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Diffusive monotonicity and threshold dynamics of delayed reaction diffusion equations [☆]

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Dedicated to Professor Yuanxun Qin (Y.-S. Chin) on the occasion of his 80th birthday

Abstract

For abstract functional differential equations and reaction–diffusion equations with delay, an exponential ordering is introduced which takes into account the spatial diffusion. The induced monotonicity of the solution semiflows is established and applied to describe the threshold dynamics (extinction or persistence/convergence to positive equilibria) for a nonlocal and delayed reaction–diffusion population model.

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1. Introduction

The purpose of this paper is to introduce a new ordering in the phase space with respect to which some reaction diffusion equations with

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nonlinear and delayed (not necessarily monotone) reaction terms generate monotone (or order-preserving) semiflows. We also use the order-preserving property and some general results of monotone dynamical systems to describe the global dynamics (in particular, threshold dynamics) of a diffusive population model with delay and nonlocal effects.

Reaction diffusion equations with delayed reaction terms and, more generally, abstract functional differential equations, have been widely used to model the evolution of a physical system distributed over a spatial domain [21]. In the celebrated work of Martin and Smith [9,10], the monotonicity of the semiflow generated by an abstract functional differential equation was established and the powerful theory of monotone dynamical systems was applied to obtain some detailed descriptions of the generic dynamics of the semiflow. In order for the semiflow to be order-preserving with respect to the pointwise ordering of the phase space, the aforementioned work requires that the nonlinear reaction term satisfy a certain quasimonotonicity condition which, in the special case of a reaction diffusion equation with delay, requires the reaction term to be monotone and thus limits the applications in some cases. It is therefore nature to ask whether the quasimonotonicity condition in the work of Martin and Smith can be relaxed. This question was addressed in Smith and Thieme [14,15] for the case of ordinary functional differential equations (that is, the spatial diffusion is absent), where they established the monotonicity of the semiflow in a restricted but sufficiently large subspace with a nonstandard exponential ordering.

Extending exponential ordering and its induced monotonicity to abstract functional differential equations and delayed reaction diffusion equations is the main goal of our work here. Such an extension, however, seems to require some new ideas, as the interaction of spatial diffusion and temporal delay requires comparison of solutions at different locations. This will be illustrated by our example in Section 3, where we consider the following nonlocal delayed and diffusive population model proposed in [20]

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} = d\Delta v(t, x) - k(x)v(t, x) + \int_{\Omega} \Gamma(x, y, r)g(y, v(t - r, y)) dy, \\ x \in \Omega, \quad t > 0, \\ Bv(t, x) = 0, \quad x \in \partial\Omega, \quad t > 0, \\ v(t, x) = \phi(t, x), \quad x \in \Omega, \quad t \in [-r, 0], \end{cases} \tag{1.1}$$

where $r \geq 0$ is the average maturation time for the species, $d > 0$ is the diffusion rate, $k(x) > 0$ is the per capita mortality rate of the species at location x , $g(x, v)$ is the recruitment rate function of an adult population (which is usually not monotone in v), B is the Dirichlet or Neumann boundary operator, and Γ is the Green's function associated with $A := d\Delta - k(\cdot)I$ and boundary condition $Bv = 0$. It should be mentioned that

such nonlocal delayed and diffusive models arise very naturally if one carefully models the delay as condensation of the underlying retarding process and takes into account that individuals move during this process (see also [2,17,18]).

The remaining part of this paper is organized as follows. In Section 2, we introduce an exponential ordering in the phase space, give an analytic characterization of such an ordering for points in the phase space with sufficient regularity, and establish the monotonicity and strong order-preserving property for mild solutions of general abstract functional differential equations with a quasi-monotone nonlinearity. In Section 3, we illustrate the exponential ordering and the quasi-monotonicity condition by the model equation (1.1) and we also apply the general theory of monotone dynamical systems to describe the threshold dynamics of the model and give explicit conditions for solutions of (1.1) to converge to either the trivial equilibrium or a positive equilibrium.

2. The exponential ordering

Let (X, P) be an ordered Banach space with $int(P) \neq \emptyset$. For $u, v \in X$, we write $u \geqslant_X v$ if $u - v \in P$; $u >_X v$ if $u - v \in P \setminus \{0\}$; $u \gg_X v$ if $u - v \in int(P)$. Since P is a closed subset of X , the topology and ordering on X are compatible in the sense that if $u_n \geqslant_X v_n$, $u_n \rightarrow u$, $v_n \rightarrow v$, then $u \geqslant_X v$.

Let $A : Dom(A) \rightarrow X$ be the infinitesimal generator of an analytic semigroup $T(t)$ satisfying $T(t)P \subset P$, $\forall t \geqslant 0$. For convenience, we denote $T(t)$ by e^{At} . Let $r \geqslant 0$ be fixed and let $C := C([-r, 0], X)$. For $\mu \geqslant 0$, we define

$$K_\mu = \{ \phi \in C : \phi(s) \geqslant_X 0, \forall s \in [-r, 0], \text{ and} \\ \phi(t) \geqslant_X e^{(A-\mu I)(t-s)} \phi(s), \forall 0 \geqslant t \geqslant s \geqslant -r \}.$$

Then K_μ is a closed cone in C . Let \geqslant_μ be the partial ordering on C induced by K_μ . The meaning of \leqslant_μ and \leqslant_X should be clear.

