Eco-evolutionary dynamics:

multilevel evolution
Degrees of freedom

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Last time

Overcoming information threshold?

first failed attempt: Hypercycles

Switch to invasion dynamics

"Everything" different in CA vs ODE
increased resistance to parasites,
pos selection for giving catalysis
no once only selection

HOWEVER

Contrived initial conditions
(multiple species/ specific catlytic interactions

NOT resistant to ongoing mutations:
loss of spirals

BUT

Multilevel evolution

CA Universe: (cf.Crutchfield, Wolfram)
Micro $->$ Macro (....$->$....$->$..... etc)
STATIC (simple) 'rockbottom' **?one more soul?**

BUT: In evolving systems also Macro $->$ Micro:

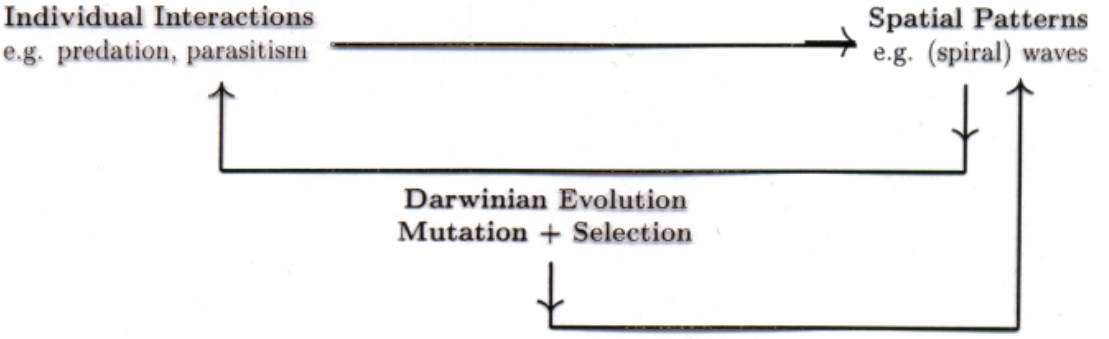


Figure 1: Relation between local interactions and spatial pattern formation in eco evolutionary models

lowest level

does not make sense except in the light of

higher level processes

Emerging higher level Darwinian Entities (waves)

a minimal eco-evolutioary model of emerging higher level of "Darwinian entities" (Takeuchi & H. PLOS Comp Biol 2009)

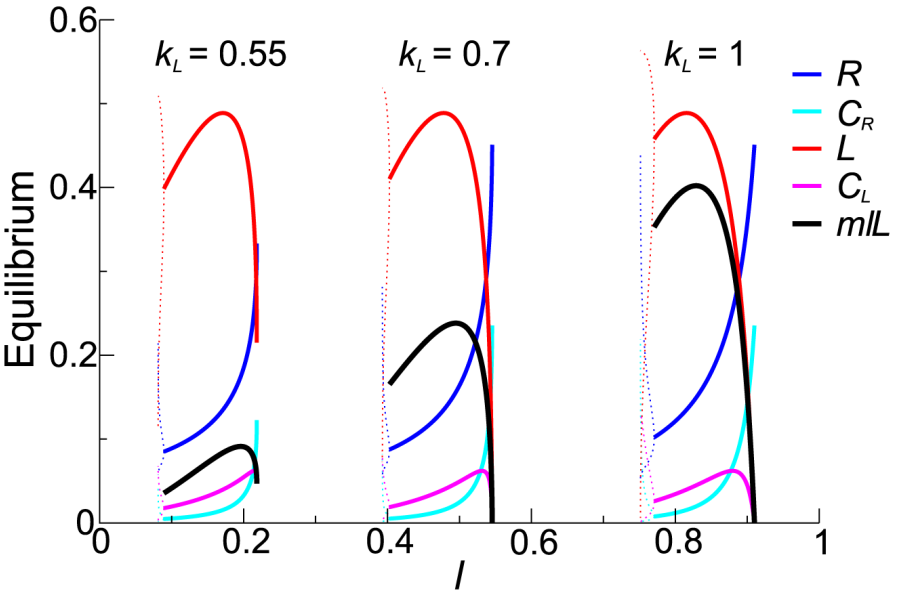
Minimal replicator system
with parasitic L's
replicated when unfolded
'functional' when folded

$$
\begin{aligned}
\dot{R} &= -2k_R R^2 + [2(1-k_R) + 3\kappa\theta + 2d]C_R - k_L RL \\
&\quad + [(1-k_L) + \kappa\theta + d]C_L - dR, \\
\dot{L} &= -k_L(1-l)RL + [(1-k_L) + 2\kappa\theta + d]C_L - dL, \qquad (2) \\
\dot{C}_R &= k_R R^2 - [(1-k_R) + \kappa\theta]C_R - 2dC_R, \\
\dot{C}_L &= k_L(1-l)RL - [(1-k_L) + \kappa\theta]C_L - 2dC_L,
\end{aligned}
$$

$$
\begin{aligned}
(a) \quad & \mathrm{R} + \mathrm{R} \underset{1-k_R}{\overset{k_R}{\rightleftharpoons}} \mathrm{C_R} \overset{\kappa\theta}{\rightarrow} 2\mathrm{R} + \mathrm{R}, \\
& \mathrm{L} + \mathrm{R} \underset{1-k_L}{\overset{k_L(1-l)}{\rightleftharpoons}} \mathrm{C_L} \overset{\kappa\theta}{\rightarrow} 2\mathrm{L} + \mathrm{R}, \\
(b) \quad & \mathrm{R,L} \overset{d}{\rightarrow} \theta, \\
& \mathrm{C_R} \overset{2d}{\rightarrow} \mathrm{R} + \theta, \\
& \mathrm{C_L} \overset{d}{\rightarrow} \mathrm{R} + \theta, \\
& \mathrm{C_L} \overset{d}{\rightarrow} \mathrm{L} + \theta, \\
(c) \quad & \mathrm{L} \overset{ml}{\rightarrow} \mathrm{L} + x,
\end{aligned}
$$

Classical problem
ODE model of RP system
evolutionary extinction (increase of k_L and decrease of I)

$$
\begin{aligned}
\dot{R} &= -2k_R R^2 + [2(1-k_R) + 3\kappa\theta + 2d]C_R - k_L RL \\
&\quad + [(1-k_L) + \kappa\theta + d]C_L - dR, \\
\dot{L} &= -k_L(1-l)RL + [(1-k_L) + 2\kappa\theta + d]C_L - dL, \qquad (2) \\
\dot{C}_R &= k_R R^2 - [(1-k_R) + \kappa\theta]C_R - 2dC_R, \\
\dot{C}_L &= k_L(1-l)RL - [(1-k_L) + \kappa\theta]C_L - 2dC_L,
\end{aligned}
$$

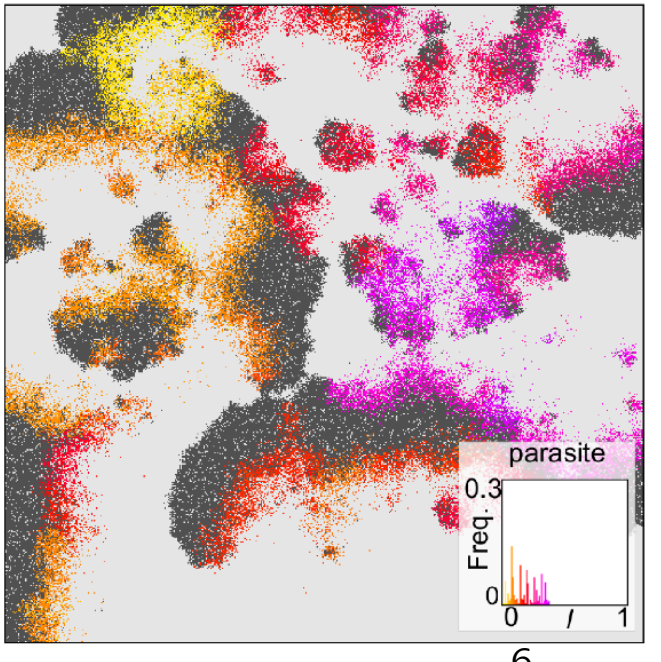


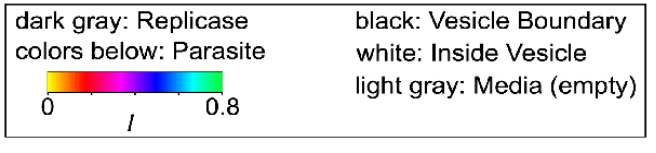
$k_R = .6$

intrinsic advantage of parasite (L)

