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Mathematics of Darwin's Diagram

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Abstract. Darwin illustrated his theory about emergence and evolution of biological species with a diagram. It shows how species exist, evolve, appear and disappear. The goal of this work is to give a mathematical interpretation of this diagram and to show how it can be reproduced in mathematical models. It appears that conventional models in population dynamics are not sufficient, and we introduce a number of new models which take into account local, nonlocal and global consumption of resources, and models with space and time dependent coefficients.

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Mathematics Subject Classification: 92D15, 35K57

1. On the origin of species

More than a century and a half after the publication of Darwin's book on the origin of species, the theory of speciation continues to attract much attention. The modern theory distinguishes allopatric speciation which implies the existence of geographic or genetic isolation where there is no gene exchange between different taxa, parapatric speciation which admits partial exchange and sympatric speciation which occurs without geographic or genetic barriers [7], [15]. It is generally accepted that allopatric speciation is biologically realistic though the mechanism which leads to the appearance of isolating barriers may be sometimes unclear. Sympatric speciation continues to instigate intensive discussions. In spite of big body of experimental data, observations in nature and theoretical models, it is difficult to make definite conclusions about its existence in nature because of the complexity of these phenomena and variety of possible mechanisms.

In this work we will study sympatric speciation with the purpose to reproduce Darwin's diagram as a graph on the (x, t) plane where x is the space variable and t is time. The space variable x corresponds to the species phenotype considered from the point of view of the type of consumed resources. In this sense, the space variable can be interpreted as characterization of resources consumed by individuals of the species.

We will introduce the models which will allow us to describe various aspects of natural selection shown in the diagram: existence of species without speciation, emergence of new species, survival of the most adapted, competition of species with distributed phenotype. These models are based on reaction-diffusion equations with nonlocal and global consumption of resources.

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1.1. Diagram

Darwin illustrated his theory on the emergence and evolution of biological species by the diagram (Figure 1). This only figure in the book is the quintessence of the theory. About a century and a half after publication of this book, we begin to understand the exact meaning of this diagram from the mathematical point of view and how to reproduce it in mathematical models.

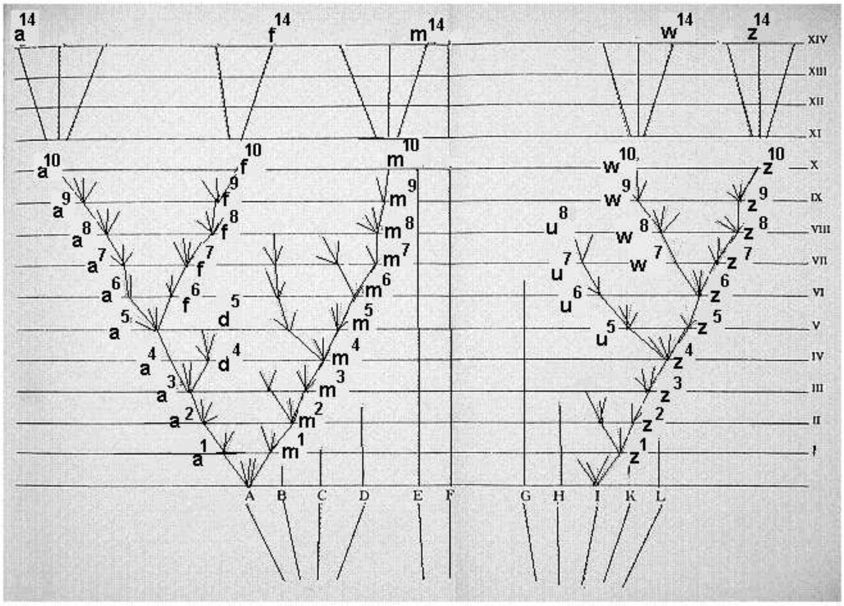

FIGURE 1. Darwin's diagram explaining emergence and evolution of biological species (adapted from [8]). More explanation in the text.

First of all, we need to understand what is shown in the diagram. Darwin described it as follows. "Let A to L represent the species of a genus large in its own country; these species are supposed to resemble each other in unequal degrees, as is so generally the case in nature, and is represented in the diagram by the letters standing at unequal distance ... The little fan of diverging dotted lines of unequal length proceeding from (A), may represent its varying offspring. The variations are supposed to be extremely slight, but of the most diversified nature, they are not supposed all to appear simultaneously, but often after long intervals of time; not are they all supposed to endure for equal periods. Only those variations which are in some way profitable will be preserved or naturally selected. And here the importance of principle of benefit being derived from divergence of character comes in; for this will generally lead to the most different or divergent variations (represented by the outer dotted lines) being preserved and accumulated by natural selection. ... After a thousand generations, species (A) is supposed to have produced two fairly well-marked varieties, namely a^1 and m^1. These two varieties will generally continue to be exposed to the same conditions which made their parents variable, and the tendency to variability is in itself hereditary, consequently they will tend to vary, and generally to vary in nearly the same manner as their parents varied. Moreover, these two varieties, being only slightly modified forms, will tend to inherit those advantages which made their common parent (A) more numerous than most of the other inhabitants of the same country" ([8], p. 104).

Thus, each line corresponds to one species. The horizontal axis measures their resemblance, that is some morphological characteristics or phenotype. The vertical axis is time. Species represents a line (trajectory) in the (x, t)-space.

Appearance of new species is shown as several lines starting from the same point. In the beginning, these are small variations inside the same species. After some time they can become different species. Among many possible variations, only favorable ones are chosen and reinforced by natural selections. The others will disappear.

One more important feature of the diagram is that lines (species) can disappear. In most cases it happens when two lines approach each other. We can suppose that it happens because the corresponding species begin to consume the same resources, compete for these resources and some of them disappear.

The goal of this work is to model the main elements of Darwin's diagram: existence of species as localized groups of individuals, their evolution (motion in the morphological space), emergence of new species, preservation of most fitted and disappearance of the others due to natural selection, competition of species when their phenotypes becomes close.

1.2. Modelling

1.2.1. Variables

We will describe biological populations by their density $u(x, t)$ which depends on space (morphology, phenotype) and on time. By localized solutions we will understand functions in the form of one or several pulses. Each of these pulses is separated from the others by the intervals where the function is close to zero. In this case, these pulses correspond in our description to biological species. They represent groups of individuals separated from each other with respect to their phenotype.

We will not discuss here a complex and not well understood question about the relation between phenotype and genotype. We will implicitly understand in the models that the genotype provides heritable properties from parents to offsprings and that mutations also concern the genotype. However we will suppose that the genotype is uniquely related to the phenotype. So we will assume that the phenotype is transmitted from parents to offsprings with small random variations. The latter are described by the diffusion term in the equations for the population density.

Specific form of pulses is shown in Figures 4 and 6. They can be characterized by the positions of their maxima. Hence we will use the coordinates of pulse maxima to trace their motion in the (x, t)-space. We will relate the trajectories of the pulses with the lines in Darwin's diagram. Thus our goal is to construct the model for which pulses have the same trajectories as species (lines) in the diagram.

One of the main properties of the diagram is the emergence of new species. In this case, several lines bifurcate from a previous line (species). According to Darwin's description, in the beginning these are small variations inside the previous species. Similarly, we will observe as one pulse gradually splits into several pulses. In the beginning, it remains as a single pulse but instead of a single maximum of the function $u(x, t)$ there appear several maxima. Each of these maxima is considered in our modelling as a new variation (sub-species). So we will trace the trajectories of these maxima. Some of them will disappear after some time, some other will become separate pulses.

1.2.2. Models

Conventional models in population dynamics do not describe desired properties of solutions. We need to introduce new models which we briefly present here and study in more detail in Sections 2-4.

