How spatial structure enables multi-level selection

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NOVEL COOPERATION EXPERIMENTALLY EVOLVED BETWEEN SPECIES

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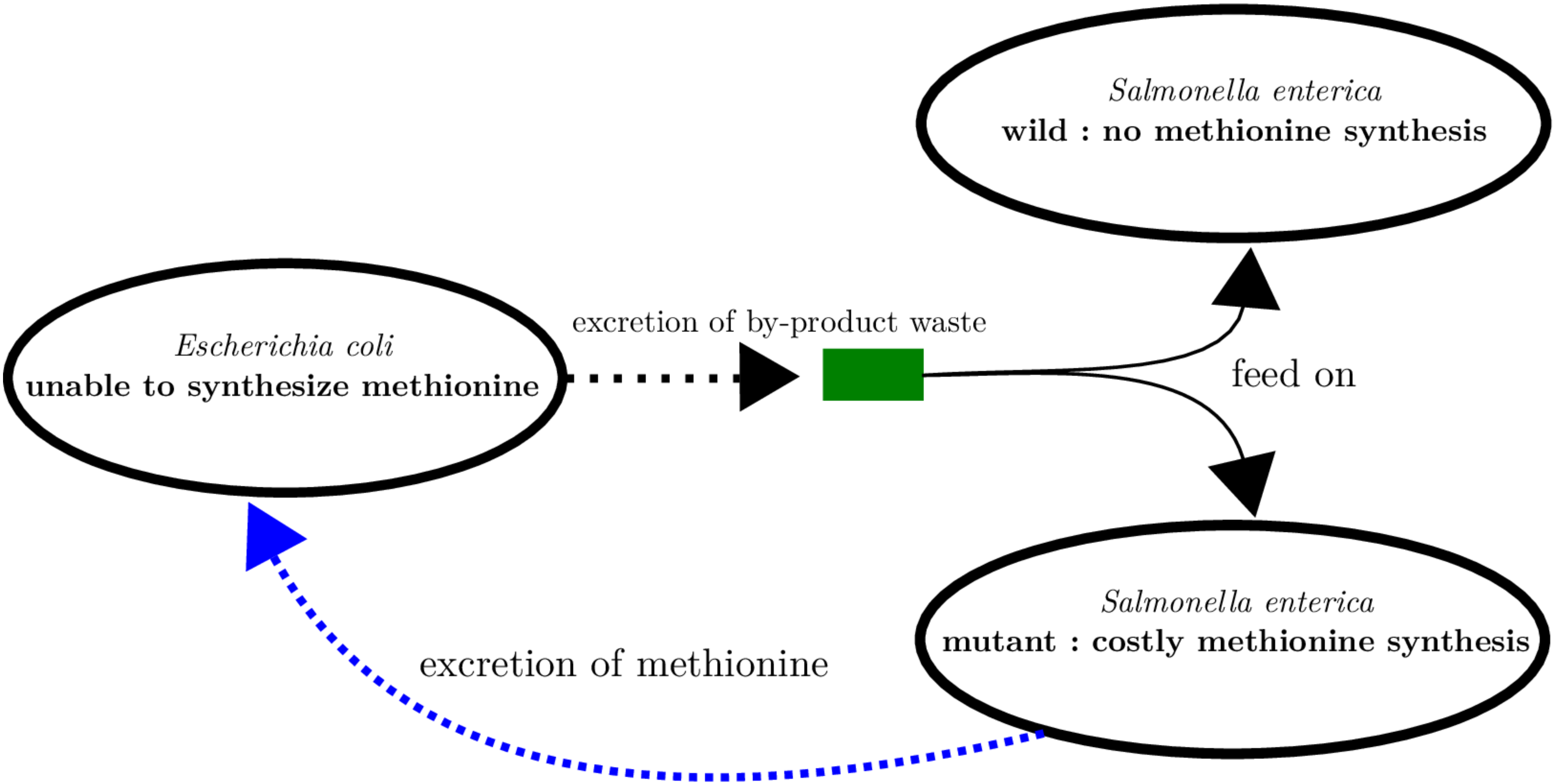

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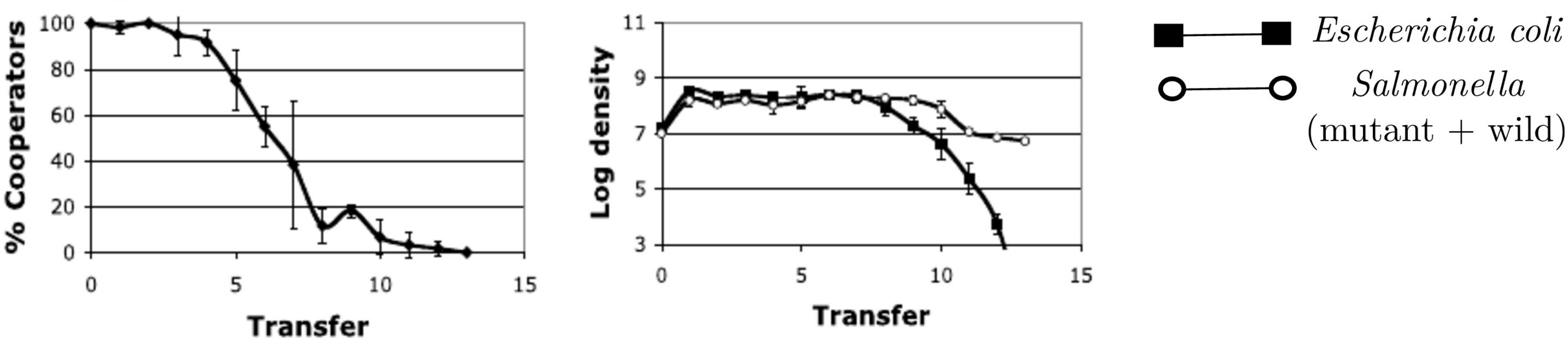
Growth in lactose liquid flasks

Salmonella mutant



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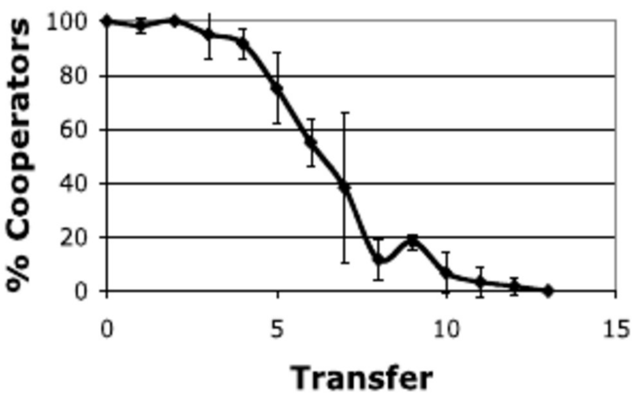

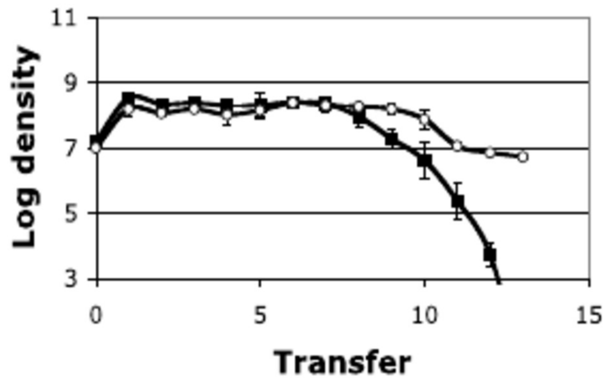

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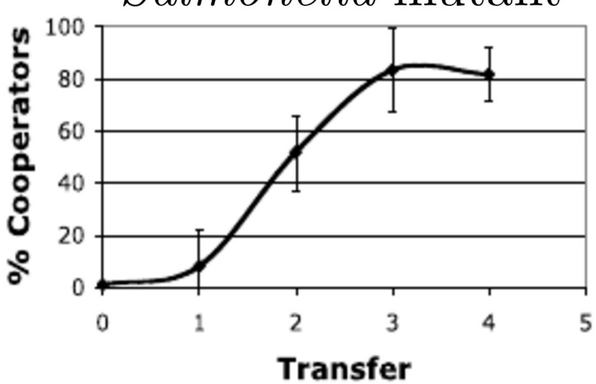

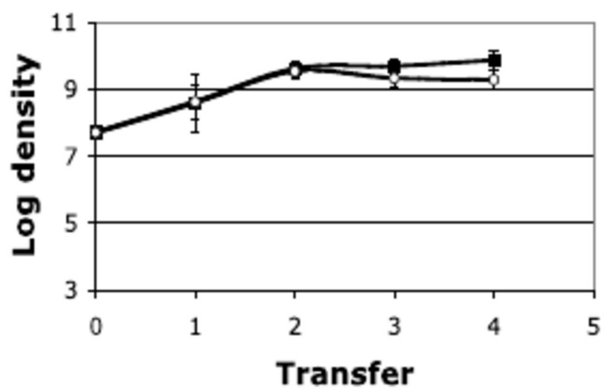

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Fitnesses of altruists (Wa) and nonaltruists (Ws) :

$$Wa = X - c + b(np\text{-}1)/(n\text{-}1)$$
$$Ws = X + bnp/(n\text{-}1)$$

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$$Ws = X + bnp/(n\text{-}1)$$

$Wa < Ws$

altruists will always be selected against within this population

Numerical example

Population size *(n)* = *100*

Frequency of altruists *(p)* = *0.5*

Baseline fitness *(X)* = *10*

Benefit to recipient *(b)* = *5*

Cost to altruist *(c)* = *1*

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Fitness of altruist : $Wa = 10 - 1 + 5*(49)/99 = 11.47$

Fitness of nonaltruist : $Ws = 10 + 5*(50)/99 = 12.53$

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Total number of offsprings : $n' = n(p*Wa + (1\text{-}p)*Ws) = 1200$

Frequency of altruists among offspring : $p' = n*p*Wa/n' = \boldsymbol{0.478}$

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If we assume that mortality operates on all types equally, returning the population to a size of $n = 100$ without changing the new frequency of altruism

→ **The altruists decline in frequency every generation and ultimately go extinct.**

What if we consider a spatial structure ?

