Dynamics of sexual populations structured by a space variable and a phenotypical trait

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Abstract

We study sexual populations structured by a phenotypic trait and a space variable, in a non-homogeneous environment. Departing from an infinitesimal model, we perform an asymptotic limit to derive the system introduced in [25]. We then perform a further simplification to obtain a simple model. Thanks to this simpler equation, we can describe rigorously the dynamics of the population. In particular, we provide an explicit estimate of the invasion speed, or extinction speed of the species. Numerical computations show that this simple model provides a good approximation of the original infinitesimal model, and in particular describes quite well the evolution of the species' range.

Key-words: gene flow, biological invasions, structured populations

1 Introduction

Biological invasion processes play an important role in ecology [18, 34, 46]. Those invasions can for instance be due to the introduction of a new species [22] or to a climate change [20]. Theoretical models, and in particular partial differential models have proven to be useful to study biological invasions as consequences of migration and reproduction [16, 34, 46]. However, those models do not take into account evolutionary processes that can appear during the invasion.

It is known experimentally that biological invasions can involve evolutionary processes which have an impact on the speed, or even on the success of the invasion [27, 19, 45, 17]. For instance, evolutionary changes in dispersal [22, 38, 19, 47, 5] can speed up the invasion process. This is also the case if the environment to invade is inhomogeneous [22, 43, 35, 23]. In this article, we will consider this second case, for a sexual population model.

To study biological invasions in heterogeneous environments, one should consider migration and reproduction, but also mutation and gene flow. It is thus a complicated phenomenon, that has been investigated in numerous articles. In [36], it was shown that the gene flow from the center of the population's range to the edge, can prevent the expansion of the species habitat

and be the cause of the limited range of some species. In [25], a model with density regulation was introduced, which showed that a simple environment clime could lead a population to either go extinct, survive in a limited range, or invade the whole environment. This model was later generalized in [9] to several interacting species. In [4], three more detailed models were proposed, describing more accurately the local diversity of the population: A continuum of allelic effect model, a model with two alleles by locus, and an infinitesimal model. The result of this study was surprising, since the various models showed qualitatively different dynamics. In particular, no populations with limited range were obtained with the continuum of allelic effect model, or the model with two alleles by locus, while for the infinitesimal model, a limited range equilibrium and populations invading the whole environment could exist at the same time. Finally, those models have been used successfully to study the effect of global warming on populations' ranges [36, 40, 1, 26].

Most of the studies presented above focus on the cases where limited range is observed. Those cases are indeed of particular interest, since they explain globally the repartition of species. In this article, we will study with equal interest the cases where the population succeeds to invades the whole territory, since we believe it can provide a good description of the dynamics of the population close to the edge of an invasion (even if globally, the range of the population will ultimately remain limited).

In this paper, we first consider an infinitesimal model, where the population is structured by both a phenotypic trait and a space variable. We show that the model of [25] can be obtained from the infinitesimal model through an asymptotic limit (similar to the hydrodynamic limits existing in physics or chemistry [51]). This asymptotic analysis allows us to clarify the derivation of the model, and in particular to highlight the importance of the ratio between the birth rate and the maximal growth rate of the population for the validity of the model of [25]. Then, we simplify the system introduced in [25], thanks to a weak selection limit, to obtain a simple model that is able to describe populations living in a limited range, or populations invading the whole environment. Thanks to that simple model, we are able to describe rigorously the dynamics of the population, and clarify the relation between propagative fronts (invasions or extinctions) and limited range scenario. This simple equation also provides an estimate of the invasion speed of the population, if invasion happens, or of the extinction front if the population dose not succeed to invade. Finally, we illustrate the results with numerical computations, and in particular present comparisons with the dynamics of the initial infinitesimal model.

2   Derivation of simplified models from a structured population model

2.1   The structured population model

We start our analysis from a classical infinitesimal model describing the evolution of a population structured by a phenotypic trait only (see e.g. [8, 14, 32], and [13, 12, 28] for mathematical properties of this kind of models). Let $n(t, v)$ be the population at time $t \geq 0$, with a phenotypic trait $v \in \mathbb{R}$. We assume that the fitness depends on the square of the distance between v and an optimal adaptation trait θ, and is altered by the population size. If we do not take into account the effect of sexual reproduction, the fitness $s[n(t, \cdot)](v)$ of an individual of phenotypic trait v,

living among a resident population $n(t, \cdot)$, is given by:

$$s[n(t, \cdot)](v) = r_{max} - \frac{1}{2V_s}(v - \theta)^2 - \frac{r_{max}}{K} \int n(t, w)\, dw, \tag{1}$$

Here $r_{max} > 0$ denotes the maximal growth rate of the population, $\frac{1}{V_s}$ is a measure of the strength of the selection toward the optimal value of the phenotypic trait θ, and K is the carrying capacity of the environment.

The fitness is well-defined in the case of asexual populations: it is the rate of births of offsprings of trait x minus the rate of deaths. In the case of sexual populations however, the situation is more complicated, since reproduction requires two parents, of traits v_* and v'_*, that give birth to an offspring of trait v, usually different from v_* or v'_*. This has two consequences (see [6]):

- We need to define $Q(\cdot, v_*, v'_*)$, the distribution function of the trait of the offspring. We will analyze briefly the properties of Q in Subsection 2.2.

- We have to define the birth rate and the death rate separately. We will assume in this article that the birth rate is a constant, denoted by $\eta > r_{max}$.

In this model, we do not distinguish between males and females (for instance because they have the same distribution) and assume that mating is random and uniform among the population. We also assume that the number of offsprings is proportional to the local population, the idea being that the number of births is proportional to the number of females. Then the evolution of the well-mixed population, structured by a phenotypic trait only, is described by (see [14]):

$$
\begin{aligned}
\partial_t n(t, v) &= \left[-(\eta - r_{max}) - \frac{1}{2V_s}(v - \theta)^2 - \frac{r_{max}}{K} \int n(t, w)\, dw \right] n(t, v) \\
&\quad + \eta \int \int \frac{n(t, v_*)n(t, v'_*)}{\int n(t, w)\, dw} Q(v, v_*, v'_*)\, dv_*\, dv'_*.
\end{aligned} \tag{2}
$$

Here η is the birth rate ($\eta \geq r_{max}$), that we assume constant within the population (the selection occurs due to the death term).

We next consider populations that are structured by a phenotypic trait v as above, but also by a space variable $x \in \mathbb{R}$. We assume that the selection-mutation process described above occurs locally in space, but that individuals move randomly in space. We model this random movement by a diffusion of rate σ. We additionally assume that the local optimal trait changes linearly in space:

$$\theta(x) = bx. \tag{3}$$

We finally obtain the following model for sexual populations (close to the numerical model used in [15, 1]):

$$
\begin{aligned}
\partial_t n(t, x, v) &- \frac{\sigma^2}{2}\Delta_x n(t, x, v) \\
&= \left[-(\eta - r_{max}) - \frac{1}{2V_s}(v - bx)^2 - \frac{r_{max}}{K} \int n(t, x, w)\, dw \right] n(t, x, v) \\
&\quad + \eta \int \int \frac{n(t, x, v_*)n(t, x, v'_*)}{\int n(t, x, w)\, dw} Q(v, v_*, v'_*)\, dv_*\, dv'_*,
\end{aligned} \tag{4}
$$

where $-\frac{\sigma^2}{2}\Delta_x n(t,x,v)$ models individuals dispersal.

The existence and uniqueness of solutions of (4) has been shown in [41]. Notice that in this article, we do not distinguish the breeding value and the phenotypic trait of an individual, assuming a full heritability of the phenotypic trait, and neglecting the effect of the environment on the phenotypes. In Subsection 6.1 of the Appendix, under the classical assumption that probability law of the phenotypic trait of an individual is a Gaussian centered in its breeding value, we obtain a model similar to (4), where only the constant $-(\eta - r_{max})$ is modified (see e.g. [7]). Our analysis can then be generalized to this more realistic assumption.

2.2 Properties of the sexual reproduction kernel Q

In this subsection, we describe some properties of the sexual reproduction that will be useful in Subsection 2.4. As in e.g. [6, 14], we consider the infinitesimal model, where the trait is affected by an infinite number of loci with infinitesimal and additive effects. For more on the infinitesimal model and discussion of more realistic models, see [50, 49]. If the parents have traits v_*, v'_*, the distribution function $Q(\cdot, v_*, v'_*)$ of the offspring traits is given by the Gaussian distribution

$$Q(v, v_*, v'_*) := \frac{1}{\sqrt{\pi V_{LE}}} e^{-\frac{\left(v - \frac{v_* + v'_*}{2}\right)^2}{V_{LE}}}, \tag{5}$$

where $V_{LE}/2 > 0$ is the genetic variance of the genotypic values at linkage equilibrium (see [50, 49, 6]), and is assumed to be constant. We consider, in this subsection only, a pure sexual reproduction model, i.e. a well mixed population structured by a phenotypic trait v only, with a constant population size, and without selection:

$$\partial_t n(t,v) = C\left[\int\int \frac{n(t,v_*)n(t,v'_*)}{\int n(t,w)\,dw} Q(v, v_*, v'_*)\,dv_*\,dv'_* - n(t,v)\right], \tag{6}$$

for some constant $C > 0$. One can check that the total population size $\int n(t,v)\,dv$ and the mean phenotypic trait of the population $\int v \frac{n(t,v)}{N(t,x)}\,dv$ are invariant by the equation (6). On the contrary, the second moment of the population phenotypic distribution converges exponentially fast to the trait genetic variance $G^2 = V_{LE}$, and the third moment of the population phenotypic distribution converges to 0: for any initial population (see Theorem 5 in the Appendix),

$$\left|\int\left(v - \int w\,n(t,w)\,dw\right)^2 \frac{n(t,v)}{\int n(t,w)\,dw}\,dv - G^2\right|$$
$$\le e^{-Ct/2}\left|\int\left(v - \int w\,n(0,w)\,dw\right)^2 \frac{n(0,v)}{\int n(0,w)\,dw}\,dv - G^2\right|, \tag{7}$$

$$\left|\int\left(v - \int w\,n(t,w)\,dw\right)^3 \frac{n(t,v)}{\int n(t,w)\,dw}\,dv\right|$$
$$\le e^{-3Ct/4}\left|\int\left(v - \int w\,n(0,w)\,dw\right)^3 \frac{n(0,v)}{\int n(0,w)\,dw}\,dv\right|, \tag{8}$$

4

It has been shown in [6, 50] that (6) has a unique steady-state, that is the Gaussian distribution of variance $G^2 = V_{LE}$. It can indeed be shown (see [29]) that the whole distribution $n(t, \cdot)$ converges exponentially fast to a Gaussian distribution (in the sense of Wasserstein distances, see e.g. [52]).

In Subsection 2.4, estimates (7) and (8) will allow us to close a system of equations describing the evolution of two first moments of the phenotypic distribution of the population $n(t, x, \cdot)$ in (4), and recover the model of [25]. They show that for sexual populations, when C is large (in Subsection 2.4, C will be defined as the ratio between the birth rate and the maximal growth rate of the population), the second and the third moment of the population depend only on Q. They are in particular independent of the fitness landscape and the spatial structure. For asexual populations, the situation would be very different: the phenotypic variance of an asexual population in a mutation-selection equilibrium depends on the fitness landscape (and the mutation model), see e.g. [24, 6, 53, 10].

2.3 Rescaling of the structured population model

Since this term will appear often in this subsection, we write r^* the maximal fitness decreased by the load of the phenotypic variance of the population:

$$r^* := r_{max} - \frac{G^2}{2V_s},$$

where $G^2 = V_{LE}$ is the trait genetic variance.

