Eco-evolutionary dynamics:

multilevel evolution
vesicles vs mesoscale patterns

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Multilevel evolution

LAST TIME:

Emerging higher level Darwinian Entities (waves)

In Hypercycle model emerging spiral waves
$->$ "everything" different relative to ODE model
Parasites evicted in "ecological time"
evolution studied as invasion of mutants vs replicator equation

in minimal eco-evolutionary replicator RP model:
waves emerge because of parasites
waves as evolving entities (birth,death,mutation, selection)
emergent trade-off, potential of novel function
bistability; parasitism induces more catalysis
degrees of freedom: speciation, symmetry breaking
need of low diffusion rate relaxed/ lowmutation rate

TODAY:

"vesicles" as higher level entities

combining vesicles first and evolution
first view of early evolution
conflict between levels of evolution
conflict resolution and evolution of novelty

explicit higher levels of selection
coupling between levels

- Classical (ecological group selection model (DS Wilson)
- Classical prebiotic evolution model
  Stochastic corrector model (Szathmary)
- direct comparison emerging and imposed higher level of selection RP model
- Evolutionary stable disequilibrium: tuning stochasticity
- Evolution of “gnomes” and Cricks dogma

(1) Static multilevel evolutionary modeling

Classical theory of group selection (DS Wilson 1975, Michod)

- vs kin selection - $>$
- construct model without kinselection
- large number of predefined "compartments/patches" (leaves)
- confined selection
- within each compartment "altruist" (X) loses
  $dX/dt = aXX - cX \;\; dY/dt = aXY$
  (HOWEVER finite number!)
- random dispersal after growth/competition
- binomial distribution of X,Y in patches
- if $c < a$ trait increases (cf single level)
- *statistically* same environment: higher level selection compensates for lower level
- more than random variation (clumping) also 'strong' altruist can evolve

NB patches do not react on lower level

NB Mathematically Kinselection == Groupslection covariance between trait and fitness

(Compare Simpson paradox)

A Theory of Group Selection 145

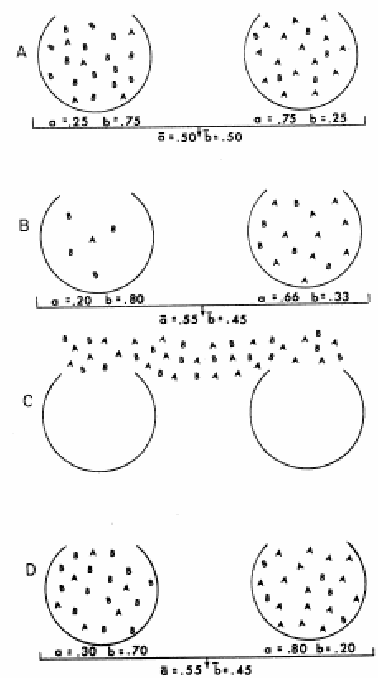


FIG. 2. Illustration of the group selection process. See *text* for explanation.

(2) (population) dynamics of macro-level (cells) explicitly modeled using param's derived from micro level

vesicle-based 'solution' of information threshold:
Stochastic Corrector model (Szathmary and Demeter 1987)

- higher level selection imposed as vesicles (cf waves)
- (like hypercycle) study 'ecological dynamics' (without mutations)
- 2 mol. form together 'replicase' (or produce metabolite) (cf RP model)

Micro level (within vesicles)

$$dX/dt = aX(XY)^{1/4} - dX - X((X+Y)/K)$$
$$dY/dt = bY(XY)^{1/4} - dY - Y((X+Y)/K)\ ;\ \mathbf{a > b}$$

(fastest growth iff X = Y)

(X outcompetes Y in ODE;
discrete stochastic version: master equation $->$
prob. distribution of mol after time=τ)

Macrolevel dynamics: vesicles
Quasispecies equation.
Species: cells with x_i, y_j molecules
"Mutations" probability to change from x_i, y_j to x_k, y_l cell

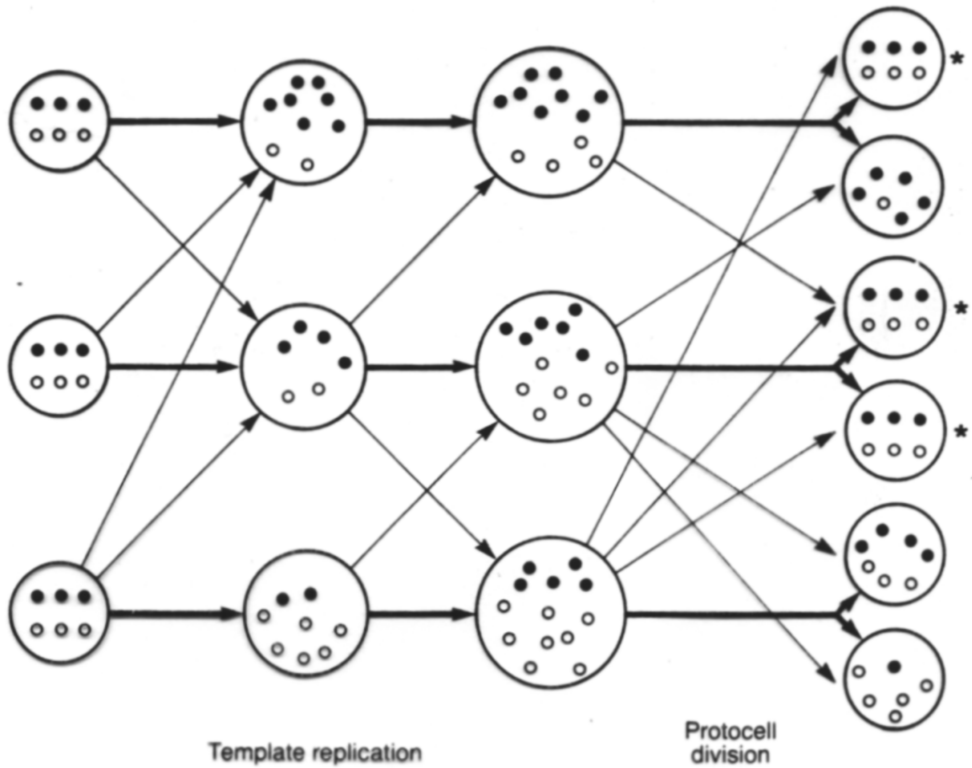
Result: master cell ($x_i = y_j$) persists!

(like group selection) can persist by stochastic fluct. in vesicle occupation (here dynamics).

NOTE: no evolution of internal replicators!

NOTE: scaling problems:
size of vesicle (should be small enough (enough stochistcity)
number of different molecules should be small enough

scheme of stochastic corrector model



NB timescales of micro vs macro dynamics

Micro and Macro level dynamics: intricate implicit mutual interactions Takeuchi and Hogeweg 2009

Micro level:
RP (replicator parasite system);
Parasite 2 states:
template (1-l), enzyme (l);
Evolutionary Unstable

Macro level:
(1) implicit: waves
(2) explicit vesicles:
growth (lL); death: # mols

$$(a) \quad \mathrm{R}+\mathrm{R} \underset{1-k_R}{\overset{k_R}{\rightleftharpoons}} \mathrm{C_R} \overset{\kappa\theta}{\rightarrow} 2\mathrm{R}+\mathrm{R},$$

$$\mathrm{L}+\mathrm{R} \underset{1-k_L}{\overset{k_L(1-l)}{\rightleftharpoons}} \mathrm{C_L} \overset{\kappa\theta}{\rightarrow} 2\mathrm{L}+\mathrm{R},$$

