

Adaptation to a gradual change of environment

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Objectives:

- Quantify (*mal*-)adaptation of a population to a changing environment
- Derive analytical formula in the regime of small phenotypical variance
- Influence of both the mode of reproduction (asexual/sexual) and the age structure

Quantitative genetics models

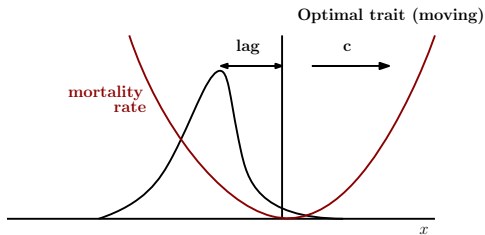
An individual is indexed by its phenotypical trait $x \in \mathbb{R}$

The phenotypical distribution is denoted by $f(t, x)$

Selection acts on mortality (but other options are possible).

The mortality rate is: $\rho(t) + m(x - ct)$, where

- $\rho(t)$ is the size of the population (competition for a single resource): $\rho(t) = \int f(t, x) dx$,
- $m(z)$ is a convex function centered at $z = 0$.



Various modes of reproduction (2 options so far)

Reproduction: (' parental trait)

- Asexual mode:

$$x' \longrightarrow x = x' + \sigma Y, \quad Y \text{ random number (any distribution)}$$

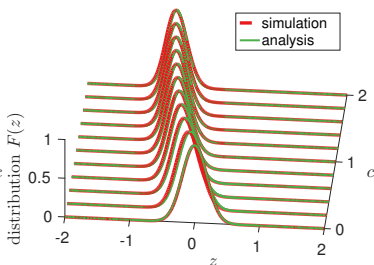
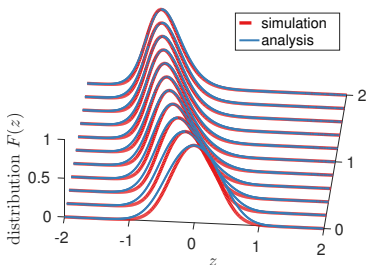
- Sexual mode (Fisher's infinitesimal model):

$$(x'_1, x'_2) \longrightarrow x = \frac{x'_1 + x'_2}{2} + \sigma Y, \quad Y \text{ normally distributed}$$

Aim: Compute the equilibrium distribution F as $\sigma \ll \text{selection unit}$ which is **stationary** in the moving frame:

$$z = x - ct, \quad \partial_t \rightarrow \partial_t - c\partial_z$$

$$\varepsilon = \frac{\sigma}{\text{selection unit}} \ll 1 \quad (*)$$



(*yields **small variance** within the population)

Models: Integro-differential equations

Asexual reproduction

$$-\varepsilon c \partial_z F(z) + (\rho + m(z)) F(z) = \frac{1}{\varepsilon} \int_{\mathbb{R}} K\left(\frac{z - z'}{\varepsilon}\right) F(z') dz'.$$

Sexual reproduction (Fisher's infinitesimal model)

$$-\varepsilon^2 c \partial_z F(z) + (\rho + m(z)) F(z) = \frac{1}{\varepsilon \sqrt{\pi}} \iint_{\mathbb{R}^2} \exp\left(-\frac{1}{\varepsilon^2} \left(z - \frac{z_1 + z_2}{2}\right)^2\right) F(z_1) \frac{F(z_2)}{\int_{\mathbb{R}} F(z'_2) dz'_2} dz_1 dz_2.$$

Equilibrium is the balance between environmental change, mortality (selection) and generation of diversity at birth.

Parameters are : ε , c , $m(z)$, and $K(z)$.

Unknowns are : F and $\rho = \int F$.

