

A NON-LINEAR DEGENERATE EQUATION FOR DIRECT AGGREGATION AND TRAVELING WAVE DYNAMICS

FAUSTINO SÁNCHEZ-GARDUÑO

Departamento de Matemáticas, Facultad de Ciencias
Universidad Nacional Autónoma de México
Circuito Exterior, Ciudad Universitaria, México, 04510, D.F., México

PHILIP K. MAINI

Centre for Mathematical Biology, Mathematical Institute
University of Oxford, 24-29 St. Giles', Oxford, OX1 3LB, England, UK and
Oxford Centre for Integrative Systems Biology, Department of Biochemistry
South Parks Road, Oxford OX1 3QU, England, UK

JUDITH PÉREZ-VELÁZQUEZ

Institute of Biomathematics and Biometry, Helmholtz Zentrum München
German Research Center for Environmental Health
Ingolstädter Landstr. 1, 85764 Neuherberg, Germany

(Communicated by Yang Kuang)

ABSTRACT. The gregarious behavior of individuals of populations is an important factor in avoiding predators or for reproduction. Here, by using a random biased walk approach, we build a model which, after a transformation, takes the general form $u_t = [D(u)u_x]_x + g(u)$. The model involves a density-dependent non-linear diffusion coefficient D whose sign changes as the population density u increases. For negative values of D aggregation occurs, while dispersion occurs for positive values of D . We deal with a family of degenerate negative diffusion equations with logistic-like growth rate g . We study the one-dimensional traveling wave dynamics for these equations and illustrate our results with a couple of examples. A discussion of the ill-posedness of the partial differential equation problem is included.

1. Introduction. By using a random walk approach and assuming that the individuals of a population have the same probability of moving from one point to another, *i.e.*, the habitat is isotropic, Skellam [38] derived the reaction-diffusion equation $u_t = D\nabla^2 u + g(u)$, for $u(\vec{r}, t)$, the population density at the point \vec{r} at time t , where $D > 0$ and g is the net rate of growth. This model has been criticized (see [7], [16] and [39]) because it does not take into account, for instance, the non-homogeneity of space and the different behavioral features of the individuals of the population. Several models have been proposed to take into account different factors which determine the spatio-temporal distribution of populations within their habitat. Among these are positive density-dependent diffusion models which describe the avoidance of crowded areas by individuals of a population. This type

2000 *Mathematics Subject Classification.* Primary: 35K65, 35C07; Secondary: 47J06.

Key words and phrases. Direct aggregation, degenerate diffusion, traveling waves, ill-posed problems, negative diffusion.

of behavior is well documented in the literature from both ecological and modeling points of view (see [6], [25] and [28]). Some of these proposed models are *degenerate* in the sense that at some value of the population density the partial differential equation (PDE) degenerates into an ordinary differential equation (ODE). This leads to interesting phenomena when the traveling wave behavior is analyzed (see [36] and [37]).

On the other hand it is also known that individuals of a population can aggregate. The gregarious behavior of species is well documented in the literature. This can be motivated by the need for survival, reproduction or to overcome a hostile environment, etc. Furthermore, this behavior can increase the animal's chance of avoiding capture by a predator (see [32], [42] and [44] for instance). Attraction between individuals of the same species can occur in two different ways:

1. **Indirect.** By this we mean the case in which a second agent produces (or facilitates) some attractive substance, *i.e.*, individuals can be attracted by diffusing mediators produced from individuals of another species. Some authors have described the indirect aggregation phenomenon in terms of different *taxis* mechanisms, such as chemotaxis, phototaxis, etc., and they incorporate them in different ways into diffusive models. One example is the so-called *chemotaxis-reaction-diffusion system* (see [24], [40] and references therein) which in one dimension, for the simple case where the individuals (with density u) produce their own attractant with concentration ρ , takes the form:

$$\begin{aligned} u_t &= [D_1 u_x - u\chi(\rho)\rho_x]_x + f(u) \\ \rho_t &= D_2 \rho_{xx} + g(u, \rho), \end{aligned} \quad (1)$$

where D_1 and D_2 are positive real numbers, χ is the chemotactic sensitivity factor, f and g are the kinetic terms. Different spatial patterns (*e.g.* spiral waves, traveling waves) have been predicted by analyzing the higher dimensional versions of these types of models ([13], [19], [24], and [40]), particularly, for example, the aggregation of the amoeba *Dictyostelium discoideum*.

2. **Direct.** Here the individuals of the species, due to social behavior (mating, settlement, etc.) or defense against predators, etc., attract other individuals of the same species (conspecific). The purely aggregative phenomena have been studied by proposing different models. By way of example we address a few of them:

The following diffusion-convection equation was proposed in [26]:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[m u^{m-1} \frac{\partial u}{\partial x} + \Psi \left(\int_{-\infty}^x u(s, t) ds \right), u \right], \quad (2)$$

where $m > 1$, with initial condition $u(x, 0) = u_0(x)$ where u_0 is a non-negative, bounded and integrable function on \mathbb{R} and $\Psi(r)$ is a smooth function in r . Ecologically the second summand in the right hand side of equation 2 can be interpreted as a dehomogenization process¹ due to a transport process which depends upon the population density on the range from $-\infty$ to the point x . In addition to analyzing the existence and uniqueness of the solution for this problem, the authors also proved the existence and the convergence of the solution to a solitary traveling wave as a pattern of aggregation of the population. An intuitive understanding of why such solutions exist is as

¹By this we mean the opposite of a strictly diffusive process.

follows: the spatial dynamics of the population is given by two factors: one (the diffusive) tends to homogenize, while the other (the convective) tends to aggregate. Thus, as both are present as time increases one can suspect that a balance among them could arise, leading to the solitary wave aggregation spatial pattern.

A model which generalizes 2 is given by the partial-integro-differential equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[D(u) \frac{\partial u}{\partial x} + \int_{\mathbb{R}} K(u(x), s) u(x+s) ds \right], \quad (3)$$

where D is such that $D(0) = 0$ and a strictly positive function for all positive values of u , and K is an odd kernel. Different types of kernels having an ecological interpretation have been proposed (see [4]).

In [12] the authors use the Ginzburg-Landau free energy approach to derive the fourth order diffusion equation:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[\chi(u) \frac{\partial u}{\partial x} - \mu(u) \frac{\partial^3 u}{\partial x^3} \right], \quad (4)$$

where $\chi(u) = (D_1 + 3D_2u^2)$ is the attractivity coefficient and $\mu(u) = D_3 > 0$. The above equation takes into account long range diffusion. These authors have shown that equation 4, with logistic growth, has spatially inhomogeneous steady state solutions. Some extensions of this approach have been carried out (see [23]) to describe an aggregation phenomenon in a plant-herbivore interaction.

In [9], the author assumes that competition between the individuals of a species (intra-specific) at a point depends not only on the population density at that point, but also on the weighted spatial average population density at neighboring points, given by,

$$v(x, t) = \int_{-\infty}^{+\infty} \frac{1}{2} c e^{-c|x-y|} u(y, t) dy.$$

This leads to a modified logistic model with constant diffusion coefficient plus an equation for v , *i.e.*, the system

$$\begin{aligned} u_t &= u[1 + \alpha u - (1 + \alpha)v] + u_{xx} \\ 0 &= c^2(u - v) + v_{xx} \end{aligned} \quad (5)$$

$\forall (x, t) \in (-\infty, +\infty) \times \mathbb{R}^+$ with the initial conditions $u(x, 0) = u_0(x)$ and $v(x, 0) = v_0(x)$. The author states conditions on the positive parameters c and α in 5 under which aggregation can occur.

Cantrell and Cosner (see, for example, [10] and [11]) have extensively worked on modeling spatial effects in ecology and population dynamics by using reaction-diffusion models. In particular, concerning the aggregation process of a population with density $u(x, t)$, these authors (see [10]) proposed and studied the following mathematical model

$$\frac{\partial u}{\partial t} = \nabla \cdot [d(x, u) \nabla u] + \lambda [m(x)u - cu^2] \text{ in } \Omega \times (0, \infty), \quad (6a)$$

$$u = 0 \text{ on } \partial\Omega \times (0, \infty), \quad (6b)$$

where $m(x)$ is a spatially varying local intrinsic growth rate, c measures the strength of logistic self-limitation, the diffusivity $d(x, u)$ depends on the population density and position, and λ measures the ratio of the respective rates of population growth and dispersal throughout Ω . The homogeneous Dirichlet boundary condition reflects the lethal character of the exterior. The tendency for the population to aggregate is modeled by assuming that the diffusion rate remains strictly positive but at low densities decreases with population density. The model allows for the diffusion rate to increase in response to overcrowding. The above authors give an example in which the model predicts a type of conditional persistence analogous to that found in models with an Allee effect.

In the model of Cantrell and Cosner, however, since the population dynamics is assumed to be logistic, the effect is induced only because of the aggregative density-dependent dispersal. This example is important because unlike non-spatial logistic models or logistic models augmented by dispersal via passive diffusion their model can predict extinction for populations with low initial densities but persistence for populations with high initial densities. They hypothesize that a biological interpretation of the mechanism is as follows: at low population densities individuals disperse rapidly and are likely to encounter the hostile exterior of their habitat, at slightly higher densities they disperse less rapidly and thus experience reduced mortality due to dispersal into hostile environments.

In [30] the author introduces a model for an aggregating population taking the form

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[\phi(u) - \lambda f(u) + \lambda \frac{\partial u}{\partial x} \right] + f(u), \quad (7)$$

where the function ϕ determines the migration rate. Homogeneous Neumann boundary conditions are imposed for a bounded domain in \mathbb{R}^n , and the case examined is that where this migration function ϕ is bounded and non-negative and given by $\phi(u) = u\psi(u)$ where, since 7 describes aggregating populations, ψ is decreasing. A further requirement imposed is that $f(u) = u\sigma(u)$ describes the Allee effect. Conditions on 7 for the survival (recovery) of a species in danger of extinction can be given.

Standard initial boundary value problems of the class

$$u_t = \nabla^2 \phi(u) + f(u) \quad (8)$$

are ill-posed when $\phi'(u)$ is negative for positive values of u . In [30] the author discusses a way to overcome this difficulty by replacing 8 by

$$u_t = \nabla^2 J + f(u), \quad (9)$$

where $J(x, t) := \int_{\Omega} K(x, y)\phi(u(y, t))dy$ and $K(x, y)$ is non-negative and zero flux boundary conditions on J are required in order to assure the isolation of Ω .

For a particular choice of J it is shown that problem 9 is equivalent to 7 with its associated boundary conditions.

Other approaches to deal with 8 being ill-posed for positive values of u have been proposed. For example, in [29] a model for aggregating populations

with migration rate ψ and constant population is studied. The functional differential equation this author proposed is

$$\frac{\partial u}{\partial t} = \nabla^2 \{ \psi(u(x, [t/\tau]\tau)) u(x, t) \}, \quad (10)$$

with boundary conditions

$$\vec{n} \cdot \nabla \{ \psi(u(x, [t/\tau]\tau)) u(x, t) \} = 0, \quad x \in \partial\Omega, \quad t > 0,$$

where \vec{n} is the normal vector at $\partial\Omega$, Ω is a bounded domain in \mathbb{R}^n and $[\theta]$ denotes the greatest integer less than or equal to θ . Padrón [29] assumed that the density dependent dispersal coefficient $\psi(u)$ gets actualized (up-dated) at certain pre-determined intervals of time, thus allowing them to overcome possible ill-posedness for the functional differential equation 10. He showed existence and uniqueness for the initial value problem 10 (with associated boundary conditions), and discussed aggregating behavior exhibited by the solutions.

The analysis of the classical mathematical problems (existence, uniqueness, continuity with respect to initial conditions, etc.) for partial-integro-differential equations such as 3 is a difficult task (see [5], [26] and [27] for instance). For this reason we suggest that the theory of diffusive models to describe aggregation can result in an easier problem. This paper deals with this approach in order to describe the direct aggregation phenomenon of individuals of one species living in a one-dimensional habitat.

The possibility of describing such aggregative phenomena by using non-linear negative degenerate diffusion equations has already been considered (see [4] and [7]). However, these authors do not provide any derivation of the negative diffusion equation, neither do they include any analysis. As far we know the first model which took into account the mutual attraction and repulsion of conspecifics was that constructed by Taylor and Taylor [41]. Because of both the formalism in its derivation and its predictions, this model was criticized (see [3] and [42]). A more consistent model was derived by Turchin (see [43]). He used a biased random walk approach to derive a model which is based on the following assumptions:

1. When there are no other individuals at adjacent positions, each animal moves randomly.
2. If there is a conspecific at an adjacent position, the animal moves there with conditional probability k (conditioned on the presence of the other animal), or ignores the neighbor with conditional probability $(1 - k)$.
3. When the local population density is low we can ignore the probability of having more than one conspecific in the immediate vicinity of each moving individual.