$$(b) \quad \mathrm{R,L} \overset{d}{\rightarrow} \theta,$$

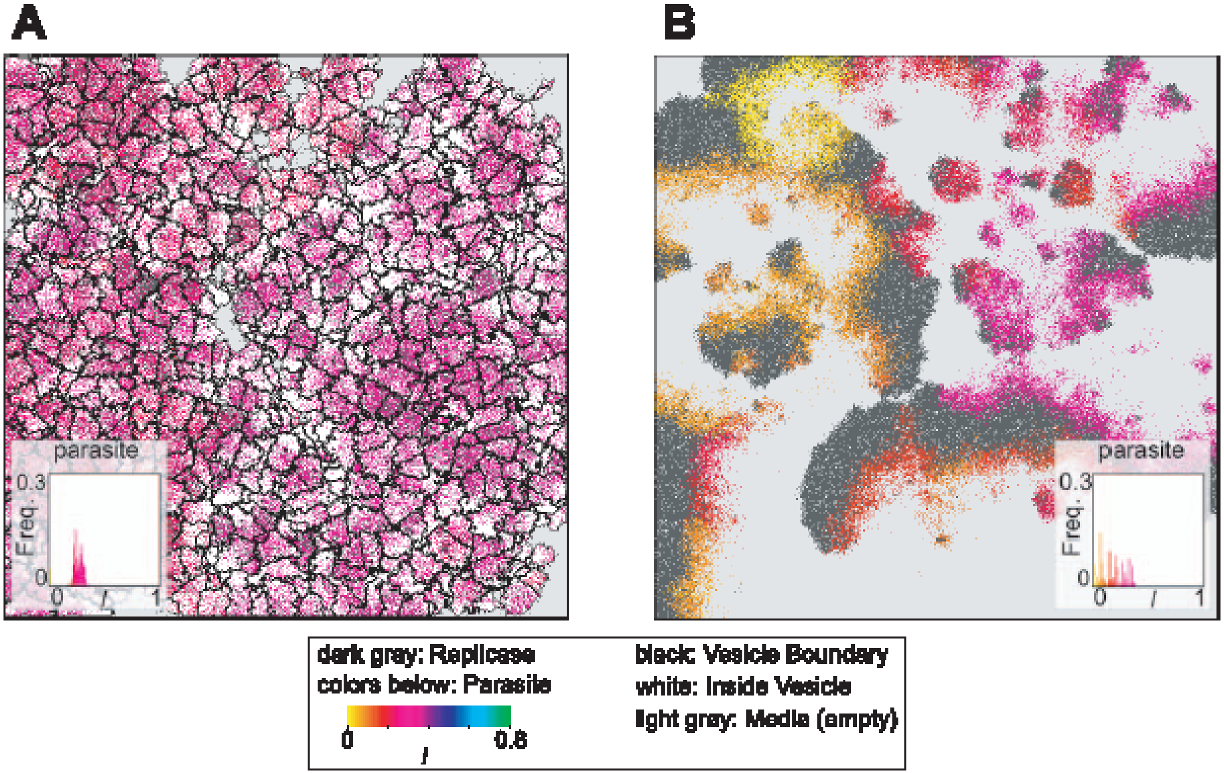
$$\mathrm{C_R} \overset{2d}{\rightarrow} \mathrm{R}+\theta,$$

$$\mathrm{C_L} \overset{d}{\rightarrow} \mathrm{R}+\theta,$$

$$\mathrm{C_L} \overset{d}{\rightarrow} \mathrm{L}+\theta,$$

$$(c) \quad \mathrm{L} \overset{ml}{\rightarrow} \mathrm{L}+x,$$

the 2 models

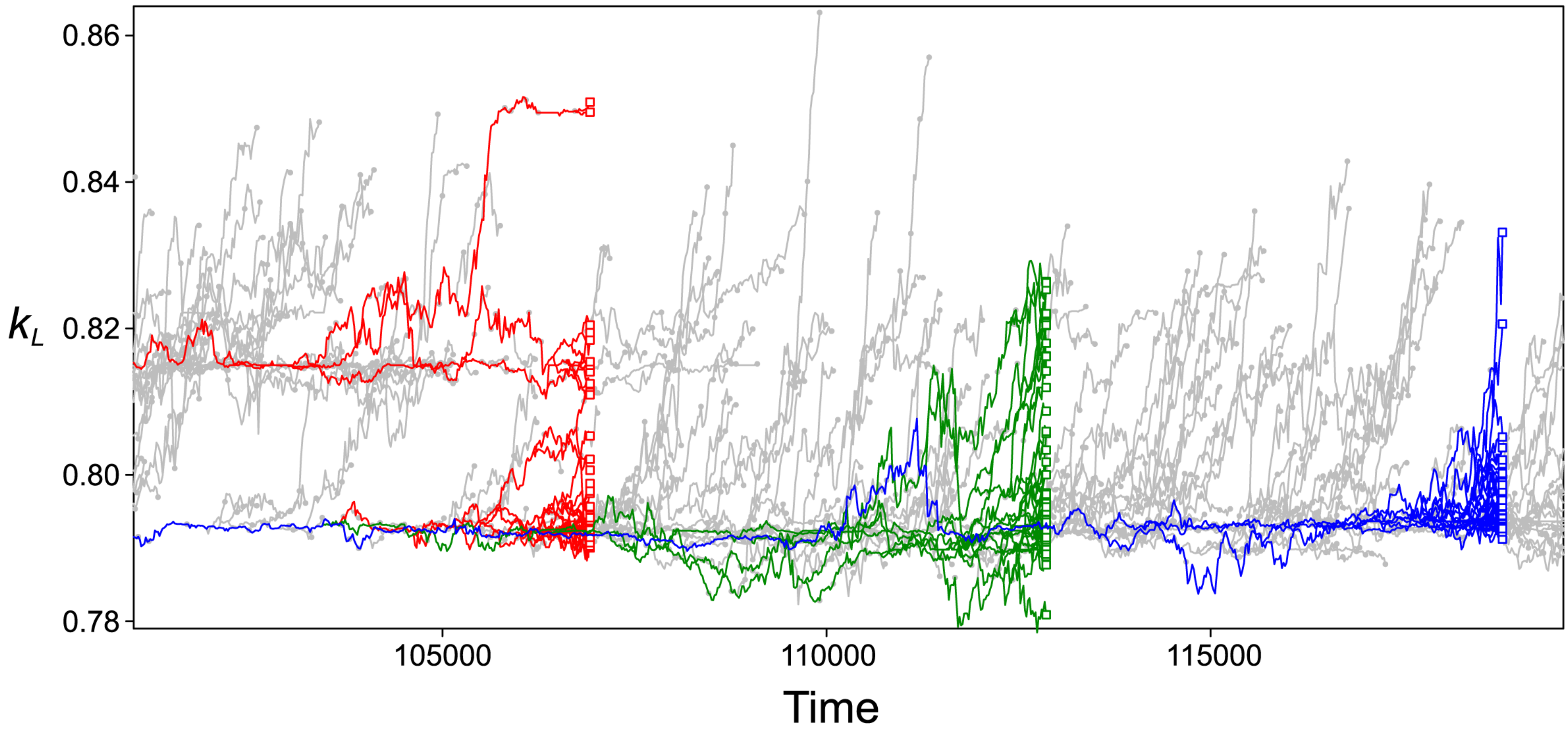


evolutionary dynamics

minimizes death rate
of vesicles

maximizes birth rate
of waves

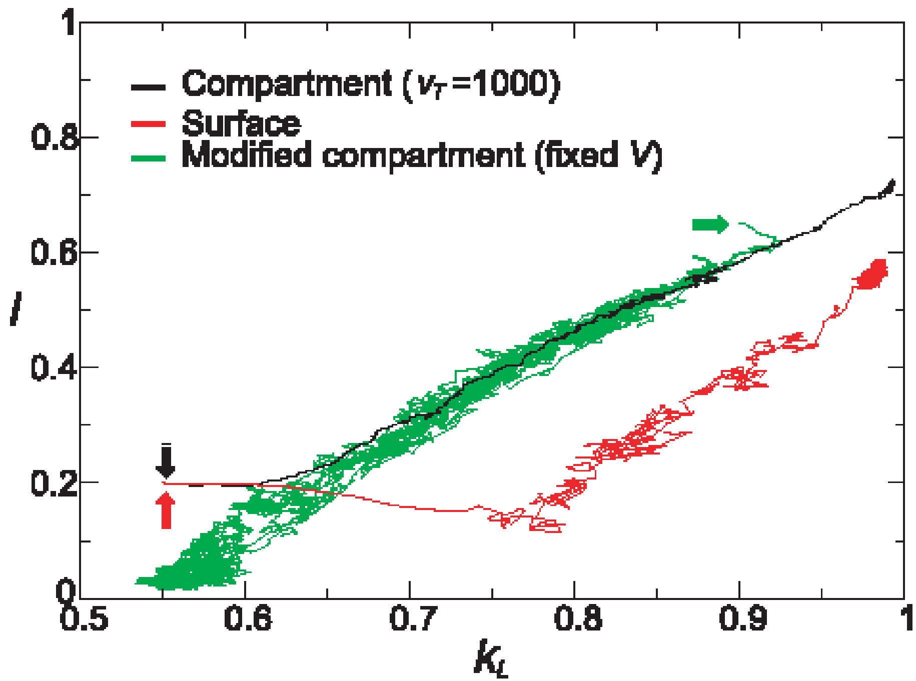
vesicle model: micro vs macro level selection

