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► **To cite this version:**

Matthieu Alfaro, Quentin Griette, Denis Roze, Benoît Sarels. The spatio-temporal dynamics of interacting genetic incompatibilities. Part I: The case of stacked underdominant clines. 2021. hal-03109887v1

HAL Id: hal-03109887

<https://hal.science/hal-03109887v1>

Preprint submitted on 14 Jan 2021 (v1), last revised 19 Mar 2021 (v2)

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The dynamics of coupled genetic incompatibilities in parapatry

Matthieu Alfaro ¹, Quentin Griette ², Denis Roze ³ and Benoît Sarels ⁴.

Abstract

In this paper, we explore the interaction between two genetic incompatibilities (underdominant loci in diploid organisms) in a population occupying a one-dimensional space. We derive a partial differential equation system describing the dynamics of allele frequencies and linkage disequilibrium between the two loci, and use a quasi linkage equilibrium approximation in order to reduce the number of variables. We investigate the solutions of this system and demonstrate the existence of a solution in which the two clines in allele frequency remain stucked together. In the case of asymmetric incompatibilities (*i.e.*, when one homozygote is favored over the other at each locus), these coupled clines move as a traveling wave. The two cases of interest (standing together and traveling together) are studied and results are established accordingly.

Keywords: genetic incompatibilities, heterozygote inferior case, quasi linkage equilibrium, standing wave, traveling wave, perturbation analysis.

1 Introduction

The evolution of reproductive isolation between incipient species corresponds to the accumulation of genetic incompatibilities among different groups of individuals, which may occur in the presence or in the absence of gene flow between them [7], [10]. Incompatibilities are thought to be mainly caused by epistatic interactions among loci (Dobzhansky–Muller incompatibilities, [8], [11]) and are revealed by experiments in which a portion of the genome of a species is introgressed into the genome of another (e.g., Table 1 in [9]). As shown by [4], different incompatibilities segregating in the same population (sympatry) are expected to become coupled through the buildup of linkage disequilibrium among them. A similar coupling phenomenon is also expected to occur in parapatry (restricted gene flow due to the limited dispersal of individuals). Indeed, genetic incompatibilities may generate clines in allele frequencies [2], while clines generated by different incompatibilities will tend to attract each other until they coincide, due to the fact that the migration of individuals generates linkage disequilibrium among loci involved in those incompatibilities [3].

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In this paper, we explore the dynamics of coupled genetic incompatibilities in a population occupying a continuous, linear habitat. As in [3], we focus on a simple example of incompatibility corresponding to selection against heterozygotes in diploid organisms (underdominance). This form of selection may generate clines in allele frequency, whose width depends on the average dispersal distance of individuals and on the strength of selection against heterozygotes [6], [2]. The interaction between several underdominant loci was explored by [3] in the symmetric case (both homozygotes have the same fitness), who showed that linkage disequilibria between loci generated by gene flow between spatial locations with different allele frequencies tend to increase the effective strength of selection against heterozygotes and steepens the clines. Here, we consider the asymmetric situation in which one homozygote is fitter than the other homozygote at each underdominant locus. In this case, the fitter homozygote tends to spread, causing the cline to move as a traveling wave [2]. We will consider the scenario in which two such incompatibilities are coupled, and use a perturbation argument to demonstrate the existence of a single traveling wave and quantify its speed.

The organization of the paper is as follows. In Section 2 we derive the mathematical model, a PDE system involving nonlinear gradient terms. Through a phase plane analysis, we construct stationary solutions in Section 3. Then, in Section 4, we construct traveling fronts thanks to a perturbation argument. We conclude and present some perspectives in Section 5.

2 Derivation of the mathematical model

The PDEs describing the dynamics of two underdominant loci in a 1-dimensional continuous habitat can be obtained by combining the works [2] and [3]. For the self-containedness of the present work, we present here a derivation of these equations, obtained by approximating a discrete-time model by a continuous-time model.

2.1 Selection stage in a discrete in time setting

We start by considering a single population of diploid, hermaphroditic individuals with nonoverlapping generations. At the end of a generation (at time t), individuals release gametes and immediately die. The next generation, at time $t+1$, is formed by the random fusion of gametes. Under these hypotheses, it is sufficient to follow the frequencies of gametes produced at each generation, which completely determine the next generation of individuals (by the law of large numbers).

Let us go into more details. We consider that the fitness of a (diploid) individual is affected by two loci: a first locus with two alleles A and a and a second locus with two alleles B and b . We assume that heterozygotes have the lowest fitness (underdominance), the fitness of the different genotypes at each locus being given by:

genotype	fitness	genotype	fitness
AA	$1 + 2s_A$	BB	$1 + 2s_B$
Aa	$1 + s_A - S_A$	Bb	$1 + s_B - S_B$
aa	1	bb	1

where the constants s_A, s_B, S_A, S_B satisfy $0 \leq s_A < S_A$, $0 \leq s_B < S_B$. We then assume multiplicative effects among loci, so that the fitnesses \mathcal{W} of two-locus genotypes are given by:

	AA	Aa	aa
BB	$(1 + 2s_B)(1 + 2s_A)$	$(1 + 2s_B)(1 + s_A - S_A)$	$1 + 2s_B$
Bb	$(1 + s_B - S_B)(1 + 2s_A)$	$(1 + s_B - S_B)(1 + s_A - S_A)$	$1 + s_B - S_B$
bb	$1 + 2s_A$	$1 + s_A - S_A$	1

(however, because we will derive expressions to the first order in s_A , s_B , S_A and S_B , assuming additive effects among loci would lead to the same results). Denote by y_A^A , y_B^A , y_B^a , y_b^a the frequencies of the different types of gametes at generation t . The fusion at random of these four combinations gives birth to sixteen types of individuals (“ordered” in the sense that $z_{i|j} \neq z_{j|i}$ for $i \neq j$)

$$z_{i|j}, \quad i, j \in \{B^A, B^a, b^A, b^a\},$$

with proportions $p_{i|j}$. Notice that, for $i \neq j$, the fusion can be male-female or female-male so that we have $p_{i|j} = 2 \times \frac{1}{2} y_i y_j$, thus

$$p_{i|j} = y_i y_j.$$

Each one of these individuals then produces gametes according to its fitness, providing the generation of gametes y_B^A , y_b^A , y_B^a , y_b^a at time $t + 1$. Here we assume that there is a probability of recombination $0 \leq r \leq \frac{1}{2}$ between the two loci. For each of the sixteen diploid genotypes, the process is as one of the three following examples:

- the individuals $z_{B^A|B^A}$, whose proportion is $y_B^A{}^2$, release gametes B^A in proportion 1.
- the individuals $z_{B^A|b^A}$, whose proportion is $y_B^A y_b^A$, release gametes B^A in proportion $\frac{1}{2}$ and gametes b^A in proportion $\frac{1}{2}$.
- the individuals $z_{B^A|b^a}$, whose proportion is $y_B^A y_b^a$, release gametes B^A and b^a both in proportion $\frac{1-r}{2}$ (no recombination), and gametes b^A and B^a both in proportion $\frac{r}{2}$ (recombination).

All these processes are weighted by the fitness of each type of individual, as in the above table. After a tedious but straightforward analysis, one obtains:

$$\begin{aligned} y_B^A &= \frac{1}{\overline{W}} \left[(1 + 2s_A)(1 + 2s_B)y_B^A{}^2 + (1 + 2s_A)(1 + s_B - S_B)y_B^A y_b^A + (1 + s_A - S_A)(1 + 2s_B)y_B^A y_B^a \right. \\ &\quad \left. + (1 - r)(1 + s_A - S_A)(1 + s_B - S_B)y_B^A y_b^a + r(1 + s_A - S_A)(1 + s_B - S_B)y_B^a y_b^A \right] \\ y_b^A &= \frac{1}{\overline{W}} \left[(1 + 2s_A)y_b^A{}^2 + (1 + 2s_A)(1 + s_B - S_B)y_b^A y_B^A + (1 + s_A - S_A)y_b^A y_b^a \right. \\ &\quad \left. + (1 - r)(1 + s_A - S_A)(1 + s_B - S_B)y_b^A y_B^a + r(1 + s_A - S_A)(1 + s_B - S_B)y_B^A y_b^a \right] \\ y_B^a &= \frac{1}{\overline{W}} \left[(1 + 2s_B)y_B^a{}^2 + (1 + s_B - S_B)y_B^a y_b^a + (1 + s_A - S_A)(1 + 2s_B)y_B^a y_B^A \right. \\ &\quad \left. + (1 - r)(1 + s_A - S_A)(1 + s_B - S_B)y_B^a y_b^A + r(1 + s_A - S_A)(1 + s_B - S_B)y_B^A y_b^a \right] \\ y_b^a &= \frac{1}{\overline{W}} \left[y_b^a{}^2 + (1 + s_A - S_A)y_b^a y_B^A + (1 + s_B - S_B)y_b^a y_B^a \right. \\ &\quad \left. + (1 - r)(1 + s_A - S_A)(1 + s_B - S_B)y_b^a y_B^A + r(1 + s_A - S_A)(1 + s_B - S_B)y_B^a y_b^A \right], \end{aligned}$$

where \overline{W} is the average fitness:

$$\overline{W} = \sum_{i,j \in \{B^A, B^a, b^A, b^a\}} z_{i|j} \mathcal{W}_{i|j}$$

$$\begin{aligned}
&= (1 + 2s_A)(1 + 2s_B)y_B^2 + (1 + 2s_A)y_b^2 + (1 + 2s_B)y_B^2 + y_b^2 \\
&+ 2(1 + 2s_A)(1 + s_B - S_B)y_B y_b^a + 2(1 + s_A - S_A)(1 + 2s_B)y_B y_b^a \\
&+ 2(1 + s_A - S_A)(1 + s_B - S_B)y_B y_b^a + 2(1 + s_A - S_A)(1 + s_B - S_B)y_b y_B^a \\
&+ 2(1 + s_A - S_A)y_b y_B^a + 2(1 + s_B - S_B)y_b y_B^a.
\end{aligned}$$

Notice that adding the four above equations, one can check $y'_B + y'_b + y'_B + y'_b = \frac{\overline{W}}{W} = 1$.

