The ecology and evolution of spatially extended systems: cellular automata and analytical approximations

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ecosystem

biodiversity, nutrient cycles

population

competition, predation, epidemiology, social interactions

individual

birth, death, development, behaviour

within-individual

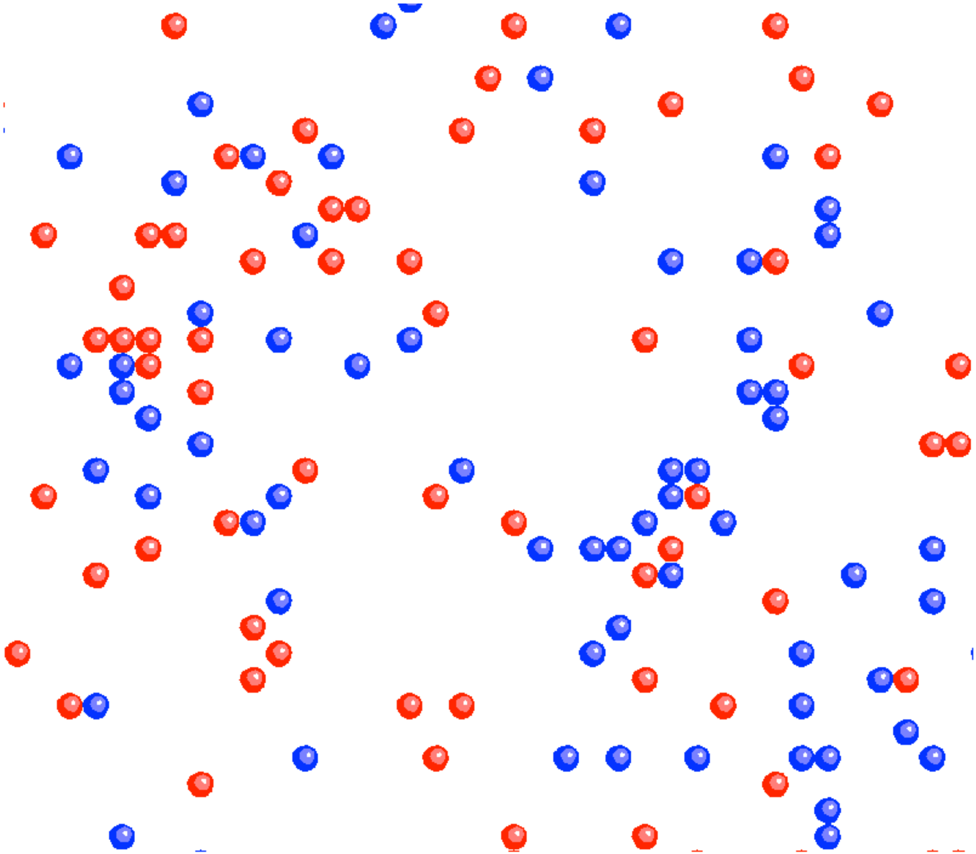
physiology, learning, infection, immune response

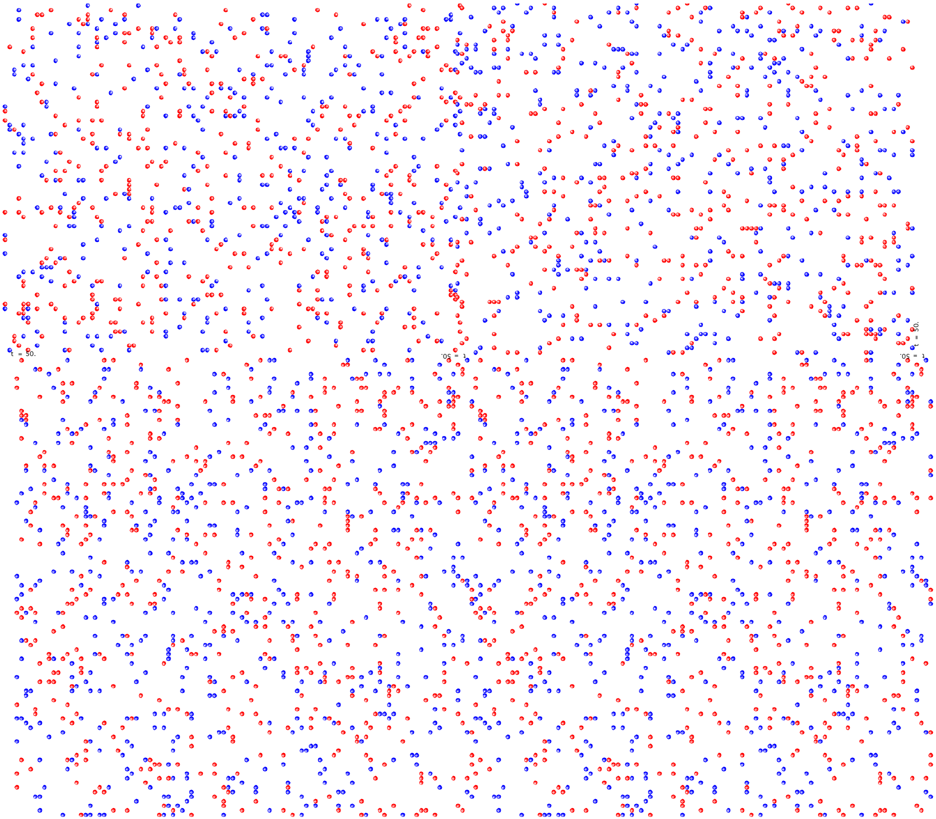
Levels of organisation

Macro-scale laws from micro-scale processes :

- Pressure & temperature from molecule movement
- Second Law: Entropy increases

Thermodynamics Success Story

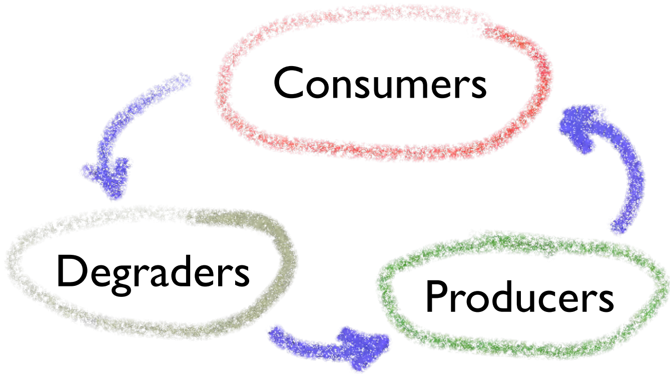



t = 50.

