Asymptotics of steady states of a selection–mutation equation for small mutation rate

Àngel Calsina and Sílvia Cuadrado

Departament de Matemàtiques, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain (acalsina@mat.uab.cat; silvia@mat.uab.cat)

Laurent Desvillettes

CMLA, ENS Cachan, IUF and CNRS, PRES UniverSud, 61 Avenue du President Wilson, 94235 Cachan Cedex, France (desville@cmla.ens-cachan.fr)

Gaël Raoul

Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France (raoul@cefe.cnrs.fr)

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We consider a selection-mutation equation for the density of individuals with respect to a continuous phenotypic evolutionary trait. We assume that the competition term for an individual with a given trait depends on the traits of all the other individuals, therefore giving an infinite-dimensional nonlinearity. Mutations are modelled by means of an integral operator. We prove existence of steady states and show that, when the mutation rate goes to zero, the asymptotic profile of the population is a Cauchy distribution.

1. Introduction

In this paper we consider a selection–mutation equation for the density of individuals of a biological population with respect to a continuous one-dimensional phenotypic evolutionary trait x, belonging to a bounded interval X of \mathbb{R} (for studies on multi-dimensional phenotypic traits see [42,43]). Selection–mutation equations in the continuous framework were introduced in [14, 25] in order to explain the maintenance of variability in a continuum of alleles. The balance of selection and mutation generates a phenotypic diversity within a species, which improves the ability of this species to adapt to a change of the environment (see, in particular, the problem of evolutionary rescue [2]), but decreases its fitness (cf. the notion of mutation load and its application to lethal mutagenesis [4,24]). Unfortunately, it is difficult to experimentally measure this diversity (on organisms such as viruses or bacteria), which legitimates its theoretical study.

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Selection-mutation equations have been previously studied in [25] under the simplifying assumption that mutations have a small effect. (The mutation can then be modelled by a diffusion. This is the Gaussian allelic approximation; see [5, 12, 25], and see, for example, [10, 25, 28, 31, 36] for applications). In this case the population has a Gaussian profile in a suitable limit. The assumption that mutations have a small effect is, however, not accurate for many species of virus or bacterium, as shown, for example, by the recent experimental results of Bell and Gonzalez [2]. Removing the assumption that mutations have a small effect (see [5, 12], and see [6, 13, 19, 32, 35, 37] for applications) can affect the profile of the population in a selection-mutation equilibrium, as shown by the so-called house-of-cards approximation (see [5, 7, 26, 38, 39]). The house-of-cards model assumes that the probability distribution of a mutant's trait is independent of its parent's trait. In that case, under some additional assumptions (in particular, the environmental feedback must be one dimensional; we comment on this below), the population profile can be explicitly found, and it is generically a Cauchy profile once a scaling imposing a small number of mutations has been performed. The house-of-cards model is a particular case of a more general model (see [7,38]) where mutations are modelled with a mutation kernel (see assumption 4.5). It is then natural to wonder whether the result found in the case of the house-of-cards model remains qualitatively true for the general model. The effect of such general mutation kernels has been studied numerically in [40, 41], and an explicit computation of the selectionmutation equilibrium for a very special mutation kernel is presented in [41]. In [7], for a general mutation kernel and independently of the fitness function, a general formula for the first-order approximation of the equilibrium mean fitness is given. Moreover, assuming that the fitness function has a unique maximum point, it is shown that the mutation load is equal (to first order) to the mutation rate. For special fitness functions and mutation kernels, higher-order approximations of the mutation load are obtained.

An important feature in most previous works (about mutation-selection equilibria) is that the feedback variable (also called the environment; see, for example, [30]) is finite-dimensional, so the equations become linear when a finite number of quantities are considered as given. This is what happens, for example, when individuals compete for a given number of different nutrients (see, for example, [11, 19]). More precisely, this means that these equations can be written in the form $f_t = A(E(f))f$, where f denotes the density of individuals with respect to the evolutionary trait, f_t is its time derivative, E is a (usually linear) function from the state space to a finite-dimensional space and A(E) is a linear operator on the state space. The problem of looking for steady states is then equivalent to finding positive eigenfunctions corresponding to the zero eigenvalue of the linear operator plus solving a fixed-point problem in a finite-dimensional space (this fixed-point problem is nonlinear because of the nonlinear dependence of the operator A(E) with respect to E; see [8,9,15]). However, in many applications, the environment is not finite dimensional (see, for example, [31, 36, 37]). We thus consider in the present paper the more general case where the competitive stress that an individual of a given trait feels (undergoes) is the sum of the individual competitions caused by all the other individuals (as in, for example, [3, 16, 20, 33], typically in such a way that those competitions are stronger when individuals have closer traits.

In this paper, we assume (see §4) that the mutation rate for the phenotype we consider is small. The mutation rate depends on the individual considered (viruses often have higher mutation rates than cells, for instance). Moreover, this mutation rate can be increased by UV light or drugs (see [4]). The typical mutation rate is estimated to be of the order of 10^{-5} per generation for a single locus (see, for example, [27]). For a given phenotype, which usually depends on many genes, the mutation rate is larger, but still small (of the order of 10^{-2} ; see [1]). The assumption that mutations are rare has been widely used in evolutionary biology, either explicitly (as in the theory of adaptive dynamics [18,29], or for pure selection models [17,19,33]), or implicitly by simplifying the fitness landscape to a parabola or a Gaussian function (see, for example, [25,39]).

In $\S 2$, we introduce the model and some notation that will be useful throughout the paper.

In $\S 3$, using Schauder's fixed-point theorem, we show (under reasonable technical assumptions on the coefficients) that the model admits a non-trivial steady state if (and only if) the per capita growth rate is positive for some value of the trait when the population is small.

Section 4 is devoted to an asymptotic analysis of the shape of steady populations, when the mutation rate tends to zero. As in [8,9,15], we consider cases where the monomorphic population $f = \delta_0$ would be globally stable in the corresponding pure selection model, and we study what happens when the mutation rate ε is small, but not zero. In order to do so, we perform a rescaling and we obtain that the steady states are asymptotically close, when the mutation rate goes to zero, to a Cauchy distribution

$$f^{\varepsilon}(x) \sim \frac{1/\varepsilon}{C_1 + C_2(x/\varepsilon)^2},\tag{1.1}$$

where the evolutionary trait x is one dimensional and belongs to a bounded interval and C_1 , C_2 are constants that can be computed explicitly.

2. The model

We consider the selection-mutation model

$$\partial_t f(t,x) = \left((1-\mu)b(x) - d_0(x) - \int_X d(x,y)f(t,y) \, \mathrm{d}y \right) f(t,x) + \mu \int_X b(y)\beta(x,y)f(t,y) \, \mathrm{d}y,$$

$$f(0,x) = f_0(x),$$
(2.1)

for a population described by its density f(t, x) of individuals, which at time t have an (abstract) phenotypic trait $x \in X$, X being a bounded interval of \mathbb{R} such that $0 \in \text{Int } X$ (the results of this paper could be generalized to an infinite phenotypic trait space, e.g. $X = \mathbb{R}$, with some additional assumptions on the behaviour of the coefficients at ∞).

In (2.1), b(x) denotes the birth rate of individuals of trait x, and $d_0(x)$ denotes their death rate in the absence of competition. For simplicity, we assume that the competition only increases the death rate of the population. We model the increase of the death rate of individuals of trait x due to cohabitation with an individual of trait y by a competition kernel d(x, y). Typically we think of a function $d(x, y) = \tilde{d}(|x - y|)$ such that the function \tilde{d} is bounded from below by a strictly positive constant (meaning that any individual competes with all individuals in the population) and having a maximum at zero (meaning that the maximum competition occurs between identical individuals). However we will make a weaker hypothesis on d (see assumption 4.3 in § 4).

Finally, the parameter $\mu \in [0, 1]$ stands for the probability of mutation in a given reproduction. If an individual of trait y gives birth to a mutant, we denote by $x \mapsto \beta(x, y)$ the probability distribution of the offspring's trait. Hence,

$$(1-\mu)b(x)f(t,x)$$

represents the newborns per unit of time due to faithful reproduction and

$$\mu \int_X b(y)\beta(x,y)f(t,y)\,\mathrm{d} y$$

the newborns that mutated.

To simplify notation in the proofs, from now on we denote by $\mu m(x, y)$ the rate of mutants of trait x produced by a genitor of trait y, where

$$m(x,y) := b(y)\beta(x,y),$$

and by a_{μ} the intrinsic growth rate:

$$a_{\mu}(x) := (1 - \mu)b(x) - d_0(x).$$

We also define the fitness of an individual of trait x when the environment is determined by a population $f(t, \cdot)$ as

$$s[f(t,\cdot)](x) = a_{\mu}(x) - \int_X d(x,y)f(t,y)\,\mathrm{d}y.$$

3. Existence of steady states

This section is devoted to proving existence of steady states of (2.1). We introduce the notation

$$d \,\tilde{\ast}\, f(x) := \int_{y \in X} d(x, y) f(y) \,\mathrm{d} y$$

and use a similar notation for the mutation kernel m. To avoid cases where the population concentrates on the boundary, we make the following assumption.

ASSUMPTION 3.1. For any $f \in L^1_+(X)$ such that

$$-\max s[f] = \min(d \,\tilde{\ast} \, f - (1-\mu)b + d_0) \leqslant 1,$$

the maximum of $s[f] = (1 - \mu)b - d_0 - d\tilde{*}f$ is reached in the interior of X.

REMARK 3.2. We do not consider in this paper the case where the maximum of the fitness is on an edge of X, as it would involve different mathematical techniques. Note that this situation is indeed interesting. It appears in some models, in particular if the phenotypic trait that is considered is the growth rate of the population without competition (see, for example, [23, 34]).

Assumption 3.1 has a simple biological meaning: for any population, the trait that maximizes the fitness is an interior point of the trait space. That trait is then a critical point of the fitness function, which will play an important role in the proof of theorem 3.5.