Under these assumptions Turchin derived a model for a population with density $u(x, t)$, of the form

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[\left(\frac{\mu}{2} - 2k(u)u \right) \frac{\partial u}{\partial x} \right], \quad (11)$$

where he then assumed that

$$k(u) = k_0 \left(1 - \frac{u}{\omega} \right),$$

where k_0 is the maximum degree of *gregariousness* (at $u = 0$) and ω is the critical density at which movement switches from aggregative to repulsive. In this way, he obtained the *aggregation-diffusion equation*² for low population density, *i.e.*, in the case where the probability, p , that one individual of the population is at point x at time t , satisfies $p \ll 1$:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[\phi'(u) \frac{\partial u}{\partial x} \right], \quad (12)$$

where $\phi(u) = (\mu/2)u - k_0u^2 + (2k_0)/(3\omega)u^3$. Turchin used the above equation to describe the aggregative movement of *Aphis varians*, a herbivore of fireweeds (*Epilobium angustifolium*). He also discussed the ill-posedness of an initial and boundary value problem associated with 12. Depending on the actual profile of ϕ , Turchin also classified in terms of *weakly aggregative* and *strongly aggregative* the different types of aggregation.

In this paper we provide an alternative derivation (for low population density) of the equation by considering the dependence of k on p prior to arriving at the diffusion approximation. The result is a slightly different equation to that derived by Turchin. In Section 2, we use a biased random walk approach to build a model to describe a direct aggregation phenomenon among individuals of one species living in a one-dimensional habitat. In Section 3 we study the existence of traveling wave solutions (t.w.s.) for a purely negative or zero diffusion equation with a logistic rate of growth. Here we include some numerical simulations on the phase portrait of the traveling wave variables. In section 4 we solve numerically a couple of initial and boundary value problems associated with two nonlinear equations where the density-dependent diffusion term is less than or equal to zero and the reactive part describes logistic growth. In Section 5 we discuss the well- and ill-posedness of certain boundary conditions associated with some purely negative diffusion equations with logistic-like kinetic part. These problems come from the analysis of existence of t.w.s. for these equations. The paper ends with section 6 where we present some conclusions and discussion.

2. Construction of the model and a comparison. Here we consider one species living in a one-dimensional habitat. To derive the model we follow a biased random walk approach plus a diffusion approximation. Thus we firstly discretize space in a regular manner. We let the distance between two successive points of the mesh be λ , and we denote by $p(x, t)$ the probability that any individual of the population is at the point x at time t . During a time period τ an individual which at time t is at position x , can either:

1. move to the right of x to the point $x + \lambda$, with probability $R(x, t)$, or
2. move to the left of x to the point $x - \lambda$, with probability $L(x, t)$ or
3. stay at the position x , with probability $N(x, t)$.

Because we allow no other possibilities of movement we have

$$N(x, t) + R(x, t) + L(x, t) = 1. \quad (13)$$

As a consequence of the above assumptions in [43], we have:

²It should be noted that in [43], $k(u)$ was introduced after the derivation of the diffusion approximation. However, including it before the approximation leads to a different form of equation to that derived in [43].

$$R(x, t) = \frac{1}{2}r(x, t) + kp(x + \lambda, t)$$

$$L(x, t) = \frac{1}{2}r(x, t) + kp(x - \lambda, t),$$

where r is the random component of the movement.

The meaning of the product kp in the above expressions is as follows: Let us consider $R(x, t)$: given that there is one conspecific to the right, $kp(x + \lambda, t)$ measures the probability of occurrence of the event: the individual moves and does so to the right.

In the above terms, the probability $p(x, t)$ can be written as follows:

$$p(x, t) = N(x, t - \tau)p(x, t - \tau) + R(x - \lambda, t - \tau)p(x - \lambda, t - \tau) + L(x + \lambda, t - \tau)p(x + \lambda, t - \tau). \quad (14)$$

Now, by using Taylor series, we obtain the well-known equation (see [28]) for p :

$$\tau \frac{\partial p}{\partial t} = -\lambda \frac{\partial}{\partial x} \{\beta(x, t)p(x, t)\} + \frac{\lambda^2}{2} \frac{\partial^2}{\partial x^2} \{\mu(x, t)p(x, t)\} + O(\lambda^3), \quad (15)$$

where $\beta(x, t) \equiv R(x, t) - L(x, t)$ and $\mu(x, t) \equiv R(x, t) + L(x, t)$ are, respectively: the *bias* and the *motility*. The above equation is sufficiently general to describe different types of random-biased movements. In order to arrive at an equation which describes the more specific movements in which we are interested, we must write the probabilities R and L into β and μ , in such a way that they take into account the assumptions stated above. In particular, the conditional probability, k , must depend on p , *i.e.*, $k = k(p)$. In ecological terms, the function k must reflect the behavioral aspects of the individuals of the species. In our derivation we assume that k is a sufficiently smooth function of p . Thus, the probabilities R and L can be re-written as follows:

$$R(x, t) = \frac{1}{2}r(x, t) + k(p(x + \lambda, t))p(x + \lambda, t) \quad (16)$$

and

$$L(x, t) = \frac{1}{2}r(x, t) + k(p(x - \lambda, t))p(x - \lambda, t), \quad (17)$$

respectively. Thus the bias and the motility are transformed as follows:

$$\beta(x, t) = R(x, t) - L(x, t) = k(p(x + \lambda, t))p(x + \lambda, t) - k(p(x - \lambda, t))p(x - \lambda, t) \quad (18)$$

and

$$\mu(x, t) = R(x, t) + L(x, t) = r(x, t) + k(p(x + \lambda, t))p(x + \lambda, t) + k(p(x - \lambda, t))p(x - \lambda, t). \quad (19)$$

Now we expand k and p in Taylor series (around (x, t)) up to the linear terms in both previous expressions. Thus, we have the following linear approximations:

$$\beta(x, t) = 2\lambda \frac{\partial}{\partial x} [k(p(x, t))p(x, t)] \quad (20)$$

and

$$\mu(x, t) = r(x, t) + 2k(p(x, t))p(x, t), \quad (21)$$

respectively. Now, we substitute 20 and 21 into 15, use the *diffusion approximation*, i.e., we assume that $\lambda^2/(2\tau) \rightarrow D > 0$ (finite) as $\tau, \lambda \rightarrow 0$, and writing down the result in a more tractable and transparent form, we obtain the *aggregation-diffusion-equation*

$$\frac{\partial p}{\partial t} = D \left[r - 2p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} - 2D \left[2p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2 + D \left(2 \frac{\partial p}{\partial x} \frac{\partial r}{\partial x} + p \frac{\partial^2 r}{\partial x^2} \right). \quad (22)$$

This equation differs from that derived in [43] as we claimed before (see footnote 2).

Nevertheless (for comparison with our calculations carried out in previous paragraphs and with Turchin's) note that if we keep a constant random component, r , then equation 22 reduces to

$$\frac{\partial p}{\partial t} = D \left[r - 2p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} - 2D \left[2p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2, \quad (23)$$

which, by setting $\mathcal{D}(p) = D \left[r - 2p^2 \frac{dk}{dp} \right]$, can be written as the more familiar density-dependent diffusion equation (see [36] and [37])

$$\frac{\partial p}{\partial t} = \mathcal{D}(p) \frac{\partial^2 p}{\partial x^2} + \mathcal{D}'(p) \left[\frac{\partial p}{\partial x} \right]^2 = \frac{\partial}{\partial x} \left[\mathcal{D}(p) \frac{\partial p}{\partial x} \right]. \quad (24)$$

This equation contains, as a particular case, that used in [43] to describe the aggregation of *Aphis varians*. In fact, one can verify that taking $k(p) = a \ln p - bp + c_1$, where a, b are such that $Da = k_0$, $Db = k_0/\omega$, $Dr = \mu/2$ and c_1 is any positive number, one obtains 12. Note that choosing k in this way, the “density-dependent diffusion coefficient” $\mathcal{D}(p) = D[r - 2ap + 2abp^2]$ is negative for all $p \in (p_1, p_2)$ and positive otherwise, where p_1 and p_2 are the roots of \mathcal{D} .

To draw a closer comparison with our equation, we now briefly review Turchin's derivation. One of the key differences between our derivation and that given by Turchin is that he does not substitute both linear approximations 20 and 21 of β and μ , respectively, into 15 before carrying out the diffusion approximation. In fact, he only substitutes 20 into 15 to obtain

$$\begin{aligned} \tau \frac{\partial p}{\partial t} = & -2\lambda^2 \left\{ \left[kp + p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} + \left[k + 3p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2 \right\} \\ & + \frac{\lambda^2}{2} \{ \mu(x, t)p(x, t) \} + O(\lambda^3). \end{aligned} \quad (25)$$

After some calculation this equation can be written as

$$\begin{aligned} \tau \frac{\partial p}{\partial t} = & -2\lambda^2 \left\{ \left[-\frac{\mu}{4} + kp + p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} + \left[k + 3p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2 \right\} \\ & + \frac{\lambda^2}{2} \left\{ 2 \frac{\partial p}{\partial x} \frac{\partial \mu}{\partial x} + p \frac{\partial^2 \mu}{\partial x^2} \right\} + O(\lambda^3). \end{aligned} \quad (26)$$

To pass to the diffusion approximation, we assume that $\frac{\lambda^2}{\tau} \rightarrow D > 0$ (finite), as λ and τ tend to zero. Equation 26 then becomes

$$\begin{aligned} \frac{\partial p}{\partial t} = 2D \left[\frac{\mu}{4} - kp - p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} - 2D \left[k + 3p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2 \\ + \frac{D}{2} \left\{ 2 \frac{\partial p}{\partial x} \frac{\partial \mu}{\partial x} + p \frac{\partial^2 \mu}{\partial x^2} \right\}. \end{aligned} \quad (27)$$

Consider the particular case in which we have space independent motility, *i.e.*, $\mu_x \equiv 0$. Then equation 27 reduces to

$$\frac{\partial p}{\partial t} = 2D \left[\frac{\mu}{4} - kp - p^2 \frac{dk}{dp} \right] \frac{\partial^2 p}{\partial x^2} - 2D \left[k + 3p \frac{dk}{dp} + p^2 \frac{d^2 k}{dp^2} \right] \left(\frac{\partial p}{\partial x} \right)^2. \quad (28)$$

If we write $k(p) = b + mp$ with $b > 0$ and $m < 0$ (as in Turchin's paper) this equation becomes

$$\frac{\partial p}{\partial t} = \left[\frac{D\mu}{2} - 2Dbp - 4Dmp^2 \right] \frac{\partial^2 p}{\partial x^2} + [-2Db - 8Dmp] \left(\frac{\partial p}{\partial x} \right)^2, \quad (29)$$

or,

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x} \left[\mathcal{D}(p) \frac{\partial p}{\partial x} \right], \quad (30)$$

where $\mathcal{D}(p) = \frac{D\mu}{2} - 2Dbp - 4Dmp^2$. Equation 30 coincides with Turchin's model by putting $D = 1$. Again, this equation has the general form 24.

Also note that equation 30 has an important feature for appropriate values of the parameters: For positive values of b satisfying $b^2 > -2m\mu$, equation 30 has negative density-dependent diffusion coefficient for all $p \in (p_1, p_2)$ where p_1 and p_2 are the roots of $\mathcal{D}(p)$, *i.e.*, they are given by³

$$p_1, p_2 = \frac{1}{4m} \left\{ -b \pm \sqrt{b^2 + 2m\mu} \right\}. \quad (31)$$

In fact equation 30 degenerates at $p = p_1, p_2$.

In addition to the aggregation or spread factors one can consider a non-linear growth rate g to obtain the equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[D(u) \frac{\partial u}{\partial x} \right] + g(u). \quad (32)$$

Whenever $D(u) < 0$ we call 32 a *reaction-aggregation equation*, while if D possesses both (positive and negative) signs we will call it a *reaction-aggregation ($D < 0$)-diffusion ($D > 0$) equation*.

In section 3 we will focus on equations where $D \leq 0$ within the domain of interest.

³Given the ecological interpretation of p the negative root has no sense. We mention it for completeness.

3. On the existence of aggregative traveling waves. Among the possible spatial patterning models for aggregation, here we study the existence of traveling wave solutions (t.w.s.) $u(x, t) = \phi(x - ct) \equiv \phi(\xi)$ connecting the stationary and homogeneous states⁴ $u(x, t) \equiv 1$ and $u(x, t) \equiv 0$ for the degenerate reaction-aggregation equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[D(u) \frac{\partial u}{\partial x} \right] + g(u), \quad \forall (x, t) \in \mathbb{R} \times \mathbb{R}^+, \quad (33)$$

where D and g are defined on $[0, 1]$ and satisfy the following conditions:

1. $g(0) = g(1) = 0$, $g(u) > 0 \forall u \in (0, 1)$,
2. $g \in C^2_{[0,1]}$, $g'(0) > 0$, $g'(1) < 0$,
3. $D(0) = 0$, $D(u) < 0 \forall u \in (0, 1]$,
4. $D \in C^2_{[0,1]}$, $D'(u) < 0 \forall u \in (0, 1]$, and $D''(u) < 0 \forall u \in [0, 1]$. In addition we distinguish the following two cases: **a)** $D'(0) = 0$ with $D'(u) < 0$ for all $u \in (0, 1]$ and **b)** $D'(u) < 0$ for all $u \in [0, 1]$.

