Contracted Fisher equation

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We apply the method of contraction, familiar in statistical mechanics applications, to reduce the Fisher equation describing population growth and dispersal in the space-time domain to an equation in the time domain. The resulting equation is identical to the well-known logistic equation with an additional correction term that depends on the global solution to the Fisher equation. This equation provides a possible basis for explaining why logistic dynamics has not always described experimental data and also for then formulating models that generalize the logistic equation.

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I. INTRODUCTION

A primary goal of statistical mechanics is the elucidation of the observed macroscopic behavior of systems both in and displaced from equilibrium. This includes determining the limitations of macroscopic laws, e.g., the time and length scales for which they provide a valid description, the generalization of these laws to regimes in which they are not applicable, as well as the relationship between the parameters they include with the underlying microscopic properties. One of the notable areas of success has been in establishing the conditions for which the various macroscopic equations describing nonturbulent, low density fluid flows are valid and in providing generalizations to these equations, e.g., in shock and boundary layers [1–3]. The procedure for this is to contract the more basic description provided by the Boltzmann equation, reducing the level of detail from the microscopic to the macroscopic level. Here we apply the method of contraction to the description of population dispersal and growth.

The simplest model describing regulated single species population growth is the logistic equation (LE) [4] that, despite obvious defects, provides a basic platform from which more detailed models can be formulated. The importance of the topic we consider here is clear, because experimentally measured population numbers versus time yield excellent fits to logistic dynamics for many biological species, such as humans [5,6], bacteria [5,6], fruit flies (Drosophila) [5], and virus strains [7], but there are also many experimental data, such as for blowflies (Lucilla cuprina) and many bird species [8–10] which do not agree with predictions based on the LE. The logistic equation is similar to, but simpler than, the rate equations [11] used to describe epitaxial crystal growth in that in both descriptions only the time dependence of the population is considered. Thus, any effects of spatial inhomogeneity that are mediated by diffusion, and possibly convection, are omitted at this most primitive level. A consequence of this simplification is that the equation of evolution in the case of the LE is an (easily solved) ordinary differential equation and only growth, but not dispersal, is described.

A higher level of description can be obtained by considering the space-dependent population density, the evolution of which is described by the Fisher equation (FE), which is a nonlinear partial differential equation [12]. Although the FE has been extensively studied, the few exact results we are aware of are the steady state solution for a finite domain embedded in a hostile environment [13] and the special traveling wave solution the evolves from some unspecified initial condition [14]. Most of the literature pertaining to the FE has focused on technical properties such as the existence and stability criteria, especially for the class of special long-time solutions that describe traveling waves [14,15]. Surprisingly, it appears that there has been no attempt to determine the connection between the FE and LE descriptions. Such a connection would be useful in providing a better understanding of the conditions for which the LE might be expected to be valid, just as the Boltzmann equation has shed light on when the Euler equations are applicable or must be superseded by the Navier-Stokes equations (or where neither are valid as in shock, boundary, and initial layers) [1–3]. Establishing this connection is the purpose of this paper. In Sec. II we consider the contracted FE for a large closed system and find that the LE must be modified by a term resembling the variance of the FE density. In Sec. III we consider the qualitative behavior of this correction term for initial conditions and times long enough so that a traveling wave solution has evolved, and show that this leads to a marked reduction in the approach to the equilibrium population.

We then conclude in Sec. IV with a discussion of how the result found here might be used to formulate generalizations of the LE.

II. CONTRACTING THE FE

The FE can be written in terms of dimensionless time and space units as [14]

$$\frac{\partial n}{\partial t} \equiv n_t = n_{xx} + n(1 - n/k), \tag{1}$$

with n the population density and k the corresponding carrying capacity density. The evolution of the total population, $N(t) = \int dx n$ is often assumed (when boundary effects can be ignored as in a large closed system) to be described by the LE,

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$$\frac{dN}{dt} = N(1 - N/K), \tag{2}$$

where K is the carrying capacity of the environment which extends from $-L \leqslant x \leqslant L$ so that $K = \int dxk$. We will consider systems large enough so that, operationally, in the limits of some integrals, $L \to \infty$, but otherwise quantities such as $K/2L = k$ are finite. The rational for Eq. (2) is the observation that it leads to the self-limiting population growth seen in many systems, and provides a simple model for predicting future growth as well as the starting point for more refined model building [4,16]. In the latter respect the connection between the LE and FE appears to have been overlooked or ignored by the population ecology community whereas it suggests itself immediately to those familiar with statistical mechanics. To provide such a connection we integrate the FE to find (as noted above, all spatial integrals extend over the entire real line)

$$\frac{dN}{dt} = N - \int dx \frac{n^2}{k}, \tag{3}$$

where we require that n and n_x vanish on the boundaries (the system is closed). This is clearly not the LE [17], and indicates that, as often occurs in statistical mechanics, we cannot obtain a closed equation following contraction without introducing approximations that effect a closure. Alternatively, it may be shown that there are conditions for which closure cannot be attained and a contracted description is not applicable.

