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

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Joint work with Sylvain Gandon (CNRS, Montpellier)

CIMPA school, Mauritius, December 2016
A model of population subject to Darwinian evolution and migration

- $z \in \mathbb{R}$: 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 $i$:
  \[ N_i = \int_{\mathbb{R}} n_i(y) dy. \]
- We consider asexual reproduction
A Hamilton-Jacobi approach to describe the evolutionary equilibria in heterogeneous environments

Introduction

A model with two habitats – equilibriums

We want to characterize the stationary solutions

$$-\varepsilon^2 n''_{\varepsilon,i}(z) = n_{\varepsilon,i}(z) R_i(z, N_i) + m_j n_{\varepsilon,j}(z) - m_i n_{\varepsilon,i}(z).$$
A model with two habitats – equilibriums

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\[-\varepsilon^2 n^{''}_{\varepsilon,i}(z) = n_{\varepsilon,i}(z)R_i(z, N_i) + m_j n_{\varepsilon,j}(z) - m_i n_{\varepsilon,i}(z).\]

The fitness of trait \(z\) in patches \(i = 1, 2\):

\[R_i(z, N_i) = r_i - g_i(z - \theta_i)^2 - \kappa_i N_i, \quad \theta_1 = -\theta, \quad \theta_2 = \theta.\]
A model with two habitats – equilibriums

We want to characterize the stationary solutions

\[-\varepsilon^2 \frac{n''}{n_i}(z) = n_{\varepsilon,i}(z)R_i(z, N_i) + m_j n_{\varepsilon,j}(z) - m_i n_{\varepsilon,i}(z).\]

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\(\varepsilon^2\) : The variance of the mutation kernel \(\times\) the probability of mutation.
A model with two habitats – equilibriums

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\[-\varepsilon^2 n_{\varepsilon,i}''(z) = n_{\varepsilon,i}(z)R_i(z, N_i) + m_j n_{\varepsilon,j}(z) - m_i n_{\varepsilon,i}(z).\]

The fitness of trait \(z\) in patches \(i = 1, 2\):

\[R_i(z, N_i) = r_i - g_i(z - \theta_i)^2 - \kappa_i N_i, \quad \theta_1 = -\theta, \quad \theta_2 = \theta.\]

\(\varepsilon^2\): The variance of the mutation kernel \(\times\) the probability of mutation.

Assumptions:

- \(\varepsilon\) is small
- \(\max(r_1 - m_1, r_2 - m_2) > 0 \implies\) Non-extinction
- \(m_1 > 0, m_2 > 0\) (can be relaxed)
What we bring comparing to previous works

Quantitative genetics:


- One or two Gaussian distributions: Yeaman, Guillaume (2009), Débarre, Ronce, Gandon (2013)
What we bring comparing to previous works

Quantitative genetics:

- One or two Gaussian distributions: Yeaman, Guillaume (2009), Débarre, Ronce, Gandon (2013)

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:

What we bring comparing to previous works

Adaptive dynamics:


What we do:

- We generalize some results in the framework of adaptive dynamics to the case of non symmetric habitats
What we bring comparing to previous works

Adaptive dynamics:


What we do:

- We generalize some results in the framework of adaptive dynamics to the case of non symmetric habitats
- 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:

- Freidlin (1985), Evans, Souganidis, Barles, ...
The Hamilton-Jacobi approach for evolutionary biology

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

- Rigorous derivation for homogeneous and heterogeneous environments, interaction with resource, etc.: Barles, Bouin, Champagnat, Jabin, Lam, Lorz, Lou, M., Méleard, Perthame, Souganidis, Taing, Turanova, Wakano
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Towards more quantitative results: characterization of the phenotypical distribution for non-vanishing mutations:
- *Homogeneous environments:* M., Roquejoffre
A Hamilton-Jacobi approach to describe the evolutionary equilibria in heterogeneous environments

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   - Some notions from adaptive dynamics
   - Identification of the ESS

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3 A method to describe selection-mutation-migration equilibria

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5 Some heuristics
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:

\[
\mathcal{A}(z; N_1, N_2) = \begin{pmatrix}
R_1(z; N_1) - m_1 & m_2 \\
m_1 & R_2(z; N_2) - m_2
\end{pmatrix}
\]
Adaptive dynamics framework–Demographic equilibria

