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# Evolution of passive movement in advective environments: General boundary condition \*

Peng Zhou a,b, Xiao-Qiang Zhao b,\*

<sup>a</sup> Department of Mathematics, Shanghai Normal University, Shanghai 200234, PR China
 <sup>b</sup> Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada

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#### Abstract

In a previous work [16], Lou et al. studied a Lotka–Volterra competition–diffusion–advection system, where two species are supposed to differ only in their advection rates and the environment is assumed to be spatially homogeneous and closed (no-flux boundary condition), and showed that weaker advective movements are more beneficial for species to win the competition. In this paper, we aim to extend this result to a more general situation, where the environmental heterogeneity is taken into account and the boundary condition at the downstream end becomes very flexible including the standard Dirichlet, Neumann and Robin type conditions as special cases. Our main approaches are to exclude the existence of co-existence (positive) steady state and to provide a clear picture on the stability of semi-trivial steady states, where we introduced new ideas and techniques to overcome the emerging difficulties. Based on these two aspects and the theory of abstract competitive systems, we achieve a complete understanding on the global dynamics. © 2017 Elsevier Inc. All rights reserved.

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E-mail address: zhao@mun.ca (X.-Q. Zhao).

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Corresponding author.

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#### 1. Introduction

Recently, Lou et al. [16] studied the following two-species Lotka-Volterra competition-diffusion-advection system

$$\begin{cases} u_{t} = du_{xx} - \alpha u_{x} + u[r_{0} - u - v], & 0 < x < L, t > 0, \\ v_{t} = dv_{xx} - \beta v_{x} + v[r_{0} - u - v], & 0 < x < L, t > 0, \\ du_{x}(0, t) - \alpha u(0, t) = du_{x}(L, t) - \alpha u(L, t) = 0, & t > 0, \\ dv_{x}(0, t) - \beta v(0, t) = dv_{x}(L, t) - \beta v(L, t) = 0, & t > 0, \\ u(x, 0) = u_{0}(x) \ge \neq 0, & 0 < x < L, \\ v(x, 0) = v_{0}(x) \ge \neq 0, & 0 < x < L, \end{cases}$$

$$(1.1)$$

which can be used to describe the competition for the same resources as measured by a constant function  $r_0 > 0$  between two aquatic species whose population densities are represented, respectively, by u(t, x) and v(t, x) at time t > 0 and location x, in a river/stream with constantly unidirectional water flow or a vertical water column that is abstracted here by a one-dimensional habitat and denoted by an interval (0, L). The no-flux boundary conditions at both ends mean that no individuals can move in or out the habitat through the boundary, that is, a closed environment is under consideration. By using the approach of adaptive dynamics [4], the authors assumed that two competitors have the same random diffusion rate d > 0 but different effective advection rates  $\alpha, \beta \ge 0$  so that they are able to figure out whether stronger or weaker advection is more helpful for species to win the competition. In the context of water column, it seems easy to understand  $\alpha \neq \beta$  since different types of nutrients or plankton species do have different sinking rates under the action of gravity. Indeed, this can also happen in river ecology; one empirical support comes from Trimbee and Harris [22], where they designed an experiment in a small reservoir, Guelph Lake, Ontario, which lasted 105 days, and finally they detected that Stephanodiscus has an advection rate of 0.4 cm/s, while Aphanizomenon has an advection rate of 0.2 cm/s. The main conclusion in [16] can be stated as follows:

**Theorem A.** Assume that  $d, r_0 > 0$  and  $0 \le \alpha < \beta$ . Then  $(\overline{u}, 0)$  is globally asymptotically stable, i.e., every solution of system (1.1) will converge to  $(\overline{u}, 0)$  as  $t \to \infty$  for any non-negative and non-trivial initial condition, where  $\overline{u}$  is the unique positive steady state of system (1.1) with  $v \equiv 0$ .

Biologically, the above result reveals that in a given closed homogeneous advective environment, species with weaker passive movement has more competitive advantages. This is because advective force will always drive individuals to the right boundary, which would cause overcrowding and overmatching of resources at right end, so the competitor with weaker advection is relatively more advantageous. Moreover, the above result also implies that the movement without advection in homogeneous environments is evolutionarily stable, as advection results in the distribution of population mismatching with the resources that are distributed evenly across space, while the species without advective movements will perfectly match the resource at the equilibrium  $u = r_0$ , which, in biology, is called ideal free distribution (introduced by Fretwell and Lucas in [5]). Generally, it is believed that strategies leading to the ideal free distribution of populations should be evolutionarily stable; see, e.g., [2] and references therein.

The main goal of the current paper is to extend the above result to a more general situation, where the resource function may depend nontrivially on the spatial variable (spatially inhomogeneous environment) and the boundary conditions at the downstream end (x = L) become very

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