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PATTERN FORMATION IN A NONLOCAL CONVECTIVE FISHER EQUATION*

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We investigate the nonlocal convective Fisher equation and the conditions for pattern formation. We observe that the width of the influence function completely determines whether the pattern is present.

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1. Introduction

Many studies on pattern formation have been carried out experimentally on systems in which convection plays an important role. The convective cells of Rayleigh–Bernard instabilities [1], moving Wigner glasses [2], and pattern formation in bacterial colonies under forced convection [3] illustrate the phenomenon of self-organization in convective motion. In these cases, a flux of particles is expected to undergo a new regime of organization at the threshold of external parameters. For the Rayleigh–Bernard effect, this parameter is the temperature difference $T - T_0$ between two plates which confine the liquid that exhibits a pattern above a certain critical value of the parameter. In the case of moving Wigner glasses [2], there is a critical electron field E_c above which the system exhibits self-organization, with the electrons moving in separate one-dimensional channels. Finally, in the case of bacterial colonies [4], the bacteria grow in a medium illuminated by fatal

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UV light. A small mask moving at velocity v shields a small region from the radiation creating a favorable patch for growth. For velocities bellow a critical value, the population becomes localized under the mask, whereas for higher velocities, the population tends to extinction. The motivation to consider such model systems of bacteria, both experimentally and theoretically, is that it may help in the understanding of infection propagation in living tissue. Generally, the theoretical investigation of such systems is carried out by modeling the population using a modified form of the Fisher equation, originally used to describe nonlinear evolution effects due to the wave propagation of advantageous genes in a population [5], and nowadays used generally in an ecological context. The Fisher equation growth and competition terms, namely.

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

describes the dynamics of a population (of bacteria, for example) with density $u(x,t)$ subject to diffusive transport with rate D, a growth term with rate a, and a growth-limiting process controlled by a local competition with rate b. It should be noted that although exact solutions for the Fisher equation exist only in special conditions [6], the theoretical investigation of a nonlinear convective equation of a form similar to that of the Fisher equation, namely

$$\frac{\partial u(x,t)}{\partial t} + v\frac{\partial u(x,t)}{\partial x} = a(x)u(x,t) - b(x)u^2(x,t)\,, \tag{2}$$

has yielded analytic solutions with rich behavior [7]. In that study, a "wind" term, responsible for convection, has been used to describe the properties of bacteria flux dynamics where the rate of growth $a(x)$ is spatially dependent.

It has been noted, however, that the inclusion of nonlocality [8, 9] in the Fisher equation can give rise to pattern formation even when we consider a system with only one species. A generalization of the Fisher equation, Eq. (1), is obtained by substituting the local competition term by a nonlocal one

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} + au(x,t) - bu(x,t)\int\limits_{\Omega} f_\mu(x-y)u(y,t)dy\,, \tag{3}$$

such that the interaction between individuals is weighed by an influence function $f_\mu(x-y)$ with a range characterized by μ and normalized in the domain Ω of the system. In this case, a nonlocal interaction term introduced in the Fisher equation may describe "nonhomogeneous" diffusion of nutrients as well as the propagation of toxic substances in bacterial colonies. Indeed nonlocality gives rise to specific patterns which are intrinsically related to the influence function f_μ; if one considers the local influence function $f_\mu(x-y) = \delta(x-y)$, then patterns are not formed.

We start with our analysis by defining the nonlocal convective Fisher equation (NLCFE)

$$\frac{\partial u(x,t)}{\partial t} + v\,\frac{\partial u(x,t)}{\partial x} = au(x,t) - bu(x,t)\int\limits_{\Omega} f_\mu(x-y)u(y,t)dy\,, \tag{4}$$

obtained by replacing the diffusive term in Fisher equation [6–8,10] by a convective one. Here v is the barycentric velocity of the fluid. Based on the NLCFE Eq. (4), we are going to analyze analytical and numerically the limits of the width μ of the influence function f_μ for the existence of pattern formation. Starting from a perturbative analysis we obtain analytically the rate of growth $\gamma(k)$, and so we show that the NLCFE is able to describe pattern formation for systems in regime of convective flux. For a fixed system of length L, we calculate numerically the critical values of μ_c in which NLCFE exhibits self-organization. Finally, we also discuss an interesting relationship between the nonlinearity of the NLCFE and the number of peaks in the population density $u(x,t)$ via a logistic map based on the different values of width μ.

