Density behavior of spatial birth-and-death stochastic evolution of mutating genotypes under selection rates *

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Abstract

We consider birth-and-death stochastic evolution of genotypes with different lengths. The genotypes might mutate that provides a stochastic changing of lengthes by a free diffusion law. The birth and death rates are length dependent which corresponds to a selection effect. We study an asymptotic behavior of a density for an infinite collection of genotypes. The cases of space homogeneous and space heterogeneous densities are considered.

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1 Description of model

We start with a heuristic discussion of a model, describing spatial evolution of mutating genotypes under selection rates. Each genotype might be characterized by a pair $\widehat{x} := (x, s_x)$. Here $x \in \mathbb{R}^d$ is a location in the Eucledian space occupied by this genotype, and a mark s_x is its quantitative characteristic. We will

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consider, cf. [4,8], a continuous-gene space model. Namely, $s_x \in \mathbb{R}_+ := [0, +\infty)$ will be understood as a length of a genotype located at site x.

We describe an infinite collection of genotypes as a configuration $\widehat{\gamma} := \{\widehat{x}\}$. Having in mind that in the reality any individual with a given genotype has not only position in space but also non-zero size, we assume that $\gamma := \{x\}$ is a locally finite subset in $\mathbb{R}^d$. Namely, $\gamma \cap \Lambda$ is a finite set for any compact $\Lambda \subset \mathbb{R}^d$. Let Γ and $\widehat{\Gamma}$ be the spaces of such γ's and $\widehat{\gamma}$'s, accordingly.

In the present paper, we deal with mutating genotypes. Omitting the nature of these mutations, we suppose that they lead to a stochastic evolution of marks s_x, given by Brownian motion on $\mathbb{R}_+$ with absorption at 0. We consider a birth-and-death stochastic dynamics of mutating genotypes. It means that at any random moment of time the existing genotype may disappear (die) from the configuration or may produce a new one. This new genotype will be placed at other location in the space. It has the parent's genotype at the moment of birth, but then it immediately involves in a mutation process. This may be understood as an expansion of genotypes along the space. The probabilistic rates of birth and death of a genotype are independent of the rest of configuration, however, we suppose that they depend on sizes of genotypes. In fact, it means that we have selection in rates of birth and death. It is natural for biological systems that genotypes with very shot as well as very long length have less possibilities for surviving and reproduction, see e. g. [1,3].

The heuristic Markov generator of the dynamics described above may be given by

$$(LF)(\widehat{\gamma}) = \sum_{x\in\gamma} b(s_x) \int_{R^d} a(x-y)\big(F(\widehat{\gamma} \cup \{y, s_x\}) - F(\widehat{\gamma})\big)dy + \sum_{x\in\gamma} d(s_x)\big(F(\widehat{\gamma} \setminus \{x, s_x\}) - F(\widehat{\gamma})\big) + \sum_{x\in\gamma} \frac{\partial^2}{\partial s_x^2} F(\widehat{\gamma}). \tag{1.1}$$

The first term in (1.1) describes the birth of genotypes. This reproduction step involves selection as well as expansion of genotypes along the space. The function a describes an expansion (migration) rate, it is independent on marks s_x, s_y. Function b is associated with stabilizing selection. It prescribes that some lengths may be ranked against the other lengths. Genotypes with optimal (or at least more optimal) lengths are assumed to breed and to spread more intensively. We assume that $0 \le a \in L^1(\mathbb{R}^d)$, a is an even non-negative function, $b : \mathbb{R}_+ \to \mathbb{R}_+$ with $b(0) = 0$. Without loss of generality we suppose that $\int_{\mathbb{R}^d} a(x)dx = 1$.

The second term in (1.1) corresponds to the death of genotypes. We assume here that the death rate $d : \mathbb{R}_+ \to \mathbb{R}_+$ depends only on a length of a genotype, and does not depend on a location of genotype in the space. The shape of d will be discussed below.

The third term describes mainly mutations of genotypes, but also can include all random changes within the genotype, such as: duplication, genetic drift, etc. This differential operator is a modification of the generator for a random jump mutation model on the continuous space. Let us note that the third term is the direct sum of operators. That means that we assume that each offspring develops independently on others and we do not consider any interaction between existing genotypes.

Note that models of this type (without expansion), so-called mutation-selection models, play an important role in analysis of many problems of population genetics, see e. g. [1,3].

To give a rigorous meaning to the expression (1.1) we consider the following classes of functions. Let $\mathcal{D}$ consist of all functions $\varphi : \mathbb{R}^d \times \mathbb{R}_+ \to \mathbb{R}$ which have bounded support in $\mathbb{R}^d \times (0, \infty)$, and φ is a continuous functions in the first variable and twice continuously differentiable in the second variable. For any $\varphi \in \mathcal{D}$ the following expression is well-defined:

$$\langle \varphi, \widehat{\gamma} \rangle := \sum_{x \in \gamma} \varphi(x, s_x),$$

since the summation will only be taken over the finite set $\gamma_\Lambda := \gamma \cap \Lambda$ for some compact $\Lambda \subset \mathbb{R}^d$. Let $\varphi_1, \ldots, \varphi_N \in \mathcal{D}$ and $f : \mathbb{R}^N \to \mathbb{R}$ be twice continuously differentiable function on $\mathbb{R}^N$ bounded together with all its partial derivatives. The class of all functions of the form

$$F(\widehat{\gamma}) = f(\langle \varphi_1, \widehat{\gamma} \rangle, \ldots, \langle \varphi_N, \widehat{\gamma} \rangle), \quad \widehat{\gamma} \in \widehat{\Gamma}$$

we denote by $\mathcal{F}$. It is worth noting that for any $F \in \mathcal{F}$ the value of $F(\widehat{\gamma})$ does not depend on on those $\widehat{x} \in \widehat{\gamma}$ which are outside of the union of supports of $\varphi_1, \ldots, \varphi_N$. In particular, the summation in the second term of (1.1) will only be taken over a finite subset of each γ, hence this term is well-defined. Analogously, for each x which is outside of the union of supports above, $\dfrac{\partial^2 F}{\partial s_x^2}(\widehat{\gamma}) = 0$. Similarly, the integral in the first term of (1.1) will be taken over a compact set. Moreover, if, additionally, a has compact support in $\mathbb{R}^d$ the sum before integral will be also finite. For a general integrable function a, this sum is a series which may converges only a.s. in the following sense.

