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Population Dynamics with Global Regulation: The Conserved Fisher Equation

T. J. Newman,[1,2,3] E. B. Kolomeisky,[2] and J. Antonovics[3]
[1]*Department of Physics and Astronomy, Arizona State University, Tempe, Arizona 85284, USA*
[2]*Department of Physics, University of Virginia, McCormick Road, Charlottesville, Virginia 22903, USA*
[3]*Department of Biology, University of Virginia, McCormick Road, Charlottesville, Virginia 22903, USA*
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We introduce and study a conserved version of the Fisher equation. Within a population biology context, this model describes spatially extended populations in which the total number of individuals is fixed due to either biotic or environmental factors. We find a rich spectrum of dynamical phases including a pseudotraveling wave and, in the presence of the Allee effect, a phase transition from a locally constrained high density state to a low density fragmented state.

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The Fisher equation is one of the most well-studied models in population biology and was originally written down to describe the spread of an advantageous allele [1,2]. Over the years the Fisher equation has been found to arise in numerous contexts in which a perturbation spreads in an excitable medium. Other examples abound and include the spread of reaction fronts in chemically bistable systems [3], switching in nonlinear optics [4], and the spreading of bacterial colonies [5].

In the language of population biology, the Fisher equation is a spatial generalization of the logistic equation, and is written in terms of $\rho(\mathbf{x}, t)$, the density of advantageous alleles:

$$\partial_t \rho = D\nabla^2 \rho + r\rho - u\rho^2, \tag{1}$$

where D is the mobility of the individuals, r is the reproduction rate in the absence of competition, and u is a parameter related to the "carrying capacity" of the system, which regulates the population density through competition. The primary feature emerging from the Fisher equation is that the density profile spreads via a traveling wave. A simpleminded calculation, however, does not provide a prediction for the velocity v. Much effort has been invested to determine the possible values of v for given initial conditions, using, primarily, the technique of marginal stability analysis [6–8]. Front propagation in the Fisher equation still poses interesting mathematical challenges, with new results recently appearing concerning the effects of discreteness [9] and internal noise [10].

The Fisher equation is the very simplest model of spatial dynamics, in which competitive interactions between individuals occur locally. It is also possible to envisage situations where population regulation occurs globally due to the presence of a secondary agent. This is most likely where the regulatory agent, whether biotic or abiotic, is itself dispersed over a scale considerably larger than the dispersal distance of the individuals themselves. For example, plant populations may be limited in size via a dependence for reproduction on pollinators that fly well beyond the limits of any particular population [11]. Microbial colonies can also be limited by a resource, such as nitrogen, that is dispersed over a scale larger than the colony itself [12]. Wide-ranging predators may key in on species once they become globally abundant and are frequently encountered [13,14]. There has been an increasing call for greater understanding of the scale over which density dependence occurs in natural populations [15–17]. A typical example in which humans play the role of secondary agent is weed or pest control, in which the total population is only tolerated below a fixed threshold [18,19]. It is therefore of interest to consider a simple model of spatial population dynamics in which the total population size is regulated via a nonlocal mechanism. In this Letter we shall describe an approach to this problem based on the Fisher equation. We find a rich spectrum of dynamical behaviors depending on spatial dimension and the type of low density reproduction.

In order to impose fixed population size N in the Fisher equation, it is necessary to allow the reproduction rate r and/or the competition parameter u to be functions of time. Thus, birth and death rates are continually adjusted to ensure that the population has a fixed size. Consequently, the conserved Fisher equation has the general form (in spatial dimension d)

$$\partial_t \rho = D\nabla^2 \rho + r(t)\rho - u(t)\rho^2, \tag{2}$$

with the auxiliary equation

$$r(t) = u(t) \int d^d x \rho(\mathbf{x}, t)^2. \tag{3}$$

We have scaled the density of individuals by N such that Eq. (3) ensures $\int d^d x \rho = 1$. As written, the conserved Fisher equation includes a continuous spectrum of models defined by a given reproduction rate $r(t)$, or equivalently by a given competition function $u(t)$. In this Letter we will study the simplest nontrivial case in which the competition rate is taken to be constant. The regulation of the population size is achieved by adjusting the linear birth rate $r(t)$. We shall take the initial density to be localized over a spatial scale ξ_0 and assume that it dynamically evolves by spreading. After some time the density will extend over a spatial scale $\xi(t)$ and have a saturated amplitude of order $\xi(t)^{-d}$.

