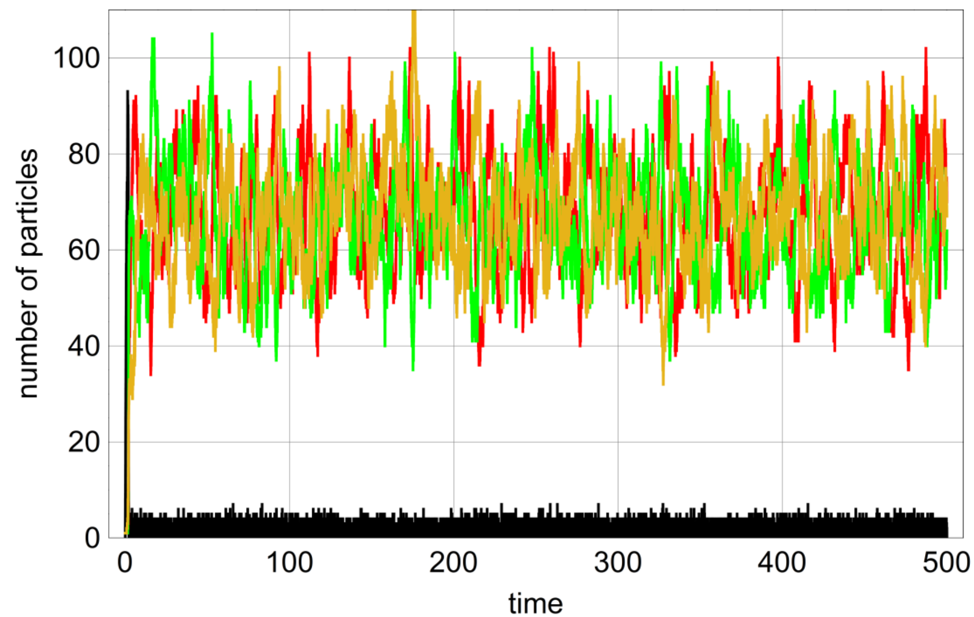
$l_1 = 0.0050$ [$\mathrm{M}^{-2}\mathrm{t}^{-1}$], $l_2 = 0.0045$ [$\mathrm{M}^{-2}\mathrm{t}^{-1}$]



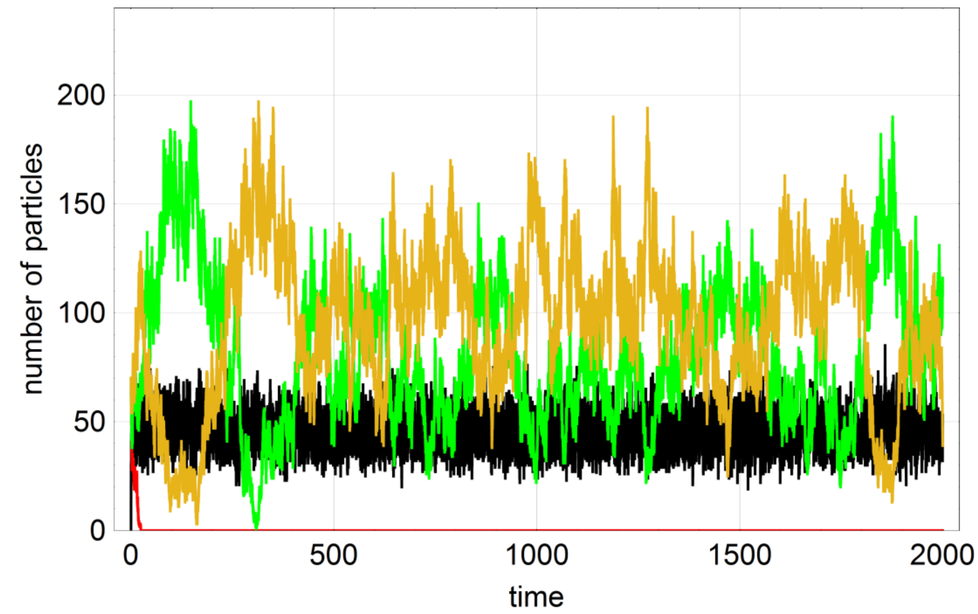
$a(0) = 0,\ x_1(0) = x_2(0) = 10$

stochastic hypercycles with n = 3



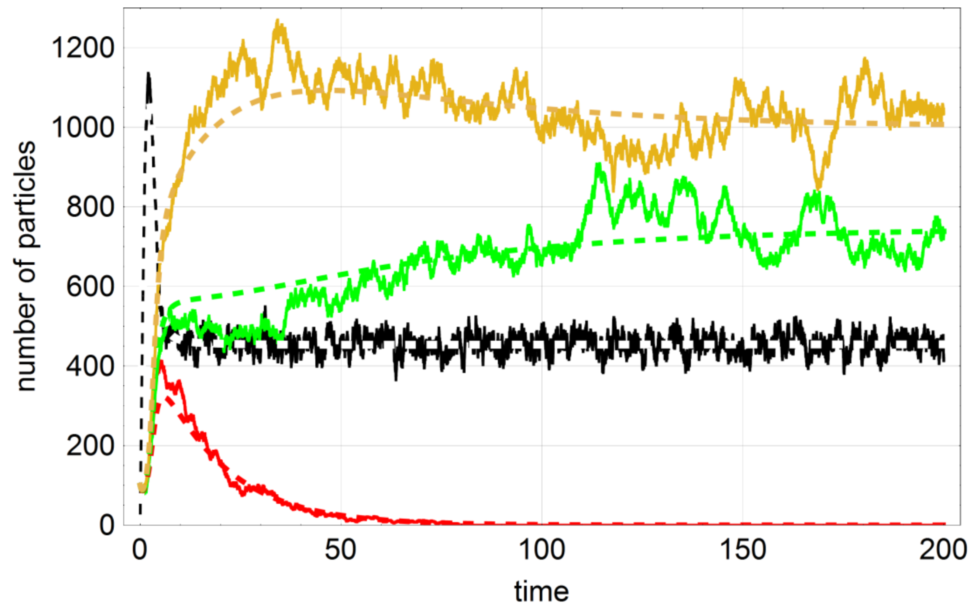


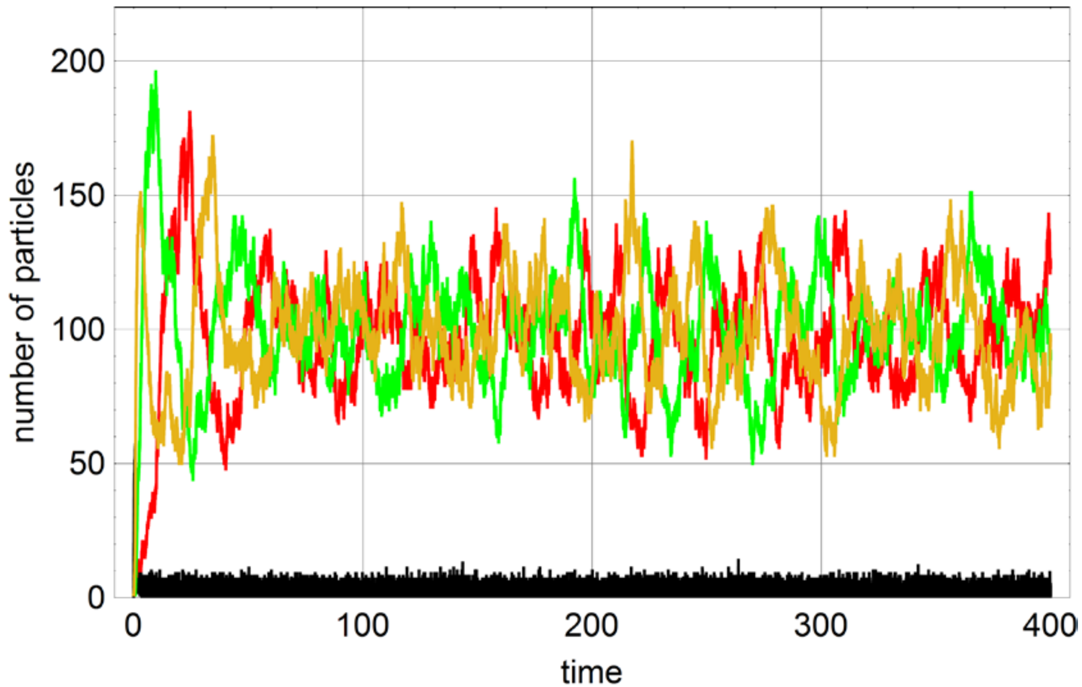
$a_0 = 220$



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

$a_0 = 2200$





n = 3, state of cooperation S_3

$$\frac{dx_i}{dt} = l_i \; x_i \;\; x_{i+1} - r \; x_i$$

$$x_{i+1} = 0 \quad \Rightarrow \quad \frac{dx_i}{dt} = -r \, x_i \le 0 \quad \Rightarrow \quad x_i \to 0$$