Derive Universal Ecological Laws from

- Physiology
- Population dynamics
- Genetics

Dream



Systems Ecology

Very few universal 'Laws of Ecology' have emerged so far

- 'Healthy' ecosystems maximise thoughput
- Complex ecosystems are more stable
- Evolution always produces more complex systems

Systems Ecology

Sole universal structuring principle

- almost faithful copying
  - reproduction + mutation
- selection

No simple emergent consequences

- no system-wide optimization
- no ‘progress’

Evolution

Why space is important

Different theoretical approaches

- Patch models
- Levins' metapopulation
- Reaction-diffusion models
- Cellular automata (& other individual-based models)
- (Correlation dynamics)

Space

http://www.idw-online.de

Parasitoid

CPB Silwood Park

Drosophila melanogaster larvae

looking for hosts

http://muextension.missouri.edu

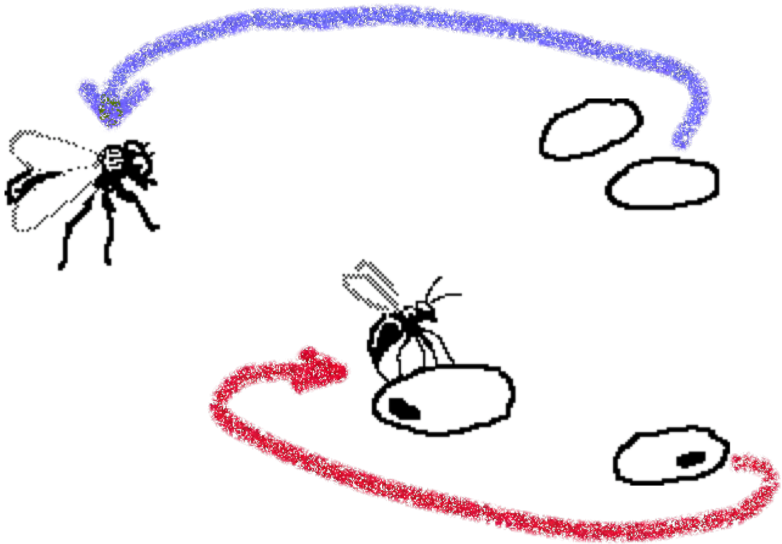
Oviposition

http://www.anbp.org

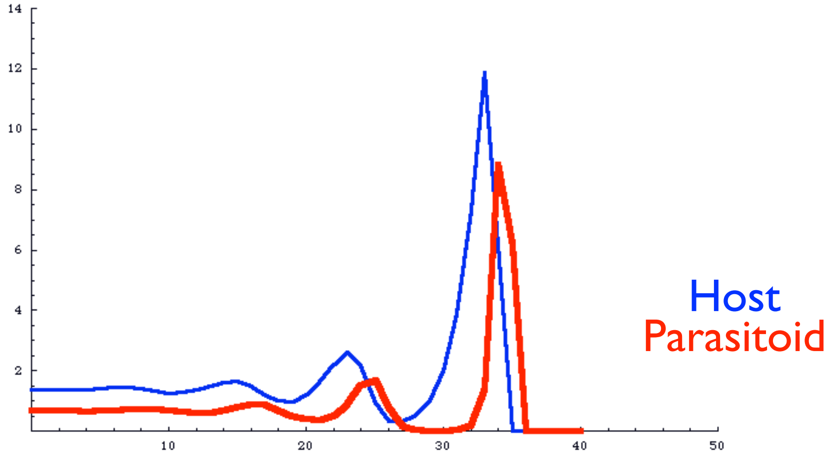
Oviposition

http://whatcom.wsu.edu

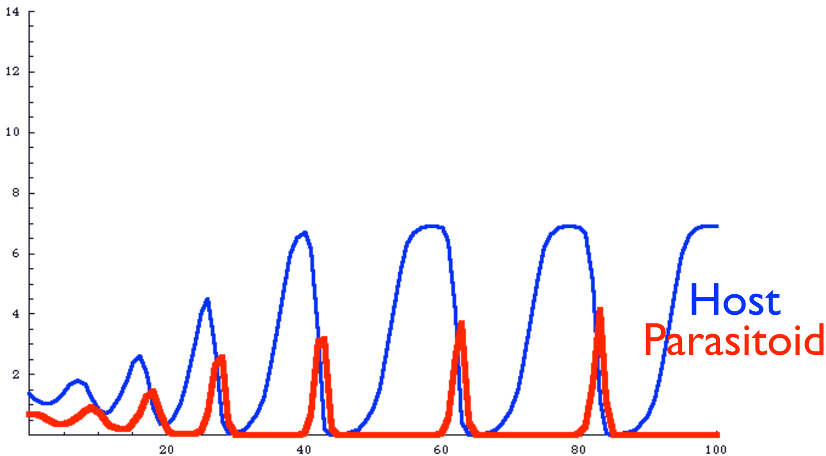
Emergence



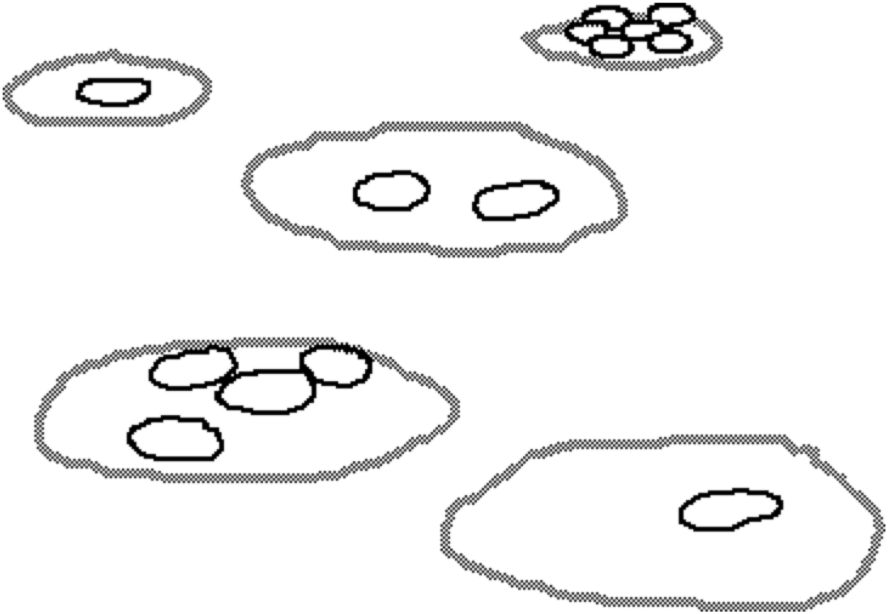
Life Cycle



Nicholson-Bailey



NB plus compétition



Heterogeneity

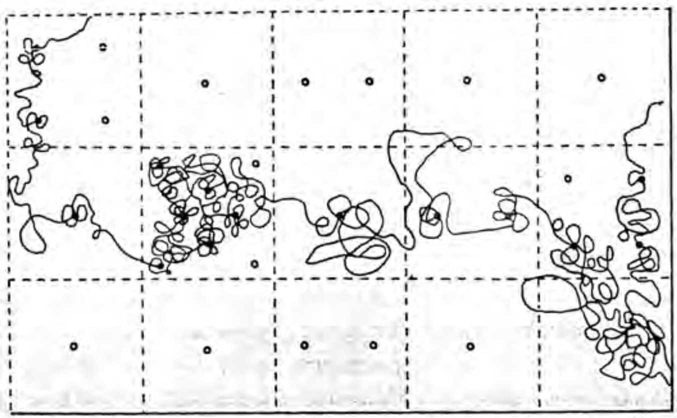
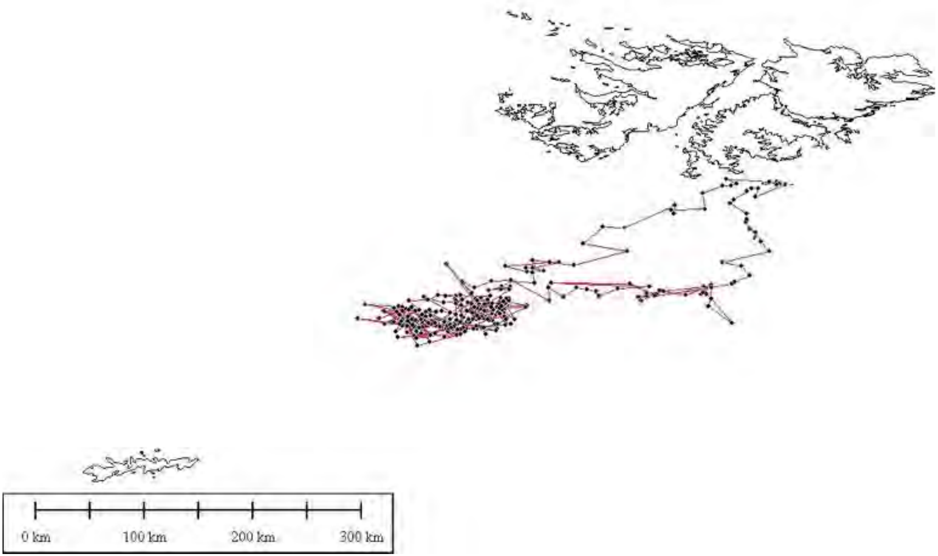
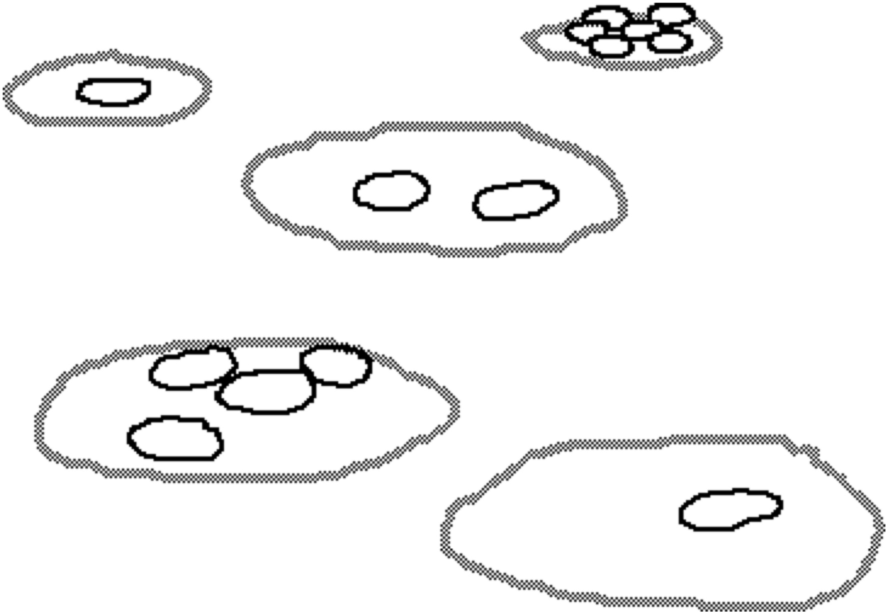


FIG. 9. Part of a track showing the movements of a tachinid parasite *Cyzenis albicans*, within an arena. The circles represent small drops of sugar solution upon which the parasite adults feed. The solid circles show where feeding occurred.