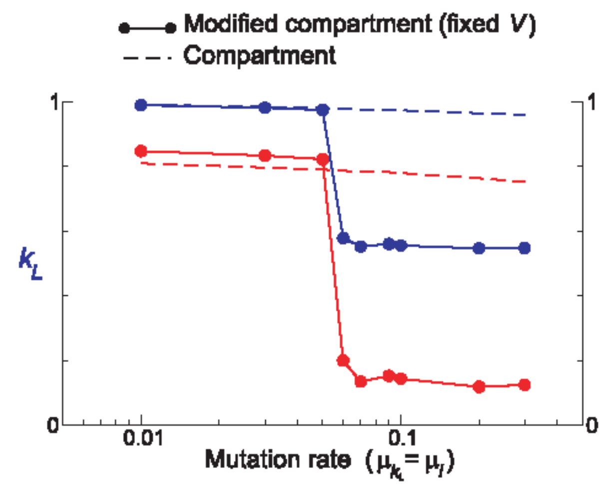


Only K_L evolves; l=0.5 vT=1000 $K_R = .6; d = 0.02$

evol rate of microsystem FAST relative to vesicle lifetime

evolutionary trajectories:
emergent trade-off and long term evolution

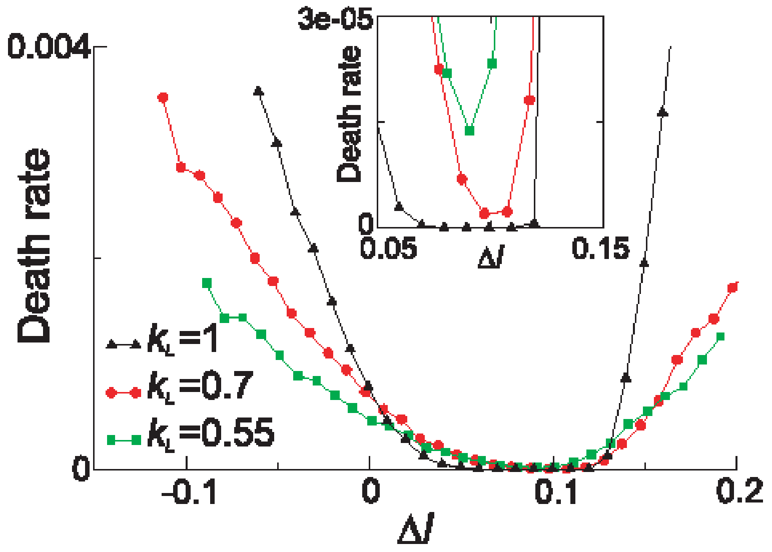


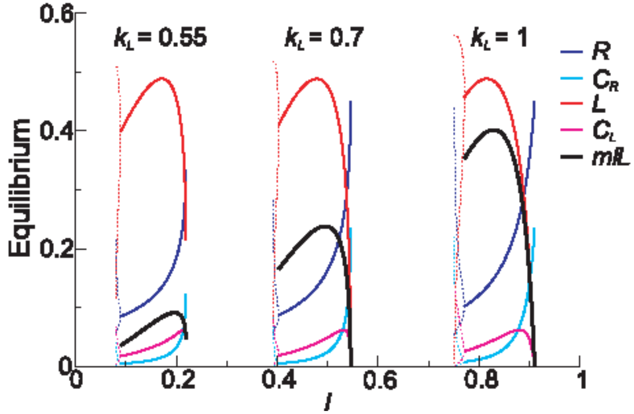


If lipid NOT needed for vesicle growth reversal of long term evolution trend *at high mutation rates*

'modified' vesicles
death rate of vesicles vs distance to replicator bifurcation

(constant vesicle size; death if no mol. or no L in vesicle)





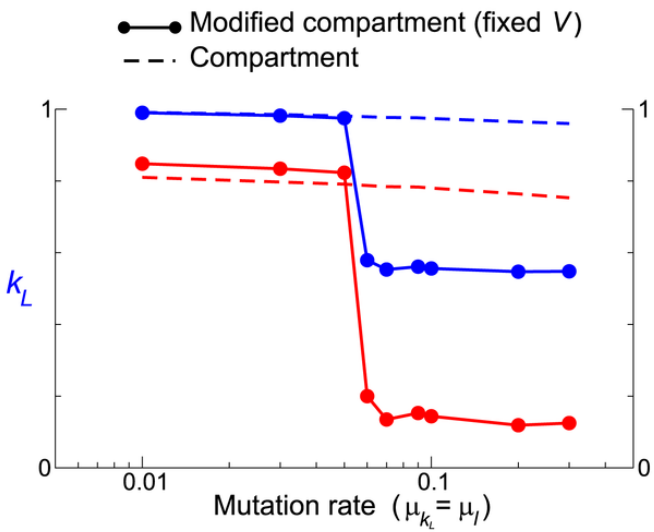
Δl from bifurcation point

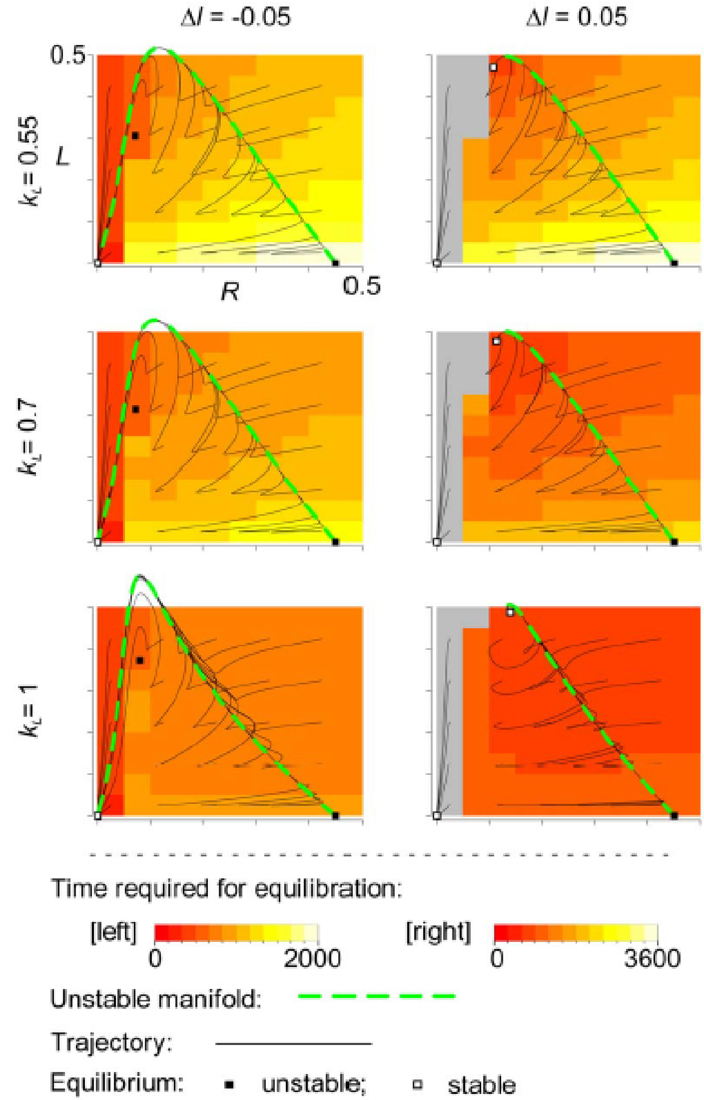
survival of the FLATTEST at high mutation rates

minimization of Death rate - max. of stoch.

