# Limiting diffusion and quasi-stationary behavior of a diploid population

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# Model

- 2 alleles, $A$ and $a$. Genotypes: $AA$, $Aa$ and $aa$.
- 3-types birth-and-death process:

$$Z_t = (Z_t^1, Z_t^2, Z_t^3).$$

- Population size: $N = Z^1 + Z^2 + Z^3$.
- Mendelian reproduction:

$$\lambda_1(Z) = \frac{bp_1}{N}\left[\left(Z^1\right)^2 + Z^1 Z^2 + \frac{(Z^2)^2}{4}\right]$$

- Logistic model:

$$\mu_1(Z) = Z^1(d_1 + c_{11}Z^1 + c_{21}Z^2 + c_{31}Z^3)$$

# Hardy-Weinberg equilibrium

Deviation from Hardy-Weinberg equilibrium:

$$\begin{aligned} Y &= \frac{4Z^1Z^3 - (Z^2)^2}{4N} \\ &= N(p_{AA} - (p_A)^2) \\ &= N(p_{Aa} - 2p_Ap_a) \\ &= N(p_{aa} - (p_a)^2) \end{aligned}$$

$$(Z^1, Z^2, Z^3) \longleftrightarrow (N, X, Y) \longleftrightarrow (N_A, N_a, Y)$$

# Large population scaling

- New scaling of individual size: $Z^K = Z/K \in (\mathbb{Z}_+)^3/K$, $K \longrightarrow +\infty$.
- New scaling of birth and natural death events:

$$
\begin{aligned}
b_i^K &= \gamma K + \beta_i \\
d_i^K &= \gamma K + \delta_i \\
K c_{ij}^K &= \alpha_{ij}
\end{aligned}
$$

# Population size and deviation from Hardy-Weinberg equilibrium

Then:

- For any $t > 0$, $Y_t^K$ converges in $L^2$ toward 0 when $K \to \infty$:

$$\frac{d\mathbb{E}\left(\left(Y_t^K\right)^2\right)}{dt} \leq -2\gamma K \mathbb{E}\left(\left(Y_t^K\right)^2\right) + C.$$

# Convergence of the sequence $(N_A^K, N_a^K)$

- $N_A^K$ (resp. $N_a^K$) is number of alleles $A$ (resp. $a$), divided by $K$.
- The sequence of processes $\left((N_A^K, N_a^K)\right)_{K\geq 0}$ converges in law in $\mathbb{D}([0,T],(\mathbb{R}_+)^2)$ toward a diffusion process $(N_A, N_a)$ such that in the neutral case:

$$dN_A(t) = \left(\beta - \delta - \alpha\,\frac{N_A(t)+N_a(t)}{2}\right) N_A(t)dt$$
$$+ \sqrt{\frac{4\gamma}{N_A(t)+N_a(t)}}N_A(t)dB_t^1 + \sqrt{2\gamma\frac{N_A(t)N_a(t)}{N_A(t)+N_a(t)}}dB_t^2$$
$$dN_a(t) = \left(\beta - \delta - \alpha\,\frac{N_A(t)+N_a(t)}{2}\right) N_a(t)dt$$
$$+ \sqrt{\frac{4\gamma}{N_A(t)+N_a(t)}}N_a(t)dB_t^1 - \sqrt{2\gamma\frac{N_A(t)N_a(t)}{N_A(t)+N_a(t)}}dB_t^2$$

# Limiting diffusion for $(N^K, X^K)$

In the neutral case,

$$dN_t = (\beta - \delta - \alpha N_t) N_t dt + \sqrt{2\gamma N_t} dB_t^1$$
$$dX_t = \sqrt{\frac{\gamma X_t (1 - X_t)}{N_t}} dB_t^2.$$

- For any $x \in \mathbb{R}_+ \times [0,1]$, $\mathbb{P}_x(T_0 < \infty) = 1$ and there exists $\lambda > 0$ such that $sup_x \mathbb{E}_x(e^{\lambda T_0}) < +\infty$ (Cattiaux et al. 2009).
- Quasi-stationary behavior of this diffusion: law of this diffusion process at time $t$ knowing that $N_t > 0$.

