FROM GAMES TO GENES… AND BACK

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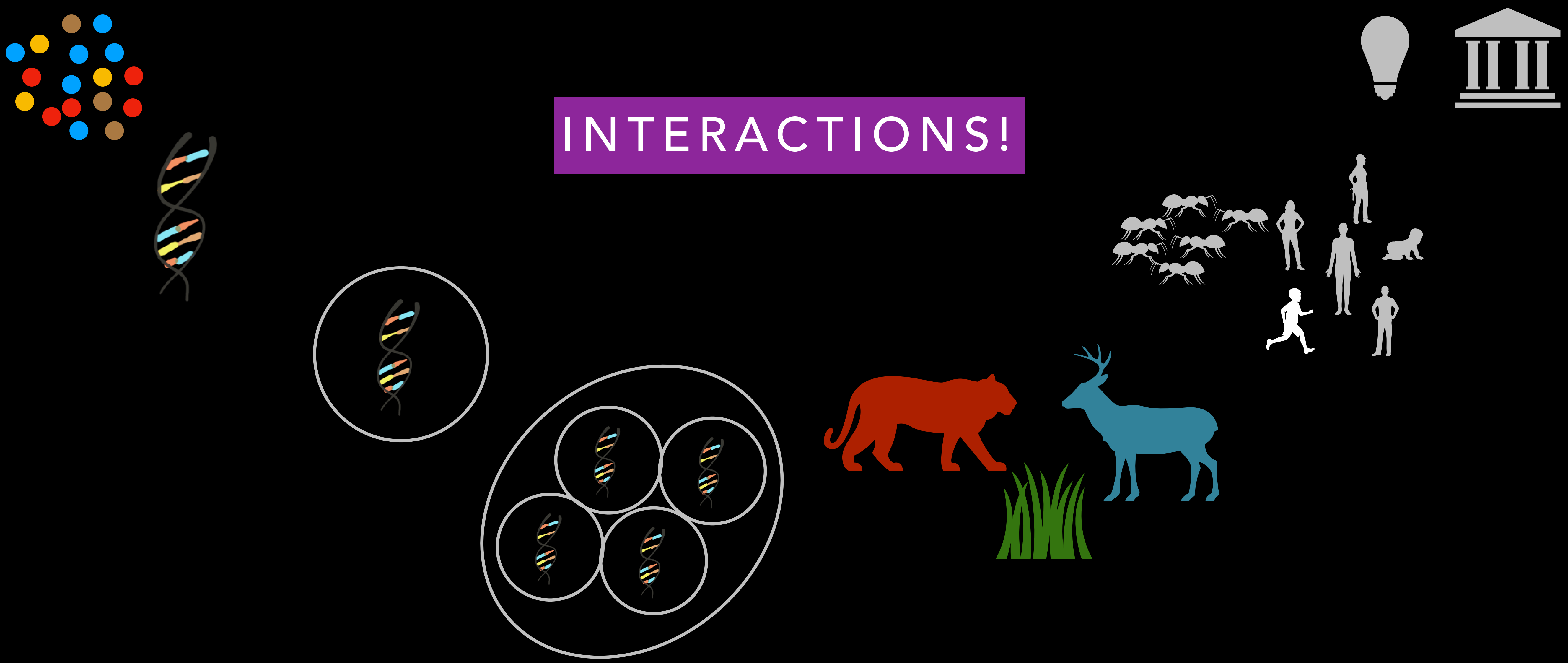
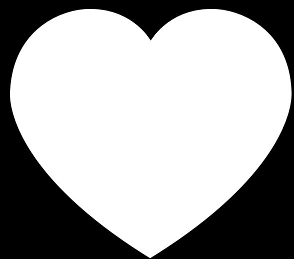
Common thread across scales of organisations?



