On the unit of adaptation in spatially structured host-parasite systems

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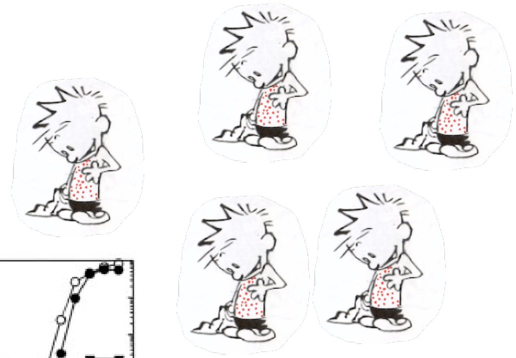
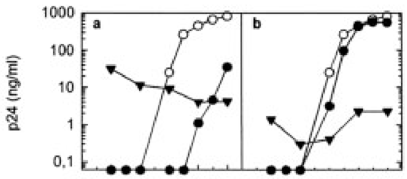
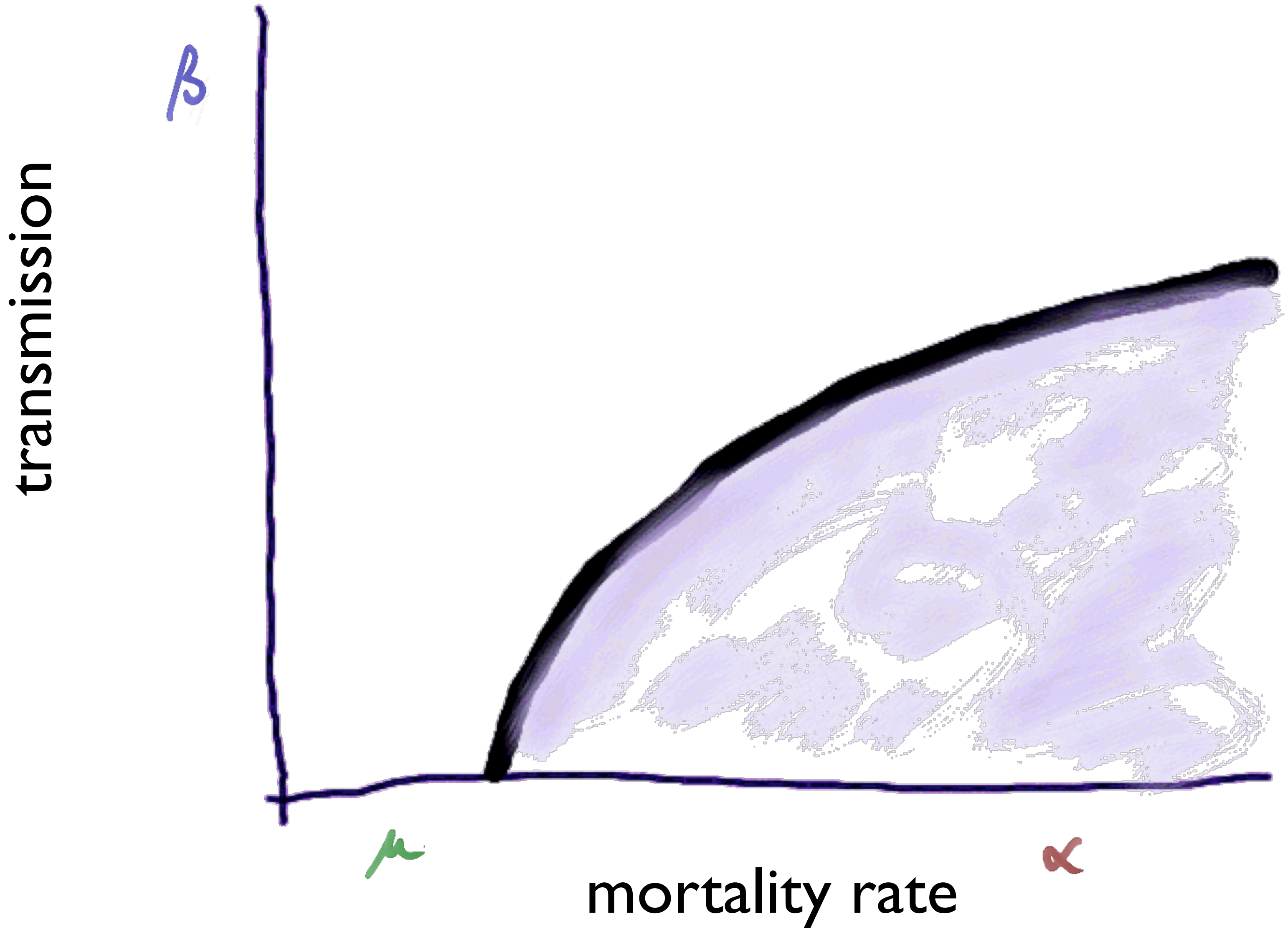
- A genetic strain?
- A quasispecies?
- An infection?
- A cluster of infections?
- A clone?
- An individual?

...ATTGCGAATATCCTCATAAGGCAC...
...ATTGCGAATATCCTCACAAGGCAC...
...ATTGCGAAAATCCTCATAAGGCAC...
...ATTGTGAATATCCTCATAAGGCAC...





What is ‘a’ parasite?



Trade-off


‘Fitness is maximised’

OK, let’s take that for granted.

But by whom or what ?

Evolutionary Theory in a Nutshell

ecosystem

biodiversity, nutrient cycles

population

competition, predation, epidemiology, social interactions

individual

birth, death, development, behaviour

within-individual

physiology, learning, infection, immune response

Levels of organisation

Fitness = Lifetime Reproductive Success

$$R_0$$

Life-history theory, epidemiology, even population genetics…

Evolutionary Theory

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biodiversity, nutrient cycles

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R_0

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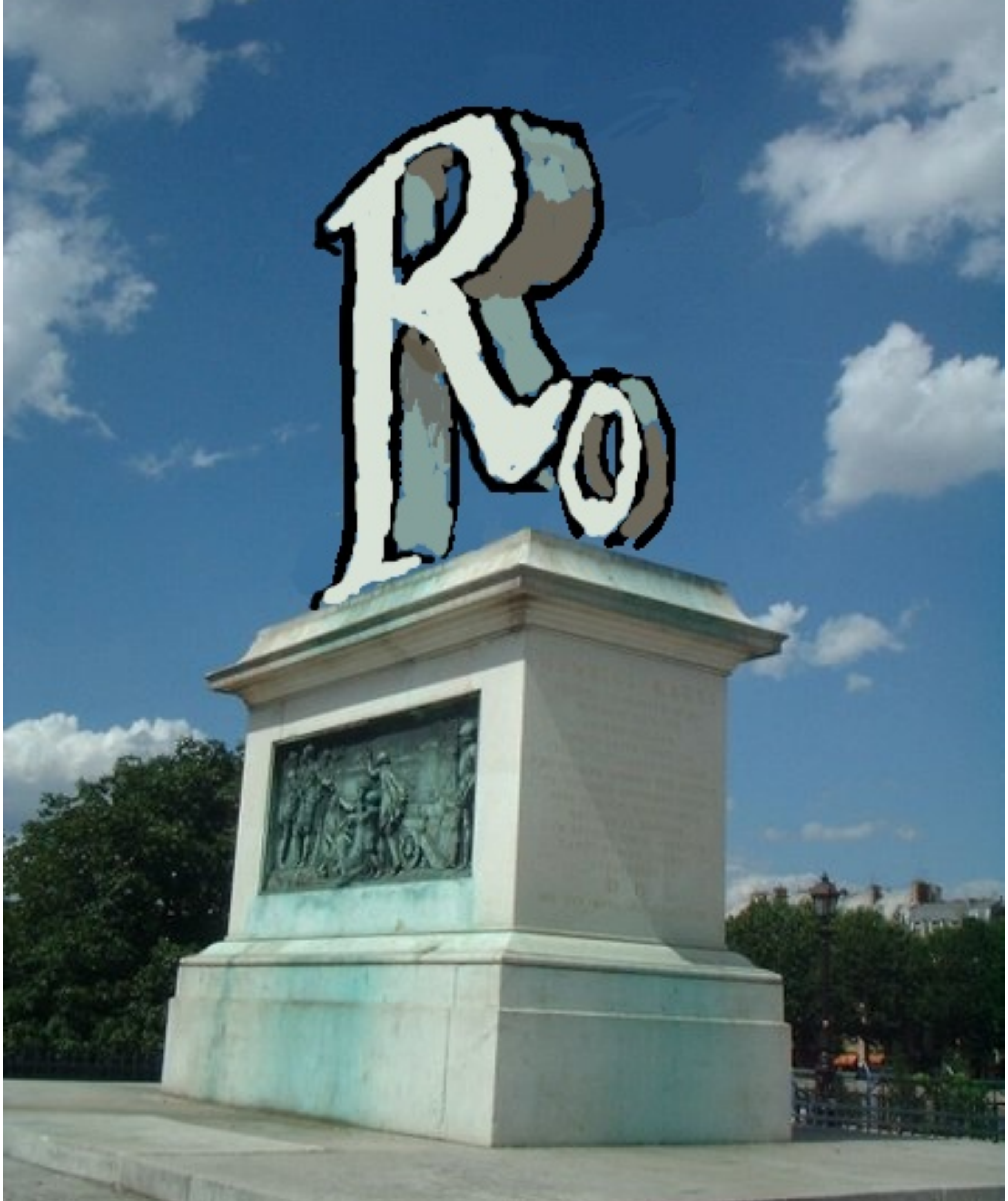
physiology, infection, immune response

