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

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Abstract

In this work, we characterize the solution of a system of elliptic integro-differential equations describing a phenotypically structured population subject to mutation, selection and migration between two habitats. Assuming that the effects of the mutations are small but nonzero, we show that the population's phenotypical distribution has at most two peaks and we give explicit conditions under which the population will be monomorphic (unimodal distribution) or dimorphic (bimodal distribution). More importantly, we provide a general method to determine the dominant terms of the population's distribution in each case. Our work, which is based on Hamilton-Jacobi equations with constraint, goes further than previous works where such tools were used, for different problems from evolutionary biology, to identify the asymptotic solutions, while the mutations vanish, as a sum of Dirac masses. The main elements for the computation of the dominant terms of the population's distribution are the convergence of the logarithmic transform of the solution to the unique solution of a Hamilton-Jacobi equation and the computation of the correctors.

This method allows indeed to go further than the Gaussian approximation commonly used by biologists and makes a connection between the theories of adaptive dynamics and quantitative genetics. Our work being motivated by biological questions, the objective of this article is to provide the mathematical details which are necessary for our biological results [30].

1 Introduction

Can we characterize the phenotypical distribution of a population which is subject to the Darwinian evolution? Several mathematical formalisms are used to study the Darwinian evolution of phenotypically structured populations. Game theory is one of the first approaches to study evolution and remains one of the important tools in this field [26, 21]. Adaptive dynamics, which is based on the study of the stability of differential systems is widely used be the theoretical evolutionary biology community (see for instance [18, 11]). Integro-differential models (usually elliptic or parabolic equations), have also contributed a lot to the understanding of evolutionary dynamics of populations (see for instance [25, 2, 12, 10, 22, 5, 23, 19]). Finally, probabilistic approaches allow to study finite populations (see for instance [4]) and also to justify the above frameworks from individual based models by proper choices of scaling on the size of the population, birth, death and mutations (see for instance [3]).

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In this work, we are interested in the integro-differential approach which is a suitable framework in the case of large populations. We are in particular interested in an approach based on Hamilton-Jacobi equations with constraint which has been developed during the last decade to describe the asymptotic solutions of the selection-mutation equations as the effect of the mutations vanishes. The asymptotic solutions of such integro-differential equations, as the mutation term vanishes, concentrate on the fittest traits. There is a large literature on this method. We refer to [12, 33, 28] 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 [16, 13]).

Such results, which are based on a logarithmic transformation (the so-called Hopf-Cole transformation) of the population's density, provide mainly the convergence along subsequences of the logarithmic transform to a viscosity solution of a Hamilton-Jacobi equation with constraint, as the effects of the mutations vanish. This allows to obtain a qualitative description of the population's phenotypical distribution for vanishing mutations' steps. To be able to characterize the population's distribution for non-vanishing effects of mutations, one should prove a uniqueness property for the viscosity solution of the Hamilton-Jacobi equation with constraint and compute the next order terms. Such properties are usually not studied due to technical difficulties. However, from the biological point of view it is usually more relevant to consider non-vanishing mutations' steps.

In this work, as announced in [17], we provide such analysis, including a uniqueness result and the computation of the correctors, in the case of a selection, mutation and migration model. Note that a recent work [32, 31] has also provided similar results in the case of homogeneous environments. We believe indeed that going further in the Hamilton-Jacobi approach for different problems from evolutionary biology, by providing higher order approximations, allows to better demonstrate the usefulness of this approach. A main objective of this project is to highlight the interest of this method for the evolutionary biology community via an example corresponding to the particular model studied in this article. The purpose of this article is to provide the mathematical details and proofs which are necessary for our biological results [30]. As explained in [30], our method allows to provide more quantitative results and correct the previous approximations obtained by biologists.

Our objective is to characterize the solutions to the following system, for $z \in \mathbb{R}$,

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

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 population that is structured by a phenotypical trait z, and which is subject to selection, mutation and migration between two habitats. We denote by $n_i(z)$ the density of the phenotypical distribution in habitat i, and by N_i the total population 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, the positive constant g_i is the strength of the selection, θ_i is the optimal trait in habitat i and the positive constant κ_i represents the intensity of the competition. The nonnegative constants m_i are the migration rates between the habitats.

Such phenomena have already been studied using several approaches by the theoretical evolutionary biologists. 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) [27, 7, 14]. 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 so that the population's distribution is continuous and is described by an integro-differential equation (see [34]–chapter 7). A main assumption in this class of works is that one considers that the population's distribution is a gaussian [20, 35] or, to take into account the possibility of dimorphic populations, a sum of one or two gaussian distributions [36, 8].

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 evolutionary stable strategy (ESS) (see Section 2 for the definition) to the case of nonsymetric habitats. Furthermore, our work makes a connection between the two approaches of adaptive dynamics and quantitative genetics.

Assumptions:
To guarantee that the population does not get extinct, we assume that

$$\max(r_1 - m_1, r_2 - m_2) > 0. \tag{3}$$

Moreover, in the first part of this article, we assume that there is positive migration rate in both directions, i.e.

$$m_i > 0, \qquad \text{i=1,2.} \tag{4}$$

The source and sink case, where for instance $m_2 = 0$, will be analyzed in the last section.

Note that in [29] the limit, as $\varepsilon \to 0$ and along subsequences, of the solutions to such system, under assumption (4), and in a bounded domain, was studied. 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. In this way, we are able to characterize the solution when the mutation's steps are not negligible.

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

$$n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{\varepsilon,i}(z)}{\varepsilon}\right). \tag{5}$$

Note that a first approximation that is commonly used in the theory of 'quantitative genetics', 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:

$$u_{\varepsilon,i} = u_i + \varepsilon v_i + \varepsilon^2 w_i + O(\varepsilon^3). \tag{6}$$

We first prove that $u_1 = u_2 = u$ is the unique viscosity solution to a Hamilton-Jacobi equation with constraint which can be computed explicitly. The uniqueness of solution of such Hamilton-Jacobi equation with constraint is related to the uniqueness of the ESS and to the weak KAM theory [15]. Such function u 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 next show how to compute formally v_i. Note that once u and v_i are known we have already a good approximation of the population's distribution with an error of order $O(\sqrt{\varepsilon})$. We then notice that, while $u(z) < 0$, $n_{\varepsilon,i}(z)$ is exponentially small. Therefore, to estimate the moments of the population's distribution only the values of v_i and w_i at the points which are close to the zero level set of u matter, i.e. the ESS points. We then compute a a fourth order Taylor expansion of u_i and a second order Taylor expansion of v_i around the ESS points, and the value of w_i at those points. These approximations are indeed enough to approximate the moments of the population's distribution with an error of order ε^2 as $\varepsilon \to 0$.

Although the computations of the correctors do not require very deep mathematical tools, they allow to complete our method and obtain the dominant terms of the population's distribution and estimate it's moments. Using the method presented in this article, a detailed biological study of this model has been provided in [30]. This analysis allows to observe new features. In particular, the computation of the correctors, v_i is important to estimate the mean phenotypical trait. This computation allows indeed to capture a gap between the mean phenotypical traits in the two patches in presence of mutations, in a case where in absence of the mutations the population is monomorphic, i.e. the distribution concentrates on a same single point in the two patches (see [30] for more details). Moreover, the analytical approximation of the moments is of particular interest in the biological community and there have been several attempts to provide such approximations (see for instance [36, 8, 9]). Our work provides a more mathematically rigorous method for such computations and improves some previous results [30]. In particular, we precise the impact of the migration rate, and other parameters of the model, on the variance of the population's distribution [30]. This is specially interesting since in classical quantitative genetics models, it is not clear how to include the influence of migration in the variance of the population's distribution that one generally assumes to be fixed. In such models the variance is usually over estimated (see for instance [8]).

Note that the part of the method where one proves the convergence of $(u_{\varepsilon,i})_\varepsilon$ to a viscosity solution of a Hamilton-Jacobi equation is very robust and can be generalized to the case of several patches with multi-dimensional trait and general growth rates R_i (see Remark 3.6). However, we use the particular structure of the model to obtain the uniqueness and the identification of the ESS. This is the reason why we chose a particular model (with two habitats and quadratic growth rates), so that we can highlight the usefulness of the Hamilton-Jacobi approach for the cases where the adaptive dynamics framework is well-understood. Note however that although with this choice of model, in absence of migration, the asymptotic analysis in each habitat is rather simple (in each patch the population will concentrate on the fittest trait in the patch), the presence of the migration makes the qualitative study non-trivial. The migration can indeed lead to dimorphism in each of the habitats. In particular a Gaussian approximation would not be adapted.

The paper is organized as follows. In Section 2 we introduce some notions from the theory of adaptive

dynamics that will be used in the following sections. In Section 3 we state our main results (theorems 3.1 and 3.5) and discuss their consequences. In this section, we also provide the method to compute the correctors and approximate the moments of the population's distribution. In Section 4 we provide the proofs of the results in the adaptive dynamics framework and in particular we prove Theorem 3.1. In Section 5 we prove Theorem 3.5. Finally, in Section 6 we generalize our results to the sink and source case where the migration is only in one direction ($m_2 = 0$).

2　Some notions from the theory of adaptive dynamics

In this section, we introduce some notions from the theory of adaptive dynamics that we will be using in the next sections [27]. Note that our objective is not to study the framework of adaptive dynamics where the mutations are assumed to be very rare. However, these notions appear naturally from our asymptotic computations.

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

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

that is

$$W(z; N_1, N_2) = \tfrac{1}{2}\Big[(R_1(z; N_1) + R_2(z; N_2) - m_1 - m_2) \\ + \sqrt{(R_1(z; N_1) - R_2(z; N_2) - m_1 + m_2)^2 + 4 m_1 m_2} \Big]. \tag{8}$$

This indeed corresponds to the *effective* growth rate associated with trait z in the whole metapopulation when the total population 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 sizes (N_1, N_2), such that

$$n_i(z) = \sum_{j=1}^{m} \alpha_{i,j} \delta(z - z_j), \quad N_i = \sum_{j=1}^{m} \alpha_{i,j}, \quad W(z_j, N_1, N_2) = 0, \quad i = 1, 2, \ j = 1, \cdots, m,$$

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 $\mathcal{A}(z_j; N_1, N_2)$.

Invasibility: We say that a mutant trait z_m can invade a resident strategy $\{z^M\}$ at its demographic equilibrium (N_1^M, N_2^M) if $W(z_m, N_1^M, N_2^M) > 0$.

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

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

where N_1^* and N_2^* are the total population sizes corresponding to the demographic equilibrium associated with the set Ω^*.

Notation: We will use the star sign * whenever we talk about an evolutionary stable strategy Ω^* (and similarly for the corresponding demographic equilibrium (n_1^*, n_2^*) and the total population sizes (N_1^*, N_2^*)). We add an index M when the strategy is monomorphic (a set of a single trait $\{z^{M*}\}$ with the corresponding demographic equilibrium (n_1^{M*}, n_2^{M*}), and the total population sizes (N_1^{M*}, N_2^{M*})) and an index D when the strategy is dimorphic (a set of two traits $\{z_{\mathrm{I}}^{D*}, z_{\mathrm{II}}^{D*}\}$ with the corresponding demographic equilibrium (n_1^{D*}, n_2^{D*}), and the total population sizes (N_1^{D*}, N_2^{D*})).

3 The main results and the details of the method

In this section, we state our main results and provide the details of our method for the approximation of the equilibrium distribution $n_{\varepsilon,i}(z)$. In Subsection 3.1 we provide the results in the framework of adaptive dynamics. In Subsection 3.2 we state our main result on the convergence to the zero order term u_i and its explicit computation. Finally, in Subsection 3.3 we show how to compute the next order terms and we provide the approximation of the moments of the population's distribution.

