

# Spatial dynamics of a nonlocal model with periodic delay and competition

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## Abstract

Each species is subject to various biotic and abiotic factors during growth. This paper formulates a deterministic model with the consideration of various factors regulating population growth such as age-dependent birth and death rates, spatial movements, seasonal variations, intra-specific competition and time-varying maturation simultaneously. The model takes the form of two coupled reaction-diffusion equations with time-dependent delays, which bring novel challenges to the theoretical analysis. Then the model is analyzed when competition among immatures is negligible, in which situation one equation for the adult population density is decoupled. The well-posedness of the system is established and the basic reproduction number  $\mathcal{R}_0$  is defined and shown to determine the global attractivity of either the zero equilibrium (when  $\mathcal{R}_0 \leq 1$ ) or a positive periodic solution ( $\mathcal{R}_0 > 1$ ) by using the dynamical system approach on an appropriate phase space. When the immature intra-specific competition is included and the immature diffusion rate is negligible, the model is neither cooperative (where the comparison principle holds) nor reducible to a single equation. In this case, the threshold dynamics about the population extinction and uniform persistence are established by using the newly defined basic reproduction number  $\tilde{\mathcal{R}}_0$  as a threshold index. Furthermore, numerical simulations are implemented on the population growth of two different species for two different cases to validate the analytic results.

*Keywords:* age structure, diffusion, seasonal effects, periodic delay, intra-specific competition

## 1 Introduction

Various continuous or discrete mathematical models have been proposed to investigate population dynamics for single species. Mathematical models allowing for more biotic and abiotic factors tend to better describe the complex behavior of populations. Age structure and spatial dispersal constitute the popular topics in recent progresses of population dynamics. For some species such as insects and mammals, juveniles and adults have very distinct characteristics, which are embodied in completely different developmental and reproductive rates. It would be natural to associate with the effects of age structure by dividing the population into different stages. The well-known McKendrick-Von Foerster model (or named as Sharp-Lotka-McKendrick model [1, 2]) is a classical framework incorporating age-dependent factors in population growth. The investigation of the

nonlinear modification and generalisation based on this classical framework has attracted increasing attention in recent years. For rigorous theoretical analysis of age-structured models, interested readers can refer to wonderful literatures [1, 2, 3, 4]. In the natural world, the environment that organisms inhabit is heterogeneously distributed. Many physiological factors such as climates and food resources may differ from place to place, which drive the organisms to keep drifting or dispersing. Spatial effects affecting population dynamics and the structures of the communities are of particular interest to scientists. Different kinds of models can be formulated to incorporate spatial effects explicitly. The patchy framework [5, 6, 7] involving a system of ordinary or delay differential equations describes the movement in a discontinuous spatial region consisting of multiple patches. Alternatively, spatial effects can be treated as a continuum and described appropriately by a reaction-diffusion model [8, 7], which is the main tool we are going to employ in this paper.

Different reaction diffusion models with age-structure and nonlocal terms have been derived and investigated theoretically in the bounded or unbounded domain [6, 9, 10, 11]. For example, a stage structured nonlocal reaction diffusion model was proposed in [12], where the threshold dynamics and global attractivity of the positive steady state were investigated through the decoupled equation for adult variable as the immature intra-specific competition was ignored. By generalizing the model in [12] to a nonautonomous version, authors in [13] established the existence of the asymptotic speed of spread in an unbounded domain and a threshold result on the global attractivity of either zero or a positive periodic solution in a bounded domain. Authors in [11] studied the global dynamics of a class of age-structured reaction diffusion models with a fixed temporal delay and a nonlocal term in an unbounded domain.

In order to simplify the analysis, two significant factors regulating population growth were ignored in these stage structured nonlocal reaction diffusion models. One factor is the immature intra-specific competition, which enables these models to be reduced into only one equation for mature variable. However, the intra-specific competition within one stage, especially the immature stage, will generate a series of variations in successive stages and greatly influences the dynamics of organisms with complex life cycles [14]. For example, the body size and longevity of adult mosquitoes are to a large extent affected by the larval competition [15, 16]. The alteration of susceptibility of adult mosquitoes to dengue virus may be induced by the competition among larval mosquitoes [17]. The density-dependent acquired host resistance to ticks leads to the increased deaths of feeding and developing ticks [18, 19, 20]. Models incorporating density dependent death terms for immature individuals are more realistic to describe complex population dynamics of some species experiencing intra-specific competition. In this study, we assume that immature (mature) individuals only compete with all other individuals in the same stage and there is no competition between immature and mature stages. This assumption is biologically reasonable since the intra-specific competition within one stage rather than between stages can be commonly founded in species such as some insects and amphibious animals, which immature and mature individuals live in different environments and have quite different requirements for food or resources [21].

The other negligible factor is the time varying maturation period, which serves as a developmental index measuring the developmental progression and addresses the timing of the transition from the previous life stage [22]. In this paper, we assume the maturation duration for juveniles is dependent on time, which is particular suitable for insects subject to climatic factors. For instance, the maturation periods of mosquitoes [23] and ticks [24] greatly rely on the temperature, which varies with time. Time-dependent maturation durations were considered in [25], where the authors derived a size structured delay differential equation (DDE) model with state-dependent delays to describe the population growth of a single species experiencing larval competition. To investigate the population growth influenced by seasonality, authors in [26] also took into account intra-specific competition and time varying development durations within each developmental stage of ticks and

developed a stage-structured DDE model with periodic delays by building a link between time dependent age thresholds and developmental durations. Based on a similar model, authors in [27] provided a rigorous analysis involving the well posedness of the solution and threshold dynamics for tick populations subject to seasonal effects.

For these aforementioned models involving time-varying maturation period, spatial movement of individuals is not considered, which motivates us to formulate an age structured nonlocal reaction diffusion growth model with consideration of immature intra-specific competition and time dependent maturation duration simultaneously. In addition, it is well known that the annual trends of population dynamics are greatly affected by the seasonal changes in rainfall, temperature and accessible food or resources. This is particular true for some insect species such as ticks, the primary vector transmitting tick-borne diseases, the distribution and abundance of which are very sensitive to the climate conditions as they need relatively high humidity and moderate temperature to survive during their prolonged nonparasitic stages [24]. Incorporating seasonal effects in the model would be a sensible choice to better investigate the population dynamics, with all the time-dependent parameter functions in our model being periodic with the same period  $T$ . The main focus of this paper is to provide a rigorous and detailed theoretical analysis on a delayed nonlocal reaction diffusion population model with age structure and time dependent delays from the perspective of periodic dynamical systems.

In the next section, a closed system related to the densities of immatures  $I(t, x)$  and adults  $M(t, x)$  is formulated by a system involving time-periodic delays due to the seasonal juvenile maturation period, individual diffusion and immature intra-specific competition. The time-dependent periodic delay in our model brings novel challenges to the theoretical analysis. Section 3 conducts theoretical analysis on the model ignoring juvenile intra-specific competition, making the model reducible to one equation for  $M(t, x)$ , based on which, the well posedness of the system and the existence of the global attractor are established. In addition, the basic reproduction number  $\mathcal{R}_0$  is formulated and the global stability of one equation in terms of  $\mathcal{R}_0$  is obtained by employing the theory of monotone and subhomogeneous semiflows. In section 4, we investigate the threshold dynamics for the obtained model under the consideration of immature intra-specific competition when the immature individuals have limited dispersal ability. It is impossible to decouple the equation for the matured population density  $M(t, x)$  from the model system as usual due to the existence of the intra-specific juvenile competition. In order to validate the theoretical results involving the threshold dynamics in terms of the basic reproduction number, numerical results are obtained by performing simulations on two different species for two different cases respectively in section 5. A discussion session in the final part concludes this paper.

## 2 Model formulation

We start with a well-accepted age-structured framework proposed in [3] and generalize it into the following spatial model with periodic coefficients to study the interactive effects of the age structure and spatial dispersal on population growth subject to seasonal effects:

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right)\rho(t, a, x) = D(a)\frac{\partial^2}{\partial x^2}\rho(t, a, x) - \mu\left(t, a, \int_0^\infty q(t, s)\rho(t, s, x)ds\right)\rho(t, a, x), \quad (2.1)$$

where  $\rho(t, a, x)$  is the population density of one species at time  $t$ , age  $a$  ( $\geq 0$ ) and location  $x$  in a bounded spatial domain  $\Omega$  with smooth boundary  $\partial\Omega$ ,  $D(a)$  ( $\geq 0$ ) is the age-dependent diffusion rate,  $\mu\left(t, a, \int_0^\infty q(t, s)\rho(t, s, x)ds\right)$  ( $\geq 0$ ) represents the per-capita death rate, which varies with the time  $t$ , age  $a$  and a weighted population density with kernel  $q(t, a)$  ( $\geq 0$ ).

By choosing appropriate weight functions as in [27], the specific form of the per-capita death rates  $\mu(t, a, \int_0^\infty q(t, s)\rho(t, s, x)ds)$  for immature and mature stages are assumed to be:

$$\mu\left(t, a, \int_0^\infty q(t, s)\rho(t, s, x)ds\right) = \begin{cases} \mu_I(t) + f(I(t, x)), & t > -\tau(0), 0 < a \leq \tau(t), x \in \Omega, \\ \mu_M(t) + g(M(t, x)), & t > -\tau(0), a > \tau(t), x \in \Omega. \end{cases}$$

In this formula,  $\mu_I(t)$  and  $\mu_M(t)$  are density-independent per capita death rates for immature and mature individuals respectively, while  $f(\cdot)$  and  $g(\cdot)$  are density-dependent death rates, which represent the intra-specific competition between individuals within the immature and mature stages respectively.

Let  $\tau(t)$  denote the juvenile maturation period at time  $t$ , that is, a newly matured individual at time  $t$  is developed from an immature individual born at time  $t - \tau(t)$ . That is, the age threshold classifying the population into immature and mature stages at time  $t$  is  $\tau(t)$ . In other words, the chronological age at time  $t$  for adults should be greater than  $\tau(t)$ . Thus, the densities of individuals within the immature stage  $I(t, x)$  and mature stage  $M(t, x)$  at time  $t$  and location  $x$  can be represented as follows:

$$I(t, x) = \int_0^{\tau(t)} \rho(t, a, x)da \quad \text{and} \quad M(t, x) = \int_{\tau(t)}^\infty \rho(t, a, x)da. \quad (2.2)$$

Provided that the developmental proportion during juvenile stage at day  $t$  is  $\sigma(t)$ , the immature individuals attain maturity when the corresponding accumulative developmental proportion during the interval  $[t - \tau(t), t]$  is unity, that is

$$\int_{t-\tau(t)}^t \sigma(r)dr = 1.$$

By taking the derivative with respect to  $t$ , it follows that

$$1 - \tau'(t) = \frac{\sigma(t)}{\sigma(t - \tau(t))}.$$

This indicates  $1 - \tau'(t) > 0$ , which guarantees that developmental processes proceed according to the chronological order and never develop back to the previous stage.

Based on (2.1), the population model incorporating both seasonal effects and spatial movements is presented as the following reaction diffusion equations with no flux boundary condition:

$$\begin{cases} \left( \frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) \rho(t, a, x) = D_1 \Delta \rho(t, a, x) - (\mu_I(t) + f(I(t, x)))\rho(t, a, x), & t > -\tau(0), 0 < a \leq \tau(t), x \in \Omega, \\ \left( \frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) \rho(t, a, x) = D_2 \Delta \rho(t, a, x) - (\mu_M(t) + g(M(t, x)))\rho(t, a, x), & t > -\tau(0), a > \tau(t), x \in \Omega, \\ \rho(t, 0, x) = b(t, M(t, x)), & t \geq -\tau(0), x \in \Omega, \\ \rho(-\tau(0), a, x) = \phi(a, x), & a \geq 0, x \in \Omega, \\ \frac{\partial \rho(t, a, x)}{\partial n} = 0, & t > -\tau(0), x \in \partial\Omega, \end{cases} \quad (2.3)$$

where  $\Delta$  is the laplacian operator,  $n$  is the outward normal vector on  $\partial\Omega$ ,  $D_1$  ( $> 0$  or  $= 0$ ) and  $D_2$  ( $> 0$ ) denote the diffusion coefficients for immature and mature individuals respectively,

$b(t, M(t, x))$  is the birth rate, which is dependent on the density of matured individuals,  $\phi(a, x)$  is the initial distribution. Note that all above functions are non-negative. Due to the seasonal factors regulating the population growth, we assume that  $\tau(t)$ ,  $b(t, M)$ ,  $\mu_I(t)$  and  $\mu_M(t)$  are periodic in time  $t$  with the same period  $T$ . Moreover, the inherent relationships between boundary and initial condition must be satisfied in order to keep the system consistent, that is,

$$\rho(-\tau(0), 0, x) = b(-\tau(0), M(-\tau(0), x)) = \phi(0, x).$$

In addition, for the sake of clarity, we introduce the following notations:

$$\hat{\tau} = \max_{t \in [0, T]} \{\tau(t)\}, \quad \bar{\tau} = \min_{t \in [0, T]} \{\tau(t)\}. \quad (2.4)$$

The basic assumptions for the coefficients are made as below, with the birth and death functions illustrated in Figure 2.

- (A1) The birth rate  $b(t, M)$  is Hölder continuous on  $\mathbb{R} \times \mathbb{R}$ , periodic in time  $t$  with the period  $T > 0$ , and increasing with respect to  $M \geq 0$ . Moreover,  $b(t, 0) \equiv 0$ ,  $b(t, M) > 0$  when  $M > 0$ ,  $\frac{\partial b(t, 0)}{\partial M} = \beta(t) > 0$  for all  $t \in \mathbb{R}$  and  $b(t, M) \leq \beta(t)M$  for all  $t \in \mathbb{R}$  and  $M > 0$ , where  $\beta(t)$  is a  $T$ -periodic continuous function. Furthermore, there exists a number  $\widetilde{M} \geq 0$  such that for all  $H > \widetilde{M}$ ,  $(1 - \tau'(t))b(t - \tau(t), H) - (\mu_M(t) + g(H))H < 0$ .
- (A2) All the per-capita death rates including natural death rates  $\mu_I(t)$  and  $\mu_M(t)$  and density dependent death rates  $f(I)$  and  $g(M)$  are Hölder continuous. In particular,  $\mu_I(t)$  and  $\mu_M(t)$  are positive functions and periodic in time  $t$  with the same period  $T > 0$ . Function  $g(M)$  is non-decreasing with respect to  $M$ . In addition,  $f(0) = 0$ ,  $g(0) = 0$ ,  $f(I) \geq 0$  and  $g(M) > 0$  when  $I > 0$  and  $M > 0$  respectively.

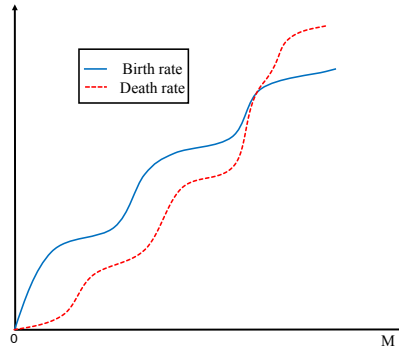


Figure 1: Model assumption for the birth rate  $b(t, M)$  and death function  $(\mu_M(t) + g(M))M$  for fixed time instant  $t$ .