Let μ be a probability measure (state) on the space $\widehat{\Gamma}$ with σ-algebra described e. g. in [7]. A function $k_\mu : \mathbb{R}^d \times \mathbb{R}_+ \to \mathbb{R}$ is called a density (or a first correlation function) of the measure μ if for any $\varphi : \mathbb{R}^d \times \mathbb{R}_+ \to \mathbb{R}$ such that $\varphi \cdot k_\mu \in L^1(\mathbb{R}^d \times \mathbb{R}_+)$ we have: the function $\langle \varphi, \cdot \rangle$ belongs to $L^1(\widehat{\Gamma}, \mu)$ and

$$\int_{\widehat{\Gamma}} \langle \varphi, \widehat{\gamma} \rangle d\mu(\widehat{\gamma}) = \int_{\mathbb{R}^d} \int_{\mathbb{R}_+} \varphi(x, s) k_\mu(x, s) dx ds.$$

In this case, $\langle \varphi, \widehat{\gamma} \rangle$ is well-defined for μ-almost all $\widehat{\gamma} \in \widehat{\Gamma}$.

It is obvious, that for $a \in L^1(\mathbb{R}^d)$ and any probability measure μ on $\widehat{\Gamma}$ with the bounded density k_μ the first term in (1.1) is well-defined for μ-almost all $\widehat{\gamma} \in \widehat{\Gamma}$ and $F \in \mathcal{F}$.

The construction of evolution of states with the generator given by (1.1) is usually related with the construction and properties of evolution of densities and higher-order correlation functions (see e. g. [9] for the case without marks). The aim of the present paper is to study the evolution of the density only. Therefore, we suppose that there exists an evolution of measures given by

$$\frac{d}{dt}\int_{\widehat{\Gamma}} F d\mu_t = \int_{\widehat{\Gamma}} LF d\mu_t, \quad F \in \mathcal{F} \tag{1.2}$$

with initial measure μ_0 at $t = 0$. We assume also that k_t be a density of μ_t. Then, for $F_\varphi(\widehat{\gamma}) := \langle \varphi, \widehat{\gamma} \rangle$, $\varphi \in \mathcal{D}$ we obtain

$$(LF_\varphi)(\widehat{\gamma}) = \sum_{x\in\gamma}\int_{\mathbb{R}^d} a(x-y)b(s_x)\varphi(y,s_x)dy - \sum_{x\in\gamma} d(s_x)\varphi(x,s_x) + \sum_{x\in\gamma}\frac{\partial^2}{\partial s_x^2}\varphi(x,s_x).$$

Therefore,

$$\begin{aligned}\int_{\widehat{\Gamma}}(LF_\varphi)(\widehat{\gamma})d\mu_t(\widehat{\gamma}) = &\int_{\mathbb{R}^d}\int_{\mathbb{R}_+} k_t(x,s)\int_{\mathbb{R}^d} a(x-y)b(s)\varphi(y,s)dydsdx \\ &- \int_{\mathbb{R}^d}\int_{\mathbb{R}_+} k_t(x,s)d(s)\varphi(x,s)dsdx \\ &+ \int_{\mathbb{R}^d}\int_{\mathbb{R}_+} k_t(x,s)\frac{\partial^2}{\partial s^2}\varphi(x,s)dsdx. \end{aligned} \tag{1.3}$$

On the other hand,

$$\frac{d}{dt}\int_{\widehat{\Gamma}} F_\varphi(\widehat{\gamma})d\mu_t(\widehat{\gamma}) = \frac{d}{dt}\int_{\mathbb{R}^d}\int_{\mathbb{R}_+} k_t(x,s)\varphi(x,s)dsdx. \tag{1.4}$$

Since $\varphi \in \mathcal{D}$ is arbitrary, by (1.2), (1.3), (1.4), the densities k_t should satisfy (in a weak sense) the following differential equation

$$\frac{\partial}{\partial t}k_t(x,s) = b(s)\int_{\mathbb{R}^d} a(x-y)k_t(y,s)dy - d(s)k_t(x,s) + \frac{\partial^2}{\partial s^2}k_t(x,s). \tag{1.5}$$

Using the assumption $\int_{\mathbb{R}^d} a(x)dx = 1$ we may rewrite (1.5) as follows

$$\frac{\partial}{\partial t}k_t(x,s) = (\mathsf{A}k_t)(x,s) - (\mathsf{H}k_t)(x,s), \tag{1.6}$$

$$(\mathsf{A}k_t)(x,s) := b(s)\int_{\mathbb{R}^d} a(x-y)\big(k_t(y,s) - k_t(x,s)\big)dy, \tag{1.7}$$

$$(\mathsf{H}k_t)(x,s) := -\frac{\partial^2}{\partial s^2}k_t(x,s) + (d(s) - b(s))k_t(x,s). \tag{1.8}$$

It is worth noting that appearance of effective potential $v(s) = d(s) - b(s)$ is inspired by the evolution mechanism of the spatial microscopic model. The function $v(s)$ has meaning of a fitness function, see e. g. [3]. The typical graphs of $b(s)$ and $d(s)$ motivated by the biological applications are given on the Figures 1 and 2, correspondingly.

In the next sections we will study the classical solution of (1.6)–(1.8) with initial conditions k_0 in different Banach spaces.

