

# Spatial Dynamics of a Discrete-Time Population Model in a Periodic Lattice Habitat

Yu Jin · Xiao-Qiang Zhao

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**Abstract** This paper is devoted to the study of spatial dynamics of a class of discrete-time population models in a periodic lattice habitat. In the general case of recruitment functions, we obtain the existence and computation formula of spreading speeds and show that they coincide with the minimal wave speeds for periodic traveling waves in the positive and negative directions.

**Keywords** Discrete time · Lattice systems · Spreading speeds · Periodic traveling waves

## 1 Introduction

The invasion speed is a fundamental characteristic of biological invasions since it describes the speed at which the geographic range of the population expands (see [9, 12, 13]). The asymptotic speed of spread (in short, spreading speed) and traveling wave fronts have received extensive investigations, see, e.g., [1, 4, 5, 15, 19–21, 23–25] and references therein. Earlier studies of biological invasions use reaction-diffusion equations in which reproduction and movement are assumed to occur continuously and the movement is subject to random dispersal, see, e.g., [6, 7, 17]. Recently, integrodifference models have been attracting more attentions since they consider the importance of nonoverlapping generations and various types of dispersal kernels, see, e.g., [10, 11, 14, 22, 25]. Among them is the following discrete-time model in a homogeneous habitat:

$$u_{n+1}(x) = \int_{\mathbb{R}} k(x-y)f(u_n(y))dy, \quad x \in \mathbb{R}, \quad n \in \mathbb{N}, \quad (1.1)$$

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Y. Jin · X.-Q. Zhao (✉)  
Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's,  
NL A1C 5S7, Canada  
e-mail: zhao@mun.ca

where  $u_n(x)$  is the density of the  $n$ -th generation of the population at location  $x \in \mathbb{R}$ ,  $k(x-y)$  is the dispersal kernel which describes the proportion of the population leaving  $y$  to  $x$ ,  $f$  is the recruitment function of the population.

Although most of earlier studies assumed that the environment is spatially homogeneous, the real environment is generally heterogeneous (see, e.g., [2, 3, 6–8, 11, 16, 17, 22, 24, 25]), due to natural phenomena or exposure to artificial disturbances. This indicates that in the study of biological invasions it is important to understand how spatial heterogeneities influence the characteristics of front propagation such as front speeds, front profiles and front location. As a generalization of (1.1), one may consider the following discrete-time model in a heterogeneous habitat:

$$u_{n+1}(x) = \int_{\mathbb{R}} k(x, y) f(y, u_n(y)) dy, \quad x \in \mathbb{R}, \quad n \in \mathbb{N}, \quad (1.2)$$

where  $k(x, y)$  is still the dispersal kernel, which may not depend only on the distance between  $x$  and  $y$ ,  $f(x, u)$  is the recruitment function of the population with density  $u$  at location  $x \in \mathbb{R}$ .

The simplest case of the spatial heterogeneity is a periodic habitat, by which we mean that the recruitment function (or the growth function) and dispersal properties vary periodically in the habitat. Freidin and Gärtner [6, 7] used probabilistic methods to study the spreading speed for an equation of Fisher type in which the mobility and the growth function vary periodically in space. In the ecological context, Shigesada et al. [17] first introduced a reaction-diffusion model for the spread of a single species in a patchy environment with periodic variations in diffusivity and growth rate. Weinberger [24] presented a general model in periodically varying environments and investigated spreading speeds and traveling waves in the case where the recursion operator is monotone. Guo and Hamel [8] studied the front propagation of a monotone lattice model in a periodic habitat. More recently, Kawasaki and Shigesada [11] considered propagating waves in a periodic environment in the framework of an integrodifference equation (an example of (1.2)), by the linearization method and numerical simulations. Weinberger et al. [25] established spreading speeds for (1.2) in a periodic habitat in the case where the recruitment function is not necessarily monotone in the density of the species. However, the proof of the existence of periodic traveling waves for (1.2) in this case is still an open problem.

As mentioned in [23], it is impractical to measure the population densities at all points at all times and computations for continuous models are often obtained as an approximation of the related discrete models. Thus, it is reasonable to consider the following lattice version of (1.2) in a periodic habitat in the case where the recruitment function is not necessarily monotone:

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u_n^j), \quad i \in \mathbb{Z}, \quad n \in \mathbb{N}, \quad (1.3)$$

where  $u_n^i$  is the density of the  $n$ -th generation of the population at the  $i$ -th location,  $P_{ij}$  is the dispersal kernel, which is the fraction of those individuals who successfully migrate from the  $j$ -th location to the  $i$ -th location,  $f_j(u) := f(j, u)$  is the recruitment function of the population with density  $u$  at location  $j \in \mathbb{Z}$ . The purpose of our current paper is to study spreading speeds and periodic traveling waves for (1.3) in both monotone and non-monotone cases of  $f_j(u)$ .

Throughout this paper, we always assume that (1.3) satisfies the following conditions:

- (H1)  $P_{ij}$  is nonnegative;  $P_{ij} = P_{i+L, j+L}$  for some  $L > 0$  for all  $i, j \in \mathbb{Z}$ ;  $\sum_{j=-\infty}^{+\infty} P_{ij} = 1$  for all  $i \in \mathbb{Z}$ ; and  $\sum_{j=-\infty}^{+\infty} P_{ij} e^{-\mu(i-j)} < \infty$  for all  $\mu \in (-\Delta^-, \Delta^+)$  and  $i \in \mathbb{Z}$ , where  $\Delta^- > 0$  and  $\Delta^+ > 0$  are the abscissas of convergence and they may be infinity.
- (H2) For any  $i \in \mathbb{Z}$ ,  $f_i \in C^1(\mathbb{R}_+, \mathbb{R})$ ;  $f_i(0) = 0$ ,  $f'_i(0) > 1$ ;  $f_i([0, b]) \subseteq [0, b]$  for some  $b > 0$ ;  $f_i(u) = f_{i+L}(u)$  for all  $u \in [0, b]$ ;  $\frac{f_i(u)}{u}$  is strictly decreasing in  $u \in (0, b]$ . There exists  $\hat{L} > 0$  such that  $|f_i(u_1) - f_i(u_2)| \leq \hat{L}|u_1 - u_2|$  for all  $u_1, u_2 \in [0, b]$ ,  $i \in \mathbb{Z}$ .

We also use the following notations:

$$\begin{aligned} X &= \{ \{\varphi^i\}_{i \in \mathbb{Z}} : \varphi^i \in \mathbb{R}_+, \forall i \in \mathbb{Z} \}, \\ X^L &= \{ \{\varphi^i\}_{i \in \mathbb{Z}} \in X : \varphi^i = \varphi^{i+L}, \forall i \in \mathbb{Z} \}, \\ X_b^L &= \{ \{\varphi^i\}_{i \in \mathbb{Z}} \in X^L : \varphi^i \in [0, b], \forall i \in \mathbb{Z} \}. \end{aligned}$$

For  $u \in X$ ,  $v \in X$ ,  $u \leq v$  means  $u^i \leq v^i$  for all  $i \in \mathbb{Z}$ ;  $u < v$  means  $u^i \leq v^i$  for all  $i \in \mathbb{Z}$  but  $u \neq v$ ; and  $u \ll v$  means  $u^i < v^i$  for all  $i \in \mathbb{Z}$ .

The rest of this paper is organized as follows. In Sect. 2, we consider that the recruitment function  $f_i(u)$  is monotone in  $u$  for all  $i \in \mathbb{Z}$  and establish the existence and computation formula of spreading speeds and their coincidence with the minimal wave speeds for periodic traveling waves in both positive and negative directions. In Sect. 3, we extend these results to the case of non-monotone recruitment functions by using the comparison method (for spreading speeds) and the Schauder fixed point theorem (for periodic traveling waves). An example is also given in Sect. 4 to illustrate the obtained analytic results.

### 2 Monotone Case

In this section, we consider model (1.3) with a monotone recruitment function. In addition to (H1) and (H2), we further assume that

- (H3)  $f_i(u)$  is nondecreasing in  $u \in [0, b]$  for all  $i \in \mathbb{Z}$ .

Define an operator  $Q$  on  $X$  by

$$(Q[\varphi])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j), \quad i \in \mathbb{Z}, \quad \varphi \in X. \tag{2.1}$$

Then for  $u_n = \{u_n^i\}_{i \in \mathbb{Z}} \in X$ , (1.3) can be written as

$$u_{n+1} = Q[u_n].$$

To find a fixed point of  $Q$  in  $X^L$ , we restrict  $Q$  on  $X^L$  as  $\bar{Q}$ :

$$(\bar{Q}[\varphi])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j), \quad i \in \mathbb{Z},$$

for any  $\varphi \in X^L$ . By using the periodicity properties of  $f$  and  $\varphi$ , we can write  $\bar{Q}$  as

$$\begin{aligned} (\bar{Q}[\varphi])^i &= \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\varphi^j) \\ &= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i,kL+m} f_{kL+m}(\varphi^{kL+m}) \\ &= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i,kL+m} f_m(\varphi^m) \\ &= \sum_{m=1}^L \left( \sum_{k=-\infty}^{+\infty} P_{i,kL+m} \right) f_m(\varphi^m), \end{aligned}$$

for any  $i \in \mathbb{Z}, \varphi \in X^L$ . Since  $P_{ij} = P_{i+L, j+L}$  for all  $i, j \in \mathbb{Z}$ , we have  $(\bar{Q}[\varphi])^{i+L} = (\bar{Q}[\varphi])^i$  for all  $i \in \mathbb{Z}$ , and hence,  $\bar{Q} : X^L \rightarrow X^L$ . By the periodicity of elements in  $X^L$ , we see that  $X^L$  is actually equivalent to  $\mathbb{R}_+^L$ . Thus,  $\bar{Q}$  can be considered as an operator from  $\mathbb{R}_+^L$  to  $\mathbb{R}_+^L$ :

$$(\bar{Q}[\varphi])^i = \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m), \quad \forall i \in \{1, 2, \dots, L\}, \quad \varphi \in \mathbb{R}_+^L,$$

where  $\bar{a}_{im} = \sum_{k=-\infty}^{+\infty} P_{i,kL+m}$ , for  $i, m \in \{1, 2, \dots, L\}$ .

Let  $\bar{L}_0 = D\bar{Q}[0]$  be the derivative of  $\bar{Q}$  at 0. It then follows that

$$(\bar{L}_0[\varphi])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) \varphi^j, \quad \forall i \in \mathbb{Z},$$

for any  $\varphi \in X^L$ . Similarly as we do for  $\bar{Q}$ , we can also show that  $\bar{L}_0 : X^L \rightarrow X^L$  and then consider  $\bar{L}_0$  as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ . Moreover,

$$\bar{L}_0[\varphi] = A\varphi, \quad \forall \varphi \in \mathbb{R}^L, \tag{2.2}$$

where  $A = (a_{im})_{L \times L}, a_{im} = \sum_{k=-\infty}^{+\infty} P_{i,kL+m} f'_m(0)$ , for  $i, m \in \{1, 2, \dots, L\}$ .

We further assume that

(H4)  $A$  is irreducible, and for any  $u_0 \in \mathbb{R}_+^L \setminus \{0\}$ , there exists  $k = k(u_0) \in \mathbb{N}$ , such that  $\bar{Q}^k[u_0] \gg 0$ .

Let

$$r(\bar{L}_0) = \max\{|\lambda| : \lambda \text{ is an eigenvalue of } A\}.$$

By [18, Theorem A.4], it then follows that  $r(\bar{L}_0)$  is a positive eigenvalue of  $A$  and that there is a strongly positive eigenvector of  $A$  associated with  $r(\bar{L}_0)$ .

**Lemma 2.1** *Let (H1)–(H4) hold. If  $r(\bar{L}_0) > 1$ , then there exists a unique fixed point  $\beta^* \gg 0$  in  $X_b^L$  such that every forward orbit of  $\bar{Q}$  in  $X_b^L \setminus \{0\}$  converges to  $\beta^*$ .*

*Proof* Let  $\hat{b} := (b, b, \dots, b) \in \mathbb{R}^L$  and  $\mathbb{R}_b^L := \{\varphi \in \mathbb{R}^L : 0 \leq \varphi \leq \hat{b}\}$ . Consider  $\bar{Q}$  and  $\bar{L}_0$  as operators on  $\mathbb{R}_+^L$  and  $\mathbb{R}^L$ , respectively. Obviously,  $\bar{Q}[0] = 0$ . For any  $\varphi \in \mathbb{R}_b^L$ , it follows from  $f_i([0, b]) \subseteq [0, b]$  that  $0 \leq (\bar{Q}[\varphi])^i \leq b$  for all  $i \in \mathbb{Z}$ . This implies that  $\bar{Q} : \mathbb{R}_b^L \rightarrow \mathbb{R}_b^L$ .