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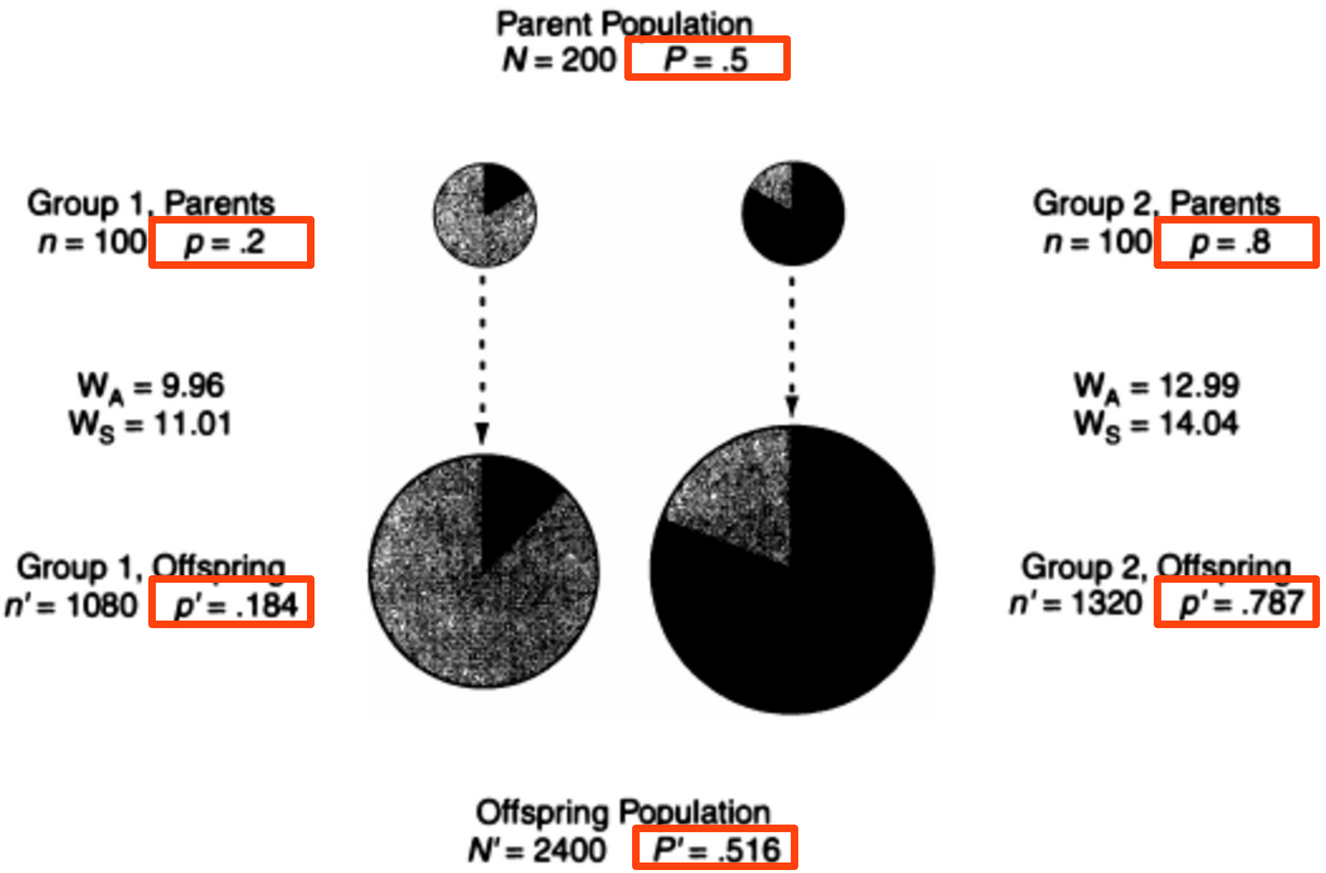

	Group 1	*Group 2*
n	100	100
p	0.2	0.8
W_A	$10 - 1 + 5(19)/99 = 9.96$	$10 - 1 + 5(79)/99 = 12.99$
W_S	$10 + 5(20)/99 = 11.01$	$10 + 5(80)/99 = 14.04$
n'	1080	1320
p'	0.184	0.787
	Global population	
N	$100 + 100 = 200$	
P	$[0.2(100) + 0.8(100)]/200 = 0.5$	
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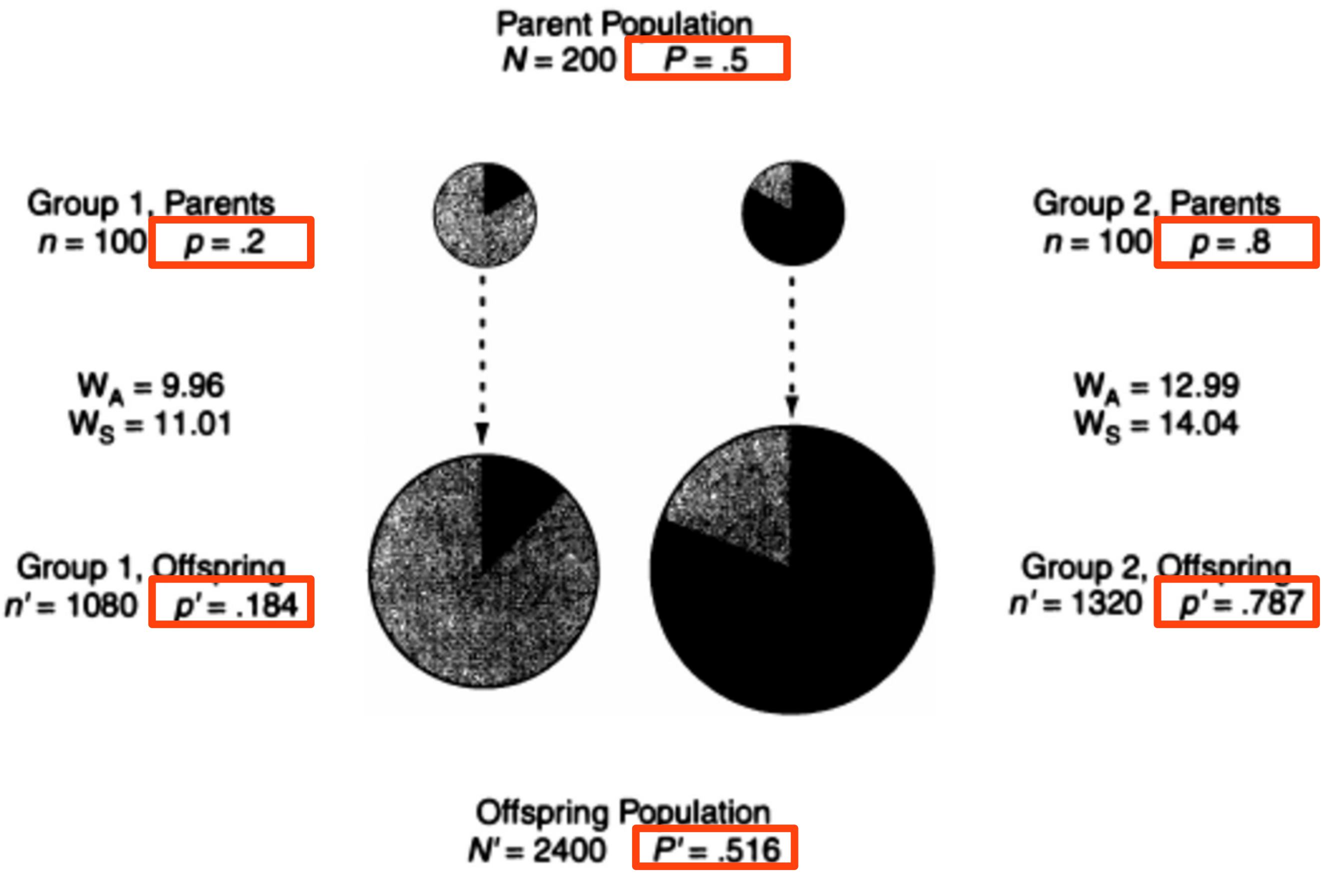
What if we consider a spatial structure ?



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Within-group selection : as previously demonstrated, altruists have a lower fitness so their frequency decreases

Between-group selection : the group with more altruists grow larger than the group with fewer altruists and so the global frequency of altruists increases.

The structured demes model (Wilson 1975, 1977)

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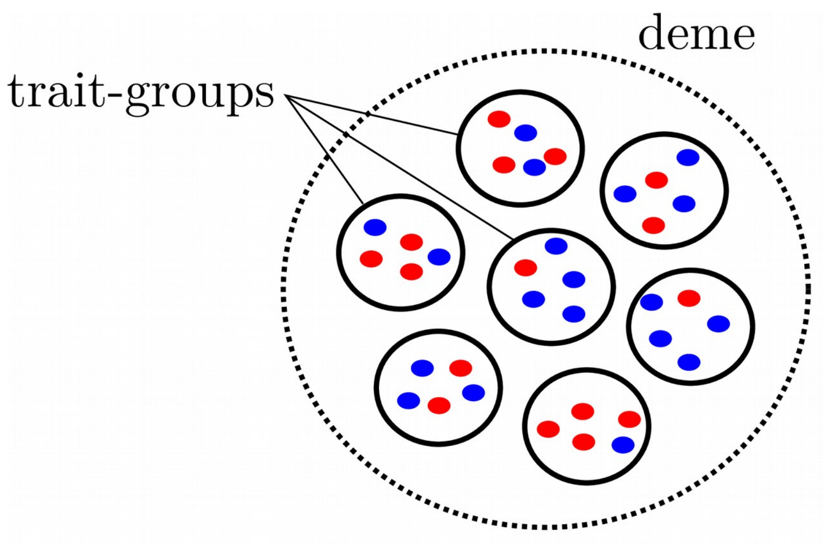
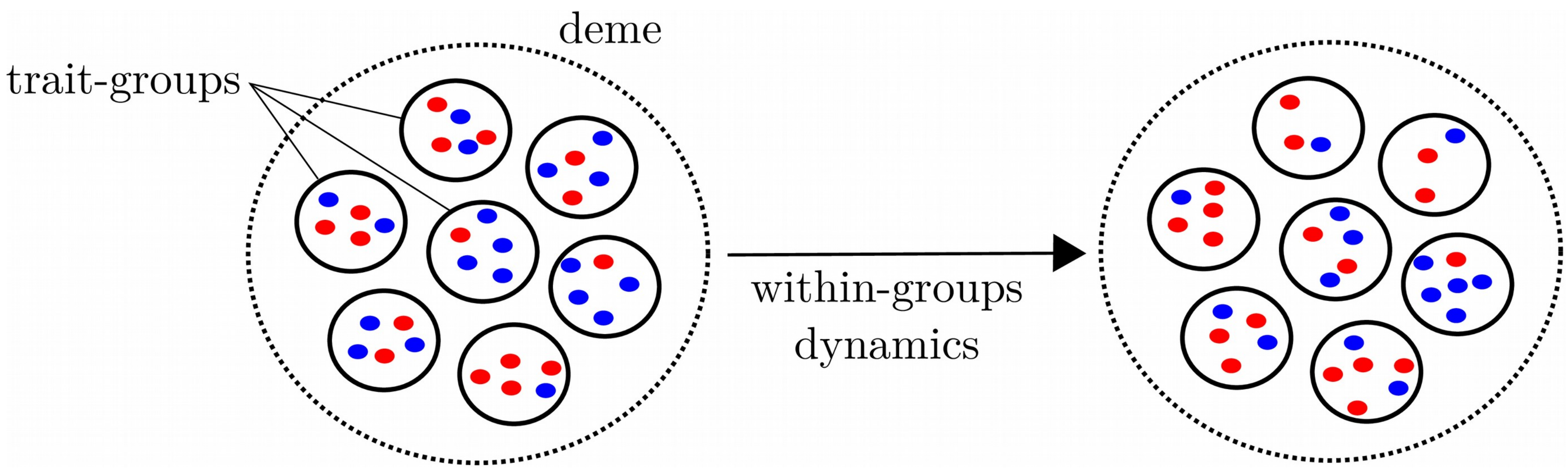


Deme : group of individuals that readily intermix during some point in their life cycle

Trait-group : group of individuals that readily interact with each other in any process of ecological interest (competition, aggression...)

