Fixation in Finite Populations

Discrete and Continuous Views

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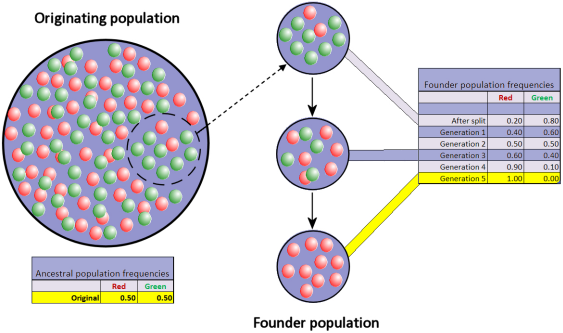
Why Fixation?

Fixation

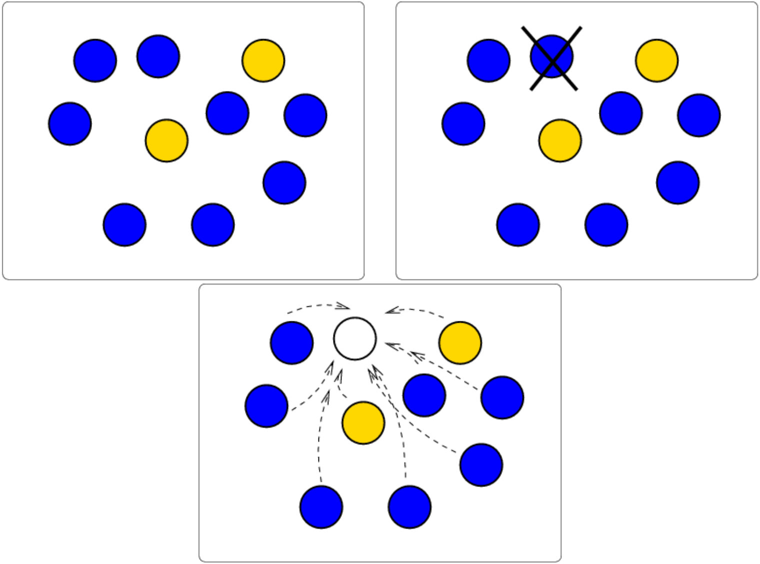


Ancestral population frequencies		
	Red	Green
Original	0.50	0.50

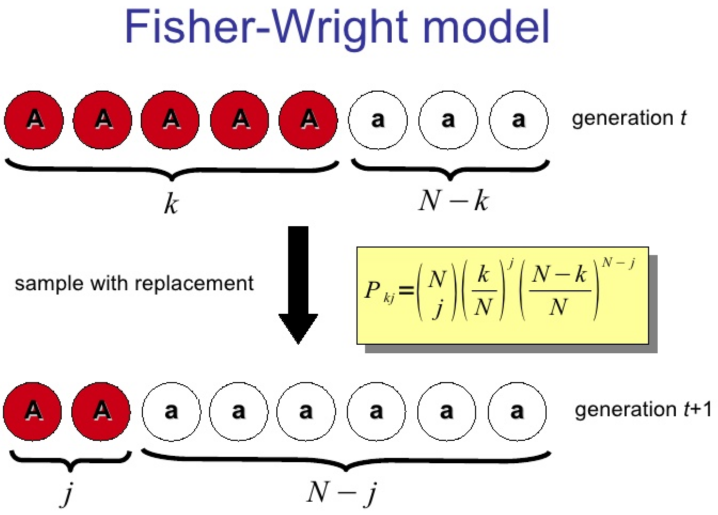
Founder population frequencies		
	Red	Green
After split	0.20	0.80
Generation 1	0.40	0.60
Generation 2	0.50	0.50
Generation 3	0.60	0.40
Generation 4	0.90	0.10
Generation 5	1.00	0.00

Discrete Views

Moran Process



Wright Fisher Model



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

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

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- $p_j \in [0, 1]$ describes the probability of a type $\mathbb{A}$ individual being selected for reproduction, with the chain in state j. We will term $\mathbf{p}$ the vector of *type selection probabilities* (TSP)

Framework

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- $p_j \in [0, 1]$ describes the probability of a type $\mathbb{A}$ 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: $\varphi^{(\mathbb{A},\mathbb{B})} : \{0, 1, \ldots, N\} \to \mathbb{R}_+$
-

$$\mathbf{p}_i = \frac{i\varphi^{(\mathbb{A})}(i)}{i\varphi^{(\mathbb{A})}(i) + (N-i)\varphi^{(\mathbb{B})}(i)}.$$

The Kimura class

Definition

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

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

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

.