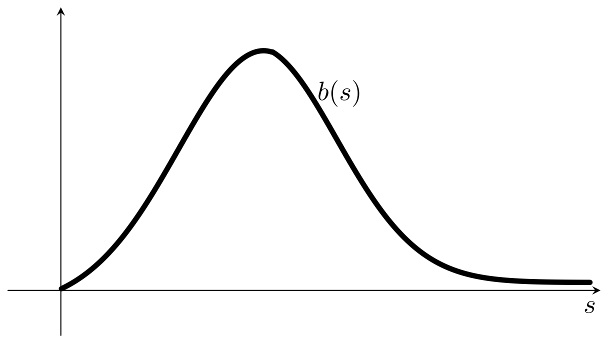

Figure 1: Fast decreasing of $b(s)$ if $s \to \infty$

2 Asymptotic of a spatially uniform density

Let $\mathcal{H} = L^2(\mathbb{R}_+)$ be a real Hilbert space. Let us define the following class of functions

$$X = \left\{ \sum_{i=1}^{n} c_i \psi_i(x) \varphi_i(s) \;\middle|\; c_i \in \mathbb{R},\ \psi_i \in L^\infty(\mathbb{R}^d),\ \varphi_i \in \mathcal{H},\ i = 1, \ldots, n,\ n \in \mathbb{N} \right\}.$$

By $\mathcal{X}$ we denote the closure of X with respect to the norm

$$\|k\|_{\mathcal{X}} := \operatorname{ess\,sup}_{x \in \mathbb{R}^d} \|k(x, \cdot)\|_{\mathcal{H}}.$$

Hence one can naturally embed $\mathcal{H}$ into $\mathcal{X}$ as set of functions which are constants in x. We will use the same notations for function $f \in \mathcal{H}$ as an element of $\mathcal{X}$.

Suppose that there exists $\omega \geq 0$ such that

$$v(s) := d(s) - b(s) \geq -\omega, \quad s \in \mathbb{R}_+. \tag{2.1}$$

Let $C_0^\infty(\mathbb{R}_+)$ consist of all smooth functions f on $\mathbb{R}_+$ with bounded support such that $f(0) = 0$. Then the operator

$$(Hf)(s) := -\frac{d^2 f(s)}{d^2 s} + v(s) f(s)$$

with a domain $C_0^\infty(\mathbb{R}_+)$ is essentially self-adjoint in $\mathcal{H}$ (see e.g. [2]). Let $\big(\bar{H}, \mathrm{Dom}(\bar{H})\big)$ be its self-adjoint closure in $\mathcal{H}$. Let $\mathsf{D} \subset \mathcal{X}$ consist of all functions $k \in \mathcal{X}$ such that, for a.a. $x \in \mathbb{R}^d$, $k(x, \cdot) \in \mathrm{Dom}(\bar{H})$.

Lemma 2.1. *Let* (2.1) *hold and* $b \in L^\infty(\mathbb{R}_+)$. *Then* $(\mathsf{A} - \mathsf{H}, \mathsf{D})$ *is a generator of a* C_0*-semigroup* $S(t)$ *in* $\mathcal{X}$.

Proof. Since v is bounded from below, $(-\bar{H} f, f)_{\mathcal{H}} \leq \omega \|f\|^2_{\mathcal{H}}$ for any $f \in \mathrm{Dom}(\bar{H})$. Therefore, by e.g. [5, Example II.3.27], $\big(-\bar{H}, \mathrm{Dom}(\bar{H})\big)$ is a generator of a C_0-semigroup $T_{\bar{H}}(t)$ in $\mathcal{H}$, and moreover, $\|T_{\bar{H}}(t)\| \leq e^{t\omega}$, $t \geq 0$. Then, by a

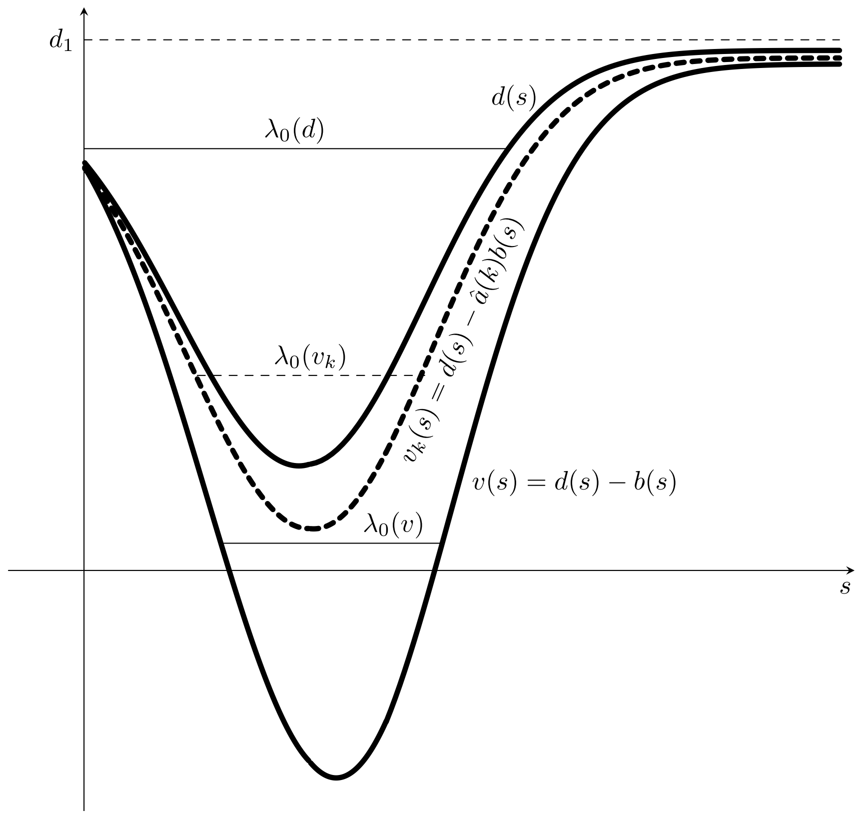

Figure 2: If $s \to \infty$ then either $d(s) \to +\infty$ or $d(s) \to d_1$, $d(s) \le d_1$, $s \in \mathbb{R}_+$ and $d(s_0) < b(s_0)$

