Scarcity is not the mother of invention!

Peter Schuster

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

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1. Motivation

2. Examples of major transitions

3. A kinetic toy model for major transitions

4. Stochastic analysis of the toy model

5. Some conclusions

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Austerity is the mother of invention.

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

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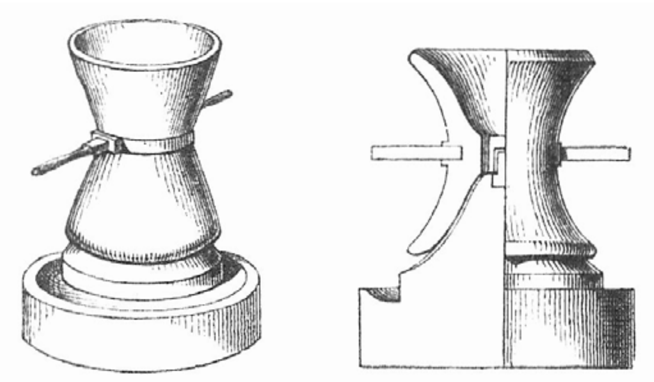


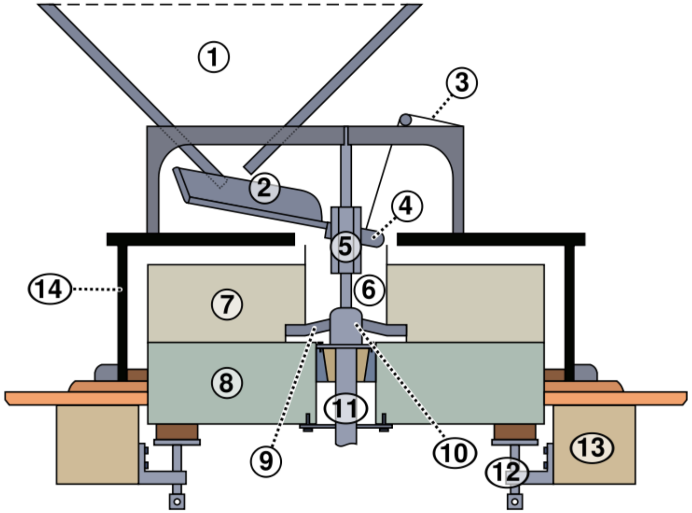
quern and motar

Meal and flour preparation in ancient worlds and with indigenous peoples

Watermill technology

Source: Wikipedia, 18.04.2016

1.Hopper 2.Shoe 3.Crook string
4.Shoe handle 5.Damsel 6.Eye
7.Runner stone 8.Bedstone
9.Rind 10.Mace 11.Stone
spindle 12.Millstone support
13.Wooden beam 14.Casing
(Tentering gear not shown)

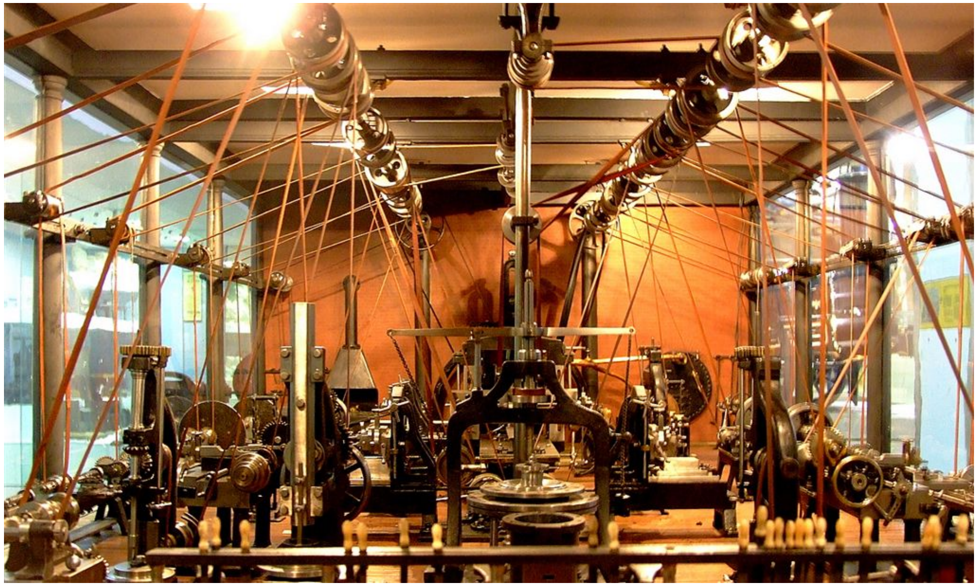


Mühlengleichnis: „Man muss übrigens notwendig zugestehen, dass die Perzeption und das, was von ihr abhängt, aus mechanischen Gründen, d. h. aus Figuren und Bewegungen, nicht erklärbar ist. Denkt man sich etwa eine Maschine, die so beschaffen wäre, dass sie denken, empfinden und perzipieren könnte, so kann man sie sich derart proportional vergrößert vorstellen, dass man in sie wie in eine Mühle eintreten könnte. Dies vorausgesetzt, wird man bei der Besichtigung ihres Inneren nichts weiter als einzelne Teile finden, die einander stoßen, niemals aber etwas, woraus eine Perzeption zu erklären wäre.“

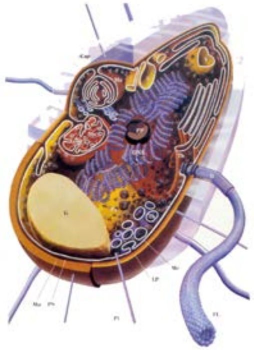
Gottfried Wilhelm Leibniz (1646-1716), Monadologie, §. 17.

Horse carriage of the emperor Qin Shihuangdis

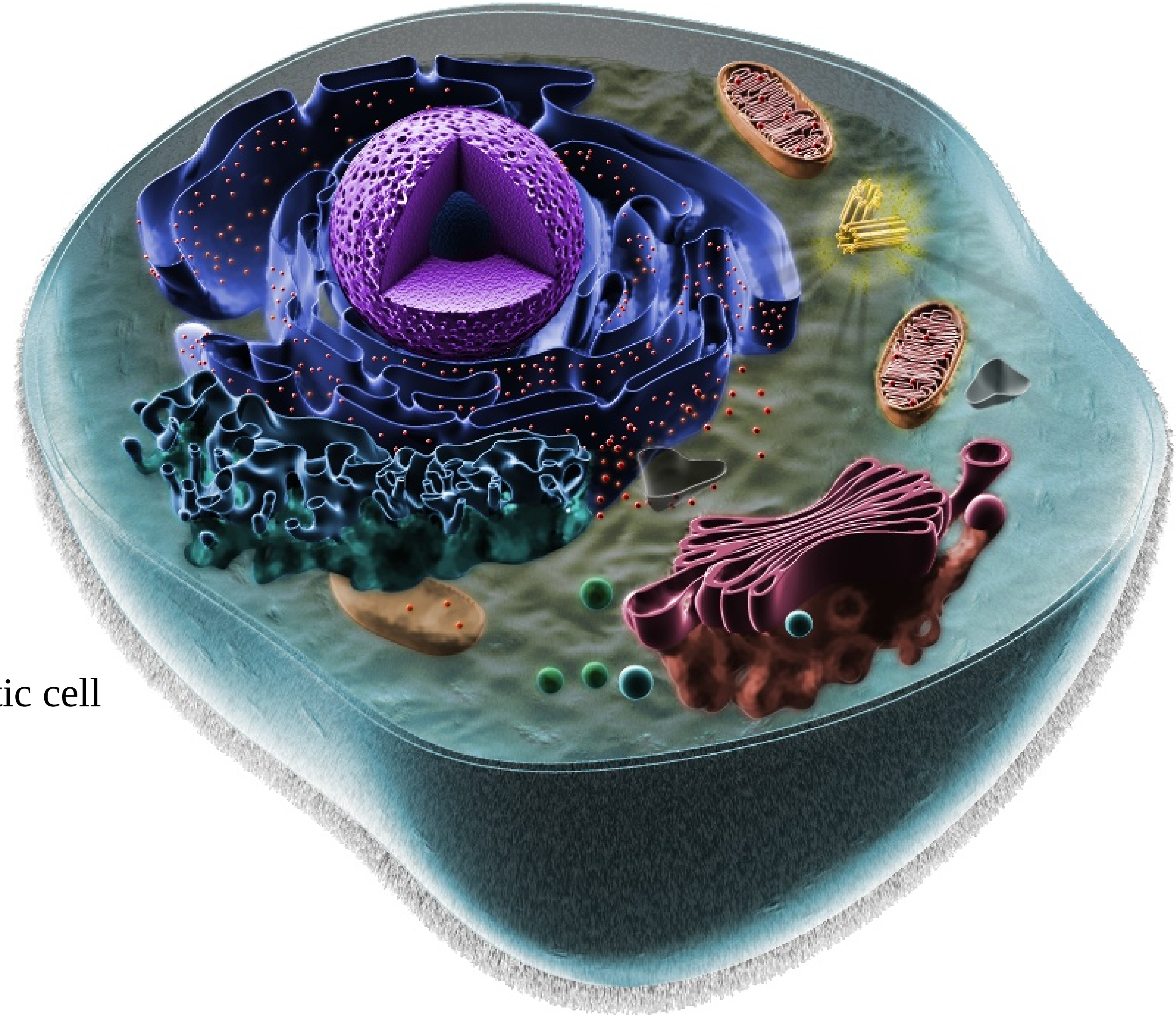
Industrial revolution and railroad



Source: Wikipedia, 18.04.2016



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

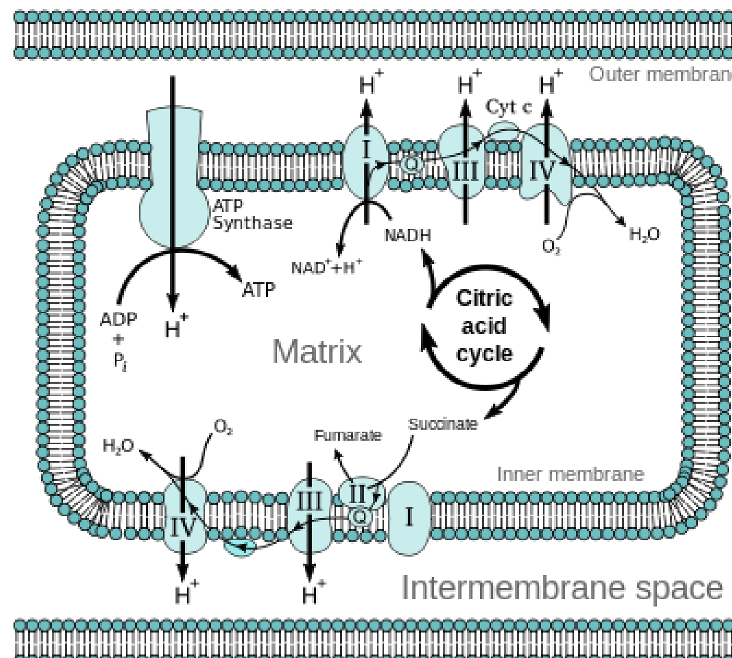
Industrial revolution 18th and 19th century:

cheap energy from fossil fuels

Origin of the eukaryotic cell 2.2×10^{9}

(1.8 – 2.7) years ago:

cheap energy from oxidative phosphorylation



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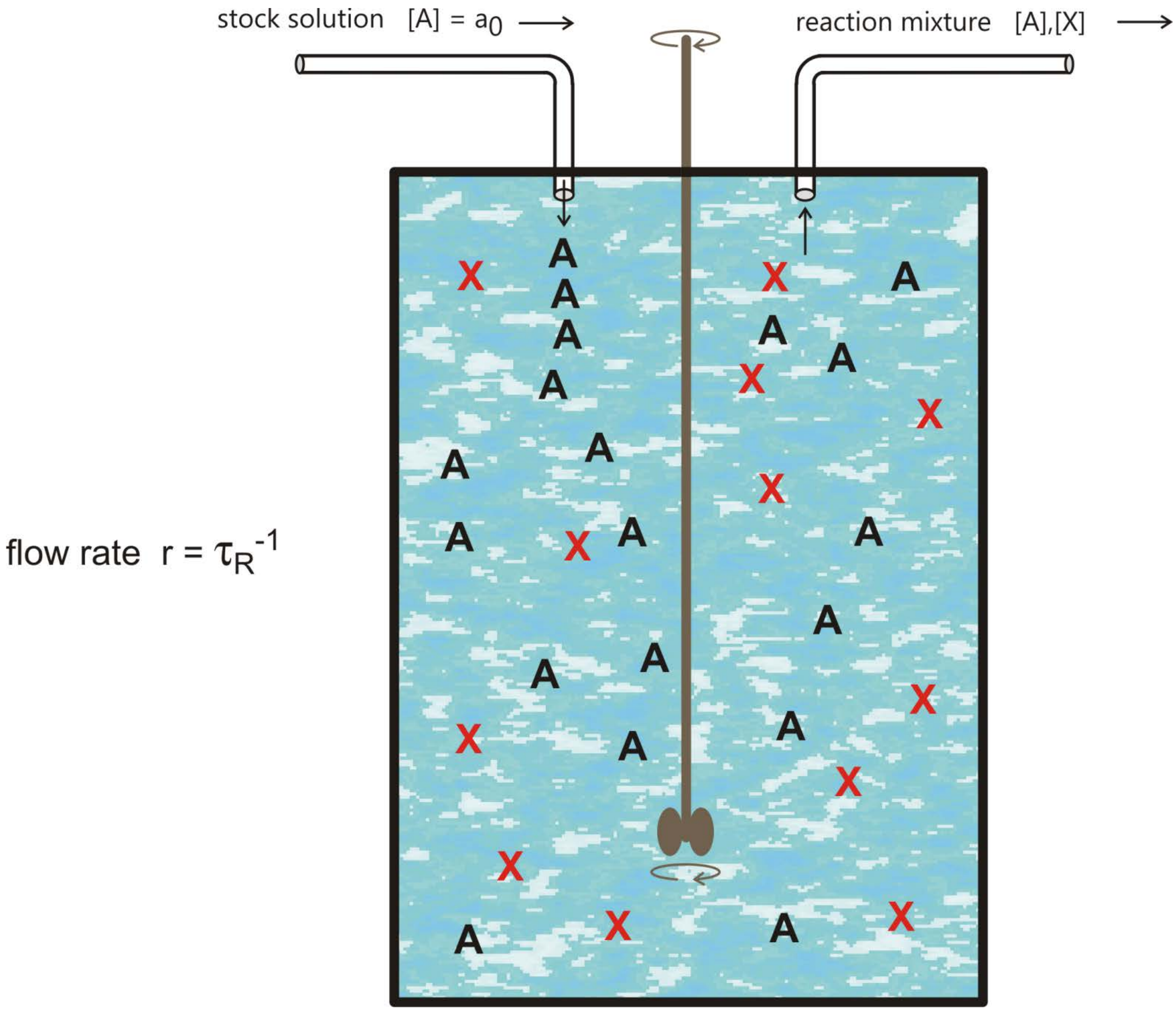


The continuously fed stirred tank reactor (CFSTR)

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

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

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

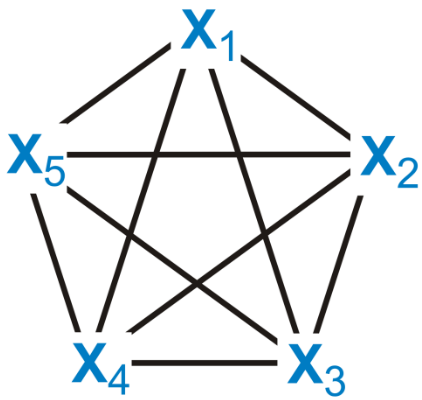
$$\mathbf{A} \xrightarrow{r} \varnothing$$

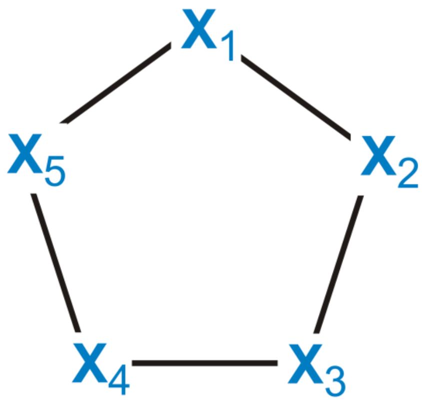
$$\mathbf{X}_j \xrightarrow{r} \varnothing\,,\; j = 1, \ldots, n$$

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

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

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

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

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

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

Toy model for the analysis of competition and cooperation

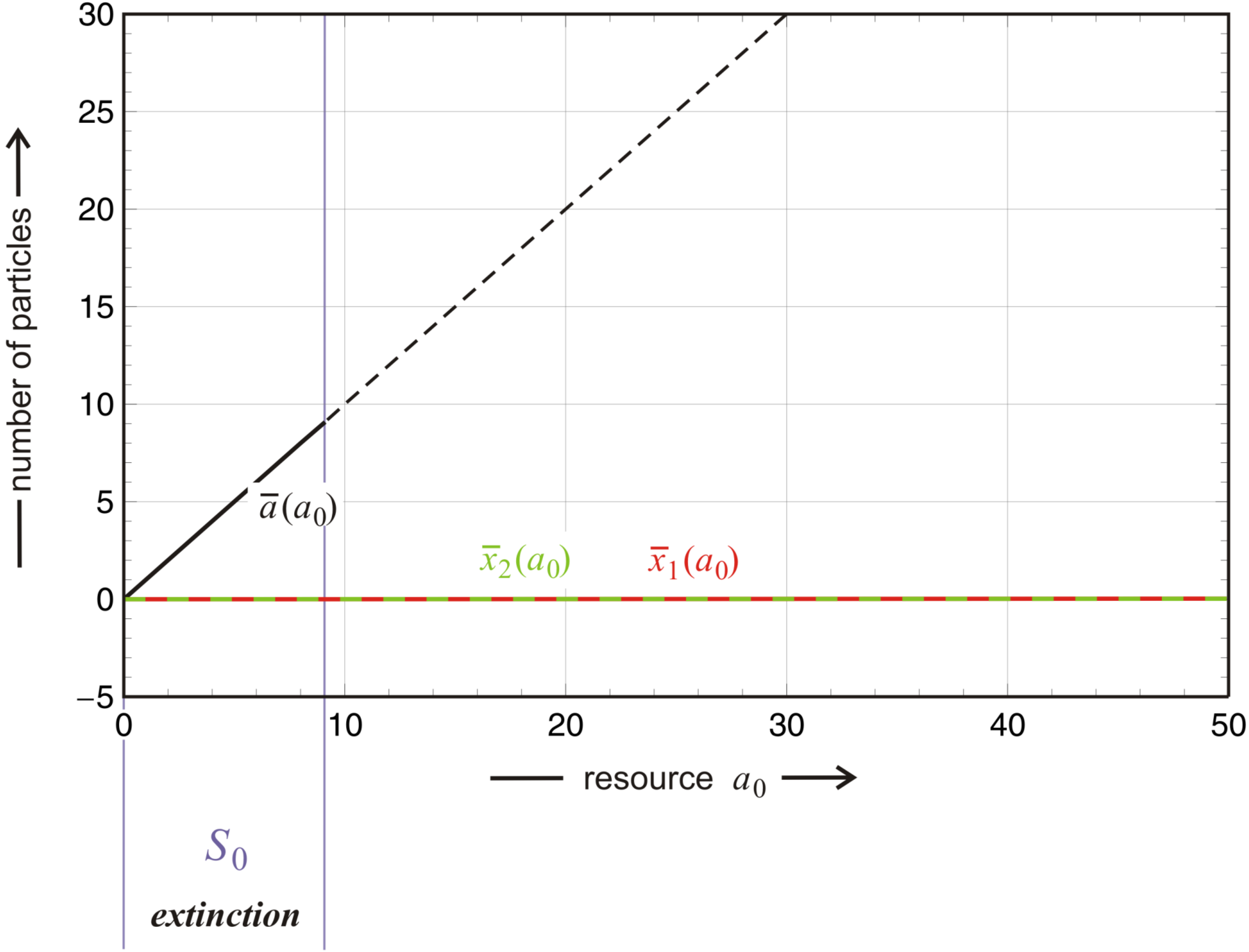
$$[\mathbf{A}] = a \quad \text{and} \quad [\mathbf{X}_j] = x_j\,;\; j = 1,\ldots,n$$

