

EXPLICIT SOLUTIONS FOR REPLICATOR-MUTATOR EQUATIONS: EXTINCTION VS. ACCELERATION

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ABSTRACT. We consider a class of nonlocal reaction-diffusion problems, referred to as *replicator-mutator* equations in evolutionary genetics. By using explicit changes of unknown function, we show that they are equivalent to the heat equation and, therefore, compute their solution explicitly. Based on this, we then prove that, in the case of beneficial mutations in asexual populations, solutions dramatically depend on the tails of the initial data: they can be global, become extinct in finite time or, even, be defined for no positive time. In the former case, we prove that solutions are accelerating, and in many cases converge for large time to some universal Gaussian profile. This sheds light on the biological relevance of such models.

1. INTRODUCTION

We consider *replicator-mutator* equations, that is nonlocal reaction-diffusion problems of the form

$$(1.1) \quad \partial_t u = \partial_{xx} u + \left(f(x) - \int_{\mathbb{R}} f(x) u(t, x) dx \right) u, \quad t > 0, x \in \mathbb{R},$$

where $f(x)$ is a given weight. In this context, $u(t, x)$ is the density of a population (at time t and per unit of a phenotypic trait) on a one-dimensional phenotypic trait space, and $f(x)$ represents the fitness. The nonlocal term then stands for the mean fitness at time t . We detail below the biological background of such models.

In this work, we mainly focus on (1.1) for the special case $f(x) = x$, namely

$$(1.2) \quad \partial_t u = \partial_{xx} u + (x - \bar{u}(t))u, \quad t > 0, x \in \mathbb{R},$$

where the nonlocal term is given by

$$(1.3) \quad \bar{u}(t) := \int_{\mathbb{R}} x u(t, x) dx.$$

We make a rigorous and detailed analysis of the Cauchy problem associated with (1.2). Precisely, we prove that it can be reduced to the heat equation, and therefore compute its solution explicitly. This enables us to describe a variety of contrasted behaviors (extinction, acceleration...) depending on the initial data.

Remark 1.1 (Generalizations to quadratic weights). As a matter of fact, our analysis is also valid for quadratic weights. Following the algebraic reductions of Section 3, one may easily collect explicit formulas for the solutions of (1.1) when $f(x) = \pm x^2$, and, based on this, explore their behaviors. Nevertheless, since the model (1.2)

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triggered a flow of studies in evolutionary genetics, we just state our results for this well-established case.

In the context of evolutionary genetics, equation (1.2) was introduced by Tsimring et al. [17], where they propose a mean-field theory for the evolution of RNA virus populations on a phenotypic trait space. Without mutations, and under the constraint of constant mass $\int_{\mathbb{R}} u(t, x) dx = 1$, the dynamics is given by

$$\partial_t u = (x - \bar{u}(t))u,$$

where $\bar{u}(t) = \int_{\mathbb{R}} xu(t, x) dx$ is the average fitness of the virus population. As a first step to take into account evolutionary phenomena, one can then model mutations by the Laplace diffusion operator so that the above integro-differential equation is transferred into (1.2). Notice also that equation (1.2) appears as a mean-field model for diffusion-limited growth [19].

A central issue in evolutionary genetics is to predict whether a population accumulates deleterious or advantageous mutations. The former case is known as the *Muller's ratchet* [11, 12]: an asexual population will accumulate deleterious mutations and, therefore, its fitness will decay. On the other hand, it recently turned out that beneficial mutations are more abundant than previously suspected. Hence, after the seminal work [17], equation (1.2) received a lot of attention since it enables to capture the effect of such beneficial mutations in asexual (clonal) populations. For more details and comments on biological assumptions and such models, we refer to [14, 4, 13], the review [15], [18] and the references therein.

However, for biological applications, the unlimited growth rate of $u(t, x)$ at large x in (1.2) is not admissible. To deal with such a problem, the authors of the aforementioned works consider a “cut-off version” of (1.2) at large x [17, 14, 15], or provide a proper stochastic treatment for large phenotypic trait region [13]. In the former cut-off regime, the existence of solitary waves (that is localized nonnegative profiles travelling at constant speed and shape) and the way they attract solutions of the Cauchy problem are investigated. In particular, the speed of the wave is determined by a matching condition, and solutions of the Cauchy problem travel at this constant speed in the large time regime.

We now go back to the original deterministic equation (1.2). As far as we know, little was known concerning existence and behaviors of solutions. Let us here mention the main result of Biktashev [1]: for compactly supported initial data, solutions converge, as $t \rightarrow \infty$, to a Gaussian profile, where the convergence is understood in terms of the moments of $u(t, x)$. One may then conjecture that this property remains valid for “arbitrary” initial data. In this work, we show in particular that this is completely false: tails of the initial data have a strong influence on solutions.

The situation for equation (1.2) is also in sharp contrast with the cut-off and stochastic approximations as studied in [17, 14, 15, 13]. First, using the Fourier transform, one can explicitly compute all solitary waves and observe that not only all positive speeds are admissible but also that all profiles are changing sign (see Appendix A for details). Next, solutions of the Cauchy problem can become extinct in finite time and, if global, are accelerating as time passes. This is the main goal of this work to rigorously prove these features for (1.2).

Throughout this work, we assume that the initial data is nonnegative, $u_0(x) \geq 0$, and satisfies

$$(1.4) \quad \int_{\mathbb{R}} u_0(x) dx = 1,$$

so that, *formally*, $\int_{\mathbb{R}} u(t, x) dx = 1$ for later times. Indeed, if we formally integrate (1.2) over $x \in \mathbb{R}$, we see that the total mass $m(t) := \int_{\mathbb{R}} u(t, x) dx$ solves the Cauchy problem

$$(1.5) \quad \frac{d}{dt} m(t) = (1 - m(t))\bar{u}(t), \quad m(0) = 1,$$

so that the Gronwall lemma yields $m(t) = 1$ as long as $\bar{u}(t)$ is meaningful. A striking result of this paper is that the above formal argument may turn out to be completely wrong, in the sense that the solution may become extinct in finite time, $u(t, x) = 0$ for all $x \in \mathbb{R}$ and $t \geq T$.

