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Doubly nonlocal reaction-diffusion equations and the emergence of species

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Abstract. The paper is devoted to a reaction-diffusion equation with doubly nonlocal nonlinearity arising in various applications in population dynamics. One of the integral terms corresponds to the nonlocal consumption of resources while another one describes reproduction with different phenotypes. Linear stability analysis of the homogeneous in space stationary solution is carried out. Existence of travelling waves is proved in the case of narrow kernels of the integrals. Periodic travelling waves are observed in numerical simulations. Existence of stationary solutions in the form of pulses is shown, and transition from periodic waves to pulses is studied. In the applications to the speciation theory, the results of this work signify that new species can emerge only if they do not have common offsprings. Thus, it is shown how Darwin's definition of species as groups of morphologically similar individuals is related to Mayr's definition as groups of individuals that can breed only among themselves.

1 Nonlocal equations in population dynamics

Nonlocal reaction-diffusion equations arise in various applications. In population dynamics they are widely used in order to describe nonlocal consumption of resources [14, 18, 21, 27] or breeding with different phenotypes [8, 15, 16]. The roles of these nonlocal terms are quite different, from the biological and from the modelling points of view. In this work we will consider both of them at the same time and will study their mutual influence. Their combination will allow us to make some important conclusions about the emergence of biological species.

We consider the nonlocal reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + a(S(u))^2(1 - J(u)) - bu, \tag{1.1}$$

where D, a and b are some positive constants,

$$S(u) = \frac{1}{2h_1}\int_{-\infty}^{\infty}\psi(x-y)u(y,t)dy, \quad \psi(z) = \begin{cases} 1, & |z| \le h_1 \\ 0, & |z| > h_1 \end{cases},$$

$$J(u) = r(h_2)\int_{-\infty}^{\infty}\phi(x-y)u(y,t)dy, \quad \phi(z) = \begin{cases} 1, & |z| \le h_2 \\ 0, & |z| > h_2 \end{cases}.$$

We take the kernels of the integrals in the form of step-wise constant functions in order to simplify analysis and simulations. Other kernels can also be considered. We will set $r(h_2) = 1/(2h_2)$ or $r(h_2) = 1$. In the first case, in the limit of small h_2 we get $J(u) = u$ similar to the local consumption of resources in the logistic equation. In the case of asymptotically large h_2 we put $r(h_2) = 1$. Then in the limit of large h_2 we obtain global consumption of resources with the integral $I(u) = \int_{-\infty}^{\infty} u(y,t)dy$ in the consumption term.

Various particular cases of this equation are studied in the literature (see [1, 27, 31] and the references therein). In the limit of small h_1 and h_2 we obtain the classical reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + au^2(1-u) - bu. \tag{1.2}$$

If $b < a/4$, then the nonlinearity has three zeros, $u_+ = 0$, $u_0 = (1-\sqrt{1-4b/a})/2$ and $u_- = (1+\sqrt{1-4b/a})/2$. In this case there is a travelling wave solution of this equation, $u(x,t) = w(x-ct)$ with the limits $w(\pm\infty) = u_\pm$. It exists for a unique value of c and it is globally asymptotically stable (see [27, 34] and the references therein). This equation also has stationary solutions in the form of pulses, that is positive solutions with zero limits at infinity. Such solutions are unstable.

If $h_1 > 0$ and $h_2 = 0$, then equation (1.1) corresponds to the local consumption of resources and breeding with possibly different phenotypes (see Appendix):

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + a(S(u))^2(1-u) - bu. \tag{1.3}$$

Similar to the previous case, existence and stability of travelling waves for this equation is proved [8, 15, 16]. The next particular case of equation (1.1) is $h_1 = 0$ and $h_2 > 0$:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + au^2(1-J(u)) - bu. \tag{1.4}$$

Contrary to the previous equation, the maximum principle is not applicable here, and the wave existence is proved only for h_2 sufficiently small [5, 6] or in some other special cases [3]. Propagation of periodic waves is observed in numerical simulations for the values of h_2 greater than some critical value h_2^* for which the homogeneous in space solution $u = u_-$ loses its stability resulting in appearance of stationary periodic solutions.

In the monostable stable case (u^2 in the production term is replaced by u), existence of waves is proved for all speeds greater than or equal to the minimal speed [2, 4, 12, 20],

stability of waves is studied in [32], their dynamics in [5, 10, 18, 23, 24]. Systems of equations are studied in [11, 25, 27, 36].

Equation (1.4) has stationary solutions in the form of pulses for all h_2 sufficiently large ($r(h_2) = 1$) [33]. Numerical simulations show that these pulses are stable [13, 28, 29], though their stability is not proved analytically.

