The evolution of dangerous liaisons

or

the ecology of common good and selfish interest

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ANAL

The evolution of eusociality

Martin A. Nowak[1], Corina E. Tarnita[1] & Edward O. Wilson[2]

Eusociality, in which some individuals reduce thei… the offspr… underlies the most advanced f… of social ins… For the past f… een the ma… attempt to ex… We argue… natural selecti… pler and s… allows the eva… terpretin… observations.

F or most o… theory has… where adult… tially) non-… young. How can ge… natural selection, w…

Rise and fall of inclusive fitness theory

For the past four decades, kin selection theory has had a profound effect on the interpretation of the genetic evolution of eusociality and, by extension, of social behaviour in general. The defining feature of kin selection theory is the concept of inclusive fitness. When evaluating an action, inclusive fitness is defined as the sum of the effect of this action on the actor's own fitness and on the fitness of the recipient multiplied by the relatedness between actor and recipient, where 'recipient' refers to anyone whose fitness is modified by the action.

The idea was first stated by J. B. S. Haldane in 1955, and a foundation of a full theory[3] was laid out by W. D. Hamilton in 1964. The pivotal … ressed by both writers was formalized by Hamilton as the … that cooperation is favoured by natural …

su… … The… eu… ha… di… dw… be… ca… by… …ruist (R = … fat… ac…natory … a d…e of so… …ract fo… eu…ested by Ham…


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‘Fitness is maximised’

OK.

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

R_0 vs λ ?

What matters is invasion capacity!

Life-history theory, epidemiology, even population genetics…

Evolutionary Theory

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R_0

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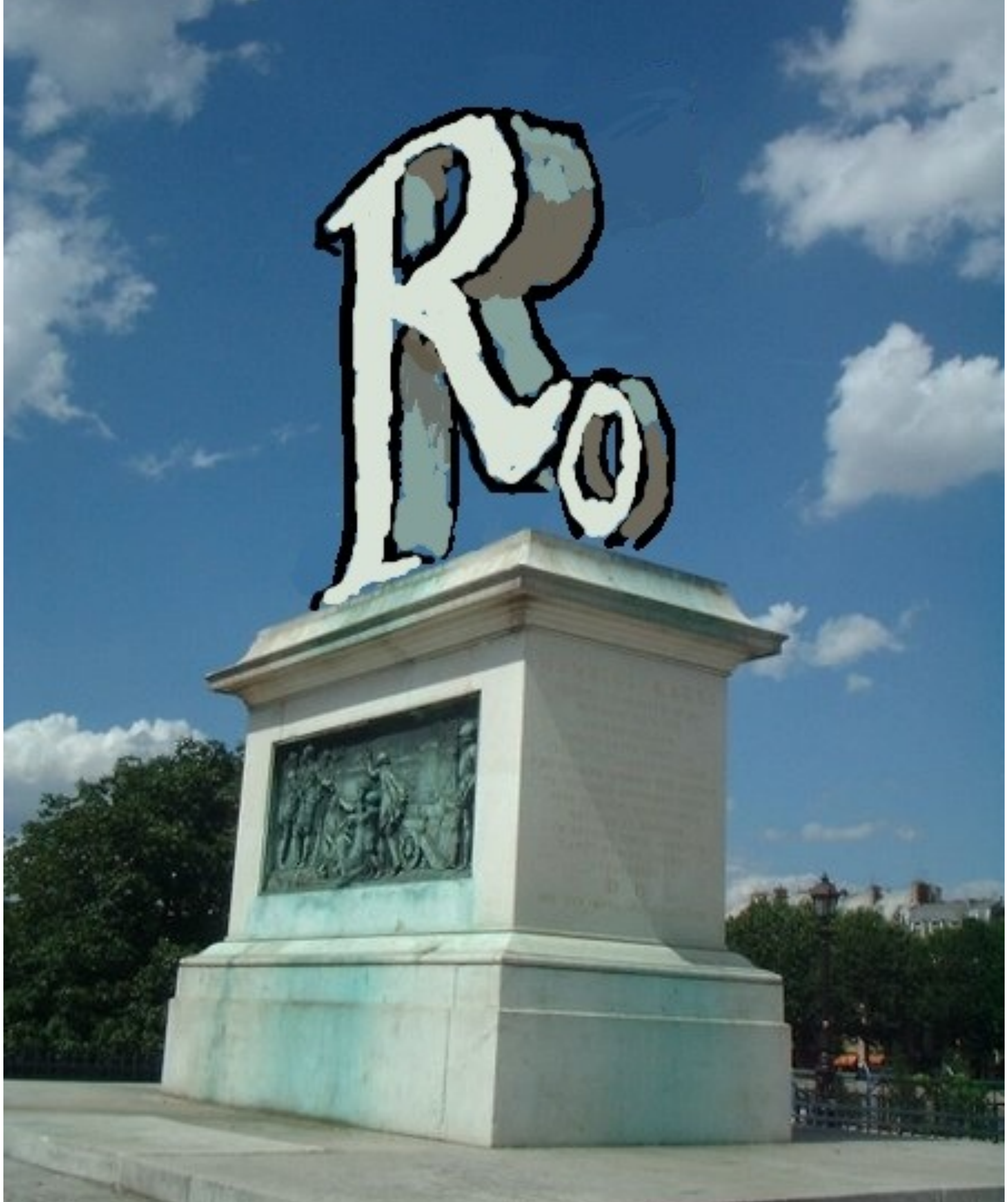
Levels of organisation