internal dynamics $->$ vesicle death rate

Modified vesicles:
Evolution of the flattest at high μ
evolution of the fittest at low μ





maximization of stochasticity!

conclusion

- Higher level of selection: waves or vesicles
- Emergent trade-off
- self-organized levels of selection more stable(!)
  $->$ Maximize birthrate (= rate of growth of replicators alone
- imposed higher levels: less stable
  especially at high mutation rates
  minimize death rate
- maximize stochasticity -¿ stochastic correction
- *Implicit interactions in explicit multilevel models automatically mutually tunes "parameters"*

Note: protocell vs cell: "genotype" - phenotype relation

Evolutionary stable disequilibrium: endless dynamics of evolution in a stationary population (Takeuchi et al 2016)

Replicator model within ce (:NO parasites)

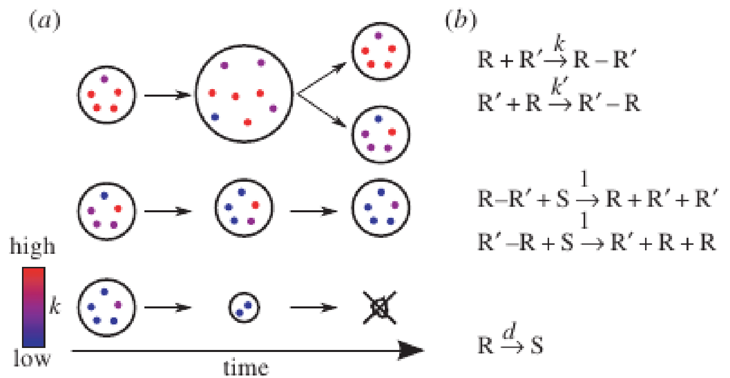
Minimization of catalysis
within cell

Maximization of cat. between cells

Internal dynamics:
ODE $-- >$ extinction

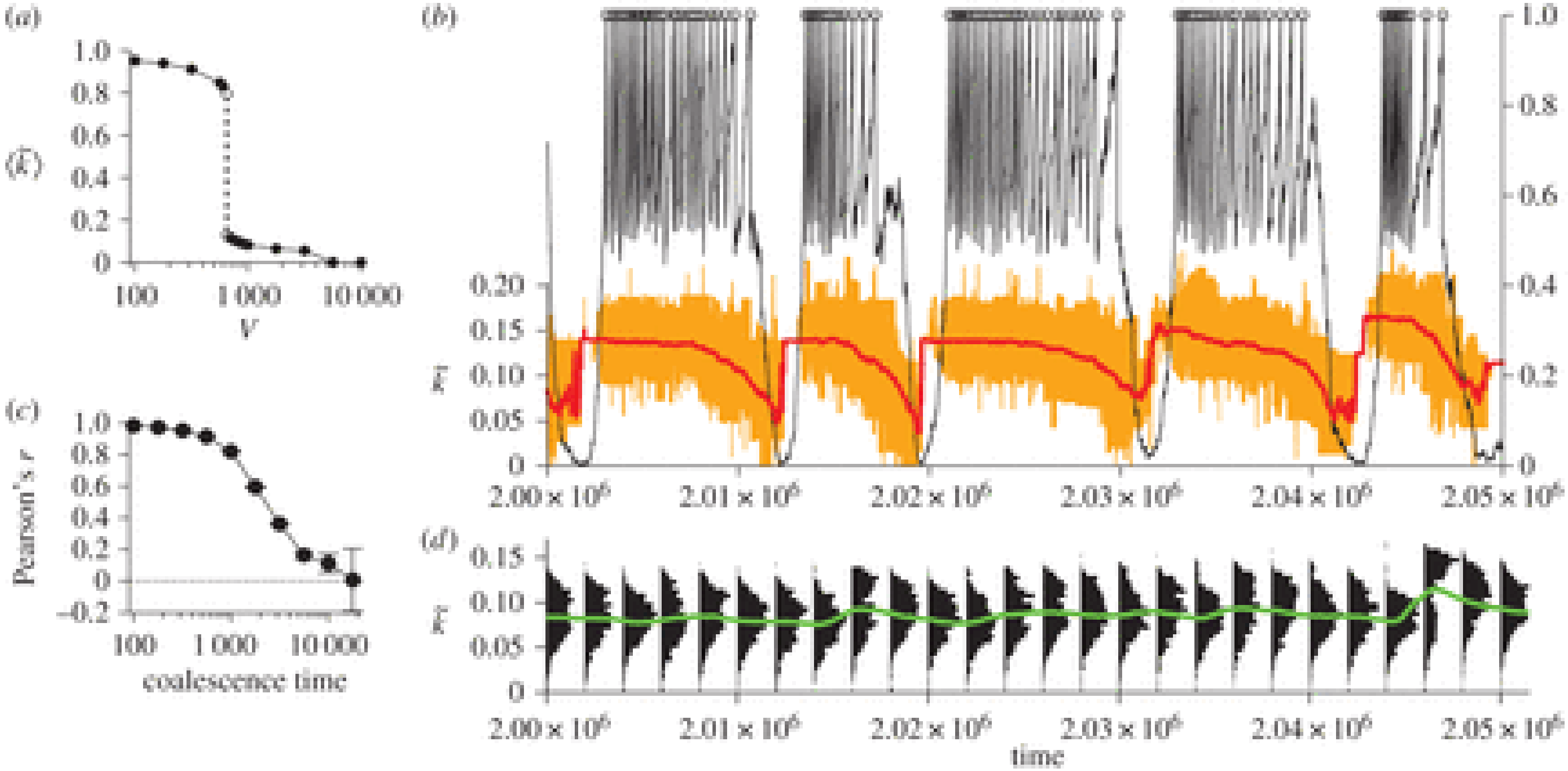
rate depends on mutation rate
(not evolvable)
and Vesicle size
(predefined at division)
(not evolvable)

Vesicle level selection
depends on variability (scales with i/V)



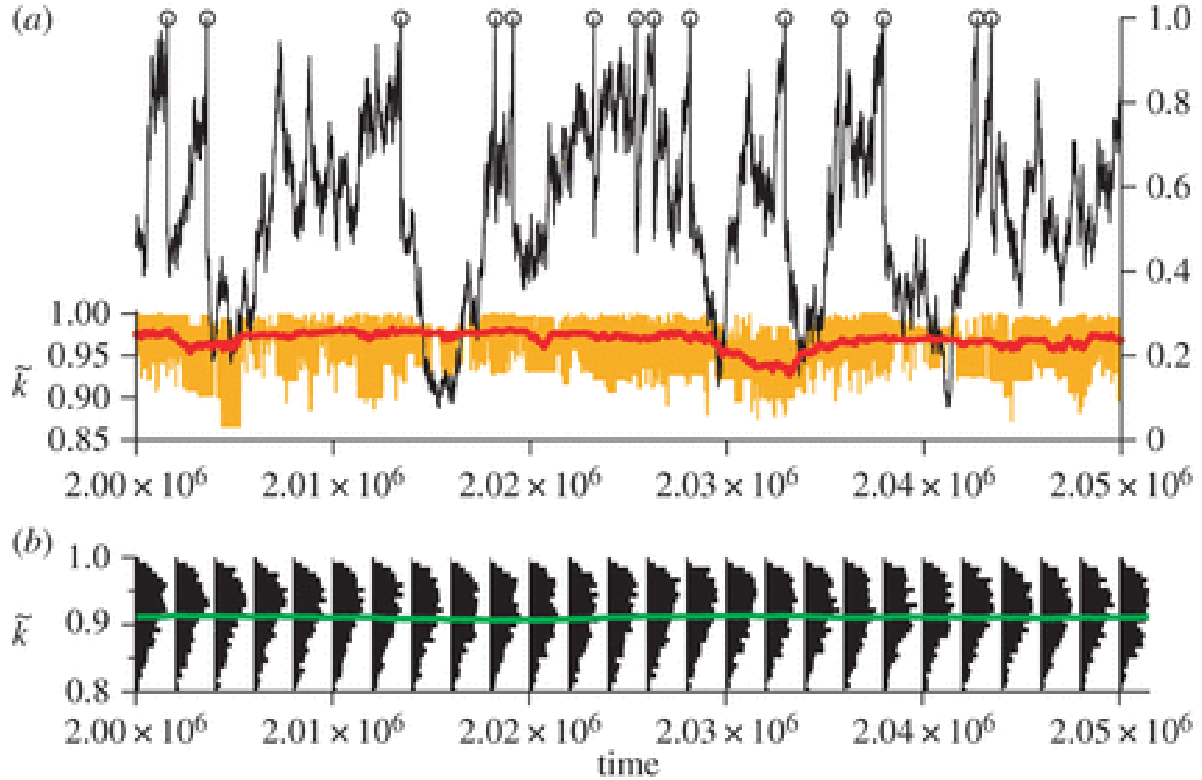
How does evolutionary dynamics cope with large cells?