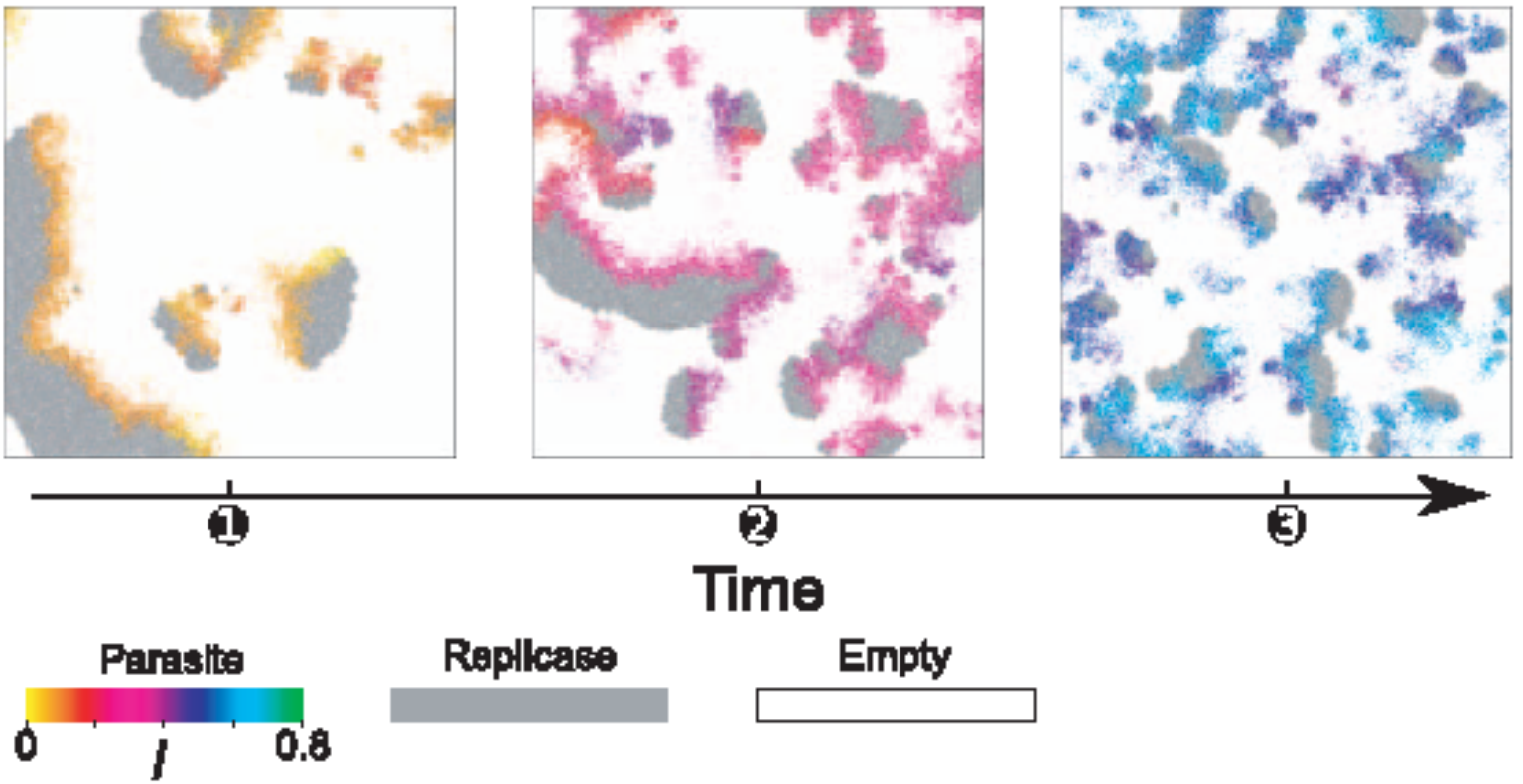
CA model of RP system
evolutionary stable (long transient)

Asynchronous CA choose random patch and random NB
perform reaction or diffusion
reaction: (complex formation (coupling 2 gp),
replication and decay)
with prob. according to
individual (evolving) parameters
of *parasites:*K_l *and* I



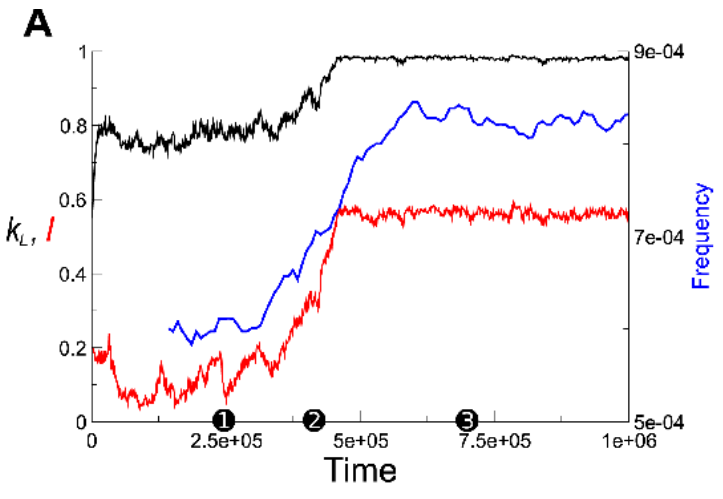


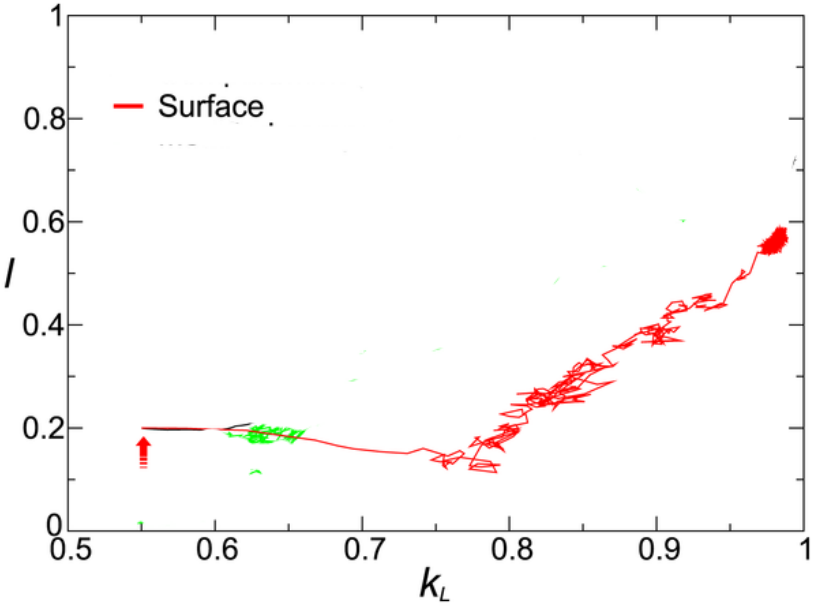
long term evolution: towards smaller waves



Long term evolution (parameters)
emergent 'trade-off' k_L and I
Maximizing I : potential 'new' function

