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

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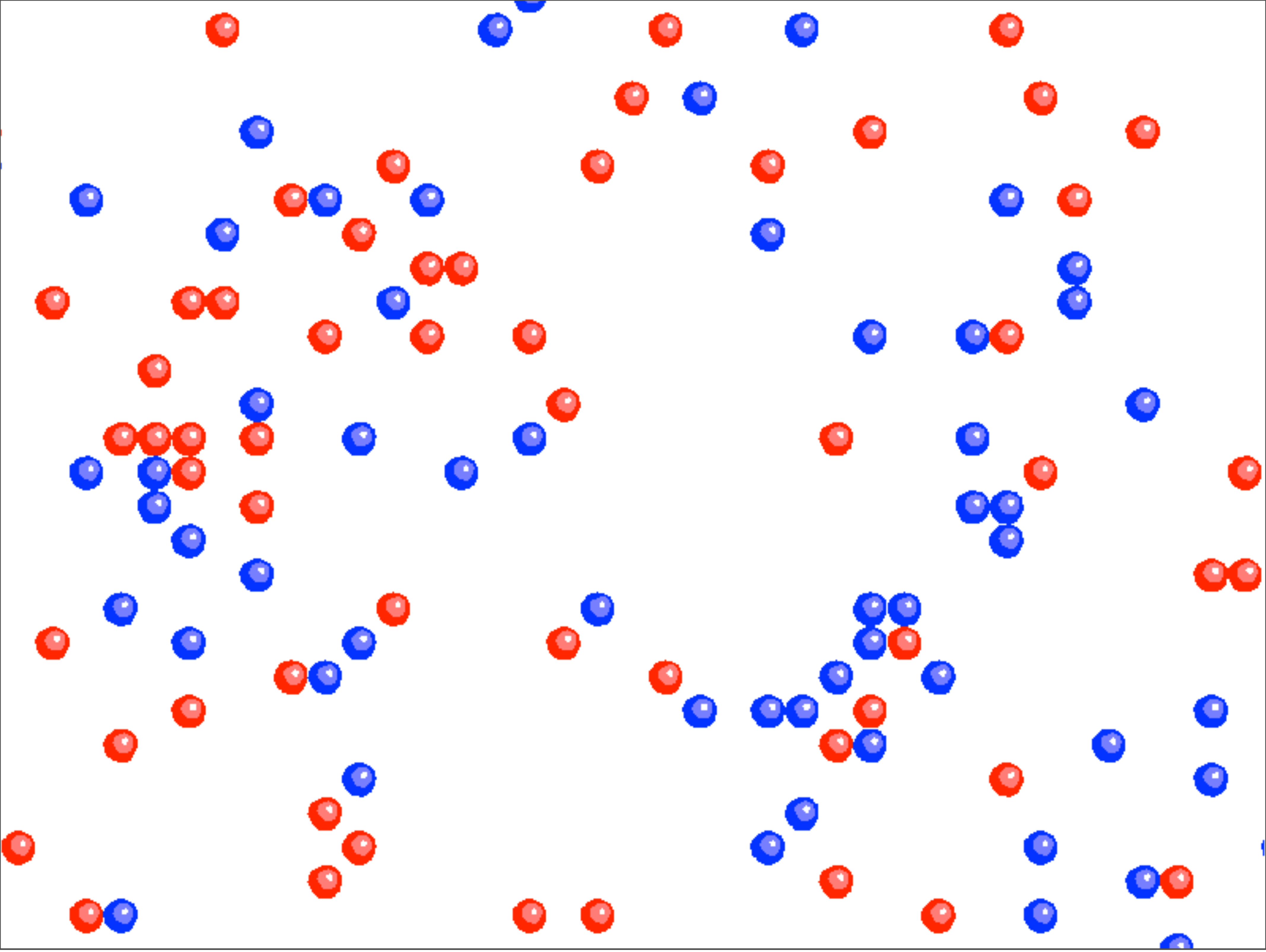
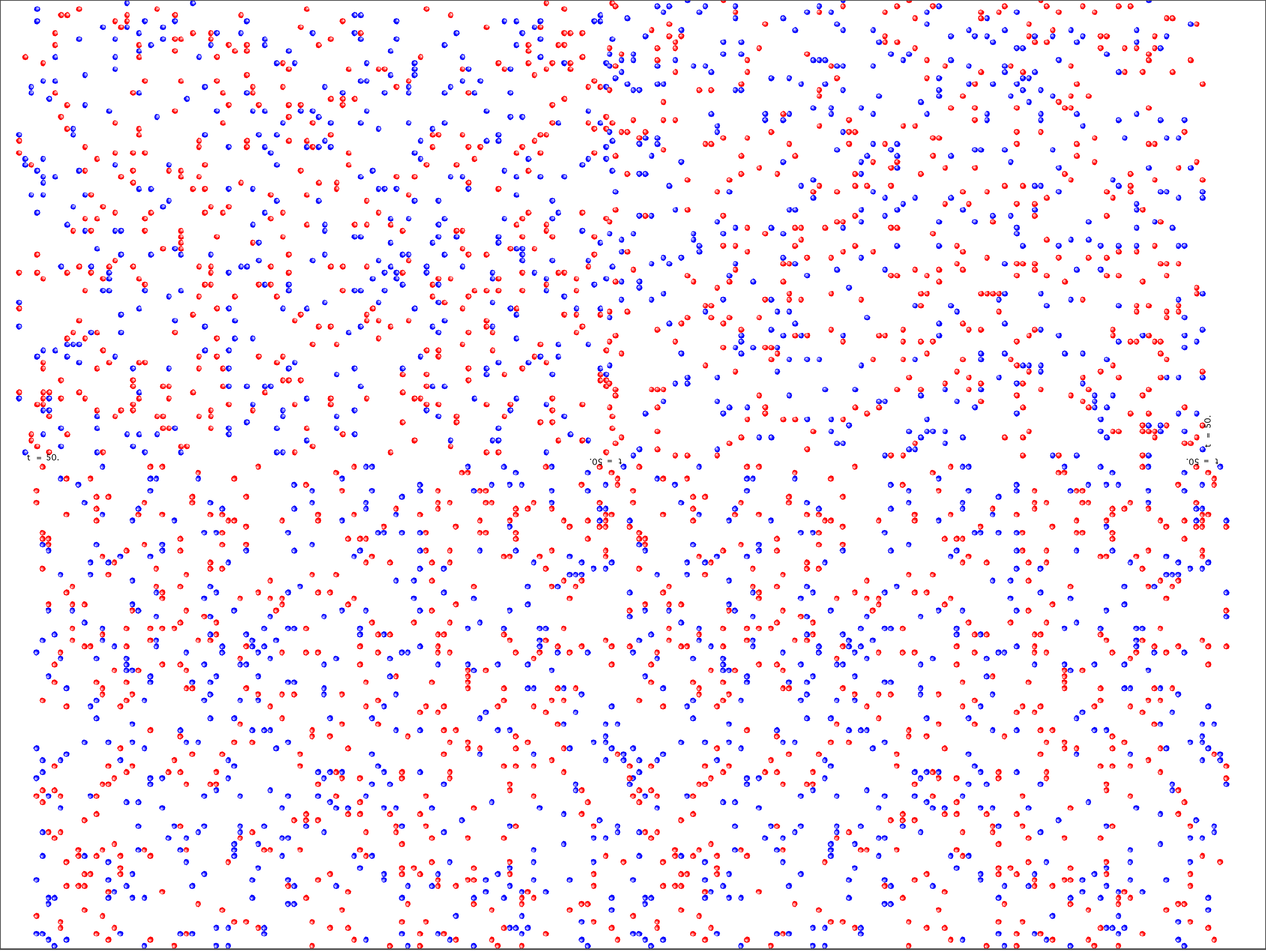
Thermodynamics Success Story

Macro-scale laws from micro-scale processes :

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

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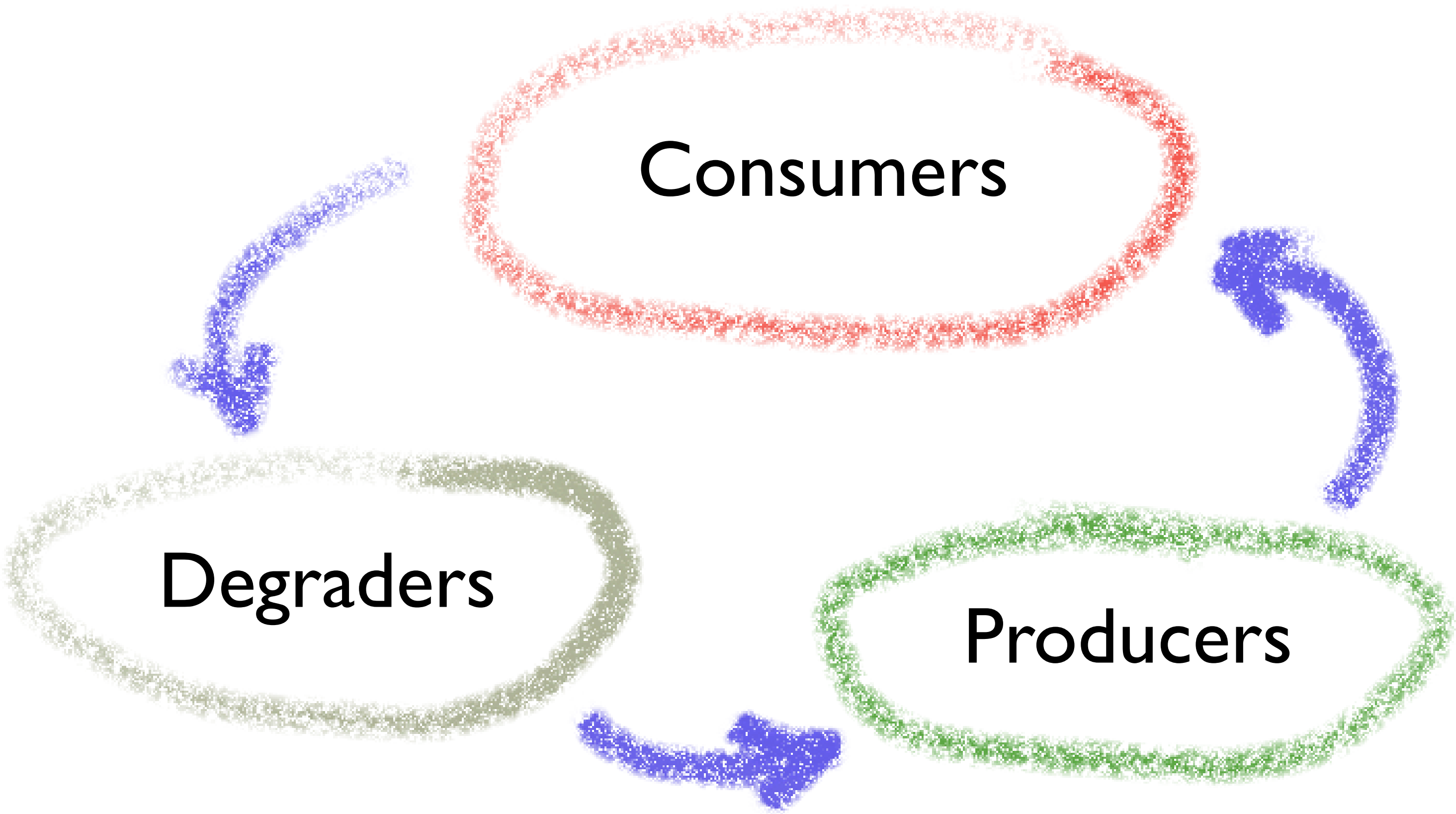
Dream

Derive Universal Ecological Laws from

- Physiology
- Population dynamics
- Genetics

Systems Ecology



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

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Evolution

Sole universal structuring principle

- almost faithful copying
  - reproduction + mutation
- selection

No simple emergent consequences

- no system-wide optimization
- no ‘progress’

