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A reaction-diffusion model with spatially inhomogeneous delays

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Abstract Motivated by population growth in a heterogeneous environment, this manuscript builds a reaction-diffusion model with spatially dependent parameters. In particular, a term for spatially uneven maturation durations is included in the model, which puts the current investigation among the very few studies on reaction-diffusion systems with spatially dependent delays. Rigorous analysis is performed, including the well-posedness of the model, the basic reproduction ratio formulation and long-term behavior of solutions. Under mild assumptions on model parameters, extinction of the species is predicted when the basic reproduction ratio is less than one. When the birth rate is an increasing function and the basic reproduction ratio is greater than one, uniqueness and global attractivity of a positive equilibrium can be established with the help of a novel functional phase space. Permanence of the species is shown when the birth function is in a unimodal form and the basic reproduction ratio is greater than one. The synthesized approach proposed here is applicable to broader contexts of studies on the impact of spatial heterogeneity on population dynamics, in particular, when the delayed feedbacks are involved and the response time is spatially varying.

Keywords Reaction-diffusion model \cdot Spatially inhomogeneous delay \cdot Stage-structured model \cdot Population dynamics

Mathematics Subject Classification (2020) 35K57 · 37N25 · 92D25

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1 Introduction

The effects of spatial heterogeneity in population dynamics have been widely evaluated through theoretical models, including those for single population growth [2], for interacting species [15], for disease transmission [5,14], and for evolution [10]. In most single population growth models, the spatial heterogeneity is characterized by spatially-dependent reproduction, survival, or/and movement rates of individuals. As a matter of fact, not only the magnitudes of feedbacks in these vital rates are spatially dependent, but also the response time of feedbacks may be spatially varying. Following are typical motivative scenarios to incorporate spatially varying feedback delays in a model system. The first example is the development of Collembola, with its egg development and hatching being affected by environmental pollution, such as copper lead, zinc [31] and other toxic substances [9]. However, these toxic substances are not evenly distributed in soil [9], which induces a non-uniform development time in the spatial scale. Another example is the spatially varying maturation duration in tick development across different spatial patches driven by patch-specific environmental conditions [29]. In addition to the species growth, a further promising direction of models with spatially-dependent delay is to evaluate the impact of regional variations of health care resources on local disease outbreaks. Significant regional variations have been observed during the viral disease outbreaks [23], including current COVID-19 outbreaks [1]. One important factor contributing to the substantial local variations in COVID-19 timing and severity is the spatial heterogeneity on hospital load [28], which in turn determines the delays in diagnosis and treatment [24]. Therefore, understanding the role of spatial heterogeneity in diagnosis and treatment delay on disease outbreak requires incorporating a spatially varying delay in epidemiological models.

This paper is going to formulate a reaction-diffusion model with spatiallyvarying delay in the context of species dynamics, which represents the spatially dependent exogenous feedbacks on the maturation process of individuals. Although spatial variations on the time taken in the feedback process have been widely observed, surprisingly few investigations have been performed on the dynamics of reaction diffusion models with spatially inhomogeneous delays. Linear stability analysis was performed by Schley and Gourley [25] for a reaction diffusion equation with a simple case of spatially inhomogeneous delay in the form of a step function of spatial coordinates. Spatially-varying delays were incorporated in a distributed actuation scheme with the consideration of uncertainty in the input control delay that may vary among different spatial regions [11]. It is important and interesting to propose a synthesized approach to (i) formulating a model which appropriately accounts the spatially inhomogeneous delay in the context of stage-structured population growth; and (ii) proposing rigorous theoretical framework to investigate the dynamics of the resultant model. These two aspects will be addressed in the next two sections. Hope this study provides a conceptual framework for further extensions when spatially-dependent delays should be involved.

2 Model formulation with spatially varying delays

To make things simple, the model will be formulated with the following biological considerations: (a) there are two stages, a non-reproductive immature stage and a reproductive adult stage, with respective densities I(t, x) and A(t, x), at time t and location x in a spatial region $\Omega \subseteq \mathbb{R}^p$ with smooth boundary; and (b) immature individuals have limited capability to move around, and their development duration $\tau(x)$ is dependent on the spatial location x. Assume w(t, a, x) (resp. $v(t, \eta, x)$) represents the density of immature (resp. adult) individuals of stage specific age a (resp. η) at time t and location $x \in \Omega$. Please note that here we are using the stage age, which measures the time of an individual remaining in a particular stage [16], instead of chronological age, to characterize each individual (please see Remark 1 for further details). Then the densities of immature and adult individuals I(t, x) and A(t, x) at location x can be represented as

$$I(t,x) = \int_0^{\tau(x)} w(t,a,x) da \quad \text{and} \quad A(t,x) = \int_0^\infty v(t,\eta,x) d\eta.$$
(1)

It becomes pivotal to describe the evolution of w(t, a, x) and $v(t, \eta, x)$, which can be achieved by the physiologically structured modeling frameworks [3,4, 8,12,20,22,30]. Assume the recruitment rate at time t and location x is a function of the adult population density, that is

$$w(t, 0, x) = b(x, A(t, x)).$$

The flow-in rate to the adult stage v(t, 0, x) is exactly the maturation rate at time t and location x, that is

$$v(t,0,x) = w(t,\tau(x),x).$$

Assume that all individuals are confined to the region $\Omega \subseteq \mathbb{R}^p$ for all times, and therefore the Neumann boundary condition is imposed on the boundary

$$\frac{\partial w(t,a,x)}{\partial \nu} = \frac{\partial v(t,\eta,x)}{\partial \nu} = 0, \; \forall t > 0, \; x \in \partial \Omega, \; a > 0, \; \eta > 0$$

where $\partial \nu$ denotes the differentiation along the outward normal ν to $\partial \Omega$. Following the diffusive McKendrick-von Foerster equation for age structured population growth [4], we have

$$\begin{pmatrix} \frac{\partial}{\partial t} + \frac{\partial}{\partial a} \end{pmatrix} w(t, a, x) = -\mu_I(x)w(t, a, x), \qquad 0 < a \le \tau(x),$$

$$\begin{pmatrix} \frac{\partial}{\partial t} + \frac{\partial}{\partial \eta} \end{pmatrix} v(t, \eta, x) = D_A(x)\Delta v(t, \eta, x) - (\mu_A(x) + g(x, A(t, x))v(t, \eta, x), \ \eta > 0,$$

$$(2)$$

where Δ is the Laplace operator with respect to $x \in \Omega$; $D_A(x)$ is the diffusion coefficient; $\mu_I(x)$ and $\mu_A(x)$ are the natural death rates of immature and adult individuals while $g(x, \cdot)$ represents the density-dependent death rate of adults.

