Decisions, Games and Evolution, ICTS

18 March, 2025

SIGILLUM UNIVERSITATIS HERBIPOLENSIS

15 83

Multiplayer Evolutionary Games

The manual

GOKHALE LAB

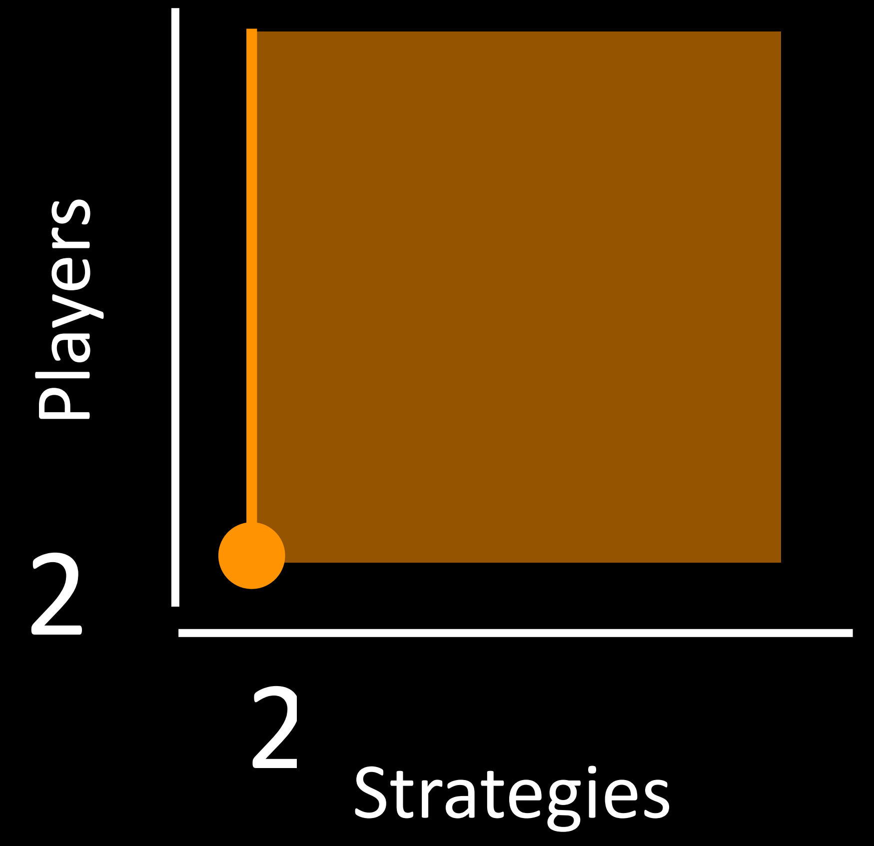
http://www.tecoevo.github.io

@GokhaleCS

Lecture 1

Introduction to MEGs

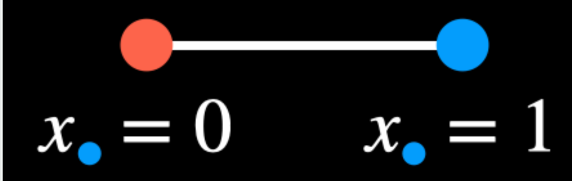
Connection to PopGen

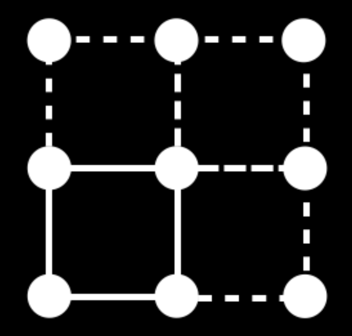


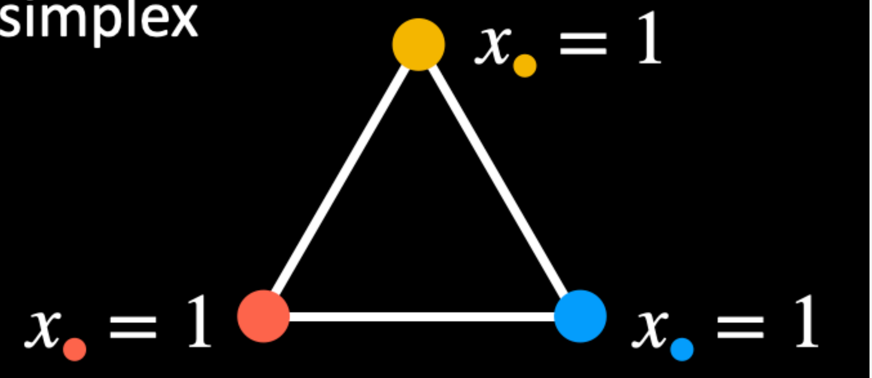
Adding a new strategy to the game

Increases the size of the payoff matrix but not the dimensions

Increases the dimensions of the simplex



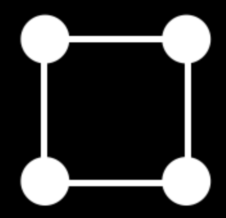


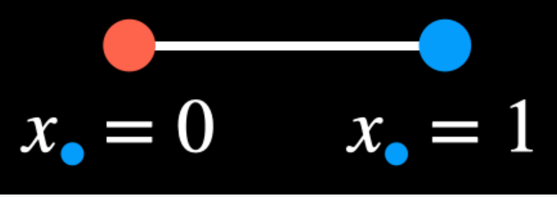


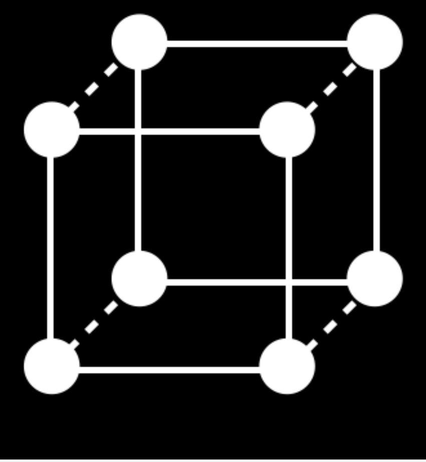
Adding a new player to the game

Increases the dimensionality of the payoff matrix

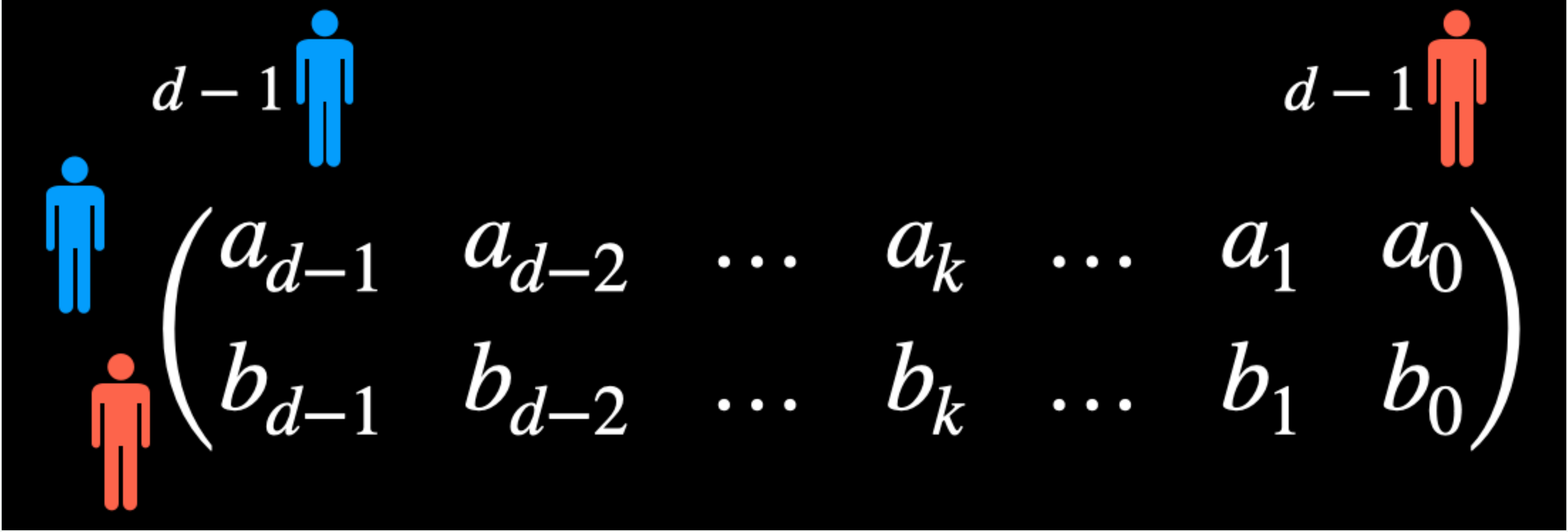
Preserves the dimensionality of the simplex







$d-$player game with 2 strategies



$$\begin{array}{c} \\ \\ \end{array}\begin{pmatrix} a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_1 & b_0 \end{pmatrix}$$

Now, assuming random pairing and mating, and correcting for the combinatorics

	a	a
A	β	
A		

	A	a
A	$(\alpha+\beta)/2$	
a		

	A	a
A	$(\alpha+\beta)/2$	
a		

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

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

	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

Thats a 4- player game with 2-strategies!

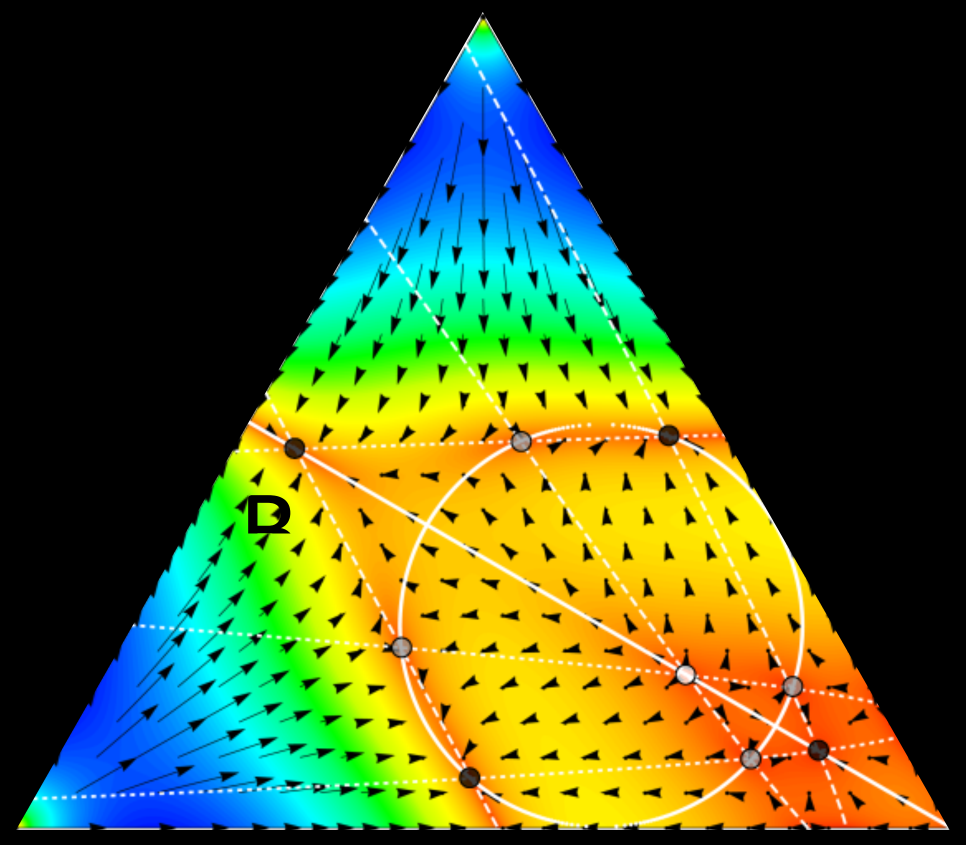
Lecture 2

If .. .when & how of MEGs in the long run

(If time permits)

MEGs in mutualism and

Eco-evolutionary dynamics



How

Also.. why??

From Static
to Dynamic

If

Fixation probability

Risk dominance

1/3rd rule

When

Fixation time

Stochastic slowdown

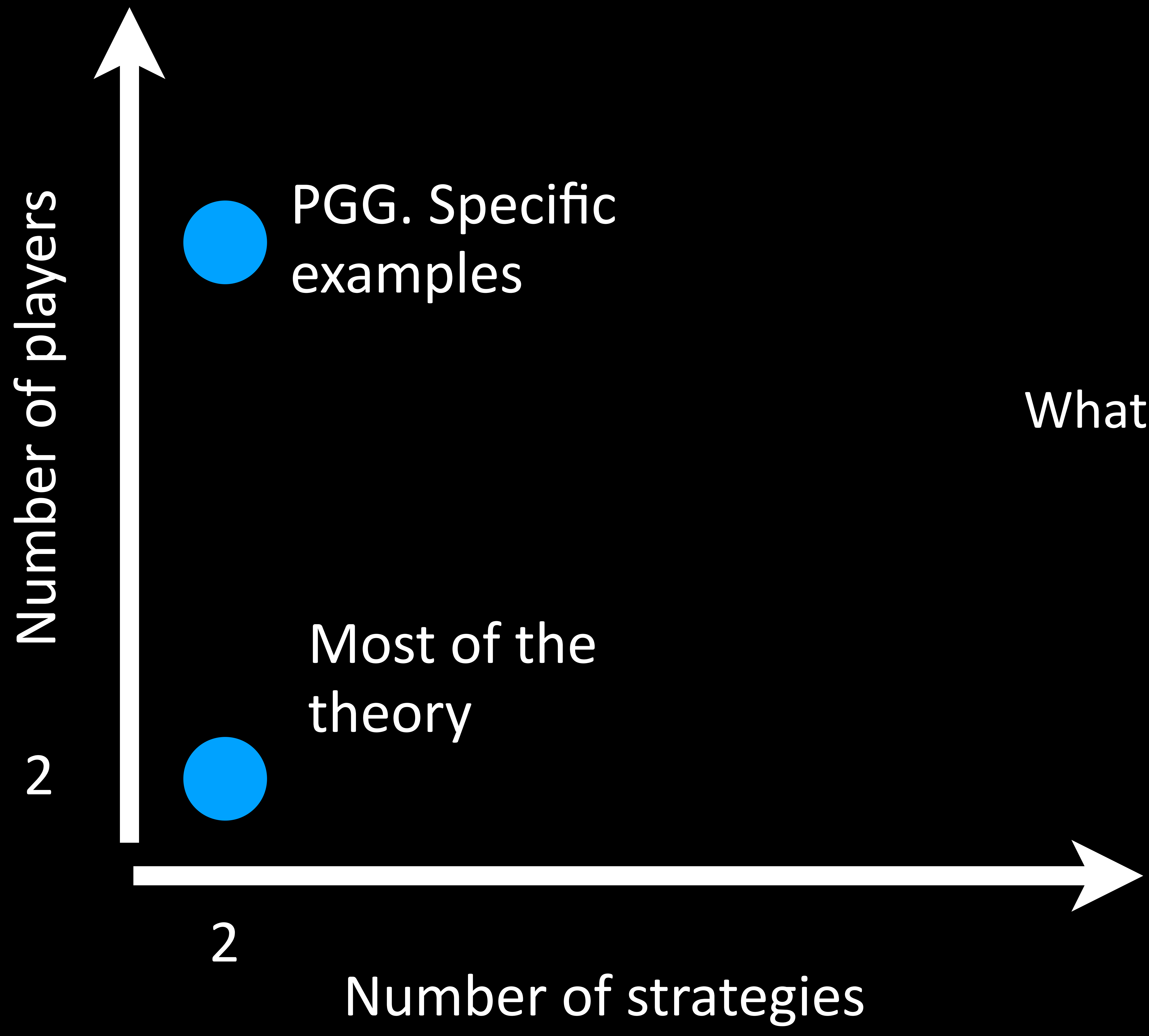
In the long run!

Mutation selection equilibrium

How

Also.. why??

From Static
to Dynamic



Number of players

PGG. Specific examples

Most of the theory

2

2

Number of strategies

What does your partner do?

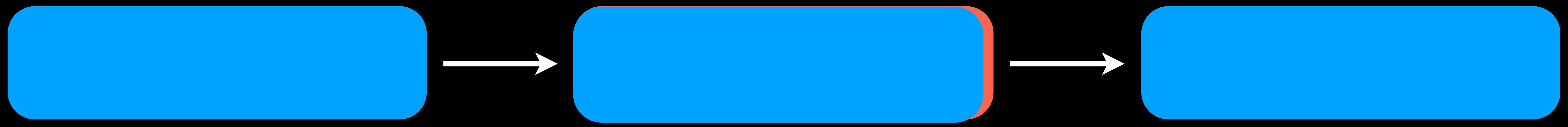
What do you do?

$$\begin{array}{ccc} & A & B \\ A & a_1 & a_0 \\ B & b_1 & b_0 \end{array}$$

Payoff matrix

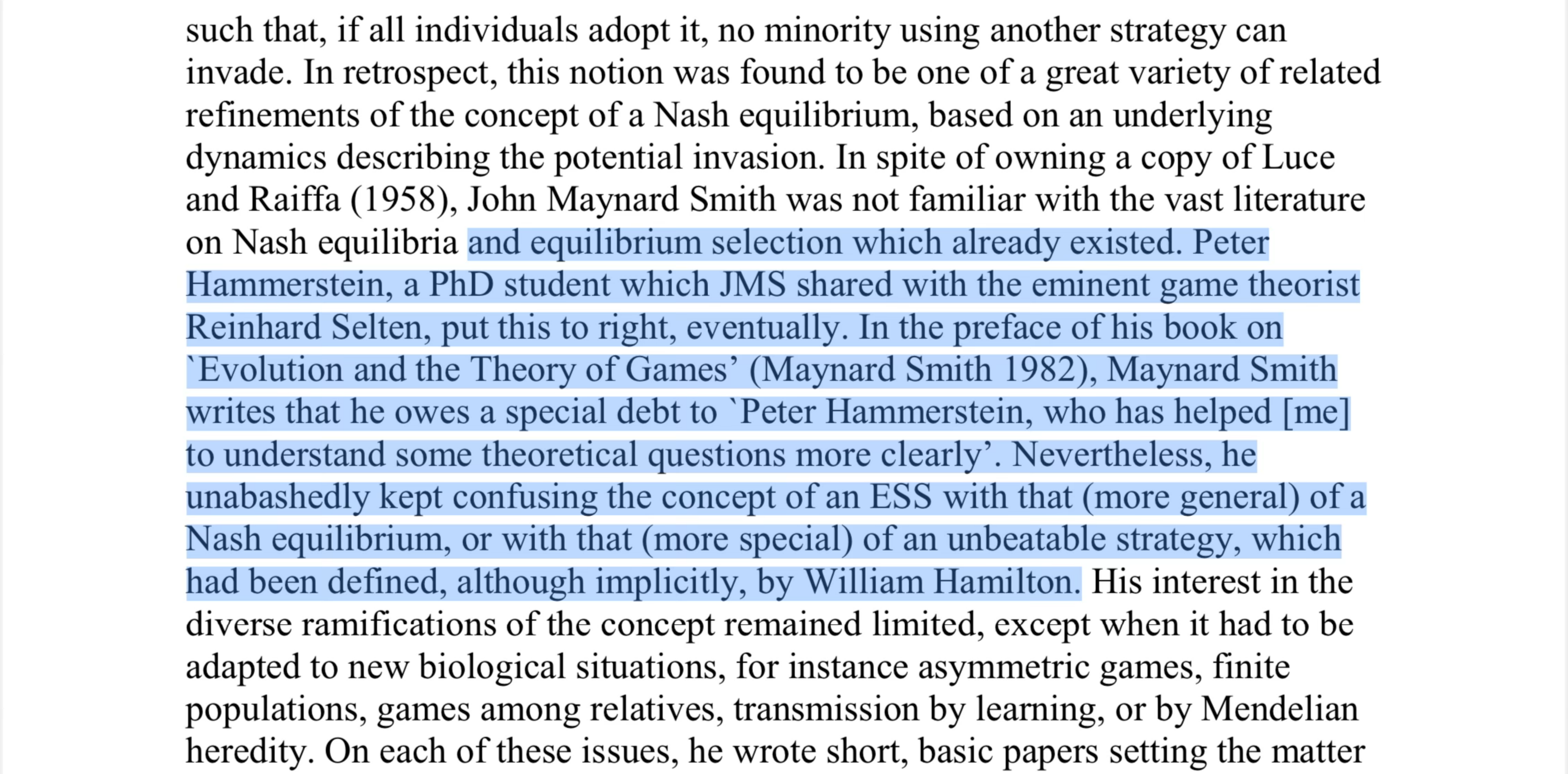
Evolutionarily Stable Strategy (for A)

$$\begin{array}{c c} & \begin{array}{cc} \text{A} & \text{B} \end{array} \\ \begin{array}{c} \text{A} \\ \text{B} \end{array} & \begin{pmatrix} a_1 & a_0 \\ b_1 & b_0 \end{pmatrix} \end{array}$$



A should be able to repel an infinitesimally small fraction of B players

$a_1 > b_1$ or $a_1 = b_1$ and $a_0 > b_0$

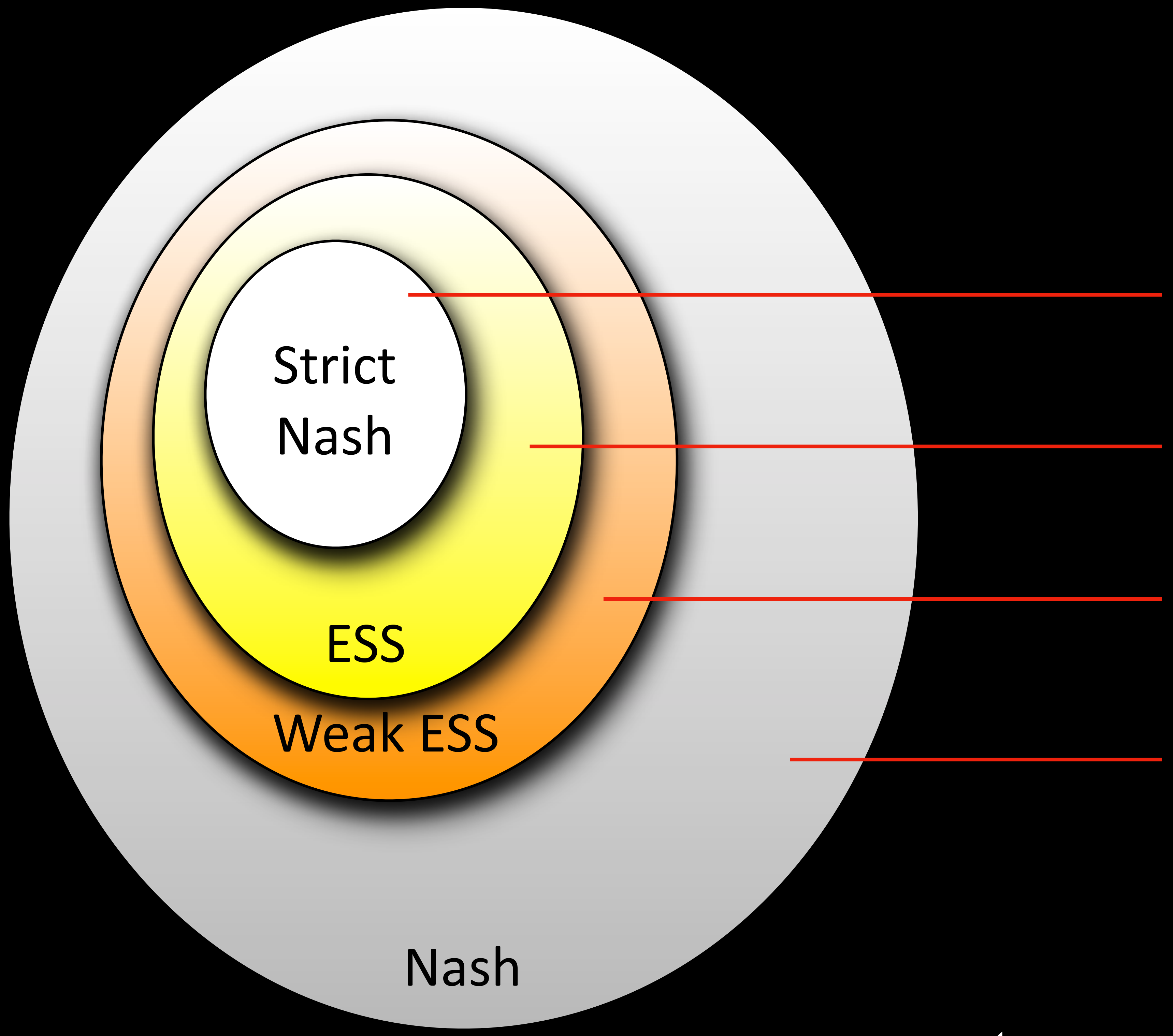


such that, if all individuals adopt it, no minority using another strategy can invade. In retrospect, this notion was found to be one of a great variety of related refinements of the concept of a Nash equilibrium, based on an underlying dynamics describing the potential invasion. In spite of owning a copy of Luce and Raiffa (1958), John Maynard Smith was not familiar with the vast literature on Nash equilibria and equilibrium selection which already existed. Peter Hammerstein, a PhD student which JMS shared with the eminent game theorist Reinhard Selten, put this to right, eventually. In the preface of his book on `Evolution and the Theory of Games' (Maynard Smith 1982), Maynard Smith writes that he owes a special debt to `Peter Hammerstein, who has helped [me] to understand some theoretical questions more clearly'. Nevertheless, he unabashedly kept confusing the concept of an ESS with that (more general) of a Nash equilibrium, or with that (more special) of an unbeatable strategy, which had been defined, although implicitly, by William Hamilton. His interest in the diverse ramifications of the concept remained limited, except when it had to be adapted to new biological situations, for instance asymmetric games, finite populations, games among relatives, transmission by learning, or by Mendelian heredity. On each of these issues, he wrote short, basic papers setting the matter

Karl Sigmund, John Maynard Smith and Evolutionary Game Theory, IIASA report

Evolutionarily Stable Strategy

For A



$a_1 > b_1 \quad a_0 > b_0$

$a_1 > b_1 \quad a_0 = b_0$

$a_1 = b_1 \quad a_0 > b_0$

$a_1 = b_1 \quad a_0 < b_0$

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

But this is static!

“We repeat most emphatically that our theory is thoroughly static.
A dynamic theory would unquestionably be more complete and therefore preferable.”

- Morgernstern and von Neumann

Replicator dynamics

$$\begin{array}{c|cc} & A & B \\ \hline A & a_1 & a_0 \\ B & b_1 & b_0 \end{array}$$

