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CENTRE DE MATHÉMATIQUES APPLIQUÉES
UMR CNRS 7641

91128 PALAISEAU CEDEX (FRANCE). Tél: 01 69 33 46 00. Fax: 01 69 33 46 46
http://www.cmap.polytechnique.fr/

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Sepideh Mirrahimi, Gaël Raoul

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Sepideh Mirrahimi
CMAP, Ecole Polytechnique, CNRS, INRIA,
Route de Saclay, 91128 Palaiseau Cedex, France.
mirrahimi@cmap.polytechnique.fr

Gaël Raoul
DAMTP,Centre for Mathematical Sciences, Cambridge University,
Wilberforce Road, Cambridge CB3 0WA, UK.
g.raoul@damtp.cam.ac.uk

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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 a structured population equation we perform a hydrodynamic-type limit to derive a model close to an existing model of theoretical biology. We then perform a further simplification to obtain a model depending on only one parameter that indicates how fast the environment is changing. We show that depending on this parameter, there exist either propagating waves, where the population invades the entire environment, or steady-states where the population survives but remains in a limited range. The corresponding propagating fronts connect an unstable steady point to a singular point. Existence of steady states with limited range distinguishes the dynamics of the sexual populations from asexual populations, where the populations whether gets extinct or propagates to the whole environment.
Numerical simulations show that the derived simplified model is a good approximation of the initial structured population model.

Key-words: Sexual populations, Structured populations, Hydrodynamic limit, Propagating fronts, gene flow

1 Introduction

In this paper, we are interested in sexual populations that are structured by a continuous phenotypic trait $v \in \mathbb{R}$ and a continuous space variable $x \in \mathbb{R}$, living in a non-homogeneous environment: we will consider a phenotypic trait of best adaptation $\theta(\cdot)$ that depends on the space variable. This type of population has been studied in [21, 15, 22, 3], using mostly numerical simulations.

This type of model can in particular be used to study the distribution of a species along an environmental gradient (such as the north-south gradient of temperature in the northern hemisphere). To study the range of the species and its local adaptation, one should consider both evolution and spatial dynamics (see [14, 15, 23, 4]). These models are also useful to study the impact of an environmental change (e.g. global warming) on a population (see [21, 15, 23]).

Our work is largely based on [15], and related articles [12, 21, 15, 22, 23]. In [15], a partial differential equation model describing the spatial and evolutionary dynamics of a population is introduced:

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

Here $N(t,x)$ is the population density at time t and location x, and $Z(t,x)$ is the population's mean phenotypic trait. The parameter A can be interpreted as the potential for adaptation to the local optimal trait and the parameter B indicates how fast the environment is changing. Numerical simulations where run for this model, and they showed that depending on A and B, three biological scenarios were possible:

- if B is large (the environment changes rapidly in space), the population goes extinct,
- for intermediate values of B, the population survives, but remains in a limited area,
- if B is small, the population invades the whole space.

In this paper, we show how (1) (indeed, the closely related equations (14)) can be derived through a hydrodynamic-type limit from a structured population model in the case of sexual populations, but is not appropriate to model asexual populations. We also introduce a simplification of the model (14) when A is small, which allows us to investigate the existence of propagating fronts and steady states, which correspond respectively to the cases where the population invades the whole space, or remains confined in a limited area.

The fact that populations can remain confined in a limited area, distinguishes the behavior of sexual population from that of asexual populations. With an equivalent model in the case of asexual populations, the population either gets extinct or it propagates to the whole space (see [20]). An origin of this difference is the phenomenon of gene flow that appears in the case of sexual populations; the traits of the individuals that are on low density areas of the domain are very influenced by the traits of the individuals in high density areas. Therefore the traits of the individuals that are on the edge of the populated area, where the population is less dense, are far from optimal (see [15]).

In Section 2, we introduce a structured population model for the evolution of sexual populations structured by both a phenotypic trait and a space variable. To construct this model, we add a spatial variable to a well established spatially homogeneous selection-mutation equation (similarly to many kinetic models in physics or chemistry, see [25]). This structured population equation can also be seen as a continuous version of the discrete model introduced in [22]. After a rescalling, three parameters appear: A, B, C. The interpretation of A and B is as above. We assume next that C is large, which means that many generations are necessary to obtain a significant growth of the population. This assumption allows us to perform formally a hydrodynamic-type limit of the structured population model (10) to obtain a model very close to (1). We explain in Remark 2 why we could not obtain exactly the system (1).

Finally, we simplify (14) further through another formal limit, assuming that A is small. This assumption is compatible with the values of A considered in [15]. With this assumption, we obtain a simpler equation on $Z(t,x)$ only:

$$\begin{aligned}\partial_t Z(t,x)-\Delta_x Z(t,x) &= -4\frac{(\partial_x Z(t,x)-B/\sqrt{2})(Z(t,x)-(B/\sqrt{2})x)}{1-(Z(t,x)-(B/\sqrt{2})x)^2}\partial_x Z(t,x)\\ &\quad +((B/\sqrt{2})x-Z(t,x)). \qquad (2)\end{aligned}$$

In Section 3, we analyze the model (2) derived in Section 2. Unfortunately, this equation has singularities that are obstacles to have a well-defined problem: we show that viscosity solutions exist, but are not unique. However, the singularities are fundamental to produce propagating fronts. We indeed prove the existence of propagating fronts, which connect an unstable steady state to a singular point. Thereby, this simple model allows us to describe two of the three possible scenarios from [15]: invasion fronts, and populations remaining in a limited area. The extinction phenomena cannot be observed here because of our assumption that A is small, as we explain in Remark 5.

We illustrate the results with numerical simulations that are presented in Section 4.

2 Structured population model

2.1 Model

We start from a classical model describing the evolution of a population structured by a phenotypic trait only (see e.g. [6, 11, 19], and [10, 9, 16] for mathematical properties of this kind of models). Let $n(t,v)$ be the density of the population of phenotypic trait $v\in\mathbb{R}$ at time $t\geq 0$. We assume that the fitness depends on the square of 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, under the latter assumptions, 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:

$$s[n(t,\cdot)](v)=r_{max}-\frac{1}{2V_s}(v-\theta)^2-\frac{r_{max}}{K}\int n(t,w)\,dw, \qquad (3)$$

Here $r_{max}>0$ denotes the maximal growth rate of the population, V_s measures the strength of the selection toward the optimal 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 [5]):

- 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 $\gamma>r_{max}$.