The starting point is to get stable localized solutions (pulses). In order to do it we need to introduce the notion of global consumption of resources. Consider the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = d \, \frac{\partial^2 u}{\partial x^2} + a u^k (1 - H(u)) - \sigma u. \tag{1.1}$$

If $k = 1$ and $H(u) = u$, it is the usual logistic equation. The term $au(1 - u)$ describes reproduction of the population, the last term in the right-hand side its mortality. The case $k = 2$ corresponds to sexual reproduction where the reproduction term is proportional to the square of the population density. The factor $(1-u)$ describes available resources, and u consumption of resources which is proportional to the population density. We call this case local consumption of resources because they are consumed at the same space point x where the individuals are located at this moment of time, where they reproduce and where they die. This equation is studied in detail both for $k=1$ (monostable case) and $k=2$ (bistable case) (see [32] and references therein).

Next, we will consider nonlocal consumption of resources where

$$H(u) = \int_{-\infty}^{\infty} \phi(x-y)u(y,t)dy,$$

$\phi(x)$ is some kernel which shows how consumption of resources depends on the distance: what is the rate of consumption of resources located at the point x by the individuals located at the point y. Here we come to another concept where consumption of resources occurs in some area around the average location of the individuals. If $k=1$, equation (1.1) with nonlocal consumption of resources is the so-called nonlocal Fisher-KPP equation actively studied during the last decade (see [6], [17], [19], [20], [26]). We will consider this equation in the case $k=2$.

Finally, we will call consumption of resources global if

$$H(u) = s\int_{-\infty}^{\infty} u(y,t)dy.$$

The integral here represents the total size of the population, s is a constant. Hence consumption of resources occurs independently of the phenotype of the individuals. Example of global resources can be water which represents a necessary resource for many species independently of their phenotype. Reaction-diffusion equations with global resources are introduced in [34].

Reaction-diffusion equations with local and nonlocal consumption of resources describe propagation of waves, nonlocal consumption of resources describes speciation. Local and global consumption of resources describe pulse solutions. They are unstable in the case of local resources and they can become stable in the case of global resources. These models will be discussed in Section 2. Section 3 is devoted to systems of competition of species with local, nonlocal and global consumption of resources. In Section 4 we consider models with space dependent coefficients. In Section 5 all these models are applied to describe Darwin's diagram.

Let us finish this section with the remark about space intervals. In real biological applications they are bounded. However from the point of view of mathematical analysis, it is often more convenient to consider the whole axis instead of a bounded interval. When we study localized solutions (pulses) and they are located sufficiently far from the boundary, the influence of the boundary can be neglected. In this case behavior of solutions in a bounded interval is close to behavior of solutions on the whole axis.

2. Single population

2.1. Local consumption (simple waves)

In classical population dynamics, the population density $u(x,t)$ is described by the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = d\,\frac{\partial^2 u}{\partial x^2} + F(u), \tag{2.1}$$

where

$$F(u) = au^k(1-u) - \sigma u.$$

The first term in the expression for $F(u)$ describes natality of the population, the second term its mortality, $k=1$ corresponds to asexual and $k=2$ to sexual reproduction. The reproduction term is proportional to the available resources $(K-u)$, where $K=1$ here is carrying capacity (production of resources) and $-u$ describes consumption of resources which is proportional to the population density. The influence of limited resources on the rate of growth of the population was first discussed by Malthus in 1798 [24]. It was introduced in mathematical models by Verhulst in 1838 [31].

If $k=1$, then $F(u)=0$ for two values of u: $u_+=0$ and $u_-=1-\sigma/a$. If $\sigma<a$, then $u_->0$, and there exist travelling wave solutions of equation (2.1) with the limits $u_\pm=u(\pm\infty)$. They were first studied in the context of population dynamics in [14], [22] and then in numerous other works (see [35] and references therein). These are solutions of the form $u(x,t)=w(x-ct)$, where c is the wave speed. They satisfy the second-order ordinary differential equation

$$dw''+cw'+F(w)=0, \quad w(\pm\infty)=u_\pm. \tag{2.2}$$

For all speeds c greater than or equal to the minimal speed $c_0=2\sqrt{dF'(0)}$ these solutions are monotonically decreasing. They are stable in properly chosen spaces.

If $k=2$ and $\sigma/a<1/4$, then the function $F(u)$ has three zeros, $u_+=0$, and two others, u^* and u_-, the roots of the equation $u(1-u)=\sigma/a$, $u_+<u^*<u_-$. There exists a solution of problem (2.2) for a unique value of speed c. The wave is monotone and globally asymptotically stable [32].

Equation (2.1) with $k=2$ has also a pulse solution, that is a stationary solution $w_0(x)$ with zero limits at infinity:

$$dw_0''+F(w_0)=0, \quad w_0(\pm\infty)=0.$$

It can be easily constructed explicitly. This solution is unstable. We will return to this question in Section 2.3. Such solution does not exist for $k=1$. Let us note that the pulse solution exists for any positive values of parameters a and σ. This means that the population persists even for high mortality rates. Moreover the maximum of the solution w_m increases for greater σ but the distribution becomes narrower.

2.2. Nonlocal consumption (simple and periodic waves)

Let us consider nonlocal consumption of resources, where the term $(1-u)$ in the reproduction rate is replaced by the term $(1-J(u))$,

$$J(u)=\int_{-\infty}^{\infty}\phi(x-y)u(y,t)dy.$$

The kernel of the integral is taken in the form of a piece-wise constant function

$$\phi(x)=\begin{cases} 1/(2N) & , |x|<N \\ 0 & , |x|\geq N \end{cases}$$

though other choice of this function is also possible. We will consider the nonlocal reaction-diffusion equation

$$\frac{\partial u}{\partial t}=d\,\frac{\partial^2 u}{\partial x^2}+F(u,J(u)), \tag{2.3}$$

where

$$F(u,J(u))=au^k(1-J(u))-\sigma u, \quad k=1,2.$$

An important property of this equation is that the homogeneous in space solution $u=u_-$ can become unstable resulting in appearance of stationary periodic in space solutions. It was first noticed in [6]. Similar to the local equation, equation (2.3) has travelling wave solutions. However their structure and dynamics become more complex.

If N is sufficiently small, then there exist monotone travelling waves with the limits $u_\pm$ at infinity. For larger values of N these waves become non-monotone but they still have the same limits at infinity. At the same time, homogeneous solution u_- loses its stability if N sufficiently large. In this case, there are two waves propagating one after another. The first one connects the stationary points u_+ and u_-. The second one provides a transition from u_- to the periodic in space structure. Depending on parameters there are different modes of propagation:

- A single periodic wave which can be represented as $w(x - ct, t)$, where $w(\xi, t)$ is a periodic function of time. There is a stationary periodic structure behind the wave (Figures 2 and 3, left),

- Transition from a simple wave $w(x - ct)$ to a stationary periodic structure (Figures 2 and 3, middle and right). The wave front represents a steady wave propagating with a constant speed and a constant profile. It is not a monotone function of x. The middle of the interval is filled by a periodic solution. There is a transition between them at some distance behind the wave front,

- If the steady wave with the limits $u_\pm$ at infinity propagates faster than transition between u_- and the periodic in space structure, then the wave runs away and the distance between them will grow [36].

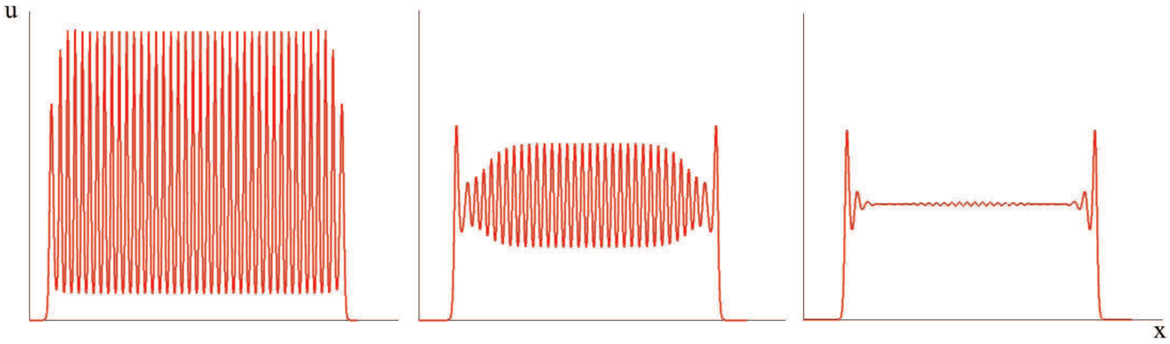

FIGURE 2. Snapshot of solution of equation (2.3) for $k = 2$, $a = 1$, $\sigma = 0.1$, $N = 3$, $d = 0.2$ (left), $d = 0.4$ (middle), $d = 0.5$ (right). The outer peaks of the solution change periodically in time in the left simulation, and they remain constant for the other two simulations.