For  $\varphi, \psi \in \mathbb{R}_b^L$  with  $\varphi \leq \psi$ , i.e.,  $0 \leq \varphi^i \leq \psi^i \leq b$  for all  $1 \leq i \leq L$ , we have

$$(\bar{Q}[\varphi])^i = \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m) \leq \sum_{m=1}^L \bar{a}_{im} f_m(\psi^m) = (\bar{Q}[\psi])^i, \quad \forall 1 \leq i \leq L.$$

Thus,  $\bar{Q}[\varphi] \leq \bar{Q}[\psi]$ , and hence,  $\bar{Q}$  is monotone on  $\mathbb{R}_b^L$ .

Let  $\alpha \in (0, 1)$  and  $\varphi \in \mathbb{R}_b^L$  with  $\varphi \gg 0$ . Since  $\frac{f_i(u)}{u}$  is strictly decreasing in  $u \in (0, b]$ , it follows that for any  $i \in \mathbb{Z}$ ,  $f_i$  is strictly subhomogeneous on  $(0, b]$  in the sense that

$$f_i(\alpha u) > \alpha f_i(u), \quad \forall u \in (0, b], \quad \alpha \in (0, 1),$$

and hence,

$$\begin{aligned} (\bar{Q}[\alpha\varphi])^i &= \sum_{m=1}^L \bar{a}_{im} f_m(\alpha\varphi^m) > \sum_{m=1}^L \bar{a}_{im} \cdot \alpha \cdot f_m(\varphi^m) = \alpha \sum_{m=1}^L \bar{a}_{im} f_m(\varphi^m) \\ &= \alpha (\bar{Q}[\varphi])^i, \quad \forall 1 \leq i \leq L. \end{aligned}$$

Then  $\bar{Q}[\alpha\varphi] \gg \alpha \bar{Q}[\varphi]$  in  $\mathbb{R}^L$ , which indicates that  $\bar{Q}$  is strongly subhomogeneous on  $\mathbb{R}_b^L$ .

Note that  $r(\bar{L}_0)$  is a positive eigenvalue of  $\bar{L}_0$  with a strongly positive eigenvector  $e \in \mathbb{R}_b^L$ . Since  $r(\bar{L}_0) > 1$ , as argued in the proof of [26, Theorem 2.1.2], we see that there exists  $\varepsilon_0 > 0$  such that  $\bar{Q}[\varepsilon e] \gg \varepsilon e$ , for all  $\varepsilon \in (0, \varepsilon_0]$ . For any given  $u \in \mathbb{R}_b^L$  with  $u \gg 0$ , there exists sufficiently small  $\varepsilon_1 \in (0, \varepsilon_0]$  such that  $u \geq \varepsilon_1 e$ . Then we have

$$\bar{Q}[u] \geq \bar{Q}[\varepsilon_1 e] \gg \varepsilon_1 e,$$

and hence,

$$\bar{Q}^n[u] \geq \varepsilon_1 e, \quad \forall n \geq 1.$$

Therefore, the  $\omega$ -limit set of  $u$ ,  $\omega(u)$ , is a nonempty compact invariant set in  $Int(\mathbb{R}_+^L)$ . By [26, Theorem 2.3.2],  $\bar{Q} : \mathbb{R}_b^L \rightarrow \mathbb{R}_b^L$  has a fixed point  $\beta^* \in Int(\mathbb{R}_+^L)$  such that every nonempty compact invariant set of  $\bar{Q}$  in  $Int(\mathbb{R}_+^L)$  consists of  $\beta^*$ . Thus, for any  $u \in Int(\mathbb{R}_+^L) \cap \mathbb{R}_b^L$ ,  $\beta^*$  attracts the forward orbit of  $u$ . Moreover, (H4) implies that  $\beta^*$  is globally attractive in  $\mathbb{R}_b^L \setminus \{0\}$ . □

To study the dynamics of invasions for (1.3), in the rest of this section we always assume that

(H5)  $r(\bar{L}_0) > 1$ .

Thus,  $Q$  admits a globally attractive fixed point  $\beta^* \gg 0$  in  $X_b^L \setminus \{0\}$ .

In order to use the theory of spreading speeds and periodic traveling waves for monotone operators on periodic habitats in [24], we first present some notations and hypotheses from there. Let  $\mathcal{H}$  be a subset of  $\mathbb{R}$ . For a recursion of the form

$$u_{n+1} = Q[u_n],$$

where  $u_n(x) \in \mathbb{R}$  for any  $x \in \mathcal{H} \subseteq \mathbb{R}$ ,  $n \in \mathbb{N}$ , we define

$$\mathcal{M} = \{u : u \text{ is continuous on } \mathcal{H}, 0 \leq u(x) \leq \pi_1(x), \forall x \in \mathcal{H}\},$$

where  $\pi_1$  is a nonnegative fixed point of  $Q$ . The following assumptions come from [24, Hypotheses 2.1].

- (A1) The habitat  $\mathcal{H}$  is a closed subset of  $\mathbb{R}$ .
- (A2)  $Q$  is monotone in the sense that if  $u(x) \leq v(x)$  on  $\mathcal{H}$ , then  $Q[u](x) \leq Q[v](x)$ . That is, an increase throughout  $\mathcal{H}$  in the population  $u_n$  at time  $n$  increases the population  $u_{n+1} = Q[u_n]$  throughout  $\mathcal{H}$  at the next time step.
- (A3) There is a closed lattice  $\mathcal{L}$  such that  $\mathcal{H}$  is invariant under translation by any element of  $\mathcal{L}$ , and  $Q$  is periodic with respect to  $\mathcal{L}$  in the sense that  $Q[T_a[u]] = T_a[Q[u]]$  holds for all  $u \in \mathcal{M}$  and  $a \in \mathcal{L}$ , where  $T$  is the translation operator defined as  $T_a[u](x) := u(x - a)$ . Moreover, there is a bounded subset  $\mathcal{P}$  of  $\mathcal{H}$  such that every  $x \in \mathcal{H}$  has a unique representation of the form  $x = z + p$  with  $z$  in  $\mathcal{L}$  and  $p$  in  $\mathcal{P}$ .
- (A4)  $Q[0] = 0$  and there are two functions  $\pi_0(x)$  and  $\pi_1(x)$  with  $\pi_i(x) = \pi_i(x + a)$  for all  $a \in \mathcal{L}$  and  $i = 0$  or  $1$ , such that  $0 \leq \pi_0 < \pi_1$ ,  $Q[\pi_0] = \pi_0$  and  $Q[\pi_1] = \pi_1$ . Moreover, if  $\pi_0 \leq u_0 \leq \pi_1$ ,  $u_0$  is periodic with respect to  $\mathcal{L}$  in the sense that  $u_0(x) = T_a[u_0](x)$  for all  $a \in \mathcal{L}$ , and  $u_0 \not\equiv \pi_0$ , then the solution  $u_n$  of the recursion  $u_{n+1} = Q[u_n]$ , which is again periodic with respect to  $\mathcal{L}$ , converges to  $\pi_1$  as  $n \rightarrow \infty$  uniformly on  $\mathcal{H}$ . (That is,  $\pi_0$  is unstable and  $\pi_1$  is stable.) In addition, any  $\mathcal{L}$ -periodic equilibrium  $\pi$  other than  $\pi_1$  which satisfies the inequalities  $0 \leq \pi \leq \pi_1$  also satisfies  $\pi \leq \pi_0$ .
- (A5)  $Q$  is continuous in the sense that if the sequence  $u_m \in \mathcal{M}$  converges to  $u \in \mathcal{M}$ , uniformly on every bounded subset of  $\mathcal{H}$ , then  $Q[u_m]$  converges to  $Q[u]$ , uniformly on every bounded subset of  $\mathcal{H}$ . That is, a change in  $u$  far from the point  $x$  has very little effect on the value of  $Q[u]$  at  $x$ .
- (A6) Every sequence  $\{u_m\}$  of functions in  $\mathcal{M}$  contains a subsequence  $\{u_{m_i}\}$  such that  $\{Q[u_{m_i}]\}$  converges to some function, uniformly on every bounded set.

**Lemma 2.2** The operator  $Q$  in (2.1) satisfies (A1)–(A6) with  $\mathcal{H} = \mathbb{Z}$ ,  $\mathcal{P} = \{1, 2, \dots, L\}$ ,  $\mathcal{L} = \{nL : n \in \mathbb{Z}\}$ ,  $\pi_0 = 0$ ,  $\pi_1 = \beta^*$ , and  $\mathcal{M} := \{\varphi \in X : 0 \leq \varphi^i \leq \beta^{*i} \text{ for all } i \in \mathbb{Z}\}$ .

*Proof* (A1) and (A2) are obvious. It remains to verify (A3)–(A6). We define the translation operator

$$(T_a[u])^i = u^{i-a}, \quad \forall i \in \mathbb{Z}, \quad a \in \mathcal{H}, \quad u \in X.$$

Clearly,  $\mathcal{H}$  is invariant under translation by any element of  $\mathcal{L}$  and every  $x \in \mathcal{H}$  has a unique representation of the form  $x = z + p$  with  $z \in \mathcal{L}$  and  $p \in \mathcal{P}$ . For any  $a \in \mathcal{L}$ ,  $u \in \mathcal{M}$ , we have

$$\begin{aligned} (T_a[Q[u]])^i &= (Q[u])^{i-a} = \sum_{j=-\infty}^{+\infty} P_{i-a,j} f_j(u^j), \\ (Q[T_a[u]])^i &= \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^{j-a}) \underbrace{z = j - a}_{z = j - a} \sum_{z=-\infty}^{+\infty} P_{i,z+a} f_{z+a}(u^z) = \sum_{z=-\infty}^{+\infty} P_{i-a,z} f_z(u^z). \end{aligned}$$

Therefore,  $(T_a[Q[u]])^i = (Q[T_a[u]])^i$  for all  $a \in \mathcal{L}$ ,  $u \in \mathcal{M}$ ,  $i \in \mathbb{Z}$ , which indicates that  $Q$  is periodic with respect to  $\mathcal{L}$ . This verifies (A3).

By Lemma 2.1, it follows that if  $0 \leq u_0 \leq \beta^*$ ,  $u_0$  is periodic with respect to  $\mathcal{L}$  and  $u_0 \not\equiv 0$ , then the solution  $u_n$  of  $u_{n+1} = Q[u_n]$  through  $u_0$ , which is again periodic with respect to  $\mathcal{L}$ , converges to  $\beta^*$  as  $n \rightarrow \infty$  uniformly on  $\mathcal{H}$ . Then (A4) is valid.

To verify (A5), let  $\{u_m\}_{m \in \mathbb{N}} \subseteq \mathcal{M}$  with  $u_m = \{u_m^i\}_{i \in \mathbb{Z}} \in X$  being a sequence such that  $u_m \rightarrow u \in \mathcal{M}$  uniformly on every bounded subset of  $\mathcal{H}$ , as  $m \rightarrow \infty$ . Given a bounded subset  $B$  of  $\mathcal{H}$ , for any  $\varepsilon > 0$ ,  $i \in B$ , we have

$$\begin{aligned} |(Q[u_m])^i - (Q[u])^i| &= \left| \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u_m^j) - \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \right| \\ &= \left| \sum_{j=-\infty}^{+\infty} P_{ij} (f_j(u_m^j) - f_j(u^j)) \right| \\ &\leq \hat{L} \sum_{j=-\infty}^{+\infty} P_{ij} |u_m^j - u^j|. \end{aligned}$$

Since  $\sum_{j=-\infty}^{+\infty} P_{ij} = 1$  for any  $i \in \mathbb{Z}$ , there exists  $M > 0$ , such that  $\sum_{|j| \geq M} P_{ij} < \varepsilon$  for all  $i \in B$ .

