Analytic Considerations in the Study of Spatial Patterns Arising from Non-local Interaction Effects in Population Dynamics

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Simple analytic considerations are applied to recently discovered patterns in a generalized Fisher equation for population dynamics. The generalization consists of the inclusion of non-local competition interactions among individuals. We first show how stability arguments yield a condition for pattern formation involving the ratio of the pattern wavelength and the effective diffusion length of the individuals. We develop a mode-mode coupling analysis which might be useful in shedding some light on the observed formation of small-amplitude versus large-amplitude patterns.

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We have shown recently that the Fisher equation used frequently for investigations of biological or ecological systems, when generalized to include spatially non-local competition interactions, leads to interesting patterns in the steady state density [1, 2]. In this Note we attempt to shed some analytic light on the formation of these patterns. The original Fisher equation [3, 4] is

$$\frac{\partial u\left(\vec{x},t\right)}{\partial t}=D\nabla^{2}u\left(\vec{x},t\right)+au\left(\vec{x},t\right)-bu^{2}\left(\vec{x},t\right), \qquad (1)$$

where $u\left(\vec{x},t\right)$ is the population density of individuals under investigation (bacteria, rodents, etc.) at position $\vec{x}$ and time t, and D, a, b are, respectively, the diffusion coefficient, population growth rate, and competition parameter. The generalized equation [1, 2] features competition interactions linking $u(\vec{x},t)$ at point $\vec{x}$ with $u(\vec{y},t)$ at point $\vec{y}$ through an influence function $f_\sigma(\vec{x},\vec{y})$ of range σ,

$$\begin{aligned}\frac{\partial u\left(\vec{x},t\right)}{\partial t} &= D\nabla^{2}u\left(\vec{x},t\right)+a\,u(\vec{x},t) \\ &\quad -b\,u(\vec{x},t)\int_{\Omega}u(\vec{y},t)f_\sigma(\vec{x},\vec{y})dy,\end{aligned} \qquad (2)$$

Ω being the domain for the non-local interaction.

In [1], we found that the introduction of the finite-range competition interactions gives rise to the emergence of patterns in the steady state density $u(\vec{x})$ with the following features:

- No patterns appear [2] in the two extremes of zero range (in which the generalization reverts to the Fisher equation) and full range (in which the population density is linked equally to all points in the domain).
- The pattern structure depends crucially on features of the influence function, specifically, its cut-off length and its width.
- Even when patterns appear, their steady-state amplitude can change abruptly from substantial to negligible as the parameters of the system are varied.
- The critical quantity determining the separation of large-amplitude patterns from small-amplitude ones appears to be the ratio of the cut-off length of the influence function to its width.

These findings raise two questions. Why do the patterns form at all? And, what causes the separation of the large-amplitude patterns from the small-amplitude ones? Both questions are interesting. The first is amenable to understanding via standard stability analysis considerations. The second is more difficult but might be approachable through a mode-mode coupling analysis, as we show below.

In order to address the first question, consider a 1-dimensional version of Eq. (2) for simplicity, and substitute in it

$$u(x,t)=u_0+\epsilon\cos(kx)\exp(\varphi t). \qquad (3)$$

Here u_0 is the homogeneous steady-state solution a/b. Considering periodic boundary conditions, and retaining only first order terms in ϵ, we obtain the following dispersion relation between the wavenumber k of any mode of the pattern and the rate φ at which it tends to grow:

$$\varphi=-Dk^2-a\mathcal{F}(k). \qquad (4)$$

In this expression, the influence function (assumed to be even) is represented by its cosine (Fourier) transform

$\mathcal{F}(k)$ defined as

$$\mathcal{F}(k) = \int_{\Omega} \cos(kz) f_{\sigma}(z) dz. \tag{5}$$

Stable steady-state patterns require that

$$\lambda > 2\pi \sqrt{\frac{D}{-a\mathcal{F}(\lambda)}}, \tag{6}$$

where $\lambda = 2\pi/k$ is the wavelength associated with the $k-$mode of the Fourier expansion of the pattern.

