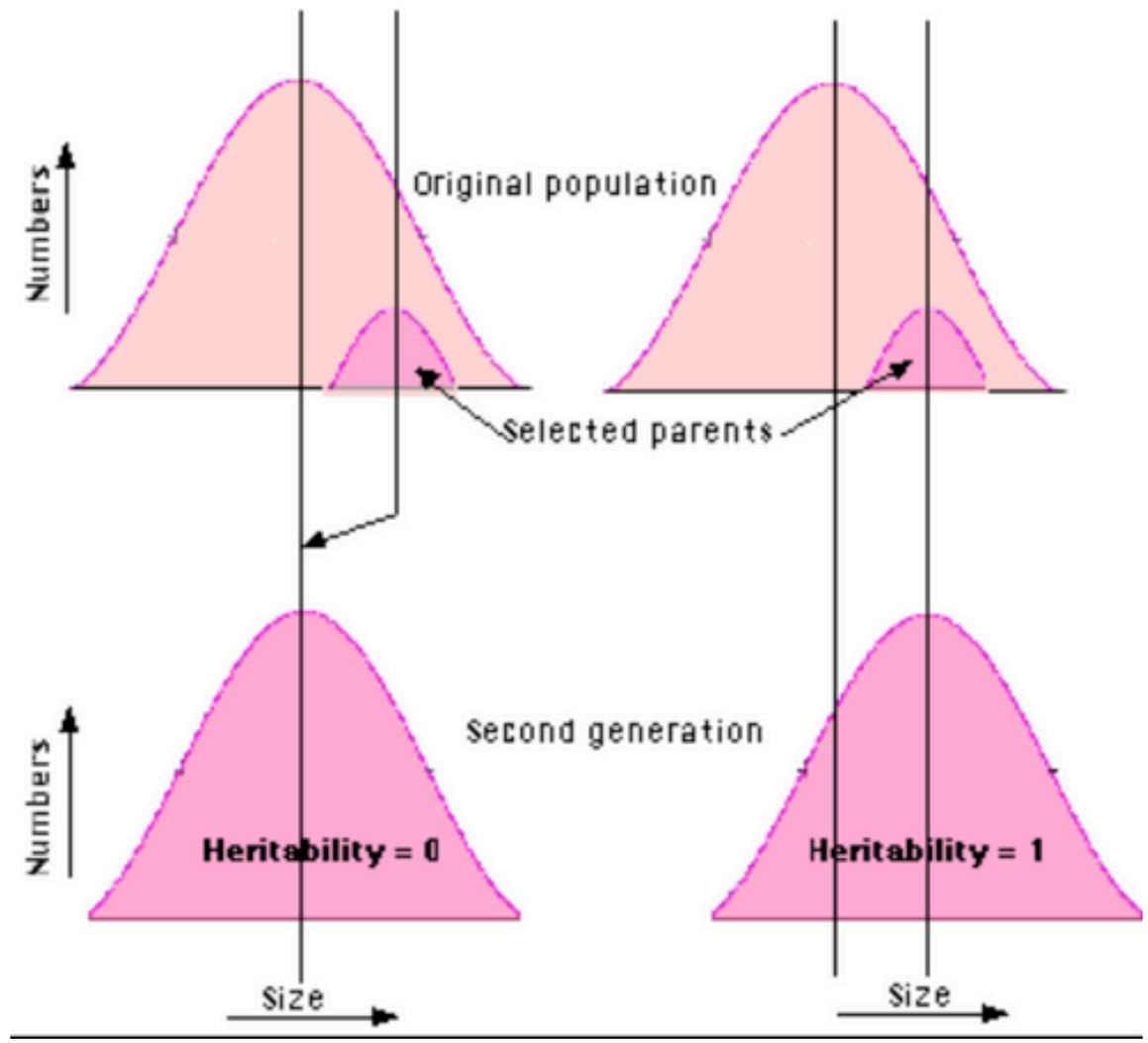
5. Dinámica Adaptativa

5.1 Evolución de estrategias de vida en un contexto ecológico

heritability



trait

number of genotypes = 3^n

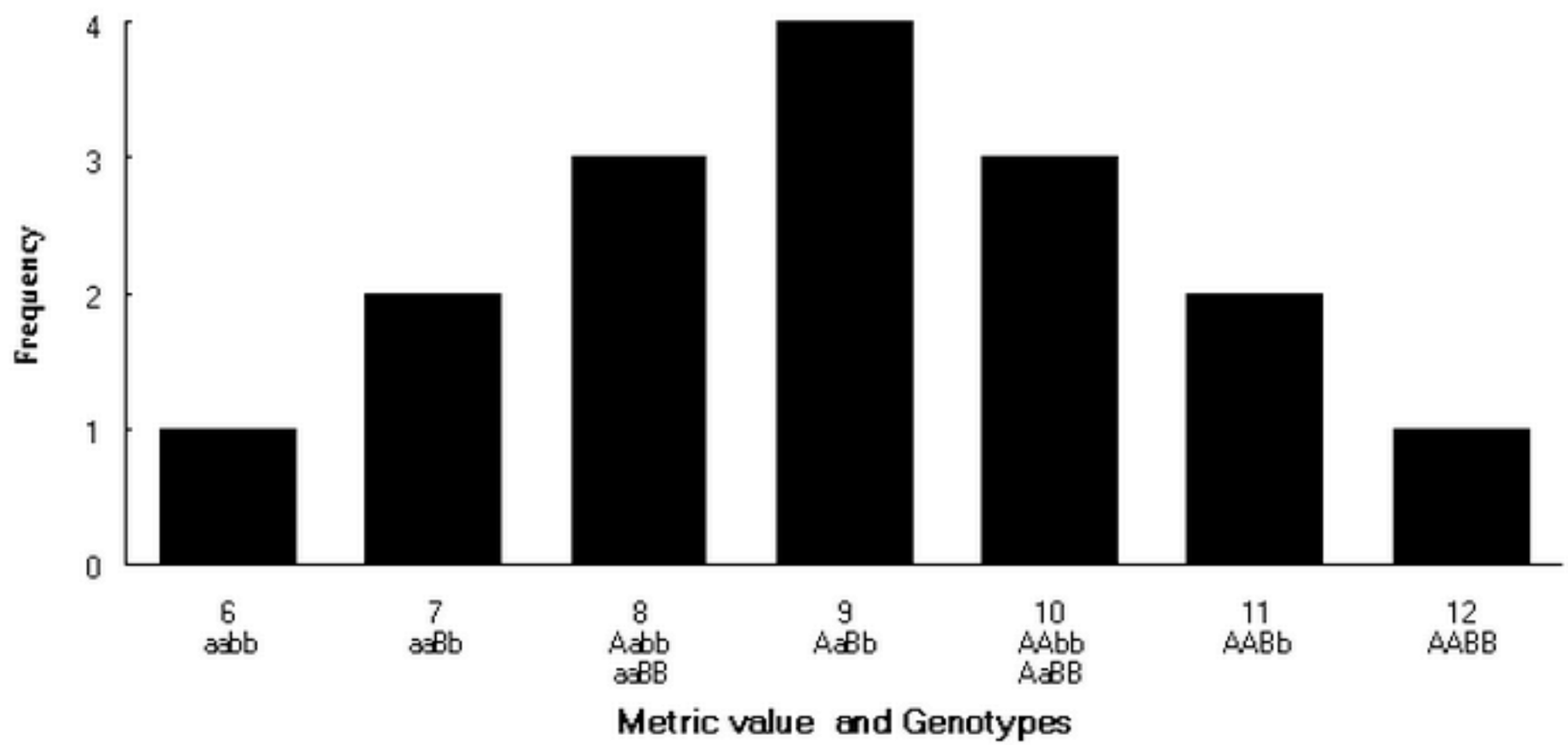
(n = number of genes involved in the expression of the trait)

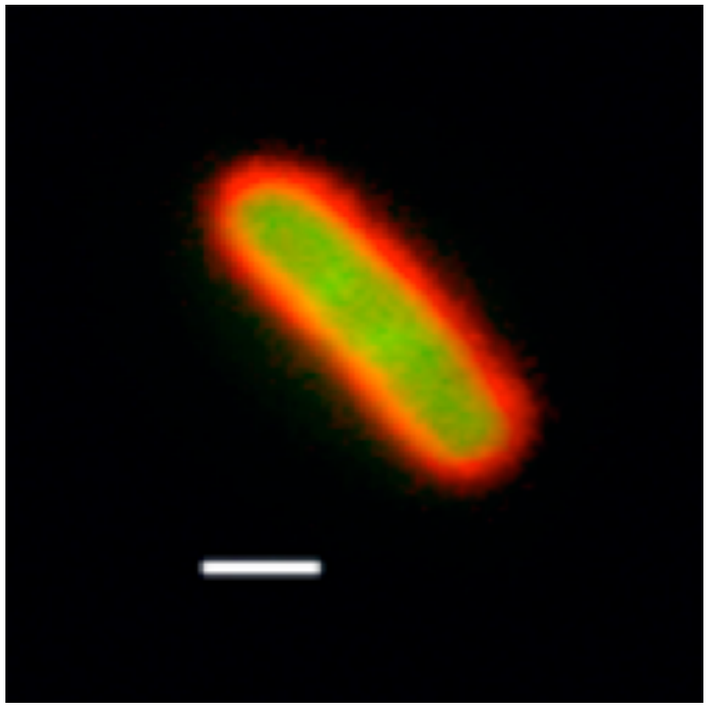
# of genes	# of genotypes
1	3
2	9
5	243
10	59,049

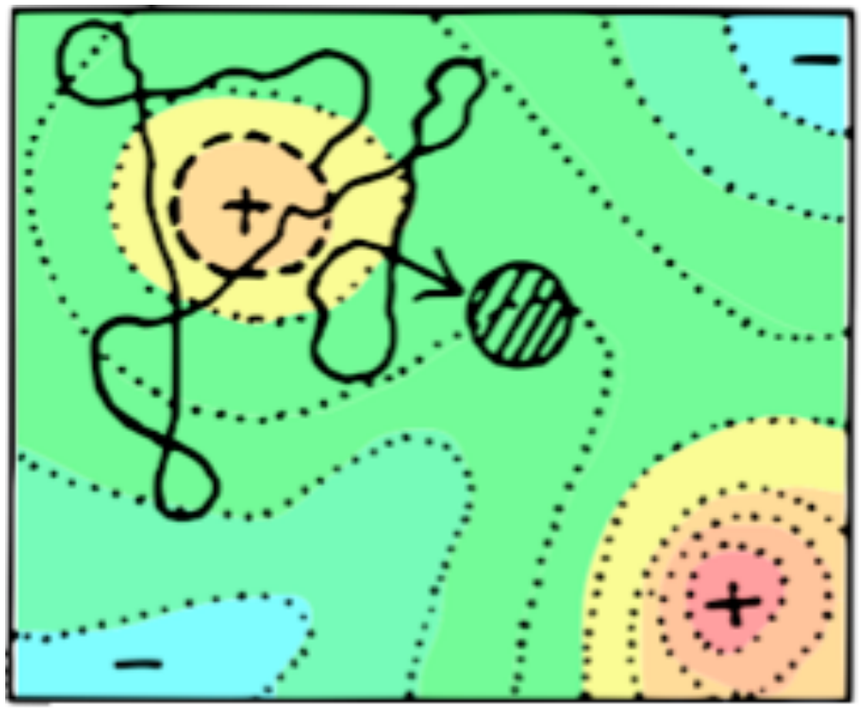
A allele = 4 units
a allele = 2 units

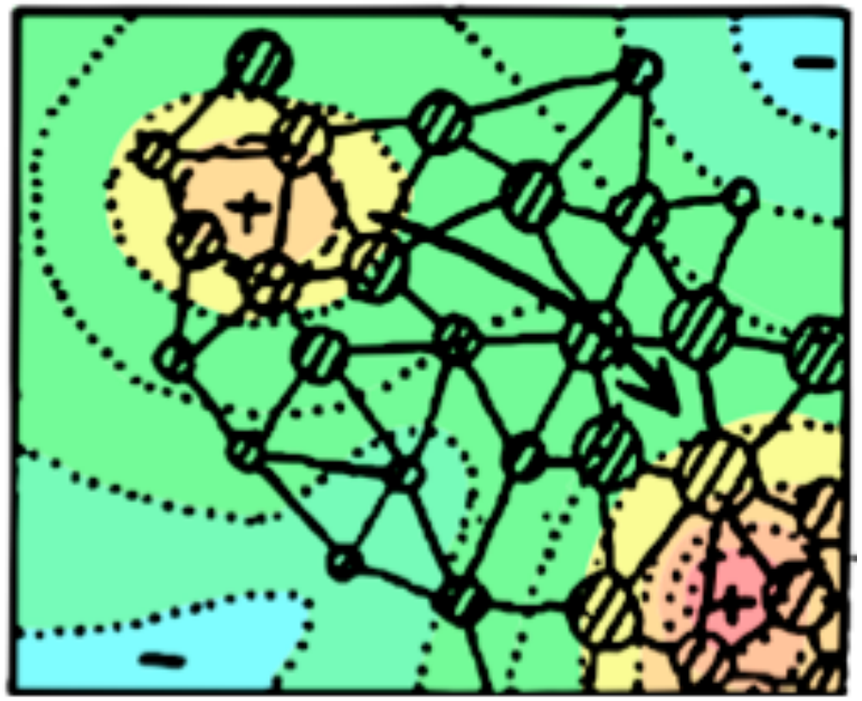
B allele = 2 units
b allele = 1 units

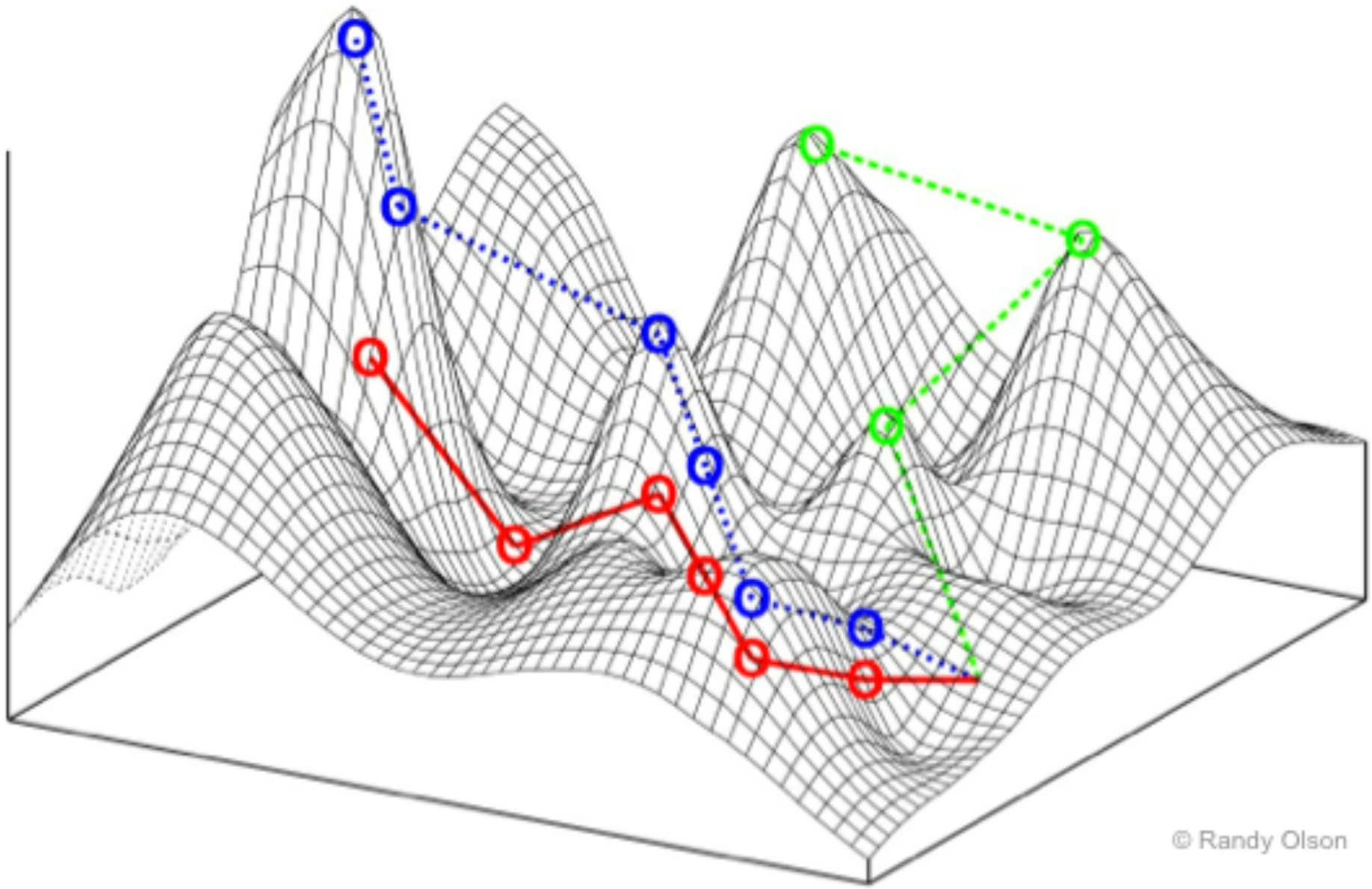
Genotype	Ratio in F_2	Metric Value
AABB	1	12
AABb	2	11
AAbb	1	10
AaBB	2	10
AaBb	4	9
Aabb	2	8
aaBB	1	8
aaBb	2	7
aabb	1	6

