Fixation in Finite Populations
Discrete and Continuous Views

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Why Fixation?
Fixation

Originating population

Founder population

<table>
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<th>Founder population frequencies</th>
<th>Red</th>
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<td>Generation 2</td>
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<td>Generation 3</td>
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<td>0.40</td>
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<td>Generation 4</td>
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<td>Generation 5</td>
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<table>
<thead>
<tr>
<th>Ancestral population frequencies</th>
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<td>Original</td>
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Discrete Views
Moran Process
Wright Fisher Model

Fisher-Wright model

\[ P_{kj} = \binom{N}{j} \left( \frac{k}{N} \right)^j \left( \frac{N-k}{N} \right)^{N-j} \]
Moran & Wright-Fisher processes
and their transition probabilities

Moran

$$M_{ij} = \begin{cases} 
\frac{i}{N}(1 - p_i), & i = j + 1, \\
\frac{i}{N} p_i + \frac{N-i}{N} (1 - p_i), & i = j, \\
\frac{N-i}{N} p_i, & i = j - 1, \\
0, & |i - j| > 1.
\end{cases}$$

Wright & Fisher

$$M_{ij} = \binom{N}{j} p_i^j (1 - p_i)^{N-j}.$$
Framework

- $M_{ij}, i, j = 0, \ldots, N;$
Framework

- $M_{ij}, i, j = 0, \ldots, N$;
- $M_{ij} = M(i, j, p, N); \quad p \in \mathbb{R}^{N+1}$
Framework

- \( M_{ij}, i, j = 0, \ldots, N; \)
- \( M_{ij} = M(i, j, p, N); \quad p \in \mathbb{R}^{N+1} \)
- \( p_j \in [0, 1] \) describes the probability of a type A individual being selected for reproduction, with the chain in state \( j \). We will term \( p \) the vector of type selection probabilities (TSP)
Framework

- \( M_{ij}, i, j = 0, \ldots, N; \)
- \( M_{ij} = M(i, j, \mathbf{p}, N); \quad \mathbf{p} \in \mathbb{R}^{N+1} \)
- \( \rho_j \in [0, 1] \) describes the probability of a type \( A \) individual being selected for reproduction, with the chain in state \( j \). We will term \( \mathbf{p} \) the vector of type selection probabilities (TSP)
- Absence of mutation:
  \[
  M_{0i} = \begin{cases} 
  1, & i = 0 \\
  0, & i = 1, \ldots, N
  \end{cases}
  \quad \text{and} \quad
  M_{Ni} = \begin{cases} 
  0, & i = 0, \ldots, N - 1 \\
  1, & i = N
  \end{cases}.
  \]
- Reproductive fitness: \( \varphi^{(A,B)} : \{0, 1, \ldots, N\} \to \mathbb{R}_+ \)
- \[
  p_i = \frac{i \varphi^{(A)}(i)}{i \varphi^{(A)}(i) + (N - i) \varphi^{(B)}(i)}.
  \]
The Kimura class

Definition
Let $M$ be a $(N + 1) \times (N + 1)$ stochastic matrix. We say that $M$ is Kimura ($M \in \mathcal{K}$), if

$$M = \begin{pmatrix}
1 & 0 & 0 \\
\tilde{a}^\dagger & \tilde{M} & \tilde{b}^\dagger \\
0 & 0 & 1
\end{pmatrix},$$

(1)

- $\tilde{M}$ is a $(N - 1) \times (N - 1)$ sub-stochastic irreducible matrix;
- $0$ is the zero vector in $\mathbb{R}^{N-1}$;
- $\tilde{a}$ and $\tilde{b}$ non-zero, non-negative vectors in $\mathbb{R}^{N-1}$. 