To simplify (4), we perform the following rescaling introduced in [25] (up to a minor modification):

$$a_1 = r^*, \qquad a_2 = \frac{\sqrt{2r^*}}{\sigma}, \qquad a_3 = (r^*V_s)^{-\frac{1}{2}},$$

$$\widetilde{n}(\widetilde{t}, \widetilde{x}, \widetilde{v}) = \frac{r_{max}}{K} \sqrt{\frac{V_s}{r^*}} n\left(\frac{\widetilde{t}}{a_1}, \frac{\widetilde{x}}{a_2}, \frac{\widetilde{v}}{a_3}\right),$$

$$\widetilde{Q}(v, v_*, v'_*) := \frac{1}{a_3} Q\left(\frac{v}{a_3}, \frac{v_*}{a_3}, \frac{v'_*}{a_3}\right).$$

We notice that the rescaled reproduction kernel $\widetilde{Q}$ satisfies (7) and (8) with $\widetilde{G}^2 = (a_3)^2 G^2 = \frac{G^2}{r^*V_s}$, that is the solution of (6) with $\widetilde{Q}$ satisfies:

$$\int \left(v - \int w\, n(t, w)\, dw\right)^2 \frac{n(t, v)}{\int n(t, w)\, dw}\, dv \to \frac{G^2}{r^*V_s} \tag{9}$$

With the above rescaling, (4) becomes, if we omit the tildes:

$$\partial_t n(t, x, v) - \Delta_x n(t, x, v) = -\left[(C - (1 + A/2)) + \tfrac{1}{2}(v - Bx)^2 + \int n(t, x, w)\, dw\right] n(t, x, v)$$
$$+ C \int \int \frac{n(t, x, v_*) n(t, x, v'_*)}{\int n(t, x, w)\, dw} Q(v, v_*, v'_*)\, dv_*\, dv'_*, \tag{10}$$

with

$$A := \frac{G^2}{r^*V_s}, \qquad B := \frac{b\sigma}{r^*\sqrt{2V_s}}, \tag{11}$$

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A	measures the strength of the potential for adaptation to the local optimal trait.
B	indicates how rapidly the environment changes over space.
C	measures the ratio between the birth rate and the maximal growth rate of the population.

Table 1: The interpretation of parameters A, B and C.

$$C := \frac{\eta}{r^*},$$

and Q satisfying (7) and (8) with $\widetilde{G}^2 = A$.

We recall the interpretation of parameters A, B and C in Table 1. Notice that in the case of a population that can only procreate through sexual reproduction, $\eta \geq r_{max}$ and thus $C \in [1, \infty)$. On the contrary, for asexual populations (which we do not consider here), $C = 0$. The parameter C characterizes indeed the strength of the phenotypic traits mixing caused by the sexual reproduction.

2.4 Derivation of the model (15)

In this subsection, we show that when C is large, the phenotypic variance of the population converges to the constant A, whereas the third moment of the phenotypic distribution of the population converges to 0. The structured population model (10) then reduces to the model (15).

We denote by N, Z, the two first moments of the distribution $n(t, x, \cdot)$:

$$N(t,x) := \int n(t,x,v)\, dv, \quad Z(t,x) := \int v \frac{n(t,x,v)}{N(t,x)}\, dv,$$

Then (see Theorem 2 in Subsection 6.3 of the Appendix), N and Z satisfy the following unclosed equations:

$$\partial_t N(t,x) - \Delta_x N(t,x)$$
$$= \left[1 + \frac{1}{2}\left(A - \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv \right) - \frac{1}{2}(Z(t,x) - Bx)^2 - N(t,x) \right] N(t,x). \quad (12)$$

$$\partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + (Bx - Z(t,x))\int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv$$
$$- \int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\, dv. \quad (13)$$

The term $2\partial_x(\log N)\partial_x Z$ is referred to as the swamping, or asymmetric gene flow term (see [31] and [36, 25, 40, 42]). This term models the fact that the mean phenotype of low density areas are greatly influenced by the phenotypes of neighboring high density areas. It is interesting to notice that this term does not come from the sexual reproduction term, but from the diffusion term:

$$\Delta_x Z(t,x) = \int v \frac{\Delta_x n(t,x,v)}{N(t,x)}\, dv - \frac{Z(t,x)}{N(t,x)}\Delta_x N(t,x) + 2\partial_x(\log N(t,x))\partial_x Z(t,x).$$

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Equations (12) and (13) can also be obtained for asexual populations. However, the moment closure that we will present next, and that will allow us to derive the model of [25] from (12) and (13) does not apply to asexual populations. This is fortunate, since the cases where the population survives in a limited range, obtained in [25] only make sense for sexual populations.

To close the equations (12) and (13), we notice that (10) can be written:

$$\partial_t n(t,x,v) - \Delta_x n(t,x,v) = C\left[\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw}Q(v,v_*,v'_*)\,dv_*\,dv'_* - n(t,x,v)\right]$$
$$+ \left[1 + \frac{A}{2} - \frac{1}{2}(v-Bx)^2 - \int n(t,x,w)\,dw\right]n(t,x,v)$$

Therefore if C is very large (that is $C >> \max\{1,A,B\}$), the first term dominates the dynamics of the population. This first term corresponds to the "pure" sexual reproduction equation (6). It does not affect the total population $N(t,x)$ or the mean phenotypic trait $Z(t,x)$, but it acts on the second and the third moments of the phenotypic distribution of the population, as described in Subsection 2.2. The recalled reproduction kernel $\tilde{Q}$ (denoted by Q here) satisfies (7) and (8) with $\tilde{G}^2 = \frac{G^2}{r^* V_s} = A$ (see (9)). If C is large, it is then natural to assume that at all time $t > 0$ and all locations $x \in \mathbb{R}$,

$$\int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\,dv \sim A, \qquad \int (v - Z(t,x))^3 \frac{n(t,x,v)}{N(t,x)}\,dv \sim 0. \qquad (14)$$

We can then use the estimates (14) to close the system of equations (12) and (13) and to obtain the model (15) of [25]:

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \left(1 - \frac{1}{2}(Z(t,x) - Bx)^2 - N(t,x)\right)N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x)), \end{cases} \qquad (15)$$

Our derivation shows that the model (15) is valid (in the sense that it is the formal asymptotic limit of the infinitesimal (4)) if:

- The reproduction is sexual,

- The reproduction kernel satisfies (7) and (8),

- C is large.

With the asymptotic that we consider in this article (C large), the phenotypic variance of the population depends only on the phenotypic variance of the offsprings ($G^2 = V_{LE}$, see Subsection 2.3), and neglects the effect of migration on the phenotypic variance. If $C \geq 1$ is small, numerical computations in Subsection 4.3 show that this simplification may not be very accurate, away from the edge of the propagating front.

Unfortunately, there is no existence and uniqueness theory for (15). The difficulty comes from the term $\partial_x(\log N(t,x)) = \frac{\partial_x N(t,x)}{N(t,x)}$, which is not defined when N is not bounded away from 0. One possibility to avoid this difficulty is to multiply the second equation of (15) by N. But even in this case, the equation on Z is not defined when $N(t,x) = 0$. This problem will persist in the simplified model that we will derive in the next subsection, where we will discuss the problem of the definition of solutions in more details (see Example 1, and Subsection 6.4 in the Appendix).

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2.5 Derivation of the model (18)

In this subsection, we show that when A and B are small, the model (15) simplifies further. To do so, we first apply the following change of variable:

$$\breve{N}\left(\breve{t},\breve{x}\right) := N\left(\frac{\breve{t}}{A},\frac{\breve{x}}{\sqrt{A}}\right), \qquad \breve{Z}\left(\breve{t},\breve{x}\right) := \frac{1}{\sqrt{2}}Z\left(\frac{\breve{t}}{A},\frac{\breve{x}}{\sqrt{A}}\right).$$

To simplify the notations, we omit the breves in the new unknown functions. The rescaled model becomes

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \frac{1}{A}\left[1 - (Z(t,x) - Dx)^2 - N(t,x)\right]N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + (Dx - Z(t,x)), \end{cases} \tag{16}$$

where $D = \frac{B}{\sqrt{2A}}$. Now, if we assume that A and B are small, while D remains constant, N and Z are related by the simple relation:

$$N(t,x) \sim 1 - (Z(t,x) - Dx)^2. \tag{17}$$

Notice that $D = \frac{b\sigma}{2\sqrt{r^*G}}$. If $\frac{1}{V_s} \to 0$, then A, $B \to 0$ while D remains constant. The model (18) can then be seen as a weak selection limit of (15). This is however not the only case where this model applies: it would also apply, for instance, if $G = \sigma \to 0$. In [25], the range of A that has been considered is $A \in [0.001, 1]$, and the range of B when the population does not go extinct is $B \in [0.01, 1]$. Thus our approximation, assuming that A and $B \sim \sqrt{A}$ are small, is coherent with [25]. As we will see in Section 3, this model will provide relevant approximations of the dynamics of the population, even when A is not very small.

Then, we obtain the simpler model (18), on Z only:

$$\begin{aligned} \partial_t Z(t,x) - \Delta_x Z(t,x) &= -4\frac{(\partial_x Z(t,x) - D)(Z(t,x) - Dx)}{1 - (Z(t,x) - Dx)^2}\partial_x Z(t,x) \\ &\quad + (Dx - Z(t,x)). \end{aligned} \tag{18}$$

Notice that $N \geq 0$ implies that this approximation makes sense only if $|Z(t,x) - Dx| \leq 1$. Therefore we consider only solutions of (18) such that $Z(t,x) \in [Dx - 1, Dx + 1]$.

As we can see in (16), the limit that we performed corresponds to an infinitely fast reaction term. This model is thus inadequate to capture the extinction phenomenon that occurs at the infinitesimal level (see Section 4). This simple model is however able to capture the two other possible behaviors of the population: propagation to the entire environment and survival in a limited range.

Remark 1 *Another simplification had been proposed in [25], where the equation on N was replaced by*

$$N := k\exp\left(\beta\left(1 - A(Z - Bx)^2\right)\right). \tag{19}$$

With this ansatz, the model (15) simplifies considerably:

$$\partial_t Z(t,x) - \Delta_x Z(t,x) = A(Bx - Z(t,x))\left[1 - 4\beta\partial_x Z(t,x)(B - \partial_x Z(t,x))\right].$$

However, the simplification (19) seems independent of (15). Our simplification has the advantage to rely on a clearer assumption: (18) is the formal limit of (15) when A is small.

The equation (18) has a singularity for $Z = Dx \pm 1$. The existence of singularities is an obstacle to have a well-defined problem. However, as we will see in Subsection 3.1, the singularities are fundamental to produce propagating fronts. We have not been able to find a good notion of solution, that is a definition of solutions that would imply both the existence of solution for general initial data, and the uniqueness of those solutions. Nevertheless we are able to show in Subsection 6.4 of the Appendix (Theorem 3) that (18) admits viscosity solutions (see Subsection 6.4 in the Appendix for the definition of viscosity solutions and [11, 2] for general introduction to the theory of viscosity solutions). Unfortunately the viscosity criterion is not enough to select a unique solution. We give a counter-example below:

Example 1 *Non-uniqueness for equation* (18)*: We have the two following solutions to equation* (18)*:*

$$Z_1(t,x) = Dx - 1, \qquad \text{for all } (t,x) \in \mathbb{R}_+ \times \mathbb{R},$$

$$Z_2(t,x) = Dx - e^{-t}, \qquad \text{for all } (t,x) \in \mathbb{R}_+ \times \mathbb{R}.$$

The first solution corresponds to $N(t,x) = 0$, while the second corresponds to $N(t,x) = 1-e^{-2t}$, that is to a the spontaneous apparition of a population. The biologically relevant solution is thus first one: if initially $Z(0,x) = Dx - 1$ for all $x \in \mathbb{R}$, we expect that $W(t,\cdot) \equiv -1$, for all $t \in \mathbb{R}_+$. However, an existence theory able to select the biologically relevant solution for any initial population doesn't exist yet (see also Subsection 6.4 in the Appendix).

3 Dynamics of the population, and propagating fronts

3.1 Theoretical study of the simplified model (18)

In this subsection, we study the existence of propagating fronts and steady states for equation (18). Since the optimal trait at the point x of space is Dx, we expect a propagating front Z, with Z a solution of (18), to be of the following form

$$Z(t,x) = Dx + U(x - \nu t).$$

Using the above notation, the equation (18) becomes

$$-\nu U' - U'' = -4 \frac{U'U}{1 - U^2}(U' + D) - U,$$

with $U : \mathbb{R} \mapsto [-1, 1]$. If we denote by $V := U'$ the derivative of U, finding a propagating front is equivalent to finding a solution defined on $\mathbb{R}$ to the ODE

$$\frac{d}{dt}(U,V)(t) = (F_U(U,V), F_V(U,V)),$$

where the vector field (F_U, F_V) is given by:

$$\begin{cases} F_U(U,V) = V, \\ F_V(U,V) = -\nu V + 4\frac{UV}{1-U^2}(V + D) + U. \end{cases} \tag{20}$$

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Using this new formulation of the problem, we show in Subsection 6.5 of the Appendix (Theorem 5) that for any $D > 0$, there exists a minimal speed $\nu_D \in \mathbb{R}$ such that (18) has a propagating front of speed ν, $Z(t, x) = Dx + U(x - \nu t)$, satisfying

$$U(x) \to 0 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty,$$

if and only if $\nu \geq \nu_D$. Just as for classical invasion models (like the Fisher-KPP model, see [34, 46]), only the front of minimal speed is biologically relevant: the fronts of speed $\nu > \nu_D$ can be obtained only with very particular initial populations. One can then consider that the propagation speed of the population is ν_D. The corresponding propagating front has a sharp edge: there exists $x(t) = x_0 + \nu_D t$ such that $N(t, x) = 1 - (Bx - Z(t, x))^2 \neq 0$ for $x < x(t)$, and $N(t, x) = 0$ for $x \geq x(t)$. Moreover, $\partial_x Z(t, x) \to 0$ as $x \to x(t)$, $x < x(t)$, that is the mean phenotypic trait of the population is almost constant close to the edge of the population's range. We represent some propagating fronts in Figure 1.

