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Spatial dynamics of a lattice population model with two age classes and maturation delay

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This paper is concerned with the spatial dynamics of a monostable delayed age-structured population model in a 2D lattice strip. When there exists no positive equilibrium, we prove the global attractivity of the zero equilibrium. Otherwise, we give some sufficient conditions to guarantee the global attractivity of the unique positive equilibrium by establishing a series of comparison arguments. Furthermore, when those conditions do not hold, we show that the system is uniformly persistent. Finally, the spreading speed, including the upward convergence, is established for the model without the monotonicity of the growth function. The linear determinacy of the spreading speed and its coincidence with the minimal wave speed are also proved.

Key words: population model in 2D lattice strip; global attractivity; spreading speed; travelling waves; linear determinacy

1 Introduction

It is well known that many species, such as mammals, exhibit distinct age stages. To study the evolution of such populations, it is natural to take into account the age structure which, in many situations, can influence population size and growth in a significant way. In the past two decades, there has been great progress in modelling and investigating dynamical behaviour of population systems with age structure. We refer to Al-Omari and Gourley [1], Cheng *et al.* [3], Gourley and Kuang [8], Kyrychko *et al.* [13], Smith and

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Thieme [21], So *et al.* [22], Weng *et al.* [27], Weng [28] and Weng and Zhao [29] for more information.

In [21], Smith and Thieme developed an approach to derive an age-structured population model with two age classes (i.e. immature and mature) and fixed maturation delay. Their approach is mainly based on the Fourier transform and the technique of integration along characteristics. Following this approach, many population models with two age classes and fixed or distributed maturation delay have been derived. These resulting models for the mature population are delayed nonlocal reaction–diffusion equations when the spatial domain is continuous (see Al-Omari and Gourley [1], Gourley and Kuang [8], So *et al.* [22] and Weng and Zhao [29]) or delayed lattice differential systems with global interaction when the spatial domain consists of discrete patches (see Cheng *et al.* [3], Kyrychko *et al.* [13], and Weng *et al.* [27]).

More recently, Weng [28] derived a population model in a two-dimensional (2D) lattice strip with two age classes and maturation delay. We sketch the outline of the derivation to illustrate the Smith–Thieme's approach. Consider a single species population distributed over a 2D lattice strip $(i,j) \in \Omega := [1,N]_{\mathbb{Z}} \times \mathbb{Z}$, where $[1,N]_{\mathbb{Z}} := \{1,\dots,N\}$ and N is a positive integer. Let $v(i,j,t,a)$ denote the density of the population on the (i,j)-th patch and at time $t \geqslant 0$ with age $a \geqslant 0$. Assuming that the spatial diffusion occurs only at the nearest neighbourhood along the horizontal and vertical directions, and is proportional to the difference of the densities of the population at adjacent patches, u is governed by

$$\begin{cases} \frac{\partial v(i,j,t,a)}{\partial t} + \frac{\partial v(i,j,t,a)}{\partial a} = D(a)\Delta v(i,j,t,a) - d(a)v(i,j,t,a) \\ v(0,j,t,a) = v(1,j,t,a),\ v(N,j,t,a) = v(N+1,j,t,a), \end{cases} \tag{1.1}$$

where $i \in [1,N]_{\mathbb{Z}}$, $j \in \mathbb{Z}$, $t > 0$, $a \geqslant 0$, $D(a)$ and $d(a)$ are the age-dependent diffusion rate and death rate, respectively, and

$$\begin{aligned} \Delta v(i,j,t,a) = {} & v(i+1,j,t,a) + v(i-1,j,t,a) \\ & + v(i,j+1,t,a) + v(i,j-1,t,a) - 4v(i,j,t,a). \end{aligned} \tag{1.2}$$

Note that, in equation (1.1), a boundary value condition is imposed to restrict the movement of individuals on the boundary of the strip.

If $\tau \geqslant 0$ is the maturation time for the species, then the total matured population at location (i,j) and time t is given by

$$u(i,j,t) = \int_{\tau}^{\infty} v(i,j,t,a)\,da,$$

and satisfies, under the biologically realistic assumption $v(i,j,t,\infty) = 0$, that

$$\frac{du(i,j,t)}{dt} = v(i,j,t,\tau) + \int_{\tau}^{\infty} \big[D(a)\Delta v(i,j,t,a) - d(a)v(i,j,t,a)\big]\,da. \tag{1.3}$$

To proceed further, we assume that the diffusion and death rates for the mature population are age independent, i.e. $D(a) = D_m$ and $d(a) = d_m$ for $a \geqslant \tau$, where D_m and d_m are constants. Then, it follows from equation (1.3) that

$$\frac{du(i,j,t)}{dt} = D_m \Delta u(i,j,t) - d_m u(i,j,t) + v(i,j,t,\tau). \tag{1.4}$$

To obtain a closed system for $u(i,j,t)$, we need to evaluate $v(i,j,t,\tau)$: the maturation rate at location (i,j) and time t. Assume that only the matured individuals can reproduce. Then, $v(i,j,t,0) = b(u(i,j,t))$, where $b(\cdot)$ is the birth function. Applying the discrete Fourier transform and the technique of integration along characteristics, they derived

$$v(i,j,t,\tau) = \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) b\big(u(i_1,j_1,t-\tau)\big). \tag{1.5}$$

In equation (1.5), $\mu = \exp\{-\int_0^\tau d(z)\,dz\}$, $\alpha = \int_0^\tau D(z)\,dz$, and

$$G(i,i_1,j,j_1,\alpha) = G_1(i,i_1,\alpha)\beta_\alpha(j-j_1),\ \beta_\alpha(k) = \frac{1}{2\pi}\int_{-\pi}^{\pi} e^{k\omega \mathbf{i} - 4\alpha \sin^2 \frac{\omega}{2}}\, d\omega,$$

where $\mathbf{i}$ is the imaginary unit, and $G_1(i,i_1,t)$ is the Green function of the boundary value problem

$$\begin{cases} \frac{dU(i,t)}{dt} = U(i+1,t) + U(i-1,t) - 2U(i,t),\ i \in [1,N]_{\mathbb{Z}}, t > 0, \\ U(0,t) = U(1,t),\ U(N,t) = U(N+1,t),\ t \geqslant 0. \end{cases} \tag{1.6}$$

Therefore, the model for the mature population finally becomes

$$\begin{cases} \frac{du(i,j,t)}{dt} = D_m \Delta u(i,j,t) - d_m u(i,j,t) \\ \qquad\qquad + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) b\big(u(i_1,j_1,t-\tau)\big), \\ u(0,j,t) = u(1,j,t),\ u(N,j,t) = u(N+1,j,t). \end{cases} \tag{1.7}$$

It is easy to explain each term in equation (1.7) naturally. The growth rate of the mature population at location (i,j) and time t is the balance of the spatial diffusion, the death rate and the maturation rate. It should be mentioned that although the patches are connected only locally through nearest neighbourhood dispersal, the mature population is governed by a delayed lattice differential system with a global interaction term.

An important issue in population dynamics is the stability of equilibria. There have been many significant results on the stability of equilibria for various equations defined on bounded domains, see e.g. Al-Omari and Gourley [1], Gourley and Ruan [9], Wu and Zhao [31] and Yang and So [33], and the references therein. However, it seems that little has been done for this aspect of equations defined on unbounded domains. Kyrychko *et al.* [13] derived a delayed stage-structured population model on an isolated lattice and studied the stability of the positive equilibrium. Recently, Wang and Li [26] further extended the method in Kyrychko *et al.* [13] to a delayed non-local reaction–diffusion equation in $\mathbb{R}^n$.

Motivated by the works of Kyrychko *et al.* [13] and Wang and Li [26], the first purpose of this paper is to study the stability of equilibria of equation (1.7) in a 2D lattice strip Ω with monotone or non-monotone birth functions. We first prove the positivity and boundedness of the solutions for the Cauchy-type problem of equation (1.7) provided that the initial value is non-negative and bounded. When no positive equilibrium exists, we show that the zero equilibrium is globally attractive. Otherwise, under monostable assumptions (see assumptions (A_1) and (A_3)), we give some sufficient conditions to guarantee the global attractivity of the unique positive equilibrium by establishing a series of comparison arguments. Finally, when those conditions do not hold, we prove that the system is uniformly persistent by constructing a "lower" auxiliary equation. Biologically, the persistence of a population model means that the species survive in the long term. On the rigorous definition of persistence, we refer to Freedman and Ruan [6].

In addition to the stability of the equilibria, two other important issues are the spreading speed and travelling wave solutions. A travelling wave solution of an evolution system is a special solution which travels without change of shape (see Definition 4.1). It can describe spatial spread/invasion of the species. In recent years, this topic has attracted much attention from the mathematical and biological community and has resulted in many significant research papers, see e.g. [3–5, 7, 8, 14–17, 19, 24, 25, 27–30, 32, 36] and the references therein. The spreading speed is a threshold constant $c_* > 0$ which gives an important description of the long time behaviour for a population system either for $c \in (0, c_*)$ or $c \in (c_*, \infty)$ (see Definition 4.2). Since the introduction of this concept by Aronson and Weinberger [2], it has been developed and applied to various of evolution systems. See [4, 10, 16, 24, 25, 27–29] and the references therein.

When equation (1.7) has only two equilibria 0 and $K > 0$ and the birth function b is non-decreasing on $[0, K]$, Weng [28] obtained the spreading speed and its coincidence with the minimal wave speed of monotone travelling wave solutions of equation (1.7) by applying the theory for monotone semiflows developed by Liang and Zhao [16]. However, the birth functions, such as logistic and Ricker type, may not be monotone in general (see Fang and Zhao [5], Hsu and Zhao [10], Li *et al.* [15] and Ma [17]). When b is not monotone in $[0, K]$, equation (1.7) is a *non-quasi-monotone* system. In this case, the solution semiflow generalized from equation (1.7) may not be monotone and Liang and Zhao's theory for monotone semiflows cannot be applied directly to establish the results on the travelling waves and spreading speed.

The second purpose of this paper is to consider the spreading speed and travelling waves for equation (1.7) with monostable nonlinearity and without the quasi-monotone condition. To overcome the difficulty for the non-quasi-monotone equations, we shall introduce two auxiliary quasi-monotone equations to "trap" equation (1.7). The method has been used by many researchers for various non-monotone evolution equations, see e.g. Fang *et al.* [4], Fang and Zhao [5], Hsu and Zhao [10], Li *et al.* [15], Ma [17], Wang [25] and Wu and Liu [30]. Based on a comparison theorem for solutions of the Cauchy problems of the three systems, the spreading speed c_* is established and the non-existence of travelling waves with speed less than c_* is also obtained. By constructing a profile set in a suitable Banach space via the monotone travelling waves of the auxiliary systems and applying Schauder's fixed-point theorem, we then establish the existence and asymptotic behaviour of travelling waves with speed $c > c_*$. Finally, the existence of travelling waves with speed $c = c_*$ (minimal waves for short) is obtained by using a limiting process. It turns out that the spreading speed is linearly determinate and coincides with the minimal wave speed of travelling waves for this class of non-quasi-monotone delayed lattice dynamical systems.

We would like to mention that it is not easy to obtain the upward convergence of the spreading speed and travelling waves, as well as the downward convergence of the minimal wave due to the non-quasi-monotone nonlinearity. We shall establish some sufficient conditions to ensure the upward convergence of the spreading speed by using a fluctuation method. This method was developed by Thieme and Zhao [23] for a non-local delayed and diffusive predator-prey model and was used in [4, 5, 10] to prove the upward convergence of the spreading speed for various non-monotone evolution systems. The upward convergence of the travelling waves are then obtained. The downward convergence of the minimal wave is also obtained by proving its integrability on $(-\infty, 0]$.

The rest of the paper is organized as follows. In Section 2, we consider the positivity and boundedness of solutions for equation (1.7). Section 3 is devoted to the stability of the equilibria. In Section 4, we first state some known results on spreading speed and travelling waves for equation (1.7) with monotone growth function b. Then by using the squeezing method combined with two auxiliary systems, we obtain the minimal wave speed and spreading speed of equation (1.7) with a non-monotone growth function, the linear determinacy of the spreading speed as well as the coincidence in between the minimal wave speed and spreading speed. In Section 5, we present two illustrative examples.

2 Positivity and boundedness of solutions

Throughout this paper, we always make the following basic assumption:

(A_1) $b \in C^1(\mathbb{R}_+, \mathbb{R})$, $b(0) = 0$, and $b(u) > 0$ for $u > 0$.

Other assumptions which will be needed later are listed as follows.

(A_2) $b(\cdot)$ is non-decreasing on $[0, +\infty)$.

$(A_2)'$ There exists a number $u_{\max} > 0$ such that $b(u)$ is non-decreasing for $0 < u < u_{\max}$ and decreasing for $u > u_{\max}$.

(A_3) There exists a constant $K > 0$ such that $\mu b(K) = d_m K$, and $\mu b(u) > d_m u$ for $u \in (0, K)$, $\mu b(u) < d_m u$ for $u > K$.

$(A_3)'$ $d_m u > \mu b(u)$ for $u > 0$.

It is easy to see that if (A_1) and (A_3) hold, then the reaction system of equation (1.7) has an unstable equilibrium 0 and a stable equilibrium K. In this case, equation (1.7) is a monostable system. The monostable assumptions will be needed in studying the global attractivity of the positive equilibrium, travelling waves and spreading speeds.