Fixation

Proposition

Let $\mathbf{M} \in \mathcal{K}$. Then, there exists a unique vector $\mathbf{F} \in \mathbb{R}^{N-1}$, with $0 < \tilde{F}_i < 1$, such that

$$\mathbf{F} = \begin{pmatrix} 0 & \tilde{\mathbf{F}} & 1 \end{pmatrix},$$

with $\mathbf{M}\mathbf{F}^\dagger = \mathbf{F}^\dagger$ and

$$\tilde{\mathbf{F}}^\dagger = \left( \mathbf{I} - \tilde{\mathbf{M}} \right)^{-1} \tilde{\mathbf{b}}^\dagger.$$

Definition (Admissible fixation vector)

A fixation vector $\mathbf{F}$ satisfying $0 < F_i < 1$, $i = 1, \ldots, N - 1$, is termed admissible.
The more the merrier?
Kimura Birth-Death processes

- Fixation given explicitly by

\[
F_i = c^{-1} \sum_{l=1}^{i} \prod_{k=1}^{l} \frac{M_{k-1,k}}{M_{k+1,k}}, \quad c = \sum_{l=1}^{N} \prod_{k=1}^{l-1} \frac{M_{k-1,k}}{M_{k+1,k}}.
\]

- Hence fixation KBD processes are \textbf{always} strictly increasing.
Regular and weakly-regular processes

**Definition**
An evolution process such that the transition matrix belongs to the Kimura class is said to be **regular** (**weakly regular**), if the associated fixation vector is increasing (non-decreasing, respect.).
Questions

- Is every model regular?
- Otherwise, is every relevant model regular?
- If not, what are the important irregular processes?
- Can we characterise regular/irregular processes?
Stochastic orderering

Definition (Vector stochastic ordering)
We say that two vectors $\mathbf{u}, \mathbf{v} \in \Delta^N := \{ \mathbf{x} \in \mathbb{R}^{N+1} | x_i \geq 0, \sum_i x_i = 1 \}$ are stochastically ordered, $\mathbf{u} \succ \mathbf{v}$, if for all $n = 1, \ldots, N$, we have that $\sum_{i=n}^{N} u_i \geq \sum_{i=n}^{N} v_i$. If all inequalities are strict, then we say $\mathbf{u} \succ\succ \mathbf{v}$.

Definition (Ordered matrices)
Consider a $N \times N$ matrix $\mathbf{A}$. We say that $\mathbf{A}$ is stochastically ordered (SO, $\mathbf{A} \in \text{StO}_N$) if all row vectors are stochastically ordered, i.e., if for all $i > j$, we have that $\mathbf{A}_{i, \cdot} \succ \mathbf{A}_{j, \cdot}$. We say that $\mathbf{A}$ is strictly stochastically ordered (SSO, $\mathbf{A} \in \text{St}^2O_N$) if for all $i > j$, we have that $\mathbf{A}_{i, \cdot} \succ\succ \mathbf{A}_{j, \cdot}$. 
Definition
We say that a $N \times N$ matrix $A$ is \textit{eventually strictly stochastically ordered} (\textit{stochastically ordered}) if there exists $k_0 \in \mathbb{N}$ such $A^k$ is strictly stochastically ordered (stochastically ordered, respect.) for $k \geq k_0$. 

\begin{flushright}
\text{Proposition}
\end{flushright}
Let $M$ be a $(N+1) \times (N+1)$ Kimura matrix. If $M$ is eventually stochastically ordered then $M$ is weakly-regular. Is it necessary?
SO/ESO => Weakly-Regular

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Let $M$ be a $(N + 1) \times (N + 1)$ Kimura matrix. If $M$ is eventually stochastically ordered then $M$ is weakly-regular.

▶ ESO is sufficient to guarantee the process is weakly-regular. Is it necessary?
Let
\[ M = \begin{pmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}. \]

Then
\[ F = \begin{pmatrix} 0 & 1 \\ \frac{1}{2} & \frac{1}{2} \end{pmatrix}; \text{ hence } M \text{ is weakly-regular.} \]

We check directly that
\[ M^\kappa = \begin{pmatrix} 1 & 0 & 0 & 0 \\ \alpha_\kappa & \delta_\kappa & \gamma_\kappa & \alpha_\kappa \\ \beta_\kappa & 2\gamma_\kappa & \delta_\kappa & \beta_\kappa \\ 0 & 0 & 0 & 1 \end{pmatrix}. \]

In particular,
\[ \alpha_{\kappa+1} = \frac{1}{8} + \frac{2\alpha_\kappa + \beta_\kappa}{4}, \quad \beta_{\kappa+1} = \frac{\alpha_\kappa + \beta_\kappa}{2}. \]

It is easily verified by induction in \( \kappa \) that \( \alpha_\kappa, \beta_\kappa < \frac{1}{2} \). On the other hand,
\[ \alpha_{\kappa+1} - \beta_{\kappa+1} = \frac{1 - 2\beta_\kappa}{8} > 0, \]
However for regularity, ESSO is equivalent to regularity:

**Theorem**

Let $\mathbf{M}$ be a $(N + 1) \times (N + 1)$ Kimura matrix. Then $\mathbf{M}$ is regular if, and only if, it is eventually strictly stochastically ordered.
The WF process

Theorem

Let $M$ be the transition matrix of the Wright Fisher process associated to the type selection probability vector $p$. The three conditions below are equivalent.