Dynamics: Change in number of A players

Frequency of A players: x

Average payoff of A players, $\pi_A = xa_1 + (1-x)a_0$

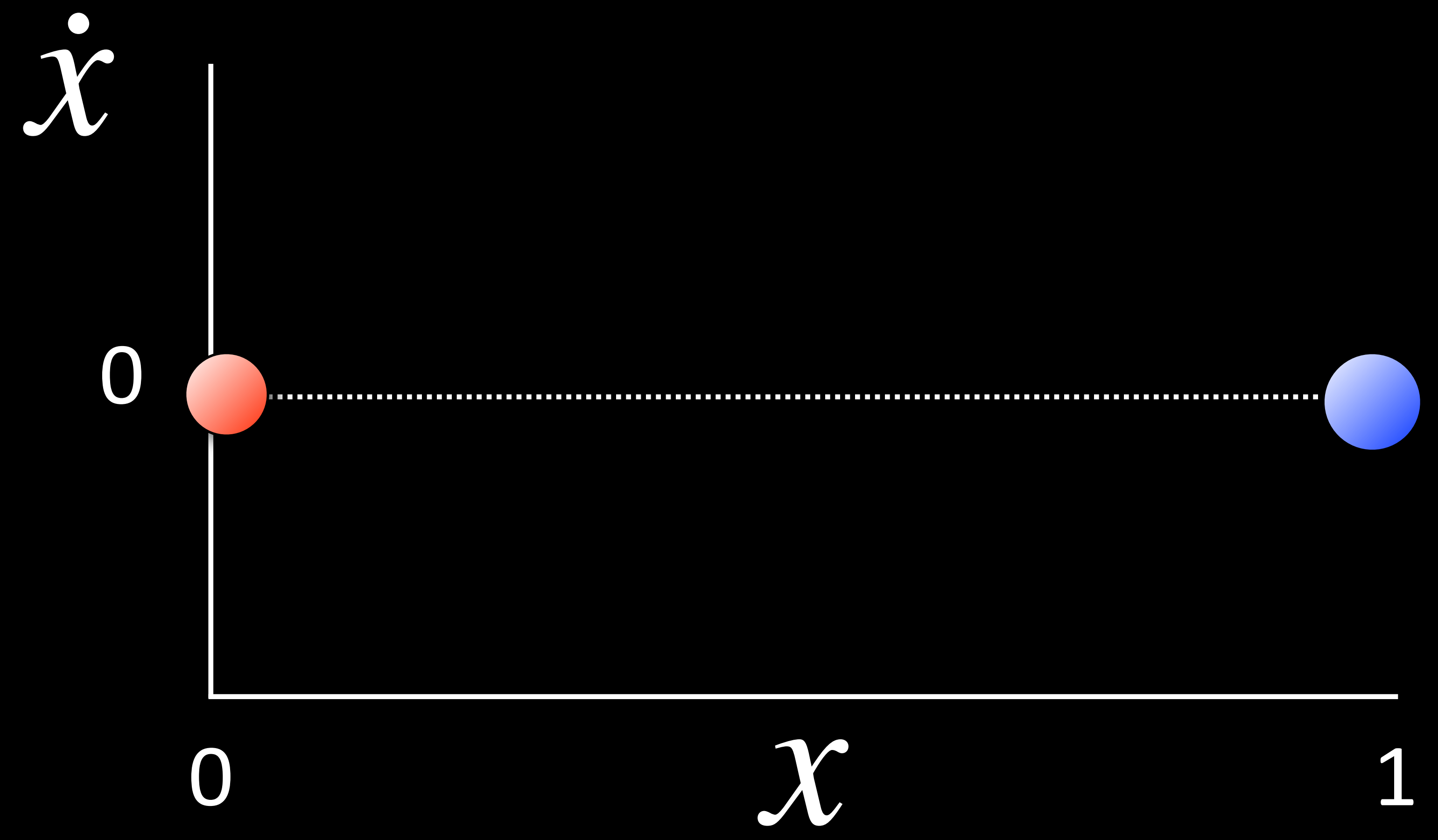
Fitness = payoff, $f_A = \pi_A$

Replicator equation

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

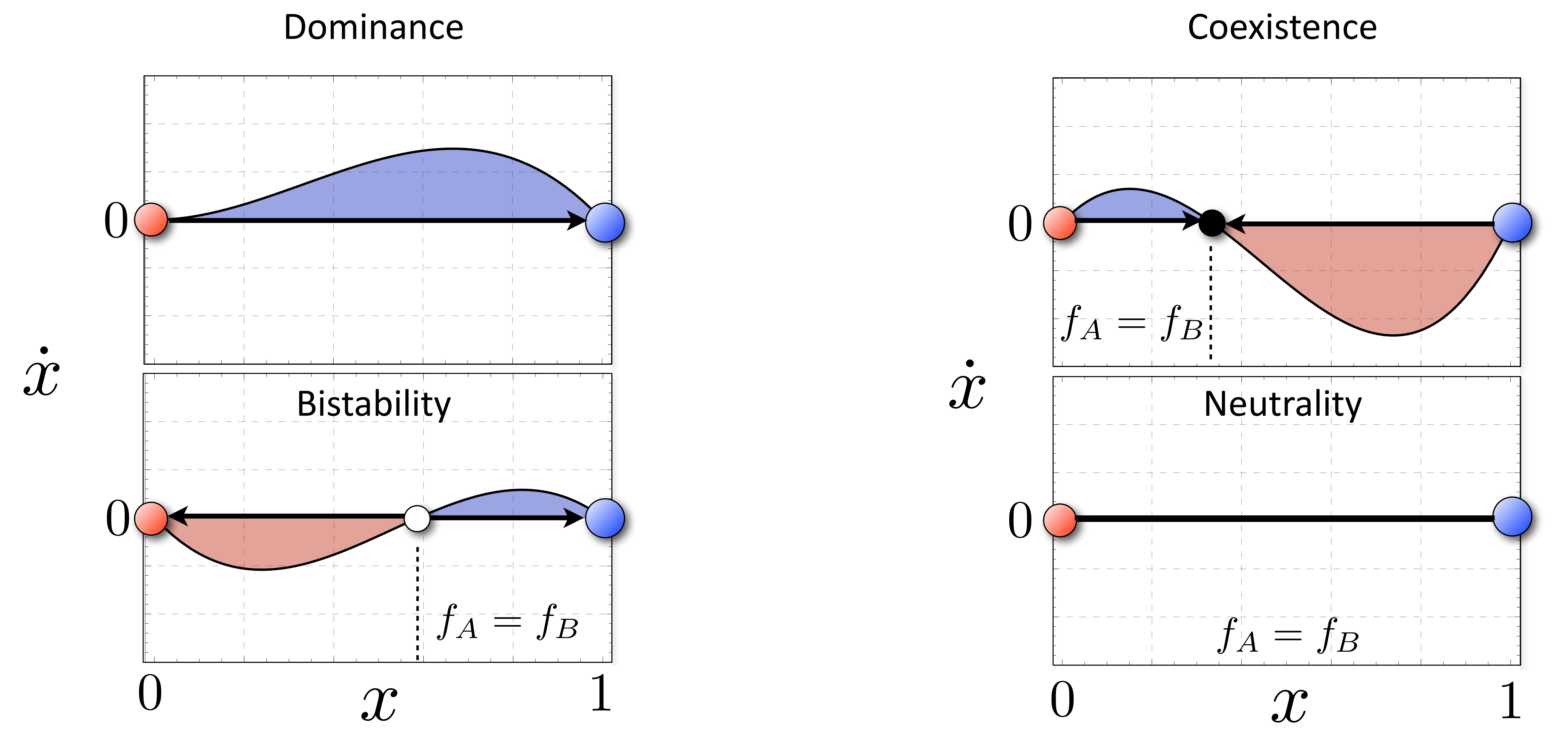
Replicator dynamics

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



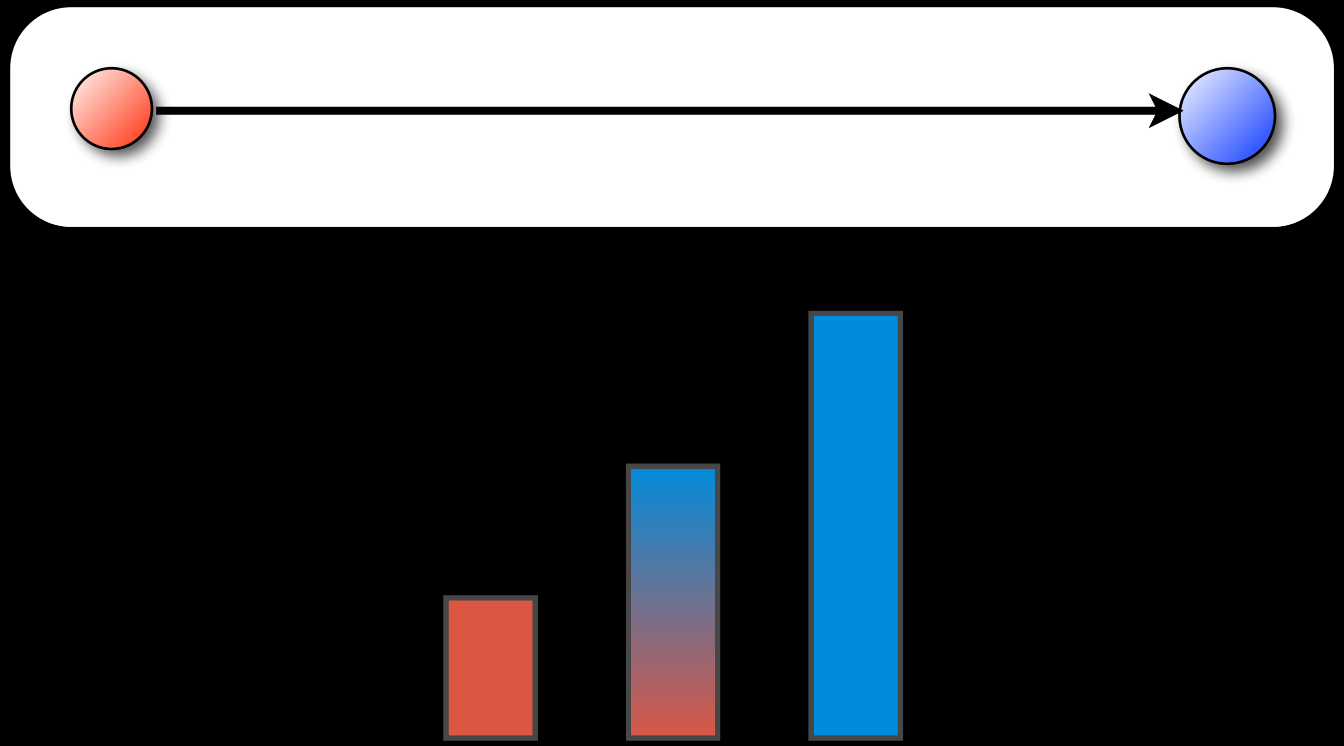
Replicator dynamics

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

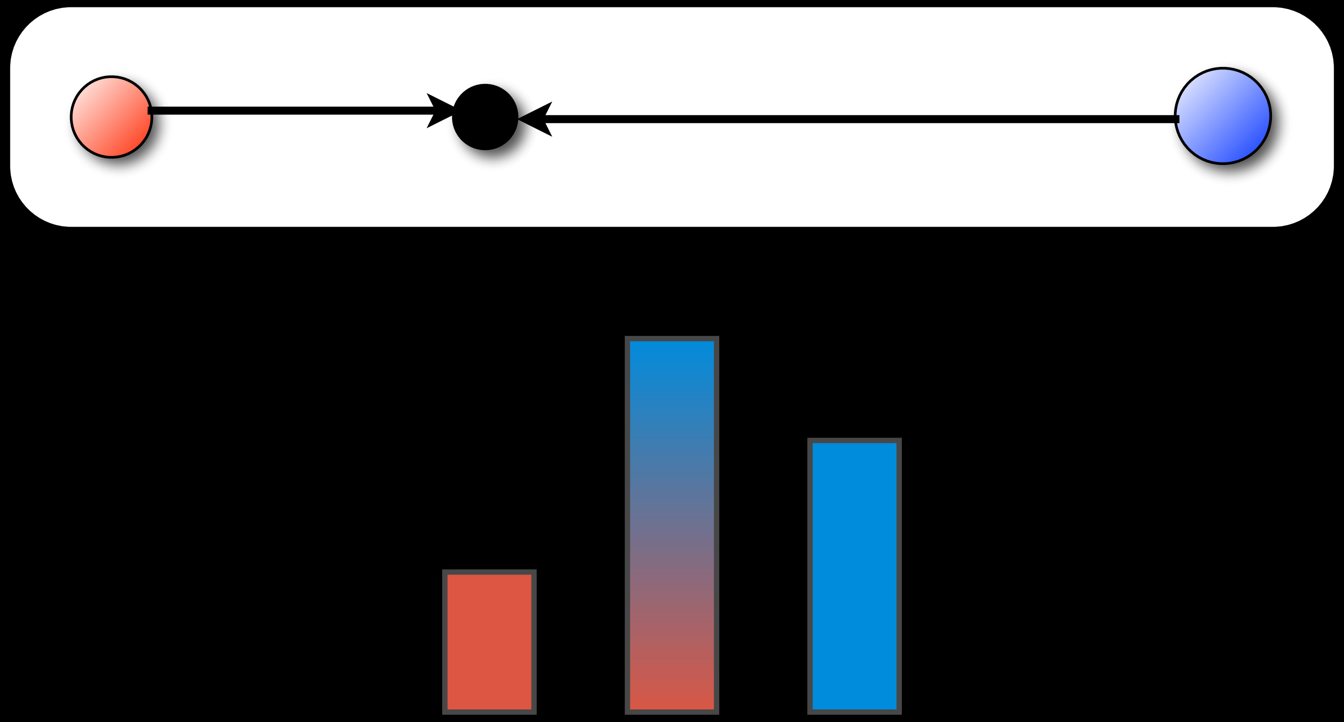


Relation to genetics

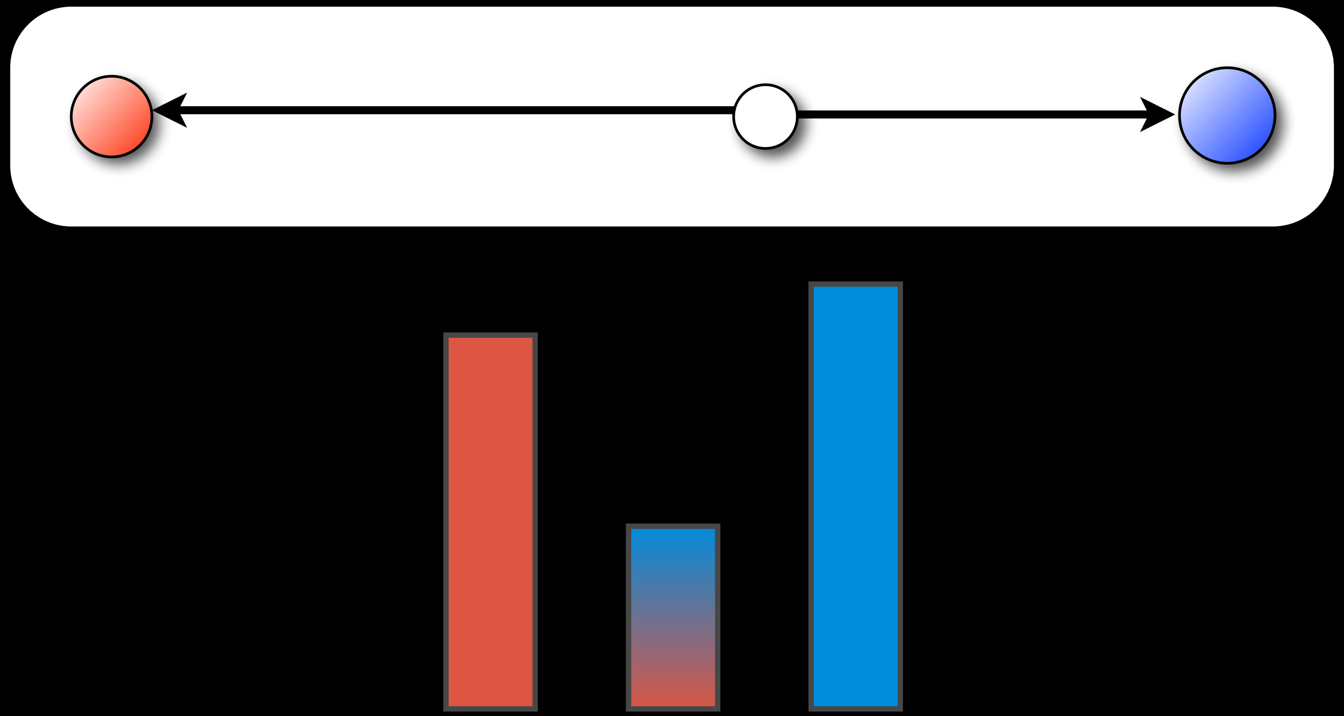
Different methodology from yesterday



Directional



Overdominance



Underdominance

Neutrality

Cressman, Evolutionary Dynamics and Extensive Form Games, MIT Press (2003)

Replicator dynamics

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

How do we calculate the internal fixed point?

When is $f_A = f_B$?

$$xa_1 + (1-x)a_0 = xb_1 + (1-x)b_0$$

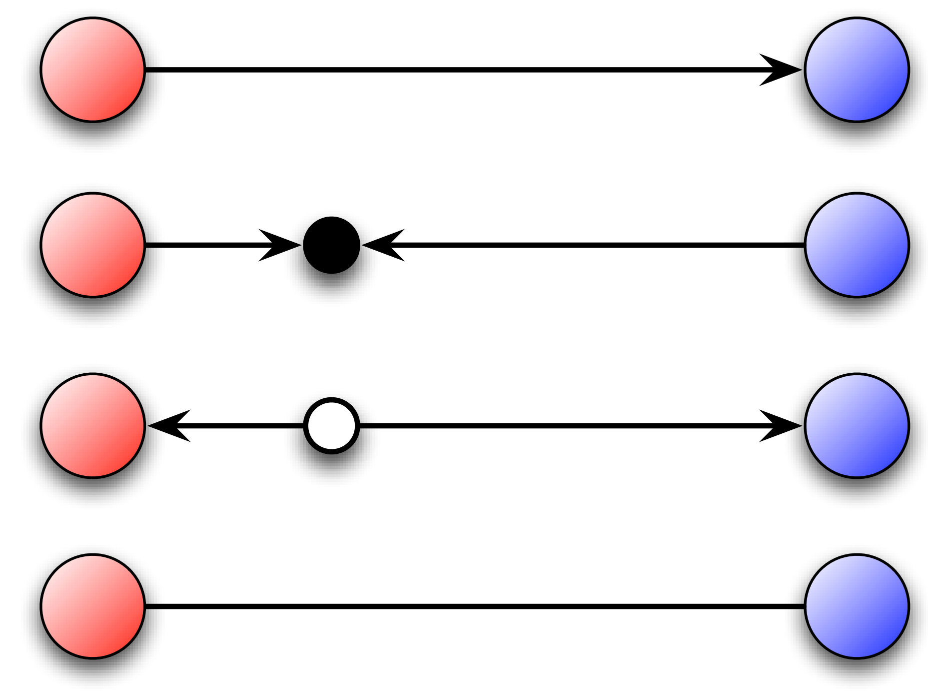
$$x^\star = \frac{b_0 - a_0}{(a_1 - a_0 - b_1 + b_0)}$$

Summary

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

Deterministic dynamics

$x_{\bullet} = 0$ $x_{\bullet} = 1$



If

Fixation probability

Risk dominance

1/3rd rule

From infinite to finite

Mathematical analysis for a finite population is more realistic

Emergence of cooperation and evolutionary stability in finite populations

Martin A. Nowak[1,2], Akira Sasaki[4], Christine Taylor[1,5] & Drew Fudenberg[3]

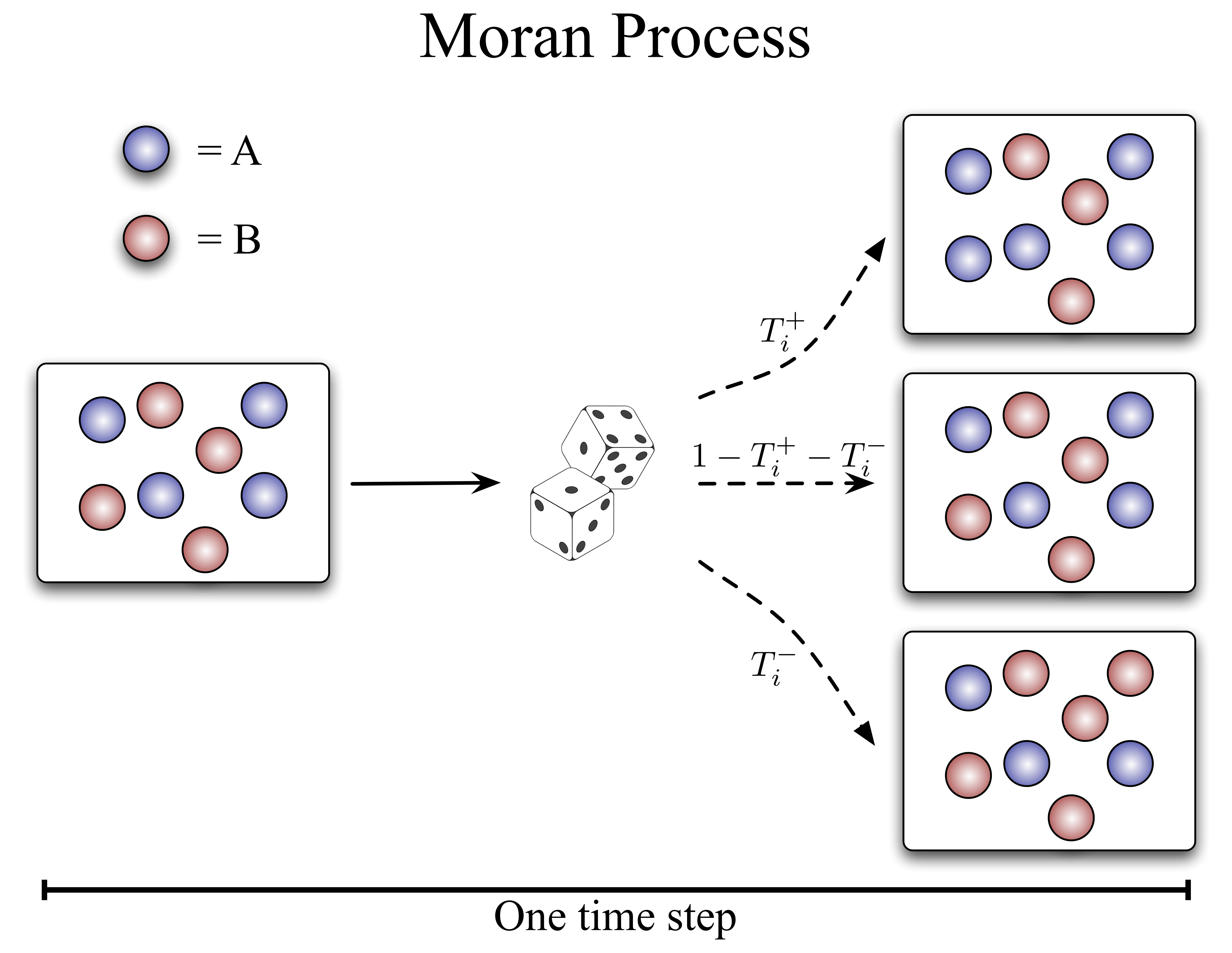
[1] Program for Evolutionary Dynamics, [2] Department of Organismic and Evolutionary Biology and Department of Mathematics, [3] Department of Economics, Harvard University, Cambridge, Massachusetts 02138, USA
[4] Department of Biology, Kyushu University, Fukuoka 812-8581, Japan
[5] Department of Mathematics, MIT, Cambridge, Massachusetts, 02139, USA

To explain the evolution of cooperation by natural selection has been a major goal of biologists since Darwin. Cooperators help others at a cost to themselves, while defectors receive the benefits of altruism without providing any help in return. The standard game dynamical formulation is the 'Prisoner's Dilemma'[1–11], in which two players have a choice between cooperation and defection. In the repeated game, cooperators using direct reciprocity cannot be exploited by defectors, but it is unclear how such cooperators can arise in the first place[12–15]. In general, defectors are stable against invasion by cooperators. This understanding is based on traditional concepts of evolutionary stability and

Publishing Group

NATURE | VOL 428 | 8 APRIL 2004 | www.nature.com/nature

Stochastic description

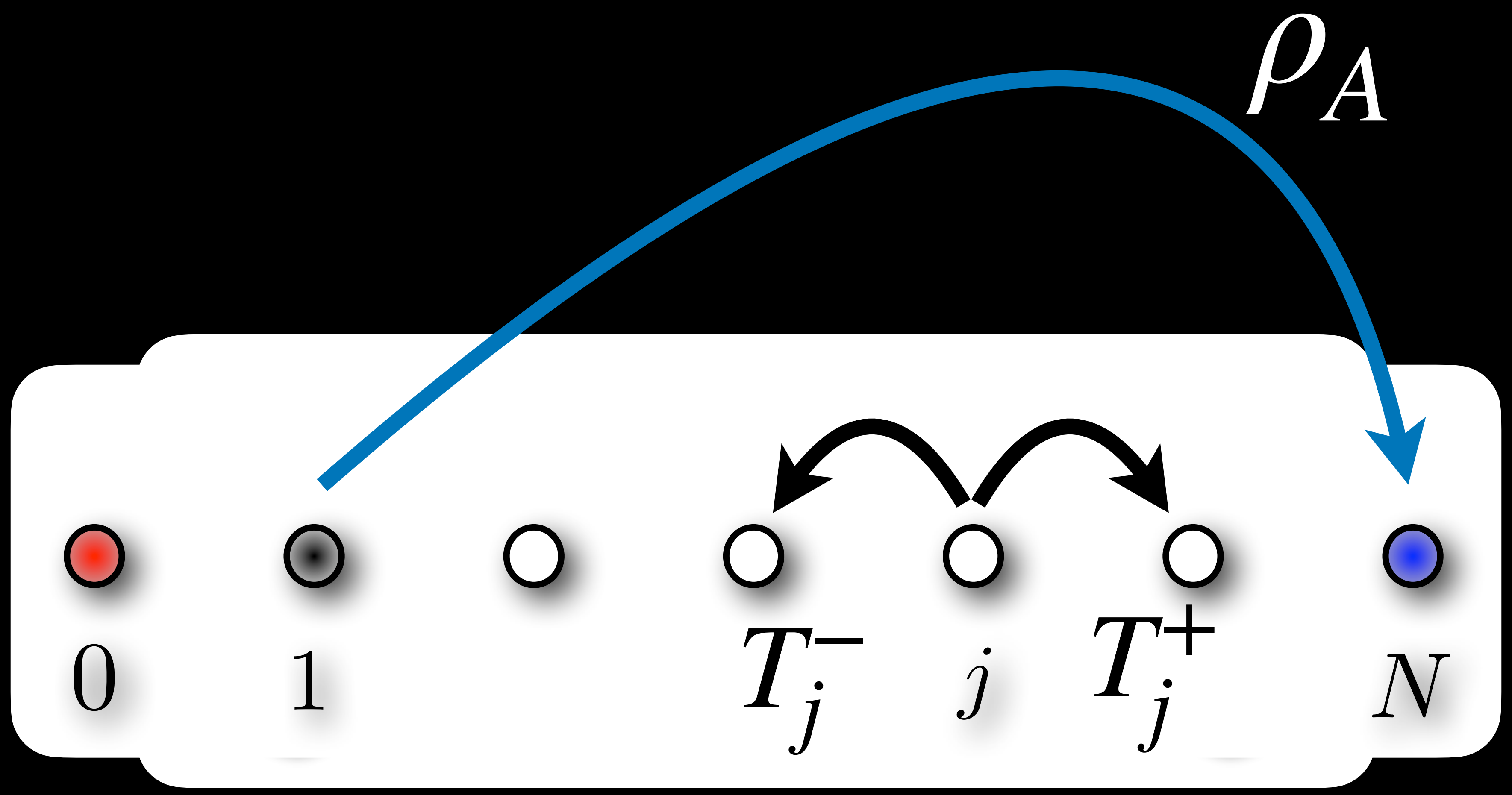


$$T_i^+ = \frac{i f_A}{i f_A + (N-i) f_B} \frac{N-i}{N},$$

$$T_i^- = \frac{(N-i) f_B}{i f_A + (N-i) f_B} \frac{i}{N}.$$

How fitness loads the dice!

Stochastic description



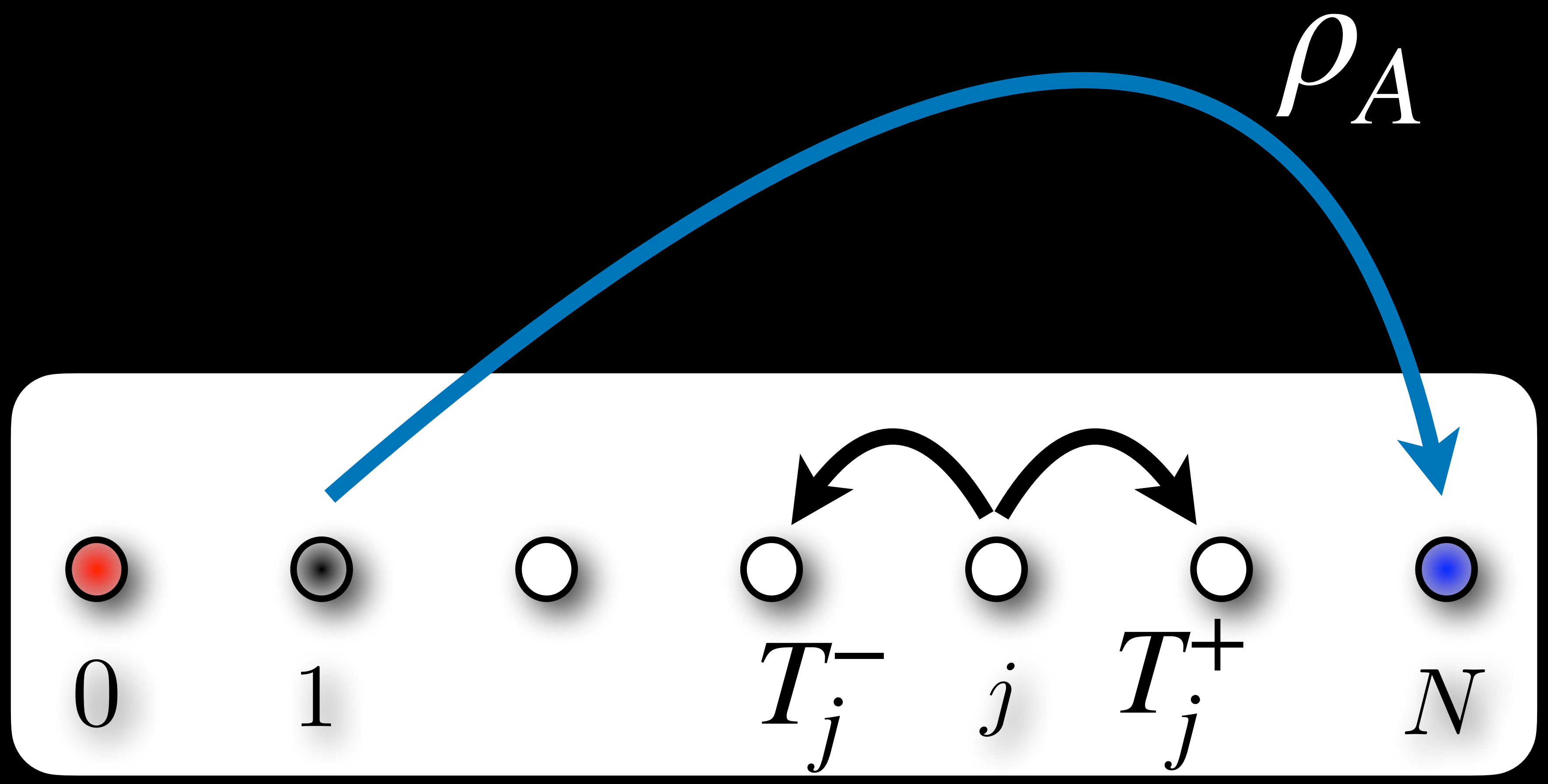
Under neutrality i.e. $T_j^+ = T_j^-$ we have $\rho_A = \dfrac{1}{N}$

New payoff to fitness mapping $f_A = 1 - \omega + \omega\pi_A$

Where ω tunes the impact of the game on the fitness

Nowak, Sasaki, Taylor, Fudenberg *Nature*. 2004

Stochastic description



Under weak selection, $\omega \ll 1$ we have,

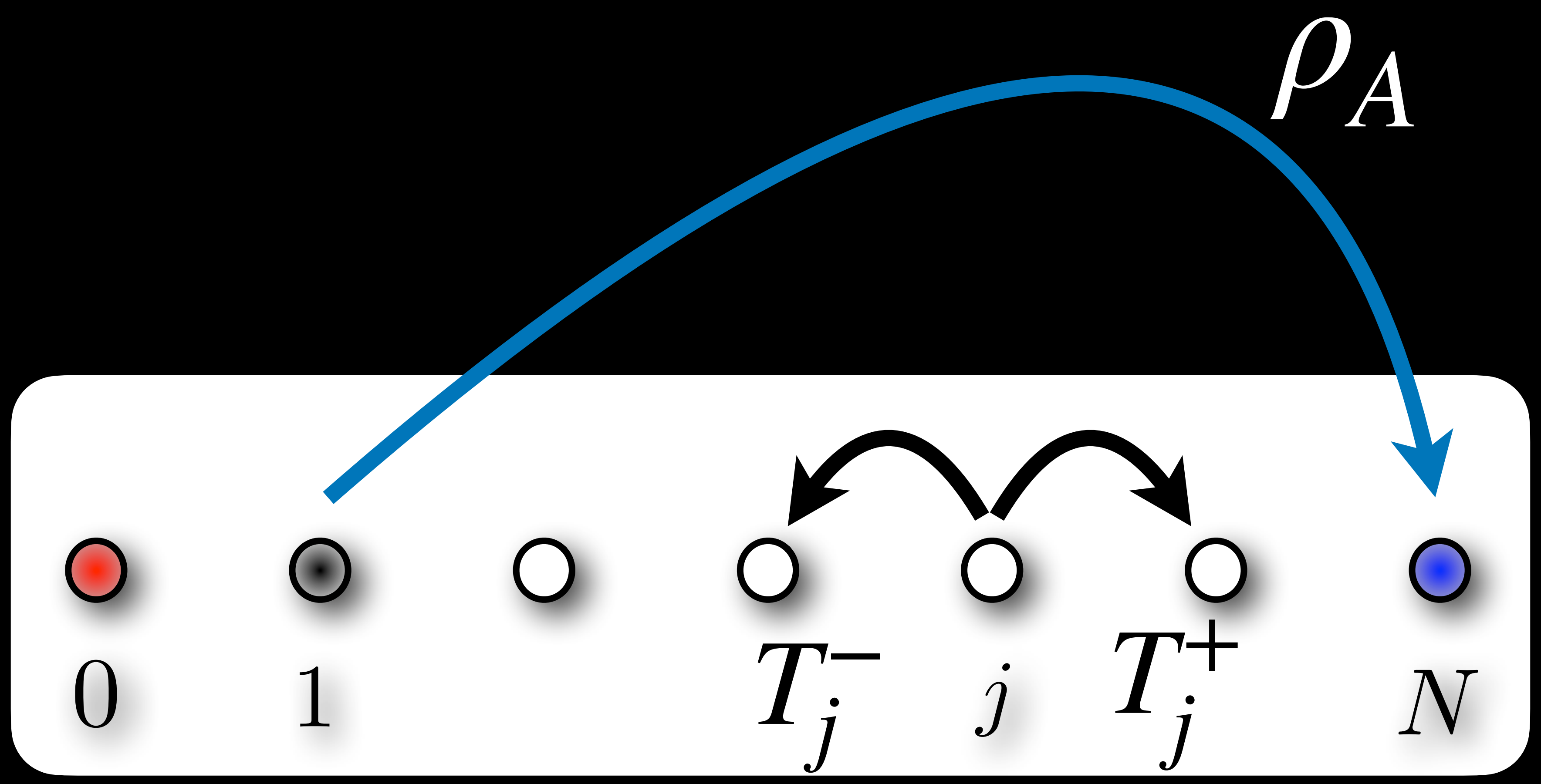
$$\rho_A \approx \frac{1}{N} + \frac{\omega}{N^2} \underbrace{\sum_{m=1}^{N-1} \sum_{j=1}^{m} (\pi_A - \pi_B)}_{\Gamma}$$

Strategy A is favoured by selection i.e. $\rho_A > 1/N$ if $\Gamma > 0$

$$a_0(2N-1) + a_1(N-2) > b_0(2N-4) + b_1(N+1)$$

Nowak, Sasaki, Taylor, Fudenberg *Nature*. 2004

Stochastic description



Thus for finite but large populations, for $\omega \ll 1$, we have $\rho_A > 1/N$ if

$$\boxed{2a_0 + a_1 > 2b_0 + b_1}$$

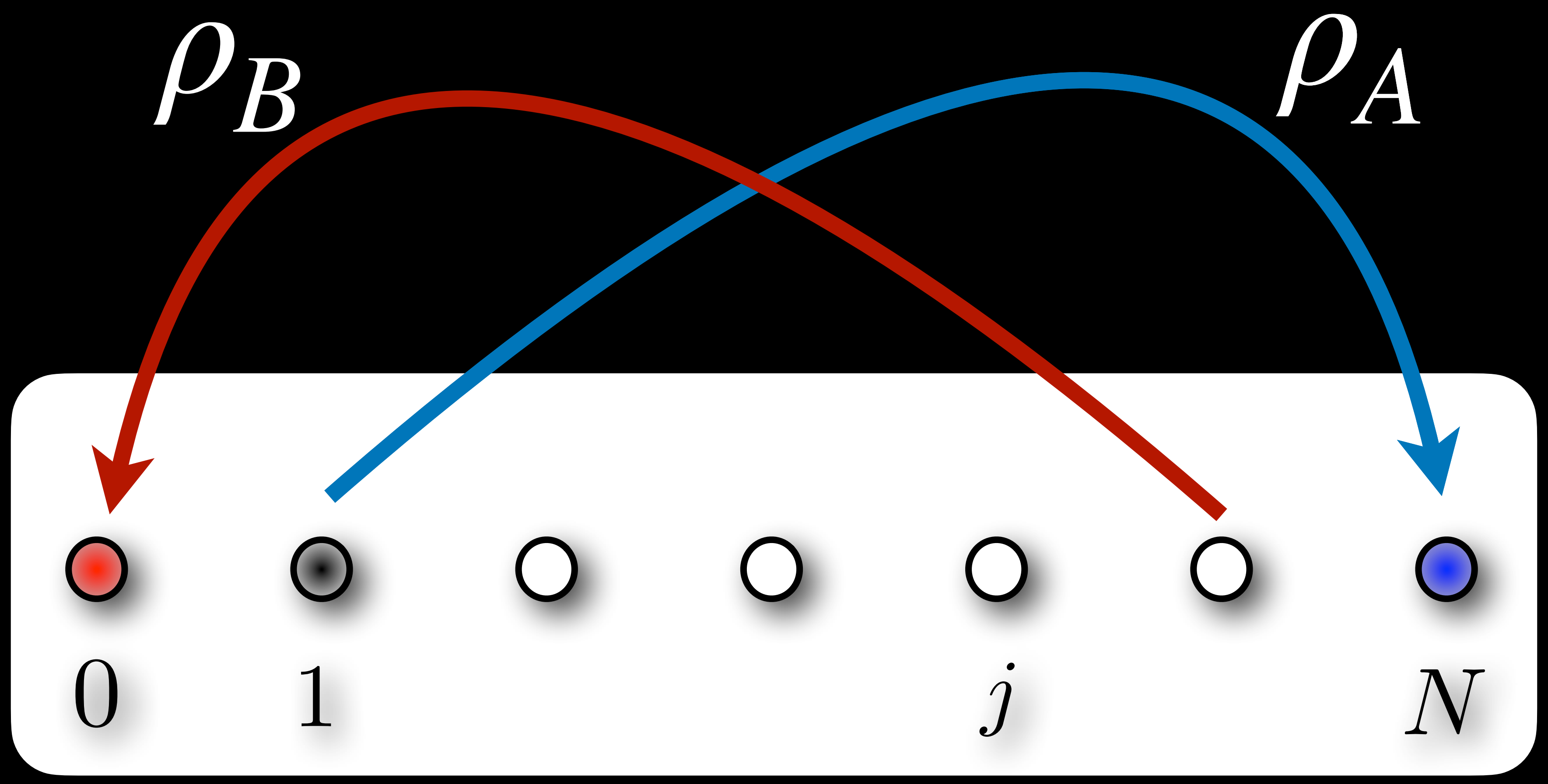
$$\begin{array}{c|cc} & \text{A} & \text{B} \\ \hline \text{A} & a_1 & a_0 \\ \text{B} & b_1 & b_0 \end{array}$$

$$x^\star = \frac{b_0 - a_0}{(a_1 - a_0 - b_1 + b_0)} < 1/3$$

One=third rule

Nowak, Sasaki, Taylor, Fudenberg Nature. 2004

Who replaces whom?

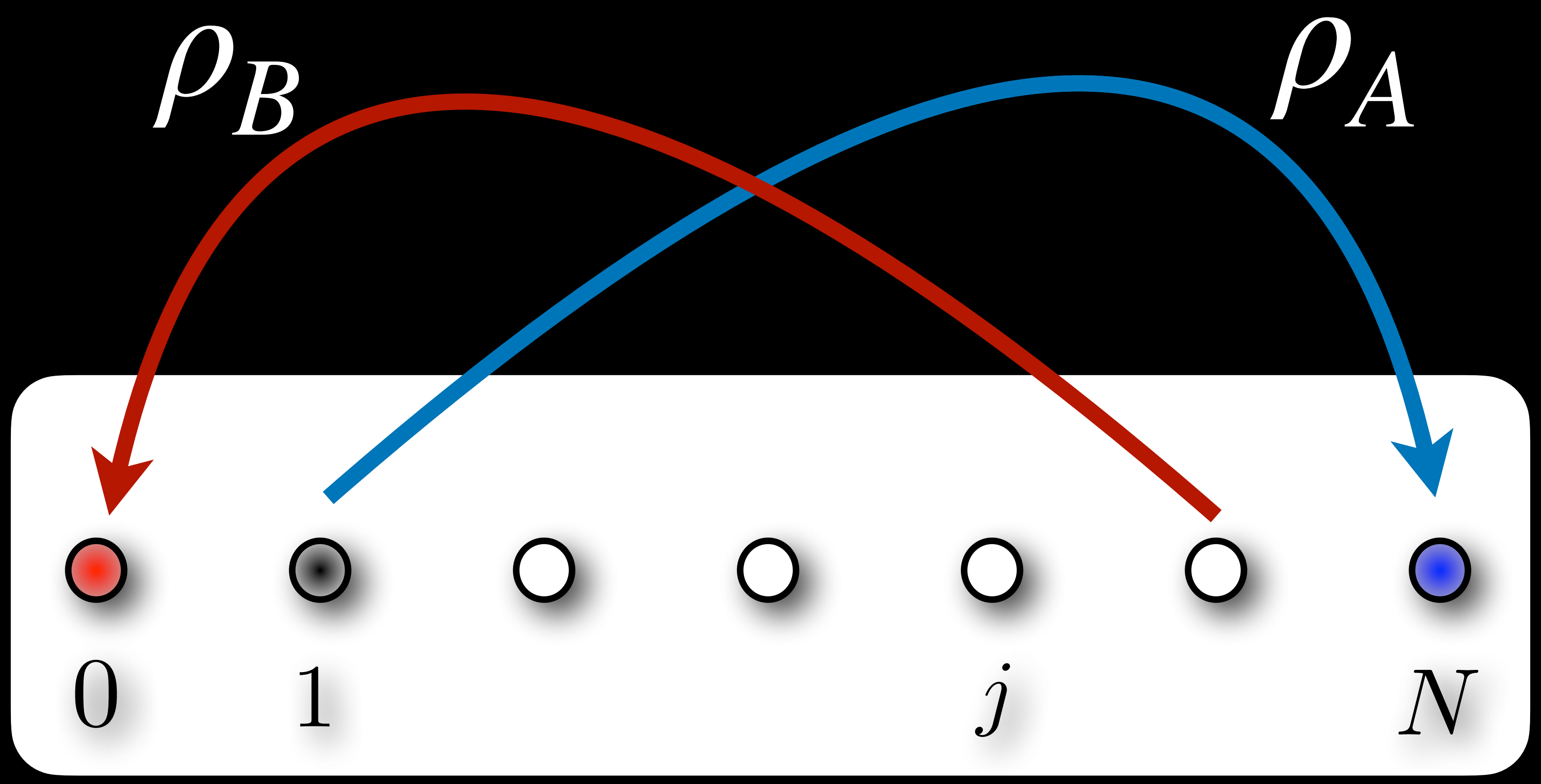


Is $\rho_A > \rho_B$? We look at the ratio $\frac{\rho_B}{\rho_A} < 1$

$$\frac{\rho_B}{\rho_A} = \prod_{j=1}^{N-1} \frac{T_j^-}{T_j^+} = exp\left[-w \sum_{j=1}^{N-1} \underbrace{(\pi_A - \pi_B)}_{\Phi}\right]$$

Nowak, Sasaki, Taylor, Fudenberg Nature. 2004

Who replaces whom?



