Selection and mutation in a shifting and fluctuating environment

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Joint work with Susely Figueroa Iglesias (IMT)

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Motivating example 1:
The influence of fluctuating temperature on bacteria

Bacteria 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):

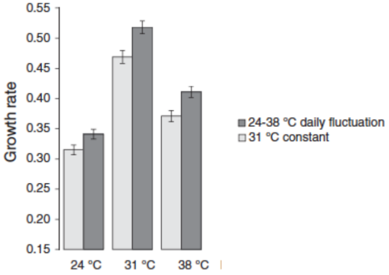

Figure from: Ketola et al. 2013

Motivating example 2:
Earth's temperature changes (increase and oscillations)

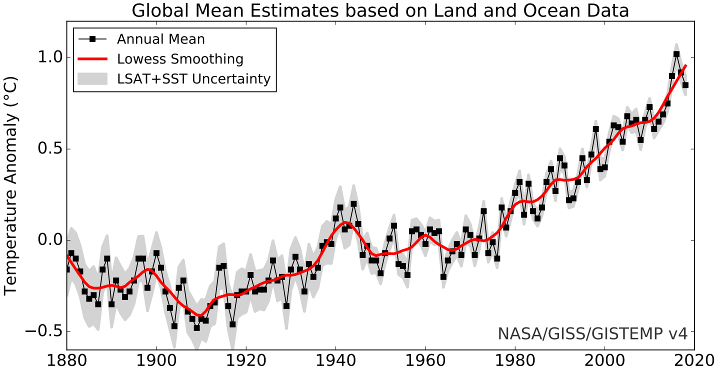

Figure from: data.giss.nasa.gov

Selection-mutation in a shifting and fluctuating environment

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

- z: phenotypic trait
- $m(t,z)$: density of trait z
- σ: mutation effective size
- $e(t)$: environment state
- $R(e,z)$: growth rate
- c: speed of the linear change
- $M(t)$: size of the population
- κ: intensity of the competition

A change of notation and questions

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

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

Objective: to characterize the phenotypic density n.

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Questions:

- Critical speed of environment change above which the population gets extinct?
- Impact of the oscillations on the critical speed and the phenotypic distribution?
- In which situation, a population evolved in a periodic environment (without linear change) would outperform a population evolved in a constant environment?

Some references

- **Time-varying environments**:

Lynch et al (1991), Lynch and Lande (1993), Burger and Lynch (1995), Lande and Shannon (1996)
(assumptions: quadratic stabilizing selection, Gaussian phenotypic distribution, the environment change acts only on the optimum)

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- The **Hamilton-Jacobi approach**:
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◦ More quantitative results:
M.–Roquejoffre (2015-2016), M.–Gandon (2017-2019)

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Assumptions

Notation:

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

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Assumptions:

- e T-periodic with respect to t
- There exists a unique $z_m \in \mathbb{R}^d$ such that

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

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

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

Critical speed for survival

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

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

Critical speed for survival

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Proposition (Figueroa Iglesias and M., SIMA 2018, Preprint 2019)

(i) $c \geq c_\sigma$*:* $N(t) \to 0$ *as* $t \to \infty$.
(ii) $c < c_\sigma$*:* $n(t,\cdot)$ *converges to a the unique positive solution to*

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

An asymptotic expansion for the critical speed

Regime of small mutations:

$$\sigma = \varepsilon^2.$$

Theorem (Figueroa Iglesias and M., Preprint 2019)

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

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Define the renormalized speeds

$$c = \widetilde{c}\,\varepsilon, \qquad c_\varepsilon = \widetilde{c}_\varepsilon\,\varepsilon.$$

Objective: to characterize the phenotypic density $n_{\varepsilon,p}$ when $\widetilde{c} < \widetilde{c}_\varepsilon$:

$$\begin{cases} \frac{\partial}{\partial t} n_{\varepsilon,p} - \varepsilon\widetilde{c}\frac{\partial}{\partial z} n_{\varepsilon,p} - \varepsilon^2\frac{\partial^2}{\partial z^2} n_{\varepsilon,p} = n_{\varepsilon,p}[R(e(t),z) - \kappa N_{\varepsilon,p}(t)], \\ N_{\varepsilon,p}(t) = \int_{\mathbb{R}} n_{\varepsilon,p}(t,y)dy, \quad n_{\varepsilon,p}(0,z) = n_{\varepsilon,p}(T,z). \end{cases}$$

The Hamilton-Jacobi approach

The **Hopf-Cole** transformation:

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

An expected asymptotic expansion:

$$u_{\varepsilon,p}(t,z) = u + \varepsilon v + O(\varepsilon^2).$$

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Theorem (Figueroa Iglesias and M., SIMA 2018, Preprint 2019)

As $\varepsilon \to 0$, $u_{\varepsilon,p}$ converges to u which is uniquely and explicitly determined. In particular, it solves

$$\begin{cases} -\left|\frac{\partial}{\partial z} u(z) + \frac{\tilde{c}}{2}\right|^2 = \overline{R}(z) - \kappa\overline{N} - \frac{\tilde{c}^2}{4}, \\ \max u(z) = u(\overline{z}) = 0. \end{cases}$$

The population follows the optimum with a constant lag

Theorem (Figueroa Iglesias and M., SIMA 2018, Preprint 2019)

