Spatially Structured Populations

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Space

Why space is important

Different theoretical approaches

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

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 Populations

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

Parasitoïde

http://www.idw-online.de

cherchant des larves cachés

CPB Silwood Park

de *Drosophila melanogaster*

Oviposition

http://muextension.missouri.edu

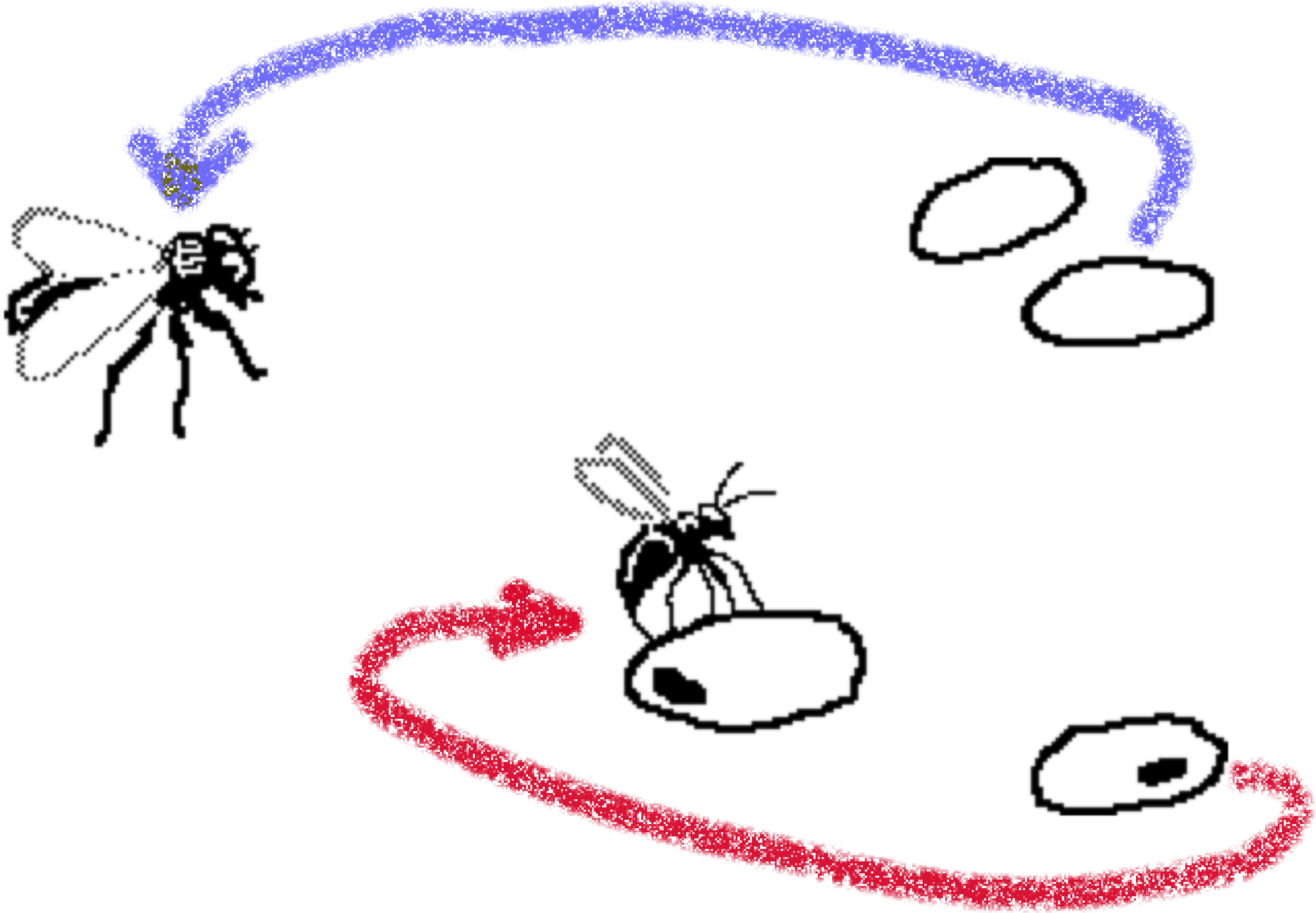