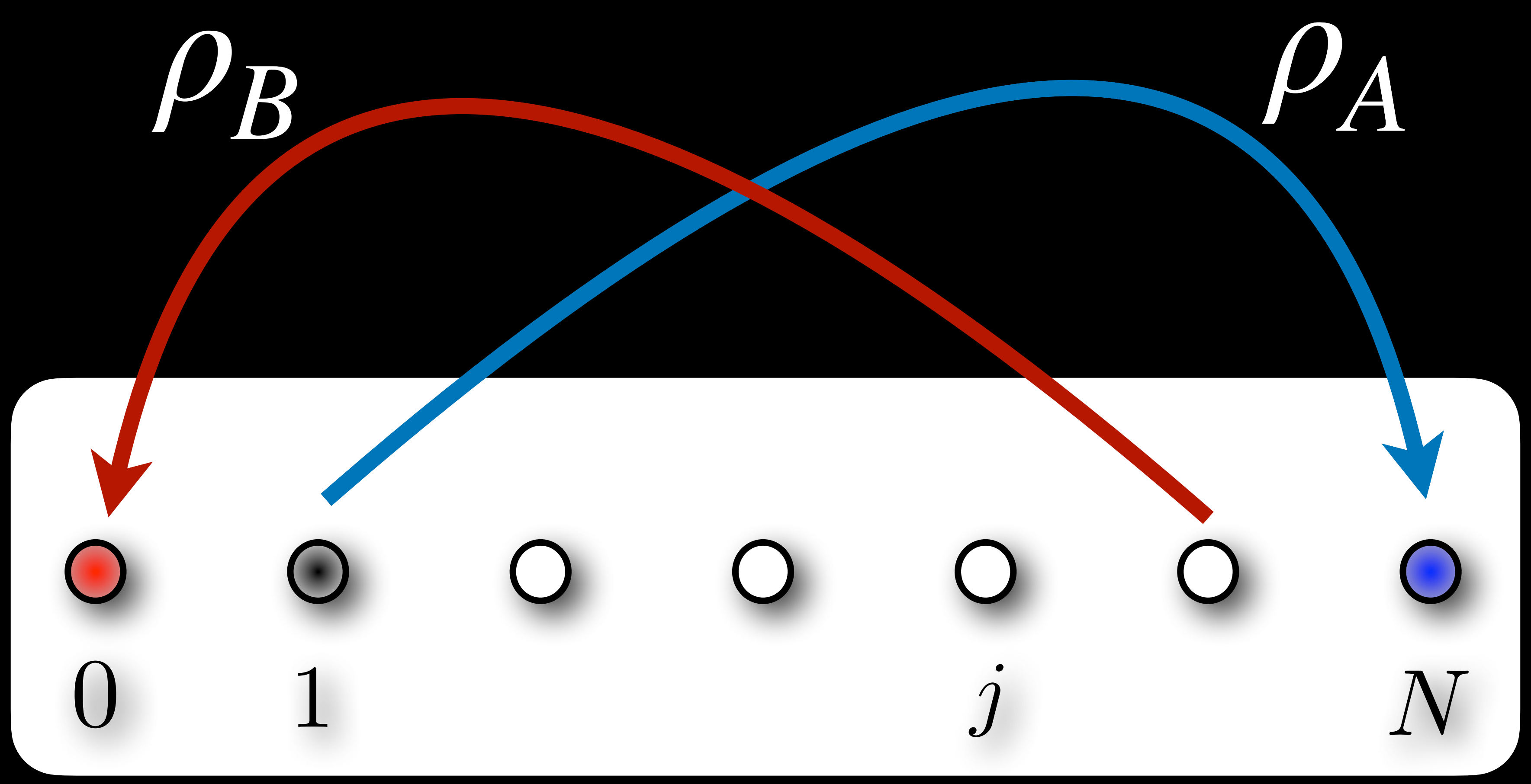
Thus $\dfrac{\rho_B}{\rho_A} < 1$ if $\Phi > 0$

Then for finite populations we have,

$$(N-2)a_1 + Na_0 > Nb_1 + (N-2)b_0$$

Nowak, Sasaki, Taylor, Fudenberg Nature. 2004

Who replaces whom?



For finite but large populations, $\rho_A > \rho_B$ if

$$\boxed{a_1 + a_0 > b_1 + b_0}$$

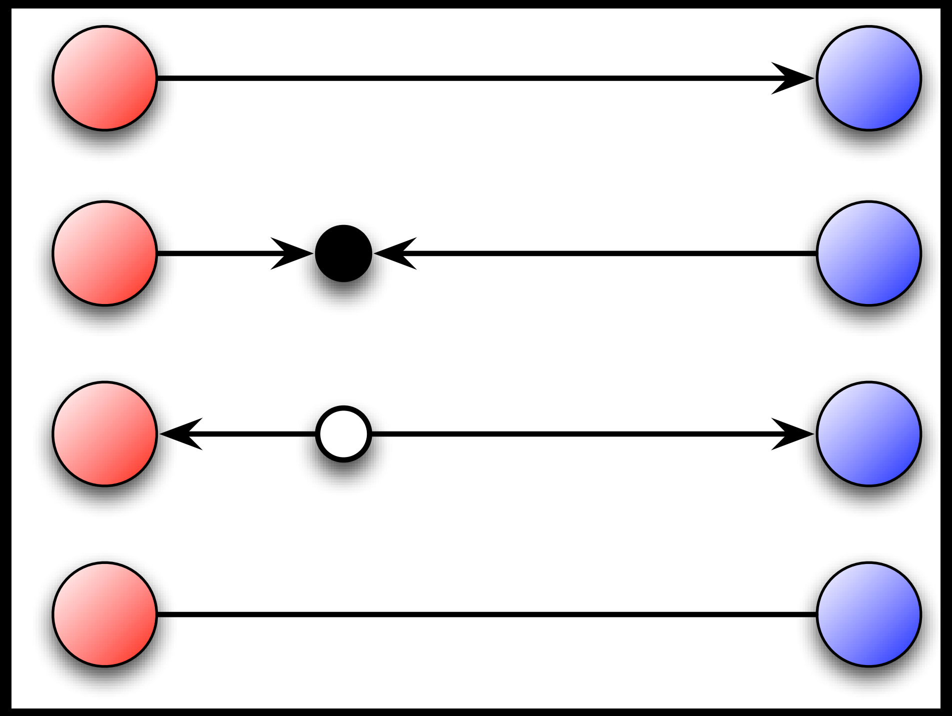
$$\begin{array}{ccc} & \text{A} & \text{B} \\ \text{A} & a_1 & a_0 \\ \text{B} & b_1 & b_0 \end{array}$$

Nowak, Sasaki, Taylor, Fudenberg Nature. 2004

Summary

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

Deterministic dynamics



Stochastic dynamics

$$\rho_A > 1/N$$

$$\rho_A > \rho_B$$

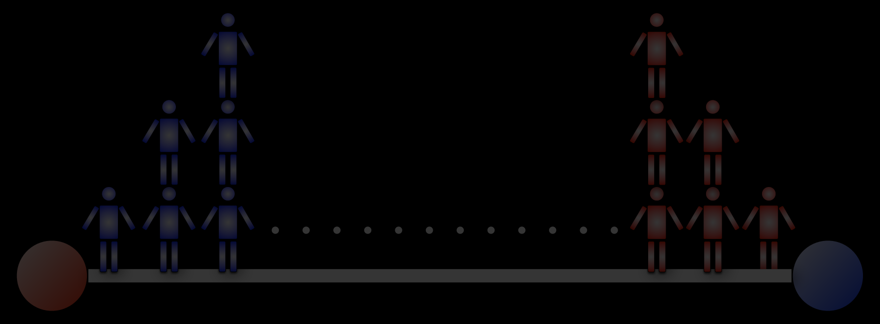
$$\boxed{2a_0 + a_1 > 2b_0 + b_1}$$

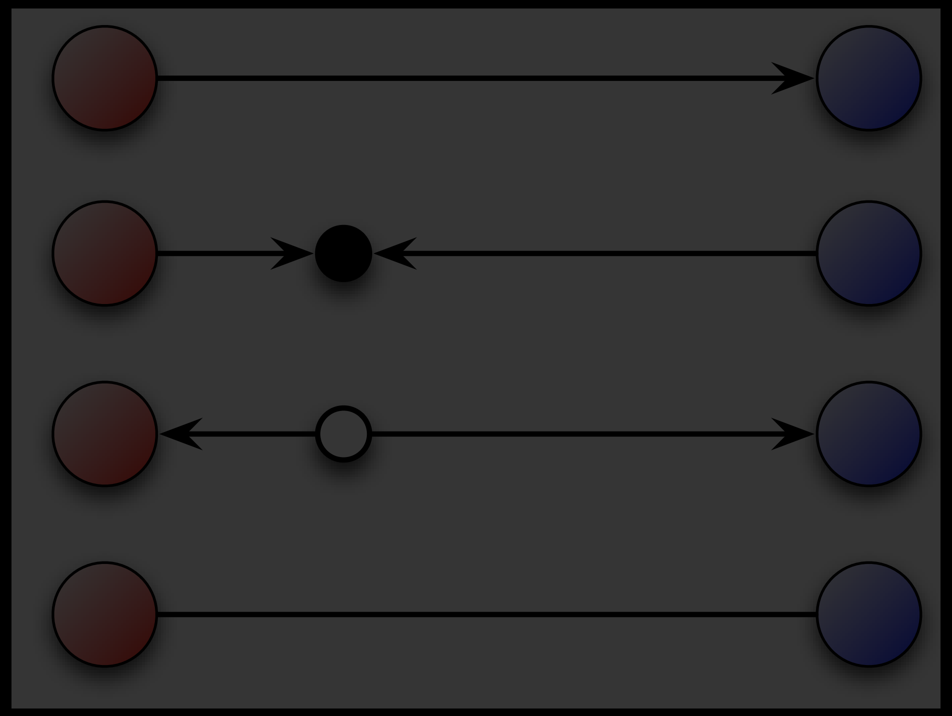
$$\boxed{a_0 + a_1 > b_0 + b_1}$$

Summary

How does this look like for multiplayer games?

Deterministic dynamics





Stochastic dynamics

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Summary

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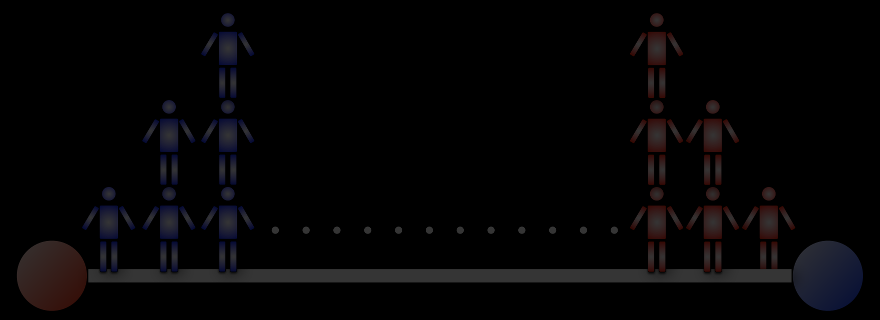
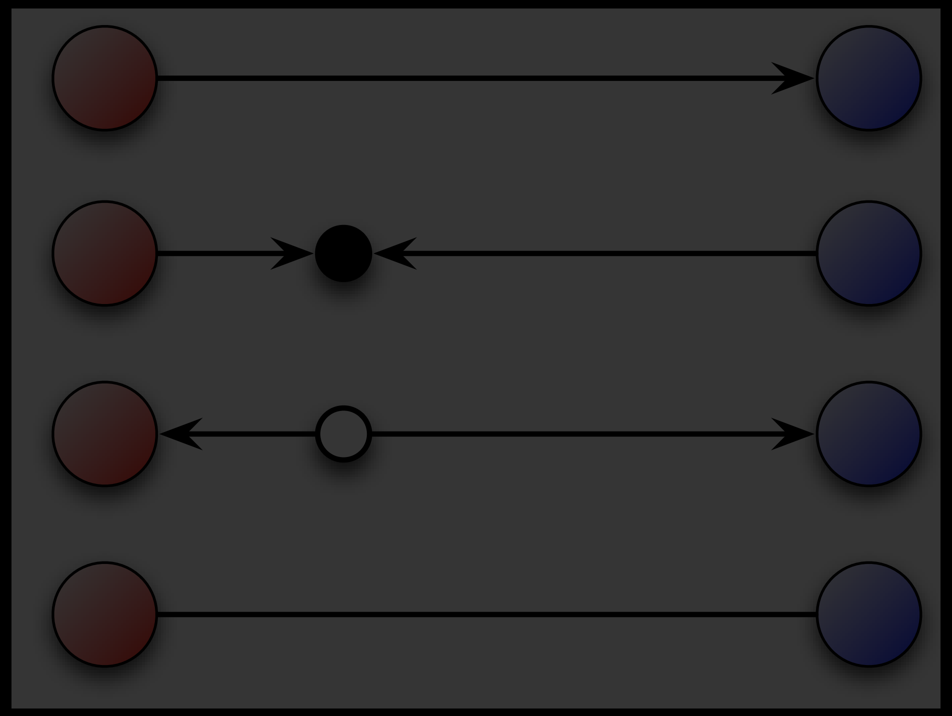
Deterministic dynamics





Stochastic dynamics

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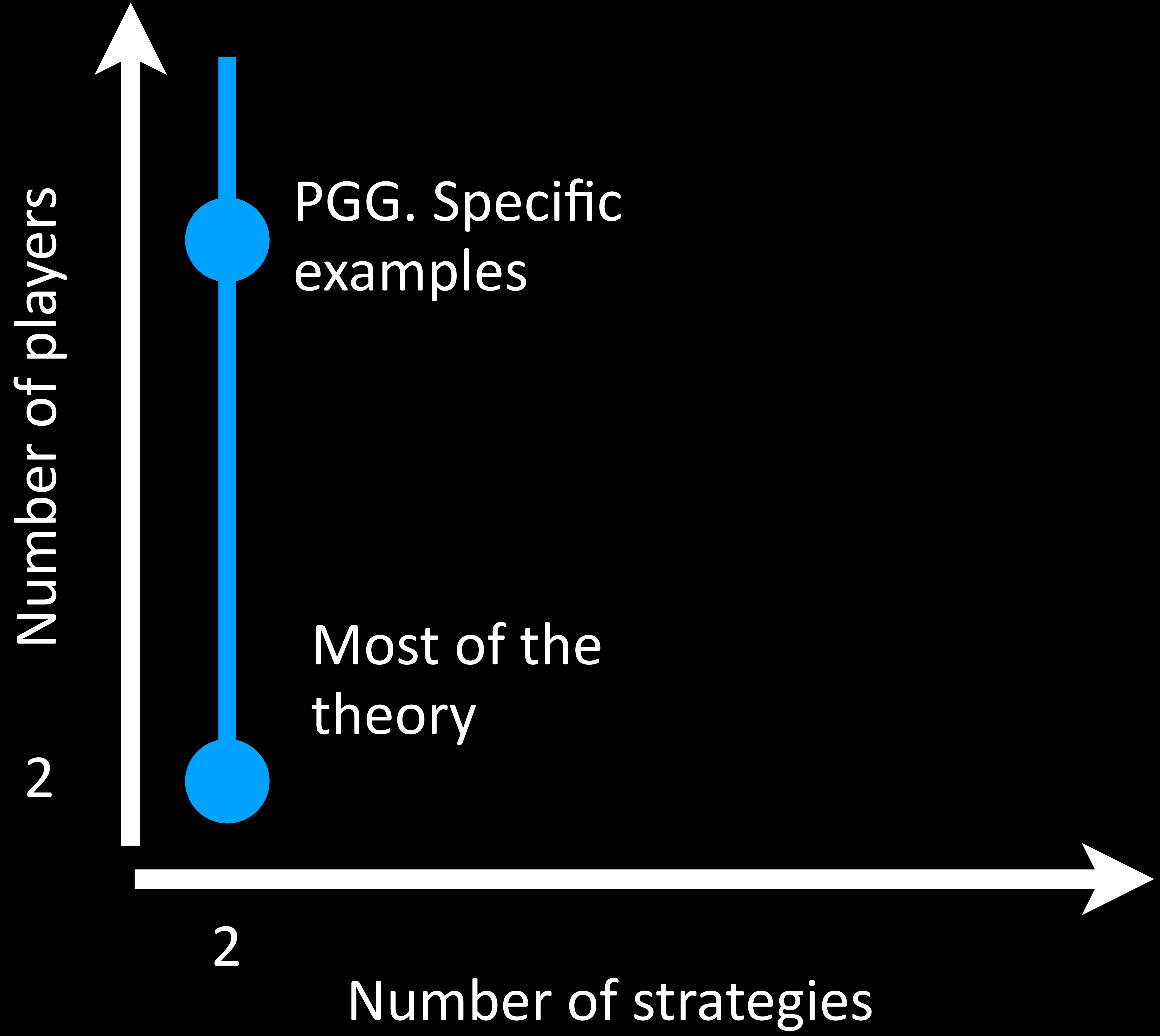
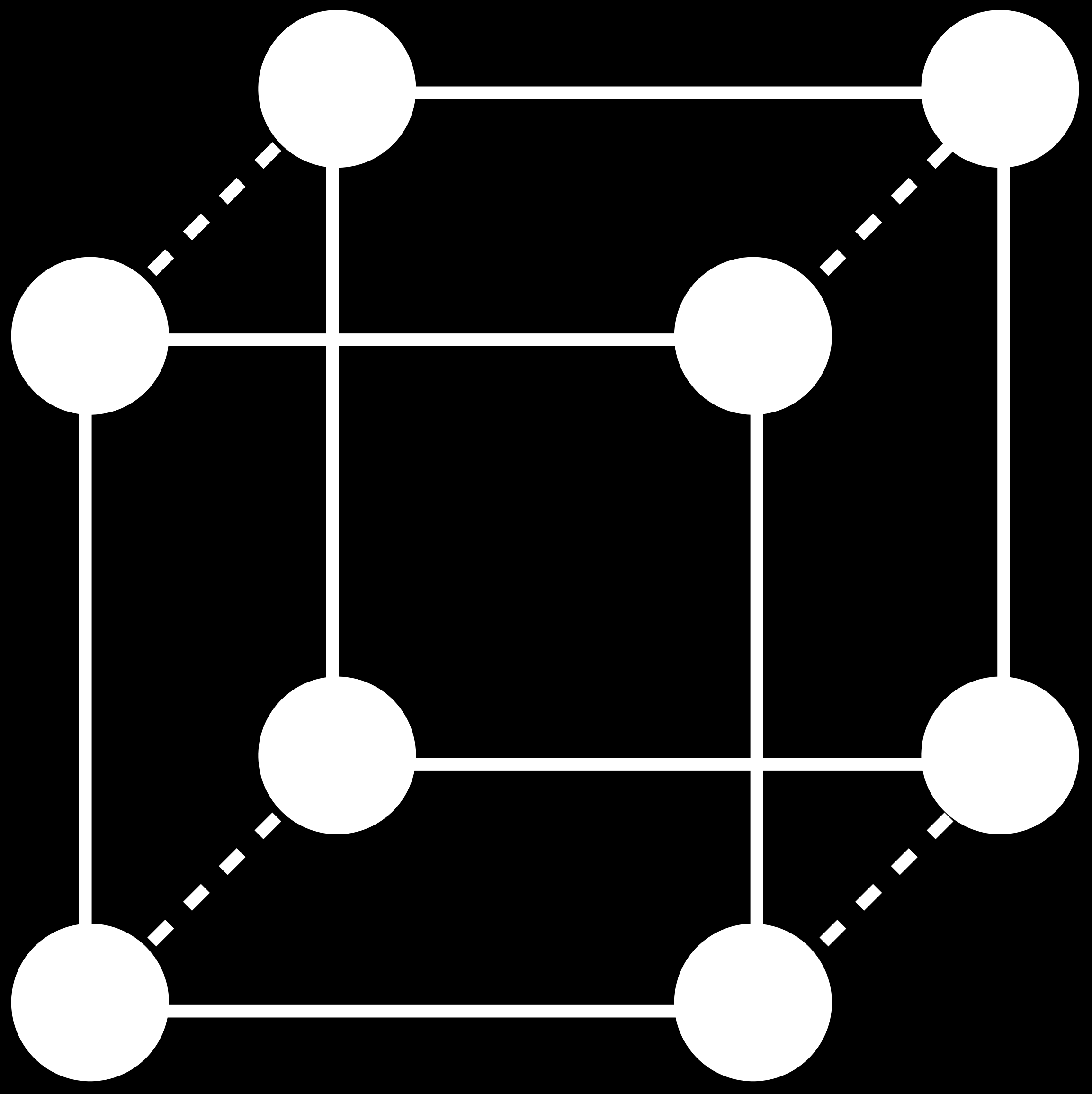
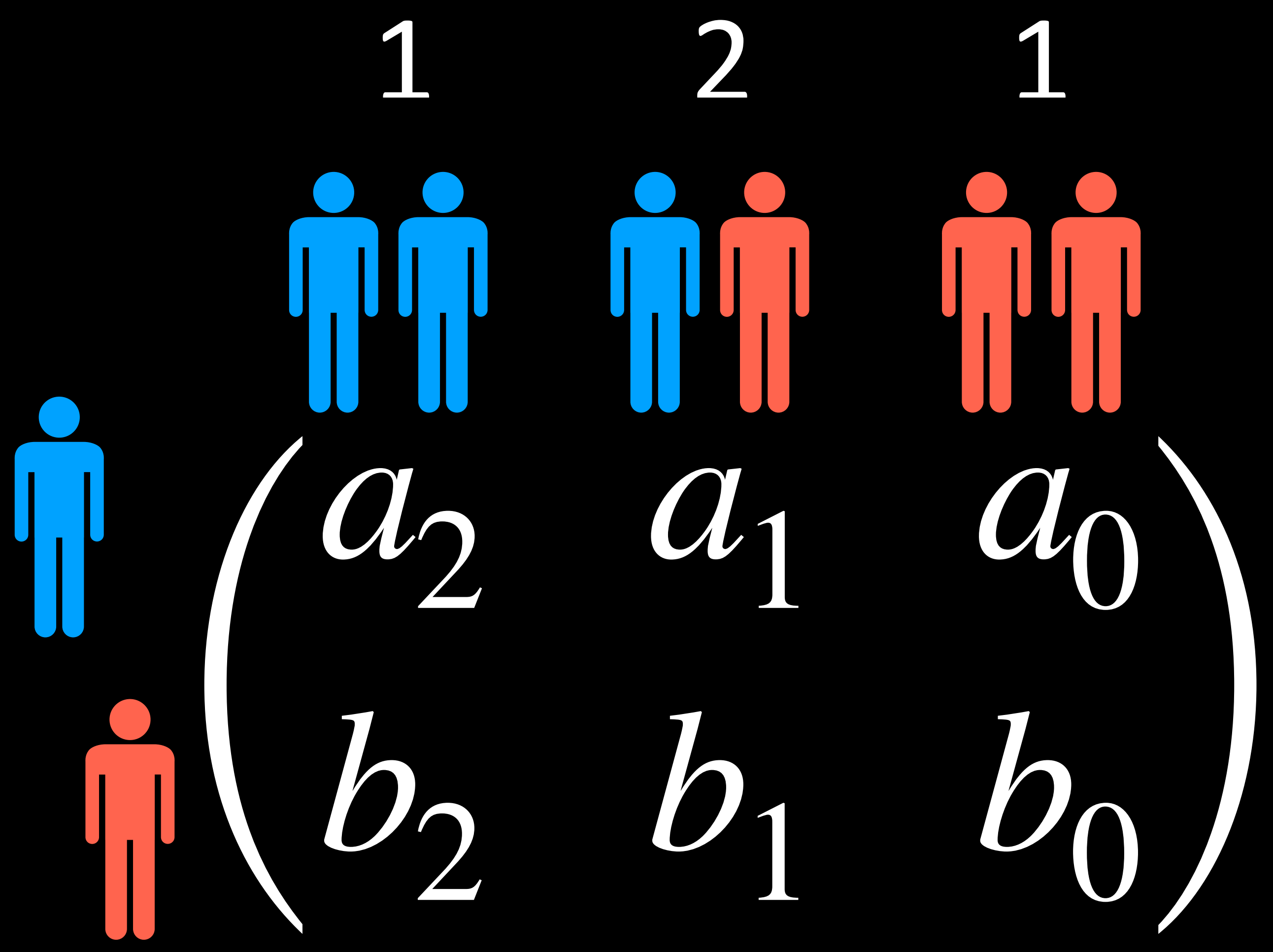


PGG. Specific examples

Most of the theory

Start simple with



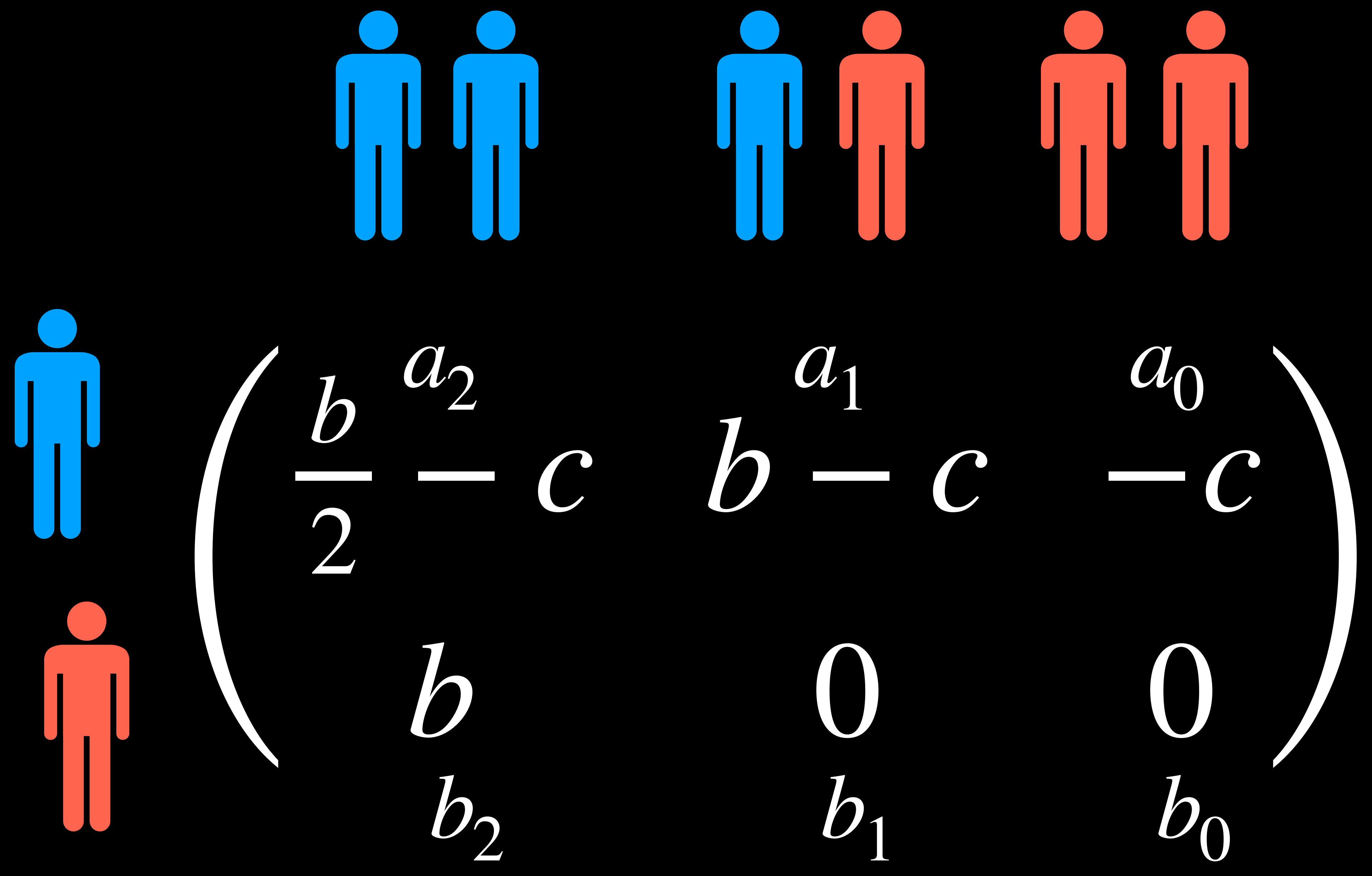


$$\begin{pmatrix} a_2 & a_1 & a_0 \\ b_2 & b_1 & b_0 \end{pmatrix}$$

$2 \times 2 \times 2$

Exercise - Too many cooks!

Lets say you want to bake a cake. For each chef, baking costs c leading to a delicious cake b . Two chefs can bake the cake perfectly but three diminish the quality.

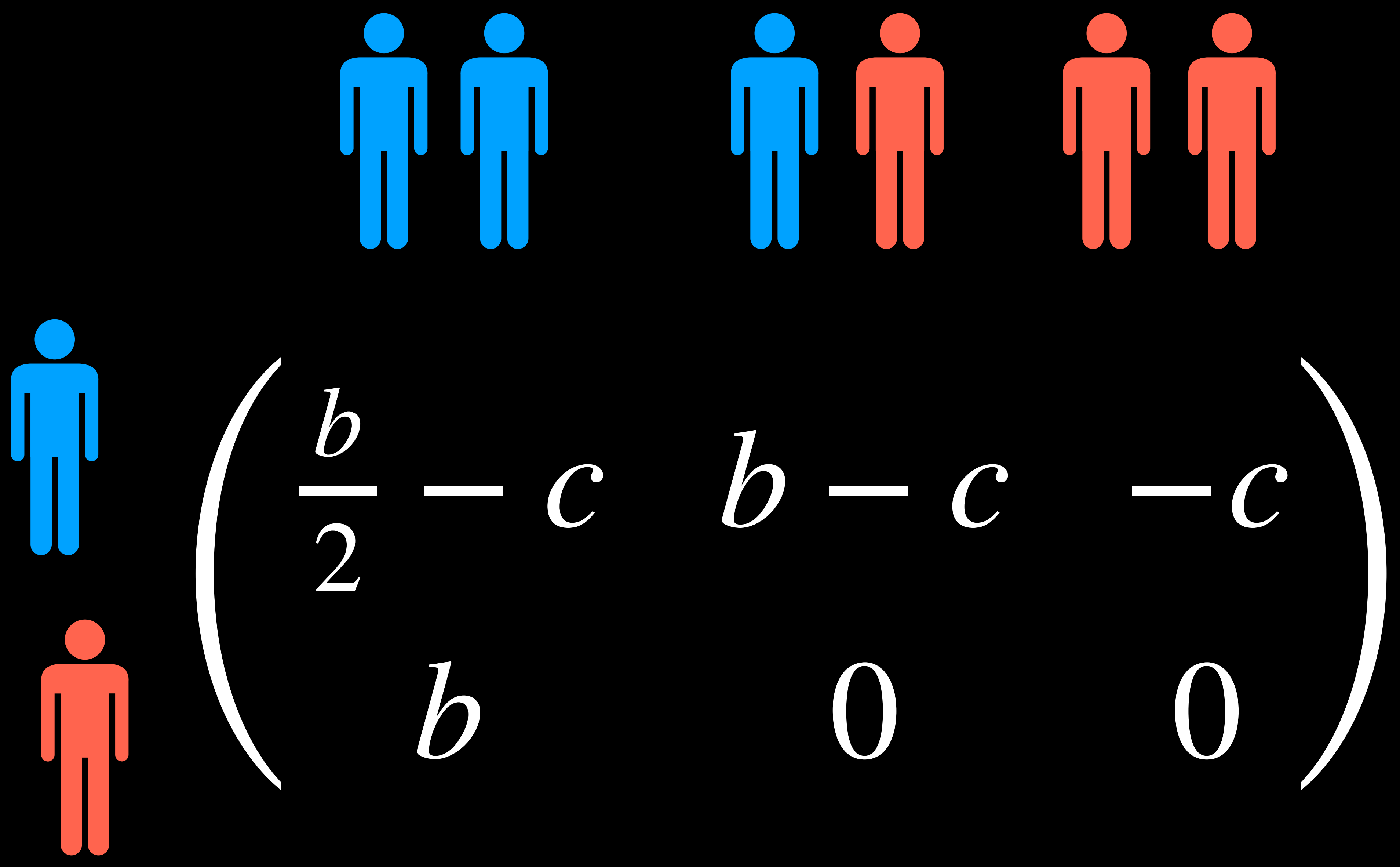


$$\begin{pmatrix} \overset{a_2}{\frac{b}{2} - c} & \overset{a_1}{b - c} & \overset{a_0}{-c} \\ \underset{b_2}{b} & \underset{b_1}{0} & \underset{b_0}{0} \end{pmatrix}$$

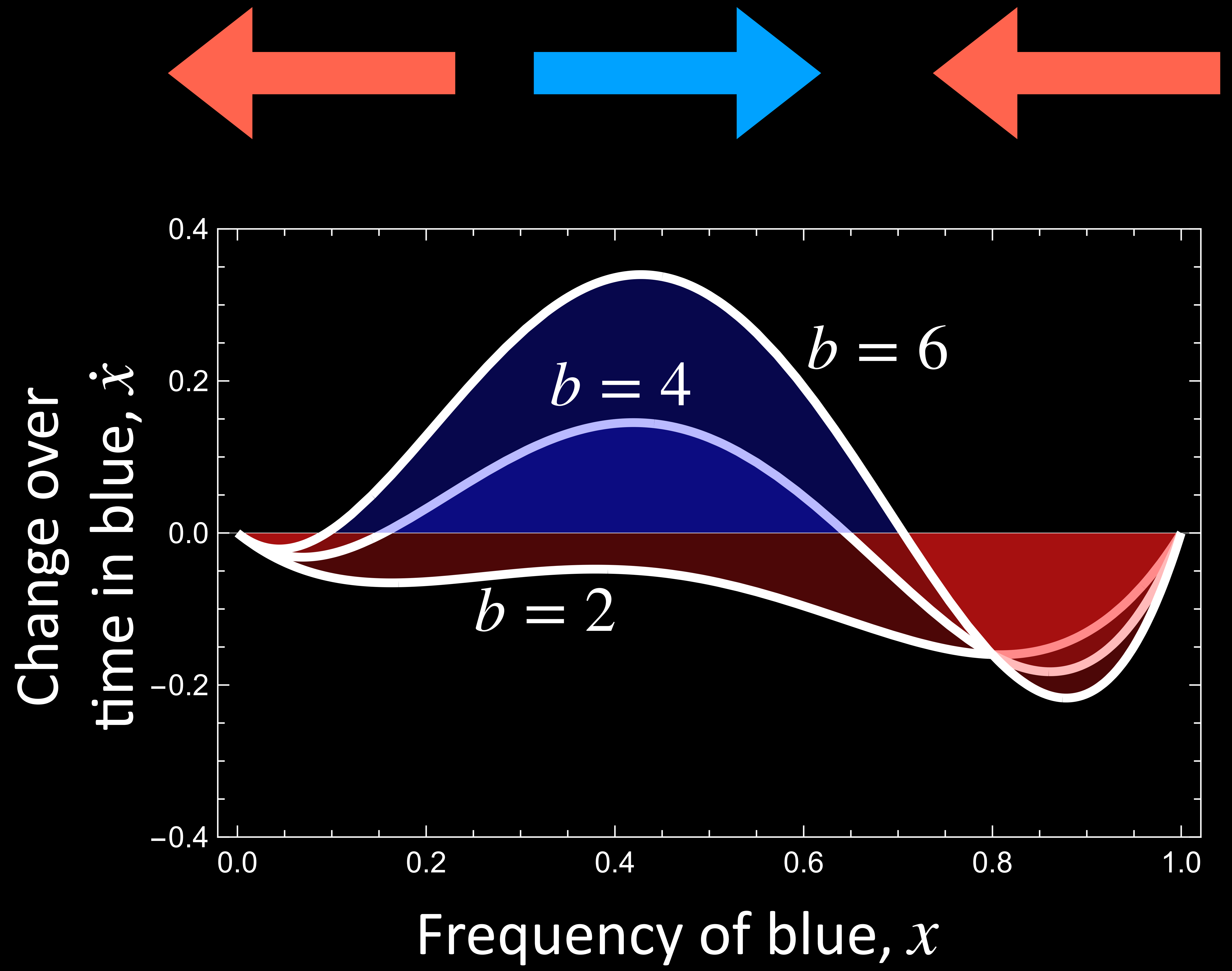
$$f_{\color{blue}\bullet} = \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} a_k \qquad f_{\color{red}\bullet} = \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} b_k$$

$$\dot{x} = x(1-x)(f_{\color{blue}\bullet} - f_{\color{red}\bullet})$$

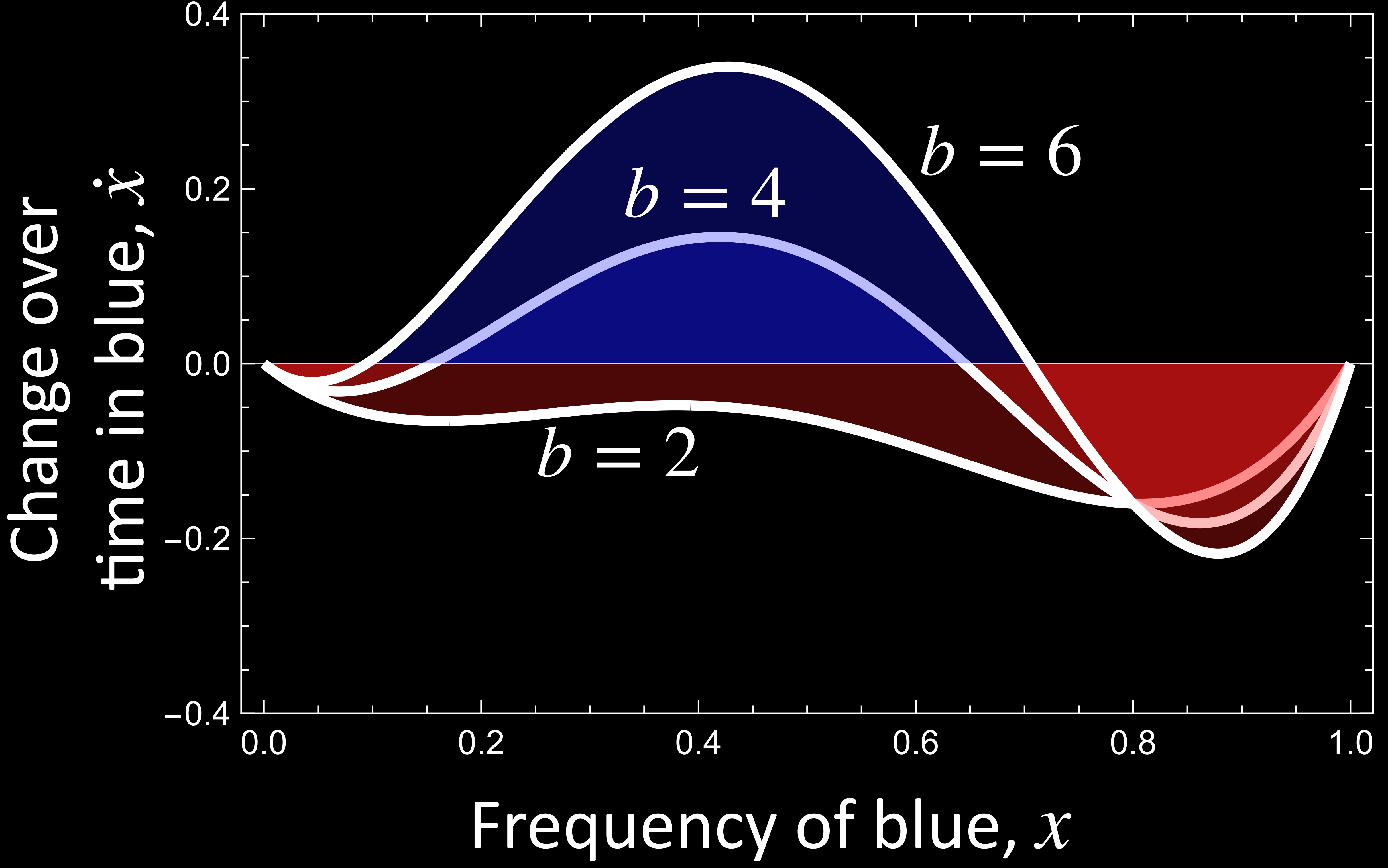
Exercise - Too many cooks!