Main analytical features

- The limit distributions need not be Gaussian functions
- The analysis is based on the Taylor expansion of

$$U = -(\varepsilon || \varepsilon^2) \log F$$

as $\varepsilon \ll 1$

After Diekmann, Jabin, Mischler and Perthame (2005), Perthame (2007), Barles and Perthame (2008), Lorz, Mirrahimi and Perthame (2011), Bouin and Mirrahimi (2015), Mirrahimi (2016), Mirrahimi and Roquejoffre (2016)... *all in the case of asexual reproduction.*

Equilibrium distribution and growth rate (λ, F)

$$\lambda F(z) = \underbrace{B(F)(z)}_{\text{Reproduction}} - \underbrace{\mu(z)F(z)}_{\text{Selection}}, \quad z \in \mathbb{R}$$

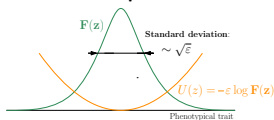
Small variance parameter – ε

$$\varepsilon := \frac{Z_{div}}{Z_{sel}}$$

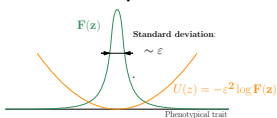
Ratio between genetic scale and selection scale

Distribution transformation – Rescaling U

Asexual Reproduction



Sexual Reproduction



Small variance Limit – $\varepsilon \rightarrow 0$

$$U(z) \approx U_0(z)$$

Global description
Full distribution

$$U(z) \approx U_0(z) + \varepsilon^2 U_1(z)$$

Macroscopic properties

λ = Malthusian growth rate
 z_0^* = dominant trait
 $\text{Var}(F)$ = phenotypical variance.

Methodology

The easy computation is on the left hand side:

$$\frac{-\varepsilon c \partial_z F(z) + (\rho + m(z)) F(z)}{F(z)} = c \partial_z U(z) + \rho + m(z)$$

The not-so-easy computation is on the right hand side:

$$\frac{1}{\varepsilon} \int_{\mathbb{R}} K \left(\frac{z - z'}{\varepsilon} \right) \frac{F(z')}{F(z)} dz' \approx ?$$

$$\frac{1}{\varepsilon \sqrt{\pi}} \iint_{\mathbb{R}^2} \exp \left(-\frac{1}{\varepsilon^2} \left(z - \frac{z_1 + z_2}{2} \right)^2 \right) \frac{F(z_1)}{F(z)} \frac{F(z_2)}{\int_{\mathbb{R}} F(z'_2) dz'_2} dz_1 dz_2 \approx ?$$

Everything boils down to compare z' – resp (z'_1, z'_2) – with z
→ to find the most likely parental traits!

Formal results (asexual case)

$$U(z) = U_0(z) + \varepsilon U_1(z) + \dots$$

where U_0 is the solution of a **stationary Hamilton-Jacobi equation**:

$$c \partial_z U_0(z) + \rho_0 + m(z) = 1 + H(\partial_z U_0(z)).$$

The function H is the Hamiltonian function:

$$H(p) = \int K(y) e^{py} dy - 1,$$

which depends only on the mutation kernel.

H comes with the Lagrangian function (convex conjugate):

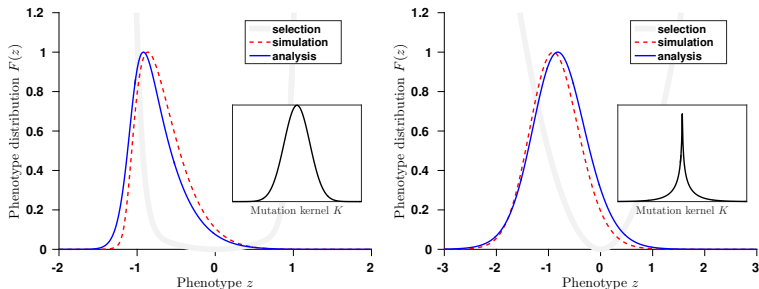
$$L(v) = \max_p (p \cdot v - H(p))$$

Explicit formula

Surprisingly, the number ρ_0 is obtained without any effort:

$$\rho_0 = 1 - m(0) - L(c).$$

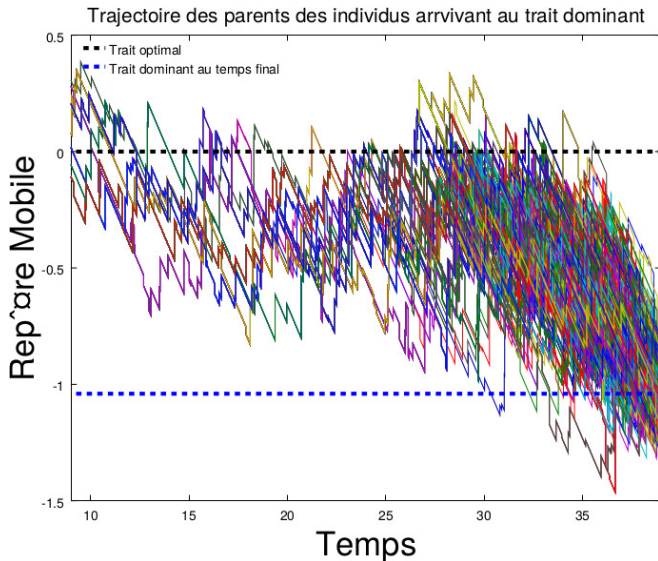
$L(c)$ comes as an additional cost due to mutations (lag load).



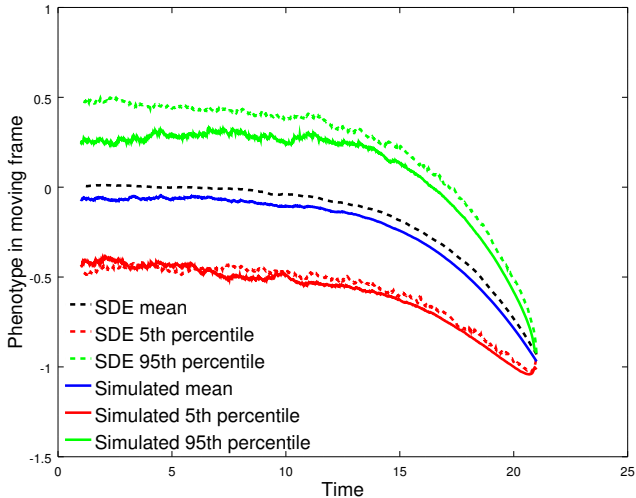
As a by-product, we obtain the value of the common trait z_0 :

$$\rho_0 + m(z_0) = 1 \quad \Longleftrightarrow \quad m(z_0) - m(0) = L(c)$$

Lineages (simulations by Florian Patout)



Lineages (simulations vs. formula)



Formal results (sexual case)

$$U(z) = \frac{(z - z_0)^2}{2} + \varepsilon^2 U_1(z) + \dots$$

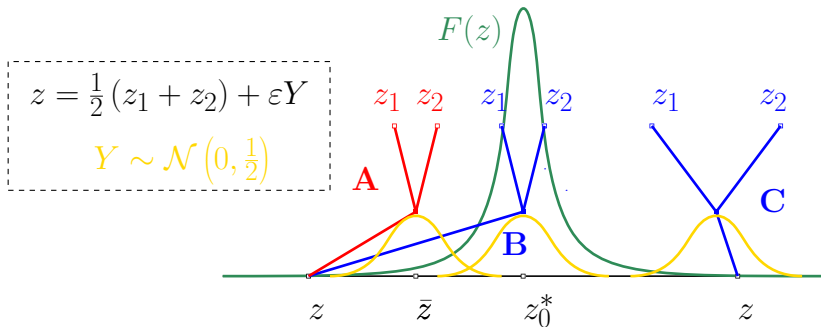
where U_1 is solution of a difference equation:

$$c(z - z_0) + \rho_0 + m(z) = \exp \left(U_1(z_0) - 2U_1 \left(\frac{z + z_0}{2} \right) + U_1(z) \right).$$