Oviposition

http://www.anbp.org

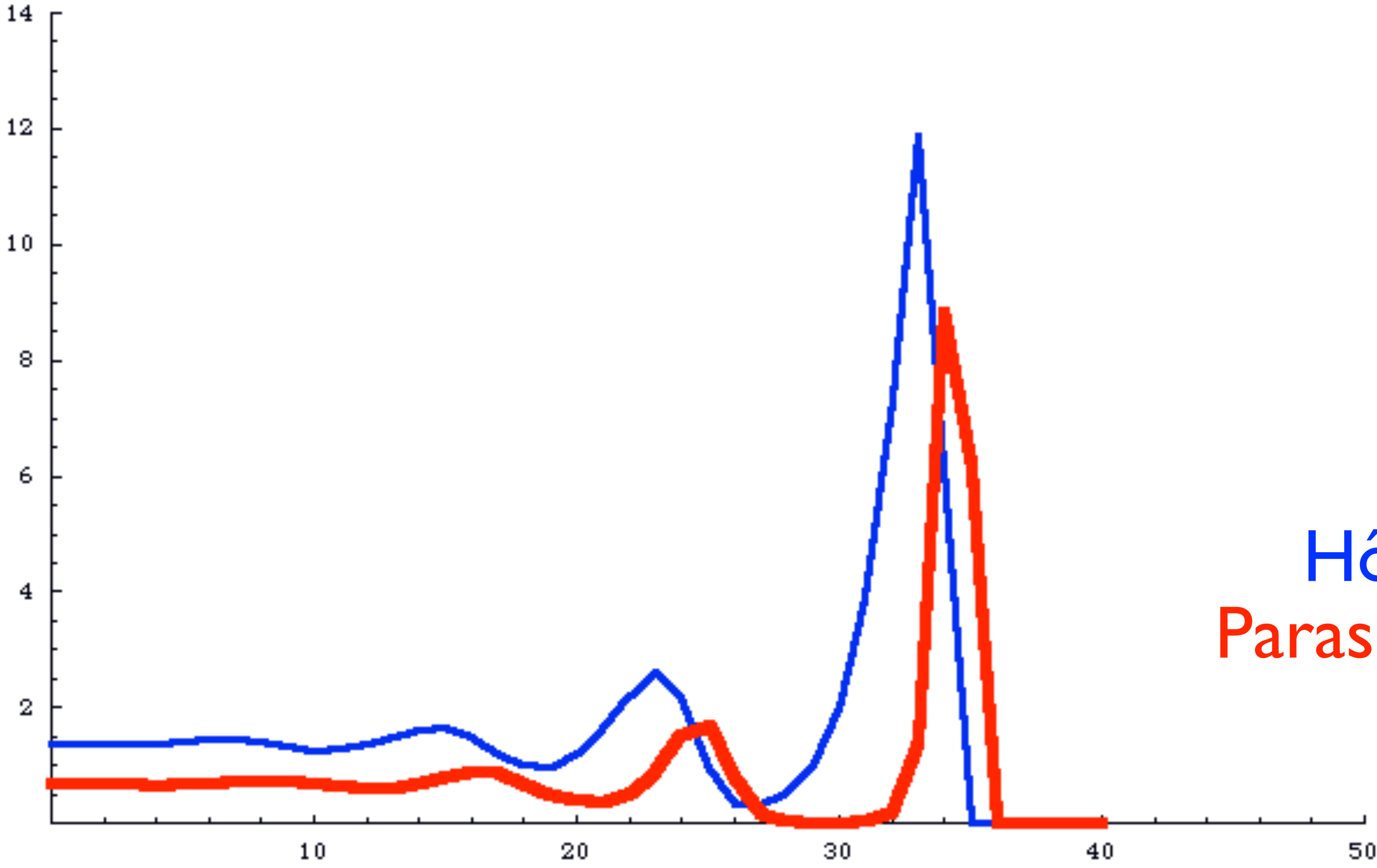
Emergence

http://whatcom.wsu.edu

Cycle de vie

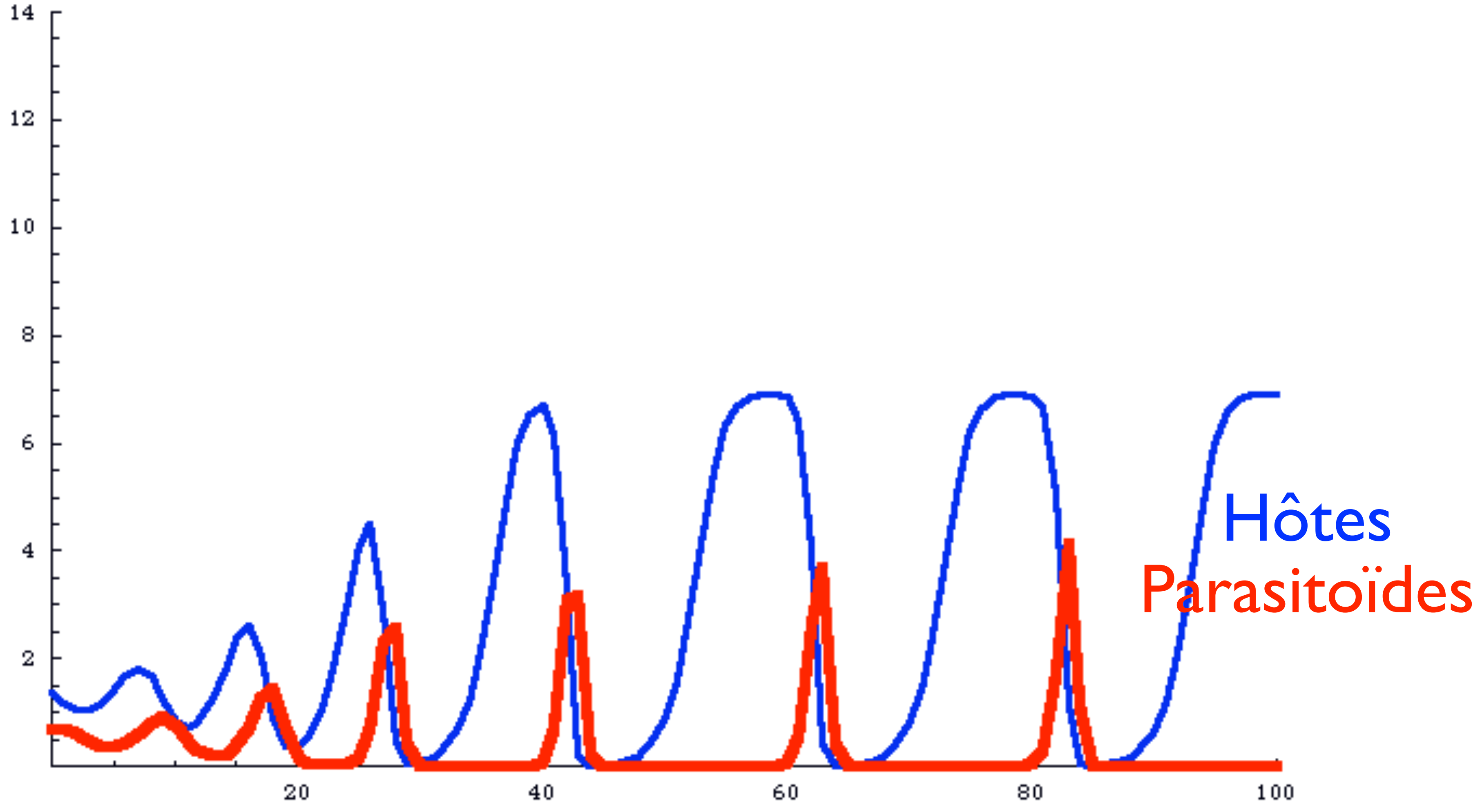


Nicholson-Bailey



Hôtes
Parasitoïdes

NB plus compétition



Hétérogénéité

Localisation

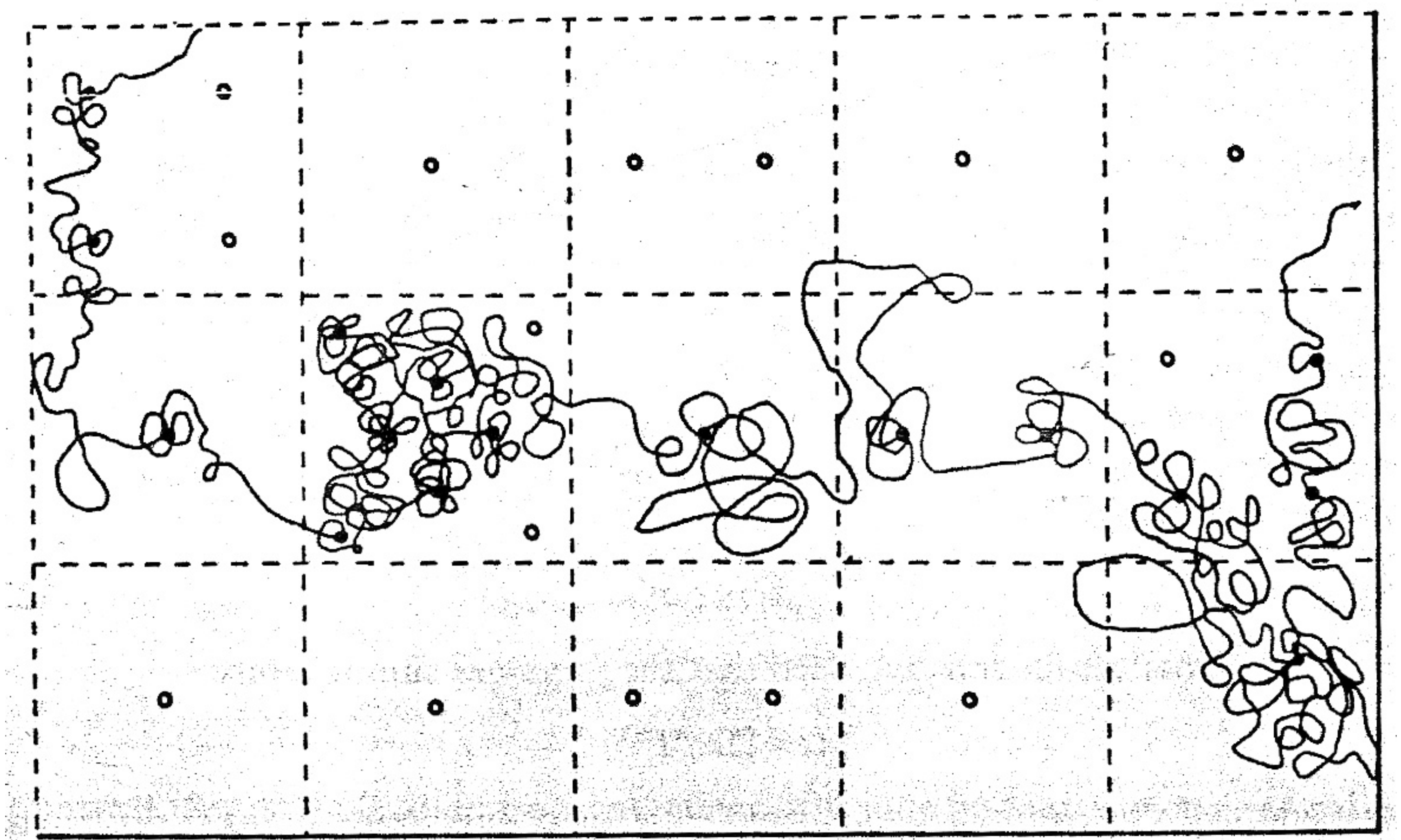


FIG. 9. Part of a track showing the movements of a tachinid parasite *Cyzenis albicans*, within an arena. The circles represent small drops of sugar solution upon which the parasite adults feed. The solid circles show where feeding occurred.