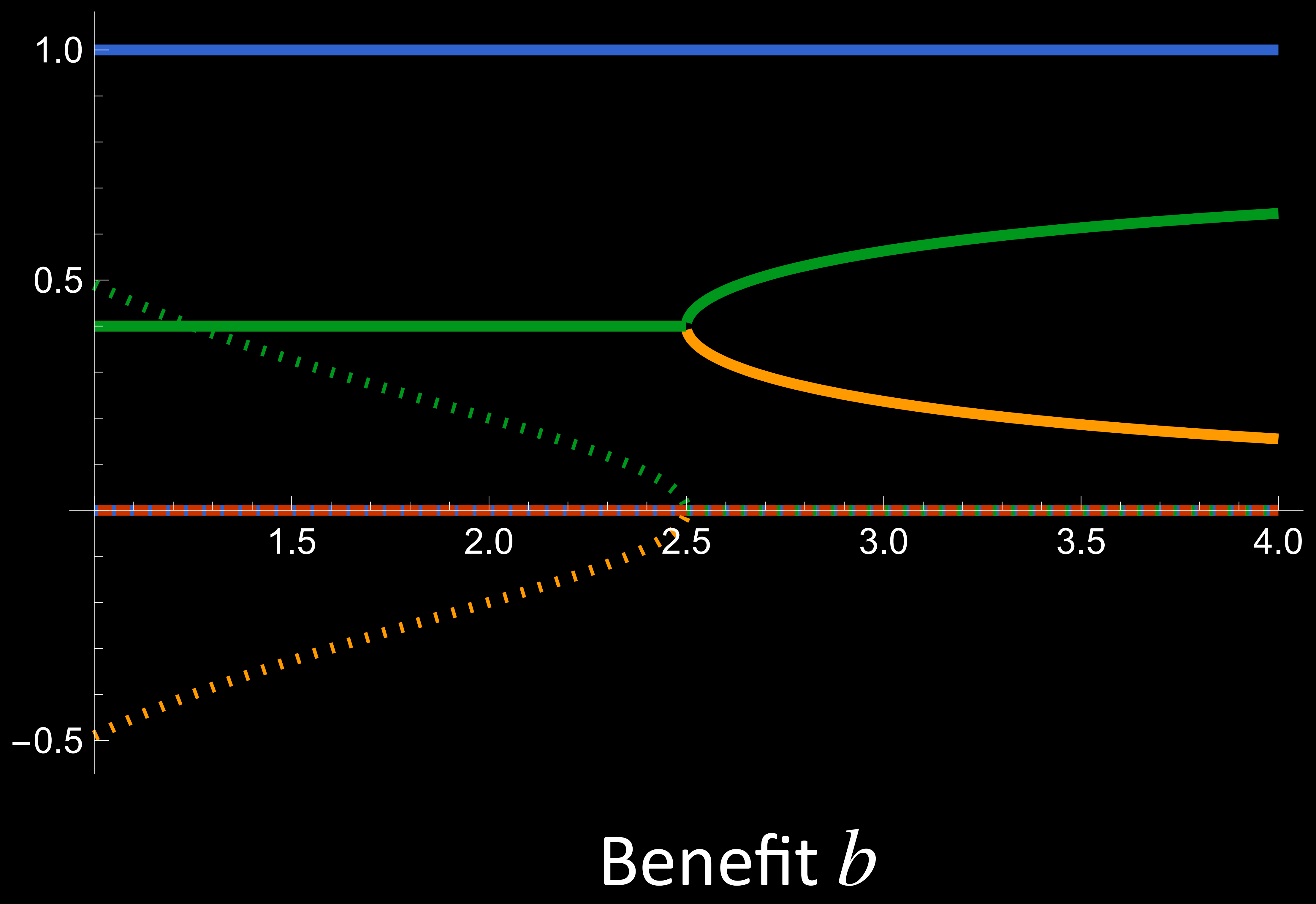
$$\begin{pmatrix} \frac{b}{2} - c & b - c & -c \\ b & 0 & 0 \end{pmatrix}$$

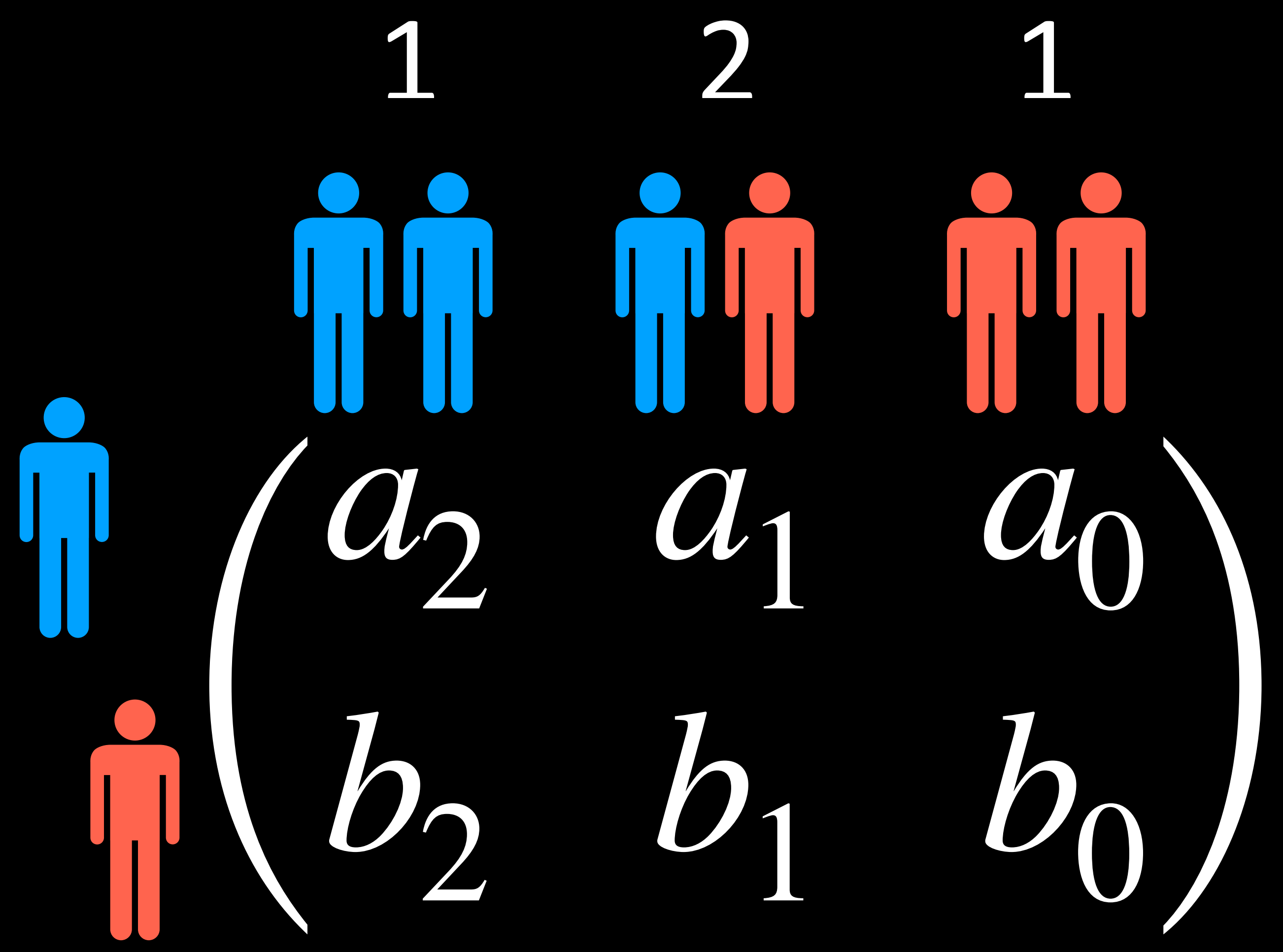


Exercise - Too many cooks!



Solution space





$$\begin{pmatrix} a_2 & a_1 & a_0 \\ b_2 & b_1 & b_0 \end{pmatrix}$$

How many sign changes?

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Gains from switching and evolutionary stability in multi-player matrix games

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HIGHLIGHTS

- We study the evolutionary dynamics of two-strategy symmetric multi-player matrix games.
- We make use of the theory of polynomials in Bernstein form.
- We unify, simplify and extend previous work on evolutionary multi-player games.

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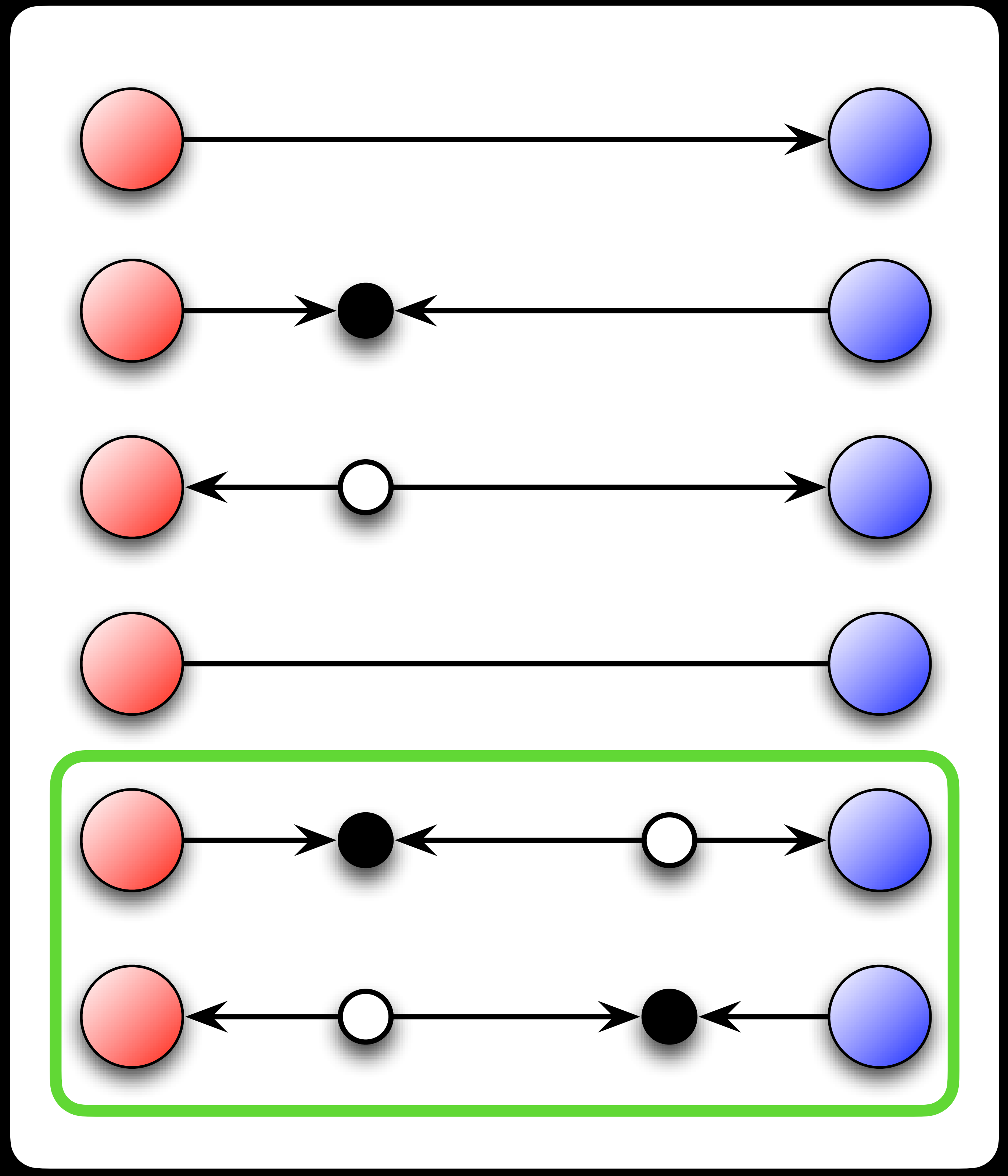
Evolutionary game theory
Replicator dynamics
Polynomials in Bernstein form
Public goods games

ABSTRACT

In this paper we unify, simplify, and extend previous work on the evolutionary dynamics of symmetric N-player matrix games with two pure strategies. In such games, gains from switching strategies depend, in general, on how many other individuals in the group play a given strategy. As a consequence, the gain function determining the gradient of selection can be a polynomial of degree $N-1$. In order to deal with the intricacy of the resulting evolutionary dynamics, we make use of the theory of polynomials in Bernstein form. This theory implies a tight link between the sign pattern of the gains from switching on the one hand and the number and stability of the rest points of the replicator dynamics on the other hand. While this relationship is a general one, it is most informative if gains from switching have at most two sign changes, as is the case for most multi-player matrix games considered in the literature. We demonstrate that previous results for public goods games are easily recovered and extended using this observation. Further examples illustrate how focusing on the sign pattern of the gains from switching obviates the need for a more involved analysis.

Deterministic dynamics

$x_{\bullet} = 0$ $x_{\bullet} = 1$

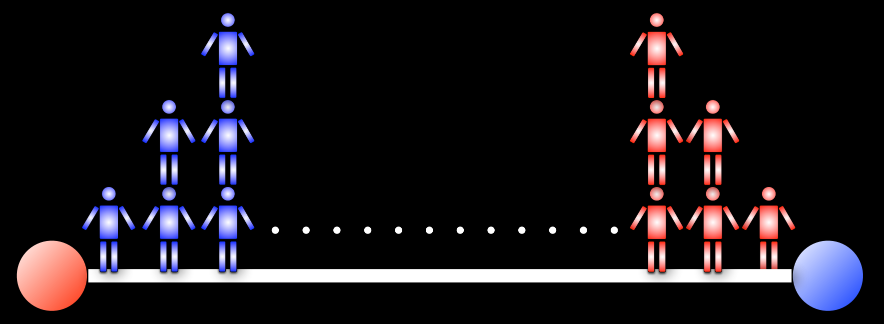


$2 \times 2 \times 2$

Summary

$$\begin{pmatrix} a_{d-1} & a_{d-2} & \cdots & a_k & \cdots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \cdots & b_k & \cdots & b_1 & b_0 \end{pmatrix}$$

Deterministic dynamics



The maximum number of internal isolated fixed points is $d-1$

Stochastic dynamics

$$\rho_A > 1/N$$

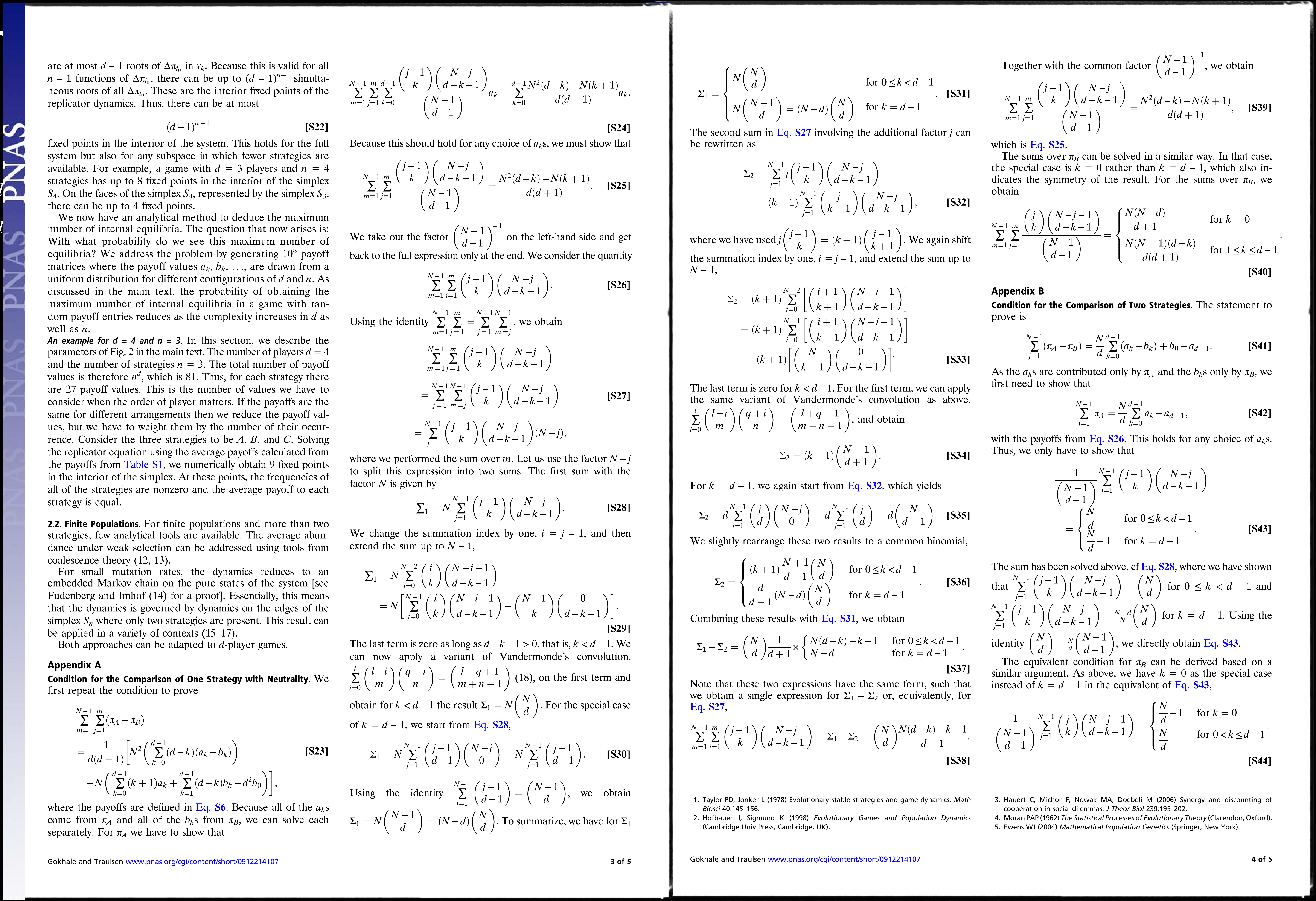
$$\rho_A > \rho_B$$

$$\boxed{2a_0 + a_1 > 2b_0 + b_1}$$

$$\boxed{a_0 + a_1 > b_0 + b_1}$$

Sur

$$\left(\begin{matrix} a_{d-1} & a_d \\ b_{d-1} & b_d \end{matrix}\right.$$



are at most $d-1$ roots of $\Delta\pi_{i_0}$ in x_k. Because this is valid for all $n-1$ functions of $\Delta\pi_{i_0}$, there can be up to $(d-1)^{n-1}$ simultaneous roots of all $\Delta\pi_{i_0}$. These are the interior fixed points of the replicator dynamics. Thus, there can be at most

$$(d-1)^{n-1} \qquad \textbf{[S22]}$$

fixed points in the interior of the system. This holds for the full system but also for any subspace in which fewer strategies are available. For example, a game with $d = 3$ players and $n = 4$ strategies has up to 8 fixed points in the interior of the simplex S_4. On the faces of the simplex S_4, represented by the simplex S_3, there can be up to 4 fixed points.

We now have an analytical method to deduce the maximum number of internal equilibria. The question that now arises is: With what probability do we see this maximum number of equilibria? We address the problem by generating 10^8 payoff matrices where the payoff values $a_k, b_k, \ldots$, are drawn from a uniform distribution for different configurations of d and n. As discussed in the main text, the probability of obtaining the maximum number of internal equilibria in a game with random payoff entries reduces as the complexity increases in d as well as n.

An example for d = 4 and n = 3. In this section, we describe the parameters of Fig. 2 in the main text. The number of players $d = 4$ and the number of strategies $n = 3$. The total number of payoff values is therefore n^d, which is 81. Thus, for each strategy there are 27 payoff values. This is the number of values we have to consider when the order of player matters. If the payoffs are the same for different arrangements then we reduce the payoff values, but we have to weight them by the number of their occurrence. Consider the three strategies to be A, B, and C. Solving the replicator equation using the average payoffs calculated from the payoffs from Table S1, we numerically obtain 9 fixed points in the interior of the simplex. At these points, the frequencies of all of the strategies are nonzero and the average payoff to each strategy is equal.

2.2. Finite Populations. For finite populations and more than two strategies, few analytical tools are available. The average abundance under weak selection can be addressed using tools from coalescence theory (12, 13).

For small mutation rates, the dynamics reduces to an embedded Markov chain on the pure states of the system [see Fudenberg and Imhof (14) for a proof]. Essentially, this means that the dynamics is governed by dynamics on the edges of the simplex S_n where only two strategies are present. This result can be applied in a variety of contexts (15–17).

Both approaches can be adapted to d-player games.

Appendix A

Condition for the Comparison of One Strategy with Neutrality. We first repeat the condition to prove

$$\begin{aligned}&\sum_{m=1}^{N-1}\sum_{j=1}^{m}(\pi_A-\pi_B)\\ &=\frac{1}{d(d+1)}\left[N^2\left(\sum_{k=0}^{d-1}(d-k)(a_k-b_k)\right)\right.\\ &\quad\left.-N\left(\sum_{k=0}^{d-1}(k+1)a_k+\sum_{k=1}^{d-1}(d-k)b_k-d^2b_0\right)\right],\end{aligned} \qquad \textbf{[S23]}$$

where the payoffs are defined in Eq. S6. Because all of the a_ks come from π_A and all of the b_ks from π_B, we can solve each separately. For π_A we have to show that

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\sum_{k=0}^{d-1}\frac{\binom{j-1}{k}\binom{N-j}{d-k-1}}{\binom{N-1}{d-1}}a_k=\sum_{k=0}^{d-1}\frac{N^2(d-k)-N(k+1)}{d(d+1)}a_k. \qquad \textbf{[S24]}$$

Because this should hold for any choice of a_ks, we must show that

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\frac{\binom{j-1}{k}\binom{N-j}{d-k-1}}{\binom{N-1}{d-1}}=\frac{N^2(d-k)-N(k+1)}{d(d+1)}. \qquad \textbf{[S25]}$$

We take out the factor $\binom{N-1}{d-1}^{-1}$ on the left-hand side and get back to the full expression only at the end. We consider the quantity

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\binom{j-1}{k}\binom{N-j}{d-k-1}. \qquad \textbf{[S26]}$$

Using the identity $\sum_{m=1}^{N-1}\sum_{j=1}^{m}=\sum_{j=1}^{N-1}\sum_{m=j}^{N-1}$, we obtain

$$\begin{aligned}&\sum_{m=1}^{N-1}\sum_{j=1}^{m}\binom{j-1}{k}\binom{N-j}{d-k-1}\\ &=\sum_{j=1}^{N-1}\sum_{m=j}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}\\ &=\sum_{j=1}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}(N-j),\end{aligned} \qquad \textbf{[S27]}$$

where we performed the sum over m. Let us use the factor $N-j$ to split this expression into two sums. The first sum with the factor N is given by

$$\Sigma_1=N\sum_{j=1}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}. \qquad \textbf{[S28]}$$

We change the summation index by one, $i = j-1$, and then extend the sum up to $N-1$,

$$\begin{aligned}\Sigma_1&=N\sum_{i=0}^{N-2}\binom{i}{k}\binom{N-i-1}{d-k-1}\\ &=N\left[\sum_{i=0}^{N-1}\binom{i}{k}\binom{N-i-1}{d-k-1}-\binom{N-1}{k}\binom{0}{d-k-1}\right].\end{aligned} \qquad \textbf{[S29]}$$

The last term is zero as long as $d-k-1>0$, that is, $k<d-1$. We can now apply a variant of Vandermonde's convolution, $\sum_{i=0}^{l}\binom{l-i}{m}\binom{q+i}{n}=\binom{l+q+1}{m+n+1}$ (18), on the first term and obtain for $k<d-1$ the result $\Sigma_1=N\binom{N}{d}$. For the special case of $k = d-1$, we start from Eq. S28,

$$\Sigma_1=N\sum_{j=1}^{N-1}\binom{j-1}{d-1}\binom{N-j}{0}=N\sum_{j=1}^{N-1}\binom{j-1}{d-1}. \qquad \textbf{[S30]}$$

Using the identity $\sum_{j=1}^{N-1}\binom{j-1}{d-1}=\binom{N-1}{d}$, we obtain $\Sigma_1=N\binom{N-1}{d}=(N-d)\binom{N}{d}$. To summarize, we have for Σ_1

$$\Sigma_1=\begin{cases}N\binom{N}{d} & \text{for } 0\le k<d-1\\ N\binom{N-1}{d}=(N-d)\binom{N}{d} & \text{for } k=d-1\end{cases}. \qquad \textbf{[S31]}$$

The second sum in Eq. S27 involving the additional factor j can be rewritten as

$$\begin{aligned}\Sigma_2&=\sum_{j=1}^{N-1}j\binom{j-1}{k}\binom{N-j}{d-k-1}\\ &=(k+1)\sum_{j=1}^{N-1}\binom{j}{k+1}\binom{N-j}{d-k-1},\end{aligned} \qquad \textbf{[S32]}$$

where we have used $j\binom{j-1}{k}=(k+1)\binom{j-1}{k+1}$. We again shift the summation index by one, $i = j-1$, and extend the sum up to $N-1$,

$$\begin{aligned}\Sigma_2&=(k+1)\sum_{i=0}^{N-2}\left[\binom{i+1}{k+1}\binom{N-i-1}{d-k-1}\right]\\ &=(k+1)\sum_{i=0}^{N-1}\left[\binom{i+1}{k+1}\binom{N-i-1}{d-k-1}\right]\\ &\quad-(k+1)\left[\binom{N}{k+1}\binom{0}{d-k-1}\right].\end{aligned} \qquad \textbf{[S33]}$$

The last term is zero for $k<d-1$. For the first term, we can apply the same variant of Vandermonde's convolution as above, $\sum_{i=0}^{l}\binom{l-i}{m}\binom{q+i}{n}=\binom{l+q+1}{m+n+1}$, and obtain

$$\Sigma_2=(k+1)\binom{N+1}{d+1}. \qquad \textbf{[S34]}$$

For $k = d-1$, we again start from Eq. S32, which yields

$$\Sigma_2=d\sum_{j=1}^{N-1}\binom{j}{d}\binom{N-j}{0}=d\sum_{j=1}^{N-1}\binom{j}{d}=d\binom{N}{d+1}. \qquad \textbf{[S35]}$$

We slightly rearrange these two results to a common binomial,

$$\Sigma_2=\begin{cases}(k+1)\,\frac{N+1}{d+1}\binom{N}{d} & \text{for } 0\le k<d-1\\ \frac{d}{d+1}(N-d)\binom{N}{d} & \text{for } k=d-1\end{cases}. \qquad \textbf{[S36]}$$

Combining these results with Eq. S31, we obtain

$$\Sigma_1-\Sigma_2=\binom{N}{d}\frac{1}{d+1}\times\begin{cases}N(d-k)-k-1 & \text{for } 0\le k<d-1\\ N-d & \text{for } k=d-1\end{cases}. \qquad \textbf{[S37]}$$

Note that these two expressions have the same form, such that we obtain a single expression for $\Sigma_1-\Sigma_2$ or, equivalently, for Eq. S27,

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\binom{j-1}{k}\binom{N-j}{d-k-1}=\Sigma_1-\Sigma_2=\binom{N}{d}\frac{N(d-k)-k-1}{d+1}. \qquad \textbf{[S38]}$$

Together with the common factor $\binom{N-1}{d-1}^{-1}$, we obtain

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\frac{\binom{j-1}{k}\binom{N-j}{d-k-1}}{\binom{N-1}{d-1}}=\frac{N^2(d-k)-N(k+1)}{d(d+1)}, \qquad \textbf{[S39]}$$

which is Eq. S25.

The sums over π_B can be solved in a similar way. In that case, the special case is $k = 0$ rather than $k = d-1$, which also indicates the symmetry of the result. For the sums over π_B, we obtain

$$\sum_{m=1}^{N-1}\sum_{j=1}^{m}\frac{\binom{j}{k}\binom{N-j-1}{d-k-1}}{\binom{N-1}{d-1}}=\begin{cases}\frac{N(N-d)}{d+1} & \text{for } k=0\\ \frac{N(N+1)(d-k)}{d(d+1)} & \text{for } 1\le k\le d-1\end{cases}. \qquad \textbf{[S40]}$$

Appendix B

Condition for the Comparison of Two Strategies. The statement to prove is

$$\sum_{j=1}^{N-1}(\pi_A-\pi_B)=\frac{N}{d}\sum_{k=0}^{d-1}(a_k-b_k)+b_0-a_{d-1}. \qquad \textbf{[S41]}$$

As the a_ks are contributed only by π_A and the b_ks only by π_B, we first need to show that

$$\sum_{j=1}^{N-1}\pi_A=\frac{N}{d}\sum_{k=0}^{d-1}a_k-a_{d-1}, \qquad \textbf{[S42]}$$

with the payoffs from Eq. S26. This holds for any choice of a_ks. Thus, we only have to show that

$$\begin{aligned}&\frac{1}{\binom{N-1}{d-1}}\sum_{j=1}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}\\ &=\begin{cases}\frac{N}{d} & \text{for } 0\le k<d-1\\ \frac{N}{d}-1 & \text{for } k=d-1\end{cases}.\end{aligned} \qquad \textbf{[S43]}$$

The sum has been solved above, cf Eq. S28, where we have shown that $\sum_{j=1}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}=\binom{N}{d}$ for $0\le k<d-1$ and $\sum_{j=1}^{N-1}\binom{j-1}{k}\binom{N-j}{d-k-1}=\frac{N-d}{N}\binom{N}{d}$ for $k = d-1$. Using the identity $\binom{N}{d}=\frac{N}{d}\binom{N-1}{d-1}$, we directly obtain Eq. S43.

The equivalent condition for π_B can be derived based on a similar argument. As above, we have $k = 0$ as the special case instead of $k = d-1$ in the equivalent of Eq. S43,

$$\frac{1}{\binom{N-1}{d-1}}\sum_{j=1}^{N-1}\binom{j}{k}\binom{N-j-1}{d-k-1}=\begin{cases}\frac{N}{d}-1 & \text{for } k=0\\ \frac{N}{d} & \text{for } 0<k\le d-1\end{cases}. \qquad \textbf{[S44]}$$

1. Taylor PD, Jonker L (1978) Evolutionary stable strategies and game dynamics. *Math Biosci* 40:145–156.
2. Hofbauer J, Sigmund K (1998) *Evolutionary Games and Population Dynamics* (Cambridge Univ Press, Cambridge, UK).
3. Hauert C, Michor F, Nowak MA, Doebeli M (2006) Synergy and discounting of cooperation in social dilemmas. *J Theor Biol* 239:195–202.
4. Moran PAP (1962) *The Statistical Processes of Evolutionary Theory* (Clarendon, Oxford).
5. Ewens WJ (2004) *Mathematical Population Genetics* (Springer, New York).

