EVOLUTIONARY BRANCHING VIA REPLICATOR-MUTATOR EQUATIONS

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Abstract. We consider a class of non-local reaction-diffusion problems, referred to as *replicator-mutator* equations in evolutionary genetics. For a confining fitness function, we prove well-posedness and write the solution explicitly, via some underlying Schrödinger spectral elements (for which we provide new and non-standard estimates). As a consequence, the long time behaviour is determined by the principal eigenfunction or *ground state*. Based on this, we discuss (rigorously and via numerical explorations) the conditions on the fitness function and the mutation rate for *evolutionary branching* to occur.

1. Introduction

In this paper we first study the existence, uniqueness and long time behaviour of solutions $u = u(t,x)$, $t > 0$, $x \in \mathbb{R}$, to the integro-differential Cauchy problem

$$\begin{cases} \dfrac{\partial u}{\partial t} = \sigma^2 \dfrac{\partial^2 u}{\partial x^2} + u\left(\mathcal{W}(x) - \displaystyle\int_{\mathbb{R}} \mathcal{W}(y)u(t,y)\,dy\right), \quad t>0,\ x\in\mathbb{R}, \\ u(0,x) = u_0(x), \end{cases} \tag{1}$$

which serves as a model for the dynamics of adaptation, and where $\mathcal{W}$ is a confining fitness function (see below for details). Next, we enquire on the possibility, depending on the function $\mathcal{W}$ and the parameter $\sigma > 0$, for a solution to split from *uni-modal* to *multi-modal* shape, thus reproducing *evolutionary branching*.

The above equation is referred to as a *replicator-mutator* model. This type of model has found applications in different fields such as economics and biology [25], [4]. In the field of evolutionary genetics, a free spatial version of equation (1) was introduced by Tsimring, Levine and Kessler in [40], where they propose a mean-field theory for the evolution of RNA virus population. Without mutations, and under the constraint of constant mass $\int_{\mathbb{R}} u(t,x)\,dx = 1$, the dynamics is given by

$$\frac{\partial u}{\partial t} = u\left(\mathcal{W}(x) - \int_{\mathbb{R}} \mathcal{W}(y)u(t,y)\,dy\right), \tag{2}$$

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with $\mathcal{W}(x) = x$ in [40]. In this context, $u(t,x)$ represents the density of a population (at time t and per unit of phenotypic trait) on a one-dimensional phenotypic trait space. The function $\mathcal{W}(x)$ represents the *fitness* of the phenotype x and models the individual reproductive success; thus the non-local term

$$\overline{u}(t) := \int_{\mathbb{R}} \mathcal{W}(y)u(t,y)\,dy$$

stands for the mean fitness at time t.

As a first step to take into account evolutionary phenomena, mutations are modelled by the local diffusion operator $\sigma^2\partial_x^2$, where σ^2 is the mutation rate, so that equation (2) is transferred into (1). We refer to the recent paper [41] for a rigorous derivation of the replicator-mutator problem (1) from individual based models.

Equation (1) is supplemented with a non-negative and bounded, initial data $u_0(\cdot) \geq 0$ such that $\int_{\mathbb{R}} u_0(x)\,dx = 1$, so that, *formally*, $\int_{\mathbb{R}} u(t,x)\,dx = 1$ for later times. Indeed, integrating formally (1) over $x \in \mathbb{R}$, the total mass

$$m(t) := \int_{\mathbb{R}} u(t,x)\,dx$$

solves the initial value problem

$$\frac{d}{dt}m(t) = (1 - m(t))\overline{u}(t),\ m(0) = 1.$$

Hence, by Gronwall's lemma, $m(t) = 1$, as long as $\overline{u}(t)$ is meaningful.

The case of linear fitness function, $\mathcal{W}(x) = x$, was the first introduced in [40], but little was known concerning existence and behaviours of solutions. Let us here mention the main result of Biktashev [5]: for compactly supported initial data, solutions converge, as t goes to infinity, to a Gaussian profile, where the convergence is understood in terms of the moments of $u(t,\cdot)$. In a recent paper [2], Alfaro and Carles proved that, thanks to a tricky change of unknown based on the Avron-Herbst formula (coming from quantum mechanics), equation (1) can be reduced to the heat equation. This enables to compute the solution explicitly and describe contrasted behaviours depending on the tails of the initial datum: either the solution is global and tends, as t tends to infinity, to a Gaussian profile which is centred around $x(t) \sim t^2$ (acceleration) and is flattening (extinction in infinite horizon), or the solution becomes extinct in finite time (or even immediately) thus contradicting the conservation of the mass, previously formally observed.

For quadratic fitness functions, $\mathcal{W}(x) = \pm x^2$, it turns out that the equation can again be reduced to the heat equation [3], up to an additional use of the generalized lens transform of the Schrödinger equation. In the case $\mathcal{W}(x) = x^2$, for any initial data, there is extinction at a finite time which is always bounded from above by $T^* = \frac{\pi}{4\sigma}$. Roughly speaking, both the right and left tails quickly enlarge, so that, in order to conserve the mass, the central part is quickly decreasing. Then the non-local mean fitness term $\int_{\mathbb{R}} y^2 u(t,y)\,dy$ becomes infinite very quickly and equation (1) becomes meaningless (extinction). On the other hand, when $\mathcal{W}(x) = -x^2$, for any initial data, the solution is global and tends, as t tends to infinity, to an universal stationary Gaussian profile.

The aforementioned cases $\mathcal{W}(x) = x$ and $\mathcal{W}(x) = x^2$ share the property of being unbounded from above, meaning that some phenotypes are infinitely well-adapted. This unlimited growth rate of $u(t, x)$ in (1) yields rich mathematical behaviours (acceleration, extinction) but is not admissible for biological applications. To deal with such a problem, for the linear fitness case, some works consider a "cut-off version" of (1) at large x [40], [35], [37], or provide a proper stochastic treatment for large phenotypic trait region [34].

On the other hand, $\mathcal{W}(x) = -x^2$ is referred to as a confining fitness function, typically preventing extinction phenomena. However, it does not suffice to take into account more realistic cases for which fitness functions are defined by a linear combination of two components (e.g. birth and death rates), each maximized by different optimal values of the underlying trait, a typical case being $\mathcal{W}(x) = x^2 - x^4$.

Our main goal is thus to provide a rigorous treatment of the Cauchy problem (1) when the fitness function $\mathcal{W}$ is confining. For a relatively large class of such fitness functions, we prove well-posedness, and show that the solution of (1) converges to the principal eigenfunction (or ground state) of the underlying Schrödinger operator divided by its mass. This requires rather non-standard estimates on the eigenelements. Also, from a modelling perspective, this enables to reproduce *evolutionary branching*, consisting of the spontaneous splitting from uni-modal to multi-modal distribution of the trait.

Such splitting phenomena have long been discussed and analysed in different frameworks, see e.g. [29] via Hamilton-Jacobi technics, [42] within finite populations, or [27] for a Lotka-Volterra system in a bounded domain. In a replicator-mutator context, let us notice that, while branching in (1) is mainly induced by the fitness function, it was recently obtained in [18] through different means. Precisely, the authors study the case of linear fitness $\mathcal{W}(x) = x$ but non-local diffusion $J * u - u$ (mutation kernel), namely

$$\partial_t u = J * u - u + u\left(x - \int_{\mathbb{R}} y u(t, y)\, dy\right).$$

Their approach [30], [18] is based on *Cumulant Generating Functions* (CGF): it turns out that the CGF satisfies a first order non-local partial differential equation that can be explicitly solved, thus giving access to many informations such as mean trait, variance, position of the leading edge. When a purely deleterious mutation kernel J balances the infinite growth rate of $\mathcal{W}(x) = x$, they reveal some branching scenarios.

The paper is organized as follows. In Section 2 we present the underlying linear material. In Section 3 we prove the well-possessedness of the Cauchy problem associated to (1). We also provide an explicit expression of the solution and studies its long time behaviour. In Section 4 we discuss, through rigorous details or numerical explorations, the conditions on the shape of the fitness function $\mathcal{W}$ and on the mutation parameter $\sigma > 0$ for branching phenomenon to occur. Finally, we briefly conclude in Section 5.

2. Some spectral properties

In this section, we present some linear material. We first quote some very classical results [39], [33], [1], [21], [22], [20], [15] for Schrödinger operators, and then prove less standard estimates on the eigenfunctions, which are crucial for later analysis.

2.1. **Confining fitness functions and eigenvalues properties.**

Confining fitness functions tend to $-\infty$ at infinity. In quantum mechanics, this corresponds to potentials describing the evolution of quantum particles subject to an external field force that prevents them from escaping to infinity, that is, particles have a high probability of presence in a bounded spatial region.

Assumption 1 (Confining fitness function)**.** *The fitness function $\mathcal{W}$ is continuous and confining, that is*

$$\lim_{|x|\to\infty} \mathcal{W}(x) = -\infty.$$

Proposition 2.1 (Spectral basis)**.** *Let $\mathcal{W}$ satisfy Assumption 1. Then the operator*

$$\mathcal{H} := -\sigma^2 \frac{d^2}{dx^2} - \mathcal{W}(x) \tag{3}$$

is essentially self-adjoint on $\mathscr{C}_c^\infty(\mathbb{R})$, and has discrete spectrum: there exists an orthonormal basis $\{\phi_k\}_{k\in\mathbb{N}}$ of $L^2(\mathbb{R})$ consisting of eigenfunctions of $\mathcal{H}$

$$\mathcal{H}\phi_k = \lambda_k \phi_k, \quad \|\phi_k\|_{L^2(\mathbb{R})} = 1,$$

with corresponding eigenvalues

$$\lambda_0 < \lambda_1 \leq \lambda_2 \leq \cdots \leq \lambda_k \to +\infty,$$

of finite multiplicity.