By differentiating (2.2) with respect to time  $t$  and combining with (2.3), we obtain the following

system:

$$\begin{aligned}
& \frac{\partial I(t, x)}{\partial t} \\
&= \int_0^{\tau(t)} \frac{\partial \rho(t, a, x)}{\partial t} da + \tau'(t) \rho(t, \tau(t), x) \\
&= \int_0^{\tau(t)} \left( -\frac{\partial \rho(t, a, x)}{\partial a} + D_1 \Delta \rho(t, a, x) - (\mu_I(t) + f(I(t, x))) \rho(t, a, x) \right) da + \tau'(t) \rho(t, \tau(t), x) \\
&= D_1 \Delta I(t, x) + \rho(t, 0, x) - \rho(t, \tau(t), x) - (\mu_I(t) + f(I(t, x))) I(t, x) + \tau'(t) \rho(t, \tau(t), x) \\
&= D_1 \Delta I(t, x) + b(t, M(t, x)) - (\mu_I(t) + f(I(t, x))) I(t, x) - (1 - \tau'(t)) \rho(t, \tau(t), x),
\end{aligned}$$

and

$$\begin{aligned}
& \frac{\partial M(t, x)}{\partial t} \\
&= \int_{\tau(t)}^{\infty} \frac{\partial \rho(t, a, x)}{\partial t} da - \tau'(t) \rho(t, \tau(t), x) \\
&= \int_{\tau(t)}^{\infty} \left( -\frac{\partial \rho(t, a, x)}{\partial a} + D_2 \Delta \rho(t, a, x) - (\mu_M(t) + g(M(t, x))) \rho(t, a, x) \right) da - \tau'(t) \rho(t, \tau(t), x) \\
&= D_2 \Delta M(t, x) + \rho(t, \tau(t), x) - \rho(t, \infty, x) - (\mu_M(t) + g(M(t, x))) M(t, x) - \tau'(t) \rho(t, \tau(t), x) \\
&= D_2 \Delta M(t, x) + (1 - \tau'(t)) \rho(t, \tau(t), x) - (\mu_M(t) + g(M(t, x))) M(t, x),
\end{aligned}$$

where the reasonable biological assumption guarantees that  $\rho(t, \infty, x)$  is zero since no individual can survive forever.

To get the closed form of the above system, we need to determine  $\rho(t, \tau(t), x)$  by integrating along characteristics. For any  $\xi \geq -\tau(0)$ , let  $v(\xi, x) = \rho(t_0 + \xi, a_0 + \xi, x)$ , where  $t_0$  and  $a_0$  are fixed. Then, when  $0 < a_0 + \xi \leq \tau(t)$ , we have,

$$\left\{ \begin{aligned} \frac{\partial}{\partial \xi} v(\xi, x) &= \left( \frac{\partial}{\partial t} + \frac{\partial}{\partial a} \right) \rho(t_0 + \xi, a_0 + \xi, x) \\ &= D_1 \Delta \rho(t_0 + \xi, a_0 + \xi, x) - (\mu_I(t_0 + \xi) + f(I(t_0 + \xi, x))) \rho(t_0 + \xi, a_0 + \xi, x) \\ &= D_1 \Delta v(\xi, x) - (\mu_I(t_0 + \xi) + f(I(t_0 + \xi, x))) v(\xi, x), \\ v(-\tau(0), x) &= \rho(t_0 - \tau(0), a_0 - \tau(0), x). \end{aligned} \right. \quad (2.5)$$

Clearly, the expression of the solutions  $v(\xi, x)$  of (2.5) depends on coefficients  $D_1$  and  $f(I)$ . More precisely, the fundamental solution corresponding to the partial differential operator  $L \equiv [\partial_t - D_1 \Delta - \mu_I(t) - f(I(t, \cdot))]$  involves  $D_1$  and  $f(I)$ . Especially, when  $D_1 > 0$  and  $f(I) > 0$ , it is very challenging for us to show such fundamental solution (see [28]). At what follows, we study the equation (2.5) in terms of  $D_1$  and  $f(I)$  with three cases: (I)  $D_1 > 0, f(I) \equiv 0$  for  $I > 0$ ; (II)  $D_1 = 0, f(I) \equiv 0$  for  $I > 0$ ; (III)  $D_1 = 0, f(I) > 0$  for  $I > 0$ , and then we show the closed form of the system on  $I$  and  $M$ . As a matter of fact, the fundamental solution based on (II) is a special case of it involved with (I) due to  $f(I) \equiv 0$ . Hence, we mainly concern cases (I) and (III).

**Case I:**  $D_1 > 0$  and  $f(I) \equiv 0$ . For some species such as mammals [29] and raptor [30], the juvenile individuals have the ability to disperse, which alleviates the intra-specific competition within immature stages [31]. Consequently, the juvenile intra-specific competition can be ignored when immature individuals can move or disperse efficiently, that is,  $f(I) \equiv 0$  when  $D_1 > 0$ . In

view of (2.5), we have

$$\begin{aligned} v(\xi, x) &= \int_{\Omega} \Gamma(t_0 + \xi, t_0 - \tau(0), x, y, D_1) v(-\tau(0), y) dy \\ &= \int_{\Omega} \Gamma(t_0 + \xi, t_0 - \tau(0), x, y, D_1) \rho(t_0 - \tau(0), a_0 - \tau(0), y) dy, \end{aligned}$$

where  $\Gamma(t, s, x, y, D_1)$  represents the fundamental solution corresponding to the partial differential operator  $L \equiv [\partial_t - D_1 \Delta - \mu_I(t)]$  (see [28, Chapter 1]). For all  $t \geq 0$ , let  $t_0 = t + \tau(0) - \tau(t)$ ,  $\xi = \tau(t) - \tau(0)$  and  $a_0 = \tau(0)$ , then  $\xi \geq -\tau(0)$  and  $\xi + a_0 = \tau(t)$ . In this case,

$$\begin{aligned} \rho(t, \tau(t), x) &= v(\tau(t) - \tau(0), x) \\ &= \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \rho(t - \tau(t), 0, y) dy, \\ &= \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), M(t - \tau(t), y)) dy. \end{aligned}$$

Therefore, the closed form of the system describing the population growth when  $t \geq 0$  can be written as:

$$\left\{ \begin{aligned} \frac{\partial I(t, x)}{\partial t} &= D_1 \Delta I(t, x) + b(t, M(t, x)) - \mu_I(t) I(t, x) \\ &\quad - (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), M(t - \tau(t), y)) dy, \\ &\quad t > 0, x \in \Omega, \\ \frac{\partial M(t, x)}{\partial t} &= D_2 \Delta M(t, x) - (\mu_M(t) + g(M(t, x))) M(t, x) \\ &\quad + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), M(t - \tau(t), y)) dy, \\ &\quad t > 0, x \in \Omega, \\ \frac{\partial I(t, x)}{\partial n} &= \frac{\partial M(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega, \end{aligned} \right. \quad (2.6)$$

When  $D_1 = 0$  and  $f(I) \equiv 0$ , the fundamental solution operator  $\Gamma(t, t - \tau(t), x, y, D_1)$  is reduced to

$$\Gamma(t, t - \tau(t), x, y, D_1) = e^{\int_{t-\tau(t)}^t \mu_I(s) ds},$$

and hence, we have the following system:

$$\left\{ \begin{aligned} \frac{\partial I(t, x)}{\partial t} &= D_1 \Delta I(t, x) + b(t, M(t, x)) - \mu_I(t) I(t, x) \\ &\quad - (1 - \tau'(t)) e^{\int_{t-\tau(t)}^t \mu_I(s) ds} b(t - \tau(t), M(t - \tau(t), y)), \quad t > 0, x \in \Omega, \\ \frac{\partial M(t, x)}{\partial t} &= D_2 \Delta M(t, x) - (\mu_M(t) + g(M(t, x))) M(t, x) \\ &\quad + (1 - \tau'(t)) e^{\int_{t-\tau(t)}^t \mu_I(s) ds} b(t - \tau(t), M(t - \tau(t), y)), \quad t > 0, x \in \Omega, \\ \frac{\partial I(t, x)}{\partial n} &= \frac{\partial M(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega, \end{aligned} \right. \quad (2.7)$$

**Case III:**  $D_1 = 0$ ,  $f(I) > 0$ . For some species such as mosquitoes [32] or frogs [33], the immature individuals are often restricted in a limited area due to inefficient dispersal ability, which

would intensify the competition for food and resources among immature individuals. In this scenario, the diffusion rate for immature individuals is negligible (i.e.  $D_1 \equiv 0$ ) while the immature intra-specific competition is taken into consideration, that is,  $f(I) > 0$  for  $I > 0$ . Then, the fundamental solution corresponding to the differential operator  $L = [\partial_t - \mu_I(t) - f(I(t, \cdot))]$  is given by  $\exp\left(\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, \cdot))) ds\right)$ . Similar to the former arguments, we obtain that

$$\begin{aligned} \rho(t, \tau(t), x) &= v(\tau(t) - \tau(0), x) \\ &= \exp\left(\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, \cdot))) ds\right) \rho(t - \tau(t), 0, y), \\ &= \exp\left(\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, \cdot))) ds\right) b(t - \tau(t), M(t - \tau(t), y)). \end{aligned}$$

Consequently, the closed form of the system describing the population growth when  $t \geq 0$  can be written as:

$$\left\{ \begin{array}{l} \frac{\partial I(t, x)}{\partial t} = b(t, M(t, x)) - (\mu_I(t) + f(I(t, x)))I(t, x) - (1 - \tau'(t)) \\ \quad \times \exp\left(-\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, x))) ds\right) b(t - \tau(t), M(t - \tau(t), x)), \\ \quad \quad \quad t > 0, x \in \Omega, \\ \frac{\partial M(t, x)}{\partial t} = D_2 \Delta M(t, x) - (\mu_M(t) + g(M(t, x)))M(t, x) + (1 - \tau'(t)) \\ \quad \times \exp\left(-\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, x))) ds\right) b(t - \tau(t), M(t - \tau(t), x)), \\ \quad \quad \quad t > 0, x \in \Omega, \\ \frac{\partial I(t, x)}{\partial n} = \frac{\partial M(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega. \end{array} \right. \quad (2.8)$$

Notice that during derivation of the above system, it is not difficult to see that

$$\rho(t, a, x) = \exp\left(-\int_{t-a}^t (\mu_I(r) + f(I(r, x))) dr\right) b(t - a, M(t - a, x))$$

for  $t \geq \tau(t) \geq a$ , while

$$\begin{aligned} I(t, x) &= \int_0^{\tau(t)} \rho(t, a, x) da \\ &= \int_0^{\tau(t)} \exp\left(-\int_{t-a}^t (\mu_I(r) + f(I(r, x))) dr\right) b(t - a, M(t - a, x)) da \\ &= \int_{t-\tau(t)}^t \exp\left(-\int_s^t (\mu_I(r) + f(I(r, x))) dr\right) b(s, M(s, x)) ds \end{aligned}$$

for  $t \geq \tau(t) \geq a$ . Letting  $t = 0$  in the above equation for  $I$ , we obtain the following constraint:

$$I(0, x) = \int_{-\tau(0)}^0 \exp\left(-\int_s^0 (\mu_I(r) + f(I(r, x))) dr\right) b(s, M(s, x)) ds. \quad (2.9)$$



When the competition among immature individuals is non-negligible, that is,  $f(I) > 0$  provided  $I > 0$ , the model (2.8) consists of two coupled equations which is not reducible to a single equation. The model structure of (2.8) is quite different from systems (2.6) and (2.7). Meanwhile, the lack of the diffusion term for immature individuals ( $D_1 \equiv 0$ ) especially make the corresponding solution maps no longer compact. A series of rigorous analysis including the well-posedness and threshold dynamics in terms of the basic reproduction number will be conducted, which constitutes the main focus of our paper. In the subsequent section, we will first investigate systems (2.6) and (2.7) where the immature intra-specific competition is negligible.

### 3 Dynamics for the model without immature intra-specific competition

In this section, we establish the global dynamics for (2.6) via the basic reproduction number. It is easy to check that the system is reducible to one single equation for  $M(t, x)$ . In fact, since the  $M$  equation in (2.6) is independent of  $I$ , it suffices to study the decoupled system:

$$\begin{cases} \frac{\partial M(t, x)}{\partial t} = D_2 \Delta M(t, x) - (\mu_M(t) + g(M(t, x)))M(t, x) \\ \quad + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), M(t - \tau(t), y)) dy, \\ \frac{\partial M(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega. \end{cases} \quad t > 0, x \in \Omega, \quad (3.1)$$

#### 3.1 Global existence and uniqueness of solutions

Without loss of generality, we choose the initial timing as the global maximum point of  $\tau(t)$  in  $[0, T]$ , that is,  $\tau(0) = \max_{t \in [0, T]} \{\tau(t)\} = \hat{\tau}$ , which is feasible with solution evolution. Let  $\mathbf{Y} := C(\bar{\Omega}, \mathbb{R})$  be the Banach space of continuous functions with the supremum norm  $\|\cdot\|_{\mathbf{Y}}$ . Define  $\mathcal{C} = C([-\tau(0), 0], \mathbf{Y})$ . For any  $\psi \in \mathcal{C}$ , define the norm  $\|\psi\| = \max_{\theta \in [-\tau(0), 0]} \|\psi(\theta)\|_{\mathbf{Y}}$ . Then,  $\mathcal{C}$  is a Banach space. Let  $\mathbf{Y}^+ := C(\bar{\Omega}, \mathbb{R}^+)$  and  $\mathcal{C}^+ = C([-\tau(0), 0], \mathbf{Y}^+)$ , then  $(\mathbf{Y}, \mathbf{Y}^+)$  and  $(\mathcal{C}, \mathcal{C}^+)$  are both strongly ordered spaces. Given a function  $u(t) : [-\tau(0), \sigma) \rightarrow \mathbf{Y}$  for  $\sigma > 0$ , define  $u_t \in \mathcal{C}$  by  $u_t(\theta, x) = u(t + \theta, x)$ , for all  $\theta \in [-\tau(0), 0]$ ,  $x \in \bar{\Omega}$  and  $t \in [0, \sigma)$ .

Define the linear operator  $\mathcal{A}$  by

$$\begin{aligned} D(\mathcal{A}(t)) &= \{\psi \in C^2(\bar{\Omega}) : \frac{\partial \psi}{\partial n} = 0 \text{ on } \partial\Omega\}, \\ \mathcal{A}(t)\psi &= D_2 \Delta \psi - \mu_M(t)\psi, \quad \forall \psi \in D(\mathcal{A}(t)). \end{aligned}$$

Define the nonlinear operator  $\mathcal{F} : \mathbb{R} \times \mathcal{C}^+ \rightarrow \mathbf{Y}$  by

$$\mathcal{F}(t, \psi) = -g(\psi(0, \cdot))\psi(0, \cdot) + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), \cdot, y, D_1) b(t - \tau(t), \psi(-\tau(t), y)) dy,$$

for  $t \geq 0$  and  $\psi \in \mathcal{C}^+$ .

