Bet-hedging strategies in expanding populations

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Outline

- Bet-hedging in jellyfish with N. Azaña, P. Mariani (DTU, Copenhagen)
- Bet-hedging waves with P.V. Martin (OIST), M.A. Muñoz (U. Granada)

Bet-hedging

In gambling:

A New Interpretation of Information Rate
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By J. L. Kelly, jr.

(Manuscript received March 21, 1956)

- Diversify investment strategy when playing an uncertain game
- Theory of bet-hedging is related with information theory

Betting on a biased coin

q: fraction of capital bet on head
p: probability of head $>1/2$
$\$(t)$: capital at round t
nH, nT: number of head and tails until t

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Betting on a biased coin

q: fraction of capital bet on head
p: probability of head >1/2
$(t): capital at round t
nH, nT: number of head and tails until t

$$\$(t) = \$(0)(1+q)^{n_H}(1-q)^{n_T}$$
$$\approx \$(0)e^{t[p\ln(1+q)+(1-p)\ln(1-q)]}$$

Maximized for $q = 2p - 1$

-> maximum average growth rate $\ln 2 + p\ln p + (1-p)\ln(1-p)$

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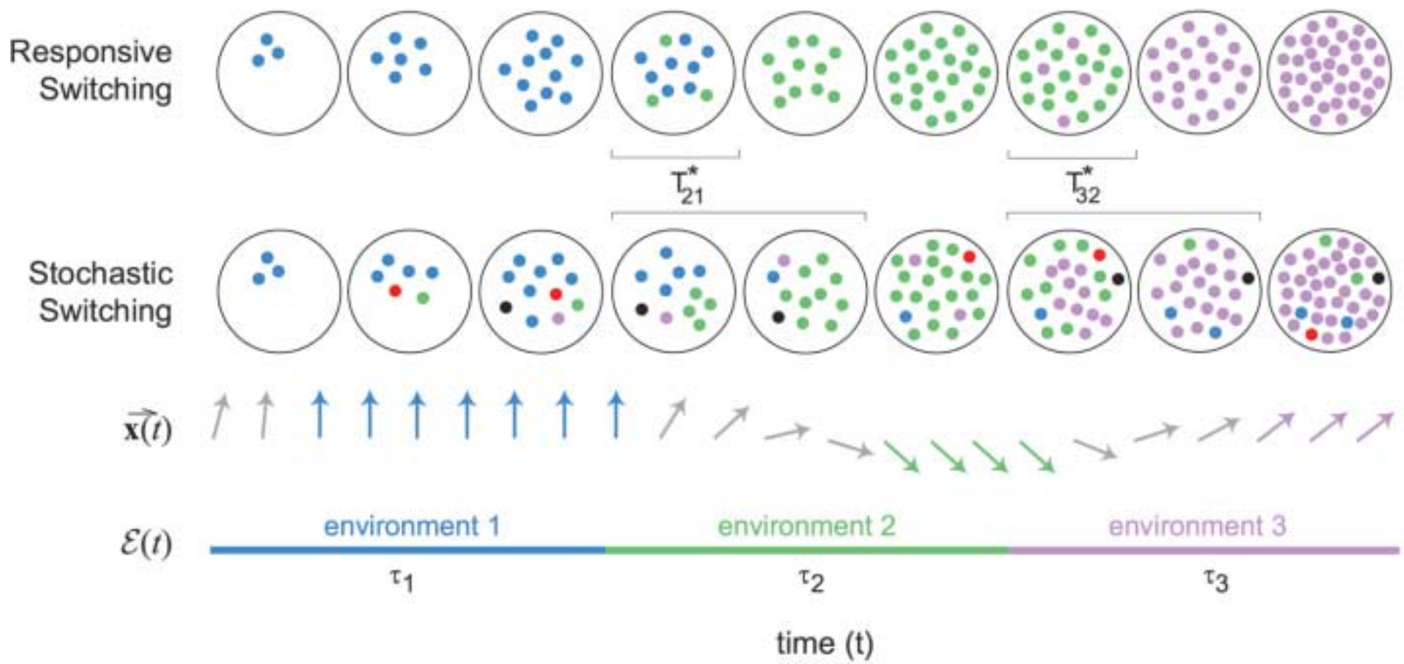
Bet-hedging in biology



Kussell, Leibler 2005

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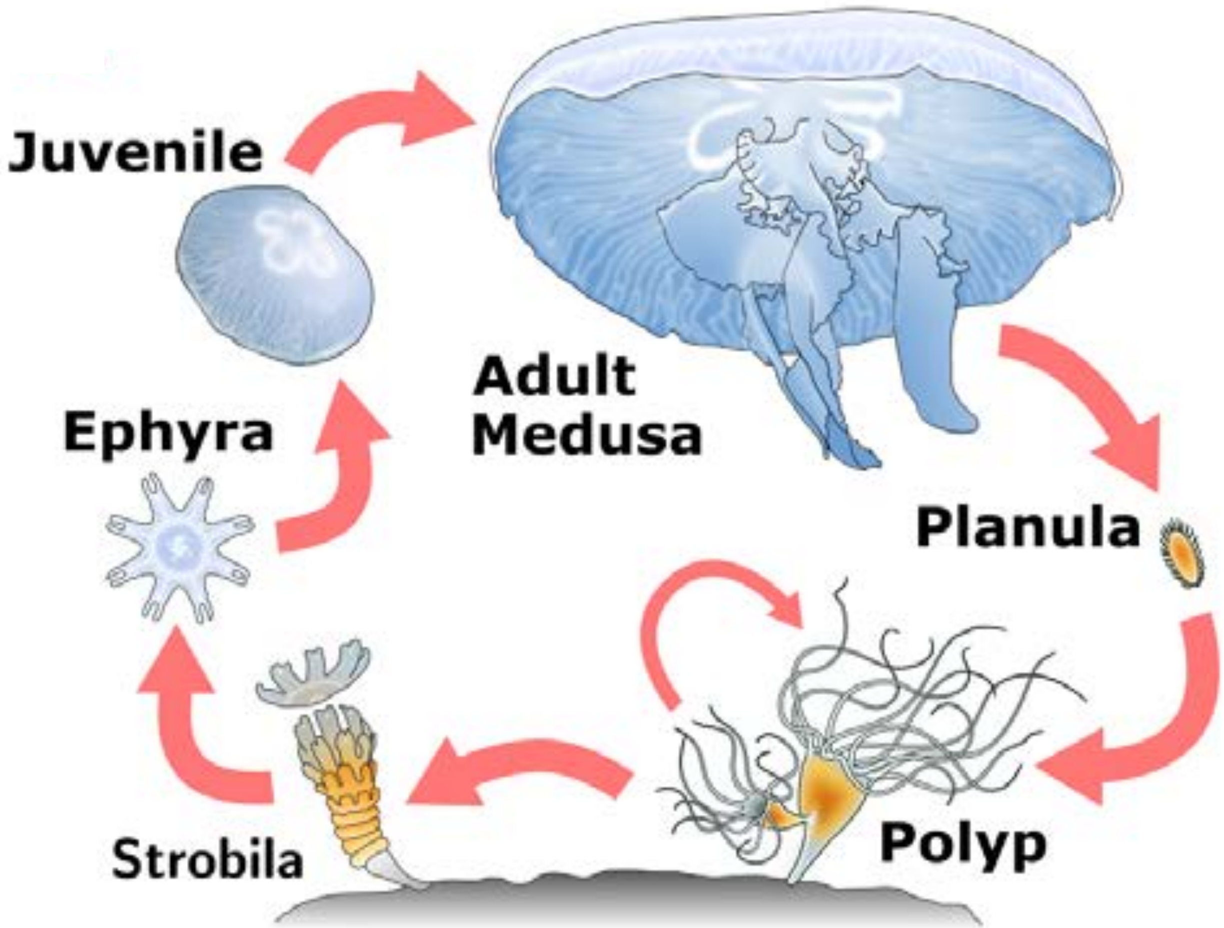
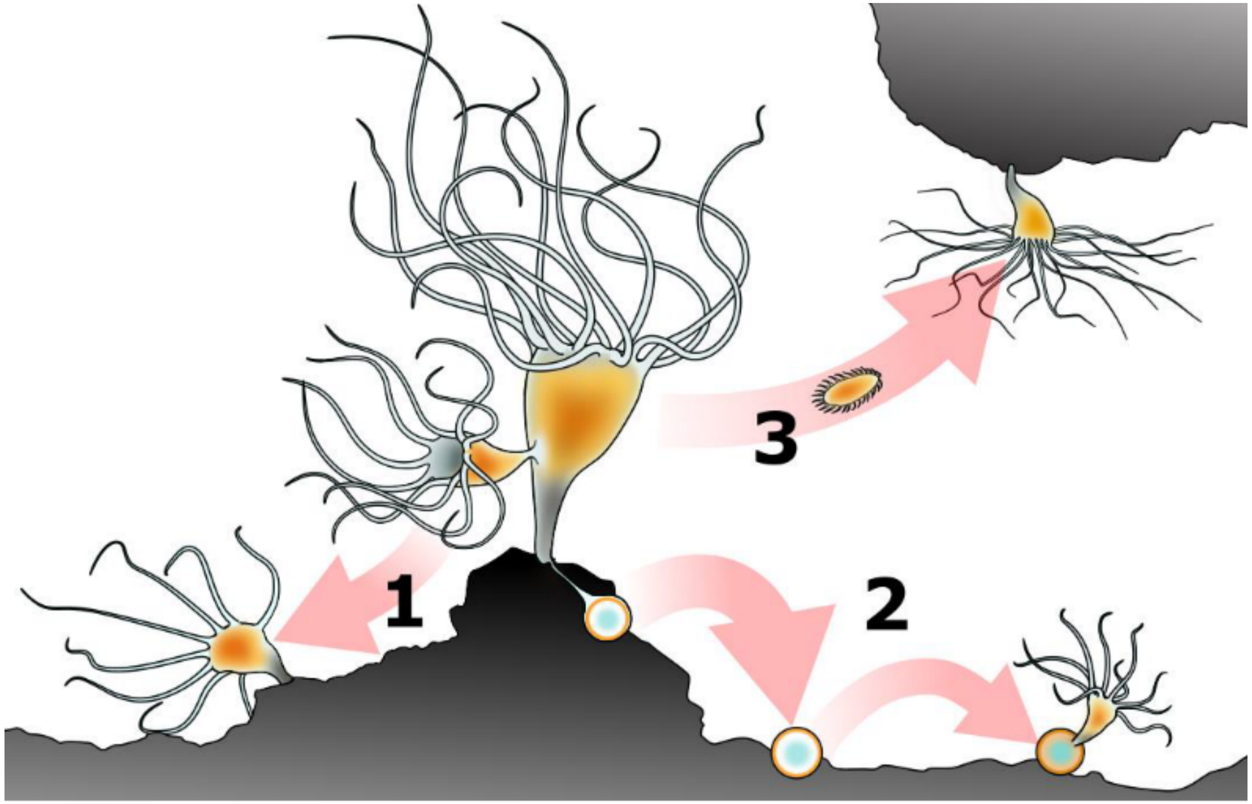
Life cycle of scyphozoan jellyfish