Space

Why space is important

Different theoretical approaches

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

Parasitoid

http://www.idw-online.de

looking for hosts

CPB Silwood Park

Drosophila melanogaster larvae

Oviposition

http://muextension.missouri.edu

Oviposition

http://www.anbp.org

Emergence

http://whatcom.wsu.edu

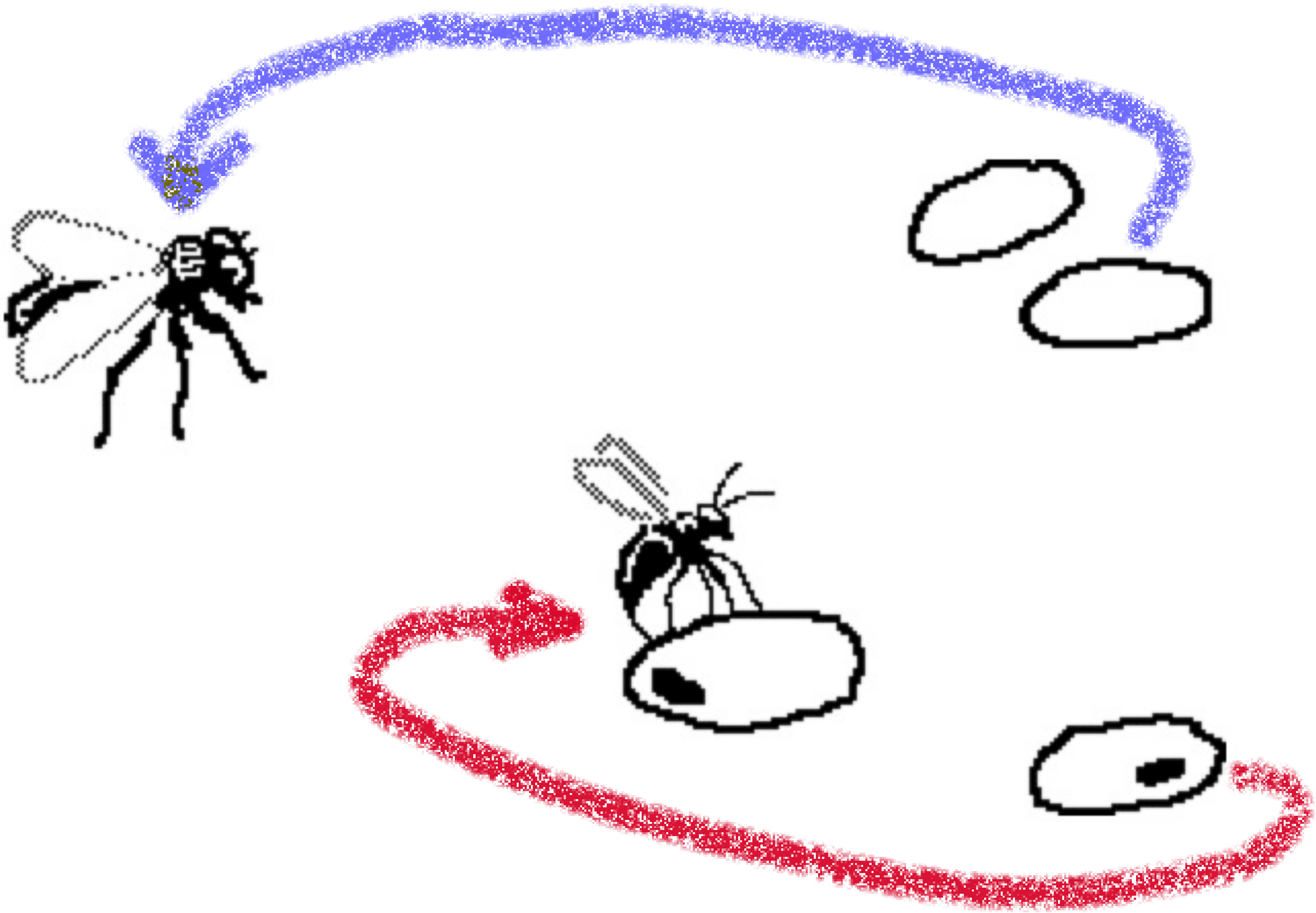
Life Cycle

Life Cycle

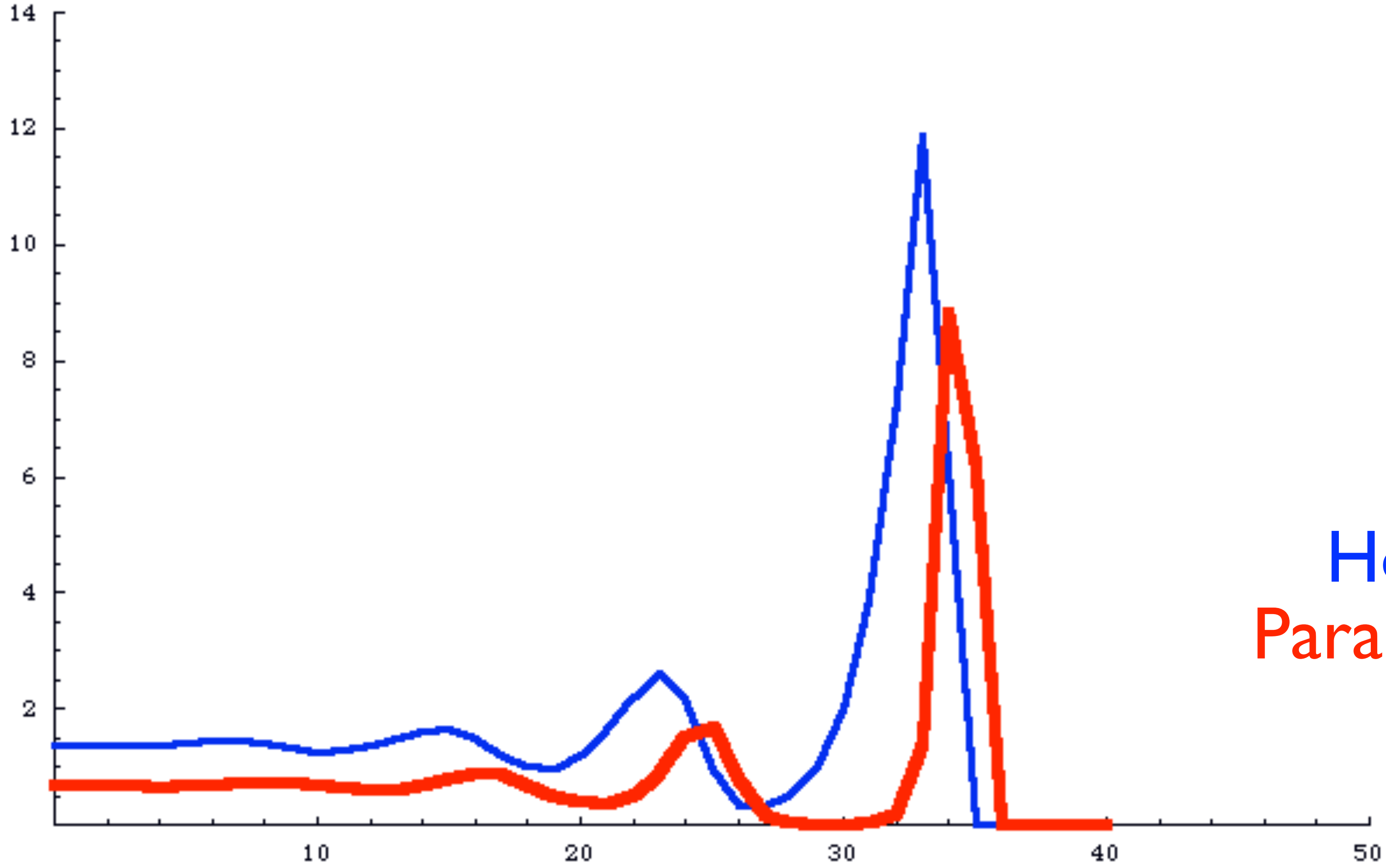
Life Cycle

Life Cycle

Life Cycle

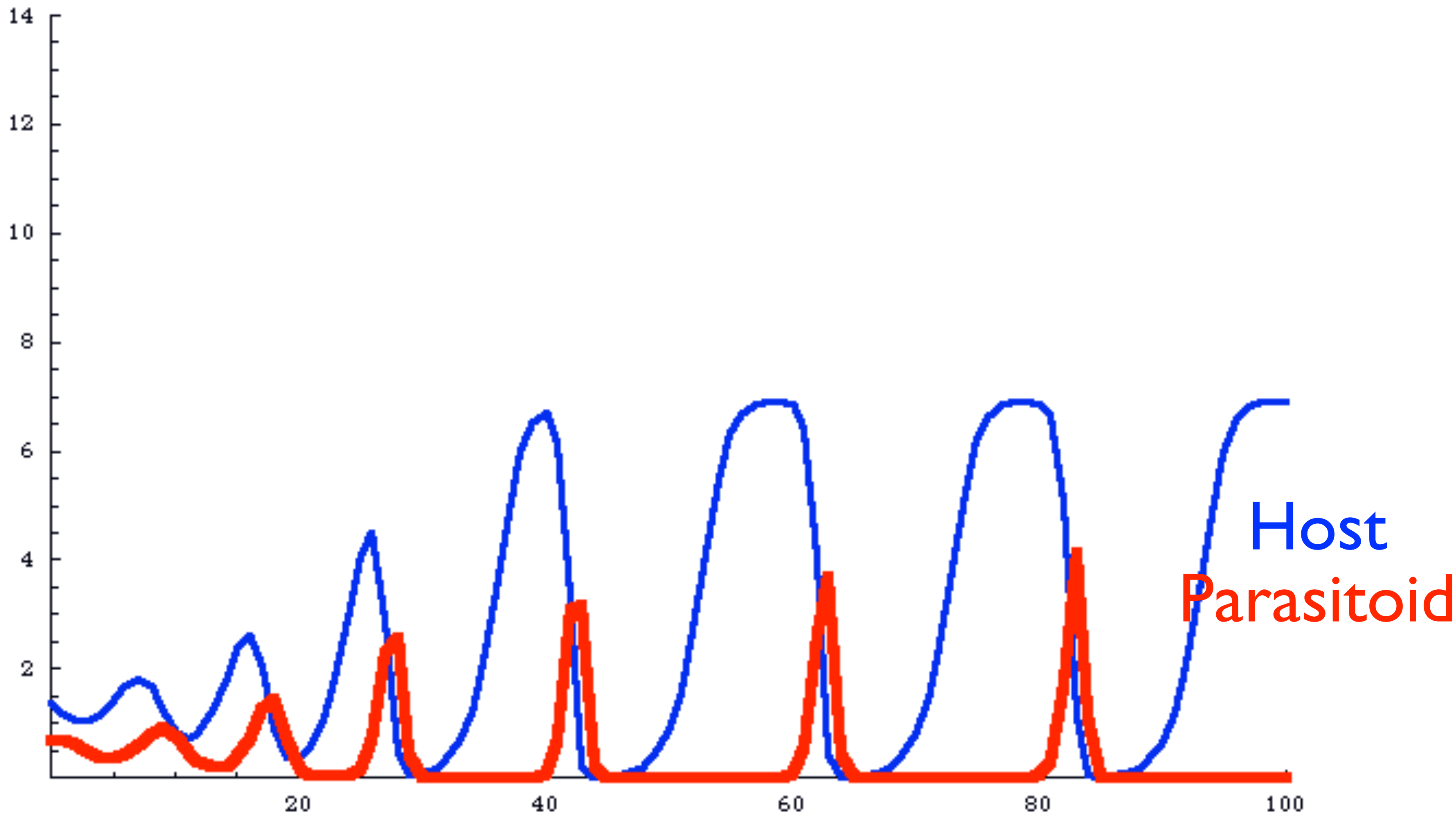


Nicholson-Bailey



Host
Parasitoid

NB plus compétition



Heterogeneity

Localisation

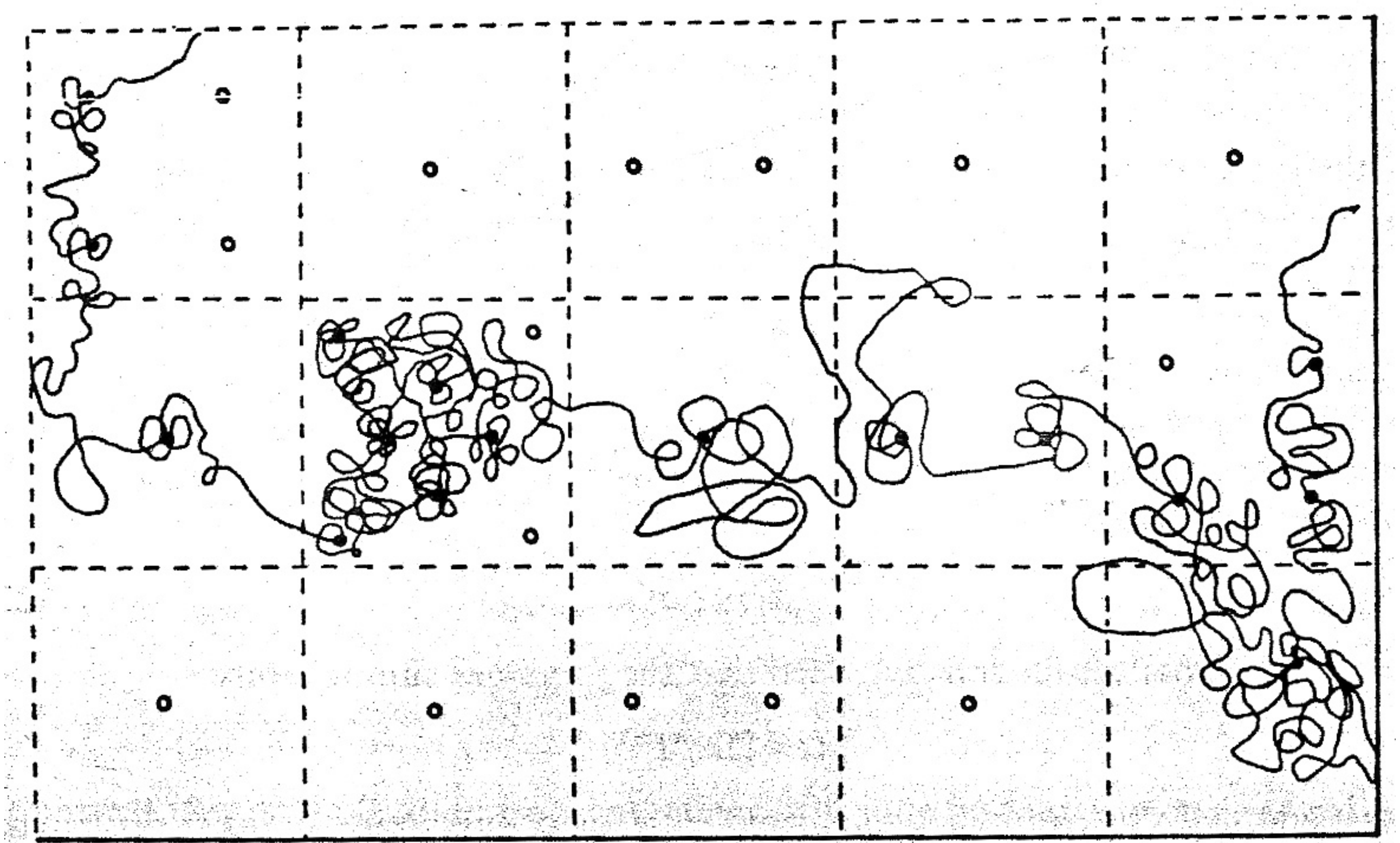
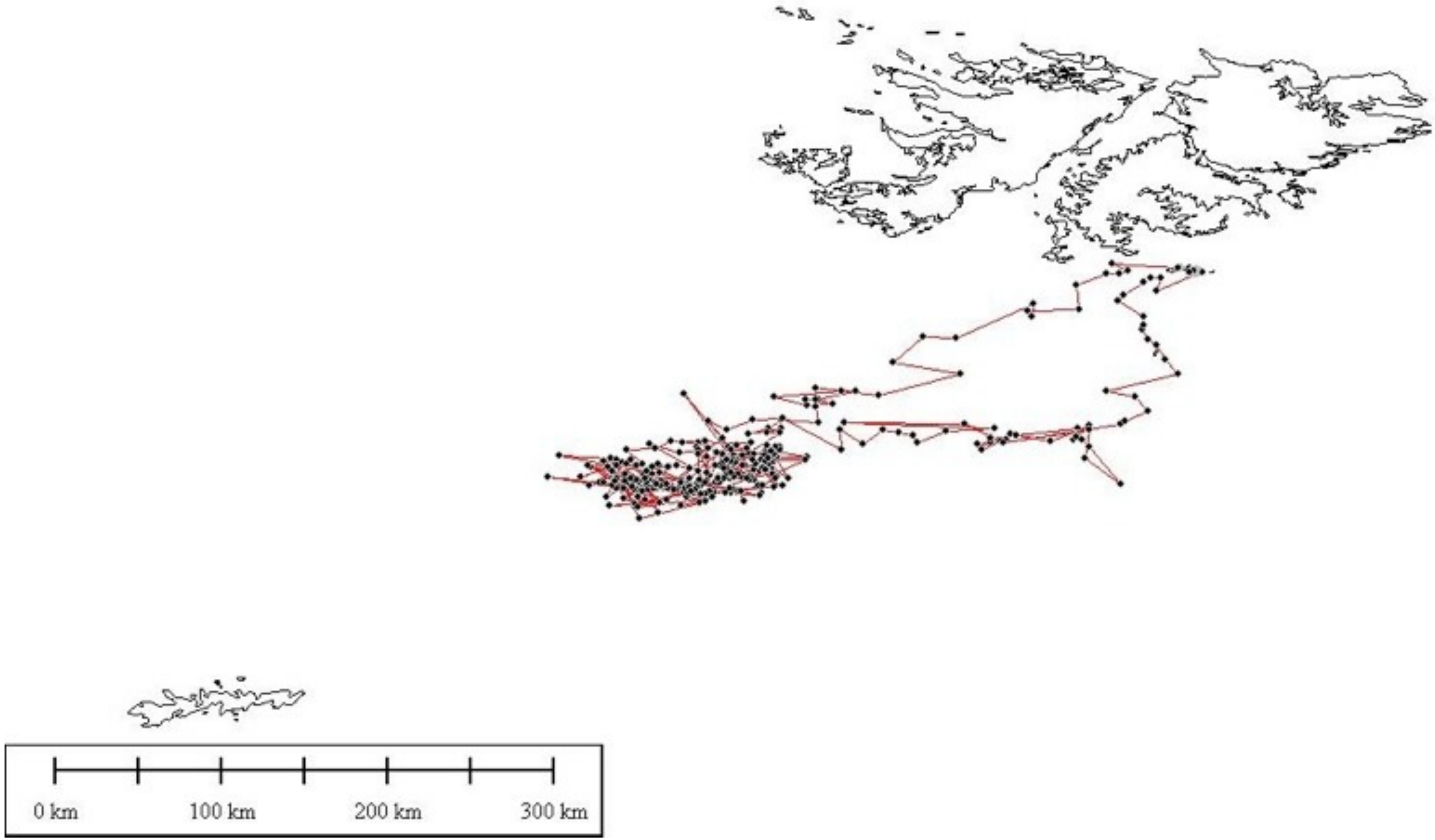


