A Hamilton-Jacobi method to describe the evolutionary equilibria in heterogeneous environments and with non-vanishing effects of mutations

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Abstract

In this note, we characterize the solution of a system of elliptic integro-differential equations describing a phenotypically structured population subject to mutation, selection and migration. Generalizing an approach based on Hamilton-Jacobi equations, we identify the dominant terms of the solution when the mutation term is small (but nonzero). This method was initially used, for different problems from evolutionary biology, to identify the asymptotic solutions, while the mutations vanish, as a sum of Dirac masses. A key point is a uniqueness property related to the weak KAM theory. This method allows to go further than the Gaussian approximation commonly used by biologists and is an attempt to fill the gap between the theories of adaptive dynamics and quantitative genetics.

Résumé

Méthode Hamilton-Jacobi pour décrire des équilibres évolutives dans les environnements hétérogènes et avec des mutations non-évanescentes. Dans cette note, nous étudions un système d'équations intégro-différentielles elliptiques, décrivant une population structurée par trait phénotypique soumise à des mutations, à la sélection et à des migrations. Nous généralisons une approche basée sur des équations de Hamilton-Jacobi pour détérminer les termes dominants de la solution lorsque les effets des mutations sont petits (mais non-nuls). Cette méthode était initialement utilisée, pour différents problèmes venant de la biologie évolutive, pour identifier les solutions asymptotiques, lorsque les effets des mutations tendent vers 0, sous forme des sommes de masses de Dirac. Un point clé est une propriété d'unicité en rapport avec la théorie de KAM faible. Cette méthode nous permet d'aller au-delà des approximations Gaussiennes habituellement utilisées par les biologistes et contribue ainsi à relier les théories de la dynamique adaptative et de la génétique quantitative.

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1. Introduction

During the last decade, an approach based on Hamilton-Jacobi equations with constraints has been developed to describe the asymptotic evolutionary dynamics of phenotypically structured populations, in the limit of vanishing mutations. The mathematical modeling of such phenomena leads to parabolic (or elliptic for the steady case) integro-differential equations, whose solutions tend, as the diffusion term vanishes, to a sum of Dirac masses, corresponding to dominant traits. These asymptotic solutions can be described using the Hamilton-Jacobi approach. There is a large literature on this method. We refer to [4,17,13] for the establishment of the basis of this approach for problems from evolutionary biology. Note that related tools were already used in the case of local equations (for instance KPP type equations) to describe the propagation phenomena (see for instance [8,5]).

In almost all the previous works, the Hamilton-Jacobi approach has been used to describe the limit of the solution, corresponding to the population's phenotypical distribution, as the mutations' steps vanish. However, from the biological point of view, it is sometimes more relevant to consider non-vanishing mutation's steps. A recent work [16] has pointed out that such tools can also be used, for a simple model with homogeneous environment, to characterize the solution while mutations' steps are small but nonzero. In this note, we show how such results can be obtained in a more complex situation with a heterogeneous environment.

Our purpose in this note is to study the solutions to the following system, for $z \in \mathbb{R}$,

$$\begin{cases} -\varepsilon^2 n''_{\varepsilon,1}(z) = n_{\varepsilon,1}(z) R_1(z, N_{\varepsilon,1}) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\ -\varepsilon^2 n''_{\varepsilon,2}(z) = n_{\varepsilon,2}(z) R_2(z, N_{\varepsilon,2}) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z), \\ N_{\varepsilon,i} = \displaystyle\int_{\mathbb{R}} n_{\varepsilon,i}(z) dz, \qquad \text{for } i = 1, 2, \end{cases} \tag{1}$$

with

$$R_i(z, N_i) = r_i - g_i(z - \theta_i)^2 - \kappa_i N_i, \qquad \text{with } \theta_1 = -\theta \text{ and } \theta_2 = \theta. \tag{2}$$

This system represents the equilibrium of a phenotypically structured population under mutation, selection and migration between two habitats. For more details on the modeling and the biological motivations, see Section 2.

Note that the asymptotic behavior, as $\varepsilon \to 0$ and along subsequences, of the solutions to this system, under the assumption $m_i > 0$, for $i = 1, 2$, and for bounded domains, was already studied in [14]. In the present work, we go further than the asymptotic limit along subsequences and we obtain uniqueness of the limit and identify the dominant terms of the solution when ε is small but nonzero.