The organization of the paper is as follows. In Section 2, we state our main results for (1.2). The keystone result is Theorem 2.1 and contains explicit formulas for solutions. Its proof (and that of some generalizations as explained in Remark 1.1) involves algebraic reductions that are given in Section 3. The different scenarios for solutions (extinction in finite time, global existence, acceleration...) are then proved in Section 4. We give a short summary of our work in Section 5. Last, the solitary waves are computed in Appendix A, and the propagation of Gaussian initial data in the case of a quadratic weight f in (1.1) is presented in Appendix B.

2. MAIN RESULTS

By using tricky algebraic manipulations, we can actually reduce the nonlocal equation (1.2) to the heat equation, and therefore compute the solution explicitly. This is our first main result and it reads as follows.

Theorem 2.1 (The solution explicitly). *Let $u_0 \geq 0$, with $\int u_0 = 1$. As long as $\bar{u}(t)$ is finite, the solution of (1.2) with initial data u_0 is given by*

$$(2.1) \quad u(t, x) = \frac{e^{tx+t^3/3} w(t, x+t^2)}{1 + \int_0^t \int_{\mathbb{R}} x e^{sx+s^3/3} w(s, x+s^2) dx ds},$$

where $w(t, x) = e^{t\partial_{xx}} u_0(x)$ is the solution of the heat equation with initial data u_0 . As a consequence, we also have

$$(2.2) \quad u(t, x) = \frac{e^{tx+t^3/3} \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi t}} e^{-(x+t^2-y)^2/4t} u_0(y) dy}{1 + \int_0^t \int_{\mathbb{R}} x e^{sx+s^3/3} \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi s}} e^{-(x+s^2-y)^2/4s} u_0(y) dy dx ds},$$

and

$$(2.3) \quad u(t, x) = \frac{e^{tx} \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi t}} e^{-(x+t^2-y)^2/(4t)} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy}.$$

Corollary 2.2 (The nonlocal term explicitly). *As long as it exists, $\bar{u}(t)$ is given by*

$$(2.4) \quad \bar{u}(t) = t^2 + \frac{\int_{\mathbb{R}} e^{ty} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy}.$$

It seems however that these explicit formulas rely on the fact that the equation has *exactly* the form (1.2): if saturation (as in [17, 14, 15]) or stochasticity (as in [13]) is introduced, then we can no longer take advantage of this “algebraic miracle”.

Equipped with the above formulas, we can prove rather different scenarii for the Cauchy problem associated with (1.2). Let us notice that, without our exact formulas, proving such behaviors seems to be far from obvious.

Theorem 2.3 (Global existence vs. extinction in finite time). *Let $u_0 \geq 0$, with $\int u_0 = 1$. Consider*

$$T = \sup \left\{ t \geq 0, \int_0^\infty e^{ty} u_0(y) dy < \infty \right\} \in [0, \infty].$$

- (i) *If $T = \infty$, then in (1.2), both $u(t, x)$ and $\bar{u}(t)$ are global in time. Typically, $u \in L_{\text{loc}}^\infty((0, \infty) \times \mathbb{R})$, $\bar{u} \in L_{\text{loc}}^\infty(0, \infty)$, and $\int_{\mathbb{R}} u(t, x) dx = 1$ for all $t \geq 0$.*
- (ii) *If $0 < T < \infty$, then extinction in finite time occurs, that is*

$$u(t, x) = 0, \quad \forall t > T, \forall x \in \mathbb{R}.$$

- (iii) *If $T = 0$, then $u(t, x)$ is defined for no $t > 0$.*

The first case holds, for instance, for Gaussian initial data whose propagation is investigated in Proposition 2.8. The proof of (i) is obvious since the assumption $\int_0^\infty e^{ty} u_0(y) dy < \infty$ for all $t > 0$ (i.e. $T = \infty$) implies $\int_0^\infty e^{ty} y u_0(y) dy < \infty$ for all $t > 0$, and therefore (notice that the integration on $(-\infty, 0)$ is harmless since ye^{ty} is bounded on this interval) both (2.4) and (2.3) are meaningful for all $t > 0$.

On the other hand, initial data not having *very light* tails at $+\infty$ make the equation completely meaningless in positive and finite time (second point). This in particular happens for initial data having *light* exponential tails. The proof of (ii) is straightforward in view of (2.3):

$$0 \leq u(t, x) \leq \frac{e^{tx}}{\sqrt{4\pi t}} \frac{\int_{\mathbb{R}} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy} = \frac{e^{tx}}{\sqrt{4\pi t} \int_{\mathbb{R}} e^{ty} u_0(y) dy}.$$

The numerator remains bounded for each (t, x) fixed, while the denominator tends to $+\infty$ near time T (possibly just after T).

Example 2.4 (Light exponential tail, extinction for $t \geq \alpha$). If

$$(2.5) \quad u_0(y) = \alpha e^{-\alpha y} \mathbf{1}_{(0, \infty)}(y), \quad \alpha > 0,$$

then in (1.2), both $u(t, x)$ and $\bar{u}(t)$ are defined on $(0, \alpha)$. They are given (see subsection 4.1 for details) by

$$(2.6) \quad \bar{u}(t) = t^2 + \frac{1}{\alpha - t} \xrightarrow{t \rightarrow \alpha} \infty,$$

and

$$(2.7) \quad u(t, x) = \frac{1}{\sqrt{2\pi}}(\alpha - t)e^{-(\alpha-t)x}e^{-\alpha t^2 + \alpha^2 t} \operatorname{Erf} \left(\frac{-(x + t^2 - 2\alpha t)}{\sqrt{2t}} \right) \xrightarrow{t \rightarrow \alpha} 0,$$

uniformly in $x \in \mathbb{R}$, where

$$\operatorname{Erf}(\theta) := \int_{\theta}^{\infty} e^{-z^2/2} dz.$$

In view of this, it seems reasonable to extend the solution by $u(t, x) \equiv 0$ for $t \geq \alpha$, which shows an extinction phenomena.