Average in population





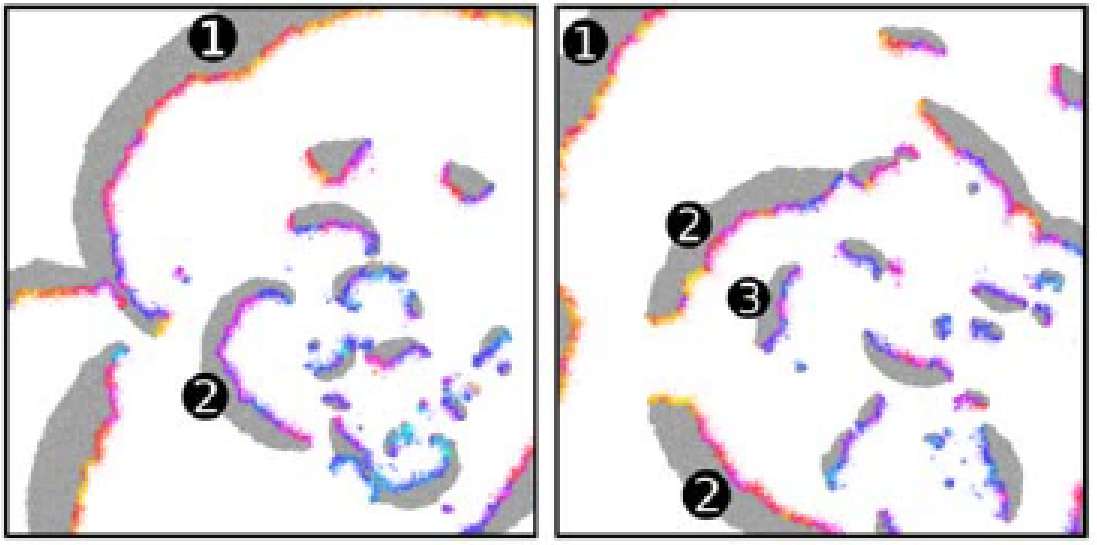
WHY?

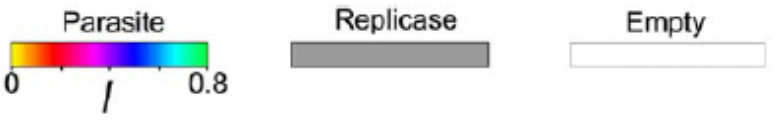
evolution of higher level entities

The waves of replicase and parasites are higher level "Darwinian" entities

Birth
Maturation
Death
Mutation
Selection
Competing

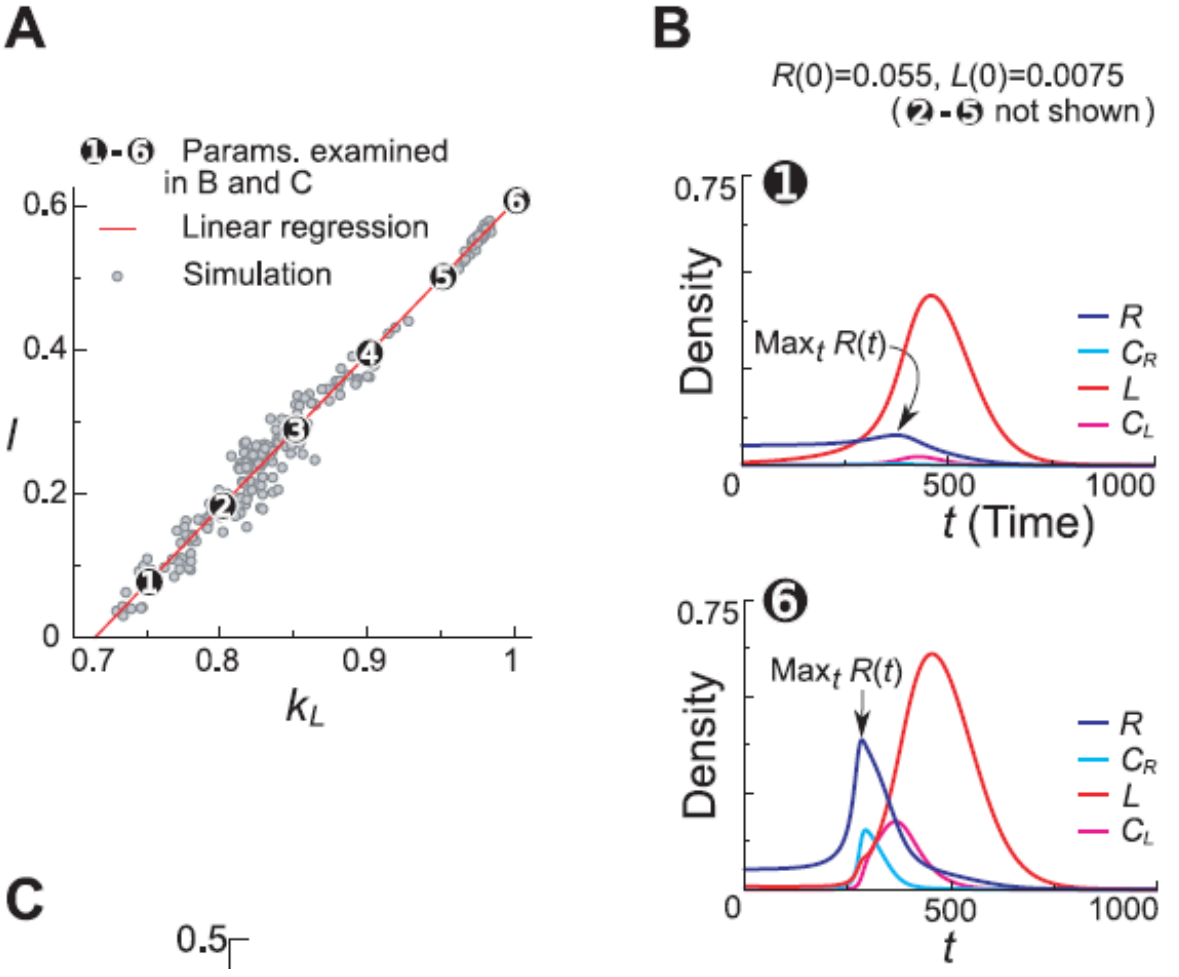
Maximizing birth rate



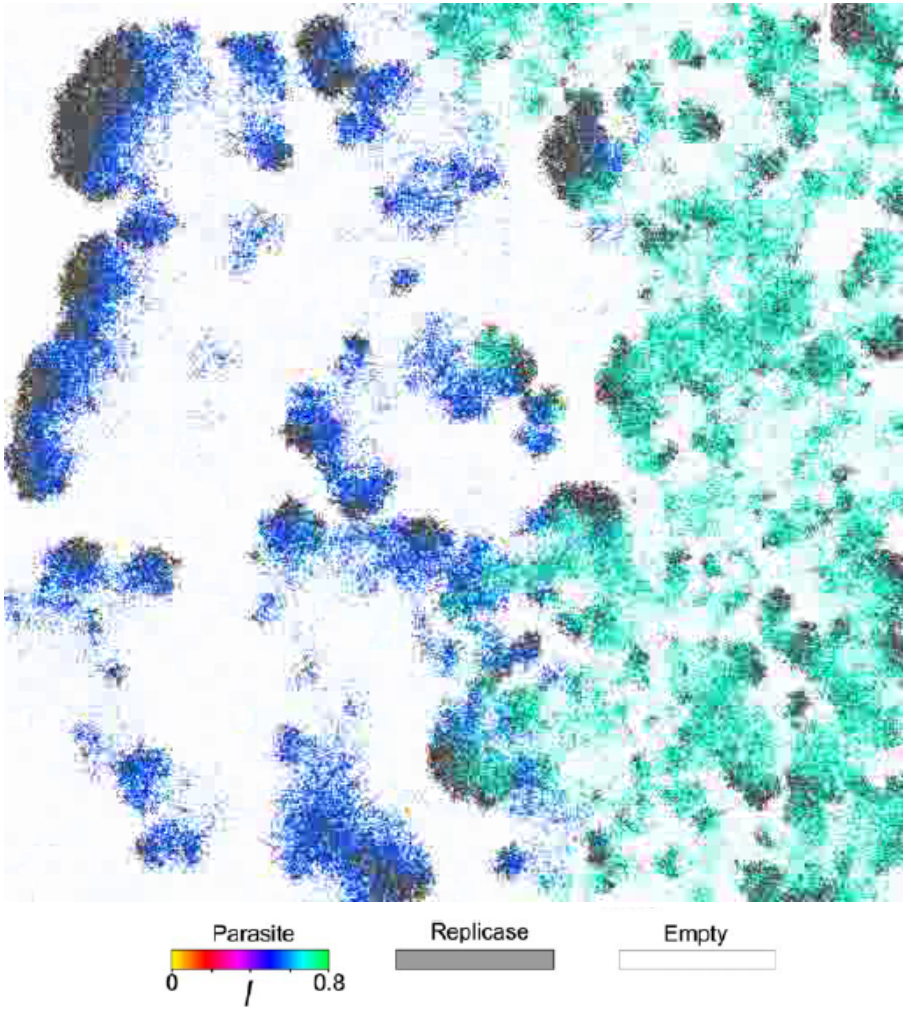


$K_L = 1$

Larger K_L and I increase birthrate of waves
analysis of transient in ODE (for evolved parameters)



evolutionary attractor
at "edge of chaos" ("border of order")