For ease of notation, we now let

$$u := y_B, \quad v := y_b, \quad w := y_B^a, \quad z := y_b^a, \quad (1)$$

so that

$$u + v + w + z = 1. \quad (2)$$

As in [3], we shall rather work on the three components system satisfied by

$$p := u + v, \quad q := u + w, \quad D := uz - vw, \quad (3)$$

where

- p measures the frequency of allele A ,
- q measures the frequency of allele B ,
- D stands for the linkage disequilibrium, measuring the association between alleles A and B within gametes (notice than, equivalently, $D = u - pq$).

Notice that

$$u = pq + D, \quad v = p(1 - q) - D, \quad w = (1 - p)q - D, \quad z = (1 - p)(1 - q) + D. \quad (4)$$

Next, we assume that s_A, s_B, S_A, S_B, r are small and of the same order of magnitude, that is

$$s_A \leftarrow s_A \alpha, \quad s_B \leftarrow s_B \alpha, \quad S_A \leftarrow S_A \alpha, \quad S_B \leftarrow S_B \alpha, \quad r \leftarrow r \alpha, \quad (5)$$

for $0 < \alpha \ll 1$. Taking into account (1), (2), (3), (4), (5), one can perform straightforward (but tedious) computations and obtain to the first order in α :

$$\begin{cases} p' &= p + \alpha \left[(S_A(2p - 1) + s_A)p(1 - p) + (S_B(2q - 1) + s_B)D \right] \\ q' &= q + \alpha \left[(S_B(2q - 1) + s_B)q(1 - q) + (S_A(2p - 1) + s_A)D \right] \\ D' &= D - \alpha \left[r + (2p - 1)(S_A(2p - 1) + s_A) + (2q - 1)(S_B(2q - 1) + s_B) \right] D. \end{cases} \quad (6)$$

2.2 Inserting a spatial structure and switching to continuous time

Finally we consider the associated problem with a spatial structure $x \in \mathbb{R}$ (corresponding to the position of individuals along space) and continuous time $t \geq 0$. More precisely, we assume that gametes migrate according to a dispersal kernel centered on 0 and with variance σ^2 . In the diffusion limit, and from (6), the equations for the frequencies $p = p(t, x)$, $q = q(t, x)$ are

$$\begin{cases} p_t &= \frac{\sigma^2}{2} p_{xx} + (S_A(2p - 1) + s_A)p(1 - p) + (S_B(2q - 1) + s_B)D \\ q_t &= \frac{\sigma^2}{2} q_{xx} + (S_B(2q - 1) + s_B)q(1 - q) + (S_A(2p - 1) + s_A)D, \end{cases}$$

where $\sigma > 0$. As for the equation for the disequilibrium $D = uz - vw$, we have additional gradient terms (e.g., [5], [3]) since

$$\begin{aligned} D_t &= \left(\frac{\sigma^2}{2} u_{xx} + \dots \right) z + u \left(\frac{\sigma^2}{2} z_{xx} + \dots \right) - \left(\frac{\sigma^2}{2} v_{xx} + \dots \right) w - v \left(\frac{\sigma^2}{2} w_{xx} + \dots \right) \\ &= \frac{\sigma^2}{2} (D_{xx} + 2(-u_x z_x + v_x w_x)) + \dots \\ &= \frac{\sigma^2}{2} (D_{xx} + 2(p_x q_x)) + \dots \end{aligned}$$

where we have used the identity

$$p_x q_x = (u + v)_x (u + w)_x = u_x (u_x + v_x + w_x) + v_x w_x = -u_x z_x + v_x w_x.$$

Hence, from (6), the equation for $D = D(t, x)$ is

$$D_t = \frac{\sigma^2}{2} D_{xx} + \sigma^2 p_x q_x - [r + (2p - 1)(S_A(2p - 1) + s_A) + (2q - 1)(S_B(2q - 1) + s_B)] D.$$

2.3 Conclusion and goals

Hence the system for the allele frequencies $p = p(t, x)$, $q = q(t, x)$ and the linkage disequilibrium $D = D(t, x)$ is written

$$\begin{cases} p_t &= \frac{\sigma^2}{2} p_{xx} + (S_A(2p - 1) + s_A) p(1 - p) + (S_B(2q - 1) + s_B) D \\ q_t &= \frac{\sigma^2}{2} q_{xx} + (S_B(2q - 1) + s_B) q(1 - q) + (S_A(2p - 1) + s_A) D \\ D_t &= \frac{\sigma^2}{2} D_{xx} + \sigma^2 p_x q_x - [r + (2p - 1)(S_A(2p - 1) + s_A) + (2q - 1)(S_B(2q - 1) + s_B)] D, \end{cases} \quad (7)$$

where $\sigma > 0$, $r > 0$, $s_A > 0$, $s_B > 0$, $S_A > 0$ and $S_B > 0$ are given parameters. When $D \equiv 0$ (no disequilibrium), the dynamics of p and q are decoupled but the gradient terms p_x and q_x cause disequilibrium and thus coupling [3].

In the sequel, we use a simplified version of system (7) by using a *quasi linkage equilibrium* approximation: assuming that recombination r is sufficiently large relative to the strength of selection against heterozygotes (S_A , S_B , determining the gradients in allele frequencies, e.g., [2]), one expects that the linkage disequilibrium D should remain small ($D \ll 1$) as well as its derivatives, see [3]. Then D approximately follows

$$D_t \approx \sigma^2 p_x q_x - r D,$$

and we then reach a quasi equilibrium situation where

$$D \approx \frac{\sigma^2}{r} p_x q_x. \quad (8)$$

As a result, the system is recast (for simplicity we select $\frac{\sigma^2}{2} = 1$)

$$\begin{cases} p_t &= p_{xx} + S_A f(p) + s_A g(p) + \frac{2}{r} (S_B(2q - 1) + s_B) p_x q_x, \\ q_t &= q_{xx} + S_B f(q) + s_B g(q) + \frac{2}{r} (S_A(2p - 1) + s_A) p_x q_x, \end{cases}$$

where

$$f(u) := u(2u - 1)(1 - u), \quad g(u) := u(1 - u).$$

Last, we assume that

$$S_A = S_B = S, \quad s_A = s_B = \varepsilon, \quad (9)$$

and thus focus on the system

$$\begin{cases} p_t = p_{xx} + Sf(p) + \varepsilon g(p) + \frac{2}{r}(S(2q-1) + \varepsilon)p_x q_x, \\ q_t = q_{xx} + Sf(q) + \varepsilon g(q) + \frac{2}{r}(S(2p-1) + \varepsilon)p_x q_x. \end{cases} \quad (10)$$

Notice that f is a balanced bistable nonlinearity, which is slightly unbalanced by the term εg .

In the sequel, our goal is to inquire on conditions insuring that the A cline, measured by p , and the B cline, measured by q , remain “sticked together”. To do so we look after $u = p = q$ solving the nonlinear equation

$$u_t = u_{xx} + Sf(u) + \varepsilon g(u) + \frac{2}{r}(S(2u-1) + \varepsilon)u_x^2. \quad (11)$$

We suspect the existence of a stationary solution connecting 1 to 0 for $\varepsilon = 0$ and that of a front connecting 1 to 0 and traveling at a speed $c_\varepsilon \sim \varepsilon$ for $\varepsilon > 0$ (at least sufficiently small). These facts are proved in Section 3 and 4.

3 Standing together ($\varepsilon = 0$)

In this section, we construct a stationary solution connecting 1 to 0 in (11) when $\varepsilon = 0$, and then prove its stability.

3.1 Construction of the standing wave

We are here looking after a $u_0 : \mathbb{R} \rightarrow \mathbb{R}$ solving

$$\begin{cases} u_0'' + Sf(u_0) + \frac{2}{r}S(2u_0-1)(u_0')^2 = 0 & \text{on } \mathbb{R}, \\ u_0(-\infty) = 1, \quad u_0(+\infty) = 0. \end{cases} \quad (12)$$

Lemma 3.1 (A priori estimates). *Any standing wave solution of (12) has to satisfy $0 < u_0 < 1$ and $u_0'(\pm\infty) = 0$.*

Proof. If $u_0 \leq 1$ is not true then, from the boundary conditions, u_0 has to reach a maximum value strictly larger than 1 at some point but, testing the equation at this point, this cannot hold. Hence $u_0 \leq 1$ and, from the strong maximum principle, $u_0 < 1$. Similarly $u_0 > 0$.

