Eco-evolutionary dynamics: multilevel evolution

Course Computational Biology 2025; Paulien Hogeweg; Theoretical Biology and Bioinformatics Grp Utrecht University

Last time

- Hypercycles were proposed as potential "ecosystem based" solution for *error catastrophe*
- Studied as ecological system (no ongoing mutations)
- ODE model: vulnerable to parasites *Parasite catastrophe*
- CA model: selforganization in spiral waves (N>5); Dynamics of spiral waves drives parasites to extinction
- All properties of ODE and CA models modeling the same interactions are opposite due to **multilevel selection**
- HOWEVER no solution for error threshold: spiral vulnerable for ongoing mutations
- spiral new level of selections but not new level of replicators.

TODAY: *can we do better??*

Multilevel evolution

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

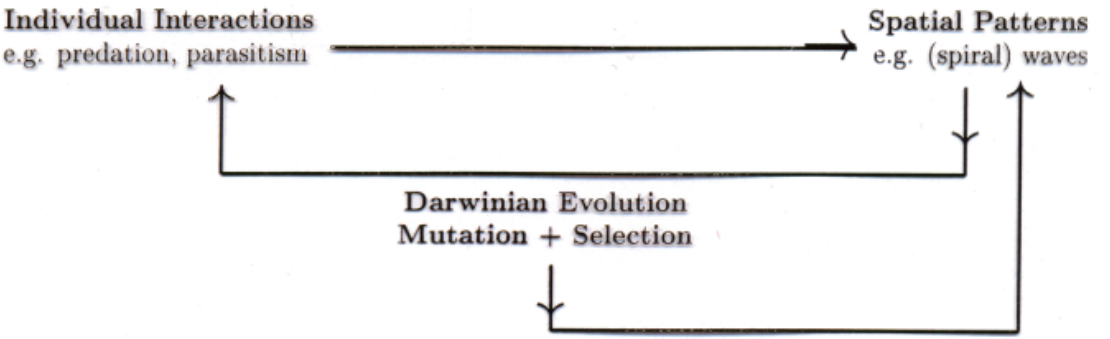


Figure 1: Relation between local interactions and spatial pattern formation in eco evolutionary models

lowest level

does not make sense except in the light of

higher level processes

Themes

Evolutionary dynamics:
ongoing mutations, selection but no predefined fitness criterion

Multiple - Multilevel selection models

Emergent higher level Darwinian entities vs
Imposed higher level (Darwinian) entities

Analysis of multilevel evolution models (ODE as tool)

Degrees of freedom of evolutionary systems

Role of parasites

"Nothing in biology makes sense except in the light of Evolution, selforganization ... and parasites

Ecosystem based information conservation examining the parasite catastrophe beyond hypercycle model

Hypercycle model has in fact
Contrived initial conditions
(multiple species/ specific catalytic interactions)

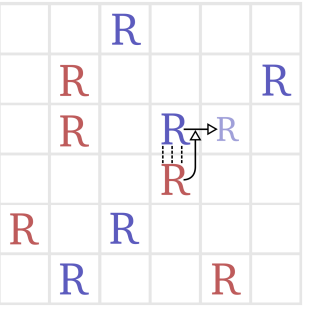
Here we simplify

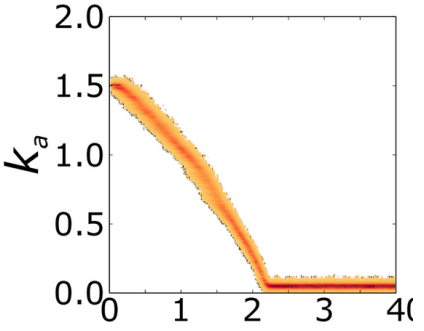
Non-cyclic interaction structure.

Ongoing mutations instead of invasion dynamics

Evolution of Replicases (and parasites)

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





replicases only: Evolve k_{ai}

well mixed: extinction

in space: minimization of k_{ai}

Role of parasites

evolve parasites in fixed replicase population

evolve replicases with different fixed parasitic population

co-evolve replicases and parasites

Takeuchi & Hogeweg 2009; Colizzi & Hogeweg 2016

Evolving parasite strength emerging higher level of "Darwinian entities"

Minimal replicase system (catalysed replication)
with parasitic L's
replicated when unfolded
'functional' when folded

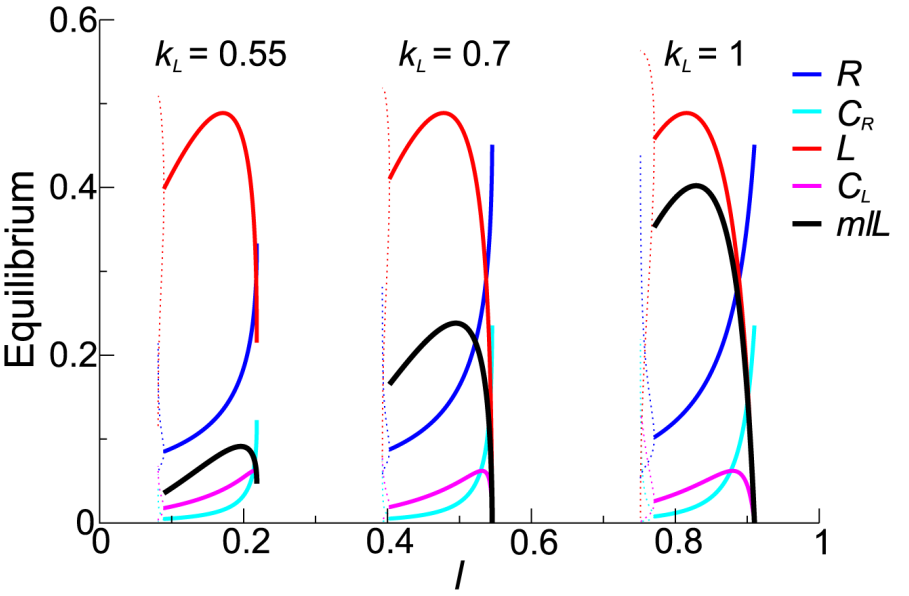
$$
\begin{aligned}
(a)\quad & \mathrm{R}+\mathrm{R} \underset{1-k_R}{\overset{k_R}{\rightleftharpoons}} \mathrm{C_R} \overset{\kappa\theta}{\rightarrow} 2\mathrm{R}+\mathrm{R}, \\
& \mathrm{L}+\mathrm{R} \underset{1-k_L}{\overset{k_L(1-l)}{\rightleftharpoons}} \mathrm{C_L} \overset{\kappa\theta}{\rightarrow}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

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

Takeuchi & Hogeweg 2009

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

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

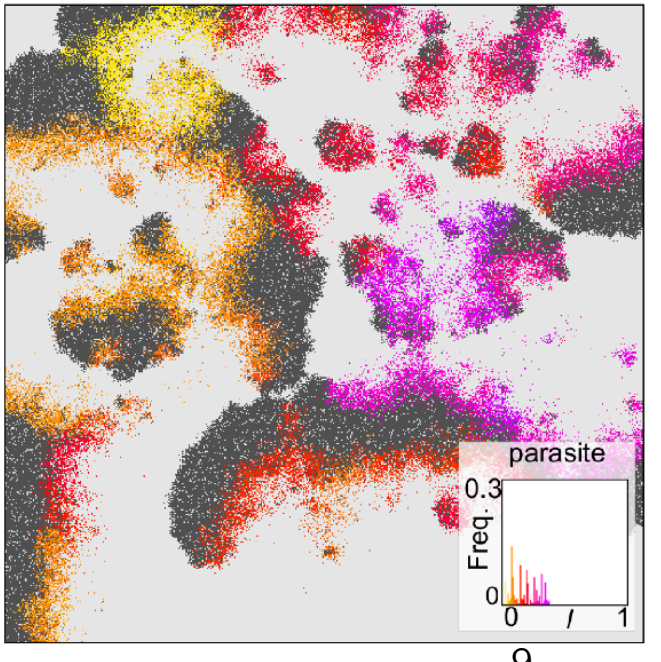


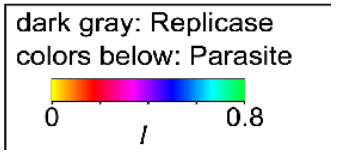
$k_R = .6$

intrinsic advantage of parasite (L)

