On the Degree of Freedom in Multilevel Evolutionary Models

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Evolution of Biotic Systems

Biotic systems:

- Large degree of freedom
  - → Great variety in possible adaptations
- Constraint and structure
  - → RNA/protein folding is not random
  - → Random mutation produces statistical order
  - → Adaptations might be conceivable, not equally achievable

How to Model Evolution

Simplicity versus Complexity in Model

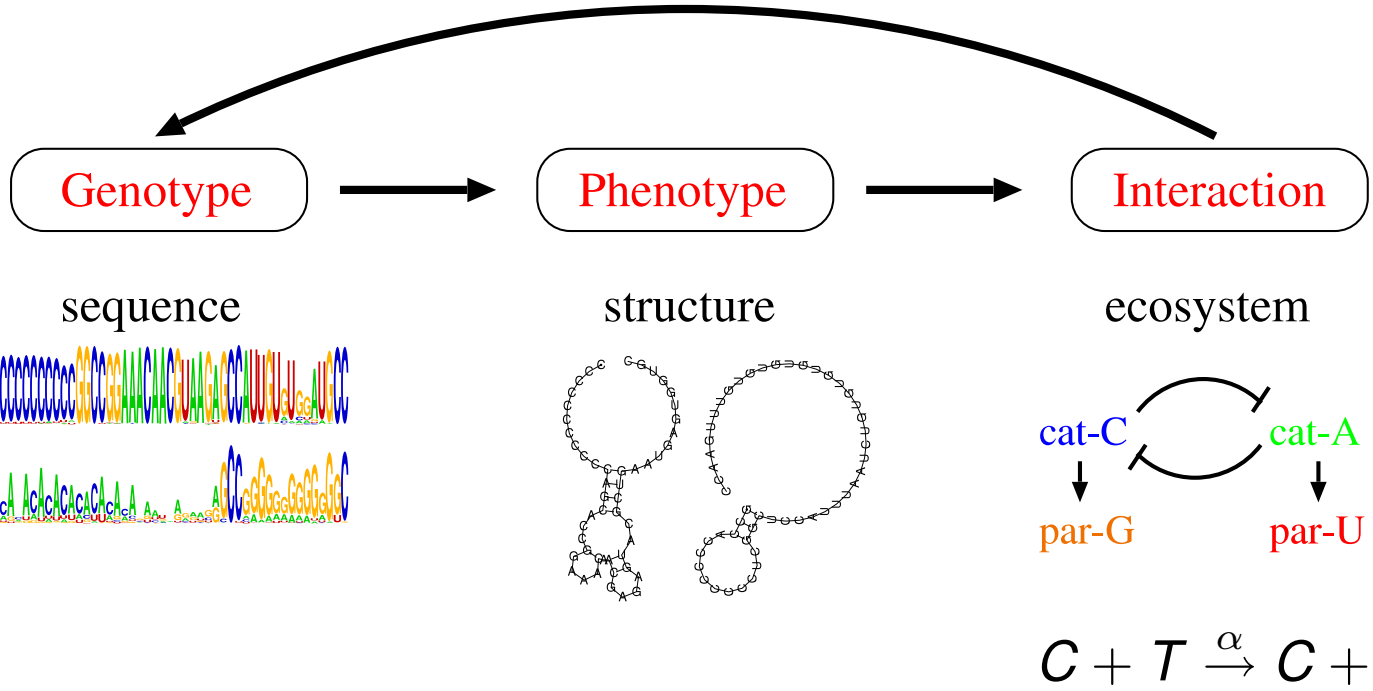
- Small degree of freedom + predefined structure
  - → Strengthening/weakening of predefined structure
    e.g.) Predator X $\xrightarrow{a_{xy}}$ Prey Y
  - → Novel structure cannot emerge (structures are predefined)
- Large degree of freedom + biological constraint
  - → Novel structure can emerge

The Purpose of This Talk

- We compare the two modeling approaches
  $\rightarrow$ small vs. large degree of freedom ($N = 2$!)
- Kinds of adaptations depend on the degree of freedom available to evolution

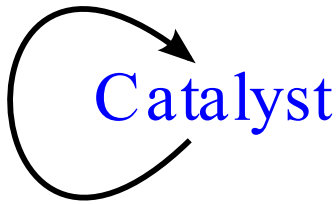
Model with Large Degree of Freedom

- Evolution of Complexity in RNA-like Replicator Systems



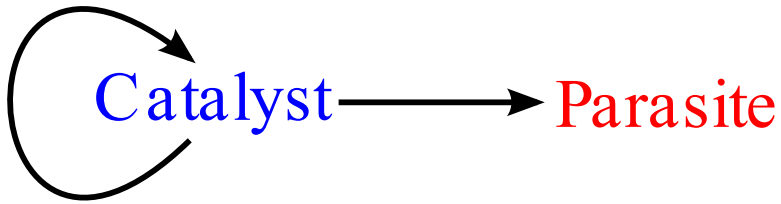
Takeuchi & Hogeweg (2008) *Biol Direct* **3**:11