We remark that the following two specific functions

$$b_1(u) = \frac{pu}{1 + \alpha u} \text{ and } b_2(u) = pue^{-\alpha u} \text{ with } p > 0 \text{ and } \alpha > 0,$$

which have been widely used in the mathematical biology literature, satisfy the conditions (A_1) and either (A_2) or $(A_2)'$, respectively. For a wide range of parameters p, μ, α and d_m, they also satisfy either (A_3) or $(A_3)'$. We also mention that the function $b_3(u) = pu^2e^{-\alpha u}$, with $p > 0$ and $\alpha > 0$, satisfies (A_1) and $(A_3)'$ provided that $d_m ae > \mu p$.

To investigate the existence, positivity and boundedness of solutions for equation (1.7), consider an initial value of equation (1.7):

$$u(i,j,s) = \varphi(i,j,s),\ (i,j,s) \in \Omega \times [-\tau, 0]. \tag{2.1}$$

For convenience, we introduce the following notation.

(1) We define

$$\begin{aligned} X &:= \{\phi : \Omega \to \mathbb{R} |\ \phi = \{\phi(i,j)\}_{(i,j)\in\Omega} \text{ is bounded}\}, \\ X^+ &:= \{\phi \in X | \phi(i,j) \geqslant 0 \text{ for } (i,j) \in \Omega\}, \\ \mathscr{A}(\phi)(i,j) &:= \Delta\phi(i,j),\ \forall \phi \in X, \\ T(t)[\phi](i,j) &:= e^{-d_m t} \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,D_m t)\phi(i_1,j_1),\ \forall \phi \in X, t > 0. \end{aligned}$$

Clearly, X^+ is a closed cone of X under the partial ordering induced by X^+.

(2) We equip X with a compact open topology, and the accompanied norm is expressed as $\|\cdot\|_X$. Then X is a Banach lattice, and $T(t) : X \to X$ is a linear C_0-semigroup with $T(t)X^+ \subseteq X^+$ for $t > 0$.

(3) Let $\mathscr{C} = C([-\tau, 0], X)$ be the Banach space of continuous functions from $[-\tau, 0]$ into X with the supremum norm $\|\cdot\|_{\mathscr{C}}$. For any given $\tilde{K} > 0$, we define the following spaces:

$$\begin{aligned} \mathscr{C}^+ &:= \{\varphi \in \mathscr{C} | \varphi(s) \in X^+, s \in [-\tau, 0]\}, \\ \mathscr{C}_{[0,\tilde{K}]} &:= \{\varphi \in \mathscr{C} | \varphi(i,j,s) \in [0,\tilde{K}], \forall (i,j,s) \in \Omega \times [-\tau, 0]\}. \end{aligned}$$

Clearly, $\mathscr{C}^+$ is a closed (positive) cone of $\mathscr{C}$.

(4) As usual, we identify an element $\varphi \in \mathscr{C}$ as a function from $\Omega \times [-\tau, 0]$ into $\mathbb{R}$ defined by $\varphi(i,j,s) = \varphi(s)(i,j)$. For any continuous function $u : [-\tau, b) \to X$, $b > 0$, we define $u_t \in \mathscr{C}$, $t \in [0, b)$ by $u_t(s) = u(t+s)$, $s \in [-\tau, 0]$. Then $t \to u_t$ is a continuous function from $[0, b)$ to $\mathscr{C}$.

(5) Define $F : \mathscr{C} \to X$ by

$$F(\varphi)(i,j) := \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) b\big(\varphi(i_1,j_1,-\tau)\big).$$

Using this notation, the initial value problem for equation (1.7) can be rewritten as

$$\begin{cases} u'(t) = D_m \mathscr{A} u - d_m u(t) + F(u_t),\ t > 0, \\ u_0 = \varphi \in \mathscr{C}^+. \end{cases} \tag{2.2}$$

Since $G(i,i_1,j,j_1,D_m t)$ is the Green function of the boundary value problem

$$\begin{cases} \frac{dU(i,j,t)}{dt} = D_m \Delta U(i,j,t),\ i \in [1,N]_{\mathbb{Z}},\ j \in \mathbb{Z},\ t > 0, \\ U(0,j,t) = U(1,j,t),\ U(N,j,t) = U(N+1,j,t),\ j \in \mathbb{Z},\ t \geqslant 0, \end{cases}$$

one can see that equation (2.2) is equivalent to the integral problem (see Weng [28]):

$$\begin{cases} u(t) = T(t)\varphi(0) + \int_0^t T(t-s)F(u_s)\,ds, \ t > 0, \\ u(s) = \varphi(s), \ s \in [-\tau, 0]. \end{cases} \tag{2.3}$$

Then, we have the following result on the existence, positivity and boundedness of solutions of equation (1.7) with monotone or non-monotone birth functions.

Theorem 2.1 *Under the assumption* (A_1)*, for any* $\varphi \in \mathscr{C}^+$*, equation* (1.7) *has a unique solution* $u(i,j,t;\varphi)$ *on* $[0,+\infty)$ *such that*

$$0 \leqslant u(i,j,t;\varphi) \leqslant \bar{K} \text{ for any } (i,j,t) \in \Omega \times [0,+\infty), \tag{2.4}$$

where $M := \max_{s\in[-\tau,,0]} \sup_{(i,j)\in\Omega} \varphi(i,j,s)$ *and*

$$\bar{K} := \begin{cases} \max\{\mu b(u_{\max})/d_m, M\}, & \text{if } (A_2)' \text{ holds;} \\ \max\{K, M\}, & \text{if } (A_2) \text{ and } (A_3) \text{ hold;} \\ M, & \text{if } (A_3)' \text{ hold.} \end{cases} \tag{2.5}$$

Furthermore, if $\varphi(0) \in \mathrm{Int}X^+$*, then* $u(t) \in \mathrm{Int}X^+$ *for* $t \geqslant 0$ *and* $u_t \in \mathrm{Int}\mathscr{C}^+$ *for* $t > \tau$.

Proof The existence and non-negativity of the solutions follow directly from the method of steps, see e.g. Smith [20, Chapter 5]. We now prove that $u(i,j,t;\varphi) \leqslant \bar{K}$ for any $(i,j,t) \in \Omega \times [0,+\infty)$.

If $(A_2)'$ holds, then for any $(i,j) \in \Omega$ and $t > 0$, we have

$$\begin{aligned} u(i,j,t;\varphi) &= T(t)\varphi(0)(i,j) + \int_0^t T(t-s)F(u_s)(i,j)\,ds \\ &\leqslant Me^{-d_m t} + \mu b(u_{\max}) \int_0^t e^{-d_m(t-s)}\,ds \\ &= Me^{-d_m t} + \mu b(u_{\max})(1 - e^{-d_m t})/d_m \\ &\leqslant \max\{\mu b(u_{\max})/d_m, M\}. \end{aligned}$$

If (A_2) and (A_3) hold, we consider two subcases: $M \leqslant K$ and $M > K$. If $M \leqslant K$, then for any $(i,j) \in \Omega$ and $t \in [0,\tau]$, we have

$$\begin{aligned} u(i,j,t;\varphi) &= T(t)\varphi(0)(i,j) + \int_0^t T(t-s)F(u_s)(i,j)\,ds \\ &\leqslant Me^{-d_m t} + \mu b(M) \int_0^t e^{-d_m(t-s)}\,ds \\ &\leqslant Ke^{-d_m t} + \mu b(K)(1 - e^{-d_m t})/d_m = K. \end{aligned}$$

Thus, for $(i,j) \in \Omega$ and $t \in [\tau, 2\tau]$, we have

$$u(i,j,t;\varphi) \leqslant Ke^{-d_m t} + \mu b(K) \int_0^t e^{-d_m(t-s)}\,ds \leqslant K.$$

Inductively, we can prove that $u(i,j,t;\varphi) \leqslant K = \max\{K, M\}$ for any $(i,j,t) \in \Omega \times [0,+\infty)$. If $M > K$, then $d_m M > \mu b(M)$ and hence for any $(i,j) \in \Omega$ and $t \in [0,\tau]$, we have

$$u(i,j,t;\varphi) \leqslant Me^{-d_m t} + \mu b(M)(1-e^{-d_m t})/d_m \leqslant M.$$

By an inductive argument, we can prove that $u(i,j,t;\varphi) \leqslant M = \max\{K, M\}$ for any $(i,j,t) \in \Omega \times [0,+\infty)$.

If $(A_3)'$ holds, then for $(i,j) \in \Omega$ and $s \in [0,\tau]$,

$$F(u_s)(i,j) \leqslant \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) d_m u(i_1,j_1,s-\tau) \leqslant d_m M.$$

Thus, for $(i,j) \in \Omega$ and $t \in [0,\tau]$, we have

$$u(i,j,t;\varphi) \leqslant Me^{-d_m t} + d_m M \int_0^t e^{-d_m(t-s)} ds = M.$$

Inductively, we can prove that $u(i,j,t;\varphi) \leqslant M$ for any $(i,j,t) \in \Omega \times [0,+\infty)$. Therefore, $u(i,j,t;\varphi) \leqslant \bar{K}$ for any $(i,j,t) \in \Omega \times [0,+\infty)$.

From the boundedness of solutions and the assumption $b \in C^1(\mathbb{R}_+, \mathbb{R})$, it is easy to prove the uniqueness of the solution by using the Gronwall's inequality. We omit it here.

If $\varphi(0) \in \mathrm{Int}X^+$, it then follows from the fact

$$u(i,j,t;\varphi) \geqslant T(t)\varphi(0)(i,j) \geqslant e^{-d_m t} \inf_{(i,j)\in\Omega} \varphi(i,j,0)$$

that $u(t) \in \mathrm{Int}X^+$ for $t \geqslant 0$ and $u_t \in \mathrm{Int}\mathscr{C}^+$ for $t > \tau$. This completes the proof. □

3 Global attractivity

This section is devoted to the stability of the equilibria for equation (1.7). We first show that when no positive equilibrium exists, the trivial equilibrium is globally stable regardless of the monotonicity of the birth function b. Then, in Subsection 3.1, we shall prove the stability of the positive equilibrium when the birth function b is non-decreasing. A similar problem with b being non-monotone will be discussed in Subsection 3.2.

For convenience, we write

$$\mathscr{C}^+_{\delta,M} := \{\varphi \in \mathscr{C}^+ : \|\varphi\|_{\mathscr{C}} \leqslant M \text{ and } \inf_{(i,j)\in\Omega} \varphi(i,j,0) \geqslant \delta\}$$

for any given constants $\delta > 0$ and $M > 0$. In the following, we also write $\|\phi\| = \sup_{(i,j)\in\Omega} |\phi(i,j)|$ for any $\phi \in X$.

Theorem 3.1 *Assume that* (A_1) *and* $(A_3)'$ *are satisfied. Then for any* $\delta > 0$ *and* $M > 0$,

$$\lim_{t\to\infty} \|u(\cdot,t;\varphi)\| = 0 \text{ uniformly for } \varphi \in \mathscr{C}^+_{\delta,M}.$$

Proof From Theorem 2.1, we have $\delta e^{-d_m t} \leqslant u(i,j,t;\varphi) \leqslant M$ for any $(i,j,t) \in \Omega \times [0,+\infty)$ and $\varphi \in \mathscr{C}^+_{\delta,M}$. Since $b(u) > 0 = b(0)$ for $u > 0$, the function b is either non-decreasing on $[0,\infty)$ or non-monotone on $[0,\infty)$. We first consider the case where b is non-decreasing on $[0,\infty)$. Let $v(t)$ solve the following problem

$$\begin{cases} \frac{dv(t)}{dt} = -d_m v(t) + \mu b(v(t-\tau)), \ t > 0, \\ v(s) = M, \ s \in [-\tau, 0]. \end{cases}$$

Since b is non-decreasing on $[0,\infty)$, by the comparison method (see Lemma 3.2 in Subsection 3.1), we have

$$0 \leqslant u(i,j,t;\varphi) \leqslant v(t) \text{ for } (i,j) \in \Omega \text{ and } t \geqslant 0. \tag{3.1}$$

Thus, to prove the assertion of this theorem in the monotone case, it is sufficient to show that $\lim_{t\to\infty} v(t) = 0$. We first prove that $\lim_{t\to\infty} v(t)$ exists. If this is not true, then

$$\alpha =: \limsup_{t\to\infty} v(t) > \liminf_{t\to\infty} v(t) \geqslant 0.$$

Applying the Fluctuation lemma (see e.g. Wu and Zou [32, Lemma 2.2]), there exists a sequence $\{t_j\}$ with $t_j \to \infty$ as $j \to \infty$ such that $\lim_{j\to\infty} v'(t_j) = 0$ and $\lim_{j\to\infty} v(t_j) = \alpha$. Set $v^j = \sup\{v(t) : t \geqslant t_j - \tau\}$. Then, we have

$$v'(t_j) = -d_m v(t_j) + \mu b(v(t_j - \tau)) \leqslant -d_m v(t_j) + \mu b(v^j).$$

Letting $j \to \infty$ in the above inequality, we obtain $0 \leqslant \mu b(\alpha) - d_m \alpha < 0$. This contradiction implies that $\lim_{t\to\infty} v(t)$ exists. Moreover, it is easy to see that $\lim_{t\to\infty} v(t) = 0$ since $d_m u > \mu b(u)$ for all $u > 0$.

