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Dynamics of a Nonlocal Dispersal Population Model With Annually Synchronized Emergence of Adults

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ABSTRACT

This paper is devoted to studying the spatial dynamics of a nonlocal dispersal species model with annually synchronized emergence of adults. In the situation of a bounded domain, we show threshold dynamics of the adult population, and provide exact persistence criterion. In the situation of a spatially homogeneous unbounded domain, we obtain the existence and computation formula of spreading speeds, which coincide with the minimal wave speed for the traveling waves. The above results are obtained in both monotone and nonmonotone cases of maturation impulse function. Numerical simulations are carried out to demonstrate the theoretical results.

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1 | Introduction

Mathematical models play a very important role in spatial ecology because they help understand and explain evolution of biological species in time and space (see, e.g., Cantrell and Cosner [8]; Murray [37, 38]; Okubo and Levin [40]). Reaction–diffusion equations, which contain random diffusion operators and reaction functions, can describe the spatial movement and growth of the population in time and space. Spatial theories about the spread and persistence of species obtained by reaction–diffusion equations agree in many cases with field observations (Cantrell and Cosner [8]; Murray [37, 38]; Shigesada and Kawasaki [43]).

For many biological species, such as birds and large mammal, there is one (or more for some species) breeding season annually, reflected by the births occurring at the beginning of the season and newly born individuals growing into adults before the end of the year. For instance, in Colorado, big brown bats usually breed only in late June [16]. For such a species, its long-term population dynamics can be more properly described by a so-called metered model that distinguishes the growths of immature and mature populations which are connected by the producing and maturing in the beginning and end of the breeding season. Within a season, the population can move in the space and population mortality depends continuously on time, while between seasons the population gives birth to offsprings in discrete form. In [28], Lewis and Li constructed an impulsive reaction–diffusion model for species with distinct reproductive and dispersal stages, which describes a seasonal birth pulse plus dispersal and nonlinear mortality throughout the year. In the one-dimensional space, they provided a critical domain size to determine whether a species is persistent or extinct in a bounded domain, and also showed the existence of spreading speed and traveling waves in the unbounded domain. These results were extended by Fazly, Lewis, and Wang [14, 15] to a general impulsive reaction–diffusion–advection system in a high-dimensional space. For a class of species of stream insects with different life stages, Vasilyeva, Lutscher, and Lewis [47] proposed a reaction–diffusion–advection system incorporating nonlocal impulse to describe the population dynamics. Considering the effects of climate changes, Wang and Wang [48] studied the persistence and propagation dynamics of a PDE and discrete-map hybrid model with habitat shift. Meng, Ge, and Lin [36] explored the effect of impulsive harvesting on the logistic model with free boundaries. Recently, Wang and Wang [49] considered an impulsive reaction–diffusion–advection system with bistable nonlinearity, and proved the existence, uniqueness, and global stability of bistable traveling wave.

It has been observed and reported that in addition to reproductive synchronization in years, many egg-laying animals may also demonstrate synchronous emergence of mature individuals, and synchronous hatching and emergence (Santos et al. [42]). One can refer to the reference [7] for the synchronous maturation of *Xiphophorus variatus*, and [22] for the synchronized emergence of adult cicadas in 13- and 17-year cycles as instances. According to such an observation, Bai, Lou, and Zhao [3] established the following impulsive reaction–diffusion population model with the annually synchronous emergence of mature individuals:

$$\begin{cases} \partial_t u_m = D_M \dfrac{\partial^2 u_m}{\partial x^2} - f(u_m), & x \in \Omega,\ 0 < t \le 1,\ t \neq \tau, \\ u_m(x, t^+) = u_m(x, t) + \mathcal{R}(x; N_m), & t = \tau, \\ u_m(x, 0) = N_m(x), & m \in \mathbb{N}, \\ N_{m+1}(x) = u_m(x, 1), \end{cases} \tag{1.1}$$

where $\tau \in (0, 1)$ and $\mathcal{R}(x; N_m)$ is value of the solution, evaluated at $t = \tau$, of the following equation:

$$\begin{cases} \partial_t v_m = D_I \dfrac{\partial^2 v_m}{\partial x^2} - d_I v_m, & x \in \Omega, t \in (0, \tau], \\ v_m(x, 0) = g(N_m(x)), & x \in \overline{\Omega}, \end{cases} \tag{1.2}$$

which is the first modeling study to qualitatively assess the effects of synchronous development activities on the persistence and invasion of population in a spatially defined habitat. In model (1.1)–(1.2), it is assumed that the whole species can be classified into two stages: mature and immature, and mature individuals reproduce offsprings at the beginning of the mth year, with $m \in \mathbb{N} = \{0, 1, 2, \dots\}$. Here, $u_m(x, t)$ and $v_m(x, t)$ are the adult and juvenile population densities, respectively, at location $x \in \overline{\Omega}$ and time $t \in [0, 1]$ within year $m \in \mathbb{N}$, $N_m(x)$ is the adult population density at the beginning of year m, and $v_m(x, 0)$ is the density of immature population at the beginning of mth year, which depends on the adult population density at the beginning of mth year (i.e., $g(\cdot)$ is a birth function). The constants $D_M > 0$ and $D_I > 0$ denote the random diffusion rates of mature and immature individuals, respectively, $f(\cdot)$ is the death rate function of adult population, including both density-independent and density-dependent mortalities, $d_I > 0$ is the nature death rate of juvenile population. The parameter $\tau \in (0, 1)$ is the impulsive time, which means that the immature individuals develop into the adult stage after time τ at each year. In [3], Bai, Lou, and Zhao investigated the spreading speed and traveling waves for model (1.1) on an unbounded spatial domain, and studied the critical domain size to reserve species persistence on a bounded domain.

The dispersal mode employed in the aforementioned references [3, 14, 15, 28, 47–49] is assumed to be random diffusion, that is, all individuals move randomly with a fixed spatial step on the real line [8]. This dispersal mode appears to be a local behavior [25], which causes small-scale results for scalar equation model [41] and may even underestimate the invasion speed [10]. However, some species can actually disperse in a nonlocal way, that is, individual walkers can randomly select their own spatial step size from some distribution [2, 18, 25, 35]. Considering the impact of birth pulse and nonlocal dispersal, Wu and Zhao [53] constructed an impulsive nonlocal dispersal population model, which is a nonlocal version of the model considered in [14, 15, 28]. They studied the threshold dynamics of such model in a bounded domain, and showed that the invasion speed of population is the same as the minimal speed of traveling waves. We point out that age structure is not considered in [53].

Note that model (1.1) contains the Laplace operator u_{xx}, which represents the local dispersal mode of immature and mature individuals in the space. However, we adopt an integral operator $[J * \phi - \phi](x) := \int_\Omega J(x, y)\phi(y)dy - \phi(x)$ to describe the spatial movement of immature and mature individuals. That is, all individuals can move from any location to other location regardless of distance. In this paper, we consider the following nonlocal dispersal population growth model with annually synchronized emergence of matured individuals:

$$\begin{cases} \partial_t u_m = D_M \left[\displaystyle\int_\Omega J(x, y) u_m(y, t) dy - u_m \right] - f_M(u_m), & x \in \overline{\Omega}, \\ & 0 < t \le 1,\ t \neq \tau, \\ u_m(x, t^+) = u_m(x, t) + v_m(x, \tau), & t = \tau, \\ u_m(x, 0) = N_m(x), & m \in \mathbb{N}, \\ N_{m+1}(x) = u_m(x, 1), \end{cases} \tag{1.3}$$

where $u_m(x, t)$ and $v_m(x, t)$ are the adult and juvenile population densities at location $x \in \Omega$ and time $t \in [0, 1]$ within year $m \in \mathbb{N}$, respectively, $v_m(x, t)$ satisfies

$$\begin{cases} \partial_t v_m = D_I \left[\displaystyle\int_\Omega J(x, y) v_m(y, t) dy - v_m \right] - f_I(v_m), & x \in \overline{\Omega}, \\ & t \in (0, \tau], \\ v_m(x, 0) = g(N_m(x)), & x \in \overline{\Omega}, \end{cases} \tag{1.4}$$

$D_M > 0$ and $D_I > 0$ denote the diffusion rates of mature and immature individuals, respectively, $f_M(\cdot)$ and $f_I(\cdot)$ are the death rate functions depending on the adult and juvenile population, respectively, $g(\cdot)$ is the birth function, and $\tau \in (0, 1)$ is the time when the immature individuals become mature. When $\tau = 0$, the model (1.3)-(1.4) becomes the scenario of the model in [53].

Throughout this paper, we assume that $J(x, y)$ satisfies the following assumption:

- **(J1)** $J(x, y)$ is nonnegative and continuous on $\mathbb{R} \times \mathbb{R}$ satisfying that $J(x, x) > 0$ for any $x \in \mathbb{R}$, $\int_{\mathbb{R}} J(x, y)dx \equiv 1$ and $\int_{\mathbb{R}} J(x, y)dy \equiv 1$.

Here, $J(x, y)$ is the probability of the species jumping from location y to location x, $\int_{\mathbb{R}} J(x, y)v_m(y, t)dy$ represents the rate where immature individuals are arriving at location x from all other places, and $-v_m(x, t) = -\int_{\mathbb{R}} J(x, y)v_m(x, t)dy$ is the rate at which they are leaving location x to travel to all other sites. At the same time, assume that the death rate functions f_M, f_I and the birth function g satisfy:

- **(H1)** $f_M(0) = 0 < f_M'(0)$, f_M is locally Lipschitz continuous in $u \in \mathbb{R}_+ := [0, \infty)$ and $f_M(u)/u$ is strictly increasing in $u \in \mathbb{R}_+$.
- **(H2)** $f_I(0) = 0 < f_I'(0)$, f_I is locally Lipschitz continuous in $u \in \mathbb{R}_+$ and $f_I(v)/v$ is strictly increasing in $v \in \mathbb{R}_+$.
- **(H3)** $g(0) = 0 < g'(0)$, $g(N) > 0$ for $N > 0$ and g is locally Lipschitz continuous in $N \in \mathbb{R}_+$. Moreover, $g(N)/N$ is nonincreasing in $N \in \mathbb{R}_+$ and there exists $\bar{N} > 0$ such that $g(\bar{N}) < \bar{N}$.
- **(H4)** There exist real numbers $\rho_M > 0, \rho_I > 0, \sigma_M > 0, \sigma_I > 0, \nu_M > 1$, and $\nu_I > 1$ such that $f_M(u) \le f_M'(0)u + \rho_M u^{\nu_M}$ for $0 \le u < \sigma_M$, and $f_I(v) \le f_I'(0)v + \rho_I v^{\nu_I}$ for $0 \le v < \sigma_I$.
- **(H5)** There exist real numbers $\rho_g > 0, \sigma_g > 0$, and $\nu_g > 1$ such that $g(N) \ge g'(0)N - \rho_g N^{\nu_g}$ for $0 \le N \le \sigma_g$.

A classical form of death functions satisfying assumptions **(H1)** and **(H2)** takes the form

$$f(u) = au + bu^2,$$

where the positive constant a in the first term is the natural death rate while the second term can be rewritten as $(bu) \cdot u$ with bu being the density-dependent death rate due to intraspecific competition. The birth rate functions satisfying **(H3)** and **(H5)** include the Beverton–Holt function

$$g(N) = \frac{pN}{q + N} \text{ with } p > 0 \text{ and } q > 0,$$

and the Ricker function

$$g(N) = Ne^{r(1-N)} \text{ with } r > 0.$$

One can refer to [14, 28, 31] and the references therein for more general forms and biological interpretation of f and g.

We remark that when $\Omega = \mathbb{R}$ or $\Omega = [0, L]$, the impulsive emergence function $\mathcal{R}(x; N_m)$ in (1.1) can be expressed explicitly (refer to [3] for details). However, $v_m(x, \tau)$ in (1.3) does not have an explicit expression by $g(N_m(x))$ due to the occurrence of nonlinear term f_I, which causes that system (1.3)-(1.4) is strongly coupled.

Notice that model (1.3) includes a maturation impulse, and the impulse occurs at time τ of each year, that is, this sudden change happens periodically. Then, we will consider the 1-year time solution map of system (1.3). Similar to the discussion in [24, Theorem 2.1] and [57, Lemma 2.4], we can derive that for any nonnegative, continuous, and bounded initial value $v_m(x, 0)$, the nonlinear equation (1.4) admits a unique nonnegative and bounded classical solution $v_m(x, t)$ for $t \in [0, 1]$. Let T_t be the time-t solution map of Equation (1.4). In the same way, let S_t be the solution map of $u_t = D_M \left[\int_\Omega J(x - y)u(y, t)dy - u\right] - f_M(u)$. For any density distribution $\phi(x)$ of adult population at location x at the beginning of the year, the density distribution at time τ is $S_\tau(\phi)(x)$. Since the newborn offsprings will develop into mature stage after time τ, the density of newly emerging adults at time τ is $T_\tau g(\phi)(x)$. Then, the adult population density will be $[S_\tau(\phi) + T_\tau g(\phi)](x)$ at time τ^+ due to the impulsive maturation emergence. During the remaining time interval $(\tau, 1]$, the spatial distribution follows Equation (1.3) and thus becomes $S_{1-\tau}[S_\tau(\phi) + T_\tau g(\phi)](x)$ at the end of year. This means that the time-1 solution map of (1.3) is given by

$$Q[\phi](x) := S_{1-\tau}[S_\tau(\phi) + T_\tau g(\phi)](x), \quad x \in \overline{\Omega}. \tag{1.5}$$

Therefore, system (1.3) can be reduced to the following discrete-time recursion:

$$N_{m+1}(x) = Q[N_m](x), \quad x \in \overline{\Omega}, \quad m \ge 0. \tag{1.6}$$

One can also refer to Liang, Yi, and Zhao [30, Section 2], Zhao [59, Section 3.1] and Wu and Zhao [53] for this type of recursion.

The main purpose of this paper is to explore the evolution dynamics of discrete-time problem (1.6) in the cases of bounded and unbounded spatial domains. The remainder of this paper is organized as follows. Section 2 is dedicated to the threshold dynamics of (1.6) in a bounded spatial domain. In Section 3, for the spatially unbounded case, we prove the existence of invasion speed of system (1.6) and show that it coincides with the minimal speed of traveling waves of (1.6). In Section 4, we present some numerical results to demonstrate our theoretical results. In Section 5, we summarize the main results, compare our results with those in literature on similar topics, and discuss some possible future research in this line.

2 | Threshold Dynamics in a Bounded Domain

This section is devoted to the threshold dynamics of system (1.6) when the spatial domain $\Omega \subset \mathbb{R}$ is a bounded and open interval containing the origin. In this situation, we observe that the nonlocal dispersal operator $\phi(x) \mapsto \int_\Omega J(x, y)\phi(y)dy - \phi(x)$ in (1.4) and (1.3) can be viewed as $\phi(x) \mapsto \int_{\mathbb{R}} J(x, y)[\phi(y) - \phi(x)]dy$ with Dirichlet-type boundary condition $\phi(x) \equiv 0, \forall x \in \mathbb{R} \setminus \overline{\Omega}$, which is the nonlocal counterpart of the elliptic operator ϕ_{xx} with homogeneous Dirichlet-type boundary condition.

We point out that in (1.3) and (1.4), the values of $u_m(x, t)$ and $v_m(x, t)$ at the boundary $\partial\Omega$ are implicitly determined by the equation itself. To explain this, we look at the equation

$$u_t = d\left[\int_\Omega J(x, y)u(y, t)dy - u\right], \quad x \in \overline{\Omega}, t > 0. \tag{2.1}$$

Let $u(x,t)$ be the unique solution to (2.1) with initial condition $u(x,0)=u_0(x)\in C(\overline{\Omega})$. Then, $u(x,t)$ satisfies

$$u(x,t)=u_0(x)+d\int_0^t\left[\int_\Omega J(x,y)u(y,s)dy-u(x,s)\right]ds,$$
$$x\in\overline{\Omega}, t\geq 0.$$

Since $u\in C(\overline{\Omega}\times\mathbb{R}_+)$, for $x_0\in\partial\Omega$, there holds that

$$u(x_0,t)=u_0(x_0)+d\int_0^t\left[\int_\Omega J(x_0,y)u(y,s)dy-u(x_0,s)\right]ds,$$
$$t\geq 0.$$

Therefore, in order to avoid the incompatible definitions of $u_m, \underline{v_m}$ for $x\in\partial\Omega$, we assume that $u_m(x,t)=0$ for $m\geq 0, x\in\mathbb{R}\setminus\overline{\Omega}, t\in[0,1]$ and $v_m(x,t)=0$ for $m\geq 0, x\in\mathbb{R}\setminus\overline{\Omega}, t\in[0,\tau]$. We also mention that under this assumption, the solution may be discontinuous on the boundary.

In next two subsections, we aim to investigate the threshold dynamics of system (1.6) in bounded domain Ω for two different cases: (i) the birth function g is monotonically increasing in N, and (ii) the birth function g is not monotone.