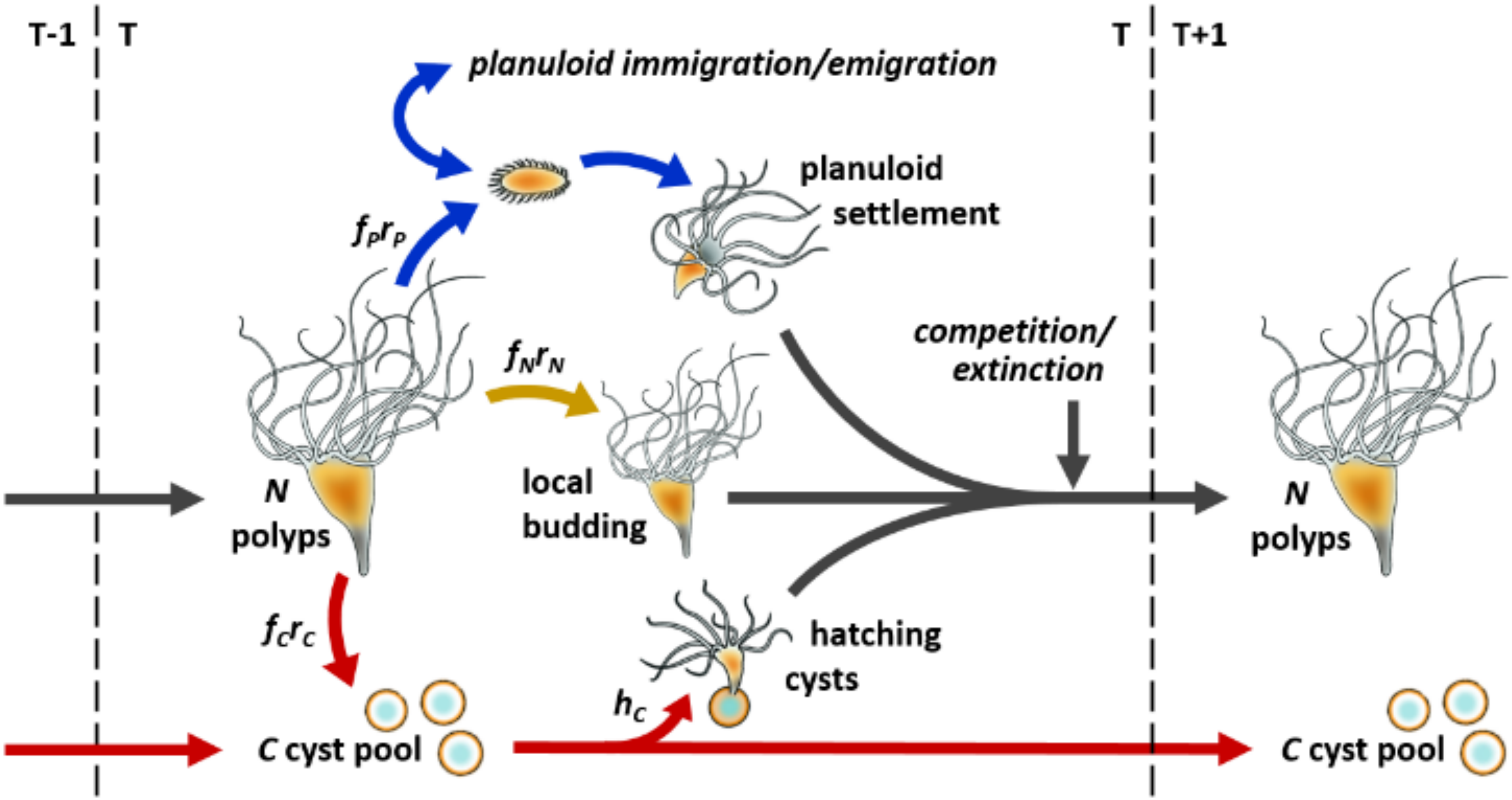
Asexual life cycle of jellyfish



1. Polyps
2. Cysts
3. Planuloids

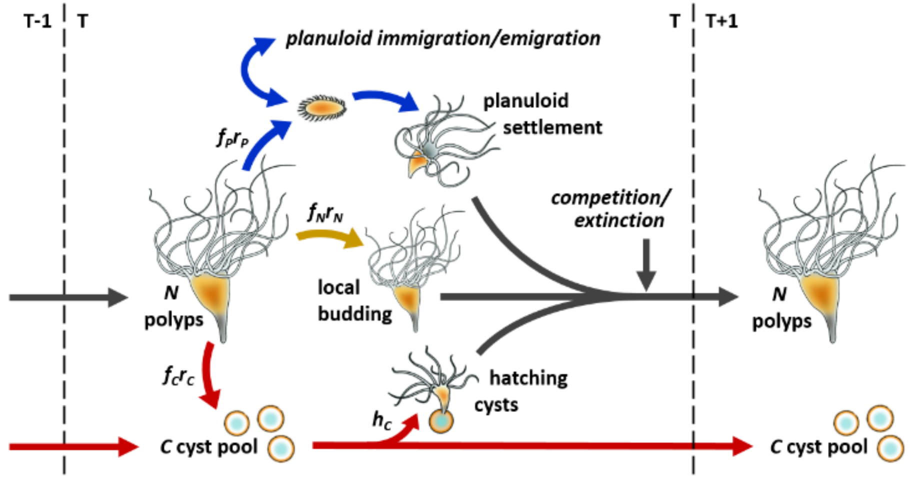
N. Azaña, SP, P. Mariani, American Naturalist (2018)

Model



T-1
T
T
T+1
planuloid immigration/emigration
$f_P r_P$
planuloid
settlement
$f_N r_N$
competition/
extinction
N
polyps
local
budding
N
polyps
$f_C r_C$
hatching
cysts
h_C
C cyst pool
C cyst pool

1. Beginning of the season

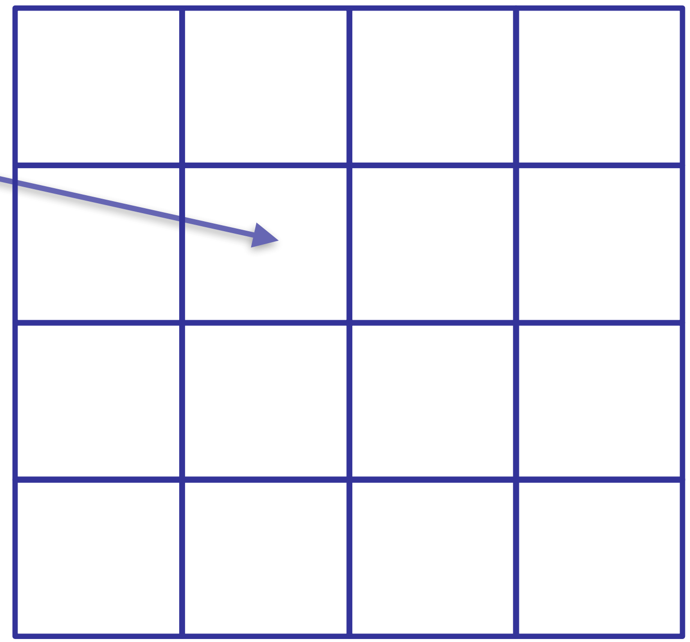


In each patch:
Wild type (*w*), mutant (*m*)

Fraction of polyps: N_t^w, N_t^m

with $N_t^w + N_t^m = 1$

Number of cysts: C_t^w, C_t^m



Sea: square lattice of LxL patches

2. Reproduction

Local budding:

$$B_{t+1}^{w} = N_t^w f_N^w r_N$$

Motile buds:

$$M_{t+1}^{w} = N_t^w f_M^w r_M$$

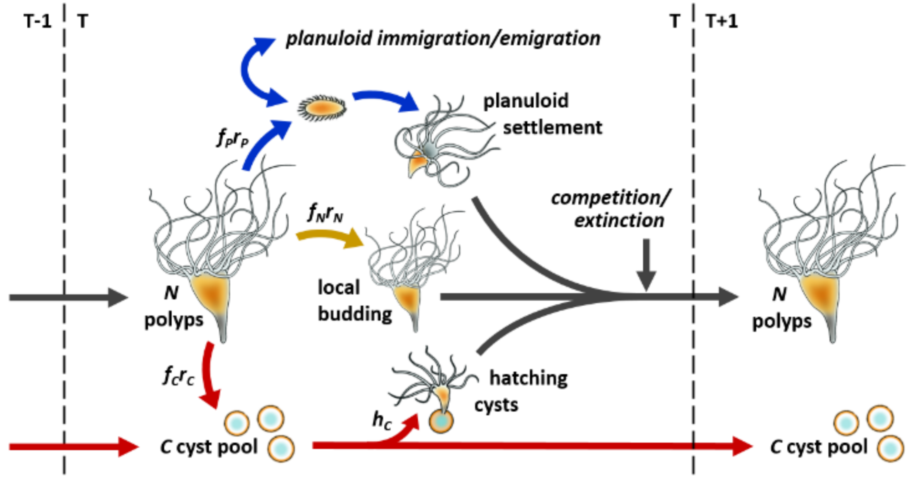
(spread among neighboring patches)

