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The spatio-temporal dynamics of interacting genetic incompatibilities.

Part I: The case of stacked underdominant clines

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

Abstract

We explore the interaction between two genetic incompatibilities (underdominant loci in diploid organisms) in a population occupying a one-dimensional space. We derive a system of partial differential equations 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 stacked together. In the case of asymmetric incompatibilities (*i.e.* when one homozygote is favored over the other at each locus), these stacked clines propagate in the form of a traveling wave. We obtain an approximation for the speed of this wave which, in particular, is decreased by recombination between the two loci but is always larger than the speed of “one cline alone”.

Keywords: genetic incompatibilities, underdominance, quasi-linkage equilibrium, standing wave, traveling wave, perturbation analysis.

AMS Subject Classifications: 92D10 (Genetics and epigenetics), 35C07 (Traveling wave solutions), 35B20 (Perturbations in context of PDEs).

1 Introduction

Genetic incompatibilities correspond to deleterious interactions between alleles (at the same locus or at different loci) within the same genome, and are the cause of the reduced fitness of hybrids between species [10], [12]. Such incompatibilities may be revealed by crosses between divergent populations or species, which may be performed experimentally [11], but may also occur naturally in hybrid zones resulting from secondary contacts between genetically divergent populations [6, 7]. Indeed, the offspring of such crosses carry a mix of alleles from the two parental populations, which may not function well together. Genetic incompatibilities may also be widespread within the same species, as suggested by recent data from *Drosophila* [9].

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How several incompatibilities segregating within the same population interfere with each other has important consequences for the evolution of reproductive isolation, and the maintenance of distinct genetic entities after a secondary contact. Barton & de Cara [4] showed that, in the case of a single population (sympatry), incompatibilities are expected to couple through the buildup of linkage disequilibrium among them, which may eventually lead to strong reproductive isolation between two distinct genetic backgrounds. In spatially structured populations with limited dispersal (parapatry), clines in allele frequencies may form between regions containing different sets of incompatible alleles [2]. In this case, linkage disequilibria generated by dispersal generally tend to pull clines together [14], again leading to the *coupling* of genetic incompatibilities which then tend to reinforce each other. This process was explored by Barton [3] in the case of a continuous, linear habitat, and when genetic incompatibilities are generated by an arbitrary number of underdominant loci: at each locus, heterozygotes (say Aa) have a lower fitness than homozygotes, while the two homozygotes (AA and aa) have equal fitness. This form of *symmetric* selection (against heterozygotes) can maintain stable clines in allele frequencies [8], [2], separating regions where AA and aa individuals are abundant (Aa hybrids being generated between these regions). When two such clines overlap in space (one separating regions where AA and aa are abundant, and the other separating regions where BB and bb are abundant), they tend to attract each other until they coincide, as illustrated by the numerical simulations in Figure 1, and then become motionless.

In the *asymmetric* situation where one allele has a selective advantage over the other (*i.e.*, one homozygous genotype, say AA , has a higher fitness than the other, aa), the cline will move in the direction of the less fit genotype [2]. The interaction between several such asymmetric incompatibilities raises several questions that remain little explored to date, such as: when clines moving at different speeds come into contact, will they remain *stacked* (increasing the degree of reproductive isolation between the two sides of the clines) or not? If they do remain stacked, what will be the speed of the resulting front? Under which conditions may an asymmetric incompatibility escape from a hybrid zone in which several incompatibilities are segregating?

This article constitutes a first step in the exploration of the spatio-temporal dynamics of interacting asymmetric incompatibilities, focusing on a simple situation involving two coupled underdominant loci (with alleles A, a at the first locus, B, b at the second) with identical fitness effects. Notice that Barton [3] has considered the situation where heterozygotes present a cost in fitness and where the fitness of the homozygotes $AB|AB$ and the one of $ab|ab$ are the same, that is the symmetric case. In Section 3, we give a mathematical proof of the existence of such a cline in this symmetric situation, see Proposition 3.2. We also prove in Proposition 3.3 that such a stationary cline is stable, *i.e.* that small perturbations of the profile may shift its spatial position but essentially do not alter its shape. In other words, a perturbed stationary cline comes back to a possibly shifted stationary cline. We refer to (12) for the equation satisfied by such a cline.