Consider a set $\Omega = \{z_1, \cdots, z_m\}$. The demographic equilibrium corresponding to this set is given by

$$n_i(z) = \sum_{j=1}^{m} \alpha_{j,i}\delta(z - z_j), \quad N_i = \sum_{j=1}^{m} \alpha_{j,i}, \quad i = 1, 2,$$

such that

$$W(z_j, N_1, N_2) = 0, \quad j = 1, \cdots, m,$$

and such that $\left( \begin{array}{c} \alpha_{j,1} \\ \alpha_{j,2} \end{array} \right)$ is the right eigenvector associated with the dominant eigenvalue $W(z_j, N_1, N_2) = 0$ of $A(z_j; N_1, N_2)$. 


Adaptive dynamics framework–Demographic equilibria

Since there are two habitats, we consider only monomorphic and dimorphic equilibria:
Adaptive dynamics framework–Demographic equilibria

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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 \( A(z^M; N_1^M, N_2^M) \).
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  \[ n_i^M(z) = N_i^M \delta(z - z^M) \]
  with \( \left( \begin{array}{c} N_1^M \\ N_2^M \end{array} \right) \) the right eigenvector associated with the dominant eigenvalue \( W(z^M; N_1^M, N_2^M) = 0 \) of \( A(z^M; N_1^M, N_2^M) \).

- **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 \( \left( \begin{array}{c} \nu_{k,1} \\ \nu_{k,2} \end{array} \right) \) the right eigenvectors associated with the largest eigenvalues \( W(z_k^D; N_1^D, N_2^D) = 0 \) of \( A(z_k^D; N_1^D, N_2^D) \).
Adaptive dynamics framework–Evolutionary equilibria

**Evolutionary stable strategies (ESS):**
A set of points \( \Omega^* = \{z_1^*, \cdots, z_m^*\} \) is called an evolutionary stable strategy (ESS) if

\[
W(z, N_1^*, N_2^*) = 0, \quad \text{for } z \in \mathcal{A} \text{ and, } \quad W(z, N_1^*, N_2^*) \leq 0, \quad \text{for } z \notin \mathcal{A},
\]

where \( N_1^* \) and \( N_2^* \) are the total population’s sizes corresponding to the demographic equilibrium associated with the set \( \Omega^* \).
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where $N_1^*$ and $N_2^*$ are the total population’s sizes corresponding to the demographic equilibrium associated with the set $\Omega^*$.

When the mutations are very rare, we expect that, in long time, the population concentrates on an ESS.
Migration in both directions – Identification of the ESS

Theorem:
There exists a unique ESS.

(i) The ESS is dimorphic if and only if

\[ \frac{m_1 m_2}{4 g_1 g_2 \theta^4} < 1 \]  
\[ C_1 < \alpha_2 r_2 - \alpha_1 r_1 \]  
\[ C_2 < \beta_1 r_1 - \beta_2 r_2. \]

with \( C_i \), \( \alpha_i \) and \( \beta_i \) 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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\]

with \( C_i, \alpha_i \) and \( \beta_i \) constants depending on \( m_1, m_2, g_1, g_2, \kappa_1, \kappa_2, \theta \) which can be determined explicitly. Then the dimorphic ESS is given by \( \{-z^{D*}, z^{D*}\} \) with
\[
z^{D*} := \sqrt{\theta^2 - \frac{m_1 m_2}{4 \theta^2 g_1 g_2}}.
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Migration in both directions – Identification of the ESS

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\[
z^{D\ast} := \sqrt{\theta^2 - \frac{m_1 m_2}{4 \theta^2 g_1 g_2}}.
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(ii) If the above conditions are not satisfied then the ESS is **monomorphic**.
Migration in both directions – Identification of the ESS

Theorem:
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\[
z^{D*} := \sqrt{\theta^2 - \frac{m_1 m_2}{4 \theta^2 g_1 g_2}}.
\]

(ii) If the above conditions are not satisfied then the ESS is monomorphic.
For symmetric habitats, the ESS is given by \( \{z^{M*} = 0\} \).
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4 Numerics and comparison with previous results