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

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

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

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



30
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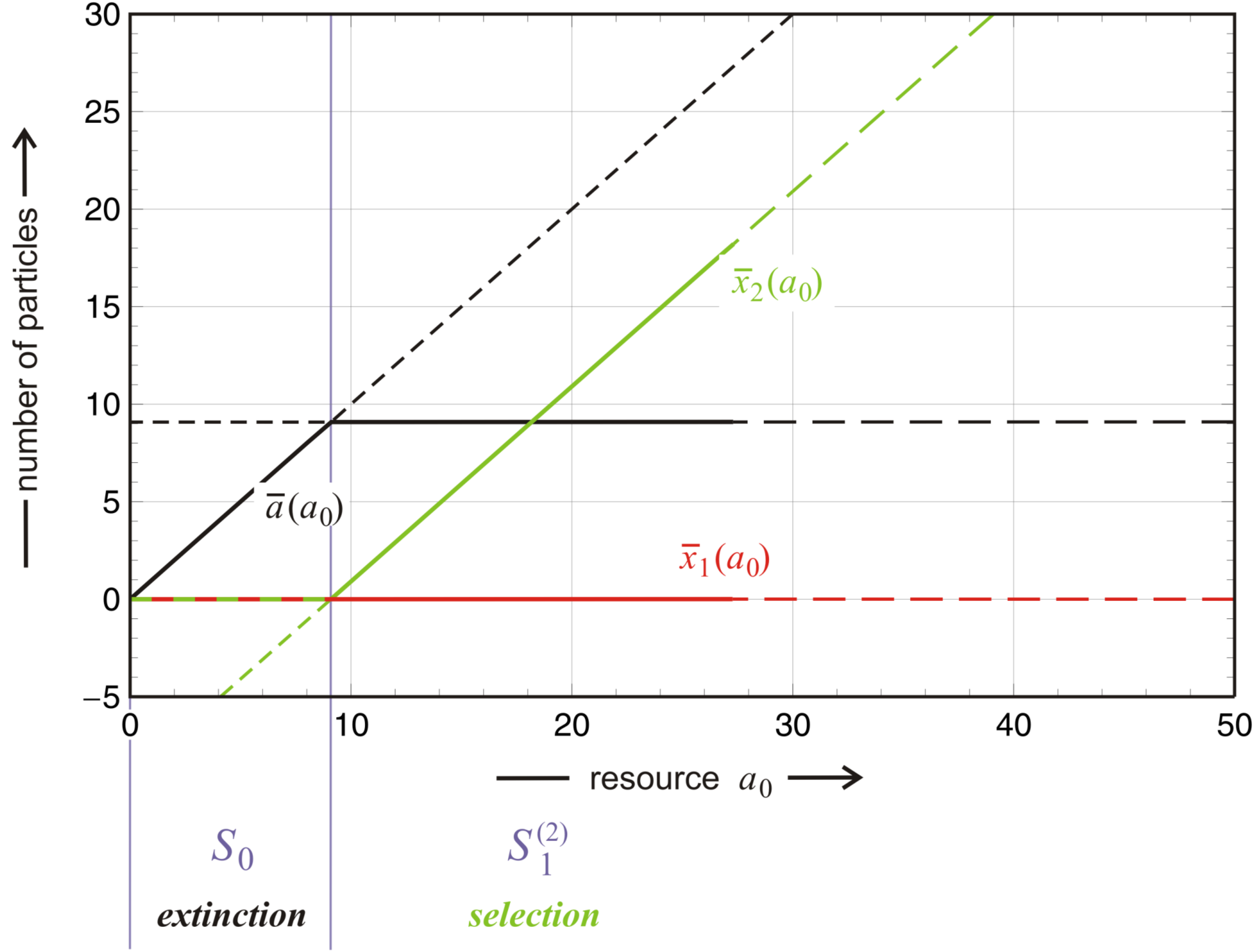
number of particles
resource a_0
$\bar{a}(a_0)$
$\bar{x}_2(a_0)$
$\bar{x}_1(a_0)$
S_0
extinction



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number of particles
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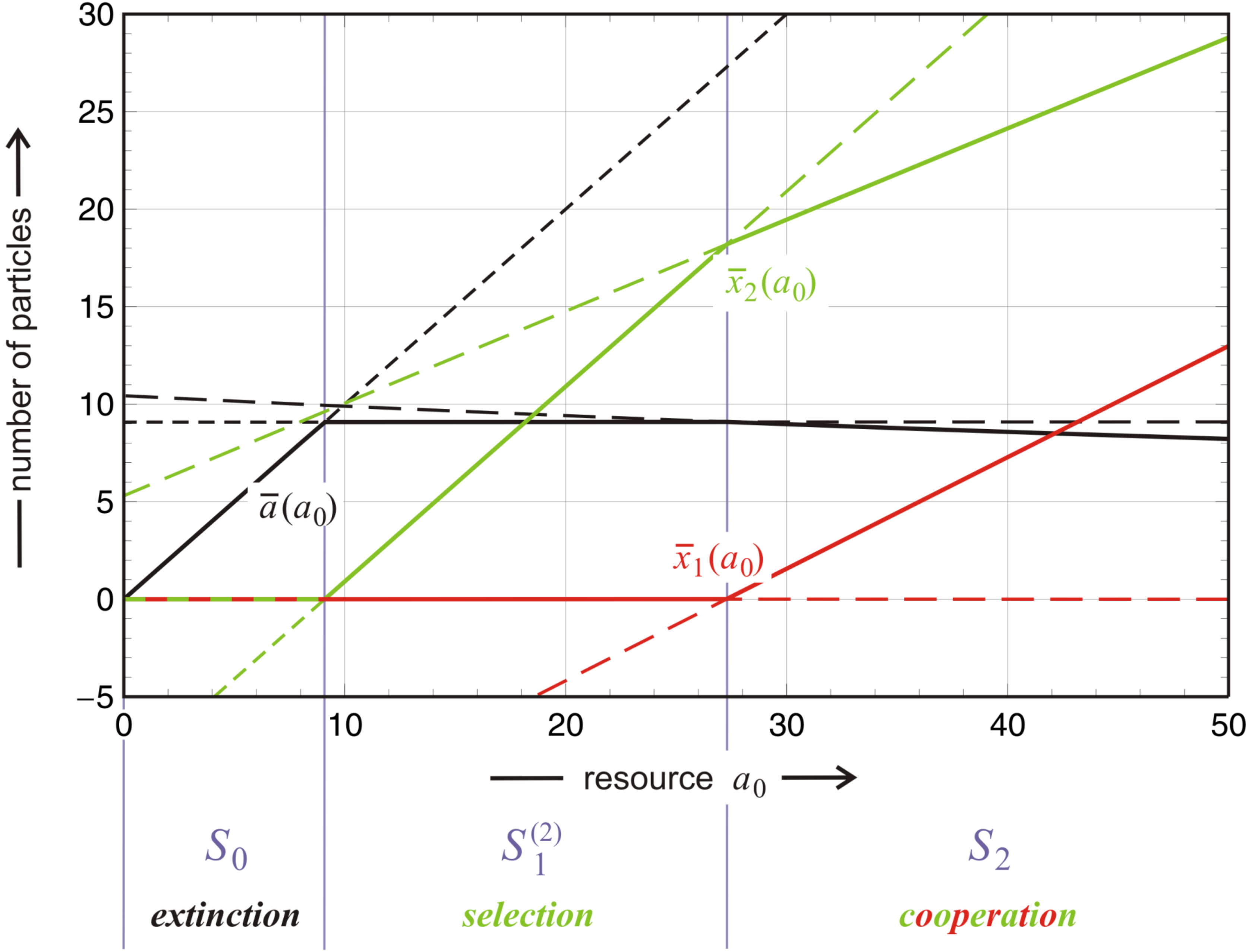
$\bar{a}(a_0)$
$\bar{x}_2(a_0)$
$\bar{x}_1(a_0)$
S_0
$S_1^{(2)}$
extinction
selection



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40
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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

$f_2 > f_1$ 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**			**stability range**
		$\overline{a}$	$\overline{x}_1$	$\overline{x}_2$	
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	$\frac{r - f_2 \alpha}{k_2 \alpha}$	$\frac{r - f_1 \alpha}{k_1 \alpha}$	$\frac{r}{f_2} + \frac{f_2 - f_1}{k_1} \leq a_0$

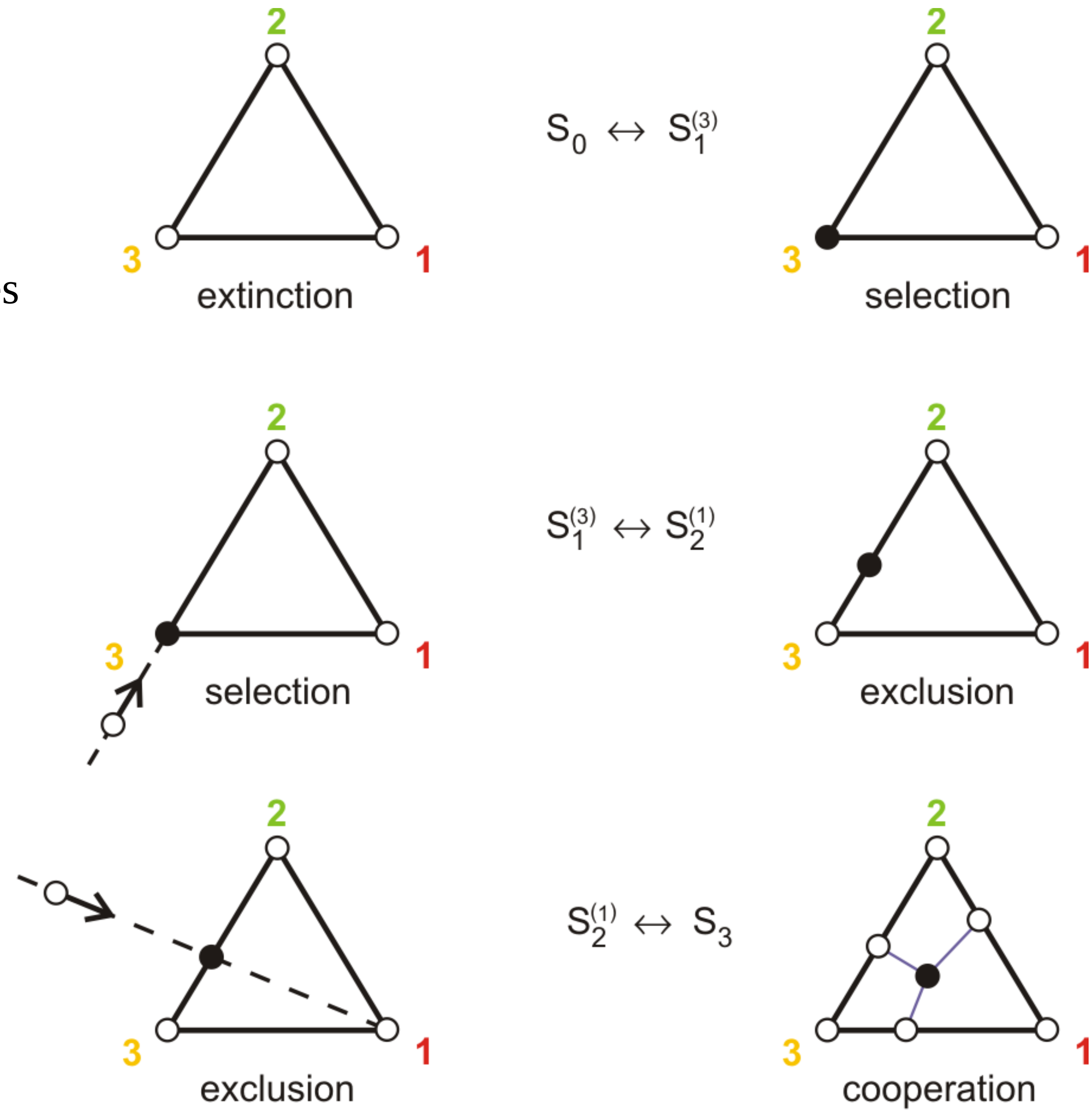
$$\overline{a} = \alpha = \frac{1}{2}\left(a_0 + \psi - \sqrt{(a_0 + \psi)^2 - 4\, r \phi}\right) \qquad r \leq (a_0 + \psi)^2 \,/\, 4\phi$$