Ecological interactions

Population Genetics

Evolutionary Game Theory

Techniques

physics, mathematics, computational techniques, experimental biology

EGT and PopGen are not just tools but also research lines in themselves

GAME THEORY

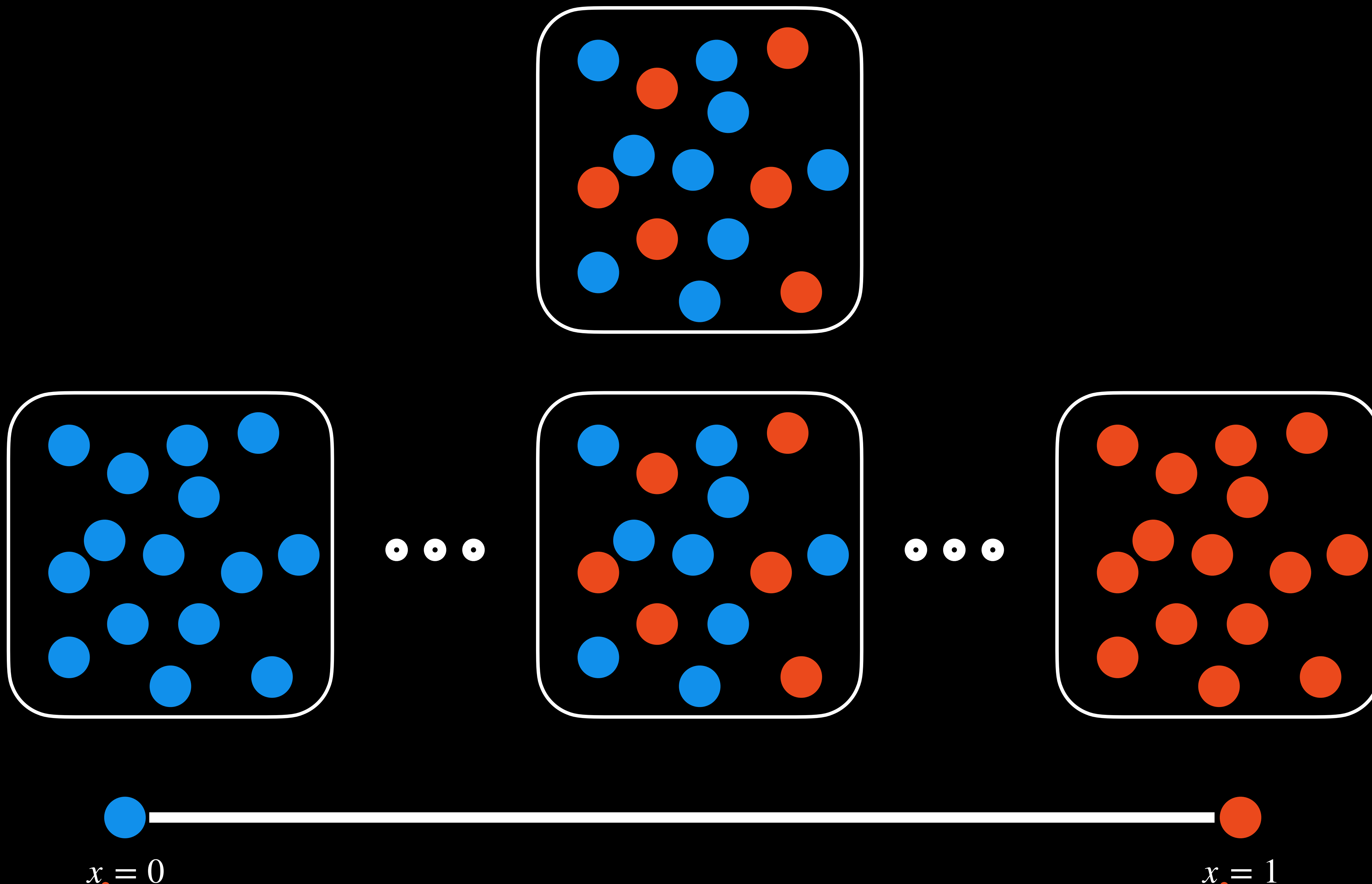
Oskar
Morgernstern

John
von Neumann

Theory of games and economic behaviour, 1944

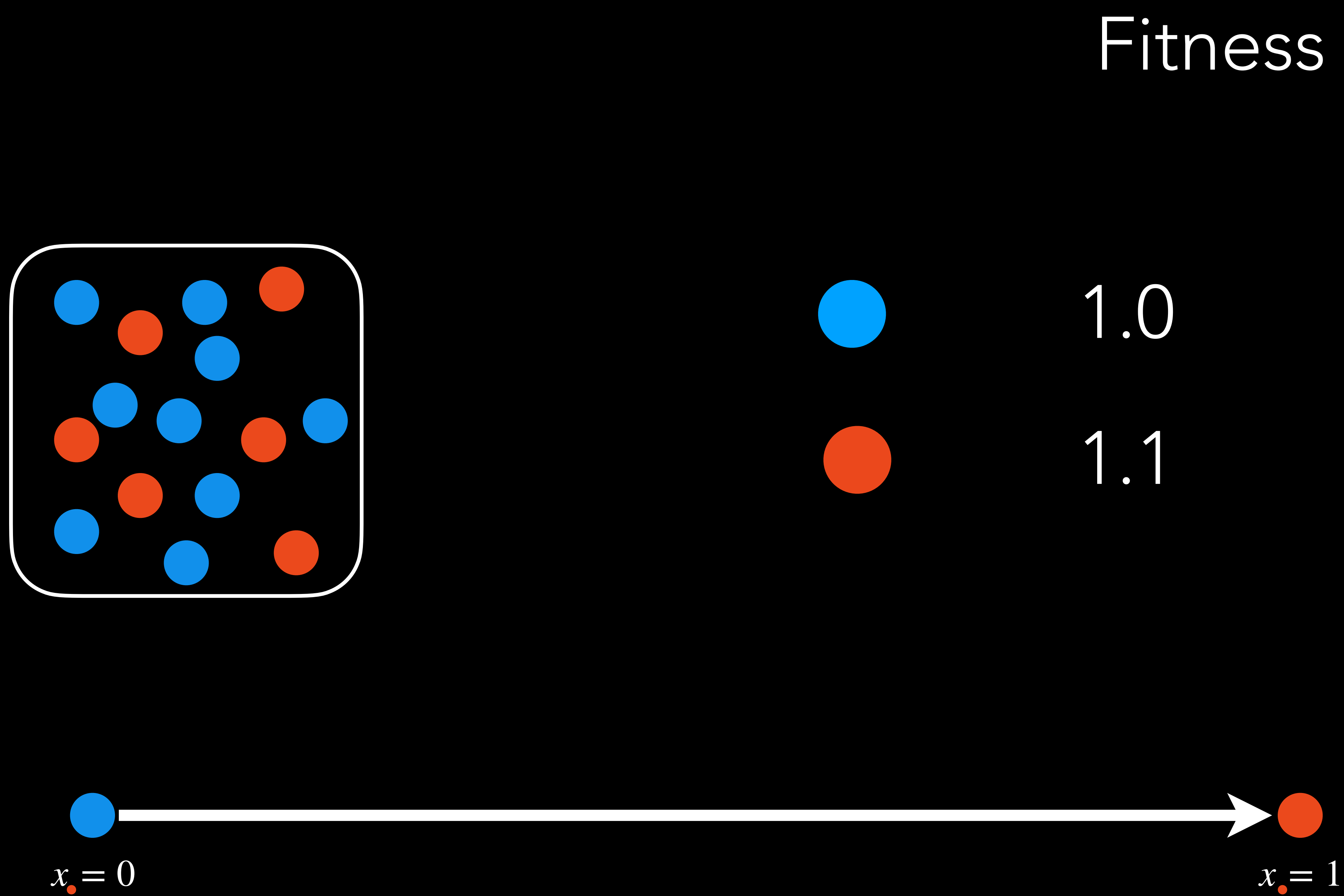
Deals with human decision-making
among interacting individuals.

EVOLUTIONARY GAME THEORY?



Possible population states

EVOLUTIONARY GAME THEORY?

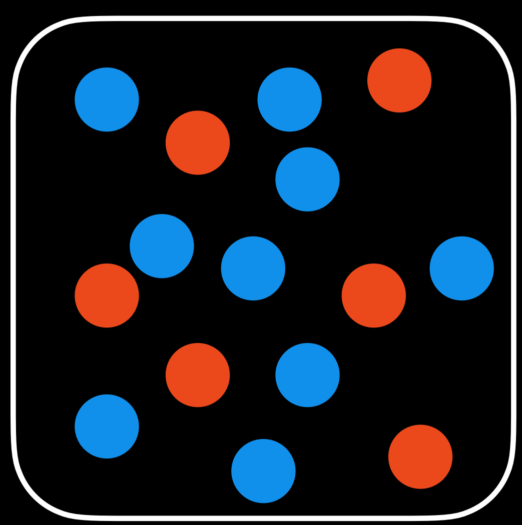


In the land of the blind, the one-eyed is king

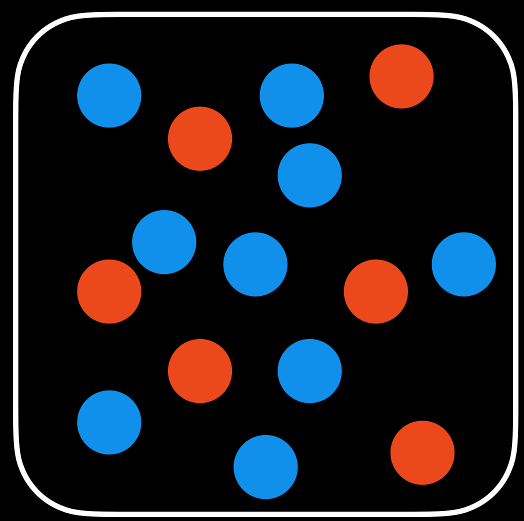
EVOLUTIONARY GAME THEORY?