Hassell & May 1974

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

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

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

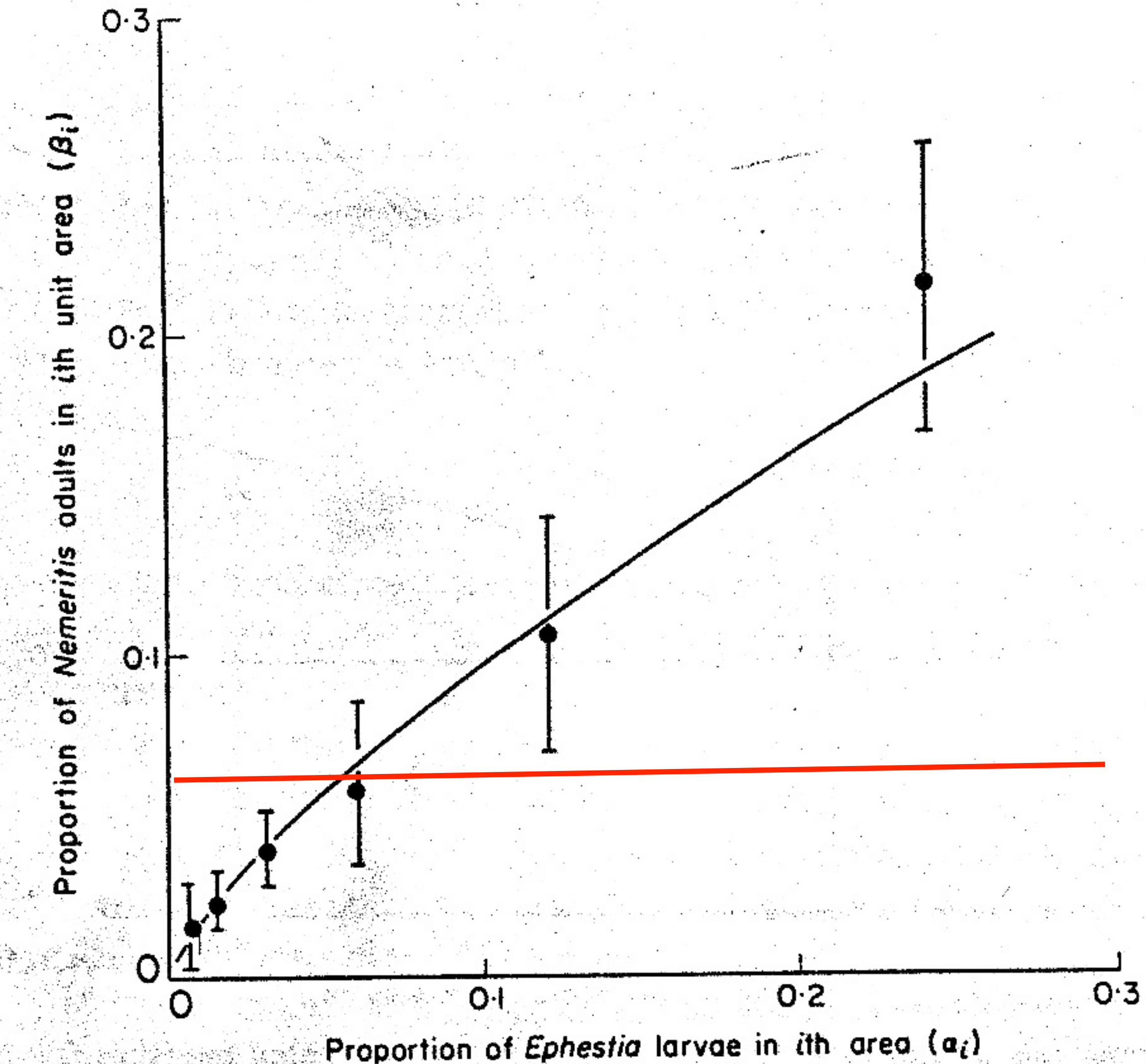
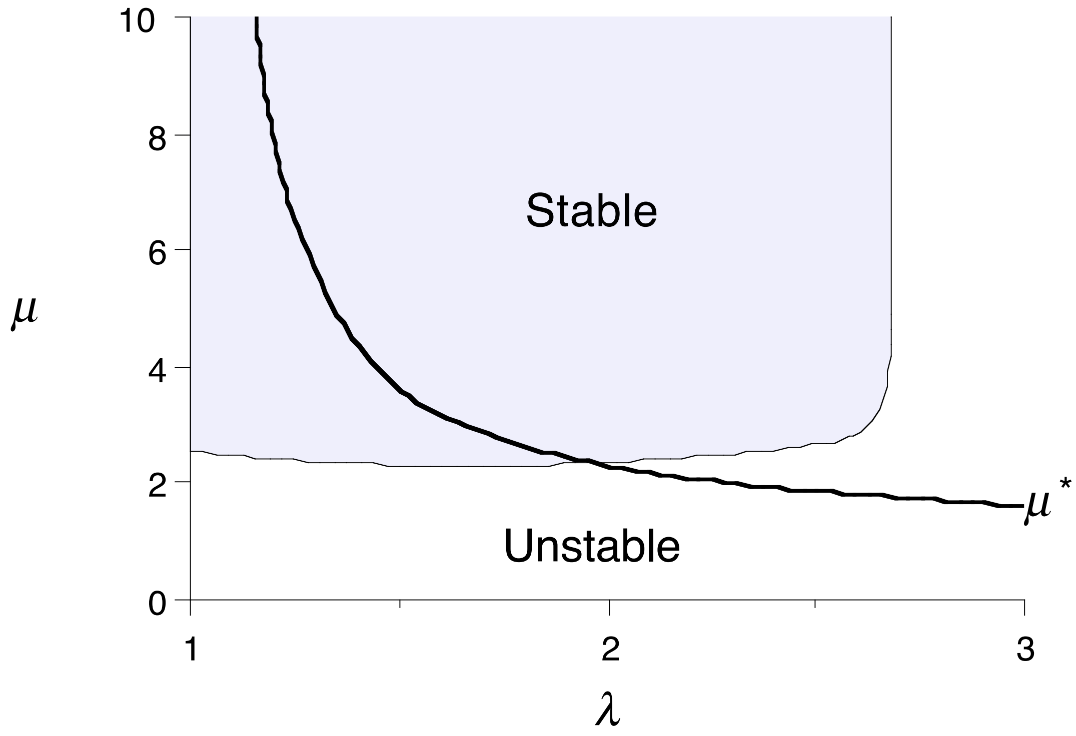


FIG. 11. The relationship between the proportion of searching *Nemeritis canescens* (β_i) and the proportion of *Ephestia cautella* larvae (α_i) per unit area from a laboratory interaction (Hassell 1971a, b). The fitted curve was derived by use of eqn (22). $\beta_i = 0{\cdot}53\ \alpha_i^{\ 0{\cdot}73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

Aggregation stabilise ?