Remark 1. *Proposition 2.1 is a classical result* [33], [38, Chapter 3, Theorem 1.4 and Theorem 1.6] *for Schrödinger operators with confining potential $V_{\mathrm{conf}}(x) = -\mathcal{W}(x)$. In this paper, the minus sign is due to the biological interpretation of the fitness function $\mathcal{W}$.*

In the quantum mechanics terminology, ϕ_0 is known as the *ground state*, corresponding to the bound-state of minimal energy λ_0. In this paper we refer to the couple (ϕ_0, λ_0) indistinctly as ground state/ground state energy or as principal eigenfunction/principal eigenvalue.

The principal eigenvalue λ_0 can be characterised by the variational formulation

$$\lambda_0 = \inf \left\{ \mathcal{E}(u) : u \in \mathscr{C}_c^\infty(\mathbb{R}), \|u\|_{L^2(\mathbb{R})} = 1 \right\}, \tag{4}$$

where $\mathcal{E}$ is the energy functional given by

$$\mathcal{E}(u) = \sigma^2 \int_{\mathbb{R}} \left| \frac{\partial u}{\partial x} \right|^2 dx + \int_{\mathbb{R}} -\mathcal{W}(x)|u(x)|^2 \, dx.$$

Using concentrated test functions, the above formula enables to understand the behaviour of the principal eigenvalue $\lambda_0 = \lambda_0(\sigma)$ as the mutation rate σ tends to 0. The following will be used in Section 4 to prove some branching phenomena.

Proposition 2.2 (Asymptotics for $\lambda_0(\sigma)$ as $\sigma \to 0$). *Let $\mathcal{W}$ satisfy Assumption 1. Assume that $\mathcal{W}$ reaches a global maximum M at $x = \alpha$. Then* $\lim_{\sigma \to 0^+} \lambda_0(\sigma) = -M$.

Proof. For the convenience of the reader, we give the proof of this standard fact. Let p be a smooth, non-negative, and compactly supported in $[-1, 1]$ function with $\|p\|_{L^2(\mathbb{R})} = 1$. We define the test function

$$p_\sigma(x) := \frac{1}{\sigma^{1/4}} p\left(\frac{x - \alpha}{\sqrt{\sigma}}\right).$$

From the variational formula (4), we have

$$-M \leq \lambda_0(\sigma) \leq \sigma^2 \int_{\mathbb{R}} |\partial_x p_\sigma(x)|^2 \, dx + \int_{\mathbb{R}} -\mathcal{W}(x)|p_\sigma(x)|^2 \, dx.$$

The first integral in the right hand side is given by

$$\sigma^2 \int_{\mathbb{R}} |\partial_x p_\sigma(x)|^2 \, dx = \sigma \|p'\|_{L^2(\mathbb{R})} \to 0,$$

as $\sigma \to 0^+$. The second integral gives

$$\int_{\mathbb{R}} -\mathcal{W}(x)|p_\sigma(x)|^2 \, dx = \int_{\mathbb{R}} -\mathcal{W}(\alpha + \sqrt{\sigma} y) p(y)^2 \, dy$$

which, by the L^1-dominated convergence theorem tends to $-M\|p\|_{L^2(\mathbb{R})} = -M$ as $\sigma \to 0^+$. □

In the subsequent sections, we will quote results on the spectral properties of Schrödinger operators, in particular an asymptotics for the eigenvalues λ_k as $k \to +\infty$. As far as we know, the available results require to assume that the fitness $\mathcal{W}$ is polynomial.

Assumption 2 (Polynomial confining fitness function). *The fitness function $\mathcal{W}$ is a real polynomial of degree $2s$:*

$$\mathcal{W}(x) = -x^{2s} + \sum_{k=0}^{2s-1} w_k x^k,$$

for some integer $s \geq 1$ and some real numbers w_k, $0 \leq k \leq 2s - 1$.

Under Assumption 2, elliptic regularity theory insures that the eigenfunctions are infinitely differentiable. Furthermore, all the derivatives of each eigenfunction are square-integrable [17]. Notice that it is also known that all eigenfunctions actually belong to the Schwartz space $\mathcal{S}(\mathbb{R})$.

Proposition 2.3 (Asymptotics for eigenvalues). *Let $\mathcal{W}$ satisfy Assumption 2. Then all eigenvalues of $\mathcal{H}$ are simple and*

$$\lambda_k \sim C_{s,\sigma} \, k^{\frac{2s}{s+1}} \qquad \text{as } k \to +\infty, \tag{5}$$

where $C_{s,\sigma} := \left(\dfrac{\sigma\sqrt{\pi}\,\Gamma(\frac{3}{2} + \frac{1}{2s})}{\Gamma(1 + \frac{1}{2s})}\right)^{\frac{2s}{s+1}}$, *with* $\Gamma(z) = \displaystyle\int_{\mathbb{R}^+} t^{z-1} e^{-t} \, \mathrm{d}t$ *being the gamma function.*

We refer to [39], [15] and the references therein for more details on the above asymptotic formula. Furthermore, in the case of a symmetric fitness $\mathcal{W}(-x) = \mathcal{W}(x)$, the simplicity of eigenvalues enforce all eigenfunctions to be even or odd. In particular the principal eigenfunction ϕ_0 (*ground state*) is even since it is known to have constant sign.

Remark 2. *Assume that $\mathcal{W}$ is such that $P - c \leq \mathcal{W} \leq P + c$ for some polynomial P as in Assumption 2 and some constant $c > 0$. From Courant-Fisher's theorem, that is the variational characterization of the eigenvalues, we deduce that $\lambda'_k - c \leq \lambda_k \leq \lambda'_k + c$, where λ'_k are the eigenvalues of the Hamiltonian with potential P. Hence, λ_k share with λ'_k the asymptotics* (5)*, which is the keystone for deriving the estimates on eigenfunctions in subsection 2.2, and thereafter our main results in Section 3. Hence, our results apply to such fitness functions, covering in particular the case of the so-called pseudo-polynomials (i.e. smooth functions which coincide, outside of a compact region, with a polynomial P as in Assumption 2), which are relevant for numerical computations.*

2.2. **L^1, L^∞ and weighted L^1 norms of the eigenfunctions.** In the study of spectral properties of Schrödinger operators, efforts tend to concentrate around asymptotic estimates of eigenvalues or on the regularity and decay of eigenfunctions [39], [1], [10], [16]. Much less attention has been given to estimate the L^1 and L^∞ norms of eigenfunctions. One reason is that the natural framework for eigenfunctions of the Hamiltonian $\mathcal{H}$, defined in (3), is $L^2(\mathbb{R})$. On the other hand, the biological nature of problem (1) suggests $L^1(\mathbb{R})$ and $L^\infty(\mathbb{R})$ as natural spaces for the solution $u(t,x)$. We therefore provide in this subsection rather non-standard estimates on the eigenfunctions.

We define

$$m_k := \int_{\mathbb{R}} \phi_k(x)\,dx,$$

the mass of the k-th eigenfunction ϕ_k of the Hamiltonian $\mathcal{H}$. In the sequel, by

$$A_k \lesssim B_k$$

we mean that there is $c > 0$ such that, for all $k \geq 1$, $A_k \leq cB_k$.

Proposition 2.4 (L^1 norm of eigenfunctions)**.** *Let $\mathcal{W}$ satisfy Assumption 2. Then we have*

$$|m_k| \leq \|\phi_k\|_{L^1(\mathbb{R})} \lesssim k^{\frac{1}{2(s+1)}}. \tag{6}$$

Before proving the above proposition, we need the following lemma which is of independent interest.

Lemma 2.5. *Let $d \in \mathbb{N}^*$ and $N \in (d, +\infty)$ be given. Then there is a constant $C = C(d,N) > 0$ such that, for all $f : \mathbb{R}^d \to \mathbb{R}$,*

$$\|f\|_{L^1(\mathbb{R}^d)} \leq C\, \|f\|^{1-\delta}_{L^2(\mathbb{R}^d)} \left\|x^{N/2} f\right\|^{\delta}_{L^2(\mathbb{R}^d)}, \quad \delta := d/N. \tag{7}$$

Proof. Let $\mathcal{B}_R$ denote the open d-dimensional ball of radius $R > 0$ and center $0_{\mathbb{R}^d}$. We write

$$\|f\|_{L^1(\mathbb{R}^d)} = \int\limits_{\mathcal{B}_R} |f(x)|\,dx + \int\limits_{\mathbb{R}^d\setminus\mathcal{B}_R} \frac{1}{|x|^{N/2}}|x|^{N/2}|f(x)|\,dx =: \mathcal{I}_1 + \mathcal{I}_2.$$

By the Cauchy-Schwarz inequality we have

$$\mathcal{I}_1 \le \|f\|_{L^2(\mathcal{B}_R)}\|1\|_{L^2(\mathcal{B}_R)} = \left[\frac{\pi^{d/2}R^d}{\Gamma\left(1+\frac{d}{2}\right)}\right]^{1/2}\|f\|_{L^2(\mathbb{R}^d)} =: C_1R^{d/2}\|f\|_{L^2(\mathbb{R}^d)},$$

and

$$\begin{aligned}
\mathcal{I}_2 &\le \Big(\int_{\mathbb{R}^d\setminus\mathcal{B}_R} \frac{1}{|x|^N}\,dx\Big)^{1/2}\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)}\\
&\le C\Big(\int_R^{+\infty}\frac{1}{r^N}\,r^{d-1}\,dr\Big)^{1/2}\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)}\\
&\le C_2R^{(d-N)/2}\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)},
\end{aligned}$$

for some $C = C(d) > 0$ and $C_2 = C_2(d,N) > 0$. Summarizing,

$$\|f\|_{L^1(\mathbb{R}^d)} \le C_1R^{d/2}\|f\|_{L^2(\mathbb{R}^d)} + C_2R^{(d-N)/2}\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)}. \tag{8}$$