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

$$f_3 > f_2 > f_1$$

$$k_3 < k_2 < k_1$$

increasing a_0-values



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

increasing a_0-values

name	**symbol**	**stationary values**				**stability range**
		$\overline{a}$	$\overline{x}_1$	$\overline{x}_2$	$\overline{x}_3$	
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	$\frac{r-f_3\alpha}{k_3\alpha}$	$\frac{r-f_1\alpha}{k_1\alpha}$	$\frac{r-f_2\alpha}{k_2\alpha}$	$\frac{r}{f_3} + \frac{f_3-f_2}{k_2} + \frac{f_3-f_1}{k_1} \le a_0$

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

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

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

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

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

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

Hypercycle dynamics in the flow reactor

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

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

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

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

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

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

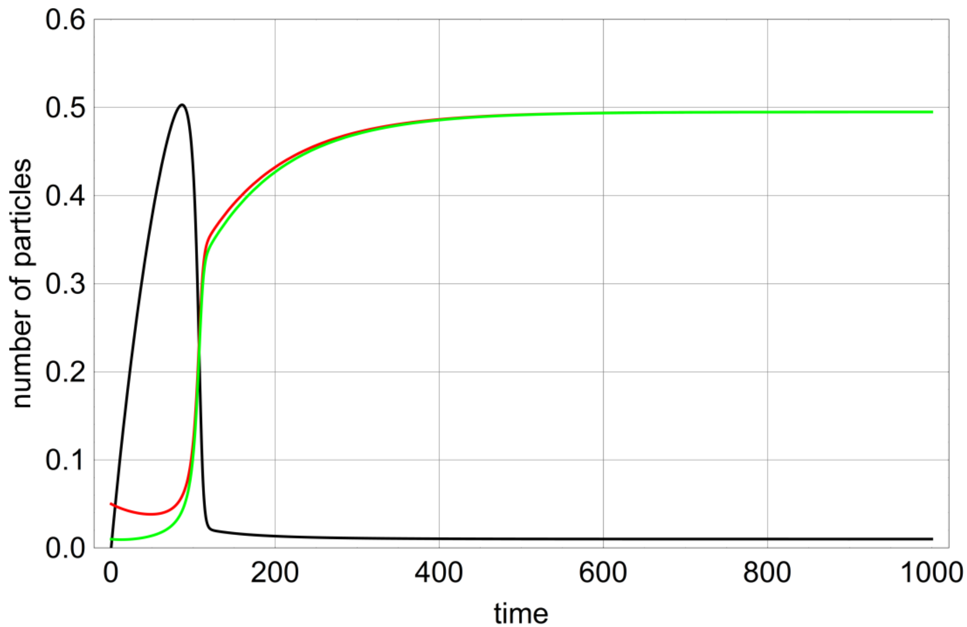
eigenvalues of the Jacobian: ω_k ; $k = 0, 1, \ldots, n-1$

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

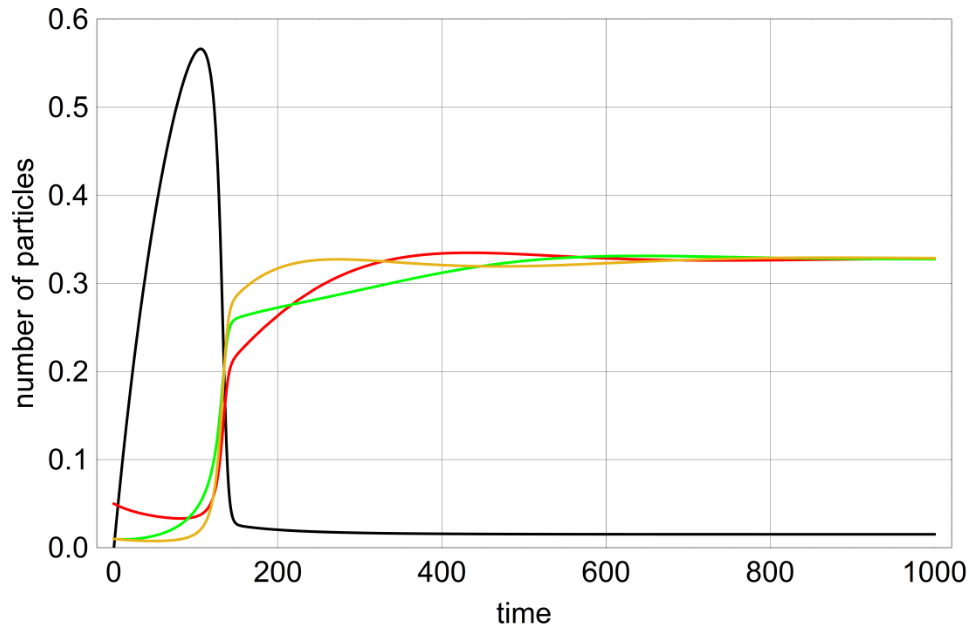
Long-time behavior of hypercycles in the flow reactor

