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Persistence and extinction of population in reaction–diffusion–advection model with strong Allee effect growth

Yan Wang[1,2] · **Junping Shi**[1] · **Jinfeng Wang**[3]

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Abstract

A reaction–diffusion–advection equation with strong Allee effect growth rate is proposed to model a single species stream population in a unidirectional flow. Here random undirected movement of individuals in the environment is described by passive diffusion, and an advective term is used to describe the directed movement in a river caused by the flow. Under biologically reasonable boundary conditions, the existence of multiple positive steady states is shown when both the diffusion coefficient and the advection rate are small, which lead to different asymptotic behavior for different initial conditions. On the other hand, when the advection rate is large, the population becomes extinct regardless of initial condition under most boundary conditions. It is shown that the population persistence or extinction depends on Allee threshold, advection rate, diffusion coefficient and initial conditions, and there is also rich transient dynamical behavior before the eventual population persistence or extinction.

Keywords Strong Allee effect · Reaction diffusion · Advection · Steady state · Extinction · Persistence

Mathematics Subject Classification 92D25 · 35K57 · 35K58 · 92D40

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✉ Junping Shi
jxshix@wm.edu

[1] Department of Mathematics, College of William and Mary, Williamsburg, VA 23187-8795, USA

[2] Department of Applied Science, College of William and Mary, Williamsburg, VA 23187-8795, USA

[3] School of Mathematical Sciences and Y.Y. Tseng Functional Analysis Research Center, Harbin Normal University, Harbin 150001, Heilongjiang, People's Republic of China

1 Introduction

The growth of a biological population is affected by both the environmental factors and the population density. The spatial structure of the natural environment influences the movement pattern of the individuals in the population, and that in turn affects the population dynamics. Individual movement can be undirected or directed. Random indirected movement of individuals in the environment is often described by a passive diffusion of a density function in continuum following the classical approach in physics. Combining with the density-dependent growth of the population, we obtain reaction–diffusion models which have been widely used to describe spatiotemporal behavior in both chemical (Epstein and Pojman 1998; Prigogine and Lefever 1968) and biological fields (Cantrell and Cosner 2003; Ni 2011; Okubo and Levin 2001).

In some situations, in addition to the random dispersal, individuals in a population also make advective movement which is from sensing and following the gradient of resource distribution (taxis) or a directional fluid/wind flow. Some examples are marine living species flowing in rivers, lakes or oceans, benthic marine species along coastlines with dominant long-shore currents, or phytoplankton species in water column experiencing gravitational downward pull (Huisman et al. 2002; Speirs and Gurney 2001). The addition of advection to reaction–diffusion models may change the long term outcome (persistence/extinction) of the population (Hsu and Lou 2010; Jin and Lewis 2011; Lam et al. 2016; Lutscher et al. 2005, 2006). When the population follows a typical logistic growth, there often exists a critical parameter value (diffusion coefficient, advection coefficient, domain size, growth rate) for the population persistence or extinction (Lam et al. 2015; Lou and Lutscher 2014; Mckenzie et al. 2012), and it is well known that the model has a unique positive steady state solution which is globally asymptotically stable when population persists (Cantrell and Cosner 2003).

Despite the universal acceptance of logistic growth as the most reasonable one, since Allee's pioneer work (Allee 1931) in 1931, ecologists have found that in many cases, the population growth could depend on the density positively instead of negative dependence as in the logistic one. When the population density is low, individual may have difficulty in finding mates or defending against predators, which will lead to low birth rate and high death rate. For high population density, population size is still restricted by the environment limits. Thus either excessively sparse or excessive crowded can inhibit the population growth, which means such species has a optimum intermediate range for the population growth. This phenomenon, frequently termed as the Allee effect, has been the focus of increasing interest over the past three decades (Courchamp et al. 2008; Lewis and Kareiva 1993; Stephens and Sutherland 1999). For instance, due to the severe harvesting, the west Atlantic cod (*Ganus morhus*) population stayed below the Allee threshold in the past few decades (De Roos and Persson 2002; Rowe et al. 2004). Although many management strategies have been implemented to reduce fishing mortality after a collapse, the cod population does not show an increase of size and such a lack of recovery indicates a reduced capacity to rebound from low densities. Another example is the case of Vancouver Island marmot (*Marmota vancouverensis*) whose population has declined by 80% since the 1980s.

The studies in Brashares et al. (2010) shows a growth rate of strong Allee effect type for the marmot due to the longer distance traveled when finding mates and change of social behavior. Overall more and more evidences of Allee effect in wild species populations have been found in recent studies (Courchamp et al. 2008; Kramer et al. 2009), especially for marine species such as blue crab, oyster whose growth rate strongly depends on the river/ocean flow (Gascoigne and Lipcius 2004a, b; Jordan-Cooley et al. 2011).

In this paper, we study the dynamic behavior of a reaction–diffusion–advection model of the density of a biological species in an open or closed river environment with a strong Allee effect population growth rate. If the river population suffers a loss on the boundary ends due to movement, then the river is an open environment and otherwise it is a closed environment. Compared to the well-studied reaction–diffusion–advection model with logistic growth rate (Cantrell and Cosner 2003; Lam et al. 2015; Lou and Lutscher 2014), the model with strong Allee effect growth possesses multiple steady state solutions, and the extinction state is always locally stable. Here we set up a framework of reaction–diffusion–advection model in a one-dimensional habitat with general growth rate functions and general boundary conditions, but focus on the strong Allee effect type growth and open or closed environment boundary conditions.

Our main results on the dynamics of reaction–diffusion–advection model with strong Allee effect type growth on a bounded habitat include:

1. The solution asymptotically always converges to a nonnegative steady state solution, and there is no temporal oscillatory behavior.
2. The population goes to extinction when the initial condition is small, or the advection rate is large and under an open environment.
3. When the initial population is properly large, the population persists if the advection rate is small and the boundary condition is favorable. In that case, a bistability exists in the system so different outcomes can be reached with different initial settings.
4. In a closed environment river system, when the advection rate is large, the population either becomes extinct or it only concentrates at the downstream end. Numerical results indicate that extinction or concentration at downstream depends on the relative position of the Allee effect threshold value.
5. The traveling wave speed of associated problem is determined by the diffusion coefficient, advection rate, baseline growth rate and the Allee effect threshold, and the traveling-wave-like transient dynamics facilitates the merge of population persistence/extinction patches.

Most of the above results are rigorously proved using theory of dynamical systems, partial differential equations, and upper–lower solution methods, and various numerical simulations are also included to verify or demonstrate theoretical results. Our focus is on the influence of various system parameters (diffusion coefficient, advection rate, Allee effect threshold, boundary condition parameters) and initial conditions on the asymptotic and transient dynamical behavior.

The question of dynamics of a spatially distributed species, moving passively in a stream or river, have been proposed to explore population persistence and the so-called "drift paradox" (Lutscher et al. Nov 2010; Pachepsky et al. 2005; Speirs and Gurney 2001). The drift paradox asks how stream-dwelling organisms can persist, without being washed out, when they are continuously subject to the unidirectional stream flow. With assumption of logistic population growth, the existence/persistence of a stream population in a constant environment have been considered in the framework of reaction–diffusion–advection in Lam et al. (2015, 2016), Lou and Lutscher (2014), Lou and Zhou (2015), Mckenzie et al. (2012), Speirs and Gurney (2001) and Vasilyeva and Lutscher (2010), and the effect of seasonal variations in environmental and climatic conditions on the stream population were considered in Jin et al. (2014), Jin and Lewis (2011, 2012). The competition of two species in stream environment have also been studied in Lam et al. (2015), Lou and Lutscher (2014), Lou et al. (2016), Vasilyeva and Lutscher (2012), Zhao and Zhou (2016), Zhou (2016) and Zhou and Zhao (2018). Several extended studies also consider the effect of river network structure (Ramirez 2012; Sarhad et al. 2014), drift-benthic structure (Huang et al. 2016; Lutscher et al. 2006), and meandering structure (Jin et al. 2017). On the other hand, integrodifferential and integrodifference models equations have also been used to describe the diffusion and advection but also long-distance dispersal, and comparable results with logistic growth on extinction, persistence and spreading of population have been obtained (Hutson et al. 2003; Jacobsen et al. 2015; Lutscher et al. 2005; Pachepsky et al. 2005). In most of the literature mentioned above and also the present paper, advection is a constant and unidirectional movement. Note that in other literature, the term "advection" was used for movement towards gradient of resource function for better quality habitat (Belgacem and Cosner 1995; Cantrell et al. 2006, 2007; Chen et al. 2008, 2012; Chen and Lou 2008; Cosner and Lou 2003; Lam 2011, 2012; Lam and Ni 2010; Zhou and Xiao 2018).

The role of the Allee effect in population spreading and invasion in reaction–diffusion or integrodifferential models has been investigated in Keitt et al. (2001), Kot et al. (1996), Lewis and Kareiva (1993), Maciel and Lutscher (2015), Sullivan et al. (2017), Wang and Kot (2001) and Wang et al. (2002), and the effect of Allee effect in population persistence on a bounded habitat has been considered in Liu et al. (2009), Ouyang and Shi (1998) and Shi and Shivaji (2006).

Our paper is organized as follows: In Sect. 2, we introduce the reaction–diffusion–advection model with strong Allee effect and the boundary conditions. Some mathematical preliminaries regarding eigenvalue problem, comparison of the boundary conditions, previous results on the non-advective case and the upper–lower methods are prepared in Sect. 3. Our main results on the dynamic properties of the model are stated and proved in Sect. 4. By using comparison method and variational method, we investigate the existence and multiplicity of positive nontrivial steady states and derive various sufficient conditions for the population persistence and extinction under an open or closed environment. We also use numerical simulation to explore the rich transient and wave-like dynamical behaviors. Some concluding remarks are made in Sect. 5.

2 Model

2.1 Equation

Following (Cantrell and Cosner 2003; Lou and Lutscher 2014), we consider a reaction–diffusion–advection equation on a one-dimensional bounded habitat $(0, L)$:

$$u_t = du_{xx} - qu_x + f(x, u), \qquad 0 < x < L,\ t > 0. \tag{2.1}$$

Here $u(x,t)$ is the population density of a biological species at location x and time t, $d > 0$ is the diffusion coefficient, $q \geq 0$ is the advection rate, and $f(x,u)$ is the growth/death rate of the species which may depend on the location and population density. As discussed in Lou and Lutscher (2014), (2.1) can be used to describe plankton growth in river flows, periphyton dynamics in the lake water column, or biological species in water flow from stream to ocean or lake.

We assume that the growth rate $f(x,u) = ug(x,u)$ satisfies the following basic technical assumptions, which are similar to the ones in Cantrell and Cosner (2003) and Shi and Shivaji (2006):

- (f1) For any $u \geq 0$, $g(\cdot, u) \in C[0, L]$, and for any $x \in [0, L]$, $g(x, \cdot) \in C^1[0, L]$.
- (f2) For any $x \in [0, L]$, there exists $r(x) \geq 0$, where $0 < r(x) < M$ and $M > 0$ is a constant, such that $g(x, r(x)) = 0$, and $g(x, u) < 0$ for $u > r(x)$.
- (f3) For any $x \in [0, L]$, there exists $s(x) \in [0, r(x)]$ such that $g(x, \cdot)$ is increasing in $[0, s(x)]$ and non-increasing in $[s(x), \infty]$; and there also exists $N > 0$ such that $g(x, s(x)) \leq N$.

Here $g(x,u)$ is the growth rate per capita at x; $r(x)$ is a local carrying capacity at x which has a uniform upper bound M; $u = s(x)$ is where $g(x, \cdot)$ reaches the maximum value, and the number N is a uniform bound for $g(x,u)$ at all (x,u). Typically the behavior of $g(x, \cdot)$ defined in (f3) can be one of the following three cases (see Shi and Shivaji 2006):

- (f4a) Logistic: $s(x) = 0$, $g(x, 0) > 0$, and $g(x, \cdot)$ is decreasing in $[0, \infty)$;
- (f4b) Weak Allee effect: $s(x) > 0$, $g(x, 0) > 0$ and $g(x, \cdot)$ is increasing in $[0, s(x)]$, non-increasing in $[s(x), \infty)$; or
- (f4c) Strong Allee effect: $s(x) > 0$, $g(x, 0) < 0$, $g(x, s(x)) > 0$ and $g(x, \cdot)$ is increasing in $[0, s(x)]$, non-increasing in $[s(x), \infty)$. Hence there exists a unique $h(x) \in (0, s(x))$ such that $g(x, h(x)) = 0$ for all $0 < x < L$.

In (f4c), the quantity $h(x)$ is the local threshold value for the extinction/persistence of the population, which is also known as the sparsity constant. Figure 1 shows typical graphs of $f(x,u)$ and $g(x,u)$ for these three cases.

Typical examples of growth rate functions satisfying (f4a) is

$$f(x, u) = u(r(x) - u), \tag{2.2}$$

while the one for Allee effect is

$$f(x, u) = u(u - h(x))(r(x) - u), \tag{2.3}$$

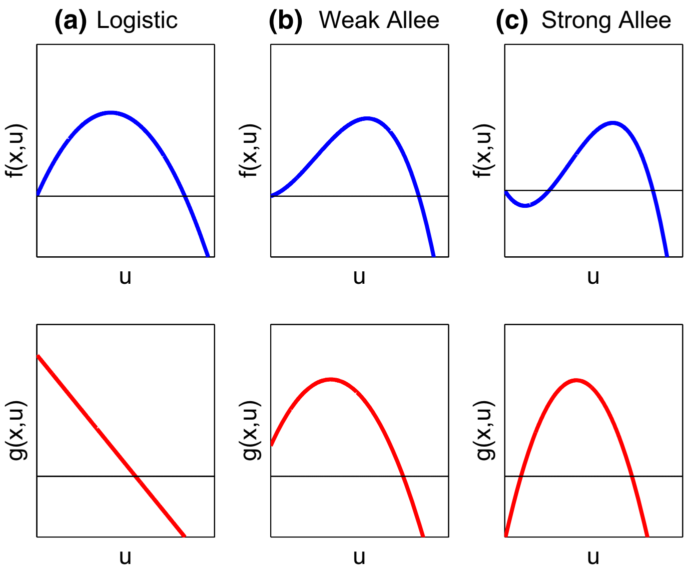

Fig. 1 **a** Logistic; **b** weak Allee effect; **c** strong Allee effect; the graphs on top row are growth rate $f(u)$, and the ones on lower row are growth rate per capita $g(u)$

where $0 < h(x) < r(x)$ represents the strong Allee effect case, and $-r(x) < h(x) < 0$ represents the weak Allee effect case. The nonlinear function $f(x, u)$ with a strong Allee effect growth rate is also called the bistable type as $u = 0$ and $u = r(x)$ are both stable solutions to the ordinary differential equation (ODE) $u' = f(x, u)$.

2.2 Boundary conditions

The boundary condition at $x = 0$ or $x = L$ can take one of the following forms (see (Lou and Lutscher 2014) for ecological interpretation of each boundary condition):

$$\begin{aligned} &\text{No Flux (NF)} \qquad du_x(x,t) - qu(x,t) = 0, && (2.4)\\ &\text{Free Flow (FF)} \qquad u_x(x,t) = 0, && (2.5)\\ &\text{Hostile (H)} \qquad u(x,t) = 0. && (2.6) \end{aligned}$$

Often at the upstream end $x = 0$ a no flux boundary condition is imposed, and at the downstream end $x = L$ a free flow boundary condition is used to indicate that there is a population loss due to the advective movement, or a hostile boundary condition is used which means no individuals can return to the habitat after leaving. The no-flux boundary condition can be interpreted as there is no loss of individuals at $x = 0$ or $x = L$.

Following (Lam et al. 2016; Lou and Lutscher 2014), we impose boundary conditions for (2.1) in a general form

$$du_x(0,t) - qu(0,t) = b_u qu(0,t), \quad du_x(L,t) - qu(L,t) = -b_d qu(L,t), \tag{2.7}$$

where $b_u \geq 0$ and $b_d \geq 0$. Here the parameters b_u and b_d determine the magnitude of population loss at the upstream end $x = 0$ and the downstream end $x = L$, respectively. For $b_u = 0$ ($b_d = 0$), that is the no-flux (NF) boundary condition (2.4); $b_d = 1$ gives the free-flow (FF) boundary condition (2.5); and for $b_u \to \infty$ ($b_d \to \infty$), we have the hostile (H) boundary condition (2.6). Note that (2.7) with $b_u \geq 0$ and $b_d \geq 0$ implies that

$$[du_x(x,t) - qu(x,t)]\Big|_0^L = -q[b_d u(L,t) + b_u u(0,t)] \leq 0. \tag{2.8}$$

When $b_u = b_d = 0$, we have a no-flux boundary condition at both ends of the stream:

$$\text{(NF/NF)} \qquad du_x(0,t) - qu(0,t) = 0, \quad du_x(L,t) - qu(L,t) = 0, \tag{2.9}$$

which represents a closed environment as there is no loss of the population due to the movement. On the other hand, if $b_u > 0$ or $b_d > 0$, then the total population has a loss over the region $[0, L]$ due to the movement and (2.7) depicts an open flowing environment. For example,

$$\text{(NF/FF)} \qquad du_x(0,t) - qu(0,t) = 0, \quad u_x(L,t) = 0, \tag{2.10}$$

In this paper, we consider the persistence and extinction of population $u(x,t)$ under the general boundary conditions (2.7) with $b_u \geq 0$ and $b_d \geq 0$. But hostile boundary condition will also be studied some time as a comparison, such as (H/H), (NF/H) or (H/NF). For example,

$$\text{(NF/H)} \qquad du_x(0,t) - qu(0,t) = 0, \quad u(L,t) = 0. \tag{2.11}$$

Summarizing the above discussions, we will consider the following reaction–diffusion–advection equation with a general Danckwerts boundary condition at the upstream ($x = 0$) and downstream ($x = L$) ends:

$$\begin{cases} u_t = du_{xx} - qu_x + f(x,u), & 0 < x < L, \ t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in (0, L). \end{cases} \tag{2.12}$$

3 Preliminaries

3.1 Eigenvalue problem and logistic model

In this section we first recall some results on the following eigenvalue problem:

$$\begin{cases} d\phi''(x) - q\phi'(x) + p(x)\phi(x) = \lambda\phi(x), & 0 < x < L, \\ d\phi'(0) - q\phi(0) = b_u q\phi(0), \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L). \end{cases} \tag{3.1}$$

Here $d > 0$, $q \geq 0$, $p(x) \in L^\infty(0, L)$, and the boundary conditions are the ones introduced in Sect. 2.2. Then we have the following properties for the eigenvalues.