FIG. 9. Part of a track showing the movements of a tachinid parasite *Cyzenis albicans*, within an arena. The circles represent small drops of sugar solution upon which the parasite adults feed. The solid circles show where feeding occurred.

A Foraging Sea-Elephant



Heterogeneity

Hassell & May 1974

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

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

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

Aggregation

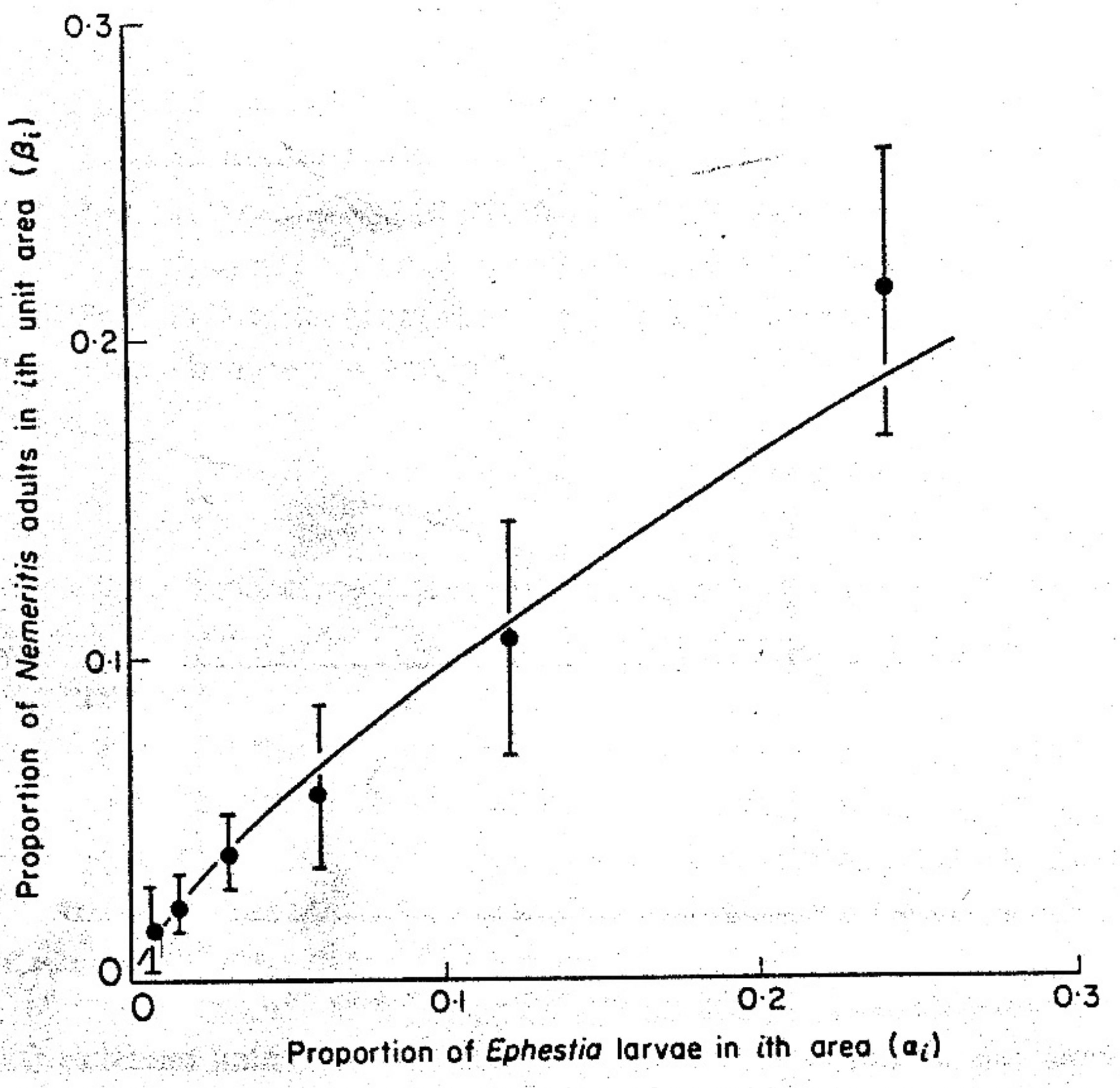
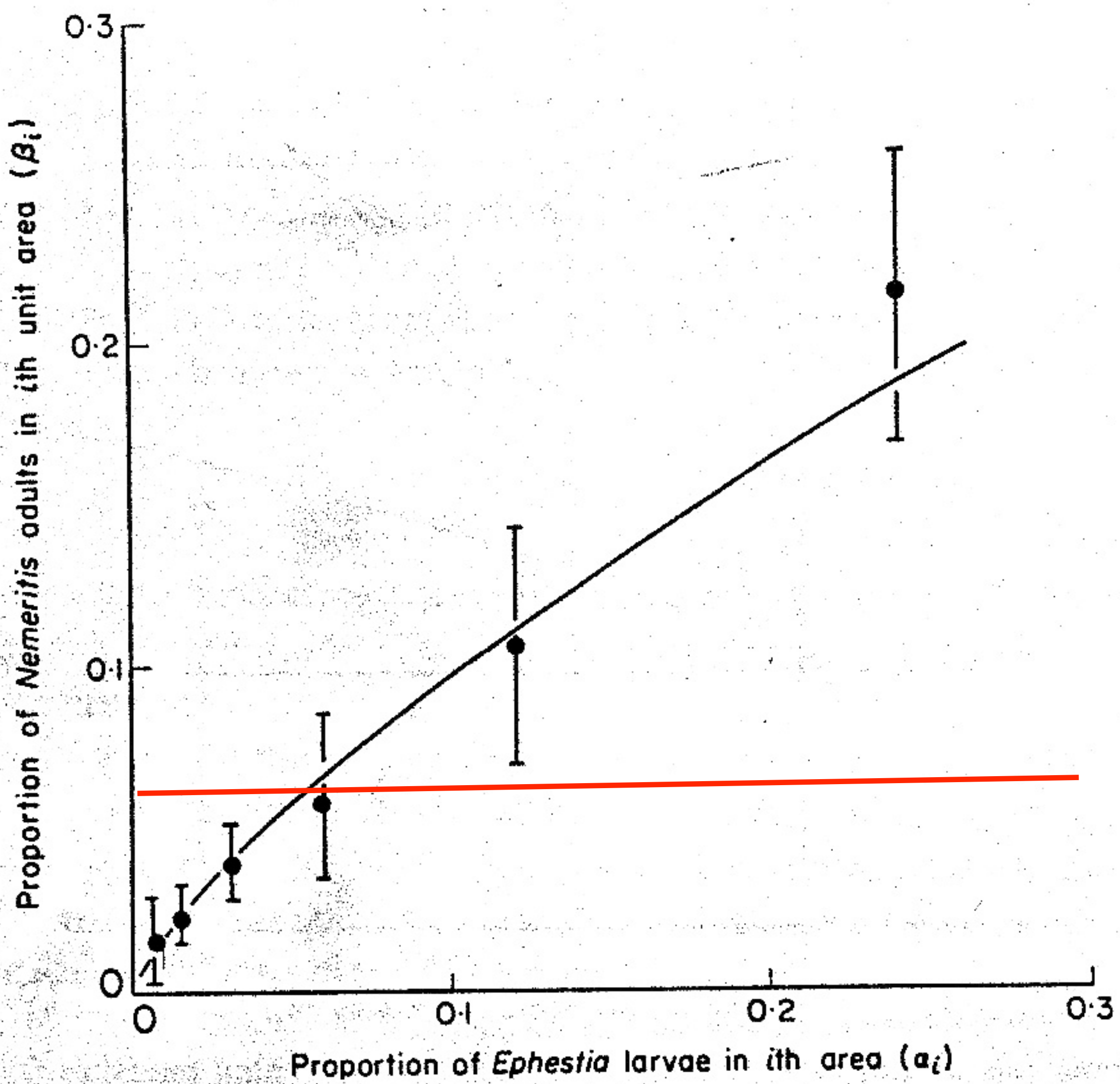


FIG. 11. The relationship between the proportion of searching *Nemeritis canescens* (β_i) and the proportion of *Ephestia cautella* larvae (α_i) per unit area from a laboratory interaction (Hassell 1971a, b). The fitted curve was derived by use of eqn (22). $\beta_i = 0{\cdot}53\ \alpha_i^{\ 0{\cdot}73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