Result



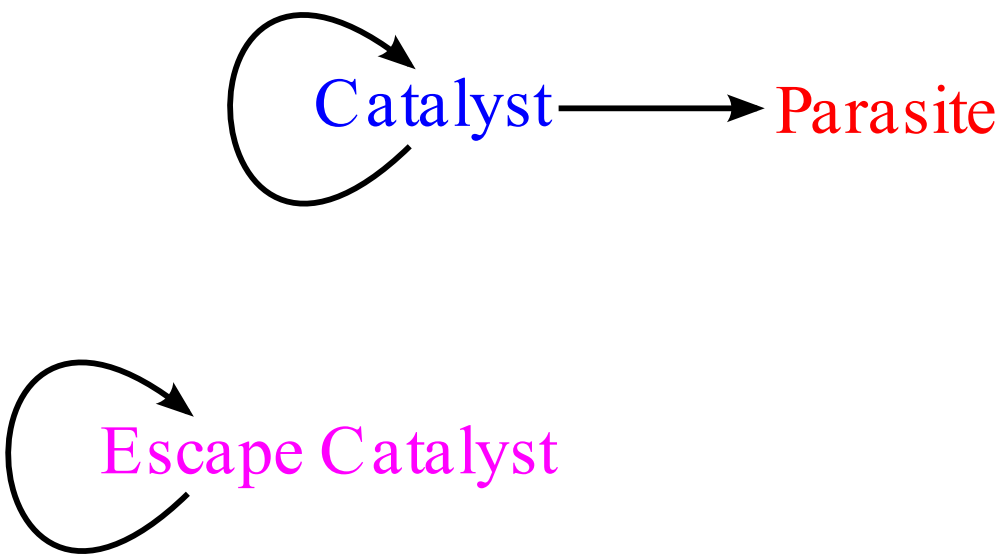
Arrows denote replication

Result



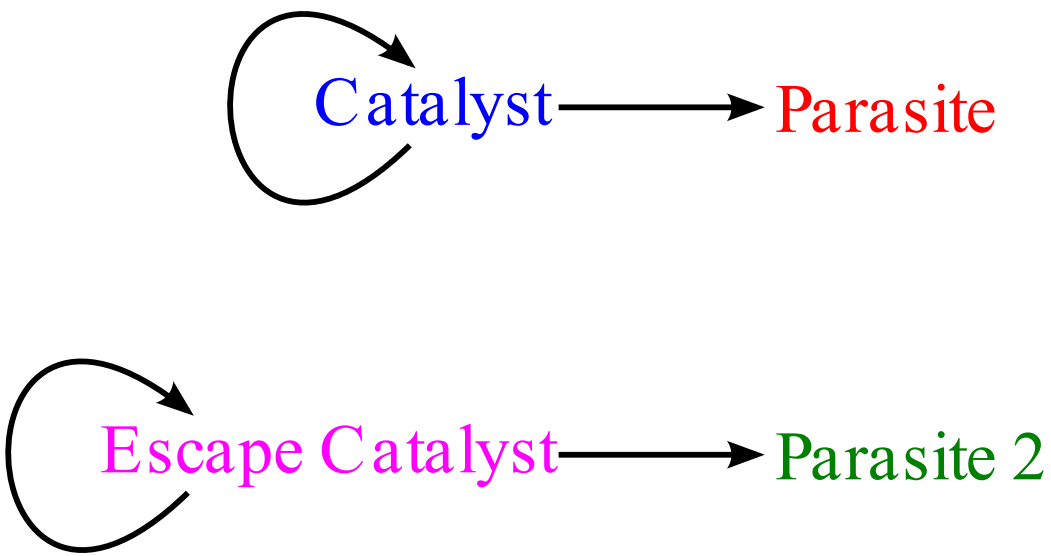
Arrows denote replication

Result



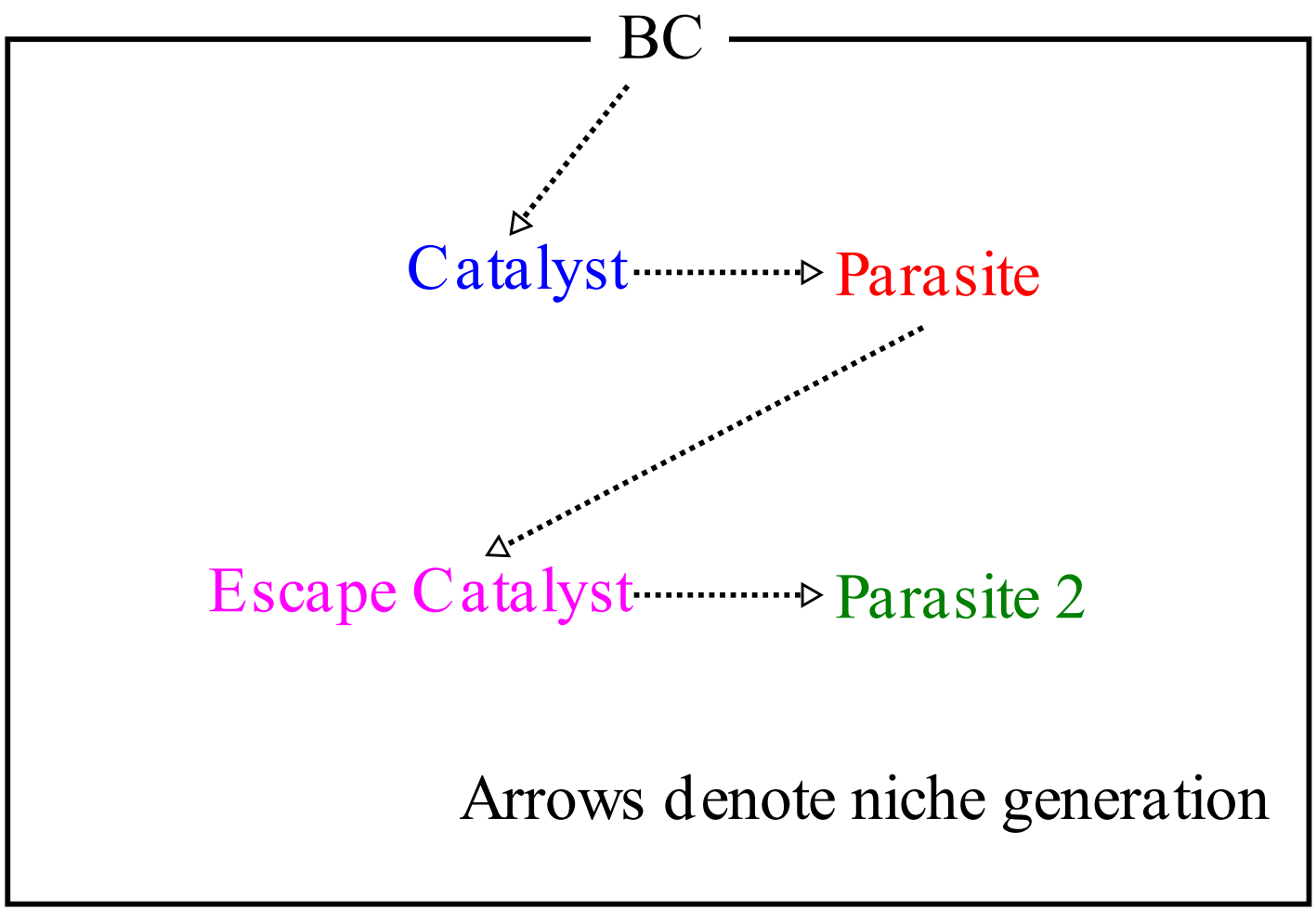
Arrows denote replication

Result



Arrows denote replication

Result


BC
Catalyst
Parasite
Escape Catalyst
Parasite 2
Arrows denote niche generation

Mess of Data

```
51 :ls -lh sequence-prototype.seq
-rw-r--r-- 1 nobuto binf 251M Sep  7 21:54 sequence-prototype.seq
nobuto@rna:~/tmp
52 :head -n 100 sequence-prototype.seq
t0 t0+ GCAUACGAUUUGCCUCUUUCGCGUUUCCUGGCGUUACAUUAUUUUCUUUC p104791 c2 ((((((H)S)I)S)I)S)R)
t0 c0- GAAAGAAAAUAAUGUAACGCCAGGAAACGCGAAAGAGGCAAAUCGUAUGC p104838 c2 ((((H)S)((H)S)M)S)R)