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 population density, the idea being that the number of births is proportional to the number of females. Then the evolution of the population, structured by a phenotypic trait only, is described by (see [11]):

$$\begin{aligned} \partial_t n(t,v) &= \left[-(\gamma - r_{max}) - \frac{I_s}{2} - \frac{1}{2V_s}(v-\theta)^2 - \frac{r_{max}}{K}\int n(t,w)\,dw\right] n(t,v) \\ &\quad +\gamma \int\int \frac{n(t,v_*)n(t,v_*')}{\int n(t,w)\,dw} Q(v,v_*,v_*')\,dv_*\,dv_*'. \end{aligned} \tag{4}$$

Here γ is the birth rate ($\gamma > r_{max}$), that we assume constant within the population, (the selection occurs in the death term), and $\frac{I_s}{2}$ is the additional death rate due to lethal mutations (see [15]).

We next consider populations that are structured by a phenotypic trait v as above, but also by a space variable $x \in \mathbb{R}$. The density is then denoted by $n(t,x,v)$. 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_x. We additionally assume that the trait of optimal adaptation changes linearly in space:

$$\theta(x) = bx. \tag{5}$$

We finally obtain the following model for sexual populations (close to the model used in [12]):

$$\begin{aligned} &\partial_t n(t,x,v) - \sigma_x^2 \Delta_x n(t,x,v) \\ &\quad = \left[-(\gamma - r_{max}) - \frac{I_s}{2} - \frac{1}{2V_s}(v-bx)^2 - \frac{r_{max}}{K}\int n(t,x,w)\,dw\right] n(t,x,v) \\ &\qquad + \gamma \int\int \frac{n(t,x,v_*)n(t,x,v_*')}{\int n(t,x,w)\,dw} Q(v,v_*,v_*')\,dv_*\,dv_*'. \end{aligned} \tag{6}$$

For an existence theory for (6), we refer to [24].

2.2 Properties of the sexual reproduction kernel Q

In Subsection 2.3, we rescale (6) to show that it indeed only depends on three parameters. To be able to do so, we first need to define more precisely the reproduction kernel Q, and analyze its properties.

The sexual reproduction has two opposite effects on the repartition of the population over the phenotypic traits:

- For each set of two chromosomes, one comes from the parent of phenotypic trait v_*, and one from the parent of trait v_*'. This process tends to give the offspring a trait between v_* and v_*'. The effect of this phenomenon is to concentrate the population traits.

- On the contrary, a variability is maintained in the population by mutations and recombinations. Recombination is the process, occurring by the crossing-over of chromosomes during meiosis, in which DNA is exchanged between a pair of chromosomes (notice that the effect of recombinations is typically much larger than the effect of mutations, see [6]).

A reasonable assumption is that in absence of selection, a sexual population phenotypic distribution converges to a given profile that only depends on Q. To make this assumption precise, we consider the homogeneous sexual reproduction model (4) without selection, and with a constant population size, that is

$$\begin{cases} \partial_t n(t,v) = \int\int Q(v,v_*,v'_*)n(t,v_*)n(t,v'_*)\,dv_*\,dv'_* - n(t,v) \\ n(0,v) = n^0(v) \in L^1(\mathbb{R}), \text{ with } \int n^0(v)\,dv = 1. \end{cases} \tag{7}$$

We also assume that the long-time dynamics of this model is simple in the sense that:

Condition 1:

- For any $v_*,\ v'_* \in \mathbb{R}$, we have $\int Q(v,v_*,v'_*)\,dv = 1$,
- For any $v_*,\ v'_* \in \mathbb{R}$, we have $\int v\,Q(v,v_*,v'_*)\,dv = \frac{v_*+v'_*}{2}$,
- There exists G (from the *genetic variance*, see [15]) such that for any initial population n^0, the phenotypic variance of the population converges to G:

$$\int \left(v - \int w\,n^0(w)\,dw\right)^2 n(t,v)\,dv \to G^2, \text{ as } t \to \infty,$$

- For any initial population n^0, the third moment of the phenotypic distribution of the population converges to 0:

$$\int \left(v - \int w\,n^0(w)\,dw\right)^3 n(t,v)\,dv \to 0, \text{ as } t \to \infty.$$

We notice that Condition 1 implies that the two first moments of n are conserved:

$$\forall t \geq 0, \quad \int n(t,v)dv = 1, \quad \int vn(t,v)dv = \int vn^0(v)dv. \tag{8}$$

The reproduction kernel that is typically used in structured population models for sexual populations (see [5, 11]) is:

$$Q(v,v_*,v'_*) := \frac{1}{\gamma\sqrt{2\pi}} e^{-\frac{\left(v-\frac{v_*+v'_*}{2}\right)^2}{2\gamma^2}}. \tag{9}$$

We show that Condition 1 is satisfied for this particular reproduction kernel:

Proposition 1 *Condition 1 is satisfied by the reproduction kernel defined in* (9)*, with* $G = \sqrt{2}\gamma$.

Remark 1 *This condition is indeed hold true for a more general reproduction kernel* $Q(v,v_*,v'_*) = \left(\widetilde{\Gamma} * \widetilde{Q}(\cdot,v_*,v'_*)\right)(v)$*, where* $\widetilde{\Gamma}$ *is symmetrical with a positive variance,* $\widetilde{Q}(\frac{v_*+v'_*}{2} + v, v_*, v'_*) = \widetilde{Q}(\frac{v_*+v'_*}{2} - v, v_*, v'_*)$ *for any* $v,\ v_*,\ v'_* \in \mathbb{R}$*, and*

$$\int \left(v - \frac{v_*+v'_*}{2}\right)^2 \widetilde{Q}(v,v_*,v'_*)\,dv = C\frac{(v_*-v'_*)^2}{4},$$

with $C < 1$*. For this and more on this type of problem, we refer to [13, 17].*

Proof of Proposition 1: The two first parts of Condition 1 can be easily checked. We only prove the third and the fourth.

We assume, without loss of generality, that $\int v\, n^0(v) = 0$. Therefore according to (8) we have

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

We multiply equation (7) 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 $G = \sqrt{2}\gamma$ for any initial condition n^0:

$$\int v^2 n(t,v)\, dv \to G^2 = 2\gamma^2, \text{ as } t \to \infty.$$

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 $\int v^3 n(t,v) \to 0$ as $t \to \infty$.