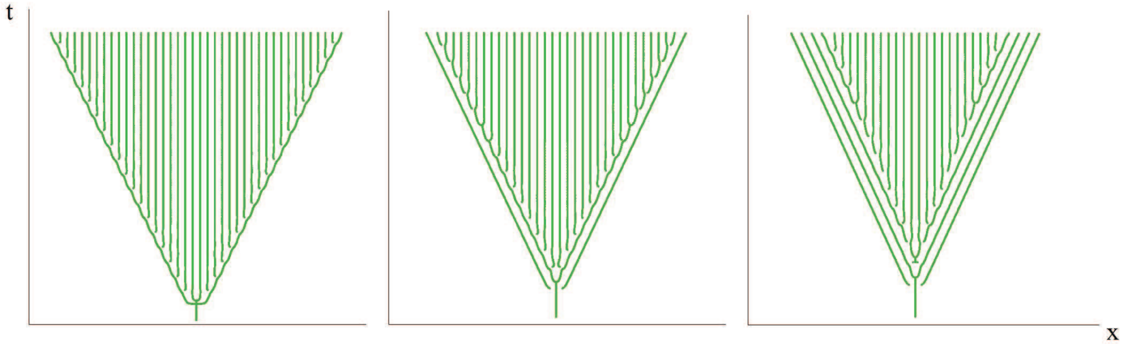

FIGURE 3. The maxima of solutions on the (x, t) plane for the same values of parameters as in the previous figure. The outer peaks in the middle and right figures move with a constant speed. There is a stationary periodic solution inside the interval.

Propagation of simple and periodic waves for the nonlocal reaction-diffusion equation was studied in [1], [16], [17], [18], [19], [20], [26], [28] for $k = 1$ (monostable case) and in [1], [2], [3] for $k = 2$ (bistable case). It is important to note that similar to the local equation, the waves exists for all speeds greater than or equal to the minimal wave in the monostable case, and the wave is unique in the bistable case.

2.3. Global consumption (pulses)

In this section we will consider the equation

$$\frac{\partial u}{\partial t} = d\,\frac{\partial^2 u}{\partial x^2} + F(u, I(u)), \tag{2.4}$$

where

$$F(u, I(u)) = au^k(1 - sI(u)) - \sigma u, \qquad I(u) = \int_{-\infty}^{\infty} u(y,t)dy.$$

It differs from the previous one by the integral $I(u)$ which is now taken over the whole space. In the other words, the kernel of the integral equals 1. Behavior of solutions is different in comparison with the previous case. The waves do not exist, the pulse exists and it becomes stable. Pulse existence can be easily studied in the one-dimensional case. In the multi-dimensional case, the existence prove is more involved (see, e.g., [29], [34]). The question about its stability is quite difficult and it is studied only for some model examples [34].

2.3.0.1. Pulse existence. In the stationary case, equation (2.4) becomes

$$w'' + w^2\left(1 - s\int_{-\infty}^{\infty} w(y)dy\right) - \sigma w = 0 \tag{2.5}$$

$(a = 1, d = 1)$. We will analyze the existence of solutions $w(x)$ which satisfy the following properties:

$$w(x) > 0,\ x \in \mathbb{R},\ \ w(x) \to 0,\ \ x \to \pm\infty,\ \ w(x) = w(-x). \tag{2.6}$$

Set

$$c = 1 - s\int_{-\infty}^{\infty} w(y)dy \tag{2.7}$$

and consider the equation

$$w'' + cw^2 - \sigma w = 0. \tag{2.8}$$

For each fixed positive c, there exists a unique solution of this equation satisfying (2.6). Its existence can be easily proved by the analysis of the phase plane of the system of two first-order equations,

$$w' = p, \quad p' = -cw^2 + \sigma w$$

or by the explicit integration of the equation

$$\frac{dp}{dw} = \frac{1}{p}\left(-cw^2 + \sigma w\right).$$

Let us note that since $\sigma > 0$, then this solution exponentially decays at infinity. Denote this solution by $w_c(x)$. Substituting it into (2.7), we obtain the equation

$$c = 1 - s\int_{-\infty}^{\infty} w_c(y)dy. \tag{2.9}$$

Denote by w_1 the solution of (2.8) with $c = 1$. Then $w_c = w_1/c$ and we can write (2.9) as

$$c^2 - c + s \int_{-\infty}^{\infty} w_1(y)dy = 0. \tag{2.10}$$

This equation has two solutions if

$$s \int_{-\infty}^{\infty} w_1(y)dy < \frac{1}{4} . \tag{2.11}$$

We note that for every σ fixed, solution $w_1(x)$ of (2.8) with $c = 1$ exists and it is independent of s. Let us take a positive value of s which satisfies condition (2.11). Then equation (2.10) has two solutions, c_1 and c_2, such that $0 < c_1 < 1/2 < c_2 < 1$. If $s \to 0$, then $c_1 \to 0, c_2 \to 1$. Therefore,

$$w_{c_1}(x) \to \infty, \quad w_{c_2}(x) \to w_1(x), \quad a \to 0.$$

The first convergence occurs uniformly on every bounded interval, the second uniformly in $\mathbb{R}$.

Denote $s_0 = 1/(4\int_{-\infty}^{\infty} w_1(y)dy)$. Then condition (2.11) is satisfied for $s < s_0$, and there are two solutions of equation (2.5). There are no solutions for $s > s_0$.

2.3.0.2. Pulse stability. The pulse solution w_0 is unstable in the case of the local reaction-diffusion equation. The operator

$$Lu = u'' + F'(w_0)u$$

has a positive eigenvalue. Indeed, the function $w_0'(x)$ is the eigenfunction of this operator corresponding to the zero eigenvalue. This eigenfunction has variable sign. On the other hand, the principal eigenvalue (with the maximal real part) of this operator is real, simple and the corresponding eigenfunction is positive [32]. Therefore, 0 is not the principal eigenvalue of this operator. Therefore there exists a positive eigenvalue, and solution $w_0(x)$ is not stable.

Numerical simulations show that the pulse solution can be stable as a solution of equation (2.4). It is proved that the corresponding operator does not have eigenvalues with positive real parts for some model examples [34]. Stability of pulses is proved for some other nonlocal equations [21] and reaction-diffusion systems [27], [38] (see the bibliographical comments in [34]).

2.4. Nonlocal and global consumption (multiple pulses)

In this section we introduce a new model:

$$\frac{\partial u}{\partial t} = d\, \frac{\partial^2 u}{\partial x^2} + F(u, I(u), J(u)), \tag{2.12}$$

where

$$F(u, J(u)) = au^k(1 - s_1 J(u))(1 - s_2 I(u)) - \sigma u.$$

It describes dynamics of the population with two resources, one of them is nonlocal and another one is global in the sense of the previous sections. Thus the reproduction term has the factor $(1 - s_1 J(u))$ as in Section 2 and the factor $(1 - s_2 I(u))$ as in Section 3. If we put one of the constants s_1 or s_2 equal zero, then we get one of the previous models.

The presence of the integral $J(u)$ provides splitting of the population into sub-populations (speciation) while the integral $I(u)$ in the reproduction term limits the total size of the population. As a result, instead of travelling waves and single pulses observed before we obtain here solutions which consists of multiple pulses (Figure 4). Their number depends on the value of the parameter s_2. If we decrease it, the number of pulses increases. Let us also note that the distance between pulses slowly grows in time. So multiple pulse solutions are not stationary but transient solutions. When the distance between pulses tends to infinity, each of them converges to the stationary single pulse solution.