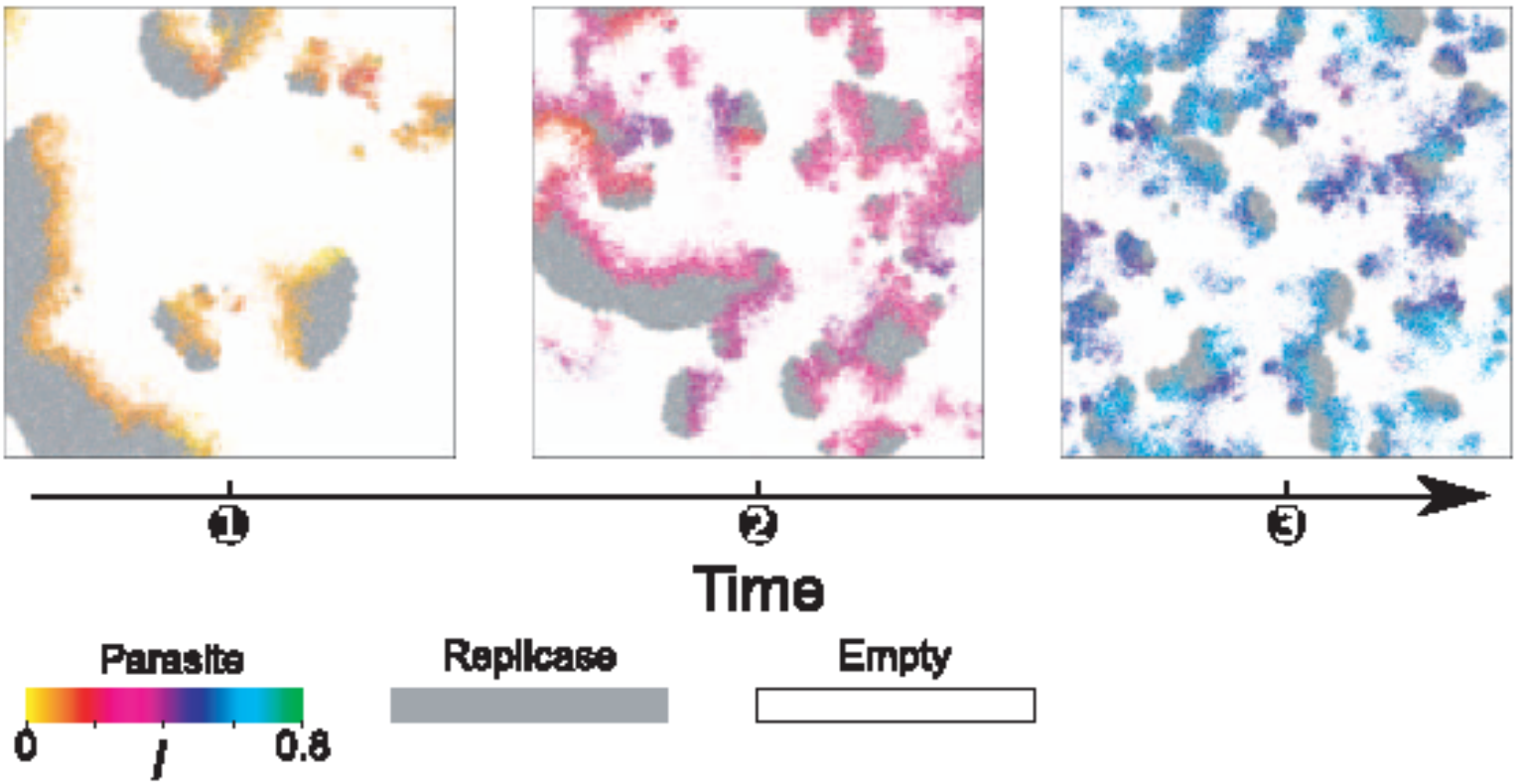
CA model of RP system
evolutionary stable (long transient)

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



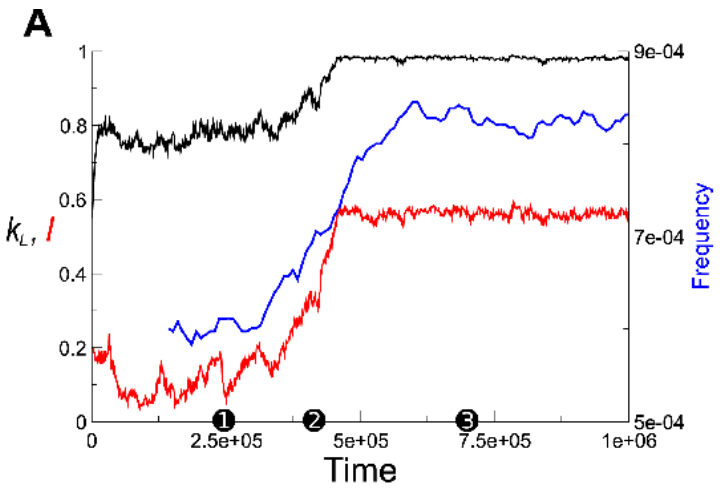


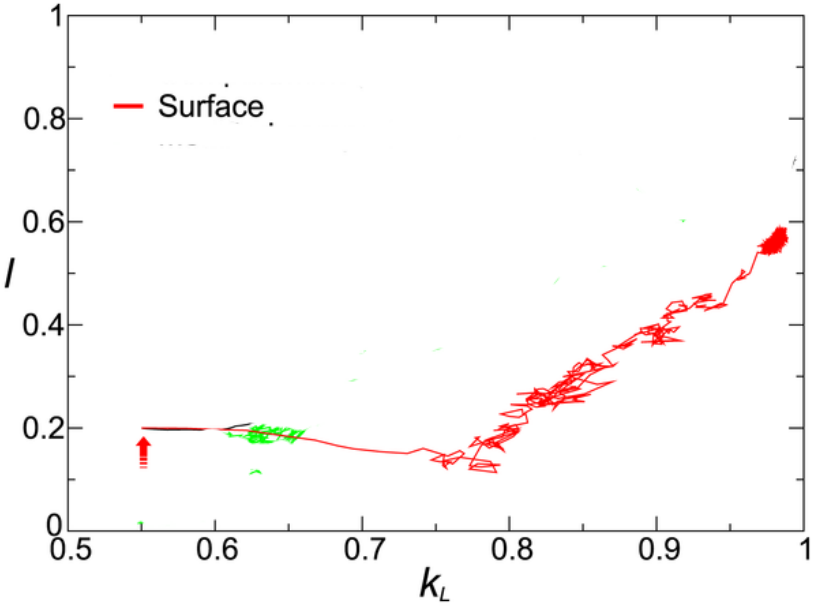
long term evolution: towards smaller waves



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

Average in population



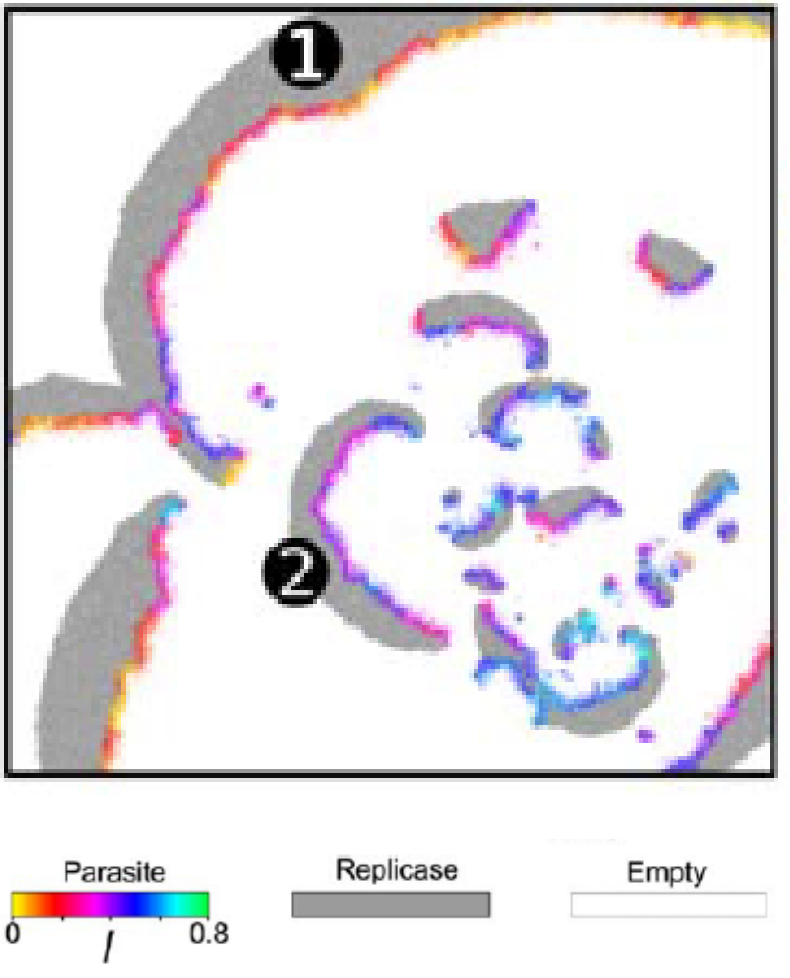


WHY?