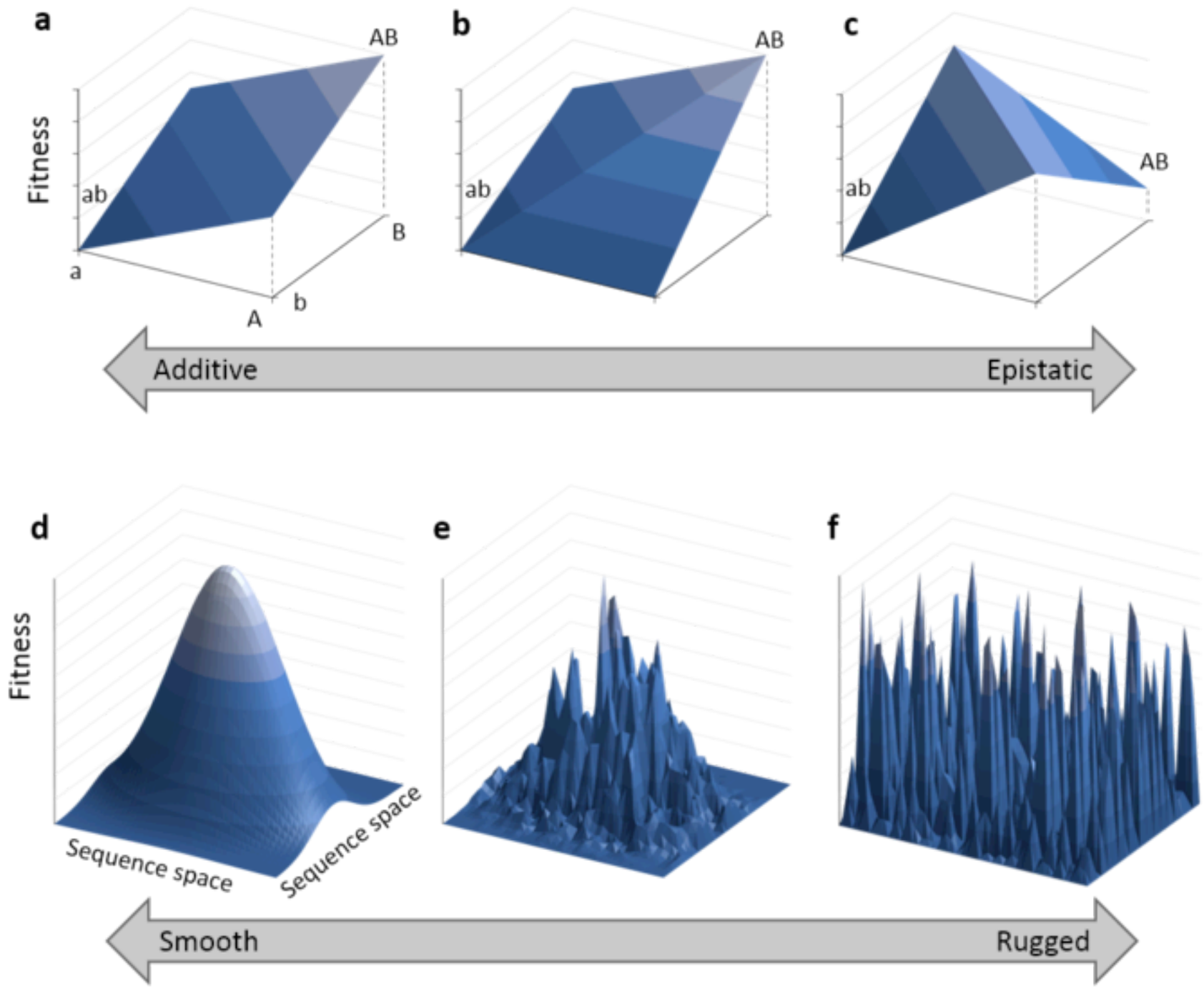


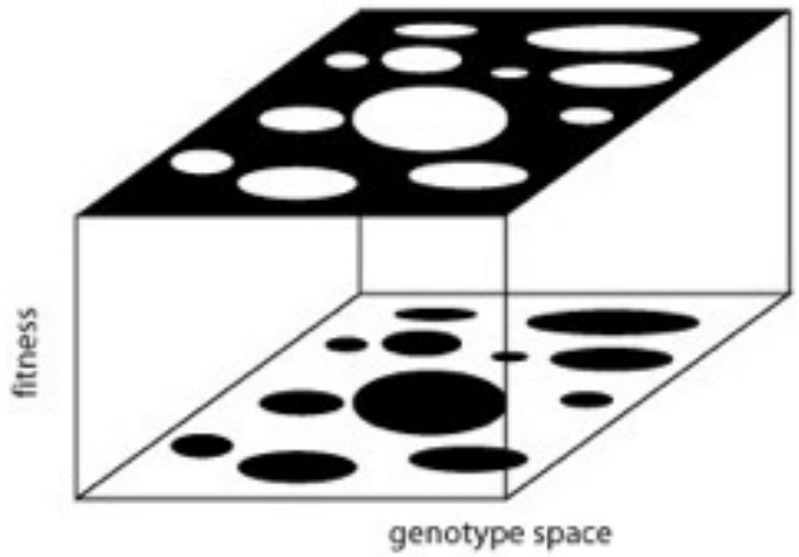


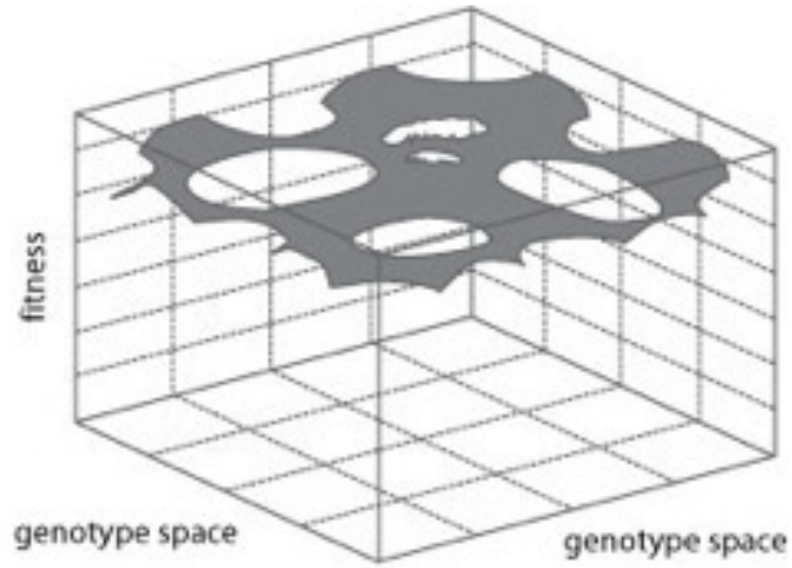




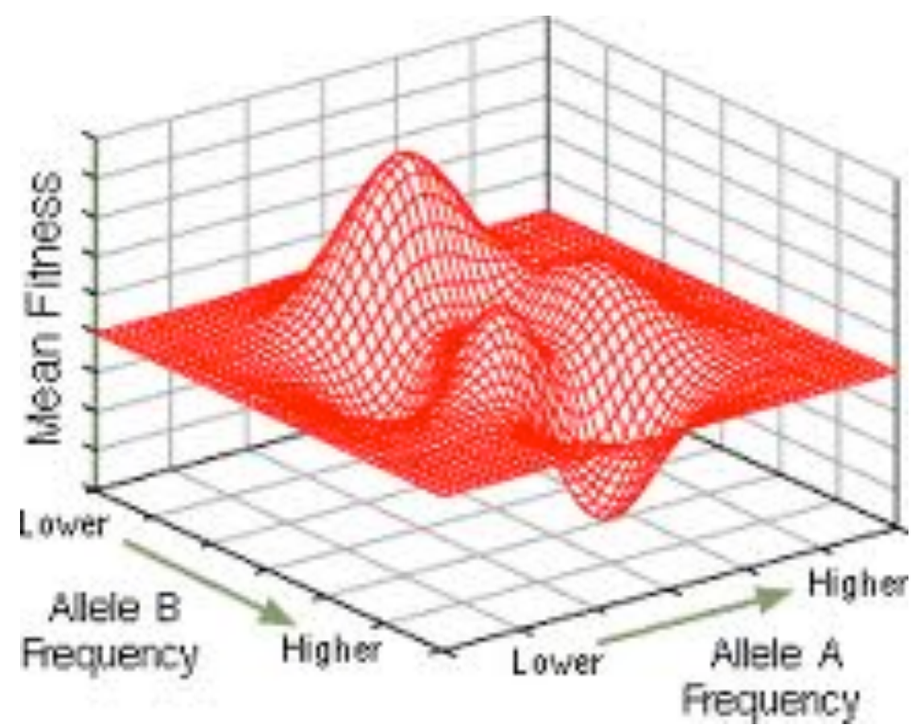

© Randy Olson


a
b
c
Fitness
ab
AB
a
A
b
B
Additive
Epistatic
d
e
f
Fitness
Sequence space
Sequence space
Smooth
Rugged

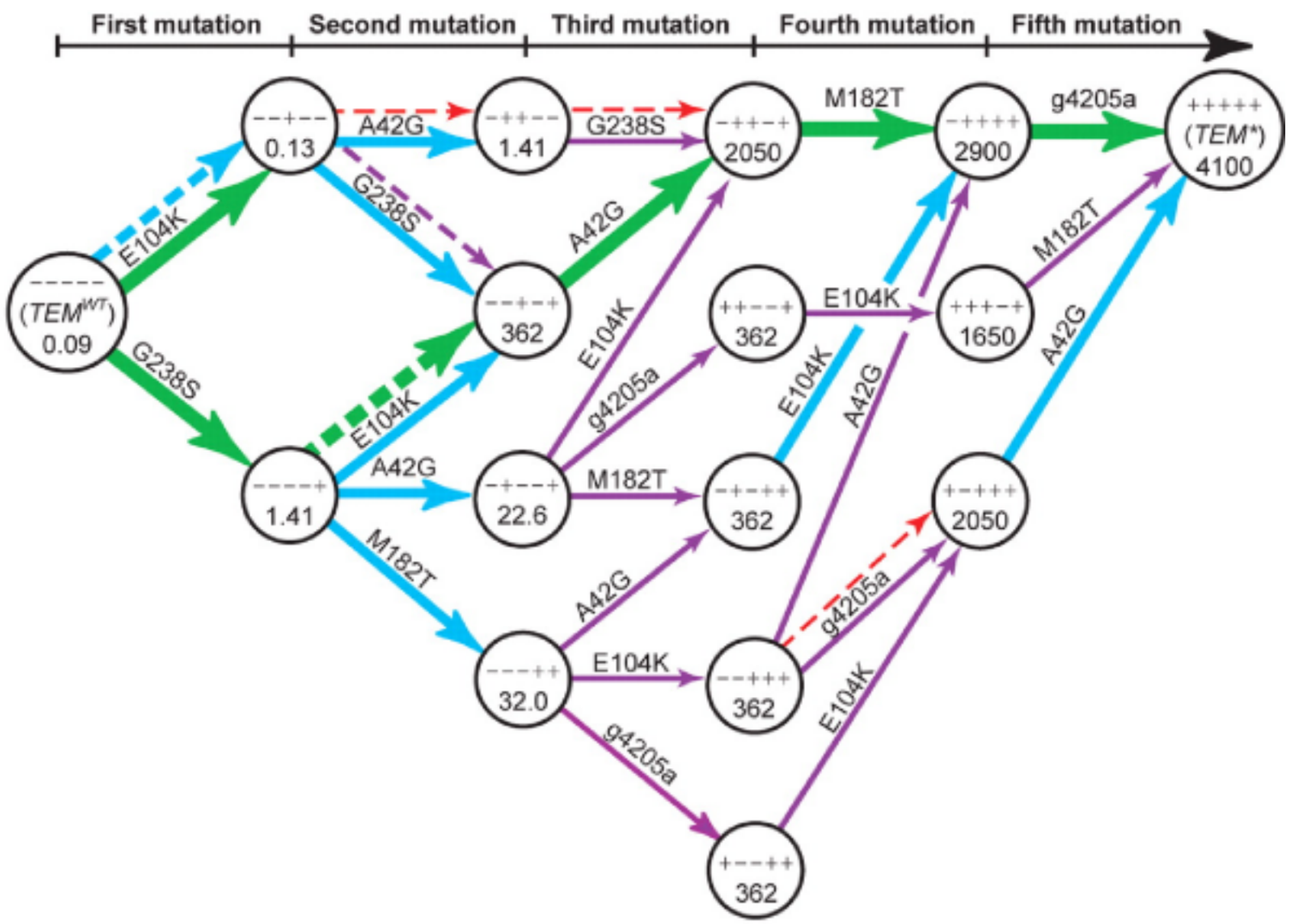


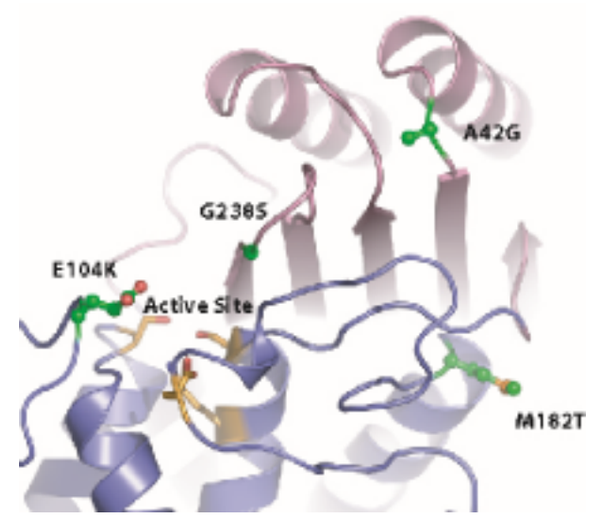


Left: From Gavrilets 1997, right from Gavrilets 2003



Microevolution



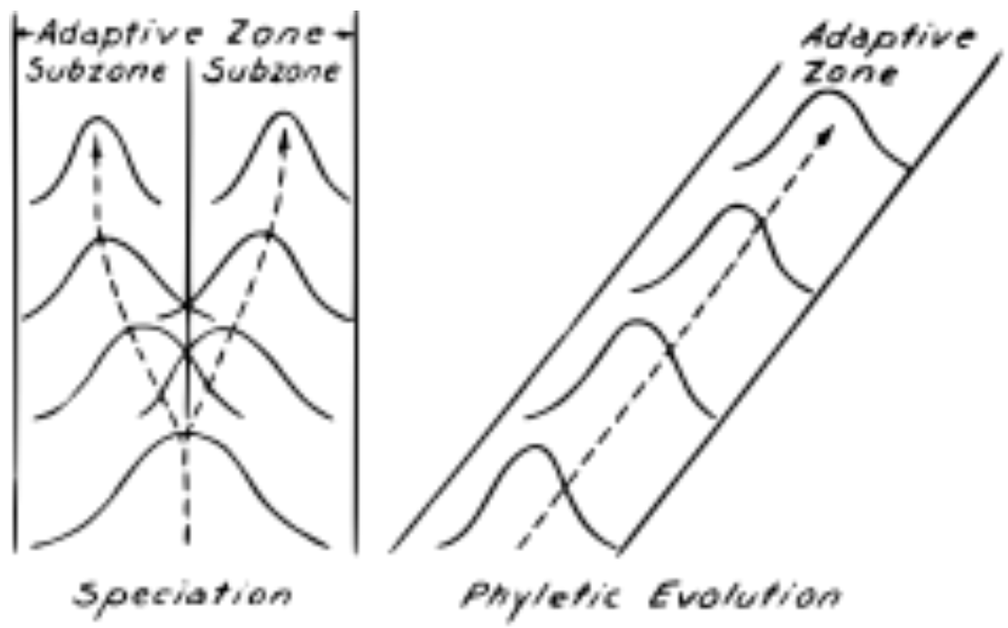


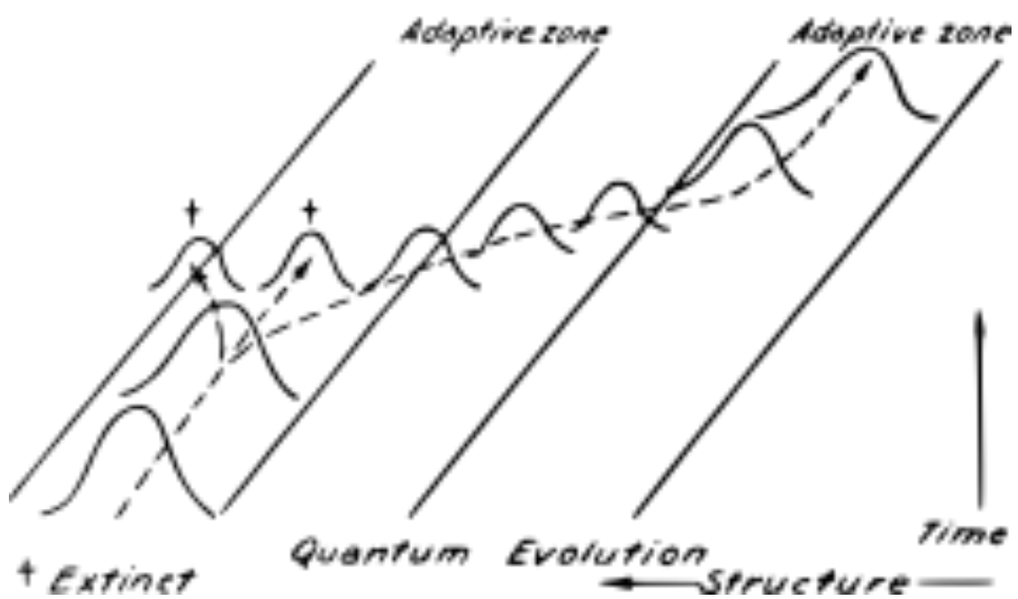
Beta-lacatamase protein

Darwinian Evolution Can Follow Only Very Few Mutational Paths to Fitter Proteins

Daniel M. Weinreich,* Nigel F. Delaney,† Mark A. DePristo, Daniel L. Hartl

Mecroevolution





article
Nature **246**, 15 - 18 (02 November 1973); doi:10.1038/246015a0

The Logic of Animal Conflict

J. MAYNARD SMITH* & G. R. PRICE†

Evolutionary Game Theory

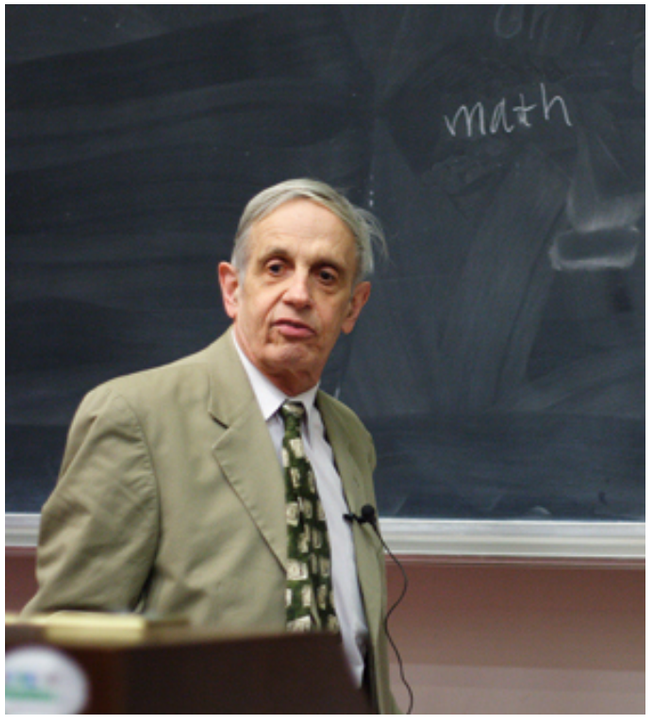
Evolutionary Stable Strategy
(ESS)