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

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



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

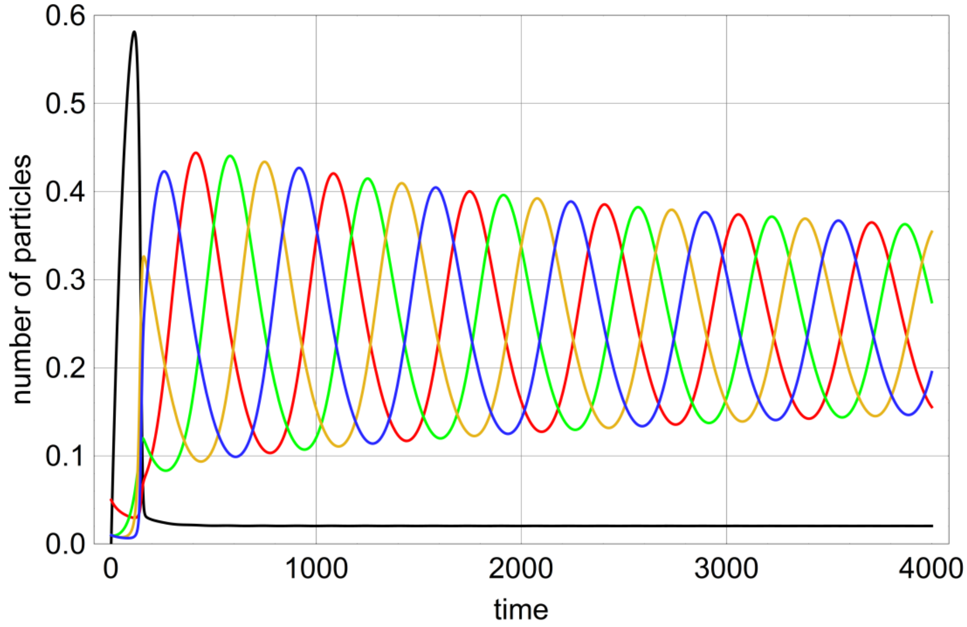


$n = 4$

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

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

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



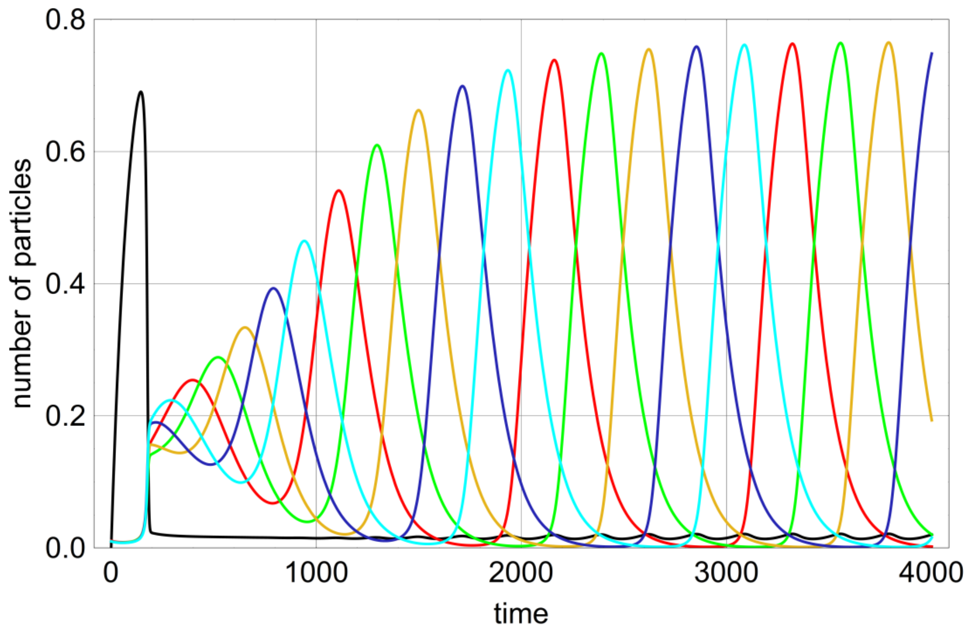
$n = 5$

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

$r = 0.01$, $a_0 = 1$

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

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



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

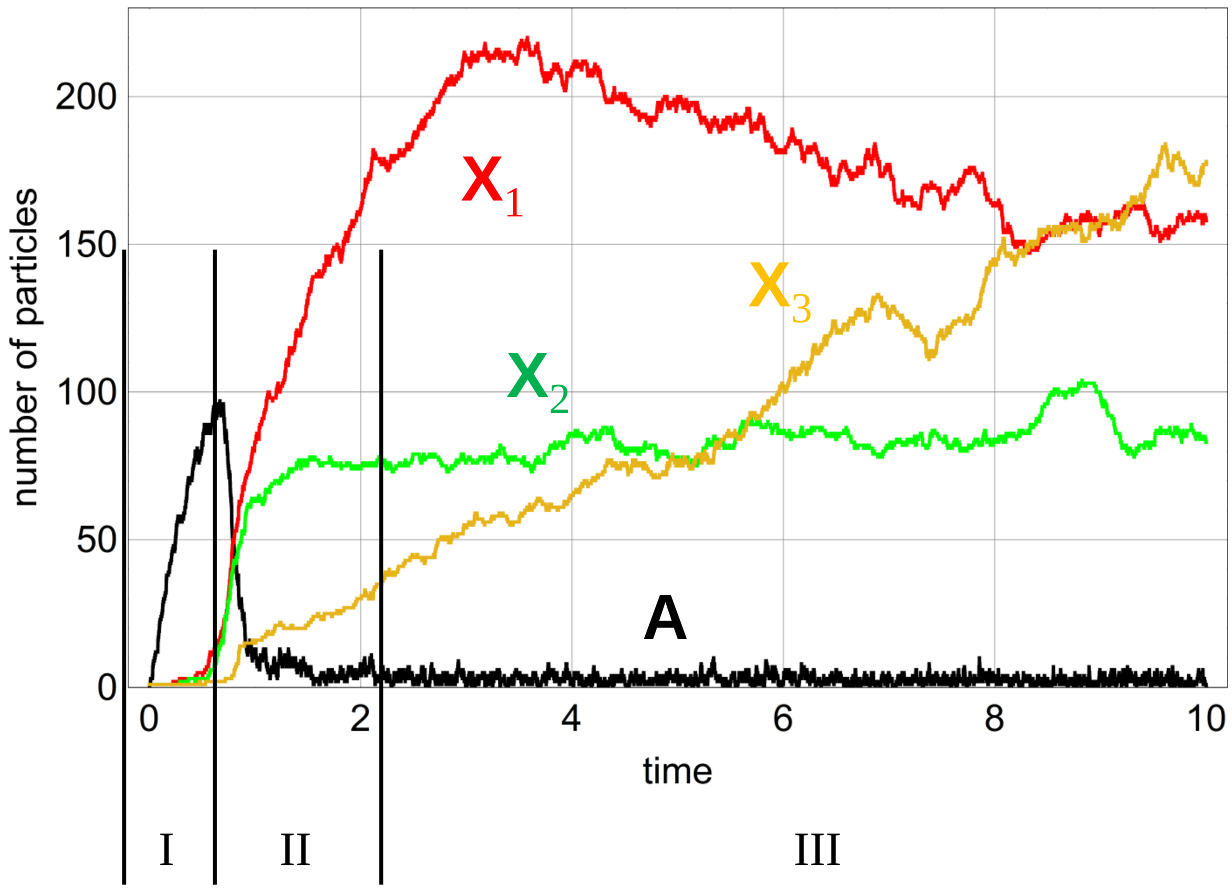
$$\mathbf{X} = (\mathrm{m}, \mathrm{s}_j; j = 1, \ldots, n)$$

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

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

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

The master equation for competition and cooperation

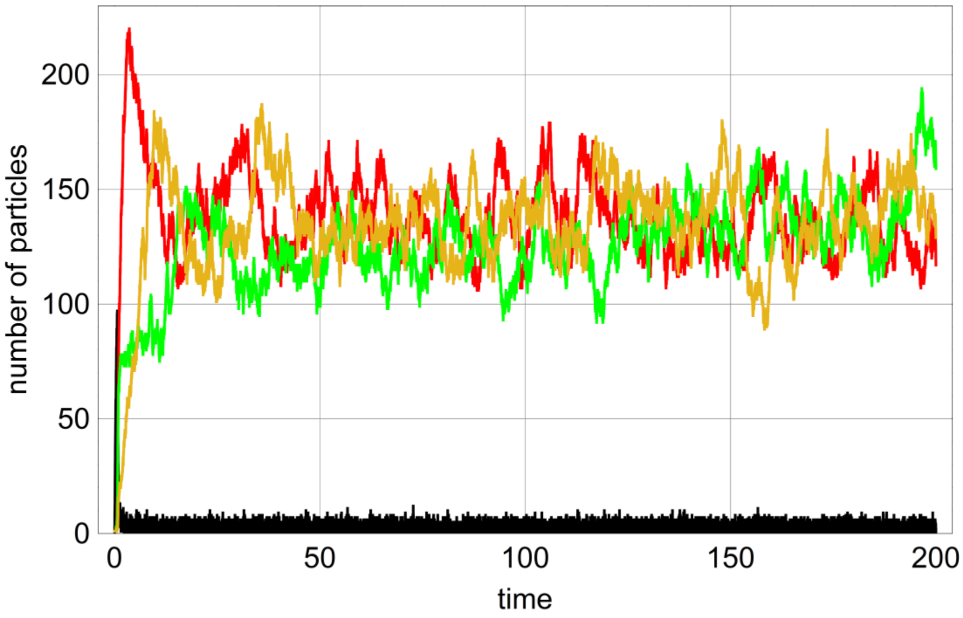


phase I: raise of [**A**] ; phase II: random choice of quasistationary state ;

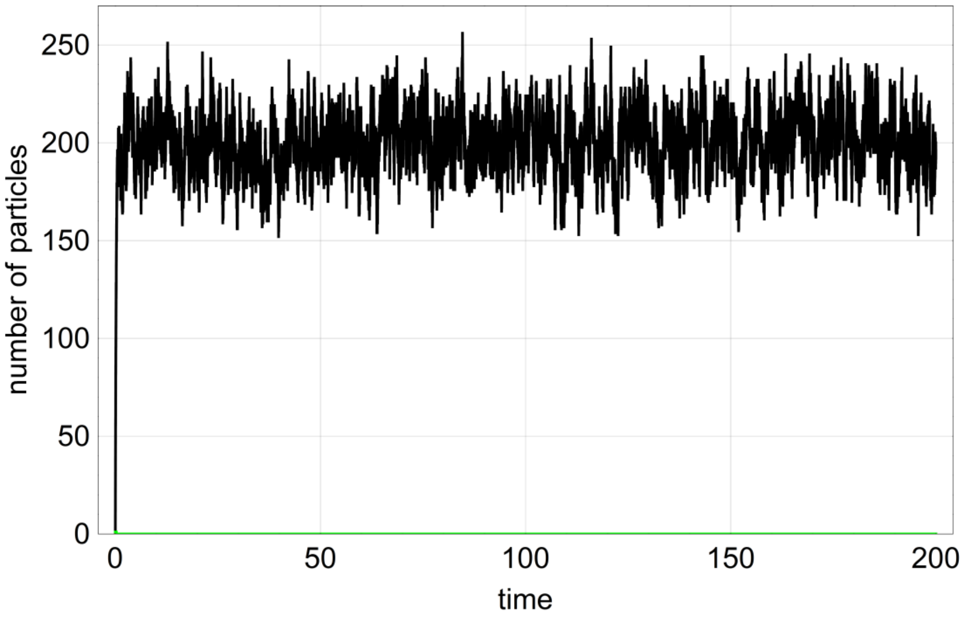
phase III: convergence to quasistationary state

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

quasistationary state of
cooperation



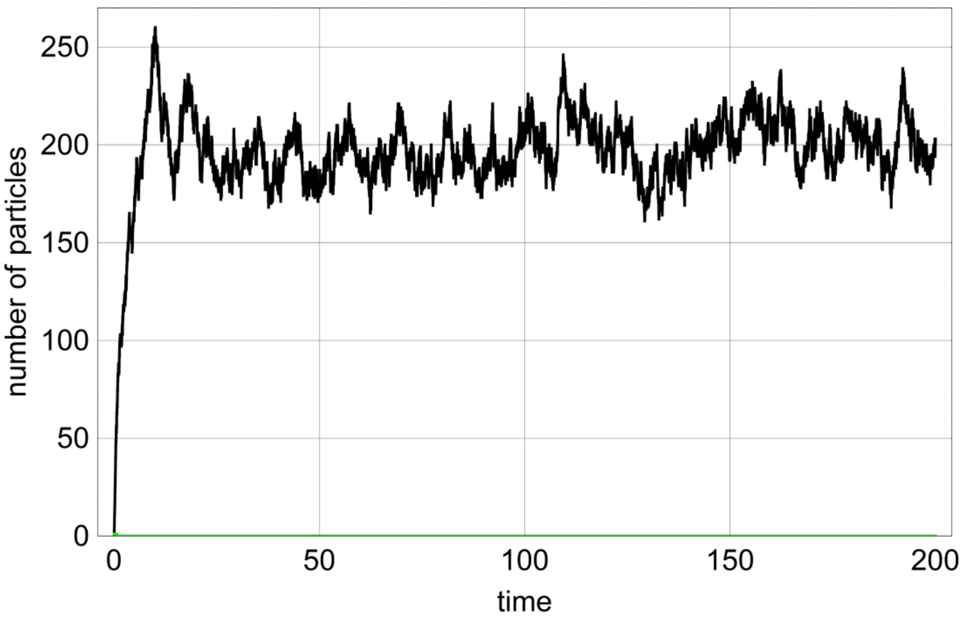
absorbing state of
extinction



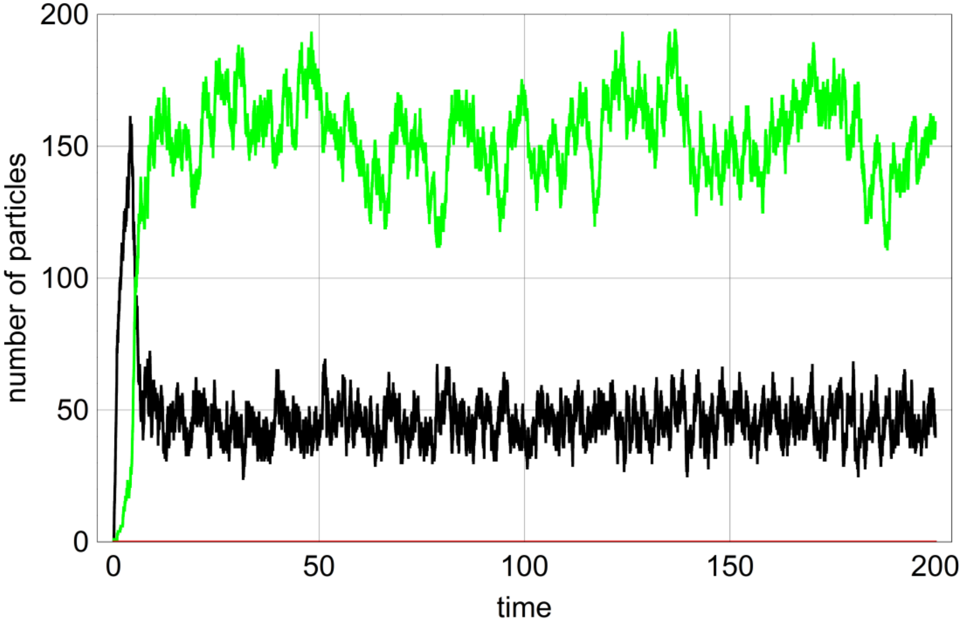
$$\frac{\mathrm{d}P_{\mathbf{X}}}{\mathrm{dt}} = a_0\, r P_{(\mathrm{m}-1)} + r\Big((\mathrm{m}+1)P_{(\mathrm{m}+1)} + \sum_{j=1}^{n}(\mathrm{s}_j+1)P_{(\mathrm{s}+1)}\Big) +$$