Now, we consider the case where b is non-monotone on $[0,\infty)$. We construct a monotone system to control the original system. Define

$$b^+(u) := \max_{v\in[0,u]} b(v), \ u \in [0,\infty). \tag{3.2}$$

It is easy to see that $b^+(0) = 0$, $b^+(u)$ is non-decreasing on $[0,\infty)$, $b^+(u) \geqslant b(u)$ for any $u \geqslant 0$, and $\mu b^+(u) < d_m u$ for any $u > 0$. Let $u^+(t;M)$ be the solution of the following auxiliary system:

$$\begin{cases} \frac{du^+(t)}{dt} = -d_m u^+(t) + \mu b^+(u^+(t-\tau)), \ t > 0, \\ u^+(s) = M, \ s \in [-\tau, 0]. \end{cases} \tag{3.3}$$

Since $b^+(u)$ is non-decreasing on $[0,\infty)$ and $\mu b^+(u) < d_m u$ for any $u > 0$, from the proof of the first case, we have $\lim_{t\to\infty} u^+(t;M) = 0$. Thus, it suffices to show that $u(i,j,t;\varphi) \leqslant u^+(t;M)$ for $(i,j) \in \Omega$ and $t \geqslant 0$. Let

$$w(i,j,t) = u(i,j,t;\varphi) - u^+(t;M) \text{ for } (i,j) \in \Omega \text{ and } t \geqslant -\tau.$$

Then, $w(i,j,s) \leqslant 0$ for $(i,j) \in \Omega$ and $s \in [-\tau, 0]$. Moreover, for $(i,j) \in \Omega$ and $t \in (0,\tau]$, we have

$$\begin{aligned}\frac{dw(i,j,t)}{dt} &= D_m \Delta w(i,j,t) - d_m w(i,j,t) + \mu b(u(i,j,t-\tau;\varphi)) - \mu b^+(u^+(t-\tau)) \\ &\leqslant D_m \Delta w(i,j,t) - d_m w(i,j,t) + \mu b^+(u(i,j,t-\tau;\varphi)) - \mu b^+(u^+(t-\tau)) \\ &\leqslant D_m \Delta w(i,j,t) - d_m w(i,j,t),\end{aligned}$$

which implies that

$$w(i,j,t) \leqslant e^{-d_m t} \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,D_m t) w(i_1,j_1,0) \leqslant 0.$$

Thus, $u(i,j,t;\varphi) \leqslant u^+(t;M)$ for $(i,j) \in \Omega$ and $t \in [0,\tau]$. Inductively, we can prove that $u(i,j,t;\varphi) \leqslant u^+(t;M)$ for $(i,j) \in \Omega$ and $t \geqslant 0$. This completes the proof. □

Theorem 3.1 guarantees that when no positive equilibrium exists, the trivial equilibrium is globally stable regardless of the monotonicity of the birth function b. In the following, we shall consider the stability of the unique positive equilibrium of equation (1.7) with monotone or non-monotone birth function b.

3.1 Monotone birth function

Assume that the birth function is non-decreasing. We first introduce the following comparison lemma.

Lemma 3.2 *Assume that* (A_1) *and* (A_2) *are satisfied. Let* $\bar{u}(i,j,t)$ *and* $\underline{u}(i,j,t)$ *be such that* $\bar{u}(i,j,s) \geqslant \underline{u}(i,j,s)$ *for all* $(i,j,s) \in \Omega \times [-\tau, 0]$ *and*

$$\begin{cases} \frac{d\bar{u}(i,j,t)}{dt} \geqslant D_m \Delta \bar{u}(i,j,t) - d_m \bar{u}(i,j,t) + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) \\ \qquad \times b\big(\bar{u}(i_1,j_1,t-\tau)\big), \ (i,j) \in \Omega, t > 0, \\ \bar{u}(0,j,t) = \bar{u}(1,j,t), \ \bar{u}(N,j,t) = \bar{u}(N+1,j,t), \ j \in \mathbb{Z}, t \geqslant 0, \end{cases}$$

and

$$\begin{cases} \frac{d\underline{u}(i,j,t)}{dt} \leqslant D_m \Delta \underline{u}(i,j,t) - d_m \underline{u}(i,j,t) + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) \\ \qquad \times b\big(\underline{u}(i_1,j_1,t-\tau)\big), \ (i,j) \in \Omega, t > 0, \\ \underline{u}(0,j,t) = \underline{u}(1,j,t), \ \underline{u}(N,j,t) = \underline{u}(N+1,j,t), \ j \in \mathbb{Z}, t \geqslant 0. \end{cases}$$

Then, $\bar{u}(i,j,t) \geqslant \underline{u}(i,j,t)$ *for* $(i,j) \in \Omega$ *and* $t > 0$.

The proof of the above lemma is similar to that of Weng [28, Lemma 3.3] and is omitted.

Theorem 3.3 *Assume that* (A_1)–(A_3) *are satisfied. Then for any* $\delta > 0$ *and* $M > 0$,

$$\lim_{t\to\infty} \|u(\cdot,t;\varphi) - K\| = 0 \text{ uniformly for } \varphi \in \mathscr{C}^+_{\delta,M}.$$

Proof If (A_3) holds, then from Theorem 2.1, we have $\delta e^{-d_m t} \leqslant u(i,j,t;\varphi) \leqslant \bar{K} = \max\{K, M\}$ for any $(i,j,t) \in \Omega \times [0,+\infty)$ and $\varphi \in \mathscr{C}^+_{\delta,M}$. Let $\bar{u}(t)$ and $\underline{u}(t)$ solve the following problems

$$\begin{cases} \frac{d\bar{u}(t)}{dt} = -d_m\bar{u}(t) + \mu b(\bar{u}(t-\tau)),\ t > \tau, \\ \bar{u}(s) = \bar{K},\ s \in [0,\tau], \end{cases}$$

and

$$\begin{cases} \frac{d\underline{u}(t)}{dt} = -d_m\underline{u}(t) + \mu b(\underline{u}(t-\tau)),\ t > \tau, \\ \underline{u}(s) = \delta e^{-d_m\tau},\ s \in [0,\tau], \end{cases}$$

respectively. It then follows from Lemma 3.2 that

$$\underline{u}(t) \leqslant u(i,j,t;\varphi) \leqslant \bar{u}(t) \text{ for } (i,j) \in \Omega \text{ and } t \geqslant \tau. \tag{3.4}$$

Moreover, using Theorem 9.1 in Kuang [12, page 159], we have

$$\lim_{t\to\infty} \underline{u}(t) = \lim_{t\to\infty} \bar{u}(t) = K,$$

and hence the assertion follows. This completes the proof. □

3.2 Non-monotone birth function

In this subsection, we consider the stability of the positive equilibrium for the non-monotone case.

We first establish the following comparison theorem for general birth functions.

Lemma 3.4 *Assume that* (A_1) *holds, and that there exists* $\bar{M} > 0$ *such that* $0 \leqslant u^-(i,j,t) \leqslant u^+(i,j,t) \leqslant \bar{M}$ *for* $(i,j,t) \in \Omega \times [-\tau,+\infty)$ *satisfying: for any function* ϕ *with* $u^-(i,j,t) \leqslant \phi(i,j,t) \leqslant u^+(i,j,t) \leqslant \bar{M}$ *for* $(i,j,t) \in \Omega \times [-\tau,\infty)$*, we have*

$$\begin{cases} \frac{du^+(i,j,t)}{dt} \geqslant D_m\Delta u^+ - d_m u^+(i,j,t) + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) \\ \qquad\qquad \times b\big(\phi(i_1,j_1,t-\tau)\big),\ (i,j) \in \Omega, t > 0, \\ u^+(0,j,t) = u^+(1,j,t),\ u^+(N,j,t) = u^+(N+1,j,t),\ j \in \mathbb{Z}, t \geqslant 0, \end{cases}$$

and

$$\begin{cases} \frac{du^-(i,j,t)}{dt} \leqslant D_m\Delta u^- - d_m u^-(i,j,t) + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) \\ \qquad\qquad \times b\big(\phi(i_1,j_1,t-\tau)\big),\ (i,j) \in \Omega, t > 0, \\ u^-(0,j,t) = u^-(1,j,t),\ u^-(N,j,t) = u^-(N+1,j,t),\ j \in \mathbb{Z}, t \geqslant 0. \end{cases}$$

Then for any function φ *with*

$$u^-(i,j,s) \leqslant \varphi(i,j,s) \leqslant u^+(i,j,s) \leqslant \bar{M} \ \textit{ for } (i,j,s) \in \Omega \times [-\tau, 0],$$

we have

$$u^-(i,j,t) \leqslant u(i,j,t;\varphi) \leqslant u^+(i,j,t) \text{ for all } (i,j) \in \Omega \text{ and } t > 0,$$

where $u(i,j,t;\varphi)$ is the solution of equation (1.7) with the initial value $\varphi \in \mathscr{C}^+$, and u^- and u^+ are called a pair of sub- and super-solutions of equation (1.7).

Proof Define $w(i,j,t) = u^+(i,j,t) - u(i,j,t;\varphi)$ for $(i,j) \in \Omega$ and $t \geqslant -\tau$. Then it is easy to see that

$$\begin{cases} \frac{dw(i,j,t)}{dt} \geqslant D_m \Delta w(i,j,t) - d_m w(i,j,t) + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i,i_1,j,j_1,\alpha) \\ \qquad \times \left[b\big(\phi(i_1,j_1,t-\tau)\big) - b\big(u(i_1,j_1,t-\tau)\big) \right],\ (i,j) \in \Omega, t > 0, \\ w(0,j,t) = w(1,j,t),\ w(N,j,t) = w(N+1,j,t),\ j \in \mathbb{Z}, t \geqslant 0, \end{cases} \tag{3.5}$$

for all ϕ with $u^-(i,j,t) \leqslant \phi(i,j,t) \leqslant u^+(i,j,t)$ for $(i,j,t) \in \Omega \times [-\tau,+\infty)$. Note that $u(i,j,s;\varphi) = \varphi(i,j,s)$ for $(i,j,s) \in \Omega \times [-\tau,0]$. Take $\phi(i,j,s) = \varphi(i,j,s)$ for $(i,j,s) \in \Omega \times [-\tau,0]$. It follows from equation (3.5) that

$$\begin{cases} \frac{dw(i,j,t)}{dt} \geqslant D_m \Delta w(i,j,t) - d_m w(i,j,t),\ (i,j) \in \Omega, t \in (0,\tau], \\ w(0,j,t) = w(1,j,t),\ w(N,j,t) = w(N+1,j,t),\ j \in \mathbb{Z}, t \geqslant 0. \end{cases} \tag{3.6}$$

Recalling the definition of the operator T, equation (3.6) implies that

$$w(i,j,t) \geqslant T(t)w(0)(i,j) \geqslant 0,\ (i,j) \in \Omega, t \in (0,\tau].$$

Hence, $u(i,j,t;\varphi) \leqslant u^+(i,j,t)$ for all $(i,j) \in \Omega$ and $t \in [0,\tau]$. Similarly, we can show that $u^-(i,j,t) \leqslant u(i,j,t;\varphi)$ for all $(i,j) \in \Omega$ and $t \in [0,\tau]$.

Now, we choose ϕ to be any function between u^+ and u^- such that $\phi(i,j,t) = u(i,j,t;\varphi)$ for $(i,j,t) \in \Omega \times [0,\tau]$. Then, from equation (3.5), we have

$$\begin{cases} \frac{dw(i,j,t)}{dt} \geqslant D_m \Delta w(i,j,t) - d_m w(i,j,t),\ (i,j) \in \Omega, t \in (\tau,2\tau], \\ w(0,j,t) = w(1,j,t),\ w(N,j,t) = w(N+1,j,t),\ j \in \mathbb{Z}, t \geqslant \tau, \end{cases}$$

which implies that

$$w(i,j,t) \geqslant T(t)w(\tau)(i,j) \geqslant 0,\ (i,j) \in \Omega, t \in (\tau,2\tau].$$

Hence, $u(i,j,t;\varphi) \leqslant u^+(i,j,t)$ for all $(i,j) \in \Omega$ and $t \in [\tau,2\tau]$. Proving that $u^-(i,j,t) \leqslant u(i,j,t;\varphi)$ for all $(i,j) \in \Omega$ and $t \in [\tau,2\tau]$ is similar.

Inductively, we can obtain $u^-(i,j,t) \leqslant u(i,j,t;\varphi) \leqslant u^+(i,j,t)$ for all $(i,j) \in \Omega$ and $t > 0$. This completes the proof. □

In the rest of this section, we always assume that (A_1), $(A_2)'$ and (A_3) hold. We shall consider two cases: $K \leqslant u_{\max}$ and $K > u_{\max}$.