Thus, equation (1.4) has travelling waves propagating with a constant speed and profile for h_2 sufficiently small. Periodic waves are observed for intermediate values of h_2 and pulses for h_2 sufficiently large. Transition from periodic waves to pulses occurs through a global bifurcation where the speed of the periodic wave converges to zero and the peaks of the wave form the pulses [29].

Equation (1.4) is a limiting case of equation (1.1) as h_1 converges to 0. In this work we will study how dynamics of solution is influenced by the integral $S(u)$ for positive h_1. The linear stability analysis of the homogeneous in space solutions is presented in Section 2. Dynamics of pulses and waves is discussed in Section 3. The derivation of the model and positiveness of solutions are discussed in the appendix.

One of the important applications of nonlocal reaction-diffusion equations concerns the theory of speciation. Nonlocal consumption of resources allows the description of the emergence of biological species [17, 18, 19, 31]. The integral $S(u)$ in the reproduction term is determined by the relation between the phenotypes of parents. We will show that speciation can occur only if this distribution is sufficiently narrow. This is related to Mayr's definition of species as a group of individuals that can breed only among themselves. We discuss these questions in Section 4.

2 Linear stability analysis

2.1 Nonlocal consumption

We begin with the stability analysis of a homogeneous in space stationary solution. Linearizing equation (1.1) about $u = u_*(= u_\pm, u_0)$, we obtain the eigenvalue problem:

$$Dv'' + 2au_*(1 - u_*)S(v) - au_*^2 J(v) - bv = \lambda v. \tag{2.1}$$

Taking the Fourier transform, we find the spectrum:

$$\lambda = -D\xi^2 + 2au_*(1 - u_*)\tilde{\psi}(\xi) - au_*^2\tilde{\phi}(\xi) - b, \tag{2.2}$$

where

$$\tilde{\psi}(\xi) = \frac{\sin(\xi h_1)}{\xi h_1}, \quad \tilde{\phi}(\xi) = \frac{\sin(\xi h_2)}{\xi h_2}.$$

In the limit of small h_1 and h_2, which corresponds to the local reaction-diffusion equation, we obtain that the solution $u = u_-$ is always stable. Since $\tilde{\phi}(\xi) \leq 1$, then the function $\tilde{\phi}$ moves

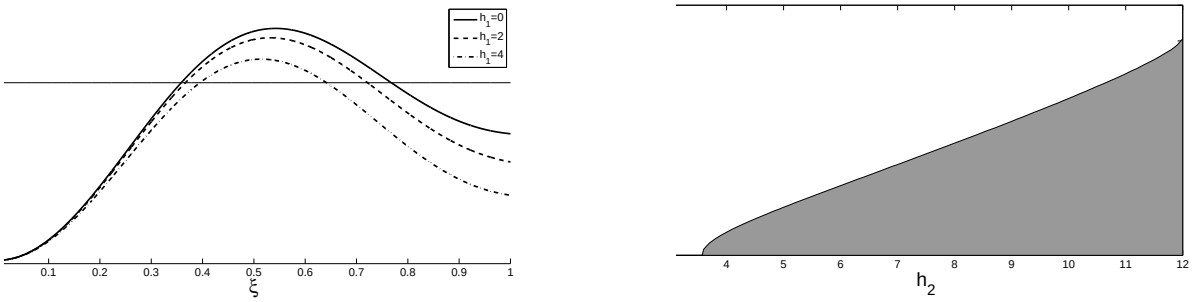

Figure 1: Linear stability analysis. The eigenvalue λ in (2.2) for $D = 0.2$, $a = 1$, $b = 0.1$, $h_2 = 5$ and for different values of h_1 (left). Stability region (white) and instability region (grey) on the (h_2, h_1) plane.

the spectrum to the right, and it can destabilize the solution. Hence nonlocal consumption of resources can lead to the instability of the homogeneous in space stationary solution. This result is known from the numerous previous works [14, 18, 19, 21]. The function $\tilde{\psi} \leq 1$ moves the spectrum to the left, and it stabilizes the solution.

The eigenvalue λ as a function of ξ is shown in Figure 1 (left). It is negative for $\xi = 0$ and positive on some interval of ξ providing the instability of the stationary solution. The interval where it is positive decreases with the increase of h_1. Stability boundary is given by the values of parameters for which the maximal value of $\lambda(\xi)$ equals 0. Stability and instability regions on the plane (h_2, h_1) are presented in Figure 1 (right). The instability region is below the curve. Increase of h_2 destabilizes the solution while increase of h_1 stabilizes it.

2.2 Global consumption

The integral $I(u) = \int_{-\infty}^{\infty} u(x,t)dx$ is well defined only for functions $u(x,t)$ integrable on the whole axis. Therefore in order to study the emergence of pulses in the case of global consumption, we will consider a similar equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + au^2(1 - I_0(u)) - bu, \quad I_0(u) = \int_0^L u(y,t)dy \tag{2.3}$$

on a bounded interval $0 < x < L$ with the no-flux boundary conditions: $x = 0, L : \partial u/\partial x = 0$. To simplify the presentation, we consider the particular case where $S(u) = u$ ($h_1 = 0$).

