



Nonlinear population dynamics in a bounded habitat

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ARTICLE INFO

Article history:

Received 26 September 2017

Revised 15 January 2018

Accepted 26 February 2018

Available online 27 February 2018

Keywords:

Habitat size

Density-dependence

Reintroduction

ABSTRACT

A key issue in ecology is whether a population will survive long term or go extinct. This is the question we address in this paper for a population in a bounded habitat. We will restrict our study to the case of a single species in a one-dimensional habitat of length L . The evolution of the population density distribution $\rho(x, t)$, where x is the position and t the time, is governed by elementary processes such as growth and dispersal, which, in standard models, are typically described by a constant per capita growth rate and normal diffusion, respectively. However, feedbacks in the regulatory mechanisms and external factors can produce density-dependent rates. Therefore, we consider a generalization of the standard evolution equation, which, after dimensional scaling and assuming large carrying capacity, becomes $\partial_t \rho = \partial_x (\rho^{\nu-1} \partial_x \rho) + \rho^\mu$, where $\mu, \nu \in \mathbb{R}$. This equation is complemented by absorbing boundaries, mimicking adverse conditions outside the habitat. For this nonlinear problem, we obtain, analytically, exact expressions of the critical habitat size L_c for population survival, as a function of the exponents and initial conditions. We find that depending on the values of the exponents (ν, μ) , population survival can occur for either $L \geq L_c, L \leq L_c$ or for any L . This generalizes the usual statement that L_c represents the minimum habitat size. In addition, nonlinearities introduce dependence on the initial conditions, affecting L_c .

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1. Introduction

The collective behavior of living organisms in an heterogeneous environment is a central issue in population ecology (Hanski, 1999). Habitats are naturally heterogeneous due to nonuniform distribution of resources and other environmental conditions that determine life development (Hanski, 1999; Turner et al., 2001). Moreover, the current days are characterized by an unprecedented influence of human activity on ecosystems (anthropocene epoch). Humans contribute to the degradation of the environment by reducing or fragmenting habitats, but can also interfere constructively, for example, through species reintroduction strategies (Seddon et al., 2007).

In order to understand the role of environment spatiotemporal structure in the persistence of the populations, many theoretical models have been developed (Giometto et al., 2015; Hanski et al., 1994; Hanski and Ovaskainen, 2000; Keymer et al., 2000; Neicu et al., 2000; Perry, 2005; Seddon et al., 2007). This question is central in the so-called metapopulation theory, which considers

sub-populations living in separate domains, coupled through the dispersion of individuals (Hanski, 1999).

The elementary unit is a single domain habitat, which can be seen as a refuge (where life is viable) immersed in a harmful background (Berti et al., 2015; Perry, 2005). The habitat neighborhood can be explicitly included in the model or incorporated into the boundary conditions (Hanski et al., 1994; Ludwig et al., 1979; Perry, 2005). The habitat size plays a crucial role in the fate of the population. This role has been investigated in the literature, both theoretically and experimentally, for particular dynamics, including diffusion, advection, growth, and features such as the Allee effect, for different types of boundary conditions (Holmes et al., 1994; Ludwig et al., 1979; Perry, 2005). Another relevant aspect that has been studied is the fact that the environment changes over time (Colombo and Anteneodo, 2016; Holmes et al., 1994; Lin et al., 2004; Neicu et al., 2000). In all these cases, the results show that the habitat must have a minimal size for population survival. This critical value L_c depends on the balance between population growth and dispersion.

Despite these many studies, one aspect that has been overlooked is the role of nonlinear diffusion and growth rate (Holmes et al., 1994), which is the question we address in this work. Our results will show, in particular, that the idea that the habitat size needs to overcome a critical value to allow population survival is not always valid. Depending on the kind of nonlineari-

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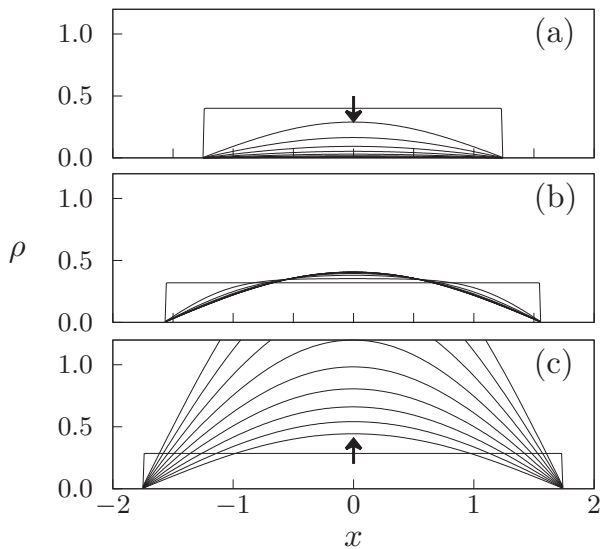


Fig. 1. Temporal evolution of the density distribution profile, in the linear case $\nu = \mu = 1$. For (a) $L < L_c$, (b) $L = L_c = \pi$ and (c) $L > L_c$, the population becomes extinct, attains a steady state or blows up, respectively. The lines are produced with Eq. (5). The arrows indicate the direction of time.

ties present, population survival occurs for $L \geq L_c$, $L \leq L_c$ or for any L . Additionally, nonlinearity introduces sensitivity to initial conditions, which affects the values of L_c .

