Integro-differential models of evolutionary adaptation in changing environments

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Motivating example 1:
Earth's temperature changes (increase and oscillations)

- Under which conditions can species adapt to (and survive) an environmental shift ?
- How the oscillations of an environment impact the adaptation to a gradual change?

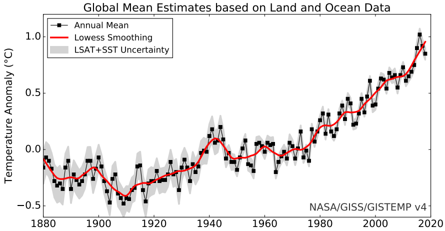

Figure from: data.giss.nasa.gov

Motivating example 2:
The influence of fluctuating temperature on bacteria

Bacteria 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).

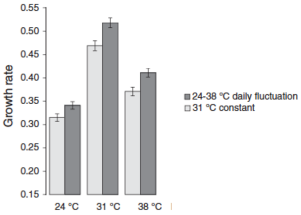

Figure from: Ketola et al. 2013

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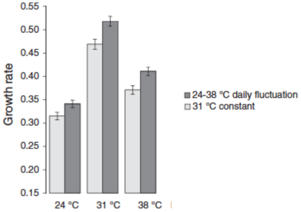

Figure from: Ketola et al. 2013

- What is the impact of an oscillating environment on the phenotypic distribution of a population ?
- Is it possible that evolving in a periodic environment would lead to a more performant population?

How to model the evolutionary dynamics of quantitative traits?

Different mechanisms contribute to the evolution of quantitative traits. Here, we consider:

- asexual reproduction: offspring arise from a single organism
- heredity: transmission of the ancestral trait to the offspring
- mutation: generates variability in the trait values
- selection: individuals with better ability will spread through the population over time
- competition for limited resources, leading to a bounded population size

Main question: predict evolutionary and demographic outcomes depending on the trade-offs between these mechanisms.

A classical model considering a homogeneous evironment

Continuum of alleles model (Kimura 1965, Champagnat, Ferrière and Méléard 2008):

$$\begin{cases} \partial_t m(t,z) = \underbrace{\int b(y)G(y-z)m(t,y)dy}_{\text{mutation}} + \underbrace{m(t,z)R(z,I(t))}_{\text{selection \& competition}}, \\ \underbrace{I(t) = \int_{\mathbb{R}^d} \psi(y)m(t,y)dy}_{\text{Environment feedback}}, \qquad (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d. \end{cases}$$

Competition modeled through $I(t)$: $R(z,I)$ decreasing w.r.t. I

Positive contribution of all traits to the competition:

$$0 < C_1 \leq \psi(z) \leq C_2.$$

Examples of growth rate R

Example 1: logistic growth

$$R(z,I) = r(z) - \kappa I, \quad I(t) = \int_{\mathbb{R}^d} m(t,y)dy, \quad \psi(z) \equiv 1.$$

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Example 2: chemostat
(considering fast dynamics for the nutrient)

$$R(z,I) = \frac{S_{\rm in}\psi(z)}{d + I(t)} - d.$$

d: renewing rate in the chemostat $\quad S_{\rm in}$: fresh nutrient income rate

$\psi(z)$: nutrient uptake rate for individuals of trait z

An alternative model: diffusive approximation

When the **mutations are rather frequent but with small effects**, the mutation term can be approximated by a Laplace term (Kimura 1965, Burger 2000, Champagnat, Ferrière and Méléard 2008)

$$\begin{cases} \partial_t m(t,z) = \sigma \Delta m + m(t,z) R(z, I(t)) \\ I(t) = \int_{\mathbb{R}^d} \psi(x) m(t,y) dy, \qquad (t,z) \in \mathbb{R}^+ \times \mathbb{R}^d. \end{cases}$$

(considering constant birth rate with mutations)

Let's focus on a simple model including the important features

$$\begin{cases} \frac{\partial}{\partial t} m - \underbrace{\sigma \frac{\partial^2}{\partial z^2} m}_{\text{mutations}} = m\Big(\underbrace{R(e,z)}_{\substack{\text{growth rate} \\ \text{(selection)}}} - \underbrace{\kappa M}_{\text{competition}} \Big), \\ M(t) = \int_{\mathbb{R}} m(t,y)\, dy, \qquad m(t=0,\cdot) = m_0(\cdot). \end{cases}$$

- z: phenotypic trait ($\in \mathbb{R}$)
- $m(t,z)$: density of trait z
- $R(e,z)$: growth rate
- e: environment state
- $M(t)$: size of the population
- κ: intensity of the competition
- σ: mutation effective size

Example of growth rate

$$R(e,z) = \underbrace{r(e)}_{\text{maximal growth rate}} - \underbrace{s(e)}_{\text{selection pressure}} (z - \underbrace{\theta(e)}_{\text{optimal trait}})^2$$

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Examples of time varying environment:

- **Shifting environment:** $R(e(t),z) = R(z-ct)$ (in the example above : $\theta(e(t)) = \theta_0 + ct$.
- **Oscillating environment:** $R(e,z)$, with $e(t)$ a periodic function.
- **Shifting and oscillating:** $R(e(t),z) = R(e(t),z-ct)$, with $e(t)$ a periodic function.
- **Piecewise constant environment:** $e(t) = e_i$, for $t_i \leq t \leq t_{i+1}$.

Some references

My lectures are based on: Figueroa Iglesias–M. (2018-2021), Costa–Etchegaray–M. (2021)

- **The Hamilton-Jacobi approach:**

Diekmann et al. (2005), Perthame–Barles (2008), Lorz–M.–Perthame (2011),...

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- **Related works on time-varying environments**:

Lynch et al. (1991), Lynch–Lande (1993), Burger–Lynch (1995), Lande–Shannon (1996), Kopp–Matuszewski (2014)

(assumptions: quadratic stabilizing selection: $R(e,z) = r_{\max} - s(z - \theta(e))^2$, Gaussian phenotypic distribution, the environment change acts only on the optimum)

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M.–Perthame–Souganidis (2015), Roques et al. (2020), Garnier et al. (preprint 2022)

Cancer therapy optimisation: Lorenzi et al. (2015), Almeida et al. (2019) Carrère and Nadin (2020)

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A shifting environment

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Density in the moving framework: $n(t,z) = m(t, z+ct)$:

$$\begin{cases} \frac{\partial}{\partial t} n - c\frac{\partial}{\partial z} n - \sigma \frac{\partial^2}{\partial z^2} n = n\big(R(z) - \kappa N\big), \\ N(t) = \int_{\mathbb{R}} n(t,y)\,dy. \end{cases}$$

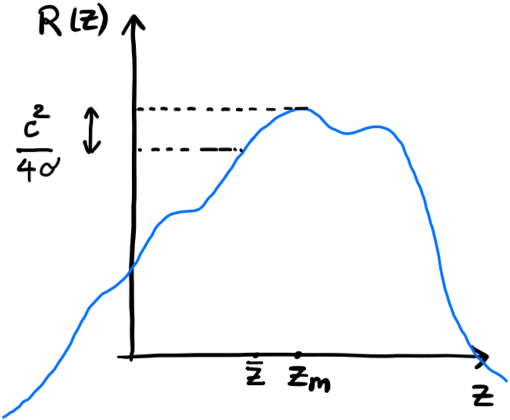
Assumptions

- $R(z)$ is smooth.
- $R(z) \to -\infty$ as $|z| \to +\infty$.
- There exists a unique $z_m \in \mathbb{R}$ such that

$$\max_{z \in \mathbb{R}} R(z) = R(z_m) > 0.$$

- There exists a unique $\bar{z} < z_m$ such that

$$R(\bar{z}) + \frac{c^2}{4\sigma} = R(z_m).$$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$\frac{c^2}{4\alpha}$
$\bar{z}$
z_m
z

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An eigenvalue problem with $c = 0$

An eigenvalue problem, by linearization and taking $c = 0$:

$$\begin{cases} -\sigma \frac{\partial^2}{\partial z^2} p_{\sigma,0} - R(z) p_{\sigma,0} = \lambda_{\sigma,0} p_{\sigma,0}, \qquad p_{\sigma,0} \in L^2(\mathbb{R}). \\ \|p_{\sigma,0}\|_{L^2} = 1. \end{cases}$$

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$\Rightarrow$ Krein-Rutman Theorem implies the existence of a unique **principal eigenpair** $(\lambda_{\sigma,0}, p_{\sigma,0})$ with $p_{\sigma,0} > 0$.