2 levels of Darwinian selection

Wave level evolution

- Waves: long lived -
  (death not by parasites but by collision)
- Maximize Birthrate + growth rate of newborns
- Birthrate higher for high l ('escape')
- However higher birthrate $->$ more (smaller) waves
- $->$ increase collision! (= deathrate of waves))

Individual level evolution

- Within waves: parasites evolve towards 'nastiness' (low l)
- However viability maintained $-->$
  "prudent" parasites
- because of higher level selection; which also
- 'frees' parasites to do other things (be folded)

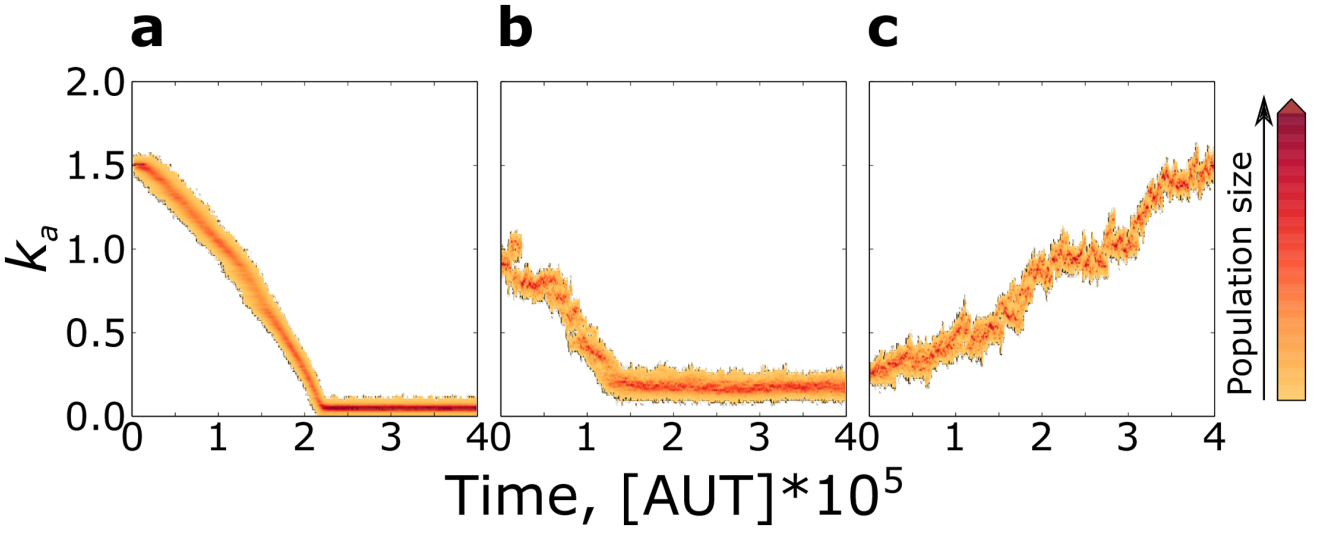
through parasites
evolution of novel functionality

Evolution of replicases in RP system
Strong parasites lead to strong replicases

The model

$$\mathrm{X_i} + \mathrm{X_j} \underset{k_{\mathrm{diss}}}{\overset{k_{a_i}}{\rightleftharpoons}} \mathrm{C_{X_j o X_i}} \xrightarrow{\rho,\theta} 2\,\mathrm{X_j} + \mathrm{X_i}$$

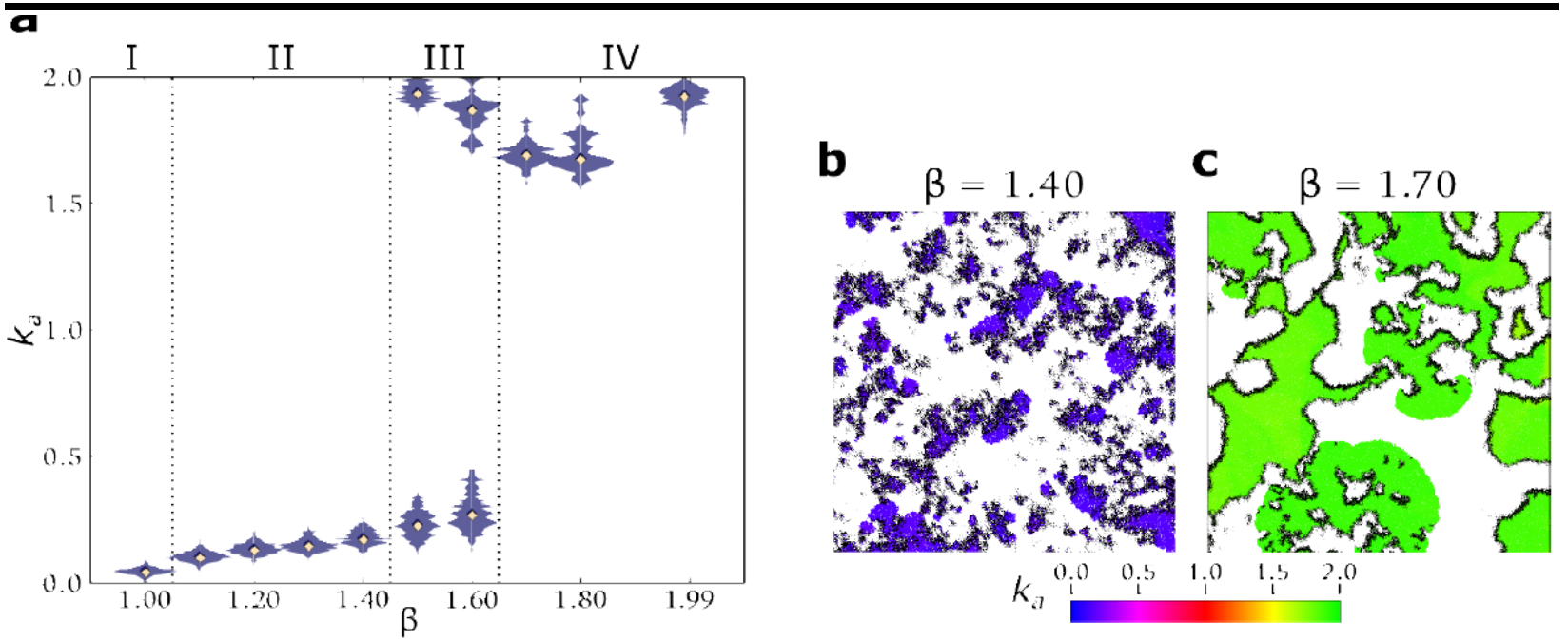
$$\mathrm{X_i} + \mathrm{P} \underset{k_{\mathrm{diss}}}{\overset{\beta \cdot k_{a_i}}{\rightleftharpoons}} \mathrm{C_{PoX}} \xrightarrow{\rho,\theta} 2\,\mathrm{P} + \mathrm{X_i}$$



