PROPPAGATION OF MONOSTABLE TRAVELING FRONTS IN DISCRETE PERIODIC MEDIA WITH DELAY

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Abstract. This paper is devoted to study the front propagation for a class of discrete periodic monostable equations with delay and nonlocal interaction. We first establish the existence of rightward and leftward spreading speeds and prove their coincidence with the minimal wave speeds of the pulsating traveling fronts in the right and left directions, respectively. The dependency of the speeds of propagation on the heterogeneity of the medium and the delay term is also investigated. We find that the periodicity of the medium increases the invasion speed, in comparison with a homogeneous medium; while the delay decreases the invasion speed. Further, we prove the uniqueness of all noncritical pulsating traveling fronts. Finally, we show that all noncritical pulsating traveling fronts are globally exponentially stable, as long as the initial perturbations around them are uniformly bounded in a weight space.

1. Introduction. In the past decades, there has been great progress in modelling and investigating the dynamical behaviour of population systems with age structure, see e.g. Gourley and Kuang [8], Smith and Thieme [28], So et al. [29], Weng et al. [37], and Weng and Zhao [39]. In particular, Smith and Thieme [28] 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 technique of integration along characteristics and the Fourier transform. Following their approach, Weng [37] further derived a delayed lattice differential model (DLDM for short) for a single species in a one-dimensional patchy environment based on the following system:

\[
\begin{align*}
\frac{\partial}{\partial t}v_j(t, a) + \frac{\partial}{\partial a}v_j(t, a) &= \tilde{d}(a)[v_{j+1}(t, a) + v_{j-1}(t, a) - 2v_j(t, a)] - \mu(a)v_j(t, a), \\
v_j(t, 0) &= b(u_j(t)), \\
u_j'(t) &= D[u_{j+1}(t) + u_{j-1}(t) - 2u_j(t)] - d(u_j(t)) + v_j(t, \tau),
\end{align*}
\]

(1)

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for \( j \in \mathbb{Z}, t > 0 \) and \( \alpha \in (0, \tau) \), where \( v_j(t, a) \) is the density of individuals at location \( j \in \mathbb{Z} \), time \( t \geq 0 \) and age \( a \geq 0 \); \( u_j(t) \) is the density of the mature population; \( \bar{d}(a) \) and \( \mu(a) \) are the diffusion and death rate of the immature population at age \( a \), respectively; \( D \) is the diffusion rate of the mature individuals; \( d(u) \) and \( b(u) \) are the mortality rate and birth rate of the mature population, respectively; \( v_j(t, \tau) \) is the adults recruitment term for those of maturation age \( \tau \). In [37], the authors studied the well-posedness of the initial-value problem of the DLDM derived from (1) and obtain the existence of monotone travelling waves for wave speeds greater than the minimal wave speed. They further showed that the minimal wave speed is also the asymptotic speed of propagation, which depends on the maturation period and the diffusion rate of mature population monotonically.

However, due to the natural phenomena or exposure to artificial distributions, the real environment is generally heterogeneous. For example, a simple but realistic and important form of heterogeneous environment is the periodic habitat. Therefore, in this paper we will consider the following spatially periodic version of system (1):

\[
\begin{align*}
\frac{\partial}{\partial t} v_j(t, a) + \frac{\partial}{\partial a} v_j(t, a) &= \bar{d}(a)[v_{j+1}(t, a) + v_{j-1}(t, a) - 2v_j(t, a)] - \mu(a)v_j(t, a), \\
v_j(t, 0) &= b_j(u_j(t)), \\
u_j^{\prime}(t) &= D_{j+1}[u_{j+1}(t) - u_j(t)] + D_j[u_{j-1}(t) - u_j(t)] - d_j(u_j(t)) + v_j(t, \tau),
\end{align*}
\]

where \( j \in \mathbb{Z}, t > 0 \) and \( \alpha \in (0, \tau) \). For simplicity, we assume that the immature individuals have the same diffusion and death rates in different patches, and hence, the equation for the immature individuals is homogeneous. In contrast to (1), the mortality rate \( d_j(\cdot) \), birth rate \( b_j(\cdot) \) and diffusion rates \( D_j \) for the mature individuals of (2) are spatially dependent.

Similarly as in [28] (see also [37]), by integrating along characteristics and using the discrete Fourier transform, we can obtain

\[
v_j(t, \tau) = \sum_{k \in \mathbb{Z}} \frac{\nu}{2\pi} \beta_j(j-k) b_k(u_k(t-\tau)),
\]

where

\[
\nu := \exp\{-\int_0^\tau \mu(s)ds\}, \quad \alpha := \int_0^\tau \bar{d}(s)ds \quad \text{and} \quad \beta_j(t) := 2e^{-2\alpha} \int_0^{\pi} \cos(ls)e^{2\alpha\cos^2 s} ds.
\]

Then the age-structured population model (2) is reduced to the following lattice periodic differential equation with delay and nonlocal interaction for mature individuals:

\[
u_j^{\prime}(t) = \Delta[u_j(t)] - d_j(u_j(t)) + \sum_{k \in \mathbb{Z}} \frac{\nu}{2\pi} \beta_j(j-k) b_k(u_k(t-\tau)),
\]

where \( j \in \mathbb{Z}, t > 0 \), and

\[
\Delta[u_j(t)] := D_{j+1}[u_{j+1}(t) - u_j(t)] + D_j[u_{j-1}(t) - u_j(t)].
\]

It is very important to understand how the heterogeneity of the medium and the delay influence the dynamics for such periodic and delayed systems.

Based on this prototype, in this paper we will consider the spatial dynamics of the general spatially periodic lattice dynamical system with delay and nonlocal
interaction:

\[ u_j'(t) = \Delta [u_j(t)] + f_j(u_j(t), \sum_{k \in \mathbb{Z}} J(j-k)S_k(u_k(t-\tau))), \quad j \in \mathbb{Z}, t > 0, \]  

(4)

where \( \tau \geq 0 \) is a constant; the kernel function \( J(\cdot) \) satisfies the following assumption:

(A0): \( J(k) \geq 0, \; J(0) > 0, \; J(-k) = J(k), \; \forall k \in \mathbb{Z}; \sum_{k \in \mathbb{Z}} J(k) = 1 \) and \( \sum_{k \in \mathbb{Z}} J(k) e^{\lambda k} < \infty, \; \forall \lambda \geq 0. \)

We also assume that the constants \( D_j \) and nonlinearities \( f_j(\cdot, \cdot) \) and \( S_j(\cdot), \; j \in \mathbb{Z} \) satisfy the following assumptions:

(A1): [Periodicity] \( f_j(\cdot, \cdot) \in C^2(\mathbb{R}_+^2, \mathbb{R}_+), \; S_j(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R}_+), \; \forall j \in \mathbb{Z}, \) and there exists a \( N \in \mathbb{N} \) such that \( D_j = D_{j+N} > 0, \; f_j(\cdot, \cdot) = f_{j+N}(\cdot, \cdot) \) and \( S_j(\cdot) = S_{j+N}(\cdot); \)

(A2): [Monostability] \( f_j(0, 0) = S_j(0) = 0, \)

\[ \partial_1 f_j(0, 0) + \partial_2 f_j(0, 0) \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0) > 0, \; \partial_2 f_j(0, 0)S'_j(0) > 0, \; \forall j \in \mathbb{Z}, \]

and there exists a \( K > 0 \) such that \( f_j(K; \sum_{k \in \mathbb{Z}} J(j-k)S_k(K)) \leq 0, \; \forall j \in \mathbb{Z}; \)

(A3): [Monotonicity] \( \partial_2 f_j(u, v) \geq 0 \) and \( S'_j(u) \geq 0 \) for all \( j \in \mathbb{Z}, \; u \in [0, K] \) and \( v \in [0, S_K], \) where \( S'_K := \max_{j \in \mathbb{Z}} S_j(K); \)

(A4): [Sub-homogeneity] For any \( \gamma \in (0, 1), \; j \in \mathbb{Z} \) and \( u, v \in (0, K], \) it holds that

\[ f_j(\gamma u, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\gamma v)) > \gamma f_j(u, \sum_{k \in \mathbb{Z}} J(j-k)S_k(v)). \]

It is clear that (4) is a generalization of (3). Under the assumptions (A0)–(A4), we shall show that (4) admits a unique positive and periodic equilibrium \( \beta = (\beta(j))_{j \in \mathbb{Z}} \) (see Lemma 6). In particular, when \( \tau = 0, \; J(0) = 1 \) and \( J(j) = 0 \) for \( j \neq 0, \) (4) becomes the following periodic lattice differential system:

\[ u_j'(t) = \Delta [u_j(t)] + g_j(u_j(t)), \]

(5)

where \( g_j(u) = f_j(u, S_j(u)) \) for \( j \in \mathbb{Z}. \) Let’s mention that the front dynamics of (5) have been studied by many researchers, see e.g. [4, 9, 10, 41].

The purpose of this work is to study the propagation phenomena of (4), including the asymptotic speed of spread (spreading speed for short) and the pulsating traveling fronts (also called spatially periodic traveling waves in the literature) connecting the uniform zero state (denoted by \( \mathbf{0} \)) and \( \beta. \) The concept of the spreading speed was first introduced by Aronson and Weinberger [1] for reaction-diffusion equations and has been an important biological metric in a wide range of biological applications. In addition, the traveling wave fronts connecting \( \mathbf{0} \) and \( \beta \) can describe the biological invasion of the \( \mathbf{0} \) state by the heterogeneous state \( \beta. \) In the past decades, there were many works devoted to the spreading speed and traveling wave solutions for evolution systems, see e.g. [12, 15–19, 21–24, 31, 35–37, 39] and the references therein. Under some reasonable assumptions, the spreading speed always coincides with the minimal wave speed of the traveling wave solutions for various monostable dynamics.

Recently, Liang and Zhao [19] generalized the earlier works in [18, 21, 22, 35, 36] on spreading speed and traveling wave fronts to some abstract monostable evolution systems with spatial structure. In this article, by applying the Liang and Zhao’s theory [19], we first establish the existence of the rightward and leftward spreading speeds \( c^+_l \) for system (4) (see Theorems 1). We emphasize that such an application
is nontrivial because we need to show that the system (4) generates a continuous semiflow with respect to the compact open topology and choose appropriate linear operators to obtain explicit expressions of the spreading speeds. Moreover, to employ the linear operator approach to estimate the spreading speeds, one needs to consider a periodic and nonlocal eigenvalue problem of delayed type. Since there is no variational formula for the principal eigenvalue, it is not easy to study its properties, such as the convexity (see Lemma 8). In particular, based on a variational formula of $c^\pm_*$ involving the linear eigenvalue problem of the system, we investigate the dependency of the spreading speeds on the heterogeneity of the medium and the delay term. We obtain that (1) the periodicity of the medium increases the invasion speed, in comparison with a homogeneous medium; (2) the delay decreases the invasion speed.

We mention that the existence of the leftward and rightward pulsating traveling fronts can also be obtained by applying the Liang and Zhao’s theory [19]. However, the applications of Liang and Zhao’s theory can not provide the decay rates of the wave profiles at $-\infty$ which reflect some important information of the pulsating traveling fronts. Therefore, in this article, we shall extend the elementary iteration method to the periodic and delayed system (4). This method was used much earlier by Diekmann [6] for an epidemic model and has been nontrivially developed by many researchers for various homogeneous systems, see e.g. [31, 38, 43]. More specifically, by constructing a pair of explicit sub- and super-solution, we show that (4) has two rightward and leftward pulsating traveling fronts with speed $c > c^+_*$ and $c > c^-_*$, respectively, which have exponential decay rates at $-\infty$ (see Theorem 4). Further, we show that the noncritical pulsating traveling front with given speed and satisfying the exponential decay rates at $-\infty$ is unique up to a translation (see Theorem 6).

Another main contribution of this article is the stability of the pulsating traveling fronts. Although the energy method, spectral method and squeezing technique are usually used to study the stability of the traveling waves, see e.g. [3, 26, 27, 34, 42]. However, for the model (4) in discrete and periodic media, such techniques seem not to work in this case. Thus, a challenging question is how to obtain the stability for the pulsating traveling fronts of (4). Inspired by the works [32,33], using the analysis of the principal eigenvalue of two non-local and periodic eigenvalue problems of delayed type, we shall show that if the initial function is within a bounded distance from a certain pulsating traveling front with respect to a weighted maximum norm, then the solution will converge to the pulsating traveling front exponentially in time (see Theorem 7). Our work provides some insights on how to obtain the stability of the pulsating traveling fronts for the general periodic and discrete systems with delay and nonlocal interaction.

The rest of this paper is organized as follows. In Section 2, we establish some preliminaries for later use. Section 3 is devoted to the study of spreading speeds. Section 4 focus on the dependency of the spreading speeds on the periodicity and delay. In Section 5, we consider the existence, non-existence, asymptotic behavior and uniqueness of the pulsating traveling fronts. Section 6 is devoted to the stability of the noncritical pulsating traveling fronts. Finally, we apply our abstract result to two concrete population models in Section 7.

2. Preliminaries. We first prove the existence and positivity of solutions and establish various comparison theorems for the super- and subsolutions of (4) and its related linear system. Then, using the analysis of the principal eigenvalue of a
2.1. Existence, positivity and comparison theorems. Let’s consider the initial value problem of (4) with initial data:
\[ u_j(\theta) = \varphi_j(\theta), \text{ for } j \in \mathbb{Z}, \theta \in [-\tau, 0]. \quad (6) \]
The definitions of supersolution and subsolution of (4) are given as follows.

**Definition 1.** A function \( u(t) = (u_j(t))_{j \in \mathbb{Z}}, t \in [0, T), T > 0, \) is called a supersolution (or subsolution) of (4) on \([0, T)\) if
\[ u_j(t) \geq (or \leq) e^{-\omega_j t} u_j(0) + \int_0^t e^{-\omega_j(t-s)} F[u](s, j) ds, \text{ for } j \in \mathbb{Z}, t \in [0, T), \quad (7) \]
where
\[ \omega_j := D_{j+1} + D_j + L_1, \quad L_1 := \max\{||\partial_1 f_j(u,v)|| \mid j \in \mathbb{Z}, u \in [0, K], v \in [S K]\}, \]
\[ F[u](t, j) := D_{j+1} u_j+1(t) + D_j u_j-1(t) \]
\[ + L_1 u_j(t) + f_j(u_j(t), \sum_{k \in \mathbb{Z}} J(j-k) S_k(u_k(t-\tau))). \]

According to Definition 1, we have the following result on the existence, eventual positivity, and comparison theorem for solutions of (4).

**Lemma 1.** Assume that (A0)–(A3) hold.

1. For any \( \varphi = (\varphi_j)_{j \in \mathbb{Z}} \) with \( \varphi_j \in C([-\tau, 0], [0, K]) \), equation (4) admits a unique solution \( u(t; \varphi) = (u_j(t; \varphi))_{j \in \mathbb{Z}} \) on \([0, +\infty)\) which satisfies \( u_j(s) = \varphi_j(s) \) and \( u_j \in C^1([0, \infty), [0, K]) \) for all \( j \in \mathbb{Z} \).

2. Suppose \( u^+(t) = (u^+_j(t))_{j \in \mathbb{Z}} \) and \( u^-(t) = (u^-_j(t))_{j \in \mathbb{Z}} \) are supersolution and subsolution of (4) on \([0, +\infty)\), respectively such that \( 0 \leq u^+_j(t), u^-_j(t) \leq K \) and \( u^+_j(s) \geq u^-_j(s) \) for \( j \in \mathbb{Z}, s \in [-\tau, 0] \) and \( t \geq 0 \), then \( u^+_j(t) \geq u^-_j(t) \) for all \( j \in \mathbb{Z} \) and \( t \geq 0 \). Moreover, if \( u^+(0) \neq u^-(0) \), then \( u^+_j(t) > u^-_j(t) \) for all \( j \in \mathbb{Z} \) and \( t > \tau \).

3. For any \( \varphi = (\varphi_j)_{j \in \mathbb{Z}} \) with \( \varphi_j \in C([-\tau, 0], [0, K]) \), if \( \varphi \neq 0 \), then \( u_j(t; \varphi) > 0 \) for all \( j \in \mathbb{Z} \) and \( t > \tau \).

**Proof.** (1)–(2) Note that \( u_j(t) = K \) is a supersolution of (4). The assertions of these two parts can be proved by using the similar arguments as those in [23, Lemma 4.1] and [24, Lemma 2.2]. We omit it here.

(3) For simplicity, we denote \( u(t; \varphi) = (u_j(t; \varphi))_{j \in \mathbb{Z}} \) by \( u(t) = (u_j(t))_{j \in \mathbb{Z}} \). By assertion (1), we have \( u_j(t; \varphi) \geq 0 \) for all \( j \in \mathbb{Z} \) and \( t \geq 0 \). According to assertion (2), it suffices to prove that there exists one \( t_0 \in [0, \tau] \) such that \( u(t_0) \neq 0 \). Suppose, by contradiction, that \( u(t) \equiv 0 \) for all \( t \in [0, \tau] \). Since \( \varphi \neq 0 \), we can choose \( j_0 \in \mathbb{Z} \) and \( \theta_0 \in [-\tau, 0] \) such that \( \varphi_{j_0}(\theta_0) > 0 \). Define \( \bar{f}(u) = f_{j_0}(0, J(0) S_{j_0}(u)) \), \( u \in [0, K] \). By our assumptions, we have \( \bar{f}(0) = 0, \bar{f}'(0) = J(0) \partial_1 f_{j_0}(0, 0, S_{j_0}'(0)) > 0 \) and \( \bar{f}'(u) = J(0) \partial_2 f_{j_0}(0, J(0) S_{j_0}(u)) S_{j_0}'(u) \geq 0 \) for all \( u \in [0, K] \). Therefore, \( \bar{f}(u) = f_{j_0}(0, J(0) S_{j_0}(u)) > 0 \) for any \( u \in [0, K] \). Letting \( t = \theta_0 + \tau \) and \( j = j_0 \) in (4), it follows that
\[ 0 = f_{j_0}(0, \sum_{k \in \mathbb{Z}} J(j_0 - k) S_k(\varphi_k(\theta_0))) \geq f_{j_0}(0, J(0) S_{j_0}(\varphi_{j_0}(\theta_0))) > 0. \]
This contradiction implies that 
\( u_j(t) > 0 \) for all \( j \in \mathbb{Z} \) and \( t > \tau \). The proof is complete.

Next, we establish the following comparison theorem for the solutions of the linear system of (4) about the trivial equilibrium 0, which will be used in investigating the stability of pulsating traveling fronts (see Section 6).

**Lemma 2.** Assume that (A0)–(A3) hold. Let \( u^+_j(t) \in C^1([0, +\infty), [0, +\infty)) \) and \( u^-_j(t) \in C^1([0, +\infty), (-\infty, K]) \) such that \( u^+_j(s) \geq u^-_j(s) \) for \( j \in \mathbb{Z}, s \in [-\tau, 0] \), and

\[
(u^+_j)'(t) \geq \Delta[u^+_j(t)] + \partial_1 f_j(0,0) u^+_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S'_k(0) u^+_k(t-\tau),
\]

\[
(u^-_j)'(t) \leq \Delta[u^-_j(t)] + \partial_1 f_j(0,0) u^-_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S'_k(0) u^-_k(t-\tau),
\]

for all \( j \in \mathbb{Z} \), and \( t > 0 \). Then \( u^+_j(t) \geq u^-_j(t) \) for \( j \in \mathbb{Z}, t \geq 0 \).

