The Kimura Equation

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FACULDADE DE CIÊNCIAS E TECNOLOGIA UNIVERSIDADE NOVA DE LISBOA
NOVA id FCT Associação para a Inovação e Desenvolvimento da FCT
FCT Fundação para a Ciência e a Tecnologia
cma fct.unl centro de matemática e aplicações
POPH PROGRAMA OPERACIONAL POTENCIAL HUMANO

IF INVESTIGADOR FCT

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History

In 1954, following previous works by Sewall Wright, the Japanese geneticist Motoo Kimura (1924–1994) wrote

If $\phi(x,t)dx$ is the probability that the gene frequency lies between x and $x+dx$ in the t-th generation, it can be proved that $\phi(x,t)$ satisfies the partial differential equation,

$$\frac{\partial \phi(x,t)}{\partial t} = \frac{\partial^2}{\partial x^2}\left[\frac{V_{\delta x}}{2}\phi(x,t)\right] - \frac{\partial}{\partial x}\left[M_{\delta x}\,\phi(x,t)\right], \qquad (1)$$

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In 1962, this problem was reformulated into a *backward equation*:

$$\frac{\partial u(p,t)}{\partial t} = \frac{V}{2}\frac{\partial^2 u(p,t)}{\partial p^2} + M\frac{\partial u(p,t)}{\partial p}$$

$$\begin{cases} M_{\delta x} = sx(1-x) \\ V_{\delta x} = x(1-x)/(2N) \end{cases}$$

$$u(0,t)=0,\ \ u(1,t)=1.$$

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Selection force → sx

Effective population → $2N$

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"A mutant gene which appeared in a finite population will eventually either be lost from the population or fixed (established) in it"

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$$\partial_t\varphi = \kappa\partial_x^2\left(x(1-x)\varphi\right) - \partial_x\left(x(1-x)\theta(x)\varphi\right)$$

$$\Big\Downarrow \, t \to \infty$$

$$\varphi \to c_0\delta_0 + c_1\delta_1$$

Outline

Stochastic Processes

Finite populations, discrete generations

Kimura Equation

Infinite populations; continuous time

Replicator Equation

Infinite populations; continuous, but short, time

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↓ $\Delta t \to 0$, $N \to \infty$, $N\Delta t = o(1)$, weak selection

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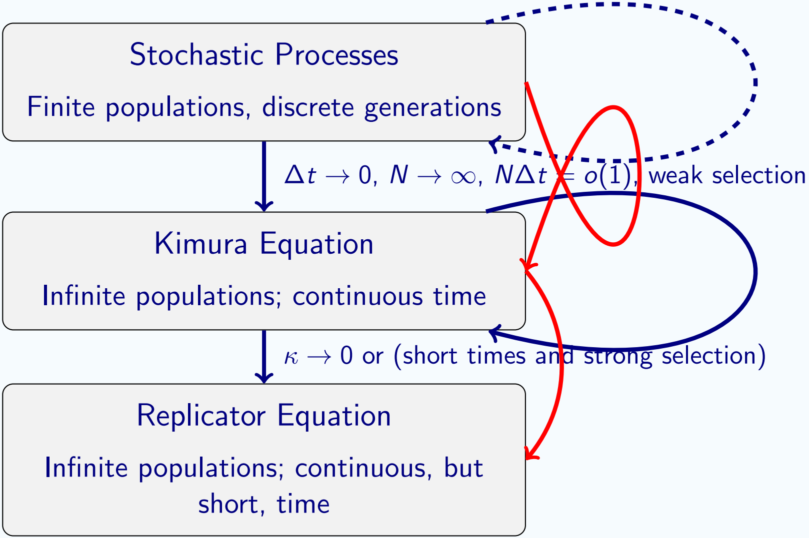
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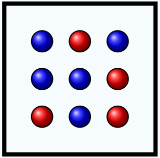
Stochastic processes

Consider a finite population of haploid individuals which reproduce asexually evolving stochastically in time.