version of Hille–Yosida theorem (see e. g. [5, Corollary II.3.6]), for each $\lambda > \omega$, $\lambda \in \rho(-\bar{H})$ and $\|R(\lambda, -\bar{H})\| \le (\lambda - \omega)^{-1}$. Here and below $\rho(B)$ and $R(\lambda, B)$ denotes a resolvent set and a resolvent of a closed operator B, correspondingly. By (1.8) and the properties of $\bar{H}$, it is evident that $(-\mathsf{H}, \mathsf{D})$ is a closed densely defined operator in $\mathcal{X}$. Moreover, $\rho(-\mathsf{H}) = \rho(-\bar{H})$, and, for each $\lambda \in \rho(-\mathsf{H})$,

$$\big(R(\lambda, -\bar{H})k(x, \cdot)\big)(s) = \big(R(\lambda, -\mathsf{H})k\big)(x, s), \quad k \in \mathcal{X}, x \in \mathbb{R}^d, s \in \mathbb{R}_+.$$

As a result,

$$\begin{aligned}\|R(\lambda, -\mathsf{H})k\|_{\mathcal{X}} &= \operatorname{ess\,sup}_{x \in \mathbb{R}^d} \big\| \big(R(\lambda, -\mathsf{H})k\big)(x, \cdot) \big\|_{\mathcal{H}} \\ &= \operatorname{ess\,sup}_{x \in \mathbb{R}^d} \big\| R(\lambda, -\bar{H})k(x, \cdot) \big\|_{\mathcal{H}} \\ &\le (\lambda - \omega)^{-1} \operatorname{ess\,sup}_{x \in \mathbb{R}^d} \|k(x, \cdot)\|_{\mathcal{H}} = (\lambda - \omega)^{-1} \|k\|_{\mathcal{X}}.\end{aligned}$$

Hence, by the version of Hille–Yosida theorem mentioned above, $(-\mathsf{H}, \mathsf{D})$ is a generator of a C_0-semigroup $T_{\mathsf{H}}(t)$ in the space $\mathcal{X}$, and moreover, $\|T_{\mathsf{H}}(t)\| \le e^{t\omega}$,

$t \geq 0$. Next, since $b \in L^\infty(\mathbb{R}_+)$, we have, for any $k \in \mathcal{X}$ and for a.a. $x \in \mathbb{R}^d$,

$$\begin{aligned}
&\|(\mathsf{A}k)(x,\cdot)\|_{\mathcal{H}} \\
&\leq \|b\|_{L^\infty(\mathbb{R}_+)} \biggl(\int_{\mathbb{R}_+} \Bigl(\int_{\mathbb{R}^d} a(x-y)\bigl(k(y,s)-k(x,s)\bigr)dy \Bigr)^2 ds \biggr)^{\frac{1}{2}} \\
&\leq \|b\|_{L^\infty(\mathbb{R}_+)} \biggl(\int_{\mathbb{R}_+} \int_{\mathbb{R}^d} a(x-y)\bigl|k(y,s)-k(x,s)\bigr|^2 dyds \biggr)^{\frac{1}{2}} \\
&\leq \sqrt{2}\,\|b\|_{L^\infty(\mathbb{R}_+)} \biggl(\int_{\mathbb{R}_+} \int_{\mathbb{R}^d} a(x-y)|k(y,s)|^2 dyds + \int_{\mathbb{R}_+} |k(x,s)|^2 ds \biggr)^{\frac{1}{2}} \\
&\leq 2\|b\|_{L^\infty(\mathbb{R}_+)} \Bigl(\operatorname{ess\,sup}_{x\in\mathbb{R}^d} \|k(x,\cdot)\|^2_{\mathcal{H}} \Bigr)^{\frac{1}{2}} \leq 2\|b\|_{L^\infty(\mathbb{R}_+)}\|k\|_{\mathcal{X}}.
\end{aligned}$$

Therefore, A is a bounded operator in $\mathcal{X}$ with $\|\mathsf{A}\| \leq 2\|b\|_{L^\infty(\mathbb{R}_+)}$. Then, by e. g. [5, Theorem III.1.3], the operator $-\mathsf{H}+\mathsf{A}$ with domain D generates a C_0-semigroup $S(t)$ in $\mathcal{X}$. Moreover,

$$\|S(t)\| \leq \exp\{(\omega + 2\|b\|_{L^\infty(\mathbb{R}_+)})t\}, \quad t \geq 0.$$

□

Our goal is to study the asymptotic behavior of $k_t(x,s) = S(t)k_0(x,s)$ as $t \to \infty$. Here $k_0 \in \mathcal{X}$. In the particular case $k_0(s) \in \mathcal{H}$, one can solve this problem in details.

Theorem 2.2. *Let* (2.1) *hold and* $b \in L^\infty(\mathbb{R}_+)$, $b(s) \geq 0$. *Suppose additionally that the operator* $\bar{H}$ *in* $\mathcal{H}$ *has either simple discrete spectrum* $\lambda_0 < \lambda_1 < \ldots < \lambda_n \to \infty$, *as* $n \to \infty$, *or continuous spectrum* $[\lambda, +\infty)$ *and a finite number of simple eigenvalues* $\lambda_0 < \lambda_1 < \ldots < \lambda_n < \lambda$. *Consider the initial condition given by* $k_0(x,s) = \varrho_0(s)$, *for a.a.* $x \in \mathbb{R}^d$, $s \in \mathbb{R}_+$, *where* $\varrho_0 \in \mathcal{H}$. *Then*

$$\bigl\|S(t)k_0(s) - e^{-t\lambda_0}c_0\psi_0(s)\bigr\|_{\mathcal{X}} = O\bigl(e^{-t\lambda_1}\bigr), \quad t \to \infty, \tag{2.2}$$

where $\psi_0(s)$ *is the eigenfunction of the operator* $\bar{H}$ *corresponding to the eigenvalue* λ_0, $c_0 = (\varrho_0, \psi_0)_{\mathcal{H}}$, *and* $\lambda_1 > \lambda_0$.