□

2.3 Rescaling of the structured population model

To simplify (6), we perform the following rescaling:

$$a_1 = \left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right), \qquad a_2 = \frac{1}{\sigma_x}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{\frac{1}{2}}, \qquad a_3 = \frac{1}{G},$$

$$\widetilde{n}(\widetilde{t},\widetilde{x},\widetilde{v}) = \frac{r_{max}G}{K}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1} n\left(\frac{\widetilde{t}}{a_1}, \frac{\widetilde{x}}{a_2}, \frac{\widetilde{v}}{a_3}\right),$$

$$\widetilde{Q}(v,v_*,v'_*) := G\, Q\left(Gv, Gv_*, Gv'_*\right),$$

where G is given by Condition 1. We notice that the rescaled reproduction kernel $\widetilde{Q}$ satisfies Condition 1 with $\widetilde{G} = 1$. With the above rescaling, (6) becomes:

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

with

$$A := \frac{G^2}{V_s}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1}, \qquad B := \frac{b\sigma_x}{G}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-\frac{1}{2}},$$

$$C := \gamma\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1} - 1.$$

Here the parameter A can be interpreted as the potential for adaptation to the local optimal trait. The parameter B indicates how fast the environment is changing along x. The parameter C measures the ratio between the birth rate and the maximal growth rate of the total population.

Remark 2 *This is not the only possible rescaling for this equation. As we will see in Subsection 2.4, this particular scaling will allow us to obtain* (14) *as a formal limit of* (10) *when C is large. In [15], the authors perform another renormalization of* (1) *and they obtain only two parameters A and B. The corresponding parameters are defined as:*

$$A = \frac{G}{2V_s}\left(r_{max} - \frac{I_s}{2}\right)^{-1}, \quad B = \frac{b\sigma_x}{\sqrt{2V_s}}\left(r_{max} - \frac{I_s}{2}\right).$$

The scaling they use does not work here, because they assume that the rescaling in the variable v does not modify G, the typical phenotypic variance of the phenotypic distribution of the population. While with (6)*, G is necessarily affected by a scaling in the v variable (see Condition 1). This is also why we could not obtain exactly* (1)*, but the slightly different model* (14).

2.4 Formal limit of the structured population model

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

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

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

We show that N and Z satisfy the following unclosed equations:

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

$$\partial_t N(t,x) - \Delta_x N(t,x) = \left[1 + \frac{A}{2}(1 - V(t,x)) - \frac{A}{2}(Z(t,x) - Bx)^2 - N(t,x)\right]N(t,x). \tag{11}$$

$$\begin{aligned}\partial_t Z(t,x) - \Delta_x Z(t,x) = {} & 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x))V(t,x) \\ & - \int (v - Z)^3\frac{n(t,x,v)}{N(t,x)}\,dv.\end{aligned} \tag{12}$$

Proof of Proposition 2: To obtain (11), we integrate (10) along v:

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

The second equation, (12), is obtained as follows:

$$\begin{aligned}
\partial_t Z(t,x) - \Delta_x Z(t,x) &= \partial_t \int v \frac{n(t,x,v)}{N(t,x)}\,dv - \Delta_x \int v \frac{n(t,x,v)}{N(t,x)}\,dv \\
&= \int \frac{v}{N(t,x)} \left(\partial_t n(t,x,v) - \Delta_x n(t,x,v)\right) dv \\
&\quad - \left(\partial_t N(t,x) - \Delta_x N(t,x)\right) \frac{Z(t,x)}{N(t,x)} \\
&\quad + 2\partial_x(\log N(t,x))\partial_x Z(t,x),
\end{aligned}$$

and thus,

$$\begin{aligned}
&\partial_t Z(t,x) - \Delta_x Z(t,x) \\
&= -\int \frac{v}{N(t,x)} \left(\left(C - \frac{A}{2}\right) + \frac{A}{2}(v - Bx)^2 + \int n(t,w)\,dw\right) n(t,x,v)\,dv \\
&\quad + (C+1) \int \frac{v}{N(t,x)} \left(\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw} Q(v,v_*,v'_*)\,dv_*\,dv'_*\right) dv \\
&\quad - \left(1 - \frac{A}{2}(Z(t,x) - Bx)^2 - N + \frac{A}{2}(1 - V(t,x))\right) N(t,x) \frac{Z(t,x)}{N(t,x)} \\
&\quad + 2\partial_x(\log N(t,x))\partial_x Z(t,x) \\
&= 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x))V(t,x) \\
&\quad - \int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\,dv.
\end{aligned}$$

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

$\square$

Remark 3 *The term $2\partial_x(\log N)\partial_x Z$ is referred to, by biologists, as the "gene flow" term (see [18] and [21, 15, 23]). 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:*

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

To close the equations on N and Z obtained in Proposition 2, we notice that (10) can be written:

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

Therefore if C is very large, the first term dominates the dynamics of the population. Since this first term corresponds to the "pure" sexual reproduction equation (7), and since the reproduction kernel Q satisfies Condition 1, it is natural to assume that at all time $t > 0$ and all locations $x \in \mathbb{R}$,

$$V(t,x)=\int (v-Z(t,x))^2\frac{n(t,x,v)}{N(t,x)}\,dv \sim G=1, \qquad \int (v-Z(t,x))^3\frac{n(t,x,v)}{N(t,x)}\,dv \sim 0. \tag{13}$$

We notice that here, thanks to the rescaling performed in the previous subsection, $G = 1$.

Using the latter properties to close the system of equations on N and Z obtained in Proposition 2, we obtain the following model:

$$\begin{cases}\partial_t N(t,x)-\Delta_x N(t,x)=\left(1-\frac{A}{2}(Z(t,x)-Bx)^2-N(t,x)\right)N(t,x),\\ \partial_t Z(t,x)-\Delta_x Z(t,x)=2\partial_x(\log N(t,x))\partial_x Z(t,x)+A(Bx-Z(t,x)).\end{cases} \tag{14}$$

This model is very close to the model (1) from [21, 15]. The model (1) was built directly, without the intermediate step of a structured population model, and the limits of its applications were unclear (see [22]). Our derivation shows that the model (14) is valid (in the sense that it is the formal limit of (6)) if:

- The reproduction is sexual,
- The reproduction kernel satisfies Condition 1,
- C is large.

Remark 4 $C=\gamma\left(r_{max}-\frac{G^2}{2V_s}-\frac{I_s}{2}\right)^{-1}-1$ *is large if the birth rate is large compared to the maximal growth rate of the total population. In other words, many generations are necessary to obtain a significant growth of the population, which seems reasonable in many biological situations.*

Notice also that in the framework of Proposition 1, the convergence criteria in Condition 1 hold true exponentially fast. Therefore the simplification (13) *might be accurate even if C is not very large. The numerical simulations in Subsection 4.3 show that, the simplified model* (2) *(which is a further simplification of* (14)*, see Subsection 2.5) seems accurate even if $C = 1$ (see Figure 8).*

The model (14) may hold in other situations, justifying the closure assumption (13) with other arguments. However, in [20], it is shown that (14) cannot hold for asexual populations for the whole range of parameters A and B.

