Phenotypic Adaptation in the Moving-Optimum Model: A Poissonian Stochastic Equation

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joint work with Etienne Pardoux and Michael Kopp

Contents

Motivation

- This work is based on an article of Hermisson and Kopp (2009) : "The genetic basis of phenotypic adaptation II : The distribution of adaptive substitutions in the moving optimum model."
- A linearly increasing optimum with slope $v > 0$.
- A Poisson Point Process of new mutations that hit the population.
- Mutations are divided between two categories: beneficial (have a **positive** fixation probability) and deleterious (with zero fixation probability). The beneficial mutations tend to reduce the gap between the population and the optimum.

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Important results :

- Derivation of an expression of the distribution of the first jump given the gap between the phenotype and the optimum just before the jump.
- Derivation of a recurrence formula for the distributions of the next jumps.

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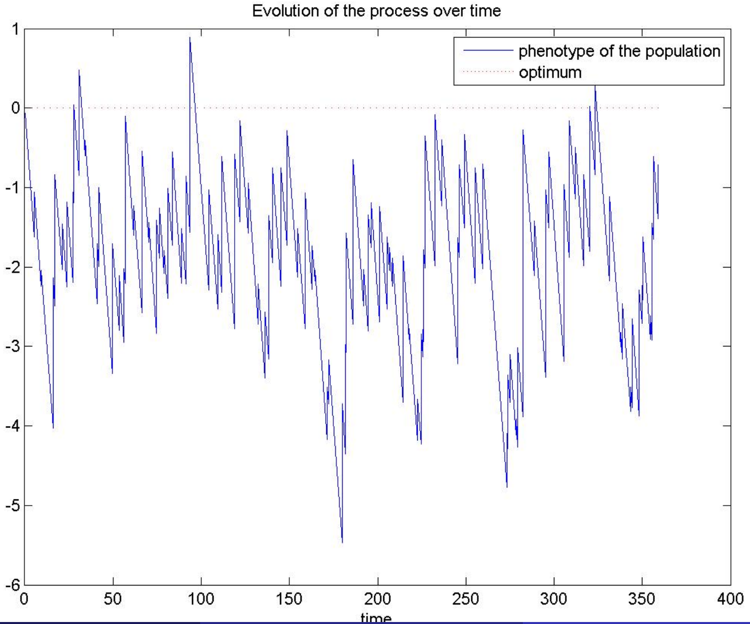
The model

Transformation : $X = Z - vt$



- Let X_t denote a one–dimensional phenotypic trait, which is in one–to–one correspondence with the fitness. The optimal fitness is zero.
- Our model for the evolution of X_t is

$$X_t = x_0 - vt + \int_{[0,t]\times\mathbb{R}\times[0,1]} w\varphi(X_{s^-}, w, \xi)N(ds, dw, d\xi)$$

where N is a PPP over $\mathbb{R}_+ \times \mathbb{R} \times [0,1]$ with mean measure

$$\mu(ds, dw, d\xi) = ds\ \nu(dw)d\xi$$

where $\nu(dw)$ is a σ–finite measure such that

$$\int_{\mathbb{R}} |w| \wedge 1\nu(dw) < \infty \qquad (1)$$

and

$$\varphi(x, w, \xi) = \mathbf{1}_{\{\xi \le g(x,w)\}}$$

- $g(x, w)$ is the fixation probability of a mutation w that hits the population whose phenotype is x.

$$g(x, w) = \left(1 - \exp\left(-2\sigma^2[|w|(2|x| - |w|)^+]\right)\right) \times \mathbf{1}_{(xw<0)}$$

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- This means that at each point (T_i, W_i) of a PPP over $\mathbb{R}_+ \times \mathbb{R}$ with mean measure $ds\ \nu(dw)$, we toss a coin with probability of success $g(X_{T_i-}, W_i)$, and the mutation gets fixed in case of success.
- The questions we asked are : what is the long–time behavior of the Markov process X_t ? Is X_t recurrent or transient ? Of course, if it is transient, $X_t \to -\infty$, as $t \to \infty$. X_t spends essentially all its time in $\mathbb{R}_-$, and we study it in $\mathbb{R}_-$ only, in which case only positive mutations have a chance to fix.
- Define

$$m(x) = \int_{\mathbb{R}_+} wg(x,w)\nu(dw), \quad m = \int_{\mathbb{R}_+} w\nu(dw);$$
$$V(x) = \int_{\mathbb{R}_+} w^2 g(x,w)\nu(dw), \quad V = \int_{\mathbb{R}_+} w^2\nu(dw);$$
$$\psi(x) = m(x) - v.$$

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It is plain that $m(x), V(x) < \infty$ for all $x < 0$, but $m, V \leq +\infty$.