2.1 | Case 1: *g* is Monotone

First, we note that the spatially homogeneous version of (1.3) has the form

$$\begin{cases} u'(t)=-f_M(u), & 0<t\leq 1,\ t\neq\tau,\\ u(t^+)=u(t)+v(\tau), & t=\tau,\\ u(0)=N_m, & m\in\mathbb{N},\\ N_{m+1}=u(1), \end{cases}\tag{2.2}$$

where $v(\tau)$ is the value of the solution, evaluated at $t=\tau$, of the following initial value problem:

$$\begin{cases} v'(t)=-f_I(v), & 0<t\leq 1\\ v(0)=g(N_m), & m\in\mathbb{N}. \end{cases}$$

Obviously, problem (2.2) also provides a discrete-time dynamical system:

$$N_{m+1}=\hat{Q}[N_m]:=\hat{S}_{1-\tau}(\hat{S}_\tau(N_m)+\hat{T}_\tau g(N_m)),\quad m\geq 0,\tag{2.3}$$

where $\hat{S}_t$ (respectively, $\hat{T}_t$) is the time-t solution map of $u'(t)=-f_M(u)$ (respectively, $v'(t)=-f_I(v)$) for $t\in[0,1]$. One can easily verify that under the assumptions **(H1)–(H5)** on birth and death functions, the map $\hat{Q}$ is monotone and strongly subhomogeneous (refer to Zhao [59]). For the recursion relationship (2.3), a straightforward calculation shows that the Fréchet derivative of $\hat{Q}$ at zero is

$$\hat{Q}'(0):=\mathrm{e}^{-f_M'(0)}+g'(0)\mathrm{e}^{-f_M'(0)(1-\tau)-f_I'(0)\tau}.$$

Define $\overline{M}:=(1+\mathrm{e}^{-f_I'(0)\tau})\hat{N}$. By **(H3)**, we see that if $0\leq N_0\leq\hat{N}$ with $\hat{N}>\overline{M}$, then $0\leq N_m\leq\hat{N}$, $\forall m\geq 1$. Hence, the map $\hat{Q}$ is continuous and compact on $\mathbb{R}$. Now by [59, Lemma 2.2.1 and Theorem 2.3.4], the following threshold dynamics for (2.3) can be obtained.

Proposition 2.1. *Assume that g is increasing in N. Then, the following statements hold:*

(i) If $\hat{Q}'(0)\leq 1$, then $N_m=0$ is a globally asymptotically stable fixed point of (2.3) in $\mathbb{R}_+$.

(ii) If $\hat{Q}'(0)>1$, then (2.3) has a unique positive fixed point, denoted by ϖ, which is globally asymptotically stable in $\mathbb{R}_+\setminus\{0\}$.

Equip the continuous function space $C(\overline{\Omega},\mathbb{R})$ with the norm $\|\phi\|=\max_{x\in\overline{\Omega}}|\phi(x)|$. Let $C(\overline{\Omega},\mathbb{R}_+):=\{\phi\in C(\overline{\Omega},\mathbb{R})|\phi(x)\geq 0\ \ \forall x\in\overline{\Omega}\}$. For any $\phi,\psi\in C(\overline{\Omega},\mathbb{R})$, we write $\phi\geq\psi$ if $\phi-\psi\in C(\overline{\Omega},\mathbb{R}_+)$; $\phi>\psi$ if $\phi-\psi\in C(\overline{\Omega},\mathbb{R}_+)\setminus\{0\}$; and $\phi\gg\psi$ if $\phi>\psi$ for all $x\in\overline{\Omega}$.

Linearizing system (1.3) at zero, we obtain

$$\begin{cases} \partial_t\tilde{u}_m=D_M\left[\int_\Omega J(x,y)\tilde{u}_m(y,t)dy-\tilde{u}_m\right]-f_M'(0)\tilde{u}_m, & x\in\overline{\Omega},\\ & 0<t\leq 1,\ t\neq\tau,\\ \tilde{u}_m(x,t^+)=\tilde{u}_m(x,t)+\tilde{v}_m(x,\tau), & t=\tau,\\ \tilde{u}_m(x,0)=\tilde{N}_m(x), & m\in\mathbb{N},\\ \tilde{N}_{m+1}(x)=\tilde{u}_m(x,1), \end{cases}\tag{2.4}$$

where $\tilde{v}(x,t)$ satisfies the linear evolution equation

$$\begin{cases} \partial_t\tilde{v}_m=D_I\left[\int_\Omega J(x,y)\tilde{v}_m(y,t)dy-\tilde{v}_m\right]-f_I'(0)\tilde{v}_m, & x\in\overline{\Omega},\\ & 0<t\leq 1,\\ \tilde{v}_m(x,0)=g'(0)\tilde{N}_m(x), & x\in\overline{\Omega}. \end{cases}$$

Similarly, we can derive from (2.4) a discrete-time recursion system as follows:

$$\tilde{N}_{m+1}(x)=\tilde{Q}[N_m](x)=\tilde{S}_{1-\tau}[\tilde{S}_\tau(N_m)+\tilde{T}_\tau g(N_m)](x),$$
$$\forall x\in\overline{\Omega},\ \forall m\geq 0,\tag{2.5}$$

where $\tilde{S}_t$ is the time-t solution map of the linear equation

$$\partial_t\tilde{u}_m=D_M\left[\int_\Omega J(x,y)\tilde{u}_m(y,t)dy-\tilde{u}_m\right]-f_M'(0)\tilde{u}_m,\ x\in\overline{\Omega},$$

and $\tilde{T}_t$ is the time-t solution map of the linear equation

$$\partial_t\tilde{v}_m=D_I\left[\int_\Omega J(x,y)\tilde{v}_m(y,t)dy-\tilde{v}_m\right]-f_I'(0)\tilde{v}_m,\ x\in\overline{\Omega}.$$

Look at the nonlocal eigenvalue problem

$$\mathcal{L}[\varphi](x):=\int_\Omega J(x,y)\varphi(y)dy=\lambda\varphi(x),\quad x\in\overline{\Omega}.\tag{2.6}$$

By [20, Lemma 3.5], the operator $\mathcal{L} : C(\overline{\Omega}, \mathbb{R}_+) \to C(\overline{\Omega}, \mathbb{R}_+)$ is compact and positive. Then, it follows from [34, Lemma 3.1] that the spectral radius $r(\mathcal{L})$ is a simple eigenvalue of $\mathcal{L}$ with a positive eigenfunction $\varphi^* \in C(\overline{\Omega}, \mathbb{R}_+)$, that is, the eigenvalue problem (2.6) has a principal eigenvalue $\lambda_0(\Omega) = r(\mathcal{L})$ corresponding to a positive eigenfunction φ^*.

Remark 2.1. As that pointed out in [2, Remark 2.4] and [21, Theorem 3.1], the principal eigenfunction φ^* is strictly positive on $\overline{\Omega}$ and vanishes in $\mathbb{R} \setminus \overline{\Omega}$. Therefore, a discontinuity occurs on $\partial\Omega$ and the boundary value is not taken in the usual "classical" sense.

According to the above discussion, the following two eigenvalue problems

$$D_M\left[\int_\Omega J(x,y)\varphi(y)dy - \varphi(x)\right] - f_M'(0)\varphi(x) = \lambda\varphi(x), \quad x \in \overline{\Omega},$$

and

$$D_I\left[\int_\Omega J(x,y)\varphi(y)dy - \varphi(x)\right] - f_I'(0)\varphi(x) = \lambda\varphi(x), \quad x \in \overline{\Omega}$$

admit the principal eigenvalues $\lambda_M(\Omega) := D_M\lambda_0(\Omega) - D_M - f_M'(0)$ and $\lambda_I(\Omega) := D_I\lambda_0(\Omega) - D_I - f_I'(0)$, respectively. Denote

$$R_0 := \mathrm{e}^{\lambda_M(\Omega)} + g'(0)\mathrm{e}^{\lambda_M(\Omega)(1-\tau)+\lambda_I(\Omega)\tau}.$$

Then, one can check that $N_m(x) = (R_0)^m \varphi^*(x), x \in \overline{\Omega}, \forall m \geq 0$, is a solution of system (2.5). Furthermore, R_0 is a threshold value on the global dynamics for system (1.6), which are read as follows.

Theorem 2.2. *Assume that* ***(J1), (H1)–(H5)*** *are satisfied, and g is monotone. Then the following statements hold:*

(i) If $R_0 < 1$, then the adult population becomes extinct eventually, that is, $\lim_{m\to+\infty} N_m(x) = 0$ uniformly for $x \in \overline{\Omega}$.

(ii) If $R_0 > 1$, then system (1.6) admits a unique positive steady state $N^* \in C(\overline{\Omega}, \mathbb{R}_+)$ with $N^* \gg 0$. Moreover, the adult population is persistent, that is, for any $N_0 \in C(\overline{\Omega}, \mathbb{R}_+) \setminus \{0\}$, there holds $\lim_{m\to+\infty} N_m(x) = N^*(x)$ uniformly for $x \in \overline{\Omega}$.

Proof.

(i) Suppose that $R_0 < 1$ and let

$$\overline{u}(x,t) = \begin{cases} \delta\mathrm{e}^{\lambda_M(\Omega)t}\varphi^*(x), & t \in [0,\tau], \\ \mathrm{e}^{\lambda_M(\Omega)(t-\tau)}[\delta\mathrm{e}^{\lambda_M(\Omega)\tau}\varphi^*(x) + \overline{v}(x,\tau)], & t \in (\tau, 1], \end{cases}$$

where δ is a positive constant and $\overline{v}(x,t) = \delta g'(0)\mathrm{e}^{\lambda_I(\Omega)t}\varphi^*(x)$ for $t \in [0,1]$. By **(H1)**, **(H3)**, and **(H4)**, we see that $\overline{v}(x,0) = \delta g'(0)\varphi^* \geq g(\delta\varphi^*) = g(\overline{u}(x,0))$,

$$\begin{aligned}
&\overline{v}_t - D_I\left[\int_\Omega J(x,y)\overline{v}(y,t)dy - \overline{v}(x,t)\right] + f_I(\overline{v}) \\
&\geq \delta\lambda_I(\Omega)g'(0)\mathrm{e}^{\lambda_I(\Omega)t}\varphi^* \\
&\quad - \delta g'(0)\mathrm{e}^{\lambda_I(\Omega)t}D_I\left[\int_\Omega J(x,y)\varphi^*(y)dy - \varphi^*\right] \\
&\quad + \delta f_I'(0)g'(0)\mathrm{e}^{\lambda_I(\Omega)t}\varphi^* \\
&= 0, \quad t \in (0,\tau], \\
&\overline{u}_t - D_M\left[\int_\Omega J(x,y)\overline{u}(y,t)dy - \overline{u}(x,t)\right] + f_M(\overline{u}) \\
&\geq \delta\lambda_M(\Omega)e^{\lambda_M(\Omega)t}\varphi^* - \delta e^{\lambda_M(\Omega)t}D_M\left[\int_\Omega J(x,y)\varphi^*(y)dy - \varphi^*\right] \\
&\quad + \delta f_M'(0)e^{\lambda_M(\Omega)t}\varphi^* \\
&= 0, \quad t \in (0,\tau],
\end{aligned}$$

and

$$\begin{aligned}
&\overline{u}_t - D_M\left[\int_\Omega J(x,y)\overline{u}(y,t)dy - \overline{u}(x,t)\right] + f_M(\overline{u}) \\
&\geq \delta\lambda_M(\Omega)\mathrm{e}^{\lambda_M(\Omega)(t-\tau)}\mathcal{K}_1\varphi^* \\
&\quad - \delta\mathrm{e}^{\lambda_M(\Omega)(t-\tau)}\mathcal{K}_1 D_M\left[\int_\Omega J(x,y)\varphi^*(y)dy - \varphi^*\right] \\
&\quad + \delta f_M'(0)\mathrm{e}^{\lambda_M(\Omega)(t-\tau)}\mathcal{K}_1\varphi^* \\
&= 0, \quad t \in (\tau, 1],
\end{aligned}$$

where $\mathcal{K}_1 = \mathrm{e}^{\lambda_M(\Omega)\tau} + g'(0)\mathrm{e}^{\lambda_I(\Omega)\tau}$. Then, $\overline{u}(x,t)$ is an upper solution of

$$\begin{cases} u_t = D_M\left[\int_\Omega J(x,y)u(y,t)dy - u_m\right] - f_M(u), & x \in \overline{\Omega}, \\ & 0 < t \leq 1,\ t \neq \tau, \\ u(x,t^+) = u(x,t) + v(x,\tau), & t = \tau, \\ u(x,0) = \delta\varphi^*(x), & x \in \overline{\Omega}, \end{cases} \tag{2.7}$$

where $v(x,\tau)$ is value of the solution, evaluated at $t = \tau$, of the following problem:

$$\begin{cases} v_t = D_I\left[\int_\Omega J(x,y)v(y,t)dy - v\right] - f_I(v), & x \in \overline{\Omega}, \\ & 0 < t \leq 1, \\ v(x,0) = g(u(x,0)), & x \in \overline{\Omega}. \end{cases}$$

Denote $\overline{N}_m(x) = \delta(R_0)^m\varphi^*(x)$ for all $m \geq 0$. For any given initial data $u_0(x,0) = N_0(x)$ in system (1.6), we can take a sufficiently large δ such that $N_0(x) \leq \overline{N}_0(x)$. Since $\overline{u}(x,t)$ is an upper solution of (2.7), by the comparison argument and mathematical induction, one can obtain that $N_m(x) \leq \overline{N}_m(x)$ for all $m \geq 0$ and $x \in \overline{\Omega}$. When $R_0 < 1$, there must be $\lim_{m\to+\infty} \overline{N}_m(x) = 0$ uniformly for $x \in \overline{\Omega}$, which implies the desired result.

(ii) Before establishing the existence and uniqueness of the positive steady state, we define the space

$$\mathcal{X} = \{\varphi : \overline{\Omega} \to \mathbb{R} | \varphi \text{ is bounded and Lebesgue measurable in } \Omega\}$$

with the norm $\|\varphi\|_{\mathcal{X}} = \sup_{x\in\overline{\Omega}} |\varphi(x)|$. Then, $(\mathcal{X}, \|\cdot\|_{\mathcal{X}})$ is a Banach space. Let $\mathcal{X}_+ = \{\varphi \in \mathcal{X} | \varphi(x) \geq 0\ \forall x \in \overline{\Omega}\}$. In this way, $\mathcal{X}_+$ becomes a positive cone of $\mathcal{X}$ and induce a partial ordering on $\mathcal{X}$. Moreover, we can check that the interior of $\mathcal{X}_+$, denoted by $\mathrm{int}(\mathcal{X}_+)$, is nonempty, and

$$\mathrm{int}(\mathcal{X}_+) = \left\{\varphi \in \mathcal{X}_+ | \inf_{x\in\overline{\Omega}} \varphi(x) > 0\right\}$$
$$= \left\{\varphi \in \mathcal{X}_+ | \varphi(x) \geq \epsilon \text{ for some } \epsilon > 0,\ \forall x \in \overline{\Omega}\right\}.$$

Recall the operator $\mathcal{L}$ defined in (2.6). An argument similar to [20, Lemma 3.5] can be carried out to obtain that $\mathcal{L}$ is compact and strongly positive from $\mathcal{X}_+$ to $\mathcal{X}_+$. Since $C(\overline{\Omega}, \mathbb{R}_+) \subset \mathcal{X}_+$, $(\lambda_0(\Omega), \varphi^*)$ is an eigen-pair of $\mathcal{L}$ in the space $\mathcal{X}_+$. Then the classical Krein–Rutman theorem [26] implies that $(\lambda_0(\Omega), \varphi^*)$ is the principal eigenpair of $\mathcal{L}$ in the space $\mathcal{X}_+$. Under the assumptions **(J1)**, **(H1)–(H5)**, we see that for any initial data $u(0;\varphi) = \varphi$ (respectively, $N_0 = \varphi$) with $\varphi \in \mathcal{X}_+$, system (1.3) (respectively, system (1.6)) admits a unique nonnegative solution $u(t;\varphi)$ (respectively, $N_m(\varphi)$). By the maximum principle of nonlocal dispersal equations (cf. [44, Propositions 2.1 and 2.2] and [18, Propositions 4.1.4 and 4.1.5]), we derive that for any $\varphi_1, \varphi_2 \in \mathcal{X}_+$ with $\varphi_1 \leq, \not\equiv \varphi_2$, we derive that $S_t[\varphi_1] < S_t[\varphi_2]$ and $T_t[\varphi_1] < S_t[\varphi_2]$ for all $t > 0$, where S_t and T_t are the time-t solution maps of the first equations in (1.3) and (1.4), respectively. Note that $Q(\varphi) = u(1;\varphi)$ and $Q^m(\varphi) = N_m(\varphi)$, where Q is defined in (1.5). Then, we have $Q[\varphi_1] < Q[\varphi_2]$ for any $\varphi_1, \varphi_2 \in \mathcal{X}_+$ with $\varphi_1 \leq, \not\equiv \varphi_2$.

Claim 2.1. The operator Q is strongly subhomogeneous in the sense that $Q(\theta\varphi) \gg \theta Q(\varphi)$ for any $\varphi \in \mathrm{int}(\mathcal{X}_+)$ and $\theta \in (0, 1)$.

For Claim 2.1, we first prove S_t is strongly subhomogeneous for $t \in (0, 1]$. Fix $\theta \in (0, 1)$. For any $\varphi \in \mathrm{int}(\mathcal{X}_+)$, let $w(x,t) = S_t[\theta\varphi](x) - \theta S_t[\varphi](x)\ \forall t \geq 0$. Then, $w(x, 0) = 0$ for $x \in \overline{\Omega}$, and for $x \in \overline{\Omega}, t \in (0, 1]$, $w(x, t)$ satisfies

$$\begin{aligned} w_t(x,t) = {} & D_M\left[\int_\Omega J(x,y)w(y,t)dy - w(x,t)\right] \\ & - f_M(S_t[\theta\varphi](x)) + f_M(\theta S_t[\varphi](x)) \\ & - f_M(\theta S_t[\varphi](x)) + \theta f_M(S_t[\varphi](x)) \\ = {} & D_M\left[\int_\Omega J(x,y)w(y,t)dy - w(x,t)\right] \\ & - H(x,t)w(x,t) - h(x,t), \end{aligned}$$

where

$$H(x,t) = \int_0^1 \frac{df_M(\xi)}{d\xi}\bigg|_{\xi = sS_t[\theta\varphi] + (1-s)\theta S_t[\varphi]} ds,$$
$$h(x,t) = f_M(\theta S_t[\varphi](x)) - \theta f_M(S_t[\varphi](x)).$$

Let $U(t,s)$, $t \geq s \geq 0$, be the evolution operator of the linear nonlocal dispersal equation

$$u_t(x,t) = D_M\left[\int_\Omega J(x,y)w(y,t)dy - w(x,t)\right] - H(x,t)w(x,t),$$
$$x \in \overline{\Omega}, t > 0.$$

Then the maximum principle of nonlocal dispersal equations (cf. [44, Propositions 2.1 and 2.2] and [18, Propositions 4.1.4 and 4.1.5]) implies that $U(t,s)[\varphi] \gg 0$ for any $\varphi > 0$. By the formula of variation of constants, there holds that

$$w(x,t) = \int_0^t U(t,s)[-h(\cdot,s)](s)ds, \quad x \in \overline{\Omega}, t \in (0,1].$$

Since $f_M(u)/u$ is strictly increasing in $u \in \mathbb{R}_+$, when $\varphi \gg 0$, we have $h(\cdot,t) < 0$ and hence $w(\cdot,t) > 0$ for $t \in (0,1]$. Thus, S_t is strongly subhomogeneous for $t \in (0,1]$. Similarly, we can prove that T_t is strongly subhomogeneous for $t \in (0,1]$. Since $g(N)/N$ is nonincreasing, we obtain that $g(N)$ is subhomogeneous. Hence, it follows from (1.5) that Q is strongly subhomogeneous.