2.5 Derivation of a simplified model

To simplify (14), we first apply the following change of variable:

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

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

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

Now, if we assume that A is very small, N and Z are related by the simple relation:

$$N(t,x) \sim 1-(Z(t,x)-(B/\sqrt{2})x)^2. \tag{16}$$

Therefore we obtain the simpler model (2), on Z only:

$$\begin{aligned} \partial_t Z(t,x) - \Delta_x Z(t,x) \quad = \quad & -4\frac{(\partial_x Z(t,x) - B/\sqrt{2})(Z(t,x)-(B/\sqrt{2})x)}{1-(Z(t,x)-(B/\sqrt{2})x)^2}\partial_x Z(t,x) \\ & +((B/\sqrt{2})x - Z(t,x)). \end{aligned}$$

In Section 4, we will show that the information given by this simple model on the dynamics of the population (see Section 3) is close to the results of numerical simulations obtained for the original structured population model (10).

Remark 5 *As we can see in* (15)*, the limit A small corresponds to an infinitly fast reaction term. In consequence, this model is not adequate to capture the extinction phenomenon that occurs at the kinetic level (see Section 4). The latter is however able to capture the two other possible behaviors of the population: propagation to the entire environment, or survival in a limited range.*

In [15], the range of A that has been considered was $A \in [0.001, 1]$. Thus our approximation, assuming that A is small, seems reasonable.

Remark 6 *Another simplification had been proposed in [15], where the equation on N was replaced by*

$$N := k\exp\left(\gamma\left(1-A(Z-Bx)^2\right)\right). \tag{17}$$

With this ansatz, the model (1) *simplifies considerably:*

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

However, the simplification (17) *seems independent of* (1)*. Our simplification has the advantage to rely on a clearer assumption:* (2) *is the formal limit of* (14) *when A is small.*

3 Dynamics of the population

3.1 Well-posedness of the model

We introduce $W = Z - (B/\sqrt{2})x$ in (2) to obtain the following equation

$$\partial_t W - \Delta_x W = -4\frac{\partial_x W W}{1-W^2}(\partial_x W + B/\sqrt{2}) - W, \tag{18}$$

with $-1 \le W \le 1$. 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 3.2, the singularities are fundamental to produce propagating fronts. In most of the cases in the classical study of propagating fronts, one proves the existence of propagating fronts that connect two steady states. Here the situation is different. The propagating fronts connect the unstable steady state $W = 0$ to the singular point $W = -1$. While the presence of singularities is crucial to observe propagating fronts, it is an obstacle to prove uniqueness or a comparison principle. Nevertheless we are able to introduce an approached model where the uniqueness and the comparison principle hold.

Since (18) is singular, we approximate it by the following model

$$\partial_t W_\delta - \Delta_x W_\delta = -4\frac{\partial_x W_\delta W_\delta}{1-W_\delta^2+\delta}(\partial_x W_\delta + B/\sqrt{2}) - \frac{(1-W_\delta^2)W_\delta}{1-W_\delta^2+\delta}, \tag{19}$$

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 3.2).

Under the assumption

$$-1 \le W_\delta^0 \le 1, \tag{20}$$

equation (19) has a smooth solution that stays between -1 and 1 by the maximum principle. We prove a regularizing effect for equation (19) and we deduce that the W_δ's converge to a viscosity solution of a variant of equation (18) (see [8, 1] for general introduction to the theory of viscosity solutions).

Theorem 1 *Under assumption* (20), W_δ *the solution of* (19) *verifies, for all* $(t,x) \in \mathbb{R}^+ \times \mathbb{R}$,

$$-1 \le W_\delta(t,x) \le 1, \qquad |\partial_x W_\delta(t,x)| \le \min(\,L_2\,, \frac{1}{2\sqrt{t}} + L_1), \tag{21}$$

with

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

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*

$$(1-W^2)\partial_t W - (1-W^2)\Delta_x W = -4\partial_x W W(\partial_x W + B/\sqrt{2}) - (1-W^2)W. \tag{22}$$

We notice that equation (22) is the original model (18) multiplied by $1 - W^2$. Furthermore, the second inequality (21) shows that equation (19) has a regularizing effect and the W_δ's become uniformly Lipschitz, for all $t > t_0 > 0$, even if they are not uniformly Lipschitz initially.

Proof of Theorem 1: We differentiate equation (18) with respect to x and obtain

$$\begin{aligned}
\partial_t \partial_x W_\delta - \Delta_x \partial_x W_\delta \quad &= -4\tfrac{W_\delta}{1-W_\delta^2+\delta}(2\partial_x W_\delta + B/\sqrt{2})\partial_x(\partial_x W_\delta) \\
&\quad -4\partial_x W_\delta^2(\partial_x W_\delta + B/\sqrt{2})\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2} \\
&\quad -\partial_x W_\delta \left(1 - \delta\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right),
\end{aligned} \tag{23}$$

where the last term comes from

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

We multiply (23) by $\partial_x W_\delta$ and divide by $|\partial_x W_\delta|$ and obtain

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

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

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

with

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

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

$$\partial_t g - \Delta_x g \quad = \alpha(t,x)\partial_x g - 4\left(\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right)(g - L_1)^3, \tag{24}$$

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 (24) 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 (21).

Now we define

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

We first consider the case with $L_2 < +\infty$. From (21), 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 latter equation, (19) and (21) 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 [2]). 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 [8, 1]), we conclude that W is a viscosity solution of (22).

□

We proved that the equation (22) has a solution in the viscosity sense. Unfortunately the viscosity criterion is not enough to select a unique solution. We give a counter-example below:

Example. Non-uniqueness for equation (22)**:** We have the two following solutions to equation (22):

$$W_1(t, x) = -1, \qquad \text{for all } (t, x) \in \mathbb{R}^+ \times \mathbb{R},$$

$$W_2(t, x) = -e^{-t}, \qquad \text{for all } (t, x) \in \mathbb{R}^+ \times \mathbb{R}.$$

Here the biological solution is the first one. Because $W = -1$ corresponds to $N = 0$. Therefore, if initially $W(0, x) = -1$ for all $x \in \mathbb{R}$, we expect that $W(t, \cdot) \equiv -1$, for all $t \in \mathbb{R}^+$. Otherwise a population is created out of nowhere. We can easily verify that if $W_\delta(t = 0, \cdot) \equiv -1$, we have $W_\delta(t, \cdot) \equiv -1$ for all $t > 0$. Therefore our approximation chooses the biological solution.

In Subsection 3.2 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 (22) 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 1 *Comparison principle: Equation* $L(D^2u, Du, u, x, t) = 0$ *verifies a comparison principle, if for any subsolution* w^1 *and supersolution* w^2 *of* L *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 (19). In particular (19) has a unique solution.