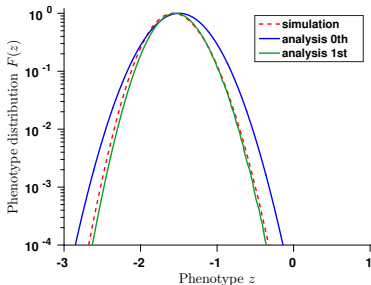
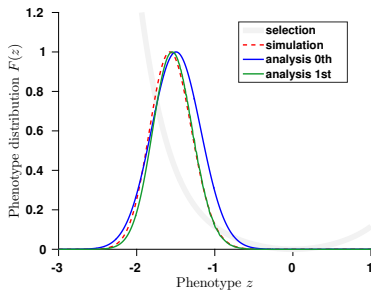
Again, the values of z_0 and ρ_0 follow directly from the equation:

$$\begin{aligned} m'(z_0) &= -c \\ \rho_0 + m(z_0) &= 1. \end{aligned}$$

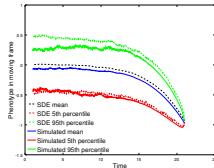
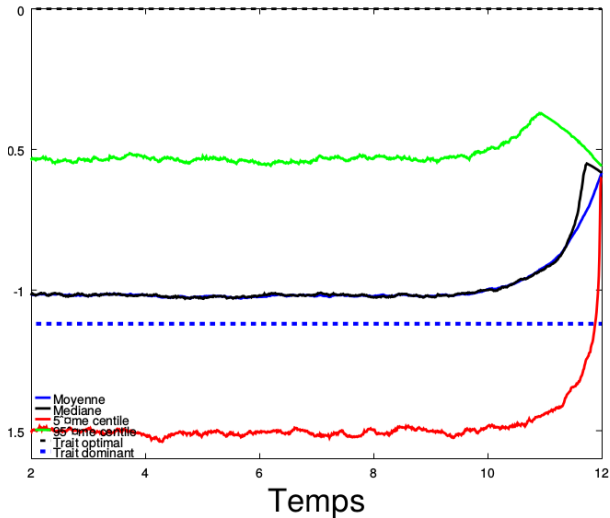
What are the most likely parental traits?



Gaussian at the leading order + corrections

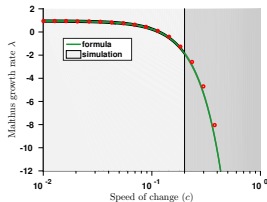
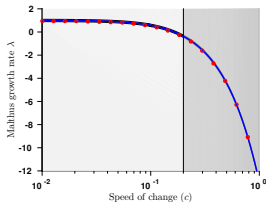


Lineages (simulations by Florian Patout)

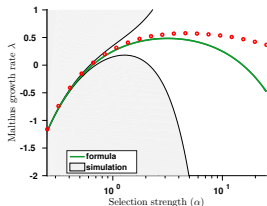
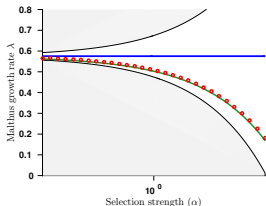


Reverse configuration as compared to the asexual case!

