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Partial differential equations

Explicit solutions in evolutionary genetics and applications

Solutions explicites en génétique évolutive et applications

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ABSTRACT

We show that the solution to a nonlocal reaction–diffusion equation, present in evolutionary genetics, can be related explicitly to the solution of the heat equation with the same initial data. As a consequence, we show different possible scenario for the solution: it can be either well-defined for all time, or become extinct in finite time, or even be defined for no positive time. In the former case, we give the leading-order asymptotic behavior of the solution for large time, which is universal.

RÉSUMÉ

Nous montrons que les solutions d'une équation de réaction–diffusion non locale, utilisée en génétique évolutive, peuvent être exprimées en fonction de la solution de l'équation de la chaleur avec même donnée initiale. Nous en déduisons plusieurs scénarios possibles pour la solution : elle peut, soit être définie pour tout temps, soit devenir identiquement nulle en temps fini, ou encore n'être définie pour aucun temps positif. Dans le premier cas, nous donnons le comportement asymptotique en temps grand de la solution, faisant intervenir un profil universel.

1. Introduction

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

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

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 trait space, and $f(x)$ represents the fitness. The nonlocal term then stands for the mean fitness at time t. In this Note, we focus on the case $f(x) = x$. We refer to [1] for explicit formulas when f is more generally of the form $f(t,x) = a(t)x^j$ for $j = 1$ or 2. We therefore consider here

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$$\partial_t u = \partial_{xx} u + \big(x - \bar{u}(t)\big)u, \quad t > 0,\ x \in \mathbb{R}, \tag{1}$$

where the nonlocal term is given by

$$\bar{u}(t) := \int_{\mathbb{R}} x u(t,x)\,\mathrm{d}x. \tag{2}$$

In the context of evolutionary genetics, Eq. (1) was introduced by Tsimring et al. [7], where they propose a mean-field theory for the evolution of RNA virus populations on a fitness space. Little seems to be known concerning existence and behaviors of solutions in (1). Let us here mention the main result of Biktashev [2]: for compactly supported initial data, solutions converge, as $t \to \infty$, 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. This suggests that the model should probably be adapted, in the spirit of the modifications presented in [7,3–5].

To be relevant from the biological point of view, (1) is associated with some initial datum u_0 that is everywhere non-negative, and such that

$$\int_{\mathbb{R}} u_0(x)\,\mathrm{d}x = 1.$$

Formally $\int_{\mathbb{R}} u(t,x)\,\mathrm{d}x = 1$ for $t \geqslant 0$. Indeed, if we formally integrate (1) over $x \in \mathbb{R}$, we see that the total mass $m(t) := \int_{\mathbb{R}} u(t,x)\,\mathrm{d}t$ solves the Cauchy problem

$$\frac{\mathrm{d}}{\mathrm{d}t}\big(m(t) - 1\big) = \frac{\mathrm{d}}{\mathrm{d}t} m(t) = \big(1 - m(t)\big)\bar{u}(t), \quad m(t) - 1_{|t=0} = 0. \tag{3}$$

Gronwall lemma yields $m(t) = 1$ as long as $\bar{u}(t)$ is finite. We show 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 $t \geqslant T$. In this Note, we always assume $u_0 \geqslant 0$, with $\int_{\mathbb{R}} u_0 = 1$.

2. Explicit formula

Theorem 2.1. *As long as $\bar{u}(t)$ is finite, the solution of (1) with initial data u_0 is given by*

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

To sketch the proof of this result, we introduce the solution of two different equations with the same initial datum,

$$\partial_t w = \partial_{xx} w, \quad t > 0,\ x \in \mathbb{R}; \quad w_{|t=0} = u_0, \tag{5}$$

which is the standard heat equation, and

$$\partial_t v = \partial_{xx} v + xv, \quad t > 0,\ x \in \mathbb{R}; \quad v_{|t=0} = u_0. \tag{6}$$

Formally, we have

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

By integrating over $x \in \mathbb{R}$ and then integrating in time, we see that so long as $\int_0^t \bar{v}(s)\,\mathrm{d}s > -1$, we have

$$u(t,x) = \frac{v(t,x)}{1 + \int_0^t \bar{v}(s)\,\mathrm{d}s}. \tag{7}$$

Note that this computation ceases to be valid if $\bar{u}(t)$ (or, equivalently, $\bar{v}(t)$) becomes infinite. Now v and w can be related thanks to a modification of the celebrated Avron–Herbst formula, known in the context of the Schrödinger equation with an external electric field (essentially, t is replaced by it; see, e.g., [6]):

$$v(t,x) = w\big(t, x + t^2\big)\exp\left(tx + \frac{t^3}{3}\right). \tag{8}$$

Theorem 2.1 then follows from the explicit formula for the heat kernel; we refer to [1] for more details.