t500 t0+ GCAUACGAUUUGCCUCUUUCGCGUUUCCUGGCGUUACAUUAUUUUCUUUC p16685 c2 ((((((H)S)I)S)I)S)R)
t500 c0- GAAAGAAAAUAAUGUAACGCCAGGAAACGCGAAAGAGGCAAAUCGUAUGC p34502 c2 ((((H)S)((H)S)M)S)R)
t500 c1+ GAAAGAAAAUAAUGUAACGCCAGGAAACGCGUAAGAGGCAAAUCGUAUGC p3382 c3 ((((H)S)((H)S)M)S)R)
t500 t1- GCAUACGAUUUGCCUCUUACGCGUUUCCUGGCGUUACAUUAUUUUCUUUC p1646 c3 (((H)S)((H)S)R)
t500 p0+ GCAUACGAUUUGCCUCUUUCGCGUUUCCUGGCGUUACAUUAUUUUCUGUC p884 c4 ((((((H)S)I)S)I)S)R)
t500 p0- GACAGAAAAUAAUGUAACGCCAGGAAACGCGAAAGAGGCAAAUCGUAUGC p1477 c4 (((H)S)((((H)S)((H)S)M)S)R)
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t500 p1- GAAAGAAAAUAAUGUAACGCCAUGAAACGCGAAAGAGGCAAAUCGUAUGC p1180 c5 ((((H)S)I)S)R)