However, it may be difficult to check whether this assumption is satisfied for a given model. In the remark below, we provide some conditions that are easier to check, and that imply assumption 3.1. The first condition given below, for instance, is satisfied by the models studied in [5] (for any mutation kernel), as soon as the fitness without competition has a maximum in the interior of X.

REMARK 3.3. Note that $-\max s[f] = \min(d \,\tilde{*} \, f - (1-\mu)b + d_0) \leqslant 1$ implies that

$$||f||_{L^1} \leq \frac{\max((1-\mu)b - d_0) + 1}{\min d}$$

Assumption 3.1 is then satisfied if one of the following two conditions is satisfied.

(i) There exists $\bar{x} \in \text{Int } X$ such that

$$(1-\mu)b(\bar{x}) - d_0(\bar{x}) = \max((1-\mu)b - d_0)$$

and, for any $x \in \partial X$,

(1

$$= -\mu)b(x) - d_0(x) \\ \leq \max((1-\mu)b - d_0) - (\|d\|_{\infty} - \min d) \frac{\max((1-\mu)b - d_0) + 1}{\min d}.$$

Indeed, this implies that, for $x \in \partial X$,

$$s[f](x) - s[f](\bar{x}) \leq ||d||_{\infty} ||f||_{L^{1}} - \max((1-\mu)b - d_{0}) - \min d||f||_{L^{1}} + ((1-\mu)b - d_{0})(x) \leq 0.$$

Then, $s[f](\bar{x}) \ge s[f](x)$, and the maximum of s[f](x) is necessarily reached in the interior of X.

(ii) Let $X = [x_1, x_2]$ and assume that

$$(1-\mu)b'(x_1) - d'_0(x_1) - \|\partial_1 d\|_{\infty} \frac{\max((1-\mu)b - d_0) + 1}{\min d} \ge 0,$$

$$(1-\mu)b'(x_2) - d'_0(x_2) + \|\partial_1 d\|_{\infty} \frac{\max((1-\mu)b - d_0) + 1}{\min d} \le 0.$$

This implies that

$$\frac{\mathrm{d}}{\mathrm{d}x}s[f](x_1) > 0 > \frac{\mathrm{d}}{\mathrm{d}x}s[f](x_2)$$

and the maximum of s[f] is then reached in the interior of X.

In order to prove the theorem of existence of steady states, we first prove the following technical lemma.

LEMMA 3.4. Let $C_1, C_2, C_3, C_4, C_5, C_6 > 0$. If $\delta > 0$ is small enough, then there exists $\hat{\alpha} > 0$ such that

$$\hat{\alpha} \leqslant \frac{(1-\delta)C_1}{C_2 + C_3(C_4 + C_5\delta/\hat{\alpha})} - C_6\delta.$$
 (3.1)

Proof. $\hat{\alpha}$ satisfies (3.1) if and only if

$$0 \ge \hat{\alpha}((C_2 + C_3C_4)\hat{\alpha} - C_1) + \delta((C_1 + C_3C_5)\hat{\alpha} + C_6(C_2\hat{\alpha} + C_3(C_4\hat{\alpha} + C_5\delta))),$$

which is satisfied (for instance) by $\hat{\alpha} = C_1/2(C_2 + C_3C_4) > 0$, if $\delta > 0$ is small enough.

The following theorem shows that (2.1) has at least one steady state, under some conditions.

THEOREM 3.5. Let $\mu \in (0,1)$, $b, d_0 \in W^{2,\infty}(X)$, $d \in W^{2,\infty}(X \times X)$, $\beta \in W^{1,\infty}(X \times X)$ such that $\min d > 0$, $\min \beta > 0$, $\min b > 0$ and such that $\max((1-\mu)b-d_0) > 0$. Under assumption 3.1 there exists a non-trivial (i.e. non-zero everywhere) steady state $\bar{f} \in W^{1,\infty}(X)$ of (2.1). Moreover, if (for some $k \in \mathbb{N}$) $b, d_0 \in W^{k,\infty}(X)$ and $d, \beta \in W^{k,\infty}(X \times X)$, then $\bar{f} \in W^{k,\infty}(X)$.

Proof. Let $\delta > 0$. We define

$$F(f) := (1 - \delta)f + \delta \frac{\mu m \,\tilde{\ast} f}{-s[f]}$$

and (for $\bar{\alpha} > 0$, $\bar{A} > 0$, $\gamma > 0$ to be chosen later) the sets

$$\mathcal{F} := \{ f \in L^1_+; \ \alpha(f) \ge \bar{\alpha}, \ \|f\|_{L^1} \le \bar{\Lambda} \}$$

where $\alpha(f) := \min\{-s[f]\}, \text{ and }$

$$\mathcal{G} := \mathcal{F} \cap \{ g \in W^{1,\infty}(X); \ \|g'\|_{\infty} \leqslant \gamma \}.$$

We note that \mathcal{G} is a convex, bounded and closed set in $(C(X), \|\cdot\|_{\infty})$ and F is continuous on \mathcal{G} . Then, due to the Ascoli theorem, it is compact in $(C(X), \|\cdot\|_{\infty})$. We show that it is not empty (see (3.9)), and that, for δ small enough, one can find $\bar{\alpha}, \bar{\Lambda}$ such that $F(\mathcal{G}) \subset \mathcal{G}$. We can then apply Schauder's fixed-point theorem to the set \mathcal{G} and obtain the existence of $\bar{f} \in \mathcal{G}$ such that

$$\bar{f} = F(\bar{f}) = (1 - \delta)\bar{f} + \delta \frac{\mu m \,\tilde{*} \,\bar{f}}{-s[\bar{f}]},$$

and, therefore,

$$0 = (s[\bar{f}])\bar{f} + \mu m \,\tilde{*}\,\bar{f},$$

which proves the existence of a steady state $\bar{f} \in W^{1,\infty}(X)$ of (2.1). Note that \bar{f} is non-trivial because $0 \notin \mathcal{F}$, since $\alpha(0) = \min(-a_{\mu}) = -\max((1-\mu)b - d_0)$.

We prove that, for δ small enough, $F(\mathcal{G}) \subset \mathcal{G}$. We present a proof in four steps.

STEP 1. We bound $\{\alpha(F(f)); f \in \mathcal{F}\}$ from below:

$$\begin{split} \alpha(F(f)) &= \min\{-s[F(f)]\} \\ &= \min\left\{d\,\tilde{*}\left[(1-\delta)f + \delta\frac{\mu m\,\tilde{*}\,f}{-s[f]}\right] - a_{\mu}\right\} \\ &\geqslant \min\{-s[f]\} + \delta\min\left\{d\,\tilde{*}\left(\frac{\mu m\,\tilde{*}\,f}{-s[f]} - f\right)\right\} \\ &\geqslant \alpha(f) + \delta\left(\mu(\min d)(\min m)\|f\|_{L^{1}}\int_{X}\frac{\mathrm{d}x}{-s[f]} - \|d\|_{\infty}\|f\|_{L^{1}}\right). \end{split}$$

Due to assumption 3.1, if $\alpha(f) \leq 1$, there exists $x_0 \in \operatorname{Int} X$ such that

$$(-s[f])(x_0) = \min(-s[f]) = \alpha(f).$$

Then, $(-s[f])'(x_0) = 0$ and

$$(-s[f])(x) \leq \alpha(f) + \frac{1}{2} ||(-s[f])''||_{\infty} (x - x_0)^2,$$

which, provided that $\alpha(f) \leq \min(\frac{1}{8} ||a''_{\mu}||_{\infty} |X|^2, 1)$, gives the following estimate on $\int_X (-s[f])^{-1} dx$:

$$\begin{split} \int_{X} \frac{\mathrm{d}x}{-s[f]} &\geq \int_{0}^{|X|/2} \frac{\mathrm{d}y}{\alpha(f) + \frac{1}{2} (\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\|f\|_{L^{1}})y^{2}} \\ &= \sqrt{\frac{2}{\alpha(f)(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\|f\|_{L^{1}})}} \\ &\qquad \times \arctan\left(\sqrt{\frac{\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\|f\|_{L^{1}}}{2\alpha(f)}}\frac{|X|}{2}\right) \\ &\geq \frac{\pi}{2\sqrt{2\alpha(f)(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\|f\|_{L^{1}})}}. \end{split}$$

Then,

$$\begin{aligned} \alpha(F(f)) &- \alpha(f) \\ &\geqslant \delta \|f\|_{L^1} \bigg\{ \mu(\min d)(\min m) \frac{\pi/2\sqrt{2}}{\sqrt{\alpha(f)(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^2 d\|_{\infty}\bar{\Lambda})}} - \|d\|_{\infty} \bigg\} \\ &\geqslant 0 \end{aligned}$$

 $\mathbf{i}\mathbf{f}$

$$\alpha(f) \leqslant \min \bigg\{ \frac{\frac{1}{8} \pi^2 \mu^2(\min d)^2(\min m)^2}{\|d\|_{\infty}^2 (\|a_{\mu}''\|_{\infty} + \|\partial_{11}^2 d\|_{\infty} \bar{A})}, \frac{\|a_{\mu}''\|_{\infty}}{8} |X|^2, 1 \bigg\}.$$

We define a constant \tilde{A} , which will be used in step 2, by

$$\tilde{A} := \frac{1}{\min d} (\mu \|m\|_{\infty} |X| + \max a_{\mu}).$$
(3.2)

We also define the constant C_{α} by

$$C_{\alpha} := \left(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\tilde{A} \right) \\ \times \min\left\{ \frac{\frac{1}{8}\pi^{2}\mu^{2}(\min d)^{2}(\min m)^{2}}{\|d\|_{\infty}^{2}(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\tilde{A})}, \frac{\|a_{\mu}''\|_{\infty}}{8} |X|^{2}, 1, \mu \|m\|_{\infty} |X| \right\}$$
(3.3)

(the last term, $\mu ||m||_{\infty}|X|$, will be useful at the end of step 3), and define $\tilde{\alpha}_{\bar{A}}$ by

$$\tilde{\alpha}_{\bar{A}} := \frac{C_{\alpha}}{(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^2 d\|_{\infty} \bar{A})}.$$
(3.4)