3.1 The adaptive dynamics framework

Our main result in the adaptive dynamics framework is that there exists a unique ESS which is whether monomorphic (a single Dirac mass) or dimorphic (a sum of two Dirac masses). We determine indeed under which conditions the ESS is monomorphic or dimorphic. To state our result, we first define

$$z^{D*} = \sqrt{\theta^2 - \frac{m_1 m_2}{4\theta^2 g_1 g_2}}, \qquad N_1^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 g_2} + r_1 - m_1}{\kappa_1}, \qquad N_2^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 g_1} + r_2 - m_2}{\kappa_2}. \tag{9}$$

Theorem 3.1 *Assume (3)–(4). Then, there exists a unique set of points Ω^* which is an ESS.*
(i) The ESS is dimorphic if and only if
$$\frac{m_1 m_2}{4 g_1 g_2 \theta^4} < 1, \tag{10}$$

$$0 < m_2 N_2^{D*} + (R_1(-z^{D*}; N_1^{D*}) - m_1) N_1^{D*}, \tag{11}$$

and
$$0 < m_1 N_1^{D*} + (R_2(z^{D*}; N_2^{D*}) - m_2) N_2^{D*}. \tag{12}$$

Then the dimorphic equilibrium is given by

$$n_i^{D*} = \nu_{\mathrm{I},i}\delta(z + z^{D*}) + \nu_{\mathrm{II},i}\delta(z - z^{D*}), \quad \nu_{\mathrm{I},i} + \nu_{\mathrm{II},i} = N_i^{D*}, \quad i = 1, 2. \tag{13}$$

(ii) If the above conditions are not satisfied then the ESS is monomorphic. In the case where condition (10) is verified but the r.h.s. of (11) (respectively (12)) is negative, the fittest trait belongs to the interval $(-\theta, -z^{D*})$ (respectively (z^{D*}, θ)). If (10) is satisfied but (11) (respectively (12)) is an equality then the monomorphic ESS is given by $\{-z^{D*}\}$ (respectively $\{z^{D*}\}$).

Note that one can compute the weights $\nu_{k,i}$, for $k = \mathrm{I}, \mathrm{II}$ and $i = 1, 2$:

$$\begin{pmatrix} \nu_{\mathrm{I},1} \\ \nu_{\mathrm{I},2} \end{pmatrix} = \frac{m_1 N_1^{D*} + (R_2(z^{D*}; N_2^{D*}) - m_2) N_2^{D*}}{m_1 m_2 - (R_1(-z^{D*}; N_1^{D*}) - m_1)(R_2(z^{D*}; N_2^{D*}) - m_2)} \begin{pmatrix} m_2 \\ -R_1(-z^{D*}; N_1^{D*}) + m_1 \end{pmatrix},$$
$$\begin{pmatrix} \nu_{\mathrm{II},1} \\ \nu_{\mathrm{II},2} \end{pmatrix} = \frac{m_2 N_2^{D*} + (R_1(-z^{D*}; N_1^{D*}) - m_1) N_1^{D*}}{m_1 m_2 - (R_1(-z^{D*}; N_1^{D*}) - m_1)(R_2(z^{D*}; N_2^{D*}) - m_2)} \begin{pmatrix} -R_2(z^{D*}; N_2^{D*}) + m_2 \\ m_1 \end{pmatrix}. \tag{14}$$

Moreover, since $W(-z^{D*}; N_1^{D*}, N_2^{D*}) = 0$, one can easily verify that condition (11) is equivalent with

$$m_1 N_1^{D*} + (R_2(-z^{D*}; N_2^{D*}) - m_2)N_2^{D*} < 0. \tag{15}$$

Similarly, since $W(z^{D*}; N_1^{D*}, N_2^{D*}) = 0$, one can easily verify that condition (12) is equivalent with

$$m_2 N_2^{D*} + (R_1(z^{D*}; N_1^{D*}) - m_1)N_1^{D*} < 0. \tag{16}$$

To prove Theorem 3.5–(iii) we will use the following result which is a corollary of Theorem 3.1.

Corollary 3.2 *Assume that*

$$m_2 N_2^{D*} + (R_1(-z^{D*}; N_1^{D*}) - m_1)N_1^{D*} \neq 0, \qquad m_1 N_1^{D*} + (R_2(z^{D*}; N_2^{D*}) - m_2)N_2^{D*} \neq 0, \tag{17}$$

and let the set Ω^* be the unique ESS of the model and (N_1^*, N_2^*) be the total population sizes at the demographic equilibrium of this ESS. Then,

$$W(z, N_1^*, N_2^*) < 0, \qquad \text{for all } z \in \mathbb{R} \setminus \Omega^*. \tag{18}$$

Note also that when the habitats are symmetric, then conditions (11) and (12) always hold under condition (10), and hence

Corollary 3.3 *Assume that the habitats are symmetric:*

$$r = r_1 = r_2, \quad g = g_1 = g_2, \quad \kappa = \kappa_1 = \kappa_2, \quad m = m_1 = m_2. \tag{19}$$

(i) Then the unique ESS is dimorphic if and only if

$$\frac{m}{2g} < \theta^2. \tag{20}$$

The dimorphic ESS is determined by (13).
(ii) When condition (20) is not satisfied, then the ESS is monomorphic and the corresponding monomorphic equilibrium is given by

$$n_1^{M*}(z) = n_2^{M*}(z) = N^{M*}\delta(z), \quad \text{with } N^{M*} = \frac{1}{\kappa}\left(r - g\theta^2\right). \tag{21}$$

The next proposition gives an interpretation of conditions (11) and (12).

Proposition 3.4 *Assume that condition (10) is satisfied and that $r_i - m_i > 0$, for $i = 1, 2$. Then,*
(i) condition (11) holds if and only if a mutant trait of type z^{D*} can invade a monomorphic resident population of type $-z^{D*}$ which is at it's demographic equilibrium.
(ii) condition (12) holds if and only if a mutant trait of type $-z^{D*}$ can invade a monomorphic resident population of type z^{D*} which is at it's demographic equilibrium.

One can indeed rewrite conditions (11) and (12) respectively as below

$$C_1 < \alpha_2 r_2 - \alpha_1 r_1, \qquad C_2 < \beta_1 r_1 - \beta_2 r_2,$$

with C_i, α_i and β_i constants depending on $m_1, m_2, g_1, g_2, \kappa_1, \kappa_2$ and θ. These conditions are indeed a measure of asymmetry between the habitats. They appear from the fact that even if condition (10), which is the only condition for dimorphism in symmetric habitats, is satisfied, while the quality of the habitats are very different, the ESS cannot be dimorphic. In this case, the population will be able to adapt only to one of the habitats and it will be maladapted to the other one.

3.2 The computation of the zero order terms u_i

The identification of the zero order terms u_i is based on the following result.

Theorem 3.5 *Assume* (3)–(4).
(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 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 $u \in C(\mathbb{R})$, such that u is a viscosity solution to the following equation

$$\begin{cases} -|u'(z)|^2 = W(z, N_1^*, N_2^*), & in \ \mathbb{R}, \\ \max_{z \in \mathbb{R}} u(z) = 0. \end{cases} \tag{22}$$

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) Under condition (17) *we have* $\operatorname{supp} n_1^* = \operatorname{supp} n_2^* = \{z \,|\, W(z, N_1^*, N_2^*) = 0\}$ *and hence*

$$\{z \,|\, u(z) = 0\} = \{z \,|\, W(z, N_1^*, N_2^*) = 0\}. \tag{23}$$

The solution of (22)–(23) *is indeed unique and hence the whole sequence $(u_{\varepsilon,i})_\varepsilon$ converge locally uniformly in $\mathbb{R}$ to u.*

Remark 3.6 *The convergence of $(u_{\varepsilon,i})_\varepsilon$ along subsequences, towards a viscosity solution of a Hamilton-Jacobi equation (i.e. part (ii) of Theorem 3.5) can be proved following similar arguments for a more general class of models. One can verify that our arguments can indeed be easily adapted to a model with an arbitrary number k of patches with corresponding growth rates $R_i(x, N_i)$, where $R_i : \mathbb{R}^d \times \mathbb{R}^+ \to \mathbb{R}$, for $i = 1, \ldots, k$, are smooth functions which satisfy*

$$\frac{\partial}{\partial N_i} R_i(x, N_i) < -C < 0, \qquad R_i(z, N_i) \to -\infty \ as \ |z| \to +\infty, \quad and \quad \max_{z \in \mathbb{R}^d} W(z, 0, \ldots, 0) > 0,$$

where $W(z, N_1, \ldots, N_k)$ is the principal eigenvalue corresponding to the matrix

$$\widetilde{\mathcal{A}} = \begin{pmatrix} R_1(x, N_1) - m_{11} & \ldots & m_{1k} \\ \vdots & \ddots & \vdots \\ m_{k1} & \ldots & R_k(x, N_k) - m_{kk} \end{pmatrix},$$

and where m_{ij}, for $i \neq j$, corresponds to the migration rate from habitat j to habitat i, $m_{ii} = \sum_{j \neq i} m_{ji}$ and the sequence $(m_{ij})_{ij}$ is such that the matrix $\widetilde{\mathcal{A}}$ is irreducible.

Note that a Hamilton-Jacobi equation of type (22) in general might admit several viscosity solutions. Here, the uniqueness is obtained thanks to (23) 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 ([24], Chapter 5 and [6]). In what follows we assume that (17) and hence (23) always hold. We then give an explicit formula for u considering two cases (one can indeed verify easily that the functions below are viscosity solutions to (22)–(23)):

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

$$u(z) = -\Big| \int_{z^{M*}}^{z} \sqrt{-W(x; N_1^{M*}, N_2^{M*})}dx \Big|. \tag{24}$$

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

$$u(z) = \max\Big(-\Big| \int_{z_{\mathrm{I}}^*}^{z} \sqrt{-W(x; N_1^{D*}, N_2^{D*})}dx \Big|, -\Big| \int_{z_{\mathrm{II}}^*}^{z} \sqrt{-W(x; N_1^{D*}, N_2^{D*})}dx \Big| \Big).$$

3.3 Next order terms and approximation of the moments

In this subsection we show how one can compute formally the first order term v_i, and in particular its second order Taylor expansion around the zero level set of u, and determine the value of w_i at those points. Next, using these expansions we estimate the moments of the population's distribution with an error of at most order $O(\varepsilon^2)$ as $\varepsilon \to 0$. We only present the method in the case of monomorphic population where the demographic equilibrium corresponding to this ESS is given by $(N_1^{M*}\delta(z - z^{M*}), N_2^{M*}\delta(z - z^{M*}))$. The dimorphic case can be treated following similar arguments.

We first note that, one can compute, using (24), a Taylor expansion of order 4 around the ESS point z^{M*}:

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

We then look for constants D_i, E_i, F_i and G_i such that

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

We will only compute D_i, E_i and F_i. The constants G_i are not necessary in the computation of the moments but they appear in our intermediate computations. Replacing the functions u, v_i and w_i by the above approximations to compute $N_{\varepsilon,i} = \int_{\mathbb{R}} n_{\varepsilon,i}(z)dz$, we obtain

$$v_i(z^{M*}) = \log\big(N_i^{M*}\sqrt{A}\big),$$

$$N_{\varepsilon,i} = N_i^{M*} + \varepsilon K_i + O(\varepsilon^2), \quad \text{with} \quad K_i = N_i^{M*}\Big(\frac{7.5\,B^2}{A^3} + \frac{3(C + BD_i)}{A^2} + \frac{E_i + 0.5\,D_i^2}{A} + F_i\Big).$$

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

$$\begin{cases} -\varepsilon u_{\varepsilon,1}''(z) = |u_{\varepsilon,1}'|^2 + R_1(z, N_{\varepsilon,1}) + m_2 \exp\big(\frac{u_{\varepsilon,2} - u_{\varepsilon,1}}{\varepsilon}\big) - m_1, \\ -\varepsilon u_{\varepsilon,2}''(z) = |u_{\varepsilon,2}'|^2 + R_2(z, N_{\varepsilon,2}) + m_1 \exp\big(\frac{u_{\varepsilon,1} - u_{\varepsilon,2}}{\varepsilon}\big) - m_2. \end{cases} \tag{25}$$

We then let $\varepsilon \to 0$ in the first line of (25) and use (22) to obtain

$$v_2(z) - v_1(z) = \log\Big(\frac{1}{m_2}\big(W(z, N_1^{M*}, N_2^{M*}) - R_1(z, N_1^{M*}) + m_1\big)\Big). \tag{26}$$

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Keeping respectively, only the terms of order $(z - z^{M*})$ and $(z - z^{M*})^2$ we find

$$\lambda_1 = D_2 - D_1 = \frac{2g_1 N_1^{M*}(z^{M*} + \theta)}{m_2 N_2^{M*}},$$

$$\lambda_2 = E_2 - E_1 = \frac{N_1^{M*}}{m_2 N_2^{M*}}(-A^2 + g_1) - \frac{2g_1^2 N_1^{M*2}}{m_2^2 N_2^{M*2}}(z^{M*} + \theta)^2.$$

Combining the above lines we obtain

$$\frac{K_2}{N_2^{M*}} - \frac{K_1}{N_1^{M*}} = \lambda_3 + \frac{0.5\,\lambda_1(D_1 + D_2)}{A} + F_2 - F_1, \quad \text{with} \quad \lambda_3 = \frac{3B}{A^2}\lambda_1 + \frac{1}{A}\lambda_2. \tag{27}$$

Next, keeping the terms of order ε in (25) we obtain, for $\{i, j\} = \{1, 2\}$,

$$-u'' = 2u' \cdot v_i' - \kappa_i K_i + m_j \exp(v_j - v_i)(w_j - w_i). \tag{28}$$

Evaluating the above equality at z^{M*} we obtain

$$A = -\kappa_i K_i + m_j \frac{N_j^{M*}}{N_i^{M*}}(F_j - F_i).$$

Replacing (27) in the above system we obtain

$$\begin{cases} A = -\kappa_1 K_1 + m_2 \frac{N_2^{M*}}{N_1^{M*}}\left(\frac{K_2}{N_2^{M*}} - \frac{K_1}{N_1^{M*}} - \lambda_3 - \frac{0.5\,\lambda_1(D_1 + D_2)}{A}\right), \\ A = -\kappa_2 K_2 + m_1 \frac{N_1^{M*}}{N_2^{M*}}\left(\frac{K_1}{N_1^{M*}} - \frac{K_2}{N_2^{M*}} + \lambda_3 + \frac{0.5\,\lambda_1(D_1 + D_2)}{A}\right). \end{cases}$$

This system allows us to identify (K_1, K_2) in a unique way, as an affine function of $(D_1 + D_2)$.

