Lecture notes for the research school of the Chaire MMB:

An asymptotic approach to study the adaptation of quantitative traits

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The objective of these notes is to introduce an asymptotic method to study the adaptation of quantitative traits in homogeneous or heterogeneous environments. The first Section is devoted to the study of the equilibrium of a phenotypically structured population subject to selection and mutation. This one-population example provides a good introduction to our method. In section 2, we show how the method can be applied to study the selection-mutation-migration equilibrium considering an environment with two habitat types. In the last section we show how the method can be applied to study the transient evolutionary dynamics of a population. See also the slides for the introduction and numerical examples.

Sections 1 and 2 in these notes are mostly based on [19, 20]. Section 3 is mostly based on [24, 2, 16].

1 One population: the selection-mutation equilibrium

In this section we start by a simple scenario with no migration. The dynamics of the phenotypic density in a single habitat is given by:

$$\frac{\partial n_0(t,z)}{\partial t} = UV_m \frac{\partial^2 n_0(t,z)}{\partial z^2} + n_0(t,z)\left(r_0(z) - \kappa\rho_0(t)\right), \quad z \in \mathbb{R}, \tag{1}$$

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where ρ_0 is the total population size:

$$\rho_0(t) = \int_{\mathbb{R}} n_0(t, y) dy.$$

For this scenario we consider a general form of growth rate $r_0(z)$. We only suppose that $r_0(z)$ is maximized for a unique optimal trait z_0. In the following we present our two-step approach. First, we analyse the evolutionary equilibria of the problem when the rate of mutation is small and we identify the evolutionary stable strategy (ESS). Second, we use this ESS to derive an approximation for the stationary solution of (1) when mutation is more frequent and maintains a standing variance at equilibrium.

Remark 1.1 *All the results in this section can be adapted to the multi-dimensional case $z \in \mathbb{R}^d$. However, to keep the notations simple we present the results for $z \in \mathbb{R}$.*

1.1 Adaptive dynamics and evolutionary stable strategies

In this section, we assume that the mutations are very rare such that a mutation is fixed or goes extinct before a new mutation arises in the population. The phenotypic distribution results from a collection of spikes. Such spikes are gradually replaced by others with the arrival of new mutations and through a competitive procedure. The theory of Adaptive Dynamics [10] is based on the study of the stable equilibrium distribution and the localization of the spikes of such equilibrium, known as evolutionary stable strategies (ESS). Note that in this first step we do not make any assumption regarding the effects of these mutations on the phenotype. We are interested in the identification of the global ESSs, i.e. when the resident population cannot be invaded by any mutation no matter its effect.

In absence of migration, the phenotype z_0 constitutes a globally stable evolutionary strategy. Indeed, when such monomorphic population reaches its demographic equilibrium, the total population size is given by $\rho_0^* = \frac{r(z_0)}{\kappa}$. The fate of a mutant with phenotype z_m introduced in such a resident population is determined by its fitness given by (i.e. per capita growth rate minus density dependence):

$$w(z_m; \rho_0^*) = r_0(z_m) - \kappa_0 \rho_0^* < w(z_0; \rho_0^*) = 0. \tag{2}$$

No mutant trait z_m can indeed invade the population since $r_0(z)$ takes its maximum at z_0.

1.2   Equilibrium distribution with mutation: presentation of the method

The ESS z_0 corresponds to the long-term evolutionary outcome in a scenario where all phenotypic strategies are present initially but where mutation is absent. In the following we study the impact of mutation on the ultimate evolutionary equilibrium of the population.

We introduce a new parameter $\varepsilon = \sqrt{UV_m}$. Hence we replace V_m by ε^2 and we approximate the phenotypic density $n_{\varepsilon,0}(z)$, the equilibrium of (1), in terms of ε, the solution to

$$0 = \varepsilon^2 n''_{\varepsilon,0}(z) + n_{\varepsilon,0}(z)\left(r_0(z) - \kappa_0 \rho_{\varepsilon,0}\right). \tag{3}$$

Our objective is to provide an approximation of the phenotypic density when the effect of mutation (measured by ε) is small while the mutation rate can be large.

To study $n_{\varepsilon,0}(z)$ we will use a method based on Hamilton-Jacobi equations which has been developed by the mathematical community during the last decade to study selection-mutation models, when the effect of mutations is vanishingly small. This method was first suggested by [8] and was developed for the case of homogeneous environments in [24, 2]. The first works in this field, which are addressed to the mathematical community, were mainly focused on the limit case where the effect of mutations ε is vanishingly small. More recent works (see for instance [23, 19, 20]) go further in the analysis and characterize the phenotypic distribution when the mutations have non-negligible effects.

The method is based on the following transformation:

$$n_{\varepsilon,0}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{\varepsilon,0}(z)}{\varepsilon}\right). \tag{4}$$

The introduction of the function $u_{\varepsilon,0}(z)$ is a mathematical trick. It is indeed easier to provide first an approximation of $u_{\varepsilon,0}(z)$ rather than directly studying $n_{\varepsilon,0}(z)$.

Note that a first approximation of the population's phenotypic density which is commonly used in the

theory of Quantitative Genetics is a Gaussian approximation of the following form around z^*:

$$n_{\varepsilon,0}(z) \approx \rho_{\varepsilon,0}\, f, \qquad f \text{ PDF of } \mathcal{N}(z^*, \varepsilon\,\sigma^2). \tag{5}$$

The Gaussian approximation, is as if we had imposed $u_{\varepsilon,0}(z)$ to be a quadratic function of z, that is $u_{\varepsilon,0}(z) = \varepsilon\log(\frac{\rho_{\varepsilon,0}^*}{\sigma}) - \frac{(z-z^*)^2}{2\sigma^2}$. Our objective, however, is to obtain more accurate results than (5) and to approximate $u_{\varepsilon,0}$ without making an a priori Gaussian assumption. To this end we postulate an expansion for $u_{\varepsilon,0}(z)$ in terms of ε:

$$u_{\varepsilon,0}(z) = u_0(z) + \varepsilon v_0(z) + O(\varepsilon^2), \tag{6}$$

and we try to compute the coefficients $u_0(z)$ and $v_0(z)$. These terms can indeed be explicitly computed and they lead to an approximation of the total population size $\rho_{\varepsilon,0}$ and the phenotypic density $n_{\varepsilon,0}(z)$:

$$\rho_{\varepsilon,0} \approx \rho_0 + \varepsilon K_0, \qquad n_{\varepsilon,0}(z) \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\Big(\frac{u_0(z) + \varepsilon v_0(z)}{\varepsilon}\Big). \tag{7}$$

Indeed we neglect the error term in (6) since when ε is small, in view of (4), it has only small contribution to the phenotypic density $n_{\varepsilon,0}(z)$.

We will prove in what follows that $\rho_0 = \rho_0^*$, with ρ_0^* the total population size at the demographic equilibrium of the ESS z_0. We will also compute the other terms of the expansions κ_0, $u_0(z)$ and $v_0(z)$. We will show in particular that u_0 solves, in the viscosity sense, the following Hamilton-Jacobi equation with constraint:

$$\begin{cases} -|u_0'(z)|^2 = w(z; \rho_0^*), \\ \max_z u_0(z) = u_0(z_0) = 0. \end{cases}$$

1.3 Regime of interest: evolutionary time scale much larger than ecological time scale

Let

$$r(z) = r_{\max} - \mu(z),$$

with $\mu(z)$ such that

$$\min_z \mu(z) = \mu(z_0) = 0, \qquad -\frac{1}{2}\mu''(z_0) = s_0.$$

Adimensional parametrization:

$$\widetilde{n}(t, z) = \frac{\kappa}{r_{\max}} n\left(\frac{t}{r_{\max}}, \frac{z}{\sqrt{s_0/r_{\max}}}\right), \qquad \widetilde{\mu}(z) = \frac{1}{r_{\max}} \mu\left(\frac{z}{\sqrt{s_0/r_{\max}}}\right).$$

Leads to

$$\frac{\partial}{\partial t}\widetilde{n} - \frac{UV_m s_0}{r_{\max}^2}\Delta\widetilde{n} = \widetilde{n}\left(1 - \widetilde{\mu}(z) - \widetilde{\rho}\right),$$

with $\widetilde{\mu}(z)$ such that

$$\min_z \widetilde{\mu}(z) = \widetilde{\mu}(z_0) = 0, \qquad \frac{1}{2}\frac{\partial^2 \widetilde{\mu}}{\partial z^2}(z_0) = 1.$$

The quantity that should be sufficiently small to have a good approximation:

$$\frac{UV_m s_0}{r_{\max}^2} << 1,$$

or equivalently

$$\sqrt{UV_m s_0} << r_{\max}.$$

This means indeed that the evolutionary time scale has to be much larger than ecological time scale.