**Proof.** The proof is similar to that of [40, Lemma 2.6] and omitted here. \( \square \)

### 2.2. Dynamics of periodic initial value problem

Let’s consider the following periodic initial value problem of (4):

\[
\begin{aligned}
&v_j'(t) = \Delta[v_j(t)] + f_j(v_j(t), \sum_{k \in \mathbb{Z}} J(j-k) S_k(v_k(t-\tau))), \\
&v_j(0) = \varphi_j(\theta) = \varphi_{j+N}(\theta), \\
&j \in \mathbb{Z}, \; t > 0,
\end{aligned}
\]

(8)

Some useful notations and definitions are introduced in the sequel.

**Notation.**

1. We denote \( \mathbb{P} := P(\mathbb{Z}, \mathbb{R}) \) by the set of all \( N \)-periodic functions from \( \mathbb{Z} \) to \( \mathbb{R} \) with the maximum norm \( \| \cdot \|_\mathbb{P} \) and \( \mathbb{P}_+ := \{ \phi \in \mathbb{P} : \phi(j) \geq 0, \; \forall j \in \mathbb{Z} \} \).
2. We denote \( \mathbb{C} := C([-\tau, 0], \mathbb{P}) \) by the set of all continuous functions from \([-\tau, 0]\) to \( \mathbb{P} \) with the maximum norm \( \| \cdot \|_\mathbb{C} \) and set \( \mathbb{C}_+ := C([-\tau, 0], \mathbb{P}_+) \).
3. For \( \zeta \in \mathbb{P} \) with \( \zeta > 0 \), we define \( [0, \zeta]_\mathbb{P} := \{ \phi \in \mathbb{P} : 0 \leq \phi(j) \leq \zeta(j), \; \forall j \in \mathbb{Z} \} \) and \( [0, \zeta]_\mathbb{C} := \{ \phi \in \mathbb{C} : \phi(\theta) \in [0, \zeta]_\mathbb{P}, \; \forall \theta \in [-\tau, 0] \} \). Moreover, for a function \( v(\cdot) \) defined on \([-\tau, b]\) with \( b > 0 \), we define \( v^t \in \mathbb{C} \) with \( t \in [0, b] \) by \( v^t(\theta) = v(t + \theta) \) for \( \theta \in [-\tau, 0] \).

Note that \( \mathbb{P}_+ \) and \( \mathbb{C}_+ \) are closed cones of \( \mathbb{P} \) and \( \mathbb{C} \), respectively.

**Definition 2.** A function \( v(t) = (v_j(t))_{j \in \mathbb{Z}} \) is called a supersolution (or subsolution) of (8) on \([0, T]\) with \( T > 0 \) if \( v(\cdot) \) is \( N \)-periodic for \( j \in \mathbb{Z} \) such that (7) holds for any \( j \in \mathbb{Z} \) and \( t \in [0, T] \).

According to Definition 2, we have the following result on the existence, monotonicity, eventual strong positivity and strongly sub-homogeneous property of solutions of (8).

**Lemma 3.** Assume that (A0)–(A3) hold.

1. For any \( \varphi \in [0, K]_\mathbb{C} \), (8) admits a unique solution \( v(t; \varphi) \) on \([0, +\infty)\) which satisfies \( v^t \in [0, K]_\mathbb{C} \) for all \( t \geq 0 \).
2. Suppose \( v^+(t) = (v^+_j(t))_{j \in \mathbb{Z}} \) and \( v^-(t) = (v^-_j(t))_{j \in \mathbb{Z}} \) are supersolution and subsolution of (8) on \([0, +\infty)\), respectively such that \( 0 \leq v^-_j(t) \leq v^+_j(t) \leq K \) and \( v^+_j(s) \geq v^-_j(s) \) for \( j \in \mathbb{Z}, s \in [-\tau, 0] \) and \( t \geq 0 \), then \( v^+_j(t) \geq v^-_j(t) \) for all \( j \in \mathbb{Z} \) and \( t \geq 0 \). Moreover, if \( v^+(0) \neq v^-(0) \), then \( v^+_j(t) > v^-_j(t) \) for all \( j \in \mathbb{Z} \) and \( t \geq 0 \).
(3) For any \( \varphi \in [0, K]_C \) with \( \varphi \not\equiv 0 \), \( v_j(t; \varphi) > 0 \) for all \( j \in \mathbb{Z} \) and \( t > \tau \).

(4) If, in addition, (A4) hold, then \( v_j(t; \gamma \varphi) > \gamma v_j(t; \varphi) \) for any \( \gamma \in (0, 1) \), \( \varphi \in [0, K]_C \) with \( \varphi \gg 0 \), \( j \in \mathbb{Z} \) and \( t > 0 \).

**Proof.** The existence and monotonicity of solutions of (8), i.e. assertions (1) and (2), can be proved by using a similar argument as that in [23, Lemma 4.1] or [24, Lemma 2.2]. It can also be proved by applying the theory of abstract functional differential equations (Martin and Smith [25, Corollary 5]). The proof of assertion (3) is similar to that of (3) in Lemma 1.

(4) We first claim that \( v_j(t; \gamma \varphi) \geq \gamma v_j(t; \varphi) \) for any \( \gamma \in (0, 1) \), \( \varphi \in [0, K]_C \), \( j \in \mathbb{Z} \) and \( t > 0 \). In fact, by the assumption (A4), it is easy to verify that the functions \( \bar{v}_j(t) := v_j(t; \gamma \varphi) \) and \( v_j(t) := \gamma v_j(t; \varphi) \) constitute a pair of sub- and supersolution of (8) with \( \bar{v}_j(s) = v_j(s) = \gamma \varphi_0(s) \) for \( j \in \mathbb{Z} \) and \( s \in [-\tau, 0] \). By comparison principle, the claim follows obviously. By assertion (2), we see that for any \( \varphi \in [0, K]_C \) with \( \varphi \gg 0 \), \( v_j(t; \varphi) > 0 \) for all \( j \in \mathbb{Z} \) and \( t \geq -\tau \).

Now we set \( w_j(t) := v_j(t; \gamma \varphi) - \gamma v_j(t; \varphi) \), for \( j \in \mathbb{Z} \), \( t \geq -\tau \); and

\[
h_j(t) := f_j(\gamma v_j(t; \varphi), \sum_{k \in \mathbb{Z}} J(j - k)S_k(\gamma v_k(t - \tau; \varphi)))
- \gamma f_j(v_j(t; \varphi), \sum_{k \in \mathbb{Z}} J(j - k)S_k(v_k(t - \tau; \varphi))).
\]

Then, \( w_j(s) = 0 \) for \( j \in \mathbb{Z} \), \( s \in [-\tau, 0] \) and \( w_j(t) \geq 0 \) for \( j \in \mathbb{Z} \), \( t \geq 0 \). By (A4), we have \( h_j(t) > 0 \) for all \( j \in \mathbb{Z} \) and \( t > 0 \). According to the assumption (A3), direct computations show that

\[
w_j'(t) = \Delta[w_j(t)] + f_j(v_j(t; \gamma \varphi), \sum_{k \in \mathbb{Z}} J(j - k)S_k(\gamma v_k(t - \tau; \varphi)))
- f_j(v_j(t; \varphi), \sum_{k \in \mathbb{Z}} J(j - k)S_k(\gamma v_k(t - \tau; \varphi))) + h_j(t)
\geq \Delta[w_j(t)] + \partial_1 f_j(\eta_j(t), \sum_{k \in \mathbb{Z}} J(j - k)S_k(\gamma v_k(t - \tau; \varphi)))w_j(t) + h_j(t)
> \Delta[w_j(t)] - L_1 w_j(t) \geq -(D_{j+1} + D_j + L_1)w_j(t),
\]

for \( j \in \mathbb{Z}, t > 0 \), where \( \eta_j(t) = \theta v_j(t; \gamma \varphi) + (1 - \theta) v_j(t; \varphi), \theta \in (0, 1) \). Therefore, it follows that

\[
w_j(t) > e^{-(D_{j+1} + D_j + L_1)t}w_j(0) = 0, \text{ for all } j \in \mathbb{Z}, \ t > 0.
\]

This completes the proof. \(\square\)

It is clear that the linearization of (8) at 0 can be represented by:

\[
\left\{
\begin{array}{ll}
v_j'(t) = \Delta[v_j(t)] + \partial_1 f_j(0, 0)v_j(t) + \partial_2 f_j(0, 0)\sum_{k \in \mathbb{Z}} J(j - k)S_k'(0)v_k(t - \tau), \\
v_j(\theta) = \varphi_j(\theta) = \varphi_{j+N}(\theta), \ j \in \mathbb{Z}, \ \theta \in [-\tau, 0].
\end{array}
\right.
\]

(9)

where \( j \in \mathbb{Z}, \ t > 0 \). By substituting \( v_j(t) = e^{\lambda t} \nu_j \) into (9), we obtain the following periodic and nonlocal eigenvalue problem of delayed type:

\[
\left\{
\begin{array}{ll}
\lambda \nu_j = \Delta[\nu_j] + \partial_1 f_j(0, 0)\nu_j + \partial_2 f_j(0, 0)e^{-\lambda \tau}\sum_{k \in \mathbb{Z}} J(j - k)S_k'(0)\nu_k, \ j \in \mathbb{Z}, \\
\nu_{j+N} = \nu_j, \ j \in \mathbb{Z}.
\end{array}
\right.
\]

(10)
To determine the sign of the principal eigenvalue of (10), we first consider the periodic and nonlocal eigenvalue problem without delay (i.e. \( \tau = 0 \)):

\[
\begin{aligned}
\lambda \nu_j &= \Delta[\nu_j] + \partial_1 f_j(0,0)\nu_j + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k)S_k'(0)\nu_k, \ j \in \mathbb{Z}, \\
\nu_{j+N} &= \nu_j, \ j \in \mathbb{Z}.
\end{aligned}
\] (11)

**Lemma 4.** Assume that (A0)–(A3) hold. Then there exists a principal eigenvalue \( \lambda_0^* > 0 \) of (11) associated with a strictly positive eigenfunction \((\nu_j)_j \in \mathbb{Z}\) with \(\nu_{j+N} = \nu_j\).

**Proof.** By Krein-Rutman Theorem (cf. [5]), we can show that (11) has a principal eigenvalue \( \lambda_0^* \) associated with a strictly positive eigenfunction \((\nu_j)_j \in \mathbb{Z}\) with \(\nu_{j+N} = \nu_j\) (see also [9, Lemma 2.1]). Letting \(i \in \{1, \cdots, N\}\) be such that \(m = \nu_i = \min_{j \in \mathbb{Z}} \nu_j > 0\), it follows from (11) that

\[
\lambda_0^* \geq [\partial_1 f_i(0,0) + \partial_2 f_i(0,0) \sum_{k \in \mathbb{Z}} J(i-k)S_k'(0)] m.
\]

Then, by (A2), we see that \( \lambda_0^* > 0 \). This completes the proof. \(\square\)

Based on Lemma 4, we can decide the sign of the principal eigenvalue of (10).

**Lemma 5.** Assume that (A0)–(A3) hold. Then there exists a principal eigenvalue \( \lambda^* \) of (10) associated with a strictly positive eigenfunction \((\nu_j^*)_j \in \mathbb{Z}\) with \(\nu_{j+N}^* = \nu_j^*\), and for any \( \tau > 0 \), \( \lambda^* \) has the same sign as \( \lambda_0^* \). In particular, \( \lambda^* > 0 \) for any \( \tau > 0 \).

**Proof.** Arguing as in the proof of part (3) of Lemma 3, one can show that the solution of the linear equation (9) is strongly positive and compact for any \( t > 2\tau \). By applying a result about the sign of spectral bound of an operator on [14, Section 4], the first part of the assertion can be proved by using the same argument as in [30, Theorem 2.2]. From Lemma 4, we have \( \lambda^* > 0 \) for any \( \tau > 0 \). This completes the proof. \(\square\)

**Lemma 6.** Assume that (A0)–(A4) hold. Then (4) admits a unique positive and periodic equilibrium \( \beta(j) \) such that \( \beta \in [0,K]_C \) and for any \( \varphi \in [0,K]_C \setminus \{0\} \),

\[
\lim_{t \to -\infty} u_j(t; \varphi) = \beta(j) \quad \text{uniformly in} \ j \in \mathbb{Z}.
\]

**Proof.** Let \( \Phi_t[\varphi] = v^t(\varphi) \) be the solution map generated by (8) on \([0,K]_C\). From Lemma 3, we see that \( \Phi_t : [0,K]_C \to [0,K]_C \), and \( \Phi \) is monotone and strongly sub-homogeneous. Moreover, the semiflow generated by equation (9) is compact and strongly positive for any \( t > 2\tau \). Based on these observations, the assertion of this lemma follows from [44, Theorem 2.3.4]. \(\square\)

3. Spreading speeds. For completeness and the readers’ convenience, we first recall the general theory of Liang and Zhao [19] on the study of spreading speeds for monotone semiflows in a periodic habitat. Then, we apply their theory to prove the existence of the spreading speeds. We also give the formula and investigate the signs of the spreading speeds.

3.1. General theory for monotone semiflows in a periodic habitat. We first give the following definitions.

**Definition 3.** (1) Let \( X := C([-\tau, 0], \mathbb{R}) \) be the set of all continuous functions from \([-\tau, 0]\) to \( \mathbb{R} \) with the maximum norm \( \| \cdot \|_X \) and the cone \( X_+ := C([-\tau, 0], \mathbb{R}_+) \).
Let $C := B(Z, X)$ be the set of all bounded functions from $Z$ to $X$ with the compact open topology. A subset $S$ of $C$ is said uniformly bounded if $\{\|\varphi(j)\|_X : \varphi \in S, j \in \mathbb{Z}\}$ is bounded.

(3) For any $\varphi, \psi \in C$, we write $\varphi \geq \psi$ (or $\varphi \gg \psi$) if $\varphi(j) \geq \psi(j)$ (or $\varphi(j) > \psi(j)$), $\forall j \in \mathbb{Z}$, and $\varphi > \psi$ if $\varphi \geq \psi$ but $\varphi \neq \psi$.

(4) For $\gamma \in X$ with $\gamma > 0$, we define $\mathcal{C}_\gamma := \{\varphi \in C : \gamma \geq \varphi \geq 0\}$ and

$$\|\varphi\|_C := \sum_{i=1}^{\infty} \max_{|j| \leq i} \frac{\|\varphi(j)\|_X}{2^i}, \forall \varphi \in C.$$ 

Clearly, any element in $X$ can be regarded as a constant function in $C$ and $(C, \| \cdot \|_C)$ is a normed space. Moreover, the topology generated by $\| \cdot \|_C$ and the compact open topology on $C$ are equivalent on any uniformly bounded subset of $C$.

For convenience, we also identify an element $\varphi \in C$ as a function form $[-\tau, 0] \times \mathbb{Z}$ to $\mathbb{R}$ defined by $\varphi(\theta, j) = \varphi(j)$. In addition, we denote the interval $[a, b]_Z := \{a, a+1, \ldots, b-1\}$ for any $a, b \in \mathbb{Z}$ with $a < b$, which has length $b-a$. Let $I := [a, b]_Z$ be a bounded and closed interval, $\varphi \in C$, $U \subseteq C$ and $h \in \mathbb{Z}$, we further define the function $\varphi_I : I \to X$, the set $U_I := \{\varphi_I : \varphi \in U\}$ and translation operator $T_h[I]$ by

$$\varphi(j) := \varphi(j), \forall j \in I, \ U_I := \{\varphi_I : \varphi \in U\} \text{ and } T_h[I][\varphi](j) = T_h[\varphi](j-h).$$

The norm $| \cdot |$ in $U_I$ is given by $|\varphi_I| := \max_{j \in I} \|\varphi(j)\|_X$.

Let $\hat{\mathcal{H}} := \{jN : j \in \mathbb{Z}\}$. Then $\mathbb{Z} = \{i+j : i \in \mathcal{H}, j \in [0,N]_Z\}$, i.e. $\hat{\mathcal{H}}$ is a sub-lattice of $\mathbb{Z}$. We say that $u \in C$ is periodic with respect to $\hat{\mathcal{H}}$ (or, more briefly, $N$-periodic) if $T_h[u] = u$ for all $h \in \hat{\mathcal{H}}$. According to [19], we set $K = \mathcal{M} := C_\beta$ with $\mathcal{Y} = X, \mathcal{D} = C$. Let $\beta \in \mathcal{D}$ be strictly positive and $N$-periodic and $Q[\cdot]$ be a map from $\mathcal{M}$ to $\mathcal{M}$. Assume that $Q[\cdot]$ satisfies the assumptions:

(E1) $Q$ is $N$-periodic, that is, $T_h[Q[u]] = Q[T_h[u]]$ for $h \in \hat{\mathcal{H}}, u \in \mathcal{M}$;

(E2) $Q[\mathcal{M}] \subseteq \mathcal{D}$ is uniformly bounded and $Q : \mathcal{M} \to \mathcal{D}$ is continuous with respect to the compact open topology;

(E3) The set $Q[\mathcal{M}](0, \cdot)$ is pre-compact in the space $C(\mathbb{Z}, \mathbb{R})$ equipped with the compact open topology, and there is an equivalent norm $\| \cdot \|_X$ on $X$ such that for any $r \geq 0$, there exists $\kappa = \kappa(r) \in [0, 1)$ such that for any interval $I = [a, b]_Z$ of the length $r$ and any $U \subseteq K$ with $U(0, \cdot)$ being pre-compact in $C(\mathbb{Z}, \mathbb{R})$, we have $\alpha(Q[\mathcal{U}](j)) \leq k(s)\alpha(\mathcal{U}(j))$, where $\alpha$ denotes the Kuratowski measure of non-compactness (see [20]) on $C(j)$ with $(X, \| \cdot \|_X)$ replaced by $(X, \| \cdot \|_X)$;

(E4) $Q : \mathcal{M} \to \mathcal{M}$ is monotone in the sense that $Q[\varphi] \geq Q[\psi]$ whenever $\varphi \geq \psi$ in $\mathcal{M}$;

(E5) $Q[\cdot]$ admits exactly two $N$-periodic fixed points $0$ and $\beta$ in $\mathcal{M}$, and for any $N$-periodic function $\varphi \in \mathcal{D}$ with $0 \ll \varphi \leq \beta$, $\lim_{n \to \infty} [Q^n[\varphi](j) - \beta(j)] = 0$ uniformly for $j \in \mathbb{Z}$.

Then it follows from [19, Theorem 5.1] that the discrete time semigroup $\{Q^n\}_{n=0}^{\infty}$ (in short, the map $Q$) on $\mathcal{M}$ admits rightward and leftward spreading speeds $c^*_p$.

Furthermore, a family of mappings $\{Q_t\}_{t \geq 0}$ is said to be a semiflow on a metric space $(X, d)$ provided that the following properties hold:

(i) $Q_0[\varphi] = \varphi, \forall \varphi \in X$;

(ii) $Q_t[Q_s[\varphi]] = Q_{t+s}[\varphi], \forall t, s \geq 0$ and $\forall \varphi \in X$;

(iii) $Q(t, \cdot) := Q_t[\cdot]$ is continuous in $(t, \varphi)$ on $[0, \infty) \times X$.