Proof. By the proof of Lemma 2.1, the operator $(-\mathsf{H}, \mathsf{D})$ is a generator of a C_0-semigroup $T_{\mathsf{H}}(t)$ in $\mathcal{X}$ and A is a bounded operator in $\mathcal{X}$. Then, by the Trotter formula (see e. g. [5, Exersise III.5.11]), we have

$$S(t)k_0 = \lim_{n\to\infty} \Bigl(T_{\mathsf{H}}\Bigl(\frac{t}{n}\Bigr) e^{\frac{t}{n}\mathsf{A}} \Bigr)^n k_0,$$

where the limit is considered in the sense of norm in $\mathcal{X}$. Note that for any $f \in \mathcal{H} \subset \mathcal{X}$, $\mathsf{A}f = 0$, therefore, $e^{t\mathsf{A}}f = f$ for all $t > 0$. Since k_0 does not depend on x, we have that $T_{\mathsf{H}}\bigl(\frac{t}{n}\bigr)e^{\frac{t}{n}\mathsf{A}}k_0 = T_{\mathsf{H}}\bigl(\frac{t}{n}\bigr)k_0$, and the latter function does not depend on x also. As a result,

$$S(t)k_0 = T_{\mathsf{H}}(t)k_0 = T_{\bar{H}}(t)\varrho_0.$$

Therefore, it is enough to show that

$$\|T_{\bar{H}}(t)\varrho_0 - e^{-t\lambda_0}c_0\psi_0\|_{\mathcal{H}} = O\big(e^{-t\lambda_1}\big), \quad \lambda_1 > \lambda_0, \quad t \to \infty.$$

The latter asymptotic follows from the general spectral theory of self-adjoint operators, see e. g. [11]. Using spectral decomposition of the self-adjoint operator $\bar{H}$ in the Hilbert space $\mathcal{H}$, we get

$$T_{\bar{H}}(t)\varrho_0 = \int_{\sigma(\bar{H})} e^{-tu} dE_{\bar{H}}(u)\varrho_0,$$

where $E_{\bar{H}}$ is the spectral measure of $\bar{H}$ and the integral is taken over the spectrum of $\bar{H}$. Then,

$$\|T_{\bar{H}}(t)\varrho_0 - e^{-t\lambda_0}c_0\psi_0\|^2_{\mathcal{H}} \le e^{-2t\lambda_1}\|P_{\mathcal{H}'}\varrho_0\|^2_{\mathcal{H}} = O(e^{-2t\lambda_1}),$$

where $P_{\mathcal{H}'}$ is the projection on $\mathcal{H}' := \mathcal{H} \ominus \{\psi_0\}$. (Note that λ_1 may be equal to λ.) The statement is proved. □

Remark 2.3. Asymptotic formula (2.2) describes, in particular, an asymptotical shape of the density. Assume that the initial density has the form $k_0(s,x) = \varrho(s)$, $x \in \mathbb{R}^d$, $\varrho \in \mathcal{H}$, which is uniform over the space $\mathbb{R}^d$ but dependent on mark s, where the dependence is defined by an arbitrary function $\varrho(s) \in \mathcal{H}$. Then on a large-time scale (when t is large enough) we get a density $k_t(s,x)$, which is again uniform over the space: $k_t(s,x) = \varrho_t(s)$, and function $\varrho_t(s)$ specifying the mark dependence in the density $k_t(s,x)$ has now a definite shape. It is shaped like the first eigenfunction $\psi_0(s)$ of the operator H. That means that an optimal range of mark values appears under the long-time evolution.

Remark 2.4. Consider the basic Schrödinger operator in $L^2(\mathbb{R}_+)$ with absorption boundary condition:

$$Hf = -\frac{d^2 f}{ds^2} + v \cdot f, \quad v \ge -\omega, \quad f(0) = 0. \tag{2.3}$$

Then the behavior of the populations in whole depends on the sign of the minimal eigenvalue λ_0 of the operator H: if $\lambda_0 > 0$, then populations are vanishing, if $\lambda_0 < 0$, then populations are increasing. The case $\lambda_0 = 0$ ("equilibrium" regime) is of particular interest. As follows from the well-known facts on spectrum of one-dimensional Schrödinger operator, see e. g. [2], the sign of λ_0 depends on the shape of the function $v(s) = d(s) - b(s)$. Let us distinguish two interesting cases.

1. Let $v(s) \to +\infty$, $s \to +\infty$, that means that $d(s) \to +\infty$; in this case the spectrum of $\bar{H}$ is discrete and simple; moreover, if $v(s) \ge 0$ then $\lambda_0 > 0$;

2. in the case $d(s) \le d_1$, $s \in \mathbb{R}_+$ and $d(s) \to d_1 > 0$, $b(s) \to 0$, $s \to \infty$ the spectrum has a continuous component $[d_1, +\infty)$ and possibly a discrete set of simple eigenvalues which are smaller than d_1. A simple sufficient condition for the existence of the ground state in this case has the following form: one can insert rectangle with the sites $h, l > 0$ such that $\sqrt{h}l > \pi/2$ between level d_1 and graph of $v(s)$ (see Figure 3).