3.2.1 *The case $K \leqslant u_{\max}$.*

Theorem 3.5 *Assume that* (A_1), $(A_2)'$ *and* (A_3) *are satisfied. If* $K \leqslant u_{\max}$, *then for any* $\delta > 0$ *and* $M > 0$,

$$\lim_{t\to\infty} \|u(\cdot,t;\varphi) - K\| = 0 \text{ uniformly for } \varphi \in \mathscr{C}^+_{\delta,M}.$$

Proof Take $\bar{K} = \max\{M, \frac{\mu}{d_m} b(u_{\max})\}$. From Theorem 2.1, we have

$$\delta e^{-d_m t} \leqslant u(i,j,t;\varphi) \leqslant \bar{K} \text{ for any } (i,j,t) \in \Omega \times [0,+\infty) \text{ and } \varphi \in \mathscr{C}^+_{\delta,M}.$$

It is easy to see that the functions $u^-(i,j,t) = 0$ and $u^+(i,j,t) = V_1(t)$ are a pair of sub- and super-solutions of equation (1.7), where $V_1(t)$ satisfies

$$\begin{cases} \frac{dV_1(t)}{dt} = -d_m V_1(t) + \mu b(u_{\max}),\ t > \tau, \\ V_1(s) = \bar{K},\ s \in [0,\tau]. \end{cases} \tag{3.7}$$

By Lemma 3.4, we have $0 \leqslant u(i,j,t;\varphi) \leqslant V_1(t)$ for $(i,j,t) \in \Omega \times [0,+\infty)$. Thus,

$$\limsup_{t\to\infty} \sup_{(i,j)\in\Omega} u(i,j,t;\varphi) \leqslant \lim_{t\to\infty} V_1(t) = \frac{\mu}{d_m} b(u_{\max}). \tag{3.8}$$

In the case where $K < u_{\max}$, we have $K \leqslant \frac{\mu}{d_m} b(u_{\max}) < u_{\max}$. Thus, there exists $T > 0$ such that

$$u(i,j,t;\varphi) \leqslant V_1(t) \leqslant \frac{1}{2}\Big[\frac{\mu}{d_m} b(u_{\max}) + u_{\max}\Big] < u_{\max}$$

for $(i,j) \in \Omega$ and $t \geqslant T$. Note that the function $b(u)$ is non-decreasing for $u \in [0,u_{\max}]$. Similar to the proof of Theorem 3.3, we can show that $\lim_{t\to\infty} \|u(\cdot,t;\varphi) - K\| = 0$ uniformly for $\varphi \in \mathscr{C}^+_{\delta,M}$.

We now consider the case when $K = u_{\max}$. Let $b^+(\cdot)$ be defined as in equation (3.2) and $u^+(t;M)$ be the solution of equation (3.3). By Theorem 9.1 in Kuang [12, page 159], we have $\lim_{t\to\infty} u^+(t;M) = K$. Then, for any $\epsilon \in (0,1)$, there exists $t_1 > 0$ such that

$$u(i,j,t;\varphi) \leqslant u^+(t;M) < K + \epsilon \text{ for any } t \geqslant t_1, \varphi \in \mathscr{C}^+_{\delta,M}.$$

Define

$$b^-_\epsilon(u) = \min\{b(u), b(K+\epsilon)\},\ u \in [0, K+\epsilon].$$

It is clear that $b^-_\epsilon(u)$ is non-decreasing on $[0, K+\epsilon]$ and $\mu b^-_\epsilon(u) = d_m u$ admits a unique positive solution K_ϵ. Moreover,

$$0 < K - K_\epsilon = \frac{\mu}{d_m}\big[b(K) - b^-_\epsilon(K_\epsilon)\big] = \frac{\mu}{d_m}\big[b(K) - b(K+\epsilon)\big] \leqslant \kappa\epsilon,$$

where $\kappa := \frac{\mu}{d_m} \max_{u\in[0,K+1]} |b'(u)|$. Let $u^-(t)$ be the solution of the following problem:

$$\begin{cases} \frac{du^-(t)}{dt} = -d_m u^-(t) + \mu b^-_\epsilon(u^-(t-\tau)),\ t > t_1 + \tau, \\ u^-(s) = \delta e^{-d_m(t_1+\tau)},\ s \in [t_1, t_1+\tau]. \end{cases}$$

Note that $K+\epsilon > u(i,j,s;\varphi) \geqslant \delta e^{-d_m(t_1+\tau)} = u^-(s)$ for any $s \in [t_1, t_1+\tau]$, $(i,j) \in \Omega$ and $\varphi \in \mathscr{C}^+_{\delta,M}$. Similar to the proof of Theorem 3.1, we can easily prove that

$$u^-(t) \leqslant u(i,j,t;\varphi) < K+\epsilon \text{ for any } t \geqslant t_1 \text{ and } (i,j) \in \Omega.$$

Since $K_\epsilon < K+\epsilon$, it is easy to show that $\lim_{t\to\infty} u^-(t) = K_\epsilon$ by the similar method used in the previous paragraph. Then there exists $t_2 > t_1$ such that $u^-(t) > K_\epsilon - \epsilon \geqslant K-(\kappa+1)\epsilon$ for any $t \geqslant t_2$ and $(i,j) \in \Omega$. Therefore,

$$K-(\kappa+1)\epsilon < u(i,j,t;\varphi) < K+\epsilon \text{ for any } t \geqslant t_2,\ (i,j) \in \Omega \text{ and } \varphi \in \mathscr{C}^+_{\delta,M}.$$

This completes the proof. □

3.2.2 *The case* $K > u_{\max}$.

To obtain the global attractivity of K in this case, we further impose the following assumptions.

(Q) $ub(u)$ is strictly increasing in $u \in \left(0, \frac{\mu}{d_m} b(u_{\max})\right]$.

(Q)′ $\frac{\mu}{d_m} b(u) \begin{cases} < 2K-u, & \text{if } u \in [u_{\max}, K), \\ \geqslant 2K-u, & \text{if } u \in [K, 2K]. \end{cases}$

Theorem 3.6 *Assume that* (A$_1$), (A$_2$)′ *and* (A$_3$) *hold and* $K > u_{\max}$. *Assume further that*

$$\frac{\mu}{d_m} b\big(\mu b(u_{\max})/d_m\big) > u_{\max} \text{ and (Q) or (Q)}' \text{ holds.} \tag{3.9}$$

Then, for any $\delta > 0$ *and* $M > 0$,

$$\lim_{t\to\infty} \|u(\cdot,t;\varphi) - K\| = 0 \text{ uniformly for } \varphi \in \mathscr{C}^+_{\delta,M}.$$

Proof Let $V_1(t)$ be the solution of the problem of equation (3.7) and $v_1(t)$ be the solution of the following problem

$$\begin{cases} \frac{dv_1(t)}{dt} = -d_m v_1(t) + \mu \min\{b(v_1(t-\tau)), b(V_1(t-\tau))\},\ t > \tau, \\ v_1(s) = \delta e^{-d_m\tau},\ s \in [0,\tau]. \end{cases} \tag{3.10}$$

Since $b(u_{\max}) \geqslant b(u)$ for all $u \geqslant 0$, we have

$$V_1(\tau) \geqslant v_1(\tau) \text{ and } \frac{dV_1(t)}{dt} + d_m V_1(t) \geqslant \frac{dv_1(t)}{dt} + d_m v_1(t),\ t > \tau.$$

It is easy to prove that $0 < v_1(t) \leqslant V_1(t)$ for all $t > \tau$. Moreover, it is not difficult to verify that v_1 and V_1 are a pair of sub- and super-solutions of equation (1.7). Thus, we have

$$0 < v_1(t) \leqslant u(i,j,t;\varphi) \leqslant V_1(t) \tag{3.11}$$

for any $(i,j,t) \in \Omega \times [0,+\infty)$ and $\varphi \in \mathscr{C}^+_{\delta,M}$. Similar to the proof of [26, Theorem 3.3], we can prove that

$$\lim_{t\to\infty} v_1(t) = \frac{\mu}{d_m} b\big(\mu b(u_{\max})/d_m\big).$$

By our assumptions, there exists $T_2 > 0$ such that

$$u_{\max} < \frac{1}{2}\Big[\frac{\mu}{d_m} b\big(\mu b(u_{\max})/d_m\big) + u_{\max}\Big] \leqslant v_1(t) \leqslant u(i,j,t;\varphi) \leqslant V_1(t)$$

for any $(i,j,t) \in \Omega \times [T_2,+\infty)$ and $\varphi \in \mathscr{C}^+_{\delta,M}$. Let

$$\delta_1 = \frac{1}{2}\Big[\frac{\mu}{d_m} b\big(\mu b(u_{\max})/d_m\big) + u_{\max}\Big].$$

We now construct a sequence of pairs of sub- and super-solutions of equation (1.7):

$$\begin{cases} \frac{dv_n(t)}{dt} = -d_m v_n(t) + \mu b(V_{n-1}(t-\tau)), \ t > T_2 + \tau, \\ \frac{dV_n(t)}{dt} = -d_m V_n(t) + \mu b(v_{n-1}(t-\tau)), \ t > T_2 + \tau, \\ v_n(s) = \delta_1, \ V_n(s) = \bar{K}, \ s \in [T_2, T_2+\tau], \end{cases}$$

where $\bar{K}$ is given by Theorem 2.1. Using Lemma 3.4 and a similar argument to that in Wang and Li [26, Theorem 3.3] and Kyrychko *et al.* [13, Theorem 5.3], we can show that

$$\begin{aligned} v_1(t) \leqslant \cdots \leqslant v_{n-1}(t) \leqslant v_n(t) < K, \ u(i,j,t;\varphi) \\ < V_n(t) \leqslant V_{n+1}(t) \leqslant \cdots \leqslant V_1(t) \end{aligned} \tag{3.12}$$

for $t > T_2 + \tau$.

By an inductive argument, $\lim_{t\to\infty} v_n(t)$ and $\lim_{t\to\infty} V_n(t)$ exist. Set $v_n^* = \lim_{t\to\infty} v_n(t)$ and $V_n^* = \lim_{t\to\infty} V_n(t)$. Then,

$$\mu b(V_{n-1}^*) = d_m v_n^* \text{ and } \mu b(v_{n-1}^*) = d_m V_n^*.$$

Define $v^* = \lim_{n\to\infty} v_n^*$ and $V_n^* = \lim_{n\to\infty} V_n^*$. Then we have

$$\mu b(V^*) = d_m v^* \text{ and } \mu b(v^*) = d_m V^*.$$

Suppose that (Q) holds. Since $\lim_{t\to\infty} V_1(t) = \frac{\mu}{d_m} b(u_{\max})$, we have $v^* \leqslant K \leqslant V^* \leqslant \frac{\mu}{d_m} b(u_{\max})$. Note that $\mu V^* b(V^*) = d_m v^* V^* = \mu v^* b(v^*)$. Then it must be $v^* = K = V^*$.

On the other hand, if (Q)$'$ holds, consider two curves $U = \frac{\mu}{d_m} b(u)$ and $u = \frac{\mu}{d_m} b(U)$ in the (u,U)-plane. Conditions $(A_2)'$, (A_3) and (Q)$'$ imply that

$$\tfrac{\mu}{d_m} b(u) < 2K - u \text{ for } u \in [0,K), \text{ and } \tfrac{\mu}{d_m} b(u) \geqslant 2K - u \text{ for } u \in [K,+\infty).$$

Since the curve $u = \frac{\mu}{d_m} b(U)$ is the reflection of the curve $U = \frac{\mu}{d_m} b(u)$ about the line $U = u$ and the line $U = 2K - u$ is symmetric with respect to the line $U = u$, the two curves $u = \frac{\mu}{d_m} b(U)$ and $U = \frac{\mu}{d_m} b(u)$ have only one positive intersection point (K,K). Hence, we have $v^* = K = V^*$. It then follows from equation (3.12) that $\lim_{t\to\infty} \|u(\cdot,t;\varphi) - K\| = 0$ uniformly for $\varphi \in \mathscr{C}^+_{\delta,M}$. This completes the proof. □

When $K > u_{\max}$, if the condition (3.9) does not hold, then we can prove that system (1.7) is uniformly persistent. For convenience, we define

$$\underline{b}(u) = \begin{cases} \min_{v\in[u,K_0]} b(v), & u \in \left[0, K_0\right], \\ b(u), & u > K_0, \end{cases}$$

where $K_0 = \frac{\mu}{d_m} b\left(u_{\max}\right) + 1$. It is clear that there exists $K_* \in (0, K)$ such that $\mu\underline{b}(K_*) = d_m K_*$, $\mu\underline{b}(u) > d_m u$ for $u \in (0, K_*)$ and $\mu\underline{b}(u) < d_m u$ for $u > K_*$. Moreover, $b(u) \geqslant \underline{b}(u)$ for all $u \geqslant 0$.

