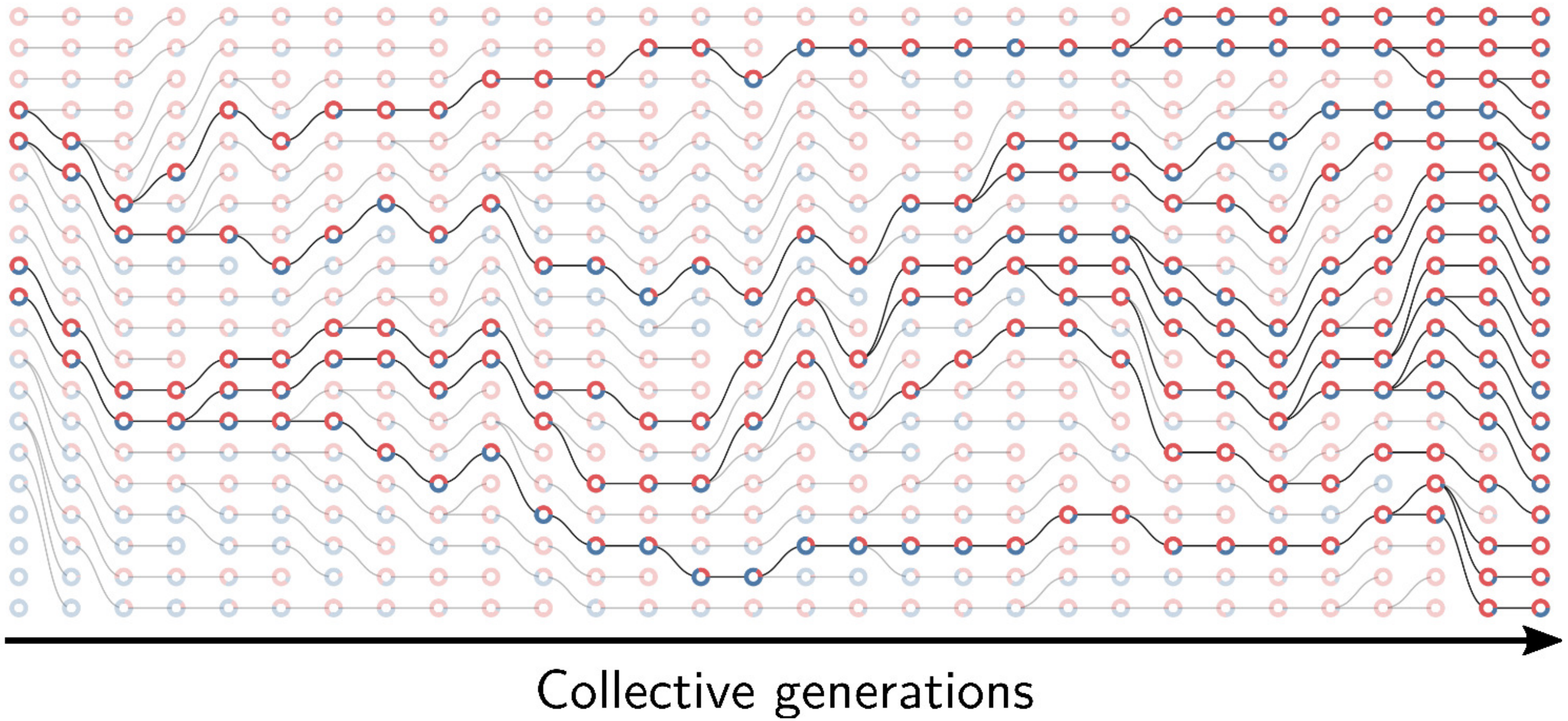
3. Community evolution under collective-level selection



Aussois, June 19, 2025

Community functions

Collective motility
Stress resistance

Primary production
Total biomass / population size
Stability
Resilience

Host health
Homeostasis

Bioremediation
Production of a compound of interest

Heterogeneity
Biodiversity
Complementarity

Are such functions selected, and how?

S. De Monte and P.B. Rainey
Nascent multicellular life and the emergence of individuality
J. Biosciences 2014

Experiments on microbial community selection

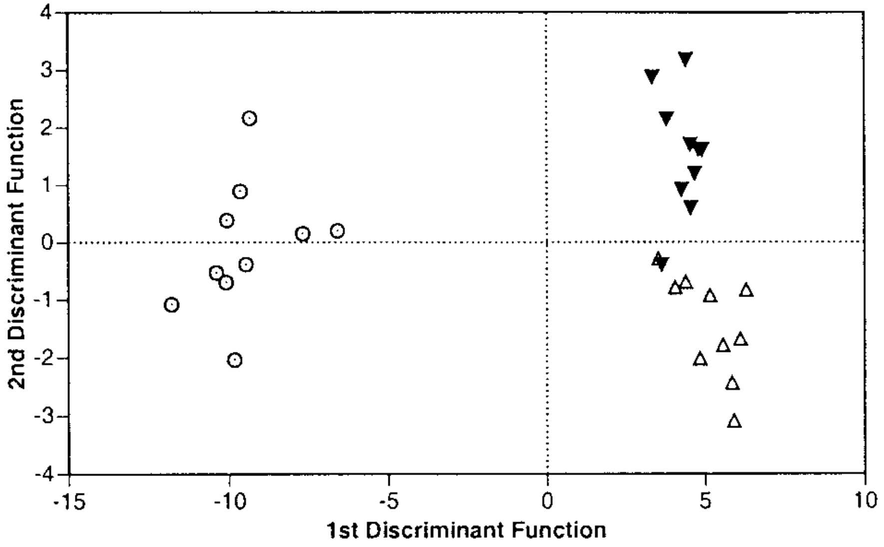
Annual Review of Biophysics

Directed Evolution of Microbial Communities

Álvaro Sánchez, Jean C.C. Vila, Chang-Yu Chang, Juan Diaz-Colunga, Sylvie Estrela, and María Rebolleda-Gomez

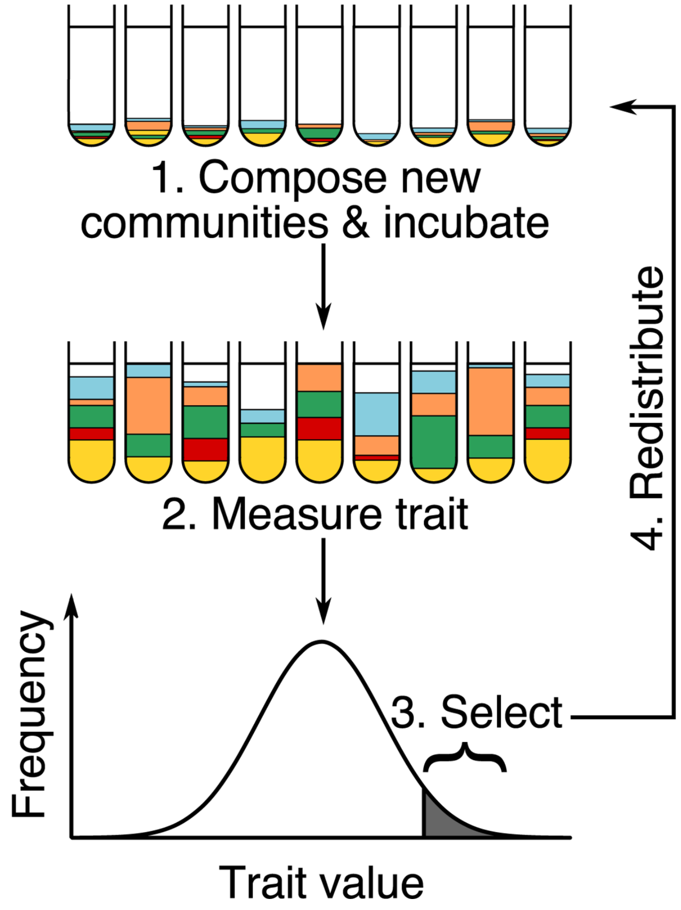
More recent studies have attempted to select microbiomes that degrade extracellular polymers (18, 121), protect plants against drought (55, 71), alter the development of animal embryos (8), and facilitate the growth of a species that could not grow on its own (18). We believe that it is fair to say that success has been mixed (some experiments succeeded while others failed or were inconclusive) and generally modest.

Annu. Rev. Biophys. 2021. 50:323–41



Swenson, Wilson & Elias
Artificial ecosystem selection
PNAS (2000)

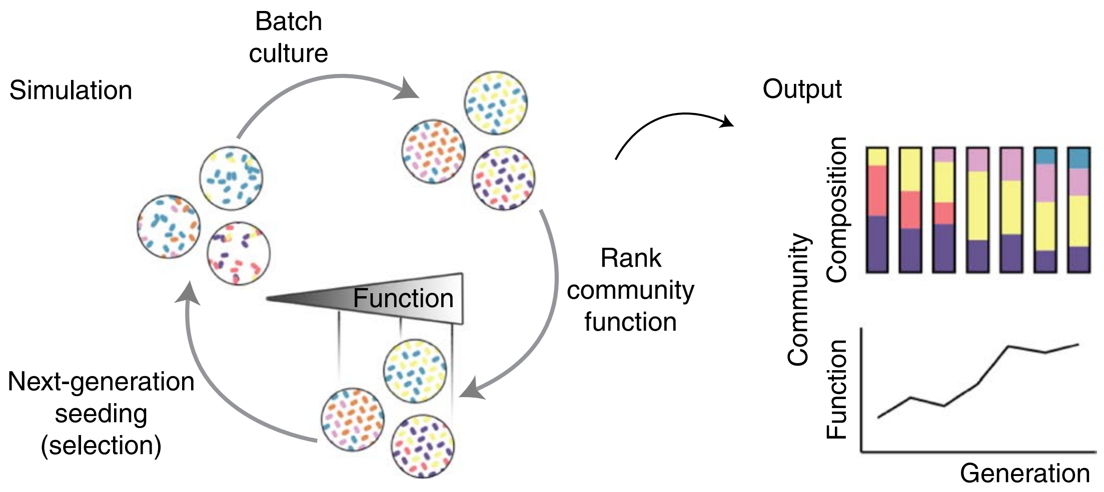
Artificial selection of community function

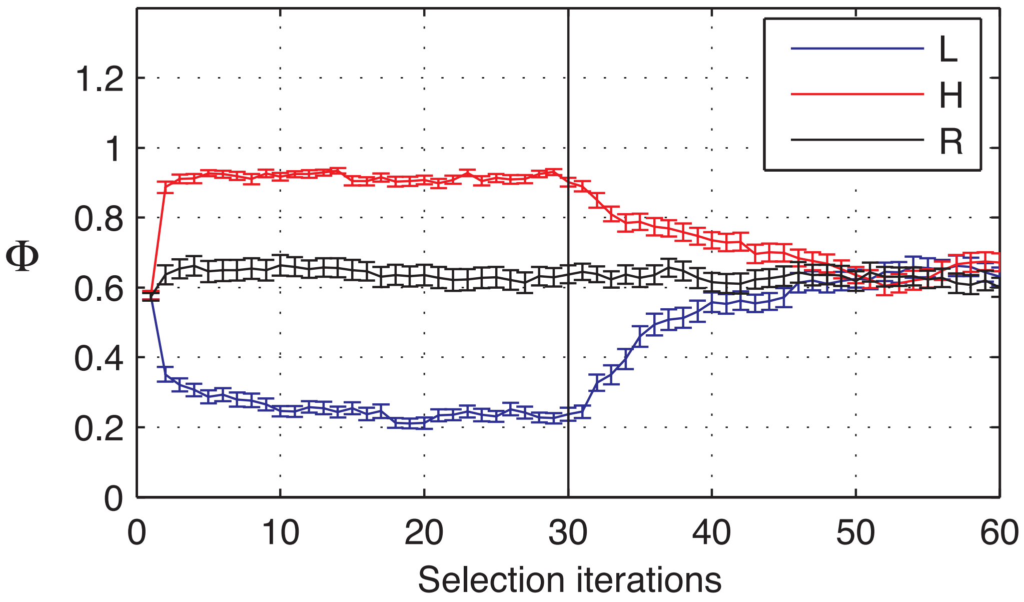


Arias-Sánchez et al.
Artificially selecting microbial communities: If we can breed dogs, why not microbiomes?
PLoS Biol (2019)

selection is applied on a measurable function of the community composition
e.g. total biomass, specific species ratios

Multi-species communities: numerical results





Chang et al.
Engineering complex communities by directed evolution
Nature Ecology & Evolution (2021)

SDM
N&V: Ecological recipes for selecting community function
Nature Ecology & Evolution (2021)

Williams & Lenton
Artificial selection of simulated microbial ecosystems
PNAS

Evolution of collective function in:

1. Two-species communities

See also Wenying Shou and van Vliet & Doebeli

2. Many-species communities

Guilhem Doulcier

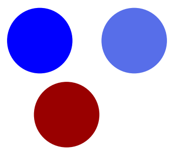
Amaury Lambert

Paul Rainey

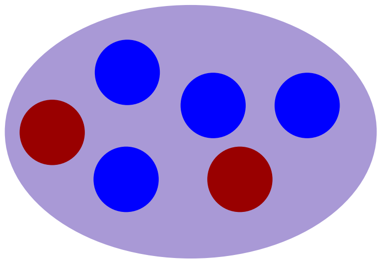
How does heredity of collective (community) traits evolve?

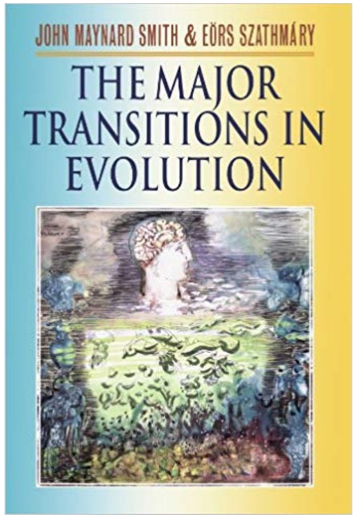
Nested population structure

Individual
(gene, cell, organism)



Collective
(chromosome, body, society, community)



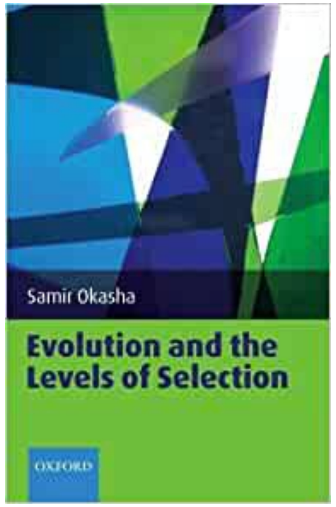


1995

Major evolutionary transitions

Evolutionary transitions in individuality

2009



Evolution by natural selection

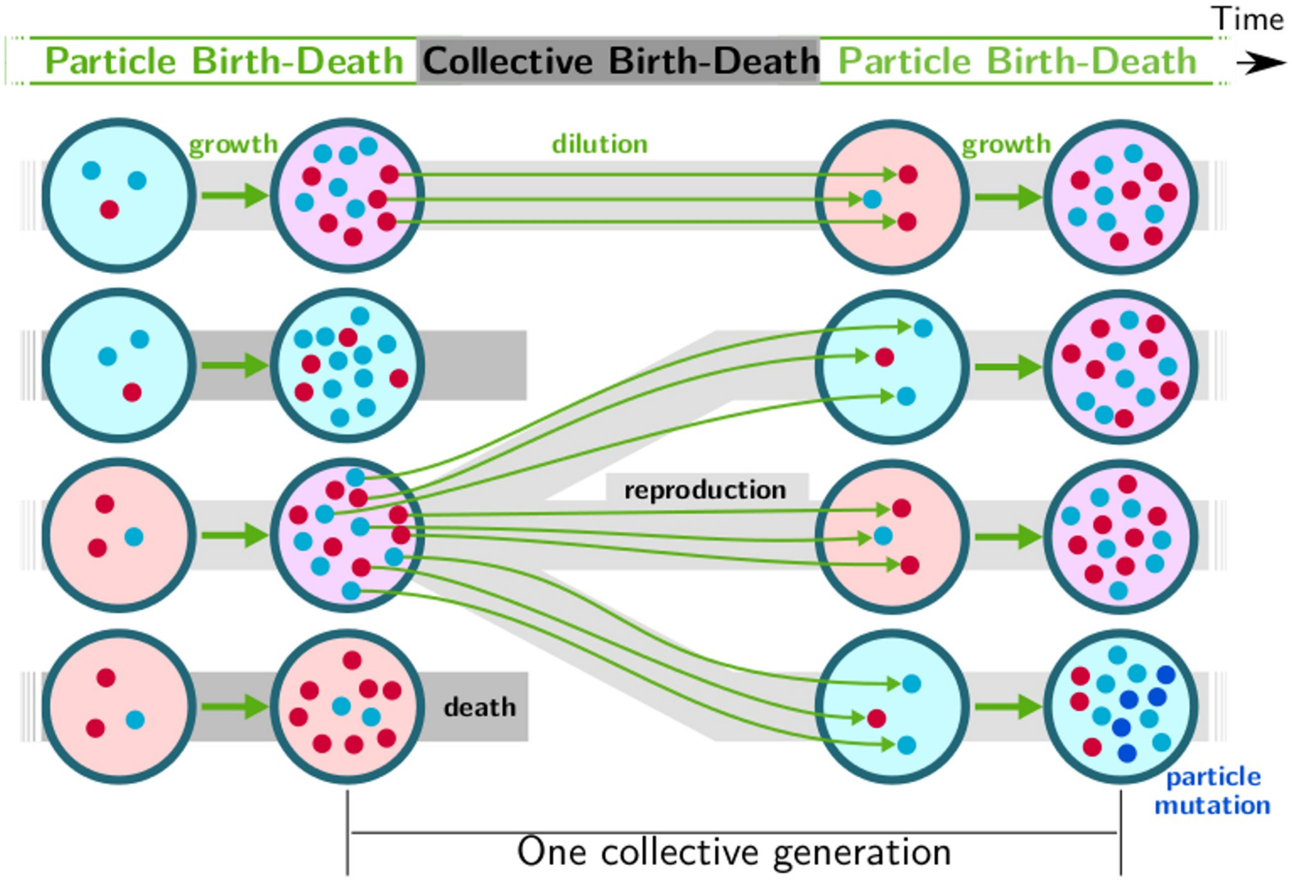
Necessary conditions for evolution by natural selection (Lewontin, 1970)