$t - 1$



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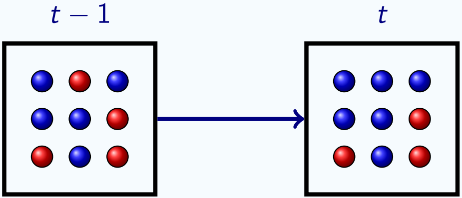

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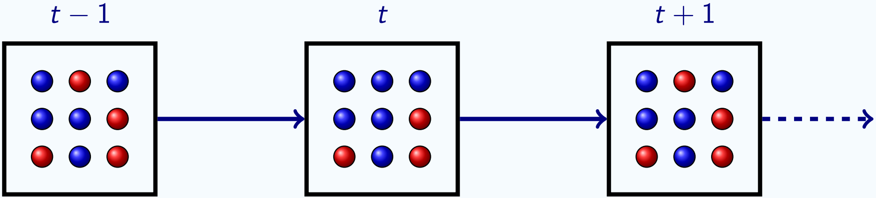

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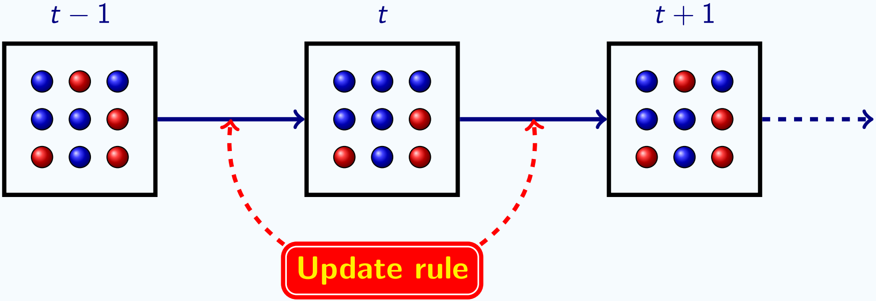
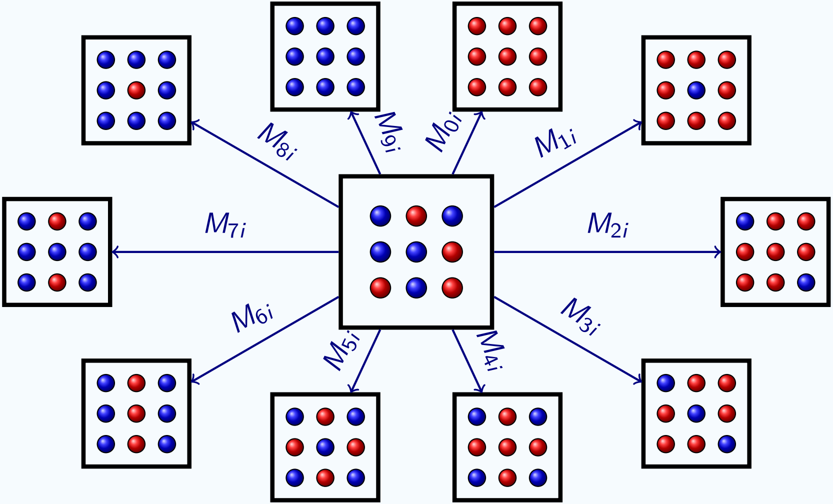


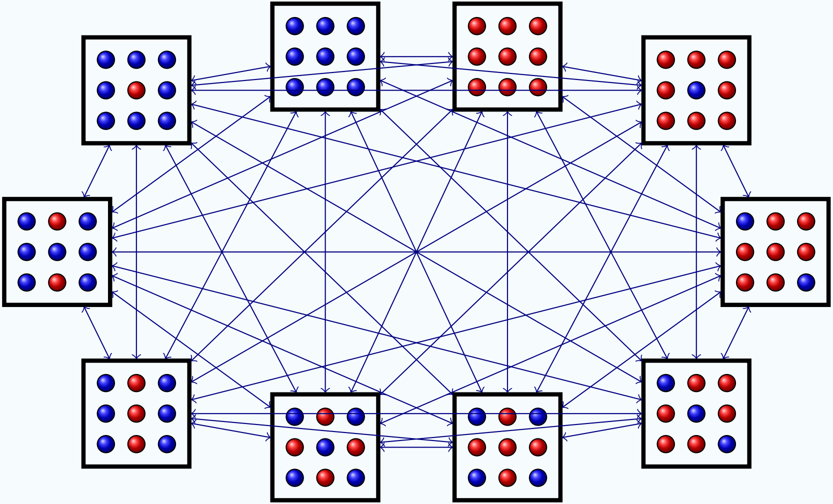
Stochastic Processes

The *update rule* attributes probabilities for all possible outcomes...



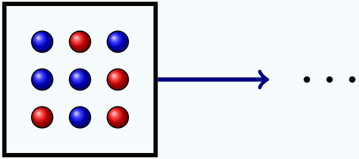
Stochastic Processes

The *update rule* attributes probabilities for all possible outcomes...
...from all initial conditions



Stochastic Processes

If there are no mutations in the population, then, after a sufficiently long time, the population will be homogeneous. We say that one type fixate, while the all the others were extinct.