Condition (6) allows us to check for the existence or absence of inhomogeneity, i.e., patterns, in the steady state. We see from (6) that the Fourier transform of the influence function at the wavelength under consideration should be *negative* for the patterns to appear and that its magnitude should be large enough. One way of understanding this condition is to recast it as requiring that 2π times the 'effective diffusion length' should be smaller than the wavelength for the patterns to occur. By the effective diffusion constant is meant D divided by $-\mathcal{F}(\lambda)$, which is a factor decided by the influence function, and by the diffusion length is meant the distance traversed diffusively in a time interval of the order of the inverse of the growth rate. If the influence function is smooth such as in the case of a Gaussian in an infinite domain, the Fourier transform is positive and no patterns appear. A cut-off in the influence function produces oscillations in the Fourier transform which can go negative for certain wavelengths. The reported finding [1] that the cut-off nature is essential to pattern formation can be understood naturally in this way.

Let us consider, in turn, three cases of the influence function which we have used in our earlier investigations [1]: square, cut-off Gaussian, and intermediate.

First we take

$$f(x-y) = \frac{1}{2w}\{\theta[w-(x-y)]\theta[w+(x-y)]\}, \tag{7}$$

where θ is the Heaviside function. The influence function is thus a square of cut-off range measured by w from its center. We will consider the case here when the range w is smaller than, or equal to, the domain length L. Equation (4) then involves an integral from 0 to w, and gives

$$\varphi = -a\frac{\sin(kw)}{kw} - Dk^2. \tag{8}$$

In terms of dimensionless parameters

$$\begin{aligned} \varphi' &= \varphi/a, \\ k' &= k\sqrt{D/a}, \\ \eta &= w\sqrt{a/D}, \end{aligned}$$

we have

$$\varphi' = -\frac{\sin(k'\eta)}{k'\eta} - k'^2, \tag{9}$$

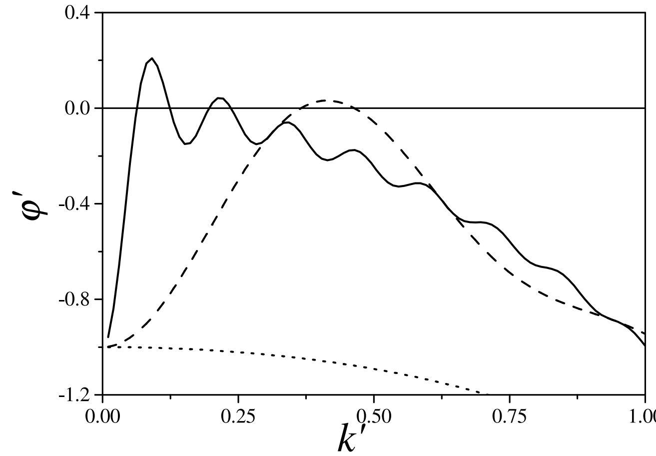

FIG. 1: The dispersion relation (9) between the dimensionless growth exponent φ' and wavenumber k' plotted for different values of the ratio η of the influence function range to the diffusion length (see text). Values of η are 50 (solid line), 10 (dashed line), and 2 (dotted line). Patterns appear for those values of k' for which φ is positive.

which we plot in Fig. 1 for three different values (50, 10 and 2) of the ratio η of the width to the diffusion length (not *effective* diffusion length). For the third case there are no patterns: diffusion is strong enough to wash them out. For the intermediate case, patterns can occur with wavelengths corresponding to values around $k' \approx 0.4$ while for the $\eta = 50$ case, they occur around $k' \approx 0.1$.

The earlier finding [1, 2] that no patterns appear for extremes of the range of the influence function is clear from Eq. (9). As the influence width vanishes, i.e., as η goes to zero, both terms in φ are negative and there can be no steady state patterns: we recover the solution for the local limit, corresponding to Eq. (1), when $w \to 0$. Since the boundary conditions are periodic in a domain of length L, there are only the allowed values $k = n\pi/L$ of the wavenumber. Therefore, in the opposite limit of full range, i.e., $w \to L$, the sine term vanishes, $\varphi' = -k'^2$, and again there are no patterns.

Precisely the same qualitative behavior occurs for other non-square influence functions such as the Gaussian with a cut-off, i.e., for

$$f(x-y) = \frac{1}{\sigma\sqrt{\pi}\mathrm{erf}(w/\sigma)} exp\left[\left(\frac{x-y}{\sigma}\right)^2\right]. \tag{10}$$

We again consider the case when the cut-off length does not exceed the domain length. This leads to the Fourier transform of the influence function involving an integral from 0 to w. In these as well as other cases considered, it should be appreciated that the domain length L, if taken to be smaller than the cut-off length, becomes itself the cut-off length: factors such as kw appearing in the Fourier transform become then kL instead.