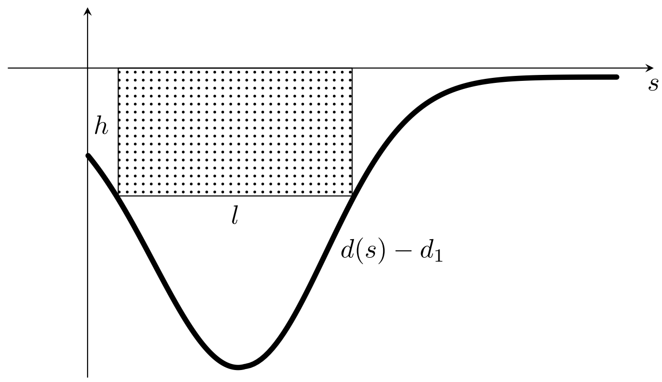

Figure 3: Sufficient condition for the existence of a ground state when $d(s) \leq d_1$, $d(s) \to d_1$, $b(s) \to 0$ as $s \to \infty$

Remark 2.5. The behavior of the populations in whole depends on the sign of the minimal eigenvalue λ_0 of the operator H: if $\lambda_0 > 0$, then populations are vanishing, if $\lambda_0 < 0$, then populations are increasing in the following sense. Denote by $n(D) = |\widehat{\gamma} \cap D|$ a random variable equal to the number of particles from the configuration lying inside of the finite volume $D = D_x \times D_s,\ D_x \subset \mathbb{R}^d,\ D_s \subset \mathbb{R}_+$. Then

$$n(D) = \sum_{\widehat{x} \in \widehat{\gamma}} \chi_D(\widehat{x}) = \langle \chi_D, \widehat{\gamma} \rangle,$$

where χ_D is the characteristic function of D. The asymptotic formula (2.2) immediately implies the following asymptotic for the average of $n(D)$ as $t \to \infty$:

$$\begin{aligned} \mathbb{E}_t n(D) = \int_{\widehat{\Gamma}} \langle \chi_D,\ \widehat{\gamma} \rangle \ d\mu_t(\widehat{\gamma}) &= \int_{\mathbb{R}^d} \int_{\mathbb{R}_+} \chi_D(x,s) k_t(x,s) dx ds \\ &= \ e^{-t\lambda_0} c_0 |D_x| \int_{D_s} \psi_0(s) ds \ (1 + o(1)) \end{aligned}$$

3 Asymptotic of a spatially local density

In this section we consider the long time behavior of the density $k_t(s,x)$ assuming that $k_t(s,x) \in L^2(\mathbb{R}_+, \mathbb{R}^d)$. Thus, we consider the Cauchy problem:

$$\frac{\partial \psi}{\partial t} = \mathcal{L}\psi, \quad \psi = \psi_t(s,x), \quad s \in \mathbb{R}_+,\ x \in \mathbb{R}^d,\ t \geq 0, \tag{3.1}$$

$$(\mathcal{L}\psi)(s,x) = \frac{\partial^2 \psi(s,x)}{\partial s^2} - v(s)\psi(s,x) b(s) \int_{\mathbb{R}^d} a(x-y)(\psi(s,y) - \psi(s,x)) dy,$$

$$\psi_0(s,x) \geq 0, \quad \psi_0 \in C_0(\mathbb{R}_+, \mathbb{R}^d),$$

$$\psi_t(0,x) = 0 \text{ (absorption boundary condition (ABC))}.$$

Here $a(x-y)$ and $v(s) = d(s) - b(s)$ are the same functions as in the preceding section.

Theorem 3.1. *Let us assume that operator H (2.3) has ground state λ_0, and additionally that*

$$a(z) \sim \frac{c_0}{|z|^{d+\alpha}}, \quad 0 < \alpha \le 2, \quad as \quad z \to \infty.$$

Then the solution of the parabolic problem (3.1) has the following asymptotic as $t \to \infty$:

$$\psi_t(s,x) = \frac{e^{-t\lambda_0}}{t^{d/\alpha}} C_d(\alpha) \ (\psi_0(s), \widehat{u}_0(s,0)) \ \psi_0(s) \ p_\alpha\Big(\frac{x}{(\tilde{c}_0 t)^{1/\alpha}}\Big)(1+o(1)), \tag{3.2}$$

where $\psi_0(s)$ is the eigenfunction of the operator H corresponding to the eigenvalue λ_0, $C_d(\alpha), \tilde{c}_0$ are positive constants depending on functions $b(s), a(x-y)$; $p_\alpha(\cdot)$ is a density of a d-dimensional symmetric α-stable distribution.

Note that for smaller $0 < \alpha \le 2$ the pre-exponential term is decreasing faster.

Remark 3.2. In the case when $|x| \ll t^{1/\alpha}$, the asymptotic of (3.2) can be written as follows:

$$\psi_t(s,x) = C_d(\alpha) \ V(\alpha) \frac{e^{-t\lambda_0}}{t^{d/\alpha}} \psi_0(s)(\psi_0(s), \widehat{u}_0(s,0))(1+o(1)), \tag{3.3}$$

where $V(\alpha) = \frac{1}{(2\pi)^d} \int_{\mathbb{R}^d} e^{-|q|^\alpha} dq$.

Proof. Since the operator

$$(B\psi)(s,x) = b(s) \int_{\mathbb{R}^d} a(x-y)(\psi(s,y) - \psi(s,x))dy$$

is bounded and self-adjoint in $L^2(\mathbb{R}_+, \mathbb{R}^d)$ as well as the operator H is essentially self-adjoint in $L^2(\mathbb{R}_+)$, we conclude that the operator $\mathcal{L}$ is self-adjoint and bounded from above in $L^2(\mathbb{R}_+, \mathbb{R}^d)$. Consequently, the operator $\mathcal{L}$ generates a C_0-semigroup in $L^2(\mathbb{R}_+, \mathbb{R}^d)$: $\psi_t(s,x) = e^{t\mathcal{L}}\psi_0(s,x)$.

