



Results from variants of the Fisher equation in the study of epidemics and bacteria

V.M. Kenkre*

*Consortium of the Americas for Interdisciplinary Science and Department of Physics and Astronomy,
University of New Mexico, Albuquerque, NM 87131, USA*

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Abstract

The Fisher equation, which combines diffusive motion of individuals with nonlinearities arising from their growth and competition processes, is analyzed, generalized, and applied to the dynamics of bacteria, pattern formation, and the spread of epidemics. Analytic solutions are also presented for some exactly soluble and physically relevant variants of the equation.

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1. Introduction

While mathematical ecology [1] is certainly not a subject so narrow that it could have a single equation which could serve as its focus point, the Fisher equation [2,3] has served as a unifying entity in various mathematical investigations in ecology and biology. The equation describes the time and space evolution of the density of individuals such as bacteria or rodents. The processes addressed are birth and death, nonlinear competition controlled by the environment leading to saturation of the population, and diffusion leading to spatial homogenization. These three respective processes are associated with the growth rate a (sometimes written as the difference of a birth rate and a

* Corresponding author. Physics Department, Center for Advanced Studies, University of New Mexico, Albuquerque, NM 87131, USA. Tel.: 505-277-4846; fax: 505-277-1520.

E-mail address: kenkre@unm.edu (V.M. Kenkre).

death rate), the environmental parameter b (sometimes written in terms of a carrying capacity), and the diffusion constant D :

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

This paper is a brief report on some investigations undertaken with the help of the equation, in formalistic as well as application contexts. Specifically, the issues addressed are

- the replacement of the diffusive character of the motion component by a convective counterpart, leading to analytic solutions,
- the understanding of pattern formation when the nonlinear competition interaction is spatially nonlocal, and
- applications to bacterial dynamics and to the spread of epidemics.

2. Analytic solutions for convective motion

The Fisher equation consists of the conjunction of the diffusion equation and the logistic equation. Except for a couple of practically uninteresting cases, no analytic solutions of the equation are known [3]. A prescription is presented below to obtain analytic solutions of a *variant* of the Fisher equation. The variant is obtained by replacing the diffusive motion component by a convective counterpart. It is surprising that, although quite straightforward, the recipe is useful in practical situations. The prescription given here generalizes to arbitrary nonlinearities work published recently by Giuggioli and the author [4] for the quadratic nonlinearity appearing in the Fisher equation.

Situations in which one may replace the diffusive term in the Fisher equation by a convective term arise in systems in which an externally imposed ‘wind’ drives the population in one direction [5] and, additionally, the wind term overwhelms the effects of diffusion. A well-known instance is in experiments on bacteria in Petri dishes [6]. The convective term is the result of a mask being moved across the Petri dish. The velocity of convection is under external experimental control. The diffusion term, typical of the ordinary Fisher equation, can be made to become small in agar through genetic engineering of the bacteria so that the velocity term overwhelms the diffusion effects. This is the physical reason for interest in a nonlinear convective equation [4]. We have seen that the convective equation with quadratic nonlinearities already gives a host of new results that do not follow from the Fisher equation [4], among them a phenomenon of velocity inversion. These results are generalized for arbitrary nonlinearity in the present paper.

Unlike in earlier analyses we are here interested in arbitrary nonlinearity. Therefore, consider the logistic terms in the Fisher equation replaced by a general nonlinearity represented by the term $F(u)$, and the diffusive term replaced by a convective counterpart:

$$\frac{\partial u}{\partial t} + v \frac{\partial u}{\partial x} = F(u). \quad (2)$$

Here v denotes the velocity with which the individuals move convectively instead of diffusively which would be the case for the Fisher equation.

The prescription for obtaining exact solutions is rather simple. One substitutes $dg/du = -1/F(u)$, rewrites the nonlinear partial differential equation for $u(x, t)$ in terms of a linear counterpart for $g(x, t)$, finds the explicit solution of the latter for the initial value problem as

$$g(x, t) = g_0(x - vt) - t, \tag{3}$$

where $g_0(x)$ is the spatial distribution $g(x, 0)$ at the initial time, and finally converts $g(x, t)$ into a solution for $u(x, t)$.

To illustrate the technique, let us consider three examples: the Fisher (quadratic) case, the Nagumo nonlinearity, and a trigonometric nonlinearity. For the first, $F(u) = au - bu^2$. Integrating $-1/F(u)$, one gets

$$g(u) = \ln \left[\left(1 - \frac{a/b}{u} \right)^{1/a} \right], \tag{4}$$

leading to the exact solution

$$u(x, t) = \frac{1}{\frac{e^{-at}}{u_0(x-vt)} + \frac{b}{a}(1 - e^{-at})} \tag{5}$$

derived and studied extensively in Ref. [4].