Localisation



A Foraging Sea-Elephant



Heterogeneity

$$N_{t+1} = \lambda N_t \sum_{i=1}^{n} \alpha_i e^{-\beta_i P_t}$$

$$P_{t+1} = c N_t \sum_{i=1}^{n} \alpha_i \left(1 - e^{-\beta_i P_t}\right)$$

Hassell & May 1974

was divided between the n unit areas with a single area of high density and the remainder of equal low density. The distribution of predators was achieved by a single parameter characterization (μ) such that

$$\beta_i = c\alpha_i^{\mu} \qquad (2)$$

where c is a normalization constant and μ is the 'relative aggregation index'.

Eqn (2) was not intended to be a realistic description of how predators aggregate. It was chosen for its simplicity and because it conveniently spans the behaviours of random search ($\mu = 0$) to complete aggregation in the highest density area, making the remainder

Hassell & May 1974

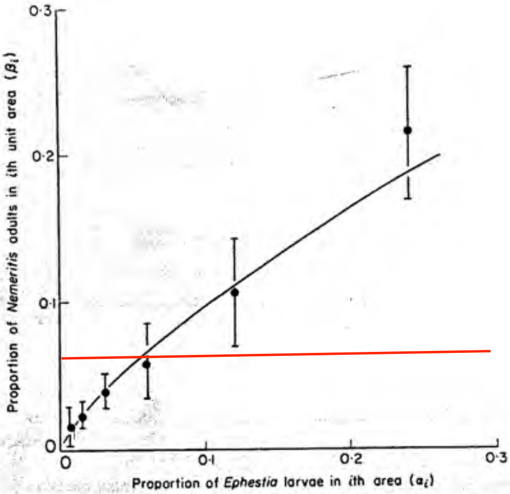


FIG. 11. The relationship between the proportion of searching *Nemeritis canescens* (β_i) and the proportion of *Ephestia cautella* larvae (α_i) per unit area from a laboratory interaction (Hassell 1971a, b). The fitted curve was derived by use of eqn (22). $\beta_i = 0{\cdot}53\ \alpha_i^{\,0{\cdot}73 \pm 0{\cdot}04}$.

Aggregation

- May determine ecological stability
- May determine persistence of species
- Allow more species to coexist
- Modify selective pressures
- …

Space is Important

Space makes life difficult for theoreticians

- as anyone who has struggled with spatially explicit models is likely to know

Space is a Pain

Modeling Space

	space	
population	continuous	discrete
continuous	diffusion models	coupled map lattices (metapopulations)
discrete	point processes	(probabilistic) cellular automaton

$$\frac{dn}{dt} = f(n)$$

$$\Longrightarrow \quad n(t)$$

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 f}{\partial x^2} + f(n)$$

$$\Longrightarrow \quad n(t, x)$$

Reaction-diffusion

innovation is to allow key model parameters to vary spatially, reflecting habitat heterogeneity.

Specifically the dynamics of the system is described by

$$\frac{\partial E}{\partial t} = \frac{\partial}{\partial x}\left(D(x)\frac{\partial E}{\partial x}\right) + r_E E(G(x) - a_E E - b_E N), \qquad (2.1a)$$

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial x}\left(d(x)\frac{\partial N}{\partial x}\right) + r_N N(g(x) - a_N N - b_N E), \qquad (2.1b)$$

which is the Lotka–Volterra competition model with difusion; see, for example, Murray (1989). The functions $D(x)$ and $d(x)$ measure the diffusion rates. The intrinsic growth rates of the organisms are reflected by the positive parameters r_E and r_N. These are scaled so that the maximum values of the functions $G(x)$ and $g(x)$, reflecting the respective carrying

Cruywagen et al (1996)

Multi-species Reaction-diffusion

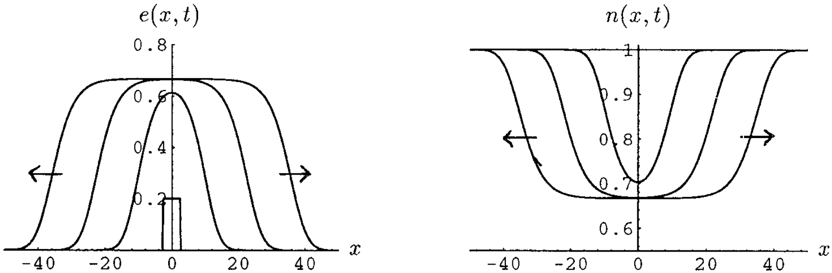


FIG. 1. A travelling wave solution connecting the native-dominant steady state to the coexistence steady state in a spatially uniform environment. Parameter values used were $\gamma_e = \gamma_n = 0.5$, $D(x) = d(x) = G(x) = g(x) = 1$, and $r = 2$, so that the coexistence state is the only stable state.

Cruywagen et al (1996)

Competition in Space

Advantages

- many mathematical tools

Disadvantages

- becomes very difficult if movement is non-random
- becomes very difficult if individuals are ‘large’

Diffusion approach

Individuality is crucially important

- in particular in spatially explicit settings
- demographic stochasticity inevitable

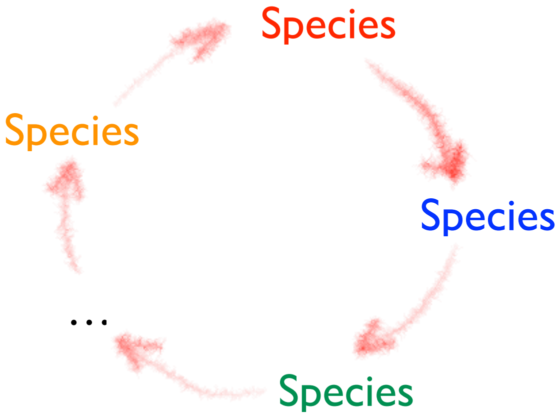
Model for the origin of life

- interactions between simple molecules
- can persist where single species cannot