Evolutionary dynamics along line of decent: evolutionary stable disequilibrium for large cells



V=1000

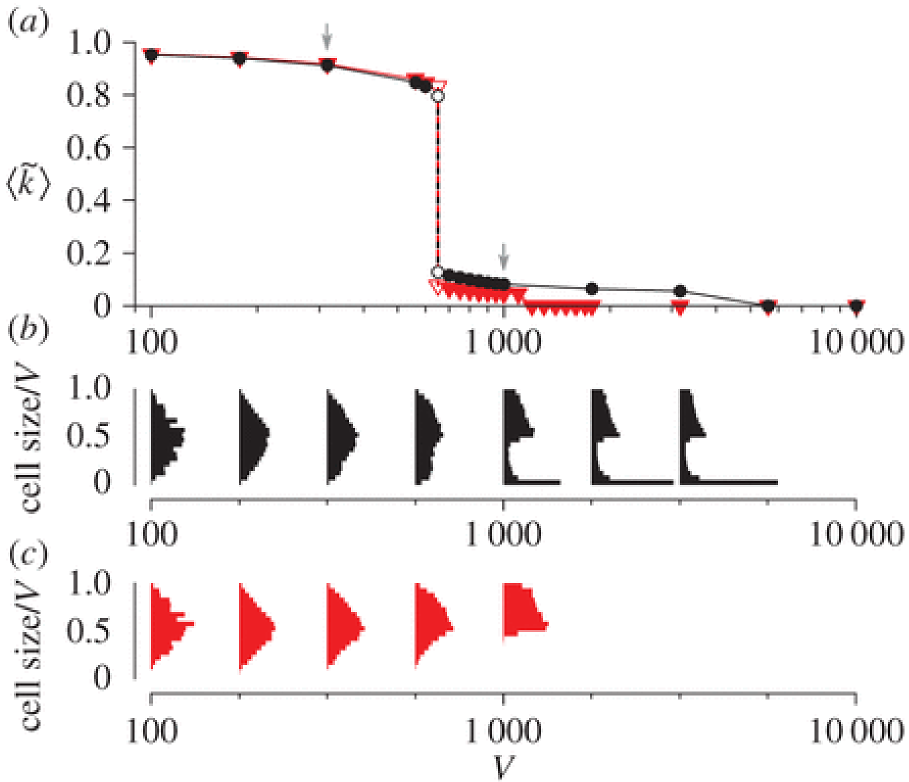
Evolutionary dynamics along line of decent: stochastic correction for small cells



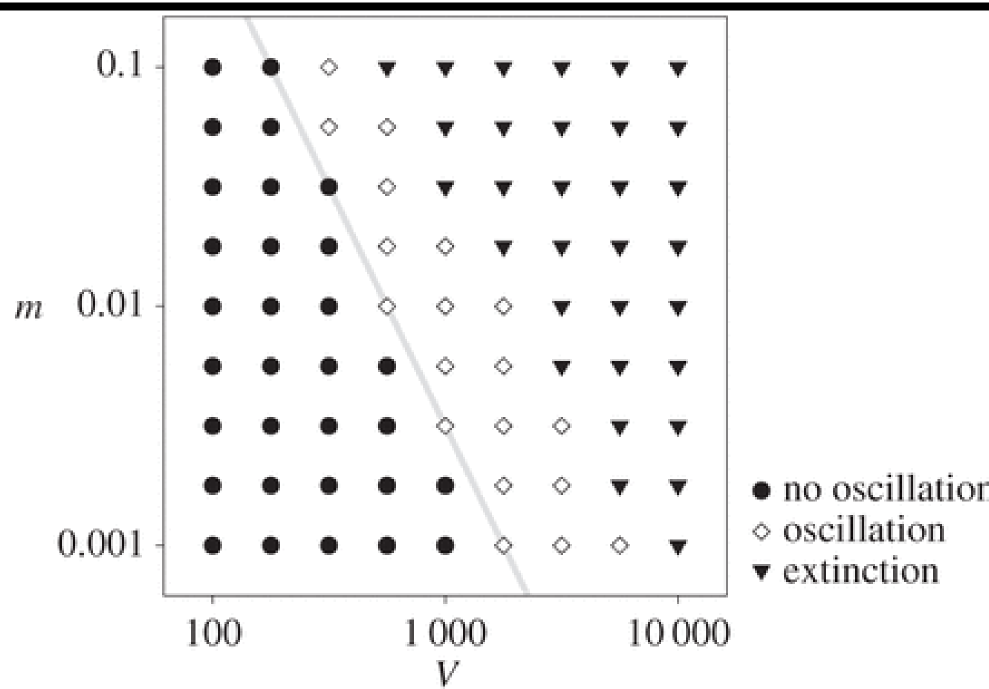
V=317

Coping with large cells by becoming small increase stochasiticy

Add extra selection
by killing small cells
only smaller cells survive



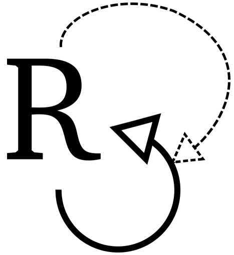
conclusion: conflict of levels of selection if similar strength: "creative solution"

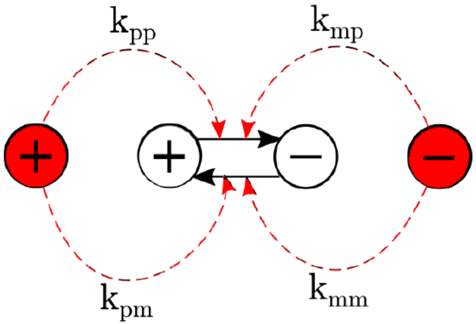


Within vesicle selection strength   mV
Between vesicle selection strength   1/V
If mV   1/V $-> mV^2 = C$ - oscillating internal dynamics.

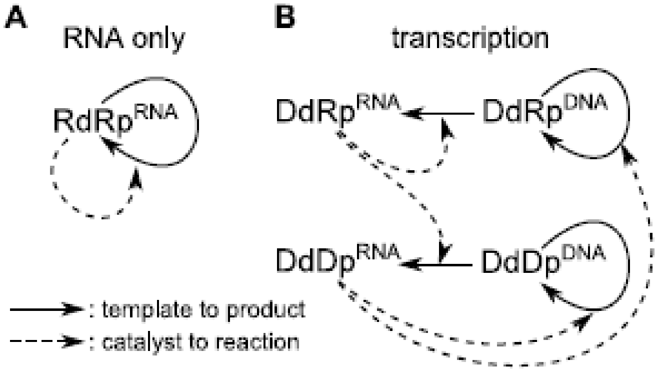
exploring evolutionary properties/advantages of more RNA-like replicators in RP systems (i.e. more degrees of freedom)