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t500 c2- GAAAGAAAAUAAUGUAACGCCAGGAAACGCGAAAGAGGCAAAUCGUUUGC p844 c6 ((((H)S)((H)S)M)S)R)
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```
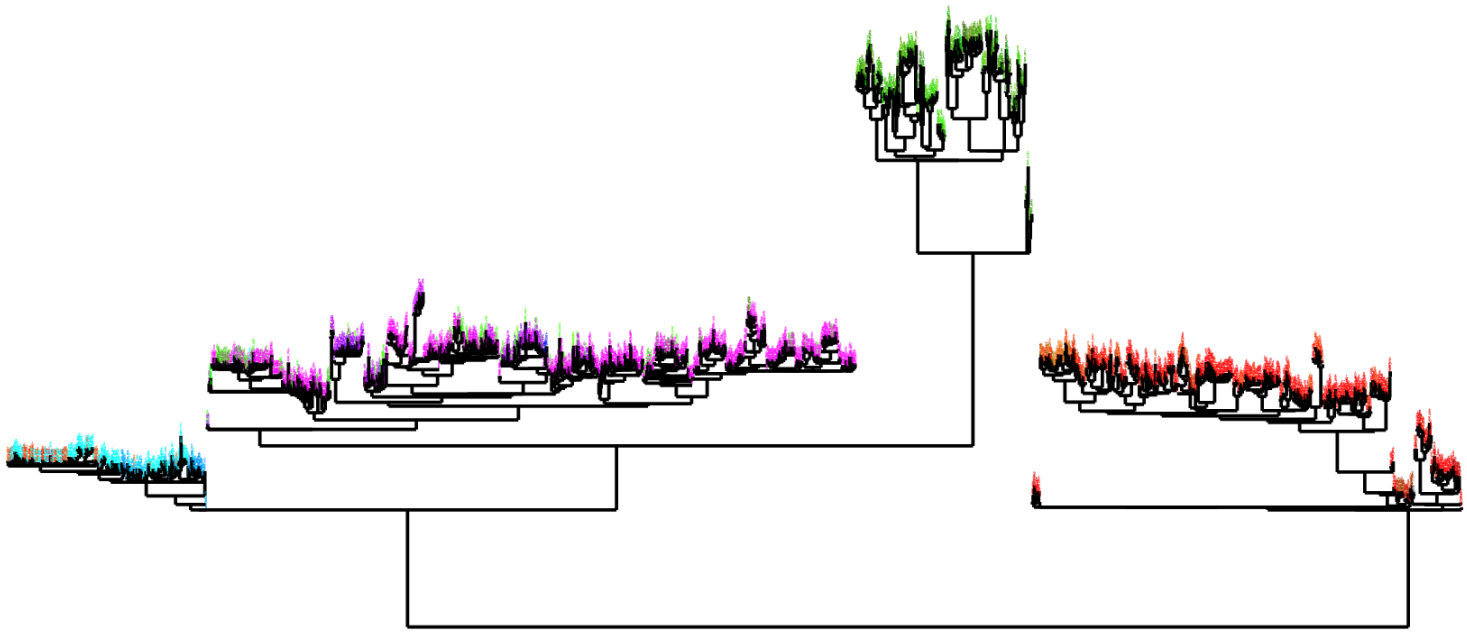
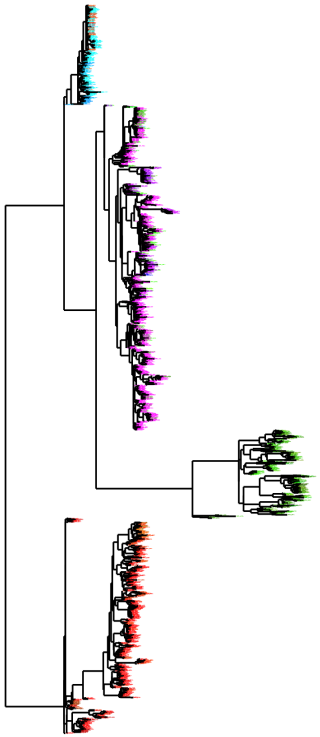

Bioinformatic pattern detection



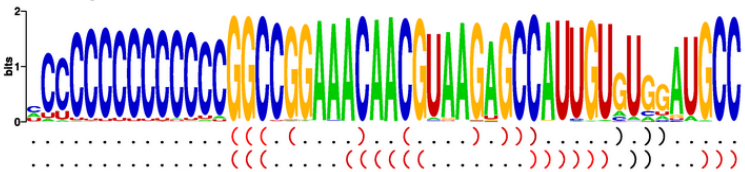
Finding Meaningful Observables

- Sequence Classes

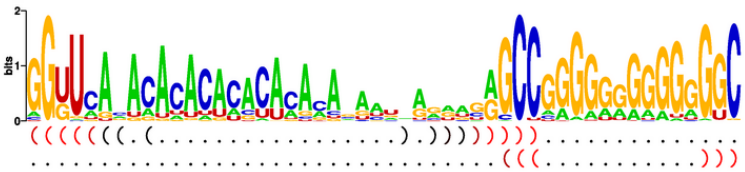


- Genotypes & Phenotypes

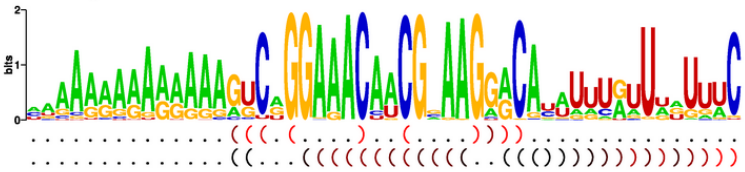
C-catalyst:



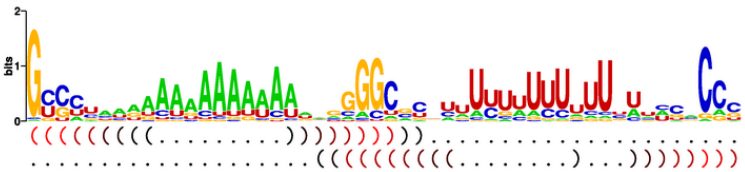
G-parasite:



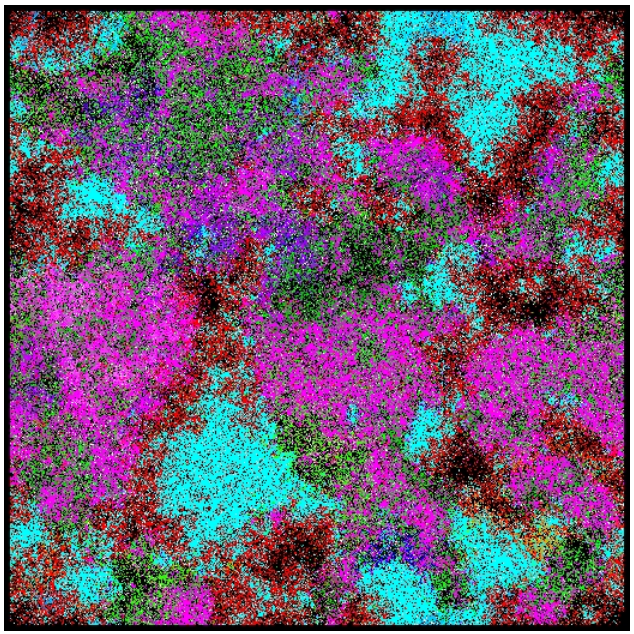