indice d'aggregation

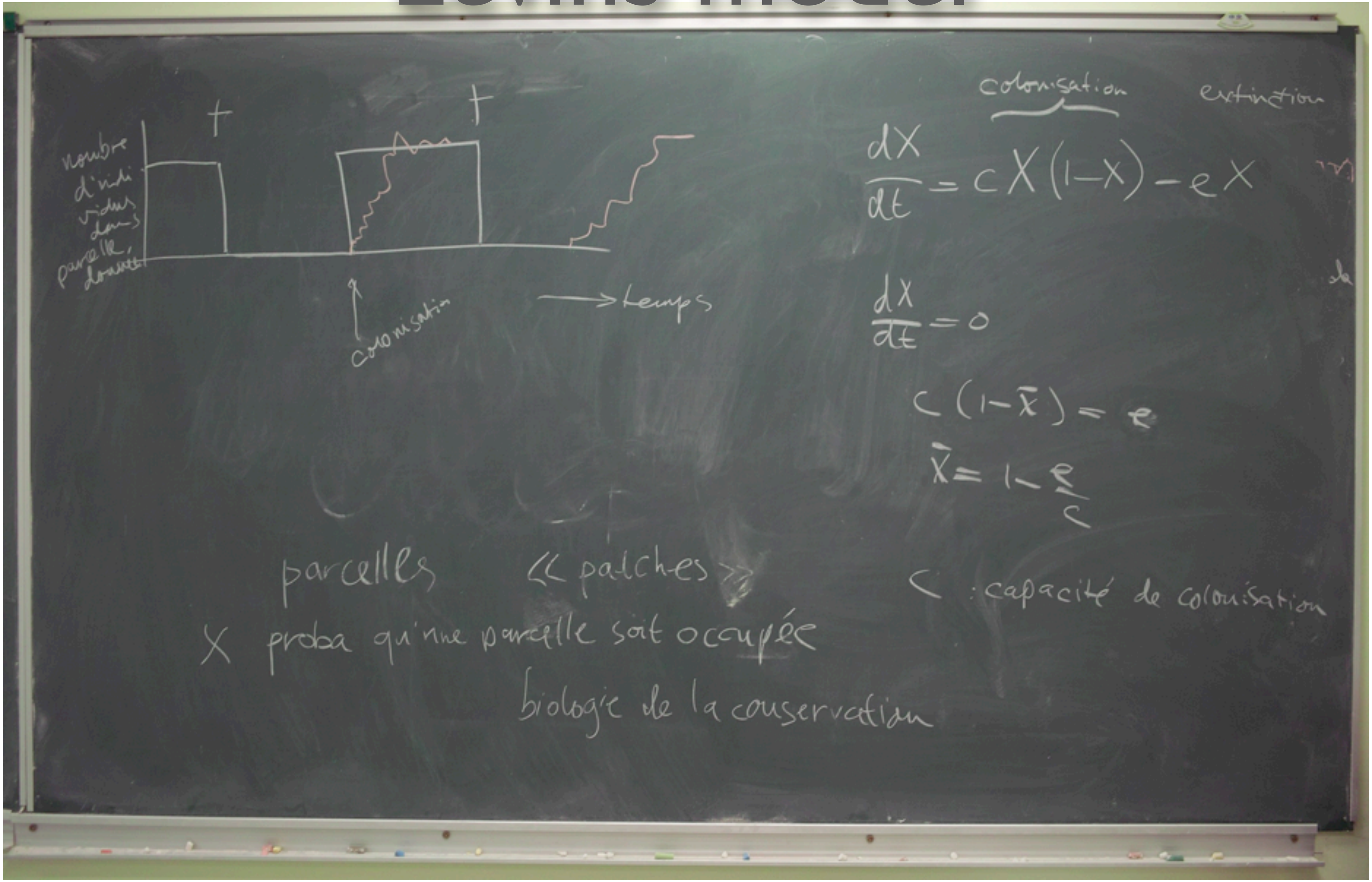


fécondité hôte

Metapopulations

- Levins model
  - occupied vs. extinct patches

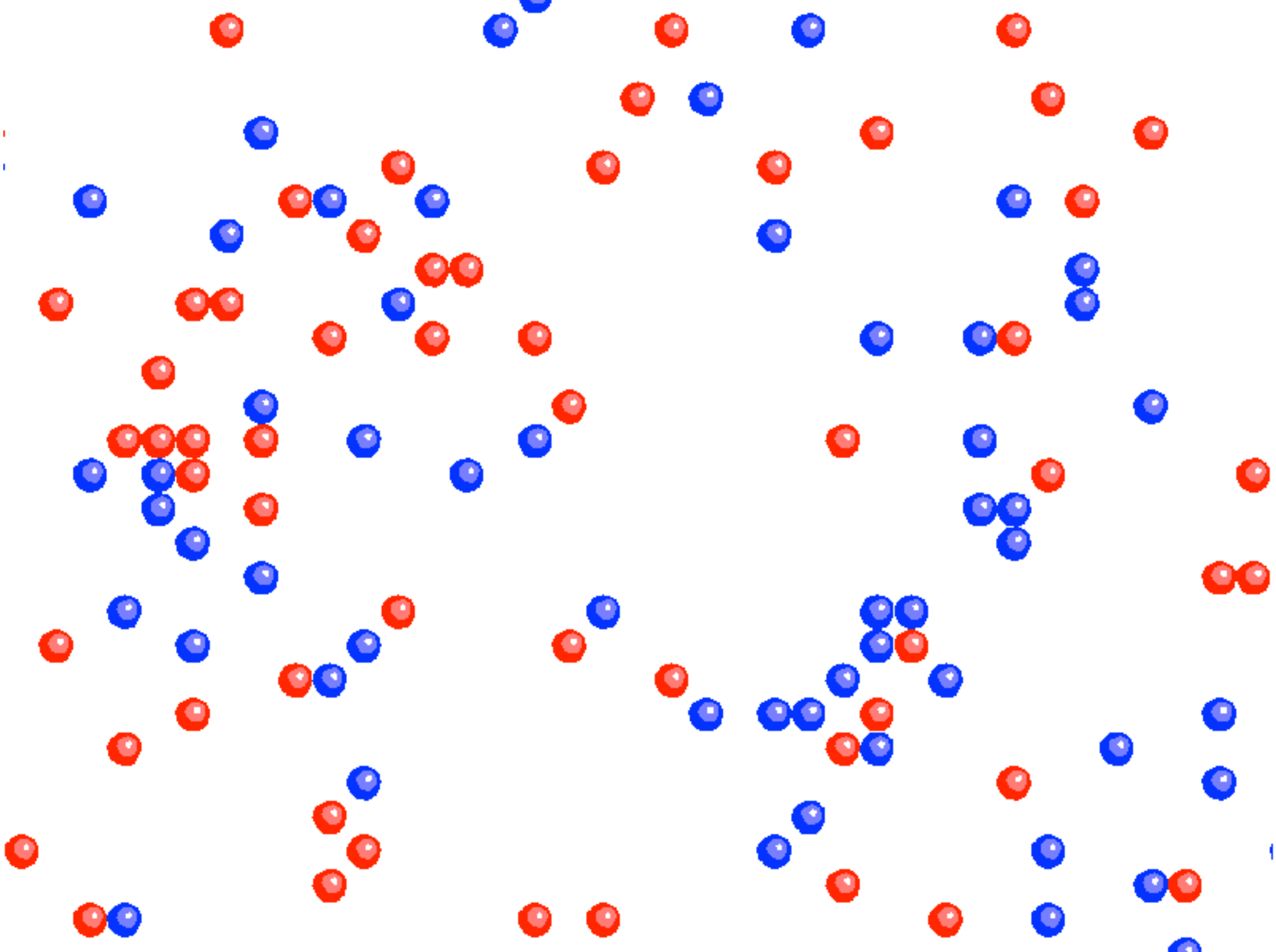
Levins model

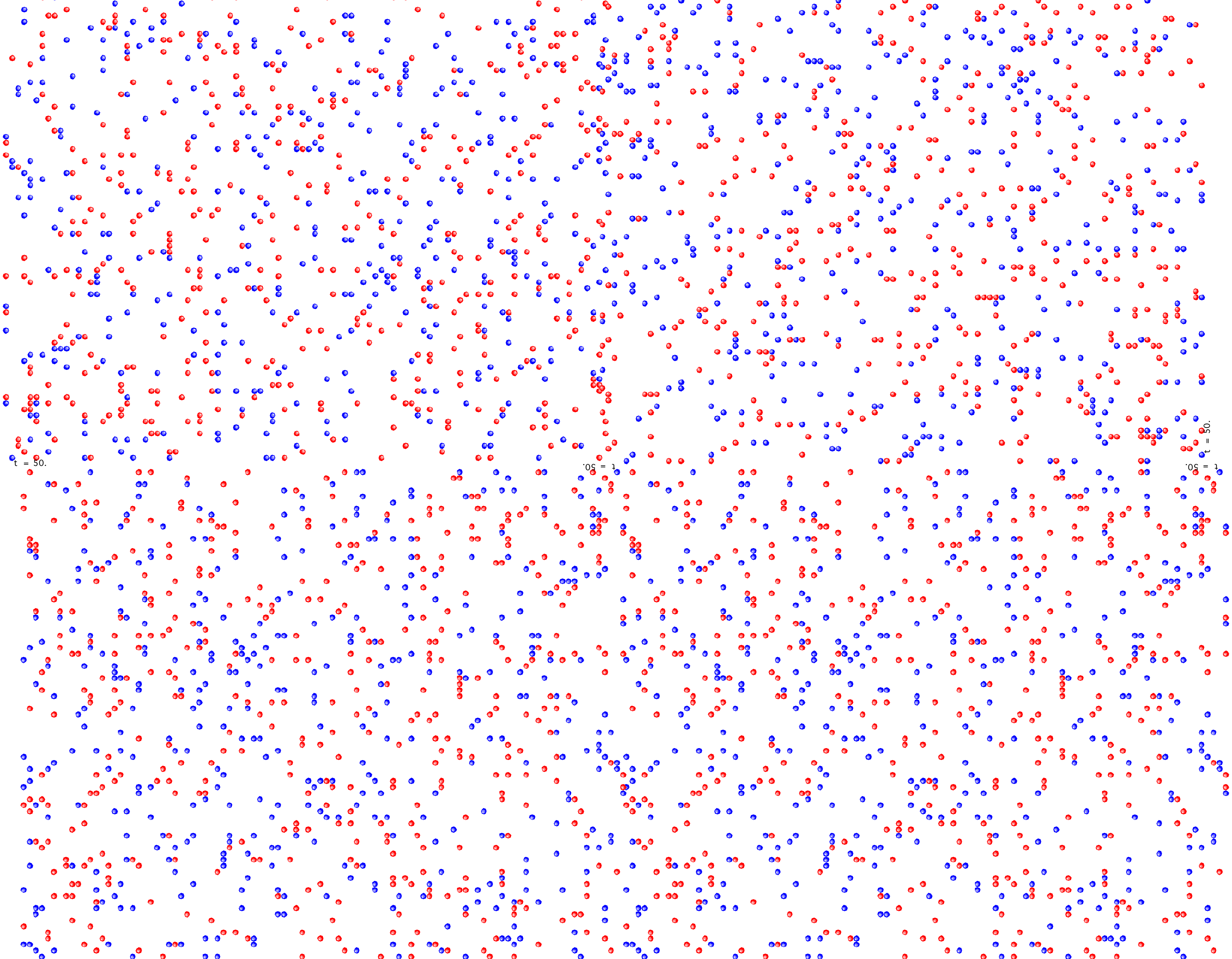


Thermodynamics Success Story

Macro-scale laws from micro-scale processes :