Aggregation



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Space is Important

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

Space is a Pain

Space makes life difficult for theoreticians

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

Modeling Space

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

Reaction-diffusion

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

Reaction-diffusion

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

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

Reaction-diffusion

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

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

Multi-species Reaction-diffusion

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

Specifically the dynamics of the system is described by

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

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

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

Competition in Space

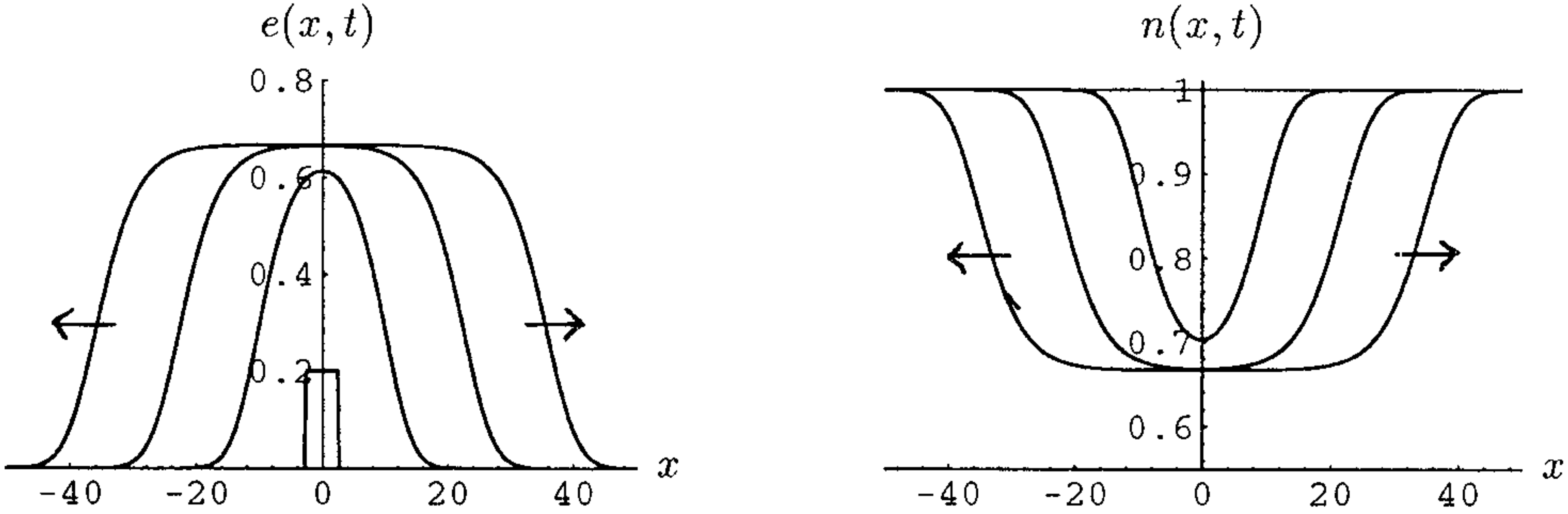


FIG. 1. A travelling wave solution connecting the native-dominant steady state to the coexistence steady state in a spatially uniform environment. Parameter values used were $\gamma_e = \gamma_n = 0.5$, $D(x) = d(x) = G(x) = g(x) = 1$, and $r = 2$, so that the coexistence state is the only stable state.

Diffusion approach

Advantages

- many mathematical tools

Disadvantages

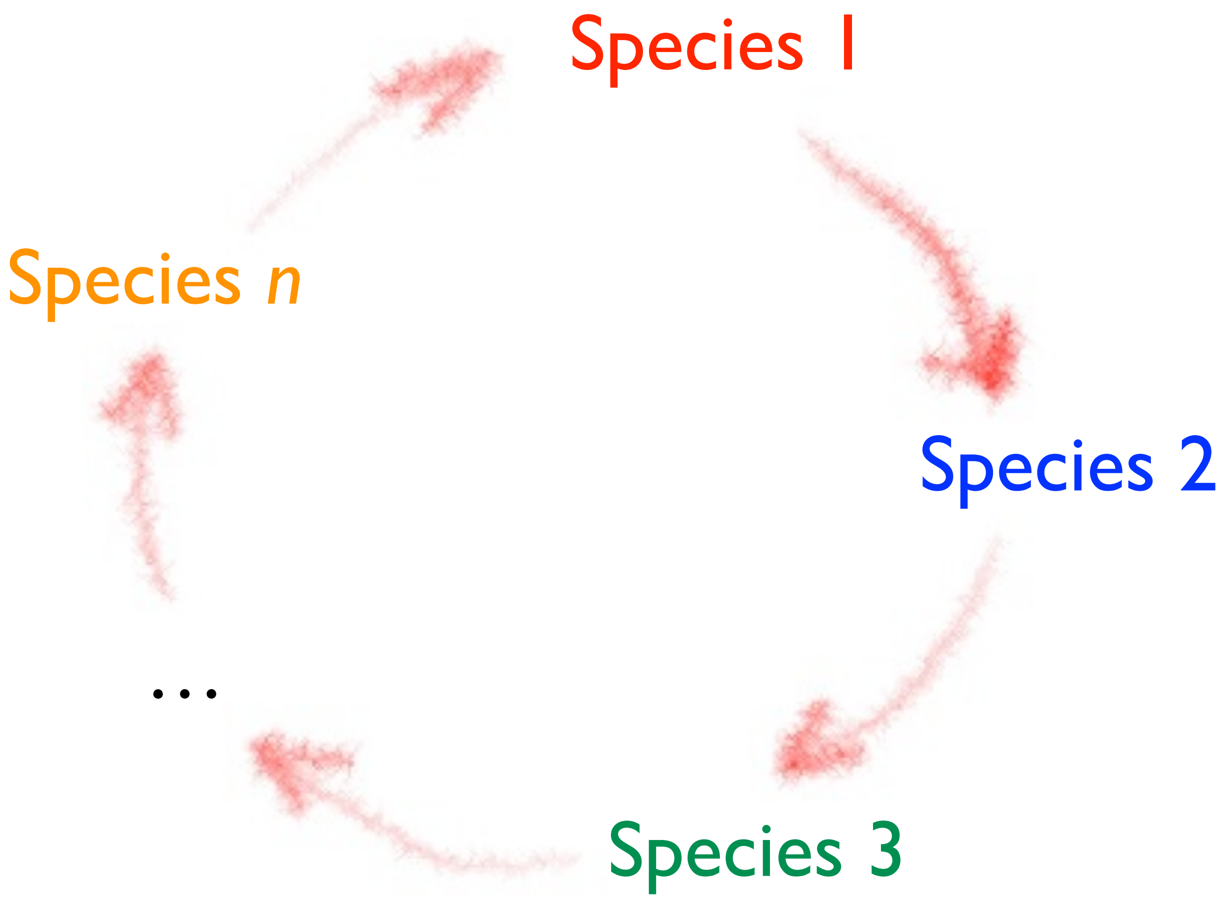
- becomes very difficult if movement is non-random
- becomes very difficult if individuals are ‘large’

Individuality

Individuality is crucially important

- in particular in spatially explicit settings
- demographic stochasticity inevitable

Hypercycle



Hypercycle

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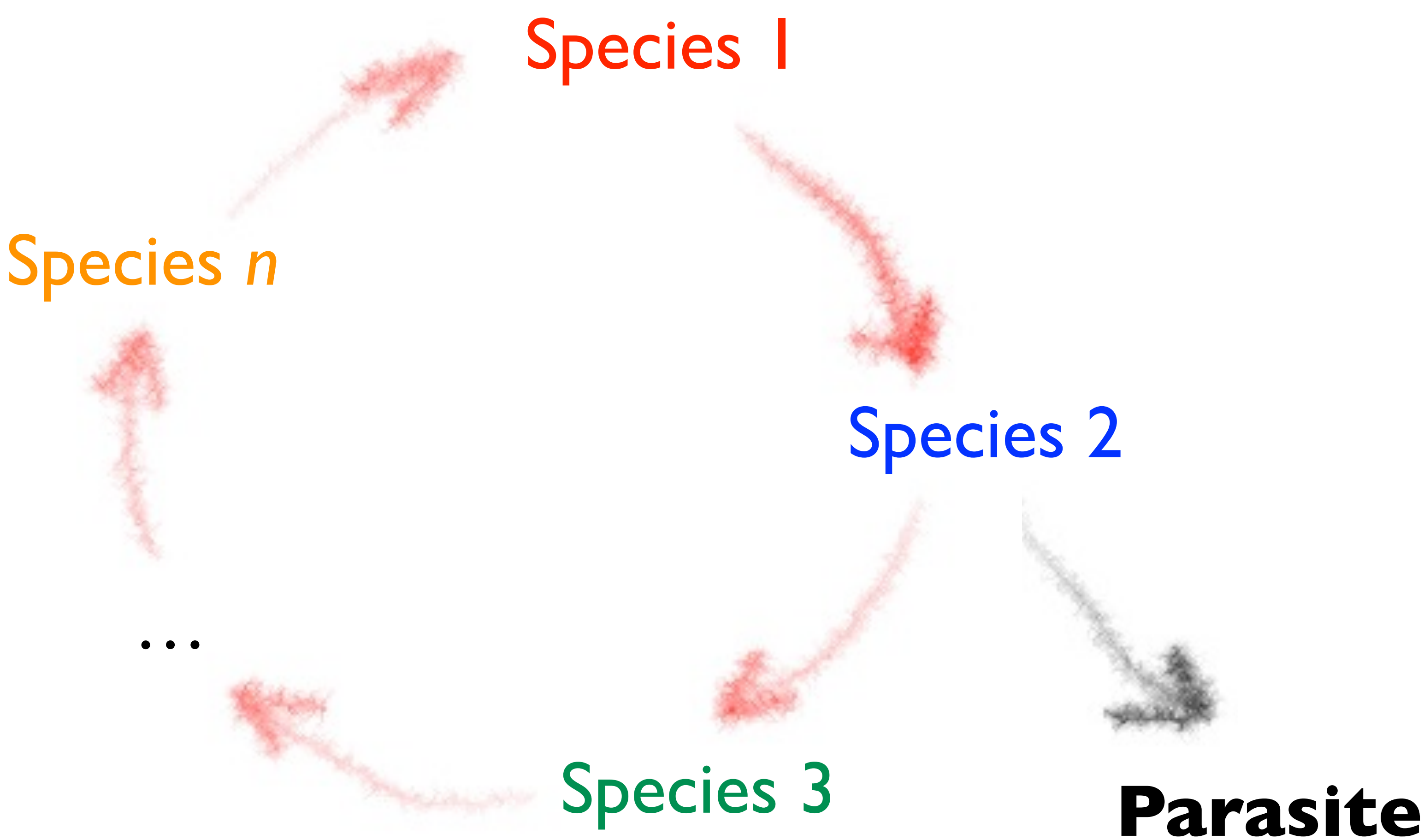
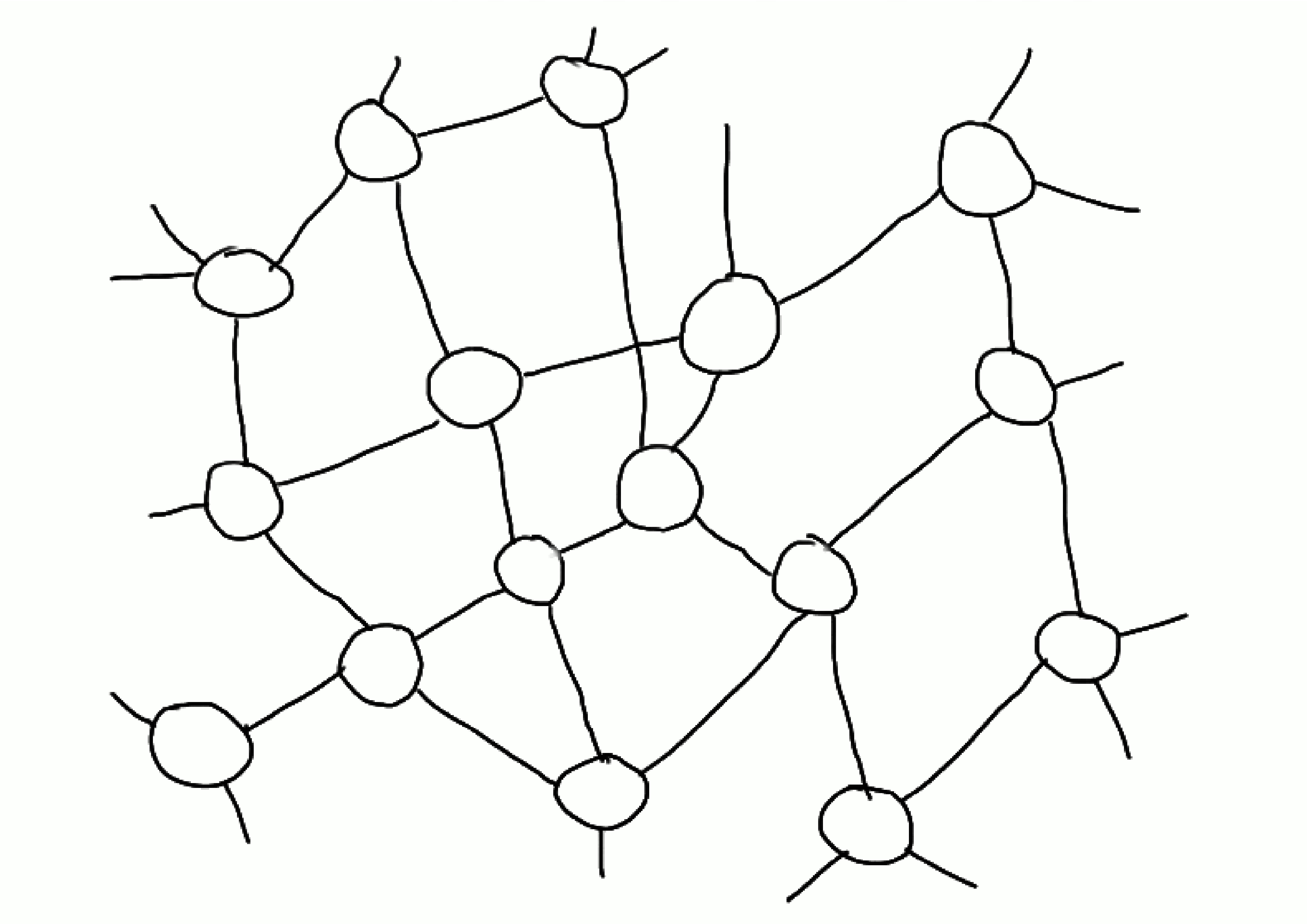