The "missing link" here is provided by the identity

$$k^{-1} \int dxnn = \frac{N^2}{K} + k \int dx \left(\frac{n}{k} - \frac{N}{K} \right)^2, \tag{4}$$

so that

$$\frac{dN}{dt} = \left(N - \frac{N^2}{K} \right) - k \int dx \left(\frac{n}{k} - \frac{N}{K} \right)^2. \tag{5}$$

The last term on the right-hand side of Eq. (5) provides the correction necessary to connect the LE with the FE. This can then serve as a basis for attempts to formulate models that generalize the LE, e.g., by replacing this term with some function of the time, and in Sec. IV we provide a simple example of how this might de done. Before doing this we will assess the possible quantitative significance of this correction term for situations where a traveling wave evolves [14,15].

III. ANALYSIS OF EQ. (5) FOR TRAVELING WAVE SOLUTIONS

The form of Eq. (5). indicates that the rate of growth experienced by N as predicted by the LE, and therefore the values of $N(t)$, will only be an upper bound in the ecologically interesting case where the density $n(x,t)$ is not uniform throughout space. The issue we address here is that of the possible significance of the correction to $N(t)$ implied by Eq. (5). In what follows we make use of the result of Kolmogoroff *et al.* [18], who showed that a for specified class of ecologically interesting, i.e., compact (nonvanishing only on a finite connected domain) initial conditions the solution of the FE evolves after an initial transient period as left and right moving traveling waves with $n \approx k$ behind these waves and $n \approx 0$ ahead of the advancing fronts. We consider here the case of an initial condition symmetric about the origin $x=0$ so that after an initial period of evolution, of $x>0$ there is a region $0<x<L_1(t)$ where $n \approx k$, a transition region of length L_T in which n decays to zero, and the region $L_1 + L_T < x < L$ in which $n \approx 0$. The wave, and hence L_1, moves to the right with speed $c=2$ [or if we write the FE in dimensional units, $n_t = Dn_{xx} + rn(1-n/k)$ with D the diffusion coefficient and r the intrinsic growth rate, $c' = 2(rD)^{1/2}$]. The transition length is $L_T = 4c$ or $4c'$ in dimensional units [14]. For $x<0$ the density profile is the mirror image of that described above for positive values of x.

Using the above information we can compare the two terms on the right--hand side of Eq. (5) for times long enough that a traveling wave solution has evolved. We will approximate the right moving wave form by a straight line of slope $-k/L_T$ connecting $x=L_1$ and $x=L_1+L_T$ so that in the transition region $n = k[1-(x/L_T)+(L_1/L_T)]$, with $n=1$ behind the wave and $n=0$ ahead of the wave. The population is then $N = 2L_1 k + L_T k$ (including contributions from both the $\pm x$ regions), so that

$$N\left(1 - \frac{N}{K}\right) = K\left[\frac{L_1}{L} + \frac{L_T}{2L} - \left(\frac{L_1}{L} + \frac{L_T}{2L}\right)^2\right]. \tag{6}$$

When the population reaches its carrying capacity K the space is uniformly filled, $L_1 \to L$, and there is no transition region, and both sides of Eq. (6) are identically zero.

We compare this term with the correction term, which his composed of three distinct parts as described above. For $0<x<L_1$ this is

$$\frac{2}{k}\int_0^{L_1} dx \left[k - \frac{N}{2L}\right]^2 = K\frac{L_1}{L}\left[1 + \left(\frac{N}{K}\right)^2 - \frac{2N}{K}\right], \tag{7}$$

where the prefactor 2 on the left side accounts for the contribution from the corresponding region where $x<0$. Similarly, using the approximation for n given above in the transition region

$$\frac{2}{k}\int_{L_1}^{L_1+L_T} dx \left[n - \frac{N}{2L}\right]^2 = K\frac{L_T}{L}\left[\frac{1}{3} - \frac{N}{K}\left(1 - \frac{N}{K}\right)\right]. \tag{8}$$

Finally, ahead of the wave.

$$\frac{2}{k}\int_{L_1+L_T}^{L} dx \left[\frac{N}{2L}\right]^2 = K\left[1 - \frac{L_1}{L} - \frac{L_T}{L}\right]\left[\frac{N}{K}\right]^2. \tag{9}$$

Combining the result of Eqs. (7)–(9) and substituting for N we find the correction term, which we denote $C(t)$ (the time dependence is through L_1), given as

$$C(t) = K\left[\frac{L_1}{L} - \left(\frac{L_1}{L}\right)^2 + \frac{L_T}{3L} - \frac{L_1 L_T}{L^2} - \left(\frac{L_T}{2L}\right)^2\right], \quad (10)$$

which also goes to zero as $L_1 \to L$ and the contribution from the transition region vanishes. Combining Eqs. (5), (6), and (10), we then find

$$N_t = \frac{KL_T}{6L}\left[1 + \frac{3L_1}{L}\right]. \quad (11)$$

In typical situations where we have a traveling wave with $L_T/L \ll L_1/L \ll 1$ we see that Eq. (11) predicts a much slower approach to quilibrium than the LE for which $N_t = O(L_1/L)$. We can conclude that there are conditions for which the correction to the LE is quantitatively significant.

