



Competitive spatially distributed population dynamics models: Does diversity in diffusion strategies promote coexistence?



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ABSTRACT

We study the interaction between different types of dispersal, intrinsic growth rates and carrying capacities of two competing species in a heterogeneous environment: one of them is subject to a regular diffusion while the other moves in the direction of most per capita available resources. If spatially heterogeneous carrying capacities coincide, and intrinsic growth rates are proportional then competitive exclusion of a regularly diffusing population is inevitable. However, the situation may change if intrinsic growth rates for the two populations have different spatial forms. We also consider the case when carrying capacities are different. If the carrying capacity of a regularly diffusing population is higher than for the other species, the two populations may coexist; as the difference between the two carrying capacities grows, competitive exclusion of the species with a lower carrying capacity occurs.

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1. Introduction

Spatial heterogeneity of the environment and species distribution is an important characteristic in population ecology. The space movements are usually modeled with a diffusion term, and a certain effort was undertaken to explain the role of diffusion coefficients in heterogeneous environments. If the environment is heterogeneous, and the per capita growth functions include a sum of population densities then the population with the slowest diffusion survives in competition with similar species which differ by diffusion coefficient only [12]. However, if we have a Lotka system with only partially shared resources, the situation changes [27]: there is an asymptotically stable coexistence equilibrium once the difference between the diffusion rates is not very significant. An interesting observation in [21] is the evolutionary advantage of space-dependent carrying capacity compared to the homogeneous carrying capacity with the same average value over space.

For diffusing populations, not only the dispersal speed but also the strategy has recently become an object of intensive discussion. This is

aimed to address the following issue: as the diffusion coefficient tends to infinity, regularly diffusing populations tend to be distributed uniformly which is not optimal in a heterogeneous environment in the following sense. The ideal free distribution describes how species can distribute themselves to maximize their total fitness in such a way that any movement in an ideally distributed population will lead to decrease in fitness; in a heterogeneous medium, this corresponds to the case when per capita available resources, not the density, is uniformly distributed. To incorporate movements in the direction of the environmental gradient, an advection term was added to the equation [1,5–10,34] which led to ideally distributed solutions, at least in the case when advection prevails over the random diffusion. The interplay of advection and diffusion coefficients in each of two competing species was explored in the recent paper [10]. The dispersal type which, independently of parameters involved in the equation, has the ideal free distribution as a solution was developed in [3], and according to [23], for a time-independent carrying capacity all positive solutions tend to the ideal free distribution. Let us note that the ideal free distribution was recently suggested as a null model for habitat patch selection in [30], see [25] for some examples of species which tend to disperse according to the inhomogeneous carrying capacity.

There were numerous studies on non-linear diffusion in biological systems, let us note [31], the recent paper [13] and references therein.

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However, the focus of the investigation was on mathematical and/or numerical modeling, in order to more exactly match the laboratory data. If, as in [13], a competition was considered, the same type of diffusion was involved in every equation. To the best of our knowledge, before [12] the influence of diffusion on evolutionary success has not been theoretically analyzed.

The evolutionarily stable strategy is understood in the sense of [11,14]: if an evolutionarily stable strategy is adopted by a resident population, it becomes impossible for a population choosing a different strategy to invade its habitat. In [25] evolutionary stability of carrying capacity driven dispersal over the regular diffusion was justified, if all other parameters of the resident and invasive populations coincide. In the present paper, both intrinsic growth rates and carrying capacities for these two populations may differ.

The idea of superiority of the carrying capacity-driven diffusion strategy compared to the regular (random) diffusion was first outlined in [24] for the logistic growth. The main contributions of the present paper compared to [24] can be summarized as follows:

1. In [24], only populations following the logistic growth law were considered. Here we consider the variety of growth rules (Gompertz, generalized logistic etc.)
2. In [24], the difference between the two populations is diffusion strategy only. While it is important to study the influence of one chosen factor only, in practice a competition involves many different factors. Here an interplay of two couples of parameters is investigated: the first factor is always the diffusion strategy, and the second one includes either carrying capacities or intrinsic growth rates. With the same diffusion strategy, higher carrying capacity would guarantee survival, but with inferior (regular) diffusion this situation may lead to coexistence. We study how optimal diffusion strategy can alleviate the negative influence of less efficient resources exploitation (a lower carrying capacity).
3. The papers [24,25] include only theoretical results in time-independent environments. The combination of theoretical and numerical analysis allows to study the situation when the carrying capacity is time-dependent (for example, due to seasonal changes), to confirm theoretical conclusions and to complement them (for instance, to explore the dependency of the limit solution on the diffusion coefficient for a regularly diffusing population).

The proofs of results of the present paper follow the schemes of the proofs in [23,24] and use some ideas of the monograph [4].