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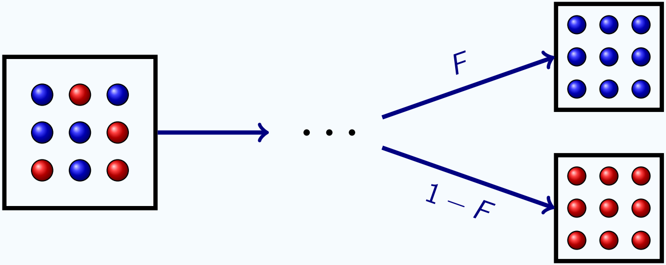

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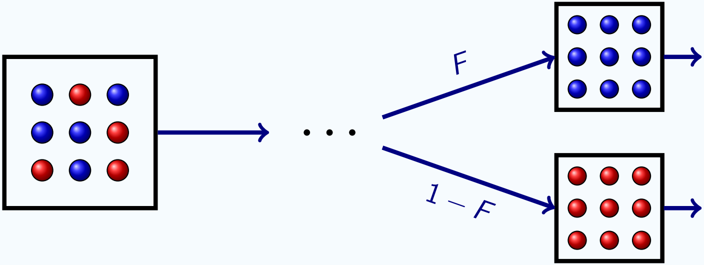

A mutant gene which appeared in a finite population will eventually either be lost from the population or fixed (established) in it. *Motoo Kimura.*

Consider a population of fixed size N composed by two types of individuals: $\mathbb{A}$ and $\mathbb{B}$ and define p_i, the probability that a type-$\mathbb{A}$ individual is selected for reproduction in a population with i type-$\mathbb{A}$ individuals and $N - i$ type-$\mathbb{B}$ individuals.

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The Moran Process

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

Moran, P. A. P. The Statistical Process of Evolutionary Theory. Clarendon Press, Oxford. (1962).

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The Wright-Fisher Process

$$M_{ij} = \binom{N}{i} p_j^i (1-p_j)^{N-i} \ .$$

Fisher, R. A. *On the dominance ratio*. Proc. Royal Soc. Edinburgh, **42**:321–341. (1922).
Wright, S. *Evolution in Mendelian populations*. Genetics, **16**(2):0097–0159. (1931).

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$$p_j = \frac{j}{N}\left[1 + (\Delta t)^{\nu}\,\frac{N-j}{N}\theta(j)\right] \;,$$

where $\theta : \{0, \ldots, N\} \to \mathbb{R}_+$ is the fitness difference.

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Direct evolution

Let $\Phi(i,t)$ be the probability to find the population at state i at time t. Then,

$$\Phi(i, t+\Delta t) = \sum_i M_{ij}\Phi(j,t)\ .$$

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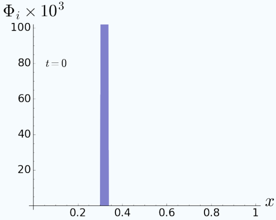
Adjoint evolution

Let $F(i,t)$ be the fixation probability at time t (or latter) if the initial condition is $\Psi(\cdot, 0) = \delta_{\cdot,i}$. Then,

$$F(j, t + \Delta t) = \sum_i F(i,t) M_{ij} \ .$$

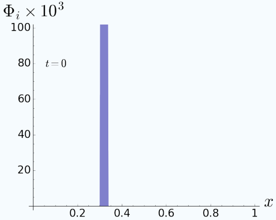
$$\begin{cases} \partial_t f = \mathcal{L}^{\dagger} f \ , \\ f(0,\cdot) = 0 \ , \quad f(1,\cdot) = 1 \ . \end{cases}$$

Dominance



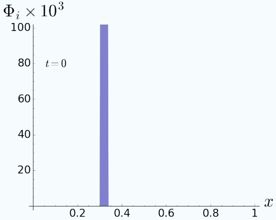
$$p_i = \frac{1.3i}{1.3i+N-i}.$$

Coexistence



$$p_i = \frac{(1.3-{}^{i}/_{135})i}{(1.3-{}^{i}/_{135})+N-i}.$$

Coordination



$$p_i = \frac{(0.7+{}^{i}/_{45})i}{(0.7+{}^{i}/_{45})i+N-i}.$$

Population size: $N = 50$

Initial condition: $\Psi(i,0) = \delta_{16,\cdot}$

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 $\langle \boldsymbol{\Psi}(t), \mathbf{1} \rangle = \langle \boldsymbol{\Psi}(0), \mathbf{1} \rangle$ and $\langle \boldsymbol{\Psi}(t), \mathbf{F} \rangle = \langle \boldsymbol{\Psi}(0), \mathbf{F} \rangle$.