Example 2.5 (Light tail, extinction for $t > \alpha$). Consider a slight modification of the above example:

$$u_0(y) = \tilde{\alpha} \frac{1}{y^2} e^{-\alpha y} \mathbf{1}_{(1, \infty)}(y), \quad \alpha > 0,$$

where $\tilde{\alpha}$ is chosen so that $\int_{\mathbb{R}} u_0 = 1$. Invoking (2.3)-(2.4), the formula that we obtain is not as explicit as (2.7). However, it is clear that $\bar{u}(t)$ is finite for $t \leq \alpha$, while $u(t, x) \equiv 0$ for $t > \alpha$.

Last, as suggested by the denominator of formula (2.3), initial data having *heavy* tails prevent the definition of the solution for any positive time, that is (iii). See Remarks 3.2 and 3.4 for a precise explanation.

Example 2.6 (Heavy tails). If

$$(2.8) \quad y \mapsto e^{ty} u_0(y) \notin L^1(0, \infty), \quad \forall t > 0,$$

then the solution $u(t, x)$ of (1.2) is defined for no $t > 0$. This is typically the case if u_0 decays only algebraically.

Remark 2.7. The fact that not enough decay of the initial data on one side leads to pathological phenomena can be compared to a situation recently studied in the framework of dispersive equations. For the L^2 -critical generalized Korteweg-de Vries equation

$$\partial_t u + \partial_x (\partial_{xx} u + u^5) = 0; \quad ; \quad u|_{t=0} = Q + \varepsilon_0,$$

where Q is the unique even positive solution to $Q'' + Q^5 = Q$, given by

$$Q(x) = \left(\frac{3}{\cosh^2(2x)} \right)^{1/4},$$

Martel, Merle and Raphaël [10] have proved that if the initial perturbation ε_0 does not decay sufficiently fast on the right, then various regimes are possible, including a continuum of blow-up rates, a continuum of growth rate at infinity, while if $\int_0^{\infty} x^{10} \varepsilon_0(x) dx < \infty$, then only three scenarii are possible. In the case of the parabolic energy critical harmonic heat flow, similar phenomena had been observed by Gustafson, Nakanishi and Tsai [6].

Let us now turn to the speed of propagation of solutions. Plugging $u_0(y) = \delta_0(y)$ the Dirac mass at 0 in (2.3) and (2.4), one gets (see subsection 4.3 for details)

$$(2.9) \quad u(t, x) = \frac{1}{\sqrt{4\pi t}} e^{-(x-t^2)^2/4t}, \quad \bar{u}(t) = t^2.$$

This suggests that the solution of the Cauchy problem are accelerating. To maintain this affirmation, we investigate the propagation of a Gaussian initial data, which is relevant for biological lectures.

Proposition 2.8 (Accelerating propagation of Gaussian initial data). *If*

$$(2.10) \quad u_0(x) = \sqrt{\frac{a}{2\pi}} e^{-a(x-m)^2/2}, \quad a > 0, \quad m \in \mathbb{R},$$

then the solution of (1.2) is

$$(2.11) \quad u(t, x) = \sqrt{\frac{a(t)}{2\pi}} e^{-a(t)(x-m(t))^2/2}, \quad a(t) := \frac{a}{1+2at}, \quad m(t) := m + t^2 + \frac{t}{a}.$$

This shows that, starting from a Gaussian profile, the solution remains a Gaussian function, is accelerating and flattening since $m(t) \sim t^2$, $a(t) \sim \frac{1}{2t}$, as $t \rightarrow \infty$. Starting from our explicit formula, the computations that prove the above proposition are presented in subsection 4.2. Notice that this family of Gaussian self-similar solutions already appears in [1], where the long time convergence of the solution of (1.2) (with a compactly supported initial data) to a Gaussian profile is also investigated. As far as this result is concerned, we can provide a sharp improvement of the convergence procedure. Precisely, the long time convergence in [1, Theorem 1] is understood in term of the moments of $u(t, x)$, whereas we can prove strong uniform convergence. Precisely the following holds.

Theorem 2.9 (Long time behavior for compactly supported initial data). *Let $u_0 \geq 0$ be compactly supported, with $\int u_0 = 1$. Let $u(t, x)$ be the global solution of (1.2) with initial data u_0 . Then there is $C > 0$ such that*

$$\sup_{x \in \mathbb{R}} \left| u(t, x) - \frac{1}{\sqrt{4\pi t}} e^{-(x-t^2)^2/4t} \right| \leq \frac{C}{t}, \quad \forall t \geq 1.$$

The above result actually measures, uniformly with respect to $x \in \mathbb{R}$, the deviation from the elementary solution (2.9). The proof is based on a combination of our explicit formulas with an elementary estimate on the long time behavior of the heat equation. It will appear in subsection 4.3.

3. ALGEBRAIC REDUCTIONS

In this section, we show how to relate the solution of various modulations of (1.2) with the solution of the standard heat equation

$$(3.1) \quad \partial_t w = \partial_{xx} w, \quad t > 0, \quad x \in \mathbb{R}; \quad w|_{t=0} = u_0,$$

or a perturbation of the heat equation. In particular, the proof of the main result Theorem 2.1 will appear in subsection 3.3.

3.1. External time-dependent factor. Consider the equation

$$(3.2) \quad \partial_t u = \partial_{xx} u + a(t)u + g(t, x)u, \quad t > 0, \quad x \in \mathbb{R}; \quad u|_{t=0} = u_0,$$

where a is a given function of time only (independent of x and v), and g is independent of u . Consider v the solution to the Cauchy problem

$$(3.3) \quad \partial_t v = \partial_{xx} v + g(t, x)v, \quad t > 0, \quad x \in \mathbb{R}; \quad v|_{t=0} = u_0.$$

Then u and v are explicitly related through the formula

$$u(t, x) = v(t, x) e^{\int_0^t a(s) ds}.$$

3.2. Generalized momentum factor. Suppose now that in (3.2), the time dependent function is related to u in the same fashion as in (1.3),

$$(3.4) \quad \partial_t u = \partial_{xx} u + g(t, x)u - \bar{u}(t)u, \quad t > 0, x \in \mathbb{R}; \quad u|_{t=0} = u_0,$$

where

$$\bar{u}(t) = \int_{\mathbb{R}} f(x)u(t, x)dx,$$

for some weight function $f(x)$. Introduce v the solution to the Cauchy problem

$$(3.5) \quad \partial_t v = \partial_{xx} v + g(t, x)v, \quad t > 0, x \in \mathbb{R}; \quad v|_{t=0} = u_0.$$