Lemma 2.1. *Assume that $\phi \in C$ is differentiable on $(-r, 0)$ and $\phi(t) \in Dom(A)$, $\forall t \in (-r, 0)$. Then $\phi \geqslant_\mu 0$ if and only if*

$$\phi(-r) \geqslant_X 0 \text{ and } \frac{d\phi(t)}{dt} - (A - \mu I)\phi(t) \geqslant_X 0, \forall t \in (-r, 0).$$

Proof. Assume that $\phi \geqslant_\mu 0$, i.e., $\phi \in K_\mu$. It then follows that $\phi(-r) \geqslant_X 0$, and for any $t \in (-r, 0)$ and $h > 0$ with $t + h \in [-r, 0]$,

$$\frac{\phi(t+h) - \phi(t)}{h} \geqslant_X \frac{e^{(A-\mu I)h} \phi(t) - \phi(t)}{h}.$$

Since ϕ is differentiable at t and $\phi(t) \in Dom(A)$, letting $h \rightarrow 0^+$ and using the definition of infinitesimal generators (see, e.g., [11]),

we get

$$\frac{d\phi(t)}{dt} = \lim_{h \rightarrow 0^+} \frac{\phi(t+h) - \phi(t)}{h} \geq_X (A - \mu I)\phi(t), \quad \forall t \in (-r, 0).$$

Conversely, assume that $\phi(-r) \geq_X 0$ and $\frac{d\phi(t)}{dt} - (A - \mu I)\phi(t) \geq_X 0$, $\forall t \in (-r, 0)$. Let $t \in (-r, 0]$ be fixed. Clearly, the function $u(s) := e^{(A-\mu I)(t-s)}\phi(s)$ is differentiable for $s \in (-r, t)$. By the property of analytic semigroups (see, e.g., [6,11]) and the positivity of $e^{(A-\mu I)(t-s)} = e^{-\mu(t-s)}e^{A(t-s)}$, we have

$$\begin{aligned} \frac{du(s)}{ds} &= -(A - \mu I)e^{(A-\mu I)(t-s)}\phi(s) + e^{(A-\mu I)(t-s)}\frac{d\phi(s)}{ds} \\ &= -e^{(A-\mu I)(t-s)}(A - \mu I)\phi(s) + e^{(A-\mu I)(t-s)}\frac{d\phi(s)}{ds} \\ &= e^{(A-\mu I)(t-s)}\left(\frac{d\phi(s)}{ds} - (A - \mu I)\phi(s)\right) \geq_X 0. \end{aligned}$$

Thus, we get $\phi(t) - e^{(A-\mu I)(t-s)}\phi(s) = u(t) - u(s) = \int_s^t \frac{du(\tau)}{d\tau} d\tau \geq_X 0$, $\forall s \in [-r, t]$. This, together with $\phi(-r) \geq_X 0$ implies $\phi \in K_\mu$. \square

Let $\sigma > 0$ and $u : [-r, \sigma) \rightarrow X$ be a continuous map. For each $t \in [0, \sigma)$, we define $u_t \in C$ by $u_t(s) = u(t + s)$, $\forall s \in [-r, 0]$. Let D be an open subset of C . Assume that $F : D \rightarrow X$ is continuous and satisfies a Lipschitz condition on each compact subset of D . We consider the abstract functional differential equation

$$\begin{cases} \frac{du(t)}{dt} = Au(t) + F(u_t), & t > 0, \\ u_0 = \phi \in D. \end{cases} \tag{2.1}$$

By the standard theory (see, e.g., [9,21]), for each $\phi \in D$, Eq. (2.1) admits a unique mild solution $u(t, \phi)$ on its maximal interval $[0, \sigma_\phi)$. Moreover, if $\sigma_\phi > r$, then $u(t, \phi)$ is a classical solution to (2.1) for $t \in (r, \sigma_\phi)$. In order to get a monotone solution semiflow of (2.1) with respect to \geq_μ , we will impose the following monotonicity condition on F .

$$(M_\mu) \quad \mu(\psi(0) - \phi(0)) + F(\psi) - F(\phi) \geq_X 0 \quad \text{for } \phi, \psi \in D \text{ with } \phi \leq_\mu \psi.$$

Theorem 2.1. *Let (M_μ) hold. If $\phi \leq_\mu \psi$, then $u_t(\phi) \leq_\mu u_t(\psi)$ for all $t \geq 0$ such that both solutions are defined.*

Proof. Let $v^* \in \text{int}(P)$ be fixed. For any $\varepsilon > 0$, define $F_\varepsilon(\phi) := F(\phi) + \varepsilon v^*$ for $\phi \in D$, and let $u^\varepsilon(t, \psi)$ be the unique mild solution of the following equation:

$$\begin{cases} \frac{du(t)}{dt} = Au(t) + F_\varepsilon(u_t), & t > 0, \\ u_0 = \psi \in D. \end{cases} \tag{2.2}$$

Without loss of generality, we assume that $u(t, \phi)$ and $u^\varepsilon(t, \psi)$ are both defined on $[0, \infty)$ (If not, we replace $[0, \infty)$ by the intersection of their maximal intervals of existence). Let $y^\varepsilon(t) := u^\varepsilon(t, \psi) - u(t, \phi)$ and define

$$P = \{t \in [0, \infty) : y_t^\varepsilon \geq_\mu 0\}.$$

Clearly, P is closed and $0 \in P$. We claim that if $t_0 \in P$, then there exists $\delta_0 > 0$ such that $[t_0, t_0 + \delta_0] \subset P$. Indeed, by the abstract integral forms of Eqs. (2.1) and (2.2), we have

$$\begin{aligned} y^\varepsilon(t) &= e^{(A-\mu I)(t-s)} y^\varepsilon(s) \\ &+ \int_s^t e^{(A-\mu I)(t-\tau)} (F(u_\tau^\varepsilon(\psi)) - F(u_\tau(\phi))) \\ &+ \mu(u^\varepsilon(\tau, \psi) - u(\tau, \phi)) + \varepsilon v^* \, d\tau, \quad t \geq s \geq 0. \end{aligned} \tag{2.3}$$

By the condition $u_{t_0}^\varepsilon(\psi) \geq_\mu u_{t_0}(\phi)$ and assumption (M_μ) , it then follows that

$$(F(u_{t_0}^\varepsilon(\psi)) - F(u_{t_0}(\phi)) + \mu(u^\varepsilon(t, \psi) - u(t, \phi)) + \varepsilon v^*)|_{t=t_0} \geq_X \varepsilon v^* \geq_X 0.$$

Thus, there exists $\delta_0 > 0$ such that

$$F(u_t^\varepsilon(\psi)) - F(u_t(\phi)) + \mu(u^\varepsilon(t, \psi) - u(t, \phi)) + \varepsilon v^* \geq_X 0, \quad \forall t \in [t_0, t_0 + \delta_0].$$

By the integral equation (2.3) and the positivity of the semigroup $e^{(A-\mu I)t}$, we then get

$$y^\varepsilon(t) \geq_X e^{(A-\mu I)(t-s)} y^\varepsilon(s), \quad \forall t_0 \leq s \leq t \leq t_0 + \delta_0,$$

which, together with the definition of (K_μ) , implies that $u_t^\varepsilon(\psi) \geq_\mu u_t(\phi)$, $\forall t \in [t_0, t_0 + \delta_0]$.