It is clear that the property (iii) holds if $Q(\cdot, \varphi)$ is continuous on $[0, \infty)$ for each $\varphi \in X$, and $Q(t, \cdot)$ is uniformly continuous for $t$ in bounded intervals in the sense
that for any $\varphi^0 \in \mathcal{X}$, bounded interval $I$, and $\epsilon > 0$, there exists $\delta = \delta(\varphi^0, I, \epsilon) > 0$ such that if $d(\varphi, \varphi^0) < \delta$, then $d(Q_t[\varphi], Q_t[\varphi^0]) < \epsilon$ for all $t \in I$. By [19, Theorem 5.2 and Remark 4.1], the following results on the spreading speed of continuous-time semiflows hold.

**Proposition 1.** Let $\{Q_t\}_{t \geq 0}$ be a semiflow on $\mathcal{M}$ with $Q_t[0] = 0$ and $Q_t[\beta] = \beta$, $\forall t \geq 0$. Suppose that $Q_t$ satisfies assumptions (E1)–(E5), and $c_+^t$ and $c_-^t$ are the rightward and leftward spreading speeds of $Q_t$, respectively. Then $c_+^t$ and $c_-^t$ are the rightward and leftward spreading speeds of $\{Q_t\}_{t \geq 0}$ in the following senses:

1. For any $c > c_+^t$ and $c < c_-^t$, if $\varphi \in \mathcal{M}$ with $0 \leq \varphi \leq \varpi$ for some $\varpi \in Y$ satisfying $\varpi \ll \beta$, and $\varphi(\cdot, j) = 0$ for $j$ outside a bounded interval, then
   \[ \lim_{t \to \infty, j \geq ct} Q_t[\varphi](j) = 0 \quad \text{and} \quad \lim_{t \to \infty, j \leq -c't} Q_t[\varphi](j) = 0 \text{ in } X. \]

2. Assume $c_+^t + c_-^t > 0$. For any $c < c_+^t$, $c < c_-^t$ and $\sigma \in Y$ with $\sigma \gg 0$, there exists an integer $r_\sigma > 0$ such that if $\varphi \in \mathcal{M}$ with $\varphi(\cdot, j) \gg \sigma$ for $j$ on an interval of length $2r_\sigma$, then
   \[ \lim_{t \to \infty, -c't \leq j \leq ct} \|Q_t[\varphi](j) - \beta(j)\|_X = 0 \text{ in } X. \]

In addition, if $Q_1[\cdot]$ is sub-homogeneous, i.e., $Q_1[\rho \varphi] \geq \rho Q_1[\varphi]$ for all $\rho \in [0, 1]$ and $\varphi \in \mathcal{M}$, then $r_\sigma$ can be chosen independently of $\sigma$.

In the rest of this section, we always assume that (A0)–(A4) hold.

### 3.2. Existence of spreading speeds

Let $\{Q_t\}_{t \geq 0}$ be the semiflow on $C_\beta$ associated with system (4), i.e.,

\[ Q_t[\varphi](\theta, j) = u_j^t(\theta; \varphi), \forall \varphi \in C_\beta, \theta \in [-\tau, 0], j \in \mathbb{Z}. \]

Then $\{Q_t[\cdot]\}_{t \geq 0}$ has the following properties.

**Lemma 7.** (1) $\{Q_t[\cdot]\}_{t \geq 0}$ is a sub-homogeneous semiflow on $C_\beta$.

(2) For any $t > 0$, the map $Q_t[\cdot]$ satisfies (E1)–(E5).

**Proof.** (1) It is clear that $Q_t[\cdot]$ satisfies the property (i). The semigroup property (ii) follows from the existence and uniqueness of solutions of (4). Now, we prove the property (iii). Given $\varphi \in C_\beta$, it follows from (4) that $\frac{d}{dt} u_j(t; \varphi)$ is bounded for all $(t, j) \in \mathbb{Z} \times [0, \infty)$. Hence, there exists a constant $L = L(\varphi) > 0$ such that

\[ |u_j(t_1; \varphi) - u_j(t_2; \varphi)| \leq L|t_1 - t_2|, \forall j \in \mathbb{Z}, t_1, t_2 \in [0, \infty). \]

Thus, for each $\varphi \in C_\beta$, $Q_t[\varphi]$ is continuous in $t \in [0, \infty)$ with respect to the compact open topology. Therefore, to prove the property (iii), it suffices to show that $Q_t[\varphi]$ is continuous in $\varphi$ with respect to the compact open topology, uniformly for $t$ in any bounded interval. Given any $\phi, \tilde{\phi} \in C_\beta$. For any given $\epsilon > 0$ and $t_0 > 0$, we define

\[ w_j(t) := |u_j(t; \phi) - u_j(t; \tilde{\phi})|, \quad k_0 := \sup_{(t, j) \in [-\tau, t_0] \times \mathbb{Z}} w_j(t), \quad \epsilon_0 := \frac{\epsilon}{2(L_f L_S t_0 + 1)e^{L_f t_0}}, \]

\[ \Omega_h(z) := [-\tau, 0] \times [z - h, z + h], \forall h \in \mathbb{Z}_+, z \in \mathbb{Z}, \]

and

\[ |\tilde{\phi}|_{\Omega_h(z)} := \sup_{(\theta, j) \in \Omega_h(z)} |\tilde{\phi}(\theta)|, \forall \phi \in C_\beta, \]

where $D := \max_{j \in \mathbb{Z}} D_j$, $L := 2D + L_f + L_f L_S$, $L_S := \max_{j \in \mathbb{Z}, u \in [0, K]} S'_j(u)$ and

\[ L_f := \max_{j \in \mathbb{Z}, (u, v) \in [0, K] \times [0, S_K]} \{ \partial_1 f_j(u, v), \partial_2 f_j(u, v) \}. \]
By the definition of $k_0$, there exists $(t_*, j_*) \in [-\tau, t_0] \times \mathbb{Z}$ such that
\[
 w_j^t(\theta) \leq k_0 \leq w_j(t_*) + \epsilon_0, \quad \forall (j, t, \theta) \in \mathbb{Z} \times [0, t_0] \times [-\tau, 0].
\]
Since $\sum_{k \in \mathbb{Z}} J(k) = 1$, we can choose an integer $M > 1$ such that $\sum_{|k| > M} J(k) < \frac{2}{N^2}$.

Then, for any $t \in [0, t_0]$, it follows that
\[
 \sum_{k \in \mathbb{Z}} J(k)w_{j-k}(t-\tau) = \sum_{|k| > M} J(k)w_{j-k}(t-\tau) + \sum_{|k| \leq M} J(k)w_{j-k}^t(\tau) \leq |w^t|_{\Omega_{j_0}} + \epsilon_0.
\]

Let $\eta = \frac{\epsilon_0}{2M} > 0$, we consider the following two sub-cases:

Case (i). $(t_*, j_*) \in [-\tau, 0] \times \mathbb{Z}$; and Case (ii). $(t_*, j_*) \in [0, t_0] \times \mathbb{Z}$.

For Case (i), if $|\tilde{\phi} - \tilde{\phi}|_{\Omega_{j_0}} < \eta$, then for any $t \in [0, t_0]$, we have
\[
 |w^t|_{\Omega_{j_0}} \leq \epsilon_0 + w_j(t_*) \leq \epsilon_0 + \eta < \epsilon.
\]

For Case (ii), direct computations show that
\[
 |f_j, (u_j, (s; \tilde{\phi}), \sum_{k \in \mathbb{Z}} J(j_* - k)S_k(u_k(s - \tau; \tilde{\phi})))
 - f_j, (u_j, (s; \tilde{\phi}), \sum_{k \in \mathbb{Z}} J(j_* - k)S_k(u_k(s - \tau; \tilde{\phi})))|
 \leq L_Jw_j(s) + L_JL_S\sum_{k \in \mathbb{Z}} J(j_* - k)w_k(s - \tau)
 \leq L_J|w^s|_{\Omega_{j_0}} + L_JL_S(|w^s|_{\Omega_{j_0}} + \epsilon_0),
\]
for any $s \in [0, t_0]$. Thus, if $|\tilde{\phi} - \tilde{\phi}|_{\Omega_{j_0}} < \eta$ and $t \in [0, t_0]$, we have
\[
 |w^t|_{\Omega_{j_0}} \leq \epsilon_0 + w_j(t_*)
 \leq \epsilon_0 + w_j(0)e^{-(D_{j_*} + D_{j_0})t_0} + \int_0^{t_0} e^{-(D_{j_*} + D_{j_0})(t_0-s)}[D_{j_*} + D_{j_0}w_{j_*}(s)
 + D_{j_*}w_{j_*-1}(s) + |f_j, (u_j, (s; \tilde{\phi}), \sum_{k \in \mathbb{Z}} J(j_* - k)S_k(u_k(s - \tau; \tilde{\phi})))
 - f_j, (u_j, (s; \tilde{\phi}), \sum_{k \in \mathbb{Z}} J(j_* - k)S_k(u_k(s - \tau; \tilde{\phi}))))|ds
 \leq \epsilon_0 + \eta + \int_0^{t_0} [2D|w^s|_{\Omega_{j_0}} + L_J|w^s|_{\Omega_{j_0}} + L_JL_S(|w^s|_{\Omega_{j_0}} + \epsilon_0)]ds
 = \epsilon_0 + \eta + L_JL_S\epsilon_0t_0 + L_J\int_0^{t_0} |w^s|_{\Omega_{j_0}}ds.
\]

It then follows from Gronwall’s inequality that
\[
 |w^t|_{\Omega_{j_0}} \leq (\epsilon_0 + \eta + L_JL_St_0\epsilon_0)e^{Lt_0} = \epsilon, \quad \forall t \in [0, t_0].
\]

Summarizing the above two cases, we conclude that for any $\epsilon > 0$, $t_0 > 0$ and compact set $A \subseteq [-\tau, 0] \times \mathbb{Z}$, there exist $\eta > 0$ and compact set $\Omega_{j_0}$ such that $A \subseteq \Omega_{j_0}$ and
\[
 |w^t|_A \leq |w^t|_{\Omega_{j_0}} < \epsilon, \quad \forall t \in [0, t_0] \text{ whenever } |\tilde{\phi} - \tilde{\phi}|_{\Omega_{j_0}} < \eta.
\]
Using this conclusion, it is easy to show that \( Q_t[\varphi] \) is continuous in \( \varphi \) with respect to the compact open topology, uniformly for \( t \in [0, t_0] \). Consequently, \( Q_t[\varphi] \) is continuous in \((t, \varphi)\) with respect to the compact open topology. Hence, \( \{Q_t[\cdot]\}_{t \geq 0} \) is a semiflow on \( C_\beta \).

Next, we prove that \( Q_t[\cdot] \) is sub-homogeneous on \( C_\beta \), i.e. \( Q_t[\gamma \varphi] \geq \gamma Q_t[\varphi] \) for all \( \gamma \in [0, 1] \) and \( \varphi \in C_\beta \). Thanks to (A4), it is easy to verify that the functions \( \bar{u}_j(t) := u_j(t; \gamma \varphi) \) and \( u_j(t) := \gamma u_j(t; \varphi) \) constitute a pair of sub- and supersolution of (4) with \( \bar{u}_j(s) = u_j(s) \) for \( j \in \mathbb{Z} \) and \( s \in [-r, 0] \). By comparison principle, we have \( u_j(t; \gamma \varphi) \geq \gamma u_j(t; \varphi) \) for any \( j \in \mathbb{Z}, t \geq 0 \), which implies that \( Q_t[\cdot] \) is sub-homogeneous on \( C_\beta \).

(2) It is clear that \( Q_t[\cdot] \) satisfies (E1), (E2) and (E4); while the assumption (E5) follows from Lemma 6. To verify (E3), let’s define a family of linear operator \( \{\bar{L}(t)\}_{t \geq 0} \) on \( X \) by

\[
\bar{L}(t)[\psi](\theta) := \begin{cases} 
\psi(t + \theta) - \psi(0), & \text{for } t + \theta < 0, \\
0, & \text{for } t + \theta \geq 0.
\end{cases}
\]

It then follows from [19, Remark 4.1] that for any given \( \gamma > 0 \), there is an equivalent norm \( \|\cdot\|_\gamma \) in \( X \) such that \( \|\bar{L}(t)\|_\gamma \leq e^{-\gamma t}, \forall t \geq 0 \). Moreover, we define

\[
L(t)[\phi](\theta, j) := \begin{cases} 
\phi(t + \theta, j) - \phi(0, j), & \text{for } t + \theta < 0, \\
0, & \text{for } t + \theta \geq 0,
\end{cases}
\]

and

\[
S(t)[\phi](\theta, j) := \begin{cases} 
\phi(0, j), & \text{for } t + \theta < 0, \\
u(t + \theta, j; \phi), & \text{for } t + \theta \geq 0.
\end{cases}
\]

Then, \( Q_t[\phi] = L(t)[\phi] + S(t)[\phi], \forall \phi \in C_\beta, t \geq 0 \). It is easy to verify that \( Q_t[C_\beta](0, \cdot) = u(t, \cdot; C_\beta) \) is pre-compact in the space \( C(\mathbb{Z}, \mathbb{R}) \) and \( S(t)[\mathcal{U}] \) is compact in \( C_\beta \) with respect to the compact open topology for any \( \mathcal{U} \in C_\beta \) with \( \mathcal{U}(0, \cdot) \) pre-compact in \( C(\mathbb{Z}, \mathbb{R}) \) (see e.g. Fang et al. [7, Lemma 2.3]). Thus, for any interval \( I = [a, b] \) of the length \( r \), we have

\[
\alpha(Q_t[\mathcal{U}]|_I) \leq \alpha(L(t)[\mathcal{U}]|_I) + \alpha(S(t)[\mathcal{U}]|_I) \leq e^{-\gamma t} \alpha(\mathcal{U}|_I),
\]

where \( \alpha \) is the Kuratowski measure of non-compactness on \( C_I \) with \( (X, \|\cdot\|_X) \) replaced by \( (X, \|\cdot\|_\gamma) \). Thus, for each \( t > 0 \), \( Q_t[\cdot] \) satisfies (E3) with \( k = e^{-\gamma t} \). The proof is complete. \( \square \)

By Lemma 7 and [19, Theorem 5.1], the map \( Q_1 : C_\beta \rightarrow C_\beta \) admits a rightward spreading speed \( c^+_\star \) and a leftward spreading speed \( c^-_\star \). Then Proposition 1 implies that \( c^{\pm}_\star \) are also the leftward and rightward spreading speeds for solutions of (4) provided that \( c^+_\star + c^-_\star > 0 \) which will be proved in Theorem 2.

**Theorem 1.** Let \( c^+_\star \) and \( c^-_\star \) be the rightward and leftward spreading speeds of \( Q_1[\cdot] \), respectively. Then the following results hold.

1. For any \( c > c^+_\star \) and \( c' > c^-_\star \), if \( \varphi \in C_\beta \) with \( 0 \leq \varphi \leq \omega \) for some \( \omega \in X \) satisfying \( \omega \ll \beta \), and \( \varphi(\cdot, j) = 0 \) for \( j \) outside a bounded interval, then

\[
\lim_{t \to -\infty} u_j(t; \varphi) = 0 \quad \text{and} \quad \lim_{t \to -\infty} u_j(t; \varphi) = 0.
\]

2. Assume \( c^+_\star + c^-_\star > 0 \). For any \( c < c^+_\star \) and \( c' < c^-_\star \), if \( \varphi \in C_\beta \) with \( \varphi \not\equiv 0 \), then

\[
\lim_{t \to -\infty} \left[ u_j(t; \varphi) - \beta(j) \right] = 0.
\]
then there exists a vector $\sigma$ defined in Proposition 1 can be chosen to be independent of $\sigma \gg 0$. Take $r_\sigma = r$. If $\varphi \in C_0$ with $\varphi(\theta,j) \gg 0$ for all $\theta \in [-\tau,0]$ and $j$ on an interval of length $2r$, then there exists a vector $\sigma \gg 0$ such that $\varphi(\theta,j) \gg \sigma$ for all $\theta \in [-\tau,0]$ and $j$ in this interval. Hence part (2) of Proposition 1 implies that $\lim_{t \to \infty} -e^{-\lambda t} u_j(\tau + \beta(j)) = 0$. For any $\varphi \in C_0$ with $\varphi \neq 0$, it follows from part (3) of Lemma 1 that $u_j(t,\varphi) > 0$ for any $j \in \mathbb{Z}$ and $t > \tau$. Fixing a $t_0 > 2\tau$ and taking $(u_j^n(\tau,\varphi))_{j \in \mathbb{Z}}$ as a new initial value, then the assertion of this part holds.

3.3. Computation of spreading speeds. We first give the formula of the spreading speeds $c_*^\pm$ by considering the linearized equation of (4) with respect to the equilibrium $0$:

$$u_j'(t) = \Delta [u_j(t)] + \partial_1 f_j(0,0)u_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k)S_k'(0)u_k(t-\tau), \quad (12)$$

where $j \in \mathbb{Z}$, $t > 0$. Let $\{L(t)\}_{t=0}^\infty$ be the solution maps associated with (12), i.e. $L(t)[\varphi] = u'(t)$. Taking $u_j(t) = e^{\lambda t}v_j(t)$ in (12), we have

$$v_j'(t) = D_{j+1}e^{-\mu v_j+1}(t) + D_{j+1}e^{\mu v_j-1}(t) - (D_{j+1} + D_j)v_j(t) + \partial_1 f_j(0,0)v_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(k)S_k'(0)e^{\mu(k-v_j-1)}v_j(t-\tau), \quad j \in \mathbb{Z}, \ t > 0. \quad (13)$$

For any $\mu \in \mathbb{R}$, let $\{L_\mu(t)\}_{t=0}^\infty$ be the solution maps associated with (13). Letting $v_j(t) = e^{\lambda t}v_j$ with $v_j = v_{j+N}$ in (13), we obtain the following eigenvalue problem:

$$\begin{cases}
\lambda v_j = D_{j+1}e^{-\mu v_j+1} + D_{j+1}e^{\mu v_j-1} - (D_{j+1} + D_j)v_j + \partial_1 f_j(0,0)v_j \\
+ \partial_2 f_j(0,0)e^{-\lambda t} \sum_{k \in \mathbb{Z}} J(k)S_k'(0)e^{\mu(j-k)}v_k, \quad j \in \mathbb{Z}, \ j \in \mathbb{Z}, \ j \in \mathbb{Z},
\end{cases} \quad (14)$$

Similar to (10), we can show that for any $\mu \in \mathbb{R}$, (14) has a principal eigenvalue $\lambda(\mu)$ with a strictly positive eigenfunction.

**Lemma 8.** The function $\lambda(\mu)$ is a convex function on $\mathbb{R}$ such that

$$\lim_{\mu \to -\infty} \lambda(\pm \mu)/\mu = \infty \text{ and } \lim_{\mu \to 0^+} \lambda(\pm \mu)/\mu = \infty.$$

**Proof.** We first prove the convexity of $\lambda(\mu)$. Given any $\mu_1, \mu_2 \in \mathbb{R}$. We denote $v_i = (v_{i,j})_{j \in \mathbb{Z}}$ by the eigenfunctions of (14) corresponding to the principal eigenvalue $\lambda_i := \lambda(\mu_i)$, $i = 1, 2$. We further set $\tilde{v}_{i,j} := e^{-\mu_i j}v_{i,j}$, $\forall j \in \mathbb{Z}$. Then, $\tilde{v}_{i,j} > 0$, $\forall j \in \mathbb{Z}$, $i = 1, 2$ and

$$\lambda_i \tilde{v}_{i,j} = \Delta [\tilde{v}_{i,j}] + \partial_1 f_j(0,0)\tilde{v}_{i,j} + \partial_2 f_j(0,0)e^{-\lambda_i t} \sum_{k \in \mathbb{Z}} J(j-k)S_k'(0)\tilde{v}_{i,k}$$

for $j \in \mathbb{Z}$, $i = 1, 2$. Now we prove the following claim.