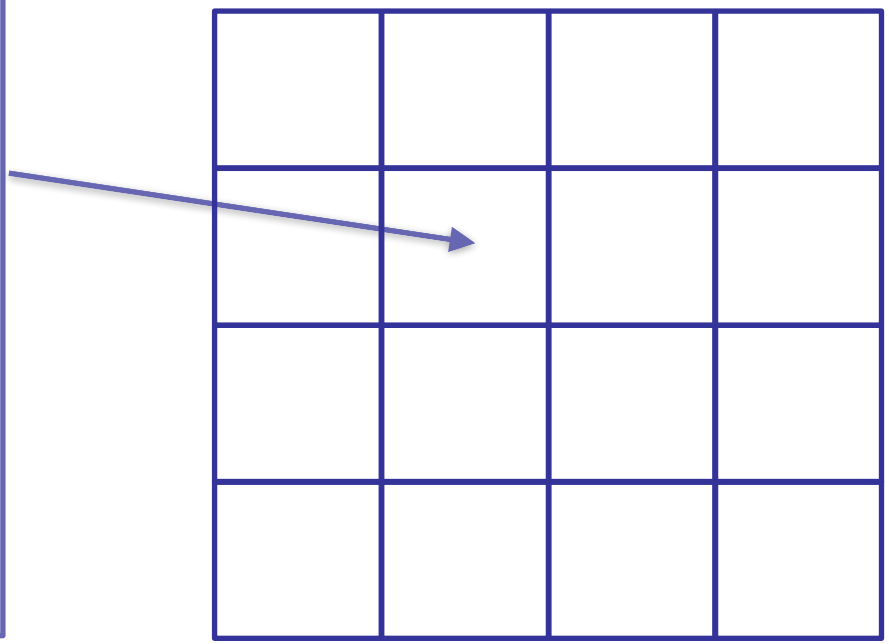
Hatching cysts:

$$H_{t+1}^{w} = C_t^w h_c$$

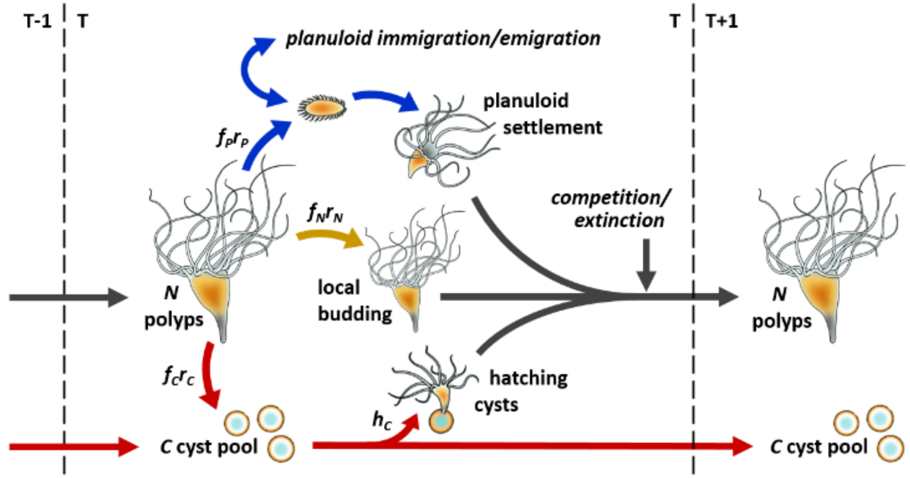
New number of cysts:

$$C_{t+1}^{w} = C_t^w (1 - h_c) + N_t^w f_C^w r_C$$





3. Competition



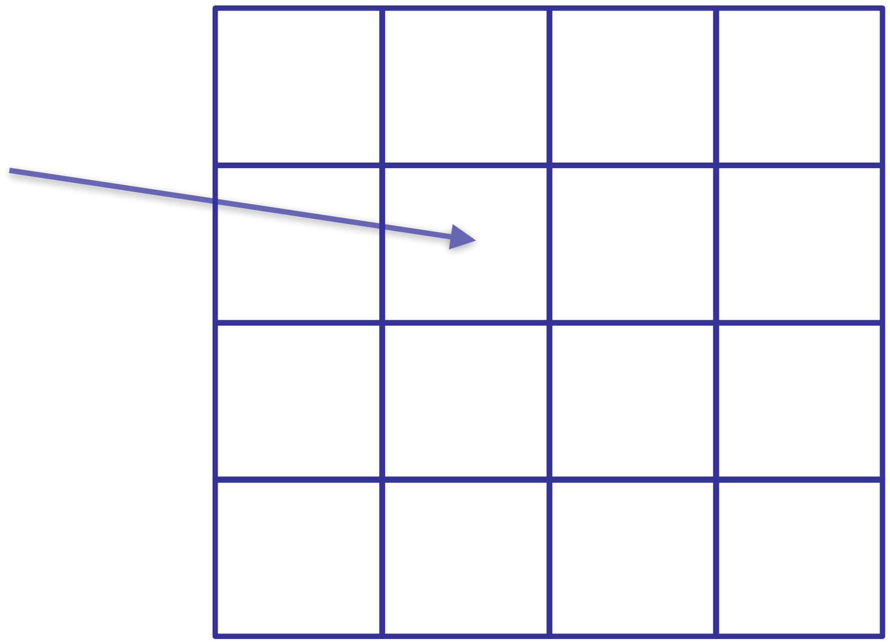
Total hatched:

$$S^w_{t+1} = B^w_{t+1} + M^w_{t+1} + H^w_{t+1}$$

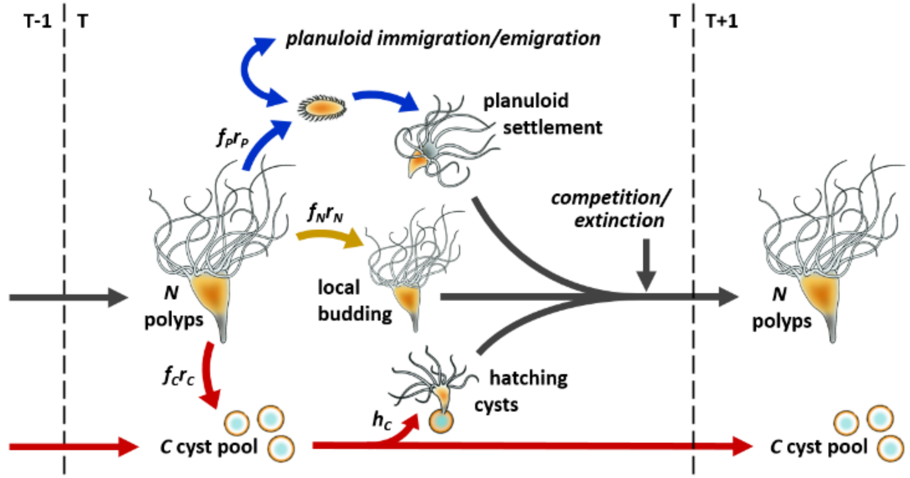
Competition:

$$N^w_{t+1} = \frac{S^w_{t+1}}{S^w_{t+1} + S^m_{t+1}}$$

$$N^m_{t+1} = \frac{S^m_{t+1}}{S^w_{t+1} + S^m_{t+1}}$$



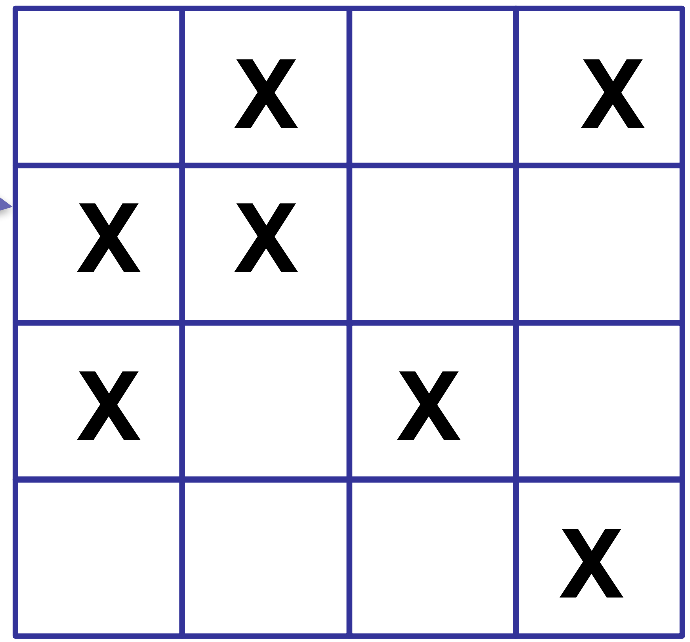
4. Extinction



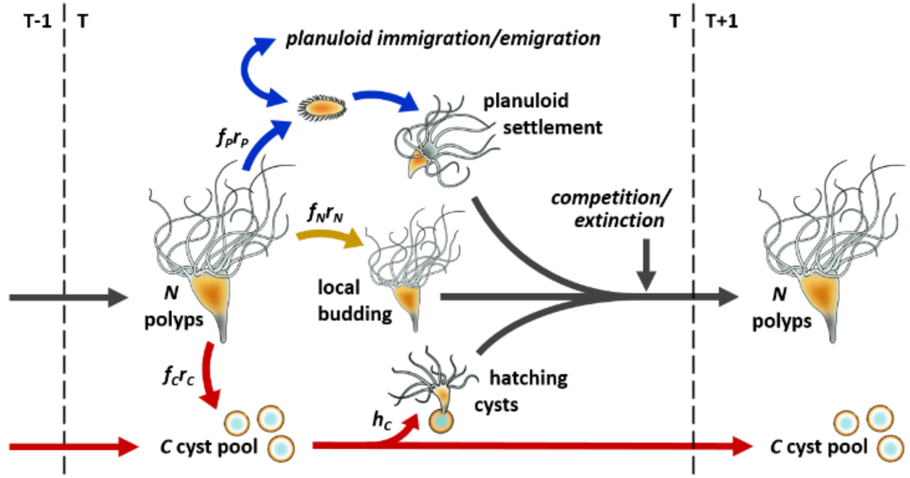
Each patch undergoes an extinction (from predation, bad environment conditions etc) with probability *e*