Let $P_1 := \{t : [0, t] \subset P\}$. We claim that $\sup P_1 = \infty$. Assume that, by way of contradiction, $t^* = \sup P_1 < \infty$. Then there is a sequence $\{t_n\} \subset P_1 \subset P$ such that $t_n \rightarrow t^*$. Thus the closedness of P implies that $t^* \in P$. By the claim in the previous paragraph, $[t^*, t^* + \delta^*] \subset P$ for some $\delta^* > 0$, and hence $t^* + \delta^* \in P_1$, which contradicts the definition of t^* . It then follows that $[0, \infty) \subset P$, and hence $P = [0, \infty)$.

By a standard argument, we have $\lim_{\varepsilon \rightarrow 0^+} u_t^\varepsilon(\psi) = u_t(\psi)$, $\forall t \geq 0$. Letting $\varepsilon \rightarrow 0^+$ in $y_t^\varepsilon = u_t^\varepsilon(\psi) - u_t(\phi) \geq_\mu 0$, we get $u_t(\psi) - u_t(\phi) \geq_\mu 0$, and hence $u_t(\psi) \geq_\mu u_t(\phi)$, $\forall t \geq 0$. \square

For simplicity, in the rest of this section we assume that for each $\phi \in C$, Eq. (2.1) admits a unique mild solution $u(t, \phi)$ defined on $[0, \infty)$. Then (2.1) generates a semiflow on C by $\Phi(t)(\phi) = u_t(\phi)$, $\phi \in C$. Clearly, condition (M_μ) is sufficient for $\Phi(t) : C \rightarrow C$ to be monotone with respect to \leq_μ in the sense that $\Phi(t)(\phi) \leq_\mu \Phi(t)(\psi)$ whenever $\phi \leq_\mu \psi$ and $t \geq 0$. In some applications of monotone dynamical systems, however, we need a strong order-preserving property (see, e.g., [13]). The semiflow $\Phi(t) : C \rightarrow C$ is said to be strongly order-preserving with respect to \leq_μ if it is monotone and whenever $\phi <_\mu \psi$ there exist open subsets U, V of C with $\phi \in U$ and $\psi \in V$ and $t_0 > 0$ such that

$\Phi(t_0)(U) \leq_{\mu} \Phi(t_0)(V)$. Next we show that the following slightly stronger condition than (M_{μ}) is sufficient for $\Phi(t)$ to be strongly order-preserving.

$$(SM_{\mu}) \quad \mu(\psi(0) - \phi(0)) + F(\psi) - F(\phi) \gg_X 0 \quad \text{for } \phi, \psi \in C \text{ with } \phi \leq_{\mu} \psi \\ \text{and } \phi(s) \leq_X \psi(s), \quad \forall s \in [-r, 0].$$

Theorem 2.2. *Assume that $T(t)(P \setminus \{0\}) \subset \text{int}(P)$, $\forall t > 0$, and (SM_{μ}) holds. Then the solution semiflow $\Phi(t)$ is strongly order-preserving on C with respect to \leq_{μ} .*

Proof. Let $v^* \in \text{int}(P)$ be fixed, and define $\phi^* \in C$ by $\phi^*(t) = e^{(A-\mu I)(t+r)}v^*$, $\forall t \in [-r, 0]$. Then $\phi^*(s) \gg_X 0$, $\forall s \in [-r, 0]$, and Lemma 2.1 implies that $\phi^* \geq_{\mu} 0$. For any $\psi \in C$, the sequence of points $\psi_n = \psi + \frac{1}{n}\phi^*$ in C satisfies $\psi <_{\mu} \psi_{n+1} <_{\mu} \psi_n$, $\forall n \geq 1$, and $\psi_n \rightarrow \psi$ as $n \rightarrow \infty$. By this property and the continuity of F , it is easy to see that (SM_{μ}) implies (M_{μ}) . Then we conclude from Theorem 2.1 that $\Phi(t)$ is monotone on C . Moreover, for each $\phi \in C$, $u(t, \phi) \in \text{Dom}(A)$, $\forall t > r$. For any $\phi <_{\mu} \psi$, the strong positivity of $T(t) = e^{At}$ implies that $\phi(0) <_X \psi(0)$, and hence, in view of $u_t(\phi) \leq_{\mu} u_t(\psi)$, $\forall t \geq 0$, there holds $u(t, \phi) \leq_X u(t, \psi)$ for all $t > 0$. Fix a real number $t_0 > 2r$ and let $\phi^0 <_{\mu} \psi^0$ be given. By condition (SM_{μ}) , the continuity of F and the compactness of $[t_0 - r, t_0]$, it then follows that there is a sufficiently small $\varepsilon_0 > 0$ such that

$$F(u_t(\psi^0)) - F(u_t(\phi^0)) + \mu(u(t, \psi^0) - u(t, \phi^0)) \geq_X \varepsilon_0 v^*, \quad \forall t \in [t_0 - r, t_0].$$

Since $\lim_{(\phi, \psi) \rightarrow (\phi^0, \psi^0)} (u(t_0 - r, \psi) - u(t_0 - r, \phi)) = u(t_0 - r, \psi^0) - u(t_0 - r, \phi^0) \geq_X 0$ and

$$\lim_{(\phi, \psi) \rightarrow (\phi^0, \psi^0)} (F(u_t(\psi)) - F(u_t(\phi)) + \mu(u(t, \psi) - u(t, \phi))) \\ = F(u_t(\psi^0)) - F(u_t(\phi^0)) + \mu(u(t, \psi^0) - u(t, \phi^0)) \text{ uniformly for} \\ t \in [t_0 - r, t_0],$$

there exist open subsets U, V of C with $\phi^0 \in U$ and $\psi^0 \in V$ such that for any $\phi \in U$ and $\psi \in V$, $u(t_0 - r, \psi) - u(t_0 - r, \phi) \geq_X 0$ and

$$\frac{d(u(t, \psi) - u(t, \phi))}{dt} - (A - \mu I)(u(t, \psi) - u(t, \phi)) \\ = F(u_t(\psi)) - F(u_t(\phi)) + \mu(u(t, \psi) - u(t, \phi)) \geq_X 0, \quad \forall t \in [t_0 - r, t_0].$$

Note that $u(t, \phi)$ and $u(t, \psi)$ are both classical solutions for $t > r$. By Lemma 2.1, we then get $u_{t_0}(\psi) - u_{t_0}(\phi) \geq_{\mu} 0$, $\forall \psi \in V, \phi \in U$, and hence $u_{t_0}(U) \leq_{\mu} u_{t_0}(V)$. \square

Remark 2.1. In the case where $X = \mathbb{R}$ and A is the zero operator, \leq_μ reduces to the exponential ordering introduced by Smith and Thieme [14] for scalar nonquasimonotone ordinary delay differential equations.