Next we substrate the two lines of the system (28) to obtain

$$w_2 - w_1 = \frac{2u' \cdot (v_2' - v_1') + \kappa_1 K_1 - \kappa_2 K_2}{m_2 \exp(v_2 - v_1) + m_1 \exp(v_1 - v_2)}. \tag{29}$$

Evaluating the above equation at z^{M*} we find

$$F_2 - F_1 = \frac{\kappa_1 K_1 - \kappa_2 K_2}{m_1 N_1^{M*}/N_2^{M*} + m_2 N_2^{M*}/N_1^{M*}},$$

and keeping the terms of order $(z - z^{M*})$ we obtain

$$G_2 - G_1 = \frac{-2A(D_2 - D_1)}{m_1 N_1^{M*}/N_2^{M*} + m_2 N_2^{M*}/N_1^{M*}} + \frac{(m_2 N_2^{M*}/N_1^{M*} - m_1 N_1^{M*}/N_2^{M*})(D_2 - D_1)}{(m_1 N_1^{M*}/N_2^{M*} + m_2 N_2^{M*}/N_1^{M*})^2}(\kappa_1 K_1 - \kappa_2 K_2).$$

We then keep the terms of order $(z - z^{M*})$ in (28) to find

$$-6B = -2AD_1 + m_2 \frac{N_2}{N_1}\left((D_2 - D_1)(F_2 - F_1) + G_2 - G_1\right).$$

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Combining the above lines, one can write D_1 as an affine function of $D_1 + D_2$. Since $D_2 - D_1$ is already known, this allows to identify, at least in a generic way, D_i and consequently K_i (see [30] for examples of such computations). Next, we replace (29) in (28) to obtain

$$-u'' = 2u' \cdot v_i' - \kappa_i K_i + \frac{m_j \exp(v_j - v_i)}{m_2 \exp(v_2 - v_1) + m_1 \exp(v_1 - v_2)} \big(2u' \cdot (v_j' - v_i') + \kappa_i K_i - \kappa_j K_j\big).$$

All the terms in the above system, except v_i', are already known. Hence one can compute v_i from the above system. In particular, keeping the terms of order $(z - z^{M*})^2$ in the above line, one can compute $E_i = \frac{1}{2} v_i''(z^{M*})$ and consequently F_i.

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 with an error of at most order $O(\varepsilon^2)$ as $\varepsilon \to 0$. We first note that, replacing $u_{\varepsilon,i}$ by the approximation (6) and using the Taylor expansions of u, v_i and w_i obtained above, we can compute

$$\int (z - z^{M*})^k n_{\varepsilon,i}(z) dz = \frac{\varepsilon^{\frac{k}{2}} \sqrt{A} N_i^{M*}}{\sqrt{2\pi}} \int_{\mathbb{R}} \big(y^k e^{-\frac{A}{2} y^2} \big(1 + \sqrt{\varepsilon}(By^3 + D_i y) + O(\varepsilon)\big) dy$$
$$= \varepsilon^{\frac{k}{2}} N_i^{M*} \Big(\mu_k(\tfrac{1}{A}) + \sqrt{\varepsilon}\big(B\mu_{k+3}(\tfrac{1}{A}) + D_i \mu_{k+1}(\tfrac{1}{A})\big)\Big) + O(\varepsilon^{\frac{k+2}{2}}),$$

where $\mu_k(\sigma^2)$ is the k-th order central moment of a Gaussian law with variance σ^2. Note that to compute the above integral, we performed a change of variable $z - z^{M*} = \sqrt{\varepsilon} y$. 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 moments 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^*. The above computation leads in particular to the following approximations of the population size, the mean, the variance and the third central moment of the population's distribution:

$$\begin{cases} N_{\varepsilon,i} = \int n_{\varepsilon,i}(z) dz = N_i^{M*}(1 + \varepsilon(F_i + \frac{E_i + 0.5 D_i^2}{A} + \frac{3(C + BD_i)}{A^2} + \frac{7.5B^2}{A^3})) + O(\varepsilon^2), \\ \mu_{\varepsilon,i} = \frac{1}{N_{\varepsilon,i}} \int z n_{\varepsilon,i}(z) dz = z^{M*} + \varepsilon(\frac{3B}{A^2} + \frac{D_i}{A}) + O(\varepsilon^2), \\ \sigma_{\varepsilon,i}^2 = \frac{1}{N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^2 n_{\varepsilon,i}(z) dz = \frac{\varepsilon}{A} + O(\varepsilon^2), \\ s_{\varepsilon,i} = \frac{1}{N_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^3 n_{\varepsilon,i}(z) dz = \frac{6B}{A^3} \varepsilon^2 + O(\varepsilon^3). \end{cases}$$

4 Identification of the ESS (the proofs of Theorem 3.1 and Proposition 3.4)

In this section, we prove Theorem 3.1, Corollary 3.2 and Proposition 3.4. We first provide a description of the ESS in Subsection 4.1. Next, we prove Theorem 3.1-(i) in Subsection 4.2. In Subsection 4.3 we prove Theorem 3.1-(ii) and Corollary 3.2. Finally in Subsection 4.4 we prove Proposition 3.4.

4.1 The description of the ESS

We first rewrite the conditions for ESS in terms of the following variables:

$$\mu_i(N_i) = \frac{\kappa_i N_i + m_i - r_i}{g_i}, \qquad i = 1, 2, \tag{30}$$

where μ_i is an indicator of the size of the population in patch i. In several parts of this paper, we will express the effective fitness as a function of μ_i instead of N_i:

$$W_\mu(z, \mu_1(N_1), \mu_2(N_2)) = W(z, N_1, N_2),$$

hence, the effective fitness in terms of μ_i is given by

$$W_\mu(z, \mu_1, \mu_2) = \frac{1}{2}\left[-g_1(\mu_1 + (z+\theta)^2) - g_2(\mu_2 + (z-\theta)^2)\right. \\ \left. +\sqrt{\left(g_1(\mu_1 + (z+\theta)^2) - g_2(\mu_2 + (z-\theta)^2)\right)^2 + 4m_1m_2}\right].$$

From the definition of ESS, we deduce that at the demographic equilibrium of an ESS, where the indicators of population size in patches 1 and 2 are given by (μ_1^*, μ_2^*), we have

$$W_\mu(z, \mu_1^*, \mu_2^*) \leq 0, \qquad \text{for } z \in \mathbb{R},$$

with the equality attained at one or two points corresponding to the monomorphic or dimorphic ESS. We then notice that the above inequality is equivalent with

$$\begin{cases} g_1(\mu_1^* + (z+\theta)^2) + g_2(\mu_2^* + (z-\theta)^2) \geq 0, \\ f(z; \mu_1^*, \mu_2^*) := (\mu_1^* + (z+\theta)^2)(\mu_2^* + (z-\theta)^2) \geq \frac{m_1m_2}{g_1g_2}. \end{cases}$$

This implies that at the ESS, $\mu_i^* > 0$ and

$$\min_x (\mu_1^* + (z+\theta)^2)(\mu_2^* + (z-\theta)^2) = \frac{m_1m_2}{g_1g_2}. \tag{31}$$

Note that the above function is a fourth order polynomial and hence has one or two minium points, which here will correspond to the monomorphic or dimorphic ESS. Conditions for the demographic equilibria will help us determine (μ_1^*, μ_2^*):

(i) If the minimum in (31) is attained at the point z^{M*}, for z^{M*} to be an ESS the following condition must be satisfied:

$$\begin{pmatrix} -g_1\left((z^{M*} + \theta)^2 + \mu_1^*\right) & m_2 \\ m_1 & -g_2\left((z^{M*} - \theta)^2 + \mu_2^*\right) \end{pmatrix} \begin{pmatrix} N_1^{M*} \\ N_2^{M*} \end{pmatrix} = 0,$$

with

$$N_i^{M*} > 0, \qquad \mu_i^* = \mu_i(N_i^{M*}) = \frac{\kappa_i N_i^{M*} + m_i - r_i}{g_i}, \qquad i = 1, 2.$$

(ii) If the minimum in (31) is attained at two points z_I^{D*} and z_{II}^{D*}, for (z_I^{D*}, z_{II}^{D*}) to be an ESS, there must exist $\nu_{k,i} > 0$, for $i = 1, 2$ and $k = I, II$, such that,

$$\begin{pmatrix} -g_1\left((z_k^{D*} + \theta)^2 + \mu_1^*\right) & m_2 \\ m_1 & -g_2\left((z_k^{D*} - \theta)^2 + \mu_2^*\right) \end{pmatrix} \begin{pmatrix} \nu_{k,1} \\ \nu_{k,2} \end{pmatrix} = 0, \qquad k = I, II, \tag{32}$$

$$\nu_{I,1} + \nu_{II,,1} = N_1^{D*}, \quad \nu_{I,,2} + \nu_{II,,2} = N_2^{D*}, \quad \mu_i^* = \mu_i(N_i^{D*}) \text{ for } i = 1, 2. \tag{33}$$

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4.2 The dimorphic ESS

To identify the dimorphic ESS we first give the following lemma

Lemma 4.1 *If $f(z; \mu_1, \mu_2)$ has two global minimum points z_{I} and z_{II}, then $\mu_1 = \mu_2$ and $z_{\mathrm{I}} = -z_{\mathrm{II}}$.*

Proof. Let's suppose that $f(z; \mu_1, \mu_2)$ has two global minimum points z_{I} and z_{II} and $\mu_2 < \mu_1$. The case with $\mu_1 < \mu_2$ can be treated following similar arguments.

Since z_{I} and z_{II} are minimum points we have

$$(\mu_1 + (z_k + \theta)^2)(\mu_2 + (z_k - \theta)^2) \leq (\mu_1 + (-z_k + \theta)^2)(\mu_2 + (-z_k - \theta)^2), \qquad k = \mathrm{I}, \mathrm{II}.$$

It follows that

$$0 \leq 4z_k \theta (\mu_1 - \mu_2), \qquad k = \mathrm{I}, \mathrm{II},$$

and hence

$$0 \leq z_k, \qquad k = \mathrm{I}, \mathrm{II}.$$

This implies in particular that all the roots of $f'(z, \mu_1, \mu_2)$ are positive. However, this is not possible since

$$f'(z, \mu_1, \mu_2) = 4z^3 + 2(\mu_1 + \mu_2 - 2\theta^2)z + 2\theta(\mu_2 - \mu_1).$$

The fact that there is no second order term in the above expression implies that the sum of the roots is zero and hence the roots change sign. This is a contradiction with the previous arguments. We hence deduce that $\mu_1 = \mu_2$. $\square$

The above lemma indicates that at a dimorphic ESS one should have $\mu_1^* = \mu_2^* = \mu^*$. Hence to find a dimorphic ESS we look for $(\mu^*, z_{\mathrm{I}}^*, z_{\mathrm{II}}^*)$ such that

$$f(z_k^*, \mu^*, \mu^*) = \min f(z; \mu^*, \mu^*) = \frac{m_1 m_2}{g_1 g_2}, \qquad k = \mathrm{I}, \mathrm{II}. \tag{34}$$

To identify the minimum points of f we differentiate f with respect to z and find

$$f'(z, \mu^*, \mu^*) = 4z^3 + 4(\mu^* - \theta^2)z.$$

For f to have two minimum points, f' must have three roots and hence one should have

$$\mu^* < \theta^2. \tag{35}$$

Then, the minimum points are given by

$$z_{\mathrm{I}}^* = -\sqrt{\theta^2 - \mu^*}, \qquad z_{\mathrm{II}}^* = \sqrt{\theta^2 - \mu^*}.$$

Then replacing the above values in (34) we obtain

$$\mu^* = \frac{m_1 m_2}{4\theta^2 g_1 g_2}.$$

Note that combining the above line with condition (35) we obtain (10).