An eigenvalue problem with $c > 0$

$$\begin{cases} -c\frac{\partial}{\partial z}p_{\sigma,c} - \sigma\frac{\partial^2}{\partial z^2}p_{\sigma,c} - R(z)p_{\sigma,c} = p_{\sigma,c}\lambda_{\sigma,c}, \\ \\ p_{\sigma,c} > 0, \qquad \|p_{\sigma,c}\|_{L^2} = 1. \end{cases}$$

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Equivalence between the eigenpairs of this operator with the one with no drift term:

Liouville transformation:

$$q(z) = p_{\sigma,c}(z)e^{\frac{c}{2\sigma}z}.$$

$$-\sigma\frac{\partial^2}{\partial z^2}q - R(z)q = q\Big(-\frac{c^2}{4\sigma} + \lambda_{\sigma,c}\Big),$$

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$$\lambda_{\sigma,c} = \lambda_{\sigma,0} + \frac{c^2}{4\sigma}.$$

Critical speed for survival

Define the critical speed :

$$c_\sigma = \begin{cases} 2\sqrt{-\sigma\lambda_{\sigma,0}}, & \text{if } \lambda_{\sigma,0} < 0 \\ 0, & \text{otherwise.} \end{cases}$$

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Theorem

(i) $c \geq c_\sigma$*:* $N(t) \to 0$ *as* $t \to \infty$*.*

(ii) $c < c_\sigma$*:* $n(t,\cdot)$ *converges to* $\overline{n}_\sigma(z) = \overline{N}_\sigma \frac{p_{\sigma,c}(z)}{\int p_{\sigma,c}(y)dy}$ *with* $(p_{\sigma,c}, \lambda_{\sigma,c})$ *the principal eigenpair:*

$$\begin{cases} -c\frac{\partial}{\partial z}p_{\sigma,c} - \sigma\frac{\partial^2}{\partial z^2}p_{\sigma,c} = p_{\sigma,c}\big(R(z) + \lambda_{\sigma,c}\big), \\ p_{\sigma,c} > 0, \end{cases}$$

and

$$\overline{N}_\sigma = -\lambda_{\sigma,c}/\kappa = -(\lambda_{\sigma,0} + \frac{c^2}{4\sigma})/\kappa.$$

The main elements of the proof

- Main elements: we prove separately convergence of N and $\frac{n}{N}$
- convergence of $\frac{n}{N}$ to $\frac{p_{\sigma,c}(z)}{\int p_{\sigma,c}(y)dy}$
- if $\lambda_{\sigma,c} > 0$: $N \to 0$ (extinction)
- if $\lambda_{\sigma,c} < 0$ convergence of N to $\overline{N} = \frac{-\lambda_{\sigma,c}}{\kappa}$

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Notation: In what follows we replace $\overline{n}_\sigma$ and $\overline{N}_\sigma$ by n_σ and N_σ.

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How to characterize c_σ and n_σ ?

Assumption: mutations with small effects

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We rescale the problem ($c \to \varepsilon c$, $c_\varepsilon \to \varepsilon c_\varepsilon$):

$$\begin{cases} -\varepsilon c \frac{\partial}{\partial z} n_\varepsilon - \varepsilon^2 \frac{\partial^2}{\partial z^2} n_\varepsilon = n_\varepsilon [R(z) - \kappa N_\varepsilon], \\ N_\varepsilon = \int_{\mathbb{R}} n_\varepsilon(y) dy. \end{cases}$$

Concentration around a trait behind the optimum

The population follows the optimum with a constant lag:

Theorem

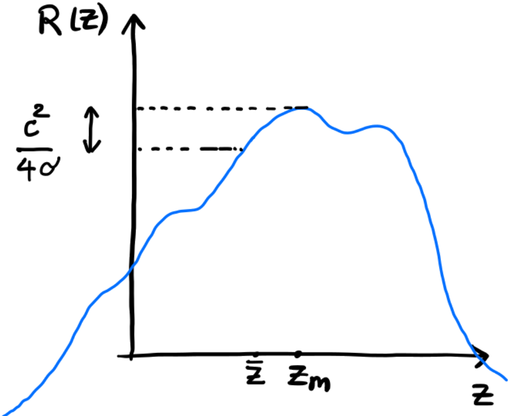
Let $c < \overline{c} := 2\sqrt{R(z_m)}$. Then, as $\varepsilon \to 0$,

$$n_\varepsilon(z) \rightharpoonup \frac{R(\overline{z})}{\kappa}\delta(z - \overline{z}).$$

In the original problem before the translation (and in long time)

$$m_\varepsilon(t, z) \approx \frac{R(\overline{z})}{\kappa}\delta(z - \overline{z} - \varepsilon\, ct).$$

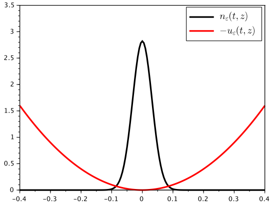
Recall: $\overline{z}$ the unique point such that $R(\overline{z}) + \frac{c^2}{4} = R(z_m)$ and $\overline{z} < z_m$.



Main ingredient: a logarithmic transformation

Hopf-Cole transformation :

$$n_\varepsilon(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_\varepsilon(z)}{\varepsilon}\right).$$



We expect that

$$u_\varepsilon(z) = u(z) + \varepsilon v(z) + o(\varepsilon).$$

Idea: to unfold the singularity of the phenotypic density.

Replacing the Hopf-Cole transformation in the equation on n_ε:

$$-c\frac{\partial}{\partial z}u_\varepsilon - \varepsilon\frac{\partial^2}{\partial z^2}u_\varepsilon - |\frac{\partial}{\partial z}u_\varepsilon|^2 = R(z) - \kappa N_\varepsilon.$$

$$\Downarrow$$

$$-\varepsilon\frac{\partial^2}{\partial z^2}u_\varepsilon - \left|\frac{\partial}{\partial z}u_\varepsilon + \frac{c}{2}\right|^2 = R(z) - \kappa N_\varepsilon - \frac{c^2}{4}.$$

Asymptotic behavior of u_ε

Proposition

(i) Assume that $c < \overline{c}$. *Then, as* $\varepsilon \to 0$ *and along subsequences,* $N_\varepsilon \to N_0$ *and* $u_\varepsilon(z)$ *converges locally uniformly to a function* $u(z) \in C(\mathbb{R})$, *a viscosity solution to*

$$\begin{cases} -\left|\dfrac{\partial}{\partial z}u + \dfrac{c}{2}\right|^2 = R(z) - \kappa N_0 - \frac{c^2}{4}, \quad z \in \mathbb{R}, \\ \max_{z\in\mathbb{R}} u(z) = 0. \end{cases} \qquad (P_u)$$

(ii) n_ε *converges in the weak sense of measures to a measure* n *with*

$$\mathrm{supp}\, n(z) \subset \{z | u(z) = 0\}.$$

The inclusion property

By integrating the equation on n_ε we obtain

$$\|n_\varepsilon\|_{L^1(\mathbb{R})} = N_\varepsilon \leq \max_{z\in\mathbb{R}} R(z),$$

$\Rightarrow$ n_ε converges, along subsequences and in the weak sense of measures to a measure n with

$$\operatorname{supp} n(z) \subset \{z | u(z) = 0\}.$$

Elements of the proof on the board.

Uniqueness and identification of u

Proposition

The viscosity solution of (P_u) is unique and it is indeed a classical solution given by

$$u(z) = \frac{c}{2}(\overline{z}-z)+\int_{\overline{z}}^{z_m} \sqrt{R(z_m)-R(y)}dy-\left|\int_{z_m}^{z} \sqrt{R(z_m)-R(y)}dy\right|.$$

Moreover, $N_0 = R(\overline{z})/\kappa$.

Recall: z_m the maximum point of R and $\overline{z}$ the unique point such that $R(\overline{z}) + \frac{c^2}{4} = R(z_m)$ and $\overline{z} < z_m$.

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Recall: z_m the maximum point of R and $\overline{z}$ the unique point such that $R(\overline{z}) + \frac{c^2}{4} = R(z_m)$ and $\overline{z} < z_m$.

Remark: $\max_z u(z) = u(\overline{z}) = 0 \Rightarrow \operatorname{supp} n = \{\overline{z}\}$.