By Claim 2.1, similar to the proof of [53, Theorem 2.2], we can easily prove that Q has at most one strongly positive fixed point in $\mathcal{X}$.

Suppose that $R_0 > 1$, then we can take $\hat{\lambda}_M < \lambda_M(\Omega)$, $\hat{\lambda}_I < \lambda_I(\Omega)$ and $\gamma \in (0, g'(0))$ such that $\mathrm{e}^{\hat{\lambda}_M} + \gamma\mathrm{e}^{\hat{\lambda}_M(1-\tau)+\hat{\lambda}_I\tau} > 1$. Let

$$\underline{u}(x,t) = \begin{cases} \varepsilon\mathrm{e}^{\hat{\lambda}_M t}\varphi^*(x), & t \in [0,\tau], \\ \mathrm{e}^{\hat{\lambda}_M(t-\tau)}[\varepsilon\mathrm{e}^{\hat{\lambda}_M\tau}\varphi^*(x) + \underline{v}(x,\tau)], & t \in (\tau,1], \end{cases}$$

where $\underline{v}(x,t) = \varepsilon\gamma\mathrm{e}^{\hat{\lambda}_I t}\varphi^*(x)$ for $t \in [0,1]$. By **(H2)** and **(H5)**, there holds that for $\varepsilon > 0$ small enough,

$$\begin{aligned} \underline{v}(x,0) &= \varepsilon\gamma\varphi^* \leq \varepsilon\gamma\varphi^* + \varepsilon\varphi^*\left(g'(0) - \gamma - \rho_g(\varepsilon\varphi^*)^{\nu_g - 1}\right) \\ &= g'(0)\varepsilon\varphi^* - \rho_g(\varepsilon\varphi^*)^{\nu_g} \leq g(\varepsilon\varphi^*) = g(\underline{u}(x,0)), \end{aligned}$$

$$\begin{aligned} & \underline{v}_t - D_I\left[\int_\Omega J(x,y)\underline{v}(y,t)dy - \underline{v}(x,t)\right] + f_I(\underline{v}) \\ & \leq \varepsilon\gamma\hat{\lambda}_I\mathrm{e}^{\hat{\lambda}_I t}\varphi^* - \varepsilon\gamma\mathrm{e}^{\hat{\lambda}_I t}D_I\left[\int_\Omega J(x,y)\varphi^*(y)dy - \varphi^*\right] \\ & + \varepsilon\gamma f_I'(0)\mathrm{e}^{\hat{\lambda}_I t}\varphi^* + \rho_I(\varepsilon\gamma\mathrm{e}^{\hat{\lambda}_I t}\varphi^*)^{\nu_I} \\ & = \varepsilon\gamma\mathrm{e}^{\hat{\lambda}_I t}\left[\hat{\lambda}_I\varphi^* - D_I\int_\Omega J(x,y)\varphi^*(y)dy + D_I\varphi^* + f_I'(0)\varphi^*\right] \\ & + \rho_I(\varepsilon\gamma\mathrm{e}^{\hat{\lambda}_I t}\varphi^*)^{\nu_I} \\ & = \underline{v}[\hat{\lambda}_I - \lambda_I(\Omega) + \rho_I\varepsilon^{\nu_I - 1}(\gamma\mathrm{e}^{\hat{\lambda}_I t}\varphi^*)^{\nu_I - 1}] \leq 0, \qquad t \in (0,\tau], \end{aligned}$$

$$\begin{aligned} & \underline{u}_t - D_M\left[\int_\Omega J(x,y)\underline{u}(y,t)dy - \underline{u}(x,t)\right] + f_M(\underline{u}) \\ & \leq \varepsilon\hat{\lambda}_M\mathrm{e}^{\hat{\lambda}_M t}\varphi^* - \varepsilon\mathrm{e}^{\hat{\lambda}_M t}D_I\left[\int_\Omega J(x,y)\varphi^*(y)dy - \varphi^*\right] \\ & + \varepsilon f_M'(0)\mathrm{e}^{\hat{\lambda}_M t}\varphi^* + \rho_M(\varepsilon\mathrm{e}^{\hat{\lambda}_M t}\varphi^*)^{\nu_M} \\ & = \varepsilon\mathrm{e}^{\hat{\lambda}_M t}\left[\hat{\lambda}_M\varphi^* - D_M\int_\Omega J(x,y)\varphi^*(y)dy + D_M\varphi^* + f_M'(0)\varphi^*\right] \end{aligned}$$

$$+\rho_M(\varepsilon e^{\hat{\lambda}_M t}\varphi^*)^{\nu_M}$$

$$=\underline{u}[\hat{\lambda}_M-\lambda_M(\Omega)+\rho_M\varepsilon^{\nu_M-1}(e^{\hat{\lambda}_I t}\varphi^*)^{\nu_M-1}]\le 0,\qquad t\in(0,\tau],$$

and

$$\underline{u}_t-D_M\left[\int_\Omega J(x,y)\underline{u}(y,t)dy-\underline{u}(x,t)\right]+f_M(\underline{u})$$

$$\le\varepsilon\hat{\lambda}_M e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2\varphi^*-\varepsilon e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2 D_M\left[\int_\Omega J(x,y)\varphi^*(y)dy-\varphi^*\right]$$

$$+\varepsilon f_M'(0)e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2\varphi^*+\rho_M(\varepsilon e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2\varphi^*)^{\nu_M}$$

$$=\varepsilon e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2\left[\hat{\lambda}_M\varphi^*-D_M\int_\Omega J(x,y)\varphi^*(y)dy+D_M\varphi^*+f_M'(0)\varphi^*\right]$$

$$+\rho_M(\varepsilon e^{\hat{\lambda}_M(t-\tau)}\mathcal{K}_2\varphi^*)^{\nu_M}$$

$$=\underline{u}[\hat{\lambda}_M-\lambda_M(\Omega)+\rho_M\varepsilon^{\nu_M-1}(e^{\hat{\lambda}_I(t-\tau)}\mathcal{K}_2\varphi^*)^{\nu_M-1}]\le 0,\qquad t\in(\tau,1],$$

where $\mathcal{K}_2=e^{\hat{\lambda}_M\tau}+\gamma e^{\hat{\lambda}_I\tau}$. Then, $\underline{u}(x,t)$ is a lower solution of (2.7) with δ replaced by ε. Meanwhile, we can choose a constant $\varepsilon_0>0$ small enough such that for any given $\varepsilon\in(0,\varepsilon_0]$, $\overline{M}>\varepsilon\varphi^*(x)\ \forall x\in\overline{\Omega}$, and

$$Q[\varepsilon\varphi^*]=S_{1-\tau}[S_\tau(\varepsilon\varphi^*)+T_\tau g(\varepsilon\varphi^*)]\ge S_{1-\tau}\left[e^{\hat{\lambda}_M\tau}\varepsilon\varphi^*+e^{\hat{\lambda}_I\tau}\gamma\varepsilon\varphi^*\right]$$

$$\ge\left(e^{\hat{\lambda}_M}+\gamma e^{\hat{\lambda}_M(1-\tau)+\hat{\lambda}_I\tau}\right)\varepsilon\varphi^*\ge\varepsilon\varphi^*,$$

which induces that

$$\overline{M}\ge Q^{m+1}(\varepsilon\varphi^*)(x)\ge Q^m(\varepsilon\varphi^*)(x),\ x\in\overline{\Omega},\ \forall m\ge 0.$$

Thus, there exists $N_*\in\operatorname{int}(\mathcal{X}_+)$ such that

$$\lim_{m\to+\infty}Q^m[\varepsilon\varphi^*](x)=N_*(x),\forall x\in\overline{\Omega},\tag{2.8}$$

and N_* is lower semicontinuous in the sense that $\liminf_{x\to x_0}N_*(x)\ge N_*(x_0)$ for any $x_0\in\overline{\Omega}$. On the other hand, noting that g is monotone, we have that $g(\overline{M})\ge g(N_*)(x)\ge g(Q^m(\varepsilon\varphi^*))(x)$. Define

$$u_m(x,t)=u(x,t;Q^m(\varepsilon\varphi^*)),\ v_m(x,t)=v(x,t;g(Q^m(\varepsilon\varphi^*))),$$

$$\forall(x,t)\in\overline{\Omega}\times[0,1],$$

where $u(x,t;Q^m(\varepsilon\varphi^*))$ (respectively, $v(x,t;g(Q^m(\varepsilon\varphi^*)))$) is the solution of (2.7) (respectively, (1.4)) with the initial condition $u(x,0;Q^m(\varepsilon\varphi^*))=Q^m(\varepsilon\varphi^*)$ (respectively, $v(x,0;g(Q^m(\varepsilon\varphi^*)))=g(Q^m(\varepsilon\varphi^*))$) for $m\ge 0$. It follows that

$$u_m(x,t)\le u_{m+1}(x,t)\le u(x,t;\overline{M})\le\max_{(x,t)\in\overline{\Omega}\times[0,1]}u(x,t;\overline{M}),$$

$$v_m(x,t)\le v_{m+1}(x,t)\le v(x,t;g(\overline{M}))\le\max_{(x,t)\in\overline{\Omega}\times[0,1]}v(x,t;g(\overline{M})).$$

Hence, the limits $u(x,t):=\lim_{m\to+\infty}u_m(x,t)$ and $v(x,t):=\lim_{m\to+\infty}v_m(x,t)$ exist for $(x,t)\in\overline{\Omega}\times[0,1]$. Especially,

$$\lim_{m\to+\infty}u_m(x,0)=\lim_{m\to+\infty}Q^m(\varepsilon\varphi^*)(x)=u(x,0),$$

$$\lim_{m\to+\infty}v_m(x,0)=\lim_{m\to+\infty}g(Q^m(\varepsilon\varphi^*))(x)=v(x,0),\ \text{for } x\in\overline{\Omega}.$$

Hence, by (2.8), $N_*(x)=u(x,0)$ for $x\in\overline{\Omega}$. Moreover, by (1.3), we have

$$u_m(x,t)-u_m(x,0)=\int_0^t D_M\left[\int_\Omega J(x,y)u_m(y,s)dy-u_m(x,s)\right]ds$$

$$-\int_0^t f_M(u_m(x,s))ds,\quad t\in[0,\tau],$$

and

$$u_m(x,t)-u_m(x,\tau)-v_m(x,\tau)$$

$$=\int_0^t D_M\left[\int_\Omega J(x,y)u_m(y,s)dy-u_m(x,s)\right]ds$$

$$-\int_0^t f_M(u_m(x,s))ds,\ t\in(\tau,1],$$

where

$$v_m(x,t)-v_m(x,0)=\int_0^t D_I\left[\int_\Omega J(x,y)v_m(y,s)dy-v_m(x,s)\right]ds$$

$$-\int_0^t f_I(v_m(x,s))ds,\quad t\in[0,\tau].$$

It then follows from Lebesgue's dominated convergence theorem that

$$u(x,t)-u(x,0)=\int_0^t D_M\left[\int_\Omega J(x,y)u(y,s)dy-u(x,s)\right]ds$$

$$-\int_0^t f_M(u(x,s))ds,\quad t\in[0,\tau],$$

and

$$u(x,t)-u(x,\tau)-v(x,\tau)$$

$$=\int_0^t D_M\left[\int_\Omega J(x,y)u(y,s)dy-u(x,s)\right]ds$$

$$-\int_0^t f_M(u(x,s))ds,\ t\in(\tau,1],$$

where

$$v(x,t)-v(x,0)=\int_0^t D_I\left[\int_\Omega J(x,y)v(y,s)dy-v(x,s)\right]ds$$

$$-\int_0^t f_I(v(x,s))ds,\quad t\in[0,\tau].$$

This shows that

$$u_t=D_M\left[\int_\Omega J(x,y)u(y,t)dy-u(x,t)\right]-f_M(u(x,t)),$$

$$t\in(0,1],t\ne\tau,$$

$$v_t = D_I\left[\int_\Omega J(x,y)v(y,t)dy - v(x,t)\right] - f_I(v(x,t)), \quad t\in(0,\tau],$$

and thus the limiting function $u(x,t)$ is a solution of (1.3), while $v(x,t)$ is a solution of (1.4). By the fact that $u(x,0) = N_*(x)$ and $v(x,0) = g(N_*)(x)$ $\forall x\in\overline{\Omega}$, we have $u(\cdot,1) = u(\cdot,1;N_*)$. Notice that $u(x,1) = \lim_{m\to+\infty} u_m(x,1)$ $\forall x\in\overline{\Omega}$, equivalently, $u(x,1) = \lim_{m\to+\infty} Q^{m+1}(\varepsilon\varphi^*)(x)$ $\forall x\in\overline{\Omega}$, which together with (2.8) implies that

$$N_*(x) = u(x,1) = u(x,1;N_*) = Q[N_*](x).$$

Hence N_* is a fixed point of the operator Q.

Recall that $\overline{M}$ is an upper solution of system (1.6), then for any given constant $\eta > 1$, there holds $Q(\eta\overline{M}) \le \eta Q(\overline{M}) \le \eta\overline{M}$, which leads to that $Q^{m+1}(\eta\overline{M}) \le Q^m(\eta\overline{M}) \le (\eta\overline{M})$ for all $m\ge 0$. Noticing that for $\varepsilon > 0$ small enough, $\varepsilon\varphi^*(x) < \overline{M} < \eta\overline{M}$ $\forall x\in\overline{\Omega}$, we have $0 < Q^m(\varepsilon\varphi^*)(x) < Q^m(\eta\overline{M})(x)$, $\forall x\in\overline{\Omega}$. Therefore, we can also find $N^*\in\mathcal{X}_+$ such that $\lim_{m\to+\infty} Q^m(\eta\overline{M})(x) = N^*(x)$, $\forall x\in\overline{\Omega}$, and N^* is upper semicontinuous in the sense that $\limsup_{x\to x_0} N^*(x) \ge N^*(x_0)$ for any $x_0\in\overline{\Omega}$. Moreover, $Q(N^*) = N^*$.

Based on the above argument, there should be $0 \ll N_* \le N^*$ in $\mathcal{X}$. Since the strongly positive fixed point of Q is unique in $\mathcal{X}$, we have $N^* = N_*$. By the upper semicontinuity of N^* and the lower semicontinuity of N_*, it follows that N^* is continuous. Moreover, we can obtain from Dini's theorem that $\lim_{m\to+\infty} Q^m(\varepsilon\varphi^*)(x) = \lim_{m\to+\infty} Q^m(\eta\overline{M})(x) = N^*(x)$ uniformly for $x\in\overline{\Omega}$.

Finally, for any given initial value $N_0 = \varphi \in C(\overline{\Omega},\mathbb{R}_+)$ with $\varphi > 0$, there holds $u(\cdot,1;\varphi) \gg 0$ (see, e.g., [25]), and thus $N_1 = u(\cdot,1;\varphi)\gg 0$. Without loss of generality, one can take N_1 as the new initial datum and choose a sufficiently small $\varepsilon\in(0,\varepsilon_0]$ and a sufficiently large $\eta > 1$ so that $\varepsilon\varphi^* \le N_1 \le \eta\overline{M}$. This causes that $Q^m(\varepsilon\varphi^*) \le Q^m(N_1) \le Q^m(\eta\overline{M})$, $\forall m\ge 0$. Consequently, $\lim_{m\to+\infty} N_m(x) = \lim_{m\to+\infty} Q^m(\varphi)(x) = N^*(x)$ uniformly for $x\in\overline{\Omega}$. The proof is completed. □

Next, we let $\Omega = (\ell_1,\ell_2)$ with $-\infty < \ell_1 < 0 < \ell_2 < +\infty$, and consider the case when the dispersal only depends on the distance between the starting location x and the destination y, namely, $J(x,y) = J(x-y)$. Look at the following linear eigenvalue:

$$(\mathcal{L}_{(\ell_1,\ell_2)} + a)[\psi](x) := d\left[\int_{\ell_1}^{\ell_2} J(x-y)\psi(y)dy - \psi(x)\right] + a\psi(x), \quad \forall\psi\in C([\ell_1,\ell_2]), \qquad (2.9)$$

where d and a are positive constants. It is well-known (see, e.g., [6, 11]) that under the following assumption:

- **(J2)** $J(x)$ is a nonnegative, symmetric, and continuous function on $\mathbb{R}$ with $J(0) > 0$, $\int_{\mathbb{R}} J(x)dx = 1$, and $\sup_{x\in\mathbb{R}} J(x) < +\infty$,

problem (2.9) admits a unique principal eigenvalue, denoted by $\lambda_p(\mathcal{L}_{(\ell_1,\ell_2)} + a)$, corresponding to a positive eigenfunction $\psi^*\in C([\ell_1,\ell_2])$. Moreover, we have some properties on the principal eigenvalue $\lambda_p(\mathcal{L}_{(\ell_1,\ell_2)} + a)$.