Then, system (3.1) can be reformulated as the following abstract functional differential equation:

$$\begin{cases} \frac{\partial M(t, \cdot)}{\partial t} = \mathcal{A}(t)M(t, \cdot) + \mathcal{F}(t, M_t), & t > 0, x \in \Omega, \\ M(\theta, x) = \psi(\theta, x), & \theta \in [-\tau(0), 0], x \in \Omega. \end{cases} \quad (3.2)$$

Let  $W(t, s)$  be the evolution operator determined by the following linear reaction-diffusion equation

$$\begin{cases} \frac{\partial M(t, x)}{\partial t} = D_2 \Delta M(t, x) - \mu_M(t) M(t, x), & t > 0, x \in \Omega, \\ \frac{\partial M(t, x)}{\partial n} = 0, & t > 0, x \in \partial\Omega. \end{cases}$$

The equivalent integral form of system (3.2) is shown as follows:

$$M(t; \psi) = W(t, 0)\psi(0) + \int_0^t W(t, s)\mathcal{F}(s, M_s)ds, \quad t \geq 0, \psi \in \mathcal{C}^+,$$

and the solution of which is a mild solution of (3.1).

Clearly,  $\mathcal{F}(t, \cdot)$  is locally Lipschitz continuous on  $\mathcal{C}^+$ , and hence for any  $\psi \in \mathcal{C}^+$ , system (3.1) admits a unique non-continuable mild solution  $M(t; \psi)$  such that  $M_t(\psi) \in \mathcal{C}$  for all  $t$  in its maximal interval of existence  $[0, \sigma_\psi)$  for  $\sigma_\psi > 0$ . Since  $W(t, s)$  is compact and analytic for  $t > s, s \in \mathbb{R}$ ,  $M(t; \psi)$  is compact and a classical solution of (3.2) for  $t > \hat{\tau}$ . In view of assumption (A1), it easily follows that for any  $H \geq \widetilde{M}$ ,  $\Sigma_H := \{\psi \in \mathcal{C}^+ : 0 \leq \psi \leq H\}$  is a positively invariant set for (3.2) (see, e.g. [34] and [35]). Thus, for any  $\psi \in \mathcal{C}^+$ ,  $M(t; \psi)$  globally exists on  $[0, \infty)$ . Recall that a family of operators  $\{Q_t\}_{t \geq 0}$  is a  $T$ -periodic semiflow on a metric space  $(\mathbf{Z}, \rho)$  with the metric  $\rho$ , provided that  $\{Q_t\}_{t \geq 0}$  satisfies: (i)  $Q_0(v) = v, \forall v \in \mathbf{Z}$ ; (ii)  $Q_t(Q_T(v)) = Q_{t+T}(v), \forall t \geq 0, \forall v \in \mathbf{Z}$ ; (iii)  $Q_t(v)$  is continuous in  $(t, v)$  on  $[0, \infty) \times \mathbf{Z}$ . Based on the  $T$ -periodicity of the coefficients in (3.1), the equation (3.1) can define a periodic semiflow  $\Psi_t : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  by

$$\Psi_t(\psi)(s, x) = M(t + s, x; \psi), \quad \forall s \in [-\tau(0), 0], x \in \overline{\Omega}.$$

Consider the following time-periodic and delayed differential equation:

$$\begin{cases} \dot{v}(t) = -(\mu_M(t) + g(v(t)))v(t) + (1 - \tau'(t))b(t - \tau(t), v(t - \tau(t))) \\ v(s) = \varphi(s) \in C([-\tau(0), 0], \mathbb{R}^+), \quad \forall s \in [-\tau(0), 0]. \end{cases} \quad (3.3)$$

Note that the function  $b(t, \cdot)$  is Lipschitz in any bounded subset of  $\mathbb{R}^+$  as defined in Assumption (A1). Consequently, for any  $\varphi \in C([-\tau(0), 0], \mathbb{R}^+)$ , the equation (3.3) admits a unique bounded solution  $v(t; \varphi)$  with  $v(s; \varphi) = \varphi(s), \forall s \in [-\tau(0), 0]$ , which globally exists on  $[0, \infty)$ . In the following, we state a comparison theorem associated with the solutions of equations (3.1) and (3.3).

**Lemma 3.1.** *For any given  $\xi \in \mathcal{C}^+$ , let  $\widehat{H}(s) = \max\{\xi(s, x), x \in \overline{\Omega}\}, \forall s \in [-\tau(0), 0]$ . Let  $v(t; \widehat{H})$  be the solution of the following differential equation:*

$$\begin{cases} \dot{v}(t) = -(\mu_M(t) + g(v(t)))v(t) + (1 - \tau'(t))b(t - \tau(t), v(t - \tau(t))), \\ v(s) = \widehat{H}(s) \in C([-\tau(0), 0], \mathbb{R}^+), \quad \forall s \in [-\tau(0), 0]. \end{cases}$$

*Then the solution  $M(t, x; \xi)$  of (3.1) with  $M_0 = \xi$  satisfies  $M(t, x; \xi) \leq v(t; \widehat{H})$  for all  $(t, x) \in (0, \infty) \times \overline{\Omega}$ .*

*Proof.* Let  $g_\alpha(t, u) = \alpha u - (\mu_M(t) + g(u))u$ , where  $\alpha$  is a sufficiently large number that makes  $g_\alpha(t, u)$  increasing with respect to all  $u \in [0, H]$ . Note that,

$$\dot{v}(t) = -\alpha v(t) + g_\alpha(t, v) + (1 - \tau'(t))b(t - \tau(t), v(t - \tau(t))),$$

and

$$\begin{aligned} \frac{\partial M(t, x)}{\partial t} &= D_2 \Delta M(t, x) - \alpha M(t, x) + g_\alpha(t, M(t, x)) \\ &\quad + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), M(t - \tau(t), y)) dy, \end{aligned}$$

Let  $\mathcal{Q}(t)$  ( $t \geq 0$ ) be the strongly continuous semigroups generated by  $D_2\Delta$  and the Neumann boundary condition. Thus,

$$v(t) = e^{-\alpha(t-s)}v(s) + \int_s^t e^{-\alpha(t-r)} [g_\alpha(r, v(r)) + (1 - \tau'(r))b(r - \tau(r), v(r - \tau(r)))] dr$$

and

$$M(t, x) = e^{-\alpha(t-s)}\mathcal{Q}(t-s)M(s, x) + \int_s^t e^{-\alpha(t-r)}\mathcal{Q}(t-r) \left[ g_\alpha(r, M(r)) + (1 - \tau'(r)) \int_\Omega \Gamma_0(r, r - \tau(r), x, y, D_1) b(r - \tau(r), M(r - \tau(r), y)) dy \right] (x) dr.$$

Set  $w(t, x) = M(t, x; \xi) - v(t; \hat{H})$  for any  $(t, x) \in [0, \bar{\tau}] \times \bar{\Omega}$ . Then, we have

$$w(t, x) \leq e^{-\alpha(t-s)}\mathcal{Q}(t-s)w(s, x) + \int_s^t e^{-\alpha(t-r)}\mathcal{Q}(t-r)(g_\alpha(r, M(r)) - g_\alpha(r, v(r)))(x)dr, \quad (3.4)$$

for  $0 \leq s < t \leq \bar{\tau}$ , where  $\bar{\tau}$  is defined as in (2.4). Let  $\hat{w}(t) = \sup_{x \in \bar{\Omega}} w(t, x)$  for  $t \in [-\tau(0), \bar{\tau}]$ . It is obvious that  $\hat{w}(t) \leq 0$  for  $t \in [-\tau(0), 0]$ . We first prove  $\hat{w}(t) \leq 0$  for any  $t \in (0, \tilde{t}]$ , where  $\tilde{t} = \min\{\bar{\tau}, \frac{1}{\rho}\}$  with  $\rho > 0$  being a constant determined later.

Suppose, by contradiction, that there exist a positive number  $\delta$  and a  $t_0 \in (0, \tilde{t}]$  such that  $0 < \hat{w}(t_0) < \delta$  and  $\hat{w}(t_0) \geq \hat{w}(t)$  for  $t \in (0, t_0]$ . By the definition of  $g_\alpha(t, u)$ , there is a  $\rho > 0$  such that  $0 \leq \frac{\partial g_\alpha}{\partial u}(t, u) \leq \rho$  for  $t \geq 0$  and  $u \in [0, H]$ . Thus,

$$\begin{aligned} g_\alpha(t, M(r, x)) - g_\alpha(t, v(r)) &= \frac{\partial g_\alpha}{\partial u}(t, \zeta(r, x))(M(r, x) - v(r)) \\ &\leq \frac{\partial g_\alpha}{\partial u}(t, \zeta(r, x))\hat{w}(t_0) \leq \rho\hat{w}(t_0), \end{aligned}$$

for any  $r \in (0, t_0]$  and  $x \in \bar{\Omega}$ , where  $\zeta(r, x)$  is between  $u(r, x)$  and  $v(r)$ . It then follows from (3.4) that

$$\begin{aligned} \hat{w}(t_0) &\leq \sup_{x \in \bar{\Omega}} e^{-\alpha t_0} \mathcal{Q}(t_0)w(0)(x) + \sup_{x \in \bar{\Omega}} \int_0^{t_0} e^{-\alpha(t_0-r)} (g_\alpha(r, M(r)) - g_\alpha(r, v(r)))(x) dr \\ &\leq e^{-\alpha t_0} \hat{w}(0) + \rho \hat{w}(t_0) \int_0^{t_0} e^{-\alpha(t_0-r)} dr \\ &\leq \rho \hat{w}(t_0) \int_0^{t_0} e^{-\alpha(t_0-r)} dr \\ &\leq \rho t_0 \hat{w}(t_0) \\ &< \hat{w}(t_0), \end{aligned}$$

which is a contradiction, and hence,  $\hat{w}(t) \leq 0$  for any  $t \in (0, \tilde{t}]$ . By repeating the above arguments for finite times, we can prove that  $\hat{w}(t) \leq 0$  for any  $(t, x) \in [0, \hat{\tau}] \times \bar{\Omega}$ . This means that

$$M(t, x) \leq v(t) \text{ for } (t, x) \in [0, \hat{\tau}] \times \bar{\Omega}.$$

Now we prove that  $M(t, x; \xi) \leq v(t, \widehat{H})$  holds for  $t \in (\hat{\tau}, \infty)$ . In this situation,  $M(t, x; \xi)$  is a classical solution of (3.1). Let  $w(t, x) = M(t, x; \xi) - v(t; \widehat{H})$ . Then we have

$$\begin{cases} \frac{\partial}{\partial t} w(t, x) - D_2 \Delta w(t, x) + \mu_M(t) w(t, x) + h(t, x) w(t, x) \\ = \frac{\partial}{\partial t} w(t, x) - D_2 \Delta w(t, x) + \mu_M(t) w(t, x) + (g(M)M - g(v)v) \leq 0, \quad \forall x \in \Omega, \\ \frac{\partial}{\partial n} w(t, x) = 0, \quad \forall x \in \partial\Omega, \end{cases}$$

for  $t \in (\hat{\tau}, \hat{\tau} + \bar{\tau})$ , where  $h(t, x) = G'(M(t, x) + \varrho[v(t) - M(t, x)])$ ,  $\varrho \in (0, 1)$ , is bounded and  $G(u) = g(u)u$ . Thus, the parabolic maximum principle implies that  $w(t, x) \leq 0$ , and hence,  $M(t, x; \xi) \leq v(t; \widehat{H})$  for any  $t \in (\hat{\tau}, \hat{\tau} + \bar{\tau}]$ . Continuing this procedure on  $t \in [\hat{\tau} + n\bar{\tau}, \hat{\tau} + (n+1)\bar{\tau}]$ ,  $n = 1, \dots, \infty$ , respectively, we can obtain that  $M(t, x; \xi) \leq v(t; \widehat{H})$  holds for  $t \in (\hat{\tau}, \infty)$ .  $\square$

**Remark 3.2.** Note that  $v(t, x) = v(t, \widehat{H})$  for all  $x \in \bar{\Omega}$  also satisfies the reaction-diffusion equation (3.1) and the comparison principle for reaction-diffusion systems with time delays [34] can also be used to establish this result. Here we use a basic approach for reader's interest.

On the basis of the above discussion and Lemma 3.1, we show the following results on the existence of a global attractor of  $\Psi_T : \mathcal{C}^+ \rightarrow \mathcal{C}^+$ .

**Theorem 3.3.** For each  $\psi \in \mathcal{C}^+$ , the equation (3.1) admits a unique solution  $M(t, x; \psi)$  on  $[0, \infty) \times \bar{\Omega}$  with  $M_0 = \psi$ . Moreover, equation (3.1) generates a  $T$ -periodic semiflow  $\Psi_t = M_t(\cdot) : \mathcal{C}^+ \rightarrow \mathcal{C}^+$ , i.e.  $\Psi_t(\psi)(\theta, x) = M(t + \theta, x; \psi)$ ,  $\forall \psi \in \mathcal{C}^+$ ,  $t \geq 0$ ,  $\theta \in [-\tau(0), 0]$ ,  $x \in \Omega$ , and  $\Psi_T : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  has a global compact attractor in  $\mathcal{C}^+$ .

*Proof.* Here we only prove the existence of a global attractor as the global existence of solutions was argued earlier. To do that, we first show the solutions of (3.1) are eventually uniformly bounded.