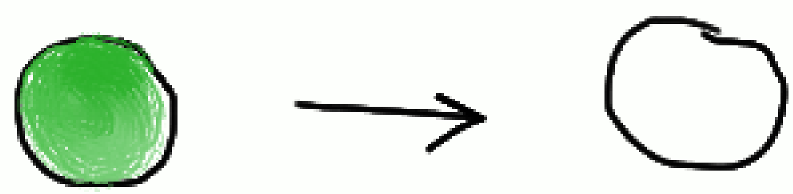
Hypercycle

Parasite

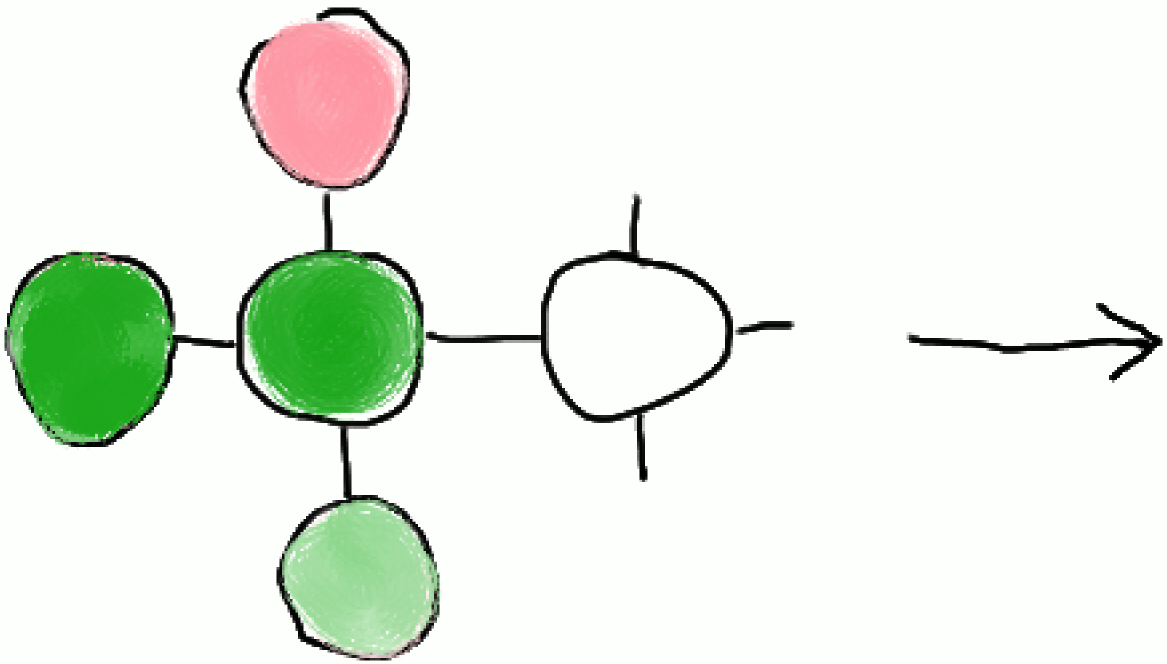
A Lattice of Sites



Death



Faithful Reproduction



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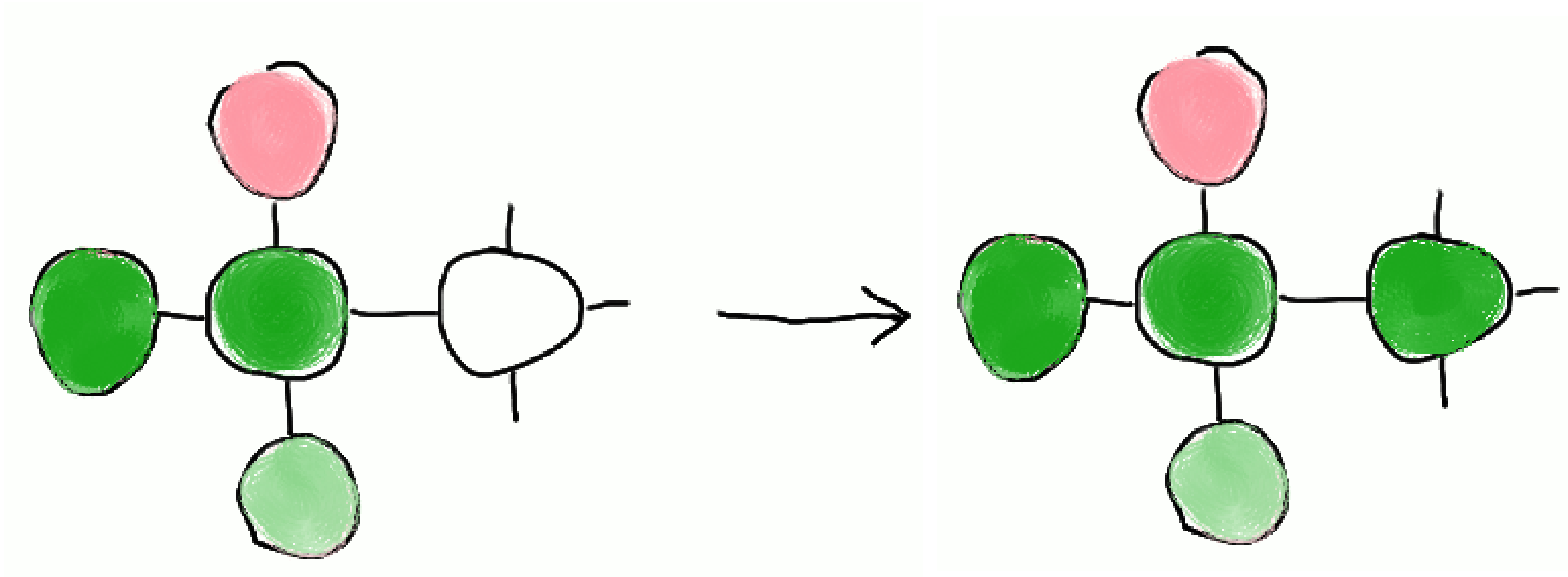
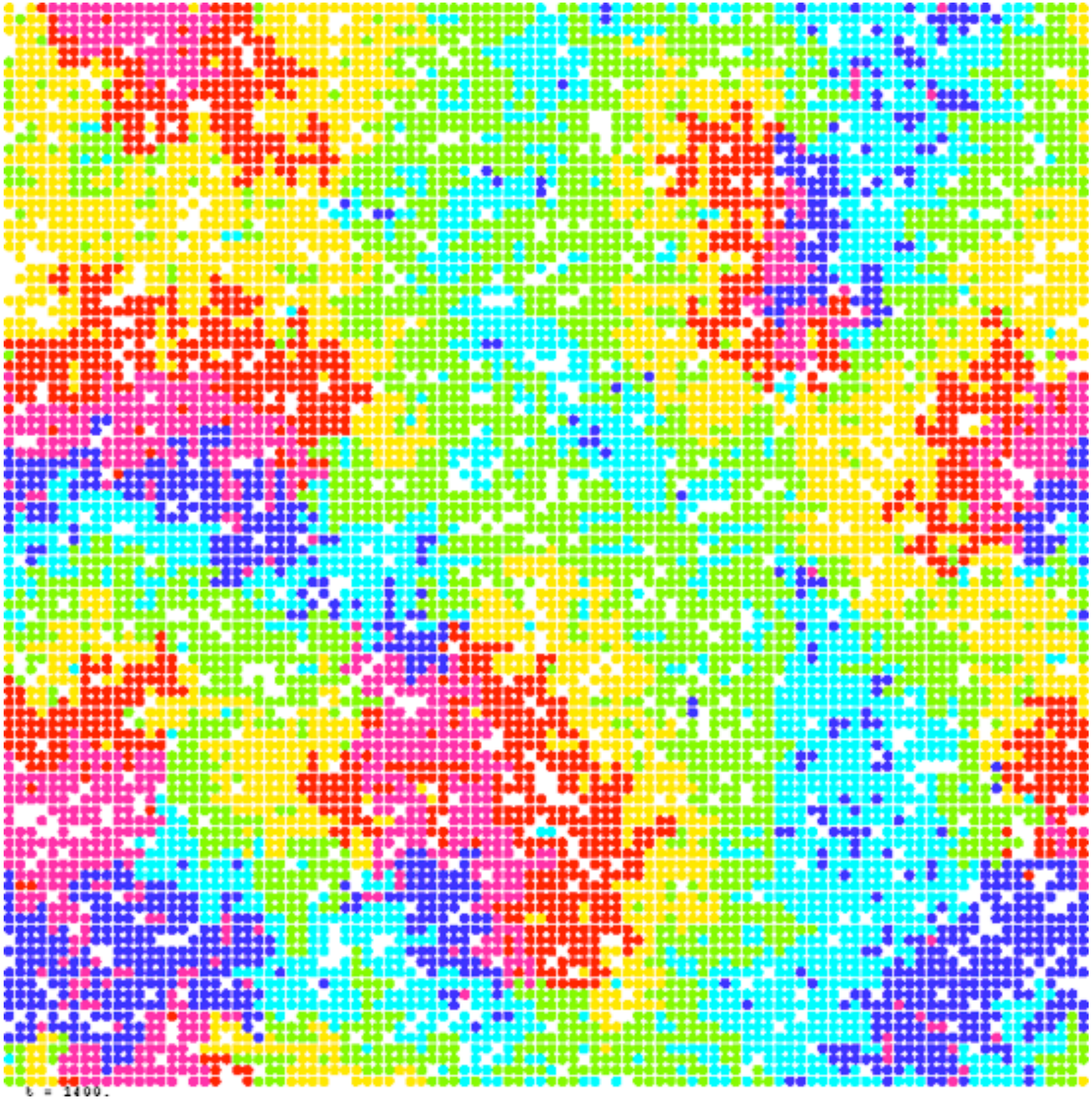
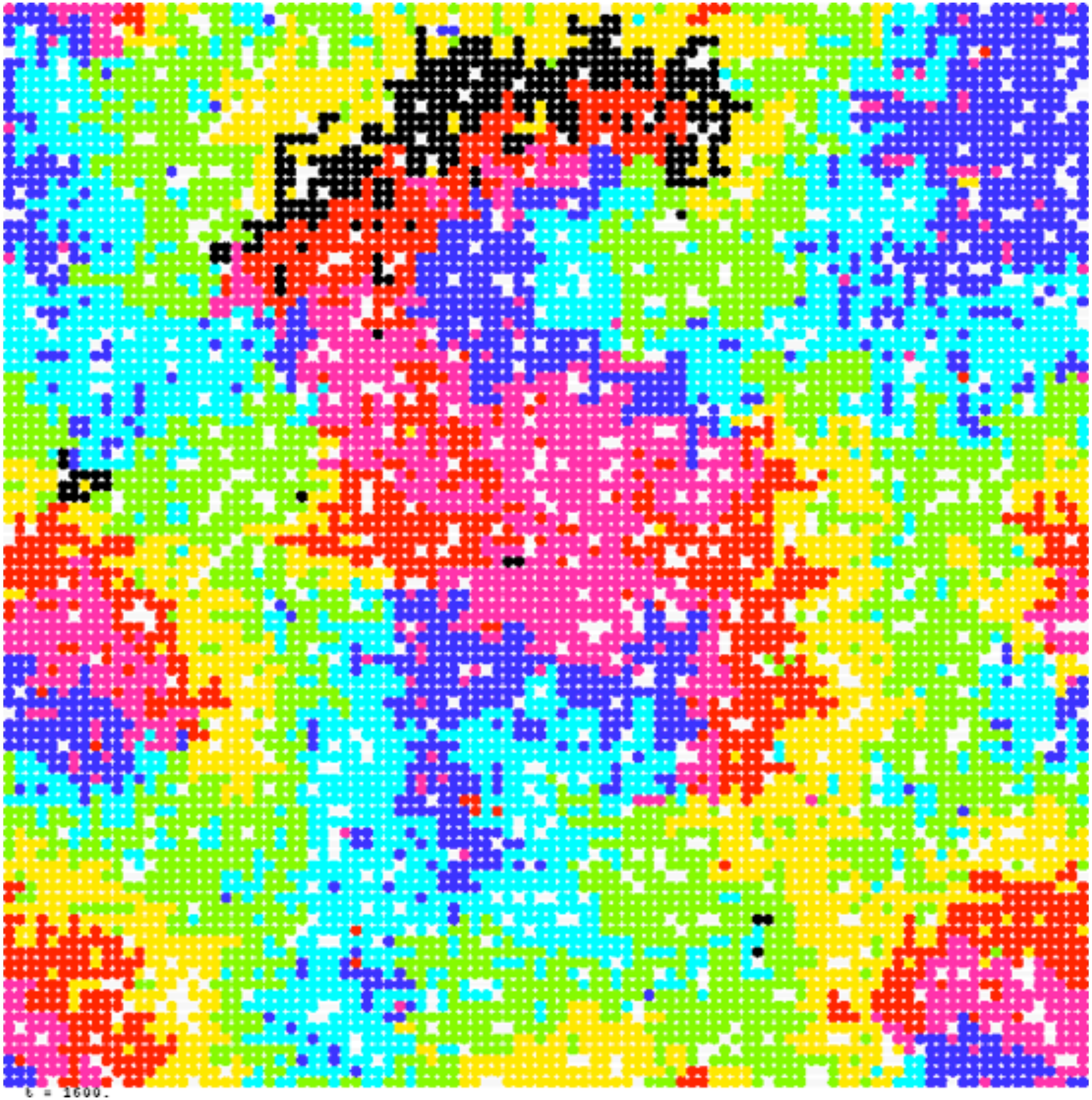