1.4   Heuristic derivation

Replacing (4) in (3) we obtain:

$$0 = \varepsilon u''_{\varepsilon,0}(z) + |u'_{\varepsilon,0}(z)|^2 + r_0(z) - \kappa_0\rho_{\varepsilon,0}. \tag{8}$$

This equation is derived using the following equalities:

$$n'_{\varepsilon,0}(z) = u'_{\varepsilon,0}(z)\frac{n_{\varepsilon,0}(z)}{\varepsilon}, \qquad n''_{\varepsilon,0}(z) = \left(\varepsilon u''_{\varepsilon,0}(z) + |u'_{\varepsilon,0}(z)|^2\right)\frac{n_{\varepsilon,0}(z)}{\varepsilon^2}.$$

We then replace the ansatz (6) in (8). We first keep the zero order terms with respect to ε (the ones in front of which there is no ε, corresponding to the dominant terms) to obtain the following equation on $u_0(z)$:

$$0 = |u_0'(z)|^2 + r_0(z) - \kappa_0 \rho_0.$$

Note also that to have a finite but positive size of population, we should have

$$\max_{z \in \mathbb{R}} u_0(z) = 0.$$

Otherwise, in view of (4), the total population size whether becomes infinite as $\varepsilon \to 0$ (if $\max_{z \in \mathbb{R}} u_0(z) > 0$) or it goes to 0 (if $\max_{z \in \mathbb{R}} u_0(z) < 0$).

At the maximum point $z_{\max}$ of u_0, we have $\partial_z u_0(z_{\max}) = 0$ and hence

$$r_0(z_{\max}) - \kappa_0 \rho_0 = 0.$$

For all other traits z

$$r_0(z) - \kappa_0 \rho_0 = -|u_0'(z)|^2 {\leq} 0.$$

We deduce that $z_{\max}$ is the maximum point of $r_0(z)$, that is $z_{\max} = z_0$. In other words, u takes its maximum at the ESS point z_0 and the zero order term ρ_0 in the approximation of the population size is given by

$$\rho_0 = \frac{r_0(z_0)}{\kappa_0}. \tag{9}$$

This corresponds indeed to the total population size ρ_0^* at the demographic equilibrium of the ESS z_0. We gather our results on u_0 in the following form [24, 2]: u_0 is indeed the unique viscosity solution to the following Hamilton-Jacobi equation

$$\begin{cases} 0 = |u_0'(z)|^2 + w(z; \rho_0^*), \\ \max_z u_0(z) = u_0(z_0) = 0, \end{cases} \tag{10}$$

where we recall that $w(z; \rho_0^*) = r_0(z) - \kappa_0 \rho_0^*$. This equation can be solved explicitly. The solution $u_0(z)$ is given by

$$u_0(z) = -\left| \int_{z_0}^{z} \sqrt{-w(y, \rho_0^*)} dy \right|. \tag{11}$$

The reader can verify that $u_0(z)$, given by the formula above, is smooth and solves (10). Note that the absolute values are necessary since the upper limit of the integral z can be smaller or larger than the lower limit z_0.

The identification of u_0 leads also to the identification of n_0, the weak limit of $n_{\varepsilon,0}$ as $\varepsilon \to 0$. The key information to identify n_0 is the following:

$$\text{supp } n_0 \subset \{z | u_0(z) = 0\}. \tag{12}$$

The above property holds since $u_0(\bar{z}) < 0$ implies that $\lim_{\varepsilon \to 0} n_{\varepsilon,i}(\bar{z}) = 0$. Furthermore, from (11) we know that

$$\{z | u_0(z) = 0\} = \{z_0\}.$$

This property together with (45) implies that n is indeed a Dirac mass:

$$n(z) = \rho^* \delta(z - z_0).$$

To compute the next order terms we then keep the terms of order ε

$$-u_0''(z) = 2v_0'(z)u_0'(z) - \kappa_0 K_0. \tag{13}$$

An evaluation of this equation at the point z_0 gives

$$K_0 = \frac{1}{\kappa_0} u_0''(z_0). \tag{14}$$

The function $v_0(z)$ can also be computed thanks to (13), that is by integrating the following quantity

$$v_0'(z) = \frac{-u_0''(z) + \kappa_0 K_0}{2u_0'(z)}. \tag{15}$$

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Note that to compute $v_0(z)$ we also need to choose the value of $v_0(z_0)$. This value is fixed in a way such that

$$\int_{-\infty}^{\infty} \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_0(z) + \varepsilon v_0(z)}{\varepsilon}\right) dz = \rho_0^* + \varepsilon K_0. \tag{16}$$

Example of quadratic growth rate. We first consider a quadratic growth rate:

$$r_0(z) = r_{\max,0} - s_0(z - \theta_0)^2. \tag{17}$$

In this example the ESS, which is indeed the maximum point of $r_0(z)$, is given by $z_0 = \theta_0$. Considering the specific fitness function (17) in (9) we first obtain that

$$\rho_0^* = \frac{r_{\max,0}}{\kappa_0}.$$

Using (11) we then obtain that

$$u_0(z) = -\left| \int_{\theta_0}^{z} \sqrt{s_0(y - \theta_0)^2} dy \right| = -\frac{\sqrt{s_0}}{2}(z - \theta_0)^2.$$

We also obtain from (14) that $K_0 = -\frac{\sqrt{s_0}}{\kappa_0}$. Moreover, from (15) we obtain that $\frac{\partial}{\partial z} v_0(z) = 0$ which means that $v_0(z)$ is a constant. Combining these informations with (16) we obtain

$$\rho_{\varepsilon,0}^* \approx \frac{1}{\kappa_0}(r_{\max,0} - \varepsilon\sqrt{s_0}), \quad n_{\varepsilon,0}(z) \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_0(z) + \varepsilon v_0(z)}{\varepsilon}\right) = \frac{\rho_{\varepsilon,0}^* s_0^{1/4}}{\sqrt{2\pi\varepsilon}} \exp\left(-\frac{\sqrt{s_0}}{2\varepsilon}(z - \theta_0)^2\right).$$

In other words, our approximation yields the Gaussian distribution (5) with:

$$\rho_{\varepsilon,0}^* \approx \frac{1}{\kappa_0}(r_{\max,0} - \varepsilon\sqrt{s_0}), \qquad \sigma^2 = \frac{1}{\sqrt{s_0}}. \tag{18}$$

Note that this Gaussian distribution is actually an exact solution of of (3) and the above $\approx$ signs can indeed be replaced by equalities (see [11] and [3]–Chapter IV).

Example of non-symmetric growth rate (19). We next consider a growth rate which is not

symmetric:

$$r_0(z) = r_{\max,0} - s(z - \theta_0)^2\big(a + (z + \theta_0)^2\big).$$ (19)

In this example similarly to the previous example the ESS z_0 is given by $z_0 = \theta_0$ and

$$\rho_0^* = \frac{r_{\max,0}}{\kappa_0}.$$

The expression of $u_0(z)$ is however different, and it is given thanks to (11) by

$$u_0(z) = -\Big| \int_{\theta_0}^z \sqrt{s(y - \theta_0)^2(a + (y + \theta_0)^2)}\,dy \Big|.$$ (20)

From this expression we can then compute K_0 and $v_0(z)$ similarly to above using (14) and (15). In Figure 1 we plot this *first approximation* and compare it with the exact distribution that we derived numerically. We observe in particular that the population distribution has a non-negligible skewness that is accurately captured by our method.

1.5   Approximation of the moments

From the above approximation, one can obtain a numerical approximation for the moments of the population distribution (except for the moment of order 0, i.e. $\rho_{\varepsilon,0}$, for which we already have obtained an analytic approximation). In order to provide more explicit formula for the moments of order $k \geq 1$ of the population's distribution in terms of the parameters of the model, we also provide a *second approximation*. This *second approximation* is based on the Laplace's method of integration and instead of using the values of u_0 and v_0 in the whole domain, uses the Taylor expansions of u_0 and v_0 around the ESS points. Our *second approximation* is by definition less accurate than the first one.