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



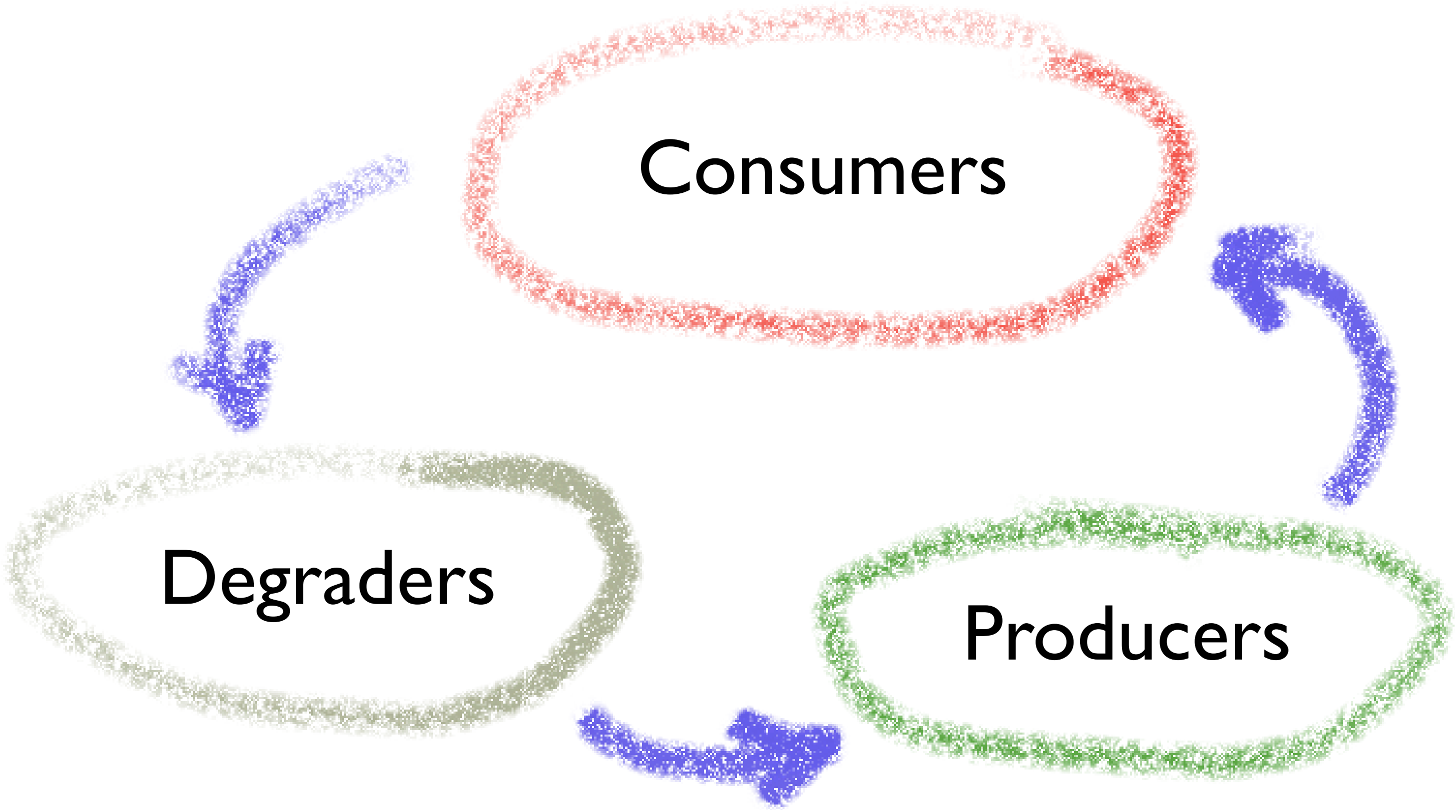

t = 50.

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

Evolution

Sole universal structuring principle

- almost faithful copying
  - reproduction + mutation
- selection

No simple emergent consequences

- no system-wide optimization
- no ‘progress’

Spatial Ecologies

Theoretical Approaches

- Reaction-Diffusion Equations
- Individual-Based Models

Reaction-diffusion

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

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

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

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

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

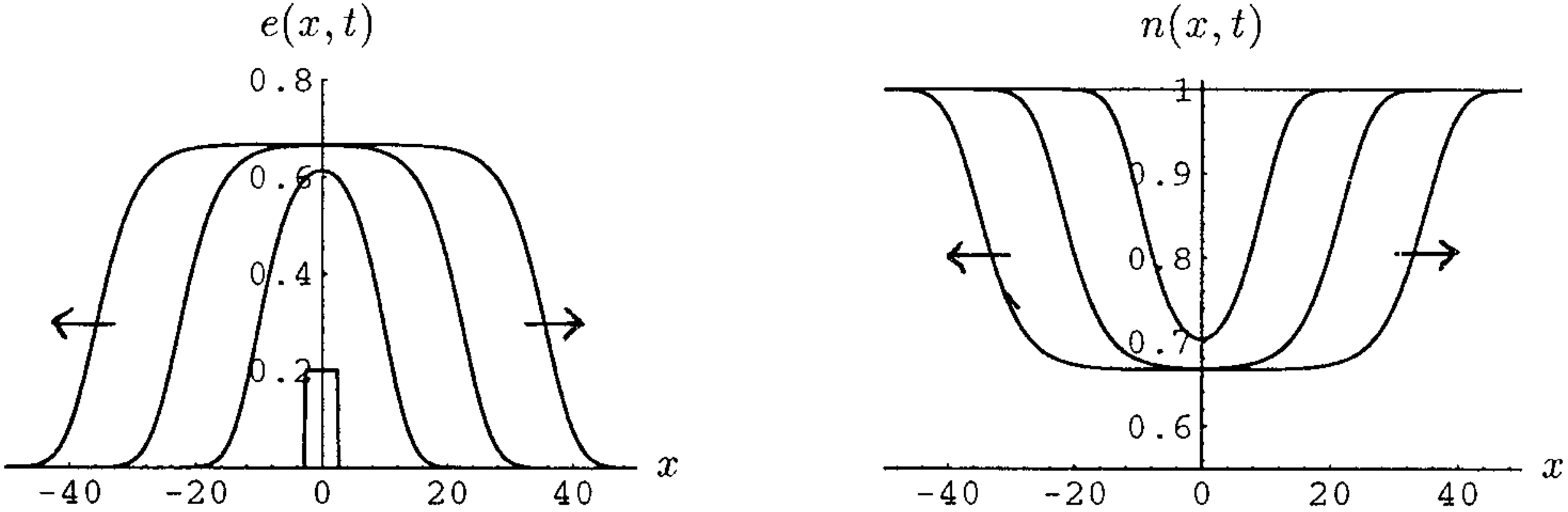


FIG. 1. A travelling wave solution connecting the native-dominant steady state to the coexistence steady state in a spatially uniform environment. Parameter values used were $\gamma_e = \gamma_n = 0.5$, $D(x) = d(x) = G(x) = g(x) = 1$, and $r = 2$, so that the coexistence state is the only stable state.

Diffusion approach

Advantages

- many mathematical tools

Disadvantages

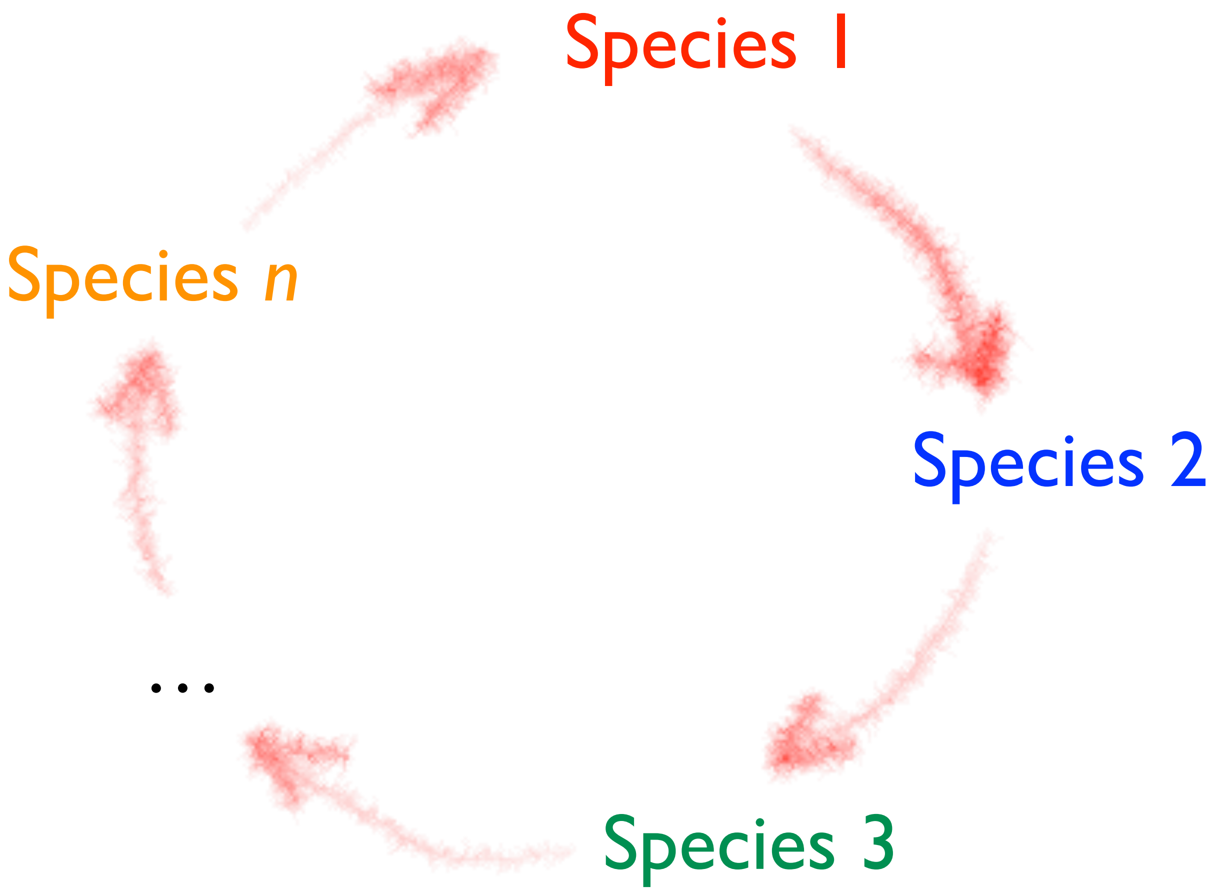
- becomes very difficult if movement is non-random
- becomes very difficult if individuals are ‘large’