Fixation

Proposition

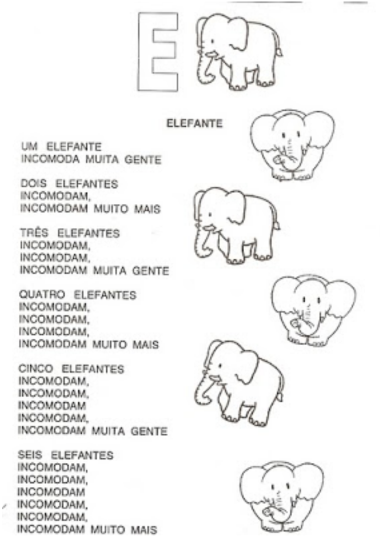
Let $\mathbf{M} \in \mathcal{K}$*. Then, there exists a unique vector* $\widetilde{\mathbf{F}} \in \mathbb{R}^{N-1}$*, with* $0 < \widetilde{F}_i < 1$*, such that* $\mathbf{F}^{=} \begin{pmatrix} 0 & \widetilde{\mathbf{F}} & 1 \end{pmatrix}$*, with* $\mathbf{M}\mathbf{F}^{\dagger} = \mathbf{F}^{\dagger}$ *and*

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

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?



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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 **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 ordering

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, $\mathbf{A} \in \mathrm{StO}_N$) 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, $\mathbf{A} \in \mathrm{St}^2\mathrm{O}_N$) if for all $i > j$, we have that $\mathbf{A}_{i,\cdot} \succ\!\succ \mathbf{A}_{j,\cdot}$.

SO/ESO => Weakly-Regular

Definition

We say that a $N \times N$ matrix **A** is *eventually strictly stochastically ordered* (*stochastically ordered*) if there exists $k_0 \in \mathcal{N}$ such A^k is strictly stochastically ordered (stochastically ordered, respect.) for $k \geq k_0$.

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Proposition

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

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- ESO is sufficient to guarantee the process is weakly-regular. Is it necessary?

Not really

Let

$$\mathbf{M} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix} .$$

Then

- $\mathbf{F} = \begin{pmatrix} 0 & \frac{1}{2} & \frac{1}{2} & 1 \end{pmatrix}$; hence $\mathbf{M}$ is weakly-regular.
- We check directly that

$$\mathbf{M}^{\kappa} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ \alpha_\kappa & \delta_\kappa & \gamma_\kappa & \alpha_\kappa \\ \beta_\kappa & 2\gamma_\kappa & \delta_\kappa & \beta_\kappa \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

- 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 κ that $\alpha_\kappa, \beta_\kappa < {}^1\!/_2$. On the other hand,

$$\alpha_{\kappa+1} - \beta_{\kappa+1} = \frac{1 - 2\beta_\kappa}{8} > 0 ,$$

Regularity in Kimura matrices

- 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 $\varphi^{(\mathbb{A})}(x) = 15 - 24x + 10x^2$ and $\varphi^{(\mathbb{B})}(x) = 1 + 14x^2$, 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 $\mathbb{A}$ ($\mathbb{B}$, respectively) player against k other players;
- Then p_i given by reproductive fitness is not increasing;
- Note that the relative fitness $\Psi^{(\mathbb{A})}/\Psi^{(\mathbb{B})} = \varphi^{(\mathbb{A})}/\varphi^{(\mathbb{B})}$ is decreasing and is associated to coexistence games (i.e., $\Psi^{(\mathbb{A})}/\Psi^{(\mathbb{B})} > 1$ for x near zero, and $\Psi^{(\mathbb{A})}/\Psi^{(\mathbb{B})} < 1$ for x near one).