5 Some heuristics
The selection-mutations-migration equilibria- the method

We want to characterize the equilibrium \((n_{\epsilon,1}(z), n_{\epsilon,2}(z))\):

\[
\begin{align*}
-\varepsilon^2 n''_{\epsilon,1}(z) &= n_{\epsilon,1} R_1(z, N_{\epsilon,1}) + m_2 n_{\epsilon,2}(z) - m_1 n_{\epsilon,1}(z), \\
-\varepsilon^2 n''_{\epsilon,2}(z) &= n_{\epsilon,2} R_2(z, N_{\epsilon,2}) + m_1 n_{\epsilon,1}(z) - m_2 n_{\epsilon,2}(z).
\end{align*}
\]

assuming that \(\varepsilon\) is small.
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\end{align*}
\]

assuming that \(\varepsilon\) is small. We make a Hopf-Cole transformation

\[
n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{\varepsilon,i}(z)}{\varepsilon}\right).
\]
The selection-mutations-migration equilibria- the method

We want to characterize the equilibrium \((n_{\epsilon,1}(z), n_{\epsilon,2}(z)):\)

\[
\begin{cases}
-\epsilon^2 n''_{\epsilon,1}(z) = n_{\epsilon,1} R_1(z, N_{\epsilon,1}) + m_2 n_{\epsilon,2}(z) - m_1 n_{\epsilon,1}(z), \\
-\epsilon^2 n''_{\epsilon,2}(z) = n_{\epsilon,2} R_2(z, N_{\epsilon,2}) + m_1 n_{\epsilon,1}(z) - m_2 n_{\epsilon,2}(z).
\end{cases}
\]

assuming that \(\epsilon\) is small. We make a Hopf-Cole transformation

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

Note that a common Gaussian approximation is given by

\[
n_{\epsilon,i}(z) = \frac{N_i}{\sqrt{2\pi\epsilon\sigma}} \exp \left( \frac{-(z-z^*)^2}{\epsilon\sigma^2} \right)
\]

\[
= \frac{1}{\sqrt{2\pi\epsilon}} \exp \left( \frac{-1/\epsilon \sigma^2 (z-z^*)^2 + \epsilon \log \frac{N_i}{\sigma}}{\epsilon} \right).
\]
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 \( n_{\varepsilon,i} \),

\[ n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp \left( \frac{u_i(z)}{\varepsilon} + v_i(z) + \varepsilon w_i(z) + O(\varepsilon^2) \right) \]
The selection-mutation-migration equilibria- the method

An expected asymptotic expansion:

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We compute these coefficients using

\[
\begin{cases}
-\varepsilon u''_{\varepsilon,1} = |u'_{\varepsilon,1}|^2 + R_1(z, N_{\varepsilon,1}) + m_2 \exp \left( \frac{u_{\varepsilon,2} - u_{\varepsilon,1}}{\varepsilon} \right) - m_1, \\
-\varepsilon u''_{\varepsilon,2} = |u'_{\varepsilon,2}|^2 + R_2(z, N_{\varepsilon,2}) + m_1 \exp \left( \frac{u_{\varepsilon,1} - u_{\varepsilon,2}}{\varepsilon} \right) - m_2.
\end{cases}
\]
How to compute $u_i$
How to compute $u_i$

**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.
How to compute $u_i$

**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

\[
\begin{align*}
-|u'(z)|^2 &= W(z, N_1^*, N_2^*), \quad \text{in } \mathbb{R}, \\
\max_{z \in \mathbb{R}} u(z) &= 0.
\end{align*}
\]

Moreover, apart from a very particular set of parameters,

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

and hence the solution $u$ is unique.
How to compute \( u \)

Such solution \( u \) can be computed explicitly:
How to compute $u$

Such solution $u$ can be computed explicitly:

(i) **Monomorphic ESS**: Assume that the unique ESS is monomorphic and is given by $\{z^M_\ast\}$. Then $u$ is given by

$$u(z) = -\left| \int_{z^M_\ast}^z \sqrt{-W(x; N^M_1, N^M_2)} \, dx \right|.$$
How to compute $u$