Variation | Inheritance | Demographic differences

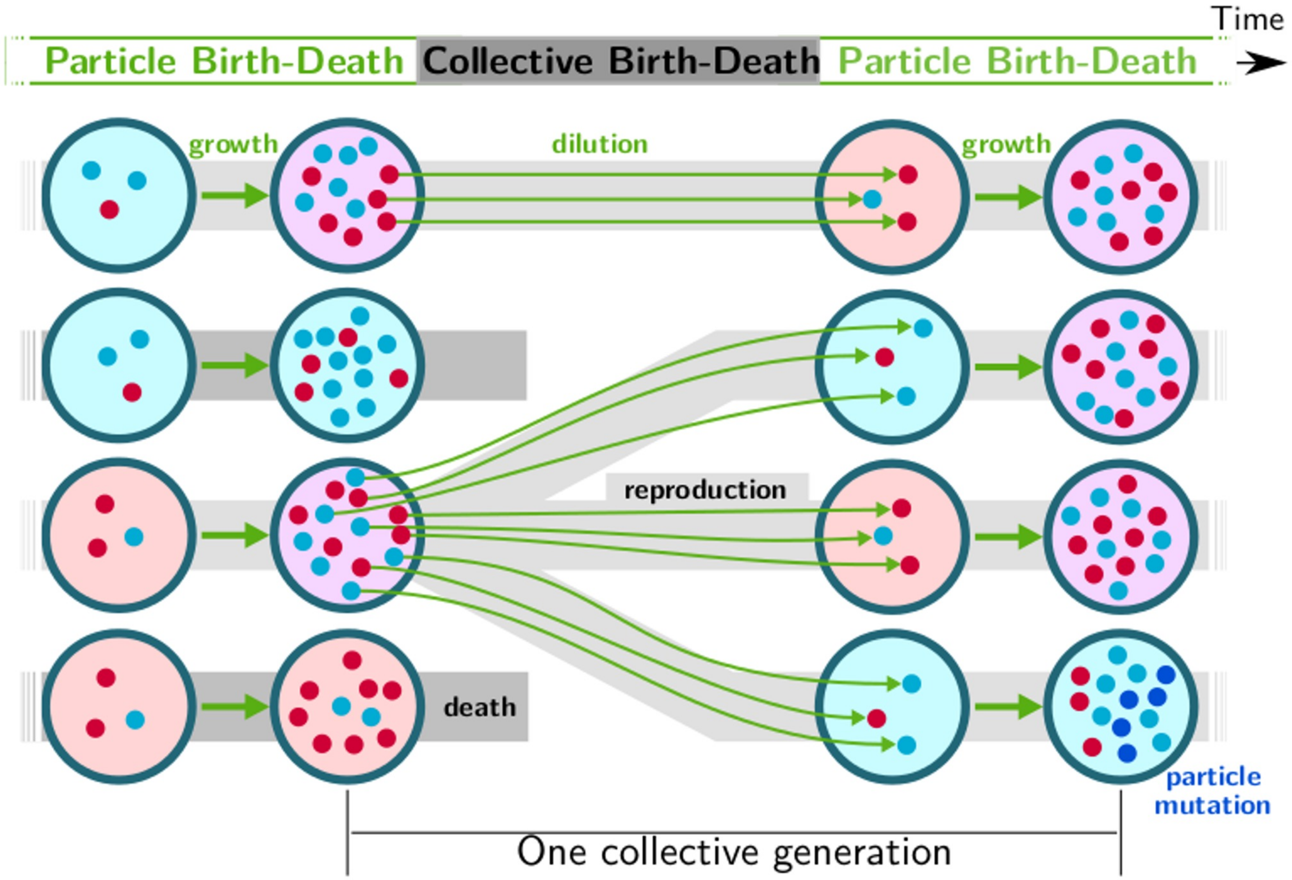
'Heritable variance in fitness'

S. De Monte and P.B. Rainey
Nascent multicellular life and the emergence of individuality
J. Biosciences 2014

Selection for community composition

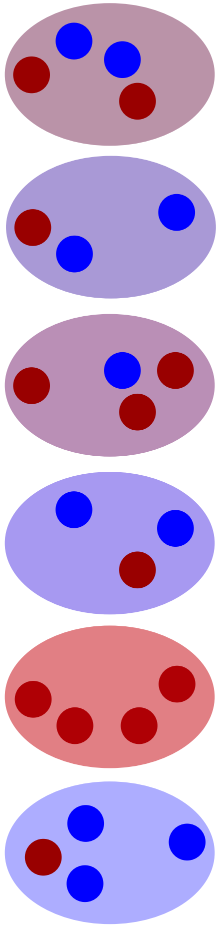


Selection for community composition

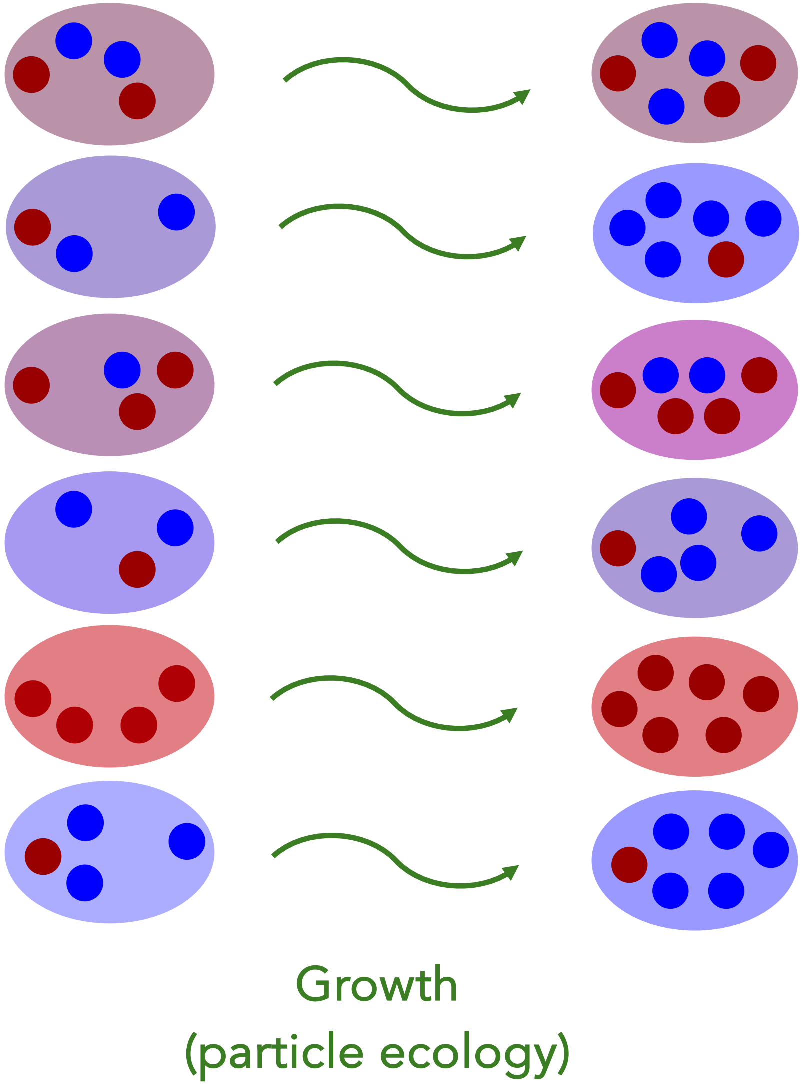


How is balanced state maintained across collective generations?

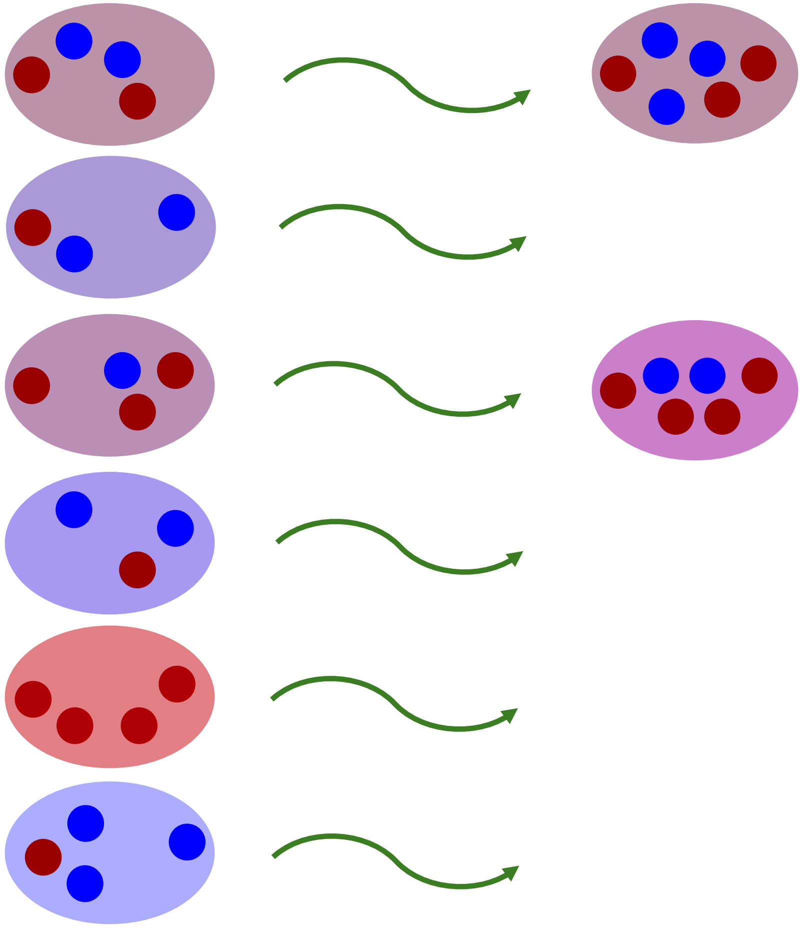
Nested Darwinian populations



Nested Darwinian populations

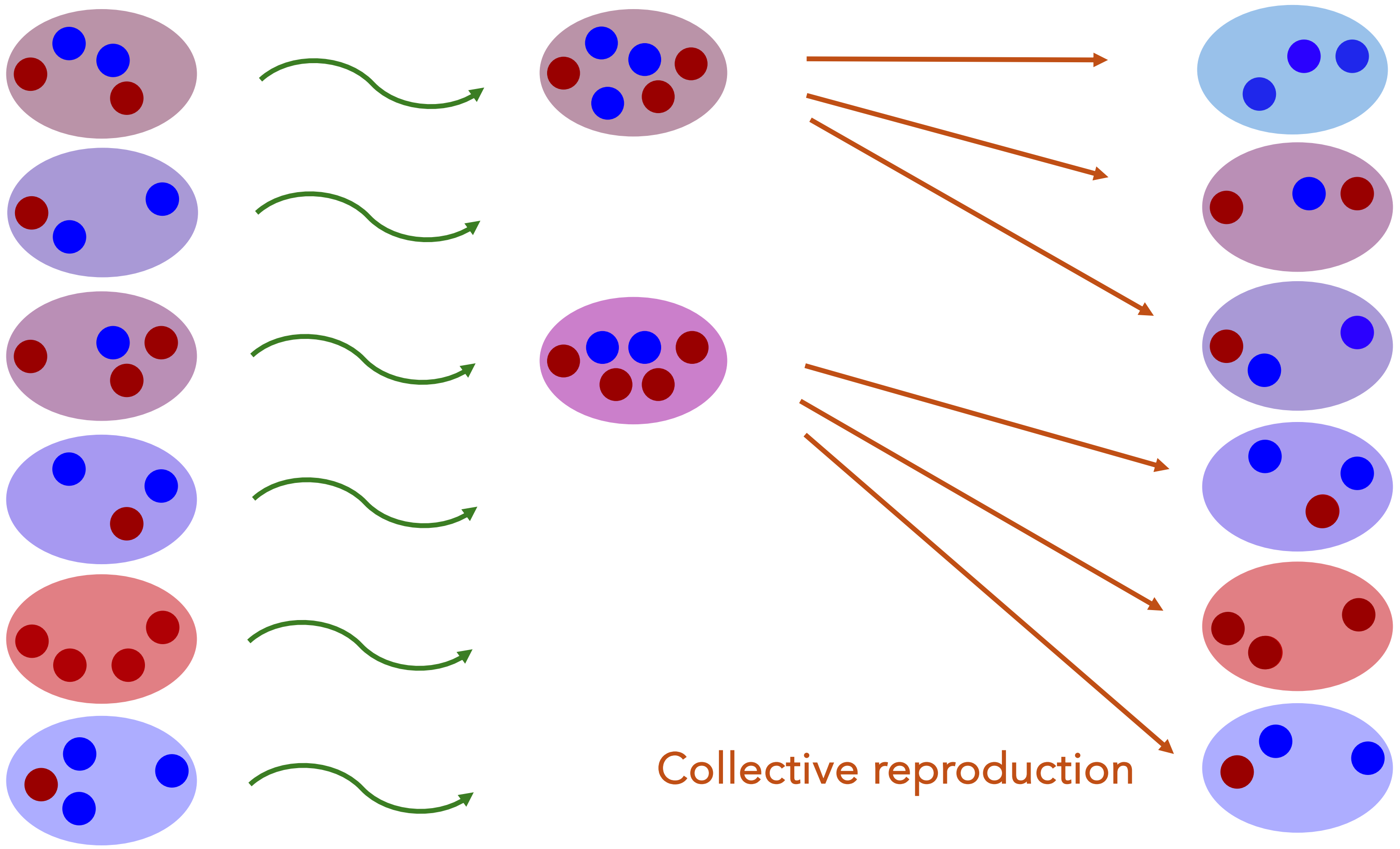


Nested Darwinian populations

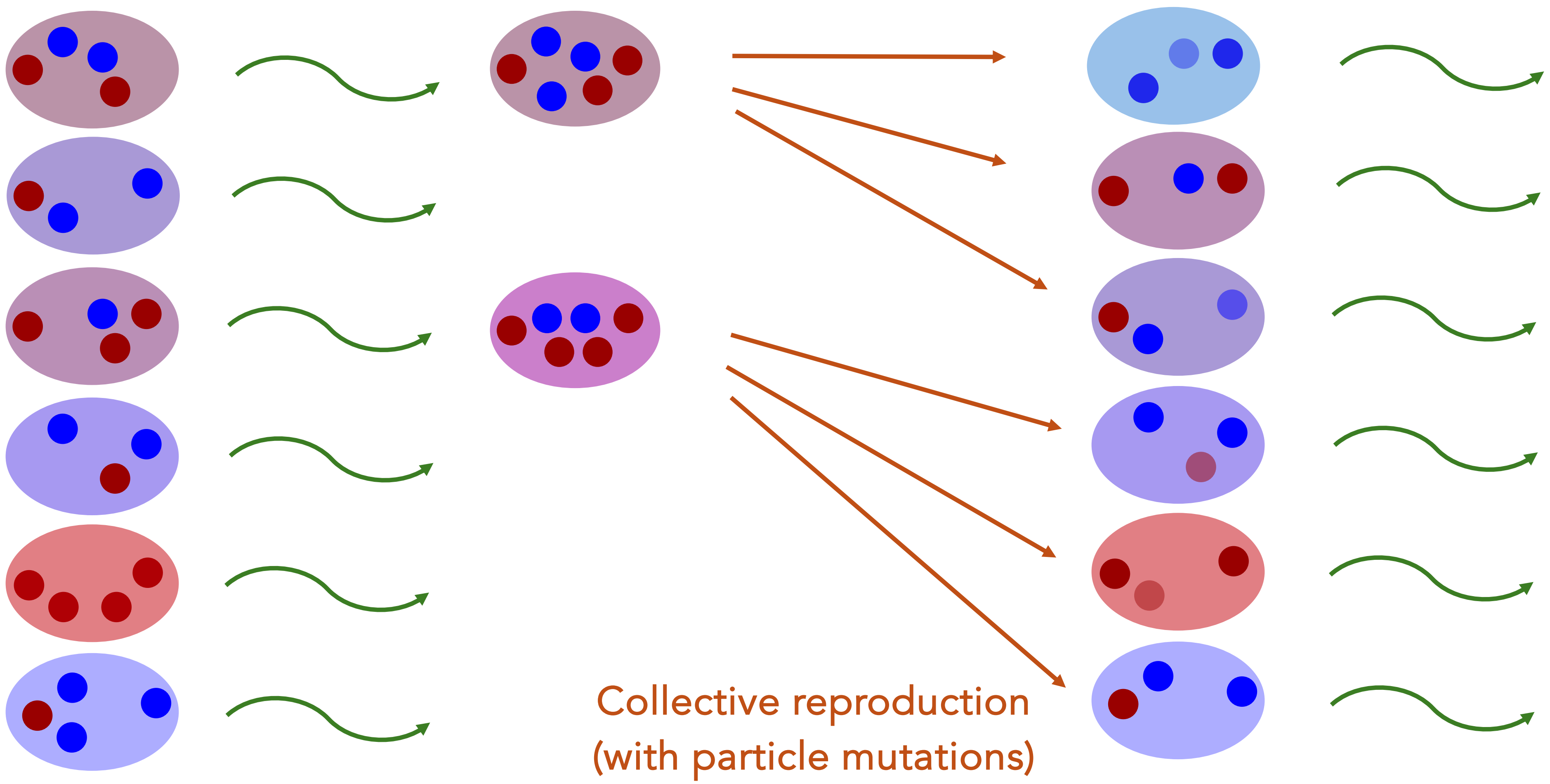


Selection on collective phenotype (50%)