**Claim.** The function $\tilde{v}_j := (\tilde{v}_{1,j}^2 + \tilde{v}_{2,j}^2)^{1/2} = e^{-\frac{\mu_1 + \mu_2}{2}}(v_{1,j}v_{2,j})^{1/2}$ satisfies

$$\frac{\lambda_1 + \lambda_2}{2} \tilde{v}_j \geq \Delta [\tilde{v}_j] + \partial_1 f_j(0,0)\tilde{v}_j + \partial_2 f_j(0,0)e^{-\frac{\lambda_1 + \lambda_2}{2} t} \sum_{k \in \mathbb{Z}} J(j-k)S_k'(0)\tilde{v}_k, \ j \in \mathbb{Z}.$$
Moreover, by the convexity of the function $e^{\tau}$, we have

$$\Delta[\tilde{\nu}_j] = \frac{1}{2}(\tilde{\nu}_{2,j} \tilde{\nu}_{1,j})^2 \left[ \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k \right] + (\tilde{\nu}_{1,j} \tilde{\nu}_{2,j}) \left[ \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k \right] - 2(\tilde{\nu}_{1,j} \tilde{\nu}_{2,j})$$

(18)

Using (15)-(18), we obtain

$$\Delta[\tilde{\nu}_j] + \partial_1 f_j(0,0)\tilde{\nu}_j + \partial_2 f_j(0,0)e^{-\lambda_1 e^{\lambda_2 t}} \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k$$

$$\leq \frac{1}{2}(\tilde{\nu}_{2,j} \tilde{\nu}_{1,j})^2 \left[ \Delta[\tilde{\nu}_j] + \partial_1 f_j(0,0)\tilde{\nu}_j \right] + \frac{1}{2}(\tilde{\nu}_{2,j} \tilde{\nu}_{1,j})^2 \left[ \Delta[\tilde{\nu}_j] + \partial_1 f_j(0,0)\tilde{\nu}_j \right]$$

$$+ \partial_2 f_j(0,0)e^{-\lambda_1 e^{\lambda_2 t}} \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k$$

$$\leq \partial_2 f_j(0,0)e^{-\lambda_1 e^{\lambda_2 t}} \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k$$

$$- \frac{1}{2}(\tilde{\nu}_{2,j} \tilde{\nu}_{1,j})^2 \left[ \Delta[\tilde{\nu}_j] + \partial_1 f_j(0,0)\tilde{\nu}_j \right] + \frac{1}{2}(\tilde{\nu}_{2,j} \tilde{\nu}_{1,j})^2 \left[ \Delta[\tilde{\nu}_j] + \partial_1 f_j(0,0)\tilde{\nu}_j \right]$$

$$- \partial_2 f_j(0,0)e^{-\lambda_1 e^{\lambda_2 t}} \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)\tilde{\nu}_k + \frac{\lambda_1 + \lambda_2}{2} \tilde{\nu}_j$$

$$\leq \frac{\lambda_1 + \lambda_2}{2} \tilde{\nu}_j.$$
where \( j \in \mathbb{Z}, t > 0 \). Denote \( \phi_j(\theta) = e^{\frac{\lambda_1 + \lambda_2}{2} t} \tilde{u}_j, \forall j \in \mathbb{Z}, \theta \in [-\tau, 0] \). By the comparison theorem for the linear equation (12) (see Lemma 2), we get
\[
e^{\frac{\lambda_1 + \lambda_2}{2} t} \tilde{u}_j = \bar{u}_j(t) \geq u_j(t; \phi), \forall j \in \mathbb{Z}, t \geq 0,
\]
where \( u_j(t; \phi) \) is the solution of (12) with the initial condition \( u^0 = \phi \). Noting that \( L(t)[\phi](j, \theta) = u_j(t + \theta; \phi) \), we further obtain
\[
e^{\frac{\lambda_1 + \lambda_2}{2} t} e^{\frac{\mu_1 + \mu_2}{2} j} \phi_j(\theta) \geq e^{\frac{\mu_1 + \mu_2}{2} j} L(t)[\phi](j, \theta), \forall j \in \mathbb{Z}, \theta \in [-\tau, 0], t \geq 0.
\]
Let’s set \( \varphi_j(\theta) = e^{\frac{\mu_1 + \mu_2}{2} j} \phi_j(\theta) \). Then
\[
e^{\frac{\lambda_1 + \lambda_2}{2} t} \varphi_j(\theta) \geq L e^{\frac{\mu_1 + \mu_2}{2} j} (t)[\varphi](j, \theta), \forall j \in \mathbb{Z}, \theta \in [-\tau, 0], t \geq 0,
\]
which implies that
\[
\left( e^{\frac{\lambda_1 + \lambda_2}{2} t} - L e^{\frac{\mu_1 + \mu_2}{2} j} (t) \right)[\varphi] \geq 0, \forall t \geq 0.
\]
Since \( \varphi_j(\theta) = e^{\frac{\lambda_1 + \lambda_2}{2} \theta} \nu_j(j) = \varphi_j(\tau) > 0, \forall \theta \in [0, 0] \) is compact and strongly positive linear operator for each \( t \geq \tau \), it follows from the Krein-Rutman Theorem that
\[
e^{\frac{\lambda_1 + \lambda_2}{2} t} \geq r(L e^{\frac{\mu_1 + \mu_2}{2} j} (t)) = e^{\lambda e^{\frac{\mu_1 + \mu_2}{2} j} t}, \forall t > \tau.
\]
Therefore, we conclude that \( \lambda(1/\mu) \leq \frac{1}{2} \lambda(\mu_1) + \frac{1}{2} \lambda(\mu_2) \), i.e. \( \lambda(\mu) \) is convex on \( \mathbb{R} \).

Let \( m = \min_{j \in \mathbb{Z}} \nu_j \). It follows from (14) that
\[
\lambda(\pm \mu) \geq D_j e^{\pm \mu} - (D_j + D_j^0) + \partial_1 f_j(0, 0) \geq \min_{j \in \mathbb{Z}} \left\{ D_j e^{\pm \mu} - (D_j + D_j^0) + \partial_1 f_j(0, 0) \right\} \geq D_{\min} \left\{ e^{\pm \mu} - 2D_{\max} + \min_{j \in \mathbb{Z}} \partial_1 f_j(0, 0) \right\},
\]
where \( D_{\min} = \min_{j \in \mathbb{Z}} D_j > 0 \) and \( D_{\max} = \max_{j \in \mathbb{Z}} D_j > 0 \), which implies \( \lambda(\pm \mu) / \mu = \infty \).

Now we show that \( \lim_{\mu \to 0^+} \lambda(\mu) / \mu = \infty \). Suppose \( \lim_{\mu \to 0^+} \lambda(\mu) / \mu \neq +\infty \), then there exist \( G_0 > 0 \) and \( \{ \mu_n \}_{n=1}^\infty \) with \( \mu_n > 0 \) and \( \lim_{n \to \infty} \mu_n = 0 \) such that \( \lambda(\mu_n) / \mu_n \leq G_0 \). From (14), we have
\[
G_0 \mu_n \geq \lambda(\mu_n) \geq \min_{j \in \mathbb{Z}} \left\{ D_j e^{\mu_n} + D_j e^{\mu_n} - D_j + \partial_1 f_j(0, 0) \right\} \geq \min_{j \in \mathbb{Z}} \left\{ D_j e^{\mu_n} + D_j e^{\mu_n} - D_j + \partial_1 f_j(0, 0) \right\} \geq \min_{j \in \mathbb{Z}} \left\{ D_j e^{\mu_n} + D_j e^{\mu_n} - D_j + \partial_1 f_j(0, 0) \right\} \geq \min_{j \in \mathbb{Z}} \left\{ D_j e^{\mu_n} + D_j e^{\mu_n} - D_j + \partial_1 f_j(0, 0) \right\}.
\]
Letting \( n \to \infty \), we obtain that
\[
\min_{j \in \mathbb{Z}} \left\{ \partial_1 f_j(0, 0) + \partial_2 f_j(0, 0) \right\} \leq 0,
\]
which contradicts to (A2). Therefore, we conclude that \( \lim_{\mu \to 0^+} \lambda(\mu) / \mu = +\infty \). Similarly, we can prove that \( \lim_{\mu \to 0^+} \lambda(-\mu) / \mu = +\infty \). This completes the proof. \( \square \)

The following result gives the formulation of the spreading speeds \( c^+ \).
Theorem 2. Let $c^+_*$ and $c^-_*$ be the rightward and leftward spreading speeds of $Q_1[\cdot]$, respectively. Then
\[
c^+_* = \inf_{\mu > 0} \lambda(\mu)/\mu \quad \text{and} \quad c^-_* = \inf_{\mu > 0} \lambda(-\mu)/\mu.
\]
Moreover, we have $c^+_* + c^-_* > 0$.

Proof. By (A4), the unique solution $u_j(t; \varphi)$ of (4) with $u^0(\varphi) = \varphi \in C_\beta$ satisfies
\[
\begin{cases}
     u_j'(t; \varphi) \leq & \Delta[u_j(t; \varphi)] + \partial_1 f_j(0,0) u_j(t; \varphi) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S_k'(0) u_k(t - \tau; \varphi), \\
     u_j(\theta; \varphi) = & \varphi_j(\theta), \ j \in \mathbb{Z}, \ \theta \in [-\tau, 0], \ t > 0.
\end{cases}
\]
Thus, the comparison theorem implies that $Q_1[\varphi] \leq \mathbb{L}(t)[\varphi], \ \forall \varphi \in C_\beta, t \geq 0$. Let $t = 1$, we have $Q_1[\varphi] \leq \mathbb{L}(1)[\varphi], \ \forall \varphi \in C_\beta$. Moreover, for any given $\mu \in \mathbb{R}$, we define a linear operator $\mathbb{L}_\mu[\cdot]$ associated with $\mathbb{L}(1)$ by
\[
\mathbb{L}_\mu[\varphi](j, \theta) := e^{\mu j} \cdot \mathbb{L}(1)[e^{-\mu j} \varphi](j, \theta) = e^{\mu j} \cdot e^{-\mu j} L_\mu(1)[\varphi](j, \theta) = L_\mu(1)[\varphi](j, \theta),
\]
$\forall j \in \mathbb{Z}, \ \theta \in [-\tau, 0], \ \varphi \in C_\beta$. Then it follows that $\mathbb{L}_\mu[\cdot] = L_\mu(1)[\cdot]$, and hence $e^{\lambda(\mu)}$ is the principal eigenvalue of $L_\mu[\cdot]$. By Lemma 7, $\ln e^{\lambda(\mu)} = \lambda(\mu)$ is a convex function of $\mu \in \mathbb{R}$. With this convexity, we can use the similar arguments as [18, Theorem 3.10(i)] and [36, Theorem 2.5] to obtain
\[
c^+_* \leq \inf_{\mu > 0} (\ln e^{\lambda(\mu)})/\mu = \inf_{\mu > 0} \lambda(\mu)/\mu.
\]
On the other hand, for any $\epsilon \in (0, 1)$, we can choose $\epsilon \in (0, K)$ such that
\[
L_1 u + f_j(u, \sum_{k \in \mathbb{Z}} J(j-k) S_k(v)) \geq (1 - \epsilon) \left[ (L_1 + \partial_1 f_j(0,0)) u + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S_k'(0) u_k(t) \right],
\]
for any $u, v \in [0, \delta], j \in \mathbb{Z}$, where $L_1$ is defined in Definition 1. Since $u_j(t; 0) \equiv 0$, there exists $\eta \in \text{Int}_\mathbb{P}$ with $\eta \leq \delta$ such that $u_j(t; \eta) \leq \delta$ for any $j \in \mathbb{Z}$ and $t \in [0, 1]$. Then for any $\varphi \in C_\eta$, $u_j(t; \varphi) \leq u_j(t; \eta) \leq \delta$ for $j \in \mathbb{Z}$ and $t \in [0, 1]$, and $u_j(t) := u_j(t; \varphi)$ satisfies
\[
u_j'(t) \geq & \Delta[u_j(t)] - L_1 u_j(t) \\
+ & (1 - \epsilon) \left[ (L_1 + \partial_1 f_j(0,0)) u_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S_k'(0) u_k(t - \tau) \right] \\
= & \Delta[u_j(t)] + [(1 - \epsilon) \partial_1 f_j(0,0) - \epsilon L_1] u_j(t) \\
+ & (1 - \epsilon) \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S_k'(0) u_k(t - \tau),
\]
where $j \in \mathbb{Z}, t \in [0, 1]$. Let $\{L^t \} t \geq 0$ be the solution maps associated with the linear system
\[
v_j'(t) = & \Delta[v_j(t)] + [(1 - \epsilon) \partial_1 f_j(0,0) - \epsilon L_1] v_j(t) \\
+ & (1 - \epsilon) \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j-k) S_k'(0) u_k(t - \tau). \quad (20)
\]
Then the comparison theorem implies that $\mathbb{L}^t[\varphi] \leq Q_1[\varphi], \ \forall \varphi \in C_\eta, t \in [0, 1]$. In particular, $L^t(1)[\varphi] \leq Q_1[\varphi], \ \forall \varphi \in C_\eta$. 

\[
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\]
Now let $\lambda'(\mu)$ be the principal eigenvalue of the eigenvalue problem associated with the linear system (20). As the above discussions, the convexity of $\lambda'(\mu)$ and the similar argument as in [18, Theorem 3.10(i)] and [36, Theorem 2.5] give rise to
\[
\inf_{\mu > 0} \lambda'(\mu)/\mu \geq \inf_{\mu > 0} (\ln e^{\lambda'(\mu)})/\mu = \inf_{\mu > 0} \lambda'(\mu)/\mu.
\]
Therefore, we have
\[
\inf_{\mu > 0} \lambda'(\mu)/\mu \leq c_*^+ \leq \inf_{\mu > 0} \lambda(\mu)/\mu, \forall \epsilon \in (0, 1).
\]
Taking $\epsilon \to 0$, we obtain $c_*^+ = \inf_{\mu > 0} \lambda(\mu)/\mu$. Moreover, changing the variable $w_j(t) = u_{-j}(t)$, then it follows that $c_*^-$ is the rightward spreading speed of the resulting equation for $w$. This fact implies that $c_*^- = \inf_{\mu > 0} \lambda(-\mu)/\mu$.

Note that $\lambda(0) = \lambda^* > 0$ (see Lemma 5). Using the convexity of $\lambda(\mu)$, we can show that $c_*^+ + c_*^- > 0$, see e.g. [19, Section 7.1]. This completes the proof. \[\square\]

Next, we study the signs of the spreading speeds $c_*^\pm$. To this end, we make the following assumption:

\[\text{(A4') One of the following conditions holds:}\]
\[
\begin{cases}
\text{(a) } S_j(\cdot) = S_0(\cdot), \forall j \in \mathbb{Z}; & \text{(b) } J(0) = 1 \text{ and } J(j) = 0 \text{ for } j \neq 0; \\
\text{(c) } \partial_1 f_j(0,0) + \partial_2 f_j(0,0)J(0)S_j'(0) > 0, \forall j \in \mathbb{Z},
\end{cases}
\]

**Lemma 9.** Let $\lambda(\mu)$ be the principal eigenvalue of (14). If (A4') holds, then $\lambda(\mu) > 0$ for any $\mu \in \mathbb{R}$ and $c_*^+ > 0$.

**Proof.** Similar to the proof of Lemma 5, we can show that $\lambda(\mu)$ has the same sign as $\lambda_0(\mu)$, where $\lambda_0(\mu)$ is the principal eigenvalue of the following eigenvalue problem without delay:

\[
\begin{cases}
\lambda \nu_j = D_{j+1} e^{-\mu \nu_{j+1}} + D_j e^{\mu \nu_{j-1}} - (D_{j+1} + D_j)\nu_j + \partial_1 f_j(0,0)\nu_j \\
+ \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(k)S_{j-k}'(0) e^{\mu k} \nu_{j-k}, \quad j \in \mathbb{Z},
\end{cases}
\]

\[\nu_j = \nu_{j+N}, \quad j \in \mathbb{Z}.
\]

Therefore, it suffices to show that $\lambda_0(\mu) > 0$ for any $\mu \in \mathbb{R}$. Let $(\nu_{j,\mu})_{j \in \mathbb{Z}}$ with $\max_{j \in \mathbb{Z}} \nu_{j,\mu} = 1$ be the strictly positive eigenfunction of (21) corresponding to $\lambda_0(\mu)$, then it follows that

\[
\begin{cases}
\lambda(\mu) \nu_{j,\mu} = D_{j+1} e^{-\mu \nu_{j+1,\mu}} + D_j e^{\mu \nu_{j-1,\mu}} - (D_{j+1} + D_j)\nu_{j,\mu} + \partial_1 f_j(0,0)\nu_{j,\mu} \\
+ \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(k)S_{j-k}'(0) e^{\mu k} \nu_{j-k,\mu}, \quad j \in \mathbb{Z},
\end{cases}
\]

\[\nu_{j,\mu} = \nu_{j+N,\mu}, \quad j \in \mathbb{Z}.
\]

\[\text{(22)}
\]

Similar to the proof of Lemma 8, $\lambda_0(\mu)$ is convex and continuous on $\mathbb{R}$.

To proceeding further, we first prove that $\lim_{\mu \to 0} \nu_{j,\mu} = \nu_{j,0}$. Let $\{\nu_{n,\mu}\}$ be an arbitrary sequence which converges to 0. By periodicity and boundedness, one can extract a subsequence $\{\nu_{j,\mu_n}\}$ such that $\lim_{n \to \infty} \nu_{j,\mu_n} = \tilde{\nu}_j$ for some $(\tilde{\nu}_j)_{j \in \mathbb{Z}}$ with $\max_{j \in \mathbb{Z}} \tilde{\nu}_j = 1$. Then, the continuity of the function $\lambda_0(\mu)$ implies that $(\tilde{\nu}_j)_{j \in \mathbb{Z}}$ satisfies (22) with $\mu = 0$. Moreover, by uniqueness, one concludes that $\tilde{\nu}_j = \nu_{j,0}, \forall j \in \mathbb{Z}$ and that the whole sequence $(\nu_{j,\mu_n})$ converges to $\nu_{j,0}$ as $n \to \infty$ for all $j \in \mathbb{Z}$. Thus, $\lim_{\mu \to 0} \nu_{j,\mu} = \nu_{j,0}$.