For this cut-off Gaussian case, the square case dispersion relation (8) is replaced by

$$\varphi = -\frac{a\exp[-(k\sigma/2)^2]}{2\mathrm{erf}(w/\sigma)} \left[\mathrm{erf}\left(\frac{w}{\sigma} - \frac{ik\sigma}{2}\right) + \mathrm{erf}\left(\frac{w}{\sigma} + \frac{ik\sigma}{2}\right)\right] - Dk^2.$$

The dimensionless version (9) is replaced by

$$\varphi' = -\frac{\exp(-k'^2\beta^2)}{2\mathrm{erf}(\alpha)}\left\{\mathrm{erf}(\alpha - ik'\beta) + \mathrm{erf}(\alpha + ik'\beta)\right\} - k'^2. \quad (11)$$

Here α and 2β are the ratios of the cut-off length to the range and of the range to the diffusion length respectively:

$$\alpha = w/\sigma,$$
$$2\beta = \sigma\sqrt{a/D}.$$

What is analogous to η in the square case is their product $2\alpha\beta = w\sqrt{a/D}$. Plots which are essentially the same as those in Fig. 1 can be drawn for this Gaussian case.

It is interesting to note that, while there is a single quantity η in the square case, there are two quantities, α and β, in the cut-off Gaussian case. This arises from the fact that, although there are generally two lengths associated with any influence function, the cut-off length and the width, the latter is infinite for the square case. The width has been defined in Ref. [1] as being inversely proportional to the second derivative of the influence function evaluated at its central point, and has been denoted by the symbol Σ. The cut-off length measures the distance beyond which the influence function is exactly zero and has been denoted [1] by ξ_c. For the cut-off Gaussian, this $\xi_c = x_c = w$. The symbol x_c has been used in Ref. [1] and w in the present Note. The width Σ obeys $\Sigma = \sigma$ for the Gaussian case and $\Sigma = \infty$ for the square case.

Both the cut-off Gaussian and the square can be obtained as particular cases of a general function [1, 5] which we call the *intermediate* influence function:

$$f(x-y) = \frac{\Gamma(1/r + 3/2)}{\sqrt{\pi}w\Gamma(1/r+1)}\left[1 - \frac{r\,(x-y)^2}{(2+3r)\sigma^2}\right]^{1/r} \{\theta[w-(x-y)]\theta[w+(x-y)]\}. \quad (12)$$

For $r \to 0$ the intermediate influence function goes to the cut-off Gaussian, while for $r \to \infty$ it yields he square function. The cut-off length of the influence function is given by

$$w = \sqrt{\frac{(2+3r)}{r}}\sigma. \quad (13)$$

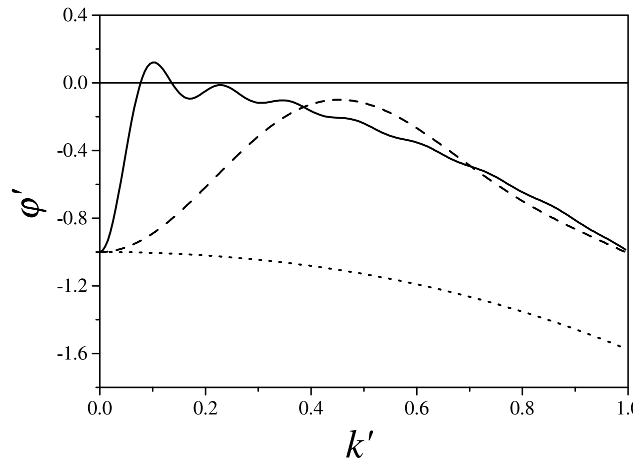

FIG. 2: The dispersion relation (15) between the dimensionless growth exponent φ' and wavenumber k' plotted for the *intermediate* influence function. Values of η are as in Fig. 1: 50 (solid line), 10 (dashed line), and 2 (dotted line). Patterns appear for those values of k' for which φ' is positive.

We will follow the notation

$$\nu = 1/r + 1/2,$$

and evaluate the Fourier transform of the influence function by calculating the integral [6]

$$\frac{2w^{-2\nu}\Gamma(\nu+1)}{\sqrt{\pi}\Gamma(\nu+\frac{1}{2})}\int_0^w \cos(ks)\left[w^2 - s^2\right]^{\nu-\frac{1}{2}} ds = \left(\frac{2}{kw}\right)^{\nu}\Gamma(\nu+1)J_\nu(kw), \quad (14)$$

for

$$k > 0, w > 0, \mathrm{Re}[\nu] > \frac{1}{2},$$

Γ and J being the gamma and the Bessel functions respectively. The dimensionless dispersion relation analogous to (9) is, for this general case,

$$\varphi' = -\left(\frac{2}{k'\eta}\right)^{\nu}\Gamma(\nu+1)J_\nu(k'\eta) - k'^2. \quad (15)$$

Here, as in the square case, $\eta = w\sqrt{a/D}$ is the ratio of the influence function width to the diffusion length.