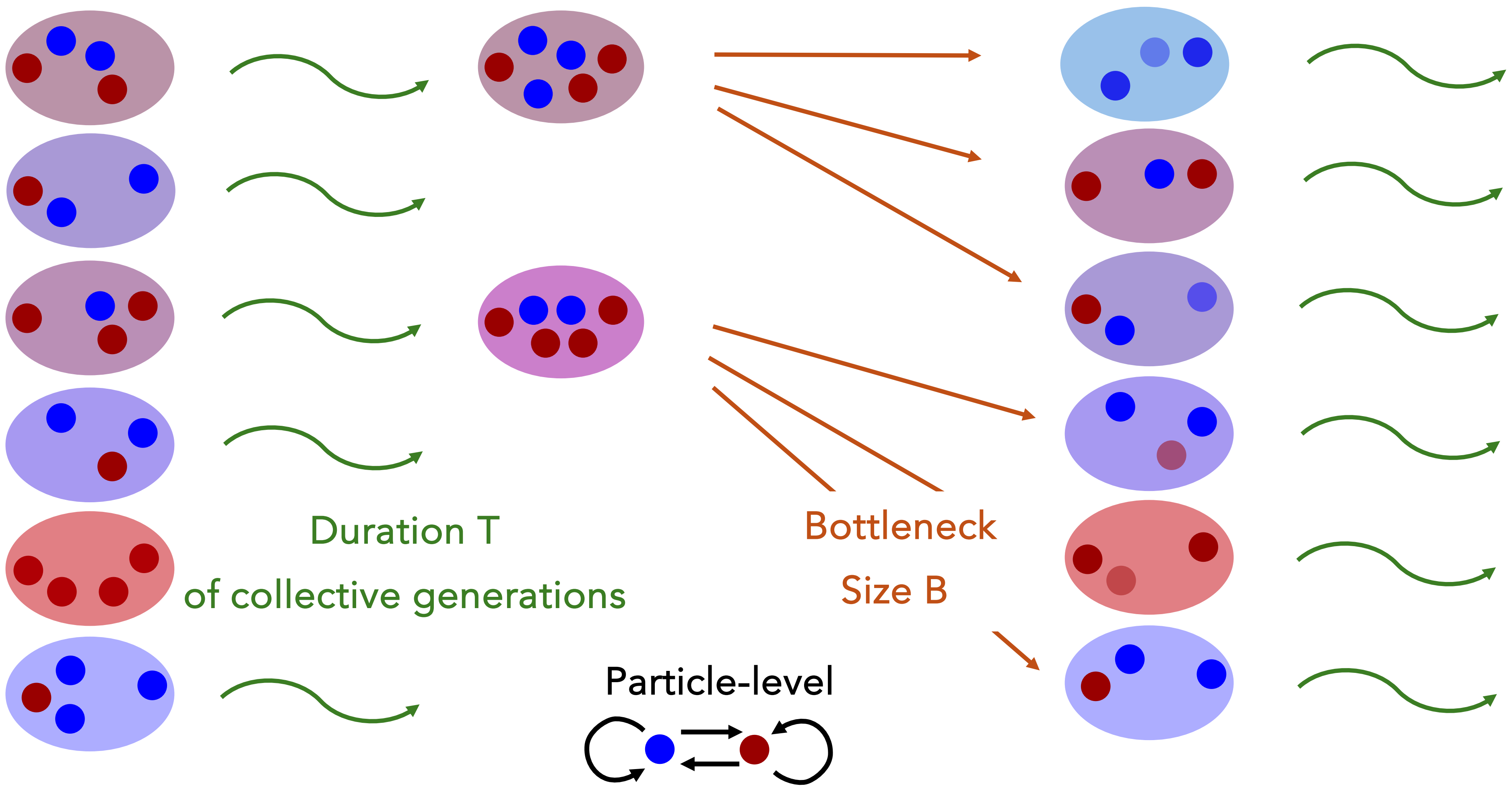
Nested Darwinian populations



Nested Darwinian populations



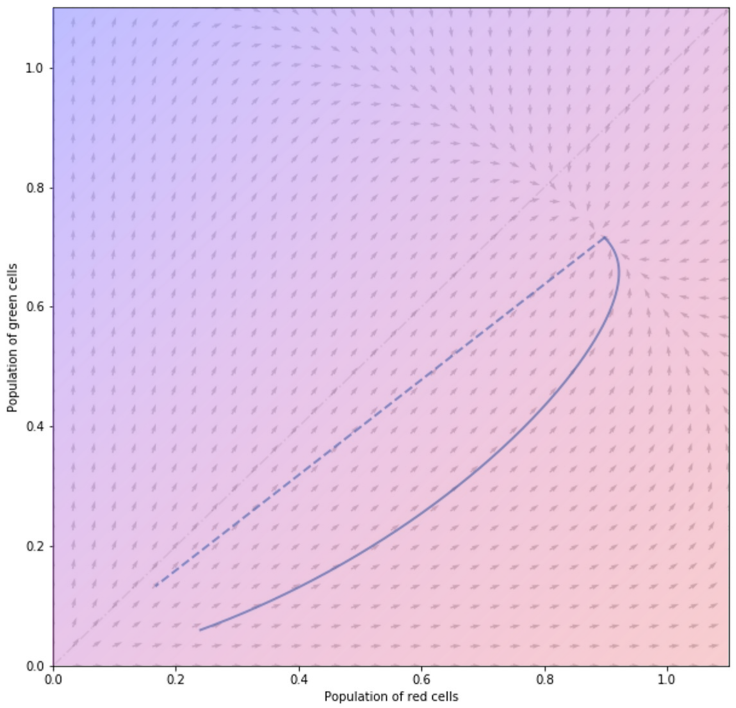
Nested Darwinian populations



Within-collective particle ecology

Lotka-Volterra competitive equations

$$\begin{cases} \frac{dN_0}{dt} = r_0 N_0 (1 - a_{00} N_0 - a_{01} N_1) \\ \frac{dN_1}{dt} = r_1 N_1 (1 - a_{10} N_0 - a_{11} N_1) \end{cases}$$



Particle traits (of the biological system):

Growth rates r_i

Intra- and Inter-specific interactions a_{ij}

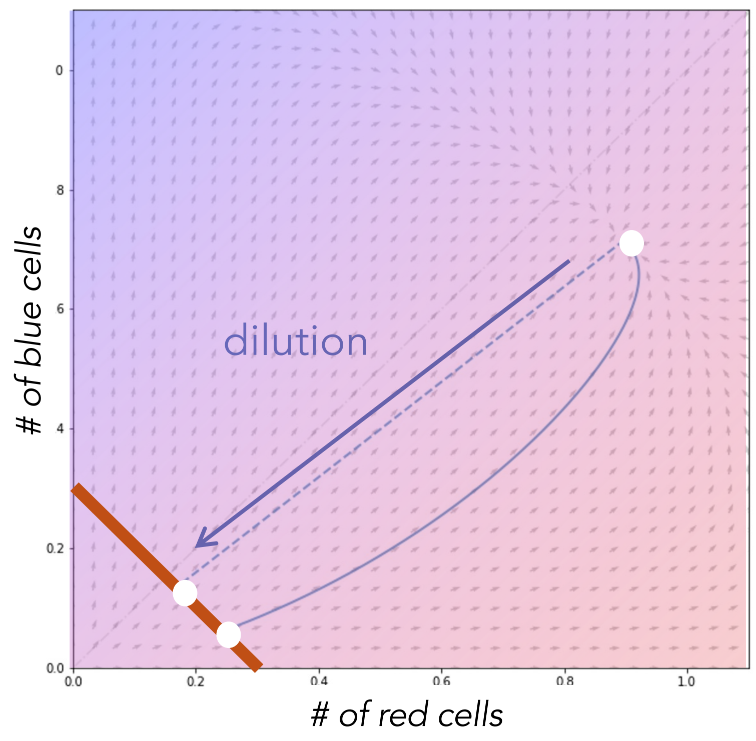
Particle ecology across collective generations

Collective parameters:

T duration of a collective generation

B bottleneck size

These are the parameters an experimenter can modify



Particle ecology across collective generations

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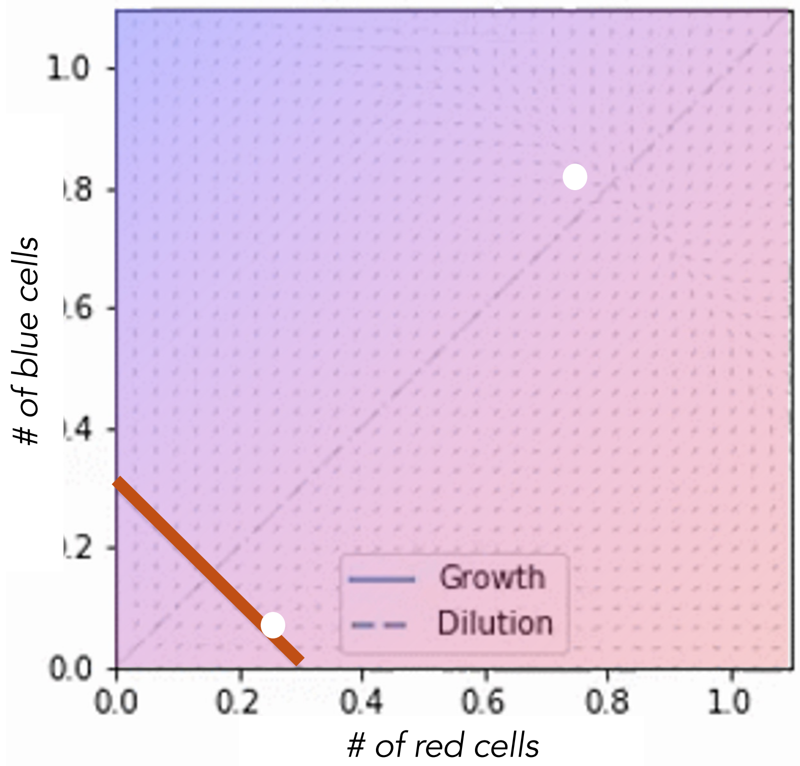
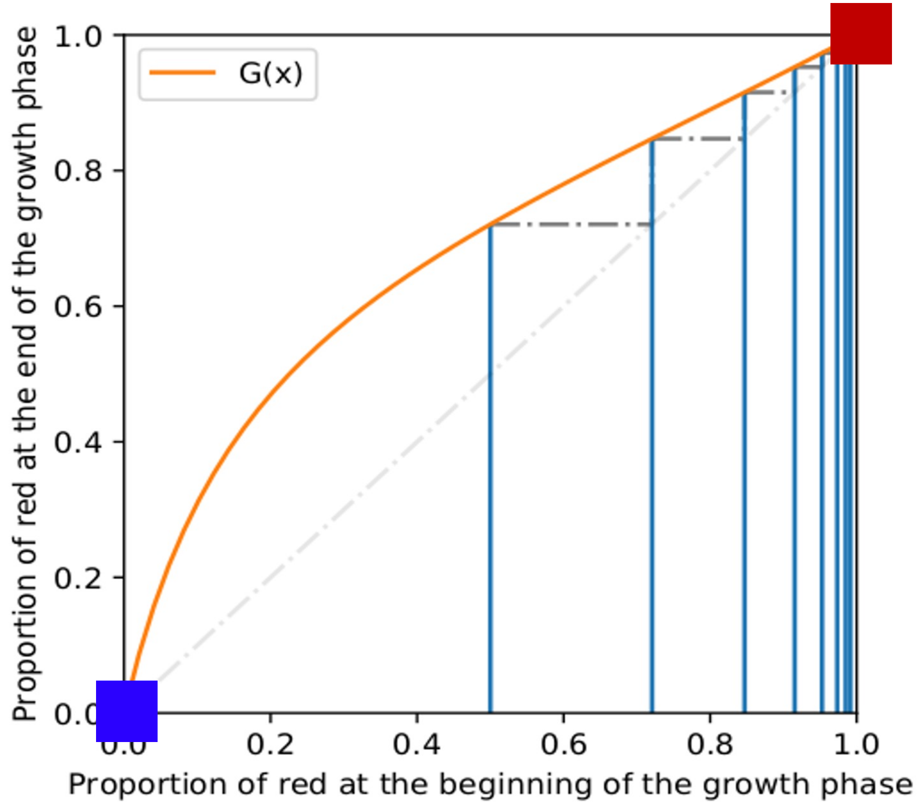


Time-discrete dynamics of collective colour

'Developmental' growth function G: colour of an adult collective as a function of newborn colour



An analogy:

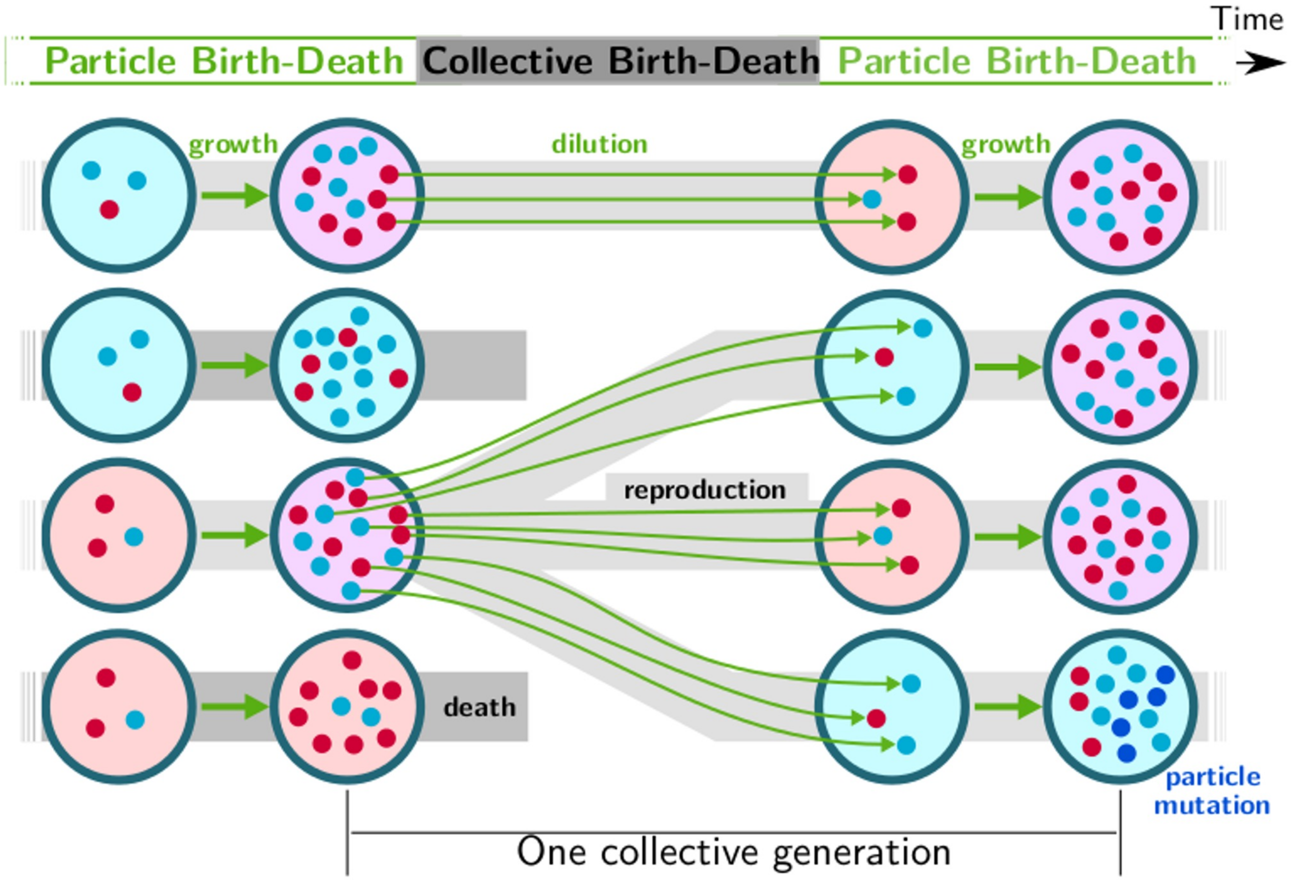
particle parameters: genotype

collective colour: phenotype

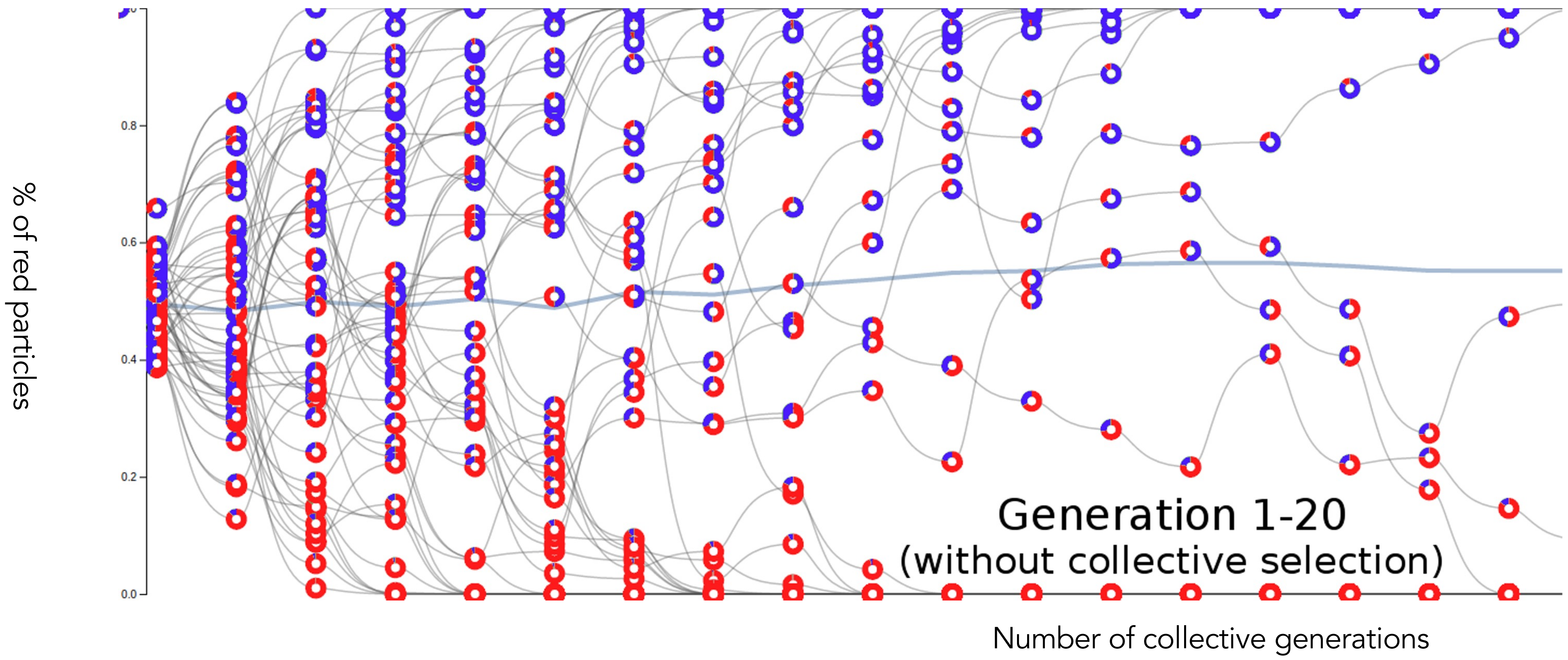
growth function: genotype-to-phenotype map

Sources of stochastic phenotype variation: sampling at birth, particle-level demography

Selection for community composition

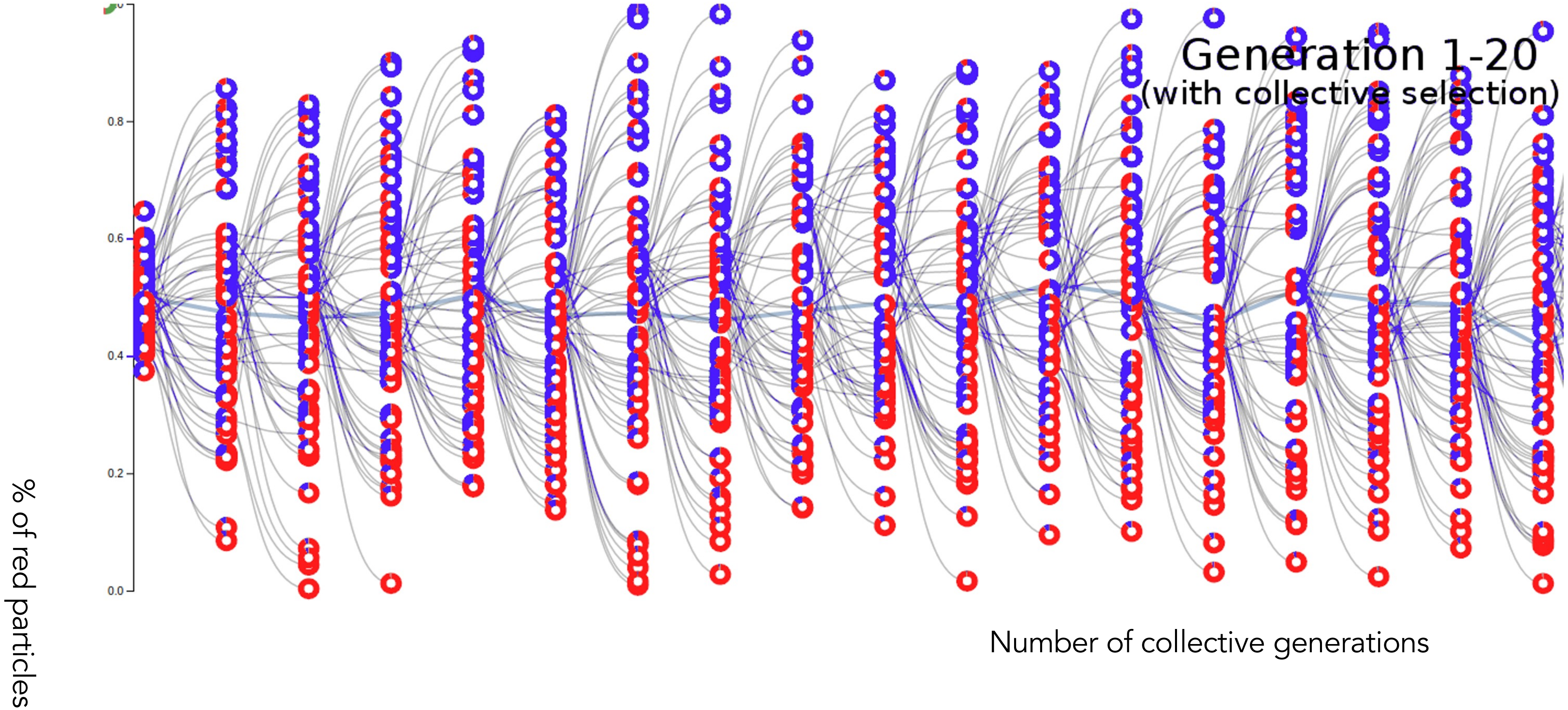


No collective-level selection



In the absence of selection, stochastic sampling leads to monochromatic lineages.