Proposition 3.1 *Suppose that $d > 0$, $L > 0$, $q \geq 0$, and $p(x) \in L^\infty(0, L)$. Then*

1. *The eigenvalue problem (3.1) has a sequence of eigenvalues*

$$\lambda_1 > \lambda_2 > \cdots > \lambda_n \to -\infty, \tag{3.2}$$

and the principal eigenvalue λ_1 has the variational characterization $-\lambda_1 = \inf_{\psi \in X_1, \psi \neq 0} R(\psi)$, where $R(\psi)$ is the Rayleigh quotient

$$R(\psi) = \frac{\displaystyle\int_0^L e^{\alpha x}[d(\psi')^2(x) - p(x)\psi^2(x)]dx + qb_u\psi^2(0) + qb_d e^{\alpha L}\psi^2(L)}{\displaystyle\int_0^L e^{\alpha x}\psi^2(x)dx}, \tag{3.3}$$

$\alpha = q/d$ and $X_1 = H^1(0, L)$.

2. *The principal eigenvalue $\lambda_1 = \lambda_1(p, d, q, b_u, b_d)$ is continuously differentiable in d, q, b_u, b_d and is decreasing with respect to b_u and b_d; if $p_1(x) \geq p_2(x)$, then $\lambda_1(p_1) \geq \lambda_1(p_2)$.*
3. *If $b_d > 0$ and $b_u \geq 0$, then $\lambda_1(q) \to -\infty$ as $q \to +\infty$; moreover if $b_d > 1/2$, then $\lambda_1(q)$ is strictly decreasing in q.*
4. *If $\int_0^L e^{\alpha x} p(x)dx > 0$ and $b_d = b_u = 0$, then there always holds $\lambda_1(q) > 0$, where $\alpha = q/d$.*
5. *If $p(x) < 0$ and $b_d, b_u \geq 0$, for $x \in [0, L]$, then $\lambda_1(q) < 0$.*

Proof We use the transform $\phi = e^{\alpha x}\psi$. Then system (3.1) becomes

$$\begin{cases} d\psi''(x) + q\psi'(x) + p(x)\psi(x) = \lambda\psi(x), & 0 < x < L, \\ d\psi'(0) = b_u q\psi(0), \quad d\psi'(L) = -b_d q\psi(L). \end{cases} \tag{3.4}$$

Part 1 is well-known as (3.4) can be written as a self-adjoint eigenvalue problem:

$$\begin{cases} (P\psi')' + (Q - \lambda S)\psi = 0, & x \in (0, L), \\ P(0)\sin\beta\psi'(0) - \cos\beta\psi(0) = 0, \quad P(L)\sin\gamma\psi'(L) - \cos\gamma\psi(L) = 0. \end{cases}$$

with

$$P(x) = de^{\alpha x}, \ Q(x) = p(x)e^{\alpha x}, \ S(x) = e^{\alpha x}, \ \beta = \operatorname{arccot}(b_u q), \ \gamma = \operatorname{arccot}(-b_d q e^{\alpha L}).$$

Then the existence of eigenvalues follows from Coddington and Levinson (1955, Theorem 8.2.1). From the definition of Rayleigh quotient (3.3), it is clear that λ_1 is decreasing in b_d or b_u and if $p_1(x) \geq p_2(x)$, then $\lambda_1(p_1) \geq \lambda_1(p_2)$, that proves part 2. For part 3, the result that $\lambda_1(q)$ is strictly decreasing and $\lim_{q\to\infty}\lambda_1(q) = -\infty$ when $b_d > 1/2$ and $b_u \geq 0$ are proved in Lou and Lutscher (2014, Lemmas 4.8, 4.9, Remark 4.10), and for $0 < b_d \leq 1/2$ and $b_u \geq 0$, we still have $\lim_{q\to\infty}\lambda_1(q) = -\infty$ following (Lou and Zhou 2015, Proposition 2.1) for the case of $b_u = 0$ and that $\lambda_1(q)$ is decreasing with respect to b_u in part 2. For part 4, since $b_d = b_u = 0$, then $\lambda_1(q) = -\inf_{\psi\in X_1, \psi\neq 0} R(\psi) \geq -R(1) > 0$, and from the definition of Rayleigh quotient (3.3), we obtain part 5. □

If $f(x, u)$ satisfies (f1)–(f3) and (f4a), then the population has a logistic type growth and the dynamics of system (2.12) in this case is well-known, see for example Cantrell and Cosner (2003), Lam et al. (2015) and Lou and Lutscher (2014). We recall the following result:

Proposition 3.2 *Suppose that $f(x, u) = ug(x, u)$ satisfy (f1)–(f3) and (f4a), $d > 0$ and $q \geq 0$. Let $\lambda_1(q)$ be the principal eigenvalue of the eigenvalue problem (3.1) with $p(x) = g(x, 0)$.*

1. *If $\lambda_1(q) \leq 0$, then $u = 0$ is globally asymptotically stable for (2.12); if $\lambda_1(q) > 0$, there exists a unique positive steady state of (2.12) which is globally asymptotically stable.*
2. *If $b_d > 0$ and $b_u \geq 0$, then there exists $q_1 > 0$ such that for $q > q_1$, $\lambda_1(q) < 0$; moreover if $b_d > 1/2$ and $b_u \geq 0$, then $\lambda_1(q) < 0$ for all $q \geq 0$ if $\lambda_1(0) < 0$, and if $\lambda_1(0) > 0$, there exists $q_2 > 0$ such that $\lambda_1(q) > 0$ for $0 < q < q_2$ and $\lambda_1(q) < 0$ for $q > q_2$.*
3. *If $b_u = b_d = 0$, then $\lambda_1(q) > 0$ for all $q > 0$.*

Proof The proof of the uniqueness and global stability of positive steady state for diffusive logistic type equation in part 1 is well known, see for example Cantrell and Cosner (2003, Proposition 3.3). Then parts 2 and 3 follow from Proposition 3.1 as $g(x, 0) > 0$ from the condition (f4a). □

Equation (2.12) with $f(x, u) = u(r(x) - u)$ has been considered in Lam et al. (2015, 2016) and Lou and Lutscher (2014), and results in Proposition 3.2 for that special case can be found in Lewis and Kareiva (2016, Theorem 3.1, 3.2) and Lou and Lutscher (Lou and Lutscher (2014), Theorem 4.1). Results in this section hold for $b_u, b_d \geq 0$, and they can also be adapted to hostile boundary condition by considering the limiting case when b_u or $b_d \to \infty$.

3.2 Comparison of boundary conditions

The dynamics of reaction–diffusion–advection system (2.12) is highly dependent on the boundary conditions. As shown in Propositions 3.1 and 3.2 , since the principal eigenvalue of system (2.12) decreases with respect to b_u or b_d, then the population with larger b_u or b_d is more likely to be extinct. This monotone property for the principal eigenvalue actually also holds for nonlinear system as shown in the following result:

Proposition 3.3 *Suppose $f(x,u)$ satisfies (f1)–(f2), $0 \le b_u \le b'_u \le \infty$ and $0 \le b_d \le b'_d \le \infty$. Let $u_1(x,t)$ be the solution of (2.12), and let $u_2(x,t)$ be the solution of*

$$\begin{cases} u_t = du_{xx} - qu_x + f(x,u), & 0 < x < L, t > 0, \\ du_x(0,t) - qu(0,t) = b'_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b'_d qu(L,t), & t > 0, \\ u(x,0) = u_0(x) \ge 0, & 0 \le x \le L. \end{cases} \tag{3.5}$$

Then $u_1(x,t) \ge u_2(x,t) \ge 0$ for $t \in (0,\infty)$, $x \in \overline{\Omega}$. In particular, if $\lim_{t\to\infty} u_1(x,t) = 0$, then $\lim_{t\to\infty} u_2(x,t) = 0$; and if $\lim_{t\to\infty} \inf u_2(x,t) \ge \delta > 0$ for some positive constant $\delta > 0$, then $\lim_{t\to\infty} \inf u_1(x,t) \ge \delta > 0$.

The proof of Proposition 3.3 follows from the maximum principle of nonlinear parabolic equations (see for example, Smoller 1983, Theorem 10.1), and we omit the details here. Note that here $b'_u = \infty$ or $b'_d = \infty$ is interpreted as the hostile boundary condition (H). The result implies the following comparison between two boundary conditions: if $b'_u \ge b_u$ and $b'_d \ge b_d$, and with identical initial condition, then the extinction in the system with parameter (b_u, b_d) implies the extinction of the system with parameter (b'_u, b'_d), and vice versa, the persistence for the system with (b'_u, b'_d) would imply the persistence for the one with (b_u, b_d).

Among all the boundary conditions, the no-flux boundary condition at $x = L$ ($b_d = 0$) is the most “friendly” for the population to persist, while the hostile boundary condition at $x = L$ ($b_d = \infty$) is the most vulnerable environment for the population. And the free flow ($b_d = 1$) is in between these two.

3.3 Non-advective case

For reaction–diffusion–advection Eq. (2.12) with the strong Allee effect growth rate in a non-advective environment, there have been several earlier papers on the existence and multiplicity of positive steady state solutions, and we recall these results here. In the environment with a hostile boundary condition, the non-advection equation in a higher dimensional domain Ω has the form

$$\begin{cases} u_t = d\Delta u + u(u-h)(r-u), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{3.6}$$

Proposition 3.4 *Suppose that Ω is a bounded smooth domain in $\mathbb{R}^n$ with $n \geq 1$, $d > 0$, and the constants h, r satisfy $0 < h < r$.*

1. *If $h > r/2$, then for any $d > 0$, the only nonnegative steady state solution of (3.6) is $u = 0$.*
2. *If $0 < h < r/2$, then there exists $d_0 > 0$ such that (3.6) has at least two positive steady state solutions for $0 < d < d_0$.*
3. *If $0 < h < r/2$ and Ω is a unit ball, then (3.6) has exactly two positive steady state solutions for $0 < d < d_0$, and has only the zero steady state when $d > d_0$.*

The nonexistence of positive steady state solution in part 1 is proven in Dancer and Schmitt (1987), and the existence of two positive steady state solutions in part 2 can be proven using variational methods (see Liu et al. 2009; Rabinowitz 1973). The exact multiplicity of positive steady state solutions in part 3 is proved in Ouyang and Shi (1998). The conditions of $h \leq r/2$ or $h > r/2$ in Proposition 3.4 are equivalent to $F(r) = \displaystyle\int_0^r u(u-h)(r-u)du \leq 0$ or > 0.

On the other hand, if the non-advective environment is with a free-flow (equivalent to no-flux) boundary condition, then the boundary value problem in a higher dimensional domain Ω has the form

$$\begin{cases} u_t = d\Delta u + u(u-h)(r-u), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{3.7}$$

The following results are proved in Wang et al. (2011, Theorems 3.3, 3.4):

Proposition 3.5 *Suppose that Ω is a bounded smooth domain in $\mathbb{R}^n$ with $n \geq 1$, $d > 0$, and the constants h, r satisfy $0 < h < r$. Let μ_m be the eigenvalues of the operator $-\Delta$ under Neumann boundary condition on Ω.*

1. *There exist three nonnegative constant steady state solutions $u = 0$, $u = h$, $u = r$ of (3.7), and all positive nonconstant steady solutions of (3.7) satisfy $0 < u(x) < r$;*
2. *Let $d_* = \dfrac{2(h+r)}{h\mu_1}$. Then for $d > d_*$, the only nonnegative steady state solutions to (3.7) are $u = 0$, $u = h$ and $u = r$.*
3. *Let $d_m = \dfrac{r-h}{\mu_m}$ with $m \geq 1$, then $d = d_m$ is a bifurcation point for the positive steady state solutions of (3.7), where a connected component Σ_m of the set of positive nonconstant steady state solutions of (3.7) bifurcates from the line of constant steady state $\{(d, u = h) : d > 0\}$.*
4. *If $n = 1$ and $\Omega = (0, L)$, then $\Sigma_m = \{(d, u_m^{\pm}(d,x)) : 0 < d < d_m\}$, the solution $u_m^{\pm}(d,\cdot) - h$ changes sign exactly m times in $(0, L)$, $u_m^{+}(d, 0) > h$ and $u_m^{-}(d, 0) < h$. In particular, (3.7) has exactly $2m$ nonconstant positive steady state solutions if $d_{m+1} < d < d_m$, and all of them are unstable.*

In particular Proposition 3.5 shows that when the diffusion coefficient d is large, the Eq. (3.7) has only the constant steady states, while for the small diffusion coefficient d case, (3.7) has a large number of positive steady states.

3.4 Upper–lower solution methods

In the following we frequently use the method of upper–lower solutions to construct steady states or study the dynamics of (2.12). We review the method in this subsection. Suppose that $u(x)$ is a steady state solution of system (2.12), then $u(x)$ satisfies

$$\begin{cases} du_{xx}(x) - qu_x(x) + f(x, u(x)) = 0, & 0 < x < L, \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L), \end{cases} \tag{3.8}$$

where $f(x, u)$ satisfies (f1)–(f3), and $r(x)$ is defined in (f2). Using the transform $u = e^{\alpha x} v$ on system (3.8), we obtain the following system

$$\begin{cases} dv_{xx} + qv_x + e^{-\alpha x} f(x, e^{\alpha x} v) = 0, & 0 < x < L, \\ -dv_x(0) + b_u qv(0) = 0, \\ dv_x(L) + b_d qv(L) = 0. \end{cases} \tag{3.9}$$

According to Pao (1992, Definition 3.2.1), $\overline{\psi}(x)$ is said to be an upper solution if it satisfies the inequalities

$$\begin{cases} d\overline{\psi}_{xx} + q\overline{\psi}_x + e^{-\alpha x} f(x, e^{\alpha x}\overline{\psi}) \le 0, & 0 < x < L, \\ -d\overline{\psi}_x(0) + b_u q\overline{\psi}(0) \ge 0, \\ d\overline{\psi}_x(L) + b_d q\overline{\psi}(L) \ge 0. \end{cases} \tag{3.10}$$

Similarly $\underline{\psi}(x)$ is called a lower solution if it satisfies all the inequalities in (3.10) with the direction of inequalities reversed. Moreover from Pao (1992, Theorem 3.2.1), if the upper and lower solutions satisfy $\overline{\psi} \ge \underline{\psi}$, then there exists a solution $\psi(x)$ of (3.9) satisfying $\underline{\psi}(x) \le \psi(x) \le \overline{\psi}(x)$. By Pao (1992, Theorem 3.2.2), system (3.9) has a maximal solution $\psi_{max}(x)$ and a minimal solution $\psi_{min}(x)$. Similarly by using $u(x, t) = e^{\alpha x} v(x, t)$, the parabolic system (2.12) can also be converted into

$$\begin{cases} v_t = dv_{xx} + qv_x + e^{-\alpha x} f(x, e^{\alpha x} v), & 0 < x < L,\ t > 0, \\ -dv_x(0) + b_u qv(0) = 0, & t > 0, \\ dv_x(L) + b_d qv(L) = 0, & t > 0, \\ v(x, 0) = v_0(x) \ge 0, & x \in (0, L), \end{cases} \tag{3.11}$$

where $v_0(x) = e^{-\alpha x} u_0(x)$. The upper and lower solutions of (3.11) can be defined in a similar fashion (see Pao 1992, Definition 2.3.1). In particular, if $\underline{\psi}$ and $\overline{\psi}$ is a pair of upper and lower solutions of (3.9), and $\underline{\psi}(x) \le v_0(x) \le \overline{\psi}(x)$, then $\underline{\psi}$ and $\overline{\psi}$ is also a pair of upper and lower solutions of (3.11). According to Pao (1992, Lemma 5.4.2), system (3.11) possesses a unique solution $v(x, t)$ satisfying

$$\underline{\psi}(x) \le v_{\underline{\psi}}(x, t) \le v(x, t) \le v_{\overline{\psi}}(x, t) \le \overline{\psi}(x), \tag{3.12}$$

where $v_{\underline{\psi}}(x,t)$ (or $v_{\overline{\psi}}(x,t)$) is the solution of (3.11) with the initial value $\underline{\psi}$ (or $\overline{\psi}$), and from Pao (1992, Theorem 5.4.2), $v_{\overline{\psi}}(x,t)$ is nonincreasing in t and $\lim_{t\to+\infty} v_{\overline{\psi}}(x,t) = \psi_{max}(x)$; $v_{\underline{\psi}}(x,t)$ is nondecreasing in t and $\lim_{t\to+\infty} v_{\underline{\psi}}(x,t) = \psi_{min}(x)$.