Laplace's method of integration. The Laplace's method of integration allows to approximate integrals of the form

$$\int_a^b e^{\frac{f(z)}{\varepsilon}}\,dz,$$

where f is twice differentiable function and ε is a small parameter. We assume indeed that f has a single maximum point at the point z_0 and that $f''(z_0) < 0$. Then one can approximate the integral above using the following property

$$\lim_{\varepsilon \to 0} \frac{\int_a^b e^{\frac{f(z)}{\varepsilon}} dz}{\sqrt{\frac{2\pi\varepsilon}{|f''(z_0)|}} e^{\frac{f(z_0)}{\varepsilon}}} = 1.$$

Analytic formula for the moments of the population's distribution. According to above there exists a unique ESS which is monomorphic and given by z_0. In order to provide an explicit approximation of the moments of the population's distribution, we compute the third order approximation of $u_0(z)$ around z_0:

$$u_0(z) = -\frac{A}{2}(z - z_0)^2 + B(z - z_0)^3 + O(z - z_0)^4, \tag{21}$$

and the first order approximation of $v_0(z)$ around z_0:

$$v_0(z) = C + D(z - z_0) + O(z - z_0)^2. \tag{22}$$

Such coefficients can be computed thanks to (11) and (15). Note that we can compute directly the constant C:

$$C = \log(\sqrt{A}\rho_0^*).$$

To obtain the zero order term in the expansion for $v_0(z)$ we use the fact that, as the mutation's variance vanishes ($\varepsilon \to 0$), the total population size $\rho_{\varepsilon,0}$ tends to ρ_0^* which corresponds to the demographic equilibrium at the ESS.

The above approximation allows us to estimate the moments of the population's distribution:

$$\begin{cases} \mu_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int z n_{\varepsilon,0}(z) dz = z_0 + \varepsilon(\frac{3B}{A^2} + \frac{D}{A}) + O(\varepsilon^2), \\[2mm] \sigma_{\varepsilon,0}^2 = \frac{1}{\rho_{\varepsilon,0}} \int (z - \mu_{\varepsilon,0})^2 \, n_{\varepsilon,0}(z) dz = \frac{\varepsilon}{A} + O(\varepsilon^2), \\[2mm] \psi_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int (z - \mu_{\varepsilon,0})^3 \, n_{\varepsilon,0}(z) dz = \frac{6B}{A^3}\varepsilon^2 + O(\varepsilon^3). \end{cases} \tag{23}$$

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Derivation of the analytic formula. To compute such approximations we use similar arguments as for the Laplace's method of integration. We can indeed use the expressions in (21) and (22) to compute for any integer $k \geq 1$,

$$\int (z-z_0)^k n_{\varepsilon,0}(z)dz = \frac{\varepsilon^{\frac{k}{2}}\sqrt{A}\rho_0^*}{\sqrt{2\pi}} \int_{\mathbb{R}} (y^k e^{-\frac{A}{2}y^2}(1+\sqrt{\varepsilon}(By^3+Dy)+O(\varepsilon))dy$$
$$= \varepsilon^{\frac{k}{2}}\rho_0^*\left(\omega_k(\tfrac{1}{A}) + \sqrt{\varepsilon}\left(B\omega_{k+3}(\tfrac{1}{A})+D\omega_{k+1}(\tfrac{1}{A})\right)\right) + O(\varepsilon^{\frac{k+2}{2}}),$$

where $\omega_k(\sigma^2)$ corresponds to the k-th order central moment of a Gaussian distribution with variance σ^2. Note that to compute the integral terms above we have performed a change of variable $z-z_0 = \sqrt{\varepsilon}\, y$, therefore each term $z-z_0$ can be considered as of order $\sqrt{\varepsilon}$ in the integrations. Note also that since the term v is multiplied by ε in (6), a first order expansion of v is enough, while a third order expansion of u is required to obtain the above approximation. The above integrations are the main ingredients to obtain the approximations given in (23), i.e. our *second approximation.*

The asymmetric growth rate (19)**:** We can use our *second approximation* to obtain analytic expressions for the moments of the phenotypic distribution in the case of example (19):
Here are the expressions for the mean phenotypic trait,

$$\mu_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int z n_{\varepsilon,0}(z)dz = \theta_0 - \frac{4\theta_0\varepsilon}{\sqrt{s}(a+4\theta_0^2)^{3/2}} + O(\varepsilon^2),$$

for the variance,

$$\sigma_{\varepsilon,0}^2 = \frac{1}{\rho_{\varepsilon,0}} \int (z-\mu_{\varepsilon,0})^2 n_{\varepsilon,0}(z)dz = \frac{\varepsilon}{\sqrt{s(a+4\theta_0^2)}} + O(\varepsilon^2),$$

and the third central moment:

$$\psi_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int (z-\mu_{\varepsilon,0})^3 n_{\varepsilon,0}(z)dz = -\frac{4\theta_0\varepsilon^2}{s_0(a+4\theta_0^2)^2} + O(\varepsilon^3).$$

In Table 1 we show that our two approximations capture accurately the first three moments of the equilibrium distribution using the parameters that we used in Figure 1. As expected, the *first approx-*

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imation is more accurate, but the analytic expressions of the *second approximation* given above allow us to capture the influence of the parameters of the model.
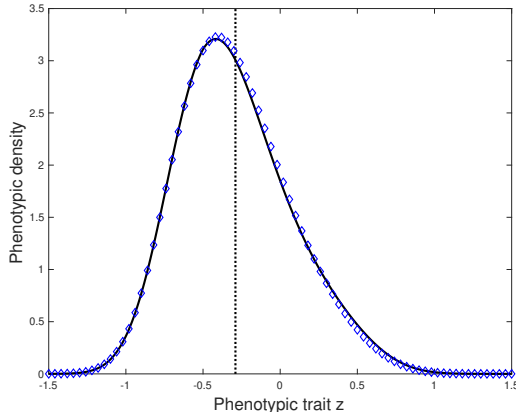
Figure 1 – The selection-mutation equilibrium of the phenotypic density $n_{\varepsilon,0}(z)$ in a single population. We plot the exact phenotypic density at equilibrium obtained from numerical computations of the equilibrium of (1) (blue dots) together with our *first approximation* (full black line) with the growth rate given in (19). The vertical dotted line indicates the mean of the phenotypic distribution. Note the skewness of the equilibrium distribution that is accurately captured with our approximation (see also Table 1). In this figure, to compute numerically the equilibrium, we have solved numerically the dynamic problem (1) and kept the solution obtained after long time when the equilibrium has been reached. Parameter values: $r_{\max} = 3$, $s_0 = 1$; $\theta = -0.5$, $\kappa = 1$, $a = 0.2$, $b = 1$, $\varepsilon = 0.1$.

1.6 Rigorous derivation

In this subsection, we provide the main elements to prove that $(u_{\varepsilon,0})$ converges locally uniformly to u_0. For the derivation of asymptotic expansions of type (6) see [9, 22].

The following proposition provides the important ingredients for the proof of the convergence of $(u_{\varepsilon,0})$.

Proposition 1.2 *For all $\varepsilon \leq \varepsilon_0$, the family $(u_{\varepsilon,0})$ is locally uniformly bounded and Lipschitz. Moreover, $(\rho_{\varepsilon,0})$ is uniformly bounded.*

The convergence of $(u_{\varepsilon,0})$ follows from the proposition above and the Arzela-Ascoli Theorem. We hence deduce that $u_{\varepsilon,0}$ converges to a certain continuous function u_0. We saw in the subsection 1.4

	Exact value	First approximation	Second approximation
Mean: $\mu_{\varepsilon,0}$	-0.29	-0.29	-0.35
Variance: $\sigma_{\varepsilon,0}^2$	0.13	0.14	0.09
Third central moment: $\psi_{\varepsilon,0}$	0.02	0.02	0.01

Table 1 – First three moments of the phenotypic distribution at mutation-selection equilibrium in a single population. We compare the values from the exact numerical resolution of (1) and our two approximations using the growth rate given in (19) (see also Figure 2). Parameter values: $r_{\max} = 3$, $s_0 = 1$; $\theta = -0.5$, $\kappa = 1$, $a = 0.2$, $b = 1$, $\varepsilon = 0.1$.

that formally we expect that u_0 solves (10):

$$0 = |u_0'(z)|^2 + w(z; \rho_0^*).$$

One can indeed prove following classical arguments that the function u_0 is indeed a viscosity solution to such Hamilton-Jacobi equation. Viscosity solutions correspond to a class of weak solutions which are particularly adapted to such stability properties (u_0 is obtained as the limit of the solution to a vanishingly viscous problem). For an introduction to the notion of viscosity solutions and their basic properties, see [1]. For similar convergence results in the context of selection-mutation models, see [2] for the dynamic version of the problem presented above, and [19] for the heterogeneous 2-habitat model.

Note that the Hamilton-Jacobi equation above in general might admit several viscosity solutions. Here, the uniqueness is obtained thanks to the constraint

$$\max_z u_0(t, z) = 0,$$

which implies that at the maximum point z_0 of $w(\cdot; \rho_0^*)$, $u_0(z_0) = 0$ and that u_0 takes negative values. Such properties allow to determine in a unique way the viscosity solution u_0 which is given by (11) ([15], Chapter 5).

