A Hamilton-Jacobi approach for models from evolutionary biology III: the case of a time-periodic environment

Sepideh Mirrahimi

CNRS, IMT, Toulouse, France

Joint work with Susely Figueroa Iglesias (IMT)

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Table of contents

Table of contents

The influence of fluctuating temperature on bacteria

Bacterial pathogen **Serratia marcesens** evolved in fluctuating temperature (daily variation between 24°C and 38°C, mean 31°C), outperforms the strain that evolved in constant environments (31°C):

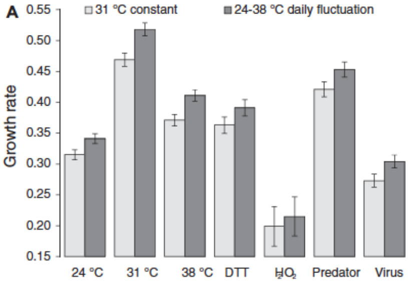

Figure from: Fluctuation temperature leads to evolution of thermal generalism and preadaptation to novel environments, Ketola et al. 2013

A model of a phenotypically structured population in a time-periodic environment

$$\begin{cases} \frac{\partial}{\partial t} n - \varepsilon^2 \Delta n = n\big(R(t,x) - \kappa\rho\big), \\ n(t=0,\cdot) = n_0(\cdot), \\ \rho(t) = \int_{\mathbb{R}^d} n(t,x)\,dx, \end{cases}$$

with R, T- **periodic** with respect to the first variable.

- $x \in \mathbb{R}^d$: phenotypical trait
- $n(t,x)$: density of trait x
- $\varepsilon^2 \propto$ variance of the mutations
- $R(t,x)$: growth rate
- $\rho(t)$: size of the population
- κ: intensity of the competition

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Some related works: Lorenzi–Chisholm–Desvillettes–Hughes 2015, M.–Perthame–Souganidis 2015

Assumptions

Notation:

$$\overline{R}(x) = \frac{1}{T}\int_0^T R(t,x)dt.$$

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- ε is small.

Table of contents

Long time behavior of the population's phenotypical distribution

Proposition (Figueroa Iglesias and M., 2018)

As $t \to \infty$, $n(t,x)$ converges to the unique periodic solution of

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The **Hopf-Cole** transformation:

$$n_\varepsilon(t,x) = \frac{1}{(2\pi\varepsilon)^{\frac{d}{2}}} \exp\left(\frac{u_\varepsilon(t,x)}{\varepsilon}\right).$$

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An expected asymptotic expansion:

$$u_\varepsilon(t,x) = u + \varepsilon v + \varepsilon^2 w + O(\varepsilon^3).$$

The main result

Theorem (Figueroa Iglesias and M., 2018)

(i) As $\varepsilon \to 0$, $n_\varepsilon(t,x) - \tilde\rho(t)\,\delta(x - x_m) \rightharpoonup 0$,

with $\tilde\rho$ *the unique T-***periodic** *solution to*

$$\frac{d\tilde\rho}{dt}(t) = \tilde\rho(t)\,(R(t,x_m) - \tilde\rho(t)).$$

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(i) As $\varepsilon \to 0$, u_ε *converges locally uniformly to the unique viscosity solution of*

$$\begin{cases} -|\nabla u|^2(x) = \overline{R}(x) - \overline{\rho}, \\ \max_{x\in\mathbb{R}^d} u(x) = 0. \end{cases}$$

For $x \in \mathbb{R}$, *this solution is indeed smooth and classical and can be computed explicitly.*

Next order terms and the approximation of the moments of the population's distribution

One can also compute (at least formally) the next order term v leading to the following approximation of the population's distribution:

$$n_\varepsilon(t,x) \approx \frac{1}{(2\pi\varepsilon)^{\frac{d}{2}}} \exp\left(\frac{u(x)}{\varepsilon} + v(t,x)\right).$$

Going further in the approximations $\Rightarrow$ **analytical formula for the moments of the population's distribution** with an error of order ε^2, in terms of the derivatives of u and v at the point x_m (using the Laplace's method for integration).

Some notations

Average **size of the population** over a period of time:

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Mean phenotypic trait of the population:

$$\mu_p(t) = \frac{1}{\rho_\varepsilon(t)}\int_{\mathbb{R}^d} x\ n_\varepsilon(t,x)dx$$

Phenotypic **variance** of the population's distribution:

$$v_p(t) = \frac{1}{\rho_\varepsilon(t)}\int_{\mathbb{R}^d} (x-\mu_p)^2 n_\varepsilon(t,x)dx$$

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Mean fitness of the population in an environment with constant temperature $\boldsymbol{\tau}$:

$$F_p(\tau) = \int_{\mathbb{R}^d} a(\tau,x)\frac{1}{T}\int_0^T \frac{n_\varepsilon(t,x)}{\rho_\varepsilon(t)}dtdx$$