4 Persistence/extinction dynamics

In this section, we consider the dynamics of (2.12) with the growth function $f(x,u)$ satisfying (f1)–(f3) and (f4c), the strong Allee effect growth.

4.1 Basic dynamics

First we have the following bound for steady states of (2.12), which was proved in Lam et al. (2015, Lemma 2.3) for $f(x,u) = r(x) - u$. We include a proof here for convenience of readers.

Proposition 4.1 *Suppose $f(x,u)$ satisfies (f1)–(f2) and $r(x)$ is defined in (f2). Let $u(x)$ be a positive steady state solution of system (2.12), then $u(x) \le e^{\alpha x} \max_{y\in[0,L]}(e^{-\alpha y} r(y))$ for $x \in [0,L]$. Moreover, if $b_d \ge 1$, then $u(x) \le M = \max_{y\in[0,L]} r(y)$ for $x \in [0,L]$.*

Proof Let $u = e^{\alpha x} v$. Then from (3.9), we have

$$e^{\alpha x}(dv_{xx} + qv_x) + f(x, e^{\alpha x} v(x)) = 0. \tag{4.1}$$

Let $v(x_0) = \max_{x\in[0,L]} v(x) > 0$ for $x_0 \in [0,L]$. If $x_0 = 0$, then $v'(0) \le 0$ as $x = 0$ is the maximum point. The boundary condition implies that $bqv(0) = dv'(0) \le 0$ which contradicts with $v(x_0) > 0$. So $x_0 \ne 0$. Similarly we have $x_0 \ne L$. Then $x_0 \in (0,L)$, and we have $v'(x_0) = 0$ and $v''(x_0) \le 0$. Therefore (4.1) implies that $f(x_0, e^{\alpha x_0} v(x_0)) \ge 0$, and consequently,

$$g(x_0, e^{\alpha x_0} v(x_0)) \ge 0. \tag{4.2}$$

According to (f2), $e^{\alpha x_0} v(x_0) \le r(x_0)$, which implies that

$$e^{-\alpha x} u(x) = v(x) \le v(x_0) \le e^{-\alpha x_0} r(x_0) \le \max_{y\in[0,L]}(e^{-\alpha y} r(y)), \tag{4.3}$$

which implies the desired result.

Next we assume that $b_d \ge 1$. From the boundary conditions, we know that $u'(0) > 0$ and since $b_d \ge 1$, $u'(L) \le 0$. Then there exists $x_* \in (0,L]$ such that $u'(x_*) = 0$ and $u(x_*) = \max_{x\in[0,L]} u(x)$. If $x_* \in (0,L)$ (which is the case if $b_d > 1$), then $u''(x_*) \le 0$. According to equation in (3.8), we have $f(x_*, u(x_*)) \ge 0$. If $x_* = L$, then $b_d = 1$, we still have $u'(x_*) = 0$ then again we have $f(x_*, u(x_*)) \ge 0$. From (f2), we have $u(x) \le u(x_*) \le r(x_*) \le M$. □

Now we show that the population dynamics defined by (2.12) is well-posed: the solution of (2.12) exists globally for $t \in (0, \infty)$ and it converges to a non-negative steady state solution when $t \to \infty$. Note here we only require (f1) and (f2), not (f3) and (f4), hence the results hold for both logistic and (weak or strong) Allee effect cases.

Theorem 4.2 *Suppose $f(x, u)$ satisfies (f1)–(f2), then (2.12) has a unique positive solution $u(x, t)$ defined for $(x, t) \in [0, L] \times (0, \infty)$, and the solutions of (2.12) generates a dynamical system in X_2, where*

$$X_2 = \{\phi \in W^{2,2}(0, L) : \ \phi(x) \geq 0, \ d\phi'(0) - q\phi(0) = b_u q\phi(0), \\ d\phi'(L) - q\phi(L) = -b_d q\phi(L)\}. \tag{4.4}$$

Moreover, for any $u_0 \in X_2$ and $u_0 \not\equiv 0$, the ω-limit set $\omega(u_0) \subset S$, where S is the set of non-negative steady state solutions.

Proof Assume that $u(x, t)$ is a solution of system (2.12), then $v(x, t) = e^{-\alpha x} u(x, t)$ is a solution of system (3.11). We choose

$$M_1 = \max \left\{ \max_{y \in [0, L]} e^{-\alpha y} r(y), \ \max_{y \in [0, L]} e^{-\alpha y} u_0(y) \right\}, \tag{4.5}$$

then M_1 is an upper solution of (3.11) and 0 is a lower solution of (3.11). Then from the discussion in Sect. 3.4, we obtain that

$$0 \leq v(x, t) \leq v_1(x, t),$$

where $v_1(x, t)$ is the solution of (3.11) with initial condition $v_1(x, 0) = M_1$. Moreover the solution $v_1(x, t)$ is nonincreasing in t and $\lim\limits_{t \to +\infty} v_1(x, t) = v_{max}(x)$ which is maximal steady state of (3.11) not larger than M_1. From Proposition 4.1, we obtain that $u(x, t)$ exists globally for $t \in (0, \infty)$ and

$$u(x, t) \geq 0, \quad \limsup_{t \to \infty} u(x, t) \leq e^{\alpha x} \max_{y \in [0, L]} e^{-\alpha y} r(y). \tag{4.6}$$

In particular, we may assume that for any initial value u_0, the solution $u(x, t)$ of (2.12) is bounded by $M_2 := e^{\alpha L} \max_{y \in [0, L]} e^{-\alpha y} r(y) + \epsilon$ for $t > T$ and some small $\epsilon > 0$.

Next we prove that the solution $u(x, t)$ is always convergent. For that purpose, we construct a Lyapunov function

$$E(u) = \int_0^L e^{-\alpha x} \left[\frac{d}{2} (u_x)^2 - F(x, u) \right] dx \\ + \frac{q}{2}(1 + b_u) u^2(0) - \frac{q}{2}(1 - b_d) e^{-\alpha L} u^2(L), \tag{4.7}$$

for $u \in X_2$, where $F(x,u) = \displaystyle\int_0^u f(x,s)ds$. Assume that $u(x,t)$ is a solution of system (2.12), we have

$$\begin{aligned}
\frac{d}{dt}E(u(\cdot,t)) &= \int_0^L e^{-\alpha x}(du_x u_{xt} - f(x,u)u_t)dx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t) - q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= \int_0^L (de^{-\alpha x}u_x)du_t - \int_0^L e^{-\alpha x} f(x,u)u_t dx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t) - q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= de^{-\alpha x}u_x u_t\Big|_0^L - \int_0^L [(e^{-\alpha x}du_x)_x + e^{-\alpha x} f(x,u)]u_t dx \\
&\quad + q(1+b_u)u(0,t)u_t(0,t) - q(1-b_d)e^{-\alpha L}u(L,t)u_t(L,t) \\
&= u_t(L,t)e^{-\alpha L}(du_x(L,t) - q(1-b_d)u(L,t)) \\
&\quad + u_t(0,t)(-du_x(0,t) + q(1+b_u)u(0,t)) - \int_0^L e^{-\alpha x}(u_t)^2 dx \\
&= -\int_0^L e^{-\alpha x}(u_t)^2 dx \le 0.
\end{aligned}$$

According to (f2), $f(x,u) < 0$ for $u > r(x)$ and $f(x,r(x)) = 0$, we have $F(x,u(x)) \le F(x,r(x))$ for $u \in X_2$ and $0 < r(x) \le M$. Hence when $t > T$,

$$\begin{aligned}
E(u(\cdot,t)) \ge -\int_0^L e^{-\alpha x}F(x,r(x))dx \\
-\frac{q}{2}e^{-\alpha L}u^2(L,t) \ge -M_3 L - \frac{qM_2^2}{2}e^{-\alpha L},
\end{aligned} \tag{4.8}$$

where $M_3 = \max_{y\in[0,L]} F(y,r(y))$. Therefore $E(u(\cdot,t)$ is bounded from below. Notice $\frac{d}{dt}E(u) = 0$ holds if and only if $u_t = 0$, which means that u is a steady state solution of system (2.12). Refer to Henry (1981, Theorem 4.3.4), the LaSalle's Invariance Principle, we have that for any initial condition $u_0(x) \ge 0$, the ω-limit set of u_0 is contained in the largest invariant subset of S. If every element in S is isolated, then the ω-limit set is a single steady state. □

In addition, if $f(x,u)$ satisfies (f4a) (logistic case), then from part 1 in Proposition 3.2, any solution of (2.12) either goes to zero steady state or converges to the unique positive steady state. In the following, we will focus on the case when $f(x,u)$ satisfies (f4c), for which the solutions of (2.12) have more complicated behavior.

4.2 Extinction

In this subsection, we consider under what condition, the population goes to extinction. The zero steady state of (2.12) is always locally asymptotically stable from Proposition 3.1 part 5, and we provide some estimates of the basin of attraction of the zero steady state. Recall that $f(x,u)$ satisfies (f4c), then we have that $h(x)$ satisfies $f(x,0) = f(x,h(x)) = f(x,r(x)) = 0$ with $0 < h(x) < r(x)$ for all $x \in [0, L]$. First we note the following property of the steady state solution $u(x)$.

Proposition 4.3 *Suppose $f(x,u)$ satisfies (f1)–(f3) and (f4c), then there is no positive solution $u(x)$ of (3.8) satisfying $u(x) < h(x)$ for all $x \in [0, L]$.*

Proof Integrating both sides of (3.8), we get

$$[du_x - qu]\Big|_0^L + \int_0^L f(x,u)dx = 0. \tag{4.9}$$

According to the boundary conditions in (3.8), the first part of (4.9) is

$$-b_d qu(L) - b_u qu(0) \le 0. \tag{4.10}$$

Thus, the second part of (4.9) is non-negative,

$$\int_0^L f(x,u)dx \ge 0. \tag{4.11}$$

which does not hold if $0 < u(x) < h(x)$. Therefore, there is no positive solution $u(x)$ satisfying $u(x) < h(x)$ for all $x \in [0, L]$. □

In the following proposition, we describe the basin of attraction of the zero steady state solution of system (2.12) for different boundary conditions.

Proposition 4.4 *Suppose $f(x,u)$ satisfies (f1)–(f3) and (f4c), and let $u(x,t)$ be the solution of (2.12) with initial condition $u_0(x)$.*

1. *When $b_u \ge 0$ and $b_d \ge 0$, if $0 < u_0(x) < e^{\alpha x}\min_{y\in[0,L]} e^{-\alpha y}h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$;*
2. *When $b_u \ge 0$ and $b_d \ge 1$, if $0 < u_0(x) < \min_{y\in[0,L]} h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$.*

Proof 1. When $b_u \ge 0$ and $b_d \ge 0$, we set $\overline{v}_1(x) = \min_{y\in[0,L]} e^{-\alpha y}h(y)$, which is a constant function. Then according to (f4c), we have

$$\begin{aligned} d(\overline{v}_1)_{xx} + q(\overline{v}_1)_x + \overline{v}_1 \cdot g(x, e^{\alpha x}\overline{v}_1) &= \min_{y\in[0,L]} e^{-\alpha y}h(y) \cdot g(x, e^{\alpha x}\min_{y\in[0,L]} e^{-\alpha y}h(y)) \\ &\le \min_{y\in[0,L]} e^{-\alpha y}h(y) \cdot g(x, e^{\alpha x}e^{-\alpha x}h(x)) = \min_{y\in[0,L]} e^{-\alpha y}h(y) \cdot g(x, h(x)) = 0, \end{aligned} \tag{4.12}$$

and the boundary conditions $-d\overline{v}_{1x}(0)+b_u q\overline{v}_1(0) \geq 0, d\overline{v}_{1x}(L)+b_d q\overline{v}_1(L) \geq 0$. Thus, $\overline{v}_1(x) = \min_{y\in[0,L]} e^{-\alpha y}h(y)$ is an upper solution of system (3.9). Let $\underline{v}_1(x) = 0$ be the lower solution of system (3.9). Now assume that $0 \leq v_0(x) \leq \min_{y\in[0,L]} e^{-\alpha y}h(y)$, and let $v(x,t)$ be the solution of (3.11). From the discussion in Sect. 3.4, there exist solutions $\overline{V}_1(x,t)$ and $\underline{V}_1(x,t)$ of system (3.11),

$$\underline{V}_1(x,t) \leq v(x,t) \leq \overline{V}_1(x,t), \tag{4.13}$$

where $\underline{V}_1(x,t)$ and $\overline{V}_1(x,t)$ are the solutions of system (3.11) with the initial condition $\underline{V}_1(x,0) = \underline{v}_1(x)$ and $\overline{V}_1(x,0) = \overline{v}_1(x)$. Moreover, $\lim_{t\to+\infty} \overline{V}_1(x,t) = v_{max}(x)$ and $\lim_{t\to+\infty} \underline{V}_1(x,t) = v_{min}(x)$, where $v_{max}(x)$, $v_{min}(x)$ are the maximal and minimal solutions of (3.9) between 0 and $\overline{v}_1(x)$. From Proposition 4.3, there is no positive solution $u(x)$ satisfying $u(x) < h(x)$ for all $x \in [0,L]$, hence $v_{min}(x) = v_{max}(x) = 0$. Therefore, if the initial value satisfies $u_0(x) < e^{\alpha x} \min_{y\in[0,L]} e^{-\alpha y}h(y)$, then $\lim_{t\to+\infty} u(x,t) = 0$.

2. When $b_u \geq 0$ and $b_d \geq 1$, we apply the upper and lower solution method directly to (2.12), and we choose $\overline{u}_1(x) = \min_{y\in[0,L]} h(y)$ to be the upper solution and $\underline{u}_1(x) = 0$ be the lower solution. We can follow the same argument in the above paragraph to reach the conclusion.

□

Proposition 4.4 only gives a partial description of the basin of attraction of the zero steady state (extinction initial values). This extinction region depends on the advection coefficient q and the boundary condition. Using a constant initial value $u_0 = K > 0$, Fig. 2 shows the threshold initial condition $K = K_0$ between persistence and extinction under the NF/H, NF/FF and NF/NF boundary conditions and varying advection coefficient q. The left panel corresponds to the case when the threshold h is relatively small and the right panel describes the case when threshold h is relatively large. For the NF/NF boundary conditions, the behavior of the population changes significantly due to the threshold while the other two exhibit almost the same tendency. For small threshold h and under the NF/NF boundary condition, as advection q increases, the basin of attraction of the zero steady state solution decreases. However, for large threshold h, there exists a critical $q^* > 0$, such that when the advection $q > q^*$, the population will go to extinction.

To provide another extinction criterion, we compare the solution of (2.12) with the strong Allee effect growth rate with the one with a comparable logistic growth rate. For that purpose, we define a function $\widetilde{f}(x,u) = u\widetilde{g}(x,u)$ as follows

$$\widetilde{g}(x,u) = \begin{cases} g(x,s(x)), & 0 < u < s(x), \\ g(x,u), & u > s(x), \end{cases} \tag{4.14}$$

where for $x \in \overline{\Omega}$, $s(x)$ is the maximum point of $g(x,u)$ defined in (f3). Thus $\widetilde{f}(x,u)$ is of logistic type and satisfies $\widetilde{f}(x,u) \geq f(x,u)$. The function $\widetilde{f}(x,u)$ is also the smallest function of logistic type which is greater than $f(x,u)$. A comparison of $\widetilde{f}$, $\widetilde{g}$ and f, g can be seen in Fig. 3.

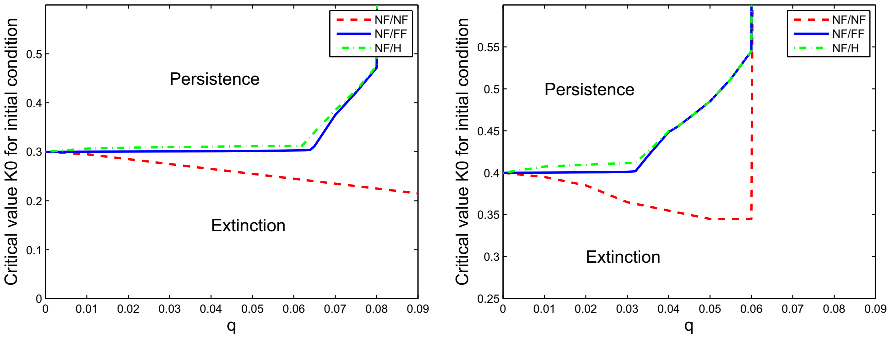

Fig. 2 Population extinction and persistence for varying advection coefficient q and the initial condition $u_0 = K$ (constant). For each of NF/H, NF/FF and NF/NF boundary conditions, a curve is plotted to show the threshold K_0 between extinction and persistence. When $u_0 \equiv K > K_0$, the population persists; and when $u_0 \equiv K < K_0$, the population becomes extinct. Persistence/extinction is determined by the solution at $t = 3000$. Here $f(x,u) = au(1-u)(u-h)$, $a = 0.5$, $L = 10$ and $d = 0.1$. Left: $h = 0.3$; Right: $h = 0.4$

Now we can define a new system with this modified growth rate:

$$\begin{cases} u_t = du_{xx} - qu_x + \widetilde{f}(x,u), & 0 < x < L,\ t > 0, \\ du_x(0,t) - qu(0,t) = b_u qu(0,t), & t > 0, \\ du_x(L,t) - qu(L,t) = -b_d qu(L,t), & t > 0. \\ u(x,0) = u_0(x) \geq 0, & 0 \leq x \leq L. \end{cases} \tag{4.15}$$

Then from the comparison principle of parabolic equations, we obtain the following comparison of solutions of (2.12) and (4.15).