In Subsection 6.5 of the Appendix, we show that (18) is also able to describe the situations where the population survives in a limited range, but does not succeed to invade the whole space. More precisely, we show that (18) has a non-trivial steady-state (that is the population has a limited range) if and only if $\nu_D < 0$ (that corresponds to the case where the propagating front described above is indeed an extinction front). Those steady-states $Z(t, x) = Dx + U(x)$ satisfy

$$U(x) \to 1 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty.$$

Similarly to the propagating fronts that we described above, provided that $\nu_D < 0$, there exists a whole family of steady-states (parameterized by $V(0) = U'(0) \in [-K_D, 0)$), only one of which being biologically relevant (the one satisfying $V(0) = U'(0) = -K_D$). Those steady states also have sharp edges: there exist x_{min}, x_{max} such that the population is present on the interval $[x_{min}, x_{max}]$ only, and close to the edges of the population's range, the mean phenotypic trait of the population is almost constant. We represent some steady populations in Figure 2. As we can see numerically in Figure 2 (or theoretically thanks to (20)), the mean phenotypic trait of the population is almost constant as soon as D is large ($D \gtrsim 4$).

3.2 Estimation of the speed of the propagating fronts

The correspondence between propagating fronts of (18) and solutions of (20) provides a simple way to determine numerically the minimal speed and shape of the propagating fronts of (18). As we show in Subsection 6.6 of the Appendix, it also provides a way to estimate analytically the speed of the propagating fronts: for $D > 0$,

$$\nu_D \sim \frac{1}{20} \left(7 \left(\frac{2}{D} - 9D \right) + 3 \sqrt{\left(\frac{2}{D} - 9D \right)^2 + 40} \right). \tag{21}$$

In Figure 9, we see that this analytical approximation of ν_D is remarkably close to the values of ν_D obtained numerically. If we come back to the scaling of (15) or (10), the population described by n or (N, Z) would then propagate at a speed $\nu_{A,B} \sim \frac{1}{\sqrt{A}} \nu_{B/\sqrt{2A}}$.

We notice that (21) provides an estimate $D_{crit} \sim \frac{2}{3}$ for the critical value of D such that $\nu_D = 0$, which corresponds to the limit between cases where the species invade the whole
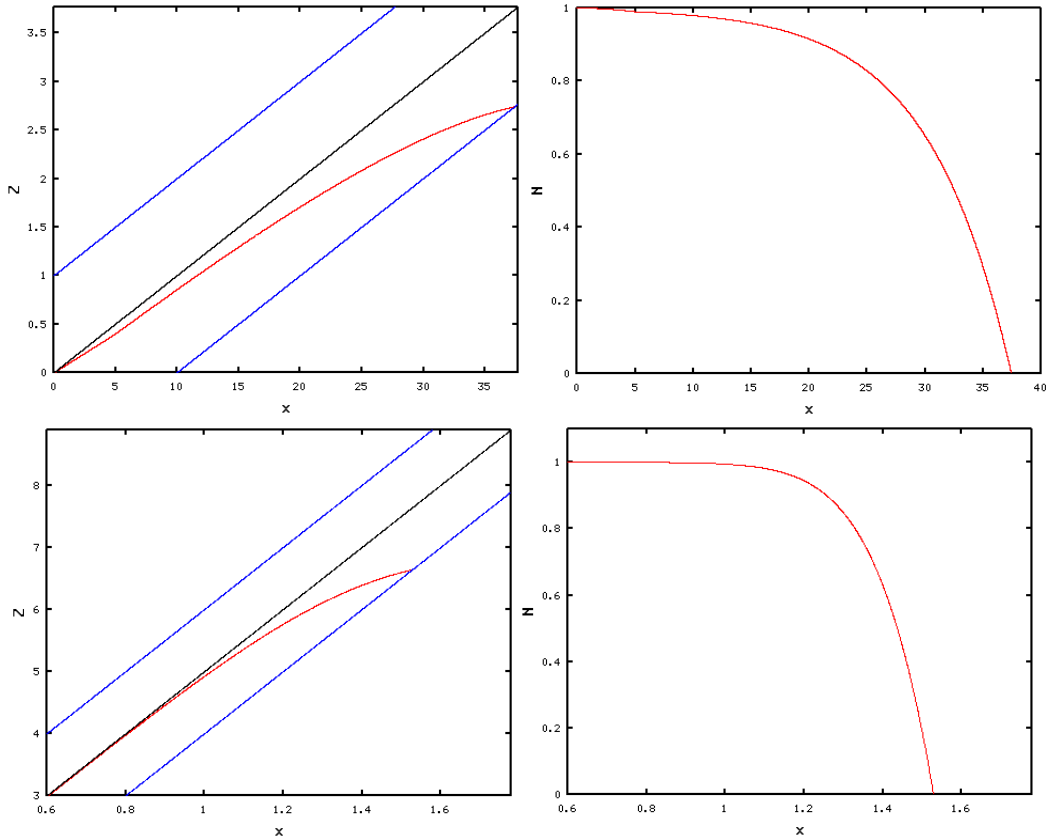
Figure 1: Propagating fronts. We represent the mean phenotypic trait $x \mapsto Z(x - \nu_D t)$ and the corresponding population size $x \mapsto N(x - \nu_D t)$, for $D = 0.1$ in the first line and $D = 5$ in the second. For $D = 0.1$, the front is an invasion front, $\nu_{0.1} \sim 9.7 > 0$, whereas for $D = 5$, it is a depopulation front, $\nu_5 \sim -9.25 < 0$. On the graphs representing the mean phenotypic traits, we also represent the optimal trait $Z = Dx$ (in black), and the two lines $Z - Dx = \pm 1$ (in blue), which correspond to the limits of the domain where Z has a meaning (we recall that $Z(t, x) \in [Dx - 1, Dx + 1]$).

territory ($D < D_{crit}$), or remain in a limited range ($D > D_{crit}$). Notice that this estimation of the critical value is different from the one obtained in [25] where $D_{crit} \sim 1$ was derived from the approximation that $N << 1$. It seems that this approximation does not apply in the weak selection limit considered here (see Subsection 2.5).

We can also derive from the above estimate an approximation of the shape of the propagating fronts:

$$Dx + U_{\nu_D}(x) \sim Dx - \left(\left(1 - \frac{\beta}{D + \beta}\right) e^{-\frac{D+\beta}{2}x} + \frac{\beta}{D + \beta} \right)^{-2}, \quad x \in \mathbb{R}_-,$$

where $\beta = \frac{1}{2} \left(\sqrt{\nu_D^2 + 4} - \nu_D \right) - D$, and $Dx + U_{\nu_D}(x) = Dx - 1$ on $\mathbb{R}_+$. Finally, N_{ν_D} can be estimated thanks to the formula $N_{\nu_D}(x) = 1 - U_{\nu_D}^2$.
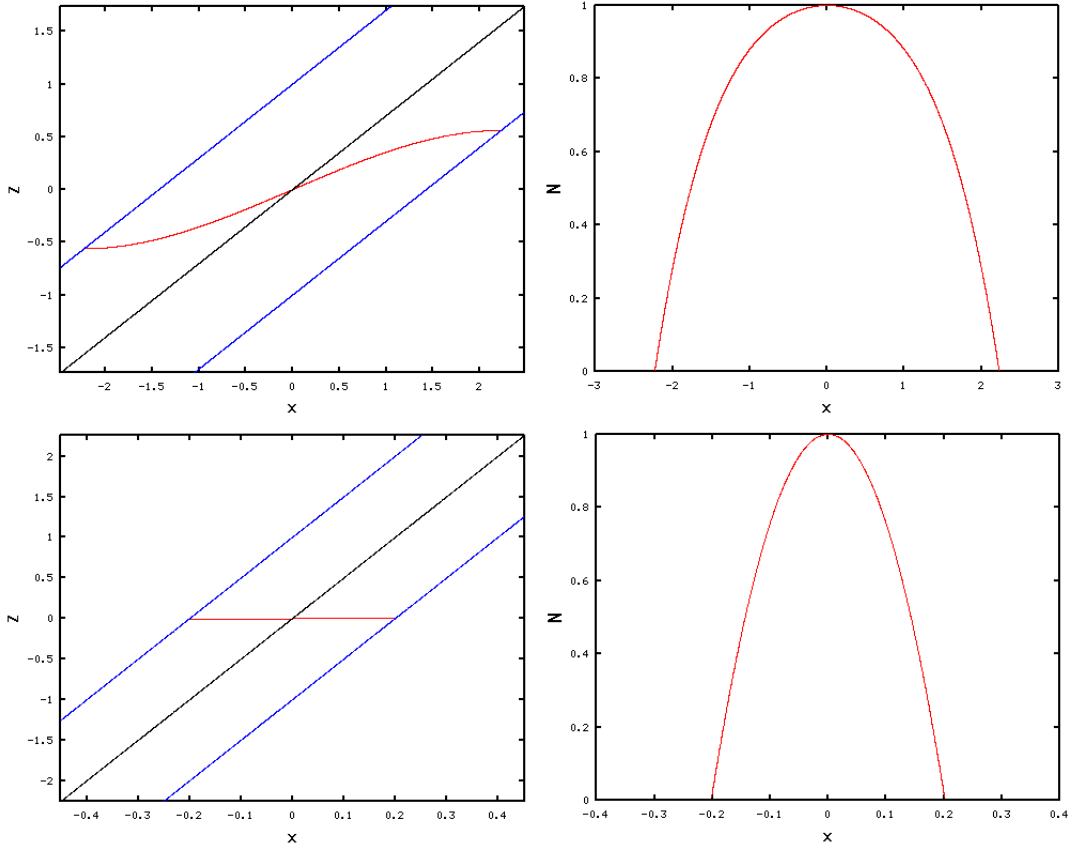
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Figure 2: Population at equilibrium with a limited range. We represent the mean phenotypic trait $Z(x)$ and the corresponding population size $N(x)$, for $D = 0.7$ in the first line and $D = 5$ in the second. On the graphs representing the mean phenotypic traits, we also represent the optimal trait $Z = Dx$ (in black), and the two lines $Z - Dx = \pm 1$ (in blue), which correspond to the limits of the domain where Z has a meaning (we recall that $Z(t, x) \in [Dx - 1, Dx + 1]$).

4   Numerics

In this section, we analyze numerically the dynamics of the structured population model (10), and compare it with the propagating fronts and steady-states obtained from the simplified model (18).

4.1   Numerical scheme

The difficulty for the numerical resolution of (10) is that a direct discretization of the birth term leads to a very slow algorithm (of order k^3, where k is the number of nodes in the v variable). Fortunately, with the classical sexual reproduction kernel (5), we can write the reproduction term as a double convolution, as noticed in [50]:

$$\int \int \frac{n(t, x, v_*) n(t, x, v'_*)}{\int n(t, x, w)\, dw} Q(v, v_*, v'_*)\, dv_*\, dv'_* = \frac{1}{\int n(t, x, w)\, dw} \left(\tilde{Q} *_v f(t, x, \cdot) *_v f(t, x, \cdot) \right)(2v),$$
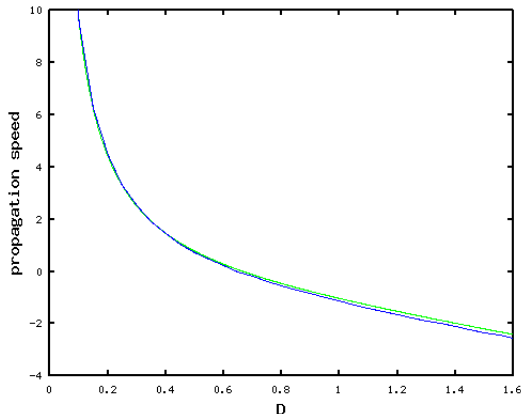
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Figure 3: Comparison of the minimal speed ν_D of propagating waves of the simplified model (18) (in blue), with the approximated speed (21) (in green).

where Q is defined by (5) with $\gamma^2 = A$, and $\tilde{Q}(v) := \frac{1}{A\sqrt{2\pi}}e^{-\frac{v^2}{8A^2}}$. This formula allows us, as described in [50] to use a spectral method to compute the reproduction term, and the computational cost of the birth term then becomes of the order of a Fast Fourier Transform, that is $k \log k$. Coupled to a classical finite difference scheme for the rest of the equation, this produces an algorithm reasonably fast.