Note that the equation (3.3) admits a unique bounded solution  $v(t; \varphi)$  with  $v(s; \varphi) = \varphi(s)$ ,  $\forall s \in [-\tau(0), 0]$ , which globally exists on  $[0, \infty)$ . Therefore, for any  $\varphi \in C([-\tau(0), 0], \mathbb{R}^+)$ , the omega limit set  $\omega(\varphi)$  of the positive orbit  $\gamma^+(\varphi) = \{v_t(\varphi) : t \geq 0\}$  is nonempty, compact and invariant. Let  $G := \{\psi(s) : \psi \in \omega(\varphi), s \in [-\tau(0), 0]\}$ . On the basis of the compactness of  $\omega(\varphi)$ , it follows that  $G$  is compact. As a result, there exist  $s_0 \in [-\tau(0), 0]$  and  $\psi \in \omega(\varphi)$  such that  $\psi(s_0) = \max\{G\} := H_G$ . For any  $t \in [0, \hat{\tau}]$ , since  $t - \tau(t)$  is increasing with respect to  $t$ , we have

$$-\tau(0) = 0 - \tau(0) \leq t - \tau(t) \leq \hat{\tau} - \tau(\hat{\tau}) \text{ while } \hat{\tau} - \tau(\hat{\tau}) \geq \hat{\tau} - \hat{\tau} = 0.$$

Hence there exists  $t_0 \in [0, \hat{\tau}]$  such that  $t_0 = \tau(t_0)$ . By means of the invariance of  $\omega(\varphi)$ , there exists  $\psi^* \in \omega(\varphi)$  such that  $v_{t_0}(\psi^*) = \psi$ , i.e.  $v(t_0 + s; \psi^*) = \psi(s)$ ,  $\forall s \in [-\tau(0), 0]$ . Without loss of generality, we assume that  $\psi(0) = H_G$ . Assume that  $H_G > \widetilde{M}$ , it then follows from assumption (A1) that

$$\begin{aligned} \dot{v}(t_0; \psi^*) &\leq -(\mu_M(t_0) + g(v(t_0; \psi^*)))v(t_0; \psi^*) + (1 - \tau'(t_0))b(0, v(0; \psi^*)) \\ &\leq -(\mu_M(t_0) + g(H_G))H_G + (1 - \tau'(t_0))b(0, H_G) < 0. \end{aligned}$$

Hence, there exists some  $s \in [-\tau(0), 0]$  such that  $\psi(s) > \psi(0) = H_G$ , a contradiction. Thus,

$$\limsup_{t \rightarrow \infty} v(t; \varphi) \leq \widetilde{M}, \quad \forall \varphi \in C([-\tau(0), 0], \mathbb{R}^+).$$

For any given  $\phi \in \mathcal{C}^+$ , let  $\widehat{\phi}(\theta) := \max\{\phi(\theta, x) : x \in \overline{\Omega}\}$ ,  $\forall \theta \in [-\tau(0), 0]$ . Then,  $\limsup_{t \rightarrow \infty} v(t; \widehat{\phi}) \leq \widetilde{M}$ . By Lemma 3.1, we have  $\limsup_{t \rightarrow \infty} M(t, x; \phi) \leq \limsup_{t \rightarrow \infty} v(t; \widehat{\phi}) \leq \widetilde{M}$ ,  $\forall x \in \overline{\Omega}$ , which means that  $\Psi_t : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  is point dissipative. According to [36, Lemma 4.1] and [37, Section 3.5],  $\Psi_T : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  is  $\kappa$ -contraction and hence asymptotically smooth. Therefore, it follows from [37, Theorem 1.1.2] that  $\Psi_T : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  has a global compact attractor.  $\square$

We further show that the periodic semiflow  $\Psi_t : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  is strongly monotone and strictly subhomogeneous in  $\mathcal{C}^+$ .

**Lemma 3.4.** *For any  $\phi$  and  $\psi$  in  $\mathcal{C}^+$  with  $\phi > \psi$  (that is,  $\phi \geq \psi$  but  $\phi \neq \psi$ ), the solutions  $u(t, x; \phi)$  and  $v(t, x; \psi)$  of system (3.1) with  $u(\theta, x) = \phi(\theta, x)$  and  $v(\theta, x) = \psi(\theta, x)$ , for all  $\theta \in [-\tau(0), 0]$  and  $x \in \overline{\Omega}$  respectively, satisfy that  $u(t, x; \phi) > v(t, x; \psi)$  for all  $t > \hat{\tau}$ , and hence  $\Psi_t(\phi) \gg \Psi_t(\psi)$  in  $\mathcal{C}$  for all  $t > 2\hat{\tau}$ .*

*Proof.* By a comparison argument on each interval  $[n\tau(0), (n+1)\tau(0)]$ ,  $\forall n \in \mathbb{N}$  as in the proof of Lemma 3.1, it is not difficult to show that  $u(t, x; \phi) \geq v(t, x; \psi)$  for all  $t \geq 0$ . Note that  $u_t$  and  $v_t$  satisfy the following integral equation for all  $t \geq 0$ :

$$M(t)(x) = e^{-\alpha t} \mathcal{Q}(t) M(0)(x) + \int_0^t e^{-\alpha(t-s)} \mathcal{Q}(t-s) \left[ g_\alpha(s, M(s)) + (1 - \tau'(s)) \int_\Omega \Gamma_0(s, s - \tau(s), x, y, D_1) b(s - \tau(s), M(s - \tau(s), y)) dy \right] (x) ds, \quad (3.5)$$

where  $g_\alpha(t, u)$  and  $\mathcal{Q}(t)$  are defined as in the proof of Lemma 3.1. Then for any  $\phi$  and  $\psi$  in  $\mathcal{C}^+$  with  $\phi > \psi$ , it follows from (3.5) and the strong positivity of  $\mathcal{Q}(t)$ ,  $t > 0$  that

$$w(t, x) := u(t, x; \phi) - v(t, x; \psi) \geq e^{-\alpha t} \mathcal{Q}(t) (\phi(0, \cdot) - \psi(0, \cdot)) > 0, \quad t > 0$$

provided that  $\phi(0, \cdot) \not\equiv \psi(0, \cdot)$ .

In the following, we show that for any  $\phi$  and  $\psi$  in  $\mathcal{C}^+$  with  $\phi > \psi$  and  $\phi(0, \cdot) = \psi(0, \cdot)$ , there exists  $t_0 \in [0, \hat{\tau}]$  such that  $w(t_0, \cdot) > 0$ . Suppose, by contradiction, that for a pair of initial values  $\phi, \psi \in \mathcal{C}^+$  with  $\phi > \psi$  and  $\phi(0, \cdot) = \psi(0, \cdot)$ , there holds  $w(t, \cdot) \equiv 0$  for  $t \in [0, \hat{\tau}]$ . In view of (3.5), we have that

$$\begin{aligned} 0 = w(t)(x) &= \int_0^t e^{-\alpha(t-s)} \mathcal{Q}(t-s) [g_\alpha(s, u(s, \cdot; \phi)) - g_\alpha(s, v(s, \cdot; \psi))] (x) ds \\ &\quad + \int_0^t e^{-\alpha(t-s)} \mathcal{Q}(t-s) (1 - \tau'(s)) \int_\Omega \Gamma(s, s - \tau(s), x, y, D_1) \\ &\quad \left[ b(s - \tau(s), u(s - \tau(s), y)) - b(s - \tau(s), v(s - \tau(s), y)) \right] (x) dy ds \end{aligned}$$

for  $t \in [0, \hat{\tau}]$ . Since  $e^{-\alpha(t-s)} \mathcal{Q}(t-s)$  is strongly positive for  $t > s \geq 0$ , and both  $g_\alpha(t, u)$  and  $b(t, u)$  are increasing functions with respect to the variable  $u$ , we must have

$$b(s - \tau(s), u(s - \tau(s), y)) - b(s - \tau(s), v(s - \tau(s), y)) \equiv 0$$

for any  $s \in [0, \hat{\tau}]$  and  $y \in \overline{\Omega}$ , which implies that  $u(s - \tau(s), y) = v(s - \tau(s), y)$  for any  $s \in [0, \hat{\tau}]$  and  $y \in \overline{\Omega}$ . This contradicts to  $\phi > \psi$ . Consequently, we have  $w(t_0, \cdot) > 0$  for some  $t_0 \in [0, \hat{\tau}]$ . Applying the strong positivity of  $e^{-\alpha(t-s)} \mathcal{Q}(t-s)$  for  $t > s \geq 0$  and (3.5) again, for any  $t > t_0$ , we see that

$$w(t, x) \geq e^{-\alpha(t-t_0)} \mathcal{Q}(t-t_0) (u(t_0, \cdot, \phi) - v(t_0, \cdot, \psi)) = e^{-\alpha(t-t_0)} \mathcal{Q}(t-t_0) w(t_0, \cdot) > 0, \quad t > t_0.$$

Therefore, for any  $\phi$  and  $\psi$  in  $\mathcal{C}^+$  with  $\phi > \psi$ , there holds  $u(t, x; \phi) > v(t, x; \psi)$  for all  $t > \hat{\tau}$  and  $x \in \overline{\Omega}$ , which further implies that  $\Psi_t$  is strongly monotone whenever  $t > 2\hat{\tau}$ .  $\square$

In order to show the periodic semiflow is strictly subhomogeneous, a further assumption about the birth rate  $b(t, M)$  should be imposed:

(A3) The birth rate  $b(t, M)$  is strictly subhomogeneous in  $M$  in the sense that for any  $k \in (0, 1)$ ,  $b(t, kM) > kb(t, M)$  for all  $M > 0$  and  $t \geq 0$ .

Based on this assumption, we can show  $\Psi_t$  is strictly subhomogeneous through the following lemma.

**Lemma 3.5.** *For each  $t > 2\hat{\tau}$ ,  $\Psi_t : \mathcal{C}^+ \rightarrow \mathcal{C}^+$  is strictly subhomogeneous.*

*Proof.* For any  $\psi \in \mathcal{C}^+$  with  $\psi \not\equiv 0$ , let  $u(t, x; \psi)$  be the solution of system (3.1) with  $u(\theta, x) = \psi(\theta, x)$  for all  $\theta \in [-\tau(0), 0]$  and  $x \in \bar{\Omega}$ . For a fixed  $k \in (0, 1)$ , by (A2) and (A3), we have

$$\begin{aligned} \frac{\partial(ku(t, x))}{\partial t} &= D_2 \Delta(ku(t, x)) - (\mu_M(t) + g(u(t, x)))(ku(t, x)) \\ &\quad + k(1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), u(t - \tau(t), y)) dy \\ &\leq D_2 \Delta(ku(t, x)) - \mu_M(t)(ku(t, x)) - g(ku(t, x))(ku(t, x)) \\ &\quad + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), ku(t - \tau(t), y)) dy. \end{aligned}$$

By a similar comparison argument to the proof of Lemma 3.1, it is not difficult to see from the above inequality that  $ku(t, x; \psi) \leq u(t, x; k\psi)$  for  $t \geq 0$ , where  $u(t, x; k\psi)$  is the solution of (3.1) with  $u(\theta, x; k\psi) = k\psi(\theta, x)$  for  $(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$ .

Let  $w(t, x) = u(t, x; k\psi) - ku(t, x; \psi)$ . Then  $w(\theta, x) = 0$  for  $(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$  and  $w(\theta, x) \geq 0$  for  $(\theta, x) \in [-\tau(0), \infty) \times \bar{\Omega}$ . In the following, we show that  $w(t, x) > 0$  for all  $t > \hat{\tau}$ ,  $x \in \bar{\Omega}$ . Let

$$\begin{aligned} &\mathbf{P}(t, u(t, x), u(t - \tau(t), x)) \\ &= -g(u(t, x))u(t, x) + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) b(t - \tau(t), u(t - \tau(t), y)) dy. \end{aligned}$$

Then we have

$$\begin{aligned} &\frac{\partial w(t, x)}{\partial t} \\ &= \frac{\partial u(t, x; k\psi)}{\partial t} - k \frac{\partial u(t, x; \psi)}{\partial t} \\ &= D_2 \Delta u(t, x; k\psi) - \mu_M(t)u(t, x; k\psi) + \mathbf{P}(t, u(t, x; k\psi), u(t - \tau(t), x; k\psi)) \\ &\quad - k[D_2 \Delta u(t, x; \psi) - \mu_M(t)u(t, x; \psi) + \mathbf{P}(t, u(t, x; \psi), u(t - \tau(t), x; \psi))] \\ &= D_2 \Delta w(t, x) - \mu_M(t)w(t, x) - g(u(t, x; k\psi))u(t, x; k\psi) + kg(ku(t, x; \psi))u(t, x; \psi) \\ &\quad + R(t, x) + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \left[ b(t - \tau(t), u(t - \tau(t), y; k\psi)) \right. \\ &\quad \left. - b(t - \tau(t), ku(t - \tau(t), y; \psi)) \right] dy \\ &\geq D_2 \Delta w(t, x) - \mu_M(t)w(t, x) - g(u(t, x; k\psi))u(t, x; k\psi) + kg(ku(t, x; \psi))u(t, x; \psi) + R(t, x) \end{aligned}$$

where

$$R(t, x) = \mathbf{P}(t, ku(t, x; \psi), ku(t - \tau(t), x; \psi)) - k\mathbf{P}(t, u(t, x; \psi), u(t - \tau(t), x; \psi)).$$

Note that

$$g(ku(t, x; \psi))(ku(t, x; \psi)) - g(u(t, x; k\psi))u(t, x; k\psi)$$

$$= -G'(ku(t, x; \psi) + \varrho[u(t, x; k\psi) - ku(t, x; \psi)])w(t, x), \quad \varrho \in (0, 1),$$

where  $G(\zeta) = g(\zeta)\zeta$ , and  $G'(\zeta)$  is bounded, that is, there exists a positive number  $l > 0$  such that  $-l \leq G'(\zeta) \leq l$ . Consequently, we have

$$\frac{\partial w(t, x)}{\partial t} \geq D_2 \Delta w(t, x) - \mu_M(t)w(t, x) - lw(t, x) + R(t, x).$$

In view of the assumption (A3), we have  $R(t, x) > 0$  for  $t > \hat{\tau}$  and  $x \in \bar{\Omega}$ . Consider the following equation

$$\begin{cases} \frac{\partial \check{w}(t, x)}{\partial t} = D_2 \Delta \check{w}(t, x) - \mu_M(t)\check{w}(t, x) - h(t, x)\check{w}(t, x) + R(t, x), & t > 0, \\ \check{w}(0, x) = 0, & x \in \bar{\Omega}, \end{cases} \quad (3.6)$$

which can be rewritten as

$$\check{w}(t, \cdot; \psi) = \int_0^t U(t, s)R(s, \cdot)ds, \quad t \geq 0,$$

where  $U(t, s), 0 \leq s \leq t$  is the evolution operator generated by

$$\begin{cases} \frac{\partial \check{w}(t, x)}{\partial t} = D_2 \Delta \check{w}(t, x) - \mu_M(t)\check{w}(t, x) - h(t, x)\check{w}(t, x), & t > 0, \\ \frac{\partial \check{w}(t, x)}{\partial n} = 0, & t > 0, x \in \partial\Omega. \end{cases}$$

Since  $R(t, x) > 0, \forall t > \hat{\tau}, x \in \bar{\Omega}$ , we can conclude from the strong positivity of  $U(t, s), 0 \leq s < t$  that the solution of (3.6) satisfies  $\check{w}(t, x) > 0$  for all  $t > \hat{\tau}$  and  $x \in \bar{\Omega}$ . It then follows from the comparison principle that  $w(t, x) \geq \check{w}(t, x) > 0$  for all  $t > \hat{\tau}$  and  $x \in \bar{\Omega}$ . Therefore,  $u(t, x; k\psi) > ku(t, x; \psi)$  for all  $t > \hat{\tau}, x \in \bar{\Omega}$ , and hence,  $\Psi_t(k\psi) > k\Psi_t(\psi)$  for all  $t > \hat{\tau}$ , which implies that for each  $t > 2\hat{\tau}$ ,  $\Psi_t$  is strictly subhomogeneous.  $\square$

### 3.2 Basic reproduction number

Set the ordered Banach space consisting of all  $T$ -periodic continuous functions from  $\mathbb{R}$  to  $\mathbf{Y}$  as  $C_T(\mathbb{R}, \mathbf{Y})$ , where  $\|\phi\|_{C_T(\mathbb{R}, \mathbf{Y})} := \max_{\theta \in [0, T]} \|\phi\|_{\mathbf{Y}}$  for any  $\phi \in C_T(\mathbb{R}, \mathbf{Y})$ . The positive cone of  $C_T(\mathbb{R}, \mathbf{Y})$  is defined as follows:

$$C_T^+(\mathbb{R}, \mathbf{Y}) := \{\phi \in C_T(\mathbb{R}, \mathbf{Y}) : \phi(t)(x) \geq 0, \forall t \in \mathbb{R}, x \in \bar{\Omega}\}.$$