- **Direct replication vs Complementary replication**





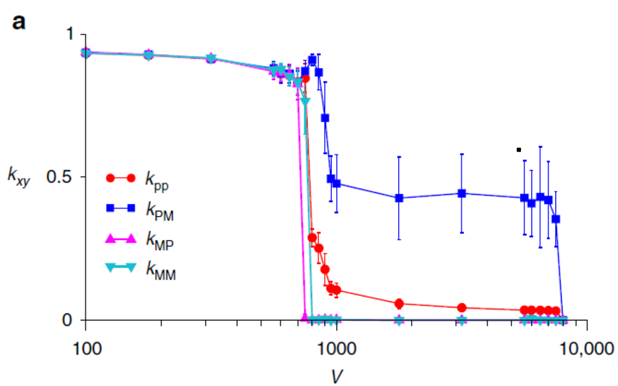
- **evolution of DNA in RNA world**

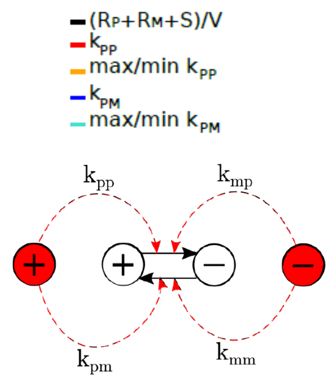


compare imposed vs emergent multilevel evolution

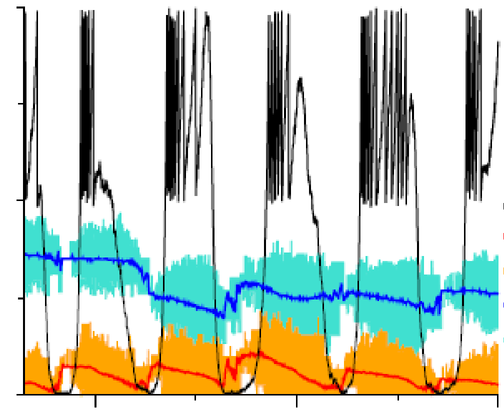
imposed levels of selection: protocells
direct vs complementary replication
symmetry breaking and robustness to larger cells

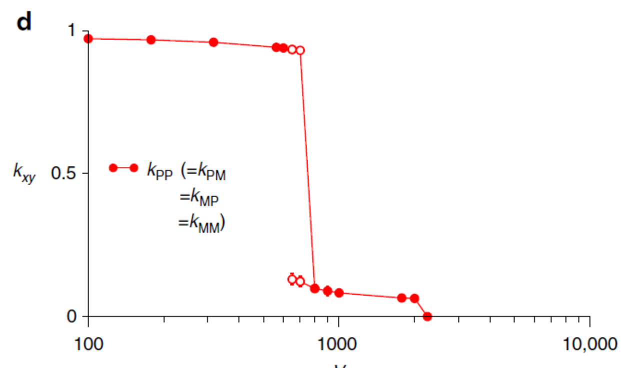
evolutionary attractors

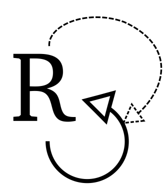


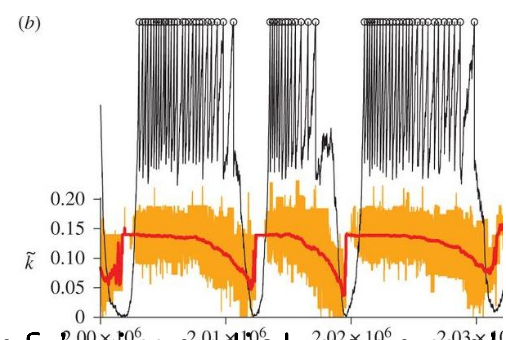


ancestor trace: bottlenecks









Evolutionary stable disequilibrium, and origin of 'primordial genome'

Takeuchi Kaneko, Hogeweg 2016; Takeuchi, Hogeweg, Kaneko 2017

Multilevel evolution and replicator strategies
protocells vs spatial self-organization

Both models:

Exploit "near death" for evolving new replication strategies

Protocells: enhanced drift in bottlenecks of dying cells

in space: creation of wave-fronts and positive selection for more catalysis (wave-level+individual level)

parasite lineage essential for survival: enabling wave-formation

Exploit complementary replication for "division of labor"

protocells: symmetry-breaking iff levels of selection similar strength

decreases within cell mutational pressure to low catalysis

One catalytic strand (+), strongly favors complementary strand (-)

Many +, few - strands (Genome-like)

maintains more catalysis in bottle necks

in space: Always symmetry breaking, different kinds

At high diffusion similar to protocells and few - strands many + strands

optimizes both availability as template and amount of catalysis (wave front/wave back)

Evolution of multiple lineages (speciation)

mutual dependence (feedback) higher level/lower level evolution

bottom line

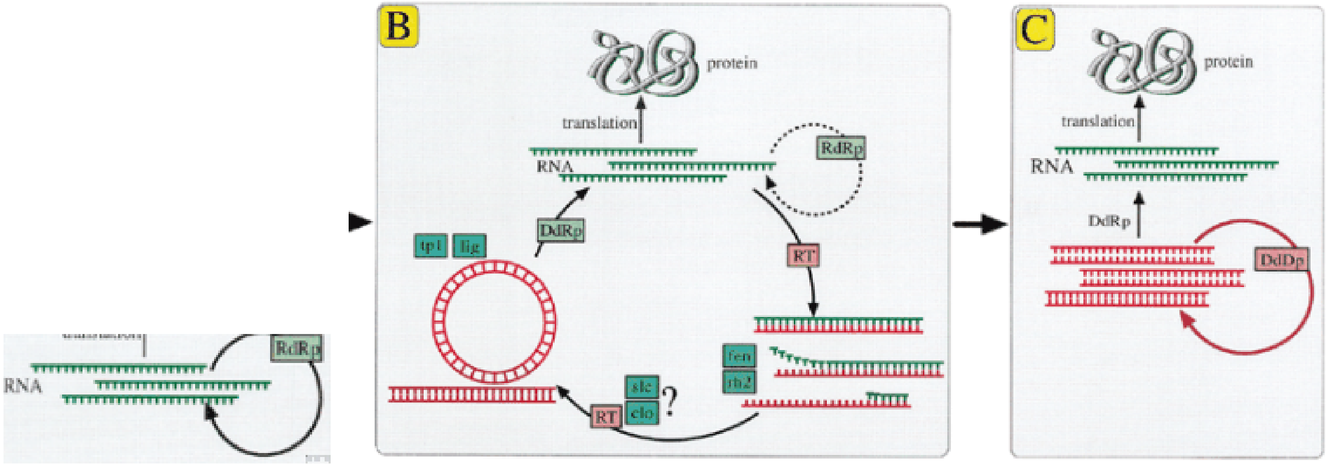
functional differentiation:
specialized catalytic reaction

generic property

multiple specific models converge to similar result

evolution of DNA in the RNA world
phylogenetic evidence

evolution of DNA replication late
core enzyme domains for DNA replicases
non-homologous between Prokaryotes and Eukaryotes
(reverse) transcriptases are homologous.



cf Leipe, Aravind and Koonin, NAR 1999

Conflict resolution between levels of selection
“major transitions in evolution”

Decoupling of information storage and function: Evolution of DNA in RNA world

RNA: information storage (template) AND ribozym;
DNA only information storage (template)

(Note in vitro DNA can also be catalyst but here defined as only template)

Evolution of DNA in the RNA world: “division of labor”

RNA “giving up” self-sufficieny - selfreplication?

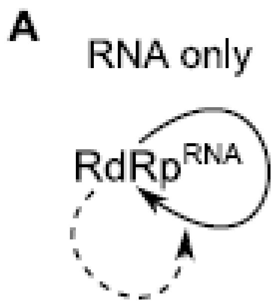
Evolution of slower replication cycle

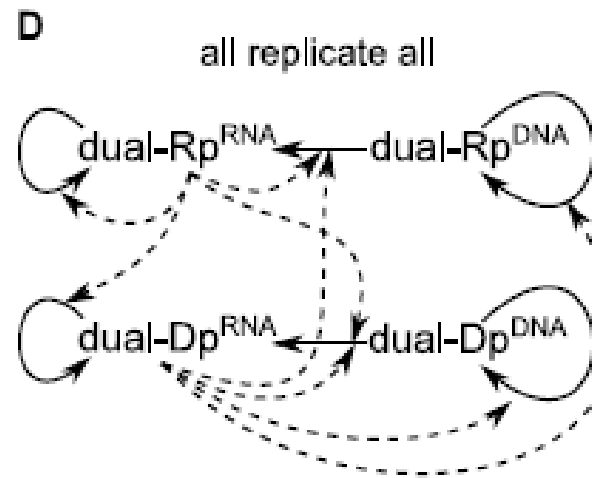
Takeuchi et al 2011 (PLOS comp biol)