Proposition 2.3 [9, Proposition 3.4]. *Assume that the kernel function J satisfies **(J2)**, then*

- *(i) $\lambda_p(\mathcal{L}_{(\ell_1,\ell_2)} + a)$ is strictly increasing and continuous with respect to $\ell := \ell_2 - \ell_1$;*
- *(ii) $\lim_{\ell_2-\ell_1\to 0^+} \lambda_p(\mathcal{L}_{(\ell_1,\ell_2)} + a) = a - d$;*
- *(iii) $\lim_{\ell_2-\ell_1\to+\infty} \lambda_p(\mathcal{L}_{(\ell_1,\ell_2)} + a) = a$.*

By Proposition 2.3 and the definition of R_0, we derive that

$$\lim_{\ell_2-\ell_1\to 0^+} R_0 = e^{-f'_M(0)-D_M} + g'(0)e^{-(f'_M(0)+D_M)(1-\tau)-(f'_I(0)+D_I)\tau} =: Q'_D,$$

$$\lim_{\ell_2-\ell_1\to+\infty} R_0 = e^{-f'_M(0)} + g'(0)e^{-f'_M(0)(1-\tau)-f'_I(0)\tau} = \hat{Q}'(0),$$

and R_0 is strictly increasing and continuous with respect to $\ell := \ell_2 - \ell_1$. Therefore, Theorem 2.2 implies the following corollary.

Corollary 2.4. *Assume that **(J2)**, **(H1)–(H5)** hold, and g is monotone. Then, the following statements are valid:*

- *(i) If $\hat{Q}'(0) < 1$, then the adult population becomes extinct eventually.*
- *(ii) If $Q'_D < 1 < \hat{Q}'(0)$, then there exists a critical value $\ell^*\in(0,+\infty)$ such that the adult population is persistent if and only if $\ell_2 - \ell_1 > \ell^*$.*
- *(iii) If $Q'_D > 1$, then the adult population is always persistent.*

2.2 | Case 2: *g* is Nonmonotone

In this subsection, we will show the threshold dynamics of systems (1.6) when the birth function g in nonmonotone. We make the following assumption:

- **(H6)** There exists $\sigma > 0$ such that $g(N)$ is nondecreasing for $0\le N\le\sigma$.

Inspired by the method used in [19, 23, 28, 46], we first define a nondecreasing function

$$g^+(N) := \max_{0\le V\le N} g(V), \quad \forall N\ge 0.$$

Clearly, g^+ is nondecreasing and locally Lipschitz continuous, and ${g^+}'(0) = g'(0)$. Then by Proposition 2.1, system (2.3) with g replaced by g^+ has a positive fixed point ϖ^+ if and only if $\hat{Q}'(0) > 1$. Similarly, we introduce another function

$$g^-(N) := \min_{N\le V\le\varpi^+} g(V), \quad \forall 0\le N\le\varpi^+.$$

Then, g^- is nondecreasing and locally Lipschitz continuous, and system (2.3) with g replaced by g^- has a positive fixed point ϖ^- when $\hat{Q}'(0) > 1$. By the definitions of $g^\pm$, we easily see that $0 < \varpi^- \le \varpi \le \varpi^+$, $g^-(N) \le g(N) \le g^+(N)$, $(g^\pm)'(0) = g'(0)$, and $g^\pm(N) \le g'(0)N$. Furthermore, there exists $\sigma_0\in(0,\sigma^*)$ with $\sigma^* = \min\{\sigma,\sigma_g\}$ so that $g^\pm(N) = g(N)$ for $0 < N\le\sigma_0$.

Next, we introduce the following two auxiliary equations:

$$\begin{cases}\partial_t u_m = D_M\left[\int_\Omega J(x,y)u_m(y,t)dy - u_m\right] - f_M(u_m), & x\in\mathbb{R},\\ & 0<t\le 1,\ t\neq\tau,\\ u_m(x,t^+) = u_m(x,t) + v_m^+(x,\tau), & t=\tau,\\ u_m(x,0) = N_m^+(x), & m\in\mathbb{N},\\ N_{m+1}^+(x) = u_m(x,1), \end{cases} \tag{2.10}$$

and

$$\begin{cases}\partial_t u_m = D_M\left[\int_\Omega J(x,y)u_m(y,t)dy - u_m\right] - f_M(u_m), & x\in\mathbb{R},\\ & 0<t\le 1,\ t\neq\tau,\\ u_m(x,t^+) = u_m(x,t) + v_m^-(x,\tau), & t=\tau,\\ u_m(x,0) = N_m^-(x), & m\in\mathbb{N},\\ N_{m+1}^-(x) = u_m(x,1), \end{cases} \tag{2.11}$$

where $v_m^+(\cdot,\tau)$ (respectively, $v_m^-(\cdot,\tau)$) is the value of the solution, evaluated at $t=\tau$, of problem (1.4) with the initial value $v_m(x,0) = g^+(N_m^+(x))$ (respectively, $v_m(x,0) = g^-(N_m^-(x))$) for $m\ge 0$. In the same way as (1.6), we can induce from (2.10) and (2.11) the following discrete-time systems:

$$N_{m+1}^+(x) = Q^+[N_m^+](x) = S_{1-\tau}[S_\tau(N_m^+) + T_\tau g^+(N_m^+)](x),$$
$$x\in\overline{\Omega}, m\ge 0, \tag{2.12}$$

and

$$N_{m+1}^-(x) = Q^-[N_m^-](x) = S_{1-\tau}[S_\tau(N_m^-) + T_\tau g^-(N_m^-)](x),$$
$$x\in\overline{\Omega}, m\ge 0. \tag{2.13}$$

Let $N_{m+1}^+(x)$ (respectively, $N_{m+1}^-(x)$) be the solution to system (2.12) (respectively, (2.13)). It follows from a comparison argument that for $0<N_0^-(x)\le N_0(x)\le N_0^+(x)\le \varpi^+$ with $N_0^-, N_0, N_0^+\in\mathcal{X}_+$, there holds that

$$0\le N_m^-(x)\le N_m(x)\le N_m^+(x)\le\varpi^+,\quad x\in\overline{\Omega},\ \forall m\ge 0.$$

By theorem 2.2, we see that models (2.10) and (2.11) have the same threshold value R_0. Then, we have the following results on the dynamics of (1.6).

Theorem 2.5. *Assume that **(J1)** and **(H1)–(H6)** hold. Then, we have the following statements:*

(i) If $R_0<1$, then $\lim_{m\to+\infty} N_m(x) = 0$ uniformly for $x\in\overline{\Omega}$.

(ii) If $R_0>1$, then for any initial datum $N_0\in C(\overline{\Omega},\mathbb{R}_+)\setminus\{0\}$, the solution $N_m(x)$ of system (1.6) satisfies

$$\limsup_{m\to+\infty}\max_{x\in\overline{\Omega}}[N_m(x) - N_*^+(x)]\le 0$$
$$\le \liminf_{m\to+\infty}\min_{x\in\overline{\Omega}}[N_m(x) - N_*^-(x)],$$

where $N_*^-(x)$ (respectively, $N_*^+(x)$) is the unique positive steady state of system (2.13) (respectively, (2.12)).

Proof.

(i) Suppose that $R_0<1$. It follows from the definition of g^+ that $g^+(N)\ge g(N)$ for all $N\ge 0$. Then by a comparison argument, we infer that $0\le N_m(x)\le N_m^+(x)$ for $x\in\overline{\Omega}, m\ge 0$. Since $(g^+)'(0) = g'(0)$, by Theorem 2.2(i), we have that $N_m^+(x)$ converges to zero uniformly for $x\in\overline{\Omega}$ as $m\to\infty$. Hence, $N_m(x)$ converges to zero uniformly for $x\in\overline{\Omega}$ as $m\to\infty$.

(ii) Suppose that $R_0>1$. A comparison argument can be carried out to obtain that $0\le N_m(x)\le N_m^+(x)$ for $x\in\overline{\Omega}, m\ge 0$. Since $(g^+)'(0) = g'(0)$, by Theorem 2.2(ii), we have that $\lim_{m\to+\infty} N_m^+(x) = N_*^+(x)$ uniformly for $x\in\overline{\Omega}$. Then,

$$\limsup_{m\to+\infty}\max_{x\in\overline{\Omega}}[N_m(x) - N_*^+(x)]\le 0. \tag{2.14}$$

Notice that ϖ^+ satisfies

$$\begin{cases}u'(t) = -f_M(u), & 0<t\le 1,\ t\neq\tau,\\ u(t^+) = u(t) + v(\tau), & t=\tau,\\ u(0) = \varpi^+ = u(1),\end{cases}$$

where $v(\tau)$ is the value of the solution, evaluated at $t=\tau$, of the following initial value problem:

$$\begin{cases}v'(t) = -f_I(v), & 0<t\le 1\\ v(0) = g^+(\varpi^+), & m\in\mathbb{N}.\end{cases}$$

By a comparison argument, there holds that $N_*^+(x)\le\varpi^+$ on $\overline{\Omega}$. Then for any $\varepsilon>0$, there exists a large integer M such that

$$N_m(x)\le\varpi^+ + \varepsilon,\quad x\in\overline{\Omega}, m\ge M. \tag{2.15}$$

In the following, we show the Lower limit of N_m. For this purpose, we choose $\varepsilon>0$ small enough and let

$$g_\varepsilon^-(N) := \min_{N\le V\le\varpi^+ + \varepsilon} g(V),\ \ \forall 0\le N\le\varpi^+ + \varepsilon.$$

Consider the following perturbed system of (2.11):

$$\begin{cases}\partial_t u_m = D_M\left[\int_\Omega J(x,y)u_m(y,t)dy - u_m\right]\\ \qquad - f_M(u_m), & x\in\mathbb{R},\\ & 0<t\le 1,\ t\neq\tau,\\ u_m(x,t^+) = u_m(x,t) + v_m(x,\tau), & t=\tau,\\ u_m(x,0) = N_{m,\varepsilon}^-(x), & m\in\mathbb{N},\\ N_{m+1,\varepsilon}^-(x) = u_m(x,1),\end{cases}$$

where $v_m(\cdot,\tau)$ is the value of the solution, evaluated at $t=\tau$, of problem (1.4) with the initial value $v_m(x,0) = g_\varepsilon^-(N_{m,\varepsilon}^-(x))$ for $m\ge 0$. It follows from (2.15) and a comparison argument that for $N_0(x)\ge N_{0,\varepsilon}^-(x)>0$ with $N_{0,\varepsilon}^-, N_0\in\mathcal{X}_+$, there holds that

$$0\le N_{m,\varepsilon}^-(x)\le N_m(x)\le\varpi^+ + \varepsilon,\quad x\in\overline{\Omega},\ \forall m\ge M.$$

Since $(g_\varepsilon^-)'(0) = g'(0)$, by Theorem 2.2(ii), we have that $\lim_{m\to+\infty} N_{m,\varepsilon}^-(x) = N_{*,\varepsilon}^-(x)$ uniformly for $x \in \overline{\Omega}$, where $N_{*,\varepsilon}^-$ is the unique positive steady state of the discrete system $\{N_{m,\varepsilon}^-\}_{m=0}^\infty$. This gives that

$$\liminf_{m\to+\infty} \min_{x\in\overline{\Omega}} [N_m(x) - N_{*,\varepsilon}^-(x)] \geq 0.$$

Finally, letting $\varepsilon \to 0$, we obtain

$$\liminf_{m\to+\infty} \min_{x\in\overline{\Omega}} [N_m(x) - N_*^-(x)] \geq 0.$$

The proof is completed. □

Remark 2.2. The persistence criterion obtained in Corollary 2.4 still applies to Theorem 2.5 since $(g^\pm)'(0) = g'(0)$.

3 | Spreading Speeds and Traveling Waves in an Unbounded Domain

In this section, we will show the existence of spreading speed and its coincidence with minimal wave speed for system (1.6) with two kinds of birth functions, that is, the function g is monotone (Section 3.1) and nonmonotone (Section 3.2), respectively. In this situation, $\Omega = \mathbb{R}$.

For simplicity, we consider the case when the dispersal only depends on the distance between the starting location x and the destination y, namely, $J(x, y) = J(x - y)$. In this section, we always assume that

- **(J3)** J is a nonnegative, symmetric, and continuous function on $\mathbb{R}$ with $J(0) > 0$, $\int_{\mathbb{R}} J(x)dx = 1$ and $\int_{\mathbb{R}} e^{\mu x} J(x)dx < +\infty, \forall \mu \in [0, \mu^*)$ for some constant $\mu^* > 0$.

Under the above assumption, we can rewrite system (1.3) as

$$\begin{cases} \partial_t u_m = D_M\left[\int_{\mathbb{R}} J(x-y)u_m(y,t)dy - u_m\right] \\ \qquad - f_M(u_m), & x \in \mathbb{R}, \\ & 0 < t \leq 1,\ t \neq \tau, \\ u_m(x, t^+) = u_m(x,t) + v_m(x,\tau), & t = \tau, \\ u_m(x,0) = N_m(x), & m \in \mathbb{N}, \\ N_{m+1}(x) = u_m(x,1), \end{cases} \tag{3.1}$$

where the impulsive perturbation term $v_m(x, \tau)$, which represents the synchronized maturation, is the value of the solution $v_m(x,t)$, evaluated at $t = \tau$, of the following initial value problem:

$$\begin{cases} \partial_t v_m = D_I\left[\int_{\mathbb{R}} J(x-y)v_m(y,t)dy - v_m\right] \\ \qquad - f_I(v_m), & x \in \mathbb{R}, t \in (0,1], \\ v_m(x,0) = g(N_m(x)), & x \in \mathbb{R}. \end{cases} \tag{3.2}$$

Clearly, problem (3.1) can still induce the discrete-time system (1.6).

Let $X := BC(\mathbb{R}, \mathbb{R})$ be the set of all continuous and bounded functions from $\mathbb{R}$ to $\mathbb{R}$ with the supreme norm. Let $X_+ := \{\phi \in X | \phi(x) \geq 0\ \forall x \in \mathbb{R}\}$. For any $\phi, \psi \in X$, we write $\phi \geq \psi$ if $\phi - \psi \in X_+$; $\phi > \psi$ if $\phi - \psi \in X_+ \setminus \{0\}$; and $\phi \gg \psi$ if $\phi > \psi$ for all $x \in \mathbb{R}$. Here, X_+ is a closed cone of X and it induces a partial ordering relation which makes X as an ordered Banach space. In addition, we equip X with the compact open topology, that is, a sequence of $\phi^n(x)$ converges to $\phi(x)$ uniformly for x in any compact subset of $\mathbb{R}$. Moreover, we denote

$$X_r = \{u \in X | 0 \leq u(x) \leq r,\ \forall\, x \in \mathbb{R}\},$$

where $r > 0$ is given real number, and define the translation operator $\mathcal{T}_a : X \to X$ by

$$\mathcal{T}_a[u](x) = u(x-a), \quad \forall\, u \in X,\ a \in \mathbb{R}.$$

3.1 | Case 1: *g* is Monotone

To study the propagation dynamics of (1.6), based on Proposition 2.1, we need to assume that $\hat{Q}'(0) > 1$, which can guarantee the existence of a positive fixed point of discrete-time system (2.3), which is globally asymptotically stable. Since the solution map S_t of (3.1) is not compact, Q in system (1.6) is not compact. In the rest of this subsection, we will apply the abstract theory in [12] for monotone semiflows with weak compactness. Accordingly, we need to state the known definition of the Kuratowski measure of noncompactness.

Definition 3.1 [59]. Let $\mathcal{E}$ be a Banach space. The *Kuratowski measure of noncompactness* in $\mathcal{E}$ is defined by

$$\kappa(B) = \inf\{r : B \text{ has a finite open cover of diameter} \leq r\}$$

for any bounded set B of $\mathcal{E}$. Clearly, $\kappa(B) = 0$ if and only if $\overline{B}$ is compact. Moreover, $\kappa(B_1 + B_2) \leq \kappa(B_1) + \kappa(B_2)$ for any bounded sets B_1 and B_2.

We are now able to establish the propagation dynamics of (1.6) by utilizing the theory developed in [12, 34].

Theorem 3.2. *Assume that* **(J3)**, **(H1)–(H5)** *hold, and g is monotone. If $\hat{Q}'(0) > 1$, then there exists a spreading speed c^* for system (1.6) such that the following statements are valid:*

- *(i) If $\phi \in X_\varpi$, where ϖ is the positive fixed point of system (2.3), and $\phi(x) = 0$ outside a bounded interval, then $\lim_{m\to\infty, |x|\geq cm} |Q^m[\phi](x)| = 0, \forall c > c^*$.*
- *(ii) If $\phi \in X_\varpi \setminus \{0\}$, then $\lim_{m\to\infty, |x|\leq cm} |Q^m[\phi](x) - \varpi| = 0, \forall c \in (0, c^*)$.*

Proof. At first, by **(H1)–(H5)**, an argument similar to that in [52, Theorem 2.2 and Lemma 3.1] can be carried out to show that for any $\phi \in X_\varpi \setminus \{0\}$, $Q(\phi) \gg 0$, and $Q(\theta\phi) \gg \theta Q(\phi)\ \forall \theta \in (0,1)$. Next, we show that Q satisfies the following properties:

(R1) $\mathcal{T}_y \circ Q = Q \circ \mathcal{T}_y$ for all $y \in \mathbb{R}$.

(R2) $Q : X_\varpi \to X_\varpi$ is continuous with respect to the compact open topology.

(R3) There exists $\theta \in [0,1)$ such that $\kappa(Q[\mathcal{V}](0)) \le \theta\kappa(\mathcal{V}(0))$ for any $\mathcal{V} \subseteq X_\varpi$.