- We have

$$m(x) \uparrow_{x \to -\infty} m, \quad V(x) \uparrow_{x \to -\infty} V.$$

- We can rewrite the SDE for X_t as follows

$$X_t = x_0 + \int_0^t (m(X_s) - v) ds + \int_{[0,t] \times \mathbb{R} \times [0,1]} w\varphi(X_{s-}, w, \xi) \overline{N}(ds, dw, d\xi),$$

where $\bar{N} = N - \mu$ is the compensated PPP.

- m increases from $m(0) = 0$ to $m(-\infty) = m$, as x goes from 0 to $-\infty$.
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Results (constant speed)

- Case $m < v$

Proposition

If $m < v$, then $X_t \to -\infty$ at speed $v - m$ as $t \to \infty$.

- Case $m > v$

Proposition

If $m > v$, then X_t is positive recurrent.

- On the other hand, in the case $m = v$, we will see that the process is essentially either null recurrent or transient.

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Proposition (Case $m = v$)

If

$$\limsup_{x \to -\infty} |x\psi(x)| < \frac{V}{2}$$

then the process is recurrent. If we have the additional assumption that

$$\lim_{x \to -\infty} \frac{V(x)}{|x|} = 0$$

then the process is null recurrent.

Proposition (Case $m = v$)

Assume that

$$\liminf_{x \to -\infty} |x\psi(x)| > \frac{V}{2}$$

If moreover ν *verifies for some* $0 < p < 1$ *and for all* $\alpha > 0$ *sufficiently small*

$$|x|^{p+2} \int_{-\alpha x}^{\infty} w^2 \nu(dw) \xrightarrow[x \to -\infty]{} 0 \tag{2}$$

then

$$X_t \to -\infty$$

$$\textit{and} \quad \frac{X_t}{t} \to 0$$

Results (speed as a function of time)

- When the speed is a function of time, we can generalize our results under the following condition

$$\frac{1}{t}\int_0^t v(s)ds \to \bar{v} \tag{3}$$

- Case $m < \bar{v}$

Proposition

If $m < \bar{v}$, then $X_t \to -\infty$ at speed $\bar{v} - m$ as $t \to \infty$.

- Case $m > \bar{v}$

Proposition

If $m > \bar{v}$, then X_t is recurrent. Moreover if $\exists K_v$ such that

$$\bar{v}t - \int_0^t v(s)ds \geq -K_v$$

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In addition to condition (3), *assume that* $v_{\sup} = \limsup v(s)$ *is finite. Now let* $\psi_{\sup}(x) = m(x) - v_{\sup}$. *If*

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In addition to condition (3), *assume that* $v_{\inf} = \liminf v(s)$ *is finite. Now let* $\psi_{\inf}(x) = m(x) - v_{\inf}$. *If*

$$\liminf_{x \to -\infty} |x \psi_{\inf}(x)| > \frac{V}{2}$$

then

$$X_t \to -\infty$$
$$\frac{X_t}{t} \to 0$$

Small Jumps Limit

- Now we assume $V < \infty$ and $\int_0^\infty w^3 \nu(dw) < \infty$ and we take the small/frequent jumps asymptotic. In other words, we introduce the change of variables :

$$\tilde{w} = \epsilon w \quad \text{and} \quad \tilde{s} = \frac{s}{\epsilon^2} \text{ with } \epsilon > 0.$$

- We have the following

Proposition

$$X_t^\epsilon \xrightarrow{proba} X_t \text{ as } \epsilon \to 0$$

such that

$$\frac{dX_t}{dt} = -v - 4\sigma^2 V X_t.$$

Moreover

$$X_t \xrightarrow[t\to\infty]{} -\frac{v}{4\sigma^2 V}.$$

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Furthermore we have the following proposition:

Proposition

For $\epsilon \ll 1$ *and for large* t

$$X_t^\epsilon \sim \mathcal{N}\left(-\frac{v}{4\sigma^2 V}, \frac{\epsilon v}{8\sigma^2 V^2}\int_{\mathbb{R}_+} w^3 \nu(dw)\right).$$