It is straightforward to obtain the two limits, square and Gaussian, from this dispersion result (15) for the intermediate influence function. In Fig. 2 we plot the intermediate case for $\nu = 1$ and see the same general behavior as in the Gaussian and the square counterparts (see, e.g., Fig. 1). Steady state patterns appear only around $k' = 0.1$.

Having understood the appearance of the patterns, we now come to the second issue mentioned in the introduction: the transition from small-amplitude to large-amplitude patterns [1]. This is much more difficult to address analytically. We present here a procedure that we believe has the potential to shed some light on this issue. We substitute the Fourier mode expansion of $u(x,t)$,

$$u\left(\vec{x},t\right) = \sum A_n(t)\cos(k_n x), \tag{16}$$

in (2), explicitly noting that $k_n = \pi n/L$, and using the orthogonality properties of trigonometric functions, obtain separate equations for the $n=0$ mode,

$$\frac{dA_0}{dt} = aA_0 - bA_0^2 - b\sum_{n=1}^{\infty}\frac{A_n^2}{2}\mathcal{F}(k_n), \tag{17}$$

and for other modes $n \neq 0$:

$$\begin{aligned}\frac{dA_n}{dt} = & -Dk_n^2 A_n + aA_n \\ & -bA_0A_n\left[1+\mathcal{F}(k_n)\right] \\ & -b\sum_{j=1}^{n-1}\frac{A_jA_{n-j}}{2}\mathcal{F}(k_j) \\ & -b\sum_{j=n+1}^{\infty}\frac{A_jA_{j-n}}{2} \\ & \left[\mathcal{F}(k_j)+\mathcal{F}(k_{j-n})\right].\end{aligned} \tag{18}$$

Equations (17) and (18) are the complete set of equations for the evolution of the amplitudes of all modes in the non-local problem given by Eq. (2). The appearance of stable patterns only for those values of k_n for which φ is positive as seen in our Figs. 1 and 2, suggests that we envisage an interaction between *only two modes*, the zero mode and the one whose growth we examine, say $n = m$. In a situation as in the plots shown in which $\varphi > 0$ only for a small $k-$ range, the discrete nature of the allowed k values could lead to only a single non-zero mode lying in the stable range. Then we would have only two coupled nonlinear equations for the mode amplitudes,

$$\begin{aligned}\frac{dA_0}{dt} &= aA_0 - bA_0^2 - b\,\frac{A_m^2}{2}\mathcal{F}(k_m), \\ \frac{dA_m}{dt} &= -Dk_m^2 A_m + aA_m - bA_0A_m\left[1+\mathcal{F}(k_m)\right]\end{aligned}$$

which lead, in the steady state, to

$$A_0 = \frac{a - Dk_m^2}{b\left[1+\mathcal{F}(k_m)\right]} \tag{19}$$

$$A_m^2 = -2\left[\frac{bA_0^2 - aA_0}{b\mathcal{F}(k_m)}\right]. \tag{20}$$

Substitution of the zero mode amplitude in A_m gives an explicit expression for the latter:

$$A_m^2 = -\frac{2}{\mathcal{F}(k_m)b}\left[\frac{(a-Dk_m^2)^2}{b(1+\mathcal{F}(k_m))^2} - \frac{a(a-Dk_m^2)}{b(1+\mathcal{F}(k_m))}\right]. \tag{21}$$

Preliminary investigations lead us to believe that the appearance of small and large amplitude patterns for different parameter regimes might emerge from considerations of (21). The two-mode approach is, however, plagued by the fact that variation of the parameters of the system can make the approach invalid in one regime even if it is valid in another. Surely steady state pattern amplitudes can always be obtained by a simultaneous solution of the algebraic equations obtained by putting the left side of (17) and (18) to zero. This is a straightforward numerical task if we can make the reasonable assumption that the number of modes to be considered has a finite cut-off. Such a cut-off is an obvious consequence of the fact the Fourier transform of a typical influence function disappears for high values of n. These and related studies will be reported in the future.

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