2. Analytical study of the NLCFE

2.1. First order perturbation

To understand how pattern formation occurs in the NLCFE and what parameters govern this regime, we start with the test function

$$u(x,t) = u_0 + \varepsilon\exp(ikx)\exp(\phi t)\,, \tag{5}$$

where u_0 is the homogeneous steady state solution a/b, constant in space and time. The term $\varepsilon\exp(ikx)\exp(\phi t)$ is a perturbation to the steady state that will grow or die out, depending on the values of the wave numbers k. Considering a static velocity field $v(x) \to v$, substituting Eq. (5) into Eq. (4) and retaining only first order perturbative terms, we find a dispersion relation between the pattern growth rate ϕ and the wave number k, given by

$$\phi(k) = -ivk - a\mathcal{F}_\mathrm{c}\{f_\mu(z)\}\,, \tag{6}$$

where $\mathcal{F}_\mathrm{c}\{f_\mu(z)\}$ is the Fourier cosine transform of the influence function $f_\mu(z)$ (assumed to be even), defined as

$$\mathcal{F}_\mathrm{c}\{f_\mu(z)\} = \int\limits_{\Omega} f_\mu(z)\cos(kz)\,dz\,. \tag{7}$$

Only the real part of the complex growth rate

$$\gamma(k) = \mathcal{R}e\left\{\phi(k)\right\} = -a \int\limits_{\Omega} f_{\mu}(z)\cos(kz)dz\,, \tag{8}$$

will be important to determine whether the perturbation with wave number k will die out or will generate a pattern, depending on it being positive or negative, what can be seen by rewriting $u(x,t)$ as

$$u(x,t) = u_0 + \varepsilon\{\cos[k(x-vt)] + i\sin[k(x-vt)]\}\, e^{\gamma t}\,, \tag{9}$$

where we used the dispersion relation, Eq. (6). Let us now consider the simple case of the square influence function which we have used in our analytical and numerical investigations

$$f_{\mu}(z) = \begin{cases} \dfrac{1}{2\mu} & |z| \leq \mu\,, \\ 0 & \text{otherwise}\,. \end{cases}$$

Here μ is the cut-off range ($0 < \mu < L$, where L is the size of the system). Equation (7) involves an integral from 0 to μ, so we find

$$\gamma(k) = -a\,\frac{\sin(k\mu)}{k\mu}\,. \tag{10}$$

2.2. Supretion of lower modes analise

We verify that $\gamma(k)$ will be positive only in the intervals $(2n+1)\pi/\mu < k < 2(n+1)\pi/\mu$ for $n = 0,1,2\,\ldots$, which indicates that in the convective dynamic regime the colony of bacteria tend to self-organization. The most important behavior that gives rise to pattern formation is the suppression of the modes $0 < k < k_{\min} = \pi/\mu$, *i.e.* the suppression of traveling waves Eq. (9) with frequency $0 < \omega < \omega_{\min} = vk_{\min}/\mu$. Very similar phenomenon has been demonstrated for diffusion using a generalized Langevin equation [11–14] there it was proven that when we eliminated the lower modes $0 < \omega < \omega_{\min}$ in the noise spectrum the system violates ergodicity and the detailed balance equations. In this case, the elimination of the lower modes induces ergodicity violation, *i.e.*, pattern formation with preferential position in the space.

3. Numerical approach for NLCFE

To solve Eq. (4) numerically, we applied the operator splitting method (OSM) [15]. By this method, the operator of the differential equation is split into several parts, which act additively on $u(x,t)$. If we write Eq. (4) as:

$$\frac{\partial u(x,t)}{\partial t} = \hat{T}u(x,t)\,, \tag{11}$$

where $\hat{T}$ is the total operator, then

$$\hat{T}u(x,t) = \hat{T}_{\text{con}}u(x,t) + \hat{T}_{\text{grow}}u(x,t) + \hat{T}_{\text{int}}u(x,t)\,, \tag{12}$$

with

$$\begin{aligned}
\hat{T}_{\text{con}}u(x,t) &= -v(x)\,\frac{\partial u(x,t)}{\partial x}\,,\\
\hat{T}_{\text{grow}}u(x,t) &= au(x,t)\,,\\
\hat{T}_{\text{int}}u(x,t) &= -bu(x,t)\int_{\Omega} f_\mu(x-y)u(y,t)\,dy\,.
\end{aligned} \tag{13}$$