Main ingredients

Define

$$\psi(z) = u(z) + \frac{c}{2} z.$$

Then,

$$-|\partial_z \psi|^2 = R(z) - \kappa N_0 - \frac{c^2}{4} =: f(z).$$

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$$-|\partial_z \psi|^2 = R(z) - \kappa N_0 - \frac{c^2}{4} =: f(z).$$

We have

$f(z) \leq 0,$ and f attains a strict maximum at z_m.

The viscosity solution to

$$\begin{cases} -|\partial_z \psi|^2 = f(z), & z \in (a,b) \\ f(z) < 0, & z \in (a,b) \end{cases}$$

can be explicitly identified by its values at the boundary.

Let $A >> |z_m|$.
For all $z \in (-A, z_m)$:

$$\psi(z) = \max\left\{\psi(-A) - \left|\int_{-A}^{z} \sqrt{-f(y)}dy\right| ; \psi(z_m) - \left|\int_{z_m}^{z} \sqrt{-f(y)}dy\right|\right\},$$

and for all $z \in (z_m, A)$:

$$\psi(z) = \max\left\{\psi(A) - \left|\int_{A}^{z} \sqrt{-f(y)}dy\right| ; \psi(z_m) - \left|\int_{z_m}^{z} \sqrt{-f(y)}dy\right|\right\}.$$

Note that

$$-f(z) = -R(z) - \kappa N_0 - \frac{c^2}{4} \to +\infty, \quad \text{as } |z| \to \infty,$$

$$\psi(\pm A) = u(\pm A) \pm \frac{c}{2}A \leq \frac{c}{2}A.$$

Therefore, the first terms in the maximum operators tend to $-\infty$ as $A \to +\infty$.

We deduce that

$$\psi(z) = \psi(z_m) - \left| \int_{z_m}^{z} \sqrt{-f(y)}dy \right|.$$

or equivalently

$$u(z) = u(z_m) + \frac{c}{2}(z_m - z) - \left| \int_{z_m}^{z} \sqrt{R(z_m) - R(y)}dy \right|.$$

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This also implies that

$$f(z_m) = R(z_m) - \kappa N_0 - \frac{c^2}{4} = 0, \quad \Rightarrow \kappa N_0 = R(z_m) - \frac{c^2}{4}.$$

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$$u(z_m) = ?$$

Identification of the maximum point of u

Note that

$$\max_z u(z) = u(z^*) = 0.$$

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From the equation on u we obtain that

$$R(z^*) = R(z_m) - \frac{c^2}{4}.$$

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From the equation on u we obtain that

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Moreover, from the expression of $u(z)$:

$$\max_z u(z) = u(z^*) = u(z_m) + \frac{c}{2}(z_m - z^*) - \left| \int_{z_m}^{z^*} \sqrt{-f(y)}dy \right| \geq u(z_m).$$

and hence

$$z^* \leq z_m.$$

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Note that

$$\max_z u(z) = u(z^*) = 0.$$

From the equation on u we obtain that

$$R(z^*) = R(z_m) - \frac{c^2}{4}.$$

Moreover, from the expression of $u(z)$:

$$\max_z u(z) = u(z^*) = u(z_m) + \frac{c}{2}(z_m - z^*) - \left| \int_{z_m}^{z^*} \sqrt{-f(y)}dy \right| \geq u(z_m).$$

and hence

$$z^* \leq z_m.$$

These two properties lead to

$$z^* = \overline{z}.$$

Identification of u

We deduce that

$$u(\overline{z}) = u(z_m) + \frac{c}{2}(z_m - z^*) - \left| \int_{z_m}^{z^*} \sqrt{-f(y)}dy \right| = 0.$$

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and hence

$$u(z_m) = -\frac{c}{2}(z_m - \overline{z}) + \left| \int_{z_m}^{\overline{z}} \sqrt{-f(y)}dy \right|.$$

This leads to the formula on $u(z)$ and completes the proof.

More precise approximation of the population size and the survival threshold

Theorem

$$N_\varepsilon = -\lambda_{c,\varepsilon}/\kappa = \left(R(z_m) - \frac{c^2}{4}\right)/\kappa - \varepsilon\frac{\sqrt{-R''(z_m)/2}}{\kappa} + o(\varepsilon),$$

$$c_\varepsilon = 2\sqrt{R(z_m)} - \varepsilon\sqrt{-\frac{R''(z_m)}{2\,R(z_m)}} + o(\varepsilon).$$

These approximations come from the harmonic approximation of the ground state energy of the Schrodinger operator.

Going to the next order approximation of u_ε

We expect that

$$u_\varepsilon(z) = u(z) + \varepsilon v(z) + o(\varepsilon),$$

which leads to a more precise approximation of the phenotypic density for nonzero ε

$$n_\varepsilon \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u(z) + \varepsilon v(z) + o(1)}{\varepsilon}\right).$$

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Moments of the population distribution: notations

Size of the population at equilibrium:

$$N_\varepsilon = \int_{\mathbb{R}} n_\varepsilon(z)dz.$$

Mean phenotypic trait:

$$\mu_\varepsilon = \frac{1}{N_\varepsilon}\int_{\mathbb{R}} z\; n_\varepsilon(z)dz.$$

Variance of the phenotypic distribution:

$$v_\varepsilon = \frac{1}{N_\varepsilon}\int_{\mathbb{R}} (z-\mu_\varepsilon)^2 n_\varepsilon(z)dz$$

Third order central moment of the phenotypic distribution:

$$\psi_{\varepsilon,0} = \frac{1}{N_{\varepsilon,0}}\int (z-\mu_\varepsilon)^3\; n_\varepsilon(z)dz).$$

Analytic approximation of the moments

We can approximate the moments of the phenotypic distribution using the **Laplace's method of integration**:

Analytic approximation of the moments

We can approximate the moments of the phenotypic distribution using the **Laplace's method of integration**:

Assume that f has a single maximum point at the point z_0 and that $f''(z_0) < 0$. Then,

$$lim_{\varepsilon \to 0} \frac{\int_a^b e^{\frac{f(z)}{\varepsilon}} dz}{\sqrt{\frac{2\pi\varepsilon}{|f''(z_0)|}}\, e^{\frac{f(z_0)}{\varepsilon}}} = 1.$$

Analytic approximation of the moments

Taylor expansions for u and v:

$$u(z) = -\frac{A}{2}(z-\overline{z})^2 + B(z-\overline{z})^3 + O(z-\overline{z})^4,$$

$$v(z) = C + D(z-\overline{z}) + O(z-\overline{z})^2.$$

Then

$$\begin{cases} \mu_\varepsilon = \frac{1}{N_\varepsilon}\int z n_\varepsilon(z)dz = \overline{z} + \varepsilon(\frac{3B}{A^2} + \frac{D}{A}) + o(\varepsilon), \\ v_\varepsilon = \frac{1}{N_\varepsilon}\int (z-\mu_\varepsilon)^2\, n_\varepsilon(z)dz = \frac{\varepsilon}{A} + o(\varepsilon), \\ \psi_\varepsilon = \frac{1}{N_\varepsilon}\int (z-\mu_\varepsilon)^3\, n_\varepsilon(z)dz = \frac{6B}{A^3}\varepsilon^2 + o(\varepsilon^2). \end{cases}$$

Analytic approximation of the moments

Main ingredient:

$$\int (z-z_0)^k n_\varepsilon(z)dz$$

$$= \frac{\varepsilon^{\frac{k}{2}}\sqrt{A}N_0}{\sqrt{2\pi}} \int_{\mathbb{R}} (y^k e^{-\frac{A}{2}y^2}\big(1+\sqrt{\varepsilon}(By^3+Dy)+O(\varepsilon)\big)dy$$

$$= \varepsilon^{\frac{k}{2}} N_0 \Big(\omega_k(\tfrac{1}{A}) + \sqrt{\varepsilon}\big(B\omega_{k+3}(\tfrac{1}{A}) + D\omega_{k+1}(\tfrac{1}{A})\big)\Big) + O(\varepsilon^{\frac{k+2}{2}}).$$

$\omega_k(v)$: k-th order central moment of a Gaussian distribution with variance v.