Universality of Moran processes

Tell me your fixation and I will tell who you are

Theorem

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

$$p_i = \frac{i(F_i - F_{i-1})}{i(F_i - F_{i-1}) + (N-i)(F_{i+1} - F_i)} \in (0,1), \quad i = 1, \dots, N-1.$$

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.

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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 $\mathbf{A}$ is totally indecomposable if there are no permutation matrices $\mathbf{P}$ and $\mathbf{Q}$ such that $\mathbf{PAQ} = \begin{pmatrix} \mathbf{B} & \mathbf{0} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}$, with $\mathbf{B}$, $\mathbf{D}$ non-trivial square matrices and $\mathbf{0}$ the null matrix. We say that a Kimura transition matrix $\mathbf{M}$ is a *Gillespie* matrix if $\widetilde{\mathbf{M}}$ 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.

Fixation

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* $\mathbf{p} \in (\epsilon_N, 1 - \epsilon_N), \quad \epsilon_N = 1/(N+1)$*.*
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

$$\mathbf{p}_1 = \left(0, \tfrac{1}{7}, \tfrac{6}{7}, 1\right) \quad \text{and} \quad \mathbf{p}_2 = \left(0, \tfrac{6}{7}, \tfrac{1}{7}, 1\right)$$

with corresponding Moran matrices:

$$\mathbf{M}_1 = \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ \frac{2}{7} & \frac{13}{21} & \frac{2}{21} & 0 \\ 0 & \frac{2}{21} & \frac{13}{21} & \frac{2}{7} \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{\text{Summer only}} \mathbf{M}_2 = \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{21} & \frac{8}{21} & \frac{4}{7} & 0 \\ 0 & \frac{4}{7} & \frac{8}{21} & \frac{1}{21} \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{\text{Winter only}}.$$

Let

$$\mathbf{M}_3 = \mathbf{M}_1\mathbf{M}_2 = \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ \frac{23}{147} & \frac{128}{441} & \frac{172}{441} & \frac{8}{49} \\ \frac{8}{49} & \frac{172}{441} & \frac{128}{441} & \frac{23}{147} \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{\text{Summer and Winter}},$$

and let $\mathbf{F}_i$, $i = 1, 2, 3$, then we have:

$$\mathbf{F}_1 = \left(0, \tfrac{1}{5}, \tfrac{4}{5}, 1\right)^{\dagger}$$

$$\mathbf{F}_2 = \left(0, \tfrac{12}{25}, \tfrac{13}{25}, 1\right)^{\dagger}$$

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 Λ_1)
  - Processes in periodic and random environments.

FACC Chalub & MO Souza, On the stochastic evolution of finite populations. J. Math. Biol Online, 2017.

Continuous Views

Suitable Birth-Death Processes (SBD)

Population of fixed size N with two types $\mathbb{A}$ and $\mathbb{B}$.
Transition probabilities given by:

$$T_N^{\pm}(x) = x(1-x)\Delta^{\pm}\left(\Psi_N^{\mathbb{A}}, \Psi_N^{\mathbb{B}}\right) .$$

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

- $\Delta^{\pm} : \mathbb{R}^{+} \times \mathbb{R}^{+} \to \mathbb{R}^{+}$ models natural selection.
- Fitnesses given by $\Psi_N^{\mathbb{A}}, \Psi_N^{\mathbb{B}} : [0,1] \to \mathbb{R}^{+}$.
- Write $\Delta_N^{\pm}(x) = \Delta^{\pm}\left(\Psi_N^{\mathbb{A}}(x), \Psi_N^{\mathbb{B}}(x)\right)$.
- 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

$$\Phi_N(x) := c_N^{-1} \sum_{s \in [1/N, x]_N} \prod_{r \in [1/N, s-1/N]_N} \frac{\Delta_N^-(r)}{\Delta_N^+(r)}, \tag{2}$$