Proposition 4.5 *Suppose $f(x,u)$ satisfies (f1)–(f3) and (f4c), and $\widetilde{f}(x,u)$ is defined as in* (4.14). *Let $u_3(x,t)$ be the solution of* (2.12), *and let $u_4(x,t)$ be the solution of* (4.15) *with the same initial value. Then $0 \leq u_3(x,t) < u_4(x,t)$ for $t \in (0,\infty)$ and $x \in \overline{\Omega}$. In particular, if $\lim_{t\to\infty} u_4(x,t) = 0$, then $\lim_{t\to\infty} u_3(x,t) = 0$; and if $\lim_{t\to\infty} \inf u_3(x,t) \geq \delta > 0$ for some positive constant $\delta > 0$, then $\lim_{t\to\infty} \inf u_4(x,t) \geq \delta > 0$.*

Now by using the previously known results for the logistic equation, we have the following result for population extinction with the strong Allee effect growth rate.

Theorem 4.6 *Suppose that $f(x,u)$ satisfies (f1)–(f3) and (f4c). If $b_u \geq 0$ and $b_d > 0$, then there exists $q_1 > 0$ such that when $q > q_1$, there is no positive steady state solution of* (2.12)*; and for any initial condition $u_0(x) \geq 0$, the solution $u(x,t)$ of* (2.12) *satisfies $\lim_{t\to+\infty} u(x,t) = 0$.*

Proof This is a direct consequence of Proposition 3.2 and Proposition 4.5. □

Here it is shown that under an open river environment, when the advection rate q is large and there is a population loss at the downstream, then the population becomes extinct no matter what initial condition is, which is the same as the case of logistic

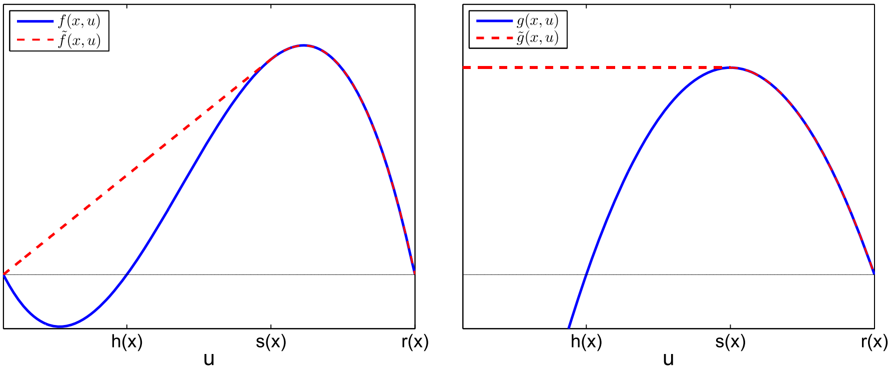

Fig. 3 Left: the graphs of $f(\cdot, u)$ and $\widetilde{f}(\cdot, u)$ for fixed $x \in [0, L]$; Right: the graphs of $g(\cdot, u)$ and $\widetilde{g}(\cdot, u)$ for fixed $x \in [0, L]$

growth (Lou and Lutscher 2014). This result confirms the numerical result shown in Fig. 2 for NF/H and NF/FF cases, but it does not include the case of NF/NF boundary condition which corresponds to the case $b_u = b_d = 0$.

In Fig. 4, the solutions of (2.12) with the strong Allee effect growth $f(x, u) = u(1-u)(u-h)$ and the ones of (4.15) with corresponding logistic growth rate

$$\widetilde{f}(x, u) = \begin{cases} \dfrac{(1-h)^2 u}{4}, & 0 < u < \dfrac{1+h}{2}, \\ u(1-u)(u-h), & u > \dfrac{1+h}{2}, \end{cases} \tag{4.16}$$

are shown. The results in Fig. 4 confirm the comparison stated in Proposition 4.5: the solution of logistic growth model is an upper solution for the case with the strong Allee effect growth. When the advection rate is small (Fig. 4 upper left), the two solutions are almost identical despite of different growth rates; but for large advection rates, the strong Allee effect growth rate leads to extinction while the logistic one supports persistence. This clearly shows the importance of the growth rate at low population density as the two growth rates are the same in high densities.

4.3 Persistence

In this subsection, we provide some criteria for the population persistence of (2.12) with the strong Allee effect growth rate. Note that in the logistic case, the persistence and extinction of population is completely determined by the stability of the extinction steady state $u = 0$ (see Proposition 3.2), but in the strong Allee effect case, the extinction state $u = 0$ is always locally stable.

We first show some properties of the set of positive steady state solutions of (2.12) if there exists any.

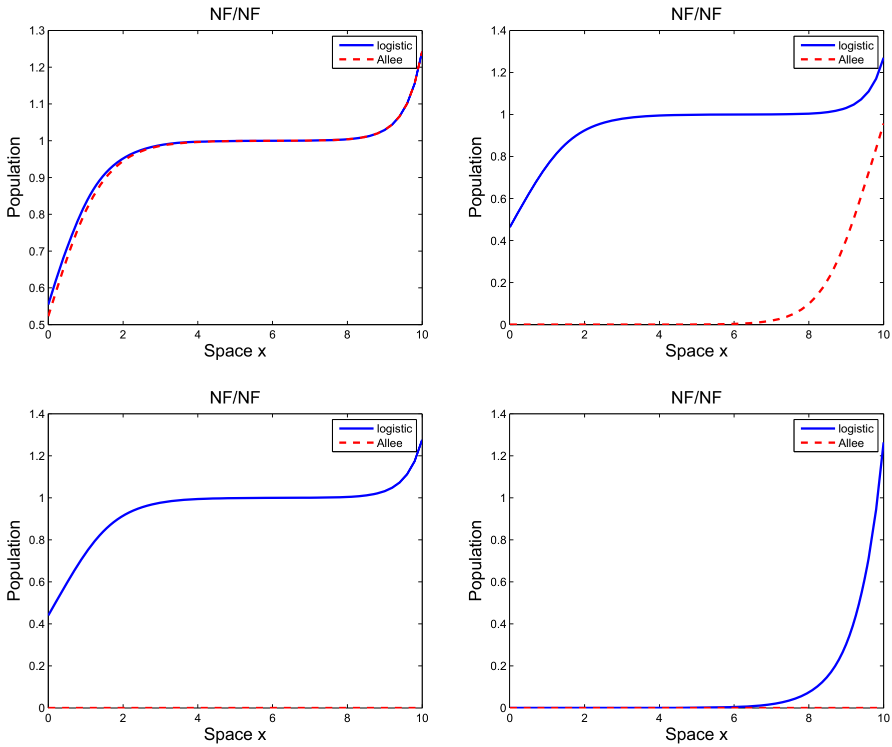

Fig. 4 Comparison of solutions of (2.12) with strong Allee effect growth $f(x, u) = u(1 - u)(u - h)$ and the one of (4.15) with corresponding logistic growth rate given in (4.16). Here $d = 0.1$, $h = 0.4$, $L = 10$, NF/NF boundary condition is used, the initial condition is $u_0 = 0.6$, and the solutions at $t = 3000$ are shown. Upper left: $q = 0.006$; Upper right: $q = 0.0068$; Lower left: $q = 0.007$; Lower right: $q = 0.2$

Proposition 4.7 *Suppose $f(x, u)$ satisfies (f1)–(f3). If there exists a positive steady state solution of (2.12), then there exists a maximal steady state solution $u_{max}(x)$ such that for any positive steady state $u(x)$ of system (2.12), $u_{max}(x) \geq u(x)$.*

Proof We consider the equivalent steady state equation (3.9). Set $\overline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y} r(y)$, which is a constant function. From (f3), we have $f_u(x, u) \leq 0$ for $u \geq r(x)$. Therefore,

$$f(x, e^{\alpha x}\overline{v}_2) = f(x, e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y} r(y)) \leq f(x, e^{\alpha x} e^{-\alpha x} r(x)) = f(x, r(x)) = 0.$$

Substituting $\overline{v}_2(x)$ into system (3.9), we have

$$\begin{cases} d\overline{v}_2'' + q\overline{v}_2' + e^{-\alpha x} f(x, e^{\alpha x}\overline{v}_2) \leq 0, & 0 < x < L, \\ -d\overline{v}_2'(0) + b_u q\overline{v}_2(0) \geq 0, \\ d\overline{v}_2'(L) + b_d q\overline{v}_2(L) \geq 0. \end{cases} \tag{4.17}$$

Thus $\overline{v}_2(x)$ is an upper solution of system (3.9). Moreover from Proposition 4.1, any positive steady state solution v of (3.9) satisfies $v(x) \leq \overline{v}_2(x)$. Since $u(x)$ is a positive steady state of (2.12), we can set the lower solution of (3.9) to be $\underline{v}_2(x) = e^{-\alpha x}u(x)$. Then from the results in Sect. 3.4, there exists a maximal solution $v_{max}(x)$ of (3.9) satisfying $\underline{v}_2(x) \leq v_{max}(x)$. Since $v_{max}(x)$ is obtained through the monotone iteration process (see Amann 1976; Pao 1992) from the upper solution $\overline{v}_2(x)$ and any positive steady state solution v of (3.9) satisfying $v(x) \leq \overline{v}_2(x)$, we conclude that $v_{max}(x)$ is the maximal steady state solution of (3.9), which implies the desired result. □

Next we show a monotonicity result for the maximal steady state solution $u_{max}(x)$.

Proposition 4.8 *Suppose $f(x,u)$ satisfies (f1)–(f3), and $b_u \geq 0$ and $0 \leq b_d \leq 1$. Then the maximal steady state solution $u_{max}(x)$ of Eq. (2.12) is strictly increasing in $[0, L]$ if one of the following conditions is satisfied:*

1. *$f(x,u) \equiv f(u)$, that is f is spatially homogeneous; or*
2. *$g(x,u)$ is also differentiable in x, $g_u(x,u) \leq 0$ and $g_x(x,u) \geq 0$ for $x \in [0, L]$ and $u \geq 0$.*

Proof For part 1, we prove it by contradiction. Assuming that the maximal solution $u_{max}(x)$ is not increasing for all $x \in [0, L]$. From boundary conditions in (2.12) and the condition $b_u \geq 0$, $0 \leq b_d \leq 1$, we have

$$(u_{max})_x(0) = \alpha(b_u + 1)u_{max}(0) > 0,$$
$$(u_{max})_x(L) = \alpha(-b_d + 1)u_{max}(L) \geq 0.$$

Then $(u_{max})_x(x)$ has at least two zero points in $(0, L)$. We choose the two smallest zero points $x_1, x_2 \in (0, L)$ $(x_1 < x_2)$ such that $(u_{max})_x(x_1) = (u_{max})_x(x_2) = 0$, $(u_{max})_x(x) < 0$ on (x_1, x_2). We claim that $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$. Indeed differentiating the equation in (3.8) with respect to x, we have

$$d(u_{max})_{xxx} - q(u_{max})_{xx} + f_u(x, u_{max})(u_{max})_x = 0. \tag{4.18}$$

Since $(u_{max})_x(x) < 0$ on (x_1, x_2), then $(u_{max})_{xx}(x_1) \leq 0$ and $(u_{max})_{xx}(x_2) \geq 0$. If $(u_{max})_{xx}(x_1) = 0$, then from (4.18) and $(u_{max})_x(x_1) = 0$, we conclude that $(u_{max})_x(x) \equiv 0$ near $x = x_1$ from the uniqueness of solution of ordinary differential equation, which contradicts with the assumption that $(u_{max})_x(x) < 0$ on (x_1, x_2). Hence we have $(u_{max})_{xx}(x_1) < 0$, and similarly we can show that $(u_{max})_{xx}(x_2) > 0$.

According to Sattinger (1971/1972, p. 992), the maximal solution u_{max} is semistable. The corresponding eigenvalue problem is (3.1) with $p(x) = f_u(u_{max}(x))$:

$$\begin{cases} d\phi_{xx} - q\phi_x + f_u(u_{max})\phi = \lambda\phi, & 0 < x < L, \\ d\phi_x(0) - q\phi(0) = b_u q\phi(0), \\ d\phi_x(L) - q\phi(L) = -b_d q\phi(L), \end{cases} \tag{4.19}$$

and the corresponding principal eigenvalue $\lambda_1(f_u(u_{max})) \le 0$ with eigenfunction $\phi > 0$. Multiplying Eq. (4.18) by $e^{-\alpha x}\phi$ and multiplying the equation in (4.19) by $e^{-\alpha x}(u_{max})_x$, then subtracting, we obtain

$$\begin{aligned} &de^{-\alpha x}((u_{max})_x\phi_{xx} - (u_{max})_{xxx}\phi) + qe^{-\alpha x}((u_{max})_{xx}\phi - (u_{max})_x\phi_x) \\ &\quad = \lambda_1(f_u(u_{max}))e^{-\alpha x}\phi(u_{max})_x. \end{aligned} \tag{4.20}$$

Integrating the above equation on $[x_1, x_2]$, the right hand side of (4.20) becomes

$$\int_{x_1}^{x_2} e^{-\alpha x}\lambda_1(f_u(u_{max}))\phi(u_{max})_x dx \ge 0.$$

Since $(u_{max})_{xx}(x_1) < 0$ and $(u_{max})_{xx}(x_2) > 0$, the left hand side of (4.20) becomes

$$\begin{aligned} &d\int_{x_1}^{x_2}[(e^{-\alpha x}\phi_x)_x(u_{max})_x - (e^{-\alpha x}(u_{max})_{xx})_x\phi]dx \\ &= de^{-\alpha x}(\phi_x(u_{max})_x - \phi(u_{max})_{xx})\,\big|_{x_1}^{x_2} - d\int_{x_1}^{x_2} e^{-\alpha x}(\phi_x(u_{max})_{xx} - \phi_x(u_{max})_{xx})dx \\ &= de^{-\alpha x_1}\phi(x_1)(u_{max})_{xx}(x_1) - de^{-\alpha x_2}\phi(x_2)(u_{max})_{xx}(x_2) < 0, \end{aligned}$$

which is a contradiction. Thus, the maximal solution $u_{max}(x)$ of (3.8) is increasing on $x \in (0, L)$. Moreover the strong maximum principle implies that u_{max} must be strictly increasing.

For part 2, we employ some idea in Lou et al. (2019, Lemma 4.2) (thanks to an anonymous reviewer for this suggestion). Let $w(x) = u'_{max}(x)/u_{max}(x)$. Then by some straightforward computation, we find that $w(x)$ satisfies

$$\begin{cases} -dw_{xx} + (q - 2dw)w_x - u_{max}g_u(x, u_{max})w = g_x(x, u_{max}), & 0 < x < L, \\ dw(0) = (1 + b_u)q > 0, \\ dw(L) = (1 - b_d)q \ge 0. \end{cases} \tag{4.21}$$

From the assumptions that $g_u(x, u) \le 0$ and $g_x(x, u) \ge 0$ for $x \in [0, L]$ and $u \ge 0$ and the maximum principle, we conclude that $w(x) > 0$ for $x \in (0, L)$, which implies that $u_{max}(x)$ is strictly increasing for $x \in (0, L)$. □

The condition $b_u \ge 0$, $0 \le b_d \le 1$ in Proposition 4.8 is optimal as $u'_{max}(L) = \alpha(1 - b_d)u_{max}(L) < 0$ if $b_d > 1$. Figure 5 shows the maximal positive steady solutions under different boundary conditions. We can see that the maximal solution $u_{max}(x)$ is increasing for the NF/FF and NF/NF cases and is decreasing near $x = L$ for the NF/H case since $b_d > 1$ under this situation. Figure 6 shows the dependence of the maximal solution $u_{max}(x)$ on the advection coefficient q. It appears that the maximum value of the maximal solution $\|u_{max}\|_\infty$ decreases in q in the NF/FF and NF/H cases, and when $q \ge q_1$ for some $q_1 > 0$, $\|u_{max}\|_\infty = 0$ which implies there is no positive steady state for such q. This verifies the extinction result proved in Theorem 4.6 for $b_d > 0$. However in the NF/NF case, $\|u_{max}\|_\infty$ is not monotone in q,

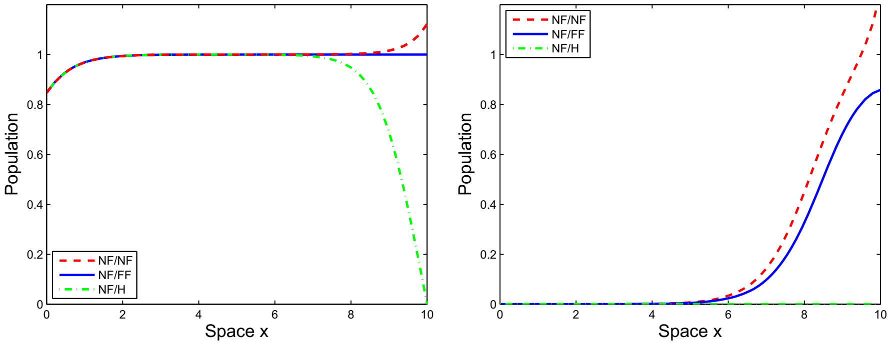

Fig. 5 The maximal steady state solution $u_{max}(x)$ of system (2.12) with $f(x,u) = u(1-u)(u-h)$ under different boundary conditions. Here $d = 0.1$, $h = 0.3$, $L = 10$, $q = 0.03$ (left) and $q = 0.082$ (right). The solutions are simulated with initial condition $u_0 = e^{qx/d}$ and the solution at $t = 3000$ is shown

and $\|u_{max}\|_\infty$ achieves the maximum at an intermediate $q_m > 0$. This suggests that an intermediate advection rate q may increase the maximum population density. Indeed under intermediate advection, the river flow pushes the population to the downstream so that the downstream end has a higher density and the upstream density is lower; but when the advection rate is high, then the population will be washed out before it can establish at the downstream. On the other hand, a larger advection always leads to a lower total steady state population (see Fig. 8). It is not clear whether the population can still persist for a large q under NF/NF boundary condition (see Sect. 4.4), but from Fig. 6, the persistence range of advection q for NF/NF boundary condition is much larger than the ones for NF/FF and NF/H cases.