Now we assume the condition (a) in (A4') holds and show that $\lambda_0'(0) = 0$. Multiplying the equations (22) by $\nu_{j,0}$ and (22) with $\mu = 0$ by $\nu_{j,0}$, we can subtract
both equations and summing them over $j = 1, \ldots, N$ to obtain
\[
[\lambda_0(\mu) - \lambda_0(0)] \sum_{j=1}^{N} \nu_j, \nu_j, 0
\]
\[
= \sum_{j=1}^{N} \left( D_{j+1} e^{-\mu} \nu_{j+1, \mu} \nu_j, 0 + D_{j} e^{\mu} \nu_j, 1, \mu - D_{j+1} \nu_j, 1, \mu - D_{j} \nu_j, 0 \right) + D_{j} \nu_j, 0, 0 \mu
\]
\[
= \sum_{j=1}^{N} \left( \partial_{2} f_j(0, 0) S_j'(0) \sum_{k \in \mathbb{Z}} J(k) \sum_{j=1}^{N} \nu_j, k, \mu, 0 - \nu_j, k, \mu, 0 \right].
\]

By the periodicity condition, it follows that
\[
\lim_{\mu \to 0} \frac{1}{\mu} \sum_{k \in \mathbb{Z}} J(k) \sum_{j=1}^{N} \left( e^{\mu} \nu_j, k, \mu, 0 - \nu_j, k, \mu, 0 \right)
\]
\[
= \lim_{\mu \to 0} \frac{1}{\mu} \sum_{k \in \mathbb{Z}} J(k) \left\{ \sum_{j=1}^{N} \left( e^{\mu} \nu_j, k, \mu, 0 - \nu_j, k, \mu, 0 \right) + \sum_{j=1}^{N} e^{-\mu} \nu_j, k, \mu, 0 \right\}
\]
\[
= \lim_{\mu \to 0} \sum_{k \in \mathbb{Z}} J(k) \left\{ \sum_{j=1}^{N} \nu_j, k, \mu, 0 - \sum_{j=1}^{N} \nu_j, k, \mu, 0 \right\} = 0.
\]

Similarly, we have
\[
\lim_{\mu \to 0} \frac{1}{\mu} \sum_{j=1}^{N} \left[ D_{j+1} e^{-\mu} \nu_{j+1, \mu} \nu_j, 0 + D_{j} e^{\mu} \nu_j, 1, \mu - D_{j+1} \nu_j, 1, \mu - D_{j} \nu_j, 0 \right]
\]
\[
= \lim_{\mu \to 0} \left[ \frac{e^{-\mu} - 1}{\mu} \sum_{j=1}^{N} D_{j+1} \nu_{j+1, \mu} \nu_j, 0 + \frac{e^{\mu} - 1}{\mu} \sum_{j=1}^{N} D_{j} \nu_j, 1, \mu, 0 \right] = 0.
\]

Thus, the function $\lambda_0(\mu)$ is differentiable at 0 and $\lambda_0(0) = 0$. Note that $\lambda_0(0) = \lambda_0^* > 0$ (see Lemma 4). Therefore, $\lambda_0(\mu) \geq \lambda_0(0) > 0$, which implies that $\lambda(\mu) > 0$ for any $\mu \in \mathbb{R}$.

Next, we assume the condition (b) in (A4) holds. Then (22) reduces to
\[
\left\{ \begin{array}{l}
\lambda_0(\mu) \nu_{j, \mu} = D_{j+1} e^{-\mu} \nu_{j+1, \mu} + D_{j} e^{\mu} \nu_j, 1, \mu - (D_{j+1} + D_{j}) \nu_j, \mu \\
+ [\partial_1 f_2(0, 0) + \partial_2 f_2(0, 0)] S_j'(0) \right\] \nu_j, \mu, 0 \\
\nu_{j, \mu} = \nu_j, \mu + N, \mu, 0 \end{array} \right. \quad (23)
\]

Note that in this case, the condition $\partial_1 f_2(0, 0) + \partial_2 f_2(0, 0) \sum_{k \in \mathbb{Z}} J(j - k) S_j'(0) > 0$ becomes $\partial_1 f_2(0, 0) + \partial_2 f_2(0, 0) S_j'(0) > 0$, $\forall j \in \mathbb{Z}$. Similar to the above argument, we can show that $\lambda(\mu) > 0$ for any $\mu \in \mathbb{R}$.

Finally, we assume the condition (c) in (A4) holds. Then it follows from (22) that
\[ \lambda_0(\mu)\nu_{j,\mu} = D_{j+1}e^{-\mu}\nu_{j+1,\mu} + D_{j}e^{\mu}\nu_{j-1,\mu} - (D_{j+1} + D_{j})\nu_{j,\mu} \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu} + \partial_2 f_j(0, 0) \sum_{k \in \mathbb{Z}} J(k)S'_{j-k}(0)e^{\mu k}\nu_{j-k,\mu} \\
\geq D_{j+1}e^{-\mu}\nu_{j+1,\mu} + D_{j}e^{\mu}\nu_{j-1,\mu} - (D_{j+1} + D_{j})\nu_{j,\mu} \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu} + \partial_2 f_j(0, 0)J(0)S'_j(0)\nu_{j,\mu}. \]

Let \( \lambda_0(\mu) \) be the principal eigenvalue of the following eigenvalue problem:

\[
\begin{align*}
\lambda \nu_{j,\mu} &= D_{j+1}e^{-\mu}\nu_{j+1,\mu} + D_{j}e^{\mu}\nu_{j-1,\mu} - (D_{j+1} + D_{j})\nu_{j,\mu} \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu} + \partial_2 f_j(0, 0)J(0)S'_j(0)\nu_{j,\mu}, \\
\nu_{j,\mu} &= \nu_{j-N,\mu}, \ j \in \mathbb{Z}.
\end{align*}
\]

Then \( \lambda_0(\mu) \geq \lambda_0(\mu), \ \forall \mu \in \mathbb{R} \). Moreover, form the second case, we know that \( \lambda_0(\mu) > 0 \) for any \( \mu \in \mathbb{R} \). Thus, \( \lambda(\mu) > 0 \) for any \( \mu \in \mathbb{R} \). This completes the proof. \( \square \)

4. Effects of periodicity and delay on \( c^+_1 \). In this section, we analyze the dependency of the spreading speeds \( c^+_1 \) with respect to the periodicity and delay. Since the influence of these facts may be opposite, we shall investigate each of them separately. For simplicity, we only consider the issue for \( c^+_1 \), since results for \( c^-_1 \) can be obtained similarly. Throughout this section, we always assume that (A0)–(A4) hold.

4.1. Effect of delay on \( c^+_1 \). For simplicity, we call \( c^+_1 = c^+_1(\tau) \), given in Theorem 2, the rightward invasion speed of (25). The following lemma means that the delay decreases the invasion speed, in comparison with the model without delay.

**Lemma 10.** If (A4)' holds, then \( c^+_1(\tau) \leq c^+_1(0) \) for all \( \tau \geq 0 \). If, in addition, \( \partial_2 f_j(0, 0) > 0 \) and \( S'_j(0) > 0 \), \( \forall j \in \mathbb{Z} \), then \( c^+_1(\tau) < c^+_1(0) \) for all \( \tau > 0 \).

**Proof.** Let \( \lambda_\mu(\tau) \) be the principal eigenvalue of the eigenvalue problem (14) and \( (\nu_{j,\mu}(\tau))_{j \in \mathbb{Z}} \) be the corresponding strictly positive eigenfunction with \( \max_{j \in \mathbb{Z}} \nu_{j,\mu}(\tau) = 1 \). It follows from Lemma 9 that \( \lambda_\mu(\tau) > 0 \) for all \( \mu \in \mathbb{R} \) and \( c^+_1(\tau) = \inf_{\mu>0} \lambda_\mu(\tau)/\mu > 0 \).

Using (14), we obtain

\[
\begin{align*}
\lambda_\mu(\tau)\nu_{j,\mu}(\tau) &= D_{j+1}e^{-\mu}\nu_{j+1,\mu}(\tau) + D_{j}e^{\mu}\nu_{j-1,\mu}(\tau) - (D_{j+1} + D_{j})\nu_{j,\mu}(\tau) \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu}(\tau) + \partial_2 f_j(0, 0)e^{-\lambda_\mu(\tau)\tau} \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)e^{\mu(j-k)}\nu_{k,\mu}(\tau) \\
\leq& D_{j+1}e^{-\mu}\nu_{j+1,\mu}(\tau) + D_{j}e^{\mu}\nu_{j-1,\mu}(\tau) - (D_{j+1} + D_{j})\nu_{j,\mu}(\tau) \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu}(\tau) + \partial_2 f_j(0, 0) \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)e^{\mu(j-k)}\nu_{k,\mu}(\tau).
\end{align*}
\]

Note that

\[
\begin{align*}
\lambda_\mu(0)\nu_{j,\mu}(0) &= D_{j+1}e^{-\mu}\nu_{j+1,\mu}(0) + D_{j}e^{\mu}\nu_{j-1,\mu}(0) - (D_{j+1} + D_{j})\nu_{j,\mu}(0) \\
+ \partial_1 f_j(0, 0)\nu_{j,\mu}(0) + \partial_2 f_j(0, 0) \sum_{k \in \mathbb{Z}} J(j-k)S'_k(0)e^{\mu(j-k)}\nu_{k,\mu}(0) \\
&= \lambda_0(\mu)\nu_{j,\mu}(0).
\end{align*}
\]
By comparison, \( \lambda_\mu(\tau) \leq \lambda_\mu(0) \) for any \( \tau \geq 0 \). Therefore, we conclude that \( c_+^*(\tau) \leq c_+^*(0) \).

Next, we set \( \tilde{v}_{j,\mu} := e^{-\lambda_\mu\tau}\psi_{j,\mu}(0) > 0, \forall j \in \mathbb{Z} \). Then, by our assumptions, for any \( \tau > 0 \),

\[
\begin{align*}
\lambda_\mu(0)\tilde{v}_{j,\mu} &= D_{j+1}\tilde{v}_{j+1,\mu} + D_j\tilde{v}_{j-1,\mu} - (D_{j+1} + D_j)\tilde{v}_{j,\mu} \\
&+ \partial_1 f_j(0,0)\tilde{v}_{j,\mu} + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j - k)S'_k(0)\tilde{v}_{k,\mu} \\
&> D_{j+1}\tilde{v}_{j+1,\mu} + D_j\tilde{v}_{j-1,\mu} - (D_{j+1} + D_j)\tilde{v}_{j,\mu} \\
&+ \partial_1 f_j(0,0)\tilde{v}_{j,\mu} + \partial_2 f_j(0,0)e^{-\lambda_\mu\tau} \sum_{k \in \mathbb{Z}} J(j - k)S'_k(0)\tilde{v}_{k,\mu}.
\end{align*}
\]

Hence, the function \( \tilde{u}_j(t) = e^{\lambda_\mu(0)t}\tilde{v}_{j,\mu} \) satisfies

\[
\tilde{u}_j'(t) > \Delta[\tilde{u}_j(t)] + \partial_1 f_j(0,0)\tilde{u}_j(t) + \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(j - k)S'_k(0)\tilde{u}_{k}(t - \tau).
\]

Let \( \phi_j(\theta) = e^{\lambda_\mu(\theta)t}\psi_{j,\mu} \). Then, one can easily show that \( e^{\lambda_\mu(0)t}\psi_{j,\mu} = \tilde{u}_j(t) > u_j(t; \phi), \forall j \in \mathbb{Z}, t \geq 0 \), where \( u_j(t; \phi) \) is the solution of (12) with the initial condition \( u^0 = \phi \). Note that \( L(t)[\phi](j, \theta) = u_j(t + \theta; \phi) \), we further obtain

\[
e^{\lambda_\mu(\theta)t}e^{\lambda_\mu(0)t}\phi_j(\theta) > e^{\lambda_\mu(0)t}L(t)[\phi](j, \theta), \forall j \in \mathbb{Z}, \theta \in [-\tau, 0], t \geq 0.
\]

Set \( \varphi_j(\theta) = e^{\lambda_\mu(\theta)t}\phi_j(\theta) \). Then

\[
e^{\lambda_\mu(\theta)t}\varphi_j(\theta) > L(\mu(t))[\varphi](j, \theta), \forall j \in \mathbb{Z}, \theta \in [-\tau, 0], t \geq 0,
\]

where \( L_\mu(t) \) be the solution maps associated with (13). It follows that \( L(\mu(t))[\varphi] < e^{\lambda_\mu(\theta)t}\varphi, \forall t \geq 0 \). Since \( \varphi_j(\theta) = e^{\lambda_\mu(\theta)t}\psi_{j,\mu}(0) = \varphi_{j+N}(\theta) > 0, \forall j \in \mathbb{Z}, \theta \in [-\tau, 0] \) and \( L_\mu(t) \) is compact and strongly positive linear operator for each \( t > \tau \), it follows from the Krein-Rutman Theorem (cf. [11, Theorem 7.3]) that

\[
\tau(L_\mu(t)) = e^{\lambda_\mu(\tau)t} < e^{\lambda_\mu(0)t}, \forall t > \tau.
\]

Therefore, \( \lambda_\mu(\tau) < \lambda_\mu(0) \) for any \( \tau > 0 \), which implies that \( c_+^*(\tau) < c_+^*(0) \) for all \( \tau > 0 \).

4.2. Effect of periodicity on \( c_+^* \). To investigate the effect of periodicity on \( c_+^* \), we assume the following conditions:

(P1) \( \tau = 0, J(0) = 1, J(j) = 0 \) for \( j \neq 0 \), and \( D_j = D_0, \forall j \in \mathbb{Z} \);

(P2) \( \forall j \in \mathbb{Z}, g_j(u) := f_j(u, S_j(u)) \) satisfies \( g_j'(0) = \rho_j + B\omega_j, \) where \( \omega_j+N = \omega_j > 0, \rho_j+\rho_j = \rho_j \geq 0 \) and \( B \in \mathbb{R} \).

According to (P1) and (P2), system (4) reduces to

\[
u_j'(t) = D_0[u_{j+1}(t) - u_j(t)] + D_0[u_{j-1}(t) - u_j(t)] + g_j(u_j(t)).
\]

In population biology, when \( \rho_j = 0, j \in \mathbb{Z} \), \( B \) can be viewed as the amplitude of the effective birth rate of the species in consideration (see Berestycki et al. [2]). If \( g_j'(0) > 0 \), we call \( c_+^* = c_+^*(B) \), given in Theorem 2, the rightward invasion speed of (25). The following result give a monotonous dependency of \( c_+^*(B) \) on \( B \) as well as some lower and upper bounds for \( c_+^*(B) \).

**Lemma 11.** Assume that (P1) and (P2) hold and \( g_j'(0) > 0 \) for all \( j \in \mathbb{Z} \).

1. If \( \rho_j = \rho_0 > 0 \) for all \( j \in \mathbb{Z} \), then \( c_+^*(B) \) is increasing in \( B \geq 0 \).
(2) Let $k(\mu) := D_0(e^{-\mu} + e^{\mu} - 2)$. For any $B > -\min_{j \in \mathbb{Z}} \rho_j/\omega_j$, we have
\[
\inf_{\mu > 0} \frac{k(\mu) + \min\{\rho_j + B\omega_j\}}{\mu} \leq c^+_B(B) \leq \inf_{\mu > 0} \frac{k(\mu) + \max\{\rho_j + B\omega_j\}}{\mu}.
\]

Proof. Let $\lambda_\mu(B)$ be the principal eigenvalue of the following eigenvalue problem and $(\nu_{j,\mu}(B))_{j \in \mathbb{Z}}$ be the corresponding strictly positive eigenfunction with $\max_{j \in \mathbb{Z}} \nu_{j,\mu}(B) = 1$:
\[
\begin{align*}
\lambda_\mu(B)\nu_{j,\mu}(B) &= D_0[e^{-\mu}\nu_{j+1,\mu}(B) + e^{\mu}\nu_{j-1,\mu}(B) - 2\nu_{j,\mu}(B)] \\
&\quad + [\rho_j + B\omega_j]\nu_{j,\mu}(B), \\
\nu_{j,\mu}(B) &= \nu_{j+N,\mu}(B), \quad j \in \mathbb{Z}.
\end{align*}
\]
(26)

It is clear that $\rho_j + B\omega_j > 0$ when $B > -\min_{j \in \mathbb{Z}} \rho_j/\omega_j$. Then it follows from Lemma 9 that $\lambda_\mu(B) > 0$ for any $\mu \in \mathbb{R}$ and $c^+_B(B) = \inf_{\mu > 0} \lambda_\mu(B)/\mu$. (1) To prove this assertion, it suffices to show that for any given $\mu > 0$, $\lambda_\mu(B)$ is increasing in $B \geq 0$. Given any $\mu > 0$, we first prove that $\lambda_\mu(B)$ is convex in $B \geq 0$. Let $K_{\text{per}} := \{\phi = (\phi_j)_{j \in \mathbb{Z}} | \phi_j > 0 \text{ and } \phi_j = \phi_{j+N}, \forall j \in \mathbb{Z}\}$. By the min-max formulation of the principal eigenvalue of a matrix, we have
\[
\lambda_\mu(B) = \min_{\phi \in K_{\text{per}}} \max_{j \in \mathbb{Z}} \left\{ \frac{D_0[e^{-\mu}\phi_{j+1} + e^{\mu}\phi_{j-1}]}{\phi_j} + \rho_0 - 2D_0 + B\omega_j \right\}.
\]

Let $B_1, B_2 \geq 0, \theta \in [0,1], \phi, \psi \in K_{\text{per}}$. Denote $\varphi = (\varphi_j)_{j \in \mathbb{Z}} = (e^{\theta \ln \phi_j + (1-\theta) \ln \psi_j})_{j \in \mathbb{Z}}$. It is clear that $\varphi \in K_{\text{per}}$. It then follows the above characterization of $\lambda_\mu(B)$ that
\[
\lambda_\mu(\theta B_1 + (1 - \theta) B_2) \leq \max_{j \in \mathbb{Z}} \left\{ \frac{D_0[e^{-\mu}\varphi_{j+1} + e^{\mu}\varphi_{j-1}]}{\varphi_j} + \rho_0 - 2D_0 + [\theta B_1 + (1 - \theta) B_2] \omega_j \right\}
\]
\[
= \max_{j \in \mathbb{Z}} \left\{ D_0[e^{-\mu}e^{\theta \ln \varphi_{j+1} + (1-\theta) \ln \varphi_{j-1}} + e^{\mu}e^{\theta \ln \varphi_{j-1} + (1-\theta) \ln \varphi_{j+1}}] \right. \\
\left. + \rho_0 - 2D_0 + [\theta B_1 + (1 - \theta) B_2] \omega_j \right\}
\]
\[
\leq \theta \max_{j \in \mathbb{Z}} \left\{ \frac{D_0[e^{-\mu}\phi_{j+1} + e^{\mu}\phi_{j-1}]}{\phi_j} + \rho_0 - 2D_0 + B_1 \omega_j \right\}
\]
\[
+ (1 - \theta) \max_{j \in \mathbb{Z}} \left\{ \frac{D_0[e^{-\mu}\psi_{j+1} + e^{\mu}\psi_{j-1}]}{\psi_j} + \rho_0 - 2D_0 + B_2 \omega_j \right\}.
\]

By the arbitrariness of $\phi, \psi \in K_{\text{per}}$, we conclude that $\lambda_\mu(\theta B_1 + (1 - \theta) B_2) \leq \theta \lambda_\mu(B_1) + (1 - \theta) \lambda_\mu(B_2)$, that is $\lambda_\mu(B)$ is convex in $B \geq 0$. In particular, it is continuous in $B \geq 0$.