Differentiating $A(t,x)=\int_0^\infty v(t,\eta,x)d\eta$ with respect to t, the growth law in (2) gives

$$\frac{\partial A(t,x)}{\partial t} = D_A(x)\Delta A(t,x) - (\mu_A(x) + g(x,A(t,x)))A(t,x) + v(t,0,x) - v(t,\infty,x).$$
(3)

As no individual can live forever, it is natural to assume $v(t, \infty, x) = 0$. Note that $v(t, 0, x) = w(t, \tau(x), x)$ represents the density of newly matured individuals at time t with age $\tau(x)$, which can be determined by the evolution process of $w(t - \tau(x), 0, x)$ after $\tau(x)$ units of time. It is clear that the solution evolution follows the growth law given in (2) for the immature population. Let $\rho(r, a, x) = w(a + r, a, x)$, where $r \ge 0$. Then the integration along characteristics argument induces that

$$\frac{\partial \rho(r, a, x)}{\partial a} = \left[\frac{\partial w(t, a, x)}{\partial t} + \frac{\partial w(t, a, x)}{\partial a}\right]_{t=a+r} = -\mu_I(x)\rho(r, a, x), \qquad (4)$$
$$\rho(r, 0, x) = w(r, 0, x) = b(x, A(r, x)).$$

Regarding r as a parameter and solving equation (4), we obtain

$$\rho(r, a, x) = \exp(-\mu_I(x)a)b(x, A(r, x)).$$
(5)

When $t \ge \tau(x)$, letting $r = t - \tau(x)$ and $a = \tau(x)$ in (5), we have

$$w(t,\tau(x),x) = \rho(t-\tau(x),\tau(x),x) = \exp(-\mu_I(x)\tau(x))b(x,A(t-\tau(x),x)).$$

Substituting $w(t, \tau(x), x)$ into (3), we formulate the following reaction-diffusion equation with spatially inhomogeneous delay when $t \ge \max_{\tau \in \overline{\Omega}} \{\tau(x)\}$:

$$\frac{\partial A(t,x)}{\partial t} = D_A(x)\Delta A(t,x) + \exp(-\mu_I(x)\tau(x))b(x,A(t-\tau(x),x)) - (\mu_A(x) + g(x,A(t,x)))A(t,x).$$
(6)

Before moving to the next section on analyzing the model equation (6), we would like to address a remark on the model formulation with the stage-specific age to characterize the physiological state of an individual.

Remark 1 Please note that the stage-specific age a and η for immature and adult individuals are used in (1), instead of the widely used chronological age. In fact, if η represents the chronological age of an adult individual, then one may possibly rewrite the total adult population density at location y as $A(t,y) = \int_{\tau(y)}^{\infty} w(t,\eta,y) d\eta$ by mistake, although it makes sense in the spatially uniform maturation delay case where $\tau(y)$ is independent of location y. We use the following special case to show that $A(t,y) = \int_{\tau(y)}^{\infty} w(t,\eta,y) d\eta$ is not appropriate when the maturation time $\tau(\cdot)$ is dependent on spatial location. Consider an individual born at time $t - \tau(x) - 0.5$ and at location x with spatially dependent maturation delay $\tau(x) = 1$. This individual matures at time t - 0.5, and is able to move to a different spatial location y. Then at time instant t, this adult individual has chronological age $\eta = \tau(x) + 0.5 =$ 1.5 at location y. However, in this scenario, $\eta \in [0, \tau(y))$, which implies that an individual with chronological age $\eta = 1.5$ at location y should remain in the immature stage, a contradiction. Therefore, $A(t, y) = \int_{\tau(y)}^{\infty} w(t, \eta, y) d\eta$ becomes invalid when the maturation duration is spatially varying and the chronological age is used as the physiological variable of individuals.

3 Theoretical analysis

For notational simplicity, replacing A(t, x), $D_A(x)$, $\mu_I(x)$ and $\mu_A(x)$ by u(t, x), D(x), $\mu(x)$ and d(x), respectively. Then system (6) can be written into

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))b(x,u(t-\tau(x),x)) \\ -d(x)u(t,x) - g(x,u(t,x))u(t,x), \ t > 0, \ x \in \Omega, \\ \frac{\partial u}{\partial \nu} = 0, \ t > 0, \ x \in \partial\Omega. \end{cases}$$
(7)

We assume the following baseline conditions for model parameters:

- (A1) Functions $\tau(x)$, $\mu(x)$, d(x) and D(x) are continuous and positive functions for $x \in \overline{\Omega}$. Functions b(x, u) and g(x, u) are in set $C^1(\overline{\Omega} \times \mathbb{R}^+, \mathbb{R}^+)$.
- (A2) b(x,0) = 0, g(x,0) = 0 and $\frac{\partial b(x,u)}{\partial u}|_{u=0} > 0$ for all $x \in \Omega$. Furthermore, $\frac{\partial g(x,u)}{\partial u} \ge 0$ for all $x \in \Omega$ and $u \ge 0$.
- (A3) For any $x \in \overline{\Omega}$, there exists some $\tilde{A} > 0$ such that

$$d(x)u + g(x, u)u \ge e^{-\mu(x)\tau(x)}b(x, u) \text{ for all } u \ge \tilde{A}.$$

We would like to make some comments on these assumptions. Condition (A1) is a standard technical assumption for the existence of solutions. Condition (A2) implies the birth rate and per-capita density-dependent death rate due to competition are negligible when the population density is zero. Furthermore, the excessive per-capita death rate g(x, u) due to intra-specific competition is a nondecreasing function of the population density. Condition (A3) is a dissipative assumption to guarantee the population density remains bounded due to the self-limiting effects specified on density-dependent birth rate b(x, u) or excessive per-capita death rate g(x, u). Now, we are in a position to establish the well-posedness of the model system.

3.1 Basic properties with the natural phase space

It is natural to introduce the maximum delay $\tau_{\max} := \max_{x \in \bar{\Omega}} \{\tau(x)\}$ and define the phase space based on τ_{\max} . Let $\mathbb{X} := C(\bar{\Omega}, \mathbb{R})$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. Define $\mathcal{X} := C([-\tau_{\max}, 0], \mathbb{X})$ with the norm $\|\phi\|_{\mathcal{X}} := \max_{\theta \in [-\tau_{\max}, 0]} \|\phi(\theta)\|_{\mathbb{X}}, \forall \phi \in \mathcal{X}$. Then \mathcal{X} is a Banach space. Introduce positive cones $\mathbb{X}^+ := C(\bar{\Omega}, \mathbb{R}_+)$ and $\mathcal{X}^+ := C([-\tau_{\max}, 0], \mathbb{X}^+)$. Then $(\mathbb{X}, \mathbb{X}^+)$

and $(\mathcal{X}, \mathcal{X}^+)$ are ordered spaces with nonempty interiors. For $\sigma > 0$ and a given function $z(t) : [-\tau_{\max}, \sigma) \to \mathbb{X}$, we define $z_t \in \mathcal{X}$ by

$$z_t(\theta) = z(t+\theta), \ \forall \ \theta \in [-\tau_{\max}, 0], \ t \in [0, \sigma).$$

Suppose that $T(t) : C(\bar{\Omega}, \mathbb{R}) \to C(\bar{\Omega}, \mathbb{R})$ is the C_0 semigroups associated with $D(\cdot)\Delta$ subject to the zero flux boundary condition. It then follows that for any $\varphi \in C(\bar{\Omega}, \mathbb{R}), t \geq 0$,

$$(T(t)\varphi)(x) = \int_{\Omega} \Gamma(x, y, t)\varphi(y)dy, \qquad (8)$$

where Γ is the Green functions associated with $D(\cdot)\Delta$ and the zero flux boundary condition. From [26, Section 7.1 and Corollary 7.2.3], it follows that $T(t): C(\bar{\Omega}, \mathbb{R}) \to C(\bar{\Omega}, \mathbb{R})$ is compact and strongly positive for all t > 0.