RNA world: minimal RP system (replicase (Rp) - parasite)

assume 2 types of polymerases: DNA pol.(Dp) and RNA pol. (Rp) can exits as RNA and DNA

both can recognition RNA and/or DNA (binding evolvable parameter)

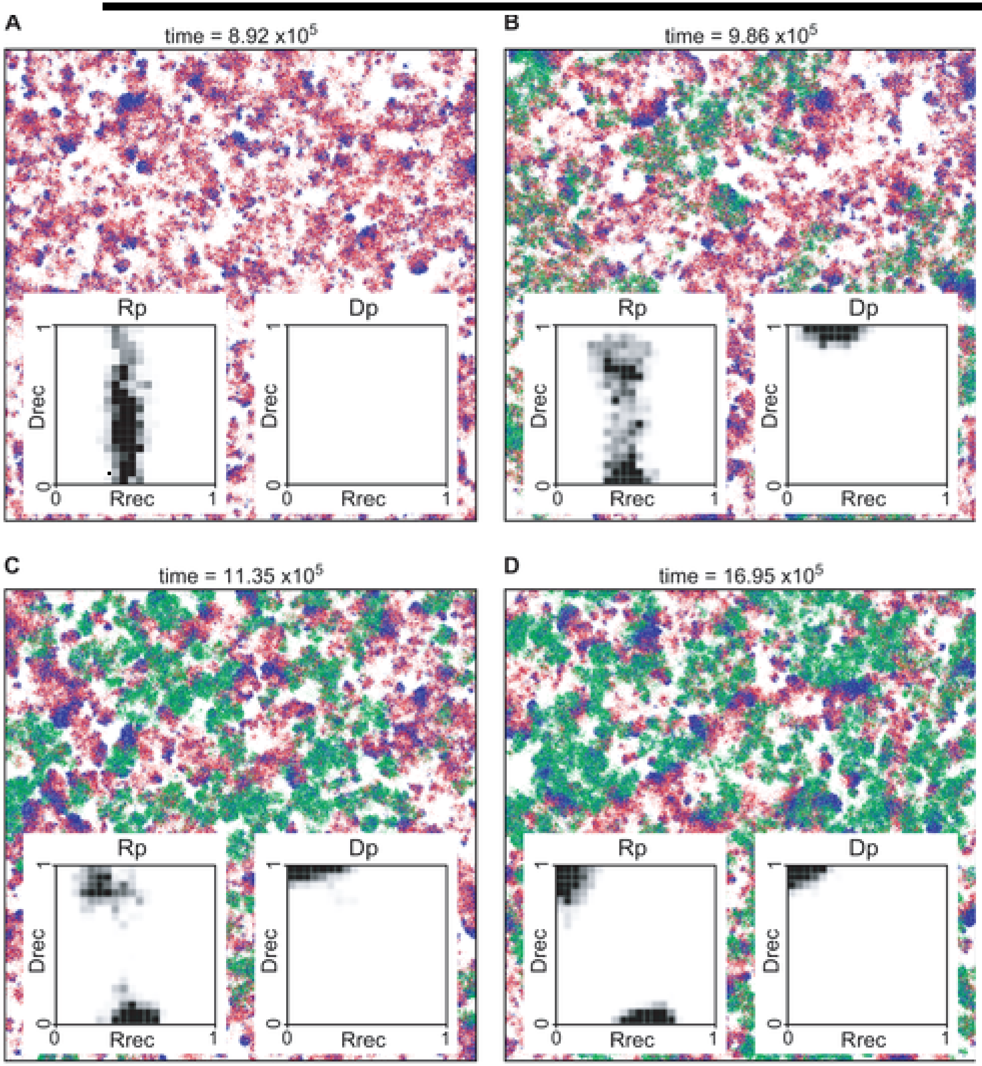


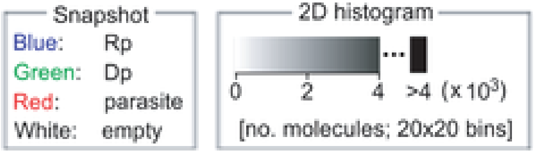


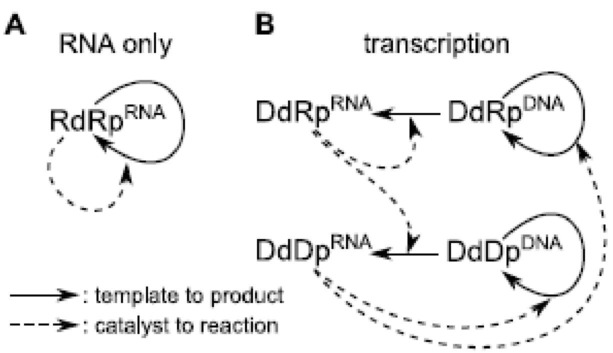
— — —? — —— >

- **Can DNA establish itself in an RNA world** *in evolutionary equilibrium*
- **If so WHY (longer replication cycle)**
- **Which type of specificity evolves?**

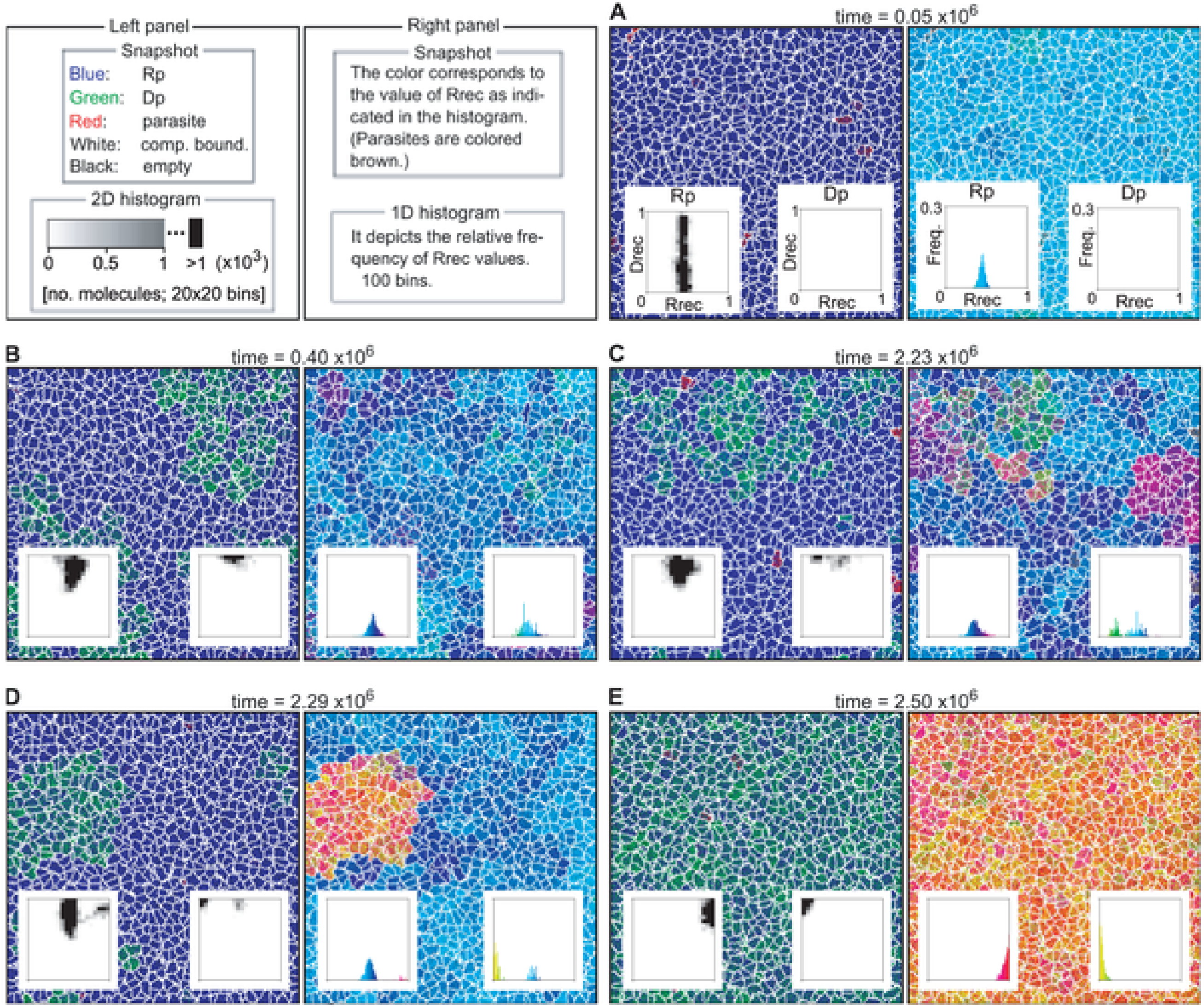
evolutionary trajectory in spatial system