Next, we show that $\lambda_\mu(0) > 0$. One can easily sees that $\lambda_\mu(0) = D_0[e^{-\mu} + e^{\mu} - 2] + \rho_0$, and that the associated eigenfunction $\nu_\mu(0)$ is equal to 1. Using (26) with $\rho_j = \rho_0$, we obtain
\[
\lambda_\mu(B) \sum_{j=1}^{N} \nu_{j,\mu}(B) = D_0[e^{-\mu} + e^{\mu} - 2] + \rho_0 \sum_{j=1}^{N} \nu_{j,\mu}(B) + B \sum_{j=1}^{N} \omega_j \nu_{j,\mu}(B)
\]
\[
= \lambda_\mu(0) \sum_{j=1}^{N} \nu_{j,\mu}(B) + B \sum_{j=1}^{N} \omega_j \nu_{j,\mu}(B),
\]
which implies that
\[(\lambda_\mu(B) - \lambda_\mu(0))/B = \sum_{j=1}^{N} \omega_j \nu_{j,\mu}(B)/\sum_{j=1}^{N} \nu_{j,\mu}(B). \tag{27}\]

By continuity, one knows that $\lambda_\mu(B) \to \lambda_\mu(0)$ as $B \to 0$. Arguing as in the proof of Lemma 9, one also knows that $\nu_{j,\mu}(B) \to \nu_{j,\mu}(0) = 1$ as $B \to 0$. Then, it follows from (27) that $\lambda'_\mu(0) = \sum_{j=1}^{N} \omega_j > 0$. From the convexity of $B \to \lambda_\mu(B)$, one deduces that the function is increasing with respect to $B \geq 0$. Therefore, $c^*_{\mu}(B)$ is increasing in $B \geq 0$.

(2) From (26), we see that $\lambda_\mu(B) \geq D_0[e^{-\mu} + e^{\mu} - 2] + \min\{\rho_j + B\omega_j\}$, which implies that
\[c^*_{\mu}(B) \geq \inf_{\mu > 0} k(\mu) + \min\{\rho_j + B\omega_j\}. \]

By the formula of $c^*_{\mu}(B)$, one can also prove that
\[c^*_{\mu}(B) = \inf\{c > 0 \mid \text{there exists } \mu > 0 \text{ such that } c\mu - \lambda_\mu(B) = 0\}. \]

Using (26) again, it follows that
\[c_\mu - \lambda_\mu(B) \geq c_\mu - D_0[e^{-\mu} + e^{\mu} - 2] - \max\{\rho_j + B\omega_j\}. \]

Note that $\lambda_0(B) > 0$. Thus, if $\epsilon \geq \inf_{\mu > 0} k(\mu) + \max\{\rho_j + B\omega_j\}$, then there exists a $\mu_0 > 0$ such that $c\mu_0 - \lambda_{\mu_0}(B) = 0$. Therefore, one concludes that
\[c^*_{\mu}(B) \leq \inf_{\mu > 0} k(\mu) + \max\{\rho_j + B\omega_j\}. \]

This completes the proof. \hspace{1cm} \Box

Lemma 11 implies that increasing the amplitude of the effective birth rate of the species increases the invasion speed.

Now, we call $c^*_\mu = c^*_\mu(\rho)$, given in Theorem 2, the rightward invasion speed of (25) with $g_j'(0) = \rho_j > 0$, where $\rho_{j+N} = \rho_j$, $\forall j \in \mathbb{Z}$. The following lemma means that the periodicity of the medium increases the invasion speed, in comparison with a homogeneous medium.

**Lemma 12.** Assume that $g_j'(0) = \rho_j > 0$ and $\sum_{j=1}^{N} \rho_j \geq N\bar{\rho} > 0$, where $\rho_{j+N} = \rho_j$. Then $c^*_\mu(\rho) \geq c^*_\mu(\bar{\rho})$.

**Proof.** Let $\lambda_\mu(\rho)$ be the principal eigenvalue of the following eigenvalue problem and $(\nu_{j,\mu}(\rho))_{j \in \mathbb{Z}}$ be the corresponding strictly positive eigenfunction with $\max_{j \in \mathbb{Z}} \nu_{j,\mu}(\rho) = 1$:
\[
\begin{cases}
\lambda_\mu(\rho) \nu_{j,\mu}(\rho) = D_0[e^{-\mu}\nu_{j+1,\mu}(\rho) + e^{\mu}\nu_{j-1,\mu}(\rho) - 2\nu_{j,\mu}(\rho)] + \rho_j \nu_{j,\mu}(\rho), \\
\nu_{j,\mu}(\rho) = \nu_{j+N,\mu}(\rho), \ j \in \mathbb{Z}.
\end{cases}
\tag{28}
\]
It follows from Lemma 9 that $c^*_\mu(\rho) = \inf_{\mu > 0} \lambda_\mu(\rho)/\mu$. Using (28) and the fact $\nu_{j,\mu}(\rho) = \nu_{j+N,\mu}(\rho), \forall j \in \mathbb{Z}$, we deduce that
\[
\lambda_\mu(\rho) = D_0\left[e^{-\mu}\sum_{j=1}^{N} \frac{\nu_{j+1,\mu}(\rho)}{\nu_{j,\mu}(\rho)} + e^{\mu}\sum_{j=1}^{N} \frac{\nu_{j-1,\mu}(\rho)}{\nu_{j,\mu}(\rho)} - 2\right] + \frac{1}{N} \sum_{j=1}^{N} \rho_j \geq D_0[e^{-\mu} + e^{\mu} - 2] + \bar{\rho} = \lambda_\mu(\bar{\rho}),
\]

where $\bar{\rho} = \inf_{\mu > 0} \lambda_\mu(\rho)/\mu$. Therefore, $c^*_\mu(\rho) \geq c^*_\mu(\bar{\rho})$. \hspace{1cm} \Box
which implies that \( c_1^+ (\rho) \geq c_1^+ (\bar{\rho}) \). The proof is complete.

5. Existence and uniqueness of pulsating traveling fronts. This section is devoted to the existence, non-existence, asymptotic behavior and uniqueness of the pulsating traveling fronts. As a direct consequence of Lemma 7 and Liang and Zhao [19, Theorem 5.3], we can show that the rightward and leftward spreading speeds \( c_1^\pm \) are exactly the minimal wave speed of the rightward and leftward pulsating traveling fronts, respectively. However, we can not obtain any information about the decay rates of the wave profiles at \(-\infty\). So, in the sequel, we reprove the existence result of the pulsating traveling fronts for \( c > c_1^+ \) by a different method. The main idea is to extend the technique of monotone iteration scheme coupled with the method of sub-super solutions to periodic system (4). Based on constructing a pair of explicit sub- and supersolutions, we show that (4) has two rightward and leftward pulsating traveling fronts with speed \( c > c_1^+ \) and \( c > c_1^- \), respectively, which have exponential decay rates at \(-\infty\). Further, we show that the noncritical pulsating traveling front with given speed and satisfying the exponential decay rates at \(-\infty\) is unique (up to a translation).

We first give the definition of the pulsating traveling wave solution.

**Definition 4.** A leftward (or rightward) pulsating traveling wave solution of (4) connecting \( 0 \) and \( \beta \) refers to a solution \( u(t) = \{u_j(t)\}_{j \in \mathbb{Z}} \), \( t \in \mathbb{R} \) satisfying

\[
\begin{align*}
\{ & u_j(t) = \psi_j(j + ct) \text{ (or) } u_j(t) = \psi_j(-j + ct) , \\
& \psi_j(\cdot) = \psi_{j+N}(\cdot) , \quad \psi_j(-\infty) = 0 \text{ and } \psi_j(+\infty) = \beta_j, \\
& \forall j \in \mathbb{Z}, \ t \in \mathbb{R},
\end{align*}
\]

(29)

where \( c \) represents the wave speed, and \( \Psi(\cdot) = (\psi_j(\cdot))_{j \in \mathbb{Z}} \) is called the wave profile. Moreover, we say that \( \Psi(\cdot) \) is a pulsating traveling (wave) front if \( \Psi(\cdot) \) is monotone.

As mentioned above, the following result on minimal wave speeds of the leftward and rightward pulsating traveling fronts is a direct consequence of Lemma 7 and [19, Theorem 5.3].

**Theorem 3.** Assume that (A0)–(A4) hold. Then, system (4) has a rightward (or leftward) pulsating traveling front with speed \( c \) connecting \( 0 \) and \( \beta \) if and only if \( c \geq c_1^+ \) (or \( c \geq c_1^- \)).

We now consider the characteristic problems of wave profiles’ equations. Let \( \Psi^+(\xi) = (\psi^+_j(-j + ct))_{j \in \mathbb{Z}} \) and \( \Psi^-(\xi) = (\psi^-_j(j + ct))_{j \in \mathbb{Z}} \) be the rightward and leftward wave profiles of (4), respectively. By (29), it is clear that

\[
\begin{align*}
\frac{d\psi^+_j}{d\xi} &= D_{j+1} \psi^+_{j+1}(\xi + 1) + D_j \psi^+_{j-1}(\xi - 1) - (D_{j+1} + D_j) \psi^+_j(\xi) \\
&\quad + f_j(\psi^+_j(\xi), \sum_{k \in \mathbb{Z}} J(k) S_{j-k}(\psi^\pm_{j-k}(\xi \pm k - \tau))), \\
\psi^+_{j+N}(\xi) &= \psi^+_j(\xi), \quad \psi^+_j(-\infty) = 0, \quad \psi^+_j(+\infty) = \beta_j, \ j \in \mathbb{Z}.
\end{align*}
\]

(30)

The characteristic problems for (30) with respect to the equilibrium \( 0 \) can be represented by

\[
\begin{align*}
\lambda \nu_j &= D_{j+1} e^{-\nu_j} + D_j e^{\nu_j} - (D_{j+1} + D_j) \nu_j + \partial_1 f_j(0, 0) \nu_j \\
&\quad + \partial_2 f_j(0, 0) e^{-\lambda \tau} \sum_{k \in \mathbb{Z}} J(j - k) S_k(0) e^{\mu(j-k)} \nu_k, \ j \in \mathbb{Z},
\end{align*}
\]

(31)

\[
\nu_j = \nu_{j+N}, \ j \in \mathbb{Z},
\]
respectively. Let $\lambda(\mu)$ be the principal eigenvalue of (31) and $\nu_j(\mu)$ be the corresponding strongly positive eigenfunction. Then $\lambda(\mu) = \lambda(-\mu)$ and $\bar{\nu}_j(\mu) = \nu_j(-\mu)$ are the principal eigenvalue and strongly positive eigenfunction of (32) respectively. By Lemma 8, we have the following result.

**Lemma 13.** The functions $\Phi^\pm(\mu) := \lambda(\pm \mu)/\mu$ have the following properties.

1. There exist $\mu_*^\pm > 0$ such that $\Phi(\mu_*^+) = \inf_{\mu > 0} \Phi^\pm(\mu) = c_*^\pm$, $\Phi^\pm(\mu) > c_*^\pm$ for any $\mu \in (0, \mu_*^\pm)$ and $\Phi^\pm(\mu)$ are strictly decreasing in $(0, \mu_*^\pm)$.
2. For any $c > c_*^\pm$, there exists a unique $\mu_*^\pm := \mu_*^\pm(c) \in (0, \mu_*^\pm)$ such that $\Phi^\pm(\mu_*^\pm) = c$ and there exist $\tilde{\mu}^\pm := \tilde{\mu}^\pm(c) \in (\mu_*^\pm, \mu_*^\pm)$ such that $\tilde{\mu}^\pm < 2\mu_*^\pm$ and $\Phi^\pm(\tilde{\mu}^\pm) < c$.

**Proof.** (1) We only prove the statement for $\Phi^+(\mu)$, since the other case can be proved similarly. By Lemma 8, $\Phi^+(\infty) = \infty$ and $\Phi^+(0^+) = \infty$. Hence there exists a unique $\mu_*^+ > 0$ such that

$$\Phi(\mu_*^+) = \inf_{\mu > 0} \Phi^+(\mu) = c_*^+ \quad \text{and} \quad \Phi^+(\mu) > c_*^+ \quad \text{for any} \quad \mu \in (0, \mu_*^+)\text{.}$$

We claim that $\Phi^+(\mu_1) \neq \Phi^+(\mu_2)$ for any $0 < \mu_1 < \mu_2 < \mu_*^+$. If the claim is false, then there exist $0 < \tilde{\mu}_1 < \tilde{\mu}_2 < \mu_*^+$ such that $\Phi^+(\tilde{\mu}_1) = \Phi^+(\tilde{\mu}_2) := \gamma$. Using the convexity of $\lambda(\mu)$, we have

$$\frac{\lambda(\mu) - \lambda(\tilde{\mu}_2)}{\mu - \tilde{\mu}_2} \leq \frac{\lambda(\tilde{\mu}_1) - \lambda(\tilde{\mu}_2)}{\mu_1 - \tilde{\mu}_2} = \gamma, \quad \forall \mu \geq \tilde{\mu}_2,$$

which implies that $\lambda(\mu) \geq \gamma \mu$ for $\mu \geq \tilde{\mu}_2$. Hence $\Phi^+(\mu_*) \geq \gamma > c_*^+$ which gives a contradiction. Suppose that there exist $0 < \tilde{\mu}_1 < \tilde{\mu}_2 < \mu_*^+$ such that $\Phi^+(\tilde{\mu}_1) < \Phi^+(\tilde{\mu}_2)$. Since $\Phi^+(\tilde{\mu}_2) > \Phi^+(\tilde{\mu}_1) > \Phi^+(\mu_*^+)$, there exists $\mu_0 \in (\tilde{\mu}_2, \mu_*^+) \subseteq (\tilde{\mu}_1, \mu_*^+)$ such that $\Phi^+(\tilde{\mu}_1) = \Phi^+(\mu_0)$, which contradicts to the above claim. Therefore, we deduce that for any $0 < \mu_1 < \mu_2 < \mu_*^+$, $\Phi^+(\mu_1) > \Phi^+(\mu_2)$, i.e. $\Phi^+(\mu)$ is strictly decreasing in $(0, \mu_*^+)$. The assertion of (2) follows directly from assertion of (1). This completes the proof.

The existence and asymptotic behaviour of the rightward and leftward pulsating traveling fronts of (4) are stated as follows.

**Theorem 4.** Assume that (A0)–(A4) and (A4)’ hold.

1. For any $c > c_*^+$, system (4) has a rightward pulsating traveling front $\Psi^+(\xi) = (\psi^+_j(\xi))_{j \in \mathbb{Z}}$ with $\xi = -j + ct$, connecting $0$ and $\beta$, and satisfies $(\psi^+_j)'(\xi) > 0$,

$$\lim_{\xi \to -\infty} \psi^+_j(\xi)e^{-\mu_1^+(c)\xi} = \nu_j(\mu_1^+(c)) \quad \text{and} \quad \psi^+_j(\xi) \leq e^{\mu_1^+(c)\xi}\nu_j(\mu_1^+(c)), \quad \forall \xi \in \mathbb{R}, \ j \in \mathbb{Z}. \quad \text{(33)}$$

2. For any $c > c_*^-$, system (4) has a leftward pulsating traveling front $\Psi^-(-\xi) = (\psi^-_j(\xi))_{j \in \mathbb{Z}}$ with $\xi = j + ct$, connecting $0$ and $\beta$, and satisfies $(\psi^-_j)'(-\xi) > 0$,

$$\lim_{\xi \to -\infty} \psi^-_j(\xi)e^{-\mu_1^-(c)\xi} = \nu_j(\mu_1^-(c)) \quad \text{and} \quad \psi^-_j(\xi) \leq e^{\mu_1^-(c)\xi}\nu_j(\mu_1^-(c)), \quad \forall \xi \in \mathbb{R}, \ j \in \mathbb{Z}. \quad \text{(34)}$$
We only prove part (1) of Theorem 4 in the sequel, since the proof for part (2) is similar.

5.1. The method of sub- and supersolutions. Recall that \( \omega_j = D_{j+1} + D_j + L_1 \), \( j \in \mathbb{Z} \), and \( L_1 = \max_{(u,v) \in [0,K] \times [0,\Lambda]} |\partial_h f_j(u,v)| \). Let’s define the operator \( H[\cdot] \) and set \( \Lambda \) by

\[
H[\psi_j](\xi) := D_{j+1} \psi_{j+1}(\xi - 1) + D_j \psi_{j-1}(\xi + 1) + L_1 \psi_j(\xi) + f_j(\psi_j(\xi), \sum_{k \in \mathbb{Z}^+} J(k) S_{j-k}(\psi_{j-k}(\xi + k - c \tau))),
\]

\[
\Lambda := \{ (\psi_j)_{j \in \mathbb{Z}} | \psi_j(\xi) \text{ is non-decreasing in } \xi \in \mathbb{R}, \psi_j(-\infty) = 0 \leq \psi_j(\xi) \leq K, \text{ and } \psi_{j+N}(\xi) = \psi_j(\xi), \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \}
\]

Assume \( c > 0 \). It is clear that \( \psi_j \in \Lambda \) satisfies the first equation of (30) if and only if \( \psi_j \) satisfies

\[
\psi_j(\xi) = T_c[\psi_j](\xi) := \frac{1}{c} \int_{-\infty}^{\xi} e^{-\frac{2c}{c+1}(\xi-s)} H[\psi_j](s) ds.
\] (35)

One can easily verify that the operator \( T_c[\cdot] \) has the following properties:

(i) \( T_c[\psi_{1,j}](\xi) \leq T_c[\psi_{2,j}](\xi) \), for any \( \psi_{1,j}, \psi_{2,j} \in C(\mathbb{R}, [0, K]) \) satisfying \( \psi_{1,j}(\cdot) \leq \psi_{2,j}(\cdot) \).

(ii) \( T_c[\psi_j](\xi) \) is non-decreasing in \( \xi \in \mathbb{R} \), if \( \psi_j(\cdot) \in C(\mathbb{R}, [0, K]) \) is non-decreasing in \( \xi \in \mathbb{R} \).

Now, we give the definitions of sub- and supersolutions of (30).

**Definition 5.** A function \((\psi_j)_{j \in \mathbb{Z}} \) with \( \psi_j \in C(\mathbb{R}, [0, K]) \) is called a supersolution (or a subsolution) of (30) if it satisfies \( \psi_j(\xi) \geq (\text{or} \leq) T_c[\psi_j](\xi) \), \( \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \).

**Remark 1.** If \((\psi_j)_{j \in \mathbb{Z}} \) with \( \psi_j \in C(\mathbb{R}, [0, K]) \) is differentiable almost everywhere and satisfies

\[
c \phi_j'(\xi) \geq (\text{or} \leq) - \omega_j \phi_j(\xi) + H[\psi_j](\xi), \ a.e. \ in \ \mathbb{R} \text{ for } j \in \mathbb{Z},
\]

then \( \phi(\xi) \) is a supersolution (or a subsolution) of (30).

**Theorem 5.** Assume that (A0)–(A4) hold, \( c > 0 \) and (30) admits a pair of sub- and super-solution \( \phi^\pm(\xi) = (\phi_j^\pm(\xi))_{j \in \mathbb{Z}} \) satisfying \( \phi^\pm \in \Lambda, \phi^\pm_j \neq 0 \) and \( 0 \leq \phi^-_j(\xi) \leq \phi^+_j(\xi) \leq K, \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \). Then there exists a monotone increasing solution of (30) connecting \( 0 \) and \( \beta \), i.e. (4) has a rightward pulsating traveling front connecting \( 0 \) and \( \beta \) with speed \( c \).