The linearized system for (3.1) at the population extinction equilibrium  $M = 0$  is shown as follows:

$$\begin{cases} \frac{\partial w(t, x)}{\partial t} = D_2 \Delta w(t, x) - \mu_M(t)w(t, x) \\ \quad + (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \beta(t - \tau(t))w(t - \tau(t), y)dy, \\ \quad t > 0, x \in \Omega, \\ \frac{\partial w(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega, \\ w(\theta, x) = \varphi(\theta, x), \quad \varphi \in \mathcal{C}, \theta \in [-\tau(0), 0], x \in \Omega. \end{cases} \quad (3.7)$$

Similar to the previous subsection, we know that (3.7) has a unique mild solution  $w(t, x; \varphi)$  with  $w_0(\cdot, \cdot; \varphi) = \varphi$  and  $w_t(\cdot, \cdot; \varphi) \in \mathcal{C}^+$  for all  $t \geq 0$ . Moreover,  $w(t, x; \varphi)$  is a classical solution when  $t > \hat{\tau}$ , and  $w_t(\cdot, \cdot; \varphi)$  is strongly positive and compact on  $\mathcal{C}^+$  for all  $t > 2\hat{\tau}$ . Define  $P : \mathcal{C} \rightarrow \mathcal{C}$  by  $P(\varphi) = w_T(\varphi)$  for all  $\varphi \in \mathcal{C}$ , where  $w_T(\varphi)(\theta, x) = w(T + \theta, x; \varphi)$  for all  $(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$ , and  $w_t$  is the solution map of (3.7). Thus, we have  $P^{n_0} = w_{n_0 T}$  is compact and strongly positive, where  $n_0 := \min\{n \in \mathbb{N} : nT > 2\hat{\tau}\}$ . Let  $r(P)$  be the spectral radius of  $P$ . By virtue of [38, Lemma 3.1] that  $r(P)$  is a simple eigenvalue of  $P$  having a strongly positive eigenvector  $\bar{\varphi}$ , and the modulus of any other eigenvalue is less than  $r(P)$ . Let  $w(t, x; \bar{\varphi})$  be the solution of (3.7) with  $w(s, x; \bar{\varphi}) = \bar{\varphi}(s, x)$  for all  $s \in [-\tau(0), 0], x \in \Omega$ . By the strong positivity of  $\bar{\varphi}$ , we have  $w(\cdot, \cdot; \bar{\varphi}) \gg 0$ . Inspired by [39, Proposition 2.1], we can prove the following observation, which indicates the existence of a special solution of system (3.7).

**Lemma 3.6.** *There exists a positive  $T$ -periodic function  $v^*(t, x)$  such that  $e^{\mu t} v^*(t, x)$  is a solution of (3.7), where  $\mu = \frac{\ln r(P)}{T}$ .*

*Proof.* Since  $\bar{\varphi}$  is the eigenvector of  $P$ , we have  $P\bar{\varphi} = r(P)\bar{\varphi}$ . That is

$$w(s + T, x; \bar{\varphi}) = r(P)\bar{\varphi}(s)(x), \quad \forall s \in [-\tau(0), 0].$$

Let  $\mu = \frac{\ln r(P)}{T}$  and  $v^*(t, x) = e^{-\mu t} w(t, x; \bar{\varphi})$  for all  $t \geq -\tau(0), x \in \Omega$ . Then  $r(P) = e^{\mu T}$ . By a following simple calculation, we can see that  $v^*(t, x)$  is periodic. In fact, for all  $s \in [-\tau(0), 0]$ , we have

$$w(s + T, x; \bar{\varphi}) = P\bar{\varphi}(s)(x) = r(P)\bar{\varphi}(s)(x).$$

Then, for all  $t \geq 0$ ,

$$w(t + T, x; \bar{\varphi}) = r(P)w(t, x; \bar{\varphi}).$$

This indicates that

$$v^*(t + T, x) = e^{-\mu(t+T)} w(t + T, x; \bar{\varphi}) = e^{-\mu t} e^{-\mu T} r(P)w(t, x; \bar{\varphi}) = e^{-\mu t} w(t, x; \bar{\varphi}) = v^*(t, x).$$

Thus, the equation (3.7) admits a positive solution  $e^{-\mu t} v^*(t, x)$  with  $v^*(t, x)$  being periodic in  $t$ .  $\square$

Let  $\phi(s, x) = \phi(s)(x) \in C_T(\mathbb{R}, \mathbf{Y}^+)$  be the initial distribution of adult individuals at time  $s \in \mathbb{R}$  and the spatial location  $x \in \bar{\Omega}$ . Define an operator  $C(t) : \mathbf{Y} \rightarrow \mathbf{Y}$  as follows:

$$(C(t)\varphi)(x) := (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \beta(t - \tau(t)) \varphi(y) dy, \quad \forall \varphi \in \mathbf{Y}.$$

Recall that  $W(t, s)$  is the evolution operator determined by the following linear reaction-diffusion equation:

$$\begin{cases} \frac{\partial w(t, x)}{\partial t} = D_2 \Delta w(t, x) - \mu_M(t) w(t, x), & t > 0, x \in \Omega, \\ \frac{\partial w(t, x)}{\partial n} = 0, & t > 0, x \in \partial\Omega. \end{cases}$$

Then,  $W(t - \tau(t), s)\phi(s)(x)$  represents the density distribution of the individuals who matured into adults at previous time  $s$  ( $s < t - \tau(t)$ ) and survived to time  $t - \tau(t)$  at location  $x$ . Hence,  $\int_{-\infty}^{t - \tau(t)} W(t - \tau(t), s)\phi(s)(x) ds$  denotes the density distribution of the accumulative individuals who



matured into adults at all previous time  $s < t - \tau(t)$  and survived to time  $t - \tau(t)$  at location  $x$ . Thus, the distribution of newborn individuals at location  $x$  and time  $t$  can be represented as follows:

$$\begin{aligned}
& (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \beta(t - \tau(t)) \left( \int_{-\infty}^{t - \tau(t)} W(t - \tau(t), s) \phi(s)(y) ds \right) dy \\
&= (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \beta(t - \tau(t)) \left( \int_{\tau(t)}^{\infty} W(t - \tau(t), t - s) \phi(t - s)(y) ds \right) dy \\
&= \int_{\tau(t)}^{\infty} (1 - \tau'(t)) \int_{\Omega} \Gamma(t, t - \tau(t), x, y, D_1) \beta(t - \tau(t)) W(t - \tau(t), t - s) \phi(t - s)(y) dy ds \\
&= \int_{\tau(t)}^{\infty} \left[ C(t) (W(t - \tau(t), t - s) \phi(t - s)) \right] (x) ds \\
&= \int_0^{\infty} \left[ H(t, s) \phi(t - s) \right] (x) ds,
\end{aligned}$$

where  $H(t, s)$ ,  $t \in \mathbb{R}$ ,  $s \geq 0$  is defined as follows:

$$H(t, s) := \begin{cases} C(t) W(t - \tau(t), t - s), & s > \tau(t), \\ 0, & s \in [0, \tau(t)]. \end{cases}$$

Thus, the next generation operator  $\mathcal{L}$  can be defined as

$$\mathcal{L}(\phi)(t) := \int_0^{\infty} H(t, s) \phi(t - s) ds, \quad \forall t \in \mathbb{R}, \phi \in C_T(\mathbb{R}, \mathbf{Y}).$$

It easily follows that  $\mathcal{L}$  is a positive and bounded linear operator on  $C_T(\mathbb{R}, \mathbf{Y})$ . The basic reproduction number can be defined as the spectral radius of  $\mathcal{L}$ , that is,

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

In the light of [36, Theorem 3.4] and [40, Remark 2.1] (see also [41, Theorem 3.7]), we obtain the subsequent result, which implies that  $\mathcal{R}_0$  serves as a threshold value for the stability of the zero solution for system (3.7).

**Lemma 3.7.**  $\mathcal{R}_0 - 1$  has the same sign as  $r(P) - 1$ .

### 3.3 Global dynamics

The main focus of this section is to show the global attractivity of the system (3.1) in terms of  $\mathcal{R}_0$  by employing the theory of monotone and subhomogeneous semiflows [37, Section 2.3]. Since the strong monotonicity and strict sub-homogeneity of the periodic semiflow  $\Psi_t$  has been proven (see Lemmas 3.4 and 3.5), it is time to show the global stability of system (3.1) when  $\mathcal{R}_0 > 1$  in  $\mathcal{C}^+$ .

**Theorem 3.8.** *If  $\mathcal{R}_0 > 1$ , then system (3.1) admits a unique positive  $T$ -periodic solution  $M^*(t, x)$ , which is globally asymptotically stable in  $\mathcal{C}^+ \setminus \{0\}$ .*

*Proof.* We can fix an integer  $n_0$  such that  $n_0 T > 2\hat{\tau}$ , then  $\Psi_t$  can be regarded as an  $n_0 T$ -periodic semiflow on  $\mathcal{C}^+$ . Furthermore,  $\Psi_{n_0 T}$  is a strongly monotone and strictly subhomogeneous map on  $\mathcal{C}^+$  as a consequence of Lemma 3.4 and 3.5. It follows from [37, Theorem 2.3.4] that system (3.1) admits a unique positive  $n_0 T$ -periodic and globally asymptotically stable solution  $M^*(t, x)$  when  $r(D\Psi_{n_0 T}(0)) > 1$ . Note that  $r(D\Psi_{n_0 T}(0)) = r(P(n_0 T)) = (r(P(T)))^{n_0}$ . It then follows from

Lemma 3.7 that  $\text{sign}(\mathcal{R}_0 - 1) = \text{sign}(r(D\Psi_{n_0 T}(0)) - 1)$ . Hence, it suffices to show the existence of the unique  $T$ -periodic positive solution  $M^*(t, x)$  when  $\mathcal{R}_0 > 1$ . This is true since

$$\Psi_T^{n_0}(\Psi_T \psi^*) = \Psi_T(\Psi_T^{n_0} \psi^*) = \Psi_T(\Psi_{n_0 T} \psi^*) = \Psi_T(\psi^*),$$

where  $\psi^*(s, \cdot) = M^*(s, \cdot)$  for all  $s \in [-\tau(0), 0]$  guaranteeing that  $\Psi_{n_0 T} \psi^* = \psi^*$ . Therefore, the uniqueness of the positive fixed point of  $\Psi_T^{n_0} = \Psi_{n_0 T}$  implies that  $\Psi_T \psi^* = \psi^*$  holds, which indicates that  $M^*(t, x)$  is a  $T$ -periodic solution of system (3.1).  $\square$

By implying [37, Theorem 2.3.4] and a similar argument as in the previous proof, we can establish the following result:

**Theorem 3.9.** *If  $\mathcal{R}_0 \leq 1$ , then the zero equilibrium 0 is globally attractive for all solutions of system (3.1).*

It can be easily checked that  $I(t, x)$  can be represented by the following equivalent integral form:

$$I(t, x) = \int_{t-\tau(t)}^t \int_{\Omega} \Gamma(t, s, x, y, D_1) b(s, M(s, y)) dy ds, \quad t > 0, \quad x \in \Omega.$$

When  $\mathcal{R}_0 > 1$ , as a consequence of the global stability of  $M(t, x)$ , we can obtain the property of the solution for the other variable  $I(t, x)$  as well by using its integral form:

$$\lim_{t \rightarrow \infty} [I(t, x) - I^*(t, x)] = 0,$$

where

$$I^*(t, x) = \int_{t-\tau(t)}^t \int_{\Omega} \Gamma(t, s, x, y, D_1) b(s, M^*(s, y)) dy ds$$

is a positive  $T$ -periodic function. The scenario when  $\mathcal{R}_0 \leq 1$  can be discussed in a similar way. Thus, the global attractivity of the full system (2.6) can be obtained and summarized in the following theorem.

**Theorem 3.10.** *If  $\mathcal{R}_0 > 1$ , then system (2.6) admits a unique positive  $T$ -periodic solution  $(I^*(t, x), M^*(t, x))$ , which is globally attractive to all nontrivial solutions. If  $\mathcal{R}_0 \leq 1$ , then the population extinction equilibrium  $(0, 0)$  is globally attractive for all solutions.*

**Remark 3.11.** *The main analytic methodologies for the system (2.6) are also applicable to (2.7). In fact, due to the absence of the intra-specific competition ( $f(I) \equiv 0$ ), the  $I$  equation can be decoupled from (2.7).*

In the next section, we will establish the well-posedness and threshold dynamics for the model when the intra-specific competition is included and the immature dispersal ability is negligible.

## 4 Dynamics under immature intra-specific competition

In this section, we devoted to dynamics for system (2.8) with the constraint (2.9), namely, intra-specific competition is taken into account. As the beginning of this section, we introduce several notations. Let  $\mathbf{X} := C(\overline{\Omega}, \mathbb{R}^2)$  be the Banach space of continuous functions with the supremum norm  $\|\cdot\|_{\mathbf{X}}$ . Define  $\mathcal{E} = C([-\tau(0), 0], \mathbf{X})$ . For any  $\phi \in \mathcal{E}$ , define the norm  $\|\phi\| = \max_{\theta \in [-\tau(0), 0]} \|\phi(\theta)\|_{\mathbf{X}}$ . Then,  $\mathcal{E}$  is a Banach space. Let  $\mathbf{X}^+ := C(\overline{\Omega}, \mathbb{R}_+^2)$  and  $\mathcal{E}^+ = C([-\tau(0), 0], \mathbf{X}^+)$ , then  $(\mathbf{X}, \mathbf{X}^+)$  and

$(\mathcal{E}, \mathcal{E}^+)$  are both strongly ordered spaces. Given a function  $\mathbf{u}(t) : [-\tau(0), \sigma] \rightarrow \mathbf{X}$  for  $\sigma > 0$ , define  $\mathbf{u}_t \in \mathcal{E}$  by  $\mathbf{u}_t(\theta, x) = \mathbf{u}(t + \theta, x)$ , for all  $\theta \in [-\tau(0), 0]$ ,  $x \in \overline{\Omega}$  and  $t \in [0, \sigma]$ .

