Physica A 391 (2012) 142–146

Contents lists available at SciVerse ScienceDirect

Physica A

journal homepage: www.elsevier.com/locate/physa

Population persistence in weakly-coupled sinks

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ARTICLE INFO

Article history:
Received 12 May 2011
Received in revised form 11 August 2011
Available online 23 August 2011

Keywords:
Population dynamics
Fisher–Kolmogorov equation
Extinctions
Patches
Diffusion

ABSTRACT

We consider a single species population obeying a saturated growth model with spatial diffusion taken into account explicitly. Strong spatial heterogeneity is considered, represented by a position dependent reproduction rate. The geometry of the problem is that of two patches where the reproductive rate is positive, surrounded by unfavorable patches where it is negative. We focus on the particular case where the population would not persist in the single patches (sinks). We find by means of an analytical derivation, supplemented by a numerical calculation, the conditions for the persistence of the population in the compound system of weakly connected patches. We show that persistence is possible even if each individual patch is a sink where the population would go extinct. The results are of particular relevance for ecological management at the landscape level, showing that small patches may harbor populations as long as the connectivity with adjacent patches is maintained. Microcosmos experiences with bacteria could be performed for experimental verification of the predictions.

1. Introduction

Single species models in population dynamics are important for the study of phenomena that take place in more complex arenas. Their simplicity allows one to inspect situations that will also be present when other species are considered. It is indeed known that single species models might be instrumental even when the interaction network contains many species [1]. In this work, we will consider such a single species model.

The description of the spatial aspects is of central importance in population dynamics. It could play a fundamental role when considering issues like the persistence or extinction of a species in a certain region. In particular, the space might be perceived as heterogeneous by the species in focus [2], resulting in, e.g., reproduction rates that depend on spatial location. The most common situation relevant for problems in ecology and epidemiology is the one where the space is composed of patches. Each patch is a limited region of space with constant properties. Patches where the population in focus has a positive reproduction rate will be called habitat patches. The space between habitat patches is called the *matrix*.

The spatial structure depicted above might be approached in at least two distinct ways. Metapopulations [3] and diffusion models [4]. The first one assumes that patches are effectively uncorrelated, being connected by colonization and subject to local extinctions. Diffusion models are motivated by statistical mechanics, assuming that populations obey a Fick law resulting in descriptions by partial differential equations of the parabolic kind, with spatial heterogeneities reflected in the spatial dependence of the coefficients in the equation. Which one is to be used to address a given situation is dependent on the knowledge of the degree of correlation between the patches.

We will consider in this work a situation described by the second approach above: two habitat patches with a matrix in between. We propose a 1-D model and we will address the question whether the population persists or goes extinct.

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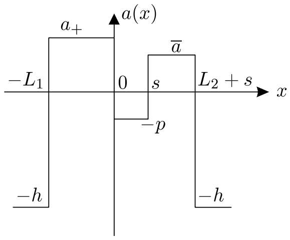
doi:10.1016/j.physa.2011.08.029



$$a(x) = \begin{cases} -h, & \text{if} \quad x < -L_1 & I \\ a_+, & \text{if} \quad -L_1 < x < 0 & II \\ -p, & \text{if} \quad 0 < x < s & III \\ \overline{a}, & \text{if} \quad s < x < s + L_2 & IV \\ -h, & \text{if} \quad L_2 + s < x & V \end{cases}$$

Fig. 1. The profile $a(x)$ showing two favorable regions (II and IV), surrounded by unfavorable ones.

Extinction will be mathematically translated as the fixed point with zero population being a global attractor. This situation is similar to the one studied in Ref. [5], but our emphasis is on a peculiar phenomenon, namely the fact that there can exist a system where the two patches would not subsist individually, but – due to coupling – the population becomes viable.

A region of space where a population cannot subsist unless it is sustained from outside is called a population sink, or shortly, a sink. A region where a population can subsist is called a source [6]. We are thus interested in a weakly coupled sink–sink system [7,8].

Our approach is based on the well-established Fisher–Kolmogorov equation (also called Fisher–Kolmogorov–Petrovski–Piskunov equation, or FKPP equation). This equation is a simple diffusion equation plus a logistic growth term. The hypotheses of locality of interactions and classical Brownian motion are implicit in this equation. More general situations have been addressed in *e.g.* Refs. [9,10]. This model (FKPP) has been studied in many different instances related to population dynamics [11–15] and plays the role of basic equation where more complex situations can be built upon [16–19]. It has also been tested in laboratory experiments [20]. Further, it plays a central role in models of biological invasions [21].

One of the central results about the Fisher–Kolmogorov equation is the following: consider the equation in a finite domain (in one dimension, to simplify the argument) of size D, with null Dirichlet boundary conditions. The large time behavior depends on D. If it is larger than a certain critical value, then the solutions are non-zero, representing a population in the domain. On the other hand, if D is smaller than the critical value, the solution tends to zero, and represents local extinction.

Thus, a simple model for a sink population is just a population in a domain smaller than a certain critical value. Our aim is to show that if two such domains are weakly connected, the population does not necessarily go to zero for large times. In order to do so, we will perform an analytical calculation for the linearized Fisher–Kolmogorov equation and then compare the result with the numerical integration of the full equation.

2. Mathematical model

As discussed previously, our model is mathematically described by the Fisher–Kolmogorov equation, which, in a convenient form, is given by

$$u_t = u_{xx} + a(x)u - u^2 \tag{1}$$

where $u = u(x, t)$ is the spatial population density and subscripts denote partial derivatives. We have used time, space and density scales in a way to avoid unnecessary constants in the equation. On the right side, we have a diffusive term (second derivative in x), a saturation term ($-u^2$) and a growth parameter $a(x)$. The spatial non-homogeneity of the medium is introduced by the dependence of the growth factor $a(x)$, on x, as in Ref. [22]. If $a(x) > 0$, the population grows locally. For x such that $a(x) < 0$ the region represents the matrix, that is, a region where the population tends locally to extinction.

A classical result [2,4] says that if Eq. (1) is solved on a finite segment of size D where $a(x) = a_0$ (a constant) and with $a(x) \to -\infty$ at the borders of the fragment, the population will asymptotically go to zero if $D < \pi\sqrt{1/a_0}$.

We now consider the situation where we have two regions with $a(x) > 0$ surrounded by regions with $a(x) < 0$. We want to find a condition for a small population to grow. This allows us to neglect the nonlinear term of Eq. (1). If the associated linear equation describes a population that gets extinguished, surely this is also true for the complete equation. On the other hand, the population is allowed to grow indefinitely, but this growth will be restrained by the nonlinear term in the complete equation. Consequently, we will work with the following equation:

$$u_t = u_{xx} + a(x)u. \tag{2}$$

The profile a(x)

Let us consider favorable patches having lengths L_1 and L_2, the adverse region between them having length s. All lengths, L_1, L_2 and s, are constant parameters. Let us take $a(x)$ given by the profile represented in Fig. 1.

This is a general form, with the reproductive rates in the favorable regions (a_+ and $\overline{a}$) allowed to assume different values on each patch. The inter-patch and outside regions have negative growth rates. As we are dealing with a linear equation, we may just suppose that the solution is of the form $u(x, t) = X(x)e^{\lambda t}$. We then have an eigenvalue problem, equivalent to the one we would obtain for the Schrödinger equation with piecewise constant potential. The critical condition separating the