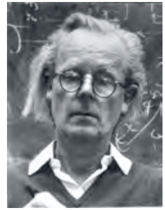
The Hypercycle

Manfred Eigen

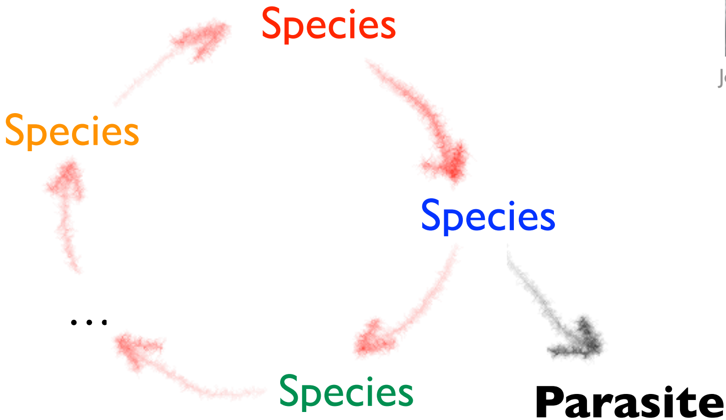
Peter Schuster



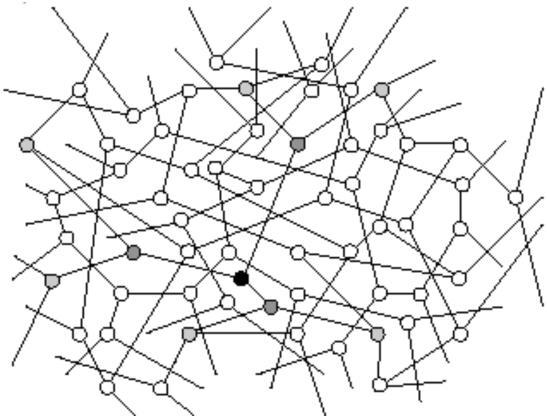
The Hypercycle

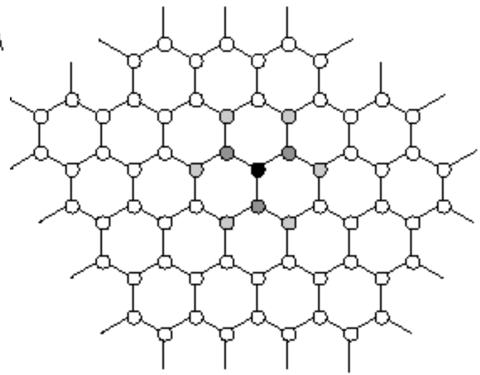


John Maynard Smith



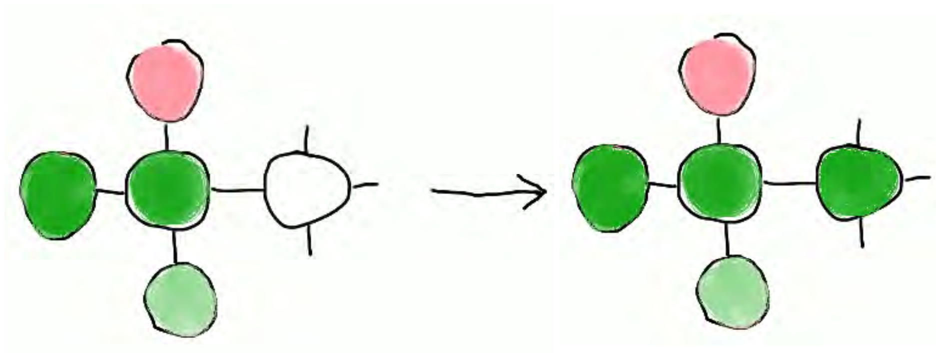
The Hypercycle



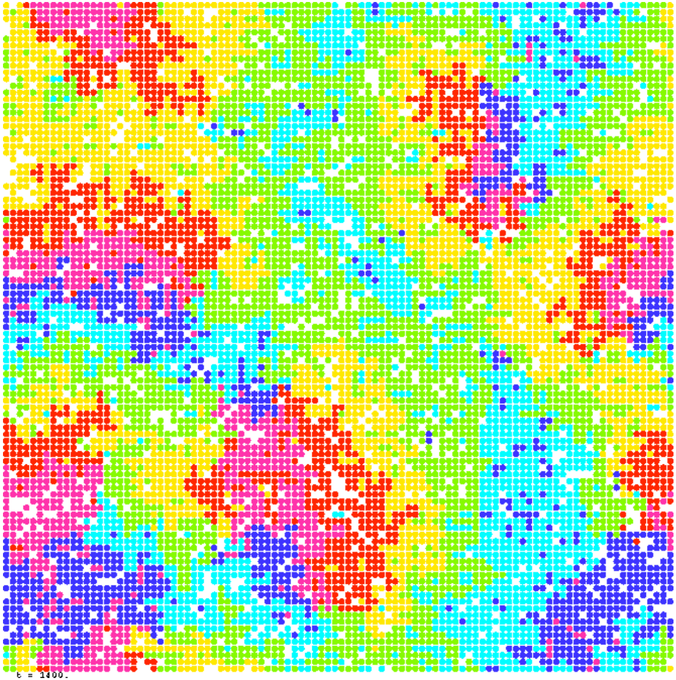


A Way to Model Space

Death

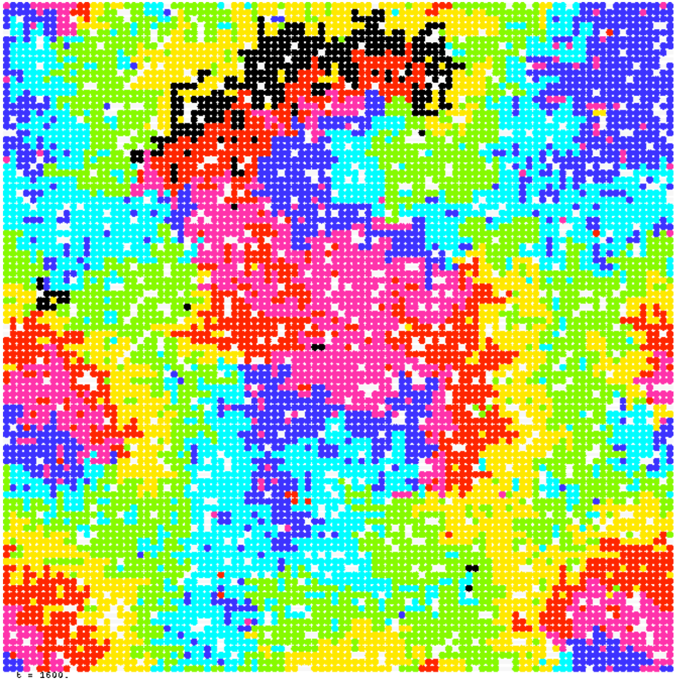


Faithful Reproduction