Define a linear operator  $\mathcal{A}$  by

$$\begin{aligned} D(\mathcal{A}) &= \{\phi \in C^2(\overline{\Omega}, \mathbb{R}) : \frac{\partial \phi}{\partial n} = 0 \text{ on } \partial\Omega\}, \\ \mathcal{A}\phi &= D_2\Delta\phi, \quad \forall \phi \in D(\mathcal{A}). \end{aligned}$$

Define a linear operator  $\mathbf{A} = \begin{pmatrix} 0 & 0 \\ 0 & \mathcal{A} \end{pmatrix}$  with  $D(\mathbf{A}) := C(\overline{\Omega}, \mathbb{R}) \times D(\mathcal{A})$  and

$$\mathbf{A}\phi = (0, \mathcal{A}\phi_2) \quad \text{for } \phi := (\phi_1, \phi_2) \in D(\mathbf{A}).$$

For  $t \geq 0$ , define nonlinear operators  $\mathbf{F}(t, \cdot) = (\mathbf{F}_1(t, \cdot), \mathbf{F}_2(t, \cdot)) : \mathcal{E}^+ \rightarrow \mathbf{X}$  by

$$\begin{aligned} \mathbf{F}_1(t, \phi) &= b(t, \phi_2(0, \cdot)) - (\mu_I(t) + f(\phi_1(0, \cdot)))\phi_1(0, \cdot) - (1 - \tau'(t)) \\ &\quad \times \exp\left(-\int_{t-\tau(t)}^t (\mu_I(s) + f(\phi_1(s, \cdot)))ds\right) b(t - \tau(t), \phi_2(-\tau(t), \cdot)), \\ \mathbf{F}_2(t, \phi) &= -(\mu_M(t) + g(\phi_2(0, \cdot)))\phi_2(0, \cdot) + (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^t (\mu_I(s) + f(\phi_1(s, \cdot)))ds\right) \\ &\quad \times b(t - \tau(t), \phi_2(-\tau(t), \cdot)), \end{aligned}$$

where  $\phi = (\phi_1, \phi_2) \in \mathcal{E}^+$ . Then, system (2.8) can be reformulated as the following abstract functional differential equations:

$$\begin{cases} \frac{\partial \mathbf{u}(t, \cdot)}{\partial t} = \mathbf{A}\mathbf{u}(t, \cdot) + \mathbf{F}(t, \mathbf{u}_t), & t > 0, \quad x \in \overline{\Omega}, \\ \mathbf{u}(\theta, x) = \phi(\theta, x), & \theta \in [-\tau(0), 0], \quad x \in \overline{\Omega}. \end{cases} \quad (4.1)$$

Let  $W(t)$  be the analytic semigroup on  $C(\overline{\Omega}, \mathbb{R})$  with the infinitesimal generator  $\mathcal{A}$ . Then, an strongly continuous semigroup on  $\mathbf{X}$  can be defined as  $\mathbf{U}(t) := \begin{pmatrix} \mathbf{I} & 0 \\ 0 & W(t) \end{pmatrix}$ , where  $\mathbf{I}$  is the identical operator on  $C(\overline{\Omega}, \mathbb{R})$ . Hence, the integral form of system (4.1) is shown as follows:

$$\mathbf{u}(t, \phi) = \mathbf{U}(t)\phi(0) + \int_0^t \mathbf{U}(t-s)\mathbf{F}(s, \mathbf{u}_s)ds, \quad t \geq 0, \quad \phi \in \mathcal{E}^+,$$

and the solution of which is a mild solution of (4.1).

Clearly,  $\mathbf{F}(t, \cdot)$  is locally Lipschitz continuous on  $\mathcal{E}^+$ , and hence for any  $\phi \in \mathcal{E}^+$ , system (2.8) admits a unique non-continuable mild solution  $\mathbf{u}(t; \phi)$  such that  $\mathbf{u}_t(\phi) \in \mathcal{E}$  for all  $t$  in its maximal interval of existence  $[0, \sigma_\phi]$  for  $\sigma_\phi > 0$  (see [34] and [35]).

It is obvious that the constraint (2.9) is equivalent to

$$\phi_1(0, x) = \int_{-\tau(0)}^0 \exp\left(-\int_s^0 (\mu_I(r) + f(\phi_1(r, x)))dr\right) b(s, \phi_2(s, x))ds. \quad (4.2)$$

Denote  $\mathcal{X}$  as the set of all  $\phi \in \mathcal{E}^+$  such that (4.2) holds. It follows that  $\mathcal{X}$  is a nonempty and closed subset of  $\mathcal{E}$ . Let  $\mathbf{u}(t, \phi)(x) = (I(t, x), M(t, x))$  for  $\phi \in \mathcal{X}$ , and define

$$w(t, x) = \int_{t-\tau(t)}^t \exp\left(-\int_s^t (\mu_I(r) + f(I(r, x)))dr\right) b(s, M(s, x))ds, \quad \forall t \in [0, \sigma_\phi].$$

Thus,

$$\begin{aligned} \frac{\partial w(t, x)}{\partial t} = & b(t, M(t, x)) - (\mu_I(t) + f(I(t, x)))I(t, x) - (1 - \tau'(t)) \\ & \times \exp\left(-\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, x)))ds\right) b(t - \tau(t), M(t - \tau(t), x)), \end{aligned}$$

and hence,

$$\frac{\partial(I(t, x) - w(t, x))}{\partial t} = -(\mu_I(t) + f(I(t, x)))(I(t, x) - w(t, x)), \quad \forall t \in [0, \sigma_\phi].$$

Since  $I(0, \cdot) = w(0, \cdot) = \phi_1(0, \cdot)$ , we have

$$I(t, \cdot) - w(t, \cdot) = V(t, 0)(I(0, \cdot) - w(0, \cdot)) = 0, \quad \forall t \in [0, \sigma_\phi],$$

which implies that for any  $\phi \in \mathcal{X}$ , the solution  $\mathbf{u}(t, x, \phi)$  satisfies

$$I(t, x) = \int_{t-\tau(t)}^t \exp\left(-\int_s^t (\mu_I(r) + f(I(r, x)))dr\right) b(s, M(s, x))ds, \quad \forall t \in [0, \sigma_\phi].$$

Applying Corollary 5 of [34] (or Corollary 1.11 of [35, Chapter 8]) to  $M(t, x)$ , we can get  $M(t, x) \geq 0$  for any  $t \in [0, \sigma_\phi]$  and  $x \in \bar{\Omega}$ . The above integral equation on  $I$  indicates that  $I(t, x)$  is also nonnegative, and hence,  $\mathbf{u}_t(\phi) \in \mathcal{E}^+$  for all  $t \in [0, \sigma_\phi]$ .

The following results asserts the existence of global solutions of system (2.8).

**Theorem 4.1.** *Let (A1) and (A2) hold. For each  $\phi \in \mathcal{X}$ , the system (2.8) admits a unique solution  $\mathbf{u}(t, x; \phi)$  on  $[0, \infty) \times \bar{\Omega}$  with  $\mathbf{u}_0 = \phi$ . Moreover, system (2.8) generates a  $T$ -periodic semiflow  $\Phi_t = \mathbf{u}_t(\cdot) : \mathcal{X} \rightarrow \mathcal{X}$ , i.e.  $\Phi_t(\phi)(\theta, x) = \mathbf{u}(t + \theta, x; \phi)$ ,  $\forall \phi \in \mathcal{X}$ ,  $t \geq T$ ,  $\theta \in [-\tau(0), 0]$ ,  $x \in \bar{\Omega}$ .*

*Proof.* For any  $\phi \in \mathcal{X}$ , let  $\mathbf{u}(t, x; \phi) = (I(t, x; \phi), M(t, x; \phi)) = (I(t, \phi)(x), M(t, \phi)(x))$  be the unique solution of (2.8) with (2.9) satisfying  $\mathbf{u}_0 = \phi$  with the maximal interval of existence  $[0, \sigma_\phi)$  for  $\sigma_\phi > 0$ . Note that

$$I(t, x; \phi) \geq 0, \quad M(t, x; \phi) \geq 0, \quad \forall t \in [0, \sigma_\phi], \quad x \in \bar{\Omega}.$$

Consider the following equation

$$\left\{ \begin{aligned} \frac{\partial \widehat{M}(t, x)}{\partial t} = & D_2 \Delta \widehat{M}(t, x) - (\mu_M(t) + g(\widehat{M}(t, x)))\widehat{M}(t, x) + (1 - \tau'(t)) \\ & \times \exp\left(-\int_{t-\tau(t)}^t \mu_I(s)ds\right) b(t - \tau(t), \widehat{M}(t - \tau(t), x)), \quad t > 0, \quad x \in \Omega, \\ \frac{\partial \widehat{M}(t, x)}{\partial n} = & 0, \quad t > 0, \quad x \in \partial\Omega, \\ \widehat{M}(\theta, x) = & \phi_2(\theta, x), \quad t \in [-\tau(0), 0], \quad x \in \Omega. \end{aligned} \right.$$

Since  $f(I) > 0$  for  $I > 0$ , then we have  $M(t, x) \leq \widehat{M}(t, x)$  for  $t \geq 0$  and  $x \in \bar{\Omega}$  by Proposition 3 of [34] (or Theorem 1.10 of [35, Chapter 8]). Thus, for any  $H > \widehat{M}$ , it follows from the proof of Theorem

3.3 that  $M(t, x)$  satisfies  $0 \leq M(t, x) \leq H$  for all  $t \geq 0$  and  $x \in \overline{\Omega}$  whenever  $0 \leq \phi_2(\theta, x) \leq H$  for  $\theta \in [-\tau(0), 0]$  and  $x \in \overline{\Omega}$ . Moreover, by assumption (A1), we have

$$\begin{aligned} 0 \leq I(t, x) &\leq \int_{t-\tau(t)}^t b(s - \tau(s), M(s - \tau(s), x)) ds \\ &\leq \int_{t-\tau(t)}^t \beta(s - \tau(s)) M(s - \tau(s), x) ds \\ &\leq \hat{\beta} \hat{\tau} H, \end{aligned}$$

for  $t \in (0, \sigma_\phi)$  and  $x \in \Omega$ , where  $\hat{\beta} = \max_{t \in [0, T]} \beta(t)$ . Hence,

$$\tilde{\Sigma}_H := C([- \tau(0), 0], [0, \hat{\beta} \hat{\tau} H] \times [0, H]),$$

is positively invariant for system (2.8). Since  $H$  can be chosen as large as we can,  $\mathbf{u}(t; \phi)$  globally exists on  $[0, \infty)$  for any  $\phi \in \mathcal{X}$ . Hence, (2.8) can define a semiflow  $\Phi_t : \mathcal{X} \rightarrow \mathcal{X}, t \geq T$  by

$$\Phi_t(\phi)(s, x) = \mathbf{u}(t + s, x; \phi), \quad \forall s \in [-\tau(0), 0], x \in \overline{\Omega}.$$

It easily follows from the periodicity of the variable coefficients that  $\Phi_t$  is a  $T$ -period semiflow.  $\square$

We remark that, due to the absence of diffusion for the first equation of system (2.8), the map  $\Phi_T$  admits no compactness. Furthermore, since the immature intra-specific competition is taken into account in (2.8), it is even hard to prove the weak compactness of  $\Phi_T$ . This gives rise to the difficulty in obtaining the existence of the global attractor for  $\Phi_T$ .

#### 4.1 Basic reproduction number

Based on assumption (A1), it is easy to check that system (2.8) has a population extinction equilibrium  $E_0 = (0, 0)$ . Linearizing system (2.8) at the extinction equilibrium  $E_0$ , we obtain the following linear system for adults:

$$\left\{ \begin{aligned} \frac{\partial v(t, x)}{\partial t} &= D_2 \Delta v(t, x) - \mu_M(t) v(t, x) + (1 - \tau'(t)) \\ &\quad \times \exp \left( - \int_{t-\tau(t)}^t \mu_I(s) ds \right) \beta(t - \tau(t)) v(t - \tau(t), x), \\ \frac{\partial v(t, x)}{\partial n} &= 0, \quad t > 0, x \in \partial\Omega, \end{aligned} \right. \quad t > 0, x \in \Omega, \quad (4.3)$$

It easily follows that (4.3) has a unique mild solution  $v(t, x; \varphi)$  with  $v_0(\cdot, \cdot; \varphi) = \varphi$  and  $v_t(\cdot, \cdot; \varphi) \in \mathcal{C}^+$  for all  $t \geq 0$ , and when  $t > \hat{\tau}$ ,  $v(t, x; \varphi)$  is a classical solution and  $v_t(\cdot, \cdot; \varphi)$  is strongly positive and compact on  $\mathcal{C}^+$  for all  $t > 2\hat{\tau}$ . Define  $\tilde{P} : \mathcal{C} \rightarrow \mathcal{C}$  by  $\tilde{P}(\varphi) = v_T(\varphi)$  for all  $\varphi \in \mathcal{C}$ , where  $v_T(\varphi)(\theta, x) = v(T + \theta, x; \varphi)$  for all  $(\theta, x) \in [-\tau(0), 0] \times \overline{\Omega}$ , and  $v_t$  is the solution map of (4.3). Thus, we have  $\tilde{P}^{n_0} = v_{n_0 T}$  is compact and strongly positive, where  $n_0 := \min\{n \in \mathbb{N} : nT > 2\hat{\tau}\}$ . Let  $r(\tilde{P})$  be the spectral radius of  $\tilde{P}$ . In view of [38, Lemma 3.1] that  $r(\tilde{P})$  is a simple eigenvalue of  $\tilde{P}$  having a strongly positive eigenvector  $\tilde{\varphi}$ , which means the modulus of any other eigenvalue is less than  $r(\tilde{P})$ . Let  $v(t, x; \tilde{\varphi})$  be the solution of (4.3) with  $v(s, x; \tilde{\varphi}) = \tilde{\varphi}(s, x)$  for all  $s \in [-\tau(0), 0], x \in \Omega$ . The strong positivity of  $\tilde{\varphi}$  implies that  $v(\cdot, \cdot; \tilde{\varphi}) \gg 0$ . Thus, we can apply analogous arguments as in Lemma 3.6 to prove the following observation, which indicates the existence of a special solution of system (4.3).

**Lemma 4.2.** *There exists a positive  $T$ -periodic function  $\tilde{v}(t, x)$  such that  $e^{\tilde{\mu}t}\tilde{v}(t, x)$  is a solution of (4.3), where  $\tilde{\mu} = \frac{\ln r(\tilde{P})}{T}$ .*

Denote the initial distribution of adult individuals at time  $s \in \mathbb{R}$  and the spatial location  $x \in \overline{\Omega}$  by  $\phi(s, x) = \phi(s)(x) \in C_T(\mathbb{R}, \mathbf{Y}^+)$ . Define an operator  $\tilde{C}(t) : \mathbf{Y} \rightarrow \mathbf{Y}$  as follows:

$$(\tilde{C}(t)\varphi)(x) := (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^t \mu_I(s)ds\right) \beta(t - \tau(t))\varphi(x), \quad \forall \varphi \in \mathbf{Y}.$$

Recall the arguments in section 3.2, we know that  $\int_{-\infty}^{t-\tau(t)} W(t - \tau(t), s)\phi(s)(x)ds$  denotes the density distribution of the accumulative individuals who matured into adults at all previous time  $s < t - \tau(t)$  and survived to time  $t - \tau(t)$  at location  $x$ . Hence, the distribution of new-born individuals at location  $x$  and time  $t$  can be represented as follows:

$$\begin{aligned} & (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^t \mu_I(s)ds\right) \beta(t - \tau(t)) \left(\int_{-\infty}^{t-\tau(t)} W(t - \tau(t), s)\phi(s)(x)ds\right) \\ &= (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^t \mu_I(s)ds\right) \beta(t - \tau(t)) \left(\int_{\tau(t)}^{\infty} W(t - \tau(t), t - s)\phi(t - s)(x)ds\right) \\ &= \int_{\tau(t)}^{\infty} (1 - \tau'(t)) \exp\left(-\int_{t-\tau(t)}^t \mu_I(s)ds\right) \beta(t - \tau(t)) W(t - \tau(t), t - s)\phi(t - s)(x)ds \\ &= \int_{\tau(t)}^{\infty} \left[\tilde{C}(t)(W(t - \tau(t), t - s)\phi(t - s))\right](x)ds \\ &= \int_0^{\infty} \left[\tilde{H}(t, s)\phi(t - s)\right](x)ds, \end{aligned}$$

where  $\tilde{H}(t, s)$ ,  $t \in \mathbb{R}$ ,  $s \geq 0$  is defined as follows:

$$\tilde{H}(t, s) := \begin{cases} \tilde{C}(t)W(t - \tau(t), t - s), & s > \tau(t), \\ 0, & s \in [0, \tau(t)]. \end{cases}$$

The next generation operator  $\tilde{\mathcal{L}}$  in this case can be defined as

$$\tilde{\mathcal{L}}(\phi)(t) := \int_0^{\infty} \tilde{H}(t, s)\phi(t - s)ds, \quad \forall t \in \mathbb{R}, \phi \in C_T(\mathbb{R}, \mathbf{Y}).$$

It can be easily shown that  $\tilde{\mathcal{L}}$  is a positive and bounded linear operator on  $C_T(\mathbb{R}, \mathbf{Y})$ . We can define the basic reproduction number as the spectral radius of  $\tilde{\mathcal{L}}$ , that is,

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

Based on [36, Theorem 3.4] and [40, Remark 2.1], we can also obtain the following similar result as in the previous section, which indicates that  $\tilde{\mathcal{R}}_0$  serves as a threshold value for the stability of the zero solution for system (3.7).