Remark 2.2. Let (X_i, P_i) , $1 \leq i \leq n$, be ordered Banach spaces with $\text{int}(P_i) \neq \emptyset$, and let $A_i : \text{Dom}(A_i) \rightarrow X_i$ be the infinitesimal generator of an analytic semigroup $T_i(t)$ satisfying $T_i(t)P_i \subset P_i, \forall t \geq 0$. Let $X = \prod_{i=1}^n X_i, P = \prod_{i=1}^n P_i, T(t) = \prod_{i=1}^n T_i(t), A = \prod_{i=1}^n A_i, \text{Dom}(A) = \prod_{i=1}^n \text{Dom}(A_i)$. Then $A : \text{Dom}(A) \rightarrow X$ is the infinitesimal generator of the analytic semigroup $T(t)$ defined on the ordered Banach space (X, P) . Let $B = (b_{ij})$ be an $n \times n$ matrix with $b_{ij} \geq 0, \forall 1 \leq i \neq j \leq n$. Define

$$K_B = \{ \phi \in C : \phi(s) \geq_X 0, \forall s \in [-r, 0], \\ \text{and } \phi(t) \geq_X e^{A(t-s)} e^{B(t-s)} \phi(s), \forall 0 \geq t \geq s \geq -r \}.$$

Then K_B is a closed cone in C and induces a partial order \geq_B on C . By an argument similar to that in Theorem 2.1, we can prove that the solution semiflow of (2.1) is monotone with respect to \leq_B under the following monotonicity condition:

$$(M_B) \quad F(\psi) - F(\phi) \geq_X B(\psi(0) - \phi(0)) \\ \text{for } \phi, \psi \in D \text{ with } \phi \leq_B \psi.$$

Clearly, in the case where $n = 1$ and $B = -\mu, \geq_B$ reduces to \geq_μ . Replacing $-\mu$ with B in (SM_μ) , we get a stronger condition (SM_B) . By a similar argument as in Theorem 2.2, we should be able to prove that the solution semiflow of (2.1) is strongly order-preserving with respect to \leq_B under (SM_B) and an additional irreducibility assumption. For the details in a special case where $X = \mathbb{R}^n$ and $A = 0$, we refer to [15].

3. A nonlocal and delayed reaction–diffusion model

In this section, we illustrate how the exponential ordering and the theory of monotone dynamical systems can be applied to nonlocal and delayed reaction–diffusion models in population dynamics.

Consider the growth of a single species with immature and mature stage structure. For simplicity, we assume that $r \geq 0$ is the average maturation time for the species, and that both matured and immatured populations have the same random diffusive rate $d > 0$ and the per capita mortality rate $k(x) > 0$ at location x . Recently, Thieme and Zhao [20] proposed and analysed a nonlocal delayed and diffusive predator–prey model. By replacing the biomass gain rate function $f(x, u, v)$ in the predator equation (1.4) of [20] with the birth rate function $g(x, v)$ of the matured population, we then get a nonlocal and diffusive model of the matured population

growth in a habitat Ω

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} = d\Delta v(t, x) - k(x)v(t, x) + \int_{\Omega} \Gamma(x, y, r)g(y, v(t - r, y)) dy, \\ x \in \Omega, \quad t > 0, \\ Bv(t, x) = 0, \quad x \in \partial\Omega, \quad t > 0, \\ v(t, x) = \phi(t, x) \geq 0, \quad x \in \Omega, \quad t \in [-r, 0], \end{cases} \tag{3.1}$$

where Ω is a bounded and open subset of \mathbb{R}^N with $\partial\Omega \in C^{2+\theta}$ for a real number $\theta > 0$, Δ denotes the Laplacian operator on \mathbb{R}^N , either $Bv = v$ or $Bv = \frac{\partial v}{\partial n} + \alpha v$ for some nonnegative function $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $\frac{\partial}{\partial n}$ denotes the differentiation in the direction of the outward normal n to $\partial\Omega$, Γ is the Green’s function associated with $A := d\Delta - k(\cdot)I$ and boundary condition $Bv = 0$, and ϕ is a given function to be specified later. Such a model equation can also be derived from the structured models (a hyperbolic partial differential equation) by integration along characteristics (see [17,18]).

Let $p \in (N, \infty)$ be fixed. For each $\beta \in (1/2 + N/(2p), 1)$, let X_{β} be the fractional power space of $L^p(\Omega)$ with respect to $(-A, B)$ (see, e.g., [6]). Then X_{β} is an ordered Banach space with the cone X_{β}^+ consisting of all nonnegative functions in X_{β} , and X_{β}^+ has nonempty interior $int(X_{\beta}^+)$. Moreover, $X_{\beta} \subset C^{1+\nu}(\bar{\Omega})$ with continuous inclusion for $\nu \in [0, 2\beta - 1 - N/p)$. We denote the norm in X_{β} by $\|\cdot\|_{\beta}$. It is well-known that A generates an analytic semigroup $T(t)$ on $L^p(\Omega)$. Moreover, the standard parabolic maximum principle implies that the semigroup $T(t) : X_{\beta} \rightarrow X_{\beta}$ is strongly positive, that is, $T(t)(X_{\beta}^+) \setminus \{0\} \subset int(X_{\beta}^+)$, $\forall t > 0$. Let $C := C([-r, 0], X_{\beta})$ and $C^+ := C([-r, 0], X_{\beta}^+)$. Then model (3.1) can be written as the following abstract functional differential equation:

$$\begin{cases} \frac{dv(t)}{dt} = Av(t) + T(r)g(\cdot, v(t - r)), \quad t > 0, \\ v_0 = \phi \in C^+. \end{cases} \tag{3.2}$$

We further assume that $k(\cdot)$ is a positive Hölder continuous function on $\bar{\Omega}$ and $g \in C^1(\bar{\Omega} \times \mathbb{R}^+, \mathbb{R}^+)$ satisfies the following condition:

- (G) $g(\cdot, 0) \equiv 0$, $\partial_v g(x, 0) > 0$, $\forall x \in \Omega$, g is bounded on $\bar{\Omega} \times \mathbb{R}^+$, and for each $x \in \Omega$, $g(x, \cdot) : \mathbb{R}^+ \rightarrow \mathbb{R}^+$ is strictly sublinear in the sense that $g(x, \alpha v) > \alpha g(x, v)$, $\forall \alpha \in (0, 1)$, $v > 0$.

