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Zhengyang Zhang

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THÈSE

PRÉSENTÉE À

L'UNIVERSITÉ DE BORDEAUX

ÉCOLE DOCTORALE DE MATHÉMATIQUES ET
D'INFORMATIQUE

par **Zhengyang Zhang**

POUR OBTENIR LE GRADE DE

DOCTEUR

SPÉCIALITÉ : MATHÉMATIQUES

**Études d'une classe d'équations à retard dépendant
de l'état et application à la croissance de forêts**

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Devant la commission d'examen composée de :

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**Études d'une classe d'équations à retard
dépendant de l'état et application à la
croissance de forêts**

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Résumé

Cette thèse est consacrée à l'étude d'une classe d'équations différentielles à retard dépendant de l'état – ces équations provenant d'un modèle structuré en taille.

La principale motivation de cette thèse provient de la volonté d'ajuster les paramètres du système d'équations étudiées vis-à-vis des données générées par un simulateur de forêts, appelé SORTIE. Deux types de forêts sont étudiés ici: d'une part une forêt ne comportant qu'une seule espèce d'arbre, et d'autre part une forêt comportant deux espèces d'arbres (au chapitre 2). Les simulations numériques du système d'équations correspondent relativement bien aux données générées par SORTIE, ce qui montre que le système considéré peut être utilisé afin d'écrire la dynamique de populations d'une forêt. De plus, un modèle plus étendu prenant en compte la position spatiale des arbres est proposé dans le chapitre 2, dans le cas de forêts possédant deux espèces d'arbres. Les simulations numériques de ce modèle permettent de visualiser la propagation spatiale des forêts.

Les chapitres 3 et 4 se concentrent sur l'analyse mathématique des équations différentielles à retard considérées. Les propriétés du semi-flot associé au système sont étudiées au chapitre 3, où l'on démontre en particulier que ce semi-flot n'est pas continu en temps. Le caractère dissipatif et borné du semi-flot, pour des modèles de forêts comportant une ou deux espèces d'arbres, est étudié dans le chapitre 4.

En outre, afin d'étudier la dynamique de population d'une forêt (d'une seule espèce d'arbre) après l'introduction d'un parasite, nous construisons dans le chapitre 5 un système proie-prédateur dont la proie (à savoir la forêt) est modélisée par le système d'équations différentielles à retard dépendant de l'état étudié auparavant, et dont le prédateur (à savoir le parasite) est modélisé par une équation différentielle ordinaire. De nombreuses simulations numériques associées à différents scénarios sont faites, afin d'explorer le comportement complexe des solutions du au couplage proie-prédateur et les équations à retard dépendant de l'état.

Mots clés: Équation différentielle à retard dépendant de l'état, semi-flot, bornage des solutions, dissipativité, dynamique des populations de forêts, système proie-prédateur.

A class of state-dependent delay differential equations and applications to forest growth

Abstract

This thesis is devoted to the studies of a class of state-dependent delay differential equations. This class of equations is derived from a size-structured model.

The motivation comes from the parameter fittings of this system to a forest simulator called SORTIE. Cases of both single species forest and two-species forest are considered in Chapter 2. The numerical simulations of the system correspond relatively very well to the forest data generated by SORTIE, which shows that this system is able to be used to describe the population dynamics of forests. Moreover, an extended model considering the spatial positions of trees is also proposed in Chapter 2 for the two-species forest case. From the numerical simulations of this spatial model one can see the diffusion of forests in space.

Chapter 3 and 4 focus on the mathematical analysis of the state-dependent delay differential equations. The properties of semiflow generated by this system are studied in Chapter 3, where we find that this semiflow is not time-continuous. The boundedness and dissipativity of the semiflow for both single species model and multi-species model are studied in Chapter 4.

Furthermore, in order to study the population dynamics after the introduction of parasites into a forest, a predator-prey system consisting of the above state-dependent delay differential equation (describing the forest) and an ordinary differential equation (describing the parasites) is constructed in Chapter 5 (only the single species forest is considered here). Numerical simulations in several scenarios and cases are operated to display the complex behaviours of solutions appearing in this system with the predator-prey relation and the state-dependent delay.

Key words: State-dependent delay differential equation, semiflow, boundedness of solutions, dissipativity, forest population dynamics, predator-prey system.

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Chapter 1

Introduction

1.1 History and applications of delay differential equations

For a very long time, people in various scientific fields have used ordinary or partial differential equations (since they were born in the late 17th century) to describe systems of which the future state was determined by the present state and the rate of change of the state. With a more and more profound understanding of the world, people gradually found out that in some cases it would be unrealistic not to consider the influence of the past on the present. At the IV International Congress of Mathematicians (Rome, April 10th 1908), Picard [174] pointed out the importance of “heredity” in the modelling of physical systems, namely the influence of the past state on the present or future state:

La Mécanique, nous l'avons rappelé, a longtemps postulé plus ou moins explicitement un principe de non-hérédité. Nous nous accommodons encore de ce principe, au moins en première approximation, dans les sciences de la nature inanimée, quoique de nombreux phénomènes indiquent que l'état actuel garde la trace des états antérieurs.

L'hérédité joue surtout un rôle capital dans les sciences de la vie.

Nous pouvons rêver d'équations fonctionnelles plus compliquées que les précédentes parce qu'elles renfermeront en outre des intégrales prises entre un temps passé très éloigné et le temps actuel, intégrales qui apporteront la part de l'hérédité.

Picard [174] also mentioned the idea of the application of functional differential equations in some systems:

Parfois, dans certaines questions, l'influence sur une partie du système des parties éloignées de ce système ne peut être négligée, et le problème pris

dans sa généralité ne se présente plus sous forme d'équations différentielles, mais sous forme d'équations fonctionnelles où entrent d'ailleurs des dérivées des fonctions inconnues, les intégrales qui figurent dans ses équations étant étendues au volume occupé par le système considéré.

Until this time did people begin to think about using delay differential equations, or functional differential equations to describe dynamics of systems in other fields of science. Although at this time, these kinds of equations had been studied for over 100 years (in the late 18th century by Condorcet, Laplace, Poisson, etc.) [15, 187].

Volterra seemed to be the first to apply this idea. In his work [208, 209, 210, 212, 214], he formulated some general differential equations incorporating the past states of systems to treat the problems about the hereditary phenomena and to model viscoelasticity in population dynamics. Unfortunately, his results were not drawing enough attention [77, 78].

In the 1940s, as mechanics was well developed in the Soviet Union, the engineers also began to consider in engineering systems and control theory the hereditary effects, which, they had always known but ignored for lack of mathematical theory support. The pioneer work was probably from Minorsky [152] in 1942 in the study of ship stabilization and automatic steering. In 1951, Mishkis published the book *Linear differential equations with retarded argument* [154], which is considered to be the first rather complete research in this area. In the '50s and '60s, several books about functional differential equations appeared [22, 23, 75, 117, 153]. They focused on the linear systems with retarded arguments and presented a well-organized theory, which also mathematically supported research in other areas. Now delay differential equations have been applied in various fields to describe behaviours with time lags, for example, in economics [19, 23, 27, 31, 137], in physics [62, 64, 192], in population dynamics [48, 59, 97, 135, 212], in botanics [99, 100, 101, 103], in epidemiology [28, 35, 47, 91, 92, 189, 207, 223], in medical science [17], even in pedagogy [68, 69, 70]. I refer to [15, 77, 78, 113] for more applications and explicit models in various sciences.

One general form of delay differential equations is given by

$$x'(t) = f(t, x(t), x(t - \tau)) \quad (1.1)$$

where $\tau > 0$ denotes the delay and f is a continuous function on \mathbb{R}^3 . The initial value problem for delay differential equations is defined by

$$\begin{cases} x'(t) = f(t, x(t), x(t - \tau)), t \geq t_0, \\ x(t) = \varphi(t), t \leq t_0. \end{cases}$$

An important type of delay differential equations is the case where the delay τ depends on the state x , which is called state-dependent delay differential

equations, for example, the analogous equation to (1.1)

$$x'(t) = f(t, x(t), x(t - \tau(x(t)))).$$

State-dependent delay differential equations can date back to Poisson [176] in 1806, but most studies were done in recent fifty years due to the arising applications in various areas [80]. I will give more information about state-dependent delay differential equation in Chapter 1.2.

Another general form of equation is given by

$$x'(t) = f(t, x_t), \tag{1.2}$$

where $f : D(\subset \mathbb{R} \times C([- \tau, 0], \mathbb{R}^n)) \rightarrow \mathbb{R}^n$ is a given functional and the function x_t is defined by

$$x_t : [-\tau, 0] \rightarrow \mathbb{R}^n, x_t(\theta) := x(t + \theta),$$

which was first introduced by Hale [76]. Equation (1.2) is also called a functional differential equation. Given the initial condition $x_{t_0} = \varphi \in C([- \tau, 0], \mathbb{R}^n)$, a solution $x(t)$ of the equation (1.2) will be a continuous function defined on an interval $[t_0 - \tau, t_0 + T)$ for some $T > 0$ such that $x(t) = \varphi(t)$ on the interval $[t_0 - \tau, t_0]$, x is continuously differentiable on $(t_0, t_0 + T)$, has a right derivative at $t = t_0$ and satisfies (1.2) on the interval $(t_0, t_0 + T)$ [15]. The basic theory regarding the solution of the equation (1.2) such as the existence, uniqueness, continuation, differentiability and dependence on initial values and parameters have been preliminarily studied in many literatures [15, 77, 78, 197]. Different theories and tools are also used in studying state-dependent delay differential equations, or functional differential equations [3, 128]. Moreover, I also refer to some other books about the fundamental theory of delay differential equations [29, 56, 53, 60]. For some recent advances about delay differential equations, I refer to [34, 66, 81, 148].

1.2 Overview of the thesis

This thesis deals with the following state-dependent delay differential equation. Let Ω be a compact subset of \mathbb{R}^n (with $n \geq 1$). Denote $C(\Omega) := C(\Omega, \mathbb{R})$ and $C_+(\Omega) := C(\Omega, [0, +\infty))$ for simplicity. The system considered in the thesis is the following: $\forall t \geq 0$ and $\forall x \in \Omega$,

$$\begin{cases} \partial_t A(t, x) = F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(t))(\cdot, \cdot))(x), \\ \int_{-\tau(t, x)}^0 f(A(t + s, \cdot))(x) ds = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \end{cases} \tag{1.3}$$

with the initial condition

$$A(t, x) = \varphi(t, x), \forall t \leq 0,$$

and φ belongs to

$$\text{Lip}_\alpha := \{\phi \in C((-\infty, 0], C(\Omega)) : t \rightarrow e^{-\alpha|t|}\phi(t, \cdot) \text{ is bounded and Lipschitz continuous from } (-\infty, 0] \text{ to } C(\Omega)\}.$$

In system (1.3) the map $A(t - \tau(t)) \in C(\Omega^2)$ is defined by

$$A(t - \tau(t))(x, y) := A(t - \tau(t, x), y).$$

In this problem the state space Lip_α is a Banach space endowed with the norm

$$\|\phi\|_{\text{Lip}_\alpha} := \|\phi_\alpha\|_\infty + \|\phi_\alpha\|_{\text{Lip}}$$

where $\phi_\alpha : (-\infty, 0] \rightarrow C(\Omega)$ is defined by

$$\phi_\alpha(t, x) := e^{-\alpha|t|}\phi(t, x), \forall t \in (-\infty, 0], \forall x \in \Omega. \quad (1.4)$$

and

$$\|\phi_\alpha\|_\infty := \sup_{t \leq 0} \|\phi_\alpha(t, \cdot)\|_\infty$$

and for fixed t ,

$$\|\phi_\alpha(t, \cdot)\|_\infty := \sup_{x \in \Omega} |\phi_\alpha(t, x)|$$

and

$$\|\phi_\alpha\|_{\text{Lip}} := \sup_{t, s \leq 0: t \neq s} \frac{\|\phi_\alpha(t, \cdot) - \phi_\alpha(s, \cdot)\|_\infty}{|t - s|}.$$

1.2.1 Comparisons with a forest simulator SORTIE

In Chapter 2, system (1.3) is used in a very specific form as a mathematical model for forest growth, and numerical simulations are conducted to fit and compare with a forest simulator SORTIE. The work of Chapter 2 has been published in [140].

Development of forest growth models has gone through more than 300 years, from the earliest model - yield tables since 1713 [43, 172, 188], to growth equations since late 1940s, especially the use of differential equations since the 1960s [178]. A rather detailed chart of the development of forest growth models can be seen in [228]. Among all the forest models, one kind, which is named individual-based model (IBM), or agent-based model, attracted people's attention very much. This kind of model focuses on each individual instead of on the stand or forest, thus has a higher resolution than the model based on the whole forest. The first individual-based forest model was developed in 1964 by Newnham [159] for pure Douglas fir stands. After, many types of IBMs for forests have been constructed.

