Regularity and time-inhomogeneity in the Wright-Fisher dynamics.

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IF INVESTIGADOR FCT

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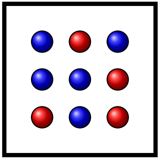
The problem

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



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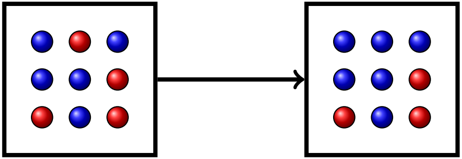

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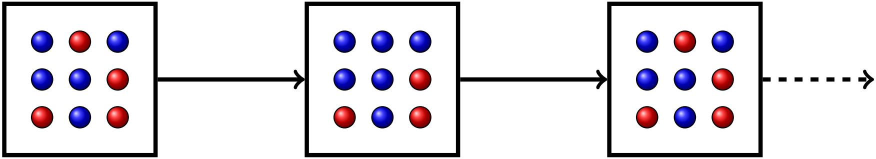

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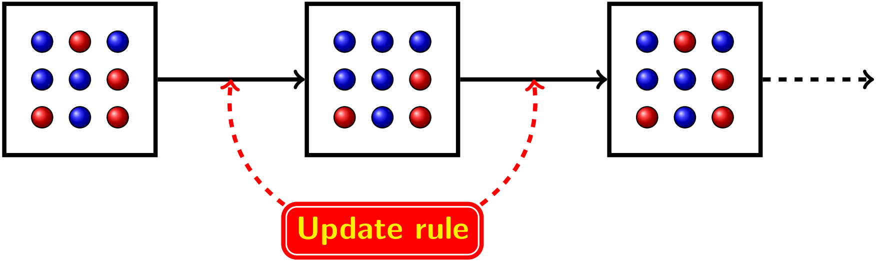

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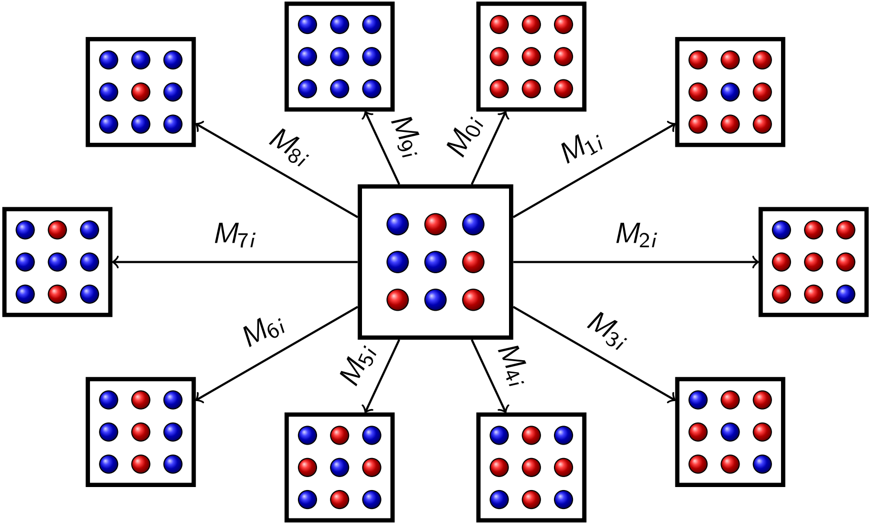

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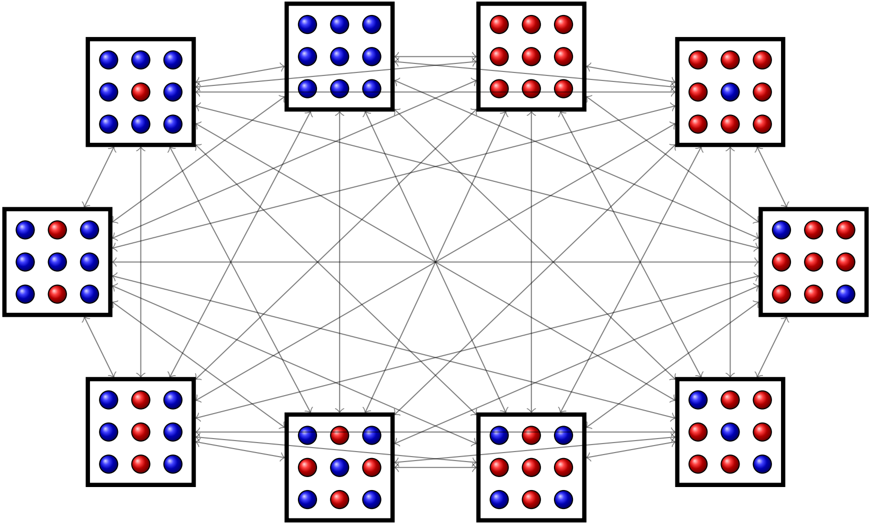

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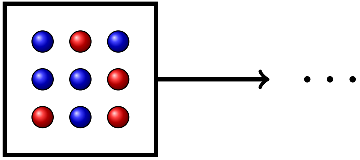
If there are no mutations in the population, then, after a sufficiently long time, the population will be homogeneous. We say that one type fixate, while the all the others were extinct.