Population Dynamics

+

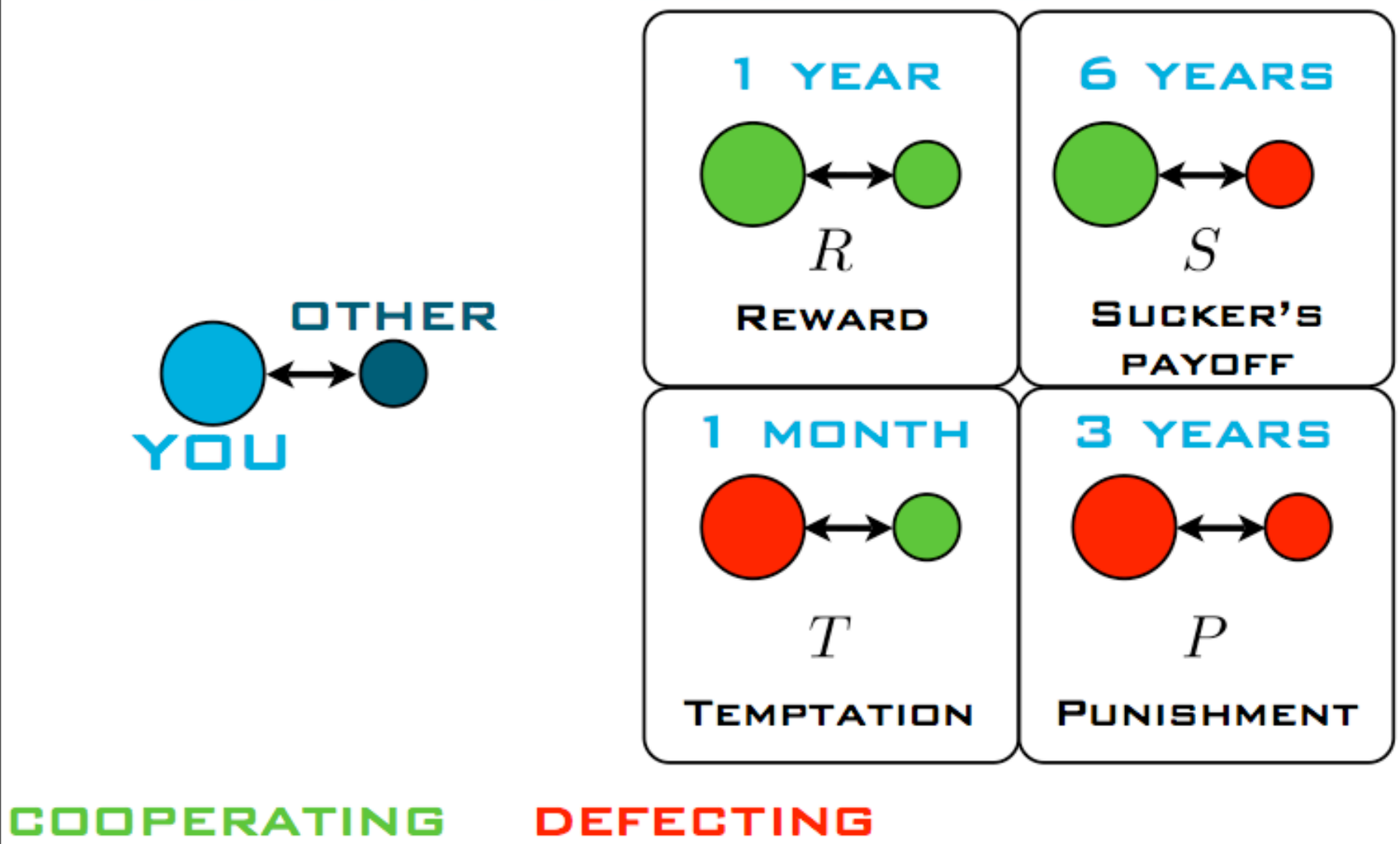
Game Theory

Nash equilibrium



Prisoner's Dilemma

Cooperative vs Defective



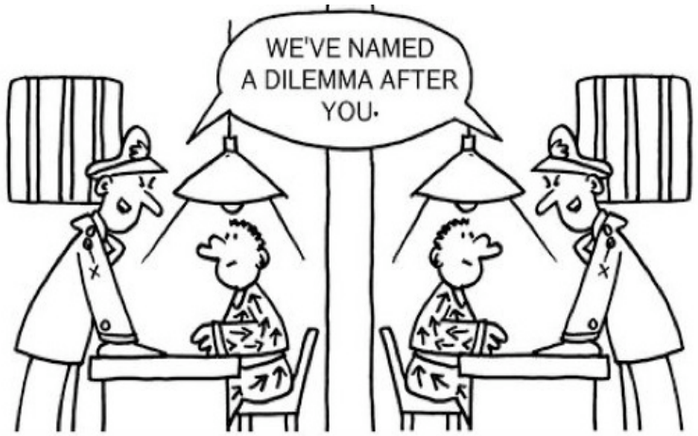
$$\mathcal{P} = \begin{pmatrix} R & S \\ T & P \end{pmatrix}$$

$$T > R > P > S$$

$\Longrightarrow$ Tragedy of the commons

Stag Hunt game

S<P<T<R



Prisoner's Dilemma

S<P<R<T

	C	D
C	R	S
D	T	P

P<S<T<R

Harmony game

P<S<R<T

Hawk and Dove game

Replicator equation

$$\boxed{\frac{\dot{p}_d}{p_d} = f_d - \bar{f}}$$

$$\bar{f} = f_c(\underbrace{1 - p_d}_{p_c}) + f_d p_d$$

$$\frac{\dot{p}_d}{p_d} = f_d - f_c(1 - p_d) - f_d p_d$$

$$\frac{\dot{p}_d}{p_d} = (f_d - f_c) - f_d p_d + f_c p_d$$

$$\frac{\dot{p}_d}{p_d} = (f_d - f_c) - (f_d - f_c) p_d$$

$$\boxed{\frac{\dot{p}_d}{p_d} = (\underbrace{f_d - f_c}_{\Delta f})(1 - p_d)}$$

Logistic equation

$$\boxed{\dot{p}_d / p_d = (f_d - f_c)(1 - p_d)}$$

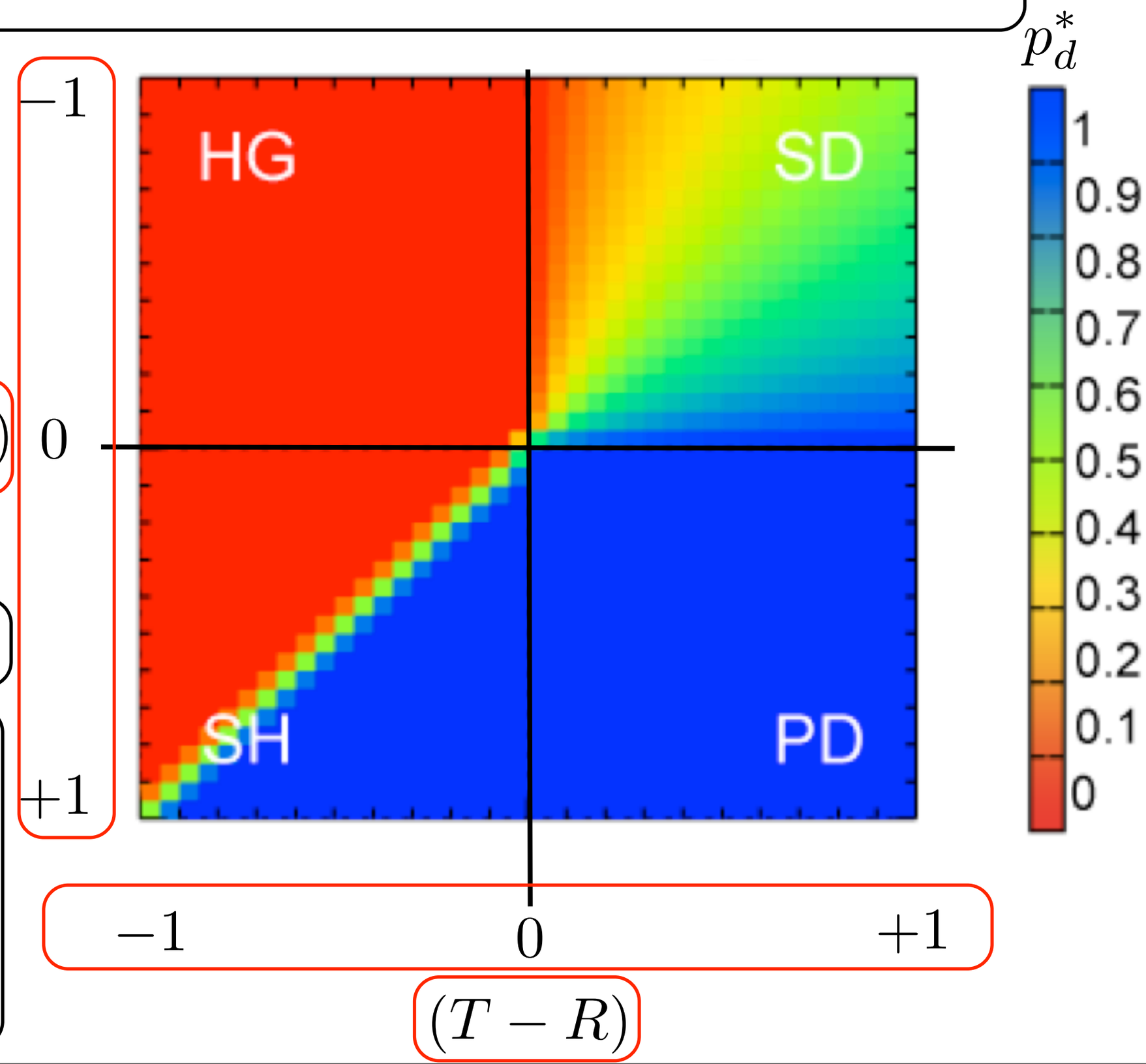
$$\Delta f = f_d - f_c$$

Interaction GAME

$$f_c = (1 - p_d) \cdot R + p_d \cdot S$$
$$f_d = (1 - p_d) \cdot T + p_d \cdot P$$

$$\boxed{\Delta f = (1 - p_d) \cdot (T - R) + p_d \cdot (P - S)}$$

$$\Delta f = (1 - p_d) \cdot (T - R) + p_d \cdot (P - S)$$

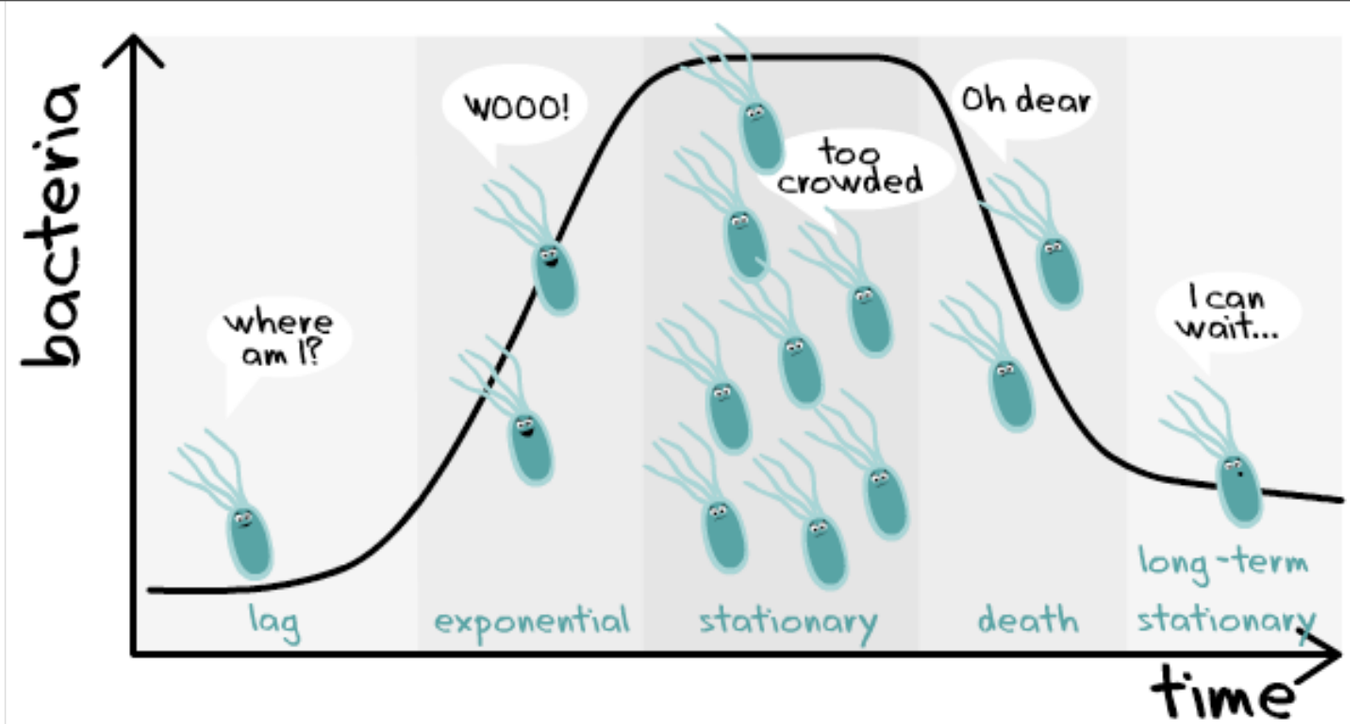


$$\dot{p}_d / p_d = (f_d - f_c)(1 - p_d)$$

$$\hat{p}_d^0 = 0$$

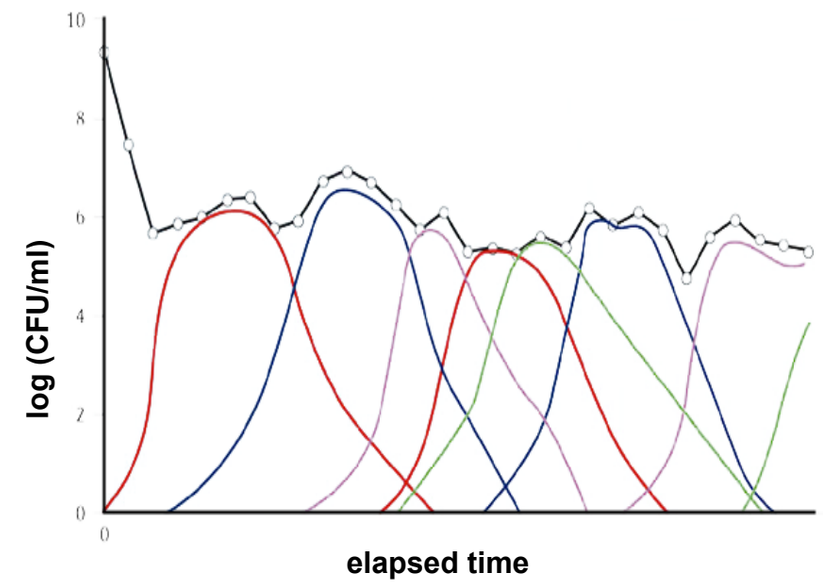
$$\hat{p}_d^1 = 1$$

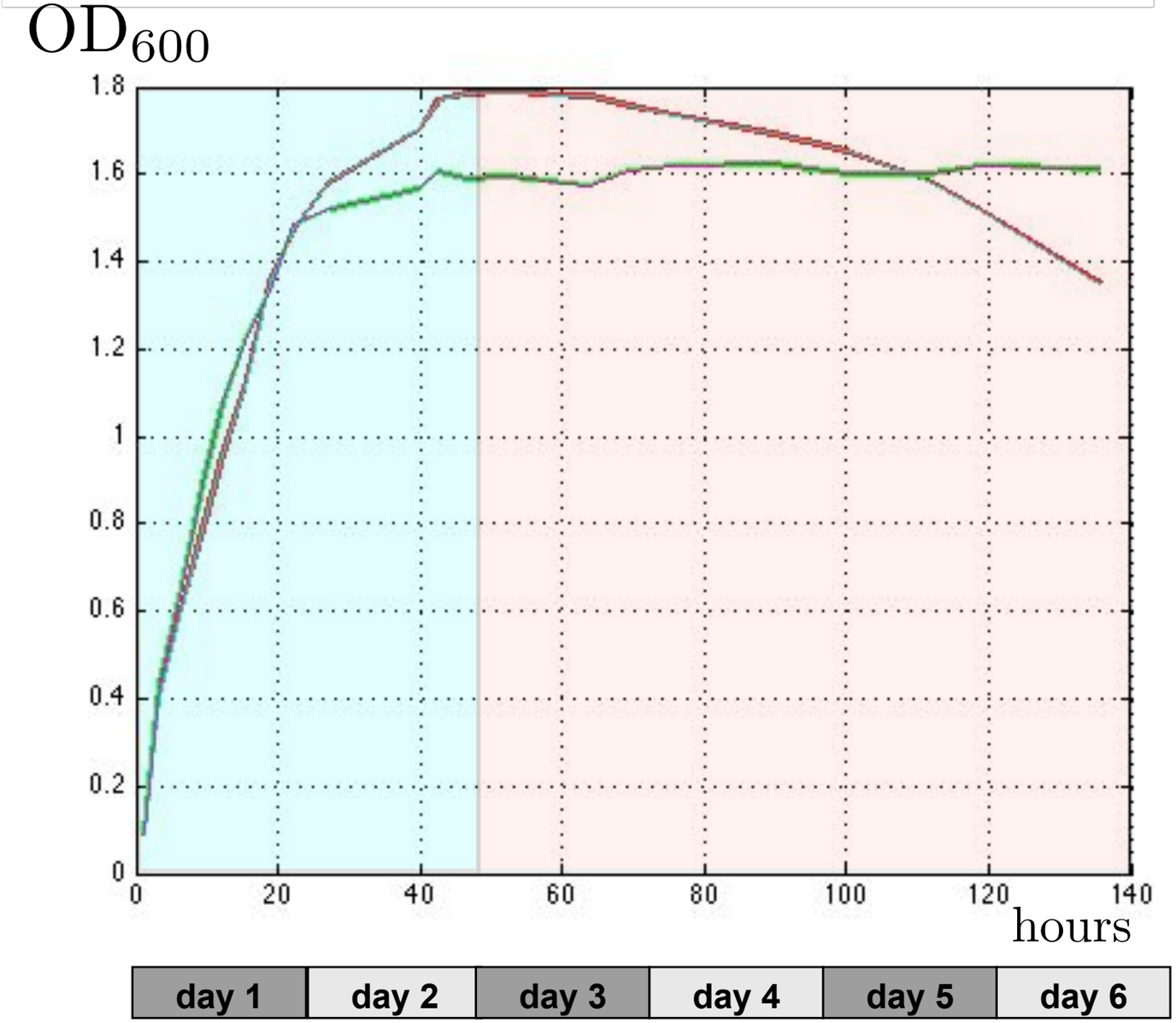
$$\hat{p}_d^{\text{mix}} = \left(1 - \frac{P - S}{T - R}\right)^{-1}$$



GASP mutants

emerge in the stationary phase





Sustainable persistence for WT

$$R > P$$

$$\dot{\phi} = r\phi(1-\phi)$$

Tragedy of the commons for GASP

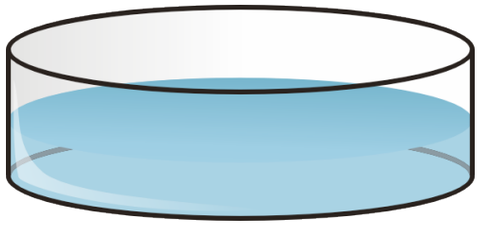
Genetics, Vol. 158, 519-526, June 2001, Copyright © 2001

Evolutionary Cheating in *Escherichia coli* Stationary Phase Cultures

GENETICS

Marin Vulić[a] and Roberto Kolter[a]

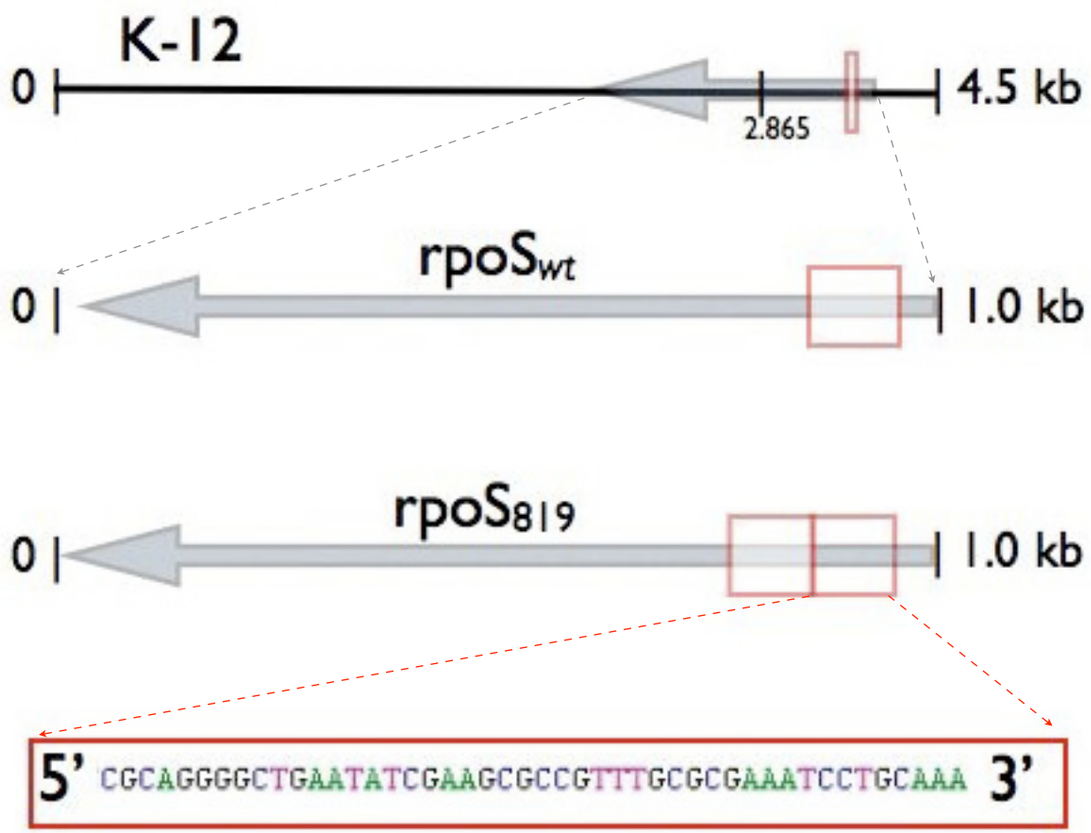
[a] Department of Microbiology and Molecular Genetics, Harvard Medical School, Boston, Massachusetts