Summary

$$\begin{pmatrix} a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_1 & b_0 \end{pmatrix}$$

Deterministic dynamics

The maximum number of internal isolated fixed points is $d-1$

Stochastic dynamics

$$\rho_A > 1/N$$

$$\rho_A > \rho_B$$

$$\boxed{2a_0 + a_1 > 2b_0 + b_1}$$

$$\boxed{a_0 + a_1 > b_0 + b_1}$$

$$\boxed{\sum_{k=0}^{d-1} (d-k)a_k > \sum_{k=0}^{d-1} (d-k)b_k}$$

$$\boxed{\sum_{k=0}^{d-1} a_k > \sum_{k=0}^{d-1} b_k}$$

Summary

$$\begin{pmatrix} a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_1 & b_0 \end{pmatrix}$$

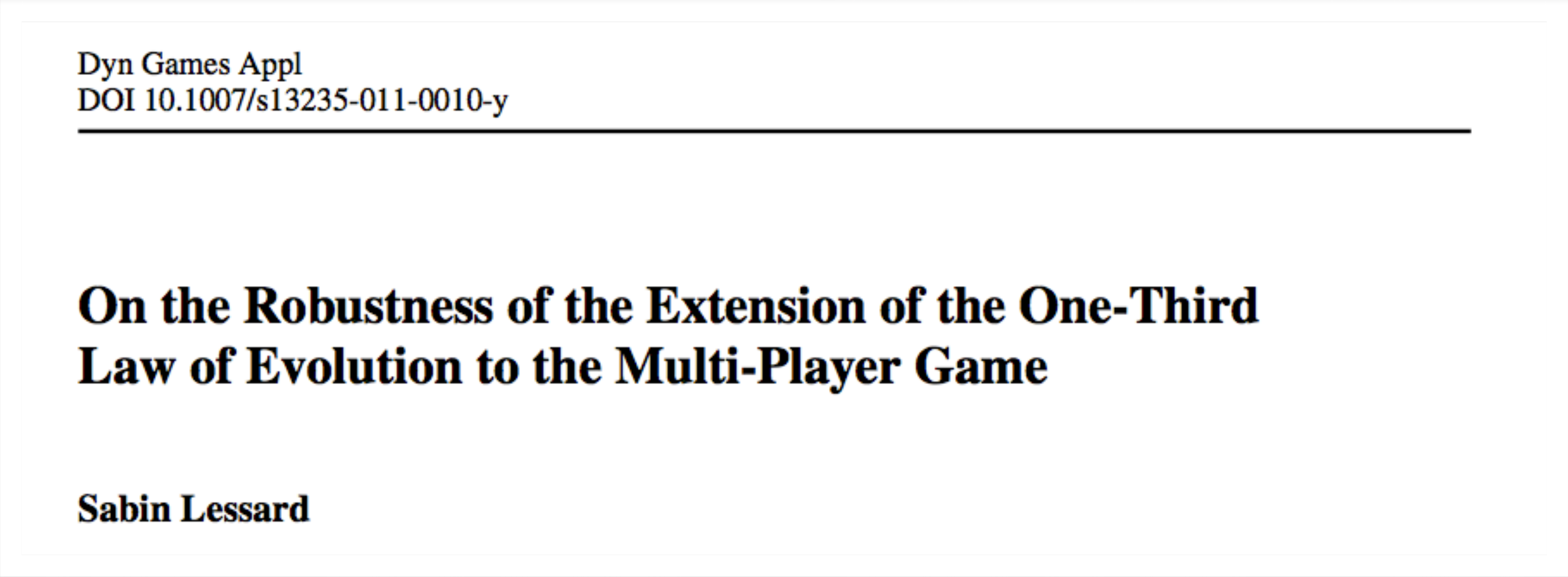
$$\rho_A > 1/N$$

$$\boxed{\sum_{k=0}^{d-1} (d-k)a_k > \sum_{k=0}^{d-1} (d-k)b_k}$$

$$\rho_A > \rho_B$$

$$\boxed{\sum_{k=0}^{d-1} a_k > \sum_{k=0}^{d-1} b_k}$$

Generalised the one third rule and risk dominance to arbirary number of players

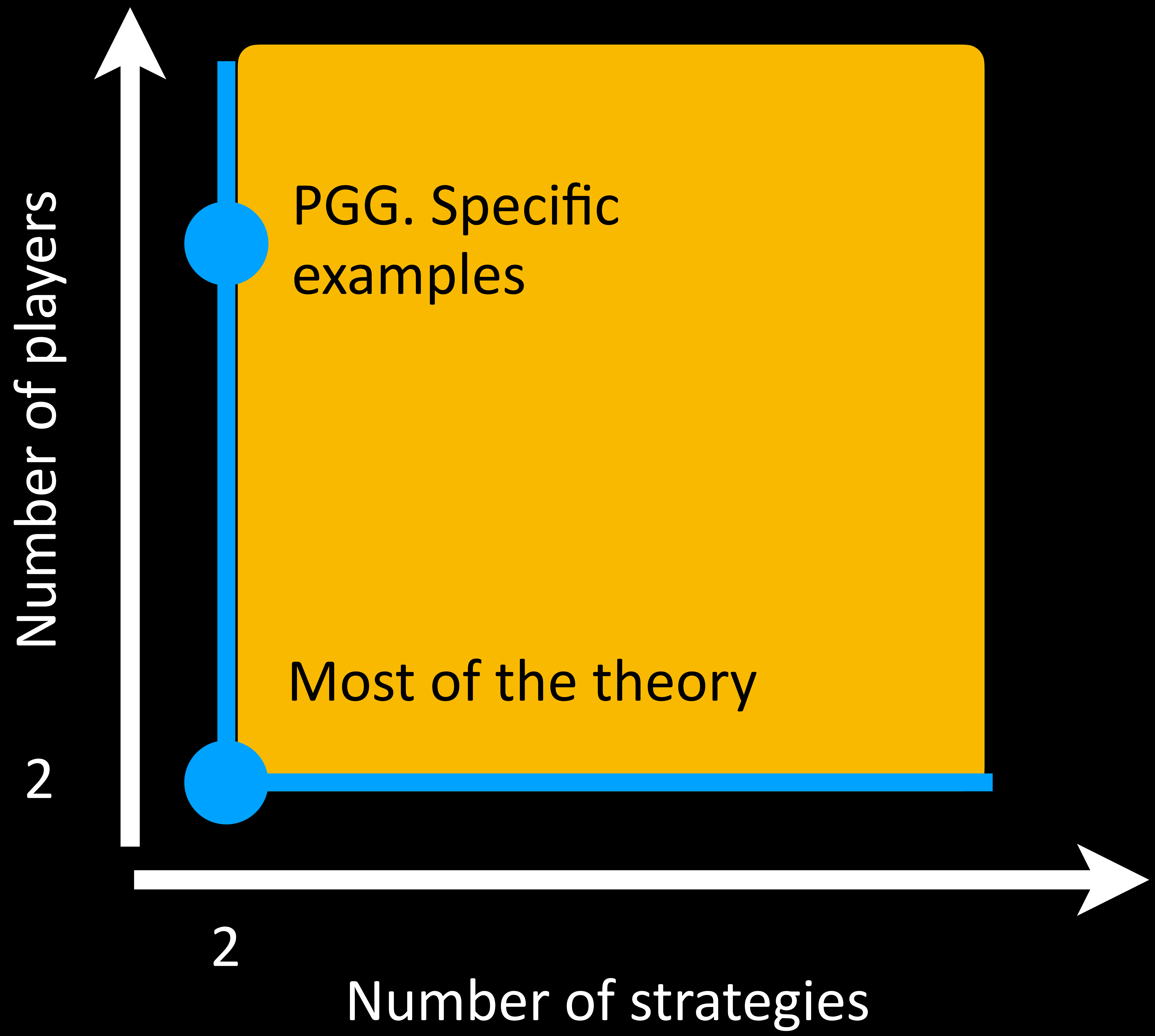


Dyn Games Appl
DOI 10.1007/s13235-011-0010-y

On the Robustness of the Extension of the One-Third Law of Evolution to the Multi-Player Game

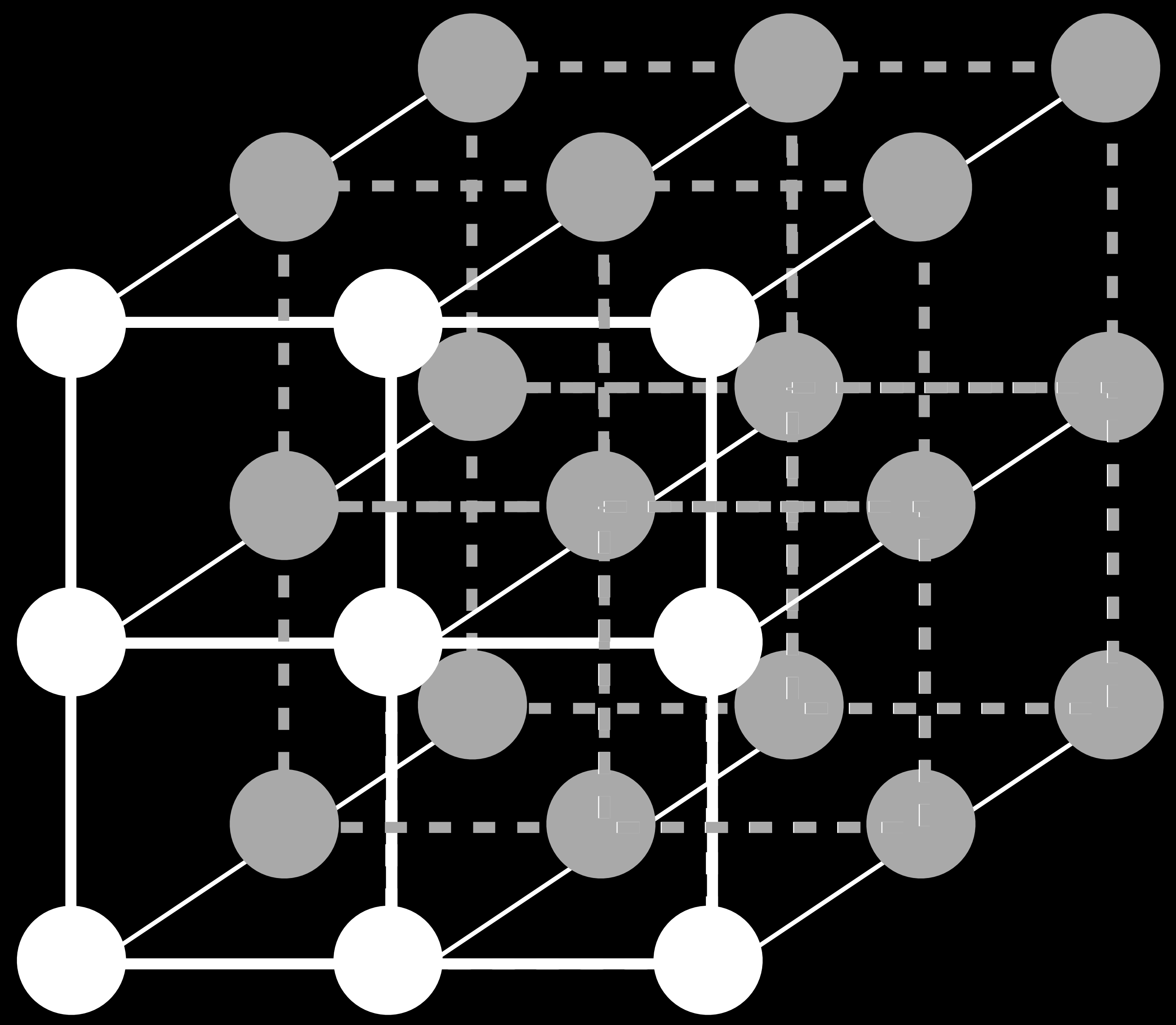
Sabin Lessard

Valid for all processes in the Kingman's coalescent



PGG. Specific examples

Most of the theory

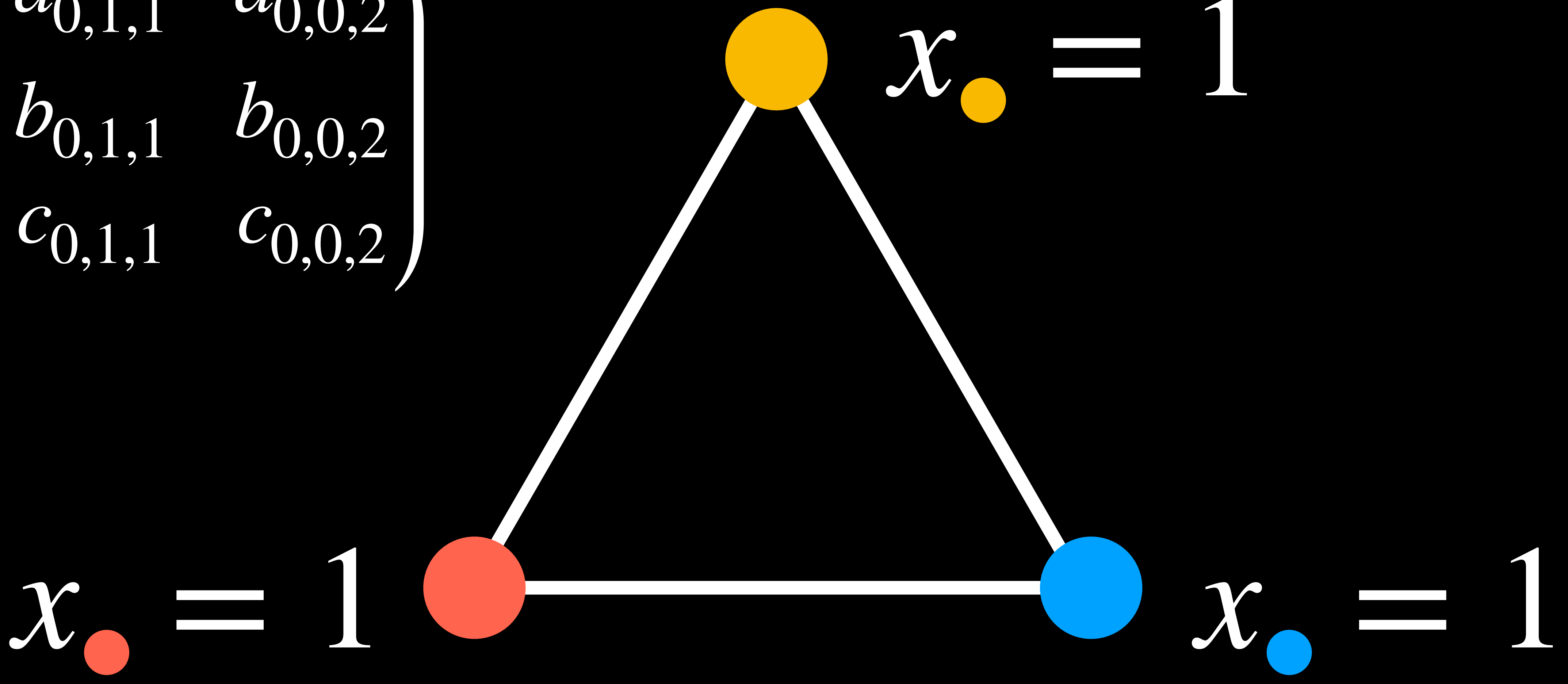


$3 \times 3 \times 3$

$$\begin{pmatrix} a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_1 & b_0 \end{pmatrix}$$

The maximum number of internal fixed points is $d-1$

$$\begin{pmatrix} a_{2,0,0} & a_{1,1,0} & a_{0,2,0} & a_{1,0,1} & a_{0,1,1} & a_{0,0,2} \\ b_{2,0,0} & b_{1,1,0} & b_{0,2,0} & b_{1,0,1} & b_{0,1,1} & b_{0,0,2} \\ c_{2,0,0} & c_{1,1,0} & c_{0,2,0} & c_{1,0,1} & c_{0,1,1} & c_{0,0,2} \end{pmatrix}$$



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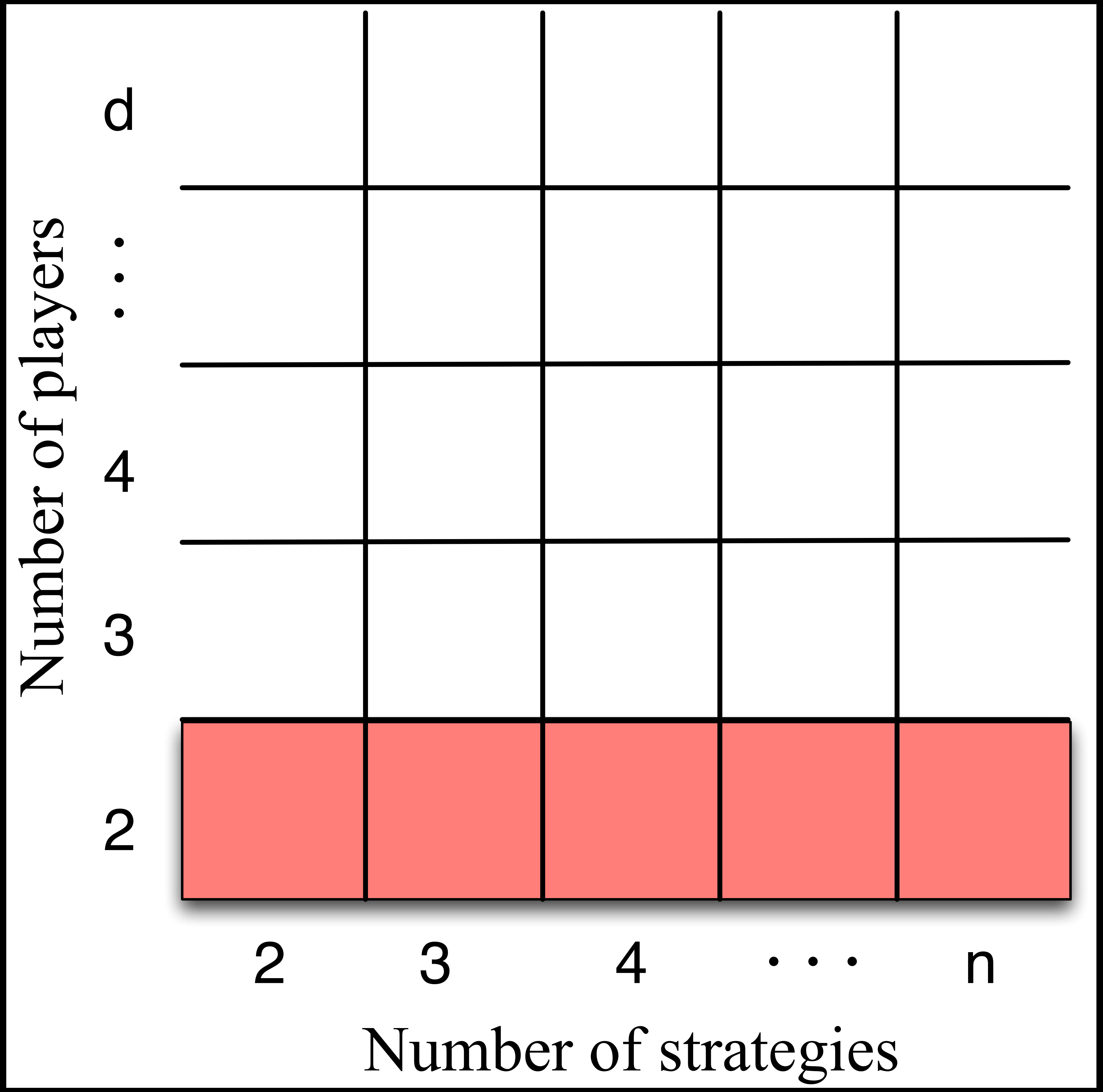
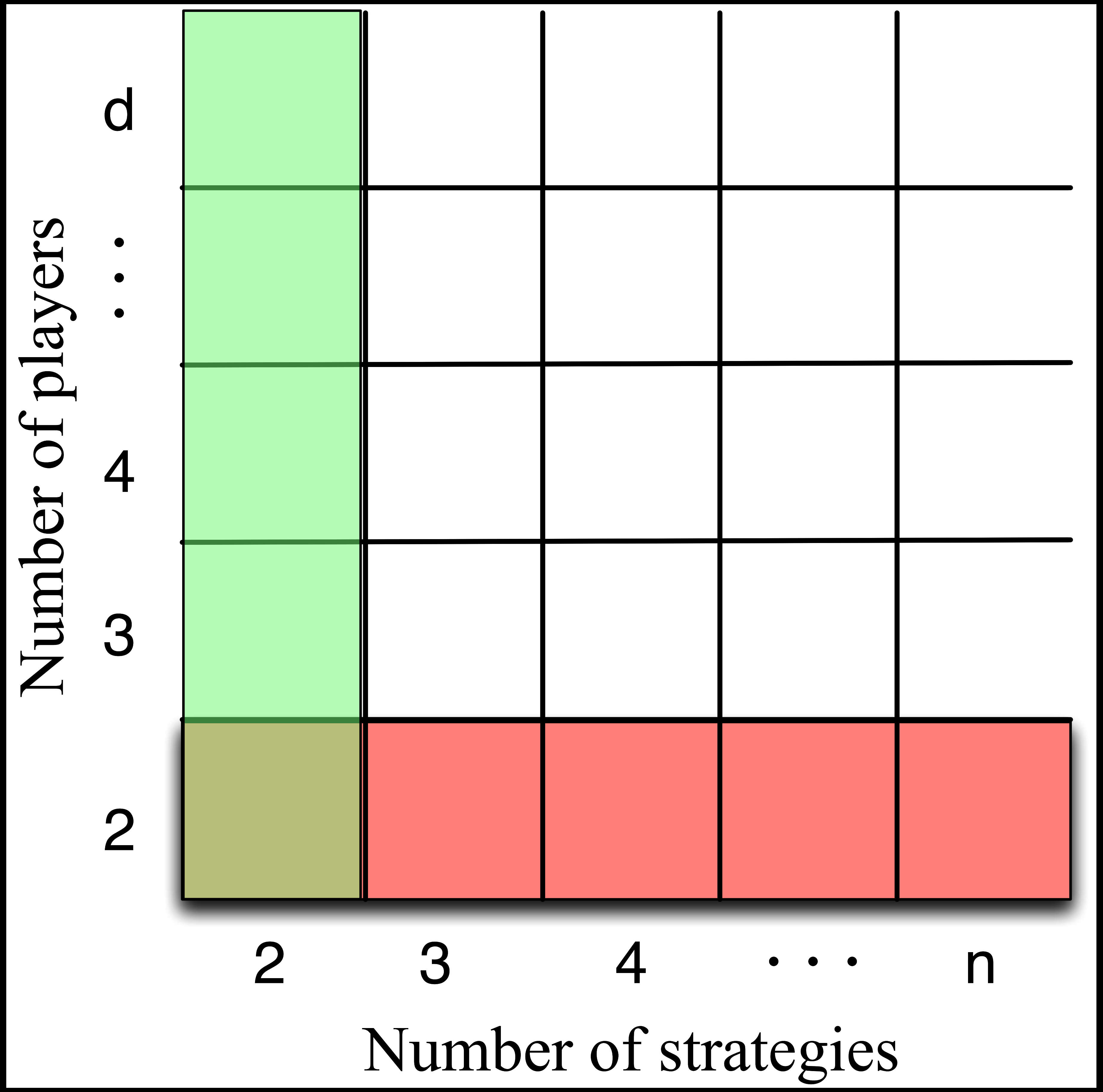


P(one internal equilibrium) = 2^{1-n}

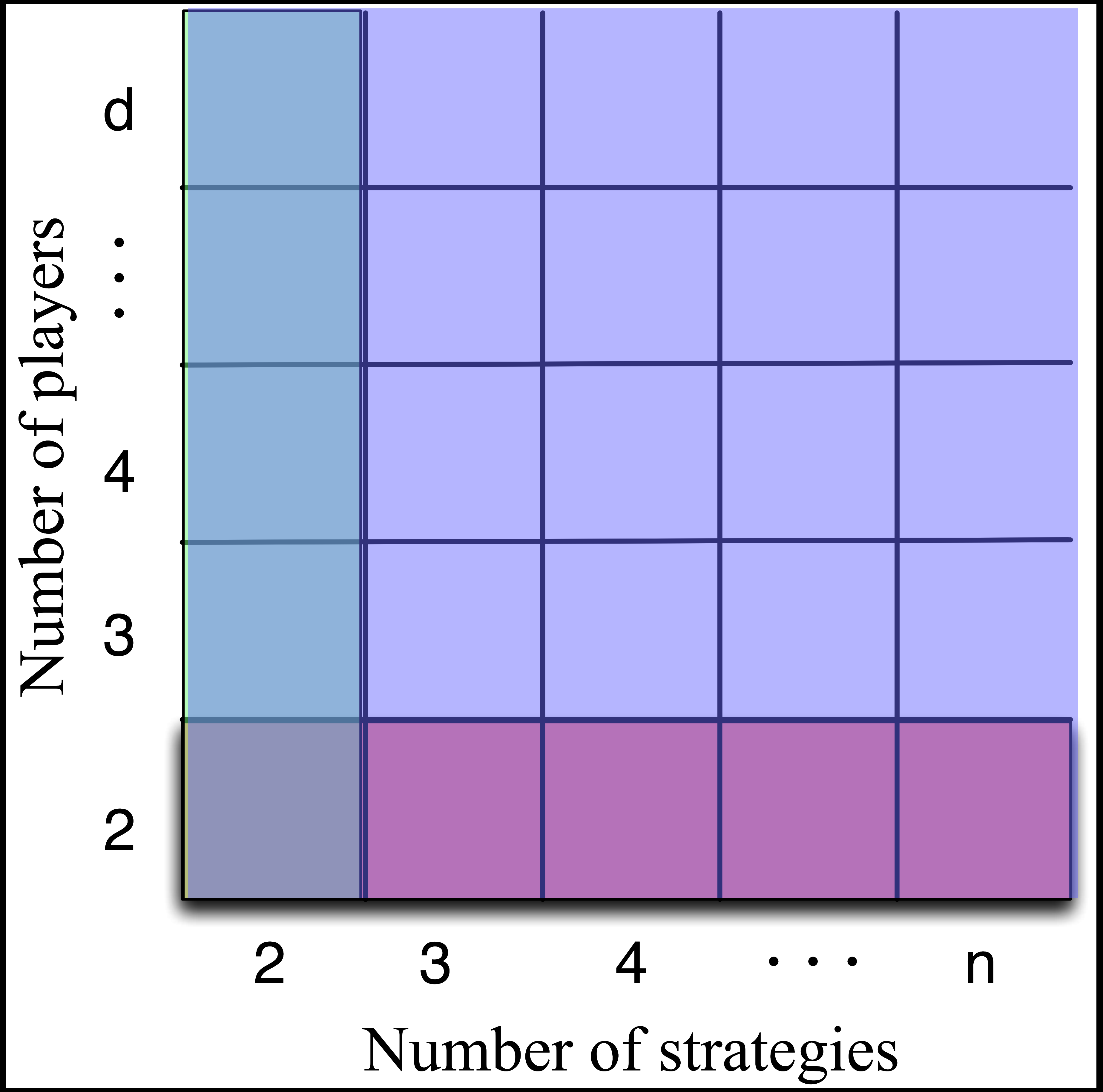
P(one internal stable equilibrium) $\leq 2^{-n}$



P(one internal equilibrium) = 2^{1-n}

P(one internal stable equilibrium) $\leq 2^{-n}$

P(given equilibrium is stable) = $1/2$

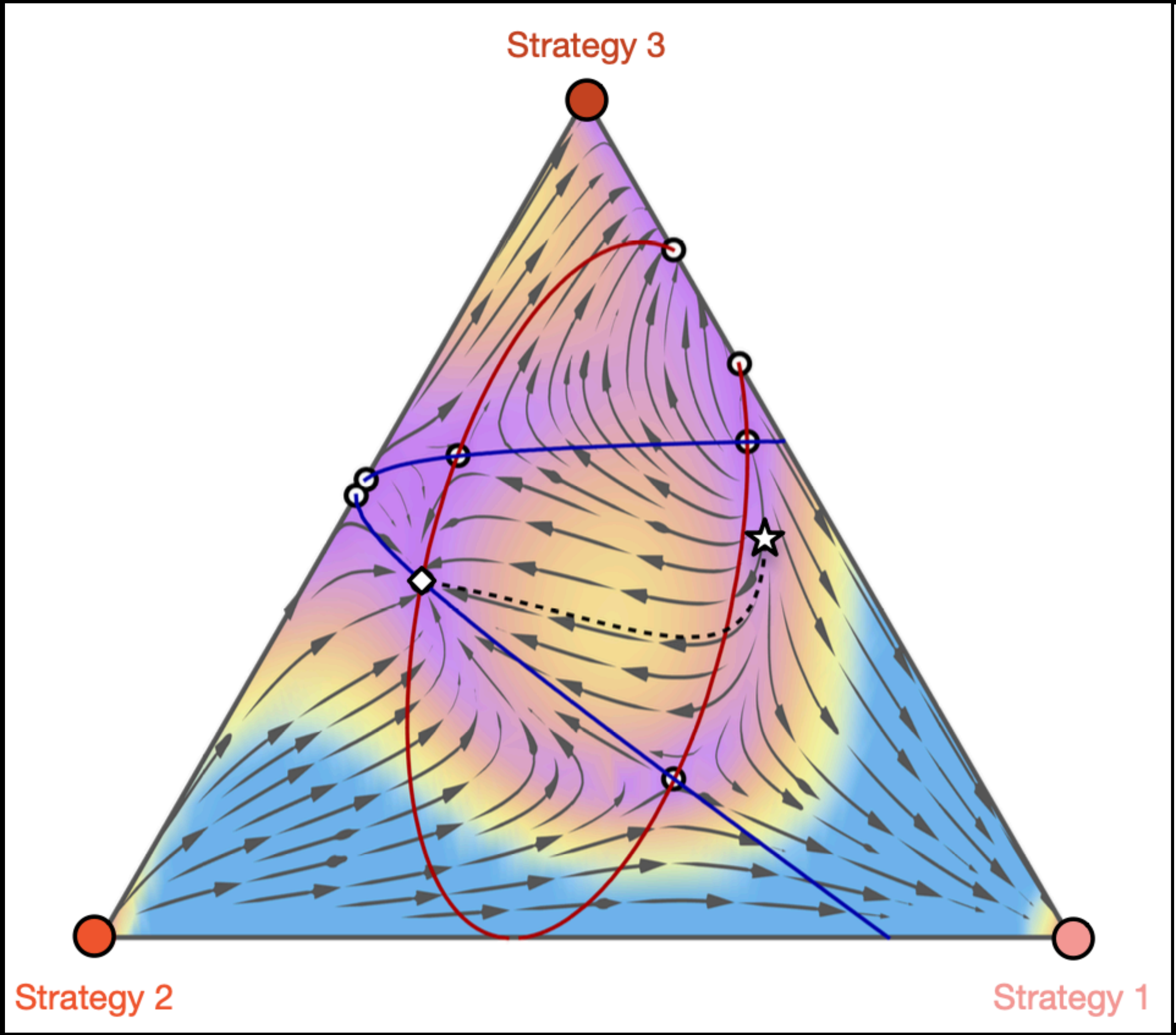


P(one internal equilibrium) = 2^{1-n}

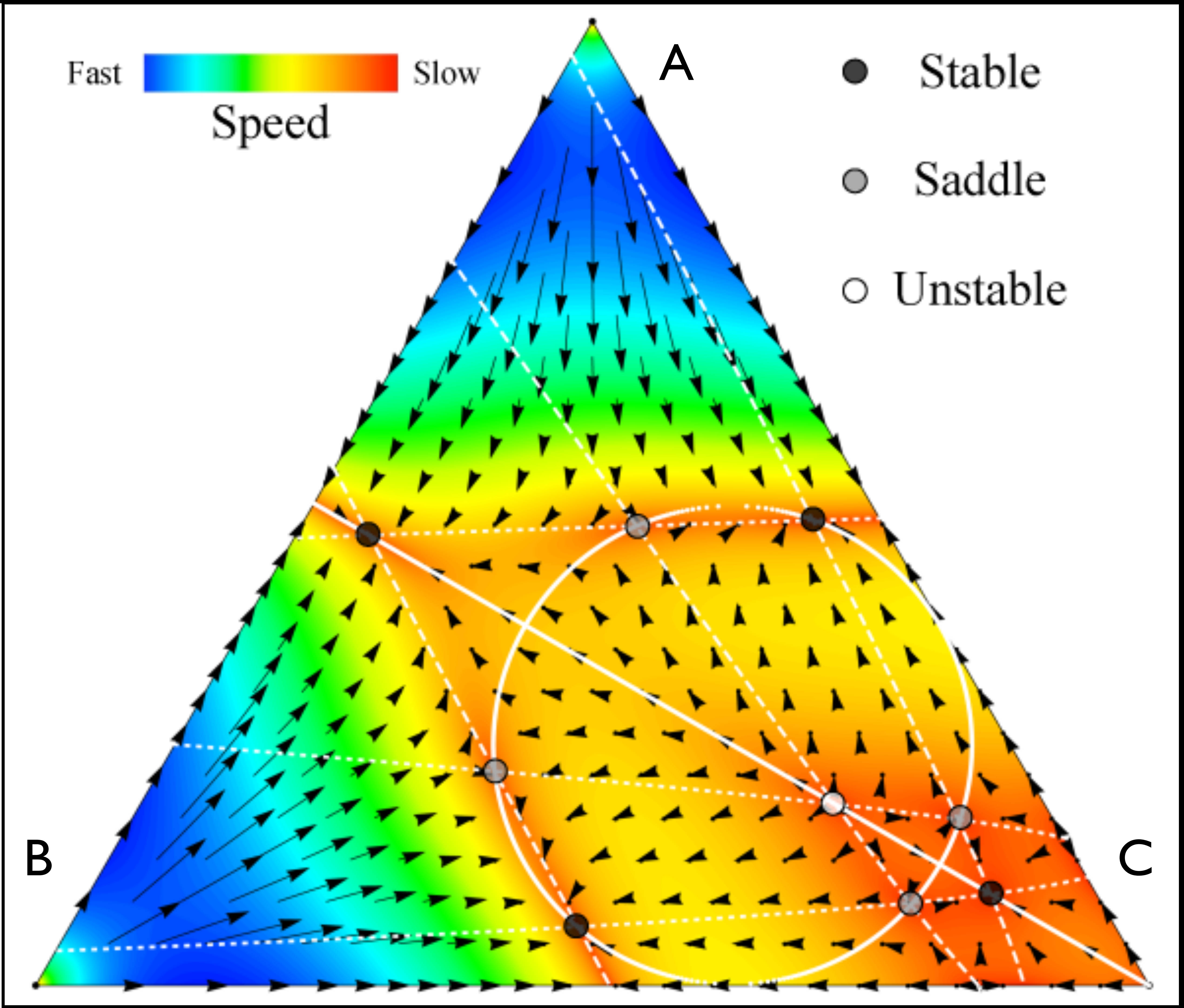
P(one internal stable equilibrium) $\leq 2^{-n}$

P(given equilibrium is stable) = $1/2$

Maximum internal
isolated equilibria = $(d-1)^{n-1}$



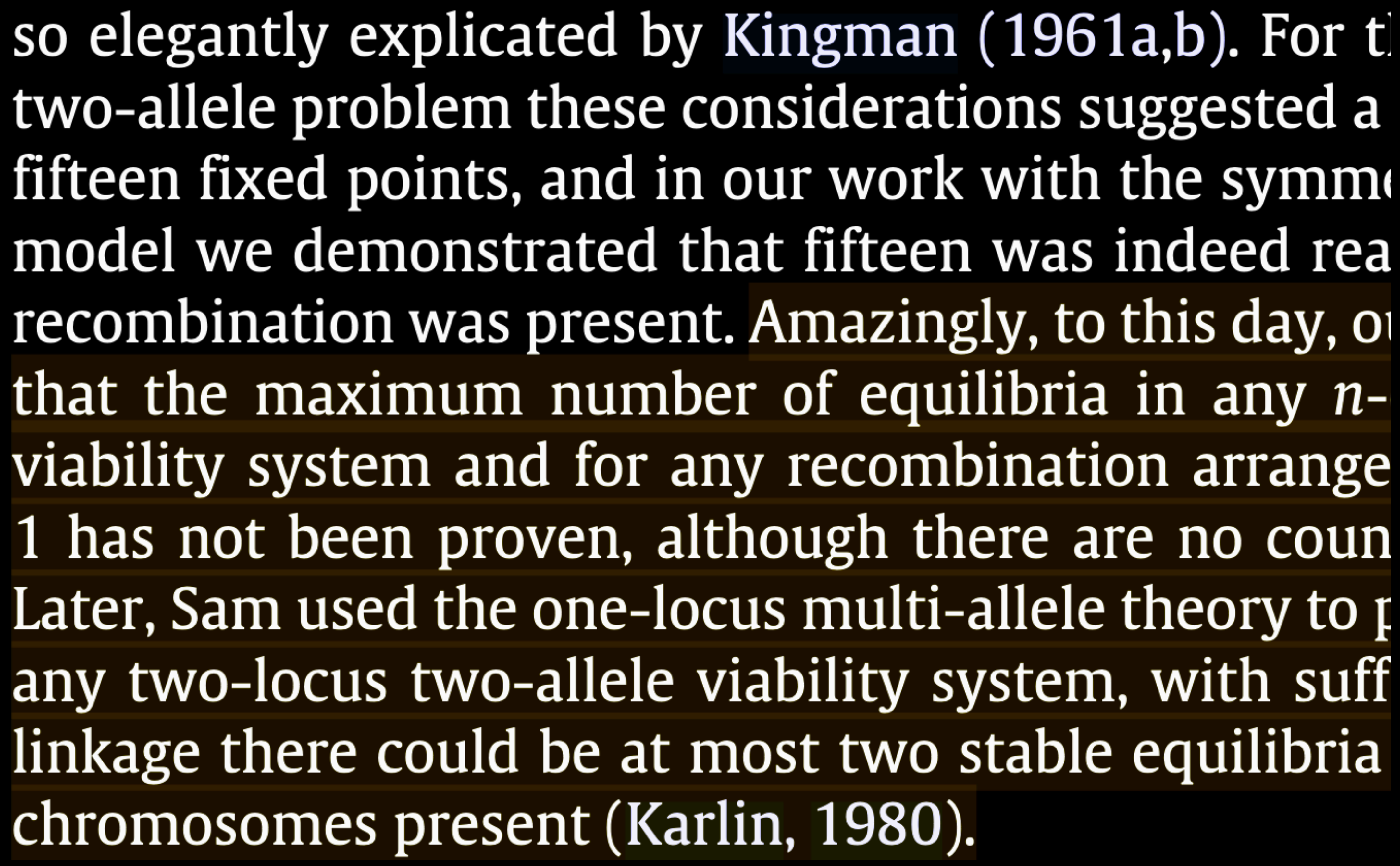
$d = 3; n = 3$



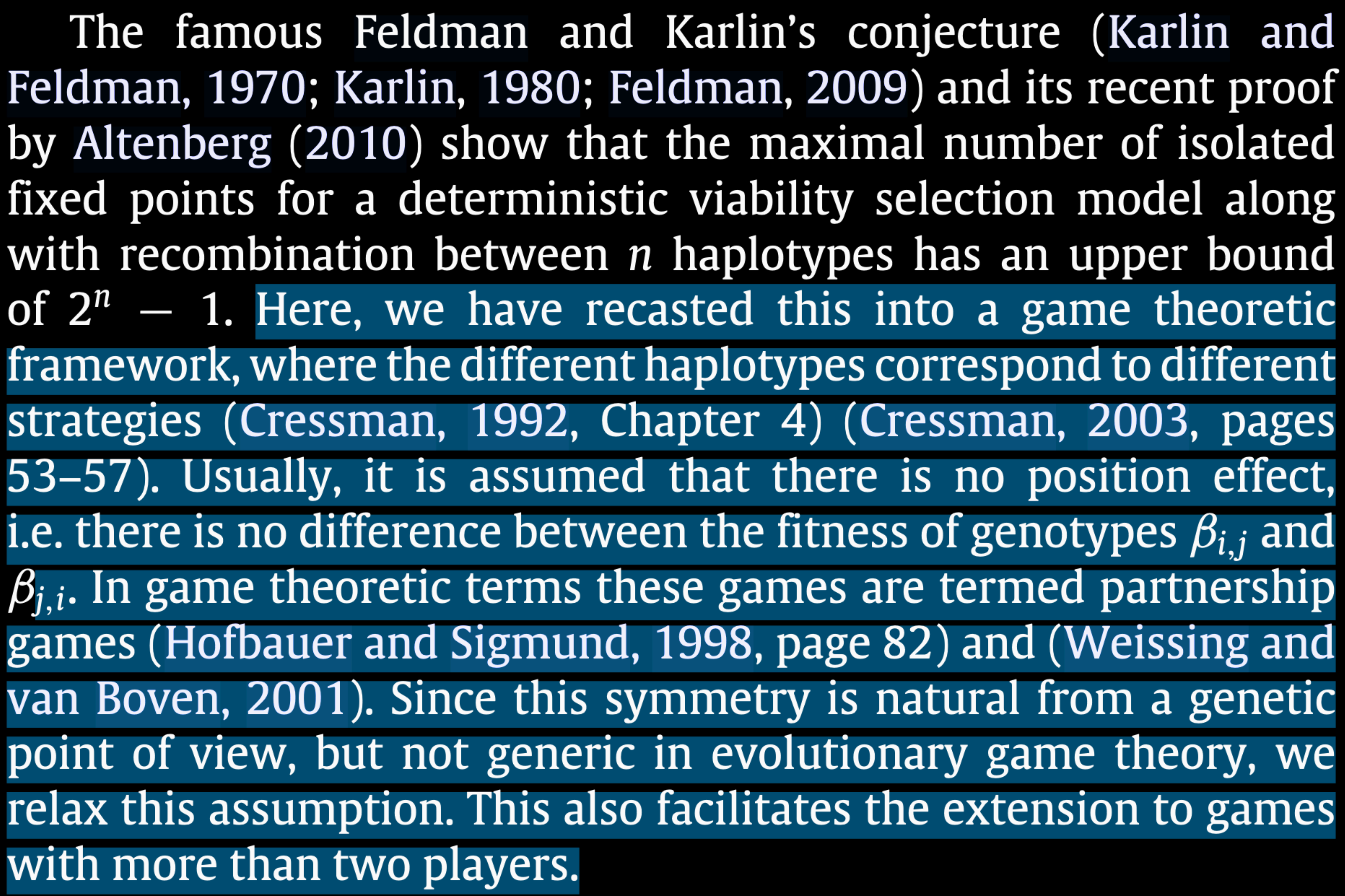
$d = 4; n = 3$

The maximum number of internal fixed points is $(d-1)^{(n-1)}$

Feldman and Karlin conjecture



so elegantly explicated by Kingman (1961a,b). For t
two-allele problem these considerations suggested a
fifteen fixed points, and in our work with the symm
model we demonstrated that fifteen was indeed rea
recombination was present. Amazingly, to this day, o
that the maximum number of equilibria in any n-
viability system and for any recombination arrange
1 has not been proven, although there are no coun
Later, Sam used the one-locus multi-allele theory to
any two-locus two-allele viability system, with suff
linkage there could be at most two stable equilibria
chromosomes present (Karlin, 1980).