Stochastic extinction of hypercycles

$$X_n \Leftarrow X_1 \Leftarrow X_2 \Leftarrow X_3 \Leftarrow X_4 \Leftarrow \cdots \Leftarrow X_{n-1} \Leftarrow X_n$$

$$X_n \Leftarrow X_1 \Leftarrow X_2 \Leftarrow X_3 \Leftarrow X_4 \Leftarrow \cdots \Leftarrow X_{n-1}$$

$$\downarrow$$

$$\downarrow$$

$$X_n \Leftarrow X_1 \Leftarrow X_2 \Leftarrow X_3 \Leftarrow X_4$$

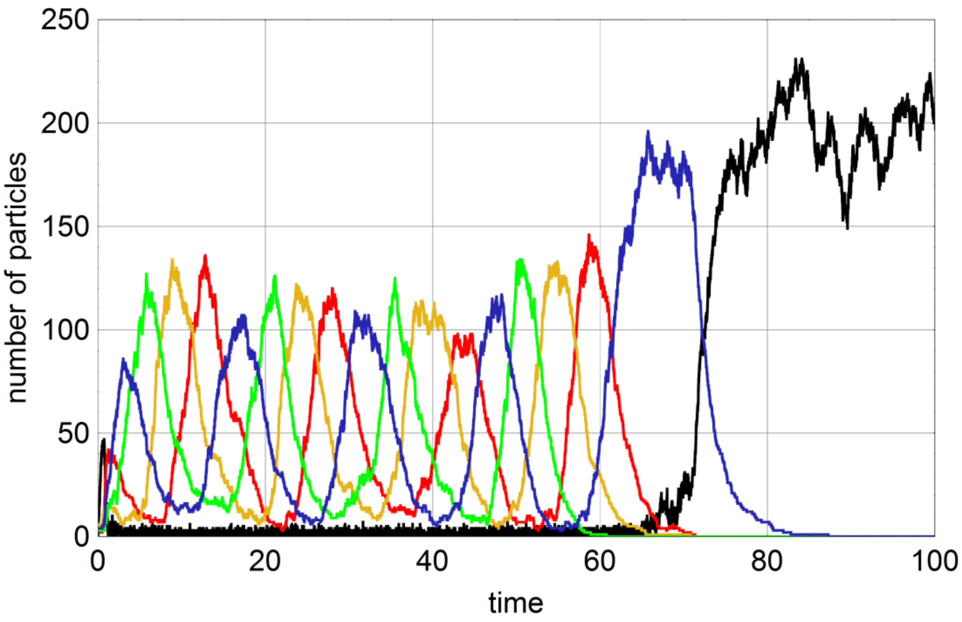
$$X_n \Leftarrow X_1 \Leftarrow X_2 \Leftarrow X_3$$

$$X_n \Leftarrow X_1 \Leftarrow X_2$$

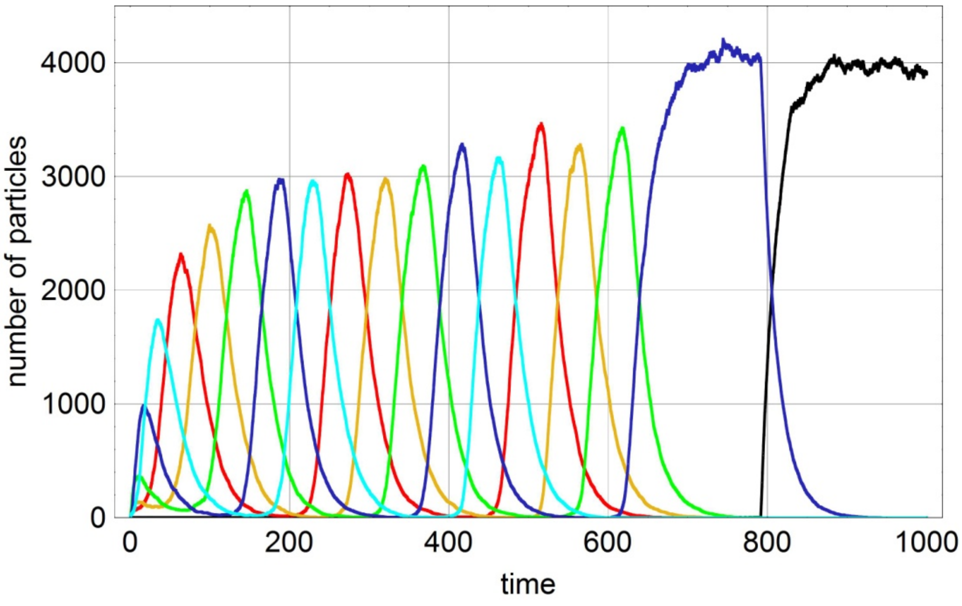
$$X_n \Leftarrow X_1$$

$$X_n$$

Stepwise consecutive extinction of a hypercycle stochastic hypercycles with $n = 4$



stochastic hypercycles with $n = 5$



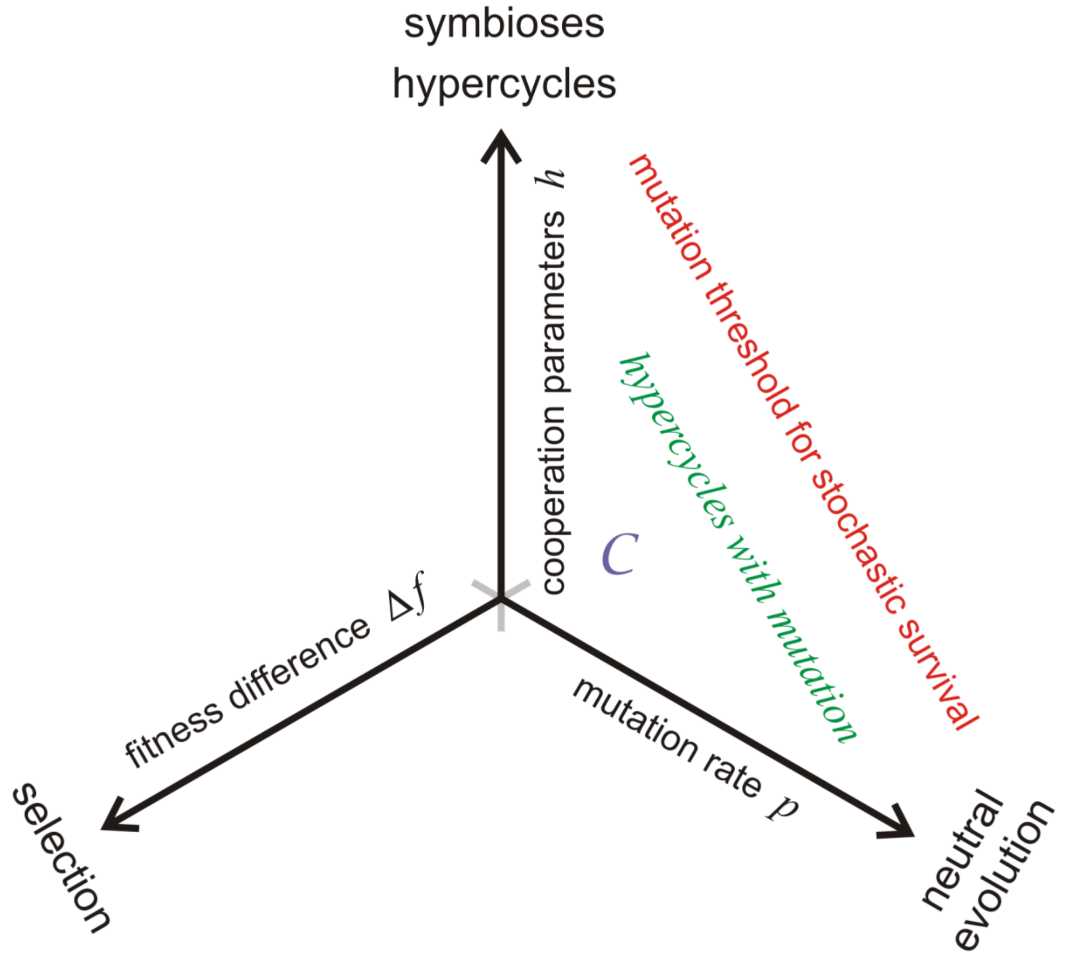
1. A general and simple model for evolution