Then formally,

$$v(t, x) = u(t, x)e^{\int_0^t \bar{u}(s)ds}.$$

We remark that this change of unknown function can be inverted: multiplying the above expression by $f(x)$ and integrating over $x \in \mathbb{R}$, we get

$$\bar{v}(t) = \bar{u}(t)e^{\int_0^t \bar{u}(s)ds} = \frac{d}{dt} \left(e^{\int_0^t \bar{u}(s)ds} \right).$$

By integrating in time, we infer

$$\int_0^t \bar{v}(s)ds = e^{\int_0^t \bar{u}(s)ds} - 1,$$

and, so long as $\int_0^t \bar{v}(s)ds > -1$,

$$(3.6) \quad u(t, x) = \frac{v(t, x)}{1 + \int_0^t \bar{v}(s)ds}.$$

In the case considered throughout this paper, $u_0 \geq 0$, which implies in the case $g(t, x) = x$, as we will see below, not only $v(t, x) > 0$, but also $\int_0^t \bar{v}(s)ds > -1$. As a result, the above computations are licit provided that \bar{u} (and therefore \bar{v}) is finite.

Example 3.1. Consider (1.2) without the drift factor xu , that is

$$\partial_t u = \partial_{xx} u - \bar{u}(t)u, \quad t > 0, x \in \mathbb{R}; \quad v|_{t=0} = u_0,$$

with

$$\bar{u}(t) = \int_{\mathbb{R}} xu(t, x)dx.$$

In that case, $v = w$, solution to the heat equation (3.1). In view of the expression of the heat kernel, we have:

$$\int_0^t \bar{w}(s)ds = \int_0^t \int_{\mathbb{R}} \int_{\mathbb{R}} x \frac{1}{\sqrt{4\pi s}} e^{-(x-y)^2/4s} u_0(y) dy dx ds.$$

We compute

$$\int_{\mathbb{R}} x e^{-(x-y)^2/4s} dx = \int_{\mathbb{R}} (x+y) e^{-x^2/4s} dx = y\sqrt{4\pi s},$$

and thus

$$(3.7) \quad u(t, x) = \frac{w(t, x)}{1 + t \int_{\mathbb{R}} y u_0(y) dy}.$$

Therefore, if u_0 is even, or if the main part of its mass lies on the right, $\int_{\mathbb{R}} y u_0(y) dy \geq 0$, then the solution u is well-defined for all times $t \geq 0$. On the other hand, if the mass of u_0 is more important on the left, $\int_{\mathbb{R}} y u_0(y) dy < 0$, then finite time blow-up occurs:

$$\exists T_* > 0, \quad u(t, x) \xrightarrow[t \rightarrow T_*]{} +\infty, \quad \forall x \in \mathbb{R}.$$

Remark 3.2. The above reduction requires to be able to consider an open time interval, in order for the integration procedure to make sense. This approach becomes meaningless if we have $\bar{u}(t) = \infty$ (hence $\bar{v}(t) = \infty$) for all $t > 0$, which is exactly the case of Theorem 2.3, (iii).

3.3. Spatially linear factor. Consider now a heat equation supplemented with an extra term involving a factor which is linear in x ,

$$(3.8) \quad \partial_t v = \partial_{xx} v + a(t)xv, \quad t > 0, x \in \mathbb{R}; \quad v|_{t=0} = u_0,$$

where a is a given function of time only (independent of x and v). In quantum mechanics, the left hand side of the equation is replaced by $i\partial_t v$, where $i = \sqrt{-1}$, and the corresponding Schrödinger equation models the evolution of particles under the effect of an electric field $a(t)x$. When the function a is constant, it is possible to relate the solution of the free Schrödinger equation to the solution of the equation with this electric field through the *Avron–Herbst formula*, see e.g. [16]. This formula can be generalized to the case where a does depend on t , see [2]. Replacing t with $-it$ in the formula given in [2], we see that the solutions to (3.1) and (3.8) are related through

$$v(t, x) = w \left(t, x + 2 \int_0^t \int_0^s a(\tau) d\tau ds \right) \exp \left(x \int_0^t a(s) ds + \int_0^t \left(\int_0^s a(\tau) d\tau \right)^2 ds \right).$$

In the case $a(t) \equiv 1$, this formula is simply

$$(3.9) \quad v(t, x) = w \left(t, x + t^2 \right) \exp \left(tx + \frac{t^3}{3} \right).$$

Proofs of Theorem 2.1 and Corollary 2.2. Combining (3.6) and (3.9), we infer (2.1). The expression (2.2) then stems from the explicit formula of the heat kernel on \mathbb{R} . Finally, to deduce (2.3), we denote by $I(t)$ the triple integral appearing in the denominator of (2.2). Using Fubini's Theorem, we first compute the integral with respect to x . Using elementary algebra (canonical form) we find

$$\begin{aligned} \int_{\mathbb{R}} x e^{sx} e^{-(x+s^2-y)^2/4s} dx &= e^{sy} \int_{\mathbb{R}} x e^{-[x-(s^2+y)]^2/(4s)} dx \\ &= e^{sy} \int_{\mathbb{R}} (z + (s^2 + y)) e^{-z^2/(4s)} dz \\ (3.10) \quad &= e^{sy} (s^2 + y) \sqrt{4\pi s}. \end{aligned}$$

As a result, we have

$$I(t) = \int_0^t \int_{\mathbb{R}} (s^2 + y) e^{s^3/3 + sy} u_0(y) dy ds = \int_{\mathbb{R}} (e^{t^3/3 + ty} - 1) u_0(y) dy.$$

Plugging this into (2.2) and using the normalization $\int_{\mathbb{R}} u_0 = 1$, we then obtain (2.3). Using (2.3) and equality (3.10) again, we see that (2.4) holds true. \square

Remark 3.3. The denominator of (3.7) in Example 3.1 corresponds to the expression obtained by considering the first two terms of the Taylor expansion of the exponential in the denominator in (2.3). Example 3.1 illustrates the fact that introducing the term xu in (1.2) prevents blow-up, as shown by the formula (2.3) and Theorem 2.3.