For the simplified model (18), we can use the phase plane (U, V) described in Subsection 3.1 to compute numerically the steady-states and propagating fronts of (18). We can in particular estimate numerically ν_D (see Theorem 5), and obtain a numerical approximation of the corresponding front.

4.2 Dynamics of the population

By performing a numerical resolution of (10), we can observe the three possible behaviors described in [25]: For given A and C, we observe extinction if B is large (see Figure 4), convergence to a steady-state for intermediate values of B (see Figure 5), and propagation if B is small (see Figure 6).

For $C = 20$, Figure 7 describes the dynamics of populations depending on A and B. The dots come from the numerical resolution of (10) and they determine the limit between the zones where populations propagate, remain in a limited range or get extinct. We can also use the simplified model (18) to determine the border between the zones where populations succeed to propagate (if $D = \frac{B}{\sqrt{2A}} < D_{crit} \sim \frac{2}{3}$), and where populations remain in a limited range (if $D = \frac{B}{\sqrt{2A}} > D_{crit} \sim \frac{2}{3}$). This border is represented by a continuous line in Figure 7. We notice that the agreement between the theoretical border and the numerical results is good.

As explained in Subsection 2.5, the simplified model (18) is unable to describe the extinction phenomena. However, we can still obtain formally the border between the zones of extinction, and limited range. Indeed, numerically we observe that when a steady population is small, it tends to have a constant mean trait, that is Z is constant. Using this purely formal ansatz, we can use (15) to get a criterion for extinction or survival of populations: it depends on the sign
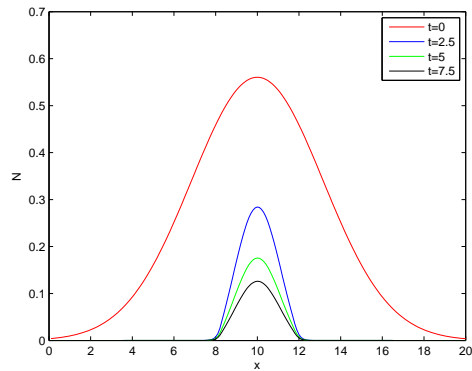
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Figure 4: Extinction for $A = 0.01$, $B = 1.3$, $C = 20$. The graph represents the total population $x \mapsto N = \int n(t, x, v)\, dv$ for four successive times.
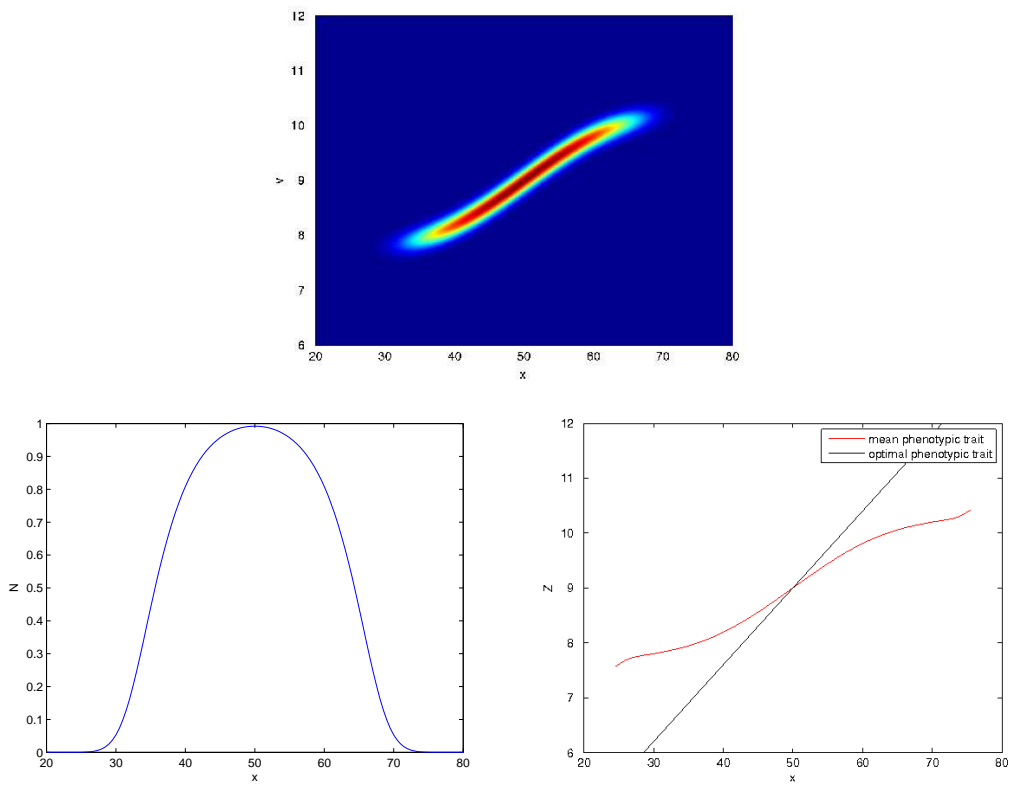

Figure 5: Limited range, for $A = 0.01$, $B = 0.3$, $C = 20$. The three graphs represent respectively the population $(x, v) \mapsto n(t, x, v)$, the total population at each location $x \mapsto N = \int n(t, x, v)\, dv$, and the mean phenotypic trait of the population, $x \mapsto Z = \int v \frac{n(t,x,v)}{N(t,x)}\, dv$.
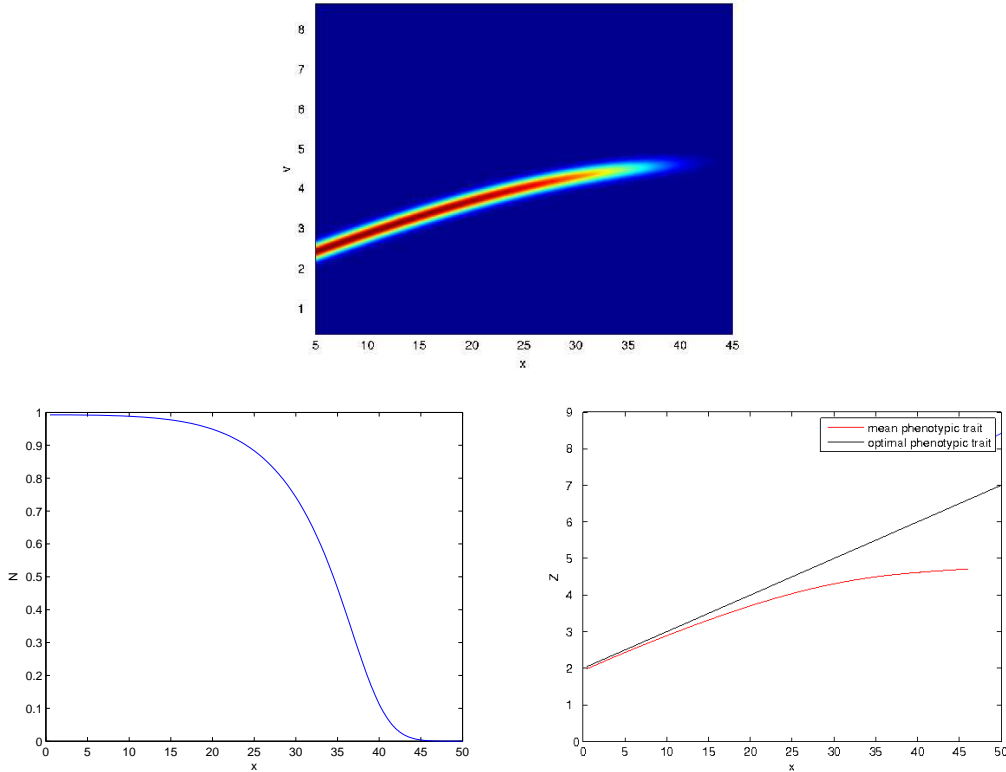
Figure 6: Propagation for $A = 0.01$, $B = 0.1$, $C = 20$. The three graphs represent respectively the population $(x, v) \mapsto n(t, x, v)$, the total population at each location $x \mapsto N(t, x) = \int n(t, x, v) \, dv$, and the mean phenotypic trait of the population, $x \mapsto Z(t, x) = \int v \frac{n(t,x,v)}{N(t,x)} \, dv$.

of the principal eigenvalue of the linear operator

$$\mathcal{L}(N)(x) = \Delta N(x) + \left(1 - \frac{B^2}{2}x^2\right) N(x),$$

that is the sign of $1 - \frac{B}{\sqrt{2}}$ (the corresponding eigenfunction being $N(x) = e^{-\frac{Bx^2}{2\sqrt{2}}}$). Following this formal argument, extinction would occur if $B > \sqrt{2}$. In Figure 7 we also represent the line $B = \sqrt{2}$, that appears to be close to the border obtained by numerical resolution of (10).

4.3 Comparison between the structured population model (10) and the simplified model (18)

In Section 2, we showed that the structured population model (10) converges formally to the simplified model (18) when C is large and A, B are small. Then, in Subsection 3.1, we have described the steady-states and traveling waves of the simplified model (18) using a phase plane analysis. In Figure (8), we compare the numerical resolution of the structured population model (10) with the propagating fronts of the simplified model (18) for $A = 0.01$, $B = 0.1$ and $C = 20$.
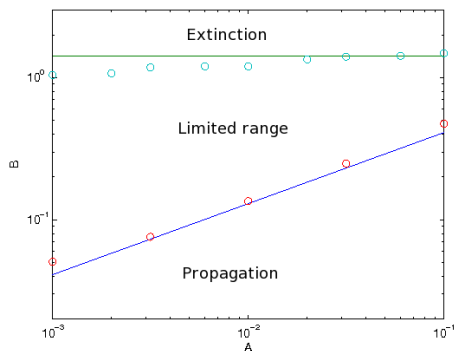
Figure 7: Dynamics of the structured population model (10). The dots come from the numerical resolution of (10) with $C = 20$. The continuous lines come from the approximations presented in Subsection 4.2.
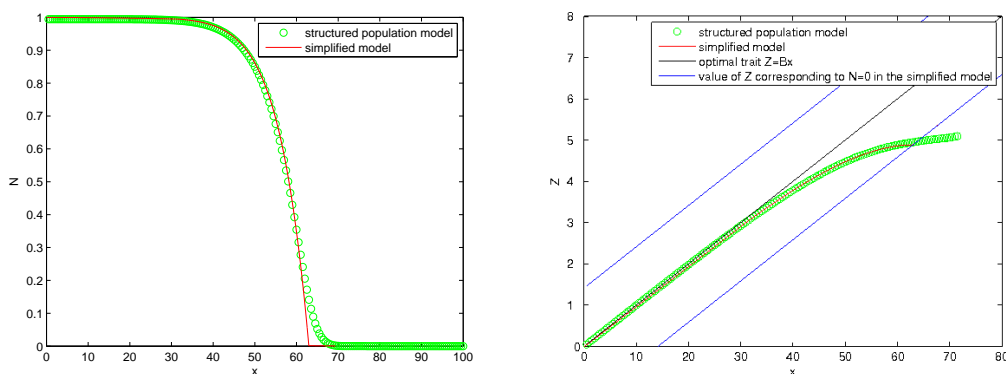

Figure 8: Comparison of propagating wave profiles of the structured population model (10) with the propagating wave of minimal speed ν_D for the simplified model (18). We depict the total population N for both models (left) and the mean phenotypic trait Z for both models (right), using the following parameters: $A = 0.01$, $B = 0.1$, and $C = 20$.

We can compare numerically the propagation speed for models (15) and (18) for $A = 0.01$ small. As we can see in Figure 9, the speed ν_D obtained from the simplified model seems a good approximation of the speed of propagating fronts from the structured population model (10) when C is large ($C = 20$ on figure 9). When C is small ($C = 1$, which is the minimal possible value of C for a sexual population), the approximation is much less accurate. The assumption that C is large, which we used to derive the model (15) from (4) in Subsection 2.4 thus seems necessary for the simpler models (15) and (18) to be relevant.