We address these issues assuming a general nonlinear population dynamics taking into account, in an effective manner, density-dependent regulatory mechanisms. We focus on the one dimensional case, where L is the length of the habitat. The evolution equation for the population density distribution $\rho(x, t)$ at position x and time t is given by

$$\partial_t \rho = \partial_x (\rho^{\nu-1} \partial_x \rho) + \rho^\mu, \quad (1)$$

where $\nu > 0$, $\mu \in \mathbb{R}$, together with the absorbing boundary condition $\rho(\pm L/2, t) = 0$ and a uniform initial condition $\rho(x, 0) = N_0/L$, where N_0 is the initial population size. The terms of Eq. (1) represent diffusion and growth, respectively, with diffusion coefficient $\rho^{\nu-1}$ and per capita growth rate $\rho^{\mu-1}$, which depend on ρ when $\nu, \mu \neq 1$. The boundary conditions take into account a nonviable neighborhood. Competition was neglected by assuming abundance of resources. Further details of the model and its biological motivations will be given in Section 2.

The emergence of these nonlinearities in population dynamics has different origins that will be discussed in Section 2 too. But beyond the biological motivation, the nonlinear mathematical problem can be also of interest for diverse other fields such as combustion theory, heat conduction and transport in porous media (Galaktionov and Vázquez, 2002; Newman, 1980). It is also related to the so-called blow-up (divergence at finite time) of solutions, found in the mathematical literature (Fujita, 1966; Galaktionov and Vázquez, 2002; Newman, 1980).

An illustrative example of the addressed problem is shown in Fig. 1, for the linear case. The population goes extinct for small habitat with $L < L_c$ (Fig. 1a), increases for $L > L_c$ (Fig. 1c) and tends to a steady state at the critical value (Fig. 1b). Our goal is to determine the critical size and characterize the regimes of extinction and survival in the general nonlinear case. In order to do that, we perform a systematic analysis, both numerically and analytically, of the asymptotic behavior of the total population $N(t) \equiv \int_{\Omega} \rho(x, t) dx$, where $\Omega \equiv [-L/2, L/2]$. For numerical integration of

the partial differential Eq. (1), the standard forward-time centered-space discretization scheme was used.¹

2. Model

In population dynamics, the Fisher-KPP equation (Fisher, 1937) has been a paradigmatic model as far as it includes the most elementary processes. In one dimension, it reads

$$\partial_t \rho = D \partial_{xx} \rho + a \rho - b \rho^2, \quad (2)$$

where D , a and b , are positive parameters that give the rates of diffusion, growth (including reproduction and death) and competition, respectively. The local part of Eq. (2) is composed by a logistic term $a \rho (1 - b \rho)$ that induces exponential growth at low densities and an upper bound to the population size when $\rho \rightarrow a/b$. The Laplacian term $D \partial_{xx} \rho$ takes into account the unbiased population fluxes through space, assuming that individuals perform a random (Brownian) motion (Turchin, 2015). In this standard case, the per capita growth rate and the diffusion coefficient are constant.

We introduce density-dependent rates, through nonlinearities in the growth and diffusion processes. These dependencies on the density represent macroscopic feedbacks in the regulatory mechanisms, that can emerge from the complex interactions at individual level, such as cooperation, competition or homophilia (the preference to be among peers) (Courchamp et al., 1999), or from the interactions with a complex environment. Assuming power-law forms, we generalize Eq. (2) as

$$\partial_t \rho = D \partial_x (\rho^{\nu-1} \partial_x \rho) + a \rho^\mu - b \rho^{\mu+\delta}, \quad (3)$$

with exponents $\nu > 0$, $\delta > 0$ and real μ .

Diffusion. In many real cases, the diffusion coefficient is not constant, which may be a consequence of the interaction between individuals (Cates et al., 2010; Murray, 2002). For instance, in populations of insects, such as grasshoppers, the diffusion coefficient is enhanced at high densities (consistent with $\nu > 1$), but, in other species, this occurs at low densities (consistent with $\nu < 1$) (Murray, 2002). The adopted form of the diffusion coefficient, $D \rho^{\nu-1}$, allows to embrace all these cases. The spread of insect swarms, bacteria and other organisms has been also described through a nonlinear diffusion equation with different values of ν (Gurtin and MacCamy, 1977; Kareiva, 1983; Murray, 2002; Newman, 1980). When $\nu > 1$, the diffusion coefficient increases with population density. Then, large dispersal takes place in dense regions ($\rho > 1$), but low mobility occurs where the population is sparse ($\rho < 1$). This indicates that individuals become more active when they encounter more individuals, a type of positive feedback that increases with ν . In contrast, when $0 < \nu < 1$, the diffusion coefficient is enhanced in regions of low density, in comparison to highly populated ones. Then, this dispersion in open space yields long tails in the distribution of individuals (Anteneodo, 2005; Lenzi et al., 2001; Tsallis and Bukman, 1996), but here we are dealing with a bounded domain.

Alternatively, nonlinear diffusion may also have external origin, from the spatial heterogeneity of the environment, such as the recently investigated case of bacteria developing in porous media (Sosa-Hernández et al., 2017). In fact, $\partial_t \rho = D \partial_x (\rho^{\nu-1} \partial_x \rho)$ is known as porous media equation (Drazer et al., 2000; Muskat and Wyckoff, 1937), which arises in other contexts too (Galaktionov and Vázquez, 2002; Newman, 1980; Newman and Sagan, 1981). Let us note that the associated random dispersal yields anomalous diffusion in open space, where $x \sim t^{1/(1+\nu)}$. That means normal diffusion for $\nu = 1$, subdiffusion for $\nu > 1$ and superdiffusion

¹ We used a forward-time centered-space (FTCS) scheme, with integration steps Δt and Δx adequate for convergence. Typically it was necessary that $\Delta t / \Delta x^2 \lesssim 10^{-3}$. See, for instance, Ref. Press et al. (2007).

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