Table of contents

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$$R(t, x) = r - g(x - c\sin(bt))^2.$$

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We can estimate the size of the population, the mean phenotypic trait and the mean variance of the population's distribution :

$$\rho_p \approx r - \frac{gc^2}{2} - \varepsilon\sqrt{g}, \quad \mu_p(t) \approx \frac{2\varepsilon c}{b}\sqrt{g}\sin\left(b(t - \frac{\pi}{2b})\right), \quad \sigma_p^2 \approx \frac{\varepsilon}{\sqrt{g}}.$$

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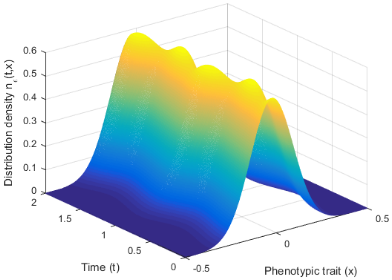
One can also estimate the **mean fitness** of this population in an environment with constant temperature $t = \frac{\pi}{b}$ and compare it with the mean fitness of a population evolved in constant environment in the same conditions :

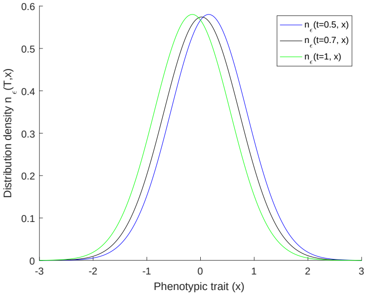
$$\widetilde{F}_c(\pi/b) \approx \widetilde{F}_p(\pi/b) \approx r - \varepsilon\sqrt{g}.$$

Example 1: when the fluctuations act on the optimal trait

Numerical computation of the phenotypic distribution density, with

$$R(t,x) = r - g(x - c\sin(bt))^2,$$
$$r = 2, \quad c = g = 1, \quad b = 2\pi, \quad \varepsilon = 0.5.$$





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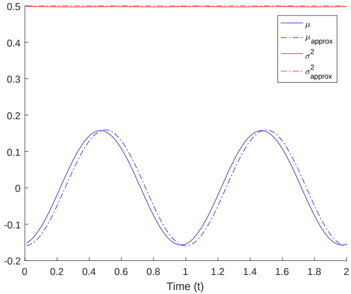

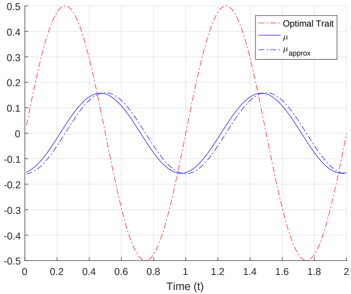

Left: comparison between the **analytical** and the **numerical** approximations of the moments of the population's density.
Right: comparison between the mean phenotypic trait (numerical and analytical approximations) and the optimal trait.

Example 2: when the fluctuations act on the pressure of the selection

$$R(t,x) = r - g(t)x^2,$$

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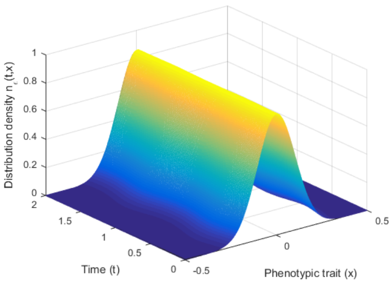
and the **mean fitness** in an environment with constant temperature $t = \frac{1}{2}$

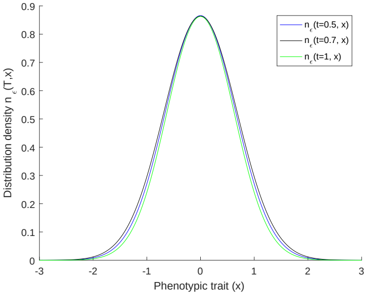
$$\widetilde{F}_c(1/2) \approx r - \varepsilon\sqrt{g(1/2)} < \widetilde{F}_p(1/2) \approx r - \varepsilon\frac{g(1/2)}{\sqrt{\overline{g}}}, \quad \text{if } \overline{g} > g(\frac{1}{2}).$$

Example 2: when the fluctuations act on the pressure of the selection

Numerical computation of the phenotypic distribution density, with

$$R(t,x) = r - (cos(bt) + 1.5)x^2,$$
$$r = 2, \qquad b = 2\pi, \quad \varepsilon = 0.5.$$





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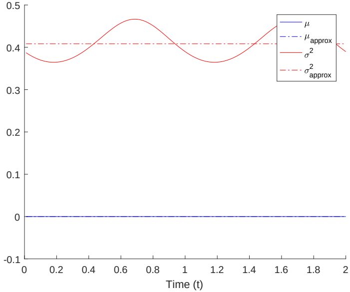

Thank you for your attention !