Next we prove the existence of positive steady state solutions of (2.12) for the NF/NF boundary condition ($b_u = b_d = 0$) case.

Theorem 4.9 *Suppose that $f(x,u)$ satisfies (f1)–(f3) and (f4c), and*

$$\max_{y\in[0,L]} e^{-\alpha y}h(y) < \min_{y\in[0,L]} e^{-\alpha y}r(y). \tag{4.22}$$

Then when $b_u = b_d = 0$, (2.12) has at least two positive steady state solutions. In particular the condition (4.22) is satisfied if

$$0 < \frac{q}{d} < \frac{1}{L}\ln\left(\frac{\min_{y\in[0,L]} r(y)}{\max_{y\in[0,L]} h(y)}\right). \tag{4.23}$$

Proof Using the transform $u = e^{\alpha x}v$, the steady state equation in this case is of the form

$$\begin{cases} dv_{xx} + qv_x + e^{-\alpha x} f(x, e^{\alpha x}v) = 0, & 0 < x < L, \\ v_x(0) = 0, \quad v_x(L) = 0. \end{cases} \tag{4.24}$$

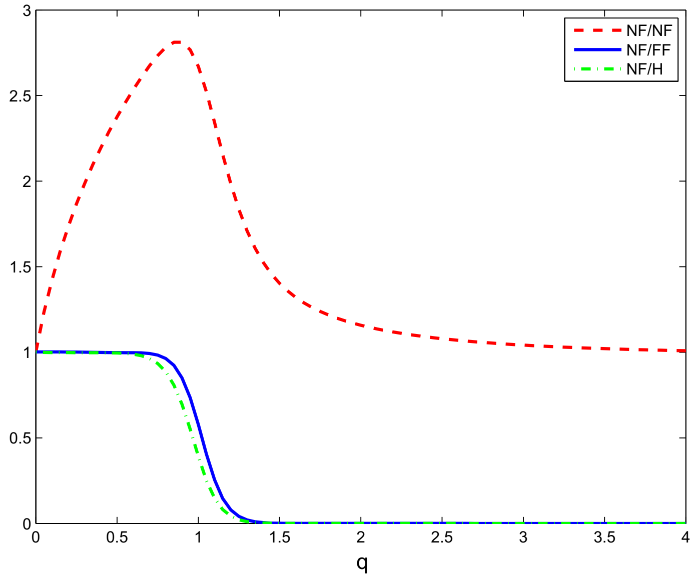

Fig. 6 The dependence of maximal steady state solution $u_{max}(x)$ of system (2.12) with $f(x,u) = u(1-u)(u-h)$ on the advection coefficient q. The horizontal axis is q and the vertical axis is $\|u_{max}\|_\infty$. Here $d = 0.02$, $h = 0.3$, $a = 0.5$

From Proposition 4.7, $\overline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y} r(y)$ is an upper solution of (4.24). Set $\underline{v}_2(x) = \max_{y\in[0,L]} e^{-\alpha y} h(y)$. Then from

$$\begin{aligned} e^{-\alpha x} f(x, e^{\alpha x}\underline{v}_2) &= \underline{v}_2 g(x, e^{\alpha x} \max_{y\in[0,L]} e^{-\alpha y} h(y)) \\ &\geq \underline{v}_2 g(x, e^{\alpha x} e^{-\alpha x} h(x)) = g(x, h(x)) = 0, \end{aligned}$$

we obtain that

$$\begin{cases} d\underline{v}_2'' + q\underline{v}_2' + e^{-\alpha x} f(x, e^{\alpha x}\underline{v}_2) \geq 0, & 0 < x < L, \\ \underline{v}_2'(0) = 0, \ \underline{v}_2'(L) = 0. \end{cases}$$

So $\underline{v}_2(x)$ is a lower solution of (4.24), and from (4.22), we have $\underline{v}_2(x) < \overline{v}_2(x)$. Therefore (4.24) has at least one positive solution between $\underline{v}_2$ and $\overline{v}_2$ by the results in Sect. 3.4. Moreover $\underline{v}_1(x) = 0$ is a lower solution of (4.24), and from Proposition 4.4, $\overline{v}_1 = \min_{y\in[0,L]} e^{-\alpha y} h(y)$ is an upper solution of (4.24), hence we have two pairs of upper and lower solutions which satisfy

$$\underline{v}_1 < \overline{v}_1 < \underline{v}_2 < \overline{v}_2.$$

From Amann (1976, Theorem 14.2), (4.24) has at least three nonnegative solutions, which implies that there exist at least two positive solutions. The condition (4.23) can be derived from (4.22) since

$$\max_{y\in[0,L]} e^{-\alpha y}h(y) \le \max_{y\in[0,L]} h(y), \quad e^{-\alpha L}\min_{y\in[0,L]} r(y) \le \min_{y\in[0,L]} e^{-\alpha y}r(y). \qquad \square$$

Note that if $h(x) \equiv h$ and $r(x) \equiv r$, then (4.23) becomes $0 < \frac{q}{d} < \frac{1}{L}\ln(\frac{r}{h})$. Also the maximal steady state solution obtained from Theorem 4.9 is the maximal steady state solution defined in Proposition 4.7 as $\overline{v}_2$ is the bound for all positive steady states. The second positive solution in Theorem 4.9 is a saddle-type solution in between two stable solutions: the maximal one and the zero solution.

The existence result in Theorem 4.9 shows that the population is able to persist when the relative advection rate q/d is relatively small. The existence of positive steady state solution of (2.12) for other boundary conditions can also be proved along the approach in the proof of Theorem 4.9 if proper upper and lower solutions can be constructed. The numerically simulated persistence region Fig. 2 suggests that positive steady state solutions of (2.12) for other boundary conditions only exist when the advection q is in a more restrictive range than the one for no-flux case.

For the open environment, *i.e.* $b_u \ge 0$ and $b_d > 0$, we can also obtain the existence of multiple positive steady states, but with more restriction on the growth rate. Here we establish a persistence result for H/H boundary condition. From Proposition 3.3, we know that the persistence for the system with H/H type boundary condition would imply the persistence for the one with other boundary conditions with $b_u \ge 0$ and $b_d \ge 0$. Indeed the positive steady states under H/H type boundary condition can be used as the lower solution to obtain the existence of the positive steady states under other boundary conditions.

Theorem 4.10 *Suppose that $f(x,u)$ satisfies (f1)–(f3) and (f4c), $d > 0$, $q \ge 0$ and there exists an interval $(x_1, x_4) \subset [0, L]$ and $\delta > 0$ such that*

$$F(x, r(x)) = \int_0^{r(x)} f(x,s)ds \ge \delta > 0, \quad x \in (x_1, x_4), \tag{4.25}$$

where $r(x)$ is defined in (f2) and here we assume that $r(x)$ is continuously differentiable for $x \in (x_1, x_4)$. Then for any $k > 0$, when $\frac{q}{d} \in [0, k]$, there exists $d_0(k) > 0$, such that when $0 < d < d_0(k)$, the following steady state problem

$$\begin{cases} du_{xx} - qu_x + f(x,u) = 0, \quad 0 < x < L, \\ u(0) = u(L) = 0, \end{cases} \tag{4.26}$$

has at least two positive solutions.

Proof We prove the result following a variational approach similar to Liu et al. (2009), see also Rabinowitz (1973/1974). Define an energy functional

$$E(u) = \int_0^L e^{-\alpha x}\left[\frac{d}{2}(u_x)^2 - F(x,u)\right]dx,$$

where $u \in X_3 \equiv W_0^{1,2}(0, L)$. Here we redefine $f(x, u)$ to be

$$\tilde{f}(x, u) = \begin{cases} f(x, u), & 0 \le u \le M, \\ 0, & u < 0 \ \ and \ \ u > M, \end{cases} \tag{4.27}$$

where $M = \max_{y \in [0,L]} r(y)$. From Proposition 4.1, all non-negative solutions of (4.26) satisfy $0 \le u(x) \le M$, so this will not affect the solutions of (4.26). In the following we assume $f(x, u)$ to be $\tilde{f}(x, u)$ as defined in (4.27).

Similar to Liu et al. (2009), we can verify that $E(u)$ satisfies the Palais–Smale condition, and similar to (4.8), we can show that $E(u)$ is bounded from below. Since any critical point of $E(u)$ is a classical solution of (4.26) and $E(u)$ satisfies the Palais-Smale condition, $\inf E(u)$ can be achieved and it is a critical value. In the following we prove that $\inf E(u) < 0 = E(0)$.

Let $[0, L] = [0, x_1] \cup (x_1, x_2] \cup (x_2, x_3) \cup [x_3, x_4) \cup [x_4, L]$ where $0 < x_1 < x_2 < x_3 < x_4 < L$. Here x_2, x_3 are to be chosen and $x_3 - x_2 \ge (x_4 - x_1)/2$. We define a test function $u_0(x)$ as follows:

$$u_0(x) = \begin{cases} 0, & x \in [0, x_1], \\ \dfrac{r(x_2)}{x_2 - x_1}(x - x_1), & x \in (x_1, x_2], \\ r(x), & x \in (x_2, x_3), \\ \dfrac{r(x_3)}{x_4 - x_3}(x_4 - x), & x \in [x_3, x_4), \\ 0, & x \in [x_4, L). \end{cases} \tag{4.28}$$

Then $u_0(x) \in X_3$. Let $v_0(x) = e^{-\alpha x}\left[\dfrac{d}{2}(u_0'(x))^2 - F(x, u_0(x))\right]$. Then

$$E(u_0) = \int_{x_1}^{x_2} v_0(x)dx + \int_{x_2}^{x_3} v_0(x)dx + \int_{x_3}^{x_4} v_0(x)dx \equiv I_1 + I_2 + I_3.$$

Since $\alpha = \dfrac{q}{d} \in [0, k]$, we have

$$\begin{aligned} I_2 &= \frac{d}{2}\int_{x_2}^{x_3} e^{-\alpha x}(r_x)^2(x)dx - \int_{x_2}^{x_3} e^{-\alpha x}F(x, r(x))dx \\ &\le \frac{d}{2}M_4^2(x_3 - x_2) - e^{-\alpha x_3}\delta(x_3 - x_2) \\ &\le \frac{d}{2}M_4^2(x_4 - x_1) - \frac{1}{2}e^{-kL}\delta(x_4 - x_1), \end{aligned} \tag{4.29}$$

where $M_4 = \max_{x_2 \le x \le x_3} |r_x(x)|$. And

$$\begin{aligned} |I_1| + |I_3| \le & \frac{d}{2} \frac{r(x_2)^2}{x_2 - x_1} + M_5(x_2 - x_1) + \frac{d}{2} \frac{r(x_3)^2}{x_4 - x_3} + M_5(x_4 - x_3) \\ \le & \frac{d}{2} \frac{M^2}{x_2 - x_1} + \frac{d}{2} \frac{M^2}{x_4 - x_3} + M_5(x_2 - x_1 + x_4 - x_3), \end{aligned} \tag{4.30}$$

where $M_5 = \max_{x_1 \le x \le x_4} F(x, r(x))$ and recall that in (f2), $0 < r(x) < M$. Now choosing x_2 sufficiently close to x_1 and x_3 sufficiently close to x_4, we can have

$$M_5(x_2 - x_1 + x_4 - x_3) < \frac{\delta(x_4 - x_1)}{8} e^{-kL}. \tag{4.31}$$

Next fixing x_2, x_3 as above, we can choose $d_0(k) > 0$ such that for $0 < d < d_0(k)$,

$$\frac{d}{2} M^2 \left(\frac{1}{x_2 - x_1} + \frac{1}{x_4 - x_3} \right) < \frac{\delta(x_4 - x_1)}{8} e^{-kL}, \tag{4.32}$$

and

$$\frac{d}{2} M_4^2 < \frac{\delta}{8} e^{-kL}. \tag{4.33}$$

Now combining (4.29), (4.30), (4.31), (4.32) and (4.33), we have, for $0 < d < d_0(k)$,

$$E(u_0) \le |I_1| + I_2 + |I_3| < -\frac{\delta(x_4 - x_1)}{8} e^{-kL} < 0. \tag{4.34}$$

Thus (4.26) has at least one positive solution $u_1(x)$ satisfying $E(u_1) = \inf E(u) < 0$ ($u_1 > 0$ follows from the definition of $f(x, u)$ in (4.27) and the strong maximum principle) from standard minimization theory in calculus of variation (Rabinowitz 1986, Theorem 2.7).

Next we apply the mountain pass theorem (Ambrosetti and Rabinowitz 1973) to obtain another positive solution (4.26). Note that

$$E''(u)[\varphi, \varphi] = \int_0^L d e^{-\alpha x} (\varphi_x)^2 dx - \int_0^L e^{-\alpha x} f_u(x, u) \varphi^2 dx.$$

So we have

$$E''(0)[\varphi, \varphi] > e^{-\alpha L} \left(d \int_0^L (\varphi_x)^2 dx + A_1 \int_0^L \varphi^2 dx \right) \ge A_2 e^{-\alpha L} ||\varphi||^2, \tag{4.35}$$

where $A_1 = \min_{x \in [0, L]} -f_u(x, 0) > 0$ and $A_2 = \min\{d, A_1\}$. Because $E(0) = E'(0) = 0$, and E is twice differentiable, then for any $\epsilon > 0$, there exists $\rho > 0$ such that for $||\varphi|| \le \rho$ (here $||\cdot||$ is the norm of X_3), we have

$$\left| E(\varphi) - \frac{1}{2}E''(0)[\varphi, \varphi] \right| \leq \epsilon ||\varphi||^2. \tag{4.36}$$

Now by choosing $\epsilon = \dfrac{A_2 e^{-\alpha L}}{4}$, and applying (4.35) and (4.36), we obtain that when $||\varphi|| = \rho$,

$$E(\varphi) \geq \frac{A_2 e^{-\alpha L}}{4} ||\varphi||^2 = \frac{A_2 e^{-\alpha L}}{4} \rho^2 > 0. \tag{4.37}$$

Along with the result that there exists $u_0 \in X_3$ such that $E(u_0) < 0$ and $\| u \| > \rho$, the mountain pass theorem (Ambrosetti and Rabinowitz 1973) implies that $E(u)$ has another critical point u_2 such that $E(u_2) \geq \dfrac{A_2 e^{-\alpha L}}{4} \rho^2 > 0 > E(u_1)$. Therefore, u_2 is a distinct positive solution of (4.26). □

Now from the comparison of boundary condition in Proposition 3.3, under the assumption of Theorem 4.10, (2.12) always has at least two positive steady state solutions as any other boundary condition is more favorable than the H/H one in Theorem 4.10.

Theorem 4.11 *Suppose that $f(x, u)$ satisfies (f1)–(f3) and (f4c), $d > 0$, $q \geq 0$, $b_u, b_d \geq 0$ and there exist an interval $(x_1, x_4) \subset [0, L]$ and $\delta > 0$ such that (4.25) holds, and $r(x)$ is continuously differentiable for $x \in (x_1, x_4)$. Then for any $k > 0$, if $\dfrac{q}{d} \in [0, k]$, there exists $d_0(k) > 0$, such that when $0 < d < d_0(k)$, (2.12) has at least two positive steady state solutions.*

Proof We use the upper–lower solution approach from Sect. 3.4. From Proposition 4.1, $\overline{v}_2(x) = e^{\alpha x} \max_{y \in [0,L]}(e^{-\alpha y} r(y))$ is an upper solution of (3.9), and the solution $\underline{v}_2(x)$ of (4.26) is a lower solution. Using the same $\overline{v}_1$ and $\underline{v}_1$, we can conclude the existence of at least two positive solutions of (3.9). □

Remark 4.12 1. The growth rate condition (4.25) is clearly the local version of the one used in Proposition 3.4, and this condition is sharp for the H/H boundary condition (see Proposition 4.15 below for a nonexistence results). Note that for the most favorable NF/NF boundary condition, Theorem 4.9 shows the existence without any restriction on $f(x, u)$, while for the most unfavorable H/H boundary condition, condition (4.25) is needed to ensure the persistence state is a more stable than the extinction state in at least some part of the habitat. Note that the potential function $F(x, u)$ is a measurement of stability, and (4.25) implies that 0 and $r(x)$ are both local minimum points of F, but $r(x)$ is a global minimum point with smaller energy.

2. The persistence result in Theorem 4.9 under NF/NF boundary condition requires q/d is smaller than a given value, but q and d are not necessarily small. On the other hand, the existence result in Theorems 4.10 and 4.11 for open environment allows q/d to be large but d to be small. In general, it is difficult to determine the exact range of (d, q) which supports population persistence.