Levels of organisation


A JOYFUL EASTER


Ro

An anthill is an individual

(almost)

http://homepage.mac.com/ldr/albums/summer2001/images/rudsmaasan2.jpg

A lichen is an association

http://en.wikipedia.org/wiki/Image:Hyella_caespitosa_hypae.jpg

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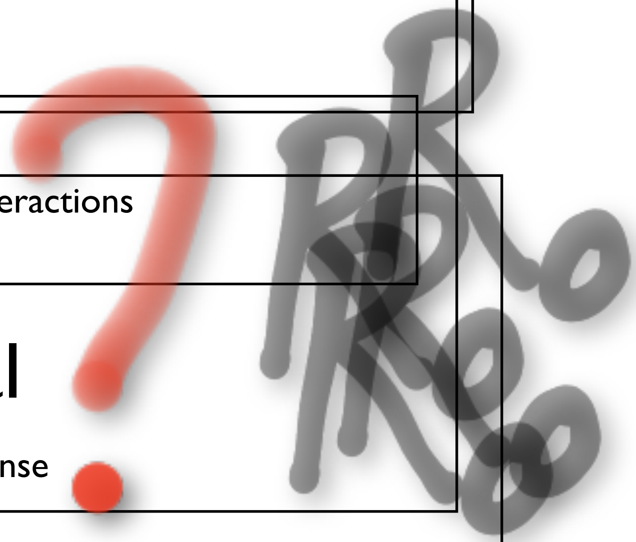
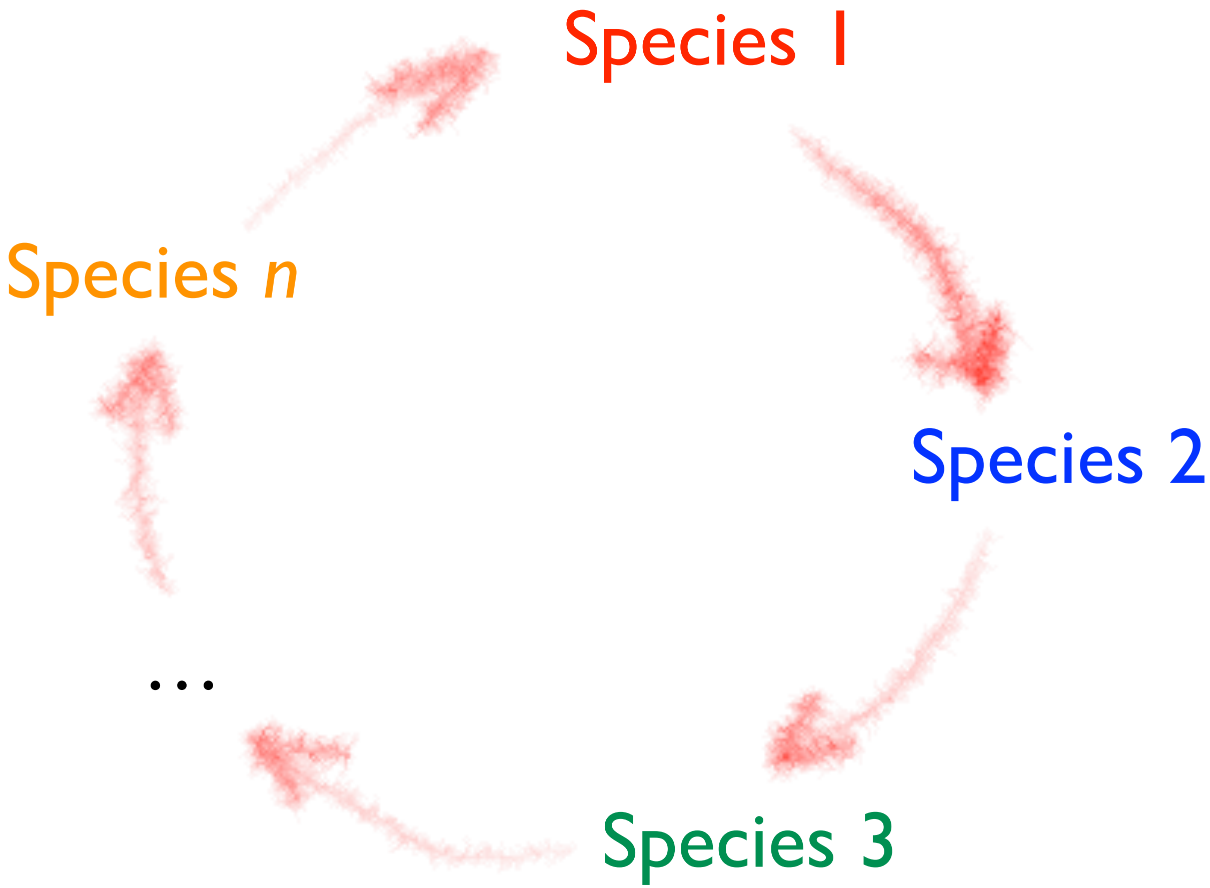


Levels of organisation

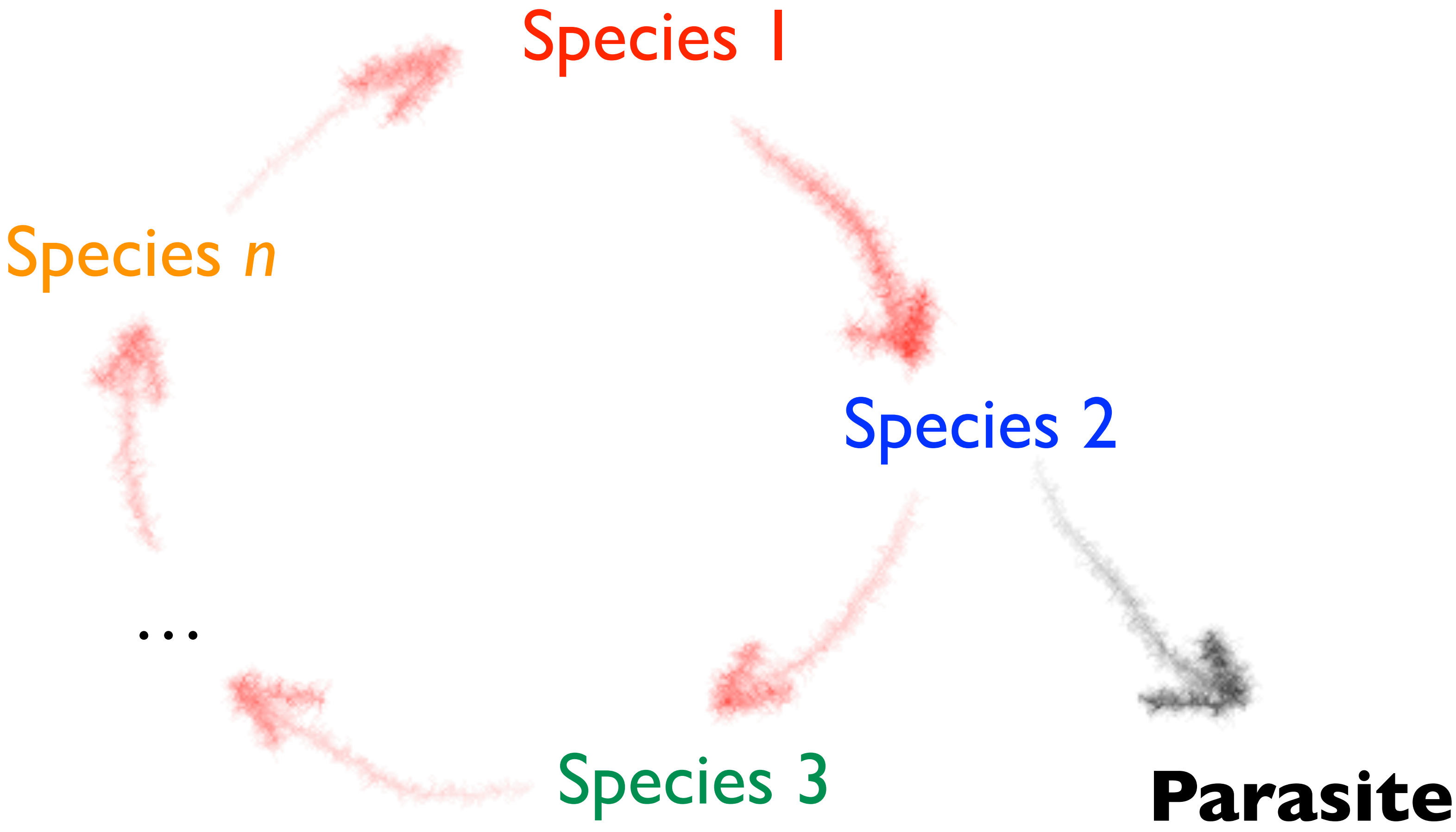
Model for the origin of life

- interactions between simple molecules
- can persist where single species cannot
- susceptible to '**parasites**'