Dynamic fitness landscape

Frequency dependent



EVOLUTIONARY GAME THEORY



	Wildtype	Mutant
Wildtype	1.0	0.9
Mutant	1.1	0.8

$$\begin{pmatrix} a_1 & a_0 \\ b_1 & b_0 \end{pmatrix}$$

"Evolutionary game theory is a way of thinking about evolution at the *phenotypic* level when the fitnesses of particular *phenotypes* depend on their frequencies"

– MAYNARD SMITH

MAYNARD SMITH, *EVOLUTION AND THE THEORY OF GAMES* (1982)

DYNAMICS?

There are different rules by which the strategies can change over time

We will focus on something closely emulating biological evolution

Replicator dynamics

DYNAMICS?

$$\begin{pmatrix} a_1 & a_0 \\ b_1 & b_0 \end{pmatrix}$$

All B ———————————— All A

x frequency of type A

$f_A = ax + b(1 - x)$

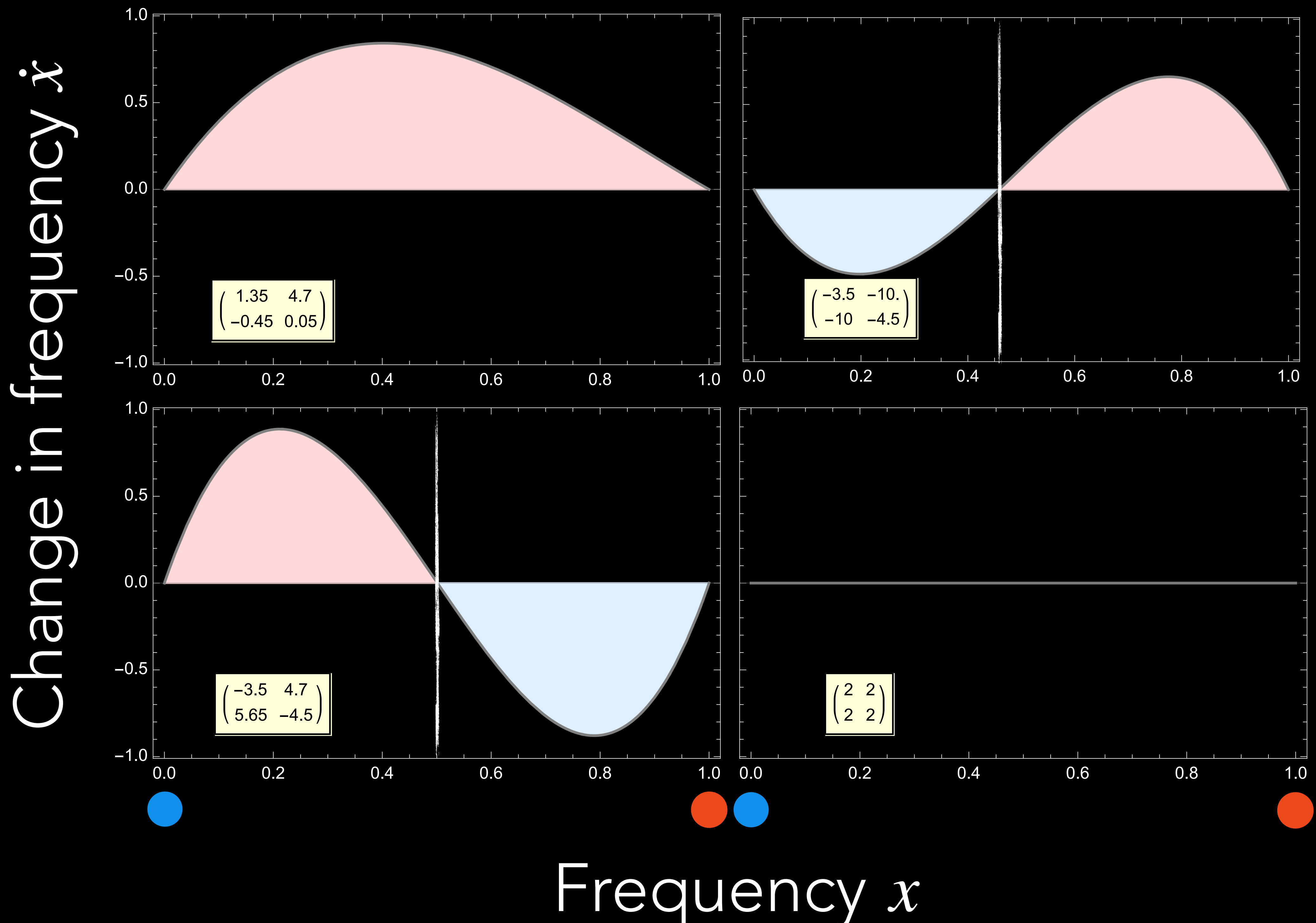
$f_B = cx + d(1 - x)$

A will increase if the average fitness is greater than the average population fitness