1. The process $M$ is regular.
2. The matrix $M$ is strictly stochastically ordered.
3. The vector $p$ is increasing.

Proposition

If fitnesses functions are positive and affine, then the type selection probability vector $p$ is increasing.
A non-regular three-player game

- Let $\varphi^{(A)}(x) = 15 - 24x + 10x^2$ and $\varphi^{(B)}(x) = 1 + 14x^2$, which are strictly positive in the interval $[0, 1]$;
- Can be obtained from 3-player game theory, with $a_0 = 15, a_1 = 3, a_2 = 1, b_0 = 1, b_1 = 1, b_2 = 15$, where $a_k (b_k)$ is the pay-off of a type $A$ ($B$, respectively) player against $k$ other players;
- Then $p_i$ given by reproductive fitness is not increasing;
- Note that the relative fitness $\Psi^{(A)}/\Psi^{(B)} = \varphi^{(A)}/\varphi^{(B)}$ is decreasing and is associated to coexistence games (i.e., $\Psi^{(A)}/\Psi^{(B)} > 1$ for $x$ near zero, and $\Psi^{(A)}/\Psi^{(B)} < 1$ for $x$ near one).
Universality of Moran processes
Tell me your fixation and I will tell who you are

**Theorem**

Let $\mathbf{F}$ be an admissible fixation vector. Then $\mathbf{F}$ is the fixation vector of some Moran process if, and only if, $\mathbf{F}$ is increasing. Moreover, in the latter case, the type fixation probabilities of the Moran process that realises such a vector are given by

$$p_i = \frac{i(F_i - F_{i-1})}{i(F_i - F_{i-1}) + (N - i)(F_{i+1} - F_i)} \in (0, 1), \quad i = 1, \ldots, N-1.$$
Universality of Wright-Fisher

Tell me your fixation and I will tell who you could be

- We already have seen that are non-regular WF processes.
Universality of Wright-Fisher
Tell me your fixation and I will tell who you could be

➤ We already have seen that are non-regular WF processes.
➤ It turns out that WF fixation can be almost anything:
We already have seen that are non-regular WF processes. It turns out that WF fixation can be almost anything:

**Theorem**

Let \( \mathbf{F} \) be an admissible fixation vector. Then there exists at least one WF matrix that has \( \mathbf{F} \) as a fixation vector. In addition, if \( \mathbf{F} \) is increasing, then such WF matrix is unique.
Definition
We say that a matrix $A$ is totally indecomposable if there are no permutation matrices $P$ and $Q$ such that $PAQ = \begin{pmatrix} B & 0 \\ C & D \end{pmatrix}$, with $B$, $D$ non-trivial square matrices and $0$ the null matrix. We say that a Kimura transition matrix $M$ is a Gillespie matrix if $\tilde{M}$ is totally indecomposable. The Gillespie class will be denoted by $\mathcal{G}$.

Proposition
The class of Gillespie matrices is a convex set and it is closed by multiplication. In particular, it is a convex semigroup.
Lemma
The intersection of the set of banded stochastically ordered matrices with the set of regular Gillespie matrices is a convex semigroup. Furthermore, let $\mathcal{R}$ be one of the following set of matrices:

1. WF matrices with increasing $\mathbf{p}$ (or, equivalently, regular WF matrices).
2. $M$ matrices with increasing $\mathbf{p}$.
3. $M$ matrices with $\mathbf{p} \in (\epsilon_N, 1 - \epsilon_N)$, $\epsilon_N = 1/(N+1)$.
4. The union of any two of the previous sets or of all three.