From the equation and the boundary condition, $u_0' > 0$ in some $(A, +\infty)$, so that u_0' is increasing on $(A, +\infty)$. As a result u_0' has a limit in $+\infty$, which has to be zero since u_0 is bounded. Similarly $u_0'(-\infty) = 0$. \square

Using a phase plane analysis $(x, y) = (u_0, u_0')$, the equation in (12) is recast

$$\begin{cases} x' = y \\ y' = -Sf(x) - \frac{2}{r}S(2x-1)y^2. \end{cases} \quad (13)$$

The phase plane analysis is depicted in Figure 1. The equilibria $(0, 0)$ and $(1, 0)$ are saddle points, the eigenvalues of the Jacobian matrix at these points being $\pm\sqrt{S}$, whereas the equilibrium $(\frac{1}{2}, 0)$ is a center, the eigenvalues of the Jacobian matrix at this point being

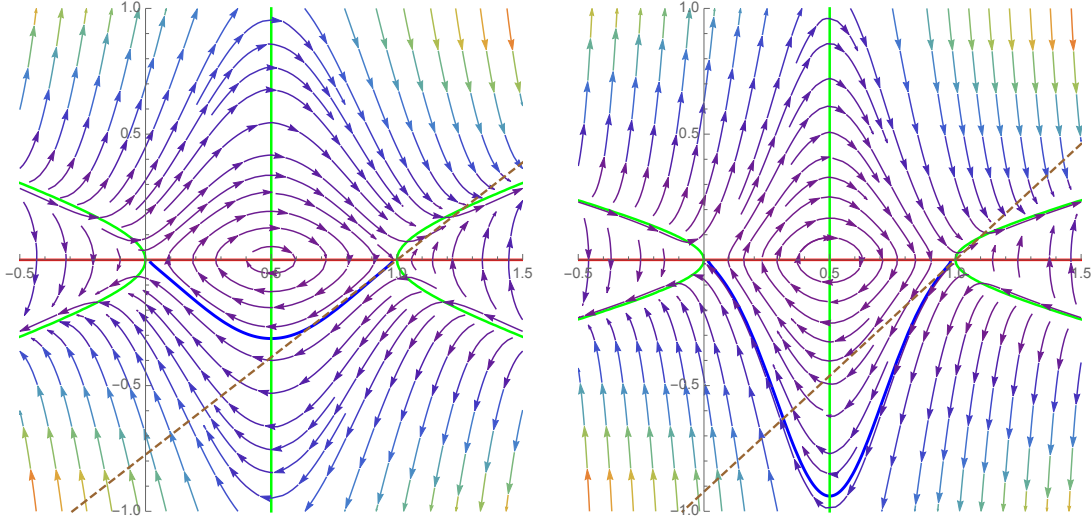


Figure 1: Phase plane analysis for (13). In red, the nullcline $x' = 0$, in green the nullcline $y' = 0$, in brown dashed the linear unstable manifold at $(1, 0)$, in blue (an approximation of) the heteroclinic orbit from $(1, 0)$ to $(0, 0)$. Left: the parameters are $S = 0.6$, $r = 0.25$ so that (14) holds. Right: the parameters are $S = 0.85$, $r = 0.15$ so that (14) does not hold.

$\pm i\sqrt{\frac{S}{2}}$. At equilibrium $(1, 0)$ the linear unstable manifold is the line $y = \sqrt{S}(x - 1)$. To prove the existence of a heteroclinic orbit from $(1, 0)$ to $(0, 0)$, we consider the orbit leaving $(1, 0)$ along the unstable manifold. As long as it has not reached $x = \frac{1}{2}$ this trajectory satisfies $x' < 0$ and $y' < 0$ (south west trajectory). In order to prove that the trajectory does cross the vertical line $x = \frac{1}{2}$, we need to construct a barrier, from below, preventing the situation $x \rightarrow l \geq \frac{1}{2}$, $y \rightarrow -\infty$. We choose the line $y = \alpha(x - 1)$ with $\alpha > 0$ to be selected large enough. Choosing $\alpha > \sqrt{S}$ insures that the trajectory is above the barrier in a neighborhood of $(1, 0)$. We thus need to show that

$$\frac{|y'|}{|x'|} < \alpha \quad \text{on the points } (x, y) \text{ such that } y = \alpha(x - 1), \frac{1}{2} \leq x < 1.$$

After some straightforward computations, this is recast

$$\varphi(x) := (2x - 1) \left| \left(1 - \frac{2\alpha^2}{r} \right) x + \frac{2\alpha^2}{r} \right| < \frac{\alpha^2}{S}, \quad \text{for all } \frac{1}{2} \leq x < 1.$$

Assuming $1 - \frac{2\alpha^2}{r} < 0$, and evaluating the maximum of φ on $[\frac{1}{2}, 1]$, we reach

$$\frac{\left(\frac{2\alpha^2}{r} + 1 \right)^2}{8 \left(\frac{2\alpha^2}{r} - 1 \right)} < \frac{\alpha^2}{S},$$

which can be obtained with α sufficiently large provided

$$S < 4r. \tag{14}$$

Notice that, from the modelling point of view, assumption (14) is consistent with the asymptotics “ S small” performed in Section 2 (quasi linkage equilibrium approximation).

On the other hand, even if (14) does not hold, the (right) phase plane analysis of Figure 1 suggests that the heteroclinic orbit joining $(1, 0)$ to $(0, 0)$ still exists, but the above argument does not apply.

As a result, under assumption (14), the orbit touches the line $x = \frac{1}{2}$ at some point $(\frac{1}{2}, -\beta)$ for some $\beta > 0$. Since the problem is symmetric with respect to $x = \frac{1}{2}$, we conclude that the orbit then converges to the equilibrium $(0, 0)$ along the stable manifold, the linear stable manifold being given by $y = -\sqrt{S}x$. This trajectory provides a positive and decreasing solution u_0 to (12).

In other words, we have (nearly) proved the following.

Proposition 3.2 (Stationary solution for $\varepsilon = 0$). *Let us assume (14). Then there is a unique $u_0 : \mathbb{R} \rightarrow \mathbb{R}$ solving (12) and satisfying the normalization condition $u_0(0) = \frac{1}{2}$.*

Moreover, u_0 is positive, decreasing, symmetric in the sense that

$$u_0(-x) = 1 - u_0(x) \quad \text{for all } x \in \mathbb{R},$$

and has the asymptotics

$$1 - u_0(x) \sim C e^{\sqrt{S}x} \text{ as } x \rightarrow -\infty, \quad u_0(x) \sim C e^{-\sqrt{S}x} \text{ as } x \rightarrow +\infty, \quad (15)$$

for some $C > 0$.

Proof. From the above phase plane analysis, we are already equipped with a positive, decreasing and symmetric u_0 solving (12). The asymptotics (15) is rather classical but, for the convenience of the reader, we sketch a short and direct proof. We work as $x \rightarrow +\infty$. We know from the phase plane analysis that $u'_0(x) \sim -\sqrt{S}u_0(x)$ so that

$$u_0(x) = e^{-\sqrt{S}x + o(x)}. \quad (16)$$

Now, from the nonlinear ODE, we have, for some $K > 0$,

$$-K u_0^2(x) \leq u_0''(x) - S u_0(x) \leq K u_0^2(x).$$

Multiplying this by $u'_0(x) < 0$ and integrating from x to $+\infty$, we have,

$$-\frac{K}{3} u_0^3(x) \leq -\frac{1}{2} (u'_0)^2(x) + \frac{S}{2} u_0^2(x) \leq \frac{K}{3} u_0^3(x),$$

so that, for some $M > 0$,

$$-M u_0^2(x) \leq u'_0(x) + \sqrt{S} u_0(x) \leq M u_0^2(x). \quad (17)$$

From this and (16) we deduce that $e^{\sqrt{S}x} (u'_0(x) + \sqrt{S} u_0(x)) = \frac{d}{dx} (e^{\sqrt{S}x} u_0(x))$ must be integrable in $+\infty$. As a result there is $C \geq 0$ such that $e^{\sqrt{S}x} u_0(x) \rightarrow C$ as $x \rightarrow +\infty$. Now the left inequality in (17) implies

$$-\sqrt{S} \leq \frac{u'_0}{u_0 + \frac{M}{\sqrt{S}} u_0^2} = \frac{u'_0}{u_0} - \frac{\frac{M}{\sqrt{S}} u'_0}{1 + \frac{M}{\sqrt{S}} u_0}.$$

Integrating this from 0 to x provides $\frac{u_0(0)}{1 + \frac{M}{\sqrt{S}} u_0(0)}$ as a positive lower bound for $e^{\sqrt{S}x} u_0(x)$ so that $C > 0$ and we are done with (15).

It remains to prove uniqueness. We use a sliding method argument. Let v_0 be “another” solution such that $v_0(0) = \frac{1}{2}$. For $K \geq 0$, define the shifted function $v_K(x) := v_0(x - K)$. Since v_0 must also have some asymptotics of the form (15), say with some constant $C' > 0$ instead of C , we see that $u_0 \leq v_K$ on \mathbb{R} for $K > 0$ sufficiently large. As a result the real number

$$K_0 := \inf \{K \in \mathbb{R} : u_0(x) \leq v_K(x), \forall x \in \mathbb{R}\}$$

is well defined and nonnegative. Assume by contradiction that $K_0 > 0$. Then there is a point $x_0 \in \mathbb{R}$ where $u_0(x_0) = v_{K_0}(x_0)$ and $u_0'(x_0) = v_{K_0}'(x_0)$ so that, from Cauchy-Lipschitz theorem, $u_0 \equiv v_{K_0}$ on \mathbb{R} , which is excluded by the normalization conditions. As a result $K_0 = 0$ and thus $u_0 \leq v_0$. Similarly $v_0 \leq u_0$ and we are done. \square

3.2 Stability of the standing wave

We prove here that the standing wave constructed in Proposition 3.2 is linearly stable in the L^∞ norm. More precisely the following holds.