Gap model is one kind of the forest IBMs that interests people very much. The principle is that, the large forest ecosystem is considered as a mosaic of

patches or gaps when it is investigated, and as a whole when it is modelled and understood [178]. The first gap model would be the JABOWA model developed by Botkin et al. [26] for Hubbard Brook Ecosystem, a northern hardwood forest in New Hampshire USA, which also laid the foundation on this direction of studies. By modifying the assumptions, functions and submodels in JABOWA in accordance with specific forests, many other forest gap models have been developed since then, like FORET [191] for an Appalachian deciduous forest, SORTIE [169, 170] for a northern hardwood forest, FORMIX and FORMIND [98, 107, 108] for a tropical forest, etc.. One may refer to [32] and [178] for a nice survey about forest gap models. One can also find more types of forest IBMs and more information in [33, 58, 124, 126, 177, 178, 205, 228].

In Chapter 2, SORTIE is chosen to be the forest simulator which generates the forest data that is needed in the comparison with the mathematical model. It is an individual-based forest model developed in the 1990s. A detailed introduction about SORTIE is presented in Chapter 2.1, and I also refer to the following original research papers about SORTIE [39, 40, 41, 42, 106, 169, 170, 171, 179]. An important principle behind SORTIE which is worth mentioning is that light is the only resource considered which influences forests' growth. The scientists have also programmed SORTIE model into a software. There is a website <http://www.sortie-nd.org> where one can find this software and help manuals.

In Chapter 2 SORTIE was run on Ubuntu 16.04 system. The data obtained from SORTIE are used as the real data of forests in the numerical simulations and parameter fitting of the following single species model describing the competition for light in forests

$$\begin{cases} \frac{dA(t)}{dt} = e^{-\mu_J \tau(t)} \frac{f(A(t))}{f(A(t - \tau(t)))} \beta b(A(t - \tau(t))) - \mu_A A(t), \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_- \end{cases} \quad (1.5)$$

where

$$f(x) = \frac{\alpha}{1 + \delta x} \text{ and } b(x) = x e^{-\xi x}.$$

In this model, $A(t)$ describes the adult tree population number. A two-species model (system (2.9), see Chapter 2.3.1) extended from system (1.5) is also fitted to the forest data in Chapter 2.

Furthermore, with all the parameter values obtained in the above parameter fitting, a two-species model with space structure (system (2.12), see Chapter 2.4) is also derived and numerically simulated. The diffusion of forests in the space thus can be observed from the simulation.

Delay differential equation applied in population dynamics started from

the following Hutchinson's equation [97]

$$\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t - \tau)}{K} \right),$$

and Nicholson's blowfly equation [160, 161, 173]

$$\frac{dN(t)}{dt} = b(N(t - \tau))N(t - \tau) - \lambda(N(t))N(t),$$

which, along with the variations, have always been a research interest [7, 72, 149, 150, 225, 226].

The single species model (1.5) has been previously considered by Smith [193, 194, 195, 196], where it was derived from the following size-structured model

$$\begin{cases} \partial_t u(t, s) + f(A(t))\partial_s u(t, s) = -\mu(s)u(t, s), & \text{for } t > 0, s > s_-, \\ f(A(t))u(t, s_-) = \beta b(A(t)), & \text{for } t > 0, \\ u(0, \cdot) = u_0(\cdot) \in L^1_+(s_-, +\infty). \end{cases} \quad (1.6)$$

Such ideas of deriving delay differential equations from structured population models have been used a lot in the literature [4, 13, 73, 84, 85, 163].

With deeper study and understanding of population dynamics, people started to consider introducing state-dependent delay into population models, as was pointed out in Arino et al. [14]:

In the context of population dynamics, the delay arises frequently as the maturation time from birth to adulthood and this time is in some cases a function of the total population.

The early work about introducing state-dependent delay into population dynamical models includes Bélair [21] in 1991 about open-access fisheries, and Aiello et al. [6] in 1992 about the maturation time of Antarctic whales and seals in Antarctica. After that, more research following their ideas came up [7, 8, 13, 14, 18, 84, 85, 232]. More studies about delay differential equation models (and also delay difference equation models) describing population dynamics can be found in [67, 114, 119, 136, 158, 197].

1.2.2 Semiflow properties

Chapter 3 deals with the semiflow properties of system (1.3), corresponding to the work in [143]. The definition of a semiflow defined on a general metric space can be seen in Chapter 3.1, Definition 3.5. The semiflow generated by system (1.3) is

$$\mathcal{U}(t)(\varphi(\cdot, x), \tau_0(x)) := (A_t(\cdot, x), \tau(t, x)),$$

where $A(t, x)$ and $\tau(t, x)$ are the solution of system (1.3) with the initial distribution $(\varphi(t, x), \tau_0(x))$.

There are several ways in understanding the delay $\tau(t, x)$. One normal understanding is that $\tau(t, x)$ is the solution of the integral equation in (1.3). In this way $\tau(t, x)$ together with $A_t(\cdot, x)$ is treated as a state variable. Another understanding is to regard $\tau(t, x)$ as the solution of a partial differential equation obtained by a differentiation on the integral equation in system (1.3), proved in Chapter 3.3, Lemma 3.9. Furthermore, the result in Chapter 3.3, Lemma 3.13 shows that this delay term is also a functional of A_t , which means that the delay is also a state-dependent delay.

There have been a number of research about the solution and the semiflow of state-dependent delay differential equations. First results regarding the general results about the existence and uniqueness of solutions and continuous dependence on initial conditions were probably from Driver [54, 55] in the study of a two-body problem in electrodynamics. Studies about state-dependent delay differential equations have been largely enriched since then, for example, about the differentiability and smoothness [82, 132], about attractors [95, 118], about the stability of solutions [74, 145, 146], about periodic solutions [9, 12, 121, 138, 144, 147, 164, 215, 219]. For a very nice survey and basic theoretical results about functional differential equations with state-dependent delay, I refer to Hartung et al. [80].

Walther did a series of work [216, 217, 218, 220, 221, 222] on the semiflow of a general autonomous state-dependent delay differential equation. Particularly, in [221], he studied the semiflow properties of a general class of state-dependent delay differential equations with locally bounded delay

$$x'(t) = g(x_t); \quad x_0 = \varphi \in M$$

in the following exponentially weighted space (with the compatibility condition)

$$M := \{\phi \in U : \phi'(0) = g(\phi)\}$$

where

$$U \subset B^1 := \{\phi \in B \cap C^1 : e^{as}\phi'(s) \rightarrow 0 \text{ as } s \rightarrow -\infty\},$$

$$B := \{\phi \in C : e^{as}\phi(s) \rightarrow 0 \text{ as } s \rightarrow -\infty\},$$

$$C := C((-\infty, 0], \mathbb{R}^n), C^1 := C^1((-\infty, 0], \mathbb{R}^n).$$

In his problem, the delay is finite, yet unbounded. One result he proved was the continuity of the semiflow with respect to time.

In Chapter 3.3, a relatively complete analysis about the delay $\tau(t, x)$ is given, where it is shown that although from the integral equation of system (1.3), the delay can be infinite due to the assumptions on the function f , however, when $A(t, x)$ is bounded, $\tau(t, x)$ is also bounded. The semiflow properties are also studied for the system (1.3) in the exponentially weighted Lipschitz

space Lip_α . The existence and the “state variable continuity” of the semiflow are proved (see Theorem 3.6). The major principle is to use fixed point theorem to find the solution of the system. The difficulty lies in how to find a proper space and how to define the fixed point problem properly. However, the semiflow is in general not continuous in time. An example where the semiflow is not continuous in time is offered in Chapter 3.1 (between Definition 3.5 and Theorem 3.6). Moreover, we also consider the system in a similar space as in Walther [221]

$$D_\alpha := \{(\phi, \tau_0) \in BUC_\alpha^1 \times C_+(\Omega) : \phi'(0, x) = F(\phi(0, \cdot), \tau_0(\cdot), \phi(-\tau_0(\cdot), \cdot))(x), \forall x \in \Omega\},$$

where

$$BUC_\alpha^1 := \{\phi \in C^1((-\infty, 0], C(\Omega)) : \phi_\alpha \in BUC((-\infty, 0], C(\Omega)) \text{ and } \partial_t \phi_\alpha \in BUC((-\infty, 0], C(\Omega))\},$$

and ϕ_α is defined in (1.4). The result is Theorem 3.7, where it is shown that we can choose two different state space for A_t (Lip_α or BUC_α^1), but only in the case of BUC_α^1 can we get a continuous (in time) semiflow, which is in accordance with the result in Walther [221]. An illustration can also be seen at the end of Chapter 3.1. Moreover, for those who might be interested, I refer to [86, 123] for the research about infinite delay.

1.2.3 Boundedness and dissipativity of solutions

Chapter 4 deals with the boundedness and dissipativity of solutions of system (1.5) and the extended n -dimensional system (see system (4.5)). This work has been published in [141]. The dissipativity result describes that the solutions will eventually go below some constant which is independent of the initial conditions. A more detailed explanation of “dissipativity” is given in Theorem 4.16 and Theorem 4.21.

Smith dealt with this kind of problem in his work [193, 194], where he used a change of variable

$$\hat{t} = \int_0^t f(A(s))ds, t \geq 0; \hat{A}(\hat{t}) = A(t),$$

and transformed the state-dependent delay into a constant delay (a general analysis of this kind of change of variable can be found in Otto [168]). Then he studied the postivity, boundedness, Hopf bifurcation, global attractor and uniform persistence in the articles. This “change of variable” idea has also been successfully used in Kloosterman et al. [104] for dealing with a nutrient-phytoplankton-zooplankton model. A similar model as (1.5) was also used in Brunner et al. [30] about larva development.

However, in the case of an n -dimensional system, we can't find a valid change of variable any more. So we turn back to the original state-dependent delay differential equation (1.5) and deal with it directly. The approach to study the boundedness of solutions contains some similar procedures as the constant delay case in Smith's work [193], but more technical details and delicate arguments are needed in the state-dependent delay case. The major idea is to firstly find a proper bound on a certain interval of time, and then to prove that for the rest of the timeline the solution won't exceed this bound. Following this idea, the dissipativity results can also be proved.

1.2.4 Numerical simulations for a predator-prey system incorporating the state-dependent delay

Inspired by the above research of the forest growth model, we come up with the idea of introducing a predator-prey relation into the forest model. The predator-prey relation in the forest is usually expressed as the forest-pest or forest-parasite relation. A simple forest-pest mathematical model has been studied in [11].

In Chapter 5, the following predator-prey system is studied numerically

$$\left\{ \begin{array}{l} \frac{dA(t)}{dt} = f(A(t)) \frac{\beta A(t - \tau(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t)} - \mu_A A(t) - \frac{\gamma_A I(t) A(t)}{1 + \kappa A(t)}, \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_-, \\ \frac{dI(t)}{dt} = \left(\frac{\varepsilon \chi \gamma_A A(t)}{1 + \kappa A(t)} - \mu_I \right) I(t) \end{array} \right. \quad (1.7)$$

with the initial distributions

$$A(t) = A_0(t) \geq 0, \forall t \in (-\infty, 0]; \quad \tau(0) = \tau_0 \geq 0; \quad I(0) = I_0 \geq 0.$$

In this model, $A(t)$ describes the adult tree population number, and $I(t)$ describes the parasite population number. In Chapter 5, this parasite is a species of pine wood nematode, which causes a serious pine disease – pine wilt disease across the world [156, 206]. As is explained in Chapter 5, the life cycle of nematode is very short compared to the pine tree, so the model uses instantaneous production of nematodes, namely there is no delay term in the nematode equation.

The predator-prey system dates back to Lotka [129] and Volterra [211, 213] in the early 20th century, which is also called consumer-resource model in a general way. The classical Lotka-Volterra model takes the form

$$\left\{ \begin{array}{l} \frac{dx}{dt} = \alpha x - \beta xy, \\ \frac{dy}{dt} = \delta xy - \gamma y, \end{array} \right.$$

where x and y denotes the number of the prey and the predator respectively. This model has been very well studied in the literature (for example, [83, 158, 201]). I refer to papers [24, 38, 79, 93, 120, 122] and books [151, 166, 224] for some general introductions and analysis about predator-prey theory.

