Continuous approximations of discrete processes

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If population dynamics is based on individuals, why do people use differential equations?

Objectives

...and side effects

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3. We use the differential equation to obtain informations of the discrete process

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The Wright-Fisher process

General definitions

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The transition probability from a state y to a new state x is given by

$$\Theta_N(y \to x) = \frac{N!}{(xN)!((1-x)N)!} \frac{\left(y\Psi^{\mathbb{B})}(y)\right)^{xN} \left((1-y)\Psi^{(\mathbb{B})}(y)\right)^{(1-x)N}}{\left(y\Psi^{(\mathbb{A})}(y) + (1-y)\Psi^{(\mathbb{B})}(y)\right)^{N}} \ .$$

Discrete and continuous modeling

The probability $P_{(N,\Delta t)}(\mathbf{x}, t)$ to find the population at the state $\mathbf{x}$ at time t evolves according to the Master equation:

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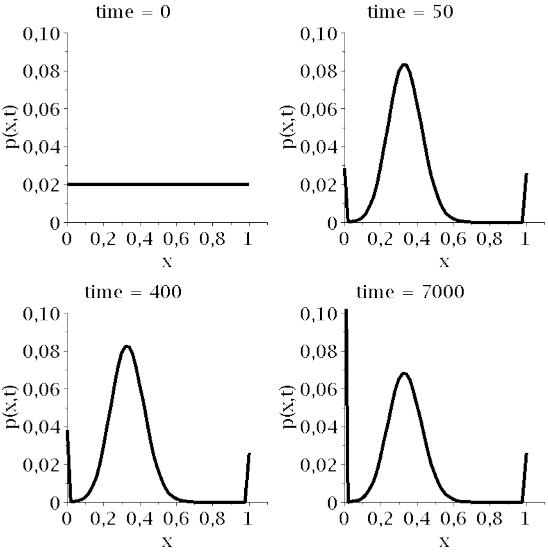
In a different approach, the evolution of a given type in population can be modelled using the replicator differential equation:

$$\dot{x} = x \left(\psi^{(\mathbb{A})}(x) - \bar{\psi}(x) \right) = x(1 - x)(\psi^{(\mathbb{A})} - \psi^{(\mathbb{B})}) \ .$$



Simulation for $N = 50$,
$\psi^{(\mathbb{A})}(x) = 2$,
$\psi^{(\mathbb{B})}(x) = 1 + 3x$.

The replicator dynamics is given by $\dot{x} = x(1-x)(1-3x)$. The probability distribution initially concentrates in three points: $x = 0$, $x = 1$ and $x = x^* = \frac{1}{3}$. We accelerate the evolution and nothing seems to happen. After a long time, a diffusion process dominates...

The Wright-Fisher process

Transition matrix for two types

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The evolution equation can be written

$$\mathbf{P}(t+\Delta t) = \mathbf{M}\mathbf{P}(t)$$

where $\mathbf{M}$ is a stochastic matrix and

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This implies that $\mathbf{P}(\kappa\Delta t) = \mathbf{M}^{\kappa}\mathcal{P}(0)$.

Theorem

$$\lim_{\kappa\to\infty} \mathbf{M}^{\kappa} = \begin{pmatrix} 1 & 1-F_1 & \cdots & 1-F_N \\ 0 & 0 & \cdots & 0 \\ & & \vdots & \\ 0 & F_1 & \cdots & F_N \end{pmatrix} .$$

where the F_n *satisfy* $F_n = \sum_{m=0}^{N} \Theta_N \left(\frac{n}{N} \to \frac{m}{N}\right) F_m$, *with* $F_0 = 0$ *and* $F_N = 1$.
In particular, any stationary state will be concentrated at the endpoints.
If $\mathbf{1}$ *denotes the vector* $(1, 1, \ldots, 1)^{\dagger}$, $\mathbf{F} = (F_0, F_1, \ldots, F_N)^{\dagger}$ *and if* $\langle \cdot, \cdot, \rangle$ *denotes the usual inner product, then we have that* $\langle \mathbf{P}(t), \mathbf{1} \rangle = \langle \mathbf{P}(0), \mathbf{1} \rangle$ *and* $\langle \mathbf{P(t)}, \mathbf{F} \rangle = \langle \mathbf{P(0)}, \mathbf{F} \rangle$.