Individuality

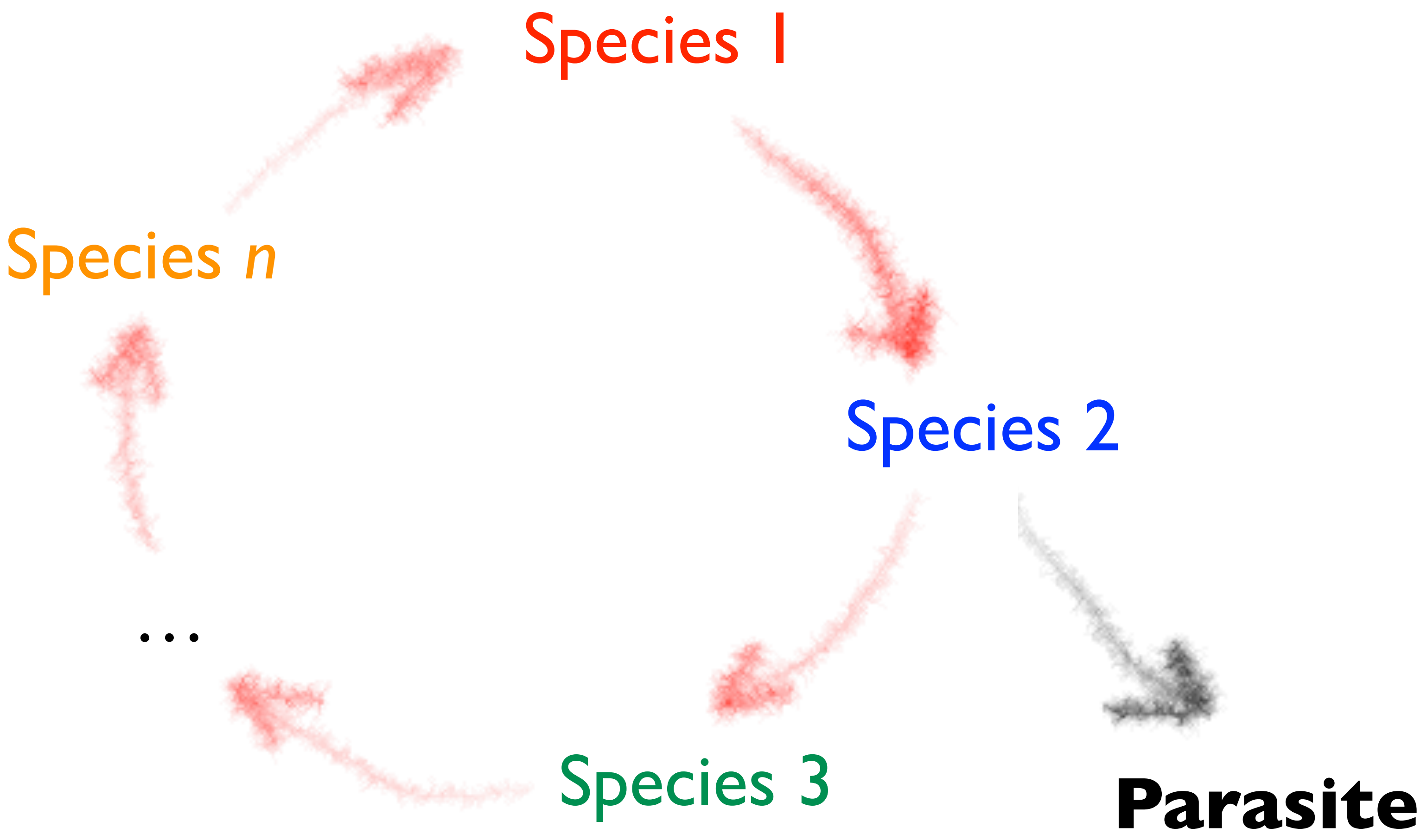
Individuality is crucially important

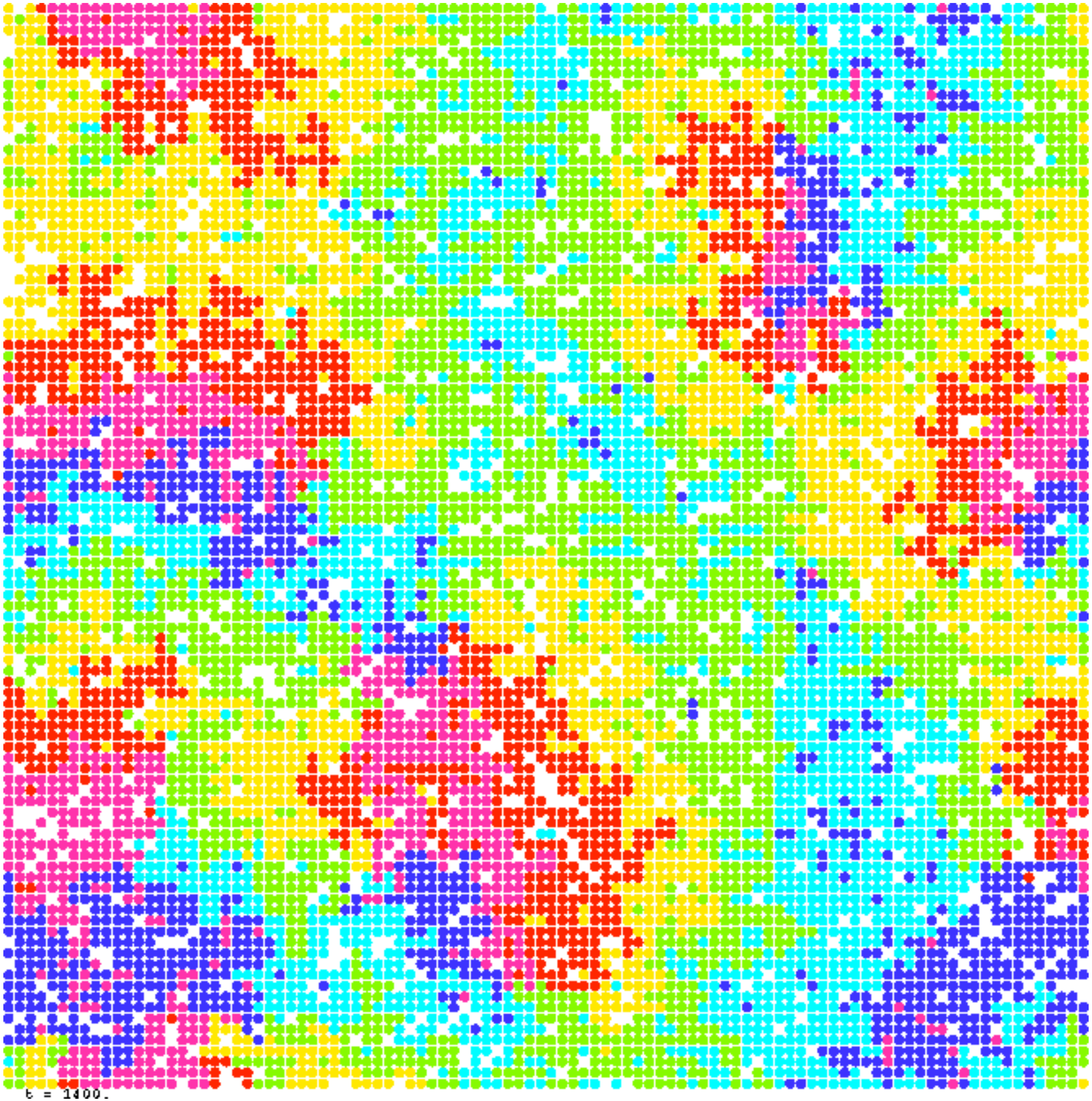
- in particular in spatially explicit settings
- demographic stochasticity inevitable