Next we show that when the growth rate is in a special form, then multiple positive steady state solutions of (2.12) exist when the diffusion coefficient d and advection rate q are in certain range. Unlike Theorem 4.9, this result holds for any $b_u, b_d \geq 0$ but not hostile boundary condition.

Theorem 4.13 *Consider the steady state solution for* (2.12)

$$\begin{cases} du_{xx} - qu_x + u(r-u)(u-h) = 0, & x \in (0, L), \\ du_x(0) - qu(0) = b_u qu(0), \\ du_x(L) - qu(L) = -b_d qu(L). \end{cases} \tag{4.38}$$

Here $0 < h < r$, $d > 0$, $q \geq 0$, *and* $b_u, b_d \geq 0$. *Let* $d_m = (r-h)L^2/(m\pi)^2$ *be defined as in Proposition* 3.5 *for* $m \in \mathbb{N}$ *and also define* $d_0 = \infty$. *Suppose that* $d_{m+1} < d < d_m$ *for* $m \in \mathbb{N} \cup \{0\}$. *Then there exists* $q_m > 0$ *such that when* $q \in [-q_m, q_m]$, (4.38) *has exactly* $2m + 2$ *nonconstant positive solutions.*

Proof We prove the result with a perturbation argument using implicit function theorem. When $q = 0$, (4.38) becomes

$$\begin{cases} du_{xx} + u(r-u)(u-h) = 0, & x \in (0, L), \\ u_x(0) = u_x(L) = 0. \end{cases} \tag{4.39}$$

From Proposition 3.5, when $d_{m+1} < d < d_m$, we know that (4.39) has exactly $2m$ nontrivial positive solutions $u_k^{\pm}(d, x)$ $(1 \leq k \leq m)$ and two trivial positive solutions $u_{m+1}^{-}(x) \equiv h$, $u_{m+1}^{+}(x) \equiv r$. Moreover all these solutions except u_{m+1}^{+} are unstable, so each of them is non-degenerate; and $u_{m+1}^{+}(x) = r$ is locally asymptotically stable. Here a solution u of (4.38) is stable (or unstable) if the principal eigenvalue λ_1 of the eigenvalue problem

$$\begin{cases} d\phi_{xx} - q\phi_x + (-3u^2 + 2(r+h)u - rh)\phi = \lambda\phi, & x \in (0, L), \\ d\phi_x(0) - q\phi(0) = b_u q\phi(0), \\ d\phi_x(L) - q\phi(L) = -b_d q\phi(L), \end{cases} \tag{4.40}$$

is negative (or positive), and u is non-degenerate if $\lambda = 0$ is not an eigenvalue of (4.40).

We use the implicit function theorem to obtain the existence of positive solutions for (4.38) when q is near 0. Define a mapping $F : \mathbb{R} \times W^{2,p}(0, L) \to L^p(0, L) \times \mathbb{R} \times \mathbb{R}$ (where $p > 2$) by

$$F(q, u) = \begin{pmatrix} du_{xx} - qu_x + u(r-u)(u-h) \\ du_x(0) - qu(0) - b_u qu(0) \\ du_x(L) - qu(L) + b_d qu(L) \end{pmatrix}.$$

Then $F(0, u_k^{\pm}) = 0$ for $1 \leq k \leq m+1$. The Frechét derivative of F with respect to u at $(0, u_k^{\pm})$ is

$$F_u(0, u_k^{\pm})[w] = \begin{pmatrix} dw_{xx} + (-3(u_k^{\pm})^2 + 2(r+h)u_k^{\pm} - rh)w \\ dw_x(0) \\ dw_x(L) \end{pmatrix}, \tag{4.41}$$

where $w \in W^{2,p}(0, L)$. From the non-degeneracy of $u_k^{\pm}$, $F_u(0, u_k^{\pm})$ is invertible, then from the implicit function theorem, we obtain the existence of a positive solution $u_k^{\pm}(q, x)$ of (4.38) when $q \in (-\delta_k, \delta_k)$ for some $\delta_k > 0$ and each of $1 \leq k \leq m+1$. One can choose $q_m = \min_{1 \leq k \leq m+1}\{\delta_k\} > 0$ so (4.38) has $2m+2$ positive solutions when $q \in [-q_m, q_m]$. Note that each of these solutions is nonconstant when $q \neq 0$. By making q_m possibly smaller, there are exactly $2m+2$ such solutions when $q \in [-q_m, q_m]$ as there are exactly $2m+2$ positive solutions when $q = 0$. □

Remark 4.14 1. The solution $u_{m+1}^{+}(q, x)$ of (4.38) is locally asymptotically stable as it is perturbed from $u_{m+1}^{+}(x) = r$ which is locally asymptotically stable, and $u_{m+1}^{+}(q, x)$ is also the maximal steady state solution in Proposition 4.7. All other positive solutions of (4.38) are unstable. The trivial state $u = 0$ remains a locally asymptotically stable steady state for all $d > 0$ and $q \geq 0$.

2. The multiplicity of positive steady state solutions in Theorem 4.13 holds for all $b_d, b_u \geq 0$, but the critical advection rate q_m is not explicitly defined and it is only for the special form growth function $f(u) = u(r-u)(u-h)$; while the result in Theorem 4.9 holds for more general growth function only requiring (f1)–(f3) and (f4c) and an explicit bound of the critical advection rate (4.23), but only for $b_d = b_u = 0$.
3. The multiplicity result in Theorem 4.13 does not include the NF/H or even H/H boundary conditions. Indeed in the hostile boundary condition case, positive steady states of (4.38) may not exist when $h > r/2$, see the following Proposition 4.15.

Finally we show a nonexistence of positive steady state solution result when the upstream boundary condition is hostile and the Allee threshold is high.

Proposition 4.15 *Suppose that $f(x, u) = f(u)$ satisfies (f1)–(f3) and (f4c), and for $r(x) \equiv M$ defined in (f2),*

$$F(M) = \int_0^M f(s)ds < 0, \tag{4.42}$$

Then the following steady state problem

$$\begin{cases} du_{xx} - qu_x + f(u) = 0, & x \in (0, L), \\ u(0) = 0, \\ du_x(L) - qu(L) = -b_d q u(L), \end{cases} \tag{4.43}$$

has no positive solution if $b_d \geq 1$.

Proof Suppose that $u(x)$ is a positive solution of (4.43). From Proposition 4.1 and $b_d \geq 1$, we have $u(x) \leq M$. Multiplying the equation in (4.43) by u_x, and integrating over an arbitrary interval $[a, b] \subseteq [0, L]$, we obtain that

$$\left[\frac{d}{2}u_x(x)^2 + F(u(x))\right]\Bigg|_{x=a}^{x=b} - q\int_a^b u_x^2(x)dx = 0, \tag{4.44}$$

as

$$\begin{aligned}\int_a^b (du_{xx}u_x + f(u)u_x)dx &= \frac{d}{2}u_x^2(x)|_{x=a}^{x=b} + \int_{u(a)}^{u(b)} f(u)du\\ &= \left[\frac{d}{2}u_x(x)^2 + F(u(x))\right]\Bigg|_{x=a}^{x=b}.\end{aligned}$$

From the boundary condition of (4.43), $u_x(0) > 0$ and $du_x(L) = (1-b_d)qu(L) \leq 0$. Hence there exists $x_0 \in (0, L]$ such that $u_x(x_0) = 0$. Applying (4.44) to the interval $[0, x_0]$, we obtain that

$$F(u(x_0)) - \frac{d}{2}u_x^2(0) - q\int_0^{x_0} u_x^2(x)dx = 0.$$

But (4.42) implies that $F(u) < 0$ for any $u > 0$. That is a contradiction. Therefore (4.43) has no positive solution if $b_d \geq 1$. □

The condition (4.42) is satisfied for $f(u) = u(r-u)(u-h)$ with $h > r/2$, so the result in Proposition 4.15 is partly similar to the nonexistence of solutions for Dirichlet boundary value problem in Proposition 3.4. The nonexistence of positive steady state of (2.12) when the upstream boundary is hostile and the Allee threshold is high also holds when the downstream boundary is hostile, but is not proven here though it can be observed numerically (see Fig. 7 lower right panel).

Theorem 4.10 and Proposition 4.15 show that the Allee effect threshold h plays an important role in the persistence/exitinction of population. In Fig. 7, the population persistence/extinction behavior for (2.12) with $f(u) = u(r-u)(u-h)$, varying advection rate q and strong Allee threshold h is shown under the three boundary conditions: NF/NF, NF/FF and NF/H, with an initial condition $u_0(x) = r = 1$. For the NF/FF boundary condition, the population persists under small q for all $h \in (0, 1)$, and it goes to extinction for large q. For the NF/H boundary condition, the persistence for small q only occurs for $0 < h < r/2$, while the behavior is similar for NF/FF case for large q. It is interesting that for small positive $q > 0$, the threshold h_c between persistence and extinction is actually slightly higher than $r/2$.

4.4 Closed environment

Theorem 4.6 shows that when $b_d > 0$, i.e. when the population has a loss at the downstream, then a large advection rate q always drives the population to extinction.

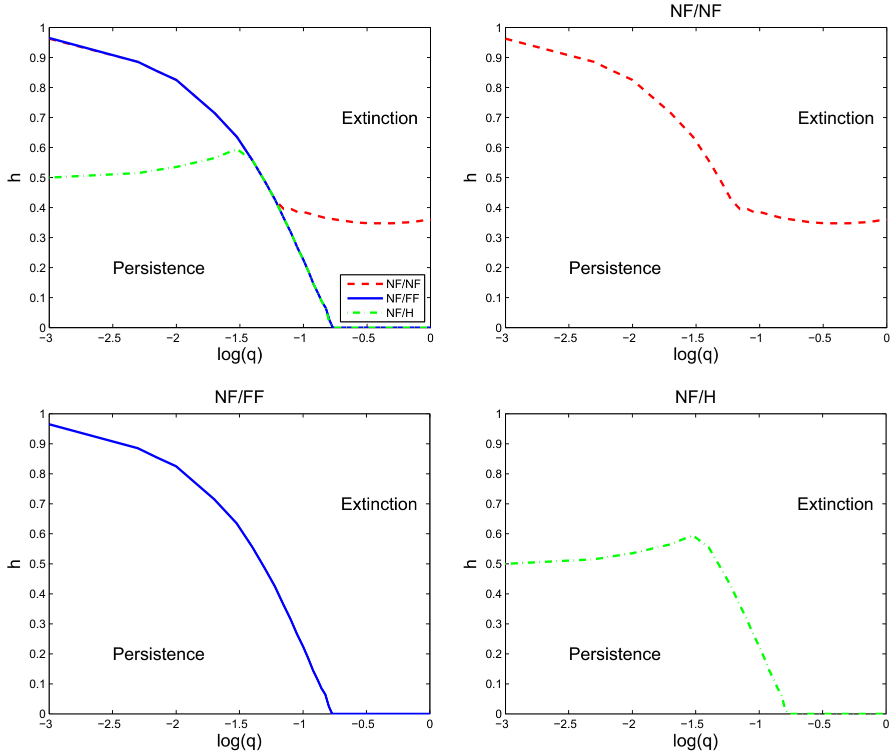

Fig. 7 Population extinction and persistence for varying advection coefficient q (log scale) and the Allee threshold h. Here $f(x,u) = au(1-u)(u-h)$, $a = 0.5$, $d = 0.1$, $L = 10$ and the initial condition is $u_0(x) = 1$. (Upper left): comparison of NF/NF, NF/FF and NF/H boundary conditions; (Upper right): NF/NF; (Lower left): NF/FF; (Lower right): NF/H

But the restriction of $b_u \geq 0$ and $b_d > 0$ in Theorem 4.6 excludes the NF/NF boundary condition for which the population does not have a loss at the downstream end, so under the NF/NF boundary condition, (2.12) could have a positive steady state solution for large advection rate q. In the subsection, we discuss the asymptotic profile of positive steady state under closed advective environment, so we consider this special case of (2.12) and (3.8) with $b_u = b_d = 0$:

$$\begin{cases} u_t = du_{xx} - qu_x + f(x,u), & 0 < x < L,\ t > 0, \\ du_x(0,t) - qu(0,t) = 0, & t > 0, \\ du_x(L,t) - qu(L,t) = 0, & t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in (0,L), \end{cases} \tag{4.45}$$

and

$$\begin{cases} du_{xx} - qu_x + f(x,u) = 0, & x \in (0,L), \\ du_x(0) - qu(0) = 0, \\ du_x(L) - qu(L) = 0. \end{cases} \tag{4.46}$$

First we have the following maximum principle (see Cui et al. 2017, Lemma 3.1).

Lemma 4.16 *Recall that* $N = \max_{y\in[0,L],u\geq 0} g(y,u)$ *from (f3). Suppose that* $f(x,u) = ug(x,u)$ *satisfies (f1)–(f3),* q*,* d *satisfy* $q^2/d \geq 4N$*, and* $u(x) \in C^2(0,L)\cap C[0,L]$ *satisfies*

$$\begin{cases} du_{xx} - qu_x + g(x,u(x))u \leq 0, & 0 < x < L, \\ -du_x(0) + qu(0) \geq 0, \quad u(L) \geq 0, & \end{cases} \tag{4.47}$$

then either $u(x) \equiv 0$ *or* $u(x) > 0$ *in* $[0,L)$.

Proof Using the change of variables $v(x) = e^{-\alpha x/2}u(x)$, we obtain that $v(x)$ satisfies

$$\begin{cases} dv_{xx} + v\tilde{g}(x, e^{\alpha x/2}v) \leq 0, & 0 < x < L, \\ -dv_x(0) + \dfrac{q}{2}v(0) \geq 0, \quad v(L) \geq 0, & \end{cases} \tag{4.48}$$

where $\tilde{g}(x,u) = g(x,u) - q^2/4d \leq 0$. From the maximum principle, $u(x) \geq 0$ in $[0,L]$. Moreover either $u(x) \equiv 0$ or $u(x) > 0$ in $[0,L)$ according to the strong maximum principle. □

For some results below, we also assume that $f(x,u) = ug(x,u)$ satisfies one of the following:

(f5) there exists constants $A, B > 0$ such that, $g(x,u) \leq A - Bu$ for $x \in [0,L]$ and $u \geq 0$.
(f6) there exists $P, Q > 0$ such that $g(x,u) \geq -P$ for any $x \in [0,L]$ and $u \geq 0$, and $g(x,u) \leq -Q$ for any $x \in [0,L]$ and $u \geq u_1$ where $u_1 > 2M$ and $M = \max_{y\in[0,L]} r(y)$.

For the growth function satisfying (f5), the growth function per capita can be controlled by a declining linear function. In (f6) the growth rate per capita is non-increasing but it has a lower bound $-P$. We will prove our limiting profile result under the condition (f5), but in the process of the proof, we first prove the result under the condition (f6). Note that the cubic function $f(u) = u(r-u)(u-h)$ satisfies (f5) but does not satisfy (f6), while the function

$$f(x,u) = \begin{cases} u(r-u)(u-h), & 0 \leq u \leq u_1, \\ u(r-u_1)(u_1-h), & u > u_1 \end{cases} \tag{4.49}$$

satisfies (f6) but does not satisfy (f5), where $u_1 > r > h > 0$.

Now we can obtain the following estimates for the positive solution $u(x)$ of (4.46), which is inspired by Cui et al. (2017, Lemma 3.2).

Proposition 4.17 *Suppose that* $f(x,u) = ug(x,u)$ *satisfies (f1)–(f3), and* $u(x)$ *is a positive solution of* (4.46)*. Let* $C_1 = 2 + N + P$*, and assume that* $q^2/d \geq C_1^2$*. Then we have:*

1.

$$u(x) \leq u^+(x) := u(L) \exp\left(\left(-\frac{q}{d} + \frac{C_1}{q}\right)(L-x)\right), \quad x \in [0, L]. \tag{4.50}$$

2. *If, in addition, we assume that $f(x, u) = ug(x, u)$ also satisfies (f6), then*

$$u(x) \geq u^-(x) := u(L) \exp\left(\left(-\frac{q}{d} - \frac{C_1}{q}\right)(L-x)\right), \quad x \in [0, L]. \tag{4.51}$$

Proof We denote $\alpha = q/d$ and $\beta = C_1/q$. Since $q^2/d \geq C_1^2 \geq 4N$, we have $d\beta^2 \leq 1$ and

$$\begin{aligned} &du^+_{xx} - qu^+_x + g(x, u(x))u^+ \\ &\quad = [d(\alpha-\beta)^2 - q(\alpha-\beta) + g(x, u(x))]u^+ \\ &\quad \leq [-C_1 + d\beta^2 + N]u^+ \\ &\quad \leq [-1 + d\beta^2]u^+ \leq 0, \end{aligned} \tag{4.52}$$

and

$$-du^+_x(0) + qu^+(0) = d\beta u^+(0) \geq 0, \quad u^+(L) = u(L). \tag{4.53}$$

Applying Lemma 4.16 to $u^+(x) - u(x)$, we obtain the estimate in (4.50).

Similarly, we have

$$\begin{aligned} &du^-_{xx} - qu^-_x + g(x, u(x))u^- \\ &\quad = [d(\alpha+\beta)^2 - q(\alpha+\beta) + g(x, u(x))]u^- \\ &\quad \geq [C_1 + d\beta^2 - P]u^+ \geq 0, \end{aligned} \tag{4.54}$$

and

$$-du^-_x(0) + qu^-(0) = -d\beta u^-(0) \leq 0, \quad u^-(L) = u(L). \tag{4.55}$$

Now applying Lemma 4.16 to $u(x) - u^-(x)$, we obtain the estimate in (4.51). □

We note that the estimates in Proposition 4.17 does not require (f4a), (f4b) or (f4c), hence it holds not only for the Allee effect case but also for the logistic case. It shows that when the advection rate q is large, the population density exhibits a spike layer profile: the population concentrates at the downstream boundary end and the density elsewhere except $x = L$ tends to zero.