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

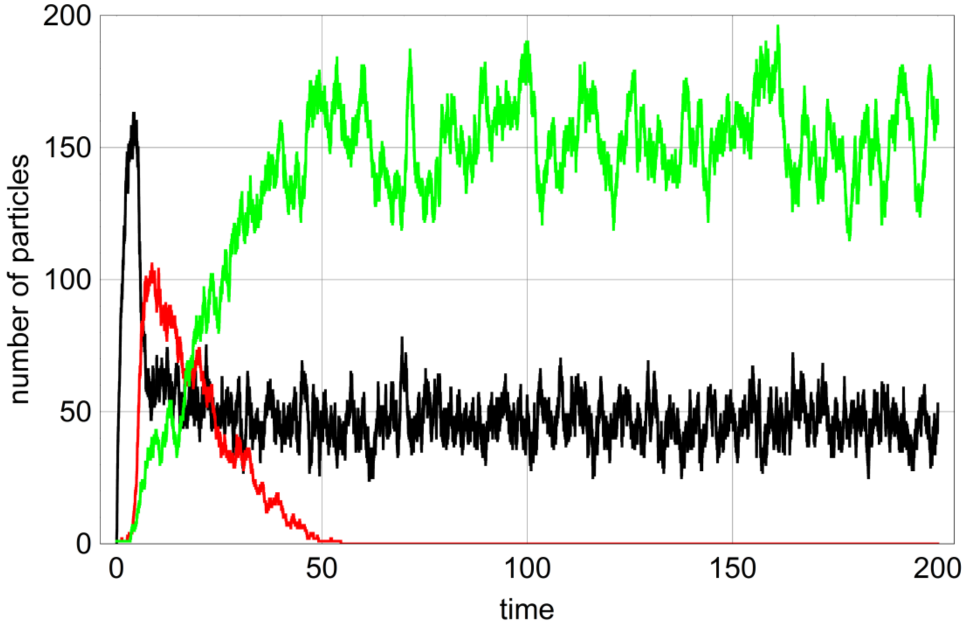
Stochastic selection

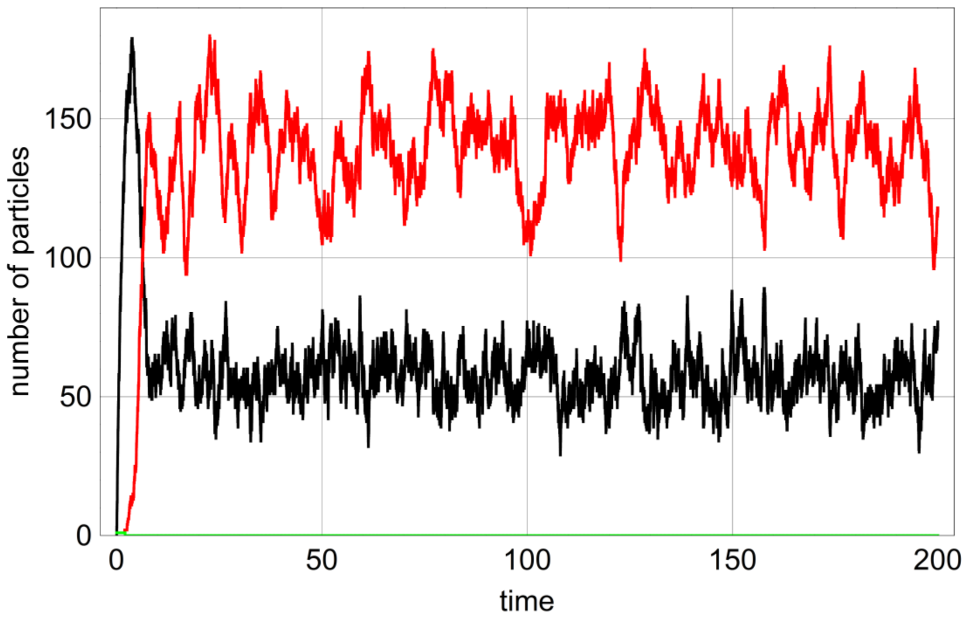


extinction and selection



other solutions





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: $f_1 = 0.11$ [$M^{-1}t^{-1}$]; $f_2 = 0.09$ [$M^{-1}t^{-1}$]; $a_0 = 200$; $r = 0.5$ [Vt^{-1}]

Counting of final states

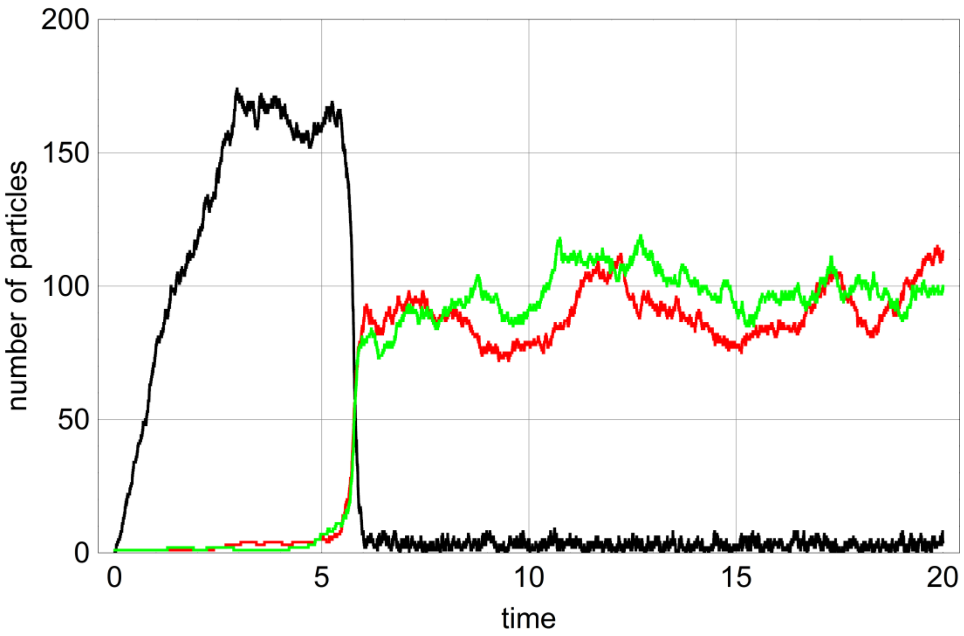
$$\frac{\mathrm{d}P_{\mathbf{X}}}{\mathrm{dt}} = a_0\, r P_{(\mathrm{m}-1)} + r\Big((\mathrm{m}+1)P_{(\mathrm{m}+1)} + \sum_{j=1}^{n}(\mathrm{s}_j+1)P_{(\mathrm{s}+1)}\Big) +$$

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

Stochastic cooperation

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

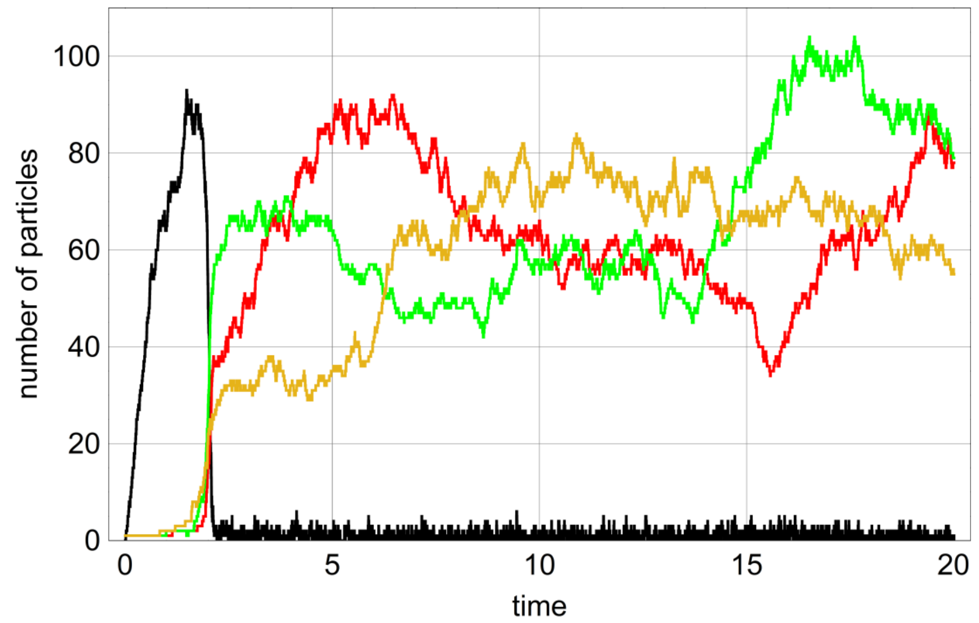
$k_1 = k_2 = 0.01$ [$M^{-1}t^{-1}$]



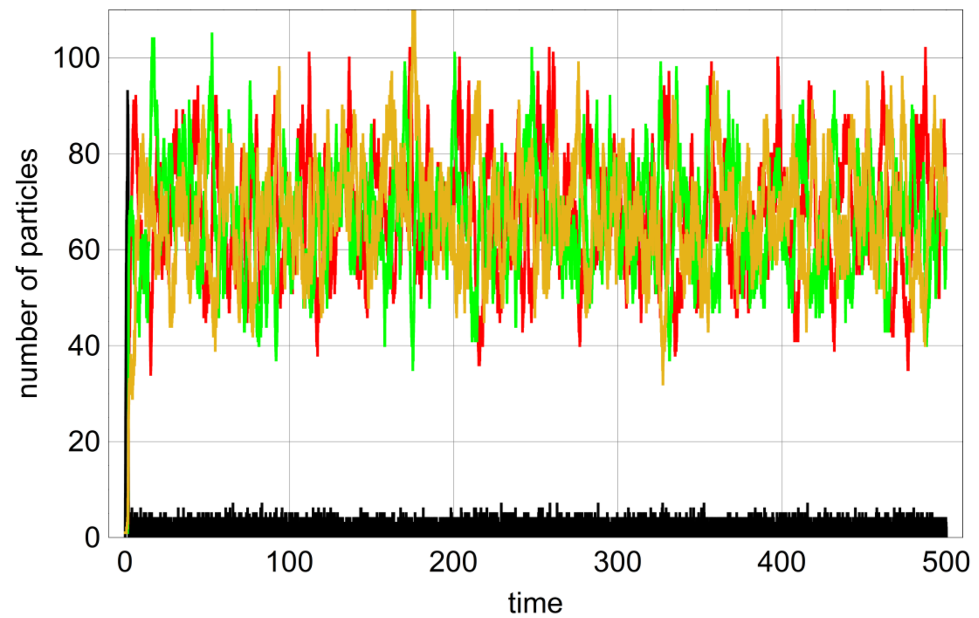
$k_1 = k_2 = 0.002$ [$M^{-1}t^{-1}$]