Proposition 3 *Equation* (19) *admits a comparison principle in the set of solutions* $\{-1 \le W \le 1\}$*.*

Proof of Proposition 3: We suppose that W_1 and W_2 are respectively subsolution and supersolution of (19) and

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

We prove that $W_1 \le W_2$ 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

$$\begin{aligned}
&\partial_t (W_1 - W_2)(\bar t, \bar x) - \Delta (W_1 - W_2)(\bar t, \bar x) \\
&\quad \le -4p\,(p + B/\sqrt{2}) \frac{(1 + W_1 W_2 + \delta)}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)} (W_1 - W_2)(\bar t, \bar x) \\
&\quad - \frac{(1+\delta)(1 - W_1^2 - W_1 W_2 - W_2^2) + W_1 W_2 + W_1^2 W_2^2}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)} (W_1 - W_2)(\bar t, \bar x).
\end{aligned}$$

In the previous section we proved that $|\partial_x W|$ is bounded. Thus $p(p + B/\sqrt{2})$ is bounded. Moreover W_1 and W_2 are bounded and

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

Therefore the coefficient of $W_1 - W_2$ is bounded. Following the classical maximum principle we deduce that equation (19) admits a comparison principle.

□

3.2 Existence of propagating fronts and steady populations

In this section, we study the existence of propagating fronts and steady states for equation (2). Since the optimal trait at the point x of space is $(B/\sqrt{2})x$, we expect that a propagating front Z, with Z a solution of (2), to be of the following form

$$Z(t,x) = (B/\sqrt{2})x + U(x - \nu t).$$

Using the above notation, the equation (2) becomes

$$-\nu U' - U'' = -4 \frac{U'U}{1 - U^2}(U' + B/\sqrt{2}) - U.$$

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 given by the vector field

$$\begin{cases} F_U(U,V) = V, \\ F_V(U,V) = -\nu V + 4\frac{UV}{1-U^2}(V + B/\sqrt{2}) + U. \end{cases} \tag{25}$$

To have a meaning with respect to (18), those solutions must satisfy $U(\cdot) \in [-1, 1]$.

We prove that propagating fronts exist for any positive constant $B > 0$ (see Figure 1).

Theorem 2 *For any positive constant $B > 0$, there exists $\nu_B \in \mathbb{R}$ such that* (18) *has a propagating front of speed ν, $Z(t,x) = (B/\sqrt{2})x + U(x - \nu t)$, satisfying*

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

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

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

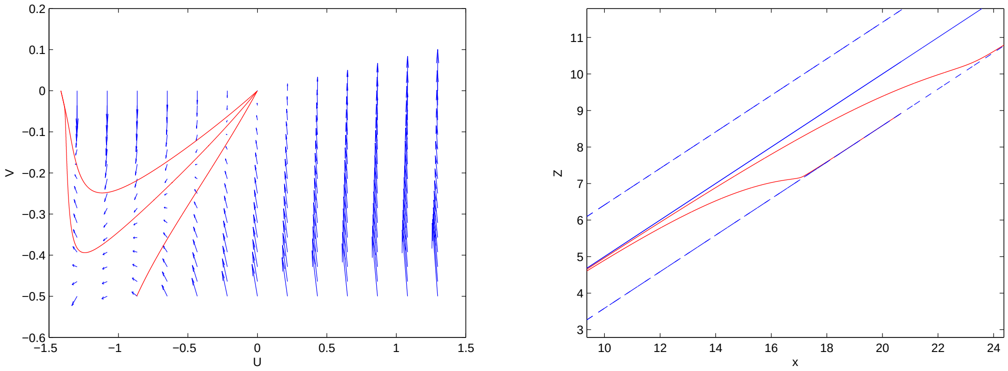

Figure 1: On the left, we represent solutions of the ODE defined by the vector field (25) for $B := 0.5$ and $\nu = 3.75, 4.75, 5.75$ (the vector field represented corresponds to $\nu = 4.75$). A propagating front exists for those two last values of ν only, which we represent on the right.

The above Theorem claims that for each $B > 0$, there exists a one-parameter family of propagating fronts. By analogy to the KPP-Fisher equation, one can expect that there is only one stable propagating front, the one with the least speed. In Section 4, numerical simulations show that the speed of propagating waves for the structured population model (10) are close to ν_B (when A is small and C is large), confirming the idea that the minimal speed ν_B is the natural speed to consider here. Since the model does not admit a comparison principle, we cannot use the usual methods from the study of the KPP-Fisher equation to study the stability of propagating fronts rigorously.

The propagating waves with minimal speed would be invasive fronts if $\nu_B > 0$, and extinction fronts if $\nu_B < 0$. In Theorem 3 we prove that steady populations exist in this second case only.

Theorem 3 *The equation* (2) *has a non-trivial steady-state if and only if $\nu_B < 0$. Steady-states $Z(t,x) = (B/\sqrt{2})x + U(x)$ satisfy*

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

As one can see in the proof, if $\nu_B < 0$, there exists indeed a whole family of steady-states. If we assume that $U(0) = 0$ (to avoid the translation invariance of the problem), then the family of steady-states can be parameterized by $V(0) = U'(0) \in (-K_B, 0)$, for some $K_B > 0$.

To prove the above Theorems, we will use the two following Lemma:

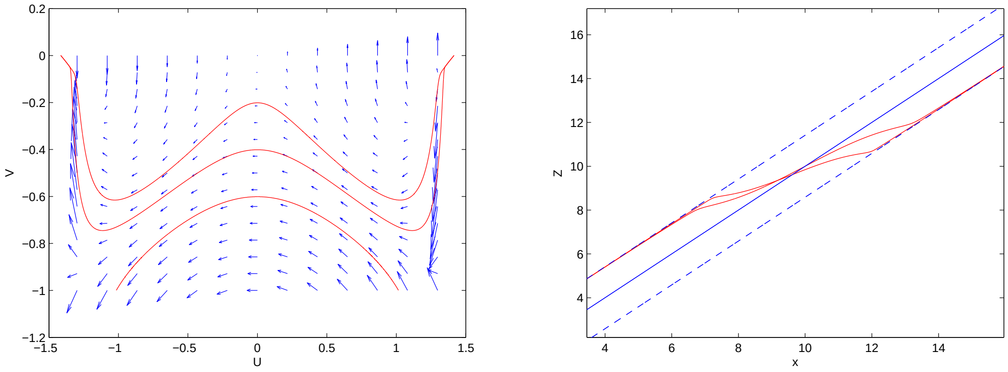

Figure 2: On the left, we represent solutions of the ODE defined by the vector field (25) for $B := 1.5$ and $\nu = 0$. Two of the three solutions represented define steady-states of (18), which we represent on the right.