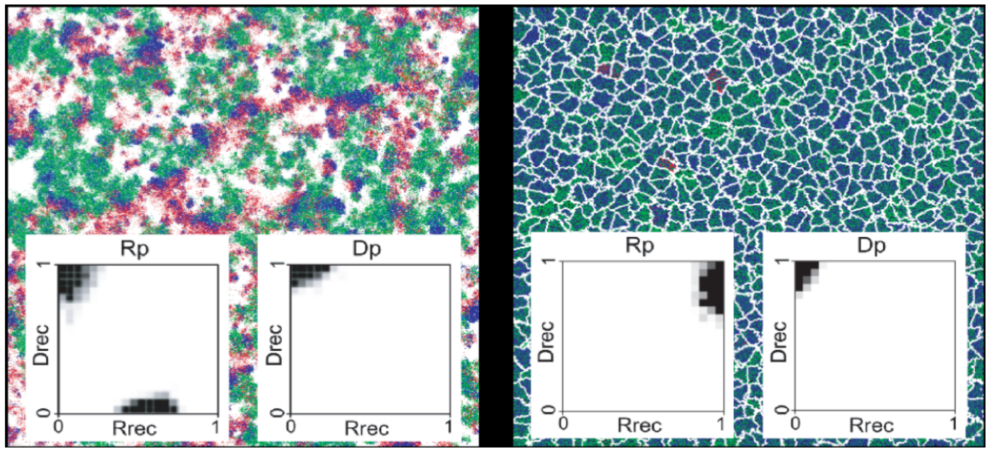


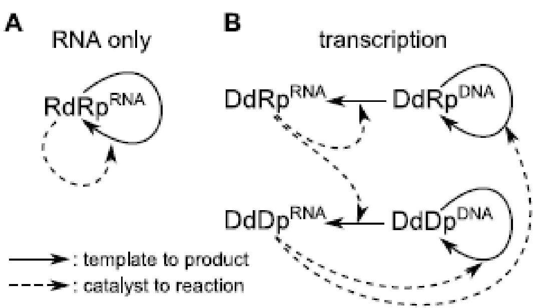


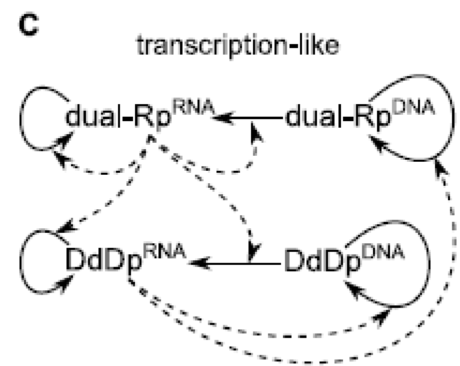
Evolutionary trajectory in vesicle system



RNA replication AND + Transcription system in vesicles and in surface system however dual functional RNA polymerses in vesicles



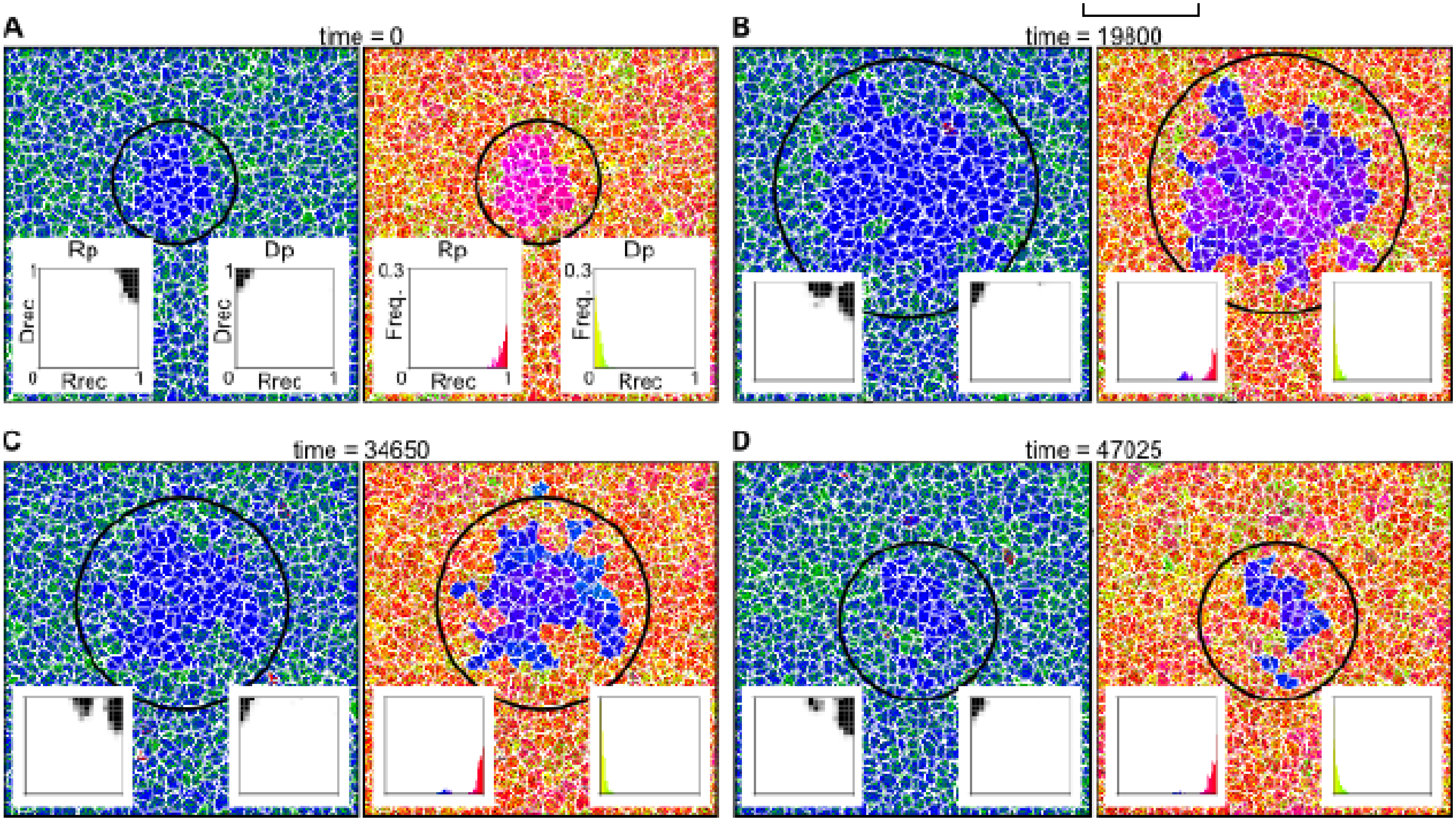




. **NO (minimal)** reverse transcription: DNA common ancestor

DNA stabilizes high catalytic RNA because division of labor of information storage and catalysis

vesicles without DNA first win, later lose competition



conclusion: reproductive division of labor

Spatial systems with local interactions prevent evolutionary collapse of cooperative replicating systems

but only to the level of 'viability': they do minimize contribution to 'common good' (in RNA world giving catalysis)

Division of labor (work vs replication) can prevent such evolutionary minimization of 'work' because inheritance via non-worker (DNA).

Evolutionary stabilization (a long term effect) can indeed evolve! (even if lower replication rate)

Conflict resolution:
Internal dynamics with DNA does not lead to catalysis minimization
Does not have to be counteracted by higher level selection

Slower replicators "out-evolve" faster ones
complexity evolves because of evolutionary "benefit"