Boerlijst & Hogeweg's (1991)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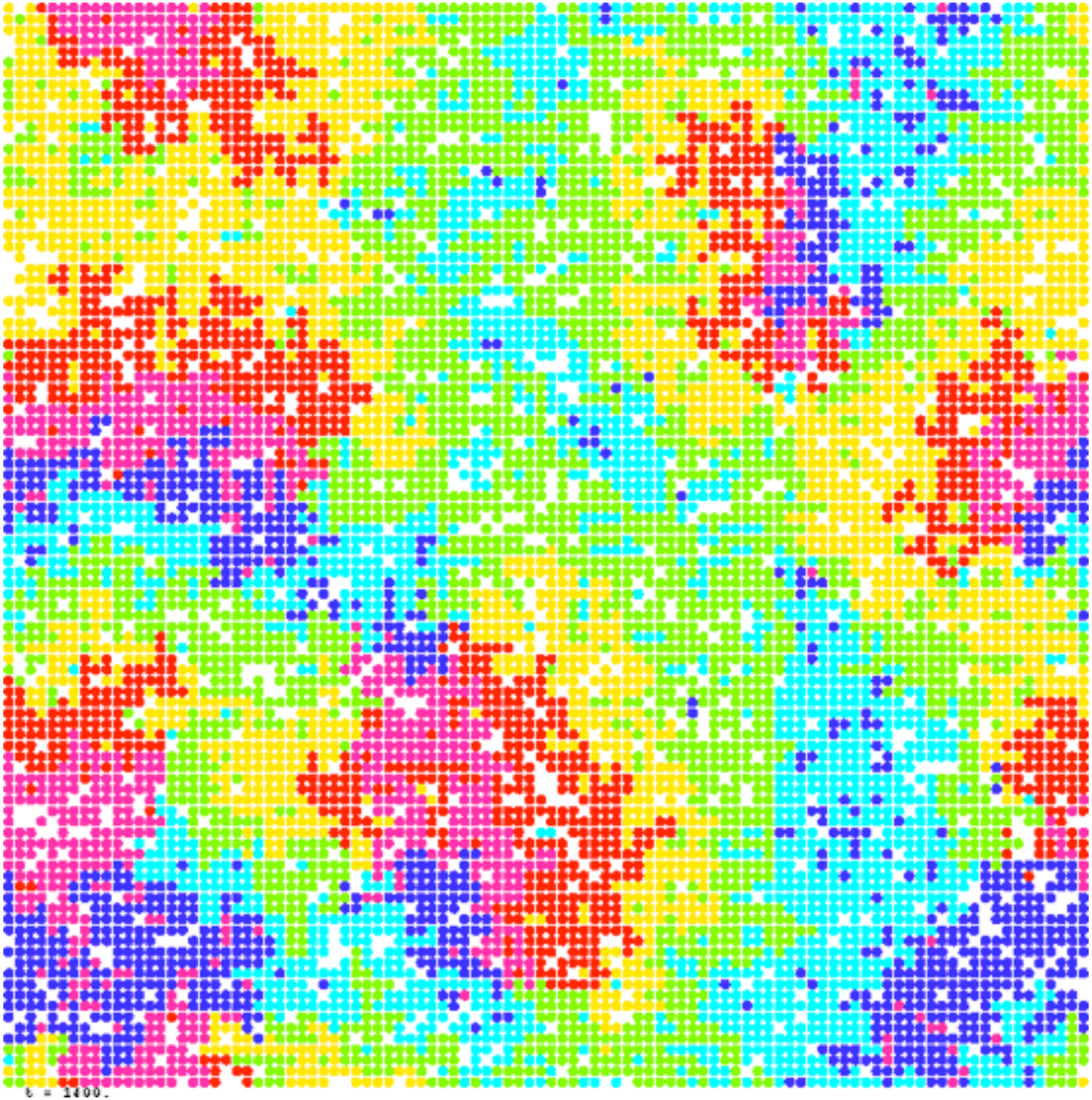

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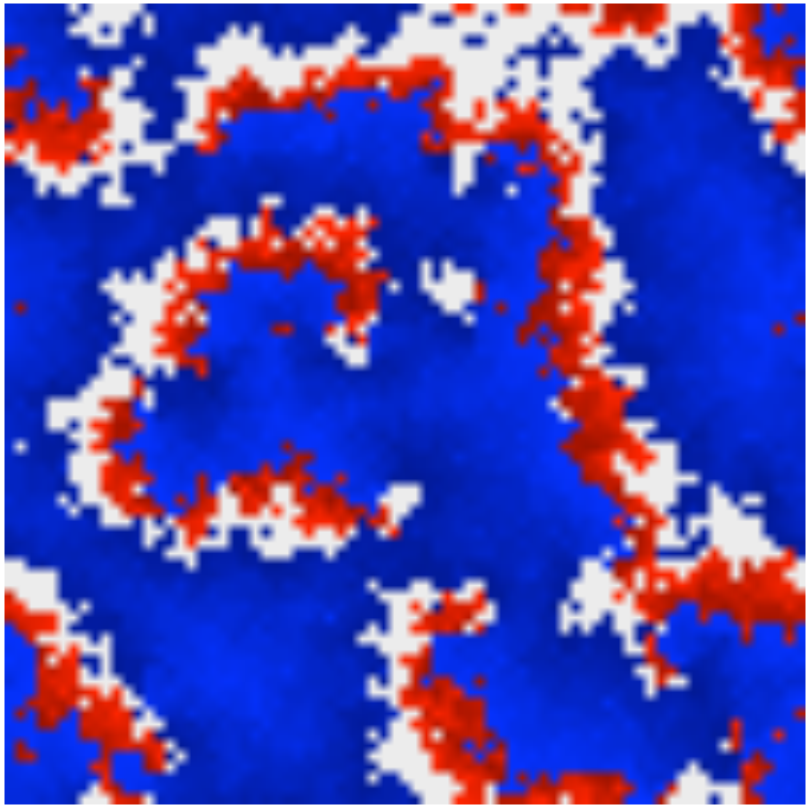


van Ballegooijen & Boerlijst 2004

Spatial Hypercycles

Boerlijst & Hogeweg's (1991) hypercycles

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

Spatial evolution

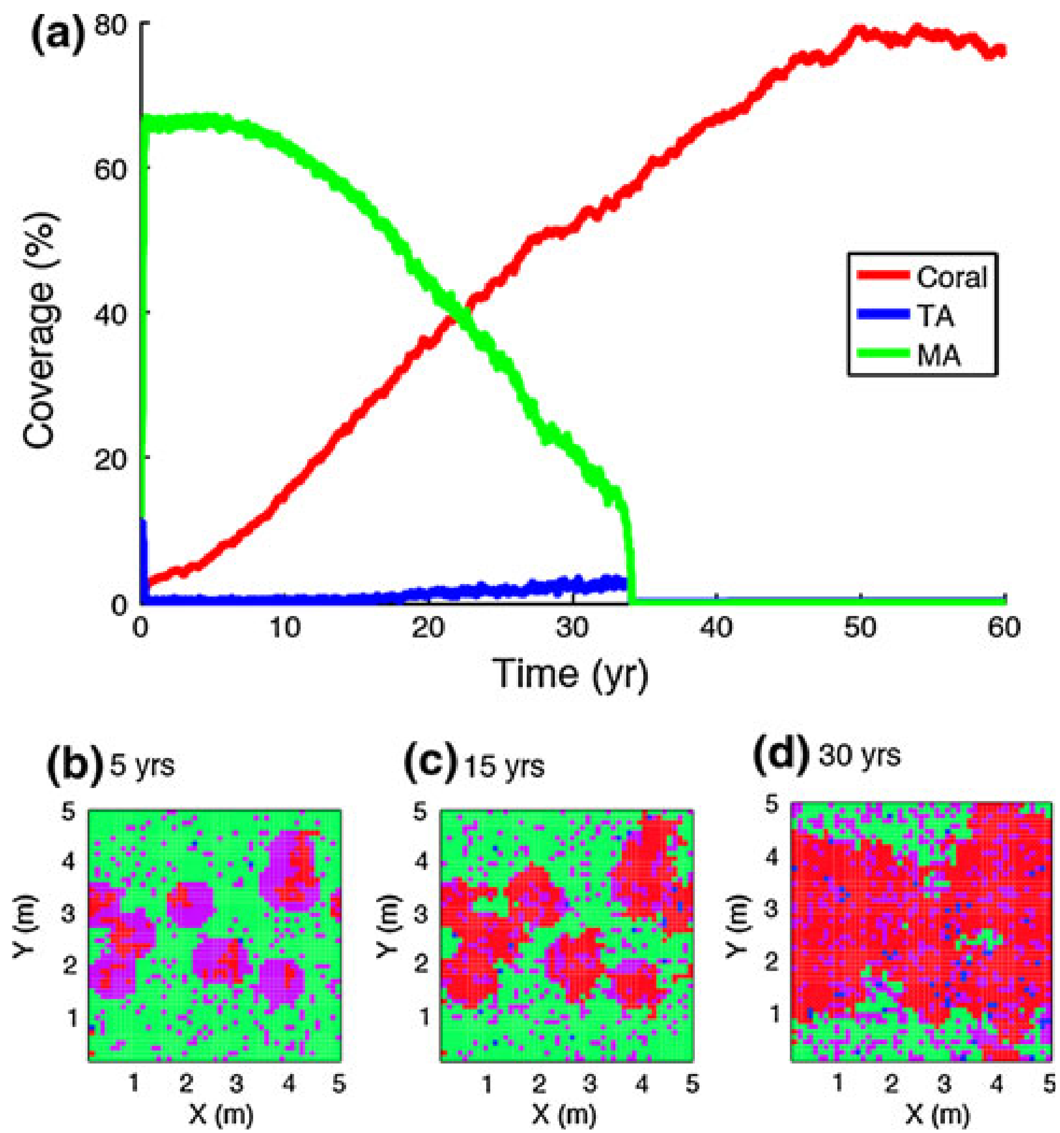
Spirals 'unit of selection'

- Rotation speed selected trait

But:

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

Coral Dynamics



Sandin & McNamara 2012

Cellular Automata

+ Nice toys

+ Colourful movies

– Difficult to generalise

– Difficult to obtain deeper insight

Viscous populations

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)

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

Bookkeeping

state of the lattice

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

Morris (1997)

event rate

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

Bookkeeping

state of the lattice

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Morris (1997)

event rate

$\delta t \to 0$

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Bookkeeping

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Morris (1997)

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"$\delta t \to 0$"

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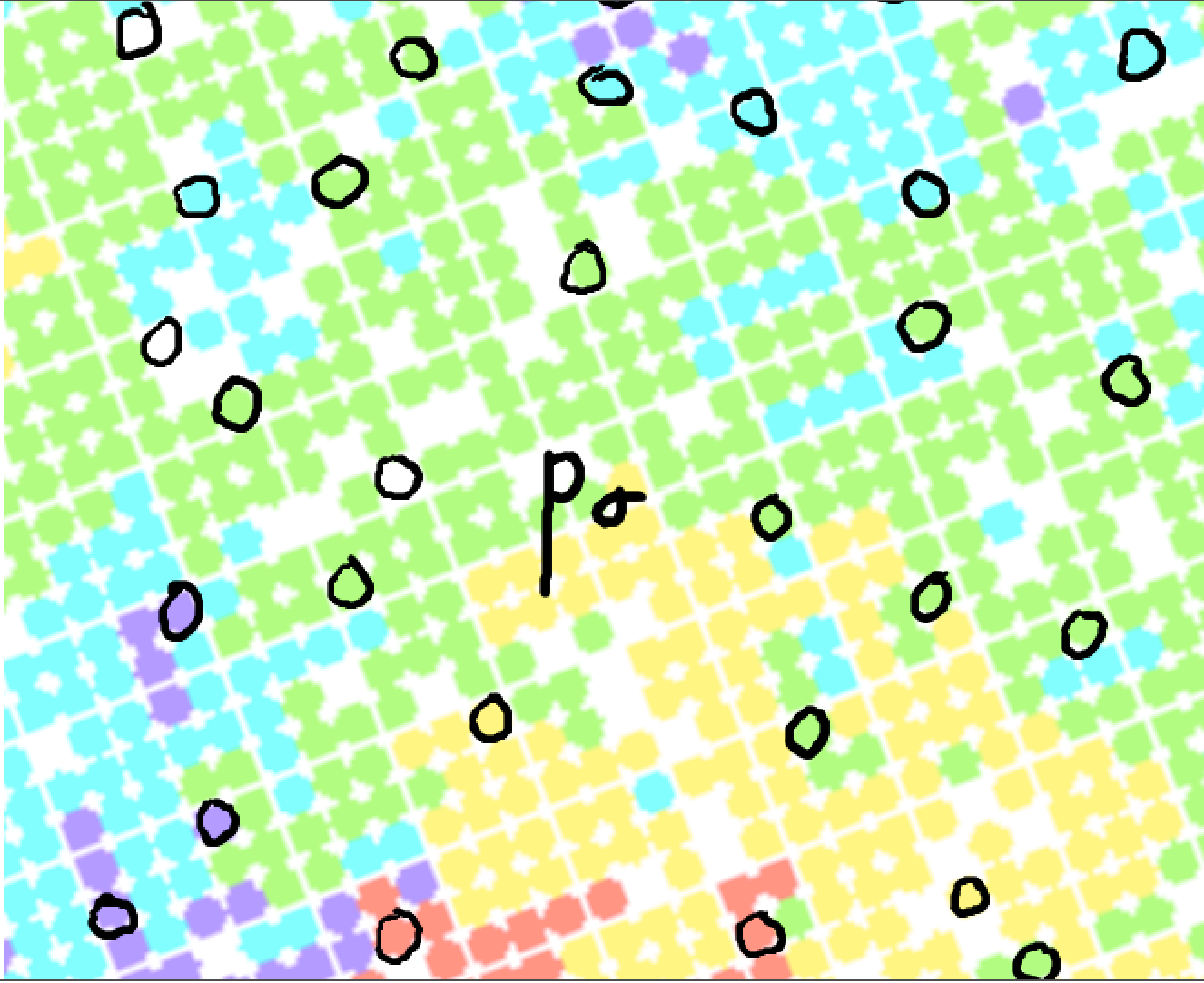
Bookkeeping


