Eco-evolutionary dynamics:
multilevel evolution
vesicles vs mesoscale patterns
Multilevel evolution

LAST TIME:

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

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 $K_{pp}K_{pm}K_{mm}K_{mp}$

Comparing emergent vs predefined mutilevel evolution

waves vs vesicles
explicit higher levels of selection
coupling between levels

• Classical (ecological group selection model (DS Wilson)

• Classical prebiotic evolution model
  Stochastic corrector model (Szathmary)

• Evolutionary stable disequilibrium: tuning stochasticity

• direct comparison emerging and imposed higher level
  of selection in RP models

• Evolution of “genomes” 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
  \[ \frac{dX}{dt} = aXX - cX \]
  \[ \frac{dY}{dt} = aXY \]
  (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)

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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)**

\[
\frac{dX}{dt} = aX(XY)^{1/4} - dX - X((X + Y)/K)
\]

\[
\frac{dY}{dt} = bY(XY)^{1/4} - dY - Y((X + Y)/K) \quad ; \quad a > b
\]

(fastest growth iff \( X = Y \))

(X outcompetes Y in ODE;
discrete stochastic version: master equation \rightarrow prob. distribution of mol after time=\( \tau \))
**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 stochasticity)
number of different molecules should be small enough
NB timescales of micro vs macro dynamics
Evolutionary stable disequilibrium: endless dynamics of evolution in a stationary population (Takeuchi et al 2016)

Replicator model within cell (NO parasites)

Minimization of catalysis within cell

Maximization of catalysis 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 $1/V$)

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 \( mV \ 1/V \rightarrow mV^2 = C \) - 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
imposed levels of selection: protocells
direct vs complementary replication
symmetry breaking and robustness to larger cells

Evolutionary stable disequilibrium, and origin of 'primordial genome'
Takeuchi Kaneko, Hogeweg 2016; Takeuchi, Hogeweg, Kaneko 2017
exploring evolutionary properties/advantages of more RNA-like replicators in R-only system (i.e. more degrees of freedom) IN SPACE

- Direct replication vs Complementary replication

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

- reciprocal \((K_{pm} - K_{mp})\)
- target \((K_{pm} - K_{mm})\)
- one-cat \((K_{pm} + << K_{pp}\)

\[\begin{align*}
&\text{Green: } k_{pp} \\
&\text{Black: } k_{pm} \\
&\text{Red: } k_{mm} \\
&\text{Purple: } k_{mp}
\end{align*}\]

Population density (N): 
- \(\leq 0.4\) (low)
- \(\geq 0.4\) (high)

Legend:
- Free
- In complex
- Empty
Evolutionary dynamics at high diffusion (D70)

selection at wave front

ancestor trace

spatial self-organization

evolution through time
“competition(?) between direct and complementary replication

Catalyst Model

Basic Model

Bas = direct replication 1 parameter $K_{xx}$
Complementary replication: here only 2 parameters: $K_{px} K_{mx}$
Both species “speciate” in replicase and parasite;
Complementary replicase: symmetry breaking

$\begin{array}{c}
\text{Bas} \\
\text{Cat.}
\end{array}$ $k_{px}$ $k_{mx}$ $k_{xx}$

$\begin{array}{c}
\text{Empty} \\
\leq 0.0 \\
1.0 \leq
\end{array}$

Bas = direct replication 1 parameter $K_{xx}$
Complementary replication: here only 2 parameters: $K_{px} K_{mx}$
Both species “speciate” in replicase and parasite;
Complementary replicase: symmetry breaking
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-sufficiency - selfreplication?

Evolution of slower replication cycle

Takeuchi et al 2011 (PLOS comp biol)
the model

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 (CPM)
RNA replication AND Transcription system in vesicles and in surface system however dual functional RNA polymerases 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
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”