We first focus on $u = u_0 > 0$, with the dynamics occurring in one spatial dimension. On the basis of preliminary numerical work, we observed that the population density does indeed spread, but that the cluster size $\xi(t)$ grows less quickly than a traveling wave, and the interfacial region separating the saturated density from zero density broadens in time. To understand this analytically, we assume a "pseudotraveling wave" form for the density for large positive x:

$$\rho(x, t) = \frac{1}{\xi(t)} f\left(\frac{x - \xi(t)}{W(t)}\right), \tag{4}$$

where $W(t)$ is a measure of the width of the interfacial region. (The function f tends to a constant for small x to match the saturated density in this region.) Solutions obtained from a direct numerical integration of Eq. (2), using a simple Euler discretization, strongly support this pseudotraveling wave. On inserting Eq. (4) into the conserved Fisher equation, we generate a number of terms with time-dependent coefficients. For large times it is straightforward to show that three of these coefficients balance each other. They are $\dot{\xi}/\xi W$, $1/\xi^2$, and $1/\xi W^2$. This immediately implies that $\xi \sim t^{2/3}$ and $W(t) \sim \xi^{1/2} \sim t^{1/3}$. Thus, the one-dimensional conserved Fisher equation, with positive competition parameter u_0, exhibits dynamical spreading, which is intermediate between a traveling wave and pure diffusion. The linear size of the population cluster grows superdiffusively as $t^{2/3}$, while the interfacial region grows subdiffusively as $t^{1/3}$. A similar analysis in two dimensions (assuming azimuthal symmetry) indicates that both ξ and W grow diffusively so that one cannot distinguish the linear size of the cluster from the interfacial region. In this case, the system is asymptotically dominated by pure diffusion. Presumably, a whole host of intermediate dynamical regimes exists for other choices of $u(t)$. With specific biological examples in mind, it would be interesting to explore other cases.

It is worth mentioning that this system shows interesting (and exactly solvable) dynamics for $D = 0$, namely, when there are no local spatial interactions. For the standard Fisher equation this is a trivial limit, since then each point in space evolves under an independent logistic process. However, in the conserved Fisher equation, the global constraint implicitly generates a coupling between different spatial regions, such that deaths at one place are balanced by births elsewhere, or vice versa. We shall not enter into details of the calculation here, which may be performed for general initial conditions, but give the results for the specific initial condition

$$\rho(x, 0) = A \exp(-|x/\xi_0|^\beta). \tag{5}$$

Setting $D = 0$ in Eq. (2), one can solve for the density, and for large times one obtains:

$$\rho(x, t) = \frac{1}{\xi(t)}\left\{\exp\left[\left|\frac{x}{\xi_0}\right|^\beta - \left(\frac{\xi(t)}{\xi_0}\right)^\beta\right] + 1\right\}^{-1}, \tag{6}$$

where $\xi(t) \sim t^{1/(1+\beta)}$. This solution is approximately uniform for $|x| \ll \xi(t)$ and decays as a stretched exponential for large x. The density interpolates between these two extremes over a length scale $W(t)$ in the region $|x| \sim \xi(t)$, and one finds $W(t) \sim \xi(t)^{1-\beta}$.

We can actually use this solution to get a glimpse of the properties of the system with local spatial interactions, meaning $D \neq 0$. By assuming that the solution found above in Eq. (6) still holds (which is not strictly true since it does not satisfy the pseudotraveling wave ansatz), we can compare the size of the Laplacian term with the other growth terms in Eq. (2). The Laplacian term is only non-negligible in the interfacial region, and thus $D\partial_x^2\rho \sim 1/\xi(t)W(t)^2$. Comparing this to the term $u_0\rho^2 \sim 1/\xi(t)^2$ immediately implies that $W(t) \sim \xi^{1/2}$. Thus including local interactions effectively selects a value of β, which from comparison with the exact result $W(t) \sim \xi(t)^{1-\beta}$ is $\beta = 1/2$. As a consequence, we have $\xi(t) \sim t^{2/3}$ and $W(t) \sim t^{1/3}$ in agreement with the predictions of the pseudotraveling wave ansatz.

For the remainder of this Letter we shall discuss some particularly striking results which arise in the conserved Fisher equation when the coefficients r and u are negative. Clearly, in the context of the nonconserved Fisher equation r and u are strictly non-negative since otherwise the equation is dynamically unstable. However, in the conserved Fisher equation, the global constraint forbids a dynamical instability. The biological motivation for studying negative values of the linear reproduction rate r is well known and arises in the following manner. Population dynamics based on the logistic equation assumes that in the absence of competition (i.e., at low densities) the reproduction rate is positive. This reasoning will break down in situations where reproduction becomes more difficult at lower population densities. In such cases one speaks of the Allee effect [20,21]. The most common example is bisexual reproduction. At low densities it is difficult for individuals to find a mate and so the effective reproduction rate becomes negative. Similar effects occur for species that require a critical number of individuals for resource collecting or for predator evasion. The conserved Fisher equation with negative $r(t)$ and $u(t)$ models the Allee effect in a population with fixed total size. We shall concentrate solely on the case of constant competition: $u_0 = -v_0 < 0$. Writing the negative reproduction rate as $r(t) = -s(t) < 0$, we have