**Lemma 4.3.**  *$\tilde{\mathcal{R}}_0 - 1$  has the same sign as  $r(\tilde{P}) - 1$ .*

In what follows, we establish the threshold dynamics of system (2.8) in terms of the basic reproduction number  $\tilde{\mathcal{R}}_0$ . Let

$$W_0 = \{\phi \in \mathcal{X} : \phi_2(0, \cdot) \not\equiv 0\},$$

and

$$\partial W_0 = \mathcal{E}^+ \setminus W_0 = \{\phi \in \mathcal{X} : \phi_2(0, \cdot) \equiv 0\}.$$

**Theorem 4.4.** *Let (A1), (A2) and (A4) hold and  $\mathbf{u}(t, x; \phi)$  be the solution of (2.8) with  $\mathbf{u}_0 = \phi \in \mathcal{X}$ , then the following statements are valid:*

- (1) *If  $\tilde{\mathcal{R}}_0 < 1$ , the population extinction equilibrium  $E_0 = (0, 0)$  is globally attractive in  $\mathcal{X}$ ;*
- (2) *If  $\tilde{\mathcal{R}}_0 > 1$ , there exists an  $\eta > 0$  such that for any  $\phi \in W_0$  guaranteeing that*

$$\limsup_{n \rightarrow \infty} \|\mathbf{u}(nT, \cdot; \phi)\|_{\mathbf{X}} \geq \eta$$

*holds uniformly for all  $x \in \bar{\Omega}$ .*

*Proof.* (1) In the case of  $\tilde{\mathcal{R}}_0 < 1$ , we have  $\tilde{\mu} = \frac{\ln r(\tilde{P})}{T} < 0$ . Note that the second equation of (2.8) for  $M(t, x)$  is dominated by (4.3), that is,  $M(t, x)$  satisfies

$$\begin{cases} \frac{\partial M(t, x)}{\partial t} \leq D_2 \Delta M(t, x) - \mu_M(t) M(t, x) \\ \quad + (1 - \tau'(t)) \exp \left( - \int_{t-\tau(t)}^t \mu_I(s) ds \right) b(t - \tau(t), M(t - \tau(t), x)), \\ \quad t > 0, x \in \Omega, \\ \frac{\partial M(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega. \end{cases} \quad (4.4)$$

It follows from Lemma 4.2 that there exists a positive  $T$ -periodic function  $\tilde{v}(t, x)$  such that  $w(t, x) = e^{\tilde{\mu}t} \tilde{v}(t, x)$  is a positive solution of (4.3). In view of the comparison principle for (4.4), we have

$$M(t, x) \leq Kw(t, x) = Ke^{\tilde{\mu}t} \tilde{v}(t, x),$$

with a constant  $K > 0$  satisfying  $M_0(\theta, x) \leq Ke^{\tilde{\mu}\theta} v_0(\theta, x)$  for all  $\theta \in [-\tau(0), 0]$ . Thus, it follows that

$$\lim_{t \rightarrow \infty} M(t, x) = 0, \quad \forall x \in \bar{\Omega}.$$

Recall the integral form of  $I(t, x)$ , we have

$$I(t, x) \leq \int_{t-\tau(t)}^t \beta(s) M(s, y) dy ds,$$

and therefore  $\lim_{t \rightarrow \infty} I(t, x) = 0$  holds when  $\tilde{\mathcal{R}}_0 \leq 1$ .

(2) In the case of  $\tilde{\mathcal{R}}_0 > 1$ , we have  $r(\tilde{P}) > 1$ , which results in  $\tilde{\mu} = \frac{\ln r(\tilde{P})}{T} > 0$ . It can be easily shown that the positivity of  $\mathbf{u}_i(t, x; \phi)$  ( $i = 1, 2$ ) holds for any  $\phi \in W_0$ ,  $t > 0$  and  $x \in \bar{\Omega}$ , which implies that  $\Phi_T^n(W_0) \subseteq W_0$  for any  $n \in \mathbb{N}$ .

Define  $\tilde{P}_\epsilon : \mathcal{C} \rightarrow \mathcal{C}$  as the Poincaré map of the following system with a small positive parameter  $\epsilon$ :

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} = D_2 \Delta v(t, x) - (\mu_M(t) + \epsilon) v(t, x) + (1 - \tau'(t)) \\ \quad \times \left[ e^{-\int_{t-\tau(t)}^t \mu_I(s) ds} \beta(t - \tau(t)) - \epsilon \right] v(t - \tau(t), x), \quad t > 0, x \in \Omega, \\ \frac{\partial v(t, x)}{\partial n} = 0, \quad t > 0, x \in \partial\Omega, \\ v(\theta, x) = \varphi(\theta, x), \quad \varphi \in \mathcal{C}, \theta \in [-\tau(0), 0], x \in \Omega. \end{cases} \quad (4.5)$$

Then,  $\tilde{P}_\epsilon(\varphi) = v_T(\varphi)$ , where  $v_T(\varphi)(\theta, x) = v(T + \theta, x; \varphi)$  for  $(\theta, x) \in [-\tau(0), 0] \times \bar{\Omega}$ , and  $v(t, x; \varphi)$  is the solution of (4.5) with  $v(\theta, x) = \varphi(\theta, x)$  for all  $\theta \in [-\tau(0), 0]$ ,  $x \in \bar{\Omega}$ . The continuity of the spectral radius indicates that there exists a sufficiently small positive number  $\epsilon_1$  such that the spectral radius of  $\tilde{P}_\epsilon$ ,  $r(\tilde{P}_\epsilon)$ , satisfies  $r(\tilde{P}_\epsilon) > 1$  for all  $\epsilon \in [0, \epsilon_1]$ . Based on assumptions (A1) and (A2), we may choose some  $\eta_1 > 0$  such that

$$e^{-\int_{t-\tau(t)}^t (\mu_I(s) + f(I(s, x))) ds} b(t, M(t, x)) \geq (e^{-\int_{t-\tau(t)}^t \mu_I(s) ds} \beta(t) - \epsilon) M(t, x),$$

and  $g(M) < g(\eta_1) < \epsilon_1$  hold for all  $I \leq \eta_1$  and  $M \leq \eta_1$ . Moreover, according to the continuous dependence of solutions on the initial value, there exists  $\eta_0 \in (0, \epsilon_1)$  such that for any  $|\phi(s, x)| < \eta_0$ ,  $s \in [-\tau(0), 0]$ ,  $x \in \bar{\Omega}$ ,

$$|(I(t, x; \phi), M(t, x; \phi))| \leq \eta_1, \quad \forall t \in [0, T], \quad x \in \bar{\Omega}.$$

Now we prove the persistence result by contradiction. Suppose that for some  $\phi_0 \in W_0$ , there exists a  $n_1 \geq 1$  such that  $\|\Phi_{nT}(\phi_0)\|_{\mathbf{X}} < \eta_0$  for all  $n \geq n_1$ . Hence, there exists a positive integer  $n_1$ , such that  $|u_i(nT + \theta, x; \phi_0)| < \eta_0$  for all  $n \geq n_1$ ,  $i = 1, 2$ ,  $\theta \in [-\tau(0), 0]$  and  $x \in \bar{\Omega}$ . Rewrite  $t = nT + \theta + t'$  with  $t' \in [0, T)$  for every  $t > n_1 T$ . Then for  $\phi_0 \in W_0$ , we have

$$0 < u_i(t, x; \phi_0) < \eta_1, \quad \forall t > n_1 T, \quad x \in \bar{\Omega}, \quad i = 1, 2. \quad (4.6)$$

Then,  $M(t, x; \phi_0)$  satisfies

$$\begin{cases} \frac{\partial M(t, x)}{\partial t} \geq D_2 \Delta M(t, x) - (\mu_M(t) + \epsilon_1) M(t, x) + (1 - \tau'(t)) \\ \quad \times \left[ e^{-\int_{t-\tau(t)}^t \mu_I(s) ds} \beta(t - \tau(t)) - \epsilon_1 \right] M(t - \tau(t), x), & t > (n_1 + 1)T, \quad x \in \Omega, \\ \frac{\partial M(t, x)}{\partial n} = 0, & t > (n_1 + 1)T, \quad x \in \partial\Omega. \end{cases} \quad (4.7)$$

Let  $\psi^*$  be the positive eigenfunction of  $\tilde{P}_{\epsilon_1}$  corresponding to  $r(\tilde{P}_{\epsilon_1})$ . For all  $t > \hat{\tau}$  and  $x \in \bar{\Omega}$ , the positivity of  $M(t, x; \phi_0)$  gives rise the existence of a constant  $\varsigma > 0$  such that

$$M((n_1 + 1)T + \theta, x; \phi_0) \geq \varsigma \psi^*, \quad \forall \theta \in [-\tau(0), 0], \quad x \in \bar{\Omega}.$$

Then, based on the comparison principle for (4.7), we have

$$M(t, x; \phi_0) \geq \varsigma v(t - (n_1 + 1)T, x; \psi^*) = \varsigma r(\tilde{P}_{\epsilon_1})^{t - (n_1 + 1)T} \psi^*(0, x), \quad \forall t \geq (n_1 + 1)T, \quad x \in \bar{\Omega},$$

where  $v(t, x; \psi^*)$  is a solution for (4.5) with  $v(\theta, x) = \psi^*(\theta, x)$  for all  $\theta \in [-\tau(0), 0]$  and  $x \in \bar{\Omega}$ . Thus, it follows that

$$\lim_{t \rightarrow \infty} M(t, x; \phi_0) = \infty,$$

a contradiction to (4.6). This completes the proof.  $\square$

## 5 Numerical simulations

In this section, we attempt to validate the analytic results involving the global dynamics in terms of the basic reproduction number numerically. For simplicity, we consider a bounded domain in one dimension, that is,  $\Omega \in \mathbb{R}$ . Without loss of generality, we choose  $\Omega$  as  $(0, 3)$ . On account of the seasonal effects, we take the period of time dependent functions as 12 months, i.e.,  $T = 12$ . In this



paper, we use modified cosine functions to approximate the seasonal effects on the time dependent developmental duration, reproduction and death rate functions. The birth rate function is assumed as the following:

$$b(t, M(t, x)) = B(t)M(t, x),$$

where the per-capita birth rate function  $B(t)$  is a positive and time periodic function with period 12. We assume the intra-specific competition for the immature mosquitoes and adult mosquitoes assume the following linear density dependent functions:

$$f(I(t, x)) = d_I I(t, x) \quad \text{and} \quad g(M(t, x)) = d_M M(t, x),$$

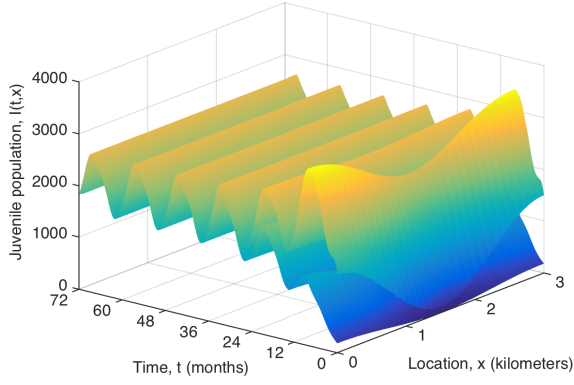
where the density dependent coefficients  $d_I$  and  $d_M$  are non-negative constants. In what follows, we will perform numerical simulations on two different species for two cases.

### 5.1 Case I: $D_1 > 0$ and $f(I) \equiv 0$

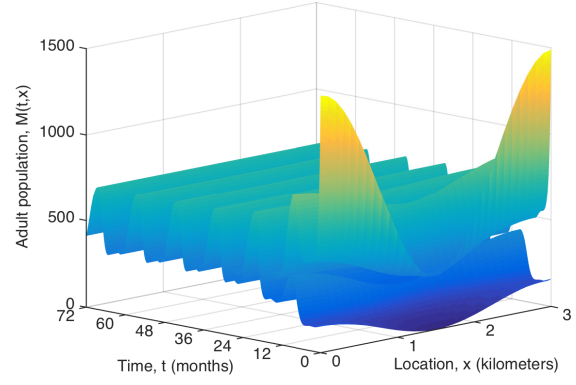
The European wild rabbit is a geographically widespread small mammal, the population of which plays critical roles in ecological community [42]. The efficient dispersal ability of juvenile rabbits may lead them to search for better quality of food and water resources, which may relieve the intra-specific competition during the juvenile stage to a certain extent [31]. Consequently, the population of the European wild rabbit is the appropriate simulating example for Case I.

The diffusion coefficients of the juveniles and adults are assumed as  $D_1 = 0.01 \text{ km}^2 \cdot \text{month}^{-1}$  and  $D_2 = 0.02 \text{ km}^2 \cdot \text{month}^{-1}$  respectively. The reproduction of the European wild rabbit is strongly related to the seasonal effects, and the breeding seasons usually begins at the end of the winter season and ends in the early autumn [43]. Therefore, we assume the per-capita birth rate function is  $B(t) = 2 - 1.2 \cos(2\pi(t+1)/12)$  per adult per month. Since the developmental duration of the juvenile rabbits ranges from 3 to 6 months [43], we assume the time periodic developmental duration as  $\tau(t) = 1.5(3 + \cos(2\pi(t-3)/12))$ . The time dependent natural death rates for juveniles and adults are approximated as  $\mu_I(t) = c_1(30 + 7 \cos(2\pi(t-3)/12))$  and  $\mu_M(t) = c_2(50 + 9 \cos(2\pi(t-3)/12))$  month<sup>-1</sup>, where  $c_1$  and  $c_2$  are positive constants. Besides, the density dependent coefficient for adults is fixed as  $d_M = 0.001$  per adult per month. The European wild rabbits usually inhabit in the rural areas because human activities in urban areas may cause the decline of their fitness [44]. Motivated by [45], we consider the area around the two ends of  $\Omega$  as the rural area and the intermediate zone of  $\Omega$  as the urban area.