If extinction occurs:

$$N^w_{t+1} = N^m_{t+1} = 0$$



5. Repeat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cysts
h_C
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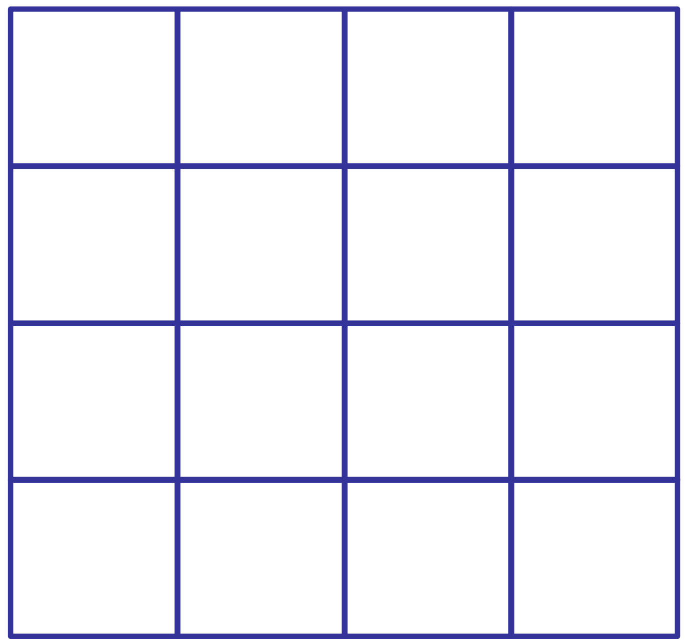
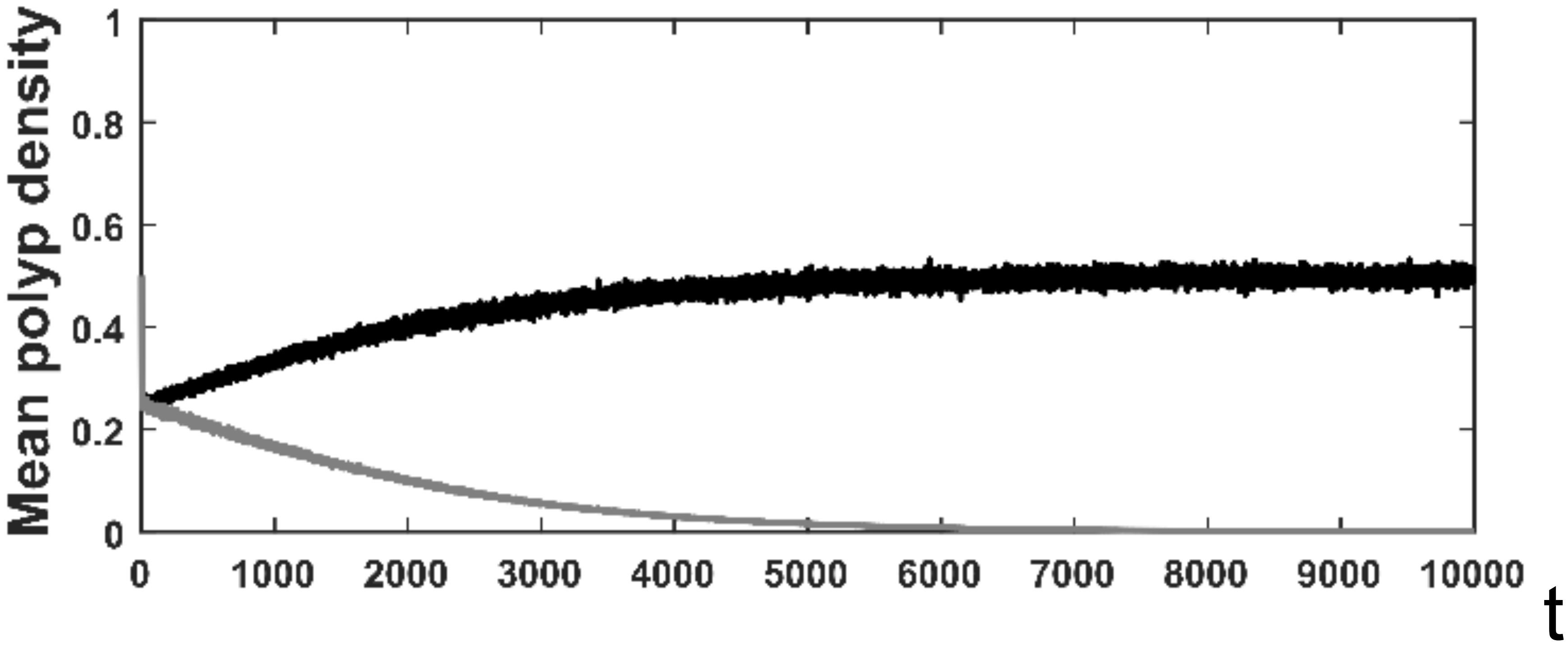
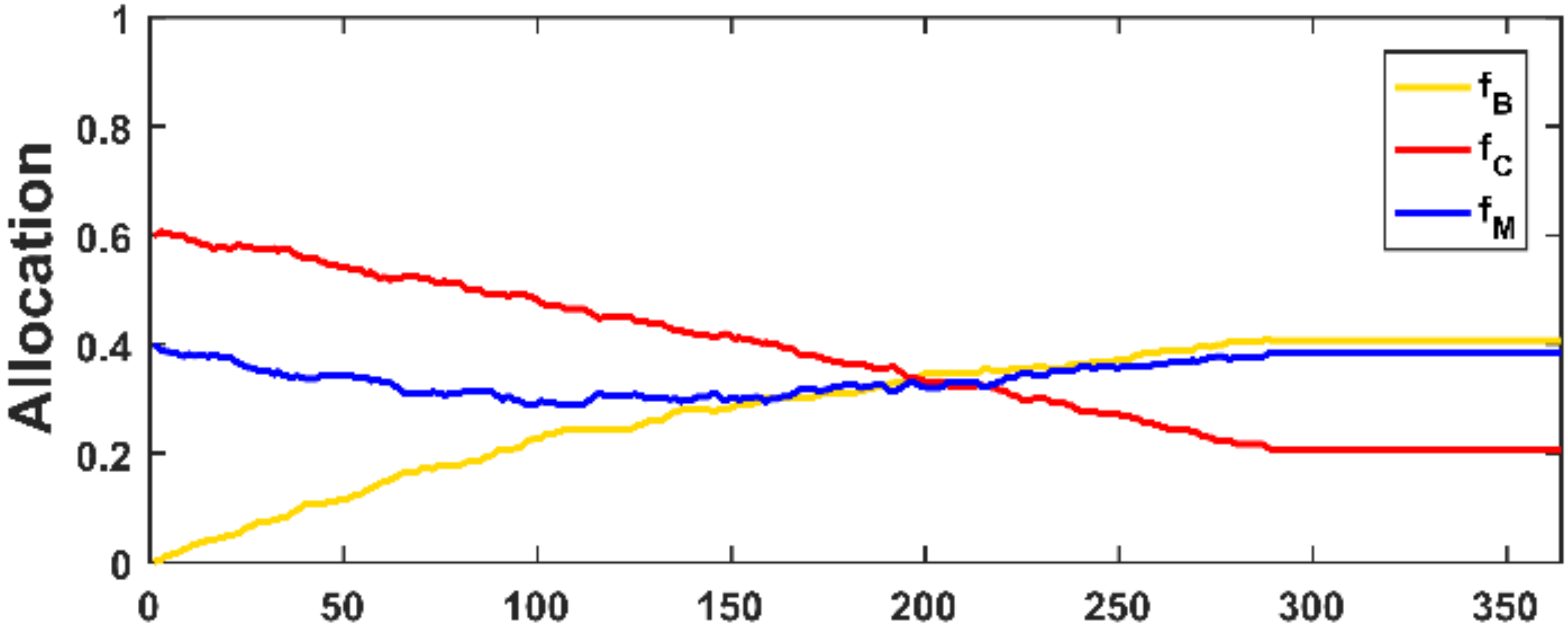