Now, we select

$$R = \left(\frac{C_2(N-d)}{C_1 d}\,\frac{\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)}}{\|f\|_{L^2(\mathbb{R}^d)}}\right)^{2/N}$$

which minimizes the right hand side of (8) and yields (7). □

Remark 3. *The correct power δ in (7) can be retrieved by a standard homogeneity argument. Indeed, defining $f_\lambda(x) := f(\lambda x)$ for $\lambda > 0$, we get*

$$\begin{aligned}
\|f_\lambda\|_{L^1(\mathbb{R}^d)} &= \frac{1}{\lambda^d}\|f\|_{L^1(\mathbb{R}^d)},\\
\|f_\lambda\|_{L^2(\mathbb{R}^d)} &= \frac{1}{\lambda^{d/2}}\|f\|_{L^2(\mathbb{R}^d)},\\
\left\|x^{N/2}f_\lambda\right\|_{L^2(\mathbb{R}^d)} &= \frac{1}{\lambda^{(N+d)/2}}\left\|x^{N/2}f\right\|_{L^2(\mathbb{R}^d)},
\end{aligned}$$

so that

$$\frac{1}{\lambda^d} \lesssim \left(\frac{1}{\lambda^{d/2}}\right)^{1-\delta}\left(\frac{1}{\lambda^{(N+d)/2}}\right)^{\delta}.$$

Powers of λ in both sides must coincide, which enforces $\delta = d/N$.

We can now estimate the mass of the eigenfunctions.

Proof of Proposition 2.4. Up to subtracting a constant to $\mathcal{W}$, we can assume without loss of generality that $\mathcal{W} < 0$. Multiplying by ϕ_k the eigenvalue equation

$$-\sigma^2\phi_k'' - \mathcal{W}\phi_k = \lambda_k\phi_k$$

and integrating over $x \in \mathbb{R}$, we get

$$\int_{\mathbb{R}} -\sigma^2\phi_k''(x)\phi_k(x)\,dx + \int_{\mathbb{R}} -\mathcal{W}(x)\phi_k(x)^2\,dx = \lambda_k\int_{\mathbb{R}}\phi_k^2(x)\,dx.$$

Integrating by parts and recalling that eigenfunctions ϕ_k are normalized in $L^2(\mathbb{R})$, we obtain

$$\sigma^2 \int_{\mathbb{R}} \phi_k'(x)^2\, dx + \int_{\mathbb{R}} -\mathcal{W}(x)\phi_k(x)^2\, dx = \lambda_k,$$

so that

$$\int_{\mathbb{R}} -\mathcal{W}(x)\phi_k(x)^2\, dx \leq \lambda_k.$$

Next, it follows from Assumption 2 (and $\mathcal{W} < 0$) that there is $\gamma > 0$ such that $-\mathcal{W}(x) \geq \gamma x^{2s}$ for all $x \in \mathbb{R}$, and thus

$$\|x^s \phi_k\|^2_{L^2(\mathbb{R})} \leq \frac{\lambda_k}{\gamma}.$$

Now, by Lemma 2.5, we have

$$\|\phi_k\|_{L^1(\mathbb{R})} \lesssim \|x^s\phi_k\|^{1/(2s)}_{L^2(\mathbb{R})} \lesssim \lambda_k^{1/4s},$$

which, combined with (5), implies (6). The proposition is proved. □

Proposition 2.6 (L^∞ norm of eigenfunctions)**.** *Let $\mathcal{W}$ satisfy Assumption 2. Then we have*

$$\|\phi_k\|_{L^\infty(\mathbb{R})} \lesssim k^{\frac{s}{2(s+1)}}. \tag{9}$$

Proof. Since $-\dfrac{1}{2}\phi_k^2(x) = \displaystyle\int_x^{+\infty} \phi_k(s)\phi_k'(s)ds$, we have

$$\|\phi_k\|^2_{L^\infty(\mathbb{R})} \lesssim \|\phi_k\|_{L^2(\mathbb{R})} \|\phi_k'\|_{L^2(\mathbb{R})} \lesssim \lambda_k^{1/2},$$

and the conclusion follows from (5). □

Proposition 2.7 (Weighted L^1 norm of eigenfunctions)**.** *Let $\mathcal{W}$ satisfy Assumption 2. Then we have*

$$\|\mathcal{W}\phi_k\|_{L^1(\mathbb{R})} \lesssim k^{\frac{5s+2}{2s+2}}.$$

Proof. From Assumption 2 and $\lambda_k \to +\infty$, we can find $k_0 \geq 0$ large enough so that the following facts hold for all $k \geq k_0$: there are $-y_k < 0$ and $x_k > 0$ such that

$$\begin{aligned} \mathcal{W}(x) + \lambda_k \geq 0 \qquad & \forall x \in (-y_k, x_k) \\ \mathcal{W}(x) + \lambda_k = 0 \qquad & \forall x \in \{-y_k, x_k\} \\ \mathcal{W}(x) + \lambda_k \leq 0 \qquad & \forall x \in \mathbb{R} \setminus (-y_k, x_k), \end{aligned}$$

and $\mathcal{W}$ is decreasing on $(-\infty, -y_k) \cup (x_k, +\infty)$. Assumption 2 implies that $x_k, y_k \sim \lambda_k^{\frac{1}{2s}}$ and thus, from Proposition 2.3, $x_k, y_k \lesssim k^{\frac{1}{s+1}}$. Next, up to enlarging k_0 if necessary, it follows from Assumption 2 that $\mathcal{W}(x) + \lambda_k \leq -1$ for all $x \in (2x_k, +\infty)$. As a result, functions

$$\phi^{\pm}(x) := \pm\|\phi_k\|_\infty e^{-(x-2x_k)}$$

are respectively super and sub-solutions of the eigenvalue equation

$$-\phi_k'' - (\mathcal{W}(x) + \lambda_k)\phi_k = 0,$$

so that

$$|\phi_k(x)| \leq \|\phi_k\|_\infty e^{-(x-2x_k)} \quad \forall x \in (2x_k, +\infty), \tag{10}$$

by the comparison principle. An analogous estimate holds on $(-\infty, 2y_k)$.

In order to estimate $\|\mathcal{W}\phi_k\|_{L^1(\mathbb{R})}$, we split the domain of integration into three parts: $\Omega_1 := \mathbb{R} \setminus (-2y_k, 2x_k)$, $\Omega_2 := (-2y_k, -y_k) \cup (x_k, 2x_k)$ and $\Omega_3 := (-y_k, x_k)$. Setting

$$I_i := \int_{\Omega_i} |\mathcal{W}(x)\phi_k(x)|\, dx = \int_{\Omega_i} -\mathcal{W}(x)|\phi_k(x)|\, dx,$$

we decompose $\|\mathcal{W}\phi_k\|_{L^1(\mathbb{R})} = I_1 + I_2 + I_3$. Notice that,

$$\int_{2x_k}^{+\infty} -\mathcal{W}(x)e^{-(x-2x_k)}\, dx = \Big[-P(x)e^{-(x-2x_k)}\Big]_{2x_k}^{+\infty} = P(2x_k),$$

where P is a polynomial of same degree as $\mathcal{W}$. Hence, from (10) and Proposition 2.6, we get

$$\begin{aligned} I_1 &\lesssim \|\phi_k\|_\infty \int_{2x_k}^{+\infty} |\mathcal{W}(x)|e^{-(x-2x_k)}\, dx \lesssim k^{\frac{s}{2(s+1)}} P(2x_k) \\ &\lesssim k^{\frac{s}{2(s+1)}} x_k^{2s} \lesssim k^{\frac{s}{2(s+1)}} k^{\frac{2s}{s+1}} = k^{\frac{5s}{2s+2}}. \end{aligned}$$

By monotonicity of $\mathcal{W}$ on Ω_2,

$$I_2 \lesssim x_k\, |\mathcal{W}(2x_k)| \|\phi_k\|_\infty \lesssim x_k^{1+2s} k^{\frac{s}{2(s+1)}} \lesssim k^{\frac{5s+2}{2s+2}}.$$

Remember that $-\mathcal{W}(x) \leq \lambda_k$ in Ω_3 so that

$$I_3 \lesssim x_k \lambda_k \|\phi_k\|_\infty \lesssim x_k k^{\frac{2s}{s+1}} k^{\frac{s}{2(s+1)}} \lesssim k^{\frac{5s+2}{2s+2}}.$$

Finally, $\|\mathcal{W}\phi_k\|_{L^1(\mathbb{R})} \lesssim k^{\frac{5s+2}{2s+2}}$. □

3. Well-posedness and long time behaviour

In this section we show that the Cauchy problem (1) has a unique smooth solution which is global in time. Keystones are the change of variable (13) that links the non-local equation (1) to a linear parabolic problem, and our previous estimates on the underlying eigenelements. Equipped with the representation (12) of the solution, we then prove convergence in any L^p, $1 \leq p \leq +\infty$, to the principal eigenfunction normalized by its mass.

Up to subtracting a constant to the confining fitness function $\mathcal{W}$, we can assume without loss of generality (recall the mass conservation property) that $\mathcal{W} \leq -1$.