We look for homogeneous in space stationary solutions of equation (2.3). If $b < a/(4L)$, then this problem has three constant solutions, $w = 0$, and two solutions of the equation

$$aw(1 - I_0(w)) = b. \tag{2.4}$$

We denote them by w_1 and w_2 assuming that $w_1 < w_2$.

Consider next the eigenvalue problem for the equation linearized about a constant solution u_*:

$$Du'' + 2au_*(1 - I_0(u_*))u - bu - au_*^2 I_0(u) = \lambda u, \quad u'(0) = u'(L) = 0. \tag{2.5}$$

Taking into account (2.4) we can write it as follows:

$$Du'' + bu - au_*^2 I_0(u) = \lambda u, \quad u'(0) = u'(L) = 0. \tag{2.6}$$

We will search its solutions in the form

$$u(x) = \cos(n\pi x/L), \quad n = 0, 1, 2, ...$$

Then we get

$$\lambda_0 = b - au_*^2 L, \quad \lambda_n = -D(n\pi/L)^2 + b, \quad n = 1, 2, ...$$

Hence the presence of the integral term influences only the eigenvalue λ_0. From (2.4) we get

$$\lambda_0 = au_*(1 - 2Lu_*).$$

If equation (2.4) has two solutions, then $\lambda_0 > 0$ for $u_* = w_1$ and $\lambda_0 < 0$ for $u_* = w_2$.

Thus, the problem linearized about solution w_2 has negative eigenvalue λ_0. The eigenvalue λ_1 can be negative or positive. If it is negative, this solution is stable, otherwise it is unstable and another solution bifurcates from it. We can consider D as bifurcation parameter with the critical value $D^* = bL^2/\pi^2$. If $D < D^*$, then a non-homogeneous stable solution emerges. Since the eigenfunction $\cos(\pi x/L)$ corresponding to the eigenvalue λ_1 has its extrema at the boundary, then the emerging solution has also its maximum at the boundary of the interval. If we consider a double interval, then this solution corresponds to the pulse solution.

3 Waves and pulses

3.1 Wave propagation

Travelling wave solution of equation (1.1) is a solution $u(x,t) = w(x - ct)$, where the function $w(\xi)$ satisfies the equation

$$Dw'' + cw' + a(S(w))^2(1 - J(w)) - bw = 0, \quad w(\pm\infty) = u_\pm. \tag{3.1}$$

The constant c is the wave speed. It is a priori unknown and should be found as a solution of the problem. We suppose here that $r(h_2) = 1/(2h_2)$. In the limit of small h_2 we have $J(w) = w$, and we obtain equation (1.3) for which the existence of waves is proved [8, 15]. Therefore we can expect that the waves also exist for all h_2 sufficiently small.

Theorem 3.1. *For any $h_1 > 0$ and for all $h_2 > 0$ sufficiently small problem (3.1) has a monotonically decreasing solution for a unique value of c.*

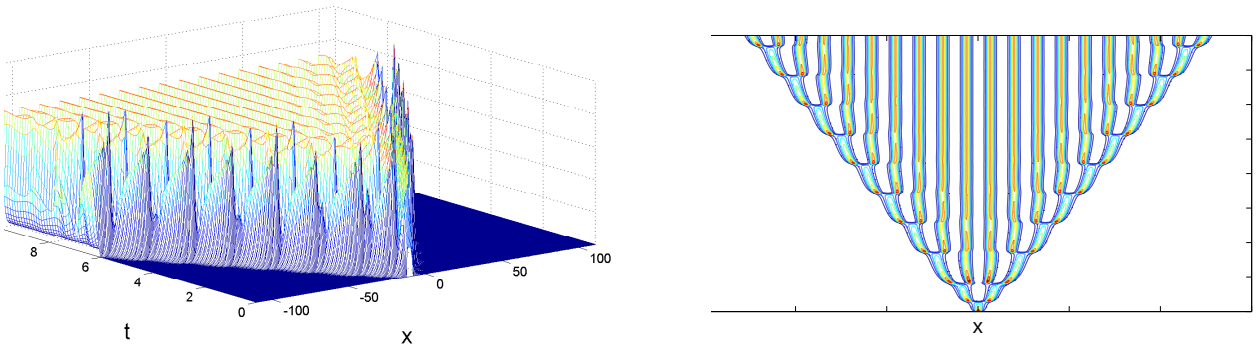

Figure 2: Propagation of periodic waves for equation (1.1). Solution $u(x,t)$ as a function of two variables (left). The same solution as levels lines of the function $u(x,t)$ on the (x,t) plane.