We also require the conditions: $u(x, 0) = u_0(x)$ with $0 \leq u_0(x) \leq 1 \forall x \in \mathbb{R}$, $0 \leq u(x, t) \leq 1 \forall (x, t) \in \mathbb{R} \times \mathbb{R}^+$.

Note that the condition $0 \leq u_0(x) \leq 1 \forall x \in \mathbb{R}$ on the initial data comes from the physical interpretation of the steady and homogeneous states 0 and 1. For example, from an ecological point of view, we can interpret the state $u(x, t) \equiv 1$ as a measure of the maximum population density sustainable in the medium while $u(x, t) \equiv 0$ is the state where there is no population. Hence we require the restriction $0 \leq u(x, t) \leq 1 \forall (x, t) \in \mathbb{R} \times \mathbb{R}^+$ on the state variable u . As we will see, this condition does not hold for any positive value of c .

We also note that, because of assumption 3., the non-linear diffusion equation 33 is no longer of parabolic type. This can be seen by noting that the function

$$F\left(u, \frac{\partial u}{\partial x}, \frac{\partial^2 u}{\partial x^2}\right) \equiv D(u) \frac{\partial^2 u}{\partial x^2} + D'(u) \left[\frac{\partial u}{\partial x} \right]^2 + g(u),$$

is not elliptic with respect to its third argument. Therefore the non-linear operator

$$L[u] \equiv F\left(u, \frac{\partial u}{\partial x}, \frac{\partial^2 u}{\partial x^2}\right) - \frac{\partial u}{\partial t},$$

⁴This imposes the following boundary conditions $\lim_{\xi \rightarrow -\infty} \phi(\xi) = 1$ and $\lim_{\xi \rightarrow +\infty} \phi(\xi) = 0$.

is not parabolic⁵. Also equation 33 degenerates at $u = 0$. It is a *simple degeneration* when $D(0) = 0$ but $D'(0) \neq 0$ and *double doubly degenerate* when $D(0) = D'(0) = 0$. By using the above we can conclude that Turchin's equation 12 is not of parabolic type on the interval (p_1, p_2) and has simple degeneracy at $u = p_1, p_2$. Here p_1 and p_2 are the roots of ϕ' in equation 12.

We can now begin the one-dimensional t.w.s. analysis for equation 33 by stating that if this equation possesses a traveling wave connecting the homogeneous stationary states $u(x, t) \equiv 1$ and $u(x, t) \equiv 0$, then $c > 0$. This can be shown in a similar way to that in [36].

By assuming that for $c > 0$, $u(x, t) = \phi(x - ct)$ is a solution of 33 we substitute it into that equation to obtain the non-linear second order ODE

$$D(\phi)\phi''(\xi) + D'(\phi)[\phi'(\xi)]^2 + c\phi'(\xi) + g(\phi) = 0, \quad \forall \xi \in (-\infty, +\infty), \quad (34)$$

where the dash on D denotes derivative with respect to ϕ while the dash on ϕ denotes derivative with respect to ξ , with the boundary conditions $\phi(-\infty) = 1$ and $\phi(+\infty) = 0$. In addition, we require $0 \leq \phi(\xi) \leq 1$ for all ξ . Now we follow the classical approach in investigating the existence of t.w.s. of a PDE introduced by Kolmogorov *et al.* ([21]). This consists of re-stating the problem 33 in terms of finding the set of parameters for which there exist homoclinic or heteroclinic trajectories of an ODE system. Thus, by setting $\phi' = v$ the above equation can be written as the following singular (at $\phi = 0$) ODE system

$$\begin{aligned} \phi' &= v \\ D(\phi)v' &= -cv - D'(\phi)v^2 - g(\phi). \end{aligned} \quad (35)$$

Here we remove the singularity by using a standard reparametrization (see [6] and [36]) of the above system, which **preserves the orientation** of the corresponding trajectories. Let τ be such that

$$\frac{d\tau}{d\xi} = -\frac{1}{D(\phi(\xi))}. \quad (36)$$

In terms of τ , system 35 can be written as the following non-singular system

$$\begin{aligned} \dot{\phi} &= -D(\phi)v \equiv f_1(\phi, v) \\ \dot{v} &= cv + D'(\phi)v^2 + g(\phi) \equiv f_2(\phi, v), \end{aligned} \quad (37)$$

where the dot on ϕ and on v means derivative with respect to τ .

⁵For this characterization we have used a standard classification for second order PDEs, in particular for nonlinear equations of the form considered in this paper. This is the precise definition (see [31]).

Let $F(\vec{x}, t, u, \vec{p}, \vec{R})$ be a continuous differentiable function of its $n^2 + 2n + 2$ variables. F is *elliptic* with respect to $u(\vec{x}, t)$ at a given point (\vec{x}, t) if, for all real vectors $\vec{\xi} = (\xi_1, \xi_2, \dots, \xi_n)$, we have

$$\sum_{i,j=1}^n \frac{\partial F}{\partial r_{ij}} \xi_i \xi_j > 0, \quad \text{for } \vec{\xi} \neq \vec{0},$$

where $p_i = \partial u / \partial x_i$ and $r_{ij} = \partial^2 u / \partial x_i \partial x_j$. Accordingly, the nonlinear operator

$$L[u] \equiv F\left(\vec{x}, t, u, \frac{\partial u}{\partial x_i}, \frac{\partial^2 u}{\partial x_i \partial x_j}\right) - \frac{\partial u}{\partial t},$$

is said to be *parabolic* whenever F is elliptic.

Depending on the local profile (at $u = 0$) of the diffusion coefficient D , the system [37](#) has different dynamics. We consider two separate cases:

Case 1. g satisfies 1-2 and D satisfies 3-4a). Here [37](#) has two “finite” equilibrium points: $P_0 = (0, 0)$ and $P_1 = (1, 0)$. Note that for $D'(0) = 0$, $(0, +\infty)$ is also an equilibrium for [37](#).

Local Analysis:

Given that the eigenvalues of the Jacobian, $J[f_1, f_2]_{(0,0)}$, of the system [37](#) at P_0 are $\lambda_1 = 0$ and $\lambda_2 = -c$, then this equilibrium is a non-hyperbolic point. The corresponding eigenvectors are

$$\vec{v}_1 = (1, -g'(0)/c)^T \quad \text{and} \quad \vec{v}_2 = (0, 1)^T.$$

The implication of the non-hyperbolicity of P_0 is that, because of the Hartman-Grobman theorem, the local dynamics (around P_0) of [37](#) is not topologically equivalent to the dynamics of the linear system defined by $J[f_1, f_2]_{(0,0)}$ (see [\[8\]](#)). In such a case, the local phase portrait of [37](#) can be obtained by carrying out a non-linear local analysis, which is based on the *center manifold theorem*. This, in addition to other things, says that the local dynamics around a non-hyperbolic equilibrium, is determined by the dynamics around the center manifold of the system. The existence of such a center manifold is also guaranteed. Here we are not including the details as the basic ideas of the analysis can be seen elsewhere ([\[35\]](#)). For our purposes, it is sufficient to say that the non-linear local analysis shows that P_0 is a *non-hyperbolic saddle-like* point for all $c > 0$ where the unstable *non-hyperbolic manifold* is the vertical axis and the *one-dimensional center manifold* (which is stable) is locally tangent to \vec{v}_1 .

The linear analysis implies that P_1 is a hyperbolic point with different features depending on the speed c . In fact, we have:

1. For $c^2 \geq 4g'(1)D(1)$, P_1 is an unstable node. Here the eigenvalues of the Jacobian matrix, $J[f_1, f_2]_{(1,0)}$ are $\lambda_1 = \left(c + \sqrt{c^2 - 4g'(1)D(1)}\right)/2$ and $\lambda_2 = \left(c - \sqrt{c^2 - 4g'(1)D(1)}\right)/2$. The corresponding eigenvectors are

$$\vec{v}_1 = (1, -\lambda_1/D(1))^T \quad \text{and} \quad \vec{v}_2 = (1, -\lambda_2/D(1))^T.$$

Note that for $c^2 = 4g'(1)D(1)$ the point P_1 is a degenerate node. Consequently we have a damped (non-oscillatory) behavior around P_1 implying that the condition $0 \leq \phi(\xi) \leq 1$ for all ξ is violated.

2. For $c^2 < 4g'(1)D(1)$, P_1 is an unstable focus. In this case, the local phase portrait of system [37](#) consists of oscillatory trajectories around P_1 . Again, the bounds on ϕ do not hold for these values of c .

Global Analysis:

For this end we need the null-clines of the system [37](#). The horizontal ($\dot{\phi} = 0$) null-cline consists of the vertical ($\phi \equiv 0$) and the horizontal ($v \equiv 0$) axes. The vertical ($\dot{v} = 0$) null-cline has two branches:

$$V_1(\phi) = \frac{-c + \sqrt{c^2 - 4D'(\phi)g(\phi)}}{2D'(\phi)} \quad \text{and} \quad V_2(\phi) = \frac{-c - \sqrt{c^2 - 4D'(\phi)g(\phi)}}{2D'(\phi)}. \quad (38)$$

For this case we have: $\lim_{\phi \rightarrow 0^+} V_1(\phi) = 0$, $V_1(1) = 0$, $V_1(\phi) < 0 \forall \phi \in (0, 1)$. $\lim_{\phi \rightarrow 0^+} V_2(\phi) = +\infty$, $V_2(1) = -c/D'(1)$, $V_2(\phi) > 0 \forall \phi \in (0, 1)$.

Additionally, one can verify that in both cases (1 and 2), for positive values, c_1 and c_2 , of c with $c_1 < c_2$, the corresponding branches $V_i^{c_j}$ with $i, j = 1, 2$ are related as follows: $V_1^{c_1}(\phi) < V_1^{c_2}(\phi)$ and $V_2^{c_1}(\phi) < V_2^{c_2}(\phi)$ for all $\phi \in (0, 1]$.

For Case 1 the qualitative behavior of V_1 and V_2 as c changes is as shown in Figure 1.

Now let us consider the coordinate system generated by the basis $\{\vec{v}_1, \vec{v}_2\}$ at P_1 . This set of vectors generates the main directions on the phase portrait. For all positive values of c such that $c^2 > 4g'(1)D(1)$, the trajectories of (37) leaving P_1 have \vec{v}_2 as tangent vector. Actually, we are only interested in those trajectories of (37) which, once they have left P_1 , enter the region $\mathcal{R} = \{(\phi, v) | 0 \leq \phi \leq 1, v \leq 0\}$. Moreover, let us consider that trajectory of (37) whose path can be approximated (around P_1) by the linear relationship $v(\phi) = -\frac{\lambda_2}{D(1)}(\phi - 1)$. It can be seen that this trajectory leaves P_1 below the graph of V_1 . In a small neighborhood of P_1 , the path of v and the graph of V_1 , are close for sufficiently large values of c .

Given that for all positive values of c , P_1 is unstable (node or focus), it follows that the system (37) has no heteroclinic trajectory coming from P_0 and ending at P_1 . For the same reason there is no trajectory coming from $(0, +\infty)$ and ending at P_1 .

By considering all the above analysis, we are at the point of drawing an analogy between the t.w.s. analysis for the classical Fisher-KPP equation $u_t = u_{xx} + g(u)$ and ours. For this goal, the key result is the following proposition.