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

Notation: For $a, b \in N^{-1}\mathbb{N}_0 = \mathbb{N} \cup \{0\}$

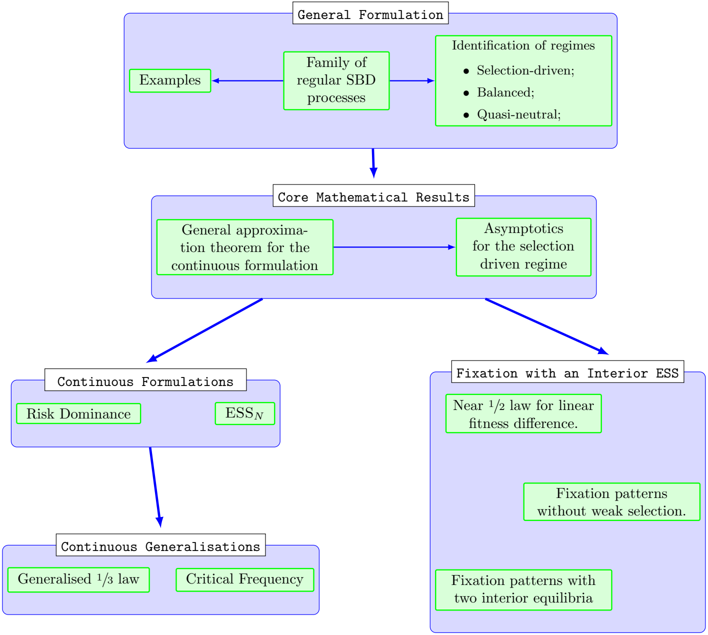
$$[a, b]_N := \left\{ a, a + \frac{1}{N}, a + \frac{2}{N}, \ldots, b \right\} .$$

Interested in large N

"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
Examples
Family of regular SBD processes
Identification of regimes
• Selection-driven;
• Balanced;
• Quasi-neutral;
Core Mathematical Results
General approximation theorem for the continuous formulation
Asymptotics for the selection driven regime
Continuous Formulations
Risk Dominance
ESS_N
Fixation with an Interior ESS
Near 1/2 law for linear fitness difference.
Fixation patterns without weak selection.
Fixation patterns with two interior equilibria
Continuous Generalisations
Generalised 1/3 law
Critical Frequency

Prelims

> 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

$$\Theta_N(x) := \log\left(\frac{\Delta_N^-(x)}{\Delta_N^+(x)}\right).$$

Asume that

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

weak selection If $\xi = 0$;

moderate selection If $\xi \ll 1$.

Formal infinite population limit

A family, indexed by population size, of frequency dependent SBD processes with log difference fitness Θ_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. θ has finitely many zeros.

Fitness potential

Define the fitness potential as

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

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

Boundary potential otherwise.

The continuous approximation

Let

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

$$\phi_N(x) = d_N^{-1} \int_0^x \exp\left(\kappa_N^{-1}\mathcal{F}(s)\right) \mathrm{d}s,$$

$$d_N = \int_0^1 \exp\left(\kappa_N^{-1}\mathcal{F}(s)\right) \mathrm{d}s \ .$$

Regular SBD processes

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

1. Θ_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, θ, does not vanish at the boundaries.
- Then, for sufficient large N, the fixation probability can be approximated as follows:

$$\Phi_N(x) = \phi_N(x) + \mathrm{O}\left(\kappa_N^{-1}\epsilon_N, \kappa_N\xi_N^2, \kappa_N^{1-b}\xi_N^2\right), \qquad (3)$$

  where $\xi_N = \|\Theta_N\|_\infty$, $b = 1$ if $\mathcal{F}$ 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 κ_N^{-1} has a limit when $N \to \infty$, then the approximation can be made uniform:

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

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

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

Different regimes

(Chalub & Souza 2009; Chalub & Souza 2014)

κ_∞^{-1}	Infinite population	Large finite population	Infinite population dynamics
∞	Deterministic	Selection-driven	for certain scalings with weak-selection: replicator dynamics
$\mathrm{O}(1)$	Balanced	Balanced	Replicator-diffusion
0	Neutral	Quasi-neutral	Pure diffusion

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

$$\phi_\kappa(x) = 1 - \exp(-\theta(0)x/\kappa). \tag{4}$$

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

$$\phi_\kappa(x) = \exp(\theta(1)(1 - x)/\kappa). \tag{5}$$

From now on: assume θ has an unique interior zero.