Let $\mathcal{A} : \mathfrak{D}(\mathcal{A}) \to C(\overline{\Omega}, \mathbb{R})$ be the generator of T(t). Then $T(t) : \mathbb{X} \to \mathbb{X}$ is a C_0 semigroup generated by the operator \mathcal{A} defined on $\mathfrak{D}(\mathcal{A})$. Define $F : \mathcal{X} \to \mathbb{X}$ by

$$F(\phi)(x) = \exp(-\mu(x)\tau(x))b(x,\phi(-\tau(x),x)) - (g(x,\phi(0,x)) + d(x))\phi(0,x),$$
(9)

for $x \in \overline{\Omega}$ and $\phi \in \mathcal{X}$. Then (7) can be rewritten into the following abstract differential equation

$$\frac{du}{dt} = \mathcal{A}u + F(u_t), \ t > 0, \ u_0 = \phi \in \mathcal{X}^+.$$

or it can be rewritten as the following integral equation

$$u(t) = T(t)\phi(0) + \int_0^t T(t-s)F(u_s)ds, \ u_0 = \phi \in \mathcal{X}^+.$$

Then we have the following result.

Lemma 1 Assume Conditions (A1)-(A3) hold. Then

- (i) For every initial value function $\phi \in \mathcal{X}^+$, system (7) admits a unique solution $u(t, x; \phi)$ on its maximal interval of existence $[0, t_{\phi})$ with $u_0 = \phi$, where $t_{\phi} \leq \infty$. Furthermore, $u(t, \cdot; \phi) \in \mathbb{X}^+$, $\forall t \in [0, t_{\phi})$ and $u(t, x; \phi)$ is a classical solution of (7) for all $t > \tau_{\max}$.
- (ii) For any $A \geq \tilde{A}$ with \tilde{A} given in Assumption (A3) and any initial value function $\phi \in \mathcal{X}^+$ with $\phi(\theta, x) \leq A$ for all $\theta \in [-\tau_{\max}, 0]$ and $x \in \bar{\Omega}$, solution $u(t, x; \phi)$ exists and $u(t, x; \phi) \leq A$ for all $t \geq 0$ and $x \in \bar{\Omega}$.

Proof (i) Obviously, for any $\phi \in \mathcal{X}^+$, $F(\phi)$ is locally Lipschitz. Furthermore, $u(t,x) \equiv 0$ is a solution to the system. In view of [21, Corollary 4] and [26, Theorem 7.3.1], it suffices to show that

$$\lim_{h \to 0^+} \frac{1}{h} dist(\phi(0) + hF(\phi), \mathbb{X}^+) = 0, \ \forall \ \phi \in \mathcal{X}^+.$$
(10)

For any $\phi \in \mathcal{X}^+$ and $h \ge 0$, we have

$$\begin{split} \phi(0,x) &+ hF(\phi)(x) \\ &= \phi(0,x) + h[\exp(-\mu(x)\tau(x))b(x,\phi(-\tau(x),x)) - (g(x,\phi(0,x)) + d(x))\phi(0,x)] \\ &\geq \phi(0,x)[1 - h\left(g(x,\phi(0,x)) + d(x)\right)], \quad \text{for} \quad x \in \Omega. \end{split}$$

The above inequality implies that when $h < \frac{1}{\max_{x \in \overline{\Omega}} \{g(x, \phi(0, x)) + d(x)\}}, \phi(0, \cdot) + hF(\phi) \in \mathbb{X}^+$, which establishes (10).

(ii) For any positive constant $A \geq \tilde{A}$, we can observe that $T(t) : [0, A] \rightarrow [0, A]$. For any function $\psi \in \mathcal{X}^+$ with $\psi(\theta, x) \leq A$ for all $\theta \in [-\tau_{\max}, 0]$ and $x \in \bar{\Omega}$, we claim that the solution through initial value ψ satisfies $u(t, x; \psi) \leq A$, for all $t \geq 0$ and $x \in \bar{\Omega}$ when it exists. Actually, for any such ψ and $h \geq 0$, we have

$$\begin{split} \psi(0,x) + hF(\psi)(x) \\ &= \psi(0,x) + h[\exp(-\mu(x)\tau(x))b(x,\psi(-\tau(x),x)) - (g(x,\psi(0,x)) + d(x))\psi(0,x)] \\ &\leq \psi(0,x) + h[(g(x,A) + d(x))A - (g(x,\psi(0,x)) + d(x))\psi(0,x)] \\ &\leq \psi(0,x) + hL(A - \psi(0,x)) \\ &\leq (1 - hL)\psi(0,x) + hLA, \end{split}$$

with L being the Lipschitz constant for the u-function (g(x, u) + d(x))u for all $x \in \overline{\Omega}$. It then follows that when h < 1/L,

$$\psi(0,x) + hF(\psi)(x) \le (1 - hL)A + hLA = A$$

Therefore, $\psi(0, \cdot) + hF(\psi)(\cdot) \in [0, A]$ if h < 1/L. Hence, [21, Corollary 4] implies that the solution $u(t, x; \psi)$ of equation (7) through initial value ψ satisfies $0 \le u(t, x; \psi) \le A$ for all $t \ge 0$ and $x \in \overline{\Omega}$ when it exists. Furthermore, the interval of existence for the solution is $[0, \infty)$. This completes the proof.

Since for any initial value $\phi \in \mathcal{X}^+$, there is $A > \tilde{A}$ such that $\phi \in [0, A]$, therefore, the solution through this initial value $u(t, x; \phi)$ exists for all $t \in [0, \infty)$ and moreover, $0 \leq u(t, x; \phi) \leq A$, for all $t \geq 0$ and $x \in \overline{\Omega}$. Therefore, the solution map $\Phi(t) = u_t(\cdot) : \mathcal{X}^+ \to \mathcal{X}^+$ can be defined by (7), i.e.,

$$(\varPhi(t)\phi)(\theta,x) = u(t+\theta,x;\phi), \ \forall \ t \ge 0, \ x \in \bar{\varOmega}, \ \theta \in [-\tau_{\max},0].$$

Without loss of generation, we may consider this solution map $\Phi(t) : \mathcal{X}_A^+ \to \mathcal{X}_A^+$, $t \ge 0$, with $A \ge \tilde{A}$ and the set \mathcal{X}_A^+ being defined as follows:

$$\mathcal{X}_A^+ = \{ \phi \in \mathcal{X}^+ : 0 \le \phi(\theta, x) \le A, \ \forall x \in \overline{\Omega}, \ \theta \in [-\tau_{\max}, 0] \}$$

Furthermore, the solution map $\Phi(t) : \mathcal{X}_A^+ \to \mathcal{X}_A^+$ admits a global compact attractor (see [33, Theorem 1.1.2]). Then we have following result.

Theorem 1 Fix a positive constant A with $A \ge \tilde{A}$ and \tilde{A} being given in Assumption (A3). For every initial function $\phi \in \mathcal{X}_A^+$, system (7) admits a unique solution $u(t, x; \phi)$ on $[0, \infty)$ with $u_0 = \phi$. Moreover, the solution map $\Phi(t) = u_t(\cdot) : \mathcal{X}_A^+ \to \mathcal{X}_A^+$ generated by (7), i.e.,

$$(\Phi(t)\phi)(\theta,x) = u(t+\theta,x;\phi), \ \forall \ t \ge 0, \ x \in \overline{\Omega}, \ \theta \in [-\tau_{\max},0]$$

admits a global compact attractor in \mathcal{X}_A^+ .