Theorem 3.7 *Assume that* (A_1), $(A_2)'$ *and* (A_3) *hold and* $K > u_{\max}$. *Then, for any* $\varphi \in \mathscr{C}^+$ *with* $\inf_{(i,j)\in\Omega} \varphi(i, j, 0) > 0$,

$$K_* \leqslant \liminf_{t\to\infty} \inf_{(i,j)\in\Omega} u(i, j, t; \varphi) \leqslant \limsup_{t\to\infty} \sup_{(i,j)\in\Omega} u(i, j, t; \varphi) \leqslant \frac{\mu}{d_m} b\left(u_{\max}\right).$$

Proof Let $V_0(t)$ and $v_0(t)$ be the solutions of the following problems:

$$\begin{cases} \frac{dV_0(t)}{dt} = -d_m V_0(t) + \mu b(u_{\max}), \ t > \tau, \\ V_0(s) = \max\left\{\mu b(u_{\max})/d_m, \sup_{(i,j,r)\in\Omega\times[-\tau,0]} \varphi(i, j, r)\right\}, \ s \in [0, \tau], \end{cases}$$

and

$$\begin{cases} \frac{dv_0(t)}{dt} = -d_m v_0(t) + \mu \min\left\{b(v_0(t-\tau)), b(V_0(t-\tau))\right\}, \ t > \tau, \\ v_0(s) = \min\left\{K_*, \ e^{-d_m\tau} \inf_{(i,j)\in\Omega} \varphi(i, j, 0)\right\}, \ s \in [0, \tau], \end{cases}$$

respectively. We can verify that v_0 and V_0 are a pair of sub- and super-solutions of equation (1.7) and it follows from Theorem 2.1 that $v_0(t) \leqslant u(i, j, t; \varphi) \leqslant V_0(t)$ for $(i, j, t) \in \Omega \times [0, \tau]$. Using Lemma 3.4, we obtain

$$v_0(t) \leqslant u(i, j, t; \varphi) \leqslant V_0(t) \text{ for } (i, j, t) \in \Omega \times [\tau, \infty). \tag{3.13}$$

It is clear that $\lim_{t\to\infty} V_0(t) = \mu b(u_{\max})/d_m$. To prove the assertion of this theorem, it suffices to show that $\liminf_{t\to\infty} v_0(t) \geqslant K_*$. From equation (3.13), there exists $T_3 > 0$ such that $0 < v_0(t) \leqslant \mu b(u_{\max})/d_m + \frac{1}{2}$ for $t \geqslant T_3$. Consider the following problem:

$$\begin{cases} \frac{d\tilde{v}(t)}{dt} = -d_m\tilde{v}(t) + \mu\underline{b}(\tilde{v}(t-\tau)), \ t > T_3 + \tau, \\ \tilde{v}(s) = \min\left\{K_*, \ \min_{t\in[T_3,T_3+\tau]} v_0(t)\right\}, \ s \in [T_3, T_3 + \tau]. \end{cases}$$

Noting that $b(u) \geqslant \underline{b}(u)$ for all $u \geqslant 0$ and $\underline{b}(u)$ is non-decreasing on $[0, K_0]$, it is easy to show that

$$\lim_{t\to\infty} \tilde{v}(t) = K_* \text{ and } v_0(t) \geqslant \tilde{v}(t) \text{ for } t > T_3 + \tau.$$

Thus, $\liminf_{t\to\infty} v_0(t) \geqslant K_*$. This completes the proof. $\square$

4 Travelling waves and spreading speed

In this section, we consider the travelling waves and spreading speed. In addition to (A_1) and (A_3), we also need the following strictly sublinear assumption:

(B_1) $b''(0)$ exists and $b(\gamma u) > \gamma b(u)$ for $\gamma \in (0,1)$ and $u \in (0,+\infty)$.

From (B_1), we see that $b(u) \leqslant b'(0)u$ for all $u \geqslant 0$. Furthermore, this fact together with the assumption (A_3) implies that $\mu b'(0) \geqslant \mu b(\frac{K}{2})\frac{2}{K} > d_m$.

4.1 Preliminaries

We first state some results on spreading speed and travelling waves for equation (1.7) with a monotone growth function b:

(B_2) $b'(u) \geqslant 0$ for all $u \in [0,K]$.

The definitions of the spreading speed and travelling waves of equation (1.7) are described as follows, see e.g. [4, 16, 24].

Definition 4.1 *A travelling wave solution of equation (1.7) refers to a solution with the form $u(i,j,t) = \Phi_i(j+ct)$, $(i,j) \in \Omega$, where $c > 0$ is the wave speed. Moreover, we say that $c_m > 0$ is the minimal wave speed if system* (1.7) *has a travelling wave with speed c if and only if its speed $c \geqslant c_m$.*

Definition 4.2 *A function $u : \Omega \times \mathbb{R}_+ \to \mathbb{R}_+$ is said to have a spreading speed $c_* > 0$ if there exists a constant $\varepsilon > 0$ such that*

$$\lim_{t\to\infty, |j|\geqslant tc} u(i,j,t) = 0 \text{ for all } c > c_*, \text{ and } \lim_{t\to\infty, |j|\leqslant tc} u(i,j,t) \geqslant \varepsilon \text{ for any } c \in (0, c_*).$$

All these limits are uniformly for $i \in [1,N]_{\mathbb{Z}}$.

According to Definition 4.2, we see that c_* and ε depend on the function u. However, if all solutions of a system with initial functions having compact supports share the same c_* and ε, then we call such c_* the spreading speed of the system.

For the sake of simplicity, we write $\mathbf{0} = (0,\dots,0) \in \mathbb{R}^N$ and $\mathbf{K} = (K,\dots,K) \in \mathbb{R}^N$. Letting $\xi = j+ct$, then the profile function of the travelling wave solution of equation (1.7) is $\Phi(\xi) = (\Phi_1(\xi),\dots,\Phi_N(\xi))$. It is obvious that the profile function $\Phi(\xi)$ of the travelling wave solution satisfies the following equation:

$$\begin{cases} c\Phi_i'(\xi) = D_m[\Phi_{i+1}(\xi) + \Phi_{i-1}(\xi) - 2\Phi_i(\xi)] \\ \qquad\qquad + D_m[\Phi_i(\xi+1) + \Phi_i(\xi-1) - 2\Phi_i(\xi)] - d_m\Phi_i(\xi) \\ \qquad\qquad + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G_1(i,i_1,\alpha)\beta_\alpha(j_1) b\big(\Phi_{i_1}(\xi - j_1 - c\tau)\big), \\ \Phi_0(\xi) = \Phi_1(\xi),\ \Phi_N(\xi) = \Phi_{N+1}(\xi). \end{cases} \tag{4.1}$$

Since $\sum_{j_1=-\infty}^{+\infty} \beta_\alpha(j_1)e^{-\lambda j_1} = e^{2\alpha(\cosh\lambda - 1)}$ (see Weng [28, Lemma 2.1]), it is clear that the characteristic problem for equation (4.1) with respect to the trivial equilibrium can be represented by

$$\begin{cases} M(\lambda)v_i = D_m[v_{i+1} + v_{i-1} - 2v_i] + [2D_m(\cosh\lambda - 1) - d_m]v_i \\ \qquad + \mu b'(0)e^{-M(\lambda)\tau}e^{2\alpha(\cosh\lambda-1)}\sum_{i_1=1}^{N} G_1(i, i_1, \alpha)v_{i_1}, \\ \qquad i \in [1, N]_{\mathbb{Z}},\ \lambda \in \mathbb{R}, \\ v_0 = v_1,\ v_N = v_{N+1}. \end{cases} \tag{4.2}$$

From Weng [28], we know that equation (4.2) has a positive principal eigenvalue $M(\lambda)$ with strictly positive eigenfunction $v(\lambda) = \{v_i(\lambda)\}_{i\in[1,N]_{\mathbb{Z}}}$. Moreover, there exist $c_* > 0$ and $\lambda_* > 0$ such that

$$c_* = \frac{M(\lambda_*)}{\lambda_*} = \inf_{\lambda>0}\frac{M(\lambda)}{\lambda}, \tag{4.3}$$

and for any $c > c_*$, there exists a unique $\lambda_1 := \lambda_1(c) \in (0, \lambda_*)$ such that $M(\lambda_1) = c\lambda_1$, and $M(\lambda) < c\lambda$ for any $\lambda \in (\lambda_1, \lambda_*)$.

Under the assumptions (A_1), (A_3), (B_1) and (B_2), Weng [28] showed that the number c_* is the minimal wave speed of monotone travelling waves connecting $\mathbf{0}$ and $\mathbf{K}$ as well as the spreading speed of equation (1.7) by employing Liang and Zhao's theory for monotone semiflows (see Liang and Zhao [16]). In fact, using the technique of monotone iteration schemes coupled with the method of sub-super solutions, one can further obtain the asymptotic behaviour of the wave tail for travelling wave fronts as $c > c_*$. The following result summarizes the above stated results which will be used in the coming subsections for proving the existence and asymptotic behaviour of the travelling wave solutions.

Proposition 4.3 ([28, Theoerems 5.2–5.3]) *Assume that* (A_1), (A_3), (B_1) *and* (B_2) *are satisfied. Then the following statements hold.*

(1) *For each* $c > c_*$, *system* (1.7) *has a non-increasing travelling wave solution* $\Phi(\xi) = (\Phi_1(\xi), \ldots, \Phi_N(\xi))$, $\xi = j + ct$ *satisfying* $\Phi(-\infty) = \mathbf{0}$ *and* $\Phi(+\infty) = \mathbf{K}$. *Moreover,*

$$\Phi'(\xi) \gg \mathbf{0},\ \lim_{\xi\to-\infty}\Phi(\xi)e^{-\lambda_1(c)\xi} = v(\lambda_1(c)) \quad \textit{and} \quad \Phi(\xi) \leqslant e^{\lambda_1(c)\xi}v(\lambda_1(c))$$

for all $\xi \in \mathbb{R}$.

(2) *For any* $c \in (0, c_*)$, *system* (1.7) *has no travelling wave solution* $\Phi(\xi)$ *connecting* $\mathbf{0}$ *and* $\mathbf{K}$.

(3) *For any* $c > c_*$, *if* $\varphi \in \mathscr{C}_{[0,K]}$ *with* $0 \leqslant \varphi \ll K$, *and* $\varphi(i, j, \cdot) = 0$ *for* $i \in [1, N]_{\mathbb{Z}}$ *and* j *outside a bounded interval, then* $\lim_{t\to\infty,|j|\geqslant ct} u(i, j, t; \varphi) = 0$ *uniformly for* $i \in [1, N]_{\mathbb{Z}}$.

(4) *For any* $0 < c < c_*$, *if* $\varphi \in \mathscr{C}_{[0,K]}$ *with* $\varphi(\cdot, 0) \not\equiv 0$, *then* $\lim_{t\to\infty,|j|\leqslant ct} u(i, j, t; \varphi) = K$ *uniformly for* $i \in [1, N]_{\mathbb{Z}}$.

Remark 4.4 From equations (4.2) and (4.3), it is easy to see that the spreading speed c_* depends on the maturation delay τ. Moreover, from equation (4.2), we can see that $M(\lambda)$ is decreasing with respect to τ on $[0, \infty)$. Thus, due to the definition of c_*, it is a decreasing function of τ, that is, the maturation time delay will slow the spreading speed. A similar phenomenon has been observed by some researchers for various spatially continuous reaction–diffusion equations with delay, see e.g. Zou [36], Li *et al.* [14] and Ou and Wu [19].

In what follows, we shall extend the results in Proposition 4.3 to the case of non-monotone growth function b. We replace the monotone condition (B_2) by the following assumption.

$(B_2)'$ There exist constants $K^{\pm}$ with $K^+ \geqslant K \geqslant K^- > 0$ and two continuous and piecewise continuously differentiable functions $b^{\pm} : [0, K^+] \to \mathbb{R}_+$ such that

(i) $\mu b^{\pm}(K^{\pm}) = d_m K^{\pm}$ and $\mu b^{\pm}(u) > d_m u$ for $u \in (0, K^{\pm})$;

(ii) $b'(0) = (b^{\pm})'(0)$, $(b^{\pm})''(0)$ exist, $b^{\pm}(u)$ are non-decreasing on $[0, K^+]$ and

$$0 \leqslant b^-(u) \leqslant b(u) \leqslant b^+(u) \leqslant b'(0)u \text{ for } u \in [0, K^+].$$

According to the assumption $(B_2)'$, we introduce two auxiliary monotone equations to "trap" the equation (1.7):

$$\begin{cases} \frac{du(i,j,t)}{dt} = D_m \Delta u(i,j,t) - d_m u(i,j,t) \\ \qquad + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i, i_1, j, j_1, \alpha) b^-\big(u(i_1, j_1, t-\tau)\big), \\ u(0,j,t) = u(1,j,t),\ u(N,j,t) = u(N+1,j,t), \end{cases} \tag{4.4}$$

and

$$\begin{cases} \frac{du(i,j,t)}{dt} = D_m \Delta u(i,j,t) - d_m u(i,j,t) \\ \qquad + \mu \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G(i, i_1, j, j_1, \alpha) b^+\big(u(i_1, j_1, t-\tau)\big), \\ u(0,j,t) = u(1,j,t),\ u(N,j,t) = u(N+1,j,t). \end{cases} \tag{4.5}$$

For simplicity, we define $\mathbf{K}^{\pm} = (K^{\pm}, \ldots, K^{\pm}) \in \mathbb{R}^N$. Note that if b is non-decreasing on $[0, K]$, then $b^{\pm} = b$ and $K^{\pm} = K$. If there exists a number $u_{\max} > 0$ such that $b(u)$ is non-decreasing for $0 < u < u_{\max}$ and decreasing for $u > u_{\max}$, then $b^{\pm}(\cdot)$ can be constructed as follows:

$$b^+(u) := \max_{v \in [0,u]} b(v) \text{ and } b^-(u) := \min_{v \in [u, K^+]} b(v),\ u \in [0, K^+],$$

where $K^+ = \mu b(u_{\max})/d_m$.