Different strategies ⇨ competitive exclusion



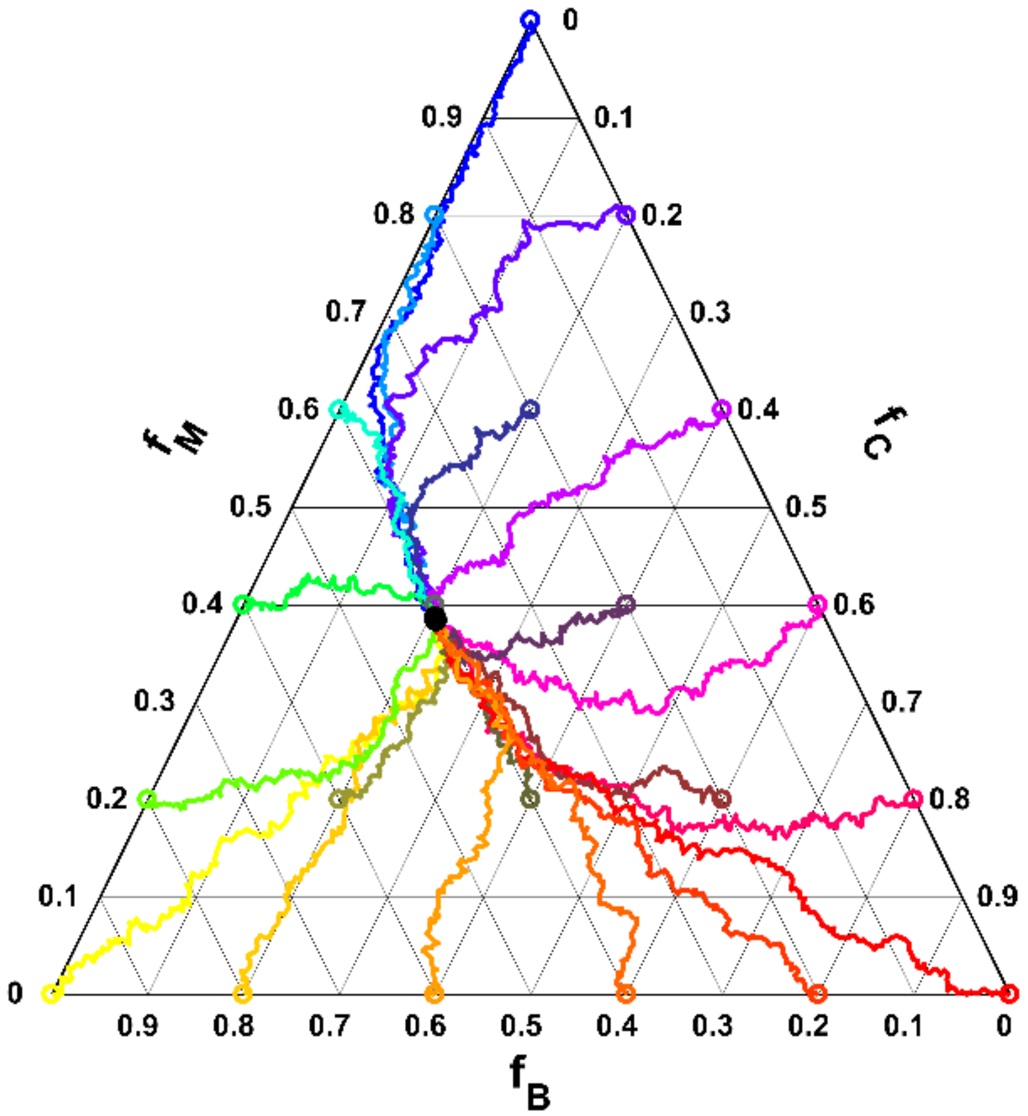
Evolution

Each round: WT vs. mutant, if mutant wins becomes new WT

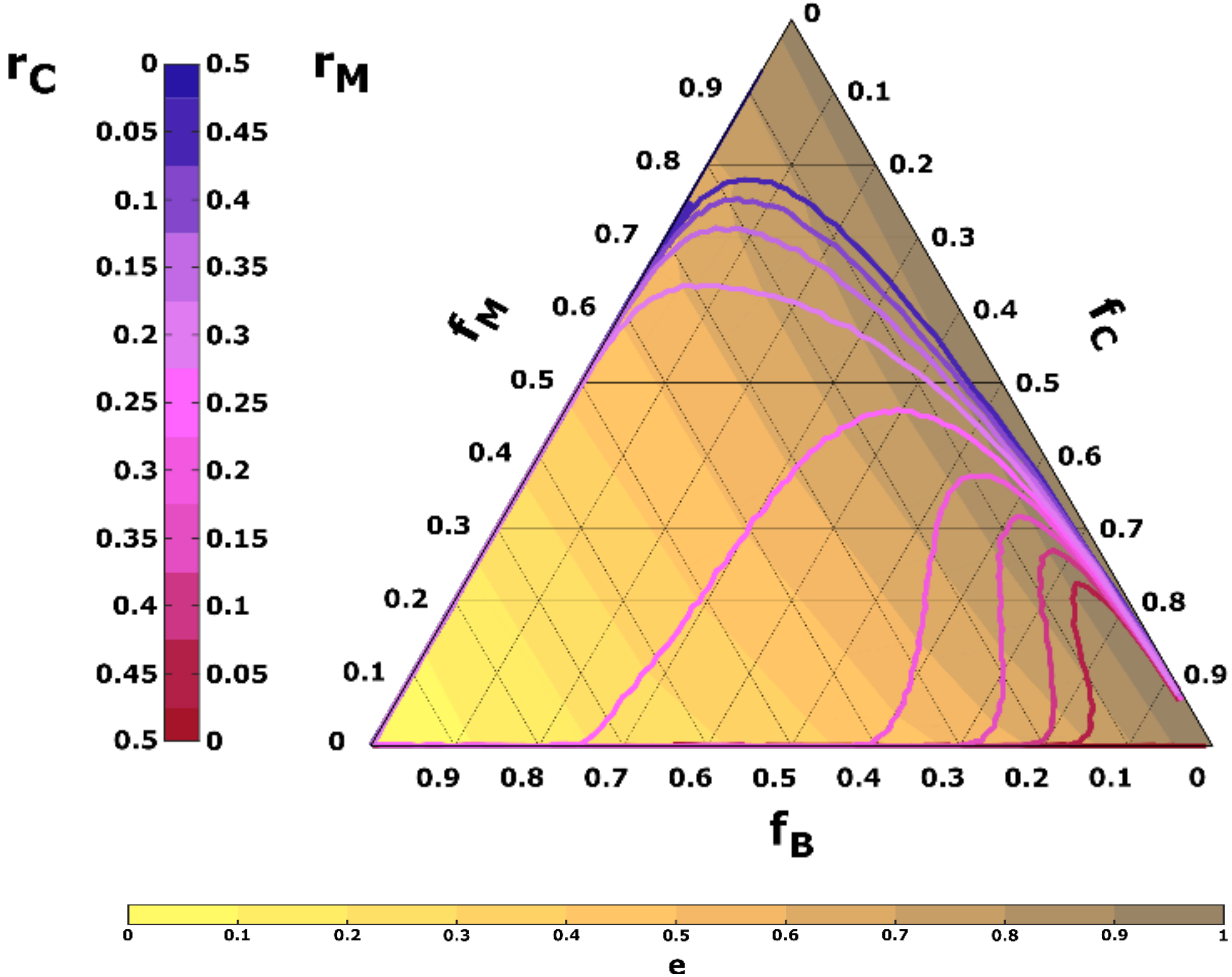


"rounds"

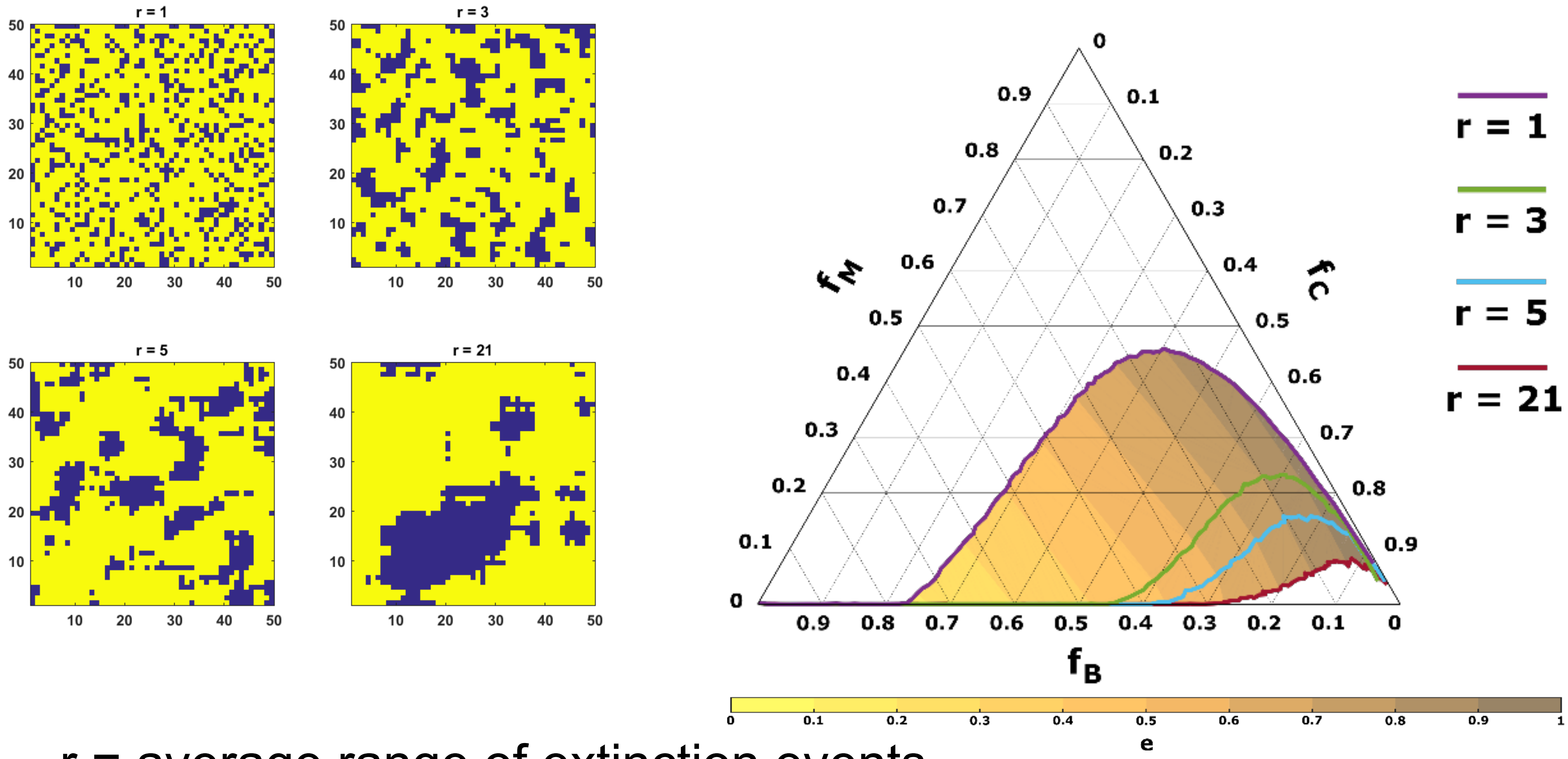
Evolutionary stable strategy



Evolutionary stable strategy



Spatially correlated extinctions



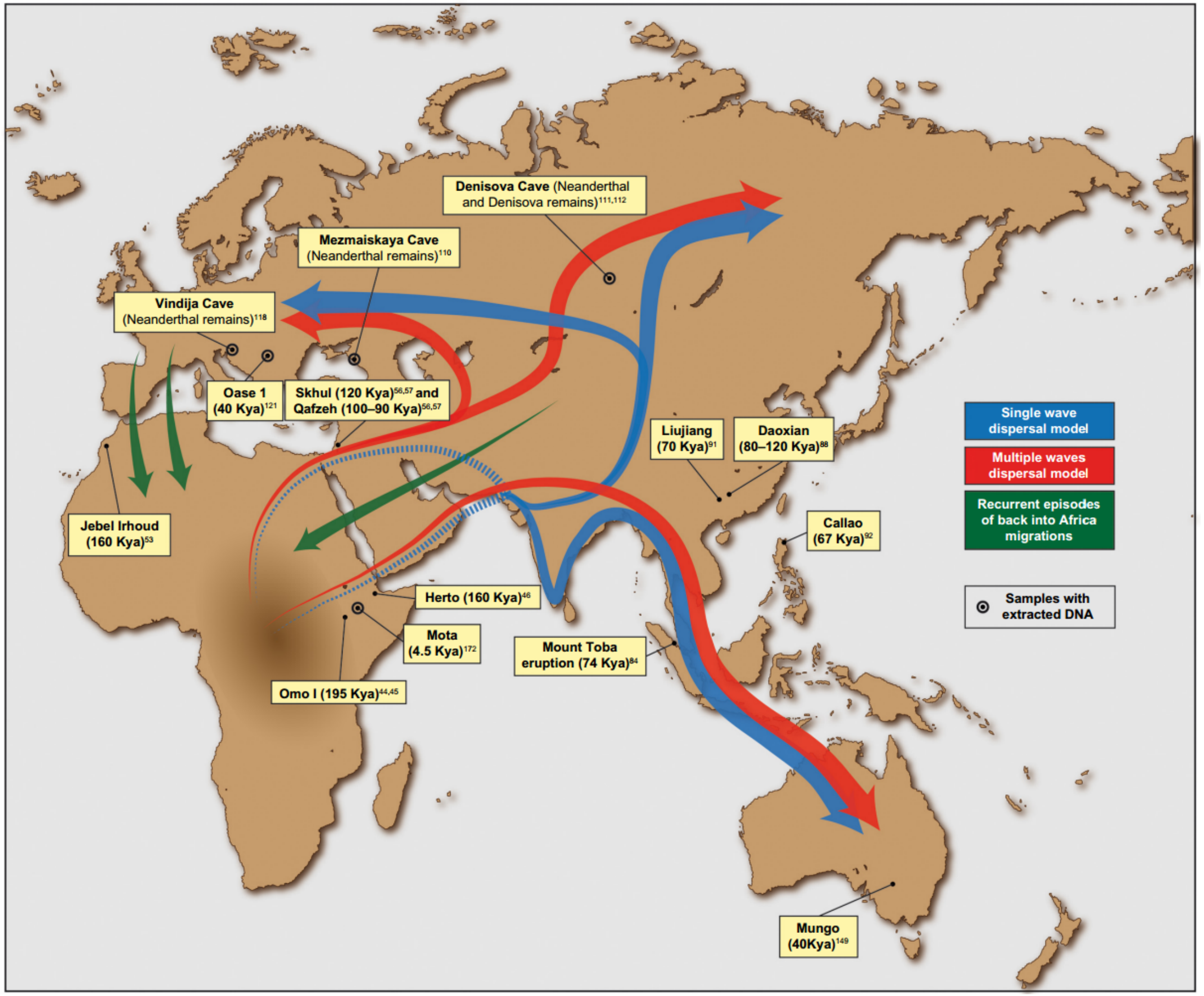
r = average range of extinction events

N. Azaña, SP, P. Mariani, American Naturalist (2018)

Conclusions

- Coexistence of multiple asexual strategies is possible ✓
- No species employ only local budding in the wild (but they do in the lab in food-rich conditions) ✓
- More common and generalist species typically employ all three modes ✓
- Cyst allocation increases in response to starvation/predation ✓
- Tradeoff between cysts and motile buds depends on level of environmental risk and spatial correlations -> “Escape in space vs time” ?