Then the set generated by convex combinations and finite products of elements of $\mathcal{R}$ is a convex sub-semigroup of regular Gillespie matrices.
Non-regularity
Parrondo-like paradox in evolution

Let
\[ p_1 = (0, \frac{1}{7}, \frac{6}{7}, 1) \quad \text{and} \quad p_2 = (0, \frac{6}{7}, \frac{1}{7}, 1) \]
with corresponding Moran matrices:

\[
M_1 = \begin{pmatrix}
1 & 0 & 0 & 0 \\
\frac{2}{7} & \frac{13}{21} & \frac{2}{21} & 0 \\
0 & \frac{2}{21} & \frac{13}{21} & \frac{2}{7} \\
0 & 0 & 0 & 1
\end{pmatrix}
\quad \text{Summer only}
\]

\[
M_2 = \begin{pmatrix}
1 & 0 & 0 & 0 \\
\frac{1}{21} & \frac{8}{21} & \frac{4}{7} & 0 \\
0 & \frac{7}{21} & \frac{8}{21} & \frac{1}{21} \\
0 & 0 & 0 & 1
\end{pmatrix}
\quad \text{Winter only}
\]

Let
\[
M_3 = M_1 M_2 = \begin{pmatrix}
1 & 0 & 0 & 0 \\
\frac{23}{49} & \frac{128}{441} & \frac{172}{441} & \frac{8}{49} \\
\frac{147}{8} & \frac{441}{441} & \frac{441}{441} & \frac{49}{23} \\
0 & 0 & 0 & 1
\end{pmatrix}
\quad \text{Summer and Winter}
\]

and let \( F_i, \ i = 1, 2, 3 \), then we have:

\[ F_1 = (0, \frac{1}{5}, \frac{4}{5}, 1)^\dagger \]
\[ F_2 = (0, \frac{12}{25}, \frac{13}{25}, 1)^\dagger \]
Summary

- Axiomatisation of evolutionary processes in finite populations;
- Qualitative study of fixation in finite populations;
- Identification and characterisation of regularity;
- Study of time-inhomogeneous processes (including mixtures);

Not presented:
- Regular fixation in large populations;
- Alternative processes (pairwise comparison; generalised Eldon-Wakeley; generalised $\Lambda_1$);
- Processes in periodic and random environments.

Continuous Views
Population of fixed size $N$ with two types $A$ and $B$. Transition probabilities given by:

$$T_N^\pm(x) = x(1-x)\Delta^\pm\left(\psi_A^N, \psi_B^N\right).$$

$$T_N^0(x) = 1 - T_N^+(x) - T_N^-(x).$$

- $\Delta^\pm : \mathbb{R}^+ \times \mathbb{R}^+ \rightarrow \mathbb{R}^+$ models natural selection.
- Fitnesses given by $\psi_A^N, \psi_B^N : [0, 1] \rightarrow \mathbb{R}^+$.
- Write $\Delta_N^\pm(x) = \Delta^\pm\left(\psi_A^N(x), \psi_B^N(x)\right)$.
- Similar class studied by Assaf & Mobilia (2010).
Examples

- Frequency dependent Moran process (Nowak et al. 2004);
- Linear Moran process (Traulsen et al. 2006);
- Local update rule (Traulsen et al. 2006);
- Fermi process (Szabo & Hauert 2002; Altrock & Traulsen 2009).
Fixation Probability

\[ \Phi_N(x) := c_N^{-1} \sum_{s \in [1/N, x]_N} \prod_{r \in [1/N, s-1/N]_N} \frac{\Delta^-_N(r)}{\Delta^+_N(r)}, \]  

(2)

with \( c_N \) chosen such that \( \Phi_N(1) = 1. \)

**Notation:** For \( a, b \in N^{-1}N_0 = \mathbb{N} \cup \{0\} \)

\[ [a, b]_N := \left\{ a, a + \frac{1}{N}, a + \frac{2}{N}, \ldots, b \right\}. \]
"Winwood Reade is good upon the subject," said Holmes. "He remarks that, while the individual man is an insoluble puzzle, in the aggregate he becomes a mathematical certainty.

Sherlock Holmes

—The Sign of the Four
General Formulation

Core Mathematical Results

Examples
Family of regular SBD processes
Identification of regimes
• Selection-driven;
• Balanced;
• Quasi-neutral;

Continuous Formulations

Continuous Generalisations
Fixation with an Interior ESS

Asymptotics for the selection driven regime
General approximation theorem for the continuous formulation

Risk Dominance
ESS

Near $1/2$ law for linear fitness difference.