$\Delta t = \text{days}$

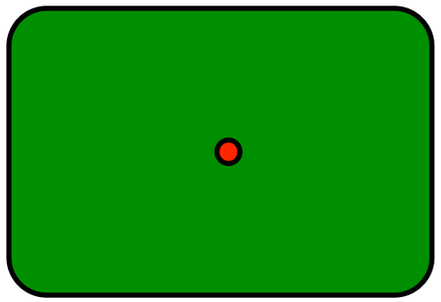
$$\begin{pmatrix} R & S \\ T & P \end{pmatrix} = \begin{pmatrix} 1 & 1-s_1 \\ 1+s_2 & 1-c \end{pmatrix}$$

$$\left.\frac{\Delta N_i}{\Delta t^*}\right|_{t^*} = f_i(p_j^{t_0}) = m_i \cdot p_j^{t_0} + A_i$$



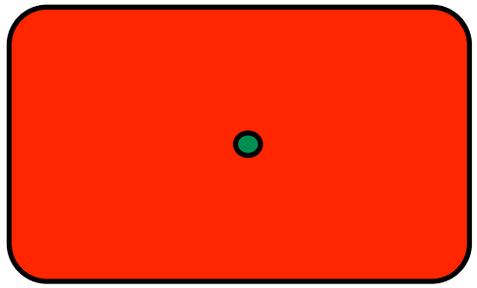
$$\Delta f = (1 - p_d) \cdot (T - R) + p_d \cdot (P - S)$$

$$\frac{\dot{p_d}}{p_d} = \Delta f \cdot (1 - p_d)$$

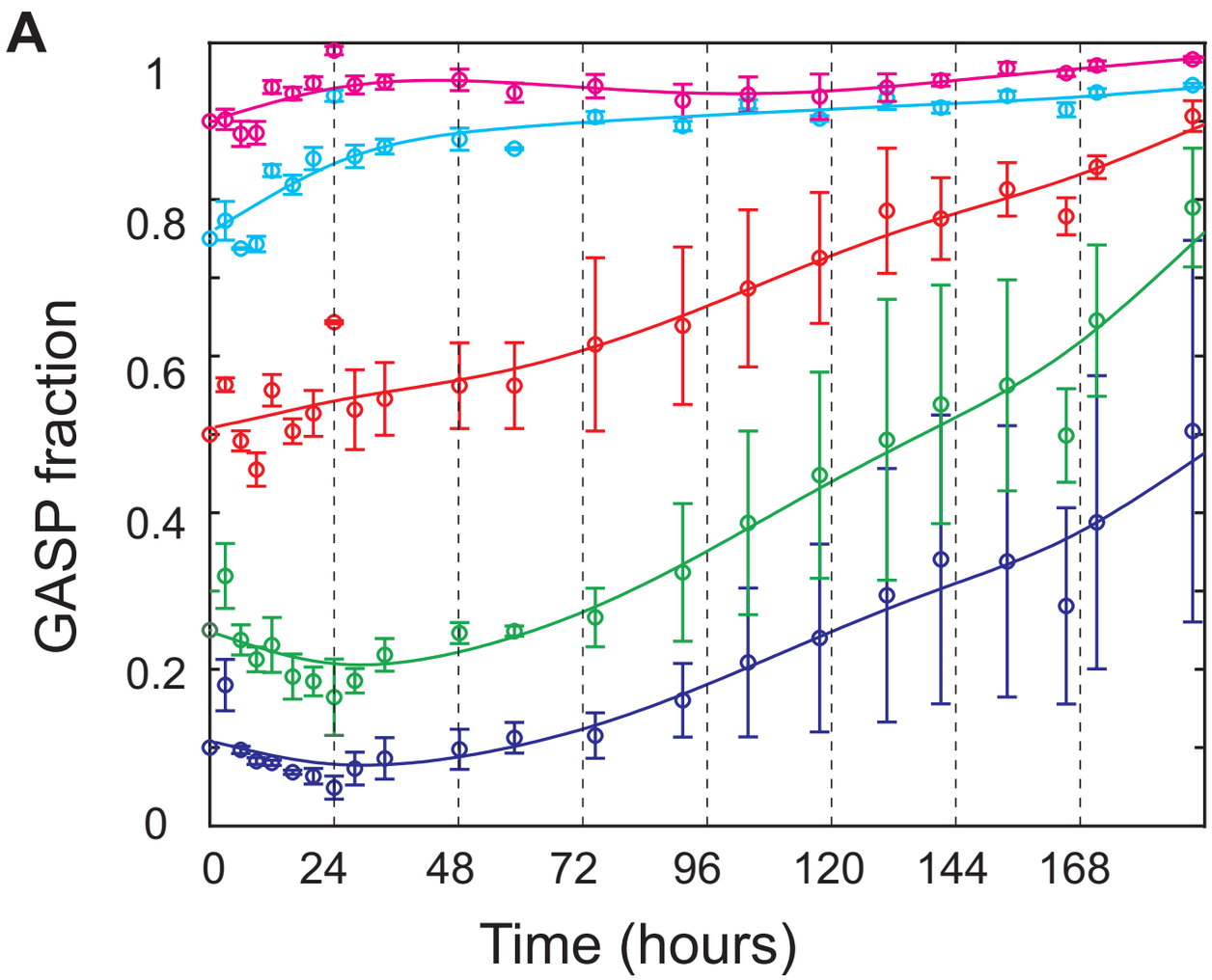


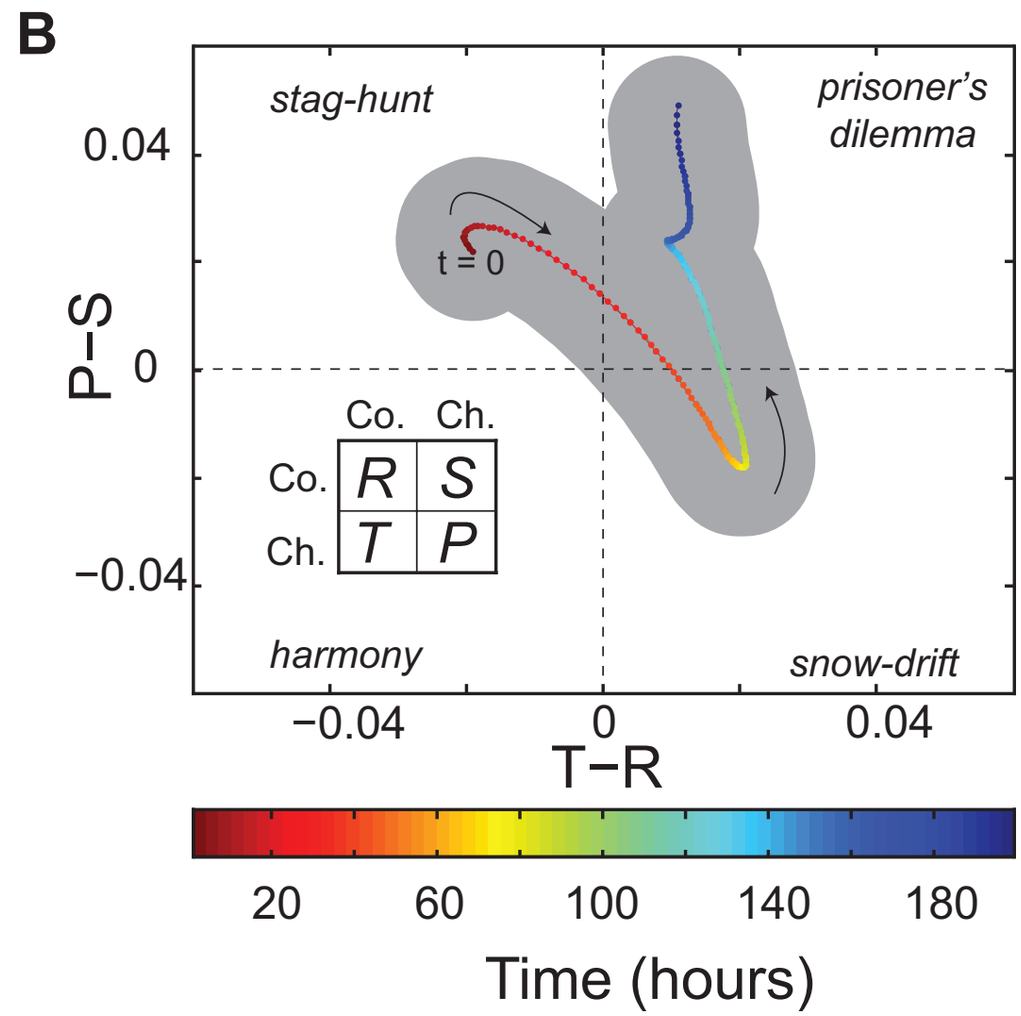
$$\left.\frac{\dot{p_d}}{p_d}\right|_{p_d \approx 0} \approx (T - R)$$

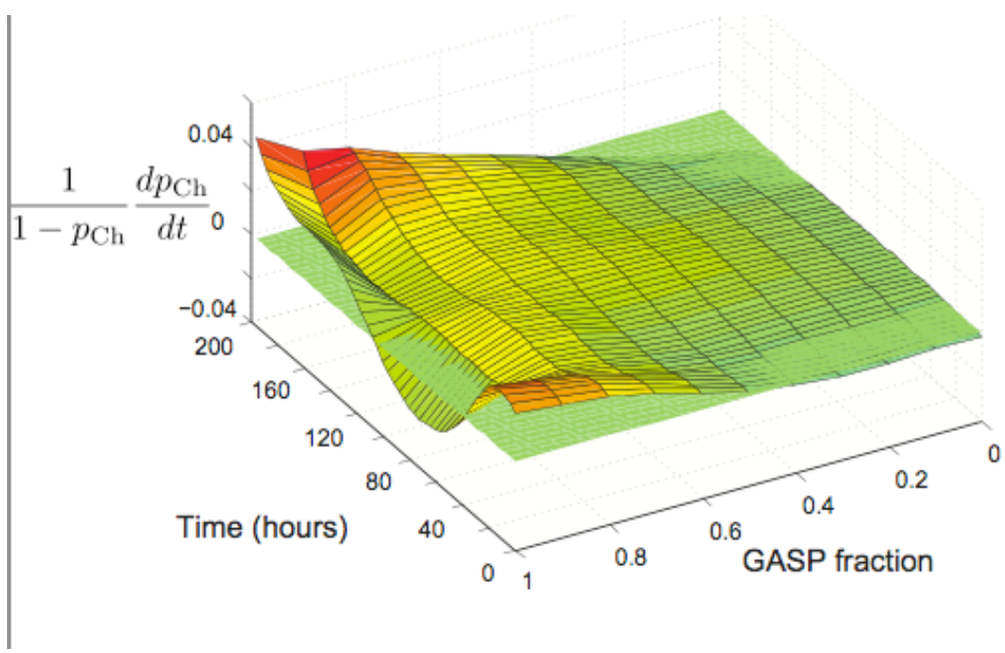
$$\frac{\dot{p_d}}{(1 - p_d)} = \Delta f \cdot p_d$$

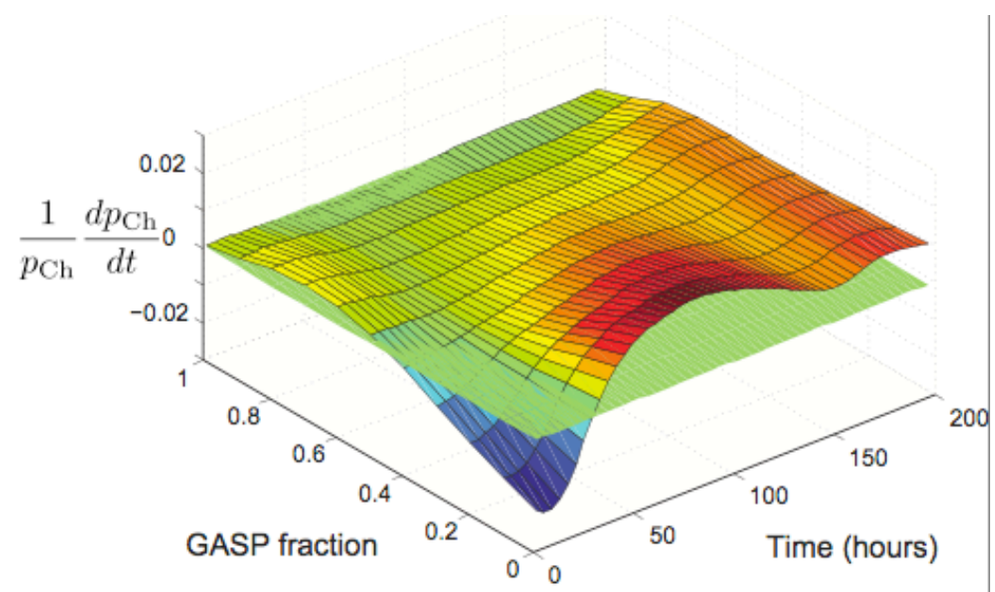


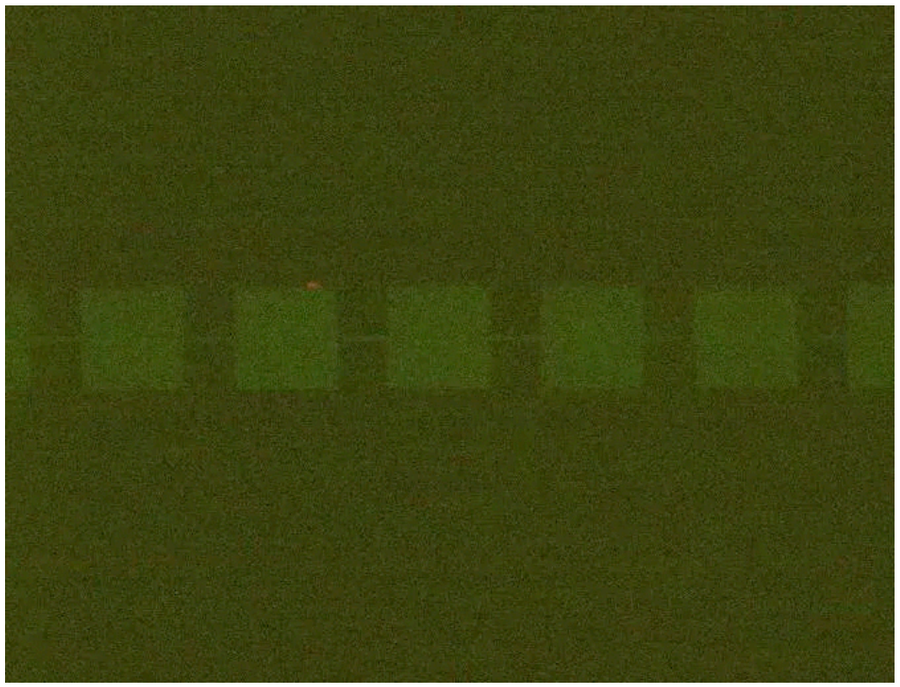
$$\left.\frac{\dot{p_d}}{(1 - p_d)}\right|_{p_d \approx 1} \approx (P - S)$$

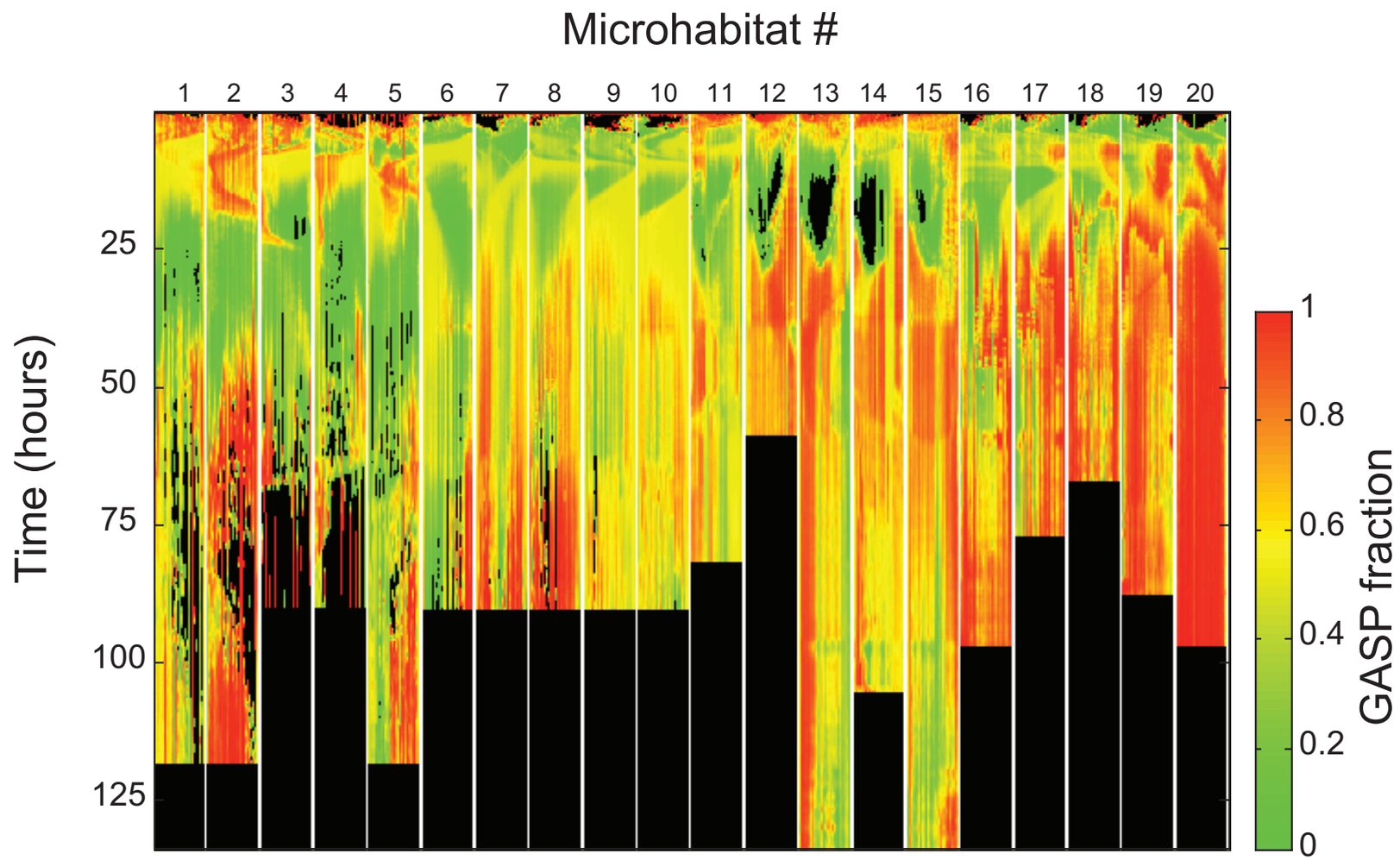

A
GASP fraction
Time (hours)
0
0.2
0.4
0.6
0.8
1
0
24
48
72
96
120
144
168

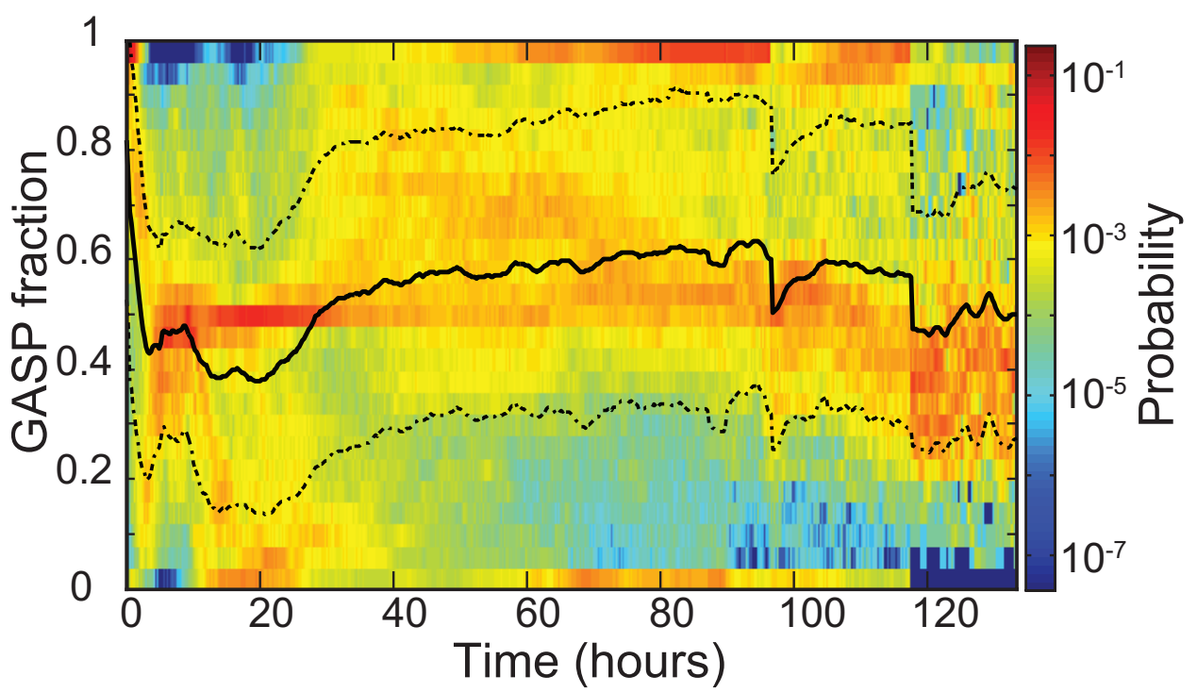

B
stag-hunt
prisoner's dilemma
harmony
snow-drift
t = 0
P−S
T−R
0.04
0
−0.04
Co. Ch.
Co. R S
Ch. T P
20
60
100
140
180
Time (hours)