We will construct now the spectral representation of $\mathcal{L}$ as the direct integral of 1-D Schrödinger operators H_k, $k \in \widehat{\mathbb{R}}^d$ using the Fourier transform over $x \in \mathbb{R}^d$. Consider $\psi(s,x) \in L^2(\mathbb{R}_+, \mathbb{R}^d)$ and present it using the Fourier duality in the form

$$\psi(s,x) = \frac{1}{(2\pi)^d} \int_{\widehat{\mathbb{R}}^d} e^{-i(k,x)} \widehat{\psi}(s,k) dk$$

Then the operator $\widehat{\mathcal{L}}$ in $L^2(\mathbb{R}_+ \times \widehat{\mathbb{R}}^d)$ has the following form

$$(\widehat{\mathcal{L}}\widehat{\psi})(s,k) = \frac{\partial^2 \widehat{\psi}(s,k)}{\partial s^2} - v(s)\widehat{\psi}(s,k) - b(s)(1-\widehat{a}(k))\widehat{\psi}(s,k), \qquad \widehat{\psi}(0,k) = 0.$$

Here

$$\widehat{a}(k) = \int_{\mathbb{R}^d} e^{i(k,z)} a(z) dz,$$

and $\widehat{a}(0) = \int_{\mathbb{R}^d} a(z)dz = 1$ by the normalization condition.

Let us introduce for each $k \in \widehat{\mathbb{R}}^d$ the Schrödinger operator $H_k := H + B_k$ where the operators H and B_k act in $L^2(\mathbb{R}_+)$ as follow

$$H\psi(s) := -\frac{d^2\psi}{ds^2} + v(s)\psi(s),$$
$$B_k\psi(s) := \ b(s)(1 - \widehat{a}(k))\psi(s),$$
$$\psi(0) = 0, \quad \psi \in C_0(\mathbb{R}_+).$$

One can rewrite

$$H_k\psi(s) = -\frac{d^2\psi(s)}{ds^2} + v_k(s)\psi(s),$$

where

$$v_k(s) := v(s) + b(s)(1 - \widehat{a}(k)) = d(s) - b(s)\widehat{a}(k).$$

It is worth noting that

$$\widehat{a}(k) < \widehat{a}(0) = \int_{\mathbb{R}^d} a(z)dz = 1, \ k \in \widehat{\mathbb{R}}^d \setminus \{0\}, \quad \widehat{a}(k) \to 0, \ |k| \to \infty, \tag{3.4}$$

and our assumption

$$a(z) \sim \frac{c_0}{|z|^{d+\alpha}}, \quad 0 < \alpha \le 2, \quad \text{as} \quad z \to \infty$$

implies that

$$\widehat{a}(k) = \int_{\mathbb{R}^d} e^{i(k,z)} a(z)dz = 1 - c_0|k|^\alpha + o(|k|^\alpha), \quad c_0 > 0, \quad 0 < \alpha \le 2, \quad |k| \to 0.$$

Each of the operators H_k is essentially self-adjoint operator in $L^2(\mathbb{R}_+)$, and for small enough k, $|k| \le \delta$, has a simple ground state $\psi_k(s) > 0$ analytically depending on the perturbation operator B_k which is a bounded operator in $L^2(\mathbb{R}_+)$. The corresponding eigenvalue λ_k is strictly greater than λ_0, since $b(s)(1 - \widehat{a}(k)) \ge 0$. In this situation one can use the standard Schrödinger perturbation theory, see e. g. [10], for the simple eigenvalue of the perturbed operator $H_k = H + B_k$. Then in the case when k is small enough: $|k| \le \delta$, the lowest eigenvalue λ_k of H_k and the corresponding eigenfunction $\psi_k(s)$ have the following representations:

$$\lambda_k = \lambda_0 + (B_k\psi_0, \psi_0) + O(||B_k||^2) \ = \ \lambda_0 + (1 - \widehat{a}(k))(b\psi_0, \psi_0) + o(|k|^\alpha), \tag{3.5}$$

and

$$\psi_k(s) = \psi_0(s) + (H - \lambda_0)^{-1}((B_k\psi_0, \psi_0)\psi_0 - B_k\psi_0) + o(|k|^\alpha), \tag{3.6}$$

where ψ_0 is the normalized eigenfunction of the operator H: $(\psi_0, \psi_0) = 1$, and the operator $(H - \lambda_0)^{-1}$ is bounded in the invariant subspace $\psi_0^\perp = L^2(\mathbb{R}_+) \ominus \{\psi_0\}$.

Consider the parabolic problem associated with operator $-H_k$ in $L^2(\mathbb{R}_+)$:

$$\frac{\partial \widehat{\psi}}{\partial t} = -H_k \widehat{\psi} = \frac{\partial^2 \widehat{\psi}}{\partial s^2} - (v(s) + b(s)(1 - \widehat{a}(k)))\widehat{\psi},$$
$$\widehat{\psi} = \widehat{\psi}_t(s,k), \ s \in \mathbb{R}_+, \ k \in \widehat{\mathbb{R}}^d,$$
$$\widehat{\psi}_0(s,k) = \widehat{u}_0(s,k) \in \ L^2(\mathbb{R}_+), \ k \in \widehat{\mathbb{R}}^d.$$

Using the spectral decomposition for $\widehat{\psi}_t(s,k)$:

$$\widehat{\psi}_t(s,k) = e^{-tH_k}\widehat{u}_0(s,k) = \int_{\sigma(H_k)} e^{-tw} dE_{H_k}(w)\widehat{u}_0(s,k)$$

we get:

1. from the continuity arguments and condition (3.4) that for any $\varepsilon > 0$ one can find $\delta = \delta(\varepsilon) > 0$ such that when $|k| \ge \delta$:

$$\|\widehat{\psi}_t(s,k)\|_{L^2(\mathbb{R}_+)} \ \le \ e^{-t(\lambda_0+\varepsilon)}\|\widehat{u}_0(s,k)\|_{L^2(\mathbb{R}_+)},$$