The main elements of the method:
To describe the solutions $n_{\varepsilon,i}(z)$ we use a WKB ansatz

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

Note that a first approximation that is commonly used in the theory of 'quantitative genetics' (a theory in evolutionary biology that investigates the evolution of continuously varying traits [18]-chapter 7), is a gaussian distribution of the following form

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

Here, we try to go further than this a priori gaussian assumption and to approximate directly $u_{\varepsilon,i}$. To this end, we write an expansion for $u_{\varepsilon,i}$ in terms of ε:

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

We prove that $u_1 = u_2 = u$ is the unique viscosity solution to a Hamilton-Jacobi equation with constraint. The uniqueness of the viscosity solution to such Hamilton-Jacobi equation with constraint is related to the uniqueness of the Evolutionary Stable Strategy (ESS), see Section 3 for definition and for the result on the uniqueness of the ESS, and to the weak KAM theory [7]. In section 4, we compute explicitly u which indeed satisfies

$$\max_{\mathbb{R}} u(z) = 0,$$

with the maximum points attained at one or two points corresponding to the ESS points of the problem. We then notice that, while $u(z) < 0$, $n_{\varepsilon,i}(z)$ is exponentially small. Therefore, only the values of v_i and w_i close to the zero level sets of u matter, i.e. the ESS points. In section 5, we provide the main elements to compute formally v_i and hence its second order Taylor expansion around the ESS points and the value of w_i at those points. Then, we show, in section 6, that these approximations together with a fourth order Taylor expansion of u around the ESS points are enough to approximate the moments of the population's distribution with an error of order ε^2.

The mathematical details of our results will be provided in [12]. The biological applications will be detailed in [15].

2. Model and motivation

The solution of (1) corresponds to the steady solution to the following system, for $(t, z) \in \mathbb{R}^+ \times \mathbb{R}$,

$$\begin{cases} \partial_t n_i(t,z) - \varepsilon^2 \dfrac{\partial^2}{\partial z^2} n_i(t,z) = n_i(t,z) R_i(z, N_i(t)) + m_j n_j(t,z) - m_i n_i(t,z), \quad i = 1,2, \quad j = 2,1, \\ N_i(t) = \displaystyle\int_{\mathbb{R}} n_i(t,z) dz, \qquad \text{for } i = 1,2. \end{cases} \tag{4}$$

This system represents the dynamics of a population that is structured by a phenotypical trait z, and which lives in two habitats. We denote by $n_i(t, z)$ the density of the phenotypical distribution in habitat i, and by N_i the total population's size in habitat i. The growth rate $R_i(z, N_i)$ is given by (2), where r_i represents the maximum intrinsic growth rate, g_i is the strength of the selection, θ_i is the optimal trait in habitat i and κ_i represents the intensity of the competition. The constants m_i are the migration rates between the habitats. In this note we assume that there is positive migration rate in both directions, i.e.

$$m_i > 0, \qquad \text{i=1,2.} \tag{5}$$

However, the source and sink case, where for instance $m_2 = 0$, can also be analyzed using similar tools. We refer to [15] for the analysis of this case. We additionally assume that

$$\max(r_1 - m_1, r_2 - m_2) > 0. \tag{6}$$

This guarantees that the population does not get extinct.

Such phenomena have already been studied by several approaches. A first class of results are based on the adaptive dynamics approach, where one considers that the mutations are very rare such that the population has time to attain its equilibrium between two mutations and hence the population's distribution has discrete support (one or two points in a two habitats model) [11,2,6]. A second class of results are based on an approach known as 'quantitative genetics', which allows more frequent mutations and does not separate the evolutionary and the ecological time scales . A main assumption in this class of

works is that one considers that the population's distribution is a gaussian [9,19] or, to take into account the possibility of dimorphic populations, a sum of one or two gaussian distributions [20,3].

In our work, as in the quantitative genetics framework, we also consider continuous phenotypical distributions. However, we don't assume any a priori gaussian assumption. We compute directly the population's distribution and in this way we correct the previous approximations. To this end, we also provide some results in the framework of adaptive dynamics and in particular, we generalize previous results on the identification of the ESS to the case of nonsymetric habitats. Furthermore, our work makes a connection between the two approaches of adaptive dynamics and quantitative genetics.

3. The adaptive dynamics framework

In this section, we introduce some notions from the theory of adaptive dynamics that we will be using in the next sections [11]. We also provide our main result in this framework.

Effective fitness: The effective fitness $W(z; N_1, N_2)$ is the largest eigenvalue of the following matrix:

$$\mathcal{A}(z; N_1, N_2) = \begin{pmatrix} R_1(z; N_1) - m_1 & m_2 \\ m_1 & R_2(z; N_2) - m_2 \end{pmatrix} \tag{7}$$

This indeed corresponds to the *effective* growth rate associated with trait z in the whole metapopulation when the total population's sizes are given by (N_1, N_2).