Two time scales

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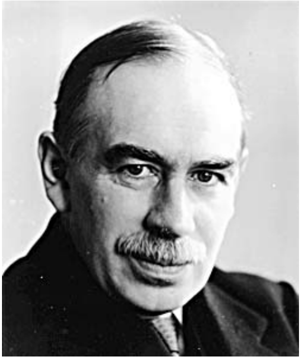

However, “in the long run, we are all dead” (J. M. Keynes).

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Continuous models

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1. The weak selection principle:

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   More precisely, we assume that $\Psi^{(i)}(x) = 1 + (\Delta t)^{\nu} \psi^{(i)}(x)$.

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3. The limit function $p = \lim_{N\to\infty,\Delta t\to 0} \frac{P_{(N,\Delta t)}}{1/N}$ is such that

$$p\left(x \pm \frac{1}{N}, t\right) = p(x,t) \pm \frac{1}{N}\partial_x p(x,t) + \frac{1}{2N^2}\partial_x^2 p(x,t) + \mathcal{O}(N^{-3}) \ ,$$

$$p\,(x, t+\Delta t) = p(x,t) + (\Delta t)\,\partial_t p(x,t) + \mathcal{O}\left((\Delta t)^2\right) \ .$$

Using all these assumptions, we find the asymptotic expansion:

$$\partial_t p = -\frac{1}{(\Delta t)^{1-\nu}} \partial_x \left(x(1-x) \left(\psi^{(\mathbb{A})}(x) - \psi^{(\mathbb{B})}(x) \right) p \right) + \frac{1}{2N\Delta t} \partial_x^2 \left(x(1-x) p \right) \ .$$

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Continuous models

Formal asymptotic: Wright-Fisher process for two types

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or the *replicator-diffusion equation* (generalized Kimura equation)

$$\partial_t p = \frac{\kappa}{2}\partial_x^2\left(x(1-x)p\right)-\partial_x\left(x(1-x)\left(\psi^{(\mathbb{A})}(x)-\psi^{(\mathbb{B})}(x)\right)p\right)\ .$$

The invariants become the following conservation laws:

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 p(x,t)\,\mathrm{d}x = 0, \qquad \frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 \pi(x)p(x,t)\,\mathrm{d}x = 0,$$

where π satisfies

$$\frac{\kappa}{2}\pi'' + \left(\psi^{(\mathbb{A})}(x) - \psi^{(\mathbb{B})}(x)\right)\pi' = 0, \quad \pi(0) = 0, \quad \pi(1) = 1 \ .$$

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$$\pi(x) = \frac{\int_0^x \exp\left[-\frac{2}{\kappa}\int_0^{x'}\left(\psi^{(\mathbb{A})}(x'') - \psi^{(\mathbb{B})}(x'')\right)\mathrm{d}x''\right]\mathrm{d}x'}{\int_0^1 \exp\left[-\frac{2}{\kappa}\int_0^{x'}\left(\psi^{(\mathbb{A})}(x'') - \psi^{(\mathbb{B})}(x'')\right)\mathrm{d}x''\right]\mathrm{d}x'} \ .$$

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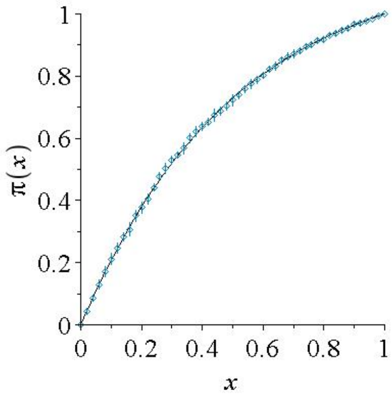
If the initial condition is $p^{\mathrm{I}} = \delta_{x_0}$, then the fixation probability is $\pi(x_0)$.

