A Hamilton-Jacobi approach to describe the evolutionary equilibria in heterogeneous environments

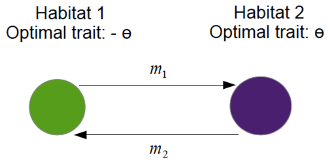
Sepideh Mirrahimi

CNRS, Institut de mathématiques de Toulouse, France

Joint work with Sylvain Gandon (CNRS, Montpellier)

CMAP, Septembre 2016

A model with two habitats



- $z \in \mathbb{R}$: **phenotypical trait**
- $n_i(z)$: the density of the population's **phenotypical distribution** in patch i
- N_i: the **total population's size** in patch i:

$$N_i = \int_{-\infty}^{\infty} n_i(y)dy.$$

- We consider **asexual reproduction**

A model with two habitats – equilibriums

We want to characterize the stationary solutions

$$-V_m\frac{\partial^2}{\partial z^2}n_{\varepsilon,i}(z) = n_{\varepsilon,i}(z)w_i(z,N_i) + m_j n_{\varepsilon,j}(z) - m_i n_{\varepsilon,i}(z).$$

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The **fitness** of trait z in patches $i = 1, 2$:

$$w_i(z, N_i) = r_i - g_i(z - \theta_i)^2 - \kappa_i N_i, \quad \theta_1 = -\theta, \quad \theta_2 = \theta.$$

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$V_m = \varepsilon^2$: The variance of the mutation kernel $\times$ the probability of mutation.

Assumptions:

- ε **is small**
- $\max\left(r_1 - m_1, r_2 - m_2\right) > 0 \quad \Longrightarrow \quad$ **Non-extinction**

What we bring comparing to previous works

Quantitative genetics:

- A single Gaussian distribution: Ronce, Kirkpatrick (2001), Hendry, Day, Taylor (2001)
- One or two Gaussian distributions: Yeaman, Guillaume (2009), Débarre, Ronce, Gandon (2013)

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What we do:

- We provide a **robust method** to characterize analytically the mutation-migration-selection equilibrium (i.e. the stationary solution $n_{\varepsilon,i}(z)$)– going **beyond the Gaussian approximation**.

What we bring comparing to previous works

Adaptive dynamics:

- Main results for symmetric habitats: Meszéna, Czibula, Geritz (1997), Day (2000), Fabre, Méléard, Porcher, Teplitsky, Robert (2012)

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- To characterize the equilibriums, we provide some preliminary results in the adaptive dynamics framework, **without** making any **symmetry assumption**.

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What we do:

- To characterize the equilibriums, we provide some preliminary results in the adaptive dynamics framework, **without** making any **symmetry assumption**.
- We make a **connection** between notions in **adaptive dynamics** and **quantitative genetics**.

The Hamilton-Jacobi approach for evolutionary biology

An old method to study the asymptotic behavior of reaction-diffusion equations:

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In evolutionary biology: asymptotic behavior of populations (nonlocal models):

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Towards more quantitative results: approximation of the phenotypical distribution:

- *Homogeneous environments :* M. , Roquejoffre

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Effective fitness

Consider a **resident population** $(n_1(z), n_2(z))$, with the total population's sizes $(N_1 = \int_{\mathbb{R}} n_1(y)dy, N_2 = \int_{\mathbb{R}} n_2(y)dy)$.

Then, **the effective growth rate** $W(z; N_1, N_2)$, associated with trait z in the resident population $(n_1(z), n_2(z))$, is **the largest eigenvalue** of :

$$\mathcal{A}(z; N_1, N_2) = \begin{pmatrix} w_1(z; N_1) - m_1 & m_2 \\ m_1 & w_2(z; N_2) - m_2 \end{pmatrix}$$

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- A **monomorphic** equilibrium is characterized by

$$n_i^M(z) = N_i^M \delta(z - z^M)$$

with $\begin{pmatrix} N_1^M \\ N_2^M \end{pmatrix}$ the **right eigenvector** associated with the dominant eigenvalue $W(z^M; N_1^M, N_2^M) = 0$ of $\mathcal{A}(z^M; N_1^M, N_2^M)$.

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- A **dimorphic** equilibrium is characterized by:

$$n_i^D(z) = \nu_{a,i}\delta(z - z_a^D) + \nu_{b,i}\delta(z - z_b^D), \quad \nu_{a,i} + \nu_{b,i} = N_i^D$$

with $\begin{pmatrix} \nu_{k,i} \\ \nu_{k,j} \end{pmatrix}$ the **right eigenvectors** associated with the largest eigenvalues $W(z_k^D; N_1^D, N_2^D) = 0$ of $\mathcal{A}(z_k^D; N_1^D, N_2^D)$.