Remark 3.4. Back to Theorem 2.3, (iii), we see that if there was a $\tau > 0$ such that \bar{u} is finite on $[0, \tau]$, then (2.3) would hold true. On the other hand, the assumption $T = 0$, along with (2.3), would imply $u(t, x) = 0$ for all $t \in (0, \tau]$ and all $x \in \mathbb{R}$, while we have seen in (1.5) that so long as \bar{u} is finite, we have $\int_{\mathbb{R}} u(t, x) dx = 1$, hence a contradiction.

3.4. Spatially quadratic factor. Consider

$$(3.11) \quad \partial_t v = \partial_x^2 v - a(t)x^2 v \quad ; \quad v|_{t=0} = u_0,$$

where a is a given function of time only (independent of x and v). In the case where a is constant (say $a = 1$), the solution to (3.11) is given by the *Mehler's formula*,

$$(3.12) \quad v(t, x) = \frac{1}{\sqrt{2\pi \sinh(2t)}} \int_{\mathbb{R}} e^{-\coth(2t)\frac{x^2+y^2}{2} - \operatorname{cosech}(2t)xy} u_0(y) dy.$$

The formula is known in the context of the heat equation ([5]) as well as in the context of the Schrödinger equation ([3]). For a general time-dependent function a , introduce the fundamental solution associated to the corresponding oscillator,

$$\begin{cases} \ddot{\mu} - a(t)\mu = 0 & ; \quad \mu(0) = 0, \quad \dot{\mu}(0) = 1, \\ \ddot{\nu} - a(t)\nu = 0 & ; \quad \nu(0) = 1, \quad \dot{\nu}(0) = 0. \end{cases}$$

For $a(t) \geq 0$, we check that $\nu(t) \geq 1$ for all $t \geq 0$, and $\mu(t) > 0$ for all $t > 0$. Adapting the generalized lens transform presented in [2], we see that the solutions to (3.11) and (3.1) are related through the formula

$$(3.13) \quad v(t, x) = \frac{1}{\sqrt{\nu(2t)}} e^{-\frac{x^2}{2} \frac{\dot{\nu}(2t)}{\nu(2t)}} w\left(\frac{\mu(2t)}{2\nu(2t)}, \frac{x}{\nu(2t)}\right).$$

Of course, this formula makes sense so long as ν is nonzero, and so long as the map $t \mapsto \mu(2t)/\nu(2t)$ is invertible. Note that this is the case for all positive times when $a \geq 0$, from the above remark.

Remark 3.5. In the case $a = 1$, we compute explicitly $\mu(t) = \sinh(t)$ and $\nu(t) = \cosh(t)$. Mehler's formula (3.12) can be viewed as the composition of the lens transform (3.13) and the explicit formula for the heat kernel.

Remark 3.6 (Multidimensional case). All the formulas presented in this section can be generalized to a multidimensional framework, $x \in \mathbb{R}^d$, $d \geq 1$. In the case considered in subsection 3.3, replace $a(t)x$ with $a(t) \cdot x$ where $a(t) \in \mathbb{R}^d$ is a vector-valued time-dependent function. In the quadratic case of subsection 3.4, it seems necessary to restrict to the isotropic case where $a(t)x^2 u$ is replaced by

$$a(t)|x|^2 u = a(t) \left(\sum_{j=1}^d x_j^2 \right) u,$$

that is, the coefficient in factor on x_j^2 is independent of j (see [2]).

4. PROOFS OF VARIOUS FEATURES OF THE CAUCHY PROBLEM

In this section, based on our explicit formulas, we prove the different behaviors as stated in Section 2.

4.1. Extinction in finite time. We present here the computations associated to Example 2.4. For the initial data (2.5), we compute

$$\int_{\mathbb{R}} e^{ty} u_0(y) dy = \frac{\alpha}{\alpha - t}, \quad \int_{\mathbb{R}} e^{ty} y u_0(y) dy = \frac{\alpha}{(\alpha - t)^2},$$

which we plug into (2.4) to get (2.6). Next, (2.3) and elementary algebra (canonical form) yields

$$\begin{aligned} u(t, x) &= \frac{e^{tx}(\alpha - t)}{\sqrt{4\pi t}} \int_0^\infty e^{-(x+t^2-y)^2/(4t)} e^{-\alpha y} dy \\ &= \frac{e^{tx}(\alpha - t)}{\sqrt{4\pi t}} e^{-\alpha(x+t^2-\alpha t)} \int_0^\infty e^{-[y-(x+t^2-2\alpha t)]^2/(4t)} dy \\ &= \frac{e^{tx}(\alpha - t)}{\sqrt{2\pi}} e^{-\alpha(x+t^2-\alpha t)} \int_{-\frac{x+t^2-2\alpha t}{\sqrt{2t}}}^\infty e^{-z^2/2} dz, \end{aligned}$$

that is formula (2.7). The fact that $u(t, x) \rightarrow 0$, as $t \rightarrow \alpha$, uniformly in $x \in \mathbb{R}$ follows from the following two facts: first, if $x \geq -\frac{1}{\alpha-t}$ then (2.7) implies $|u(t, x)| \leq C(\alpha-t)$; next, for t sufficiently close to α , if $x \leq -\frac{1}{\alpha-t}$ then, using $\text{Erf}(\theta) \sim \frac{1}{\theta} e^{-\theta^2/2}$ as $\theta \rightarrow \infty$, (2.7) implies that

$$|u(t, x)| \leq C e^{-(\alpha-t)x} \text{Erf}\left(-\frac{x}{\sqrt{2\alpha}}\right) \leq C e^{-(\alpha-t)x} 2 \frac{\sqrt{2\alpha}}{-x} e^{-x^2/(4\alpha)},$$

so that $|u(t, x)| \leq C' e^{-\frac{x^2}{4\alpha}(1+4\alpha\frac{\alpha-t}{x})} \leq C' e^{-\frac{x^2}{8\alpha}} \leq C' e^{-\frac{1}{8\alpha(\alpha-t)^2}}$.