3.1. **Functional framework.**

For $\mathcal{W}$ a negative confining fitness function (see Assumption 1), we set

$$L^2_{-\mathcal{W}}(\mathbb{R}) := \left\{ v : \mathbb{R} \to \mathbb{R}, \|v\|^2_{L^2_{-\mathcal{W}}(\mathbb{R})} := \int_{\mathbb{R}} -\mathcal{W}(x)v^2(x)\, dx < +\infty \right\}.$$

Recall that the Sobolev space $W^{1,2}(\mathbb{R})$ is defined as

$$W^{1,2}(\mathbb{R}) = \{f : \mathbb{R} \to \mathbb{R}, f \in L^2(\mathbb{R}), f' \in L^2(\mathbb{R})\},$$

where the derivative f' is understood in the distributional sense. We denote by $V := W^{1,2}(\mathbb{R}) \cap L^2_{-\mathcal{W}}(\mathbb{R})$ the Hilbert space with inner product defined by

$$(v, \mathsf{v})_V := \int_{\mathbb{R}} \frac{dv}{dx}(x)\frac{d\mathsf{v}}{dx}(x)\, dx + \int_{\mathbb{R}} -\mathcal{W}(x)v(x)\mathsf{v}(x)\, dx,$$

and $H := L^2(\mathbb{R})$ with usual inner product

$$(v, \mathsf{v})_H = \int_{\mathbb{R}} v(x)\mathsf{v}(x)\,dx.$$

By Assumption 1, it is straightforward that $L^2_{-\mathcal{W}}(\mathbb{R}) \subset L^2(\mathbb{R})$, so that $V \subset H$. Moreover, the following holds.

Lemma 3.1. *The embedding $V \hookrightarrow H$ is dense, continuous and compact.*

Proof. This is very classical but, for the convenience of the reader, we present the details. Since $\mathscr{C}_c^\infty(\mathbb{R}) \subset V$ and $\mathscr{C}_c^\infty(\mathbb{R})$ is dense in $L^2(\mathbb{R}) = H$, it follows that V is dense in $L^2(\mathbb{R})$. Next, since for $\mathsf{v} \in V$,

$$\int_{\mathbb{R}} \mathsf{v}^2(x)\,dx \leq \frac{1}{-\sup \mathcal{W}} \|\mathsf{v}\|_V^2,$$

the embedding $V \hookrightarrow H$ is continuous.

The proof of compactness follows by the Riesz-Fréchet-Kolmogorov theorem, see e.g. [8, Theorem 4.26]. Let $(\mathsf{v}_n)_{n\geq 0}$ a bounded sequence of functions of V: there is $M > 0$ such that, for all $n \geq 0$,

$$\|\mathsf{v}_n\|_V^2 = \int_{\mathbb{R}} \mathsf{v}_n'(x)^2\,dx + \int_{\mathbb{R}} -\mathcal{W}(x)\mathsf{v}_n(x)^2\,dx < M.$$

We first need to show the uniform smallness of the tails of v_n^2. Let $\varepsilon > 0$. Select $a > 0$ large enough so that $\dfrac{1}{-\mathcal{W}(x)} \leq \varepsilon$ for all $|x| \geq a$. Then

$$\begin{aligned}\|\mathsf{v}_n\|^2_{L^2(\mathbb{R}\setminus[-a,a])} &= \int_{-\infty}^{-a} \mathsf{v}_n(x)^2\,dx + \int_a^{+\infty} \mathsf{v}_n(x)^2\,dx \\ &\leq \varepsilon \int_{-\infty}^{-a} -\mathcal{W}(x)\mathsf{v}_n(x)^2\,dx + \varepsilon \int_a^{+\infty} -\mathcal{W}(x)\mathsf{v}_n(x)^2\,dx \\ &\leq M\varepsilon.\end{aligned}$$

Next, for a compact set K, we need to show the uniform smallness of the $L^2(K)$ norm of $\mathsf{v}_n(\cdot + h) - \mathsf{v}_n$. Let $\varepsilon > 0$. By Morrey's theorem, there is $C > 0$ such that, for all $h \in \mathbb{R}$ and $n \geq 0$,

$$|\mathsf{v}_n(x+h) - \mathsf{v}_n(x)| \leq C|h|^{1/2}\left\|\mathsf{v}_n'\right\|_{L^2(\mathbb{R})} \leq C|h|^{1/2}M^{1/2},$$

so that

$$\|\mathsf{v}_n(\cdot + h) - \mathsf{v}_n\|^2_{L^2(K)} \leq C^2 M|K||h| \leq \varepsilon,$$

for all $n \geq 0$, if $|h|$ is sufficiently small. The lemma is proved. $\square$

3.2. **Main results.** We first define the notion of solution to the Cauchy problem (1).

Definition 3.2 (Admissible initial data)**.** *We say that a function u_0 is an admissible initial data if $u_0 \in L^1(\mathbb{R}) \cap L^\infty(\mathbb{R})$, $u_0(\cdot) \geq 0$ and $\int_{\mathbb{R}} u_0(x)\,dx = 1$.*

Definition 3.3 (Solution of the Cauchy problem (1))**.** *Let u_0 be an admissible initial data. We say that $u = u(t,x)$ is a (global) solution of the Cauchy problem (1) if, for any $T > 0$, $u \in \mathscr{C}^0(0,T;H) \cap L^2(0,T;V)$, $u(0,\cdot) = u_0$, and* *(i) For all* $\mathsf{v} \in V$*, all* $t \in (0, T]$*,*

$$\frac{d}{dt}\int_{\mathbb{R}} u(t,x)\mathsf{v}(x)\,dx + \sigma^2 \int_{\mathbb{R}} \frac{\partial u}{\partial x}(t,x)\frac{d\mathsf{v}}{dx}(x)\,dx + \int_{\mathbb{R}} -\mathcal{W}(x)u(t,x)\mathsf{v}(x)\,dx + \overline{u}(t)\int_{\mathbb{R}} u(t,x)\mathsf{v}(x)\,dx = 0,$$

where the time derivative is understood in the distributional sense. Equivalently, for all $\mathsf{v} \in V$*, all* $\varphi \in \mathscr{C}^1_{\mathrm{c}}(0,T)$*,*

$$\begin{aligned} &-\int_0^T \left(\int_{\mathbb{R}} u\mathsf{v}\,dx\right)\varphi'(t)\,dt + \sigma^2\int_0^T \left(\int_{\mathbb{R}} \frac{\partial u}{\partial x}\frac{d\mathsf{v}}{dx}\,dx\right)\varphi(t)\,dt \\ &+\int_0^T \left(\int_{\mathbb{R}} -\mathcal{W}u\mathsf{v}\,dx\right)\varphi(t)\,dt + \int_0^T \left(\int_{\mathbb{R}} u\mathsf{v}\,dx\right)\overline{u}(t)\varphi(t)\,dt = 0. \end{aligned} \tag{11}$$

(ii) $\overline{u} : t \mapsto \int_{\mathbb{R}} \mathcal{W}(y)u(t,y)\,dy$ *is a continuous function on* $(0,T]$.

(iii) $C_T := \int_0^T |\overline{u}(t)|\,dt < +\infty$.

Here is our main mathematical result.

Theorem 3.4 (Solving replicator-mutator problem)**.** *Let* $\mathcal{W}$ *satisfy Assumption 2. For any admissible initial condition* u_0*, there is a unique solution* $u = u(t,x)$ *to the Cauchy problem (1), in the sense of Definition 3.3. Moreover the solution is smooth on* $(0,+\infty) \times \mathbb{R}$ *and is given by*

$$u(t,x) = \frac{\displaystyle\sum_{k=0}^{+\infty} (u_0,\phi_k)_{L^2(\mathbb{R})}\phi_k(x)e^{-\lambda_k t}}{\displaystyle\sum_{k=0}^{+\infty} (u_0,\phi_k)_{L^2(\mathbb{R})} m_k e^{-\lambda_k t}}, \quad t > 0,\ x \in \mathbb{R}, \tag{12}$$

where (λ_k, ϕ_k) *are the eigenelements defined in Proposition 2.1, and*

$$m_k = \int_{\mathbb{R}} \phi_k(x)\,dx.$$

Proof. We proceed by necessary and sufficient condition. Let u be a solution, in the sense of Definition 3.3. We define the function v as

$$v(t,x) := u(t,x)\exp\left(\int_0^t \overline{u}(\tau)\,d\tau\right), \quad 0 \le t \le T,\ x \in \mathbb{R}. \tag{13}$$

This function is well defined since by Definition 3.3 (iii), the integral in the exponential is finite for all $t \in [0,T]$. Since $C_T < \infty$ and $u(t,\cdot) \in H \cap V$, it is straightforward to see that, for all $t \in (0,T]$, $v(t,\cdot) \in H \cap V \equiv V$. Additionally, from $C_T < \infty$ and $u \in \mathscr{C}^0(0,T;H)$, one can see that $v \in \mathscr{C}^0(0,T;H)$. Last, $v \in L^2(0,T;V)$ due to

$$\int_0^T \|v(t,\cdot)\|_V^2\,dt = \int_0^T \left\| u(t,\cdot)e^{\int_0^t \overline{u}(\tau)\,d\tau}\right\|_V^2 dt \le e^{2C_T}\int_0^T \|u(t,\cdot)\|_V^2\,dt < \infty,$$

since $u \in L^2(0,T;H)$.