In the predator-prey system, a concept “functional response” is very important in describing the relationship between the predator and the prey. It is the intake rate of the predator as a function of prey density. On the other words, it describes the change in the rate of consumption of prey by a predator when the prey density varies [49]. This concept was first introduced in Holling’s papers [89, 90]. In the papers Holling also derived three types of functional responses. Holling’s type I functional response is a linear function

$$g(x) = \beta x,$$

which is basically the one in the Lotka-Volterra model, except that the linear relation in Holling’s type I functional response only exists up to a certain value of x and after this certain value, the function $g(x)$ takes a constant value, while there is no such limitation in Lotka-Volterra model. Holling’s type II functional response takes the form

$$g(x) = \frac{ax}{1 + ahx},$$

and Holling’s type III functional response is

$$g(x) = \frac{ax^k}{1 + ahx^k}.$$

Different population species will display different functional responses, for example, type I for algae and fungi, type II for the invertebrates and type III for the vertebrates [45]. Predator-prey systems with Holling’s type functional responses have been extensively studied in the literature (for example [5, 16, 46, 94, 105, 133] and with delays [131, 162, 229]). More kinds of functional responses were also raised and used in different situations [20, 50, 96, 102, 185].

In system (1.7), Holling’s type I and II functional response are combined together, namely the function $g(A) = \frac{\gamma_A A}{1 + \kappa A}$, which becomes type I when $\kappa = 0$ and type II when $\kappa > 0$.

One will observe that when $I_0 = 0$ then $I(t) = 0, \forall t \geq 0$, then system (1.7) corresponds to system (1.5), the one without parasite. On the other hand, when $\tau_0 = 0$ then by Remark 3.10, $\tau(t) = 0, \forall t \geq 0$, then system (1.7) becomes the following ODE predator-prey system

$$\begin{cases} \frac{dA(t)}{dt} = (\beta - \mu_A)A(t) - \frac{\gamma_A I(t)A(t)}{1 + \kappa A(t)}, \\ \frac{dI(t)}{dt} = \left(\frac{\varepsilon \chi \gamma_A A(t)}{1 + \kappa A(t)} - \mu_I \right) I(t). \end{cases}$$

This chapter is to investigate the influence of introducing nematode into a pine forest numerically, which can be regarded as a predator-prey system where the prey has (possibly) a complex dynamics described by a state-dependent delay differential equations. Three scenarios of forest population (steady solution, damped oscillating solution and periodic solution) with the introduction of nematodes are investigated via numerical simulations. Comparisons on two levels, namely i) forest population with and without nematodes, ii) predator-prey system with and without state-dependent delay are also studied. Both cases, either introducing the nematodes or introducing the state-dependent delay will bring significant changes in the population dynamics. The work of this chapter has been published in [142].

1.2.5 Discussion

This thesis studies a class of state-dependent delay differential equations.

The motivation comes from the comparison results between the state-dependent delay differential equation and a forest simulator SORTIE. Adult population numbers of two species of trees in two cases: single species case and two-species case are considered. These two species of trees represent two scenarios of forest population growth: i) going directly to a steady state; ii) oscillating to a steady state. From the numerical simulations, we observe that the state-dependent delay differential equation fits the forest data generated by the simulator SORTIE very well in both cases. Moreover, a spatial version of the state-dependent delay differential equation for two-species case, which includes the spatial position of trees, is also proposed in the thesis. Numerical simulations are also conducted for this spatial model, but there is no fitting to the forest data due to the reason that we cannot obtain the specific data of adult population numbers in each spatial position from the simulator SORTIE. However, from the numerical simulations one can still observe the spatial disperse of the forests. And, by changing parameters which influence the interactions of the two species, we can obtain different evolutionary consequences in the long term: competitive exclusion or coexistence. This actually shows that in order for the species to coexist, they must have different advantages in different levels, otherwise one that has no advantages in any aspect must die out. Specifically speaking, in Figure 2.9, the decrease of ζ_{21} changes the forest system from competitive exclusion to coexistence. This can be explained as the fact that although the species A_2 has some advantage before so that it can dominate, the decrease of ζ_{21} means that the species A_1 has some advantage on some other level such that the species A_2 can influence it less stronger, thus two species can coexist.

Inspired by the nice simulation results, we propose a general class of state-dependent delay differential equations which can derive the above one. Similar systems have been considered in the literature, but the state space is differ-

ent. Most papers dealt with systems in the space of continuous differentiable functions, or in addition, with an exponential weight. In this thesis, I consider this problem in an exponentially weighted Lipschitz space, which, to my best knowledge, has not been studied before. The existence of the maximal semiflow is studied via the fixed point method and the lower semi-continuity of the maximal time of existence with respect to the initial conditions is also studied. A big difference from before is that in general there is no time continuity of this maximal semiflow. Furthermore, the boundedness of solutions and the dissipativity of the system are also studied, where we extend the method which was used before by Smith on constant delay system to adapt to our varying delay problem.

Lastly, we naturally turn to the thought of the predator-prey relation in forest, which obviously has influences on forest population growth. Combined with the serious pine wilt disease, we consider introducing the parasite of the disease into the forest population growth model, and construct the predator-prey system with a state-dependent delay differential equation. Preliminary analysis are from the numerical point of view. From the simulations of the predator-prey system in three scenarios, we observe the complexity of the dynamics in two levels: introducing the state-dependent delay into a predator-prey system and introducing the predator-prey relationship into a single population model. Although there haven't been any mathematical analysis of this kind of system, the numerical simulations help to understand this system intuitively.

More work can be done in this direction. Firstly, since the time when this kind of system was raised more than 20 years ago, very little studies have been done. Yet there are a lot of interesting research prospects of this system in a mathematical point of view, for example, the stability analysis, the bifurcation analysis, the travelling wave problem. Moreover, there are other forest simulators in the literature. Is our system capable of fitting other forest simulators? Different forests might compete for different resources, thus light might no longer be the main ingredient. So what kind of changes need to be done accordingly to our system in order to adapt to other forests? These questions are issued for further research.

Chapter 2

Comparisons between a forest computer simulator and a mathematical model

2.1 Introduction

In the natural ecosystem, forests play an important role. This has motivated a lot of people to propose computer simulators as well as mathematical models to describe the dynamical properties of forests. Many computer simulators (also sometimes called Individual Based Models (IBMs)) have been proposed and we refer to JABOWA [25, 26], FORET [191], SORTIE [170], FORMIND [107, 108] and others. These models consist of stochastic processes describing individual behaviors, such as birth, death, movement, reproduction and so on. Moreover, these models also permit us to describe the behavior of the entire plant community. The main advantage is that it provides simulated data which can be used to analyze such a complex system. Of course this is a rough description of the real plant community. However, they do supply powerful experimental tools and describe the forest dynamics reasonably well [125]. We refer to [126, 177] for a general review about forest IBMs.

SORTIE is a forest simulator based on the forest data observed in and around Great Mountain Forest (GMF), a privately owned 2500ha forest located in northwestern Connecticut (41°57'N, 73°15'W), USA (see Figure 2.1) in the year 1990-1992. In SORTIE, four submodels (resource, growth, mortality, and recruitment) are included to determine the behaviour of each individual. As is explained in [169], from the point of view of the resource competition, SORTIE includes only the light competition, since from extra experiments very little evidence of water or nitrogen limitation has been observed for this particular forest. Nevertheless water or nitrogen limitation might be vital in other forests. The lighting mechanism in SORTIE is rather complex and we refer to the subsection *Resource submodel* page 3 in [169] for more about this. Tree growth



Figure 2.1: *The location of the forest - Great Mountain Forest - studied by SORTIE: northwestern Connecticut ($41^{\circ}57'N$, $73^{\circ}15'W$), USA.*

is described by change of tree size, which is denoted here as the diameter at a certain height. Two concepts "diam₁₀ (Diameter at 10cm Height)" and "DBH (Diameter at Breast Height)" are often used to describe the tree growth and represent the tree size in the analysis of forest dynamics [169, 170, 179]. Thereinto, the diam₁₀ can be used almost throughout the whole life of an individual, from seedling to adult, while DBH can only be used for adults in most cases, as it is measured at a higher height. The definition of the breast height (of an adult human being) is different in different regions, for example, 1.4m in the US and 1.3m in Europe and Canada. But it makes little difference to the measuring result in many cases. We refer to [106, 169, 170, 171, 179, 202] for more details of SORTIE.

In this chapter we will extend the model proposed by Hal Smith in [193, 194] to describe the dynamic of a population that is structured in size with intra-specific competition for light. For a single species, we will compare such a mathematical model with SORTIE model for two types of tree (American beech (FAGR) and eastern hemlock (TSCA)). The reason why we choose particularly these two types of tree is that after a tentative run of SORTIE, we find that FAGR and TSCA dominates the forest in an obvious way (see Figure 2.2). Moreover, based on the parameters estimated separately for each kind of tree, we will investigate the inter-specific competition for light by assuming that the growth rate of juveniles is influenced by the number of adults due to the competition for light between them. We will also extend our modelling effort by considering the case of two populations distributed in space and competing for light.

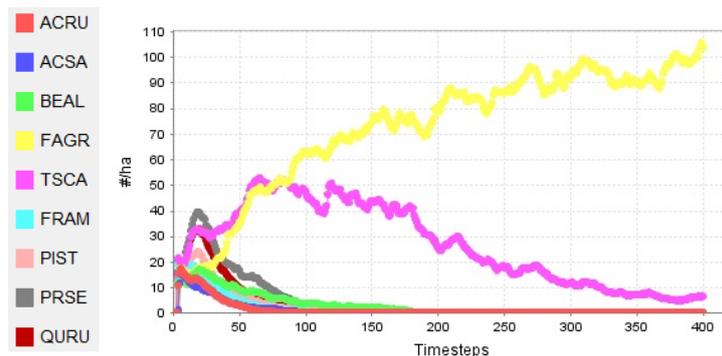


Figure 2.2: *The output of one run of SORTIE for all the nine species on a period of 2000 years (1 time step=5 years).*

Several mathematical models describing the forest growth were proposed in the literature. Zavala et al. [231] studied a stage-structured population model incorporating the light competition respectively in growth, mortality and recruitment, and gave the conditions for the existence of a steady state distribution. Angulo et al. [10] continued with a similar model, but they considered the light competition only in recruitment, and after that they extended the model to a two-species stand, and gave the positive stationary distribution for both single-species and two-species model and the conditions for the coexistence. Cammarano [37] studied a system of Lotka-Volterra type, incorporating also the light competition and discussed the equilibria and the coexistence conditions. In this article, based on SORTIE simulated data, we will exclude the competition occurring in the mortality and recruitment. In other words, we will see that the best fit for SORTIE model is obtained by using a model where the competition for light influences only the growth rate of trees. We also refer to [65, 109, 111, 165, 183, 200, 230] and the references therein for other models and relevant research.

This chapter is organized as follows. In section 2 we will give a mathematical model for single species, and we will conduct numerical simulations to compare with SORTIE. In section 3 a mathematical model for two species is obtained likewise, and we also conduct the comparison with SORTIE. Then in section 4 we extend it to a 2-dimension spatial model, and conduct numerical simulations to see the spread of trees in space.

2.2 Single species model

2.2.1 Mathematical modelling

In this section we consider the following model describing the growth of trees of single species

$$\begin{cases} \partial_t u(t, s) + \underbrace{f(A(t))\partial_s u(t, s)}_{\text{growth of juvenile trees}} = - \underbrace{\mu(s)}_{\text{mortality}} u(t, s), & \text{for } t > 0, s > s_-, \\ f(A(t))u(t, s_-) = \underbrace{\beta b(A(t))}_{\text{flux of newborns}}, & \text{for } t > 0, \\ u(0, \cdot) = u_0(\cdot) \in L^1_+(s_-, +\infty). \end{cases} \quad (2.1)$$

Here $u(t, s)$ denotes the population density of trees with size s at time t , so $\int_{s_1}^{s_2} u(t, s) ds$ is the number of trees with size $s \in [s_1, s_2]$ at time t , and $A(t)$ is the number of adult population at time t . As it will be explained in Appendix A, the size s is described by a function of diam_{10}

$$s(t) := \ln \frac{r(t)}{r_-}, \text{ and } r(t) = \frac{\text{diam}_{10}(t)}{2}$$

where r_- is the minimal radius of the juvenile. The function $\mu(s) > 0$ is the natural mortality. In the following derivation we will assume for simplicity that

$$\mu(s) = \begin{cases} \mu_A > 0, & \text{if } s \geq s^*, \\ \mu_J > 0, & \text{if } s \in [s_-, s^*), \end{cases}$$

where $s_- > 0$ is the minimal size of a juvenile and s^* satisfying $s^* > s_-$ is the maximal size of a juvenile (or the minimal size of an adult). The parameter β is the birth rate in absence of birth limitation, and the term $\beta b(A(t))$ describes the flux of newborns into the population, where $b(x) = xe^{-\xi x}$ is the Ricker's type birth limitation [180, 181]. The nonlinear growth function $f(x)$ takes the form

$$f(x) = \frac{\alpha}{1 + \delta x}, \quad \alpha, \delta > 0, \quad (2.2)$$

which is decreasing, thus taking care of the fact that the more large trees there are, the slower the growth rate of small trees is. So this shows the type of competition for light between adults and juveniles. A similar size-structured population dynamical model with a nonlinear growth rate (taking into account the competition for a resource) has been studied in Calsina and Saldaña [36]. The function $u_0(\cdot)$ represents the initial distribution of the species. Normally we want the number of the total population to be finite at each time, hence we have

$$\int_{s_-}^{+\infty} u(t, s) ds < +\infty, \quad \forall t \geq 0.$$

So the natural state space for this model is $L^1(s_-, +\infty)$.