To investigate further the influence of C on the properties of the population, we consider the case where $A = 0.01$, $B = 0.5$ and $C = 1$ or $C = 20$. We observe in Figure 10 that the values of the total population $N(t, x) = \int n(t, x, v) \, dv$ and the mean phenotypic trait $Z(t, x) = \int v \frac{n(t,x,v)}{N(t,x)} \, dv$ for the propagating fronts obtained numerically for $C = 1$ and $C = 20$ are close.

However, in the case $C = 1$, the value of the phenotypic variance of the population is far from the value $\int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)} \, dv = A$ used in our asymptotic analysis (see Subsection 2.4). This is because in our asymptotic analysis (Subsection 2.4), we have neglected the phenotypic variance produced by the migration, which probably explains the dependence of the population's propagation speed in the coefficient C.

Notice however that close to the edge of the propagating front, the assumption that the phenotypic variance of the population is A seems accurate. This is probably due to the fact that in this region, the mean phenotype Z is almost constant in x (see Subsection 3.1), migration has then little effect on the phenotypic variance of the population. Our approximation that C is large thus fails to reproduce the phenotypic variance of a population far from the edge of the habitat (for $C \geq 1$ small), but describes it quite well at the edge of the habitat (even for $C = 1$, see Fig. 10).
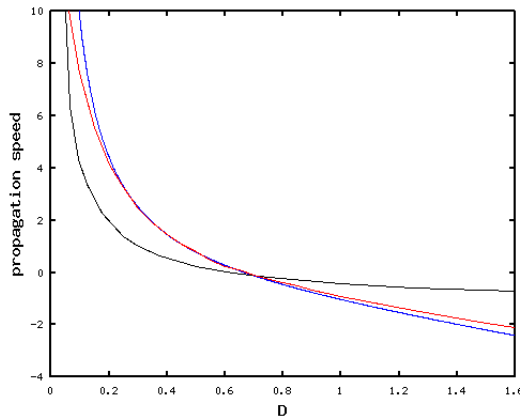

Figure 9: Comparison of the propagating wave speed of the structured population model (10) for $C = 1$ (in black), $C = 20$ (in red) and the minimal speed ν_D of propagating waves of the simplified model (18) (in blue).

5   Discussion

The study of populations living in heterogeneous environments is challenging, since many biological processes are combined: migration, mutation, gene flow... Understanding the dynamics of such populations is however crucial to study the repartition area of species, or the effect of global warming on a species' range. Several models have been proposed to study such populations.

In [36], a model describing the evolution of the mean phenotypic trait and the size of the population was introduced (the model also allowed the optimal phenotypic trait to evolve in time). This model has an exact solution, which is very useful in practice (see e.g. [26]). The model however does not allow for any density dependence in the fitness function, which is problematic, since the population's size can grow indefinitely. The absence of density regulation leads indeed to a strong gene flow from the center of the habitat to the edge, which prevents any species to invade the whole environment.

A density dependence was then introduced in [25], which leads to a model able to capture three possible outcomes: the population can either go extinct, survive in a limited area, or spread to
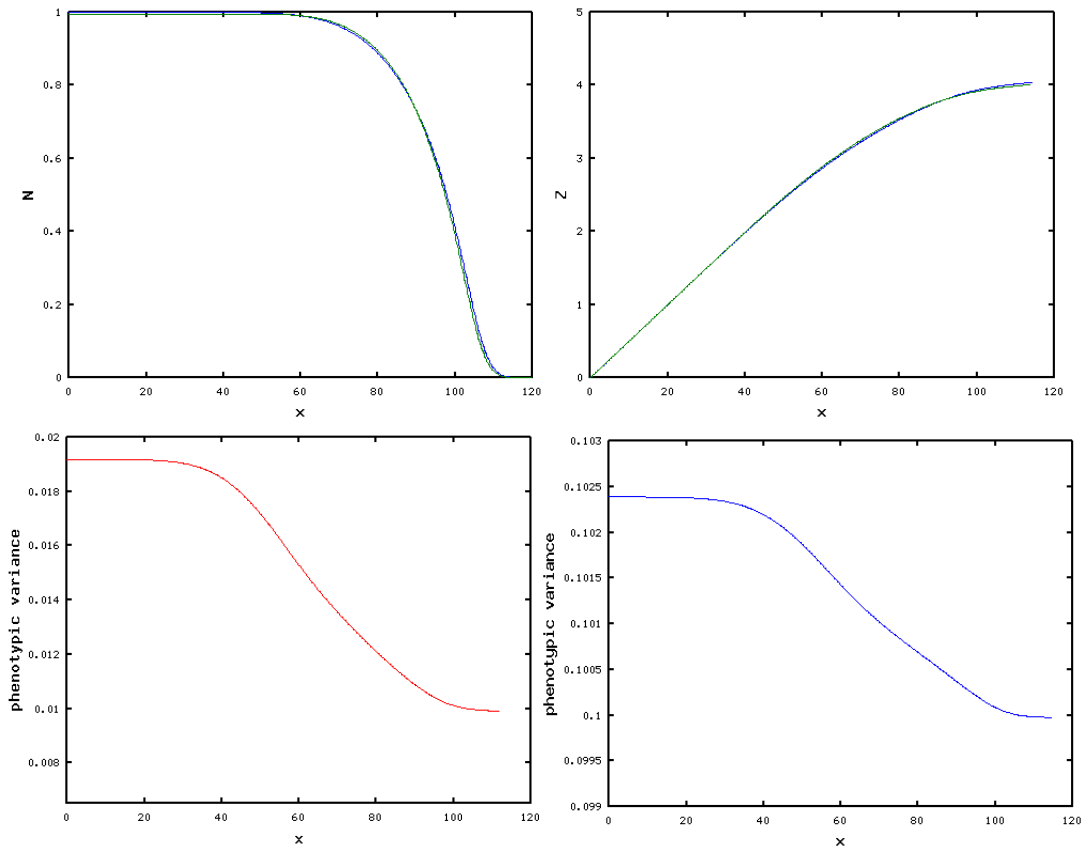
Figure 10: Comparison of propagating wave profiles of the structured population model (10) for $C = 1$ (in red) and $C = 20$ (in blue). The other parameters are $A = 0.01$, $B = 0.5$, and the speeds of propagation are respectively 0.237 and 0.792. We depict the total population N (left), the mean phenotypic trait Z (right), and the phenotypic variance (bottom) of the population. Notice the different scales for the phenotypic trait axis in those two last plots. The variance of the population when C is very large is $G^2 = A = 0.01$.

the entire environment. No exact solution is known for this more realistic model (except for a population that is perfectly adapted everywhere), and simplifications are then necessary to understand its dynamics.

In [25], the phenotypic variance of the population was assumed constant, which may not be realistic. More detailed models where thus introduced in [4]: a continuum of alleles model, a model for two alleles per locus, and an infinitesimal model. Surprisingly, the conclusion was then very different from [25]: no stationary populations were observed for the two first models, whereas both convergence to a steady population with limited range or invasion to the whole space were possible for the infinitesimal model. In Figure 10, numerical resolutions of the infinitesimal model suggest that the phenotypic variance in the population is minimal at the edge of the population range. This result is quite different from the results of [4], where it is explained that gene flow can inflate the genetic variance at the edge of the population's range, enabling its propagation.

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In this article, we have shown that the model of [25] can be obtained from the infinitesimal model through an asymptotic limit (see Subsection 2.4). This asymptotic analysis shows an explicit link between those two models, which enables us to compare them numerically. Numerically, we observe no qualitative difference between the dynamics of the infinitesimal model and the model of [25]. In particular, the existence of steady populations seems equivalent to the existence of extinction fronts, just as for the simplified model (18). Our analysis emphasizes the importance of the parameter C (the birth rate divided by the maximal growth rate of the population): the model of [25] is the asymptotic limit of the infinitesimal model when C is large. Notice that the cases where $C \leq 1$ may be interesting, since it allows the investigation of populations that do not only reproduce sexually.

In our asymptotic analysis, we have assumed (as a consequence of our asymptotic limit C large) that the phenotypic variance of the population is constant, and is not affected by migration. As we showed, this assumption is quite rough when C is small, but it remains accurate close to the edge of the invasion front for any $C \geq 1$. This result is quite different from the result obtained in [4] with the continuum of alleles model and the model for two alleles per locus. It was observed there that close to the edge of the species' range, mutations increase the phenotypic variance of the population ultimately allowing the population to invade the whole environment under any circumstance. A natural continuation of our work would be to modify our asymptotic limit to allow the phenotypic variance of the population to evolve. Numerically, an approximation of the type $\int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)} \, dv \sim A + \varepsilon(A,B,C)\partial_x Z(t,x)^2$ (where $\varepsilon(A,B,C) \to 0$ as $C \to 0$) seems to be very close to the numerical resolution of the infinitesimal model. This would be the next step to understand the connections between the infinitesimal model and the continuum of alleles model proposed in [4].

From the model of [25], we have derived the simplified model (18). This new model can be seen as a weak selection limit of [25], and is interesting because its simplicity allows a good understanding of its dynamics, as well as a good approximation of the invasion speed or extinction speed. If a steady population with limited range exists (for a given set of parameters of the equation (4)), we have shown using the simplified model (18) that depopulation fronts exist. A perfectly adapted population occupying the entire space may be stable, but as soon as the population has a bounded range ($N(0,x) = 0$ outside a bounded interval, that is $Z(0,x) = Dx+1$ when $x < -C$, $Z(0,x) = Dx - 1$ when $x > C$ for some $C > 0$), a depopulation front will shrink that range, and finally the population will converge to the limited range steady population.

Following [36], the models proposed in [36, 25, 4] are mostly used in the case of limited range. We believe however that those models can also be interesting to study invasion or extinction processes, as an extension of classical invasion models (see [16, 34, 46]) including evolutionary effects. In particular, the mathematical tools presented here may be useful to study the evolution of species' range under the effect of global warming. The idea would not be to model the whole population, but simply a part of it, close to an edge of its range. In the context of global warming (where this type of model have been widely used in the case of limited range [1, 26]) those models could be used to understand how fast the species will invade towards the north (if we consider a population living in the northern hemisphere), or how fast it will go extinct on the southern edge of its range. Our explicit approximation of those speeds, provided in Subsection 3.2 can then be useful (after a modification to include the effect of global warming, that we did not consider here).

As noticed in Subsections 2.4 and 2.5, a good definition of solutions of (15) and (18) is still

missing, when the population $N(t, x)$ is not initially bounded away from 0. This case is of particular importance, since those models can be used to study invasions of new environments. This theoretical problem has the concrete implication that classical finite difference schemes, for (18) at least, fail to select the biologically relevant solutions of the model (see Example 1). An investigation of an existence and uniqueness theory would then be interesting. It seems that the approximation scheme (25) (or a similar approximation for (15)) could be a good intermediate step.

6 Appendix

6.1 Case of a population structured by a Breeding value

The phenotypic trait is produced by a combination of the breeding trait, determined by the genotype of the individual, and environmental factors. A common assumption is to consider that the probability distribution of the phenotype v of an individual is given by a Gaussian distribution centered around its breeding value p, with variance V_E. The fitness of a population of breeding value p is then given by the average fitness of the Gaussian distribution. If $n(t, x, p)$ is a population at time $t \geq 0$ structured by a space variable x and a breeding value p, (4) then becomes:

$$
\partial_t n(t, x, p) - \frac{\sigma^2}{2} \Delta_x n(t, x, p)
$$
$$
= \left[-\left(\eta + \frac{1}{2V_s} V_E - r_{max} \right) - \frac{1}{2V_s}(p - bx)^2 - \frac{r_{max}}{K} \int n(t, x, q)\, dq \right] n(t, x, p)
$$
$$
+ \eta \int \int \frac{n(t, x, p_*) n(t, x, p_*')}{\int n(t, x, q)\, dq} Q(p, p_*, p_*')\, dp_*\, dp_*',
$$

since

$$
\int -\frac{1}{2V_s}(v - bx)^2 \frac{e^{\frac{-(v-p)^2}{2V_E}}}{\sqrt{2\pi V_E}}\, dv = -\frac{1}{2V_s}(p - bx)^2 - \frac{1}{2V_s} V_E.
$$

6.2 Evolution of the moments of the population density for the pure selection model (6)

Theorem 1 *If Q is defined by* (5), *any solution of* (6) *satisfies* (7) *and* (8).