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 ecosystem

biodiversity, nutrient cycles

population

individual

competition, predation, epidemiology, social interactions

birth, death, development, behaviour

within-individual

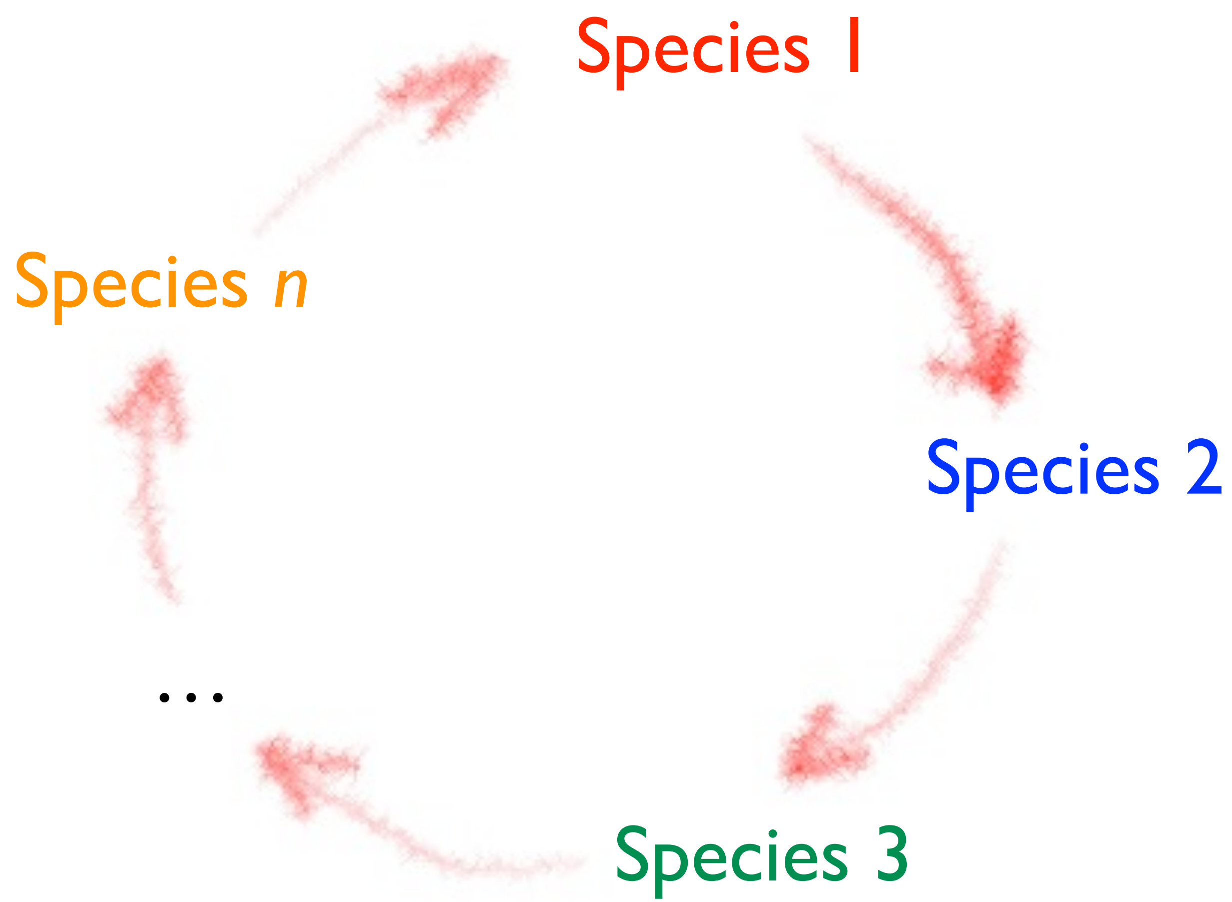
physiology, infection, immune response

Levels of organisation

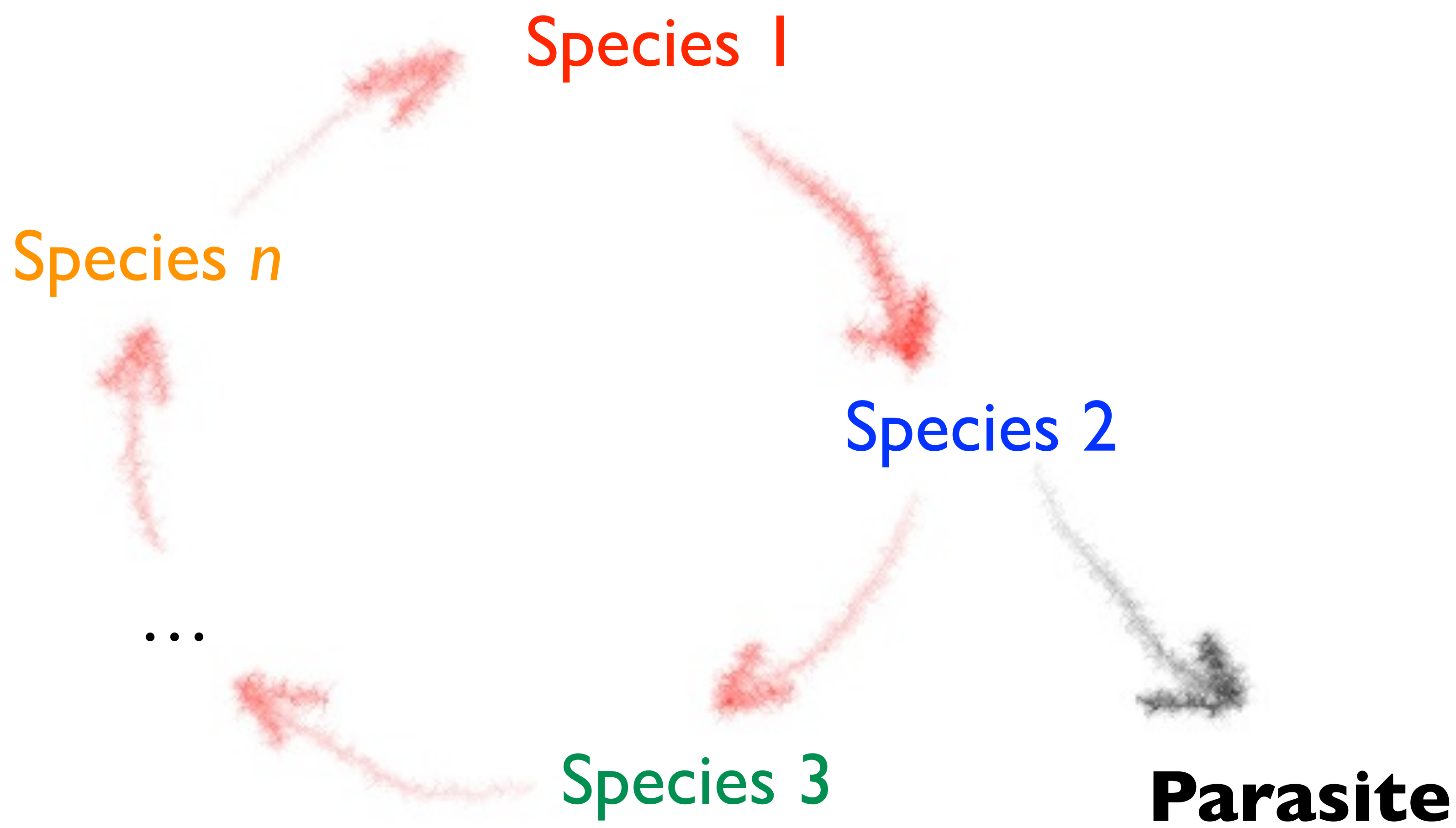
Model for the origin of life

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