Thus, there exists  $N_1 \in \mathbb{Z}$ ,  $N_1 > 0$ , such that  $|(Q[u_m])^i - (Q[u])^i| \leq \hat{L}(\varepsilon \cdot 2\beta_0 + \varepsilon)$  for any  $i \in B$ , where  $\beta_0 = \max_{i \in \{1, 2, \dots, L\}} |\beta^{*i}|$  and  $N_1$  satisfies that for  $m \geq N_1$ ,  $|u_m^j - u^j| < \varepsilon$ , for all  $j \in \{-M, \dots, M\}$ . This implies that  $Q[u_m]$  converges to  $Q[u]$  uniformly on every bounded subset of  $\mathcal{H}$ .

Any sequence  $\{u_m\}_{m \in \mathbb{N}}$  in  $\mathcal{M}$  is uniformly bounded. Moreover, since  $\mathcal{H}$  is countable, it is easy to see that  $\{Q[u_m]\}_{m \in \mathbb{N}}$  is equicontinuous on  $\mathcal{H}$ . Therefore, there exists a subsequence  $\{u_{m_k}\}_{k \in \mathbb{N}}$  of  $\{u_m\}_{m \in \mathbb{N}}$  such that  $\{Q[u_{m_k}]\}_{k \in \mathbb{N}}$  converges to some function uniformly on every bounded subset of  $\mathcal{H}$ . Thus, (A6) is valid. □

Let  $L_0 = DQ[0] : X \rightarrow X$  be the derivative of  $Q$  at 0. For any  $n \in \mathbb{Z}$ , let  $\varphi_n = \{\varphi_n^i\}_{i \in \mathbb{Z}} \in X$  with  $\varphi_n^i = \min\{n, e^{|\mu|i}\}$  for all  $i \in \mathbb{Z}$ . Then

$$\begin{aligned} (L_0[\varphi_n])^i &= \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0)\varphi_n^j = \sum_{|j| > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0)n + \sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0)e^{\mu|j|}, \\ &\forall i \in \mathbb{Z}, \quad n \in \mathbb{N}. \end{aligned}$$

Given a bounded subset  $B$  of  $\mathbb{Z}$ . Since  $\sum_{j=-\infty}^{+\infty} P_{ij} e^{\mu j}$  converges for all  $\mu \in [0, \Delta^-)$ ,  $i \in \mathbb{Z}$ , and

$$\sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0)e^{\mu|j|} \leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} e^{\mu|j|},$$

we can obtain that  $\sum_{|j| \leq \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0)e^{\mu|j|}$  converges for all  $i \in B$ ,  $\mu \in [0, \Delta^-)$  and  $n > 0$ .

Fix  $\alpha \in (0, \Delta^-)$  such that  $0 < \mu < \alpha < \Delta^-$ . Since  $\sum_{j=-\infty}^{+\infty} P_{ij} e^{\alpha j} < \infty$ , we have  $P_{ij} e^{\alpha j} \rightarrow 0$  as  $j \rightarrow \infty$  uniformly for  $i \in B$ . Then there exists  $N > 0$  such that  $P_{ij} e^{\alpha j} < 1$  for  $i \in B$ ,  $j > N$ , and hence,  $P_{ij} < e^{-\alpha j}$  for  $i \in B$ ,  $j > N$ . Therefore, when  $\lfloor \frac{\ln n}{\mu} \rfloor > N$ , for any  $i \in B$ , we have

$$\begin{aligned} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} n \\ &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} e^{-\alpha j} n \\ &\leq \max_{j \in \{1, 2, \dots, L\}} \{f'_j(0)\} \frac{n e^{\alpha(1 - \frac{\ln n}{\mu})}}{e^\alpha - 1}, \end{aligned}$$

which indicates that  $\sum_{j > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  tends to 0 as  $n \rightarrow \infty$  uniformly for  $i \in B$ . Similarly, we can prove that  $\sum_{j < -\lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  tends to 0 as  $n \rightarrow \infty$  uniformly for  $i \in B$ . Thus,

$\sum_{|j| > \lfloor \frac{\ln n}{\mu} \rfloor} P_{ij} f'_j(0) n$  is uniformly bounded for all  $i \in B$  and  $n > 0$ , and hence,  $(L_0[\varphi_n])^i$  is uniformly bounded for all  $i \in B$  and  $n > 0$ . The equicontinuity of  $\{L_0[\varphi_n]\}_{n \in \mathbb{N}}$  in  $i \in B$  is obvious since  $B \subseteq \mathbb{Z}$ . Then the Arzelà-Ascoli theorem implies that  $\{L_0[\varphi_n]\}_{n \in \mathbb{N}}$  has a subsequence  $\{L_0[\varphi_{n_k}]\}_{k \in \mathbb{N}}$ , which converges to some function  $\tilde{f}$  on every bounded set of  $\mathbb{Z}$ . By the definitions of  $L_0$  and  $\varphi_n$ , it is easy to see that  $\{L_0[\varphi_n]\}_{n \in \mathbb{N}}$  is increasing in  $n$ . Thus,  $\{L_0[\varphi_n]\}_{n \in \mathbb{N}}$  itself converges to  $\tilde{f}$  on every bounded set of  $\mathbb{Z}$ . Then we define  $L_0[e^{\mu|\cdot|}] = \tilde{f}$ . Similarly, by a limiting process, we can define  $L_0[\{e^i u^i\}]$  and  $L_0[\{e^{-i} u^i\}]$  for any bounded sequence  $u \in X$ .

Consider the negative direction  $\vec{\xi} = -1$ . Following [24, Sect. 2], for any  $\mu \in (0, \Delta^-)$  and  $u \in X^L$ , let  $v = \{e^{\mu i} u^i\}_{i \in \mathbb{Z}}$  and define  $L_{-\mu}$  by

$$\begin{aligned} (L_{-\mu}[u])^i &= e^{-\mu i} (L_0[v])^i \\ &= e^{-\mu i} \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) e^{\mu j} u^j \\ &= \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0) e^{-\mu(i-j)} u^j \\ &= \sum_{k=-\infty}^{+\infty} \sum_{m=1}^L P_{i, kL+m} f'_{kL+m}(0) e^{-\mu(i-kL-m)} u^{kL+m} \\ &= \sum_{m=1}^L \left( \sum_{k=-\infty}^{+\infty} (P_{i, kL+m} e^{\mu kL}) \cdot e^{\mu m} f'_m(0) e^{-\mu i} \right) u^m, \end{aligned} \tag{2.3}$$

for any  $i \in \mathbb{Z}$ . We then obtain that  $L_{-\mu} : X^L \rightarrow X^L$  and that  $(L_{-\mu}[u])^i = (L_{-\mu}[u])^{i+L}$  for all  $i \in \mathbb{Z}$  and  $u \in X^L$ . Thus,  $L_{-\mu}$  can be considered as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ :

$$L_{-\mu}[u] = A_{-\mu} u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_{-\mu} = (a_{im}^{-\mu})_{L \times L}$ ,  $a_{im}^{-\mu} = \sum_{k=-\infty}^{+\infty} (P_{i, kL+m} e^{\mu kL}) e^{\mu m} f'_m(0) e^{-\mu i}$  for all  $i, m \in \{1, 2, \dots, L\}$ .

For the positive direction  $\vec{\xi} = 1$ , we can similarly define  $L_\mu : X^L \rightarrow X^L$  by

$$(L_\mu[u])^i = e^{\mu i} (L_0[v])^i, \quad \forall i \in \mathbb{Z}, \tag{2.4}$$



for  $\mu \in (0, \Delta^+)$ ,  $u \in X^L$ , where  $v = \{e^{-\mu i} u^i\}_{i \in \mathbb{Z}}$ . Furthermore,  $L_\mu$  can also be considered as a linear operator from  $\mathbb{R}^L$  to  $\mathbb{R}^L$ :

$$L_\mu[u] = A_\mu u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_\mu = (a_{im}^\mu)_{L \times L}$  with  $a_{im}^\mu = \sum_{k=-\infty}^{+\infty} (P_{i,kL+m} e^{-\mu kL}) e^{-\mu m} f'_m(0) e^{\mu i}$  for all  $i, m \in \{1, 2, \dots, L\}$ .

Let

$$c^*(1) = \inf_{0 < \mu < \Delta^+} \frac{1}{\mu} \ln \lambda_\mu \tag{2.5}$$

and

$$c^*(-1) = \inf_{0 < \mu < \Delta^-} \frac{1}{\mu} \ln \lambda_{-\mu}, \tag{2.6}$$

where  $\lambda_\mu$  and  $\lambda_{-\mu}$  are principle eigenvalues of  $A_\mu$  and  $A_{-\mu}$ , respectively.

**Lemma 2.3** *Let (H1), (H2) and (H4) hold. If  $P_{ij} = P_{ji}$  for all  $i, j \in \mathbb{Z}$ , then  $c^*(1) = c^*(-1)$ .*

*Proof* Let  $C = \text{diag}(f'_1(0) \dots f'_L(0))$  and  $B = (B_{im})_{L \times L}$  with

$$B_{im} = \sum_{k=-\infty}^{+\infty} (P_{i,kL+m} e^{\mu kL}) e^{\mu m} e^{-\mu i}, \quad \forall i, m \in \{1, 2, \dots, L\}.$$

It is easy to see that  $\Delta^+ = \Delta^-$  and  $A_{-\mu} = BC$ . Moreover, we have

$$\begin{aligned} a_{mi}^\mu &= \sum_{k=-\infty}^{+\infty} (P_{m,kL+i} e^{-\mu kL}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{m,-kL+i} e^{\mu kL}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{m+kL,i} e^{\mu kL}) e^{-\mu i} f'_i(0) e^{\mu m} \\ &= \sum_{k=-\infty}^{+\infty} (P_{i,m+kL} e^{\mu kL}) e^{-\mu i} f'_i(0) e^{\mu m}, \end{aligned}$$

for all  $i, m \in \{1, 2, \dots, L\}$ . Then  $A_\mu = B^\top C$ , where  $B^\top$  is the transpose of  $B$ , and hence,  $A_\mu^\top = CB$ . Since  $C$  is invertible, we obtain  $C \cdot BC \cdot C^{-1} = CB$ , which indicates that  $BC$  and  $CB$  are similar, and hence,  $\sigma(A_{-\mu}) = \sigma(A_\mu^\top) = \sigma(A_\mu)$ , where  $\sigma(M)$  denotes the set of all eigenvalues of matrix  $M$ . By the definition of  $c^*(\vec{\xi})$ , it then follows that  $c^*(1) = c^*(-1)$ .  $\square$

The following result shows that  $c^*(\vec{\xi})$  is the spreading speed in the directions  $\vec{\xi} = \pm 1$ .

**Theorem 2.1** *Let (H1)–(H5) hold. Then the following statements are valid:*

- (i) *For any  $u_0 \in \mathcal{M} := \{\varphi \in X : 0 \leq \varphi^i \leq \beta^{*i}, \forall i \in \mathbb{Z}\}$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , the solution of (1.3) satisfies  $\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0$  for all  $c > c^*(1)$ .*

For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (1.3) satisfies  $\lim_{n \rightarrow \infty, i \leq cn} (u_n^i - \beta^{*i}) = 0$  for all  $c < c^*(1)$ .

(ii) For any  $u_0 \in \mathcal{M}$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \leq K$  for some  $K \in \mathbb{Z}$ , the solution of (1.3) satisfies  $\lim_{n \rightarrow \infty, i \leq -cn} u_n^i = 0$  for all  $c > c^*(-1)$ .

For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (1.3) satisfies  $\lim_{n \rightarrow \infty, i \geq -cn} (u_n^i - \beta^{*i}) = 0$  for all  $c < c^*(-1)$ .

(iii) For any  $u_0 \in \mathcal{M}$  with  $u_0^i = 0$  for  $i$  outside a bounded subset of  $\mathbb{Z}$ , the solution of (1.3) satisfies

$$\lim_{n \rightarrow \infty} u_n^i = 0, \quad \forall c_1 > c^*(-1), \quad \forall c_2 > c^*(1),$$

$$i \leq -c_1 n \text{ or } i \geq c_2 n$$

(iv) For any  $u_0 \in \mathcal{M} \setminus \{0\}$ , the solution of (1.3) satisfies

$$\lim_{n \rightarrow \infty, -c_1 n \leq i \leq c_2 n} (u_n^i - \beta^{*i}) = 0, \quad \forall c_1 < c^*(-1), \quad \forall c_2 < c^*(1).$$

*Proof* In view of Lemma 2.2, it suffices to verify conditions in [24, Corollary 2.1].