$$\partial_t\rho = D\nabla^2\rho - s(t)\rho + v_0\rho^2, \tag{7}$$

with the auxiliary equation

$$s(t) = v_0 \int d^d x \rho(\mathbf{x}, t)^2. \tag{8}$$

This equation supports a steady-state solution for the density, but only in one dimension. Setting $\partial_t\rho = 0$ and solving the resulting ordinary differential equation in $d = 1$, we find the stable solution

$$\rho(x) = \frac{1}{2\xi_0}\operatorname{sech}^2\left(\frac{|x|}{\xi_0}\right), \tag{9}$$

where $\xi_0 = 12D/v_0$. This solution has been verified by the direct numerical integration of (7). It is interesting that this functional form commonly arises in $1D$ soliton problems, a physical example being the polaron [22].

In higher dimensions there is no steady-state solution. We proceed by assuming a dynamical scaling relation for a density depending only on the radial coordinate:

$$\rho(\mathbf{x}, t) = \frac{1}{\xi(t)^d} F\left(\frac{|\mathbf{x}|}{\xi(t)}\right). \tag{10}$$

So long as the Laplacian term is balanced with the time variation of the density, the length scale $\xi(t) \sim (Dt)^{1/2}$. Then, for $d > 2$, the remaining terms are subdominant and this process reduces to pure diffusion. It may well be that new dynamical behavior arises in three dimensions in the strong-coupling regime.

The case of two dimensions is most interesting since the Laplacian term is perfectly balanced with the nonlinear terms. Furthermore, from a population biology viewpoint, two dimensions is clearly the case of most empirical relevance. Defining the "dimensionless coupling constant" $\lambda = v_0/D$, we find (in the scaling limit of large $|\mathbf{x}|$ and t with $z = |\mathbf{x}|/\sqrt{Dt}$ finite) that the scaling function $F(z)$ satisfies the nonlinear ordinary differential equation

$$F'' + (z/2 + 1/z)F' + F + \lambda F(F - F_0) = 0, \tag{11}$$

where $F_0 = 2\pi \int_0^\infty dzzF(z)^2$.

Numerical analysis of this equation proceeds by adding a fictitious time derivative $\partial_\tau F$ to the right-hand side and iterating the equation under this "dynamics" using an Euler discretization. The solution of (11) is the "steady state" arising from this iteration method. We find that as λ is increased the function $F(z)$ becomes progressively more localized, collapsing to a δ function at a critical value of $\lambda = \lambda_c$. This transition in the scaling function signals a localization transition for the density: for $\lambda < \lambda_c$ the population spreads in a diffusive manner (albeit with a non-Gaussian scaling function), while for $\lambda > \lambda_c$ the population becomes strictly localized in space. By monitoring the approach to criticality as a function of the grid scale, we have estimated $\lambda_c \sim 31.005(5)$ (close in value to the integer 31 and $\pi^3 = 31.006\ldots$, although equal to neither as we shall see).

To further understand this phase transition for the dynamical scaling function $F(z)$, we make a critical scaling ansatz for F itself, in the spirit of Widom scaling at a critical point. We write (for $\lambda \leq \lambda_c$)

$$F(z) = \frac{1}{(\lambda_c - \lambda)^\alpha} h\left(\frac{z}{(\lambda_c - \lambda)^{\alpha/2}}\right). \tag{12}$$

Precisely at the critical point, the new scaling function $h(w)$ satisfies

$$h'' + h'/w + \lambda_c h(h - h_0) = 0, \tag{13}$$

where $h_0 = 2\pi \int_0^\infty dwwh(w)^2$ and the scaling variable $w = z/(\lambda_c - \lambda)^{\alpha/2}$. This equation can be cast into dimensionless form for $Q(u) = h(w)/h_0$:

$$Q'' + Q'/u + Q^2 - Q = 0, \tag{14}$$

where $u = w(\lambda_c h_0)^{1/2}$. By substituting these rescalings into the definition of h_0, we find a self-consistent expression for the critical coupling:

$$\lambda_c = 2\pi \int_0^\infty duuQ(u) = 2\pi \int_0^\infty duuQ(u)^2. \tag{15}$$

This reduces the calculation of the critical point to a single well-defined numerical problem. We have solved Eq. (14) to high precision (using iteration under fictitious dynamics as described above, along with matching at small u to an exact perturbative result). Using Eq. (15) we find $\lambda_c = 31.0032(1)$ and $Q(0) = 2.39196(1)$. The critical scaling function is shown in Fig. 1. For large values of u, Q is proportional to the modified Bessel function $K_0(u)$, which is significantly broader than the Gaussian obtained for pure diffusion.