In the following subsections, we always assume that (A_1), (A_3), (B_1) and $(B_2)'$ are satisfied.

4.2 Spreading speeds and non-existence of travelling waves

We shall consider the spreading speed and the non-existence of travelling waves for equation (1.7) with non-monotone growth function b. Similar to Theorem 2.1, it is easy to show that for any $\varphi \in \mathscr{C}_{[0,K^+]}$, equation (1.7) admits a unique solution $u(i,j,t;\varphi)$ on $[0, +\infty)$ such that $u(i,j,s;\varphi) = \varphi(i,j,s)$ and $0 \leqslant u(i,j,t;\varphi) \leqslant K^+$ for $(i,j) \in \Omega$, $s \in [-\tau, 0]$ and $t \geqslant 0$.

To obtain the spreading speed of equation (1.7) in the non-monotone case, we need to establish a comparison theorem for solutions to systems (1.7), (4.5) and (4.4). Its proof is similar to that of Zhao *et al.* [35, Lemma 4.2] and is omitted here.

Lemma 4.5 *Assume that* $\varphi, \varphi^+ \in \mathscr{C}_{[0,K^+]}$ *and* $\varphi^- \in \mathscr{C}_{[0,K^-]}$ *with*

$$\varphi^-(i,j,s) \leqslant \varphi(i,j,s) \leqslant \varphi^+(i,j,s) \text{ for } (i,j,s) \in \Omega \times [-\tau, 0].$$

Let $u^-(i,j,t;\varphi^-)$, $u(i,j,t;\varphi)$ *and* $u^+(i,j,t;\varphi^+)$ *be the unique solutions of systems* (4.4), (1.7) *and* (4.5) *through* φ^-, φ *and* φ^+, *respectively. Then,*

$$u^-(i,j,t;\varphi^-) \leqslant u(i,j,t;\varphi) \leqslant u^+(i,j,t;\varphi^+) \text{ for } (i,j) \in \Omega \text{ and } t \geqslant 0.$$

Applying the comparison Lemma 4.5, we have the following results on the spreading speed for system (1.7) with non-monotone growth function b.

Theorem 4.6 *The following statements hold:*

(1) *For any* $c > c_*$, *if* $\varphi \in \mathscr{C}_{[0,K^+]}$ *with* $0 \leqslant \varphi \ll K^+$, *and* $\varphi(i,j,\cdot) = 0$ *for* $i \in [1,N]_{\mathbb{Z}}$ *and* j *outside a bounded interval, then* $\lim_{t\to\infty,|j|\geqslant ct} u(i,j,t;\varphi) = 0$ *uniformly for* $i \in [1,N]_{\mathbb{Z}}$.

(2) *For any* $0 < c < c_*$, *if* $\varphi \in \mathscr{C}_{[0,K^+]}$ *with* $\varphi(\cdot,0) \not\equiv 0$, *then*

$$K^- \leqslant \liminf_{t\to\infty,|j|\leqslant ct} u(i,j,t;\varphi) \leqslant \limsup_{t\to\infty,|j|\leqslant ct} u(i,j,t;\varphi) \leqslant K^+$$

uniformly for $i \in [1,N]_{\mathbb{Z}}$. *Moreover, if, in addition, one of the following holds:*

(i) $(\mathrm{A}_2)'$ *holds and* $K \leqslant u_{\max}$;

(ii) $b(u)/u$ *is strictly decreasing for* $u \in [K^-, K^+]$ *and* $b(u)$ *has the property (P) that for any* $u, v \in [K^-, K^+]$ *satisfying* $v \leqslant K \leqslant u$, $d_m v \geqslant \mu b(u)$ *and* $d_m u \leqslant \mu b(v)$, *we have* $u = v$,

then $\lim_{t\to\infty,|j|\leqslant ct} u(i,j,t;\varphi) = K$ *uniformly for* $i \in [1,N]_{\mathbb{Z}}$.

Proof For any $\varphi \in \mathscr{C}_{[0,K^+]}$, define $\tilde{\varphi} \in \mathscr{C}_{[0,K^-]}$ by $\tilde{\varphi}(i,j,t) = \min\{\varphi(i,j,t), K^-\}$. It follows from Lemma 4.5 that

$$u^-(i,j,t;\tilde{\varphi}) \leqslant u(i,j,t;\varphi) \leqslant u^+(i,j,t;\varphi) \text{ for } (i,j) \in \Omega \text{ and } t \geqslant 0.$$

Since $b'(0) = (b^{\pm})'(0)$, it is clear that equation (4.2) is also the characteristic problem of equations (4.5) and (4.4) with respect to the trivial equilibrium 0. Further, by Proposition 4.3, we see that c_* is the spreading speed of solutions for both auxiliary quasi-monotone systems (4.4) and (4.5), which together with the above inequalities implies that c_* satisfies the statement (1) and the first part of (2). That is, c_* is the spreading speed of system (1.7).

Now, we prove the upward convergence in the property of spreading speeds. In the case where (i) holds, we see that $b^{\pm}(\cdot) = b(\cdot)$ and $K^{\pm} = K$, and the upward convergence follows.

In the case where (ii) holds, we shall use a fluctuation method which was developed by Thieme and Zhao [23] and used in [4, 5, 10] to prove the upward convergence of the spreading speed for various non-monotone systems. Since the process is very similar, we only sketch the outline here. Define $h \in C(\mathbb{R}_+^2, \mathbb{R})$ by

$$h(u,v) = \begin{cases} \min_{w\in[u,v]} b(w), & \text{if } u \leqslant v, \\ \max_{w\in[v,u]} b(w), & \text{if } v \leqslant u. \end{cases}$$

Clearly, $h(u,v)$ is non-decreasing in u and non-increasing in v, and $h(u,u) = b(u)$. For simplicity, we denote $u(i,j,t;\varphi)$ by $u(i,j,t)$. For $\beta \in (0,c_*)$, we set

$$V_*(\beta) = \min_{i=1,\ldots,N} \liminf_{t\to\infty,|j|\leqslant\beta t} u(i,j,t) \text{ and } V^*(\beta) = \max_{i=1,\ldots,N} \limsup_{t\to\infty,|j|\leqslant\beta t} u(i,j,t).$$

Then there exists a sequence $\{t_j\} \subset (0,\infty)$ such that $|j| \leqslant \beta t_j$, $t_j \to \infty$ as $j \to \infty$ and $\lim_{j\to\infty} u(i,j,t_j) = V_*(\beta)$ for some $i \in \{1,\ldots,N\}$.

Rewrite equation (1.7) in the following way:

$$\begin{aligned} u(i,j,t) = e^{-\kappa t}u(i,j,0) + D_m \int_{-t}^{0} e^{\kappa s}[u(i+1,j,t+s) \\ + u(i-1,j,t+s) + u(i,j+1,t+s) + u(i,j-1,t+s)]ds \\ + \mu \int_{-t}^{0} e^{\kappa s} \sum_{i_1=1}^{N} \sum_{j_1=-\infty}^{+\infty} G_1(i,i_1,\alpha)\beta_\alpha(j_1) \\ \times h\big((u(i_1,j-j_1,s-\tau),(u(i_1,j-j_1,t+s-\tau)\big)ds, \end{aligned} \tag{4.6}$$

where $\kappa = 4D_m + d_m$. Let $\gamma \in (\beta, c_*)$. Then, for any given $s \in \mathbb{R}$ and $k \in \mathbb{Z}$, there holds $|j-k| \leqslant \gamma(t_j+s)$ when j is sufficiently large. Using Fatou's lemma, it then follows from equation (4.6) that

$$V_*(\beta) \geqslant \frac{4D_m}{\kappa} V_*(\gamma) + \frac{\mu}{\kappa} h(V_*(\gamma), V^*(\gamma)).$$

Set

$$W_*(c,\gamma) = \inf_{c<\beta<\gamma} V_*(\beta) \text{ and } W^*(c,\gamma) = \sup_{c<\beta<\gamma} V^*(\beta).$$

Then, we obtain

$$W_*(c,\gamma) \geqslant \frac{4D_m}{\kappa} W_*(c,\gamma) + \frac{\mu}{\kappa} h(W_*(c,\gamma), W^*(c,\gamma)),$$

which implies that

$$W_*(c,\gamma) \geqslant \frac{\mu}{d_m} h(W_*(c,\gamma), W^*(c,\gamma)). \tag{4.7}$$

Similarly, we have

$$W^*(c,\gamma) \leqslant \frac{\mu}{d_m} h(W^*(c,\gamma), W_*(c,\gamma)). \tag{4.8}$$

By the definition of function h, we can find $u, v \in [W_*(c,\gamma), W^*(c,\gamma)] \subset [K^-, K^+]$ such that

$$h(W_*(c,\gamma), W^*(c,\gamma)) = b(u) \text{ and } h(W^*(c,\gamma), W_*(c,\gamma)) = b(v).$$

Hence,

$$\frac{\mu}{d_m} b(u) \leqslant W_*(c,\gamma) \leqslant u, v \leqslant W^*(c,\gamma) \leqslant \frac{\mu}{d_m} b(v), \tag{4.9}$$

which yields that

$$\frac{\mu}{d_m}\frac{b(u)}{u} \leqslant 1 = \frac{\mu}{d_m}\frac{b(K)}{K} \leqslant \frac{\mu}{d_m}\frac{b(v)}{v}.$$

This, together with the strict monotonicity of $b(u)/u$ on $[K^-, K^+]$, implies that $v \leqslant K \leqslant u$. By equation (4.9) and the property (P), we obtain $u = v$. Hence, $u = v = K$. It then follows from equation (4.9) that $W_*(c,\gamma) = W^*(c,\gamma) = u = v = K$. Consequently,

$$K = W_*(c,\gamma) \leqslant V_*(\gamma) \leqslant V^*(\gamma) \leqslant W^*(c,\gamma) = K,$$

which implies that $\lim_{t\to\infty, |j|\leqslant ct} u(i,j,t;\varphi) = K$ uniformly for $i \in [1,N]_{\mathbb{Z}}$. This completes the proof. □

Remark 4.7 As pointed out by Fang *et al.* [4], Fang and Zhao [5] and Hsu and Zhao [10], either of the following two conditions is sufficient for (P) to hold:

(P_1) $ub(u)$ is strictly increasing for $u \in [K^-, K^+]$, or

(P_2) $b(u)$ is non-increasing for $u \in (K, K^+]$ and $b(\frac{\mu}{d_m} b(u))/u$ is strictly decreasing for $u \in (0, K]$.

The non-existence of travelling waves is a consequence of the result on the spreading speed. Its proof is similar to that of Thieme and Zhao [24, Theorem 3.5], see also Wang [25, Theorem 2.1]. We omit it here.

Theorem 4.8 *For any* $0 < c < c_*$, *equation* (1.7) *does not admit a travelling wave solution* $\Phi(\xi)$ *with* $\liminf_{\xi\to\infty} \Phi(\xi) \gg \mathbf{0}$ *and* $\Phi(-\infty) = \mathbf{0}$.

4.3 Existence of travelling waves

In this Subsection, we shall prove the existence of the travelling waves (Φ, c) for system (1.7) with a non-monotone growth function b and $c \geqslant c_*$. For the case $c > c_*$, we shall employ the Schauder's fixed-point theorem and construct a suitable profile set in a Banach space by using the travelling fronts of the lower auxiliary system (4.4). Such a construction of the profile set has the merit that we can obtain the asymptotic behaviour of the travelling waves at $-\infty$ (see equation (4.10) below).

Note that system (4.4) has the characteristic problem (4.2). From Proposition 4.3, we have the following result on the travelling fronts for the lower auxiliary system (4.4).

Proposition 4.9 *For any $c > c_*$, system* (4.4) *has a non-increasing travelling wave solution $\Phi_c^-(\xi)$ which satisfies $\Phi_c^-(-\infty) = \mathbf{0}$ and $\Phi_c^-(+\infty) = \mathbf{K}^-$. Moreover,*

$$\frac{d}{d\xi}\Phi_c^-(\xi) \gg \mathbf{0}, \ \lim_{\xi\to-\infty} \Phi_c^-(\xi)e^{-\lambda_1(c)\xi} = v(\lambda_1(c)) \ \ \textit{and} \ \ \Phi_c^-(\xi) \leqslant e^{\lambda_1(c)\xi}v(\lambda_1(c))$$

for all $\xi \in \mathbb{R}$.

Now, we state the main result in this subsection.

Theorem 4.10 *For each $c > c_*$, equation* (1.7) *admits a travelling wave $\Phi(\xi) = (\Phi_1(\xi),\ldots,\Phi_N(\xi))$ such that $\mathbf{0} \ll \Phi(\xi) \leqslant \mathbf{K}^+$ for $\xi \in \mathbb{R}$, $\Phi(-\infty) = \mathbf{0}$,*

$$\mathbf{K}^- \leqslant \liminf_{\xi\to\infty} \Phi(\xi) \leqslant \limsup_{\xi\to\infty} \Phi(\xi) \leqslant \mathbf{K}^+,$$

and

$$\lim_{\xi\to-\infty} \Phi(\xi)e^{-\lambda_1(c)\xi} = v(\lambda_1(c)). \tag{4.10}$$

Moreover, if, in addition, one of the following holds:

(i) $(\mathrm{A}_2)'$ *holds and $K \leqslant u_{\max}$;*

(ii) *$b(u)/u$ is strictly decreasing for $u \in [K^-,K^+]$ and $b(u)$ has the property (P),*

then $\lim_{\xi\to\infty} \Phi(\xi) = \mathbf{K}$.