2. Mutation and quasispecies

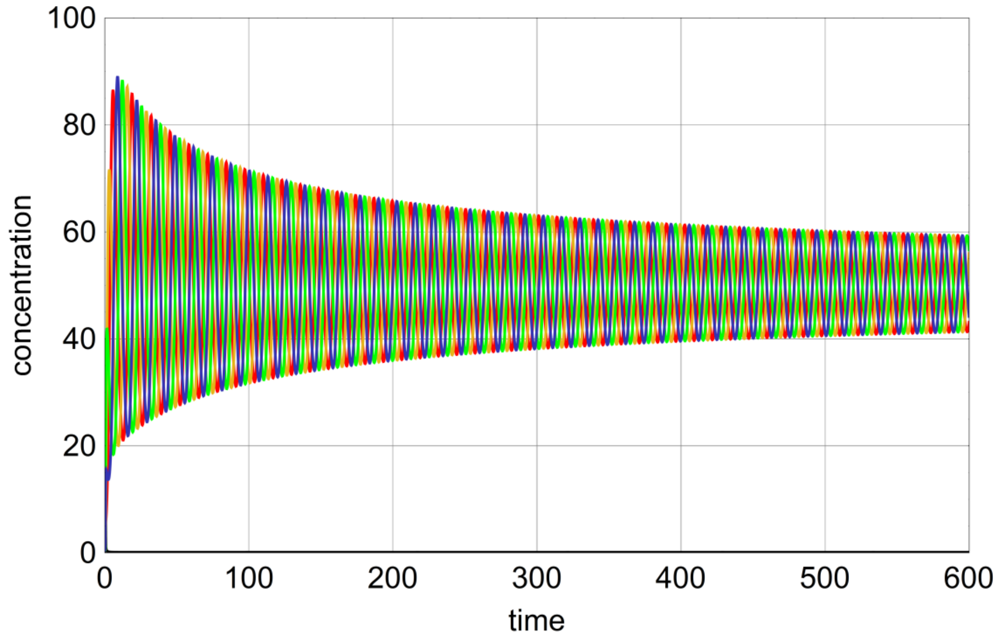
3. Cooperation and major transitions

4. **Can mutations counteract extinction ?**

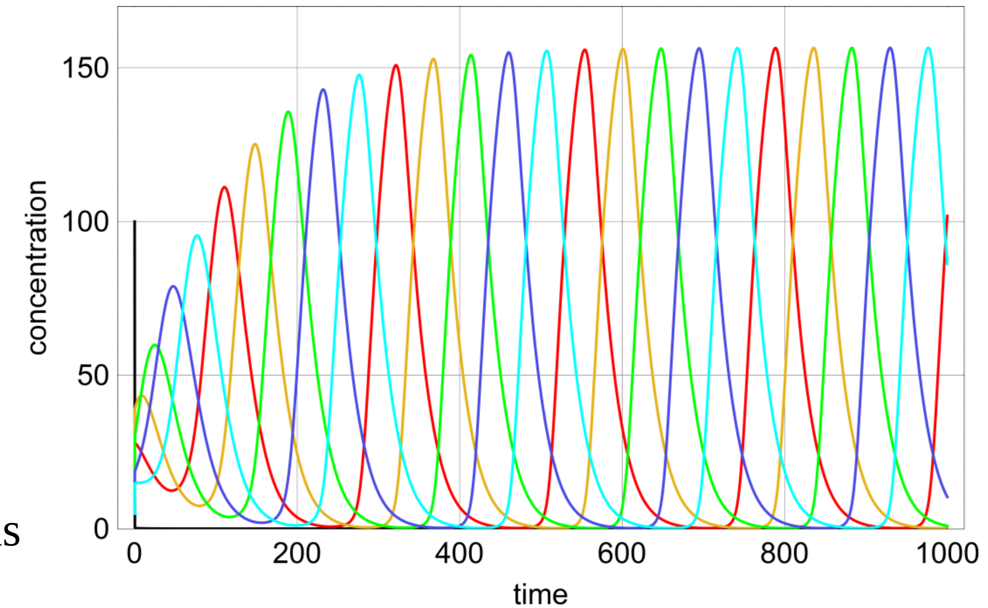
5. Some conclusions



Cooperation and mutation: stochastic escape from extinction n = 4

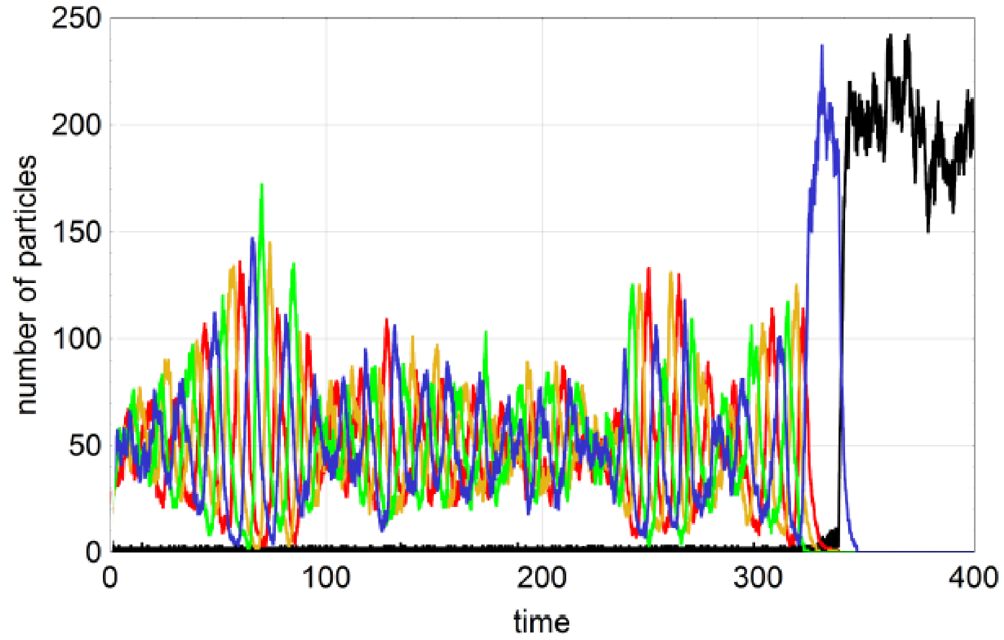


n = 5

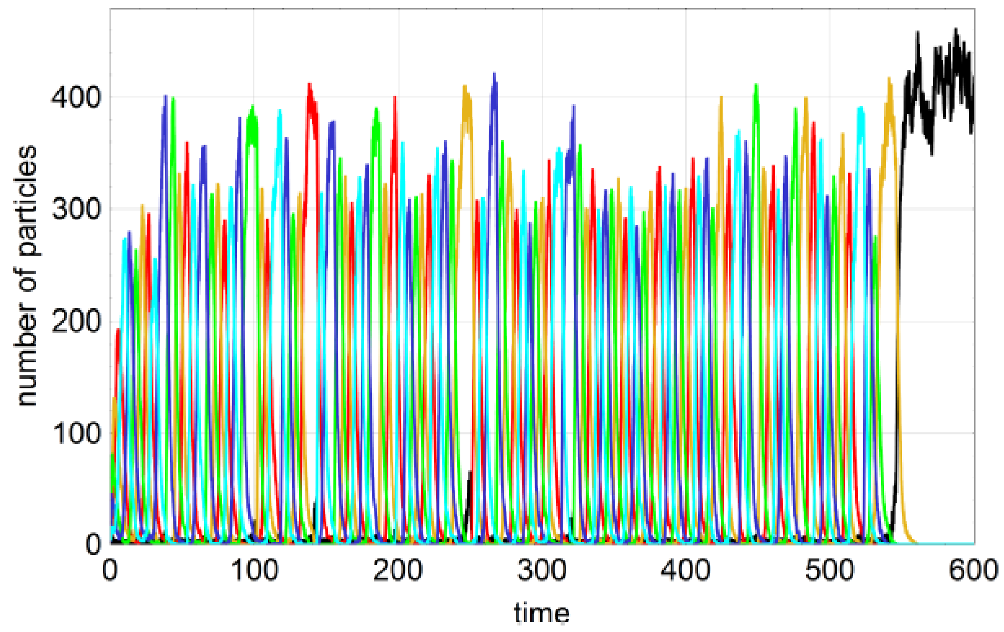


oscillatory hypercycles: ODE solutions

n = 4

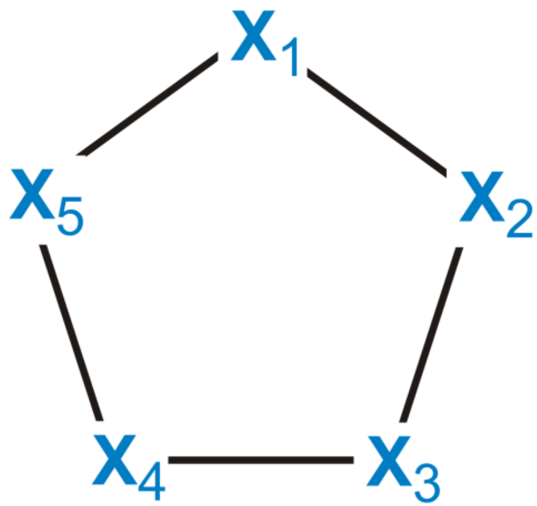