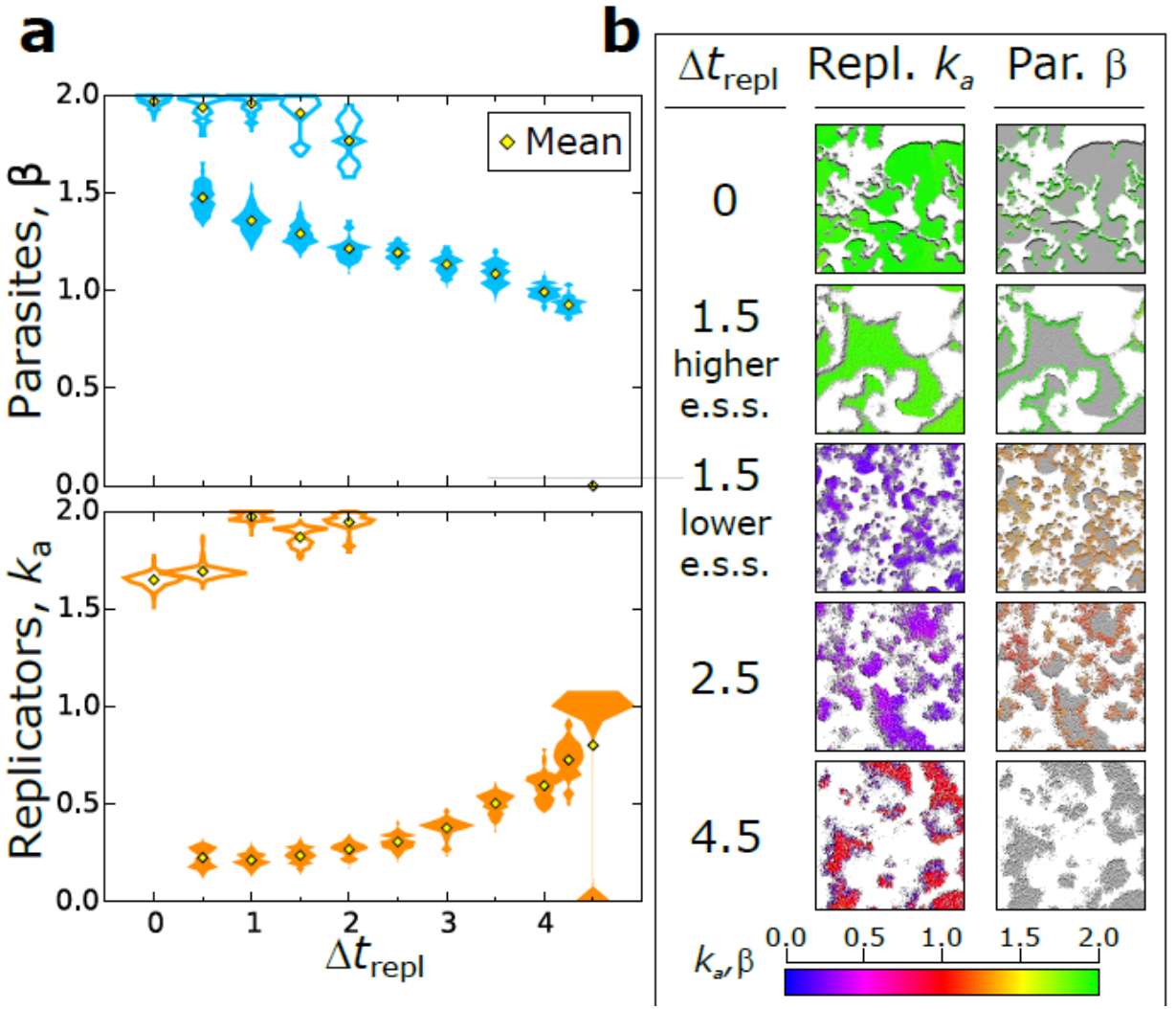
R only RP $\beta = 1,4$ $RP\beta = 1.7$

Colizzi and Hogeweg Plos Comp Biol 2016

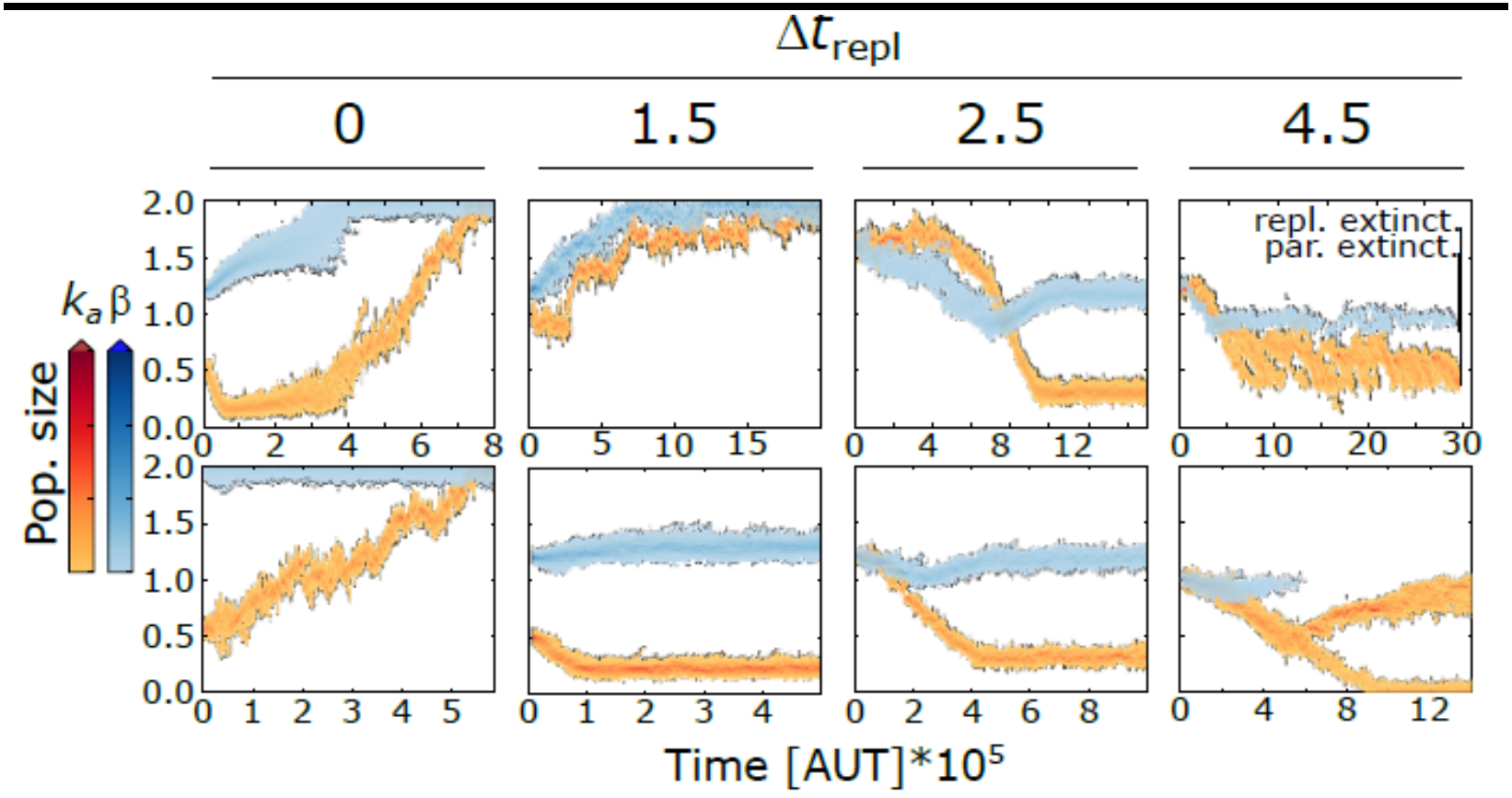
Phase transition and bistability maximizing birth rate of waves OR maximizing invasion rate of empty space



coevolution of replication (k_i) and parasite strength β for different time in complex


a
b
Parasites, β
Mean
Replicators, k_a
Δt_{repl}
0.0
0.5
1.0
1.5
2.0
0
1
2
3
4
Δt_{repl}
Repl. k_a
Par. β
0
1.5 higher e.s.s.
1.5 lower e.s.s.
2.5
4.5
k_a, β
0.0
0.5
1.0
1.5
2.0