Using a similar argument as in [13, Theorem 7.6.1], we can show that the

nonlocal elliptic eigenvalue problem

$$\begin{cases} \lambda w(x) = d\Delta w - k(x)w(x) + \int_{\Omega} \Gamma(x, y, r) \partial_v g(y, 0) w(y) dy, & x \in \Omega, \\ Bw = 0, & x \in \partial\Omega \end{cases} \tag{3.3}$$

has a principal eigenvalue, which is denoted by $\lambda_0(d, r, \partial_v g(\cdot, 0))$.

For any $\phi \in C^+$, let $v(t, \phi)$ denote the solution of (3.1). Define $k_0 := \min\{k(x) : x \in \bar{\Omega}\}$, and

$$\begin{aligned} b(r) &:= \sup \left\{ \int_{\Omega} \Gamma(x, y, r) g(y, \varphi(y)) dy : x \in \bar{\Omega}, \varphi \in X_{\beta}^+ \right\}, & M(r) &:= \frac{b(r)}{k_0}, \\ L(r) &:= \min \{ \partial_v g(x, v) : x \in \bar{\Omega}, v \in [0, M(r)] \}. \end{aligned}$$

Then we have the following threshold dynamics for model system (3.1): if the zero solution of (3.1) is linearly stable, then the species goes to extinction; if it is linearly unstable, then the species is uniformly persistent.

Theorem 3.1. *Let $v^* \in \text{int}(X_{\beta})$ be fixed and let (G) hold.*

- (1) *If $\lambda_0(d, r, \partial_v g(\cdot, 0)) < 0$, then $\lim_{t \rightarrow \infty} \|v(t, \phi)\|_{\beta} = 0$ for every $\phi \in C^+$;*
- (2) *If $\lambda_0(d, r, \partial_v g(\cdot, 0)) > 0$, then (3.1) admits at least one steady-state solution φ^* with $\varphi^*(x) > 0, \forall x \in \Omega$, and there exists a $\delta > 0$ such that for every $\phi \in C^+$ with $\phi(0, \cdot) \not\equiv 0$, there is $t_0 = t_0(\phi) > 0$ such that $v(t, \phi) \geq \delta v^*(x), \forall x \in \bar{\Omega}, t \geq t_0$.*

Proof. Define $F : C^+ \rightarrow X_{\beta}$ by $F(\phi) = T(r)g(\cdot, \phi(-r)), \forall \phi \in C^+$. Then Eq. (3.1) can be written as the following abstract functional differential equation:

$$\begin{cases} \frac{dv(t)}{dt} = Av(t) + F(v_t), & t > 0, \\ v_0 = \phi \in C^+. \end{cases} \tag{3.4}$$

Since $T(t) : X_{\beta} \rightarrow X_{\beta}$ is strongly positive, we have

$$\lim_{h \rightarrow 0^+} \frac{1}{h} \text{dist}(\phi(0) + hF(\phi), X_{\beta}^+) = 0, \quad \forall \phi \in C^+.$$

By Martin and Smith [9, Proposition 3 and Remark 2.4] and using a similar argument in the case of Dirichlet boundary condition (see also [9, Remark 1.10]), we conclude that for every $\phi \in C^+$, (3.1) admits a unique noncontinuable mild solution $v(t, \phi)$ satisfying $v_0 = \phi$ and $v(t, \phi) \in X_{\beta}^+$ for any t in its maximal interval of existence $[0, \sigma_{\phi})$. Thus $v(t, \phi)(x)$ satisfies the following parabolic inequality:

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} \leq d\Delta v(t, x) - k_0 v(t, x) + b(r), & x \in \Omega, t \in (0, \sigma_{\phi}), \\ Bv(t, x) = 0, & x \in \partial\Omega, t \in (0, \sigma_{\phi}). \end{cases} \tag{3.5}$$

Let $u(t)$ be the unique solution of the ordinary differential equation $\frac{du(t)}{dt} = -k_0u(t) + b(r)$ satisfying $u(0) = \max_{x \in \bar{\Omega}} \phi(0)(x)$. Using the standard parabolic comparison theorem, we then get

$$v(t, \phi)(x) \leq u(t) = \left(\max_{x \in \bar{\Omega}} \phi(0)(x) - M(r) \right) e^{-k_0 t} + M(r), \quad \forall x \in \Omega, \forall t \in (0, \sigma_\phi). \tag{3.6}$$

Thus $\sigma_\phi = \infty$, $\forall \phi \in C^+$, and (3.1) defines a semiflow $\Phi(t) : C^+ \rightarrow C^+$ by $\Phi(t)\phi = v_t(\phi)$. By inequality (3.6) and the properties of the fractional power space X_β , it follows that $\Phi(t) : C^+ \rightarrow C^+$ is point dissipative. Moreover, $\Phi(t) : C^+ \rightarrow C^+$ is compact for each $t > r$ (see [21, Theorem 2.2.6]). Then $\Phi(t)$ admits a global compact attractor on C^+ (see [4, Theorem 3.4.8]).