Fixation patterns without weak selection.

Generalised $1/3$ law
Critical Frequency

Fixation patterns with two interior equilibria
I fear that I bore you with these details, but I have to let you see my little difficulties, if you are to understand the situation.

Sherlock Holmes

—A Scandal in Bohemia
Definition (Generalised log relative fitness)

We define the *generalised log difference of fitness* as

\[ \Theta_N(x) := \log \left( \frac{\Delta^-_N(x)}{\Delta^+_N(x)} \right). \]

Assume that

\[ \lim_{N \to \infty} \|\Theta_N\|_{\infty} = \xi. \]

- **weak selection** if \( \xi = 0 \);
- **moderate selection** if \( \xi \ll 1 \).
A family, indexed by population size, of frequency dependent SBD processes with log difference fitness $\Theta_N$ has a formal infinite population limit, if

1. If $\|\Theta_N\|_\infty$ is uniformly bounded;

2. There exists $\theta \in C^0([0, 1])$, with $\|\theta\|_\infty = 1$ such that

$$\lim_{N \to \infty} \epsilon_N = 0, \quad \epsilon_N = \left\| \frac{\Theta_N}{\|\Theta_N\|_\infty} - \theta \right\|_\infty;$$

3. $\theta$ has finitely many zeros.
Fitness potential

Define the fitness potential as

$$\mathcal{F}(s) = -\int_0^s \theta(r) \, dr.$$  

Interior potential  global maximum of $\mathcal{F}$ over $[0,1]$ is only attained at the interior; 
Boundary potential  otherwise.
The continuous approximation

Let

\[ \kappa_N^{-1} = N \| \Theta_N \|_\infty. \]

\[ \phi_N(x) = d_N^{-1} \int_0^x \exp \left( \kappa_N^{-1} \mathcal{F}(s) \right) \, ds, \]

\[ d_N = \int_0^1 \exp \left( \kappa_N^{-1} \mathcal{F}(s) \right) \, ds. \]
Regular SBD processes

A family, indexed by population size, of frequency dependent SBD processes with log difference fitness $\Theta_N$ is regular, if

1. $\Theta_N$ is $C^1$ and it has a formal infinite population limit $\theta \in C^2([0, 1])$.

2. If

$$\lim_{N \to \infty} \kappa_N^{-1} = \infty,$$

then we also require that

$$\lim_{N \to \infty} \kappa_N^{-1} \epsilon_N = 0.$$
The approximation theorem

Assume a regular family of SBD processes, such that the formal infinite population limit, $\theta$, does not vanish at the boundaries.

Then, for sufficient large $N$, the fixation probability can be approximated as follows:

$$
\Phi_N(x) = \phi_N(x) + O \left( \kappa_N^{-1} \epsilon_N, \kappa_N \xi_N^2, \kappa_N^{1-b} \xi_N^2 \right),
$$

where $\xi_N = \|\Theta_N\|_\infty$, $b = 1$ if $F$ is a boundary potential, and $b = 0$ otherwise, and

Furthermore, the left hand side in Equation (3) is exponentially small if, and only if, both terms in the right hand side of (3) are exponentially small.
The approximation theorem
Continued

- If $\kappa_N^{-1}$ has a limit when $N \to \infty$, then the approximation can be made uniform:

$$\Phi_N(x) = \phi_N(x) \left[ 1 + O \left( \kappa_N^{-1} \epsilon_N, \kappa_N \xi_N^2, N^{-1} \right) \right], \quad x \in \left[ \frac{1}{N}, 1 \right].$$

- Finally, let $x \in \left[ \frac{1}{N}, 1 \right]$ be the smallest frequency such that $\phi_N(x) \geq \frac{1}{N}$. Then, provided that either $\mathcal{F}$ is an interior potential, or that $\mathcal{F}$ is a boundary potential, and $\kappa_N^{-1} = O(N^\alpha)$, with $\alpha < \frac{1}{2}$, we have the uniform approximation

$$\Phi_N(x) = \phi_N(x) \left[ 1 + O \left( \kappa_N^{-1} \epsilon_N, \kappa_N \xi_N^2, \kappa_N^{1-b} \xi_N \right) \right], \quad x \in [x, 1].$$
Different regimes
(Chalub & Souza 2009; Chalub & Souza 2014)