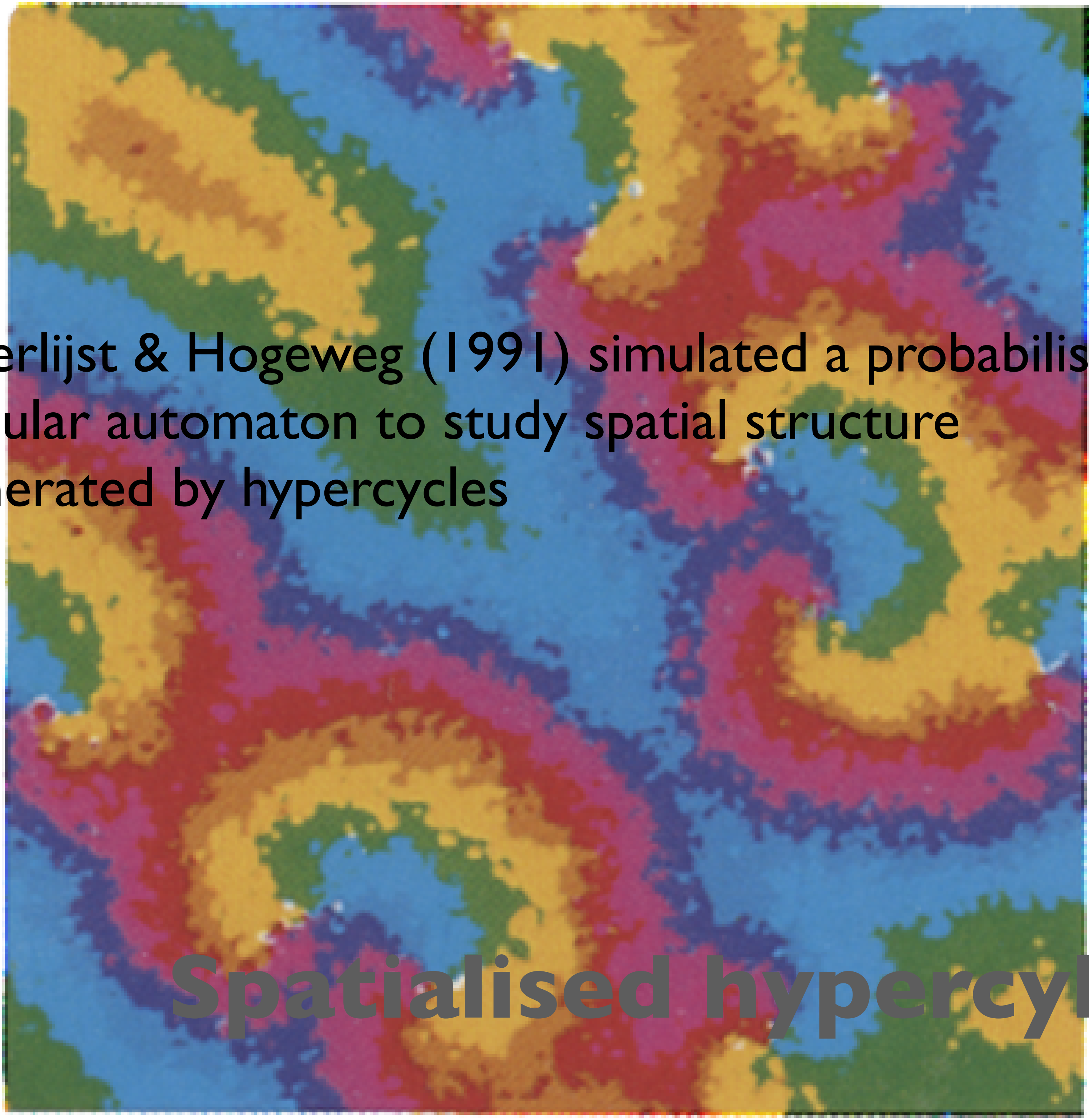
The Hypercycle



Hypercycle



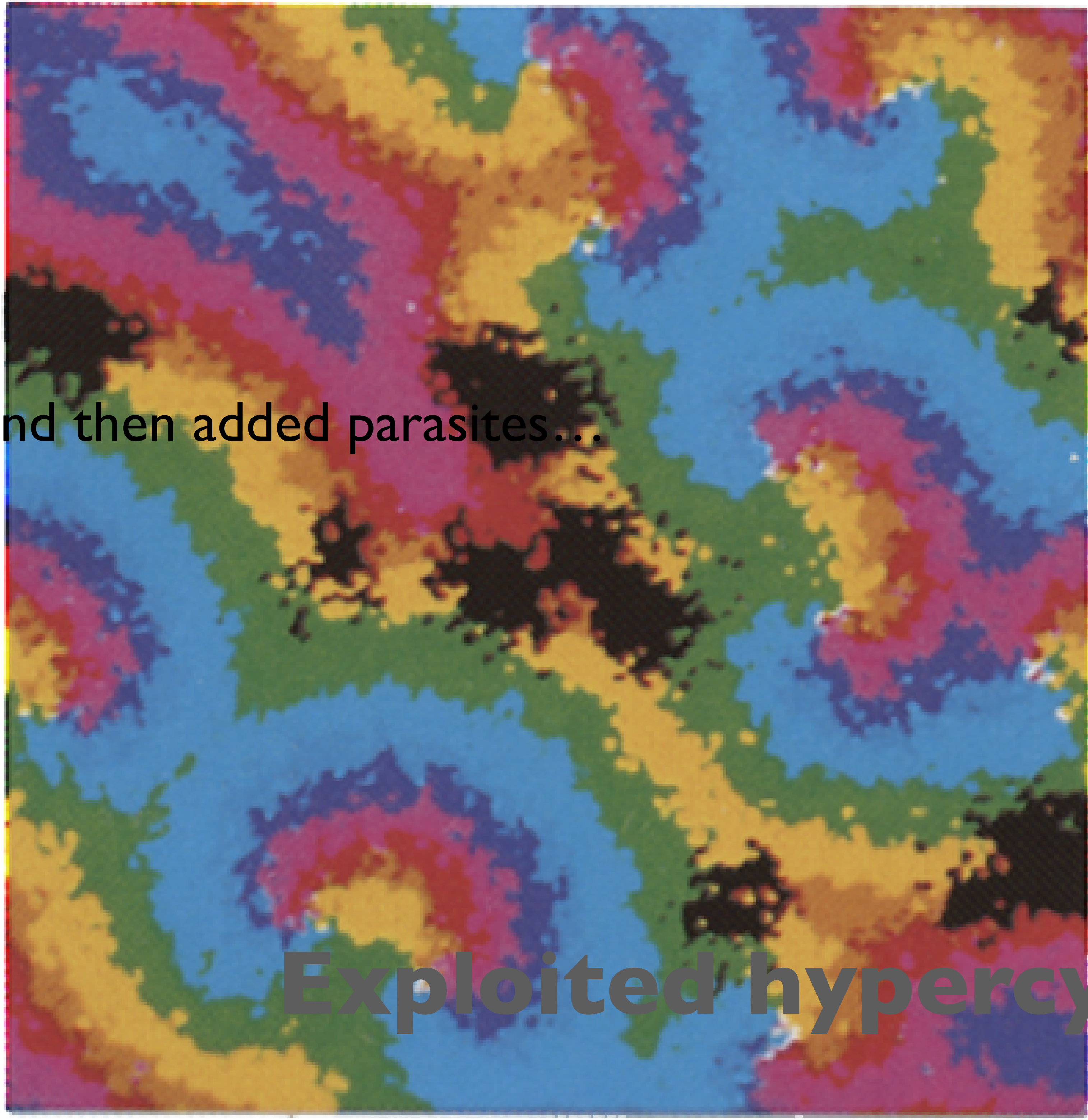
Exploited Hypercycle



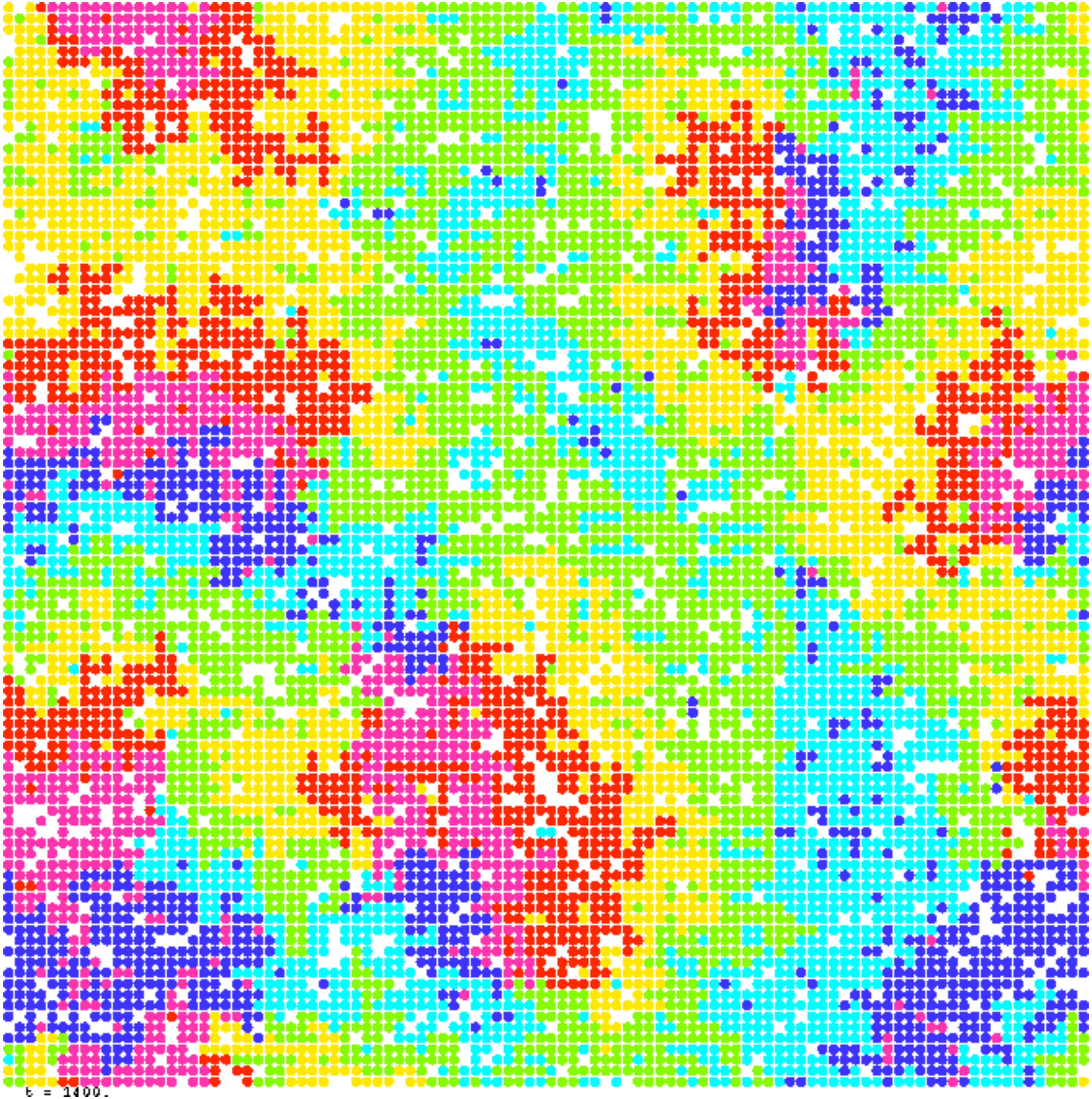
Boerlijst & Hogeweg (1991) simulated a probabilistic cellular automaton to study spatial structure generated by hypercycles

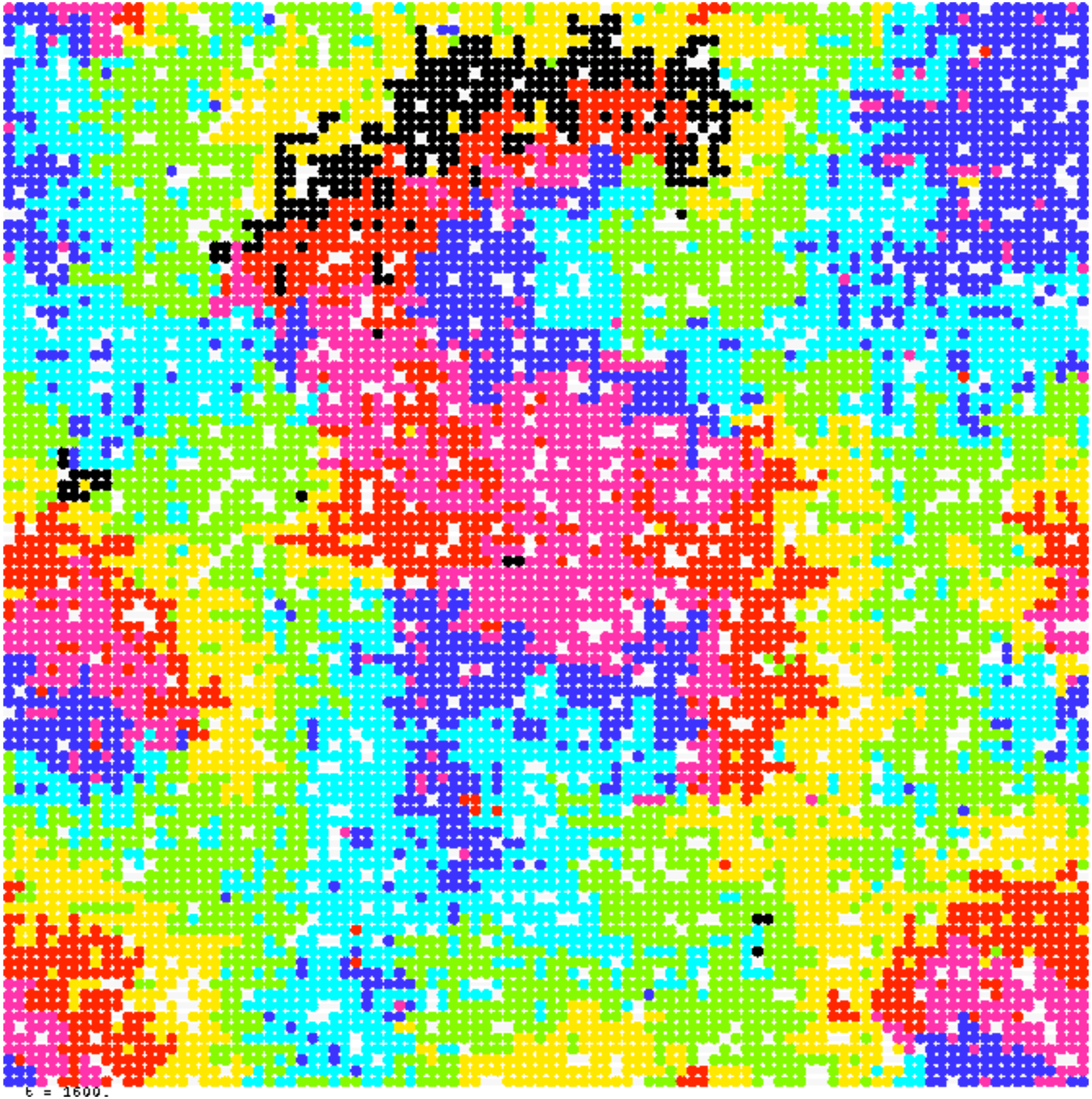
Spatialised hypercyle

and then added parasites…