In the latter equations $\hat{T}_{\text{con}}$, $\hat{T}_{\text{grow}}$ and $\hat{T}_{\text{int}}$ are convection, growth and non-local interaction operators, respectively. In our numerical calculations, we have used periodic boundary conditions $u(x=0,t) = u(x=L,t)$ with spatial period L. For each part of the operator, we apply a known difference scheme for updating the function $u(x,t)$ from step j to step $j+1$.

We start our numerical study by using the following initial distribution of bacterial colony

$$u(x,0) = \frac{1}{\Gamma}\exp\left[-\frac{(x-x_0)^2}{2\sigma^2}\right]\,, \tag{14}$$

where

$$\Gamma = \sqrt{\frac{\pi}{2}}\sigma\left[\text{erf}\left(\frac{x_0}{\sqrt{2}\sigma}\right) + \text{erf}\left(\frac{L-x_0}{\sqrt{2}\sigma}\right)\right]\,. \tag{15}$$

Here, $\sigma = 0.04$ is the width of the Gaussian and L is length of the system. In order to see how this distribution evolves in time, we shall employ two types of influence function: square influence function, which has been used in the last section; and the gaussian influence function which we shall present in this section.

3.1. Behavior of μ in a velocity flux

In Fig. 1 we present the time evolution of $u(x,t)$. Here $v = 0.020$ and the square influence function has width $\mu = 0.10$. In this illustration, we began our temporal evolution with an initial gaussian distribution of bacteria centered at $x_0 = 0.5$. We verified that the temporal evolution of $u(x,t)$ for the initial condition $u(x,0)$ when submitted to a flux convection tends to a self-organization regime.

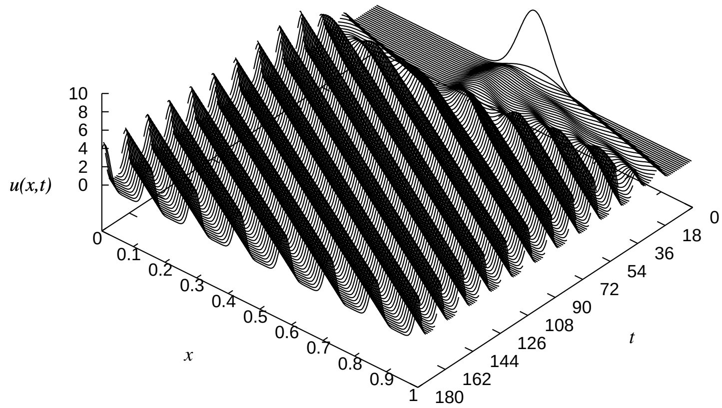

Fig. 1. The density $u(x,t)$ as a function of x and t for $v = 0.010$, $L = 1.0$ $a = 1.0$, $b = 1.0$ for the case of the square influence function with width $\mu = 0.10$. The waves move from $x = 0$ to $x = L$ with velocity $v > 0$.

In Fig. 2, we show snapshots of the stationary state $u(x)$ for several values of μ in the case of the square influence function. In this illustration we can observe the beginning of pattern formation, which occurs for $\mu = 0.484$, the value at which a new density peak appears. For the value $\mu = 0.028$ (snapshot F) we observe that pattern become negligible which caracterize a critical limit. For the limits $\mu \to 0$ and $\mu \to L/2$, our simulations do not present pattern formation, indicating an agreement with the limits of the influence function reported in [16].