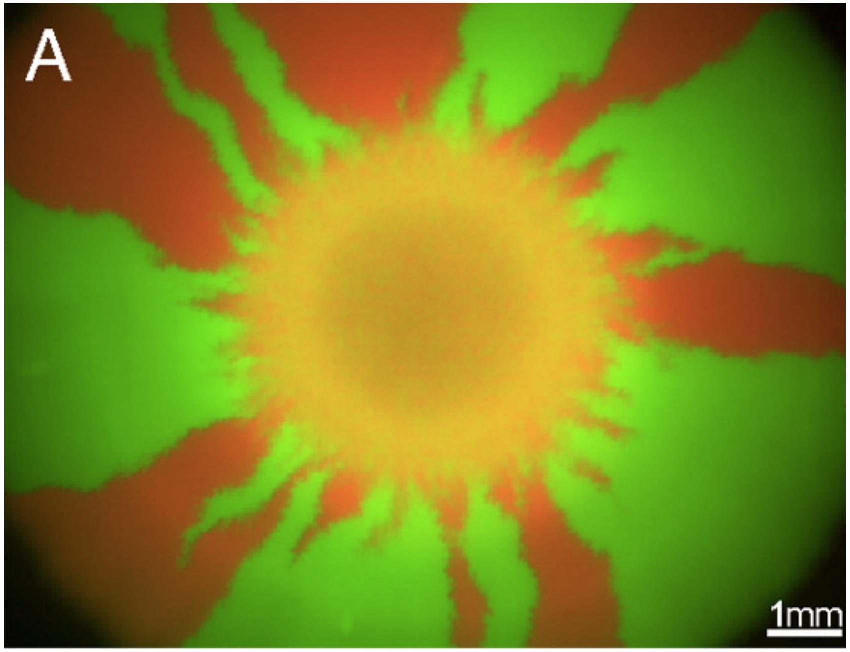
Range expansion



López et al. 2015

OIST

Neutral competition



growth of a colony of two neutral
E.Coli strains

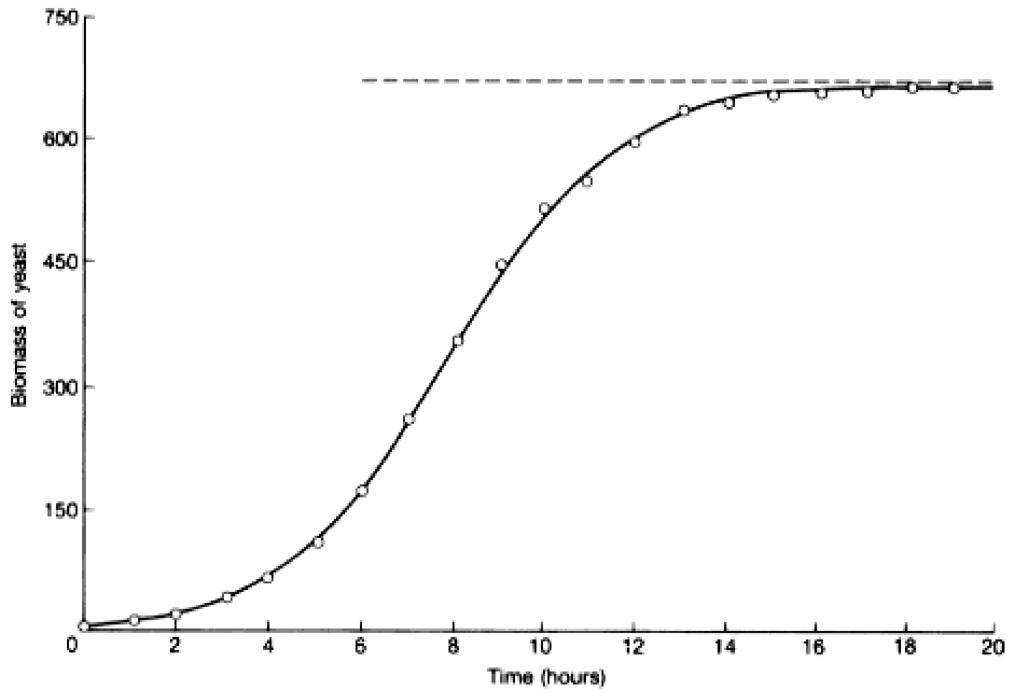
Hallatscheck and Nelson (2007)

Logistic growth

$$\frac{d}{dt}c = ac - bc^2$$

- exponential growth at small density
- saturation at higher density (finite resources)

interpretation: growth of a population
OR spread in a population of an advantageous mutation



from J. Maynard Smith, “Evolutionary Genetics”, 1998

Fisher equation

$$\partial_t c = D\partial_x^2 c + sc(1-c)$$

Spread of a population (or advantageous mutation) in space

Fisher (1937)

Fisher equation

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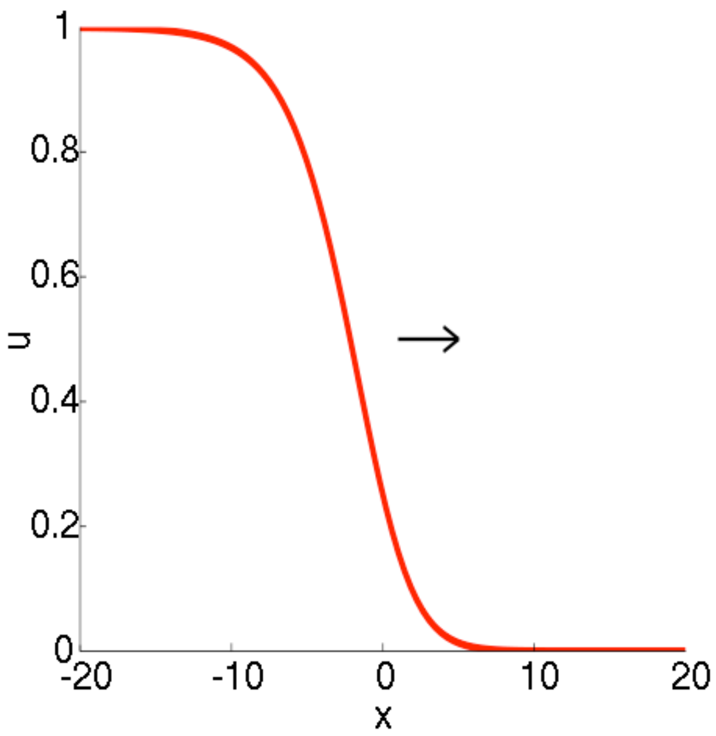
Spread of a population (or advantageous mutation) in space

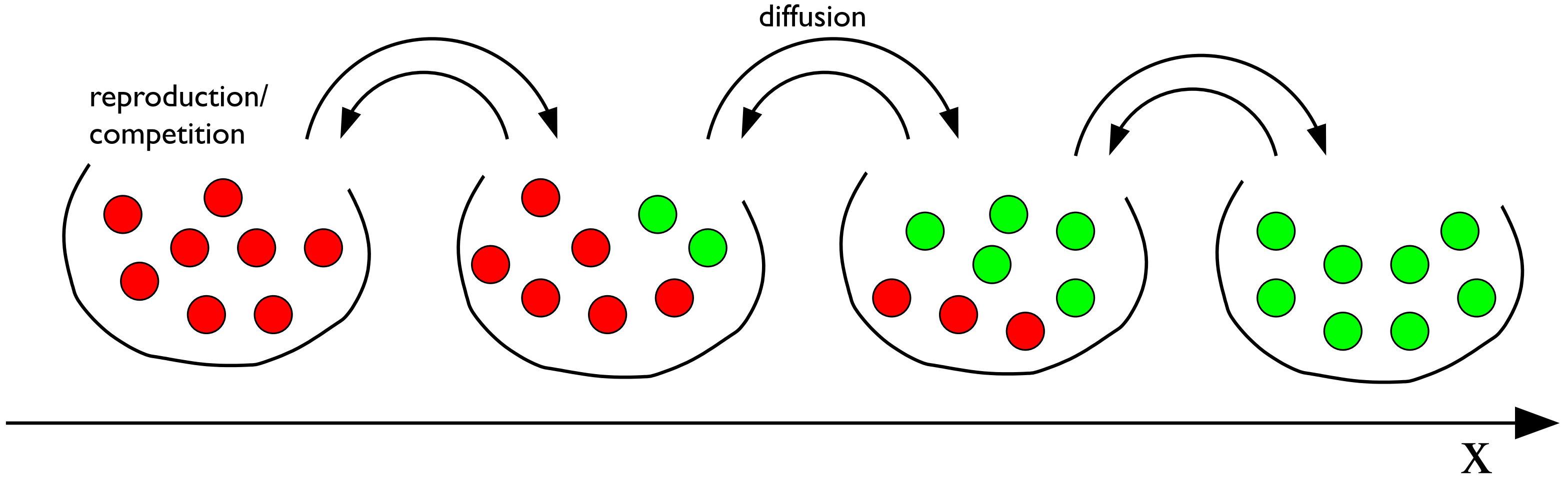


Basic result: propagating front of velocity

$$v = 2\sqrt{Ds}$$

Fisher (1937)

Individual-based models and stochasticity



continuum limit: stochastic Fisher equation

$$\partial_t c(x,t) = D\nabla^2 c + sc(1-c) + \sqrt{2\mu c(1-c)/N}\,\xi(x,t)$$

where:

c(x,t) = fraction of one of the two species
μ = reproduction rate
s = selective advantage
N = local population size
D = diffusion constant