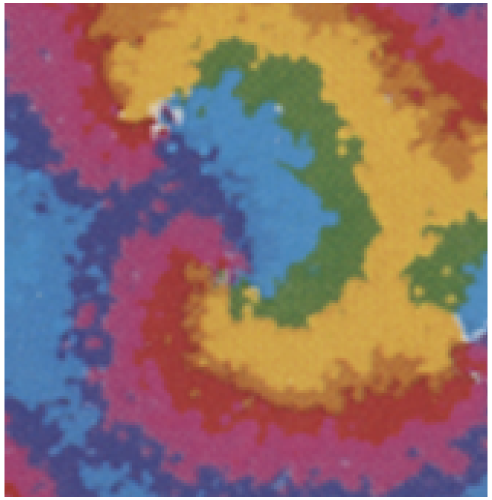


Exploited hypercyle


t = 1400.


t = 1600.

Boerlijst & Hogeweg's (1991) results



- Tend to form rotating spirals
- Parasites swept outward
- Selection on rotation speed
  - favouring higher mortality

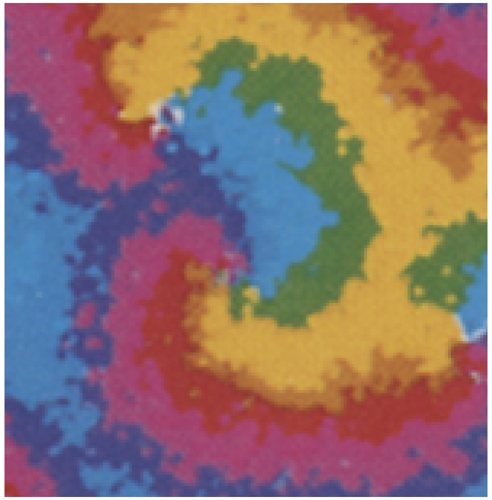
Spatial Hypercycles

Selection at the level of the spiral

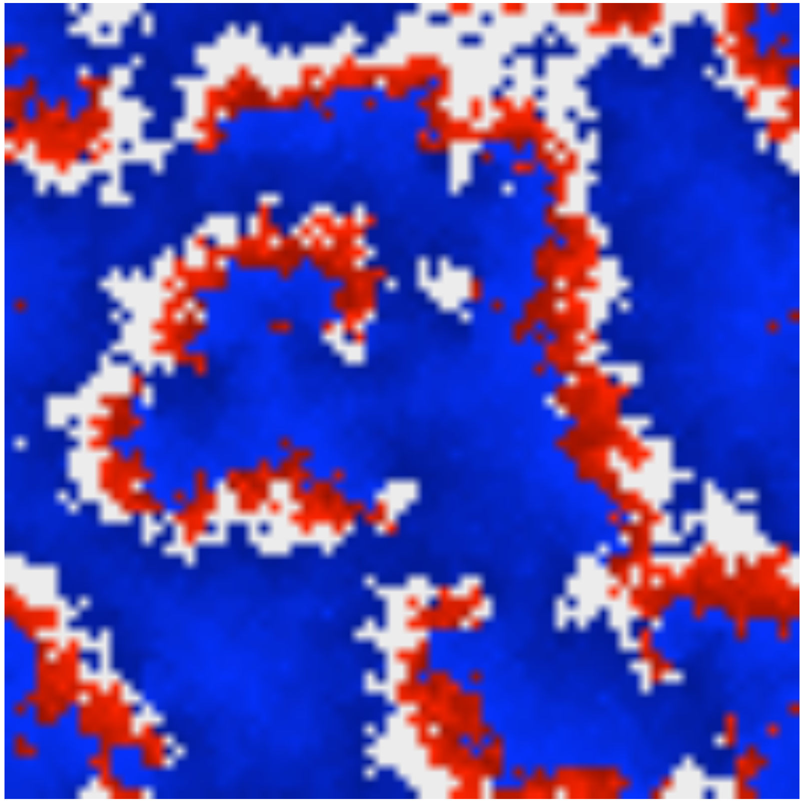
- Rotation speed selected trait

But:

- Rapidly rotating spirals ‘fly apart’
- Evolution towards criticality
  - Rand, Keeling & Howard 1995



Spatial evolution



van Ballegooijen & Boerlijst 2004

Mutants create clusters

Clusters unit of adaptation

- unit of selection is a confusing term

Mathematical characterisation

- Correlation dynamics
  - Matsuda *et al.* (1992), Van Baalen & Rand (1998), Van Baalen (2000), Ferrière & Le Galliard (2001), Lion & van Baalen (2007)

Viscous populations

state of the lattice

$$\mathbb{E}\left[f(\sigma^{t+\delta t})\right] = f(\sigma^t) + \sum_{e\in E^\sigma} \left(r^\sigma(e)\delta t + O(\delta t^2)\right)\left(f(\sigma^t_e) - f(\sigma^t)\right)$$

Morris (1997)

event rate

"$\delta t \to 0$"

$$\frac{df}{dt}(\sigma) = \sum_{e\in E} r^\sigma(e)\delta f_e$$

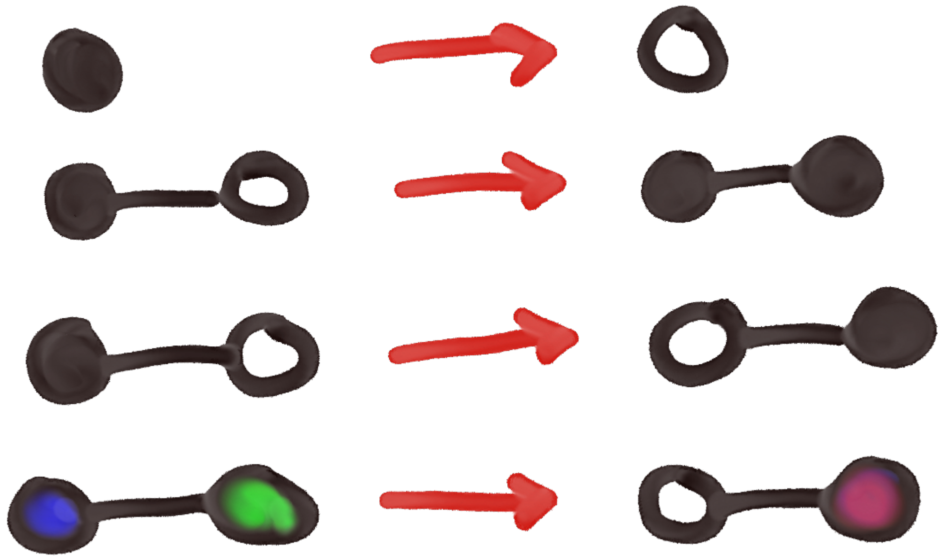
Bookkeeping

death:

birth:

movement:

predation:

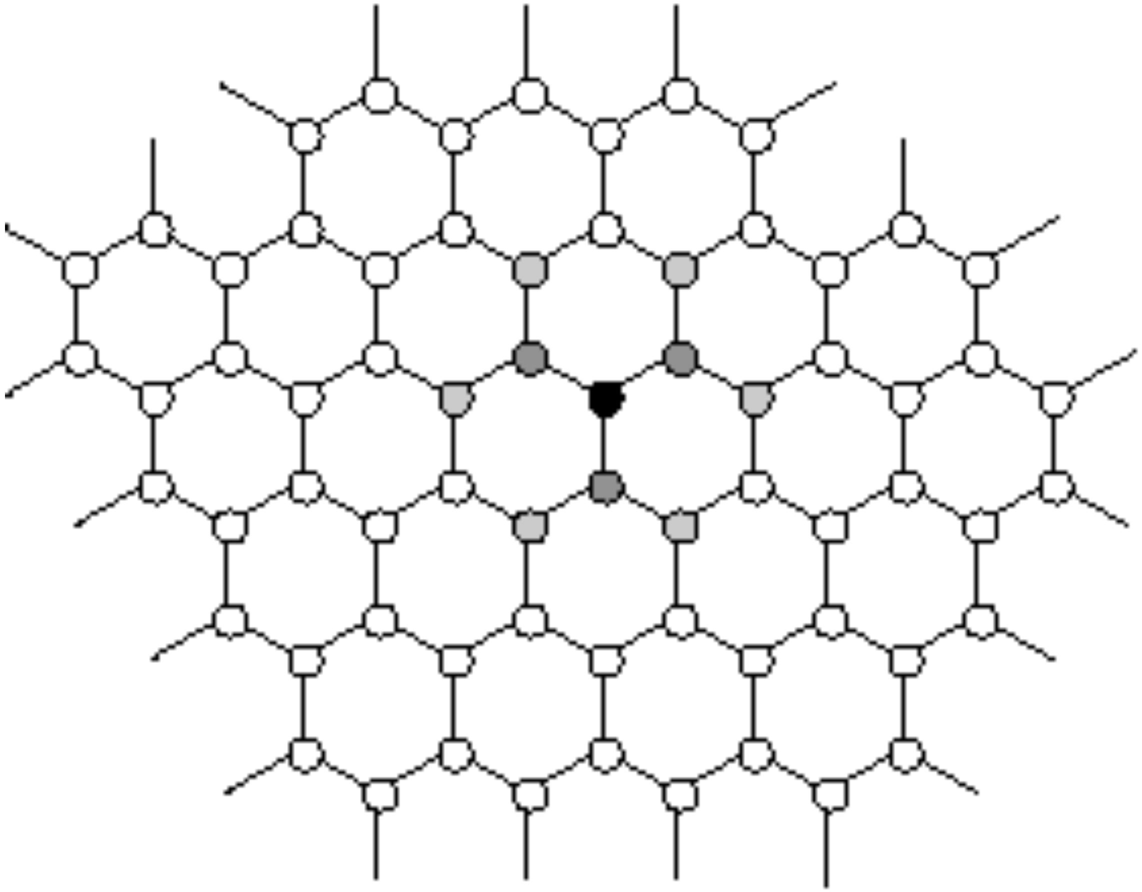


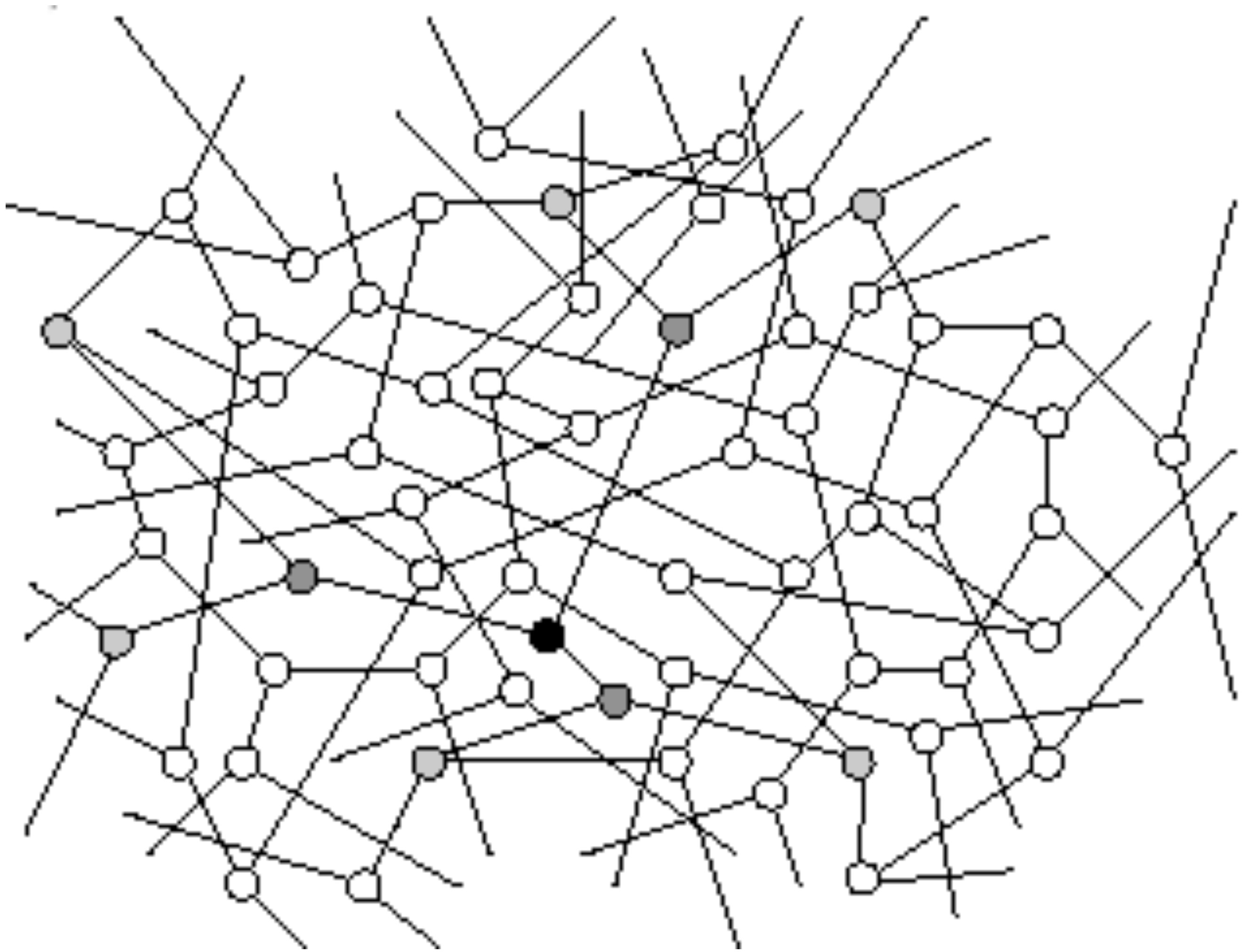
growth, infection, long-range dispersal, cooperation, spite, …