The proof of this theorem is similar to the proof of the corresponding theorem in [5, 6]. We use here the existence of solutions for the limiting equation (1.3) and the implicit function theorem. The spectrum of the operator linearized about the solution is completely in the left-half plane except for a simple zero eigenvalue [16]. Therefore the operator is invertible on the subspace orthogonal to the corresponding eigenfunction. This perturbation method is conventionally used for travelling waves [27].

The wave existence is proved only for sufficiently small values of h_2. For larger h_2 we can study wave propagation in numerical simulations. When we increase h_2, the wave becomes non-monotone with respect to x. For h_2 sufficiently large, the homogeneous in space solution $u = u_-$ becomes unstable resulting in appearance of a stable stationary space periodic solution. For such values of h_2 we observe propagation of a periodic wave where its speed and its profile change periodically in time (Figure 2). This behavior is qualitatively similar to the behavior of solutions of equation (1.4).

3.2 Existence of pulses

Equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + au^2(1 - I(u)) - bu, \tag{3.2}$$

where

$$I(u) = \int_{-\infty}^{\infty} u(x,t)dx$$

is the limiting case of equation (1.4) as $h_2 \to \infty$ ($r(h_2) = 1$). It can be easily verified that it has a pulse solution if $a > a_c$, where the critical value a_c depends on D and b [27]. Equation (3.2) is formally obtained from equation (1.1) in the limit of small h_1 and large h_2. Existence of pulses for equation (1.1) is given by the following theorem.

Theorem 3.2. *For any D, b and $a > a_c(D, b)$ equation (1.1) has a positive stationary solution vanishing at infinity for all h_1 sufficiently small and h_2 sufficiently large ($r(h_2) = 1$).*

The proof of this theorem is similar to the proof of the existence of pulses for equation (1.4) [33]. It is based on the existence result for equation (3.2), implicit function theorem and spectral properties of the linearized operator. Existence of pulses for a system of two equations describing male and female density distributions is proved in [30]. Example of a pulse solution obtained in numerical simulations is shown in Figure 3 (left).

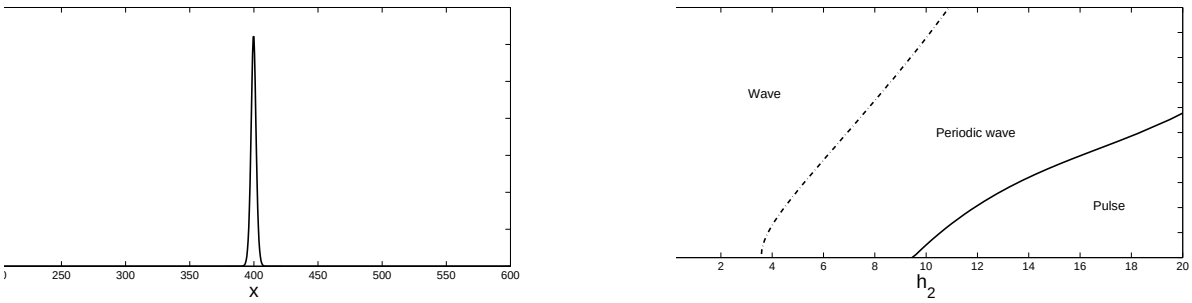

Figure 3: Pulse solution for equation (1.1) (left). The regions with different regimes on the (h_2, h_1) plane (right).

3.3 Transition between different regimes

Depending on the values of parameters equation (1.1) can have solutions of different types. For all other parameters fixed, usual travelling waves (with a constant speed and profile) are observed for sufficiently small values of h_2. Periodic travelling waves exist for intermediate values and stable pulses for sufficiently large h_2. Pulses exist also for other values of h_2 but they are unstable. The regions on the (h_2, h_1) plane where simple waves, periodic waves and stable pulses are observed numerically are shown in Figure 3 (right).

Transition from simple to periodic waves occurs due to the essential spectrum crossing the imaginary axis. This type of bifurcations is discussed in [29] for equation (1.4). The homogeneous in space stationary solution $u = u_-$ loses its stability resulting in appearance of a stationary periodic solution. The travelling wave connects the constant value $u = u_+$ for $x = +\infty$ with this periodic solution for $x \to -\infty$. Therefore the wave becomes also periodic.

Transition from periodic travelling waves to pulses occurs according to the following scenario. The average speed of periodic travelling waves decreases when h_2 increases. For h_2 sufficiently large this speed becomes zero. Instead of a periodic travelling wave we obtain one or several pulses. If there are more than one pulse, then they slowly move from each other with a speed decaying in time. The number of pulses depends on the initial condition (Figure 4).

Both transitions are influenced by the value of h_1. Increase of h_1 stabilizes simple waves versus periodic waves, and periodic waves versus pulses.