□

4.2. Propagation of Gaussian initial data. We now present the straightforward computations that prove Proposition 2.8. We plug the initial data (2.10) into the formula (2.3) for $u(t, x)$ and denote by $N(t, x)$, $D(t)$ the numerator, denominator respectively. Using elementary algebra (canonical form), we get

$$\begin{aligned} D(t) &= \sqrt{\frac{a}{2\pi}} \int_{\mathbb{R}} e^{ty} e^{-a(y-m)^2/2} dy \\ &= \sqrt{\frac{a}{2\pi}} \int_{\mathbb{R}} e^{-a[y-(m+\frac{t}{a})]^2/2} e^{mt+t^2/(2a)} dy \\ &= e^{mt+t^2/(2a)}, \end{aligned}$$

and

$$\begin{aligned}
N(t, x) &= \frac{1}{\sqrt{4\pi t}} e^{tx} \sqrt{\frac{a}{2\pi}} \int_{\mathbb{R}} e^{-(x+t^2-y)^2/(4t)} e^{-a(y-m)^2/2} dy \\
&= \frac{1}{\sqrt{4\pi t}} e^{tx} \sqrt{\frac{a}{2\pi}} \int_{\mathbb{R}} e^{-\frac{1+2at}{(4t)} \left(y - \frac{x+t^2+2amt}{1+2at}\right)^2} e^{-\frac{a}{2} \frac{(x+t^2-m)^2}{1+2at}} dy \\
&= \frac{1}{\sqrt{4\pi t}} e^{tx} \sqrt{\frac{a}{2\pi}} e^{-\frac{a}{2} \frac{(x+t^2-m)^2}{1+2at}} \sqrt{2\pi \frac{2t}{1+2at}} \\
&= \sqrt{\frac{a}{2\pi}} \frac{1}{\sqrt{1+2at}} e^{-\frac{a}{2(1+2at)} \left(x - \frac{at^2+am+t}{a}\right)^2} e^{\frac{t}{2} \frac{2am+t}{a}}.
\end{aligned}$$

Finally, $u(t, x) = N(t, x)/D(t)$ easily yields (2.11). \square

4.3. Long time behavior for compactly supported initial data. We now prove Theorem 2.9. Using elementary algebra, (2.3) is recast as

$$(4.1) \quad u(t, x) = \frac{1}{\sqrt{4\pi t}} \frac{\int_{\mathbb{R}} e^{-(x-t^2-y)^2/(4t)} e^{ty} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy},$$

which, in particular, is the appropriate form to compute the elementary solution (2.9) for $u_0(y) = \delta_0(y)$. It follows from (4.1) that the deviation

$$\psi(t, x) := u(t, x) - \frac{1}{\sqrt{4\pi t}} e^{-(x-t^2)^2/4t}$$

is given by

$$\psi(t, x) = \frac{\int_{\mathbb{R}} \left(e^{-(x-t^2-y)^2/(4t)} - e^{-(x-t^2)^2/(4t)} \right) e^{ty} u_0(y) dy}{\sqrt{4\pi t} \int_{\mathbb{R}} e^{ty} u_0(y) dy}.$$

Using Taylor formula we write

$$\begin{aligned}
\left| e^{-(x-t^2-y)^2/(4t)} - e^{-(x-t^2)^2/(4t)} \right| &= \left| \int_0^1 \frac{y}{\sqrt{t}} \frac{x-t^2-\theta y}{2\sqrt{t}} e^{-(\frac{x-t^2-\theta y}{2\sqrt{t}})^2} d\theta \right| \\
&\leq \frac{|y|}{\sqrt{t}} \sup_{z \in \mathbb{R}} |ze^{-z^2}|,
\end{aligned}$$

and get

$$|\psi(t, x)| \leq \frac{C}{t} \frac{\int_{\mathbb{R}} e^{ty} |y| u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy} \leq \frac{C}{t} M,$$

where $\text{supp } u_0 \subset [-M, M]$. Theorem 2.9 is proved. \square

5. BRIEF SUMMARY

We are concerned with evolutionary genetics models for asexual populations (viruses, microbes). In contrast with Muller's ratchet we aim at understanding the dynamics when accumulation of deleterious mutations is neglected. In order to incorporate the effects of mutations, we use the nonlocal reaction-diffusion deterministic model proposed in [17], and referred to as the replicator-mutator equation.

Our mathematical analysis shows that one can reduce the replicator-mutator equation to the heat equation. As a result, solutions are completely explicit which enables to prove various nontrivial behaviors. First, for initial data with heavy tails, the equation is immediately meaningless. Next, for light initial tails, the solution becomes extinct in finite time, which violates the mass constraint formally observed. Last, for very light initial tails, we prove that solutions are global and are accelerating as time passes. This prevents the convergence to a solitary wave, as observed for some perturbations (cut-off approximation or stochastic treatment) of the original equation.

APPENDIX A. SOLITARY WAVES FOR (1.2)

In this Appendix, we compute explicitly the solitary waves for (1.2). In particular, all positive speeds are admissible and, the Airy function being involved, all solitary waves are changing sign, which enforces some cut-off arguments for applications to biology.

We plug the ansatz $u(t, x) = \phi(x - ct)$ into equation (1.2). We are therefore looking for a speed c and a profile ϕ such that

$$(A.1) \quad \begin{cases} \phi'' + c\phi' + (x - \bar{\phi})\phi = 0 & \text{on } \mathbb{R}, \\ \phi(\pm\infty) = 0, \quad \int_{\mathbb{R}} \phi = 1, \end{cases}$$

where $\bar{\phi} := \int_{\mathbb{R}} x\phi(x) dx$.