Adaptive dynamics framework–Evolutionary equilibria

Evolutionary stable strategies (ESS):

• The monomorphic strategy z^{M*} is an **ESS** if for any mutant $z_0 \neq z^{M*}$,

$$W(z_0; N_1^{M*}, N_2^{M*}) < 0.$$

• The dimorphic strategy $\{z_a^{D*}, z_b^{D*}\}$ is an **ESS** if for any mutant $z_0 \notin \{z_a^{D*}, z_b^{D*}\}$,

$$W(z_0; N_1^{D*}, N_2^{D*}) < 0.$$

Migration in both directions – Identification of the ESS

Theorem:

Assume that $m_1 > 0$, $m_2 > 0$. There exists a **unique ESS**.

(i) The ESS is **dimorphic** if and only if

$$\frac{m_1 m_2}{4 g_1 g_2 \theta^4} < 1 \tag{1}$$

$$C_1 < \alpha_2 r_2 - \alpha_1 r_1 \tag{2}$$

$$C_2 < \beta_1 r_1 - \beta_2 r_2. \tag{3}$$

with C_i, α_i and β_i constants depending on $m_1, m_2, g_1, g_2, \kappa_1, \kappa_2, \theta$ which can be determined explicitly.

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For **symmetric habitats**, the ESS is given by $\{z^{M*} = 0\}$.

The source-sink case; identification of the ESS

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- There exists a **unique ESS** in each habitat (not necessarily the same).

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(ii) Otherwise, the ESS in the second patch is also **monomorphic** and is given by $\{-\theta\}$.

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The selection-mutations-migration equilibria- the method

We want to **approximate the equilibrium** $(n_{\varepsilon,1}(z), n_{\varepsilon,2}(z))$:

$$\begin{cases} -\varepsilon^2 \frac{\partial^2}{\partial z^2} n_{\varepsilon,1}(z) = n_{\varepsilon,1} w_1(z, N_{\varepsilon,1}) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\ \\ -\varepsilon^2 \frac{\partial^2}{\partial z^2} n_{\varepsilon,2}(z) = n_{\varepsilon,2} w_2(z, N_{\varepsilon,2}) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z). \end{cases}$$

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assuming that ε is **small**. We make a WKB ansatz

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

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

Note that a common Gaussian approximation is given by

$$\begin{aligned} n_{\varepsilon,i}(z) &= \frac{N_i}{\sqrt{2\pi\varepsilon}\sigma} \exp\left(\frac{-(z-z^*)^2}{\varepsilon\sigma^2}\right) \\ &= \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{-\frac{1}{2\sigma^2}(z-z^*)^2 + \varepsilon \log \frac{N_i}{\sigma}}{\varepsilon}\right). \end{aligned}$$

The selection-mutation-migration equilibria- the method

An expected asymptotic expansion:

$$u_{\varepsilon,i}(z) = u_i(z) + \varepsilon v_i(z) + \varepsilon^2 w_i(z) + O(\varepsilon^3),$$

which means, in terms of $n_{\varepsilon,i}$,

$$n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_i(z)}{\varepsilon} + v_i(z) + \varepsilon w_i(z) + O(\varepsilon^2)\right)$$

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We compute these coefficients using

$$\begin{cases} -\varepsilon \frac{\partial^2}{\partial z^2} u_{\varepsilon,1} = |\frac{\partial}{\partial z} u_{\varepsilon,1}|^2 + w_1(z, N_{\varepsilon,1}) + m_2 \exp\left(\frac{u_{\varepsilon,2} - u_{\varepsilon,1}}{\varepsilon}\right) - m_1, \\ \\ -\varepsilon \frac{\partial^2}{\partial z^2} u_{\varepsilon,2} = |\frac{\partial}{\partial z} u_{\varepsilon,2}|^2 + w_2(z, N_{\varepsilon,2}) + m_1 \exp\left(\frac{u_{\varepsilon,1} - u_{\varepsilon,2}}{\varepsilon}\right) - m_2. \end{cases}$$

How to compute u_i

We present the method in the case : $m_1 > 0, \quad m_2 > 0.$

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Theorem:
(i) As $\varepsilon \to 0$, $(n_{\varepsilon,1}, n_{\varepsilon,2})$ **converges to** (n_1^*, n_2^*), the equilibrium corresponding to the **unique ESS** of the metapopulation.