2. if $|k| \le \delta$, then

$$\widehat{\psi}_t(s,k) = e^{-t\lambda_k}\psi_k(s)(\psi_k(s), \widehat{u}_0(s,k)) \ + \ \widehat{\phi}_t(s,k),$$

where

$$\|\widehat{\phi}_t(s,k)\|_{L^2(\mathbb{R}_+)} \ \le \ e^{-t(\lambda_0+\varepsilon)}\|\widehat{u}_0(s,k)\|_{L^2(\mathbb{R}_+)}.$$

This implies

$$\begin{aligned} \psi_t(s,x) &= \frac{1}{(2\pi)^d}\int_{\widehat{\mathbb{R}}^d} e^{-i(k,x)}\widehat{\psi}_t(s,k)dk \\ &= \frac{1}{(2\pi)^d}\int_{\{|k|\le\delta\}} e^{-i(k,x)}e^{-\lambda_k t}\psi_k(s)(\psi_k(s), \widehat{u}_0(s,k))dk \\ &\quad + \frac{1}{(2\pi)^d}\int_{\{|k|\le\delta\}} e^{-i(k,x)}\widehat{\phi}_t(s,k)dk + \frac{1}{(2\pi)^d}\int_{\{|k|\ge\delta\}} e^{-i(k,x)}\widehat{\psi}_t(s,k)dk \\ &= \frac{1}{(2\pi)^d}\int_{\{|k|\le\delta\}} e^{-i(k,x)-\lambda_k t}\psi_k(s)(\psi_k(s), \widehat{u}_0(s,k))dk + \Psi_\varepsilon(t,s,x), \end{aligned} \tag{3.7}$$

with

$$\|\Psi_\varepsilon(t,s,x)\|_{L^2(\mathbb{R}_+,\mathbb{R}^d)} \ \le \ e^{-t(\lambda_0+\varepsilon)}\|u_0(s,x)\|_{L^2(\mathbb{R}_+,\mathbb{R}^d)}.$$

Finally we will find the asymptotic of the integral in (3.7). Using decompositions (3.5)–(3.6) and after the change of variables $q = k(t\tilde{c}_0)^{1/\alpha}$ the integral in (3.7) can be written as follows

$$\frac{e^{-\lambda_0 t}}{(2\pi)^d}\int_{\{|k|\le\delta\}} e^{-i(k,x)}e^{-\tilde{c}_0|k|^\alpha t}\psi_0(s)(\psi_0(s),\widehat{u}_0(s,0))dk\ \left(1+O\left(\frac{1}{t^{1/\alpha}}\right)\right)$$

$$=\frac{e^{-\lambda_0 t}}{t^{d/\alpha}}\frac{C_d(\alpha)}{(2\pi)^d}\ \psi_0(s)(\psi_0(s),\widehat{u}_0(s,0))$$

$$\times\int_{\mathbb{R}^d} e^{-i\left(q,\frac{x}{(\tilde{c}_0 t)^{1/\alpha}}\right)-|q|^\alpha}dq\ \left(1+O\left(\frac{1}{t^{1/\alpha}}\right)\right), \tag{3.8}$$

where the integral in (3.8)

$$\frac{1}{(2\pi)^d}\int_{\mathbb{R}^d} e^{-i\left(q,\frac{x}{(\tilde{c}_0 t)^{1/\alpha}}\right)-|q|^\alpha}dq = p_\alpha\left(\frac{x}{(\tilde{c}_0 t)^{1/\alpha}}\right)$$

represents a density of a d-dimensional symmetric α-stable distribution, see e. g. [6], and it is an integer function of $\frac{x}{t^{1/\alpha}}$.

Note that $\psi_0(s)>0,\ s\in(0,\infty)$ and $\widehat{u}_0(s,k)>0$ for small enough k (due to positivity of $u_0(s,x)$).

Theorem is proved. □

References

[1] Baake E. and Gabriel W., Biological evolution through mutation, selection and drift: an introduction review, *Ann. Rev. Comp. Phys.* VII, 203–264 (2000).

[2] Berezin F.A. and Shubin M.A., *The Schrödinger equation*, (Moscow State University Publ., 1983) (Russian), (Kluwer, 1991) (English).

[3] Burger R., *The mathematical theory of selection, recombination and mutation*, (NY: Wiley, 2000).

[4] Crow J.F. and Kimura M., The theory of genetic loads, *In:* Proc. XI Int. Congr. Genetics, vol.2, 495–505, (Oxford: Pergamon Press, 1964).

[5] Engel K.-J. and Nagel R., *One-parameter semigroups for linear evolution equations*, vol. 194 of *Graduate Texts in Mathematics*, (Springer-Verlag, 2000).

[6] Feller W., *An introduction to probability theory and its applications*, vol. II, (John Wiley & Sons, Inc., New York–London–Sydney, 1966).

[7] Kallenberg O., *Random Measures*, 4th edition, (Academic Press; Akademie-Verlag, Berlin 1986).

[8] Kimura M., A stochastic model concerning the maintenance of genetic variability in quantitative characters, *Proc. Natl. Acad. Sci. USA* **54**, 731–736 (1965).

[9] Kondratiev Y., Kutoviy O., and Pirogov S., Correlation functions and invariant measures in continuous contact model. *Infin. Dimens. Anal. Quantum Probab. Relat. Top.* **11**(2), 231–258 (2008).

[10] Reed M. and Simon B., *Methods of Modern Mathematical Physics*, Vol. 4: Analysis of Operators. Academic Press, 1978.

[11] Riesz F. and Szökefalvi-Nagy B., *Functional Analysis*, (NY: Dover 1990).