Demographic equilibrium: Consider a set of points $\Omega = \{z_1, \cdots z_m\}$. The demographic equilibrium corresponding to this set is given by $(n_1(z), n_2(z))$, with the total population's sizes (N_1, N_2), such that

$$n_i(z) = \sum_{j=1}^{m} \alpha_{i,j}\delta(z - z_j), \qquad N_i = \sum_{j=1}^{m} \alpha_{i,j}, \qquad W(z_j, N_1, N_2) = 0,$$

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

Evolutionary stable strategy: 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^*, N_2^*) is the total population's sizes corresponding to the demographic equilibrium associated with the set Ω^*.

Since, there are only two habitats we expect that at most two distinct traits coexist at the evolutionary stable equilibrium. We prove indeed the following:

Theorem 3.1 *Assume* (5)–(6). *There exists a unique set of points Ω^* which is an evolutionary stable strategy. Such set has at most two elements.*

We call an evolutionary stable strategy which has one (respectively two) element, a monomorphic (respectively dimorphic) ESS. We can indeed give a criterion to have monomorphic or dimorphic ESS, and we can identify the dimorphic ESS in the general case (see [12] for more details).

4. How to compute the zero order terms u_i

The identification of the zero order terms u_i is based on the following result. Note that the part (ii) of the theorem below is a variant of Theorem 1.1 in [14].

Theorem 4.1 *Assume* (5)–(6).
(i) As $\varepsilon \to 0$, $(n_{\varepsilon,1}, n_{\varepsilon,2})$ *converges to* (n_1^*, n_2^*), *the demographic equilibrium of the unique ESS of the model. Moreover, as* $\varepsilon \to 0$, $N_{\varepsilon,i}$ *converges to* N_i^*, *the total population's size in patch* i *corresponding to this demographic equilibrium.*
(ii) As $\varepsilon \to 0$, *both sequences* $(u_{\varepsilon,i})_\varepsilon$, *for* $i = 1, 2$, *converge along subsequences and locally uniformly in* $\mathbb{R}$ *to a continuous function* $u \in \mathrm{C}(\mathbb{R})$, *such that* u *is a viscosity solution to the following equation*

$$\begin{cases} -|u'|^2 = W(z, N_1^*, N_2^*), & \text{in } \mathbb{R}, \\ \max\limits_{z\in\mathbb{R}} u(z) = 0. \end{cases} \tag{8}$$

Moreover, we have the following condition on the zero level set of u*:*

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

(iii) There exists constants (λ_i, ν_i), *for* $i = 1, 2$, *which can be determined explicitly from* m_1, m_2, g_1, g_2, κ_1, κ_2 *and* θ, *such that, under the condition*

$$r_2 \neq \lambda_1 r_1 + \nu_1, \qquad r_1 \neq \lambda_2 r_2 + \nu_2, \tag{9}$$

we have

$$\operatorname{supp} n_1^* = \operatorname{supp} n_2^* = \{z \,|\, u(z) = 0\} = \{z \,|\, W(z, N_1^*, N_2^*) = 0\}. \tag{10}$$

The solution of (8)–(10) *is unique and hence the whole sequence* $(u_{\varepsilon,i})_\varepsilon$ *converge locally uniformly in* $\mathbb{R}$ *to* u.

Note that a Hamilton-Jacobi equation of type (8) in general might admit several viscosity solutions. Here, the uniqueness is obtained thanks to (10) and a property from the weak KAM theory, which is the fact that the viscosity solutions are completely determined by one value taken on each static class of the Aubry set ([10], Chapter 5 and [1]). In what follows we assume that (9) and hence (10) always hold. We then give an explicit formula for u considering two cases:

(i) **Monomorphic ESS :** We consider the case where there exists a unique monomorphic ESS z^* and the corresponding demographic equilibrium is given by $(N_1^*\delta(z^*), N_2^*\delta(z^*))$. Then u is given by

$$u(z) = -\Big|\int_{z^*}^{z} \sqrt{-W(x; N_1^*, N_2^*)}dx\Big|. \tag{11}$$

(ii) **Dimorphic ESS :** We next consider the case where there exists a unique dimorphic ESS (z_a^*, z_b^*) with the demographic equilibrium: $n_i = \nu_{a,i}\delta(z - z_a^*) + \nu_{b,i}\delta(z - z_b^*)$, and $\nu_{a,i} + \nu_{b,i} = N_i^*$. Then u is given by

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

5. How to compute the next order terms

In this section, we give the main elements to compute formally v_i and the value of w_i at the ESS point, with v_i and w_i the correctors introduced by (3), in the case of monomorphic population. For the details of the computations for both monomorphic and dimorphic populations, we refer the interested reader to [12].