3.2 Basic reproduction ratio

The basic reproduction ratio is a summary measure to quantify the net reproduction of a typical individual during its whole life cycle when the population density is small (near the extinction state so that the density-dependent regulations are ignored). For the reaction-diffusion model (7) with spatially varying delay, we can define the reproduction ratio by using approaches developed in [13,32] through the functional space \mathcal{X} with the maximum delay τ_{max} . Here, we technically regard the autonomous system as a periodic system and employ the theories in [13,32]. Linearizing system (7) at u = 0 gives

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))p(x)u(t-\tau(x),x) \\ -d(x)u(t,x), \ x \in \Omega \\ \frac{\partial u}{\partial \nu} = 0, \ x \in \partial\Omega, \end{cases}$$
(11)

where

$$p(x) = \left[\frac{\partial b(x,u)}{\partial u}\right]_{u=0} > 0.$$

Based on the structure of (11), we define $\mathbb{F}(t) : \mathcal{X} \to \mathbb{X}$ by

$$\mathbb{F}(t)\varphi = \exp(-\mu(\cdot)\tau(\cdot))p(\cdot)\varphi(-\tau(\cdot),\cdot), \ \forall \ t \in \mathbb{R}, \ \varphi \in \mathcal{X}$$

and $-\mathbb{V}(t): \mathbb{X} \to \mathbb{X}$ by

$$-\mathbb{V}(t)w = D(\cdot)\Delta w - d(\cdot)w, \ \forall \ t \in \mathbb{R}, \ w \in \mathbb{X},$$

with the Neumann boundary condition on $\partial \Omega$. Note that $\mathbb{F}(t)$ and $\mathbb{V}(t)$ are independent of time t, hence, $\mathbb{F}(\cdot)$ and $\mathbb{V}(\cdot)$ can be regarded as 1-periodic functionals.

It is easy to see that $\mathbb{F}(t) : \mathcal{X} \to \mathbb{X}$ is positive in the sense that $\mathbb{F}(t)\mathcal{X}^+ \subset \mathbb{X}^+$, and hence, the condition (H1) in [13] holds. Next, suppose $\{\mathbb{Y}(t,s), t \geq s\}$ is the evolution family on \mathbb{X} associated with the following system

$$\frac{dv(t)}{dt} = -\mathbb{V}(t)v(t).$$

Then $\mathbf{Y}(t-s) := \mathbb{Y}(t,s)$ is a positive operator in the sense that $\mathbf{Y}(t-s)\mathbb{X}^+ \subset \mathbb{X}^+$ for all $t \geq s$. Furthermore, if $\omega(\mathbf{Y}(\mathbf{s}))$ is the exponential growth bound

of evolution family $\{\mathbf{Y}(s), s \ge 0\}$, then $\omega(\mathbf{Y}(s))$ is negative. Therefore, the condition (H2) in [13] holds.

Assume that $C_1(\mathbb{R}, \mathbb{X})$ stands for the ordered Banach space of all continuous and 1-periodic functions from \mathbb{R} to \mathbb{X} , which is equipped with the maximum norm and the positive cone

$$C_1^+(\mathbb{R},\mathbb{X}) = \{ v \in C_1(\mathbb{R},\mathbb{X}) : v(t) \ge 0 \text{ in } \mathbb{X} \text{ for } t \in \mathbb{R} \}$$

By the results in [13], we define a linear operator on $C_1(\mathbb{R}, \mathbb{X})$ by

$$[\mathbb{L}v](t) := \int_0^\infty \mathbb{Y}(t, t-s) \mathbb{F}(t-s) v_{t-s} ds, \ \forall \ t \in \mathbb{R}, \ v \in C_1(\mathbb{R}, \mathbb{X}).$$

That is,

$$[\mathbb{L}v](t) := \int_0^\infty \mathbb{Y}(t, t-s) \mathbb{F}(t-s) v(t-s+\cdot) ds, \ \forall \ t \in \mathbb{R}, \ v \in C_1(\mathbb{R}, \mathbb{X}).$$

Motivated by the concept of next generation operators (see, e.g., [13,27]), we define the spectral radius of \mathbb{L} as the basic reproduction ratio for system (7), that is,

$$\mathcal{R}_0 := r(\mathbb{L}).$$

For any given $t \ge 0$, let S(t) be the solution maps of linear system (11) on \mathcal{X} , that is, $S(t)\phi = z_t(\phi)$ with $z_0 = \phi \in \mathcal{X}$, where

$$z_t(\phi)(\theta, x) = z(t+\theta, x; \phi)$$

for all $\theta \in [-\tau_{\max}, 0]$, $x \in \Omega$, and $z(t, x; \phi)$ is the unique solution of system (11) with $z(\theta, \cdot; \phi) = \phi(\theta, \cdot)$ for all $\theta \in [-\tau_{\max}, 0]$. Then the following result can be obtained from [13], which shows that the basic reproduction ratio can illustrate the stability of linear system (11) on the phase space \mathcal{X} with the maximum delay τ_{\max} .

Lemma 2 $\mathcal{R}_0 - 1$ has the same sign as r(S(1)) - 1, where r(S(1)) is the spectral radius of time-1 solution map S(1) of (11).

3.3 Monotonicity of the solution map

This subsection is devoted to the establishment of some monotonicity properties of the solution maps, $\Phi(t)$, associated with system (7) when additional assumptions are imposed. For this purpose, further biologically reasonable assumptions should be imposed:

- (M) Function b(x, u) is non-decreasing for $u \ge 0$ and $x \in \overline{\Omega}$.
- (S1) Function b(x, u) is strictly subhomogeneous in the sense that $b(x, \lambda u) > \lambda b(x, u)$ for all $u > 0, \lambda \in (0, 1)$ and $x \in \overline{\Omega}$.
- (S2) Function b(x, u) is subhomogeneous in the sense that $b(x, \lambda u) \ge \lambda b(x, u)$ and g(x, u) is strictly increasing for $u \ge 0$ and $x \in \overline{\Omega}$.

Assumption (M) will be used to guarantee the solution map admits monotonicity property while assumptions (S1)-(S2) will be used to ensure the solution map has subhomogeneity property (see Lemmas 3 and 4 presented later). Fix a positive constant A with $A \ge \tilde{A}$ and \tilde{A} being given in Assumption (A3). For any two functions ϕ_1 , $\phi_2 \in \mathcal{X}_A^+$ with $\phi_2 \le \phi_1$, that is, $\phi_1, \phi_2 \in \mathcal{X}^+$ and $0 \le \phi_2(\theta, x) \le \phi_1(\theta, x) \le A$ for all $\theta \in [-\tau_{\max}, 0], x \in \bar{\Omega}$, under Assumption (M), we have

$$\begin{split} & [\phi_1(0,x) - \phi_2(0,x)] + h[F(\phi_1) - F(\phi_2)](x) \\ & = [\phi_1(0,x) - \phi_2(0,x)] + h \exp(-\mu(x)\tau(x))[b(x,\phi_1(-\tau(x),x)) - b(x,\phi_2(-\tau(x),x))] \\ & -h[(g(x,\phi_1(0,x)) + d(x))\phi_1(0,x) - (g(x,\phi_2(0,x)) + d(x))\phi_2(0,x)] \\ & \geq [\phi_1(0,x) - \phi_2(0,x)] - hL[\phi_1(0,x) - \phi_2(0,x)] \\ & = (1 - hL)[\phi_1(0,x) - \phi_2(0,x)], \end{split}$$

with $h \ge 0$ and F defined in (9). Here L is a constant such that

 $|(g(x,u) + d(x))u - (g(x,v) + d(x))v| \le L|u - v|, \ \forall x \in \overline{\Omega}, \ u, v \in [0,A].$

Therefore, when h < 1/L,

$$[\phi_1(0,\cdot) - \phi_2(0,\cdot)] + h[F(\phi_1) - F(\phi_2)] \in \mathbb{X}^+.$$

Hence, the functional $F(\cdot)$ defined in (9) is quasi-monotone in the sense that

$$\lim_{h \to 0^+} \frac{1}{h} dist([\phi_1(0, \cdot) - \phi_2(0, \cdot)] + [F(\phi_1) - F(\phi_2)]; \mathbb{X}^+) = 0$$

for $\phi_1, \phi_2 \in \mathcal{X}_A^+$ with $\phi_2 \leq \phi_1$. Hence [21, Corollary 5] implies the monotonicity of the solution map $\Phi(t)$ for t > 0 as follows:

Lemma 3 Assume Assumptions (A1)-(A3) and (M) hold. If $u(t, x; \phi)$ and $u(t, x; \psi)$ are solutions of equation (7) through different initial value functions ϕ and ψ in \mathcal{X}^+ with $\phi \geq \psi \in \mathcal{X}^+_A$, then $u(t, x; \phi) \geq u(t, x; \psi)$ for all $t \geq 0$ and $x \in \overline{\Omega}$.