Theorem 4.18 *Suppose that $g(x, u)$ satisfy (f1)–(f3), (f5) and $g_x(x, u) \geq 0$, and $u_q(x)$ is a positive solution of* (4.46). *Recall C_1 is the constant defined in Proposition* 4.17. *Then*

1. *There exist positive constants C_2 and C_3, such that when $q^2/d \geq C_1^2$ and $\dfrac{q}{d} \geq C_2$, we have*

$$u_q(x) < C_3 \frac{q}{d} \exp\left(\left(-\frac{q}{d} + \frac{C_1}{q}\right)(L - x)\right). \tag{4.56}$$

2. *Let $d > 0$, $L > 0$ be fixed, then $\lim_{q \to +\infty} \int_0^L u_q(x)dx = 0$ and $\lim_{q \to +\infty} u_q(x) = 0$ for any $x \in [0, L)$.*

Proof It is clear that if the conclusions hold for the maximal solution of (4.46), then the conclusions also hold for any other positive solutions. So without loss of generality, we assume that $u_q(x)$ is the maximal solution of (4.46). To prove (4.56) under the assumptions (f1)–(f3) and (f5), we first prove (4.56) under the assumptions (f1)–(f3) and (f6). From (f1)–(f3) and (f6), there exist positive constants A, B and Q, such that

$$g(x, u) \leq \begin{cases} A - Bu, & x \in [0, L],\ 0 \leq u \leq u_1, \\ -Q, & x \in [0, L],\ u \geq u_1. \end{cases} \tag{4.57}$$

Integrating the first equation of (4.46) over $(0, L)$ and applying the boundary condition, we have

$$\int_0^L u_q g(x, u_q)dx = 0. \tag{4.58}$$

From Proposition 4.8, $u_q(x)$ is strictly increasing over $x \in [0, L]$. We assume that $u_q(L) > u_1$ [otherwise (4.56) obviously holds]. Then there exists $0 < L_1 < L$, such that $u_q(L_1) = u_1$, recalling u_1 is defined in (f6). Now (4.58) combined with (4.57) yields

$$B \int_0^{L_1} u_q^2 dx + Q \int_{L_1}^L u_q dx \leq A \int_0^{L_1} u_q dx \leq ALu_1. \tag{4.59}$$

According to Proposition 4.17, when $q^2/d \geq C_1^2$, we have $u_q^-(x) \leq u_q(x) \leq u_q^+(x)$, where $u_q^\pm = u_q(L) \exp((-\alpha \mp \beta)(L - x))$, $\alpha = q/d$ and $\beta = C_1/q$. Now substituting u_q^- into (4.59), we obtain

$$\begin{aligned} &\frac{Bu_q^2(L)}{2(\alpha + \beta)}[\exp(-2(\alpha + \beta)(L - L_1)) - \exp(-2(\alpha + \beta)L)) \\ &\quad + \frac{Qu_q(L)}{\alpha + \beta}(1 - \exp(-(\alpha + \beta)L)] \leq ALu_1. \end{aligned} \tag{4.60}$$

Claim 4.19 *As $\alpha \to \infty$, we have*

$$\exp(-(\alpha + \beta)(L - L_1)) = \frac{u_1}{u_q(L)}(1 + O(\alpha^{-1})). \tag{4.61}$$

Proof of Claim 4.19 Since $u_q^-(x) \le u_q(x) \le u_q^+(x)$, there exist $x_1, x_2 \in (0, L)$ satisfying $x_1 < L_1 < x_2$ such that $u_q^-(x) = u_q^+(x) = u_1$, that is

$$\exp\left(-(\alpha+\beta)(L-x_1)\right) = \exp\left(-(\alpha-\beta)(L-x_2)\right) = \frac{u_1}{u_q(L)}. \tag{4.62}$$

Notice that for fixed $d > 0$ when $\alpha \to \infty$, $\beta = O(\alpha^{-1})$. Thus,

$$\exp\Big((-\alpha + O(\alpha^{-1}))(L-x_1)\Big) = \exp\Big((-\alpha + O(\alpha^{-1}))(L-x_2)\Big) = \frac{u_1}{u_q(L)}. \tag{4.63}$$

Since $x_1 \le L_1 \le x_2$, we have

$$\exp\Big((-\alpha + O(\alpha^{-1}))(L-L_1)\Big) = \frac{u_1}{u_q(L)}, \tag{4.64}$$

which implies the claim. □

Substituting (4.61) into (4.60), we have (as $\alpha \to \infty$)

$$\frac{1}{\alpha+\beta}\Big[Bu_1^2 - Bu_q^2(L)\exp\Big(-2(\alpha+O(\alpha^{-1}))L\Big) + Qu_q(L) - Qu_1 + O(\alpha^{-1})\Big] \le ALu_1. \tag{4.65}$$

From Proposition 4.1, $u_q(L) \le C_4 e^{\alpha L}$, where C_4 is a constant. Therefore (4.65) implies that

$$\frac{1}{\alpha+\beta}\big[Qu_q(L) + O(1)\big] \le ALu_1, \quad \text{as} \alpha \to \infty. \tag{4.66}$$

From (4.66), we conclude that there exist positive constants C_2, C_3 such that $u_q(L) \le C_3\alpha$ whenever $\alpha \ge C_2$ and $q^2/d \ge C_1^2$. Together with (4.50), we obtain (4.56). This proves (4.56) when (f1)–(f3) and (f6) are satisfied.

Now suppose that $f(x,u) = ug(x,u)$ satisfy (f1)–(f3) and (f5), then we can define a $\tilde{f}(x,u) = u\tilde{g}(x,u)$ satisfying (f1)–(f3) and (f6), and $g(x,u) \le \tilde{g}(x,u)$. Then a comparison argument implies that the solutions of (4.46) satisfy $u_q(x) \le \tilde{u}_q(x)$, where $u_q(x)$ is the solution of (4.46) with $f(x,u)$, and $\tilde{u}_q(x)$ is a solution of (4.46) with $\tilde{f}(x,u)$. Indeed this can be shown using argument as in the proof of Theorem 4.9, as $\tilde{u}_q(x)$ can be constructed with $u_q(x)$ as the lower solution and $e^{\alpha x}\max_{y\in[0,L]} e^{-\alpha y} r(y)$ as the upper solution. Now the estimate (4.56) holds for $\tilde{u}_q(x)$, then it also holds for $u_q(x)$ under the conditions (f1)–(f3) and (f5). This completes the proof of part 1.

For part 2, we follow the proof of Lemma 2.5 in Lam et al. (2015). From (f5), there exist constants $A, B > 0$ such that $g(x,u) \le A - Bu$ for $x \in [0, L]$ and $u \ge 0$.

Then from comparison method as in the last paragraph, it is sufficient to consider the solution $u_q(x)$ of

$$\begin{cases} du_{xx} - qu_x + u(A - Bu) = 0, & x \in (0, L), \\ du_x(0) - qu(0) = 0, \\ du_x(L) - qu(L) = 0. \end{cases} \tag{4.67}$$

Integrating (4.67) on $(0, L)$ and applying the boundary condition, we obtain

$$B\int_0^L u_q^2(x)dx = A\int_0^L u_q(x)dx \le A\sqrt{L}\sqrt{\int_0^L u_q^2(x)dx}. \tag{4.68}$$

In particular, $\int_0^L u_q^2(x)dx$ is bounded by a quantity independent of q. Choosing any function $m(x) \in C^2[0, L]$ with $m_x(0) = m_x(L) = 0$, multiplying the equation in (4.67) by $m(x)$ and integrating by parts, we obtain

$$d\int_0^L m_{xx}u_q dx + q\int_0^L m_x u_q dx + \int_0^L m u_q(A - Bu_q)dx = 0. \tag{4.69}$$

Since both $\int_0^L u_q(x)dx$ and $\int_0^L u_q^2(x)dx$ are bounded and $q \to +\infty$, then (4.69) implies that $\int_0^L m_x(x)u_q(x)dx \to 0$ and consequently $\int_0^L u_q(x)dx \to 0$ as $q \to +\infty$. For the pointwise convergence, suppose it is not true. Then there exists a constant $\delta > 0$ and a $x^* \in [0, L)$, such that $\liminf_{q\to+\infty} u_q(x^*) \ge \delta > 0$. Since $u_q(x)$ is strictly increasing, we have

$$\int_0^L u_{q_n}(x)dx \ge \int_{x^*}^L u_{q_n}(x)dx \ge \delta(L - x^*) > 0,$$

for a sequence $q_n \to \infty$, which contradicts with $\int_0^L u_q dx \to 0$ as $q \to +\infty$. Therefore, we have $\lim_{q\to+\infty} u_q(x) = 0$ for any $x \in [0, L)$. □

We remark that the results of Theorem 4.18 hold under the assumption that such a steady state solution $u_q(x)$ exists for (4.46) when the advection rate q is large, and the results hold for logistic (f4a), weak Allee effect (f4b), and strong Allee effect (f4c) cases. The existence of such steady state solutions for the logistic case and any $q > 0$ has been proven in Lam et al. (2015, Lemma 2.1), and the existence for the weak Allee effect case can also be established (see our forthcoming work). So the results of Theorem 4.18 are relevant for these two cases. However, the existence for the strong Allee effect case for large q remains an open question. Nevertheless, the properties of the solution profile established in Theorem 4.18 indicates that when q is large, then the population concentrates at the downstream end but the total biomass becomes very

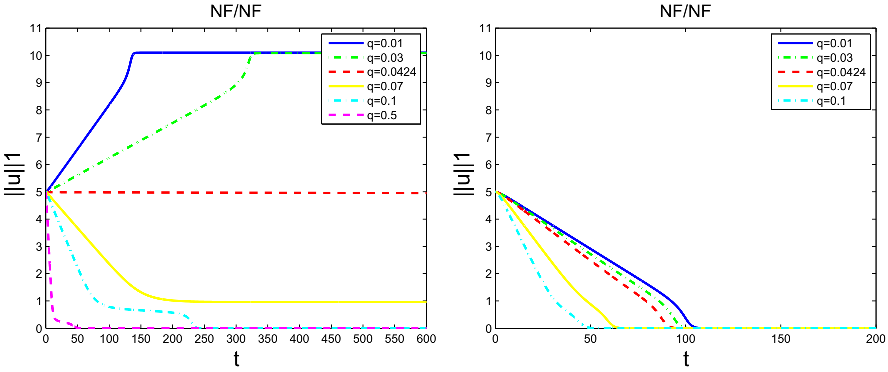

Fig. 8 The evolution of total biomass of (4.45) with respect to time under NF/NF boundary condition and varying advection coefficient q. The horizontal axis is t and the vertical axis is $\|u(\cdot,t)\|_1 = \int_0^L u(x,t)dx$. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. Left: $h = 0.4$; Right: $h = 0.6$

small regardless of the type of growth rate. In Fig. 8, the time series of total biomass of (4.45) for different advection rate q are plotted. It can be observed that the total biomass always decreases with respect to q. For small advection rate, the population is close to carrying capacity; but for large advection rate, the total population tends to near zero (or indeed zero) when $t \to \infty$.

4.5 Transient dynamics and traveling waves

From Fig. 8 left panel, the total biomass of the species increases in time t for small advection rate q, but it decreases in time t for large q; while in the right panel, the total biomass always decreases in time. Moreover, in all cases, the total biomass increases or decreases in an almost linear fashion for a long time period until it is near the equilibrium level, and the slope of linear change before the total biomass reaching the equilibrium level decreases with respect to q.

Such wave-propagating-like transient dynamics of (4.45) is closely related to the traveling wave solution of the reaction–diffusion–advection equation:

$$u_t = du_{xx} - qu_x + au(r-u)(u-h), \quad t > 0, \ x \in (-\infty, \infty), \tag{4.70}$$

where $d > 0$, $a > 0$, $q \in \mathbb{R}$, and $0 < h < r$. It is well-known (Hadeler and Rothe 1975; Lewis and Kareiva 1993) that (4.70) has a unique pair of traveling wave solutions $U_\pm(x - c_\pm t)$ satisfying

$$\begin{cases} dU''_\pm(y) - (q - c_\pm)U'_\pm(y) + aU_\pm(y)(r - U_\pm(y))(U_\pm(y) - h) = 0, & y \in (-\infty, \infty), \\ c_- : \quad U_-(-\infty) = 0, \ U_-(\infty) = r, \\ c_+ : \quad U_+(-\infty) = r, \ U_+(\infty) = 0, \end{cases} \tag{4.71}$$

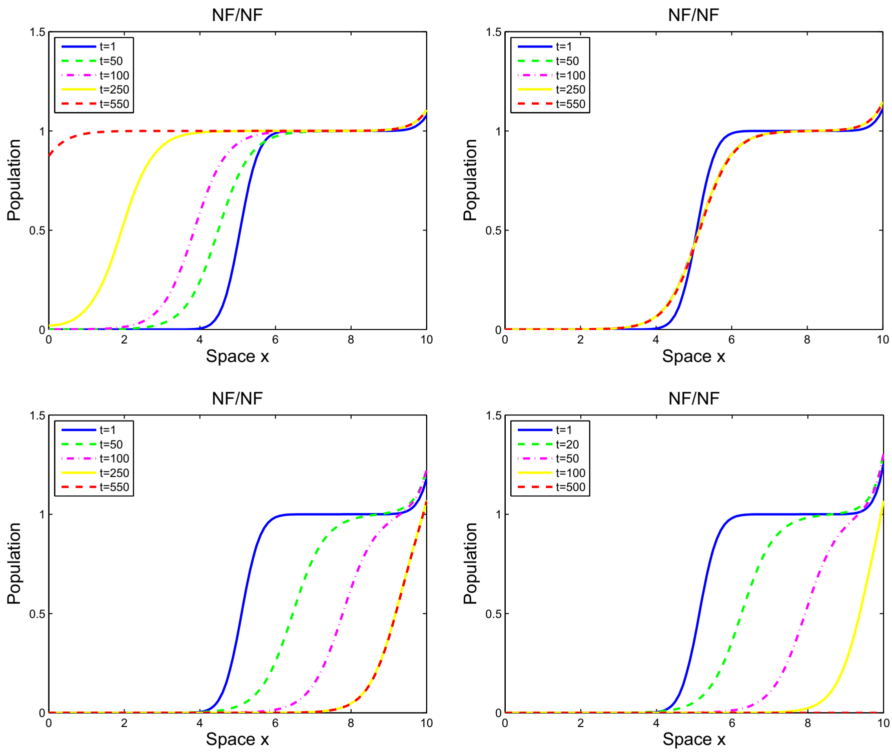

Fig. 9 Propagation of interface and formation of boundary layer in (4.45). Here $f(x,u) = u(1-u)(u-h)$, $h = 0.4$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. Upper left: $q = 0.03$; Upper right: $q = 0.043$; Lower left: $q = 0.07$; Lower right: $q = 0.1$

with

$$c_{\pm} = q \pm \sqrt{2ad}\left(\frac{r}{2} - h\right). \tag{4.72}$$

Indeed it can be explicitly computed that

$$U_{\pm}(y) = \frac{r}{1 + e^{\pm ky}}, \quad \text{where} \quad k = \sqrt{\frac{a}{2d}}r. \tag{4.73}$$

The initial condition used in Figs. 8 and 9 is a step function, which represents that the initial population only exists over the region $[L/2, L]$. The profile of this initial condition resembles the shape of U_-. The formula for c_- in (4.72) shows that when $h < r/2$, the wave speed c_- is negative for small q, so the wave front moves upstream and the population persists in the entire river (see Figs. 8 left panel and 9 upper left panel); for large q, the wave speed is positive, the wave front moves downstream, and the population could form a boundary layer steady state at downstream end (see Figs. 8 left panel and 9 lower left panel), or the population could become extinct (see Figs. 8 left panel and 9 lower right panel). Between the waves of two opposite directions,

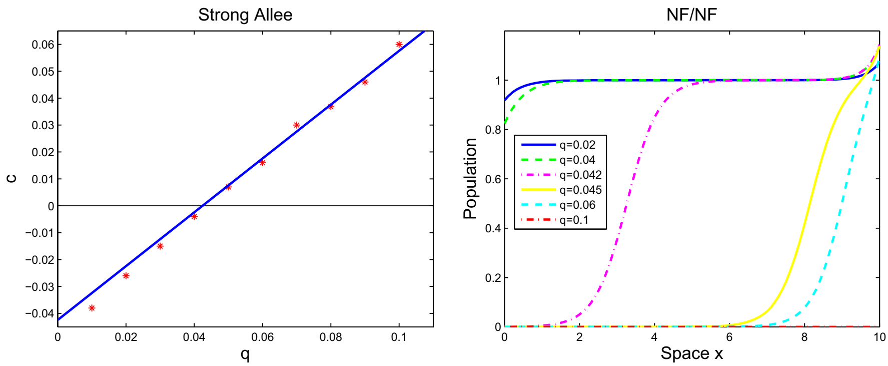

Fig. 10 Effect of advection rate q to the population propagation in (4.45). Left: The dependence of traveling wave speed c with respect to the advection rate q; Right: The dependence of maximal steady state solution on the advection rate q. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$ and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$

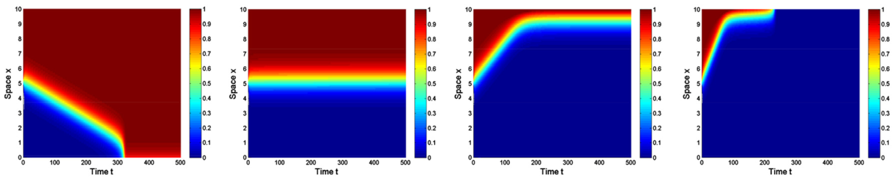

Fig. 11 Traveling-wave-like dynamics for different advection rate q. Here $f(x,u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$, $L = 10$, and the initial condition is $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$. The advection rate from left to right is $q = 0.03$, $q = 0.043$, $q = 0.07$ and $q = 0.1$

there is a "break-even" advection rate q_0 (that is ≈ 0.042 for parameters in Figs. 8 and 9) such that the total biomass is almost unchanged for all time, and the traveling wave is a standing one with $c_- \approx 0$ (see Fig. 9 upper right panel). On the other hand, when $h > r/2$, the formula of c_- in (4.72) shows that the wave speed c_- is always positive, hence for any advection rate q, the population cannot invade the upstream region (see Fig. 8 right panel). Indeed, Fig. 8 right panel suggests that extinction always occurs in this case for any advection rate q when the initial condition is a step function from 0 to 1. Note that positive steady states of (4.45) still exist for small q even when $h > r/2$ (see Theorem 4.9). However, this phenomenon of population is unable to persist in the upstream region when $h > r/2$ echoes the nonexistence of positive steady states in Propositions 3.4 and 4.15 when the upstream end has Dirichlet boundary condition.