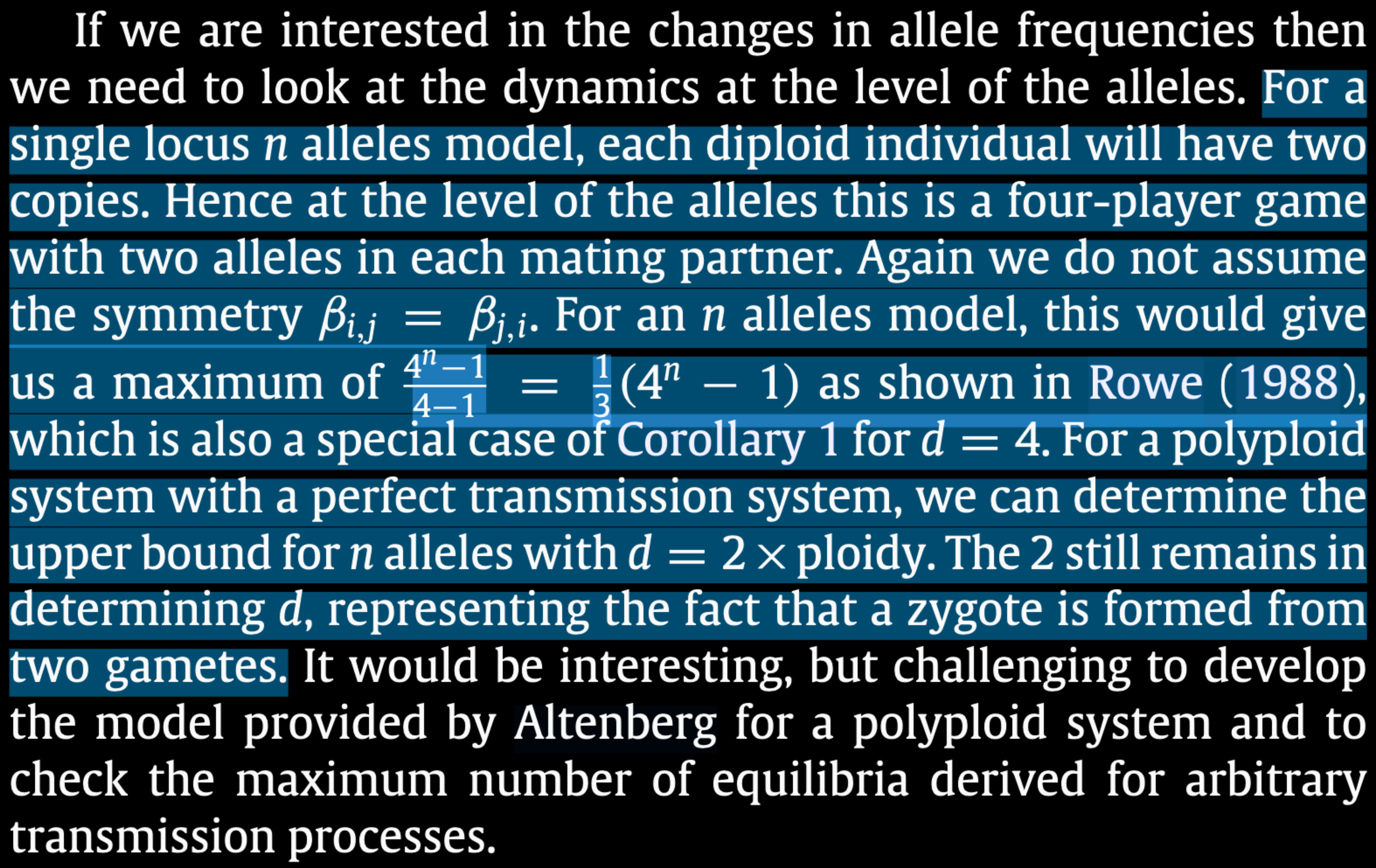


The famous Feldman and Karlin's conjecture (Karlin and Feldman, 1970; Karlin, 1980; Feldman, 2009) and its recent proof by Altenberg (2010) show that the maximal number of isolated fixed points for a deterministic viability selection model along with recombination between n haplotypes has an upper bound of $2^n - 1$. Here, we have recasted this into a game theoretic framework, where the different haplotypes correspond to different strategies (Cressman, 1992, Chapter 4) (Cressman, 2003, pages 53–57). Usually, it is assumed that there is no position effect, i.e. there is no difference between the fitness of genotypes $\beta_{i,j}$ and $\beta_{j,i}$. In game theoretic terms these games are termed partnership games (Hofbauer and Sigmund, 1998, page 82) and (Weissing and van Boven, 2001). Since this symmetry is natural from a genetic point of view, but not generic in evolutionary game theory, we relax this assumption. This also facilitates the extension to games with more than two players.

Feldman, Marcus W. "Sam Karlin and Multi-Locus Population Genetics." *Theoretical Population Biology* 75, 2009: 233–35.

Han, The Anh, Arne Traulsen, and Chaitanya S. Gokhale. "On Equilibrium Properties of Evolutionary Multi-Player Games with Random Payoff Matrices." *Theoretical Population Biology* 81, 2012: 264–72.

In fact we can extend the analysis to



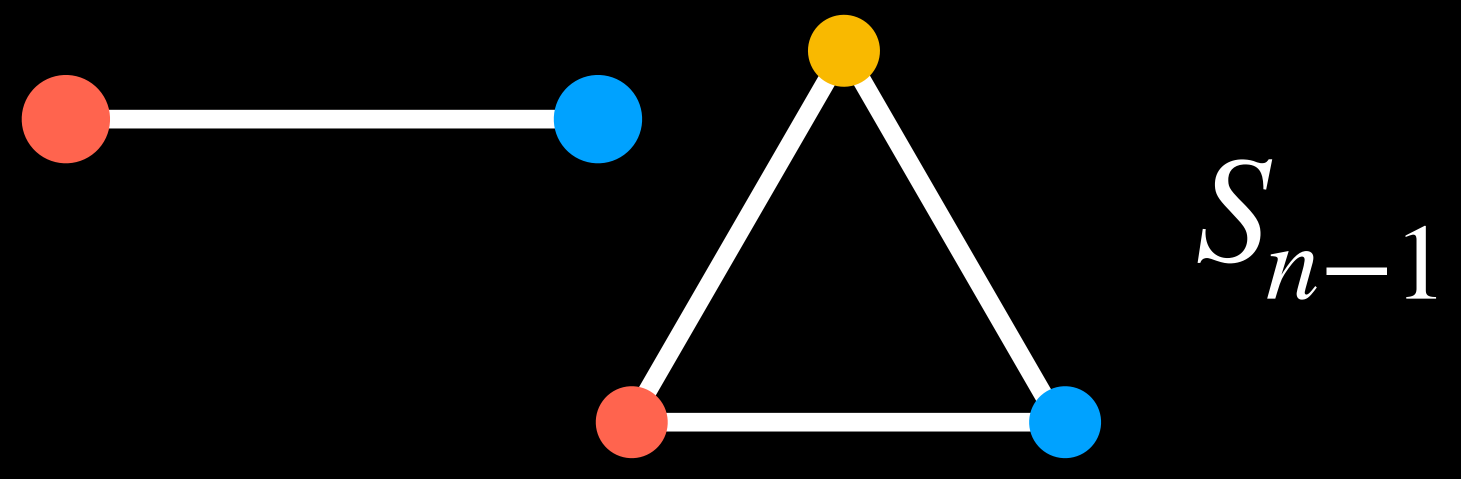
If we are interested in the changes in allele frequencies then we need to look at the dynamics at the level of the alleles. For a single locus n alleles model, each diploid individual will have two copies. Hence at the level of the alleles this is a four-player game with two alleles in each mating partner. Again we do not assume the symmetry $\beta_{i,j} = \beta_{j,i}$. For an n alleles model, this would give us a maximum of $\frac{4^n-1}{4-1} = \frac{1}{3}(4^n - 1)$ as shown in Rowe (1988), which is also a special case of Corollary 1 for $d = 4$. For a polyploid system with a perfect transmission system, we can determine the upper bound for n alleles with $d = 2 \times$ ploidy. The 2 still remains in determining d, representing the fact that a zygote is formed from two gametes. It would be interesting, but challenging to develop the model provided by Altenberg for a polyploid system and to check the maximum number of equilibria derived for arbitrary transmission processes.

Han, The Anh, Arne Traulsen, and Chaitanya S. Gokhale. "On Equilibrium Properties of Evolutionary Multi-Player Games with Random Payoff Matrices." ***Theoretical Population Biology*** **81, 2012: 264–72.**

Summary

d- player games with n strategies

Deterministic dynamics



The maximum number of internal isolated fixed points is $(d-1)^{(n-1)}$

Stochastic dynamics

$$\rho_A > 1/N$$

$$\boxed{\sum_{k=0}^{d-1}(d-k)a_k > \sum_{k=0}^{d-1}(d-k)b_k}$$

$$\rho_A > \rho_B$$

$$\boxed{\sum_{k=0}^{d-1}a_k > \sum_{k=0}^{d-1}b_k}$$

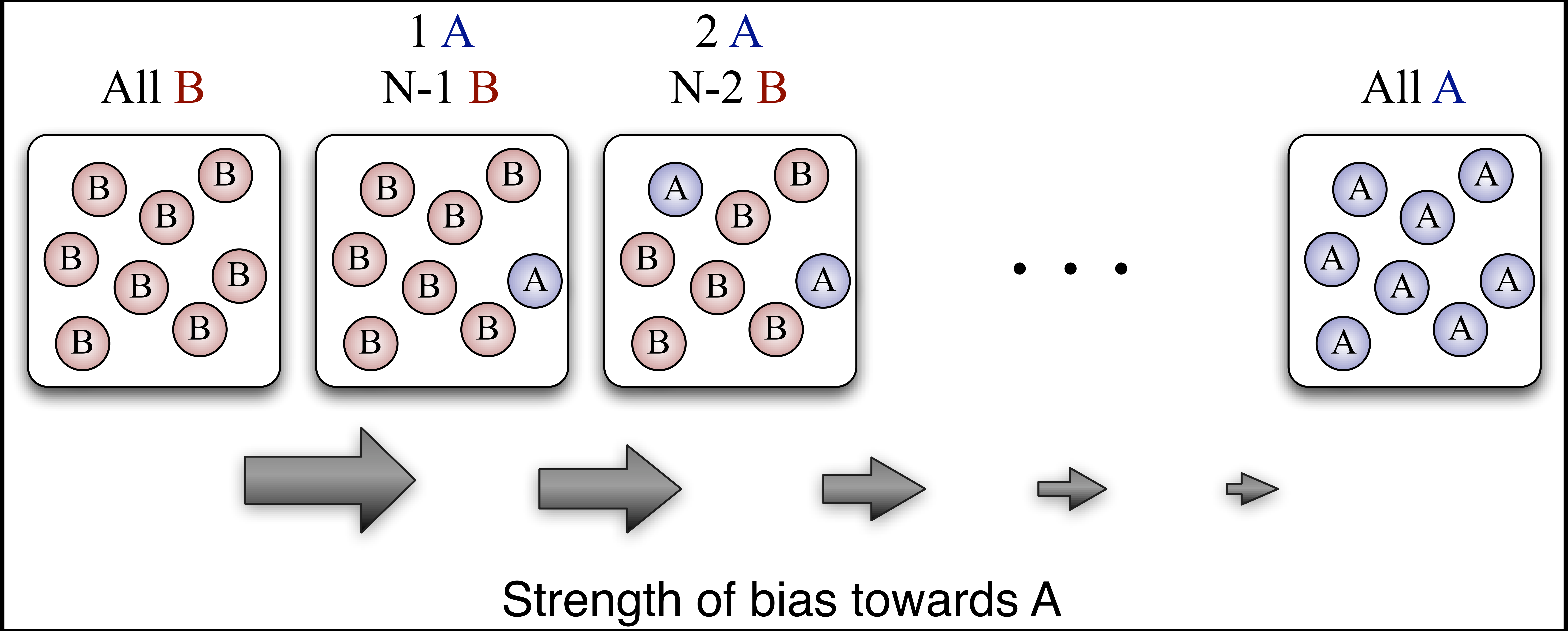
When

Fixation time

Stochastic slowdown

Fixation time

Conditional



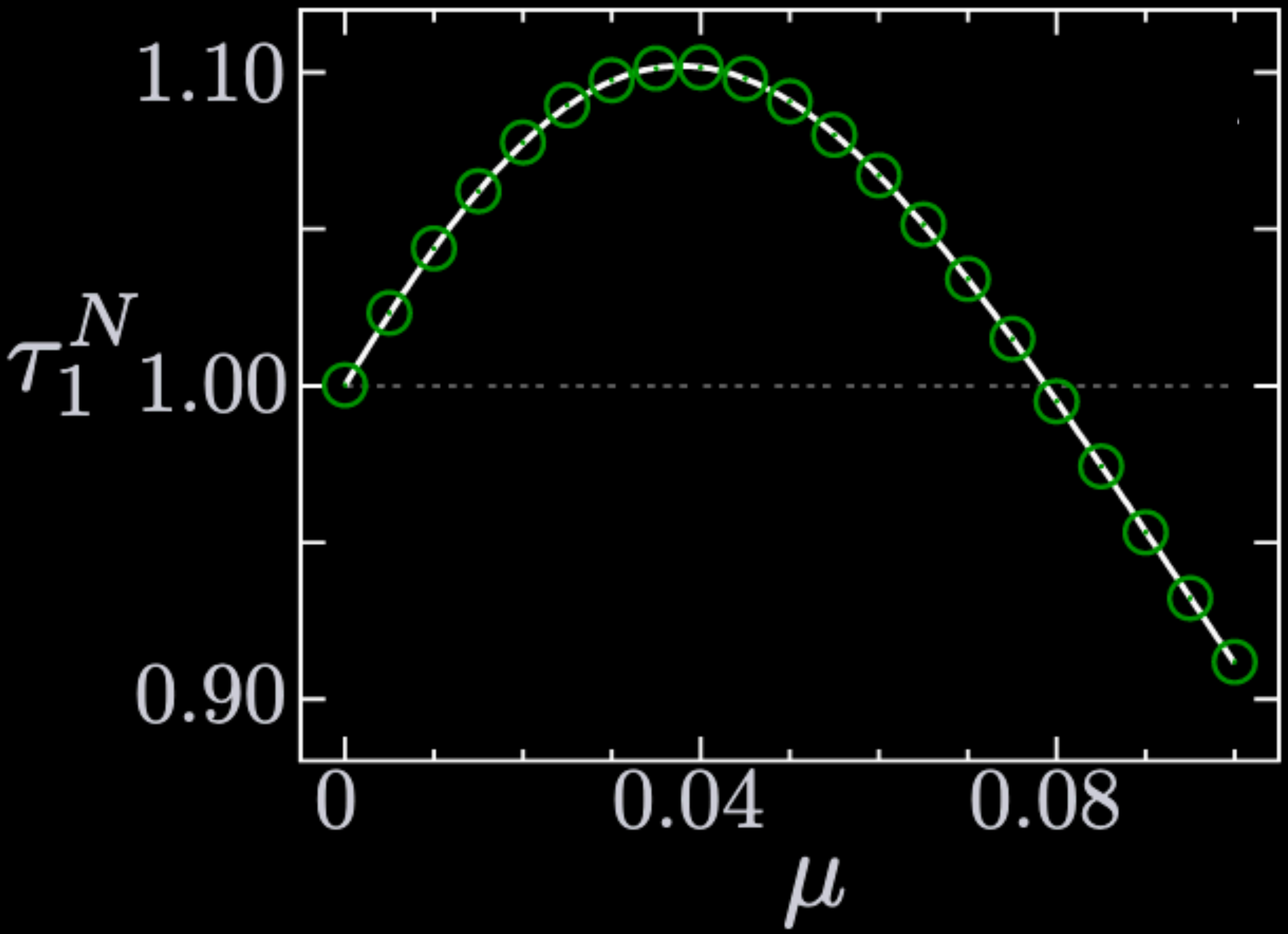
Strength of bias towards A

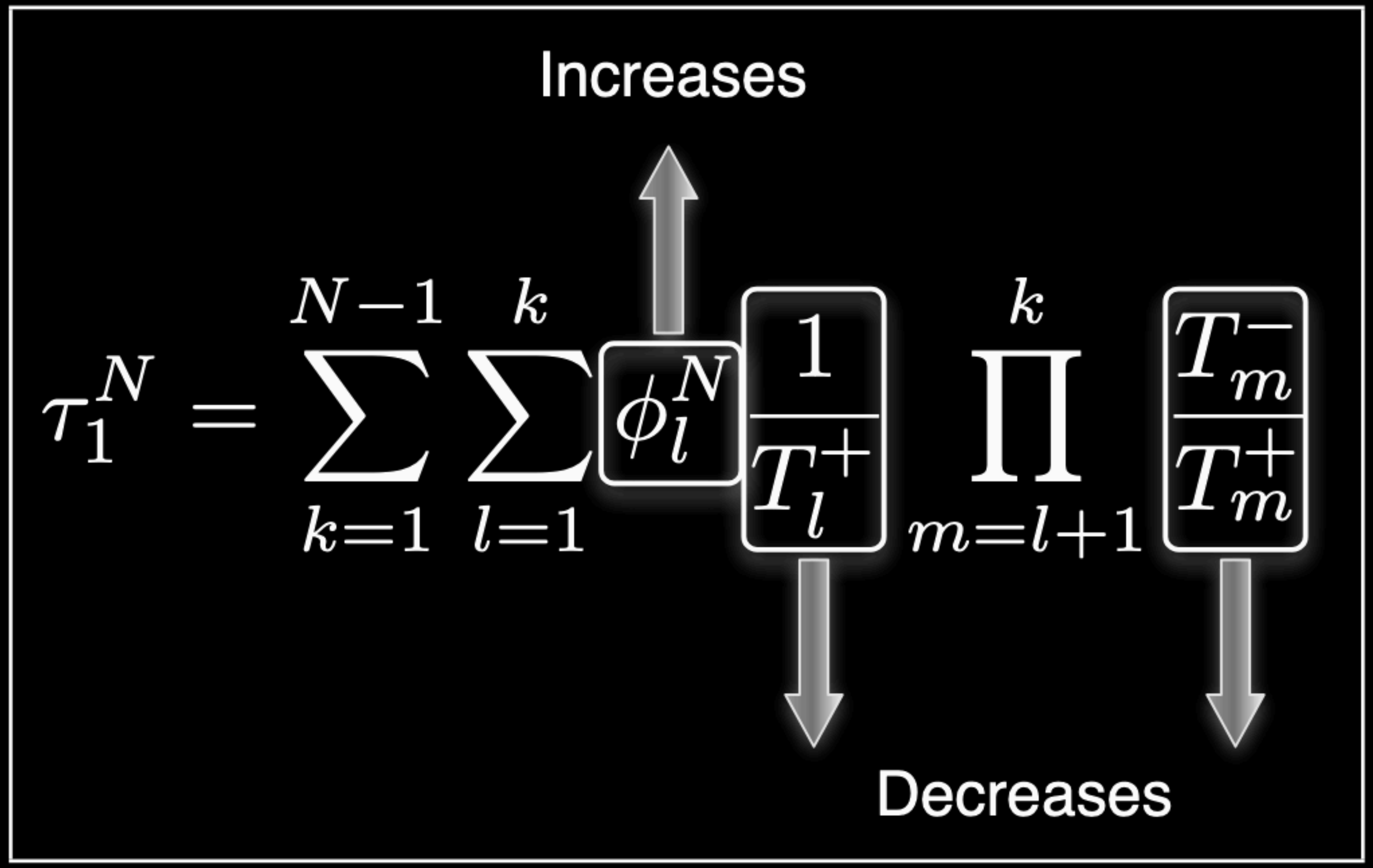
$$T_i^+ = \frac{i}{N}\frac{N-i}{N} + \frac{N-i}{N}\mu\frac{N-i}{N}.$$

$$T_i^- = \frac{N-i}{N}(1-\mu)\frac{i}{N}.$$

Fixation time

Conditional





Increases

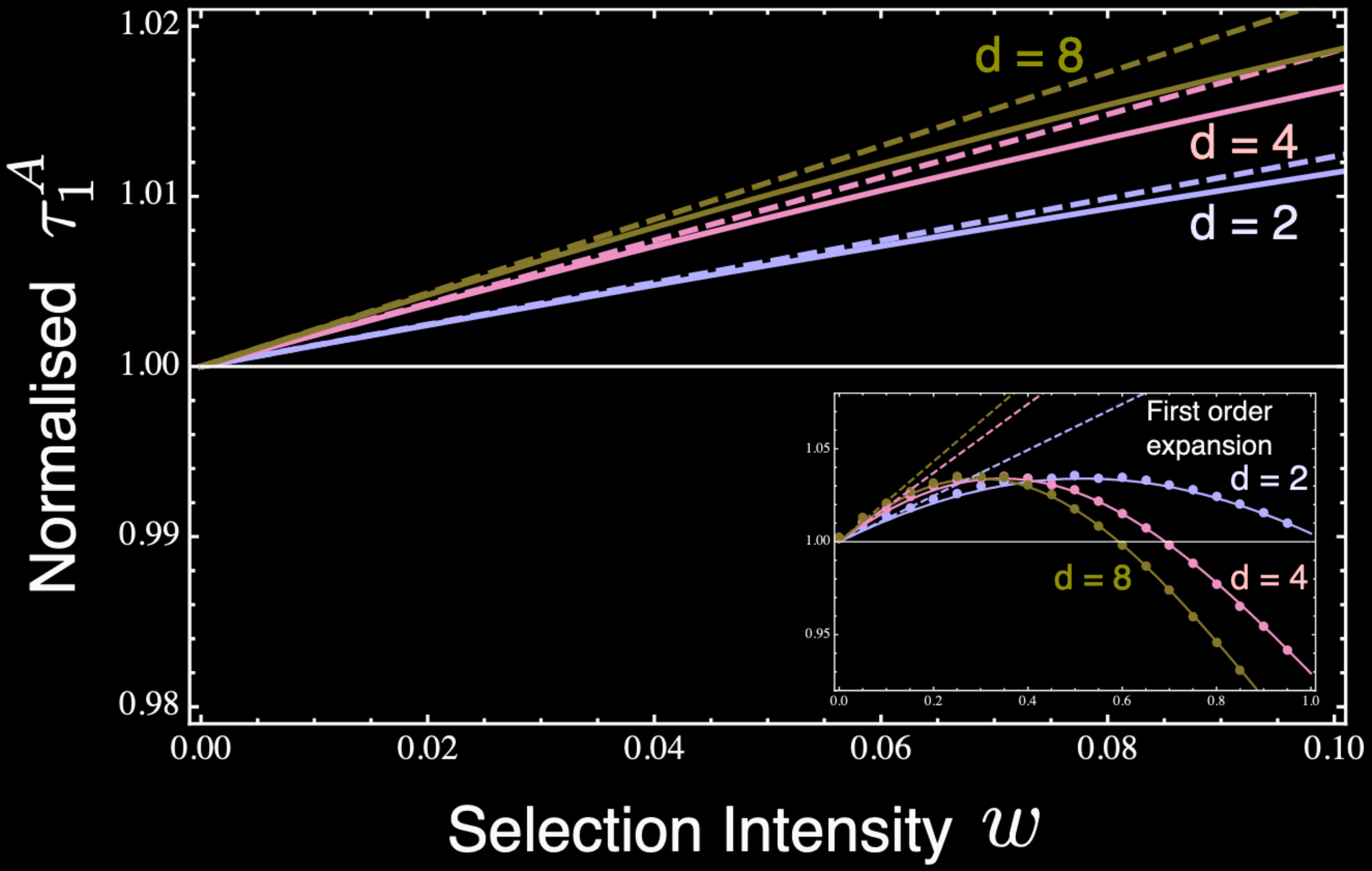
$$\tau_1^N = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \boxed{\phi_l^N} \boxed{\frac{1}{T_l^+}} \prod_{m=l+1}^{k} \boxed{\frac{T_m^-}{T_m^+}}$$

Decreases

For a slightly different biased process

Fixation time

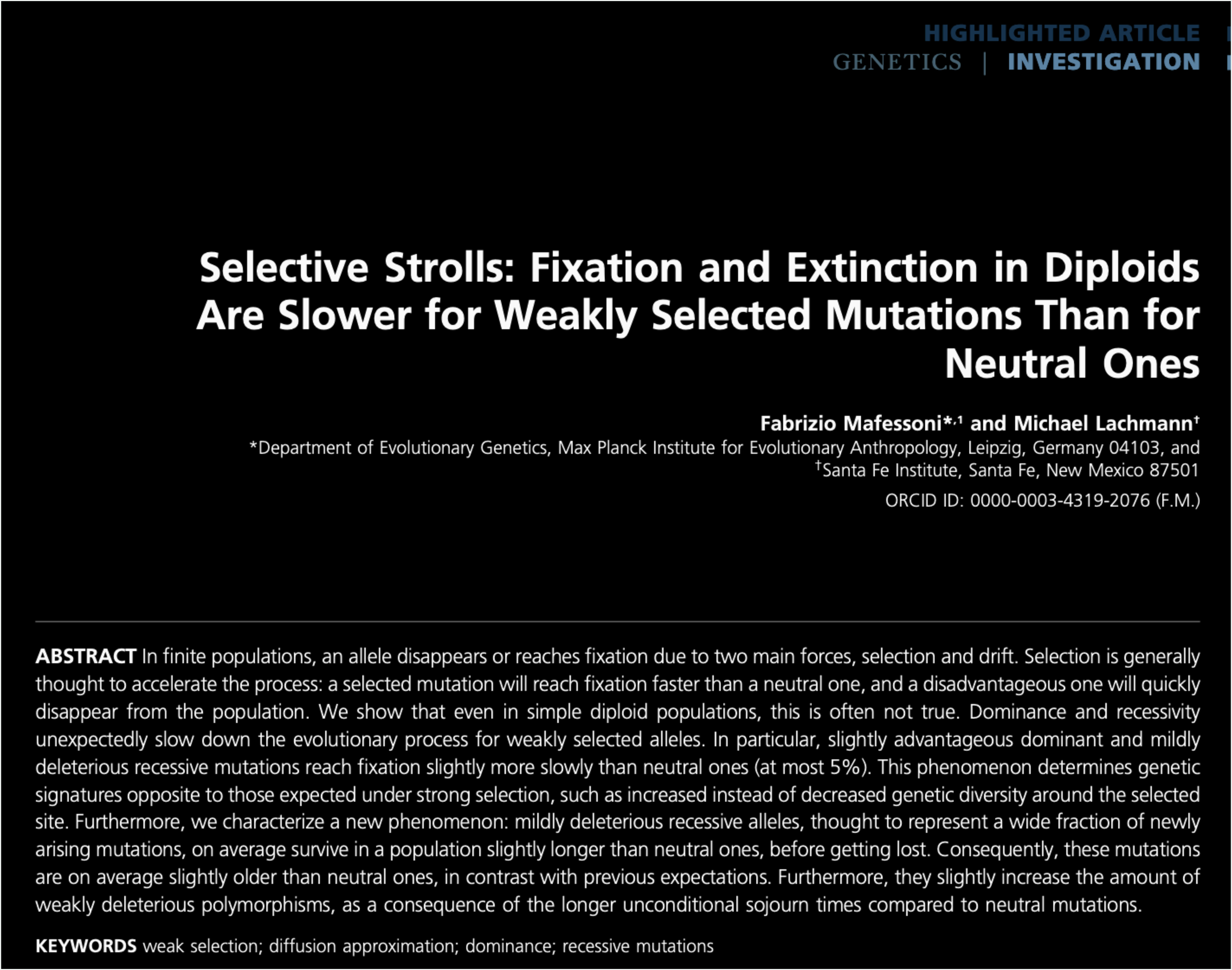
Conditional



For multi-player games we see that stochastic slowdown is even more pronounced

Fixation time

Conditional



HIGHLIGHTED ARTICLE
GENETICS | INVESTIGATION

Selective Strolls: Fixation and Extinction in Diploids Are Slower for Weakly Selected Mutations Than for Neutral Ones

Fabrizio Mafessoni*,1 and Michael Lachmann†
*Department of Evolutionary Genetics, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany 04103, and
†Santa Fe Institute, Santa Fe, New Mexico 87501
ORCID ID: 0000-0003-4319-2076 (F.M.)

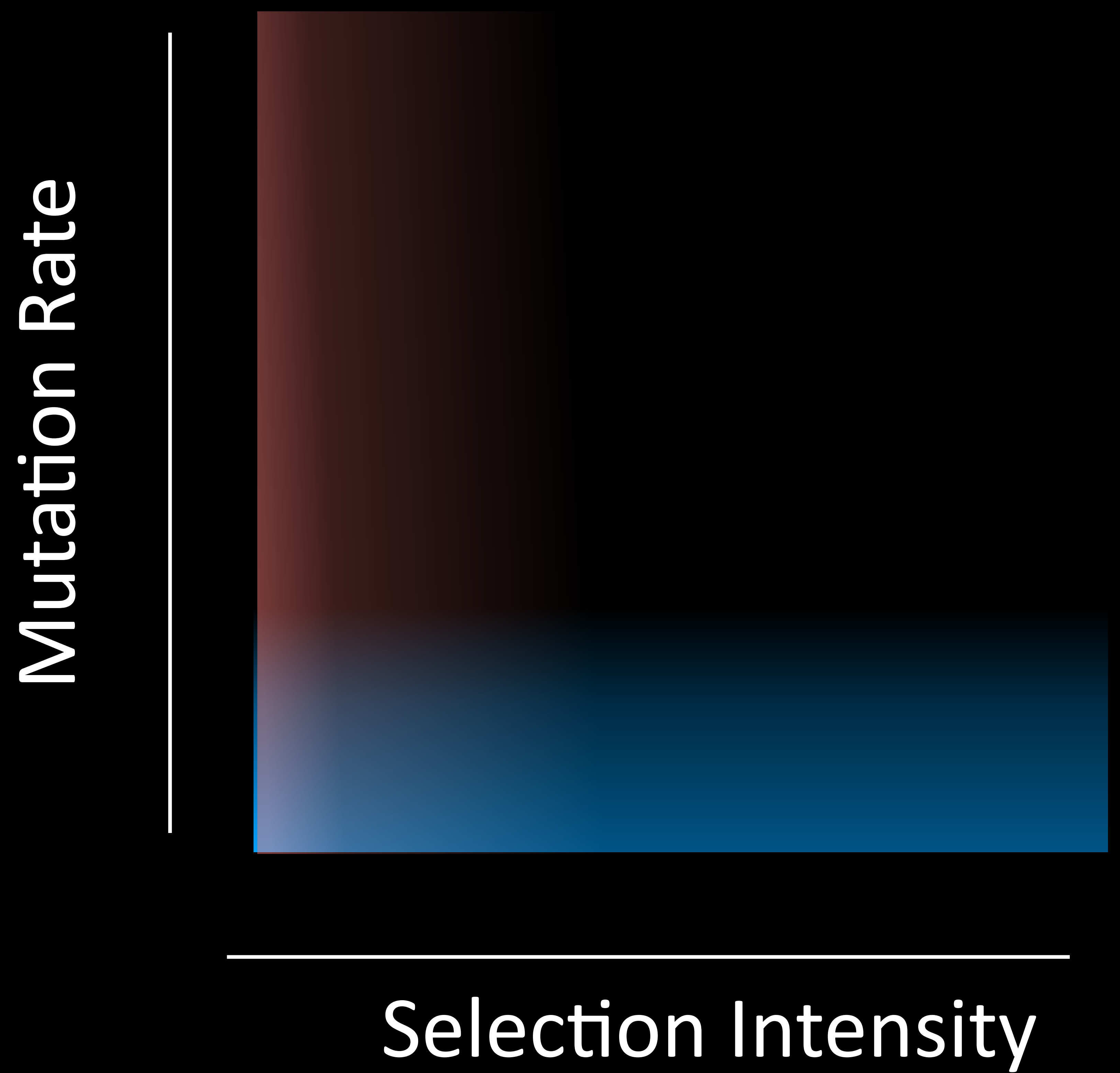
ABSTRACT In finite populations, an allele disappears or reaches fixation due to two main forces, selection and drift. Selection is generally thought to accelerate the process: a selected mutation will reach fixation faster than a neutral one, and a disadvantageous one will quickly disappear from the population. We show that even in simple diploid populations, this is often not true. Dominance and recessivity unexpectedly slow down the evolutionary process for weakly selected alleles. In particular, slightly advantageous dominant and mildly deleterious recessive mutations reach fixation slightly more slowly than neutral ones (at most 5%). This phenomenon determines genetic signatures opposite to those expected under strong selection, such as increased instead of decreased genetic diversity around the selected site. Furthermore, we characterize a new phenomenon: mildly deleterious recessive alleles, thought to represent a wide fraction of newly arising mutations, on average survive in a population slightly longer than neutral ones, before getting lost. Consequently, these mutations are on average slightly older than neutral ones, in contrast with previous expectations. Furthermore, they slightly increase the amount of weakly deleterious polymorphisms, as a consequence of the longer unconditional sojourn times compared to neutral mutations.