Up until now, we have proven that if a dimorphic ESS exists (10) is verified and the dimorphic ESS is given by $(z_{\mathrm{I}}^{D*}, z_{\mathrm{II}}^{D*}) = (-\sqrt{\theta^2 - \mu^*}, \sqrt{\theta^2 - \mu^*})$. However, for this point to be an ESS, as explained

in the previous subsection, there must exist $\nu_{k,i} > 0$, for $i = 1, 2$ and $k = \mathrm{I}, \mathrm{II}$ such that (32)–(33) are satisfied. Replacing z_k^{D*} by their values and solving (32)–(33), we obtain that $\nu_{k,i}$, for $i = 1, 2$ and $k = \mathrm{I}, \mathrm{II}$, are identified in a unique way by (14). One can verify by simple computations that the weights $\nu_{k,i}$ are positive if and only if conditions (11)–(12) are satisfied. As a conclusion, we obtain that a dimorphic ESS exists if and only if the conditions (10)–(12) are satisfied. Moreover, when it exists, such dimorphic ESS is unique.

4.3 The monomorphic ESS

In this subsection we prove Theorem 3.1-(ii) and Corollary 3.2. To this end, we assume thanks to (3) and without loss of generality that $r_1 - m_1 > 0$ and then we consider two cases:

(i) We first suppose that condition (10) does not hold. We then introduce the following functions:

$$\begin{cases} F = (F_1, F_2) : (0, +\infty) \to (0, +\infty) \times [-\theta, \theta] \\ \mu_2 \mapsto (\mu_1, \overline{z}), \end{cases} \qquad \begin{cases} G : (0, +\infty) \times [-\theta, \theta] \to \mathbb{R} \\ (\mu_1, \overline{z}) \mapsto \overline{\mu}_2, \end{cases}$$

where μ_1 and $\overline{z}$ are chosen such that

$$f(\overline{z}, \mu_1, \mu_2) = \min f(z; \mu_1, \mu_2) = \frac{m_1 m_2}{g_1 g_2},$$

and $\overline{\mu}_2$ is given by

$$\overline{\mu}_2 = \frac{1}{g_2} \left[\frac{\kappa_2 g_1}{m_2} ((\overline{z} + \theta)^2 + \mu_1) \left(\frac{g_1 \mu_1 + r_1 - m_1}{\kappa_1} \right) + m_2 - r_2 \right]. \tag{36}$$

We claim the following lemma which we will prove at the end of this paragraph.

Lemma 4.2 *If* (10) *does not hold, then the functions F and G are well-defined. Moreover, F_1 and F_2 are decreasing with respect to μ_2 and G is increasing with respect to μ_1 and $\overline{z}$.*

Following the arguments in Section 4.1, one can verify that a trait z^* is a monomorphic ESS with a demographic equilibrium (μ_1^*, μ_2^*) if and only if $F(\mu_2^*) = (\mu_1^*, z^*)$ and $G \circ F(\mu_2^*) = \mu_2^*$. Therefore, identifying monomorphic evolutionary stable strategies is equivalent with finding the fixed points of $G \circ F$.

In the one hand, from Lemma 4.2 we deduce that $G \circ F$ is a decreasing function . In the other hand, one can verify that, as $\mu_2 \to 0$, $G \circ F(\mu_2) \to +\infty$. In particular $G \circ F(\mu_2) > \mu_2$ for μ_2 small enough. It follows that there exists a unique μ_2^* such that $G \circ F(\mu_2^*) = \mu_2^*$. We deduce that there exists a unique ESS which is given by $z^{M*} = F_2(\mu_2^*)$. Moreover, $(F_1(\mu_2^*), \mu_2^*)$ corresponds to its demographic equilibrium.

Note that for such ESS to make sense, one should also have $N_i^{M*}(\mu_i^*) > 0$. This is always true for such fixed point. Note indeed that, since $\mu_1^* = F_1(\mu_2^*) \in (0, \infty)$ and $r_1 - m_1 > 0$ we deduce that $N_1^{M*} > 0$. Moreover, the positivity of N_2^{M*} follows from $N_2^{M*} = (g_2 \mu_2^* + r_2 - m_2)/\kappa_2$, (36) and the positivity of $r_1 - m_1$ and μ_1^*.

Proof of Lemma 4.2. The fact that $G : (0, +\infty) \times [-\theta, \theta] \to \mathbb{R}$ (and respectively $F_1 = (0, +\infty) \to (0, \infty)$) is well-defined and increasing (respectively decreasing) is immediate. We only show that F_2 is well-defined and decreasing. To this end, we notice that since f is a fourth order polynomial, it

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admits one or two minimum points. However, from the arguments in Subsection 4.2 we know that the only possibility to have two global minima is that (10) holds and $\mu_2 = \mu^* = \frac{m_1 m_2}{4\theta^2 g_1 g_2}$. Since we assume that (10) does not hold, f always admits a unique minimum point in $\mathbb{R}$. This minimum point is indeed attained in $[-\theta, \theta]$ since for all $z < -\theta$, $f(z; \mu_1, \mu_2) > f(-\theta; \mu_1, \mu_2)$ and for all $z > \theta$, $f(z; \mu_1, \mu_2) > f(\theta; \mu_1, \mu_2)$. Hence $\overline{z}$ is defined in a unique way in $[-\theta, \theta]$.

Finally, it remains to prove that $F_2 : (0, \infty) \to [-\theta, \theta]$ is a decreasing function. To this end, let's suppose that $\widetilde{\mu}_2 > \mu_2$. Therefore, $F_1(\widetilde{\mu}_2) = \widetilde{\mu}_1 < F_1(\mu_2) = \mu_1$. We want to prove that $F_2(\widetilde{\mu}_2) = \widetilde{z} < F_2(\mu_2) = \overline{z}$. To this end, we write

$$
\begin{aligned}
f(z; \widetilde{\mu}_1, \widetilde{\mu}_2) &= f(z; \mu_1, \mu_2) + (\widetilde{\mu}_1 - \mu_1)(z - \theta)^2 + (\widetilde{\mu}_2 - \mu_2)(z + \theta)^2 + \widetilde{\mu}_1 \widetilde{\mu}_2 - \mu_1 \mu_2 \\
&= f(z; \mu_1, \mu_2) + h(z; \mu_1, \mu_2, \widetilde{\mu}_1, \widetilde{\mu}_2),
\end{aligned}
$$

where h is increasing with respect to z. Since $f(z, \mu_1, \mu_2)$ attains its minimum at $\overline{z}$ and $f(z, \widetilde{\mu}_1, \widetilde{\mu}_2)$ attains its minimum at $\widetilde{z}$ we find that

$$
f(\overline{z}; \mu_1, \mu_2) < f(\widetilde{z}; \mu_1, \mu_2),
$$

$$
f(\widetilde{z}; \mu_1, \mu_2) + h(\widetilde{z}; \mu_1, \mu_2, \widetilde{\mu}_1, \widetilde{\mu}_2) < f(\overline{z}; \mu_1, \mu_2) + h(\overline{z}; \mu_1, \mu_2, \widetilde{\mu}_1, \widetilde{\mu}_2).
$$

Combining the above inequalities, we obtain that

$$
h(\widetilde{z}; \mu_1, \mu_2, \widetilde{\mu}_1, \widetilde{\mu}_2) < h(\overline{z}; \mu_1, \mu_2, \widetilde{\mu}_1, \widetilde{\mu}_2).
$$

and since h is an increasing function, we conclude that $\widetilde{z} < \overline{z}$.

□

(ii) We next suppose that (10) holds. Consequently, F is not well-defined at $\mu_2 = \mu^* = \frac{m_1 m_2}{4\theta^2 g_1 g_2}$ since $F_1(\mu^*) = \mu^*$ and $\max_z f(z; \mu^*, \mu^*)$ is attained at two points $\pm z^{D*}$. Therefore, we only can define F in $(0, \infty) \setminus \{\mu^*\}$:

$$
\begin{cases}
\widetilde{F} = (\widetilde{F}_1, \widetilde{F}_2) : (0, +\infty) \setminus \{\mu^*\} \to (0, +\infty) \times [-\theta, \theta] \\
\mu_2 \mapsto (\mu_1, \overline{z}),
\end{cases}
\qquad
\begin{cases}
G : (0, +\infty) \times [-\theta, \theta] \to \mathbb{R} \\
(\mu_1, \overline{z}) \mapsto \overline{\mu}_2,
\end{cases}
$$

where μ_1, $\overline{z}$ and $\overline{m}_2$ are chosen as above. Following similar arguments as in the proof of Lemma 4.2 we obtain

Lemma 4.3 *Under condition* (10) *the functions* $\widetilde{F}$ *and* G *are well-defined. Moreover,* $\widetilde{F}_1$ *and* $\widetilde{F}_2$ *are decreasing with respect to* μ_2 *in the intervals* $(0, \mu^*)$ *and* $(\mu^*, +\infty)$ *and* G *is increasing with respect to* μ_1 *and* $\overline{z}$.

As above, identifying monomorphic evolutionary stable strategies is equivalent with finding the fixed points of $G \circ \widetilde{F}$, which is a decreasing function in the intervals $(0, \mu^*)$ and $(\mu^*, +\infty)$ thanks to the lemma 4.3. We then compute

$$
\widetilde{F}(\mu^{*-}) = (\mu^*, z^{D*}), \qquad F(\mu^{*+}) = (\mu^*, -z^{D*}),
$$

$$
G \circ \widetilde{F}(\mu^{*-}) = \frac{1}{g_2} \left[\frac{\kappa_2}{m_2} g_1 \big((z^{D*} + \theta)^2 + \mu^* \big) \left(\frac{g_1 \mu^* + r_1 - m_1}{\kappa_1} \right) + m_2 - r_2 \right],
$$

$$G \circ \widetilde{F}(\mu^{*+}) = \frac{1}{g_2} \left[\frac{\kappa_2}{m_2} g_1 \big((-z^{D*} + \theta)^2 + \mu^* \big) \left(\frac{g_1 \mu^* + r_1 - m_1}{\kappa_1} \right) + m_2 - r_2 \right],$$

where μ^{*+} and μ^{*-} correspond respectively to the limits from the right and from the left as $\mu \to \mu^*$. One can easily verify that $G \circ \widetilde{F}(\mu^{*+}) < \mu^*$ if and only if (11) holds, and similarly $G \circ \widetilde{F}(\mu^{*-}) > \mu^*$ if and only if (16), or equivalently (12), holds. We hence deduce, from the latter property and the fact that $G \circ \widetilde{F}$ is decreasing in the intervals $(0, \mu^*)$ and $(\mu^*, +\infty)$, that:

1. If (11) and (12) hold there is no monomorphic ESS. Note that, under these conditions there exists a unique dimorphic ESS.

2. if (11) holds and the r.h.s. of (12) is negative, then there exists a unique monomorphic ESS in $\mu_2^{M*} \in (0, \mu^*)$, $\mu_1^{M*} \in (\mu^*, \infty)$ and $z^{M*} \in (z^{D*}, \theta)$.

3. if (12) holds and the r.h.s. of (11) is negative, then there exists a unique monomorphic ESS with $\mu_2^{M*} \in (\mu^*, \infty)$, $\mu_1^{M*} \in (0, \mu^*)$ and $z^{M*} \in (-\theta, -z^{D*})$.

4. if (11) holds and (12) is an equality, then there exists a unique monomorphic ESS which is given by $\{z^{D*}\}$ and $\mu_1^* = \mu_2^* = \mu^*$.

5. if (12) holds and (11) is an equality, then there exists a unique monomorphic ESS which is given by $\{-z^{D*}\}$ and $\mu_1^* = \mu_2^* = \mu^*$.

6. Finally, from the fact that (11) and (12) are respectively equivalent to (15) and (16) we deduce that at least one of conditions (11) and (12) always holds. Therefore, all the possible cases have been considered.

Note that, following similar arguments to the previous case, the total population sizes $N_i^{M*}(\mu_i^*)$, for $i = 1, 2$, corresponding to the unique fixed point, are positive and hence the obtained monomorphic ESS is indeed valid. This concludes the proof of Theorem 3.1. It remains to prove Corollary 3.2:

Proof of Corollary 3.2 We first notice from the arguments above that $W(z, N_1^*, N_2^*) = W_\mu(z, \mu_1^*, \mu_2^*)$ has at most two global maximum points. Therefore, for (18) not to hold, the unique ESS should be monomorphic while $W_\mu(z, \mu_1^*, \mu_2^*)$ has two maximum points. However, from the arguments in Section 4.2 we know that if $W_\mu(z, \mu_1^*, \mu_2^*)$ has two maximum points, then (10) holds, $\mu_1^* = \mu_2^* = \mu^*$ and the maximum points are given by $\{\pm z^{D*}\}$. Finally, from the results in the above paragraph, we know that the only possibility to have a monomorphic ESS in this case, is that either (11) or (12) is an equality, which is in contradiction with (17). $\square$

4.4   The interpretation of conditions (11) and (12)

In this subsection we prove Proposition 3.4. We only prove the first claim. The second claim can be derived following similar arguments.