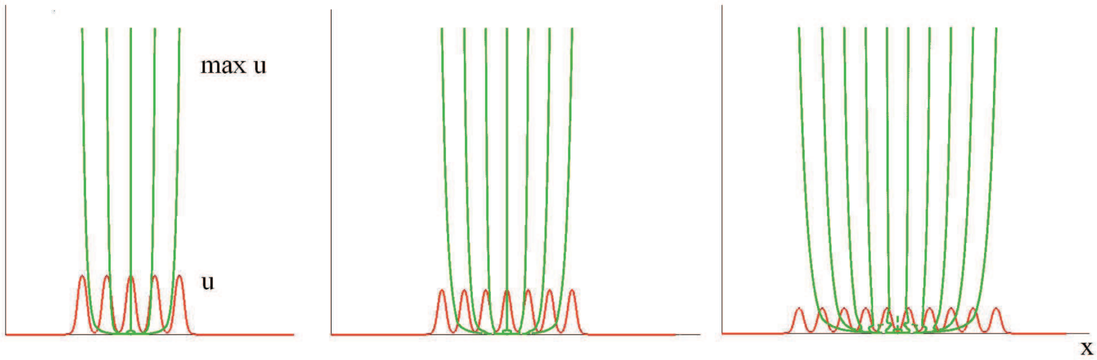

Figure 4. Five, seven and ten pulse solutions obtained respectively for $s_2 = 0.2; 0.15; 0.1$ and the values of other parameters $k = 2, D = 0.1, N = 3, a = 1, b_1 = 2, b_2 = 10, \sigma = 0.1, s_1 = 1$. The red curves are the function $u(x,t)$ at a given moment of time, the green curves show the positions of the maxima of the solution in the (x,t)-plane.

3. Competition of species

The models of competition of species were suggested by Lotka [23] and Volterra [37]. The corresponding systems with diffusion were intensively studied in relation with various problems in biology (see, e.g., [25], [34]). We will consider a system of competition of species with local, nonlocal and global consumption of resources:

$$\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{11} u - b_{12} v - b_{13} J(u) - b_{14} J(v) - b_{15} I(u) - b_{16} I(v)) - \sigma_1 u, \tag{3.1}$$

$$\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{21} u - b_{22} v - b_{23} J(u) - b_{24} J(v) - b_{25} I(u) - b_{26} I(v)) - \sigma_2 v. \tag{3.2}$$

We will discuss some important particular cases and will use them below in order to describe Darwin's diagram.

3.1. Local consumption

The system of competition of species with local consumption

$$\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^k (1 - b_{11} u - b_{12} v) - \sigma_1 u, \tag{3.3}$$

$$\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + a_2 v^k (1 - b_{21} u - b_{22} v) - \sigma_2 v \tag{3.4}$$

is usually considered in the case of asexual reproduction ($k = 1$). Depending on the values of parameters, the two species can coexist or one of them can expand replacing another one. From the mathematical point of view, this corresponds to travelling waves between two stable equilibria. Their existence and stability are well known.

We will consider the case $k = 2$ which corresponds to sexual reproduction. Stationary points of this system can be found from the algebraic system of equations

$$a_1 u (1 - b_{11} u - b_{12} v) = \sigma_1, \quad a_2 v (1 - b_{21} u - b_{22} v) = \sigma_2. \tag{3.5}$$

It can have up to four positive solutions. As before, existence and stability of travelling waves for this system can be studied by the reduction to a monotone system of equations for which the Jacobian matrix of the nonlinearity has non-negative off-diagonal elements [32].

Moreover, this system has solutions in the form of stationary pulses. Indeed, they exist in the decoupled system where $b_{12} = b_{21} = 0$ similar to the scalar equation. Consequently, they exist at least for small values of these coefficients by virtue of the implicit function theorem. Its application requires some special construction because of the presence of the zero eigenvalue of the linearized operator [33].

In the next sections we will discuss travelling waves and stationary pulses for nonlocal systems of competition of species.

3.2. Nonlocal consumption

The system of competition of species with nonlocal consumption

$$\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{13} J(u) - b_{14} J(v)) - \sigma_1 u, \tag{3.6}$$

$$\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{23} J(u) - b_{24} J(v)) - \sigma_2 v \tag{3.7}$$

was introduced in [3]. Each of the two species can propagate as a periodic wave. When these two waves meet, then begin to compete. The result of this competition depends on parameters.

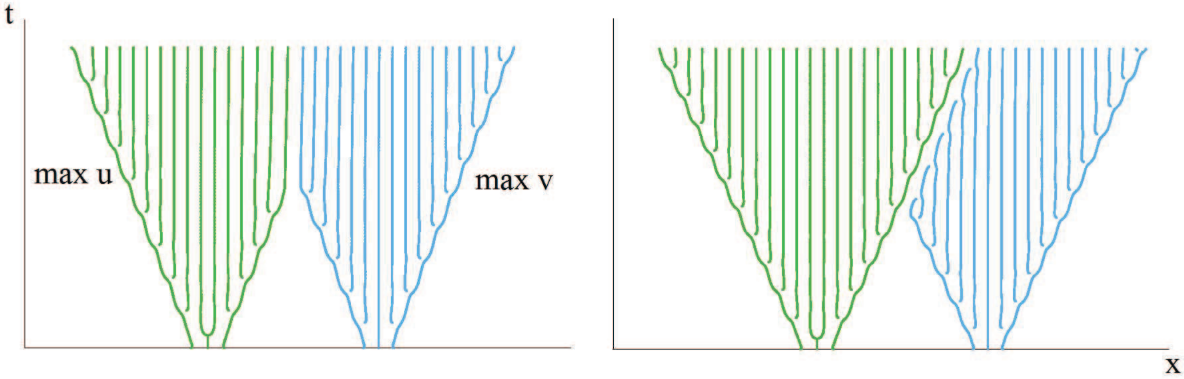

FIGURE 5. Numerical simulations of system (3.6), (3.7). The graphs show the positions of the maxima of the functions $u(x, t)$ and $v(x, t)$ on the (x, t)-plane. The interface between the two species slowly moves (left figure) if the interaction coefficients are not very different ($b_{14} = 1, b_{23} = 2$). If the difference between them is greater, then one species strongly expands while another one retreats (right figure, $b_{14} = 0.1, b_{23} = 2$). Other parameters are as follows: $d_1 = d_2 = 1$, $\sigma_1 = \sigma_2 = 1$, $a_1 = a_2 = 10$, $b_{13} = b_{24} = 0.4$.

An example of numerical simulations is shown in Figure 5. For all other parameters of the two equations equal to each other, the values of b_{14} and b_{23} determined the expansion of the species. If these two coefficients are equal, then expansion of u and v is symmetric. If they are different but close, then the interface between them slowly moves in the direction of the expanding species (Figure 5, left). If the difference is large, then the stronger species expands and the weaker one extincts (Figure 5, right).

3.3. Global consumption

We consider the system of competition of species with global consumption

$$\frac{\partial u}{\partial t} = d_1 \, \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{15} I(u) - b_{16} I(v)) - \sigma_1 u, \tag{3.8}$$

$$\frac{\partial v}{\partial t} = d_2 \, \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{25} I(u) - b_{26} I(v)) - \sigma_2 v, \tag{3.9}$$

where the functions u and v in the consumption terms are replaced by the integrals $I(u)$ and $I(v)$ [34]. We will construct a positive stationary solution of this system which vanish at infinity. Set

$$c_1 = 1 - b_{15} I(u) - b_{16} I(v), \quad c_2 = 1 - b_{25} I(u) - b_{26} I(v). \tag{3.10}$$

Then we get the equations:

$$d_1 u'' + a_1 c_1 u^2 - \sigma_1 u = 0, \qquad d_2 v'' + a_2 c_2 v^2 - \sigma_2 v = 0. \tag{3.11}$$

Denote by w_1 a positive solution of the equation

$$w'' + w^2 - w = 0, \qquad w(\pm\infty) = 0.$$

Its existence can be easily verified (cf. Section 2.3). Then

$$u(x) = \frac{\sigma_1}{a_1 c_1} \, w_1(\sqrt{\sigma_1/d_1} x), \quad v(x) = \frac{\sigma_2}{a_2 c_2} \, w_1(\sqrt{\sigma_2/d_2} x).$$

Substituting these expressions into (3.10), we obtain the equations with respect to c_1 and c_2 which we write in the new variables

$$\mu_i = \sqrt{\frac{\sigma_i}{d_i}} \, I_0, \quad z_i = \frac{\mu_i}{c_i} \, , \quad i = 1, 2,$$

where $I_0 = \int_{\mathbb{R}} w_1(x) dx$, as follows:

$$a_1 z_1 (1 - b_{15} z_1 - b_{16} z_2) = \mu_1, \quad a_2 z_2 (1 - b_{25} z_1 - b_{26} z_2) = \mu_2. \tag{3.12}$$

Each nonzero and non-negative solution of this system provides a pulse solution of system (3.8), (3.9). Let us note that these solutions are invariant with respect to translation in space. Moreover each component of the solution can be translated independently of the other one.