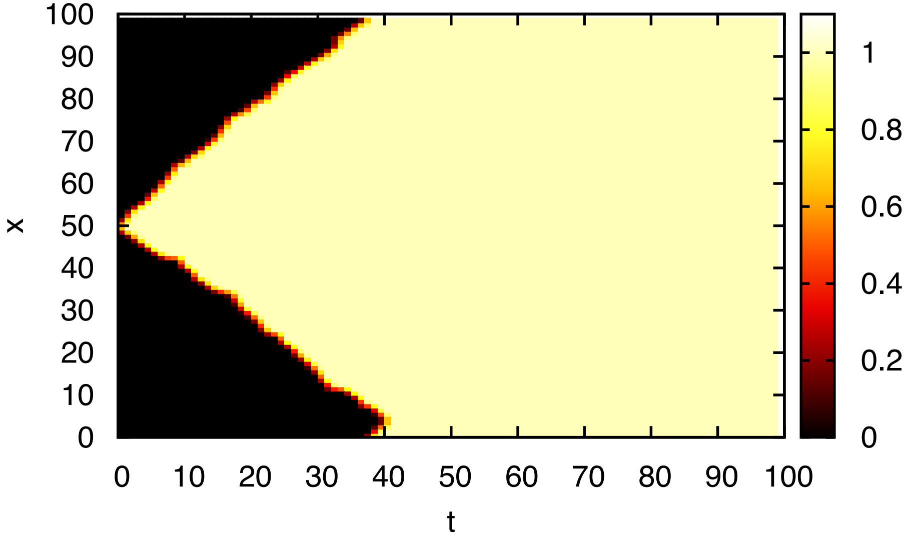
Kimura et al (1964)

Two different fixation mechanisms

continuum limit: stochastic Fisher equation

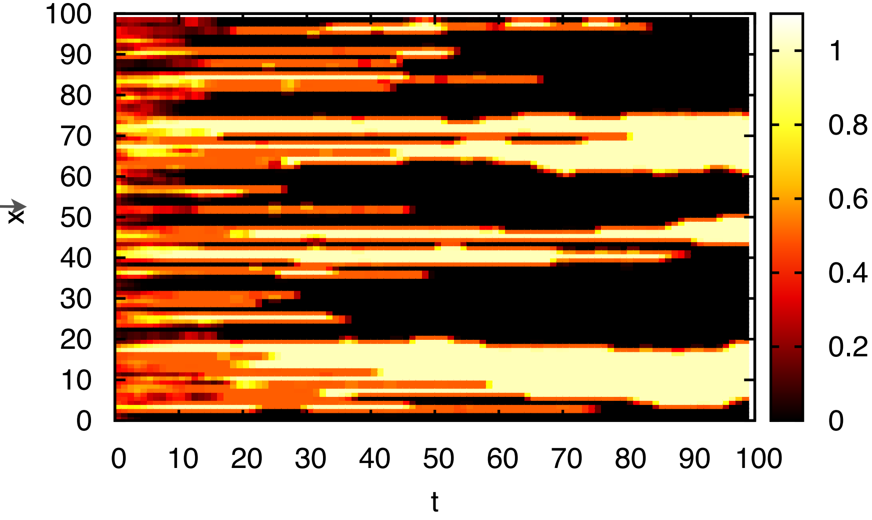
$$\partial_t c(x,t) = D\nabla^2 c + sc(1-c) + \sqrt{2\mu c(1-c)/N}\,\xi(x,t)$$

$s \gg 1/N$



Fisher wave, speed $v = 2\sqrt{Ds}$

$s \ll 1/N$



Stochastic fixation

Bet-hedging in expanding populations

$$\partial_t f(x,t) = D\nabla^2 f + \sigma(x,t)\ f(1-f)$$

$$\sigma(x,t) = \sigma_{i(x,t)} = \sum_j s_{ij}\alpha_j \qquad \text{with} \quad \sum_j \alpha_j = 1$$

Environmental states ($\sigma_{i(x,t)}$)

Frequencies of strategies (α_j)

P. Villa-Martín, M.A. Muñoz, SP, Plos Comp. Biol (2019)

Well-mixed limit

$$\frac{d}{dt} f = \sigma(t) f$$

For long times: $$f(t) \sim e^{t\langle\sigma\rangle} f(0)$$

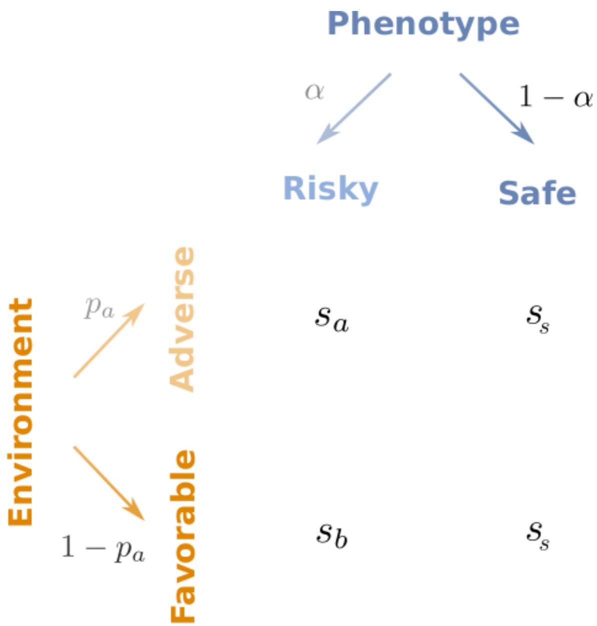
$$\sigma_i = \sum_j s_{ij} \alpha_j$$

- “Fitness” is a linear function of the frequencies
- Optimal strategy is a pure strategy
- Bet-hedging is never advantageous