The above result shows that the comparison principle holds for the solution map with condition (M). However, for two initial value functions ϕ and ψ in \mathcal{X}_A^+ , with $\phi(\theta, x) = \psi(\theta, x)$ for $\theta \in [-\tau(x), 0]$ and $\phi(\theta, x_0) > \psi(\theta, x_0)$ for some $x_0 \in \Omega$ such that $\tau(x_0) < \tau_{\max}$ and $\theta \in [-\tau_{\max}, -\tau(x_0))$, it is easy to see from the integral form of the solution for (7) that solutions through these two initial values should be identical, that is $u(t, x; \phi) = u(t, x; \psi)$ for all $t \geq 0$. Therefore, the solution map $\Phi(t) : \mathcal{X}_A^+ \to \mathcal{X}_A^+$ is not strongly monotone. However, sometimes, strong monotonicity is needed to analyze the global dynamics of system (see for example, [26,33]). For that purpose, a more suitable phase space other than \mathcal{X} should be used to exclude the redundant information in the initial value $\phi(\theta, x)$ for $x \in \Omega$ and $\theta \in [-\tau_{\max}, -\tau(x))$, which will be discussed in the coming subsection.

3.4 A new phase space and further properties

Introduce $\tilde{\mathcal{X}} := C(\tilde{\Omega}; \mathbb{R})$, where $\tilde{\Omega} = \{(\theta, x) \in \mathbb{R} \times \bar{\Omega} : -\tau(x) \leq \theta \leq 0\}$ with the norm

$$\|\phi(\theta, x)\|_{\tilde{\mathcal{X}}} := \max_{x \in \bar{\Omega}, \ \theta \in [-\tau(x), 0]} | \phi(\theta, x) |, \ \forall \ \phi \in \tilde{\mathcal{X}}.$$

Then $\tilde{\mathcal{X}}$ is a Banach space. Introduce the positive cone $\tilde{\mathcal{X}}^+ := \{\phi \in \tilde{\mathcal{X}} : \phi(\theta, x) \geq 0 \text{ for all } x \in \overline{\Omega}, \theta \in [-\tau(x), 0] \}$. Then $(\tilde{\mathcal{X}}, \tilde{\mathcal{X}}^+)$ is an ordered space with a nonempty interior. For $\sigma > 0$ and a given function $z(t, x) : [-\tau(x), \sigma) \times \overline{\Omega} \to \mathbb{R}$, we denote $z_t \in \tilde{\mathcal{X}}$ by

$$z_t(\theta, x) = z(t+\theta, x), \ \forall \ \theta \in [-\tau(x), 0], \ t \in [0, \sigma).$$

When initial data ϕ is specified from the phase space \hat{X} , the existence and uniqueness of solution $u(t, x; \phi)$ to model (7) can be established through discussing the equation on each time interval $[n \min_{x \in \hat{\Omega}} \{\tau(x)\}, (n+1) \min_{x \in \hat{\Omega}} \{\tau(x)\}]$ for

 $n = 0, 1, 2, \cdots$ With the help of this new phase space $\tilde{\mathcal{X}}$, we can establish the following result.

Lemma 4 In addition to Assumptions (A1)-(A3), if (M) and one of assumptions (S1)-(S2) hold, then the solution map is eventually strongly subomogeneous. That is, for any $\phi \in \tilde{\mathcal{X}}^+$ with $\phi(\theta_0, x_0) > 0$ for some $x_0 \in \overline{\Omega}$, $\theta_0 \in [-\tau(x_0), 0]$ and for $\lambda \in (0, 1)$, solutions $u(t, x; \phi)$ and $u(t, x; \lambda \phi)$ of system (7) through ϕ and $\lambda \phi$, respectively, satisfy the following inequality

$$u(t, x; \lambda \phi) > \lambda u(t, x; \phi), \ \forall \ t > 2\tau_{\max}, \ x \in \overline{\Omega}.$$

Proof We will use the integral form of the solution (3.1) on the new phase space, which is copied here for easy reference:

$$u(t, \cdot; \phi) = T(t)\phi(0, \cdot) + \int_0^t T(t-s)F(u_s)(\cdot)ds,$$
(12)

with $u_0 = \phi \in \tilde{\mathcal{X}}^+$, and $F : \tilde{\mathcal{X}} \to \mathbb{X}$ is defined by

$$F(\phi)(x) = \exp(-\mu(x)\tau(x))b(x,\phi(-\tau(x),x)) - (g(x,\phi(0,x)) + d(x))\phi(0,x),$$

for $x \in \overline{\Omega}$ and $\phi \in \mathcal{X}$ and $T(t) : C(\overline{\Omega}, \mathbb{R}) \to C(\overline{\Omega}, \mathbb{R})$ is defined as in (8). Then we can show the follow claim.

Claim: $u(t, x; \phi) > 0$ for all $t \ge \tau_{\max}$ and $x \in \overline{\Omega}$. Given $\phi \in \tilde{\mathcal{X}}^+$ with $\phi(\theta_0, x_0) > 0$ for some $x_0 \in \overline{\Omega}, \theta_0 \in [-\tau(x_0), 0]$. By Lemma 3, it is easy to see that $u(t, x; \phi) \ge 0$ for all $t \ge 0$ and $x \in \overline{\Omega}$. In the following, we first show that there is $t_0 \in [0, \tau(x_0)]$ such that $u(t_0, \cdot; \phi) \not\equiv 0$. Assume by contradiction that $u(t, x; \phi) \equiv 0$, for all $t \in [0, \tau(x_0)], x \in \overline{\Omega}$. At $t = \tau(x_0) + \theta_0 \in [0, \tau(x_0)]$ and $x = x_0$, it follows from the integral form (12) that $b(\cdot, u(\theta_0, \cdot; \phi)) \equiv 0$, that implies, $b(x_0, \phi(\theta_0, x_0)) = 0$. This, together with assumptions (A1)-(A3) and (M), show that $\phi(\theta_0, x_0) = 0$, which is a contradiction. Thus, $u(t_0, \cdot; \phi) \not\equiv 0$,

for some $t_0 \in [0, \tau(x_0)]$. Then the strong monotonicity of T(t) and the integral form (12) indicate that $u(t, x; \phi) > 0$ for all $t > \theta_0 + \tau(x_0)$ and $x \in \overline{\Omega}$.