From now on we assume that $\overline{A} \ge \widetilde{A}$ and $\overline{\alpha} \le \widetilde{\alpha}_{\overline{A}}$. We take $f \in \mathcal{F}$. If $\alpha(f) \le \widetilde{\alpha}_{\overline{A}}$, then we have just proved that $\alpha(F(f)) \ge \alpha(f) \ge \overline{\alpha}$. On the other hand, if $\alpha(f) \ge \tilde{\alpha}_{\bar{\Lambda}}$, then

$$\begin{aligned} \alpha(F(f)) &= \min\left\{ (1-\delta)(-s[f]) + \delta \left[d\tilde{*} \left(\frac{\mu m \tilde{*} f}{-s[f]} \right) - a_{\mu} \right] \right\} \\ &\geqslant (1-\delta)\tilde{\alpha}_{\bar{A}} + \delta \min\left\{ d\tilde{*} \left(\frac{\mu m \tilde{*} f}{-s[f]} \right) - a_{\mu} \right\} \\ &\geqslant (1-\delta)\tilde{\alpha}_{\bar{A}} - \delta \max a_{\mu} \\ &= \frac{(1-\delta)C_{\alpha}}{(\|a_{\mu}''\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\bar{A})} - \delta \max a_{\mu}. \end{aligned}$$

That is, we have shown that, for any $f \in \mathcal{F}$,

$$\alpha(F(f)) \ge \frac{(1-\delta)C_{\alpha}}{(\|a_{\mu}^{\prime\prime}\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\bar{\Lambda})} - \delta \max a_{\mu} \quad \text{or} \quad \alpha(F(f)) \ge \bar{\alpha}.$$
(3.5)

STEP 2. We bound $\{ \|F(f)\|_{L^1}; f \in \mathcal{F} \}$ from above:

$$\begin{split} \|F(f)\|_{L^{1}} &= \int \left[f + \delta \left(\frac{\mu m \,\tilde{*}\, f}{-s[f]} - f \right) \right] \mathrm{d}x \\ &= \|f\|_{L^{1}} + \delta \left[\int \frac{\mu m \,\tilde{*}\, f}{-s[f]} \,\mathrm{d}x - \|f\|_{L^{1}} \right] \\ &\leqslant \|f\|_{L^{1}} + \delta \left[\frac{\mu \|m\|_{\infty} |X|}{\min(-s[f])} - 1 \right] \|f\|_{L^{1}} \\ &\leqslant \|f\|_{L^{1}} + \delta \left[\frac{\mu \|m\|_{\infty} |X|}{\|f\|_{L^{1}} \min d - \max a_{\mu}} - 1 \right] \|f\|_{L^{1}}. \end{split}$$

So, if

$$||f||_{L^1} \ge \frac{\mu ||m||_{\infty} |X| + \max a_{\mu}}{\min d} = \tilde{\Lambda},$$

then $||F(f)||_{L^1} \leq ||f||_{L^1} \leq \bar{\Lambda}$.

We next consider $f \in \mathcal{F}$ such that $||f||_{L^1} \leq \tilde{\Lambda}$. Then,

$$\begin{split} \|F(f)\|_{L^{1}} &\leq (1-\delta) \|f\|_{L^{1}} + \delta\mu \|m\|_{\infty} \|f\|_{L^{1}} \frac{|X|}{\alpha(f)} \\ &\leq (1-\delta)\tilde{A} + \delta\mu \|m\|_{\infty} \tilde{A} \frac{|X|}{\bar{\alpha}} \\ &\leq \tilde{A} \bigg(1 + \delta\mu \|m\|_{\infty} \frac{|X|}{\bar{\alpha}} \bigg). \end{split}$$

That is, we have shown that, for any $f \in \mathcal{F}$,

$$\|F(f)\|_{L^1} \leqslant \tilde{\Lambda} \left(1 + \delta \mu \|m\|_{\infty} \frac{|X|}{\bar{\alpha}}\right) \quad \text{or} \quad \|F(f)\|_{L^1} \leqslant \bar{\Lambda}.$$
(3.6)

STEP 3. We show that if $\delta > 0$ is small enough, there exist $0 < \bar{\alpha}$, $\bar{\Lambda} < \infty$ such that $F(\mathcal{F}) \subset \mathcal{F}$ and $\mathcal{F} \neq \emptyset$.

Due to steps 1 and 2, in order to show that $F(\mathcal{F}) \subset \mathcal{F}$, we need to show that, for $\delta > 0$ small enough, $\bar{\alpha} > 0$ and $\bar{A} < \infty$ can be chosen in such a way that

$$\bar{\alpha} \leqslant \frac{(1-\delta)C_{\alpha}}{(\|a_{\mu}^{\prime\prime}\|_{\infty} + \|\partial_{11}^{2}d\|_{\infty}\bar{\Lambda})} - \delta \max a_{\mu},$$

$$\bar{\Lambda} \geqslant \tilde{\Lambda} \left(1 + \delta\mu \|m\|_{\infty} \frac{|X|}{\bar{\alpha}}\right).$$
(3.7)

In order to show that such a choice of $\bar{\alpha}$, $\bar{\Lambda}$ is possible, we apply lemma 3.4 and get that, for $\delta > 0$ small enough, there exists $\hat{\alpha} > 0$ satisfying

$$\hat{\alpha} \leqslant \frac{(1-\delta)C_{\alpha}}{\|a_{\mu}''\|_{\infty} + \|\partial_{11}^2 d\|_{\infty} (\tilde{A}(1+\delta\mu\|m\|_{\infty}|X|/\hat{\alpha}))} - \delta \max a_{\mu}.$$
(3.8)

We then define $\bar{\alpha} := \hat{\alpha}$ and $\bar{A} := \tilde{A}(1 + \delta \mu ||m||_{\infty} |X|/\hat{\alpha})$. The second equation of (3.7) is satisfied due to the definition of \bar{A} , and the first equation of (3.7) is satisfied due to (3.8). Also, $\bar{\alpha} \leq \tilde{\alpha}_{\bar{A}}$ and $\bar{A} \geq \tilde{A}$ due to (3.8). It follows that $F(\mathcal{F}) \subset \mathcal{F}$.

Finally, in order to show that \mathcal{F} is not empty, we consider the constant function $g \in L^1(X)$:

$$g(x) := \frac{\tilde{A}}{|X|}.$$
(3.9)

Then, $\|g\|_{L^1} = \tilde{\Lambda} \leq \bar{\Lambda}$, and

$$\begin{aligned} \alpha(g) &= \min\{-s[g]\} \\ &\geqslant \frac{\tilde{\Lambda}}{|X|} |X| \min d - \max a_{\mu} \\ &= \mu \|m\|_{\infty} |X| \\ &\geqslant \tilde{\alpha}_{\bar{\Lambda}}, \end{aligned}$$

due to the definitions of (3.2)–(3.4). Then, $\alpha(g) \ge \overline{\alpha}$ and $g \in \mathcal{F}$, which cannot be empty. Note that $g \in \mathcal{G}$.

STEP 4. We conclude by applying Schauder's fixed-point theorem.

We choose $\delta, \bar{\alpha}, \bar{\Lambda} > 0$ such that $F(\mathcal{F}) \subset \mathcal{F}$, which is possible due to step 3. We compute the first derivative of F(f) as

$$F(f)' = (1-\delta)f' + \delta \left[\frac{\mu\partial_1 m\,\tilde{\ast}\,f}{-s[f]} + (\mu m\,\tilde{\ast}\,f)\frac{a'_{\mu} - \partial_1 d\,\tilde{\ast}\,f}{(-s[f])^2}\right],$$

and then, if $f \in \mathcal{F} \cap W^{1,\infty}(X)$,

$$||F(f)'||_{\infty} \leq (1-\delta)||f'||_{\infty} + \gamma\delta, \qquad (3.10)$$

where

$$\gamma := \frac{\mu \|\partial_1 m\|_{\infty} \bar{\Lambda}}{\bar{\alpha}} + \mu \|m\|_{\infty} \bar{\Lambda} \frac{\|a'_{\mu}\|_{\infty} + \|\partial_1 d\|_{\infty} \bar{\Lambda}}{\bar{\alpha}^2}.$$

Then, $F(\mathcal{G}) \subset \mathcal{G}$ due to step 3 and (3.10). Thus, we can apply Schauder's fixed-point theorem, which proves the existence of a steady state $\overline{f} \in W^{1,\infty}(X)$ of (2.1) and concludes the proof.

REMARK 3.6. If $b, d_0 \in W^{k,\infty}(X), d, \beta \in W^{k,\infty}(X \times X)$, the same argument can be used to build a set $\mathcal{G}^k \subset W^{k,\infty}(X)$ such that $F(\mathcal{G}^k) \subset \mathcal{G}^k$. It then follows that the steady state \overline{f} given by theorem 3.5 can be taken in $W^{k,\infty}(X)$.

4. Asymptotics

In this section we perform an asymptotic analysis of the steady states for small mutation rates. We denote it, from now on, by ε . Model (2.1) then reads (for notation see § 2)

$$\partial_t f^{\varepsilon}(t,x) = s[f^{\varepsilon}(t,\cdot)](x)f^{\varepsilon}(t,x) + \varepsilon \int_X m(x,y)f^{\varepsilon}(t,y) \,\mathrm{d}y \quad \text{for } t \ge 0, \ x \in X.$$
(4.1)

We now present those assumptions on the coefficients that will enable us to perform our asymptotic study.