We provide below, the proof of the main regularity result in Proposition 1.2, that is the Lipschitz

bound.

Proof of the Lipschitz bound of Proposition 1.2.

$$-\varepsilon u''_{\varepsilon,0} = |u'_{\varepsilon,0}|^2 + w(z; \rho_{\varepsilon,0}). \tag{24}$$

We differentiate the above equation with respect to z and multiply it by $u'_{\varepsilon,0}$ to obtain

$$-\varepsilon u'_{\varepsilon,0} u'''_{\varepsilon,0} = 2u'^2_{\varepsilon,0} u''_{\varepsilon,0} + r'_0(z) u'_{\varepsilon,0}.$$

We then define $p_{\varepsilon,0} := |u'_{\varepsilon,0}|^2$ and notice that

$$p'_{\varepsilon,0} = 2u'_{\varepsilon,0} u''_{\varepsilon,0}, \qquad p''_{\varepsilon,0} = 2u''^2_{\varepsilon,0} + 2u'_{\varepsilon,0} u'''_{\varepsilon,0}.$$

Combining the above lines we obtain that

$$-\frac{\varepsilon}{2} p''_{\varepsilon,0} + \varepsilon u''^2_{\varepsilon,0} = 2p'_{\varepsilon,0} u'_{\varepsilon,0} + r'_0(z) u'_{\varepsilon,0}. \tag{25}$$

Let's first assume that $p_{\varepsilon,0}$ takes its maximum at a point z_m. Evaluating the equation above at z_m we obtain that

$$\varepsilon u''^2_{\varepsilon,0}(z_m) \leq -\frac{\varepsilon}{2} p''_{\varepsilon,0}(z_m) + \varepsilon u''^2_{\varepsilon,0}(z_m) = r'_0(z_m) u'_{\varepsilon,0}(z_m).$$

Let's also assume that $r'(z)$ is bounded (note that this assumption does not hold for instance if r_0 is a quadratic function). Then we would obtain that

$$\varepsilon u''^2_{\varepsilon,0}(z_m) \leq C|u'_{\varepsilon,0}(z_m)|.$$

Using again (8) we obtain that

$$\frac{1}{\varepsilon}(|u'_{\varepsilon,0}(z)|^2 + r_0(z) - \kappa_0 \rho_{\varepsilon,0})^2 \leq C|u'_{\varepsilon,0}(z_m)|.$$

One can deduce then from the inequality above, and assuming that r_0 and $\rho_{\varepsilon,0}$ are bounded, that

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$|u'_{\varepsilon,0}(z_m)|$ is bounded.

However, in the above argument we made some assumptions which do not necessarily hold. We do not know a priori that $p_{\varepsilon,0}$ takes its maximum at a point in the interior of $\mathbb{R}$. Moreover, $r'_0(z)$ may be unbounded. We may overcome these difficulties, by introducing cut-off functions and providing a local argument, showing that $|u'_{\varepsilon,0}|$ is locally bounded. See [19] for more details. $\quad\square$

2 Two populations: the selection-mutation-migration equilibrium

The objective of this section is to provide an approximation of the phenotypic densities $(n_1(z), n_2(z))$ solution to the following system:

$$
\begin{cases}
0 = \varepsilon^2 n''_{\varepsilon,1}(z) + n_{\varepsilon,1}(z)\left(r_1(z) - \kappa_1\rho_{\varepsilon,1}\right) + m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z), \\
0 = \varepsilon^2 n''_{\varepsilon,2}(z) + n_{\varepsilon,2}(z)\left(r_2(z) - \kappa_2\rho_{\varepsilon,2}\right) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z),
\end{cases}
\tag{26}
$$

with

$$
r_i(z) = r_{\max,i} - s(z - \theta_i)^2.
$$

As previously we also assume that $\varepsilon^2 = UV_m$ is a small parameter. We follow the two-step approach we used to obtain the stationary phenotypic distribution in a single population. First, we analyse the evolutionary equilibria of the system when mutations are rare using the Adaptive Dynamics framework. We identify monomorphic or dimorphic globally evolutionary stable strategies (ESS). Second, we use these ESSs to derive approximations of the solution of (26) when mutation is more frequent and maintains a standing variance at equilibrium.

In the analysis presented below, we will assume that migration rates are positive $m_i > 0$. However the extreme source and sink case, where for instance $m_1 > 0$ but $m_2 = 0$ can also be treated using the same approach. For the derivation of our approximation in this case, see [19, 20].

2.1 Adaptive dynamics in presence of migration

In this section, we provide the conditions for a global evolutionary stable strategy. To be able to characterize the ESS one should first characterize the demographic equilibrium corresponding to a set

of traits. Because there are only two habitats, at most two distinct traits can co-exist. Therefore, we only need to consider two scenarios where the phenotypic distribution is either monomorphic (with phenotype z^M) or dimorphic (with phenotypes z_I^D and z_II^D, where the subscripts I and II indicate that the phenotype is best adapted to habitat 1 and 2, respectively).

The monomorphic equilibrium is given by $n_i^M(z) = \rho_i^M \delta(z - z^M)$ where $\delta(.)$ is the dirac delta function, $\left(\rho_1^M, \rho_2^M\right)^T$ is the right eigenvector associated with the dominant eigenvalue $W(z^M; \rho_1^M, \rho_2^M) = 0$ of $\mathcal{A}(z^M; \rho_1^M, \rho_2^M)$, with

$$\mathcal{A}(z_m; \rho_1, \rho_2) = \begin{pmatrix} w_1(z_m; \rho_1) - m_1 & m_2 \\ m_1 & w_2(z_m; \rho_2) - m_2 \end{pmatrix}. \tag{27}$$

In a similar way the dimorphic equilibrium is characterized by: $n_i^D(z) = \nu_{\mathrm{I},i}\delta(z - z_\mathrm{I}^D) + \nu_{\mathrm{II},i}\delta(z - z_\mathrm{II}^D)$, where $\nu_{\mathrm{I},i} + \nu_{\mathrm{II},i} = \rho_i^D$ and $(\nu_{k,1}, \nu_{k,2})^T$ are the right eigenvectors associated with the largest eigenvalues $W(z_k^D; \rho_1^D, \rho_2^D) = 0$ (for $k = \mathrm{I}, \mathrm{II}$) of $\mathcal{A}(z_k^D; \rho_1^D, \rho_2^D)$.

The evolutionary stability of a resident strategy z^{M*} can be studied with the analysis of the invasion of a new mutant strategy z_m at the demographic equilibrium $\left(\rho_1^{M*}, \rho_2^{M*}\right)$ set by the resident strategy. The monomorphic strategy z^{M*} is an evolutionary stable strategy if for any mutant $z_m \neq z^{M*}$, the effective fitness is negative: $W(z_m; \rho_1^{M*}, \rho_2^{M*}) < 0$. In a similar way, the dimorphic strategy $\{z_\mathrm{I}^{D*}, z_\mathrm{II}^{D*}\}$ is an evolutionary stable strategy if for any mutant $z_m \notin \{z_\mathrm{I}^{D*}, z_\mathrm{II}^{D*}\}$, the effective fitness is negative: $W(z_m; \rho_1^{D*}, \rho_2^{D*}) < 0$.

To determine the global ESS, we first define

$$z^{D*} = \sqrt{\theta^2 - \frac{m_1 m_2}{4\theta^2 s_1 s_2}}, \qquad \rho_1^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 s_2} + r_{\max,1} - m_1}{\kappa_1}, \qquad \rho_2^{D*} = \frac{\frac{m_1 m_2}{4\theta^2 s_1} + r_{\max,2} - m_2}{\kappa_2}.$$

Theorem 2.1 [19] *There exists a unique global ESS.*

(i) The ESS is dimorphic if

$$\frac{m_1 m_2}{4 s_1 s_2 \theta^4} < 1, \tag{28}$$

$$0 < m_2 \rho_2^{D*} + (w_1(-z^{D*}; \rho_1^{D*}) - m_1) \rho_1^{D*}, \tag{29}$$

and

$$0 < m_1 \rho_1^{D*} + (w_2(z^{D*}; \rho_2^{D*}) - m_2) \rho_2^{D*}. \tag{30}$$

Then the dimorphic equilibrium is given by

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

where $\nu_{k,i}$ can be explicitly determined (see [20]).