We will derive the following equations for adults and juveniles under some assumptions

$$\begin{cases} \frac{dA(t)}{dt} = f(A(t))j(t, s^*) - \mu_A A(t), \text{ for } t > 0, \\ \partial_t j(t, s) + f(A(t))\partial_s j(t, s) = -\mu_J j(t, s), \text{ for } s \in [s_-, s^*), t > 0, \\ f(A(t))j(t, s_-) = \beta b(A(t)), \text{ for } t > 0, \\ A(0) = A_0 \geq 0, \\ j(0, s) = j_0(s) \geq 0, \text{ for } s \in [s_-, s^*), \end{cases} \quad (2.3)$$

where $j(t, s)$ represents the population density of juveniles with size $s \in [s_-, s^*)$ at time t . Hence the total number of juveniles at time t is

$$J(t) = \int_{s_-}^{s^*} j(t, s) ds = \int_{s_-}^{s^*} u(t, s) ds.$$

And we can assume as follows the adult population number

$$A(t) = \int_{s^*}^{+\infty} u(t, s) ds. \quad (2.4)$$

By integrating along the characteristic line of the second equation (of juvenile) in (2.3), the first equation (of adult) in (2.3) can be rewritten as the following state-dependent Functional Differential Equation (FDE)

$$\begin{cases} \frac{dA(t)}{dt} = e^{-\mu_J \tau(t)} \frac{f(A(t))}{f(A(t - \tau(t)))} \beta b(A(t - \tau(t))) - \mu_A A(t), \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_- \end{cases} \quad (2.5)$$

when $t > t^*$, where t^* is defined as

$$\int_0^{t^*} f(A(\sigma)) d\sigma = s^* - s_-.$$

Differentiation of the second equation with respect to t gives the following system

$$\begin{cases} A'(t) = e^{-\mu_J \tau(t)} \frac{f(A(t))}{f(A(t - \tau(t)))} \beta b(A(t - \tau(t))) - \mu_A A(t), \\ \tau'(t) = 1 - \frac{f(A(t))}{f(A(t - \tau(t)))}. \end{cases} \quad (2.6)$$

The initial conditions are

$$A(t) = A_0(t) \geq 0, \forall t \in (-\infty, 0]; \tau(0) = \tau_0 \geq 0, \quad (2.7)$$

where $A_0(t)$ is continuous and exponentially bounded, namely for some $\vartheta > 0$

$$\sup_{t \leq 0} e^{\vartheta t} A_0(t) < +\infty.$$

From the second equation of (2.5), as f is decreasing, the delay $\tau(t)$ can become large enough, namely we may have infinite delay. For all the derivations here, see Appendix A. The semiflow properties of such a state-dependent delay differential equation will be studied in Chapter 3.

2.2.2 Numerical simulations of two special cases

We conduct numerical simulations for two special cases of the system (2.5).

Special case 1 ($f(x)$ is constant): Assume that $f(x)$ is a constant function (so the delay $\tau(t)$ is also constant by the second equation of (2.5)) and $b(x) = xe^{-x}$. Then since the PDE model (2.1) can be transformed (by making a simple change of variable in time) into an age-structured model, it is known (see Magal and Ruan [139]) that the system has a Hopf bifurcation around the positive equilibrium when β increases (see in Figure 2.3).

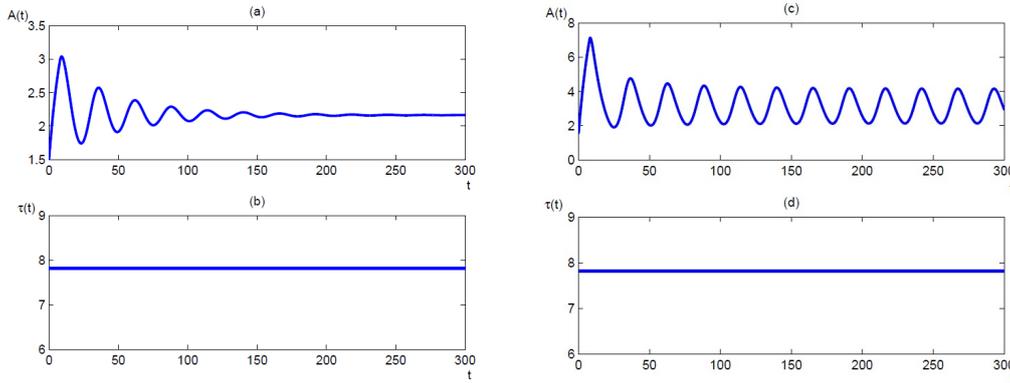


Figure 2.3: We plot the adult population number $A(t)$ in figure (a) and (c), and the corresponding delay $\tau(t)$ in figure (b) and (d). We fix the parameter values $\mu_J = 0.2$, $\mu_A = 0.1$, $\alpha = 0.5$, $\delta = 0$, $\xi = 1$, $s^* = \ln 50$, $s_- = 0$, and the initial distribution $A_0(t) = 1.5$, $\forall t \in [-100, 0]$. In (a) and (b) we set $\beta = 9$. The solution oscillates and then converges to the positive equilibrium. In (c) and (d) we set $\beta = 25$. Changing β from 9 to 25, we observe a Hopf bifurcation.

Special case 2 ($b(x) = x$): Assume $b(x) = x$, namely the Ricker's type birth function doesn't appear in system (2.5). It is known that when τ is constant in the first equation (which becomes linear) of system (2.5), this system is either exponentially increasing or exponentially decreasing when the time goes to infinity. However, it has been proved by Smith [193] that Hopf bifurcation can occur when we take state-dependent delay. This is illustrated in Figure 2.4.

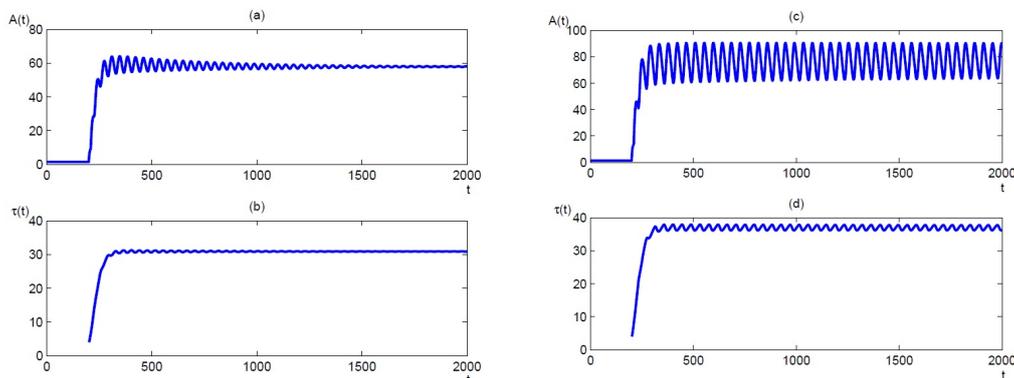


Figure 2.4: We plot the adult population number $A(t)$ in figure (a) and (c), and the corresponding delay $\tau(t)$ in figure (b) and (d). We fix the parameter values $\mu_J = \mu_A = 0.1$, $\delta = 0.1$, $\xi = 0$ (remember this means that $b(x) = x$), and the initial delay $\tau_0 = 4$. The initial distribution is $A_0(t) = 1.5, \forall t \in [0, 200]$. In (a) and (b) we set $\beta = 2.2$, then we have the damped oscillating solution which converges to the positive equilibrium; In (c) and (d) we set $\beta = 4$. Changing β from 2.2 to 4, we observe a Hopf bifurcation.

2.2.3 Comparison with SORTIE

We run the simulator SORTIE with the parameter values given in [106, 170, 179, 202] and get the simulation for the density of adult trees (adults are defined here as trees having a DBH ≥ 10 cm). And as we can see from this simulation, American beech(FAGR) and eastern hemlock(TSCA) become the dominant species after a period time. So in this article we will focus on these two species in two cases: one single species and two-species.

The basic idea of the numerical simulation of (2.5) and comparison is as follows. Before starting, we need to get the forest data from SORTIE. Since every run of SORTIE is initiated with a random seed, we conduct 50 runs and take the average values as our actual data. Moreover, the data that SORTIE gives are actually the density of the adult population per hectare. As the area of the sample square is 90000m^2 (a square of $300\text{m} \times 300\text{m}$) = 9 hectares, we multiply the data by 9 to obtain the total adult population number. We plot the 50 runs and the average in Figure 2.5 to see the stochastic variation. Now we will compare our model (2.5) with the mean value over these 50 runs of SORTIE, and find the best fit. First we need to decide the initial time (for example, $t = 100$ as the initial time), and we will use the data from SORTIE over the time interval $[0, 100]$ as the initial condition. Next we discretize the parameters $\mu_J, \mu_A, \beta, \xi, \delta, \tau_0$, and for each set of parameters, we calculate the solution of (2.5) by using the common approximation of the derivative (the numerical scheme will be conducted via the equivalent system (2.6)), and we compare the numerical solutions with the data from SORTIE by using the least

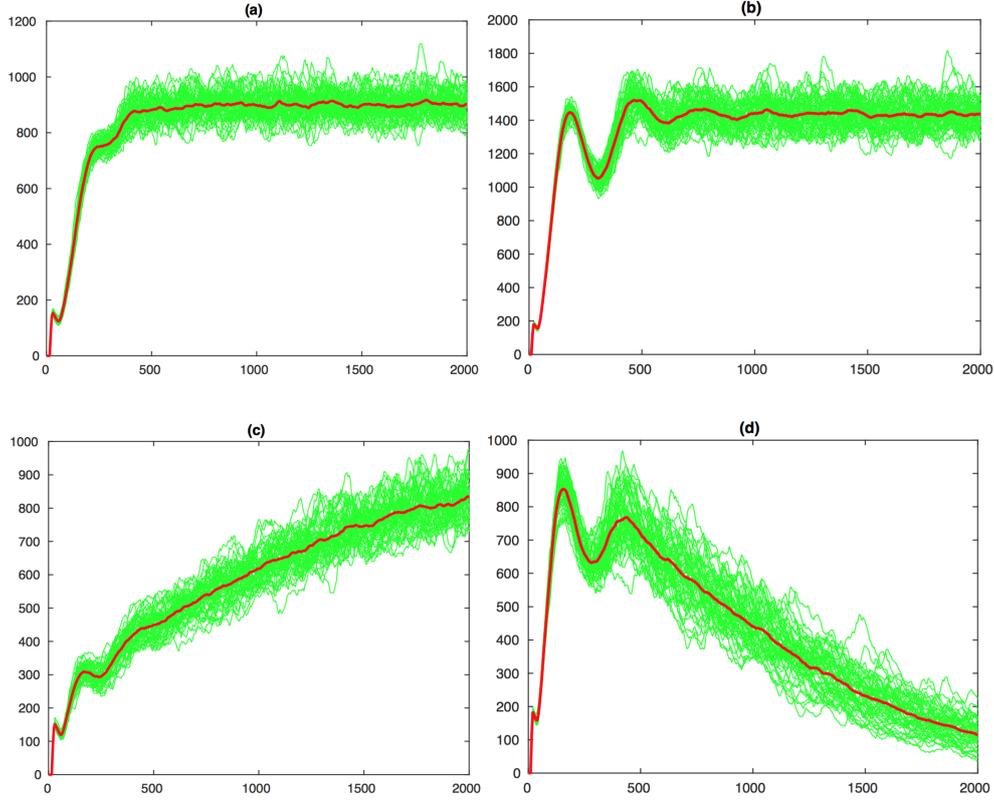


Figure 2.5: Population numbers of 50 random runs from SORTIE for the adults of two species American beech and eastern hemlock (green curve) and the average number (red curve) respectively, in a period of 400 timesteps. (a). One single species American beech; (b). One single species eastern hemlock; (c). Two-species case: American beech; (d). Two-species case: eastern hemlock.

square method, to find the set of parameter values with which the numerical result of the model (2.5) and the data have the least difference. Then we use the following formula (see Appendix A)

$$\int_{-\tau_0}^0 \frac{\alpha}{1 + \delta A(\sigma)} d\sigma = s^* - s_-,$$

to compute α , where we use the Simpson's rule to calculate the integral. Now we can keep this set of parameter values, and we have the best fit to SORTIE.