Since  $f_i(u)/u$  is strictly decreasing for  $i \in \mathbb{Z}, u \in (0, b]$ , we see that  $f_i$  is strictly subhomogeneous in  $u \in (0, b]$  for any  $i \in \mathbb{Z}$ . This implies that  $f_i(u) \leq f'_i(0)u$  for any  $i \in \mathbb{Z}$  and  $u \in [0, b]$ , and hence, for any  $u \in \mathcal{M}$ ,

$$(Q[u])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \leq \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0)u^j = (L_0[u])^i, \quad \forall i \in \mathbb{Z}.$$

Thus,  $Q[u] \leq L_0[u]$  for all  $u \in \mathcal{M}$ .

Clearly,  $L_0$  is  $\mathcal{L}$ -periodic and strictly positive in the sense that if  $u \in X$  with  $u > 0$  then  $L_0[u] > 0$ .

Since  $f_i(u) < f'_i(0)u$  for all  $i \in \mathbb{Z}, u \in (0, b]$ , we have

$$(L_0[\beta^*])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f'_j(0)\beta^{*j} > \sum_{j=-\infty}^{+\infty} P_{ij} f_j(\beta^{*j}) = (Q[\beta^*])^i = \beta^{*i},$$

i.e.,  $L_0[\beta^*] > \beta^*$ . Define an operator  $Q^{[L_0, \beta^]}$  by

$$Q^{[L_0, \beta^]}[u] = \min\{L_0[u], \beta^*\}, \quad \forall u \in X \text{ with } 0 \leq u^i \leq \beta^{*i}, \quad i \in \mathbb{Z}.$$

Then  $Q^{[L_0, \beta^]}[0] = 0, Q^{[L_0, \beta^]}[\beta^*] = \min\{L_0[\beta^*], \beta^*\} = \beta^*$ . We further have the following observation.

*Claim.*  $Q^{[L_0, \beta^]}$  satisfies (A1)–(A6) with  $\mathcal{H} = \mathbb{Z}, \mathcal{P} = \{1, 2, \dots, L\}, \mathcal{L} = \{nL : n \in \mathbb{Z}\}$ , and  $\mathcal{M} = \{\{\varphi^i\}_{i \in \mathbb{Z}} \in X : 0 \leq \varphi^i \leq \beta^{*i}, \forall i \in \mathbb{Z}\}$ .

Indeed, (A1) is obvious. By the monotonicity of  $L_0$ , for  $u, v \in \mathcal{M}$  with  $u \leq v$ , we have

$$(Q^{[L_0, \beta^]}[u])^i = \min\{(L_0[u])^i, \beta^{*i}\} \leq \min\{(L_0[v])^i, \beta^{*i}\} = (Q^{[L_0, \beta^]}[v])^i, \quad \forall i \in \mathbb{Z}.$$

Thus,  $Q^{[L_0, \beta^]}$  is monotone.  $L_0$  is periodic with respect to  $\mathcal{L}$ , so is  $Q^{[L_0, \beta^]}[u]$ . By the properties of  $L_0$ , if  $0 \leq u_0 \leq \beta^*$  with  $u_0$  periodic with respect to  $\mathcal{L}$  and  $u_0 \not\equiv 0$ , then the the solution  $u_n$  of  $u_{n+1} = Q^{[L_0, \beta^]}[u_n]$  is again periodic with respect to  $\mathcal{L}$ . Since  $\bar{Q}[u_0] \leq L_0[u_0]$  and  $\bar{Q}[u_0] \leq \bar{Q}[\beta^*] = \beta^*$ , we have  $\bar{Q}[u_0] \leq Q^{[L_0, \beta^]}[u_0] \leq Q^{[L_0, \beta^]}[\beta^*] = \beta^*$ . Then it follows from  $\bar{Q}[u_n] \rightarrow \beta^*$  as  $n \rightarrow \infty$  that  $u_{n+1} = Q^{[L_0, \beta^]}[u_n] \rightarrow \beta^*$  as  $n \rightarrow \infty$ . Let  $\{v_m\}_{m \in \mathbb{N}} \subseteq \mathcal{M}$  be a sequence such that  $v_m \rightarrow v \in \mathcal{M}$  as  $m \rightarrow \infty$  uniformly on every

bounded subset of  $\mathbb{Z}$ . Given a bounded subset  $B$  of  $\mathbb{Z}$ . For any  $\varepsilon > 0$  and  $i \in B$ , by the continuity of  $L_0$  and uniform convergence of  $v_m$  on  $B$ , we can obtain

$$\begin{aligned} & |(Q^{[L_0, \beta^*]}[v_m])^i - (Q^{[L_0, \beta^*]}[v])^i| \\ &= |\min\{(L_0[v_m])^i, \beta^{*i}\} - \min\{(L_0[v])^i, \beta^{*i}\}| \\ &= \begin{cases} |(L_0[v_m])^i - (L_0[v])^i|, & \text{if } \beta^{*i} \geq \max\{(L_0[v_m])^i, (L_0[v])^i\} \\ |\beta^{*i} - \beta^{*i}|, & \text{if } \beta^{*i} \leq \min\{(L_0[v_m])^i, (L_0[v])^i\} \\ |(L_0[v_m])^i - \beta^{*i}|, & \text{if } (L_0[v_m])^i \leq \beta^{*i} \leq (L_0[v])^i \\ |\beta^{*i} - (L_0[v])^i|, & \text{if } (L_0[v])^i \leq \beta^{*i} \leq (L_0[v_m])^i \end{cases} \\ &\leq |(L_0[v_m])^i - (L_0[v])^i| \\ &< \varepsilon, \end{aligned}$$

for all  $m > N_i$  with some  $N_i > 0$ . Note that  $B$  is a finite subset of  $\mathbb{Z}$ . We can further find an  $N > 0$ , such that

$$|(Q^{[L_0, \beta^*]}[v_m])^i - (Q^{[L_0, \beta^*]}[v])^i| < \varepsilon, \quad \forall i \in B, \quad m > N.$$

Since  $\{v_m\}_{m \in \mathbb{N}} \subseteq \mathcal{M}$ ,  $\{Q^{[L_0, \beta^*]}[v_m]\}_{m \in \mathbb{N}}$  is uniformly bounded by  $\beta^*$ . For any bounded subset  $B$  of  $\mathbb{Z}$ , the equicontinuity of  $\{Q^{[L_0, \beta^*]}[v_m]\}_{m \in \mathbb{N}}$  on  $B$  follows from the fact that  $N$  contains only countable elements. Therefore,  $\{v_m\}_{m \in \mathbb{N}}$  contains a subsequence  $\{v_{m_k}\}_{k \in \mathbb{N}}$  such that  $\{Q[v_{m_k}]\}_{k \in \mathbb{N}}$  converges to some function on every bounded subset of  $\mathbb{Z}$ . Therefore,  $Q^{[L_0, \beta^*]}$  satisfies (A1)–(A6). This proves our claim above.

Since  $r(\bar{L}_0) > 1$ , there exists  $\delta_0 > 0$  such that  $r((1 - \delta)\bar{L}_0) > 1$  for all  $\delta \in [0, \delta_0)$ . Then there exists  $\varphi \in X_b^L$  such that  $\varphi$  is an eigenvector of  $(1 - \delta)\bar{L}_0$ , corresponding to the eigenvalue  $r((1 - \delta)\bar{L}_0)$ . Note that  $f_i(u)/u \rightarrow f'_i(0)$  as  $u \rightarrow 0^+$  for all  $i \in \mathbb{Z}$ . It follows that for any  $\delta$  in  $(0, \delta_0)$ , there exists  $\varsigma > 0$  such that  $f_i(u) > (1 - \delta)f'_i(0)u$  for all  $u \in (0, \varsigma]$ ,  $i \in \{1, 2, \dots, L\}$ . Thus, for any  $u \in X_\varsigma := \{\phi \in X : 0 \leq \phi^i \leq \varsigma, \forall i \in \mathbb{Z}\}$ ,

$$(Q[u])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(u^j) \geq \sum_{j=-\infty}^{+\infty} P_{ij} (1 - \delta) f'_j(0) u^j = (1 - \delta)(L_0[u])^i, \quad \forall i \in \mathbb{Z},$$

i.e.,  $Q[u] \geq (1 - \delta)L_0[u]$  for all  $u \in X_\varsigma$ .

For simplicity, let  $M := (1 - \delta)L_0$ . The properties of  $L_0$  imply that  $M$  is  $\mathcal{L}$ -periodic and that if  $u \in X$  with  $u > 0$  then  $M[u] > 0$ . Similarly as we did for  $L_0$ , we can define  $(1 - \delta)L_0[e^{\mu \cdot | \cdot |}]$  for all  $\mu \in (0, \Delta^-)$ . Noting that  $(1 - \delta)\bar{L}_0$  is the restriction of  $M$  on  $X_b^L$ , we have  $M[\varphi] = r((1 - \delta)\bar{L}_0)\varphi > \varphi$ . Moreover, we can restrict  $\varphi \in X_\varsigma$ , and define

$$(Q^{[M, \varphi]}[u])^i = \min\{(M[u])^i, \varphi^i\}, \quad \forall u \in X_\varsigma, \quad i \in \mathbb{Z}.$$

Then  $Q^{[M, \varphi]}[0] = 0$  and  $Q^{[M, \varphi]}[\varphi] = \varphi$ . By similar arguments as in [15, Lemma 3.3], we can prove that  $Q^{[M, \varphi]}$  admits exactly two fixed points  $0$  and  $\varphi$  in  $[0, \varphi] \subseteq X_b^L$ . Note that  $Q^{[M, \varphi]}$  is monotone increasing in  $u \in X_\varsigma$  and that  $Q^{[M, \varphi]}[u] > 0$  whenever  $u > 0$ . Similarly as we did for  $Q^{[L_0, \beta^*]}$ , we can verify that  $Q^{[M, \varphi]}$  satisfies (A1)–(A6).

By [24, Corollary 2.1], it then follows that the statements (i) and (ii) are valid. Statements (iii) and (iv) are straightforward consequences of (i) and (ii) (see also [25, Remarks 2]).  $\square$

Motivated by [24, Definition 2.1], below we introduce the concept of periodic traveling waves for system (1.3).

**Definition 2.1** A solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of the recursion (1.3) is called a periodic traveling wave with speed  $c$  in the direction of the unit vector  $\bar{\xi} = -1$  if it has the form  $u_n^i = W(i, i + cn)$ , for some function  $W : \mathbb{Z} \times \{j + cn : j \in \mathbb{Z}, n \in \mathbb{N}\} \rightarrow \mathbb{R}_+$ , with  $W(i, s)$  being  $L$ -periodic

in  $i$  for each  $s$ ; Such a wave is said to be nondecreasing if  $W(i, s)$  is nondecreasing in  $s$ , and to connect 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  if  $\lim_{s \rightarrow -\infty} W(i, s) = 0$  and  $\lim_{s \rightarrow +\infty} W(i, s) = \beta^{*i}$  uniformly for  $i \in \mathbb{Z}$ .

Similarly, a solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of the recursion (1.3) is called a periodic traveling wave with speed  $c$  in the direction of the unit vector  $\xi = 1$  if it has the form  $u_n^i = W(i, i - cn)$ , for some function  $W : \mathbb{Z} \times \{j - cn : j \in \mathbb{Z}, n \in \mathbb{N}\} \rightarrow \mathbb{R}_+$ , with  $W(i, s)$  being  $L$ -periodic in  $i$  for each  $s$ ; Such a wave is said to be nonincreasing if  $W(i, s)$  is nonincreasing in  $s$ , and to connect  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0 if  $\lim_{s \rightarrow -\infty} W(i, s) = \beta^{*i}$  and  $\lim_{s \rightarrow +\infty} W(i, s) = 0$  uniformly for  $i \in \mathbb{Z}$ .

The subsequent result is a consequence of Lemma 2.2, Theorem 2.1 and [24, Theorem 2.6]. It shows that  $c^*(\xi)$  is the minimal wave speed for periodic traveling waves in the direction  $\xi$ .