We now show that v solves the linear Cauchy problem

$$\begin{cases} \partial_t v = \sigma^2 \partial_x^2 v + \mathcal{W}(x) v \\ v(0,x) = u_0(x). \end{cases} \tag{14}$$

Indeed, formally for the moment,

$$\partial_t v = (\partial_t u) e^{\int_0^t \overline{u}(\tau)\, d\tau} + u\overline{u}$$
$$\partial_x^2 v = (\partial_x^2 u) e^{\int_0^t \overline{u}(\tau)\, d\tau},$$

so that

$$\partial_t v - \sigma^2 \partial_x^2 v - \mathcal{W}(x) v = (\partial_t u + u\overline{u} - \sigma^2 \partial_x^2 u - \mathcal{W}(x) u) e^{\int_0^t \overline{u}(\tau)\, d\tau} = 0$$

since u solves (1). Those computations can be made rigorous in the distributional sense. Indeed, for a test function $\psi \in \mathscr{C}_c^1(0,T)$, set

$$\varphi(t) := \psi(t) e^{\int_0^t \overline{u}(\tau)\, d\tau},$$

and by Definition 3.3 (ii), φ belongs to $\mathscr{C}_c^1(0,T)$. Writing (11) with φ as test function yields the weak formulation of (14) with ψ as test function, that is

$$- \int_0^T \left(\int_{\mathbb{R}} v(t,x) \mathsf{v}(x)\, dx \right) \psi'(t)\, dt + \sigma^2 \int_0^T \left(\int_{\mathbb{R}} \frac{\partial v}{\partial x}(t,x) \frac{d\mathsf{v}}{dx}(x)\, dx \right) \psi(t)\, dt$$
$$+ \int_0^T \left(\int_{\mathbb{R}} -\mathcal{W}(x) v(t,x) \mathsf{v}(x)\, dx \right) \psi(t)\, dt = 0,$$

for all $\mathsf{v} \in V$.

The well-posedness of the linear Cauchy problem (14) is postponed to the next subsection: from Proposition 3.6, we know that, for all $t \in (0,T]$,

$$v(t) = \sum_{k=0}^{+\infty} (u_0, \phi_k)_{L^2(\mathbb{R})} \phi_k e^{-\lambda_k t} \quad \text{in } L^2(\mathbb{R}).$$

Now, the estimates on the eigenvalues and the L^∞ norm of eigenfunctions, namely Proposition 2.3 and Proposition 2.6, allow to write

$$v(t,x) = \sum_{k=0}^{+\infty} (u_0, \phi_k)_{L^2(\mathbb{R})} \phi_k(x) e^{-\lambda_k t}, \quad 0 < t \leq T,\ x \in \mathbb{R}.$$

Also, we know from the parabolic regularity theory and the comparison principle, that $v \in \mathscr{C}^\infty((0,T) \times \mathbb{R})$ and that $v(t,x) > 0$ for all $t > 0$, $x \in \mathbb{R}$.

Now, we show that the change of variable (13) can be inverted. For $t > 0$, multiplying (13) by $\mathcal{W}(x)$ and integrating over $x \in \mathbb{R}$, we get

$$\begin{aligned} \overline{v}(t) := \int_{\mathbb{R}} \mathcal{W}(x) v(t,x)\, dx &= \overline{u}(t) \exp\left(\int_0^t \overline{u}(\tau)\, d\tau \right) \\ &= \frac{d}{dt} \left(\exp\left(\int_0^t \overline{u}(\tau)\, d\tau \right) \right). \end{aligned} \tag{15}$$

On the other hand, we claim that, for all $t > 0$,

$$\frac{d}{dt} m_v(t) = \overline{v}(t), \tag{16}$$

which follows formally by integrating (14) over $x \in \mathbb{R}$. To prove (16) rigorously, notice first that by Proposition 2.3 and 2.4, the series

$$\sum_{k=0}^{+\infty} \left|(u_0, \phi_k)_{L^2(\mathbb{R})}\right| e^{-\lambda_k t} \int_{\mathbb{R}} |\phi_k(x)|\, dx$$

converges for all $t > 0$. Hence $m_v(t)$, the total mass of v, is given by

$$m_v(t) = \sum_{k=0}^{+\infty} (u_0, \phi_k)_{L^2(\mathbb{R})} m_k e^{-\lambda_k t}.$$

Next, for any $t_0 > 0$, $\displaystyle\sum_{k=0}^{+\infty} \left|(u_0, \phi_k)_{L^2(\mathbb{R})}\right| |m_k| \lambda_k e^{-\lambda_k t_0} < +\infty$ thanks to Proposition 2.3 and 2.4, so that m_v is differentiable on $(0, T]$ and

$$\frac{d}{dt} m_v(t) = \sum_{k=0}^{+\infty} (u_0, \phi_k)_{L^2(\mathbb{R})} m_k (-\lambda_k) e^{-\lambda_k t} = \overline{v}(t),$$

the last equality following by similar arguments based on Proposition 2.7. Hence (16) is proved. From (15), (16) and $m_v(0) = 1$, we deduce that

$$\exp\left(\int_0^t \overline{u}(\tau)\, d\tau\right) = m_v(t),$$

for all $t \geq 0$. As a conclusion, (13) is inverted into

$$u(t,x) = \frac{v(t,x)}{m_v(t)}, \quad m_v(t) := \int_{\mathbb{R}} v(t,x)\, dx > 0, \tag{17}$$

for all $0 \leq t \leq T$, $x \in \mathbb{R}$.

Conversely, we need to show that the function u given by (17) is the solution of (1) in the sense of Definition 3.3. Let $T > 0$.

Since $\overline{u}(t) = \dfrac{\overline{v}(t)}{m_v(t)} = \dfrac{\frac{d}{dt} m_v(t)}{m_v(t)}$, the function $\overline{u}$ is continuous on $(0, T]$, which shows item (ii) of Definition 3.3.

Next, since $m_v > 0$ and $\overline{v} < 0$,

$$\int_0^T |\overline{u}(t)|\, dt = -\int_0^T \frac{\frac{d}{dt} m_v(t)}{m_v(t)}\, dt = -\ln(m_v(T)) < +\infty,$$

which shows item (iii) of Definition 3.3.

Last, since $v \in \mathscr{C}^0(0,T;H) \cap L^2(0,T;V)$ and $0 < m_v(T) \leq m_v(t) \leq 1$ for any $0 \leq t \leq T$, then $u \in \mathscr{C}^0(0,T;H) \cap L^2(0,T;V)$. For a test function $\varphi \in \mathscr{C}^1_c(0,T)$, set

$$\psi(t) := \varphi(t) e^{-\int_0^t \overline{u}(\tau)\, d\tau},$$

writing the weak formulation of (14) with ψ as test function, we see that u given by (17) satisfies the weak formulation (11) with φ as test function, which shows item (i) of Definition 3.3.

Theorem 3.4 is proved. $\square$

We are now in the position to understand the long time behaviour of the solution, of crucial importance for the biological interpretation (branching phenomena) in Section 4.

Corollary 3.5 (Long time behaviour)**.** *Let $\mathcal{W}$ satisfy Assumption 2. Let u_0 be an admissible initial data u_0. Then the solution u to the Cauchy problem (1) converges, at large time, to the ground state ϕ_0 divided by its mass $m_0 := \int_{\mathbb{R}} \phi_0(x)\,dx$. Precisely, for any $1 \le p \le +\infty$,*

$$u(t,\cdot) - \frac{\phi_0(\cdot)}{m_0} \longrightarrow 0 \quad \text{in } L^p(\mathbb{R}), \quad \text{as } t \to +\infty.$$

Proof. We denote $a_k := (u_0, \phi_k)_{L^2(\mathbb{R})}$ and observe that $a_0 > 0$ since $\phi_0 > 0$ and $u_0 \ge 0$, $u_0 \not\equiv 0$. Thus, from (12) we have

$$u(t,x) = \frac{\phi_0(x) + \dfrac{1}{a_0}\displaystyle\sum_{k=1}^{+\infty} a_k \phi_k(x) e^{-(\lambda_k-\lambda_0)t}}{m_0 + \dfrac{1}{a_0}\displaystyle\sum_{k=1}^{+\infty} a_k m_k e^{-(\lambda_k-\lambda_0)t}}.$$

Recall that $\lambda_0 < \lambda_1 \le \lambda_k$ for all $k \in \mathbb{N}^*$ and that we are equipped with the asymptotics of Proposition 2.3. Hence, by Proposition 2.4 and the dominated convergence theorem, the denominator tends to m_0 as $t \to +\infty$. Similarly, by Proposition 2.6, Proposition 2.4 respectively, the numerator tends to ϕ_0 in $L^\infty(\mathbb{R})$, $L^1(\mathbb{R})$ respectively, as $t \to +\infty$. For $1 < p < +\infty$, the result follows by interpolation. □

In particular, Corollary 3.5 implies that, whatever the number of maxima of the initial date u_0, the long time shape is determined by that of the ground state ϕ_0. We illustrate this property with numerical simulations in Section 4.

Note that Corollary 3.5 is an extension of the long time convergence result proved in [2], for to the particular case of a quadratic fitness, $\mathcal{W}(x) = -x^2$, for which it is well known that the principal eigenfunction is a Gaussian.

3.3. **Linear parabolic equation.** For the convenience of the reader, we recall here how to deal with the linear Cauchy problem (14).

Proposition 3.6 (The linear problem)**.** *For any $u_0 \in L^1(\mathbb{R}) \cap L^\infty(\mathbb{R})$, for any $T > 0$, the problem (14) posses a unique weak solution $v = v(t,x)$, in the sense that $v \in \mathscr{C}^0(0,T;H) \cap L^2(0,T;V)$, $v(0,\cdot) = u_0$ and for all $\mathsf{v} \in V$, all $t \in (0,T]$,*

$$\frac{d}{dt}\int_{\mathbb{R}} v(t,x)\mathsf{v}(x)\,dx + \sigma^2 \int_{\mathbb{R}} \partial_x v(t,x)\partial_x \mathsf{v}(x) + \int_{\mathbb{R}} -\mathcal{W}(x)v(x)\mathsf{v}(x)\,dx = 0,$$

where the time derivative is understood in the distributional sense. Furthermore,

$$v(t) = \sum_{k=0}^{+\infty} (u_0, \phi_k)_{L^2(\mathbb{R})} \phi_k e^{-\lambda_k t}$$

and the convergence of the sequence of partial sums is uniform in time.