ASSUMPTION 4.1. Assume that $b, d_0 \in W^{3,\infty}(X), d \in W^{3,\infty}(X \times X)$ satisfy $b'(0) = d'_0(0) = 0$ and

$$\max_{x \in X} (b''(x) - d_0''(x)) + \frac{\max(b - d_0)}{\min d} \|\partial_{11}^2 d\|_{\infty} \leqslant -\delta < 0.$$

Remark 4.2. This assumption is the cornerstone of our study. It implies that there exist $\bar{\varepsilon} > 0$, $\tilde{\delta} > 0$ such that

$$\max_{x \in X} \max(b''(x), (1 - \bar{\varepsilon})b''(x)) - \min_{x \in X} d_0''(x) + \frac{\max(b - d_0) + \bar{\varepsilon} \max_{y \in X} \|m(\cdot, y)\|_{L^1(X)}}{\min d} \|\partial_{11}^2 d\|_{\infty} \leqslant -\tilde{\delta} < 0.$$
(4.2)

In other words, assumption 4.1 ensures that the fitness $s[f](\cdot)$ is concave as soon as the total population is less than a constant

$$\int_X f(x) \, \mathrm{d}x \leqslant \frac{\max(b - d_0) + \bar{\varepsilon} \max_{y \in X} \|m(\cdot, y)\|_{L^1(X)}}{\min d}.$$

An integration over X of (4.1) shows that any steady population satisfies this last inequality when $\varepsilon \leq \bar{\varepsilon}$.

Assumption 4.1 implies, in particular, that $a_{\varepsilon} = (1 - \varepsilon)b - d_0$ has a unique maximum at x = 0, and that

$$-\left[\frac{a_0''(0)}{a_0(0)} - \frac{\partial_{11}^2 d(0,0)}{d(0,0)}\right] > 0$$

This last quantity appears in the asymptotic result provided by theorem 4.7. It also means, exactly, that the Dirac mass $a_0(0)\delta_0/d(0,0)$ is a linearly stable steady solution of (4.1) when $\varepsilon = 0$ (cf. [16]).

Assumption 4.1 is, for instance, satisfied when $b(x) - d_0(x) = 1 - x^2$, d(x, y) = 1 (see, for example, [25]).

ASSUMPTION 4.3. The following 'symmetry' condition holds:

$$\forall x \in X, \quad \partial_1 d(x, x) = 0$$

REMARK 4.4. This assumption is satisfied in the classical case when the competition between two individuals is maximal when they have the same trait $(x \mapsto d(x, y))$ is maximal when x = y. Our analysis could, however, be generalized to cases when this condition is not satisfied.

ASSUMPTION 4.5. The mutation kernel satisfies

$$\min_{X \times X} m > 0, \quad m \in C^1(X \times X) \cap L^\infty(X \times X).$$

REMARK 4.6. This assumption is quite general, apart from the strict positivity condition. This last condition could probably be replaced by the weaker assumption that $m \ge 0$, m(0,0) > 0, but this generalization would most likely require long and technical estimates (see [32], where a similar generalization is made).

The next theorem describes the asymptotic profile of the steady states when the mutation rate is small. It shows that f^{ε} has the shape of a Cauchy distribution centred at $\varepsilon \bar{x}^{\varepsilon} = O(\varepsilon^{2/3})$.

THEOREM 4.7. Suppose that assumptions 4.1, 4.3 and 4.5 hold. For $\varepsilon \in (0, \overline{\varepsilon})$ (where $\overline{\varepsilon}$ is defined as in remark 4.2) let f^{ε} be a steady state of (4.1) (such as obtained in theorem 3.5, for example). Then, there exists $\overline{x}^{\varepsilon} = O(\varepsilon^{-1/3})$, such that

$$\begin{split} \varepsilon f^{\varepsilon}(\varepsilon(\bar{x}^{\varepsilon} + x)) &= \left(m(0,0) \frac{a_0(0)}{d(0,0)} + O(\sqrt{\varepsilon}) + O(\varepsilon x) \right) \\ &\times \left(\frac{2(m(0,0)\pi)^2}{-[a_0''(0) - a_0(0)\partial_{11}^2 d(0,0)/d(0,0)]} + O(\sqrt{\varepsilon}) \right. \\ &+ \frac{1}{2} \left(- \left[a_0''(0) - \frac{a_0(0)}{d(0,0)} \partial_{11}^2 d(0,0) \right] + O(\sqrt{\varepsilon}) + O(\varepsilon x) \right) x^2 \right)^{-1}. \end{split}$$

REMARK 4.8. This result shows that, for a small mutation rate, the profile of the steady states for general mutation and competition kernels is indeed similar to the

profile obtained when the house-of-cards model is used (see [5, 39]). In particular, it is different from the Gaussian profiles (see [22, 25]) obtained when mutations are modelled through a diffusion (that is, roughly speaking, when one assumes that mutations have a very small effect; see [12]). For a discussion of the population profile depending on the mutations rate, see [7].

In particular, our result shows that the steady populations have fat tails (that is, $f^{\varepsilon}(x) \equiv C\varepsilon/x^2$ for εx large). This feature is not at all in accordance with the usual assumption that populations have a Gaussian distribution. Those tails may lead to different values of the mutation load (see [4,7]) and may have a significant role in rapidly changing environments, as in evolutionary rescue experiments (see [2,21]). In [2], the success of the evolutionary rescue is directly related to the number of resistant (to the new environment) cells initially present in the population. A precise estimate of the tails of the population distribution is then especially interesting.

Note that the mutation rate ε is linked to the concentration of the population at the point x = 0, as was previously noted in [7]. Assuming that ε is small then allows us to describe the profile of the population using only the values of the coefficients and their derivatives at the point x = 0.

We observe that the competition in our asymptotics only changes the coefficients in the Cauchy profile, not the general shape of the profile.

Finally, we note that the fact that X is bounded does not play an important role in the asymptotics, since the quantity that is studied is $\varepsilon f^{\varepsilon}(\varepsilon(\bar{x}^{\varepsilon} + x))$. In the limit $\varepsilon \to 0$ the whole Cauchy profile is recovered, since, for any $x \in \mathbb{R}$, $\varepsilon(\bar{x}^{\varepsilon} + x) \in X$ for $\varepsilon > 0$ small enough.

Proof. We introduce the change of variable $f^{\varepsilon}(t, x) = g^{\varepsilon}(t, x/\varepsilon)/\varepsilon$, and consider the non-trivial steady states $u^{\varepsilon} \ge 0$ for the equation on g^{ε} :

$$\forall x \in \varepsilon^{-1} X, \quad 0 = s^{\varepsilon} [u^{\varepsilon}](x) u^{\varepsilon}(x) + \varepsilon^2 \int_{\varepsilon^{-1} X} m(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y, \tag{4.3}$$

where

$$s^{\varepsilon}[u^{\varepsilon}](x) := a_{\varepsilon}(\varepsilon x) - \int_{\varepsilon^{-1}X} d(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y.$$

Then,

$$u^{\varepsilon}(x) = \frac{1}{-s^{\varepsilon}[u^{\varepsilon}](x)/\varepsilon^2} \int_{\varepsilon^{-1}X} m(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y.$$
(4.4)

Let $\bar{x}^{\varepsilon} \in \varepsilon^{-1}X$ be such that

$$s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) := \max_{x \in \varepsilon^{-1}X} s^{\varepsilon}[u^{\varepsilon}](x).$$
(4.5)

REMARK 4.9. Note that, since $u^{\varepsilon}(x) \ge 0$, the second term of the right-hand side of (4.3) is strictly positive and, therefore, $u^{\varepsilon}(x) > 0$ and $s^{\varepsilon}[u^{\varepsilon}](x) < 0$ for $x \in \varepsilon^{-1}X$.

STEP 1. We show that $\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}] / \varepsilon^2 \leq -\delta$.

Since u^{ε} satisfies (4.3),

$$\begin{split} 0 &= \int_{\varepsilon^{-1}X} \left[\left(a_{\varepsilon}(\varepsilon x) - \int_{\varepsilon^{-1}X} d(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right) u^{\varepsilon}(x) \right] \mathrm{d}x \\ &+ \int_{\varepsilon^{-1}X} \left[\varepsilon^2 \int_{\varepsilon^{-1}X} m(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right] \mathrm{d}x \\ &\leqslant (\max a_{\varepsilon} - (\min d) \| u^{\varepsilon} \|_{L^1(\varepsilon^{-1}X)}) \| u^{\varepsilon} \|_{L^1(\varepsilon^{-1}X)} \\ &+ \varepsilon \Big(\max_{y \in X} \| m(\cdot, y) \|_{L^1(X)} \Big) \| u^{\varepsilon} \|_{L^1(\varepsilon^{-1}X)}, \end{split}$$

we can bound $||u^{\varepsilon}||_{L^{1}(\varepsilon^{-1}X)}$ from above as

$$\|u^{\varepsilon}\|_{L^{1}(\varepsilon^{-1}X)} \leqslant \frac{\max a_{\varepsilon} + \varepsilon \max_{y \in X} \|m(\cdot, y)\|_{L^{1}(X)}}{\min d}.$$
(4.6)

Moreover, $\partial_{xx}^2 s^{\varepsilon}[u^{\varepsilon}]$ satisfies

$$\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](x) = \varepsilon^2 a_{\varepsilon}''(\varepsilon x) - \varepsilon^2 \int_{\varepsilon^{-1}X} \partial_{11}^2 d(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y$$
$$\leqslant \varepsilon^2 \Big[\max_X a_{\varepsilon}'' + \|u^{\varepsilon}\|_{L^1(\varepsilon^{-1}X)} \|\partial_{11}^2 d\|_{L^{\infty}(X \times X)} \Big].$$

Due to (4.6) and assumption 4.1,

$$\frac{1}{\varepsilon^2} \partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](x)$$

$$\leq \max_X a_{\varepsilon}'' + \frac{\max_X a_{\varepsilon} + \varepsilon \max_{y \in X} \|m(\cdot, y)\|_{L^1(X)}}{\min d} \|\partial_{11}^2 d\|_{L^{\infty}(X \times X)}$$

$$\leq -\delta < 0,$$

which proves step 1.

REMARK 4.10. Step 1 proves that $s^{\varepsilon}[u^{\varepsilon}]$ is concave. Then, \bar{x}^{ε} is well defined (that is, unique) due to (4.5).

STEP 2. We show that $|\varepsilon \bar{x}^{\varepsilon}| = O(\sqrt{\varepsilon})$.

We prove that if $\varepsilon \bar{x}^{\varepsilon} > 0$, then $\varepsilon \bar{x}^{\varepsilon} \leq O(\sqrt{\varepsilon})$. The case $\varepsilon \bar{x}^{\varepsilon} < 0$ can be dealt with in the same way.