The last theorem states that " A mutant gene which appeared in a finite population will eventually either be lost from the population or fixed (established) in it. " (M. Kimura).

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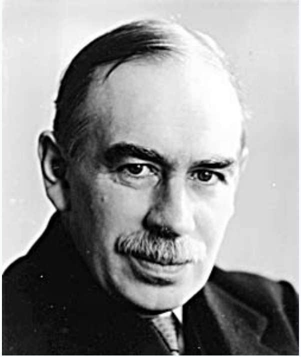

However, "in the long run, we are all dead" (J. M. Keynes).

From WF & Moran to Kimura

We look for a differential equation that approximates the discrete evolution of Ψ when $N \to \infty$ and $\Delta t \to 0$.

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... and imposing a time-step such that $\kappa(\Delta t)^{\mu} = N^{-1} = z$ we conclude

$$\left\langle \mathbf{\Psi}, \frac{\mathcal{T}_{-\Delta t} - 1}{\Delta t}\mathbf{\Phi} \right\rangle = \left\langle \mathbf{\Psi}, \kappa\,(\Delta t)^{\mu+\nu-1}\,x(1-x)\theta(x)\partial_x\mathbf{\Phi} + \kappa^2\,(\Delta t)^{2\mu-1}\,x(1-x)\partial_x^2\mathbf{\Phi} \right\rangle + \mathrm{o}\Big((\Delta t)^{2\mu}, (\Delta t)^{\mu+\nu}\Big) \ .$$

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$$+\,\mathrm{o}\Big((\Delta t)^{2\mu}, (\Delta t)^{\mu+\nu}\Big) \ .$$

In the strong formulation, with $\Delta t \to 0$, and with the right choice of μ and ν, we have the *generalized Kimura equation*:

$$\partial_t\varphi = \frac{\kappa}{2}\partial_x^2\left(x(1-x)\varphi\right) - \partial_x\left(x(1-x)\theta(x)\varphi\right) \ .$$

From WF & Moran to Kimura

The invariants become the following conservation laws:

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

where π satisfies

$$\frac{\kappa}{2}\pi'' + \theta(x)\pi' = 0, \quad \pi(0) = 0, \quad \pi(1) = 1 \ .$$

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This implies:

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

The Kimura Equation

A weak solution is a function $\varphi \in L^\infty([0,\infty);\mathcal{BM}_+([0,1]))$ that satisfies for test functions $\phi \in C_0^\infty([0,\infty)\times[0,1])$

$$-\int_0^\infty \int_0^1 \varphi(t,x)\partial_t\psi(t,x)\mathrm{d}x\mathrm{d}t$$
$$= \int_0^\infty \int_0^1 \varphi(t,x)x(1-x)\left[\partial_x^2\psi + \theta(x)\partial_x\psi\right]\mathrm{d}x\mathrm{d}t + \int_0^1 \varphi(0,x)\psi(0,x)\mathrm{d}x \;.$$

Theorem

There exists a unique solution $\varphi \in L^\infty([0,\infty);\mathcal{BM}_+([0,1]))$ *such that*

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 \varphi(x,t)\mathrm{d}x = \frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 \pi(x)\varphi(x,t)\mathrm{d}x = 0 \;.$$

In fact $\varphi(x,t) \in C^\infty(\mathbb{R}_+;\mathcal{BM}_+([0,1])) \cap C^\infty(\mathbb{R}_+;C^\infty((0,1)))$ *i.e.,*

$$\varphi(t,x) = \Pi_0(t)\delta_0(x) + r(x,t) + \Pi_1(t)\delta_1(x) \;.$$

Furthermore, Π_0 *and* Π_1 *are non-decreasing and* $\lim_{t\to\infty} r(x,t) = 0$ *uniformly.*

The Kimura Equation

Therefore,

$$\lim_{t\to\infty} \varphi(t,\cdot) = \Pi_0\delta_0 + \Pi_1\delta_1$$

with the fixation probability given by

$$\Pi_1 = 1 - \Pi_0 = \int_0^1 \pi(x)\varphi(x,0)\mathrm{d}x \ .$$

Note that if $\varphi(x,0) = \delta_{x_0}(x)$, then $\Pi_1 = \pi(x_0)$.