Hypercycle

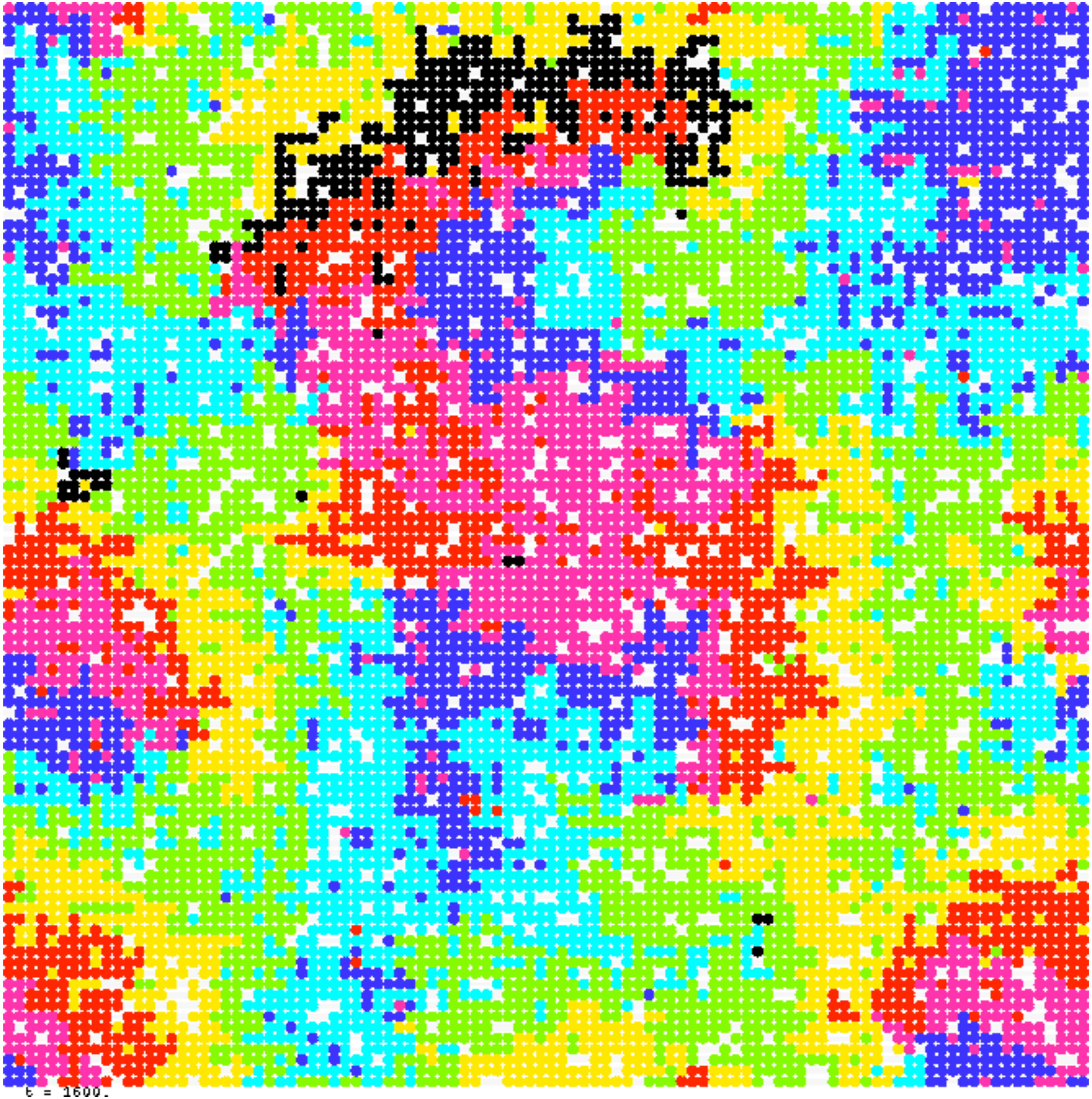


Hypercycle

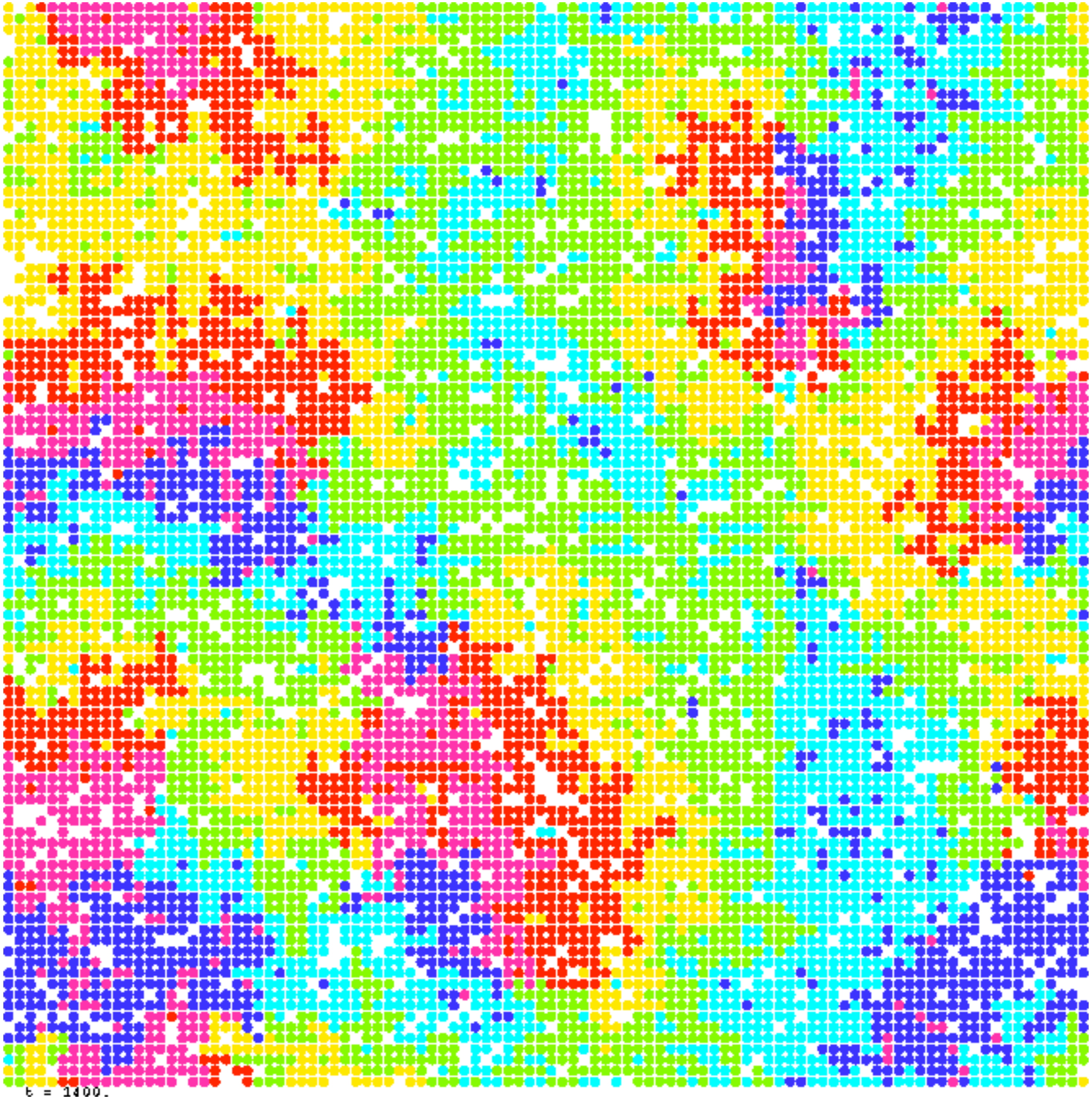




Boerlijst & Hogeweg's (1991)



t = 1600.