(R4) Q is order preserving in the sense that if $\phi \ge \psi$ for $\phi, \psi \in X_\varpi$, then $Q[\phi] \ge Q[\psi]$.

(R5) $Q : [0,\varpi] \to [0,\varpi]$ admits two fixed points 0 and ϖ, and for any $\phi \in X_\varpi$ with $0 \ll \phi \le \varpi$, it holds that $\lim_{m\to\infty} Q^n[\phi](x) = \varpi$.

Let $\lfloor \tilde{t} \rfloor$ be the nearest integer less than or equal to $\tilde{t}$. If $u(x,\tilde{t})$ is a solution of (3.1) with $n = \lfloor \tilde{t} \rfloor$ and $t = \tilde{t} - \lfloor \tilde{t} \rfloor \in [0,1)$, then $u(x+y,\tilde{t}), \forall y \in \mathbb{R}$ is also a solution. This verifies (R1). One can prove property (R2) by the arguments similar to those in Weng and Zhao [52, Lemma 3.1]. To show property (R3), we take $x = 0$. Since any bounded set in $\mathbb{R}$ is precompact, we have $\kappa(Q[\mathcal{V}](0)) = 0$. On the other hand, by the boundedness of $\mathcal{V}(0)$, there holds that $\kappa(\mathcal{V}(0)) = 0$. Hence, $\kappa(Q[\mathcal{V}](0)) = \kappa(\mathcal{V}(0)) = 0$. In view of the monotonicity of g, we obtain that Q is order preserving and (R4) holds. By part (ii) in Proposition 2.1, we see that Q satisfies property (R5). Therefore, Q satisfies all conditions in [12, Remark 3.7], and discrete-time system (1.6) admits a spreading speed c^* such that the statements (i) and (ii) hold. □

In the following, we consider the linearized system at zero to compute c^*, which has the form

$$\begin{cases} \partial_t u_m = D_M\left[\int_{\mathbb{R}} J(x-y)u_m(y,t)dy - u_m\right] \\ \qquad - f_M'(0)u_m, & x\in\mathbb{R}, \\ & 0<t\le 1,\ t\ne\tau, \\ u_m(x,t^+) = u_m(x,t) + \mathcal{R}(x;N_m), & t=\tau, \\ u_m(x,0) = N_m(x), & m\in\mathbb{N}, \\ N_{m+1}(x) = u_m(x,1), \end{cases} \tag{3.3}$$

where $\mathcal{R}(x;N_m) = \mathrm{e}^{-f_I'(0)\tau} g'(0)\int_{\mathbb{R}} \mathcal{G}(D_I\tau, x-y)N_m(y)dy$ with $\mathcal{G}(\alpha,x) = \frac{1}{2\pi}\int_{\mathbb{R}} \mathrm{e}^{\alpha(\hat{J}(w)-1)}\mathrm{e}^{-iwx}dw$ and $\hat{J}(w) = \int_{\mathbb{R}} \mathrm{e}^{iwy}J(y)dy$, in which i is the imaginary unit. More details on derivation of $\mathcal{G}(\alpha,x)$ can be found in A. For any $\mu \in \mathbb{R}_+$, set $u(x,t) = \mathrm{e}^{-\mu x}\eta(t)$. Then, we have

$$\begin{cases} \dfrac{d\eta(t)}{dt} = \left[D_M\int_{\mathbb{R}} J(y)\mathrm{e}^{\mu y}dy - D_M - f_M'(0)\right]\eta(t), & 0<t\le 1, \\ & t\ne\tau, \\ \eta(t^+) = \eta(t) + \mathrm{e}^{-f_I'(0)\tau}g'(0)\displaystyle\int_{\mathbb{R}} \mathcal{G}(D_I\tau,y)\mathrm{e}^{\mu y}dy\,\eta(0), & t=\tau, \end{cases}$$

where $\int_{\mathbb{R}} \mathcal{G}(D_I\tau,y)\mathrm{e}^{\mu y}dy$ is finite by Lemma A.4. Solving the above equation, we obtain a time-1 solution map

$$\eta(1) = \left[\mathrm{e}^{C_\mu} + g'(0)\mathrm{e}^{C_\mu(1-\tau)}\mathrm{e}^{-f_I'(0)\tau}\int_{\mathbb{R}} \mathcal{G}(D_I\tau,y)\mathrm{e}^{\mu y}dy\right]\eta(0),$$

where

$$C_\mu = D_M\int_{\mathbb{R}} J(y)\mathrm{e}^{\mu y}dy - D_M - f_M'(0),\ \mu\in\mathbb{R}_+.$$

Hence, we can rewrite system (3.3) as

$$N_{m+1}(x) = \mathrm{e}^{-\mu x}\left[\mathrm{e}^{C_\mu} + g'(0)\mathrm{e}^{C_\mu(1-\tau)}\mathrm{e}^{-f_I'(0)\tau}\int_{\mathbb{R}} \mathcal{G}(D_I\tau,y)\mathrm{e}^{\mu y}dy\right]N_m(x). \tag{3.4}$$

Since the dispersal kernel function J is symmetric, a comparison argument similar to that in [34, Proposition 3.9] and [52, Theorem 3.2] can be conducted to show the formula of the spreading speed c^* as follows:

$$c^* = \inf_{\mu>0}\frac{1}{\mu}\ln\left[\mathrm{e}^{C_\mu} + g'(0)\mathrm{e}^{C_\mu(1-\tau)}\mathrm{e}^{-f_I'(0)\tau}\int_{\mathbb{R}} \mathcal{G}(D_I\tau,y)\mathrm{e}^{\mu y}dy\right]. \tag{3.5}$$

Theorem 3.3. *Assume that **(J3)**, **(H1)–(H5)** hold, and $g(N)$ is monotone with respect to N. Let c^* be defined as in (3.5). Then for each $c \ge c^*$, there exists a traveling wave solution $W(x+cm)$ for system (1.6), where $W(\xi)$ is nondecreasing in ξ and connects 0 to ϖ, while for any $c \in (0,c^*)$, there is no traveling wave solution for system (1.6), which connects 0 to ϖ.*

Proof. Denote $\mathcal{M}$ the set of all nonincreasing and bounded functions from $\mathbb{R}$ to X. Then, one can verify that Q still satisfies the properties (R1)–(R5) in the proof of Theorem 3.2 with X_ϖ replaced by $\mathcal{M}_\varpi$, where $\mathcal{M}_\varpi = \{\phi \in \mathcal{M} | 0 \le \phi \le \varpi\}$. Therefore, we can obtain the existence and nonexistence of monotone traveling wave by using Theorem 3.8 in [12]. □

3.2 | Case 2: g is Nonmonotone

This subsection is devoted to propagation dynamics of system (1.6) with a nonmonotone birth function g. Similar to the discussion in Section 2.2, we always assume that **(H6)** are satisfied.

Next, we introduce the following two auxiliary equations:

$$\begin{cases} \partial_t u_m = D_M\left[\int_{\mathbb{R}} J(x-y)u_m(y,t)dy - u_m\right] \\ \qquad -(u_m), & x\in\mathbb{R}, \\ & 0<t\le 1,\ t\ne\tau, \\ u_m(x,t^+) = u_m(x,t) + v_m^+(x,\tau), & t=\tau, \\ u_m(x,0) = N_m^+(x), & m\in\mathbb{N}, \\ N_{m+1}^+(x) = u_m(x,1), \end{cases} \tag{3.6}$$

and

$$
\begin{cases}
\partial_t u_m = D_M\left[\int_{\mathbb{R}} J(x-y)u_m(y,t)dy - u_m\right] \\
\qquad - f(u_m), & x\in\mathbb{R}, \\
 & 0<t\le 1,\ t\neq\tau, \\
u_m(x,t^+) = u_m(x,t) + v_m^-(x,\tau), & t=\tau, \\
u_m(x,0) = N_m^-(x), & m\in\mathbb{N}, \\
N_{m+1}^-(x) = u_m(x,1),
\end{cases}
\tag{3.7}
$$

where $v_m^+(x,\tau)$ (respectively, $v_m^-(x,\tau)$) is the value of the solution, evaluated at $t=\tau$, of problem (3.2) with the initial value $v_m(x,0)=g^+(N_m^+(x))$ (respectively, $v_m(x,0)=g^-(N_m^-(x))$) for $m\ge 0$.

By the same argument for the recursion operator Q in (1.6), we can process (3.6) and (3.7) to two discrete-time recursion systems for N_m^+ and N_m^- as

$$
N_{m+1}^+(x) = Q^+[N_m^+](x) = S_{1-\tau}[S_\tau(N_m^+) + T_\tau g^+(N_m^+)](x), \quad x\in\mathbb{R}, m\ge 0, \tag{3.8}
$$

and

$$
N_{m+1}^-(x) = Q^-[N_m^-](x) = S_{1-\tau}[S_\tau(N_m^-) + T_\tau g^-(N_m^-)](x), \quad x\in\mathbb{R}, m\ge 0, \tag{3.9}
$$

respectively. Let N_m^+ and N_m^- be the solutions of (3.8) and (3.9), respectively. It follows from comparison arguments that when $0< N_0^-(x)\le N_0(x)\le N_0^+(x)\le \varpi^+$,

$$
0\le N_m^-(x)\le N_m(x)\le N_m^+(x), \quad x\in\mathbb{R},\ m\ge 0. \tag{3.10}
$$

We have obtained in Section 3.1 that c^* given in (3.5) is the spreading speed of (1.6) when the birth function g is monotone. Notice that the value of the spreading speed c^* is determined only by the linearized system (3.4). Meanwhile, models (3.6) and (3.7) have the same linearized system at $u=0$, that is, Equation (3.3). Then, Theorem 3.2 can be employed to show that c^* is also the spreading speed of models (3.8) and (3.9). At this point, we can use a comparison argument together with (3.10) to prove that c^* is also a spreading speed for system (1.6) when g is nonmonotone, which is read as follows.

Theorem 3.4. *Assume that **(J3)**, **(H1)–(H6)** are satisfied. If $\hat{Q}'(0)>1$, then the following statements hold:*

(i) If $\phi\in X_{\varpi^+}$ and $\phi(x)=0$ outside a bounded interval, then $\lim_{m\to\infty,|x|\ge cm}|Q^m[\phi](x)|=0, \forall c>c^*$.

(ii) If $\phi\in X_{\varpi}\setminus\{0\}$, then

$$
\varpi^-\le \liminf_{m\to\infty,|x|\le cm} Q^m[\phi](x)\le \limsup_{m\to\infty,|x|\le cm} Q^m[\phi](x)\le\varpi^+, \quad \forall c\in(0,c^*).
$$

Before proving the existence of traveling waves of system (1.6), we state the following definition and lemmas.

Definition 3.5 [59]. Let $\mathcal{E}$ be a Banach space. A continuous mapping $F:\mathcal{E}\to\mathcal{E}$ is called κ-condensing if it is bounded and $\kappa(F(B))<\kappa(B)$ for any nonempty bounded closed set $B\subset\mathcal{E}$ with $\kappa(B)>0$; and it is compact dissipative if there is a bounded set $B_0\subset\mathcal{E}$ such that B_0 attracts each compact set in $\mathcal{E}$. Clearly, a compact map is κ-condensing.

Lemma 3.6 Asymptotic fixed point theorem [39]. *Let $\mathcal{E}$ be a Banach space. If $F:\mathcal{E}\to\mathcal{E}$ is κ-condensing and compact dissipative, then F admits a fixed point.*

To show that an operator is κ-condensing (see the proof of Theorem 3.9), we introduce the following property of the Kuratowski measure of noncompactness (cf. [4, Lemma 5].)

Lemma 3.7. *Let $\mathcal{E}$ be a Banach space, $a<b$ be two real numbers and $\Gamma\subset C([a,b],\mathcal{E})$ be a bounded set. Define $\Gamma(s):=\{f(s)|f\in\Gamma\}$, $\forall s\in[a,b]$. If Γ is equicontinuous on $[a,b]$, then $\kappa\left(\int_a^b\Gamma(s)ds\right)\le\int_a^b\kappa(\Gamma(s))ds$, where $\int_a^b\Gamma(s)ds=\{\int_a^b f(s)ds|f\in\Gamma\}$.*

Choose $\rho=\rho(c)\in(0,\frac{\hat{D}}{c})$ for any given $c>c^*$, where $\hat{D}=\min\{D_I,D_M\}$. Set

$$
\mathbb{X}_\rho := \{\phi\in C(\mathbb{R},\mathbb{R})|\sup_{x\in\mathbb{R}}|\phi(x)|e^{-\rho|x|}<+\infty\},
$$

and $\|\phi\|_\rho:=\sup_{x\in\mathbb{R}}|\phi(x)|e^{-\rho|x|}$. Then, $(\mathbb{X}_\rho,\|\cdot\|_\rho)$ is a Banach space. Define a set $Y_{\mathbb{L}^+}:=\{\phi\in\mathbb{X}_\rho|0\le\phi\le\mathbb{L}^+\}$. We see that $Y_{\mathbb{L}^+}$ is a nonempty, convex, and closed subset of $\mathbb{X}_\rho$ since $0,\mathbb{L}^+\in Y_{\mathbb{L}^+}$. Next, we recall some known results for the following linear integro–differential equation

$$
\begin{cases}
u_t = d\left[\int_{\mathbb{R}} J(x-y)u(y,t)dy - u\right], & x\in\mathbb{R}, t>0, \\
u(x,0)=\phi(x),
\end{cases}
\tag{3.11}
$$

where d is a given positive constant. By [52, Lemma 3.1], the above equation generates a strongly continuous semigroup $P_d(t)$ on X. Moreover, the unique mild solution of (3.11) has the form of

$$
[P_d(t)\phi](x) = e^{-dt}\sum_{k=0}^{\infty}\frac{(dt)^k}{k!}a_k(\phi)(x), \tag{3.12}
$$

where $a_0(\phi)(x)=\phi(x)$ and $a_k(\phi)(x)=\int_{\mathbb{R}}J(x-y)a_{k-1}(\phi)(y)dy$ for any integer $k\ge 1$.

Lemma 3.8.

(i) For any given nonempty and bounded interval $I:=[a,b]\subset\mathbb{R}$ and $t\ge 0$, it holds that $\kappa((P_d(t)\mathcal{U})_I)\le e^{-dt}\kappa((\mathcal{U})_I)$ for each set $\mathcal{U}\subset Y_{\mathbb{L}^+}$.

(ii) The map $\mathcal{T}_c P(1)$ is a κ-contraction on $Y_{\mathbb{L}^+}$ with the contraction coefficient $e^{\rho c-d}$.

Proof. Part (i) comes from [13, Lemma 2]. Part (ii) can be seen in [53, Lemma 3.4]. ☐

We now are ready to establish the existence of traveling wave solutions.

Theorem 3.9. *Assume that **(J3)**, **(H1)–(H6)** are satisfied. Suppose that $\hat{Q}'(0) > 1$, then the following statements are true:*

(i) For any $c \in (0, c^*)$, system (1.6) admits no traveling wave $W(x + cm)$ satisfying $W(-\infty) = 0$.

(ii) If, further, $D_M > D^*$, where D^* satisfies

$$e^{L_M - D^*} + e^{(L_M - D^*)(1-\tau) + (L_I - D_I)\tau} L_g = 1, \tag{3.13}$$

with L_M, L_I, and L_g being the Lipschitz coefficients of f_M, f_I, and g on $[0, \varpi^+]$, respectively, then for any $c > c^*$, system (1.6) admits a continuous traveling wave $W(x + cm)$ satisfying that $W(-\infty) = 0$ and $\varpi^- \le \liminf_{\xi \to +\infty} W(\xi) \le \limsup_{\xi \to +\infty} W(\xi) \le \varpi^+$.

Proof.

(i) On the contrary, we suppose that there exists $c_0 \in (0, c^*)$ such that system (1.6) admits a traveling wave solution $N_m(x) = W(x + c_0 m)$ with $W(-\infty) = 0$. It follows from Theorem 3.4(ii) that

$$\liminf_{m \to +\infty, |x| \le cm} N_m(x) \ge \varpi^- > 0, \ \forall c \in (0, c^*).$$

If we take $\tilde{c} \in (c_0, c^*)$ and set $x = -\tilde{c}m$, then $\liminf_{m \to +\infty} N_m(-\tilde{c}m) = \liminf_{m \to +\infty} W((c_0 - \tilde{c})m) > 0$, which contradicts with the fact that $\lim_{m \to +\infty} W((c_0 - \tilde{c})m) = W(-\infty) = 0$.

(ii) Given any $c > c^*$, we take $\rho = \rho(c)$ as in the definition of $\mathbb{X}_\rho$. Define the operators

$$Q_c[\phi](x) := \mathcal{T}_c Q[\phi](x) = \mathcal{T}_c\{S_{1-\tau}[S_\tau(\phi) + T_\tau g(\phi)]\}(x), \quad \forall \phi \in \mathbb{X}_\rho,$$

and

$$Q_c^\pm[\phi](x) := \mathcal{T}_c Q^\pm[\phi](x) = \mathcal{T}_c\{S_{1-\tau}[S_\tau(\phi) + T_\tau g^\pm(\phi)]\}(x), \quad \forall \phi \in \mathbb{X}_\rho.$$

Recall that the operators $Q^\pm$ are order preserving. We see from Theorem 3.3 that systems (3.8) and (3.9) admit nontrivial traveling wave solutions $W^+(x + cm)$ and $W^-(x + cm)$, respectively, where $W^\pm(+\infty) = \varpi^\pm$ and $W^\pm(-\infty) = 0$. Then, we define a positively invariant set of Q_c which was introduced in [3]. For any $c \ge c^*$, we denote

$$\mathcal{E}_c := \{\phi \in \mathbb{X}_\rho | \delta W^+(x) \le \phi(x) \le W^+(x), \ x \in \mathbb{R}\}$$

with $\delta \in (0, 1)$ and $\delta W^+(x) \le \sigma_0$. Clearly, the set $\mathcal{E}_c$ is a nonempty, bounded, closed, and convex subset of $\mathbb{X}_\rho$. Furthermore, the following four claims hold.