When the fitness of the homozygote $AB|AB$ becomes slightly larger than the one of $ab|ab$, it is not *a priori* obvious whether the stationary cline stays stationary or begins to move. Here we answer this question by showing that invasion does occur even if the difference in fitness between homozygotes has a lower order of magnitude (measured by $0 < \varepsilon \ll 1$) compared to the fitness cost of heterozygotes. By using a rather involved perturbation analysis, we show in Theorem 4.1 that a front traveling at a constant speed $c_\varepsilon > 0$ emerges from the stationary cline u_0 solving (12) when ε becomes positive. Such a traveling front is a solution to the reaction-diffusion equation involving nonlinear gradient terms (11). We give an explicit approximation of the speed c_ε which is, from the modelling

point of view, the main contribution of the present work. Among other implications, it reveals not only that recombination between the two loci tends to slow down the propagation of the front but also that the stacked clines always travel faster than one cline alone.

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. In Section 5, a trick enables to derive an explicit approximation of the speed c_ε which sheds light on the original model. We conclude and present some perspectives in Section 6.

2 Derivation of the mathematical model

2.1 Biological assumptions

The population is homogeneous in a one-dimensional space, along which density is supposed uniform and large. We focus on the variations of the genetic composition of the population. 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 in Table 1.

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

Table 1: Fitness of the different genotypes at each locus.

Here 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 in Table 2.

	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

Table 2: Fitness of diploid individuals.

Note that, 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.

We assume that recombination occurs with probability r , so that $AB|ab$ individuals may produce Ab and aB gametes. Throughout the paper, the population occupying the left-hand side of the linear habitat will consist mostly of $AB|AB$ individuals, while the right-hand side will be mostly composed of $ab|ab$ individuals. In the symmetric situation ($s_A = s_B = 0$), if the clines of A and B are shifted in space, linkage disequilibrium will develop between the two loci and will pull both fronts together until they are stacked [14], [3], as illustrated in Figure 1. This paper is concerned with the established regime where the fronts are stacked (this situation may also result from a secondary contact between two

divergent populations, as considered by [3]). Note that in the general case ($s_A, s_B \neq 0$), shifted clines may not necessarily become stacked; however, we postpone the analysis of the conditions for stacking to future works.

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. In Section 2.2 we present the genetic model that drives the genetic dynamics. In Section 2.3 we introduce the spatial structure and the corresponding equations. Finally in Section 2.4, we precise our assumptions on the parameters and their respective magnitudes, as well as our precise objectives.

2.2 Recursions on gamete frequencies 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). Denote by $y_B^A, y_b^A, y_B^a, y_b^a$ 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 , 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:

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

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

where $\overline{\mathcal{W}}$ is the average fitness:

$$\begin{aligned}
\overline{\mathcal{W}} &= \sum_{i,j \in \{A, a, B, b\}} z_{i|j} \mathcal{W}_{i|j} \\
&= (1 + 2s_A)(1 + 2s_B)y_A^2 + (1 + 2s_A)y_b^2 + (1 + 2s_B)y_B^2 + y_b^2 \\
&\quad + 2(1 + 2s_A)(1 + s_B - S_B)y_B^a y_b^A + 2(1 + s_A - S_A)(1 + 2s_B)y_B^a y_B^a \\
&\quad + 2(1 + s_A - S_A)(1 + s_B - S_B)y_B^a y_b^a + 2(1 + s_A - S_A)(1 + s_B - S_B)y_b^a y_B^a \\
&\quad + 2(1 + s_A - S_A)y_b^a y_b^A + 2(1 + s_B - S_B)y_B^a y_b^a.
\end{aligned}$$

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

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 :

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

2.3 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 $\sigma > 0$. Notice that, since we assumed that the density of individuals is uniform and large, no advection term appears in the above system. 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

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

2.4 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. Observe that, starting from $D \equiv 0$ (no disequilibrium) the dynamics of p and q are decoupled but the gradient terms p_x and q_x in the D -equation cause disequilibrium and thus interaction [3], see Figure 1.