We also show in Fig. 3 our study of pattern formation using a Gaussian influence function, given by

$$f_\mu(z) = \frac{1}{\Lambda} \exp\left[-\frac{z^2}{2\mu^2}\right], \tag{16}$$

where μ is the width of the Gaussian function and

$$\Lambda = \sqrt{\frac{\pi}{2}}\mu \operatorname{erf}\left(\frac{L}{\sqrt{2}\mu}\right), \tag{17}$$

is the normalization factor. For a Gaussian influence function we noticed that there exists a critical value of μ, $\mu_c = 0.46$, below which the system tends to self-organize. Again for this type of influence function, we verified that for small values of the width $\mu \to 0$, as well as for values of μ that tend to the size of the system divided by two $\mu \to L/2$, we will not have self-organization. We yet do not have a complete and conclusive physical explanation for this phenomenon once the critical value μ_c was obtained

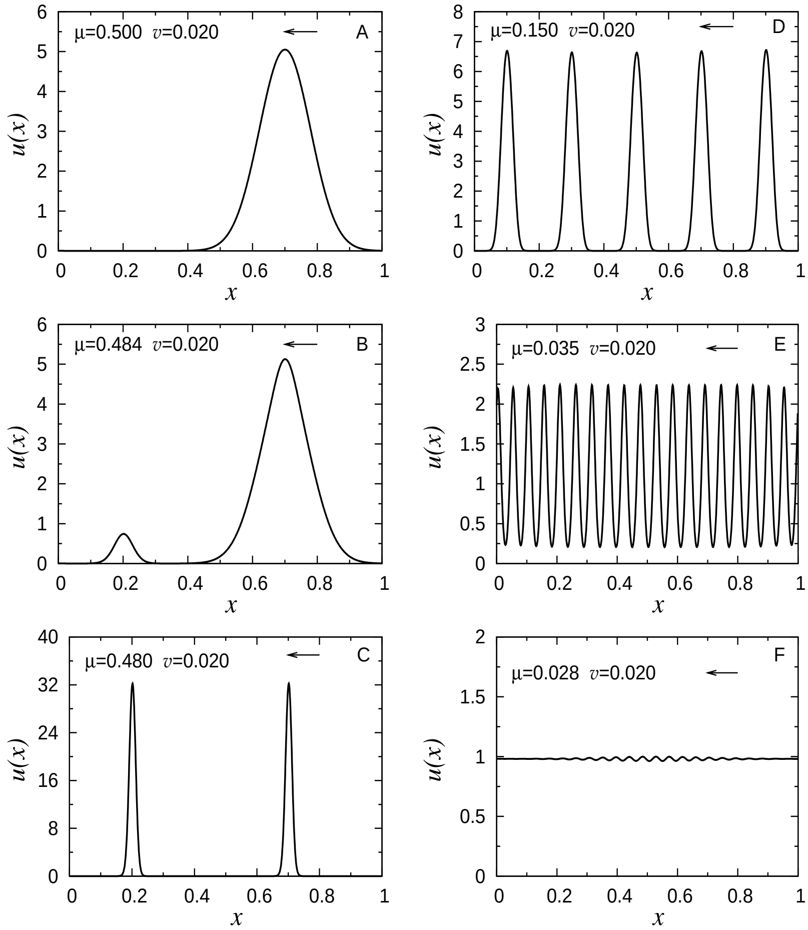

Fig. 2. Snapshots of the steady state $u(x)$ for several values of μ for the square influence function. For large times, the form and number of peaks no longer changes; the unchanging peaks move in the direction indicated in the figure. In these graphs $v = 0.020$, $a = 1.0$ and $b = 1.0$. The value $\mu = 0.484$ (snapshot B) indicates the first value where a new density peak appears, what illustrates the appearance of pattern formation. The pattern become negligible for $\mu = 0.023$ (snapshot F).

from numerical simulations. Nevertheless, we believe that below 0.5 the interaction between the elements are nonhomogeneous, the distribution of toxins (interactions) is different in each point generating a nonlocal effective behavior by its surrounding. On the other hand, above 0.5 the interaction becomes homogeneous, *i.e.*, all individuals "feel" the same interaction and so there is no pattern. This result is similar to those obtained using a diffusive term [5, 7, 8].