pσ

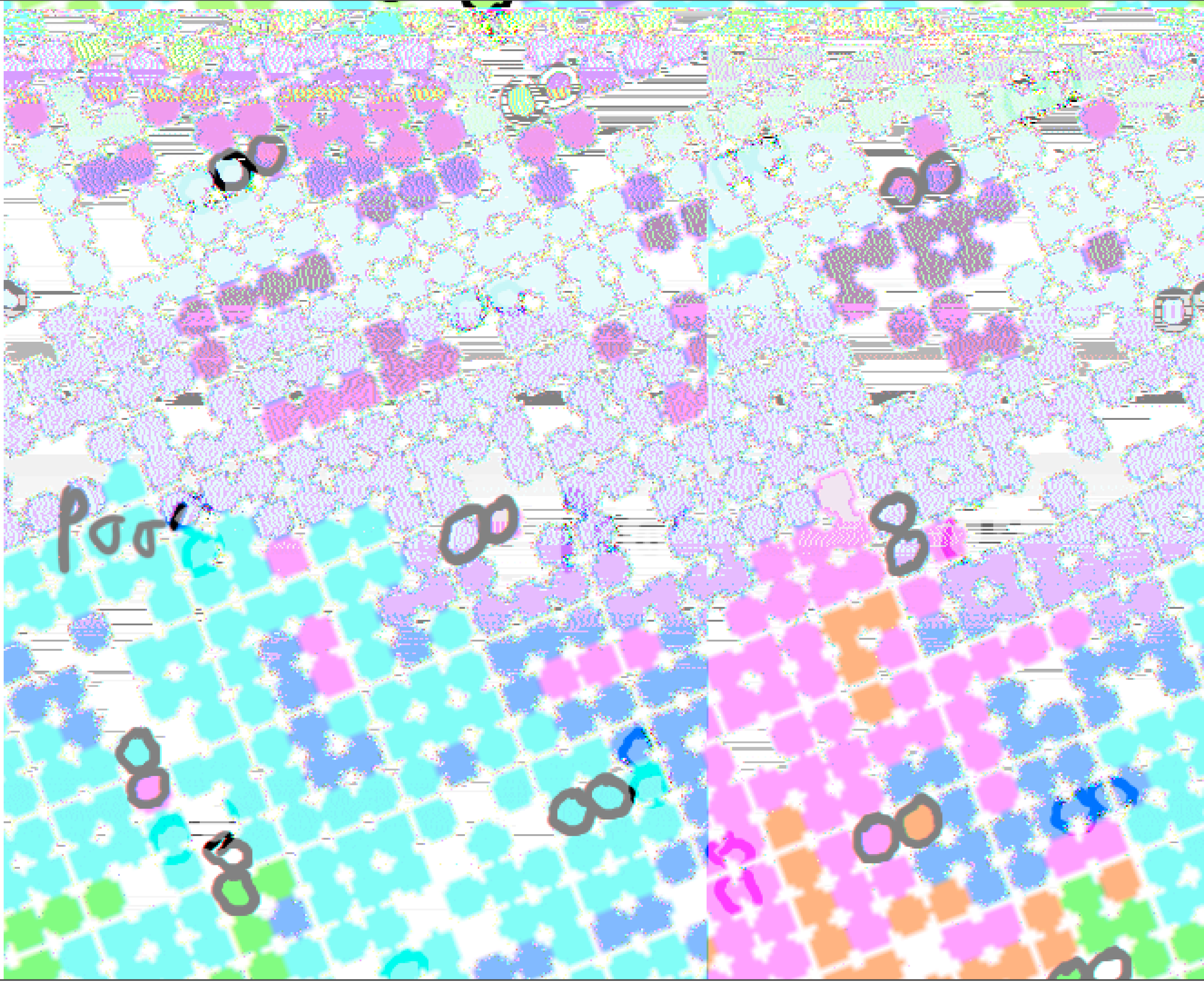
Dynamics of densities

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

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

[redacted]

no space
("mean field")



Pairs of Neighbours

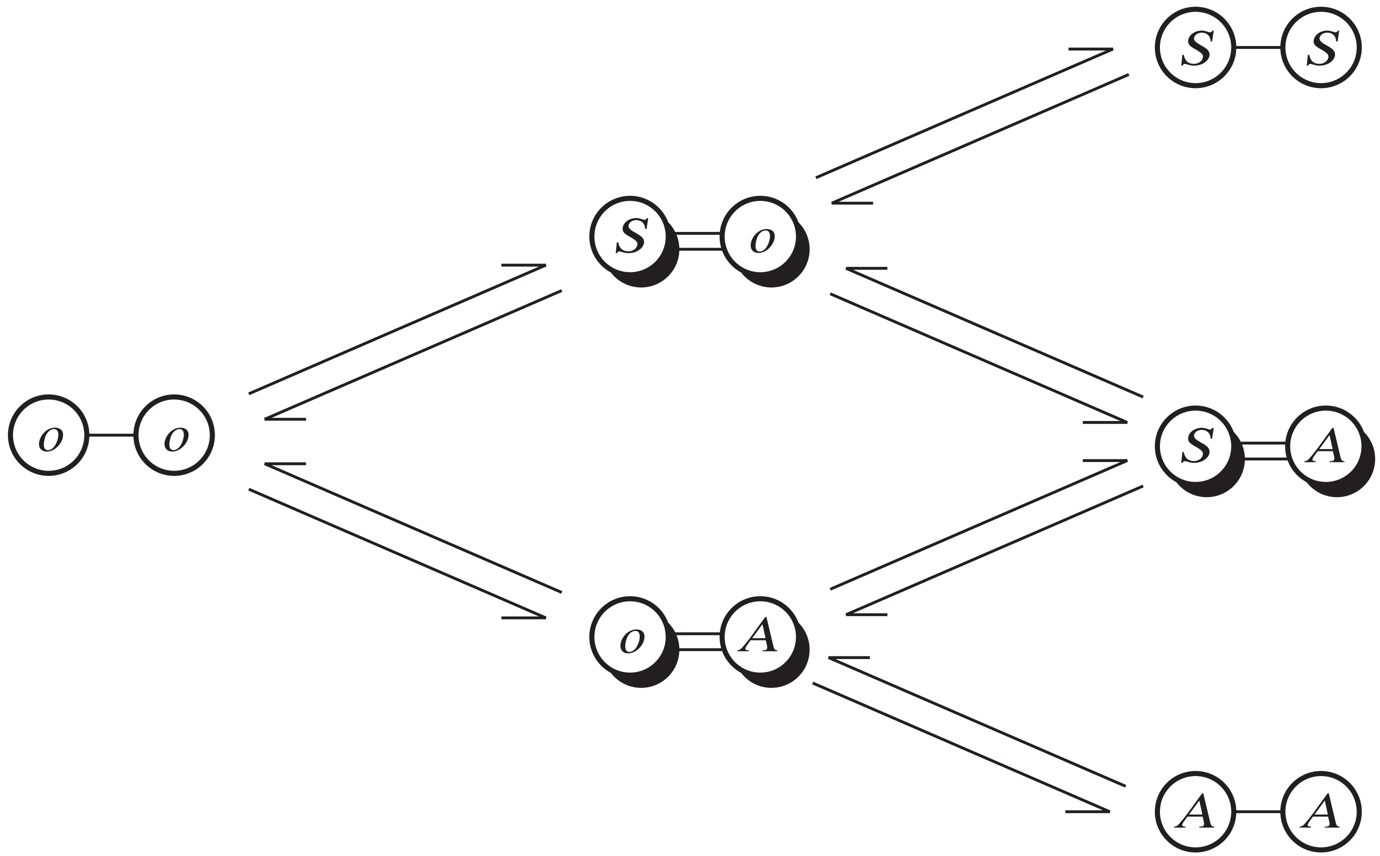


FIG. 2. The possible transitions between the state of doublets (pairs of neighbouring sites). Pairs that have a symmetric counterpart are shaded.