Colour selection without particle trait evolution



Target colour is maintained by ‘stochastic correction’

Eörs Szathmáry and J. Maynard Smith
The Major Transitions in Evolution. Oxford, 1995

Stochastic corrector

PROS

Collective colour is maintained in spite of differences in growth rate thanks to stochastic fluctuations at birth

Eörs Szathmáry and J. Maynard Smith
The Origins of Life, Oxford University Press, 1999

CONS

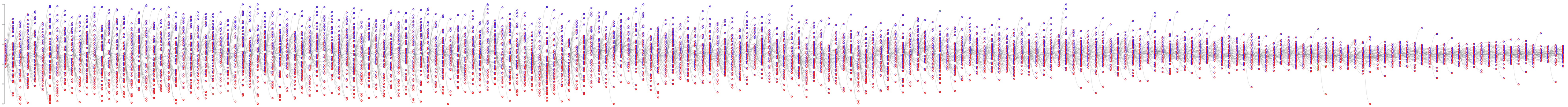
Small populations with too large bottlenecks may not avoid extinction

Inefficient process: most collectives get discarded at each generation

The target colour is rapidly lost if selection is discontinued

Colour selection with particle trait (slow) evolution

The particles of any colour can produce ‘mutants’ with different traits.
If the mutant increases in frequency, it substitutes the resident.



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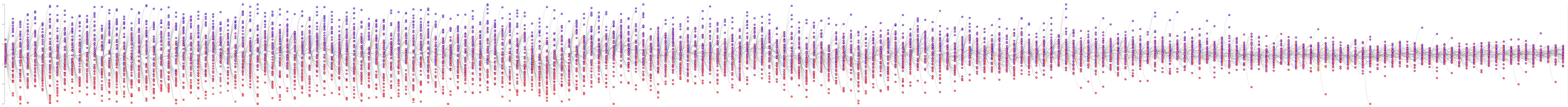
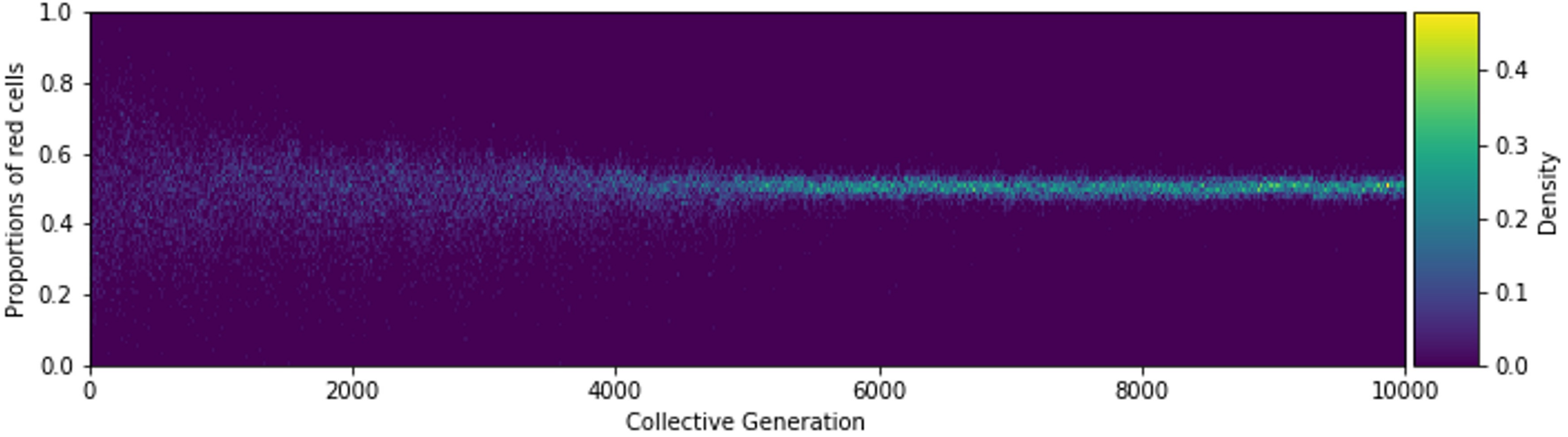
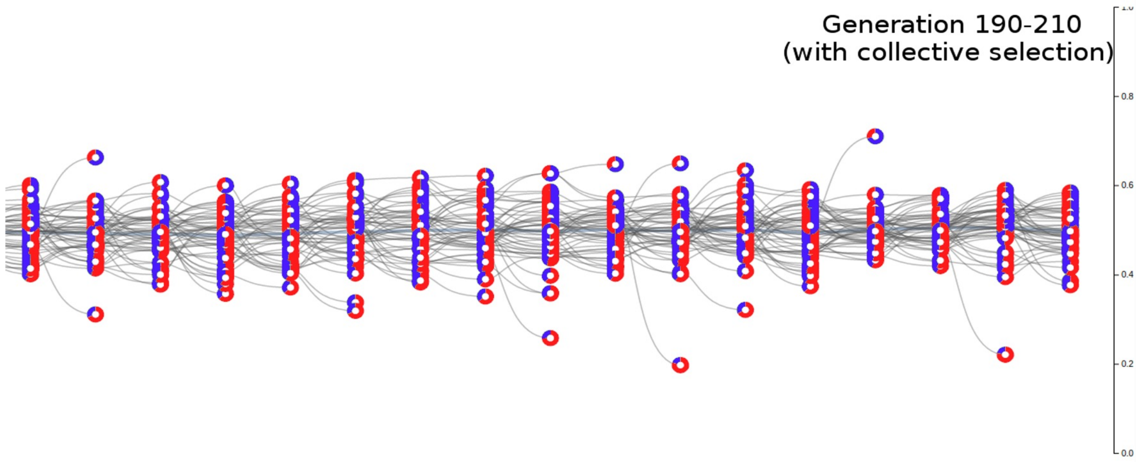




Collective colour has become heritable

Permanence of the collective phenotype across collective generations



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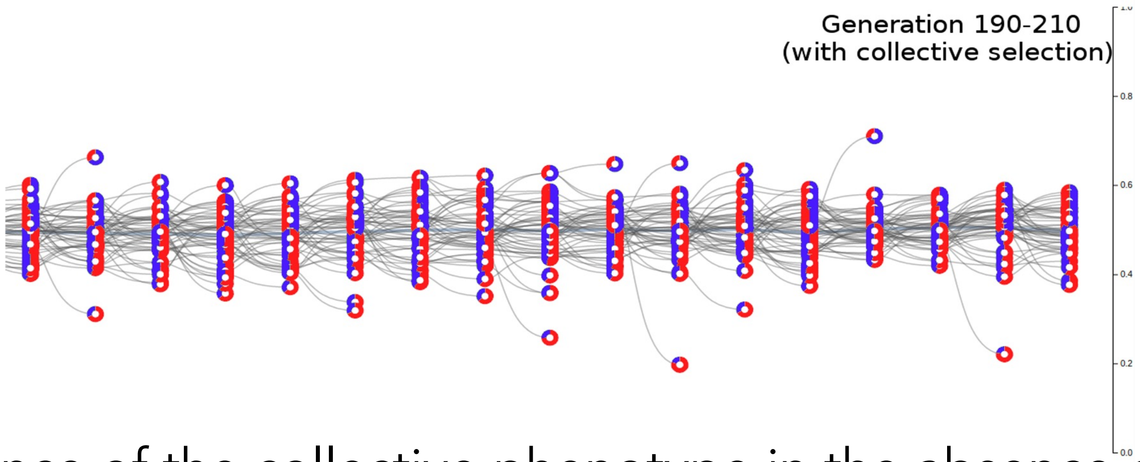
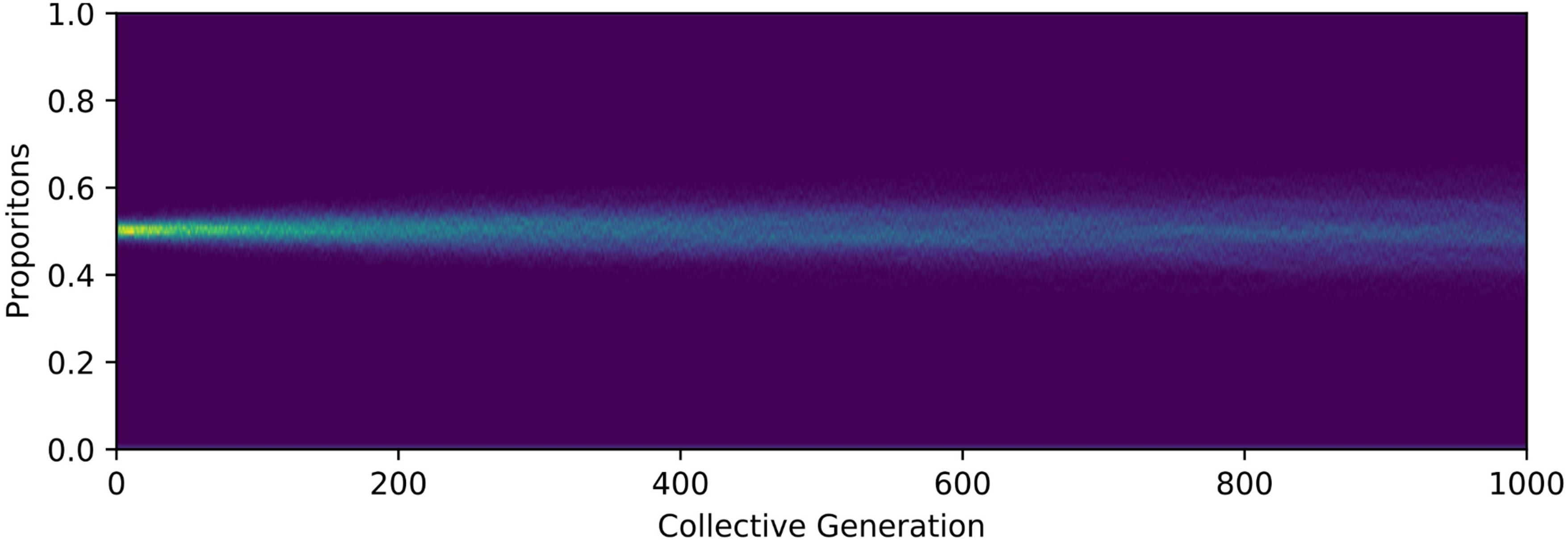
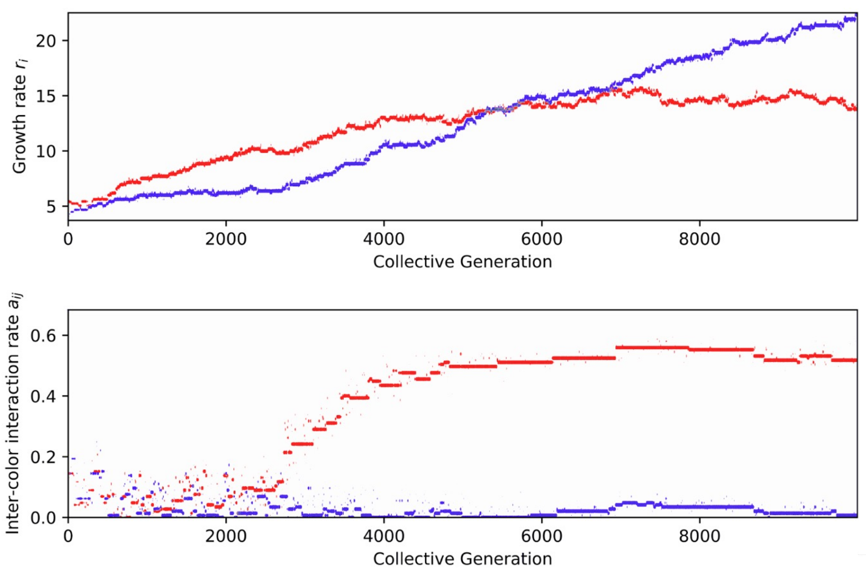


Permanence of the collective phenotype in the absence of selection



Evolution of a 'Developmental Corrector'

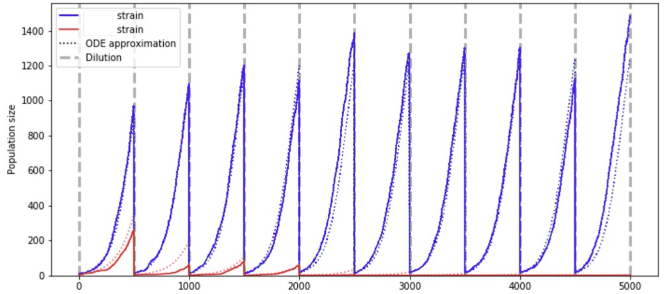


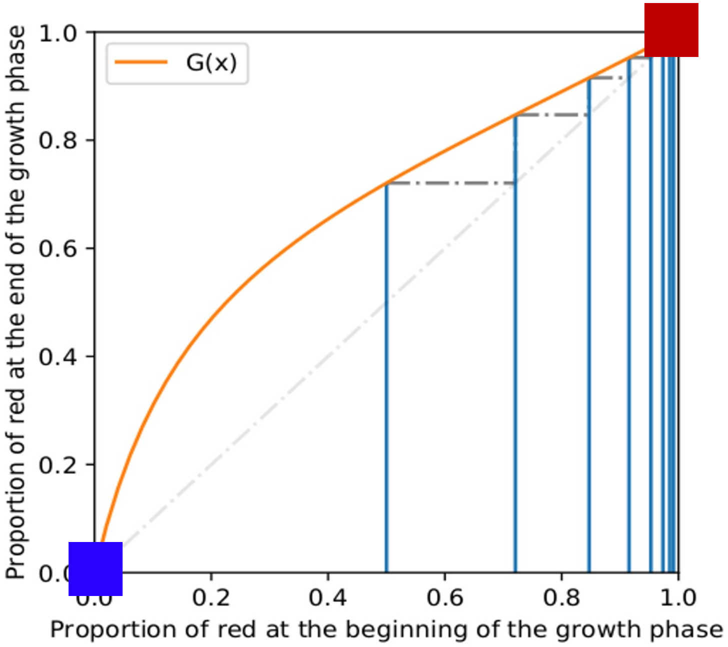
Growth and interaction rates evolve (if unconstrained) so that:

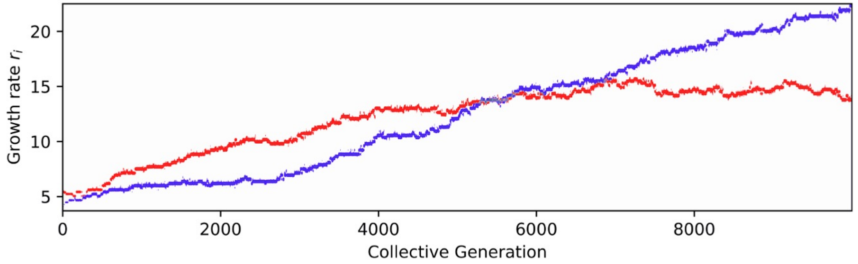
1. Particle growth increases: interactions/ecology become important within a collective generation
2. Interactions become increasingly asymmetric
3. Colour becomes increasingly heritable in spite of fluctuations at birth

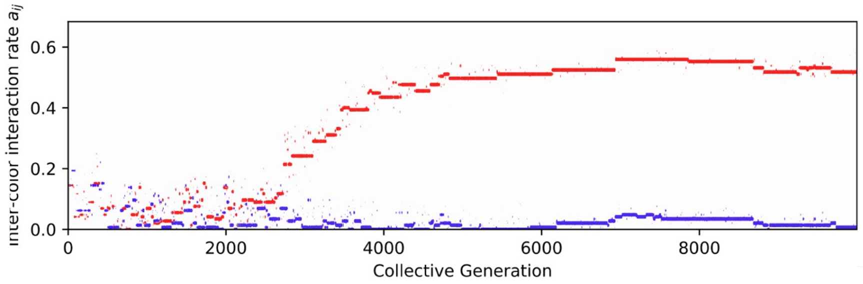
Evolution of a ‘Developmental Corrector’