It is easy to see that $g(x, v) \leq \partial_v g(x, 0)v$, $\forall x \in \bar{\Omega}, v \geq 0$. Then the comparison theorem for quasimonotone abstract functional differential equations (see [9,10]) implies that

$$v(t, \phi)(x) \leq u(t, \phi)(x), \quad \forall x \in \Omega, t \geq 0,$$

where $u(t, \phi)$ is the unique solution of the following linear, nonlocal and delayed parabolic equation:

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} = d\Delta v(t, x) - k(x)v(t, x) + \int_\Omega \Gamma(x, y, r) \partial_v g(y, 0) v(t-r, y) dy, & x \in \Omega, t > 0, \\ Bv(t, x) = 0, & x \in \partial\Omega, t > 0, \\ v(t, x) = \phi(t, x), & x \in \Omega, t \in [-r, 0]. \end{cases} \tag{3.7}$$

By Thieme and Zhao [20, Theorem 2.2] and a similar argument in the case of Dirichlet boundary condition, the nonlocal elliptic eigenvalue problem

$$\begin{cases} \lambda w(x) = d\Delta w - k(x)w(x) + e^{-\lambda r} \int_\Omega \Gamma(x, y, r) \partial_v g(y, 0) w(y) dy, \\ x \in \Omega, \\ Bw = 0, \quad x \in \partial\Omega \end{cases} \tag{3.8}$$

has a principal eigenvalue $\bar{\lambda}_0(d, r, \partial_v g(\cdot, 0))$, and $\bar{\lambda}_0(d, r, \partial_v g(\cdot, 0))$ has the same sign as $\lambda_0(d, r, \partial_v g(\cdot, 0))$. Then in the case where $\lambda_0(d, r, \partial_v g(\cdot, 0)) < 0$, the properties of principal eigenvalues and linear semigroups imply that $\lim_{t \rightarrow \infty} \|u(t, \phi)\|_\beta = 0$, $\forall \phi \in C$, and hence $\lim_{t \rightarrow \infty} \|v(t, \phi)\|_\beta = 0$, $\forall \phi \in C^+$.

In the case where $\lambda_0(d, r, \partial_v g(\cdot, 0)) > 0$, let $Z_0 = \{\phi \in C^+ : \phi(0, \cdot) \neq 0\}$, $\partial Z_0 := C^+ \setminus Z_0$. Since $g(x, v) \geq 0$, Eq. (3.1) implies that

$$\frac{\partial v(t, x)}{\partial t} \geq d\Delta v(t, x) - k(x)v(t, x), \quad \forall x \in \Omega, t > 0.$$

By the standard parabolic maximum principle, it then follows that $\Phi(t)Z_0 \subset \text{int}(C^+)$, $\forall t > 0$. Let $Z_1 = \{\phi \in \partial Z_0 : \Phi(t)\phi \in \partial Z_0, \forall t \geq 0\}$. Then $\bigcup_{\phi \in Z_1} \omega(\phi) = \{0\}$, where $\omega(\phi)$ denotes the omega limit set of the orbit $\gamma^+(\phi) := \{\Phi(t)\phi, \forall t \geq 0\}$. Clearly, $g(x, v)$ can be written as $g(x, v) = vh(x, v)$

with $h(x, 0) = \partial_v g(x, 0)$. By the condition $\bar{\lambda}_0(d, r, \partial_v g(\cdot, 0)) > 0$ and an argument of contradiction similar to that in the proof of [12, Lemma 3.1], we can prove that $\{0\}$ is a uniform weak repeller for Z_0 , that is, there exists $\delta_0 > 0$ such that $\limsup_{t \rightarrow \infty} \|\Phi(t)\phi\|_\beta \geq \delta_0, \forall \phi \in Z_0$. By Thieme [19, Theorem 4.6], $\Phi(t)$ is uniformly persistent with respect to Z_0 in the sense that there exists an $\eta > 0$ such that $\liminf_{t \rightarrow \infty} \text{dist}(\Phi(t)\phi, \partial Z_0) \geq \eta, \forall \phi \in Z_0$. As $\Phi(t) : C^+ \rightarrow C^+$ is compact for $t > r$, the order persistence in (2) follows from [16, Theorem A.2] with $e = v^* \in \text{int}(C^+)$. It remains to prove the existence of a positive steady state of (3.1). Let $\Phi_0(t) : X_\beta^+ \rightarrow X_\beta^+, t \geq 0$, be the solution semiflow of the following nonlocal reaction–diffusion equation

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = d\Delta u(t, x) - k(x)u(t, x) + \int_\Omega \Gamma(x, y, r)g(y, u(t, y)) dy, \\ x \in \Omega, t > 0, \\ Bu(t, x) = 0, x \in \partial\Omega, t > 0, \\ u(0, x) = \varphi(x), x \in \Omega. \end{cases} \tag{3.9}$$

Since $\frac{\partial u(t, x)}{\partial t} \geq d\Delta u(t, x) - k(x)u(t, x)$, the standard parabolic maximum principle implies that $\Phi_0(t)(X_\beta^+ \setminus \{0\}) \subset \text{int}(X_\beta^+), \forall t > 0$. As proven for $\Phi(t) : C^+ \rightarrow C^+$, it follows that $\Phi_0(t)$ is point dissipative on X_β^+ , compact for each $t > 0$ and uniformly persistent with respect to $X_\beta^+ \setminus \{0\}$. Then by Zhao [22, Theorem 2.4], $\Phi_0(t)$ has an equilibrium $\varphi^* \in X_\beta^+ \setminus \{0\}$, i.e., $\Phi_0(t)\varphi^* = \varphi^*$ for all $t \geq 0$. Fix a $t > 0$, we then get $\varphi^* = \Phi_0(t)\varphi^* \in \text{int}(X_\beta^+)$. \square

As an application of the theory in Section 2, we are able to get sufficient conditions under which the species stabilizes eventually at positive steady states in case (2) of Theorem 3.1.

Theorem 3.2. *Assume that (G) holds and $\lambda_0(d, r, \partial_v g(\cdot, 0)) > 0$.*

- (1) *If $L(r) \geq 0$, then (3.1) admits a unique positive steady state φ^* , and $\lim_{t \rightarrow \infty} \|v(t, \phi) - \varphi^*\|_\beta = 0$ for every $\phi \in C^+$ with $\phi(0, \cdot) \neq 0$.*
- (2) *If $L(r) < 0$ and $r|L(r)| < 1/e$, then there exists an open and dense subset S of C^+ with the property that for every $\phi \in S$ with $\phi(0, \cdot) \neq 0$, there is a positive steady state φ of (3.1) such that $\lim_{t \rightarrow \infty} \|v(t, \phi) - \varphi\|_\beta = 0$.*

Proof. Let $\Phi(t) : C^+ \rightarrow C^+$ be the solution semiflow of (3.1), and $\Phi_0(t) : X_\beta^+ \rightarrow X_\beta^+$ be the solution semiflow of (3.9). Define

$$Y := \{\phi \in C^+ : \phi(s, x) \leq M(r), \forall s \in [-r, 0], x \in \Omega\}$$

and

$$Y_0 := \{\phi \in X_\beta^+ : \phi(x) \leq M(r), \forall x \in \Omega\}.$$

Then inequality (3.6) implies that every omega limit set $\omega(\phi)$ of $\Phi(t)$ is contained in Y , and Y is positively invariant for $\Phi(t)$. In particular, every nonnegative steady state φ of (3.1) is contained in Y_0 .