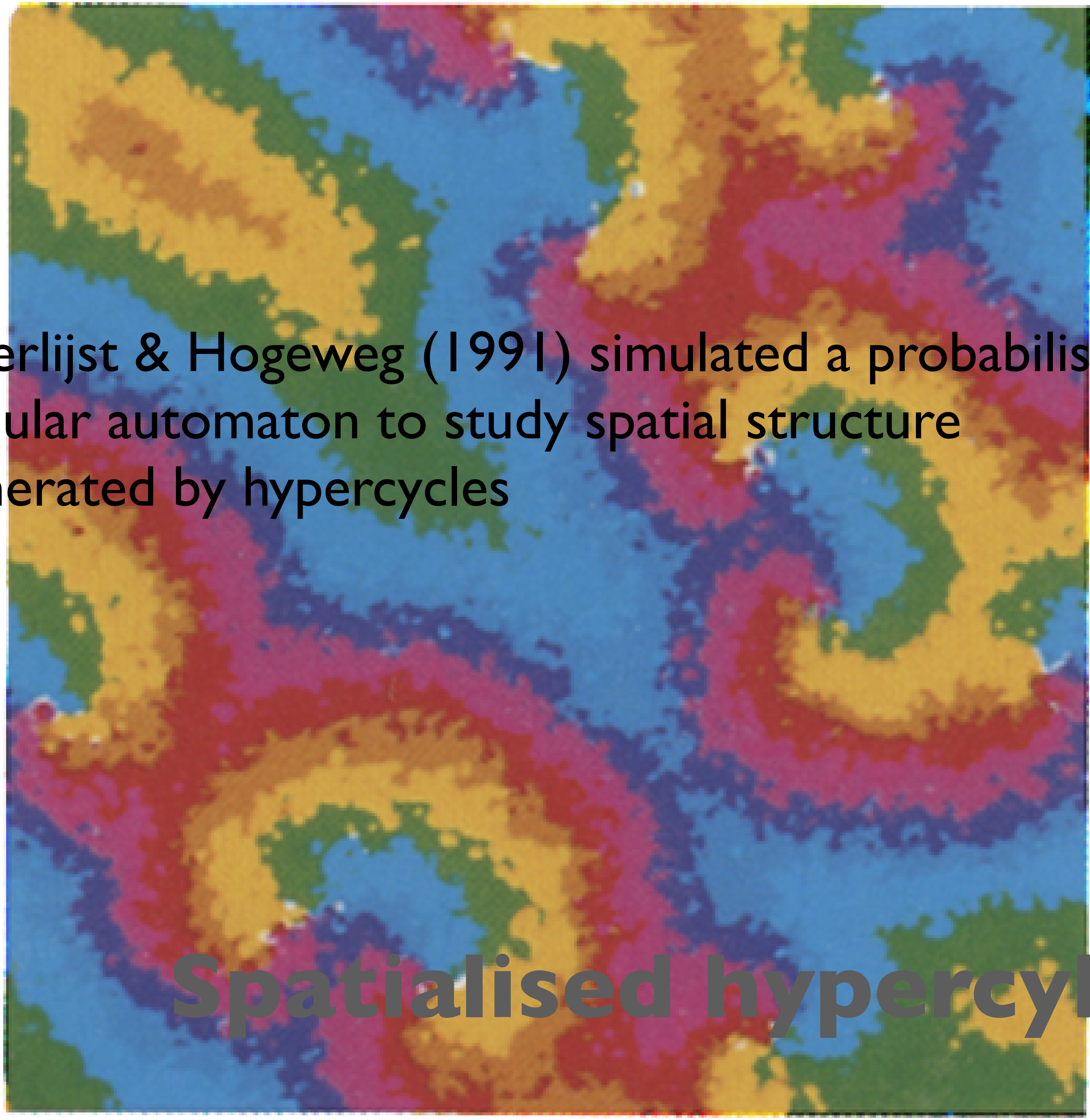
The Hypercycle



Hypercycle

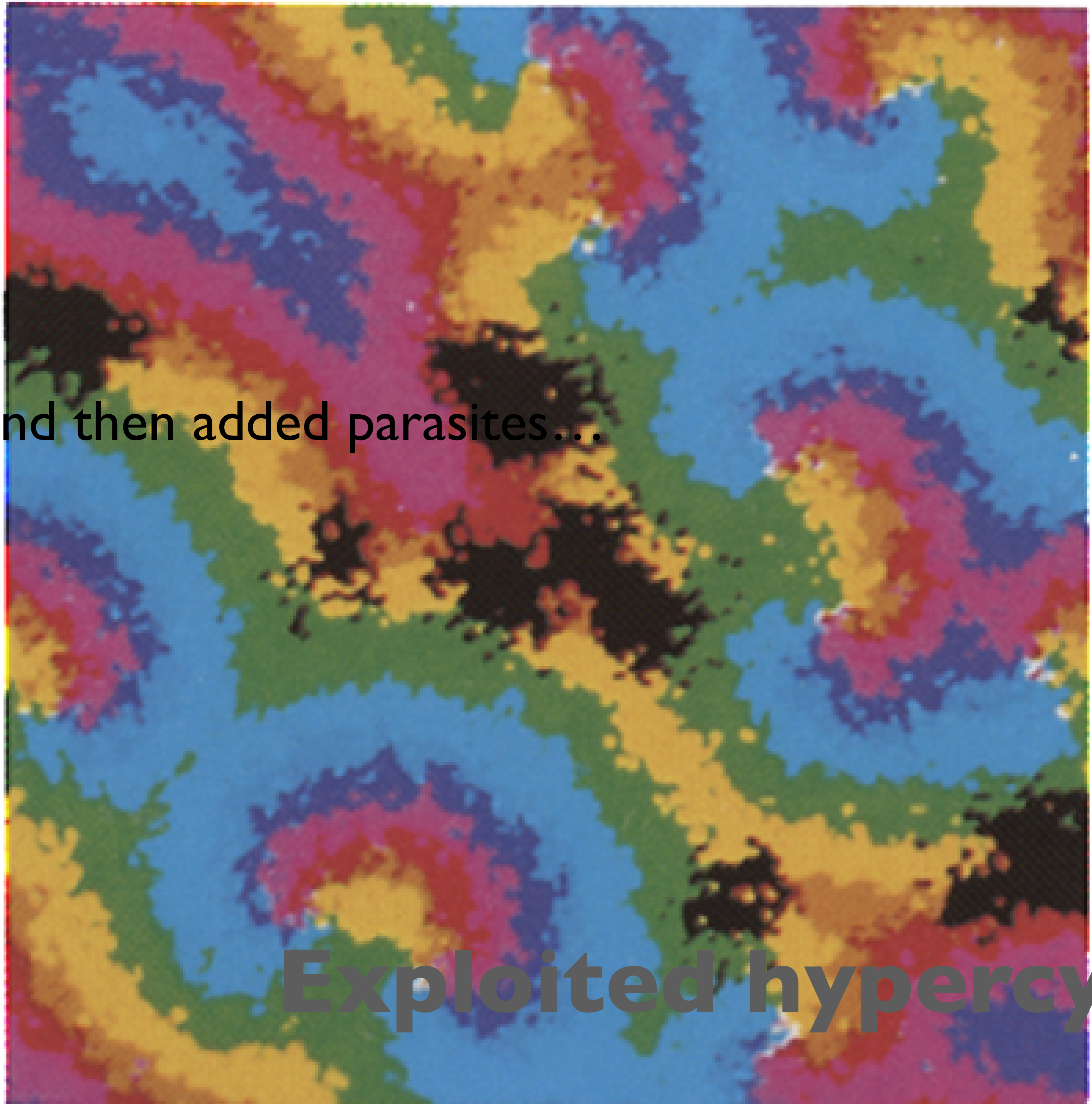


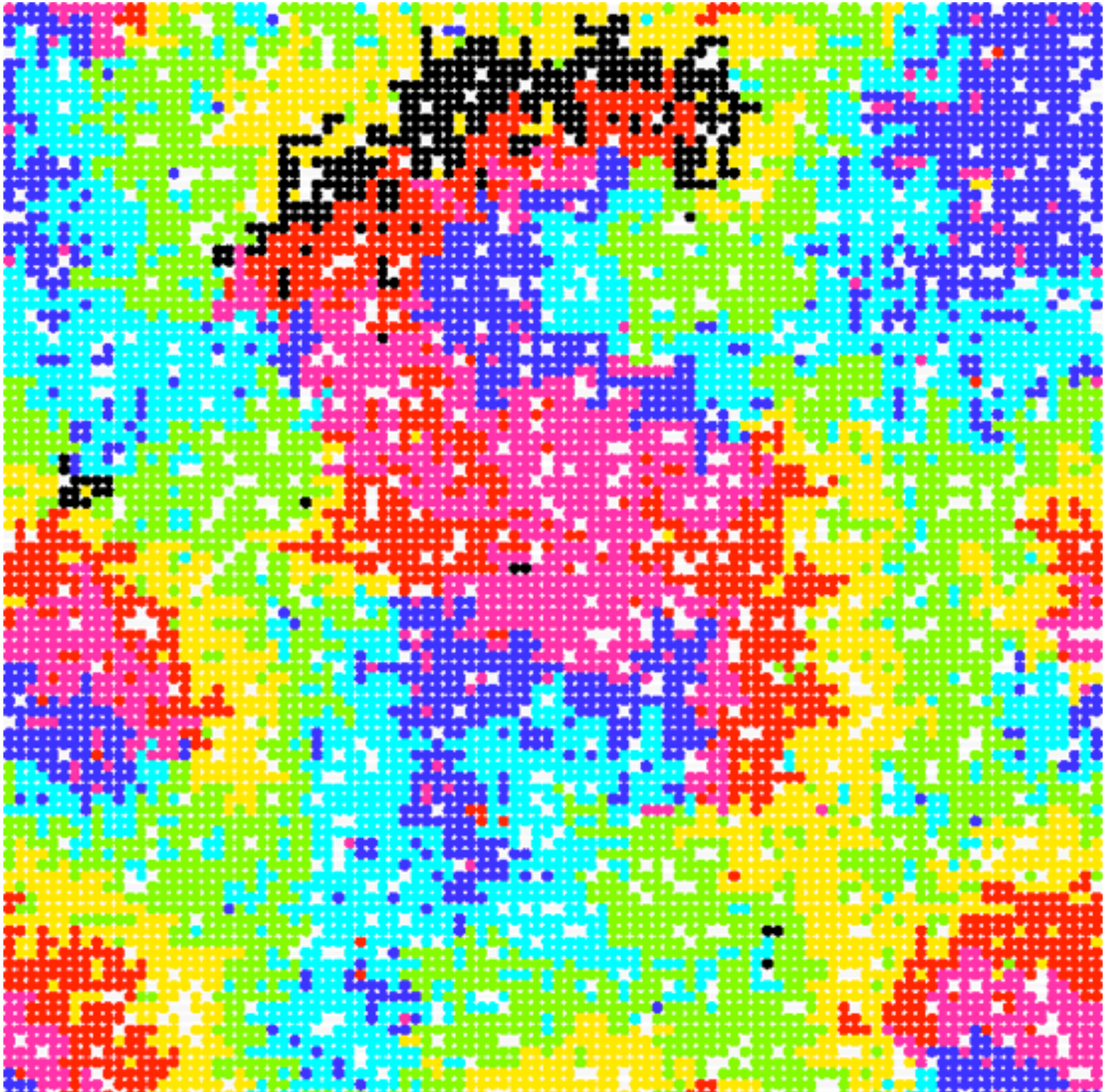
Exploited Hypercycle



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

Spatialised hypercyle


and then added parasites…
Exploited hypercyle



t = 1600.

Boerlijst & Hogeweg's (1991) results

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

Spatial Hypercycles

Spirals 'unit of selection'

- Rotation speed selected trait

But:

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

Spatial evolution

Mutants create clusters

Clusters unit of selection (unit of adaptation)

Mathematical characterisation

- Correlation dynamics
  - Van Baalen & Rand (1998), Van Baalen (2000), Ferrière & Le Galliard (2001), Lion & van Baalen (2007)

Viscous populations

$$\overline{\mathrm{d}t} = (b_S + m_S)\overline{\phi} q_{S|oo} p_{oo}$$

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

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

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

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

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

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

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

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

Van Baalen & Rand (1998)