(ii) As $\varepsilon \to 0$, both sequences $(u_{\varepsilon,i})_\varepsilon$ **converge to** a viscosity solution to

$$\begin{cases} -|\frac{\partial}{\partial z} u|^2 = W(z, N_1^*, N_2^*), & \text{in } \mathbb{R}, \\ \max_{z \in \mathbb{R}} u(z) = 0. \end{cases}$$

Moreover, apart from a very particular set of parameters,

$$\mathrm{supp}\, n_1^* = \mathrm{supp}\, n_2^* = \{z \mid u(z) = 0\} = \{z \mid W(z, N_1^*, N_2^*) = 0\}.$$

and hence the solution u is unique.

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(ii) **Dimorphic ESS :** Assume that the unique ESS is dimorphic and is given by $\{z_a^{D*}, z_b^{D*}\}$. Then u is given by

$$u(z) = \max\Big(-\left| \int_{z_a^{D*}}^{z} \sqrt{-W(x; N_1^{D*}, N_2^{D*})}dx \right|, -\left| \int_{z_b^{D*}}^{z} \sqrt{-W(x; N_1^{D*}, N_2^{D*})}dx \right| \Big).$$

Asymptotic expansions for u, v_i and w_i

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When $u < 0$, $n_{\varepsilon,i}$ is exponentially small.
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When $u < 0$, $n_{\varepsilon,i}$ is exponentially small.
$\Rightarrow$ **Only the values of v_i and w_i near the ESS point z^{M*} matter**.

We indeed compute

$$u(z) = -\frac{A}{2}(z - z^{M*})^2 + B(z - z^{M*})^3 + C(z - z^{M*})^4 + O(z - z^{M*})^5.$$

$$v_i(z) = \log(\sqrt{A} N_i^{M*}) + D_i(z - z^{M*}) + E_i(z - z^{M*})^2 + O(z - z^{M*})^3.$$

$$w_i(z) = F_i + O(z - z^{M*}).$$

This is **enough** to obtain a good approximation of the population's distribution : **moments** approximated with an **error of order** ε^2.

Approximation of the moments

- **Total population**: $N_{\varepsilon,i} = N_i^{M*}(1 + \varepsilon(F_i + \frac{E_i}{A} + \frac{3C}{A^2}) + O(\varepsilon)$.
- **Mean**: $\mu_{\varepsilon,i} = \frac{1}{N_{\varepsilon,i}} \int z n_{\varepsilon,i} dz = z^{M*} + \varepsilon\big(3\frac{B}{A^2} + \frac{D_i}{A}\big) + O(\varepsilon^2)$.
- **Variance**: $\sigma^2_{\varepsilon,i} = \frac{1}{N_{\varepsilon,i}} \int (z - \mu^M_{\varepsilon,i})^2 n_{\varepsilon,i}(z) dz = \frac{\varepsilon}{A} + O(\varepsilon^2)$.
- **Skewness**:
$s_{\varepsilon,i} = \frac{1}{\sigma^3_{\varepsilon,i} N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^3 n_{\varepsilon,i}(z) dz = 6\frac{B}{A^{\frac{3}{2}}}\sqrt{\varepsilon} + O(\varepsilon^{\frac{3}{2}})$.

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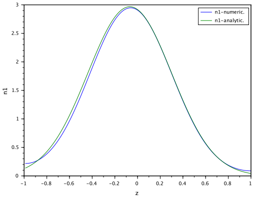
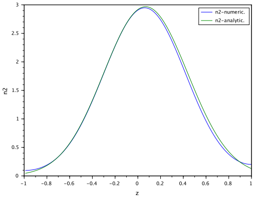
Symmetric habitats with monomorphic ESS





Comparison between **numerical** and **analytical** solution for $n_{\varepsilon,1}(z)$(at left) and $n_{\varepsilon,2}(z)$ (at right) with $\varepsilon = 0.1$.

$$r_{max} = 3, \quad g = 1, \quad \theta = 0.5, \quad \kappa = 1, \quad m = 1.$$

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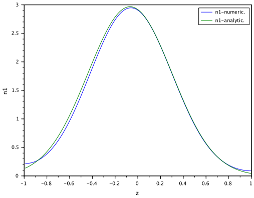