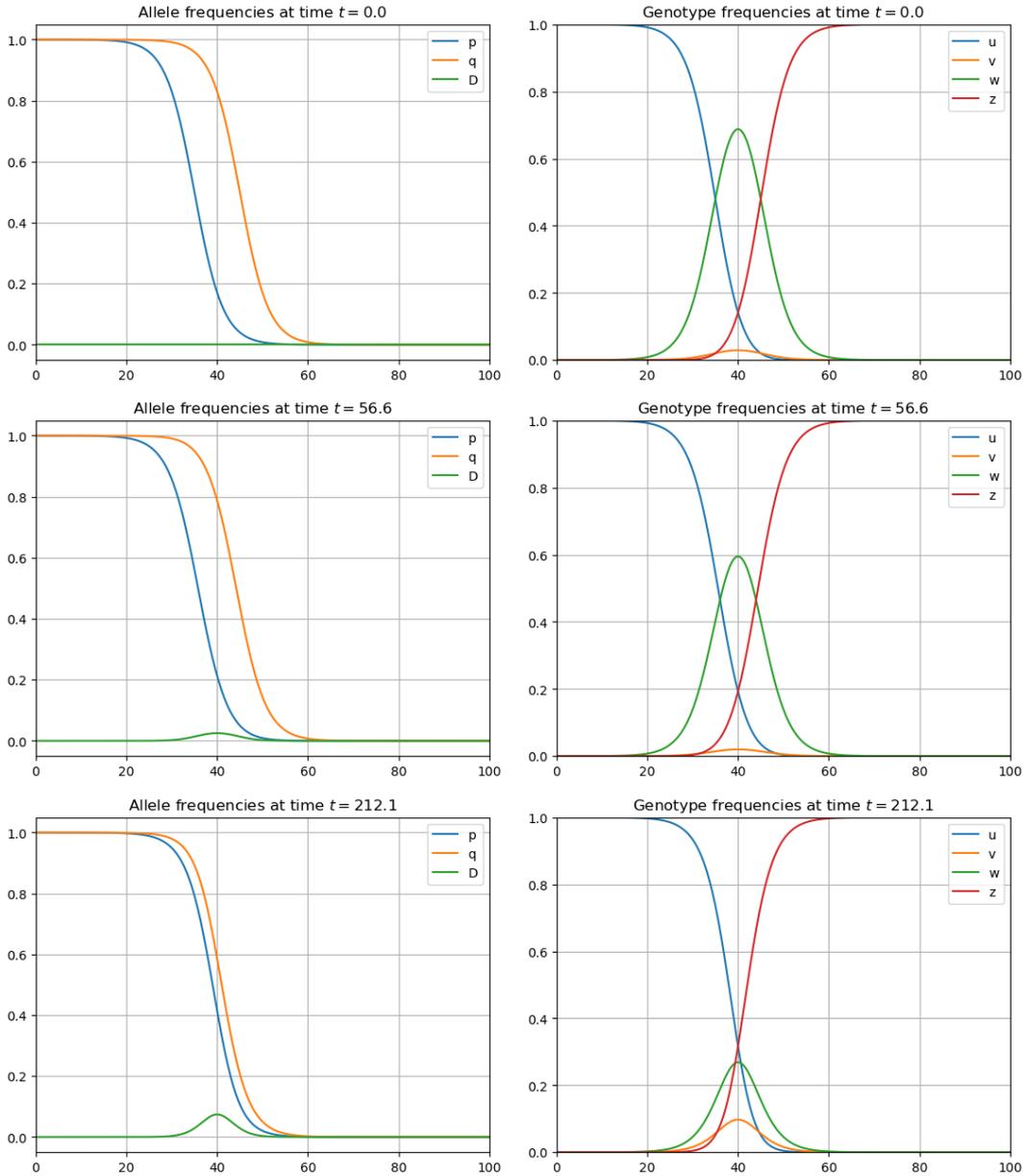


Figure 1: Numerical solutions with parameters $s_A = s_B = 0$ (symmetric case), $S_A = S_B = r = 0.1$ and $\frac{\sigma^2}{2} = 1$. Left column: p , q and D ; the clines are initially uncoupled; next, in a transitory regime, they are driven closer to each other, and eventually become stacked. Right column: the original unknowns, that is the frequencies of gametes u , v , w , z . Remark: the partial differential system in (u, v, w, z) is a reaction-diffusion system for which a standard Strang splitting method was used; numerical simulations were done in python 3.9.2 with the NumPy package version 1.20.1.