The structured demes model (Wilson 1975, 1977)



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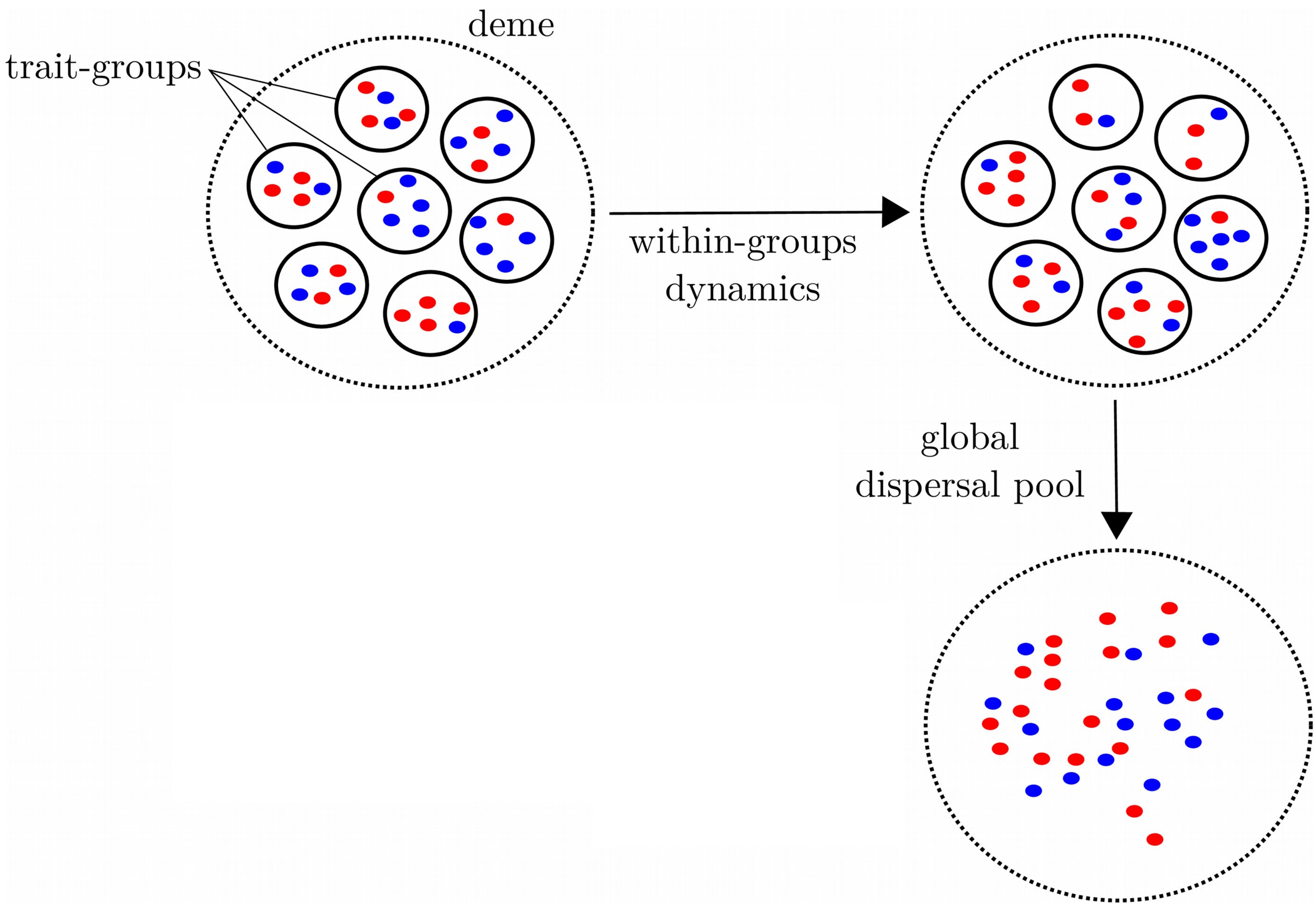

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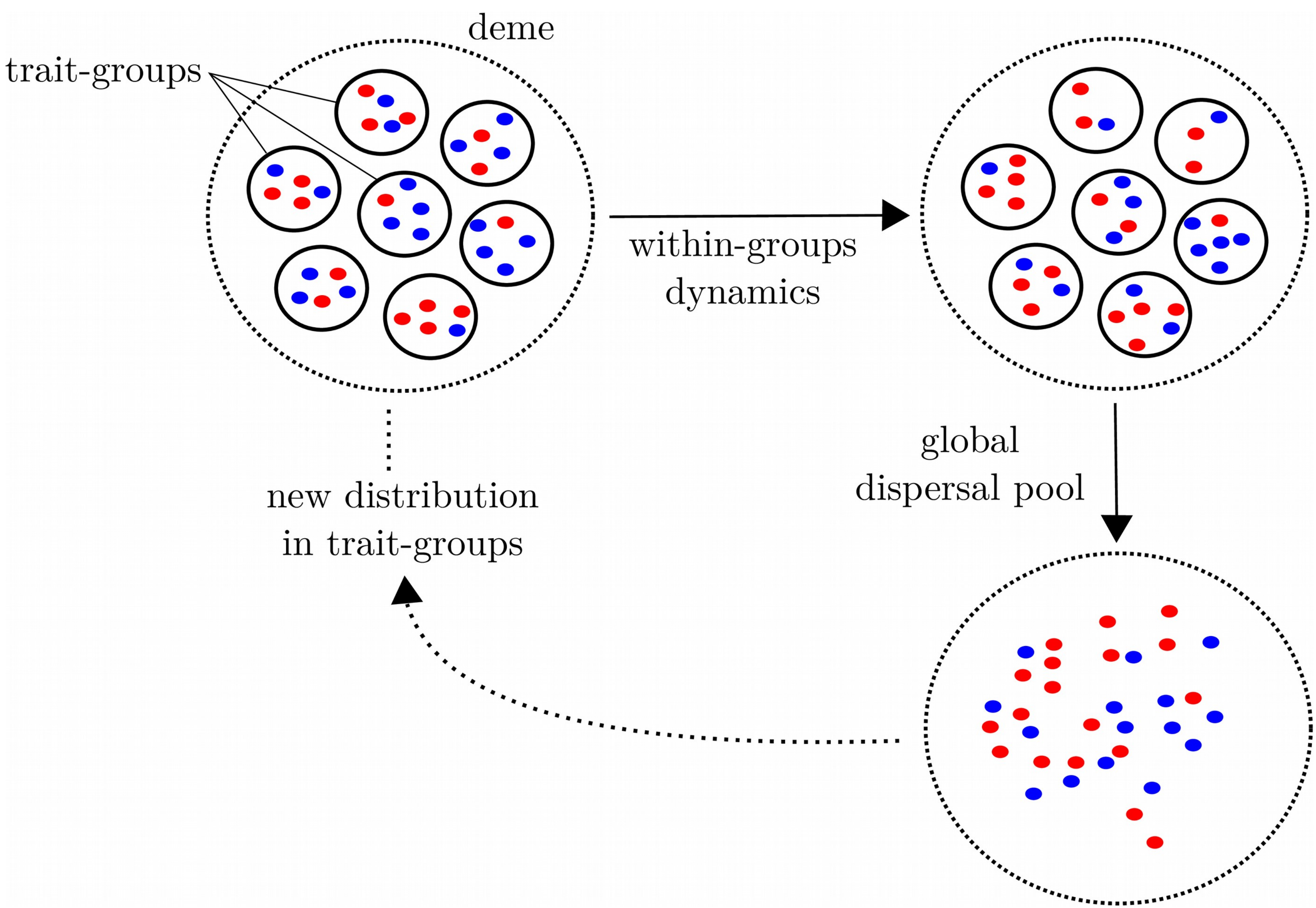

The structured demes model and evolution on the level of communities (Wilson 1976)

Consider two plant species (A and B) that benefit equally from earthworm activity but differ in their effect on the earthworm (E).