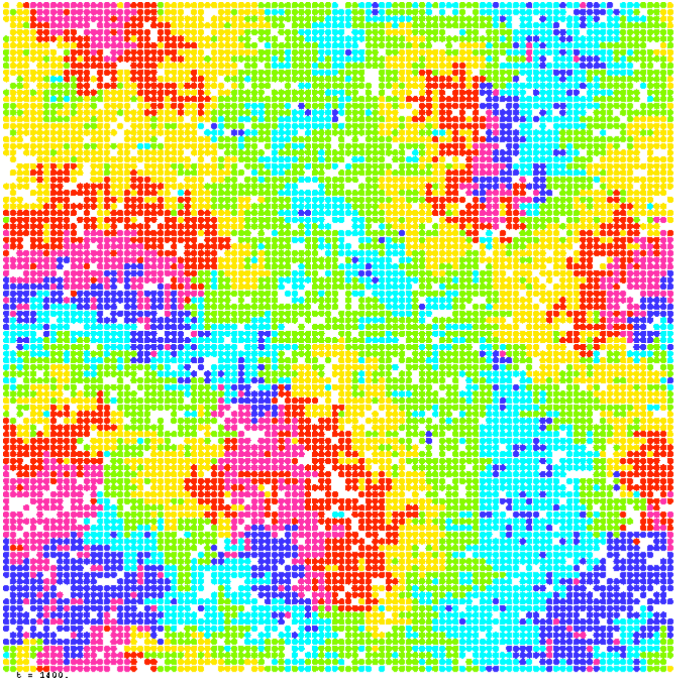


Boerlijst & Hogeweg (1991)

Spatial Selfstructuring...

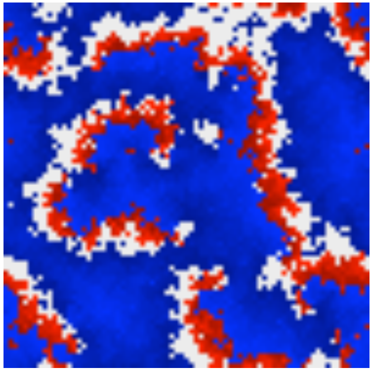


...Kills the Parasites



Boerlijst & Hogeweg's (1991)

Parasite-free Hypercycle



van Ballegooijen & Boerlijst 2004

Boerlijst & Hogeweg's (1991) hypercycles

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

Spatial Hypercycles

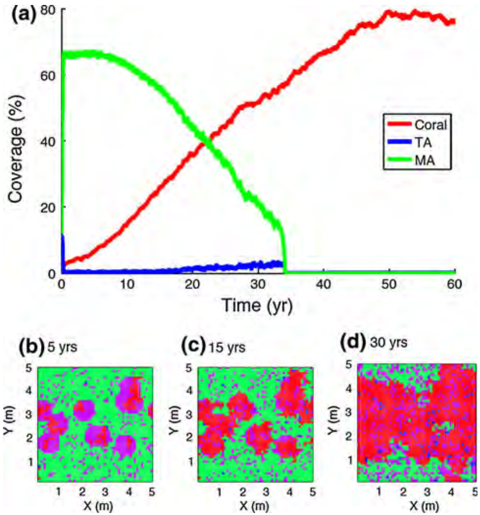
Spirals ‘unit of selection’

- Rotation speed selected trait

But:

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

Spatial evolution



Sandin & McNamara 2012

Coral Dynamics

+ Nice toys

+ Colourful movies

– Difficult to generalise

– Difficult to obtain deeper insight

Cellular Automata

Probabilistic Cellular Automata

Computer Simulations

Mathematical characterisation

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

Viscous populations

state of the lattice

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

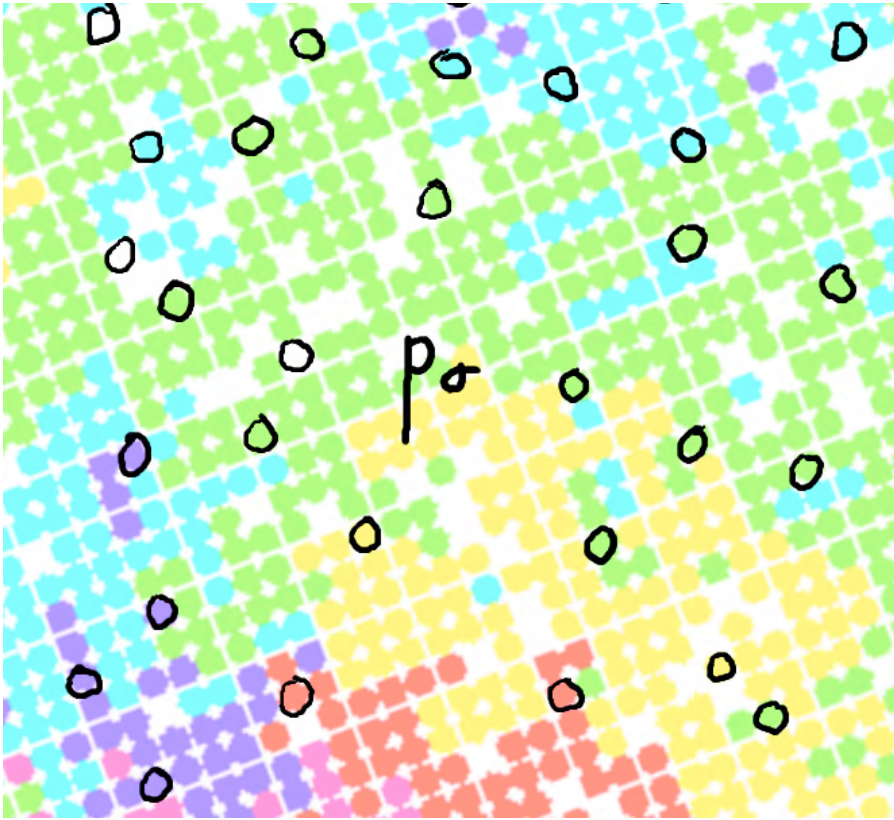
event rate

"δt → 0"

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

Morris (1997)

Bookkeeping


pσ

Dynamics of densities

$$\dot{p}_A = p_0 r_{0\to A} - p_A r_{A\to 0}$$

Dynamics of densities

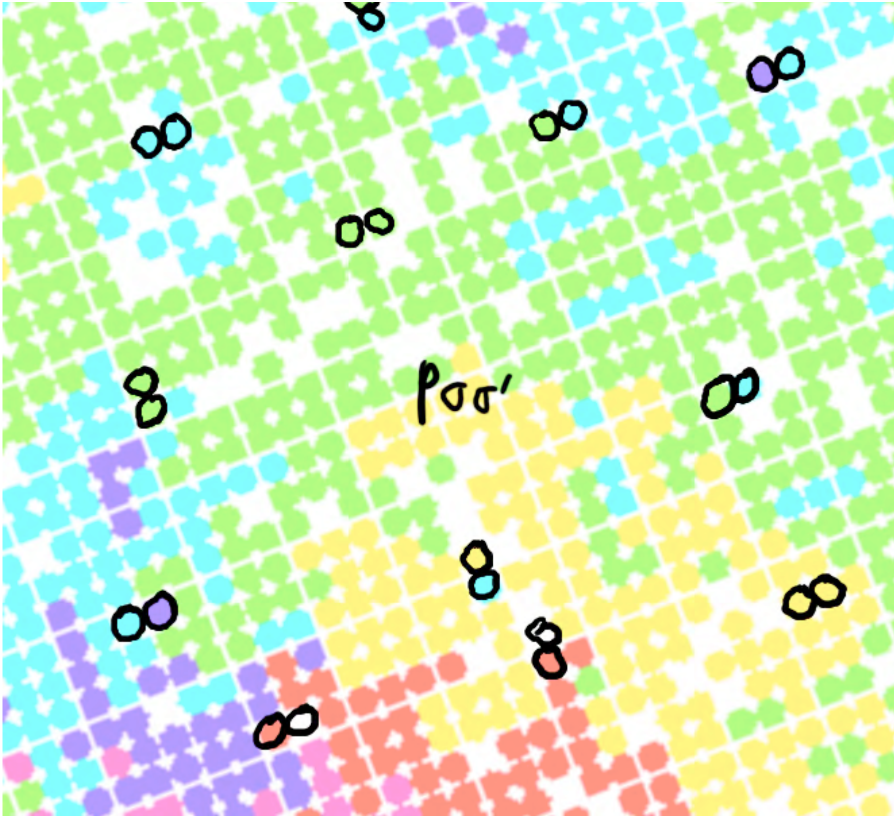
$$\frac{dp_A}{dt} = \left(b_A q_{0|A} - d_A\right) p_A$$

$$q_{0|A} \approx p_0$$

no space
("mean field")

$$q_{0|A} = \frac{p_{0A}}{p_A}$$

space


ρσσ'

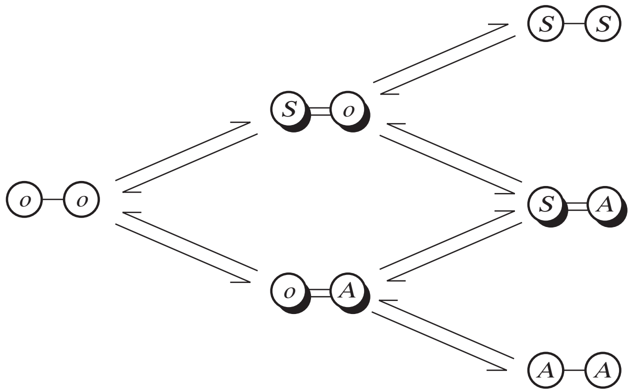


FIG. 2. The possible transitions between the state of doublets (pairs of neighbouring sites). Pairs that have a symmetric counterpart are shaded.