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

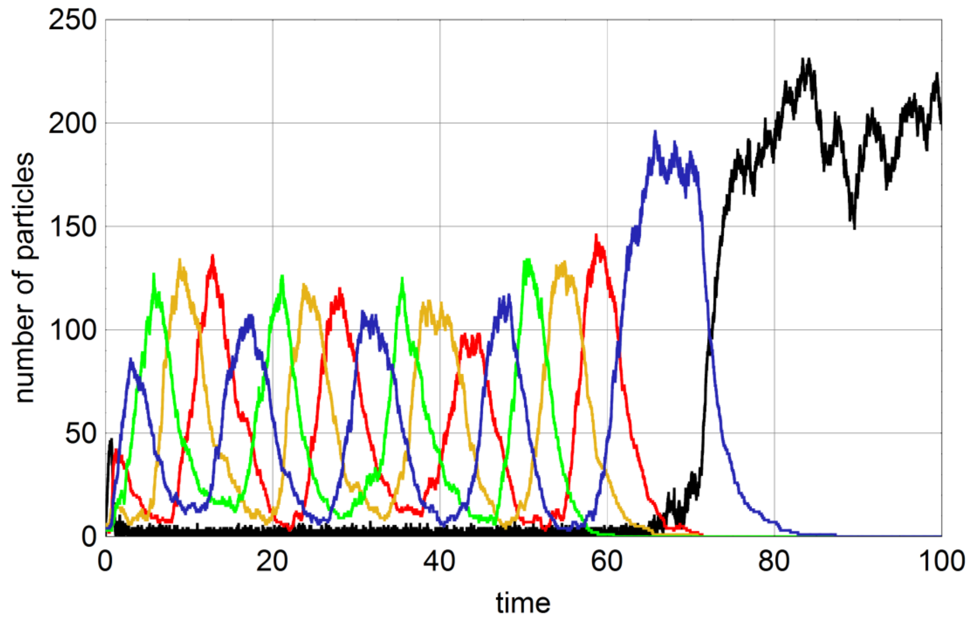
Stochastic cooperation with $n = 2$



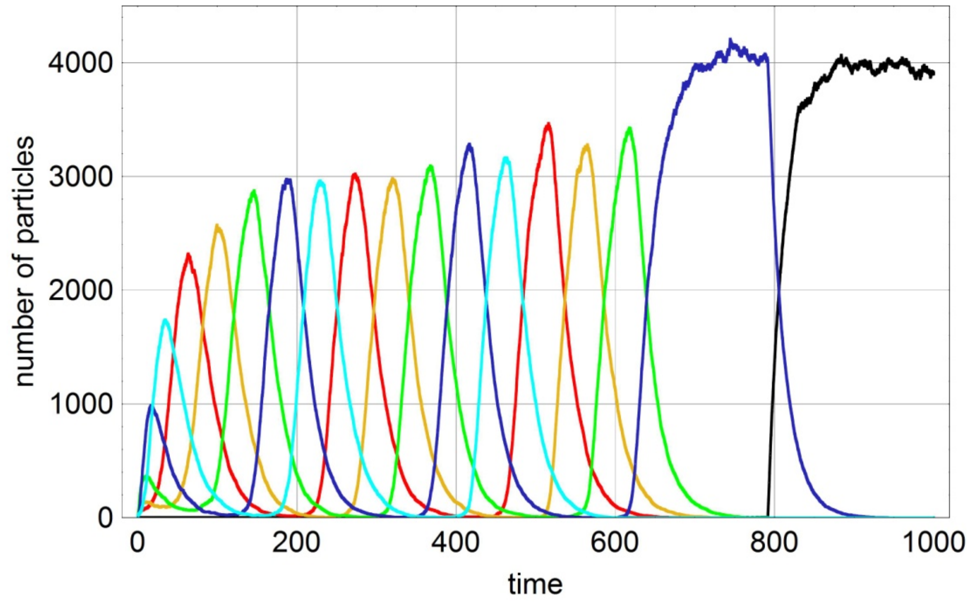
stochastic hypercycles with $n = 3$

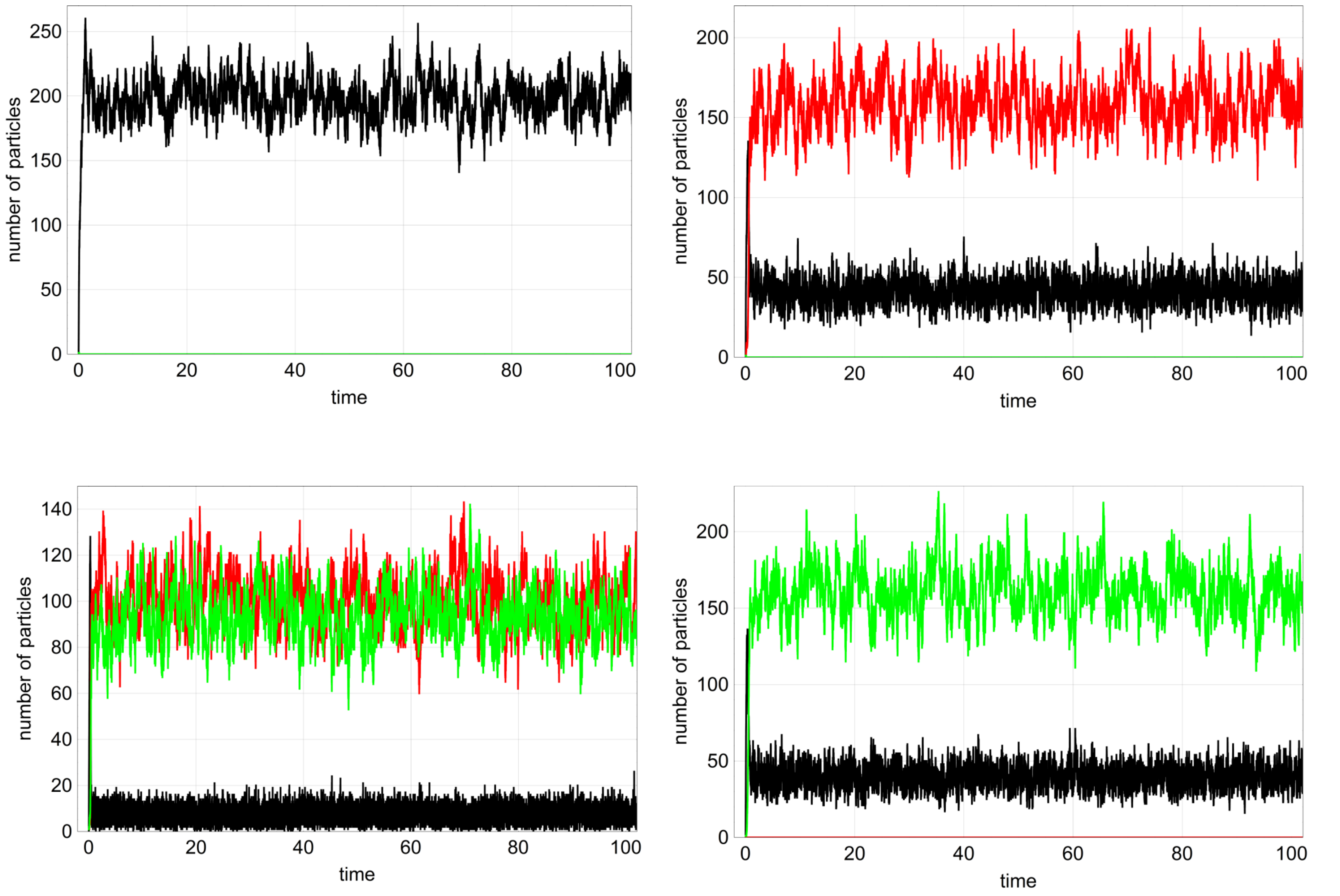


stochastic hypercycles with $n = 4$



stochastic hypercycles with $n = 5$





Competition and cooperation with $n = 2$

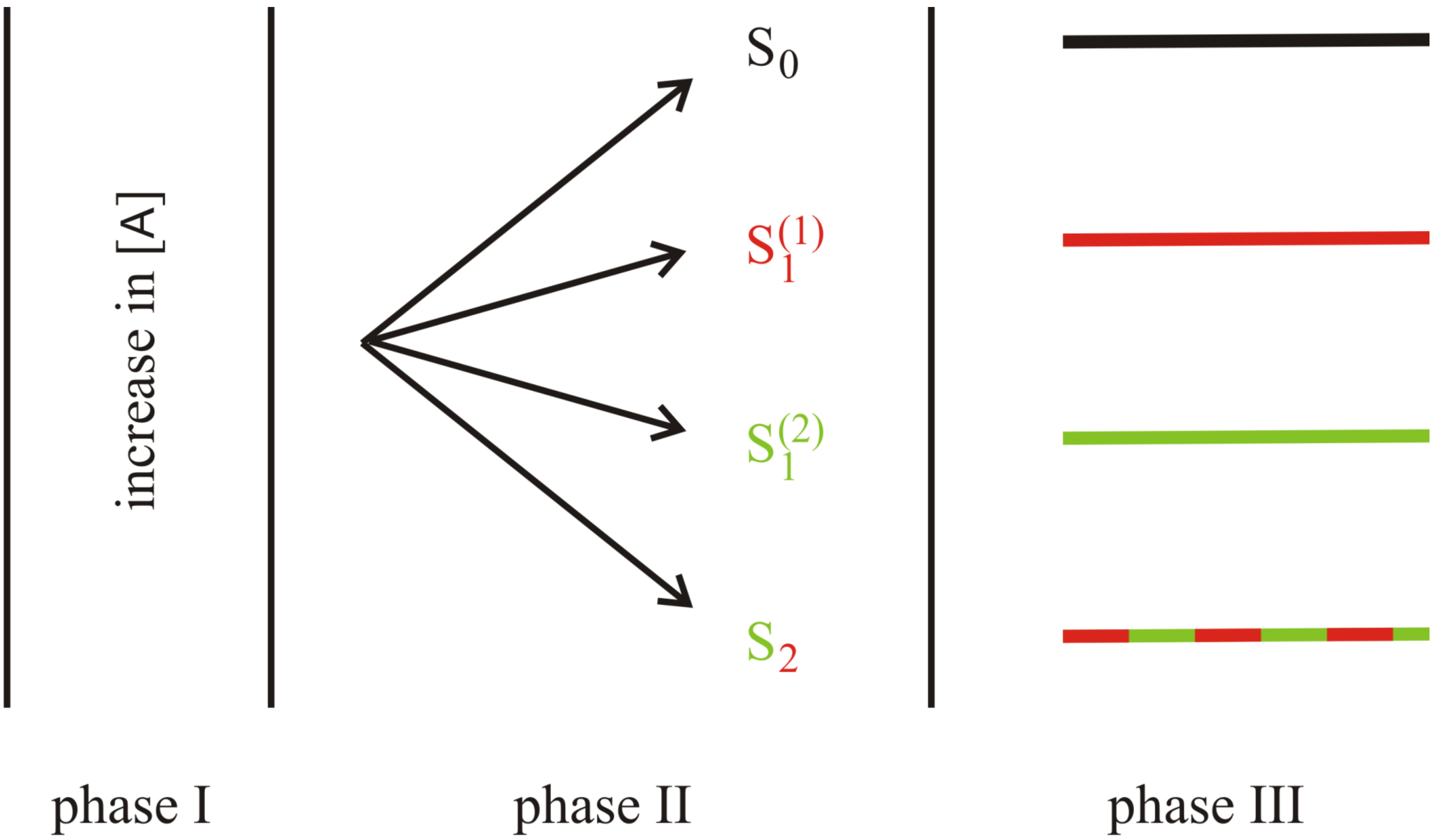
Initial values		Final states			
$X_1(0)$	$X_2(0)$	N_{S_0}	$N_{S_1^{(1)}}$	$N_{S_1^{(2)}}$	N_{S_2}
1	1	385.1 ± 23.6	1481.0 ± 36.8	1719.6 ± 37.8	6414.3 ± 53.8
2	2	14.9 ± 2.6	303.7 ± 16.0	354.5 ± 23.8	9326.8 ± 22.7
3	3	0	70.2 ± 10.0	106.2 ± 10.9	9823.4 ± 15.7
4	4	0	12.1 ± 2.6	28.0 ± 5.0	9959.9 ± 6.4