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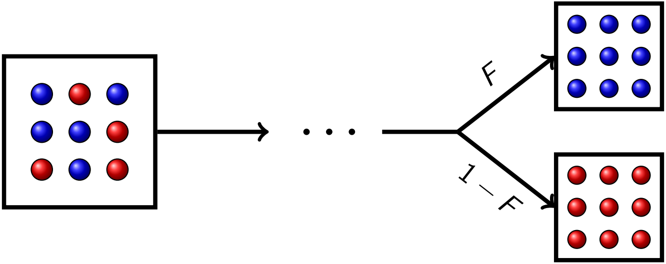

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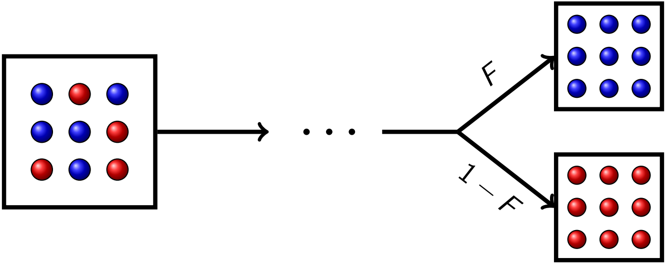

A mutant gene which appeared in a finite population will eventually either be lost from the population or fixed (established) in it. *Motoo Kimura.*

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2. How the fixation probability behaves with respect to the initial condition?
3. What changes if reproduction is time-dependent?

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Let p_i is the probability to select an individual of type $\mathbb{A}$ in a population with i individuals of type $\mathbb{A}$ and $N - i$ individuals of type $\mathbb{B}$.

$$p_0 = 0, \qquad p_i \in (0,1) \text{ for } i = 1\ldots, N-1, \qquad p_N = 1.$$

We call $\mathbf{p} = (p_0, p_1, \ldots, p_N)$ the type selection probability vector.

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The transition matrix of the Wright-Fisher process is given by

$$M_{ij} = \binom{N}{i} p_j^i (1-p_j)^{N-i} \ , i,j = 0, \ldots, N \ , \qquad \mathbf{M} = \begin{pmatrix} 1 & * & 0 \\ \mathbf{0} & \widetilde{\mathbf{M}} & \mathbf{0} \\ 0 & * & 1 \end{pmatrix}$$

with $\widetilde{\mathbf{M}} > \mathbf{0}$ (i.e., $M_{ij} > 0$ for $i,j = 1, \ldots, N-1$).

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We define F_i, the fixation probability of type $\mathbb{A}$ given an initial condition with i individuals of type $\mathbb{A}$.

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We say that a vector is $\mathbf{a} = (a_0, a_1, \dots, a_N)$ is *increasing* if $a_0 < a_1 < a_2 < \cdots < a_N$.

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Remember: $\boxed{M_{ij} = \binom{N}{i} p_j^i (1-p_j)^{N-i} \text{ and } \mathbf{F} = \mathbf{F}\mathbf{M}, \quad F_0 = 0, F_N = 1.}$

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Neutral evolution: $$\left.\begin{array}{l} p_i = \frac{i}{N} \\ i = 0, \ldots, N \end{array}\right\} \Longrightarrow \left\{\begin{array}{l} F_i = \frac{i}{N} \\ i = 0, \ldots, N \end{array}\right.$$

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Main results

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If $\mathbf{M}_1$ *and* $\mathbf{M}_2$ *are two Wright-Fisher matrices such that the associated fixation vectors are increasing, then the fixation vector of the matrices* $\mathbf{M}_1\mathbf{M}_2$ *and* $\mu\mathbf{M}_1 + (1-\mu)\mathbf{M}_2$ *are increasing.*

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$\Longrightarrow$ We define

$$\Upsilon_{\mathbf{F}}(p) = \sum_{i=0}^{N} F_i \binom{N}{i} p^i (1-p)^{N-i} \ .$$

$\Upsilon_{\mathbf{F}}(0) = 0$, $\Upsilon_{\mathbf{F}}(1) = 1$, $\Upsilon_{\mathbf{F}}$ is continuous and increasing. Furthermore $\Upsilon_{\mathbf{F}}(p_i) = F_i$, i.e., $p_i = \Upsilon_{\mathbf{F}}^{-1}(F_i)$ is increasing.