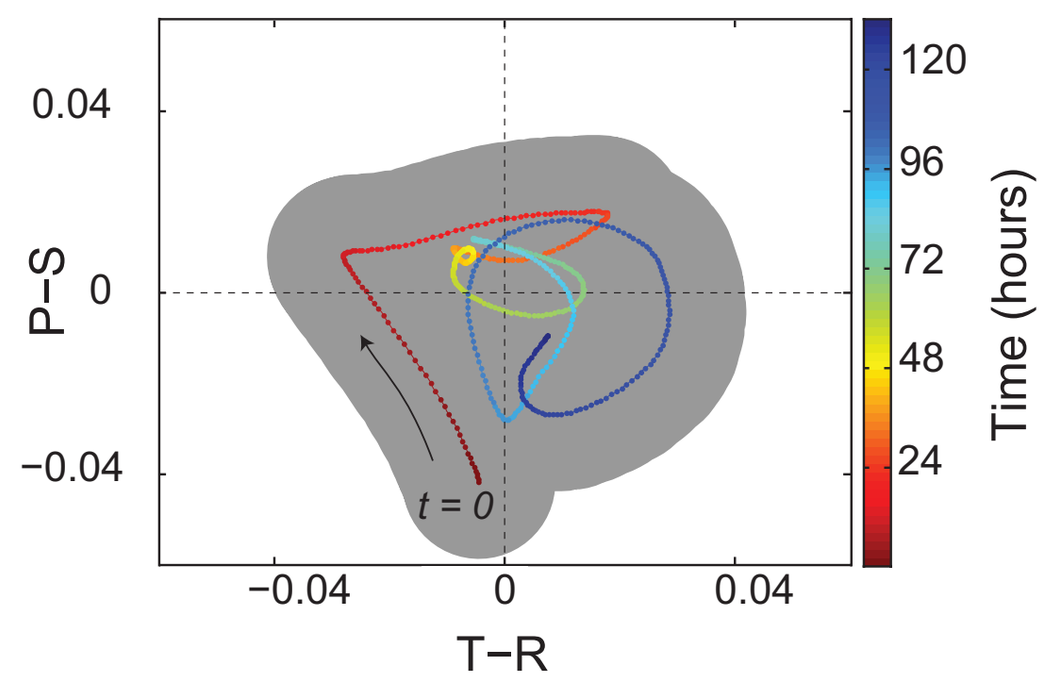

$\frac{1}{1-p_{\mathrm{Ch}}}\frac{dp_{\mathrm{Ch}}}{dt}$
0.04
0
−0.04
Time (hours)
200
160
120
80
40
0
GASP fraction
1
0.8
0.6
0.4
0.2
0


$\frac{1}{p_{\mathrm{Ch}}}\frac{dp_{\mathrm{Ch}}}{dt}$
0.02
0
−0.02
GASP fraction
1
0.8
0.6
0.4
0.2
0
Time (hours)
0
50
100
150
200




Microhabitat #
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Time (hours)
25
50
75
100
125
GASP fraction
1
0.8
0.6
0.4
0.2
0


A
GASP fraction
1
0.8
0.6
0.4
0.2
0
0 20 40 60 80 100 120
Time (hours)
Probability
10^{-1}
10^{-3}
10^{-5}
10^{-7}


B
P−S
0.04
0
−0.04
−0.04 0 0.04
T−R
t = 0
Time (hours)
120
96
72
48
24

article
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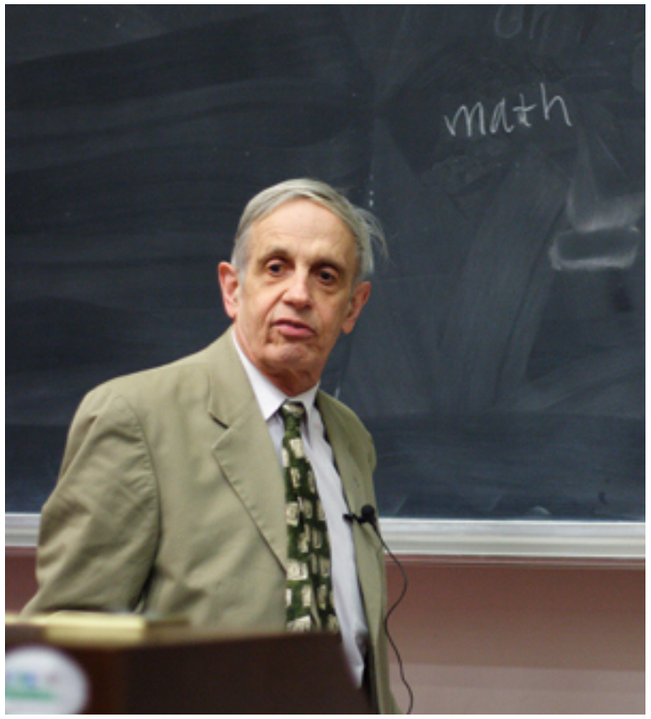
Nash equilibrium



Monomorphic evolution (meso-evolution)

Invasion fitness and selection gradient

$$\frac{n'}{n} = b - n \cdot d$$

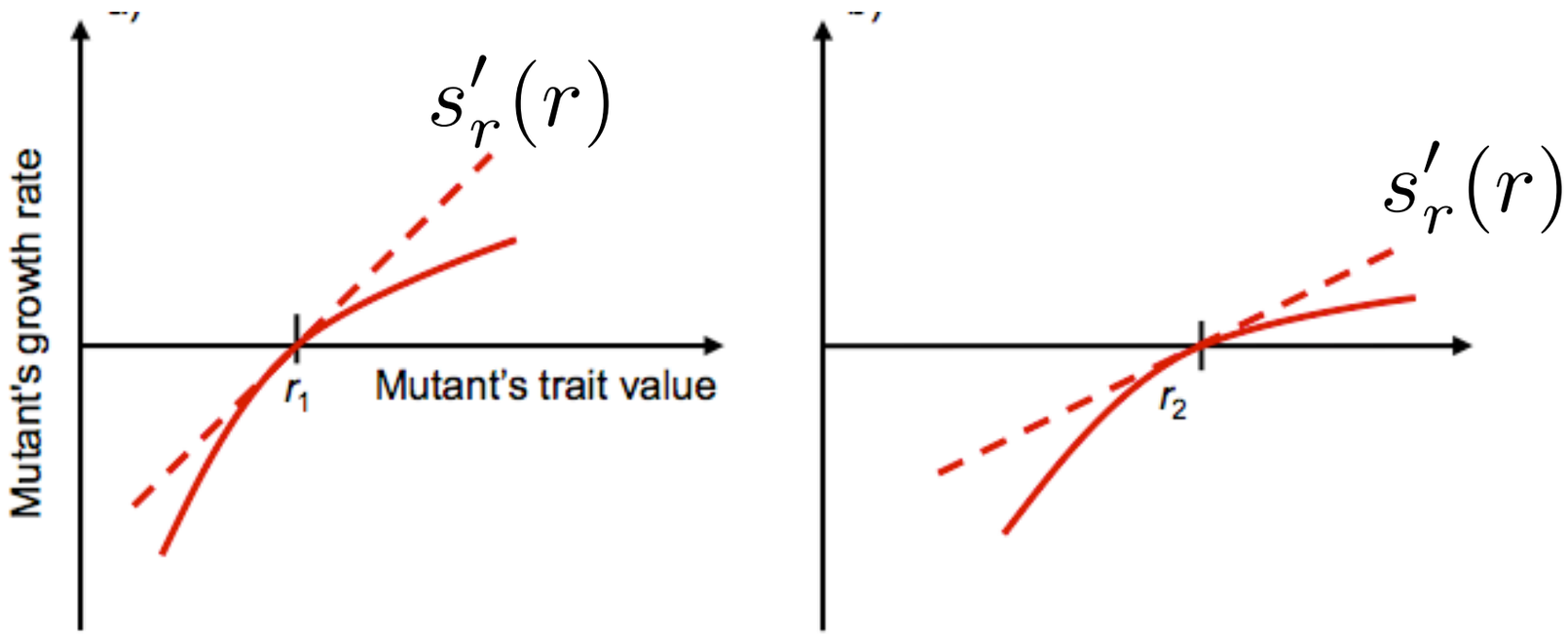
$S_r(m)$:= per capita growth rate

of a rare mutant with trait value m

in the context of a resident population of trait value r

fitness landscape changes after invasion

$s_r(m)$



$$s_r(m) \approx s'_r(r) \cdot (m - r)$$

$m > r$?

$r_1 \to m_1$

$r_2 = m_1 \to m_2$

$S_r(m)$ vanishes exactly at $m = r$

Deriving Invasion fitness and selection gradient for a demographic model

$$n'(t) = n(t) \cdot [b - n(t) \cdot d]$$

per capita growth rate

$s_r(m)$

$$\frac{n'}{n} = b - n \cdot d$$

long-term equilibrium

$$0 = n^* \cdot [b - n^* \cdot d]$$

$$n^* = b/d$$

$$n_r'(t) = n_r(t) \cdot [r - n(t) \cdot d]$$

$$n_m'(t) = n_m(t) \cdot [m - n(t) \cdot d]$$

$$n = n_r + n_m$$

of a rare mutant with trait value m

in the context of a resident population of trait value r

$$n_m(t) \to 0$$

$$n(t) \approx n_r(t) \approx n_r^* = r/d$$

$$n_r'(t) = n_r(t) \cdot [r - n(t) \cdot d]$$

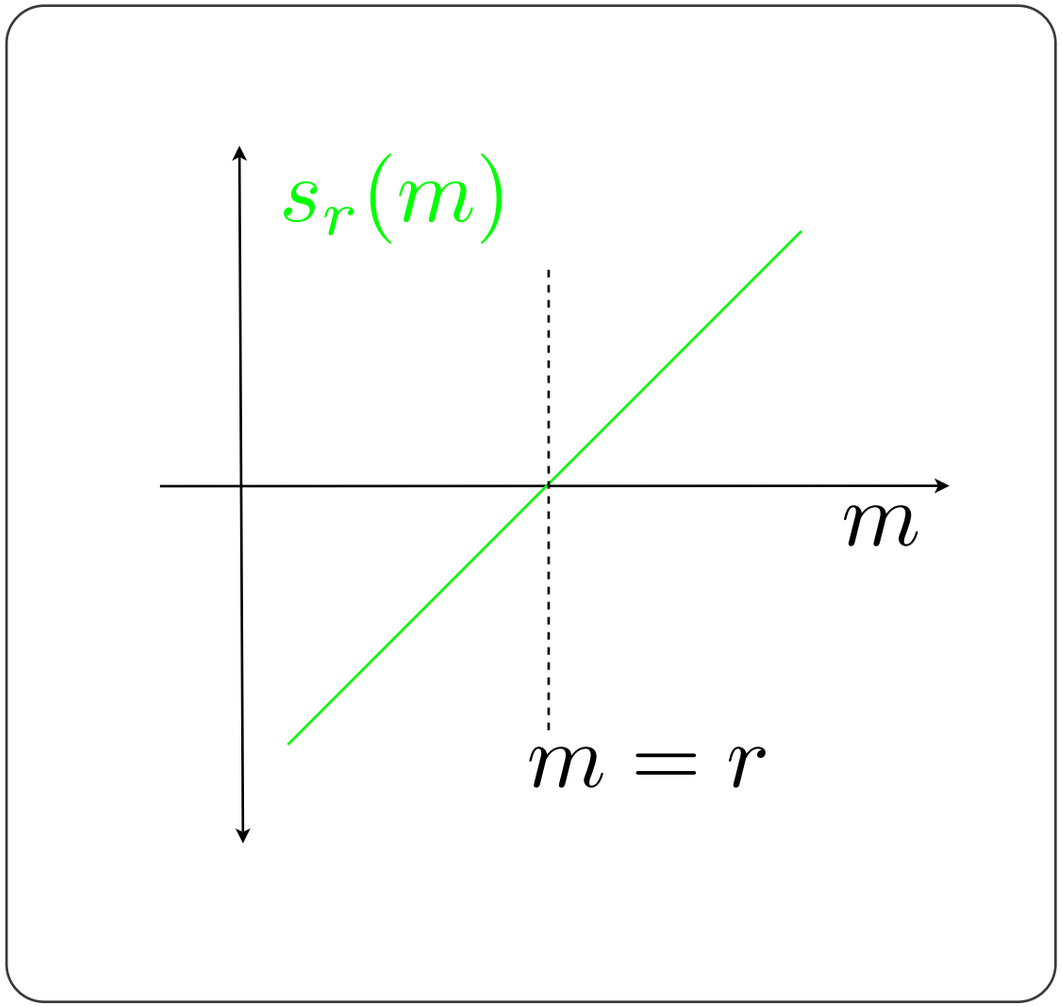
$$n_m'(t) = n_m(t) \cdot [m - n(t) \cdot d]$$

$$n = n_r + n_m$$

$$n_m(t) \to 0$$

$$n(t) \approx n_r(t) \approx n_r^* = r/d$$

$$s_r(m) = \frac{n_m'(t)}{n_m(t)} = m - n_r^* \cdot d$$



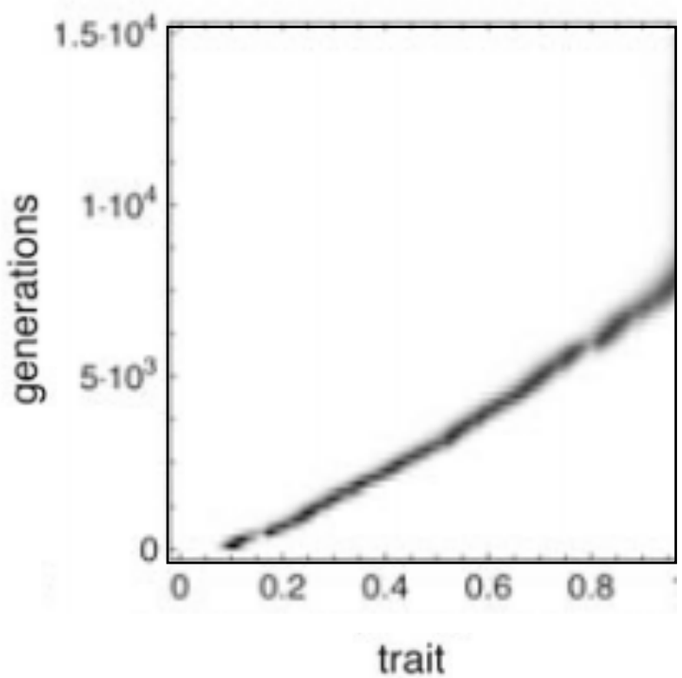
$$s_r(m) = m - r$$

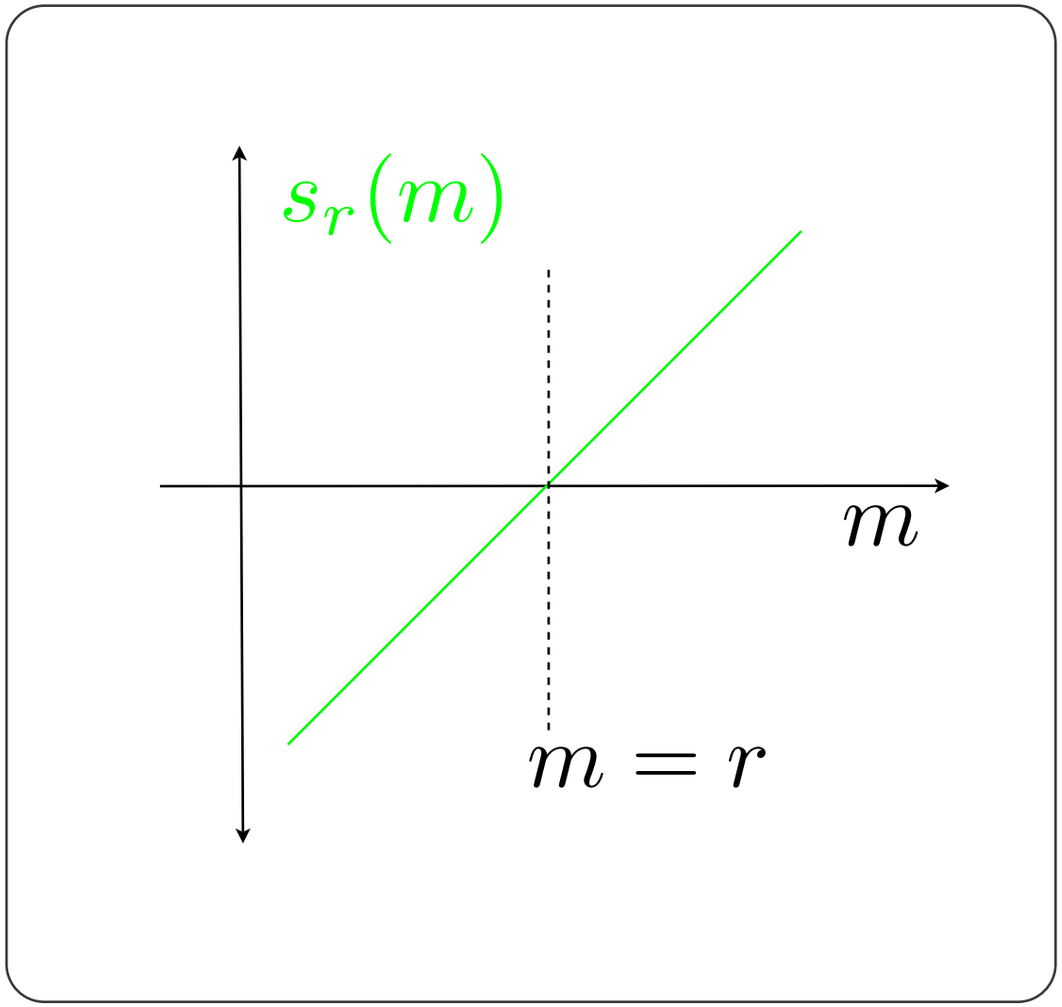
$$s_r(r) = 0$$

$$\left.\frac{d}{dm}\right|_{m=r} s_r(m) = s_r'(r) = 1$$

$$s_r'(r) = 1$$

directional selection





$$s_r(r) = 0$$

$$s_r'(r) = 1$$

$c(r)$ cost function

$$\frac{n'}{n} = b - c(b) - d \cdot n$$

at equilibrium

$$n^* = \frac{b - c(b)}{d}$$

$c(r)$ cost function

$$n_r'(t) = n_r(t) \cdot [r - c(r) - n(t) \cdot d]$$

$$n_m'(t) = n_m(t) \cdot [m - c(m) - n(t) \cdot d]$$

$$n = n_r + n_m$$

invasion fitness

$$s_r(m) = \frac{n_m'(t)}{n_m(t)} = m - c(m) - r + c(r)$$

$$s_r(r) = 0$$

$$s_r'(r) = 1 - c'(r)$$

$$s_r'(r) = 0 \text{ if } c'(r) = 1$$

selection gradient

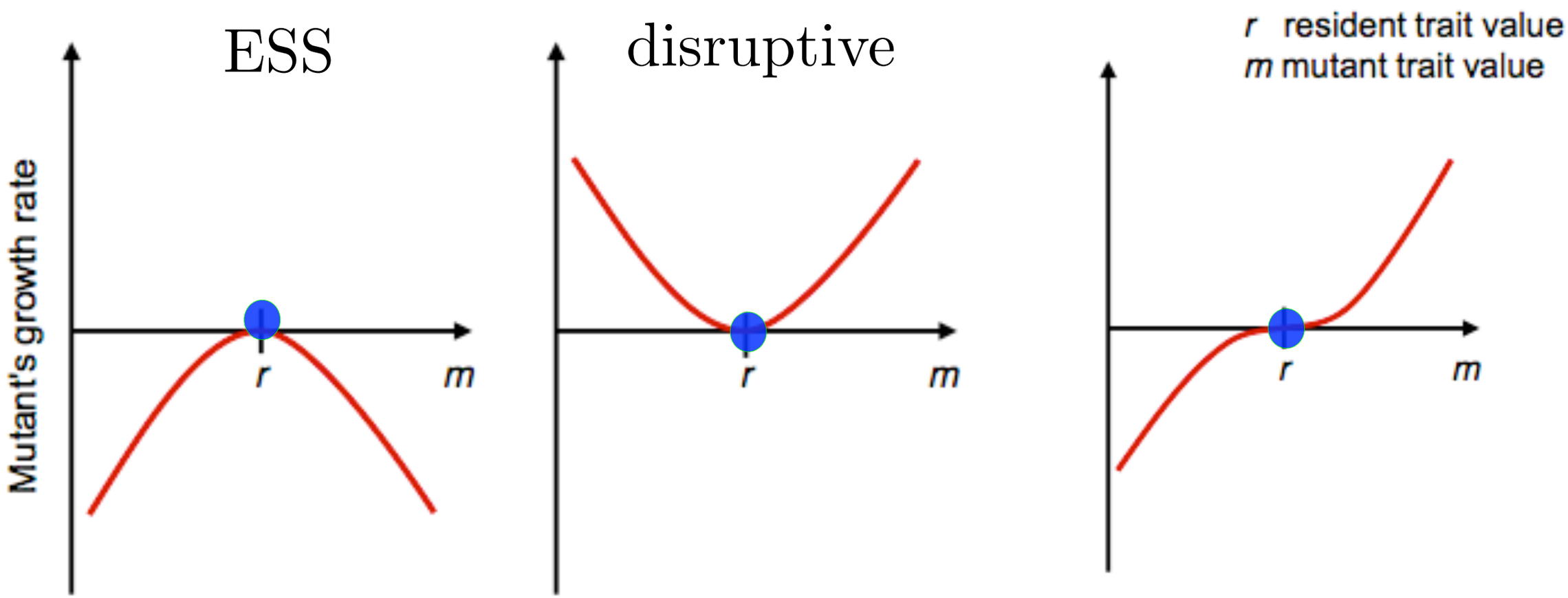
Evolutionary Singular Strategy $s'_r(r) = 0$?