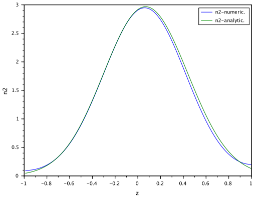

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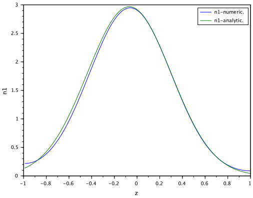

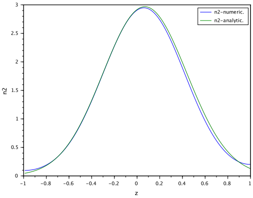

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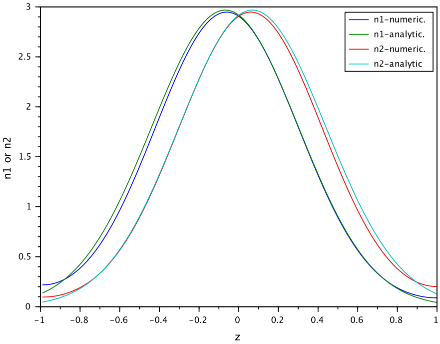
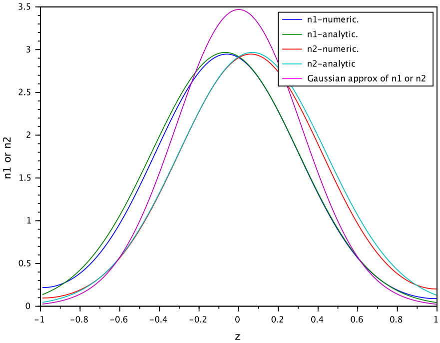


Symmetric habitats with monomorphic ESS



Comparison of the solutions n_1 and n_2 with Gaussian distribution with fixed variance (previous approximation given in Debarre et al. 2013).

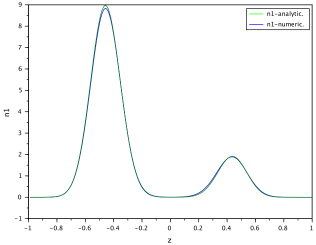
Symmetric habitats with monomorphic ESS

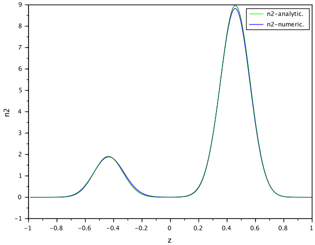
	Numerical	Analytical	Gaussian approx
N_1	2.68	2.68	2.75
N_2	2.68	2.68	2.75
μ_1	- 0.06	- 0.07	0
μ_2	0.06	0.07	0
σ_1^2	0.13	0.14	0.03
σ_2^2	0.13	0.14	0.03
s_1	0.04	0	0
s_2	- 0.04	0	0

Comparison between **numerical** and **analytical** values for the total populations, the mean trait, the variance and the skewness in the two habitats, for $\varepsilon = 0.1$.

Symmetric habitats with dimorphic ESS

$$r_{max} = 3, \quad g = 1, \quad \theta = 0.5, \quad \kappa = 1, \quad m = 0.2.$$

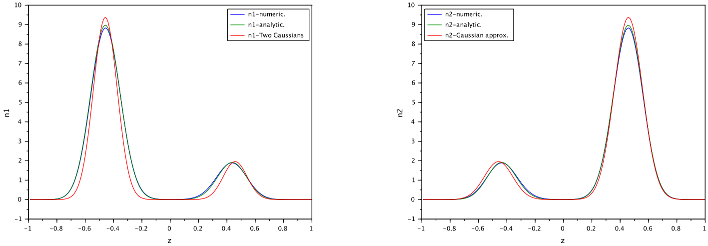




Comparison between **numerical** and **analytical** solution for $n_{\varepsilon,1}(z)$(at left) and $n_{\varepsilon,2}(z)$ (at right) with $\varepsilon = 0.01$.

Symmetric habitats with dimorphic ESS

$$r_{max} = 3, \quad g = 1, \quad \theta = 0.5, \quad \kappa = 1, \quad m = 0.2.$$



Comparison of the solutions $n_{\varepsilon,1}(z)$(at left) and $n_{\varepsilon,2}(z)$ (at right) with the Gaussian approximations with fixed variance.