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 (25) 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.

Lemma 2 *Let $\nu_1 \le \nu_2$, 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, $t_2 \in \mathbb{R}$,*

$$\left\{ \begin{array}{l} u_{\nu_1}(t_1) = u_{\nu_2}(t_2) \\ v_{\nu_1}(t_1) \le v_{\nu_2}(t_2), \end{array} \right. \tag{26}$$

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 $v_{\nu_1}(t_1') \le v_{\nu_2}(t_2')$, 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.

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.

□

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,

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

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.

□

Proof of Theorem 2: *Step 1:* We show that the solution (u, v) given by Lemma 1 satisfies either $v(\bar{t}) = -B/\sqrt{2}$ 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 $V \in (-B/\sqrt{2}, 0)$, only two situations are possible: either $v(\bar{t}) = -B/\sqrt{2}$ for some $\bar{t} < +\infty$, or $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t} \in \mathbb{R} \cup \{+\infty\}$.

If $v(\bar{t}) = -B/\sqrt{2}$, then $v(t) < -B/\sqrt{2}$ for all $t \geq \bar{t}$. This is because

$$F_V(U, -B/\sqrt{2}) = \nu B/\sqrt{2} + U \leq F_V(u(\bar{t}), -B/\sqrt{2}) \leq 0$$

for $U \in (-1, u(\bar{t}))$ and since u is decreasing. Therefore, $u'(t) = v(t) \leq -B/\sqrt{2}$ for all $t \geq \bar{t}$. From the latter, together with $F_V(-1, V) = -\infty$ for $V < -B/\sqrt{2}$, 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 $F_V(U,V) \sim \frac{-2B}{\sqrt{2}}\frac{V}{1+U} - 1$. We deduce that,

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

if $v(t) \leq \frac{-\sqrt{2}}{3B}(1+u(t))$ 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, $\frac{v(t)}{1+u(t)} \geq \min\left(\frac{v(\widetilde{t})}{1+u(\widetilde{t})}, \frac{-\sqrt{2}}{3B}\right)$ 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_B such that, there exists a propagating front if and only if $\nu > \nu_B$.

If $\nu > \frac{\sqrt{2}}{B}$, we have $F_V(U, -B/\sqrt{2}) = \nu B/\sqrt{2} - U > 0$ for $U \in (-1,1)$. Therefore, the solution given by Lemma 1 cannot cross the line $V = -B/\sqrt{2}$, 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 $[-1/\sqrt{2}, 0] \times [-B/\sqrt{2}, 0]$ and for $\nu \leq -5B$, we have

$$F_V(U,V) \leq -\nu V - 4\sqrt{2}\,V(V + B/\sqrt{2}) \leq BV \leq B\,F_U(U,V).$$

It follows that the solution given by Lemma 1 necessarily crosses the line $V = -B$, 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_B is a decreasing function of B. Firstly we notice that, for $B_1 \leq B_2$, we have $F_U^{B_1} = F_U^{B_2}$, and $F_V^{B_1} \leq F_V^{B_2}$ in $(-1,0] \times \mathbb{R}_-$. We deduce that, using Step 1, if the solution given by Lemma 1 for B_1 converges to $(-1,0)$ as $t \to \infty$, so does the one associated to B_2. This proves that ν_B is a decreasing function of B.

□

Proof of Theorem 3: We assume that $\nu_B < 0$. Then, for $\nu = \frac{\nu_B}{2}$, the solution $(u_{\nu_B/2}, v_{\nu_B/2})$ given by Lemma 1, is globally defined, and it satisfies $(u_{\nu_B/2}, v_{\nu_B/2})(t) \to (-1, 0)$ as $t \to +\infty$. Moreover we have

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

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

Consider now the vector field (25) 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 $(u_{\nu_B/2}, v_{\nu_B/2})$. 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 $(u_{\nu_B/2}, v_{\nu_B/2})$. We define $(\bar u, \bar v)$ to be the solution of the ODE given by the vector fields (25) 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 3.

□

4 Numerical simulations

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 (2).

4.1 Numerical scheme

The difficulty for the simulation of (10) is that a direct discretization of the birth term leads to a very slow algorithm (of order n^3, where n is the number of nodes in the v variable). Fortunately, with the classical sexual reproduction kernel (9), we can write the reproduction term as a double convolution:

$$\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw} Q(v, v_*, v'_*)\,dv_*\,dv'_* = \frac{1}{\int n(t,x,w)\,dw} \left(\tilde{Q} *_v f(t,x,\cdot) *_v f(t,x,\cdot)\right)(2v),$$

where Q is defined by (9) with $\gamma = 1$, and $\tilde{Q}(v) := \frac{1}{\sqrt{2\pi}} e^{-\frac{v^2}{8}}$. This formula allows us 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 $n \log n$. Coupled to a classical finite difference scheme for the rest of the equation, this produces an algorithm reasonably fast.

For the simplified model (2), we can use the phase plane (U, V) described in Subsection 3.2 to compute numerically the steady-states and propagating fronts of (2). We can in particular estimate numerically ν_B (see Theorem 2), and obtain a numerical approximation of the corresponding front.

4.2 Dynamics of the population

By performing a numerical simulation of (10), we can observe the three possible behaviors described in [15]: For given A and C, we observe extinction if B is large (see Figure 3), propagation if B is small (see Figure 4), and convergence to a steady-state for intermediate values of B (see Figure 5). Moreover we observe that at any position x of space the population, if it has reached the latter point, tends to concentrates on the line $v = Bx$ that is the optimal trait.

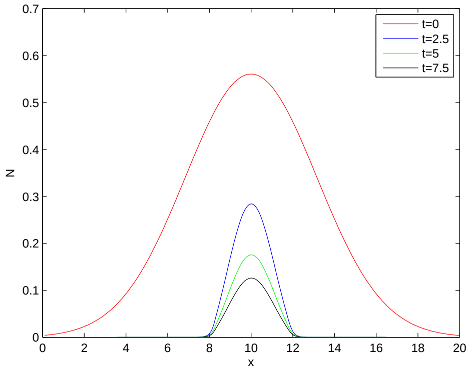

Figure 3: Extinction for $A = 0.01$, $B = 13$, $C = 40$. The graph represents the total population $x \mapsto N = \int n(t,x,v)\,dv$ for four successive times.

Given that C is a large constant (here $C = 40$), in Figure 6 we represent graphically dynamics of populations depending on A and B. The dots come from the simulation 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 (2) to determine the border between the zones where populations succeed to propagate (if $B < B_{crit}$), and where populations remain in a limited range (if $B > B_{crit}$). This border corresponds to the horizontal line in Figure 6. We notice that this line is close to the dots coming from the simulation of (10).