Stochastic corrector



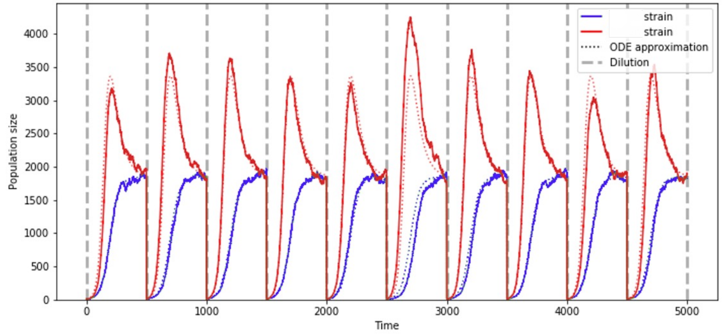


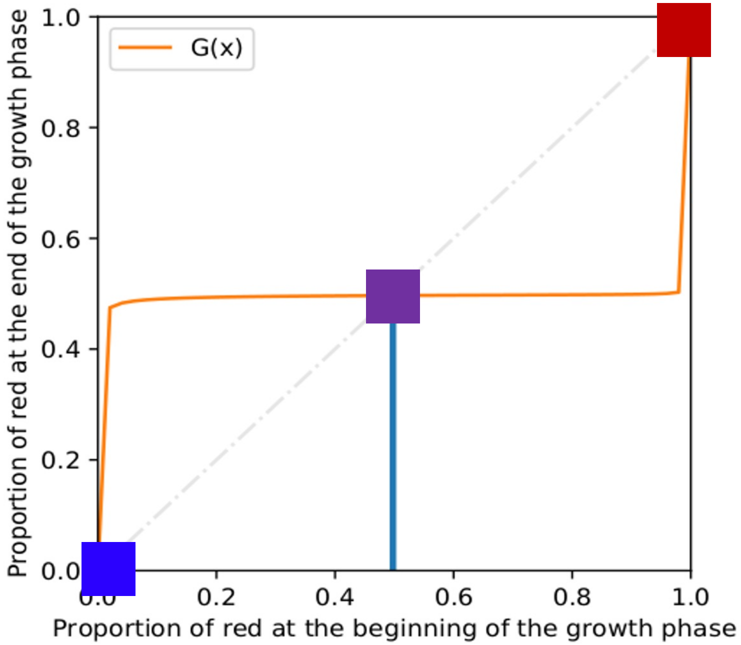




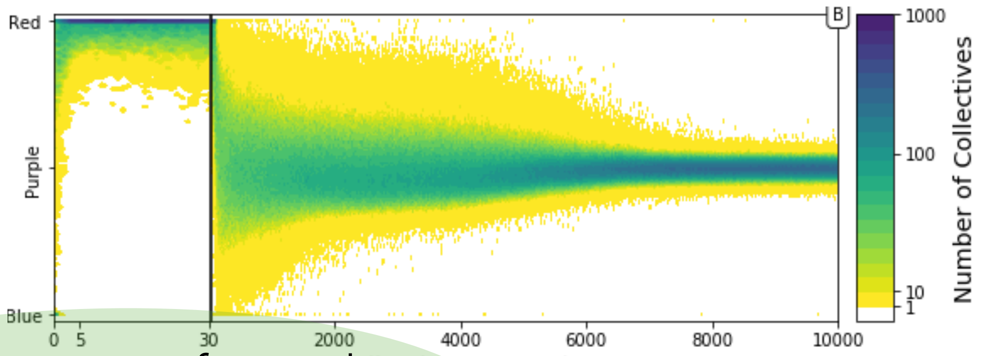
The target colour becomes a fixed point of the growth function

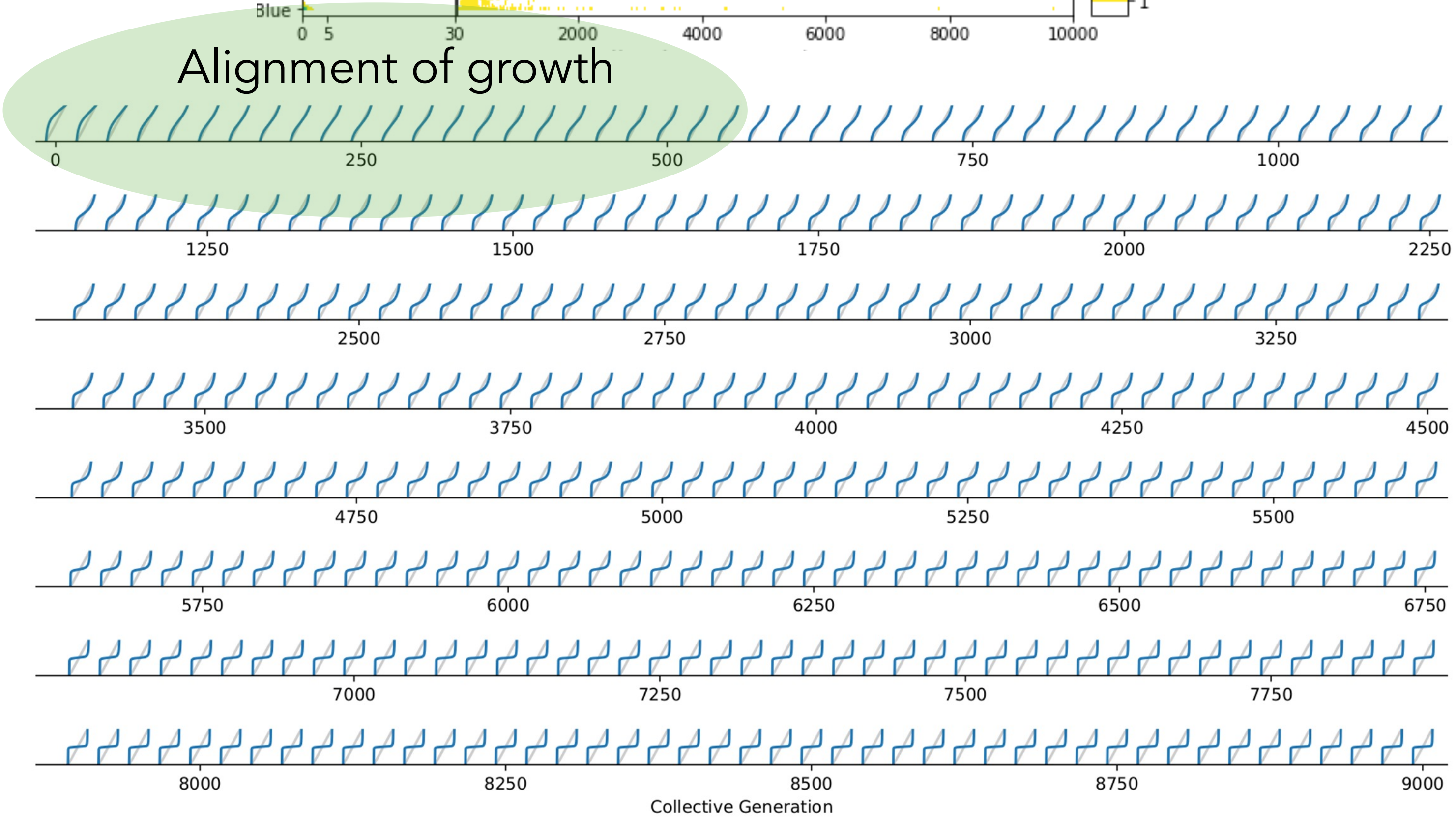
Developmental corrector



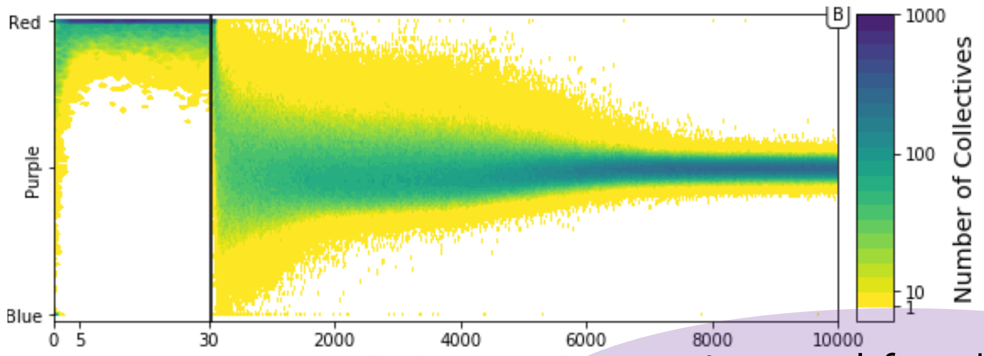


Evolution of the G function

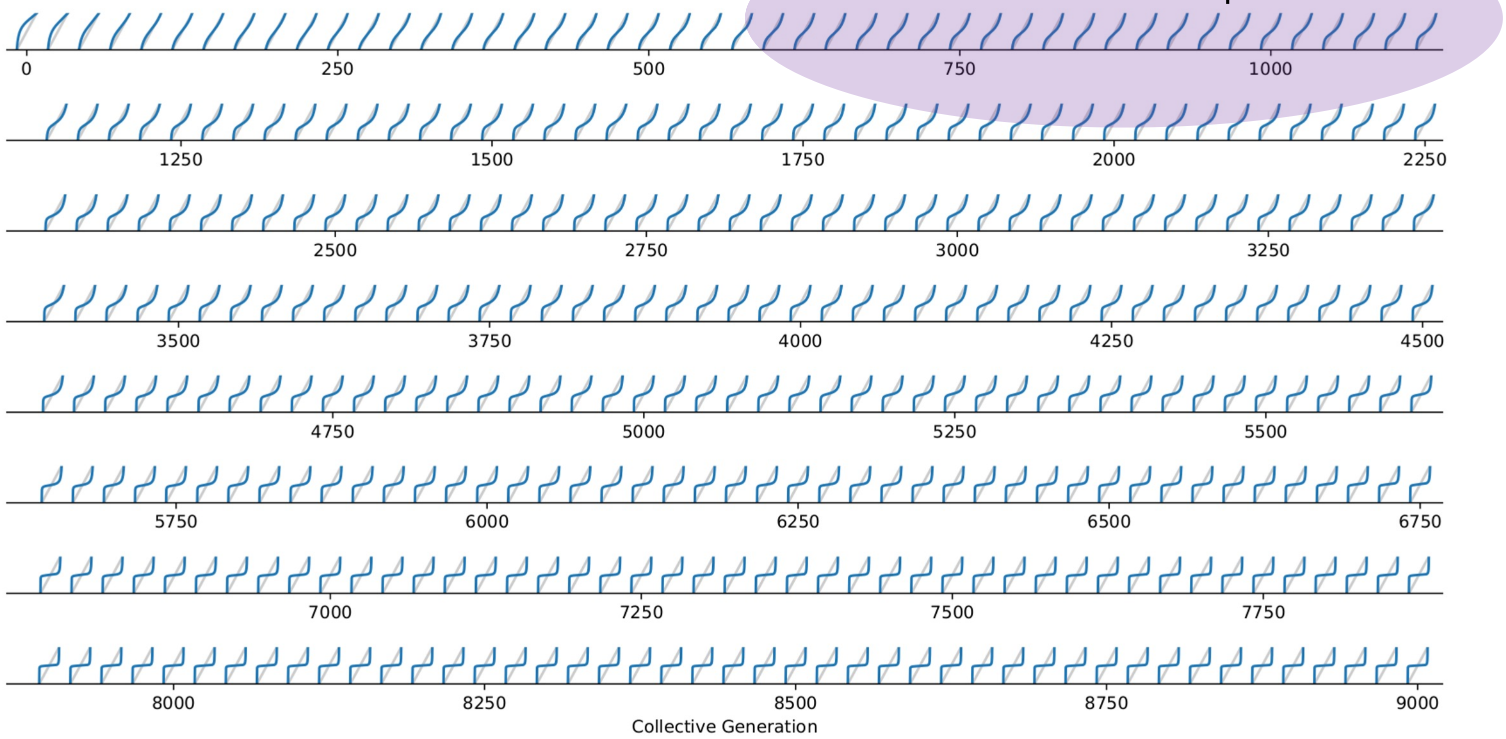




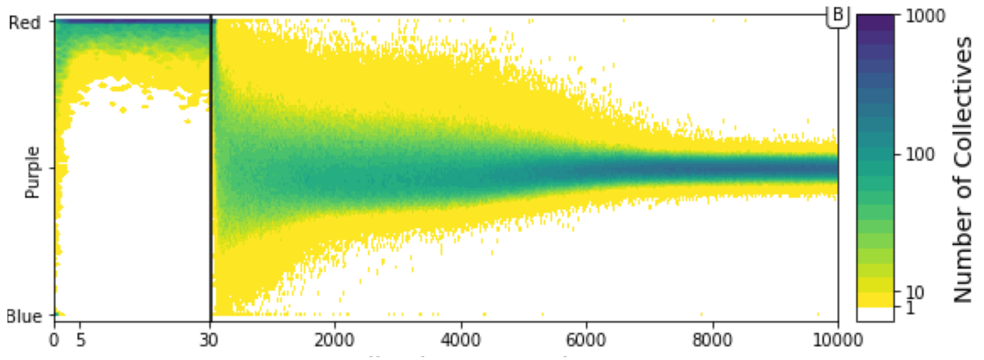
Evolution of the G function

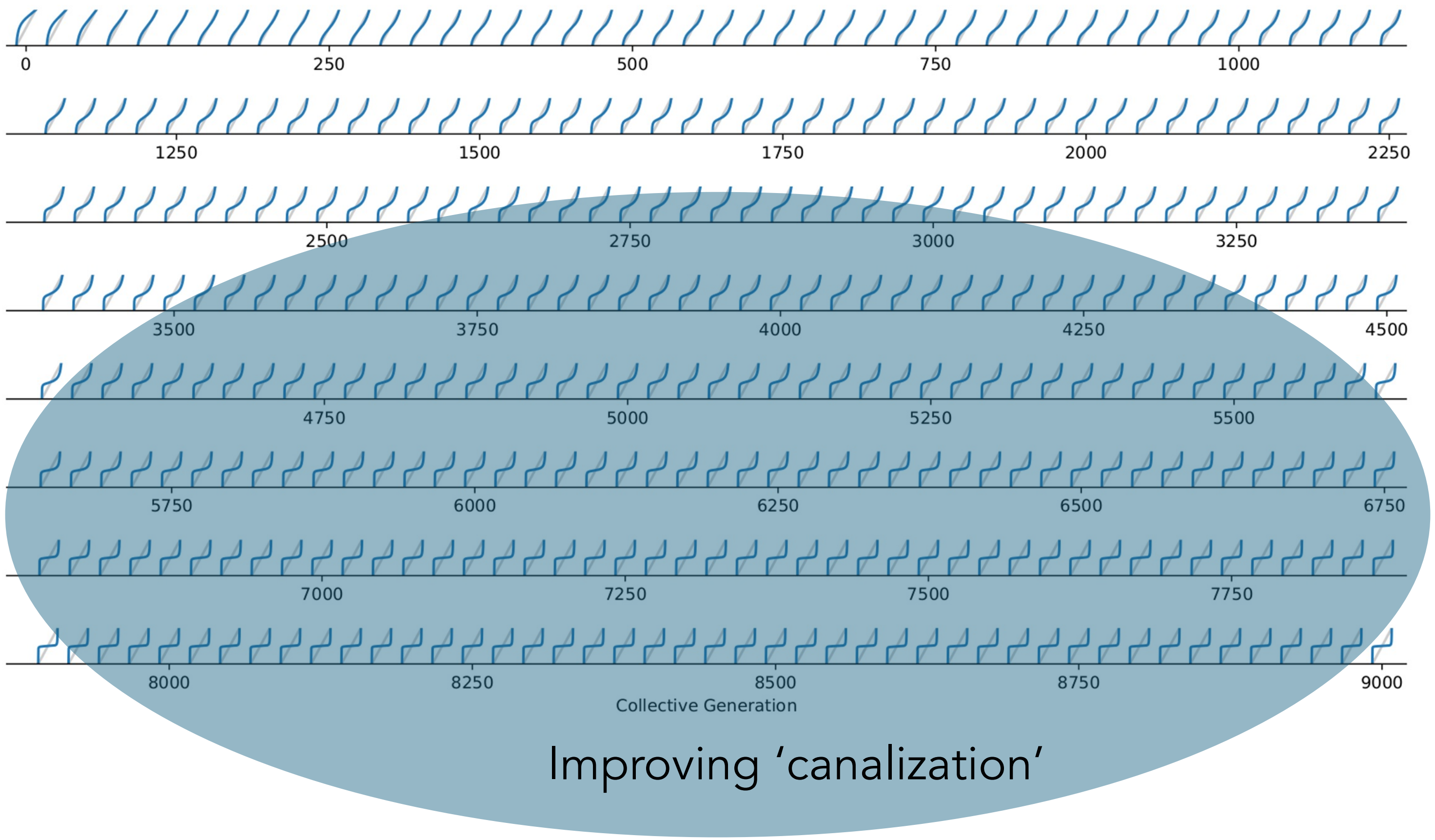


Internal fixed point

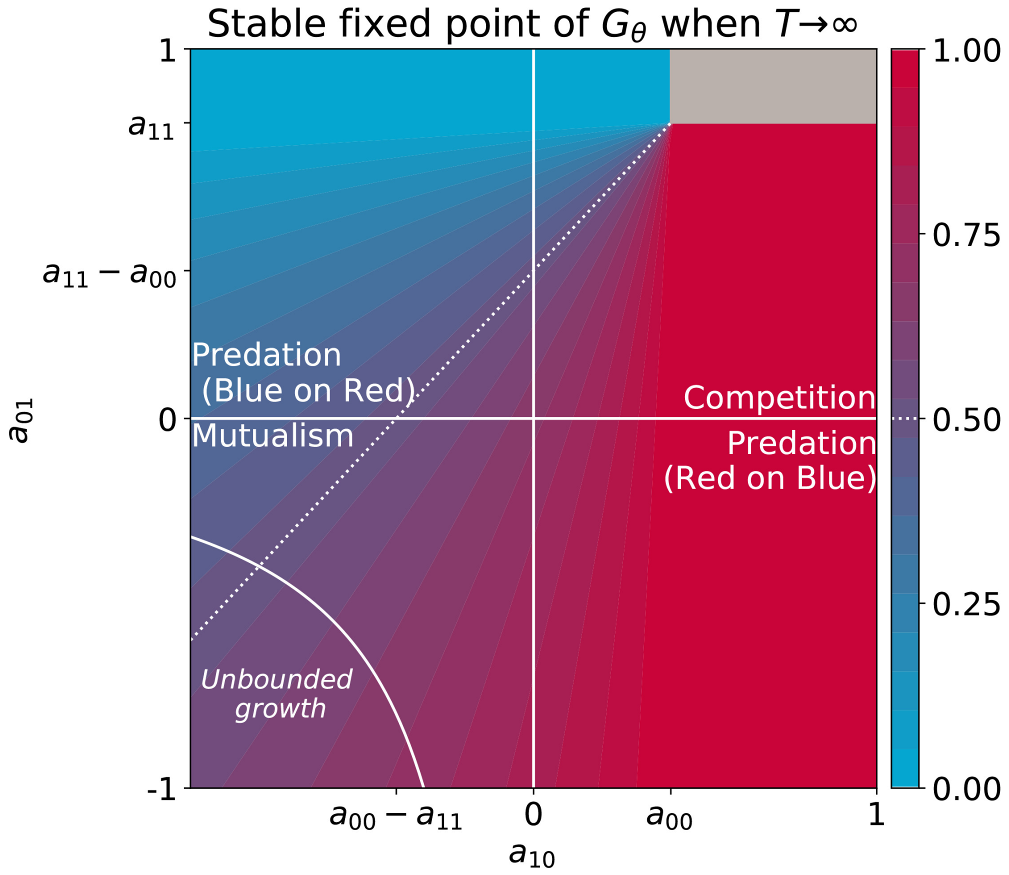


Evolution of the G function



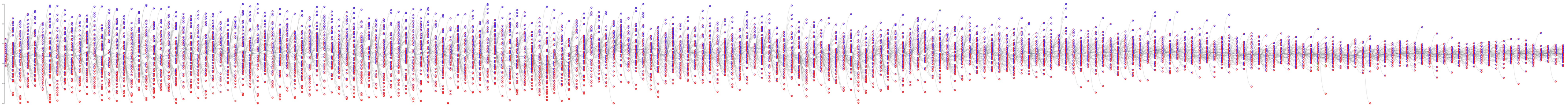


Evolution as gradient climbing



(when time scales are well separated)