n = 5



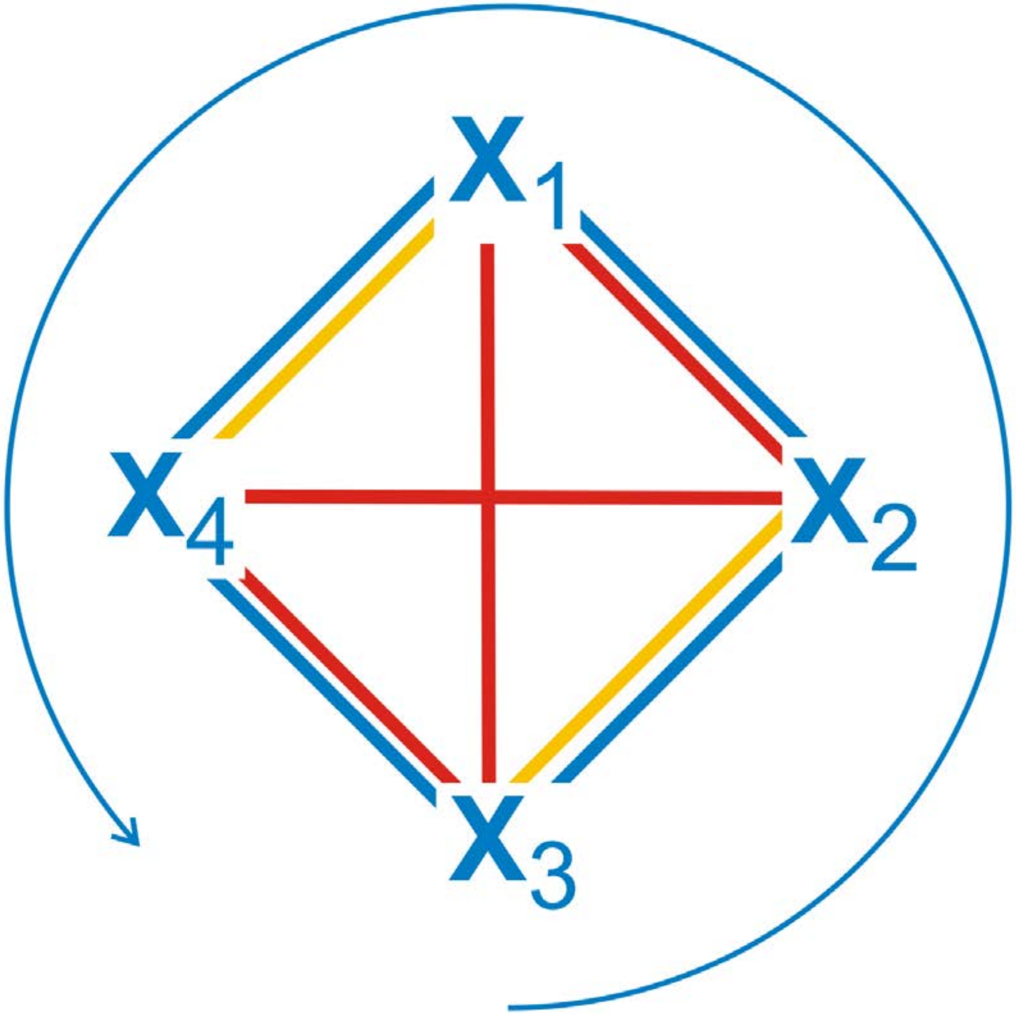
oscillatory hypercycles: simulations

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

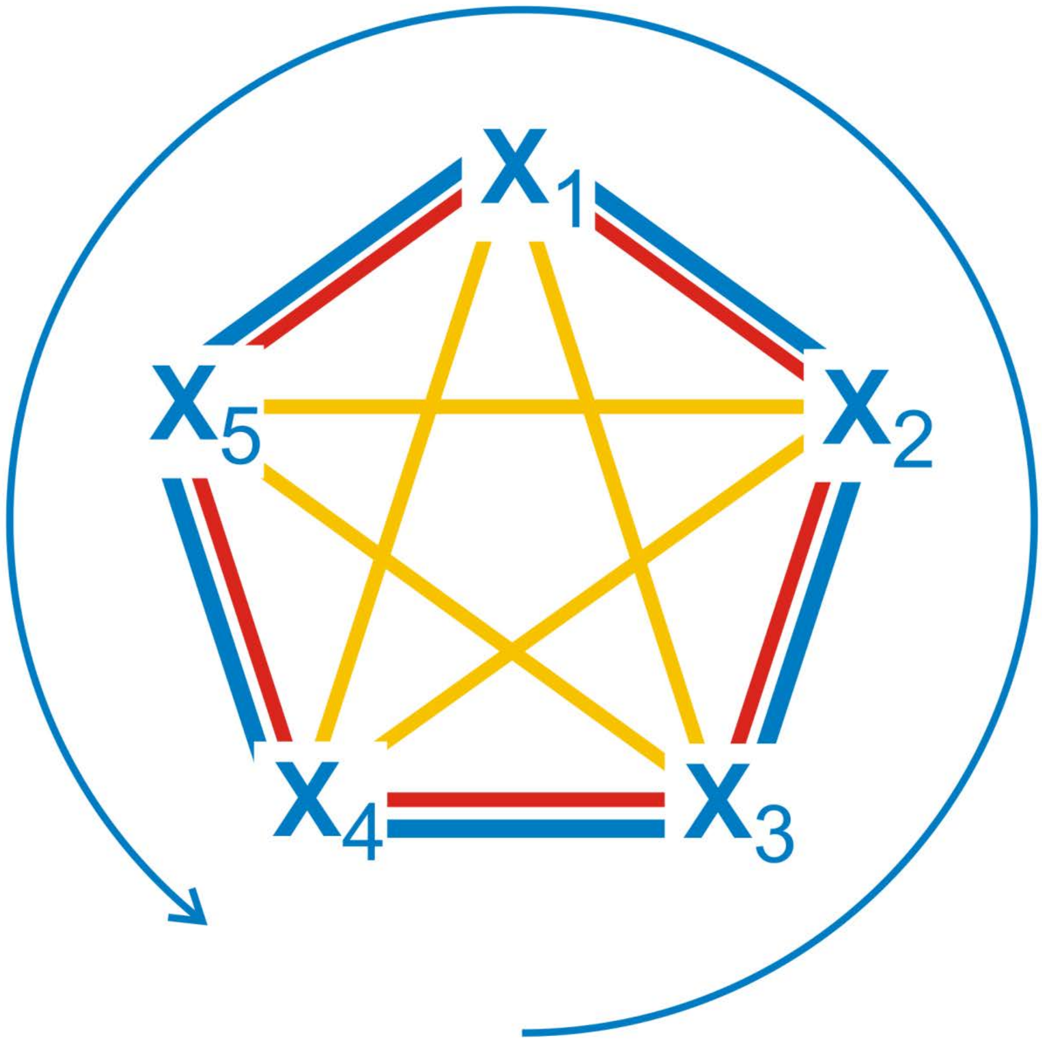


$$\mathbf{X}_n \Leftarrow \mathbf{X}_1 \Leftarrow \mathbf{X}_2 \Leftarrow \cdots \Leftarrow \mathbf{X}_{n-1} \Leftarrow \mathbf{X}_n$$

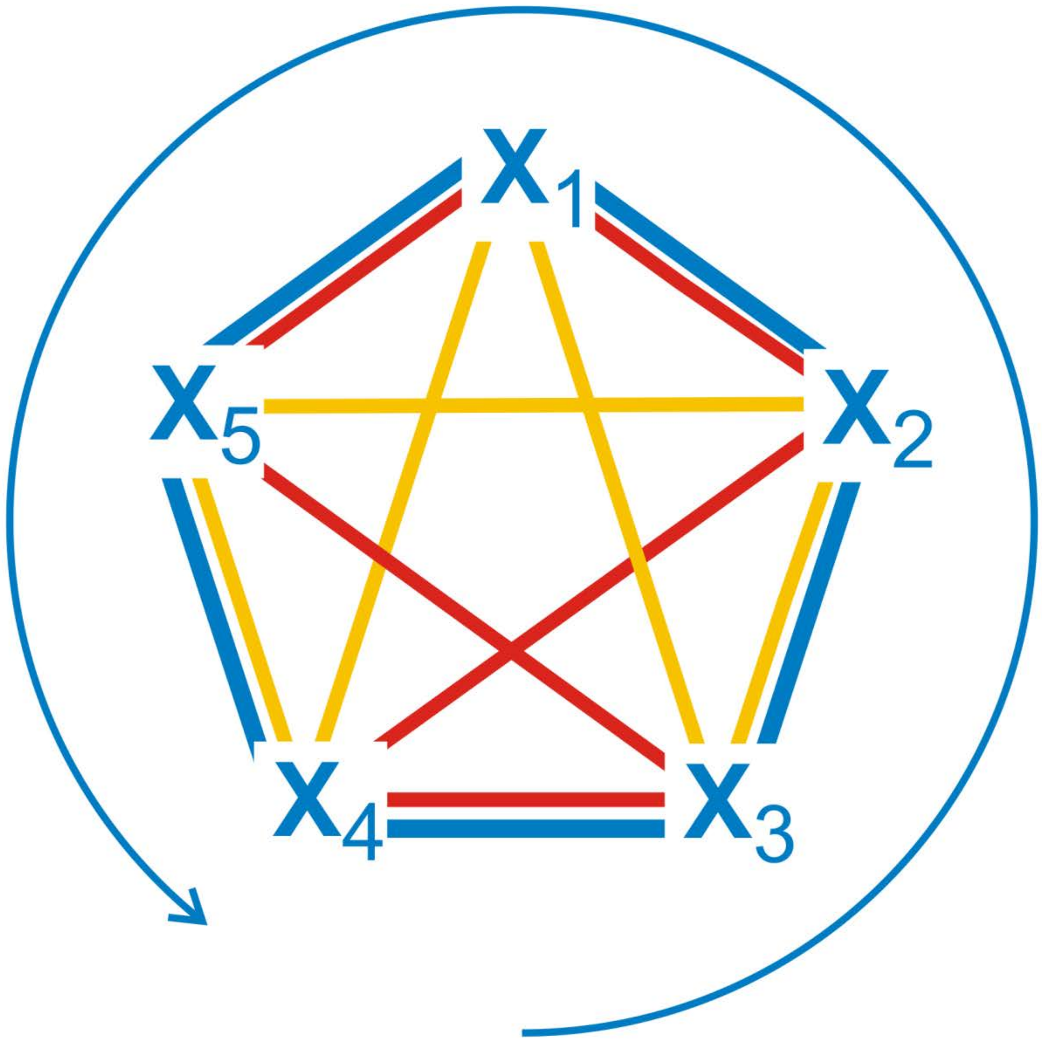
Catalytic hypercycles



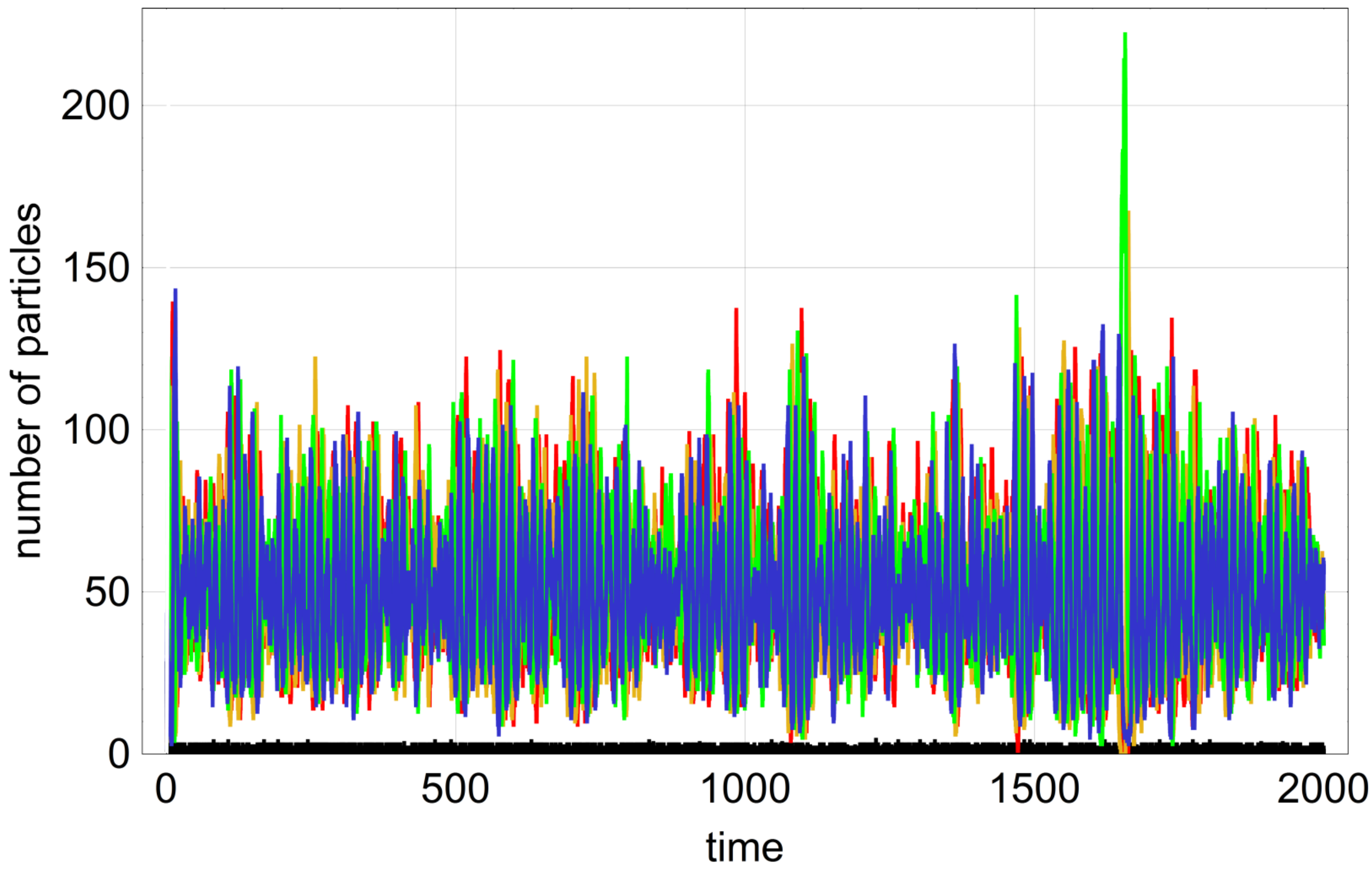
mutation mechanism, N = 4: ‚sequence space‘