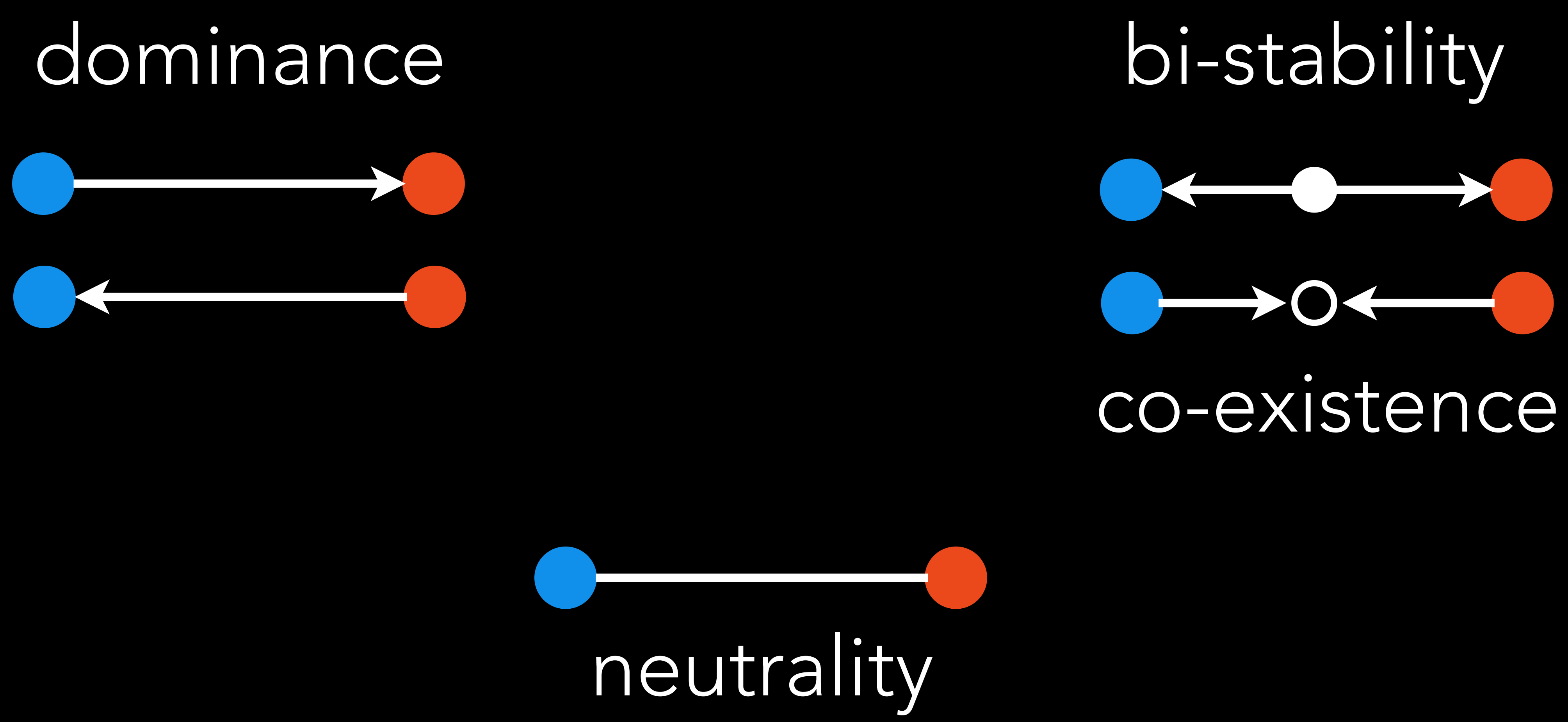
$$\bar{f} = xf_A + (1 - x)f_B$$

$$\dot{x} = x(1 - x)(f_A - f_B)$$

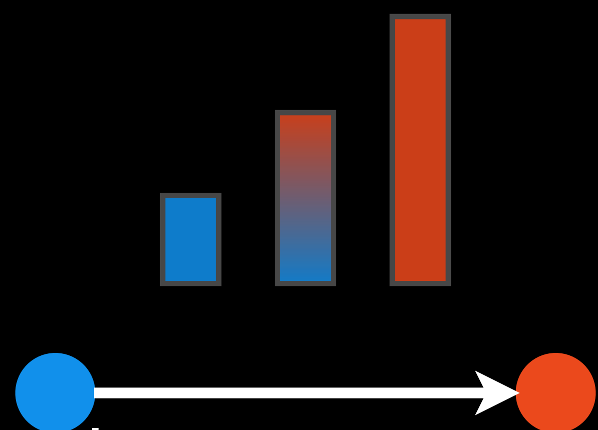
$$\dot{x} = x(1 - x)(f_A - f_B)$$



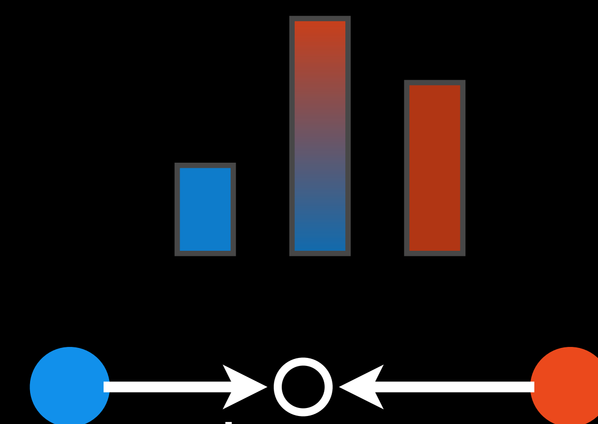
Classical outcomes of the replicator dynamics for two player and two strategies



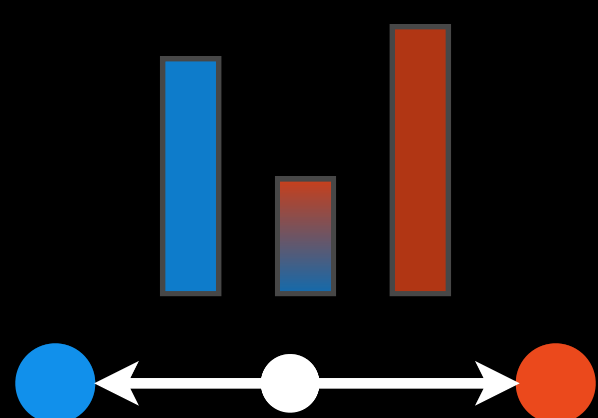
GAMES TO GENES?



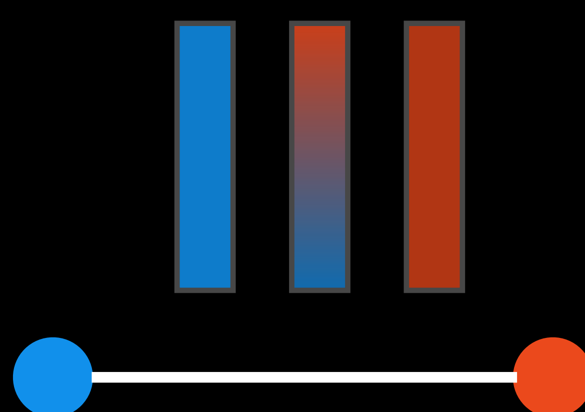
dominance



over-dominance



under-dominance



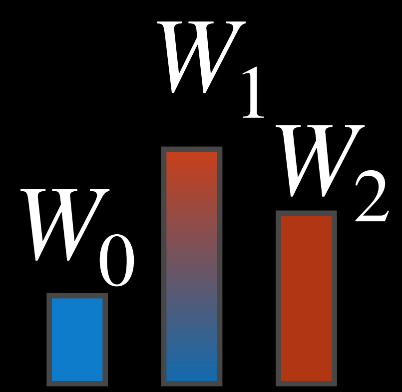
neutrality

HOW DID WE GET HERE?