Conclusions on the two-species model



Collective-level selection acting on two particle types:

1. Optimizes collective function despite within-collective conflicts

2. Makes such function **heritable**, increasing efficiency of natural selection at the collective level

3. Improves stability of such function through evolution of interactions

G. Doulcier, A. Lambert, SDM, P. Rainey
Eco-evolutionary dynamics of nested Darwinian populations and the emergence of community-level heredity
eLife 2020

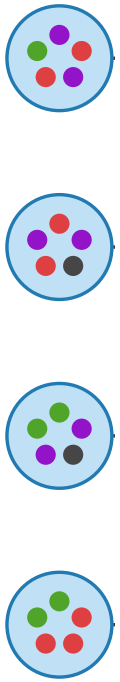
The evolution of structure in species-rich communities

Jules Fraboul

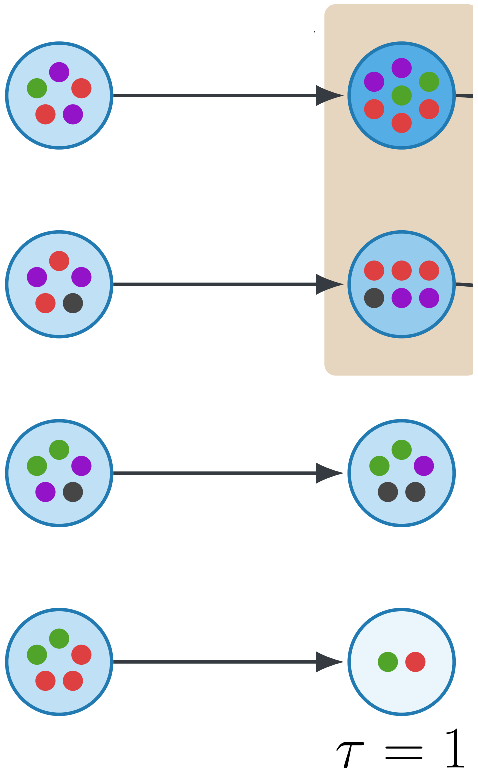
Giulio Biroli

Dept. of Physics, ENS, Paris

Community selection and reproduction

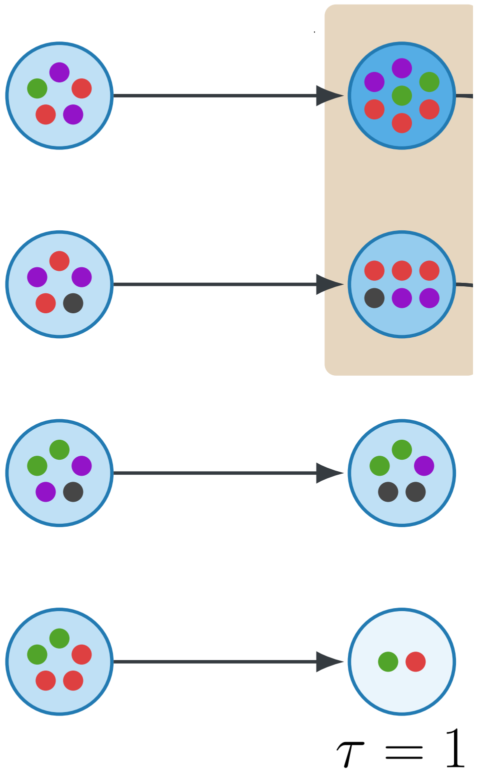


Community selection and reproduction



Community selection and reproduction

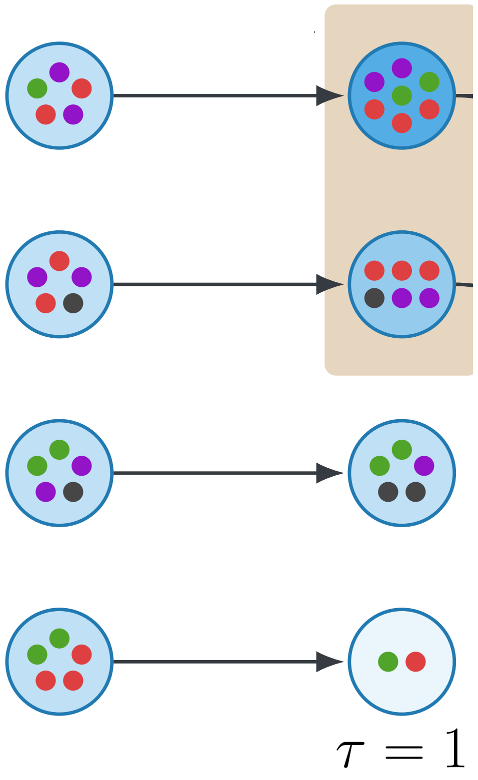
Selection for a target function $\vec{T}$



Community selection and reproduction

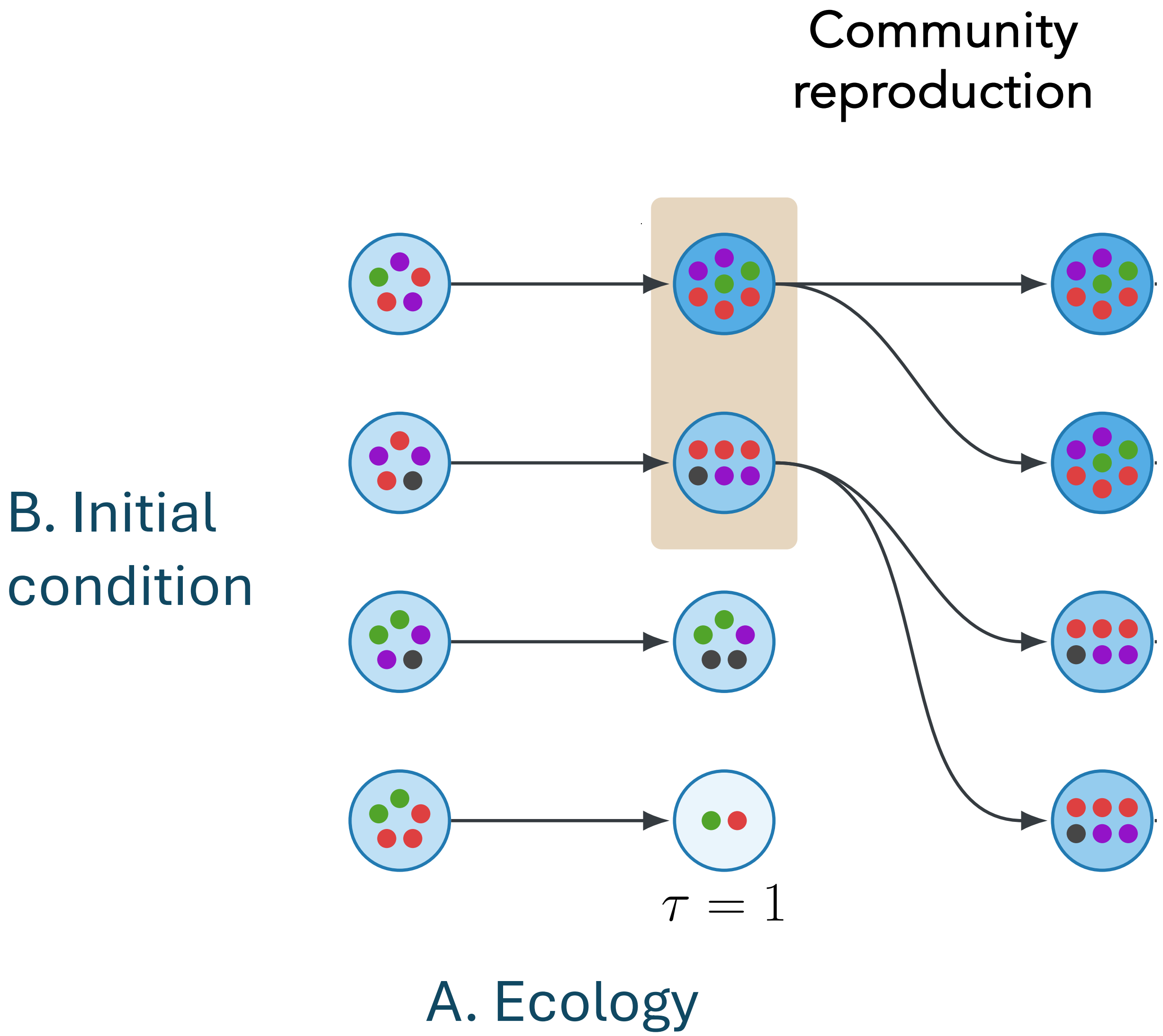
Selection for a target function $\vec{T}$

B. Initial condition

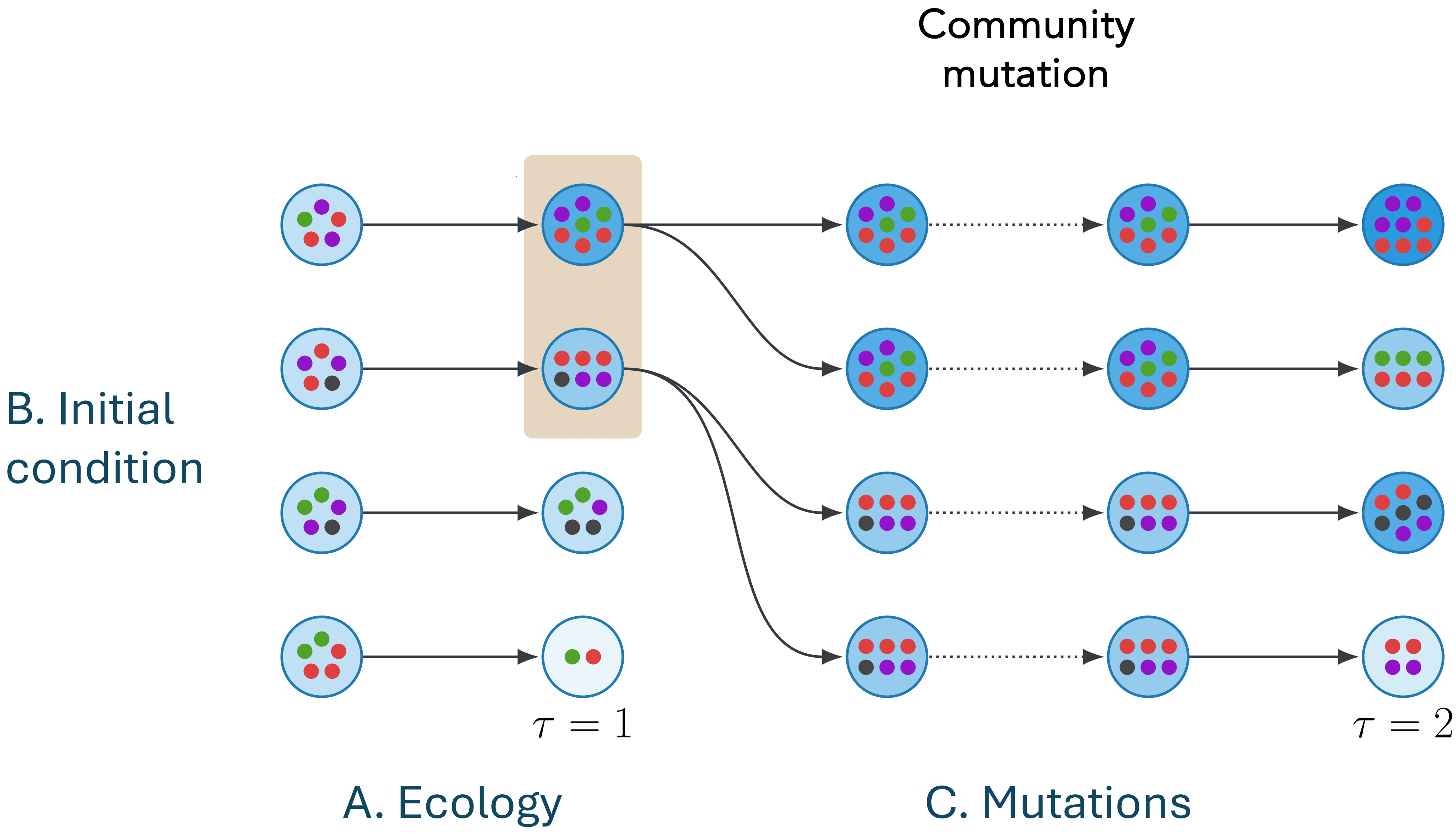


A. Ecology

Community selection and reproduction



Community selection and reproduction



A. Community ecology

Generalized disordered Lotka-Volterra model

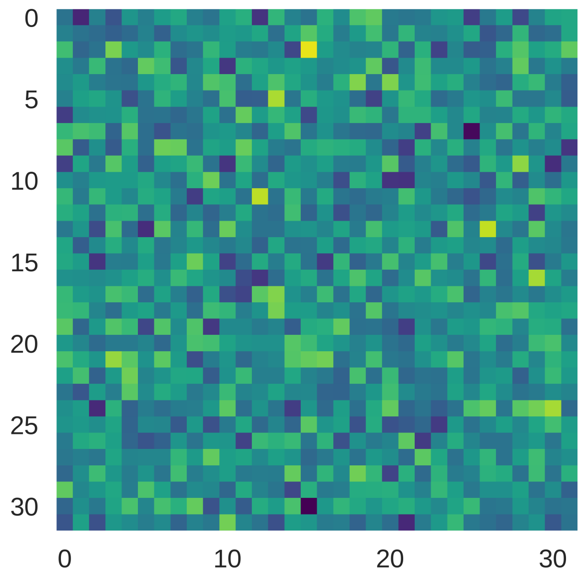
$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \frac{N_i}{K_i}\left(K_i - N_i - \sum_{j \neq i} \alpha_{ij} N_j\right)$$

$$\mathbb{E}(\alpha_{ij}) = \mu/S$$

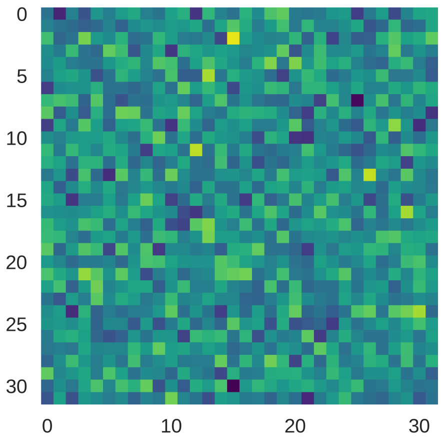
$$\mathrm{Var}(\alpha_{ij}) = \sigma^2/S$$

$$\mathrm{Corr}(\alpha_{ij}, \alpha_{ji}) = \gamma$$

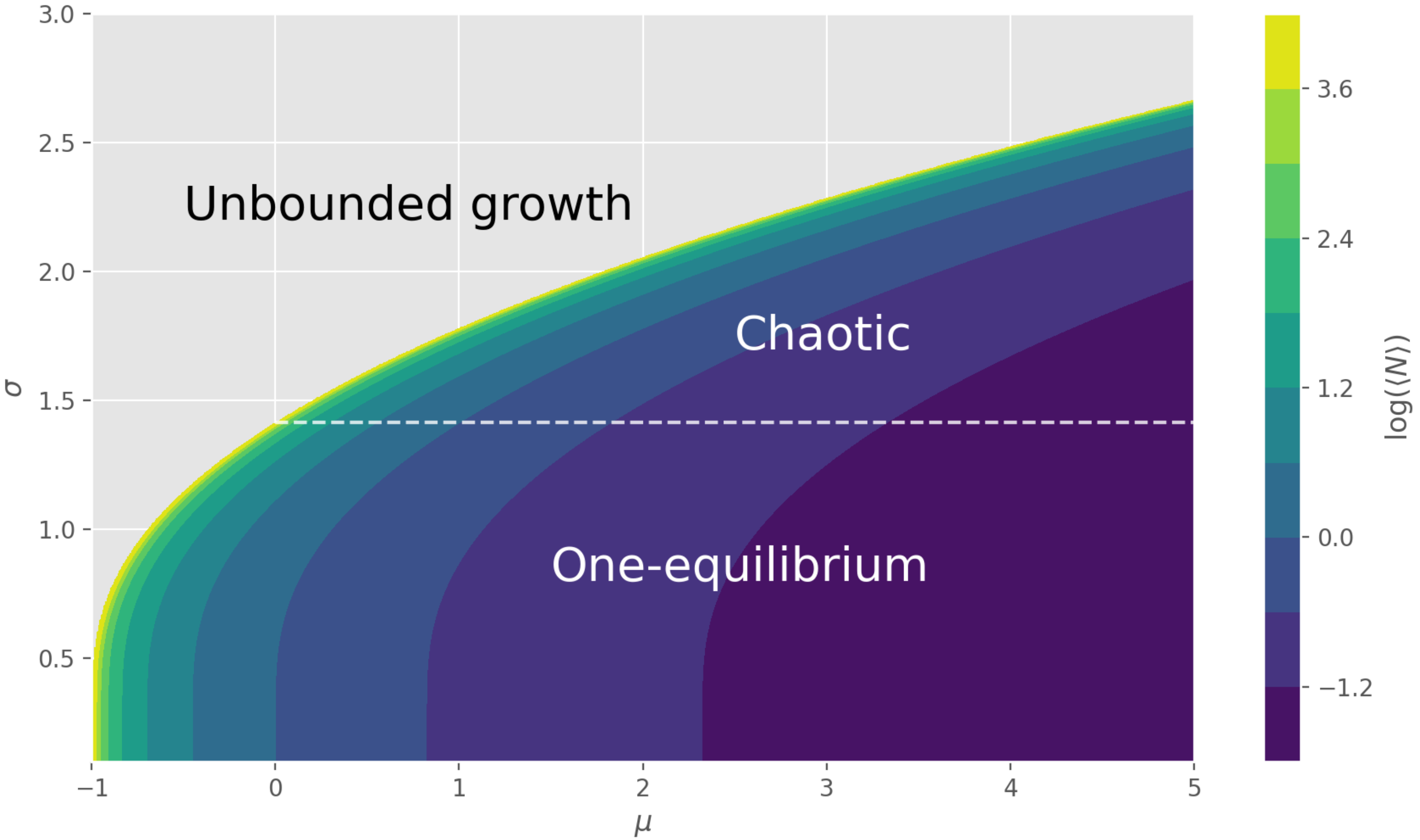
Carrying capacities $\vec{K}$
(uniform distribution)