For the first dominant species American beech, we choose the SORTIE data in the time interval $[0,200]$ as the initial distribution. We have the best fit in Table 1 and Figure 2.6.

2. Forest models

Parameter	Interpretation	value	Reference
μ_{J_1}	natural mortality rate for juveniles	0.03	estimated
μ_{A_1}	natural mortality rate for adults	0.001	estimated
β_1	birth rate in absence of birth limitation	2	estimated
s_-	minimal size for juvenile	0	[170]
s^*	minimal size for adult	$\ln 50$	[179]
ξ_1	parameter in the Ricker type function	0	estimated
τ_{01}	time delay of the juveniles present at time 0 to become adults	121	estimated
α_1	growth rate of juveniles without adults	0.1709	computed
δ_1	parameter describing the descending speed of the growth rate when adult population increases	0.1	estimated

Table 1: Parameter values of the best fit for species 1: American beech.

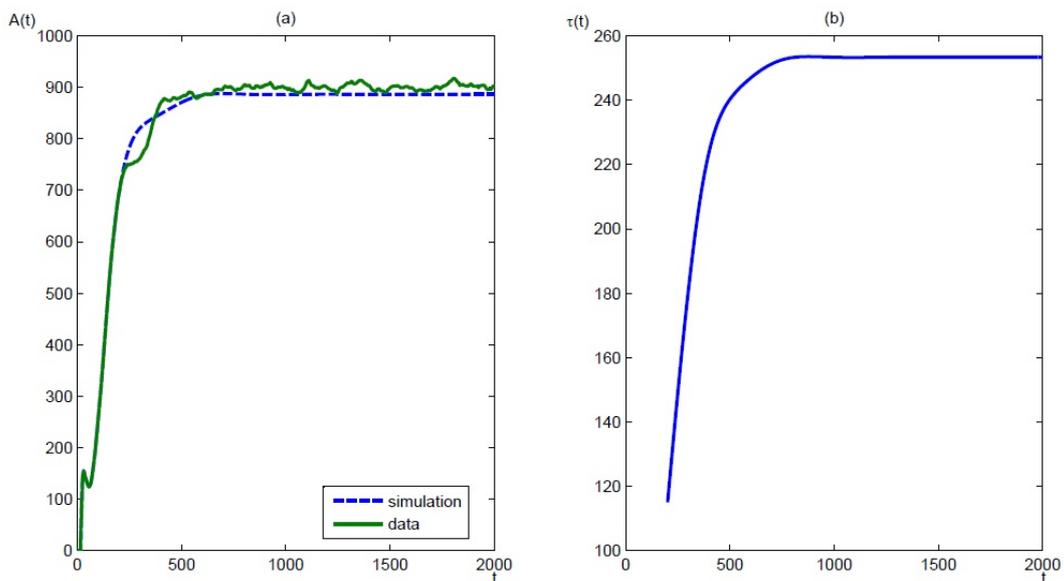


Figure 2.6: In this figure we show the comparison between SORTIE data and numerical simulation for American beech. The adult population number $A(t)$ is plotted in (a) and the delay $\tau(t)$ is shown in (b).

Similarly, for the second dominant species eastern hemlock we choose the SORTIE data in the time interval $[0,180]$ as the initial distribution. We get the best fit in Table 2 and Figure 2.7.

Parameter	Interpretation	value	Reference
μ_{J_2}	natural mortality rate for juveniles	0.031	estimated
μ_{A_2}	natural mortality rate for adults	0.0037	estimated
β_2	birth rate in absence of birth limitation	4	estimated
s_-	minimal size for juvenile	0	[170]
s^*	minimal size for adult	$\ln 50$	[179]
ξ_2	parameter in the Ricker type function	0	estimated
τ_{02}	time delay of the juveniles present at time 0 to become adults	127	estimated
α_2	growth rate of juveniles without adults	0.249	computed
δ_2	parameter describing the descending speed of the growth rate when adult population increases	0.1	estimated

Table 2: Parameter values of the best fit for species 2: eastern hemlock.

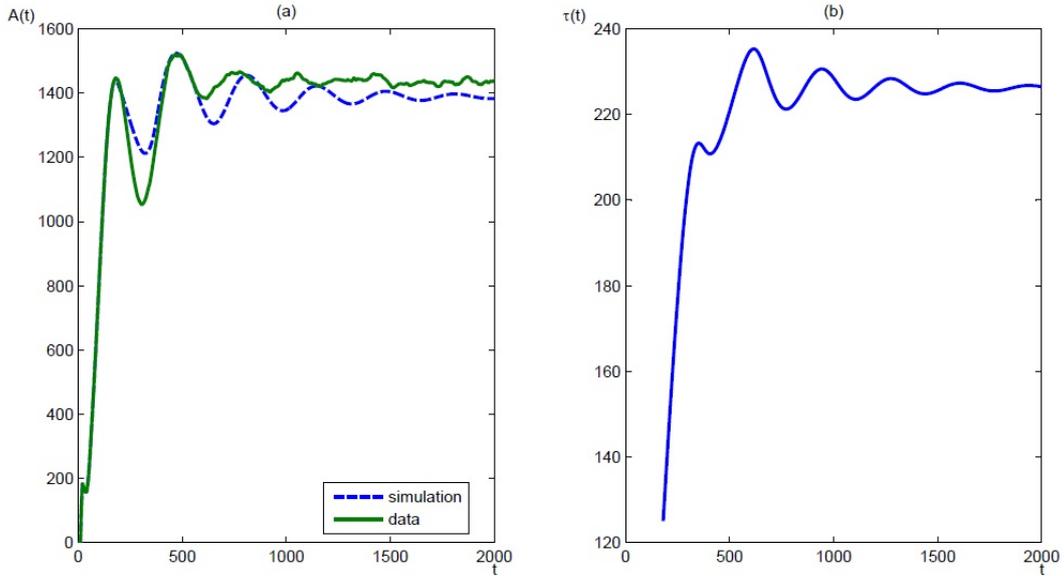


Figure 2.7: In this figure we show the comparison between SORTIE data and numerical simulation for eastern hemlock. The adult population number $A(t)$ is plotted in (a) and the delay $\tau(t)$ is shown in (b). Notice that this species will have an oscillation before it converges to the stable positive equilibrium.

Notice that for both species in the single species case, we have $\xi_1 = \xi_2 = 0$ as the best fit, which means that there is no Ricker's type birth limitation here.

2.3 Two-species model

2.3.1 Mathematical modelling

System (2.1) can be extended to the case of two species. Taking the previous best fit $\xi_1 = \xi_2 = 0$ into account, we obtain the following system

$$\begin{cases} \partial_t u_1(t, s) + f_1(Z_1(t)) \partial_s u_1(t, s) = -\mu_1(s) u_1(t, s), & \text{for } t > 0, s > s_-, \\ \partial_t u_2(t, s) + f_2(Z_2(t)) \partial_s u_2(t, s) = -\mu_2(s) u_2(t, s), & \text{for } t > 0, s > s_-, \\ f_1(Z_1(t)) u_1(t, s_-) = \beta_1 A_1(t), & \text{for } t > 0, \\ f_2(Z_2(t)) u_2(t, s_-) = \beta_2 A_2(t), & \text{for } t > 0, \\ u_1(0, \cdot) = u_{10}(\cdot) \in L^1_+(s_-, +\infty), \\ u_2(0, \cdot) = u_{20}(\cdot) \in L^1_+(s_-, +\infty), \end{cases} \quad (2.8)$$

where

$$Z_i(t) = \zeta_{i1} A_1(t) + \zeta_{i2} A_2(t), \quad f_i(x) = \frac{\alpha_i}{1 + \delta_i x}, \quad \mu_i(s) = \begin{cases} \mu_{A_i} > 0, & \text{if } s \geq s^*, \\ \mu_{J_i} > 0, & \text{if } s \in [s_-, s^*), \end{cases}$$

and $\zeta_{ij} \geq 0$ are non-negative constants, $\alpha_i, \delta_i > 0$, $i, j = 1, 2$. A specific explanation of the meaning of ζ_{ij} can be found in Table 3. Notice that we use the same minimal juvenile size s_- and minimal adult size s^* for both species (see [169]). After a similar derivation, we have the following state-dependent delay differential equations

$$\begin{cases} A'_i(t) = e^{-\mu_{J_i} \tau_i(t)} \frac{f_i(Z_i(t))}{f_i(Z_i(t - \tau_i(t)))} \beta_i A_i(t - \tau_i(t)) - \mu_{A_i} A_i(t), \\ \int_{t - \tau_i(t)}^t f_i(Z_i(t)) d\sigma = s^* - s_-, \end{cases} \quad (2.9)$$

$i = 1, 2$. We give the following expression for the sake of numerical simulation

$$\begin{cases} A'_i(t) = e^{-\mu_{J_i} \tau_i(t)} \frac{f_i(Z_i(t))}{f_i(Z_i(t - \tau_i(t)))} \beta_i A_i(t - \tau_i(t)) - \mu_{A_i} A_i(t), \\ \tau'_i(t) = 1 - \frac{f_i(Z_i(t))}{f_i(Z_i(t - \tau_i(t)))}. \end{cases} \quad (2.10)$$

2.3.2 Comparison with SORTIE

We use the same method of comparison as before and we use the parameters in Table 1 and Table 2 to simulate the two-species model. We discretize the new parameters ζ_{ij} appeared in the competition term, and also by the least square method, we get the best fit for them: $\zeta_{11} = 1$, $\zeta_{12} = 0.6$, $\zeta_{21} = 1.6$, $\zeta_{22} = 1$, and the delay τ_{01} is increased to 201, τ_{02} increased to 208. We list these values in Table 3. The comparison figure is in Figure 2.8.

Parameter	Interpretation	value	Reference
ζ_{11}	parameter in the competition term describing the intraspecific competition among American beech	1	estimated
ζ_{12}	parameter in the competition term describing the interspecific influence of eastern hemlock on American beech	0.6	estimated
ζ_{21}	parameter in the competition term describing the interspecific influence of American beech on eastern hemlock	1.6	estimated
ζ_{22}	parameter in the competition term describing the intraspecific competition among eastern hemlock	1	estimated
τ_{01}	time delay of the American beech juveniles present at time 0 to become adults	201	estimated
τ_{02}	time delay of the eastern hemlock juveniles present at time 0 to become adults	208	estimated

Table 3: New parameter values for two-species model.

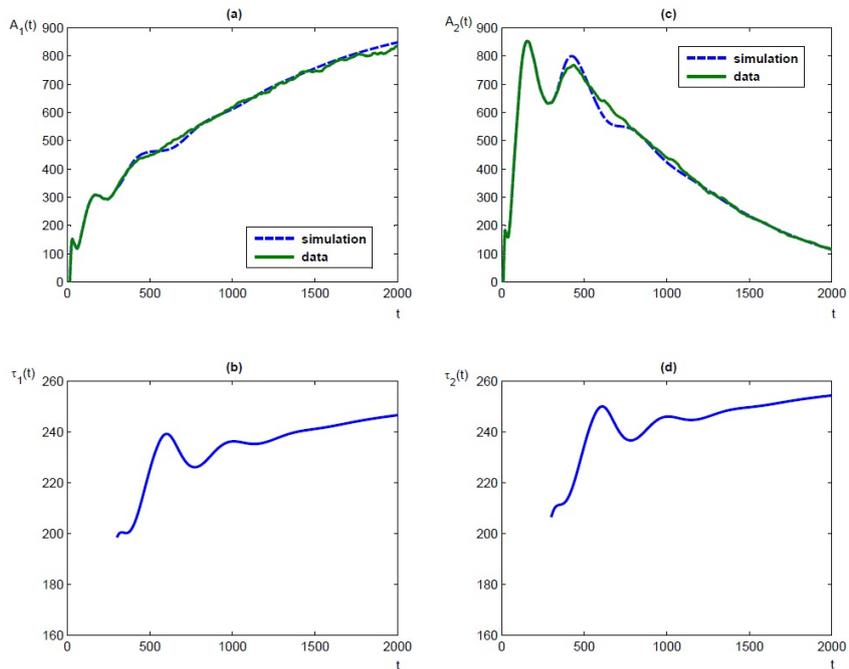


Figure 2.8: *In this figure we plot the comparison between SORTIE data and numerical simulation for two-species model (2.9). The figures (a) and (c) show the adult population number for species 1 American beech and species 2 eastern hemlock respectively. The figures (b) and (d) show the corresponding time delay.*

By analyzing the existence of positive (coexisting) equilibrium (see Appendix B), we can also obtain the coexistence of both American beech and eastern hemlock in Figure 2.9.