Proposition 3.3 (Stability of standing waves). *Let u_0 be the standing wave constructed in Proposition 3.2. Let $h \in C_b^1(\mathbb{R})$ be given. Let v solve the parabolic Cauchy problem*

$$\begin{cases} v_t(t, x) = v_{xx}(t, x) + S f(v(t, x)) + \frac{2}{r} S (2v(t, x) - 1)(v_x(t, x))^2, & t > 0, x \in \mathbb{R}, \\ v(0, x) = u_0(x) + \varepsilon h(x), & x \in \mathbb{R}. \end{cases}$$

Then there is $\lambda_0 > 0$ such that, for any $0 < \lambda < \lambda_0$, the following holds: for sufficiently small ε , there is a continuous function $\gamma(\varepsilon)$ satisfying

$$\gamma(0) = \int_{\mathbb{R}} h(x) u_0'(x) e^{\frac{4S}{r}(u_0^2(x) - u_0(x))} dx,$$

and a constant $K > 0$ such that, for all $t > 0$,

$$\|v(t, \cdot) - u_0(\cdot + \varepsilon \gamma(\varepsilon))\|_{C_b^1(\mathbb{R})} \leq K e^{-\lambda t}.$$

Proof. We aim at applying a result of Sattinger, namely [12, Theorem 4.1]. To do so, we need to show that the linear operator (obtained by linearizing (12) around the solution u_0)

$$Lh := h'' + \frac{4S}{r}(2u_0 - 1)u_0'h' + S \left(f'(u_0) + \frac{4}{r}(u_0')^2 \right) h,$$

satisfies the assumptions (i) and (ii) of [12, Lemma 3.4]. Since equation (12) is a scalar quasilinear second-order differential equation set on \mathbb{R} and with a smooth nonlinearity, the assumption (ii) of [12, Lemma 3.4] can be readily checked thanks to [12, Lemma 5.4]. As for the assumption (i) of [12, Lemma 3.4], we point out that [12, Corollary 5.7] does not apply to our situation, and we thus need to determine the spectrum of L .

The linear operator L admits u_0' as principal eigenvector with eigenvalue 0. We remark that L can be written as

$$Lh = e^{-\frac{2S}{r}(u_0^2 - u_0)} M \left(h e^{\frac{2S}{r}(u_0^2 - u_0)} \right),$$

where

$$Mk := k'' + \left(\frac{2S^2}{r}(2u_0 - 1)f(u_0) + S f'(u_0) \right) k =: k'' + c(x)k.$$

Since the weight function $e^{\frac{4S}{r}(u_0^2-u_0)}$ is bounded and uniformly positive, the operators L and M can be considered as acting on the same space $C_b^0(\mathbb{R})$. In particular, $\lambda I - L$ admits a bounded inverse if and only if $\lambda I - M$ does (where I is the identity mapping on $C_b^0(\mathbb{R})$), and we have

$$(\lambda I - L)^{-1} = e^{-\frac{2S}{r}(u_0^2-u_0)}(\lambda I - M)^{-1}e^{\frac{2S}{r}(u_0^2-u_0)}.$$

Below, by following ideas of [12], we analyze, for $g \in C_b^0(\mathbb{R})$, the set of solutions to the resolvent equation

$$(\lambda I - M)k = -k'' + (\lambda - c(x))k = g(x), \quad (18)$$

and then determine the spectrum of M .

1. System of fundamental solutions to the homogeneous equation: we first look for a system of fundamental solutions to

$$-k'' + (\lambda - c(x))k = 0, \quad (19)$$

whose behaviour near $\pm\infty$ can be determined (see [12, Lemma 5.1] for related arguments) for $\lambda \in \mathbb{C}$ such that $\lambda + S \notin \mathbb{R}^-$.

Near $+\infty$, this is performed by substituting $\varphi_1(x) = z_1(x)e^{-\gamma_+x}$ in (19), where $\gamma_+ \in \mathbb{C}$ solves $\gamma_+^2 = \lambda + S$ and $\text{Re } \gamma_+ > 0$. We obtain

$$-z_1'' + 2\gamma_+z_1' - (S + c(x))z_1 = 0, \quad (20)$$

which is recast

$$-(z_1'e^{-2\gamma_+x})' - (S + c(x))z_1e^{-2\gamma_+x} = 0,$$

so that, assuming $z_1'(+\infty) = 0$,

$$z_1'(x) = \int_x^{+\infty} e^{-2\gamma_+(y-x)}(S + c(y))z_1(y)dy, \quad (21)$$

and thus, assuming $z_1(+\infty) = 1$,

$$z_1(x) = 1 + \int_x^{+\infty} \frac{e^{2\gamma_+(x-y)} - 1}{2\gamma_+}(S + c(y))z_1(y)dy. \quad (22)$$

Hence z_1 is written as the solution of a fixed-point problem (22) set on $C_b^0(\mathbb{R}^+)$. Notice that the asymptotic behaviour (15) of u_0 implies $y \mapsto S + c(y) \in L^1(\mathbb{R}^+)$. As a result, for a given $x_0 > 0$, the right-hand side operator appearing in (22) is globally Lipschitz continuous on $C_b^0([x_0, +\infty))$ with Lipschitz constant $\frac{1}{2|\gamma_+|} \int_{x_0}^{+\infty} |S + c(y)|dy$. Hence, equation (22) has a unique solution z_1 on $C_b^0([x_0, +\infty))$ for x_0 sufficiently large, and this z_1 can be extended to $(-\infty, x_0)$ by solving the adequate Cauchy problem associated with (20). We have therefore constructed a solution $\varphi_1(x) = z_1(x)e^{-\gamma_+x}$ to (19) with $z_1 \in C_b^0(\mathbb{R}^+)$, $z_1(+\infty) = 1$.

By the same procedure, but integrating on $[x_0, x]$ instead of $[x, +\infty)$ in (21), we can construct a solution $\varphi_2(x) = z_2(x)e^{\gamma_+x}$ to (19) with $z_2 \in C_b^0(\mathbb{R}^+)$ provided by the fixed-point problem

$$z_2(x) = 1 + \int_{x_0}^x \frac{1 - e^{-2\gamma_+(x-y)}}{2\gamma_+}(S + c(y))z_2(y)dy.$$

By the continuous dependence of the fixed-point with respect to the parameter x_0 [15, Proposition 1.2], and by selecting x_0 sufficiently large, $z_2(x)$ can be made arbitrarily close to 1. Indeed $z_2(x + x_0)$ is the unique fixed point of the operator

$$T_{x_0}z(x) := 1 + \int_0^x \frac{1 - e^{-2\gamma_+(x-y)}}{2\gamma_+}(S + c(x_0 + y))z(y)dy,$$

and T_{x_0} converges uniformly to the constant operator $T_{+\infty}z \equiv 1$ as $x_0 \rightarrow +\infty$:

$$\|T_{x_0}z - 1\|_{C_b^0([0,+\infty))} \leq \left(\frac{1}{2|\gamma_+|} \int_{x_0}^{+\infty} |S + c(y)|dy \right) \|z\|_{C_b^0([0,+\infty))} \xrightarrow{x_0 \rightarrow \infty} 0.$$

Therefore we have found a system of fundamental solutions (φ_1, φ_2) to (19) whose behaviour near $+\infty$ is known. We can proceed similarly near $-\infty$ and find another system of fundamental solutions (ψ_1, ψ_2) whose behaviour near $-\infty$ is known.

Summarizing, for each $\lambda \in \mathbb{C} \setminus (-\infty, -S]$, we have

$$\varphi_1(x) \approx_{+\infty} e^{-\gamma+x}, \quad \varphi_2(x) \approx_{+\infty} e^{\gamma+x}, \quad \psi_1(x) \approx_{-\infty} e^{\gamma+x}, \quad \psi_2(x) \approx_{-\infty} e^{-\gamma+x}, \quad (23)$$

$$\varphi'_1(x) \approx_{+\infty} e^{-\gamma+x}, \quad \varphi'_2(x) \approx_{+\infty} e^{\gamma+x}, \quad \psi'_1(x) \approx_{-\infty} e^{\gamma+x}, \quad \psi'_2(x) \approx_{-\infty} e^{-\gamma+x}, \quad (24)$$

where $A(x) \approx_{+\infty} B(x)$ means $0 < \liminf_{x \rightarrow +\infty} \frac{|A(x)|}{|B(x)|} \leq \limsup_{x \rightarrow +\infty} \frac{|A(x)|}{|B(x)|} < +\infty$. Notice that, if λ is not an eigenvalue of M , we further know that φ_1 is unbounded as $x \rightarrow -\infty$ (or else it would be an eigenvector), and ψ_1 is unbounded as $x \rightarrow +\infty$. Notice also that the constants involved in the above estimates are locally uniform in λ .