Phase diagram for random matrixes

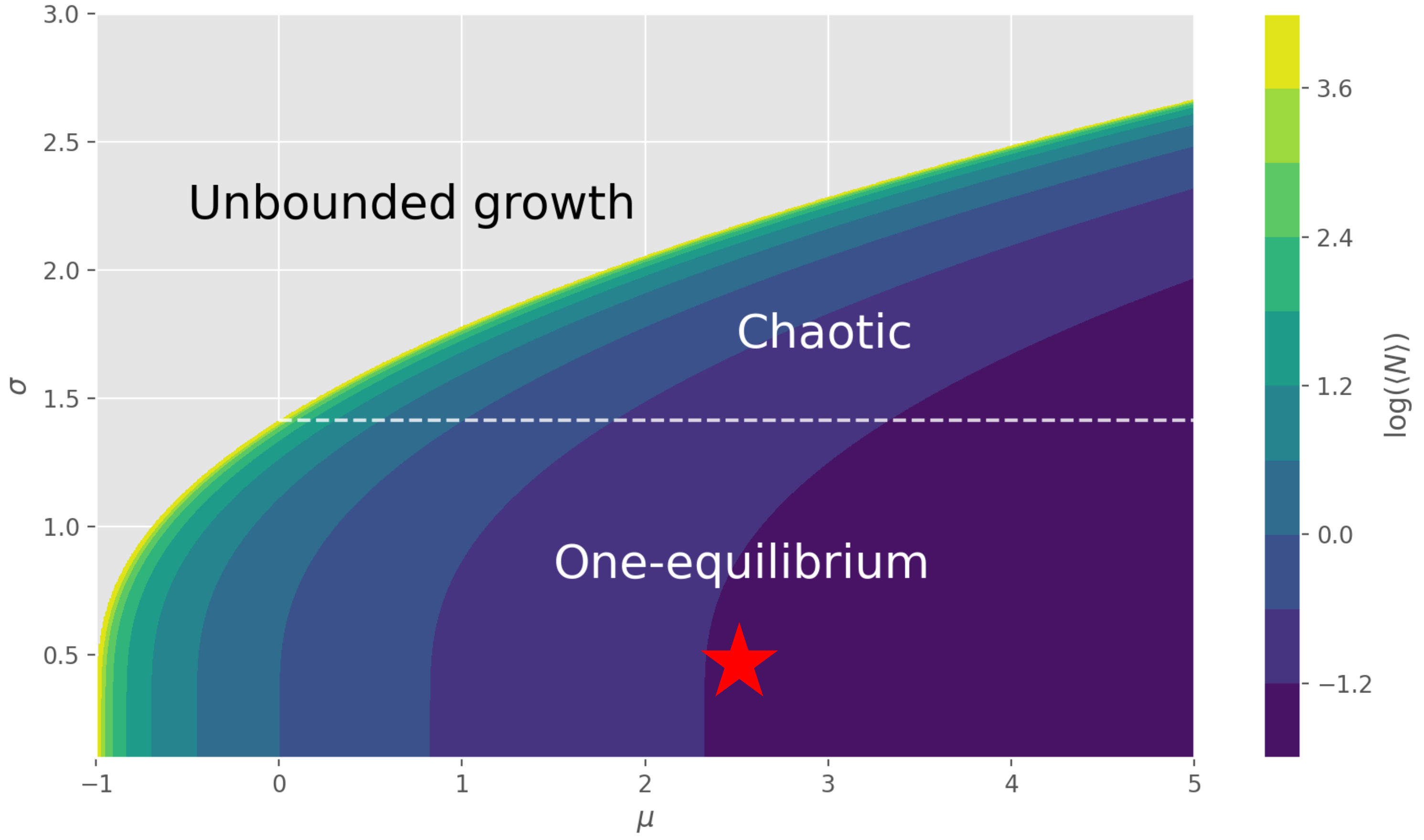


$$\mathbb{E}(\alpha_{ij}) = \mu/S$$
$$\mathrm{Var}(\alpha_{ij}) = \sigma^2/S$$
$$\mathrm{Corr}(\alpha_{ij}, \alpha_{ji}) = \gamma$$



G Bunin
Ecological communities with Lotka-Volterra dynamics.
Phys. Rev. E (2017)

B. 'Ancestral' community



Initial condition: random, competitive, stable community

C. Community-level mutations

$$\alpha_{ij}(\tau+1) = \mathrm{mean}[\alpha(\tau)] + \mathrm{std}[\alpha(\tau)]\, \hat{b}_{ij}(\tau)$$

$$\hat{b}_{ij}(\tau) = \frac{b_{ij}(\tau) + \varepsilon \eta_{ij}(\tau)}{\sqrt{1+\varepsilon^2}}$$

$$\mathbb{E}(\eta_{ij}) = 0$$

$$\mathrm{Var}(\eta_{ij}) = 1$$

$$\mathrm{Corr}(\eta_{ij}, \eta_{ji}) = \gamma$$

The mutant matrix is similar to the parental, and maintains the same expectations

phenotypic effects of mutations are stochastic and unbiased

$\epsilon \ll 1$ mutations have small effects on total abundance

C. Community-level mutations

$$\alpha_{ij}(\tau+1) = \mathrm{mean}[\alpha(\tau)] + \mathrm{std}[\alpha(\tau)]\,\hat{b}_{ij}(\tau)$$

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$$\mathbb{E}(\eta_{ij}) = 0$$

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$$\mathrm{Corr}(\eta_{ij}, \eta_{ji}) = \gamma$$

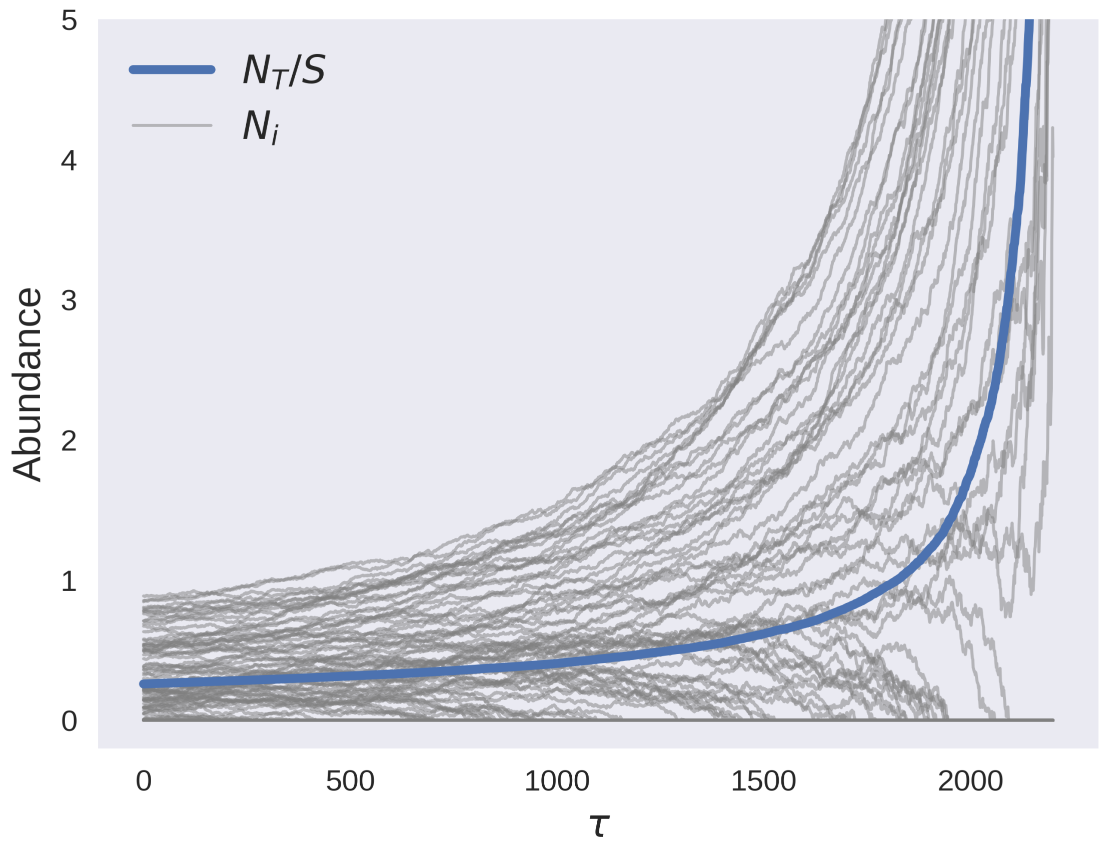
The mutant matrix is similar to the parental, and maintains the same expectations

phenotypic effects of mutations are stochastic and unbiased

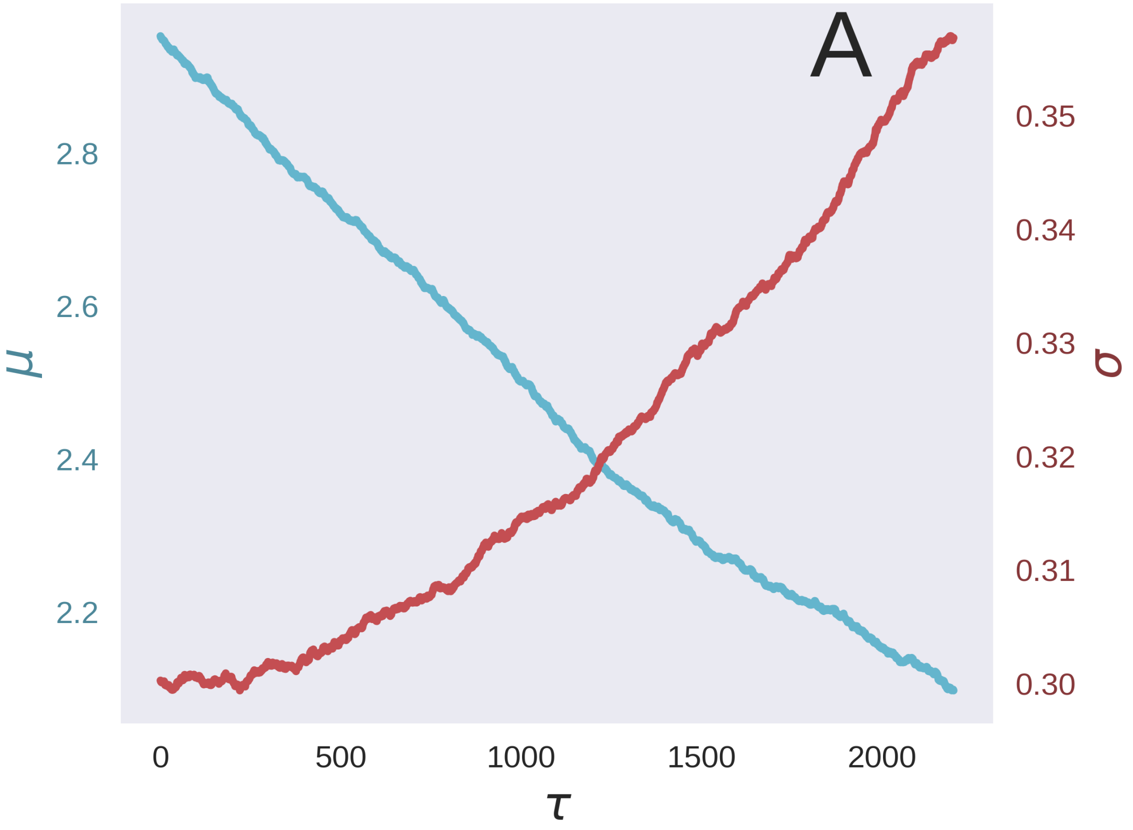
$\epsilon \ll 1$ mutations have small effects on total abundance

Selection chooses among the realizations the one maximizing $\vec{N} \cdot \vec{1}$