evolution of higher level entities

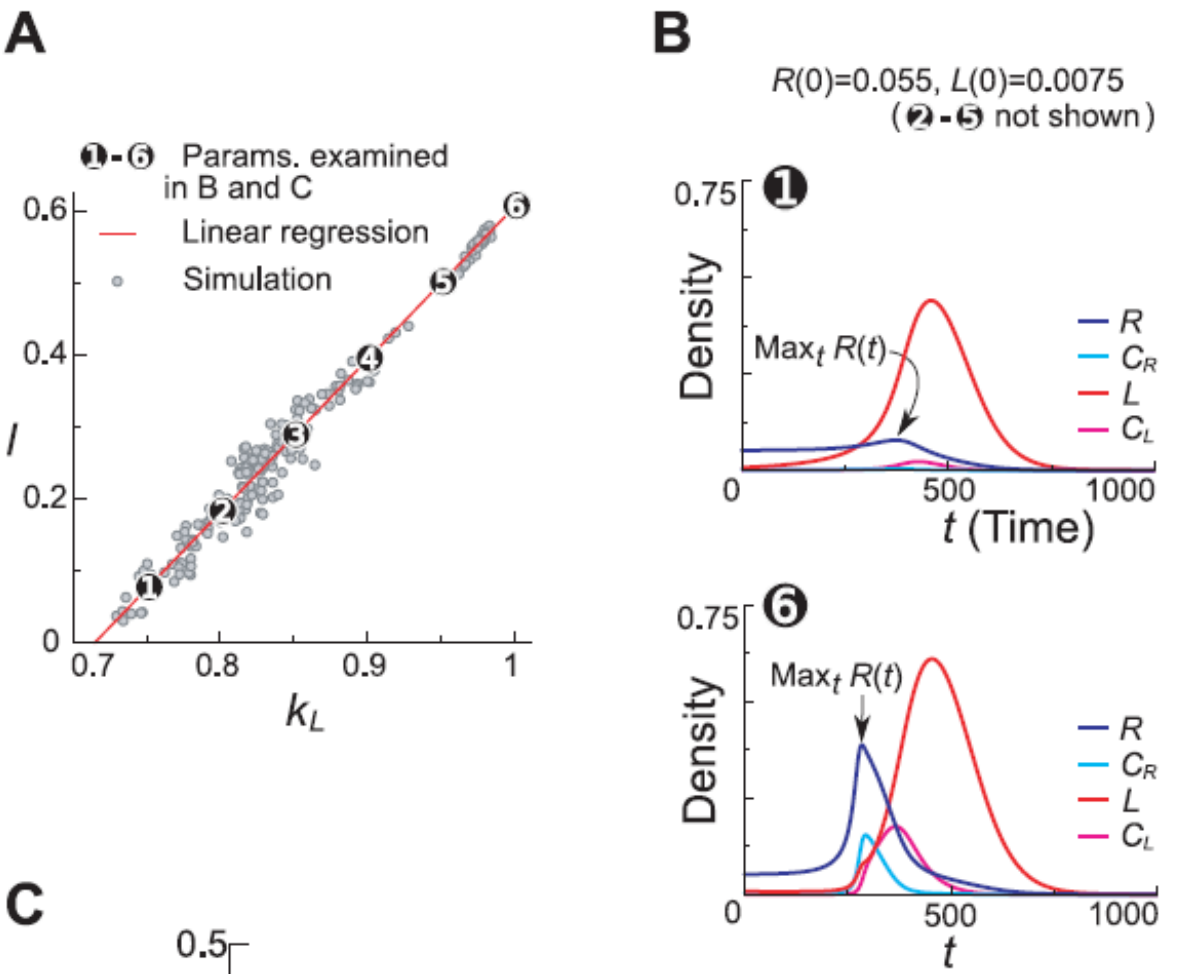
The waves of replicase and parasites are higher level "Darwinian" entities

Birth
Maturation
Death
Mutation
Selection
Competing

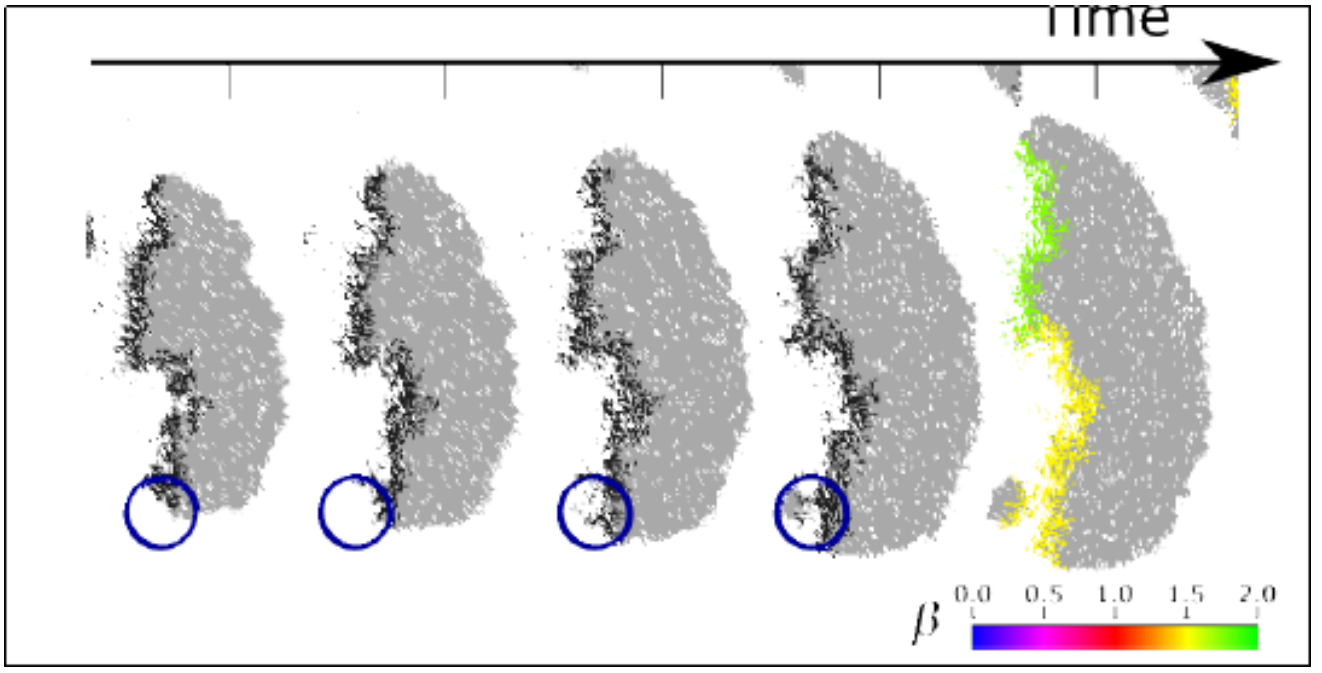


$K_L = 1$

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

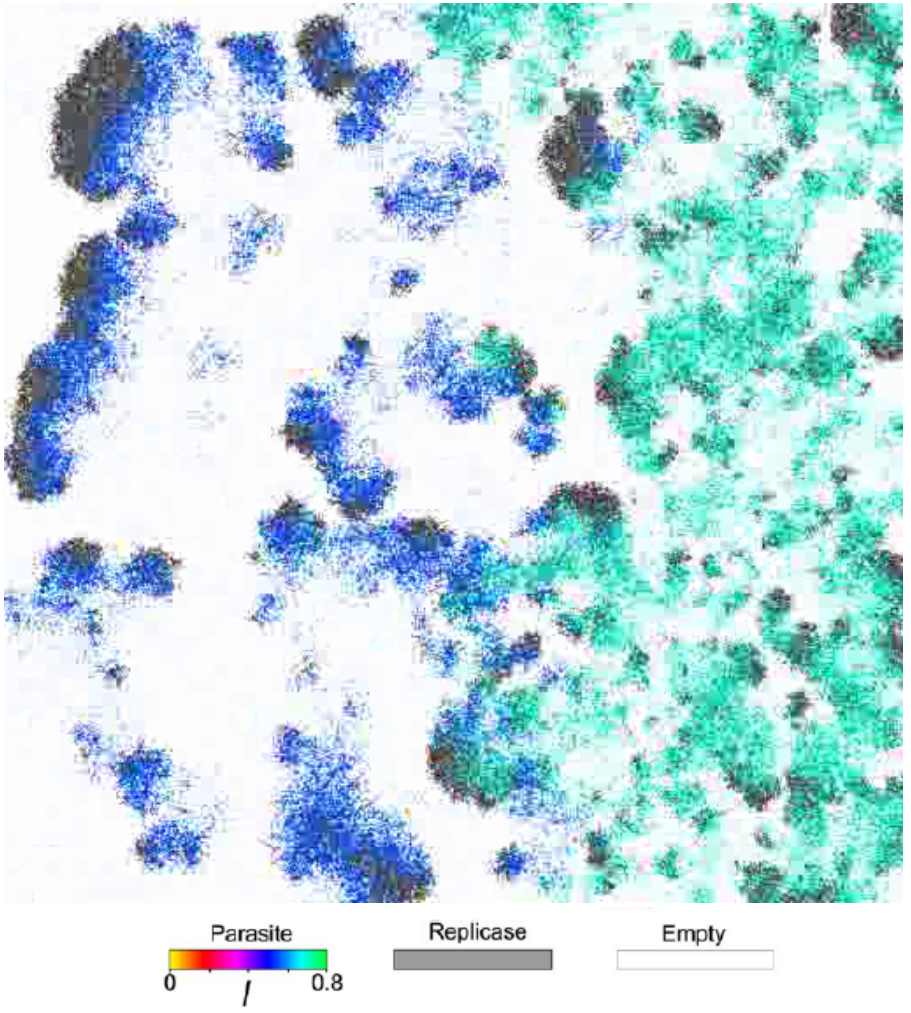


Example of birth of new waves, happening at relatively weak parasites



Colizzi & Hogeweg 2016

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)

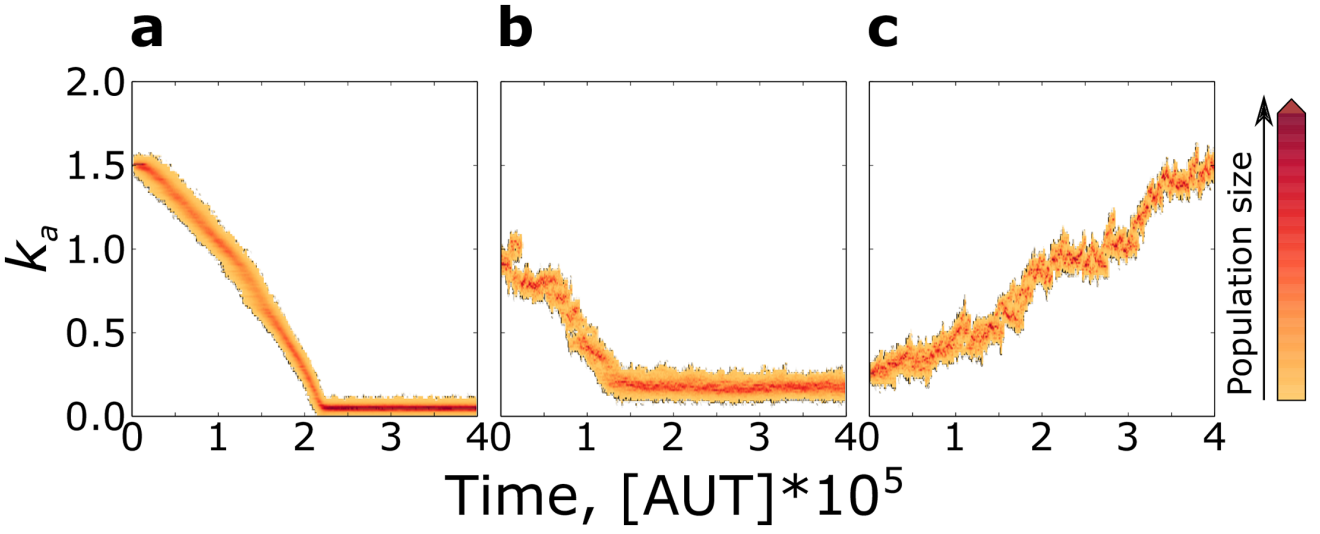
through parasites
evolution of novel functionality