System (3.12) is similar to system (3.5) for stationary points in the system with local consumption, that is for the system of competition of species without space distribution. If $d_i = I_0^2/\sigma_i$, $i = 1, 2$, then the right-hand sides of these systems coincide, and the conditions of existence of solutions are equivalent. In the general case they can be different. This means that conditions of existence species with distributed genotypes can be different in comparison with the classical model of competition of species.

3.4. Nonlocal and global consumption

We considered above three examples where local, nonlocal and global consumption terms were taken separately. We will finish this section with another important example where nonlocal and global terms interact:

$$\frac{\partial u}{\partial t} = d_1 \, \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{14} J(v) - b_{15} I(u)) - \sigma_1 u, \tag{3.13}$$

$$\frac{\partial v}{\partial t} = d_2 \, \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{23} J(u) - b_{26} I(v)) - \sigma_2 v. \tag{3.14}$$

In the first equation consumption of resources is global for the first species and nonlocal for the second one. It is opposite in the second equation. If $b_{14} = b_{23} = 0$, then the two equations are decoupled. Each of them has a stationary pulse solution. Denote them by $u_0(x)$ and $v_0(x)$ respectively. There are two families of stationary solutions, $u_0(x+h_1)$ for the first equation, $v_0(x+h_2)$ for the second equation, $h_1, h_2 \in \mathbb{R}$.

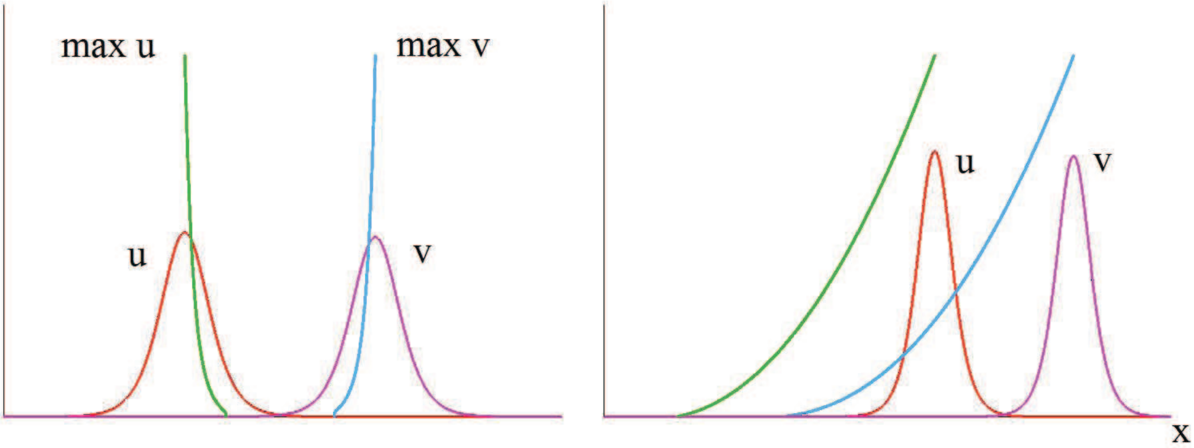

Figure 6. Pulse dynamics described by system (3.13), (3.14). Pulses go away from each other (left) if the interaction coefficients are positive ($b_{14} = b_{23} = 0.1$). One pulse pursuits another one if the coefficients have different signs ($b_{14} = -0.1, b_{23} = 0.1$). The other parameters are as follows: $a_1 = a_2 = 10, \sigma_1 = \sigma_2 = 0.1$, $b_{15} = b_{26} = 0.02$, $d_1 = d_2 = 2$ (left), $d_1 = d_2 = 1$ (right).

If the coefficients b_{14} and b_{23} are different from zero, then the nonlocal terms provide interaction between the pulses. These interaction is repulsive if both parameters are positive: the pulses slowly move away (Figure 6, left). When the distance between them increases and tends to infinity, the cross terms decay, and each of the pulses approaches a stationary solution for the corresponding equation.

Behavior of solutions is different if one of these two parameters is negative and another one is positive. If $b_{14} < 0$ and $b_{23} > 0$, then the first pulse ($u(x,t)$) pursuits the second one ($v(x,t)$) (Figure 6, right), while the later tries to escape. It is a variant of predator-pray model with distributed genotypes. Nevertheless, the distance between the pulses grow and they approach stationary solutions for the corresponding equations. For greater values of the diffusion coefficients, the pulses becomes larger and their interaction stronger. We observe complex oscillations where the pulses can cross each other (Figure 7).

4. Space dependent coefficients

At the next step of modelling, we need to introduce equations with the coefficients which depend on the space variable x. From the biological point of view this means that the rate of mortality and other characteristics of the population depend on the genotype.

4.1. Pulse dynamics

We begin with the scalar equation with global consumption of resources (Section 2.3) where the mortality rate depends on x. Consider the equation

$$\epsilon \frac{\partial u}{\partial t} = d \frac{\partial^2 u}{\partial x^2} + au^2(1 - sI(u)) - \sigma(x)u, \quad I(u) = \int_{-\infty}^{\infty} u(y,t)dy \; , \tag{4.1}$$

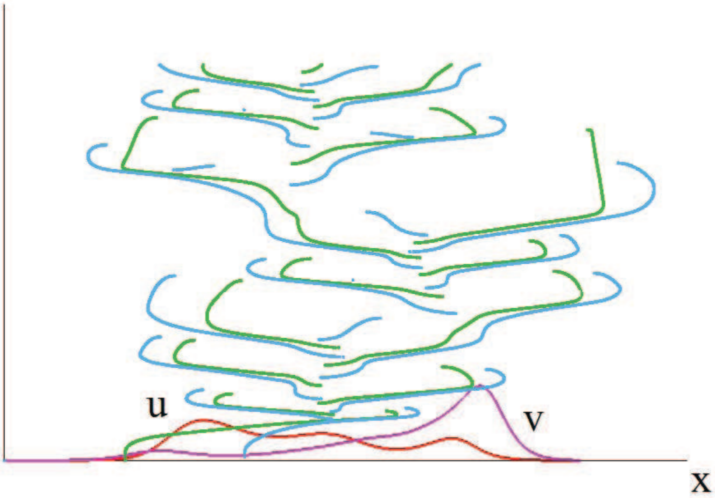

FIGURE 7. Complex oscillations are observed for greater values of diffusion coefficients ($d_1 = d_2 = 5$). Other parameters are the same as in Figure 6 (right).