Claim 3.1. $Q_c[\mathcal{E}_c] \subset \mathcal{E}_c$.

Since $g^+ \ge g \ge g^-$ and g^+ and g^- are nondecreasing, we obtain that when $\phi \le W^+$,

$$Q_c[\phi] \le Q_c^+[\phi] \le Q_c^+[W^+] = W^+,$$

while when $\phi \ge \delta W^+$,

$$\begin{aligned} Q_c[\phi] \ge Q_c^-[\phi] \ge Q_c^-[\delta W^+] \\ &= \mathcal{T}_c\{S_{1-\tau}[S_\tau(\delta W^+) + T_\tau g^-(\delta W^+)]\} \\ &\ge \delta \mathcal{T}_c\{S_{1-\tau}[S_\tau(W^+) + T_\tau g^+(W^+)]\} \\ &= \delta Q_c^+[W^+] = \delta W^+, \end{aligned}$$

where we have used the fact that $g^-(\delta W^+) = g^+(\delta W^+) \ge \delta g^+(W^+)$. Hence, Claim 3.1 is proved.

Claim 3.2. The operator $Q_c : \mathcal{E}_c \to \mathcal{E}_c$ is continuous in the norm $\|\cdot\|_\rho$.

For any $\phi_i \in \mathcal{E}_c (i = 1, 2)$ and $t \in [0, 1]$, we let $\Phi_t[\phi_i](x) = u(x, t; \phi_i), x \in \mathbb{R} (i = 1, 2)$ be the solution of (3.1) with initial value ϕ_i. By constant-variation formula, we can obtain

$$u(x, t; \phi_i) = \begin{cases} P_{D_M}(t)[\phi_i](x) \\ - \int_0^t P_{D_M}(t-s) f_M(u(\cdot, s; \phi_i))(x) ds, & t \in [0, \tau], \\ P_{D_M}(t-\tau)[u(\cdot, \tau; \phi_i) + v(\cdot, \tau; g(\phi_i))](x) \\ - \int_\tau^t P_{D_M}(t-s) f_M(u(\cdot, s; \phi_i))(x) ds, & t \in (\tau, 1], \end{cases} \tag{3.14}$$

where $v(x, t; g(\phi_i)) = P_{D_I}(t)[g(\phi_i)](x) - \int_0^t P_{D_I}(t-s) f_I(v(\cdot, s; \phi_i))(x) ds, \forall t \in [0, \tau]$. Then by (3.14), we have that for $t \in [0, \tau]$,

$$\begin{aligned} &\left|u(x, t; \phi_1) - u(x, t; \phi_2)\right| e^{-\rho|x|} \\ &\le \left|P_{D_M}(t)[\phi_1](x) - P_{D_M}(t)[\phi_2](x)\right| e^{-\rho|x|} \\ &+ \int_0^t \left|P_{D_M}(t-s) f_M(u(\cdot, s; \phi_1))(x) \right. \\ &\left. - P_{D_M}(t-s) f_M(u(\cdot, s; \phi_2))(x)\right| e^{-\rho|x|} ds \\ &\le \mathcal{P}\|\phi_1 - \phi_2\|_\rho + \int_0^t \mathcal{P} L_M \|u(\cdot, s; \phi_1) - u(\cdot, s; \phi_2)\|_\rho ds, \end{aligned}$$

where $\mathcal{P} = \max_{s \in [0,1]} \|P_{D_M}(t)\|$. The above inequality together with Gronwall's inequality implies that

$$\|u(\cdot, t; \phi_1) - u(\cdot, t; \phi_2)\|_\rho \le \mathcal{P}\|\phi_1 - \phi_2\|_\rho e^{\mathcal{P} L_M t}, \ \forall t \in [0, \tau],$$

and thus

$$\|S_\tau(\phi_1) - S_\tau(\phi_2)\|_\rho \le \mathcal{P}\|\phi_1 - \phi_2\|_\rho e^{\mathcal{P} L_M \tau}.$$

This means that the operator S_τ is continuous on $\mathcal{E}_c$. Similarly, we can verify that $\mathcal{T}_c$, $T_\tau g$, and $S_{1-\tau}$ are all continuous on $\mathcal{E}_c$. Hence, the continuity of the operator Q_c with respect to $\|\cdot\|_\rho$ is obtained.

Claim 3.3. For any given closed set $B \subset \mathcal{E}_c$, $P_{D_M}(t-s) f_M(u(\cdot, s; B))$ is equicontinuous in $s \in [0, t]$ for any $t \in [0, \tau]$, and is equicontinuous in $s \in (\tau, t]$ for any $t \in (\tau, 1]$.

Let B be a closed subset of $\mathcal{E}_c$. We obtain from Claim 3.1 that for any $\psi \in B$, $u(\cdot, t; \psi)$ is uniformly bounded and hence $u_t(\cdot, t; \psi)$ is uniformly bounded in $t \in [0, \tau]$ by (1.3) and (1.4). According to the definition of $\phi_k(\phi)$ in (3.12), by an argument of induction, we deduce that for any integer $k \geq 0$,

$$|a_k(f_M(u(\cdot, s; \psi)))(x)| \leq \int_{\mathbb{R}} J(x-y)|a_{k-1}(f_M(u(\cdot, s; \psi)))(y)|dy$$
$$\leq \cdots \leq |f_M(u(\cdot, s; \psi))| \leq C_1 := C_1(B),$$

for any $\psi \in B$, $x \in \mathbb{R}$, and $s \in [0, \tau]$. Notice that for any $\psi \in B$, $\iota \in [0, \tau]$, and $s \in [0, \tau]$, $P_{D_M}(\iota) f_M(u(\cdot, s; \psi))$ is the unique solution to (3.11) with $\phi = f_M(u(\cdot, s; \psi))$ and $t = \iota$. Then by (3.12),

$$|P_{D_M}(\iota) f_M(u(\cdot, s; \psi))(x)| \leq e^{-D_M \iota} \sum_{k=0}^{\infty} \frac{(D_M \iota)^k}{k!} |a_k(f_M(u(\cdot, s; \psi)))(x)|$$
$$\leq C_1 e^{-D_M \iota} \sum_{k=0}^{\infty} \frac{(D_M \iota)^k}{k!} = C_1$$

for any $\psi \in B$, $x \in \mathbb{R}$, $t \in [0, \tau]$, $\iota \in [0, t]$, and $s \in [0, t]$, which together with (3.11) leads to that

$$\left| \frac{\partial P_{D_M}(\iota) f_M(u(\cdot, s; \psi))(x)}{\partial \iota} \right|$$
$$\leq D_M \int_{\mathbb{R}} J(x-y)|P_{D_M}(\iota) f_M(u(\cdot, s; \psi))(y)|dy$$
$$+ D_M |P_{D_M}(\iota) f_M(u(\cdot, s; \psi))(x)|$$
$$\leq 2 D_M C_1, \quad \forall x \in \mathbb{R}$$

for any $\psi \in B$, $t \in [0, \tau]$, $\iota \in [0, t]$, and $s \in [0, t]$. Then, for any $\psi \in B$, $t \in [0, \tau]$, and $s_1, s_2 \in [0, t]$, we have

$$|P_{D_M}(t-s_1) f_M(u(\cdot, s_1; \psi))(x) - P_{D_M}(t-s_2) f_M(u(\cdot, s_2; \psi))(x)| e^{-\rho|x|}$$
$$\leq |P_{D_M}(t-s_1) f_M(u(\cdot, s_1; \psi))(x) - P_{D_M}(t-s_2) f_M(u(\cdot, s_1; \psi))(x)|$$
$$+ |P_{D_M}(t-s_2) f_M(u(\cdot, s_1; \psi))(x) - P_{D_M}(t-s_2) f_M(u(\cdot, s_2; \psi))(x)|$$
$$\leq |s_1 - s_2| \cdot \max_{t-\tilde{s} \leq \iota \leq t-\hat{s}} \left| \frac{\partial P_{D_M}(\iota) f_M(u(\cdot, s_1; \psi))(x)}{\partial \iota} \right|$$
$$+ |s_1 - s_2| \cdot \max_{\hat{s} \leq \iota \leq \tilde{s}} \left| P_{D_M}(t-s_2)\left[f'_M(u(\cdot, \iota; \psi)) u_t(\cdot, \iota; \psi) \right](x) \right|$$
$$\leq C_2 |s_1 - s_2|, \quad \forall x \in \mathbb{R},$$

where $\hat{s} = \min\{s_1, s_2\}$, $\tilde{s} = \max\{s_1, s_2\}$, and $C_2 = C_2(B)$ is a constant independent of x, t, s_1, and s_2. Hence, for any $t \in [0, \tau]$, $P_{D_M}(t-s) f_M(u(\cdot, s; B))$ is equicontinuous with respect to $s \in [0, t]$ in the norm $\|\cdot\|_\rho$. By a similar argument, we have that for any $t \in (\tau, 1]$, $P_{D_M}(t-s) f_M(u(\cdot, s; B))$ is equicontinuous with respect to $s \in (\tau, t]$ in the norm $\|\cdot\|_\rho$. This proves Claim 3.3.

Claim 3.4. The operator $Q_c : \mathcal{E}_c \to \mathcal{E}_c$ is a κ-contraction in the norm $\|\cdot\|_\rho$.

By (3.14), Claim 3.3, Lemmas 3.7 and 3.8(i), we obtain that for any given closed set $B \subset \mathcal{E}_c$ and $t \in [0, \tau]$,

$$\kappa(u(\cdot, t; B)) \leq \kappa\big(P_{D_M}(t)[B]\big) + \int_0^t \kappa\big(P_{D_M}(t-s) f_M(u(\cdot, s; B))\big) ds$$
$$\leq e^{-D_M t} \kappa(B) + \int_0^t e^{-D_M(t-s)} L_M \kappa(u(\cdot, s; B)) ds,$$

equivalently,

$$e^{D_M t} \kappa(u(\cdot, t; B)) \leq \kappa(B) + \int_0^t L_M e^{D_M s} \kappa(u(\cdot, s; B)) ds.$$

It follows from Gronwall's inequality that $e^{D_M t} \kappa(u(\cdot, t; B)) \leq \kappa(B) e^{L_M t}$, that is, $\kappa(u(\cdot, t; B)) \leq \kappa(B) e^{(L_M - D_M)t}$. Hence, $\kappa(u(\cdot, \tau; B)) \leq \kappa(B) e^{(L_M - D_M)\tau}$. Similarly, there holds $\kappa(v(\cdot, \tau; B)) \leq L_g \kappa(B) e^{(L_I - D_I)\tau}$. By (3.14), Claim 3.3, Lemmas 3.7 and 3.8(i), we derive that for $t \in (\tau, 1]$,

$$\kappa(u(\cdot, t; B)) \leq \kappa\big(P_{D_M}(t-\tau)[u(\cdot, \tau; B) + v(\cdot, \tau; B)]\big)$$
$$+ \int_\tau^t \kappa\big(P_{D_M}(t-s) f_M(u(\cdot, s; B))\big) ds$$
$$\leq e^{-D_M(t-\tau)} [\kappa(u(\cdot, \tau; B)) + \kappa(v(\cdot, \tau; B))]$$
$$+ \int_\tau^t e^{-D_M(t-s)} L_M \kappa(u(\cdot, s; B)) ds$$
$$\leq e^{-D_M(t-\tau)} \left[e^{(L_M - D_M)\tau} \kappa(B) + e^{(L_I - D_I)\tau} L_g \kappa(B) \right]$$
$$+ \int_\tau^t e^{-D_M(t-s)} L_M \kappa(u(\cdot, s; B)) ds,$$

equivalently,

$$e^{D_M t} \kappa(u(\cdot, t; B)) \leq \left[e^{L_M \tau} + e^{(D_M + L_I - D_I)\tau} L_g \right] \kappa(B)$$
$$+ \int_\tau^t L_M e^{D_M s} \kappa(u(\cdot, s; B)) ds.$$

Using Gronwall's inequality again, we can deduce that

$$e^{D_M t} \kappa(u(\cdot, t; B)) \leq \left[e^{L_M \tau} + e^{(D_M + L_I - D_I)\tau} L_g \right] \kappa(B) e^{L_M(t-\tau)}, \ \forall t \in (\tau, 1],$$

that is, $\kappa(u(\cdot, t; B)) \leq \left[1 + e^{(D_M + L_I - D_I - L_M)\tau} L_g \right] \kappa(B) e^{(L_M - D_M)t}, \forall t \in (\tau, 1]$. Notice that

$$Q[B] = P_{D_M}(1-\tau) \left[P_{D_M}[B] - \int_0^\tau P_{D_M}(\tau - s) f_M(u(\cdot, s; B)) ds \right.$$
$$\left. + v(\cdot, \tau; B) \right]$$
$$- \int_\tau^1 P_{D_M}(1-s) f_M(u(\cdot, s; B)) ds,$$

where $v(x, \tau; B) = P_{D_I}[g(B)] - \int_0^\tau P_{D_I}(\tau - s) f_I(v(\cdot, s; B)) ds$. Therefore, by Lemma 3.8(ii),

$$\kappa(Q_c[B]) \leq e^{\rho c - D_M} \kappa(B) + e^{(\rho c - D_M)(1-\tau)}$$
$$\times \int_0^\tau e^{(\rho c - D_M)(\tau - s)} L_M e^{(L_M - D_M)s} \kappa(B) ds$$

$$+\mathrm{e}^{(\rho c-D_M)(1-\tau)}\mathrm{e}^{(L_I-D_I)\tau}L_g\kappa(B)$$

$$+\int_\tau^1 \mathrm{e}^{(\rho c-D_M)(1-s)}L_M\left[1+\mathrm{e}^{(D_M+L_I-D_I-L_M)\tau}L_g\right]$$

$$\times\kappa(B)\mathrm{e}^{(L_M-D_M)s}ds$$

$$=\mathrm{e}^{\rho c-D_M}\left[1+\frac{L_M(\mathrm{e}^{L_M-\rho c}-1)}{L_M-\rho c}+\mathrm{e}^{(D_M+L_I-D_I-\rho c)\tau}L_g\right.$$

$$\left.\times\left(1+\frac{L_M(\mathrm{e}^{(L_M-\rho c)(1-\tau)}-1)}{L_M-\rho c}\right)\right]\kappa(B)$$

$$=:C(\rho)\kappa(B).$$

Now by (3.13), it holds that for $D_M > D^*$,

$$\lim_{\rho\to 0^+} C(\rho)=\mathrm{e}^{L_M-D_M}+\mathrm{e}^{(L_M-D_M)(1-\tau)+(L_I-D_I)\tau}L_g<1,$$

which implies that there exists sufficiently small $\rho\in(0,\frac{\hat{D}}{c})$ such that $C(\rho)<1$. Consequently, the operator Q_c is a κ-contraction with the coefficient $C(\rho)$.

We see that the operator $Q_c:\mathcal{E}_c\to\mathcal{E}_c$ is κ-condensing, since Q_c is a κ-contraction by Claim 3.4. Clearly, Q_c is also compact dissipative by the boundedness of $\mathcal{E}_c$ in $\mathbb{X}_\rho$ and the fact that $(Q_c)^m(\mathcal{E}_c)\subset\mathcal{E}_c$ for any $m\geq 1$. Then, it follows from the asymptotic fixed point theorem (Lemma 3.6) that the operator Q_c admits a fixed point $W\subset\mathcal{E}_c$, that is, $Q_c(W)=\mathcal{T}_c Q(W)=W$. Hence, $Q(W)(x)=W(x+c)$, and $Q^m(W)(x)=W(x+cm)$ is a traveling wave solution of system (1.6). Furthermore, $W(-\infty)=0$ since $W^-(\xi)\leq W(\xi)\leq W^+(\xi),\forall\xi=x+c\in\mathbb{R}$.

For a fixed $c>c^*$, we let $u_m(x):=W(x+cm)$, $\forall m\geq 0$. Fix a constant $\hat{c}_0\in(0,c^*)$. We see from Theorem 3.4(ii) that

$$\varpi^-\leq\liminf_{m\to+\infty,|x|\leq\hat{c}_0 m}u_m(x)\leq\limsup_{m\to+\infty,|x|\leq\hat{c}_0 m}u_m(x)\leq\varpi^+,$$

and thus,

$$\varpi^-\leq\liminf_{m\to+\infty}u_m(km)\leq\limsup_{m\to+\infty}u_m(km)\leq\varpi^+$$

uniformly for $k\in[0,\hat{c}_0]$.

This means that $\varpi^-\leq\liminf_{m\to+\infty}u_m(sm)\leq\limsup_{m\to+\infty}u_m(sm)\leq\varpi^+$ uniformly for $s\in[c-\hat{c}_0,c]$. Let $a_m=m(c-\hat{c}_0)$ and $b_m=cm$, $\forall m\geq 1$. Thus, there is $j_0>0$ such that $a_{m+1}-b_m<0$, $\forall m\geq j_0$, and hence, $\cup_{m\geq j}[a_m,b_m]=[a_j,+\infty)$, $\forall j\geq j_0$. Therefore, we obtain that $\varpi^-\leq\liminf_{\xi\to+\infty}W(\xi)\leq\limsup_{\xi\to+\infty}W(\xi)\leq\varpi^+$. The proof is completed. □

4 | Numerical Simulations

In this section, we present some numerical simulations to illustrate the analytic results obtained in the previous sections and explore the impacts of the mature emergence delay on the spatial dynamics. Referring to Bai, Lou, and Zhao [3], Lewis and Li [28], and Wu and Zhao [53], we take the mortality functions $f_I(v)=a_1v+b_1v^2$ and $f_M(u)=a_2u+b_2u^2$ with $a_1=0.5$ and $a_2=1$ being the natural death rates of the immature individuals and adult population, respectively, and $b_1=0.01$ and $b_2=0.01$ being the strength of the intraspecific competition for immature individuals and adult population, respectively. We use two types of birth functions, the Beverton–Holt function $g(N)=\frac{pN}{q+N}$ and Ricker function $g(N)=N\mathrm{e}^{r(1-N)}$, to simulate two different cases for g: monotone and nonmonotone, respectively. Unless otherwise specified, we set the parameter values as $p=2, q=0.2$, and $r=2.5$ by default. For the nonlocal dispersal operator, we choose the kernel function as Laplace kernel $J(x)=\frac{1}{2D}\mathrm{e}^{-\frac{|x|}{D}},\forall x\in\mathbb{R}$, where $D=0.56$ is the mean dispersal distance.