Noting that $\varepsilon \bar{x}^{\varepsilon} > 0$, $[0, \varepsilon \bar{x}^{\varepsilon}) \subset X$, and using definition (4.5) of \bar{x}^{ε} , we see that

$$0 \leqslant \partial_x s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}). \tag{4.7}$$

Then,

$$\begin{aligned} a_{\varepsilon}'(\varepsilon\bar{x}^{\varepsilon}) \geqslant \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon\bar{x}^{\varepsilon},\varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y \\ &= \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon\bar{x}^{\varepsilon},\varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y + \int_{|y-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon\bar{x}^{\varepsilon},\varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y. \end{aligned}$$

$$(4.8)$$

We perform a Taylor expansion to estimate the first term of the right-hand side of the equality in (4.8), using assumption 4.3 and (4.6),

$$\begin{split} \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ & \geqslant \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \bar{x}^{\varepsilon}) u^{\varepsilon}(y) \, \mathrm{d}y \\ & + \varepsilon \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \partial_{12}^2 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \theta(y)) (y - \bar{x}^{\varepsilon}) u^{\varepsilon}(y) \, \mathrm{d}y \\ & \geqslant 0 - \varepsilon \|\partial_{12}^2 d\|_{\infty} \frac{1}{\sqrt{\varepsilon}} \|u^{\varepsilon}\|_{L^1} \\ & \geqslant -C_1 \sqrt{\varepsilon} \end{split}$$

for some $C_1 > 0$. To estimate the second term of (4.8), we first estimate $s^{\varepsilon}[u^{\varepsilon}]$ using a Taylor expansion: for $\varepsilon x \in X$,

$$s^{\varepsilon}[u^{\varepsilon}](x) = s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) + (x - \bar{x}^{\varepsilon})\partial_{x}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) + \frac{1}{2}(x - \bar{x}^{\varepsilon})^{2}\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\theta)$$

$$\leqslant s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) - \frac{1}{2}\varepsilon^{2}\delta(x - \bar{x}^{\varepsilon})^{2}, \qquad (4.9)$$

where we used (4.7) to estimate $\partial_x s^{\varepsilon}[u^{\varepsilon}](x)$, and step 1 to estimate $\partial_{xx}^2 s^{\varepsilon}[u^{\varepsilon}](\theta)$. Then, using (4.4), we get (from remark 4.9) that

$$\begin{split} \int_{|y-\bar{x}^{\varepsilon}| \ge 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ \ge -\|\partial_1 d\|_{\infty} \int_{|y-\bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}} \frac{\|m\|_{\infty} \|u^{\varepsilon}\|_{L^1}}{-s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^2 + \delta(y-\bar{x}^{\varepsilon})^2/2} \, \mathrm{d}y, \end{split}$$

and then (due to remark 4.9 and (4.6)),

.

$$\int_{|y-\bar{x}^{\varepsilon}| \ge 1/\sqrt{\varepsilon}} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y$$

$$\geq -\|\partial_1 d\|_{\infty} \|u^{\varepsilon}\|_{L^1} \int_{|y-\bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}} \frac{\|m\|_{\infty}}{0 + \delta(y-\bar{x}^{\varepsilon})^2/2} \, \mathrm{d}y$$

$$\geq -C_2\sqrt{\varepsilon} \tag{4.10}$$

for some $C_2 > 0$. Finally, due to (4.9) and (4.10), (4.8) becomes

$$a_{\varepsilon}'(\varepsilon \bar{x}^{\varepsilon}) \geqslant -C\sqrt{\varepsilon},$$

where $C = C_1 + C_2$. We assumed that $\varepsilon \bar{x}^{\varepsilon} > 0$. Then, due to assumption 4.1, $a'_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) \leq -\varepsilon \bar{x}^{\varepsilon} \delta$, and thus

$$\varepsilon \bar{x}^{\varepsilon} \leqslant \frac{-a_{\varepsilon}'(\varepsilon \bar{x}^{\varepsilon})}{\delta} \leqslant \frac{C}{\delta} \sqrt{\varepsilon}.$$

REMARK 4.11. Step 2 implies, in particular, that, for $\varepsilon > 0$ small enough, $\varepsilon \bar{x}^{\varepsilon} \in$ Int X, and then

$$0 = \partial_x s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}).$$

Due to this equality and a Taylor expansion, (4.4) becomes

$$u^{\varepsilon}(x) = \frac{\int_{\varepsilon^{-1}X} m(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y}{-s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^{2} + (-\partial_{xx}^{2}(s^{\varepsilon} [u^{\varepsilon}])(\theta))(x - \bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}},\tag{4.11}$$

where $\theta \in [\bar{x}^{\varepsilon}, x]$ (or $\theta \in [x, \bar{x}^{\varepsilon}]$ if $x < \bar{x}^{\varepsilon}$).

STEP 3. We bound $Q^{\varepsilon} := -s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^2$ from above and below.

We recall what we showed in step 1, that is,

$$\forall x \in \varepsilon^{-1} X, \quad -\partial_{xx}^2 (s^{\varepsilon} [u^{\varepsilon}])(x) \ge \delta \varepsilon^2 > 0.$$
(4.12)

Then, due to (4.11) $(Q^{\varepsilon} > 0$ from remark 4.9),

$$u^{\varepsilon}(\bar{x}^{\varepsilon} + x) \leqslant \frac{\int_{\varepsilon^{-1}X} m(\varepsilon(\bar{x}^{\varepsilon} + x), \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y}{Q^{\varepsilon} + \delta x^2/2}$$
$$\leqslant \|m\|_{\infty} \frac{\int_{\varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y}{Q^{\varepsilon} + \delta x^2/2}.$$
(4.13)

Then,

$$\begin{split} \int_{\varepsilon^{-1}X} u^{\varepsilon} &\leqslant \|m\|_{\infty} \bigg(\int_{\varepsilon^{-1}X} u^{\varepsilon} \bigg) \int_{\varepsilon^{-1}X - \bar{x}^{\varepsilon}} \frac{\mathrm{d}x}{Q^{\varepsilon} + \delta x^{2}/2} \\ &\leqslant \|m\|_{\infty} \bigg(\int_{\varepsilon^{-1}X} u^{\varepsilon} \bigg) \int_{\mathbb{R}} \frac{\mathrm{d}x}{Q^{\varepsilon} + \delta x^{2}/2} \\ &= \|m\|_{\infty} \bigg(\int_{\varepsilon^{-1}X} u^{\varepsilon} \bigg) \frac{\sqrt{2\pi}}{\sqrt{Q^{\varepsilon}\delta}}, \end{split}$$

which yields the following (uniform in ε) upper bound on Q^{ε} :

$$Q^{\varepsilon} \leqslant \frac{2\pi^2 \|m\|_{\infty}^2}{\delta}.$$

On the other hand, since (using (4.6))

$$\begin{aligned} \frac{1}{\varepsilon^2} \partial_{xx}^2 s^\varepsilon [u^\varepsilon](x) &= a_\varepsilon''(\varepsilon x) - \int_{\varepsilon^{-1} X} \partial_{11}^2 d(\varepsilon x, \varepsilon y) u^\varepsilon(y) \, \mathrm{d}y \\ &\geqslant [\min a_\varepsilon'' - \|u^\varepsilon\|_{L^1(\varepsilon^{-1} X)} \|\partial_{11}^2 d\|_{L^\infty(X \times X)}] \\ &\geqslant \left[\min a_\varepsilon'' - \frac{\max a_{\overline{\varepsilon}} + \overline{\varepsilon} \max_{y \in X} \|m(\cdot, y)\|_{L^1(X)}}{\min d} \|\partial_{11}^2 d\|_{\infty}\right] \\ &=: -\tilde{\delta}, \end{aligned}$$

we obtain, using (4.11), the estimate

$$\int_{\varepsilon^{-1}X} u^{\varepsilon} \ge (\min m) \| u^{\varepsilon} \|_{L^{1}(\varepsilon^{-1}X)} \int_{\varepsilon^{-1}X - \bar{x}^{\varepsilon}} \frac{\mathrm{d}x}{Q^{\varepsilon} - \partial_{xx}^{2} s^{\varepsilon} [u^{\varepsilon}](\theta) x^{2}/2\varepsilon^{2}} \\ \ge (\min m) \| u^{\varepsilon} \|_{L^{1}(\varepsilon^{-1}X)} \int_{\varepsilon^{-1}X - \bar{x}^{\varepsilon}} \frac{\mathrm{d}x}{Q^{\varepsilon} + \tilde{\delta}x^{2}/2}.$$

Since X is an interval, $\varepsilon^{-1}X - \bar{x}^{\varepsilon}$ contains the interval $(-|X|/2\varepsilon, 0]$ or $[0, |X|/2\varepsilon)$. Then,

$$\frac{1}{\min m} \ge \int_0^{|X|/2\varepsilon} \frac{\mathrm{d}x}{Q^\varepsilon + \frac{1}{2}\tilde{\delta}x^2}$$
$$= \frac{\pi}{\sqrt{2Q^\varepsilon\tilde{\delta}}} - \int_{|X|/2\varepsilon}^\infty \frac{\mathrm{d}x}{Q^\varepsilon + \frac{1}{2}\tilde{\delta}x^2}$$
$$\ge \frac{\pi}{\sqrt{2Q^\varepsilon\tilde{\delta}}} - O(\varepsilon).$$