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

The model

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

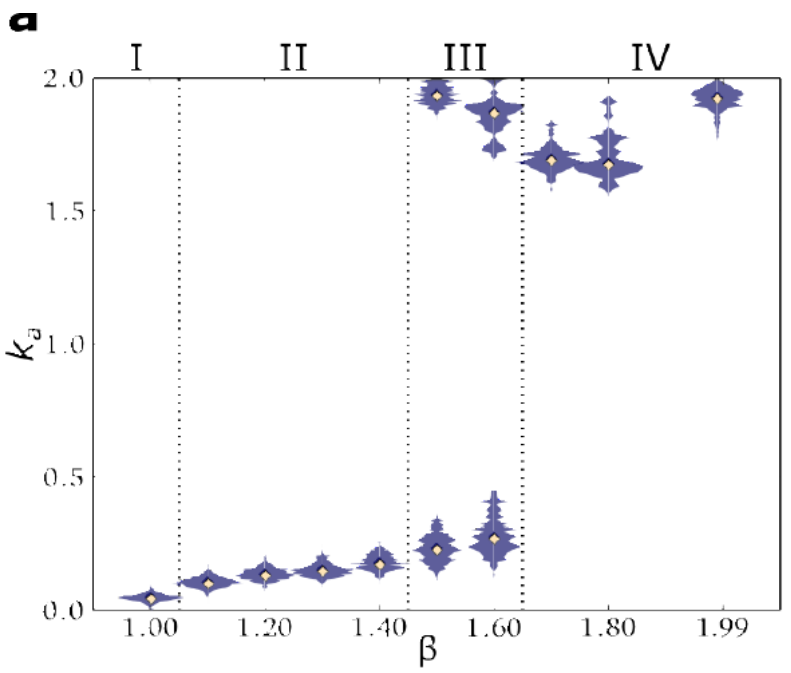
$$\mathrm{X_i} + \mathrm{P} \underset{k_{\mathrm{diss}}}{\overset{\beta \cdot k_{a_i}}{\rightleftharpoons}} \mathrm{C_{PoX}} \xrightarrow{\rho,\theta} 2\,\mathrm{P} + \mathrm{X_i}$$