p Allele 1

$$\Delta q = \frac{pq\left(q(W_2 - W_1) + p(W_1 - W_0)\right)}{\bar{W}}$$

q Allele 2

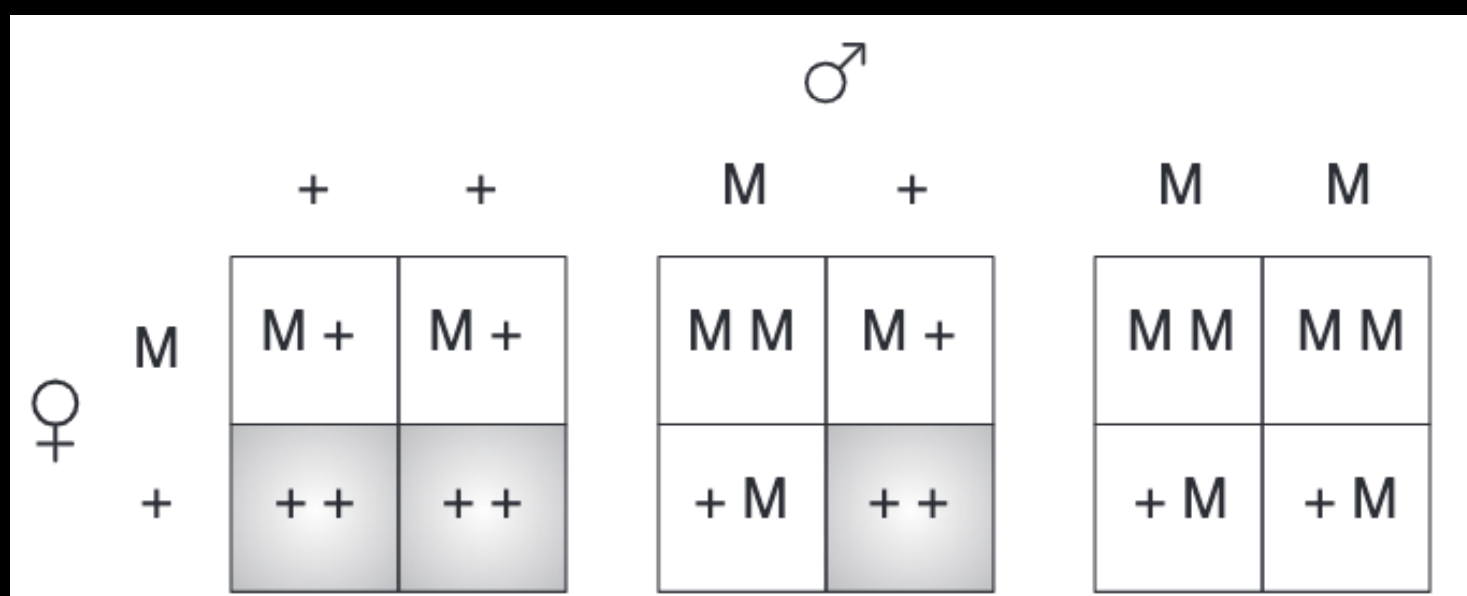


$$\dot{q} = (1-q)q\left(qf_q + (1-q)f_p\right)$$

But genetics can be quite complicated!

MEDEA

Medea is a naturally occurring selfish genetic element. Natural Maternal effect dominant embryonic arrest.



Medea in a fresco from Herculaneum.

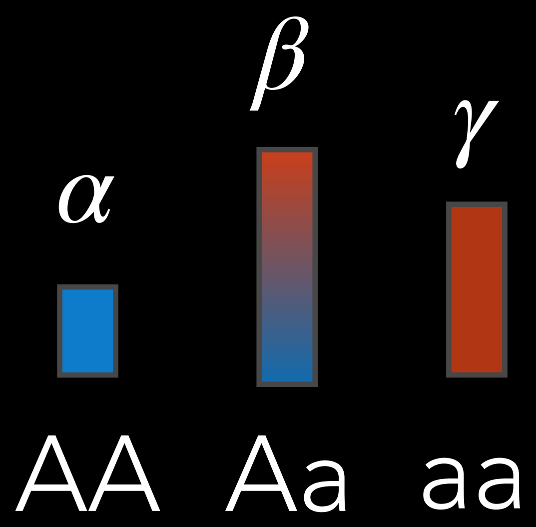
GAMES THAT ALLELES PLAY

A and a are two alleles

	AAA	AAa	Aaa	aaa
A	a_3	a_2	a_1	a_0
a	b_3	b_2	b_1	b_0

GOKHALE, C. S. & TRAULSEN, A. EVOLUTIONARY MULTIPLAYER GAMES. *DYN GAMES APPL* **4**, 468–488 (2014)

	AAA	AAa	Aaa	aaa
A	a_3	a_2	a_1	a_0
a	b_3	b_2	b_1	b_0



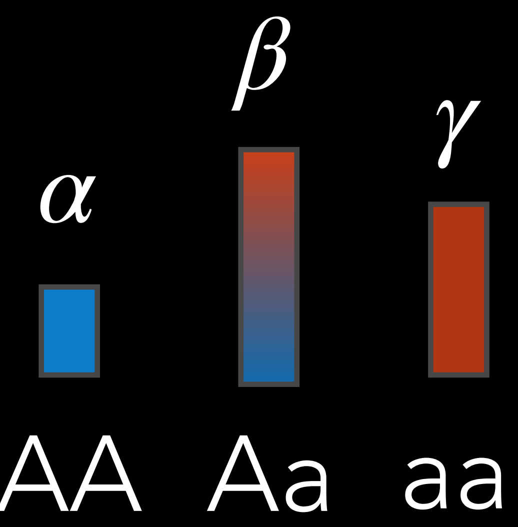
	a	a
A	β	β
A	β	β

	A	a
A	α	β
a	β	γ

	A	a
A	α	β
a	β	γ

$$a_1 = \frac{\beta + (\alpha + \beta)/2 + (\alpha + \beta)/2}{3} = \frac{\alpha + 2\beta}{3}$$

	AAA	AAa	Aaa	aaa
A	α	$\frac{2\alpha+\beta}{3}$	$\frac{\alpha+2\beta}{3}$	β
a	β	$\frac{2\beta+\gamma}{3}$	$\frac{\beta+2\gamma}{3}$	γ



…in retrospect!

$$\pi_A = \alpha x + \beta(1-x)$$

$$\pi_a = \beta x + \gamma(1-x)$$

$$\begin{array}{c} \\ \text{A} \\ \text{a} \end{array} \begin{array}{c} \begin{array}{cc} \text{A} & \text{a} \end{array} \\ \begin{pmatrix} \alpha & \beta \\ \beta & \gamma \end{pmatrix} \end{array}$$

BACK TO MEDEA

		♀		
		$++$	$+M$	MM
♂	$++$	$\sim$	!	$\sim$
	$+M$	$\sim$	!	$\sim$
	MM	$\sim$	$\sim$	$\sim$

$\sim$ Normal offspring
! ++ die with probability t

MM	+M	++
ν	ω	1

	MMM	MM+	M++	+++
M	ν	$\frac{\omega + 2\nu}{3}$	$\frac{2\omega + \nu}{3}$	ω
+	ω	$\frac{2\omega + 1 - t}{3}$	$\frac{2 + \omega - t}{3}$	1

Medea in a fresco from Herculaneum.