In the case where $L(r) \geq 0$, [9, Corollary 5] implies that $\Phi(t) : Y \rightarrow Y$ is a monotone semiflow with respect to the pointwise ordering of C induced by C^+ . We further claim that (3.1) admits at most one positive steady state. Indeed, it suffices to prove that the semiflow $\Phi_0(t)$ has at most one positive equilibrium in Y_0 . By Martin and Smith [9, Corollary 5] with $\tau = 0$, it then follows that $\Phi_0(t) : Y_0 \rightarrow Y_0$ is a monotone semiflow with respect to the pointwise ordering of X_β induced by X_β^+ . Moreover, for any $\varphi_1, \varphi_2 \in Y_0$ with $\varphi_1 - \varphi_2 \in X_\beta^+ \setminus \{0\}$, $w(t) := \Phi_0(t)\varphi_1 - \Phi_0(t)\varphi_2$ satisfies

$$\frac{\partial w(t, x)}{\partial t} \geq d\Delta w(t, x) - k(x)w(t, x), \quad \forall x \in \Omega, t > 0.$$

Then the standard parabolic maximum principle implies that $w(t) \in \text{int}(X_\beta^+)$, $\forall t > 0$, that is, $\Phi_0(t) : Y_0 \rightarrow Y_0$ is strongly monotone. By the strict sublinearity of g , it easily follows that for each $t > 0$, $\Phi_0(t) : Y_0 \rightarrow Y_0$ is strictly sublinear (see, e.g., [23]). Now fix a real number $t_0 > 0$, then [23, Lemma 1] implies that the map $\Phi_0(t_0)$ has at most one positive fixed point in Y_0 , and hence, the semiflow $\Phi_0(t)$ has at most one positive equilibrium in Y_0 . As shown in Theorem 3.1, $\Phi(t) : C^+ \rightarrow C^+$ is compact for each $t > r$, admits a global compact attractor in C^+ , and is uniformly persistent with respect to Z_0 . By Hale and Waltman [5, Theorem 3.2], $\Phi(t) : Y \cap Z_0 \rightarrow Y \cap Z_0$ has a global attractor A_0 . Clearly, Theorem 3.1 (2), together with the uniqueness of positive steady state, implies that A_0 contains only one equilibrium φ^* . By Hirsch [7, Theorem 3.3], it then follows that φ^* attracts every point in $Y \cap Z_0$. Consequently, every orbit in Y converges to either the trivial equilibrium or the positive equilibrium φ^* , and hence, together with Theorem 3.1 (2), equilibria 0 and φ^* are also two isolated invariant sets in Y , respectively, and there is no cyclic chain of equilibria. By Hirsch et al. [8, Theorem 3.2 and Remark 4.6], every compact internally chain transitive sets of $\Phi(t) : Y \rightarrow Y$ is an equilibrium. Let $\phi \in C^+$ be given. As mentioned above, there holds $\omega(\phi) \subset Y$. Since every compact omega limit set is an internally chain transitive set (see [8, Lemma 2.1']), $\omega(\phi)$ is an equilibrium. If $\phi \in C^+$ with $\phi(0, \cdot) \neq 0$, we then get $\omega(\phi) = \varphi^*$ in view of Theorem 3.1 (2).

In the case where $L(r) < 0$ and $r|L(r)| < 1/e$, we define $f(\alpha) := \alpha + L(r)e^{r\alpha}$, $\forall \alpha \in [0, \infty)$. It then follows that $f(0) < 0$ and $f''(\alpha) \leq 0$, $\forall \alpha \in [0, \infty)$. If $r = 0$, then $f(\alpha) > 0$ for all $\alpha > |L(0)|$. If $0 < r|L(r)| < \frac{1}{e}$, then $f(\alpha)$ reaches its maximum value at $\alpha_0 = -\frac{1}{r} \ln(r|L(r)|) > 0$ and $f(\alpha_0) > 0$. Consequently, we can fix a real number $\mu > 0$ such that $f(\mu) = \mu + L(r)e^{r\mu} > 0$. Let $F : C^+ \rightarrow X_\beta$ be defined as in the proof of Theorem 3.1, and let K_μ be defined as in Section 1 with $X = X_\beta$, $P = X_\beta^+$ and $A = d\Delta - k(\cdot)I$. By the definition of $L(r)$,

there holds

$$g(x, v_2) - g(x, v_1) \geq L(r)(v_2 - v_1), \quad \forall x \in \bar{\Omega}, \quad 0 \leq v_1 \leq v_2 \leq M(r).$$

Assume that $\phi, \psi \in Y$ satisfy $\phi \leq_\mu \psi$ and $\phi(s) \ll_{X_\beta} \psi(s), \forall s \in [-r, 0]$. Clearly, $\psi - \phi \in K_\mu$ implies that

$$\begin{aligned} \psi(0) - \phi(0) &\geq_{X_\beta} e^{(A-\mu)r}(\psi(-r) - \phi(-r)) \\ &= T(r)e^{-\mu r}(\psi(-r) - \phi(-r)). \end{aligned} \tag{3.10}$$

It then follows that

$$\begin{aligned} &\mu(\psi(0) - \phi(0)) + F(\psi) - F(\phi) \\ &\geq_{X_\beta} \mu(\psi(0) - \phi(0)) + L(r)T(r)(\psi(-r) - \phi(-r)) \\ &\geq_{X_\beta} (\mu + L(r)e^{\mu r})e^{-\mu r}T(r)(\psi(-r) - \phi(-r)) \gg_{X_\beta} 0. \end{aligned} \tag{3.11}$$