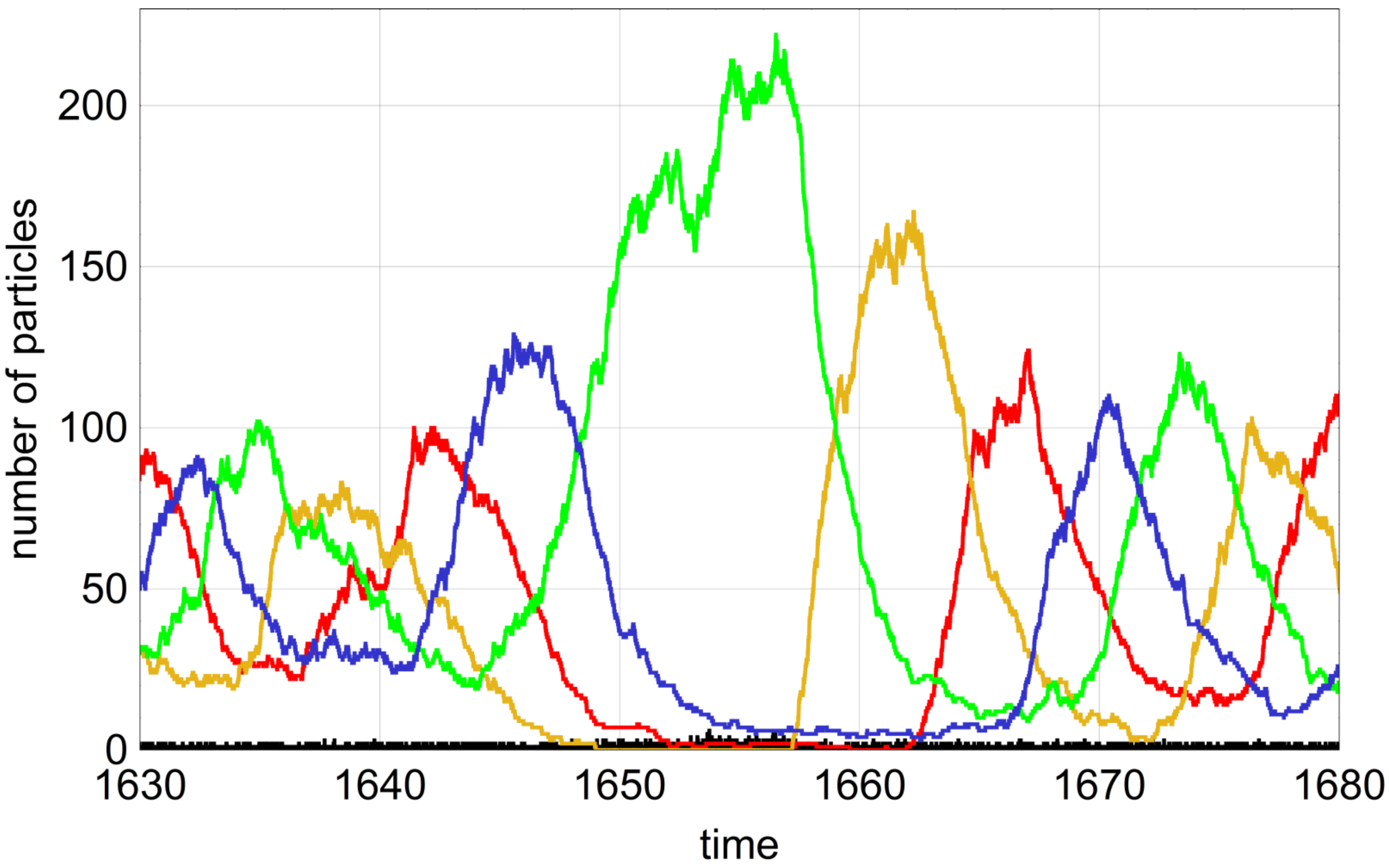
mutation mechanism, N = 5: ‚pentagram‘



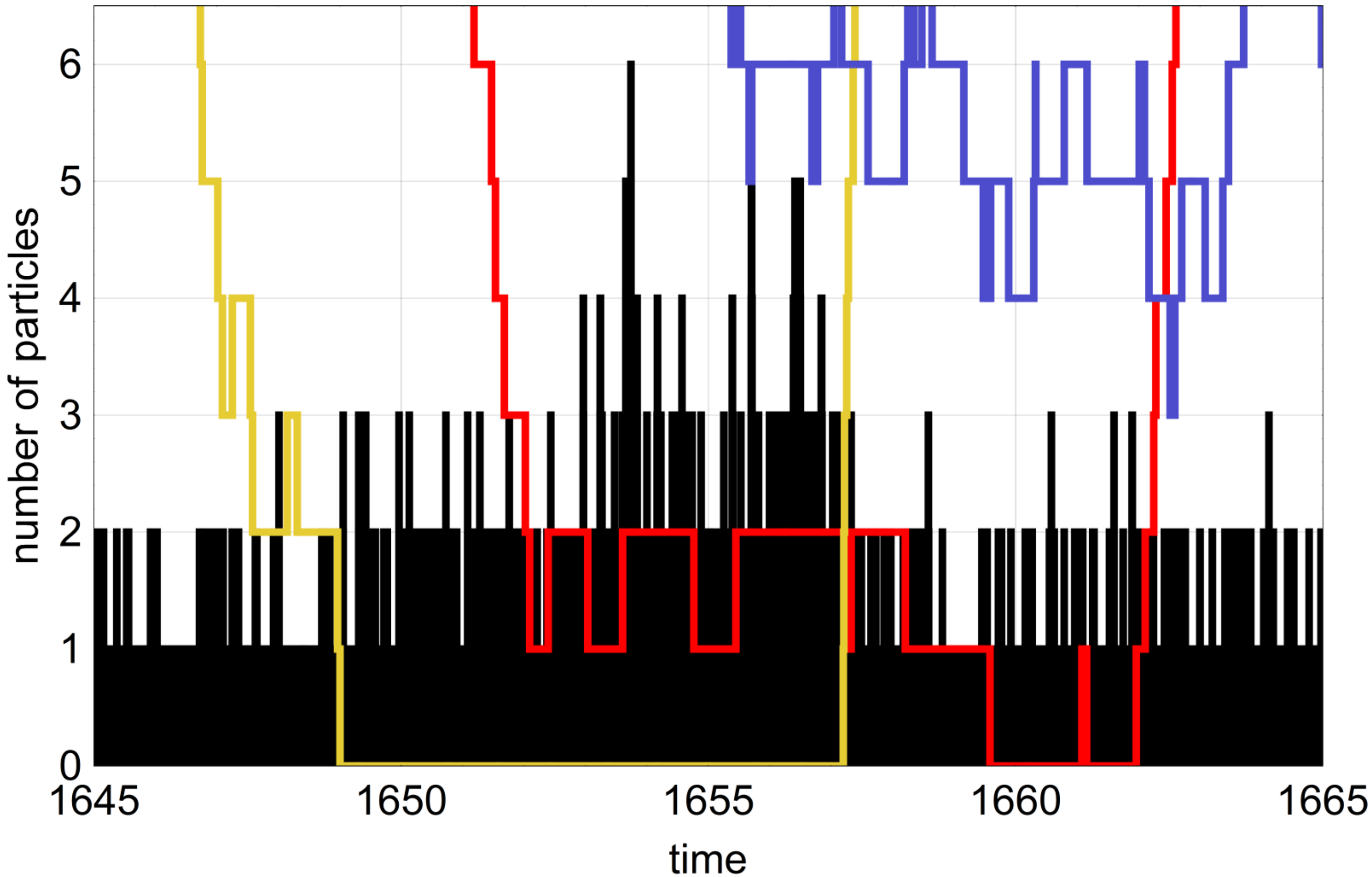
mutation mechanism, N = 5: ‚pentagramvariant‘



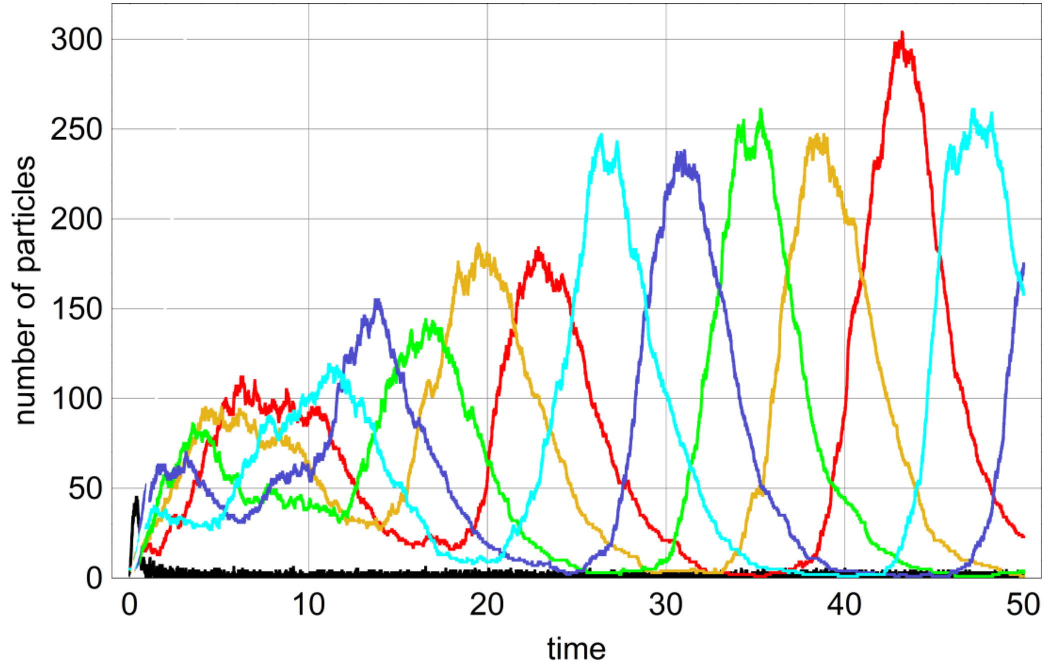
Oscillatory hypercycles:simulation for n=4