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$\Longleftarrow$ We define $h_n(p) = \sum_{i=n}^{N} \binom{N}{i} p^i (1-p)^{N-i}$. $h_0(p) = 1$ and for $p \in (0,1)$, $n \geq 1$, $h_n'(p) > 0$. Therefore $\sum_{i=n}^{N} M_{ij} = h_n(p_j) > h_n(p_{j-1})$, and the matrix $\mathbf{M}$ is *strictly stochastically ordered*.

A matrix $\mathbf{A}$ is *strictly stochastically ordered* if $\sum_{i=n}^{N} A_{ij} > \sum_{i=n}^{N} A_{i,j-1}$ for all $n \geq 1$. Products and convex combinations of strictly stochastically ordered matrices are strictly stochastically ordered[a].

[a] Keilson, J. and Kester, A. (1977). Stoch. Proc. Appl., 5(3):231–241

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We finish the proof with a lemma:

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If the matrix $\mathbf{M}$ *is strictly stochastically ordered, then* $\mathbf{F}$ *is increasing.*

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Note that the fact that $\mathbf{M}^{\kappa}$ is strictly stochastically ordered for every $\kappa \in \mathbb{N}$ proves only that $\mathbf{F}$ is non-decreasing.

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3. If $p_i = i\Psi^{(\mathbb{A})}(i)/(i\Psi^{(\mathbb{A})}(i) + (N-i)\Psi^{(\mathbb{B})}(i)$, with affine $\Psi^{(\mathbb{A},\mathbb{B})}$ (two player game theory), then **p** and **F** are increasing.

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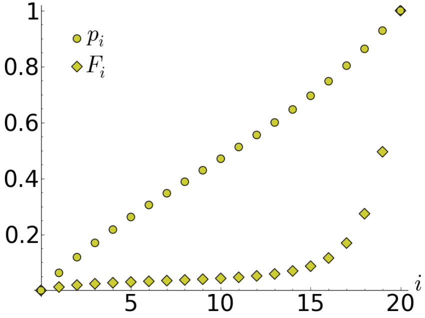

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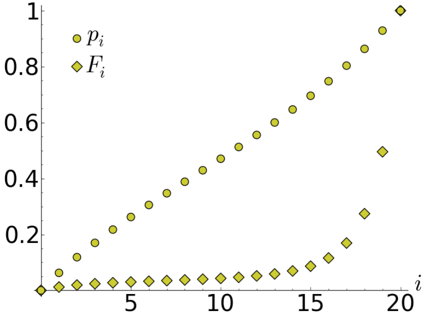

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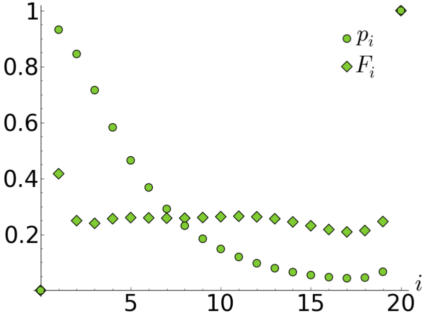

$\Psi^{\mathbb{A})}(x) = 9(0.7 - x) + 3x^3$, $\Psi^{(\mathbb{B})}(x) = 0.01 + 100x^3$.

Observations

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1. Any fixation vector **F** is realized by at least one Wright-Fisher process (i.e., at least one vector **p**). If **F** is increasing, then **p** is unique.
2. All Birth-Death processes are regular. In this case, the matrix **M** is tri-diagonal, and

$$F_k = \frac{\sum_{i=1}^{k} \prod_{j=1}^{i-1} \frac{M_{j-1,j}}{M_{j+1,j}}}{\sum_{i=1}^{N} \prod_{j=1}^{i-1} \frac{M_{j-1,j}}{M_{j+1,j}}} \ .$$

Time inhomogeneous Wright-Fisher process

Let us assume two transition matrices, $\mathbf{M}_1$ and $\mathbf{M}_2$. Consider two static environment: $\cdots \mathbf{M}_1\mathbf{M}_1$ (*summer*) and $\cdots \mathbf{M}_2\mathbf{M}_2$ (*winter*).