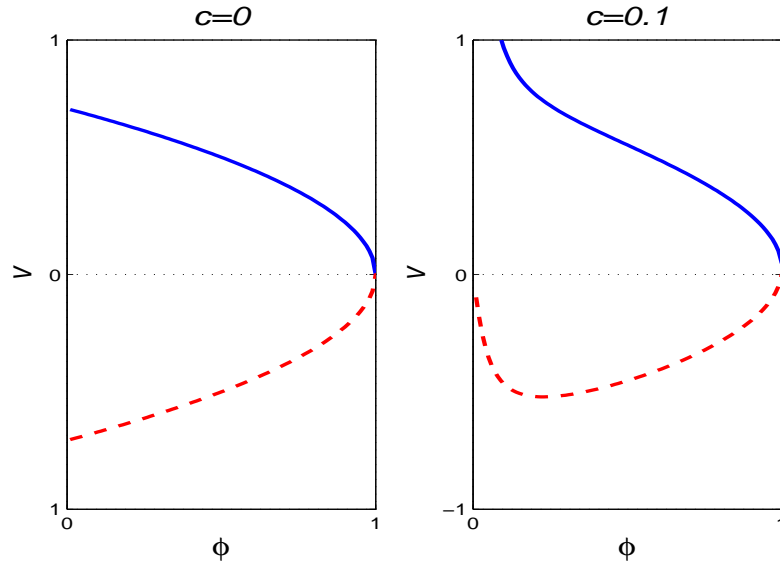
Proposition 1. *The system (37), with D and g as in Case 1, has a heteroclinic trajectory connecting P_1 with P_0 (in this order) for $c > 0$ if and only if the system*

$$\begin{aligned} \dot{\phi} &= D(\phi)v \\ \dot{v} &= -cv - D'(\phi)v^2 - g(\phi), \end{aligned} \quad (39)$$

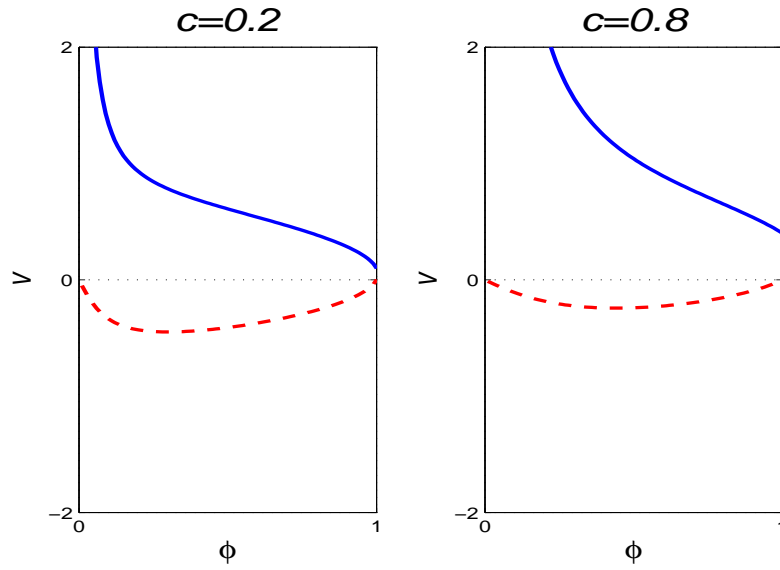
for the same value of c , has a heteroclinic trajectory connecting P_0 with P_1 (in this order).

Proof. Suppose that for $c > 0$, $(\phi_c(\tau), v_c(\tau))$ is the trajectory of (37) connecting P_1 with P_0 , i.e., satisfying the boundary conditions $(\phi_c(-\infty), v_c(-\infty)) = (1, 0)$ and $(\phi_c(+\infty), v_c(+\infty)) = (0, 0)$. We claim that the trajectory $(\tilde{\phi}_c(\tau), \tilde{v}_c(\tau)) \equiv (\phi_c(-\tau), v_c(-\tau))$ is the corresponding trajectory of the system (39) connecting P_0 with P_1 . It is easy to verify that $(\tilde{\phi}_c(\tau), \tilde{v}_c(\tau))$ is a solution of the system (39). Moreover, given that time for this system is in the reverse sense compared with that of (37), the boundary conditions for $(\tilde{\phi}_c(\tau), \tilde{v}_c(\tau))$ are as they are stated in the proposition. One can verify the reverse reasoning in a straightforward way. Hence the proof follows. \square

Recall that, in the classical Fisher-KPP t.w.s. analysis on the appropriate phase portrait, for each $c \geq c_0 = 2\sqrt{g'(0)}$ it is possible to choose a positive number m in such a way that the triangle \mathcal{T} with boundaries: the segments $0 \leq \phi \leq 1$, $v_0 \leq v \leq 0$, and $v(\phi) = -m\phi$ where $v_0 = v(1) = -m$, is a positive invariant set for the ODE system $\phi' = v$, $v' = -cv - g(\phi)$. Therefore, by a direct consequence of the Poincaré-Bendixson theorem, for each $c \geq c_0$ the trajectory leaving P_1 (which is a hyperbolic saddle point for all $c > 0$) through the left unstable manifold and entering the set \mathcal{T} , ends at P_0 (which, for $c > 2\sqrt{g'(0)}$, is a stable node) as ξ tends to $+\infty$.



(a)



(b)

FIGURE 1. Behavior of the vertical null-clines of 37 for Case 1, as c changes. The dashed line is that of V_2 for four values of c ; the solid line corresponds to that for V_1 for the same values of c . Here we consider $D(\phi) = -\phi^2$ and $g(\phi) = \phi(1 - \phi)$. (a) For small values of c ($c = 0$ and $c = 0.1$). (b) For larger values of c ($c = 0.2, 0.8$). Note that the graph of V_1 tends to the horizontal axis for large values of c .

In our case, the positions of the equilibria are not the same (they are inverted compared with the Fisher-KPP equation) but the required local behavior and all the additional properties of the vertical null-cline, the relative position of the main direction and the vertical null-cline at P_1 (in terms of Proposition 1) are the same. Additionally, because of the stronger non-linearities in our system, we do not suspect that the positive invariant set for 39 will be as simple as a triangle. To construct the appropriate set, let us consider a $C^1_{[0,1]}$ function f , such that: a) $f < 0 \ \forall \ \phi \in (0, 1)$, $f(0) = v_0 < 0$, $f(1) = 0$, b) $f' > 0 \ \forall \ \phi \in [0, 1]$ with $f'(1) > -\lambda_2/D(1)$.

The following reasoning is close to that given by Haderer (see [18]). For this we define the region \mathcal{R}_f as follows: $\mathcal{R}_f = \{(\phi, v) | 0 < \phi < 1, \ f(\phi) \leq v \leq 0\}$. We have the following proposition:

Proposition 2. *For functions f with the properties listed above, there exist positive values of c such that the region \mathcal{R}_f is a positive invariant set for the system 39.*

Proof. We denote by $\vec{N}_{int} = (-f'(\phi), 1)$ the normal vector to the graph of f at $(\phi, f(\phi))$ pointing inwards towards \mathcal{R}_f (see Figure 2).

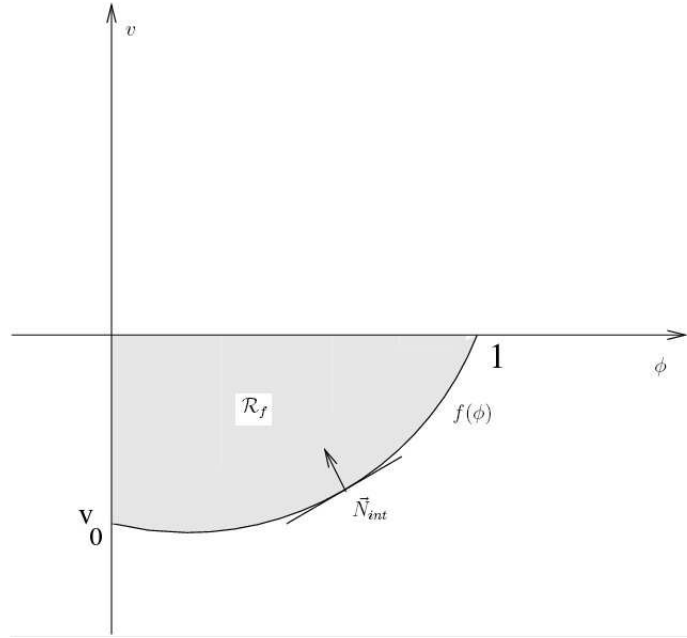


FIGURE 2. Proof of Proposition 2. For appropriate function f , the region \mathcal{R}_f is a positive invariant set for system 39. See text for details.

We now restrict the vector field defined by 39 on the graph of f . The restriction results in the system

$$\begin{aligned} \dot{\phi} &= D(\phi)f(\phi) \\ \dot{v} &= -cf(\phi) - D'(\phi)[f(\phi)]^2 - g(\phi). \end{aligned} \quad (40)$$

Given that on the segment $0 < \phi < 1$ the vector field defined by 40 points inwards on \mathcal{R}_f , the proposition follows if we choose values of c such that the inner product

$\vec{N}_{int} \cdot (\dot{\phi}, \dot{v})$ is greater than or equal to zero on the graph of f for all $\phi \in (0, 1)$. A simple calculation gives us

$$\vec{N}_{int} \cdot (\dot{\phi}, \dot{v}) = -(D(\phi)f(\phi)f'(\phi) + cf(\phi) + D'(\phi)(f(\phi))^2 + g(\phi)).$$

We need $(\vec{N}_{int} \cdot (\dot{\phi}, \dot{v})) \geq 0$. This happens if, for $\phi \in (0, 1)$, we take c such that

$$c \geq -\frac{d}{d\phi} [D(\phi)f(\phi)] - \frac{g(\phi)}{f(\phi)}.$$

Moreover

$$c \geq \sup \left\{ -\frac{d}{d\phi} [D(\phi)f(\phi)] - \frac{g(\phi)}{f(\phi)} \right\},$$

where the *supremum* is taken on $\phi \in (0, 1)$. In fact, if now we consider the set of functions f as above, the following condition on c characterizes the lowest value, c_0 , of c for which \mathcal{R}_f is a positive invariant set for 39,

$$c_0 = \inf \sup \left\{ -\frac{d}{d\phi} [D(\phi)f(\phi)] - \frac{g(\phi)}{f(\phi)} \right\}, \quad (41)$$

where the *infimum* is taken on the set of functions f . Then the proposition follows. \square

By using Propositions 1 and 2, we conclude:

Proposition 3. *For each $c > 0$ such that $c \geq c_0$ where c_0 satisfies 41 and for functions D and g as in Case 1, the system 37 has a heteroclinic trajectory connecting the equilibrium P_1 with P_0 .*

Remark 1. In order to remove the singularity at $\phi = 0$ we have re-parametrized the system 35. To make explicit the analogy with the Fisher-KPP t.w.s. analysis we consider the system 39 whose trajectories run in opposite directions to those of 37. Note that we could have carried out a simple reparametrization for doing both things simultaneously.

Remark 2. For a given f , a comparison between the values c_0 and $2\sqrt{g'(1)D(1)}$ can be useful to determine which type of connections the system 37 could have. Our numerical simulations (see Examples 1 and 2) strongly suggest that the set $\{c > 0 | c^2 > 4g'(1)D(1)\}$ is contained in the set $\{c | c \geq c_0\}$. Also, these simulations show that the set $\{c | 0 < c < 2\sqrt{g'(1)D(1)}\}$ is part of the above mentioned set.

We can summarize the above analysis by stating the following lemma:

Lemma 3.1. *If the functions D and g satisfy the conditions mentioned in Case 1, then for each positive value of c such that $c > c_0$, where c_0 satisfies 41, the equation 33 has a t.w.s. which is:*

1. *of monotone decreasing front type connecting the states $u(x, t) \equiv 1$ and $u(x, t) \equiv 0$ if c satisfies the additional condition $c^2 > 4g'(1)D(1)$. Here ϕ satisfies the condition $0 \leq \phi \leq 1$ for all values of its argument;*
2. *of oscillatory (around the state $u(x, t) \equiv 1$) type connecting the states $u(x, t) \equiv 1$ and $u(x, t) \equiv 0$, for $c > 0$ satisfying the additional condition $c^2 < 4g'(1)D(1)$. Here the bounds, $0 \leq \phi \leq 1$, for ϕ are violated;*

3. a damped (around $u(x, t) \equiv 1$) t.w.s. connecting $u(x, t) \equiv 1$ and $u(x, t) \equiv 0$ for $c > 0$ satisfying the extra condition $c^2 = 4g'(1)D(1)$. Again, here the bounds on ϕ are violated.

To illustrate the t.w.s. dynamics involved, we consider the following example:

Example 1. The simplest equation satisfying the conditions in Case 1 is

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[-u^2 \frac{\partial u}{\partial x} \right] + u(1 - u). \quad (42)$$

The corresponding system [37](#) is

$$\begin{aligned} \dot{\phi} &= \phi^2 v \\ \dot{v} &= cv - 2\phi v^2 + \phi(1 - \phi). \end{aligned} \quad (43)$$

The phase portrait of system [43](#) is shown in Figure [3](#). This shows the different heteroclinic trajectories of [43](#) as c varies.

Thus we have the different types of aggregation t.w.s. for equation [42](#), namely: monotonic fronts (corresponding to the node-saddle-like heteroclinic trajectory), damped fronts and damped oscillatory fronts (associated with the focus-saddle-like connection), depending on the values of c . These are illustrated in Figure [3](#). Note the damped behavior in the back of the t.w.s. in Figures [4\(a\)](#) and [4\(b\)](#).

Case 2. g satisfies [1-2](#) and D satisfies [3-4b](#)). (see these conditions at the beginning of Section [3](#)) Here, in addition to P_0 and P_1 , the system [37](#) has a third equilibrium point: $P_c = (0, v_c) = (0, -c/D'(0))$ which, because of the condition $D'(0) \neq 0$, comes from $(0, +\infty)$ (see Case 1). Note that P_c moves away monotonically on the positive vertical axis as c increases.