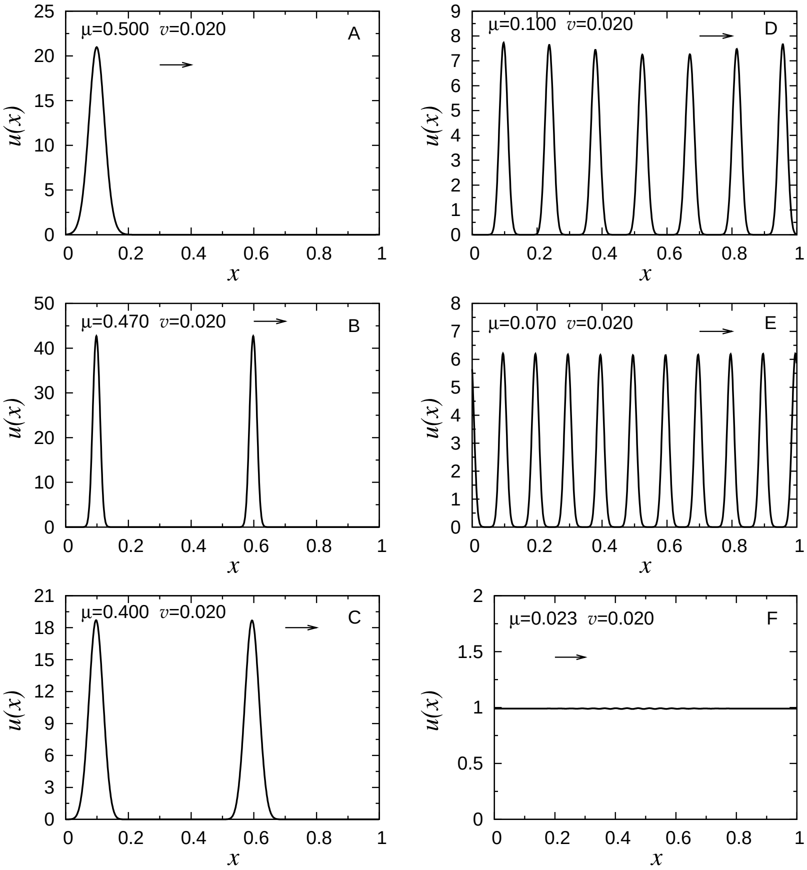

Fig. 3. Snapshots of the steady state $u(x)$ for several values of μ for the Gaussian influence function. For large times, the form and number of peaks no longer changes; the unchanging peaks move in the direction indicated in the figure. In these graphs $v = 0.020$, $a = 1.0$ and $b = 1.0$. The value $\mu = 0.470$ (snapshot B) indicates the first value where a new density peak appears, what illustrates the appearance of pattern formation. The pattern become negligible for $\mu = 0.028$ (snapshot F).

3.2. Independence of initial condictions

In Fig. 4 we address the problem of independence of the initial conditions. In panel (A) and (C) we start with three different distributions. (B) is the final pattern for (A) while (D) is the final pattern for (C). In all cases, the three initial distributions converge to a unique solution which is independent of the initial conditions. It depends only on the parameter μ. In reality, there are small differences among the curves due to numerical errors.

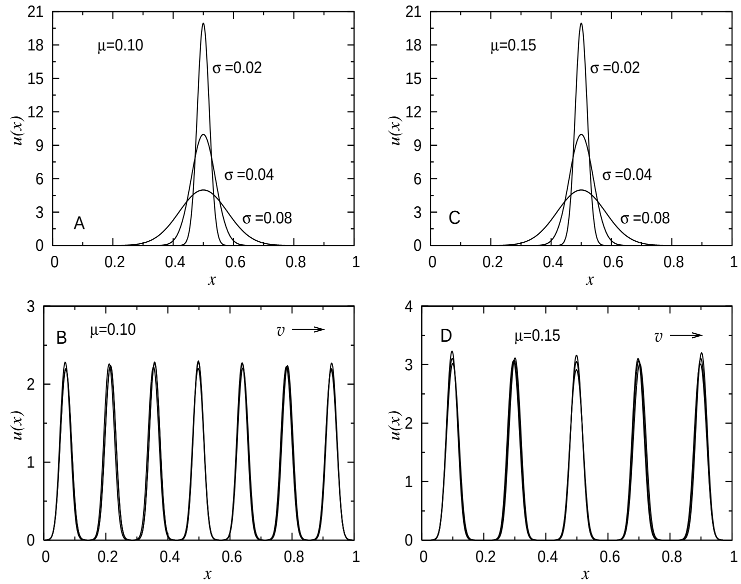

Fig. 4. Independence of the initial conditions for pattern formation using a square influence function. Figs. (A) and (B) are for $\mu = 0.10$ while figures (C) and (D) are for $\mu = 0.15$. σ denotes the width of initial distribution. In figures (A) and (C) we have initial conditions $u(x, 0)$; the figures (B) and (D) show the steady state of pattern formation $u(x)$ for large times, in which the peaks remain unchanged, but more to right.