We denote by (μ_1^{eq}, μ_2^{eq}) the demographic equilibrium of a monomorphic population of trait $-z^{D*}$ and we first claim the following lemma.

Lemma 4.4 *There exists a unique demographic equilibrium $n_i = N_i \delta(z + z^{D*})$ corresponding to the the set $\Omega = \{-z^{D*}\}$.*

Proof. We introduce two functions K and H which are respectively close to F_1 and G introduced above:

$$\begin{cases} K : (-(z^{D*}+\theta)^2, +\infty) \to \mathbb{R} \\ \mu_2 \mapsto \mu_1, \end{cases} \qquad \begin{cases} H : \mathbb{R} \to \mathbb{R} \\ \mu_1 \mapsto \overline{\mu}_2, \end{cases}$$

where μ_1 is chosen such that

$$f(-z^{D*}; \mu_1, \mu_2) = \frac{m_1 m_2}{g_1 g_2},$$

and $\overline{\mu}_2$ is given by

$$\overline{\mu}_2 = \frac{1}{g_2}\left[\frac{\kappa_2 g_1}{m_2}((z^{D*}-\theta)^2 + \mu_1)\Big(\frac{g_1\mu_1 + r_1 - m_1}{\kappa_1}\Big) + m_2 - r_2\right].$$

Then the demographic equilibrium $(\mu_1^{\text{eq}}, \mu_2^{\text{eq}})$ of a monomorphic resident population of type $-z^{D*}$ corresponds to a fixed point of $H \circ K$:

$$H \circ K(\mu_2^{\text{eq}}) = \mu_2^{\text{eq}}, \qquad K(\mu_2^{\text{eq}}) = \mu_1^{\text{eq}}.$$

Note also that, for such equilibrium to make sense, one should have $0 \leq N_i(\mu_i^{\text{eq}})$ or equivalently

$$\frac{m_i - r_i}{g_i} \leq \mu_i^{\text{eq}}.$$

Moreover, since $W_\mu(-z^{D*}, \mu_1^{\text{eq}}, \mu_2^{\text{eq}}) = 0$, we have the additional condition

$$0 < \mu_1^{\text{eq}} + (z^{D*}-\theta)^2, \qquad 0 < \mu_2^{\text{eq}} + (z^{D*}+\theta)^2.$$

Reciprocally, a pair (μ_1, μ_2) which satisfies the above conditions corresponds to a demographic equilibrium.

We next notice, on the one hand, that K is a decreasing function, and hence, in view of the above conditions, a fixed point $(\mu_1^{\text{eq}}, \mu_2^{\text{eq}})$ of $H \circ K$, is a demographic equilibrium if and only if $\mu_2^{\text{eq}} \in \big(-(-z^{D*}+\theta)^2, \widetilde{\mu}_2\big)$, with $\widetilde{\mu}_2 = K^{-1}(\max(\frac{m_1-r_1}{g_1}, -(z^{D*}-\theta)^2)$. On the other hand, H, restricted to $\big(\max(\frac{m_1-r_1}{g_1}, -(z^{D*}-\theta)^2), +\infty\big)$, is an increasing function. Therefore $H \circ K$, restricted to the set $\big(-(z^{D*}+\theta)^2, \widetilde{\mu}_2\big)$, is decreasing. We deduce that a demographic equilibrium, if it exists, is unique.

We then note that, as $\mu_2 \to -(z^{D*}+\theta)^{2+}$, $H \circ K(\mu_2) \to +\infty$. In particular, for μ_2 close to $-(z^{D*}+\theta)^2$, $H \circ K(\mu_2) > \mu_2$. Furthermore, $H \circ K(\widetilde{\mu}_2) = \frac{m_2-r_2}{g_2} < 0$. Note also that, $K(\widetilde{\mu}_2) < 0$ and $K(\mu^*) = \mu^* > 0$ and hence $0 < \mu^* < \widetilde{\mu}_2$, which implies that $H \circ K(\widetilde{\mu}_2) < \widetilde{\mu}_2$. We deduce from the intermediate value theorem that, $H \circ K : \big(-(z^{D*}+\theta)^2, \widetilde{\mu}_2\big) \to \mathbb{R}$ has a unique fixed point $(\mu_1^{\text{eq}}, \mu_2^{\text{eq}})$ and hence there exists a unique demographic equilibrium. $\square$

We next observe that, since $W_\mu(-z^{D*}, \mu_1^{\text{eq}}, \mu_2^{\text{eq}}) = 0$, we have $W_\mu(z^{D*}, \mu_1^{\text{eq}}, \mu_2^{\text{eq}}) > 0$ if and only if $\mu_2^{\text{eq}} < \mu_1^{\text{eq}}$. Moreover, since $W_\mu(-z^{D*}, \mu^*, \mu^*) = 0$, this is equivalent with $\mu_2^{\text{eq}} < \mu^* < \mu_1^{\text{eq}}$.

We are now ready to conclude. Let's first suppose that (11) holds which implies that $H \circ K(\mu^*) < \mu^*$. Then, thanks to the fact that $\mu^* < \widetilde{\mu}_2$ and from the monotonicity of K and $H \circ K$ we deduce that the unique fixed point, μ_2^{eq}, of $H \circ K$ satisfies

$$\mu_2^{\text{eq}} < \mu^* < K(\mu_2^{\text{eq}}) =: \mu_1^{\text{eq}}.$$

This implies that $W_\mu(z^{D*}, \mu_1^{eq}, \mu_2^{eq}) > 0$ or equivalently, a mutant trait z^{D*} can invade a resident population of trait $-z^{D*}$ at its demographic equilibrium.

Let's now suppose that $W_\mu(z^{D*}, \mu_1^{eq}, \mu_2^{eq}) > 0$ and hence $\mu_2^{eq} < \mu^* < \mu_1^{eq}$. We then deduce from $H \circ K(\mu_2^{eq}) = \mu_2^{eq}$ and that the monotonicity of $H \circ K$ that $H \circ K(\mu^*) < \mu^*$. This implies (11).

5 The proof of Theorem 3.5

In this section, we prove Theorem 3.5. To this end, we first provide a convergence result along subsequences in Subsection 5.1. We next conclude using a uniqueness argument in Subsection 5.2.

5.1 Convergence to the Hamilton-Jacobi equation with constraint

In this section, we prove that as $\varepsilon \to 0$, both sequences $(u_{\varepsilon,i})_\varepsilon$, for $i = 1, 2$, converge along subsequences and locally uniformly to a function $u \in \mathrm{C}(\mathbb{R})$, such that u is a viscosity solution to the following equation

$$\begin{cases} -|u'(z)|^2 = W(z, N_1, N_2), & \text{in } \mathbb{R}, \\ \max_{z \in \mathbb{R}} u(z) = 0, \end{cases} \tag{37}$$

$$\mathrm{supp}\, n_1 = \mathrm{supp}\, n_2 \subset \{z \mid u(z) = 0\} \subset \{z \mid W(z, N_1, N_2) = 0\}, \tag{38}$$

where (n_1, n_2) (respectively (N_1, N_2)) is a limit, along subsequences, of $(n_{\varepsilon,1}, n_{\varepsilon,2})$ (respectively $(N_{\varepsilon,1}, N_{\varepsilon,2})$) as ε vanishes. Moreover,

$$N_i = \int_{\mathbb{R}} n_i(z)dz.$$

Note that this is indeed the claim of Theorem 3.5, except that we don't know yet if $(n_1, n_2) = (n_1^*, n_2^*)$. To this end, we first claim the following

Proposition 5.1 *Assume* (3)–(4).
(i) For all $\varepsilon > 0$, we have

$$N_{\varepsilon,1} + N_{\varepsilon,2} \le N_M = 2\max(r_1, r_2). \tag{39}$$

In particular, for $i = 1, 2$, $(n_{\varepsilon,i})_\varepsilon$ converge along subsequences and weakly in the sense of measures to n_i and $N_{\varepsilon,i}$ converges along subsequences to N_i.
(ii) For any compact set $K \subset \mathbb{R}$, there exists a constant $C_M = C_M(K)$ such that, for all $\varepsilon \le 1$,

$$n_{\varepsilon,i}(x) \le C_M n_{\varepsilon,j}(y), \qquad for \quad i, j \in \{1, 2\}, |x - y| \le \varepsilon. \tag{40}$$

(iii) For all $\eta > 0$ there exists a constant R large enough such that

$$\int_{|z|>R} n_{\varepsilon,i}(z)dz < \eta, \quad for\ i = 1, 2. \tag{41}$$

Consequently $N_i = \int_{\mathbb{R}} n_i(z)dz$.

We postpone the proof of this proposition to the end of this paragraph and we pursue giving the scheme of the proof of Theorem 3.5. The next step, is to introduce functions $(l_{\varepsilon,1}, l_{\varepsilon,2})$ as below

$$l_{\varepsilon,i} := \alpha_\varepsilon n_{\varepsilon,i}, \quad \text{for } i = 1, 2,$$

with α_ε chosen such that

$$\int_{\mathbb{R}} \big(l_{\varepsilon,1}(z) + l_{\varepsilon,2}(z)\big)dz = 1. \tag{42}$$

Moreover, we define

$$v_{\varepsilon,i} := \varepsilon \log(l_{\varepsilon,i}), \quad \text{for } i = 1, 2.$$

We next prove the following

Proposition 5.2 *Assume (3)–(4).*
(i) For $i = 1, 2$ and all $\varepsilon \le \varepsilon_0$, the families $(v_{\varepsilon,i})_\varepsilon$ are locally uniformly bounded and locally uniformly Lipschitz.
(ii) As $\varepsilon \to 0$, both families $(v_{\varepsilon,i})_\varepsilon$, for $i = 1, 2$, converge along subsequences and locally uniformly in $\mathbb{R}$ to a continuous function $v \in C(\mathbb{R})$ and $(N_{\varepsilon,i})_\varepsilon$, for $i = 1, 2$, converge along subsequences to N_i, such that v is a viscosity solution to the following equation

$$\begin{cases} -|v'(z)|^2 = W(z, N_1, N_2), & \text{in } \mathbb{R}, \\ \max_{z \in \mathbb{R}} v(z) = 0. \end{cases} \tag{43}$$

(iii) We have

$$W(z, N_1, N_2) \le 0. \tag{44}$$

Consequently, there exists $\delta > 0$ such that

$$N_i \ge \delta, \quad \text{for } i = 1, 2. \tag{45}$$

The proof of this proposition is given at the end of this subsection. Note that (45) implies that, for ε small enough, $N_{\varepsilon,i} \ge \frac{\delta}{2}$. This together with (39) imply that, for $\varepsilon \le \varepsilon_1$ with ε_1 small enough,

$$\frac{1}{2\max(r_1, r_2)} \le \alpha_\varepsilon \le \frac{1}{\delta},$$

and consequently

$$v_{\varepsilon,i} + \varepsilon \log(\delta) \le u_{\varepsilon,i} \le v_{\varepsilon,i} + \varepsilon \log(2\max(r_1, r_2)).$$

We then conclude from the above inequality together with Proposition 5.2–(ii) that $(u_{\varepsilon,i})_\varepsilon$, for $i = 1, 2$, converge along subsequences and locally uniformly to a function $u \in C(\mathbb{R})$ which is a viscosity solution of (37).
To prove (38) we use the following lemma:

Lemma 5.3 *The function v is semiconvex.*

Then (38) is immediate from the WKB ansatz (5) and the fact that v is differentiable at its maximum points (since it is a semiconvex function). Finally, lemma 5.3 can be proved following similar arguments as in [29]–Theorem 1.2, but using cut-off functions to treat the unbounded case as in the proof of Proposition 5.2-(i).

Proof of Proposition 5.1. (i) We first prove (39). To this end, we integrate the equations in (1) with respect to z to obtain

$$\int_{\mathbb{R}} n_{\varepsilon,i}(z)(r_i - m_i - g_i(z - \theta_i)^2 - N_{\varepsilon,i})dz + m_j N_{\varepsilon,j} = 0, \quad i = 1, 2, \ j = 2, 1.$$

Adding the two equations above, it follows that

$$N_{\varepsilon,1}^2 + N_{\varepsilon,2}^2 \leq r_1 N_{\varepsilon,1} + r_2 N_{\varepsilon,2},$$

and hence (39).