# Appropriate change of variable

$$S_t^1 = \sqrt{\frac{\gamma N_t}{2}} \cos\left(\frac{\arccos(2X_t - 1)}{\sqrt{2}}\right)$$
$$S_t^2 = \sqrt{\frac{\gamma N_t}{2}} \sin\left(\frac{\arccos(2X_t - 1)}{\sqrt{2}}\right).$$

$S = (S^1, S^2)$ satisfies

$$dS_t = dW_t - \nabla Q(S_t)dt.$$

# Values taken by $S$ and absorbing sets

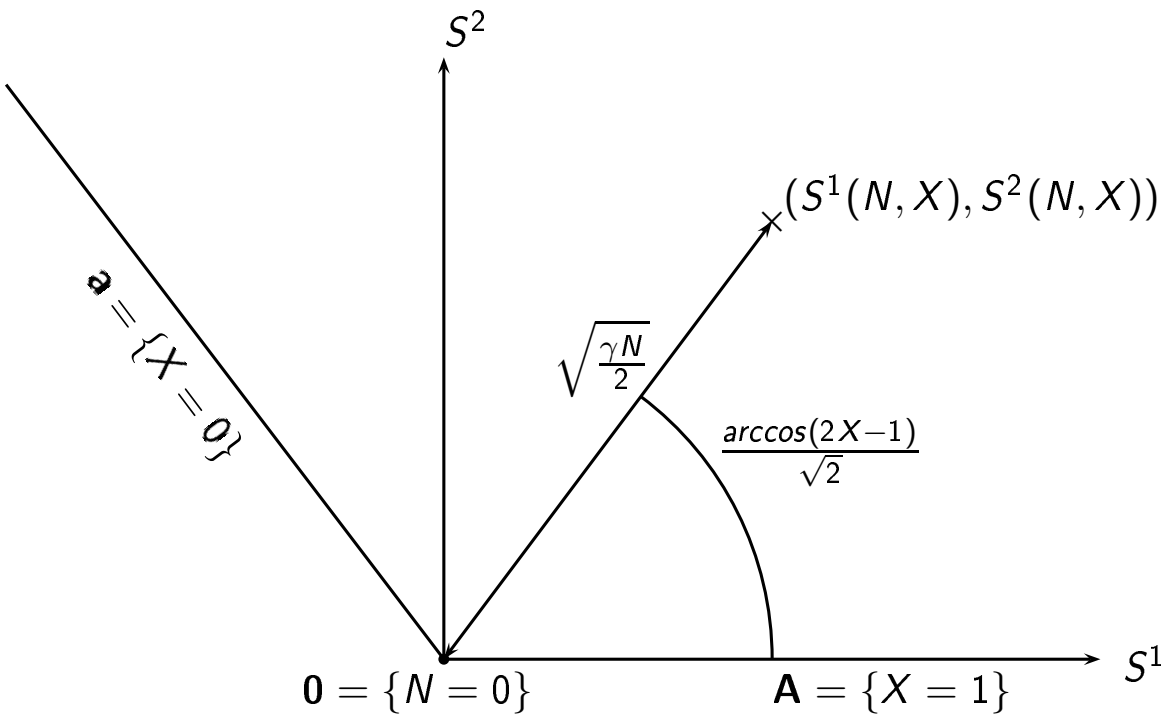


Figure : Values taken by $S_t$ for any $t$.

# Absorption: properties

## Theorem

(*i*) *For any* $x \in D \setminus \mathbf{0}$, $\mathbb{P}_x(T_{\mathbf{A}} \wedge T_{\mathbf{a}} < T_{\mathbf{0}}) = 1$.

- *True for Brownian motion.*
- *Girsanov theorem on* $D_\epsilon \Rightarrow \mathbb{P}_x(T_{\mathbf{A}_\epsilon} \wedge T_{\mathbf{a}_\epsilon} < T_{\mathbf{0}}) = 1$
- *Martingale argument in the neutral case.*

(*ii*) *For any* $x \in D \setminus \partial D$, $\mathbb{P}_x(T_{\mathbf{A}} < T_{\mathbf{0}}) > 0$, *and* $\mathbb{P}_x(T_{\mathbf{a}} < T_{\mathbf{0}}) > 0$.

- *In the neutral case,* $\mathbb{P}_x(T_{\mathbf{a}} < T_{\mathbf{0}}) = 1/2$ *for all* $x \in \mathbf{a}_{\tan(\pi/(2\sqrt{2}))}$.
- *Markov property to conclude in the neutral case.*
- *Girsanov theorem in the general case.*

# Quasi-stationary behavior

From Cattiaux & Méléard (2009) and the previous theorem,

**Theorem**

*There exists a unique distribution $\nu$ on $D \setminus \mathbf{0}$ such that*
$\lim_{t\to\infty} \mathbb{P}_x(S_t \in E | T_0 > t) = \nu(E) \quad \forall x \in D \setminus \partial D$ *and* $E \subset D \setminus \mathbf{0}$.