If ϕ solves (A.1) then

$$(A.2) \quad \psi(x) := \phi(x + \bar{\phi})$$

solves

$$\begin{cases} \psi'' + c\psi' + x\psi = 0 & \text{on } \mathbb{R} \\ \psi(\pm\infty) = 0, \quad \int_{\mathbb{R}} \psi = 1, \quad \bar{\psi} = 0. \end{cases}$$

Applying Fourier transform to this linear problem yields

$$-\xi^2 \hat{\psi} + ci\xi \hat{\psi} + i \frac{d\hat{\psi}}{d\xi} = 0, \quad \hat{\psi}(0) = 1,$$

which is solved as

$$\hat{\psi}(\xi) = e^{-i\frac{\xi^3}{3} - c\frac{\xi^2}{2}}.$$

This enforces $c > 0$ (if not then $\lim_{\pm\infty} \hat{\psi} = 0$ would not hold) so that $\hat{\psi}$ belongs to the Schwartz space $\mathcal{S}(\mathbb{R})$, and so does ψ . The inverse Fourier transform then yields

$$\psi(x) = \frac{1}{2\pi} \int_{\mathbb{R}} \hat{\psi}(\xi) e^{ix\xi} d\xi.$$

But the canonical transformation yields

$$\hat{\psi}(\xi) = e^{-\frac{i}{3}(\xi - i\frac{c}{2})^3} e^{-i\frac{c^2}{4}\xi - \frac{c^3}{24}}.$$

Recalling that the Airy function can be written as

$$(A.3) \quad \text{Ai}(x) = \frac{1}{2\pi} \int_{\mathbb{R}} e^{i\xi^3/3 + ix\xi} d\xi = \frac{1}{2\pi} \int_{\text{Im } \xi = \eta > 0} e^{i\xi^3/3 + ix\xi} d\xi,$$

(see e.g. [7]), we infer, since ψ is real-valued,

$$\begin{aligned}\psi(x) &= \frac{1}{2\pi} \int_{\mathbb{R}} e^{-\frac{i}{3}(\xi - i\frac{c}{2})^3} e^{-i\frac{c^2}{4}\xi - \frac{c^3}{24}} e^{ix\xi} d\xi \\ &= \frac{1}{2\pi} \int_{\mathbb{R}} e^{\frac{i}{3}(\xi + i\frac{c}{2})^3} e^{i\frac{c^2}{4}\xi - \frac{c^3}{24}} e^{-ix\xi} d\xi \\ &= \frac{1}{2\pi} \int_{\text{Im } \zeta = c/2} e^{i\zeta^3/3} e^{i\frac{c^2}{4}(\zeta - ic/2) - \frac{c^3}{24}} e^{-ix(\zeta - ic/2)} d\zeta,\end{aligned}$$

where we have used the property $c > 0$ to change the contour of integration in the complex plane according to (A.3). Thus,

$$(A.4) \quad \psi(x) = e^{-cx/2 + c^3/12} \text{Ai}\left(\frac{c^2}{4} - x\right),$$

which is the form announced in [17].

Hence, in view of (A.2), ϕ must be of the form $\phi(x) = \psi(x - \alpha)$, with ψ given by (A.4). Conversely, if $\phi(x) = \psi(x - \alpha)$ for some $\alpha \in \mathbb{R}$, then $\bar{\psi} = 0$ enforces $\bar{\phi} = \alpha$ and it is obvious that ϕ solves (A.1).

Theorem A.1 (Solitary waves). *Let $c > 0$ be given. Then there exists a unique solitary wave (c, ψ_c) solution of (A.1) and such that $\bar{\psi}_c = 0$. It is given by (A.4). Other solutions are translations of this ψ_c :*

$$\phi_{\alpha,c}(x) := \psi_c(x - \alpha), \quad \alpha \in \mathbb{R},$$

so that in particular $\bar{\phi}_{\alpha,c} = \alpha$.

For $c \leq 0$, problem (A.1) has no solution.

APPENDIX B. GAUSSIAN INITIAL DATA UNDER A QUADRATIC POTENTIAL

Since the weight $f(x)$ in (1.1) may be quadratic (see e.g. [9]), we present the explicit computations stemming from Section 3 as far as the propagation of Gaussians is concerned. For $m \in \mathbb{R}$ and $a > 0$, consider the Cauchy problem

$$(B.1) \quad \partial_t u = \partial_{xx} u - \left(x^2 - \int_{\mathbb{R}} x^2 u(t, x) dx\right) u \quad ; \quad u(0, x) = \sqrt{\frac{a}{2\pi}} e^{-a(x-m)^2/2}.$$

From subsection 3.2, (B.1) is equivalent to

$$(B.2) \quad \partial_t v = \partial_{xx} v - x^2 v \quad ; \quad v(0, x) = \sqrt{\frac{a}{2\pi}} e^{-a(x-m)^2/2},$$

through the relation

$$u(t, x) = \frac{v(t, x)}{1 - \int_0^t \int_{\mathbb{R}} x^2 v(s, x) dx ds}.$$

Relation (3.13) shows that

$$v(t, x) = \frac{1}{\sqrt{\cosh(2t)}} e^{-\tanh(2t)\frac{x^2}{2}} w\left(\frac{\tanh(2t)}{2}, \frac{x}{\cosh(2t)}\right),$$

where w , solution to the heat equation

$$\partial_t w = \partial_{xx} w \quad ; \quad w(0, x) = \sqrt{\frac{a}{2\pi}} e^{-a(x-m)^2/2},$$

is given by

$$w(t, x) = \sqrt{\frac{a}{2\pi(1+2at)}} e^{-\frac{a}{2(1+2at)}(x-m)^2}.$$

We infer

$$\begin{aligned} v(t, x) &= \sqrt{\frac{a}{2\pi(\cosh(2t) + a \sinh(2t))}} e^{-\tanh(2t)\frac{x}{2}} e^{-\frac{a}{2(1+a \tanh(2t))}(\frac{x}{\cosh(2t)} - m)^2} \\ &= \sqrt{\frac{a}{2\pi(\cosh(2t) + a \sinh(2t))}} e^{-\frac{am^2 \sinh(2t)}{2(a \cosh(2t) + \sinh(2t))}} e^{-\frac{a(t)}{2}(x-m(t))^2}, \end{aligned}$$

where

$$a(t) = \frac{a \cosh(2t) + \sinh(2t)}{\cosh(2t) + a \sinh(2t)}, \quad m(t) = \frac{am}{a \cosh(2t) + \sinh(2t)},$$

hence

$$\begin{aligned} \int_{\mathbb{R}} x^2 v(t, x) dx &= \frac{\sqrt{a} e^{-\frac{am^2 \sinh(2t)}{2(a \cosh(2t) + \sinh(2t))}}}{(a \cosh(2t) + \sinh(2t))^{5/2}} \\ &\quad \times ((\cosh(2t) + a \sinh(2t))(a \cosh(2t) + \sinh(2t)) + a^2 m^2). \end{aligned}$$