KEYWORDS weak selection; diffusion approximation; dominance; recessive mutations

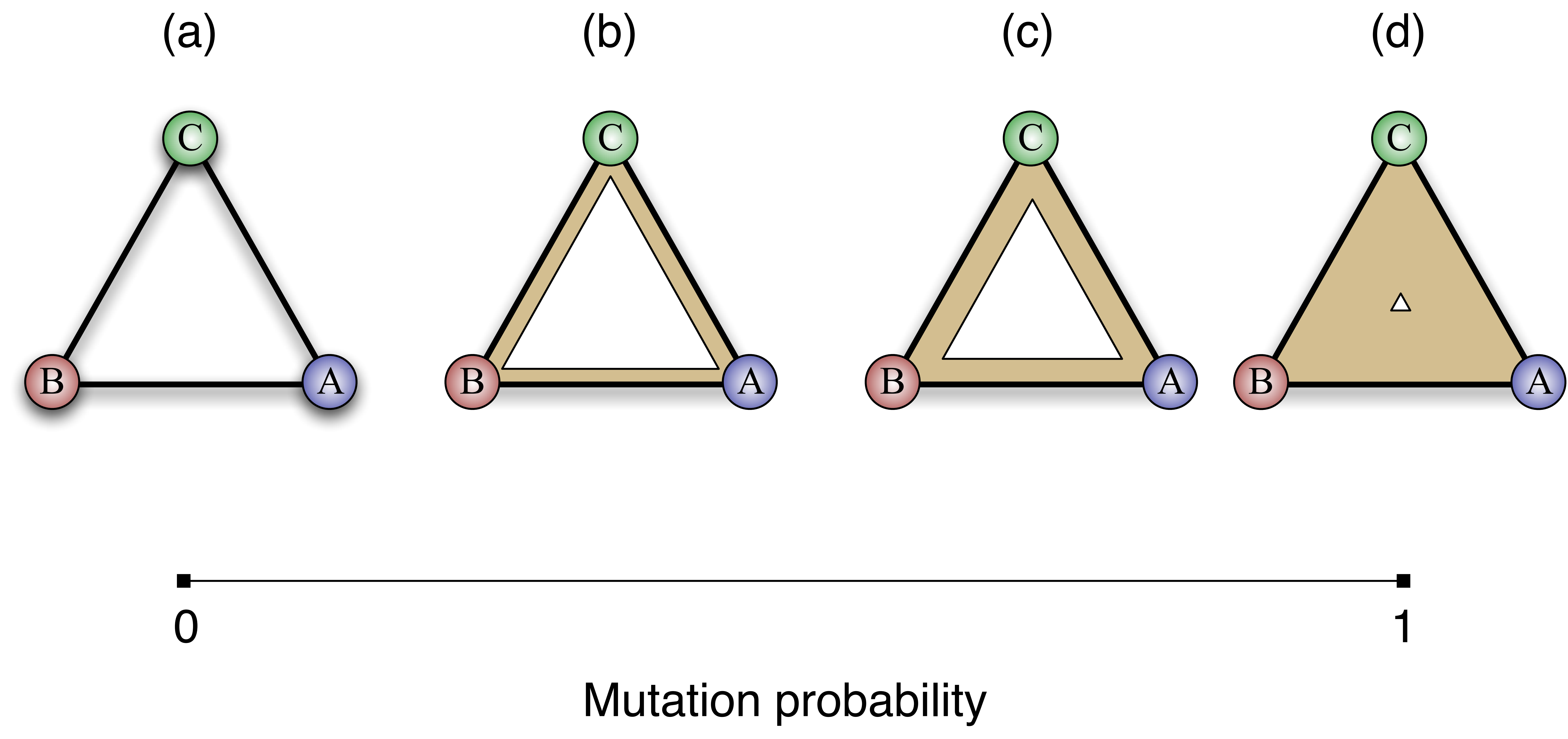
In the long run!

Mutation selection equilibrium

Until now we dealt with selection… what about mutations?



The problem



In the long run

Average frequency of a strategy in the mutation-selection equilibrium

$$\langle x_k \rangle_\delta = \frac{1}{n} + N \frac{1-u}{u} \langle \Delta x_k^{sel} \rangle_\delta .$$

$$\langle x_k \rangle_\delta = \frac{1}{n} + \text{something}$$

$\langle x_k \rangle_\delta > \frac{1}{n}$ if "something" is positive

Antal, Nowak & Traulsen, *Jour. Theor. Biol.*, 2009

In the long run

The “something” is the average change in the frequency of strategy k under weak selection $\delta \ll 1$

For d = 3

$$\langle \Delta x_k^{sel} \rangle_\delta = \frac{\delta\mu(L_k + M_k\mu + H_k\mu^2)}{Nn(1+\mu)(2+\mu)(3+\mu)}$$

$$L_k + M_k\mu + H_k\mu^2 > 0$$

Where L_k, M_k and H_k are functions consisting only of the number of strategies n and payoff values $a_{k,h,i}$

For an arbitrary d

$$L_k + \ldots + H_k\mu^{(d-1)} > 0$$

In the long run

A transformation

Games details

$L_k, \ldots, H_k$

+ Process details

Process details

(Pop. Structure,
update rule etc)

σ

+ game details

For d = 2;n=2

$$L_k + H_k\mu > 0$$

$$\sigma a_1 + a_0 > b_1 + \sigma b_0$$

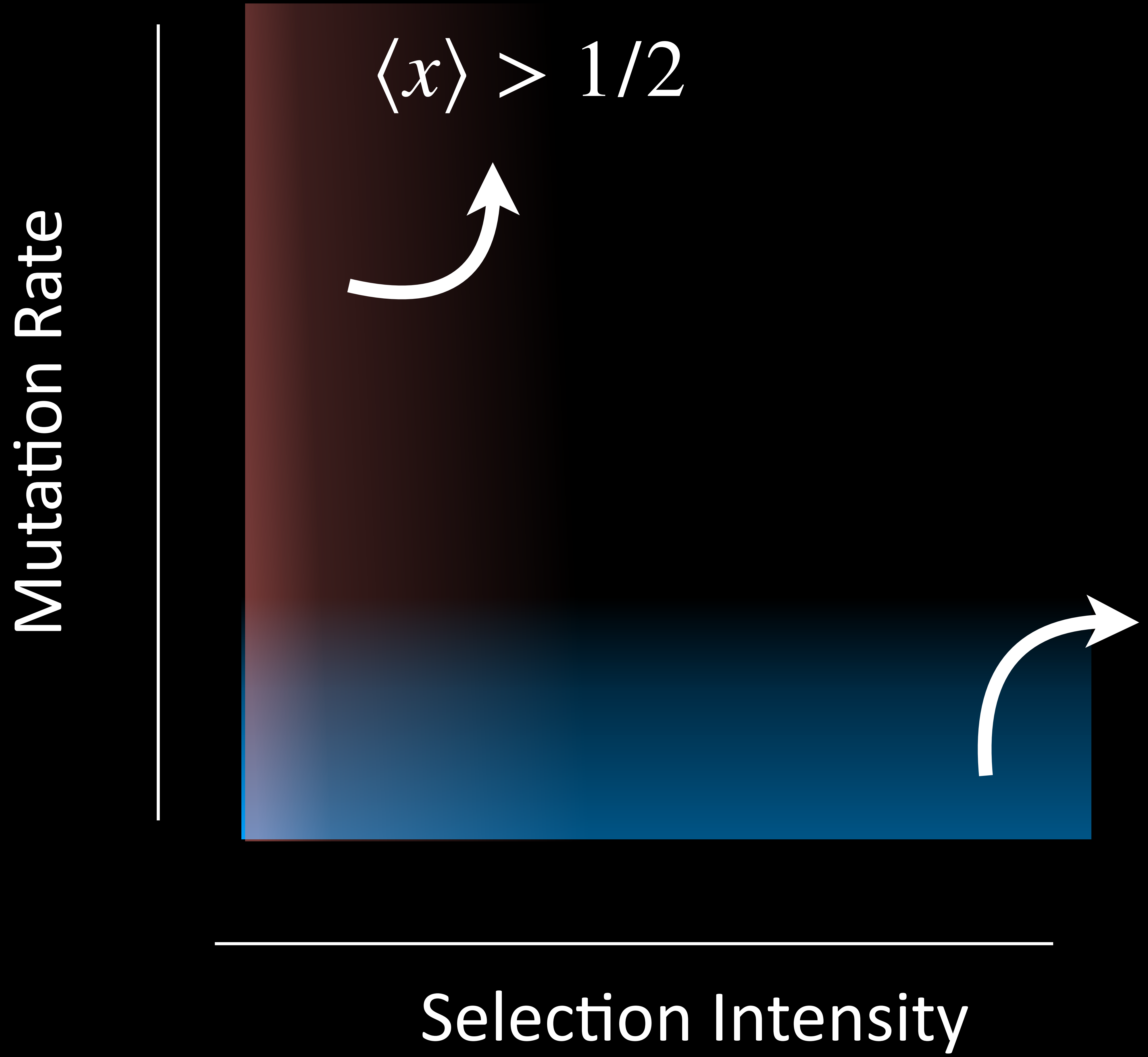
Harsanyi & Selten. A general theory of equilibrium selection in games, MIT Press, Cambridge, 1988

Tarnita, Antal, Ohtsuki, Fu, Nowak, *Jour. Theor. Biol.*, 2009

For n = 2

$$\sum_{\substack{0\le i\le d-1\\ i\neq i^*}} \sigma_i a_i + a_{i^*} > \sum_{\substack{0\le i\le d-1\\ i\neq i^*}} \sigma_i b_{d-1-i} + b_{d-1-i^*}$$

$$\langle x \rangle > 1/2$$



$$\rho_A > \rho_B$$

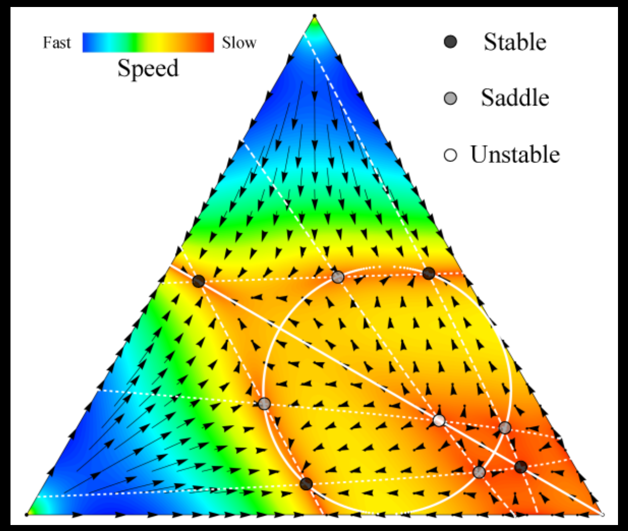
$$\sum_{k=0}^{d-1} a_k > \sum_{k=0}^{d-1} b_k$$

Wu, Bin, Arne Traulsen, and Chaitanya Gokhale. “Dynamic Properties of Evolutionary Multi-Player Games in Finite Populations.” *Games* 2013: 182–99.

How

Also.. why??

From Static
to Dynamic



If

Fixation probability

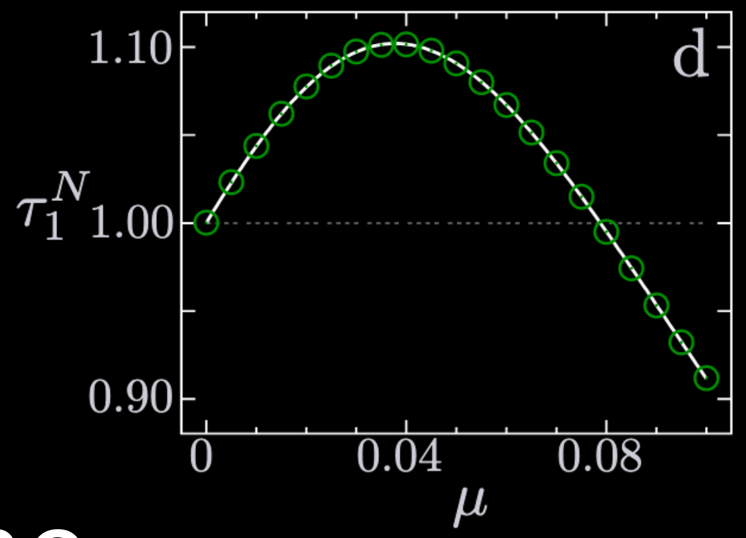
Risk dominance

1/3rd rule

$$\sum_{k=0}^{d-1} a_k > \sum_{k=0}^{d-1} b_k$$

$$\sum_{k=0}^{d-1} (d-k)a_k > \sum_{k=0}^{d-1} (d-k)b_k$$

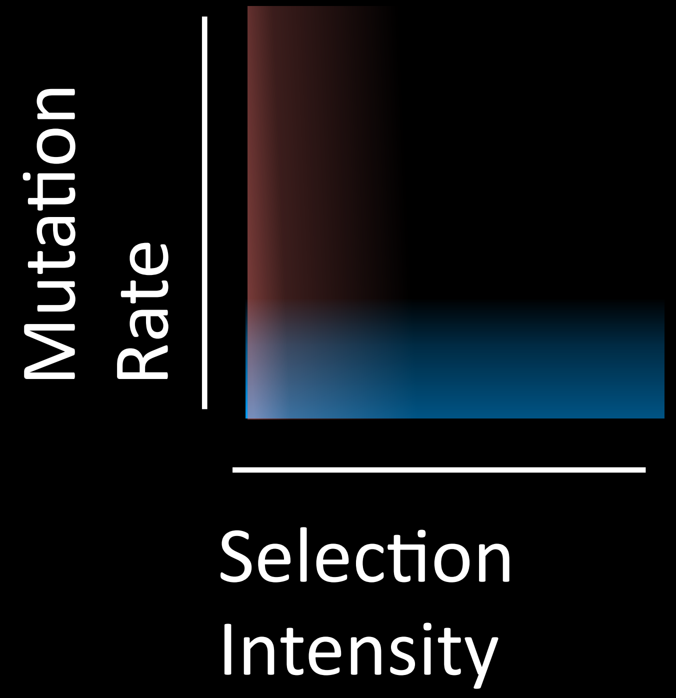
When



Fixation time

Stochastic slowdown

In the long run!



Mutation selection equilibrium

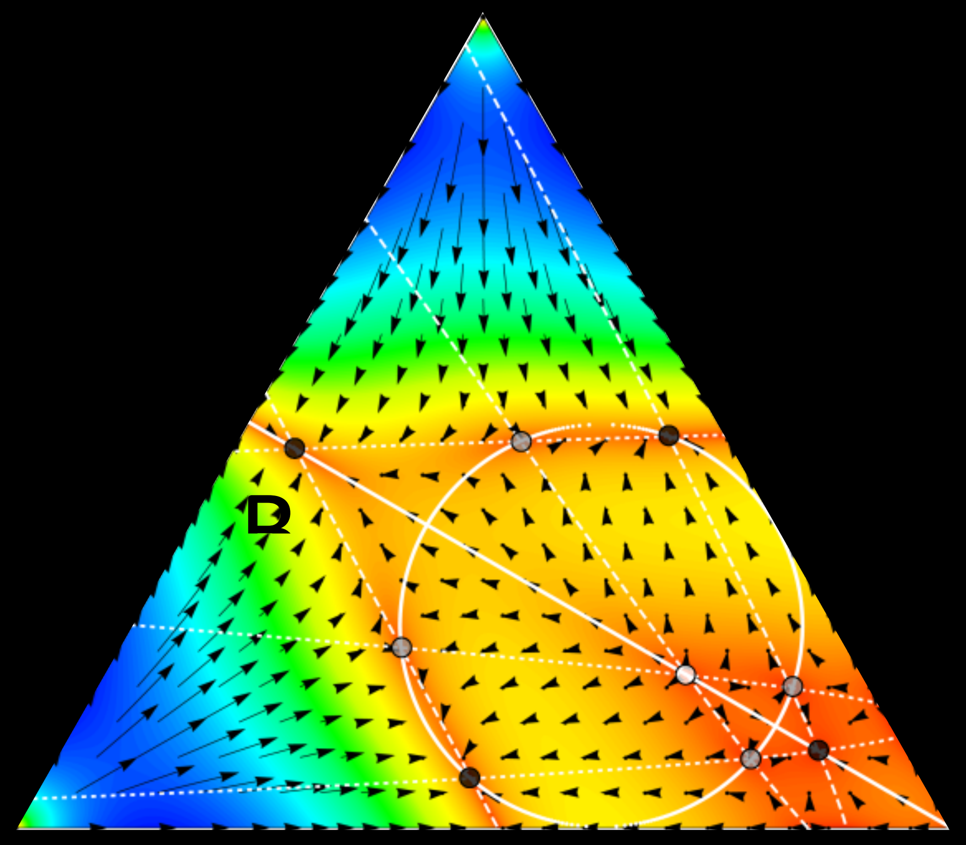
Lecture 2

If .. .when & how of MEGs in the long run

(If time permits)

MEGs in mutualism and

Eco-evolutionary dynamics



Mutualism and Evolutionary Multiplayer Games

How do they evolve and what keeps them from breaking down?

How the evolutionary process distributes the benefits of mutualism?

PGGs, Prisoners dilemma

Reciprocal altruism

Partner choice

Byproduct benefits

Pseudoreciprocity

…

Gokhale, Chaitanya S., and Arne Traulsen. "Mutualism and Evolutionary Multiplayer Games: Revisiting the Red King." ***Proceedings of the Royal Society B: Biological Sciences*** **279, 2012: 4611–16.**

Mutualism and Evolutionary Multiplayer Games

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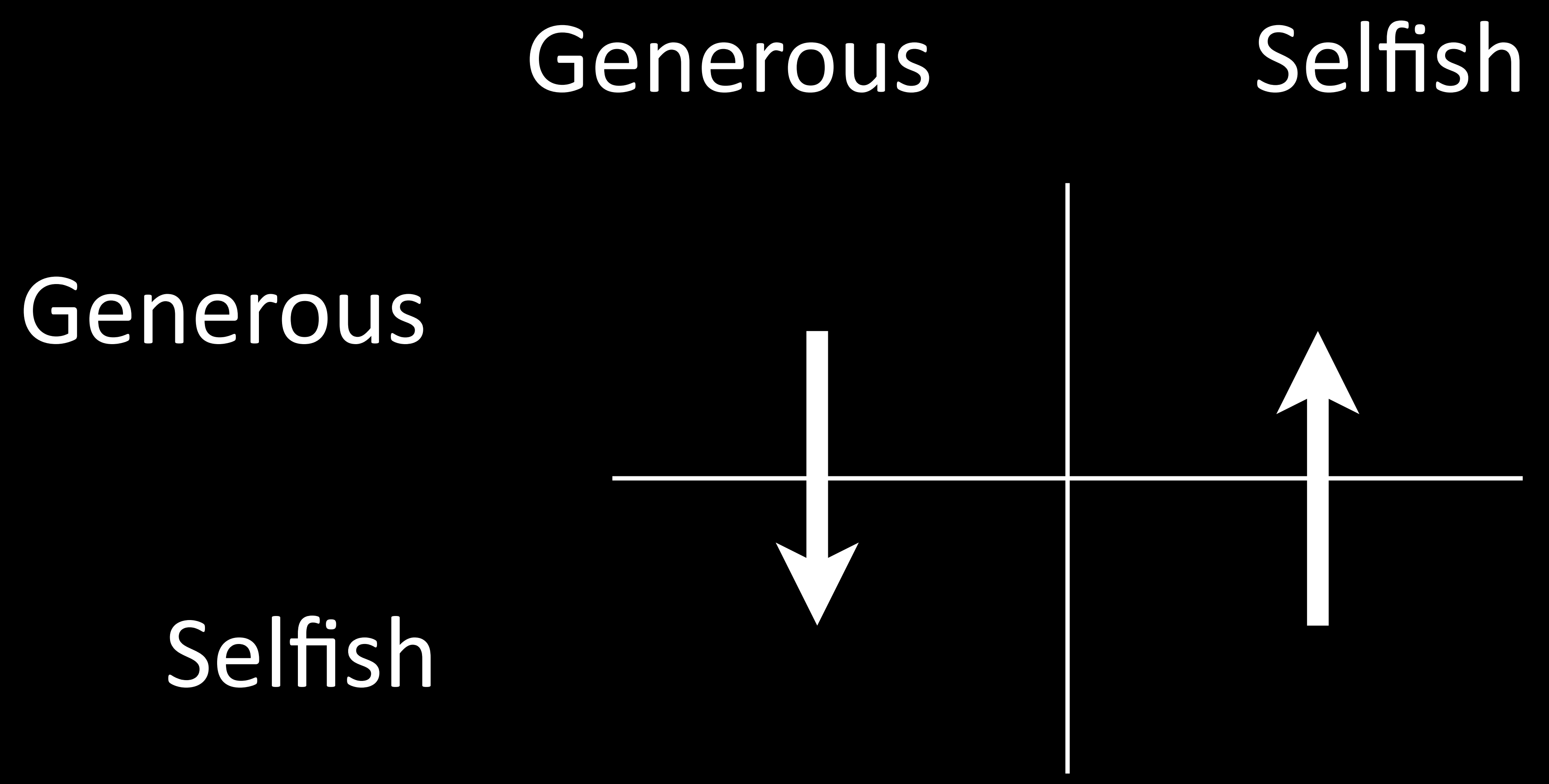

$$\dot{x} = x(f_G(x) - \bar{f}(x))$$

Mutualism and Evolutionary Multiplayer Games

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PGGs, Prisoners dilemma

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Byproduct benefits

Pseudoreciprocity

…

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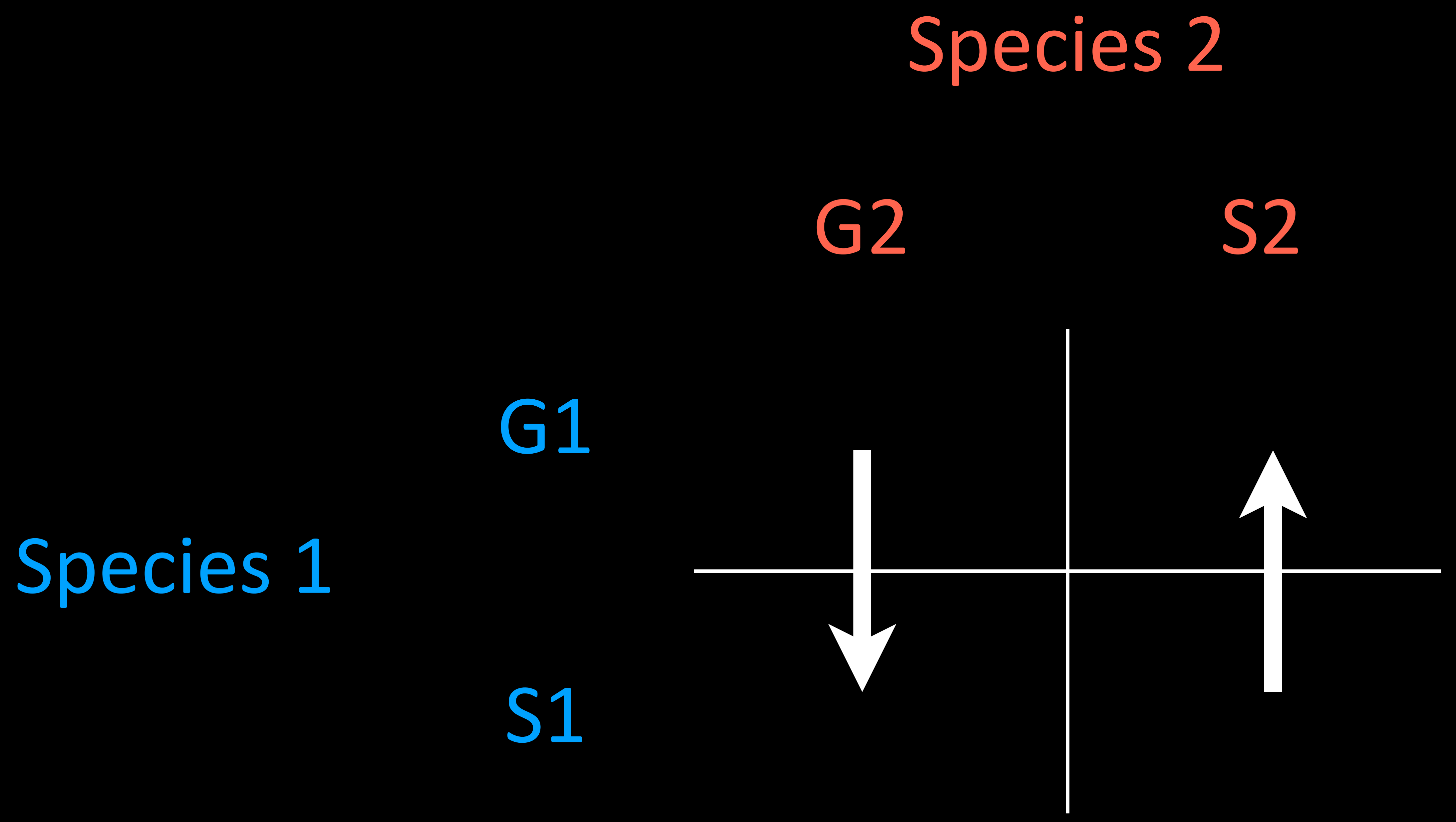


Species 2

G2 S2

Species 1

G1

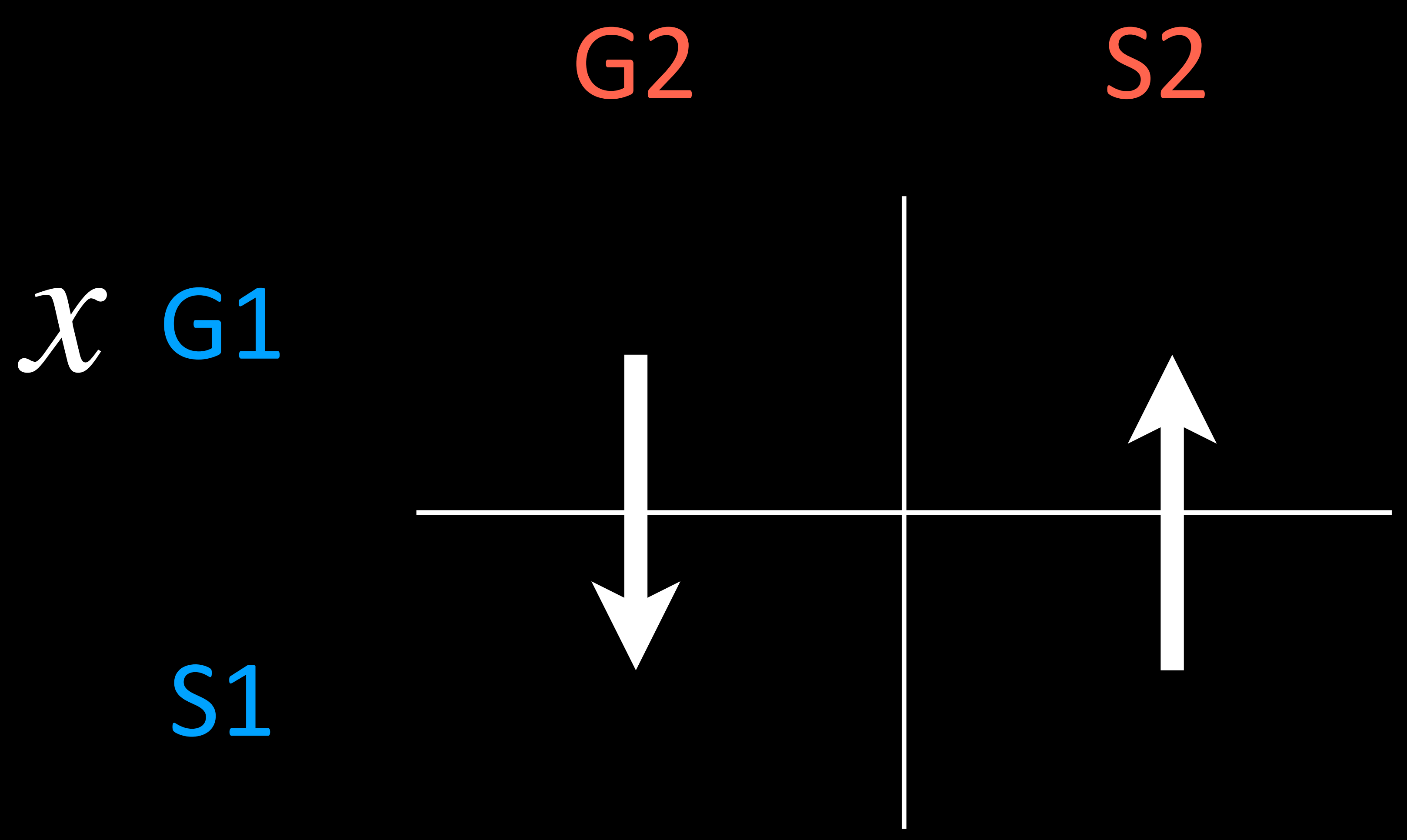
S1

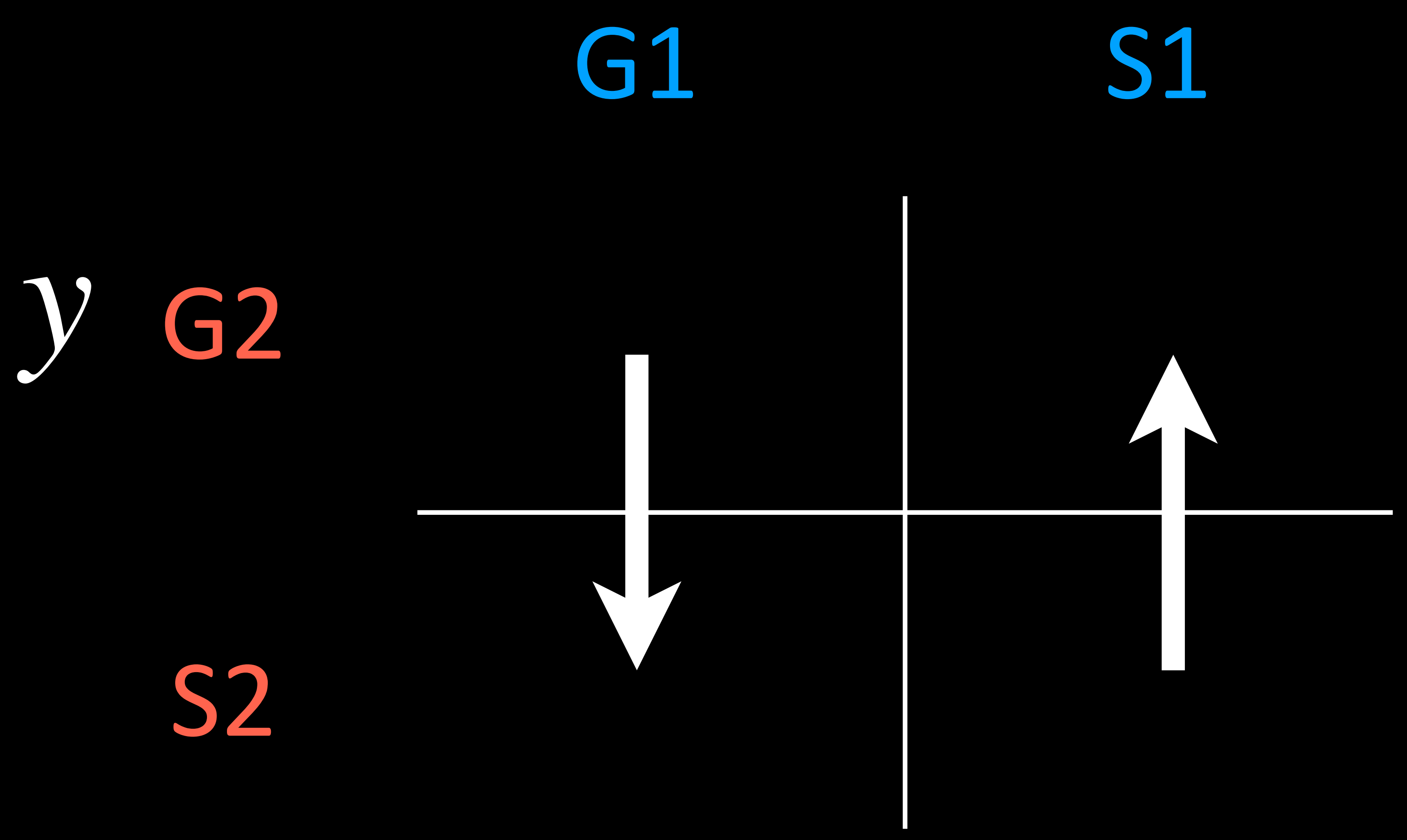
Mutualism and Evolutionary Multiplayer Games

$$\dot{x} = x\left(f_{G_1}(y) - \bar{f}_1(x,y)\right)$$

$$\dot{y} = y\left(f_{G_2}(x) - \bar{f}_2(x,y)\right)$$

How the evolutionary process distributes the benefits of mutualism?

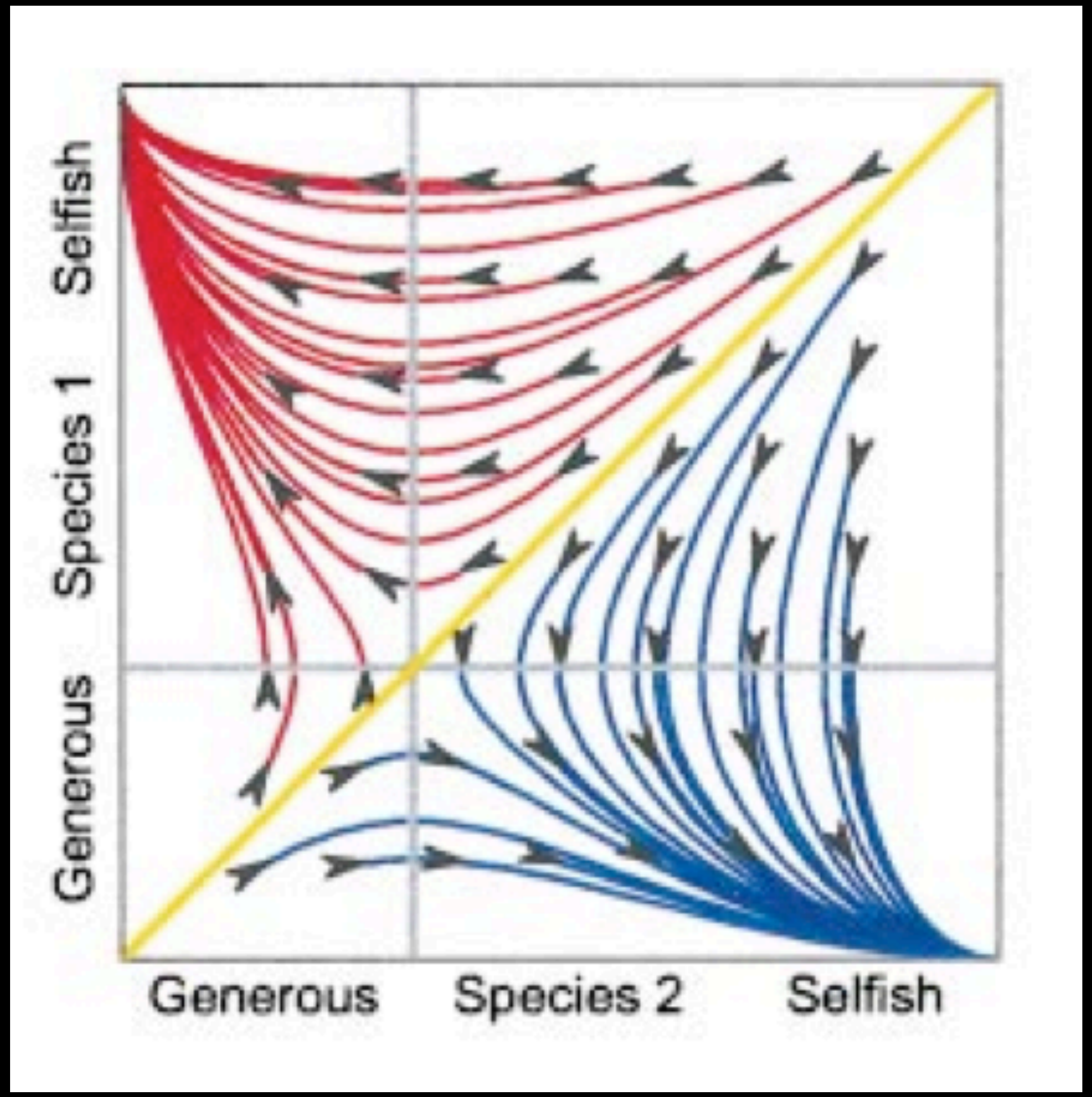




Mutualism and Evolutionary Multiplayer Games

$$\dot{x} \;=\; x\left(f_{G_1}(y) - \bar{f}_1(x,y)\right)$$

$$\dot{y} \;=\; y\left(f_{G_2}(x) - \bar{f}_2(x,y)\right)$$

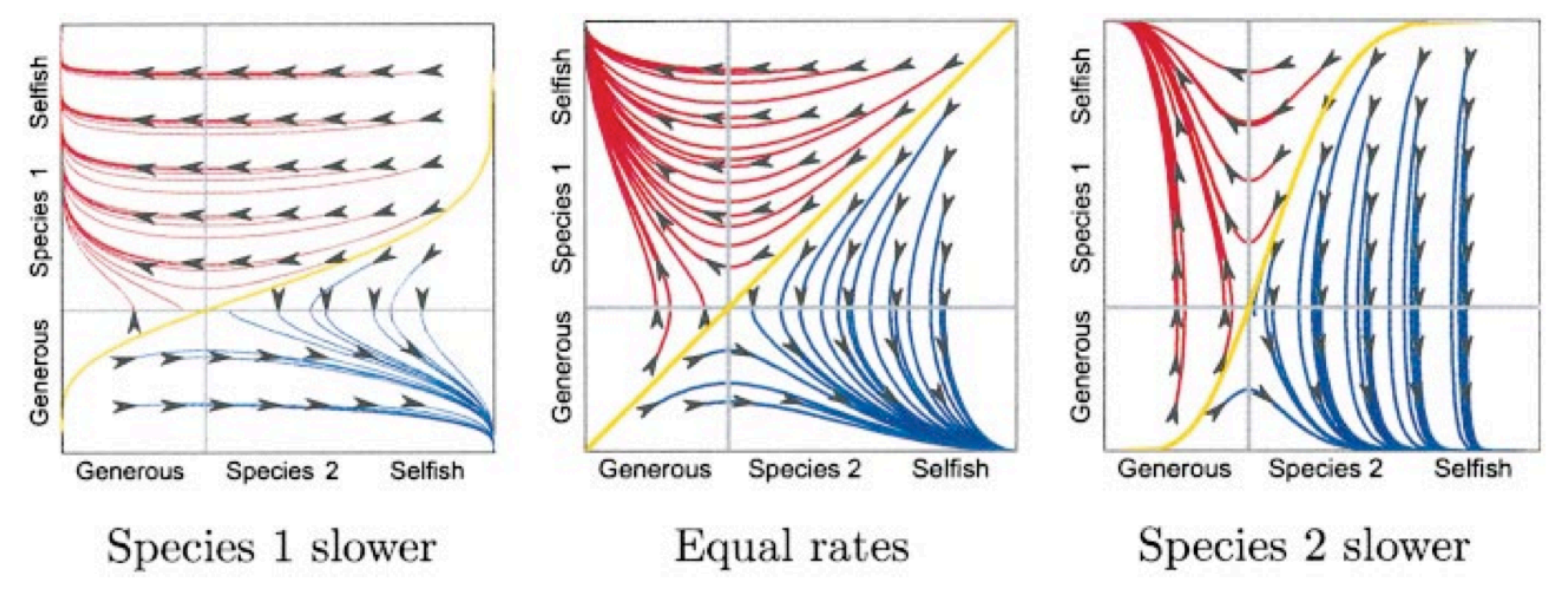


How the evolutionary process distributes the benefits of mutualism?