The example of quadratic growth rate

$$R(z) = r - s(z-\theta)^2.$$

$$\begin{cases} N_\varepsilon = r - \underbrace{c^2/4}_{\substack{\text{load due to}\\ \text{environmental shift}}} - \underbrace{\varepsilon\sqrt{s}}_{\text{mutation load}} + o(\varepsilon), \\ \mu_\varepsilon = \theta - \underbrace{c/(2\sqrt{s})}_{\text{phenotypic lag due to environmental shift}} + o(\varepsilon), \\ v_\varepsilon = \frac{\varepsilon}{\sqrt{s}} + o(\varepsilon), \qquad \psi_\varepsilon = o(\varepsilon^2), \\ c_\varepsilon = 2\sqrt{r} - \sqrt{\frac{s}{r}}\,\varepsilon + o(\varepsilon). \end{cases}$$

A strong selection pressure reduces the phenotypic lag but also leads to a lower threshold of speed of environmental change above which the population goes extinct.

Non-confining growth rates R

We have made the assumption:

$$R(z) \to -\infty, \qquad \text{as } |z| \to \infty.$$

This assumption was made to guarantee the existence of a principal eigenpair.

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This assumption may be relaxed to consider bounded growth rates:

$$\exists\, L >> 1,\ \delta > 0, \qquad \text{such that}$$

$$R(z) + \delta \leq R(z_m) - \frac{c^2}{4}, \qquad \text{for all } |z| \geq L.$$

Then, for ε small enough, there exists a principal eigenpair and all the theory above applies (Figueroa Iglesias–M. 2021).

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Then, for ε small enough, there exists a principal eigenpair and all the theory above applies (Figueroa Iglesias–M. 2021).

Question: what happens as c approaches the threshold c_{crit} such that

$$\min R(z) = R(z_m) - \frac{c_{\mathrm{crit}}^2}{4} \ ?$$

Example of non-confining growth rate and **evolutionary tipping points**

$$R(z) = \frac{r}{2}\left(1 + e^{-s(z-z_m)^2}\right).$$

$$R(z_m) = r, \qquad \min_z R(z) = r/2.$$

$$c_{\text{crit}} = \sqrt{2r}.$$

How the moments of the phenotypic distribution behave as $c \to c_{\text{crit}}$?

$$\bar{z} \to -\infty, \quad A \to 0, \quad \frac{3B}{A^2} + \frac{D}{A} \to -\infty, \quad \frac{6B}{A^3} \to -\infty.$$

Example of non-confining growth rate and evolutionary tipping points

As $c \to c_{\mathrm{crit}}$:

$$\begin{cases} N_\varepsilon \to r/2 \\ \mu_\varepsilon \to -\infty \\ v_\varepsilon \to +\infty \\ \psi_\varepsilon \to -\infty \end{cases}$$

With environment change speed $c < c_{\mathrm{crit}}$ positive population size.

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At the speed c_{crit} the phenotypic lag diverges and the population collapses suddenly.

This is called an **evolutionary tipping point**.

(Discussed in Garnier et al. 2022)

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The influence of fluctuating temperature on bacteria

Bacteria 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).

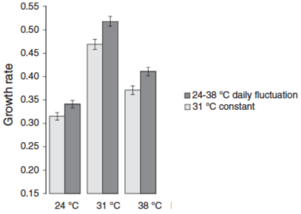

Figure from: Ketola et al. 2013

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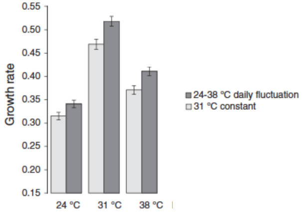

Figure from: Ketola et al. 2013

- What is the impact of an oscillating environment on the phenotypic distribution of a population ?
- Is it possible that evolving in a periodic environment would lead to a more performant population?

A periodic environment

$$\begin{cases} \frac{\partial}{\partial t} n - \underbrace{\sigma \frac{\partial^2}{\partial z^2}}_{\text{mutations}} n = n\big(\underbrace{R(e(t), z)}_{\text{growth rate}} - \underbrace{\kappa N}_{\text{competition}} \big), \\ N(t) = \int_{\mathbb{R}} n(t, y)\, dy, \qquad n(t = 0, \cdot) = n_0(\cdot), \qquad z \in \mathbb{R}. \end{cases}$$

$$e : \mathbb{R}^+ \to \mathbb{R}, \qquad T\text{-periodic.}$$

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Example:

$$R(e,z) = \underbrace{r(e)}_{\text{maximal growth rate}} - \underbrace{s(e)}_{\text{selection pressure}}\big(z - \underbrace{\theta(e)}_{\text{optimal trait}}\big)^2$$

Assumptions

- R is smooth and bounded from above
- R takes small values for large z.

  Notation:
  $$\overline{R}(z) = \frac{1}{T}\int_0^T R(e(t), z)dt.$$
- There exists a unique $z_m \in \mathbb{R}$ such that
  $$\max_{z\in\mathbb{R}} \overline{R}(z) = \overline{R}(z_m) > 0.$$

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An eigenvalue problem

There exists a unique pair $(\lambda_\sigma, p_\sigma)$:

$$\begin{cases} \frac{\partial}{\partial t} p_\sigma(t,z) - \sigma \frac{\partial^2}{\partial z^2} p_\sigma(t,z) - R(e(t),z) p_\sigma(t,z) = \lambda_\sigma p_\sigma(t,z), \\ p_\sigma(t,z) = p_\sigma(t+T,z), \;\; p_\sigma > 0, \quad . \end{cases}$$

$(\lambda_\sigma, p_\sigma)$: the principal eigenpair.

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- If $R(z) \to -\infty$ as $|z| \to +\infty$, the operator is with compact resolvent and one can apply the Krein-Rutman theorem.

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$(\lambda_\sigma, p_\sigma)$: the principal eigenpair.

- If $R(z) \to -\infty$ as $|z| \to +\infty$, the operator is with compact resolvent and one can apply the Krein-Rutman theorem.
- One can relax this assumption as before to consider finite growth rates.

The long time behavior

Proposition (Figueroa Iglesias and M. 2018)

(i) If $\lambda_\sigma \geq 0$*:* $N(t) \to 0$ *as* $t \to \infty$.

(ii) If $\lambda_\sigma < 0$*:* $n(t,\cdot)$ *converges to the unique positive solution to*

$$\begin{cases} \frac{\partial}{\partial t} n_{p,\sigma} - \sigma \frac{\partial^2}{\partial z^2} n_{p,\sigma} = n_{p,\sigma}\big(R(e,z) - \kappa N_{p,\sigma}\big), \\ N_{p,\sigma}(t) = \int_{\mathbb{R}} n_{p,\sigma}(t,y)\,dy, \qquad n_{p,\sigma}(t+T,z) = n_{p,\sigma}(t,z). \end{cases}$$

Main elements

$$Q_\sigma(t) = \frac{\int_{\mathbb{R}^d} R(e(t), z) p_\sigma(t, z) dz}{\int_{\mathbb{R}^d} p_\sigma(t, z) dz}, \quad P_\sigma(t, z) = \frac{p_\sigma(t, z)}{\int_{\mathbb{R}^d} p_\sigma(t, y) dy}.$$

(i) $$\left\| \frac{n(t, x)}{N(t)} - P(t, x) \right\|_{L^\infty} \longrightarrow 0, \text{ as } t \to \infty \ .$$

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(ii) If $\lambda_\sigma \geq 0$, $N(t) \to 0$, as $t \to \infty$.

(iii) If $\lambda_\sigma < 0$, $|N(t) - N_{p,\sigma}(t)| \to 0$, with $N_{p,\sigma}$ the unique solution to

$$\begin{cases} N'_{p,\sigma}(t) = N_{p,\sigma}(t) \left[Q_\sigma(t) - \kappa N_{p,\sigma}(t) \right], & t \in (0, T), \\ N_{p,\sigma}(0) = N_{p,\sigma}(T). \end{cases}$$

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How to characterize the periodic solution $n_{p,\sigma}$?

Assumption: mutations with small effects

$$\sigma = \varepsilon^2, \qquad \varepsilon << 1.$$

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Assumption: mutations with small effects

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Objective: to characterize the solution to

$$\begin{cases} \frac{\partial}{\partial t} n_{p,\varepsilon} - \varepsilon^2 \frac{\partial^2}{\partial z^2} n_{p,\varepsilon} = n_{p,\varepsilon}\big(R(e,z) - \kappa N_{p,\varepsilon}\big), \\ N_{p,\varepsilon}(t) = \int_{\mathbb{R}} n_{p,\varepsilon}(t,y)\,dy, \qquad n_{p,\varepsilon}(t+T,z) = n_{p,\varepsilon}(t,z). \end{cases}$$

Asymptotic behavior of the population density

Let $N_p(t)$ be the unique solution to

$$\begin{cases} N_p'(t) = N_p(t)\left[R(e(t), z_m) - \kappa N_p(t)\right], \quad t \in (0, T), \\ N_p(0) = N_p(T). \end{cases}$$

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Theorem (Figueroa Iglesias and M. 2018)

As $\varepsilon \to 0$,

$$\|N_{p,\varepsilon}(t) - N_p(t)\|_{L^\infty} \to 0,$$

and

$$n_{p,\varepsilon}(t,z) - N_p(t)\delta(z - z_m) \rightharpoonup 0,$$

weakly in the sense of measures.