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Plant per capita fitnesses

$$\frac{N(A)_{t+1}}{N(A)_t} = \frac{N(B)_{t+1}}{N(B)_t} = 1 + m_{A,B}\left(\frac{N(E)_t}{L+N(E)_t}K_{A,B} - N(A)_t - N(B)_t\right)$$

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Earthworm per capita fitness

$$\frac{N(E)_{t+1}}{N(E)_t} = 1 + m_E\left(\frac{N(A)_t}{N(A)_t+N(B)_t}K_E - N(E)_t\right)$$

The earthworm only benefits from plant A

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Two initial conditions :

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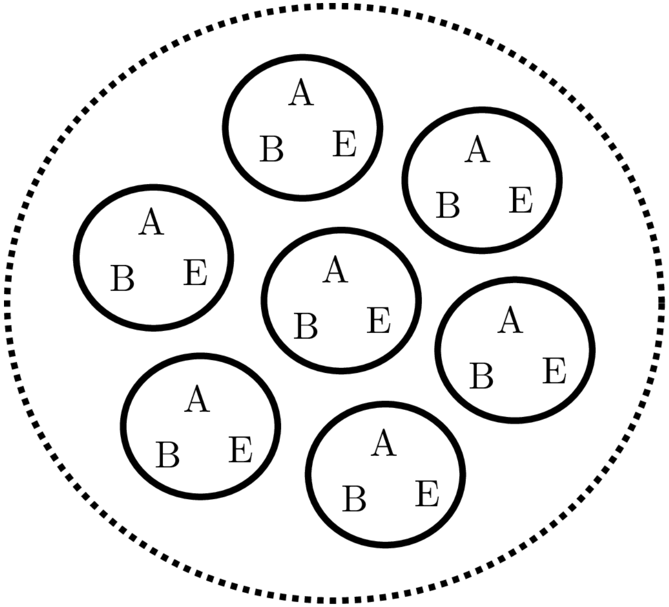
Without spatial variation



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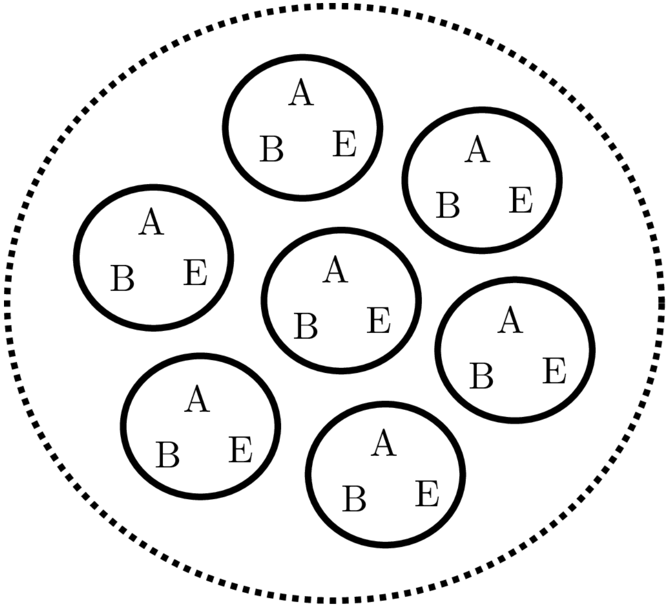
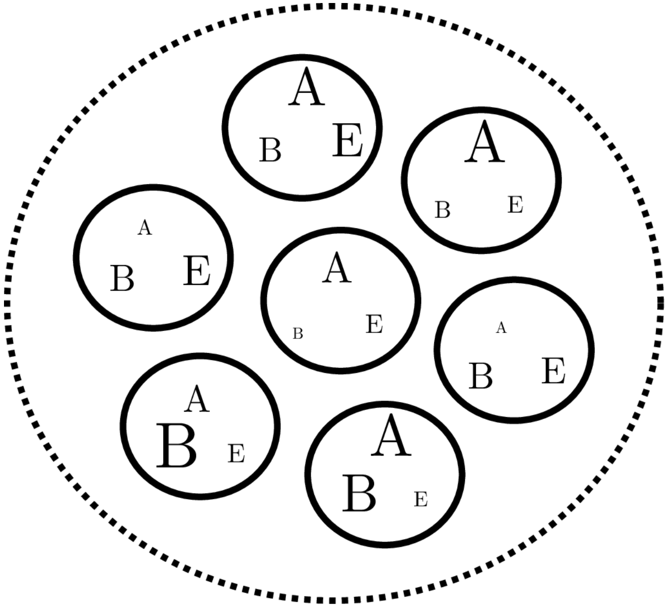


With random spatial variation



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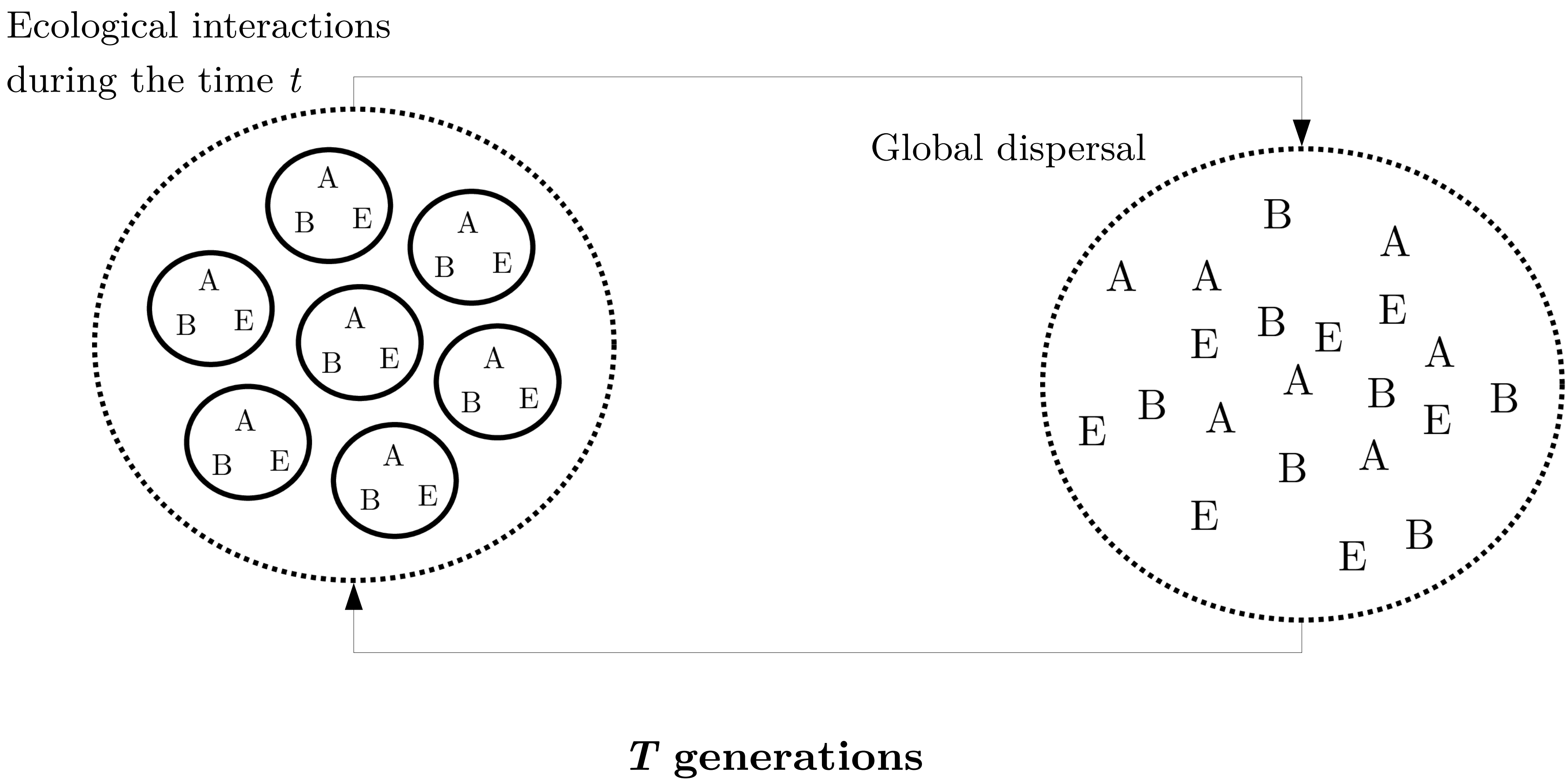

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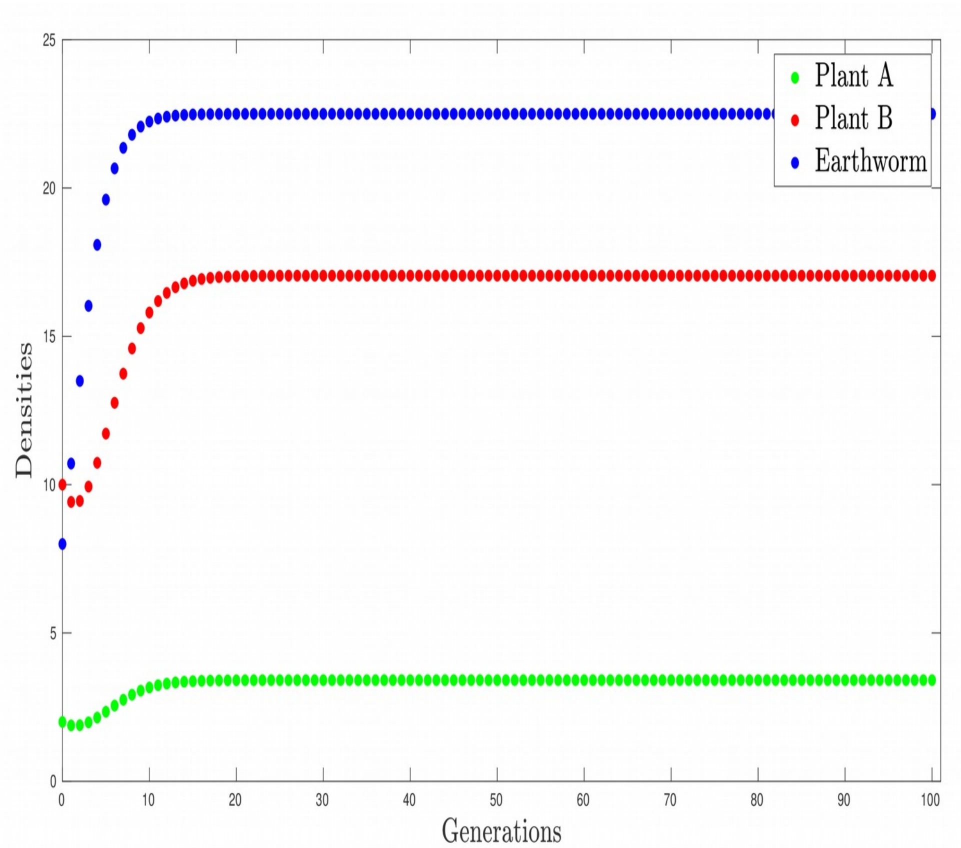