The second example is $F = -bu(u - h)(u - c)$. In the absence of the last term, this corresponds to $h = a/b$ for the Fisher equation but generally produces the Nagumo nonlinearity [3,7]. For this case,

$$g(u) = (1/b) \ln [u^{1/hc}(u - c)^{-1/[c(h-c)]}(u - h)^{1/[h(h-c)]}]. \tag{6}$$

The solution for $u(x, t)$ is obtained analytically, but implicitly, as

$$u^{1/hc}(u - c)^{-1/[c(h-c)]}(u - h)^{1/[h(h-c)]} = u_0^{1/hc}(u_0 - c)^{-1/[c(h-c)]}(u_0 - h)^{1/[h(h-c)]} e^{-bt}, \tag{7}$$

where the argument of u is (x, t) and the argument of u_0 is $x - vt$. By boosting x to $x - vt$ in the known initial spatial dependence $u_0(x)$, each side of the equation is obtained explicitly.

The third example is the sinusoidal nonlinearity: $F(u) = p \sin mu$. Using the fact that the integral of $\sin x$ is $\ln(\tan(x/2))$, one gets

$$g(u) = \frac{1}{mp} \ln \left(\cot \frac{mu}{2} \right). \tag{8}$$

This means that the solution can be written explicitly as

$$u(x, t) = \frac{2}{m} \tan^{-1} \left(e^{mpt} \tan \frac{mu_0(x - vt)}{2} \right). \tag{9}$$

Generally, integrating $-1/F(u)$ leads often to a g which is naturally in the form of a logarithm: $g(u) = \ln \zeta(u)$. Then, the final solution is

$$u(x, t) = \zeta^{-1} [e^{-t} \zeta(u_0(x - vt))]. \tag{10}$$

The general prescription is thus to (i) find $\xi(u)$ in the given problem, (ii) boost the initial spatial dependence by vt , (iii) apply the ξ to the boosted initial dependence and multiply the result by e^{-t} , and, finally, (iv) apply the inverse ξ^{-1} to obtain the solution $u(x, t)$.

This near-trivial method of obtaining exact solutions to nonlinear partial differential equations of the convective type should not be underestimated regarding its practical use. The reader is referred to the extensive discussion in Ref. [4] where a number of useful results have been obtained in the analysis of the special quadratic case. They include a rich diversity of evolutions for exponential and nonexponential tails in the initial distribution, a curious phenomenon of velocity inversion, and the potential for application to the dynamics of bacteria in a Petri dish.

3. Pattern formation with spatially nonlocal interactions

The competition interaction in the Fisher equation is local in space: individuals are assumed to compete for resources in their immediate neighborhood. What happens if the spatial locality is relaxed and the Fisher equation is generalized to include long-range competition interactions? Fuentes et al. have shown that such a generalization leads to interesting patterns in the steady state density [8,9]. The generalized equation in arbitrary dimensions 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 ,

$$\frac{\partial u(\vec{x}, t)}{\partial t} = D\nabla^2 u(\vec{x}, t) + a u(\vec{x}, t) - b u(\vec{x}, t) \int_{\Omega} u(\vec{y}, t) f_\sigma(\vec{x}, \vec{y}) d\mathbf{y}, \tag{11}$$

Ω being the domain for the non-local interaction.

The patterns that emerge [8] in the steady state density $u(\vec{x})$ from such finite-range competition interactions, have the following primary features: (1) No patterns appear 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). (2) The pattern amplitude can change abruptly from substantial to negligible as the parameters of the system are varied, the critical quantity being apparently the ratio of the cut-off length of the influence function to its width. (3) The diffusion coefficient has a strong influence on the patterns in that, if large enough, it can destroy the patterns. (4) A finite cut-off in the influence function appears crucial to the existence of the patterns. The first feature can be proved [9] quite simply. The second is difficult to understand quantitatively although attempts have been made [10]. The third and the fourth are addressed below.

Linear stability analysis applied to the one-dimensional version of Eq. (11) shows [10] that the dispersion relation between the wavenumber k of any mode of the pattern and the rate φ at which it tends to grow, is

$$\varphi = -Dk^2 - a\mathcal{F}(k), \tag{12}$$

where $\mathcal{F}(k)$ is defined as $\int \cos(kz) f_\sigma(z) dz$, the cosine (Fourier) transform of the influence function (assumed even). It follows immediately that stable steady-state

patterns require that

$$2\pi\sqrt{\frac{D}{-a\mathcal{F}(\lambda)}} < \lambda, \quad (13)$$

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

Condition (13) specifies clearly when patterns can arise in the steady state. The Fourier transform of the influence function at the wavelength under consideration should be *negative* and its magnitude should be large enough. For a Gaussian in an infinite domain (for instance), 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. Negativity of the Fourier transform is essential to the patterns but does not guarantee their appearance unless the diffusion constant is small enough. Four lengths are important: λ , the wavelength of the pattern, $\sqrt{D/a}$, the diffusion length which is the distance traversed diffusively within the growth time $1/a$, the cut-off length w of the influence function beyond which there is no interaction, and the range σ which shows how the influence function behaves near its center. Needless to say, a fifth length, the size of the domain L , is also important, partly in determining allowed k values, and particularly because it effectively serves as the cut-off length if it is smaller than the influence function cut-off length.