$s_r(m)$

& the fitness landscape

r^*

$s'_{r^*}(r^*) = 0$



branching

Max

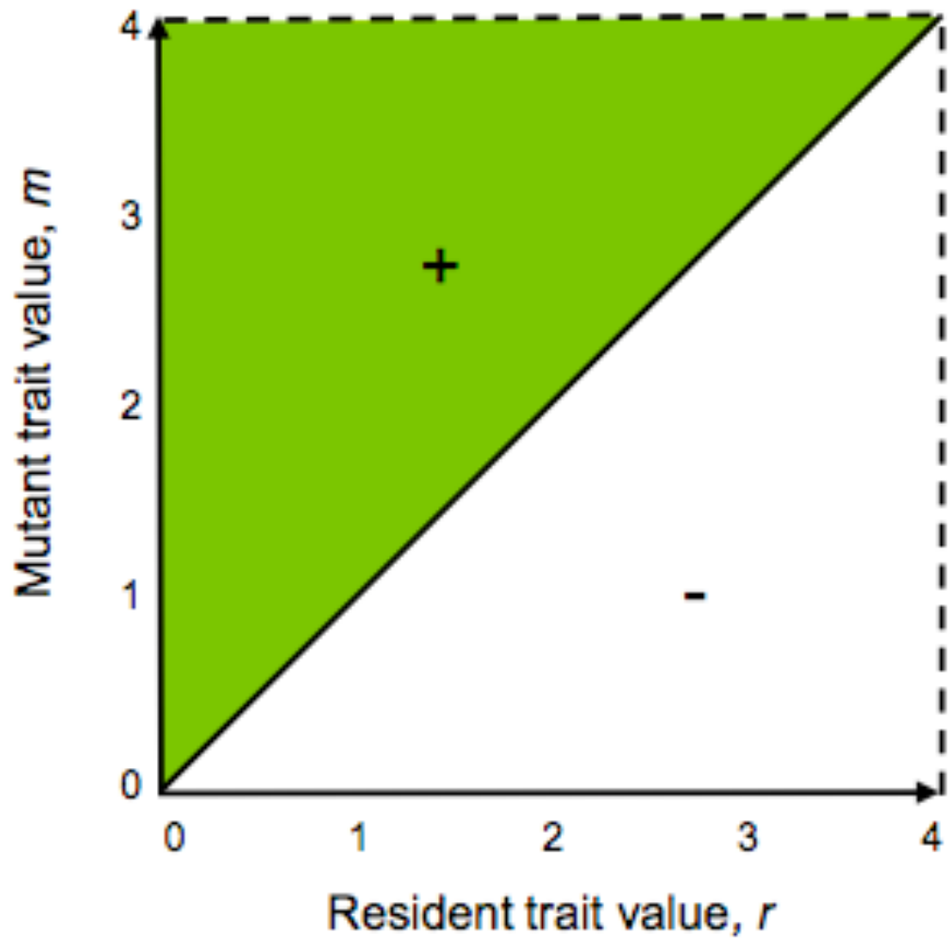
Min

n/a

Pairwise Invasibility Plots (PIPs)

$$n = n_r + n_m$$

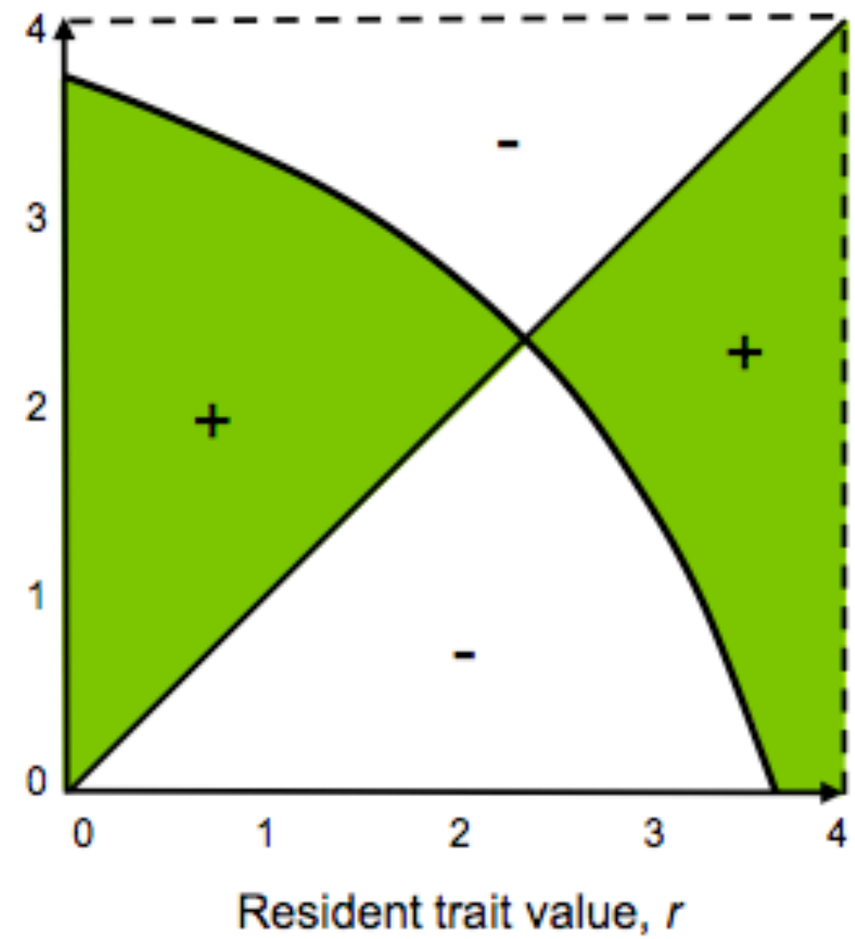
$s_r(m)$ $\quad$ sign $[f(r,m) = s_r(m)]$



$$n'_r(t) = n_r(t) \cdot [r - n(t) \cdot d]$$

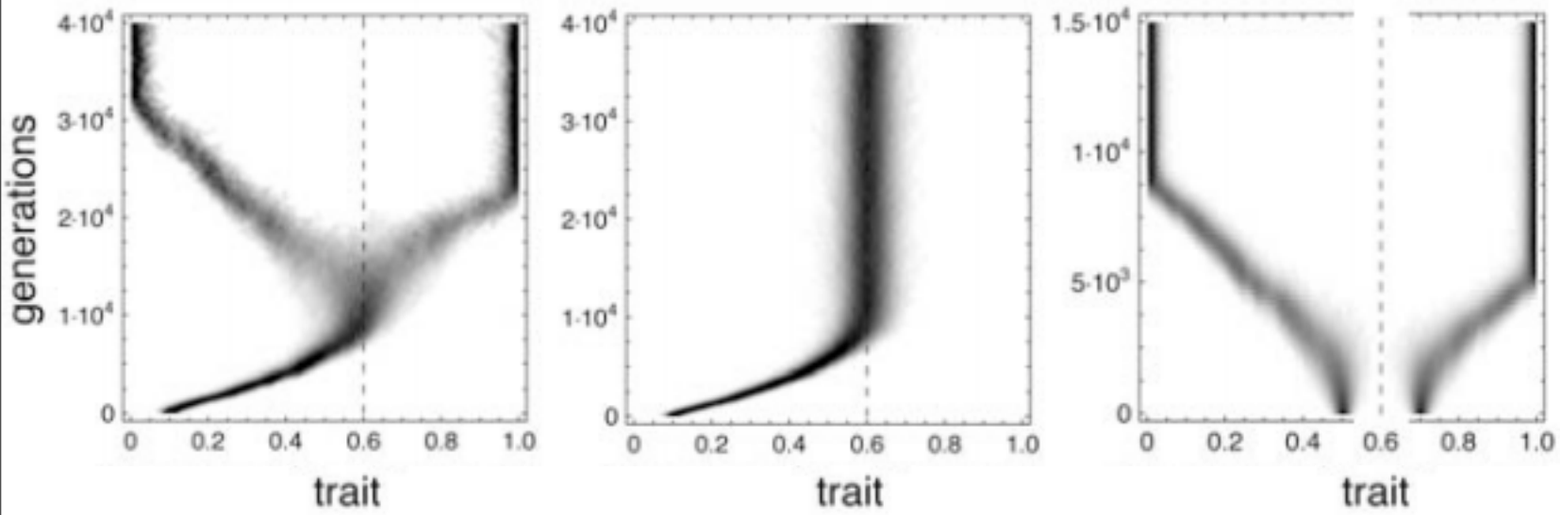
$$n'_m(t) = n_m(t) \cdot [m - n(t) \cdot d]$$

$c(r) = 10^{-1} \cdot e^r$

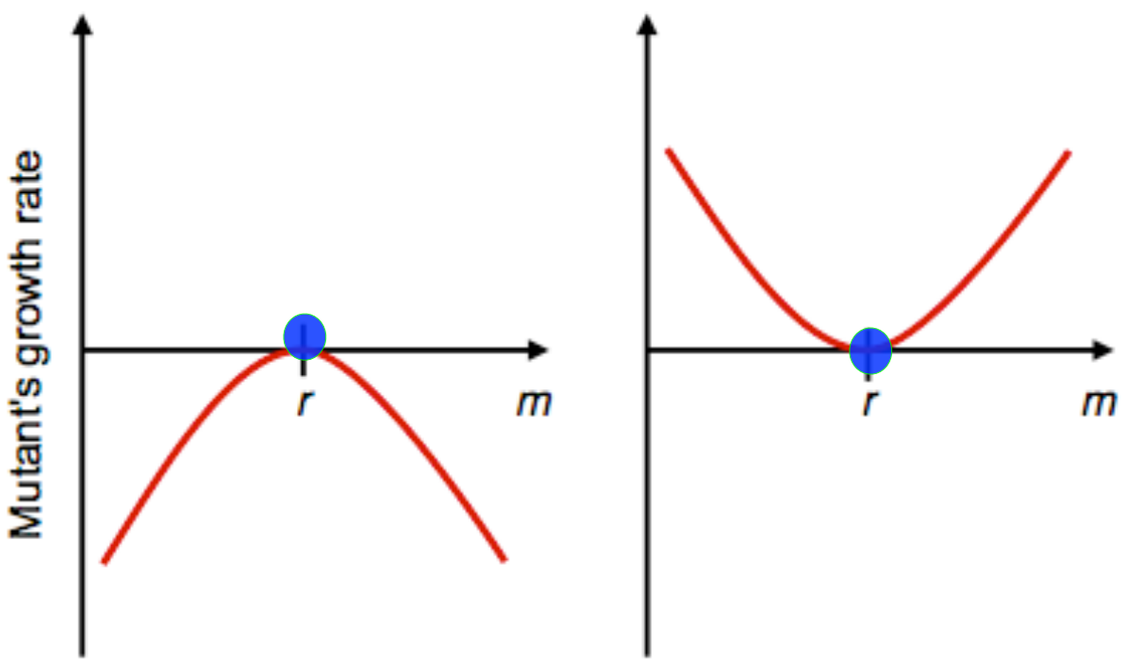


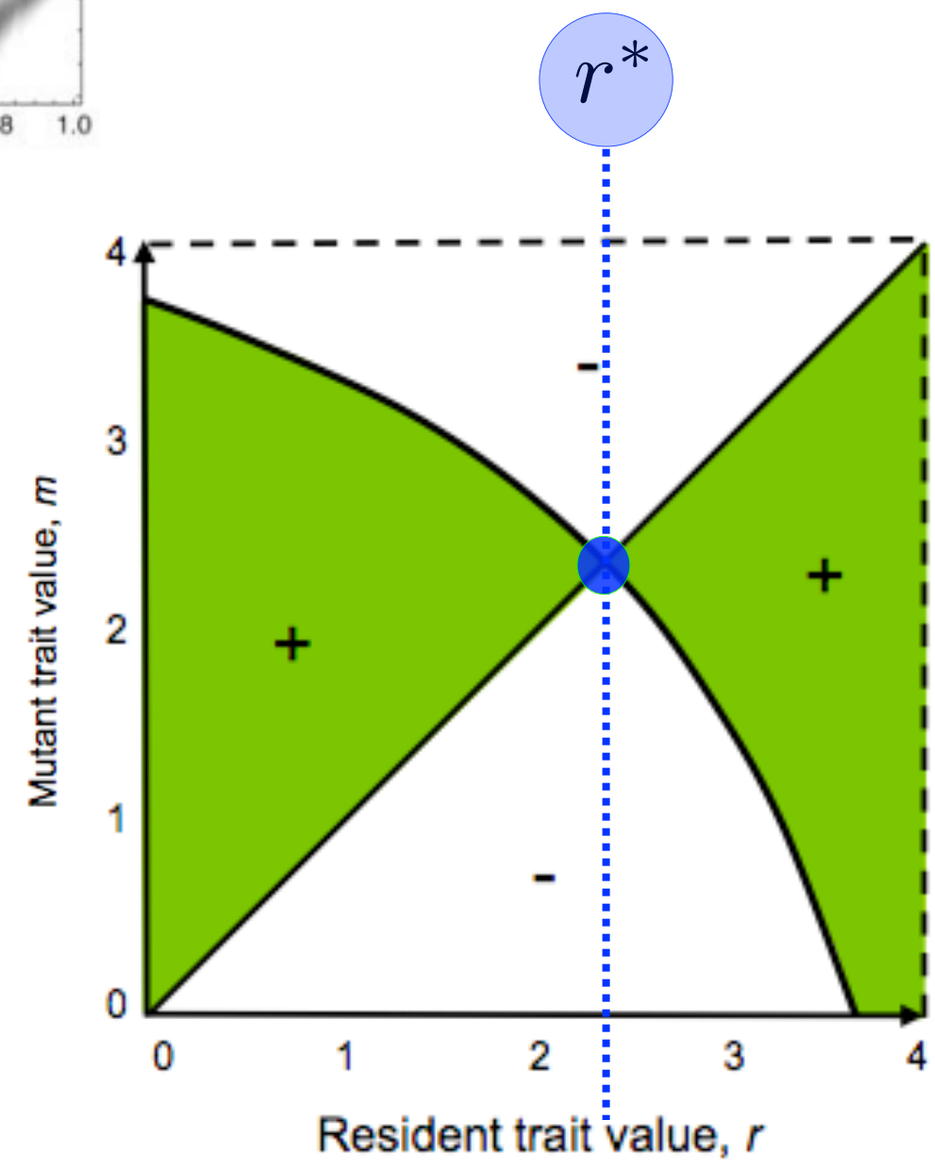
$$n'_r(t) = n_r(t) \cdot [r - c(r) - n(t) \cdot d]$$

$$n'_m(t) = n_m(t) \cdot [m - c(m) - n(t) \cdot d]$$



$$n = n_r + n_m$$





$$n_r'(t) = n_r(t) \cdot [r - c(r) - n(t) \cdot d]$$

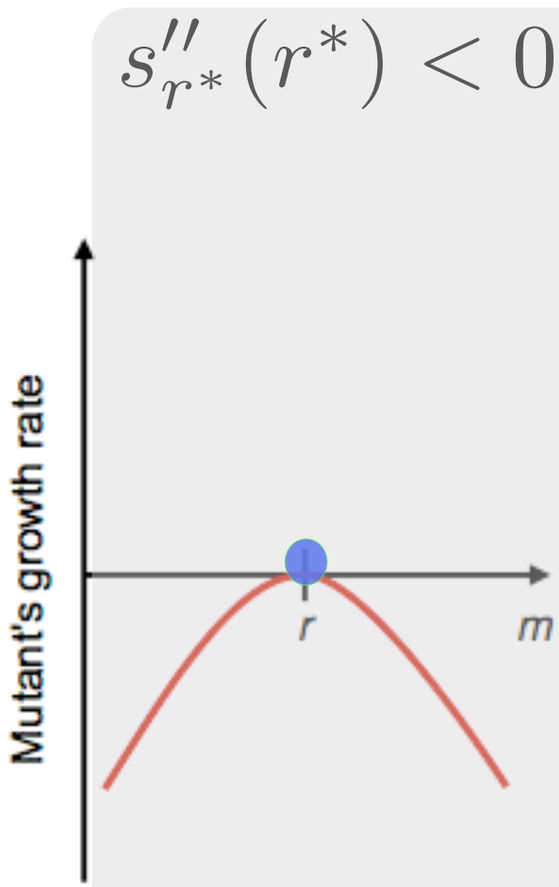
$$n_m'(t) = n_m(t) \cdot [m - c(m) - n(t) \cdot d]$$