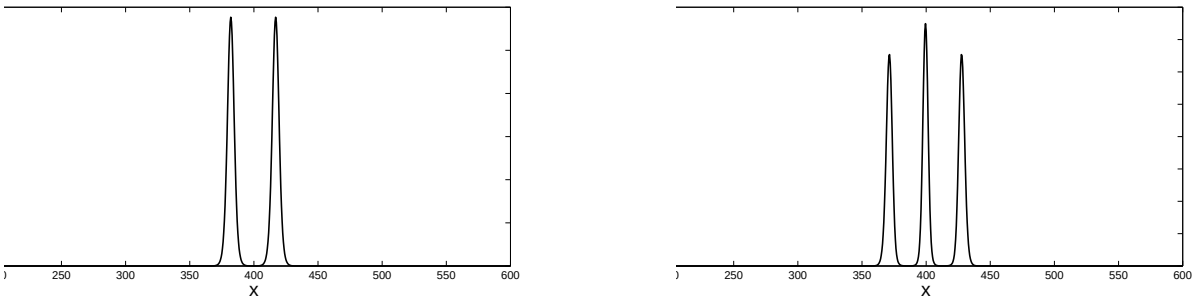

Figure 4: Solutions of equation (1.1) with two and three pulses. The pulses slowly move from each other.

4 Discussion

Nonlocal consumption of resources in reaction-diffusion equations changes dynamics of solutions resulting in appearance of periodic travelling waves and stable pulses that do not exist for the usual (scalar) reaction-diffusion equations. In this work we introduce an additional nonlocal term in the reproduction rate. From the biological point of view, it shows that offsprings can have phenotype different from the phenotype of parents. If nonlocal consumption of resources destabilizes solutions, the second nonlocal term stabilizes them. This conclusion concerns the transition from the homogeneous in space solution to a periodic solution, transition from simple waves to periodic waves, and transition from periodic waves to stable pulses.

Spectrum, stability, bifurcations. The influence of integral terms on stability can be studied analytically for the homogeneous in space stationary solution. Nonlocal consumption destabilizes this solution leading to the bifurcation of periodic in space solutions due to a real eigenvalue crossing the origin.

The situation is different in the case of global consumption where the kernel of the integral identically equals 1. The integral $I(u)$ is defined only for integrable functions. Therefore we cannot consider the homogeneous in space stationary solution on the whole axis if it is different from 0. In order to study stability of such solutions and the emergence of pulses, we consider this equation on a bounded interval.

The origins of the instability for nonlocal and global consumption are different. Consider first the eigenvalue problems (2.1). Since $\tilde{\phi}(\xi) = 1$ for $\xi = 0$ and $\tilde{\phi}(\xi)$ can be negative for some $\xi \neq 0$, then the integral term can lead to the instability of solution with some periodicity determined by this value of ξ. In this case the instability occurs due to the principal eigenvalue crossing the origin from the left half-plane to the right half-plane.

On the other hand, in problem (2.6), $I_0(u) = 0$ for $\xi \neq 0$ (admissible ξ are determined by the length L of the interval) and $I_0(u) \neq 0$ only for $\xi = 0$. Hence $I_0(u)$ changes only the principal eigenvalue and does not influence other eigenvalues. Since $b > 0$, then the principal eigenvalue of the operator $Tu = Du'' + bu$ is positive. The integral $I_0(u)$ moves it

to the left half-plane. Hence stability of solutions is determined by the second eigenvalue of the operator T. If it is positive, then the homogeneous in space stationary solution loses its stability resulting in appearance of the solution with a half period on the interval L ($n = 1$). This solution corresponds to the pulse on the interval $2L$.

Thus, the cases of nonlocal and global consumption differ not only by the origin of instability but also by periodicity of solutions. For the nonlocal consumption, solution can have several periods on the interval $[0, L]$ while for the global consumption only half period. If L increases, the period of nonlocal solution can remain the same while the period of global solution will increase together with L. In this limit as L tends to infinity, we obtain a periodic solution in the nonlocal case and a pulse solution in the global case.

Stability and bifurcations of solutions are determined not only by the eigenvalues but also by the essential spectrum. It can be explicitly determined for the local and nonlocal reaction-diffusion equations [7, 9, 26, 35]. Transition from simple to periodic waves is related to the essential spectrum crossing the imaginary axis. Such bifurcations cannot be studied by conventional methods of the bifurcation theory.

Another unusual bifurcation is observed for the transition from periodic waves to pulses. It is a global bifurcation where peaks of the periodic wave become stationary or slowly moving pulses as the speed of the wave converges to zero.

Emergence of species. One of the important applications of reaction-diffusion equations with nonlocal consumption of resources concerns the emergence of species due to natural selection. In this case, the space variable x corresponds to the phenotype, t is time, $u(x, t)$ is the density distribution with respect to the phenotype (for each t fixed).