(ii) If the above conditions are not satisfied then the ESS is monomorphic. In the case where condition (28) is verified but the r.h.s. of (29) (respectively (30)) is negative, the fittest trait belongs to the interval $(-\theta, -z^{D*})$ (respectively (z^{D*}, θ)). If (28) is satisfied but (29) (respectively (30)) is an equality then the monomorphic ESS is given by $\{-z^{D*}\}$ (respectively $\{z^{D*}\}$).

If the habitats are symmetric, then the second and the third conditions (29)–(30) above are always satisfied and the dimorphism occurs under the only condition (28). In other words, if migration is weak with respect to the selection or the difference of the optimal traits in the two habitats, then the ESS will be dimorphic. When the habitats are non-symmetric the extra conditions (29) and (30) appear which are conditions of mutual invasibility. Condition (29) (respectively condition (30)) means indeed that a mutant trait of type z^{D*} (respectively $-z^{D*}$) can invade a monomorphic resident population of type $-z^{D*}$ (respectively z^{D*}) which is at it's demographic equilibrium (see [19]-Proposition 3.4). We can indeed rewrite conditions (29) and (30) respectively as below

$$\eta_1 < \beta_2 r_{\mathrm{max},2} - \alpha_1 r_{\mathrm{max},1}, \qquad \eta_2 < \beta_1 r_{\mathrm{max},1} - \alpha_2 r_{\mathrm{max},2},$$

with η_i, α_i and β_i constants depending on m_1, m_2, g_1, g_2, κ_1, κ_2 and θ (see [20] for the expressions of these coefficients). These conditions are indeed a measure of asymmetry between the habitats. They appear from the fact that even if condition (28), 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 (see Figure 2). The proof of Theorem (2.1) is given in [19]–Section 4.
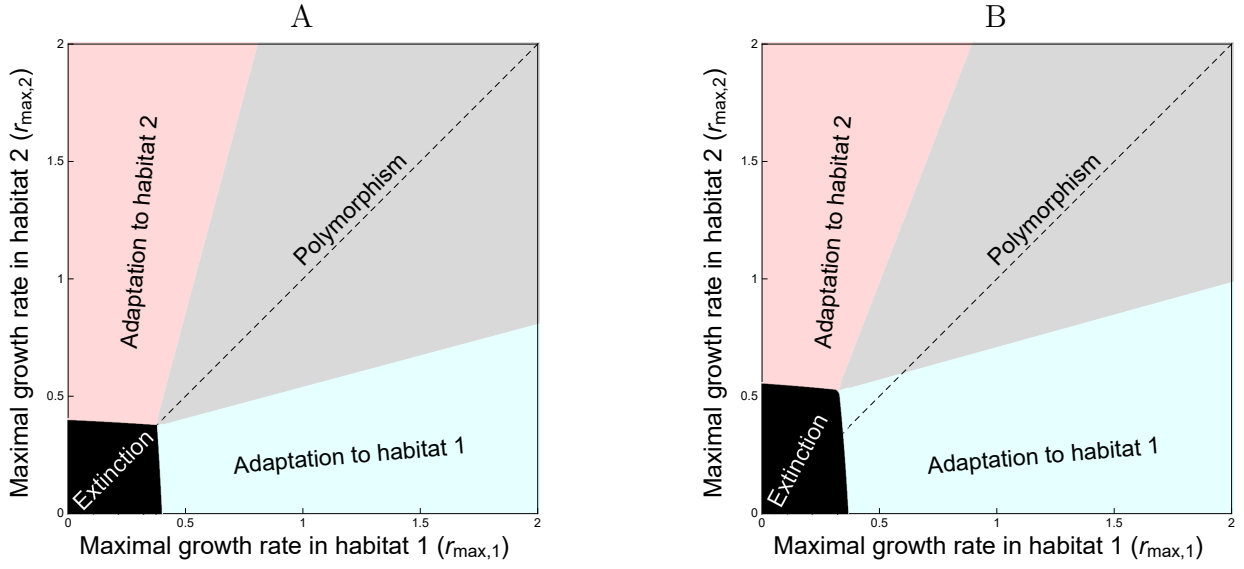
Figure 2 – Maintenance of polymorphism and non-symmetric adaptation as a function of the maximal growth rates $r_{max,1}$ and $r_{max,2}$ in the two habitats. In (A) we examine a symmetric situation where all the parameters are identical in the two habitats: $m_1 = m_2 = 0.5$, $s_1 = s_2 = 2$, $\kappa_1 = \kappa_2 = 1$. In (B) we show a non-symmetric case with the same parameters as in (A) except $m_1 = 0.5$ and $m_2 = 0.7$. The black area indicates the parameter space where the population is driven to extinction because the maximal growth rates are too low. In the grey area some polymorphism can be maintained in the two-habitat population as long as the difference in the maximal growth rates are not too high. When this difference reaches a threshold polymorphism cannot be maintained and the single type that is maintained is more adapted to the good-quality habitat (the habitat with the highest maximal growth rate).

2.2 Selection-mutation-migration equilbirum

In the following we allow mutation rate to increase and we study the impact of mutations on the ultimate evolutionary equilibrium of the phenotypic densities, i.e. the solution of (26). We present below the general principle of the approach before examining specific case studies.

Our objective is to provide an approximation of the phenotypic density in each habitat when the effect

of mutation (measured by ε) is small. We use analogous transformation to (4):

$$n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_{\varepsilon,i}(z)}{\varepsilon}\right). \tag{31}$$

Our objective is then to estimate $u_{\varepsilon,i}(z)$. We proceed as in Section 1.2 and we postulate an expansion for $u_{\varepsilon,i}$ in terms of ε:

$$u_{\varepsilon,i}(z) = u_i(z) + \varepsilon v_i(z) + O(\varepsilon^2), \tag{32}$$

and we try to compute the coefficients $u_i(z)$ and $v_i(z)$. First we can show that, when there is migration in both directions (i.e. $m_i > 0$ for $i = 1, 2$), the zero order terms are the same in both habitats: $u_1(z) = u_2(z) = u(z)$ (see Section 2.3 below). We can indeed compute explicitly $u(z)$ which is given by (37) in the monomorphic case and by (38) in the dimorphic case. As we observe in the formula (37) and (38), $u(z)$ attains its maximum (which is equal to 0) at the ESS points identified in the previous subsection. This means that the peaks of the population's distribution are around the ESS points (z^{M*} in the case of the monomorphic ESS and $(z_\mathrm{I}^{D*}, z_\mathrm{II}^{D*})$ for the dimorphic ESS). Note that the fact that $u_1(z) = u_2(z) = u(z)$ means that the peaks of the population distribution are placed approximately at the same points (ESS points) in both habitats. However, the size of the peaks may be different since $v_1(z)$ is not necessarily equal to $v_2(z)$.

We are also able to compute the first order term $v_i(z)$ (see Section 2.3). This allows us to obtain an approximation (that we call *first approximation*) of the phenotypic density $n_{\varepsilon,i}(z)$.

As in section 1.2 we can also derive more explicit formula for the moments of order $k \geq 1$ of the stationary phenotypic distribution. This *second approximation*, instead of using the values of $u(z)$ and $v_i(z)$ in the whole domain, is based on the computation of the Taylor expansions of $u(z)$ and $v_i(z)$ around the ESS points and can be computed following similar types of arguments as in Section 1.5.

2.3 Heuristic derivation

As mentioned above, our *first approximation* is based on the computation of the terms $u_i(z)$ and $v_i(z)$.

Based on such computations we can provide an approximation of the population's total density $\rho_{\varepsilon,i}$ and the phenotypic density $n_{\varepsilon,i}(z)$ in the following form

$$\rho_{\varepsilon,i} \approx \rho_i + \varepsilon K_i, \qquad n_{\varepsilon,i}(z) \propto \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_i(z) + \varepsilon v_i(z)}{\varepsilon}\right). \tag{33}$$