Proof. The form $\mathbf{a} : V \times V \to \mathbb{R}$

$$\mathbf{a}(v,\mathsf{v}) := \sigma^2 \int_{\mathbb{R}} \frac{dv(x)}{dx}\frac{d\mathsf{v}(x)}{dx} + \int_{\mathbb{R}} -\mathcal{W}(x)v(x)\mathsf{v}(x)\,dx$$

is symmetric and bilinear. It is continuous since, for all $v, \mathsf{v} \in V$,

$$\begin{aligned}|\mathbf{a}(v,\mathsf{v})| &\leq \sigma^2 \left| \int_{\mathbb{R}} v'(x)\mathsf{v}'(x)\,dx \right| + \left| \int -\mathcal{W}(x)v(x)\mathsf{v}(x)\,dx \right| \\ &\leq \sigma^2 \|v'\|_{L^2(\mathbb{R})} \|\mathsf{v}'\|_{L^2(\mathbb{R})} + \|v\|_{L^2_{-\mathcal{W}}(\mathbb{R})} \|\mathsf{v}\|_{L^2_{-\mathcal{W}}(\mathbb{R})} \\ &\leq (\sigma^2+1)\|v\|_V \|\mathsf{v}\|_V.\end{aligned}$$

It is coercive since, for all $\mathsf{v} \in V$,

$$\begin{aligned}\mathbf{a}(\mathsf{v},\mathsf{v}) &= \sigma^2 \int_{\mathbb{R}} (\mathsf{v}'(x))^2\,dx + \int_{\mathbb{R}} -\mathcal{W}(x)\mathsf{v}^2(x)\,dx \\ &\geq \min(\sigma^2,1)\|\mathsf{v}\|_V^2.\end{aligned}$$

The conclusion then follows from Lemma 3.1 and Lions' Theorem for parabolic equations. $\square$

We state Lions' theorem covering parabolic Cauchy problems of the form

$$\begin{cases} \partial_t v = \sigma^2 \partial_x^2 v + \mathcal{W}(x)v + f(t,x) \\ v(0,x) = u_0(x). \end{cases}$$

Theorem 3.7 (Lions' theorem, see [28] or [32])**.** *Let V be a separable Hilbert space with inner product $(\cdot,\cdot)_V$ and norm $\|\cdot\|_V$. Let H be a Hilbert space with inner product $(\cdot,\cdot)_H$ and norm $\|\cdot\|_H$, such that $H \simeq H'$. Assume that the embedding $V \hookrightarrow H$ is dense, continuous and compact. Let $\mathbf{a} : V \times V \to \mathbb{R}$ be a symmetric, continuous and coercive bilinear form. Let $T > 0$ and $f \in L^2(0,T;H)$ be given. Let $u_0 \in H$ be given.*

Then, there is a unique function $v \in \mathscr{C}^0(0,T;H) \cap L^2(0,T;V)$ such that, for all $\mathsf{v} \in V$,

$$\begin{cases} \dfrac{d}{dt}(v(t),\mathsf{v})_H + \mathbf{a}(v(t),\mathsf{v}) = \langle f(t),\mathsf{v}\rangle_{V',V} \quad \text{in } \mathscr{D}'(0,T) \\ v(0) = u_0. \end{cases}$$

Moreover, for all $t \in [0,T]$, v is written as the Hilbertian sum

$$v(t) = \sum_{j=0}^{+\infty} g_j(t)\phi_j,$$

where $(\phi_j)_{j\geq 0}$ is the spectral basis of H defined by $\mathbf{a}(\phi_j,\mathsf{v}) = \lambda_j(\phi_j,\mathsf{v})$ for all $\mathsf{v} \in V$,

$$g_j(t) := (u_0,\phi_j)_H e^{-\lambda_j t} + \int_0^t f_j(s)e^{-\lambda_j(t-s)}\,ds, \qquad f_j(s) := (f(s),\phi_j)_H.$$

Also, the sequence $v_n(t) := \sum_{j=0}^{n} g_j(t)\phi_j$ uniformly converges to $v(t)$, that is

$$\sup_{0\leq t\leq T} \|v_n(t) - v(t)\|_H \to 0, \qquad \text{as } n \to +\infty.$$

4. Branching or not

Evolutionary branching is a corner stone in the theory of evolutionary genetics [19], [26]. It consists in the splitting from uni-modal to multi-modal distribution of the phenotypic trait. By Corollary 3.5, if the principal eigenfunction ϕ_0 has two or more maxima, it follows that for any uni-modal initial condition u_0, the solution will split to multi-modal distribution in the limit $t \to +\infty$. From a biological point of view, the fitness function $\mathcal{W}$ is the key element for branching to occur. However, the mutation rate σ is another main parameter involved in the branching process. Indeed, if σ is large, then the population distribution tends to homogenize. As a consequence, a too large value of σ may enforce uni-modality of the principal eigenfunction ϕ_0 and thus of the solution $u(t,\cdot)$ as t tends to $+\infty$. In this section, we enquire on the conjunct influence of $\mathcal{W}$ and of σ on the shape of the principal eigenfunction ϕ_0. This is far from being straightforward, and we therefore combine some rigorous results and numerical explorations. We start with some particular cases of analytic ground states.

4.1. **Some explicit ground states.** The search for eigenvalues and eigenfunctions of Schrödinger operators has long been motivated by applications in physics and chemistry. Some closed-form formulas of eigenfunctions, in particular the ground state, for specific potentials are available in the literature. For example in [6], the authors get for $\sigma = 1$,

$$\begin{cases} -\mathcal{W}(x) = x^{10} - x^8 + x^6 - \frac{43}{8}x^4 + \frac{105}{64}x^2 \\ \phi_0(x) = A\exp\left(-\dfrac{3}{16}x^2 + \dfrac{1}{8}x^4 - \dfrac{1}{6}x^6\right) \\ \lambda_0 = \frac{3}{8}, \end{cases}$$

with $A > 0$ a normalization constant. In this case the potential $-\mathcal{W}$ is symmetric and double-well shaped, but the ground state is uni-modal because of a too large σ.

Xie, Wang and Fu [43] provide exact solutions for a class of rational potentials using the confluent Heun functions: for any $\omega > 0$, $g > 0$ and $V_2 < g$, they obtain

$$\begin{cases} -\mathcal{W}(x) = \dfrac{\omega^2}{4}x^2 + \dfrac{g(g-V_2) + g\omega + \sqrt{g(g-V_2)}(g+\omega)}{g\,(1+gx^2)} + \dfrac{V_2}{(1+gx^2)^2} \\ \phi_0(x) = A\exp\left(-\dfrac{\omega}{4}x^2 + \frac{g+\sqrt{g(g-V_2)}}{2g}\ln\left(1+gx^2\right)\right) \\ \lambda_0 = \left(\frac{\sqrt{g(g-V_2)}}{g} + \frac{3}{2}\right)\omega \\ \sigma = 1. \end{cases}$$

Here, the potential is symmetric. At least for some parameters, see [43], both the potential and the ground state are double-well shaped (branching occurs).

In [44], authors give some explicit formulas for potentials defined by trigonometric hyperbolic functions: for any $B > 0$ and $C \geq 0$, they obtain

$$\begin{cases} -\mathcal{W}(x) = \frac{B^2}{4}\left(\sinh(x) - \frac{C}{B}\right)^2 - B\cosh(x) \\ \phi_0(x) = A(e^{\frac{x}{2}} - \frac{1}{B}(C - \sqrt{B^2+C^2})e^{-\frac{x}{2}})e^{\frac{C}{2}x - \frac{B}{2}\cosh(x)} \\ \lambda_0 = -\dfrac{1}{2}\sqrt{B^2+C^2} - \dfrac{1}{4} \\ \sigma = 1. \end{cases}$$

In particular, when $C = 0$ the potential is symmetric and is a double-well for $0 < B < 2$ but a single-well when $B > 2$; on the other hand the ground state has then two local maxima for $0 < B < 1/2$ but only one when $B > 1/2$. If we slightly increase $C > 0$, thus breaking the symmetry of the potential, and keep $B > 0$ small, we see that a second local maximum appears in the ground state. This shows that the shape of the ground state is very sensitive to the symmetry or not of the potential.

To conclude this subsection, let us observe that the ansatz $\phi_0(x) := e^{-q(x)}$ is positive and satisfies $-\phi_0'' - (q''(x) - (q'(x))^2)\phi_0 = 0$. It is therefore the ground state associated with $\sigma = 1$, $\mathcal{W}(x) = q''(x) - (q'(x))^2$, $\lambda_0 = 0$. This provides a way to construct many examples.

4.2. **Obstacles to branching.** As already mentioned above, a too large σ prevents the branching phenomenon.

Next, if the fitness $\mathcal{W}$ is concave it is known [7, Theorem 6.1], see also [23], that the ground state is log-concave and therefore uni-modal. For instance, the harmonic potential $-\mathcal{W}(x) = x^2$ has the ground state $\phi_0(x) = \frac{1}{\sqrt{\pi\sigma}}\exp\left(-\frac{x^2}{2\sigma}\right)$ which is log-concave.