Part of the analysis carried out in Case 1 holds here. Thus, except where there are major differences, we do not go into great detail for this case.

Local Analysis:

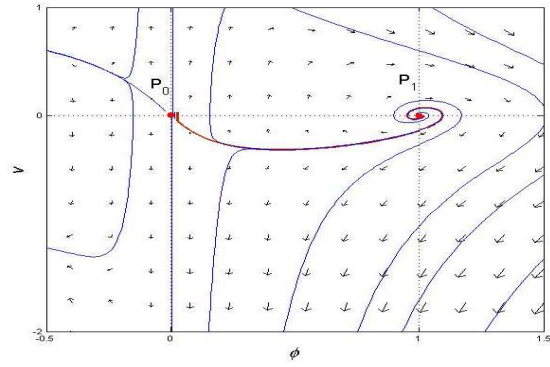
The linear local analysis shows that for all positive values of c , P_c is a hyperbolic saddle point where the eigenvalues of the Jacobian matrix $J[f_1, f_2]_{(0, v_c)}$ are $\lambda_1 = c$ and $\lambda_2 = -c$. The corresponding eigenvectors are $\vec{v}_1 = (1, r/2c)^T$ and $\vec{v}_2 = (0, 1)^T$, where $r = \left[\frac{D''(0)c^2}{(D'(0))^2} + g'(0) \right]$. Note that, depending on the values of c , the local unstable manifold of [37](#) at P_c has a different slope which varies as follows: it is zero for $c^2 = \frac{-g'(0)(D'(0))^2}{D''(0)}$, it is negative for $c^2 > \frac{-g'(0)(D'(0))^2}{D''(0)}$ and it is positive when this last inequality is reversed.

P_0 is a non-hyperbolic point. The non-linear local analysis around P_0 implies that this equilibrium is a *saddle-node* point with the saddle-like sector to the right of P_0 and the node-like region to the left. The behavior of the trajectories of [37](#) around P_1 is the same as in Case 1, *i.e.*, they depend on the values of c as was stated in that case.

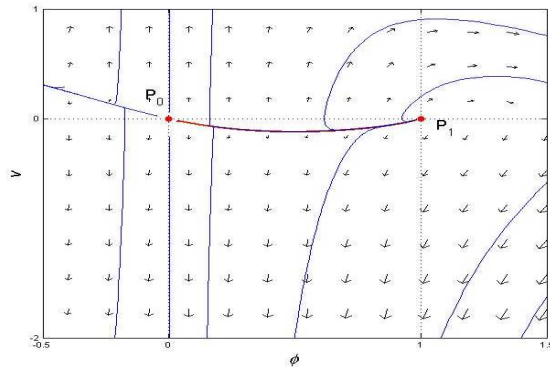
Global Analysis:

The ϕ null-clines are the same as in Case 1. One can verify: $V_1(0) = 0$, $V_1(1) = 0$, $V_1(\phi) < 0 \forall \phi \in (0, 1)$; meanwhile for V_2 , we have: $V_2(0) = -c/D'(0)$, $V_2(1) = -c/D'(1)$ and $V_2(\phi) > 0 \forall \phi \in (0, 1)$. Here the qualitative behavior of the v null-clines [38](#) of the system [37](#) as c changes is shown in Figure [5](#).

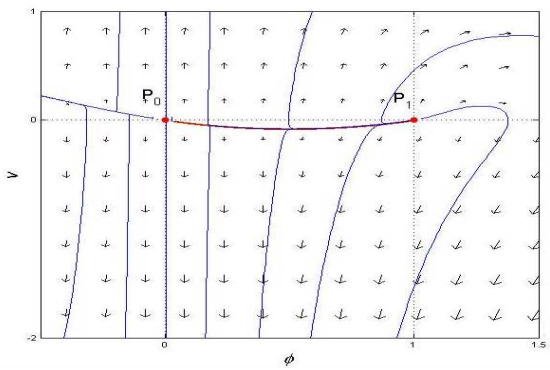
The following proposition holds:



(a)

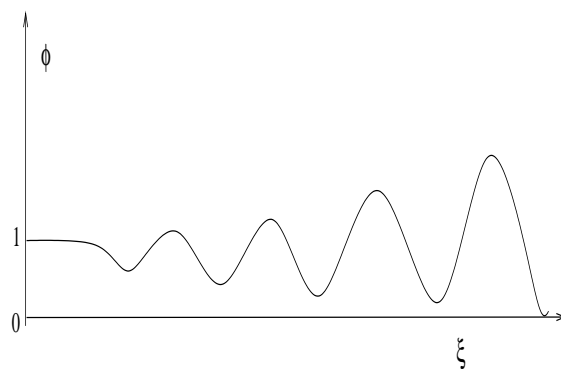


(b)

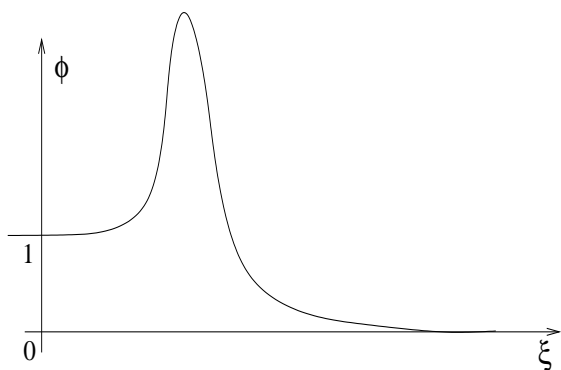


(c)

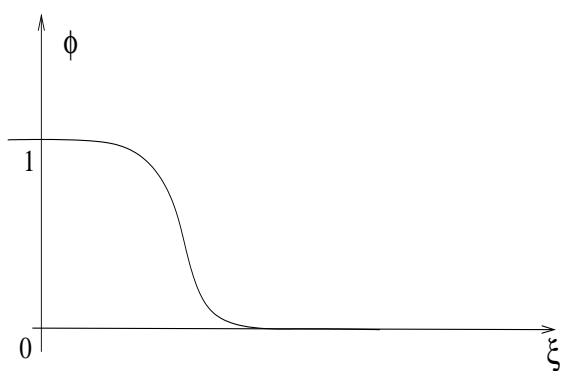
FIGURE 3. Phase portrait for [43](#) for different values of c : (a) $c = 0.5$, (b) $c = 2.0$ and (c) $c = 3.0$. The heteroclinic connections in (a) and (b) violate the bounds of ϕ . See text for details.



(a)



(b)



(c)

FIGURE 4. Different aggregative t.w.s. of front type for equation 42: (a) oscillatory front, (b) damped front and (c) monotonic front. The cases (a) and (b) violate the condition $0 \leq \phi(\xi) \leq 1$ on ϕ .

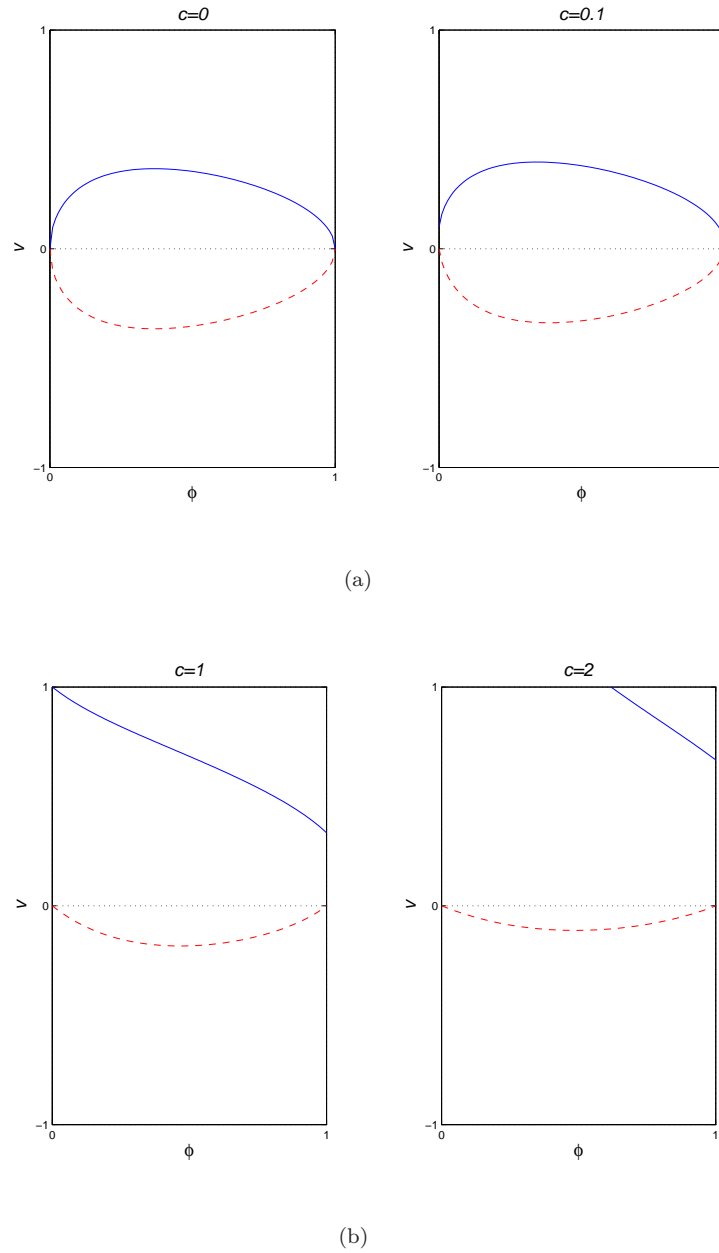


FIGURE 5. Behavior of the v -null-clines of 37 for Case 2 as c changes. Here, by way of example, we take $D(\phi) = -(2\phi + \phi^2)$ and $g(\phi) = \phi(1 - \phi)$. (a) For small values of c ($c = 0, 0.1$). (b) For bigger values of c ($c = 1, 2$). For large c the graph of V_1 (dashed line) tends to the horizontal axis. The continuous line corresponds to the graph of V_2 .

Proposition 4. *For functions D and g as above and for $c = 0$, the system 37 has a homoclinic trajectory based at P_0 which surrounds the equilibrium P_1 .*

Proof. Firstly, we note that for $c = 0$ and D and g as above, the equilibrium P_c collapses into P_0 , and P_1 becomes a center. Secondly, if we multiply the right hand sides of 37 by the strictly positive function $-D(\phi)$ with $\phi > 0$, the resulting system has the same dynamics as 37 on the first and fourth quadrants. Moreover, the constructed system is Hamiltonian-like. One can verify that the Hamiltonian is

$$H(\phi, v) = \frac{1}{2}[D(\phi)v]^2 + \int_{\phi_0}^{\phi} D(s)g(s)ds,$$

where $\phi_0 \in (0, 1)$. The path of the trajectory of 37 passing through P_0 coincides with the contour curve $H(\phi, v) = 0$. By the properties of D and g apart from the origin, its positive branch touches the horizontal axis at $\tilde{\phi}_0 > 1$ with a vertical tangent vector. Since the contour curves of H are symmetrical with respect to the horizontal axis, we have that the trajectory associated with this path is the homoclinic connection of the proposition. \square

Remark 3. Corresponding to the homoclinic trajectory of the system 37 we have a *standing wave* of pulse type for equation 33. This wave violates the stated bounds for ϕ . Additionally, this trajectory is the boundary of a region on which the system has a *continuum* of closed trajectories around P_1 .

Given that for $c > 0$ the equilibrium P_1 is unstable (focus or node, depending on c), there is no trajectory of 37 connecting P_c with P_1 for all $c > 0$.

Now let us denote by $\theta(\phi, v; c)$ the angle formed by the positive ϕ -axis (θ grows in the counter-clockwise direction) and the vector field defined by 37 at the point (ϕ, v) for the speed c . The following monotonicity property holds.

Proposition 5. *For fixed (ϕ, v) with $\phi > 0$ and all $v \neq 0$, $\theta(\phi, v; c)$ is a monotonic increasing function of c .*

Proof. We have that

$$\tan \theta(\phi, v; c) = \frac{f_2(\phi, v)}{f_1(\phi, v)},$$

where f_1 and f_2 are the components of the vector field associated with system 37.

From the above equation

$$\frac{d\theta}{dc}(\phi, v; c) = \frac{-D(\phi)v^2}{[D(\phi)v]^2 + [cv + D'(\phi)v^2 + g(\phi)]^2} > 0,$$

for all (ϕ, v) and c as in the proposition. Then the proof follows. \square

Now, we focus on analyzing the behavior of the right unstable manifold, $W_c^u(P_c)$, of 37 as c increases. For this aim, we denote by $W_{c_1}^u(P_{c_1})$ and $W_{c_2}^u(P_{c_2})$ the right unstable manifolds of 37 at P_c corresponding to the speed values c_1 and c_2 , respectively with $c_1 < c_2$. Then the following result holds:

Proposition 6. *For any two positive values of c , c_1 and c_2 with $c_1 < c_2$:*

1. $W_{c_1}^u(P_{c_1})$ runs below $W_{c_2}^u(P_{c_2})$ in the first quadrant as time increases,
2. $W_{c_1}^u(P_{c_1})$ runs above $W_{c_2}^u(P_{c_2})$ in the fourth quadrant, as time increases.