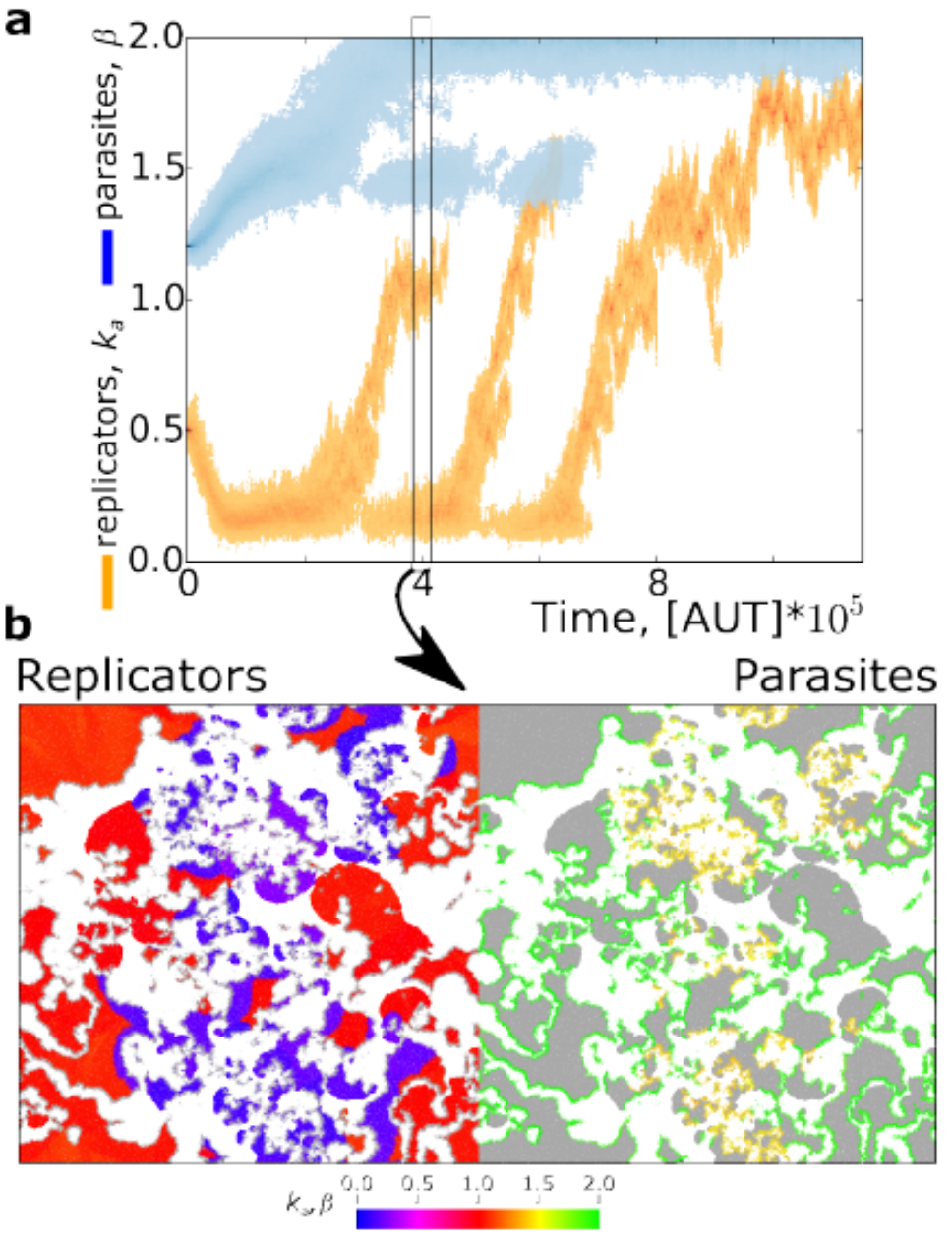
coevolution of replication (k_i) and parasite strength β for different time in complex : timeplots



$\Delta T_{repl} = 0$

“Ghost” attractor

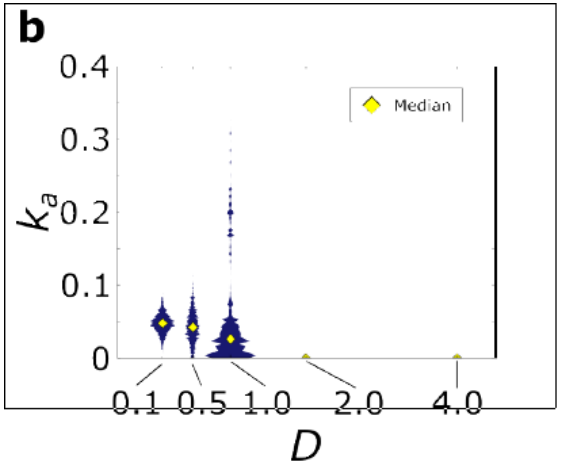
(bistabity)



conclusion

Because of wave-level selection
Parasites enhance replication potential

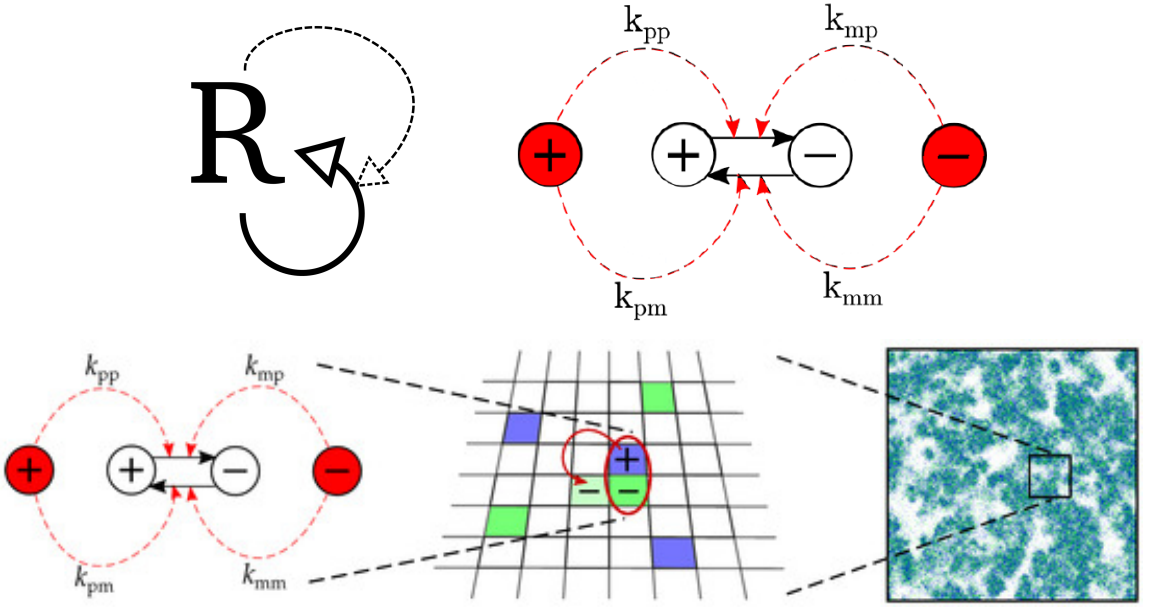
Bistability:
maximizing birth rate of waves vs maximizing wave stability
minimizing 'altruism' of replicators vs maximizing invasion rate
BUT:



limited diffusion

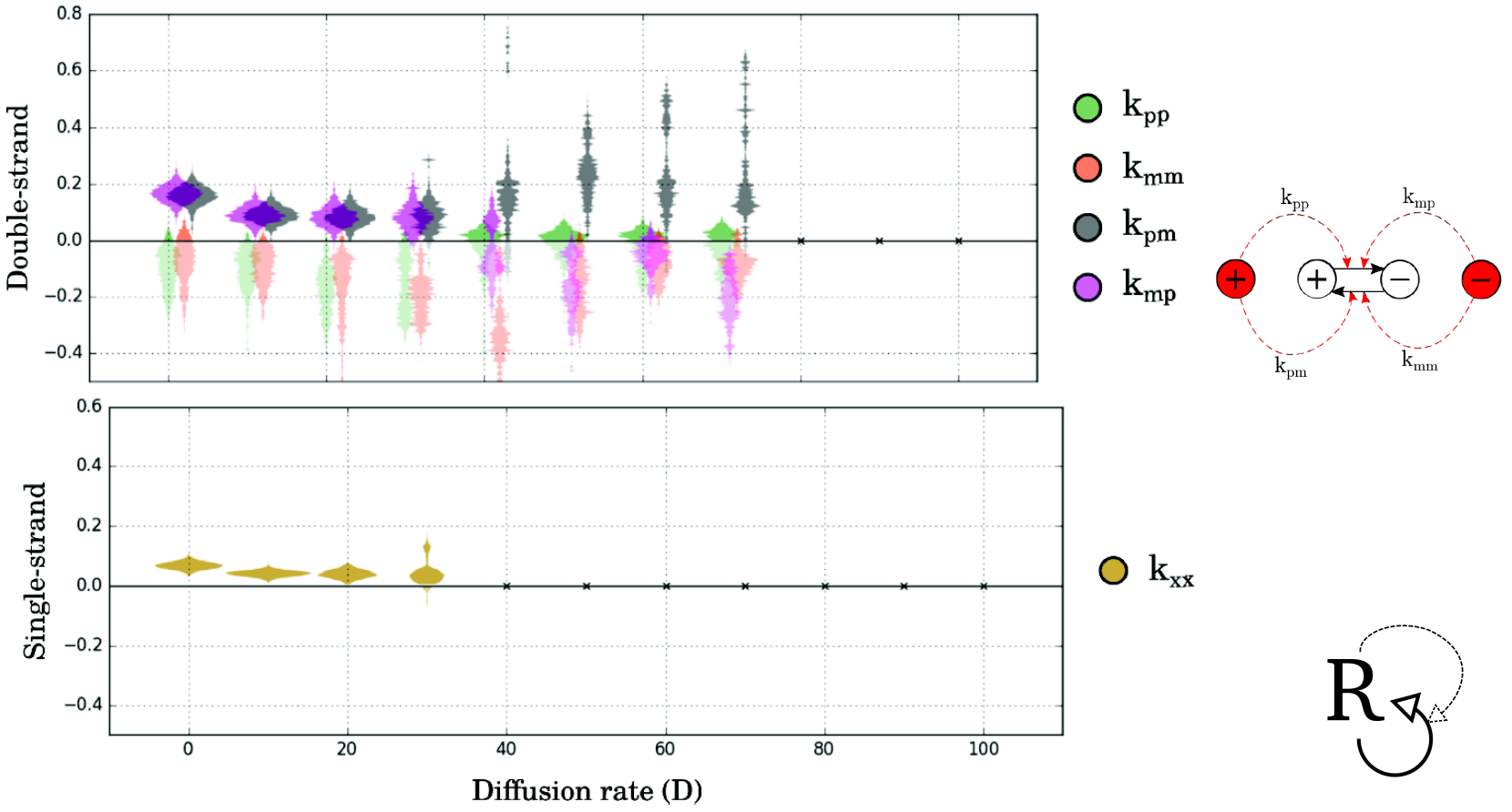
exploring evolutionary properties/advantages of more RNA-like replicators in R-only system (i.e. more degrees of freedom)

- **Direct replication vs Complementary replication**



1 vs 4 evolving parameters: K_{xx} vs $K_{pp}K_{pm}K_{mm}Kmp$

emergent levels of selection
direct vs complementary replication
symmetry breaking robustness to diffusion



symmetry breaking and speciation von den Dunk, Colizzi Hogeweg 2017

initial decrease of catalysis

Only if small enough emergent higher level selection leads to

3 types of symm breaking:

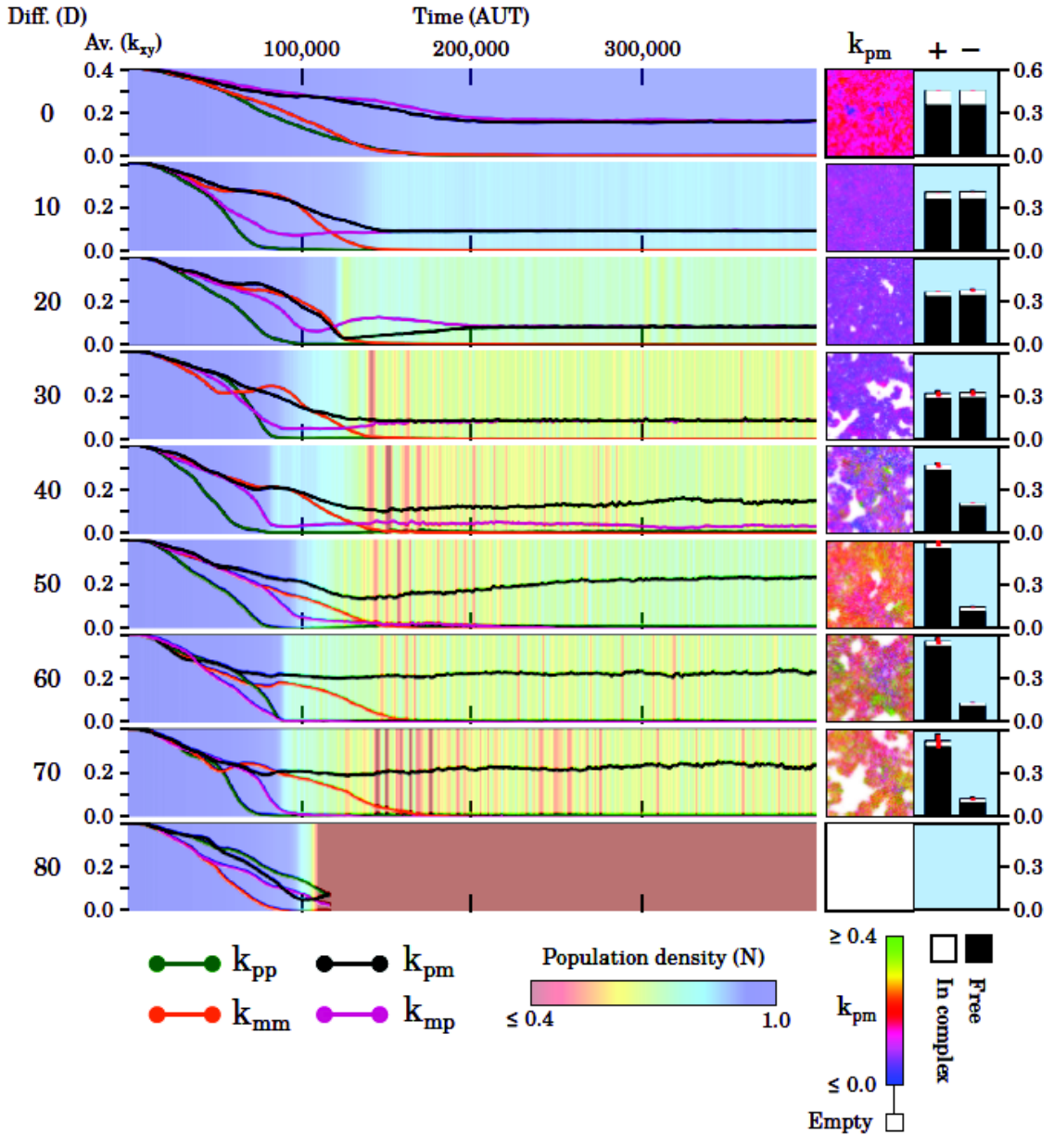
reciprocal $(K_{pm} - K_{mp})$

target $(K_{pm} - K_{mm})$

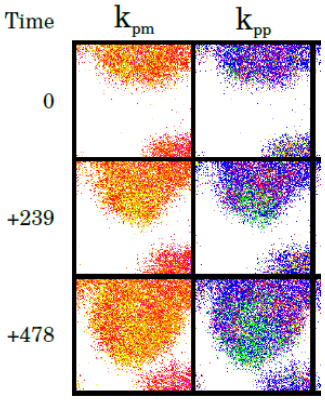
one-cat

$(K_{pm} +$

$<< K_{pp}$

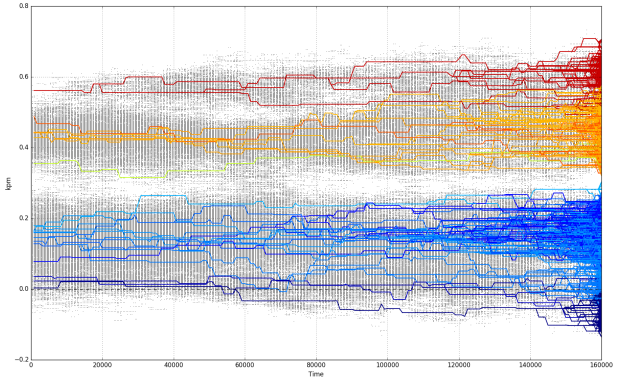


Evolutionary dynamics at high diffusion (D70)

