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Dynamical behavior of a general reaction–diffusion–advection model for two competing species

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ABSTRACT

It is well known that the studies of the evolution of biased movement along a resource gradient could create very interesting phenomena. This paper deals with a general two-species Lotka–Volterra competition model for the same resources in an advective non-homogeneous environment, where the individuals are exposed to unidirectional flow (advection) but no individuals are lost through the boundary. It is assumed that the two species have the same population dynamics but different diffusion and advection rates. It is shown that at least five scenarios can occur (i) If one with a very strong biased movement relative to diffusion and the other with a more balanced approach, the species with much larger advection dispersal rate is driven to extinction; (ii) If one with a very strong biased movement and the other is smaller compare to its diffusion, the two species can coexist since one species mainly pursues resources at places of locally most favorable environments while the other relies on resources from other parts of the habitat; (iii) If both of the species random dispersal rates are sufficiently large (respectively small), two competing species coexist; (iv) If one with a sufficiently large random dispersal rate and the other with a sufficiently small one, two competing species still coexist; (v) If one with a sufficiently small random dispersal rate and the other with a suitable diffusion, which causes the extinction of the species with smaller random movement. Where (iii), (iv) and (v) show the global dynamics of (5) when both of the species dispersal rates are sufficiently large or sufficiently small. These results provide a new mechanism for the coexistence of competing species, and they also imply that selection is against excessive advection along environmental gradients (respectively, random dispersal rate), and an intermediate biased movement rate (respectively, random dispersal rate) may evolve. Finally, we also apply a perturbation argument to illustrate the evolution of these rates.

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1. Introduction

Ecologically, positive solutions correspond to the existence of steady states of species. So, the set of positive solutions may contain crucial clues for the stationary patterns. From the mathematical viewpoint, it is important to derive some information about the set of positive solutions by means of the coefficients. Hence, many researchers focused on this topic. To begin our

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discussion, we first recall the following logistic model proposed by Verhulst:

$$u_t = u(a - u), \quad t \in \mathbb{R}^+ := (0, \infty), \tag{1}$$

where u denotes the total population of a species and a is a positive constant representing the carrying capacity of the environment. It is well known that the equilibrium $u = a$ is globally asymptotically stable, i.e., for all initial value $u(0) > 0$,

$$\lim_{t \rightarrow \infty} u(t) = a.$$

Spatial characteristics of the environment play an important role in ecology and evolution. Many researchers pay more attention on the interaction between migration and the resources, one can refer to [1–3]. When taking the interaction between migration and the resources into consideration, we turn to the following diffusive equation

$$\begin{cases} u_t = \mu \Delta u + u(m(x) - u), & \text{in } \Omega \times \mathbb{R}^+, \\ \nabla u \cdot \vec{n} = 0, & \text{on } \partial\Omega \times \mathbb{R}^+, \end{cases} \tag{2}$$

where $\mu > 0$ denotes the dispersal rate and $u(x, t)$ denotes the population density of the species at location x and time t . The habitat Ω is a bounded domain in \mathbb{R}^n with smooth boundary, denoted by $\partial\Omega$. The function $m(x)$ represents the local carrying capacity or the common (spatially inhomogeneous) intrinsic growth rate. The zero Neumann (no-flux) boundary condition means that no individual crosses the boundary of the habitat; \vec{n} denotes the outward unit normal vector on $\partial\Omega$. When $m(x) \equiv a$, i.e., the resources are distributed uniformly, then all solutions of (2) with non-trivial non-negative initial values converge to a in Ω as $t \rightarrow \infty$. However, if $m(x) \neq \text{const}$ with $\int_{\Omega} m \geq 0$, then all solutions converge to $\theta(x; \mu)$ as $t \rightarrow \infty$ for non-trivial non-negative initial values, where $\theta(x; \mu)$ is the unique positive solution of

$$\begin{cases} \mu \Delta \theta + \theta(m(x) - \theta) = 0, & \text{in } \Omega, \\ \nabla \theta \cdot \vec{n} = 0, & \text{on } \partial\Omega. \end{cases} \tag{3}$$

(See, e.g. [4] for the proof of existence and uniqueness results of (3).)

In the aforementioned literature, the authors only discuss the case in a spatially varying but temporally constant environment. Usually, faster dispersal is always selected against if dispersal is completely random, see also [5,6]. However, organisms sometimes are forced to move in certain directions, for example, in advective environments such as rivers, water columns or the gut [7–12], or when environmental conditions shift, such as, movement of temperature isoclines caused by global climate change [3,13]. Active movement of organisms may also be biased in certain directions, for example, moving up a resource gradient [14–16], or a fitness gradient [17,18]. Along these clues, we assume further that the species obeys the logistic growth law, then we derive the following reaction–diffusion–advection model:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m - u), & \text{in } \Omega \times \mathbb{R}^+, \\ (\mu \nabla u - \alpha u \nabla m) \cdot \vec{n} = 0, & \text{on } \partial\Omega \times \mathbb{R}^+, \end{cases} \tag{4}$$

where ∇ is the gradient operator, $\nabla \cdot$ is the divergence operator; $\alpha > 0$ measures the tendency of the biased movement of species along the environmental gradient; no-flux boundary condition is imposed on the boundary $\partial\Omega$ of a bounded smooth domain Ω in \mathbb{R}^n . It is shown in [14] that for all $\mu > 0$, $\alpha \geq 0$ and $m > 0$, a unique coexistence state $\theta(x; \mu, \alpha)$ for (4) exists. Moreover, $\theta(x; \mu, \alpha)$ is globally asymptotically stable among non-negative, non-trivial initial data. In particular, if the species has almost the same weight as the water, then the upward (or downward) movement caused by buoyancy (or gravity) can be ignored, i.e., $\alpha \approx 0$, and so in this case problem (4) reduces to problem (2)–(3).

Many researchers pay more attention on the studies of evolution of biased movement along a resource gradient, one can refer to [19–21]. Evolutionarily stable dispersal strategies are found to be those that have comparable dispersal and advection rates. On the one hand, if individuals move upward along the gradient of a resource distribution, and the advection rate is large relative to the dispersal rate, then the individuals become overcrowded at only the best locations and stay there, reasonably beneficial areas. Besides, higher dispersal rates can help individuals utilize those resources as well. Hence, slower dispersal is selected against. On the other hand, when random dispersal is large in comparison to resource tracking, the species will spread widely in habitat so that it only utilizes some average quality of the resource. This implies the fast dispersal is also selected against. Altogether, intermediated dispersal rate can evolve. However, much less is known about the evolution of dispersal in advection environments, where movement bias is caused by external forces such as river flow, gravity or climate. In this paper, we will address these questions.

In view of the limited ability of a predator to consume its prey, a general functional response of the predator $G(u)$ was introduced by Solomon [22] and Holling [23,24], and hence we propose two aquatic species which are competing for the same resources in the water column, as described by the following general Lotka–Volterra competition model including advection forces:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m - u) - G(u)v, & \text{in } \Omega, \\ v_t = \nabla \cdot [v \nabla v - \beta v \nabla m] + v(m - v - G(u)), & \text{in } \Omega, \\ (\mu \nabla u - \alpha u \nabla m) \cdot \vec{n} = (v \nabla v - \beta v \nabla m) \cdot \vec{n} = 0, & \text{on } \partial\Omega, \end{cases} \tag{5}$$

where u and v , represent the population densities of two competing species with random dispersal rates $\mu, v > 0$ respectively, are therefore non-negative functions of x and t ; $m(x)$ denotes the local intrinsic growth rate and is assumed to

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