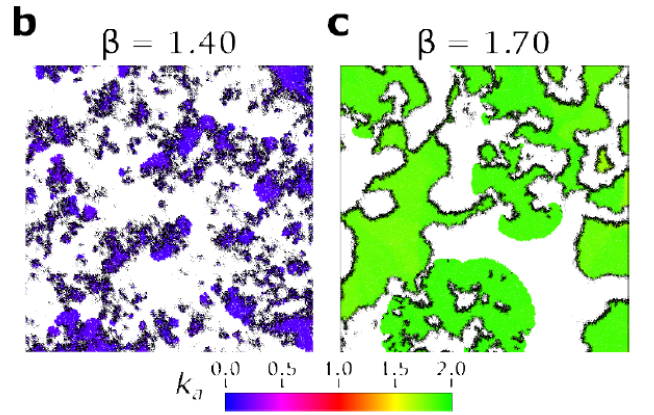


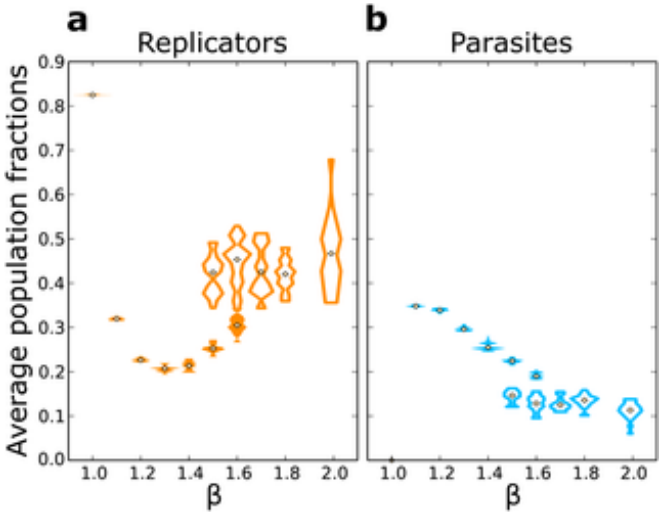
R only RP $\beta = 1.4$ $RP\beta = 1.7$

Colizzi and Hogeweg Plos Comp Biol 2016

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







stronger parasites $->$
more replicases and less parasites

Maximizing invasion of empty space vs maximization of birthrate of waves

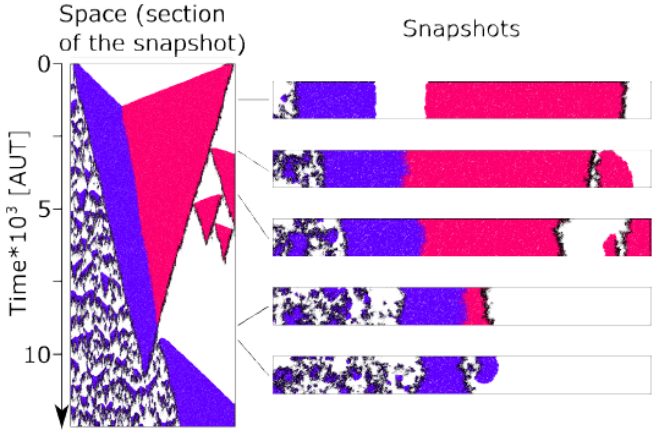
LOW $\beta = 1.3$

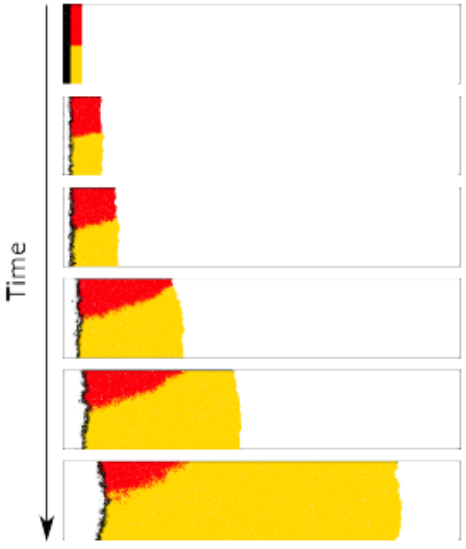
blue: $k_a = .2$; red $k_a = .8$

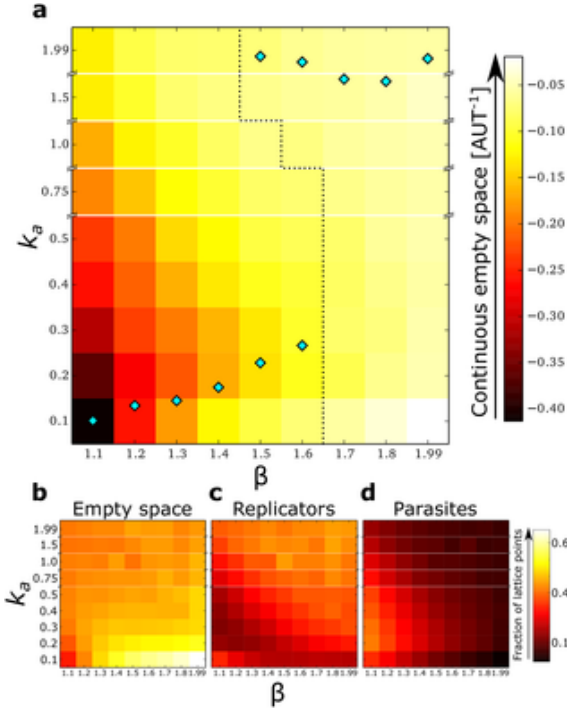
HIGH $\beta = 1.8$

redk$_a = 1$ yellow $k_a = 1.2$

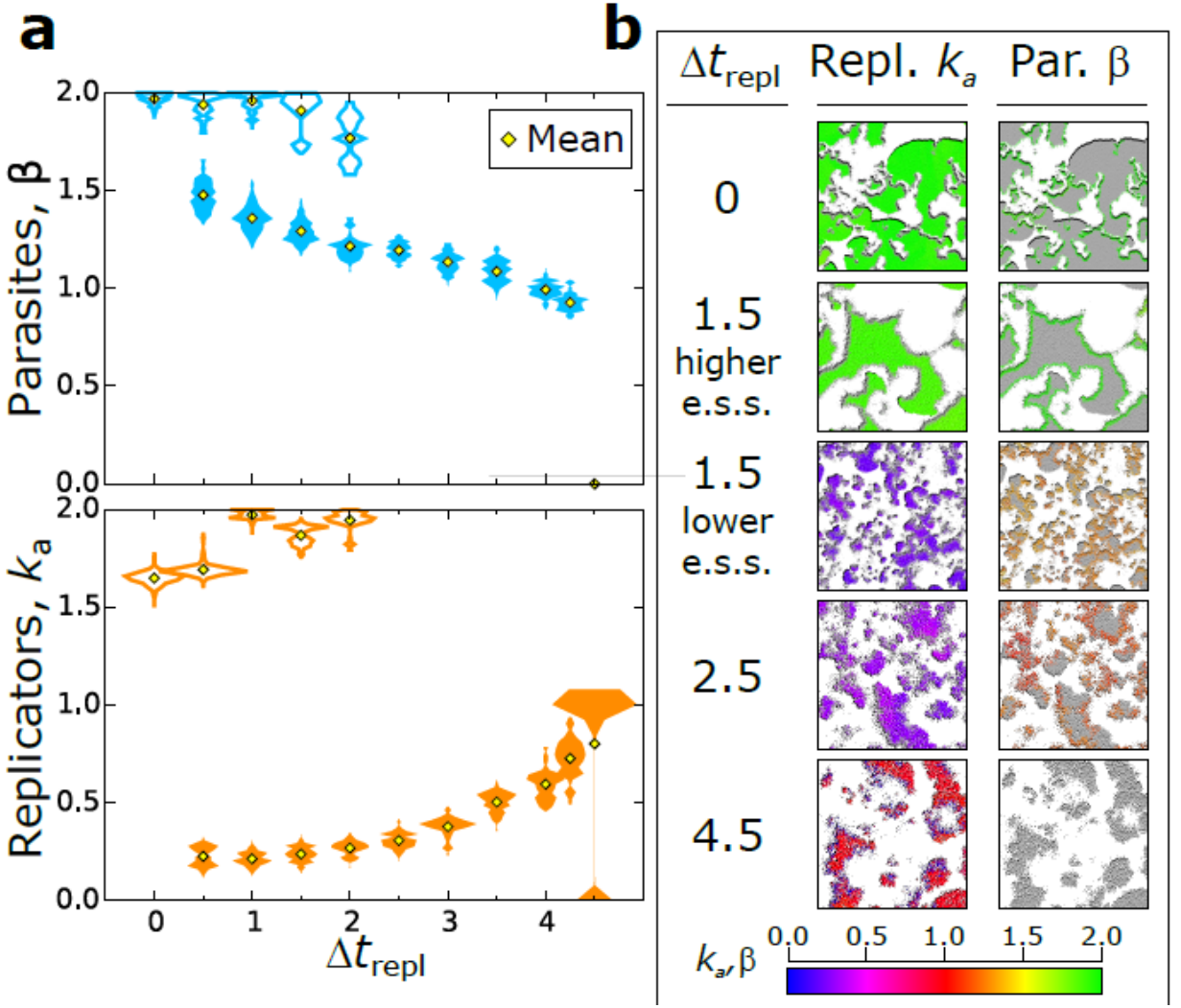
empty space





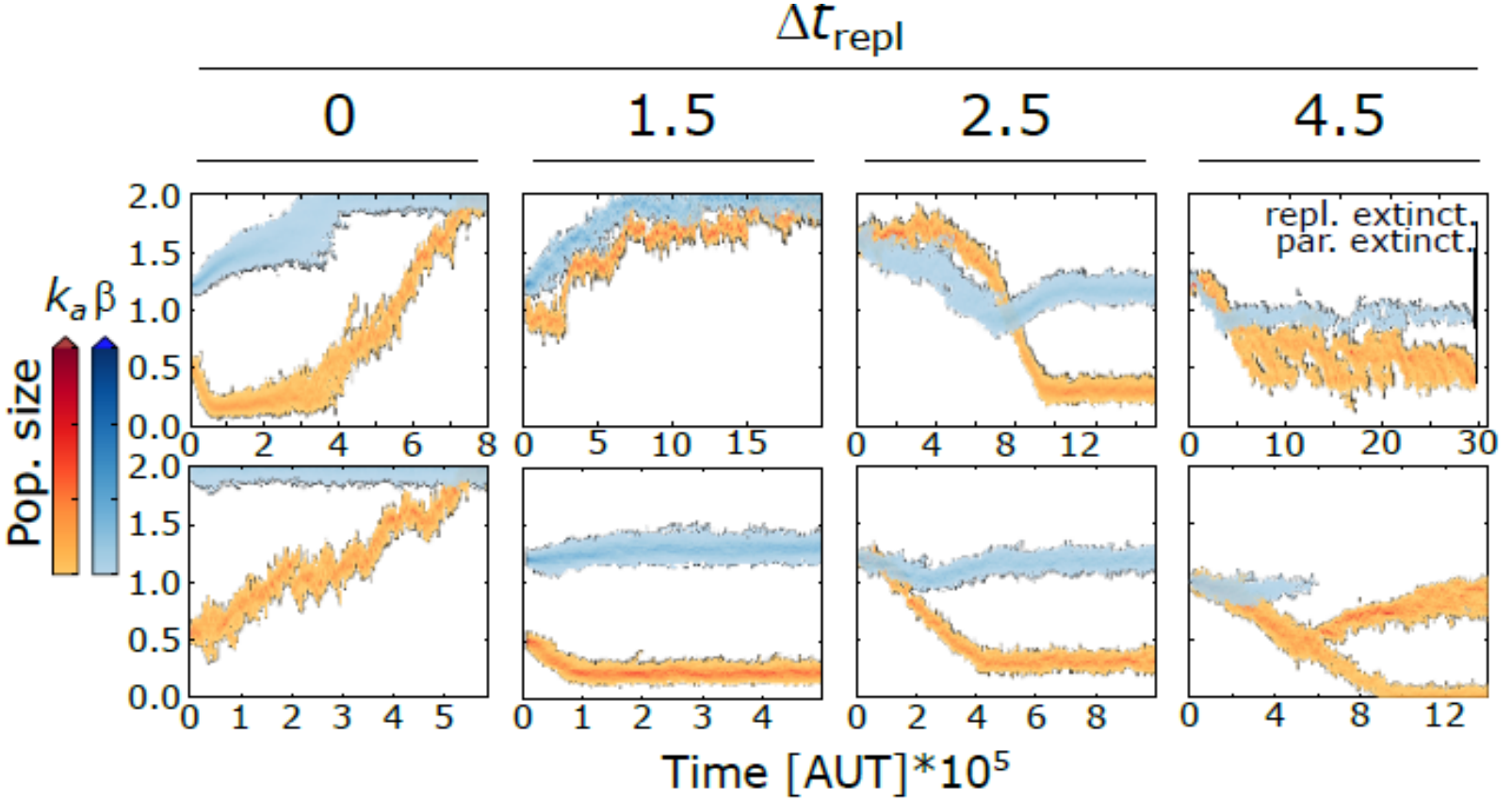


Coevolution of replication (k_i) and parasite strength β

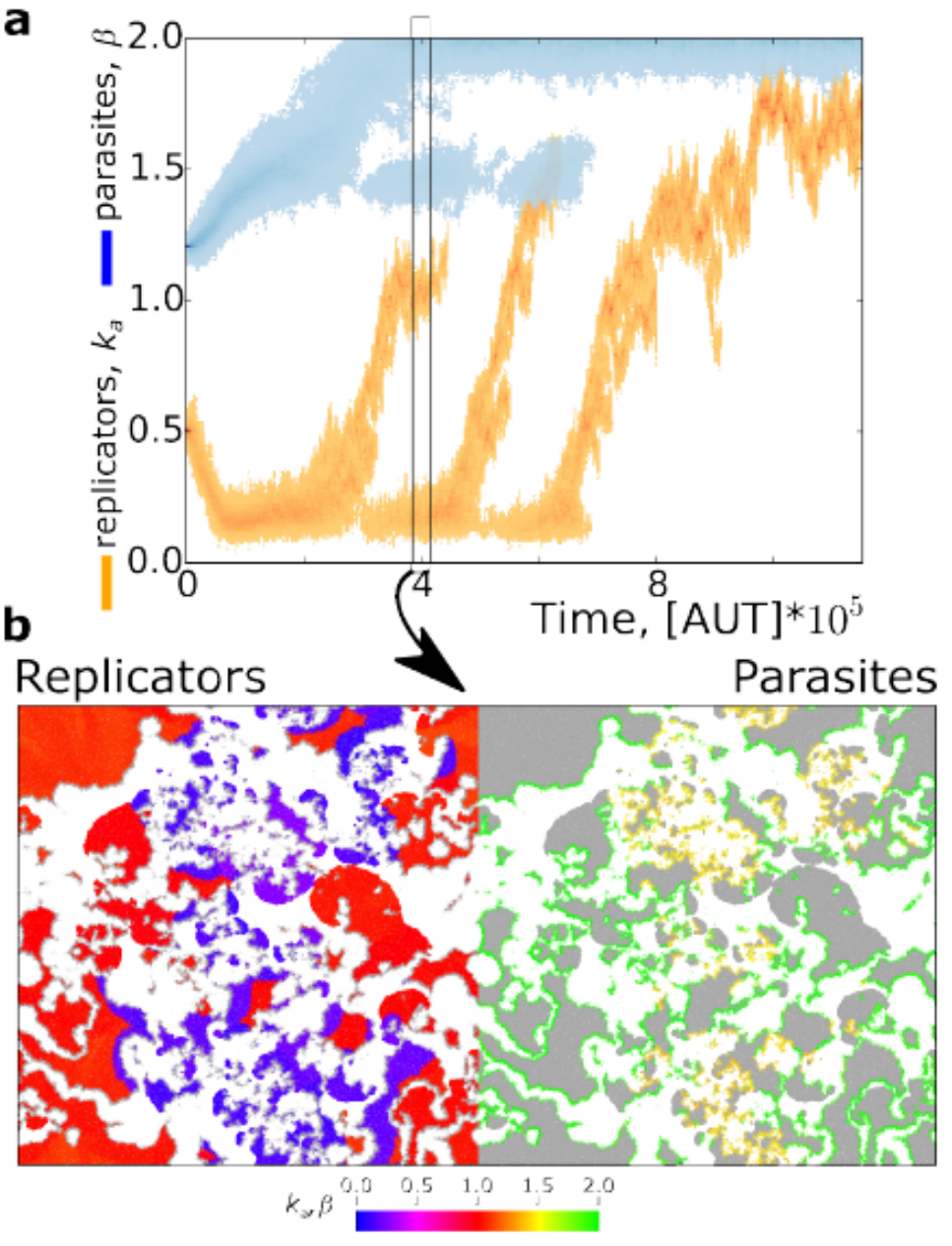


varying duration in complex

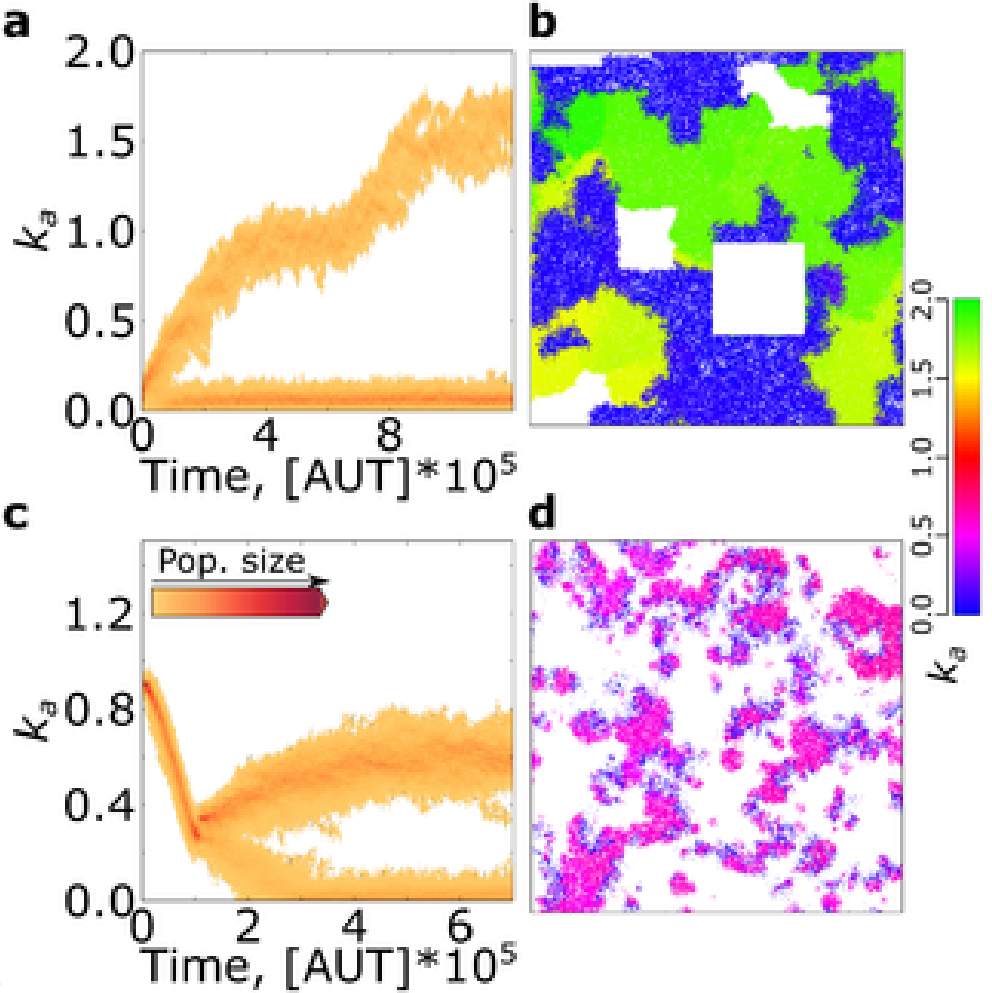
coevolution of replication (k_i) and parasite strength β for different time in complex : timeplots