3.3. Pattern formation and finite size

In our analysis, patterns occur only for finite systems due to the need of shelter, *i.e.*, as $L \to \infty$ the patterns disappear. As we have discussed, the NLCFE presents patterns only in the presence of a nonlocal interaction term. Then rescaling the gaussian distribution Eq. (16) for $z = Lx$, we get

$$f_\mu(x) = \frac{1}{\Lambda_x} \exp\left[-\frac{x^2}{2\mu_x^2}\right],$$

with $\mu_x^2 = \mu_z^2/L^2$ and $\Lambda_x = L\sqrt{(\pi/2)}\,\mu_x \operatorname{erf}(1/\sqrt{2}\mu_x)$. Consequently, as $L \to \infty$ the influence function becomes a delta one and we return to the local Fisher Equation; in this case there is no pattern. Note that this result is unchanged even when the other parameters are rescaled in the Fisher Equation. This implies that the mean square value $\mu_z^2 = \int f(z)z^2dz$ must be finite. Furthermore, for the existence of patterns we must have $\mu_{\mathrm{mim}} < \mu_z < \mu_{\mathrm{max}}$. Note that for a Gaussian we get $\mu_z = \mu$, while for a step function $\mu_z = \mu/\sqrt{3}$. Moreover, for large μ_z, $\mu_z > \mu_{\mathrm{max}}$, the system becomes homogeneous, and we see no pattern. For $\mu_z < \mu_{\mathrm{mim}}$, the influence function behaves as a delta one and again we have no pattern. Unfortunately for such nonlinear system we have not yet found a way to determine the limits analytically.

3.4. Parameter μ and nonlinearity

For the influence functions and initial conditions used, we see a general tendency: for large μ we do not have a distribution with pattern. As μ decreases we reach a value μ_2, where the original crest bifurcates. The process continues in such way that we can associate a μ_n to the value of μ for which we have n crests. For very small μ, n can be very large, implying negligible differences between crests and troughs, in such way that it may be considered uniform as in Fig. 2 (D) or Fig. 3 (D). This is similar to a logistic map $z_{n+1} = g(\beta, z_n)$ where the variation of the parameter β yields bifurcation [17]. Nonlinearity in general cause extreme dependence on the initial conditions. However, in our patterns, what bifurcates is the crest of the density $u(x,t)$, and so the bifurcations do not induce different solutions, but an unique solution with several crests. This, roughly speaking, reminds us of the synchronization phenomena where systems with [18] or without memory [19, 20] are driven from distinct initial conditions to a unique final state.

4. Conclusions

Using a perturbation analysis in Eq. (4), we verified that the real part of the growth rate $\gamma(k)$ is positive for some values of the wave number k, in this way, we can have pattern formation for certain values of the parameters that determine the behavior of $\gamma(k)$. Therefore, using the numerical approach OSM, we show that the NLCFE is able to describe the pattern formation in regime of convective motion in bacterial systems in which the diffusion dynamics is negligible. Our numerical calculation about the NLCFE shows that the system exhibits self-organization in regime of low velocity. In fact it indicates that nonlocal interaction stated in nonlinear terms of Fisher equation is a very important element to describe patterns, where the linear dynamic of the system becomes as a secondary element. We also show that pattern formation occurs for a specific value of critical width $\mu_{\rm c}$ for a given system with fixed length L. This is a relevant information in the study of self-organization of dynamic systems in general. In this model, we also observe an analogy with the logistic map $z_{n+1} = g(\beta, z_n)$ which associates the number of crests in the population density $u(x,t)$ with a bifurcation parameter β. However, this model does not exhibit chaos due to nonlocal effects on nonlinear term imposed in NLCFE. Indeed, the bifurcations do not allow different solutions, but an unique solution with several crests which can be associated to a synchronization phenomenon.

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