Therefore $\lim_{t\to\infty} \mathbb{P}(X_t \in B | N_t > 0)$ exists.

# Numerical result 1: neutral case

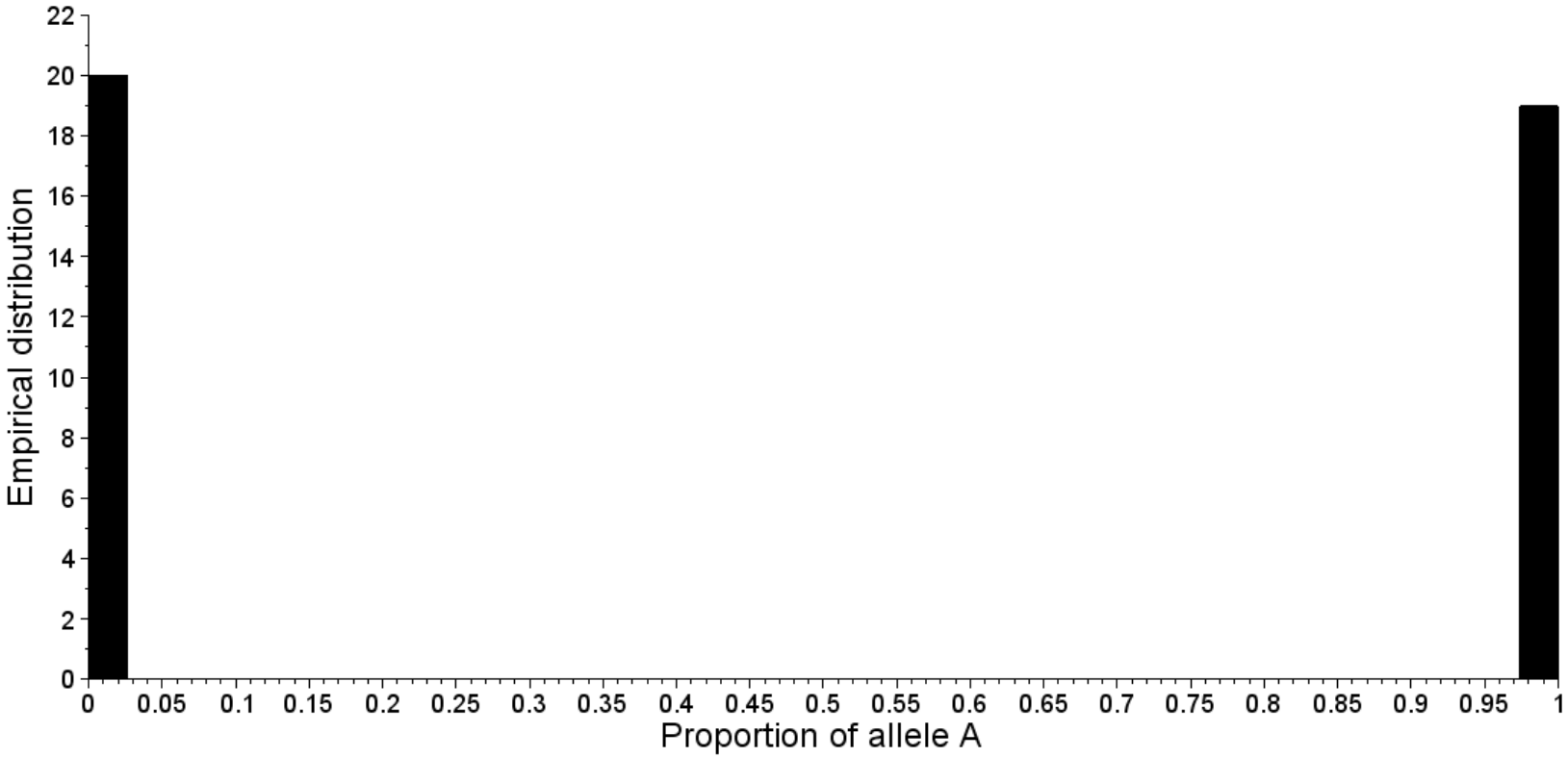


Figure : Distribution of the proportion $X_t$ of alleles $A$ in the neutral case, knowing that $N_t \neq 0$. In this figure, $\beta_i = 1 = \delta_i$, and $\alpha_{ij} = 0.1$ for any $i$, $j$.