BACK TO MEDEA

$$\pi_M = \nu x + \omega(1 - x)$$

$$\pi_+ = \omega x + (1 - xt)(1 - x)$$

The nonlinearity, which is brought about in the dynamics of the + allele arises naturally from considering a *four player game*.

Looking for a two player game which reflects this scenario would make the payoff entries themselves frequency dependent.

Medea in a fresco from Herculaneum.

MULTIPLAYER GAMES

UN CLIMATE
CHANGE
CONFERENCE
UK 2021

IN PARTNERSHIP WITH ITALY

INCLUDING MORE PLAYERS?

All B ——— All A

x frequency of type A

# of other A players	1	0
A	a_1	a_0
B	b_1	b_0

TWO PLAYER GAME

$$f_A = ax + b(1-x) \qquad f_B = cx + d(1-x)$$

A will increase if the average fitness is greater than the average population fitness

$$\dot{x} = x(1-x)(f_A - f_B)$$

INCLUDING MORE PLAYERS?

All B ———————————————— All A

x frequency of type A

# of other A players	*d-1*	*d-2*		1	0
A	a_{d-1}	a_{d-2}	$\cdots$	a_1	a_0
B	b_{d-1}	b_{d-2}	$\cdots$	b_1	b_0

d – PLAYER GAME

$$f_A = \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} a_k$$

$$f_B = \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} b_k$$

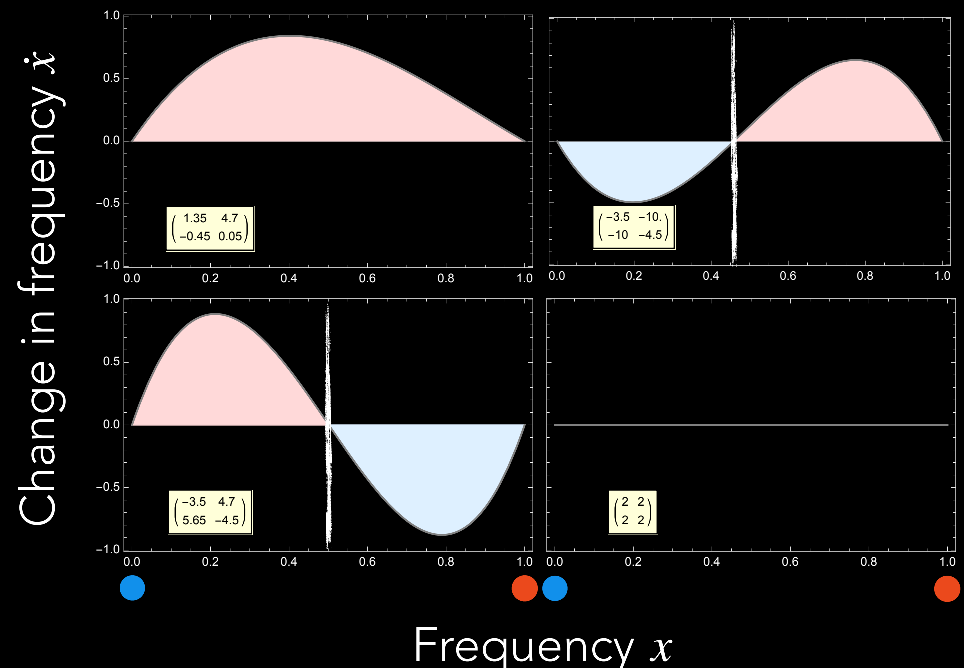
A will increase if the average fitness is greater than the average population fitness

$$\dot{x} = x(1-x)(f_A - f_B)$$

INCLUDING MORE PLAYERS?