Slightly more generally, if the fitness has a unique global maximum, it is expected that, whatever the values of σ, the ground state remains uni-modal, see Figure 1 for numerical simulations.

4.3. **The typical situation leading to branching.** In order to obtain branching, the above considerations drive us to consider a fitness function $\mathcal{W}$ reaching multiple times its global maximum combined with a small enough parameter $\sigma > 0$. Hence, in the particular case of a double-well potential $-\mathcal{W}$, it is proved in [36, Theorem 2.1] that, far from the minima of the potential (in particular between the two wells), the ground state $\phi_0 = \phi_0(\sigma)$ is exponentially small as $\sigma \to 0^+$, which indicates that branching occurs.

Nevertheless, one can come to a similar conclusion through direct arguments under the assumption that the fitness function $\mathcal{W}$ is even, satisfies Assumption 2 and $\mathcal{W}(0) < \max \mathcal{W}$. Indeed, since $\mathcal{W}$ is even, so is the ground state and therefore $\phi_0'(0) = 0$. Next, testing the equation at $x = 0$, we get

$$\sigma^2\phi_0''(0) = -(\mathcal{W}(0) + \lambda_0)\phi_0(0).$$

We know from Lemma 2.2 that $\lambda_0 = \lambda_0(\sigma) \to -\max \mathcal{W}$ as $\sigma \to 0$, and therefore, for σ sufficiently small, $\phi_0''(0) > 0$. This shows that the ground state is at least bi-modal. For instance, in Figure 2 we show $-\mathcal{W}(x) := \dfrac{1}{12}(x^2-2)^2$

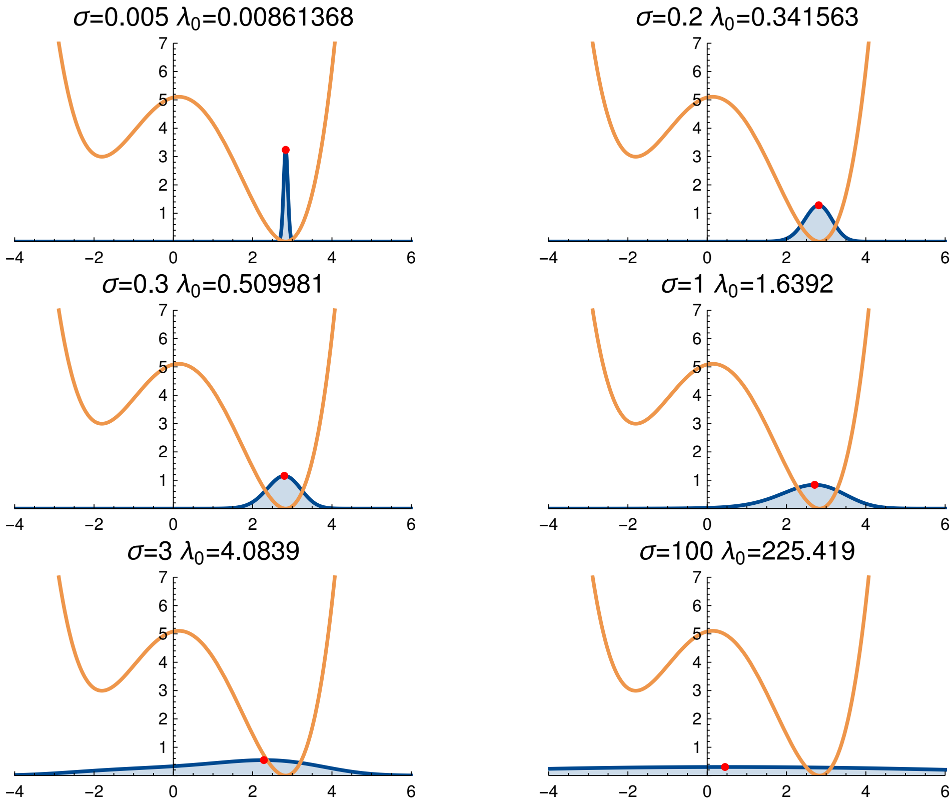

FIGURE 1. Ground state $\phi_0(\sigma)$, increasing parameter σ, in the case $-\mathcal{W}(x) = \frac{299}{2520}x^4 - \frac{233}{1260}x^3 - \frac{2971}{2520}x^2 + \frac{139}{420}x + \text{constant}$. The ground state remains uni-modal, and the global maximum is shifted towards left, asymptotically reaching 0.

and the associated principal eigenfunction $\phi_0 = \phi_0(\sigma)$, for different values of the parameter σ.

As far as the Cauchy problem (1) is concerned, we present here some numerical simulations where one can observe the branching phenomenon. For this example we choose the double-well fitness function

$$-\mathcal{W}(x) = \left(x^2 - 4\right)x^2 + 4, \tag{18}$$

and $\sigma = 10^{-3}$, which is sufficiently small to ensure that ϕ_0 is bi-modal. To numerically compute the solution $u(t,x)$ to (1) we follow the proof of Theorem 3.4: using finite element method we first compute a numerical approximation $v_{\mathrm{num}}(t,x)$ of the solution $v(t,x)$ to the linear Cauchy problem (14); next, using standard quadrature methods, we compute the mass $m_{v_{\mathrm{num}}}(t)$ of the numerical approximation $v_{\mathrm{num}}(t,x)$; last, we use the relation (17) to obtain $u_{\mathrm{num}}(t,x)$. The results are plotted for different times in Figure 3 and Figure 4. In Figure 3, we use the Gaussian initial condition $u_0(x) = \frac{1}{\sqrt{\pi}}e^{-x^2}$. As for Figure 4, we use

$$u_0(x) = \frac{1}{\sqrt{\pi}}\frac{e^{-(x-4)^2} + \varepsilon e^{-x^2}}{1+\varepsilon}, \quad \varepsilon = 10^{-2},$$

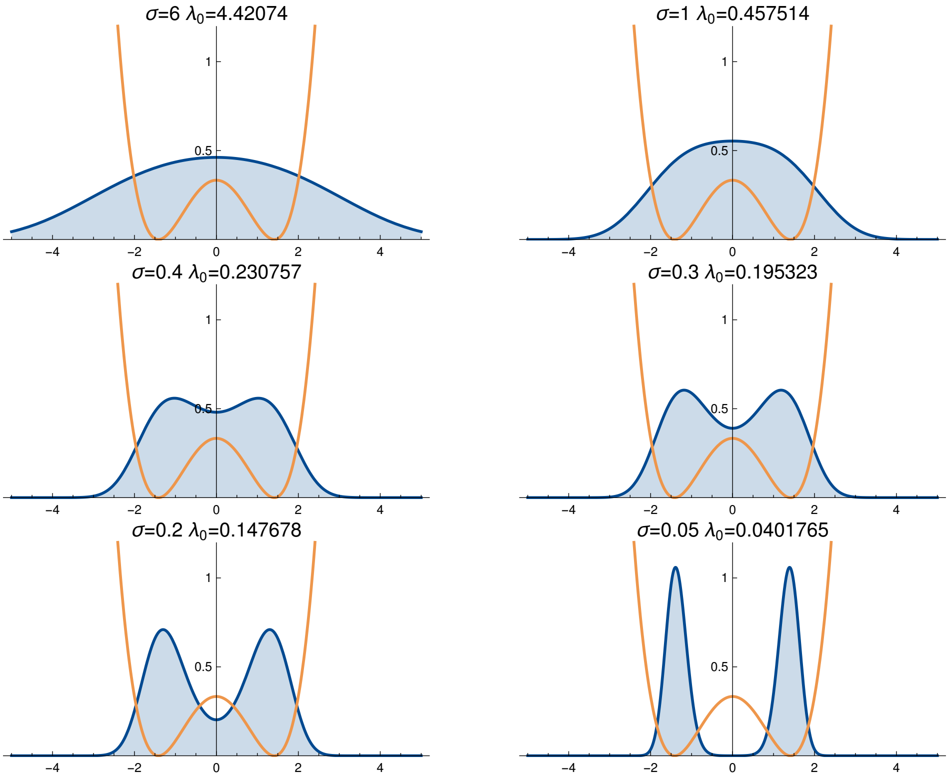

FIGURE 2. Ground state $\phi_0(\sigma)$, decreasing parameter σ, in the case $-\mathcal{W}(x) = \frac{1}{12}(x^2 - 2)^2$. Top left: for large σ the ground state is uni-modal. Bottom right: for small σ the ground state tends to concentrate into the wells of $-\mathcal{W}$.

the role of ε being to avoid some numerical instabilities. The initial condition lies on the right of the two wells. The solution remains not symmetric but, gradually, it converges to the symmetric ground state, with some possible transient complicated patterns.

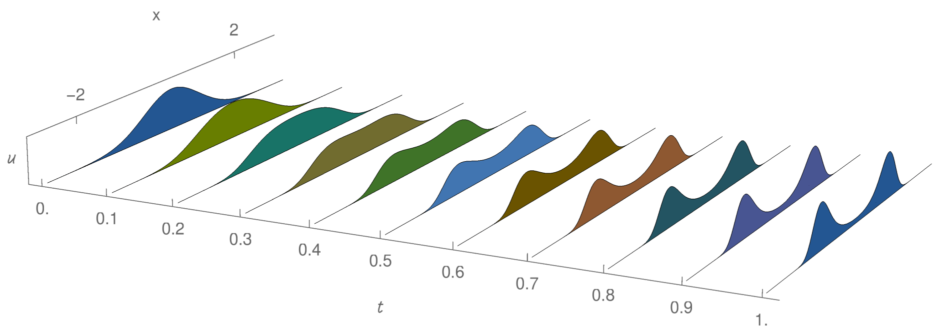

FIGURE 3. Numerical solution of the Cauchy problem (1) exhibiting a branching phenomenon. Here $\sigma = 10^{-3}$, fitness is as in (18) and the initial data is centered.