Proof. By contradiction. Let us start with item 1. Suppose that for c_1 and c_2 as in the statement, in a certain range $W_{c_1}^u(P_{c_1})$ runs above $W_{c_2}^u(P_{c_2})$. This means that there exists at least one point, (ϕ^*, v^*) , at which these manifolds intersect each other. Although the argument is valid if the intersection occurs at any other point, let us assume that this happens below the graph of the v -null-cline V_2 . At the intersection point, the angles $\theta_1 = \theta_1(\phi^*, v^*; c_1)$ and $\theta_2 = \theta_2(\phi^*, v^*; c_2)$, are related by $\theta_2 < \theta_1$ which contradicts Proposition 5. Therefore our supposition is false. The same argument can be used in proving item 2. Hence the proof follows. \square

Let us take $\tilde{\phi}_0$ as in the proof of Proposition 4 and for $c > 0$ we denote by $\tilde{\phi}_c$ the point at which $W_c^u(P_c)$ crosses the horizontal axis. The following proposition holds:

Proposition 7. *$\tilde{\phi}_0 < \tilde{\phi}_c$ for all $c > 0$. Moreover, $\tilde{\phi}_c$ increases monotonically on the positive ϕ (horizontal) axis as c increases.*

Proof. The monotonicity of $\tilde{\phi}_c$ with respect to c is a consequence of the continuity of the vector field 37 with respect to ϕ, v and c and Proposition 5. The existence of $\tilde{\phi}_c$ for all $c > 0$ follows from the behavior of the vector field defined by 37. For example, for small c , namely such that $c^2 > \frac{-g'(0)(D'(0))^2}{D''(0)}$, the trajectory $W_c^u(P_c)$ enters the second quadrant below the graph of V_2 , then the vector field 37 pushes up until it reaches the graph of V_2 , where its tangent vector must be horizontal pointing towards the right. Then $W_c^u(P_c)$ is pushed down until it touches the horizontal axis at $\tilde{\phi}_c$. Except for some qualitative and quantitative changes on the graph of V_2 (see Figure 3) which do not change the essential behavior of $W_c^u(P_c)$, similar arguments can be used to conclude that, for bigger values of c , $W_c^u(P_c)$ touches the positive ϕ -axis further away. \square

Once $W_c^u(P_c)$ reaches the horizontal axis, where does it go as time increases? The following two propositions contain part of the answer.

Proposition 8. *If for some $c > 0$, $W_c^u(P_c)$ connects the equilibrium P_c with P_0 it does so in such a way that, except at the origin, it never crosses the existing homoclinic trajectory of 37 for $c = 0$.*

Proof. Follows by using continuity arguments and Propositions 6 and 7. \square

Proposition 9. *For positive values of c satisfying $c^2 \geq 4g'(1)D(1)$, $W_c^u(P_c)$ does not connect P_c with P_0 . Moreover, $W_c^u(P_c)$ behaves such that ϕ is finite but v is unbounded and negative, as time goes to $+\infty$.*

Proof. By Proposition 7 we have that for sufficiently large values of c , $W_c^u(P_c)$ crosses the positive horizontal axis far away from $\tilde{\phi}_0$. On the other hand, for those values of c , the branch V_1 of the v -null-cline is much closer to the horizontal axis (see Figure 5(b)). Thus the vector field 37 pushes $W_c^u(P_c)$ down leftwards with decreasing vertical component. The norm of this component is bigger as v is more negative. \square

To illustrate the t.w.s. dynamics studied in Case 2 we consider an example.

Example 2. Consider the equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[-(\gamma u + u^2) \frac{\partial u}{\partial x} \right] + u(1 - u), \quad (44)$$

where $\gamma > 0$. The corresponding system [37](#) is

$$\begin{aligned} \dot{\phi} &= (\gamma\phi + \phi^2)v \\ \dot{v} &= cv - (\gamma + 2\phi)v^2 + \phi(1 - \phi). \end{aligned} \quad (45)$$

The phase portrait of the above system is shown in [Figure 6](#) for different values of c . Note the homoclinic trajectory based at P_0 for $c = 0$, and the focus (P_1) to saddle-node (P_0), and the node (P_1) to saddle-node (P_0), heteroclinic trajectories.

The above homo- and heteroclinic connections of [45](#) correspond to a standing wave, an oscillatory front and monotonic front solutions, respectively, for equation [44](#). See [Figure 6](#).

4. Numerical solutions. The degenerate diffusion term in equation [33](#) can lead to problems for numerical simulation. To determine the origin of these problems, note that the nonlinear density-dependent diffusion term —once the x -derivative in calculated in [33](#)— can be written as the sum of two terms: a strictly density-dependent diffusive term and a convective term. When the convective term dominates the diffusive term, oscillations or wiggles will appear in the numerical solution if classical finite element, finite difference or finite box methods are used. This is caused by the negative diffusion arising from the numerical discretization method.

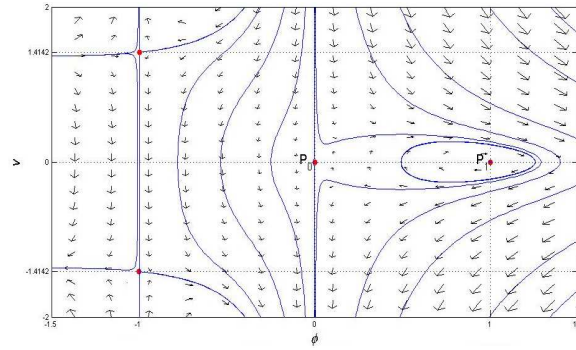
There are several numerical techniques that can be used to treat these numerical difficulties. Some of these are developed in [\[14\]](#) and [\[15\]](#). A sufficiently fine spatial grid may be useful but this strategy can prove to be computationally expensive. Another method is to stabilize the discretization by adding numerical diffusion, *i. e.* the addition of a diffusion term $\epsilon \frac{\partial^2 u}{\partial x^2}$, where $\epsilon \ll 1$, a common practice to eliminate or reduce non-physical oscillations near discontinuities [\[1, 20\]](#). This method avoids the spread of errors in the calculation or accumulation of errors leading to “blow up”. In particular the addition of the diffusion term leads to the recovery of the stability conditions of the numerical scheme.

The difficulty with problems of this kind is the treatment of the numerical flux and in setting up the problem to enable such treatment. We have chosen to use an approach (by introducing a change of variable) that allows us to deal with the degeneracy in equation [33](#) and then solve it by using a conventional method for convection-diffusion equations.

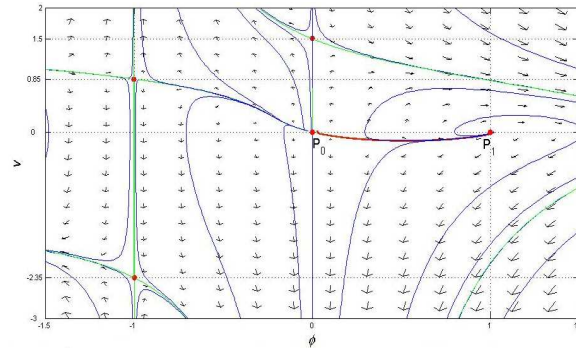
In this section we present the numerical solutions of Examples [1](#) and [2](#). We used the routine D03PSF from the NAG Fortran Library for convection-diffusion one space dimension problems. D03PSF integrates the system of convection-diffusion equations in conservative form:

$$\sum_{j=1}^N P_{i,j} \frac{\partial U_j}{\partial t} + \frac{\partial F_i}{\partial x} = C_i \frac{\partial D_i}{\partial x} + S_i \quad (46)$$

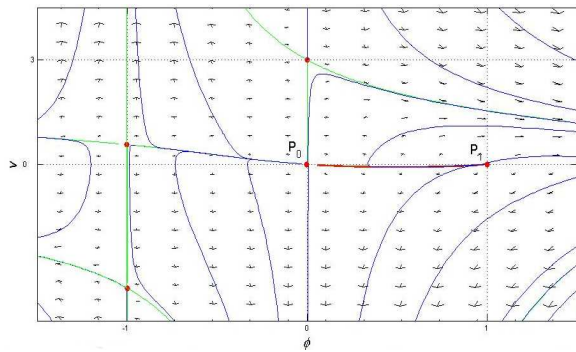
for $i = 1, 2, \dots, N$ (with N = number of equations), $a \leq x \leq b, t \geq t_0$, where U_j are the state variables. In [46](#), $P_{i,j}$, F_i and C_i depend on x, t , and U ; where the vector U denotes the solution of the initial and boundary value problem associated with the PDE system; D_i depends on x, t, U and U_x ; and S_i depends on x, t , and U .



(a)



(b)



(c)

FIGURE 6. Phase portrait of system 45 illustrating different types of connections for different values of c : (a) homoclinic trajectory based on P_0 for $c = 0$, (b) a focus to saddle-node connection for $c = 1.5$ and (c) a node to saddle-node heteroclinic trajectory for $c = 3.0$. In (a) and (b) the bounds on ϕ are violated. See text for details.

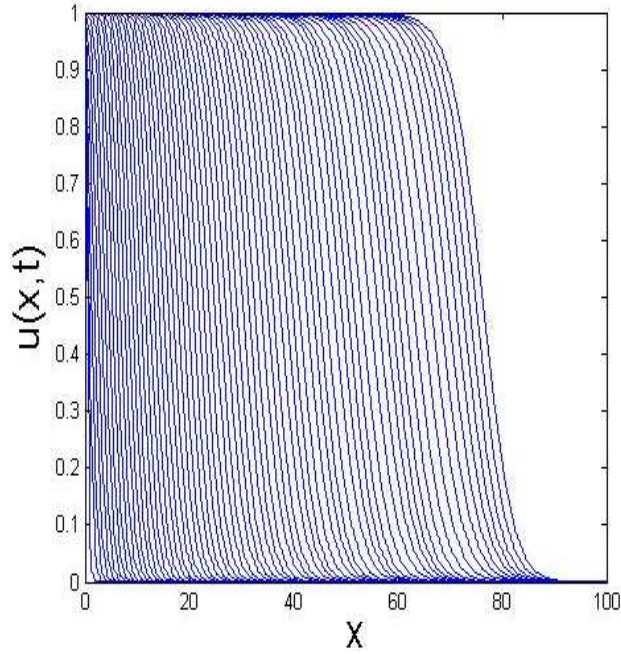


FIGURE 7. Numerical results showing how the initial and boundary value problem associated with equation 42 evolves in time. The profiles are shown at regular time intervals $t = 0, 0.5, \dots$. Boundary condition $u(0, t) = 1$ is imposed at $x = 0$ and $x = 100$. Initial conditions are $u(x, 0) = 0.5 \left(1 + \tanh\left(\frac{0.4-x}{0.1}\right)\right)$.

$P_{i,j}, F_i, C_i$ and S_i must not depend on any space derivatives, and $P_{i,j}, F_i, C_i$ and D_i must not depend on any time derivatives.

In order to use this numerical method, we must transform equations 42 and 44 to the conservative form 46, and we do this by means of a change of variable. In Example 1, equation 42, by putting $v = u^3$ (then $\frac{\partial v}{\partial x} = 3u^2 \frac{\partial u}{\partial x}$) can be rewritten as the algebraic-partial differential system

$$\begin{aligned} 0 &= v - u^3 \\ \frac{\partial u}{\partial t} &= -\frac{1}{3} \frac{\partial^2 v}{\partial x^2} + u(1 - u). \end{aligned}$$

We will then have that D in 46 is u^3 , $C = -\frac{1}{3}$ and $F = 0$.