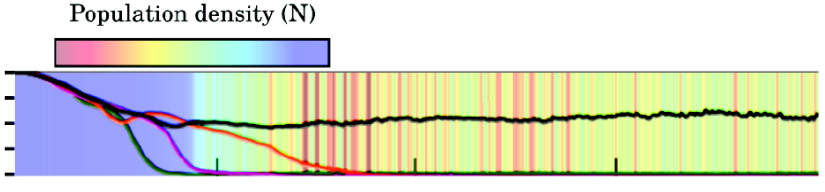


selection at wave front

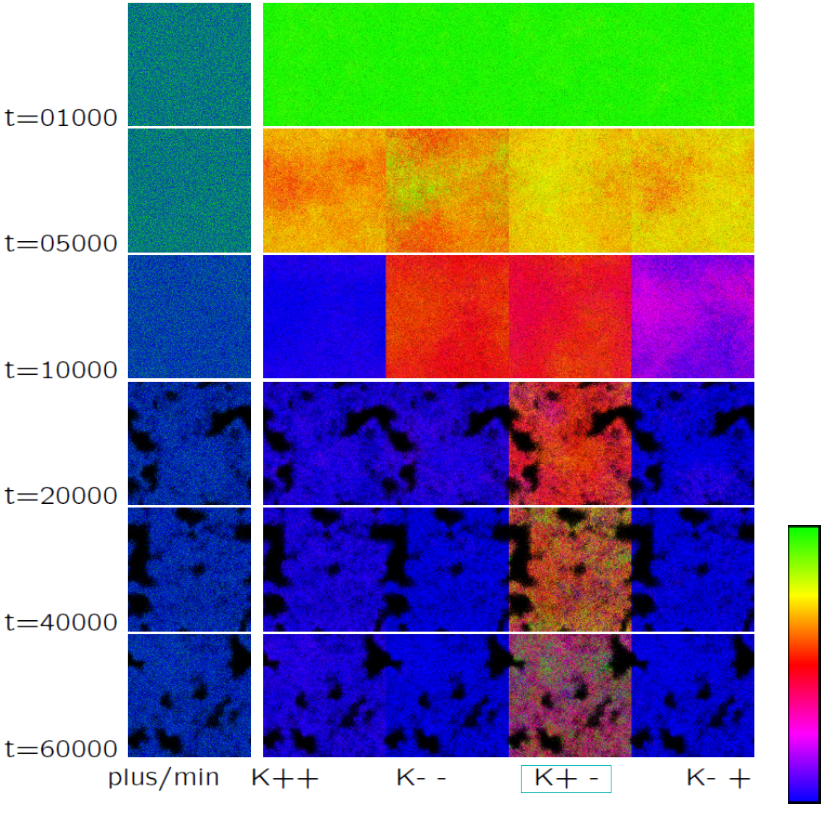
ancestor trace



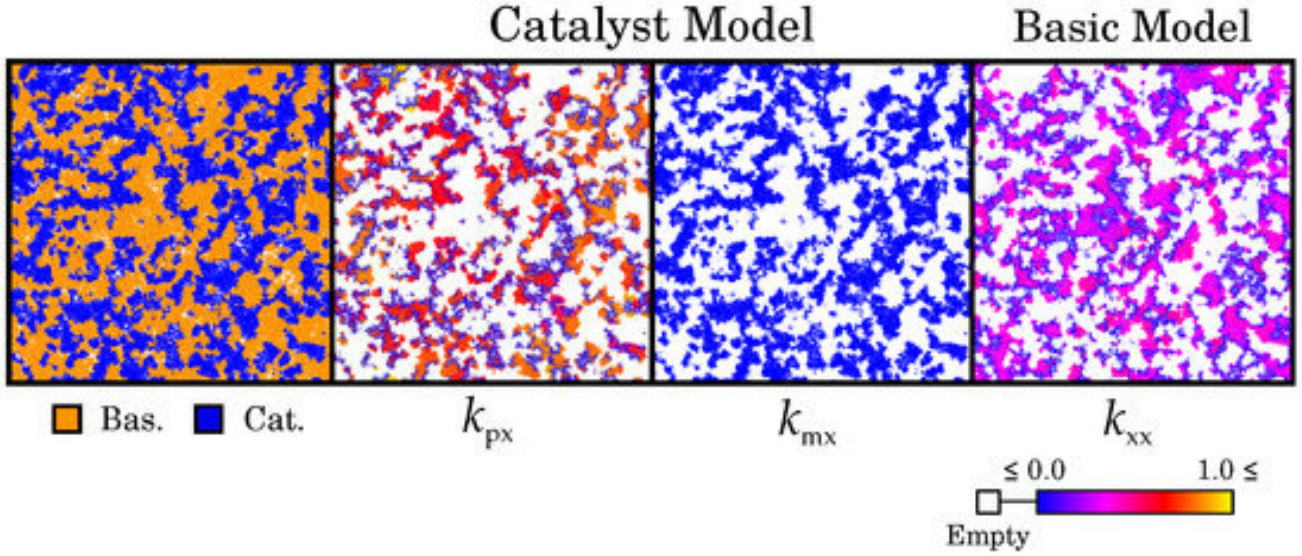
evolution through time



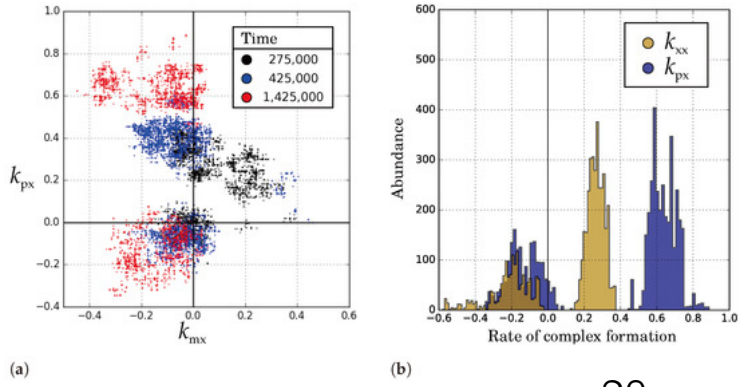
spatial self-organization



"competition(?) between direct and compementary replication



Bas = directreplication 1 parameter Kxx
Complemetary replication: here only 2 parameters: $K_{px}K_{mx}$
Both species "speciate" in replicase and parasite;
Compementary replicase: symmetry breaking



Conclusion
Symmetry breaking and division of labor
to resolve conflict between high catalysis and being template

Exploit "near death" for evolving new replication strategies
creation of wave-fronts and positive selection for more catalysis
(wave-level+individual level)
evolved parasite lineage essential for survival:
enabling wave-formation

Exploit complementary replication for "division of labor"
Always symmetry breaking, different kinds
At high diffusion
One catalytic strand (+), strongly favors complementary strand (-)
Many +, few - strands (Genome-like)
Therefore less selection to minimize catalysis
optimizes both availability as template and amount of catalysis
(wave front/wave back)
maximizes evolvability to adapt to wavefront (increase K_{++})
Evolution of multiple lineages (speciation)
mutual dependence (feedback) higher level/lower level evolution

conclusions

Feedback between levels of selection

speciation, parasites

More evolutionary degrees of freedom: BETTER results:

here: higher diffusion, higher mutation rates