The integral in time of this quantity involves elliptic integrals in general, so we consider special values of the parameters. In the particular case of an initial Gaussian centered at the origin, $m = 0$, with $a = 1$, the above formula becomes much simpler,

$$\int_{\mathbb{R}} x^2 v(t, x) dx = e^{-t},$$

and we check that

$$(B.3) \quad u(t, x) = \frac{1}{\sqrt{2\pi}} e^{-x^2/2} = u_0(x), \quad \forall t \in \mathbb{R}.$$

In other cases, the initial Gaussian propagates as a Gaussian in a non-trivial way, for which in general explicit computations seem rather intricate. The fact that the solution in (B.3) does not depend on time can be understood as follows: the Gaussian $e^{-x^2/2}$ is the ground state associated to the harmonic oscillator, that is the eigenfunction associated to the lowest eigenvalue of the harmonic oscillator (see e.g. [8]):

$$(-\partial_{xx} + x^2) e^{-x^2/2} = e^{-x^2/2},$$

so the solution to (B.2) is simply

$$v(t, x) = \frac{1}{\sqrt{2\pi}} e^{-t} e^{-x^2/2},$$

hence

$$\int_{\mathbb{R}} x^2 v(t, x) dx = e^{-t},$$

and $u(t, x) = u_0(x)$ from (3.6). Note that this specific case (stationary solution) does not extend to other biologically relevant cases: the eigenfunctions associated to the harmonic oscillator are Hermite functions,

$$\psi_n(x) = e^{x^2/2} \frac{d^n}{dx^n} e^{-x^2},$$

which are associated with the eigenvalue $\lambda_n = 1 + 2n$, but except in the case $n = 0$, they change signs.

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REFERENCES

- [1] V. N. BIKTASHEV, *A simple mathematical model of gradual Darwinian evolution: emergence of a Gaussian trait distribution in adaptation along a fitness gradient*, J. Math. Biol., 68 (2014), pp. 1225–1248.
- [2] R. CARLES, *Nonlinear Schrödinger equation with time dependent potential*, Commun. Math. Sci., 9 (2011), pp. 937–964.
- [3] R. P. FEYNMAN AND A. R. HIBBS, *Quantum mechanics and path integrals (International Series in Pure and Applied Physics)*, Maidenhead, Berksh.: McGraw-Hill Publishing Company, Ltd., 365 p., 1965.
- [4] P. J. GERRISH, A. COLATO, A. S. PERELSON, AND P. D. SNIEGOWSKI, *Complete genetic linkage can subvert natural selection*, Proc. Natl. Acad. USA, 104 (2007), pp. 6266–6271.
- [5] A. GRIGOR'YAN, *Heat kernel and analysis on manifolds*, vol. 47 of AMS/IP Studies in Advanced Mathematics, American Mathematical Society, Providence, RI; International Press, Boston, MA, 2009.
- [6] S. GUSTAFSON, K. NAKANISHI, AND T.-P. TSAI, *Asymptotic stability, concentration and oscillations in harmonic map heat flow, Landau Lifschitz and Schrödinger maps on \mathbb{R}^2* , Comm. Math. Phys., 300 (2010), pp. 205–242.
- [7] L. HÖRMANDER, *The analysis of linear partial differential operators*, Springer-Verlag, Berlin, 1994.
- [8] L. D. LANDAU AND E. M. LIFSHITZ, *Quantum mechanics: non-relativistic theory. Course of Theoretical Physics, Vol. 3*, Addison-Wesley Series in Advanced Physics, Pergamon Press Ltd., London-Paris, 1958. Translated from the Russian by J. B. Sykes and J. S. Bell.
- [9] A. LORZ, S. MIRRAHIMI, AND B. PERTHAME, *Dirac mass dynamics in multidimensional non-local parabolic equations*, Comm. Partial Differential Equations, 36 (2011), pp. 1071–1098.
- [10] Y. MARTEL, F. MERLE, AND P. RAPHAËL, *Blow up for the critical gKdV equation III: exotic regimes*, Ann. Sc. Norm. Super. Pisa Cl. Sci. (5), (2014). archived as <http://arxiv.org/abs/1209.2510>.
- [11] H. J. MULLER, *Some genetic aspects of sex*, Am. Nat., 66 (1932), pp. 118–138.
- [12] ———, *The relation of recombination to mutational advance*, Mutat. Res., 1 (1964), pp. 2–9.
- [13] I. M. ROUZINE, E. BRUNET, AND C. O. WILKE, *The traveling-wave approach to asexual evolution: Muller's ratchet and speed of adaptation*, Theor. Popul. Biol., 73 (2008), pp. 24–46.
- [14] I. M. ROUZINE, J. WAKEKEY, AND J. M. COFFIN, *The solitary wave of asexual evolution*, Proc. Natl. Acad. USA, 100 (2003), pp. 587–592.
- [15] P. D. SNIEGOWSKI AND P. J. GERRISH, *Beneficial mutations and the dynamics of adaptation in asexual populations*, Phil. Trans. R. Soc. B, 365 (2010), pp. 1255–1263.
- [16] W. THIRRING, *A course in mathematical physics. Vol. 3*, Springer-Verlag, New York, 1981. Quantum mechanics of atoms and molecules, Translated from the German by Evans M. Harrell, Lecture Notes in Physics, 141.
- [17] L. S. TSIMRING, H. LEVINE, AND D. A. KESSLER, *RNA Virus Evolution via a Fitness-Space Model*, Phys. Rev. Lett., 76 (1996), pp. 4440–4443.
- [18] J. Y. WAKANO AND Y. IWASA, *Evolutionary Branching in a Finite Population: Deterministic Branching vs. Stochastic Branching*, Genetics, 193 (2013), pp. 229–241.
- [19] T. A. WITTEN AND L. M. SANDER, *Diffusion-limited aggregation*, Phys. Rev. B (3), 27 (1983), pp. 5686–5697.

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