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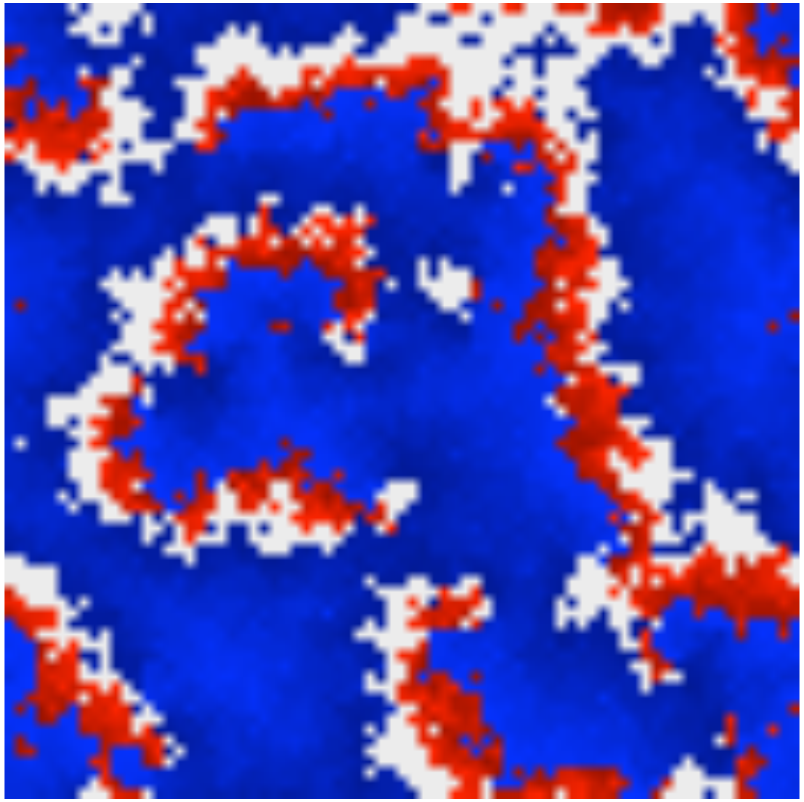
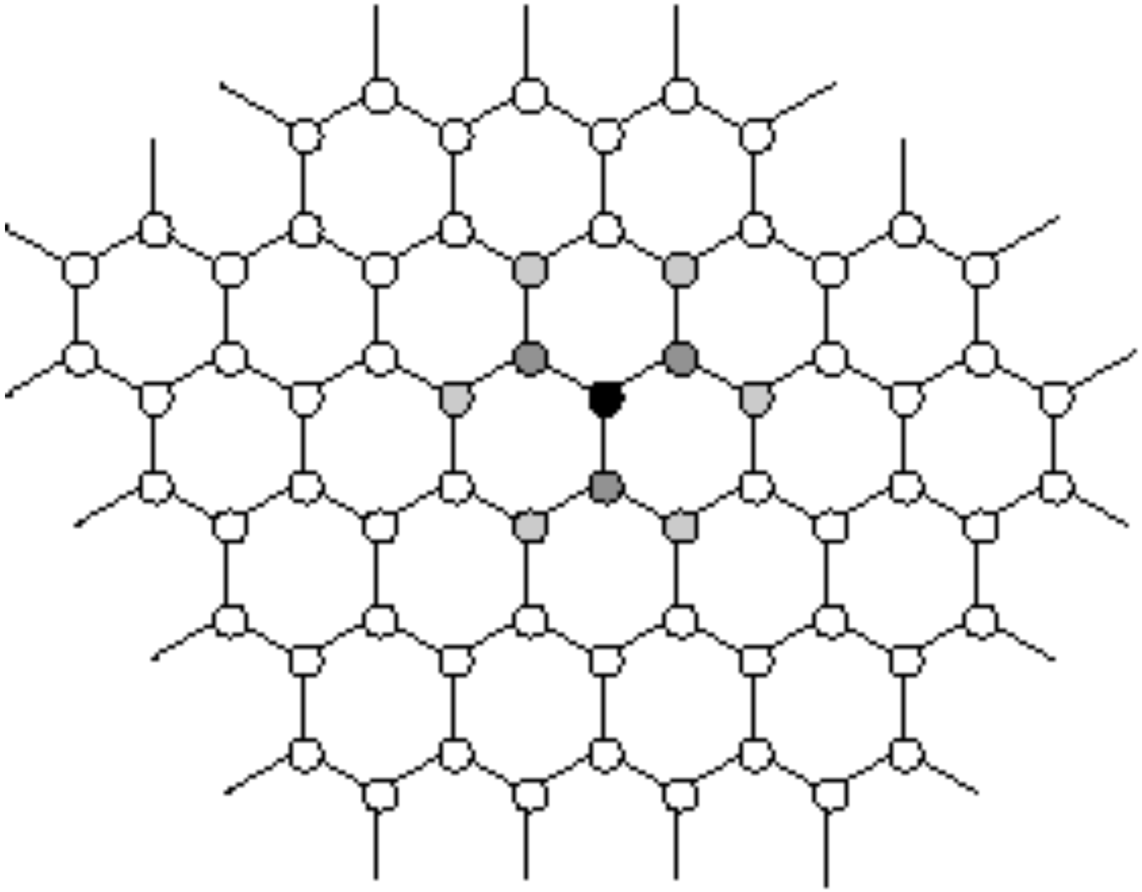
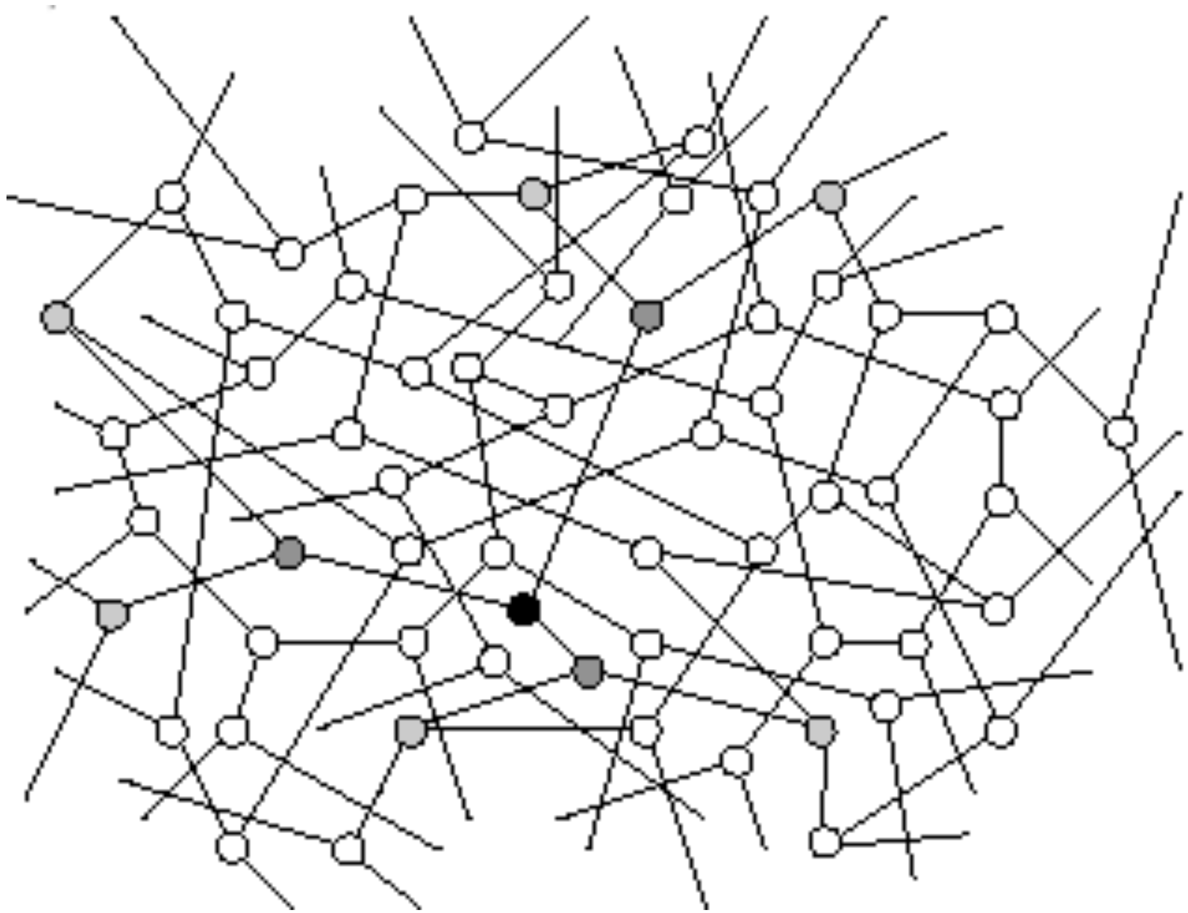


van Ballegooijen & Boerlijst 2004

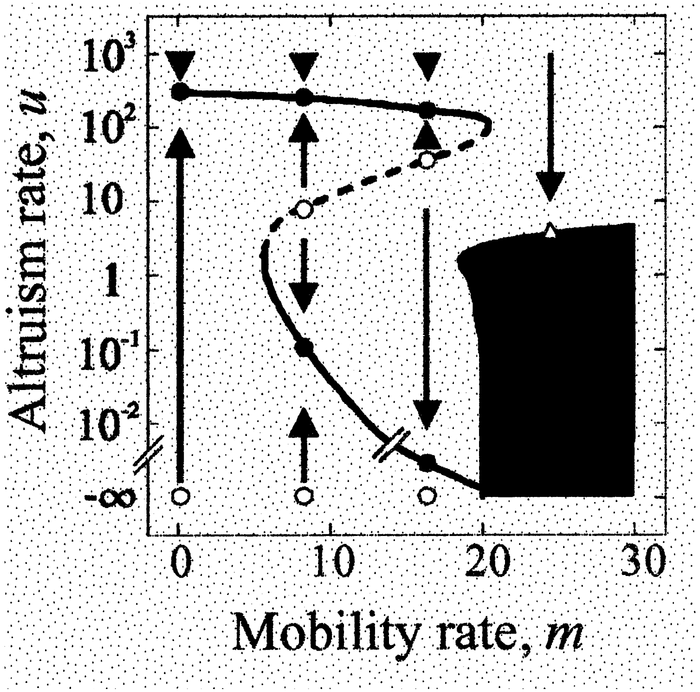




New Outcomes

Evolutionary cycling

Evolutionary suicide



Le Galliard *et al* 2003

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

Cellular Automata

+ Nice toys

+ Colourful movies

– Difficult to generalise

– Difficult to obtain deeper insight

Modeling Populations

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

Levels of organisation

population-level processes

competition, predation, epidemiology, social interactions

individual-level

birth, death, development, behaviour

within-individual level

physiology, infection, immune response

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