In our present study, we consider different intrinsic growth rates for both populations. If they are spatially similar (for example, proportional), the situation does not differ from the equal growth rates, which means competitive exclusion of a regularly diffusing population. However, if the ratio of intrinsic growth rates is spatially heterogeneous, coexistence is possible. The two equations can also involve different diffusion coefficients; their relation and values influence the transient behavior and convergence rates to the stable equilibrium state.

It is a common belief that a higher carrying capacity of an invader leads to successful invasion and even extinction of the resident. For example, in [33] the carrying capacity was associated with cell mutations, where only the colony (mutating or not) with a higher carrying capacity survived in a competition, see also [2]. The recent paper [18] explored the conjecture whether the main reason for an invader to replace antagonistic indigenous populations can be ascribed to the larger carrying capacity of the former.

In our study, we considered two cases. In the first case, the mortality term is referred to the crowding effect, the two types of species have similar physical characteristics, including food consumption, but may have different crowding tolerance: a population starts to decrease when the local density exceeds some K which may be different for the two types. If higher (or at least not less) crowding tolerance is incorporated with the directed dispersal while the other

population adopts random diffusion, the regularly diffusing population goes extinct. If random diffusion is combined with a higher crowding tolerance, we prove that this guarantees survival. If the prevalence of this crowding tolerance over the one combined with the directed dispersal is not very significant both populations coexist. Thus diversity in dispersal strategies provides coexistence in this range of parameters. Higher ratios of carrying capacities will bring the population with a lower one to extinction, as numerical examples illustrate. In the second case, the two species have different (space-dependent) consumption rates. However, if these rates are proportional, still competitive exclusion of a regularly diffusing population is observed.

Spatial heterogeneity of the environments plays a crucial role in our study; for the recent investigation of spreading or vanishing of invasive species see, for example, the recent paper [35] and references therein.

The paper is organized as follows. Section 2 describes the model and verifies positivity, existence and uniqueness of a solution for any non-negative (and not identically equal to zero) initial conditions. Section 3 explores the equilibria, in particular, outlines the cases when there is no coexistence. Section 4 includes the main results of the paper: the strategy leading to the ideal free distribution has the advantage of evolutionary stability if intrinsic growth rates are constant and the randomly diffusing population does not have a higher carrying capacity. If it does have, its survival is guaranteed, and numerical examples in Section 5 illustrate that both coexistence and competitive exclusion of the population with the carrying capacity driven dispersal are possible. Section 5 also presents an example of coexistence for different intrinsic growth rates, and Section 6 contains a brief summary of the results of the paper and discussion.

2. Description of the model

In the present paper, we consider the system describing two populations competing for the resources which exist in the isolated domain Ω . This corresponds to the initial-boundary value problem with the Neumann boundary conditions

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u(t, x)}{K_1(x)} \right) + r_1(x)u(t, x)g(x, u(t, x), v(t, x), K_1(x)), \\ \frac{\partial v(t, x)}{\partial t} = D_2 \nabla \cdot (d(x)\nabla v(t, x)) \\ \quad + r_2(x)v(t, x)g(x, v(t, x), u(t, x), K_2(x)), \\ t > 0, x \in \Omega, \frac{\partial}{\partial n} \left(\frac{u}{K_1(x)} \right) = d(x) \frac{\partial v}{\partial n} = 0, x \in \partial\Omega \end{cases} \quad (2.1)$$

and the initial conditions

$$u(0, x) = u_0(x), v(0, x) = v_0(x). \quad (2.2)$$

We assume that $K_i(x)$, $r_i(x)$, $i = 1, 2$ are in the class $C^{1+\alpha}(\overline{\Omega})$, and $K_i(x) > 0$, $r_i(x) > 0$ for any $x \in \overline{\Omega}$, and $r_i(x) > 0$ in an open nonempty subdomain of Ω . Here Ω is an open nonempty bounded domain of \mathbb{R}^n with $\partial\Omega \in C^{2+\alpha}$, $0 < \alpha < 1$, and $J_1 \times J_2$ a bounded subset of \mathbb{R}^2 . The set $J_1 \times J_2$ corresponds to the range of the solutions to (2.1) and is determined by the corresponding upper and lower solutions.

For future reference, we denote $Q = (0, \infty) \times \Omega$, $\overline{Q} = [0, \infty) \times \overline{\Omega}$, $\partial Q = (0, \infty) \times \partial\Omega$. To state the assumptions on the functions $f_1(x, u, v, K) = r_1 u g(x, u, v, K)$ and $f_2(x, u, v, K) = r_2 v g(x, v, u, K)$, we will need the following definition [28].

Definition 1. A function $f_i = f_i(x, u_1, u_2, K)$ is said to be quasimonotone nonincreasing if for fixed x, K, u_i , f_i is nonincreasing in u_j for $j \neq i$.

A vector-function $\mathbf{f} = (f_1, f_2)$ is called quasimonotone nonincreasing in $J_1 \times J_2$ if both f_1 and f_2 are quasimonotone nonincreasing in $(u_1, u_2) \in J_1 \times J_2$.

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