where ϵ is a small positive parameter, $\sigma(x) = \sigma_0 + \epsilon\sigma_1(x)$, σ_0 is a constant and $\sigma_1(x)$ is some given function. We will look for a solution in the form of a moving pulse:

$$u(x,t) = w_0(x - \xi(t)) + \epsilon w_1(x - \xi(t)), \tag{4.2}$$

where $w_0(x)$ is a solution of the equation

$$w'' + aw^2(1 - I(w)) - \sigma_0 w = 0 \tag{4.3}$$

($d = 1, s = 1$). It is a positive even function with zero limits at infinity. We substitute the function (4.2) into equation (4.1) and keep the first-order terms with respect to ϵ:

$$w_1''(x) + 2aw_0(x)w_1(x)(1 - I(w_0)) - aw_0^2(x)I(w_1) - \sigma_0 w_1(x) =$$

$$\sigma_1(x + \xi(t))w_0(x) - w_0'(x)\xi'. \tag{4.4}$$

This is a linear equation with respect to w_1. The corresponding formally adjoint operator has a unique eigenfunction w_0' corresponding to the zero eigenvalue [34]. Applying the solvability condition in the form of orthogonality in L^2 to this eigenfunction, we obtain the equation

$$\xi' = -\frac{1}{2I_2}\int_{-\infty}^{\infty} \sigma_1'(x + \xi)w_0^2(x)dx, \quad I_2 = \int_{-\infty}^{\infty} (w_0'(x))^2 dx \tag{4.5}$$

which determines pulse dynamics. In particular, if $\sigma(x)$ is a decreasing function, the pulse coordinate $\xi(t)$ increases. It moves in the direction where the mortality rate decreases. If $\sigma(x)$ is a linear function, then equation (4.5) gives a constant speed of pulse motion:

$$\xi' = -\frac{I_1}{2I_2}\sigma_1', \quad I_1 = \int_{-\infty}^{\infty} w_0^2(x)dx.$$

Numerical simulations of equation (4.1) show that indeed the speed of pulse motion is close to constant at the intervals where $\sigma(x)$ is linear (Figure 8).

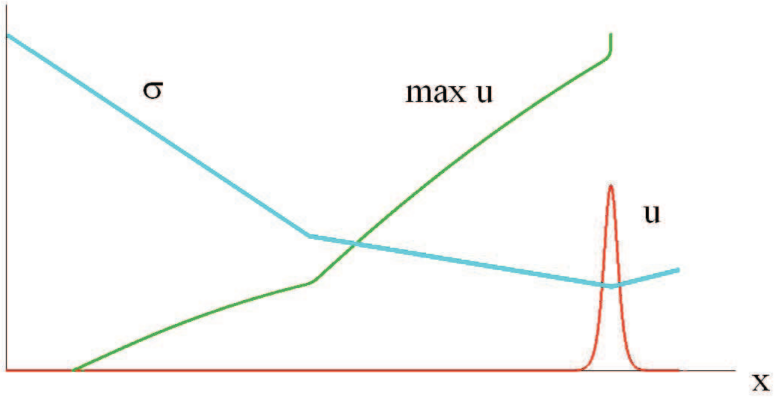

FIGURE 8. Motion of the pulse described by equation (4.1) in the (x, t)-plane (green curve). The function $\sigma(x)$ is piecewise linear (blue curve). In the intervals where it is linear, the pulse speed is close to a constant in agreement with the analytical formula. The pulse arrives to the minimum of the function $\sigma(x)$ and stays there. The values of parameters: $\epsilon = 1, d = 0.5, a = 10, s = 0.02, N = 3$, $\sigma(0) = 1$, $\sigma(x) = 0.25$ at the point of minimum.

Pulse dynamics is studied for some reaction-diffusion systems [27], [30], [38], [39].

4.2. Competition of species

We are now ready to study pulse motion in the system of competition of species with space dependent coefficients. We will restrict ourselves to the particular examples which we need to model Darwin's diagram. Our goal is to obtain extinction of species due to competition with another species when they approach each other in the space of phenotypes. Conventional models of competition of species do not describe this effect. We consider the system of equations with nonlocal and global consumption:

$$\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{14} J(v) - b_{15} I(u)) - \sigma_1(x) u, \tag{4.6}$$

$$\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{23} J(u) - b_{26}(x) I(v)) - \sigma_2(x) v. \tag{4.7}$$

It is similar to system (3.13), (3.14) but some coefficients depend on x. We set $\sigma_1(x) = 1 - x/L$, $\sigma_2(x) = x/L$. Hence the first mortality rate decreases and the second one increases as functions of x. Let us begin with a simpler case where $b_{14} = 0$ and b_{26} is a constant. Then the first equation of this system is independent of the second one, and it is similar to the equation considered in Section 4.1.

The integral $J(u)$ in the second equation provides interaction of two pulses. When the distance between them is sufficiently large, the second species does not feel the presence of the first one. When this distance decreases, the integral grows, and the second species moves away from the first one. Figure 9 (left) shows position of the pulses in time, that is the maxima of the functions $u(x, t)$ and $v(x, t)$. The first pulse increases its coordinate (green curve) since the mortality rate $\sigma_1(x)$ is a decreasing function. The second pulse (blue curve) moves in the opposite direction since the function $\sigma_2(x)$ is increasing. The speed of its motion is slower since the diffusion coefficients are taken different, $d_1 > d_2$. However, when the first pulse approaches, the second one changes its direction of motion trying to escape. They move in the same way though the mortality rate for the second species increases. Therefore the first pulse pushes the second one in the conditions unfavorable for it. However, the second species persists. It does not disappear since equation (4.3) has a solution for any values of σ_0. It becomes narrower with a greater maximal value.

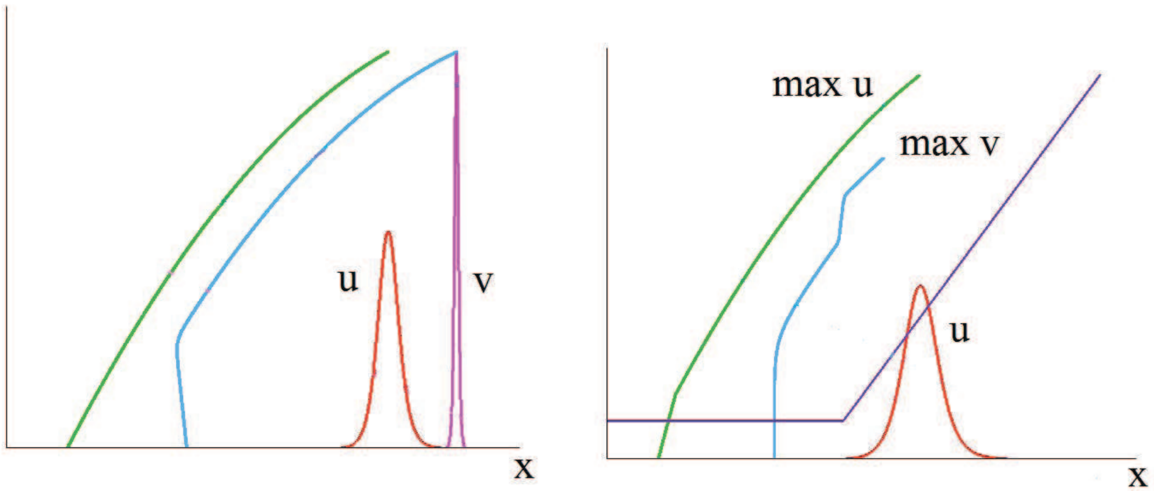

FIGURE 9. Numerical simulations of system (4.6), (4.7). Left: $\sigma_1(x)$ is a decreasing function, $\sigma_2(x)$ is an increasing function, $b_{14} = 0$, b_{26} is constant. The first pulse increases its coordinate (green curve) and pushes the second pulse in the same direction (blue curve). Right: simulations of the cold war model. The first pulse pushes the second one in the direction where it increases global consumption (coefficient $b_{26}(x)$, magenta curve). The second pulse resists but finally disappears. The values of parameters: $d_1 = 1, d_2 = 0.2, a_1 = a_2 = 10, b_{14} = 0, b_{15} = 0.02, b_{23} = 1, b_{26} = 0.02$ (left); $d_1 = 1, d_2 = 1, a_1 = a_2 = 10, b_{14} = 0, b_{15} = 0.02, b_{23} = 1, b_{26}(x) = 0.1 - 0.5$, $\sigma_2 = 10$ (right).

Thus we come to the important conclusion that competition of species with distributed genotype does not result in the extinction of one of them when they meet in the space of phenotypes. The second species survives since it constantly changes its phenotype and, as a consequence, the type of resources which it consumes. It happens even if the second species worsens its living conditions due to increasing mortality.

