Eco-evolutionary dynamics: multilevel evolution
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 catalytic interactions

NOT resistant to ongoing mutations:
loss of spirals

BUT
Multilevel evolution

- CA Universe: (cf. Crutchfield, Wolfram)
  Micro $\rightarrow$ Macro ($\ldots \rightarrow \ldots \rightarrow \ldots$ etc.)
  *STATIC (simple) 'rockbottom'*

- BUT: In evolving systems also Macro $\rightarrow$ Micro:

  ![Diagram](image)

  **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)
Ecosystem based information conservation beyond hypercycle model

Ongoing mutations instead of invasion dynamics

Non-cyclic interaction structure.
Evolution of Replicases (and parasites)

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

coevolve replicases and parasites

Takeuchi & Hogeweg 2009; Colizzi & Hogeweg 2016
Evolving parasite strength
emerging higher level of "Darwinian entities"

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

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

Takeuchi & Hogeweg 2009
Classical problem

ODE model of RP system

evolutionary extinction (increase of $k_L$ and decrease of $l$)

\[
\begin{align*}
\dot{R} &= -2k_R R^2 + [2(1 - k_R) + 3\kappa \theta + 2d] C_R - k_L R L \\
&\quad + [(1 - k_L) + \kappa \theta + d] C_L - d R, \\
\dot{L} &= -k_L (1 - l) R L + [(1 - k_L) + 2\kappa \theta + d] C_L - d L, \quad (2) \\
\dot{C}_R &= k_R R^2 - [(1 - k_R) + \kappa \theta] C_R - 2d C_R, \\
\dot{C}_L &= k_L (1 - l) R L - [(1 - k_L) + \kappa \theta] C_L - 2d C_L,
\end{align*}
\]

\[k_R = .6\]

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 $l$
long term evolution: towards smaller waves
Long term evolution (parameters) 
emergent 'trade-off' $k_L$ and $l$
Maximizing $l$: potential 'new' function

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 $l$ 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

\[
\begin{align*}
X_i + X_j & \xrightleftharpoons[k_{\text{diss}}]{k_{\alpha_i}} C_{X_jX_i} \xrightarrow[\rho,\theta]{\rho,\theta} 2X_j + X_i \\
X_i + P & \xrightleftharpoons[k_{\text{diss}}]{\beta \cdot k_{\alpha_i}} C_{P_0X} \xrightarrow[\rho,\theta]{\rho,\theta} 2P + X_i
\end{align*}
\]

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 \( \beta \)
for different time in complex
(a) Graph showing Parasites, $\beta$, and Replicators, $k_a$, against $\Delta t_{repl}$.

(b) Table and images showing changes in $\Delta t_{repl}$, with corresponding $k_a$, $\beta$, and visual representations.

- $\Delta t_{repl}$: 0, 1.5, 2.5, 4.5
- Repl. $k_a$: various values indicated
- Par. $\beta$: various visual representations

色度準拠カラーバー: 0 から 2 までのレベルを示しています。
coevolution of replication ($k_i$) and parasite strength $\beta$
for different time in complex : timeplots

$\Delta t_{\text{repl}}$

<table>
<thead>
<tr>
<th>0</th>
<th>1.5</th>
<th>2.5</th>
<th>4.5</th>
</tr>
</thead>
</table>

$\kappa_\beta$

Pop. size

Time [AUT]*10^5
$\Delta T_{repl} = 0$

“Ghost” attractor (bistability)
Speciation: From replicases only to replicases and parasites
Disruptions or cost (duration) of replication
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
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