TWO PLAYER GAME

At most one internal equilibrium



d – PLAYER GAME

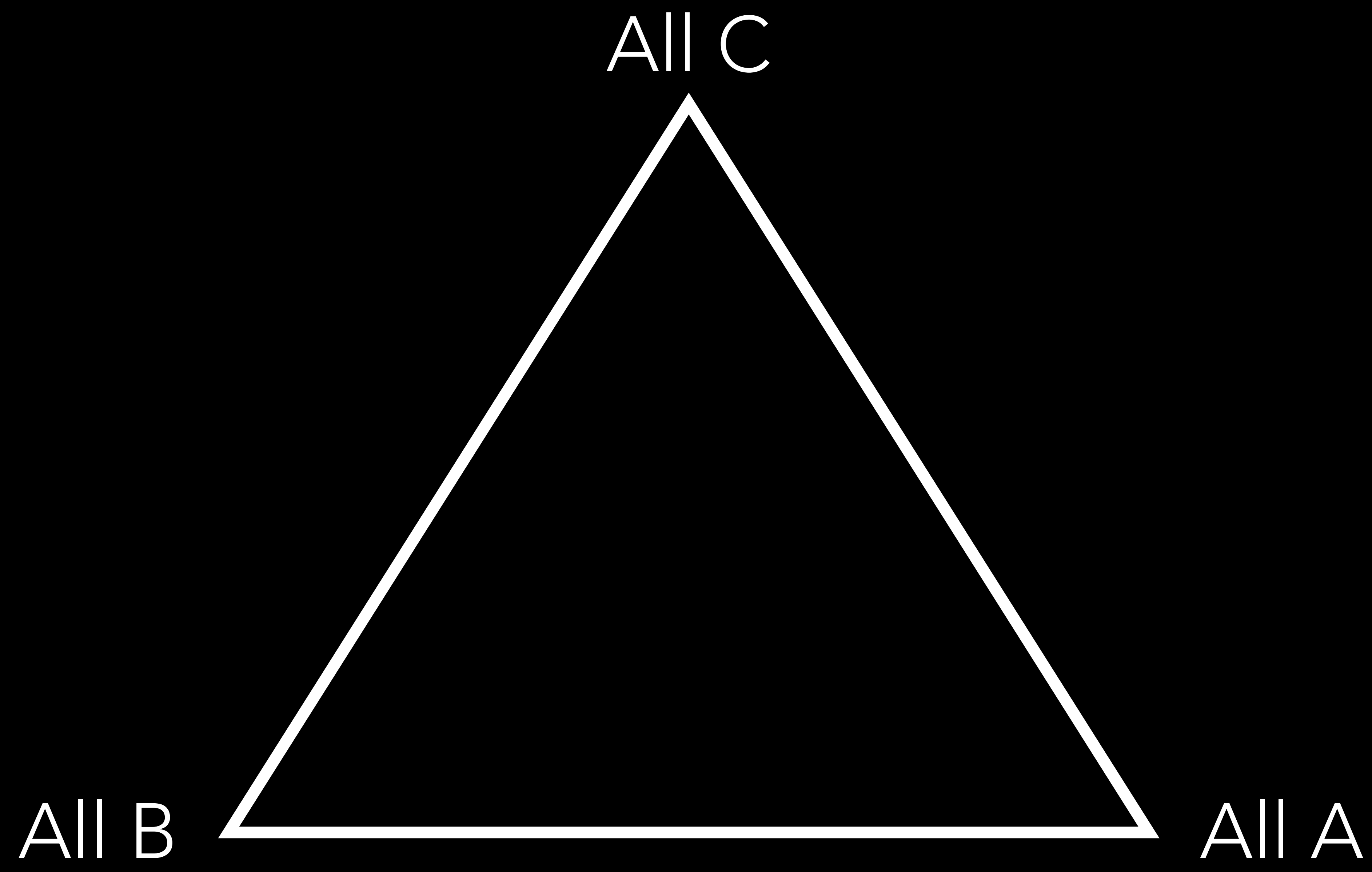
At most $d - 1$ internal equilibria

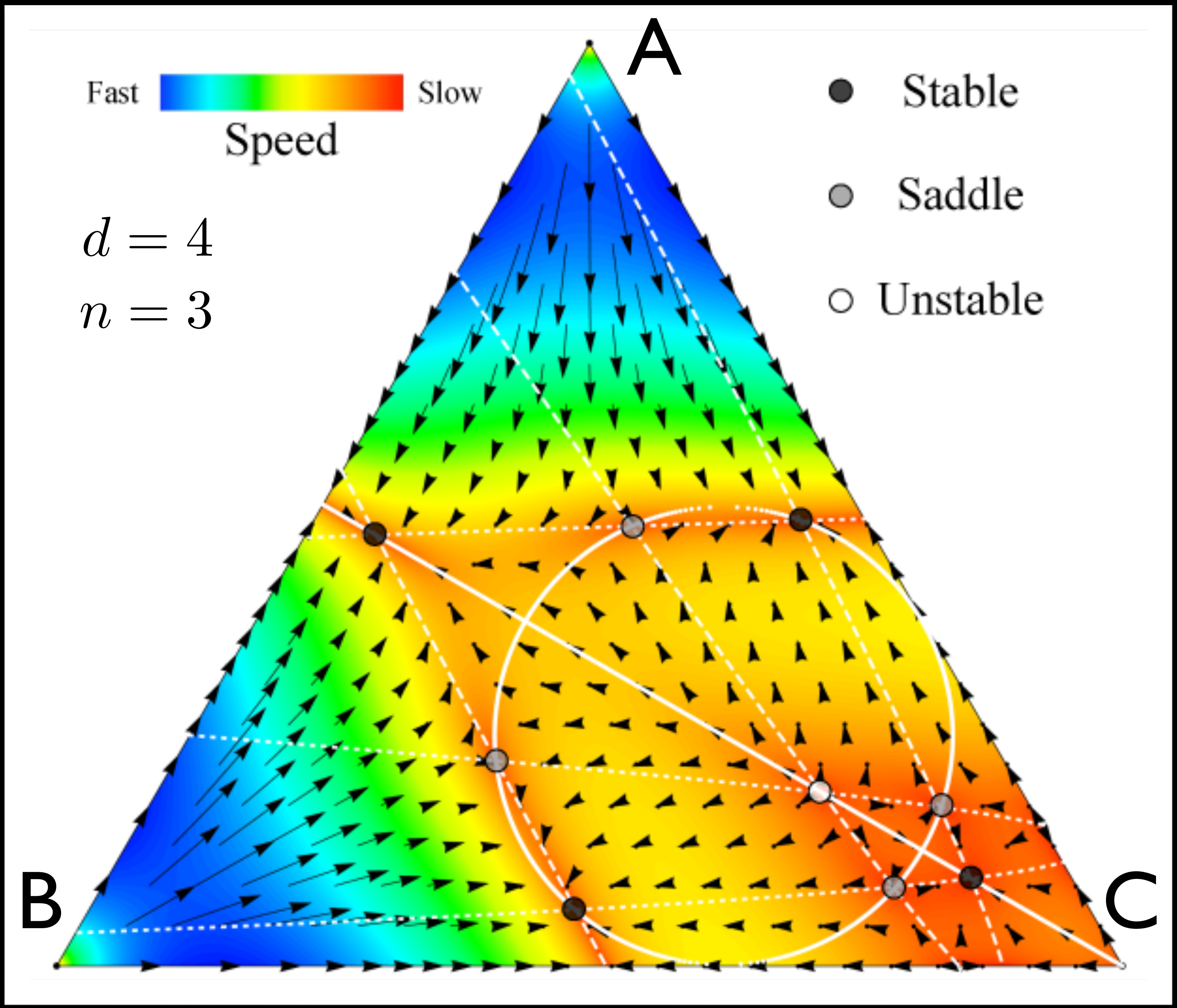
PLAYER FILE

HAN, T. A., TRAULSEN, A. & GOKHALE, C. S. ON EQUILIBRIUM PROPERTIES OF EVOLUTIONARY MULTI-PLAYER GAMES WITH RANDOM PAYOFF MATRICES. *THEOR POPUL BIOL* **81**, 264–272 (2012).

GOKHALE, C. S. & TRAULSEN, A. EVOLUTIONARY GAMES IN THE MULTIVERSE. *PROC NATIONAL ACAD SCI* **107**, 5500–5504 (2010).

MULTIPLE STRATEGIES? MULTIPLE ALLELES?





Maximum number of internal fixed points

$$(d-1)^{(n-1)}$$

Maximum fixed points

$$\frac{d^n - 1}{d - 1}$$

GOKHALE, C. S. & TRAULSEN, A. EVOLUTIONARY GAMES IN THE MULTIVERSE. *PROC NATIONAL ACAD SCI* **107**, 5500–5504 (2010).

BACK TO GENETICS

234 *M.W. Feldman / Theoretical Pop*

so elegantly explicated by Kingman (1961a,b). For the two-locus two-allele problem these considerations suggested a maximum of fifteen fixed points, and in our work with the symmetric viability model we demonstrated that fifteen was indeed realizable when recombination was present. Amazingly, to this day, our conjecture that the maximum number of equilibria in any n-chromosome viability system and for any recombination arrangement is $2^n - 1$ has not been proven, although there are no counterexamples. Later, Sam used the one-locus multi-allele theory to prove that for any two-locus two-allele viability system, with sufficiently tight linkage there could be at most two stable equilibria with all four chromosomes present (Karlin, 1980).