Variations of the Malthus growth rate λ ($\rho = \lambda_+$)

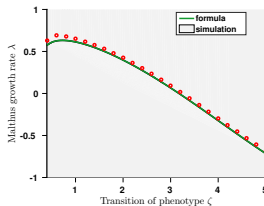
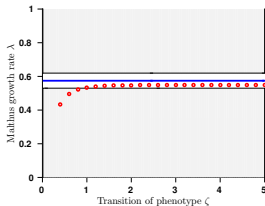


Influence of the **environmental change**

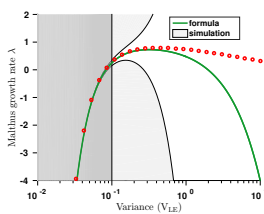
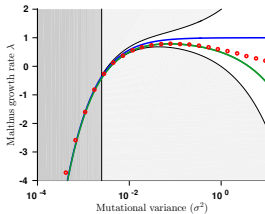


Influence of the **selection strength**

Variations of the Malthus growth rate λ ($\rho = \lambda_+$)



Influence of the **shape of selection**

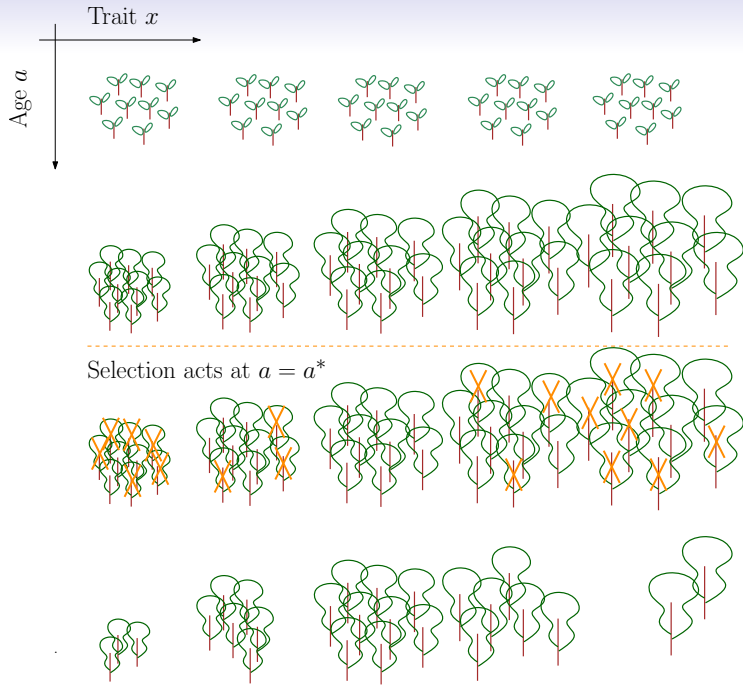


Influence of the **diversity at birth**

Age-dependent selection



Suppose selection acts at a given age (or after some age threshold)





MALADAPTATION AS A SOURCE OF SENESCENCE IN HABITATS VARIABLE IN SPACE AND TIME

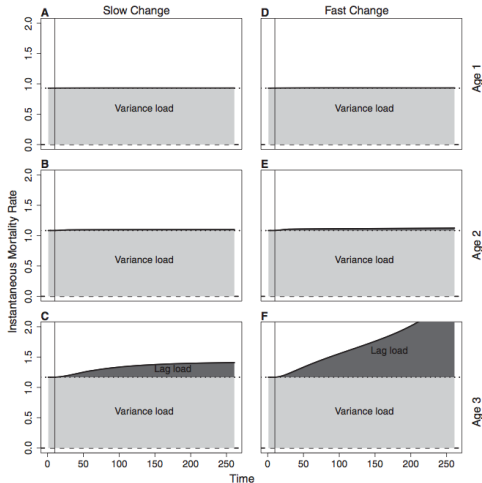
Olivier Cotto¹ and Ophélie Ronce^{1,2}

In this study, we use a quantitative genetics model of structured populations to investigate the evolution of senescence in a variable environment. Adaptation to local environments depends on phenotypic traits whose optimal values vary with age and

**– a changing environment can have a
different impact on different age classes. –**

results highlight the need to study age-specific adaptation, as a changing environment can have a different impact on different age classes.