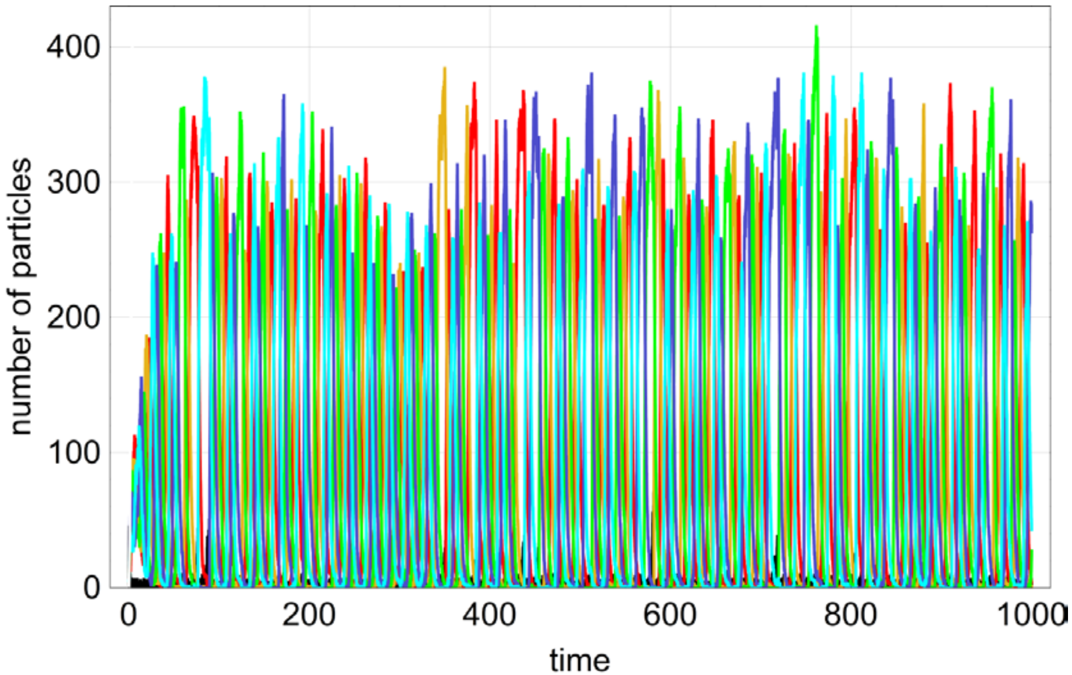


Oscillatory hypercycles:simulation for n=4, enlargement

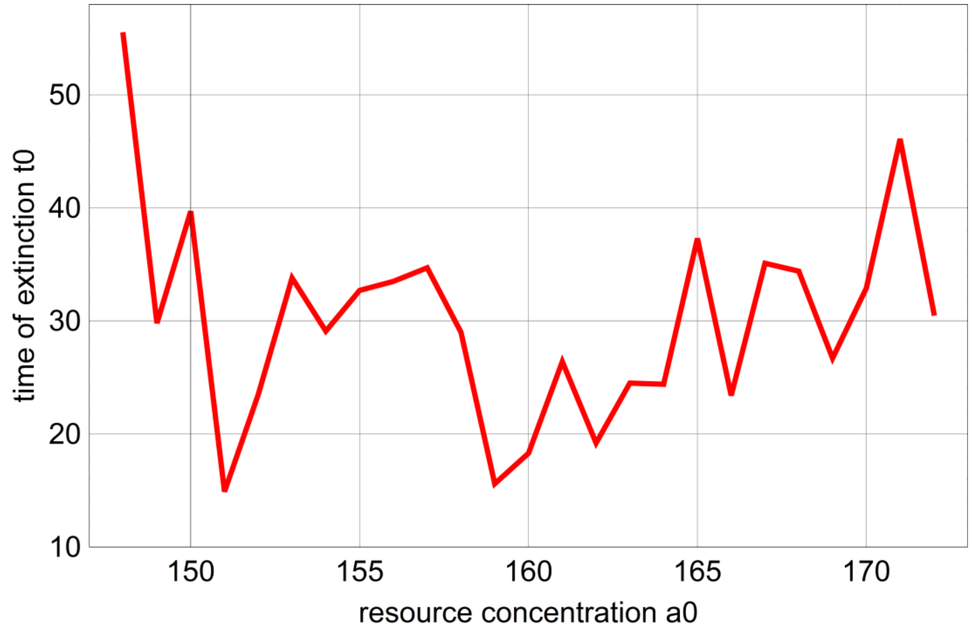


Oscillatory hypercycles:simulation for n=4, enlargement



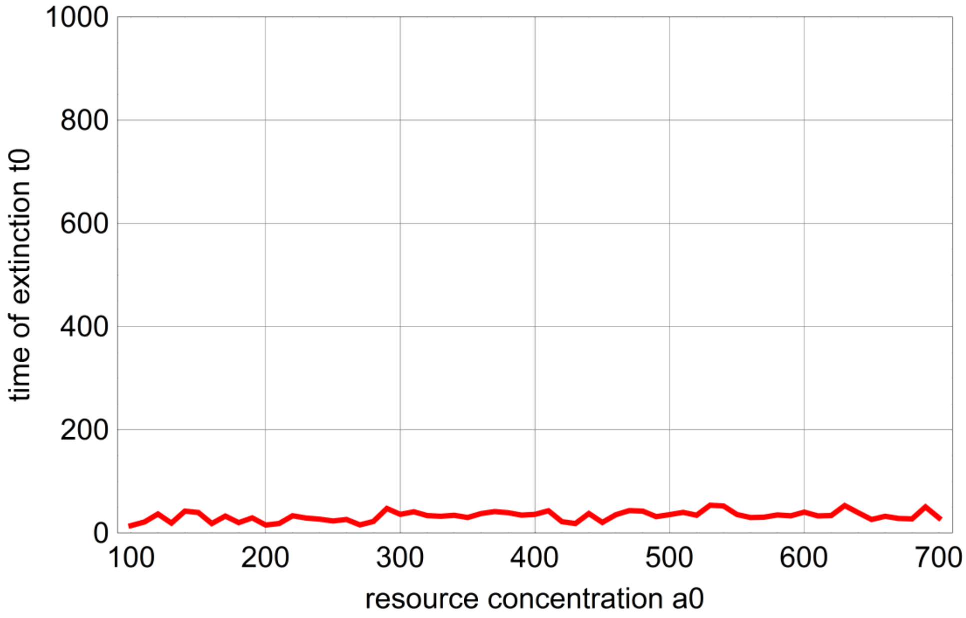


Oscillatory hypercycles:
simulation for n = 5



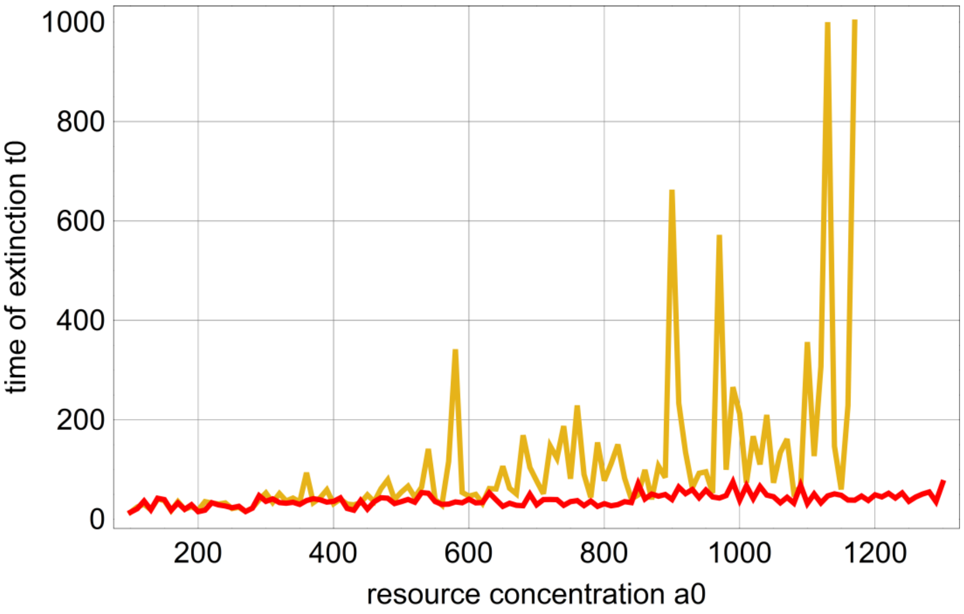
mutation rate: p = **0.0000**

Oscillatory hypercycles: simulation for n = 5



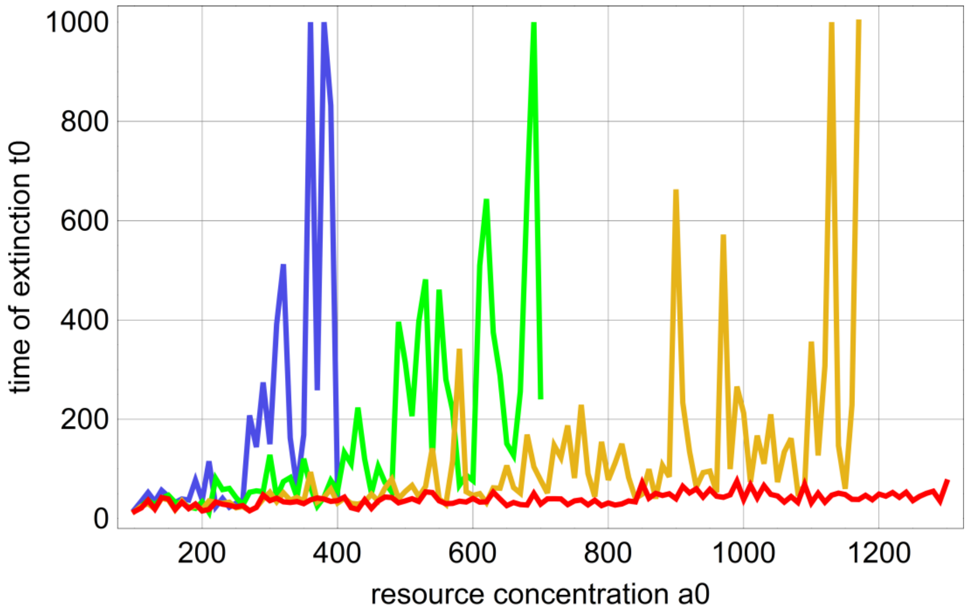
mutation rate: p = **0.0000**

Oscillatory hypercycles: simulation for n = 5



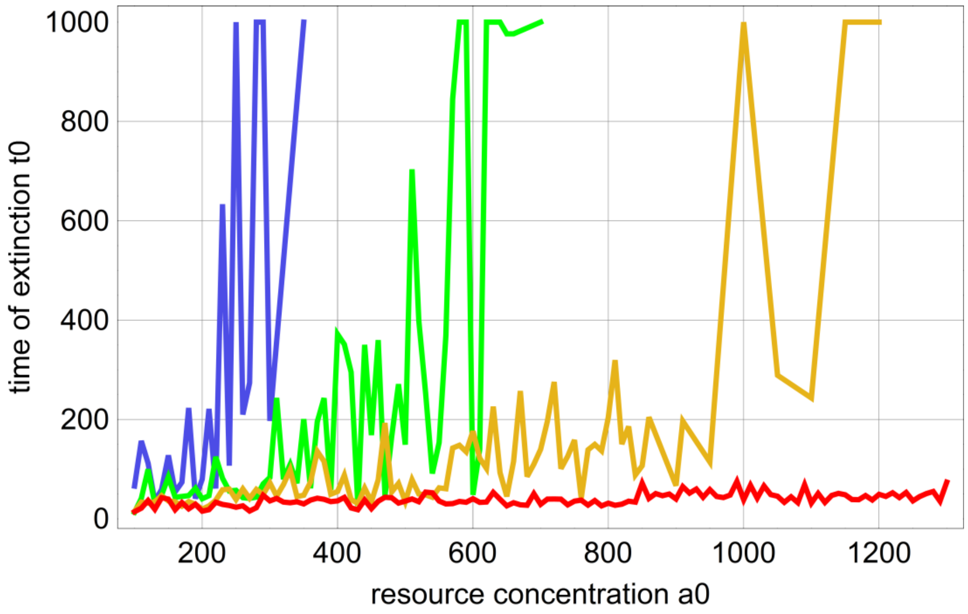