We refer the reader to Ref. [10] for details but point out here for illustrative purposes the dispersion relation for the square influence function of width $2w$:

$$\varphi = -a \frac{\sin(kw)}{kw} - Dk^2. \quad (14)$$

The range σ of the square influence function is infinite and therefore does not appear in the dispersion relation. Positivity of φ , required for the stability of patterns is only possible for some regions in k space where the sinc function attains negative values and the diffusion constant is not strong enough to pull φ into the negative region.

4. Applications to bacterial dynamics and to epidemics

Space restrictions make it impossible to address our application work in any manner other than largely descriptive. Our applications of the Fisher equation and its modified versions have been to bacterial dynamics in Petri dishes and to epidemics, particularly the hantavirus and the West Nile virus.

Bacterial colonies form a subject of obvious medical importance and have been studied recently [6,11,12] experimentally as well as theoretically [5,7]. In contemporary experiments [6] a moving mask is used to protect the bacteria dynamically from ultraviolet light which kills them in regions outside the mask, and the population distribution is observed. The static mask situation can be analyzed in terms of explicit Jacobian elliptic function solutions of the time-independent Fisher equation. As a result of the competition between diffusion into hostile regions outside the mask and growth within the mask, a critical size of the mask exists below which the mask cannot support

bacteria. This size is $\pi\sqrt{D/a}$ and, from estimated values of the diffusion constant D and the growth rate a , it appears [7] to be of the order of half a cm, which is certainly accessible to experiment.

We have also studied bacterial dynamics (theoretically) under situations in which the mask oscillates either in size or in position. We call the former the case of the breathing mask and the latter the case of the oscillating mask. Ballard et al. have predicted [13] interesting effects which await experimental testing. When the speed with which the breathing or oscillations occur is large enough, diffusion can be considered a small perturbation and the dynamics understood from the analytic predictions of the diffusionless Fisher equation. For illustrative purposes let us consider the oscillating mask with a velocity $v(t)$. It can be represented by $b(x, t) = b(x - \int_{t'}^t ds v(s))$, and the spatio-temporal distribution of $u(x, t)$ obtained explicitly:

$$u(x, t) = \frac{u_0 \left(x - \int_0^t ds v(s) \right)}{e^{-at} + u_0 \left(x - \int_0^t ds v(s) \right) \int_0^t dt' e^{-a(t-t')} b \left(x - \int_{t'}^t ds v(s) \right)}. \tag{15}$$

If the b parameter has value b inside the mask and B outside the mask, and the mask has width $2w$ centered around the origin, the spatial dependence to be employed in the above analysis is

$$b(x) = B - (B - b)[\Theta(x + w) - \Theta(x - w)], \tag{16}$$

where Θ is the Heaviside step function. A less abrupt transition expression may be written with the help of a smooth function such as a Gaussian of width $2w$.

At the macroscopic end of the application spectrum of the Fisher equation is the spread of epidemics. We have studied the hantavirus extensively [14–17]. It is a terrifying epidemic [18] discovered in the last decade, and transmitted from mouse to mouse and then passed on to human beings from the mice. Appropriate description [14] is in terms of two classes of mice, susceptible and infected, represented by M_S and M_I , respectively (with $M = M_S + M_I$):

$$\frac{\partial M_S}{\partial t} = bM - cM_S - \frac{MM_S}{K} - aM_I M_S + D \frac{\partial^2 M_S}{\partial x^2}, \tag{17}$$

$$\frac{\partial M_I}{\partial t} = -cM_I - \frac{MM_I}{K} + aM_I M_S + D \frac{\partial^2 M_I}{\partial x^2}. \tag{18}$$

Here c is the decay rate by natural death, a is the rate at which encounters of the two types of mice convert susceptible to infected, and D is the diffusion constant of the mice moving over the terrain, whether infected or susceptible. The resources (food, water, vegetation) are described by K which is generally time and space dependent. We have used the symbols a and b here differently from the first part of this paper to maintain compatibility with the literature.

It is possible to explain a number of observed spatio-temporal patterns regarding the hantavirus, such as refugia and the effect of seasonal variations, and to generalize the analysis to other epidemics such as the West Nile virus [19] which are characterized by cross-infection and time scale disparity between the two taxa involved in the

dynamics (mosquitoes and birds in the case of West Nile virus). The Fisher equation and its variants thus continue to provide useful insights into the dynamics of diverse ecological systems.

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