Computers and Mathematics with Applications 72 (2016) 653–662

Contents lists available at ScienceDirect

Computers and Mathematics with Applications

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

Competitive–cooperative models with various diffusion strategies

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ARTICLE INFO

Article history:
Received 26 November 2015
Received in revised form 12 April 2016
Accepted 18 May 2016
Available online 16 June 2016

Keywords:
Ideal free distribution
Ideal free pair
Dispersal strategy
Global attractivity
System of partial differential equations
Coexistence

ABSTRACT

The paper is concerned with different types of dispersal chosen by competing species. We introduce a model with the diffusion-type term $\nabla \cdot [a\nabla (u/P)]$ which includes some previously studied systems as special cases, where a positive space-dependent function P can be interpreted as a chosen dispersal strategy. The well-known result that if the first species chooses P proportional to the carrying capacity while the second does not then the first species will bring the second one to extinction, is also valid for this type of dispersal. However, we focus on the case when the ideal free distribution is attained as a combination of the two strategies adopted by the two species. Then there is a globally stable coexistence equilibrium, its uniqueness is justified. If both species choose the same dispersal strategy, non-proportional to the carrying capacity, then the influence of higher diffusion rates is negative, while of higher intrinsic growth rates is positive for survival in a competition. This extends the result of Dockery et al. (1998) for the regular diffusion to a more general type of dispersal.

1. Introduction

The study of population dynamics started with the description of the total population size and its dynamics. However, taking into account the spatial structure is essential for understanding of invasion, survival and extinction of species. In order to involve movements in spatially distributed systems, the dispersal strategy should be specified. The ideas of spreading over the domain to avoid overcrowding combined with advection towards higher available resources were incorporated in the model in [1–5]. Dispersal design in [3] was based on the notion of the ideal free distribution, i.e. such distribution that any movement in an ideally distributed system will decrease the fitness of moving individuals. An ideal free distribution in a temporally constant but spatially heterogeneous environment is expected to be a solution of the system. There were several possible approaches to model dispersal in such a way that the ideal free distribution is a stationary solution of the equation, see, for example, [3–6].

Most of the previous research [3–5,7–9] was focused on evolutionarily stable strategies which provide advantages in a competition. This allowed to answer the question: what parameters or strategies should a spatially distributed population choose so that its habitat cannot be invaded by a species choosing alternative strategy and having other parameters? The effect of environment heterogeneity was studied in [10]. The case when a preferred diffusion strategy alleviated a negative effect of less efficient resources exploitation leading to possible coexistence was recently studied in [11]. However, the question how spatial distribution can promote coexistence compared to homogeneous environment got much less attention. Coexistence of various species relying on the same resources is quite common in nature. Survival of a certain population can

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http://dx.doi.org/10.1016/j.camwa.2016.05.017

be secured if it finds a certain niche in the resource consumption. Adaptation of different parts of the habitat (for example, shallow waters and deep waters) by two (or more) competing for resources populations can lead to coexistence.

The purpose of this paper is two-fold.

1. The first goal is to unify different approaches to diffusion strategies and dispersal, for example, the advection to better environments in [2] and the model where not the population density but its ratio to locally available resources diffuses [6]. A type of dispersal which includes [2,6] is introduced in Section 2.
2. The second goal is to consider the case when dispersal strategies guarantee coexistence. If the carrying capacity of the environment is a combination of these strategies, the ideal free distribution is attained at the coexistence stationary solution where the first population can be more abundant in some areas of the habitat, while the second one can be dense in other areas. Altogether, the two populations use the resources in an optimal way, and the sum of two densities coincides with the carrying capacity at any place of the spatial domain. This coexistence equilibrium is unique and globally attractive, see Section 3.

In addition, we extend the results of [7] to the case when the diffusion is not necessarily regular but the diffusion strategy is the same for both species, and it is different from [6] where, as the diffusion coefficient tends to infinity, the solution tends to the carrying capacity which coincides with the ideal free distribution. If this is the case, higher diffusion coefficient leads to a disadvantage in a competition. However, Section 4 also gives an alternative interpretation to this result: higher intrinsic growth rates (assuming the two have the same dispersal strategy) give an evolutionary advantage. Finally, Section 5 includes discussion of the results obtained and states some open questions.