2. Solving equation (18) if $\lambda \in \mathbb{C} \setminus (-\infty, -S]$ is not an eigenvalue of M : from the behaviours near $-\infty$, the functions φ_1 and ψ_1 are linearly independent. Therefore, up to redefining $\varphi_2 = \psi_1$, we may consider that (φ_1, φ_2) is a system of fundamental solutions satisfying

$$\begin{aligned} \varphi_1(x) &\approx_{+\infty} e^{-\gamma+x}, & \varphi_2(x) &\approx_{+\infty} e^{\gamma+x}, & \varphi_1(x) &\approx_{-\infty} e^{-\gamma+x}, & \varphi_2(x) &\approx_{-\infty} e^{\gamma+x}, \\ \varphi'_1(x) &\approx_{+\infty} e^{-\gamma+x}, & \varphi'_2(x) &\approx_{+\infty} e^{\gamma+x}, & \varphi'_1(x) &\approx_{-\infty} e^{-\gamma+x}, & \varphi'_2(x) &\approx_{-\infty} e^{\gamma+x}. \end{aligned}$$

We use the method of variation of constants to solve (18) and straightforwardly reach

$$k(x) = \left(C_1 - \frac{1}{W} \int_{-\infty}^x \varphi_2(y)g(y)dy \right) \varphi_1(x) + \left(C_2 - \frac{1}{W} \int_x^{+\infty} \varphi_1(y)g(y)dy \right) \varphi_2(x),$$

where C_1 and C_2 are arbitrary constants and W is the constant Wronskian $W = W(x) = \varphi_1(x)\varphi'_2(x) - \varphi'_1(x)\varphi_2(x)$. Therefore, there is a unique bounded solution $k(x)$, which corresponds to $C_1 = C_2 = 0$.

Hence, for each $g \in C_b^0(\mathbb{R})$ there exists a unique $k \in C_b^2(\mathbb{R})$ such that $(\lambda I - M)k = g$. By the open mapping theorem, the operator $\lambda I - M$ has a bounded inverse $(\lambda I - M)^{-1} : C_b^0(\mathbb{R}) \rightarrow C_b^2(\mathbb{R}) \hookrightarrow C_b^0(\mathbb{R})$. In particular,

if $\lambda \in \mathbb{C} \setminus (-\infty, -S]$ is not an eigenvalue of M , then λ is in the resolvent set of M .

3. The eigenvalues in $\mathbb{C} \setminus (-\infty, -S]$ of M : if $\lambda \in \mathbb{C} \setminus (-\infty, -S]$ is an eigenvalue of M then, from (23), the eigenvector must be proportional to both φ_1 and ψ_1 , hence φ_1 and ψ_1 are not linearly independent. Hence the Wronskian $\varphi_1\psi'_1 - \varphi'_1\psi_1$ must vanish. Since the Wronskian is analytic in λ (see [12, Lemma 5.2]) and not identically zero, the eigenvalues of M in $\mathbb{C} \setminus (-\infty, -S]$ are isolated.

Let $\lambda \in \mathbb{C} \setminus (-\infty, -S]$ be an eigenvalue of M . Then the associated eigenvector φ is a solution to (18) and the former analysis applies. In particular, φ and φ' converge exponentially fast to 0 near $\pm\infty$ (at rate $\mp\gamma_+$, $\text{Re } \gamma_+ > 0$) and therefore $\varphi \in H^1(\mathbb{R})$. Since M is symmetric on $H^1(\mathbb{R})$, we have in fact $\lambda \in \mathbb{R}$. Reproducing the argument of [12, Theorem 5.5], we see that there are no positive eigenvalues of M .

We conclude from the above analysis that the eigenvalues of M in $\mathbb{C} \setminus (-\infty, -S]$ form a sequence $(\lambda_n)_{n \in \mathbb{N}}$ (with $\lambda_0 = 0$) of isolated values in $(-S, 0]$. As a result the spectrum of M satisfies

$$\sigma(L, C_b^0(\mathbb{R})) = \sigma(M, C_b^0(\mathbb{R})) \subset (-\infty, -S] \cup \{\lambda_n, n \geq 0\}.$$

This shows that the assumption (i) of [12, Lemma 3.4] holds in our case and concludes the proof of Proposition 3.3. \square

4 Traveling together ($0 < \varepsilon \ll 1$)

In this section, we construct a traveling front connecting 1 to 0 in (11), when $0 < \varepsilon \ll 1$, through a perturbation argument from the case $\varepsilon = 0$ studied above.

We are here looking after a nonnegative profile $u : \mathbb{R} \rightarrow \mathbb{R}$ and a speed $c \in \mathbb{R}$ solving

$$\begin{cases} u'' + cu' + Sf(u) + \varepsilon g(u) + \frac{2}{r}(S(2u-1) + \varepsilon)(u')^2 = 0 & \text{on } \mathbb{R}, \\ u(-\infty) = 1, \quad u(+\infty) = 0. \end{cases} \quad (25)$$

Observe that, from the strong maximum principle we have $u > 0$. Also, as in the proof of Lemma 3.1, we have $u < 1$. Hence, we *a priori* know $0 < u < 1$.

We use a perturbation technique and look for u in the form

$$u = u_0 + h,$$

where u_0 is provided by Proposition 3.2 and with, typically, $h(\pm\infty) = h'(\pm\infty) = 0$. Plugging this ansatz into the equation, we see that we need $\mathcal{F}(\varepsilon, c, h) = 0$, where

$$\mathcal{F} : \mathbb{R} \times \mathbb{R} \times E \rightarrow \tilde{E}$$

is defined by

$$\begin{aligned} \mathcal{F}(\varepsilon, c, h) &:= h'' + cu_0' + ch' + S(f(u_0 + h) - f(u_0)) + \varepsilon g(u_0 + h) \\ &\quad + \frac{2}{r}(S(2u_0 + 2h - 1) + \varepsilon)(u_0' + h')^2 - \frac{2}{r}S(2u_0 - 1)(u_0')^2. \end{aligned} \quad (26)$$

As for the function spaces, we choose the weighted Hölder spaces

$$E := C_\mu^{2,\alpha}(\mathbb{R}), \quad \tilde{E} := C_\mu^{0,\alpha}(\mathbb{R}), \quad 0 < \alpha < 1, \quad (27)$$

where, for $k \in \mathbb{N}$,

$$C_\mu^{k,\alpha}(\mathbb{R}) := \left\{ f \in C^k(\mathbb{R}) : \|f\|_{C_\mu^{k,\alpha}(\mathbb{R})} < +\infty \right\}, \quad \|f\|_{C_\mu^{k,\alpha}(\mathbb{R})} := \left\| x \mapsto e^{\mu\sqrt{1+x^2}} f(x) \right\|_{C^{k,\alpha}(\mathbb{R})},$$

for well-chosen $\mu \geq 0$. Here, $C^{k,\alpha}(\mathbb{R})$ denotes the Hölder space consisting of functions of the class C^k , which are continuous and bounded on the real axis \mathbb{R} together with their derivatives of order k , and such that the derivatives of order k satisfy the Hölder condition with the exponent $0 < \alpha < 1$. The norm in this space is the usual Hölder norm.

Our main result in this section then reads as follows.

Theorem 4.1 (Traveling waves for $0 < \varepsilon \ll 1$). *Let $0 \leq \mu < \sqrt{S}$ be given. Let $\mathcal{F} : \mathbb{R} \times \mathbb{R} \times C_\mu^{2,\alpha}(\mathbb{R}) \rightarrow C_\mu^{0,\alpha}(\mathbb{R})$ be defined as in (26).*

Then there is $\varepsilon_0 > 0$ such that, for any $0 \leq \varepsilon \leq \varepsilon_0$, there exists $(c_\varepsilon, h_\varepsilon) \in \mathbb{R} \times E$ such that $\mathcal{F}(\varepsilon, c_\varepsilon, h_\varepsilon) = 0$. Moreover the map $\varepsilon \mapsto (c_\varepsilon, h_\varepsilon)$ is continuous, the speed c_ε satisfies

$$c_\varepsilon = \frac{-\int_{\mathbb{R}} \left(g(u_0) + \frac{2}{r}(u'_0)^2 \right) u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)} dx}{\int_{\mathbb{R}} (u'_0)^2 e^{\frac{4S}{r}(u_0^2 - u_0)} dx} \varepsilon + o(\varepsilon), \quad \text{as } \varepsilon \rightarrow 0, \quad (28)$$

whereas the perturbation profile h_ε satisfies

$$\int_{\mathbb{R}} h_\varepsilon u'_0 dx = 0, \quad \text{for all } 0 \leq \varepsilon \leq \varepsilon_0. \quad (29)$$

In what follows we aim at applying the Implicit Function Theorem A.1 to the operator \mathcal{F} defined in (26), see [1] for a related argument. We straightforwardly compute the derivatives with respect to c and h at the origin $(0, 0, 0)$:

$$\partial_c \mathcal{F}(0, 0, 0)(c) = cu'_0,$$

and

$$Lh := \partial_h \mathcal{F}(0, 0, 0)(h) = h'' + \frac{4S}{r} u'_0 (2u_0 - 1) h' + S \left(f'(u_0) + \frac{4}{r} (u'_0)^2 \right) h. \quad (30)$$

We need to show that $\partial_{c,h} \mathcal{F}(0, 0, 0)$ given by

$$(c, h) \mapsto Lh + cu'_0$$

is bijective from and to a well-chosen pair of function spaces. Our strategy is as follows. In subsection 4.1, thanks to some results of [14], [13] (recalled in Appendix), we show that L is a Fredholm operator and compute its index (which depends on the choice of μ). Next, in subsection 4.2, we determine the kernel of L . In particular u'_0 is the only bounded solution. We also determine the kernel of L^* thanks to an algebraic symmetric formulation in a well-chosen weighted L^2 space, from which we deduce the surjectivity of $\partial_{c,h} \mathcal{F}(0, 0, 0)$. Then we conclude the proof of Theorem 4.1 in subsection 4.3.