Fixation asymptotics

Coexistence

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

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

Then the asymptotic approximation is given by

$$\phi_\kappa(x) = \frac{C}{C+\gamma} \underbrace{\exp(\theta(1)(1-x)/\kappa)}_{\text{dominance by } \mathbb{B}} + \frac{\gamma}{C+\gamma} \underbrace{(1-\exp(-\theta(0)x/\kappa))}_{\text{dominance by } \mathbb{A}}, \tag{6}$$

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

Fixation asymptotics

Coordination

$$\phi_\kappa(x) = \frac{\mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(x - x^*)\right) - \mathcal{N}\left(-\sqrt{\frac{\theta'(x^*)}{\kappa}}x^*\right)}{\mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(1 - x^*)\right) - \mathcal{N}\left(-\sqrt{\frac{\theta'(x^*)}{\kappa}}x^*\right)}, \qquad (7)$$

where $\mathcal{N}(x)$ is the normal cumulative distribution.
For $x^* \gg \sqrt{\kappa}$, and $1 - x^* \gg \sqrt{k}$ then (7) can be simplified to

$$\phi_\kappa(x) = \mathcal{N}\left(\sqrt{\frac{\theta'(x^*)}{\kappa}}(x - x^*)\right). \qquad (8)$$

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

$$\phi_\kappa(x^*) = \frac{1}{2}.$$

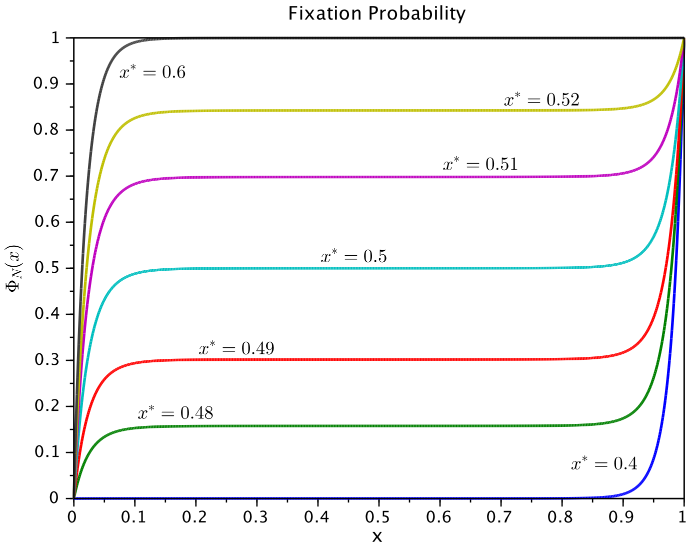
The near $\frac{1}{2}$ law

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

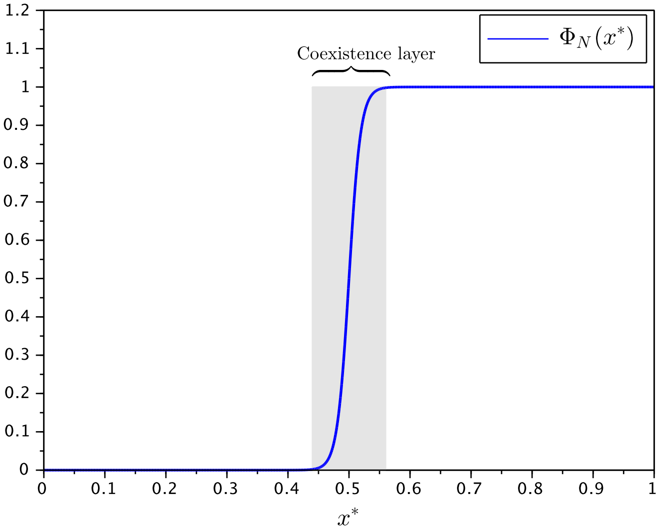
$$\theta(x) = \bar{\gamma}(x^* - x), \quad x^* \in (0,1), \quad \bar{\gamma} := \frac{1}{\max\{x^*, 1 - x^*\}}.$$