As explained in Remark 5, the simplified model (2) is too simple 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 (14) to get a criterion for extinction or survival of populations: it depends on the sign of the principal eigenvalue of the linear operator

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

that is the sign of $1 - B\sqrt{A/2}$ (the corresponding eigenfunction being $N(x) = e^{-\frac{\sqrt{A}Bx^2}{\sqrt{8}}}$). Following this formal argument, extinction would occur if $AB^2 > 2$. In Figure 6 we also represent the line $AB^2 = 2$, that appears to be close to the border, which we had obtained earlier using (10), between the zones of extinction and survival.

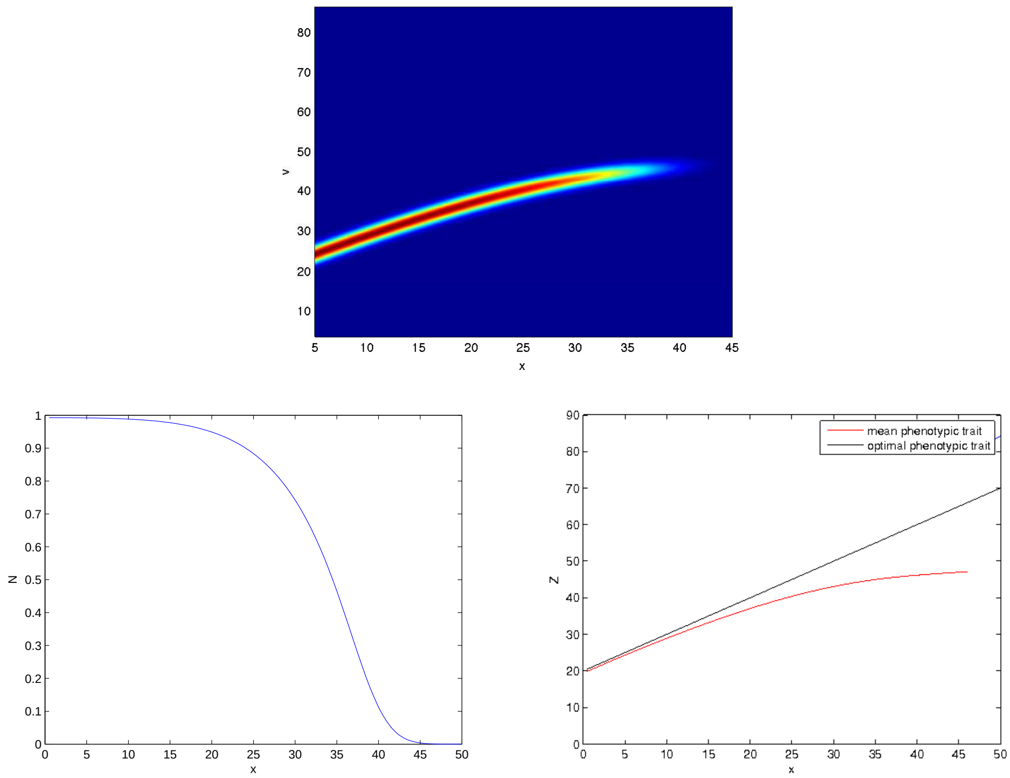

Figure 4: Propagation for $A = 0.01$, $B = 1$, $C = 40$. The three graphs represent respectively the population density $(x, v) \mapsto n(t, x, v)$, the total population $x \mapsto N = \int n(t, x, v)\, dv$, and the mean phenotypic trait of the population, $x \mapsto N = \int v \frac{n(t,x,v)}{N(t,x)}\, dv$.

4.3 Comparison between the structured population model (10) and the simplified model (2)

As presented in Section 2, the structured population model (10) converges formally to the simplified model (2) while C is large and A is small. In Section 3, we have described the steady-states and traveling waves of the simplified model (2) using a phase plane. As it is presented in Figure (7), numerical simulations show that the latter results for the simplified model (2) give a good approximation of the dynamics of the structured population model (10).

Indeed, the dependence of the structured population model (10) in the parameter C does not seem to be strong (see Remark 4). We observe in Figure 8 that the propagating fronts obtained numerically for $C = 1$ and $C = 40$ are similar.

A biologically important property for this type of population is the speed of their propagating fronts. We can compute numerically this speed for both models. As we can see in Figure 9, the speed ν_B obtained from the simplified model seems a good approximation of the speed of propagating fronts from the structured population model (10). Moreover, we observe that when A becomes small and C becomes large, the speed of propagating fronts of the structured population model (10) converges to ν_B (see Figure 10).

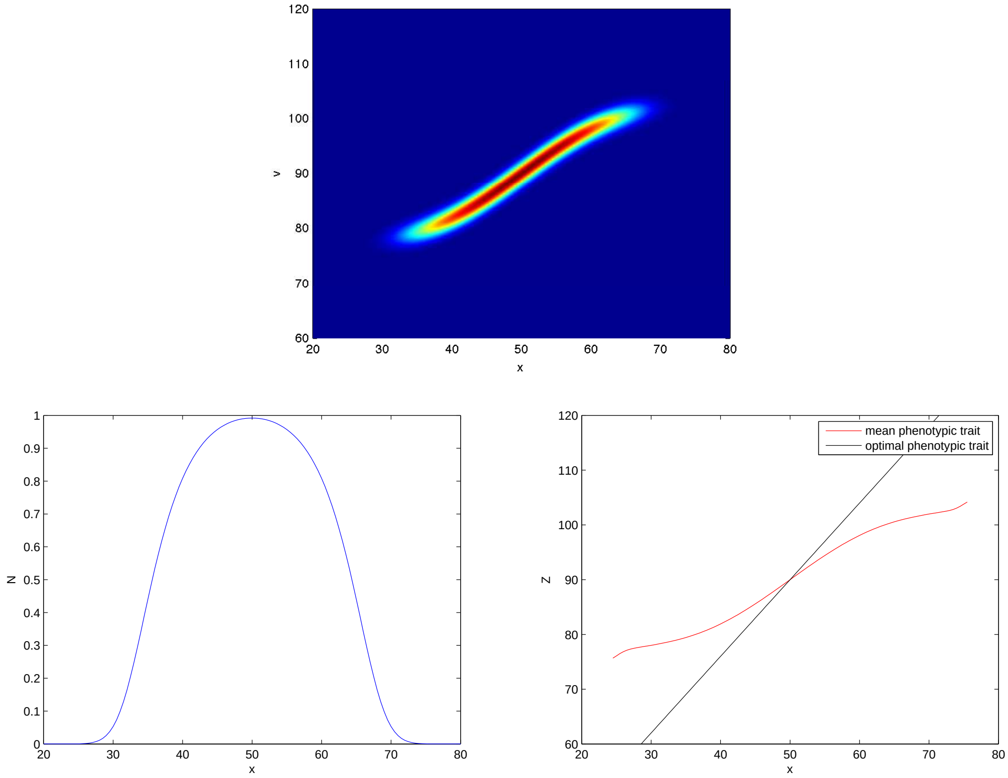

Figure 5: Limited range, for $A = 0.01$, $B = 3$, $C = 40$. The three graphs represent respectively the population density $(x, v) \mapsto n(t, x, v)$, the total population $x \mapsto N = \int n(t, x, v)\, dv$, and the mean phenotypic trait of the population, $x \mapsto N = \int v \frac{n(t,x,v)}{N(t,x)}\, dv$.