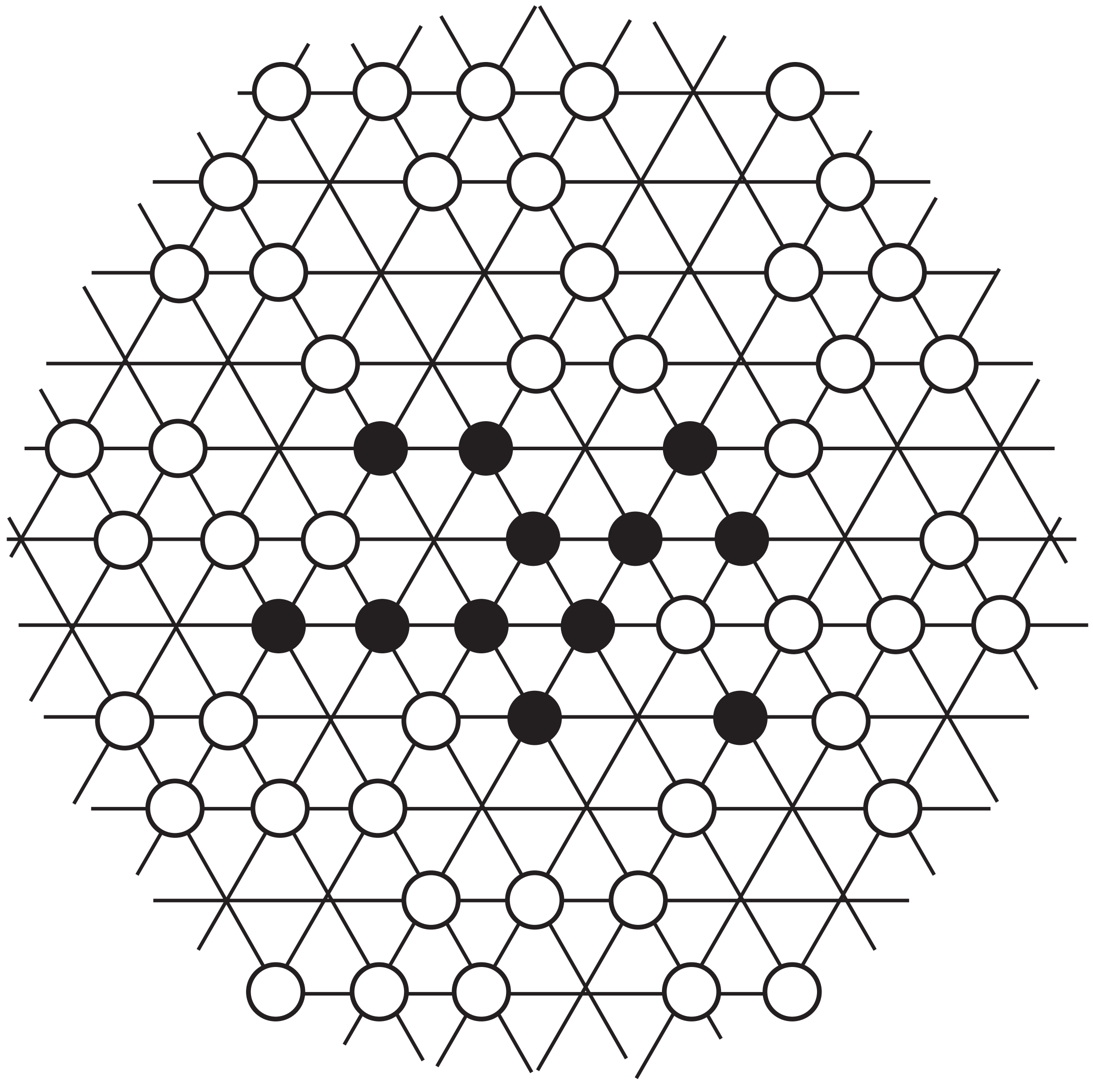
$$+ [d_S + \overline{\phi} m_S q_{o|SA}]p_{SA}$$

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

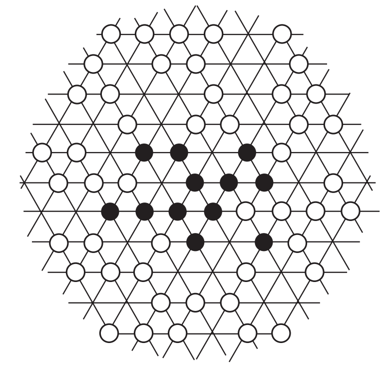
Dynamics of mutant given by sets of equations

- Fitness: dominant Lyapunov exponent
- Unit of selection: corresponding eigenvalue

Viscous populations



Characteristic cluster



Traits of the cluster determine invasion success

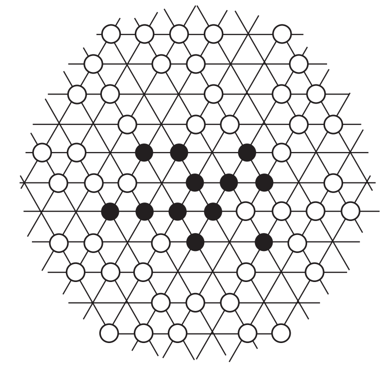
Close link with Hamilton's inclusive fitness

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

$$Br > C$$

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

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

Many mutualistic symbioses presumably evolved from parasitic interactions

- What governs the transition between parasitism and mutualism?

Evolution

According to ecological theory

type of interaction given by

sign structure in the interaction matrix

Ecology

Mutualism: the density of species *x* goes up in the presence of species *y* and *vice versa*

An interaction is either mutualistic or it is not

No ‘grey area’

Ecological definition

But what about those parasites that

1. cause mild negative effects

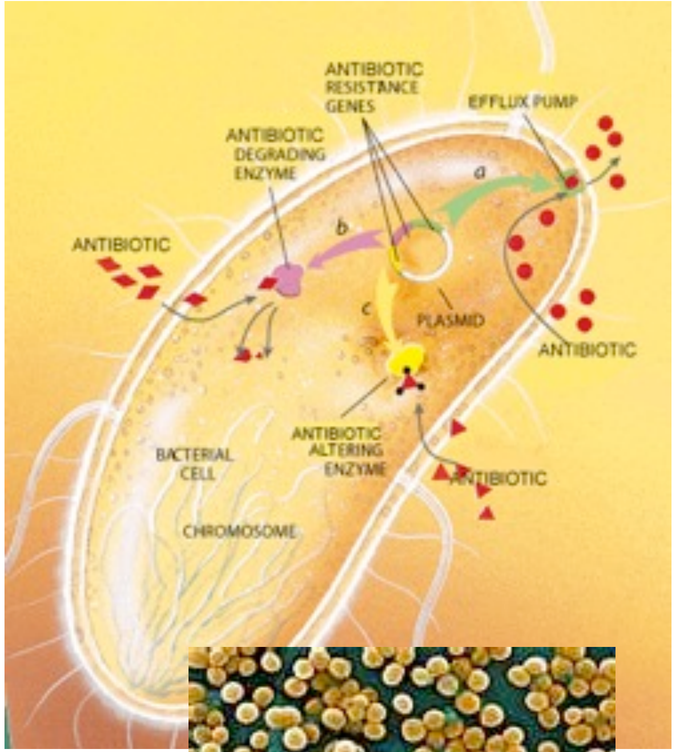
2. protect against other risks

Exx:
Plasmids that code for resistance
'Probiotic' intestinal flora
Cowpox that vaccinates against smallpox