Evolution of species abundances

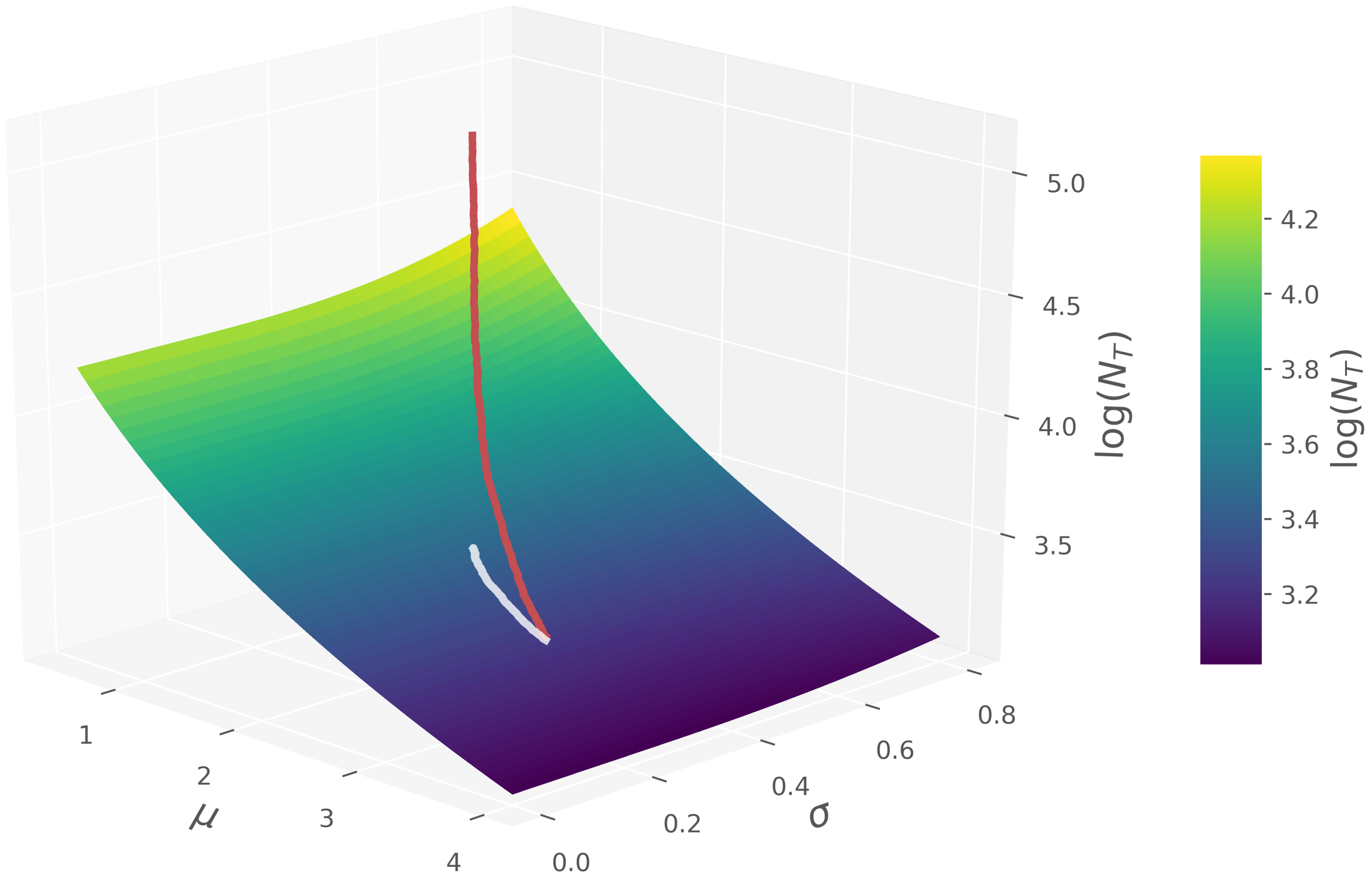


Evolution of interaction statistics



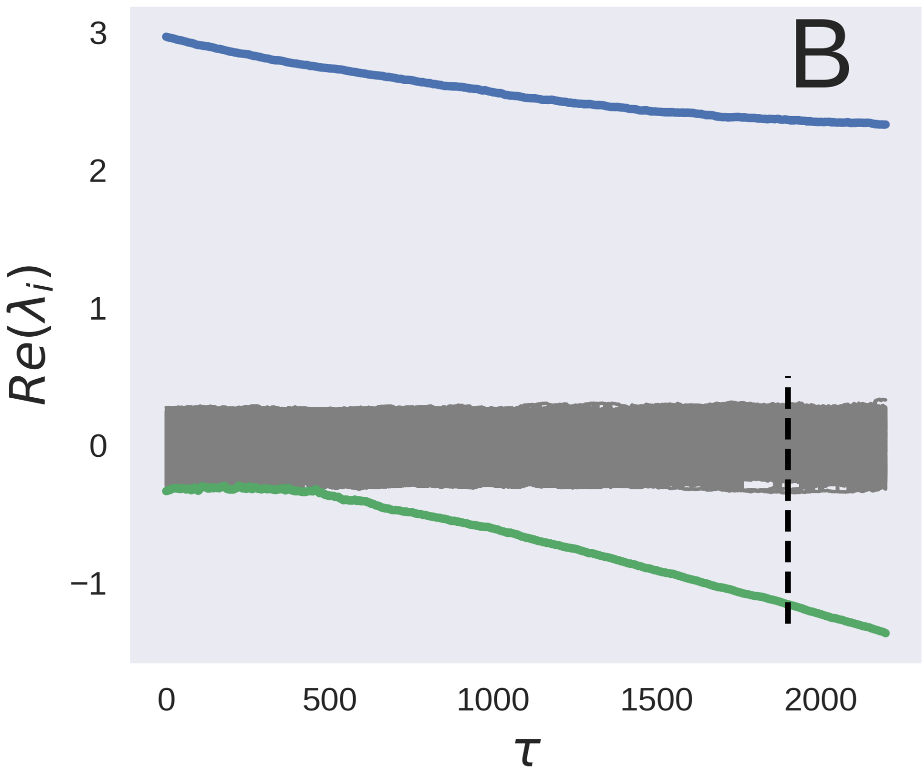
Moments of the interaction matrix

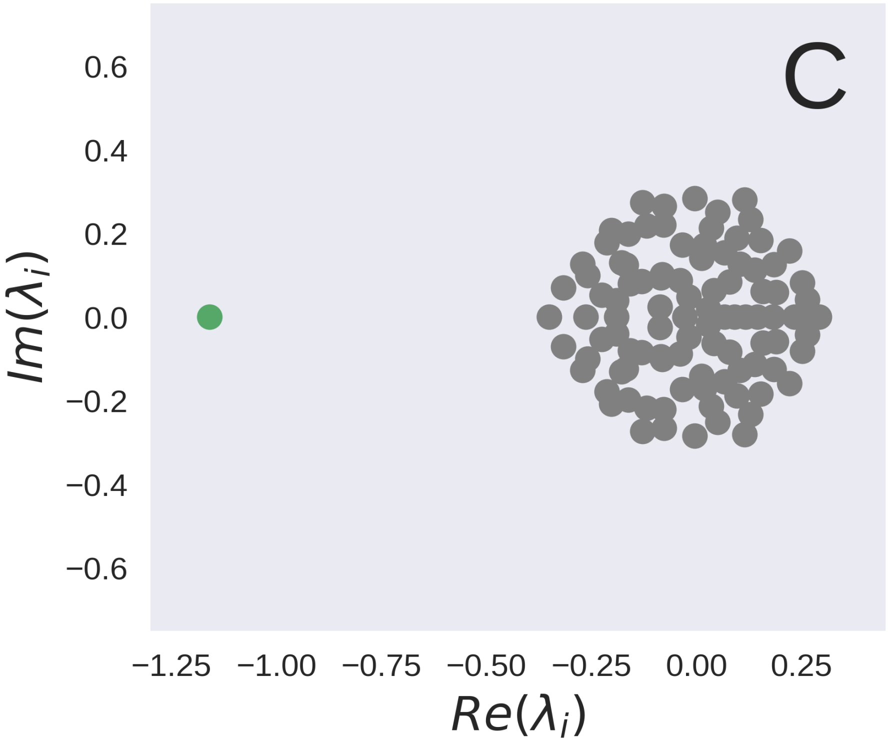
Evolution of total abundance



Change of total abundance cannot be explained by purely random interactions

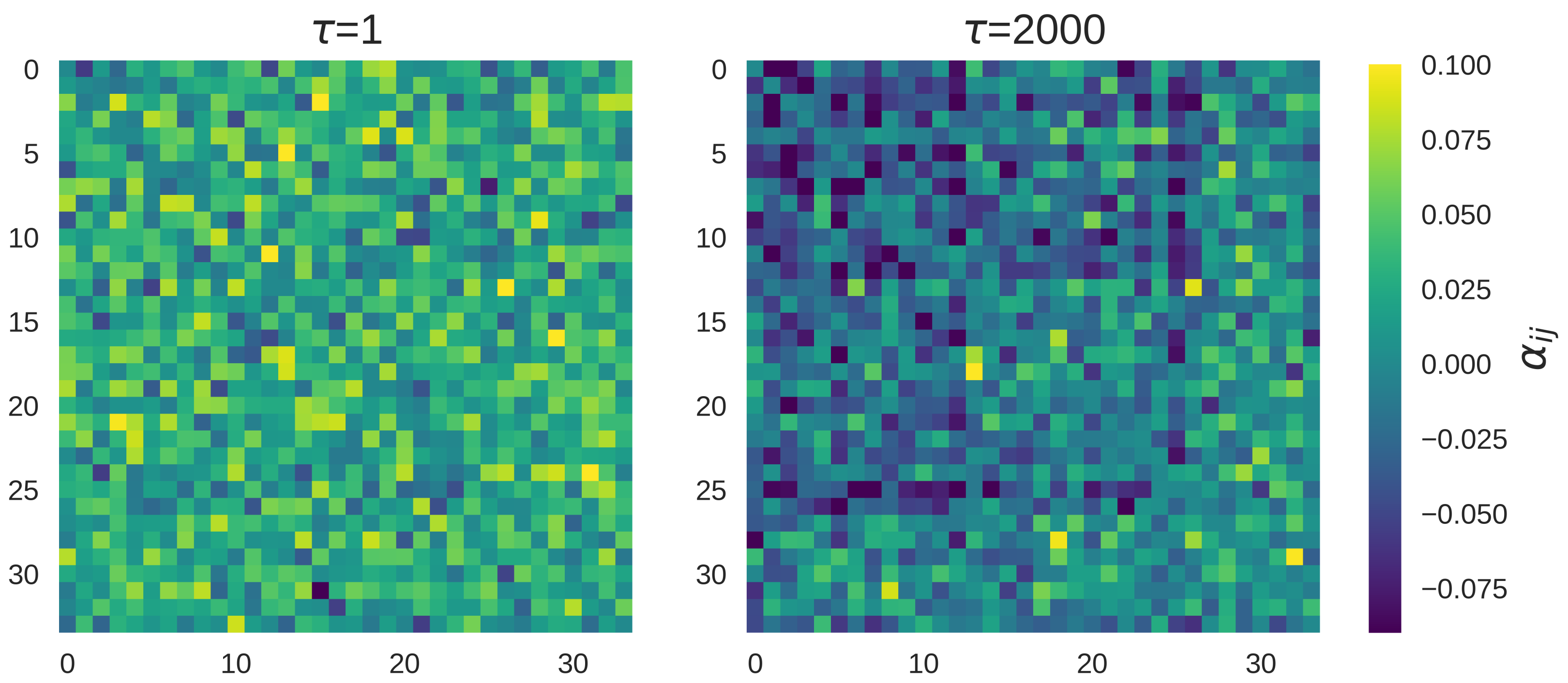
Spectrum of the interaction matrix





Emergence of a negative eigenvalue: global mutualistic interaction term

Selection imprints a structure on the interactions



Equations for the quasi-equilibrium total abundance

$(\gamma = 0)$

$$N_T(\tau+1) = N_T(\tau) + M_n(\tau)\frac{\varepsilon\sigma(\tau)}{\sqrt{S}}\|\mathbf{v}(\tau)\|\|\mathbf{N}(\tau)\|$$

M_n is a stochastic variable distributed as the maximum of n independent Gaussian values

$\overline{M_n} \propto \sqrt{\log(n)}$

$$\mathbf{N}^\star(\tau) = (\mathbb{I}^\star + \alpha^\star(\tau))^{-1}\mathbf{K}^\star$$

$$\mathbf{v}^\star(\tau) \;=\; (\mathbb{I}^\star + \alpha^\star(\tau)^\top)^{-1}\mathbf{1}^\star$$

Equations for the quasi-equilibrium total abundance

$$N_T(\tau+1) = N_T(\tau) + M_n(\tau)\frac{\varepsilon\sigma(\tau)}{\sqrt{S}}\|\mathbf{v}(\tau)\|\|\mathbf{N}(\tau)\|$$

M_n is a stochastic variable distributed as the maximum of n independent Gaussian values

$\overline{M_n} \propto \sqrt{\log(n)}$

number of communities

$$\mathbf{N}^\star(\tau) = (\mathbb{I}^\star + \alpha^\star(\tau))^{-1}\mathbf{K}^\star$$

Intraspecific interactions

$$\mathbf{v}^\star(\tau) = (\mathbb{I}^\star + \alpha^\star(\tau)^\top)^{-1}\mathbf{1}^\star$$

Selection target

Equations for the quasi-equilibrium interactions

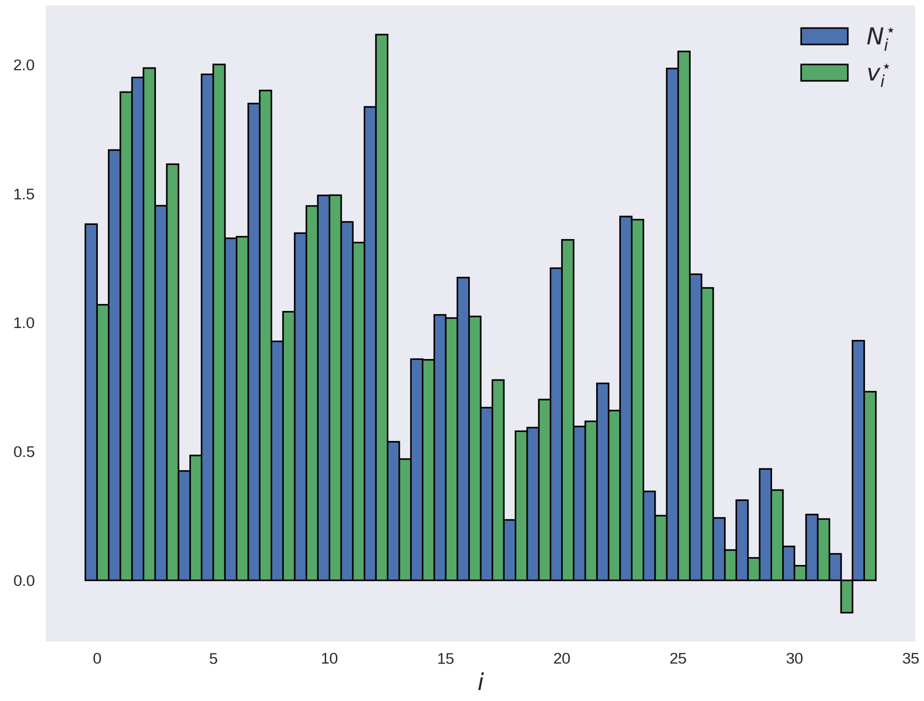
$$\alpha_{ij}(\tau+1) = \alpha_{ij}(\tau) - \frac{\varepsilon\sigma(\tau)}{\sqrt{S}} \left(M_n(\tau)\frac{v_i(\tau)}{\|\mathbf{v}(\tau)\|}\,\frac{N_j(\tau)}{\|\mathbf{N}(\tau)\|} + B_{ij} \right)$$

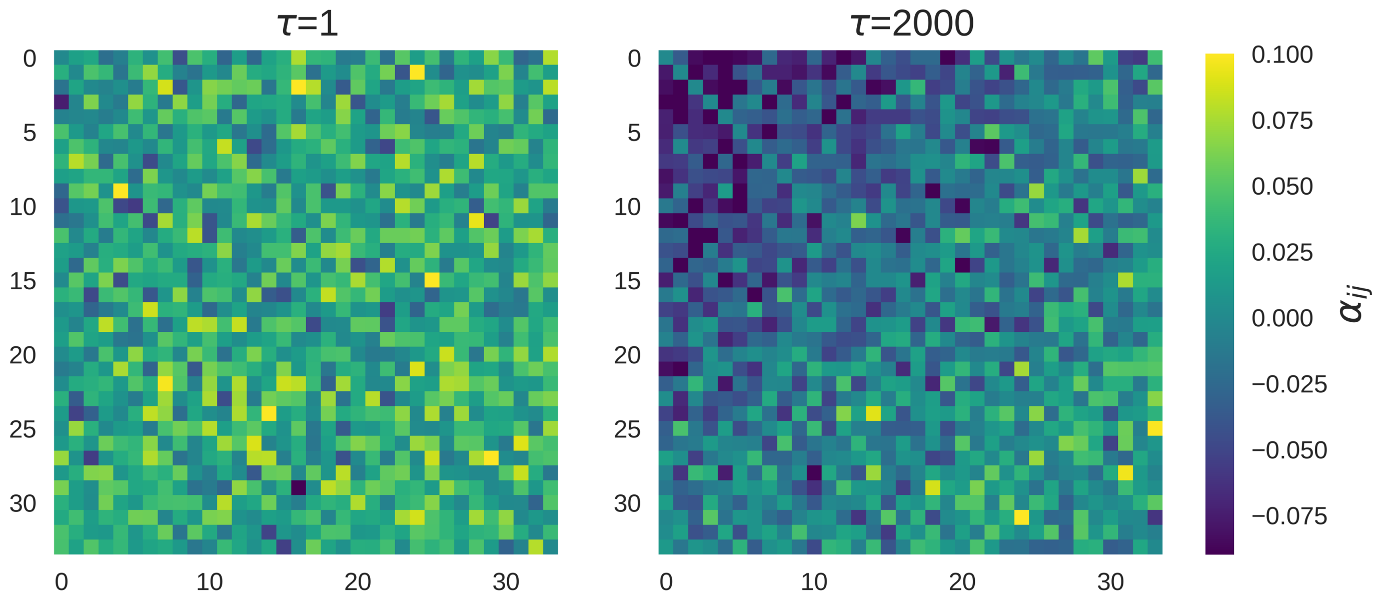
$$\mathbf{v}(\tau) = \frac{\partial N_T}{\partial \mathbf{K}}(\tau)$$

Evolutionary change affects differently different species, depending on the how their perturbations modify the target function.

Equations for the quasi-equilibrium interactions

Vectors become correlated:
more abundant species are also those that (have) become more mutualistic



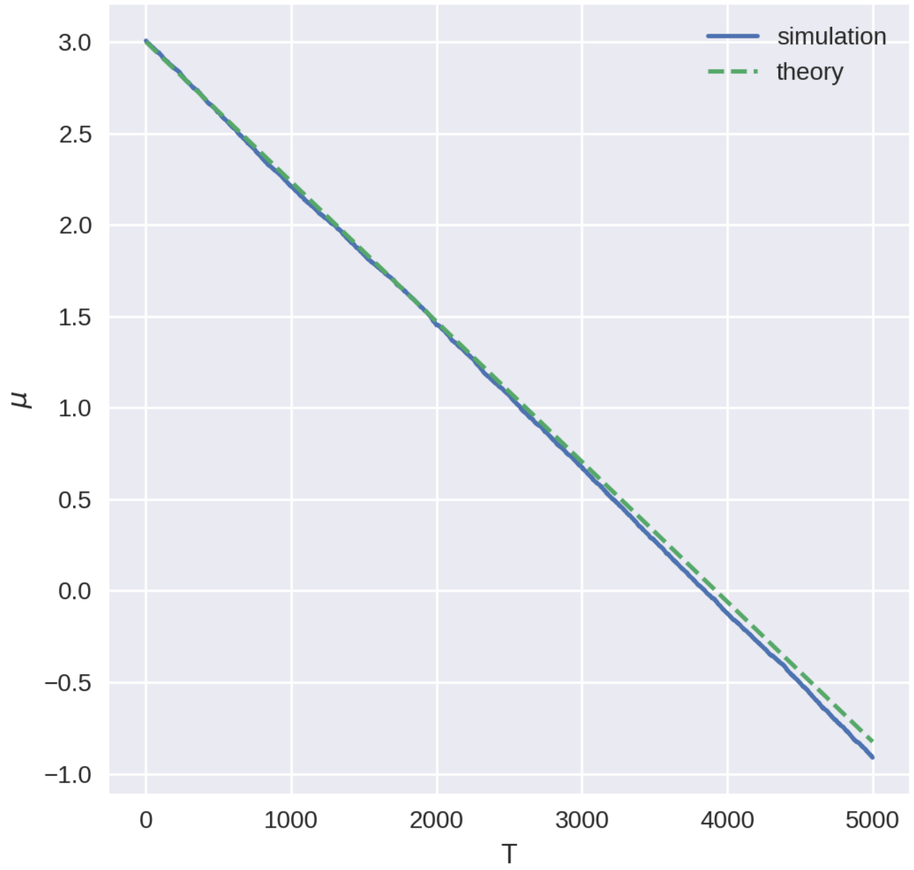


Evolutionary equations in the limit case of small σ

$$\mu(\tau) = \mu(0) - \tau \cdot \frac{\varepsilon\sigma}{\sqrt{S}} \overline{M_n} \sqrt{1+\gamma}$$

The average interaction strength decreases linearly in time.

Scaling of the speed of community evolution:
it is faster for bigger mutational steps, in smaller populations, for larger initial diversity, when there are many communities to choose from and when the interactions are more symmetric.

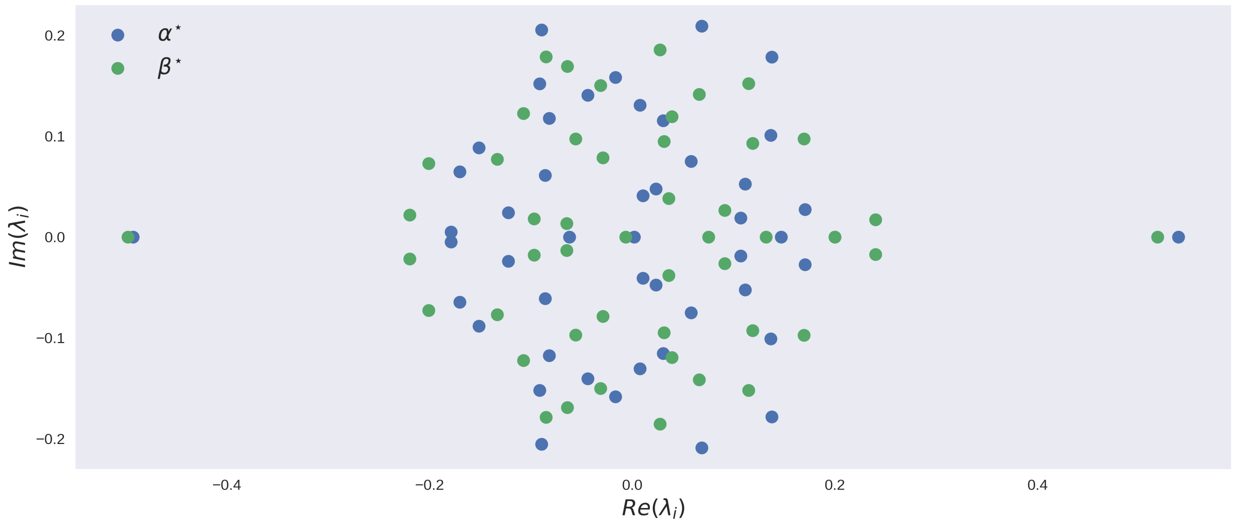


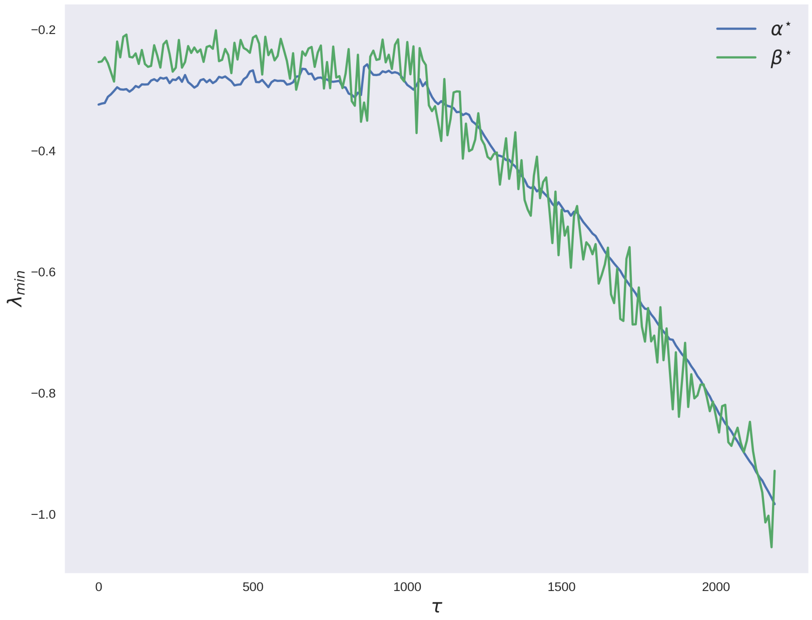
No directional change in neutral regimes and for fully symmetric interactions

General structure of the evolved matrix

Synthetic matrix inferred from the evolved equilibrium abundances and mean interaction

Barbier, M., de Mazancourt, C., Loreau, M., and Bunin, G.
Fingerprints of high-dimensional coexistence in complex ecosystems
Physical Review X (2021)





The evolved matrix resembles the most likely matrix, which has an isolated eigenvalue

Conclusions

Applying community-level selection to complex interacting ecosystems:

1. Optimizes collective function

2. Makes interactions more mutualistic

3. Imprints a structure on the evolved matrix, which remains nonetheless unpredictable except in statistical terms

Jules Fraboul, Giulio Biroli* and Silvia De Monte*

Artificial selection of communities drives the emergence of structured interactions

Journal of Theoretical Biology (2023)