**Theorem 2.2** *Let (H1)–(H5) hold. Then the following statements are valid.*

- (i) *For any  $c \geq c^*(1)$ , (1.3) admits a nonincreasing periodic traveling wave  $W(i, i - cn)$  connecting  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0; and for any  $c < c^*(1)$ , (1.3) has no periodic traveling wave  $W(i, i - cn)$  connecting  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$  to 0.*
- (ii) *For any  $c \geq c^*(-1)$ , (1.3) admits a nondecreasing periodic traveling wave  $W(i, i + cn)$  connecting 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$ ; and for any  $c < c^*(-1)$ , (1.3) has no periodic traveling wave  $W(i, i + cn)$  connecting 0 to  $\{\beta^{*i}\}_{i \in \mathbb{Z}}$ .*

### 3 Non-Monotone Case

In this section, we study spatial dynamics of system (1.3) with a non-monotone recruitment function. Motivated by recent works in [10,25], we employ the comparison method and Schauder fixed point theorem to establish spreading speeds and periodic traveling waves for (1.3).

Firstly, we define a nondecreasing function

$$f_i^+(u) := \max_{v \in [0, u]} \{f_i(v)\}, \quad \forall i \in \mathbb{Z}, u \in [0, b].$$

It follows that  $f_i^+$  is Lipschitz continuous in  $u$  with the Lipschitz constant  $\hat{L}$ , i.e.,

$$|f_i^+(u_1) - f_i^+(u_2)| \leq \hat{L}|u_1 - u_2|, \quad \forall i \in \mathbb{Z}, u_1, u_2 \in [0, b].$$

Then for the monotone system

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^+(u_n^j), \quad i \in \mathbb{Z}, n \in \mathbb{N}, \tag{3.1}$$

by Lemma 2.1, there exists  $u_{+*} = \{u_{+*}^i\}_{i \in \mathbb{Z}} \in X_b^L$  with  $u_{+*}^i = u_{+*}^{i+L}$  for all  $i \in \mathbb{Z}$ , such that  $u_{+*}$  is a fixed point of (3.1).

We define another function

$$f_i^-(u) = \min_{v \in [u, u_{+*}^i]} \{f_i(v)\}, \quad \forall u \in [0, u_{+*}^i], i \in \mathbb{Z}.$$

It then follows that  $f_i^-$  is nondecreasing in  $u \in [0, u_{+*}^i]$  for all  $i \in \mathbb{Z}$ , and that  $f_i^-$  is Lipschitz continuous in  $u \in [0, u_{+*}^i]$  with the Lipschitz constant  $\hat{L}$ , i.e.,

$$|f_i^-(u_1) - f_i^-(u_2)| \leq \hat{L}|u_1 - u_2|, \quad \forall u_1, u_2 \in [0, u_{+*}^i], i \in \mathbb{Z}.$$

Similarly, by Lemma 2.1, the monotone system

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^-(u_n^j), \quad i \in \mathbb{Z}, \quad n \in \mathbb{N} \tag{3.2}$$

admits a fixed point  $u_{-*} = \{u_{-*}^i\}_{i \in \mathbb{Z}} \in X_{u_{+*}}^L$  with  $u_{-*}^i = u_{-*}^{i+L}$  for all  $i \in \mathbb{Z}$ .

By the definitions of  $f^\pm$ , it is easy to see that the recruitment function  $f$  is bounded above and below by  $f^+$  and  $f^-$ , i.e.,

$$f_i^-(u) \leq f_i(u) \leq f_i^+(u), \quad \forall i \in \mathbb{Z}, \quad u \in [0, u_{+*}^i],$$

and  $0 < u_{-*}^i \leq u_{+*}^i \leq b$ . Moreover, it follows from Theorem 2.1 that (3.1) and (3.2) admit spreading speeds  $c_+^*(\vec{\xi})$  and  $c_-^*(\vec{\xi})$  (in the directions of  $\vec{\xi} = \pm 1$ ), respectively. By the fact that  $f_i'(0) > 1$  for all  $i \in \mathbb{Z}$  and the periodicity of  $f_i$ , there exists  $\delta_0 \in (0, \min_{j \in \{1, 2, \dots, L\}} u_{-*}^j]$ , such that  $f_i^\pm(u) = f_i(u)$  for all  $i \in \mathbb{Z}, u \in [0, \delta_0]$ , and hence,  $f_i^{+'}(0) = f_i^{-'}(0) = f_i'(0)$ . Since  $c_+^*(\vec{\xi})$  and  $c_-^*(\vec{\xi})$  are determined by the linearization systems of (3.1) and (3.2) at  $u = 0$ , respectively, we then obtain  $c_+^*(1) = c_-^*(1)$  and  $c_+^*(-1) = c_-^*(-1)$ . Let  $c^*(1) := c_+^*(1) = c_-^*(1)$  and  $c^*(-1) := c_+^*(-1) = c_-^*(-1)$ . By Theorem 2.1,  $c^*(1)$  and  $c^*(-1)$  are actually defined by (2.5) and (2.6), respectively.

We restrict  $Q$  on  $X^L$  as  $\bar{Q}$  as we did in Sect. 2 and consider that  $\bar{Q}$  is an operator from  $\mathbb{R}_+^L$  to  $\mathbb{R}_+^L$ . It then follows that

$$u_{-*} = Q^-[u_{-*}] \leq Q^-[u] \leq \bar{Q}[u] \leq Q^+[u] \leq Q^+[u_{+*}] = u_{+*}, \quad \forall u \in [u_{-*}, u_{+*}] \subseteq \mathbb{R}_+^L,$$

and hence,  $\bar{Q} : [u_{-*}, u_{+*}] \rightarrow [u_{-*}, u_{+*}]$ . By the Brouwer fixed point theorem,  $\bar{Q}$  admits a fixed point  $\beta^*$  in  $[u_{-*}, u_{+*}] \subseteq \mathbb{R}_+^L$ , and hence,  $Q$  admits a fixed point  $\beta^*$  in  $X_b^L$  with  $u_{-*}^i \leq \beta^{*i} \leq u_{+*}^i$  for all  $i \in \mathbb{Z}$ .

Instead of hypothesis (H3), we assume that

$$(H3)' \quad \text{There exist } \sigma > 1, \delta^* > 0 \text{ and } \alpha > 0 \text{ such that } f_i(u) \geq f_i'(0)u - \alpha u^\sigma \text{ for all } i \in \mathbb{Z} \text{ and } u \in [0, \delta^*] \subseteq [0, \min_{j \in \{1, 2, \dots, L\}} u_{+*}^j].$$

We then have the following result on spreading speeds for (1.3).

**Theorem 3.1** *Let (H1), (H2), (H3)', (H4) and (H5) hold. Then the following statements are valid:*

- (i) *For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , the solution of (1.3) satisfies*

$$\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0, \quad \forall c > c^*(1),$$

*and for any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , the solution of (1.3) satisfies*

$$\limsup_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{+*}^i) \leq 0 \leq \liminf_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{-*}^i), \quad \forall c < c^*(1).$$

- (ii) *For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \leq K$  with some  $K \in \mathbb{Z}$ , the solution of (1.3) satisfies*

$$\lim_{n \rightarrow \infty, i \leq -cn} u_n^i = 0, \quad \forall c > c^*(-1),$$

and for any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , the solution of (1.3) satisfies

$$\limsup_{n \rightarrow \infty, i \geq -cn} (u_n^i - u_{+*}^i) \leq 0 \leq \liminf_{n \rightarrow \infty, i \geq -cn} (u_n^i - u_{-*}^i), \quad \forall c < c^*(-1).$$

*Proof* For convenience, we define

$$(Q^+[\varphi])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^+(\varphi^j), \quad (Q^-[\varphi])^i = \sum_{j=-\infty}^{+\infty} P_{ij} f_j^-(\varphi^j), \quad i \in \mathbb{Z},$$

for any  $\varphi \in X$  with  $\varphi^i \in [0, u_{+*}^i]$  for all  $i \in \mathbb{Z}$ . Then  $Q^+$  and  $Q^-$  are monotone on  $X$  and  $Q^-[\varphi] \leq Q[\varphi] \leq Q^+[\varphi]$ , for any  $\varphi \in X$  with  $\varphi^i \in [0, u_{+*}^i]$ . Moreover,  $c^*(+1)$  and  $c^*(-1)$  are spreading speeds for  $u_{n+1} = Q^+[u_n]$  and  $u_{n+1} = Q^-[u_n]$  (i.e., (3.1) and (3.2)), in the directions of  $\vec{\xi} = 1$  and  $\vec{\xi} = -1$ , respectively.

We only show that statement (i) is valid since the proof of statement (ii) is similar. For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}]$  with  $u_0^i = 0$  for  $i \in \mathbb{Z}$  and  $i \geq K$  for some  $K \in \mathbb{Z}$ , let

$$u_n = Q^n[u_0], \quad u_n^+ = (Q^+)^n[u_0], \quad \forall n \geq 0.$$

By the comparison principle, we have

$$0 \leq u_n^i \leq u_n^{+i}, \quad \forall i \in \mathbb{Z}, \quad n \geq 0.$$

For any  $c > c^*(1)$ , Theorem 2.1 implies that  $\lim_{n \rightarrow \infty, i \geq cn} u_n^{+i} = 0$ , and hence,  $\lim_{n \rightarrow \infty, i \geq cn} u_n^i = 0$ .

For any  $u_0 = \{u_0^i\}_{i \in \mathbb{Z}} \in [0, u_{+*}] \setminus \{0\}$ , define  $v_0 = \{v_0^i\}_{i \in \mathbb{Z}}$  with  $v_0^i = \min\{u_0^i, u_{-*}^i\}$  for all  $i \in \mathbb{Z}$ . Then  $v_0 \in [0, u_{-*}] \setminus \{0\}$ . Let

$$u_n^- = (Q^-)^n[v_0], \quad u_n = Q^n[u_0], \quad u_n^+ = (Q^+)^n[u_0], \quad \forall n \geq 0.$$

Since  $v_0 \leq u_0$ , it follows from the comparison principle that

$$0 \leq u_n^{-i} \leq u_n^i \leq u_n^{+i}, \quad \forall i \in \mathbb{Z}, \quad n \geq 0.$$

For any  $c < c^*(1)$ , Theorem 2.1 implies that

$$\lim_{n \rightarrow \infty, i \leq cn} (u_n^{-i} - u_{-*}^i) = 0, \quad \lim_{n \rightarrow \infty, i \leq cn} (u_n^{+i} - u_{+*}^i) = 0.$$

Thus, for any  $c < c^*(1)$ , we have

$$\begin{aligned} \liminf_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{-*}^i) &\geq \liminf_{n \rightarrow \infty, i \leq cn} (u_n^{-i} - u_{-*}^i) = 0, \\ \limsup_{n \rightarrow \infty, i \leq cn} (u_n^i - u_{+*}^i) &\leq \limsup_{n \rightarrow \infty, i \leq cn} (u_n^{+i} - u_{+*}^i) = 0. \end{aligned}$$

This completes the proof of statement (i). □

Now we consider periodic traveling waves in the direction  $\vec{\xi} = -1$ . Let  $c \in \mathbb{R}$  and  $a > 0$  be given, and define

$$X_c := \{i + cn : i \in \mathbb{Z}, n \in \mathbb{N}\}$$

and  $\mathcal{F}_{c,a}$  the set of all functions from  $\mathbb{Z} \times X_c$  to  $[0, a]$ . Let  $U \in \mathcal{F}_{c,b}$ . By Definition 2.1, we say that  $U(i, i + cn)$  is a periodic traveling wave solution of (1.3) with wave speed  $c$  if  $\{u_n^i\}_{i \in \mathbb{Z}} = \{U(i, i + cn)\}_{i \in \mathbb{Z}}, \forall n \in \mathbb{N}$ , satisfies (1.3) and  $U(i, s) = U(i + L, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ .

We note that one should take  $X_c := \{i - cn : i \in \mathbb{Z}, n \in \mathbb{N}\}$  and replace  $U(i, i + cn)$  with  $U(i, i - cn)$  in order to obtain periodic traveling waves in the direction  $\vec{\xi} = 1$ .