Let us begin this discussion with equation (1.4). The first term in the right-hand side of this equation describes small random mutations, the second term reproduction of the population, the last term its mortality. The reproduction term is proportional to the second power of the population density (sexual reproduction) and to available resources. Nonlocal consumption of resources $J(u)$ is related to the intraspecific competition. Indeed, since each individual consumes resources in some area around its average location, then these areas overlap and the individuals compete for resources. This nonlocal term leads to the appearance of separated peaks of the density distribution which do not exist in conventional local models. These peaks in the density distribution correspond to different phenotypes, and we can interpret them as different species. This interpretation corresponds to Darwin's definition of species as groups of morphologically similar individuals. From this point of view, appearance of new peaks in the process of propagation of periodic waves describes the emergence of species [13, 18, 19]. This is sympatric speciation where species are not separated by genetic or geographic barriers.

Emergence of species in this model is based on three assumptions: random mutations (diffusion), intraspecific competition (nonlocal consumption) and reproduction with the same phenotype. Let us discuss the last assumption. The density square in the reproduction term in equation (1.4) corresponds to the product of densities of males and females taken at the same space point x, that is for the same phenotype. Therefore this model implies that the

phenotypes of parents are the same, and the phenotype of offsprings is the same as phenotype of parents. This assumption is restrictive and it is not biologically realistic.

Suppose now that phenotypes of males and females in the production term can be different. How this assumption will influence the emergence of species? Instead of equation (1.4) we consider now equation (1.1). In this case, males and females can have different phenotypes. We suppose that offsprings with phenotype x can be born from males and females with the phenotypes from the interval $(x - h_1, x + h_1)$. This assumption about the phenotypes can be different. We expect that the qualitative behavior of solutions will remain the same.

Since the emergence of species in our model is associated with a periodic wave, then we should determine how the integral $S(u)$ influences the transition from simple to periodic waves. From Figure 3 (right) we conclude that periodic waves exist if h_1 is sufficiently small. Hence if the interval of admissible phenotypes of parents is sufficiently large, then the speciation does not occur.

Furthermore, this figure allows us to conclude that periodic waves appear if $h_1 < h_2$. Let us recall that nonlocal consumption of resources determines periodicity of solutions. Namely, there is one peak of the population density in the interval $2h_2$. Condition $h_1 < h_2$ means that the individuals from the two neighboring peaks (species) cannot have common offsprings; species are reproductively isolated. The impossibility to have common offsprings can be determined by morphological or by genetic differences in the individuals and not by some imposed exterior barriers at it is the case in the allopatric speciation.

This conclusion corresponds to Mayr's definition of species. He suggested that a species is not just a group of morphologically similar individuals, but a group of individuals that can breed only among themselves, excluding all others [22]. Thus we show that species in the sense of Darwin can emerge only if Mayr's condition is satisfied. In terms of the model considered here this condition can be formulated as $h_1 < h_2$.

Emergence of species gives a selective advantage since the total biomass increases [27]. As we discussed above, the species emerge due to the intraspecific competition under the condition of separation of reproduction. On the other hand, separation of reproduction occurs due to the exclusion of the different from the process of reproduction. Therefore we can suppose that exclusion of the different, often observed in nature, is formed in the process of evolution as one of the mechanisms of speciation.

References

[1] M. Alfaro, N. Apreutesei, F. Davidson, V. Volpert. Preface to the Issue Nonlocal Reaction-Diffusion Equations Math. Model. Nat. Phenom., 10 (2015), no. 6, 1-5.

[2] M. Alfaro, J. Coville. Rapid travelling waves in the nonlocal Fisher equation connect two unstable states. Applied Mathematics Letters, 25 (2012), 2095-2099.

[3] M. Alfaro, J. Coville, G. Raoul. Bistable travelling waves for nonlocal reaction diffusion equations. DCDS A. 34 (2014), 1775–1791.

[4] N. Apreutesei, N. Bessonov, V. Volpert, V. Vougalter. Spatial structures and generalized travelling waves for an integro-differential equation. DCDS B, 13 (2010), No. 3, 537-557.

[5] A. Apreutesei, A. Ducrot, V. Volpert. Competition of species with intra-specific competition. Math. Model. Nat. Phenom., 3 (2008), No. 4, 1-27.

[6] N. Apreutesei, A. Ducrot, V. Volpert. Travelling waves for integro-differential equations in population dynamics. DCDS B, 11 (2009), No. 3, 541-561.

[7] N. Apreutesei, V. Volpert. Properness and topological degree for nonlocal reaction-diffusion operators. Abstract and Applied Analysis, 2011, Art. ID 629692, 21 pp.

[8] N. Apreutesei, V. Volpert. Existence of travelling waves for a class of integro-differential equations from population dynamics. International Electronic Journal of Pure and Applied Mathematics, Volume 5 No. 2 2012, 53-67

[9] N. Apreutesei, V. Volpert. Properness and topological degree for nonlocal integro-differential systems. TMNA, 43 (2014), no. 1, 215-229.