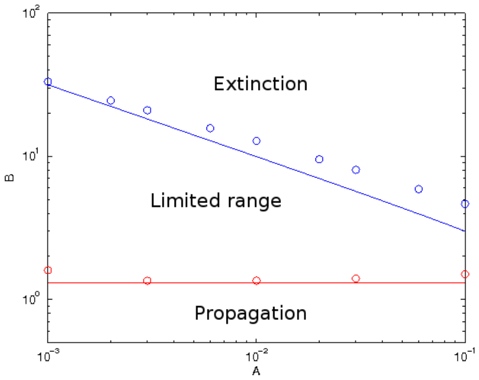

Figure 6: Dynamics of the structured population model (10). The dots come from the simulations of (10) with $C = 40$. The continuous lines come from the approximations presented in Subsection 4.2.

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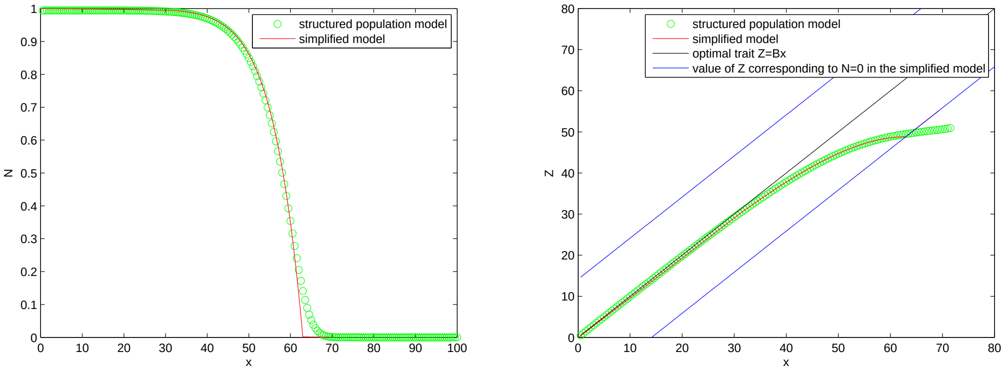

Figure 7: Comparison of propagating wave profiles of the structured population model (10) with the propagating wave of minimal speed ν_B for the simplified model (2). We depict the total population N for both models (left) and the mean phenotypic trait Z for both models (right), using the following parameters: $A = 0.01$, $B = 1$, and $C = 20$.

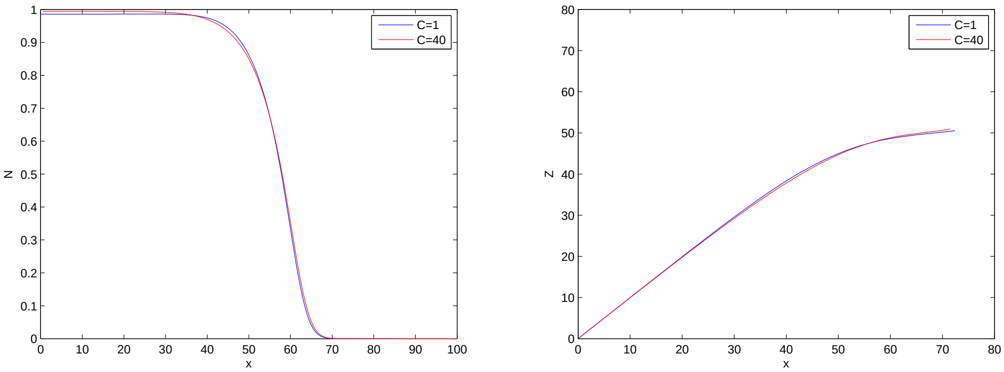

Figure 8: Comparison of propagating wave profiles of the structured population model (10) for $C = 1$ and $C = 40$. The other parameters are $A = 0.01$, $B = 1$, and the speeds of propagation are respectively 1.32 and 1.12. We depict the total population N (left) and the mean phenotypic trait Z (right).

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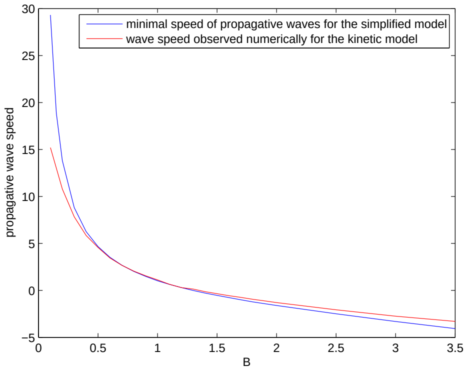

Figure 9: Comparison of the propagating wave speed of the structured population model (10), with the minimal speed ν_B of propagating waves of the simplified model (2).

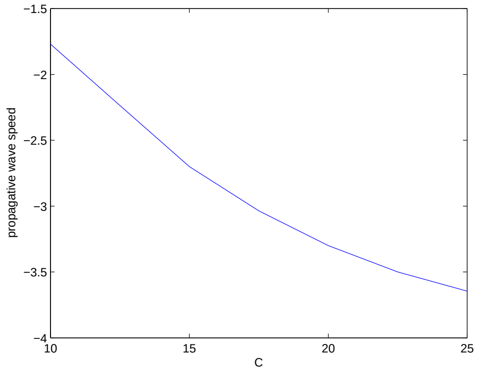

Figure 10: propagating wave speed of the structured population model (10) for $B = 3.5$, $C \in [10, 25]$ and $A = e^{20.7-2.3C}$ (that is $A = 0.1$ to $A = 0.0178$). The speed of the propagating wave of the structured population model (10) seems to converge to the minimal speed $\nu_{3.5} \sim -4$ of propagating waves of the simplified model (2).

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