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

- $x^* < y_1$ Then, for all $x < x_2$, the fixation probability of $\mathbb{B}$ is near unity.
- $x^* = 1/2$ Then, for all $x \in (x_1, x_2)$, we have near ½ probability of fixation for both types.
- $x^* > y_2$ Then, for all $x > x_1$, we have that the fixation probability of $\mathbb{A}$ is near unity.



Fixation Probability
$x^* = 0.6$
$x^* = 0.52$
$x^* = 0.51$
$x^* = 0.5$
$x^* = 0.49$
$x^* = 0.48$
$x^* = 0.4$
$\Phi_N(x)$
x
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1



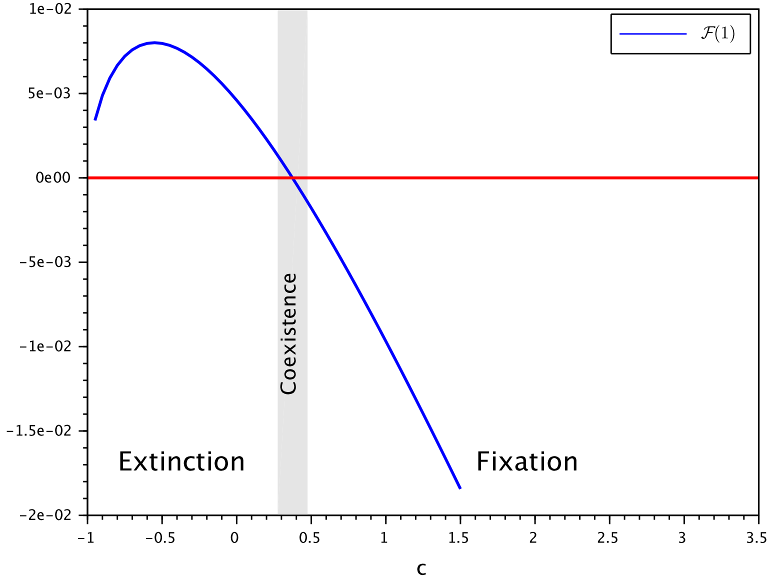
Coexistence layer
$\Phi_N(x^*)$
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
x^*

When there is no weak-selection

Consider the payoff matrix of Hawk and Dove game:

	$\mathbb{A}$	$\mathbb{B}$
$\mathbb{A}$	1+c	50.075+c
$\mathbb{B}$	1.025+c	50+c

for $c > -1$. Then, for any vale of c, the equilibrium is $x^* = 3/4$.



1e−02
5e−03
0e00
−5e−03
−1e−02
−1.5e−02
−2e−02
−1
−0.5
0
0.5
1
1.5
2
2.5
3
3.5
c
$\mathcal{F}(1)$
Coexistence
Extinction
Fixation

ESS in finite populations

(Nowak et al. 2004; Nowak 2006)

Definition (ESS_N)

Consider a SBD process with a population size N, with Φ_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 $\mathrm{ESS_N}$ definition

—for large populations

Theorem

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

1. $\phi_\kappa''(0) > 0$;
2. $\phi_\kappa(1/N) < 1/N$.

Quasi-neutral fixation asymptotics

Consider a regular family of SBD processes in the quasi-neutral regime. Then we have that

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

with $\mathcal{R} = \mathrm{O}(1)$ and smooth. Moreover, its derivatives are also order one.