4.2.0.3. Cold war model. We need to add one more element in the model in order to obtain the desired effect. We will suppose that the coefficient b_{26} is also space dependent. This coefficient shows the rate of global consumption of resources. As before, the first species pushes the second one in the direction of increasing coordinate where the mortality rate for the first species is less. The second species, when it moves in this direction, increases the coefficient $b_{26}(x)$ at the pulse location. It results in its extinction since pulse solutions do not exist when the coefficient of global consumption is sufficiently large (Section 2.3).

Figure 9 (right) shows the dynamics of pulses. The first pulse (green curve) increases its coordinate, the second pulse (blue curve) in the beginning does not move ($\sigma_2(x)$ is constant). When the first pulse approaches the second one, they begin to move together in the same direction till the point where the function $b_{26}(x)$ begins to increase (violate curve). At this point the second species becomes subject to two unfavorable effects, action from the first species and increase of global consumption rate for itself. During some time the second pulse does not move. However the influence of the first species continuous to increase and the second pulse starts again its motion. After that it rapidly extincts.

Thus, the first species pushes the second one in unfavorable conditions where it increases its global consumption. This increasing consumption (and not the direct action of the first species) results in its extinction. We will call it the cold war model keeping in mind other possible applications.

4.2.0.4. Competition with multiple pulses. We will finish this section with the model which describes competition of a single pulse with multiple pulses:

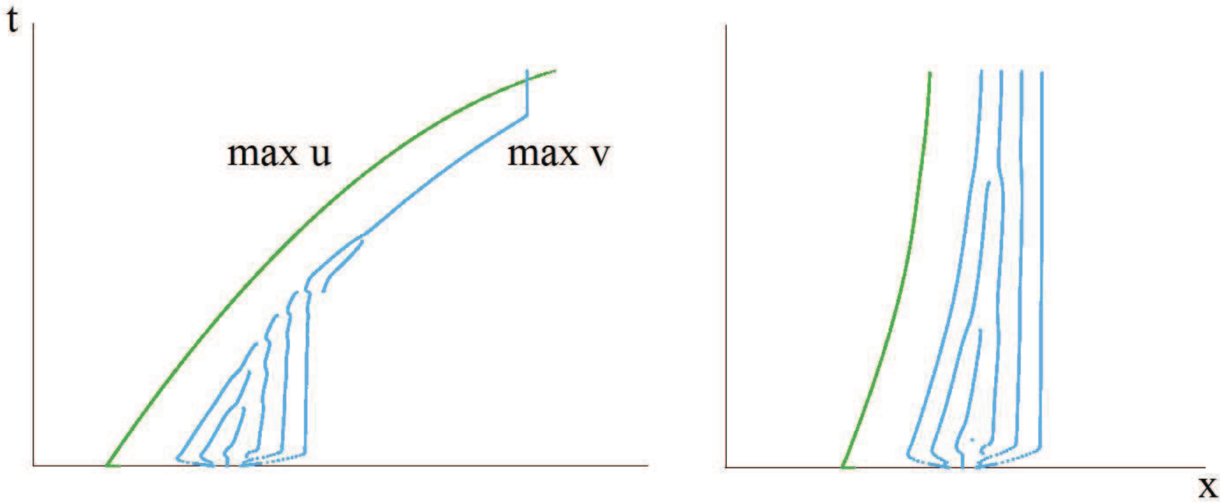

Figure 10. Numerical simulations of system (4.8), (4.9). The first pulse (green curve) increases its coordinate moving in the direction where $\sigma_1(x)$ is less. If $b_{14} = 0$ (left), then it eliminates all pulses of the second species (blue curves) except for the last one. If $b_{14} > 0$ (right), then it stops after eliminating some pulses of the second species. The values of parameters: $d_1 = 5, d_2 = 1, a_1 = a_2 = 10, b_{15} = 0.02, b_{23} = 2, b_{24} = 0.4, b_{26} = 0.02 - 4$.

$$\frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{14} J(v) - b_{15} I(u)) - \sigma_1(x) u, \tag{4.8}$$

$$\frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + a_2 v^2 (1 - b_{23} J(u) - b_{24} J(v) - b_{26}(x) I(v)) - \sigma_2(x) v. \tag{4.9}$$

This system differs from the previous one by the term $b_{24}J(v)$ in the second equation. Similar to the model considered in Section 2.2, this term leads to appearance of a periodic wave for the second variable. However its propagation is bounded by the presence of the first species from one side and by increasing coefficient $b_{26}(x)$ from the other side. The interaction of a single pulse (first species) with multiple pulses (second species) is shown in Figure 10. If $b_{14} = 0$, that is the second species does not act on the first one, then the first five pulses of the second species (blue curves) disappear one after another while the last one persists (Figure 10, left). If the coefficient b_{14} is positive, then the first species stops after eliminating several pulses of the second species (Figure 10, right).

5. Modelling of the diagram

We have introduced all models which we need to reproduce the main elements of Darwin's diagram.

5.0.0.5. Species. If we consider the diagram from the bottom upwards (in the direction of growing time), then it begins with nine lines denoted by the letters $A, B, ..., L$. Each line corresponds to one species. The horizontal axis measures "resemblance of species" which can be considered as some their morphological characteristics (phenotype). Hence each species is considered as a group of individuals localized in the space of morphological variable.

In the models, we consider the density $u(x,t)$ of the population as a function of the morphological variable x and of time t. In order to be interpreted as a species, the population density should have localized peaks or pulses separated from each other. We obtain stable single pulses in the model with sexual reproduction and global consumption (Section 2.3). Multiple pulses are obtained in the model with nonlocal and global consumption (Section 2.4). The species $A, B, ..., L$ can be considered either as ensemble of single pulses each of them described by its own variable (Section 3.3) or as ensemble of single and multiple pulses. An example is shown in Figure 12 (right lower image) where the species G, H, I, K, L are modelled as a multiple pulse described by a single variable.

5.0.0.6. Speciation. The key point of Darwin's theory is emergence of new species. This is shown in the diagram on many occasions: points $A, a^1, a^2, ..., m^1, m^2, ..., I, z^1, z^2, ...$ Each time there are several lines starting from a single point. These lines are not yet, according to Darwin, real species, but only small variations in the existing species which can give new species in the future. Speciation can be described by the model with nonlocal consumption of resources (sexual and asexual, Section 2.2) and by the model with nonlocal and global consumption of resources (Section 2.4). The difference between them is that the former gives unlimited spreading of the population while the latter only a finite number of pulses.

Let us note that the question about possibility of sympatric speciation was intensively debated in the literature. There are various mathematical models developed to study it [4], [10], [11], [12], [17], [18].

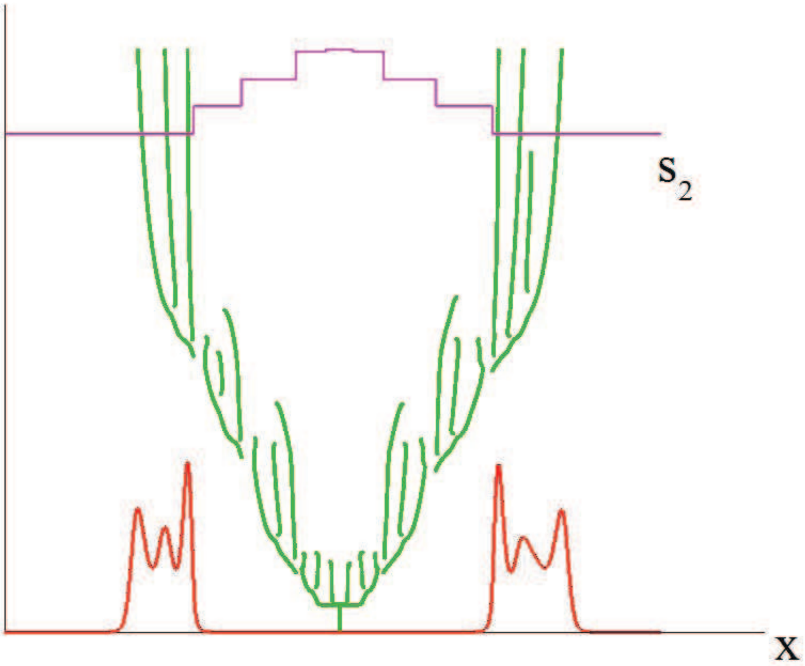

Figure 11. Modelling of the part of the diagram which begins at the point z^6 with equation (2.12). The green lines show the trajectories of the maxima of the function $u(x,t)$, the red curve is a snapshot of solution, the violet line shows the function $s_2(x)$.