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 D approximately follows

$$D_t \approx \frac{\sigma^2}{2} D_{xx} + \sigma^2 p_x q_x - r D.$$

In the sequel, we use a *quasi-linkage equilibrium* approximation [3], meaning that the dynamics on D is much faster than the one of p and q . As a result,

$$\frac{\sigma^2}{2}D_{xx} + \sigma^2 p_x q_x - rD \approx 0,$$

whose solution is given by (one may use the Fourier transform to see it)

$$D(t, x) \approx \frac{\sigma^2}{r} \rho_\sigma * (p_x q_x(t, \cdot))(x), \quad \rho_\alpha(x) := \frac{1}{2} \sqrt{\frac{2r}{\sigma^2}} e^{-\sqrt{\frac{2r}{\sigma^2}} |x|}.$$

For σ sufficiently small, the kernel ρ_α “approaches” the Dirac delta function, and thus

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

As a result, using (8) and writing $(p, q)(t, x) = (\tilde{p}, \tilde{q})\left(t, \frac{\sqrt{2}}{\sigma}x\right)$, we reach a simplified version of system (7), namely

$$\begin{cases} \tilde{p}_t &= \tilde{p}_{xx} + S_A f(\tilde{p}) + s_A g(\tilde{p}) + \frac{2}{r}(S_B(2\tilde{q} - 1) + s_B)\tilde{p}_x \tilde{q}_x, \\ \tilde{q}_t &= \tilde{q}_{xx} + S_B f(\tilde{q}) + s_B g(\tilde{q}) + \frac{2}{r}(S_A(2\tilde{p} - 1) + s_A)\tilde{p}_x \tilde{q}_x, \end{cases}$$

where

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

For ease of notation in the mathematical analysis, we now drop the tildes but keep in mind that, when returning to the original model, the traveling waves speeds we will find have to be multiplied by the factor $\frac{\sigma}{\sqrt{2}}$. Last, we assume that

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

and thus focus on the system

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

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 the situation where the A cline, measured by p , and the B cline, measured by q , remain stacked together. To do so we look after $u = p = q$ solving the nonlinear equation

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

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 $c_\varepsilon \sim c_1 \varepsilon$ for some $c_1 > 0$ and $0 < \varepsilon \ll 1$. These facts are proved in Section 3 and 4, while c_1 is explicitly identified in Section 5.

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.