4.1 Fredholm property

Lemma 4.2 (Fredholm property). *The operator $L : C_\mu^{2,\alpha}(\mathbb{R}) \rightarrow C_\mu^\alpha(\mathbb{R})$, defined in (30), is Fredholm if $\mu \neq \sqrt{S}$ and we have*

$$\text{ind } L = \begin{cases} 0 & \text{if } 0 \leq \mu < \sqrt{S}, \\ -2 & \text{if } \mu > \sqrt{S}. \end{cases}$$

Proof. In view of Remark A.4 it suffices to study the limiting operators $(L^\mu)^\pm$ associated with L^μ defined as in (38), namely

$$(L^\mu)^\pm h = h'' \mp 2\mu h' + (\mu^2 - S)h,$$

thanks to Theorem A.3. First since $-\xi^2 \mp 2\mu i\xi + \mu^2 - S = 0$, corresponding to (36), has no real solution, L is Fredholm. Next, the associated characteristic equation, corresponding to (37), writes

$$X^2 \pm 2\mu X + (\mu^2 - S) = 0,$$

and has the following roots:

$$\begin{aligned} X_{1,2}^+ &= -\mu \pm \sqrt{S}, \\ X_{1,2}^- &= +\mu \pm \sqrt{S}. \end{aligned}$$

If $0 \leq \mu < \sqrt{S}$ we deduce that $\kappa^+ = 1$ and $\kappa^- = 1$ (in the notations of Theorem A.3), hence $\text{ind } L = 0$; if $\sqrt{S} < \mu$ we have $\kappa^+ = 0$ and $\kappa^- = 2$, hence $\text{ind } L = -2$. This completes the proof of Lemma 4.2. \square

4.2 Kernels of L , L^* and surjectivity of $\partial_{c,h}\mathcal{F}(0,0,0)$

Lemma 4.3 (The kernel of L). *Two linearly independent solutions to the linear homogeneous ordinary differential equation*

$$Lh := h'' + \frac{4S}{r}u_0'(2u_0 - 1)h' + S \left(f'(u_0) + \frac{4}{r}(u_0')^2 \right) h = 0 \quad (31)$$

are given by

$$u_0' \quad \text{and} \quad v_0 : x \mapsto u_0'(x) \int_0^x \frac{1}{(u_0')^2(z)} e^{-\frac{4S}{r}(u_0^2(z) - u_0(z))} dz.$$

Among the two, u_0' is the only bounded solution.

As a result, for $0 \leq \mu < \sqrt{S}$, the kernel of the operator L acting on the space $C_\mu^{2,\alpha}(\mathbb{R})$ into $C_\mu^{0,\alpha}(\mathbb{R})$ is given by

$$\ker L = \text{span } u_0'.$$

Proof. We investigate the solutions h to (31). This is a second-order linear homogeneous ordinary differential equation and we already know a solution u_0' (as seen by differentiating (12)). In this case a second solution v_0 can be sought in the form $v_0(x) = z(x)u_0'(x)$. Indeed plugging this ansatz into (31) yields the following first order linear ordinary differential equation for z' :

$$z'' + \left(2\frac{u_0''}{u_0'} + \frac{4S}{r}(2u_0 - 1)u_0' \right) z' = 0,$$

or, equivalently,

$$z'' + \left(\ln((u_0')^2) + \frac{4S}{r}(u_0^2 - u_0) \right)' z' = 0.$$

As a result, we can select the solution

$$z'(x) = \frac{1}{(u_0')^2(x)} e^{-\frac{4S}{r}(u_0^2(x) - u_0(x))},$$

which we integrate to reach $z(x)$, and thus

$$v_0(x) = u_0'(x) \int_0^x \frac{1}{(u_0')^2(z)} e^{-\frac{4S}{r}(u_0^2(z) - u_0(z))} dz. \quad (32)$$

Now, from the analysis in Section 3, we know that, for some $C > 0$,

$$u_0'(z) \sim Ce^{-\sqrt{S}z}, \quad \text{as } z \rightarrow +\infty. \quad (33)$$

Since $u_0(+\infty) = 0$, the integrand in (32) is equivalent to $\frac{1}{C^2}e^{2\sqrt{S}z}$ as $z \rightarrow +\infty$, and thus

$$v_0(x) \sim \frac{1}{C2\sqrt{S}}e^{\sqrt{S}x}, \quad \text{as } x \rightarrow +\infty. \quad (34)$$

Thus v_0 is unbounded and, in particular, $v_0 \notin C_\mu^{2,\alpha}(\mathbb{R})$. Since solutions to (31) are the linear combinations of $u'_0 \in C_\mu^{2,\alpha}(\mathbb{R})$ when $0 \leq \mu < \sqrt{S}$, $v_0 \notin C_\mu^{2,\alpha}(\mathbb{R})$, and since $L : C_\mu^{2,\alpha}(\mathbb{R}) \rightarrow C_\mu^\alpha(\mathbb{R})$, we conclude that $\ker L = \text{span } u'_0$ when $0 \leq \mu < \sqrt{S}$. \square

Lemma 4.4 (The kernel of L^*). *If $0 \leq \mu < \sqrt{S}$ then the kernel of the adjoint operator L^* is*

$$\ker L^* = \text{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right).$$

On the other hand, if $\mu > \sqrt{S}$ then

$$\ker L^* = \text{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)}, v_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right),$$

where $v_0(x) := u'_0(x) \int_0^x \frac{1}{(u'_0)^2(z)} e^{-\frac{4S}{r}(u_0^2(z) - u_0(z))} dz$ is as in Lemma 4.3.

Proof. Our starting point is to notice that the coefficient of the first-order term in the definition of L , that is $u'_0(2u_0 - 1)$, is the derivative of $u_0^2 - u_0$ so that

$$Lh = h'' + \frac{4S}{r}(u_0^2 - u_0)'h' + S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h,$$

from which we deduce the formulation

$$Lh = \left(h' e^{\frac{4S}{r}(u_0^2 - u_0)} \right)' e^{-\frac{4S}{r}(u_0^2 - u_0)} + S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h,$$

which is symmetric in the adequate weighted L^2 space:

$$\begin{aligned} \int_{\mathbb{R}} k(Lh) e^{\frac{4S}{r}(u_0^2 - u_0)} &= - \int_{\mathbb{R}} k' h' e^{\frac{4S}{r}(u_0^2 - u_0)} + \int_{\mathbb{R}} S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h k e^{\frac{4S}{r}(u_0^2 - u_0)} \\ &= \int_{\mathbb{R}} (Lk) h e^{\frac{4S}{r}(u_0^2 - u_0)}. \end{aligned}$$

In particular, for any $k \in C_\mu^{2,\alpha}(\mathbb{R})$, we have

$$\begin{aligned} \int_{\mathbb{R}} k(Lh) &= \int_{\mathbb{R}} k \left(h' e^{\frac{4S}{r}(u_0^2 - u_0)} \right)' e^{-\frac{4S}{r}(u_0^2 - u_0)} + S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h k \\ &= \int_{\mathbb{R}} - \left(k e^{-\frac{4S}{r}(u_0^2 - u_0)} \right)' h' e^{\frac{4S}{r}(u_0^2 - u_0)} \\ &\quad + \int_{\mathbb{R}} S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h \left(k e^{-\frac{4S}{r}(u_0^2 - u_0)} \right) e^{\frac{4S}{r}(u_0^2 - u_0)} \\ &= \int_{\mathbb{R}} h \left(L \left(k e^{-\frac{4S}{r}(u_0^2 - u_0)} \right) \right) e^{\frac{4S}{r}(u_0^2 - u_0)}. \end{aligned}$$

Therefore, if $v e^{-\frac{4S}{r}(u_0^2 - u_0)} = k \in \ker L$, then we have

$$\begin{aligned} \int_{\mathbb{R}} (L^* v) h &= \int_{\mathbb{R}} v(Lh) \\ &= \int_{\mathbb{R}} h \left(L \left(v e^{-\frac{4S}{r}(u_0^2 - u_0)} \right) \right) e^{\frac{4S}{r}(u_0^2 - u_0)} = 0, \end{aligned}$$

provided each integral is finite. In particular, since $C_\mu^{2,\alpha}(\mathbb{R})$ is dense in $C_\mu^{0,\alpha}(\mathbb{R})$, this shows that

$$\text{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right) \subset \ker L^*.$$

Assume $0 \leq \mu < \sqrt{S}$. Then we deduce from Lemma 4.2 and Lemma 4.3 that $\dim \ker L^* = -\operatorname{ind} L + \dim \ker L = 0 + 1 = 1$, and therefore we do have $\ker L^* = \operatorname{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right)$.