Proof The proof of the first assertion is similar to those of [17, Theorem 1.1] and [10, Theorem 3.1]. So, we only sketch the outline in the following three steps.

Step 1. Define the operator $H = (H_1,\ldots,H_N) : C(\mathbb{R},[0,K^+]^N) \to C(\mathbb{R},\mathbb{R}^N)$ by

$$\begin{aligned} H_i[\Psi](\xi) := {} & D_m[\psi_{i+1}(\xi) + \psi_{i-1}(\xi) + \psi_i(\xi+1) + \psi_i(\xi-1)] \\ & + \mu\sum_{i_1=1}^{N}\sum_{j_1=-\infty}^{+\infty} G_1(i,i_1,\alpha)\beta_\alpha(j_1)b\big(\psi_{i_1}(\xi - j_1 - c\tau)\big). \end{aligned} \tag{4.11}$$

We also define H^+ and H^- by replacing b with b^+ and b^- in equation (4.11), respectively. Since $b^\pm(u)$ are non-decreasing for all $u \in [0,K^+]$, $H^\pm(\cdot)$ are non-decreasing in $C(\mathbb{R},[0,K^+]^N)$. Furthermore, we define $T = (T_1,\ldots,T_N) : C(\mathbb{R},[0,K^+]^N) \to C(\mathbb{R},\mathbb{R}^N)$ by

$$T_i(\Psi)(\xi) = \frac{1}{c}\int_{-\infty}^{\xi} e^{-\frac{\mu_0}{c}(\xi-s)}H_i(\Psi)(s)ds, \tag{4.12}$$

where $\mu_0 = 4D_m + d_m$. Similarly, we define T^+ and T^- by replacing H with H^+ and H^- in equation (4.12), respectively. It is clear that $T^\pm(\Psi)$ are non-decreasing in $C(\mathbb{R},[0,K^+]^N)$, and

$$T^-(\Psi) \leqslant T(\Psi) \leqslant T^+(\Psi) \text{ for any } \Psi \in C(\mathbb{R},[0,K^+]^N).$$

Step 2. Define $\tilde{\Phi}^+(\xi) = (\tilde{\Phi}_1^+(\xi), \dots, \tilde{\Phi}_N^+(\xi))$ by

$$\tilde{\Phi}_i^+(\xi) = \min\{K^+, v_i(\lambda_1(c))e^{\lambda_1(c)\xi}\},\ i = 1, \dots, N.$$

Using the assumption $b^+(w) \leqslant b'(0)w$ for all $w \in [0, K^+]$, it is easy to show that $T^+(\tilde{\Phi}^+)(\xi) \leqslant \tilde{\Phi}^+(\xi)$ for $\xi \in \mathbb{R}$.

For a given $\lambda \in (0, \lambda_1(c))$, let

$$X_\lambda = \left\{\Psi = (\psi_1, \dots, \psi_N) \in C(\mathbb{R}, \mathbb{R}^N) : \sup_{\xi \in \mathbb{R}} \|\Psi(\xi)\| e^{-\lambda\xi} < +\infty\right\}$$

with $\| \Psi \|_\lambda = \sup_{\xi\in\mathbb{R}} \|\Psi(\xi)\|e^{-\lambda\xi}$. Then $(X_\lambda, \|\cdot\|_\lambda)$ is a Banach space. It is easy to see that $\Phi_c^-, \tilde{\Phi}^+ \in X_\lambda$.

Define a subset $\mathbf{Y} \subset X_\lambda$ by $\mathbf{Y} = \{\Psi \in X_\lambda :\ \Phi_c^- \leqslant \Psi \leqslant \tilde{\Phi}^+\}$. Then, $\mathbf{Y}$ is a convex and closed subset of X_λ and for any $\Psi \in \mathbf{Y}$,

$$\Phi_c^- = T^-(\Phi_c^-) \leqslant T^-(\Psi) \leqslant T(\Psi) \leqslant T^+(\Psi) \leqslant T^+(\tilde{\Phi}^+) \leqslant \tilde{\Phi}^+,$$

which implies that $T : \mathbf{Y} \to \mathbf{Y}$.

Step 3. We show that T is compact on $\mathbf{Y}$. We first show that T is continuous on $\mathbf{Y}$. For any $\Phi = (\phi_1, \dots, \phi_N)$, $\Psi = (\psi_1, \dots, \psi_N) \in \mathbf{Y}$, we have

$$\begin{aligned}
&|H_i(\Phi)(\xi) - H_i(\Psi)(\xi)|e^{-\lambda\xi} \\
&\leqslant D_m\big[|\phi_{i+1}(\xi) - \psi_{i+1}(\xi)| + |\phi_{i-1}(\xi) - \psi_{i-1}(\xi)|\big]e^{-\lambda\xi} \\
&\quad + D_m\big[|\phi_i(\xi+1) - \psi_i(\xi+1)| + |\phi_i(\xi-1) - \psi_i(\xi-1)|\big]e^{-\lambda\xi} \\
&\quad + \mu\sum_{i_1=1}^{N}\sum_{j_1=-\infty}^{+\infty} G_1(i, i_1, \alpha)\beta_\alpha(j_1) \\
&\qquad\qquad \times |b\big(\phi_{i_1}(\xi - j_1 - c\tau)\big) - b\big(\psi_{i_1}(\xi - j_1 - c\tau)\big)|e^{-\lambda\xi} \\
&\leqslant \|\Phi - \Psi\|_\lambda\Big[D_m(3 + e^\lambda) + \mu L_1\sum_{i_1=1}^{N}\sum_{j_1=-\infty}^{+\infty} G_1(i, i_1, \alpha)\beta_\alpha(j_1)e^{-\lambda j_1}\Big] \\
&=: L_2\|\Phi - \Psi\|_\lambda,\ i = 1, \dots, N,
\end{aligned}$$

where $L_1 = \max_{u\in[0,K^+]} |b'(u)|$, which implies that

$$|T_i(\Phi)(\xi) - T_i(\Psi)(\xi)|e^{-\lambda\xi} \leqslant \frac{L_2}{c\lambda + \mu_0}\|\Phi - \Psi\|_\lambda,\ i = 1, \dots, N.$$

Hence, T is continuous on $\mathbf{Y}$.

Next, we show that $T(\mathbf{Y})$ is compact X_λ. For any $\Psi \in \mathbf{Y}$ and $\xi \in \mathbb{R}$, it is easy to see that

$$|H_i(\Psi)(\xi)| \leqslant 4D_mK^+ + \mu\max_{u\in[0,K^+]}|b(u)| =: L_3,\ i = 1, \dots, N,$$

which implies that $|T_i(\Psi)(\xi)| \leqslant L_3/\mu_0,\ i = 1, \dots, N$. Noting that

$$T_i(\Psi)'(\xi) = -\frac{\mu_0}{c}T_i(\Psi)(\xi) + \frac{1}{c}H_i(\Psi)(\xi),$$

we have $|T_i(\Psi)'(\xi)| \leqslant 2L_3/c$, $i = 1, \ldots, N$. Therefore, $T(\mathbf{Y})$ is a family of uniformly bounded and equi-continuous functions on $\mathbb{R}$. Further, using the method as in Fang *et al.* [4] and Hsu and Zhao [10], we can show that $T(\mathbf{Y})$ is compact in X_λ.

Therefore, using the Schauder's fixed-point theorem, we know that the operator T has a fixed point Φ in $\mathbf{Y}$ which is a travelling wave solution of equation (1.7) for $c > c_*$. Since $\mathbf{0} \ll \Phi_c^-(\xi) \leqslant \Phi(\xi) \leqslant \tilde{\Phi}^+(\xi)$ for $\xi \in \mathbb{R}$, it is easy to see that $\mathbf{0} \ll \Phi(\xi) \leqslant \mathbf{K}^+$ for $\xi \in \mathbb{R}$. Moreover, $\Phi(-\infty) = \mathbf{0}$, $\lim_{\xi\to-\infty} \Phi(\xi)e^{-\lambda_1(c)\xi} = v(\lambda_1(c))$, and

$$\mathbf{K}^- \leqslant \liminf_{\xi\to\infty} \Phi(\xi) \leqslant \limsup_{\xi\to\infty} \Phi(\xi) \leqslant \mathbf{K}^+.$$

When $(A_2)'$ holds and $K \leqslant u_{\max}$, $b^\pm(\cdot) = b(\cdot)$ and $\mathbf{K}^\pm = \mathbf{K}$. Hence $\lim_{\xi\to\infty} \Phi(\xi) = \mathbf{K}$. In the case where (ii) holds, by using the upward convergence in the property of spreading speeds, the proof of the limit $\lim_{\xi\to\infty} \Phi(\xi) = \mathbf{K}$ is very similar to that of [10, Theorem 2.3], see also [4, Theorem 4.1]. We omit it here. This completes the proof. □

Using a limiting process, we can obtain the existence of travelling waves Φ^* with the minimal wave speed c_*. Moreover, we can show that $\Phi^*(-\infty) = \mathbf{0}$ and give some sufficient conditions to ensure the upward convergence of the minimal wave. In fact, we have the following result.

Theorem 4.11 *For $c = c_*$, equation (1.7) admits a nonconstant travelling wave solution $\Phi^* = (\Phi_1^*, \ldots, \Phi_N^*)$ such that $\Phi^*(-\infty) = \mathbf{0}$ and*

$$\mathbf{K}^- \leqslant \liminf_{\xi\to\infty} \Phi^*(\xi) \leqslant \limsup_{\xi\to\infty} \Phi^*(\xi) \leqslant \mathbf{K}^+. \tag{4.13}$$

Moreover, if, in addition, one of the following holds:

(i) $(A_2)'$ *holds and* $K \leqslant u_{\max}$*;*

(ii) $b(u)/u$ *is strictly decreasing for* $u \in [K^-, K^+]$ *and* $b(u)$ *has the property (P);*

then $\lim_{\xi\to\infty} \Phi(\xi) = \mathbf{K}$.

Proof Since $\sum_{j_1=-\infty}^{+\infty} \beta_\alpha(j_1) = 1$ and $\mu b'(0) > d_m$, there exists $M_1 > 0$ such that

$$\frac{b'(0)\mu + d_m}{2} \sum_{|j_1|\leqslant M_1} \beta_\alpha(j_1) - d_m > 0.$$

In addition, there exists $\delta_0 > 0$ such that

$$b(u) \geqslant \tfrac{b'(0)+d_m/\mu}{2} u =: \rho_1 u \text{ for all } u \in [0, \delta_0].$$

We first show that for any vector $\sigma \in \mathbb{R}^N$ with $\sigma \gg \mathbf{0}$, equation (1.7) admits a nonconstant travelling wave solution $\Phi^* = (\Phi_1^*, \ldots, \Phi_N^*)$ such that $\mathbf{0} \leqslant \Phi^*(\xi) \leqslant \mathbf{K}^+$ for $\xi \in \mathbb{R}$, and $\Phi^*(\xi) \leqslant \sigma$ for $\xi \leqslant M_1$. Choosing a sequence $\{c_j\} \subset (c_*, +\infty)$ such that $\lim_{j\to\infty} c_j = c_*$. According to Theorem 4.10, there exists a travelling wave $(\Phi^{(j)}, c_j)$ of equation (1.7) for each j such that

$$\mathbf{K}^- \leqslant \liminf_{\xi\to\infty} \Phi^{(j)}(\xi) \leqslant \limsup_{\xi\to\infty} \Phi^{(j)}(\xi) \leqslant \mathbf{K}^+.$$

Given any vector $\sigma \in \mathbb{R}^N$ with $\sigma \gg \mathbf{0}$. Since $\Phi^{(j)}(\xi+h)$, $h \in \mathbb{R}$, is also such a solution, $\Phi^{(j)}(-\infty) = \mathbf{0}$, we can assume that $\Phi^{(j)}(\xi) \leqslant \sigma$ for $\xi \leqslant M_1$. Similar to the proof of Theorem 4.10, we can prove that $\{\Phi^{(j)}(\xi)\}_{j=1}^{\infty}$ is an equi-continuous and uniformly bounded sequence of functions on $\mathbb{R}$. By Arzera–Ascoli's theorem and a nested subsequence argument, there exists a subsequence of $\{c_j\}$, still denoted by $\{c_j\}$, such that $\Phi^{(j)}(\xi)$ converges uniformly on every bounded interval, and hence pointwise on $\mathbb{R}$ to a function $\Phi^*(\xi) := (\Phi_1^*(\xi), \ldots, \Phi_N^*(\xi))$. Note that $\Phi^{(j)}(\xi) = T(\Phi^{(j)})(\xi)$, $\xi \in \mathbb{R}$, where

$$T_i(\Phi^{(j)})(\xi) = \frac{1}{c}\int_{-\infty}^{\xi} e^{-\frac{\mu_0}{c}(\xi-s)} H_i(\Phi^{(j)})(s)ds, \; i = 1, \ldots, N.$$

Letting $j \to \infty$ in the above equation and using the dominated convergence theorem, we get $\Phi^*(\xi) = T(\Phi^*)(\xi)$, $\xi \in \mathbb{R}$, $\Phi^*(\xi) \leqslant \sigma$ for $\xi \leqslant M_1$, and $\mathbf{K}^- \leqslant \liminf_{\xi\to\infty} \Phi^*(\xi) \leqslant \limsup_{\xi\to\infty} \Phi^*(\xi) \leqslant \mathbf{K}^+$.