Events

- Empty sites (o), healthy (S) and infected (I) individuals
- Full correlation dynamics model tracks oo, So, SS, Io, II, and SI pairs
- Depends on 'higher moments'
- SI pairs give insight in contact rate
- Not equal to product of S and I !

Contact epidemics





- Empty sites o, altruistic A and selfish S individuals
- Full correlation dynamics model tracks oo, So, SS, Ao, AS, and AA pairs

Altruism

$$\frac{\quad}{\mathrm{d}t} = (b_S + \cdots$$

$$- [\phi b_S + \overline{\phi}(b_S + m_S) q_{S|oS} + \overline{\phi}(b_A + m_A) q_{A|oS} + d_s - \overline{\phi} m_S q_{o|So}] p_{So}$$

$$+ [d_S + \overline{\phi} m_S q_{o|SS}] p_{SS}$$

$$+ [d_A + \overline{\phi} m_A q_{o|AS}] p_{SA}$$

$$\frac{\mathrm{d}p_{SS}}{\mathrm{d}t} = 2[\phi b_S + \overline{\phi}(b_S + m_S) q_{S|oS}] p S_o$$

$$- 2[d_S + m_s \overline{\phi} q_{o|SS}] p_{SS}$$

$$\frac{\mathrm{d}p_{Ao}}{\mathrm{d}t} = (\mathrm{b_A} + \mathrm{m_A}) \overline{\phi} \mathrm{q_{A|oo} p_{oo}} \qquad (A.1)$$

$$- [\phi b_A + \overline{\phi}(b_A + m_A) q_{A|oA} + \overline{\phi}(b_S + m_S) q_{S|oA} + d_A + \overline{\phi} m_A q_{o|Ao}] p_{Ao}$$

$$+ [d_A + \overline{\phi} m_A q_{o|AA}] p_{AA}$$

Van Baalen & Rand (1998)

$$+ [d_S + \overline{\phi} m_S q_{o|SA}] p_{SA}$$

- Empty sites o, altruistic A and selfish S individuals

- Full correlation dynamics model tracks oo, So, SS, Ao, AS, and AA pairs

- Resident system: (oo, So, SS)

- Mutant invader: (Ao, AS, AA)

$$\mathbf{p}_A = \begin{pmatrix} p_{Ao} \\ p_{AS} \\ p_{AA} \end{pmatrix}$$

Adaptive Dynamics

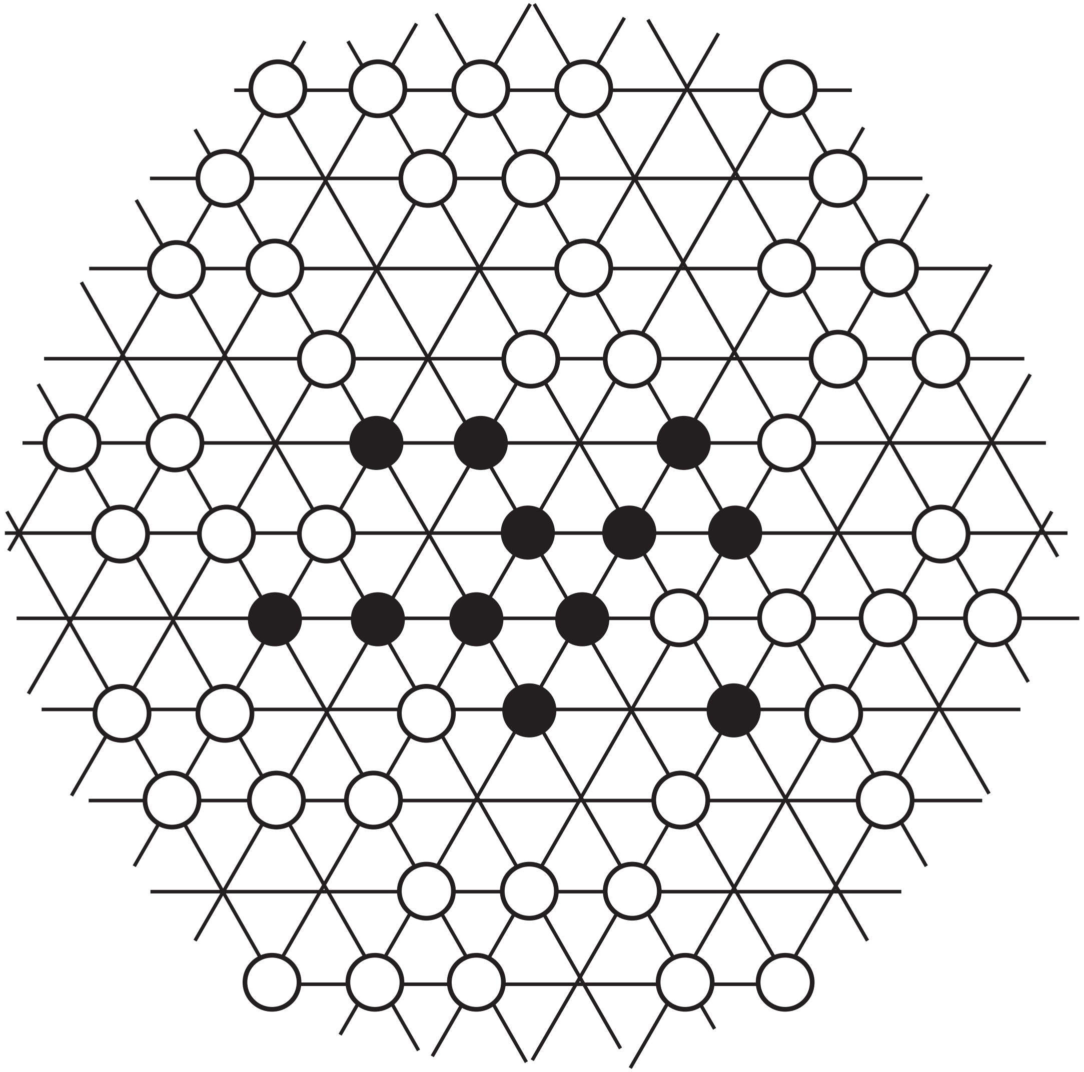
$$\mathbf{p}_A = \begin{pmatrix} p_{Ao} \\ p_{AS} \\ p_{AA} \end{pmatrix}$$

$$\frac{\mathrm{d}\mathbf{p}_A}{\mathrm{d}t} = \mathbf{M}(\mathbf{q}_A)\mathbf{p}_A$$

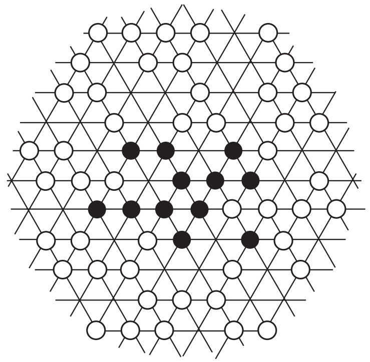
Dynamics of mutant given by sets of equations

- Matrix formalism
- Fitness: dominant Lyapunov exponent
- Unit of selection: corresponding eigenvector

Invasion of altruist mutant



Characteristic cluster



Traits of the cluster determine invasion success

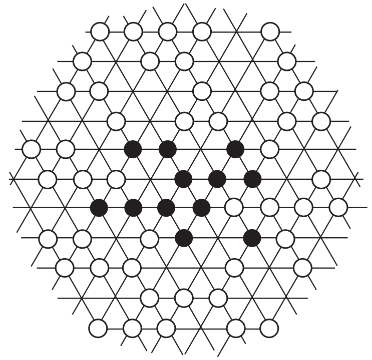
Close link with Hamilton's inclusive fitness