3. Finite time extinction

It is clear from (4) that if the initial datum u_0 does not decay sufficiently *on the right*, then u may become identically zero in finite time: the denominator becomes infinite, while the numerator remains finite. More precisely, let

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

(i) If $T = \infty$, then in (1), both $u(t,x)$ and $\bar{u}(t)$ are global in time. Typically, $u \in L^\infty_{\mathrm{loc}}((0,\infty)\times\mathbb{R})$, $\bar{u} \in L^\infty_{\mathrm{loc}}(0,\infty)$, and $\int_{\mathbb{R}} u(t,x)\mathrm{d}x = 1$ for all $t \geqslant 0$.

(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 $t > 0$.

To illustrate the second case, let

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

In (1), both $u(t,x)$ and $\bar{u}(t)$ are defined on $(0,\alpha)$. They are given by (see [1] for detailed computations)

$$\bar{u}(t) = t^2 + \frac{1}{\alpha - t} \underset{t\to\alpha}{\longrightarrow} \infty,$$

and

$$u(t,x) = \frac{1}{\sqrt{2\pi}} (\alpha - t)\, \mathrm{e}^{-(\alpha-t)x}\, \mathrm{e}^{-\alpha t^2 + \alpha^2 t}\, \mathrm{erf}\left(\frac{-(x + t^2 - 2\alpha t)}{\sqrt{2t}} \right) \underset{t\to\alpha}{\longrightarrow} 0,$$

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

$$\mathrm{erf}(\theta) := \int_\theta^\infty \mathrm{e}^{-z^2/2}\,\mathrm{d}z.$$

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

4. Universal Gaussian profile

The first case in the previous section is met typically when u_0 is compactly supported.

Theorem 4.1. *If u_0 is compactly supported, there exists $C > 0$ such that*

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

Note that the asymptotic profile is universal in the sense that it does not depend on the profile u_0: it merely stems from the three properties satisfied by u_0 (nonnegative, total mass equal to one, and compact support). This estimate is a clarified version of the main result in [2]. Note that according to the previous section, the above result cannot be true for all initial data u_0, for too little decay on the right annihilates the solution.

Theorem 4.1 can be proved as follows. Using elementary algebra, (4) is recast as

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

It follows that the deviation ψ estimated in Theorem 4.1 is given by

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

Using Taylor formula we write

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

and get

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

where $\operatorname{supp} u_0 \subset [-M, M]$.

References

[1] Matthieu Alfaro, Rémi Carles, Explicit solutions for replicator–mutator equations: extinction vs. acceleration, preprint. Archived as, http://arxiv.org/abs/1405.2768.

[2] Vadim 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 (5) (2014) 1225–1248.

[3] Igor M. Rouzine, Johan Wakekey, John M. Coffin, The solitary wave of asexual evolution, Proc. Natl. Acad. Sci. USA 100 (2003) 587–592.

[4] Igor M. Rouzine, Éric Brunet, Claus O. Wilke, The traveling-wave approach to asexual evolution: Muller's ratchet and speed of adaptation, Theor. Popul. Biol. 73 (2008) 24–46.

[5] Paul D. Sniegowski, Philip J. Gerrish, Beneficial mutations and the dynamics of adaptation in asexual populations, Philos. Trans. R. Soc. B 365 (2010) 1255–1263.

[6] W. Thirring, Quantum mechanics of atoms and molecules, in: A Course in Mathematical Physics, vol. 3, Springer-Verlag, New York, 1981. Translated from the German by Evans M. Harrell, Lecture Notes in Physics, 141.

[7] Lev S. Tsimring, Herbert Levine, David A. Kessler, RNA virus evolution via a fitness-space model, Phys. Rev. Lett. 76 (23) (1996) 4440–4443.