FELDMAN, M. W. SAM KARLIN AND MULTI-LOCUS POPULATION GENETICS. *THEOR POPUL BIOL* **75**, 233–235 (2009).

KARLIN, S. THE NUMBER OF STABLE EQUILIBRIA FOR THE CLASSICAL ONE-LOCUS MULTIALLELE SELECTION MODEL. *JOURNAL OF MATHEMATICAL BIOLOGY* **9**, 189–192 (1980).

BACK TO GENETICS

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Maximum fixed points

$$\frac{d^n - 1}{d - 1}$$

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BACK TO GENETICS

The number of players *d* corresponds to the ploidy level.

Hence, we provide estimates for polyploid systems!

Maximum fixed points

$$\frac{d^n - 1}{d - 1}$$

HAN, T. A., TRAULSEN, A. & GOKHALE, C. S. ON EQUILIBRIUM PROPERTIES OF EVOLUTIONARY MULTI-PLAYER GAMES WITH RANDOM PAYOFF MATRICES. *THEOR POPUL BIOL* **81**, 264–272 (2012).

ROWE, G. W. TO EACH GENOTYPE A SEPARATE STRATEGY—A DYNAMIC GAME THEORY MODEL OF A GENERAL DIPLOID SYSTEM. *JOURNAL OF THEORETICAL BIOLOGY* **134**, 89–101 (1988).

$$\dot{x}_i = \sum_{j=1}^{n} x_j f_i(\mathbf{x}) q_{ji} - x_i \bar{f}$$

Replicator-Mutator equation

Neglecting mutations

Neglecting frequency dependent fitness

$$\dot{x}_i = x_i f_i(\mathbf{x}) - x_i \bar{f}$$

Replicator equation

$$\dot{x}_i = \sum_{j=1}^{n} x_j f_i q_{ji} - x_i \bar{f}$$

Quasispecies equation

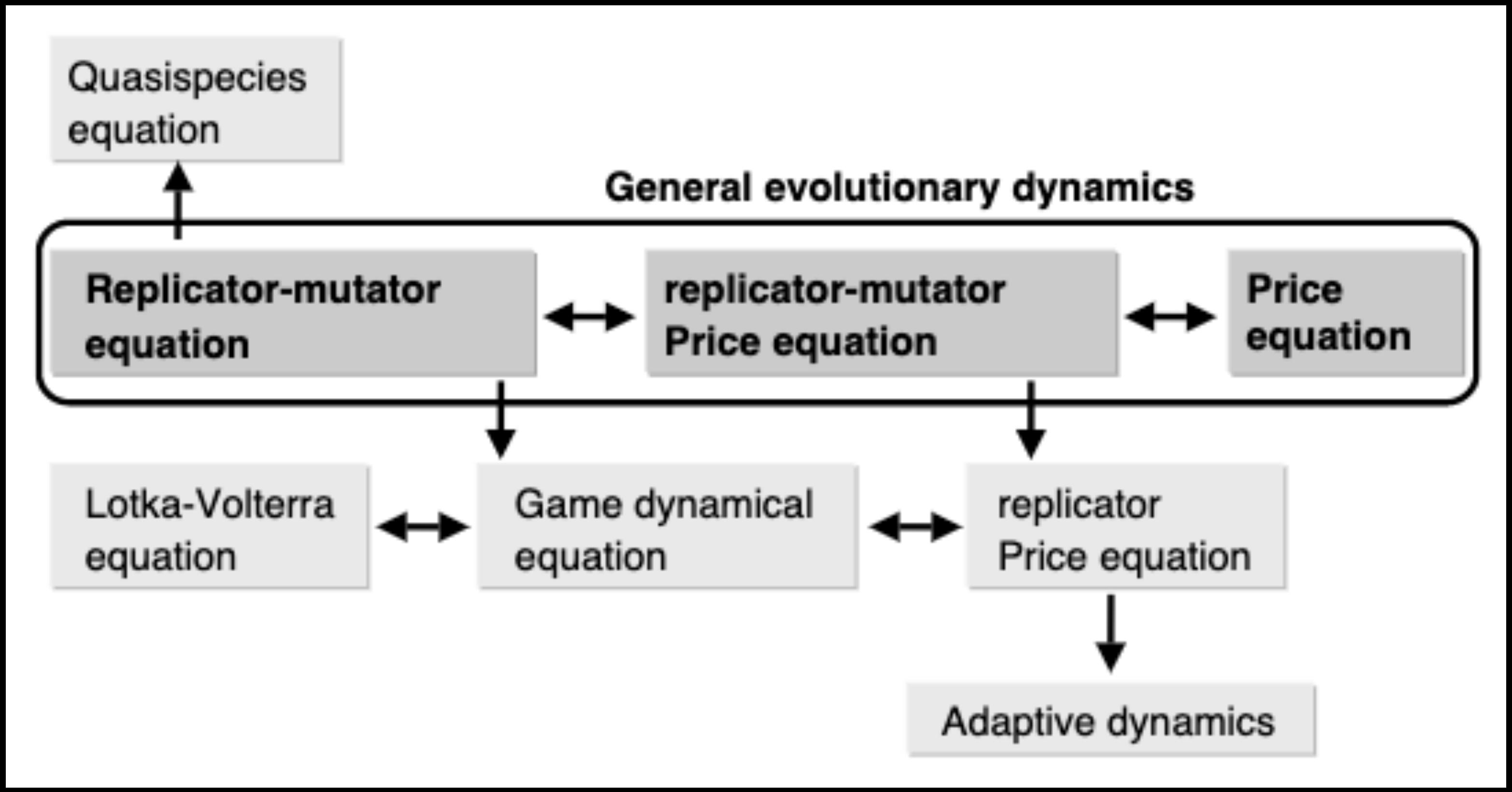
$\dot{x}$ Frequency of type i

q_{ji} Mutation probability from j to i

$\bar{f}$ Average fitness of the population

f_i Frequency independent fitness of type i

$f_i(\mathbf{x})$ Frequency dependent fitness of type i



Extend to genetic evolution

PAGE, K. M. & NOWAK, M. A. UNIFYING EVOLUTIONARY DYNAMICS. *JOURNAL OF THEORETICAL BIOLOGY* **219**, 93–98 (2002).

A CASE FOR PLURALITY

A broad strategy coming from diverse fields enriches the approaches themselves

It can speed up the progress in one field by the ideas and methods ported from another

CAVEAT!

Interpretation is paramount as assumptions may get lost in translation!

PAGE, K. M. & NOWAK, M. A. UNIFYING EVOLUTIONARY DYNAMICS. *JOURNAL OF THEORETICAL BIOLOGY* **219**, 93–98 (2002).

THANK YOU!