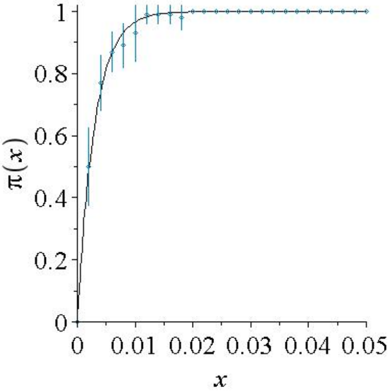


Fixation probability for $N = 50$ and pay-off matrix $\begin{pmatrix} 51 & 51 \\ 50 & 50 \end{pmatrix}$. The line indicates the function $\pi(x) = \frac{1-e^{-\mathbf{1.986x}}}{1-e^{-\mathbf{1.986}}}$.

In the quasi-neutral case, $\pi(x) \approx \frac{1-e^{-\frac{2\psi(0)x}{\kappa}}}{1-e^{-\frac{2\psi(0)}{\kappa}}}$.

Fixation probability

The dominance case ($\kappa \ll 1$ and $\psi > 0$)

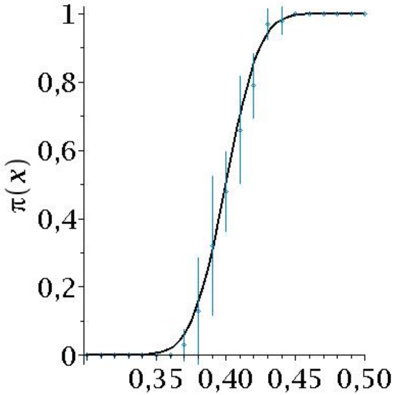


Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 11 & 12 \\ 10 & 9 \end{pmatrix}$. The line indicates the function $\pi(x) = 1 - \mathrm{e}^{-339.6x}$.

In the dominance case, $\pi(x) \approx 1 - \mathrm{e}^{-\frac{2(\psi(0))x}{\kappa}}$.

Fixation probability

The coordination case ($\kappa \ll 1$ and $\psi(0) < 0 < \psi(1)$).

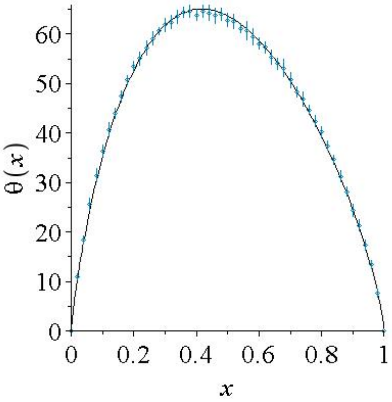


Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 4 & 1 \\ 1 & 3 \end{pmatrix}$. The line indicates the function $\pi(x) = \mathcal{N}(73.8(x - 0.40)^2)$.

In the coordination case, $\pi(x) \approx \mathcal{N}\left(\sqrt{\frac{\psi'(x*)}{\kappa}}(x - x*)\right)$, where $\mathcal{N}(z) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{z} \mathrm{e}^{-s^2/2} \mathrm{d}s$ is the cumulative Normal distribution.