Pairs of Neighbours

Correlation Dynamics

$$\frac{dp_{So}}{dt} = (b_S + m_S)\phi q_{S|oo} p_{oo}$$

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

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

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

$$\frac{dp_{SS}}{dt} = 2[\phi b_S + \overline{\phi}(b_S + m_S)q_{S|oS}]pS_o$$

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

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

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

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

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

$$\frac{dp_{AA}}{dt} = 2[\phi b_A + \overline{\phi}(b_A + m_A)q_{A|oA}]p_{Ao}$$

$$- 2[d_A + \overline{\phi} m_A q_{o|AA}]p_{AA}$$

$$\frac{dp_{AS}}{}$$

The dynamics of Singletons depend on Pairs, who depend on Triplets, who depend on…

Closure approximation

$$q_{a|bc} \approx q_{a|b}$$

A Cascade

$$\dot{p}_{øA} = \quad + \left[(b_A + m_A) \frac{n-1}{n} q_{A|ø} \right] \bar{p}_{øø} - \left[d_A + m_A \frac{n-1}{n} q_{ø|A} \right] p_{øA}$$

$$- \left[(b_S + m_S) \frac{n-1}{n} q_{S|ø} \right] p_{øA} + \left[d_S + m_S \frac{n-1}{n} q_{ø|S} \right] p_{SA}$$

$$- \left[(b_A + m_A) \frac{n-1}{n} q_{A|ø} + \frac{1}{n} b_A \right] p_{øA}$$

$$+ \left[d_A + m_A \frac{n-1}{n} q_{ø|A} \right] p_{AA}$$

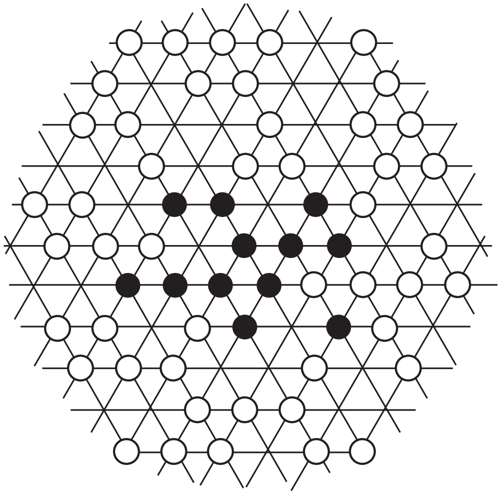
A closed equation for pair dynamics

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

Dynamics of mutant given by sets of equations

- Fitness: dominant eigenvalue
- Unit of adaptation: corresponding eigenvector

Invasion of a mutant



“Unit of adaptation”

ecosystem

biodiversity, nutrient cycles

population

competition, predation, epidemiology, social interactions

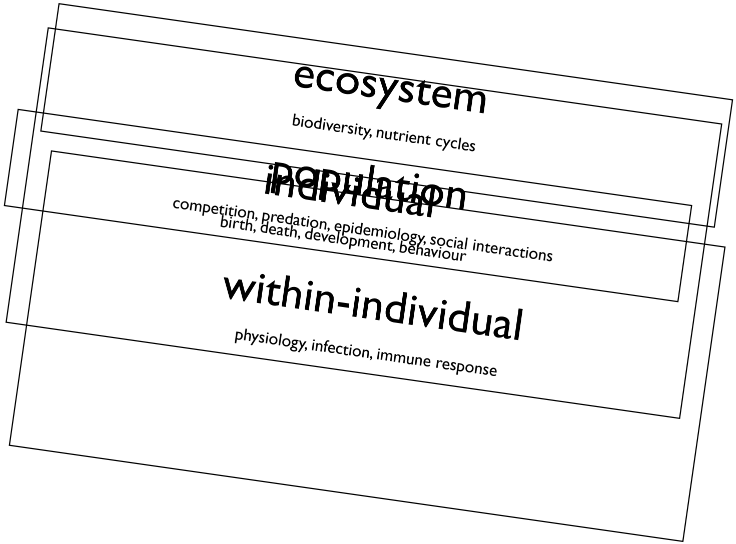
individual

birth, death, development, behaviour

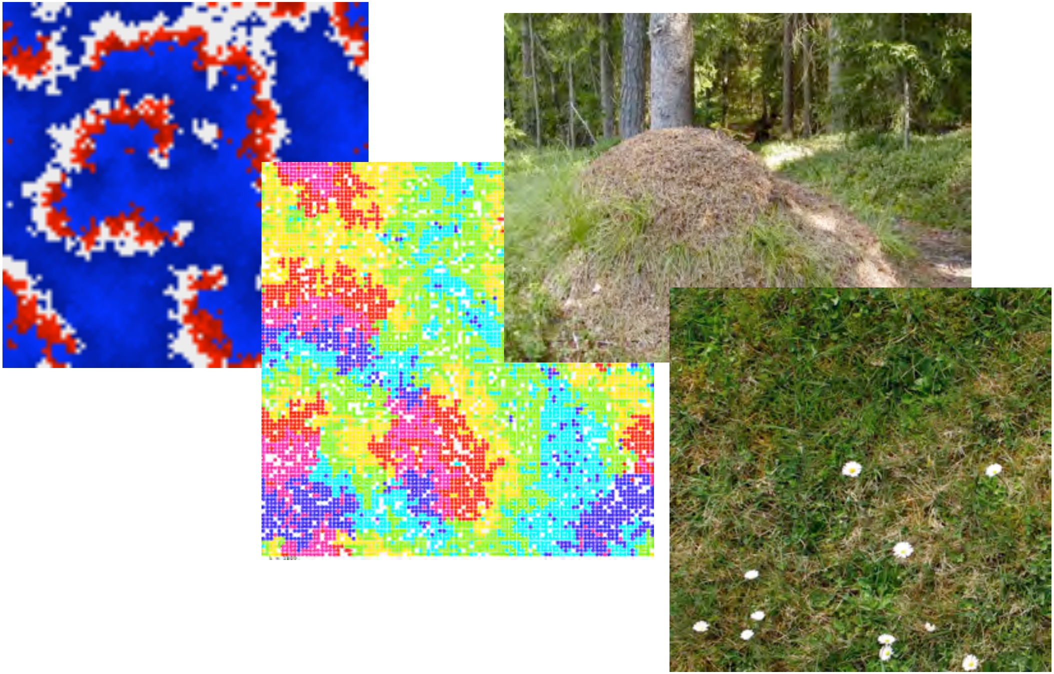
within-individual

physiology, learning, infection, immune response

Levels of organisation



Consequence of Space



Where is the individual?