Assume $\mu > \sqrt{S}$. This time, the asymptotics for v_0 being given in (34), terms $\int_{\mathbb{R}} v_0 h e^{\frac{4S}{r}(u_0^2 - u_0)}$ are finite as soon as $h \in C_{\mu}^{0,\alpha}(\mathbb{R})$, and therefore

$$\operatorname{span} \left(v_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right) \subset \ker L^*,$$

by a density argument. Then we deduce from Lemma 4.2 and Lemma 4.3 that $\dim \ker L^* = -\operatorname{ind} L + \dim \ker L = -(-2) + 0 = 2$. Since $u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)}$ and $v_0 e^{\frac{4S}{r}(u_0^2 - u_0)}$ are linearly independent, we do have $\ker L^* = \operatorname{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)}, v_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right)$. \square

Lemma 4.5 (Surjectivity of $\partial_{c,h}\mathcal{F}(0,0,0)$). *Let $0 \leq \mu < \sqrt{S}$ be given. Then, the application*

$$\begin{aligned} \partial_{c,h}\mathcal{F}(0,0,0) : \mathbb{R} \times C_{\mu}^{2,\alpha}(\mathbb{R}) &\rightarrow C_{\mu}^{0,\alpha}(\mathbb{R}) \\ (c, h) &\mapsto Lh + cu'_0 \end{aligned}$$

is surjective.

Proof. We check that u'_0 is not in the range of L . Since L has closed range we have $\operatorname{rg} L = (\ker L^*)^{\perp}$, and thus $\operatorname{rg} L = \left(\operatorname{span} \left(u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right) \right)^{\perp}$ from Lemma 4.4. But

$$\left\langle u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)}, u'_0 \right\rangle_{(C_{\mu}^{0,\alpha}(\mathbb{R}))^*, C_{\mu}^{0,\alpha}(\mathbb{R})} = \int_{\mathbb{R}} (u'_0)^2 e^{\frac{4S}{r}(u_0^2 - u_0)} > 0$$

so that $u'_0 \notin \operatorname{rg} L$. Since $\operatorname{rg} L$ has codimension 1 by Lemma 4.2 and 4.3, we have $C_{\mu}^{0,\alpha}(\mathbb{R}) = \operatorname{rg} L \oplus \operatorname{span} u'_0$. This shows that $\partial_{c,h}\mathcal{F}(0,0,0)$ is surjective. \square

Remark 4.6. We present here an alternate way to prove that $u'_0 \notin \operatorname{rg} L$ remains true when $\mu \geq \sqrt{S}$. To do so, let us solve the second-order linear ordinary differential equation

$$w'' + \frac{4S}{r} u'_0 (2u_0 - 1) w' + S \left(f'(u_0) + \frac{4}{r} (u'_0)^2 \right) w = u'_0. \quad (35)$$

Recall that the solutions of the associated homogeneous equation are spanned by u'_0 and v_0 provided by Lemma 4.3. To find a particular solution to (35), we use the method of variation of constants. We see that $\varphi(x) := \lambda_1(x)u'_0(x) + \lambda_2(x)v_0(x)$ solves (35) as soon as

$$\begin{cases} u'_0 \lambda'_1 + v_0 \lambda'_2 &= 0 \\ u''_0 \lambda_1 + v'_0 \lambda'_2 &= u'_0, \end{cases}$$

which yields

$$\lambda'_2 \frac{u'_0 v'_0 - u''_0 v_0}{u'_0} = u'_0, \quad \lambda'_1 = -\frac{v_0}{u'_0} \lambda'_2.$$

Since $u'_0 v'_0 - u''_0 v_0$ is nothing else than the Wronskian, it is equal to $\theta^{-1} e^{-\frac{4S}{r}(u_0^2 - u_0)}$ for some $\theta \neq 0$, and thus

$$\begin{cases} \lambda'_2(x) = \theta (u'_0)^2(x) e^{\frac{4S}{r}(u_0^2(x) - u_0(x))} \sim \theta C^2 e^{-2\sqrt{S}x} \\ \lambda'_1(x) = -\theta v_0(x) u'_0(x) e^{\frac{4S}{r}(u_0^2(x) - u_0(x))} \sim -\frac{\theta}{2\sqrt{S}}, \end{cases}$$

where the equivalents are taken as $x \rightarrow +\infty$ and where we have used (33) and (34). Hence, we can select

$$\begin{cases} \lambda_2(x) = -\int_x^{+\infty} \theta(u'_0)^2(z) e^{\frac{4S}{r}(u_0^2(z)-u_0(z))} dz \sim \frac{\theta C^2}{2\sqrt{S}} e^{-2\sqrt{S}x} \\ \lambda_1(x) = -\int_0^x \theta v_0(z) u'_0(z) e^{\frac{4S}{r}(u_0^2(z)-u_0(z))} dz \sim -\frac{\theta}{2\sqrt{S}} x. \end{cases}$$

Hence the solutions to (35) are

$$w(x) = (C_1 + \lambda_1(x))u'_0(x) + (C_2 + \lambda_2(x))v_0(x)$$

for any $C_1 \in \mathbb{R}$, $C_2 \in \mathbb{R}$. If $C_2 \neq 0$ then, from all the above asymptotic, w is unbounded. If $C_2 = 0$ then, from all the above asymptotics,

$$w(x) \sim -\frac{\theta C}{2\sqrt{S}} x e^{-\sqrt{S}x}, \quad \text{as } x \rightarrow +\infty.$$

This above asymptotics shows that $w \notin C_\mu^{2,\alpha}(\mathbb{R})$ when $\mu \geq \sqrt{S}$, and thus $u'_0 \notin \text{rg } L$.

4.3 Construction of traveling waves

We are now in the position to complete the proof of Theorem 4.1, that is the construction of traveling waves for (25) when $0 < \varepsilon \ll 1$.

Proof of Theorem 4.1. Assume $0 \leq \mu < \sqrt{S}$. Let us recall that $\mathcal{F} : \mathbb{R} \times \mathbb{R} \times C_\mu^{2,\alpha}(\mathbb{R}) \rightarrow C_\mu^{0,\alpha}(\mathbb{R})$ is given by (26). It is Fréchet differentiable (even of the class C^1) with respect to each of its variables, and we have

$$\begin{aligned} \partial_\varepsilon \mathcal{F}(0, 0, 0) &= g(u_0) + \frac{2}{r}(u'_0)^2, \\ \partial_c \mathcal{F}(0, 0, 0) &= u'_0 \\ L = \partial_h \mathcal{F}(0, 0, 0) &: h \mapsto Lh = h'' + \frac{4S}{r} u'_0(2u_0 - 1)h' + S \left(f'(u_0) + \frac{4}{r}(u'_0)^2 \right) h. \end{aligned}$$

We have shown, in Lemma 4.2, that L is a Fredholm operator with indice 0 and, in Lemma 4.3, that the kernel of L is $\text{span } u'_0$ in the considered weighted Hölder space.

Our concern is the derivative $\partial_{c,h} \mathcal{F}(0, 0, 0) : (c, h) \mapsto Lh + cu'_0$. It has been shown in Lemma 4.5 that it is surjective. It is not difficult to show that

$$\ker \partial_{c,h} \mathcal{F}(0, 0, 0) = \{0\} \times \text{span } u'_0,$$

and that the restriction of $\partial_{c,h} \mathcal{F}(0, 0, 0)$ to $\mathbb{R} \times N$, where

$$N := \left\{ f \in C_\mu^{2,\alpha}(\mathbb{R}) : \int_{\mathbb{R}} f u'_0 = 0 \right\}$$

is a topological complement of $\ker L$, is injective and still surjective. Therefore we can apply the Implicit Function Theorem A.1 to the restriction of \mathcal{F} to $\mathbb{R} \times \mathbb{R} \times N$. We deduce the existence of a branch $(c_\varepsilon, h_\varepsilon)$, $0 \leq \varepsilon \ll 1$, of solutions with $\varepsilon \mapsto (c_\varepsilon, h_\varepsilon)$ continuous and h_ε satisfying (29).

It remains to prove (28). Since \mathcal{F} is C^1 in all its variables we deduce from $\mathcal{F}(\varepsilon, c_\varepsilon, h_\varepsilon) = 0$ and the chain rule that

$$\partial_\varepsilon \mathcal{F}(\varepsilon, c_\varepsilon, h_\varepsilon) + \frac{dc_\varepsilon}{d\varepsilon} \partial_c \mathcal{F}(\varepsilon, c_\varepsilon, h_\varepsilon) + \partial_h \mathcal{F}(\varepsilon, c_\varepsilon, h_\varepsilon) \left(\frac{dh_\varepsilon}{d\varepsilon} \right) = 0,$$

which we evaluate at $\varepsilon = 0$ to get

$$g(u_0) + \frac{2}{r}(u_0')^2 + \left. \frac{dc_\varepsilon}{d\varepsilon} \right|_{\varepsilon=0} u_0' + L \left(\left. \frac{dh_\varepsilon}{d\varepsilon} \right|_{\varepsilon=0} \right) = 0.$$

Since $\text{rg } L = (\ker L^*)^\perp = \left(\text{span} \left(u_0' e^{\frac{4S}{r}(u_0^2 - u_0)} \right) \right)^\perp$, multiplying the above by $u_0' e^{\frac{4S}{r}(u_0^2 - u_0)}$ and integrating over \mathbb{R} , we reach

$$\left. \frac{dc_\varepsilon}{d\varepsilon} \right|_{\varepsilon=0} = \frac{- \int_{\mathbb{R}} \left(g(u_0) + \frac{2}{r}(u_0')^2 \right) u_0' e^{\frac{4S}{r}(u_0^2 - u_0)}}{\int_{\mathbb{R}} (u_0')^2 e^{\frac{4S}{r}(u_0^2 - u_0)}} > 0,$$

which yields (28) and concludes the proof of Theorem 4.1. \square

5 Conclusion and perspectives

In this paper we have investigated the solutions of equation (11), describing the dynamics of two coupled, asymmetric genetic incompatibilities (underdominant loci) with identical fitness effects, in a quasi linkage equilibrium regime. The two main results are as follows: first, we have shown that when $\varepsilon = 0$, there is a unique standing wave u_0 under a normalization condition; then, in Section 4, we have shown that when $\varepsilon > 0$ is small enough, there exists a traveling wave u_ε defined as a perturbation of u_0 .