We consider the case of monomorphic population where the demographic equilibrium corresponding to the monomorphic ESS is given by $(N_1^*\delta(z - z^*), N_2^*\delta(z - z^*))$. One can compute, using (11), a Taylor expansion of order 4 around the ESS point z^*:

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

To provide an approximation of the moments of the population's distribution, we have to compute constants D_i, E_i and F_i such that

$$v_i(z) = v_i(z^*) + D_i(z - z^*) + E_i(z - z^*)^2 + O(z - z^*)^3, \qquad w_i(z^*) = F_i.$$

A first element of the computations is obtained by replacing the functions u, v_i and w_i by the above approximations to compute $N_{\varepsilon,i} = \int_{\mathbb{R}} n_{\varepsilon,i}(z)dz$. This leads to

$$v_i(z^*) = \log\big(N_i^*\sqrt{A}\big), \quad N_{\varepsilon,i} = N_i^* + \varepsilon K_i^* + O(\varepsilon^2), \quad \text{with} \quad K_i^* = N_i^*\big(\frac{3C}{A^2} + \frac{E_i}{A} + F_i\big).$$

Note also that writing (1) in terms of $u_{\varepsilon,i}$ we obtain

$$\begin{cases} -\varepsilon u''_{\varepsilon,1}(z) = |u'_{\varepsilon,1}|^2 + R_1(z, N_{\varepsilon,1}) + m_2 \exp\big(\frac{u_{\varepsilon,2} - u_{\varepsilon,1}}{\varepsilon}\big) - m_1, \\ -\varepsilon u''_{\varepsilon,2}(z) = |u'_{\varepsilon,2}|^2 + R_2(z, N_{\varepsilon,2}) + m_1 \exp\big(\frac{u_{\varepsilon,1} - u_{\varepsilon,2}}{\varepsilon}\big) - m_2. \end{cases} \tag{12}$$

A second element, is obtained by keeping the zero order terms in the first line of (12) and using (8) to obtain

$$v_2(z) - v_1(z) = \log\Big(\frac{1}{m_2}\big(W(z, N_1^*, N_2^*) - R_1(z, N_1^*) + m_1\big)\Big). \tag{13}$$

The last element, is derived from keeping the terms of order ε in (12) which leads to

$$-u'' = 2u'v'_i - \kappa_i K_i^* + m_j \exp(v_j - v_i)(w_j - w_i), \quad \text{for } \{i, j\} = \{1, 2\}. \tag{14}$$

The functions v_i and the coefficients D_i, E_i and F_i can be computed by combining the above elements.

6. Approximation of the moments

The above approximations of u, v_i and w_i around the ESS points allow us to estimate the moments of the population's distribution. In the monomorphic case these approximations are given below:

$$\begin{cases} N_{\varepsilon,i} = \displaystyle\int n_{\varepsilon,i}(z)dz = N_i^*(1 + \varepsilon(F_i + \frac{E_i}{A} + \frac{3C}{A^2})) + O(\varepsilon^2), \\ \mu_{\varepsilon,i} = \displaystyle\frac{1}{N_{\varepsilon,i}} \int z n_{\varepsilon,i}(z)dz = z^* + \varepsilon(\frac{3B}{A^2} + \frac{D_i}{A}) + O(\varepsilon^2), \\ \sigma^2_{\varepsilon,i} = \displaystyle\frac{1}{N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^2 n_{\varepsilon,i}(z)dz = \frac{\varepsilon}{A} + O(\varepsilon^2), \\ s_{\varepsilon,i} = \displaystyle\frac{1}{\sigma^3_{\varepsilon,i} N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^3 n_{\varepsilon,i}(z)dz = \frac{6B}{A^{\frac{3}{2}}}\sqrt{\varepsilon} + O(\varepsilon^{\frac{3}{2}}). \end{cases}$$

One can obtain similar approximations in the case of dimorphic ESS. To compute the above integrals, replacing the approximation (3) in the integrals, a natural change of variable is to take $z - z^* = \sqrt{\varepsilon}y$. Therefore each term $z - z^*$ can be considered as of order $\sqrt{\varepsilon}$ in the integration. This is why, to obtain a first order approximation of the integrals in terms of ε, it is enough to have a fourth order approximation of $u(z)$, a second order approximation of $v_i(z)$ and a zero order approximation of $w_i(z)$, in terms of z around z^*.

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