For any ψ with $\psi(\theta, x) > 0$ for all $x \in \overline{\Omega}$ and $\theta \in [-\tau(x), 0]$ and any $\lambda \in (0, 1)$, assumption (A2) together with one of (S1)-(S2) imply that

 $F(\lambda\psi)(x) = \exp(-\mu(x)\tau(x))b(x,\lambda\psi(-\tau(x),x)) - (g(x,\lambda\psi(0,x)) + d(x))\lambda\psi(0,x)$ > $\lambda[\exp(-\mu(x)\tau(x))b(x,\psi(-\tau(x),x)) - (g(x,\psi(0,x)) + d(x))\psi(0,x)]$ = $\lambda F(\psi)(x).$

For any $\phi \in \mathcal{X}^+$ and $\phi \not\equiv 0$, the previous claim shows that $u_t(\theta, x; \phi) > 0$ for all $x \in \overline{\Omega}$ and $\theta \in [-\tau(x), 0]$, when $t > 2\tau_{\text{max}}$. Therefore,

$$\lambda u(t,x;\phi) = \lambda T(t)(\phi(0,x)) + \int_0^t T(t-s)(\lambda F(u_s))(x)ds$$

$$< T(t)(\lambda\phi(0,x)) + \int_0^t T(t-s)F(\lambda u_s)(x)ds$$

$$= u(t,x;\lambda\phi).$$

Hence, this lemma holds.

Lemma 4 shows that the solution map $\tilde{\Phi}(t) : \tilde{\mathcal{X}} \to \tilde{\mathcal{X}}$ with the new phase space $\tilde{\mathcal{X}}$ is monotone and strongly subhomogeneous when $t \geq 2\tau_{\max}$ (see, e. g., [33]). Then global stability results can be predicted by the local stability of the zero solution (see for example [33, Theorem 2.3.4]). However, Lemma 2 indicates that \mathcal{R}_0 can determine the local stability of the linearized equation (11) on the natural phase space \mathcal{X} , but not on the novel phase space $\tilde{\mathcal{X}}$. It remains to show that the stability of the solution maps on both phase spaces, \mathcal{X} and $\tilde{\mathcal{X}}$, are identical.

Recall that $S(t) : \mathcal{X} \to \mathcal{X}$ are the solution maps of system (11) on \mathcal{X} , which is defined in subsection 3.2. For any given $t \geq 0$, we can define another solution map for the same linearized equation (11) on the new phase space $\tilde{\mathcal{X}}$, denoted by $\tilde{S}(t)$. That is, $\tilde{S}(t)\phi = \tilde{z}_t(\phi) \in \tilde{\mathcal{X}}$, where $\tilde{z}(t, x; \phi)$ is the unique solution of (11) with $\tilde{z}_0 = \phi \in \tilde{\mathcal{X}}$. Furthermore, Lemma 2 implies that the basic reproduction ratio \mathcal{R}_0 determines the sign of r(S(1)) - 1. Now we would like to show that \mathcal{R}_0 also illustrates the sign of $r(\tilde{S}(1)) - 1$, by using a similar argument to that in [18].

Lemma 5 The time-one solution maps $S(1) : \mathcal{X} \to \mathcal{X}$ and $\tilde{S}(1) : \tilde{\mathcal{X}} \to \tilde{\mathcal{X}}$ have the same spectral radius, that is, $r(S(1)) = r(\tilde{S}(1))$.

Proof Using similar arguments as those in the Claim of Lemma 4, it is easy to see that $\tilde{S}^n(1) = \tilde{S}(n)$ is strongly positive on $\tilde{\mathcal{X}}$ when $n \geq 2\tau_{\max}$. Furthermore, $\tilde{S}(n)$ is compact [6, Theorem 3.6.1] when $n \geq 2\tau_{\max}$. Fix $n \geq 2\tau_{\max}$, then Krein-Rutmann theorem implies that the spectral radius $r(\tilde{S}^n(1)) = \left(r(\tilde{S}(1))\right)^n > 0$. For any $\phi \in \tilde{\mathcal{X}}$, define

$$\lceil \phi \rceil(\theta, x) = \begin{cases} \phi(-\tau(x)), \text{ if } \theta \in [-\tau_{\max}, -\tau(x)], \\ \phi(\theta), & \text{ if } \theta \in [-\tau(x), 0]. \end{cases}$$

Then $\lceil \phi \rceil \in \mathcal{X}$ and $\| \phi \|_{\tilde{\mathcal{X}}} = \| \lceil \phi \rceil \|_{\mathcal{X}}$. Moreover, solutions of the same linear equation (11) through two initial values, $\phi \in \tilde{\mathcal{X}}$ and $\lceil \phi \rceil \in \mathcal{X}$ in two functional spaces, coincide when time t > 0. Hence

$$\|\tilde{S}(n)\phi\|_{\tilde{\mathcal{X}}} \le \|S(n)[\phi]\|_{\mathcal{X}} \le \|S(n)\|_{\mathcal{X}} \cdot \|[\phi]\|_{\mathcal{X}} = \|S(n)\|_{\mathcal{X}} \cdot \|\phi\|_{\tilde{\mathcal{X}}}, \ \forall \phi \in \tilde{\mathcal{X}},$$

which implies that $\|\tilde{S}(n)\|_{\tilde{\mathcal{X}}} \leq \|S(n)\|_{\mathcal{X}}$. Therefore,

$$0 < r(\tilde{S}(1)) = \lim_{n \to \infty} \|\tilde{S}^n(1)\|_{\tilde{\mathcal{X}}}^{\frac{1}{n}} = \lim_{n \to \infty} \|\tilde{S}(n)\|_{\tilde{\mathcal{X}}}^{\frac{1}{n}} \le \lim_{n \to \infty} \|S(n)\|_{\mathcal{X}}^{\frac{1}{n}} = r(S(1)).$$

It remains to prove $r(S(1)) \leq r(\tilde{S}(1))$. Since the linear solution map $S(1)^n = S(n)$ is positive and compact on \mathcal{X} ([26, Theorem 5.1.1] and [6, Theorem 3.6.1]) and $r(S(1)^n) > 0$, the Krein-Rutmann theorem (see, e.g., [7, Theorem 7.1]) implies that $r(S(1)^n)$ is an eigenvalue of $S(1)^n$ with a corresponding positive eigenvector function $\phi^* > 0$ in \mathcal{X} . Then we can introduce a conjugate function $|\phi^*| \in \tilde{\mathcal{X}}$ as

$$\lfloor \phi^* \rfloor (\theta, x) = \phi^* (\theta, x)$$
 for any $x \in \overline{\Omega}$ and $\theta \in [-\tau(x), 0]$

Moreover, solutions through two initial values $\phi^* \in \mathcal{X}$ and $\lfloor \phi^* \rfloor \in \tilde{\mathcal{X}}$ for the same linear equation (11) are exactly the same when time t > 0. Furthermore, we claim that $\lfloor \phi^* \rfloor > 0$ in $\tilde{\mathcal{X}}$. Suppose not, that is $\lfloor \phi^* \rfloor \equiv 0$, then the same solution through $\lfloor \phi^* \rfloor$ is zero. This also implies that the solution through ϕ^* is zero, contradicting to the fact that ϕ^* is the positive eigenvector function with the positive eigenvalue $r(S(1)^n)$. By the identity of solutions, we have

$$\tilde{S}(1)^n \lfloor \phi^* \rfloor = \lfloor S(1)^n \phi^* \rfloor = \lfloor r(S(1))^n \phi^* \rfloor = (r(S(1)))^n \lfloor \phi^* \rfloor$$

Therefore, $(r(S(1)))^n$ is a positive eigenvalue of $\tilde{S}(1)^n$ with a positive eigenvector $\lfloor \phi^* \rfloor \in \tilde{\mathcal{X}}$. That means $(r(S(1)))^n \leq r(\tilde{S}(1)^n) = (r(\tilde{S}(1)))^n$, and hence $r(S(1)) \leq r(\tilde{S}(1))$. Consequently, we have $r(S(1)) = r(\tilde{S}(1))$.