We emphasize that this large dimensionless critical coupling constant was obtained for a density function normalized to unity. If we work in terms of the original density, normalized to N, with a dimensionless coupling constant $\lambda^{(N)}$, then it is straightforward to show that

$$\lambda_c^{(N)} = \lambda_c/N = (31.0031\ldots)/N. \tag{16}$$

By working backwards through our scaling transformations, we find that, close to the localization transition, the original density function has the scaling form

$$\rho(\mathbf{x}, t) = \frac{1}{\lambda_c \eta(t)} Q\left(\frac{|\mathbf{x}|}{\eta(t)}\right), \tag{17}$$

where the dynamical length scale $\eta(t)$ grows as

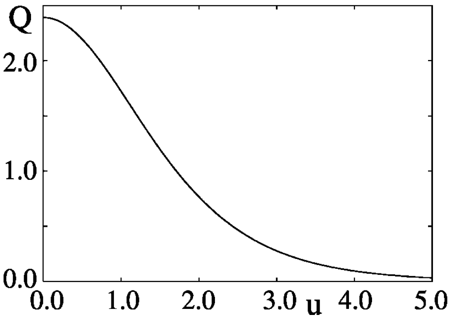

FIG. 1. The universal critical scaling function $Q(u)$.

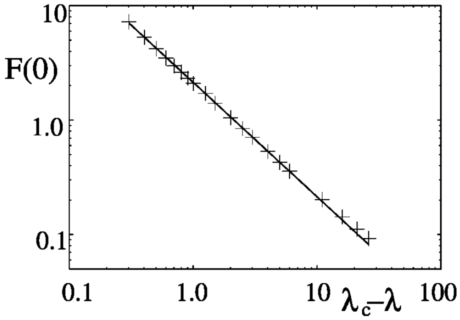

FIG. 2. The value of the dynamical scaling function evaluated at the origin, $F(0)$, which diverges at λ_c, shown on a log-log plot against $\lambda_c - \lambda$. The straight line has a slope of -1 and an amplitude of 2.139, which allows for a determination of h_0.

$$\eta(t) = (\lambda_c - \lambda)^{\alpha/2}\sqrt{\frac{Dt}{\lambda_c h_0}}. \tag{18}$$

The exponent α and the number h_0 can be extracted by studying the phase transition at the level of the dynamical scaling function $F(z)$. By varying λ in Eq. (11) and solving numerically, we measure the divergence of $F(0)$, which according to the critical scaling ansatz should behave as

$$F(0) = h_0 Q(0)(\lambda_c - \lambda)^{-\alpha}. \tag{19}$$

In Fig. 2 we show a log-log plot of this quantity as the critical point is approached. The straightness of the curve validates *a posteriori* the critical scaling ansatz. The data is consistent to within 1% error with the simple result $\alpha = 1$. Assuming this to be true, we can use the data to infer $h_0 \simeq 1.12$. Thus, we can rewrite Eq. (18) as

$$\eta(t) = \sqrt{\frac{Dt}{1.12}\left(1 - \frac{\lambda}{\lambda_c}\right)}. \tag{20}$$

The existence of a localization transition in two dimensions is consistent with the results from a discrete stochastic simulation of a population in two dimensions with bisexual reproduction [23]. The global regulation of population size is enforced by randomly selecting an individual to die each time a successful mating event occurs. The critical parameter λ_c is related to a critical reproduction rate in this discrete process. The microscopic model corresponding to the case of asexual reproduction is essentially the contact process with conserved total particle number, which has been studied recently in the context of directed percolation [19,24]. It would be interesting to look for the pseudotraveling wave in this case.

In conclusion, we have introduced a biologically motivated variant of the Fisher equation in which the integrated density is fixed due to global regulation. We have found several novel dynamical behaviors for the simplest case in which global regulation is enforced via the linear growth term. When this term is positive, we find that the conventional traveling wave solution of the one-dimensional Fisher equation is replaced by a pseudotraveling wave described by the scaling form in Eq. (4). The density profile spreads in time as $\xi(t) \sim t^{2/3}$, while the interfacial region slowly broadens as $W(t) \sim t^{1/3}$. When the linear growth term is negative, which corresponds to the Allee effect, we find a stationary density profile in one dimension (which has a classic soliton profile) and a phase transition in two dimensions, separating spreading and strongly localized density profiles. We have analyzed this phase transition in some detail, and, by using a critical scaling ansatz, deduced the precise location of the transition and the form of the critical scaling function.

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