Main ingredients

Hopf-Cole transformation:

$$n_{p,\varepsilon}(t,z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{p,\varepsilon}(t,z)}{\varepsilon}\right).$$

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Replacing the Hopf-Cole transformation in the equation on $n_{p,\varepsilon}$:

$$\frac{1}{\varepsilon}\partial_t u_{p,\varepsilon} - \varepsilon \partial_{zz} u_{p,\varepsilon} = |\partial_z u_{p,\varepsilon}|^2 + R(e(t),z) - \kappa N_{p,\varepsilon}(t).$$

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Expected asymptotic expansions, with T-periodic coefficients:

$$u_{p,\varepsilon}(t,z) = u(t,z) + \varepsilon v(t,z) + o(\varepsilon), \quad N_{p,\varepsilon}(t) = N(t) + \varepsilon K(t) + o(\varepsilon).$$

Heuristic computations

Substituting the expansions into the equation and regrouping by powers of ε:
Terms of order ε^{-1}:

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Terms of order ε^0:

$$\partial_t v(t,z) = |\partial_z u|^2 + R(e(t),z) - \kappa N(t).$$

Computing the time average of the equation in $[0, T]$:

$$0 = |\partial_z u|^2 + \overline{R}(z) - \kappa \overline{N}.$$

Asymptotic behavior of u

Let

$$\overline{N} = \frac{1}{T}\int_0^T N_p(s)ds.$$

Proposition

(i) $u_{p,\varepsilon}(t,z)$ *converges locally uniformly to* $u(z)$ *the unique viscosity solution to*

$$\begin{cases} -\left|\frac{\partial}{\partial z}u(z)\right|^2 = \overline{R}(z) - \kappa\overline{N}, \\ \max u(z) = 0. \end{cases} \qquad \text{(HJ)}$$

(ii) Moreover, $\frac{n_{p,\varepsilon}}{N_{p,\varepsilon}}$ *converges in the sense of measures to* f_p*, with* f_p *such that*

$$\mathrm{supp}\ f_p(t,\cdot) \subset \{u(z) = 0\}.$$

Uniqueness and identification of u

Proposition (Figueroa Iglesias, M. 2018)

The viscosity solution of (HJ) *is unique and it is indeed a classical solution given by*

$$u(z) = -\left| \int_{z_m}^{z} \sqrt{R(z_m) - R(y)}dy \right|.$$

Recall: z_m the maximum point of R

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Remark: z_m the unique maximum point of $u \Rightarrow \mathrm{supp}\, n = \{z_m\}$.

Going to the next order approximation of u_ε

We expect that

$$u_\varepsilon(z) = u(z) + \varepsilon v(z) + o(\varepsilon),$$

which leads to a more precise approximation of the phenotypic density for nonzero ε

$$n_\varepsilon \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u(z) + \varepsilon v(z) + o(1)}{\varepsilon}\right).$$

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Moments of the phenotypic distribution

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

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Variance of the phenotypic distribution:

$$v_{p,\varepsilon}(t) = \frac{1}{N_{p,\varepsilon}}\int_{\mathbb{R}}(z-\mu_{p,\varepsilon})^2 n_{p,\varepsilon}(t,z)dz$$

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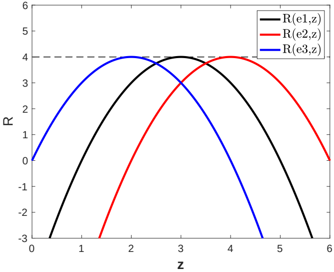
$$v_{p,\varepsilon}(t) = \frac{1}{N_{p,\varepsilon}}\int_{\mathbb{R}}(z-\mu_{p,\varepsilon})^2 n_{p,\varepsilon}(t,z)dz$$

Mean fitness in an environment with constant state $\overline{e}$:

$$F_{p,\varepsilon}(\overline{e}) = \int_{\mathbb{R}} R(\overline{e},z)\frac{1}{T}\int_0^T \frac{n_{p,\varepsilon}(t,z)}{N_{p,\varepsilon}(t)}dtdz$$

Biological case study 1: Fluctuating optimal trait

$$R(e,z) = r_{\max} - s(z-\theta(e))^2, \quad \theta(e) = e, \quad e(t)\text{: periodic},$$
$$\kappa = 1.$$



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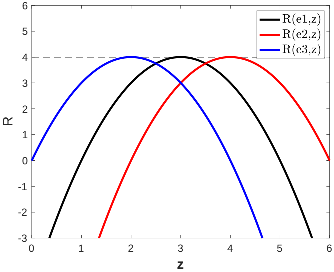

Define

$$\bar{\theta} = \frac{1}{T}\int_0^T \theta(e(s))ds, \qquad V_\theta = \frac{1}{T}\Big(\int_0^T \theta^2(e(t))dt - \bar{\theta}^2\Big).$$

The effect of a fluctuating optimal trait

$$\overline{N}_{p,\varepsilon} = r_{\max} - \underbrace{sV_\theta}_{\text{load due to fluctuations}} - \underbrace{\varepsilon\sqrt{s}}_{\text{mutation load}} + o(\varepsilon),$$

The fluctuations of the optimal trait reduce the population size.

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The fluctuations of the optimal trait reduce the population size.
Next order moments:

$$\mu_{p,\varepsilon}(t) = \bar{\theta} + \varepsilon D(t) + o(\varepsilon), \qquad v_{p,\varepsilon}(t) = \frac{\varepsilon}{\sqrt{s}} + o(\varepsilon^2),$$

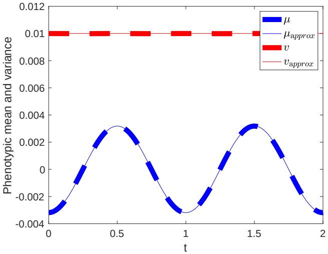
D: periodic and of average 0

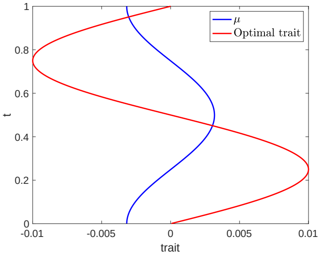
Example: Let $e(t) = d\sin\left(2\pi t/b\right)$, then

$$\mu_{p,\varepsilon}(t) = \frac{\varepsilon d b\sqrt{s}}{\pi}\sin\left(\frac{2\pi}{b}(t - b/4)\right) + o(\varepsilon).$$

The mean phenotypic trait follows the oscillations of the optimal trait with a delay and a small amplitude

$$R(e,x) = 2 - (x - \theta(e))^2, \qquad \theta(e) = e, \qquad e(t) = \sin(2\pi t), \quad \varepsilon = 0.01.$$





Left: comparison between the **analytical** and the **numerical** approximations of the moments of the phenotypic density.

Right: comparison between the mean phenotypic trait and the (rescaled) optimal trait.

The effect of a fluctuating optimal trait on the mean fitness

Mean fitness of the population when placed at environment $\bar{e}$:

$$F_{p,\varepsilon}(\bar{e}) = r - \varepsilon\sqrt{s} - \underbrace{\frac{s}{T}\int_0^T (\mu_{p,\varepsilon}(t) - \theta(\bar{e}))^2 dt}_{\text{load due to maldaptation}} + o(\varepsilon).$$

Recall: mean fitness of a population evolved in the constant environment $\bar{e}$:

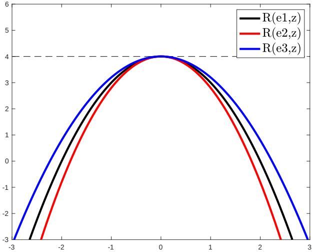
$$F_{0,\varepsilon}(\bar{e}) = r - \varepsilon\sqrt{s} + o(\varepsilon).$$

The fluctuations of the optimal trait are not beneficial for the mean fitness of the population.