A changing environment can have a different impact on different age classes



A quantitative genetics model of aging populations

(adapted from Cotto and Ronce 2014 to a continuous setting)

$$\begin{cases} \partial_t f(t, a, z) + \partial_a f(t, a, z) + (\rho(t) + \mu(a, m(z))) f(t, a, z) = 0 \\ f(t, 0, z) = \int_{\mathbb{R}} K(z - z') \left(\int_0^\infty \beta(a) f(t, a, z') da \right) dz' . \end{cases}$$

Ex. $\mu(a, m) = \mu(a) + m\delta_{a=a^*}$, $m(z) = \alpha|z|^2$.

Rk. Here, **asexual reproduction**, but similar framework in the case of sexual reproduction.

Goal: Investigate the mutation/selection balance as a function of the **age class a^*** .

A quantitative genetics model of aging populations

(adapted from Cotto and Ronce 2014 to a continuous setting)

$$\begin{cases} \partial_t f(t, a, z) + \partial_a f(t, a, z) + (\mu(a, m(z - ct)) + \rho(t)) f(t, a, z) = 0 \\ f(t, 0, z) = \int_{\mathbb{R}} K(z - z') \left(\int_0^\infty \beta(a) f(t, a, z') da \right) dz' . \end{cases}$$

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Goal: Investigate the mutation/selection balance as a function of the **age class a^* in a changing environment**.

Maladaptation under age structure (I)

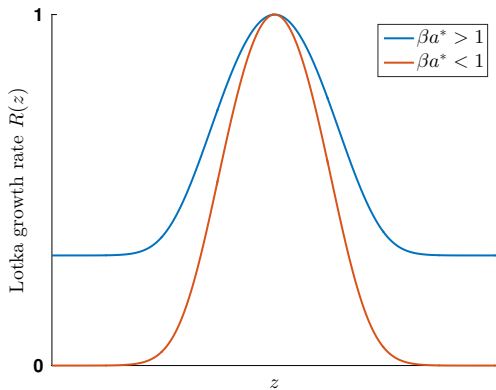
$$\begin{cases} -\varepsilon c \partial_z F(a, z) + \partial_a F(a, z) + (\mu(a, m(z)) + \rho) F(a, z) = 0 \\ F(0, z) = \int_{\mathbb{R}} K_{\varepsilon}(z - z') \left(\int_0^{\infty} \beta(a) F(a, z') da \right) dz'. \end{cases}$$

Dynamics of an **isolated trait** (without mutations) are encoded in the spectral problem:

$$\begin{cases} r(m) G(a, m) + \partial_a G(a, m) + \mu(a, m) G(a, m) = 0 \\ G(0, m) = \int_0^{\infty} \beta(a) G(a, m) da, \end{cases}$$

where the eigenvalue $r(m)$ is given by:

$$\int_0^{\infty} \beta(a) \exp \left(-r(m)a - \int_0^a \mu(a', m) da' \right) da = 1.$$



Shape of the eigenvalue $r(m(z))$ (effective fitness)

Maladaptation under age structure (II)

The logarithmic density

$$U^\varepsilon(a, z) = -\varepsilon \log \left(\frac{F^\varepsilon(a, z)}{G(a, m(z))} \right) .$$

converges towards a viscosity solution of the Hamilton-Jacobi equation

$$\rho_0 + c \partial_z U(z) = R(m(z), \partial_z U(z)) .$$

where the hamiltonian $R(m, p)$ is defined by

$$\int_0^\infty \beta(a) \exp \left(-a R(m, p) - \int_0^a \mu(a', m) da' \right) da = \frac{1}{\widehat{K}(p)} .$$

(Severe) maladaptation

In the homogeneous model (no age class), the lag z_0 increases gradually with c .