Those results were obtained under a series of assumptions that we recall here for discussion:

$$s_A, s_B < S \tag{H1}$$

$$s_A, s_B, S \ll r \tag{H2}$$

$$S_A = S_B, \quad s_A = s_B \tag{H3}$$

$$p = q. \tag{H4}$$

Assumption (H1) is the frame of this work which was devoted to the heterozygote inferior case. It is therefore not a hypothesis we want to discuss *per se*.

Assumption (H2) expresses that we are in the case of small selective advantages. When it does not hold, D may not be small, in which case the quasi linkage equilibrium approximation (that allowed us to reduce the number of variables) is no longer valid. It can easily be seen that $-\frac{1}{4} \leq D \leq \frac{1}{4}$ always holds, and that, as shown by the D equation in (7), positive D is generated whenever p and q travel in the same direction (that is $p_x q_x > 0$), while negative D is generated otherwise. These facts help to understand the kind of contribution D makes to the coupling between p and q in (7).

Assumption (H3) is basically a hypothesis of symmetry between loci. Although this allowed us to simplify the algebra, different incompatibility loci should have different fitness effects, and it would thus be of interest to relax this hypothesis.

Last but not least, assumption (H4) conveys the strong argument that the A cline and the B cline have stucked together forever in the past and will stick together forever in the future. This is indeed a good starting point from a mathematical perspective. Nevertheless, in the context of population genetics, more interesting questions arise when (H4) does not hold. In such a situation, the coupling in (7) can give rise to non-standard behaviours, such as *adaptation of the speed*. The questions that arise are such as: can a traveling front be pinned by a standing front? Will a front traveling at a large speed

crossing a slower traveling front adapt its speed so as to remain sticked with the slower one? A preliminary numerical exploration has shown that there can be a vast zoology of situations. We hope to present them in a future work.

A Some useful results and tools

We recall the *Implicit Function Theorem*, see [15, Theorem 4.B] for instance.

Theorem A.1 (Implicit Function Theorem). *Let X, Y and Z be three Banach spaces. Suppose that:*

- (i) *The mapping $\mathcal{F} : U \subset X \times Y \rightarrow Z$ is defined on an open neighbourhood U of $(x_0, y_0) \in X \times Y$ and $\mathcal{F}(x_0, y_0) = 0$.*
- (ii) *The partial Fréchet derivative of \mathcal{F} with respect to y exists on U and*

$$\mathcal{F}_y(x_0, y_0) : Y \rightarrow Z \text{ is bijective.}$$

- (iii) *\mathcal{F} and \mathcal{F}_y are continuous at (x_0, y_0) .*

Then, the following properties hold:

- (a) *Existence and uniqueness. There exist $r_0 > 0$ and $r > 0$ such that, for every $x \in X$ satisfying $\|x - x_0\| \leq r_0$, there exists a unique $y(x) \in Y$ such that $\|y - y_0\| \leq r$ and $\mathcal{F}(x, y(x)) = 0$.*
- (b) *Continuity. If \mathcal{F} is continuous in a neighbourhood of (x_0, y_0) , then the mapping $x \mapsto y(x)$ is continuous in a neighbourhood of x_0 .*
- (c) *Higher regularity. If \mathcal{F} is of the class C^m , $1 \leq m \leq \infty$, on a neighbourhood of (x_0, y_0) , then $x \mapsto y(x)$ is also of the class C^m in a neighbourhood of x_0 .*

In Section 4 we apply Theorem A.1 to the operator \mathcal{F} defined in (26), with $X = \mathbb{R}$, $x = \varepsilon$, $x_0 = 0$, $Y = \mathbb{R} \times C_\mu^{2,\alpha}(\mathbb{R})$, $y = (c, h)$, $y_0 = (0, 0)$, and $Z = C_\mu^{0,\alpha}(\mathbb{R})$.

Next, we quote some results on Fredholm operators. Let us recall that the operator L has the Fredholm property with index 0 if $\ker L$ has a finite dimension, $\text{rg } L$ is closed and has finite codimension and

$$\text{ind } L := \dim \ker L - \text{codim } \text{rg } L = 0.$$

In particular, since its range is closed, such an operator is *normally solvable*:

$$\exists u \neq 0, Lu = f \quad \Leftrightarrow \quad \forall \phi \in (\text{rg } L)^\perp, \phi(f) = 0,$$

and remark that $(\text{rg } L)^\perp = \ker L^*$.

We recall below a theorem from Volpert, Volpert and Collet [14, Theorem 2.1 and Remark p787].

Theorem A.2 (Fredholm property on the line). *For $0 < \alpha < 1$, consider the operator $L : C^{2,\alpha}(\mathbb{R}) \rightarrow C^\alpha(\mathbb{R})$ defined by*

$$Lu := a(x)u'' + b(x)u' + c(x)u,$$

where the coefficients $a(x)$, $b(x)$, $c(x)$ are smooth, and $a(x) \geq a_0$ for some $a_0 > 0$. Assume further that the coefficients $a(x)$, $b(x)$, and $c(x)$ have finite limits as $x \rightarrow \pm\infty$ and denote

$$a^\pm := \lim_{x \rightarrow \pm\infty} a(x), \quad b^\pm := \lim_{x \rightarrow \pm\infty} b(x), \quad c^\pm := \lim_{x \rightarrow \pm\infty} c(x).$$

Finally, let us define the limiting operators

$$L^\pm u := a^\pm u'' + b^\pm u' + c^\pm u,$$

and assume that for any $\lambda \geq 0$, the equation

$$L^\pm u - \lambda u = 0$$

has no nontrivial solution in $C^{2,\alpha}(\mathbb{R})$.

Then L is Fredholm with index 0.

Let us also recall a Fredholm property result for second-order ordinary differential equations, see the monograph of Volpert [13, Chapter 9, Theorem 2.4 p. 366].

Theorem A.3 (Fredholm property for second-order ODEs). *With the notations of Theorem A.2, the operator L is Fredholm provided the two equations*

$$-a^\pm \xi^2 + b^\pm i\xi + c^\pm = 0 \tag{36}$$

has no real solution $\xi \in \mathbb{R}$. In this case the index of L is given by the formula

$$\text{ind } L = \kappa^+ - \kappa^-,$$

where κ^\pm is the number of complex solutions to the characteristic equation

$$a^\pm X^2 - b^\pm X + c^\pm = 0 \tag{37}$$

which have a positive real part.

Remark A.4 (Fredholm property in weighted Hölder spaces). We cannot directly apply Theorem A.2 and Theorem A.3 to our situation since we consider the operator L acting from $C_\mu^{2,\alpha}(\mathbb{R})$ into $C_\mu^\alpha(\mathbb{R})$, and not from $C^{2,\alpha}(\mathbb{R})$ into $C^{0,\alpha}(\mathbb{R})$. To circumvent this, we consider the operator $L^\mu : C^{2,\alpha}(\mathbb{R}) \rightarrow C^\alpha(\mathbb{R})$ defined by:

$$\begin{aligned} L^\mu(u) &:= e^{\mu\sqrt{1+x^2}} L \left(u e^{-\mu\sqrt{1+x^2}} \right) \\ &= a(x)u'' + \left[\frac{-2\mu x}{\sqrt{1+x^2}} a(x) + b(x) \right] u' \\ &\quad + \left[\left(\frac{\mu^2 x^2}{1+x^2} + \frac{\mu x^2}{(1+x^2)^{\frac{3}{2}}} - \frac{\mu}{\sqrt{1+x^2}} \right) a(x) - \frac{\mu x}{\sqrt{1+x^2}} b(x) + c(x) \right] u. \end{aligned} \tag{38}$$

Since $T_\mu : u \in C_\mu^{2,\alpha}(\mathbb{R}) \mapsto e^{\mu\sqrt{1+x^2}} u \in C^{2,\alpha}(\mathbb{R})$ is continuously invertible, and $T_\mu^{-1} : u \in C^{0,\alpha}(\mathbb{R}) \mapsto e^{-\mu\sqrt{1+x^2}} u \in C_\mu^{0,\alpha}(\mathbb{R})$ is continuously invertible, the map $L = T_\mu^{-1} L^\mu T_\mu$ shares the same Fredholm property and index as L^μ . As a result, if L^μ satisfies the assumptions of Theorem A.2, or Theorem A.3, then L is a Fredholm operator with the same index as that of L^μ .

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