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

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

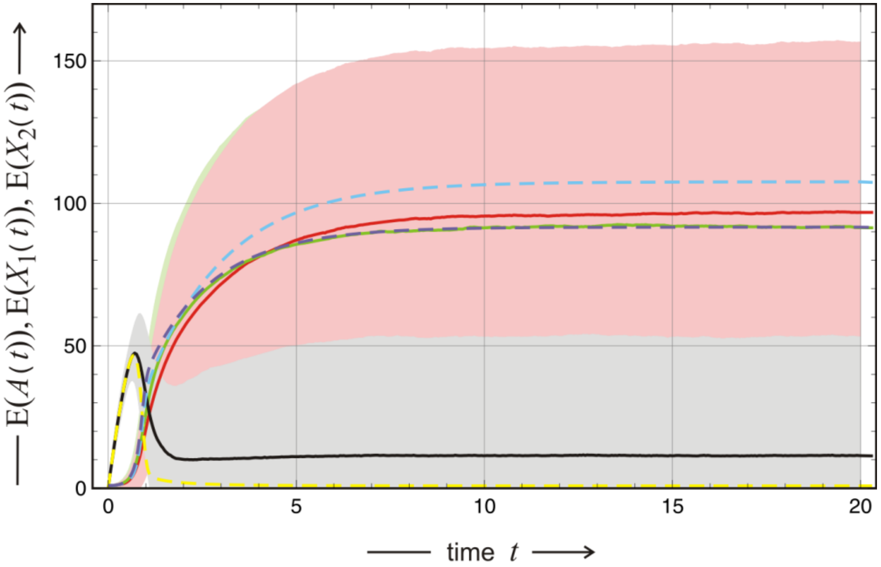
$a_0 = 200$; $r = 0.5$ [Vt^{-1}]; $a(0) = 0$

Competition and cooperation with $n = 2$



Random decision in the stochastic process

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

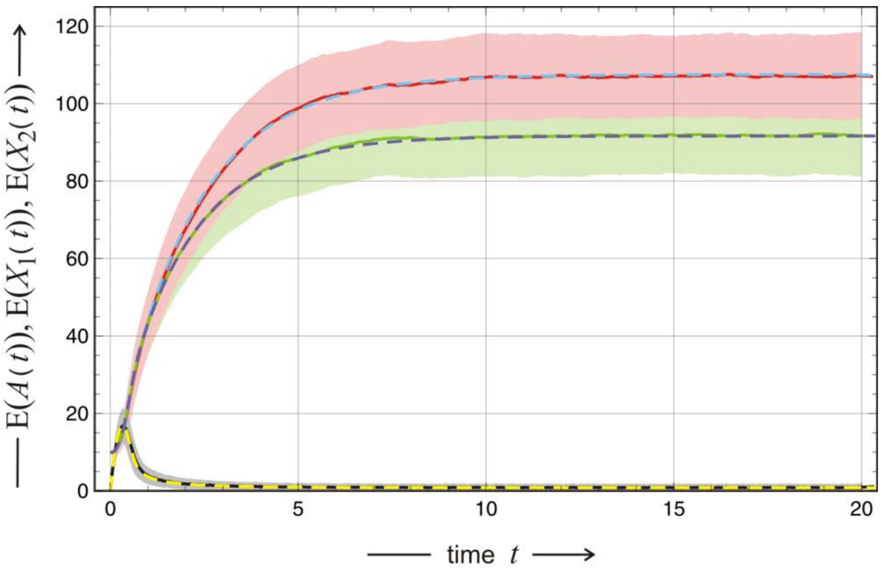


expectation values and 1σ-bands

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

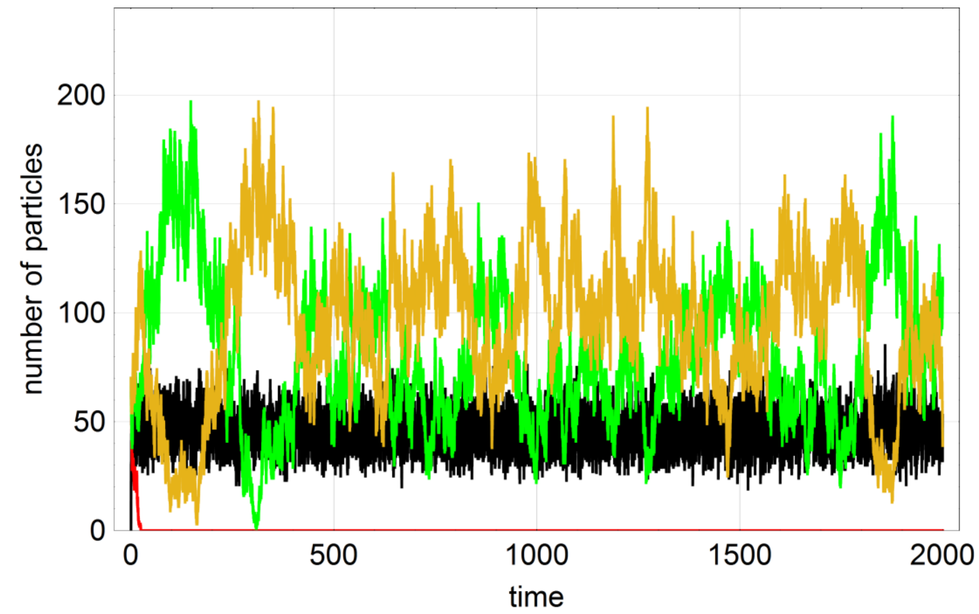
$f_1 = 0.09$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$], $f_2 = 0.11$ [$\mathrm{M}^{-1}\mathrm{t}^{-1}$],

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



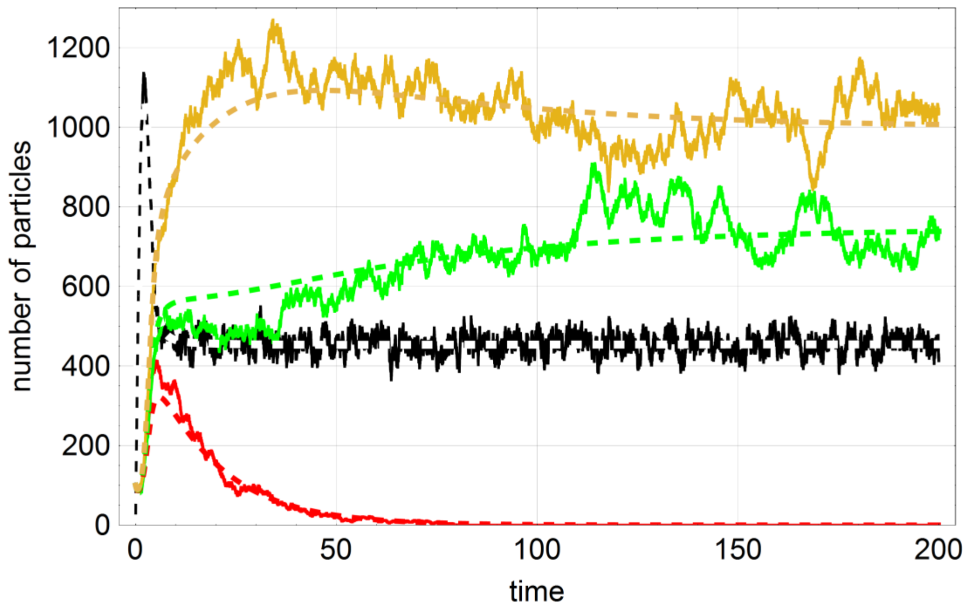
$a(0) = 0,\ x_1(0) = x_2(0) = 10$

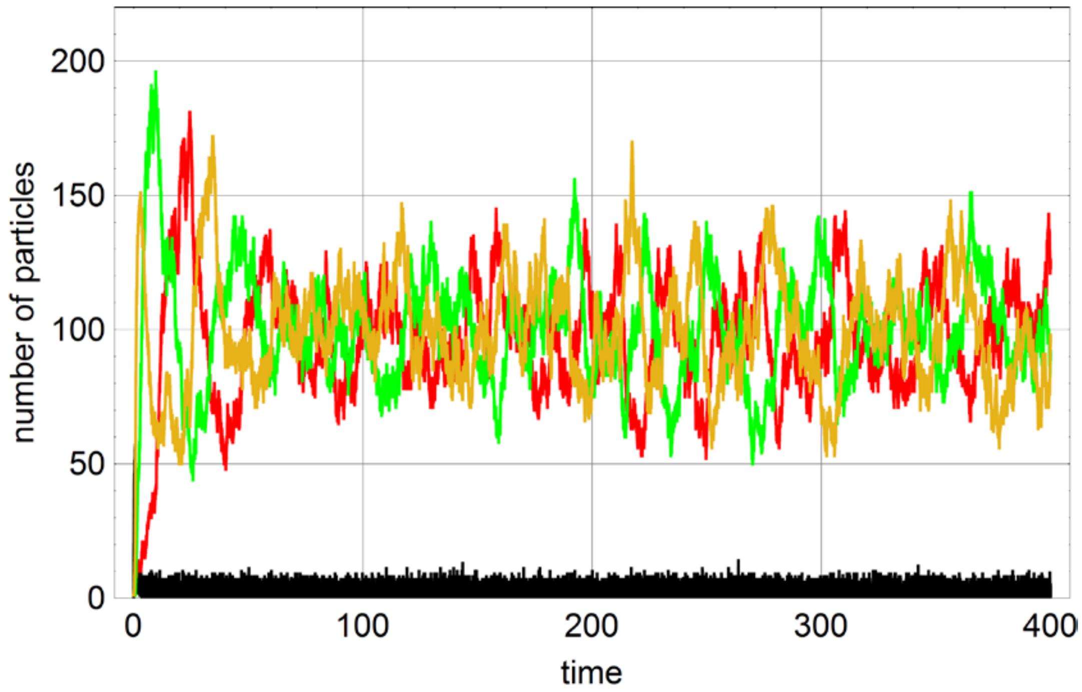
$a_0 = 220$



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

$a_0 = 2200$





$n = 3$, state of cooperation S_3

1. Motivation
2. Examples of major transitions
3. A kinetic toy model for major transitions
4. Stochastic analysis of the toy model
5. **Some conclusions**

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

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Thank you for your attention!

Web-Page for further information:

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