Let  $u_n^i = U(i, i + cn)$  for all  $i \in \mathbb{Z}, n \in \mathbb{N}$ . Then (1.3) becomes

$$U(i, i + c + cn) = \sum_{j=-\infty}^{+\infty} P_{ij} f_j(U(j, j + cn)).$$

Let  $s = i + c + cn$ . This equation can be written as

$$\begin{aligned} U(i, s) &= \sum_{j=-\infty}^{+\infty} P_{ij} f_j(U(j, j + s - i - c)) \\ &\stackrel{\text{---}}{=} \sum_{k=i-j}^{-\infty} P_{i,i-k} f_{i-k}(U(i - k, s - k - c)) \\ &\stackrel{\text{---}}{=} \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}(U(i - j, s - j - c)). \end{aligned}$$

Thus, we only need to consider the following wave profile equation

$$U(i, s) = \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}(U(i - j, s - j - c)). \tag{3.3}$$

Define

$$\begin{aligned} T[U](i, s) &:= \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}(U(i - j, s - j - c)), \quad \forall U \in C(\mathbb{Z} \times X_c, [0, b]), \\ &i \in \mathbb{Z}, s \in X_c. \end{aligned} \tag{3.4}$$

Similarly, we define  $T^+$  and  $T^-$  as in (3.4) with  $f$  replaced by  $f^+$  and  $f^-$ , respectively. It then follows that  $T^\pm$  are nondecreasing and that

$$T^-[U](i, s) \leq T[U](i, s) \leq T^+[U](i, s), \quad \forall U \in C(\mathbb{Z} \times X_c, [0, b]), i \in \mathbb{Z}, s \in X_c.$$

**Theorem 3.2** *Let (H1), (H2), (H3)', (H4) and (H5) hold. Then the following statements are valid:*

- (i) *For any  $c < c^*(-1)$ , (1.3) has no periodic traveling wave  $U(i, i + cn)$  such that  $U \in \mathcal{F}_{c,u_{+*}} \setminus \{0\}$  and  $U(i, -\infty) = 0$  for all  $i \in \mathbb{Z}$ .*
- (ii) *For any  $c > c^*(-1)$ , (1.3) has a periodic traveling wave  $U(i, i + cn)$  such that  $U \in \mathcal{F}_{c,u_{+*}} \setminus \{0\}$ ,  $U(i, -\infty) = 0$ , and for any  $i \in \mathbb{Z}, \bar{c} < c^*(-1)$ ,*

$$\min_{1 \leq j \leq L} \{u_{-*}^j\} \leq \liminf_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\}.$$

- (iii) *For  $\vec{\xi} = 1$ , similar results hold for periodic traveling waves  $U(i, i - cn)$  with  $U(i, \infty) = 0$ .*

*Proof* We only assume  $\vec{\xi} = -1$  and prove (i) and (ii) since the proof in the case of  $\vec{\xi} = 1$  is similar.

Assume, by contradiction, that for some  $c_0 < c^*(-1)$ , (1.3) has a periodic traveling wave  $U(i, i + c_0n)$  with  $U \in C(\mathbb{Z} \times X_{c_0}, [0, u_{+*}]) \setminus \{0\}$  and  $U(i, -\infty) = 0$  for all  $i \in \mathbb{Z}$ . Let  $u_n^i = U(i, i + c_0n)$ . Fix two real numbers  $c_1$  and  $c_2$  such that  $c_0 < c_1 < c_2 < c^*(-1)$ . Since

$U(i, i + c_0n) \not\equiv 0$ , there exist  $n_0$  and  $i_0$ , such that  $U(i_0, i_0 + c_0n_0) \neq 0$ , i.e.,  $u_{n_0}^{i_0} \neq 0$ . Regarding  $u_{n_0}$  as a new initial value, we see from Theorem 3.1 (ii) that  $\liminf_{n \rightarrow \infty, i \geq -c_2n} (u_n^i - u_{-c_2n}^i) \geq 0$ , and hence,  $\liminf_{n \rightarrow \infty, i \geq -c_2n} u_n^i > 0$ . Letting  $i = \lfloor -c_1n \rfloor$ , we then obtain  $\liminf_{n \rightarrow \infty} u_n^{\lfloor -c_1n \rfloor} = \liminf_{n \rightarrow \infty} U(\lfloor -c_1n \rfloor, c_0n + \lfloor -c_1n \rfloor) > 0$ . Since  $\lim_{s \rightarrow -\infty} U(i, s) = 0$  uniformly for  $i \in \mathbb{Z}$ , we have  $\liminf_{n \rightarrow \infty} U(\lfloor -c_1n \rfloor, c_0n + \lfloor -c_1n \rfloor) = 0$ , a contradiction.

Let  $c > c^*(-1)$  be given. It follows that there exists  $\mu_1 \in (0, \Delta^-)$  such that  $\frac{\ln \lambda_{-\mu_1}}{\mu_1} = c$ . Without loss of generality, suppose that  $\mu_1$  is the smallest  $\mu$  such that  $\frac{\ln \lambda_{-\mu}}{\mu} = c$ . Thus,  $\lambda_{-\mu_1} = e^{c\mu_1}$ . Let  $\{\psi_*^i\}_{i \in \mathbb{Z}}$  be the nonnegative eigenvector of  $L_{-\mu_1}$  corresponding to  $\lambda_{-\mu_1}$  with  $\psi_*^i = \psi_*^{i+L}$  for all  $i \in \mathbb{Z}$ . Then

$$(L_{-\mu_1}[\psi_*])^i = \sum_{j=-\infty}^{\infty} P_{ij} f'_j(0) \psi_*^j e^{-\mu_1(i-j)} = e^{c\mu_1} \psi_*^i, \quad \forall i \in \mathbb{Z}.$$

Define  $\phi^+$  on  $\mathbb{Z} \times X_c$  as

$$\phi^+(i, s) = \min\{\psi_*^i e^{\mu_1 s}, u_{+*}^i\}, \quad \forall i \in \mathbb{Z}, s \in X_c.$$

Then for any  $i \in \mathbb{Z}, s \in X_c$ ,

$$\begin{aligned} T^+[\phi^+](i, s) &= \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}^+(\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}^+(u_{+*}^{i-j}) \\ &= \sum_{j=-\infty}^{\infty} P_{ij} f_j^+(u_{+*}^j) \\ &= u_{+*}^i. \end{aligned}$$

Since  $f_i(u) \leq f'_i(0)u$  for all  $u \in [0, b], i \in \mathbb{Z}$ , we have

$$f_i^+(u) = \max_{v \in [0, u]} f_i(v) \leq \max_{v \in [0, u]} f'_i(0)v = f'_i(0)u, \quad \forall u \in [0, b], i \in \mathbb{Z},$$

and hence,

$$\begin{aligned} T^+[\phi^+](i, s) &= \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}^+(\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i,i-j} f'_{i-j}(0) (\phi^+(i-j, s-j-c)) \\ &\leq \sum_{j=-\infty}^{\infty} P_{i,i-j} f'_{i-j}(0) \psi_*^{i-j} e^{\mu_1(s-j-c)} \\ &= e^{\mu_1(s-c)} e^{c\mu_1} \psi_*^i \\ &= \psi_*^i e^{\mu_1 s}, \end{aligned}$$

for any  $i \in \mathbb{Z}, s \in X_c$ . Thus,

$$T^+[\phi^+](i, s) \leq \min\{u_{+*}^i, \psi_*^i e^{\mu_1 s}\} = \phi^+(i, s), \quad \forall i \in \mathbb{Z}, s \in X_c.$$

Let  $\varepsilon > 0$  be sufficiently small such that  $0 < \varepsilon \leq \mu_1(\sigma - 1)$ ,  $\mu_\varepsilon := \mu_1 + \varepsilon \in (0, \Delta^-)$ , and  $c_\varepsilon := \frac{\ln \lambda_{-\mu_\varepsilon}}{\mu_\varepsilon} \in (c^*(-1), c)$ . Then  $\lambda_{-\mu_\varepsilon} = e^{c_\varepsilon \mu_\varepsilon}$  is the principle eigenvalue of  $L_{-\mu_\varepsilon}$



with a nonnegative eigenvector  $\{\psi_{*\varepsilon}^i\}_{i \in \mathbb{Z}}$  with  $\psi_{*\varepsilon}^i = \psi_{*\varepsilon}^{i+L}$  for all  $i \in \mathbb{Z}$ , that is,

$$(L_{-\mu_\varepsilon}[\psi_{*\varepsilon}])^i = \sum_{j=-\infty}^{\infty} P_{ij} f'_j(0) \cdot \psi_{*\varepsilon}^j \cdot e^{-\mu_\varepsilon(i-j)} = e^{c_\varepsilon \mu_\varepsilon} (\psi_{*\varepsilon}^i), \quad \forall i \in \mathbb{Z}.$$

Define  $\phi^-$  on  $\mathbb{Z} \times X_c$  as

$$\phi^-(i, s) = \max\{0, \psi_*^i e^{\mu_1 s} - \psi_{*\varepsilon}^i e^{\mu_\varepsilon s}\}, \quad \forall i \in \mathbb{Z}, s \in X_c.$$

Fix  $\{\psi_{*\varepsilon}^i\}_{i \in \mathbb{Z}}$ . We can further restrict  $\{\psi_*^i\}_{i \in \mathbb{Z}}$  such that  $\psi_*^i \leq \min\{\delta^*, u_{+*}^i, \psi_{*\varepsilon}^i\}$  for all  $i \in \mathbb{Z}$ , and

$$\psi_{*\varepsilon}^i \cdot f'_i(0) + \alpha(\psi_*^i)^\sigma \leq e^{(c-c_\varepsilon)\mu_\varepsilon} \psi_{*\varepsilon}^i \cdot f'_i(0), \quad \forall i \in \mathbb{Z}.$$

Then  $\phi^-(i, s) \in [0, \delta^*]$  and  $\phi^-(i, s) \leq \phi^+(i, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ . We claim that

$$(\phi^-(i, s))^\sigma \leq (\psi_*^i)^\sigma e^{\mu_\varepsilon s}, \quad \forall i \in \mathbb{Z}, s \in X_c.$$

If  $\phi^-(i, s) = 0$ , it is obvious. If  $\phi^-(i, s) > 0$ , then  $s < 0$ . Since  $0 < \varepsilon \leq \mu_1(\sigma - 1)$ , we have  $\varepsilon s + \mu_1 s \geq \mu_1 \sigma s$ . Thus,

$$(\phi^-(i, s))^\sigma \leq e^{\mu_1 \sigma s} (\psi_*^i)^\sigma \leq e^{\mu_1 s + \varepsilon s} (\psi_*^i)^\sigma = e^{\mu_\varepsilon s} (\psi_*^i)^\sigma,$$

and hence,  $(\phi^-(i, s))^\sigma \leq (\psi_*^i)^\sigma e^{\mu_\varepsilon s}$  for all  $i \in \mathbb{Z}, s \in X_c$ .

Clearly,  $T^-[ \phi^- ](i, s) \geq 0$  for all  $i \in \mathbb{Z}, s \in X_c$ . Moreover,

$$\begin{aligned} & T^-[ \phi^- ](i, s) \\ &= \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}^-(\phi^-(i-j, s-j-c)) \\ &\geq \sum_{j=-\infty}^{\infty} P_{i,i-j} \left( f_{i-j}'(0) \phi^-(i-j, s-j-c) - \alpha(\phi^-(i-j, s-j-c))^\sigma \right) \\ &\geq \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}'(0) \left( \psi_*^{i-j} e^{\mu_1(s-j-c)} - \psi_{*\varepsilon}^{i-j} e^{\mu_\varepsilon(s-j-c)} \right) \\ &\quad - \sum_{j=-\infty}^{\infty} P_{i,i-j} \alpha(\psi_*^{i-j})^\sigma e^{\mu_\varepsilon(s-j-c)} \\ &= e^{\mu_1(s-c)} \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}'(0) \psi_*^{i-j} e^{-\mu_1 j} \end{aligned}$$

$$\begin{aligned}
 & -e^{\mu_\varepsilon(s-c)} \sum_{j=-\infty}^{\infty} P_{i,i-j} \left( f'_{i-j}(0) \psi_{*\varepsilon}^{i-j} e^{-\mu_\varepsilon j} + \alpha (\psi_*^{i-j})^\sigma e^{-\mu_\varepsilon j} \right) \\
 \geq & e^{\mu_1(s-c)} \sum_{j=-\infty}^{\infty} P_{i,j} f'_j(0) \psi_*^j e^{-\mu_1(i-j)} \\
 & - e^{\mu_\varepsilon(s-c)} \sum_{j=-\infty}^{\infty} P_{i,i-j} f'_{i-j}(0) \psi_{*\varepsilon}^{i-j} e^{-\mu_\varepsilon j} \cdot e^{(c-c_\varepsilon)\mu_\varepsilon} \\
 = & e^{\mu_1(s-c)} \cdot e^{c\mu_1} \cdot \psi_*^i - e^{\mu_\varepsilon(s-c)} \cdot e^{(c-c_\varepsilon)\mu_\varepsilon} \sum_{j=-\infty}^{\infty} P_{ij} f'_j(0) \psi_{*\varepsilon}^j \cdot e^{-\mu_\varepsilon(i-j)} \\
 = & e^{\mu_1 s} \psi_*^i - e^{\mu_\varepsilon(s-c_\varepsilon)} e^{c_\varepsilon \mu_\varepsilon} \psi_{*\varepsilon}^i \\
 = & e^{\mu_1 s} \psi_*^i - e^{\mu_\varepsilon s} \psi_{*\varepsilon}^i,
 \end{aligned}$$

for any  $i \in \mathbb{Z}, s \in X_c$ . Thus,  $T^-[ \phi^- ](i, s) \geq \phi^-(i, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ .

Fix some  $\mu \in (0, \mu_1)$  and define

$$\begin{aligned}
 X_\mu := & \{ \phi \in C(\mathbb{Z} \times X_c, \mathbb{R}) : \phi(i, s) = \phi(i + L, s), \forall (i, s) \in \mathbb{Z} \times X_c, \\
 & \sup_{s \in X_c} \max_{1 \leq i \leq L} |\phi(i, s)| e^{-\mu s} < \infty \}
 \end{aligned}$$

and  $\|\phi\|_\mu = \sup_{s \in X_c} \max_{1 \leq i \leq L} |\phi(i, s)| e^{-\mu s}$  for all  $\phi \in X_\mu$ . It follows that  $(X_\mu, \|\cdot\|_\mu)$  is a Banach space. Clearly,  $\phi^+, \phi^- \in X_\mu$ . Let

$$Y := \{ \phi \in X_\mu : \phi^-(i, s) \leq \phi(i, s) \leq \phi^+(i, s), \forall i \in \mathbb{Z}, s \in X_c \}.$$

It is easy to see that  $Y$  is nonempty, closed and convex in  $X_\mu$ . For any  $\phi \in Y$ ,

$$\phi^- \leq T^-[ \phi^- ] \leq T^-[ \phi ] \leq T[ \phi ] \leq T^+[ \phi ] \leq T^+[ \phi^+ ] \leq \phi^+.$$

Moreover, we have

$$\begin{aligned}
 T[ \phi ](i + L, s) &= \sum_{j=-\infty}^{\infty} P_{i+L,i+L-j} f_{i+L-j}(\phi(i + L - j, s - j - c)) \\
 &= \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}(\phi(i - j, s - j - c)) \\
 &= T[ \phi ](i, s)
 \end{aligned}$$

for any  $i \in \mathbb{Z}$  and  $s \in X_c$ , and

$$\begin{aligned}
 0 &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} |T[\phi](i, s)|e^{-\mu s} \\
 &= \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}(\phi(i-j, s-j-c))e^{-\mu s} \\
 &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i,i-j} f_{i-j}^+(\phi^+(i-j, s-j-c))e^{-\mu s} \\
 &= \sup_{s \in X_c} \max_{1 \leq i \leq L} T^+[\phi^+](i, s)e^{-\mu s} \\
 &\leq \sup_{s \in X_c} \max_{1 \leq i \leq L} \phi^+(i, s)e^{-\mu s} \\
 &= \|\phi^+\|_{\mu}.
 \end{aligned} \tag{3.5}$$

Therefore, for any  $\phi \in Y$ ,  $T[\phi] \in Y$ , and hence,  $T(Y) \subseteq Y$ .

For any  $\varphi, \psi \in Y$ , we have

$$\begin{aligned}
 &\|T[\varphi] - T[\psi]\|_{\mu} \\
 &= \sup_{s \in X_c} \max_{1 \leq i \leq L} |T[\varphi](i, s) - T[\psi](i, s)|e^{-\mu s} \\
 &= \sup_{s \in X_c} \max_{1 \leq i \leq L} \left| \sum_{j=-\infty}^{\infty} P_{i,i-j} [f_{i-j}(\varphi(i-j, s-j-c)) - f_{i-j}(\psi(i-j, s-j-c))] \right| e^{-\mu s} \\
 &\leq \hat{L} \sup_{s \in X_c} \max_{1 \leq i \leq L} \sum_{j=-\infty}^{\infty} P_{i,i-j} |\varphi(i-j, s-j-c) - \psi(i-j, s-j-c)|e^{-\mu s} \\
 &\leq \hat{L} \sum_{j=-\infty}^{\infty} P_{i,i-j} \sup_{s \in X_c} \max_{1 \leq i \leq L} |\varphi(i-j, s-j-c) - \psi(i-j, s-j-c)|e^{-\mu(s-j-c)} e^{-\mu(j+c)} \\
 &= \hat{L} \sum_{j=-\infty}^{\infty} P_{i,i-j} \|\varphi - \psi\|_{\mu} e^{-\mu(j+c)} \\
 &\leq \tilde{L} \|\varphi - \psi\|_{\mu}
 \end{aligned}$$

for some  $\tilde{L} > 0$  since  $\sum_{j=-\infty}^{\infty} P_{i,i-j} e^{-\mu j} < \infty$ . Thus,  $T : Y \rightarrow Y$  is continuous.

By (3.5), it follows that  $\{T[\phi] : \phi \in Y\}$  is uniformly bounded. Since both  $\mathbb{Z}$  and  $X_c$  consist of countable elements, it is obvious that  $\{T[\phi] : \phi \in Y\}$  is equicontinuous on any bounded subset of  $\mathbb{Z} \times X_c$ . It follows from the Arzela-Ascoli theorem that for any given sequence  $\{\psi_n\}_{n \geq 1}$  in  $T(Y)$ , there exist  $n_k \rightarrow \infty$  and  $\psi : \mathbb{Z} \times X_c \rightarrow \mathbb{R}$  such that

$$\lim_{k \rightarrow \infty} \psi_{n_k}(i, s) = \psi(i, s)$$

uniformly for  $(i, s)$  in any bounded subset of  $\mathbb{Z} \times X_c$ . Since  $\phi^-(i, s) \leq \psi_{n_k}(i, s) \leq \phi^+(i, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ , we have  $\phi^-(i, s) \leq \psi(i, s) \leq \phi^+(i, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ . Moreover, by the periodicity of  $\psi_{n_k}$  with respect to  $L$ , we also have  $\psi(i, s) = \psi(i + L, s)$  for all  $i \in \mathbb{Z}, s \in X_c$ . The boundedness of  $\sup_{s \in X_c} \max_{1 \leq i \leq L} |\psi(i, s)|e^{-\mu s}$  is obvious. Therefore,  $\psi \in Y$ .

Note that

$$\begin{aligned} \lim_{s \rightarrow +\infty} (\phi^+(i, s) - \phi^-(i, s))e^{-\mu s} &= 0, \\ \lim_{s \rightarrow -\infty} (\phi^+(i, s) - \phi^-(i, s))e^{-\mu s} &= 0, \end{aligned}$$

uniformly for  $i \in \{1, 2, \dots, L\}$ . Therefore, for any  $\varepsilon > 0$ , there exists  $M > 0$  such that

$$0 \leq (\phi^+(i, s) - \phi^-(i, s))e^{-\mu s} < \varepsilon, \quad \forall s \in X_c, \quad |s| \geq M, \quad 1 \leq i \leq L,$$

and hence,

$$\begin{aligned} |\psi_{n_k}(i, s) - \psi(i, s)|e^{-\mu s} &\leq |\phi^+(i, s) - \phi^-(i, s)|e^{-\mu s} < \varepsilon, \quad \forall s \in X_c, \quad |s| \geq M, \\ 1 \leq i \leq L. \end{aligned}$$

Since  $\lim_{k \rightarrow \infty} |\psi_{n_k}(i, s) - \psi(i, s)|e^{-\mu s} = 0$  uniformly for  $1 \leq i \leq L$  and  $s \in X_c$  with  $|s| \leq M$ , there exists an integer  $N > 0$  such that

$$|\psi_{n_k}(i, s) - \psi(i, s)|e^{-\mu s} < \varepsilon, \quad \forall 1 \leq i \leq L, \quad s \in X_c, \quad |s| \leq M, \quad k \geq N.$$

It then follows that

$$\|\psi_{n_k} - \psi\|_\mu = \sup_{s \in X_c} \max_{1 \leq i \leq L} |\psi_{n_k}(i, s) - \psi(i, s)|e^{-\mu s} < \varepsilon, \quad \forall k \geq N,$$

and hence,  $\lim_{k \rightarrow \infty} \psi_{n_k} = \psi$  in  $X_\mu$ . Thus,  $T(Y)$  is precompact in  $X_\mu$ .

Thus, by the Schauder fixed point theorem, there exists  $U \in Y$  such that  $U = T[U]$ , and hence,  $U(i, s)$  is a traveling wave of (1.3). Since  $\phi^-(i, s) \leq U(i, s) \leq \phi^+(i, s)$  for all  $i \in \mathbb{Z}$ ,  $s \in X_c$ , we have  $U(i, -\infty) = 0$  and  $U \in C(\mathbb{Z} \times X_c, [0, u_{+*}]) \setminus \{0\}$ .

Let  $u_n^i = U(i, i + cn)$  for all  $i \in \mathbb{Z}, n \in \mathbb{N}$ . Fix  $\bar{c} < c^*(-1)$ . By Theorem 3.1 (ii), we have

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} (u_n^i - u_{-*}^i) \geq 0, \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} (u_n^i - u_{+*}^i) \leq 0.$$

Then for sufficiently small  $\varepsilon > 0$ , we have

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} u_n^i \geq \min_{1 \leq j \leq L} \{u_{-*}^j\} - \varepsilon > 0, \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} u_n^i \leq \max_{1 \leq j \leq L} \{u_{+*}^j\} + \varepsilon,$$

that is,

$$\liminf_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \geq \min_{1 \leq j \leq L} \{u_{-*}^j\} - \varepsilon, \quad \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\} + \varepsilon.$$

Letting  $\varepsilon \rightarrow 0$ , we obtain

$$\min_{1 \leq j \leq L} \{u_{-*}^j\} \leq \liminf_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \limsup_{n \rightarrow \infty, i \geq -\bar{c}n} U(i, i + cn) \leq \max_{1 \leq j \leq L} \{u_{+*}^j\}.$$

This completes the proof. □

As a remark of this section, we point out that the domains for all periodic traveling wave profiles with speed  $c > c^*(\vec{\xi})$  are not the same, and hence, it is not easy to use these wave profiles to approximate the possible periodic traveling wave profile with  $c = c^*(\vec{\xi})$ . Thus, we are not able to prove the existence of the periodic traveling wave with speed  $c = c^*(\vec{\xi})$  at this moment.

### 4 An Example

In this section, we present an example of (1.3) with some specific recruitment function and dispersal kernel to illustrate our main analytic results.