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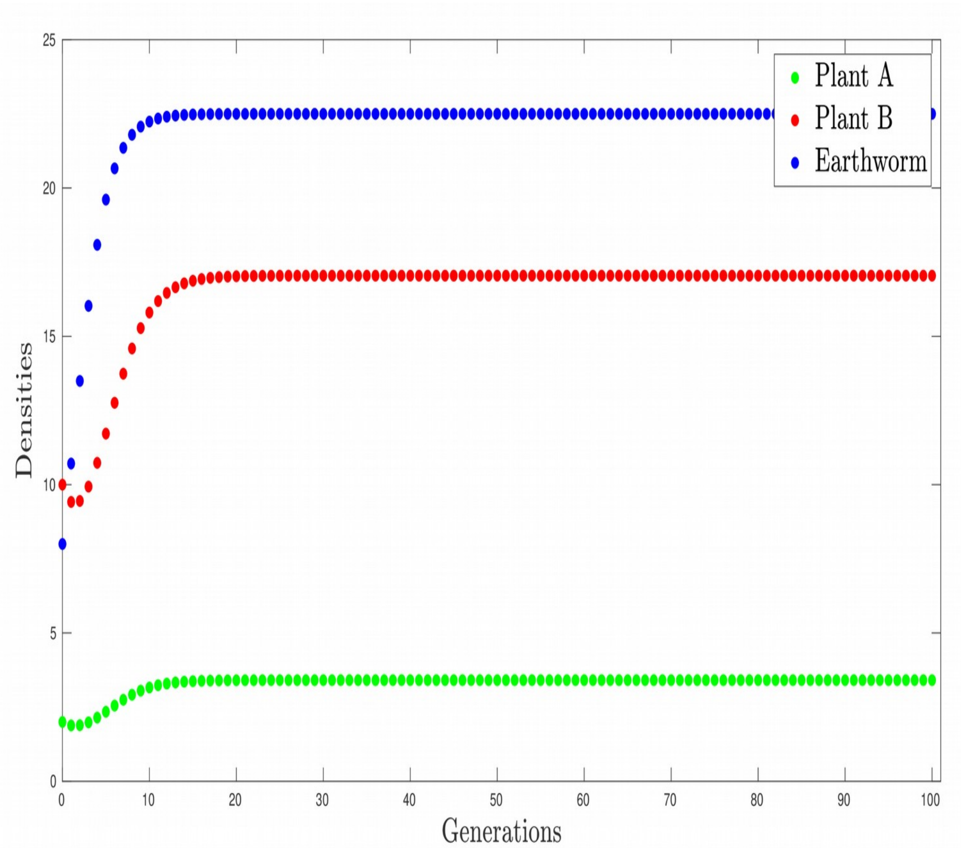

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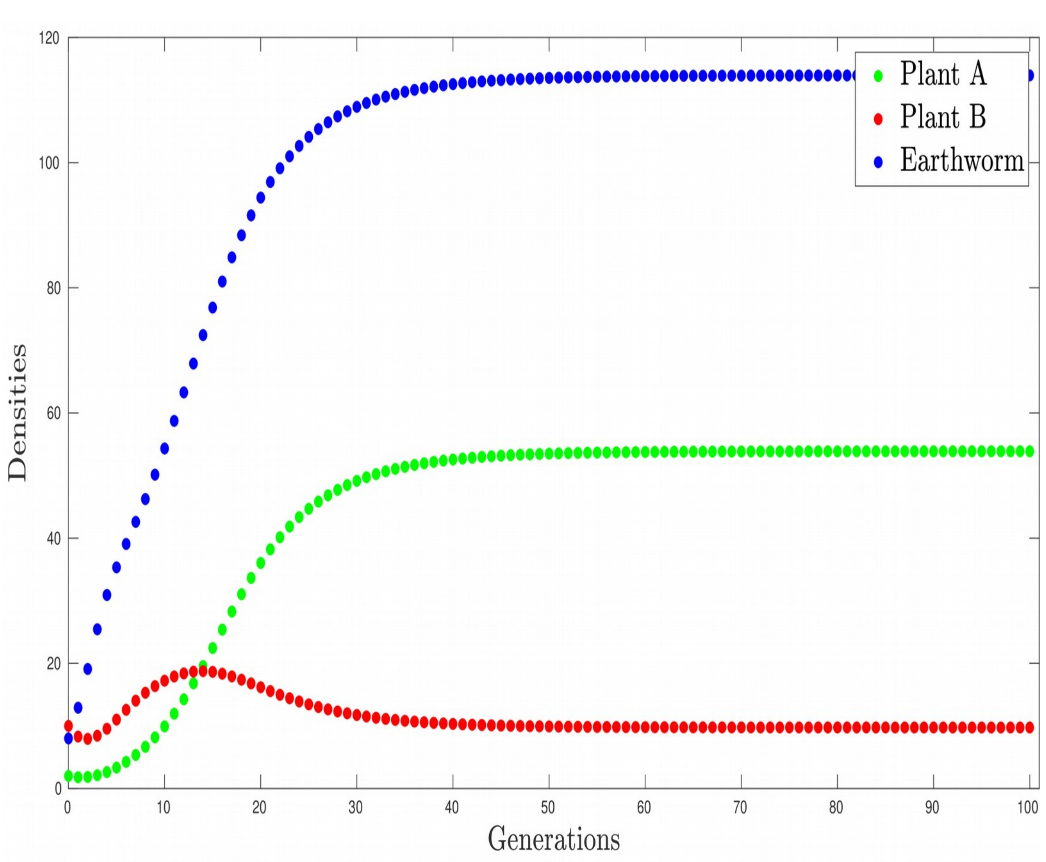

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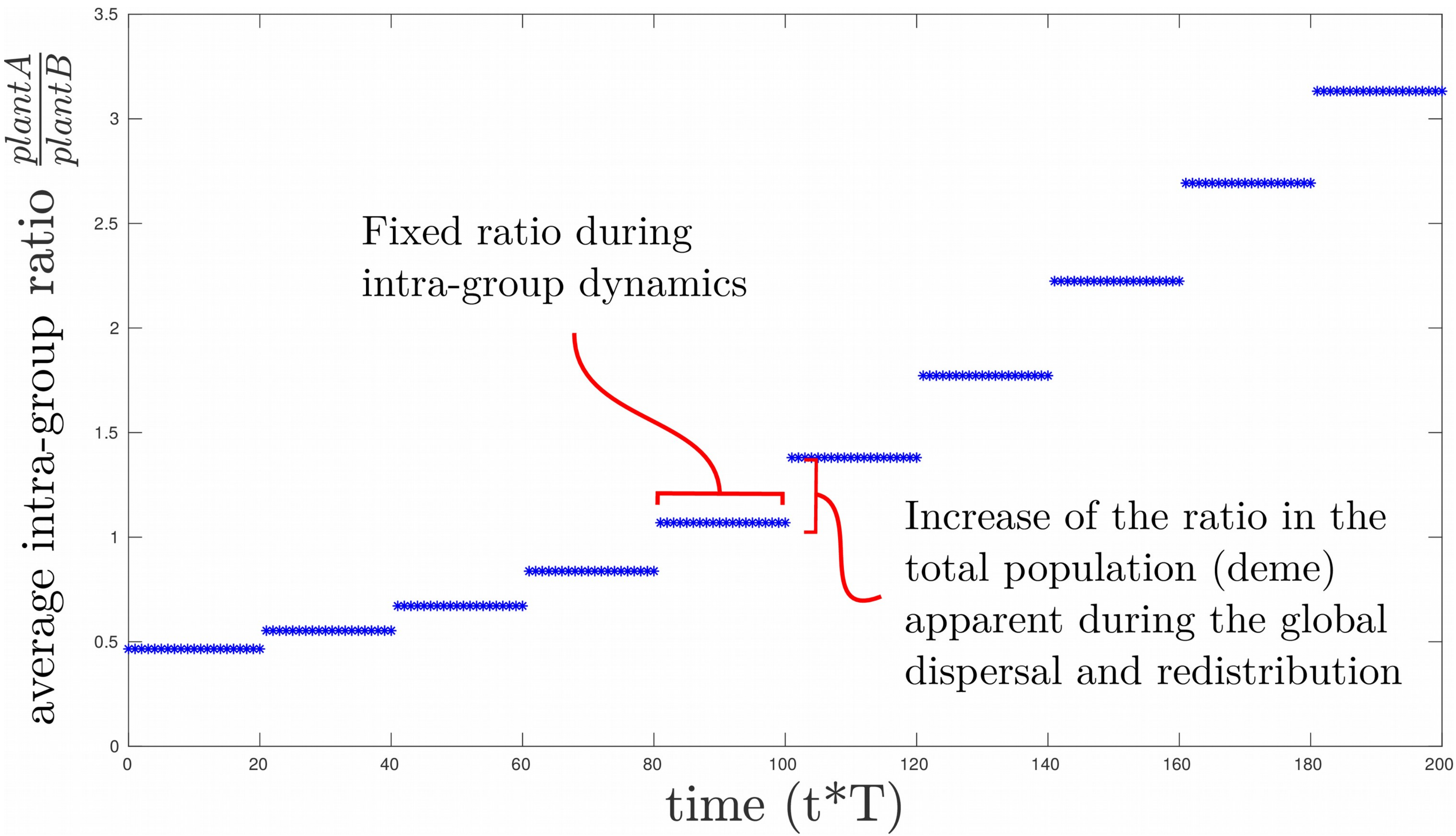