mutation rate: p = **0.0005**

Oscillatory hypercycles: simulation for n = 5,‘pentagram‘



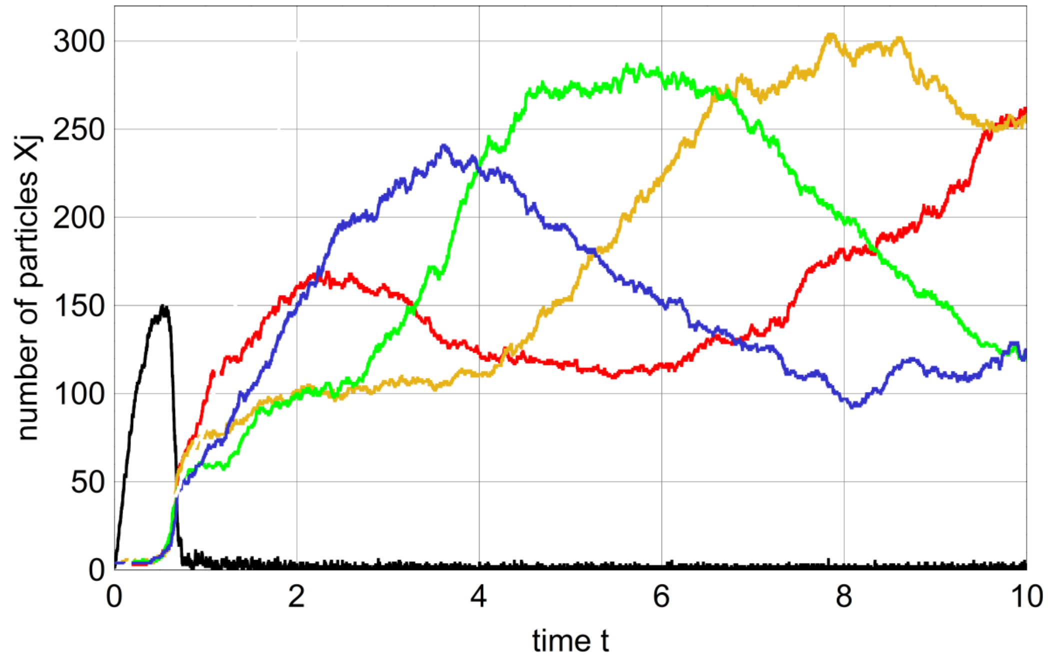
mutation rate: p = **0.0000**, p=**0.0005**, p = **0.0010** and p = **0.0020**

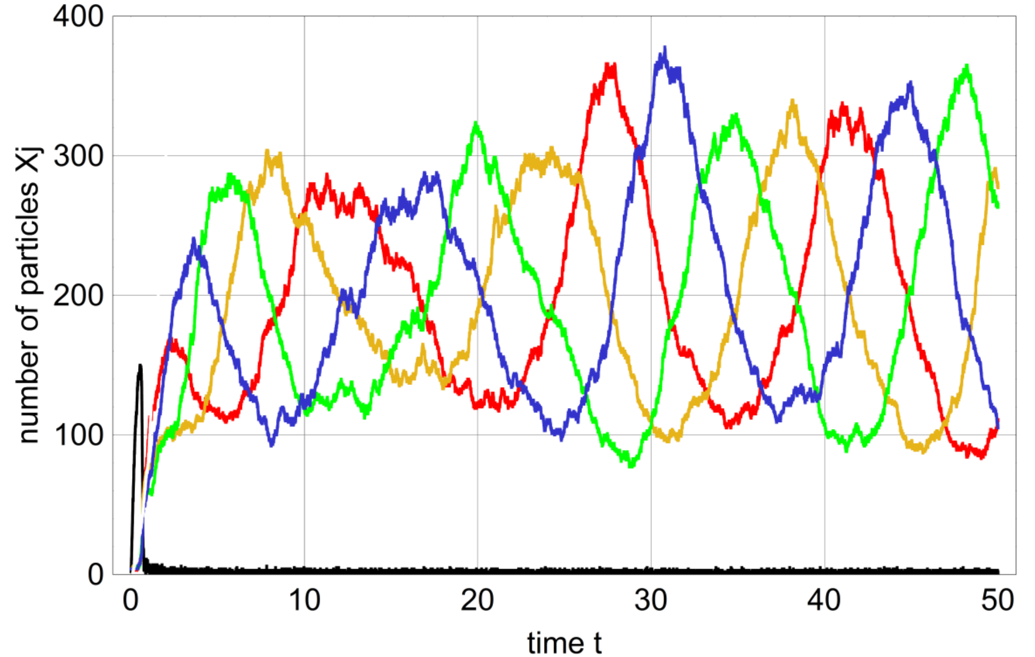
Oscillatory hypercycles: simulation for n = 5, ‚pentagram‘



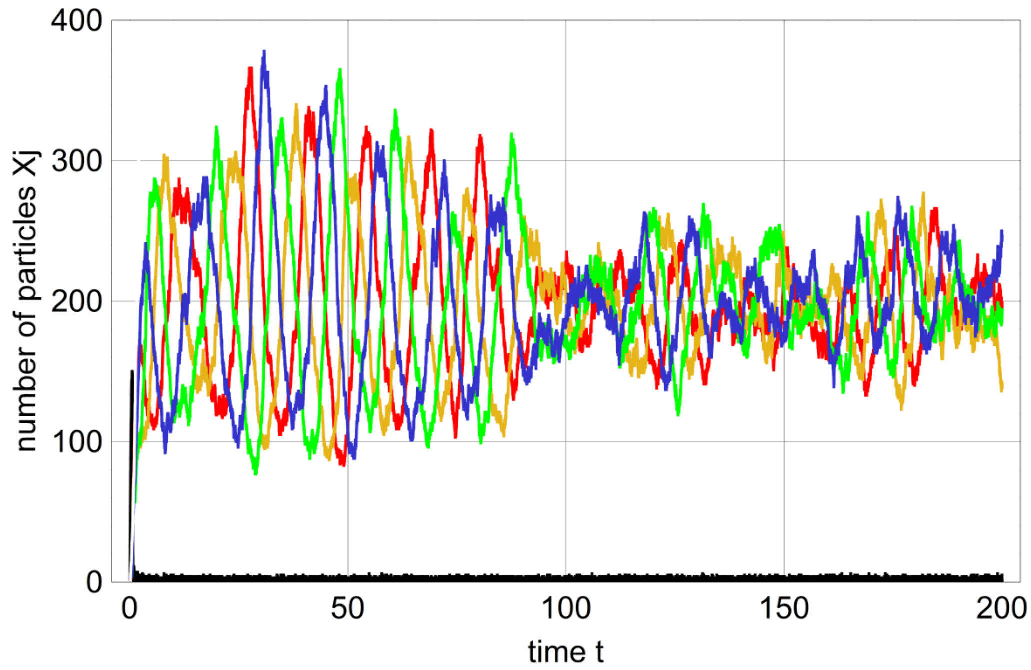
mutation rate: p = **0.0000**, p=**0.0005**, p = **0.0010** and p = **0.0020**

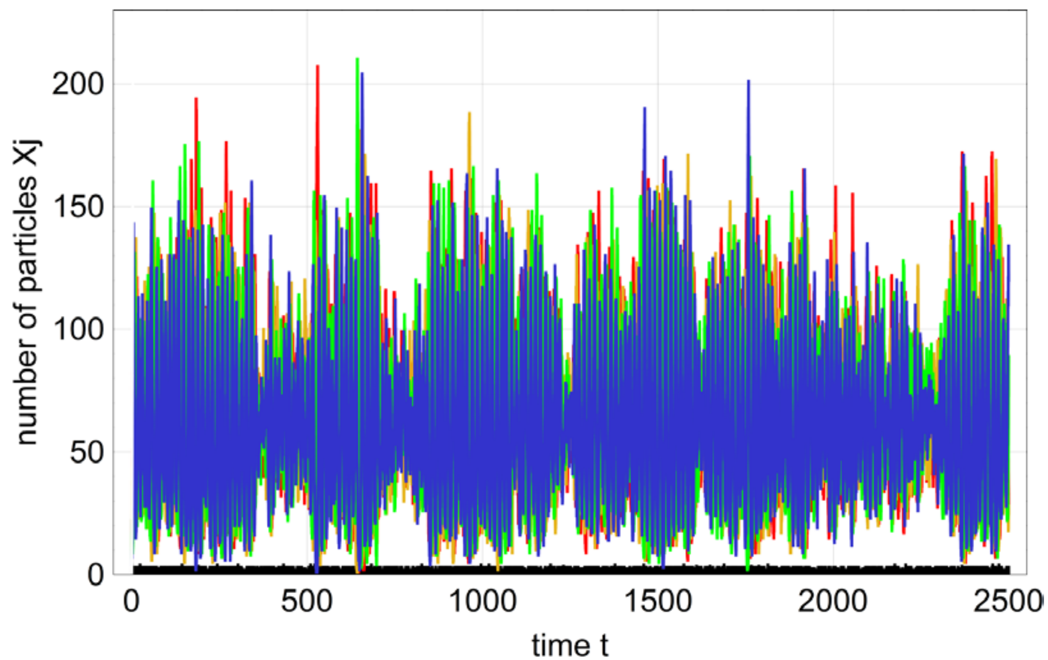
Oscillatory hypercycles: simulation for n = 5, ‚pentagramvariant'