A-catalyst:



U-parasite:



- Visualization with “designed” observables

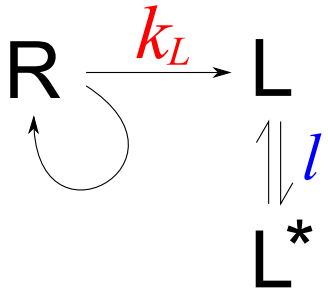


Simplicity & Complexity of a Complex Model

- Simplicity:
  - General results are simple
    $\longrightarrow$ importance of the results
- Complexity:
  - Results are unforeseeable
    general ecological organization, let alone sequence & structure
  - Recognition of results is nontrivial

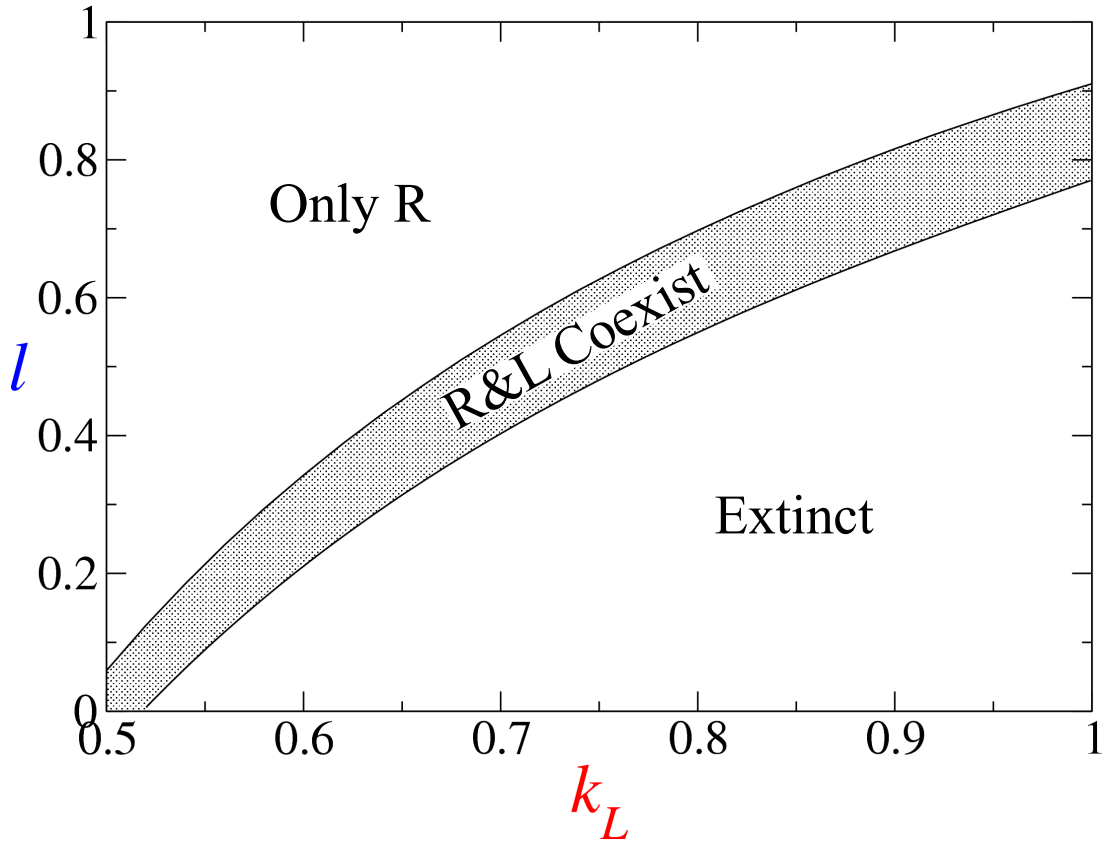
Model with Small Degree of Freedom

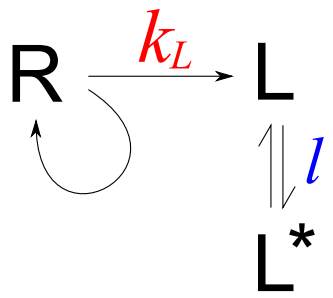
- System has predefined structure
- Only two parameters can evolve



R : replicase
L : parasites in template state
L^*: parasites in folded state