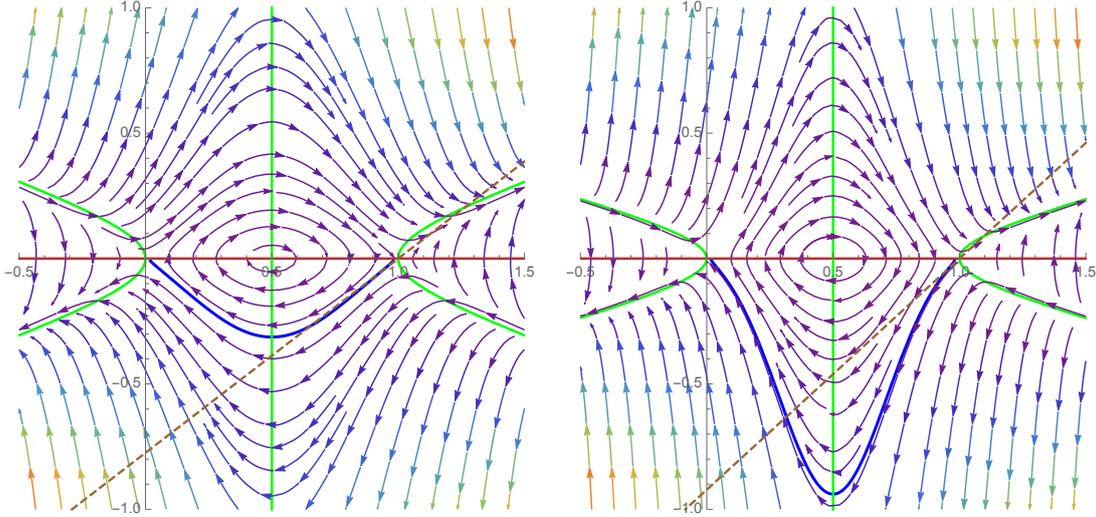


Figure 2: Phase plane analysis for (13). In red, the nullcline $x' = 0$, in green the nullcline $y' = 0$, in brown dashed the linear unstable manifold at $(1, 0)$, in blue (an approximation of) the heteroclinic orbit from $(1, 0)$ to $(0, 0)$. Left: the parameters are $S = 0.6$, $r = 0.25$ so that (14) holds. Right: the parameters are $S = 0.85$, $r = 0.15$ so that (14) does not hold.

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 2. 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 $\pm i\sqrt{\frac{S}{2}}$. 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 2 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

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

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

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

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

$$-Ku_0^2(x) \leq u_0''(x) - Su_0(x) \leq Ku_0^2(x).$$

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 $M > 0$,

$$-Mu_0^2(x) \leq u_0'(x) + \sqrt{S}u_0(x) \leq Mu_0^2(x). \quad (17)$$

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*

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

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 $t > 0$,

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

Proof. We aim at applying a result of Sattinger, namely [13, 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 [13, 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 [13, Lemma 3.4] can be readily checked thanks to [13, Lemma 5.4]. As for the assumption (i) of [13, Lemma 3.4], we point out that [13, 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 [13], 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 [13, 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 [17, 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 [13, 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 [13, 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 [13, 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

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

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

$$\int_{\mathbb{R}} h_\varepsilon u_0' = 0, \quad \text{for all } 0 \leq \varepsilon \leq \varepsilon_0. \quad (29)$$

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 [16], [15] (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 (41), 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 (39), has no real solution, L is Fredholm. Next, the associated characteristic equation, corresponding to (40), 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 $C > 0$,

$$u'_0(z) \sim C e^{-\sqrt{S}z}, \quad \text{as } z \rightarrow +\infty. \quad (33)$$

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

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

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 $\dim \ker L^* = -\text{ind } L + \dim \ker L = 0 + 1 = 1$, and therefore we do have $\ker L^* = \text{span} \left(u_0' e^{\frac{4S}{r}(u_0^2 - u_0)} \right)$.

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

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

by a density argument. Then we deduce from Lemma 4.2 and Lemma 4.3 that $\dim \ker L^* = -\text{ind } L + \dim \ker L = -(-2) + 0 = 2$. 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 $\ker L^* = \text{span} \left(u_0' e^{\frac{4S}{r}(u_0^2 - u_0)}, v_0 e^{\frac{4S}{r}(u_0^2 - u_0)} \right)$. \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 $\text{rg } L = (\ker L^*)^\perp$, and thus $\text{rg } L = \left(\text{span} \left(u_0' e^{\frac{4S}{r}(u_0^2 - u_0)} \right) \right)^\perp$ 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 $u_0' \notin \text{rg } L$. Since $\text{rg } L$ has codimension 1 by Lemma 4.2 and 4.3, we have $C_\mu^{0,\alpha}(\mathbb{R}) = \text{rg } L \oplus \text{span } u_0'$. 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 $u'_0 \notin \text{rg } L$ 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

$$\lambda'_2 \frac{u'_0v'_0 - u''_0v_0}{u'_0} = u'_0, \quad \lambda'_1 = -\frac{v_0}{u'_0}\lambda'_2.$$

Since $u'_0v'_0 - u''_0v_0$ 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

$$\begin{aligned} \partial_\varepsilon \mathcal{F}(0, 0, 0) &= g(u_0) + \frac{2}{r}(u'_0)^2, \\ \partial_c \mathcal{F}(0, 0, 0) &= u'_0 \end{aligned}$$

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

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

$$g(u_0) + \frac{2}{r} (u'_0)^2 + \frac{dc_\varepsilon}{d\varepsilon} \Big|_{\varepsilon=0} u'_0 + L \left(\frac{dh_\varepsilon}{d\varepsilon} \Big|_{\varepsilon=0} \right) = 0.$$