It can be more singular in the age-structured model. It can even diverge for some **critical speed** c^{**} :

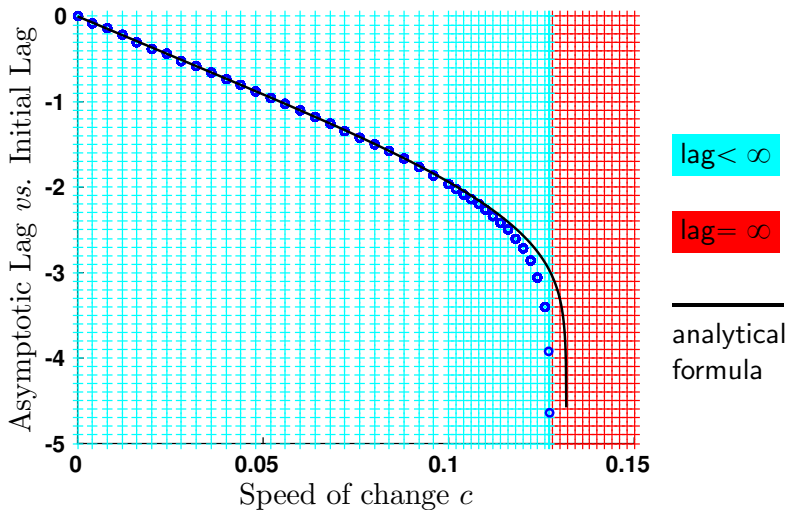
$$\lim_{c \rightarrow c^{**}} z_0(c) = \infty$$

It means that the population in the age classes $a > a^*$ goes extinct if $c^{**} < c < c^*$ (the critical speed for population extinction)

More precisely, we find,

$$z_0 = \left(-\frac{1}{\alpha} \log \left(1 - \frac{L(c)e^{-L(c)a^*}}{\beta e^{-\beta a^*}} \right) \right)^{1/2}$$

Numerical vs. analytical results (asexual mode)

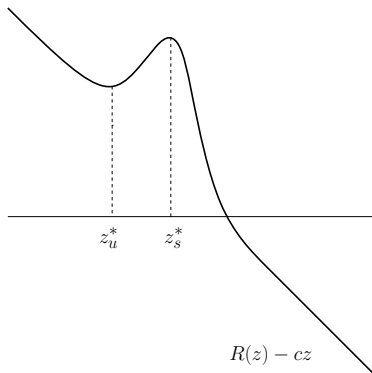


Severe maladaptation

Similar analysis in the case of sexual reproduction.

In this case, the lag is given by the simple formula:

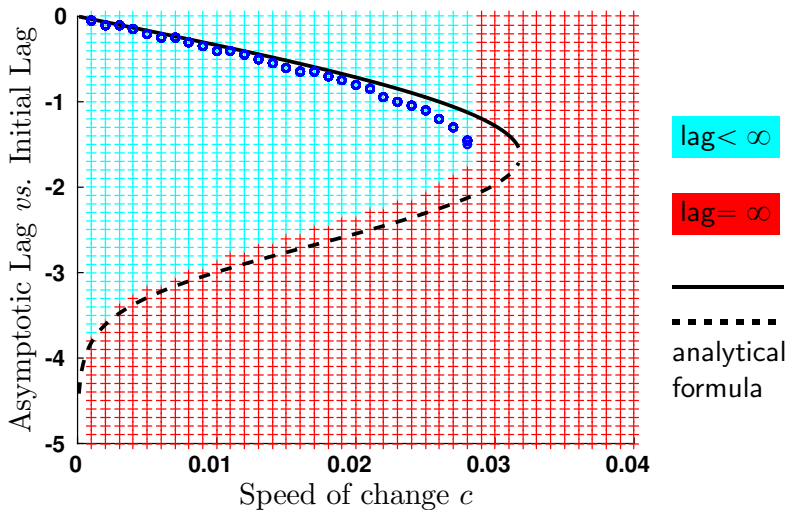
$$\frac{d}{dz}r(m(z)) = c$$



\Longleftrightarrow critical point for the
modified fitness $r(m(z)) - cz$

\Rightarrow **Bistability!**

Numerical vs. analytical results (sexual mode)



Thanks for your attention!