<table>
<thead>
<tr>
<th>$\kappa_\infty^{-1}$</th>
<th>Infinite population</th>
<th>Large finite population</th>
<th>Infinite population dynamics</th>
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<tbody>
<tr>
<td>$\infty$</td>
<td>Deterministic</td>
<td>Selection-driven</td>
<td>for certain scalings with weak-selection: replicator dynamics</td>
</tr>
<tr>
<td>$O(1)$</td>
<td>Balanced</td>
<td>Balanced</td>
<td>Replicator-diffusion</td>
</tr>
<tr>
<td>0</td>
<td>Neutral</td>
<td>Quasi-neutral</td>
<td>Pure diffusion</td>
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In the sequel: assume $N$ is large and write

$$\kappa := \kappa_N \quad \phi_\kappa := \phi_N.$$
Selection driven fixation asymptotics

Dominance

Dominance by $\mathbb{A}$ here, $\theta(x) > 0$ and

$$
\phi_\kappa(x) = 1 - \exp(-\theta(0)x / \kappa).
$$

(4)

Dominance by $\mathbb{B}$ here, $\theta(x) < 0$ and

$$
\phi_\kappa(x) = \exp(\theta(1)(1 - x) / \kappa).
$$

(5)

From now on: assume $\theta$ has an unique interior zero.
Fixation asymptotics

Coexistence

Let $|\mathcal{F}(1)| \sim \kappa$ and

$$C = \exp(\mathcal{F}(1)/\kappa) \quad \text{and} \quad \gamma = \frac{|\theta(1)|}{\theta(0)}$$

Then the asymptotic approximation is given by

$$\phi_\kappa(x) = \frac{C}{C + \gamma} \left( \exp(\theta(1)(1 - x)/\kappa) \right) + \frac{\gamma}{C + \gamma} \left( 1 - \exp(-\theta(0)x/\kappa) \right),$$

with $\theta(0) > 0 > \theta(1)$.

(6)
Fixation asymptotics

Coordination

\[ \phi_\kappa(x) = \frac{\mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(x - x^*)\right) - \mathcal{N}\left(-\sqrt{\frac{\theta'(x^*)}{\kappa}}x^*\right)}{\mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(1 - x^*)\right) - \mathcal{N}\left(-\sqrt{\frac{\theta'(x^*)}{\kappa}}x^*\right)}, \]  

(7)

where \( \mathcal{N}(x) \) is the normal cumulative distribution.

For \( x^* \gg \sqrt{\kappa} \), and \( 1 - x^* \gg \sqrt{\kappa} \) then (7) can be simplified to

\[ \phi_\kappa(x) = \mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(x - x^*)\right). \]  

(8)

Thus, for \( x^* \) far from the endpoints we have the interesting result that

\[ \phi_\kappa(x^*) = \frac{1}{2}. \]
The near $\frac{1}{2}$ law

Assume the we are in the coexistence case, selection-driven regime, with weak selection, and that we have linear limiting fitness differences, i.e.,

$$\theta(x) = \bar{\gamma}(x^* - x), \quad x^* \in (0, 1), \quad \bar{\gamma} := \frac{1}{\max\{x^*, 1 - x^*\}}.$$ 

Then there are values $0 < x_1 < y_1 < \frac{1}{2} < y_2 < x_2 < 1$, with $x_1$ near zero, $x_2$ near one, $y_1, y_2$ near $\frac{1}{2}$ such that:

- $x^* < y_1$ Then, for all $x < x_2$, the fixation probability of $B$ is near unity.
- $x^* = \frac{1}{2}$ Then, for all $x \in (x_1, x_2)$, we have near $\frac{1}{2}$ probability of fixation for both types.
- $x^* > y_2$ Then, for all $x > x_1$, we have that the fixation probability of $A$ is near unity.
When there is no weak-selection

Consider the payoff matrix of Hawk and Dove game:

<table>
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<th>A</th>
<th>B</th>
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<tbody>
<tr>
<td>A</td>
<td>$1+c$</td>
<td>$50.075+c$</td>
</tr>
<tr>
<td>B</td>
<td>$1.025+c$</td>
<td>$50+c$</td>
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for $c > -1$. Then, for any value of $c$, the equilibrium is $x^* = \frac{3}{4}$. 
ESS in finite populations
(Nowak et al. 2004; Nowak 2006)