$\Delta T_{repl} = 0$
"Ghost" attractors
(bistabity)



Speciation:
From replicases only to replicases and parasites
Disruptions or cost (duration) of replication



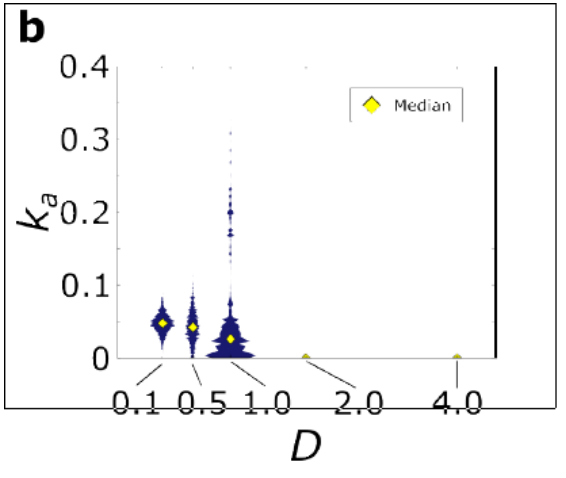
$\Delta T_{repl} = 4$

conclusion

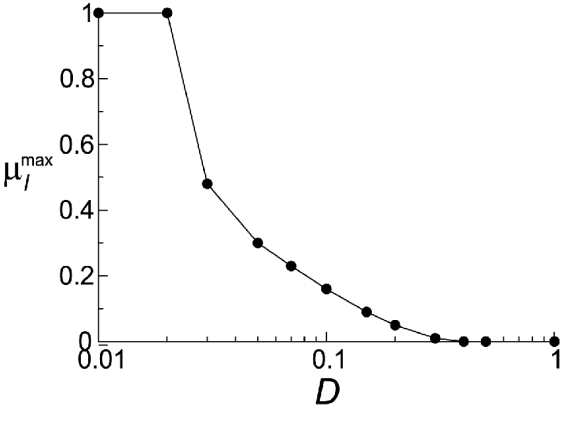
Because of wave-level selection
Parasites enhance replication potential

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

BUT:



limited diffusion (replicase model)



errorthreshold (parasite model)

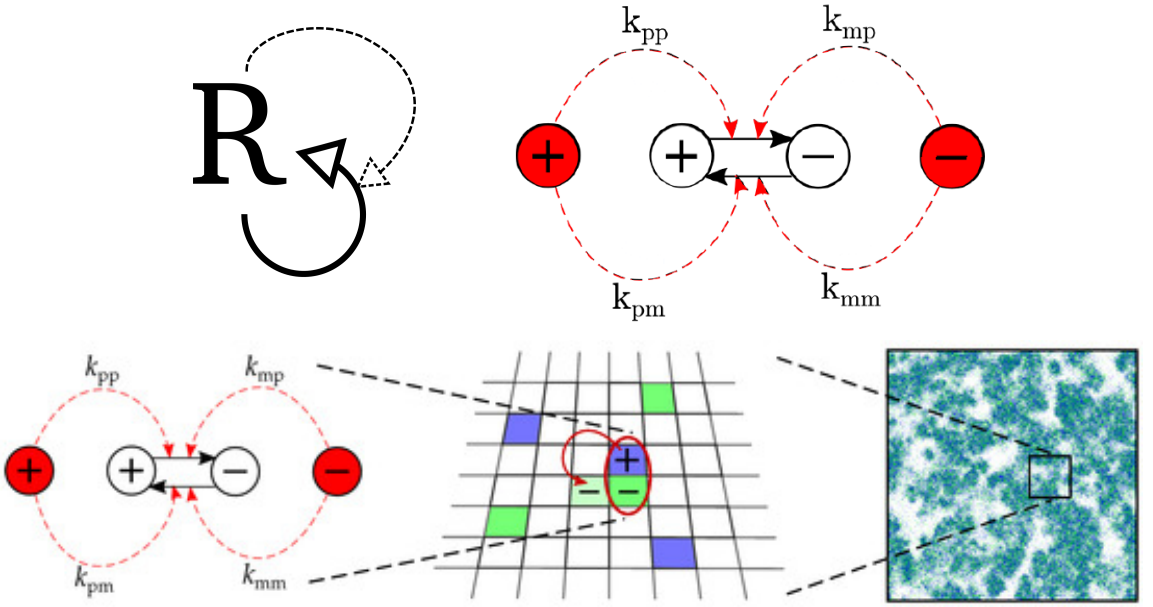
conclusion

Emerging higher level Darwinian Entities (waves)

in minimal eco-evolutionary replicator RP model:
waves emerge because of parasites
waves as evolving entities (birth,death,mutation, selection)
emergent trade-off
bistability; parasitism induces more catalysis
, potential of novel function
parasites emerge in disturbed environments
and when giving catalysis is costly enough