Theorem

For any T, there is $\varphi \in L^\infty([0,T], \mathcal{BM}_+([0,1]))$ such that

$$\Psi_{(N,\Delta t)} \to \varphi \text{ weakly, when } \Delta t \to 0 \ .$$

From Kimura to the Replicator Equation

Theorem

Assume θ and $\varphi(\cdot,0)$ are smooth. Let r_κ be the regular part of the solution of the Kimura equation with $\kappa > 0$. then, there is $C > 0$ such that for $t < C/\kappa$

$$\|r_\kappa(\cdot,t) - \varphi_0(\cdot,t)\|_\infty \leq C\kappa \ ,$$

where φ_0 is the solution of the Kimura equation with $\kappa = 0$, i.e., the solution of the replicator equation.

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The Replicator Equation

$$x' = x(1-x)\theta(x) \ .$$

Taylor PD, Jonker L. *Evolutionarily stable strategies and game dynamics*. Math Biosci. **40**(1):145–156 (1978).

Hofbauer J, Sigmund K. Evolutionary Games and Population Dynamics. Cambridge, UK: Cambridge Univ Press; 1998.

Strategy dominance and finite populations

Theorem

Let $\theta(x) > 0$ for all x. Then $\pi(x) > x$ for all x. In particular, if $\mathbb{A}$ is the Nash strategy, then the fixation probability of type $\mathbb{A}$ is larger than the neutral probability.

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Public Goods Game

1. N players can contribute 1 euro or 0 euro to a common pool.
2. After all strategic decisions, the total contribution in the pool is multiplied by $r < N$ and divided in equal shares.

Strategy dominance and finite populations

Theorem

Let $\theta(x) > 0$ for all x. Then $\pi(x) > x$ for all x. In particular, if $\mathbb{A}$ is the Nash strategy, then the fixation probability of type $\mathbb{A}$ is larger than the neutral probability.

What happens if the population is small?

Public Goods Game

1. N players can contribute 1 euro or 0 euro to a common pool.
2. After all strategic decisions, the total contribution in the pool is multiplied by $r < N$ and divided in equal shares.

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Evolution will take us to a non rational state! Spite?

Finite populations and fixation probability

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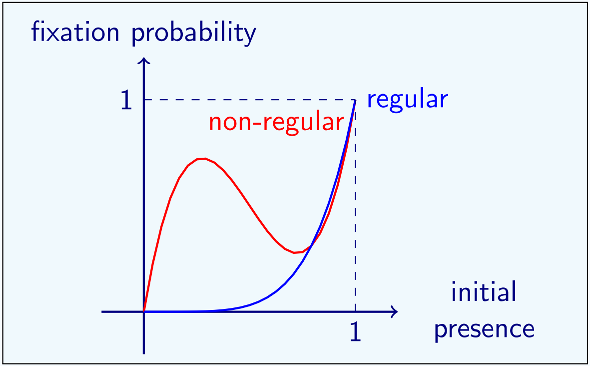

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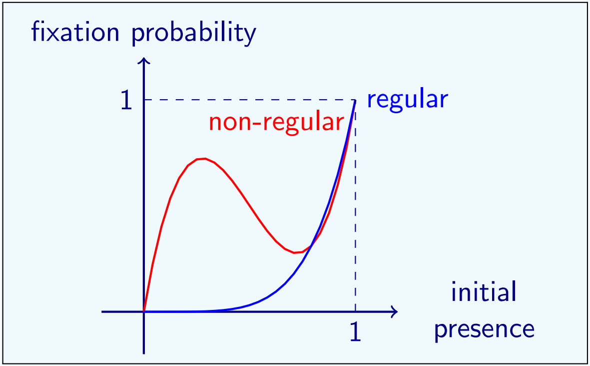
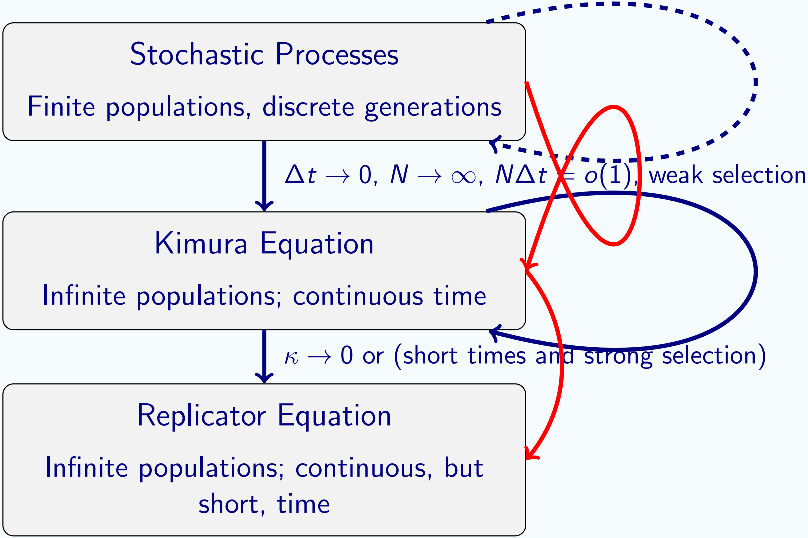