[10] O. Aydogmus. Patterns and transitions to instability in an intraspecific competition model with nonlocal diffusion and interaction. Math. Model. Nat. Phenom., 10 (2015), no. 6, 17–29.

[11] A. Bayliss, V.A. Volpert. Patterns for competing populations with species specific nonlocal coupling. Math. Model. Nat. Phenom., 10 (2015), no. 6, 30–47.

[12] H. Berestycki, G. Nadin, B. Perthame, L. Ryzhik. The non-local Fisher-KPP equation: travelling waves and steady states. Nonlinearity, 22 (2009), no. 12, 2813–2844.

[13] N. Bessonov, N. Reinberg, V. Volpert. Mathematics of Darwin's diagram. Math. Model. Nat. Phenom., Vol. 9, No. 3, 2014, 5-25.

[14] N.F. Britton. Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model. SIAM J. Appl. Math., 6 (1990), 1663–1688.

[15] I. Demin, V. Volpert. Existence of waves for a nonlocal reaction-diffusion equation. Math. Model. Nat. Phenom., 5 (2010), No. 5, 80-101.

[16] A. Ducrot, M. Marion, V. Volpert. Spectrum of some integro-differential operators and stability of travelling waves. Nonlinear Analysis Series A: Theory, Methods and Applications, 74 (2011), no. 13, 4455-4473.

[17] S. Genieys, N. Bessonov, V. Volpert. Mathematical model of evolutionary branching. Mathematical and computer modelling, 49 (2009), no. 11-12, 2109–2115.

[18] S. Genieys, V. Volpert, P. Auger. Pattern and waves for a model in population dynamics with nonlocal consumption of resources. Math. Model. Nat. Phenom., 1 (2006), No. 1, 63-80.

[19] S. Genieys, V. Volpert, P. Auger. Adaptive dynamics: modelling Darwin's divergence principle. Comptes Rendus Biologies, 329 (11), 876-879 (2006).

[20] S.A. Gourley. Travelling front solutions of a nonlocal Fisher equation, J. Math. Biol., 41 (2000), 272–284.

[21] S.A. Gourley, M.A.J. Chaplain, F.A. Davidson. Spatio-temporal pattern formation in a nonlocal reaction-diffusion equation. Dynamical systems, 16 (2001), no. 2, 173–192.

[22] E. Mayr. Systematics and the Origin of Species, from the Viewpoint of a Zoologist. Cambridge: Harvard University Press, 1942. *https://en.wikipedia.org/wiki/Ernst_Mayr*

[23] G. Nadin, L. Rossi, L. Ryzhik, B. Perthame. Wave-like solutions for nonlocal reaction-diffusion equations: a toy model. Math. Model. Nat.Phenom., 8 (2013), no. 3, 33–41.

[24] B. Perthame, S. Genieys. Concentration in the nonlocal Fisher equation: the Hamilton-Jacobi limit. Math. Model. Nat. Phenom., 4 (2007), 135–151.

[25] B.L. Segal, V.A. Volpert, A. Bayliss. Pattern formation in a model of competing populations with nonlocal interactions. Physica D, 253 (2013), 12-22.

[26] V. Volpert. Elliptic partial differential equations. Volume 1. Fredholm theory of elliptic problems in unbounded domains. Birkhäuser, 2011.

[27] V. Volpert. Elliptic partial differential equations. Volume 2. Reaction-diffusion equations. Birkhäuser, 2014.

[28] V. Volpert. Branching and aggregation in self-reproducing systems. ESAIM: Proceedings and Surveys, 47 (2014), 116-129.

[29] V. Volpert. Pulses and waves for a bistable nonlocal reaction-diffusion equation. Applied Mathematics Letters, 44 (2015), 21-25.

[30] V. Volpert, N. Reinberg, M. Benmir, S. Boujena. On pulse solutions of a reaction-diffusion system in population dynamics Nonlinear Analysis 120 (2015), 76-85.

[31] V. Volpert, S. Petrovskii. Reaction-diffusion waves in biology. Physics of Life Reviews, 6 (2009), 267-310.

[32] V. Volpert, V. Vougalter. Emergence and propagation of patterns in nonlocal reaction-diffusion equations arising in the theory of speciation. In: "Dispersal, individual movement and spatial ecology", Eds. M. Lewis, Ph. Maini, S. Petrovskii. Springer, Heidelberg, 2013, 331–353.

[33] V. Vougalter, V. Volpert. Existence of stationary pulses for nonlocal reaction-diffusion equations, Documenta Mathematica, 19 (2014) 1141-1153.

[34] A. Volpert, Vit. Volpert, Vl. Volpert. Traveling wave solutions of parabolic systems. Translation of Mathematical Monographs, Vol. 140, Amer. Math. Society, Providence, 1994.