Assume that $\widetilde{c} < \lim_{\varepsilon \to 0} \widetilde{c}_\varepsilon$. *Then, as* $\varepsilon \to 0$,

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

with $N_p(t)$ *the unique periodic solution of*

$$\frac{dN_p}{dt} = N_p\left[R(e,\overline{z}) - N_p\right].$$

In the original problem before the translation

$$m_{\varepsilon,p}(t,x) \rightharpoonup \varrho(t)\delta(z-\overline{z}-ct).$$

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

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A constant environment: Non-Gaussian distribution

$$R(e,z) = R_0(z) = 3 - (z+0.5)^2\left(0.2 + (z-0.5)^2\right), \qquad \varepsilon = 0.1$$

Blue dots:
numerical computation of equilibrium

Black line:
our approximation

Vertical dotted line:
mean phenotypic trait

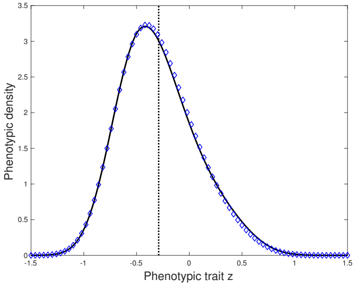

Figure from Mirrahimi–Gandon 2019

Some notations

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

$$\overline{N}_{\varepsilon,p} = \frac{1}{T}\int_0^T N_{\varepsilon,p}(t)dt$$

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Mean phenotypic trait:

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

Variance of the phenotypic distribution:

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

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

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

A constant environment: approximation of the moments

$R(e,z) = R_0(z)$ with a unique maximum at $\theta_{\mathbf{0}}$: **optimal trait**

$$R_0(z) = r - s(z-\theta_0)^2 + a(z-\theta_0)^3 + O(z-\theta_0)^4$$

r: maximal growth rate, **s: selection pressure**,

a: asymmetry parameter

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average population size, mean phenotypic trait and variance:

$$N_{\varepsilon,0} = r - \varepsilon\sqrt{s} + o(\varepsilon), \quad \mu_{\varepsilon,0} = \theta_0 + \frac{a\varepsilon}{s\sqrt{s}} + o(\varepsilon), \quad v_{\varepsilon,0} = \frac{\varepsilon}{\sqrt{s}} + o(\varepsilon),$$

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and the mean fitness in such constant environment:

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

Case 1: Fluctuating optimal trait (no shift $c = 0$)

$$R(e, z) = r - s(z - \theta(e))^2, \quad \theta(e) = e, \quad e(t) = d \sin\left(2\pi t/b\right).$$

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average population size, mean phenotypic trait and variance:

$$\overline{N}_{\varepsilon,p} \approx r - \frac{sd^2}{2} - \varepsilon\sqrt{s}, \quad \mu_{\varepsilon,p}(t) \approx \frac{\varepsilon db\sqrt{s}}{\pi} \sin\left(\frac{2\pi}{b}(t - b/4)\right),$$

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Comparison between the **mean fitness** of this population in an environment with constant state ($\bar{e} = 0$) and the mean fitness of a population evolved in the constant environment $\bar{e} = 0$:

$$F_{\varepsilon,c}(\bar{e}) \approx F_{\varepsilon,p}(\bar{e}) \approx r - \varepsilon\sqrt{s}.$$

Case 2: Fluctuating selection pressure (no shift $c = 0$)

$$R(e,z) = r - s(e)z^2 + O(z^4), \qquad \overline{s} = \frac{1}{T}\int_0^T s\big(e(\tau)\big)\,d\tau.$$

average population size, mean phenotypic trait and variance:

$$\overline{N}_{\varepsilon,p} \approx r - \varepsilon\sqrt{\overline{s}}, \qquad \mu_{\varepsilon,p}(t) \approx 0, \qquad v_{\varepsilon,p}(t) \approx \frac{\varepsilon}{\sqrt{\overline{s}}}.$$

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and the mean fitness in an environment with constant state $\bar{e}$

$$F_{\varepsilon,c}(\bar{e}) = r - \varepsilon\sqrt{s(\bar{e})} < F_{\varepsilon,p}(\bar{e}) \approx r - \varepsilon\frac{s(\bar{e})}{\sqrt{\overline{s}}}, \quad \text{if } \overline{s} > s(\bar{e}).$$

The population evolved in the periodic environment may outperform the population evolved in a constant environment.

Case 3: Fluctuating selection pressure with shift ($c > 0$)

Same growth rate (with varying selection pressure):

Critical speed of survival:

Periodic $s(e)$: $\widetilde{c}_{\varepsilon,p} \approx 2\sqrt{r} - \varepsilon \frac{\sqrt{\overline{s}}}{\sqrt{r}}$

Constant $s = s(\overline{e})$: $\widetilde{c}_{\varepsilon,c} \approx 2\sqrt{r} - \varepsilon \frac{\sqrt{s(\overline{e})}}{\sqrt{r}}$

$$\text{if} \quad \overline{s} < s(\overline{e}) \quad \Rightarrow \quad \widetilde{c}_{\varepsilon,c} < \widetilde{c}_{\varepsilon,p}$$

$\Rightarrow$ oscillations help the population to follow the environment shift

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$\Rightarrow$ oscillations help the population to follow the environment shift

Note: opposite condition to have a more performant population in absence of linear change $\Rightarrow$ what is beneficial in a (in average) constant environment is disadvantageous in a changing environment

Thank you for your attention !