# Numerical result 2: overdominance

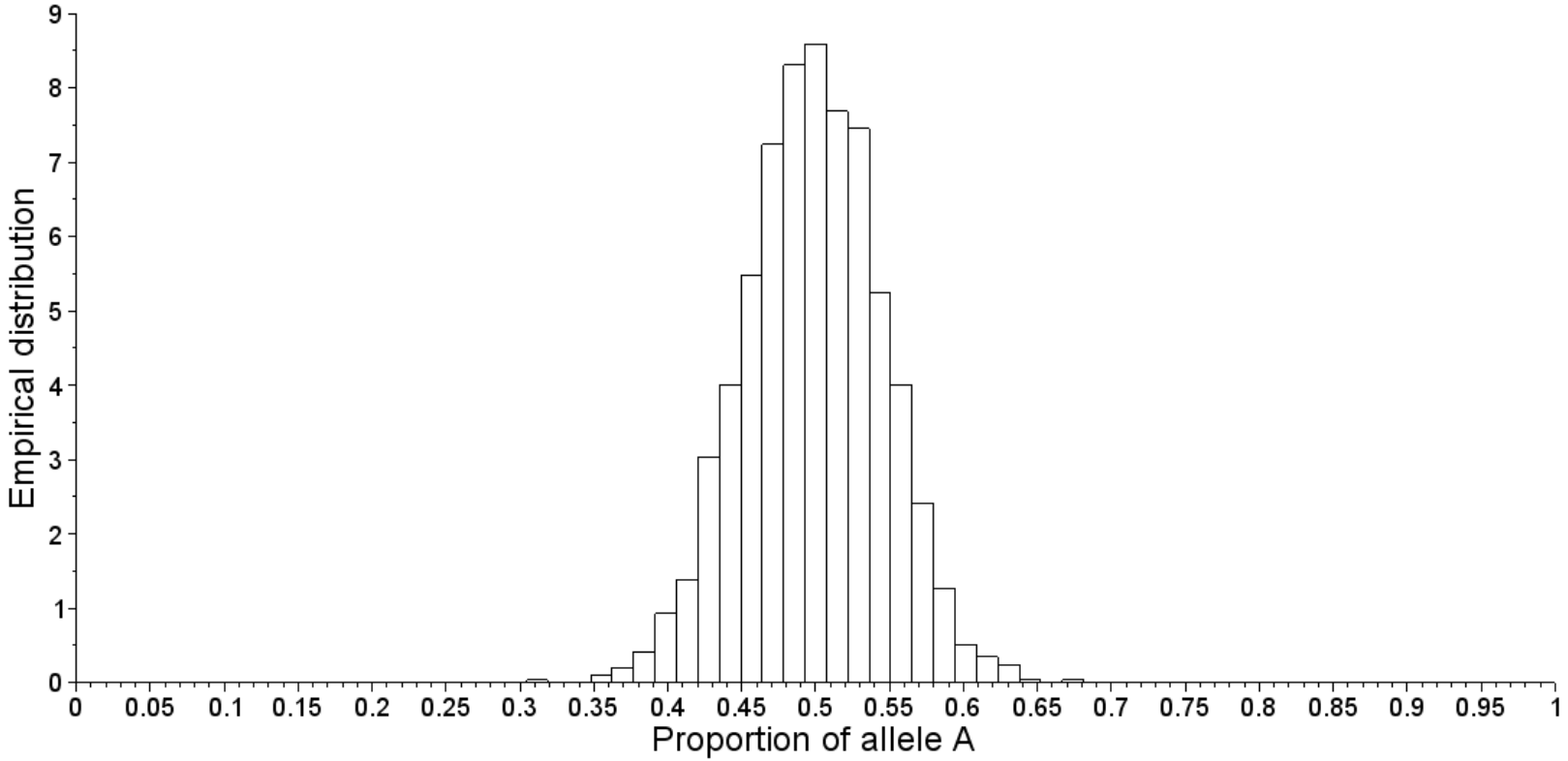


Figure : Distribution of the proportion $X_t$ of alleles $A$ in an overdominance case, knowing that $N_t \neq 0$. In this figure, $\beta_2 = 5$, $\beta_1 = \beta_3 = 1$, $\delta_i = 0$, and $\alpha_{ij} = 0.1$ for any $i$, $j$.

# Perspectives

- Exact conditions under which coexistence is possible.
- More alleles

# Bibliography


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- Cattiaux, P., and Méléard, S. (2009): Competitive or weak competitive stochastic Lotka-Volterra systems conditioned on non-extinction. Journal of Mathematical Biology. 60:797–829.