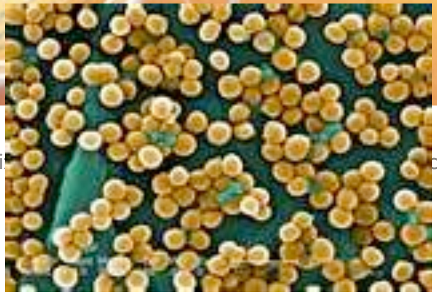
Grey Area

A plasmid may be

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



http://microvet.ari ... tRes/

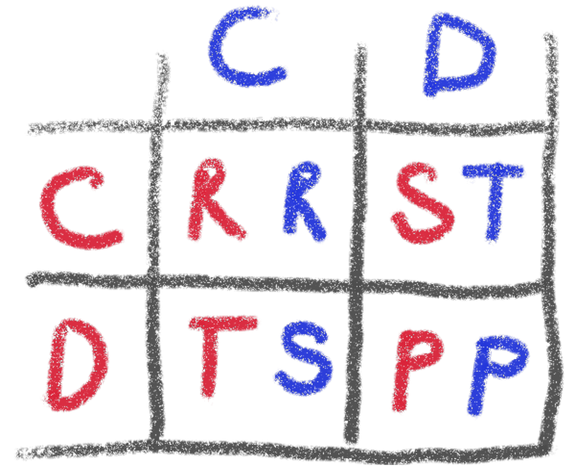


MRSA

Grey Area

Theory often supposes dilemma right from the start

- Prisoners Dilemma!



But where does the dilemma come from?