Correlation Dynamics

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

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

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

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

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

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

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

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

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

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

A Cascade

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

Closure approximation

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

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

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

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

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

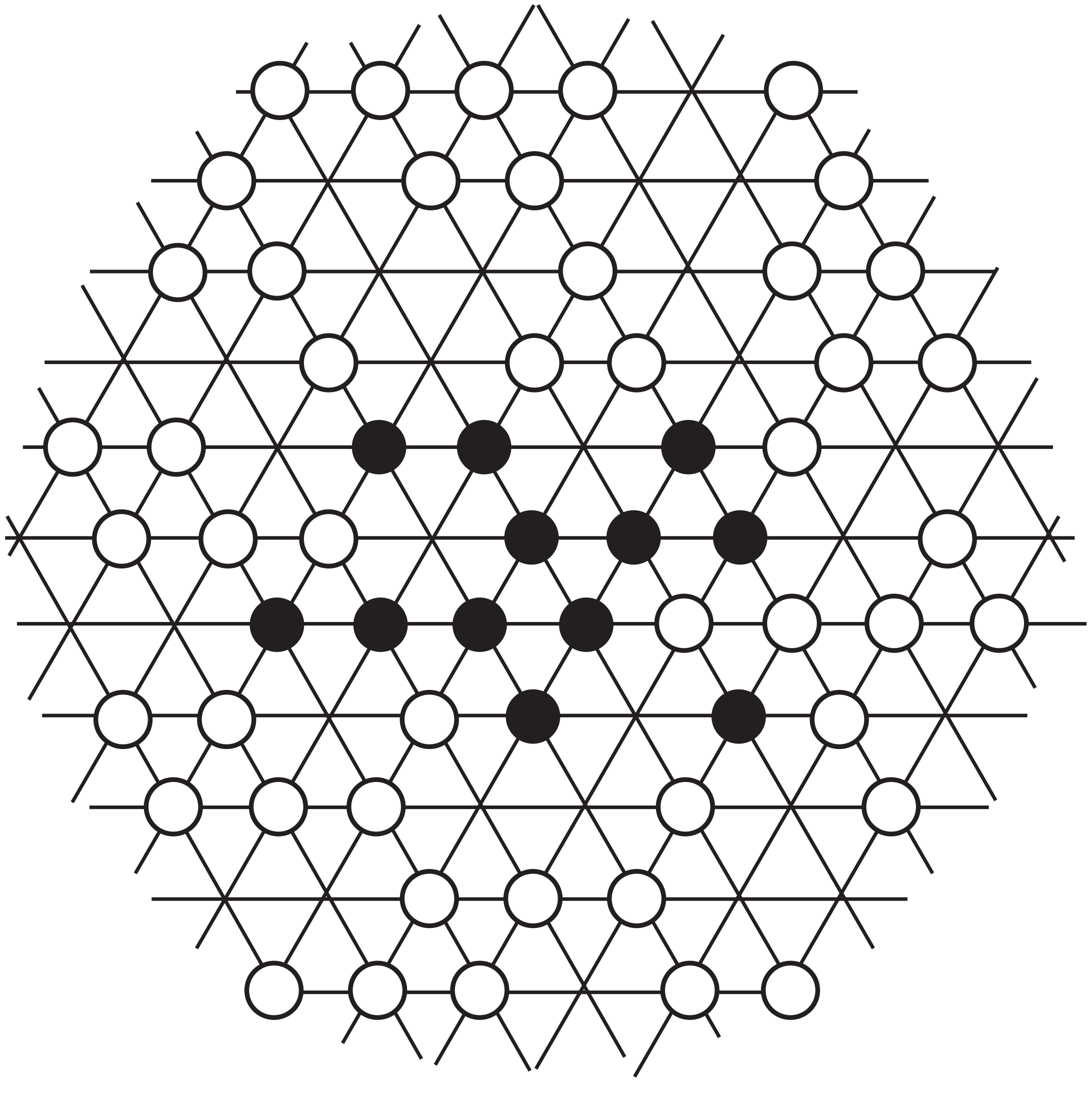
Invasion of a mutant

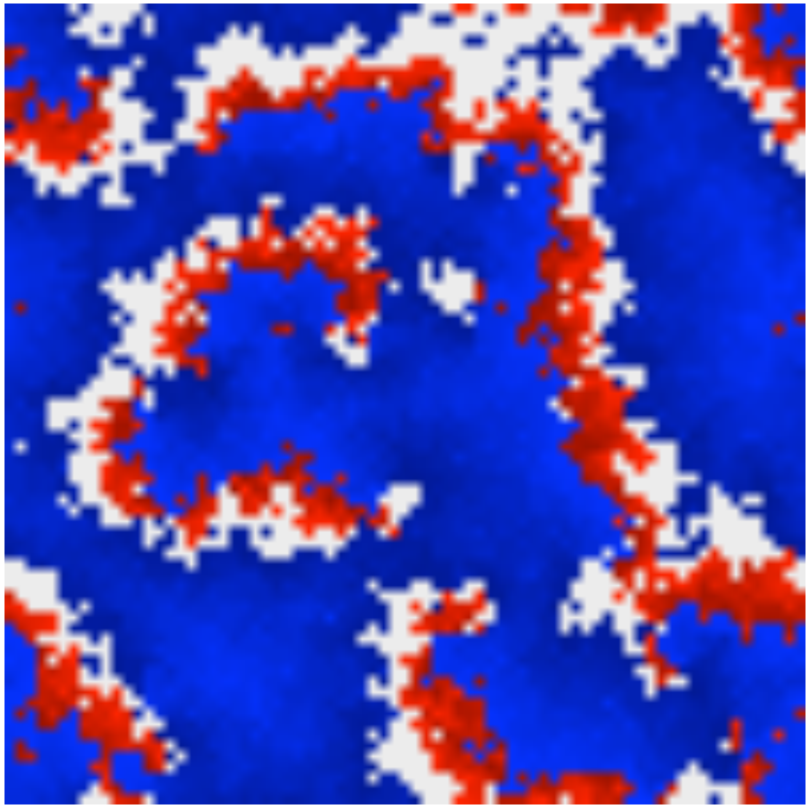
$$\frac{\mathrm{d}\mathbf{p}_A}{\mathrm{d}t} = \mathbf{M}(\mathbf{q}_A)\mathbf{p}_A$$

Dynamics of mutant given by sets of equations

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

Unit of adaptation





van Ballegooijen & Boerlijst 2004

ecosystem

biodiversity, nutrient cycles

population

competition, predation, epidemiology, social interactions

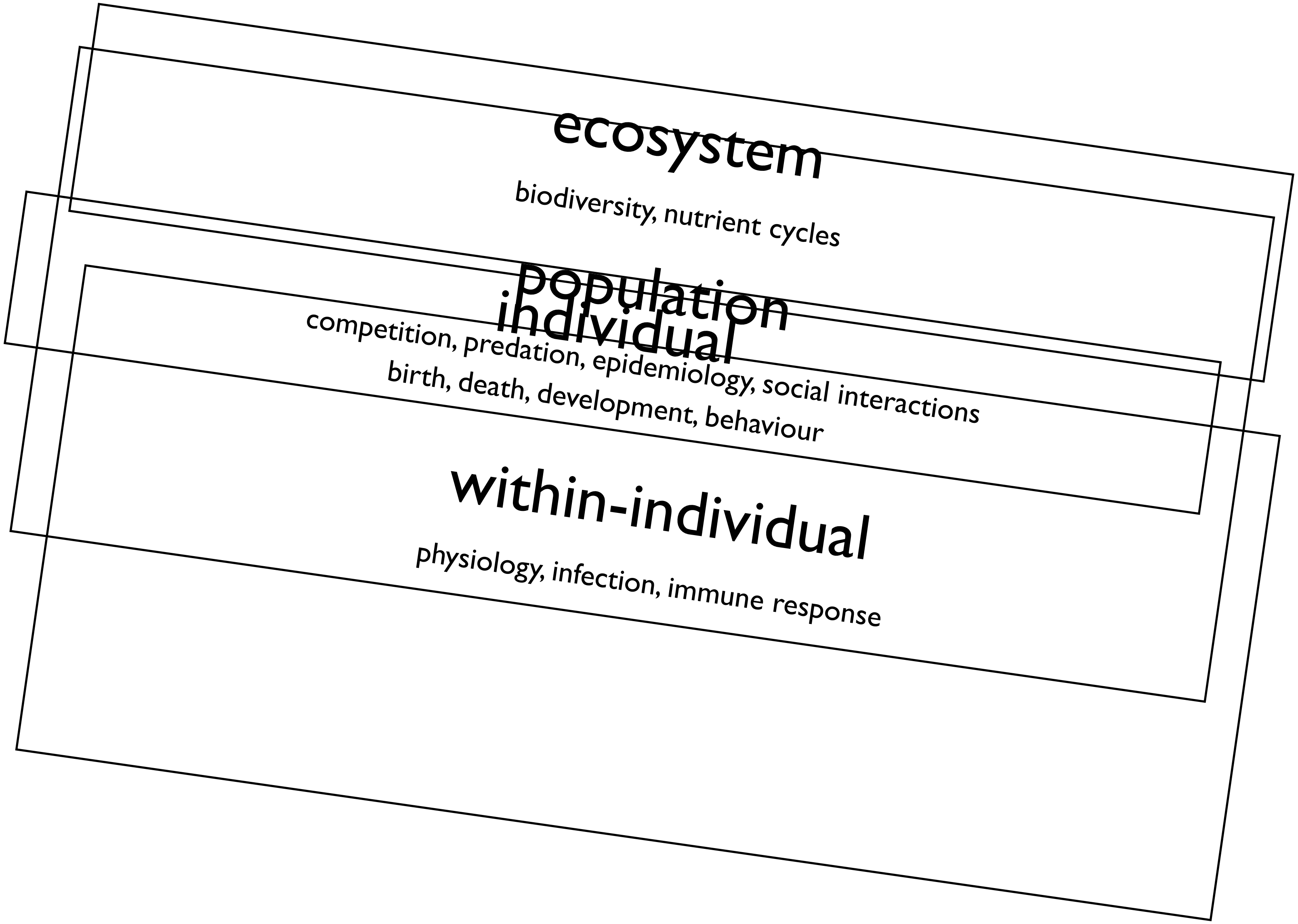
individual

birth, death, development, behaviour

within-individual

physiology, learning, infection, immune response

Levels of organisation



Consequence of Space

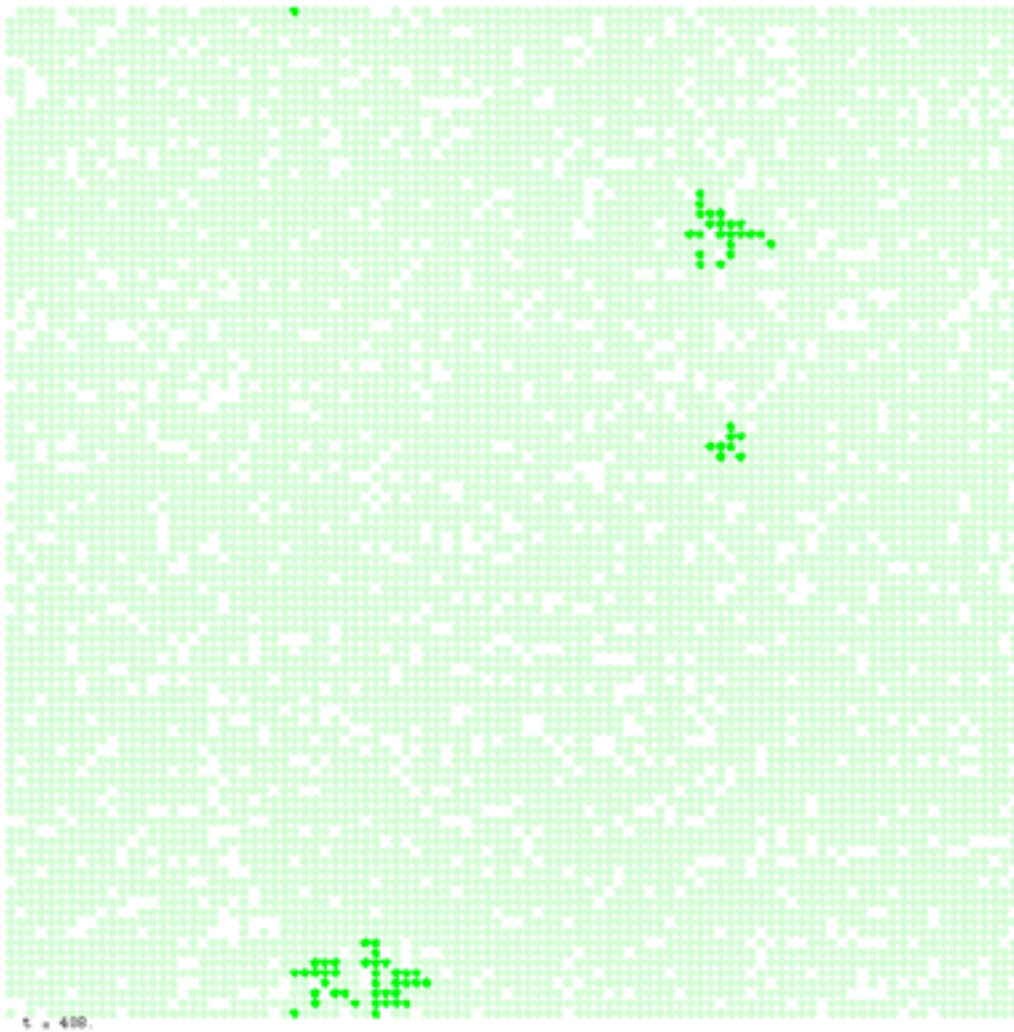
jeudi 19 septembre 2013

ALLES IS OVERAL

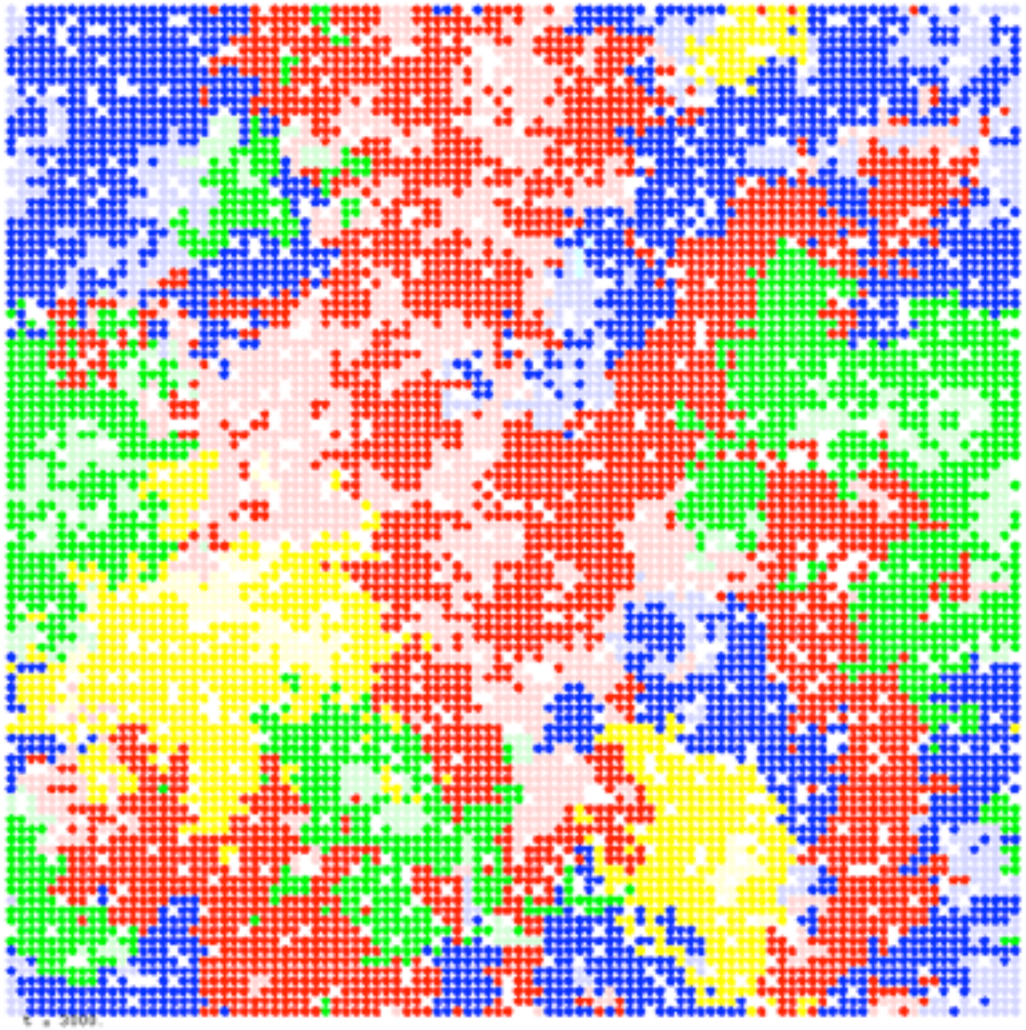
maar het milieu selecteert

EVERYTHING IS EVERY WHERE

but the environment selects



van Baalen & Jansen (2006)



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