Such solution $u$ can be computed explicitly:

(i) **Monomorphic ESS**: Assume that the unique ESS is monomorphic and is given by $\{z^{M*}\}$. Then $u$ is given by

$$u(z) = -\left| \int_{z^{M*}}^{Z} \sqrt{-W(x; N_{1}^{M*}, N_{2}^{M*})} \, dx \right|.$$

(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

$$u(z) = \max \left( -\left| \int_{z_{a}^{D*}}^{Z} \sqrt{-W(x; N_{1}^{D*}, N_{2}^{D*})} \, dx \right|, \right.$$

$$\left. -\left| \int_{z_{b}^{D*}}^{Z} \sqrt{-W(x; N_{1}^{D*}, N_{2}^{D*})} \, dx \right| \right).$$
Asymptotic expansions for $u$, $v_i$ and $w_i$

We present the results in the **monomorphic case**. The dimorphic case can be analyzed following similar arguments.
Asymptotic expansions for $u$, $v_i$ and $w_i$

We present the results in the **monomorphic case**. The dimorphic case can be analyzed following similar arguments.

When $u < 0$, $n_{\varepsilon,i}$ is exponentially small.

⇒ Only the values of $v_i$ and $w_i$ near the ESS point $z^{M*}$ matter.
Asymptotic expansions for $u$, $v_i$ and $w_i$

We present the results in the monomorphic case. The dimorphic case can be analyzed following similar arguments.

When $u < 0$, $n_{\varepsilon,i}$ is exponentially small.

⇒ 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 $\varepsilon^2$. 
Approximation of the moments

- **Total population:**
  \[ N_{\varepsilon,i} = N_{i}^{M*}(1 + \varepsilon(F_{i} + \frac{E_{i} + 0.5D_{i}^{2}}{A} + \frac{3(C + BD_{i})}{A^{2}} + \frac{7.5B_{i}^{2}}{A^{3}})) + O(\varepsilon^{2}). \]

- **Mean:**
  \[ \mu_{\varepsilon,i} = \frac{1}{N_{\varepsilon,i}} \int z n_{\varepsilon,i}dz = z^{M*} + \varepsilon \left(3 \frac{B}{A^{2}} + \frac{D_{i}}{A}\right) + O(\varepsilon^{2}). \]

- **Variance:**
  \[ \sigma_{\varepsilon,i}^{2} = \frac{1}{N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i}^{M})^{2} n_{\varepsilon,i}(z)dz = \frac{\varepsilon}{A} + O(\varepsilon^{2}). \]

- **Skewness:**
  \[ s_{\varepsilon,i} = \frac{1}{\sigma_{\varepsilon,i}^{3} N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^{3} n_{\varepsilon,i}(z)dz = 6 \frac{B^{3}}{A^{3}} \sqrt{\varepsilon} + O(\varepsilon^{3/2}). \]
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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 $\varepsilon = 0.1$.

$$r_{\text{max}} = 3, \quad g = 1, \quad \theta = 0.5, \quad \kappa = 1, \quad m = 1.$$
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 $\varepsilon = 0.1$.

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

In particular, we correct the approximation of the variance:

$$\sigma_{\varepsilon,i}^2 = \varepsilon / \sqrt{g(1 - 2g\theta^2 / m)} + O(\varepsilon^2),$$
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

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

<table>
<thead>
<tr>
<th></th>
<th>Numerical</th>
<th>Analytical</th>
<th>Gaussian approx</th>
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<tbody>
<tr>
<td>$N_1$</td>
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<td>$N_2$</td>
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<td>$\sigma_2^2$</td>
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<tr>
<td>$s_2$</td>
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</tr>
</tbody>
</table>

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

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

Comparison between \textbf{numerical} and \textbf{analytical} solution for \( n_{\varepsilon,1}(z) \) (at left) and \( n_{\varepsilon,2}(z) \) (at right) with \( \varepsilon = 0.01 \).
A Hamilton-Jacobi approach to describe the evolutionary equilibria in heterogeneous environments