4.1 | Critical Domain Size and Persistence

As shown in [53, Section 3.2], the eigenvalue problem

$$\int_{\ell_1}^{\ell_2}J(x-y)\psi(y)dy=\int_{\ell_1}^{\ell_2}\frac{1}{2D}\mathrm{e}^{-\frac{|x-y|}{D}}\psi(y)dy=\lambda\psi(x),$$
$$x\in[\ell_1,\ell_2],$$

admits a principal eigenvalue λ_0 satisfying that

$$\tan\frac{\ell\sqrt{1/\lambda_0-1}}{2D}=\frac{1}{\sqrt{1/\lambda_0-1}}\quad\text{with }\ell=\ell_2-\ell_1. \tag{4.1}$$

According to Theorem 2.2, the threshold equation is

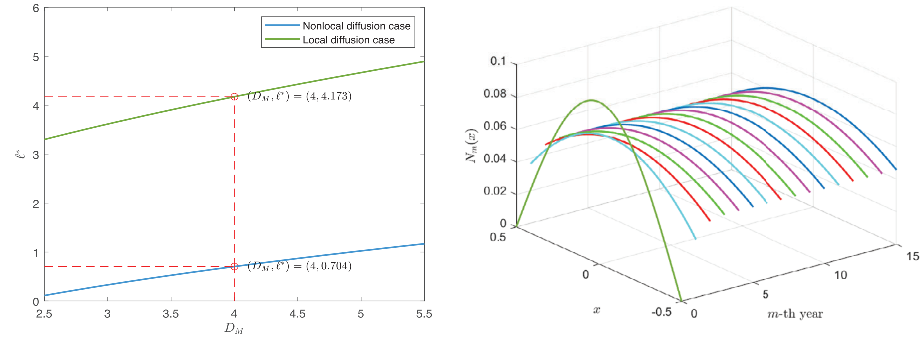
$$R_0(\ell):=\mathrm{e}^{D_M\lambda_0-D_M-a_2}+g'(0)\mathrm{e}^{[D_M(1-\tau)+D_I\tau]\lambda_0-[(D_M+a_2)(1-\tau)+(D_I+a_1)\tau]}$$
$$=1. \tag{4.2}$$

Then by Corollary 2.4, when $\mathrm{e}^{-a_2-D_M}+g'(0)\mathrm{e}^{-(a_2+D_M)(1-\tau)-(a_1+D_I)\tau}<1<\mathrm{e}^{-a_2}+g'(0)\mathrm{e}^{-a_2(1-\tau)-a_1\tau}$, there is a unique critical domain size ℓ^* satisfying (4.1) and (4.2). Notice that the principal eigenvalue of the local diffusion operator ψ_{xx} over (l_1,l_2) with zero Dirichlet boundary condition is $-\frac{\pi^2}{\ell^2}$. When the nonlocal diffusion operator $[J*\psi-\psi](x)$ is replaced by the local diffusion operator ψ_{xx} with zero Dirichlet boundary condition, the threshold equation corresponding to Corollary 2.4(ii) becomes

$$\tilde{R}_0(\ell):=\mathrm{e}^{-\frac{D_M\pi^2}{\ell^2}-a_2}+g'(0)\mathrm{e}^{-\frac{D_M\pi^2(1-\tau)}{\ell^2}-a_2(1-\tau)-\frac{D_I\pi^2\tau}{\ell^2}-a_1\tau}=1, \tag{4.3}$$

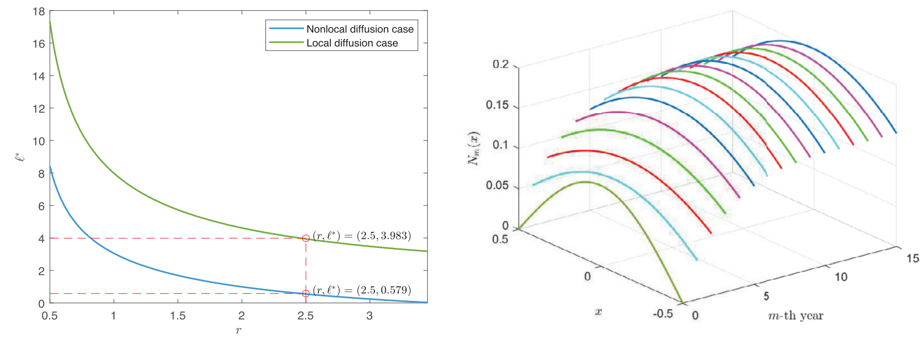
whose derivation is quite similar to [3, Theorem 4.1] and the details are omitted here.

In the scenario where g is taken as the Beverton–Holt function (monotone birth function), we can see the dependence of ℓ^* on dispersal rate D_M with $\tau=0.4$ and $D_I=\frac{D_M}{5}$ in Figure 1a. When $D_M=4$, the critical domain size corresponding to impulsive nonlocal diffusion population model (respectively, impulsive local diffusion population model) is $\ell^*\approx 0.704$ (respectively, $\ell^*\approx 4.173$), and $\hat{Q}'(0)=4.8612>1$. Then, Figure 1b shows that the adult population with nonlocal dispersal and initial datum $N_0(x)=\cos(\pi x),\forall x\in[-0.5,0.5]$ is persistent and converges to a positive steady state of (1.6) when the domain size $\ell=\ell_2-\ell_1=1>\ell^*$, which verifies Corollary 2.4(ii).



(a) Dependence of critical domain size ℓ^* on D_M. (b) Temporal dynamics of $N_m(x)$.

FIGURE 1 | Numerical simulations for system (1.6) in bounded domain when g is the Beverton–Holt function.



(a) Dependence of critical domain size ℓ^* on r. (b) Temporal dynamics of $N_m(x)$.

FIGURE 2 | Numerical simulations for system (1.6) in bounded domain when g is the Ricker function.

In the scenario where g is taken as the Ricker function (non-monotone birth function), it is shown in Figure 2a that ℓ^* is decreasing with respect to the intrinsic birth rate r when $D_M = 4, D_I = 0.8$, and $\tau = 0.4$. When $r = 2.5$, the critical domain size corresponding to impulsive nonlocal diffusion population model (respectively, impulsive local diffusion population model) is $\ell^* \approx 0.579$ (respectively, $\ell^* \approx 3.983$), and $\hat{Q}'(0) = 5.8418 > 1$. Then, Figure 2b depicts the temporal dynamics of $N_m(x)$ for system (1.6) with the domain size $\ell = \ell_2 - \ell_1 = 1 > \ell^*$ and the initial datum $N_0(x) = \cos(\pi x), \forall x \in [-0.5, 0.5]$.

Figures 1a and 2a clearly indicate that the critical domain size for the nonlocal dispersal model is significantly less than that for the local dispersal model. This observation seems to suggest that nonlocal dispersal is more beneficial than and superior to the local dispersal strategy for a biological species.

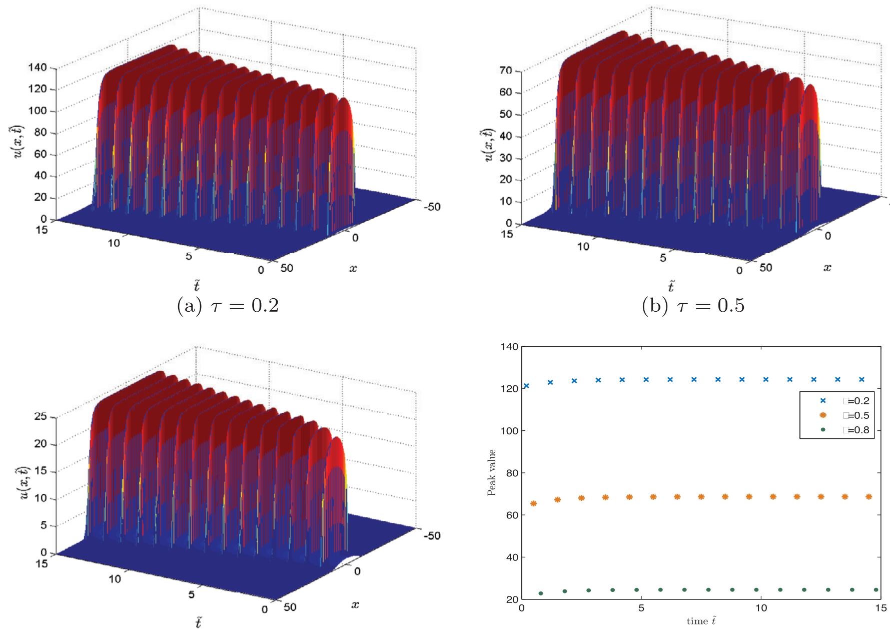
4.2 | The Effect of Maturation Delay on the Spatial Spread

To observe the propagation phenomenon, we choose the initial function as

$$u_0(x,0) = N_0(x) = \begin{cases} \cos\left(\dfrac{\pi}{20}x\right), & x \in [-10, 10], \\ 0, & x \in [-50, 10) \cup (10, 50], \end{cases}$$

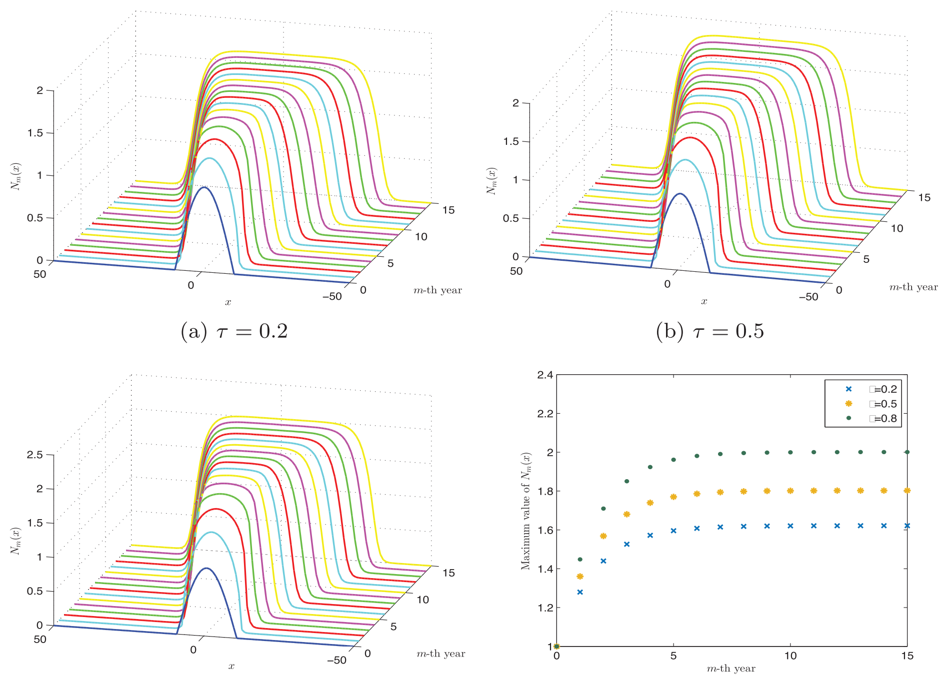
which has a compact support $[-10, 10]$ in the domain $[-50, 50]$. By fixing $D_M = 1$ and $D_I = 0.2$, we show the dynamics behavior of species in Figures 3–6 when g is taken as the Beverton–Holt and Ricker birth functions, respectively, and observe that the adult population spreads in two directions and oscillates in time (see Figures 3 and 5). Figures 3 and 5 also exhibit the effects of the maturation delay τ on the adult population density $u_m(x,t)$ for (1.3) with g taking the Beverton–Holt and Ricker birth functions, respectively. We can see in Figures 3d and 5d that the peaking value of the population density $u_m(x,t)$ for $x \in [-50, 50]$ and $t \in [0, 1]$ will converge to a positive constant eventually, which is negatively related to the maturation delay τ. This can be interpreted as that the longer the maturity time is, the lower the survival rate of juvenile to adult. Meanwhile, the peaking time, at which the adult population density $u_m(x,t)$ arrives its maximum in mth year, coincides with the moment of maturation emergence. Figures 4 and 6 illustrate the effects of the maturation delay τ on the adult population density $N_m(x)$ at the end of year m for (1.6) with g taking the Beverton–Holt and Ricker birth functions, respectively. We can see in Figures 4d and 6d that the maximum value of the adult population density $N_m(x)$ for $x \in [-50, 50]$ at the end of each year will converge to a positive constant eventually, which is positively related to the maturation delay τ. This is because the shorter the interval between the pulse time and the end of the year, the less the reduction of adult population density due to dispersal and mortality.

In Section 3.2, we also calculate the formula of the spreading speed c^* of system (1.6), which is given by (3.5). We note that there are Fourier and inverse Fourier transforms occurring in (3.5), which cannot be computed numerically through Matlab



(a) $\tau = 0.2$ (b) $\tau = 0.5$ (c) $\tau = 0.8$ (d) Peak value of $u(x, \tilde{t})$ in time $\tilde{t}$.

FIGURE 3 | The effects of the maturation delay on the distribution of adult population for (1.3) with g taking the Beverton–Holt function. The delay τ chosen in subgraphs (a), (b), and (c) are 0.2, 0.5, and 0.8, respectively, and $u(x, \tilde{t}) = u_m(x, t)$ with $\tilde{t} = m + t$ and $m = \lfloor \tilde{t} \rfloor$. Subgraph (d) depicts the peaking time and peaking value of the adult population distribution $u_m(x, t)$ in mth year.



(a) $\tau = 0.2$ (b) $\tau = 0.5$ (c) $\tau = 0.8$ (d) Maximum value of $N_m(x)$ in m-th year.

FIGURE 4 | The effects of the maturation delay on the distribution of adult population for (1.6) with g taking the Beverton–Holt function. The delay τ chosen in subgraphs (a), (b), and (c) are 0.2, 0.5, and 0.8, respectively. Subgraph (d) depicts the maximum value of the adult population distribution $N_m(x)$ at the end of mth year.

software. However, when the immature individuals cannot move in the space, that is, $D_I = 0$, the formula of the spreading speed c^* of system (1.6) can be given as

$$c^* = \inf_{\mu > 0} \frac{1}{\mu} \ln \left[e^{C_\mu} + g'(0) e^{C_\mu (1-\tau) - f_I'(0)\tau} \right].$$

We only examine the impact of the maturation delay τ on the spreading speed c^* when $D_M > 0$ and $D_I = 0$. Since we cannot determine the sign of $\int_{\mathbb{R}} J(y) e^{\mu y} dy - 1$, the sign of $C_\mu(1-\tau) - f_I'(0)\tau$ is also unknown. This means that the monotonicity of c^* with respect to τ is unclear. In Figure 7, we see that the monotonicity of c^* with respect to τ is very complicated, which

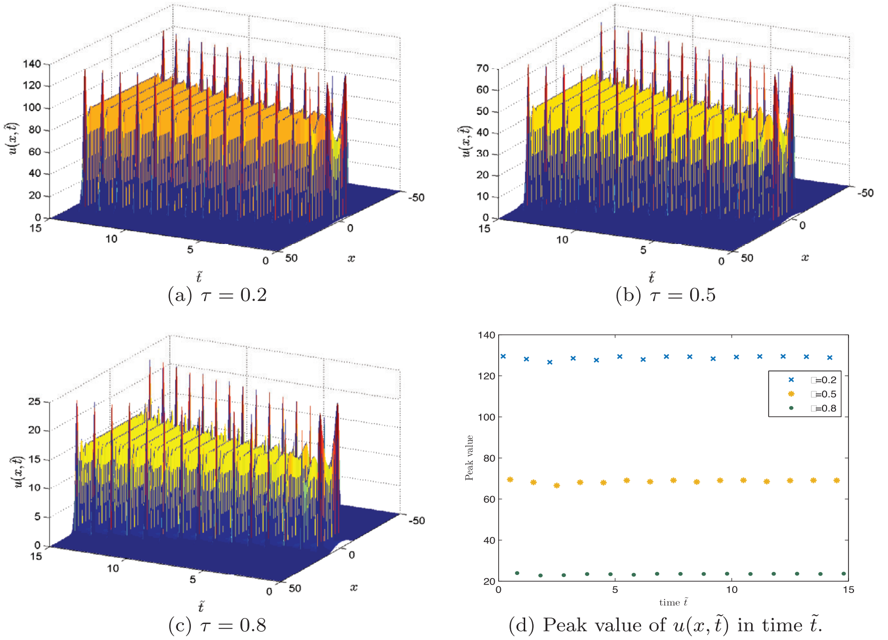


FIGURE 5 | The effects of the maturation delay on the distribution of adult population for (1.3) with g taking the Ricker function. The delay τ chosen in subgraphs (a), (b), and (c) are 0.2, 0.5, and 0.8, respectively, and $u(x,\tilde{t}) = u_m(x,t)$ with $\tilde{t} = m + t$ and $m = \lfloor \tilde{t} \rfloor$. Subgraph (d) depicts the peaking time and peaking value of the adult population distribution $u_m(x,t)$ in mth year.