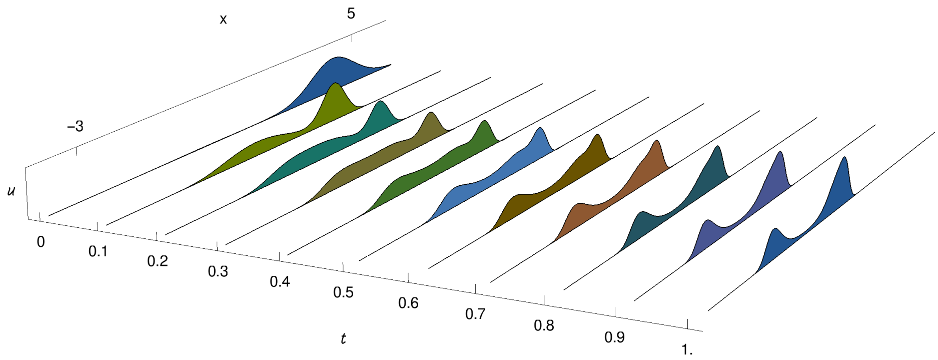

FIGURE 4. Numerical solution of the Cauchy problem (1) exhibiting a branching phenomenon. Here $\sigma = 10^{-3}$, fitness is as in (18) and the initial data is off-centered.

4.4. **The number of modes.** When the fitness function (assumed to be symmetric) reaches its global maximum at $N \geq 2$ points, say $x_1 < \cdots < x_N$, it is expected [14] that, as $\sigma \to 0$, the ground state concentrates in the x_i points where the biological niche is the widest since, at these points, individuals suffer less when their traits are slightly changed by mutations. Mathematically this means that ϕ_0 is p-modal where

$$p := \# \left\{ 1 \leq i \leq N : |\mathcal{W}''(x_i)| = \min_{1 \leq j \leq N} |\mathcal{W}''(x_j)| \right\}.$$

As a first example, consider the symmetric, triple-well potential

$$-\mathcal{W}(x) = \tfrac{1}{200} x^4 (6x-8)^2 (6x+8)^2,$$

whose wells are localized at 0 and $\pm\frac{4}{3}$. The well at zero is wider than the two other ones. In this case, the ground state is, as explained above, uni-modal for small σ. Moreover in this "narrow-wide-narrow" situation, the ground state remains uni-modal when we increase σ, as numerically observed in Figure 5.

On the other hand, as the bifurcation parameter σ increases, it may happen that, because of the position of the wells, the number of global maxima of the population distribution varies. Such an example is provided by the symmetric, triple-well potential

$$-\mathcal{W}(x) = \tfrac{1}{200} x^2 (x-2)^4 (x+2)^4, \tag{19}$$

which is of the "wide-narrow-wide" type. We numerically depict in Figure 6 the ground state associated to this fitness function, for different values of the mutation rate. As explained above, the ground state is bi-modal for small σ and uni-modal for large σ. More interestingly is that, for intermediate values of σ, the ground state is trimodal. Hence, the combination of the position of the wells of the potential and of the value of the parameter σ is of great importance on the number of emerging phenotypes.

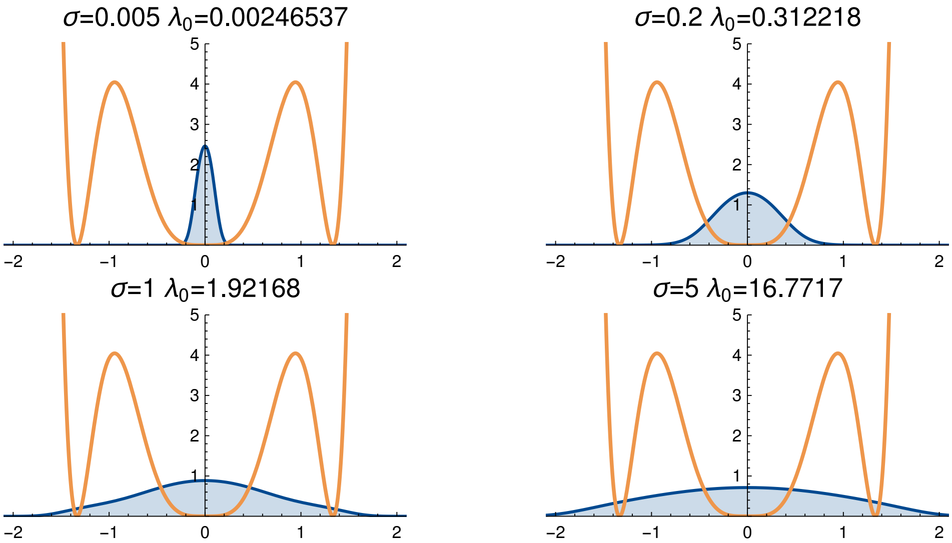

FIGURE 5. Ground state $\phi_0(\sigma)$, increasing parameter σ, in the case of a "narrow-wide-narrow" potential.

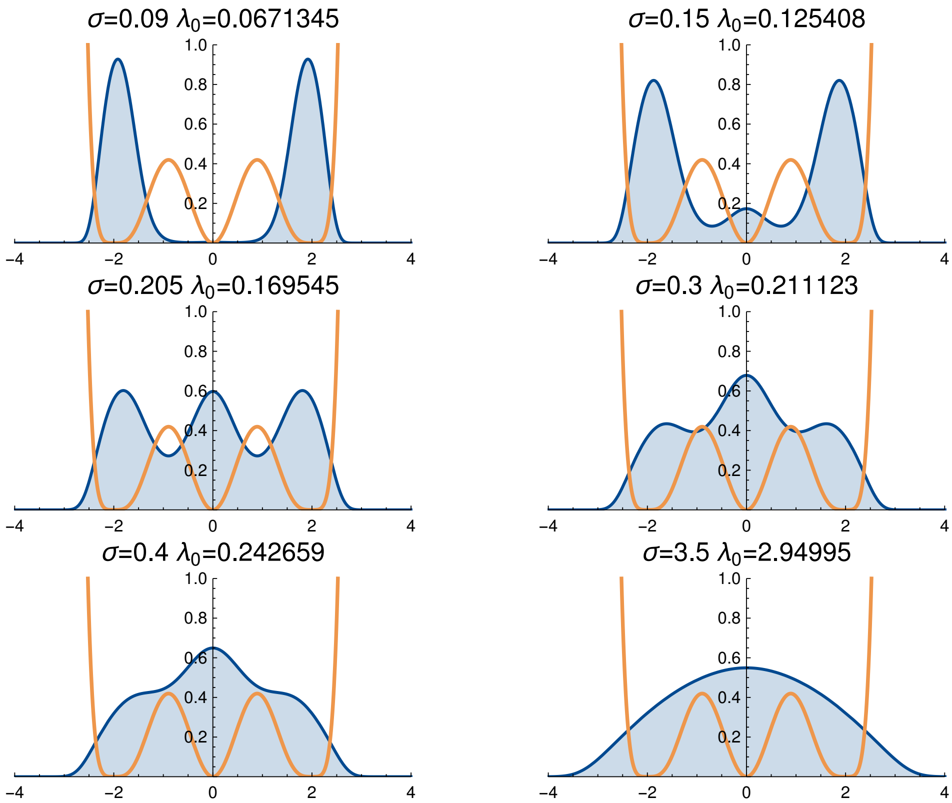

FIGURE 6. Ground state $\phi_0(\sigma)$, increasing parameter σ, in the case of a "wide-narrow-wide" potential.

5. Discussion

Our motivation is to understand the so-called branching phenomena, that is the splitting of a population structured by a phenotypic trait from uni-modal to multi-modal distribution.

We consider a population submitted to mutation and selection, thus standing in the framework of the dynamics of adaptation, see [11], [12], [13], [31], [9] among others. The retained model is the replicator-mutator equation, which is a deterministic integro-differential model [40], [5], [2, 3], [18]. The growth term involves a confining fitness function — which prevents the possibility of "escaping to infinity"— to which the mean fitness is subtracted. Hence, if the initial data is a probability density then so is the solution for later times.

For this model, we have shown the following new mathematical results: the associated Cauchy problem is well-posed and the solution is written explicitly thanks to some underlying Schrödinger eigenelements. This requires the reduction to a linear equation via a change of unknown, the use of Lions' theorem and the derivation of rather non-standard estimates on the eigenelements. As a consequence of the expression of the solution, we deduce that the long time behaviour is determined by the principal eigenfunction or ground state.

Hence, the issue of branching reduces to the issue of the shape of the ground state. In a small mutation regime, we have presented sufficient conditions on the fitness function (symmetric, with two global maxima) for the population to split to bi-modality. Also, still in the small mutation and symmetric fitness regime, the widest global maxima of the fitness function are selected, thus revealing the number of emerging phenotypes. Last, we have underlined that the number of maxima of the ground state and their value are determined by a combination of the fitness function (symmetric or not, position of the wells) and the mutation parameter: the population density can be concentrated around some intervals of phenotypic trait in different proportions, corresponding to the emergence of well identified phenotypes.

The branching phenomena have recently received more attention [42], [27], [24], [18], but to the best of our knowledge, this is the first work where it is obtained through the rather simple replicator-mutator equation (1). However, further investigations remain to be performed for a better understanding of the interplay between the fitness function and the mutation parameter, as sketched in Section 4. Another relevant information for biological purposes would be an estimate of the time needed for a uni-modal population to branch.

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