Consider the Ricker type recruitment function

$$f_i(u) = aue^{r(i)-qu}, \quad \forall i \in \mathbb{Z}, u \in \mathbb{R},$$

where  $q > 0$ ,  $r$  is an  $L$ -periodic function defined on  $\mathbb{Z}$  for some  $L \in \mathbb{N}$ , and  $ae^{r(i)} > 1$  for all  $i \in \mathbb{Z}$ . Inspired by the exponentially damping kernel function for a continuous habitat (see

[11]), we choose  $P_{ij} = \frac{e^{\frac{1}{d}-1}e^{-\frac{|i-j|}{d}}}{e^{\frac{1}{d}+1}}$  with  $d > 0$ , for any  $i, j \in \mathbb{Z}$ . Then (1.3) becomes

$$u_{n+1}^i = \sum_{j=-\infty}^{+\infty} \frac{e^{\frac{1}{d}-1}}{e^{\frac{1}{d}+1}} e^{-\frac{|i-j|}{d}} au_n^j e^{r(j)-qu_n^j}, \quad i \in \mathbb{Z}, n \in \mathbb{Z}. \tag{4.1}$$

Clearly, for any  $i \in \mathbb{Z}$ ,  $f_i \in C^1(\mathbb{R}, \mathbb{R})$ ,  $f_i(0) = 0$ ,  $f_i(u) = aue^{r(i)-qu} = aue^{r(i+L)-qu} = f_{i+L}(u)$  for all  $u \in \mathbb{R}$ ,  $f_i(u)/u = ae^{r(i)-qu}$  is strictly decreasing in  $u \in \mathbb{R}$ ,  $f_i'(0) = ae^{r(i)} > 1$ . Moreover, for any  $i \in \mathbb{Z}$ ,  $\max_{u \in [0, +\infty)} f_i(u) = f_i\left(\frac{1}{q}\right) = \frac{a}{q}e^{r(i)-1}$ . Let

$$\hat{b} = \{b\}_{i \in \mathbb{Z}} \in X \quad \text{with } b = \max_{i \in \mathbb{Z}} f_i\left(\frac{1}{q}\right),$$

and

$$\hat{L} = \max_{1 \leq i \leq L, u \in [0, b]} |f_i'(u)| = \max_{1 \leq i \leq L, u \in [0, b]} ae^{r(i)-qu}|1-qu|.$$

Then  $\hat{b} \in X^L$ ,  $f_i([0, b]) \subseteq [0, b]$  for all  $i \in \mathbb{Z}$  and

$$|f_i(u_1) - f_i(u_2)| \leq \hat{L}|u_1 - u_2|, \quad \forall i \in \mathbb{Z}, u_1, u_2 \in [0, b].$$

It is easy to see that  $P_{ij} = P_{i+L, j+L}$  for all  $i, j \in \mathbb{Z}$  and  $\sum_{j=-\infty}^{\infty} P_{ij} = 1$ . Moreover, for  $\mu \in [0, \frac{1}{d})$ ,  $i \in \mathbb{Z}$ ,

$$\begin{aligned} \sum_{j=-\infty}^{\infty} P_{ij}e^{-\mu(i-j)} &= \frac{e^{\frac{1}{d}-1}}{e^{\frac{1}{d}+1}} \sum_{j=-\infty}^{\infty} e^{-\frac{|i-j|}{d}} e^{-\mu(i-j)} \\ &= \frac{\left(e^{\frac{1}{d}-1}\right)e^{\mu} \left(e^{\frac{2}{d}-1}\right)}{\left(e^{\frac{1}{d}+1}\right) \left(e^{\mu+\frac{1}{d}}-1\right) \left(e^{\frac{1}{d}}-e^{\mu}\right)}. \end{aligned}$$

This indicates that  $\sum_{j=-\infty}^{\infty} P_{ij}e^{-\mu(i-j)} \rightarrow \infty$  as  $\mu \rightarrow 1/d$ . Similarly, we can obtain that when  $\mu \in (-1/d, 0]$ ,  $\sum_{j=-\infty}^{\infty} P_{ij}e^{-\mu(i-j)} \rightarrow \infty$  as  $\mu \rightarrow -1/d$ . Thus,  $\sum_{j=-\infty}^{\infty} P_{ij}e^{-\mu(i-j)}$  converges for all  $\mu \in (-1/d, 1/d)$  for all  $i \in \mathbb{Z}$ , and hence,  $\Delta^+ = \Delta^- = 1/d$ .

For  $\sigma = 2$  and  $\alpha$  satisfies  $0 < \frac{ae^{r(i)}}{\alpha} \leq \frac{1}{q}$  for all  $i \in \mathbb{Z}$ , we have

$$f_i(u) \geq f_i'(0)u - \alpha u^\sigma, \quad \forall i \in \mathbb{Z}, u \in [0, b].$$

Define  $\bar{L}_0 : \mathbb{R}^L \rightarrow \mathbb{R}^L$  as

$$\bar{L}_0[\varphi] = A\varphi, \quad \forall \varphi \in \mathbb{R}^L,$$

where  $A = (a_{im})_{L \times L}$  with  $a_{im} = \sum_{k=-\infty}^{+\infty} P_{i,kL+m} f'_m(0)$ , for  $i, m \in \{1, 2, \dots, L\}$ , and

$$r(\bar{L}_0) = \max\{|\lambda|, \lambda \text{ is an eigenvalue of } A\}.$$

In this case, we have

$$a_{im} = ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} \sum_{k=-\infty}^{\infty} e^{-\frac{|i-(kL+m)|}{d}}$$

$$= \begin{cases} ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{(e^{\frac{1}{d}} + 1)(1 - e^{-\frac{L}{d}})} \left( e^{-\frac{i+m}{d}} + e^{-\frac{i-m-L}{d}} \right), & \text{if } i \geq m, \\ ae^{r(m)} \frac{e^{\frac{1}{d}} - 1}{(e^{\frac{1}{d}} + 1)(1 - e^{-\frac{L}{d}})} \left( e^{-\frac{i+m-L}{d}} + e^{-\frac{i-m}{d}} \right), & \text{if } i < m, \end{cases}$$

for  $i, m \in \{1, 2, \dots, L\}$ .

If we further have  $r(\bar{L}_0) > 1$ , then assumptions (H1), (H2), (H3)', (H4) and (H5) hold, and hence, Theorems 3.1 and 3.2 hold for system (4.1). The spreading speed in the direction of  $\vec{\xi} = -1$  is

$$c^*(-1) = \inf_{\mu \in (0, \frac{1}{d})} \frac{\ln \lambda_{-\mu}}{\mu},$$

where  $\lambda_{-\mu}$  is the principle eigenvalue of  $L_{-\mu} : \mathbb{R}^L \rightarrow \mathbb{R}^L$ :

$$L_{-\mu}[u] = A_{-\mu}u, \quad \forall u \in \mathbb{R}^L,$$

where  $A_{-\mu} = (a_{im}^{-\mu})_{L \times L}$  with

$$a_{im}^{-\mu} = \sum_{k=-\infty}^{+\infty} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\frac{|i-(kL+m)|}{d}} e^{r(m)} e^{-\mu(i-(kL+m))}$$

$$= \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m)-\mu(i-m)} \left( \frac{e^{-\frac{m-i}{d}}}{1 - e^{-(\mu L + \frac{L}{d})}} + \frac{e^{-\frac{i-m-L}{d} + \mu L}}{1 - e^{(\mu L - \frac{L}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m)-\mu(i-m)} \left( \frac{e^{-\frac{m-i-L}{d} - \mu L}}{1 - e^{-(\mu L + \frac{L}{d})}} + \frac{e^{-\frac{i-m}{d}}}{1 - e^{(\mu L - \frac{L}{d})}} \right), & \text{if } i < m, \end{cases}$$

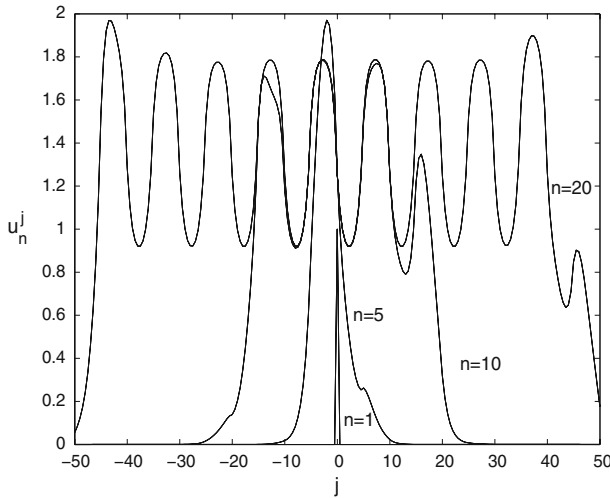
for  $i, m \in \{1, 2, \dots, L\}$ .

The spreading speed in the direction of  $\vec{\xi} = 1$  can be similarly obtained as

$$c^*(1) = \inf_{\mu \in (0, \frac{1}{d})} \frac{\ln \lambda_{\mu}}{\mu},$$

where  $\lambda_{\mu}$  is the principle eigenvalue of  $L_{\mu} : \mathbb{R}^L \rightarrow \mathbb{R}^L$ :

$$L_{\mu}[u] = A_{\mu}u, \quad \forall u \in \mathbb{R}^L,$$



**Fig. 1** A solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of (4.1) when  $n = 1, 5, 10, 20$

where  $A_\mu = (a_{im}^\mu)_{L \times L}$  with

$$a_{im}^\mu = \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) + \mu(i-m)} \left( \frac{e^{\frac{m-i}{d}}}{1 - e^{-(\mu L - \frac{L}{d})}} + \frac{e^{\frac{i-m-L}{d} - \mu L}}{1 - e^{-(\mu L - \frac{L}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{r(m) + \mu(i-m)} \left( \frac{e^{\frac{m-i-L}{d} + \mu L}}{1 - e^{-(\mu L - \frac{L}{d})}} + \frac{e^{\frac{i-m}{d}}}{1 - e^{-(\mu L - \frac{L}{d})}} \right), & \text{if } i < m, \end{cases}$$

for  $i, m \in \{1, 2, \dots, L\}$ .

Since  $P_{ij} = P_{ji}$  for all  $i, j \in \mathbb{Z}$ , it follows from Lemma 2.3 that spreading speeds in the directions of  $\vec{\xi} = 1$  and  $\vec{\xi} = -1$  are the same, i.e.,  $c^*(1) = c^*(-1)$ . Indeed, it is easy to see that  $A_{-\mu} = BC$  and  $A_\mu = B^\top C$ , where

$$B_{im} = \begin{cases} a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\mu(i-m)} \left( \frac{e^{\frac{m-i}{d}}}{1 - e^{-(\mu L + \frac{L}{d})}} + \frac{e^{\frac{i-m-L}{d} + \mu L}}{1 - e^{-(\mu L - \frac{L}{d})}} \right), & \text{if } i \geq m, \\ a \frac{e^{\frac{1}{d}} - 1}{e^{\frac{1}{d}} + 1} e^{-\mu(i-m)} \left( \frac{e^{\frac{m-i-L}{d} - \mu L}}{1 - e^{-(\mu L + \frac{L}{d})}} + \frac{e^{\frac{i-m}{d}}}{1 - e^{-(\mu L - \frac{L}{d})}} \right), & \text{if } i < m, \end{cases}$$

for  $i, m \in \{1, 2, \dots, L\}$ , and  $C = \text{diag}\{e^{r(1)}, e^{r(2)}, \dots, e^{r(L)}\}$ .

In particular, we choose

$$r(i) = \begin{cases} r_1, & nL - L_1 \leq i < nL, \\ r_2, & nL \leq i < nL + L_2, \end{cases}$$

for any  $i \in \mathbb{Z}$ , where  $n \in \mathbb{N}$ ,  $L_1, L_2 \in \mathbb{N}$  and  $L_1 + L_2 = L$ . This indicates that each period part of the whole habitat is composed of a favorable habitat (corresponding to  $\max\{r_1, r_2\}$ ) and an unfavorable habitat (corresponding to  $\min\{r_1, r_2\}$ ). Let  $a = 1.2, q = 1, d = 1, L = 2, L_1 = L_2 = 1, r_1 = 0, r_2 = 1$ . Then we have

$$A = \begin{bmatrix} 1.979266244 & 0.4718686397 \\ 1.282671949 & 0.7281313600 \end{bmatrix}$$

and  $r(\bar{L}_0) = 2.351990990 > 1$ . Moreover,

$$A_{-\mu} = \left[ \begin{array}{cc} \frac{1.2e(e-1) \left( \frac{1}{1-e^{-2\mu-2}} + \frac{e^{-2+2\mu}}{1-e^{-2+2\mu}} \right)}{(e+1)} & \frac{1.2e^\mu(e-1) \left( \frac{e^{-1-2\mu}}{1-e^{-2\mu-2}} + \frac{e^{-1}}{1-e^{-2+2\mu}} \right)}{(e+1)} \\ \frac{1.2e^{1-\mu}(e-1) \left( \frac{e^{-1}}{1-e^{-2\mu-2}} + \frac{e^{-1+2\mu}}{1-e^{-2+2\mu}} \right)}{(e+1)} & \frac{1.2(e-1) \left( \frac{1}{1-e^{-2\mu-2}} + \frac{e^{-2+2\mu}}{1-e^{-2+2\mu}} \right)}{(e+1)} \end{array} \right]$$

and

$$c^*(1) = c^*(-1) \approx 2.069595656.$$

As a verification of the analytic results, choosing the initial function  $u_1$  as

$$u_1^i = \begin{cases} 1, & i = 0, \\ 0, & i \neq 0, i \in \mathbb{Z}, \end{cases}$$

we show the solution  $\{u_n^i\}_{i \in \mathbb{Z}}$  of (4.1) at times  $n = 1, 5, 10, 20$  in Fig. 1.

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