ESS_N in the quasi-neutral regime

Assume that we are in the quasi-neutral regime with $\kappa^{-1} = \mathrm{o}\left(1/N\right)$, and that we are in the coordination case. Then strategy $\mathbb{B}$ is an ESS_N if, and only if,

1. $\theta(0) \ll -N^{-1}$
2. $$\int_0^1 (1-s)\theta(s)\,\mathrm{d}s < \frac{\theta(0)}{2N} + \mathrm{o}\left(\frac{1}{N}\right).$$

For large N, and if looking only for sufficient conditions: $\theta(0) < 0$, and

$$\int_0^1 (1-s)\theta(s)\,\mathrm{d}s < 0.$$

One-third law

Consider the case that θ is linear, i.e., $\theta(x) = \gamma(x - x^*)$, and assume that we are in the quasi-neutral regime. Then

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

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

Generalised one-third law for d-player games

(Kurokawa & Ihara 2009; Gokhale & Traulsen 2010; Lessard 2011)

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

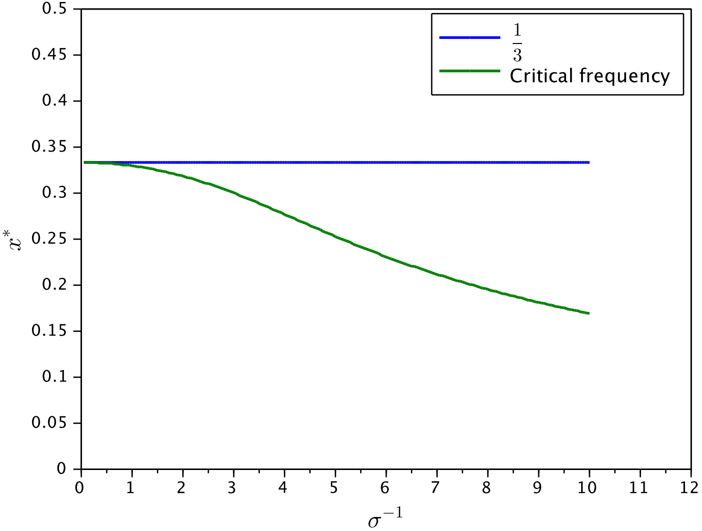
$$\theta(x) = \gamma \sum_{k=0}^{d-1} \binom{d-1}{k} x^k (1-x)^{d-1-k} (a_k - b_k),$$

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

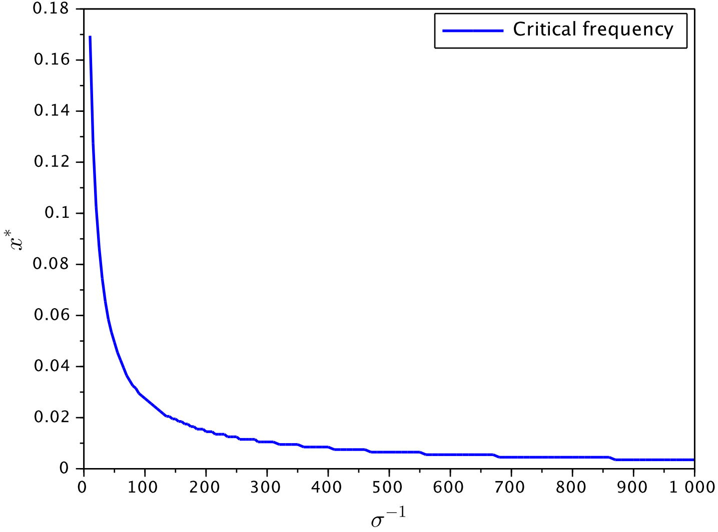
$$\sum_{k=0}^{d-1} (d-k) a_k > \sum_{k=0}^{d-1} (d-k) b_k$$

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 θ, critical frequency extends the 1/3 law outside the quasi-neutral regime.

Discussion

other stuff

- Risk dominance: under weak selection $\mathbb{A}$ 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.

FACC Chalub & MO Souza, Fixation in large populations: a continuous view of a discrete problem. J. Math. Biol 72(1-2):283–330, 2016.

Discussion

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Thanks for listening!