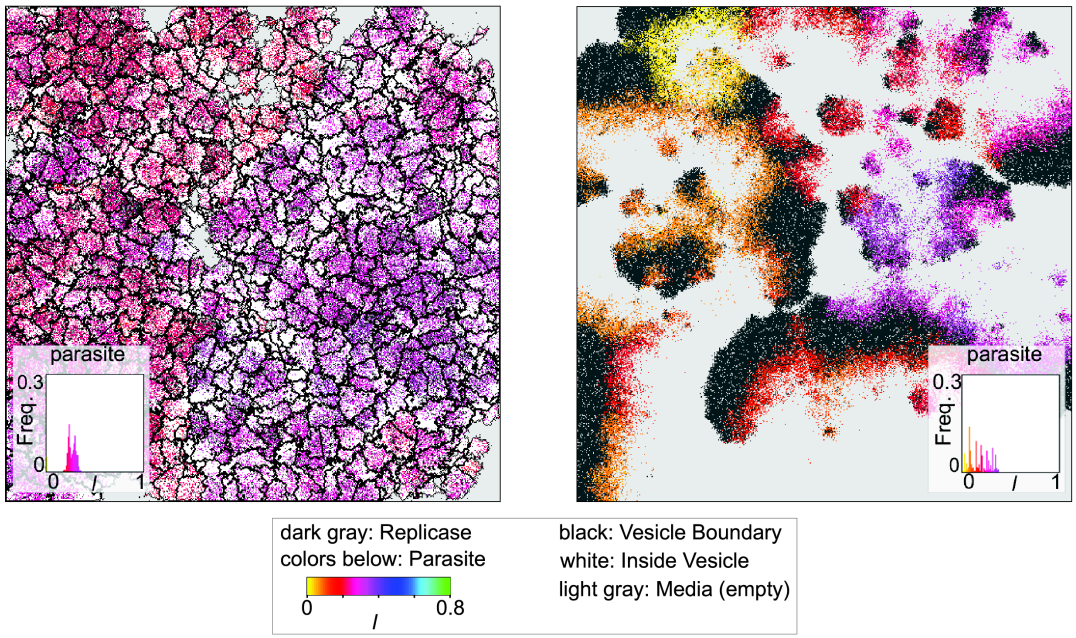
Survival Region in a Well-mixed System



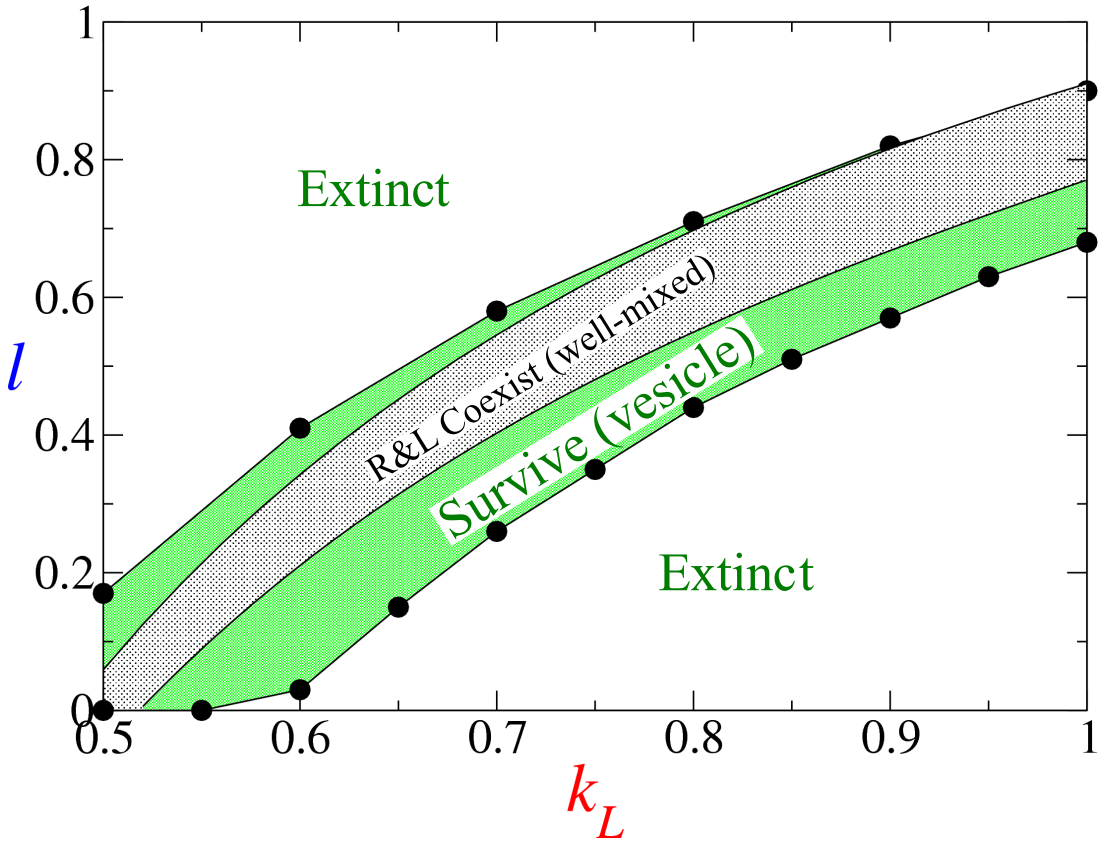


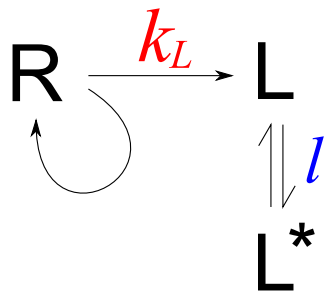
Multilevel Selection

compartmentalization (vs. spatial self-organization)

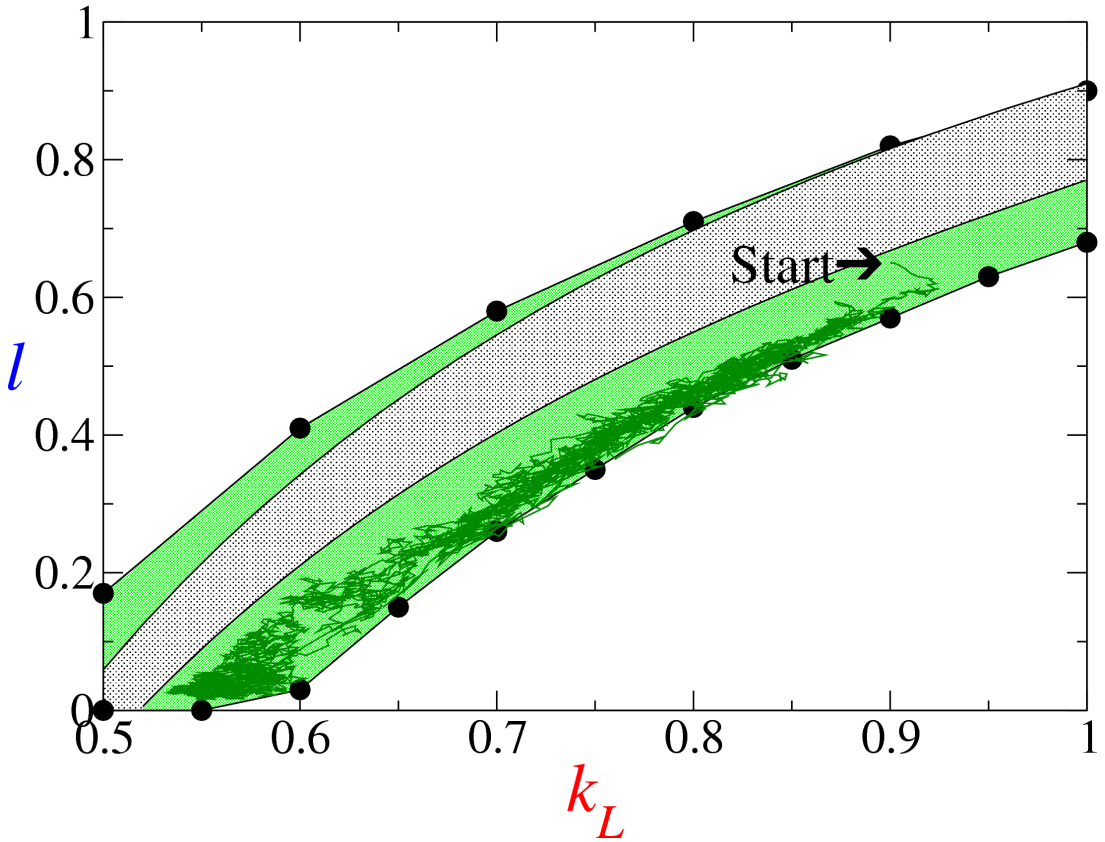


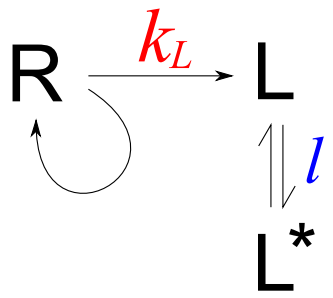
Survival Region with Compartmentalization



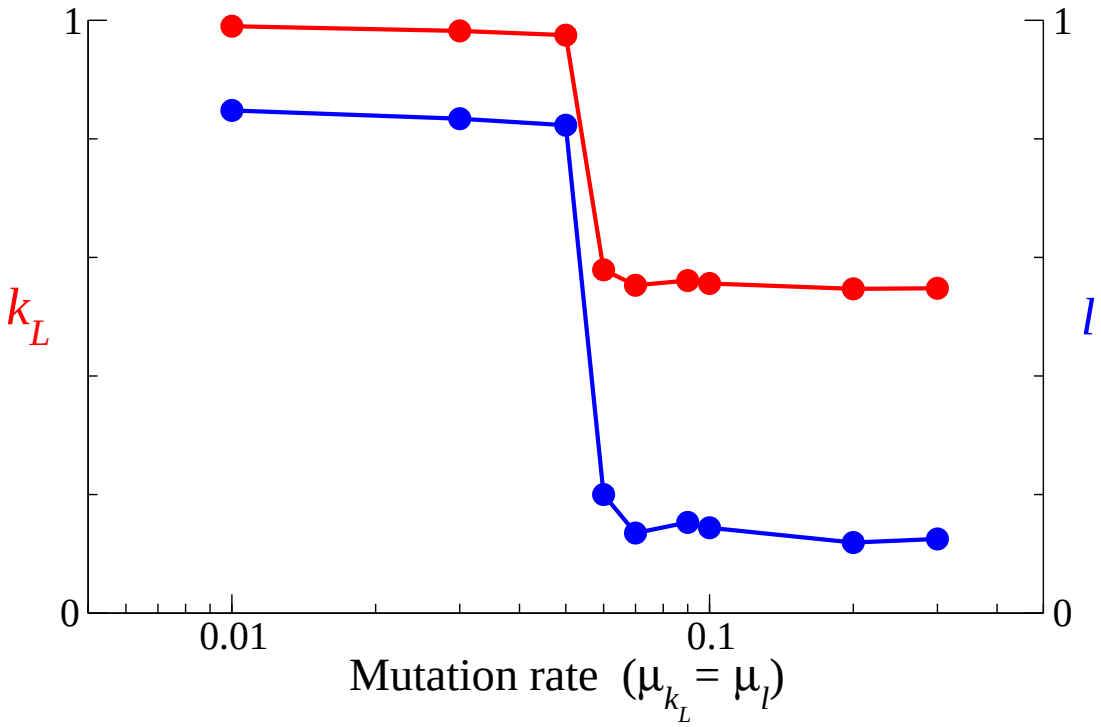


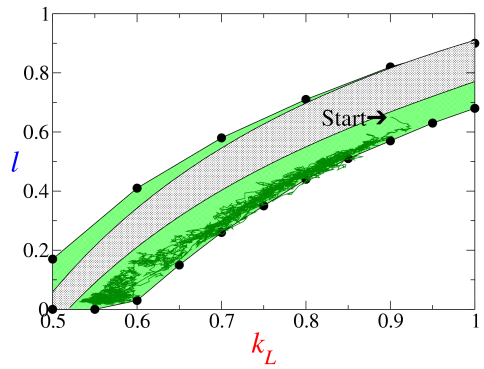
Long-term Evolutionary Trend

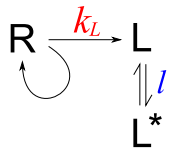


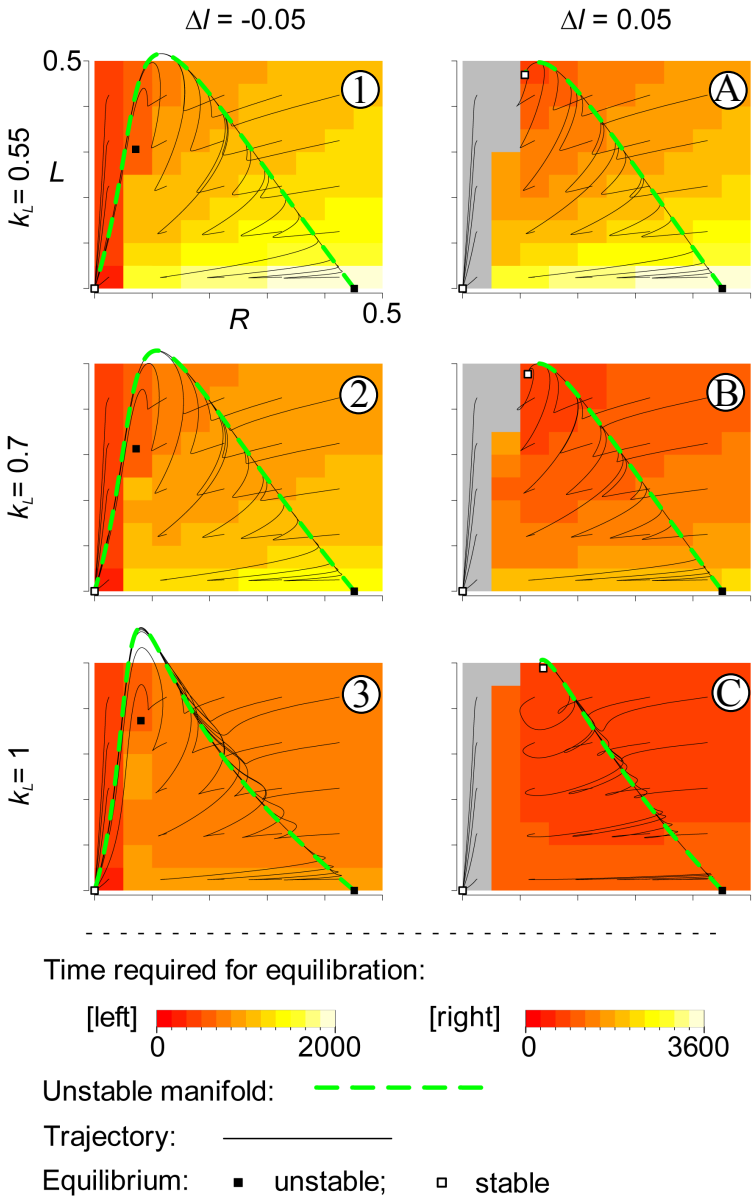


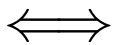
Transition Happens in Evolutionary Trend