Definition (ESS$_N$)
Consider a SBD process with a population size $N$, with $\Phi_N$ denoting the probability of fixation of $\mathbb{A}$. We say that strategy $\mathbb{B}$ is an ESS$_N$ if the following is satisfied:

1. $\Theta_N(1/N) < 0$;
2. $\Phi_N(1/N) < 1/N$;
A continuous ESS$_N$ definition
—for large populations

Theorem
Consider a family of regular SBD processes with generalised log relative fitness $\Theta_N$ and let $\phi_{\kappa}$ be the continuous approximation to the fixation probability. Then, for sufficiently large $N$, $B$ is an ESS$_N$ if, and only if, we have that

1. $\phi''_{\kappa}(0) > 0$;
2. $\phi_{\kappa}(1/N) < 1/N$. 
Consider a regular family of SBD processes in the quasi-neutral regime. Then we have that

$$
\phi_\kappa(x) = x + \kappa^{-1} \left[ x \int_0^1 (1 - s) \theta(s) \, ds - \int_0^x (x - s) \theta(s) \, ds \right] + \kappa^{-2} x \mathcal{R}(x; \kappa) + O \left( \kappa^{-3} \right),
$$

with $\mathcal{R} = O(1)$ and smooth. Moreover, its derivatives are also order one.
Assume that we are in the quasi-neutral regime with 
\( \kappa^{-1} = o\left(\frac{1}{N}\right) \), and that we are in the coordination case. Then strategy B is an ESS\(_N\) if, and only if, 

1. \( \theta(0) \ll -N^{-1} \)

2. 
\[
\int_0^1 (1 - s)\theta(s) \, ds < \frac{\theta(0)}{2N} + o\left(\frac{1}{N}\right).
\]

For large \( N \), and if looking only for sufficient conditions: 
\( \theta(0) < 0 \), and 
\[
\int_0^1 (1 - s)\theta(s) \, ds < 0.
\]
Consider the case that $\theta$ is linear, i.e., $\theta(x) = \gamma(x - x^*)$, and assume that we are in the quasi-neutral regime. Then

$$\int_0^1 (1 - s)\theta(s) \, ds = \frac{\gamma}{2} \left[ \frac{1}{3} - x^* \right].$$

Hence, strategy $B$ is an ESS if, and only if, $x^* > 1/3 + O\left(1/N, \kappa^{-1}\right)$. 

Consider a $d$-player game, in a large population. Then

$$\theta(x) = \gamma \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} (a_k - b_k),$$

We have that $\mathbb{B}$ is an $\text{ESS}_N$, if $a_0 - b_0 < 0$, and if

$$\sum_{k=0}^{d-1} (d-k)a_k > \sum_{k=0}^{d-1} (d-k)b_k$$
Beyond the quasi-neutral limit

2 player games parametrised by $\sigma^2 = \kappa / \gamma$ and $x^*$
Far beyond the quasi-neutral limit
Discussion

- Defined a class of evolutionary processes that can be well approximated by a continuous representation.
- Proof uses the idea of inverse numerical analysis—as in Chalub & Souza (2009).
- New asymptotics for coexistence and slightly improved asymptotics for coordination.
- Asymptotics in the quasi-neutral regime.
Discussion continued

- New insights in the fixation in the presence of a mixed ESS.
- Continuous definition of an ESS$_{N}$.
- Generalised one third-law: contains previous cases in the literature.
- For linear $\theta$, critical frequency extends the 1/3 law outside the quasi-neutral regime.
Risk dominance: under weak selection $A$ is risk dominant if, and only if,

$$\mathcal{F}(1) < 0.$$ 

Fixation patterns with two interior equilibria. In particular, may have

- Evolution blocking if ordering is unstable-stable
- Evolution tunnelling if ordering is stable-unstable.

Risk dominance: under weak selection $A$ is risk dominant if, and only if,

$$F(1) < 0.$$ 

Fixation patterns with two interior equilibria. In particular, may have

- Evolution blocking if ordering is unstable-stable
- Evolution tunnelling if ordering is stable-unstable.


Thanks for listening!