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

$$\frac{dc_\varepsilon}{d\varepsilon} \Big|_{\varepsilon=0} = \frac{- \int_{\mathbb{R}} \left(g(u_0) + \frac{2}{r} (u'_0)^2 \right) u'_0 e^{\frac{4S}{r}(u_0^2 - u_0)}}{\int_{\mathbb{R}} (u'_0)^2 e^{\frac{4S}{r}(u_0^2 - u_0)}} > 0,$$

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

5 The speed of the traveling stacked clines

In this section, we obtain an explicit form for $c_1 = c_1(r, S)$ appearing in the asymptotic formula for the speed $c_\varepsilon = c_1 \varepsilon + o(\varepsilon)$ as given in (28). This in turn provides valuable insights on the model for coupled underdominant clines.

For convenience let us temporarily denote $u = u_0$ the standing wave solution constructed in Proposition 3.2. From (12), we see that $v := u'^2$ solves the linear first order ODE

$$v' + \frac{4S}{r} (u^2 - u)' v = -2S u' (2u - 1) u (1 - u),$$

which is solved as

$$u'^2(x) = e^{-\frac{4S}{r}(u^2 - u)(x)} \left(C - 2S \int_0^x (u^2 - u)'(t) e^{\frac{4S}{r}(u^2 - u)(t)} (u - u^2)(t) dt \right),$$

for some constant C . We integrate by parts and, up to changing the value of the constant C , reach

$$\begin{aligned} u'^2(x) &= e^{-\frac{4S}{r}(u^2-u)(x)} \left(C - \frac{r}{2} \left(e^{\frac{4S}{r}(u^2-u)(x)} (u-u^2)(x) + \int_0^x e^{\frac{4S}{r}(u^2-u)(t)} (u^2-u)'(t) dt \right) \right) \\ &= e^{-\frac{4S}{r}(u^2-u)(x)} \left(C - \frac{r}{2} \left(e^{\frac{4S}{r}(u^2-u)(x)} (u-u^2)(x) + \frac{r}{4S} e^{\frac{4S}{r}(u^2-u)(x)} \right) \right). \end{aligned}$$

Letting for instance $x \rightarrow +\infty$ enforces $C = \frac{r^2}{8S}$ and, returning to the notation u_0 , we finally obtain

$$u_0'^2(x) = \frac{r^2}{8S} e^{\frac{4S}{r}(u_0-u_0^2)(x)} - \frac{r}{2}(u_0-u_0^2)(x) - \frac{r^2}{8S}. \quad (36)$$

The fact that u_0' can be expressed in terms of u_0 , already observed in [3], enables to obtain an explicit form $c_1 = c_1(r, S)$ appearing in $c_\varepsilon = c_1\varepsilon + o(\varepsilon)$ as given in (28). Indeed, using (36) and recalling that $u_0' < 0$, we obtain

$$c_1 = \frac{- \int_{\mathbb{R}} \frac{r}{4S} u_0'(x) \left(1 - e^{-\frac{4S}{r}(u_0-u_0^2)(x)} \right) dx}{- \int_{\mathbb{R}} u_0'(x) \left(\frac{r^2}{8S} e^{\frac{4S}{r}(u_0-u_0^2)(x)} - \frac{r}{2}(u_0-u_0^2)(x) - \frac{r^2}{8S} \right)^{\frac{1}{2}} e^{-\frac{4S}{r}(u_0-u_0^2)(x)} dx}.$$

Performing the change of variable $u = u_0(x)$ this is recast

$$c_1 = \frac{\int_0^1 \frac{r}{4S} \left(1 - e^{-\frac{4S}{r}(u-u^2)} \right) du}{\int_0^1 \left(\frac{r^2}{8S} e^{\frac{4S}{r}(u-u^2)} - \frac{r}{2}(u-u^2) - \frac{r^2}{8S} \right)^{\frac{1}{2}} e^{-\frac{4S}{r}(u-u^2)} du}.$$

Expanding with respect to $\frac{S}{r} \ll 1$, we reach, after a straightforward computation,

$$c_1 = \frac{1}{\sqrt{S}} \left(1 + \frac{4}{15} \frac{S}{r} + \frac{2}{45} \frac{S^2}{r^2} + \dots \right). \quad (37)$$

In the sequel we denote

$$c_1^* := \frac{1}{\sqrt{S}} \left(1 + \frac{4}{15} \frac{S}{r} \right), \quad (38)$$

the first order term of expansion (37).