Proof of Theorem 1:

We assume, without loss of generality, that $\int n(0, v)\, dv = 1$, $\int v\, n(0, v) = 0$, and $C = 1$ (all cases can be deduced through a change of variables). Then for all times $t \geq 0$,

$$
\int v\, n(t, v)\, dv = 0.
$$

We multiply equation (6) by v^2 and integrate to obtain

$$
\begin{aligned}
\frac{d}{dt} \int v^2 n(t,v)\, dv &= \int\int \left(\int v^2 Q(v, v_*, v'_*)\, dv \right) n(t, v'_*) n(t, v_*)\, dv_*\, dv'_* - \int v^2 n(t,v) dv \\
&= \int\int \left(\gamma^2 + \left(\frac{v_* + v'_*}{2} \right)^2 \right) n(t, v'_*) n(t, v_*)\, dv_*\, dv'_* - \int v^2 n(t,v) dv \\
&= \gamma^2 - \frac{1}{2} \int v^2 n(t,v) dv.
\end{aligned}
$$

We deduce that the variance of n converges exponentially fast to $G^2 = 2\gamma^2$ for any initial condition n^0:

$$
\left| \int v^2 n(t,v)\, dv - 2\gamma^2 \right| \le e^{-t/2} \left| \int v^2 n(0,v)\, dv - 2\gamma^2 \right|.
$$

Similarly we have

$$
\begin{aligned}
\frac{d}{dt} \int v^3 n(t,v)\, dv &= \int\int \left(\int v^3 Q(v, v_*, v'_*)\, dv \right) n(t, v_*) n(t, v'_*)\, dv_*\, dv'_* - \int v^3 n(t,v) dv \\
&= \int\int \left(\frac{v_* + v'_*}{2} \right)^3 n(t, v_*) n(t, v'_*)\, dv_*\, dv'_* - \int v^3 n(t,v) dv \\
&= -\frac{3}{4} \int v^3 n(t,v) dv.
\end{aligned}
$$

It follows that $\left| \int v^3 n(t,v)\, dv \right| \le e^{-3t/4} \left| \int v^3 n(0,v)\, dv \right|$.

$\square$

6.3 Unclosed equations on the moments of the population distribution moments

Theorem 2 *If n is a solution of (10), then the moments of the phenotypic distribution of n satisfy:*

$$
\begin{aligned}
&\partial_t N(t,x) - \Delta_x N(t,x) \\
&= \left[1 + \frac{1}{2} \left(A - \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv \right) - \frac{1}{2}(Z(t,x) - Bx)^2 - N(t,x) \right] N(t,x). \quad (22)
\end{aligned}
$$

$$
\begin{aligned}
\partial_t Z(t,x) - \Delta_x Z(t,x) &= 2\partial_x(\log N(t,x))\partial_x Z(t,x) + (Bx - Z(t,x)) \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv \\
&\quad - \frac{1}{2} \int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\, dv. \quad (23)
\end{aligned}
$$

Proof of Theorem 2: To obtain (22), we integrate (10) along v:

$$\partial_t N(t,x) - \Delta_x N(t,x) = \int \partial_t n(t,x,v) - \Delta_x n(t,x,v)\, dv$$

$$= \left[1 + \frac{A}{2} - N(t,x)\right] N(t,x) - \frac{1}{2}\int (v - Bx)^2 n(t,x,v)\, dv$$

$$= \left[1 + \frac{1}{2}\left(A - \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv\right)\right.$$

$$\left. - \frac{1}{2}(Z(t,x) - Bx)^2 - N(t,x)\right] N(t,x).$$

The second equation, (23), is obtained as follows:

$$\partial_t Z(t,x) - \Delta_x Z(t,x) = \partial_t \int v \frac{n(t,x,v)}{N(t,x)}\, dv - \Delta_x \int v \frac{n(t,x,v)}{N(t,x)}\, dv$$

$$= \int \frac{v}{N(t,x)}\left(\partial_t n(t,x,v) - \Delta_x n(t,x,v)\right)\, dv$$

$$- (\partial_t N(t,x) - \Delta_x N(t,x))\frac{Z(t,x)}{N(t,x)}$$

$$+ 2\partial_x(\log N(t,x))\partial_x Z(t,x),$$

and thus,

$$\partial_t Z(t,x) - \Delta_x Z(t,x)$$

$$= -\int \frac{v}{N(t,x)}\left(\left(C - \left(1 + \frac{A}{2}\right)\right) + \frac{1}{2}(v - Bx)^2 + \int n(t,w)\, dw\right) n(t,x,v)\, dv$$

$$+ C\int \frac{v}{N(t,x)}\left(\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\, dw} Q(v,v_*,v'_*)\, dv_*\, dv'_*\right)\, dv$$

$$- \left(1 - \frac{1}{2}(Z(t,x) - Bx)^2 - N + \frac{1}{2}\left(A - \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv\right)\right) N(t,x)\frac{Z(t,x)}{N(t,x)}$$

$$+ 2\partial_x(\log N(t,x))\partial_x Z(t,x)$$

$$= 2\partial_x(\log N(t,x))\partial_x Z(t,x) + (Bx - Z(t,x))\int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv$$

$$- \frac{1}{2}\int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\, dv.$$

Here we use the fact that the reproduction kernel does not affect the mean phenotypic trait: $\int vQ(v,v',v'_*)\, dv = \frac{v'+v'_*}{2}$.

$\square$

6.4 Existence theory for the simplified model

We introduce $W = Z - Dx$ in (18) to obtain the following equation

$$\partial_t W - \Delta_x W = -4\frac{\partial_x W W}{1 - W^2}(\partial_x W + D) - W, \tag{24}$$

with $-1 \leq W \leq 1$. This equation has a singularity for $W = \pm 1$.

The existence of singularities is an obstacle to have a well-defined problem. However, as we will see in Subsection 3.1, the singularities are fundamental to produce propagating fronts.

Similarly, we introduce $W_\delta := Z_\delta - Dx$. Then, (24) becomes

$$\partial_t W_\delta - \Delta_x W_\delta = -4\frac{\partial_x W_\delta W_\delta}{1 - W_\delta^2 + \delta}(\partial_x W_\delta + D) - \frac{(1 - W_\delta^2)W_\delta}{1 - W_\delta^2 + \delta}, \tag{25}$$

with

$$W_\delta(t = 0, \cdot) = W_\delta^0(\cdot).$$

With this choice of approximation we avoid the singularities and transform the singularity in -1 into a stable steady state (the stability is for the ODE formulation presented in Subsection 3.1).

Under the assumption

$$-1 \leq W_\delta^0 \leq 1, \tag{26}$$

equation (25) has a smooth solution that stays between -1 and 1 by the maximum principle (see e.g. [2]). We prove a regularizing effect for equation (25) and we deduce that the W_δ's converge to a viscosity solution of a variant of equation (24). Before stating the result, we first give the definition of viscosity solutions (see also [11, 2] for general introduction to this theory).

Definition 1 *Viscosity solution: The function $u \in \mathrm{C}([0, \infty) \times \mathbb{R})$ is a viscosity solution of the equation*

$$L\left(\partial_{xx}^2 u, \partial_x u, \partial_t u, t, x\right) = 0, \qquad (t, x) \in (0, \infty) \times \mathbb{R},$$

if and only if for all $\phi \in \mathrm{C}^\infty((0, \infty) \times \mathbb{R})$, we have

  1. *if $u - \phi$ has a local maximum at a point $(t_0, x_0) \in (0, \infty) \times \mathbb{R}$ then*

$$L\left(\partial_{xx}^2 \phi(t_0, x_0), \partial_x \phi(t_0, x_0), \partial_t \phi(t_0, x_0), u(t_0, x_0), t_0, x_0\right) \leq 0.$$

  2. *if $u - \phi$ has a local minimum at a point $(t_0, x_0) \in (0, \infty) \times \mathbb{R}$ then*

$$L\left(\partial_{xx}^2 \phi(t_0, x_0), \partial_x \phi(t_0, x_0), \partial_t \phi(t_0, x_0), u(t_0, x_0), t_0, x_0\right) \geq 0.$$

Theorem 3 *Under assumption (26), W_δ the solution of (25) verifies, for all $(t, x) \in \mathbb{R}_+ \times \mathbb{R}$,*

$$-1 \leq W_\delta(t, x) \leq 1, \qquad |\partial_x W_\delta(t, x)| \leq \min(L_2, \frac{1}{2\sqrt{t}} + L_1), \tag{27}$$

with

$$L_2 = \max\left(\sup_{x \in \mathbb{R}} |\partial_x W_\delta(x, 0)|, L_1\right) \in \mathbb{R}_+ \cup +\infty,$$

and L_1 a positive constant independent of δ. Moreover, after extraction of a subsequence, the W_δ's converge to a continuous function W that is a viscosity solution of

$$(1 - W^2)\partial_t W - (1 - W^2)\Delta_x W = -4\partial_x WW(\partial_x W + D) - (1 - W^2)W. \tag{28}$$

We can easily verify that if the initial solution is as in Example 1, i.e. $W_\delta(t = 0, \cdot) \equiv -1$, then we have $W_\delta(t, \cdot) \equiv -1$ for all $t > 0$. Therefore our approximation chooses the biological solution.

Proof of Theorem 3: We differentiate equation (24) with respect to x and obtain

$$
\begin{aligned}
\partial_t \partial_x W_\delta - \Delta_x \partial_x W_\delta \;\; &= -4 \frac{W_\delta}{1 - W_\delta^2 + \delta} (2 \partial_x W_\delta + D) \partial_x (\partial_x W_\delta) \\
&\quad - 4 \partial_x W_\delta^2 (\partial_x W_\delta + D) \frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \\
&\quad - \partial_x W_\delta \left(1 - \delta \frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \right),
\end{aligned} \tag{29}
$$

where the last term comes from

$$
\partial_x \left(\frac{W_\delta(1 - W_\delta^2)}{1 - W_\delta^2 + \delta} \right) = \partial_x \left(W_\delta - \frac{\delta W_\delta}{1 - W_\delta^2 + \delta} \right) = \partial_x W_\delta \left(1 - \delta \frac{1 - W_\delta^2 + \delta + 2 W_\delta^2}{(1 - W_\delta^2 + \delta)^2} \right).
$$

We multiply (29) by $\partial_x W_\delta$ and divide by $|\partial_x W_\delta|$ and obtain

$$
\begin{aligned}
\partial_t |\partial_x W_\delta| - \Delta_x |\partial_x W_\delta| \;\; &\leq -4 \frac{W_\delta}{1 - W_\delta^2 + \delta} (2 \partial_x W_\delta + D) \partial_x (|\partial_x W_\delta|) \\
&\quad - 4 \partial_x W_\delta^2 (\partial_x W_\delta + D) \left(\frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \right) \operatorname{sgn}(\partial_x W_\delta) \\
&\quad - \left(1 - \delta \frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \right) |\partial_x W_\delta|.
\end{aligned}
$$

It follows that, for $\delta < 1$,

$$
\begin{aligned}
\partial_t |\partial_x W_\delta| - \Delta_x |\partial_x W_\delta| \;\; &\leq \alpha(t, x) \partial_x |\partial_x W_\delta| + \left(\frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \right) \cdot \\
&\quad \left(-4 |\partial_x W_\delta|^3 + 4D |\partial_x W_\delta|^2 + |\partial_x W_\delta| \right),
\end{aligned}
$$

with

$$
\alpha(t, x) = -4 \frac{W_\delta}{1 - W_\delta^2 + \delta} (2 \partial_x W_\delta + D).
$$

Therefore for L_1 large enough and for $\delta < 1$, we have that $|\partial_x W_\delta|$ is a subsolution of the following equation

$$
\partial_t g - \Delta_x g \;\; = \alpha(t, x) \partial_x g - 4 \left(\frac{1 + W_\delta^2 + \delta}{(1 - W_\delta^2 + \delta)^2} \right) (g - L_1)^3, \tag{30}
$$

One can easily verify that, for $\delta < 1$, the functions $g_1(t, x) := L_2$ and $g_2(t, x) := \frac{1}{2\sqrt{t}} + L_1$ are supersolutions to equation (30) and they satisfy

$$
|\partial_x W_\delta(0, x)| \leq g_1(0, x), \qquad |\partial_x W_\delta(0, x)| \leq g_2(0, x).
$$

It follows that, for $\delta < 1$,

$$
|\partial_x W_\delta(t, x)| \leq \min(g_1(t, x), g_2(t, x)),
$$

and thus (27).