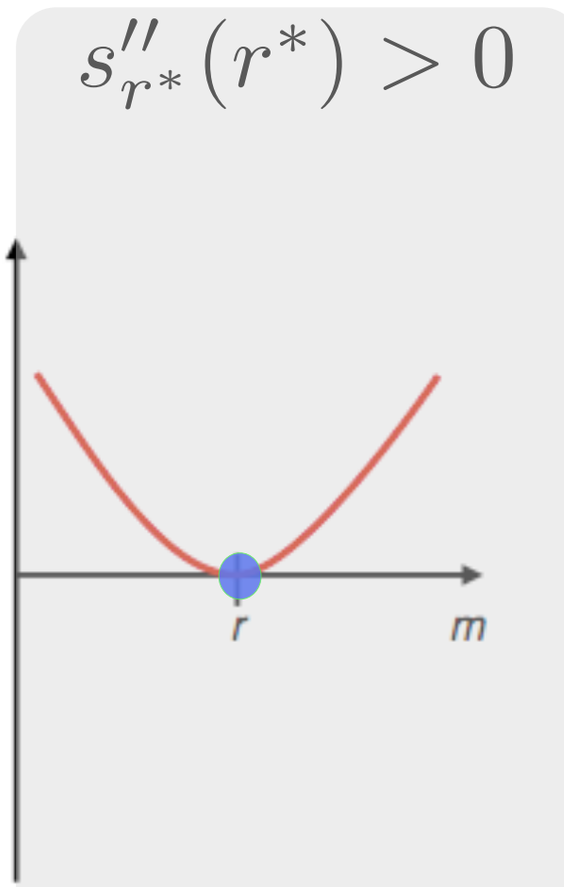
Evolutionary Stability Analysis

r^* can be classified

$s''_{r^*}(r^*) < 0 \quad ?$

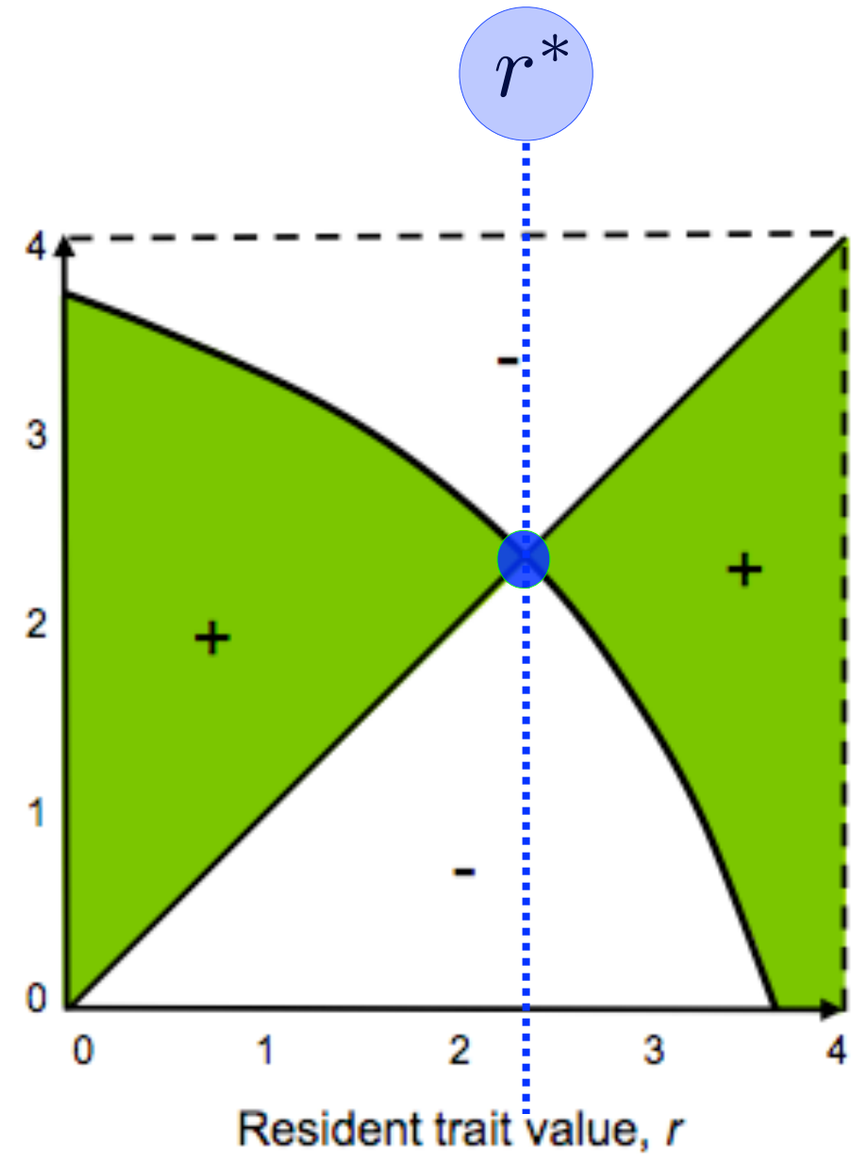
ESS





Max

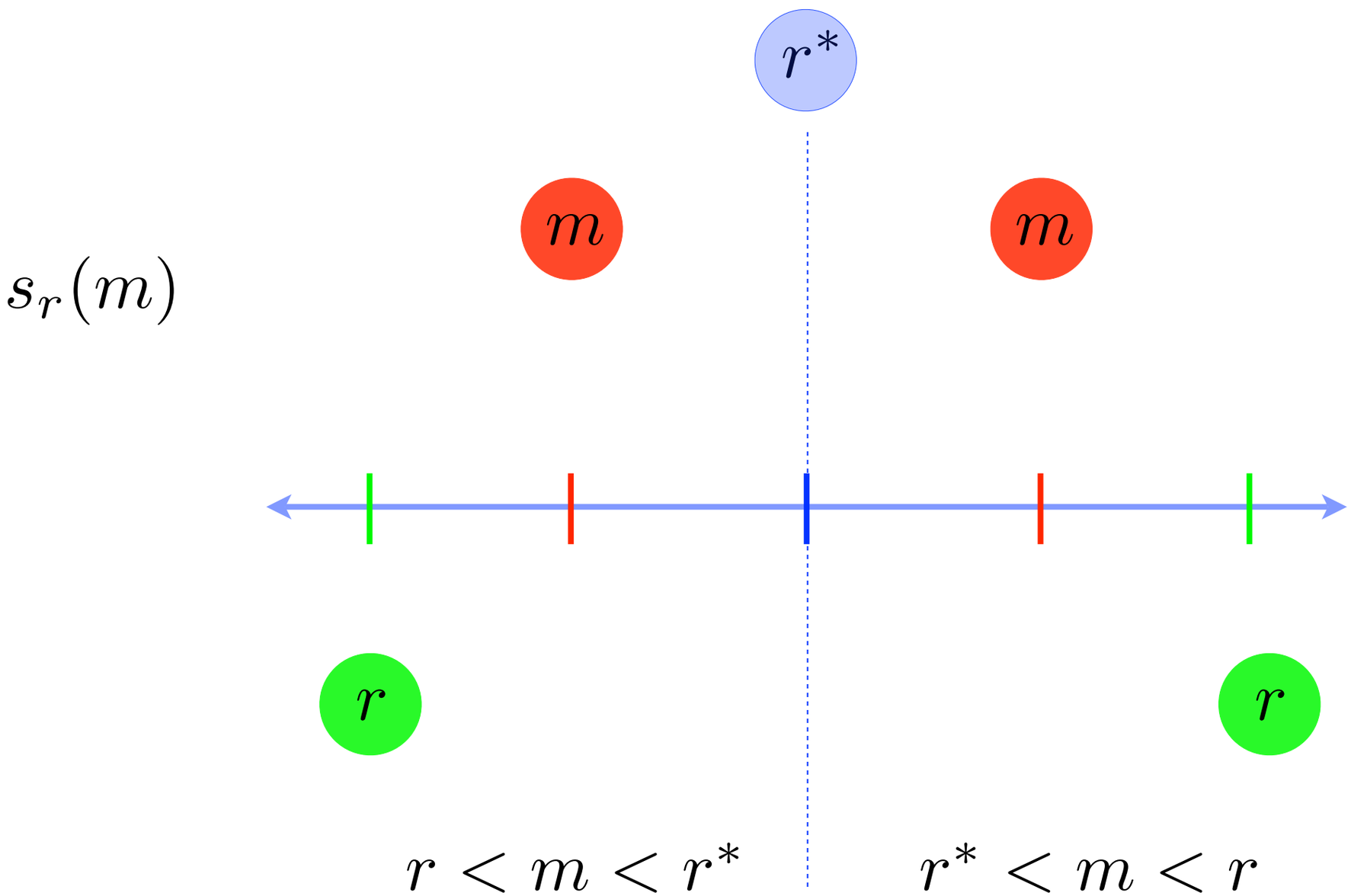
Min



Convergence stability if gradient points towards r^*

$$\frac{d}{dr} s_r'(r)\Big|_{r=r^*} < 0$$

$$\frac{\partial^2 s}{\partial r^2}\Big|_{r=m=r^*} > \frac{\partial^2 s}{\partial m^2}\Big|_{r=m=r^*}$$

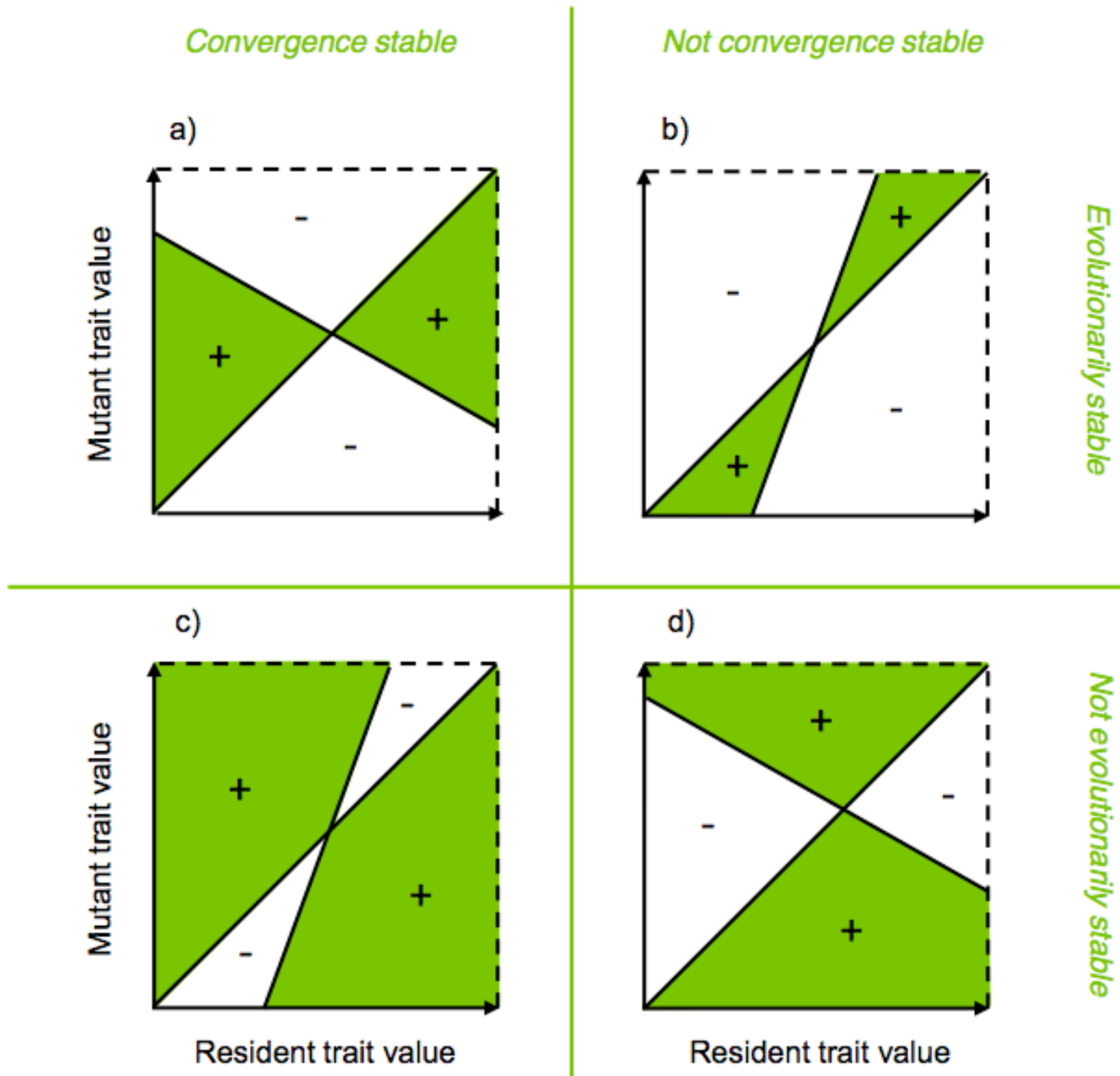


$$\left.\frac{d}{dr} s_r'(r)\right|_{r=r^*} < 0$$

attractor repeller

ESS

disruptive



$$\frac{\partial^2 s_r(m)}{\partial m^2} < 0$$

$$s_{r^*}''(r^*) < 0$$

$$\frac{\partial^2 s_r(m)}{\partial m^2} > 0$$

$$s_{r^*}''(r^*) > 0$$

Polymorphic Evolution

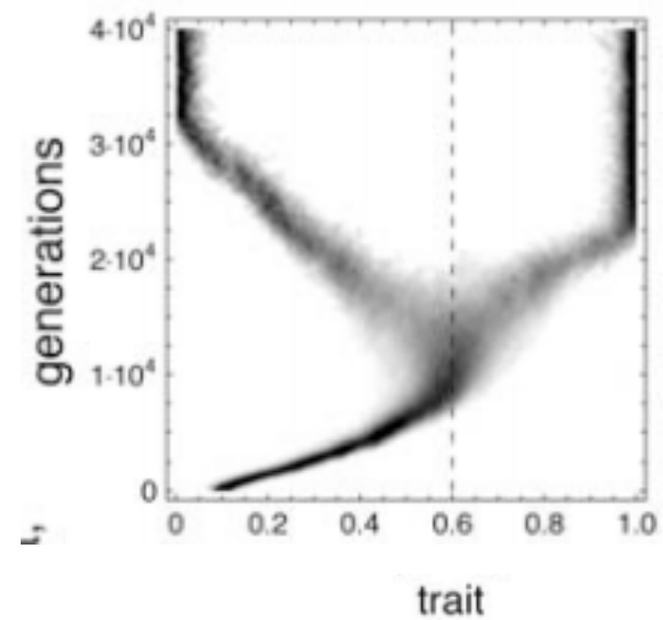
protected dimorphism

two resident

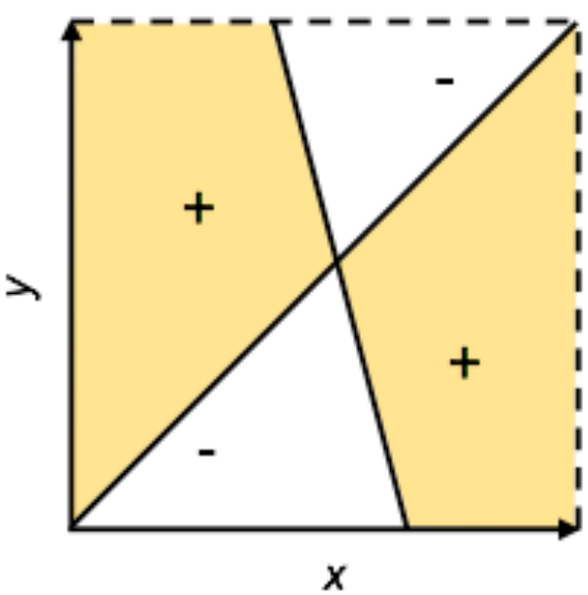
(r_1, r_2)

$s_{r_1}(r_2) > 0 \qquad s_{r_2}(r_1) > 0$

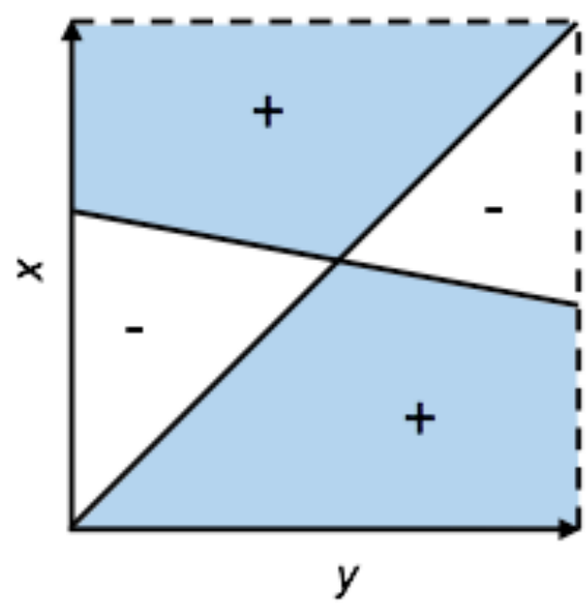
$s_{r_1,r_2}(m) \qquad s'_{r_1,r_2}(m)$



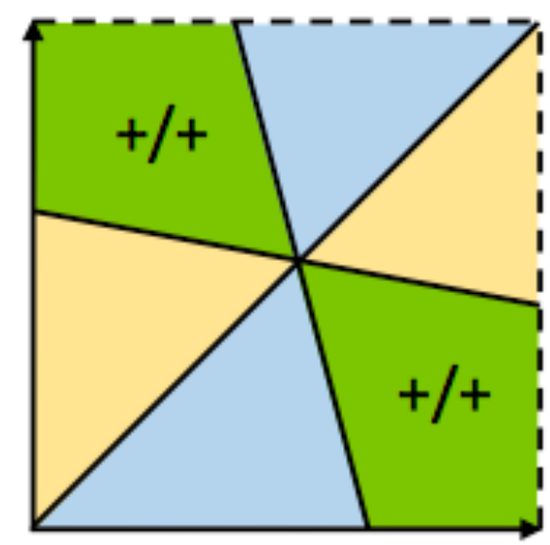
PIP Snow Drift



mirror



coexistence

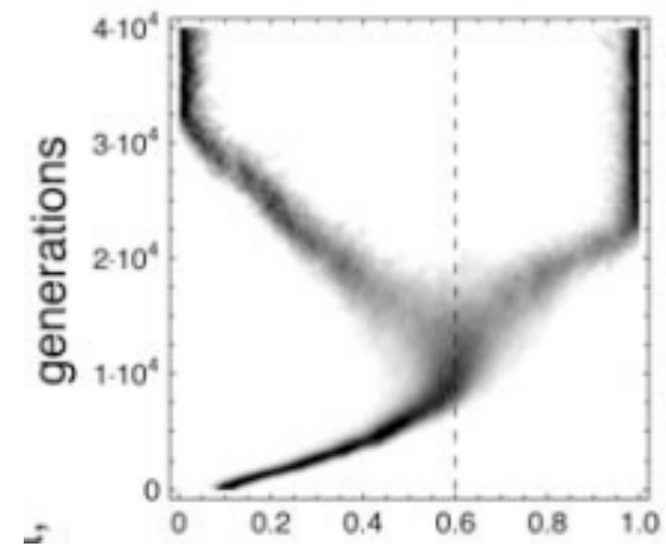


Polymorphic Evolution

protected dimorphism

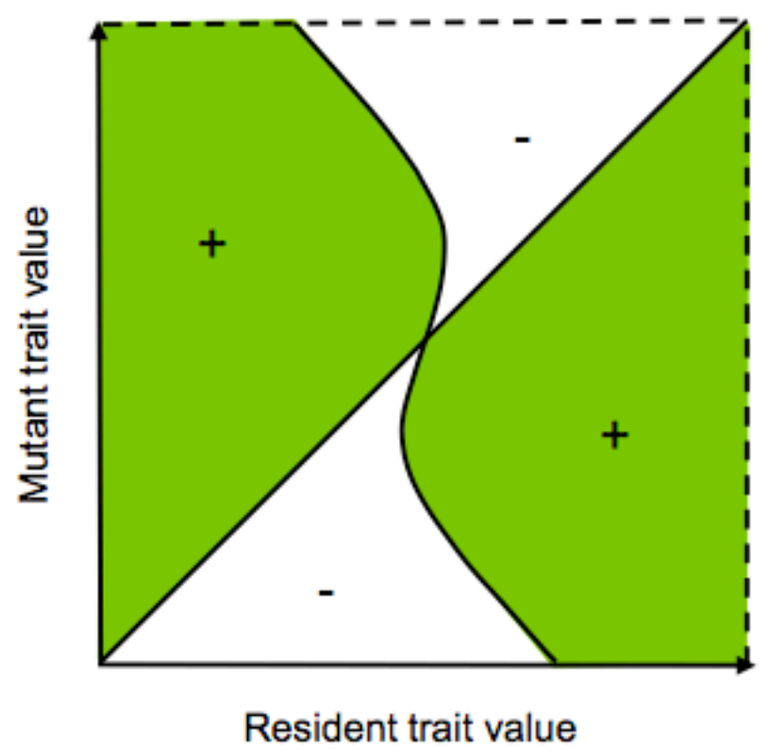
two resident

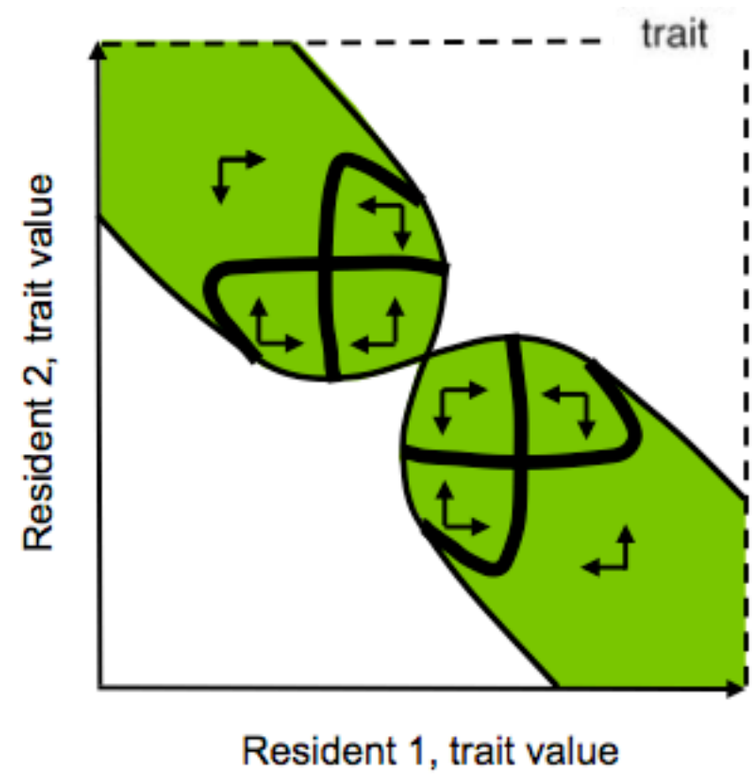
(r_1, r_2)