Biological case study 2: Fluctuating selection pressure

$$R(e,z) = r_{\max} - s(e)z^2 + O(z^4), \quad s(e) = e, \quad e(t) > 0: \text{ periodic},$$

$$\kappa = 1.$$



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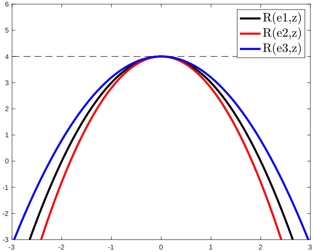

Define

$$\bar{s} = \frac{1}{T}\int_0^T s\big(e(\tau)\big)\,d\tau.$$

The effect of a fluctuating selection pressure

The size of a population evolved in the changing environment :

$$\overline{N}_{p,\varepsilon} = r_{\max} - \underbrace{\varepsilon\sqrt{\overline{s}}}_{\text{mutation load}} + o(e).$$

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$$\overline{N}_{0,\varepsilon} = r_{\max} - \underbrace{\varepsilon\sqrt{s(e)}}_{\text{mutation load}} + o(e).$$

Depending on whether $\overline{s} < s(\bar{e})$ or $\overline{s} > s(\bar{e})$, the fluctuations of the selection pressure may increase or decrease the population size.

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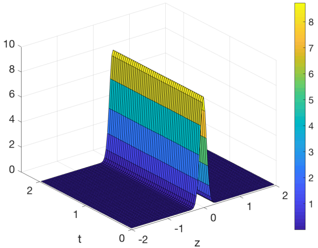
Next order moments:

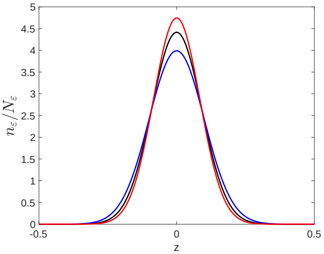
$$\mu_{p,\varepsilon}(t) = o(\varepsilon), \qquad v_{p,\varepsilon}(t) = \frac{\varepsilon}{\sqrt{\overline{s}}} + o(\varepsilon).$$

The fluctuations of the selection pressure may increase or decrease the phenotypic variance

$$R(e,z) = 2 - s(e)z^2, \qquad s(e) = e, \quad \varepsilon = 0.01.$$



Dynamics of the phenotypic density over 2 periods of e.
$e(t) = 1.5 + \cos(2\pi t)$



Black curve: constant env. $s = 1.5$
Blue curve: periodic env. $\bar{s} = 1$
Red curve: periodic env. $\bar{s} = 2$

The effect of a fluctuating selection pressure on the mean fitness ($\widetilde{c} = 0$)

Mean fitness of the population when placed at environment $\bar{e}$:

$$F_{p,\varepsilon}(\bar{e}) = r - \varepsilon \frac{s(\bar{e})}{\sqrt{\bar{s}}} + o(\varepsilon).$$

Mean fitness of a population evolved in the constant environment $\bar{e}$:

$$F_{\varepsilon,0}(\bar{e}) = r - \varepsilon \sqrt{s(\bar{e})} + o(\varepsilon).$$

Depending on whether $\overline{s} > s(\bar{e})$ or $\overline{s} < s(\bar{e})$, the fluctuations of the selection pressure may increase or decrease the mean fitness of the population

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Earth's temperature changes (increase and oscillations)

How the oscillations of an environment impact the adaptation to a gradual change?

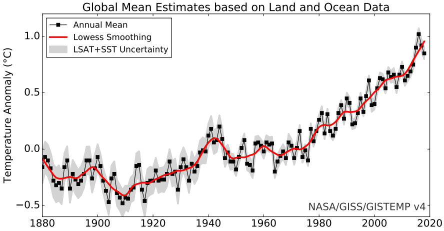

Figure from: data.giss.nasa.gov

A shifting and oscillating environment

$$\begin{cases} \frac{\partial}{\partial t}n - \underbrace{\sigma\frac{\partial^2}{\partial z^2}n}_{\text{mutations}} = n\Big(\underbrace{R(e(t), z - ct)}_{\text{growth rate}} - \underbrace{\kappa N}_{\text{competition}}\Big), \\ N(t) = \int_{\mathbb{R}} n(t,y)\,dy, \qquad n(t=0,\cdot) = n_0(\cdot), \qquad z \in \mathbb{R}. \end{cases}$$

$$e : \mathbb{R}^+ \to \mathbb{R}, \qquad T\text{-periodic.}$$

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Example: $R(e,z) = r(e) - s(e)(z - \theta(e))^2$.

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Density in the moving framework: $n(t,z) = m(t, z+ct)$:

$$\begin{cases} \frac{\partial}{\partial t} m - c\frac{\partial}{\partial z} m - \sigma \frac{\partial^2}{\partial z^2} m = m\big(R(e(t), z) - \kappa M\big), \\ M(t) = \int_{\mathbb{R}} m(t,y)\, dy. \end{cases}$$

Assumptions

- R is smooth and bounded from above
- R takes small values for large z.

Notation:

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

- There exists a unique $z_m \in \mathbb{R}$ such that

$$\max_{z\in\mathbb{R}} \overline{R}(z) = \overline{R}(z_m) > 0.$$

- There exists a unique $\overline{z} < z_m$ such that

$$\overline{R}(\overline{z}) + \frac{c^2}{4\sigma^2} = \overline{R}(z_m).$$

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An eigenvalue problem

$$\begin{cases} \frac{\partial}{\partial t} p_{\sigma,c} - c\frac{\partial}{\partial z} p_{\sigma,c} - \sigma\frac{\partial^2}{\partial z^2} p_{\sigma,c} - R(e(t),z)p_{\sigma,c} = \lambda^{p}_{\sigma,c} p_{\sigma,c}, \\ p_{\sigma,c} > 0, \qquad p_{\sigma,z}(t+T,z) = p_{\sigma,z}(t,z). \end{cases}$$

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Equivalence between the eigenpairs of this operator with the one with no drift term:

Liouville transformation:

$$q(z) = p_{\sigma,c}(z)e^{\frac{c}{2\sigma}z}.$$

$$\frac{\partial}{\partial t} q - \sigma\frac{\partial^2}{\partial z^2} q - R(e(t),z)q = q\Big(-\frac{c^2}{4\sigma} + \lambda^p_{\sigma,c}\Big),$$

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$$\lambda^p_{\sigma,c} = \lambda^p_{\sigma,0} + \frac{c^2}{4\sigma}.$$

Critical speed for survival

Define the critical speed :

$$c_\sigma = \begin{cases} 2\sqrt{-\sigma \lambda^p_{\sigma,0}}, & \text{if } \lambda^p_{\sigma,0} < 0 \\ 0, & \text{otherwise.} \end{cases}$$

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Proposition (Figueroa Iglesias and M. 2021)

(i) $c \geq c_\sigma$: $N(t) \to 0$ *as* $t \to \infty$.

(ii) $c < c_\sigma$: $n(t,\cdot)$ *converges to the unique positive solution to*

$$\begin{cases} \frac{\partial}{\partial t} n_{p,\sigma} - c\frac{\partial}{\partial z} n_{p,\sigma} - \sigma\frac{\partial^2}{\partial z^2} n_{p,\sigma} = n_{p,\sigma}\big(R(e,z) - \kappa N_{p,\sigma}\big), \\ N_{p,\sigma}(t) = \int_{\mathbb{R}} n_{p,\sigma}(t,y)\,dy, \qquad n_{p,\sigma}(t+T,z) = n_{p,\sigma}(t,z). \end{cases}$$

Main elements

$$Q(t) = \frac{\int_{\mathbb{R}^d} R(e(t), z) p_{\sigma,c}(t,z) dz}{\int_{\mathbb{R}^d} p(t,z) dz}, \quad P_{\sigma,c}(t,z) = \frac{p_{\sigma,c}(t,z)}{\int_{\mathbb{R}^d} p_{\sigma,c}(t,y) dy}.$$

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(iii) If $\lambda_\sigma < 0$, $|N(t) - N_{p,\sigma}(t)| \to 0$, with $N_{p,\sigma}$ the unique solution to

$$\begin{cases} N'_{p,\sigma}(t) = N_{p,\sigma}(t)\left[Q(t) - \kappa N_{p,\sigma}(t)\right], & t \in (0,T), \\ N_{p,\sigma}(0) = N_{p,\sigma}(T). \end{cases}$$

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How to characterize the periodic solution $n_{p,\sigma}$?