In a similar way to the previous example, for Example 2, equation 44 can be rewritten by using $v = -\frac{1}{3}u^3 - \frac{1}{2}\gamma u^2$, so $\frac{\partial v}{\partial x} = -u^2 \frac{\partial u}{\partial x} - \gamma u \frac{\partial u}{\partial x} = -(u^2 + \gamma u) \frac{\partial u}{\partial x}$. Thus, the above equation results in the algebraic-partial differential system

$$\begin{aligned} 0 &= v + \frac{1}{3}u^3 + \frac{1}{2}\gamma u^2 \\ \frac{\partial u}{\partial t} &= \frac{\partial^2 v}{\partial x^2} + u(1 - u). \end{aligned}$$

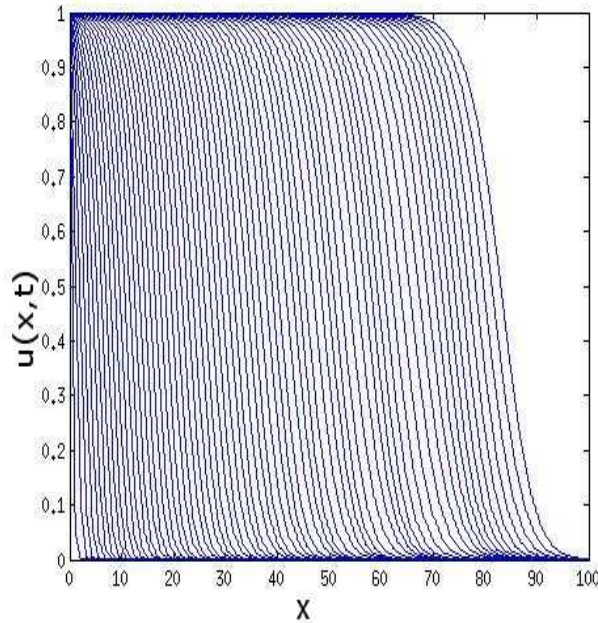


FIGURE 8. Numerical results showing how the initial and boundary value problem associated with equation 44 evolves with time. The profiles are shown at regular time intervals $t = 0, 0.5, \dots$. Here $\gamma = 1$, the boundary condition $u(0, t) = 1$ is imposed at $x = 0$ and $x = 100$, as initial conditions, we take $u(x, 0) = 0.5 \left(1 + \tanh\left(\frac{0.4-x}{0.1}\right)\right)$.

Numerical solutions of Example 1 (equation 42) can be seen in Figure 7, while those for Example 2 (equation 44) can be seen in Figure 8. Profiles are shown at regular time intervals. Traveling wave profiles can be seen in both examples. The specific initial and boundary values are given in the corresponding figure captions.

Apart from being able to display the traveling wave behavior of the solutions, the numerical results also contain data that can be used to compute the wavespeed. The wavespeed of the t.w.s. of interest is bounded by the minimum wavespeed c_{min} (this ensures we have positive solutions). Equations with known traveling wave solutions raise the question of stability. Studies on the stability of these types of solutions have already established a relationship between the stability of the wave and its speed. For example, for the FitzHugh-Nagumo equation it was shown [33, 34] that slow waves are unstable while faster waves are stable. These are the ones that can usually be obtained numerically.

Time-asymptotic behavior of the traveling wave solutions of nonlinear equations of Fisher type has also been previously considered [17, 22], making clear why typical numerical simulations of the Fisher-KPP equation result in a stable wavefront solution with speed 2 (minimum speed).

For qualitative comparison, we draw the solution of the system 43 corresponding to the speed $c = 2.8$. In Figure 11 the reader can see the pair of functions $\phi_c(\tau), v_c(\tau)$ which defines the heteroclinic trajectory connecting P_1 and P_0 . The first component,

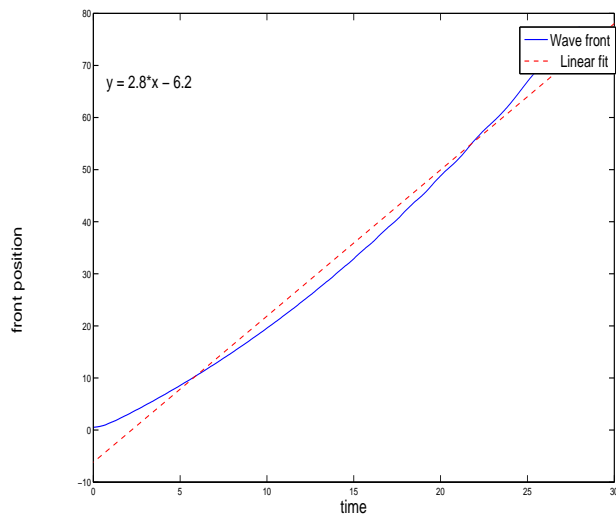


FIGURE 9. Wavespeed of traveling wave solutions of 42, determined from the numerical solution in Figure 7. Solid line denotes the wavefront and the dotted line is the best linear fit, suggesting a wavespeed c of approximately 2.8.

$\phi_c(\tau)$, has the same qualitative behavior of (the profiles of) the numerical solution of the full PDE 42 with the appropriate initial and boundary conditions (Fig. 7). Similarly, in the Figure 12 the corresponding case can be seen for the solutions of the ODE system 45 and PDE 44.

From the PDE solutions we can approximate the wavespeed by selecting a point on the solution profile, say $u = u_0$, then we plot how it changes as a function of time and compute its slope (see Figures 9 and 10). We now use this approximation to produce the corresponding ODE profiles (see Figures 11 and 12). ODE profiles were generated with MATLAB, using the software (pplane7) developed by John C. Polking, Department of Mathematics, Rice University. The aim of presenting the solution of the associated ODE systems (43 and 45) corresponding to the wavespeed approximation is to compare it to the t.w.s. found numerically and point out the qualitative agreement.

5. A note on the general approach. In section 3 we have used a phase portrait analysis to prove the existence of different types of heteroclinic trajectories for two families of autonomous ODE systems. Those give us the t.w.s. for equation 33 in two main cases. Some of the t.w.s., for appropriate values of c , violate the bounds $0 \leq \phi \leq 1$ on ϕ which means that for those values of c the original problem (as stated at the beginning of Section 3) does not have a solution. For this reason, the analysis of existence of t.w.s. in the full PDE equation satisfying some prescribed initial and boundary conditions and its re-statement in terms of looking for the values of c for which there exist heteroclinic or homoclinic trajectories of an ODE system in the t.w.s. variables, must be studied more carefully. This is the aim of this section.

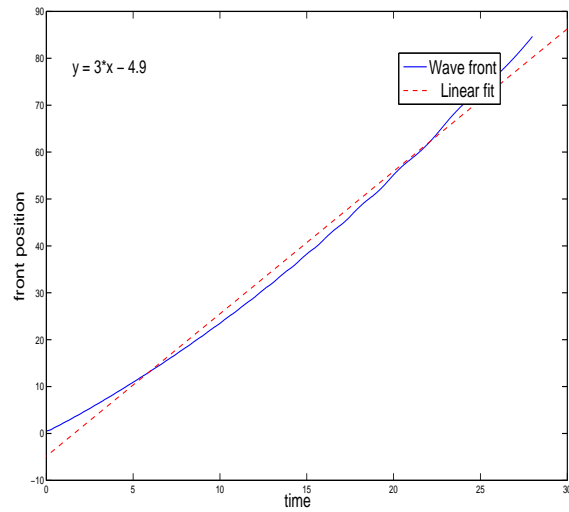


FIGURE 10. Wavespeed of traveling wave solutions of 44, determined from the numerical solution in Figure 8. Solid line denotes the wavefront and the dotted line is the best linear fit, suggesting a wavespeed c of approximately 3.

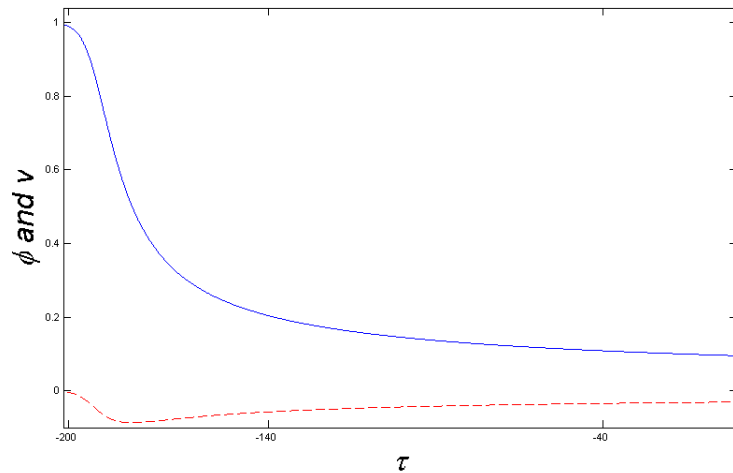


FIGURE 11. Numerical solutions of the ODE system 43 with $c = 2.8$. Key: ϕ continuous line, v dashed line. Note that, qualitatively, $\phi(\tau)$ displays similar behavior as the profile of its PDE solution counterpart (Fig. 7), for example for $\phi, \phi(-\infty) = 1$ and $\phi(+\infty) = 0$ and therefore for $u(x, t)$ conditions $u(x, 0) = u_0(x)$ with $0 \leq u_0(x) \leq 1, x \in \mathbb{R}, 0 \leq u(x, t) \leq 1, (x, t) \in \mathbb{R} \times \mathbb{R}^+$, are met. See equivalence of problems in Section 5.

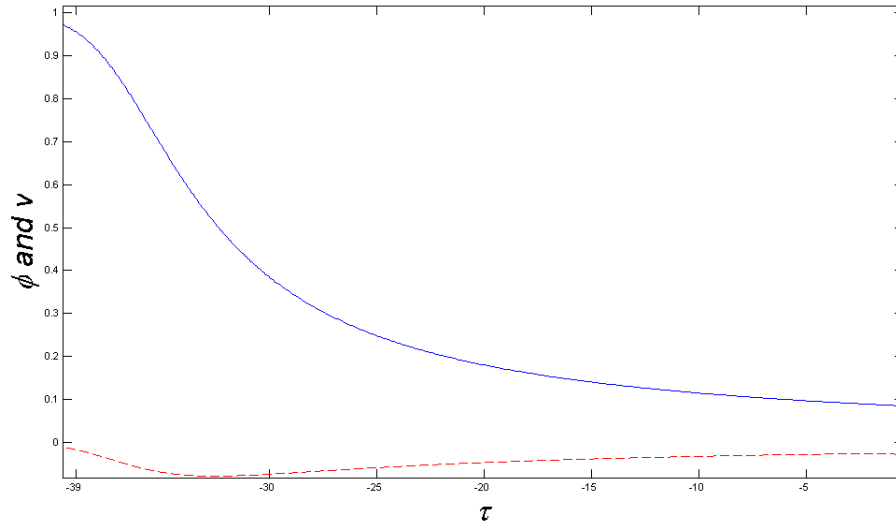


FIGURE 12. Numerical solutions of the ODE system 45 with $c = 3$.
Key: ϕ continuous line, v dashed line.

Part of the analysis here consists of investigating the relationship between the following two problems:

Problem. [PROBLEM 1 (P1)] To search for the existence of t.w.s., $u(x, t) = \phi(x - ct)$, of 33 satisfying the following conditions:

1. $\phi(-\infty) = 1$, $\phi'(-\infty) = 0$; $\phi(+\infty) = 0$, $\phi'(+\infty) = 0$,
2. $u(x, 0) = u_0(x)$, with $0 \leq u_0(x) \leq 1$ and $0 \leq \phi(\xi) \leq 1 \forall \xi \in \mathbb{R}$.

Problem. [PROBLEM 2 (P2)] To search for the existence of solutions of the boundary value problem:

$$\begin{aligned} \dot{\phi} &= -D(\phi)v \\ \dot{v} &= cv + D'(\phi)v^2 + g(\phi), \end{aligned}$$

with $\phi(-\infty) = 1$, $v(-\infty) = 0$ and $\phi(+\infty) = 0$, $v(+\infty) = 0$ with $0 \leq \phi(\tau) \leq 1 \forall \tau \in (-\infty, +\infty)$, where τ satisfies 36.

We introduce the following definition:

Definition 5.1. We say that P1(P2) implies P2(P1) whenever the existence of a solution of P1(P2) implies the existence of a solution of P2(P1). When the implication is in both senses we will say that problems P1 and P2 are equivalent.

Let us denote by \mathcal{C}_E the set of values of c for which P1 (5) has a t.w.s. $u(x, t) = \phi(x - ct)$. The following proposition holds:

Proposition 10. If \mathcal{C}_E is a non-empty set, then for each $c \in \mathcal{C}_E$, P1 (5) implies P2 (5).

Proof. For c as in the statement, let $u(x, t) = \phi(x - ct)$ be a solution of P1 (5). Then ϕ satisfies

$$D(\phi)\phi''(\xi) + D'(\phi)[\phi'(\xi)]^2 + c\phi'(\xi) + g(\phi) = 0,$$

plus the conditions 1. and 2. in P1 (5). If we set $\phi' = v$, then $(\phi(\xi), v(\xi))$ is a solution of the singular boundary value problem

$$\begin{aligned} \phi' &= v \\ D(\phi)v' &= -cv - D'(\phi)v^2 - g(\phi), \end{aligned}$$

$\phi(-\infty) = 1$, $\phi(+\infty) = 0$ and $v(-\infty) = 0$, $v(+\infty) = 0$ with $0 \leq \phi(\xi) \leq 1$. Therefore, writing

$$\phi(\tau) \equiv \phi(\xi(\tau)) \text{ and } v(\tau) \equiv v(\xi(\tau)),$$

where τ satisfies 39, and substituting into the above system we conclude that the pair $(\phi(\tau), v(\tau))$ is a solution of the non-singular boundary value problem P2 (5). Hence the result follows. \square

Now we consider the converse: Let \mathcal{C}_S be the set of values of c for which problem P2 (5) has a solution. Our results, and the illustrative examples in the previous section, show us that the above is a non-empty set. Because of the condition $0 \leq \phi(\tau) \leq 1$ we note that if problem P2 (5) has solution for each $c \in \mathcal{C}_S$, such a set must be included in (or is equal to) the set $\{c | c^2 > 4g'(1)D(1)\} \cap \{c | c \geq c_0\}$, where c_0 satisfies 41.