To verify the accuracy of our previsions, we ran simulations of the full system (7), the one established before simplification thanks to the quasi-linkage equilibrium approximation. We numerically estimate the instantaneous speed by following the movement of the center of the fronts. The comparison with the theoretical speed $\varepsilon c_1^* = s c_1^*$ (let us recall that s appearing in the original model is nothing else than ε , see (9)) is shown in Figure 3. We observe that formula (38) gives a very good approximation of the instantaneous speed when $\frac{S}{r}$ is not too small (right of the figure). This validates *a posteriori* the quasi-linkage equilibrium approximation.

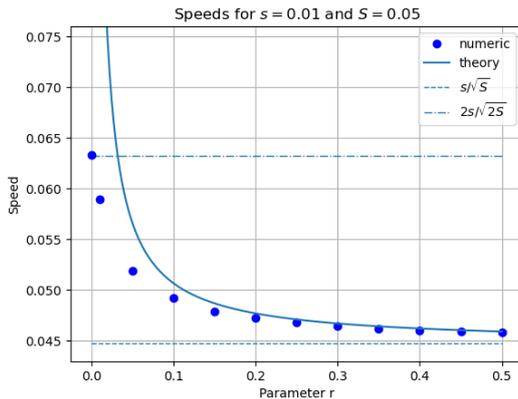


Figure 3: Comparison of the theoretical speed sc_1^* and of the numerically estimated speed of the stacked fronts.

When $r = 0.5$ (free recombination), the linkage disequilibrium stays small and the coupled clines move at a speed which is close to the one each cline would have if travelling alone, that is s/\sqrt{S} (or $s\sigma/\sqrt{2S}$ in the original spatial scale, as obtained by Barton [2] in a single-locus model). Indeed, without interaction, we are left with $u_t = u_{xx} + Sf(u) + sg(u)$, which is nothing else than the bistable equation ($0 < \frac{s}{S} < 1$)

$$u_t = u_{xx} + Su(1-u) \left(2u - 1 + \frac{s}{S} \right),$$

whose traveling wave, explicitly computed as $\frac{1}{2} - \frac{1}{2} \tanh \left(\frac{\sqrt{S}}{2} \left(x - \frac{s}{\sqrt{S}} t \right) \right)$, has speed s/\sqrt{S} .

At the other extreme, when $r = 0$ (no recombination) the system becomes equivalent to a single locus where one allele has a fitness advantage $2s$ and with a cost for heterozygotes $2S$, leading to a bistable wave speed of $2s/\sqrt{2S}$.

When $r \in (0, 0.5)$, the speed of the coupled clines decreases monotonously as recombination r increases.

Our concluding remark is as follows: whatever the values of the parameters, interacting and eventually stacked clines travel faster than one cline alone.

6 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 , and we obtained a simple approximation for its speed.

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 exchangeability between loci. Although this allowed us to simplify the algebra, different 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 were stacked in the past and will remain stacked 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 stacked 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 [17, 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, $\operatorname{rg} L$ is closed and has finite codimension and

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

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

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

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

We recall below a theorem from Volpert, Volpert and Collet [16, 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 [15, 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*

$$-a^\pm \xi^2 + b^\pm i\xi + c^\pm = 0 \tag{39}$$

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

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

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

$$a^\pm X^2 - b^\pm X + c^\pm = 0 \tag{40}$$

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:

$$\begin{aligned} L^\mu(u) &:= e^{\mu\sqrt{1+x^2}} L \left(u e^{-\mu\sqrt{1+x^2}} \right) \\ &= a(x)u'' + \left[\frac{-2\mu x}{\sqrt{1+x^2}} a(x) + b(x) \right] u' \\ &\quad + \left[\left(\frac{\mu^2 x^2}{1+x^2} + \frac{\mu x^2}{(1+x^2)^{\frac{3}{2}}} - \frac{\mu}{\sqrt{1+x^2}} \right) a(x) - \frac{\mu x}{\sqrt{1+x^2}} b(x) + c(x) \right] u. \end{aligned} \quad (41)$$

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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