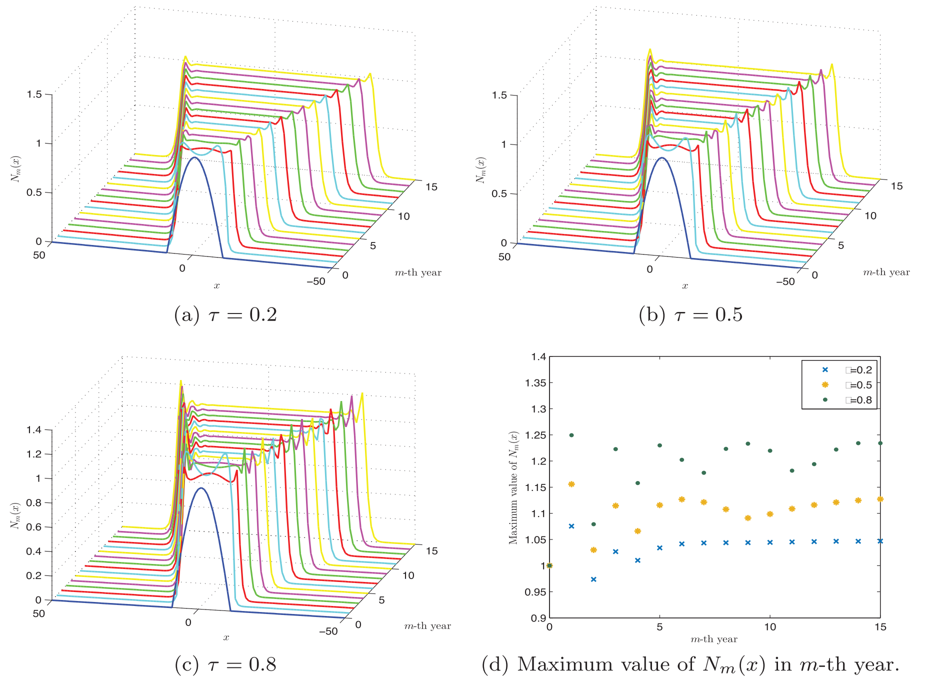
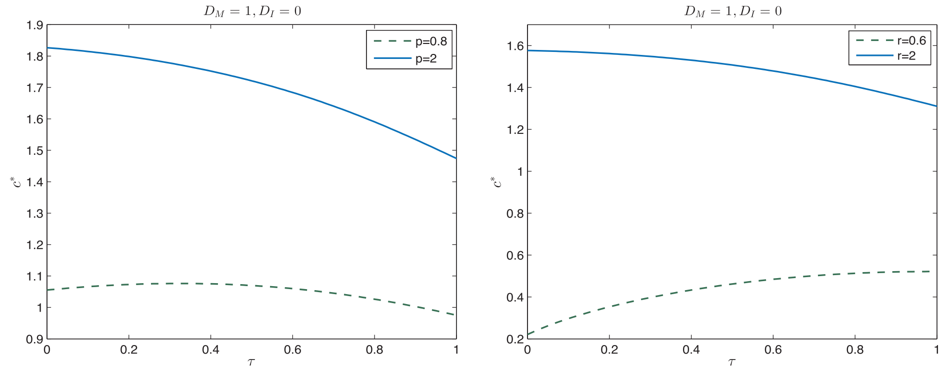


FIGURE 6 | The effects of the maturation delay on the distribution of adult population for (1.6) with g taking the Ricker function. The delay τ chosen in subgraphs (a), (b), and (c) are 0.2, 0.5, and 0.8, respectively. Subgraph (d) depicts the maximum value of the adult population distribution $N_m(x)$ at the end of mth year.

can be increasing, decreasing, or neither of them. Obviously, the form of the kernel function $J(y)$ has an impact.

5 | Conclusions

In this paper, we proposed an impulsive integro–differential equation to describe the evolution of a population growth model with annually synchronized emergence of mature individuals. Different from the model considered in [3], the model studied here cannot be decoupled and contains nonlocal dispersal describing the movement of the species in space. Based on the pulse time τ, by using the solution maps in time intervals $[0,\tau]$ and $[\tau,1]$, we deduced a discrete-time semiflow on an infinite dimension space to account for the evolution of the adult population density at the end of each year. When the spatial habitat is a bounded domain, we show a threshold dynamics of the adult population,



(a) g is the Beverton-Holt function. (b) g is the Ricker function.

FIGURE 7 | The effects of the maturation delay τ on the spreading speed c^* regarding different intrinsic birth rate.

and provide exact persistence criterion of the species. When the spatial habitat is spatially homogeneous unbounded domain, we investigated the existence and computation formula of spreading speed, which coincide with the minimal wave speed for the traveling waves. The above results are obtained in both monotone and nonmonotone cases of maturation impulse function.

Due to the lack of compactness of the solution maps, the method applied in this paper is different from that in [3]. In Section 2, where Ω is assumed to be bounded interval, we constructed a pair of upper and lower semicontinuous limiting functions to prove the existence and uniqueness of a positive steady state to system (1.6) when the birth function g is monotone (see Theorem 2.2). In Section 3, where the habitat is assume to be the 1-D full space $\mathbb{R}$, we used the asymptotic fixed point theorem rather than Schauder fixed point theorem to obtain the existence of traveling wave solutions when the birth function g is nonmonotone.

From Proposition 2.1 and Corollary 2.4, we found that in the bounded domain case $\Omega = (l_1, l_2)$, when $\hat{Q}'(0) < 1$, the solutions of discrete-time systems (1.6) and (2.3) tend to zero as $m \to \infty$, that is, the adult population becomes extinct eventually; when $Q_D' < 1 < \hat{Q}'(0)$, the discrete-time systems (1.6) has a similar persistence-extinction critical value l^* as that in [3, Theorem 4.1], and numerical simulations in Figures 1 and 2 show that the critical domain size corresponding to nonlocal diffusion model can be significantly smaller than that for corresponding local diffusion model. This observation seems to suggest that a nonlocal dispersal strategy is more superior to a random diffusion strategy as far as species survival is concerned. When $Q_D' > 1$, system (1.6) is always persistent—this cannot occur for the local diffusion model (1.1) with mature pulse (cf. [3, Theorem 4.1]). In the unbounded domain case $\Omega = \mathbb{R}$, an additional condition $D_M > D^*$ in Theorem 3.9 is required to ensure the existence of traveling wave solution. However, such condition is not needed for local diffusion model (1.1) (cf. [3, Theorem 3.4]). Notice that our main results are concerned with the evolution of the adult population density at the end of each year. By a similar argument, one can still derive the same threshold dynamics and spreading property of the juvenile population density at the mature time of each year.

For a nonlocal dispersal autonomous population model with monotone nonlinearity and with continuous births (instead of impulsive births), the corresponding solution either converges to zero steady state, or converges to a positive steady state as time goes to infinity (cf. [5, 55]). As in the discussion of [3, Section 2], we can infer that for any time $\tilde{t} \geq 0$, the time-$\tilde{t}$ solution map of system (1.3) has the expression

$$\Phi_{\tilde{t}}[\phi](x) = \begin{cases} S_{\tilde{t}-\lfloor \tilde{t} \rfloor} \circ Q^{\lfloor \tilde{t} \rfloor}[\phi](x), & 0 \leq \tilde{t} - \lfloor \tilde{t} \rfloor \leq \tau, \\ S_{\tilde{t}-\lfloor \tilde{t} \rfloor - \tau} \circ [S_\tau(Q^{\lfloor \tilde{t} \rfloor}[\phi]) \\ \quad + T_\tau g(Q^{\lfloor \tilde{t} \rfloor}[\phi])](x), & \tau < \tilde{t} - \lfloor \tilde{t} \rfloor < 1 \end{cases}$$

for any given initial data $\phi = N_0$, where $\lfloor \tilde{t} \rfloor$ is the nearest integer less than or equal to $\tilde{t}$. Moreover, one can verify that $\Phi_{\tilde{t}} \circ \Phi_1 = \Phi_{\tilde{t}+1}$ for any $\tilde{t} \geq 1$, $\Phi_{\tilde{t}}[\phi]$ is continuous in $\tilde{t} \in \mathbb{R}_+ \setminus \{m + \tau : m \in \mathbb{N}\}$ for any given ϕ, and $\Phi_{\tilde{t}}[\phi]$ is continuous in ϕ uniformly for $\tilde{t}$ in any bounded interval. This combined with our results show that (1.3) is actually a time-periodic nonlocal dispersal model with monotone nonlinearity, and its solution either converges to zero steady state, or converges to a positive 1-periodic solution (corresponding to positive fixed point of (1.6)) as time goes to infinity.

Recently, there are many works on local/nonlocal dispersal population model with age structure (cf. [32, 33, 45, 51, 54, 56]), exploring the spreading speed of the population and the existence, asymptotic behaviors and uniqueness of traveling waves of these models. However, these works have little discussion about the effect of maturation delay on the dynamics of the population. In Section 4, we performed some numerical simulations on the effect of maturation delay on the spatial spread of system (1.3). Figures 3 and 5 show that the peaking value of the population density $u_m(x,t)$ will converge to a positive constant eventually, which is negatively related to the maturation delay τ. This can be interpreted as that the longer the maturity time is, the lower the survival rate of juvenile to adult. Figures 4 and 6 show that the maximum value of the adult population density $N_m(x)$ at the end of each year will converge to a positive constant eventually, which is positively related to the maturation delay τ. This can be interpreted as that the shorter the interval between the pulse time and the end of the year, the less the reduction of adult population density due to dispersal and mortality.

We remark that the nonlinear terms g, f_M, f_I used in (3.2) are of monostable type. Another frequently encountered type of nonlinearities is the so-called bistable nonlinearity which may account for the Allee Effect—a phenomenon in which there is a positive correlation between the population unit growth rate and the population density when the population density is very low. However, at a very low density, the species will be endangered and may go to extinction [1, 27]. Recently, Wang and Wang [49] and Wang, Salmaniw, and Wang [50] studied the persistence and propagation dynamics of a discrete-time map and PDE hybrid model with the mortality function satisfying strong Allee effect and the birth function satisfying strong Allee effect, respectively. The nonlinearly bistable assumptions employed in [49, 50] are different from our nonmonotone assumption **(H6)**. This motivates us to incorporate the Allee Effect into our model in this paper. The resulting model system should demonstrate some essential difference(s), and we leave the analysis of such a model system as a future research project.

To conclude this section and the paper, we would like to point out that in our model and the model in [3], the model parameters are all assumed to be spatially homogeneous. However, spatial heterogeneity exists ubiquitously in the real world. Mathematically incorporating spatial heterogeneity brings in some big challenges, making analysis much more difficult. With respect to this aspect, our attention was just brought to a most recent paper [29] by the authors where they incorporated spatially periodic heterogeneity into the model in [3] and analyzed the resulting model system. Other types of heterogeneity, particularly those caused by climate change or industrialization or human activities are of more significant reality and importance, and thus, are surely worth investigating for their impacts on the population dynamics.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that no data are used for the research described in this article.

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Appendix A: Derivation of $\mathcal{G}(\alpha, x)$

The derivation of $\mathcal{G}(\alpha, x)$ comes from [2, Section 1.1.1], [54, Section 2], and [32, Section 3]. In this section, we consider the following linear equation:

$$\begin{cases} v_t = D_I\left[\int_{\mathbb{R}} J(x-y)v(y,t)dy - v\right] - d_I v, & x \in \mathbb{R}, t \in (0,1], \\ v(x,0) = v_0(x), & x \in \mathbb{R}, \end{cases} \tag{A.1}$$

where D_I, d_I are positive constants, J satisfies assumption **(J3)**, and v_0 is a nonnegative, continuous, and bounded function on $\mathbb{R}$.

Given any function g defined on $\mathbb{R}$, we define the Fourier transform $\mathcal{F}[g] = \hat{g}$ and inverse Fourier transform $\mathcal{F}^{-1}[\hat{g}] = g$ as

$$\hat{g}(w) = \int_{\mathbb{R}} e^{iwx} g(x)dx, \quad g(x) = \frac{1}{2\pi}\int_{\mathbb{R}} e^{-iwx}\hat{g}(w)dw.$$

The following three lemmas show some properties of the Fourier transform $\mathcal{F}[g] = \hat{g}$.

Lemma A.1 [58, p. 111]. *Assume that $g(x)$ and $g'(x)$ are both absolutely integrable on $\mathbb{R}$, then*

$$\mathcal{F}[g'](w) = (iw)\mathcal{F}[g](w).$$

Moreover, it holds that

$$\mathcal{F}[g^{(n)}](w) = (iw)^n \mathcal{F}[g](w), \quad n \geq 1 \text{ is an integer.}$$

Lemma A.2 [17, p. 20]. *Suppose that $f, g \in L^1(\mathbb{R})$ and let*

$$(f * g)(x) := \int_{\mathbb{R}} f(x-y)g(y)dy.$$

Then, $\mathcal{F}[f * g] = \mathcal{F}[f] \times \mathcal{F}[g]$.

Lemma A.3 [17, p. 27]. *Suppose that $\varphi(z)$ is analytic for $|z| < \varepsilon$ with $\varepsilon > 0$, and $\varphi(0) = 0$. If $h \in L^1(\mathbb{R})$ such that $\|h\|_{L^1} < \varepsilon$, then $\varphi(\hat{h})$ is a Fourier transform. This is to say, there is $H \in L^1(\mathbb{R})$ such that $\varphi(\hat{h}(w)) = \hat{H}(w)$ ($w \in \mathbb{R}$).*

Let $\hat{v}(w,t)$ and $\hat{J}(w)$ be the Fourier transforms of $v(x,t)$ and $J(x)$, respectively. Then, by Lemma A.2, we obtain that

$$\begin{aligned}\frac{\partial \hat{v}(m,t)}{\partial t} &= \int_{\mathbb{R}} \mathrm{e}^{iwx}\left\{D_I \int_{\mathbb{R}} J(x-y)v(y,t)dy - D_I v(x,t) - d_I v(x,t)\right\}dx \\ &= \left[D_I \hat{J}(w) - D_I - d_I\right]\hat{v}(w,t).\end{aligned}$$

The above equation can be solved as

$$\hat{v}(w,t) = \mathrm{e}^{[D_I \hat{J}(w) - D_I - d_I]t} \int_{\mathbb{R}} \mathrm{e}^{iwy} v_0(y)dy.$$

Then, we can infer from the inverse Fourier transform that

$$\begin{aligned}v(x,t) &= \frac{\mathrm{e}^{-d_I t}}{2\pi} \int_{\mathbb{R}} \mathrm{e}^{-iwx}\left[\mathrm{e}^{D_I[\hat{J}(w)-1]t} \int_{\mathbb{R}} \mathrm{e}^{iwy} v_0(y)dy\right]dw \\ &= \frac{\mathrm{e}^{-d_I t}}{2\pi} \int_{\mathbb{R}} \left[\int_{\mathbb{R}} \mathrm{e}^{D_I[\hat{J}(w)-1]t} \mathrm{e}^{iw(y-x)}dw\right] v_0(y)dy \\ &= \mathrm{e}^{-d_I t} \int_{\mathbb{R}} \mathcal{G}(D_I t, x-y) v_0(y)dy,\end{aligned}$$

where

$$\mathcal{G}(\alpha, x) = \frac{1}{2\pi} \int_{\mathbb{R}} \mathrm{e}^{\alpha(\hat{J}(w)-1)} \mathrm{e}^{-iwx} dw.$$

Clearly, $\mathcal{G}(\alpha, x)$ is the inverse Fourier transform of $g(w) := \mathrm{e}^{\alpha(\hat{J}(w)-1)}$. Here, the existence of $\mathcal{G}(\alpha, x)$ can be obtained from Lemma A.3 (see [32, Section 3] for details).

Under the assumption **(J3)**, some basic properties for $\mathcal{G}(\alpha, x)$ can be derived as follows:

Lemma A.4 [32, Lemma 3.1]. *Assume that J satisfies **(J3)**. Then, we have*

1. *$\int_{\mathbb{R}} \mathcal{G}(\alpha, x)dx = 1$ for $\alpha \geq 0$;*
2. *$\mathcal{G}(\alpha, x) = \delta(x) \geq 0$ on $\mathbb{R}$ for $\alpha = 0$, where $\delta(x)$ is the Dirac-delta function; $\mathcal{G}(\alpha, x) > 0$ on $\mathbb{R}$ for $\alpha > 0$;*
3. *$\hat{J}(w)$ is an even function in w, and hence $\mathcal{G}(\alpha, -x) = \mathcal{G}(\alpha, x)$ for $x \in \mathbb{R}$;*
4. *$\int_{\mathbb{R}} \mathcal{G}(\alpha, x-y)\mathcal{G}(\beta, y-z)dy = \mathcal{G}(\alpha+\beta, x-z)$ for $x, y, z \in \mathbb{R}$ and $\alpha, \beta \geq 0$;*
5. *$\mathcal{G}(\alpha, x) = \frac{e^{-\alpha}}{2\pi} \sum_{k=0}^{\infty} \int_{\mathbb{R}} \frac{\alpha^k [\hat{J}(w)]^k}{k!} e^{-iwx} dw = e^{-\alpha} \sum_{k=0}^{\infty} \frac{\alpha^k}{k!} \mathcal{F}^{-1}[\hat{J}^k](x) = e^{-\alpha} \sum_{k=0}^{\infty} \frac{\alpha^k}{k!} J_k(x)$, where $J_0(x) = \delta(x)$, $J_1(x) = J(x)$, and $J_k(x) = [J * J_{k-1}](x)$ for $k \geq 2$;*
6. *for each $\mu \geq 0$, if $\int_{\mathbb{R}} J(x)e^{\mu x}dx < \infty$, then $\int_{\mathbb{R}} \mathcal{G}(\alpha, x)e^{\mu x}dx < \infty$.*