Time to fixation

The quasi-neutral case ($\kappa \gg 1$)

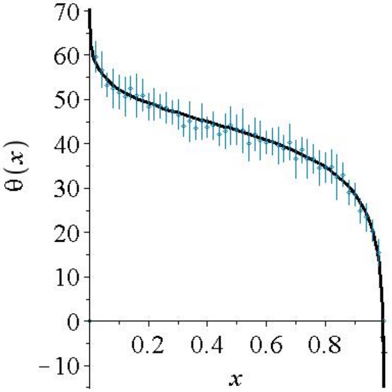


Time to fixations for $N = 50$ and pay-off matrix $\begin{pmatrix} 51 & 51 \\ 50 & 50 \end{pmatrix}$. The line indicates the function $\theta(x)$ with $\frac{2}{\kappa} \approx 91.9$ and $\frac{2\psi(0)}{\kappa^2} \approx 85.4$.

$$\theta(x) \approx -\frac{2}{\kappa}\left[x \log x + (1-x)\log(1-x)\right] + \frac{2\psi(0)}{\kappa^2}\left[x^2 \log x - (1-x)^2 \log(1-x)\right]$$

Time to fixation

The dominance case ($\kappa \ll 1$ and $\psi > 0$)

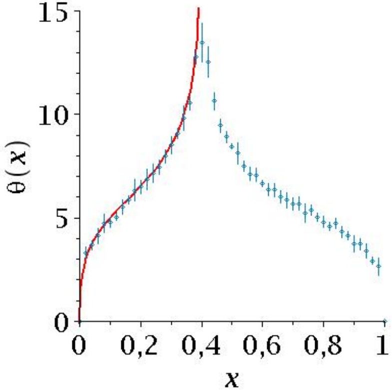


Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 11 & 12 \\ 10 & 9 \end{pmatrix}$. The line indicates the function below with with $\beta^{-1} = 3.53$, $\gamma = 2.51$ and $\alpha^{-1} \log \kappa = -49.7$.

$$\theta(x) = -\frac{1}{\beta} \log \frac{x(x + \gamma(1-x))^{\gamma - 1}}{(1-x)^{\gamma}} - \frac{1}{\alpha} \log \kappa,$$

Time to fixation

The coordination case ($\kappa \ll 1$ and $\psi(0) < 0$ and $\psi(1) > 0$)



Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 4 & 1 \\ 1 & 3 \end{pmatrix}$. The red line is given by the equation below with $(\gamma, A, B) = (0.620, 2.57, 4.28)$

$$\theta(x) \approx A \log \frac{x^{1-\gamma}(1-x)^{\gamma}}{|x - x^*|} + B$$

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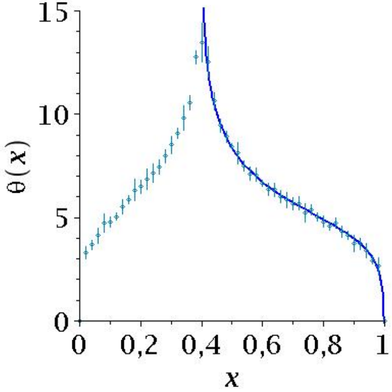

Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 4 & 1 \\ 1 & 3 \end{pmatrix}$. The red line is given by the equation below with $(\gamma, A, B) = (0.298, 2.62, 4.16)$

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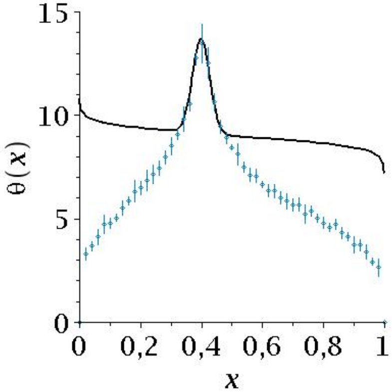

Fixation probability for $N = 500$ and pay-off matrix $\begin{pmatrix} 4 & 1 \\ 1 & 3 \end{pmatrix}$. The black line is given by the equation below with $(A, B, C, D, E) = (4.57, 618, -0.245, 9.03, -0.0573)$.

$$\theta(x) \approx A e^{-B(x-x^*)^2} + C \log \frac{x}{1-x} + D + E\pi(x)$$

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