Trait Evolution Plots (TEP)

PIP

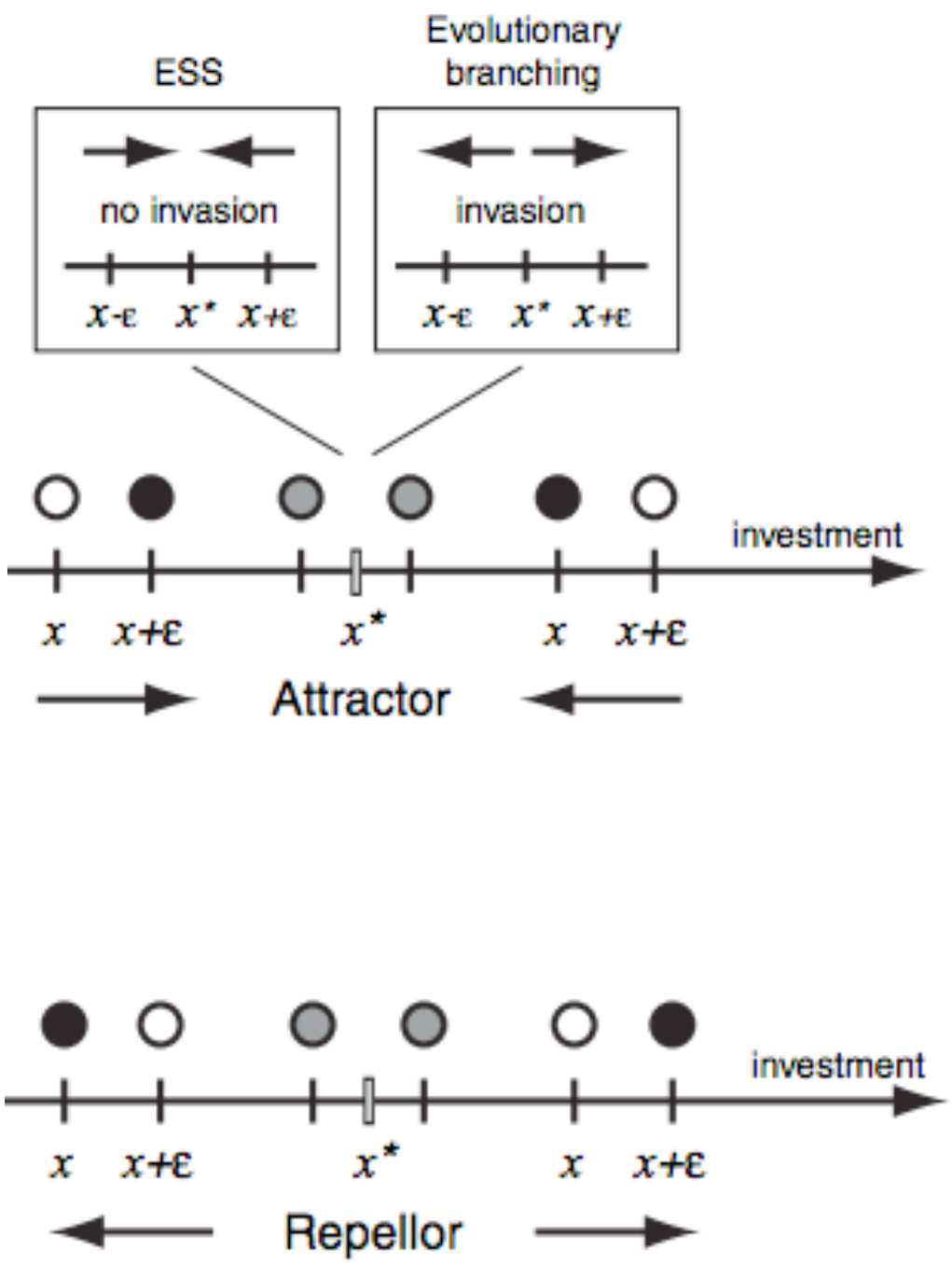


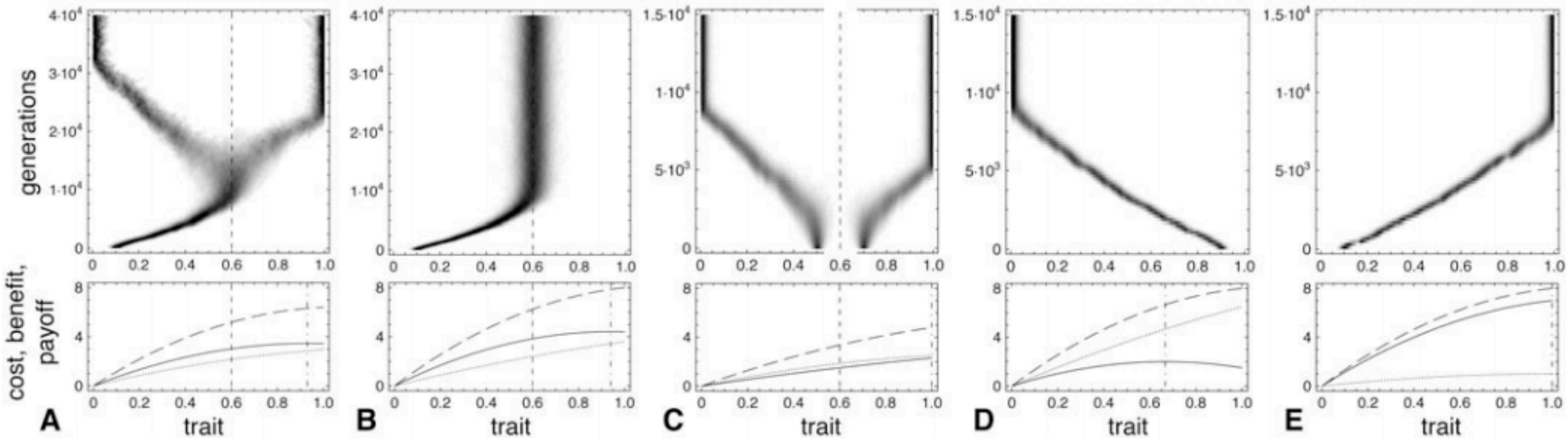


PIP Snow Drift

The Evolutionary Origin of Cooperators and Defectors

Michael Doebeli,[1*] Christoph Hauert,[1†] Timothy Killingback[2]





SD $P(x, y) = B(x + y) - C(x)$

$$B(0) = 0$$
$$C(0) = 0$$

$$B(x) = b_2 \cdot x^2 + b_1 \cdot x$$

$$C(x) = c_2 \cdot x^2 + c_1 \cdot x$$

$Q(x, y) = B(y) - C(x)$ PD

$$P(x, y) = B(x + y) - C(x)$$

$$B(x) = b_2 \cdot x^2 + b_1 \cdot x$$

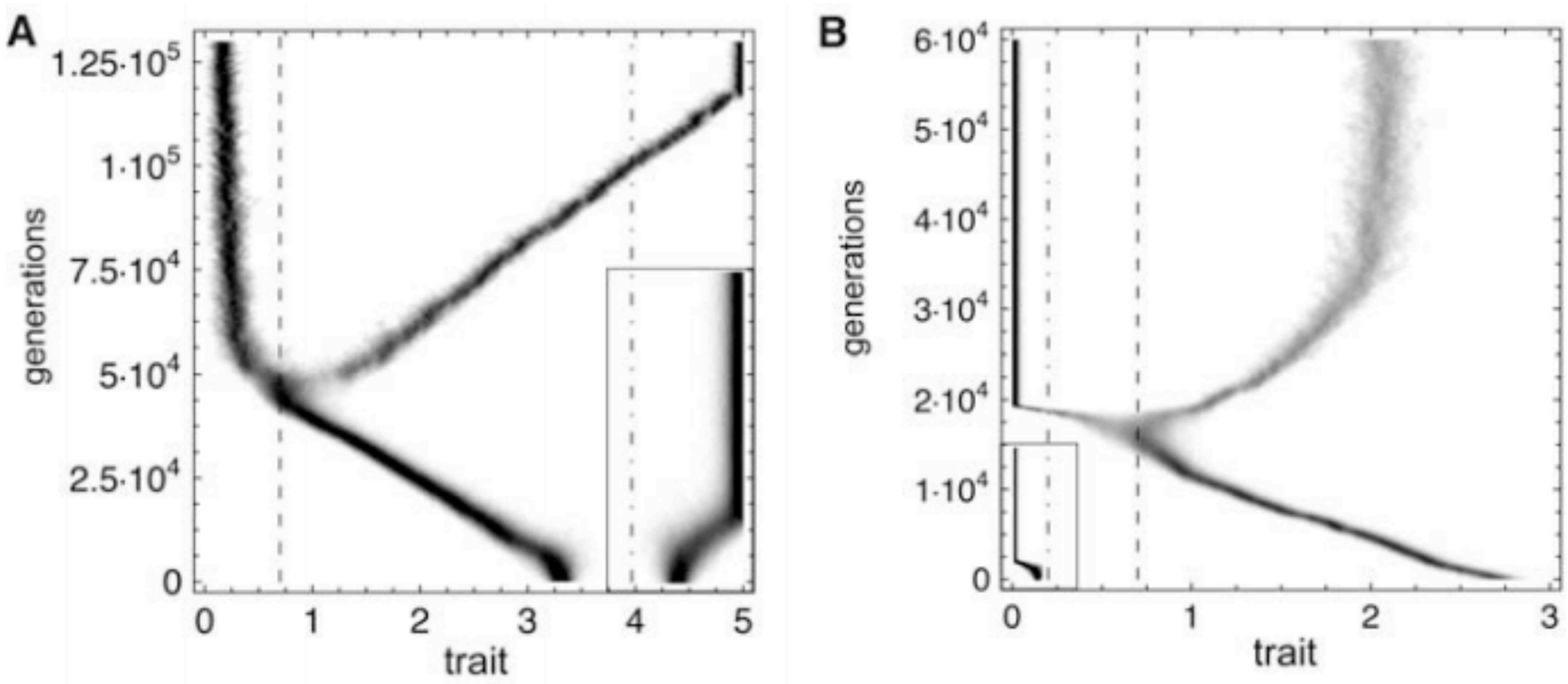
$$C(x) = c_2 \cdot x^2 + c_1 \cdot x$$

replicator dynamics

$$f_x(y) = P(y, x) - P(x, x)$$

selection gradient

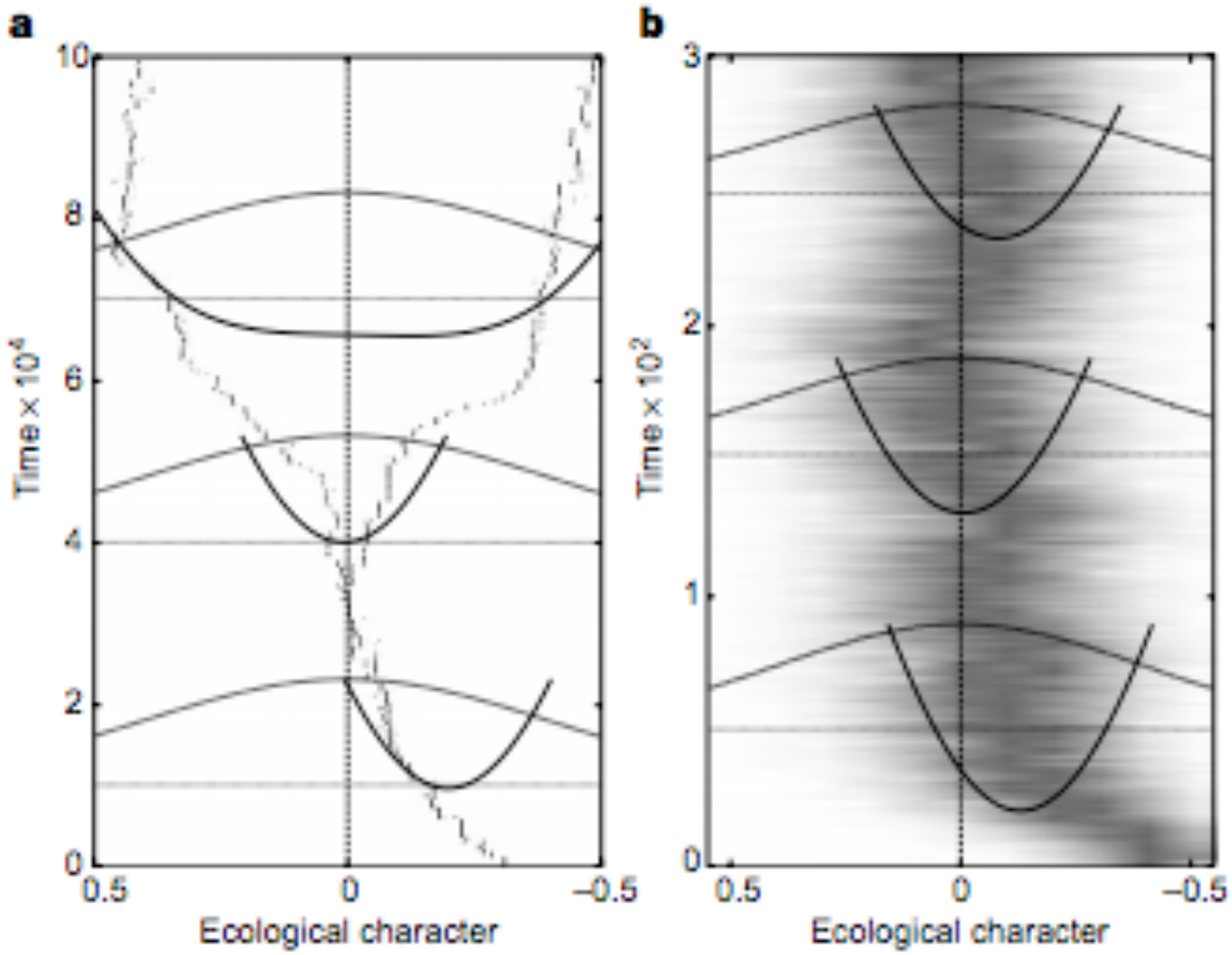
$$D(x) = \left.\frac{\partial f_x(y)}{\partial y}\right|_{y=x} = B'(2x) - C'(x)$$

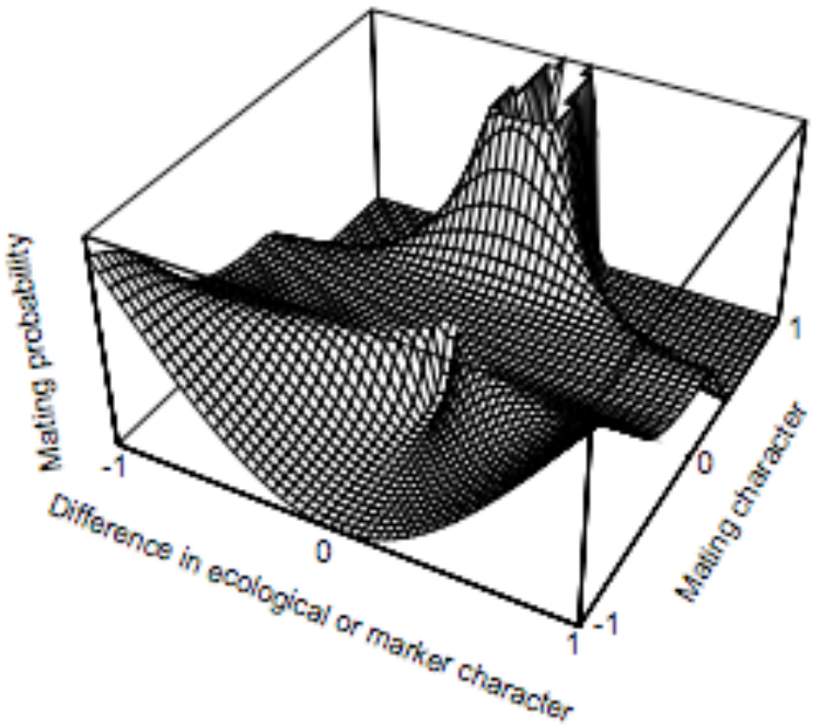

A
1.25·10^5
1·10^5
7.5·10^4
5·10^4
2.5·10^4
0
generations
0
1
2
3
4
5
trait
B
6·10^4
5·10^4
4·10^4
3·10^4
2·10^4
1·10^4
0
generations
0
1
2
3
trait

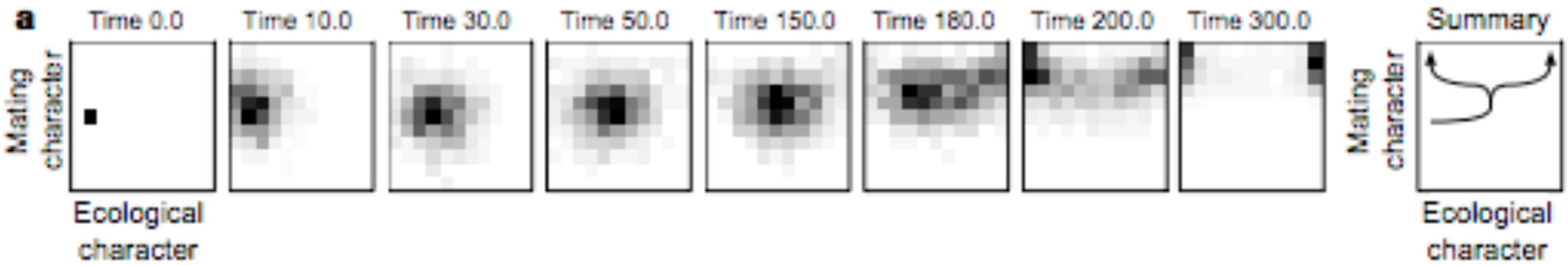
On the origin of species by sympatric speciation

Ulf Dieckmann & Michael Doebeli

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland




Mating probability
-1
0
1
Difference in ecological or marker character
-1
0
1
Mating character


a
Time 0.0
Time 10.0
Time 30.0
Time 50.0
Time 150.0
Time 180.0
Time 200.0
Time 300.0
Summary
Mating character
Ecological character
Mating character
Ecological character