For $\varepsilon > 0$ small enough, we thus get a (uniform in ε) lower bound on Q^{ε} :

$$Q^{\varepsilon} \geqslant \frac{\pi^2 (\min m)^2}{2\tilde{\delta}} > 0.$$

STEP 4. We estimate $\int_{\varepsilon^{-1}X} u^{\varepsilon}$ and Q^{ε} . We first estimate $\int_{\varepsilon^{-1}X} u^{\varepsilon}$. Due to step 3, $Q^{\varepsilon} = O(1)$. Then,

$$\begin{split} O(1) &= \frac{1}{\varepsilon^2} s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) \\ &= \frac{1}{\varepsilon^2} \left(a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - \int_{\varepsilon^{-1}X} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right) \\ &= \frac{1}{\varepsilon^2} \left(a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - \int_{|y - \bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right) \\ &- \frac{1}{\varepsilon^2} \left(\int_{|y - \bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}, \, y \in \varepsilon^{-1}X} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right) \\ &\geqslant \frac{1}{\varepsilon^2} \left(a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - \int_{|y - \bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} (d(\varepsilon \bar{x}^{\varepsilon}, 0) + O(\varepsilon y)) u^{\varepsilon}(y) \, \mathrm{d}y \right) \\ &- \frac{1}{\varepsilon^2} \left(\|d\|_{\infty} \int_{|y - \bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}, \, y \in \varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y \right). \end{split}$$

We estimate (using (4.6), step 2 and (4.13) for the second estimate) that

$$\begin{split} \left| \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} O(\varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right| &\leqslant \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} Cst \|\varepsilon y\|_{\infty} u^{\varepsilon}(y) \, \mathrm{d}y \\ &\leqslant Cst\sqrt{\varepsilon} \|u^{\varepsilon}\|_{L^{1}(\varepsilon^{-1}X)} \\ &= O(\sqrt{\varepsilon}), \qquad (4.14) \\ \int_{|y-\bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}, \, y \in \varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y \right| &\leqslant \|m\|_{L^{\infty}(X \times X)} \|u^{\varepsilon}\|_{L^{1}(\varepsilon^{-1}X)} \int_{|y| > 1/\sqrt{\varepsilon}} \frac{\mathrm{d}y}{\frac{1}{2}\delta y^{2}} \\ &= O(\sqrt{\varepsilon}). \qquad (4.15) \end{split}$$

Then,

$$O(\varepsilon^{2}) \ge a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - d(\varepsilon \bar{x}^{\varepsilon}, 0) \int_{|y - \bar{x}^{\varepsilon}| \le 1/\sqrt{\varepsilon}} u^{\varepsilon}(y) \, \mathrm{d}y - C\sqrt{\varepsilon}$$
$$= a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - d(\varepsilon \bar{x}^{\varepsilon}, 0) \int_{\varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y - O(\sqrt{\varepsilon}).$$

We thus obtain

$$d(\varepsilon \bar{x}^{\varepsilon}, 0) \int_{\varepsilon^{-1} X} u^{\varepsilon}(y) \, \mathrm{d}y \ge a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - O(\varepsilon^2) - O(\sqrt{\varepsilon}). \tag{4.16}$$

On the other hand, since

$$\begin{split} O(1) &= \frac{1}{\varepsilon^2} s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) \\ &\leqslant \frac{1}{\varepsilon^2} \bigg(a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - \int_{|y - \bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} (d(\varepsilon \bar{x}^{\varepsilon}, 0) + O(\varepsilon y)) u^{\varepsilon}(y) \, \mathrm{d}y \bigg) \\ &\quad + \frac{1}{\varepsilon^2} \bigg(\|d\|_{\infty} \int_{|y - \bar{x}^{\varepsilon}| > 1/\sqrt{\varepsilon}, \, y \in \varepsilon^{-1} X} u^{\varepsilon}(y) \, \mathrm{d}y \bigg), \end{split}$$

we obtain that

$$d(\varepsilon \bar{x}^{\varepsilon}, 0) \int_{\varepsilon^{-1} X} u^{\varepsilon}(y) \, \mathrm{d}y \leq a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon}) - O(\varepsilon^2) + O(\sqrt{\varepsilon}).$$
(4.17)

From (4.16) and (4.17) we obtain

$$\int_{\varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y = \frac{a_{\varepsilon}(\varepsilon \bar{x}^{\varepsilon})}{d(\varepsilon \bar{x}^{\varepsilon}, 0)} + O(\sqrt{\varepsilon})$$
$$= \frac{a_0(0)}{d(0, 0)} + O(\sqrt{\varepsilon}). \tag{4.18}$$

Next, using (4.11) and (4.15), we estimate Q^{ε} as

$$\begin{split} &\int_{\varepsilon^{-1}X} u^{\varepsilon}(x) \,\mathrm{d}x \\ &= \int_{|x-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} u^{\varepsilon}(x) \,\mathrm{d}x + \int_{|x-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}, \, x \in \varepsilon^{-1}X} u^{\varepsilon}(x) \,\mathrm{d}x \\ &= \int_{|x-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \frac{\int_{\varepsilon^{-1}X} m(\varepsilon x, \varepsilon y) u^{\varepsilon}(y) \,\mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2} s^{\varepsilon} [u^{\varepsilon}](\theta))(x-\bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}} \,\mathrm{d}x \\ &+ \int_{|x-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}, \, x \in \varepsilon^{-1}X} u^{\varepsilon}(x) \,\mathrm{d}x \\ &= \int_{|x-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \frac{\int_{\varepsilon^{-1}X} (m(0,\varepsilon y) + O(\varepsilon/\sqrt{\varepsilon})) u^{\varepsilon}(y) \,\mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2} s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\varepsilon 1/\sqrt{\varepsilon}))(x-\bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}} \,\mathrm{d}x + O(\sqrt{\varepsilon}). \end{split}$$
(4.19)

We compute, using (4.14) and (4.15), that

$$\begin{split} &\int_{\varepsilon^{-1}X} m(0,\varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ &= \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} m(0,\varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y + \int_{|y-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}} m(0,\varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ &= \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} (m(0,0) + O(\varepsilon 1/\sqrt{\varepsilon})) u^{\varepsilon}(y) \, \mathrm{d}y + \int_{|y-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}} m(0,\varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ &= m(0,0) \int_{\varepsilon^{-1}X} u^{\varepsilon}(x) \, \mathrm{d}x + O(\sqrt{\varepsilon}), \end{split}$$

and we estimate

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$$\begin{split} \int_{|x-\bar{x}^{\varepsilon}|\leqslant 1/\sqrt{\varepsilon}} \frac{\mathrm{d}x}{Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\sqrt{\varepsilon}))(x-\bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}} \\ &= \int_{\mathbb{R}} \frac{\mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\sqrt{\varepsilon}))y^{2}/2\varepsilon^{2}} \\ &- \int_{|y|\geqslant 1/\sqrt{\varepsilon}} \frac{\mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\sqrt{\varepsilon}))y^{2}/2\varepsilon^{2}} \\ &= \frac{\sqrt{2}\pi}{\sqrt{Q^{\varepsilon}}(-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^{2} + O(\sqrt{\varepsilon}))} + O(\sqrt{\varepsilon}), \end{split}$$

because, from step 1, we know that

$$\begin{split} 0 &\leqslant \int_{|y| \geqslant 1/\sqrt{\varepsilon}} \frac{\mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) + \varepsilon^2 O(\sqrt{\varepsilon}))y^2/2\varepsilon^2} \\ &\leqslant \int_{|y| \geqslant 1/\sqrt{\varepsilon}} \frac{\mathrm{d}y}{\frac{1}{2}\delta y^2} \\ &= \frac{4\sqrt{\varepsilon}}{\delta}. \end{split}$$

Then, (4.19) becomes

$$\begin{split} \int_{\varepsilon^{-1}X} u^{\varepsilon}(x) \, \mathrm{d}x &= \left(m(0,0) \int_{\varepsilon^{-1}X} u^{\varepsilon}(x) \, \mathrm{d}x + O(\sqrt{\varepsilon}) \right) \\ &\times \left(\frac{\sqrt{2}\pi}{\sqrt{Q^{\varepsilon}(-\partial_{xx}^2 s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^2 + O(\sqrt{\varepsilon}))}} + O(\sqrt{\varepsilon}) \right), \end{split}$$

 \mathbf{SO}

$$Q^{\varepsilon} = \frac{2(m(0,0)\pi)^2}{(-\varepsilon^{-2}\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) + O(\sqrt{\varepsilon}))} + O(\sqrt{\varepsilon})$$
$$= \frac{2(m(0,0)\pi)^2}{-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^2} + O(\sqrt{\varepsilon}).$$

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To get a better approximation of Q^{ε} , we estimate $-\partial_{xx}^2 s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon})/\varepsilon^2$ using (4.18):

$$\begin{split} \partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}) &= \varepsilon^2 a_{\varepsilon}''(\varepsilon \bar{x}^{\varepsilon}) - \int_{\varepsilon^{-1}X} \varepsilon^2 \partial_{11}^2 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ &= \varepsilon^2 \Big[a_{\varepsilon}''(\varepsilon \bar{x}^{\varepsilon}) - \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} \partial_{11}^2 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \\ &- \int_{|y-\bar{x}^{\varepsilon}| \geqslant 1/\sqrt{\varepsilon}} \partial_{11}^2 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \Big] \\ &= \varepsilon^2 \Big[a_{\varepsilon}''(0) + O(\varepsilon \bar{x}^{\varepsilon}) \\ &- \int_{|y-\bar{x}^{\varepsilon}| \leqslant 1/\sqrt{\varepsilon}} (\partial_{11}^2 d(0,0) + O(\varepsilon \bar{x}^{\varepsilon}) + O(\varepsilon y)) u^{\varepsilon}(y) \, \mathrm{d}y + O(\sqrt{\varepsilon}) \Big] \\ &= \varepsilon^2 \Big[a_0''(0) - \partial_{11}^2 d(0,0) \int_{\varepsilon^{-1}X} u^{\varepsilon} + O(\sqrt{\varepsilon}) \Big] \\ &= \varepsilon^2 \Big[a_0''(0) - \frac{a(0)}{d(0,0)} \partial_{11}^2 d(0,0) + O(\sqrt{\varepsilon}) \Big]. \end{split}$$

Finally, we obtain the following estimate on $Q^{\varepsilon} {:}$

$$Q^{\varepsilon} = \frac{2(m(0,0)\pi)^2}{-[a_0''(0) - a_0(0)\partial_{11}^2 d(0,0)/d(0,0)]} + O(\sqrt{\varepsilon}).$$

STEP 5. We show that asymptotically f^{ε} has a Cauchy-like profile.