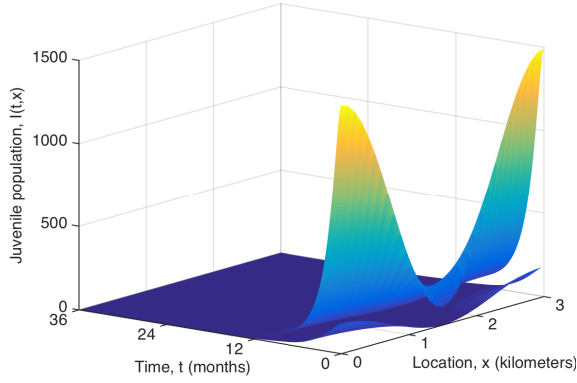
In order to simulate the long term dynamics of system (2.6), it is imperative to numerically compute the basic reproduction number  $\mathcal{R}_0$ . In this paper, we employ the method provided in Remark 3.2 in [41] to calculate the numeric value of  $\mathcal{R}_0$  for periodic abstract functional differential systems. After fixing  $c_1 = 0.01$  and  $c_2 = 0.001$  for natural death rates  $\mu_I(t)$  and  $\mu_M(t)$ , and choosing two different initial conditions, some numeric figures are plotted to describe the long term dynamical behavior of juvenile (shown in Fig. 2(a)) and adult (shown in Fig. 2(b)) rabbit population respectively. Under above parameter values, we obtain  $\mathcal{R}_0 = 11.7578$ . These figures indicate that solutions of system (2.6) with various positive initial conditions tend to keep persist and stabilize at a positive, spacial homogeneous and periodic solution when  $\mathcal{R}_0 > 1$ . If we enlarge the natural death rates  $\mu_I(t)$  and  $\mu_M(t)$  by setting  $c_1 = 0.03$  and  $c_2 = 0.01$ , it then follows that  $\mathcal{R}_0 = 0.0767$ . In this case, all the solutions of system (2.6) (shown in Figs. 2(c) and 2(d)) with different initial conditions approach to zero when  $\mathcal{R}_0 = 0.0767 < 1$ . These numeric results shown in Fig. 2 are consistent with the analytic results about the threshold dynamics in terms of  $\mathcal{R}_0$  in section 3.



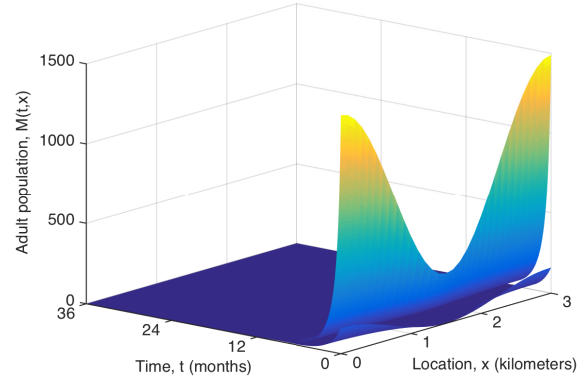
(a)



(b)



(c)



(d)

Figure 2: Long term dynamics of the European wild rabbit population under two different initial conditions when the immature intra-specific competition is negligible. Dynamics for juvenile (a) and adult (b) population densities during 6-year period when  $\mathcal{R}_0 = 11.7578 > 1$ . Dynamics for juvenile (c) and adult (d) population densities during 3-year period when  $\mathcal{R}_0 = 0.0767 < 1$ .

## 5.2 Case III: $D_1 = 0$ and $f(I) > 0$

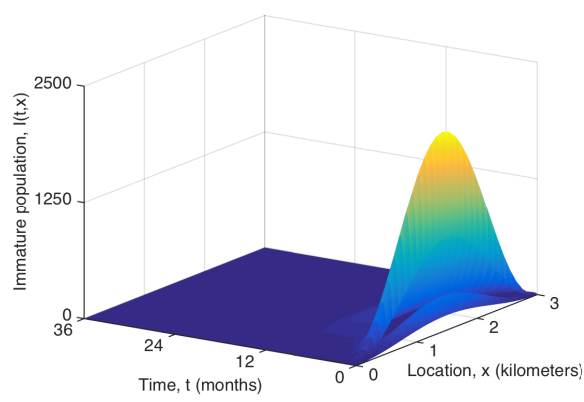
Mosquitoes as the main agent can transmit a wide variety of mosquito borne diseases such as dengue fever, malaria, West Nile fever, Zika fever, chikungunya and so on [46]. The investigation of mosquito population growth is imperative for the sake of controlling mosquito-born diseases. Compared to adult mosquitoes, the aquatic immature mosquitoes with ignorable dispersal ability are often confined in limited habitats such as the little pool or small container, which may intensify the intra-specific competition during the immature stage [32]. Indeed, one non-negligible phenomenon in modelling mosquito population growth is larval competition, which often results in increased larval deaths and lower developmental rate, and may further affects the situations of emerging adults [47]. Thus, we choose *Aedes aegypti* mosquito population as the simulating example for Case III.

Here, we fix the density dependent death coefficients for immature and adult individuals as  $d_I = 0.000001$  per immature per month and  $d_M = 0.000001$  per adult per month respectively. The adult diffusion coefficient is assumed as  $D_2 = 0.0002 \text{ km}^2 \cdot \text{month}^{-1}$ . It is well known that the population growth of *Aedes aegypti* is greatly influenced by the seasonal variations such as ambient temperature and rainfall [48]. Thus, we approximate the time-periodic developmental duration by  $\tau(t) = 0.5(1 + 0.6 \cos(2\pi(t - 2.5)/12))$  month due to the fact that the developmental duration for immature individuals ranges from 6 days to 24 days (i.e.  $0.2 \sim 0.8$  month) [49]. By virtue of the fitted time varying oviposition rate of mosquitoes in [50], the per capita birth rate is assumed as  $B(t) = 8 - 1.2 \cos(2\pi(t - 2.5)/12)$  per adult per month. Based on the time varying immature death rate fitted in [51] and the adult death rate fitted in [50], it is analogous to approximate the natural mortality rates for immatures and adults by the following modified cosine functions respectively:  $\mu_I(t) = h_1(30 + 7 \cos(2\pi(t - 3)/12))$  and  $\mu_M(t) = h_2(50 + 9 \cos(2\pi(t - 3)/12)) \text{ month}^{-1}$ , where  $h_1$  and  $h_2$  are positive constants. *Aedes aegypti* as the most prevalent mosquito species tends to inhabit in urban and sub-urban area rather than the semi-rural area [52]. Consequently, we make analogical assumptions of the bounded domain as the previous subsection, that is, the area around the two ends of  $\Omega$  is assumed as the semi-rural area and the middle zone of  $\Omega$  as the urban and sub-urban area.

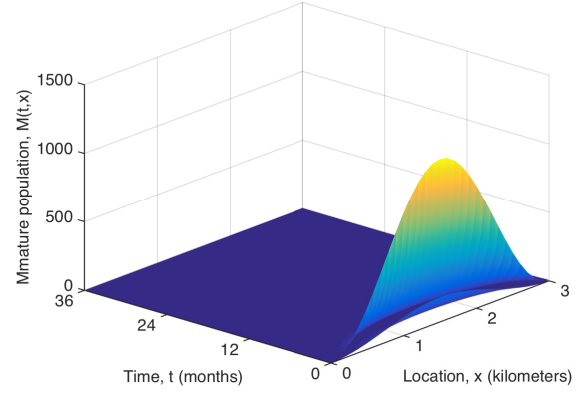
By applying similar simulating procedures as the previous subsection, we obtain the numeric plot (shown in Fig. 3) depicting the long term dynamic of solutions of system (2.8) in terms of the basic reproduction number  $\tilde{\mathcal{R}}_0$ . We compute the basic reproduction number  $\tilde{\mathcal{R}}_0 = 0.7866$  when  $h_1 = 0.05$  and  $h_2 = 0.06$  for the natural mortality rates of immature and mature individuals respectively. Under this set of parameters, solutions with various initial conditions (shown in Figs. 3(a) and 3(b)) keep decreasing and approach to zero for a long time when  $\tilde{\mathcal{R}}_0 = 0.7866 < 1$ . Then, we obtain  $\tilde{\mathcal{R}}_0 = 2.725$  if we reduce the death rates by fixing  $h_1 = 0.008$  and  $h_2 = 0.05$ . It then follows from Figs. 3(c) and 3(d) that both immature and mature population are inclined to increase and maintain at a stable positive, oscillating, and spacial homogeneous state respectively. These numeric results shown in Fig. 3 may not only validate the theoretic results in section 4, but also provide further implications of the existence of the positive periodic solution of system (2.8) when  $\tilde{\mathcal{R}}_0 > 1$ , which is a challenging problem for further consideration.

## 6 Discussion

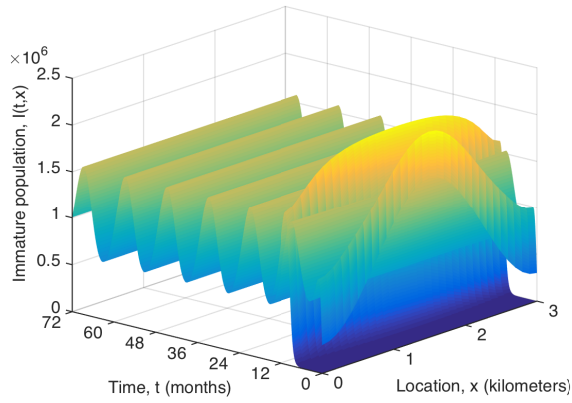
In this paper, an age-structured reaction-diffusion population model with the consideration of seasonal effects, intra-specific competition and seasonal maturation duration based on a generalized age-structured modeling framework was formulated. By applying the method of integration along characteristics, the full system related to the population densities of juveniles  $I(t, x)$  and adults



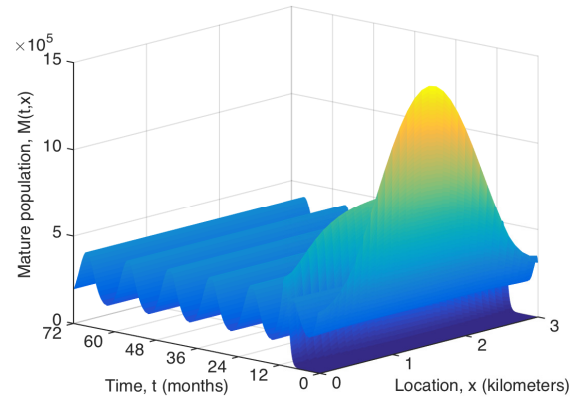
(a)



(b)



(c)



(d)

Figure 3: Long term behavior for the *Aedes aegypti* population with considering immature intra-specific competition under two different initial conditions. Dynamics for juvenile (a) and adult (b) mosquito densities during 3-year period when  $\tilde{R}_0 = 0.7866$ . Dynamics for juvenile (c) and adult (d) mosquito densities during 6-year period when  $\tilde{R}_0 = 2.725$ .

$M(t, x)$  at time  $t$  and location  $x$  was obtained with two nonlocal periodic reaction diffusion equations involving periodic delays and no flux boundary condition. The introduction of juvenile intra-specific competition and periodic delays, making the system non-cooperative and irreducible, bring more challenges to the theoretical analysis of our model. As a start, a simple case when the immature competition can be ignored due to dispersal capability of immature individuals, reduces the model to one equation for the density of matured individuals. For this single equation, the global existence, uniqueness of the solution and the existence of a global attractor were first shown. Inspired by the work [36, 40], the basic reproduction number  $\mathcal{R}_0$  as the spectral radius of the next generation operator was defined and the global attractivity of the single equation in terms of  $\mathcal{R}_0$  was established by exploring the theory of monotone and subhomogeneous semiflows. When immature competition exists, the analysis becomes somewhat tough as it is impossible to decouple two equations. In this case, we assumed the immature diffusion rate is negligible, which is justified biologically as follows: For some species such as mosquitoes and frogs experiencing the immature intra-specific competition, their juveniles have to compete food and resources with conspecifics in a restricted area due to inefficient mobility. Consequently, the new model consists of a delay differential equation coupled with a delayed reaction diffusion equation with periodic delays. We obtained the global existence, uniqueness of the solution. Moreover, the extinction and uniform persistence of the population were proved in terms of the newly defined basic reproduction number  $\tilde{\mathcal{R}}_0$ . It should be pointed out that the persistence stated in Theorem 4.4 is just “weak persistence” rather than uniform persistence (see [37, Definitions 1.3.2 and 1.3.3]). Since the existence of global attractor of  $\Phi_T$  is not obtained in Theorem 4.1, it is hard for us to prove the much stronger persistence by uniform persistence theory (see [53, 37]). How to overcome the noncompactness of  $\Phi_T$  to get the uniform persistence will be a challenging but meaningful problem.

It is worth mentioning that our model involves time-varying delays  $\tau(t)$ . An appropriate space for theoretical analysis should be introduced to analyze it. In this paper, without loss of generality, the initial timing was chosen as the maximum point of  $\tau(t)$  in  $[0, T]$ , that is,  $\tau(0) = \max_{t \in [0, T]} \{\tau(t)\} = \hat{\tau}$ , which is feasible by considering the evolution of solutions. If the initial timing instant  $t_0 = 0$  does not satisfies  $\tau(t_0) = \hat{\tau}$ , by applying similar arguments in [51, 27], we may need to introduce two spaces. One is  $C([-\hat{\tau}, 0], \mathbf{Y})$  to show the existence and uniqueness of the solution. To verify the global attractivity of the positive periodic solution, the other space  $C([-\tau(0), 0], \mathbf{Y})$  is needed, on which we can show the solution semiflow is eventually strongly monotone and strictly homogeneous. Besides that, we need to confirm that the solution can define a periodic semiflow on the new space  $C([-\tau(0), 0], \mathbf{Y})$  and the basic reproduction number can determine the stability of the system on both phase spaces.

The modified cosine functions were employed to approximate the seasonal effects on the developmental duration, the reproduction and mortality rates, which may be less accurate than estimating these constant and periodic coefficients via fitting true weather conditions. Employing more precise parameterization method will be an interesting problem for future investigation. Moreover, the diffusion coefficients in our model are assumed to be constant. In reality, the spatial dispersion and diffusion are greatly influence by the seasonal variations in biotic or abiotic factors such as resources and climate [36]. Organisms have a high mobility with warmer temperature and tend to keep motionless for the sake of saving energy to survive in colder days. Due to the heterogeneity of resource distribution in spatial scale, nonlinear diffusion or spatial dependent coefficients can also be incorporated in the system. Incorporating these biological factors in model formulation and analysing the resultant models would be good topics for further studies.

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