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 \( n_{\epsilon,1}(z) \) (at left) and \( n_{\epsilon,2}(z) \) (at right) with the Gaussian approximations with fixed variance.
### Symmetric habitats with dimorphic ESS

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<tbody>
<tr>
<td>(\mu_{a,1})</td>
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<tr>
<td>(\mu_{a,2})</td>
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<tr>
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<tr>
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<td>(\sigma_{b,1}^2)</td>
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</tr>
<tr>
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</tr>
<tr>
<td>(s_{a,1})</td>
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<td>0.036</td>
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<tr>
<td>(s_{a,2})</td>
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<td>0.036</td>
<td>0</td>
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<tr>
<td>(s_{b,1})</td>
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<td>(s_{b,2})</td>
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Some heuristic arguments to understand the results

The Hopf-Cole transformation $u_{\epsilon,i} = \epsilon \log(n_{\epsilon,i})$ leads to

$$-\epsilon u_{\epsilon,i}'' = |u_{\epsilon,i}'|^2 + R_i(z, N_{\epsilon,i}) + m_j \exp\left(\frac{u_{\epsilon,j} - u_{\epsilon,i}}{\epsilon}\right) - m_i,$$

with $i = 1, 2$ and $j = 2, 1$. 
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We expect the following expansion

$$u_{\epsilon,i} = u_i + \epsilon v_i + \epsilon^2 w_i + O(\epsilon^3).$$
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Then, keeping the zero order terms we obtain

$$-|u'(z)|^2 = R_i(z, N_i) + m_j \exp(v_j(z) - v_i(z)) - m_i.$$
The last line means
\[
\begin{pmatrix}
R_1(z; N_1) - m_1 & m_2 \\
m_1 & R_2(z; N_2) - m_2
\end{pmatrix}
\begin{pmatrix}
ev_1(z) \\
ev_2(z)
\end{pmatrix}
= -|u'(z)|^2
\begin{pmatrix}
ev_1(z) \\
ev_2(z)
\end{pmatrix}.
\]
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\begin{pmatrix}
R_1(z; N_1) - m_1 & m_2 \\
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\end{pmatrix}
\begin{pmatrix}
e^{v_1(z)} \\
e^{v_2(z)}
\end{pmatrix}
= -|u'(z)|^2 \begin{pmatrix}
e^{v_1(z)} \\
e^{v_2(z)}
\end{pmatrix}.
\]

It follows that \(-|u'(z)|^2\) is the dominant eigenvalue of the matrix \(A\) and hence
\[-|u'(z)|^2 = W(z, N_1, N_2).\]
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Moreover, from the boundedness of the total population, we obtain
\[u \leq 0, \quad \text{supp } n_1 = \text{supp } n_2 = \{u = 0\},\]

and hence
\[\text{supp } n_1 = \text{supp } n_2 = \{u = 0\} \subset \{W(z, N_1, N_2) = 0\}.\]
In particular:

\[ W(z, N_1, N_2) \leq 0, \quad \text{for } z \notin \mathcal{O}, \quad W(z, N_1, N_2) = 0, \quad \text{for } z \in \mathcal{O}, \]

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Moreover, one can indeed show that

\[ W(z, N_1^*, N_2^*) < 0, \quad \text{for } z \notin \mathcal{O}, \quad W(z, N_1^*, N_2^*) = 0, \quad \text{for } z \in \mathcal{O}, \]
We recall that

\[
\begin{cases}
-|u'(z)|^2 = W(z, N_1^*, N_2^*), \\
\max_{\mathbb{R}} u(z) = 0.
\end{cases}
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A property related to the \textbf{weak KAM} theory: any viscosity solution of the above equation is determined by its values at the maximum points of $W$. 
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A property related to the weak KAM theory: any viscosity solution of the above equation is determined by its values at the maximum points of $W$.

However, we already know that at the maximum points of $W$, $u(z) = 0$. This allows us to determine $u$ in a unique way.
Conclusion

- We provide an analytic approximation of the selection–mutation–migration equilibrium which goes beyond the Gaussian approximations.
- We make a connection between the theories of quantitative genetics and adaptive dynamics.
- We introduce a robust method based on Hamilton-Jacobi equations that can also be used in other contexts.
Thank you for your attention!