3.5 Global dynamics with two different types of birth functions

This subsection is devoted to applying results in previous subsections to investigate the global dynamics of system (7). As commented, assumptions (A1)-(A3) are natural assumptions for a population growth model. In this subsection, we will investigate some special types of the density-dependent regulations on birth and death rates. Various birth rate functions have been employed in population growth models to validate the psychological effect of density on the reproduction rate. For example, the Beverton-Holt type function $b(u) = \frac{cu}{1+au}$, the Mackey-Glass function $b(u) = \frac{cu}{1+au^m}$ with $m \ge 1$ and the Ricker type function $b(u) = cNe^{-au}$ have been widely used. Motivated by these typical birth functions, we will study two general cases when the birth function is an increasing (for example, the Beverton-Holt type function) or a unimodal function (for example, the Ricker type function or Mackey-Glass function with m > 1).

3.5.1 The birth rate is a nondecreasing function

When the birth rate is a nondecreasing function of the population density, in particular, if (M) and one of assumptions (S1-S2) hold, then we can tell from Lemma 3 and Lemma 4 that the solution map $\tilde{\Phi}(n) : \tilde{\mathcal{X}} \to \tilde{\mathcal{X}}$ is monotone and strongly subhomogeneous when $n \geq 2\tau_{\max}$. Fix $n_0 \geq 2\tau_{\max}$. Note that

$$D\Phi(t)(0) = S(t)$$
 and $D\tilde{\Phi}(t)(0) = \tilde{S}(t), \forall t \ge 0$,

and hence, $r(D\Phi(n_0)(0)) = r(S(n_0)) = (r(S(1)))^{n_0}$ and $r(D\tilde{\Phi}(n_0)(0)) = r(\tilde{S}(n_0)) = (r(\tilde{S}(1)))^{n_0}$. Based on [33, Theorem 2.3.4], the following threshold results hold:

- (i) If $r(D\tilde{\Phi}(n_0)(0)) \leq 1$, then every positive orbit of $\tilde{\Phi}(n_0)$ in $\tilde{\mathcal{X}}^+$ converges to 0;
- (ii) If $r(D\tilde{\Phi}(n_0)(0)) > 1$, then there exists a unique fixed point $u^* \gg 0$ in $\tilde{\mathcal{X}}^+$ such that every positive orbit of $\tilde{\Phi}(n_0)$ in $\tilde{\mathcal{X}}^+ \setminus \{0\}$ converges to u^* .

For the second case, it follows that

$$\tilde{\varPhi}(n_0)(\tilde{\varPhi}(t)(u^*)) = \tilde{\varPhi}(t)(\tilde{\varPhi}(n_0)(u^*)) = \tilde{\varPhi}(t)(u^*), \ \forall \ t \ge 0.$$

By uniqueness of positive fixed point of $\tilde{\Phi}(n_0)$, we see that $\tilde{\Phi}(t)(u^*) = u^*, \forall t \geq 0$. Thus, system (7) admits a unique positive steady-state $u^*(x)$, which is globally attractive for system (7) in $\tilde{\mathcal{X}}^+ \setminus \{0\}$.

Fix a positive constant A with $A \ge \tilde{A}$ and \tilde{A} being given in Assumption (A3). Let the set $\tilde{\mathcal{X}}_A^+ := \{\phi \in \tilde{\mathcal{X}} : \phi(\theta, x) \in [0, A] \text{ for all } x \in \bar{\Omega}, \theta \in [-\tau(x), 0]\}$. Based on Lemma 2, Lemma 5 and the above discussions, we have the following global dynamics when the birth function is non-decreasing.

Theorem 2 In addition to Assumptions (A1-A3), if (M) and one of assumptions (S1-S2) hold, then the following statements are valid:

(i) If R₀ ≤ 1, then zero is globally asymptotically stable for system (7) in X⁺_A.
(ii) If R₀ > 1, then system (7) admits a unique positive steady-state u*(x) which is globally attractive for (7) in X⁺_A \ {0}.

3.5.2 The birth rate is in a unimodal form

If the birth function b(x, u) is not a nondecreasing function of the species density u, but in a unimodal form, we propose the following general assumption for the birth rate function:

(A4) For each $x \in \overline{\Omega}$, there is $\hat{u}(x)$ such that $\frac{\partial b(x,u)}{\partial u} > 0$ when $u < \hat{u}(x)$ (resp. $\frac{\partial b(x,u)}{\partial u} < 0$ when $u > \hat{u}(x)$). Furthermore, $\frac{b(x,u)}{u}$ is a strictly decreasing function of u for all u > 0 and $x \in \overline{\Omega}$.

This assumption shows that the per-capita birth rate is a decreasing function of the species density. Then we can study the global dynamics of (7) by using the following auxiliary function as constructed in [17, 19]:

$$b^{+}(x,u) = \begin{cases} b(x,u), & u \le \hat{u}(x), \\ b(x,\hat{u}(x)), & u > \hat{u}(x) \end{cases}$$

Based on the definition of $b^+(x, u)$ and the Assumption (A4), we have $b(x, u) \leq b^+(x, u)$ for all $x \in \overline{\Omega}$ and $u \geq 0$. Using a similar argument as that in Lemma 1, we can show that there is $\hat{A} > 0$ such that the set

$$\tilde{\mathcal{X}}_{\hat{A}}^{+} := \{ \phi \in \tilde{\mathcal{X}} : \phi(\theta, x) \in [0, \hat{A}] \text{ for all } x \in \bar{\Omega}, \theta \in [-\tau(x), 0] \}$$

is invariant for the solution map defined by the following by auxiliary equation

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))b^+(x,u(t-\tau(x),x)) \\ -(d(x) + g(x,u(t,x)))u(t,x), \ t > 0, \ x \in \Omega, \\ \frac{\partial u}{\partial \nu} = 0, \ t > 0, \ x \in \partial\Omega. \end{cases}$$
(13)

Furthermore, we introduce another function

$$b^{-}(x,u) = \begin{cases} \min\{b(x,u), b(x,\hat{A})\}, & 0 \le u \le \hat{A}, \\ b(x,\hat{A}), & u > \hat{A}(x), \end{cases}$$

and the corresponding auxiliary equation

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))b^{-}(x,u(t-\tau(x),x)) \\ -(d(x) + g(x,u(t,x)))u(t,x), \ t > 0, \ x \in \Omega, \end{cases}$$
(14)
$$\frac{\partial u}{\partial \nu} = 0, \ t > 0, \ x \in \partial\Omega.$$

Then we can establish the following global dynamics result for the unimodal birth function.

Theorem 3 Assume conditions (A1), (A2), (A3) and (A4) hold. Let $u(t, x; \phi)$ be the solution of (7) with initial value $\phi \in \tilde{X}^+$. Then the following statements are valid:

- (i) If $\mathcal{R}_0 < 1$, then $\lim_{t \to \infty} u(t, x; \phi) = 0$ uniformly for $x \in \overline{\Omega}$.
- (ii) If $\mathcal{R}_0 > 1$, then for any $\phi \in \tilde{\mathcal{X}}_{\hat{A}}^+ \setminus \{0\}$, there exist $u^{+*}(x) > u^{-*}(x) > 0$ for all $x \in \overline{\Omega}$, which are independent of the initial value such that

$$u^{-*}(x) \le \liminf_{t \to \infty} u(t, x; \phi) \le \limsup_{t \to \infty} u(t, x; \phi) \le u^{+*}(x)$$

for $x \in \overline{\Omega}$.