2. Dispersal modeling

When choosing the type of diffusion, we focus on the ideal free distribution which is expected to be a solution of the equation, in the absence of other species. A related idea is that there is a movement towards higher available resources, not just lower densities, as the regular diffusion Δu would suggest. For our modeling, we assume the null hypothesis that not u but u/P is subject to advection or diffusion, where P is a diffusion strategy chosen by a species whose density at time t and point x is $u(t,x)$. Here P is a positive and smooth in the domain Ω function. Assuming space-dependent rate of advection $a(x)$, we consider

$$\nabla \cdot \left[a(x) \nabla \left(\frac{u(t,x)}{P(x)} \right) \right] = \nabla \cdot \left[\frac{a(x)}{P(x)} \left(\nabla u(t,x) - u(t,x) \frac{\nabla P}{P} \right) \right]. \tag{2.1}$$

The space-distributed P is treated as a diffusion strategy in the following sense: if $a(x) \to +\infty$, the density $u(t,x)$ would be proportional to P, whatever growth law we choose. Accepting (2.1) as a dispersal model, we consider the following system of two competing species obeying the logistic growth rule, with the Neumann boundary conditions

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot \left[\dfrac{a_1(x)}{P(x)} \left(\nabla u(t,x) - u(t,x) \dfrac{\nabla P}{P} \right) \right] + r(x) u(t,x) \left(1 - \dfrac{u(t,x)+v(t,x)}{K(x)} \right), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot \left[\dfrac{a_2(x)}{Q(x)} \left(\nabla v(t,x) - v(t,x) \dfrac{\nabla Q}{Q} \right) \right] + r(x) v(t,x) \left(1 - \dfrac{u(t,x)+v(t,x)}{K(x)} \right), \\ t > 0, \ x \in \Omega, \\ \dfrac{\partial u}{\partial n} - \dfrac{u}{P} \dfrac{\partial P}{\partial n} = \dfrac{\partial v}{\partial n} - \dfrac{v}{Q} \dfrac{\partial Q}{\partial n} = 0, \quad x \in \partial\Omega, \\ u(0,x) = u_0(x), \qquad v(0,x) = v_0(x), \quad x \in \Omega. \end{cases} \tag{2.2}$$

Let us note that, for smooth positive P and Q, the boundary conditions in (2.2) are equivalent to

$$\frac{\partial}{\partial n} \left(\frac{u}{P} \right) = 0, \qquad \frac{\partial}{\partial n} \left(\frac{v}{Q} \right) = 0, \quad x \in \partial\Omega. \tag{2.3}$$

The three most common particular cases are outlined below:

1. If either both P and a_1 or both Q and a_2 are constant, then either the first or the second equation incorporates a regular diffusion term $d_1 \Delta u$ or $d_2 \Delta v$, where $d_1 = a_1/P$ or $d_2 = a_2/Q$.
2. If a_1 is space-independent, in the first equation of (2.2) we obtain the type of dispersal $\Delta(u/P)$. In the particular case when $P \equiv K$ (or P is proportional to K) we have the term $\Delta(u/K)$, first introduced in [6] and later considered in [8,12,13]. If Q is constant, while a_2 is proportional to $1/K$, we have the dispersal type $\nabla \cdot (\frac{1}{K} \nabla v)$ which was considered in [8,9].
3. If $a_1 = \mu_1 P$, $\ln P = \mu_2 K$, where μ_i, $i = 1, 2$ are space-independent, and $r = K$, we obtain the directed advection model of the type

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu \nabla u - \alpha u \nabla K] + u(K - u), \tag{2.4}$$

where $\mu = \mu_1$, $\alpha = \mu_1 \mu_2$. Eq. (2.4) was considered in [1–5], see also references therein.