Assumption: mutations with small effects

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$\Rightarrow$ adaptation only to environments that vary slowly
We rescale the problem ($c \to \varepsilon c$, $c_\varepsilon \to \varepsilon c_\varepsilon$):

$$\begin{cases} \frac{\partial}{\partial t} n_{p,\varepsilon} - \varepsilon c \frac{\partial}{\partial z} n_{p,\varepsilon} - \varepsilon^2 \frac{\partial^2}{\partial z^2} n_{p,\varepsilon} = n_{p,\varepsilon}\big(R(e,z) - \kappa N_{p,\varepsilon}\big), \\ N_{p,\varepsilon}(t) = \int_{\mathbb{R}} n_{p,\varepsilon}(t,y)\, dy, \qquad n_{p,\varepsilon}(t+T,z) = n_{p,\varepsilon}(t,z). \end{cases}$$

Asymptotic behavior of the population density

Let $N_p(t)$ be the unique solution to

$$\begin{cases} N_p'(t) = N_p(t)\left[R(e(t), \overline{z}) - N_p(t)\right], \quad t \in (0, T), \\ N_p(0) = N_p(T). \end{cases}$$

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Theorem (Figueroa Iglesias and M. 2021)

As $\varepsilon \to 0$,

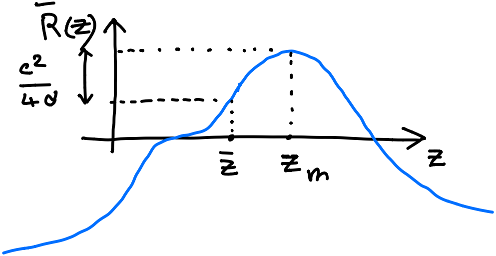
$$\|N_{p,\varepsilon}(t) - N_p(t)\|_{L^\infty} \to 0,$$

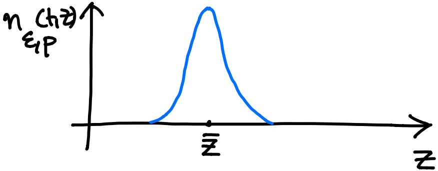
and

$$n_{p,\varepsilon}(t,z) - N_p(t)\delta(z-\overline{z}) \rightharpoonup 0,$$

weakly in the sense of measures.

Recall: $\overline{z}$ the unique point such that $\overline{R}(\overline{z}) + \frac{c^2}{4\varepsilon^2} = \overline{R}(z_m)$ and $\overline{z} < z_m$.





Main ingredients

Hopf-Cole transformation:

$$n_{p,\varepsilon}(t,z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{p,\varepsilon}(t,z)}{\varepsilon}\right).$$

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Replacing the Hopf-Cole transformation in the equation on $n_{p,\varepsilon}$:

$$\frac{1}{\varepsilon}\partial_t u_{p,\varepsilon} - c\partial_z u_{p,\varepsilon} - \varepsilon\partial_{zz} u_{p,\varepsilon} = |\partial_z u_{p,\varepsilon}|^2 + R(e(t),z) - \kappa N_{p,\varepsilon}(t).$$

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Expected asymptotic expansions, with T-periodic coefficients:

$$u_{p,\varepsilon}(t,z) = u(t,z) + \varepsilon v(t,z) + o(\varepsilon), \quad N_{p,\varepsilon}(t) = N_p(t) + \varepsilon K(t) + o(\varepsilon).$$

Heuristic computations

Substituting the expansions into the equation and regrouping by powers of ε:

Terms of order ε^{-1}:

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$$\partial_t u(t,z) = 0, \qquad u(t,z) = u(z).$$

Terms of order ε^0:

$$\partial_t v(t,z) - \left|\partial_z u + \frac{c}{2}\right|^2 = R(e(t),z) - \frac{c^2}{4} - \kappa N_p(t).$$

Computing the time average of the equation in $[0, T]$:

$$-\left|\partial_z u + \frac{c}{2}\right|^2 = \overline{R}(z) - \frac{c^2}{4} - \kappa \overline{N},$$

with $\overline{N} = \frac{1}{T}\int_0^T N_p(t)dt$.

Asymptotic behavior of u_ε

Let

$$\overline{N} = \frac{1}{T}\int_0^T N_p(s)ds.$$

Proposition (Figueroa Iglesias, M. 2021)

(i) $u_{p,\varepsilon}(t,z)$ *converges locally uniformly to* $u(z)$ *the unique viscosity solution to*

$$\begin{cases} -\left|\frac{\partial}{\partial z}u(z)\right|^2 = \overline{R}(z) - \kappa\overline{N}, \\ \max u(z) = 0. \end{cases} \qquad \text{(HJ)}$$

(ii) Moreover, $\frac{n_{p,\varepsilon}}{N_{p,\varepsilon}}$ *converges in the sense of measures to* f_p*, with* f_p *such that*

$$\mathrm{supp}\ f_p(t,\cdot) \subset \{u(z) = 0\}.$$

Uniqueness and identification of u

Proposition (Figueroa Iglesias, M. 2021)

The viscosity solution of (HJ) *is unique and it is indeed a classical solution given by*

$$u(z) = \frac{c}{2}(\overline{z} - z) + \int_{\overline{z}}^{z_m} \sqrt{\overline{R}(z_m) - \overline{R}(y)}dy - \left| \int_{z_m}^{z} \sqrt{\overline{R}(z_m) - \overline{R}(y)}dy \right| .$$

Recall: z_m the maximum point of R and $\overline{z}$ the unique point such that $R(\overline{z}) + \frac{c^2}{4} = R(z_m)$ and $\overline{z} < z_m$.

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Recall: z_m the maximum point of R and $\overline{z}$ the unique point such that $R(\overline{z}) + \frac{c^2}{4} = R(z_m)$ and $\overline{z} < z_m$.

Remark: $\max_z u(z) = u(\overline{z}) = 0 \Rightarrow \mathrm{supp}\, n = \{\overline{z}\}$.

More precise approximation of the average population size and the survival threshold

Note that

$$\overline{N}_{p,\varepsilon} := \frac{1}{T}\int_0^T N_{p,\varepsilon}(t)dt = \frac{1}{T}\int_0^T Q(t)dt = -\lambda_{c,\varepsilon}/\kappa.$$

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Theorem (Figueroa Iglesias–M., 2021)

$$\overline{N}_{p,\varepsilon} = -\lambda_{c,\varepsilon}/\kappa = \big(\overline{R}(z_m) - \frac{c^2}{4}\big)/\kappa - \varepsilon\frac{\sqrt{-\overline{R}''(z_m)/2}}{\kappa} + o(\varepsilon),$$

$$c_\varepsilon = 2\sqrt{\overline{R}(\overline{z}_m)} - \varepsilon\sqrt{-\frac{\overline{R}''(z_m)}{2\,\overline{R}(\overline{z}_m)}} + o(\varepsilon).$$

Going to the next order approximation of u_ε

We expect that

$$u_\varepsilon(z) = u(z) + \varepsilon v(z) + o(\varepsilon),$$

which leads to a more precise approximation of the phenotypic density for nonzero ε

$$n_{p,\varepsilon} \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u(z) + \varepsilon v(z) + o(1)}{\varepsilon}\right).$$

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Moments of the phenotypic distribution

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

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Mean phenotypic trait:

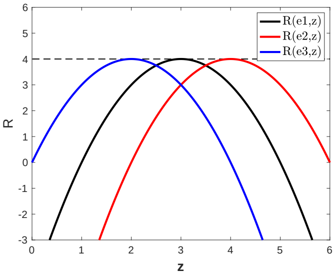
$$\mu_{p,\varepsilon}(t) = \frac{1}{N_{p,\varepsilon}(t)}\int_{\mathbb{R}} z\ n_{p,\varepsilon}(t,z)dz, \quad \overline{\mu}_{p,\varepsilon} = \frac{1}{T}\int_0^T \mu_{p,\varepsilon}(t)dt.$$

Variance of the phenotypic distribution:

$$v_{p,\varepsilon}(t) = \frac{1}{N_{p,\varepsilon}}\int_{\mathbb{R}}(z-\mu_{p,\varepsilon})^2 n_{p,\varepsilon}(t,z)dz$$

