

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

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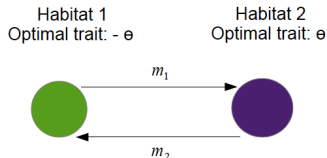
CNRS, Institut de mathématiques de Toulouse, France

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 model with two habitats – equilibriums

We want to characterize the stationary solutions

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

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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 $i = 1, 2$:

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

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Assumptions:

- ε 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:

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

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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:

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

- *Heuristics by:* Diekmann, Jabin, Mischler, Perthame (2005)
- *Rigorous derivation for homogeneous and heterogeneous environments, interaction with resource, etc.:* Barles, Bouin, Champagnat, Jabin, Lam, Lorz, Lou, M., Méléard, 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

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- 2 Preliminary results in adaptive dynamics
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- 3 A method to describe selection-mutation-migration equilibria
- 4 Numerics and comparison with previous results
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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 :

$$\mathcal{A}(z; N_1, N_2) = \begin{pmatrix} R_1(z; N_1) - m_1 & m_2 \\ m_1 & R_2(z; N_2) - m_2 \end{pmatrix}$$

Adaptive dynamics framework–Demographic equilibria

Consider a set $\Omega = \{z_1, \dots, z_m\}$. 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

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

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

Adaptive dynamics framework–Demographic equilibria

Since there are two habitats, we consider only monomorphic and dimorphic 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 $\mathcal{A}(z^M; N_1^M, N_2^M)$.

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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 $\begin{pmatrix} \nu_{k,1} \\ \nu_{k,2} \end{pmatrix}$ 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):

A set of points $\Omega^* = \{z_1^*, \dots, z_m^*\}$ 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 Ω^* .

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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

$$\frac{m_1 m_2}{4g_1 g_2 \theta^4} < 1 \quad (1)$$

$$C_1 < \alpha_2 r_2 - \alpha_1 r_1 \quad (2)$$

$$C_2 < \beta_1 r_1 - \beta_2 r_2. \quad (3)$$

with C_i , α_i and β_i constants depending on m_1 , m_2 , g_1 , g_2 , κ_1 , κ_2 , θ which can be determined explicitly.

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

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(ii) If the above conditions are not satisfied then the ESS is **monomorphic**.

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

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The selection-mutations-migration equilibria- the method

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

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

assuming that ε is **small**.

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assuming that ε is **small**. We make a Hopf-Cole transformation

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

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assuming that ε is **small**. We make a Hopf-Cole transformation

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

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

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

How to compute u_i

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Theorem:

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

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Theorem:

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

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

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

Moreover, apart from a very particular set of parameters,

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

and hence the solution u is unique.

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

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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

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

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.

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When $u < 0$, $n_{\epsilon,i}$ 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

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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

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

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

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

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:**

$$N_{\varepsilon,i} = N_i^{M*} \left(1 + \varepsilon \left(F_i + \frac{E_i + 0.5D_i^2}{A} + \frac{3(C + BD_i)}{A^2} + \frac{7.5B^2}{A^3} \right) \right) + O(\varepsilon^2).$$

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

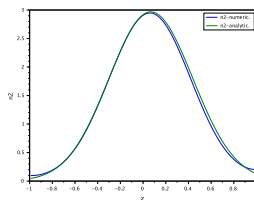
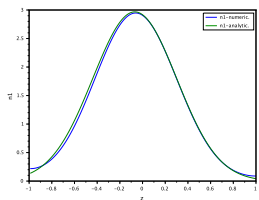
- **Skewness:**

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

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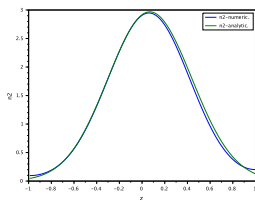
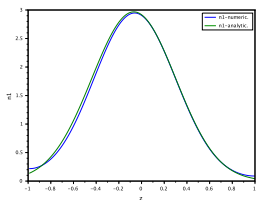
Symmetric habitats with monomorphic ESS



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

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

Symmetric habitats with monomorphic ESS



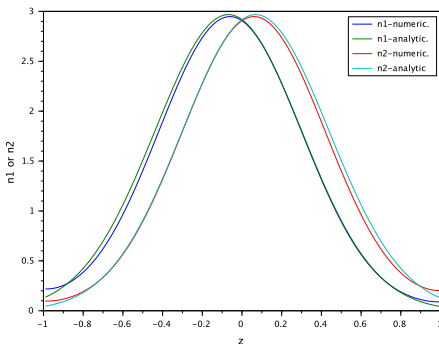
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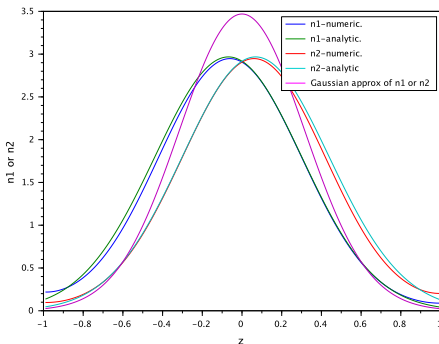
In particular, we correct the approximation of the variance:

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

Symmetric habitats with monomorphic ESS



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

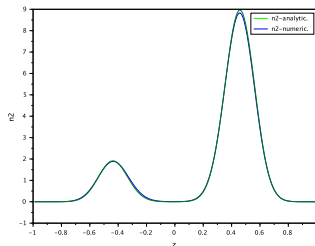
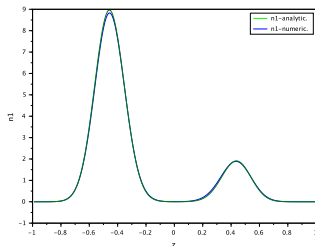
Symmetric habitats with monomorphic ESS

	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

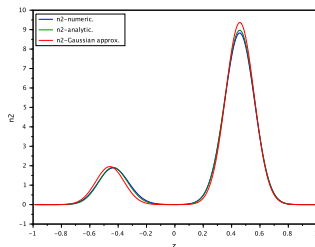
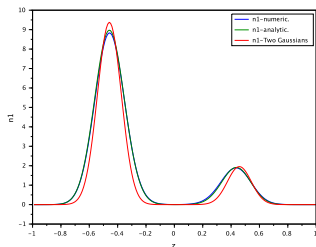
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Comparison between **numerical** and **analytical** solution for $n_{\epsilon,1}(z)$ (at left) and $n_{\epsilon,2}(z)$ (at right) with $\epsilon = 0.01$.

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

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	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
$\sigma_{a,1}^2$	0.011	0.011	0.010
$\sigma_{a,2}^2$	0.012	0.011	0.010
$\sigma_{b,1}^2$	0.012	0.011	0.010
$\sigma_{b,2}^2$	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

Some heuristic arguments to understand the results

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

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

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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

$$\begin{pmatrix} R_1(z; N_1) - m_1 & m_2 \\ m_1 & R_2(z; N_2) - m_2 \end{pmatrix} \begin{pmatrix} e^{v_1(z)} \\ e^{v_2(z)} \end{pmatrix} = -|u'(z)|^2 \begin{pmatrix} e^{v_1(z)} \\ e^{v_2(z)} \end{pmatrix}.$$

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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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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 !