Simpson's paradox

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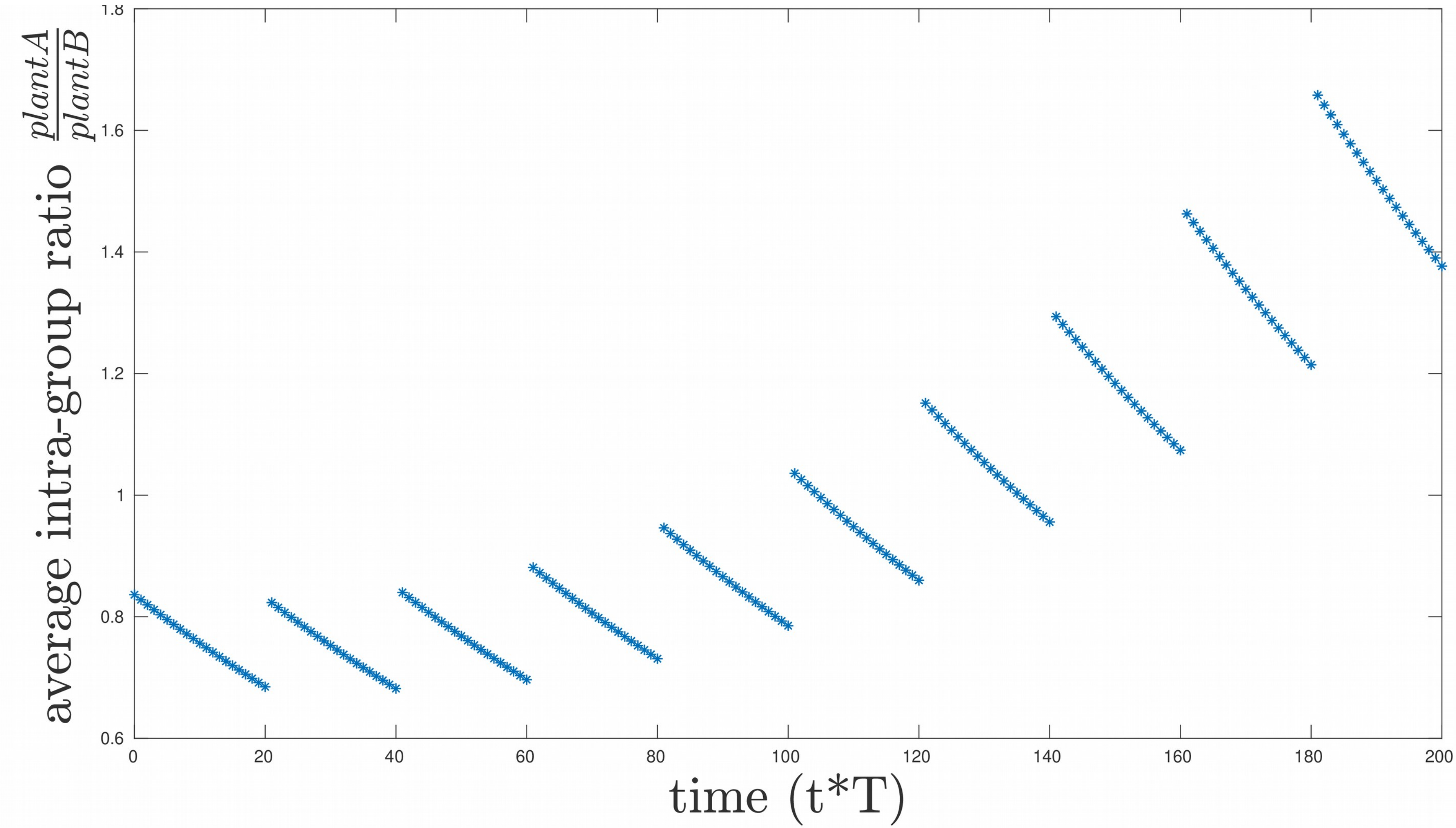
What if A has a cost on his fitness (altruism) ?



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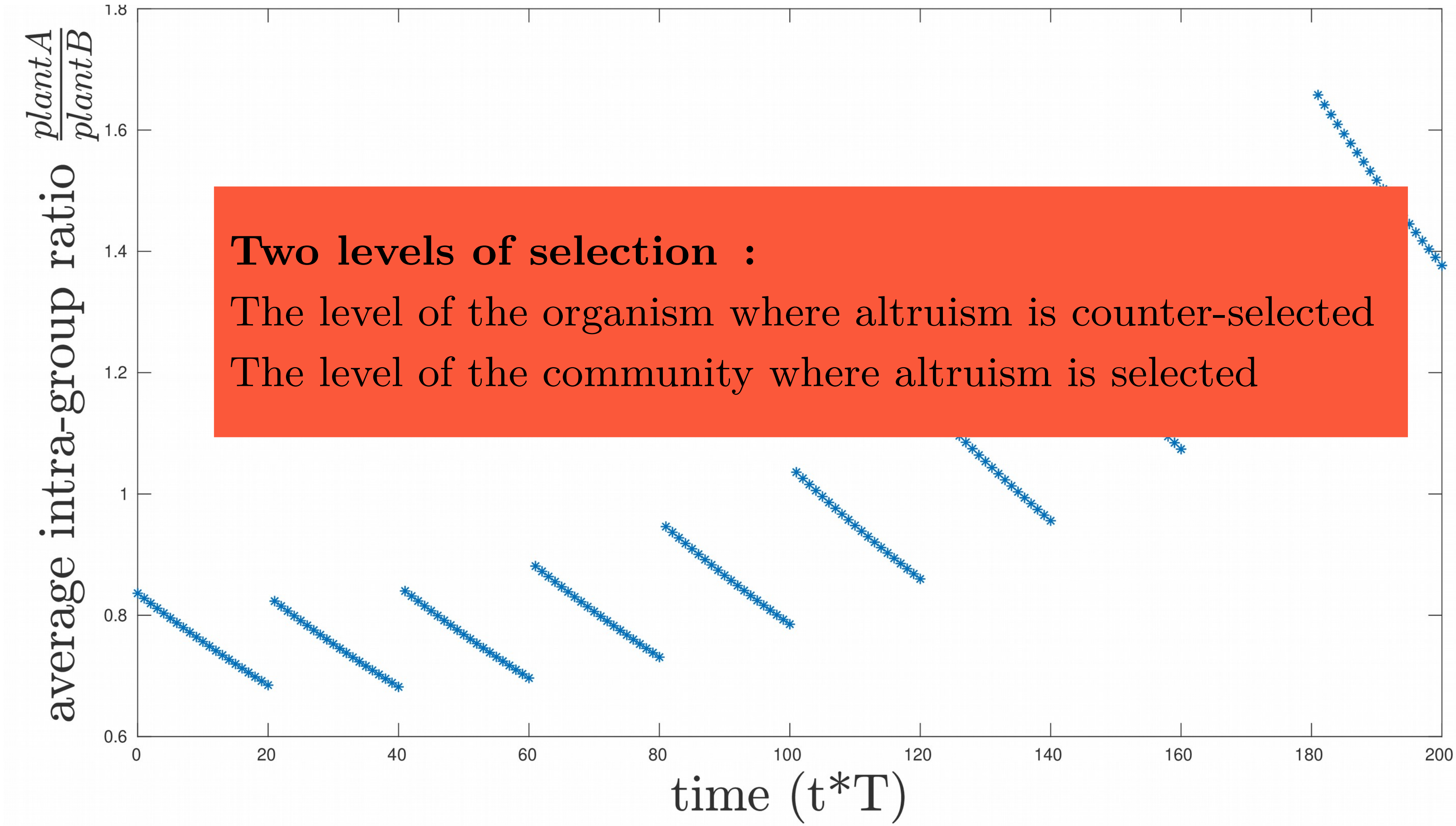

Two levels of selection :

The level of the organism where altruism is counter-selected

The level of the community where altruism is selected

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local ecological interactions ⟷ global dispersal

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local ecological interactions ⟺ global dispersal

Can a multi-level selection exist without the alternating population viscosity process ?

Requires a stronger than random spatial structure

Population viscosity and fluctuating environment (Mitteldorf and Wilson, 2000)

Individual based model with altruists and non-altruists

Ws = fitness of altruist = *1-c + Na*b/5*

Wa = fitness of non-altruist = *1 + Na*b/5*

c = cost of altruism ; b = benefit of altruism

N = population size ; a = proportion of altruists

On a two-dimensional space :

Na/5 = average proportion of altruistic neighbors (including itself)

Population viscosity and fluctuating environment (Mitteldorf and Wilson, 2000)

$$Ws = \textit{fitness of altruist} = 1\text{-}c + Na{*}b/5$$

$$\text{Wa} = \text{fitness of non-altruist} = 1 + Na{*}b/5$$

$$c = 0.2 \ ; \ \ b = 0.5$$

Fitness $= 1 + 3{*}0.5/5$
$= 1,3$

Fitness $= 1 - 0.2 + 3{*}0.5/5$
$= 1.1$

Fitness $= 1 - 0.2 + 2{*}0.5/5$
$= 1$

Altruists' fitness $= 2{*}1,1 + 1 = 3.2$

Selfishs' fitness $= 2{*}1.3 = 2.6$

Probability that the central site will be occupied by an A in the next generation

$$= 3.2/(3.2{+}2.6) = 0.552 < 3/5$$

Population viscosity and fluctuating environment (Mitteldorf and Wilson, 2000)

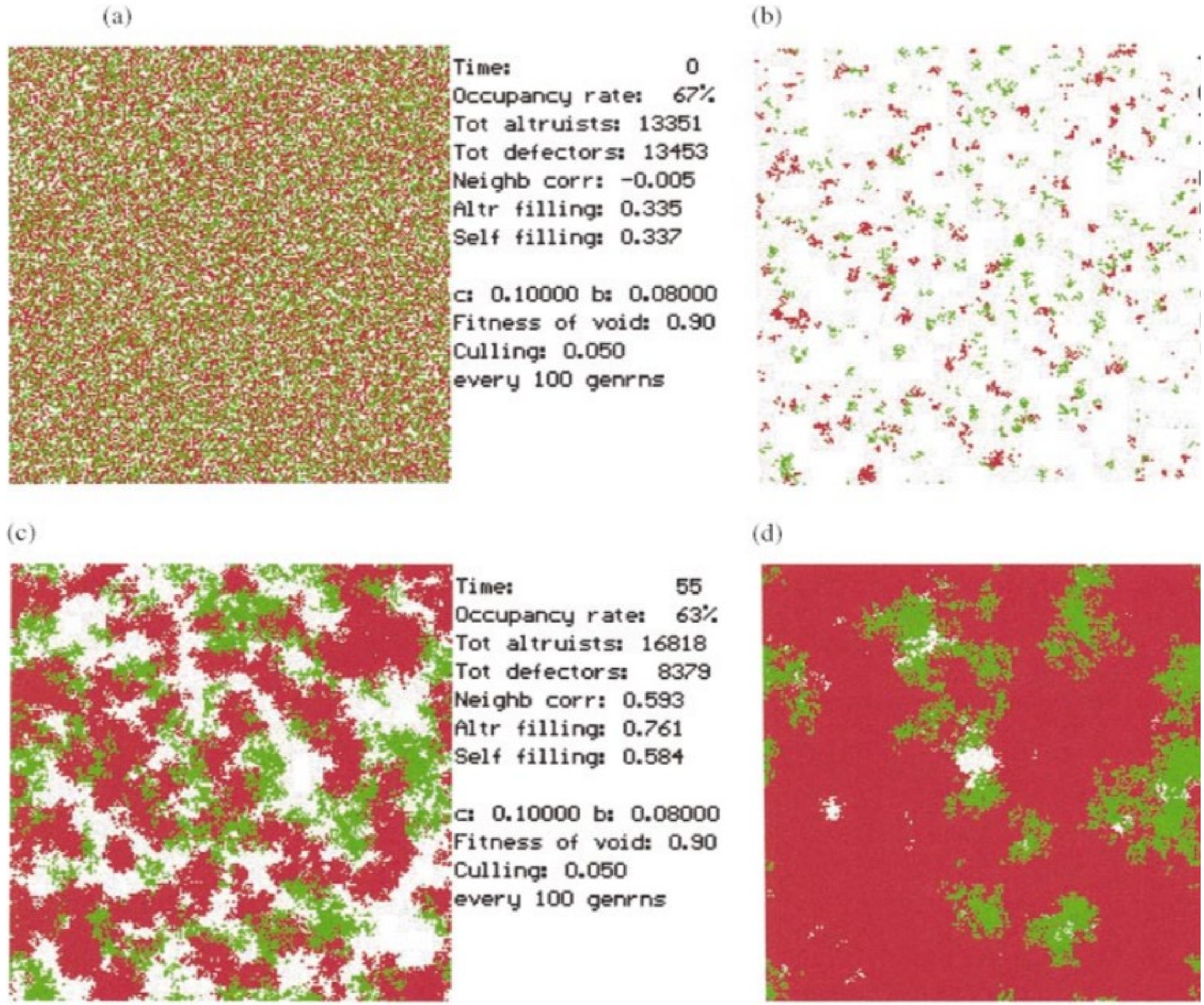
V	A	S	V	S
A	A	**S**	A	A
A	V	**A**	**A**	V
A	S	V	S	A
S	V	S	A	A