Biological case study 1: Fluctuating optimal trait

$$R(e,z) = r_{\max} - s(z-\theta(e))^2, \quad \theta(e) = e, \quad e(t)\text{: periodic},$$
$$\kappa = 1.$$



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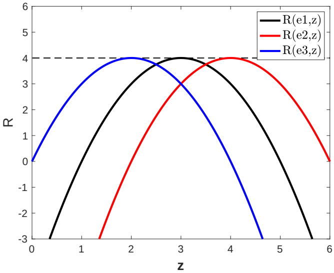

Define

$$\bar{\theta} = \frac{1}{T}\int_0^T \theta(e(s))ds, \qquad V_\theta = \frac{1}{T}\Big(\int_0^T \theta^2(e(t))dt - \bar{\theta}^2\Big).$$

The effect of a fluctuating optimal trait on the ability of the population to follow a gradual change

$$\overline{N}_{\varepsilon,p} = r_{\max} - \underbrace{sV_\theta}_{\substack{\text{load due to}\\ \text{fluctuations}}} - \underbrace{c^2/4}_{\substack{\text{load due to}\\ \text{environmental shift}}} - \underbrace{\varepsilon\sqrt{s}}_{\text{mutation load}} + o(\varepsilon),$$

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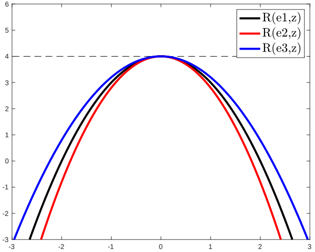
The critical speed of linear change decreases with $V_\theta \Rightarrow$
The fluctuations on the optimal trait are disadvantageous for the population's ability to follow the environmental shift.

Biological case study 2: Fluctuating selection pressure

$$R(e,z) = r_{\max} - s(e)z^2 + O(z^4), \quad s(e) = e, \quad e(t) > 0\text{: periodic},$$
$$\kappa = 1.$$



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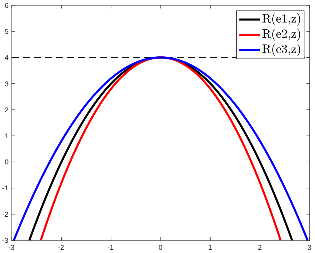

Define

$$\overline{s} = \frac{1}{T}\int_0^T s\big(e(\tau)\big)\,d\tau.$$

The effect of a fluctuating selection pressure on the ability of the population to follow a gradual change

$$\overline{N}_{p,\varepsilon} = r_{\max} - \underbrace{c^2/(4\varepsilon^2)}_{\substack{\text{load due to}\\ \text{environmental shift}}} - \underbrace{\varepsilon\sqrt{\overline{s}}}_{\text{mutation load}} + o(\varepsilon),$$

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Depending on whether $\overline{s} < s(\bar{e})$ or $\overline{s} > s(\bar{e})$, the fluctuations of the selection pressure may be beneficial or non-beneficial for the population's ability to follow the environmental shift.

Table of contents

A piecewise constant environment

Let's consider a periodic environment with two states e_1 and e_2:

$$e(t) = \begin{cases} e_1, & \text{for } t \bmod T \in [0, aT), \\ e_2, & \text{for } t \bmod T \in [aT, T). \end{cases}$$

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The dynamics of the population density:

$$\begin{cases} \frac{\partial}{\partial t} n - \sigma \Delta n = n\big(R(e(t), z) - \kappa N\big), \\ N(t) = \int_{\mathbb{R}} n(t, z) dz, \\ n(0, z) = n_0(z). \end{cases}$$

The outcome with the previous scaling

In the previous scalings, $\sigma = \varepsilon^2 << 1$ and $T = O(1)$.
$\Rightarrow$ the population does not have time to adapt to each environment; we observe only **adaptation to an average environment** with growth rate

$$\overline{R}(z) = aR(e_1, z) + (1-a)R(e_2, z).$$

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As $\varepsilon \to 0$,

$$n_{\varepsilon,p}(t,z) \rightharpoonup N_p(t)\,\delta(z - z_m), \quad \mu_{\varepsilon,p}(t) = z_m + O(\varepsilon).$$

with z_m such that

$$\max_z \overline{R}(z) = \overline{R}(z_m).$$

Considering small mutation steps (ε) but large period (T) for time variations

Let's now assume that $T = \frac{\widetilde{T}}{\varepsilon}$ (**the environment varies slowly**). In this case, the population has the time to adapt to a state of environment before the switch to another state.

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Initial condition: $\widetilde{n}_\varepsilon(0, z) = \widetilde{n}_{\varepsilon,0}(z) = \exp(\frac{u_{\varepsilon,0}(z)}{\varepsilon})$.

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Letting $\varepsilon \to 0$:

$$\frac{\partial}{\partial t}u = |\nabla u|^2 + R(e(t,z)) - \kappa N(t).$$

The asymptotic behavior of u_ε

If $N(t) > 0$, then

$$\max_z u(t,z) = 0.$$

(u, N) determined by:

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Etchegaray, Costa, M. 2021: fine analysis to determine precise conditions of survival.

The concave framework

Assume that $R(\widetilde{e}, \cdot)$ and $u_{\varepsilon,0}(\cdot)$ are strictly concave.
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Moreover, the solution is smooth and one can derive a canonical equation describing the dynamics of the dominant trait:

$$\dot{\overline{z}}(t)=(-D^2u(t,\overline{z}(t))^{-1}\nabla R(\widetilde{e}(t),\overline{z}(t)).$$

(Lorz, M., Perthame 2011)

The asymptotic behavior of the phenotypic density

Assume that $R(\widetilde{e},\cdot)$ and $u_{\varepsilon,0}(\cdot)$ are strictly concave.

Theorem (Costa, Etchegaray and M., 2021)

(i) As long as the population persists, as $\varepsilon \to 0$,

$$\widetilde{n}_\varepsilon(t,z) \longrightarrow \widetilde{\rho}(t)\,\delta(z-\overline{z}(t)), \quad \textit{with} \quad \dot{\overline{z}}(t)\cdot\nabla R(\widetilde{e}(t),\overline{z}(t)) \geq 0.$$

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which means that the dominant trait follows the gradient of the environment.

(i) Let's suppose that the environment switches from state e_1 to state e_2 at time t_0. Then, the **population goes extinct***, asymptotically as $\varepsilon \to 0$,* **if**

$$R(e_2, \overline{z}(t_0)) \leq 0.$$

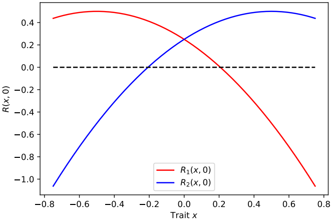
Otherwise, the population persists until the next switch.

An example with two different behaviors depending on the scales

$$R(e_1, z) = r - s(z+\theta)^2, \qquad R(e_2, z) = r - s(z-\theta)^2,$$

with

$$r = .5, \quad s = 1, \quad \theta = .5, \quad a = .5, \quad \varepsilon = .001.$$



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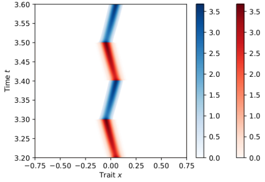
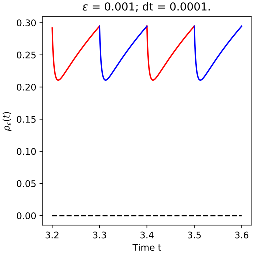
$T = O(1/\varepsilon)$ (period$= \frac{\widetilde{T}}{\varepsilon}$): **for $\widetilde{T}$ small, the population persists**, and the dominant trait $\overline{z}(t)$ moves successively to the left and to the right. Here : $\widetilde{T} = .2$:



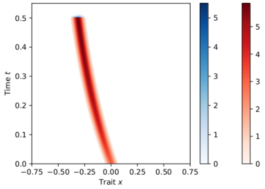
Phenotypic density



Total size of the population

An example with two different behaviors depending on the scales

For $\widetilde{T}$ large, when the environment switches to state e_2, the population is well adapted to the first environment but maladapted to the second one. As a consequence it **goes extinct** asymptotically (as $\varepsilon \to 0$). Here: $\widetilde{T} = 1$.



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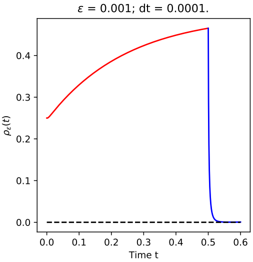

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Thank you for your attention !