In order to identify the functions u_i, v_i, ρ_i and K_i, we first let $\varepsilon \to 0$ in (26) to obtain that $n_{\varepsilon,i}(z) \to n_i(z)$ and $\rho_{\varepsilon,i} \to \rho_i$ with

$$\begin{cases} 0 = n_1(z)\left(r_1(z) - \kappa_1 \rho_1\right) + m_2 n_2(z) - m_1 n_1(z), \\[2mm] 0 = n_2(z)\left(r_2(z) - \kappa_2 \rho_2\right) + m_1 n_1(z) - m_2 n_2(z), \\[2mm] \rho_i = \int_{\mathbb{R}} n_i(z) dz, \end{cases}$$

which is equivalent with

$$\mathcal{A}(z, \rho_1, \rho_2) \begin{pmatrix} n_1(z) \\[2mm] n_2(z) \end{pmatrix} = 0, \qquad \rho_i = \int_{\mathbb{R}} n_i(z) dz,$$

with $\mathcal{A}(z, \rho_1, \rho_2)$ given by (27). This means that (ρ_1, ρ_2) corresponds to the sizes of the populations 1 and 2 at the demographic equilibrium $(n_1(z), n_2(z))$, in absence of mutations. We will show that this equilibrium corresponds indeed to a global evolutionary stable strategy and hence $\rho_i = \rho_i^*$. To this end, we replace (31) in (26) and obtain

$$\begin{cases} 0 = \varepsilon u_{\varepsilon,1}''(z) + |u_{\varepsilon,1}'(z)|^2 + r_1(z) - \kappa_1 \rho_{\varepsilon,1} + m_2 \exp\left(\frac{u_{\varepsilon,2}(z) - u_{\varepsilon,1}(z)}{\varepsilon}\right) - m_1, \\[2mm] 0 = \varepsilon u_{\varepsilon,2}''(z) + |u_{\varepsilon,2}'(z)|^2 + r_2(z) - \kappa_2 \rho_{\varepsilon,2} + m_1 \exp\left(\frac{u_{\varepsilon,1}(z) - u_{\varepsilon,2}(z)}{\varepsilon}\right) - m_2. \end{cases} \tag{34}$$

Similarly to above, this system is derived using the following equalities

$$n_{\varepsilon,i}'(z) = u_{\varepsilon,i}'(z)\frac{n_{\varepsilon,i}(z)}{\varepsilon}, \qquad n_{\varepsilon,i}''(z) = \left(u_{\varepsilon,i}''(z) + |u_{\varepsilon,i}'(z)|^2\right)\frac{n_{\varepsilon,i}(z)}{\varepsilon^2}.$$

We can determine $u_i(z)$, $v_i(z)$ from the above equation and (32).

Note that the exponential terms in (43) suggest that, when $m_i > 0$ for $i = 1, 2$, as $\varepsilon \to 0$ $u_{\varepsilon,1}(z)$ and

$u_{\varepsilon,2}(z)$ converge to the same limit $u(z)$. Otherwise, one of these exponential terms tends to infinity while the other terms are bounded. Keeping the zero order terms (the ones in front of which there is no ε, corresponding to the dominant terms) we obtain

$$\begin{cases} 0 = |u'(z)|^2 + r_1(z) - \kappa_1\rho_1 + m_2\exp(v_2(z) - v_1(z)) - m_1, \\ 0 = |u'(z)|^2 + r_2(z) - \kappa_2\rho_2 + m_1\exp(v_1(z) - v_2(z)) - m_2. \end{cases} \tag{35}$$

We then multiply the first line by $\exp(v_1(z))$ and the second line by $\exp(v_2(z))$ and write the system in the matrix form to obtain

$$\begin{pmatrix} w_1(z;\rho_1) - m_1 & m_2 \\ m_1 & w_2(z;\rho_2) - m_2 \end{pmatrix} \begin{pmatrix} \exp(v_1(z)) \\ \exp(v_2(z)) \end{pmatrix} = -|u'(z)|^2 \begin{pmatrix} \exp(v_1(z)) \\ \exp(v_2(z)) \end{pmatrix}.$$

Note that the matrix in the l.h.s. is nothing but $\mathcal{A}(z,\rho_1,\rho_2)$ given by (27). The equality above means that $-|u'(z)|^2$ is indeed the principal eigenvalue of $\mathcal{A}(z;\rho_1,\rho_2)$, that is (see Section 2.1)

$$-|u'(z)|^2 = W(z;\rho_1,\rho_2).$$

Similarly to Subsection 1.4, to have a finite but positive size of population, we should have

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

Otherwise, in view of (31), the total population size whether becomes infinite as $\varepsilon \to 0$ (if $\max_{z\in\mathbb{R}} u(z) > 0$) or it goes to 0 (if $\max_{z\in\mathbb{R}} u(z) < 0$). Similarly we obtain

$$\text{supp}\, n_i \subset \{z \,|\, u(z) = 0\},$$

where $\text{supp}\, n_i$ is the set of traits z such that the density $n_i(z)$ is positive. The above property holds since $u(z_0) < 0$ implies that $\lim_{\varepsilon\to0} n_{\varepsilon,i}(z_0) = 0$.

Let $\bar{z}$ be such that $u(\bar{z}) = 0$ which means that it is a maximum point of $u(z)$. Then, $u'(\bar{z}) = 0$ and

hence

$$W(\bar{z}; \rho_1, \rho_2) = 0.$$

Moreover in all the points $z \in \mathbb{R}$, we have

$$W(z; \rho_1, \rho_2) = -|u'(z)|^2 \leq 0.$$

This implies that

$$\text{if } z \in \text{supp}\, n_1 = \text{supp}\, n_2 \text{ then } W(z; \rho_1, \rho_2) = 0,$$

$$\text{if } z \notin \text{supp}\, n_1 = \text{supp}\, n_2 \text{ then } W(z; \rho_1, \rho_2) \leq 0.$$

In other words $(n_1(z), n_2(z))$ corresponds to the demographic equilibrium corresponding to the global ESS and hence $n_i(z) = n_i^*(z)$ and $\rho_i = \rho_i^*$, with $n_i^*(z)$ and ρ_i^* given in Subsection 2.1.

We gather the informations that we obtained on $u(z)$:

$$\begin{cases} -|u'(z)|^2 = W(z; \rho_1^*, \rho_2^*), \\ \max_{z \in \mathbb{R}} u(z) = 0, \end{cases} \tag{36}$$

with the maximum points of $u(z)$ attained at the ESS points. We can indeed prove that u solves the above equation in the viscosity sense.

Similarly to Section 1.6, this property allows us to identify u in a unique way and to provide explicit formula for $u(z)$.

In the case of monomorphic ESS, $u(z)$ is given by

$$u(z) = -\left| \int_{z^{M*}}^{z} \sqrt{-W(x; \rho_1^{M*}, \rho_2^{M*})} dx \right|. \tag{37}$$

The reader can verify that $u(z)$, given by the formula above, is smooth and solves (36) with its maximum point at z^{M*}.

In the case of dimorphic ESS, $u(z)$ is given by

$$u(z) = \max\left(-\left| \int_{z_I^{D*}}^{z} \sqrt{-W(x; \rho_1^{M*}, \rho_2^{M*})} dx \right|, -\left| \int_{z_{II}^{D*}}^{z} \sqrt{-W(x; \rho_1^{M*}, \rho_2^{M*})} dx \right| \right). \tag{38}$$

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The reader can also verify that the above function is smooth at all points except at the point where the two functions in the maximum operator intersect. Moreover, $u(z)$ solves (36) at the smooth points and it attains its maximum at the ESS points z_I^{D*} and z_{II}^{D*}. See ([19] and ([15], Chapter 5)) for the details on why u can be determined by the above formulas.

Computation of the next order terms $v_i(z)$:

The derivation of the next order terms $v_i(z)$ follows also similar arguments as in Section 1.4. However, since here we have a system the computations are less straight forward. We present the main ingredients to compute these terms.

From (35) and (36) we can compute $v_2(z) - v_1(z)$ thanks to the following formula

$$v_2(z) - v_1(z) = \log\left(\frac{1}{m_2}\left(W(z, \rho_1^{M*}, \rho_2^{M*}) - w(z, \rho_1^{M*}) + m_1\right)\right).$$

We next keep the first order terms in (43), i.e. the terms with an ε in front of them. To do so, we need to go further than (32) in the approximation of $u_{\varepsilon,i}(z)$ and also keep the term of order ε^2, $l_i(z)$:

$$u_{\varepsilon,i}(z) = u(z) + \varepsilon v_i(z) + \varepsilon^2 l_i(z) + O(\varepsilon^3).$$

Then, keeping the first order terms in (43) we obtain

$$\begin{cases} 0 = u''(z) + 2u'(z)v_1'(z) - \kappa_1 K_1 + m_2 \exp(v_2(z) - v_1(z))(l_2(z) - l_1(z)), \\ 0 = u''(z) + 2u'(z)v_2'(z) - \kappa_2 K_2 + m_2 \exp(v_1(z) - v_2(z))(l_1(z) - l_2(z)). \end{cases} \tag{39}$$

Using the above equalities and by evaluating them at the ESS points we can compute $v_i(z)$ and K_i for $i = 1, 2$. See [19]–Section 3.3 for the details of such computations.

3 The transient dynamics

The Hamilton-Jacobi approach allows also to study the transient evolutionary dynamics of populations. This method was indeed initially introduced to study dynamic equations [8, 24, 2]. In this section we

show briefly how the method can be applied to study the transient dynamics of a population.