0 < fitness of void cells < 1

Population viscosity and fluctuating environment (Mitteldorf and Wilson, 2000)

Spatial structure (positive assortment) promotes by large disturbance

0 < fitness of void cells < 1



Red = altruist

Green = non-altruist

White = void

Population viscosity and fluctuating environment (Mitteldorf and Wilson, 2000)

Spatial structure (positive assortment) promotes by a minimum probability that sites become void **even when there are no void cells nearby**

Red = altruist

Green = non-altruist

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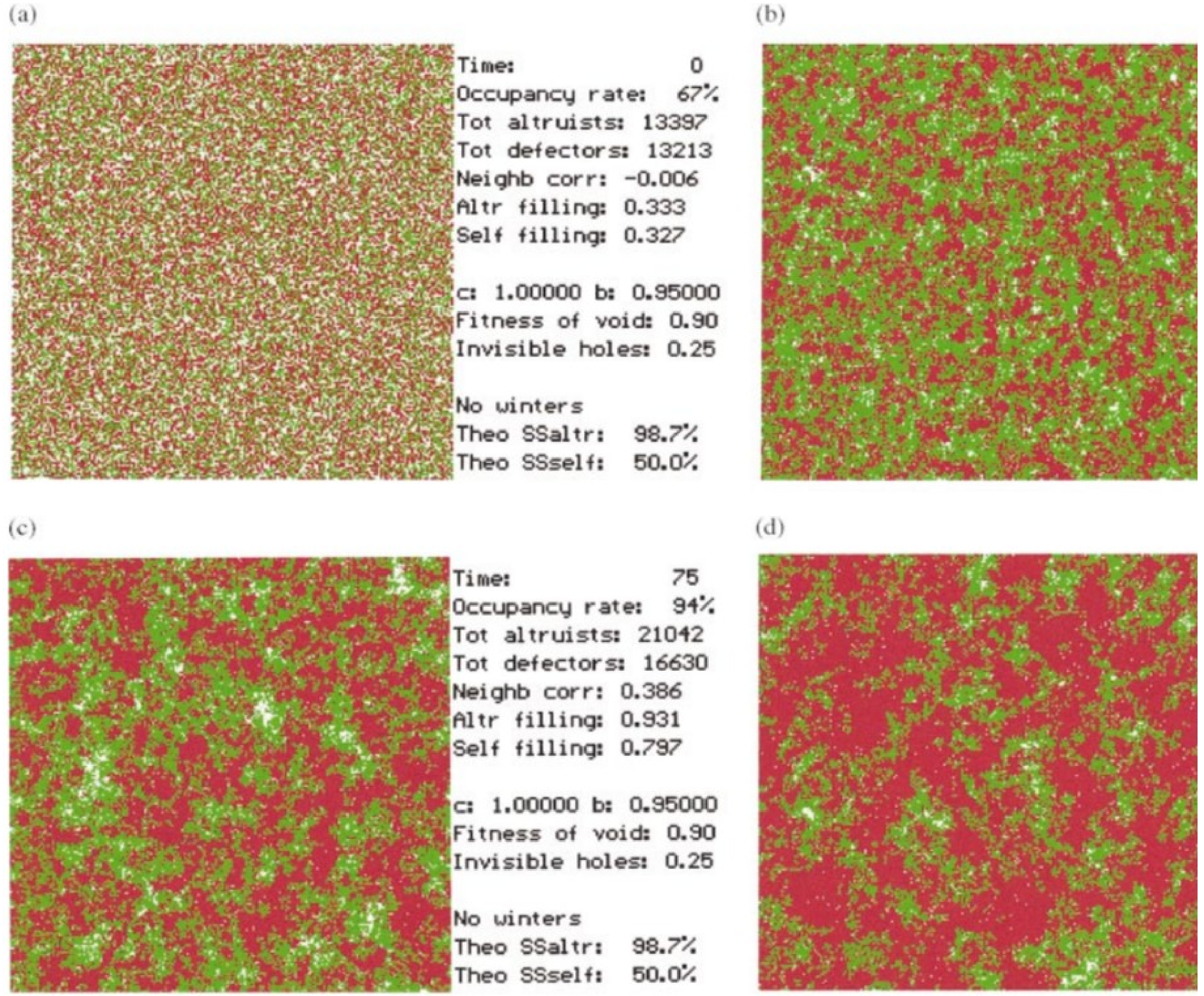
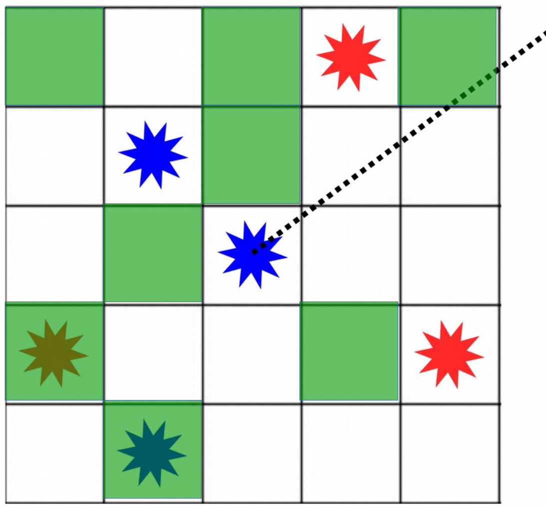


Environmental feedback (Pepper and Smuts, 2000)

Plant's growth

$$\Delta S = RS\frac{K-S}{K}$$



- Examine its current and eight adjacent cells

- From those not occupied by another forager, chose the cell containing the plant with the most energy

- If the chosen cell would yield enough food to meet its metabolic cost for one time step, it move there

- If not, it move instead to a randomly chosen adjacent cell not occupied by another forager

Lead to emigration of foragers from depleted patches

restrained forager : take 50% of the plant's energy

unrestrained forager : take 99% of the plant's energy

Foragers lost energy at each time step as a fixed metabolic cost, if energy = 0 they die.
If a forager's energy level reach an upper fertility threshold it reproduced asexually.

Environmental feedback (Pepper and Smuts, 2000)