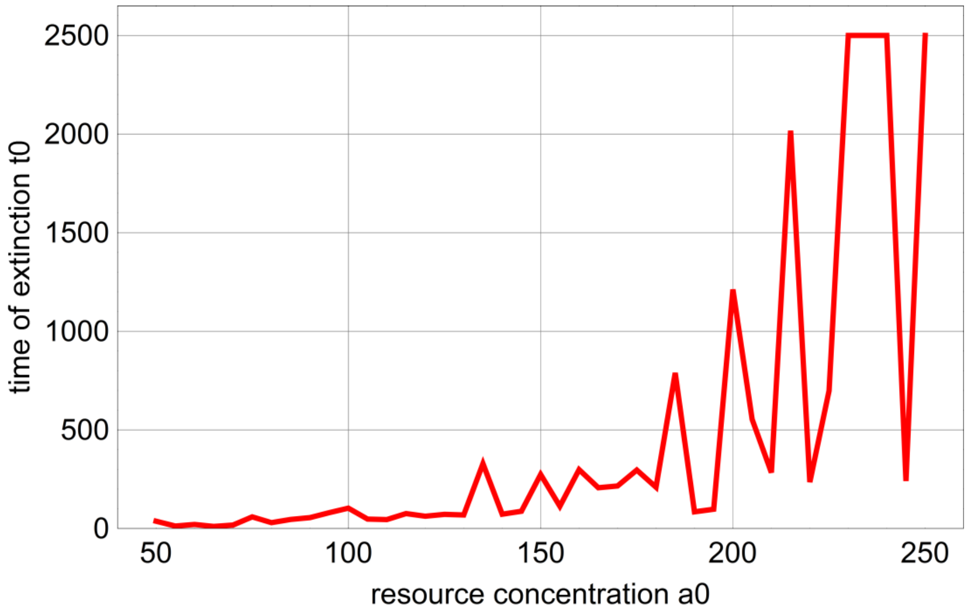


Oscillatory hypercycles:
simulation for n = 4



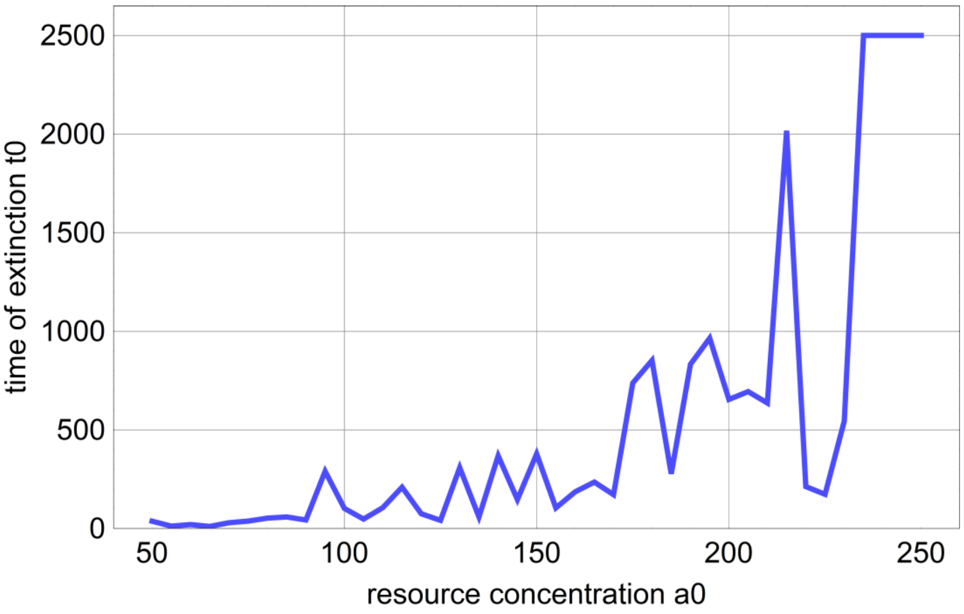


Oscillatory hypercycles:
simulation for n = 4



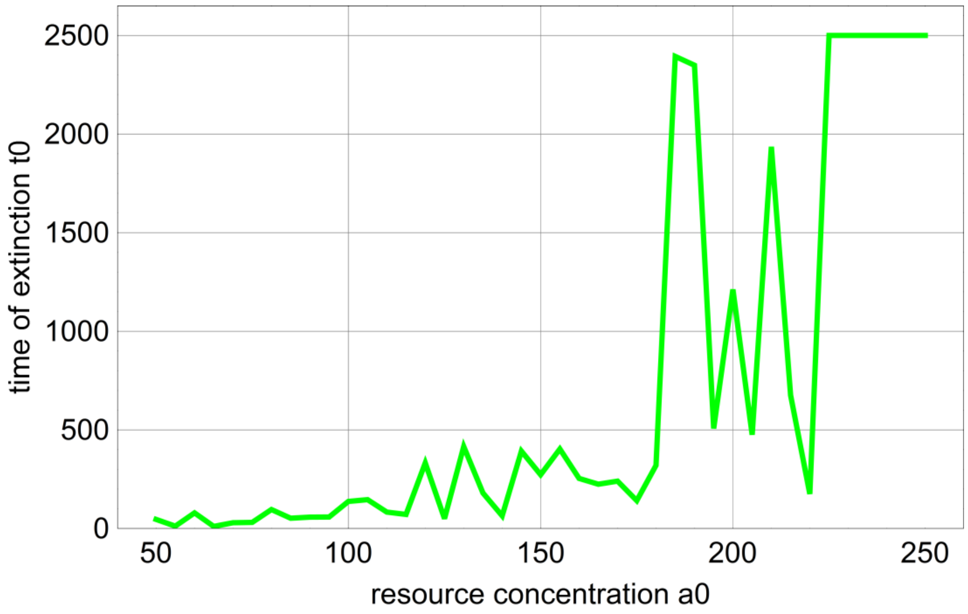
mutation rate: p = 0.0000

Oscillatory hypercycles: simulation for n = 4



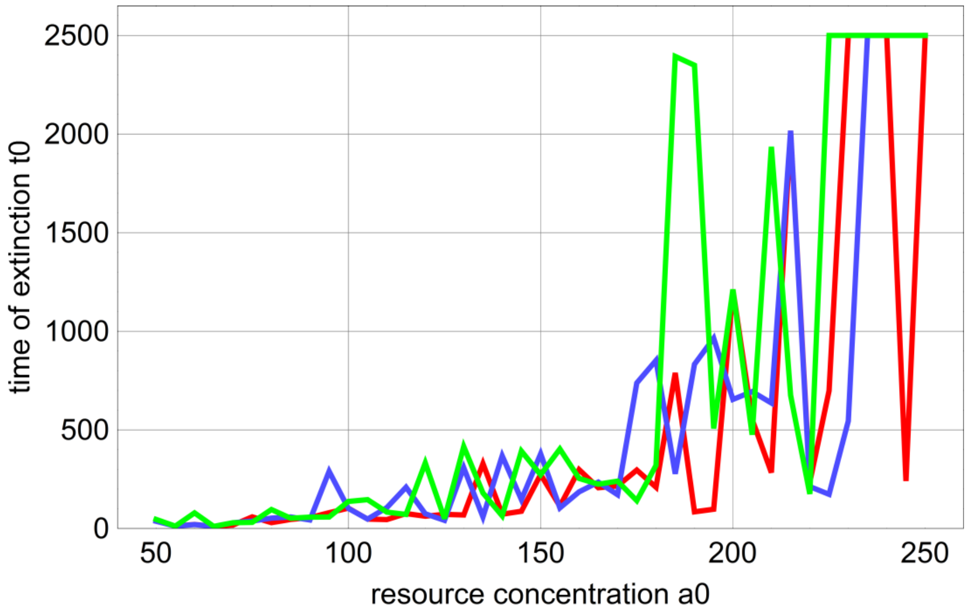
mutation rate: p = 0.0010

Oscillatory hypercycles: simulation for n = 4



mutation rate: p = 0.0020

Oscillatory hypercycles: simulation for n = 4



mutation rate: p = 0.0000, 0.0010 and 0.0020

Oscillatory hypercycles: simulation for n = 4

1. A general and simple model for evolution
2. Mutation and quasispecies
3. Cooperation and major transitions
4. Can mutations counteract extinction ?
5. **Some conclusions**

The model despite its simplicity illustrates and provides explanations for features observed in real biology.

A Cartesian space with competition, cooperation, and variation plotted on the axes is used to classify processes that lead to transition phenomena. Commonly - but not always - these transitions are sharp in the sense of 'phase transitions' in finite systems or they are represented by bifurcations.

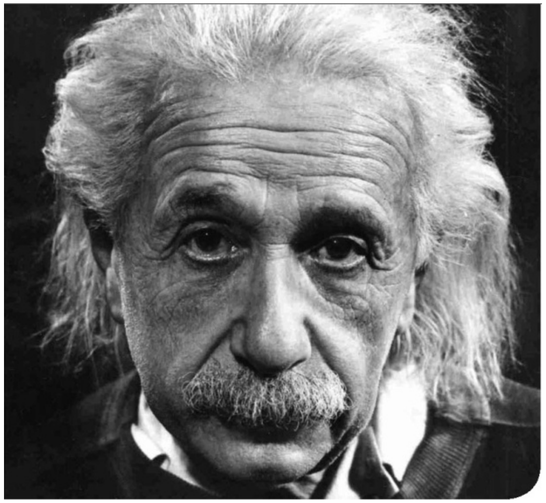
These transitions are:

i. A transition from ordered reproduction to random replication on the face constituted by differential fitness and mutation.
ii. A transition from selection to cooperation in the sense of the initiation of a 'major transition' driven by the availability of resources on the face of differential fitness and cooperation.
iii. A transition from stochastic extinction to survival on the face of cooperation and mutation.

A conjecture states that all transitions smoothen out in the interior of the Cartesian space.

Insofern sich Sätze der Mathematik auf die Wirklichkeit beziehen, sind sie nicht sicher, und insofern sie sicher sind, beziehen sie sich nicht auf die Wirklichkeit.

As far as the laws of mathematics refer to reality, they are not certain, and as far as they are certain, they don't refer to reality.



Albert Einstein. Geometrie und Erfahrung. Sitzungsberichte der Preussischen Akademie der Wissenschaften, 1921 (1), 123-130

Thank you for your attention!

Web-Page for further information:

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

Peter Schuster. Some mechanistic requirements for major transitions. *Phil. Trans. R. Soc.B* 371:e20150439, 2016

Peter Schuster. Increase in complexity and information through molecular evolution. *Entropy*, in press, 2016