We can prove the following proposition:

Proposition 11. *For each c belonging to the set \mathcal{C}_S , P2 (5) implies P1 (5).*

Proof. Let $(\phi(\tau), v(\tau))$ be the solution of P2 (5) corresponding to $c \in \mathcal{C}_S$. Since

$$\frac{d\xi}{d\tau} = -D(\phi) > 0 \text{ for } \phi \neq 0,$$

the function $\xi = \xi(\tau)$ has an inverse $\tau = \tau(\xi)$. Define

$$\phi(\xi) \equiv \phi(\tau(\xi)) \text{ and } v(\xi) \equiv v(\tau(\xi)).$$

By using 39 we have

$$\phi'(\xi) = -\frac{\dot{\phi}}{D(\phi(\xi))} \text{ and } v'(\xi) = -\frac{\dot{v}}{D(\phi(\xi))}.$$

Substituting $\dot{\phi}$ and \dot{v} into 40 we obtain the ODE system appearing in the proof of Proposition 10. This was derived from the second order ODE in P1 (5). Conditions 1. and 2. in P1 (5) are also satisfied because of the conditions at the boundary in P2 (5). \square

Remark 4. Clearly for c such that $c^2 \leq 4g'(1)D(1)$ P2 (5) has no solution because the damped behavior (with oscillations when the strict inequality holds or without them in case of equality) around P_1 violates the bound $(0 \leq \phi(\xi) \leq 1)$ of ϕ .

In light of Remark 4, it is necessary to analyze the eventual equivalence between P1 (5) and P2 (5) in a more general context. In particular, we consider the case of *ill-posedness*. Here we adopt the definition given in [2]:

Definition 5.2. A boundary or initial value problem for a partial differential equation is said to be ill-posed (or improperly posed) in the sense of Hadamard, if at least one of the following conditions fails:

1. The existence of the solution,
2. The uniqueness of the solution,

3. The continuity of the solution with respect to the prescribed initial data. The problem is a well-posed one when the above conditions hold.

The above definition is made precise by indicating the space in which the solution must belong and the measure in which the continuous dependence is desired.

In terms of the above definition we can re-state part of our results as follows:

Proposition 12. *For functions D and g as in Case 1 or Case 2, and for each $c > 0$ such that $c^2 \leq 4g'(1)D(1)$ the problem P2 (5), hence P1 (5) is an ill-posed one. Meanwhile for each $c > 0$ belonging to the set $\{c | c^2 > 4g'(1)D(1)\} \cap \{c | c \geq c_0\}$ that problem (hence P1 (5)) is well-posed.*

6. Conclusions and discussion. By way of conclusion and discussion we address the following items:

1. The analysis of the existence of t.w.s. $u(x, t) = \phi(x - ct)$ for equations of the form 33 with $D(u) \leq 0 \ \forall u \in [0, 1]$ and $g(0) = g(1) = 0$ with $g(u) > 0 \ \forall u \in (0, 1)$ satisfying some suitable initial and boundary conditions is less understood than that for the case $D(u) \geq 0$ (see [6, 26] and [27]). In fact, some of these problems are ill-posed (see Section 5) and not well studied.
2. The description of direct aggregation phenomena by using negative diffusion equations perhaps deals with relatively simple models but encounters problems with ill-posedness.
3. The derivation of the aggregation equation 23 took into account the mutual attraction between conspecifics. This has a clear interpretation. This is an important difference between our model and other approaches, namely, integro-differential equations or the Ginzburg-Landau equation, whose interpretation is not derived from first principles at the level of individual behavior within the population. Our derivation is motivated by the work of Turchin and builds on it.
4. We have only treated the t.w.s dynamics of strictly negative diffusion equations for which, as far as we know, there is no stability theory available. The analysis of the existence of t.w.s. for the case when the density dependent diffusion coefficient changes sign would, we feel, also raise challenging problems.

Acknowledgments. Part of this work was supported by *Dirección General de Asuntos del Personal Académico (DGAPA)-UNAM, proyecto IN108496*. Part of this work was carried out while PKM (FSG) was visiting the *Facultad de Ciencias, UNAM* (Centre for Mathematical Biology at Oxford) under the Exchange Scheme between the *Academia Mexicana de Ciencias* and The Royal Society of London. PKM was partially supported by a Royal Society Wolfson Research Merit Award.

We thank the NAG Response Centre Support Team for their helpful suggestions.

REFERENCES

- [1] K. Alhumaizi, R. Henda and M. Soliman, *Numerical analysis of a reaction-diffusion-convection system*, Computers & Chemical Engineering, **27** (2003), 579–594.
- [2] K. A. Ames, *Improperly posed problems in non-linear partial differential equations*, in “Non-linear Equations in the Applied Sciences” (Mathematics in Science and Engineering), W. F. Ames, C. Rogers (eds.), **185** (1992).
- [3] R. M. Anderson, D. M. Gordon, M. J. Crawley and M. P. Hassell, *Variability in the abundance of animal and plant species*, Nature, **296** (1982), 245–248.
- [4] W. Alt, *Models for mutual attraction and aggregation of motile individuals*, in “Lecture Notes in Biomathematics,” **57** (1985), 33–38.

- [5] W. Alt, *Degenerate diffusion equations related with drift functional modelling aggregation*, Nonlinear Anal., **9** (1985), 811–836.
- [6] D. G. Aronson, *Density-dependent interaction systems*, in “Dynamics and Modelling of Reactive Systems,” W. H. Steward and W. H. Ray and C. C. Conley (eds.), New York: Academic Press, 1980.
- [7] D. G. Aronson, *The role of the diffusion in mathematical biological population biology: Skellam revisited*, in “Lecture Notes in Biomathematics,” A. Fasano and M. Primicerio (eds.), 57, Berlin Heidelberg New York: Springer, 1985.
- [8] D. K. Arrowsmith and C. M. Place, “An Introduction to Dynamical Systems,” Cambridge University Press, 1990.
- [9] N. F. Britton, *Aggregation and the competitive exclusion principle*, J. Theor. Biol., **136** (1989), 57–66.
- [10] R. S. Cantrell and C. Cosner, *Conditional persistence in logistic models via nonlinear diffusion*, Proceedings of the Royal Society of Edinburgh: Section A Mathematics, **132** (2002), 267–281.
- [11] R. S. Cantrell and C. Cosner, *Spatial ecology via reaction-diffusion equations*, in “Wiley Series in Mathematical and Computational Biology,” John Wiley & Sons Ltd., Chichester, 2003.
- [12] D. S. Cohen and J. D. Murray, *A generalized diffusion model for growth and dispersal in a population*, J. Math. Biol., **12** (1981), 237–249.
- [13] J. C. Dallan and H. G. Othmer, *A discrete cell model with adaptative signaling for aggregation of Dictyostelium discoideum*, Phil. Trans. R. Soc. Lond. B, **352** (1997), 391–417.
- [14] M. Dehghan, *On the numerical solution of the one-dimensional convection-diffusion equation*, Math. Probl. Eng., **1** (2005), 61–74.
- [15] H. J. Eberl and L. Demaret, *A finite difference scheme for a degenerated diffusion equation arising in microbial ecology*, Sixth Mississippi State Conference on Differential Equation and Computational Simulations, Electron. J. Differential Equations, Conference, **15** (2007), 77–95.
- [16] W. S. C. Gurney and R. M. Nisbet, *The regulation of inhomogeneous population*, J. Theor. Biol., **52** (1975), 441–457.
- [17] P. Hagan, *Travelling wave and multiple travelling wave solutions of parabolic equations*, SIAM J. Math. Anal., **13** (1982), 717–38.
- [18] K. P. Hadeler, *Travelling fronts and free boundary value problems*, in “Numerical Treatment of Free Boundary Value Problems,” J. Albrecht and L. Collatz and K.H. Hoffman (Eds.), Birkhauser-Verlag, 1982.
- [19] T. Höfer, J. A. Sherratt and P. K. Maini, *Cellular pattern formation during Dictyostelium aggregation*, Physica D, **85** (1995), 425–444.
- [20] J. King, J. Pérez-Velázquez and H. Byrne, *Singular travelling waves in a model for tumour encapsulation*, Discrete and Continuous Dynamical Systems (DCDS-A), **25** (2009), 195–230.
- [21] A. Kolmogorov, I. Petrovsky and N. Piskounov, *Study of the diffusion equation with growth of the quantity of matter and its application to a biological problem*, in “Applicable Mathematics of Non-Physical Phenomena” (eds. F. Oliveira-Pinto and B.W. Conolly), John Wiley and Sons, 1982.
- [22] D. A. Larson, *Transient bounds and time-asymptotic behavior of solutions to nonlinear equations of Fisher type*, SIAM J. Appl. Math., **34** (1978), 93–103.
- [23] M. Lewis, *Spatial coupling of plant and herbivore dynamics: The contribution of herbivore dispersal to transient and persistent “waves” of damage*, Theor. Pop. Biol., **45** (1994), 277–312.
- [24] J. D. Murray, “Mathematical Biology. I: An introduction,” Springer, 2001.
- [25] J. H. Myers and C. J. Krebs, *Population cycles in rodents*, Sci. Am., **230** (1974), 38–46.
- [26] T. Nagai and M. Mimura, *Asymptotic behaviour for a non-linear degenerate diffusion equation in population dynamics*, SIAM J. Appl. Math., **43** (1983), 449–464.
- [27] T. Nagai and M. Mimura, *Some non-linear degenerate diffusion equations related to population dynamics*, J. Math. Soc. Japan, **35** (1983), 539–562.
- [28] A. Okubo, “Diffusion and Ecological Problems: Mathematical Models,” Springer Verlag, 1980.
- [29] V. Padrón, *Aggregation on a nonlinear parabolic functional differential equation*, Divulgaciones Matemáticas, **6** (1998), 149–164.
- [30] V. Padrón, *Effect of aggregation on population recovery modeled by a forward-backward pseudo parabolic equation*, T. Am. Math. Soc., **356** (2004), 2739–2756.
- [31] M. H. Protter and H. F. Wienberger, “Maximum Principles in Differential Equations,” Springer Verlag, 1984.

- [32] H. R. Pulliman and T. Caraco, *Living in groups: Is there an optimal group size?*, in “Behavioural Ecology: An Evolutionary Approach,” J. R. Krebs and N. B. Davies (eds.), Sinauer, Sunderland Massachusetts, 1984.
- [33] J. Rinzel and J. B. Keller, *Traveling wave solutions of a nerve conduction equation*, Biophys. J. **13** (1973), 1313–1337.
- [34] J. Rinzel, *Spatial stability of traveling wave solutions*, Biophys. J., **15** (1975), 975–988.
- [35] F. Sánchez-Garduño, “Travelling Waves in One-Dimensional Degenerate Non-Linear Reaction-Diffusion Equations,” D.Phil. thesis, University of Oxford, 1993.
- [36] F. Sánchez-Garduño and P. K. Maini, *Existence and uniqueness of a sharp travelling wave in degenerate non-linear diffusion Fisher-KPP equations*, J. Math. Biol., **33** (1994), 163–192.
- [37] F. Sánchez-Garduño and P. K. Maini, *Travelling wave phenomena in non-linear degenerate Nagumo equations*, J. Math. Biol., **35** (1997), 713–728.
- [38] J. G. Skellam, *Random dispersal in theoretical populations*, Biometrika, **38** (1951), 196–218.
- [39] J. G. Skellam, *The formulation and interpretation of mathematical models of diffusional processes in population biology*, in “The Mathematical Theory of the Dynamics of Biological Population,” M. S. Bartlett, *et al.* (eds.) New York: Academic Press, 1973.
- [40] H. L. Swinney and V. I. Krinsky (eds.), “Waves and Patterns in Chemical and Biological Media,” MIT Press, Cambridge, MA, 1992.
- [41] R. L. Taylor and R. A. J. Taylor, *Aggregation, migration and population mechanics*, Nature, **265** (1977), 415–421.
- [42] K. Thorarinsson, *Population density and movement: A critique of Δ -models*, Oikos, **46** (1986), 70–81.
- [43] P. Turchin, *Population consequences of aggregative movement*, J. of Animal Ecol., **58** (1989), 75–100.
- [44] P. Turchin and P. Kareiva, *Aggregation in aphids: An effective strategy for reducing predation risk*, Ecology, **70** (1989), 1008–1016.

Received April 2009; revised October 2009.

E-mail address: faustino@servidor.unam.mx

E-mail address: maini@maths.ox.ac.uk

E-mail address: perez-velazquez@helmholtz-muenchen.de