5.0.0.7. Survival of better adapted. The next crucial point of the theory is that among several new sub-species only one, at most two survive, the others disappear after relatively short time. However we do not observe this effect in the models introduced before. Once a species appear, it persists. We do not discuss here extinction of species due to change of the environment. This is not the case in Darwin's description. He suggested that survive those which are better adapted (usually located at the exterior with respect to the others).

If we accept that some species (or sub-species) are better adapted than the others, this implies that they differ from each other. For example, their mortality rate or some other parameters can be different. This means that the coefficients of the equation depend on the phenotype, that is on the space variable

x. Once we justify the introduction of space dependent coefficients, we can choose them in such a way that some species survive and some other disappear. It can be regulated through the mortality rate σ or through the parameter s_2 (Section 2.4) which controls the size of the population. Let us emphasize that we consider here the model with nonlocal and global consumption where the total size of the population is limited. Therefore if one of the species grows then the others will decline. This is the mechanism which ensures development of the most adapted to the prejudice of the others. If we consider for example only nonlocal consumption where the size of the population is not limited, then this mechanism does not work.

5.0.0.8. V-pattern. Figure 11 shows an example of numerical simulations of the scalar equation with nonlocal and global consumption of resources and a space dependent function $s_2(x)$. The initial condition is a narrow pulse located at the center of the interval. Due to speciation it gives six pulses.The outer two of these pulses reach the points where the function $s_2(x)$ decreases (step-wise constant function in the same figure). As a consequence, these two outer pulses begin to grow while the others disappear. A similar behavior repeats several times at each step of the function $s_2(x)$. We obtain a specific V-pattern which is one of the main repeating patterns in the diagram. Similar patterns start at the points $A, a^3, a^5, m^4, z^4, z^6$.

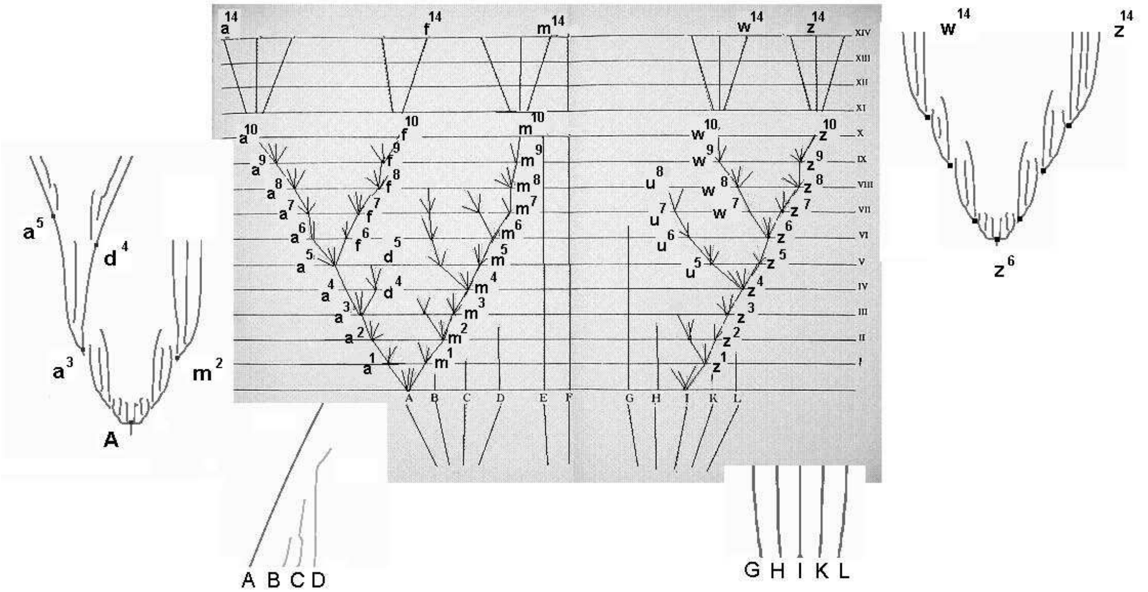

FIGURE 12. Darwin's diagram (center) and numerical simulations showing its main patterns: coexistence of several species (bottom right), V-pattern (top right), extinction of species due to competition (bottom left), time dependent coefficients allowing the species d to return back in the space of phenotypes.

5.0.0.9. Competition of species. Another repeating pattern in the diagram is disappearance of one of the species when two of them approach each other. These are for the example the species B, C and D when the meet the line m. It also happens for G and u and in several other cases. So we need to describe the situation where two species coexist when they have very different morphological characteristics and one of them disappears when their distance in the morphological space is small enough. It happens because they begin to compete for the same resources.

Thus we need to describe a) motion of species in the morphological space, b) their competition when two species are close and the absence of competition when they are far from each other in this space, c) some of the species disappear due to this competition. Clearly, these properties are not described by the conventional model of competition of species which does not take into account their distance in the space of phenotypes.

We use here the cold war model (Section 4.2) for a single or for multiple species. It includes space dependent coefficients, nonlocal and global consumption. An example of its application is shown in Figure 12 (bottom left) where the species B, C and D disappear when they meet the line m starting from the point A.

Let us emphasize some difference of the simulations in comparison with the diagram. In order to survive the species evolve and change their phenotype, that is the corresponding pulse moves before it disappears. Such behavior is observed in all simulations but it is not shown in the diagram.

5.0.0.10. Time dependent coefficients. In order to finish modelling of Darwin's diagram, we need to introduce time dependent coefficients. Let us explain why it is necessary. The pulse moves in such a way that it tends to improve living conditions of the population: decrease the mortality rate, increase natality and the total size of the population. These conditions determine the direction of its motion, and it cannot move in the opposite direction because it would be unfavorable for the population. These observations are in agreement with the biological meaning of the considered models, and they are confirmed by all obtained results.

Consider the line from the point A till a^5 of the diagram. It moves to the left. However the line f, which starts at the point a^5, returns back. If the parameters of the model remain the same, this should not happen because either the line a or the line f would deteriorate life conditions of the corresponding species. Similar behavior is shown in other parts of the diagram (m^4, z^4, z^6). Hence we need to conclude that at the moment when the curve a reaches the point a^5 the coefficients of the equation change. Biologically, this means that the new species possess new properties which modify the corresponding coefficients in the model.

An example of numerical simulations is shown in Figure 12 (left). It starts as the simulation shown in Figure 11. After some time we change the function $s_2(x)$ in order to describe appearance of the branch d starting at the point a^3.

6. Conclusions

Darwin's diagram contains several repeating patterns which play an important role in his theory: coexistence of several species, speciation, survival of most adapted and disappearance of the others, motion of species in the space of phenotypes, competition of species with close phenotypes and disappearance of some of the species due to this competition, species can change the direction of their motion in the space of phenotypes and return back.

These properties are not described by the classical population dynamics. In order to reproduce them in modelling we had to introduce several new models with nonlocal and global consumption of resources, and with space and time dependent coefficients.

Localized solutions (pulses) which correspond to species are described by the model with sexual reproduction and global consumption of resources. Multiple pulses exist in the model with two resources, nonlocal and global. Space dependent coefficients provide pulse motion.

The model of competition of species with nonlocal and global consumption of resources and with space dependent coefficients is used to describe coexistence of species with different phenotypes and disappearance of some of them when the phenotypes become sufficiently close to each other.

Finally, we need to introduce time dependent coefficients to describe inversion of the direction of motion of species in the morphological space.

All these models are reasonable from the biological point of view. They will require more detailed mathematical and numerical investigations. The questions about existence, stability and dynamics of pulses for the models presented here are not yet sufficiently well studied.

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