Now we define

$$
T_\delta := F(W_\delta) = (1 + \delta) W_\delta - \frac{W_\delta^3}{3}.
$$

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We first consider the case with $L_2 < +\infty$. From (27), we deduce that the T_δ's are uniformly bounded and Lipschitz in $[0, +\infty) \times \mathbb{R}$. Moreover we have

$$\partial_t T_\delta - \Delta T_\delta = (1 - W_\delta^2 + \delta)\partial_t W_\delta - (1 - W_\delta^2 + \delta)\Delta W_\delta + 2W_\delta|\nabla W_\delta|^2.$$

From the above equation, (25) and (27) we deduce that $\partial_t T_\delta - \Delta T_\delta$ is uniformly bounded in $[0, +\infty) \times \mathbb{R}$. It follows that the T_δ's are uniformly continuous in time in $[0, +\infty) \times \mathbb{R}$ (see [3]). Using the Arzela Ascoli Theorem we conclude that, after extraction of a subsequence, the T_δ's converge locally uniformly to a continuous function T in $[0, +\infty) \times \mathbb{R}$.

In the case with $L_2 = +\infty$, following the arguments above we obtain that the T_δ's are uniformly bounded and locally uniformly Lipschitz in $(0, +\infty) \times \mathbb{R}$. The locally uniform convergence of the T_δ's, along subsequences, is also hold in $(0, +\infty) \times \mathbb{R}$.

Finally from the fact that

$$F'(W_\delta) = 1 + \delta - W_\delta^2 > 0, \qquad \text{for } -1 \le W_\delta \le 1,$$

we obtain that F is an invertible function. We write

$$W_\delta = F^{-1}(T_\delta),$$

with F^{-1} continuous. Therefore the W_δ's converge locally uniformly to the continuous function $W = F^{-1}(T)$ along subsequences. The convergence takes place in $[0, +\infty) \times \mathbb{R}$, if $L_2 < +\infty$ and in $(0, +\infty) \times \mathbb{R}$ if $L_2 = +\infty$.

By the stability of viscosity solutions (see [11, 2]), we conclude that W is a viscosity solution of (28).

$\square$

In Subsection 3.1 we study the propagating fronts for this model. To be able to compare the solutions with the propagating fronts and to show the propagation of the density in space, we need a comparison principle. Unfortunately as we saw above, the equation (28) does not have a unique viscosity solution and therefore it does not admit a comparison principle. However we can prove a comparison principle for the approached model. We first recall its definition:

Definition 2 *Comparison principle: Equation $L(\partial_{xx}^2 u, \partial_x u, u, x, t) = 0$ verifies a comparison principle, if for any subsolution w^1, that is*

$$L(\partial_{xx}^2 w^1, \partial_x w^1, w^1, x, t) \le 0,$$

and supersolution w^2 of L, that is

$$L(\partial_{xx}^2 w^2, \partial_x w^2, w^2, x, t) \ge 0,$$

such that $w^1(0, x) \le w^2(0, x)$, we have

$$w^1(t, x) \le w^2(t, x), \qquad \text{for all } (t, x) \in \mathbb{R}_+ \times \mathbb{R}.$$

We prove that there is a comparison property for (25). In particular (25) has a unique solution.

Theorem 4 *Equation (25) admits a comparison principle in the set of solutions $\{-1 \le W \le 1\}$.*

Proof of Theorem 4: We suppose that W_1 and W_2 are respectively subsolution and supersolution of (25) and

$$W_1(t = 0, \cdot) \leq W_2(t = 0, \cdot).$$

We prove that $W_1 \leq W_2$ for all $(t, x) \in \mathbb{R}_+ \times \mathbb{R}$. Let $(\bar{t}, \bar{x})$ be a maximum point of $W_1 - W_2$. Since it is a maximum point we have $\partial_x W_1(\bar{t}, \bar{x}) = \partial_x W_2(\bar{t}, \bar{x}) = p$. Therefore we have

$$\partial_t (W_1 - W_2)(\bar{t}, \bar{x}) - \Delta(W_1 - W_2)(\bar{t}, \bar{x})$$
$$\leq -4p\,(p + D)\frac{(1 + W_1 W_2 + \delta)}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)}(W_1 - W_2)(\bar{t}, \bar{x})$$
$$- \frac{(1 + \delta)(1 - W_1^2 - W_1 W_2 - W_2^2) + W_1 W_2 + W_1^2 W_2^2}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)}(W_1 - W_2)(\bar{t}, \bar{x}).$$

In the previous section we proved that $|\partial_x W|$ is bounded. Thus $p(p + D)$ is bounded. Moreover W_1 and W_2 are bounded and

$$1 - W_i^2 + \delta \geq \delta, \qquad \text{for } i = 1, 2.$$

Therefore the coefficient of $W_1 - W_2$ is bounded. Following the classical maximum principle we deduce that equation (25) admits a comparison principle.

$\square$

6.5 Existence of propagating fronts

Theorem 5 *For any $D > 0$, there exists $\nu_D \in \mathbb{R}$ such that (24) has a propagating front of speed ν, $Z(t, x) = Dx + U(x - \nu t)$, satisfying*

$$U(x) \to 0 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty,$$

if and only if $\nu > \nu_D$.

The propagating front with speed ν is unique (up to a translation), and ν_D is a decreasing function of D.

Theorem 6 *The equation (18) has a non-trivial steady-state if and only if $\nu_D < 0$. Those steady-states $Z(t, x) = Dx + U(x)$ satisfy*

$$U(x) \to 1 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty.$$

To prove Theorems 5 and 6, we will use the two following Lemma:

Lemma 1 *Let $\nu \in \mathbb{R}$. There exist only two, up to a shift in the t variable, solutions (u, v) to the ODE defined by the vector field (20) such that $(u, v)(t) \to (0, 0)$ as $t \to -\infty$. At most one of them is globally defined, which satisfies:*

$$(u, v)(t) \sim -C_- e^{\frac{\sqrt{\nu^2 + 4} - \nu}{2}t}(1, \frac{\sqrt{\nu^2 + 4} - \nu}{2}).$$

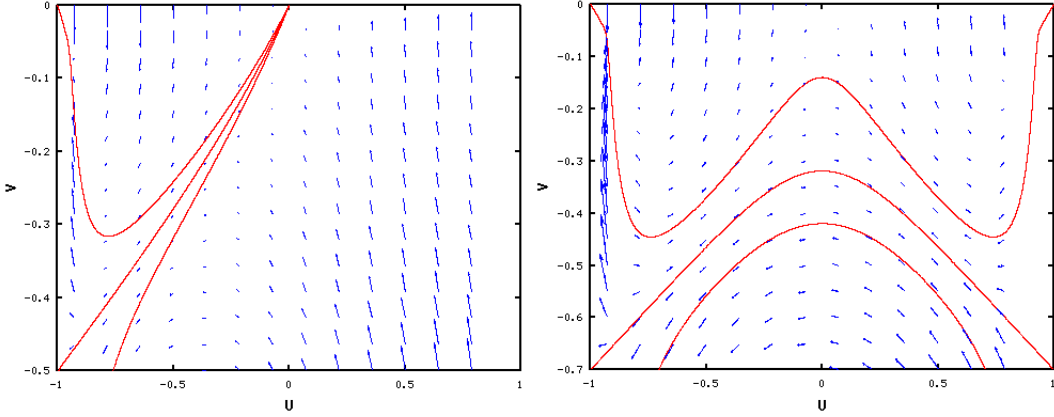*Moreover, for this solution, u is strictly decreasing.*

Figure 11: Solutions of the ODE defined by the vector field (20), on the left for $D := 0.7$ and $\nu = 0.5$, 0.73141, 1 (the vector field represented corresponds to $\nu = 0.73141$). A propagating front then exists for $\nu \geq 0.73141$ only, and the biologically relevant solution is obtained for $\nu = \nu_D \sim 0.73141$. On the right, we represent solutions of the ODE defined by the vector field (20), with $\nu = 0$ and $D = 0.7$.

Lemma 2 *Let $\nu_1 \leq \nu_2$, and (u_{ν_1}, v_{ν_1}), (u_{ν_1}, v_{ν_1}) be the corresponding solutions given by Lemma 1. If for t_1, $t_2 \in \mathbb{R}$,*

$$\begin{cases} u_{\nu_1}(t_1) = u_{\nu_2}(t_2) \\ v_{\nu_1}(t_1) \leq v_{\nu_2}(t_2), \end{cases} \tag{31}$$

then, for any $t'_1 > t_1$, $t'_2 > t_2$ such that $u_{\nu_1}(t'_1) = u_{\nu_2}(t'_2)$, we have $v_{\nu_1}(t'_1) \leq v_{\nu_2}(t'_2)$, and this inequality is strict if $\nu_1 < \nu_2$.

Proof of Lemma 1: The Differential of the vector field F in $(0,0)$ is

$$DF_{(0,0)} = \begin{pmatrix} 0 & 1 \\ 1 & -\nu \end{pmatrix}.$$

Therefore $(0,0)$ is a hyperbolic equilibrium point ($\det DF_{(0,0)} < 0$). The Hartman-Grobman Theorem applies, and thus there exist only two (non-trivial) solutions (u,v) satisfying $(u,v)(t) \to_{t\to-\infty} (0,0)$. Since the eigenvector associated to the positive eigenvalue of $DF_{(0,0)}$ is $(1, \frac{\sqrt{\nu^2+4}-\nu}{2})$, the corresponding solutions are equivalent to

$$(u,v)(t) \sim_{t\to-\infty} \pm C_\pm \, e^{\frac{\sqrt{\nu^2+4}-\nu}{2}t} \left(1, \frac{\sqrt{\nu^2+4}-\nu}{2} \right),$$

for some C_-, $C_+ > 0$.

The solution such that $(u,v)(t) \sim_{t\to-\infty} C_+ e^{\frac{\sqrt{\nu^2+4}-\nu}{2}t} \left(1, \frac{\sqrt{\nu^2+4}-\nu}{2} \right)$ satisfies $u(\bar{t}) > 0$, $v(\bar{t}) > 0$ for some $\bar{t}$. Since $F_U(u(\bar{t}), V) > 0$ for $V \geq v(\bar{t})$ and $F_V(U, v(\bar{t})) \geq F_V(u(\bar{t}), v(\bar{t})) > 0$ for $U \in [u(\bar{t}), 1)$, the solution cannot escape $[u(\bar{t}), 1) \times [v(\bar{t}), \infty)$. In particular, for $t \geq \bar{t}$, $u'(t) = v(t) \geq v(\bar{t}) > 0$ and since the vector field is not defined for $U = 1$, the solution cannot be global.

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The other solution satisfies $u(\bar{t}) < 0$, $v(\bar{t}) < 0$ for some $\bar{t}$ arbitrarily small. Since $F_U(0, V) \leq 0$ for $V \leq 0$ and $F_V(U, 0) \leq 0$ for $U \leq 0$, the solution cannot escape $\mathbb{R}^2_-$. In particular, we have $u'(t) = v(t) \leq 0$, which shows that u is strictly decreasing with respect to t.

$\square$

Proof of Lemma 2: Since u_ν is strictly decreasing, we can define the graph of (u_{ν_1}, v_{ν_1}).

We assume that $\bar{t}_1$, $\bar{t}_2$ are the smallest points respectively in (t_1, ∞) and in (t_2, ∞) such that $(u_{\nu_2}, v_{\nu_2})(\bar{t}_2) = (u_{\nu_1}, v_{\nu_1})(\bar{t}_1)$. We have,

$$
\begin{aligned}
v'_{\nu_1}(\bar{t}_1) &= -\nu_1 v_{\nu_1}(\bar{t}_1) + 4 \frac{u_{\nu_1}(\bar{t}_1) v_{\nu_1}(\bar{t}_1)}{1 - u_{\nu_1}(\bar{t}_1)^2} (v_{\nu_1}(\bar{t}_1) + D) + u_{\nu_1}(\bar{t}_1) \\
&= v'_{\nu_2}(\bar{t}_2) + (\nu_2 - \nu_1) v_{\nu_1}(\bar{t}_1) \\
&\leq v'_{\nu_2}(\bar{t}_2),
\end{aligned}
$$

this inequality being strict if $\nu_1 < \nu_2$. It follows that $\frac{v'_{\nu_1}(\bar{t}_1)}{u'_{\nu_1}(\bar{t}_1)} > \frac{v'_{\nu_2}(\bar{t}_2)}{u'_{\nu_2}(\bar{t}_2)}$. The graph of (u_{ν_2}, v_{ν_2}) can thus only cross the graph of (u_{ν_1}, v_{ν_1}) from below to above, when t increases. This is enough to conclude that $v_{\nu_1}(t'_1) \leq v_{\nu_2}(t'_2)$, for all $t'_1 > t_1$ and $t'_2 > t_2$. Moreover, the latter inequality is strict if $\nu_1 < \nu_2$. This completes the proof of Lemma 2.