Symmetric habitats with dimorphic ESS

	Numerical	Analytical	Gaus. approx
$\mu_{a,1}$	- 0.455	- 0.455	-.458
$\mu_{a,2}$	- 0.431	- 0.433	- 0.458
$\mu_{b,1}$	0.431	0.433	.458
$\mu_{b,2}$	0.455	0.455	0.458
$\sigma^2_{a,1}$	0.011	0.011	0.010
$\sigma^2_{a,2}$	0.012	0.011	0.010
$\sigma^2_{b,1}$	0.012	0.011	0.010
$\sigma^2_{b,2}$	0.011	0.011	0.010
$s_{a,1}$	0.049	0.036	0
$s_{a,2}$	0.081	0.036	0
$s_{b,1}$	- 0.081	- 0.036	0
$s_{b,2}$	- 0.049	- 0.036	0

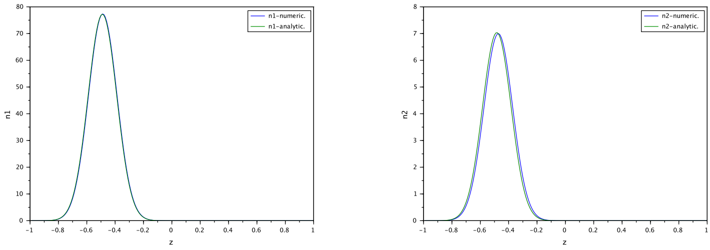
Conclusion

- We provide an analytic approximation of the selection–mutation–migration equilibrium which goes beyond the Gaussian approximations.
- We make a connection between the tools in quantitative genetics and adaptive dynamics.
- The method could be adapted to study : other fitness functions or mutation kernels, several habitats, the dynamics of the poplation's distribution.
- **We introduce a robust method based on Hamilton-Jacobi equations that can also be used in other contexts.**

Thank you for your attention !

Non-symmetric habitats with monomorphic ESS

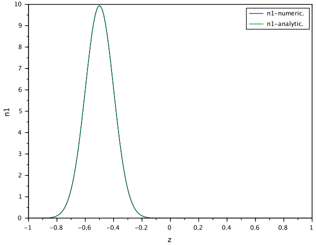
$$r_1 = 20, \quad g_1 = 1, \quad \kappa_1 = 1, \quad m_1 = 0.5, \quad \theta = 0.5.$$
$$r_2 = 0.3, \quad g_2 = 4, \quad \kappa_2 = 1, \quad m_2 = 0.2.$$

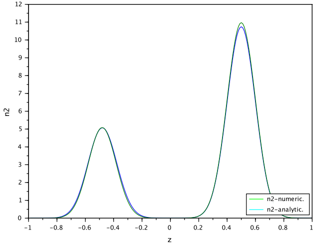


Comparison between **numerical** and **analytical** solution for $n_{\varepsilon,1}(z)$ and $n_{\varepsilon,2}(z)$ with $\varepsilon = 0.01$.

Source–sink case with dimorphic ESS

$$r_1 = 3, \quad g_1 = 1, \quad \kappa_1 = 1, \quad m_1 = 0.5, \quad \theta = 0.5.$$
$$r_2 = 4, \quad g_2 = 1, \quad \kappa_2 = 1, \quad m_2 = 0.$$

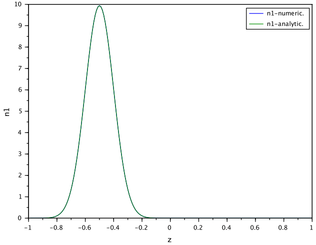


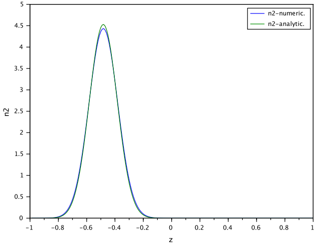


Comparison between **numerical** and **analytical** solution for $n_{\varepsilon,1}(z)$ and $n_{\varepsilon,2}(z)$ with $\varepsilon = 0.01$.

Source-sink case with monomorphic ESS

$$r_1 = 3, \quad g_1 = 1, \quad \kappa_1 = 1, \quad m_1 = 0.5, \quad \theta = 0.5.$$
$$r_2 = 1, \quad g_2 = 1, \quad \kappa_2 = 1, \quad m_2 = 0.$$





Comparison between **numerical** and **analytical** solution for $n_{\varepsilon,1}(z)$ and $n_{\varepsilon,2}(z)$ with $\varepsilon = 0.01$.