**Proof.** The proof is standard and sketched as follows. Consider the monotone iteration scheme:

\[
\begin{align*}
\psi_j^{(n)}(\xi) &= T_c[\psi_j^{(n-1)}](\xi), \ n = 1, 2, \cdots, \\
\psi_j^{(0)}(\xi) &= \phi^+_j(\xi), \ \xi \in \mathbb{R}, \ j \in \mathbb{Z}.
\end{align*}
\]

Due to the properties of the operator \( T_c \) and the supersolution, we can verify that \( \psi_j^{(n)} \in \Lambda \) and

\[
\phi^-_j(\xi) \leq \psi_j^{(n+1)}(\xi) \leq \psi_j^{(n)}(\xi) \leq \phi^+_j(\xi), \ \xi \in \mathbb{R}, j \in \mathbb{Z}.
\]

Then, (30) has a monotone increasing solution \( \phi = (\phi_j(\xi))_{j \in \mathbb{Z}} \) with \( \phi \in \Lambda \).
Next, we prove \( \phi_j(\pm \infty) = \beta_j \). Let \( \phi_j(\pm \infty) = \gamma_j \). Since \( \phi_j \neq 0 \) and \( \phi_j(\cdot) \) is non-decreasing, we have \( 0 < \gamma_j \leq K, \forall j \in \mathbb{Z} \). Note that
\[
cot \phi_j(\xi) = \int_{-\infty}^{\xi} e^{-\frac{s}{\nu_j}(c-s)} H[\phi_j](s)ds, \ j \in \mathbb{Z}, \ \xi \in \mathbb{R}.
\]
Using the L. Hopital’s rule, we obtain
\[
0 = D_{j+1}[\gamma_{j+1} - \gamma_j] + D_j[\gamma_{j-1} - \gamma_j] + f_j(\gamma_j, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\gamma_k)), \ j \in \mathbb{Z}.
\]
That is, \( \gamma = (\gamma_j)_{j \in \mathbb{Z}} \) is a positive and periodic equilibrium of (4). By Lemma 6, \( \beta = \gamma \).

5.2. Existence and asymptotic behavior of pulsating traveling fronts. Given any \( c > c_1^+ \), we denote \( \nu^+ := \nu(\mu^+_1(c)) \) and \( \bar{\nu} := \nu(\tilde{\mu}^+(c)) \) by the strongly positive eigenfunctions of (31) with respect to \( \mu^+_1(c) \) and \( \tilde{\mu}^+(c) \), respectively. For simplicity, in this subsection we write \( \mu^+_1 \) and \( \tilde{\mu}^+ \) by \( \mu_1 \) and \( \bar{\mu} \). We further denote
\[
\mathcal{L}[\psi_j(\xi)] := D_{j+1}\psi_j(\xi-1) + D_j\psi_j-1(\xi+1) - (D_{j+1} + D_j)\psi_j(\xi).
\]
Based on Lemma 13, we can construct a pair of supersolution and subsolution of (30).

**Lemma 14.** Assume that (A0)–(A4) hold, \( c > c_1^+ \) and \( q > 1 \). Denote \( \phi_j^+(\xi) \) by
\[
\phi_j^+(\xi) := \min\{\beta_j, e^{\mu_1 \xi} \nu_j^1\} \quad \text{and} \quad \phi_j^-(\xi) := \max\{0, e^{\tilde{\mu} \xi} \nu_j^1 - q e^{\nu_j^1} \}
\]
Then \( \phi_j^+(\xi) \) is a supersolution of (30), and \( \phi_j^-(\xi) \) is a subsolution of (30) provided that \( q \) is large enough.

**Proof.** Let’s define
\[
\mathcal{H}[\psi_j](\xi) := e^{\psi_j(\xi)} - \mathcal{L}[\psi_j(\xi)] - f_j(\psi_j(\xi), \sum_{k \in \mathbb{Z}} J(k)S_{j-k}(\psi_{j-k}(\xi+k-c\tau))).
\]
We first show that \( \phi_j^+(\xi) \) is a supersolution of (30). If \( \xi \geq \xi_j^+ := (\ln \beta_j - \ln \nu_j^1)/\mu_1 \), then \( \phi_j^+(\xi) = \beta_j \). It follows from (A3) that
\[
\mathcal{H}[\phi_j^+](\xi) \geq -\Delta[\beta_j] - f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(k)S_{j-k}(\beta_{j-k})) = 0. \quad (36)
\]
If \( \xi \leq \xi_j^+ \), then \( \phi_j^+(\xi) = e^{\mu_1 \xi} \nu_j^1 \). Note that \( \phi_j^+(\xi) \leq e^{\mu_1 \xi} \nu_j^1 \) for all \( \xi \in \mathbb{R} \), then it follows (A4) that
\[
\mathcal{H}[\phi_j^+](\xi) \geq e^{\phi_j^+(\xi)} - \mathcal{L}[\phi_j^+(\xi)] - \partial_1 f_j(0,0)\phi_j^+(\xi)
- \partial_2 f_j(0,0) \sum_{k \in \mathbb{Z}} J(k)S_{j-k}(0)\phi_j^+(\xi+k-c\tau)
\geq e^{\mu_1 \xi} \{c \mu_1 \nu_j^1 - [D_{j+1} e^{-\mu_1 \nu_j^1} + D_j e^{\mu_1 \nu_j^1} (D_{j+1} + D_j)\nu_j^1]
- \partial_1 f_j(0,0)\nu_j^1 - \partial_2 f_j(0,0)e^{-\mu_1 \tau} \sum_{k \in \mathbb{Z}} J(k)S_{j-k}(0)e^{\mu_1 k} \nu_j^1 \}
\]
\[
= e^{\mu_1 \xi} \{\lambda(\mu_1) \nu_j^1 - [D_{j+1} e^{-\mu_1 \nu_j^1} + D_j e^{\mu_1 \nu_j^1} (D_{j+1} + D_j)\nu_j^1]
- \partial_1 f_j(0,0)\nu_j^1 - \partial_2 f_j(0,0) e^{-\lambda(\mu_1) \tau} \sum_{k \in \mathbb{Z}} J(k)S_{j-k}(0)e^{\mu_1 k} \nu_j^1 \}
= 0. \quad (37)
\]
By (36) and (37), we see that \( \phi_j^+(\xi) \) is a supersolution of (30). Similarly, we can show that \( \phi_j^-(\xi) \) is a subsolution of (30) provided that \( q \) is sufficiently large. The proof is complete.

By Theorem 5 and Lemma 14, we are ready to prove the results of Theorem 4.

Proof of Theorem 4. As mentioned before, we only prove the results for the rightward pulsating traveling fronts. According to Lemma 9, we know that \( c^+_r > 0 \). Thus, by Theorem 5 and Lemma 14, for each \( c > c^+_r \), system (4) has a rightward pulsating traveling front \( \Psi^+ (\xi) := (\psi_j^+(\xi))_{j \in \mathbb{Z}} \) connecting 0 and \( \beta \), which satisfies

\[
\phi_j^-(\xi) \leq \psi_j^+(\xi) \leq \phi_j^+(\xi) \quad \text{for all} \quad \xi \in \mathbb{R}, \quad j \in \mathbb{Z}. 
\]

It is clear that (33) holds. Moreover, using \( (\psi_j^+)'(\xi) \geq 0 \), we deduce that

\[
e(\psi_j^+)^{\prime\prime} (\xi) \geq -\omega_j(\psi_j^+)'(\xi), \quad \forall j = 1, \cdots, n \text{ and } \xi \in \mathbb{R},
\]

which implies that

\[
(\psi_j^+)'(\xi) \geq (\psi_j^+)'(s) e^{-\lambda_j(s-\xi)} \geq 0, \quad \forall s \leq \xi. \tag{38}
\]

Suppose that the assertion \( (\psi_j^+)'(\xi) > 0 \) for all \( \xi \in \mathbb{R}, j \in \mathbb{Z} \) is false, then there exist \( j_0 \in \{1, \cdots, n\} \) and \( \xi_0 \in \mathbb{R} \) such that \( (\psi_{j_0}^+)'(\xi_0) = 0 \). By (38), we see that \( (\psi_{j_0}^+)'(s) = 0 \) for all \( s \leq \xi_0 \), which contradicts the fact \( \lim_{\xi \to -\infty} \psi_{j_0}^+(\xi) e^{-\mu_1(c)\xi} = \nu_j(\mu_1(c)) > 0 \). Therefore, \( (\psi_j^+)(\xi) \geq 0 \) for all \( \xi \in \mathbb{R}, j \in \mathbb{Z} \). The proof of Theorem 4 is complete.

5.3. Uniqueness of noncritical pulsating traveling fronts. Theorem 4 guarantees that system (4) has two rightward and leftward pulsating traveling fronts with speed \( c > c^+_r \) and \( c > c^-_l \), respectively, which have exponential decay rates at \(-\infty\). In this section, we shall show that the noncritical pulsating traveling front with given speed and satisfying the exponential decay rates at \(-\infty\) is unique (up to a translation). We only prove the uniqueness of the leftward pulsating traveling front, since the same issue for the rightward pulsating traveling front can be discussed similarly. In addition to the assumptions of Theorem 4, we also need the following assumption:

(5A): \( \partial_i f_j(u,v) \leq \partial_i f_j(0,0), i = 1,2, \) and \( S_{j}^{\prime}(u) \leq S_{j}^{\prime}(0) \) for all \( j \in \mathbb{Z} \).

Recall that \( \tilde{\lambda}(\mu) \) is the principal eigenvalue of (32) and \( \tilde{\nu}_j(\mu) \) is the corresponding strongly positive eigenfunction.

Theorem 6. Assume the assumptions of Theorem 4 and (5A) hold. Let \( \Psi(\xi) = (\psi_j(\xi))_{j \in \mathbb{Z}} \) and \( \Phi(\xi) = (\phi_j(\xi))_{j \in \mathbb{Z}} \), \( \xi = j + ct \), be two leftward pulsating traveling fronts of system (4) connecting 0 and \( \beta \) with speed \( c > c^-_l \), and satisfy

\[
\lim_{\xi \to -\infty} e^{\mu_1(c)\xi} \psi_j(\mu_1(\xi)) = h_1 \quad \text{and} \quad \lim_{\xi \to -\infty} e^{\mu_1(c)\xi} \phi_j(\mu_1(\xi)) = h_2, \tag{39}
\]

where \( h_1, h_2 \) are positive constants. Then there exists \( \xi_0 \in \mathbb{R} \) such that \( \Psi(\xi) = \Phi(\xi + \xi_0) \).

Proof. For convenience, we denote \( \mu_1^{-} \) by \( \mu_1 \). By a translation if necessary, we may assume

\[
\lim_{\xi \to -\infty} e^{\mu_1^{-}\xi} \psi_j(\mu_1) = \lim_{\xi \to -\infty} e^{\mu_1^{-}\xi} \phi_j(\mu_1) = 1. \tag{40}
\]
Let’s define
\[
Q_j(\xi) := \frac{\phi_j(\xi) - \psi_j(\xi)}{e^{\mu_1 \nu_j(\mu_1)}}, \ j \in \mathbb{Z} \text{ and } Q(\xi) := \max_{j \in \{1, \cdots, N\}} Q_j(\xi), \ \forall \xi \in \mathbb{R}.
\]

It is clear that \(Q_j(\cdot) = Q_{j+N}(\cdot), \ Q_j(\pm \infty) = 0, \ \forall j \in \mathbb{Z}, \) and \(Q(\pm \infty) = 0.\) We first prove that \(\phi_j(\xi) \leq \psi_j(\xi), \ \forall \xi \in \mathbb{R}, \ j \in \mathbb{Z}.\) It is sufficient to show that \(Q(\xi) \leq 0, \ \forall \xi \in \mathbb{R}.\) Suppose for the contrary that there exists \(\xi_* \in \mathbb{R} \) such that \(Q(\xi_*) = \max_{\xi \in \mathbb{R}} Q(\xi) > 0.\) By the definition of \(Q(\xi),\) there exists \(j_* \in \{1, \cdots, N\} \) such that \(Q(\xi_*) = Q_{j_*}(\xi_*).\) For the function \(Q_{j_*}(\xi),\) we have
\[
Q_{j_*}(\xi) \leq Q(\xi) \leq Q_{j_*}(\xi_*), \ \forall \xi \in \mathbb{R},
\]
which implies that \(Q_{j_*}(\xi)\) attains its maximum at \(\xi_*\). Since \(Q_{j_*}(\pm \infty) = 0,\) we can redefine \(\xi_*\) such that \(Q_{j_*}(\xi_*) = \max_{\xi \in \mathbb{R}} Q_{j_*}(\xi) \) and \(Q_{j_*}(\xi) < Q_{j_*}(\xi_*)\) for any \(\xi < \xi_*\). Clearly, \(Q'_{j_*}(\xi_*) = 0.\) Since
\[
Q'_{j_*}(\xi) = \frac{1}{\nu_j(\mu_1)}[\phi'_{j_*}(\xi) - \psi'_{j_*}(\xi)]e^{-\mu_1 \xi} - \mu_1 Q_{j_*}(\xi),
\]
it follows from (A5) that
\[
c\mu_1 \bar{\nu}_{j_*}(\mu_1)Q_{j_*}(\xi_*)e^{\mu_1 \xi_*} = c[\phi'_{j_*}(\xi_*) - \psi'_{j_*}(\xi_*)] \\
\leq c[\phi_{j_*}(\xi_*) - \psi_{j_*}(\xi_*)] + \partial_1 f_{j_*}(0, 0)[\phi_{j_*}(\xi_*) - \psi_{j_*}(\xi_*)] \\
+ \partial_2 f_{j_*}(0, 0) \sum_{k \in \mathbb{Z}} J(k)S_{j_*-k}(0) \max \{0, \phi_{j_*-k}(\xi_* - k - c\tau) - \psi_{j_*-k}(\xi_* - k - c\tau)\}
\]
\[
= D_{j_*+1}Q_{j_*+1}(\xi_* + 1)e^{\mu_1(\xi_* + 1)}\bar{\nu}_{j_*+1}(\mu_1) + D_{j_*}Q_{j_*-1}(\xi_* - 1)e^{\mu_1(\xi_* - 1)}\bar{\nu}_{j_*-1}(\mu_1) \\
- (D_{j_*+1} + D_{j_*})Q_{j_*}(\xi_*)e^{\mu_1 \xi} \bar{\nu}_{j_*}(\mu_1) + \partial_1 f_{j_*}(0, 0)Q_{j_*}(\xi_*)e^{\mu_1 \xi} \bar{\nu}_{j_*}(\mu_1) \\
+ \partial_2 f_{j_*}(0, 0) \sum_{k \in \mathbb{Z}} J(k)S_{j_*-k}(0) \max \{0, \ Q_{j_*-k}(\xi_* - k - c\tau)\}e^{\mu_1(\xi_* - k - c\tau)}\bar{\nu}_{j_*-k}(\mu_1).
\]

Note that \(Q_{j_*+1}(\xi_* + 1) \leq Q(\xi_* + 1) \leq Q(\xi_*) = Q_{j_*}(\xi_*)\) and
\[
Q_{j_*-k}(\xi_* - k - c\tau) \leq Q(\xi_* - k - c\tau) \leq Q(\xi_*) = Q_{j_*}(\xi_*) \quad \forall k \in \mathbb{Z}. \tag{42}
\]

According to (41) and (42), we see that
\[
c\mu_1 \bar{\nu}_{j_*}(\mu_1)Q_{j_*}(\xi_*) \\
\leq [D_{j_*+1}e^{\mu_1 \nu_{j_*+1}(\mu_1)} + D_{j_*}e^{-\mu_1 \nu_{j_*-1}(\mu_1)} - (D_{j_*+1} + D_{j_*})\bar{\nu}_{j_*}(\mu_1)]Q_{j_*}(\xi_*) + \partial_1 f_{j_*}(0, 0)e^{-c\mu_1 \tau} \\
\times \sum_{k \in \mathbb{Z}} J(k)S_{j_*-k}(0)\bar{\nu}_{j_*-k}(\mu_1) \max \{0, \ Q_{j_*-k}(\xi_* - k - c\tau)\}e^{-\mu_1 k}. \tag{43}
\]

Moreover, from (32) and the fact \(\bar{\lambda}(\mu_1) = c\mu_1,\) we obtain
\[
c\mu_1 \bar{\nu}_{j_*}(\mu_1) = D_{j_*+1}e^{\mu_1 \nu_{j_*+1}(\mu_1)} + D_{j_*}e^{-\mu_1 \nu_{j_*-1}(\mu_1)} \\
- (D_{j_*+1} + D_{j_*})\bar{\nu}_{j_*}(\mu_1) + \partial_1 f_{j_*}(0, 0)\bar{\nu}_{j_*}(\mu_1) \\
+ \partial_2 f_{j_*}(0, 0)e^{-c\mu_1 \tau} \sum_{k \in \mathbb{Z}} J(k)S_{j_*-k}(0)e^{-\mu_1 k}\bar{\nu}_{j_*-k}(\mu_1). \tag{44}
\]
From (42), (43) and (44), we have
\[
0 \leq \partial_2 f_j(0,0)e^{-\rho_1 \tau} \sum_{k \in \mathbb{Z}} J(k)S_j'(-k)(0)e^{-\mu_1 k}\bar{\nu}_j(-k)(\mu_1)
\times [Q_j, (\xi_*) - \max \{0, Q_j, (\xi_*) - k - \epsilon\tau\}] \leq 0,
\]
which implies that
\[
\partial_2 f_j(0,0)e^{-\rho_1 \tau} J(0)S_j'(0)\bar{\nu}_j(\mu_1)[Q_j, (\xi_*) - \max \{0, Q_j, (\xi_*) - \epsilon\tau\}] = 0.
\]
By the assumption \( \partial_2 f_j(0,0) J(0)S_j'(0) > 0 \) and the fact \( Q_j, (\xi_*) > 0 \), we have \( Q_j, (\xi_*) = \max \{0, Q_j, (\xi_*) - \epsilon\tau\} \) which contradicts to the fact \( Q_j, (\xi_*) < Q_j, (\xi_*) \) for any \( \xi < \xi_* \). Thus, we conclude that \( \phi_j(\xi) \leq \psi_j(\xi), \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \). Exchanging the roles of \( \phi_j(\xi) \) and \( \psi_j(\xi) \), we also obtain \( \psi_j(\xi) \leq \phi_j(\xi), \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \). Thus \( \psi_j(\xi) = \phi_j(\xi), \forall \xi \in \mathbb{R}, j \in \mathbb{Z} \). This completes the proof. \( \square \)

6. Stability of pulsating traveling fronts. In this section, we consider the stability of the pulsating traveling fronts. We only prove the stability of the leftward pulsating traveling fronts, since the same issue for the rightward pulsating traveling fronts can be discussed similarly.

First, we consider the following two related eigenvalue problems:

\[
\begin{aligned}
\lambda w_j &= \Delta[w_j] + \partial_1 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) w_j \\
+ e^{-\lambda \tau} \partial_2 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k)S_k'(\beta_k) w_k, \\
w_{j+N} &= w_j, \quad j \in \mathbb{Z},
\end{aligned}
\]

(45)

and

\[
\begin{aligned}
\lambda w_j &= \Delta[w_j] + \partial_1 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) w_j \\
+ \partial_2 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k)S_k'(\beta_k) w_k, \\
w_{j+N} &= w_j, \quad j \in \mathbb{Z},
\end{aligned}
\]

(46)

To determine the sign of the principal eigenvalues of (45) and (46), we impose the following additional assumption.

\( (A6) \): For any \( \forall j \in \mathbb{Z}, \)

\[
\partial_1 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) + \partial_2 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k)S_k'(\beta_k) < 0.
\]

Lemma 15. Assume that \( (A0)–(A3) \) and \( (A6) \) hold. Then there exists a principal eigenvalue \( \tilde{\lambda} \) of (45) associated with a strictly positive eigenfunction \( (w_j)_{j \in \mathbb{Z}} \) with \( w_{j+N} = w_j \). Moreover, for any \( \tau > 0, \tilde{\lambda} \) has the same sign as \( \lambda_0 < 0 \) which is the principal eigenvalue of (46).