3.1 One population: the transient dynamics of a population subject to selection and mutation

In this section, we present the method for a more general model than the one studied above:

$$\begin{cases} \frac{\partial}{\partial t}n - UV_m\Delta n = nR(z,I), & z \in \mathbb{R}^d \\ I(t) = \int_{\mathbb{R}^d} \eta(y)n(t,y)dy, \end{cases} \tag{40}$$

This model, takes into account the competition for the resources which are consumed by the individuals of trait y the rate $\eta(y)$. The growth rate of individuals of trait z, i.e. $R(z,I)$, depends in a decreasing way on the total consumption of the population $I(t)$. Note that if

$$\eta \equiv 1, \qquad R(z,I) = r_0(z) - \kappa I,$$

then the model is equivalent to the model (1). Note also that here we let $z \in \mathbb{R}^d$ while in Section 1 we considered $z \in \mathbb{R}$. While we chose the simpler model studied in Section 1 to simplify the notations and to insist on the general principles of the method, all the results in Section 1 can be generalized to the model (40).

Here are the main assumptions on η and R (for the whole set of assumptions see [5]):

$$0 < C_1 \leq \eta \leq C_2,$$

$$-C_3 \leq \frac{\partial R}{\partial I}(z,I) \leq -C_4 < 0,$$

$$\max_{z \in \mathbb{R}^d} R(z, I_M) = 0.$$

A typical example is

$$R(z,I) = r_0(z) - \kappa I, \quad \text{with } r_0(z) \text{ a concave function.}$$

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3.1.1 The regime of small mutations

As in Section 1, we assume that the mutations have small effects, that is $UV_m = \varepsilon^2$, with ε a small parameter. In order to observe the small effect of the mutations on the dynamics of the phenotypic density, we also make a change of variable in time to accelerate the dynamics:

$$t \mapsto \frac{t}{\varepsilon}, \quad n_\varepsilon(t, z) = n(\frac{t}{\varepsilon}, z).$$

Replacing this in (40), the equation on n_ε is written

$$\begin{cases} \varepsilon \frac{\partial}{\partial t} n_\varepsilon - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon R(z, I_\varepsilon), \\ I_\varepsilon(t) = \int \eta(y) n_\varepsilon(t, y) dy. \end{cases} \quad (41)$$

As previously, the method starts with a Hopf-Cole transformation

$$n_\varepsilon(t, z) = \frac{1}{(2\pi\varepsilon)^{d/2}} \exp\left(\frac{u_\varepsilon(t, z)}{\varepsilon}\right). \quad (42)$$

We can show that the function u_ε converges locally uniformly to a continuous function which is the viscosity solution to a Hamilton-Jacobi equation with constraint. Under suitable assumptions we can also provide an asymptotic expansion for u_ε:

$$u_\varepsilon = u + \varepsilon v + O(\varepsilon^2).$$

This allows us to provide an approximation of the phenotypic density and its moments as in the stationary case. We will also provide a differential equation describing the dynamics of the dominant trait in the population. This equation is related to Lande's equation in Quantitative Genetics (and also to the canonical equation of Adaptive Dynamics). However, it is more general since it takes into account the dynamics of the variance of the phenotypic distribution.

3.1.2 Derivation of the Hamilton-Jacobi equation with constraint

Replacing (42) in (41) we obtain

$$\partial_t u_\varepsilon - \varepsilon^2 \Delta u_\varepsilon = |\nabla u_\varepsilon|^2 + R(z, I_\varepsilon). \tag{43}$$

Similarly to above, this equation is obtained using the following relations:

$$\frac{\partial}{\partial t} n_\varepsilon(t, z) = \frac{\partial}{\partial t} u_\varepsilon(t, z) \frac{n_\varepsilon(t, z)}{\varepsilon},$$

$$\nabla n_\varepsilon(t, z) = \nabla u_\varepsilon(t, z) \frac{n_\varepsilon(t, z)}{\varepsilon}, \qquad \Delta n_\varepsilon(t, z) = \left(\Delta u_\varepsilon(t, z) + |\nabla u_\varepsilon(z)|^2 \right) \frac{n_\varepsilon(t, z)}{\varepsilon^2}.$$

Let's suppose that $(u_\varepsilon, I_\varepsilon)$ converges, as $\varepsilon \to 0$, to (u, I), with

$$0 < I_1 \leq I(t) \leq I_2.$$

Such properties can be indeed proved under suitable assumptions [2, 5]. Following similar arguments as in the previous section, we obtain

$$\max_z u(t, z) = 0, \qquad \text{for all } t,$$

and

$$\text{supp } n(t, z) \subset \{z | u(t, z) = 0\}.$$

Here, $n(t, z)$ is a measure obtained as the limit of $n_\varepsilon(t, z)$ as $\varepsilon \to 0$. Passing formally to the limit in (43) we also obtain that

$$\frac{\partial}{\partial t} u - |\nabla u|^2 = R(z, I).$$

Note moreover, that at the maximum point z_m of $u(t, \cdot)$, we have

$$\frac{\partial}{\partial t} n_\varepsilon(t, z_m) = 0, \qquad \frac{\partial}{\partial z} n_\varepsilon(t, z_m) = 0,$$

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and hence

$$R(z_m, I(t)) = 0.$$

We deduce that

$$\{z | u(t, z) = 0\} \subset \{z | R(z, I(t)) = 0\}.$$

Combining the above properties we obtain that

$$
\begin{cases}
\frac{\partial}{\partial t} u - |\nabla u|^2 = R(z, I), \\
\max_z u(t, z) = 0, \qquad \text{for all } t, \\
u(0, z) = u_0(z).
\end{cases}
\tag{44}
$$

$$\text{supp } n(t, \cdot) \subset \{z | u(t, z) = 0\} \subset \{z | R(z, I(t)) = 0\}. \tag{45}$$

We can indeed prove rigorously that u_ε converges to the viscosity solution of (44) [24, 2, 5]. Moreover the solution (u, I) to the Hamilton-Jacobi equation with constraint (44) is unique [21, 4]. Note that describing the solution u is more difficult in the dynamic case, since it depends on the identification of $I(t)$ which is more complex in the dynamic case. In what follows, we will show which type of information on the phenotypic density we could obtain from such result.

3.1.3 Concentration of the phenotypic density at a single point (monomorphism)

As the effect of the mutations ε vanishes, we expect that n_ε converges to a Dirac mass $\rho(t)\delta(z - \overline{z}(t))$. This means that the phenotypic density would concentrate at a single dominant trait $\overline{z}(t)$ which evolves under the effects of the mutations and selection. In this model, since the growth rate suffers from the competition for only one nutrient, via the term $I(t)$, we expect indeed to have a single dominant trait, as the effect of the mutations vanishes. This is indeed a consequence of the principle of the competitive exclusion [14, 25] which states that when there are k limiting factors for the population, no more than k distinct traits may coexist. When ε is small but non-zero, we then expect that the phenotypic density $n_\varepsilon(t, \cdot)$ would have a continuous uni-modal distribution, with its peak close to this dominant trait $\overline{z}(t)$.

A key information that allows to show such concentration phenomenon is given by (45). If we can prove that either the set $\{z|u(t,z)=0\}$ or the set $\{z|R(z,I(t))=0\}$ has a single point, we will then deduce that supp $n(t,\cdot)$ has a single point and hence, the phenotypic density n is a single Dirac mass: $n(t,\cdot)=\rho(t)\delta(\cdot-\overline{z}(t))$.

Let's assume for instance that $z\in\mathbb{R}$ and that $R(\cdot,I)$ is a monotonic function with respect to its first variable. This then implies that the set $\{z|R(z,I(t))=0\}$ has a singe point and hence n is a single Dirac mass. This is not the only situation where we can prove such property. In the next section, we will introduce a framework, which not only allows to obtain such concentration property but it also leads to more quantitative results.