Next, we show that $\Phi^*(-\infty) = \mathbf{0}$. It suffices to show that $\Phi^*(-\infty)$ exists. We first prove that

$$\int_{-\infty}^{0} \Phi_i^*(\xi)d\xi < +\infty, \; i = 1, \ldots, N.$$

Note that $\Phi^*(\xi) \leqslant \sigma$ for any $\xi \leqslant M_1$. Choose $\sigma \gg \mathbf{0}$ with $\|\sigma\| \leqslant \delta_0$. Then, for any $i \in \{1, \ldots, N\}$, $\xi \leqslant 0$ and $|j_1| \leqslant M_1$, $\Phi_i^*(\xi - j_1 - c\tau) \leqslant \delta_0$, and hence for any $\xi \leqslant 0$, we have

$$\begin{aligned}
&\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{j_1=-\infty}^{+\infty} G_1(i,i_1,\alpha)\beta_\alpha(j_1)b\big(\Phi_{i_1}^*(\xi - j_1 - c\tau)\big)\\
&\quad\geqslant \sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1} G_1(i,i_1,\alpha)\beta_\alpha(j_1)b\big(\Phi_{i_1}^*(\xi - j_1 - c\tau)\big)\\
&\quad\geqslant \rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1} G_1(i,i_1,\alpha)\beta_\alpha(j_1)[\Phi_{i_1}^*(\xi - j_1 - c\tau) - \Phi_{i_1}^*(\xi)]\\
&\qquad + \rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1} G_1(i,i_1,\alpha)\beta_\alpha(j_1)\Phi_{i_1}^*(\xi)\\
&\quad= \rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1} G_1(i,i_1,\alpha)\beta_\alpha(j_1)[\Phi_{i_1}^*(\xi - j_1 - c\tau) - \Phi_{i_1}^*(\xi)]\\
&\qquad + \rho_1\sum_{i=1}^{N}\sum_{|j_1|\leqslant M_1} \beta_\alpha(j_1)\Phi_i^*(\xi).
\end{aligned}$$

It follows from equation (4.1) that

$$
\begin{aligned}
c\sum_{i=1}^{N}\frac{d}{d\xi}\Phi_i^*(\xi) \geqslant{}& D_m\sum_{i=1}^{N}[\Phi_{i+1}^*(\xi)+\Phi_{i-1}^*(\xi)-2\Phi_i^*(\xi)]\\
&+D_m\sum_{i=1}^{N}[\Phi_i^*(\xi+1)+\Phi_i^*(\xi-1)-2\Phi_i^*(\xi)]-d_m\sum_{i=1}^{N}\Phi_i^*(\xi)\\
&+\mu\rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1}G_1(i,i_1,\alpha)\beta_\alpha(j_1)[\Phi_{i_1}^*(\xi-j_1-c\tau)-\Phi_{i_1}^*(\xi)]\\
&+\mu\rho_1\sum_{i=1}^{N}\sum_{|j_1|\leqslant M_1}\beta_\alpha(j_1)\Phi_i^*(\xi)\\
={}& D_m\sum_{i=1}^{N}[\Phi_i^*(\xi+1)+\Phi_i^*(\xi-1)-2\Phi_i^*(\xi)]\\
&+\mu\rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1}G_1(i,i_1,\alpha)\beta_\alpha(j_1)[\Phi_{i_1}^*(\xi-j_1-c\tau)-\Phi_{i_1}^*(\xi)]\\
&+\sum_{i=1}^{N}\Big[\mu\rho_1\sum_{|j_1|\leqslant M_1}\beta_\alpha(j_1)-d_m\Big]\Phi_i^*(\xi). \qquad (4.14)
\end{aligned}
$$

Define $\rho_2=\mu\rho_1\sum_{|j_1|\leqslant M_1}\beta_\alpha(j_1)-d_m>0$. Integrating (4.14) over $[y,0]$, we obtain

$$
\begin{aligned}
&c\sum_{i=1}^{N}[\Phi_i^*(0)-\Phi_i^*(y)]\\
&\quad\geqslant D_m\sum_{i=1}^{N}\int_y^0[\Phi_i^*(\xi+1)+\Phi_i^*(\xi-1)-2\Phi_i^*(\xi)]d\xi+\rho_2\sum_{i=1}^{N}\int_y^0\Phi_i^*(\xi)\,d\xi\\
&\quad\quad+\ \mu\rho_1\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1}G_1(i,i_1,\alpha)\beta_\alpha(j_1)\int_y^0[\Phi_{i_1}^*(\xi-j_1-c\tau)-\Phi_{i_1}^*(\xi)]\,d\xi. \qquad (4.15)
\end{aligned}
$$

Direct computation shows that

$$
\begin{aligned}
&\Big|\int_y^0[\Phi_i^*(\xi+1)+\Phi_i^*(\xi-1)-2\Phi_i^*(\xi)]\,d\xi\Big|\\
&\quad=\Big|\int_0^1\Phi_i^*(\xi)d\xi-\int_{-1}^0\Phi_i^*(\xi)d\xi-\int_y^{y+1}\Phi_i^*(\xi)d\xi+\int_{y-1}^{y}\Phi_i^*(\xi)\,d\xi\Big|\leqslant 4K^+,
\end{aligned}
$$

and

$$
\Big|\sum_{i=1}^{N}\sum_{i_1=1}^{N}\sum_{|j_1|\leqslant M_1}G_1(i,i_1,\alpha)\beta_\alpha(j_1)\int_y^0[\Phi_{i_1}^*(\xi-j_1-c\tau)-\Phi_{i_1}^*(\xi)]\,d\xi\Big|
$$

$$
\begin{aligned}
&= \Big| \sum_{i=1}^{N} \sum_{i_1=1}^{N} \sum_{|j_1| \leqslant M_1} G_1(i, i_1, \alpha) \beta_\alpha(j_1) \int_y^0 \int_0^1 (j_1 + c\tau) [(\Phi_{i_1}^*)'(\xi - (j_1 + c\tau)\theta) d\theta \, d\xi \Big| \\
&= \Big| \sum_{i=1}^{N} \sum_{i_1=1}^{N} \sum_{|j_1| \leqslant M_1} G_1(i, i_1, \alpha) \beta_\alpha(j_1) (j_1 + c\tau) \\
&\quad \times \int_0^1 [\Phi_{i_1}^*(-(j_1 + c\tau)\theta) - \Phi_{i_1}^*(y - (j_1 + c\tau)\theta)] \, d\theta \Big| \\
&\leqslant 2K^+ N \sum_{|j_1| \leqslant M_1} \beta_\alpha(j_1)(|j_1| + c\tau).
\end{aligned}
$$

Therefore, from equation (4.15), we obtain that $\int_y^0 \Phi_i^*(\xi) d\xi$ $(i = 1, \ldots, N)$ is bounded on $(-\infty, 0]$, and hence $\int_{-\infty}^0 \Phi_i^*(\xi) d\xi < +\infty$, $i = 1, \ldots, N$. By using the uniform boundedness of $(\Phi^*)'$ and the proof by contradiction, it is easy to verify that $\Phi^*(-\infty)$ exists. Therefore, $\Phi_*(-\infty) = \mathbf{0}$.

The proof of the upward convergence $\Phi_*(+\infty) = \mathbf{K}$ is similar to that of Theorem 4.11 and omitted. This completes the proof. □

5 Discussions

In this paper, we have studied the spatial dynamics of a monostable age-structured population model for the dynamics of growth of a single species on a 2D lattice strip with Neumann boundary conditions. We have given some sufficient conditions for the stability of the equilibria and the persistence of the model with monotone or non-monotone birth functions. We have also considered the spreading speed and the traveling wave solutions, including the upward convergence, for the model without the monotonicity of the birth function. Our result implies that the spreading speed is linearly determinate and coincides with the minimal wave speed of travelling waves for this class of non-quasi-monotone lattice differential systems. Our main methods are based on the comparison argument, the constructions of two auxiliary quasi-monotone systems, the Schauder's fixed-point theorem and the fluctuation method.

Now, we present illustrative examples by choosing two types of birth functions from population biology.

First, we consider the Holling-II type function $b(u) = \frac{pu}{1+\alpha u}$ with $p, \alpha > 0$. It is clear that this function is non-decreasing on $[0, \infty)$ and (A_1) and (A_2) hold. Moreover, if $p\mu/d_m > 1$, then system (1.7) has a unique positive equilibrium $K := (p\mu - d_m)/(d_m \alpha)$ and (A_3) holds. By Theorems 3.1 and 3.3, we have the following result.

Example 5.1 Let $b(u) = \frac{pu}{1+\alpha u}$ with $p, \alpha > 0$. Then, the following statements are valid:

(1) If $0 < \frac{p\mu}{d_m} \leqslant 1$, then the zero equilibrium 0 is globally attractive.

(2) If $\frac{p\mu}{d_m} > 1$, the positive equilibrium K is globally attractive.

Next, we consider the Ricker type function $b(u) = pue^{-\alpha u}$ with $p, \alpha > 0$. Clearly, $b(u)$ is non-decreasing on $[0, u_{\max}]$ while non-increasing on $[u_{\max}, \infty)$, where $u_{\max} := \alpha^{-1}$. When

$p\mu/d_m > 1$, system (1.7) has a unique positive equilibrium $K := \alpha^{-1}\ln\frac{p\mu}{d_m}$. Moreover, if $p\mu/d_m > e$, then $K > u_{\max}$ and the condition (3.9) equals to

$$2\ln\tfrac{\mu p}{d_m} - \tfrac{\mu p}{d_m e} - 1 > 0 \text{ and } \tfrac{p\mu}{d_m} \leqslant e^2.$$

It is easy to see that the above first inequality holds for $e < \frac{p\mu}{d_m} \leqslant e^2$. Therefore, equation (3.9) is equivalent to $e < \frac{p\mu}{d_m} \leqslant e^2$. By Theorems 3.1, 3.5, 3.6 and 3.7, we have the following result.

Example 5.2 Let $b(u) = pue^{-\alpha u}$ with $p, \alpha > 0$. Then, the following statements hold:

(1) If $0 < \frac{p\mu}{d_m} \leqslant 1$, then the zero equilibrium 0 is globally attractive.

(2) If $1 < \frac{p\mu}{d_m} \leqslant e$, then $K \leqslant u_{\max}$ and the positive equilibrium K is globally attractive.

(3) If $e < \frac{p\mu}{d_m} \leqslant e^2$, then $K > u_{\max}$ and the positive equilibrium K is globally attractive.

(4) If $\frac{p\mu}{d_m} > e^2$, then $\mathscr{C}_{[K_*,K^*]}$ is a global attractor, where

$$K_* = \tfrac{\mu}{d_m} b\big(\tfrac{p\mu}{d_m\alpha e} + 1\big) \text{ and } K^* = \tfrac{p\mu}{d_m\alpha e}.$$

In addition, the conclusions of Theorems 4.6, 4.10 and 4.11 are valid, that is, the spreading speed for equation (1.7) with the Ricker type birth function is linearly determinate and coincides with the minimal wave speed of travelling wave solutions. In particular, it is easy to verify that (P_2) holds in the case where $e < \frac{p\mu}{d_m} \leqslant e^2$. Hence, the upward convergence of the spreading speed and travelling waves holds provided that $1 < \frac{p\mu}{d_m} \leqslant e^2$.

We mention that the monostable assumptions are needed in studying the global attractivity of the positive equilibrium, travelling waves and spreading speeds; while they are not needed in the results on the global attractivity of the zero equilibrium. Let's consider equation (1.7) with the birth function $b(u) = pu^2e^{-\alpha u}$ with $p, \alpha > 0$. Obviously, $b(u)$ is non-decreasing on $[0, u_{\max}]$ and non-increasing on $[u_{\max}, \infty)$, where $u_{\max} := 2/\alpha$. Moreover,

(i) if $d_m > \frac{p\mu}{\alpha e}$, then 0 is the only equilibrium for equation (1.7);

(i) if $d_m = \frac{p\mu}{\alpha e}$, then system (1.7) admits a unique positive equilibrium K_1 and $d_m u > \mu b(u)$ for any $u \in (0, K_1)$;

(iii) if $d_m < \frac{p\mu}{\alpha e}$, then system (1.7) has two positive equilibria (i.e. bistable case).

It is easy to see that (A_1) and (A_3)$'$ hold provided that $d_m > \frac{p\mu}{\alpha e}$. From Theorem 3.1, if $d_m > \frac{p\mu}{\alpha e}$, then the zero equilibrium is globally attractive. However, when $d_m \leqslant \frac{p\mu}{\alpha e}$, one can see that ($A_3$) does not hold. Hence, for $b(u) = pu^2e^{-\alpha u}$ with $d_m \leqslant \frac{p\mu}{\alpha e}$, our main results on the global attractivity of positive equilibrium, travelling waves and spreading speed cannot be applied. We conjecture that the saddle-point behaviour may occur for the case when $d_m < \frac{p\mu}{\alpha e}$, see e.g. Jiang *et al.* [11].

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