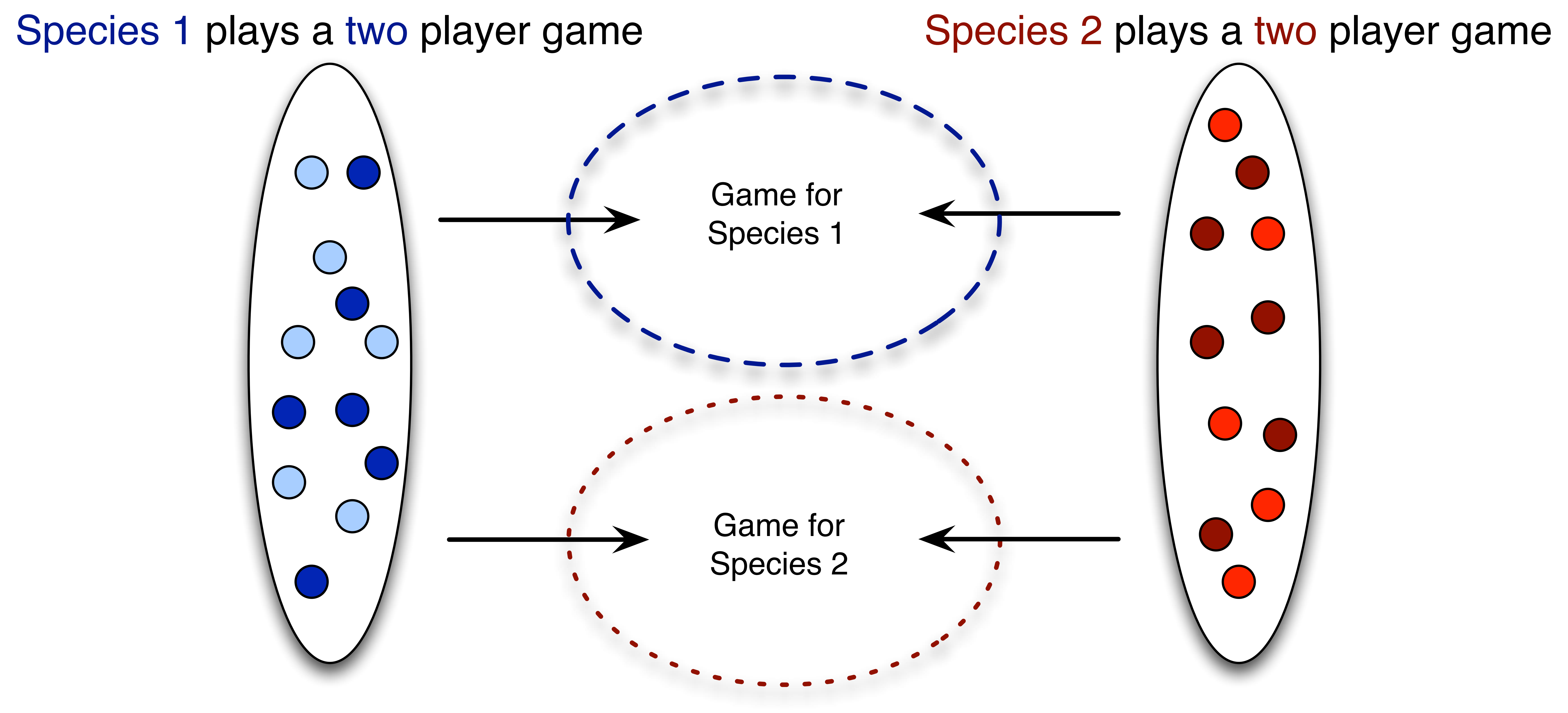
Mutualism and Evolutionary Multiplayer Games

The Red King Effect

…the slower a species evolves, the higher chance it has of reaching its favoured equilibrium.



Bergstrom, Carl T., and Michael Lachmann. "The Red King Effect: When the Slowest Runner Wins the Coevolutionary Race." *Proceedings of the National Academy of Sciences* 100, 2003: 593–98



$$\dot{x} = r_x x(f_{G_1}(y) - \bar{f}_1(x,y))$$
$$\dot{y} = r_y y(f_{G_2}(x) - \bar{f}_2(x,y)).$$

		Species 2	
		G_2	S_2
Species 1	G_1	$b-c/2$	$b-c$
	S_1	b	0

		Species 1	
		G_1	S_1
Species 2	G_2	$b-c/2$	$b-c$
	S_2	b	0

$$\begin{aligned} f_{G_1}(y) &= a_{G_1,G_2}y + a_{G_1,S_2}(1-y) \\ f_{S_1}(y) &= a_{S_1,G_2}y + a_{S_1,S_2}(1-y) \\ f_{G_2}(x) &= a_{G_2,G_1}x + a_{G_2,S_1}(1-x) \\ f_{S_2}(x) &= a_{S_2,G_1}x + a_{S_2,S_1}(1-x). \end{aligned}$$

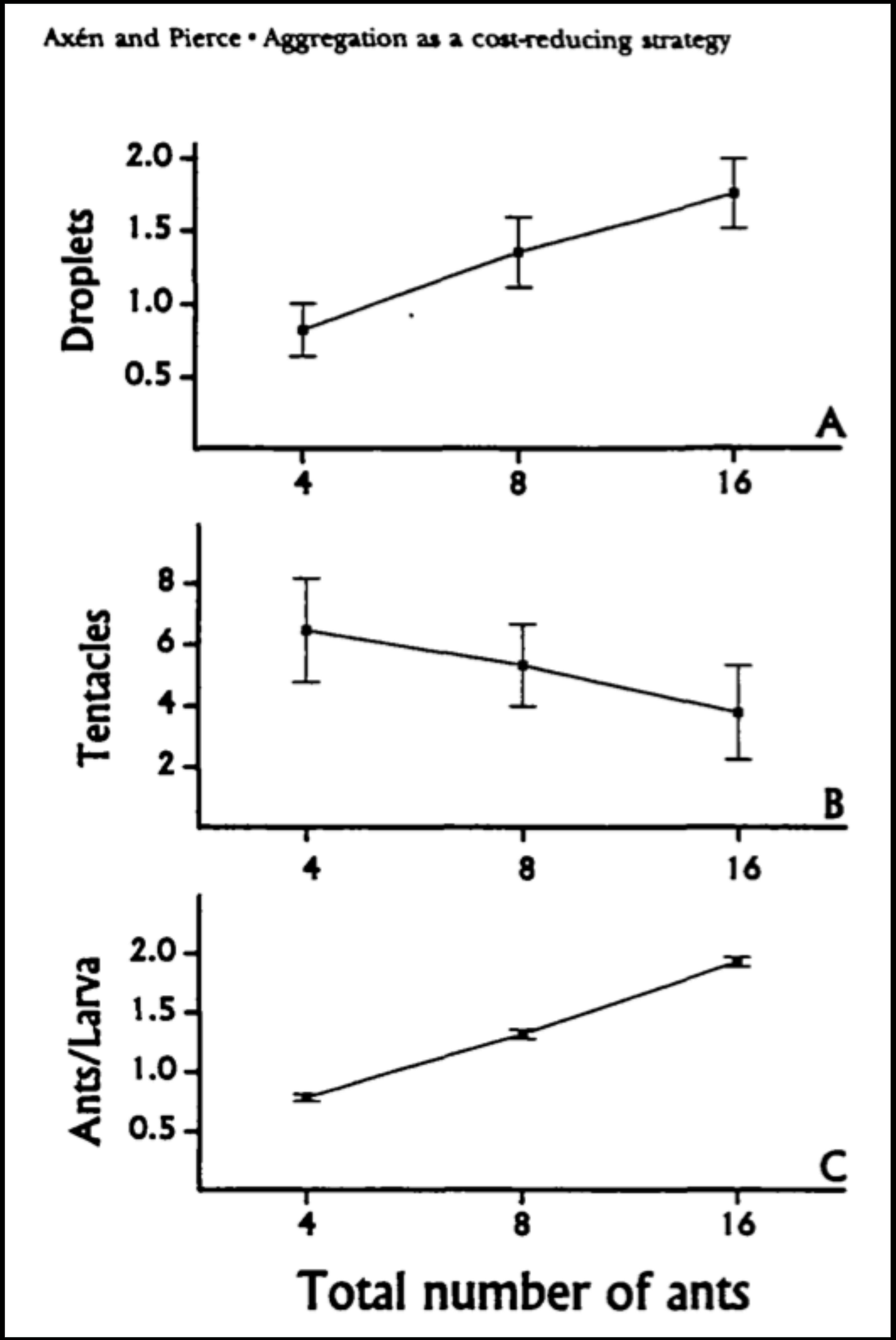
$b > c$

Behavioral Ecology Vol. 9 No. 2: 109–115

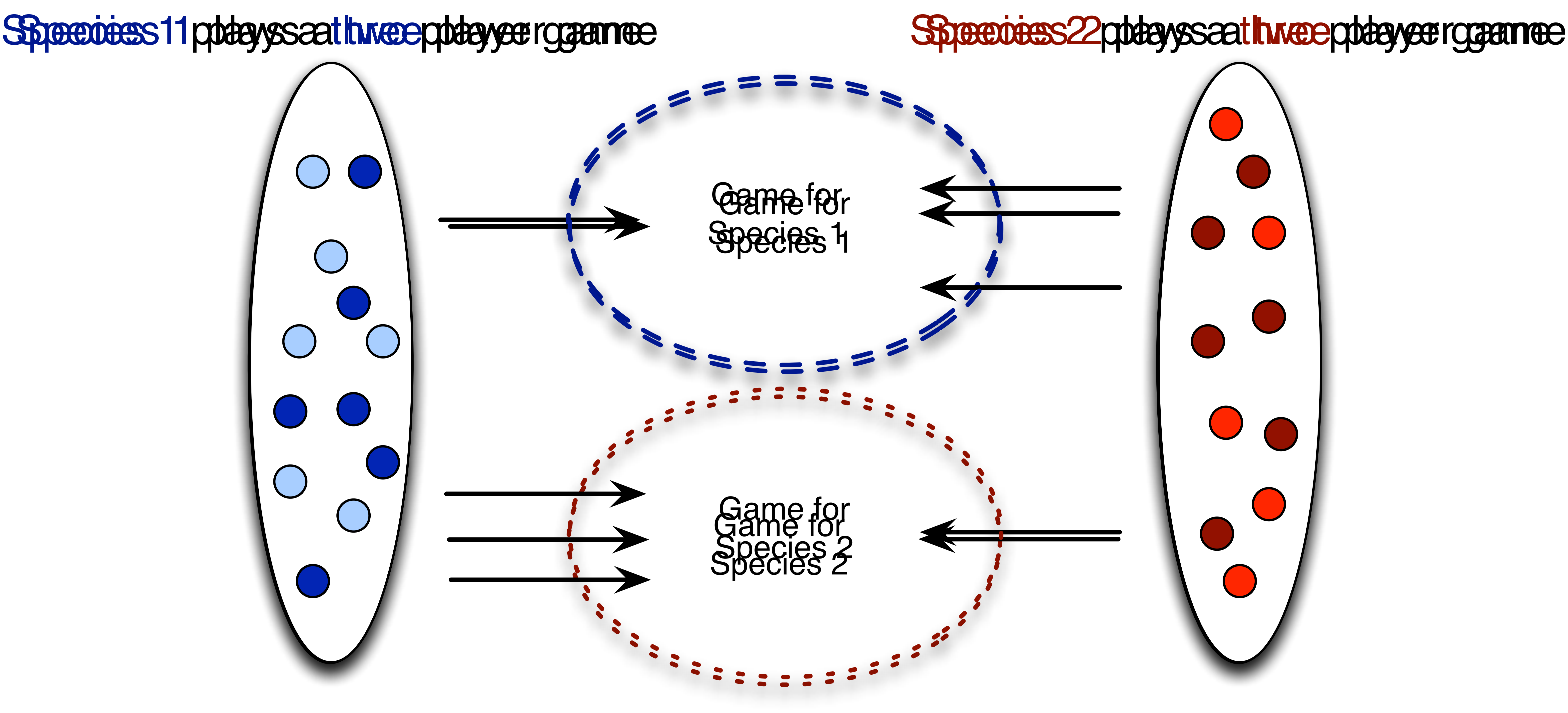
Aggregation as a cost-reducing strategy for lycaenid larvae

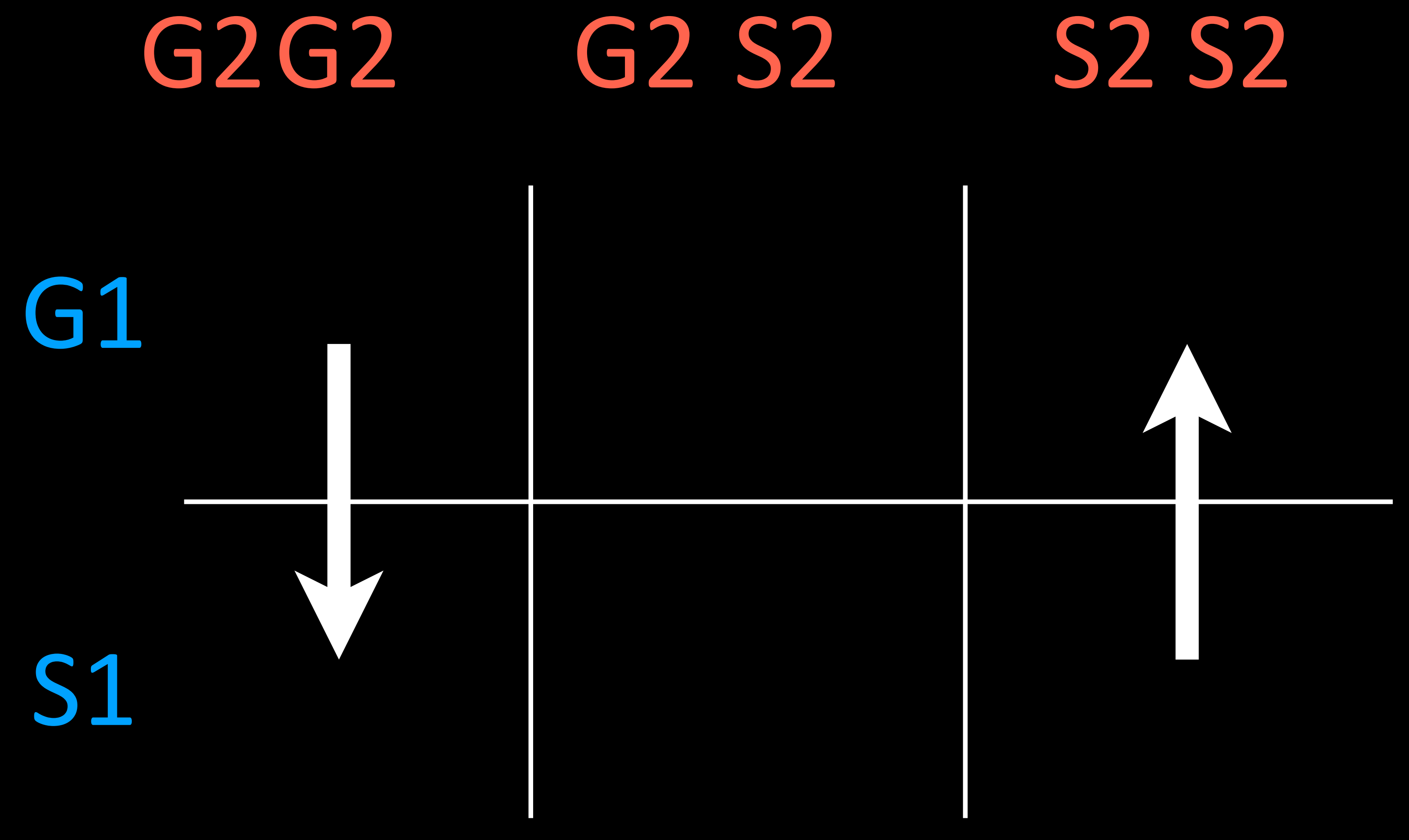
Annkristin H. Axén[a] and Naomi E. Pierce[b]
[a]Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden, and
[b]Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

If a mutualistic relationship entails providing services at a cost, selection will favor individuals that maximize the net benefits of the interaction and minimize the costs. Larvae of many species of lycaenid butterflies secrete nutritious food rewards to attending ants and, in return, receive protection against predators and parasitoids. Because ants typically recruit more workers to larger resources, by forming groups the larvae may ensure more reliable access to ants and thereby gain better protection. A further consequence of aggregating should be a change of the cost–benefit relationship for individual larvae. The larger the group, the smaller a single larva's influence will be on total ant density, which could lead to a smaller investment in secretion, thus reducing the per capita cost of cooperation. In this study, the influence of ant attendance, group size, and companion quality on larval investment was investigated. The interaction between the obligately ant-dependent lycaenid, *Jalmenus evagoras*, and its attendant *Iridomyrmex* ants was manipulated and the effect on larval secretion measured. As the level of ant attendance increased, the delivery of food rewards increased, both for solitary and for aggregated larvae. When aggregated, larvae provided less food rewards to ants than when solitary, and secretion rate decreased with increasing group size. Furthermore, larvae had lower secretion rates when paired with a bigger, more attractive larva than when paired with a smaller one. The considerable reduction in secretion rates for larvae in groups suggests that gaining protection at a lower secretion cost could be one factor that promotes aggregation in myrmecophilous lycaenids. *Key words:* aggregation, ants, butterflies, cooperation, cost–benefit relationship, food rewards, *Iridomyrmex*, *Jalmenus evagoras*, Lycaenidae, mutualism, protection, strategic behavior. *[Behav Ecol 9:109–115 (1998)]*



Axén and Pierce • Aggregation as a cost-reducing strategy





$$\dot{x} = r_x x(f_{G_1}(y) - \bar{f}_1(x,y))$$
$$\dot{y} = r_y y(f_{G_2}(x) - \bar{f}_2(x,y)).$$

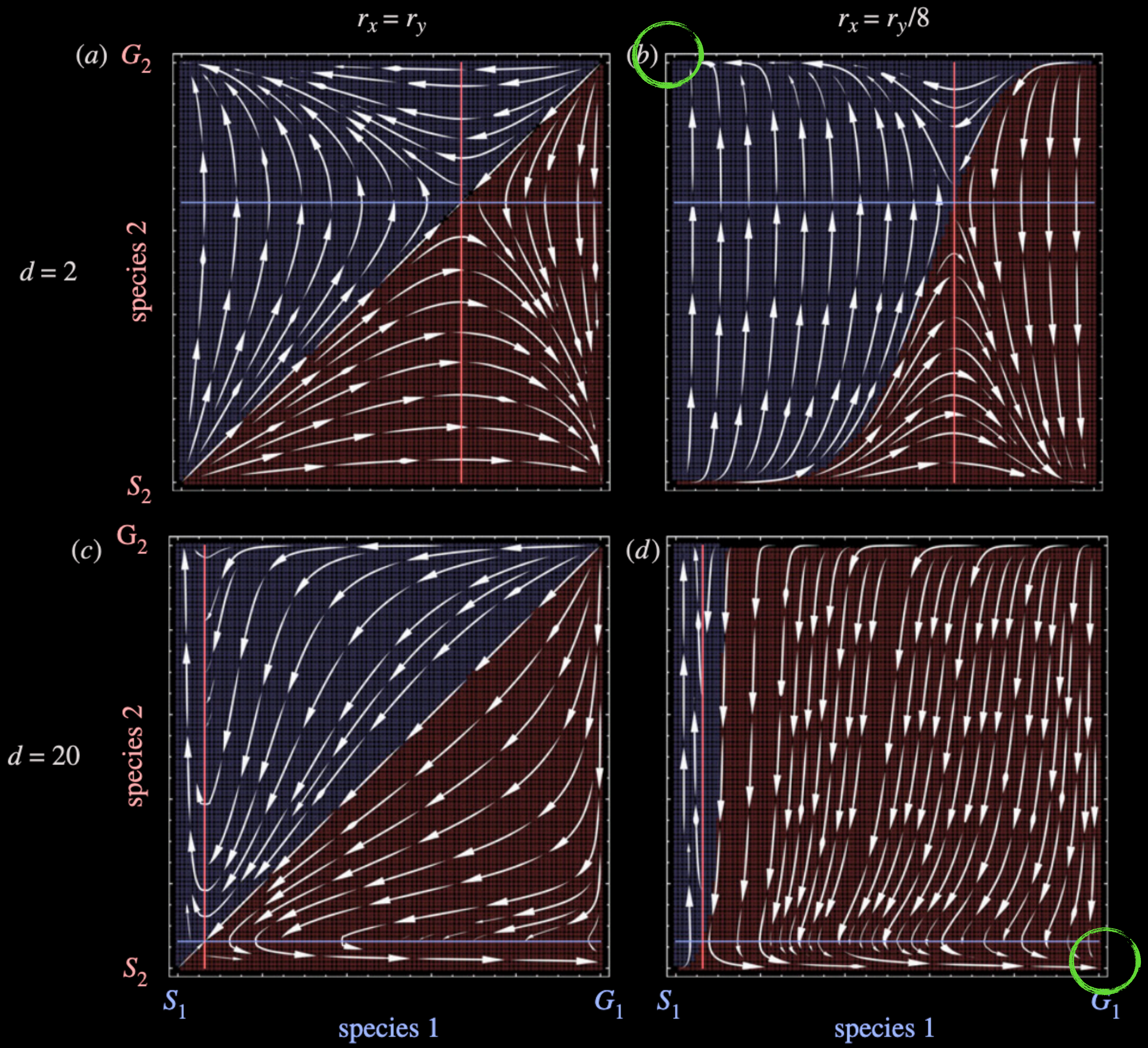
$$\Pi_{G_1}(k) = \begin{cases} b - \frac{c}{k} & \text{if } k \geq M \\ -\frac{c}{M} & \text{if } k < M \end{cases}$$

$$\Pi_{S_1}(k) = \begin{cases} b & \text{if } k \geq M \\ 0 & \text{if } k < M. \end{cases}$$

$$f_{G_1}(y) = \sum_{i=0}^{d-1} \binom{d-1}{i} y^i (1-y)^{d-1-i} \Pi_{G_1}(i+1)$$

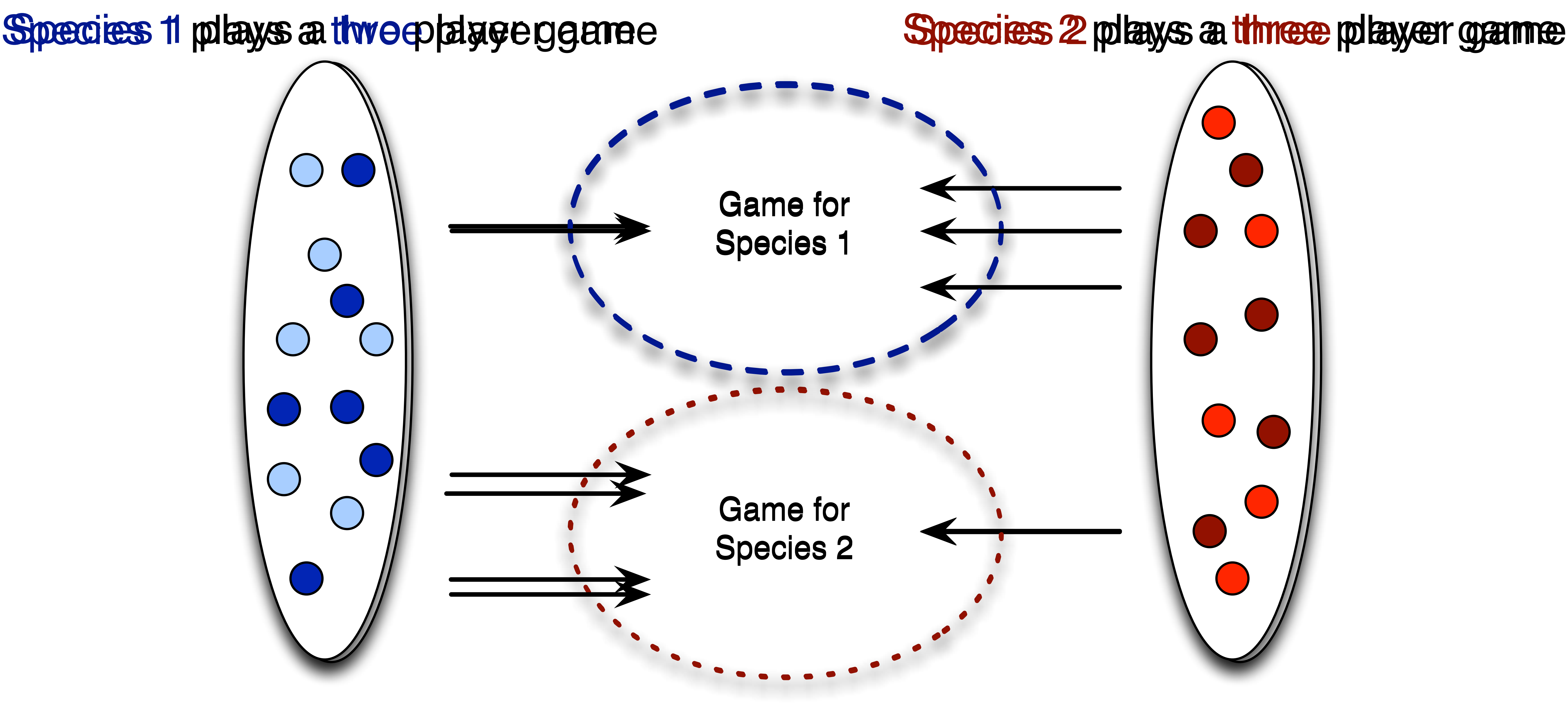
$$f_{S_1}(y) = \sum_{i=0}^{d-1} \binom{d-1}{i} y^i (1-y)^{d-1-i} \Pi_{S_1}(i).$$

…and similarly for Species 2

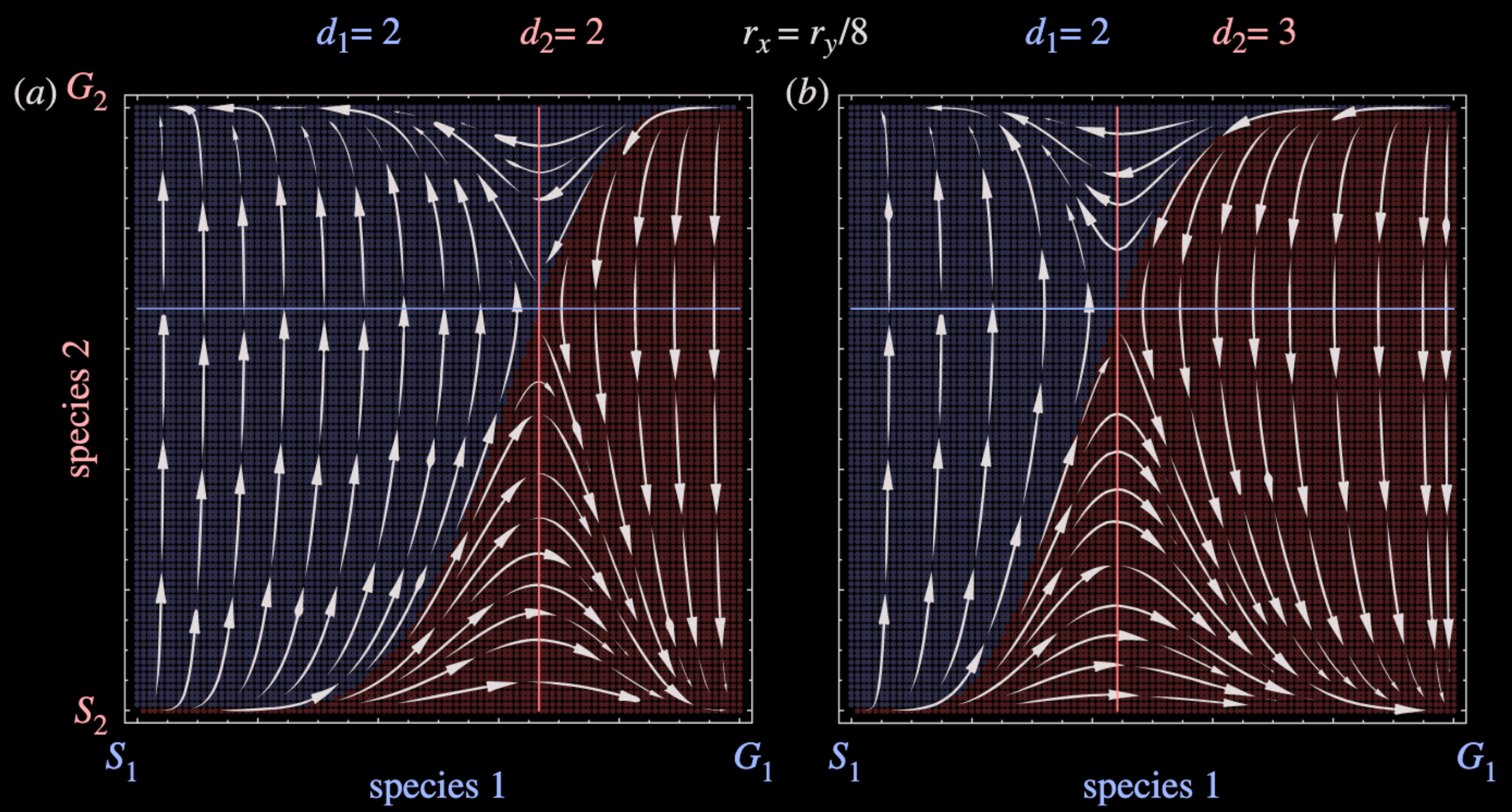


For multiplayer games the Red King effect is reversed

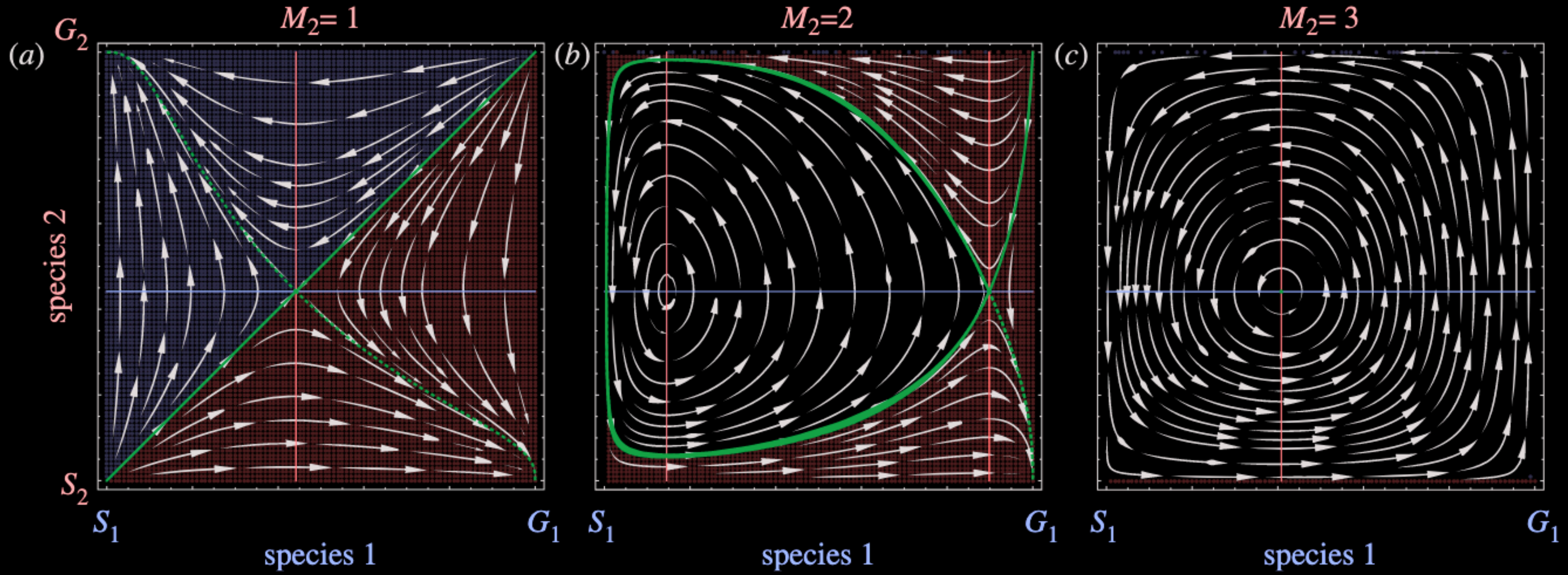
Multiplayer games allow us to incoporate additional bits of realism



Asymmetric number of players



Asymmetric thresholds



Mutualism and Evolutionary Multiplayer Games

Why is this cool?

$$\dot{x} = r_x x(f_{G_1}(y) - \bar{f}_1(x,y))$$
$$\dot{y} = r_y y(f_{G_2}(x) - \bar{f}_2(x,y)).$$

Asymmetry in the number of players / thresholds and other game parameters may be more under control of the interactors than evolutionary rates

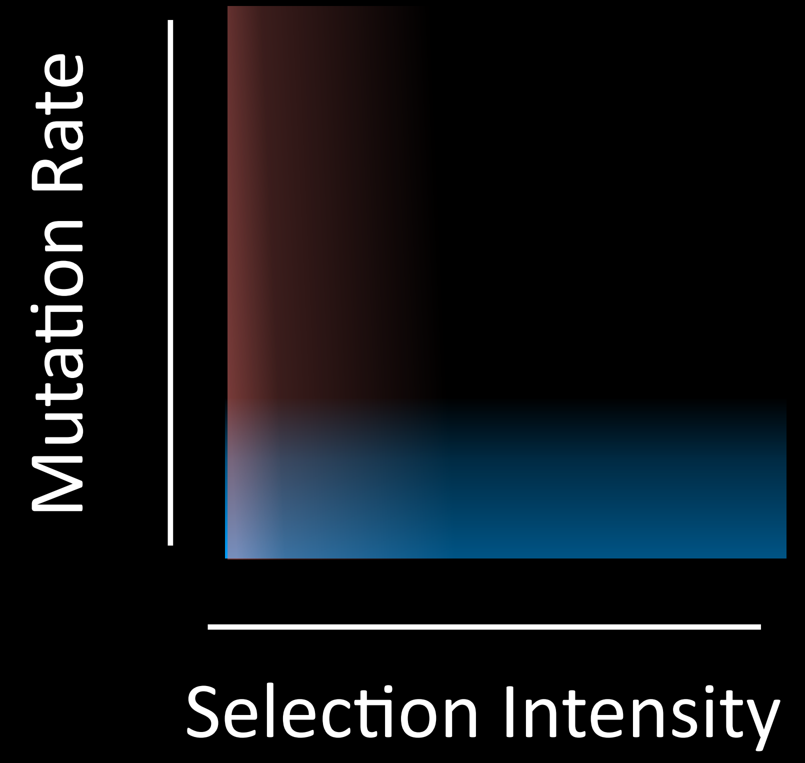
Interesting questions about how mutualism benefits can be manipulated where the exploited option is also preferred by the type being exploited

Note we are considering only interspecies dynamics and not intraspecies

For that see..

Gokhale, Chaitanya S, Marcus Frean, and Paul B Rainey. "Eco-Evolutionary Logic of Mutualisms." *Dynamic Games and Applications*, 2023

Lecture 2



If .. .when & how of MEGs in the long run

(If time permits)

MEGs in mutualism and

~~Eco-evolutionary dynamics~~