Is this related to discontinuities in the fossil record?

Variational Formulation

Ongoing work &...almost done!



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Stochastic Processes

Finite populations, discrete generations

Kimura Equation

Infinite populations; continuous time

Replicator Equation

Infinite populations; continuous, but short, time

Variational Formulation
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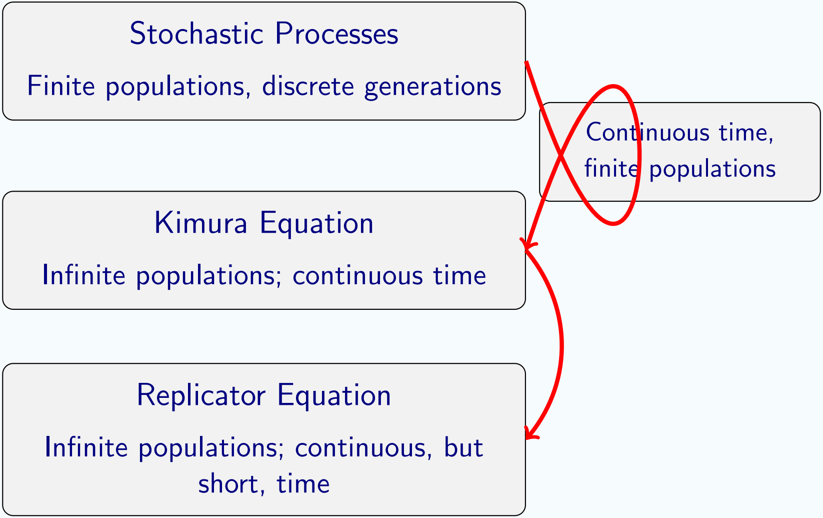

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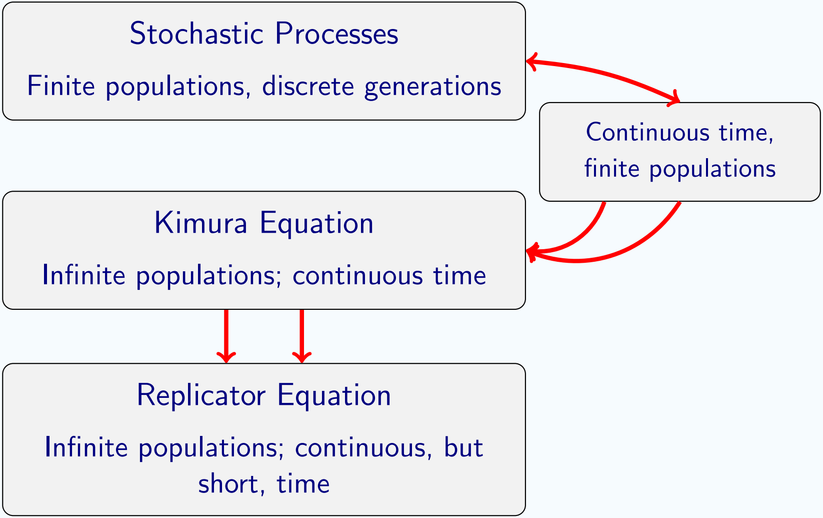

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1. Reformulate all finite population, continuous-in-time models as Gradient Flows, i.e., a define a *Wasserstein* distance $\mathcal{W}_N$ and a potential H:

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Free energy: $\sum_i \pi_i q_i \log q_i$

Shashahani metric: $\int_x^y \frac{\mathrm{d}s}{\sqrt{s(1-s)}}$

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