$\square$

Proof of Theorem 5: *Step 1:* We show that the solution (u, v) given by Lemma 1 satisfies either $v(\bar{t}) = -D$ for some $\bar{t}$, or $(u, v)(t) \to (-1, 0)$ as $t \to +\infty$. Moreover, the solution is global in this last case only.

Since u is strictly decreasing and $F_V(-1, V) = +\infty$ for $V \in (-D, 0)$, only two situations are possible: either $v(\bar{t}) = -D$ for some $\bar{t} < +\infty$, or $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t} \in \mathbb{R} \cup \{+\infty\}$.

If $v(\bar{t}) = -D$, then $v(t) < -D$ for all $t \geq \bar{t}$. This is because

$$F_V(U, -D) = \nu D + U \leq F_V(u(\bar{t}), -D) \leq 0$$

for $U \in (-1, u(\bar{t}))$ and since u is decreasing. Therefore, $u'(t) = v(t) \leq -D$ for all $t \geq \bar{t}$. From the latter, together with $F_V(-1, V) = -\infty$ for $V < -D$, we obtain that the solution cannot be globally defined.

Now let $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t} \in \mathbb{R} \cup \{\infty\}$. We prove that $\bar{t} = \infty$. For (U, V) close to $(-1, 0)$, we have $F_V(U, V) \sim -2D \frac{V}{1+U} - 1$. We deduce that,

$$
\begin{aligned}
\frac{d}{dt}\left(\frac{v}{1+u}\right)(t) &= \frac{F_V(u(t), v(t))(1 + u(t)) - v(t) F_U(u(t), v(t))}{(1 + u(t))^2} \\
&\sim \frac{1}{(1 + u(t))^2}\left[\left(-2D \frac{v(t)}{1 + u(t)} - 1\right)(1 + u(t)) - v(t)^2\right] \\
&\sim \frac{1}{(1 + u(t))^2}\left[-2D v(t) - v(t)^2 - (1 + u(t))\right] \\
&\geq 0,
\end{aligned}
$$

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if $v(t) \leq \frac{-1}{3D}(1 + u(t))$ and $(u(t), v(t))$ is close to $(-1, 0)$.

We assume that $\widetilde{t}$ is such that $(u, v)(t)$ is close to $(-1, 0)$ for $t \geq \widetilde{t}$. We then have, $\frac{v(t)}{1+u(t)} \geq$ $\min\left(\frac{v(\widetilde{t})}{1+u(\widetilde{t})}, \frac{-1}{3D}\right)$ for all $t \geq \widetilde{t}$. It follows that $u'(t) = v(t) \geq -C(u(t) + 1)$, which implies the estimate

$$u(t) \geq -1 + (u(\widetilde{t}) + 1)e^{-C(t-\widetilde{t})}.$$

Since $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t}$, we deduce that $\bar{t} = +\infty$, and (u, v) is indeed globally defined.

Step 2: We next prove that there exists a constant ν_D such that, there exists a propagating front if and only if $\nu > \nu_D$.

If $\nu > \frac{1}{D}$, we have $F_V(U, -D) = \nu D - U > 0$ for $U \in (-1, 1)$. Therefore, the solution given by Lemma 1 cannot cross the line $V = -D$, and thus it defines a propagating front thanks to Step 1. We deduce that, there exists a propagating front if ν is large enough.

In $[-1/\sqrt{2}, 0] \times [-D, 0]$ and for $\nu \leq -(4\sqrt{2} + 1)D$, we have

$$F_V(U, V) \leq -\nu V - 4\sqrt{2}\, V(V + D) \leq DV \leq D\, F_U(U, V).$$

It follows that the solution given by Lemma 1 necessarily crosses the line $V = -D$, and thus it does not define a propagating front according to Step 1. We deduce that the model does not admit a propagating front if $-\nu$ is large enough.

We consider a solution $(u_{\nu_1}, v_{\nu_1})(t)$ given by Lemma 1 for some ν_1, that converges to $(-1, 0)$ as $t \to +\infty$, and $\nu_2 > \nu_1$. Since $\frac{\sqrt{\nu^2+4}-\nu}{2}$ is a decreasing function of ν and

$$(u_{\nu_i}, v_{\nu_i})(t) \sim -C_- e^{\frac{\sqrt{\nu_{\nu_i}^2+4}-\nu_{\nu_i}}{2}}\left(1, \frac{\sqrt{\nu_{\nu_i}^2+4}-\nu_{\nu_i}}{2}\right),$$

the graph of $(u_{\nu_1}, v_{\nu_1})(t)$ is below the graph of $(u_{\nu_2}, v_{\nu_2})(t)$ for $t << 0$. Thanks to Lemma 2, this implies that the whole graph of (u_{ν_1}, v_{ν_1}) is below the graph of (u_{ν_2}, v_{ν_2}). Using the latter and Step 1 we obtain that (u_{ν_2}, v_{ν_2}) defines a propagating front.

Finally, we show that ν_D is a decreasing function of D. Firstly we notice that, for $D_1 \leq D_2$, we have $F_U^{D_1} = F_U^{D_2}$, and $F_V^{D_1} \leq F_V^{D_2}$ in $(-1, 0] \times \mathbb{R}_-$. We deduce that, using Step 1, if the solution given by Lemma 1 for D_1 converges to $(-1, 0)$ as $t \to \infty$, so does the one associated to D_2. This proves that ν_D is a decreasing function of D.

$\square$

Proof of Theorem 6: We assume that $\nu_D < 0$. Then, for $\nu = \frac{\nu_D}{2}$, the solution $(u_{\nu_D/2}, v_{\nu_D/2})$ given by Lemma 1, is globally defined, and it satisfies $(u_{\nu_D/2}, v_{\nu_D/2})(t) \to (-1, 0)$ as $t \to +\infty$. Moreover we have

$$(u_{\nu_D/2}, v_{\nu_D/2})(t) \sim_{t \to -\infty} -C_- e^{\frac{\sqrt{(\nu_D/2)^2+4}-\nu_D/2}{2}t}\left(1, \frac{\sqrt{(\nu_D/2)^2+4}-\nu_D/2}{2}\right),$$

and $\frac{\sqrt{(\nu_D/2)^2+4}-\nu_D/2}{2} > 1$.

Consider now the vector field (20) for $\nu = 0$. Since $(u_0, v_0)(t) \sim_{t \to -\infty} -C'_- e^t(1, 1)$, for $\bar{t}$ small enough, $(u_0, v_0)(\bar{t})$ is strictly above the graph of $(u_{\nu_D/2}, v_{\nu_D/2})$. Let $\widetilde{v}$ be such that $(u_0(\bar{t}), \widetilde{v})$ is strictly between $(u_0, v_0)(\bar{t})$ and the graph of $(u_{\nu_D/2}, v_{\nu_D/2})$. We define $(\bar{u}, \bar{v})$ to be the solution of the ODE given by the vector fields (20) such that $(\bar{u}, \bar{v})(0) = (u_0(\bar{t}), \widetilde{v})$ and $\nu = 0$. Then, according to Lemma 2, $(\bar{u}, \bar{v})$ is defined in $\mathbb{R}_+$. Moreover, since $(u_0, v_0)(t) \to (0, 0)$ as $t \to -\infty$ and $(0, 0)$ is a hyperbolic equilibrium point, there exists $\widetilde{t} > 0$ such that $\bar{u}(\widetilde{t}) = 0$.

By symmetry, we have $(\bar{u}, \bar{v})(\widetilde{t} + t) = (-\bar{u}, \bar{v})(\widetilde{t} - t)$. Thus, $(\bar{u}, \bar{v})$ is globally defined and satisfies $(\bar{u}, \bar{v})(t) \to (\pm 1, 0)$ as $t \to \pm \infty$. This completes the proof of Theorem 6.

$\square$

6.6   Approximation of the propagating fronts

In this subsection, we will study in more detail the propagating fronts of (18). As mentioned in Subsection 3.1, for each $D > 0$, there exists a one-parameter family of propagating fronts: for any $\nu \geq \nu_D$, there exists a unique propagating front of speed ν_D. By analogy to the KPP-Fisher equation (see e.g. [34, 46]), one can expect that there is only one stable propagating front, the one with the least speed $\nu = \nu_D$. In Section 4, numerical computations have confirmed the idea that the minimal speed ν_D is the natural speed to consider here.

For $\nu > \nu_D$, the propagating front $Dx + U_\nu$ is smooth (see Subsection 6.5), and corresponds to a solution (U, U') of (20) such that $(U, U')(x) \to_{x \to -\infty} (0, 0)$ and $(U, U')(x) \to_{x \to \infty} (-1, 0)$. The front with the minimal speed is slightly different: it is the uniform limit of the fronts $Dx + U_\nu$ as $\nu \to \nu_D$ (see Figure 11). The limit front $Dx + U_{\nu_D}$ has a singularity and cannot be a classical solution of (18). It is however a viscosity solution of (18). In the phase plane, this minimal speed front corresponds to a solution $(U, V)|_{\mathbb{R}_-}$ of (20), defined on $\mathbb{R}_-$, such that $(U, V)(x) \to_{x \to -\infty} (0, 0)$, $(U, V)(x) \to_{x \to 0^-} (-1, -D)$, and $Dx + U_{\nu_D}(x) = Dx - 1$ for $x > 0$.

Our aim is to approach the particular solutions (U, V) of (20) that joint $(0, 0)$ to $(-1, -D)$. To do this, we introduce the ansatz that for $x \in (-\infty, 0]$,

$$V = \alpha U + \beta |U|^{3/2}. \tag{32}$$

To estimate α and β, we proceed as follows:

- Since $(U, V)(0) = (-1, -D)$, necessarily, $\alpha = D + \beta$.

- Since $(0, 0)$ is a saddle point of the vector field (20), (U, V) must be tangent to the eigenvector $(1, (\sqrt{\nu^2 + 4} - \nu)/2)$ close to $(0, 0)$ (see Subsection 6.5 in the appendix). Then,

$$\beta = \frac{1}{2}\left(\sqrt{\nu_D^2 + 4} - \nu_D\right) - D. \tag{33}$$

- Finally, close to $(-1, -D)$,

$$\begin{cases} F_U(U, V) \sim -D \\ F_V(U, V) \sim \nu_D D + 2D\frac{V+D}{U+1} - 1 \end{cases}$$

$\frac{\partial V}{\partial U}(x = 0)$ should then satisfy

$$\frac{\partial V}{\partial U}(x = 0) = \frac{-1}{D}\left(\nu_D D + 2D\frac{\partial V}{\partial U}(x = 0) - 1\right),$$

and our ansatz yields $\frac{\partial V}{\partial U}(x = 0) = D - \beta/2$.

If we combine the estimates above, we obtain

$$0 = \frac{1}{D} - \frac{9D}{2} - \frac{7}{4}\nu_D + \frac{3}{4}\sqrt{\nu_D^2 + 4},$$

and thus, ν_D satisfies:

$$\nu_D \sim \frac{1}{20}\left(7\left(\frac{2}{D} - 9D\right) + 3\sqrt{\left(\frac{2}{D} - 9D\right)^2 + 40}\right).$$

This approximation of ν_D is not rigorous, but it is however very close to the numerical estimations of ν_D, as shown in Figure 3. This speed can be positive (the population then invades the empty territory), or negative (the population disappears).

We can go further and give an approximation of the propagating front with minimal speed, which satisfies

$$U'(x) = (D + \beta)U(x) + \beta|U(x)|^{3/2}, \tag{34}$$

for $x \in \mathbb{R}_-$, and $U(x) = -1$ for $x > 0$. We recall that β is given by (33), with ν_D estimated by (21). To solve (34), we use the change of variable $U(x) = -\phi^{-2}$. Replacing this in (34) we obtain that $\phi' = -\frac{D+\beta}{2} + 2\beta$ on $\mathbb{R}_-$, and thus $\phi(x) = Ce^{-\frac{D+\beta}{2}x} + \frac{\beta}{D+\beta}$. We can then compute U, recalling that $U(0) = -1$:

$$U(x) = -\left(\left(1 - \frac{\beta}{D+\beta}\right)e^{-\frac{D+\beta}{2}x} + \frac{\beta}{D+\beta}\right)^{-2}, \quad x \in \mathbb{R}_-,$$

and $U(x) = -1$ on $\mathbb{R}_+$.

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