The 1000000€ Question

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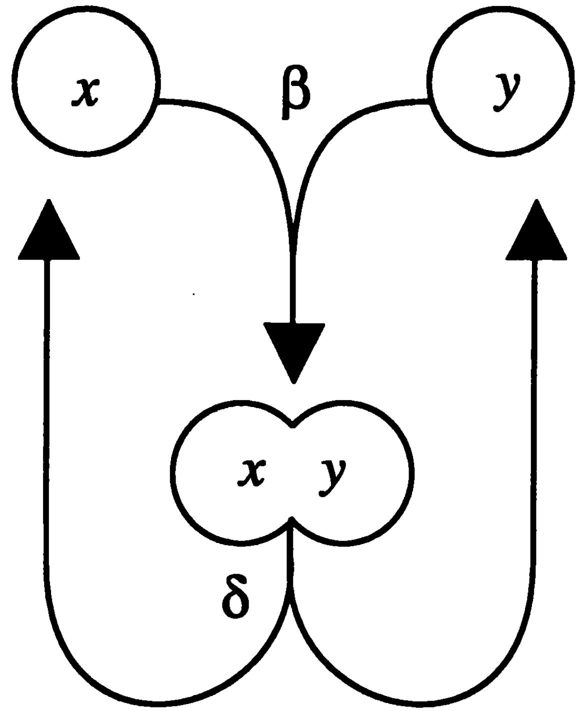
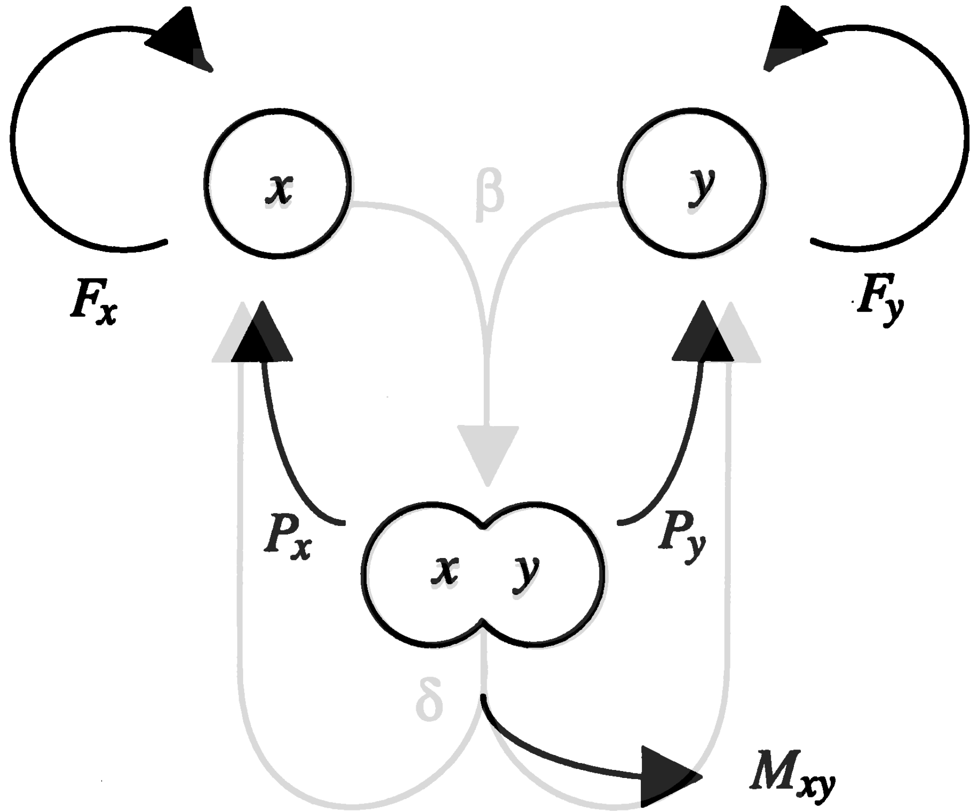
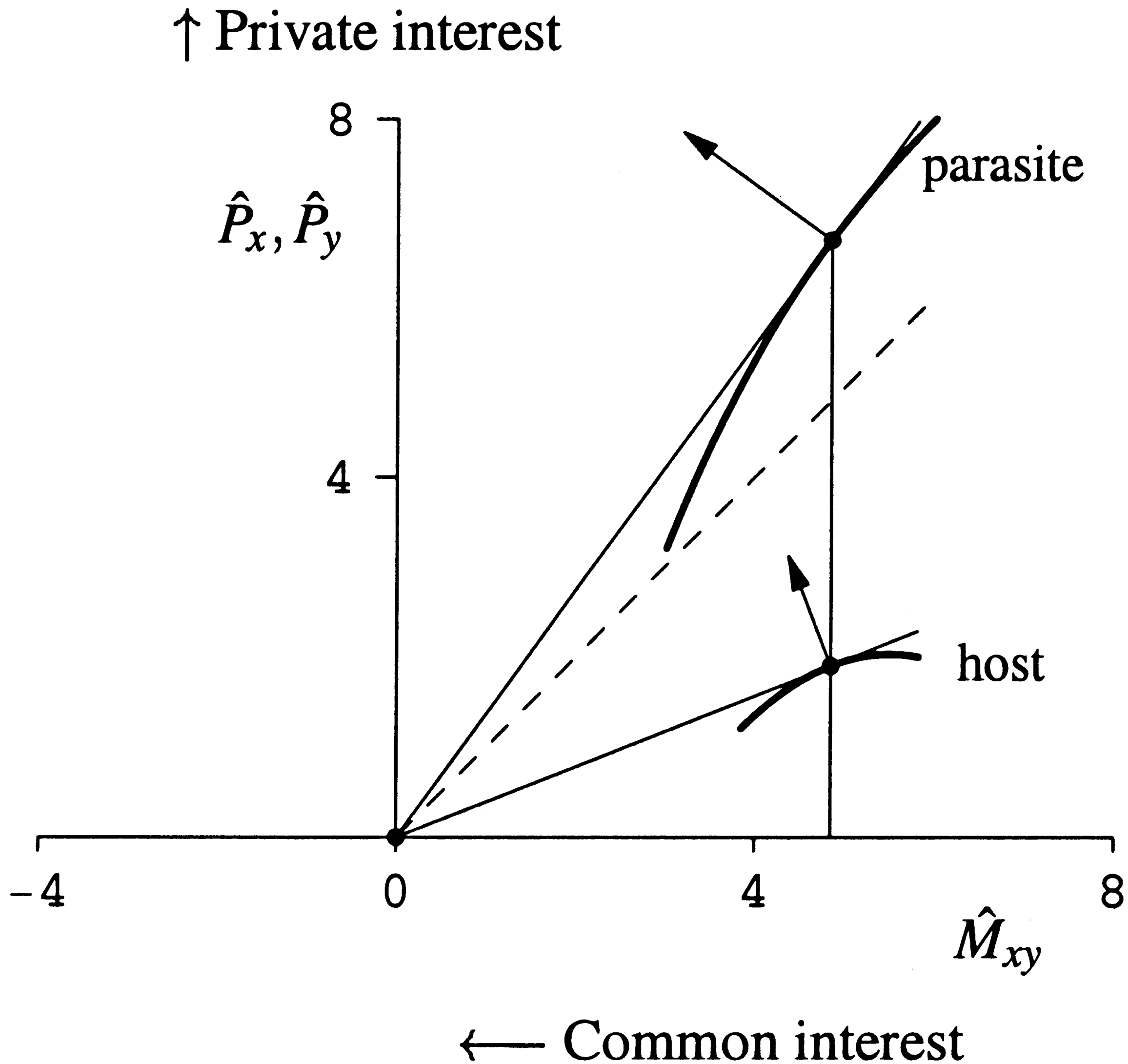


Kostitzin, V. A. (1934). *Symbiose, Parasitisme et Évolution (Étude Mathématique)*. Hermann et Cie, Paris.

‘Dangerous liaisons’



‘Dangerous liaisons’



Private interest vs Common good

Table 1. The effect of changes in demographic rates on the fitness of partners x and y, as a function of their respective private-to-common interest ratios Q_x and Q_y. (See Appendix E for how these weights are derived.)

Change	Effect on fitness		Alignment
	x	y	
increase σ_x	1	0	no
increase σ_y	0	1	no
increase σ_{xy}	Q_x	Q_y	always
decrease ν_x	Q_x	$Q_y - 1$	if $Q_y > 1$
decrease ν_y	$Q_x - 1$	Q_y	if $Q_x > 1$
decrease ν_{xy}	Q_x	Q_y	always
decrease δ	$Q_x - 1$	$Q_y - 1$	if $Q_x - 1$ and $Q_y - 1$ of same sign

Alignment of interests

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