Invasion condition $$\frac{\partial B}{\partial y} q_{M/M} > -\frac{\partial(b_M q_{o/M})}{\partial y}$$

$$Br > C$$

Coefficient of relatedness *r* ecological variable

Viscous populations



Cluster functions as unit of adaptation

Individuals balance selfish interests with common good

Viscous populations

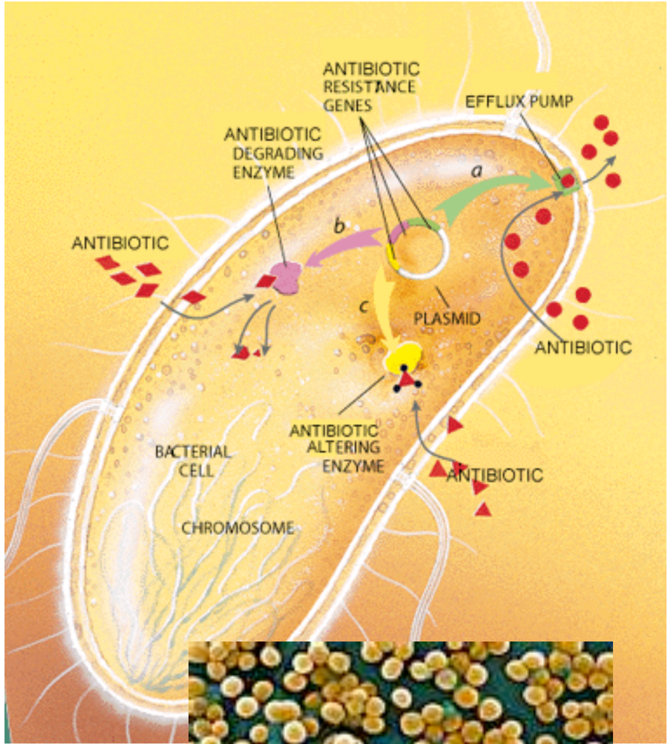
Individuals but associations of more-or-less independent smaller entities

- genes — chromosomes
- haploid — diploid
- organelles — cells
- cells — multicellular organisms
- individuals — symbioses
- populations — 'superindividuals'

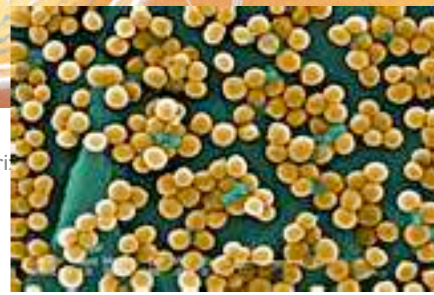
Individuals are not really

A plasmid is

- a parasite in absence of antibiotics
- a mutualist in its presence



http://microvet.ari ... cRes/



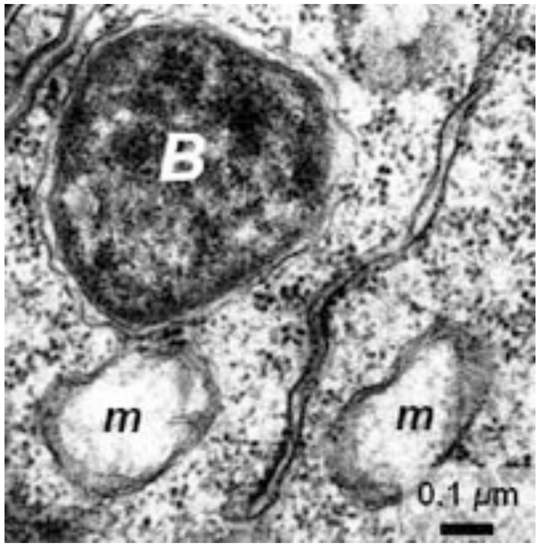
MRSA

Grey Area

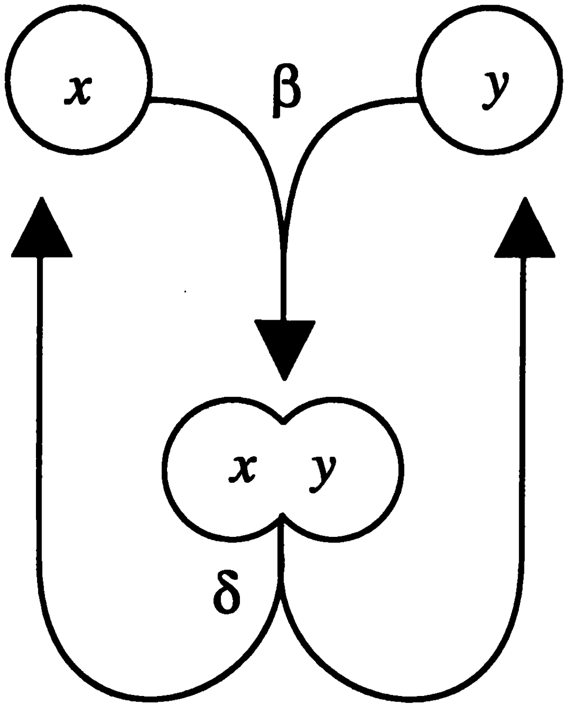
Parasites that

1. cause mild negative effects
2. protect against other risks

Exx:
Plasmids that code for resistance
'Probiotic' intestinal flora
Cowpox that vaccinates against smallpox
Wolbachia protects against RNA virus

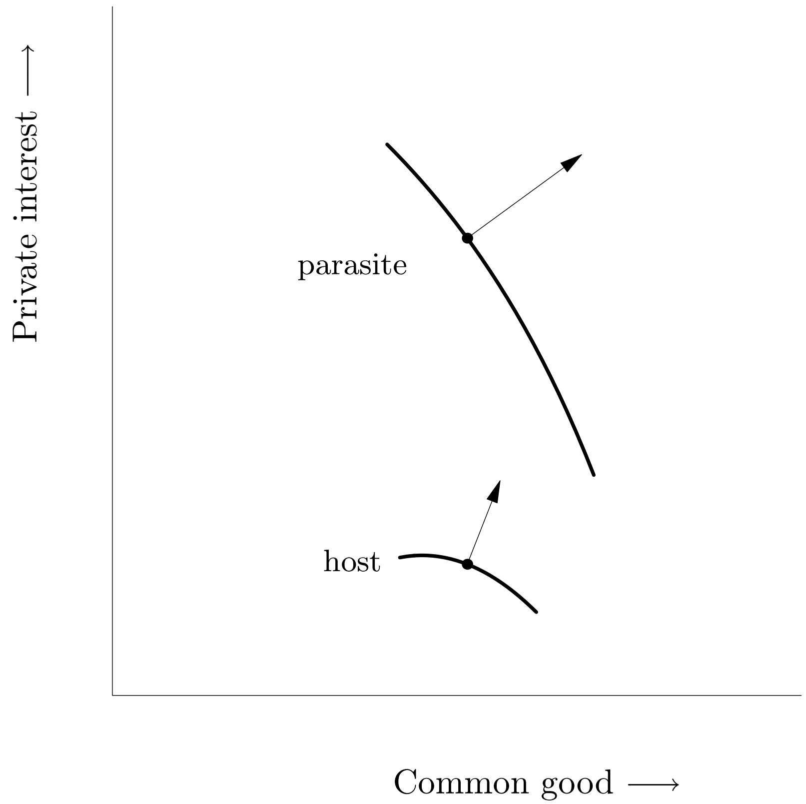


Grey Area



Kostitzin, V. A. (1934). *Symbiose, Parasitisme et Évolution (Étude Mathématique)*. Hermann et Cie, Paris.

'Dangerous liaisons'



Private interest vs Common good

Whenever two individuals interact they will have aligned interests

- favouring (limited) cooperation
- survival, competitiveness
  - e.g. plant-rhizosphere
- not individual reproduction
  - a host should not help its parasites to spread

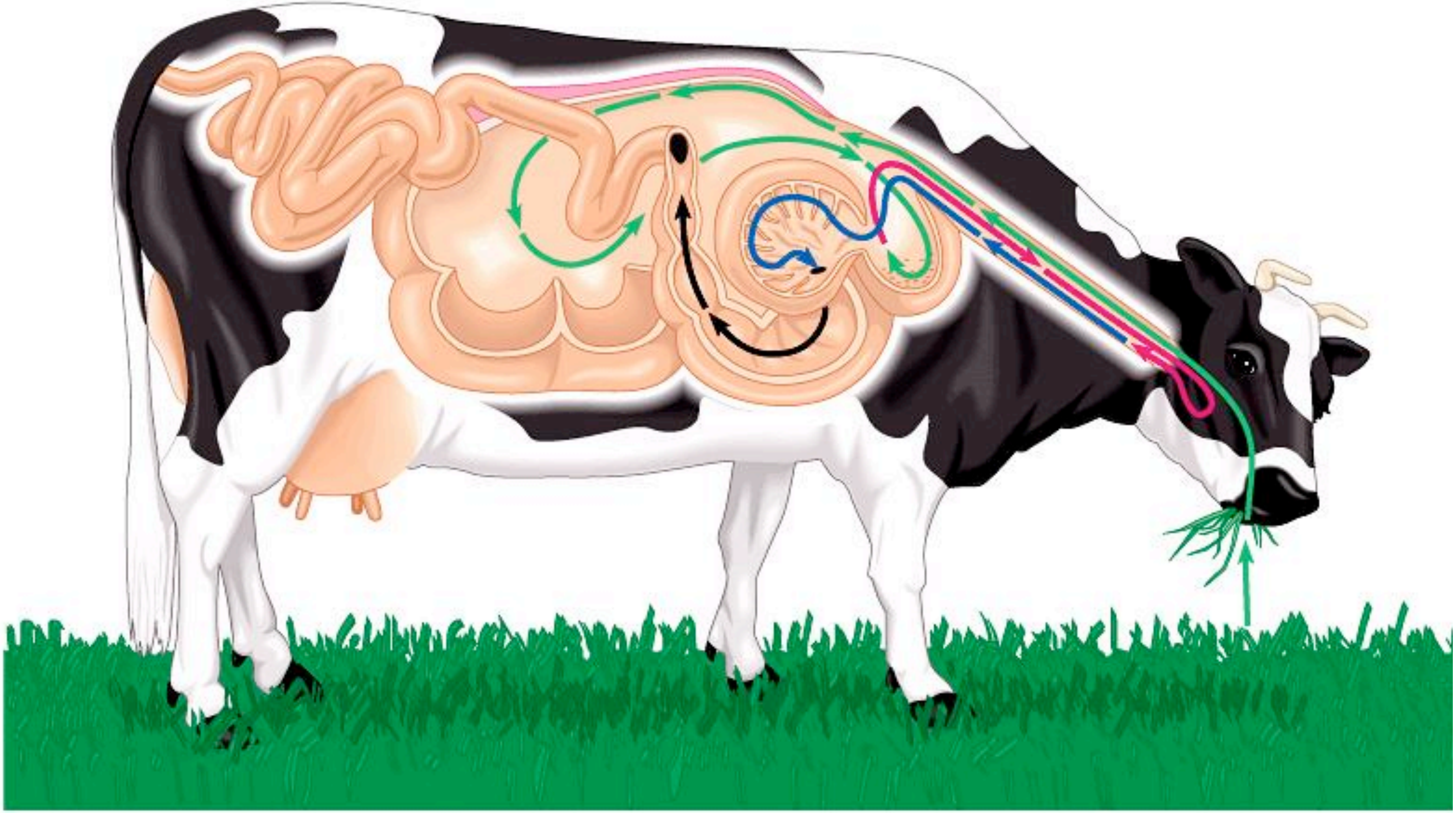
If there is relatedness, it helps!