(ii) We define

$$K_\varepsilon = \left\{ \frac{x}{\varepsilon} \mid x \in K \right\}, \qquad \widetilde{n}_{\varepsilon,i}(y) = n_{\varepsilon,i}(\varepsilon y), \qquad \text{for } i = 1,\, 2.$$

From (1) we have, for $z \in \mathbb{R}$,

$$\begin{cases} -\widetilde{n}_{\varepsilon,1}''(z) = \widetilde{n}_{\varepsilon,1}(z) R_1(\varepsilon z, N_{\varepsilon,1}) + m_2 \widetilde{n}_{\varepsilon,2}(z) - m_1 \widetilde{n}_{\varepsilon,1}(z), \\ -\widetilde{n}_{\varepsilon,2}''(z) = \widetilde{n}_{\varepsilon,2}(z) R_2(\varepsilon z, N_{\varepsilon,2}) + m_1 \widetilde{n}_{\varepsilon,1}(z) - m_2 \widetilde{n}_{\varepsilon,2}(z). \end{cases} \qquad (46)$$

Moreover, from (2) and (39) we obtain that there exists a constant $C = C(K)$ such that

$$-C \leq R_i(\varepsilon z, N_{\varepsilon,i}) \leq C, \qquad \text{for all } z \in K_\varepsilon.$$

Therefore the coefficients of the linear elliptic system (46) are bounded uniformly in K_ε. It follows from the classical Harnack inequality ([1], Theorem 8.2) that there exists a constant $C_M = C_M(K)$ such that, for all $z_0 \in K_\varepsilon$ such that $B_1(z_0) \subset K_\varepsilon$ and for $i, j = 1, 2$,

$$\sup_{z \in B_1(z_0)} \widetilde{n}_\varepsilon^i(z) \leq C_M \inf_{z \in B_1(z_0)} \widetilde{n}_\varepsilon^j(z).$$

Rewriting the latter in terms of n_ε^1 and n_ε^2 and replacing (z, z_0) by $(\frac{z'}{\varepsilon}, \frac{z_0'}{\varepsilon})$ we obtain

$$\sup_{z' \in B_\varepsilon(z_0')} n_\varepsilon^i(z') \leq C_M \inf_{z' \in B_\varepsilon(z_0')} n_\varepsilon^j(z'),$$

and hence (40).

(iii) We integrate the equations in (1) with respect to z to obtain

$$0 \leq \int_{\mathbb{R}} n_{\varepsilon,i}(z)(r_i - g_i(z + \theta)^2) dz + m_j N_{\varepsilon,j}(z). \qquad (47)$$

We choose a constant $R > 0$ large enough such that for all $|z| > R$, we have

$$r_i - g_i(z - \theta_i)^2 < -\frac{N_M}{\eta} \max(r_1 + m_2, r_2 + m_1), \qquad i = 1, 2.$$

Splitting the integral term in the r. h. s. of (47) into two parts we obtain

$$0 < r_i \int_{|z| \leq R} n_{\varepsilon,i}(z) dz - \frac{N_M}{\eta} \max(r_1 + m_2, r_2 + m_1) \int_{|z| > R} n_{\varepsilon,i}(z) dz + m_j N_{\varepsilon,j}.$$

Next, using (39), we obtain

$$\frac{N_M}{\eta} \max(r_1 + m_2, r_2 + m_1) \int_{|z| > R} n_{\varepsilon,i}(z) dz < (r_i + m_j) N_M,$$

and hence (41).

□

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Proof of Proposition 5.2. (i) We first prove that for all $a > 0$ and any compact set K, there exists ε_0 such that for all $\varepsilon \leq \varepsilon_0$, we have

$$v_{\varepsilon,i}(z) \leq a, \quad \text{for } i = 1, 2, \quad z \in K.$$

Note that, thanks to (40), for any compact set K, there exists a constant $C_M = C_M(K)$ such that

$$|v_{\varepsilon,i}(x) - v_{\varepsilon,j}(y)| \leq \varepsilon \log C_M, \quad \text{for } |x - y| \leq \varepsilon \text{ and } i = 1, 2. \tag{48}$$

We fix a compact set K. Let $z_0 \in K$, $i \in \{1, 2\}$ and $\varepsilon \leq \varepsilon_0 = \frac{a}{2 \log C_M}$ be such that

$$a < v_{\varepsilon,i}(z_0).$$

Therefore, for all $|y - z_0| \leq \varepsilon$, we find

$$\frac{a}{2} < a - \varepsilon \log C_M < v_{\varepsilon,i}(y).$$

It follows that

$$\varepsilon \exp(\frac{a}{2\varepsilon}) \leq \int_{|y-z_0| \leq \varepsilon} \exp(\frac{v_{\varepsilon,i}(y)}{\varepsilon}) dy \leq \int_{\mathbb{R}} l_{\varepsilon,i}(y) dy.$$

Note that the l. h. s. of the above inequality tends to $+\infty$ as $\varepsilon \to 0$, while the r. h. s. is bounded by 1, which is a contradiction. Such z_0 therefore does not exists and for all $z \in K$, $\varepsilon \leq \varepsilon_0$ and $i = 1, 2$, we find

$$v_{\varepsilon,i}(z) \leq a.$$

(ii) We next notice that, similarly to the proof of Theorem 5.1-(iii), one can prove that, for all $\eta > 0$ there exists a constant R large enough such that

$$\int_{|z| > R} l_{\varepsilon,i}(z) dz < \eta, \quad \text{for } i = 1, 2. \tag{49}$$

(iii) Next, we prove that there exists $\varepsilon_0 > 0$ such that for all $\varepsilon \leq \varepsilon_0$, the families $(v_{\varepsilon,i})_\varepsilon$ are locally uniformly bounded from below. To this end, we first observe from (42) and (49) that, for $\eta \in (0, \frac{1}{4})$ there exists a constant $R_0 > 0$ such that

$$\int_{|z| \leq R_0} (l_{\varepsilon,1}(z) + l_{\varepsilon,2}(z)) dz > 1 - 2\eta > \frac{1}{2}.$$

Consequently, for $\varepsilon \leq \varepsilon_0$, with ε_0 small enough, there exists $z_0 \in \mathbb{R}$ and $i \in \{1, 2\}$ such that $|z_0| \leq R_0$ and $-1 \leq v_{\varepsilon,i}(z_0)$. We deduce, thanks to (48), that for any compact set $K = \overline{B}_R(0)$, with $R \geq R_0$,

$$-1 - 2 \log(C_M(K)) R \leq v_{\varepsilon,i}(z), \quad \text{for } i = 1, 2, \ \varepsilon \leq \varepsilon_0, \ z \in K.$$

(iv) We prove that, for any compact set K, the families $(v_{\varepsilon,i})_\varepsilon$ are uniformly Lipschitz in K. To this end, we first notice that $(v_{\varepsilon,i})_\varepsilon$ solves the following system:

$$- \varepsilon v_{\varepsilon,i}'' = |v_{\varepsilon,i}'|^2 + R_i(z, N_{\varepsilon,i}) + m_j \exp\left(\frac{v_{\varepsilon,j} - v_{\varepsilon,i}}{\varepsilon}\right) - m_i, \quad i = 1, 2, \ j = 2, 1. \tag{50}$$

We differentiate the above equation with respect to z and multiply it by $v_{\varepsilon,i}'$ to obtain

$$-\varepsilon v_{\varepsilon,i}' v_{\varepsilon,i}''' = 2 v_{\varepsilon,i}'^2 v_{\varepsilon,i}'' + \frac{\partial}{\partial z} R_i(z, N_{\varepsilon,i}) v_{\varepsilon,i}' + m_j v_{\varepsilon,i}' \left(\frac{v_{\varepsilon,j}' - v_{\varepsilon,i}'}{\varepsilon}\right) \exp\left(\frac{v_{\varepsilon,j} - v_{\varepsilon,i}}{\varepsilon}\right).$$

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We then define $p_{\varepsilon,i} := |v'_{\varepsilon,i}|^2$ and notice that

$$p'_{\varepsilon,i} = 2v'_{\varepsilon,i}v''_{\varepsilon,i}, \qquad p''_{\varepsilon,i} = 2v''^2_{\varepsilon,i} + 2v'_{\varepsilon,i}v'''_{\varepsilon,i}.$$

Combining the above lines we obtain that

$$-\frac{\varepsilon}{2}p''_{\varepsilon,i} + \varepsilon v''^2_{\varepsilon,i} = 2p'_{\varepsilon,i}v'_{\varepsilon,i} + \frac{\partial}{\partial z}R_i(z, N_{\varepsilon,i})v'_{\varepsilon,i} + m_j v'_{\varepsilon,i}\left(\frac{v'_{\varepsilon,j} - v'_{\varepsilon,i}}{\varepsilon}\right) \exp\left(\frac{v_{\varepsilon,j} - v_{\varepsilon,i}}{\varepsilon}\right). \tag{51}$$

We then fix a point $\xi \in K$ and introduce a cut-off function $\varphi \in C^\infty(\mathbb{R})$ which satisfes

$$\varphi(\xi) = 1, \quad 0 \le \varphi \le 1 \text{ in } \mathbb{R}, \quad \varphi \equiv 0 \text{ in } B_1(\xi)^c, \quad |\varphi'| \le C\varphi^{\frac{1}{2}}, \quad |\varphi''| \le C. \tag{52}$$

We then define $P_{\varepsilon,i} = p_{\varepsilon,i}\varphi$ and notice that

$$P'_{\varepsilon,i} = p'_{\varepsilon,i}\varphi + p_{\varepsilon,i}\varphi', \qquad P''_{\varepsilon,i} = p''_{\varepsilon,i}\varphi + 2p'_{\varepsilon,i}\varphi' + p_{\varepsilon,i}\varphi''.$$

We then multiply (51) by φ to obtain

$$\begin{aligned}
-\frac{\varepsilon}{2}P''_{\varepsilon,i} + \varepsilon\varphi v''^2_{\varepsilon,i} &= 2P'_{\varepsilon,i}v'_{\varepsilon,i} + \frac{\partial}{\partial z}R_i(z, N_{\varepsilon,i})\varphi v'_{\varepsilon,i} + m_j\varphi v'_{\varepsilon,i}\left(\frac{v'_{\varepsilon,j} - v'_{\varepsilon,i}}{\varepsilon}\right) \exp\left(\frac{v_{\varepsilon,j} - v_{\varepsilon,i}}{\varepsilon}\right) \\
&\quad -\frac{\varepsilon}{2}\varphi'' p_{\varepsilon,i} - \varepsilon\varphi' p'_{\varepsilon,i} - 2p_{\varepsilon,i}\varphi' v'_{\varepsilon,i}.
\end{aligned}$$

Let's suppose that

$$\max_{z\in\mathbb{R}}(P_{\varepsilon,1}(z), P_{\varepsilon,2}(z)) = P_{\varepsilon,1}(z_0), \quad \text{for } z \in B_1(\xi).$$

Then, evaluating the equation on $P_{\varepsilon,1}$ at z_0 we obtain

$$\varepsilon\varphi(z_0)v''^2_{\varepsilon,1}(z_0) \le \frac{\partial}{\partial z}R_1(z_0, N_{\varepsilon,i})\varphi(z_0)v'_{\varepsilon,1}(z_0) - \frac{\varepsilon}{2}\varphi''(z_0)p_{\varepsilon,1}(z_0) - \varepsilon\varphi'(z_0)p'_{\varepsilon,1}(z_0) - 2p_{\varepsilon,1}(z_0)\varphi'(z_0)v'_{\varepsilon,1}(z_0).$$

Using (52) and $0 = (\varphi p_{\varepsilon,1})'(z_0) = \varphi'(z_0)p_{\varepsilon,1}(z_0) + \varphi(z_0)p'_{\varepsilon,1}(z_0)$, we obtain

$$\varepsilon\varphi(z_0)v''^2_{\varepsilon,1}(z_0) \le \frac{\partial}{\partial z}R_1(z, N_{\varepsilon,1})\varphi(z_0)v'_{\varepsilon,1}(z_0) + \frac{3C\varepsilon}{2}|v'_{\varepsilon,1}(z_0)|^2 + 2C\varphi(z_0)^{\frac{1}{2}}|v'_{\varepsilon,1}(z_0)|^3.$$

We deduce thanks to (50) and the above line that,

$$\begin{aligned}
\frac{\varphi(z_0)}{\varepsilon}\left(|v'_{\varepsilon,1}(z_0)|^2 + R_1(z_0, N_{\varepsilon,1}) + m_2\exp\left(\frac{v_{\varepsilon,2}(z_0) - v_{\varepsilon,1}(z_0)}{\varepsilon}\right) - m_1\right)^2 &\le \\
\frac{\partial}{\partial z}R_1(z, N_{\varepsilon,1})\varphi(z_0)v'_{\varepsilon,1}(z_0) + \frac{3C\varepsilon}{2}|v'_{\varepsilon,1}(z_0)|^2 + 2C\varphi(z_0)^{\frac{1}{2}}|v'_{\varepsilon,1}(z_0)|^3.&
\end{aligned}$$

Since $\xi \in K$, $R_1(z, N_{\varepsilon,1})$ and $\frac{\partial}{\partial z}R_1(z, N_{\varepsilon,1})$ are bounded uniformly by a constant depending only on K. We thus deduce that there exists a constant $D = D(K)$ such that for all $\varepsilon \le \varepsilon_0$ we have

$$|v'_{\varepsilon,1}(z_0)|^2 \le \frac{D}{\varphi(z_0)},$$

which leads to

$$P_{\varepsilon,1}(z_0) \le D.$$

Since z_0 was the maximum point of $P_{\varepsilon,i}$, we obtain that

$$\varphi(\xi)|v'_{\varepsilon,i}(\xi)|^2 = P_{\varepsilon,i}(\xi) \le D.$$

However, $\varphi(\xi) = 1$ and hence

$$|v'_{\varepsilon,i}(\xi)| \leq \sqrt{D}.$$

It is possible to do the above computations for any $\xi \in K$ and the above bound $\sqrt{D}$, depending only on K, will remain unchanged. We conclude that the families $(v_{\varepsilon,i})_\varepsilon$ are uniformly Lipschitz in K.