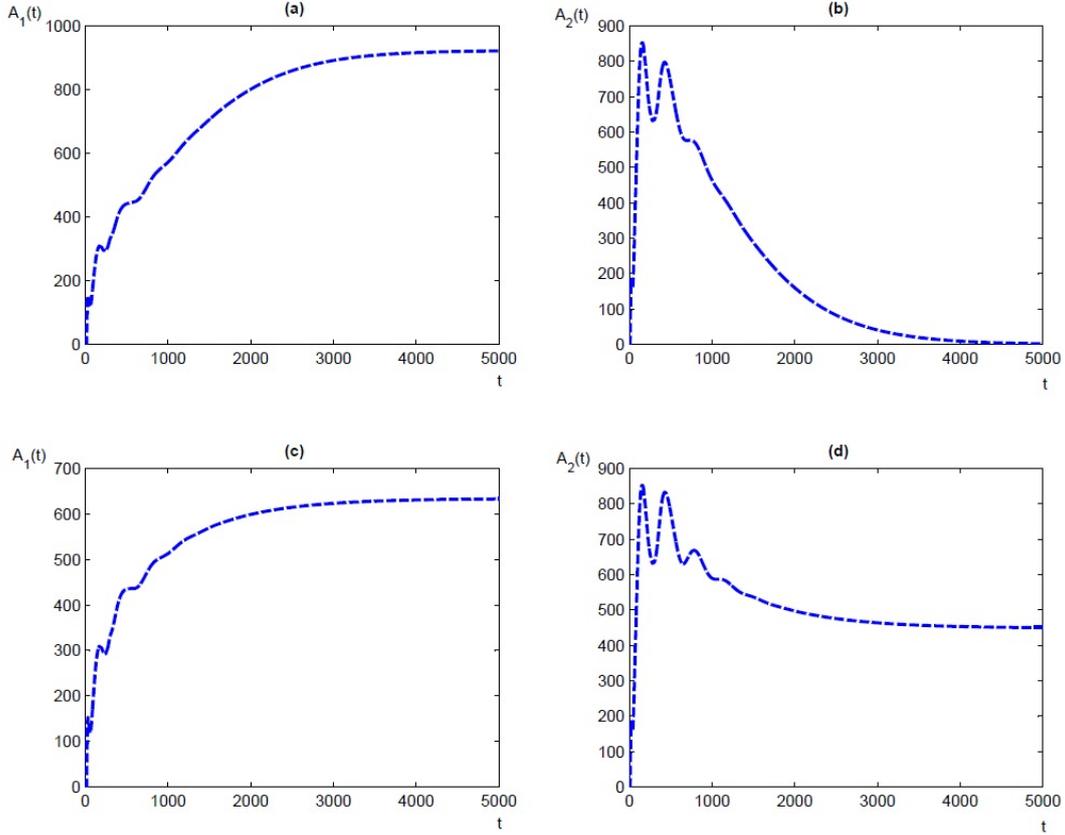


Figure 2.9: *In this figure we demonstrate that we can pass from competitive exclusion (a)(b)(which corresponds to Figure 2.8) to coexistence (c)(d) by changing one parameter ζ_{21} . The other parameters are the same as in Figure 2.8. When $\zeta_{21} = 1.6$, American beech (a) reaches to a positive steady state while eastern hemlock (b) disappears gradually. After we decrease the value of ζ_{21} to 1, both American beech (c) and eastern hemlock (d) go to a positive steady state, which means coexistence.*

2.4 Two-species spatial model

Now we take the spatial position of the individuals into account to see the spread of the adult population. We assume that the diffusion of individuals is due to the spreading of seeds around the trunk. This corresponds to assume that the distribution of seeds, when they fall down around the trunk, follows a Gaussian distribution. The same idea has already been proposed by Ducrot

[57]. The spatial model with two species reads as follows

$$\begin{cases} \partial_t u_i(t, s, x, y) + f_i(Z_i(t, x, y)) \partial_s u_i(t, s, x, y) = -\mu_i(s) u_i(t, s, x, y), \\ \quad \text{for } t > 0, s > s_-, x \in [0, x_{\max}], y \in [0, y_{\max}], \\ f_i(Z_i(t, x, y)) u_i(t, s_-, x, y) = (I - \varepsilon_i \Delta)^{-1} (\beta_i A_i(t, \cdot, \cdot))(x, y), \\ \quad \text{for } t > 0, x \in [0, x_{\max}], y \in [0, y_{\max}], \\ u_i(t, x, 0) = u_i(t, x, y_{\max}), \text{ for } x \in [0, x_{\max}], \\ u_i(t, 0, y) = u_i(t, x_{\max}, y), \text{ for } y \in [0, y_{\max}], \\ u_i(0, s, x, y) = u_{i0}(s, x, y) \in L^1_+((s_-, +\infty) \times [0, x_{\max}] \times [0, y_{\max}]), \end{cases} \quad (2.11)$$

where

$$Z_i(t, x, y) = \zeta_{i1} A_1(t, x, y) + \zeta_{i2} A_2(t, x, y), f_i(x) = \frac{\alpha_i}{1 + \delta_i x},$$

$\zeta_{ij} \geq 0$, $\alpha_i, \delta_i > 0$, $i = 1, 2$, and Δ is the Laplacian operator with periodic boundary condition. Similarly, we assume the adult population number

$$A_i(t, x, y) = \int_{s^*}^{+\infty} u_i(t, s, x, y) ds, i = 1, 2,$$

and by following a similar procedure as before, we get the state-dependent delay differential equation for the adult

$$\begin{cases} \frac{\partial A_i(t, x, y)}{\partial t} = e^{-\mu_{J_i} \tau_i(t, x, y)} \frac{f_i(Z_i(t, x, y))}{f_i(Z_i(t - \tau_i(t, x, y), x, y))} (I - \varepsilon_i \Delta)^{-1} [\beta_i A_i(t - \\ \quad \tau_i(t, x, y), \cdot, \cdot)](x, y) - \mu_{A_i} A_i(t, x, y), \text{ for } t > t^*, \\ \int_{t - \tau_i(t, x, y)}^t f_i(Z_i(\sigma, x, y)) d\sigma = s^* - s_-, \text{ for } t > t^*. \end{cases} \quad (2.12)$$

Remark 2.1. *The inverted operator $(I - \varepsilon_i \Delta)^{-1}$ is defined by using the resolvent of the Laplacian operator Δ , which is specifically explained in Appendix C. It is an operator which maps bounded uniformly continuous functions defined on \mathbb{R} to a space of periodic functions.*

We conduct numerical simulations for system (2.12), using the parameters in Table 1-3, and setting the diffusion coefficient $\varepsilon_1 = 0.01$, $\varepsilon_2 = 0.005$, in order to observe the growth and spread of adult population of the two species. The simulation is conducted in a $300 * 300$ square of the $x - y$ plane, as in the reference [169]. We choose the square $[0, 300] \times [0, 300]$ for simplicity. We use a random initial distribution $A_i(0, x, y)$ defined as follows for both species: first we discretize the interval $[0, 300]$, then we choose 25 random points in the square by taking randomly 5 points on x -axis and y -axis respectively and we assign a non-zero random number to each of the 25 points as the population

number of adults $A_i(0, x, y)$. For the rest discretized points in the square, we assign 0 to them.

Next we plot the solutions of system (2.12) at several specified time in Figure 2.10. The x - and y -axis describe the spatial coordinates, and the z -axis is the adult population number. In this figure we will observe the growth of the two species and the spread in space, and we can also see vividly that the model generates obvious species isolates after some time.

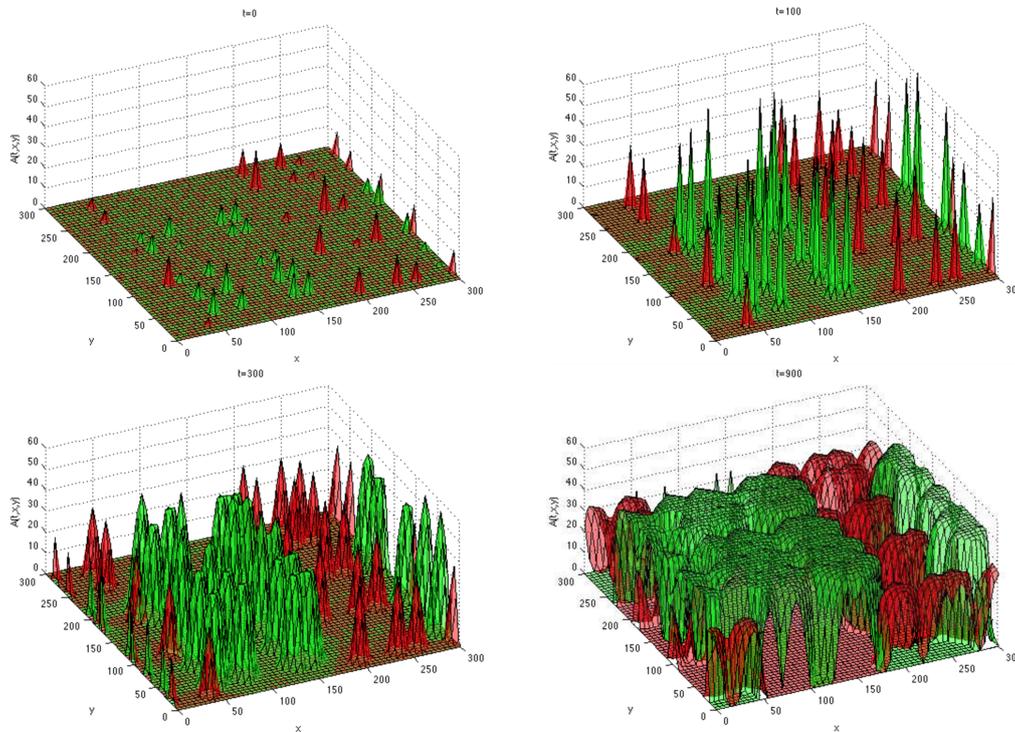


Figure 2.10: *In this figure we show the numerical simulations for the spatial model (2.12), describing the spread of adult population of the two species. The red part represents species 1 American beech, and the green part represents species 2 eastern hemlock.*

2. Forest models

We also conduct the simulation for longer time, and we get the following results (of competitive exclusion) in Figure 2.11.

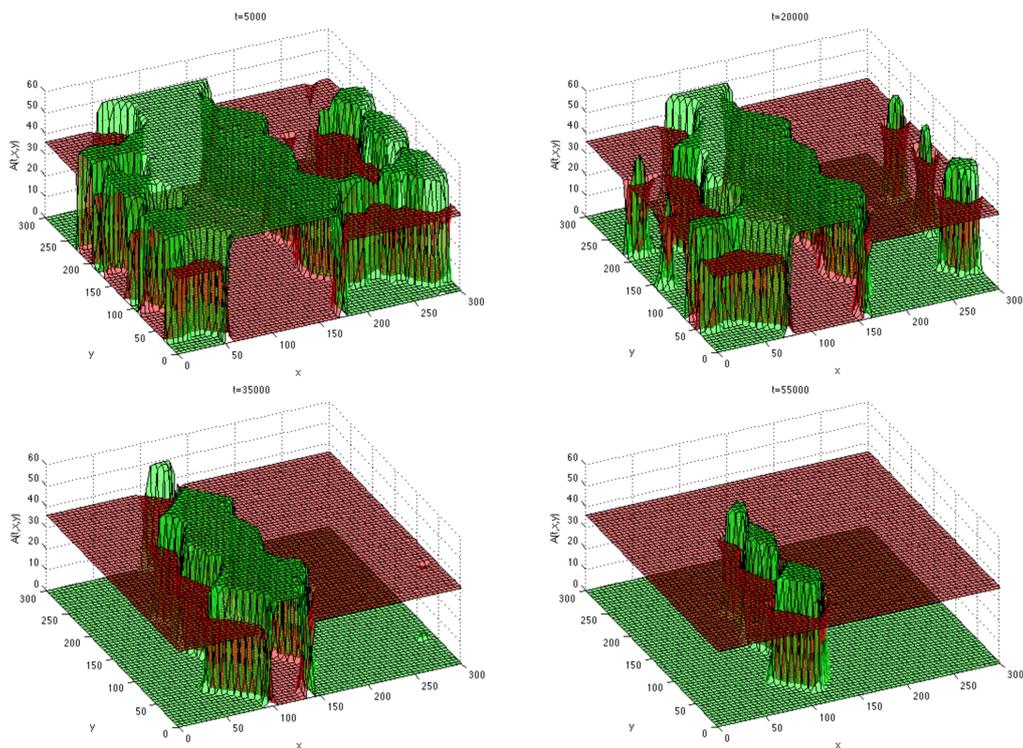


Figure 2.11: *This figure shows the change of the distribution of adult population of two species in the long run. Notice that eastern hemlock(green) is disappearing and American beech(red) becomes dominant.*

Summarizing all the figures above, we may conclude that eastern hemlock(green) grows and spreads faster than American beech(red) at first, but after long enough time, American beech begins to show its competency and gradually becomes the dominant species. This result also coincides with our previous result without considering the space in Figure 2.8.