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

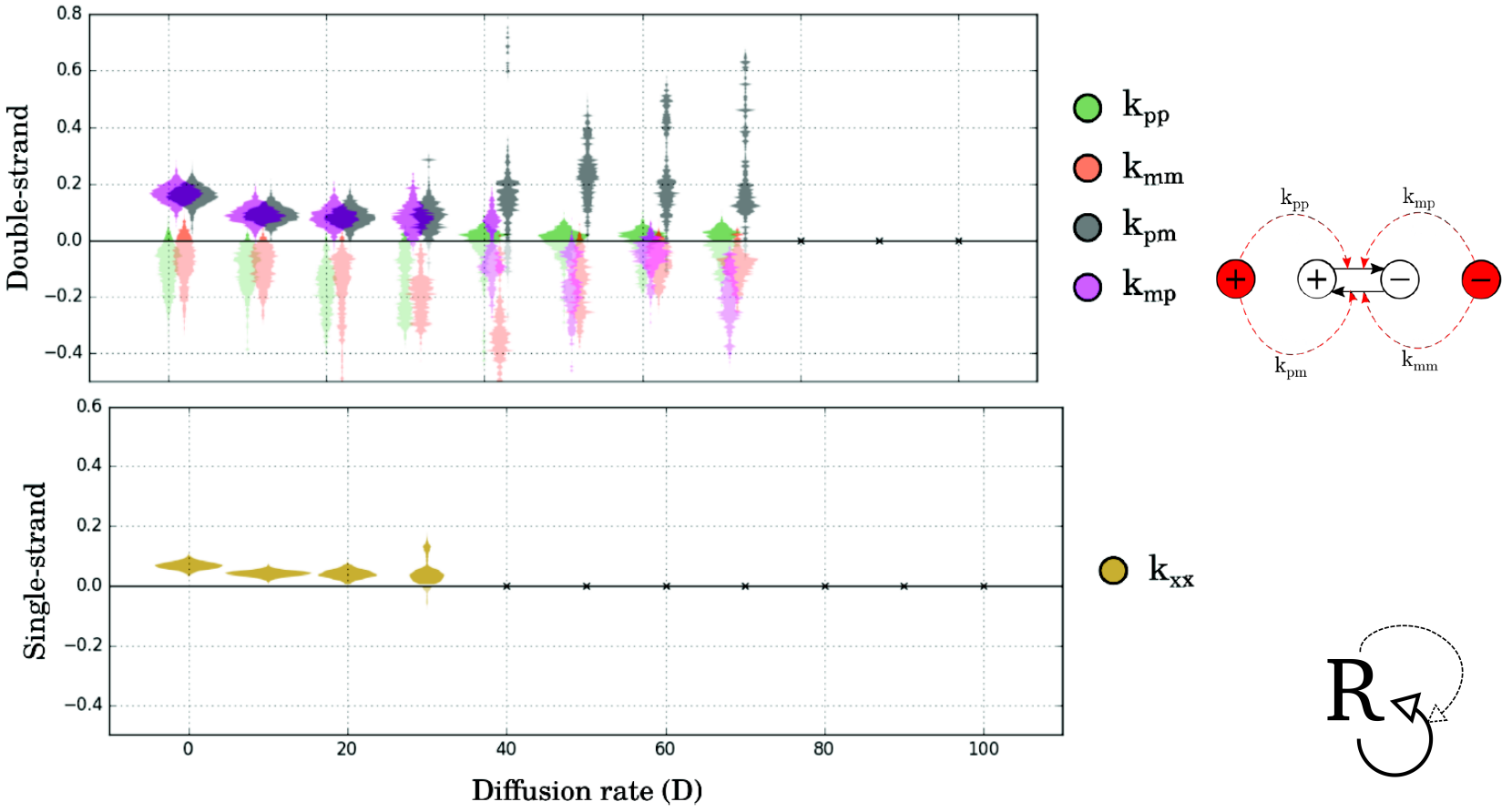
- **Direct replication vs Complementary replication**



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

von den Dunk, Colizzi Hogeweg 2017

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

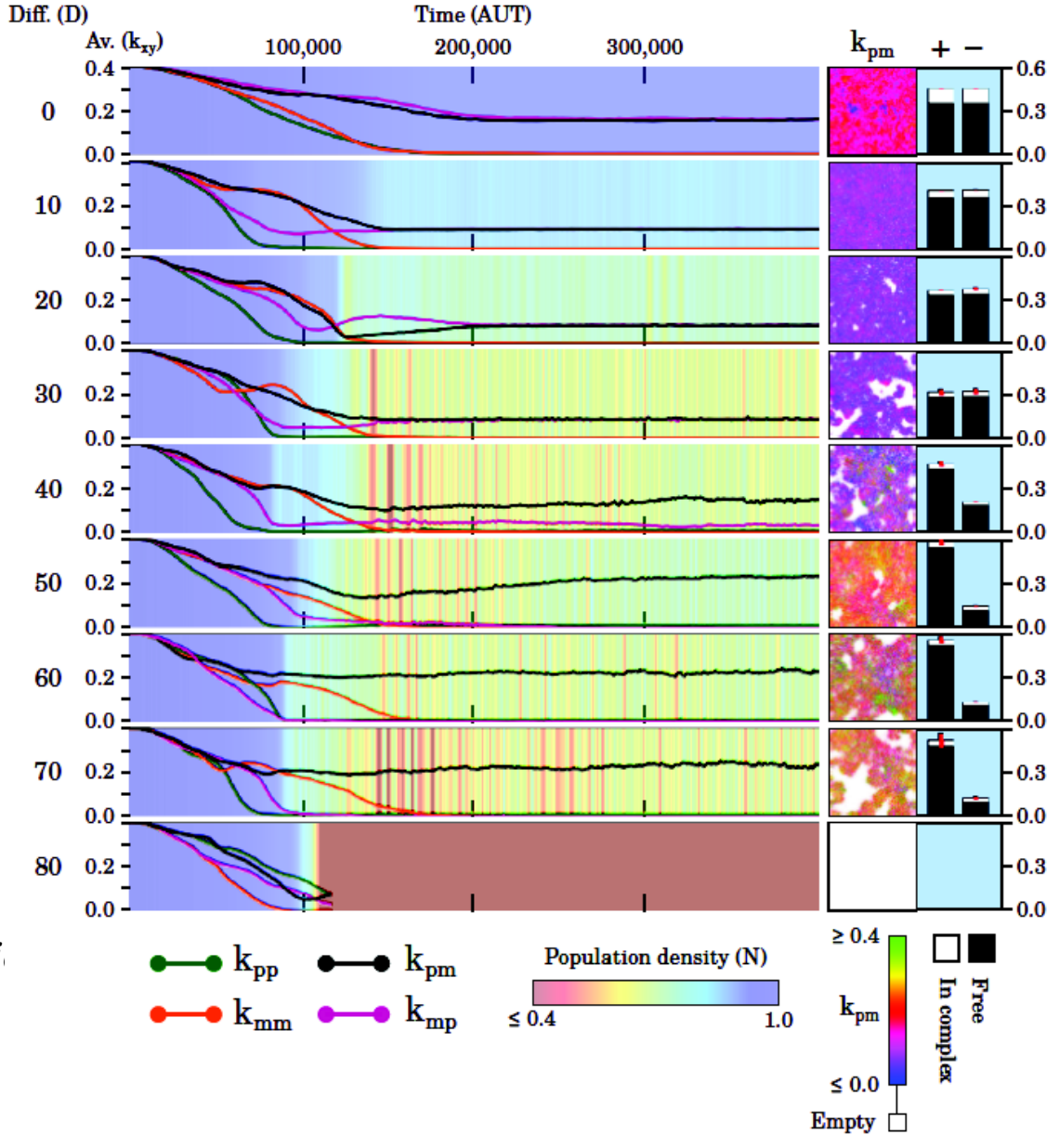
3 types of symm breaking:

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

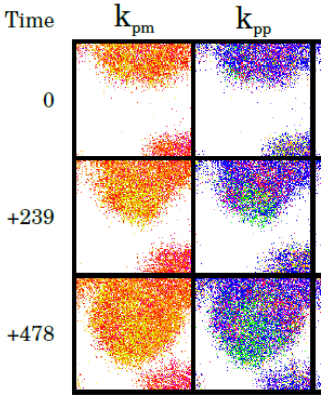
target ($K_{pm} - K_{mm}$)

one-cat ($K_{pm} + << K_{pp}$

LOSS of functi

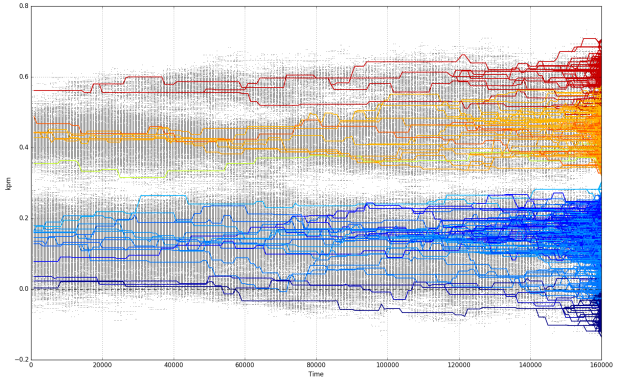


Evolutionary dynamics at high diffusion (D70)