(v) The next step is to prove the convergence along subsequences of the families $(v_{\varepsilon,i})_\varepsilon$ to a viscosity solution of (43). Note that thanks to the previous steps we know that the families $(v_{\varepsilon,i})_\varepsilon$ are locally uniformly bounded and Lipschitz. Therefore, from the Arzela-Ascoli Theorem, they converge along subsequences to functions $v_i \in C(\mathbb{R})$. Moreover, we deduce from (48) that $v_1 = v_2 = v$. The fact that v is a viscosity solution to (43) can be derived using the method of perturbed test functions similarly to the proof of Theorem 1.1 in [29].

(vi) We next prove (44). Let's suppose in the contrary that there exists $z_0 \in \mathbb{R}$ such that $W(z_0, N_1, N_2) > 0$. Then, there exists an interval (a_0, b_0) such that $z_0 \in (a_0, b_0)$ and $W(z, N_1, N_2) > 0$ for $z \in (a_0, b_0)$. We then notice that v being locally uniformly Lipschitz, is differentiable almost everywhere. Let's $z_1 \in (a_0, b_0)$ be a differentiability point of v. Then from (37) we obtain that

$$-|v'(z_1)|^2 = W(z_1, N_1, N_2),$$

which is a contradiction with the fact that $W(z_1, N_1, N_2) > 0$.

(vii) Finally, we prove (45). Note from the expression of $W(z, N_1, N_2)$ in (8) and from (3) that $0 < \max\big(W(-\theta, 0, 0), W(\theta, 0, 0)\big)$. We assume, without loss of generality, that $0 < W(-\theta, 0, 0)$. Therefore, there exists an interval (a_1, b_1) with $-\theta \in (a_1, b_1)$ and $\overline{\delta}$ such that

$$0 < W(z, N_1, N_2), \qquad \text{for all } N_1, N_2 < \overline{\delta}, \text{ and } z \in (a_1, b_1).$$

We deduce from the above line and step (vi) that there exists $i \in \{1, 2\}$ such that $N_i > \overline{\delta}$. Without loss of generality, we suppose that $i = 1$. From the fact that $(N_{\varepsilon,i})_\varepsilon$ converges to N_i and from Proposition 5.1-(iii) we obtain that there exists a compact set K and a constant $\varepsilon_0 > 0$ such that

$$\frac{\overline{\delta}}{2} \leq \int_K n_{\varepsilon,1}(z)dz, \qquad \text{for all } \varepsilon \leq \varepsilon_0.$$

We then deduce from 5.1-(ii) that

$$\delta := \frac{\overline{\delta}}{2C_M(K)} \leq \int_K n_{\varepsilon,2}(z)dz \leq N_{\varepsilon,2}.$$

This completes the proof of (45). $\quad\square$

5.2 Convergence to the demographic equilibrium of the ESS and consequences (the proof of Theorem 3.5)

We are now ready to prove Theorem 3.5.

Proof of Theorem 3.5. (i) We first prove the first part of the theorem. Note that we already proved in the previous section that as $\varepsilon \to 0$, $n_{\varepsilon,i}$ converges in the sense of measures to n_i and $N_{\varepsilon,i}$ converges to N_i such that $\int_{\mathbb{R}} n_i(z)dz = N_i$. Moreover, thanks to (38) and (44) we have

$$W(z, N_1, N_2) = 0, \quad \text{for } z \in \operatorname{supp} n_i \quad \text{and,} \quad W(z, N_1, N_2) \leq 0, \quad \text{for } z \notin \operatorname{supp} n_i.$$

Furthermore, one can verify using (8) that W can take its maximum only at one or two points and hence the support of n_i contains only one or two points. This implies indeed that $\operatorname{supp} n_i$ is indeed an ESS. We then deduce from the uniqueness of the ESS (see Theorem 3.1) that $n_i = n_i^*$ and $N_i = N_i^*$, for $i = 1, 2$ and (n_1^*, n_2^*) the demographic equilibrium corresponding to the unique ESS.

(ii) The second part of Theorem 3.5 is immediate from it's first part and the previous subsection.

(iii) We first notice from part (i) that $\Omega = \operatorname{supp} n_1^* = \operatorname{supp} n_2^*$ is the unique ESS of the model. Moreover, from Corollary 3.2 and under condition (17) we obtain (18) and consequently

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

The above equalities together with (38) lead to (23). It then remains to prove that the solution of (22)–(23) is unique. The uniqueness of u indeed derives from the fact that any negative viscosity solution of (22) can be uniquely determined by its values at the maximum points of W ([24], Chapter 5). However, (23) implies that $u = 0$ at such points and hence such solution is unique.

Note indeed that restricting to a bounded domain $\mathcal{O}$ and following similar arguments as in [24]–Chapter 5, we obtain that a viscosity solution of (22) in the domain $\mathcal{O}$, verifies

$$u(z) = \sup \left\{ L(y, z) + u(y) \mid \text{with } y \text{ a maximum point of } W(\cdot, N_1^*, N_2^*) \text{ or } y \in \partial\mathcal{O} \right\},$$

with

$$L(y, z) = \sup \left\{ -\int_0^T \sqrt{-W(\gamma(s), N_1^*, N_2^*)} \, ds \mid (T, \gamma) \text{ such that } \gamma(0) = y, \gamma(T) = z, \\ \left|\frac{d\gamma}{ds}\right| \leq 1, \text{ a.e. in } [0, T], \ \gamma(t) \in \overline{\mathcal{O}}, \ \forall t \in [0, T] \right\}.$$

Although here we have an unbounded domain, the trajectories which come from infinity do not change the value of the solution since u is negative and W is strictly negative for $|z|$ large enough. This allows to conclude that the solution u of (22) is indeed determined by its values at the maximum points of W. Note also that the above property is indeed a particular case of 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 [6].

6   A source and sink case

In this section, we consider a particular case where there is migration only from one habitat to the other, that is

$$m_1 > 0, \qquad m_2 = 0. \tag{53}$$

We also assume that

$$r_1 - m_1 > 0. \tag{54}$$

Following similar arguments to the case of migration in both directions, one can characterize the mutation, selection and migration equilibria. However, since the migration is only in one direction, we should study the equilibria in the two habitats separately.

Note that since $m_2 = 0$, there is no influence of the second habitat on the first habitat. One can indeed compute explicitly $n_{\varepsilon,1}$:

$$n_{\varepsilon,1}(z) = \frac{g_1^{\frac{1}{4}} N_{\varepsilon,1}}{\sqrt{2\pi\varepsilon}} \exp\left(-\frac{\sqrt{g_1}(z+\theta)^2}{2\varepsilon}\right), \qquad N_{\varepsilon,1} = \frac{r_1 - m_1 - \varepsilon\sqrt{g_1}}{\kappa_1}. \tag{55}$$

Note that as $\varepsilon \to 0$, $n_{\varepsilon,1}$ converges in the sense of measures to n_1^{M*} with

$$n_1^{M*}(z) = N_1^{M*}\delta(z+\theta), \qquad N_1^{M*} = \frac{r_1 - m_1}{\kappa_1}.$$

Here, $\{-\theta\}$ is indeed the unique ESS in the first habitat and n_1^* corresponds to the demographic equilibrium at the ESS.

In the second habitat however, there is an influence of the population coming from the first habitat. The natural quantity that appears in this case as the effective fitness in the second habitat is still the principal eigenvalue of (7) which is, in this case, given by

$$\begin{aligned} W(z, N_2) &= \max(r_1 - g_1(z+\theta)^2 - \kappa_1 N_1^{M*} - m_1, r_2 - g_2(z-\theta)^2 - \kappa_2 N_2) \\ &= \max(-g_1(z+\theta)^2, r_2 - g_2(z-\theta)^2 - \kappa_2 N_2). \end{aligned}$$

Then one can introduce the notion of the ESS for this habitat similarly to Section 2.

6.1 The results in the adaptive dynamics framework

We can indeed always identify the unique ESS:

Theorem 6.1 *Assume* (53)–(54). *In each patch there exists a unique ESS. In patch 1 the ESS is always monomorphic and it is given by $\{-\theta\}$ with the following demographic equilibrium:*

$$n_1^{M*} = N_1^{M*}\delta(z+\theta), \quad N_1^{M*} = \frac{r_1 - m_1}{\kappa_1}. \tag{56}$$

In patch 2 there are two possibilities:
(i) the ESS is dimorphic if and only if

$$\frac{m_1(r_1 - m_1)}{\kappa_1} < \frac{4g_2\theta^2 r_2}{\kappa_2}. \tag{57}$$

The dimorphic ESS is given by $\{-\theta, \theta\}$ with the following demographic equilibrium:

$$n_2^{D*} = \alpha\delta(z+\theta) + \beta\delta(z-\theta), \quad N_2^{D*} = \alpha + \beta = \frac{r_2}{\kappa_2}, \quad \alpha = \frac{m_1(r_1 - m_1)}{4g_2\theta^2\kappa_1}, \quad \beta = \frac{r_2}{\kappa_2} - \frac{m_1(r_1 - m_1)}{4g_2\theta^2\kappa_1}.$$

(ii) If condition (57) *is not satisfied then the ESS in the second patch is monomorphic. The ESS is given by $\{-\theta\}$ with the following demographic equilibrium:*

$$n_2^{M*} = N_2^*\,\delta(z+\theta), \quad N_2^{M*} = \frac{1}{2\kappa_2}\left(r_2 - 4g_2\theta^2 + \sqrt{(r_2 - 4g_2\theta^2)^2 + 4\frac{\kappa_2}{\kappa_1}m_1(r_1 - m_1)}\right).$$

The proof of the above theorem is not difficult and is left to the interested reader.

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6.2 The computation of the zero order term u_2

We then proceed with the method presented in the introduction to characterize the evolutionary equilibrium $n_{\varepsilon,2}(z)$. To this end, we first identify the zero order term u_2 (introduced in (5)–(6)):

Theorem 6.2 *Assume* (53)–(54).
(i) As $\varepsilon \to 0$, $(n_{\varepsilon,1}, n_{\varepsilon,2})$ converges to (n_1^{M*}, n_2^*), the demographic equilibrium of the unique ESS of the metapopulation, given by Theorem 6.1. Moreover, as $\varepsilon \to 0$, $(N_{\varepsilon,1}, N_{\varepsilon,2})$ converges to (N_1^{M*}, N_2^*), the total populations in patch 1 and 2 corresponding to this demographic equilibrium.
(ii) As $\varepsilon \to 0$, $(u_{\varepsilon,1})_\varepsilon$ converges locally uniformly in $\mathbb{R}$ to $u_1(z) = -\frac{\sqrt{g_1}}{2}(z+\theta)^2$. As $\varepsilon \to 0$, $(u_{\varepsilon,2})_\varepsilon$ converges along subsequences and locally uniformly in $\mathbb{R}$ to a function $u_2 \in C(\mathbb{R})$ which satisfies

$$-|u_2'|^2 \leq \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2^*)), \quad -|u_2'|^2 \geq R_2(z, N_2^*), \quad u_1(z) \leq u_2(z), \quad \max_{z \in \mathbb{R}} u_2(z) = 0, \tag{58}$$

where the first two inequalities are in the viscosity sense. Moreover, we have the following condition on the zero level set of u_2:

$$\operatorname{supp} n_2^* \subset \{z \,|\, u_2(z) = 0\} \subset \{z \,|\, \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2^*)) = 0\}. \tag{59}$$

Proof. The proof of Theorem 6.2 is close to the proof of Theorem 3.5-(i) and (ii). We only provide the steps of the proof and discuss the main differences.
(i) We first notice that the convergence of $(n_{\varepsilon,1})_\varepsilon$, $(N_{\varepsilon,1})_\varepsilon$ and $(u_{\varepsilon,1})_\varepsilon$ is trivial from (55).