Moreover, we plot the total population in the sample square for each species with respect to time in Figure 2.12. And we can see that the total adult population for eastern hemlock increases faster than American beech at first, and then it decreases.

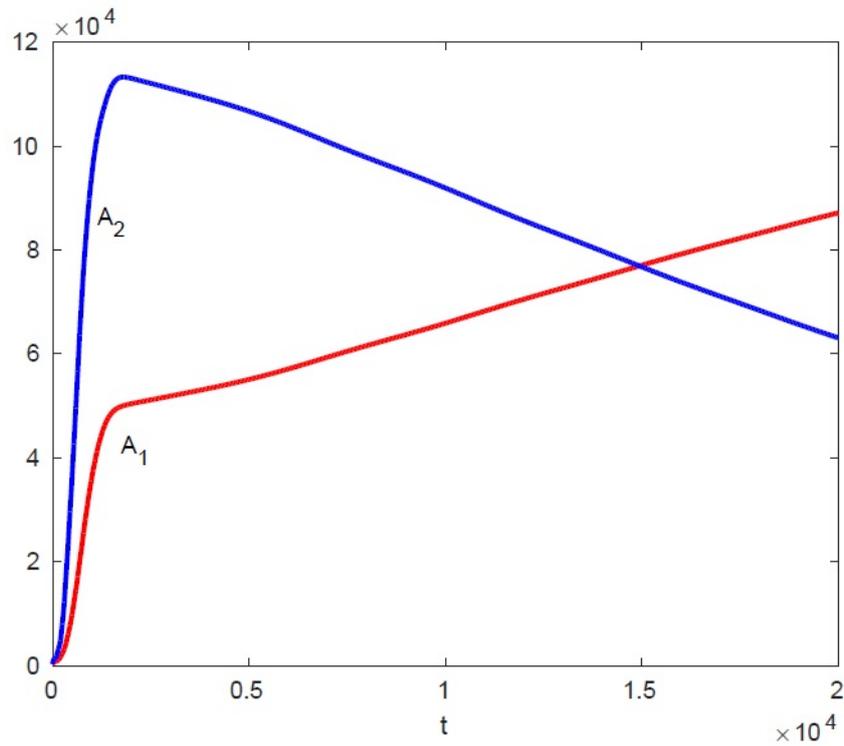


Figure 2.12: In this figure we show the total population in the $300m \times 300m$ square for each species in 20000 years. A_1 represents species 1 American beech, and A_2 represents species 2 eastern hemlock.

As in Figure 2.9, we can also observe the coexistence of both species in the spatial model. In Figure 2.13 we plot the long term distributions after the same change of parameters as in Figure 2.9.

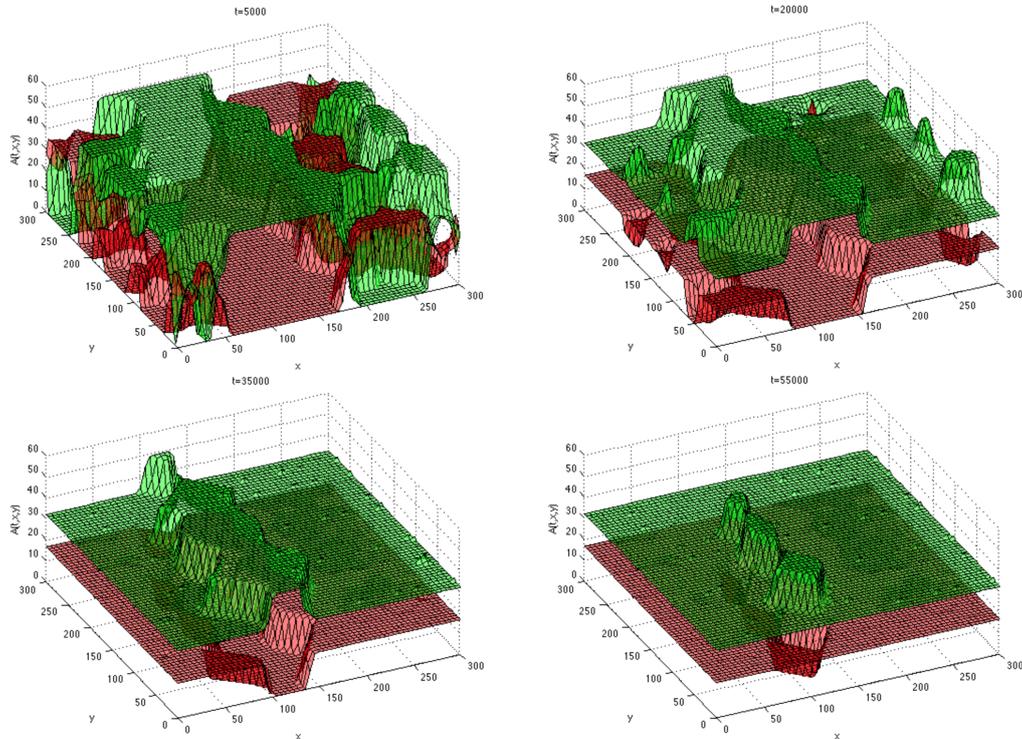


Figure 2.13: *The longterm simulation for the spatial model with a change of the parameter ζ_{21} from 1.6 to 1. All the other parameters are the same as in Figure 2.11. We observe the coexistence of both species.*

2.5 Discussion

Studies of forest dynamics have a long history[25, 51, 167, 178, 190]. There have been a large amount of research on either the descriptive model (consisting of several submodels to describe separately every process of the whole life of individuals) for forests reached by observed data, or the pure mathematical model with numerical computations, separated from data. Here we first construct a mathematical model and compare this model to the computer forest simulator SORTIE. Size-structured model with another type of growth function have been previously used by Strigul et al. [200] for a single species.

We start by fitting the parameters of the model by considering the case of a single species. Then for two species, we only fit the parameters corresponding to the competition for light between the two species of trees. Specifically speaking, we use a classical size-structured model, from which we derive a state-dependent delay differential equation, and we use this differential equation to

fit the forest data from SORTIE. This differential equation is mathematically more tractable than the submodels in SORTIE.

In order to compare our mathematical model with SORTIE, we conduct numerical simulations and we get the best fit to the SORTIE forest data and the corresponding parameter values. One result we get is that the type of birth function of these two species is not of Ricker's type, as we have $\xi = 0$ in both best fits. We then extend our mathematical model to a two-species case with interspecific competition, and similarly we conduct the numerical comparison with SORTIE forest data, where we also get a very good fit.

Based on this, we go further and propose a model incorporating the spatial position parameter, to describe the density of population, or further, the number of population at every specific spatial position. We can see vividly the spread and succession in our numerical simulation. By using a spatial model, given the initial distribution we will be able to predict specifically the population at certain spatial position and time, which is more practical in reality. We refer to [52, 171] for more results about SORTIE model and spatially distributed forest.

We should mention that our model improves the computer simulator SORTIE from the following perspectives. First, in SORTIE model, every behaviour of each individual is described separately by a submodel which calculates specific relevant variables (for example, in the resource submodel, they calculate the light transmissivity through the crown and determine how much light is intercepted in each angle, which will be used in the growth submodel), and then all the behaviours are combined together to get the dynamics of the entire community. In our mathematical model, we simplify the above complicated processes of tree physiology by using only several functions instead to describe the mean behaviour of individuals, which is still effective. Thus there are fewer parameters to input in our mathematical model (8 parameters (or 4 more parameters in two-species model), while more than 20 parameters in SORTIE). This obviously makes it easier to operate the simulation. Second, the time it takes to run a simulation is much shorter due to the different computing mechanism. Thus, it's possible for us to explore the forest dynamics in a very long time scale. Third, the analysis of the mathematical model also permit us to study the coexistence of species in ecological time scale, which allows the maintenance of species diversity in nature. In our simulation, we reach a result that the population number of eastern hemlock decreases to 0 after a long enough time, which conforms to the competitive exclusion principle. However, by analyzing the existence of the interior coexistent equilibrium, we are able to establish a range of parameters in which the exclusion principle is no longer true. The coexistence result has also been confirmed by numerical simulations (with and without space). We refer to [2, 10, 37, 110, 111, 231] for more results going into that direction. But there are few results analyzing mathematically the coexistence for the solution of the structured model

with partial differential equations (2.8). Also it is well known that light is a key influence in many forest systems [204], and our model can be used to reproduce the complicated mechanisms included into SORTIE model. But in reality, there are so many influencing factors, such as carbon, nitrogen, water, etc. [44, 112, 116, 130, 203], not only restricted to light. More work about these other influencing factors is left for future investigation.

Chapter 3

Semiflow properties of a system of state-dependent delay differential equation

3.1 Introduction

Let Ω be a compact subset of \mathbb{R}^n (with $n \geq 1$). Denote for simplicity that $C(\Omega) := C(\Omega, \mathbb{R})$, $C(\Omega^2) := C(\Omega^2, \mathbb{R})$ and $C_+(\Omega) := C(\Omega, [0, +\infty))$. In this chapter we consider the following class of state-dependent delay differential equation: $\forall t \geq 0$ and $\forall x \in \Omega$,

$$\begin{cases} \partial_t A(t, x) = F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(t))(\cdot, \cdot))(x), \\ \int_{-\tau(t, x)}^0 f(A(t + s, \cdot))(x) ds = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \end{cases} \quad (3.1)$$

where $F : C(\Omega)^2 \times C(\Omega^2) \rightarrow C(\Omega)$ and $f : C(\Omega) \rightarrow C(\Omega)$ and $A(t - \tau(t)) \in C(\Omega^2)$ is the map defined by

$$A(t - \tau(t))(x, y) := A(t - \tau(t, x), y) \quad (3.2)$$

with the initial condition

$$A(t, x) = \varphi(t, x), \forall t \leq 0 \text{ and } \tau(0) = \tau_0 \in C_+(\Omega),$$

and the initial distribution φ belongs to

$$\text{Lip}_\alpha := \{\phi \in C((-\infty, 0], C(\Omega)) : t \rightarrow e^{-\alpha|t|}\phi(t, \cdot) \text{ is bounded and Lipschitz continuous from } (-\infty, 0] \text{ to } C(\Omega)\}, \alpha \geq 0.$$

Recall that the space Lip_α is a Banach space endowed with the norm

$$\|\phi\|_{\text{Lip}_\alpha} := \|\phi_\alpha\|_\infty + \|\phi_\alpha\|_{\text{Lip}}$$

where $\phi_\alpha : (-\infty, 0] \rightarrow C(\Omega)$ is defined by

$$\phi_\alpha(t, x) := e^{-\alpha|t|}\phi(t, x), \forall t \in (-\infty, 0], \forall x \in \Omega. \quad (3.3)$$

and

$$\|\phi_\alpha\|_\infty := \sup_{t \leq 0} \|\phi_\alpha(t, \cdot)\|_\infty$$

and for fixed t ,

$$\|\phi_\alpha(t, \cdot)\|_\infty := \sup_{x \in \Omega} |\phi_\alpha(t, x)|$$

and

$$\|\phi_\alpha\|_{\text{Lip}} := \sup_{t, s \leq 0: t \neq s} \frac{\|\phi_\alpha(t, \cdot) - \phi_\alpha(s, \cdot)\|_\infty}{|t - s|}.$$

In the rest of this chapter the product space $\text{Lip}_\alpha \times C(\Omega)$ will be endowed with the usual product norm

$$\|(\phi, r)\|_{\text{Lip}_\alpha \times C(\Omega)} := \|\phi\|_{\text{Lip}_\alpha} + \|r\|_\infty, \forall \phi \in \text{Lip}_\alpha, \forall r \in C(\Omega).$$

We will make the following assumptions throughout this chapter.