IV. DISCUSSION

The main result of this paper is Eq. (5), which connects the LE to the FE. Although this is a formal result, we believe it to be of significance for two distinct reasons. First, it provides an explicit connection between the LE and the FE, and indicates why the former may not be valid in situations where the latter is valid. In addition, this can provide guidance to attempts to generalize the LE in situations where the FE provides a valid description. One apparent qualitative feature of Eq. (5) is that for every value of N it predicts a rate of population growth less than that predicted by the LE. Since the correction term in Eq. (5) decays from some initial value to zero as the traveling wave solution develops and progresses, the simplest analytically tractable model that incorporates these features as well as $dN/dt = 0, N = 0, K$ is

$$\frac{dN}{dt} = N - \frac{N^2}{K} - \alpha\left(N - \frac{N^2}{K}\right)\exp - \beta t, \quad (12)$$

with α and β parameters that reflect the initial condition (α) and the relaxation time for the correction term to decay (β). The solution of Eq. (12) is

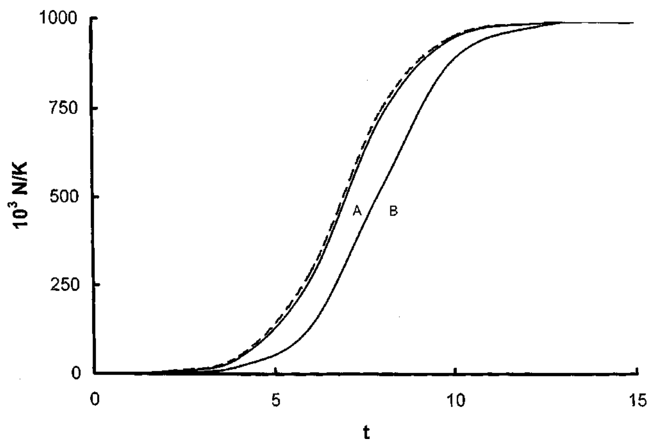

FIG. 1. $10^3 N/K$ vs time for solutions of the logistic equation (-----) and the solutions of Eq. (12) with $\alpha = 0.1$ and $\beta = 1.0$ (curve *A*) and $\alpha = 0.5$ and $\beta = 0.5$ (curve *B*). The initial condition in each case is $N(0) = 10^{-3}$ K.

$$N(t) = N(0)/[N(0) + (K - N(0))e^{-t}e^{\alpha(1-\exp-\beta t)/\beta}]. \quad (13)$$

Bearing in mind that Eq. (12), like the LE and its generalizations, is a model incorporating parameters that must be determined from data in specific applications, in Fig. 1 we show the differences between LE solution and the solution to Eq. (12) for two choices of the model parameters with $N(0) = 10^{-3}$ K. For small α and moderate β we see that the solution of Eq. (12) only slightly lags the LE solution; however, increasing α and decreasing β results in an increased lag.

In summary, it has been long known that the LE does not follow by contraction from the FE. We have determined the explicit connection between these two levels of description, introducing a correction term to the LE that can provide an alternative starting point for the development of more accurate phenomenological population growth models.

[1] H. Grad, in *Handbuch der Physik XII*, edited by S. Flugge (Springer, Berlin, 1958), pp. 205–294.
[2] M. Kogan, *Rerefied Gas Dynamics* (Plenum, New York, 1969).
[3] S. Harris, *An Introduction to the Theory of the Boltzmann Equation* (Holt, Rinehart and Winston, New York, 1971).
[4] P. Turchin, *Complex Population Dynamics* (Princeton University Press, Princeton, NJ, 2003).
[5] A Lotka , *Elements of Mathematical Biology* (Dover, New York, 1924).
[6] V. Kostitzin, *Mathematical Biology* (G. G. Harrap, London, 1939).
[7] J. Fort and V. Mendez, Phys. Rev. Lett. **89**, 178101 (2002).
[8] W. Gurney, S. Blythe, and R. Nisbet, Nature (London) **287**, 17 (1980).
[9] B.-E. Saether, S. Engen, and E. Mattysen, Science **295**, 2070 (2002).
[10] R. Law, D. Murrrell, and J. Diekmann, Ecology **84**, 252 (2003).
[11] J. Venables, G. Spiller, M. Hanbrucken, Rep. Prog. Phys. **47**, 300 (1984).
[12] R. Fisher, Ann. Eugenics **7**, 353 (1937).
[13] J. Skellam, Biometrika **38**, 196 (1951).
[14] J. Murray, *Mathematical Biology* (Springer, Berlin, 1993).
[15] N. Britton, *Reaction-Diffusion Equations and their Applications to Biology* (Academic, New York, 1986).
[16] J. Vandermeer and D. Goldberg, *Population Biology* (Princeton University Press, Princeton, NJ, 2003).
[17] This observation is not new here; we can recall having seen it stated, en passant, "somewhere" in the population ecology literature.
[18] A. Kolmogoroff, I. Petrovsky, and N. Piscounoff, Moscow Univ. Bull. Math. **1**, 1 (1937)