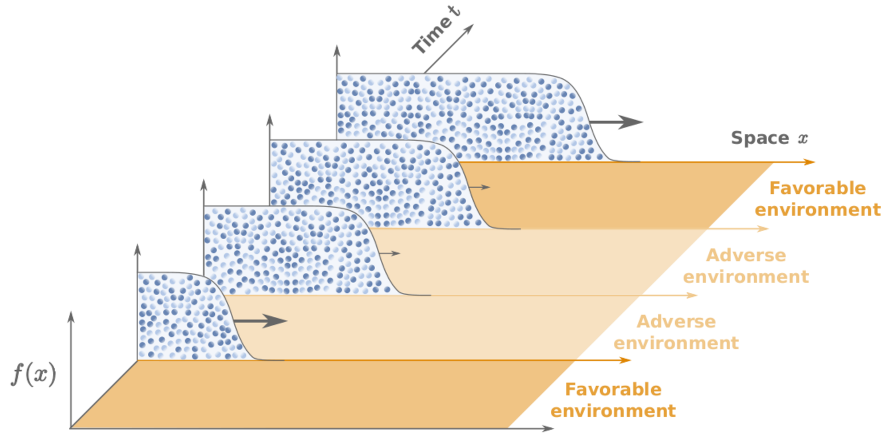
Simpler case

$$\partial_t f(x,t) = D\nabla^2 f + \sigma(x,t)\ f(1-f)$$

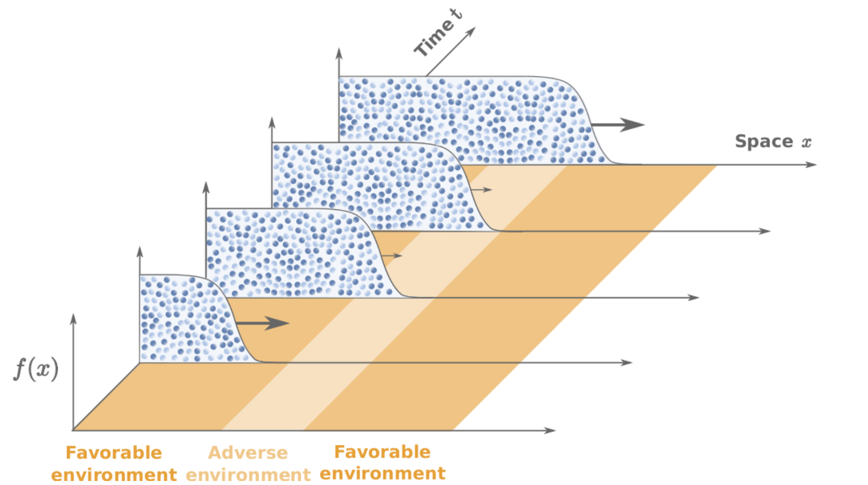
$$\sigma_i = \sum_j s_{ij}\alpha_j$$



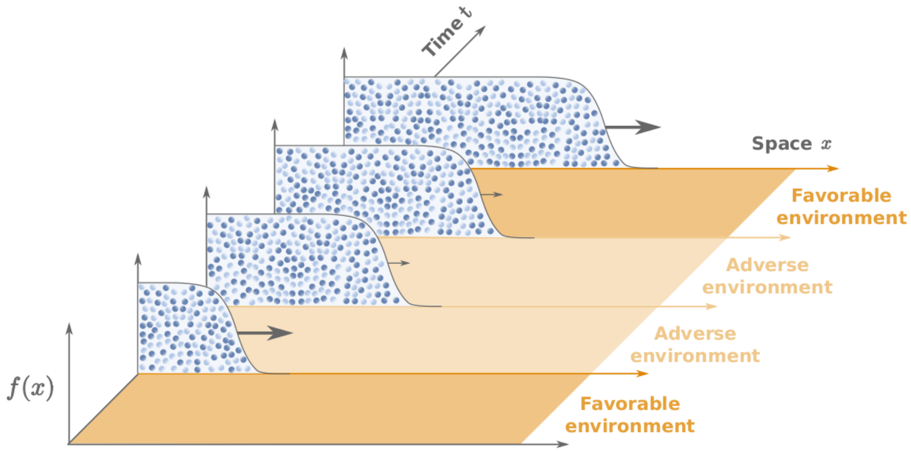
Temporal environmental variations, or

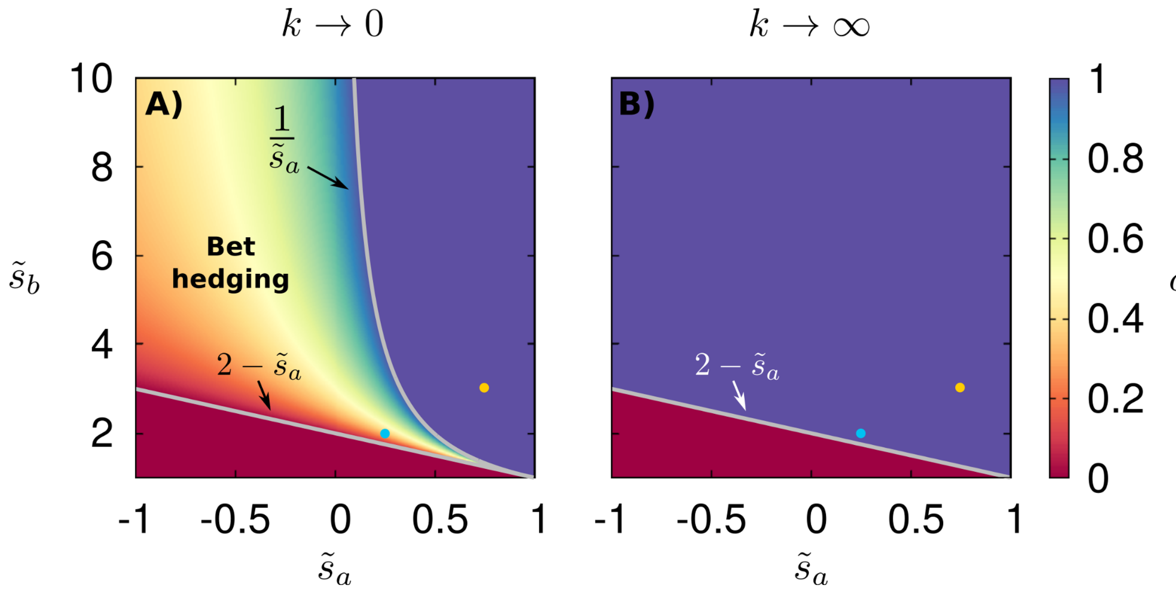


spatial environmental variations



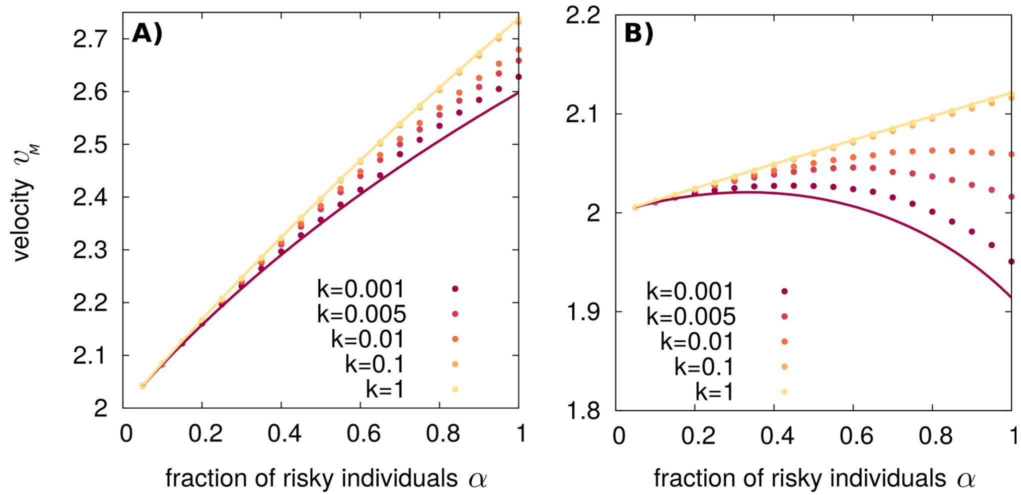
Temporal fluctuations



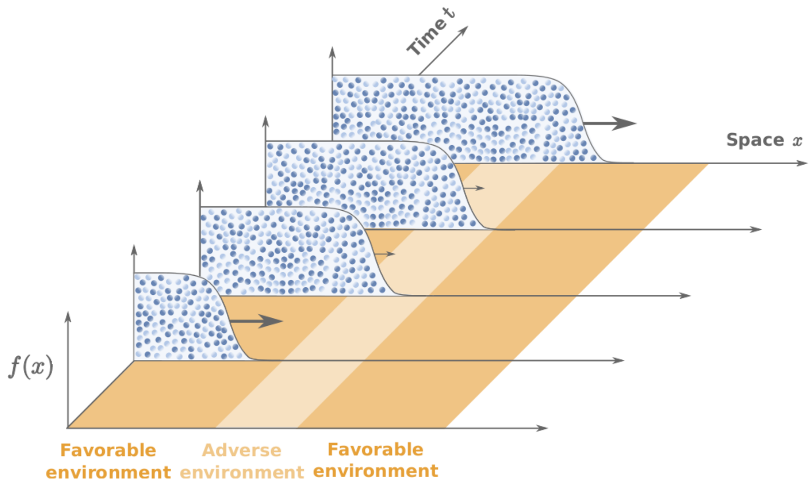


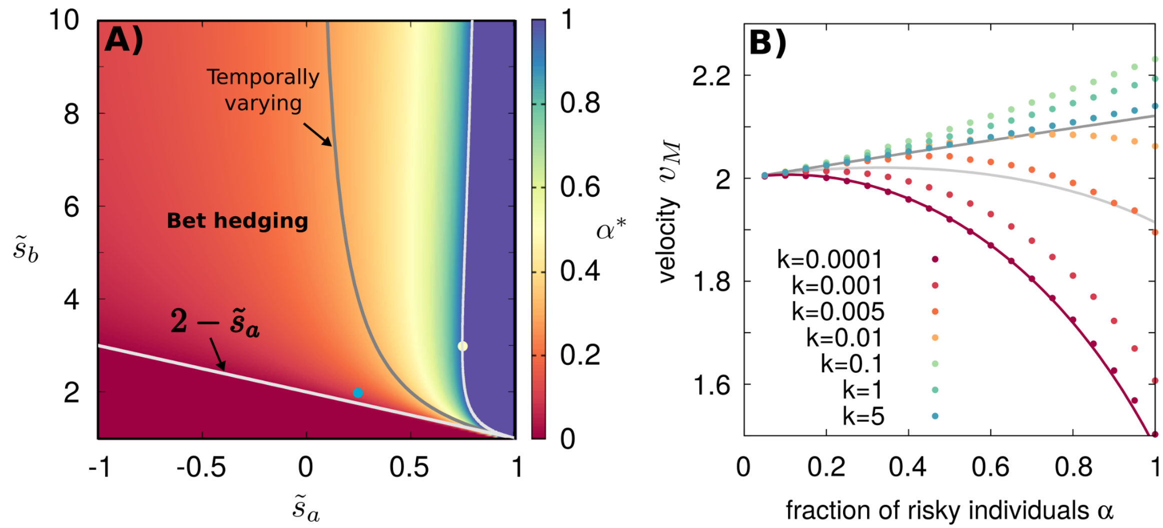
$$\langle v \rangle_{k\to\infty} = 2\sqrt{D\langle \sigma(\alpha)\rangle}$$

$$\langle v \rangle_{k\to 0} = \left\langle 2\sqrt{D\sigma(\alpha)} \right\rangle$$



Spatial fluctuations





$$\langle v \rangle_{k_M \to \infty} = 2\sqrt{D\langle\sigma(\alpha)\rangle}$$

$$\frac{1}{\langle v \rangle_{k_M \to 0}} = \left\langle \frac{1}{2\sqrt{D\sigma(\alpha)}} \right\rangle$$

- The wave front spends less time in the advantageous environment
- Bet-hedging region is broader than for temporal fluctuations

General case

$$\partial_t f(x,t) = D\nabla^2 f + \sigma(x,t)\ f(1-f)$$

$$\sigma(x,t) = \sigma_{i(x,t)} = \sum_j s_{ij}\alpha_j$$

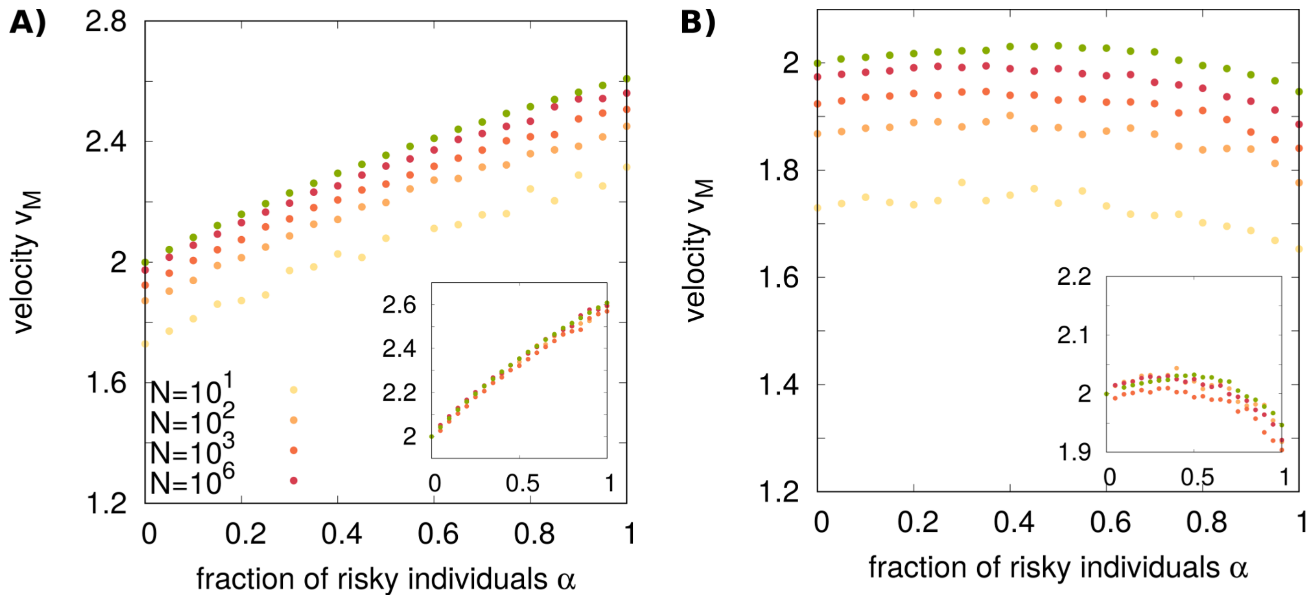
with $i = 1 \ldots M$, $j = 1 \ldots N$ and arbitrary $M, N, s_{ij} > 0$

- Frequent environmental change rate: no bet-hedging
- Slow environmental change rate: bet-hedging is favored for spatial fluctuations

Role of finite population size

Stochastic Fisher equation:

$$\partial_t f(x,t) = D\nabla^2 f + \sigma(t) f(1-f) + \sqrt{\frac{2}{N} f(1-f)}\,\xi(x,t)$$



Slightly reduced velocity, otherwise similar physics

Conclusions

Bet-hedging is:

- favored in range expansions compared to well-mixed populations
- favored at low rather than high frequency of environmental change
- favored for spatially rather than temporally varying environments
- not much dependent on demographic stochasticity

Lots of possible generalization: finite switching rates, pushed waves etc.

P. Villa-Martín, M.A. Muñoz, SP, Plos Comp. Biol (2019)