(ii) Following similar arguments as in Proposition 5.1–(i) and (iii) we find that $N_{\varepsilon,2}$ is bounded from above and that $n_{\varepsilon,2}$ has small mass at infinity. Hence, as $\varepsilon \to 0$ and along subsequences, respectively $(n_{\varepsilon,2})_\varepsilon$ and $(N_{\varepsilon,2})_\varepsilon$ converges to n_2 and N_2 with $N_2 = \int n_2(z)dz$.

(iii) Note that since $m_2 = 0$, (40) does not hold anymore but a weaker version of it still holds true. We can indeed obtain, following similar arguments and still referring to [1], Theorem 8.2, that for any compact set $K \subset \mathbb{R}$, there exists indeed a constant $C_M = C_M(K)$ such that, for all $\varepsilon \leq 1$, we have

$$n_{\varepsilon,1}(x) \leq C_M n_{\varepsilon,2}(y), \qquad \text{for} \quad |x - y| \leq \varepsilon. \tag{60}$$

(iv) We deduce from (60) and the fact that $n_{\varepsilon,1}$ has small mass at infinity, that there exists ε_0 such that, for all $\varepsilon \leq \varepsilon_0$, $N_{\varepsilon,2}$ is uniformly bounded from below by a positive constant.

(v) Following similar arguments as in the proof of Proposition 5.2 we obtain that there exists $\varepsilon_0 > 0$, such that for all $\varepsilon \leq \varepsilon_0$, $(u_{\varepsilon,2})_\varepsilon$ is locally uniformly bounded and Lipschitz. Therefore, as $\varepsilon \to 0$ and along subsequences, $(u_{\varepsilon,2})_\varepsilon$ converges to a function $u_2 \in C(\mathbb{R})$ such that $\max_{z \in \mathbb{R}} u_2(z) = 0$. Moreover, from (60) we obtain that $u_1(z) \leq u_2(z)$, for all $z \in \mathbb{R}$.

(vi) Note that $u_{\varepsilon,2}$ solves the following equation

$$-\varepsilon u_{\varepsilon,2}'' = |u_{\varepsilon,2}'|^2 + R_2(z, N_{\varepsilon,2}) + m_1 \exp\left(\frac{u_{\varepsilon,1} - u_{\varepsilon,2}}{\varepsilon}\right). \tag{61}$$

Passing to the limit as $\varepsilon \to 0$ and using the fact that the last term above is positive we obtain that

$$-|u_2'|^2 \geq R_2(z, N_2),$$

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in the viscosity sense.

(vii) Next, we prove that

$$-|u_2'|^2 \leq \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2)).$$

To this end, we consider two cases. Let's first suppose that z_0 is such that $u_2(z_0) = u_1(z_0)$. Moreover, let φ be a smooth test function such that $u_2 - \varphi$ has a local maximum at z_0. Then, since $u_1(z) \leq u_2(z)$, $u_1 - \varphi$ has also a local maximum at z_0 and hence

$$-|\varphi'(z_0)|^2 \leq R_1(z, N_1^{M*}) - m_1 \leq \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2)).$$

Next we assume that $u_1(z_0) < u_2(z_0)$. In this case, as $\varepsilon \to 0$, the last term in (61) tends to 0 at z_0 and hence

$$-|u_2'(z_0)|^2 \leq R_2(z, N_2) \leq \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2)),$$

in the viscosity sense.

(viii) We then prove (59). The fact that $\mathrm{supp}\, n_2 \subset \{z \,|\, u_2(z) = 0\}$ is immediate from (5). To prove the second property, we first notice that, considering 0 as a test function, $-|u_2'|^2 \leq \max(R_1(z, N_1) - m_1, R_2(z, N_2))$ implies that

$$0 \leq \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2)), \qquad \text{in } \{z \,|\, u_2(z) = 0\}.$$

Moreover, $-|u_2'|^2 \geq R_2(z, N_2)$, implies that $R_2(z, N_2) \leq 0$. We also know that $R_1(z, N_1^{M*}) - m_1 \leq 0$. Hence, (59).

(ix) Finally, we deduce from the previous step that

$$W(z, N_2) \leq 0, \text{ in } \mathbb{R}, \qquad W(z, N_2) = 0, \text{ for } z \in \mathrm{supp}\, n_2.$$

This means that $\mathrm{supp}\, n_2$ is an ESS and hence, thanks to Theroem 6.1, we obtain that $n_2 = n_2^*$ and $N_2 = N_2^*$, where n_2^* and N_2^* are given by Theorem 6.1. We then deduce in particular that the whole sequences $(n_{\varepsilon,2})_\varepsilon$ and $(N_{\varepsilon,2})_\varepsilon$ converge respectively to n_2^* and N_2^*.

$\square$

Theorem 6.2 allows us to identify u in a neighborhood of the ESS points:

Proposition 6.3 *(i) There exists a connected and open set $\mathcal{O}_\mathrm{I} \subset \mathbb{R}$, with $-\theta \in \mathcal{O}_\mathrm{I}$, such that*

$$u_2(z) = -\frac{\sqrt{g_1}}{2}(z + \theta)^2.$$

(ii) Assume that (57) holds. Then, there exists a connected and open set $\mathcal{O}_\mathrm{II} \subset \mathbb{R}$, with $\theta \in \mathcal{O}_\mathrm{II}$, such that

$$u_2(z) = -\frac{\sqrt{g_2}}{2}(z - \theta)^2.$$

(iii) Assume that

$$\frac{4g_2\theta^2 r_2}{\kappa_2} < \frac{m_1(r_1 - m_1)}{\kappa_1}. \tag{62}$$

Then $u_2(\theta) < 0$.

Note that when $\frac{m_1(r_1-m_1)}{\kappa_1} = \frac{4g_2\theta^2 r_2}{\kappa_2}$ we don't know the value of $u_2(\theta)$. In particular, it can vanish. This is why we cannot provide an approximation of $n_{\varepsilon,2}$ in this degenerate case.

Proof of Proposition 6.3. (i) Note that using similar arguments as in the proof of Theorem 3.5-(iii), where we used properties from the weak KAM theory, and using

$$-|u_2'|^2(z) \leq W(z; N_2^*) = \max(R_1(z, N_1^{M*}) - m_1, R_2(z, N_2^*)) \leq 0, \quad u_2(z) \leq 0,$$

which holds thanks to (58), we obtain that

$$u_2(z) \leq \max\left(-|\int_\theta^z \sqrt{-W(x; N_2^*)}dx|, -|\int_{-\theta}^z \sqrt{-W(x; N_2^*)}dx|\right). \tag{63}$$

From the above inequality it is immediate that there exists a connected and open set $\mathcal{O}_I \subset \mathbb{R}$, with $-\theta \in \mathcal{O}_I$, such that

$$u_2(z) \leq u_1(z) = -\frac{\sqrt{g_1}}{2}(z + \theta)^2.$$

Combining this with the third property in (58) we deduce the first claim of Proposition 6.3.

(ii) Note that under condition (57) the ESS is dimorphic and that supp $n_2^{D*} = \{-\theta, \theta\}$. Therefore, we deduce thanks to (59) that $u_2(\theta) = 0$. This property combined with the second property in (58) implies that

$$u_2(z) \geq -\frac{\sqrt{g_2}}{2}(z - \theta)^2.$$

The second claim of the theorem then follows from (63).

(iii) Finally, we prove the third claim of the theorem. To this end, we assume that (62) holds, and hence the ESS in the second patch is monomorphic and given by $\{-\theta\}$, but $u_2(\theta) = 0$. Note that similarly, to the case of migration in both directions, u_2 is a semiconvex function. Therefore it is differentiable at its maximum points and in particular at θ. Hence, the first claim of (58) implies that

$$0 \leq \max(R_1(\theta, N_1^{M*}) - m_1, R_2(\theta, N_2^{M*})).$$

However, this is in contradiction with (62). □

6.3 Next order terms

In this subsection we compute the next order terms in the approximation of $u_{\varepsilon,i}$ and $N_{\varepsilon,i}$:

$$u_{\varepsilon,i} = u_i + \varepsilon v_i + \varepsilon^2 w_i + o(\varepsilon^2), \qquad N_{\varepsilon,i} = N_i^* + \varepsilon K_i + O(\varepsilon^2).$$

We first notice that, thanks to (55) we already know explicitly $u_{\varepsilon,1}$ and $N_{\varepsilon,1}$:

$$u_{\varepsilon,1} = -\frac{\sqrt{g_1}(z + \theta^2)}{2} + \varepsilon \log\left(g_1^{\frac{1}{4}}\left(N_1^{M*} - \varepsilon\frac{\sqrt{g_1}}{\kappa_1}\right)\right), \quad N_{\varepsilon,1} = \frac{r_1 - m_1 - \varepsilon\sqrt{g_1}}{\kappa_1},$$

and hence

$$v_1 \equiv \log\left(g_1^{\frac{1}{4}} N_1^{M*}\right), \qquad w_1 \equiv -\frac{\sqrt{g_1}}{\kappa_1 N_1^{M*}}, \qquad K_1 = -\frac{\sqrt{g_1}}{\kappa_1}. \tag{64}$$

We next compute v_2 and w_2 around the ESS points. We only present the method to compute v_2 and w_2 around $-\theta$, in the case where

$$\frac{m_1(r_1 - m_1)}{\kappa_1} > \frac{4g_2\theta^2 r_2}{\kappa_2},$$

so that the ESS is monomorphic and is given by $\{-\theta\}$. The dimorphic case, where (57) is satisfies, can be analyzed following similar arguments. We recall that in the degenerate case where $\frac{m_1(r_1-m_1)}{\kappa_1} = \frac{4g_2\theta^2 r_2}{\kappa_2}$, we don't provide an approximation of $n_{\varepsilon,2}$.

To compute v_2, we keep the zero order terms in (61) in $\mathcal{O}_I$ and using (64) we obtain

$$v_2(z) = \log\Big(\frac{m_1 g_1^{\frac{1}{4}} N_1^{M*}}{-g_1(z+\theta)^2 + g_2(z-\theta)^2 - r_2 + \kappa_2 N_2^{M*}}\Big), \quad \text{for } z \in \mathcal{O}_I.$$

Similarly to Section 3.3 we write a Taylor expansion for v_2 around $-\theta$:

$$v_2(z) = v_2(-\theta) + D_2(z+\theta) + E_2(z+\theta)^2 + O(z+\theta)^3, \quad \text{with } v_2(-\theta) = \log(g_1^{\frac{1}{4}} N_2^{M*}),$$

and we define $w_2(-\theta) = F_2$. Note that D_2 and E_2 are known thanks to the explicit computation of $v_2(z)$ given above. Similarly to Section 3.3, keeping the first order terms in $\frac{1}{\sqrt{2\pi\varepsilon}} \int_{\mathcal{I}} \exp\big(\frac{u_{\varepsilon,2}(z)}{\varepsilon}\big)dz$ we obtain that

$$K_2 = N_2^{M*}\Big(\frac{E_2 + 0.5D_2^2}{\sqrt{g_1}} + F_2\Big). \tag{65}$$

Moreover, keeping the first order terms in (61) in $\mathcal{O}_I$ we obtain that

$$\sqrt{g_1} = -2\sqrt{g_1}(z+\theta)v_2' - \kappa_2 K_2 + m_1 \frac{N_1^{M*}}{N_2^{M*}}(w_1 - w_2). \tag{66}$$

We evaluate the above equation at $-\theta$ to obtain

$$F_2 = -\frac{\sqrt{g_1}}{\kappa_1 N_1^{M*}} - \frac{N_2^{M*}}{m_1 N_1^{M*}}\big(\sqrt{g_1} + \kappa_2 K_2\big).$$

One can then compute K_2 and F_2 combining the above equation with (65). Note finally that, once K_2 is known, one can compute w_2 in $\mathcal{I}$ thanks to (66).

Acknowledgements

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