Thanks to (4.11), (4.15) and the estimates obtained in step 4, we find (with $\theta \in [\bar{x}^{\varepsilon}, x]$, or $\theta \in [x, \bar{x}^{\varepsilon}]$ if $x < \bar{x}^{\varepsilon}$),

$$\begin{split} u^{\varepsilon}(\bar{x}^{\varepsilon} + x) \\ &= \frac{\int_{\varepsilon^{-1}X} m(\varepsilon(\bar{x}^{\varepsilon} + x), \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2}(s^{\varepsilon}[u^{\varepsilon}])(\theta)) x^{2}/2\varepsilon^{2}} \\ \\ &= \frac{\int_{|y-\bar{x}^{\varepsilon}| \leq 1/\sqrt{\varepsilon}} (m(\varepsilon(\bar{x}^{\varepsilon} + x), \varepsilon \bar{x}^{\varepsilon}) + O(\varepsilon(y - \bar{x}^{\varepsilon}))) u^{\varepsilon}(y) \, \mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2}(s^{\varepsilon}[u^{\varepsilon}])(\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\varepsilon(\theta - \bar{x}^{\varepsilon}))) x^{2}/2\varepsilon^{2}} \\ \\ &+ \frac{\int_{|y-\bar{x}^{\varepsilon}| \geq 1/\sqrt{\varepsilon}} m(\varepsilon(\bar{x}^{\varepsilon} + x), \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y}{Q^{\varepsilon} + (-\partial_{xx}^{2}(s^{\varepsilon}[u^{\varepsilon}])(\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\varepsilon(\theta - \bar{x}^{\varepsilon}))) x^{2}/2\varepsilon^{2}} \\ \\ &= \frac{m(\varepsilon(\bar{x}^{\varepsilon} + x), \varepsilon \bar{x}^{\varepsilon}) \int_{\varepsilon^{-1}X} u^{\varepsilon}(y) \, \mathrm{d}y + O(\sqrt{\varepsilon})}{Q^{\varepsilon} + (-\partial_{xx}^{2}(s^{\varepsilon}[u^{\varepsilon}])(\bar{x}^{\varepsilon}) + \varepsilon^{2}O(\varepsilon x) + \varepsilon^{2}O(\varepsilon \bar{x}^{\varepsilon})) x^{2}/2\varepsilon^{2}} \\ \\ &= \left(m(0, 0) \frac{a(0)}{d(0, 0)} + O(\sqrt{\varepsilon}) + O(\varepsilon x)\right) \\ \\ &\times \left(\frac{2(m(0, 0)\pi)^{2}}{-[a_{0}''(0) - a_{0}(0)\partial_{11}^{2}d(0, 0)/d(0, 0)]} + O(\sqrt{\varepsilon}) + O(\varepsilon x)\right) x^{2}\right)^{-1}. \end{split}$$

STEP 6. We improve our estimate on \bar{x}^{ε} .

Due to remark 4.11,

$$0 = \partial_x s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon})$$
$$= \varepsilon a_{\varepsilon}'(\varepsilon \bar{x}^{\varepsilon}) - \varepsilon \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y$$
$$= \varepsilon^2 a_{\varepsilon}''(\varepsilon \theta) \bar{x}^{\varepsilon} - \varepsilon \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y,$$

where $\theta \in [0, \bar{x}^{\varepsilon}]$ (or $\theta \in [\bar{x}^{\varepsilon}, 0]$ if $\bar{x}^{\varepsilon} < 0$). Then,

$$\bar{x}^{\varepsilon} = \frac{1}{\varepsilon a_{\varepsilon}''(\varepsilon\theta)} \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y.$$

We consider C > 0 small enough that

$$[\bar{x}^{\varepsilon} - C, \bar{x}^{\varepsilon} + C] \subset \varepsilon^{-1} X$$

(C will be chosen precisely later). Then,

$$\begin{split} \left| \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right| &\leqslant \left| \int_{|y - \bar{x}^{\varepsilon}| \leqslant C} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right| \\ &+ \left| \int_{|y - \bar{x}^{\varepsilon}| > C, \, y \in \varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right|. \end{split}$$

We estimate the first term using a Taylor expansion of $y \mapsto \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, y)$ around $y = \varepsilon \bar{x}^{\varepsilon}$ (assuming that $d \in W^{2,\infty}$), and we estimate the second term using (4.13). Then, keeping assumption 4.3 in mind,

$$\begin{split} \left| \int_{\varepsilon^{-1}X} \partial_{1} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right| \\ &\leqslant \left| \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} [\partial_{1} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \bar{x}^{\varepsilon}) + \partial_{12}^{2} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \bar{x}^{\varepsilon}) \varepsilon(y - \bar{x}^{\varepsilon}) + O(\varepsilon^{2} |\bar{x}^{\varepsilon} - y|^{2})] u^{\varepsilon}(y) \, \mathrm{d}y \right| \\ &+ \|\partial_{1} d\|_{\infty} \int_{|z| > C, z \in \mathbb{R}} \frac{\|m\|_{\infty} \|u^{\varepsilon}\|_{L^{1}(\varepsilon^{-1}X)}}{\frac{1}{2} \delta z^{2}} \, \mathrm{d}z \\ &\leqslant \left| \varepsilon \partial_{12}^{2} d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \bar{x}^{\varepsilon}) \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} (\bar{x}^{\varepsilon} - y) u^{\varepsilon}(y) \, \mathrm{d}y \right| + O(\varepsilon^{2} C^{2}) \|u^{\varepsilon}\|_{L^{1}(\varepsilon^{-1}X)} \\ &+ O(C^{-1}). \end{split}$$
(4.20)

To estimate

$$\int_{|y-\bar{x}^{\varepsilon}|\leqslant C} (\bar{x}^{\varepsilon}-y)u^{\varepsilon}(y)\,\mathrm{d}y,$$

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we use (4.11) as (with $\theta \in (y, \bar{x}^{\varepsilon})$ if $y \leq \bar{x}^{\varepsilon}$, or with $\theta \in (\bar{x}^{\varepsilon}, y)$ otherwise, and, in particular, $|\theta - \bar{x}^{\varepsilon}| \leq C$)

$$\begin{split} \int_{|y-\bar{x}^{\varepsilon}|\leqslant C} (\bar{x}^{\varepsilon} - y)u^{\varepsilon}(y) \,\mathrm{d}y \\ &= \int_{|y-\bar{x}^{\varepsilon}|\leqslant C} \frac{(\bar{x}^{\varepsilon} - y)(\int_{\varepsilon^{-1}X} m(\varepsilon y, \varepsilon z)u^{\varepsilon}(z) \,\mathrm{d}z)}{Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\theta))(y - \bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}} \,\mathrm{d}y \\ &= \int_{|y-\bar{x}^{\varepsilon}|\leqslant C} \frac{(\bar{x}^{\varepsilon} - y)(\int_{\varepsilon^{-1}X} m(\varepsilon y, \varepsilon z)u^{\varepsilon}(z) \,\mathrm{d}z)}{Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}))(y - \bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}} \,\mathrm{d}y \\ &- \int_{|y-\bar{x}^{\varepsilon}|\leqslant C} \frac{(\bar{x}^{\varepsilon} - y)[\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}) - \partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\theta)]/2\varepsilon^{2}}{[Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\theta))(y - \bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}]} \\ &\times \frac{(y - \bar{x}^{\varepsilon})^{2}(\int_{\varepsilon^{-1}X} m(\varepsilon y, \varepsilon z)u^{\varepsilon}(z) \,\mathrm{d}z)}{[Q^{\varepsilon} + (-\partial_{xx}^{2}s^{\varepsilon}[u^{\varepsilon}](\bar{x}^{\varepsilon}))(y - \bar{x}^{\varepsilon})^{2}/2\varepsilon^{2}]} \,\mathrm{d}y \\ &=: I_{1} + I_{2}. \end{split}$$

$$(4.21)$$

We use symmetry arguments to estimate I_1 :

$$\begin{split} I_1 &= \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} \frac{(\bar{x}^{\varepsilon} - y) [\int_{\varepsilon^{-1}X} (m(\varepsilon \bar{x}^{\varepsilon}, \varepsilon z) + O(\varepsilon(\bar{x}^{\varepsilon} - y))) u^{\varepsilon}(z) \, \mathrm{d}z]}{Q^{\varepsilon} + (-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}))(y - \bar{x}^{\varepsilon})^2 / 2\varepsilon^2} \, \mathrm{d}y \\ &= 0 + \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} \frac{(\bar{x}^{\varepsilon} - y) O(\varepsilon(\bar{x}^{\varepsilon} - y))}{Q^{\varepsilon} + (-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}))(y - \bar{x}^{\varepsilon})^2 / 2\varepsilon^2} \, \mathrm{d}y \int_{\varepsilon^{-1}X} u_{\varepsilon}(z) \, \mathrm{d}z \\ &= O(\varepsilon C^2) \left\| \frac{1}{Q^{\varepsilon} + (-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}))(y - \bar{x}^{\varepsilon})^2 / 2\varepsilon^2} \right\|_{L^1(\varepsilon^{-1}X)} \\ &= O(\varepsilon C^2). \end{split}$$

To estimate the term I_2 of (4.21), we note that (recalling that $|\theta - \bar{x}^{\varepsilon}| \leq C$)

$$\begin{aligned} |\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\theta) - \partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon})| &\leq \|\partial_{xxx}^3 s^{\varepsilon} [u^{\varepsilon}]\|_{\infty} (\theta - \bar{x}^{\varepsilon}) \\ &\leq \varepsilon^3 (\|a_{\varepsilon}\|_{W^{3,\infty}} + Cst \|d\|_{W^{3,\infty}}) (\theta - \bar{x}^{\varepsilon}) \\ &\leq Cst \varepsilon^3 C, \end{aligned}$$

and that, due to step 1 (see (4.12)),

$$\frac{(y-\bar{x}^{\varepsilon})^2}{Q_{\varepsilon}+(-\partial_{xx}^2 s^{\varepsilon}[u^{\varepsilon}](\theta))(y-\bar{x}^{\varepsilon})^2/2\varepsilon^2} < \frac{1}{\delta/2}.$$
(4.22)