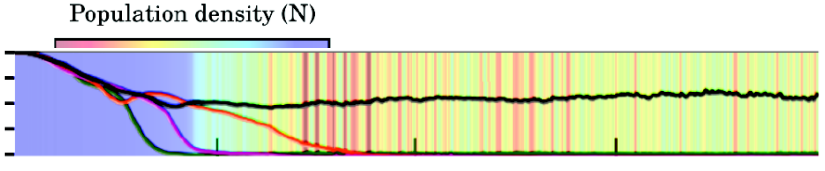


selection at wave fvront

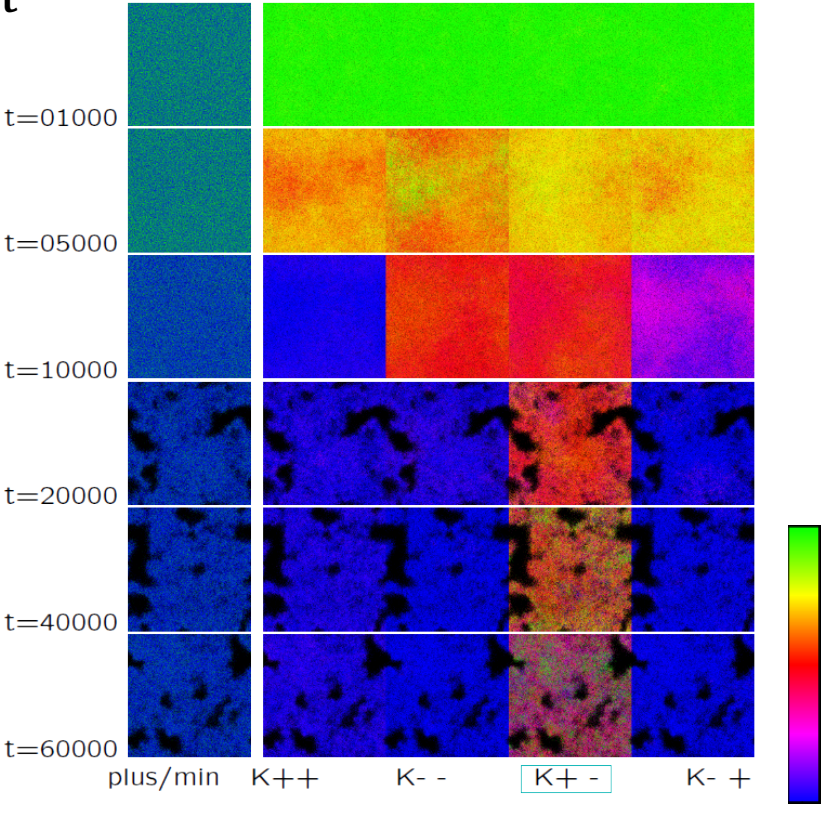
ancestor trace



evolution through time



spatial self-organization



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 - multiple 'niches'/selections pressure

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

Less well defined, distinct "level of selection"

Conflict resolution between levels

Multiple niches

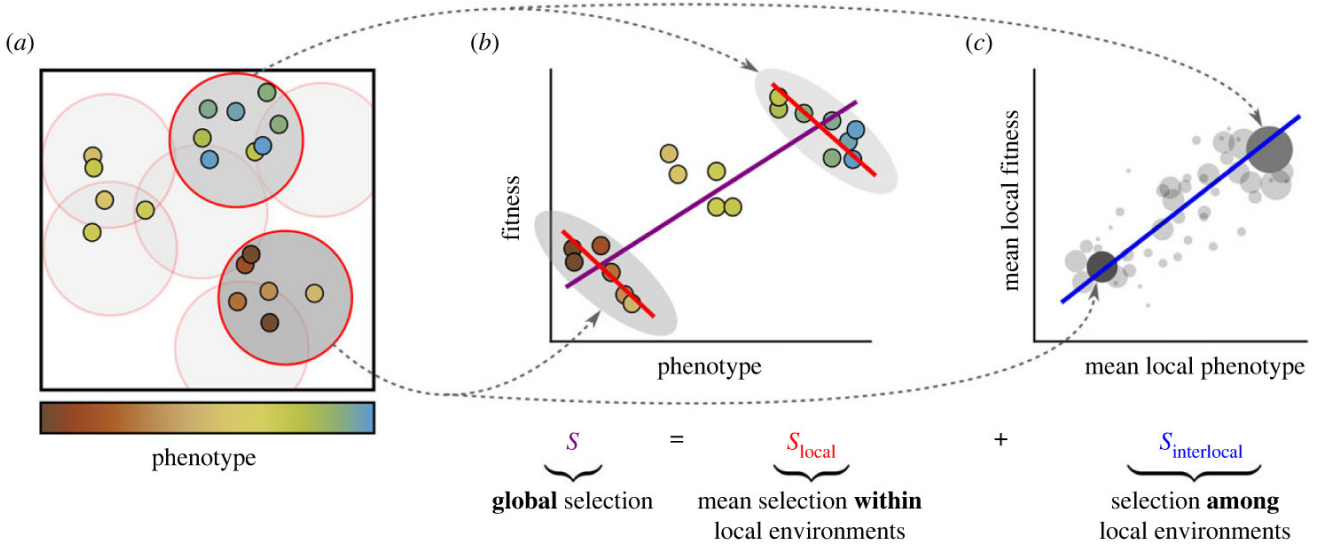
More evolutionary degrees of freedom: BETTER results:

here: higher diffusion
higher mutation rates (not shown)

Quantifying selection at different scales
Multiscale selection in spatially structured populations Hilje M. Doekes and Rutger Hermsen 2024

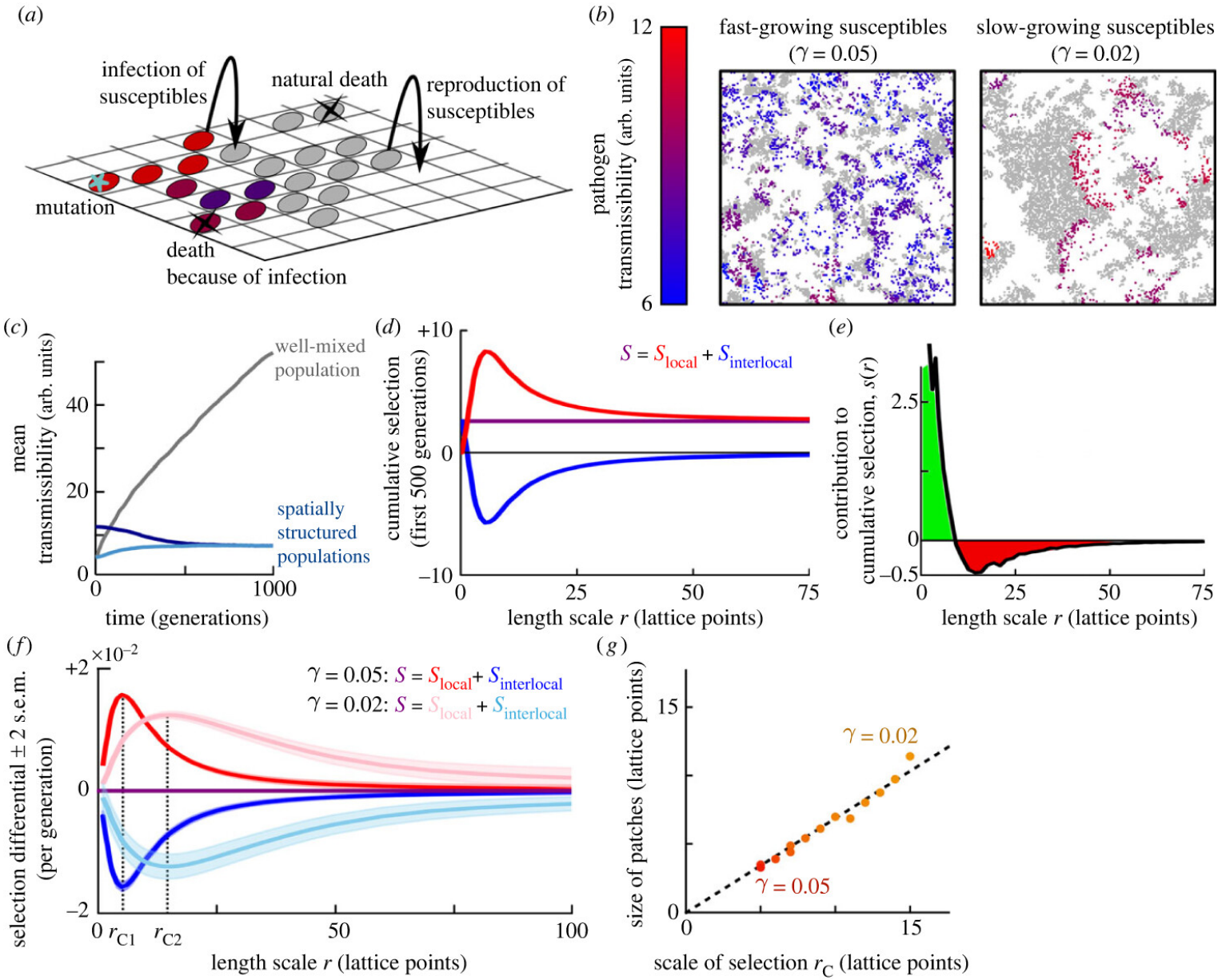
define selection of a trait as the covariance between the trait value and the number of offspring after a period δt. (Pierce equation)

measure selection at in areas of different size different locations.



$$S = \mathbf{mean}\big(\mathrm{LSD}\big) + \mathbf{Cov}\big(\text{local mean}(\phi), \text{local mean}(w)\big)$$
$$\equiv S_{\text{local}}(r) + S_{\text{interlocal}}(r),$$

Example: SI (susceptable-infectious) model in space


(a)
infection of susceptibles
natural death
reproduction of susceptibles
mutation
death because of infection
(b)
12
6
pathogen transmissibility (arb. units)
fast-growing susceptibles (γ = 0.05)
slow-growing susceptibles (γ = 0.02)
(c)
mean transmissibility (arb. units)
well-mixed population
spatially structured populations
time (generations)
(d)
cumulative selection (first 500 generations)
S = S_local + S_interlocal
length scale r (lattice points)
(e)
contribution to cumulative selection, s(r)
length scale r (lattice points)
(f)
selection differential ± 2 s.e.m. (per generation)
γ = 0.05: S = S_local + S_interlocal
γ = 0.02: S = S_local + S_interlocal
r_C1
r_C2
length scale r (lattice points)
(g)
size of patches (lattice points)
γ = 0.02
γ = 0.05
scale of selection r_C (lattice points)