The traveling-wave-like transient dynamics of (4.45) occurs when the diffusion coefficient d and advection rate q are relatively small, the river length L is comparably large, and the interface between extinction and persistence is far away from the boundary. Figure 10 left panel shows the comparison of the numerical wave speeds in Fig. 8 right panel and the theoretical one in (4.72); Fig. 10 right panel shows that the maximal steady state solution of (4.45) decreases in q, and the solution maintains a transition layer profile between the extinction and persistence states. Figure 11 shows the traveling-wave-like behavior of the solutions for different q. The slope of the interface is approximately c_-: it is negative when $q = 0.03$, and it is positive when

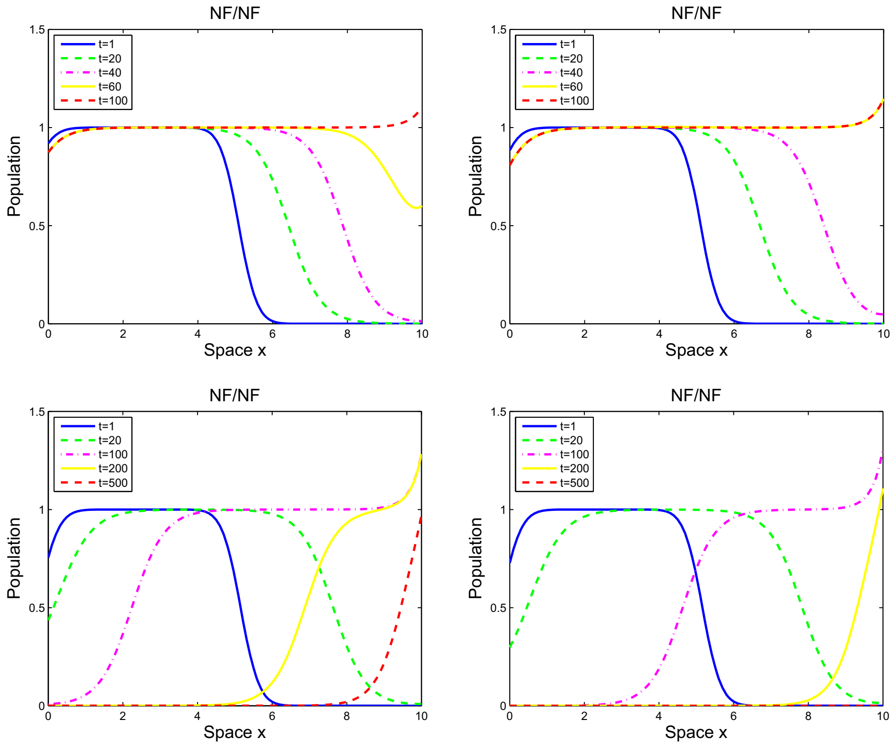

Fig. 12 Formation of boundary layer. Here $f(x, u) = u(1 - u)(u - h)$, $h = 0.4$, $d = 0.09$, $L = 10$ and the initial condition is $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$. Upper left: $q = 0.03$; Upper right: $q = 0.043$; Lower left: $q = 0.09$; Lower right: $q = 0.1$

$q = 0.07$ and $q = 0.1$. It is almost zero when $q = 0.043$ (the break-even advection rate).

Figure 12 shows the evolution of population profile under different q when the initial condition is a step function $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$. That is, the population initially is at upstream end, but not downstream end. Then in all cases, the population can invade the downstream as $c_+ > 0$ in this case. The invasion is successful for small q case and the population is established in the entire river (see Fig. 12 upper left and upper right panels). But for large q, another wave is formed at the upstream end and propagates at $c_- > 0$ downstream. Hence for some time period, there are two wave propagating: the front invasion wave with speed c_+, and the back extinction wave with speed c_-. Although the back wave never catches up with the front wave as $c_+ > c_-$, the back extinction wave eventually wipes out the entire population in the upstream region. Either it ends at a boundary layer steady state at downstream end (see Fig. 12 lower left panel), or the population becomes extinct (see Fig. 12 lower right panel).

In Fig. 13, the dynamics of (4.45) for small diffusion coefficient $d = 0.0001$ and various q is shown with the initial condition $u_0(x) = h + 0.1 \sin x$. It is known that when there is no advection present, sharp interfaces between the two stable states

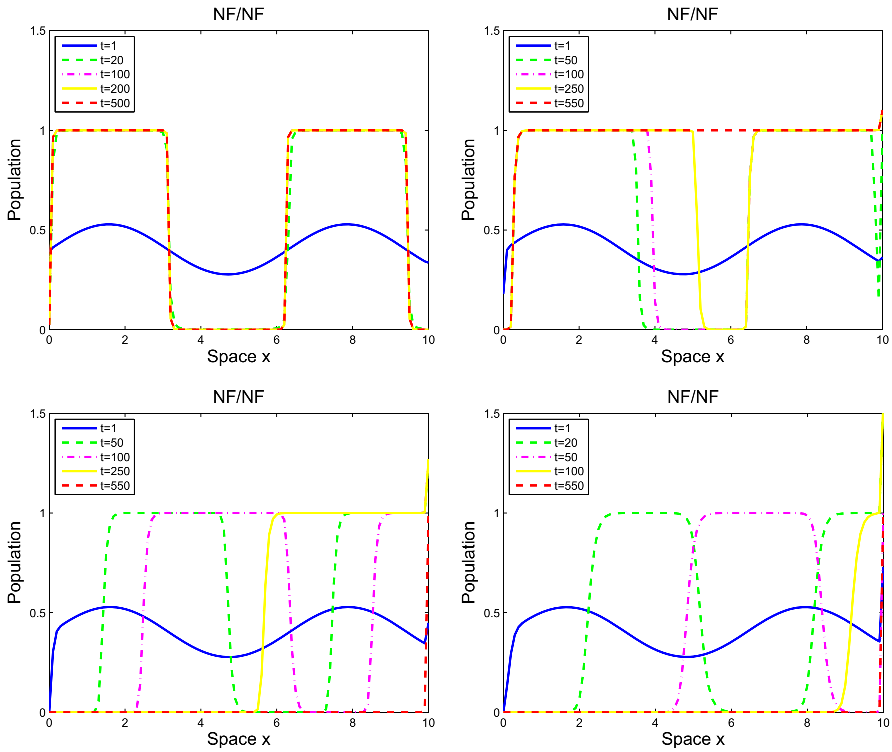

Fig. 13 Slow interface motion, persistence and extinction with advection in (4.45). Here $f(x, u) = u(1 - u)(u - h)$, $h = 0.4$, $d = 0.0001$, $L = 10$ and the initial condition is $u_0 = h + 0.1 \sin x$. Upper left: $q = 0.001$; Upper right: $q = 0.008$; Lower left: $q = 0.03$; Lower right: $q = 0.1$

are generated quickly, then the interfaces move slowly if the bistable nonlinearity is balanced ($h = r/2$) (Carr and Pego 1989; Fusco and Hale 1989), or the interfaces move with traveling wave speed if it is unbalanced ($h \neq r/2$) (Fusco et al. 1996). Here we observe that the sharp interfaces between the two stable states are still formed quickly in all cases of advection rate q. Next a properly small $q = 0.001$ can facilitate the slow movement of the interfaces (see Fig. 13 upper left panel); or a larger $q = 0.008$ can speed up the transition layer from 1 to 0 to catch the transition layer from 0 to 1, so the two transition layers merge and the two patches of high density population collide into one (see Fig. 13 upper right panel). However if the advection rate q increases further, then the strong flow will push all population patches downstream before they can establish in the middle sections (see Fig. 13 lower panel). In the large q case (Fig. 13 lower panel), a very sharp boundary layer appears to persist, which demonstrates that the boundary layer solution as in Theorem 4.18 exists for such q.

The merging of the interfaces and the collision of persistence/extinction patches can be clearly observed in Fig. 14. In the upper panel ($h = 0.4$), the persistence patches merge through coarsening as $c_+ > c_-$; and in the lower panel ($h = 0.6$), the extinction patches merge as $c_+ < c_-$. When the advection rate q is large, the extinction wave starting from the upstream end point prevails so the extinction eventually occurs

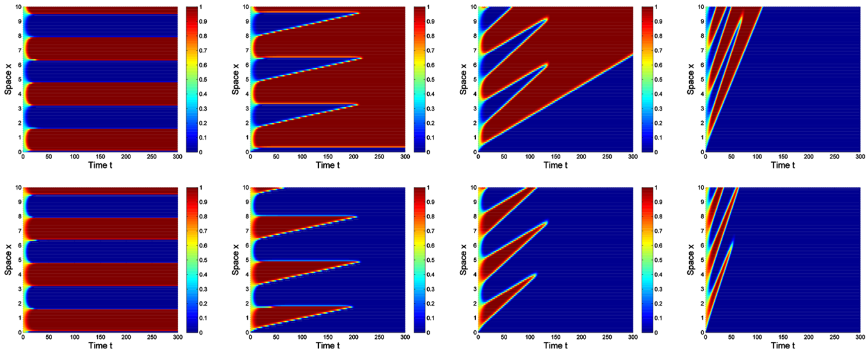

Fig. 14 Interface merging, persistence and extinction with advection in (4.45). Here $f(x, u) = u(1 - u)(u - h)$, $d = 0.0001$, $L = 10$ and the initial condition is $u_0 = h + 0.1 \sin 2x$. Upper row: $h = 0.4$; Lower row: $h = 0.6$; The advection rate from left to right: $q = 0.001$, $q = 0.008$, $q = 0.03$, and $q = 0.1$

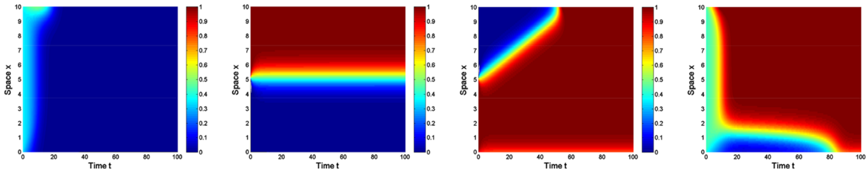

Fig. 15 Bistable dynamics for different initial conditions. Here $f(x, u) = u(1 - u)(u - h)$, $d = 0.09$, $h = 0.4$, $L = 10$, and $q = 0.043$. The initial conditions from left to right are $u_0(x) = 0.36$; $u_0(x) = 0$ for $x \in [0, L/2]$ and $u_0(x) = 1$ for $x \in [L/2, L]$; $u_0(x) = 1$ for $x \in [0, L/2]$ and $u_0(x) = 0$ for $x \in [L/2, L]$, and $u_0(x) = 0.43$

despite there being a large merged persistence patch (Fig. 14 upper row $q = 0.03$ or $q = 0.1$). Also when the advection rate q is sufficiently small, the steady state with multiple interfaces appears to be metastable regardless of $h = 0.4$ or $h = 0.6$ (see Fig. 14 first column).

Finally Figs. 15 and 16 demonstrate the bistable nature of (4.45) for different initial conditions. In Fig. 15, the population becomes extinct when starting from an initial population which is entirely smaller than the Allee threshold (first panel); and the population reaches the maximal steady state when starting from relatively large initial population (third and fourth panels). Both of the extinction and maximal steady state solutions are locally asymptotically stable (see Proposition 4.8), and we expect that there are the only stable ones. But the second panel also shows a stable pattern with a transition layer. We conjecture that the transition layer solution is unstable and metastable (with a small positive eigenvalue), so the pattern can be observed for a long time in numerical simulation. The stability of such steady states will be a question for further studies.

Figure 16 shows a well-known feature of the spreading/extinction bistable structure. For bistable equation on unbounded domain ($\mathbb{R}$) (4.70) with $q = 0$, it is known that when the initial condition is a function $u_L(x) = 1$ when $|x| \leq L$ and $u_L(x) = 0$ otherwise, then there is a sharp threshold $L_0 > 0$, such that the corresponding solution converges to 0 if $L < L_0$, and the solution converges to a traveling wave if $L > L_0$

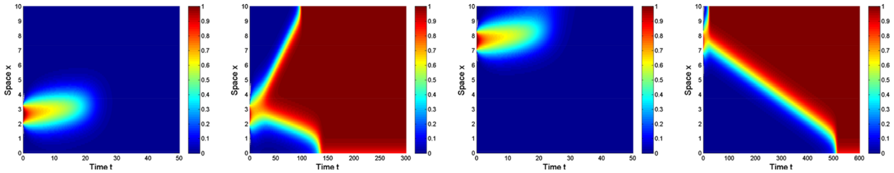

Fig. 16 Minimal initial patch size for invasion. Here $f(x, u) = u(1-u)(u-h)$, $d = 0.09$, $h = 0.4$, $L = 10$, $q = 0.03$, and the initial condition is $u_0(x) = 1$ for $x \in [C - W, C + W]$ and $u_0(x) = 0$ otherwise. Values of (C, W) from left to right: $(C, W) = (0.25L, 0.065L)$; $(C, W) = (0.25L, 0.07L)$; $(C, W) = (0.75L, 0.065L)$; and $(C, W) = (0.75L, 0.07L)$

(Zlatoš 2006), and such threshold phenomenon hold for more general situations (Du and Matano 2010; Muratov and Zhong 2013). Figure 16 illustrates this phenomenon (bistability between extinction and maximal steady state) with $q > 0$ and no-flux boundary condition. It can be seen that here $L_0 \approx 0.07L$ where L is the length of habitat, and the value of L_0 appears to be independent of location of initial patch.

5 Conclusion

The persistence or extinction of a stream population can be modeled by a reaction–diffusion–advection equation defined on a one-dimensional habitat (river environment). While it is typical that the growth rate exhibits logistic type, it is also common that the growth rate of the species exhibits a strong Allee effect so that the growth is negative at lower density. It is shown that other than the extinction of population due to the small initial condition, a strong advection can also drive the population to extinction in an open environment regardless of initial condition. On the other hand, in a closed environment, the population becomes extinct in the upstream region but may concentrate near the downstream end under strong flow rate. In general, a large increase of the advection rate makes the extinction more likely, but there are a few numerical simulations indicating that an intermediate advection rate may increase the population size or possibility of persistence (see Figs. 6 NF/NF case and 7 NF/H case).

The logistic growth usually leads to an unconditional persistence of the population for all initial condition, and the Allee effect growth rate causes a bistability in the population dynamics. For a species with Allee effect type growth, multiple stable states are possible and different initial conditions can lead to different asymptotic behavior, so the persistence is always conditional. The question of persistence or extinction also depends on the boundary conditions, advection rate, diffusion rate and the Allee threshold. From both analytical and numerical approaches, we can see that in general, a higher Allee threshold or a higher advection rate often lead to a wider range of the extinction region.

Our numerical results also suggest that when the Allee threshold satisfies certain condition, a global extinction for all initial conditions is possible even in a closed environment. For example, in Figs. 2 and 7, under NF/NF boundary condition and the growth function $f(x, u) = u(1-u)(u-h)$, a global extinction occurs if $h = 0.4$ for all large advection rate q, but for $h = 0.3$, the population appears to at least survive at the downstream end not in a total extinction. A theoretical verification of this phenomenon is an interesting open question. Similar global extinction when $h > 0.5$ has been observed and proved for a two-patch ODE model with strong Allee effect growth function $f(u) = u(1-u)(u-h)$ and no loss due to dispersal (Swift et al. 2018).

Most of our results in this paper allow a spatially heterogeneous nonlinear growth function $f(x,u)$ with a bistable structure. A multiplicity result for the steady state solutions with a homogeneous growth function is obtained for small advection rate (see Theorem 4.13), and the number of such solution can be large if the diffusion coefficient is sufficiently small. In the absence of advection, the existence of steady state solutions with multiple transition layers or spike layers has been proved in Ai et al. (2006), Alikakos et al. (1993), Hale and Sakamoto (1988) and Nakashima (2003) for one-dimensional case and many others for higher dimensional case. The existence and profile of such solutions under small diffusion and appropriate advection rate is another interesting question for future investigation.

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