[35] G. Zhao, S. Ruan. The decay rates of traveling waves and spectral analysis for a class of nonlocal evolution equations. Math. Model. Nat. Phenom., 10 (2015), no. 6, 142–162.

[36] P. Zwolenski. Trait evolution in two-sex populations. Math. Model. Nat. Phenom., 10 (2015), no. 6, 163–181.

5 Appendix

5.1 Derivation of the model

Let $w(x,t)$ and $v(x,t)$ be the density distributions of males and females depending on the phenotype x and time t. Suppose that males with phenotype y_1 and females with phenotype y_2 can have offsprings with phenotype x with probability $P(x,y_1,y_2)$. Then in the case of unlimited resources the natality rate of offspring with phenotype x is given by the integral

$$Q(w,v) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} P(x,y_1,y_2)w(y_1,t)v(y_2,t)dy_1dy_2.$$

Taking into account that natality rate depends on the available resources, we obtain the following equations for the distributions of males and females:

$$\frac{\partial w}{\partial t} = D_1\frac{\partial^2 w}{\partial x^2} + a_1Q(w,v)(1-J(w)-J(v)) - b_1w, \tag{5.1}$$

$$\frac{\partial v}{\partial t} = D_2\frac{\partial^2 v}{\partial x^2} + a_2Q(w,v)(1-J(w)-J(v)) - b_2v, \tag{5.2}$$

where

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

Assuming that $D_1 = D_2$, $a_1 = a_2$, $b_1 = b_2$, we get $w = v$ (if the initial conditions are equal), and we can reduce this system to the single equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + aQ(u,u)(1-J(u)) - bu, \tag{5.3}$$

where $D = D_1$, $a = a_1/2$, $b = b_1$.

In order to study this equation, we need to specify the function P. We will suppose that $P(x, y_1, y_2) = p(x - y_1, x - y_2)$, that is the probability density function depends on the difference between the phenotypes. We will consider $p(\xi_1, \xi_2)$ as a piece-wise constant function,

$$p(\xi_1, \xi_2) = r(N) \times \begin{cases} 1 & , \quad |\xi_1| \leq N \text{ and } |\xi_2| \leq N \\ 0 & , \quad |\xi_1| > N \text{ or } |\xi_2| > N \end{cases}, \tag{5.4}$$

where we set $r(N) = 1/N^2$ to get the integral of p equal 1. Then $p(\xi_1, \xi_2) = r(N)\psi(\xi_1)\psi(\xi_2)$, where

$$\psi(\xi) = \begin{cases} 1 & , \quad |\xi| \leq N \\ 0 & , \quad |\xi| > N \end{cases},$$

and $Q(u, u) = (S(u))^2$, where

$$S(u) = \frac{1}{N} \int_{-\infty}^{\infty} \psi(x - y) u(y, t) dy.$$

Hence equation (5.3) can be written as follows:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a(S(u))^2 (1 - J(u)) - bu. \tag{5.5}$$

The particular form of the function P considered above simplifies the analysis of this equation. We expect that the main properties of solutions remain the same for other functions.

5.2 Positiveness of solutions

We will begin with a more complete model for the density u of the population and R of resources:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a(S(u))^2 R - bu, \tag{5.6}$$

$$\epsilon \frac{dR}{dt} = K - f(R) \int_{-\infty}^{\infty} \phi(x - y) u(y, t) dy - \sigma R. \tag{5.7}$$

Here the natality term $S^2 R$ is proportional to available resources. The first term is the right-hand side of equation (5.7) describes production of resources with a constant rate. Consumption of resources $f(R)J(u)$ at space point x depends on available resources through the function $f(R) \geq 0$, $f(0) = 0$, and on the density of individuals $J(u)$ coming from spaces points y.

If we formally put $\epsilon = 0$, then we get

$$R = (K - f(R)J(u))/\sigma.$$

We can substitute this expression into (5.6) but it contains R, and this equation does not represent a closed model. We set

$$f(R) = \begin{cases} f_0 & , \quad R > 0 \\ 0 & , \quad R = 0 \end{cases}.$$

This means that the consumption rate by each individual is constant if there are available resources, and it becomes zero when there are no resources. Then for $R > 0$ we get

$$R = (K - f_0 J(u))/\sigma.$$

Hence equation (5.6) can now be written as

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + a(S(u))^2(K - f_0 J(u))/\sigma - bu, \tag{5.8}$$

assuming that

$$J(u) < K/f_0. \tag{5.9}$$

This equation coincides with equation (1.1) up to the change of variables.

It can be easily verified that if initial condition of system (5.6), (5.7) considered on the whole axis is non-negative, then the solution is also non-negative. Positiveness of solution is preserved for equation (5.8) if condition (5.9) is satisfied. If this condition is not satisfied, then positiveness can be violated. Numerical simulations presented in this work satisfy the positiveness condition.