Dangerous Liaisons

Better mathematical definition of

- Individual as unit of adaptation
  - "who benefits"
- Common good (relative to selfish interest)
- Ecological conditions that affect balance

Challenge



Unit of selection

- any structure that has differential dynamics

ecosystem

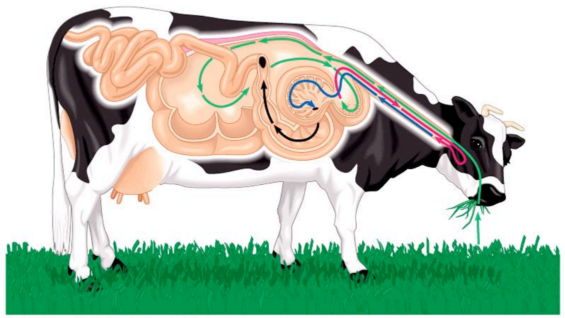
population

individual

within-individual

Unit of adaptation

- that what benefits from an adaptation



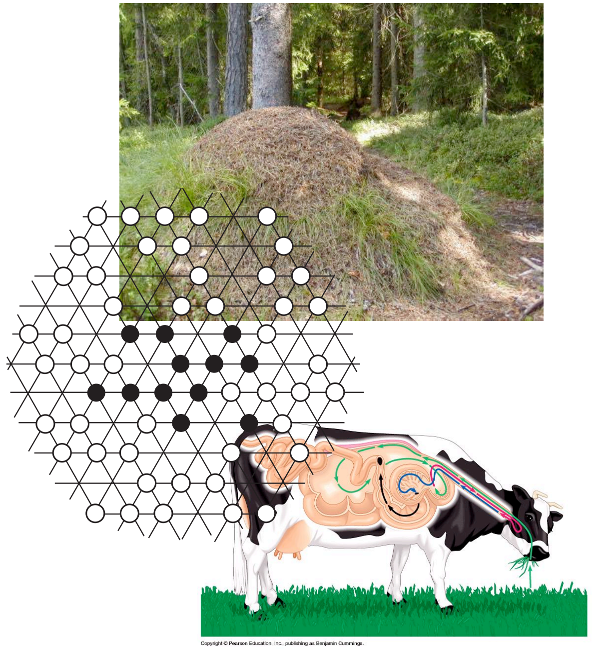
Definitions...

Who benefit from adaptation:

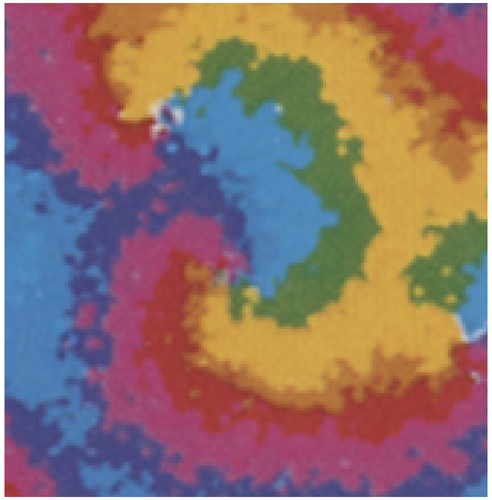
- sometimes individuals
- often clearly associations

Whatever the case unit of adaptation:

- cooperative association
- balance of selfish interest and common good



Unit of adaptation



Counterintuitive outcomes

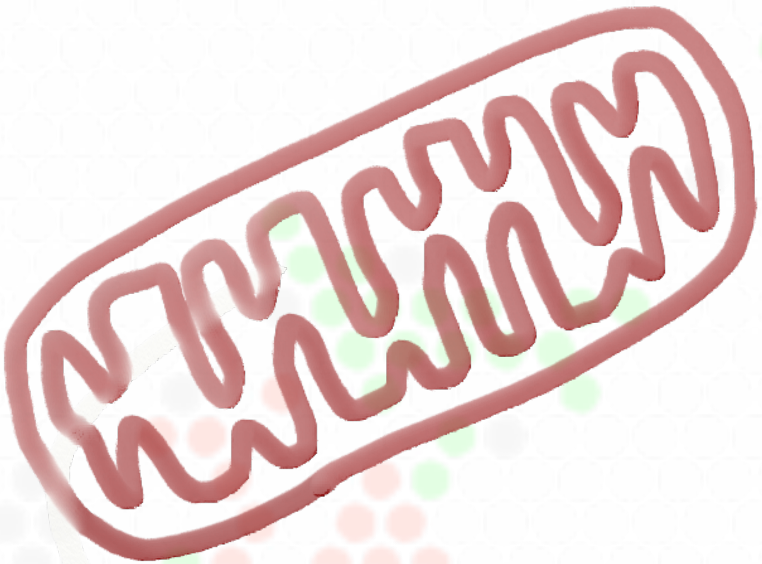
- Tend to form rotating spirals
- Selection on rotation speed
  - favouring higher mortality
- Infective disease could help the spiral to compete

Spatial Hypercycles

- How to deal with dynamic associations?
- Disentangling common good/private benefit

Questions & challenges

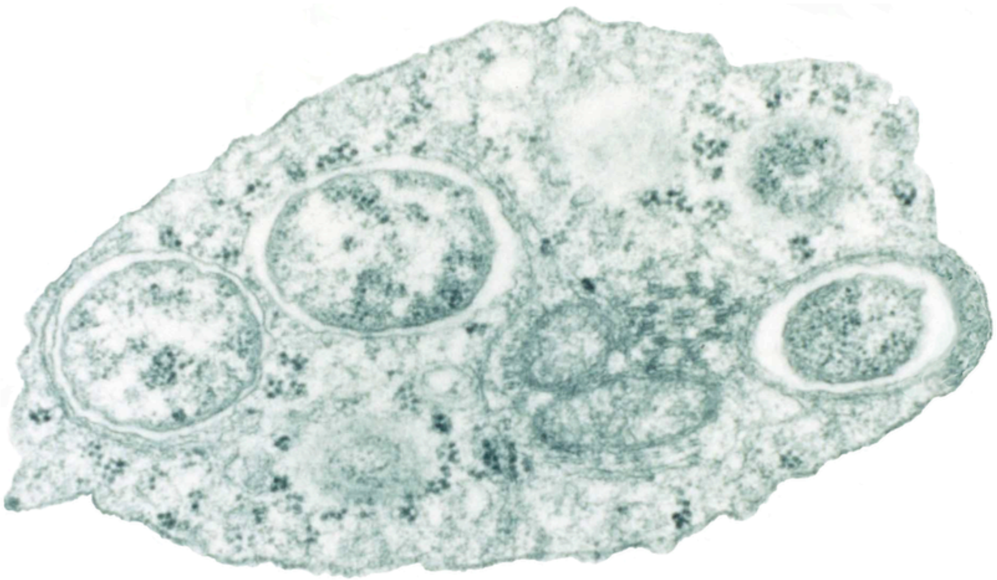
- How to deal with dynamic associations?
- Disentangling common good/private benefit
- What would favour increased integration?
- What governs eventual evolutionary transitions?



Questions & challenges

Many mutualistic symbioses presumably evolved from parasitic interactions

- What governs the transition between parasitism and mutualism?



Evolution

On every level there is potential for conflict between private interest and common good :

- genes — selfish DNA
- chromosomes — meiotic drive
- organelles — 'mitochondrial wars'
- cells — cancer
- symbionts — disease
- mutualists — cheaters
- local populations — nepotism

Conflict

ecosystem

population

individual

within-individual