Without spatial structure : plant in each cell

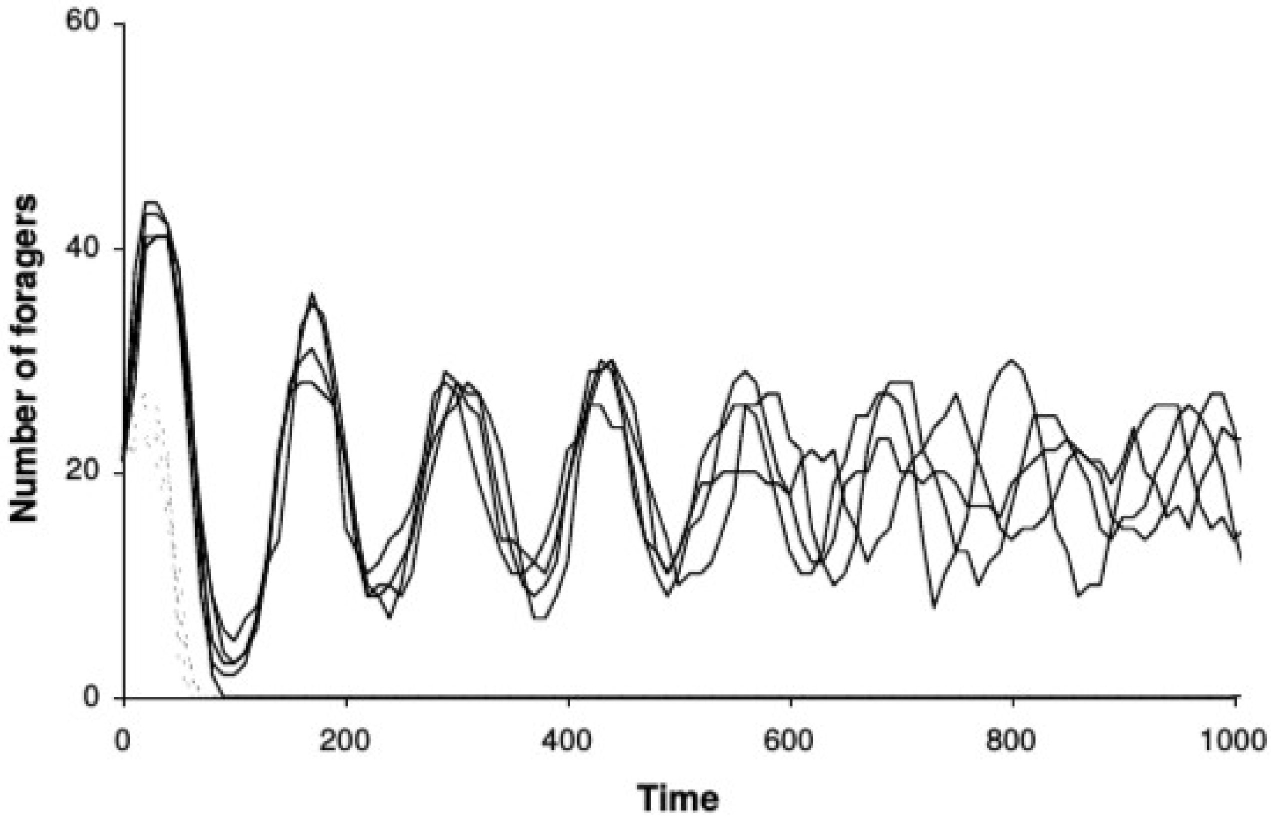


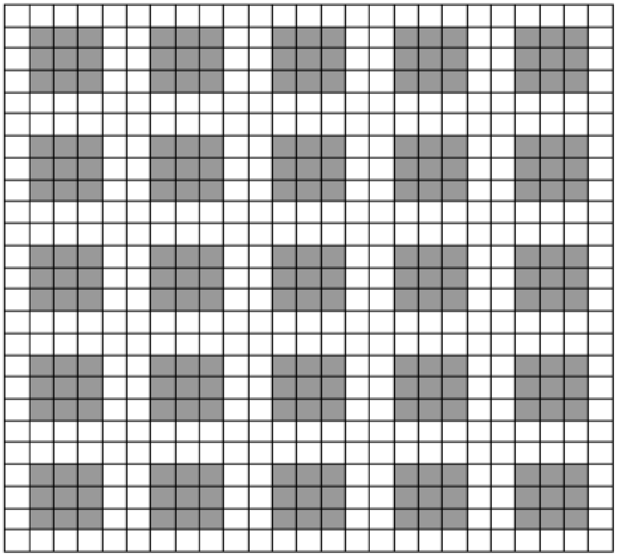
Figure 6. Number of restrained (dotted lines) and unrestrained (solid lines) foragers over time in mixed populations in a uniform environment (single patch width = 529, gap width = 0). Five runs are shown, each using the same parameter settings (see Table 1) but different random number seeds. The restraint allele was always lost, leading either to the population's extinction (in one of the five runs) or to a pure population of unrestrained foragers that oscillated in size, as in Figure 5.

Environmental feedback (Pepper and Smuts, 2000)

With spatial structure : plant in a patchy distribution

TABLE 3 Final frequency of restrained feeders as a function of patch and gap width. One run of 10,000 time steps was performed at each parameter setting. Averages over the last 1,000 time steps are shown. Boldface indicates frequencies > 0.5. *Population went extinct.

Patch width	Gap width 1	2	3	4	5	6	7	8	9	10
1	0	*	*	*	*	*	*	*	*	*
2	0	0	0	*	*	*	*	*	*	*
3	0	0	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
4	0	0	0	**1**	**1**	**1**	**1**	**1**	**1**	**1**
5	0	0	0	0	0	**1**	**1**	**1**	**1**	**1**
6	0	0	0	0	0	0	0	**1**	**1**	**1**
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0



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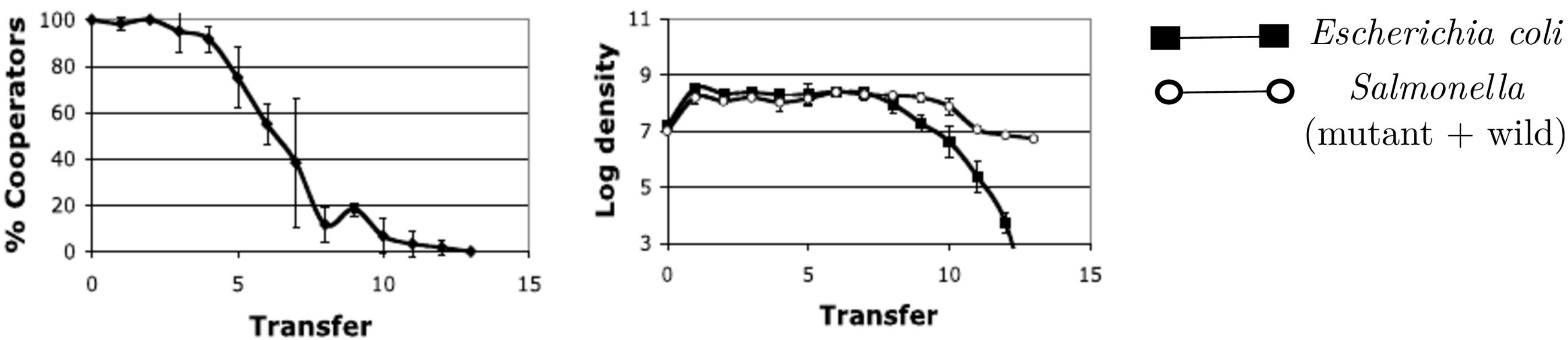

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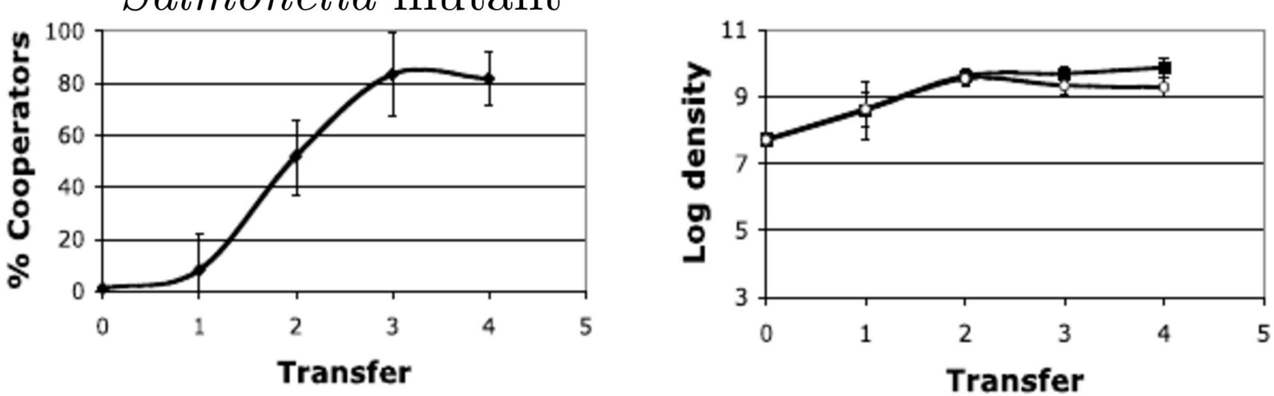
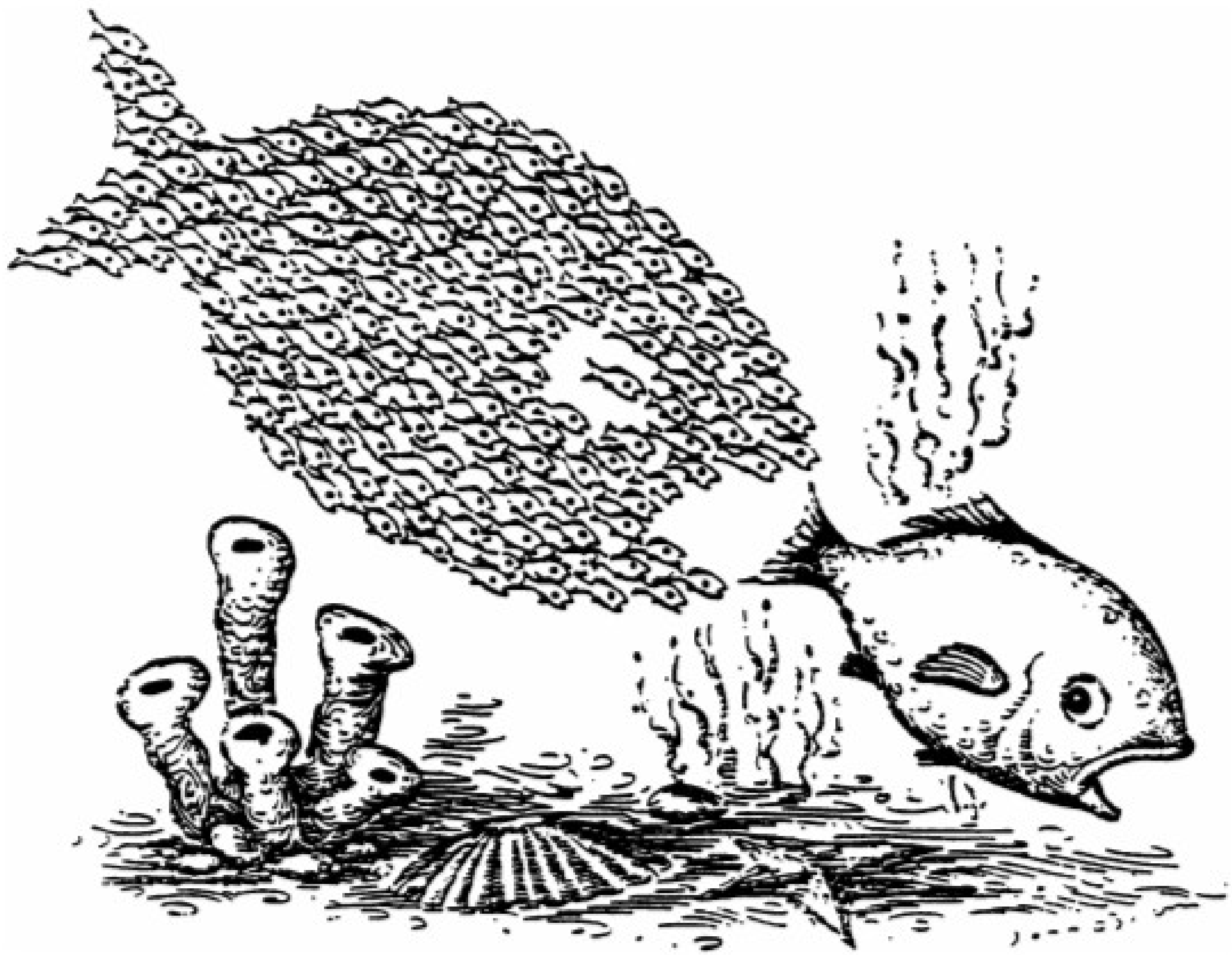


Summary

Without spatial structure	→	individual level selection
With spatial structure	→	multi-level selection : possibility of selection level conflict
Structure deme model multi-	→	only random spatial variation is sufficient to have a level selection process
Other models	→	the emergence of a stronger than random spatial structure allows for a multi-level selection process

Thanks for your attention !



John O'Brien. Reprinted by permission of *The New Yorker* from October 28, 1991, p. 39.

In Sober and Wilson, 1998