(iii) If $\mathcal{R}_0 > 1$ and $\hat{A}(x) \leq \hat{u}(x)$ for all $x \in \overline{\Omega}$, then for all $\phi \in \tilde{\mathcal{X}}_{\hat{A}}^+ \setminus \{0\}$, there is a unique positive steady-state $u^*(x)$, which is globally attractive, that is $\lim_{t \to \infty} u(t, x; \phi) = u^*(x)$ uniformly for $x \in \overline{\Omega}$.

Proof (i) It is easy to see that

$$\begin{split} & \frac{\partial u(t,x)}{\partial t} \\ &= D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))b(x,u(t-\tau(x),x)) - (d(x) + g(x,u(t,x)))u(t,x) \\ &\leq D(x)\Delta u(t,x) + \exp(-\mu(x)\tau(x))\frac{\partial b(x,y)}{\partial y}\Big|_{y=0} u(t-\tau(x),x) - d(x)u(t,x), \end{split}$$

with Neumann boundary condition. Assume that $v(t, x; \phi)$ is the solution of the linearized system (11) through an initial value $\phi \in \tilde{\mathcal{X}}^+$. Then comparison arguments imply that

$$0 \le u(t, x; \phi) \le v(t, x; \phi), \ \forall \ t \ge 0, \ x \in \Omega.$$

When $\mathcal{R}_0 < 1$, we have $\lim_{t \to \infty} v(t, x; \phi) = 0$ uniformly for $x \in \overline{\Omega}$. Hence, $\lim_{t \to \infty} u(t, x; \phi) = 0$ uniformly for $x \in \overline{\Omega}$.

(ii) Please note that both functions $b^+(x, u)$ and $b^-(x, u)$ are nondecreasing in $u \in [0, \hat{A}]$. Furthermore, for any u > 0 and $\lambda \in (0, 1)$, we have the following arguments for different cases (a) When $\lambda u < u \leq \hat{u}(x)$, we have $b^+(x, \lambda u) =$ $b(x, \lambda u) > \lambda b(x, u) = \lambda b^+(x, u)$; (b) If $\lambda u \leq \hat{u}(x) \leq u$, then $b^+(x, \lambda u) =$ $b(x, \lambda u) \geq b(x, \lambda \hat{u}(x)) > \lambda b(x, \hat{u}(x)) = \lambda b^+(x, u)$; (c) For the case $\hat{u}(x) \leq \lambda u < u$, we have $b^+(x, \lambda u) = b(x, \hat{u}(x)) > \lambda b(x, \hat{u}(x)) = \lambda b^+(x, u)$. Similar arguments remain valid for function $b^-(x, u)$. These arguments show that both functions $b^+(x, u)$ and $b^-(x, u)$ are strictly subhomogeneous in u.

Since $b^{-}(\cdot, u) \leq b(\cdot, u) \leq b^{+}(\cdot, u)$ for all $u \in [0, \hat{A}]$ and both $b^{-}(\cdot, u)$ and $b^{+}(\cdot, u)$ are nondecreasing functions in $u \geq 0$, by using the upper and lower solution arguments in [21], we can show that for any $\phi \in \tilde{\mathcal{X}}_{\hat{A}}^{+}$,

$$0 \le u^-(t, x; \phi) \le u(t, x; \phi) \le u^+(t, x; \phi) \le \hat{A} \text{ for all } t \ge 0 \text{ and } x \in \bar{\Omega}.$$

Since two systems (13) and (14) have the same linearized system as that of (7), similar arguments as those in the proof of Theorem 2 to systems (13) and (14) show that system (13) (resp. (14)) has a positive steady-state $u^{+*}(x)$ (resp. $u^{-*}(x)$) which is globally attractive for all nontrivial solutions in the invariant set $\tilde{\mathcal{X}}_{4}^{+}$. Hence, we have

$$u^{-*}(x) \le \liminf_{t \to \infty} u(t, x; \phi) \le \limsup_{t \to \infty} u(t, x; \phi) \le u^{+*}(x) \text{ for all } x \in \overline{\Omega}.$$

(iii) When $\hat{A} \leq \hat{u}(x)$ for all $x \in \overline{\Omega}$, then $b^{-}(\cdot, u) = b^{+}(\cdot, u)$ for $0 \leq u \leq \overline{A} \leq \hat{u}(\cdot)$. The above arguments on the invariant set $\tilde{\mathcal{X}}^{+}_{\hat{A}}$ indicates that $u^{-*}(x) = u^{+*}(x)$ for all $x \in \overline{\Omega}$. Hence the result holds.

4 Conclusion and discussion

The manuscript builds a population growth model in the form of a reactiondiffusion equation with time delay. The most significant component included is the spatially varying maturation delay driven by location-specific environmental conditions. A physiological state, the stage-age, instead of widely used chronological age, should be used to categorize the individuals in different stages in the model formulation (see (1)). Basic properties of solutions, such as the existence, uniqueness and non-negativeness are shown. Under a further condition that the birth rate is a non-decreasing function, the monotonicity of the solution map holds (Lemma 3). Furthermore, the basic reproduction ratio \mathcal{R}_0 for the population growth can be derived through the next generation operator approach. All these results are illustrated through employing the natural phase space \mathcal{X} with the maximum delay, which is similar to the arguments widely used in other studies for reaction-diffusion systems with spatially-constant delays (for example, [17]).

However, stronger properties for the solution map are essential sometimes to establish the global attractivity, such as strong monotonicity and strong sub-homogeneity [26,33]. On the other hand, solutions $u(t, x; \phi)$ and $u(t, x; \psi)$ through two different initial values ϕ and ψ in space \mathcal{X} with $\phi > \phi$ under the usual positive cone may become identical. This observation shows that arguments on the natural phase space fail to establish these fine properties. To overcome the challenge, a novel phase space $\tilde{\mathcal{X}}$ is introduced in subsection 3.4 and further properties of the solution map become possible (see for example Lemma 4) when dealing with the functional space $\tilde{\mathcal{X}}$. Although different functional spaces, \mathcal{X} and $\tilde{\mathcal{X}}$, have been employed for different purposes, equivalence of the linear stability of the system in different phase spaces can be shown (Lemma 5). This further implies that \mathcal{R}_0 determines the linear stability of the extinction state when analyzing the model on $\tilde{\mathcal{X}}$.

All further properties established for $\hat{\mathcal{X}}$ are applied to investigate the long term behaviors of the solutions. In particular, when the birth function takes an increasing form, the global attractivity of either zero (when $\mathcal{R}_0 \leq 1$) or positive state (when $\mathcal{R}_0 > 1$) can be shown. If the birth function takes a unimodal form, the permanence of species can be established when $\mathcal{R}_0 > 1$.

In summary, the manuscript proposes a synthesized framework to investigate the spatial dynamics of the species growth in a spatially heterogeneous environment. It is expected that the approach can be applied to broader contexts of studies on the impact of spatial heterogeneity, in particular, when the delayed feedbacks are involved and the response time is spatially varying.

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Declarations

Ethical Approval: not applicable.

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Authors' contributions: Both authors conceived of the presented idea, performed theoretical analysis and contributed to the final manuscript.

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