3.1.4 The concave framework; more precise results

In this section we assume additionally that $R(\cdot,I)$ and $u_{\varepsilon,0}(\cdot)$ are strictly concave functions, where

$$u_{\varepsilon,0}(z)=\varepsilon\log((2\pi\varepsilon)^{d/2}n_{\varepsilon}(0,z)).$$

We assume indeed that

$$-D_1\leq D^2u_{\varepsilon,0}(z)\leq -D_2<0,$$

$$-D_3\leq D^2R(z,I)\leq -D_4<0,$$

Theorem 3.1 *[16, 21] In the concave framework, $u(t,\cdot)$ the viscosity solution to (44) is indeed smooth and a classical solution. Moreover, $u(t,\cdot)$ is a strictly concave function and hence, for all $t\geq 0$, there exists a unique point $\overline{z}(t)$ such that*

$$\max_z u(t,z)=u(t,\overline{z}(t))=0,$$

which implies that

$$n(t,z)=\rho(t)\delta(z-\overline{z}(t)).$$

Finally, the following equation describes the dynamics of the dominant trait $\overline{z}(t)$:

$$\dot{\overline{z}}(t) = (-D^2 u(t, \overline{z}(t)))^{-1} \nabla R(\overline{z}(t), I(t)). \tag{46}$$

Theorem 3.2 *[23, 22] In the concave framework, and under regularity assumptions, we have*

$$u_\varepsilon(t, z) = u(t, z) + \varepsilon v(t, z) + o(\varepsilon), \qquad I_\varepsilon(t) = I(t) + \varepsilon J(t) + o(\varepsilon).$$

Similarly to the previous sections, Theorem 3.2 leads to the following approximation of the phenotypic density:

$$n_{\varepsilon, 0}(z) \approx \frac{1}{(2\pi\varepsilon)^{d/2}} \exp\left(\frac{u(t, z) + \varepsilon v(t, z)}{\varepsilon}\right).$$

It also allows to provide analytic approximations of the moments of the phenotypic distribution. In particular, we can compute the covariance matrix of the phenotypic distribution as follows

$$\mathbf{V}_{\varepsilon, t} = \varepsilon(-D^2 u)^{-1}(t, \overline{z}(t)) + o(\varepsilon),$$

where $\mathbf{V}_{\varepsilon, t} = (v_{i,j}(t))$ with $v_{i,j} = \int z_i z_j \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dx - (\int z_i \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dz)(\int z_j \frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} dz)$. Note that here we find again the term $(-D^2 u)^{-1}(t, \overline{z}(t))$ which also appeared in equation (46). This property allows to provide a biological interpretation of this equation and in particular to compare it to the so-called canonical equation in Adaptive Dynamics [7, 6] or to Lande's equation in Quantitative Genetics [17, 12, 13]. In these equations, which are very related equations under different formalisms, the change in the dominant/average trait is given by the product of the gradient of the fitness and a term that scales the rate of evolutionary change (proportional to mutational variance or genetic variance respectively in adaptive dynamics and quantitative genetics). In (46), the dynamics of the dominant trait $\dot{\overline{z}}(t)$ is also given by the product of the gradient of the fitness $\nabla_z R$ and the term $(-D^2 u(t, \overline{z}(t)))^{-1}$ which, when multiplied by ε, approximates well the phenotypic covariance matrix (note that here we do not consider any environmental contribution in the phenotype, therefore the phenotypic variance is equal to the genetic variance). In this way, (46) may be seen as a generalization of the canonical equation or Lande's equation to a case where the mutations are not assumed to be very rare (on the contrary

to adaptive dynamics) and such that the evolution of the genetic variance is included in the dynamics (the phenotypic density is not assumed to be of Gaussian type with fixed variance).

3.1.5   Example of quadratic fitness

Let's consider the following fitness function:

$$R(z, I) = r_{\max} - sz^2 - \kappa I.$$

One can solve explicitly the selection-mutation model (40) with such growth rate when the initial condition is a Gaussian. However, it is less trivial to do so when the initial condition is arbitrary. Here, we show how to provide an approximation of the solution, when ε is small, assuming arbitrary initial condition using the Hamilton-Jacobi approach. An alternative way to do so is to use the method based on cumulated generating functions [18] which provides an explicit solution for arbitrary ε. This method works particularly well when one considers a quadratic stabilizing selection. The Hamilton-Jacobi approach has the advantage to apply to arbitrary forms of growth rates $R(z, I)$ and with possible heterogeneities.

In this case study, the corresponding Hamilton-Jacobi equation is written

$$\begin{cases} \frac{\partial}{\partial t} u(t, z) - |\frac{\partial}{\partial z} u|^2 (t, z) = r_{\max} - sz^2 - \kappa I, \\ \max_z u(t, z) = u(t, \overline{z}(t)) = 0, \\ u(0, z) = u_0(z). \end{cases}$$

Note that, since

$$R(\overline{z}(t), I(t)) = 0,$$

one can then express the value of I in terms of $\overline{z}(t)$:

$$I(t) = \frac{1}{\kappa} \left(r_{\max} - s\overline{z}^2(t) \right).$$

We can also provide an analytic formula for the dominant trait $\overline{z}(t)$ (which is a good approximation

of the mean phenotypic trait when ε is small):

$$\overline{z}(t) = \frac{2e^{2\sqrt{s}t}}{1 + e^{4\sqrt{s}t}} \arg\max_{C} \{u_0(C) - C^2 \frac{\sqrt{s}}{2} \tanh\left(2\sqrt{s}t\right)\}.$$

Computation of $\overline{z}(t)$:

We next show how to identify analytically $\overline{z}(t)$. Note that the function u solves

$$\frac{\partial}{\partial t}u(t,z) - |\frac{\partial}{\partial z}u|^2(t,z) = -sz^2 + s\overline{z}^2(t).$$

The viscosity solution of the above equation is indeed given by the following representation formula:

$$u(t,z) = \sup_{\substack{\gamma \in W^{1,\infty}([0,t]) \\ \gamma(t)=z}} u_0(\gamma(0)) - \int_0^t \left(\frac{|\dot{\gamma}|^2}{4}(\tau) + s\gamma^2(\tau) - s\overline{z}^2(\tau)\right)d\tau.$$

The maximizing trajectory satisfies the following Euler-Lagrange equation:

$$\ddot{\gamma}(\tau) = 4s\gamma(\tau).$$

As a consequence $\gamma(\tau)$ can be written as follows

$$\gamma(\tau) = Ae^{2\sqrt{s}\,\tau} + (C - A)e^{-2\sqrt{s}\,\tau}, \qquad \text{with } A \text{ and } C \text{ some constants.}$$

We deduce that

$$
\begin{aligned}
u(t,z) &= \sup_{\substack{A,C \in \mathbb{R} \\ Ae^{2\sqrt{s}\,t}+(C-A)e^{-2\sqrt{s}\,t}=z}} u_0(C) - s\int_0^t \left(2A^2 e^{4\sqrt{s}\,\tau} + 2(C-A)^2 e^{-4\sqrt{s}\,\tau} - \overline{z}^2(\tau)\right)d\tau \\
&= \sup_{\substack{A,B \in \mathbb{R} \\ Ae^{2\sqrt{s}\,t}+(C-A)e^{-2\sqrt{s}\,t}=z}} u_0(C) - \frac{\sqrt{s}}{2}\left(A^2(e^{4\sqrt{s}\,t} - 1) + (C-A)^2(1 - e^{-4\sqrt{s}\,t})\right) + s\int_0^t \overline{z}^2(\tau)d\tau.
\end{aligned}
$$

We are interested in identifying the point $\overline{z}(t)$ which corresponds to the maximum point of $u(t,\cdot)$.

Let's define

$$F(A,C) = u_0(C) - \frac{\sqrt{s}}{2}\left(A^2(e^{4\sqrt{s}\,t} - 1) + (C-A)^2(1 - e^{-4\sqrt{s}\,t})\right).$$

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If the maximum of F is taken at some point (A_m, C_m). Then,

$$\overline{z}(t) = A_m e^{2\sqrt{s}\,t} + (C_m - A_m)e^{-2\sqrt{s}\,t},$$

is a maximum point of $u(t, \cdot)$. Note that the maximum point A_m can be expressed in terms of C_m:

$$A_m = C_m \frac{1 - e^{-4\sqrt{st}}}{e^{4\sqrt{st}} - e^{-4\sqrt{st}}} = C_m \frac{1}{1 + e^{4\sqrt{st}}}.$$

We deduce that

$$
\begin{aligned}
C_m &= \arg\max_C u_0(C) - C^2 \frac{\sqrt{s}}{2} \left(\frac{e^{4\sqrt{s}\,t} - 1}{(1 + e^{4\sqrt{st}})^2} + \frac{e^{8\sqrt{s}\,t} - e^{4\sqrt{s}\,t}}{(1 + e^{4\sqrt{st}})^2} \right) \\
&= \arg\max_C u_0(C) - C^2 \frac{\sqrt{s}}{2} \tanh\left(2\sqrt{st}\right).
\end{aligned}
$$

This implies that

$$\overline{z}(t) = \frac{2e^{2\sqrt{st}}}{1 + e^{4\sqrt{st}}} \arg\max_C \left\{ u_0(C) - C^2 \frac{\sqrt{s}}{2} \tanh\left(2\sqrt{st}\right) \right\}.$$

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