We can thus estimate the second term of (4.21) using step 1:

$$\begin{split} |I_2| &\leqslant \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} \frac{C[Cst\varepsilon^3 C]/2\varepsilon^2}{\delta/2} \frac{\|m\|_{\infty} Cst}{[Q^{\varepsilon} + (-\partial_{xx}^2 s^{\varepsilon} [u^{\varepsilon}](\bar{x}^{\varepsilon}))(y-\bar{x}^{\varepsilon})^2/2\varepsilon^2]} \, \mathrm{d}y \\ &\leqslant Cst\varepsilon C^2 \int_{\mathbb{R}} \frac{\mathrm{d}y}{[Q^{\varepsilon} + \delta y^2/2]} \\ &\leqslant O(\varepsilon C^2). \end{split}$$

Using these estimates in (4.20), we obtain

$$\left| \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} (\bar{x}^{\varepsilon} - y) u^{\varepsilon}(y) \, \mathrm{d}y \right| \leqslant O(\varepsilon C^2),$$

and then \bar{x}^{ε} can be estimated, due to (4.20), as

$$\begin{split} |\bar{x}^{\varepsilon}| &\leqslant \frac{1}{\varepsilon |a_{\varepsilon}''(\varepsilon\theta)|} \left| \int_{\varepsilon^{-1}X} \partial_1 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon y) u^{\varepsilon}(y) \, \mathrm{d}y \right| \\ &= \frac{1}{\varepsilon |a_{\varepsilon}''(\varepsilon\theta)|} \left[\left| \varepsilon \partial_{12}^2 d(\varepsilon \bar{x}^{\varepsilon}, \varepsilon \bar{x}^{\varepsilon}) \int_{|y-\bar{x}^{\varepsilon}| \leqslant C} (\bar{x}^{\varepsilon} - y) u^{\varepsilon}(y) \, \mathrm{d}y \right| \\ &\quad + O(\varepsilon^2 C^2) + O(C^{-1}) \right] \\ &\leqslant \frac{1}{\varepsilon} [\varepsilon O(\varepsilon C^2) + O(\varepsilon^2 C^2) + O(C^{-1})] \\ &\leqslant O(\varepsilon C^2) + O(\varepsilon^{-1} C^{-1}). \end{split}$$

If we choose $C := \varepsilon^{-2/3}$, then, for $\varepsilon > 0$ small enough, the assumption $[\bar{x}^{\varepsilon} - C, \bar{x}^{\varepsilon} + C] \subset \varepsilon^{-1}X$ (assumed on C at the beginning of this proof) is satisfied since, by step 2,

$$[\bar{x}^{\varepsilon} - C, \bar{x}^{\varepsilon} + C] \subset B(0, |\bar{x}^{\varepsilon}| + \varepsilon^{-2/3})$$
$$\subset B(0, O(\varepsilon^{-1/2}) + \varepsilon^{-2/3})$$
$$\subset \varepsilon^{-1}X.$$

Our estimates then apply to this specific choice of C, and yield the following estimate on \bar{x}^{ε} :

$$\bar{x}^{\varepsilon} = O(\varepsilon^{-1/3}).$$

This last result ends the proof of the theorem.

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References

- N. H. Barton and M. Turelli. Evolutionary quantitative genetics: how little do we know? A. Rev. Genet. 23 (1989), 337–370.
- 2 G. Bell and A. Gonzalez. Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* **12** (2009), 942–948.
- 3 S. Brown and T. L. Vincent. Coevolution as an evolutionary game. *Evolution* **41** (1987), 66–79.

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- 4 J. J. Bull, R. Sanjuán and C. O. Wilke. Theory of lethal mutagenesis for viruses. J. Virol. 81 (2007), 2930–2939.
- 5 R. Bürger. The mathematical theory of selection, recombination, and mutation, Wiley Series in Mathematical and Computational Biology (Chichester: Wiley, 2000).
- 6 R. Bürger and I. M. Bomze. Stationary distributions under mutation-selection balance: structure and properties. *Adv. Appl. Prob.* **28** (1996), 227–251.
- 7 R. Bürger and J. Hofbauer. Mutation load and mutation-selection balance in quantitative genetic traits. J. Math. Biol. **32** (1994), 193–218.
- 8 À. Calsina and S. Cuadrado. Small mutation rate and evolutionarily stable strategies in infinite-dimensional adaptive dynamics. J. Math. Biol. 48 (2004), 135–159.
- 9 À. Calsina and S. Cuadrado. Stationary solutions of a selection mutation model: the pure mutation case. Math. Models Meth. Appl. Sci. 15 (2005), 1091–1117.
- À. Calsina and C. Perelló. Equations for biological evolution. Proc. R. Soc. Edinb. A 125 (1995), 939–958.
- À. Calsina, C. Perelló and J. Saldaña. Non-local reaction-diffusion equations modelling predator-prey coevolution. *Publ. Mat.* 38 (1994), 315–325.
- 12 N. Champagnat, R. Ferrière and S. Méléard. Unifying evolutionary dynamics: from individual stochastic processes to macroscopic models. *Theor. Population Biol.* 69 (2006), 297–321.
- 13 J. Cleveland and A. S. Ackleh. Evolutionary game theory on measure spaces: well-posedness. Nonlin. Analysis Real World Applic. 14 (2013), 785–797.
- 14 J. F. Crow and M. Kimura. The theory of genetic loads. In Proc XIth International Congress of Genetics, pp. 495–505 (Oxford: Pergamon, 1964).
- 15 S. Cuadrado. Equilibria of a predator–prey model of phenotype evolution. J. Math. Analysis Applic. **354** (2009), 286–294.
- 16 L. Desvillettes, P. E. Jabin, S. Mischler and G. Raoul. On selection dynamics for continuous structured population models. *Commun. Math. Sci.* **6** (2008), 729–747.
- 17 U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. Nature 400 (1999), 354–357.
- 18 U. Dieckmann and R. Law. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34 (1996), 579–612.
- 19 O. Diekmann, P. E. Jabin, S. Mischler and B. Perthame. The dynamics of adaptation: an illuminating example and a Hamilton–Jacobi approach. *Theor. Population Biol.* 67 (2005), 257–271.
- 20 M. Doebeli and U. Dieckmann. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. Am. Nat. 156 (2000), 77–101.
- 21 R. Gomulkiewicz and R. D. Holt. When does evolution by natural selection prevent extinction? *Evolution* 49 (1995), 201–207.
- 22 I. Gudelj, C. D. Coman and R. E. Beardmore. Classifying the role of trade-offs in the evolutionary diversity of pathogens. *Proc. R. Soc. Lond.* A **462** (2006), 97–116.
- 23 O. Hallatschek. The noisy edge of traveling waves. Proc. Natl Acad. Sci. USA 108 (2011), 1783–1787.
- 24 D. L. Hartl and A. G. Clark. *Principles of population genetics*, 4th edn (Sunderland, MA: Sinauer, 2007).
- 25 M. Kimura. A stochastic model concerning the maintenance of genetic variability in quantitative characters. Proc. Natl Acad. Sci. USA 54 (1965), 731–736.
- 26 J. F. C. Kingman. A simple model for the balance between selection and mutation. J. Appl. Probab. 15 (1978), 1–12.
- 27 A. S. Kondrasov. Deleterious mutations and the evolution of sexual reproduction. *Nature* 336 (1988), 435–440.
- 28 P. Magal and G. F. Webb. Mutation, selection and recombination in a model of phenotype evolution. Discrete Contin. Dynam. Syst. 6 (2000), 221–236.
- 29 J. A. J. Metz, S. A. H. Geritz, G. Meszéna, F. A. J. Jacobs and J. S. van Heerwaasden. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and spatial structures of dynamical systems* (ed. S. J. van Strien and S. M. Verduyn Lunel), pp. 183–231 (Amsterdam: North-Holland, 1996).

- 30 S. D. Mylius and O. Diekmann. On evolutionary unbeatable life histories, optimization and the need to be specific about density dependence. *Oikos* 74 (1995), 218–224.
- J. Polechová and N. H. Barton. Speciation through competition: a critical review. *Evolution* 59 (2005), 1194–1210.
- 32 G. Raoul. Long time evolution of populations under selection and vanishing mutations. Acta Appl. Math. **114** (2011), 1–14.
- 33 J. Roughgarden and J. Roughgarden. *Theory of population genetics and evolutionary ecology* (New York, NY: Macmillan, 1979).
- 34 D. B. Saakian. A new method for the solution of models of biological evolution: derivation of exact steady-state distributions. J. Statist. Phys. 128 (2007), 781–798.
- 35 J. Saldaña, S. F. Elena and R. V. Solé. Coinfection and superinfection in RNA populations: a selection–mutation model. *Math. Biosci.* **183** (2003), 135–160.
- 36 A. Sasaki. Clumped distribution by neighborhood competition. J. Theor. Biol. 186 (1997), 415–430.
- 37 A. Sasaki and H. C. J. Godfray. A model for the coevolution of resistance and virulence in coupled host-parasitoid interactions. Proc. R. Soc. Lond. B 266 (1999), 455–463.
- 38 M. Turelli. Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theor. Population Biol.* 25 (1984), 138–193.
- 39 M. Turelli. Effects of pleiotropy on predictions concerning mutation-selection balance for polygenic traits. *Genetics* **111** (1985), 165–195.
- D. Waxman. Numerical and exact solutions for continuum of alleles models. J. Math. Biol.
 46 (2003), 225–240.
- 41 D. Waxman and J. Feng. Implications of long tails in the distribution of mutant effects. *Physica* D 206 (2005), 265–274.
- 42 D. Waxman and J. R. Peck. Pleiotropy and the preservation of perfection. Science 279 (1998), 1210–1213.
- 43 D. Waxman and J. R. Peck. The frequency of the perfect genotype in a population subject to pleiotropic mutation. *Theor. Population Biol.* **69** (2006), 409–418.

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