Thus condition (SM_μ) holds for $F : Y \rightarrow X_\beta$, and hence, by Theorem 2.2, $\Phi(t) : Y \rightarrow Y$ is strongly order-preserving with respect to \leq_μ . Let $\phi^* \geq_\mu 0$ be defined as in the proof of Theorem 2.2. Recall that $\phi^*(s) \gg_{X_\beta} 0, \forall s \in [-r, 0]$. Then for any $\psi \in Y$, either the sequence of points $\psi + \frac{1}{n}\phi^*$ or $\psi - \frac{1}{n}\phi^*$ is eventually contained in Y and approaches ψ as $n \rightarrow \infty$, and hence, each point of Y can be approximated either from above or from below in Y . Clearly, $\Phi(t) : Y \rightarrow Y$ has a global compact attractor in Y . Note that the cone K_μ has empty interior in C . Fix a $\psi(\cdot) \in \text{int}(X_\beta^+)$ such that $d\Delta\psi - k(x)\psi \leq 0, \forall x \in \Omega$, and $B\psi = 0, \forall x \in \partial\Omega$ (e.g., taking $\psi(x)$ as a positive steady state of (3.1)). Then Lemma 2.1 implies that $\psi \in K_\mu$. Define

$$C_\psi = \{\phi \in C : \text{there exists } \beta \geq 0 \text{ such that } -\beta\psi \leq_\mu \phi \leq_\mu \beta\psi\}$$

and

$$\|\phi\|_\psi = \inf\{\beta \geq 0 : -\beta\psi \leq_\mu \phi \leq_\mu \beta\psi\}, \quad \forall \phi \in C_\psi.$$

Then $(C_\psi, \|\cdot\|_\psi)$ is a Banach space and $C_\psi^+ := C_\psi \cap K_\mu$ is a closed cone in C_ψ with nonempty interior (see [1]). Using the smoothing property of the semiflow $\Phi(t)$ on C^+ and the fundamental theory of abstract functional differential equations, we can show that for each $t > r$, $\Phi(t)Y \subset Y \cap C_\psi, \Phi(t) : Y \rightarrow Y \cap C_\psi$ is continuous, $\Phi(t)\phi_2 - \Phi(t)\phi_1 \in \text{int}(C_\psi^+)$ for any $\phi_1, \phi_2 \in Y$ with $\phi_2 >_\mu \phi_1$, and for each nonnegative equilibrium φ of $\Phi(t)$, the Frechet derivative at φ of $\Phi(t) : Y \cap C_\psi \rightarrow Y \cap C_\psi$ exists and is compact and strongly positive on C_ψ^+ (see, e.g., [15]). By Smith [13, Theorem 2.4.7 and Remark 2.4.1], it then follows that there is an open and dense subset U of Y such that every orbit of $\Phi(t)$ starting from U converges to an equilibrium in Y . Clearly, the condition that $L(r) < 0$ and $r|L(r)| < 1/e$ still holds under small perturbations of $b(r)$. It then follows that there is a small $\varepsilon > 0$ such that the generic convergence also holds in

$$Y_\varepsilon := \{\phi \in C^+ : \phi(s, x) \leq M_\varepsilon(r), \forall s \in [-r, 0], x \in \Omega\},$$

where $M_\varepsilon(r) := b_\varepsilon(r)/k_0 = M(r) + \varepsilon/k_0$ and $b_\varepsilon(r) := b(r) + \varepsilon$. By inequality (3.6), every orbit of $\Phi(t)$ in C^+ eventually enters into Y_ε . Now conclusion (2) follows from the generic convergence in Y_ε and Theorem 3.1 (2). \square

Example 3.1. Consider model (3.1) with $k(x) = k$, $g(x, v) = g(v) := pve^{-qv}$, where k, p and q are all positive constants. The function $g(v)$ was introduced in [3]. Let $T_0(t)$ be the analytic semigroup generated by $d\Delta$ with boundary condition $Bv = 0$. Clearly, $T(t) = e^{-kt}T_0(t)$ and condition (G) is satisfied. A direct computation shows that $g'(v) = pe^{-qv}(1 - qv)$, $g''(v) = -pqe^{-qv}(2 - qv)$, and $g(v)$ reaches its maximum value $g(1/q) = \frac{p}{q}e^{-1}$.

In the case of Neumann boundary condition $Bv = \frac{\partial v}{\partial n} = 0$, it easily follows that

$$\lambda_0(d, r, g'(0)) = pe^{-kr} - k, \quad b(r) = \frac{p}{q}e^{-(1+kr)}, \quad M(r) = \frac{p}{kq}e^{-(1+kr)}$$

and

$$L(r) = g'(M(r)) = p\left(1 - \frac{p}{k}e^{-(1+kr)}\right)\exp\left(-\frac{p}{k}e^{-(1+kr)}\right) \quad \text{if } M(r) \leq 2/q,$$

$$L(r) = g'(2/q) = -pe^{-2} \quad \text{if } M(r) > 2/q.$$

Clearly, if $\lambda_0(d, r, g'(0)) > 0$, the model has a positive constant steady state $\frac{1}{q}\ln\left(\frac{p}{ke^{d\pi r}}\right)$.

In the case of Dirichlet boundary condition $Bv = v = 0$, $\lambda_0(d, r, g'(0))$, $b(r)$ and $L(r)$ depend nontrivially on the diffusion rate d and the domain Ω , and any positive steady state is spatially inhomogeneous. It is possible to get the explicit expressions or estimates for these quantities in some special cases of the dimensions and shapes of Ω . For example, let $\Omega = \prod_{i=1}^N(0, \pi)$, and define $w_0(x) := \prod_{i=1}^N \sin x_i$, $\forall x = (x_1, \dots, x_N) \in \Omega$. It is easy to verify that $T_0(t)w_0 = e^{-Ndt}w_0$, $\forall t \geq 0$, and that $w_0(x)$ is a positive solution of the nonlocal elliptic eigenvalue problem (3.3) with $k(x) = k$, $g(x, v) = g(v)$ and $\lambda = g'(0)e^{-(Nd+k)r} - (Nd + k)$. It then follows that $\lambda_0(d, r, g'(0)) = g'(0)e^{-(Nd+k)r} - (Nd + k)$.

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