Two dimensional case

- The adaptive landscape is described by the matrix $\Sigma = \sigma^2 Id$.
- The distribution of new mutations $W \sim \mathcal{N}(0, M)$ such that $\det(M) = 1$.
- The speed vector v is horizontal.
- The fixation probability

$$g(x, w) = \left(1 - \exp(2\sigma^{-2}\langle 2x + w, w\rangle)\right) \times \mathbf{1}_{\{\langle 2x+w,w\rangle \leq 0\}}$$

  This means that if the process is at x then the mutations that have a positive probability of fixation belong to a circle around $-x$ that passes by 0.
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$$X_t = X_0 - vt + \int_0^t m(X_s)ds + \mathcal{M}_t$$

where $m(x) = \int_{\mathbb{R}^2} wg(x,w)\nu(dw)$.

- For all x, define the direction vector $u = \frac{x}{|x|}$.

Proposition

$$m(x) \xrightarrow[|x|\to\infty]{} \bar{m}(u).$$

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- Define $A^- = \mathbb{R}_- \times \mathbb{R}$ and $T_0 = \inf\{t > 0, X_t \in A^-\}$.

Proposition

If $X_0 \notin A^-$ then $T_0 < \infty$.

- For all unit vector u we associate an angle α such that $u = \begin{pmatrix} \cos\alpha \\ \sin\alpha \end{pmatrix}$.

Proposition

There exists a unique $\alpha_0 \in \left[\frac{\pi}{2}, \frac{3\pi}{2}\right]$ such that $\bar{m}_2(\alpha_0) = 0$.

- It is difficult to find α_0 explicitly but we think that if the process is transient then it will fluctuate around this direction while getting further from zero.

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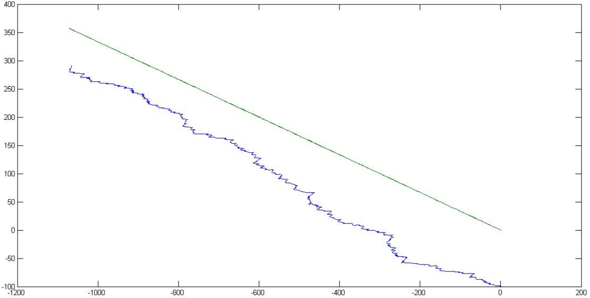
Cas $v > \bar{m}_1(\alpha_0)$

Let $M = \begin{pmatrix} a & c \\ c & b \end{pmatrix}$.

Proposition

If $c \leq 0$ *then* $\alpha_0 \in \left[S_c^1, \pi\right]$, *where* $S_c^1 = \arctan\left(\frac{c}{b}\right) + \frac{\pi}{2}$.



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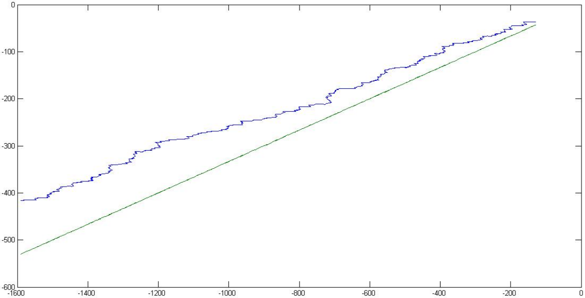

Cas $v < \bar{m}_1(\alpha_0)$

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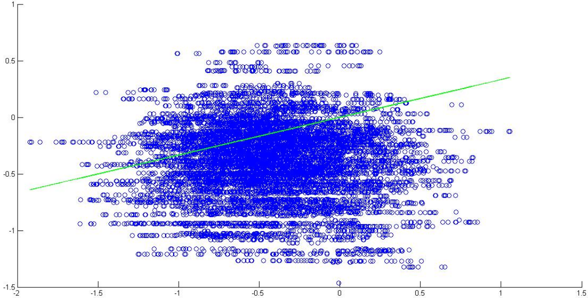

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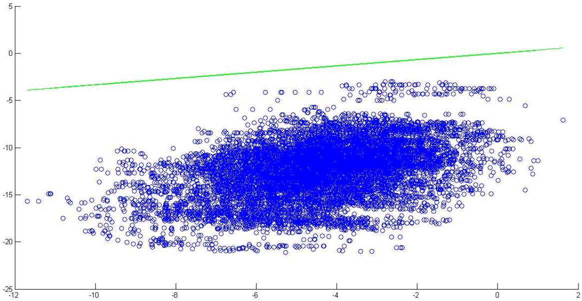

THANK YOU FOR YOUR ATTENTION !