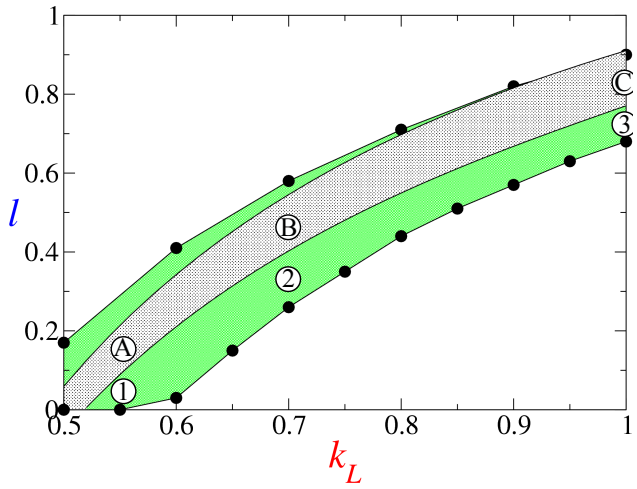


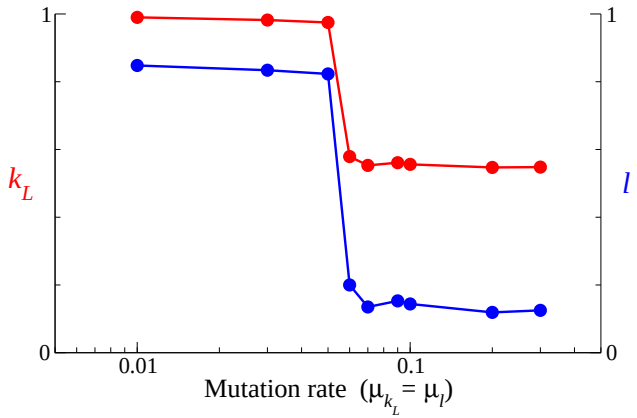





Δl = -0.05
Δl = 0.05
0.5
k_L = 0.55
L
R
0.5
1
A
k_L = 0.7
2
B
k_L = 1
3
C
Time required for equilibration:
[left]
0
2000
[right]
0
3600
Unstable manifold:
Trajectory:
Equilibrium: unstable; stable




1
0.8
0.6
l
0.4
0.2
0
0.5
0.6
0.7
0.8
0.9
1
k_L
A
B
C
1
2
3


1
k_L
0
1
l
0
0.01
0.1
Mutation rate (μ_{k_L} = μ_l)

Simplicity & Complexity of a Simple Model

- Simplicity:
  - Recognition of results is trivial ← only 2 parameters change
- Complexity:
  - Results (i.e. adaptations) are unforeseeable
  - Results are intricate/subtle

Multilevel Evolutionary Models

- Adaptations (i.e. results) are unforeseeable.
- Depending on the degree of freedom available to evolution
  $\longrightarrow$ Evolution generates different kinds of adaptation.

Complex Simplicity vs. Simple Complexity

- Small degree of freedom → Evolution "sensitively" detects possible adaptations (despite strong restriction)
  - → Trivial to recognize
    (predefined structures & a few parameters)
  - → Intricate/Subtle in adaptive effect

- Large degree of freedom → Evolution "inventively" generates best adaptations (also attainability & maintainability)
  - → Non-trivial to recognize
    (lack of search images & predefined observables)
  - → Obviously adaptive in hindsight and, thus, important