Proof. Using \( (A6) \), the proof is similar to that of Lemmas 4 and 5. We omit it here. \( \square \)

Let \( \epsilon \in (0, -\tilde{\lambda}) \) be a fixed number. Due to the periodicity, we can choose \( \epsilon_1 > 0 \) such that

\[
\epsilon w_j \geq \epsilon_1 [w_j + \partial_2 f_j (\beta_j, \sum_{k \in \mathbb{Z}} J(j - k)S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k)e^{-\lambda \tau} w_k.
\]
Furthermore, we choose a small $\delta > 0$ such that for any $z = (z_j)_{j \in \mathbb{Z}}$ and $v = (v_j)_{j \in \mathbb{Z}}$ satisfying $\beta_j - \delta < z_j < \beta_j$, $\beta_j - \delta < v_j < \beta_j$ for all $j \in \mathbb{Z}$, there holds

$$
\partial_t f_j(z_j, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\beta_k)) < \partial_t f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\beta_k)) + \epsilon_1, \quad i = 1, 2,
$$

$$
S'_j(z_j) < S'_j(\beta_j) + \epsilon_1.
$$

The stability result of pulsating traveling fronts is stated in the following theorem.

**Theorem 7.** Assume that (A0)–(A6) hold. Let $\Psi^-(j + ct) = (\psi^-_j(j + ct))_{j \in \mathbb{Z}}$ be a leftward pulsating traveling front of system (4) with $c > c^-$ connecting 0 and $\beta$. For a sufficiently small $\epsilon > 0$, we denote $\mu_\epsilon = \mu^-(c) + \epsilon$ and define the weight function $W^\epsilon : \mathbb{Z} \to \mathbb{R}_+$ as follows:

$$
W^\epsilon(j) := \begin{cases} 
  e^{-\mu_\epsilon(j-J_0)}, & j \leq J_0, \\
  1, & j > J_0,
\end{cases}
$$

where $J_0 \in \mathbb{Z}$ is chosen such that $\beta_j - \delta \leq \psi^-_j(j + ct), \psi^-_j(j + c(t - \tau)) \leq \beta_j$ for any $j + ct \geq J_0$. Then, there exists a number $\epsilon_0 > 0$ such that for any given initial value $u^0_j(s)$ with

$$
0 \leq u^0_j(s) \leq \beta_j \quad \text{and} \quad [u^0_j(s) - \psi^-_j(j + cs)]W^\epsilon(j) \in L^\infty(\mathbb{Z}, \mathbb{R}), \quad \forall j \in \mathbb{Z}, \ s \in [-\tau, 0],
$$

the unique solution $u_j(t; u^0)$ of (4) satisfies $0 \leq u_j(t; u^0) \leq \beta_j, \forall j \in \mathbb{Z}, t \geq 0$, and for some $C > 0$,

$$
\sup_{j \in \mathbb{Z}} |u_j(t; u^0) - \psi^-_j(j + ct)| \leq Ce^{-\epsilon_0 t}, \quad \forall \ t \geq 0.
$$

**Proof.** We define two functions

$$
U^+_j(s) := \max\{u^0_j(s), \psi^-_j(j + cs)\}, \forall j \in \mathbb{Z}, \ s \in [-\tau, 0],
$$

$$
U^-_j(s) := \min\{u^0_j(s), \psi^-_j(j + cs)\}, \forall j \in \mathbb{Z}, \ s \in [-\tau, 0].
$$

Let $U^+_j(t)$ be the solutions of (4) with the initial values $U^+_j(s)$ and $U^-_j(s)$, respectively. Then, a simple application of the comparison principle implies that

$$
0 \leq U^-_j(t) \leq u_j(t; u^0), \psi^-_j(j + ct) \leq U^+_j(t) \leq \beta_j, \forall j \in \mathbb{Z}, t \geq 0,
$$

which yields that

$$
|u_j(t; u^0) - \psi^-_j(j + ct)| \leq \max\{|U^+_j(t) - \psi^-_j(j + ct)|, |U^-_j(t) - \psi^-_j(j + ct)|\}.
$$

Thus, to prove the assertion of this theorem, it is sufficient to show that $U^+_j(t)$ converges to $\psi^-_j(j + ct)$ exponentially in time. By symmetry, we only prove that $U^+_j(t)$ converges to $\psi^-_j(j + ct)$. Define $V_j(t) := U^+_j(t) - \psi^-_j(j + ct)$. It is clear that

$$
0 \leq V_j(t) \leq |u^0_j(s) - \psi^-_j(j + cs)|, \forall j \in \mathbb{Z}, s \in [-\tau, 0],
$$
which yields that $V_j(s)W^R(j)$ is uniformly bounded on $Z$ for any $s \in [-\tau, 0]$. In the sequel, we consider two cases $j + ct \leq J_0$ and $j + ct > J_0$, respectively.

**Case 1.** $j + ct \leq J_0$. By the assumption (A5), we obtain
\[
V_j'(t) = \Delta [V_j(t)] + f_j(U_j^+(t), \sum_{k \in Z} J(j - k)S_k(U_k^+(t - \tau)))
- f_j(\psi_j^-(j + ct), \sum_{k \in Z} J(j - k)S_k(\psi_k^-(k + c(t - \tau))))
\leq \Delta [V_j(t)] + \partial_1 f_j(0, 0)V_j(t) + \partial_2 f_j(0, 0)\sum_{k \in Z} J(j - k)S_k'(0)V_k(t - \tau)
\]
for any $j \in Z$, $t > 0$. Let $\bar{\nu} = (\bar{\nu}_j)_{j \in Z}$ be the eigenfunction of (32) with $\mu = \mu_\epsilon$ corresponding to the principal eigenvalue $\lambda_\epsilon := \lambda(\mu_\epsilon)$. Since $V_j(s)W^R(j)$ is uniformly bounded on $Z$ for any $s \in [-\tau, 0]$, we can choose a sufficiently large $M_1 > 0$ such that
\[
M_1 \bar{\nu}_j e^{\mu_\epsilon(j - J_0) + \lambda_\epsilon s} \geq V_j(s), \forall j \in Z, s \in [-\tau, 0].
\]
Now, we define
\[
\tilde{V}_j(t) = M_1 \bar{\nu}_j e^{\mu_\epsilon(j - J_0) + \lambda_\epsilon t}, \forall j \in Z, t \geq -\tau.
\]
One can easily verify that the function $\tilde{V}_j(t)$ satisfies
\[
\tilde{V}_j'(t) = \Delta [\tilde{V}_j(t)] + \partial_1 f_j(0, 0)\tilde{V}_j(t) + \partial_2 f_j(0, 0)\sum_{k \in Z} J(j - k)S_k'(0)\tilde{V}_k(t - \tau)
\]
for $j \in Z$, $t > 0$. Then it follows from Lemma 2 that $V_j(t) \leq \tilde{V}_j(t), \forall j \in Z, t \geq 0$. Thus, for any $j \in Z$ and $t \geq 0$ with $j + ct \leq J_0$, we have
\[
V_j(t) \leq M_1 \bar{\nu}_j e^{\mu_\epsilon(j - J_0) + \lambda_\epsilon t} \leq M_1 \bar{\nu}_j e^{\mu_\epsilon(j - J_0)} t e^{-(\epsilon\mu_\epsilon - \lambda_\epsilon) t}
\leq (M_1 \lambda_\epsilon^{\max}) t e^{-(\epsilon\mu_\epsilon - \lambda_\epsilon) t}.
\]

**Case 2.** $j + ct > J_0$. Note that $\psi_j^-(j + ct) \leq U_j^+(t) \leq \beta_j, \forall j \in Z, t \geq 0$ and $\beta_j - \delta \leq \psi_j^-(j + ct), \psi_j^-(j + c(t - \tau)) \leq \beta_j$, for any $j + ct \geq J_0$. It follows from (48) that for any $j + ct \geq J_0$, we have
\[
f_j(U_j^+(t), \sum_{k \in Z} J(j - k)S_k(U_k^+(t - \tau)))
- f_j(\psi_j^-(j + ct), \sum_{k \in Z} J(j - k)S_k(\psi_k^-(k + c(t - \tau))))
= \partial_1 f_j(\eta_j(t), \sum_{k \in Z} J(j - k)S_k(\psi_k^-(k + c(t - \tau))))\bar{V}_j(t)
+ \partial_2 f_j(\psi_j^-(j + ct), \sum_{k \in Z} J(j - k)S_k(\eta_k(t)))\sum_{k \in Z} J(j - k)S_k'(\eta_k(t))V_k(t - \tau)
\leq [\partial_1 f_j(\beta_j, \sum_{k \in Z} J(j - k)S_k(\beta_k)) + \epsilon_1]V_j(t)
+ [\partial_2 f_j(\beta_j, \sum_{k \in Z} J(j - k)S_k(\beta_k)) + \epsilon_1]\sum_{k \in Z} J(j - k)[S_k'(\beta_k) + \epsilon_1]V_k(t - \tau),
\]
where $\eta_j(t) \in [\psi_j^-(j + ct), U_j^+(t)] \subset [\beta_j - \delta, \beta_j]$ and
\[ \mathbf{\bar{\nu}}_j(t) \in [\nu_j^-(j + c(t - \tau)), U_j^+(t - \tau)] \subset [\beta_j - \delta, \beta_j]. \]

Consequently, \( V_j(t) \) satisfies
\[
V_j''(t) \leq \Delta[V_j(t)] + [\partial_t f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) + \epsilon_1] V_j(t) + [\partial_2 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) + \epsilon_1] \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) + \epsilon_1] V_k(t - \tau),
\]
for all \((j, t)\) in the domain \( \Omega := \{ (j, t) : j + ct > J_0, t > 0 \} \).

Recall that \( \tilde{\epsilon} \in (0, -\lambda) \), where \( \lambda < 0 \) is the principal eigenvalue of (45) associated with a strictly positive eigenfunction \((w_j)_{j \in \mathbb{Z}}\) with \( w_{j+N} = w_j \). Take \( \epsilon_0 = \min \{ \epsilon \mu - \lambda, -\tilde{\lambda} - \tilde{\epsilon} \} \). By the result obtained from Case 1 and the fact \( \epsilon_0 \leq \epsilon \mu - \lambda \), we can choose \( M_2 > 0 \) such that \( V_j(t) \leq M_2 w_j e^{-\epsilon_0 t} \) on the boundary
\[
\partial \Omega := \{ (j, t) : j + ct > J_0, t \in [-\tau, 0] \} \cup \{ (j, t) : j + ct = J_0, t \geq -\tau \}.
\]

Now, we define
\[
\hat{V}_j(t) := M_2 w_j e^{-\epsilon_0 t}, \quad \forall j \in \mathbb{Z}, \ t \geq -\tau.
\]
In view of \( \epsilon_0 \leq -\tilde{\lambda} - \tilde{\epsilon} \leq -\tilde{\lambda} \), we have \( \hat{V}_k(t - \tau) \leq \hat{V}_k(t)e^{-\tilde{\lambda} \tau} \), and hence,
\[
\hat{V}_j''(t) = -\epsilon_0 \hat{V}_j(t) \geq (\tilde{\lambda} + \tilde{\epsilon}) \hat{V}_j(t)
\]
\[
\geq \Delta[\hat{V}_j(t)] + [\partial_t f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) + \epsilon_1] \hat{V}_j(t) + \partial_2 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) \hat{V}_k(t - \tau).
\]

From (47), we get
\[
\tilde{\epsilon}_1 \hat{V}_j(t) \geq \epsilon_1 \hat{V}_j(t) + \epsilon_1 \partial_2 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k)e^{-\tilde{\lambda} \tau} \hat{V}_k(t) + \epsilon_1 \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) e^{-\tilde{\lambda} \tau} \hat{V}_k(t) + \epsilon_1 \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) \hat{V}_k(t - \tau)
\]
\[
+ \epsilon_1 \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) \hat{V}_k(t) + \epsilon_1 \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) \hat{V}_k(t - \tau).
\]

Thus, the function \( \hat{V}_j(t) \) satisfies
\[
\hat{V}_j''(t) \geq \Delta[\hat{V}_j(t)] + [\partial_t f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) + \epsilon_1] \hat{V}_j(t) + \partial_2 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k)) \sum_{k \in \mathbb{Z}} J(j - k) S_k(\beta_k) + \epsilon_1] \hat{V}_k(t - \tau).
\]

Then, by (51)-(52) and the comparison principle in the domain \( \Omega \), we obtain
\[
V_j(t) \leq \hat{V}_j(t) = M_2 w_j e^{-\epsilon_0 t} \leq (M_2 \max_{j \in \mathbb{Z}} w_j) e^{-\epsilon_0 t}
\]
for all \( j \in \mathbb{Z} \) and \( t \geq 0 \) with \( j + ct > J_0 \).

Combining the above two cases, we conclude that
0 \leq V_j(t) = U_j^+(t) - \psi^-_j(j + ct) \leq Me^{-ct} \text{ for all } j \in \mathbb{Z} \text{ and } t \geq 0,

where \( M := \max \{ M_1 \max_{j \in \mathbb{Z}} \bar{\psi}_j^+, M_2 \max_{j \in \mathbb{Z}} w_j \} \), that is, \( U_j^+(t) \) converges to \( \psi^-_j(j + ct) \) exponentially in time. This completes the proof.

Remark 2. Theorem 7 implies that all noncritical pulsating traveling fronts are globally exponentially stable, as long as the initial perturbations around them are uniformly bounded in a weight space. It remains open whether the critical pulsating traveling front is stable. We leave the challenging problem for future researches.

7. Examples. In this section, we apply our abstract results to two concrete models in population biology.

Example 1. [Nicholson’s blowflies model] Consider the system:

\[ u_j'(t) = \Delta [u_j(t)] - \delta_j u_j(t) + b_j(u_j(t - \tau)), \quad (53) \]

where \( j \in \mathbb{Z}, t > 0, b_j(u) = p_j u e^{-a_j u}, \ a_{j+N} = a_j > 0, \ p_{j+N} = p_j > 0, \text{ and } \delta_{j+N} = \delta_j > 0 \) for some positive integer \( N \). Assume that \( p_j > \delta_j \) and

\[
\max_{j \in \mathbb{Z}} (a_j^{-1}(\ln p_j - \ln \delta_j)) \leq \min_{j \in \mathbb{Z}} (a_j^{-1}). \quad (54)
\]

It is clear that the condition (54) equals to \( p/\delta \leq e \) when \( p_j \equiv p \) and \( \delta_j = \delta \) are constants. In fact, when \( D_j, p_j, \delta_j \) are constants, the spreading speed and the pulsating traveling fronts of (53) have been studied by many researchers, see e.g. [18, 37].

Now, let \( S_j(u) = b_j(u) = p_j u e^{-a_j u} \) and \( f_j(u, v) = -\delta_j u + v \). Then,

\[
\partial_t f_j(0, 0) + \partial_2 f_j(0, 0) S_j'(0) = p_j - \delta_j > 0 \quad \text{and} \quad \partial_2 f_j(0, 0) S_j'(0) = p_j > 0, \ \forall j \in \mathbb{Z}.
\]

Take \( K = \max_{j \in \mathbb{Z}} (a_j^{-1}(\ln p_j - \ln \delta_j)) \). Then,

\[ S_k := \max_{j \in \mathbb{Z}} S_j(K) = \max_{j \in \mathbb{Z}} p_j K e^{-a_j K} \text{ and } f_j(K, S_j(K)) \leq 0, \ \forall j \in \mathbb{Z}. \]

Also, the condition (54) implies that \( S_j'(u) = p_j (1 - a_j u) e^{-a_j u} \geq 0, \ \forall u \in [0, K], \) and for any \( \gamma \in (0, 1), j \in \mathbb{Z} \) and \( u, v \in (0, K], \) it holds that

\[
f_j(\gamma u, S_j(\gamma v)) - \gamma f_j(u, S_j(v)) = S_j(\gamma v) - \gamma S_j(v) = p_j \gamma v [e^{-a_j \gamma v} - e^{-a_j v}] > 0.
\]

From the above observations, we see that the assumptions (A0)–(A5) and (A4)’ hold. Hence Lemma 6 implies that (53) admits a unique positive and periodic equilibrium \( (\beta_j)_{j \in \mathbb{Z}}, \) i.e.,

\[
\Delta [\beta_j] - \delta_j \beta_j + b_j(\beta_j) = 0 \quad \text{and} \quad \beta_{j+N} = \beta_j, \ j \in \mathbb{Z}.
\]

Then, the conclusions of Theorems 1, 2, 3, 4 and 6 hold for (53). By Lemma 8, the following eigenvalue problem

\[
\lambda \bar{\psi}_j = D_j e^{-\mu} \bar{\psi}_{j+1} + D_j e^{\mu} \bar{\psi}_{j-1} - (D_{j+1} + D_j) \bar{\psi}_j - \delta_j \bar{\psi}_j + p_j e^{-\lambda \tau} \bar{\psi}_j
\]

and \( \bar{\psi}_j = \bar{\psi}_{j+N}, \ j \in \mathbb{Z} \)

has a principal eigenvalue \( \lambda(\mu) \) with a strictly positive eigenfunction. From Lemma 9, we have \( c_+^2 = \inf_{\mu \geq 0} \lambda(\pm \mu) > 0 \). Moreover, if

\[
\partial_t f_j(\beta_j, S_j(\beta_j)) + \partial_2 f_j(\beta_j, S_j(\beta_j)) S_j'(\beta_j) = -\delta_j + p_j (1 - a_j \beta_j) e^{-a_j \beta_j} < 0, \ \forall j \in \mathbb{Z},
\]

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i.e. (A6) holds, then the conclusions of Theorem 7 hold true for (53).

Example 2. [Other population model] We consider the system:

\[ u_j'(t) = \Delta [u_j(t)] - d_j u_j^2(t) + \sum_{k \in \mathbb{Z}} J(j-k)q_k u_k(t-\tau), \]

for \( j \in \mathbb{Z}, t > 0 \), where \( d_{j+N} = d_j > 0 \) and \( q_{j+N} = q_j > 0 \) for some positive integer \( N \). Let \( S_j(u) = q_j u \) and \( f_j(u,v) = -d_j u^2 + v \). Assume that \( J(\cdot) \) satisfies (A0). It is easy to verify that (A1)-(A5) and (A4)' hold with

\[ K = \max_{j \in \mathbb{Z}} \frac{1}{d_j} \sum_{k \in \mathbb{Z}} J(j-k)q_k. \]

Hence, our main results in Sections 3–5 on the spreading speeds and pulsating traveling fronts hold for (55). By Lemma 6, (55) has a unique positive and periodic equilibrium \((\beta_j)_{j \in \mathbb{Z}}\), i.e.,

\[ \Delta [\beta_j(t)] - d_j \beta_j^2 + \sum_{k \in \mathbb{Z}} J(j-k)q_k \beta_k = 0 \quad \text{and} \quad \beta_{j+N} = \beta_j, \quad j \in \mathbb{Z}. \]

Moreover, if

\[ \partial_1 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\beta_j)) + \partial_2 f_j(\beta_j, \sum_{k \in \mathbb{Z}} J(j-k)S_k(\beta_j)) \sum_{k \in \mathbb{Z}} J(j-k)S_k'(\beta_k) \]

\[ = -2d_j \beta_j + \sum_{k \in \mathbb{Z}} J(j-k)q_k < 0, \quad \forall j \in \mathbb{Z}, \]

then (A6) holds, and hence the results in Section 6 on the stability of the pulsating traveling fronts hold for (55).

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