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Parrondo's paradox

A combination of losing strategies becomes a winning strategy[1]

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Assume the following Birth-Death (in fact, Moran) processes:

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

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$$\mathbf{F}_1 = \left(0, \tfrac{1}{5}, \tfrac{4}{5}, 1\right)^\dagger, \quad \mathbf{F}_2 = \left(0, \tfrac{12}{25}, \tfrac{13}{25}, 1\right)^\dagger, \quad \mathbf{F}_3 = \left(0, \tfrac{244}{485}, \tfrac{241}{485}, 1\right)^\dagger.$$

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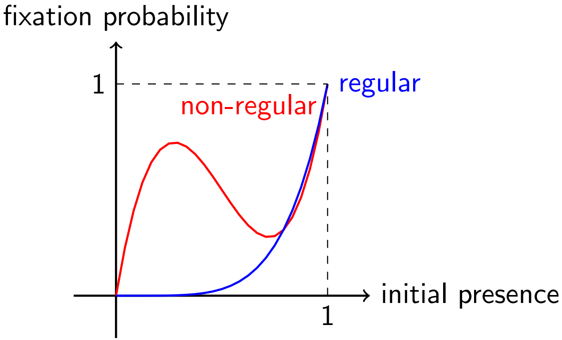
$$\mathbf{F}_1 = \left(0, \frac{1}{5}, \frac{4}{5}, 1\right)^\dagger, \quad \mathbf{F}_2 = \left(0, \frac{12}{25}, \frac{13}{25}, 1\right)^\dagger, \quad \mathbf{F}_3 = \left(0, \frac{244}{485}, \frac{241}{485}, 1\right)^\dagger.$$

Hence $\mathbf{M}_3$ is not regular despite the fact that $\mathbf{M}_1$ and $\mathbf{M}_2$ are regular.

[1] Parrondo, J. M. R. *et al* (2000). Phys. Rev. Lett., 85(24):5226–5229.

Conclusions & open questions

•We show that there are situations, that are by no means exceptional, where an increase in the initial presence of a type can lead to a decrease in the fixation probability of this type in the Wright-Fisher process. Note that this is not possible in any Birth-Death process.



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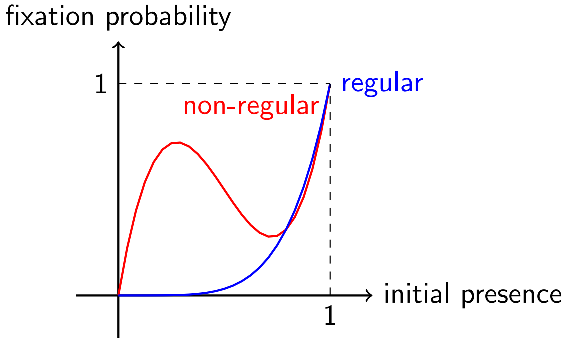
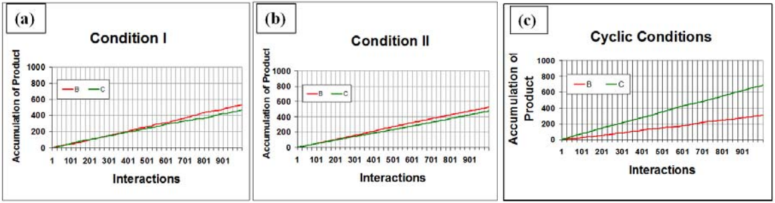


Is this related to discontinuities in the fossil record?

Conclusions & open questions

•Periodic environment may result in fixation patterns completely different from the fixation pattern of any instantaneous environment. This may happen for the Moran process but not for the Wright-Fisher process.

Figure 3. Accumulation of Products Predicted from the Stochastic Model: (a) Condition I alone; (b) Condition II alone; (c) Cycling between Conditions I and II



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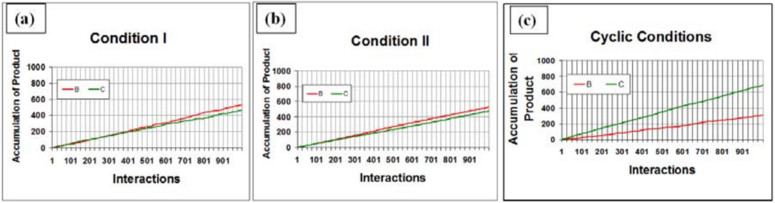

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Is there any example in nature that species $\mathbb{A}$ drives $\mathbb{B}$ to extinction in any static environment, but $\mathbb{B}$ drives $\mathbb{A}$ to extinction if the environment oscillates in time?

The end

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Chalub, Fabio A. C. C.; Souza, Max O. http://arxiv.org/abs/1602.00478.

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