Assumption 3.1. *We assume that the map $F : C(\Omega)^2 \times C(\Omega^2) \rightarrow C(\Omega)$ is Lipschitz continuous on bounded sets, that is to say that for each constant $M > 0$, there exists a constant $L(M) > 0$ satisfying*

$$\|F(u, v, w) - F(\hat{u}, \hat{v}, \hat{w})\|_\infty \leq L(M) [\|u - \hat{u}\|_\infty + \|v - \hat{v}\|_\infty + \|w - \hat{w}\|_\infty]$$

whenever $\|u\|_\infty, \|\hat{u}\|_\infty, \|v\|_\infty, \|\hat{v}\|_\infty, \|w\|_\infty, \|\hat{w}\|_\infty \leq M$.

We also assume that the map $f : C(\Omega) \rightarrow C(\Omega)$ is Lipschitz continuous and there exist real numbers $M_f > 0$ such that

$$0 < f(\varphi)(x) \leq M_f, \forall x \in \Omega \text{ and } \forall \varphi \in C(\Omega),$$

and f is monotone non-increasing, that is to say that

$$\varphi(x) \leq \hat{\varphi}(x), \forall x \in \Omega \Rightarrow f(\varphi)(x) \geq f(\hat{\varphi})(x), \forall x \in \Omega.$$

Examples of state-dependent delay differential equations of this form have been considered first by Smith [193, 194, 195, 196], and has been successfully used in [30, 104] (see also the references therein). The motivation to consider in this chapter such a class of state-dependent delay differential equations comes from modelling the competition for light in forests in Chapter 2.

Example 3.2 (Finite number of species). *The m -species case corresponds to the case $n = 1$ and the domain Ω contains exactly m elements. We can choose for example*

$$\Omega = \{1, 2, \dots, m\}$$

and for $x = 1, \dots, m$,

$$F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(t))(\cdot, \cdot))(x) = G(x, A(t, \cdot), \tau(t, x), A(t - \tau(t, x))(\cdot))$$

where $G : \Omega \times \mathbb{R}^3 \rightarrow \mathbb{R}$ is a map (see Chapter 2 for more details).

3. Semiflow properties

Example 3.3 (Spatially structured case). For the spatially structured case, we can choose

$$\Omega = [0, x_{\max}] \times [0, y_{\max}].$$

Moreover assume (for simplicity) that we have a single species, then we can choose

$$F(A(t, \cdot), \tau(t, \cdot), A_1(t, \cdot))(x, y) := -\mu_A A(t, x, y) + e^{-\mu_J \tau(t, x, y)} \frac{f(A(t, x, y))}{f(A_1(t, x, y))} \\ (I - \varepsilon \Delta)^{-1}[\beta A_1(t, \cdot)](x, y),$$

where Δ is the Laplacian operator on the domain Ω with periodic boundary conditions. This model corresponds to the spatially structured model in Chapter 2.

Let $A \in C((-\infty, r], C(\Omega))$ (for some $r \geq 0$) be given. Then for each $t \leq r$, we will use the standard notation $A_t \in C((-\infty, 0], C(\Omega))$, which is the map defined by

$$A_t(\theta, \cdot) = A(t + \theta, \cdot), \forall \theta \leq 0.$$

For clarity we will specify the notion of a solution.

Definition 3.4. Let $r \in (0, +\infty]$. A solution of the system (3.1) on $[0, r)$ is a pair of continuous maps $A : (-\infty, r) \rightarrow C(\Omega)$ and $\tau : [0, r) \rightarrow C_+(\Omega)$ satisfying

$$A(t, x) = \begin{cases} \varphi(0, x) + \int_0^t F(A(l, \cdot), \tau(l, \cdot), A(l - \tau(l))(\cdot, \cdot))(x) dl, \forall t \in [0, r), \forall x \in \Omega, \\ \varphi(t, x), \forall t \leq 0, \forall x \in \Omega, \end{cases}$$

and

$$\int_{t-\tau(t, x)}^t f(A(s, \cdot))(x) ds = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \forall t \in [0, r), \forall x \in \Omega.$$

In this problem the initial distribution is (φ, τ_0) . The semiflow generated by (3.1) is

$$\mathcal{U}(t)(\varphi(\cdot, x), \tau_0(x)) := (A_t(\cdot, x), \tau(t, x)),$$

where A and τ are the solution of (3.1) with the initial distribution (φ, τ_0) .

In order to clarify the notion of semiflow in this context, we introduce the following definition.

Definition 3.5. Let (M, d) be a metric space. Let $\mathcal{U} : D_{\mathcal{U}} \subset [0, +\infty) \times M \rightarrow M$ be a map defined on the domain

$$D_{\mathcal{U}} := \{(t, x) \in [0, +\infty) \times M : 0 \leq t < T_{BU}(x)\},$$

where $T_{BU} : M \rightarrow (0, +\infty]$ is a lower semi-continuous map (the blow-up time). We will use the notation

$$\mathcal{U}(t)x := \mathcal{U}(t, x), \forall (t, x) \in D_{\mathcal{U}}.$$

We say that \mathcal{U} is a **maximal semiflow on M** if the following properties are satisfied:

- (i) $T_{BU}(\mathcal{U}(t)x) + t = T_{BU}(x), \forall x \in M, \forall t \in [0, T_{BU}(x))$;
- (ii) $\mathcal{U}(0)x = x, \forall x \in M$;
- (iii) $\mathcal{U}(t)\mathcal{U}(s)x = \mathcal{U}(t+s)x, \forall t, s \in [0, T_{BU}(x))$ with $t+s < T_{BU}(x)$;
- (iv) If $T_{BU}(x) < +\infty$, then

$$\lim_{t \nearrow T_{BU}(x)} d(\mathcal{U}(t)x, y) = +\infty$$

for some $y \in M$.

We will say that the semiflow \mathcal{U} is **state variable continuous** if for each $t \geq 0$, the map $x \mapsto \mathcal{U}(t)x$ is continuous whenever $\mathcal{U}(t)$ is defined for x . We will say that the semiflow \mathcal{U} is **locally uniformly state variable continuous** if for each $r \in [0, T_{BU}(x_0))$,

$$\lim_{x \rightarrow x_0} \sup_{t \in [0, r]} d(\mathcal{U}(t)x, \mathcal{U}(t)x_0) = 0 \tag{3.4}$$

whenever the map $\mathcal{U}(t)$ is defined for x and x_0 and each $t \in [0, r]$.

We will say that the semiflow \mathcal{U} is **continuous** if the map $(t, x) \mapsto \mathcal{U}(t)x$ is continuous from $D_{\mathcal{U}}$ into M .

Actually the semiflow of the state-dependent delay differential equation (3.1) is not always continuous in time. Assume for example that $\alpha = 0, \Omega = \{1\}$ and $\forall u, v \in C(\Omega), \forall w \in C(\Omega^2), \forall x \in \Omega$,

$$F(u, v, w)(x) \equiv 1 \text{ and } f(u)(x) \equiv 1.$$

Consider $(A(t), \tau(t))$ (we omit the x variable since there is only one element in Ω) the solution of (3.1) with the initial distribution

$$(\varphi, \tau_0) = (0_{\text{Lip}_\alpha}, \tau_0).$$

This solution can be solved explicitly:

$$A(t) = \begin{cases} t, \forall t > 0, \\ 0, \forall t \leq 0, \end{cases} \quad \tau(t) = \tau_0, \forall t \geq 0.$$

3. Semiflow properties

And the semiflow will be defined by $\mathcal{U}(t)(0_{\text{Lip}_\alpha}, \tau_0) = (A_t, \tau)$. Notice that the map $t \mapsto A(t)$ is differentiable almost everywhere and

$$A'(t) = \begin{cases} 1, & \text{if } t > 0, \\ 0, & \text{if } t < 0. \end{cases}$$

Therefore for each $\hat{t} \geq 0$,

$$\lim_{t \rightarrow \hat{t}} \|A_t - A_{\hat{t}}\|_{\text{Lip}} = \lim_{t \rightarrow \hat{t}} \|A'(t + \cdot) - A'(\hat{t} + \cdot)\|_{L^\infty(-\infty, 0)} = 1.$$

Therefore due to the discontinuity of $A'(t)$ at time $t = 0$, the semiflow is not continuous in time.

The following theorem is the main result of this chapter.

Theorem 3.6. *There exists a maximal semiflow $\mathcal{U} : D_{\mathcal{U}} \subset [0, +\infty) \times \text{Lip}_\alpha \times C_+(\Omega) \rightarrow \text{Lip}_\alpha \times C_+(\Omega)$ and its corresponding blow-up time $T_{BU} : \text{Lip}_\alpha \times C_+(\Omega) \rightarrow (0, +\infty]$ such that for each initial distribution $(\varphi, \tau_0) \in \text{Lip}_\alpha \times C_+(\Omega)$, there exists a unique solution $A : (-\infty, T_{BU}(\varphi, \tau_0)) \rightarrow C_+(\Omega)$ and $\tau : [0, T_{BU}(\varphi, \tau_0)) \rightarrow C_+(\Omega)$ of (3.1) satisfying*

$$\mathcal{U}(t)(\varphi, \tau_0)(x) = (A_t(\cdot, x), \tau(t, x)), \forall t \in [0, T_{BU}(\varphi, \tau_0)), \forall x \in \Omega.$$

Moreover if $T_{BU}(\varphi, \tau_0) < +\infty$, then

$$\limsup_{t \nearrow T_{BU}(W_0)} \|A(t, \cdot)\|_\infty = +\infty.$$

Furthermore the semiflow \mathcal{U} has the following properties:

- (i) The map T_{BU} is lower semi-continuous and $D_{\mathcal{U}}$ is relatively open in $[0, +\infty) \times \text{Lip}_\alpha \times C_+(\Omega)$.
- (ii) The semiflow \mathcal{U} is locally uniformly state variable continuous in $\text{Lip}_\alpha \times C_+(\Omega)$.

In the sequel we will use the notation

$$BUC_\alpha := \{\phi \in C((-\infty, 0], C(\Omega)) : \phi_\alpha \in BUC((-\infty, 0], C(\Omega))\}, \alpha \geq 0$$

where

$$\phi_\alpha(t, x) := e^{-\alpha|t|}\phi(t, x)$$

and $BUC((-\infty, 0], C(\Omega))$ denotes the space of bounded uniformly continuous maps from $(-\infty, 0]$ to $C(\Omega)$. The space BUC_α is again a Banach space endowed with the norm

$$\|\phi\|_{BUC_\alpha} = \sup_{t \leq 0} \|\phi_\alpha(t, \cdot)\|_\infty.$$

We will also use the notation

$$BUC_\alpha^1 := \{\phi \in C^1((-\infty, 0], C(\Omega)) : \phi_\alpha \in BUC((-\infty, 0], C(\Omega)) \\ \text{and } \partial_t(\phi_\alpha) \in BUC((-\infty, 0], C(\Omega))\}$$

and the space BUC_α^1 is again a Banach space endowed with the norm

$$\|\phi\|_{BUC_\alpha^1} := \|\phi_\alpha\|_\infty + \|\partial_t(\phi_\alpha)\|_\infty = \|\phi_\alpha\|_\infty + \|\phi_\alpha\|_{\text{Lip}}.$$

Now we consider the following set D_α containing the couple (ϕ, τ_0) satisfying a compatibility condition:

$$D_\alpha := \{(\phi, \tau_0) \in BUC_\alpha^1 \times C_+(\Omega) : \partial_t \phi(0, x) = F(\phi(0, \cdot), \tau_0(\cdot), \phi(-\tau_0(\cdot), \cdot))(x), \\ \forall x \in \Omega\}.$$

One can note that D_α is a closed subset of $BUC_\alpha^1 \times C_+(\Omega)$. Therefore D_α is a complete metric space endowed with the distance

$$d_{D_\alpha} \left((\phi, \tau_0), (\hat{\phi}, \hat{\tau}_0) \right) := \|\phi - \hat{\phi}\|_{BUC_\alpha^1} + \|\tau_0 - \hat{\tau}_0\|_\infty.$$

We also have

$$D_\alpha \subset BUC_\alpha^1 \times C_+(\Omega) \subset \text{Lip}_\alpha \times C_+(\Omega),$$

and the topologies of $BUC_\alpha^1 \times C_+(\Omega)$ and $\text{Lip}_\alpha \times C_+(\Omega)$ coincide on D_α . We have the following results.

Theorem 3.7. *The subdomain D_α is dense in $BUC_\alpha \times C_+(\Omega)$, namely*

$$\overline{D_\alpha}^{BUC_\alpha \times C_+(\Omega)} = BUC_\alpha \times C_+(\Omega).$$

Moreover we have the following properties:

- (i) *The subdomain D_α is positively invariant by the semiflow \mathcal{U} , that is to say that for each $(\varphi, \tau_0) \in D_\alpha$,*

$$\mathcal{U}(t)(\varphi, \tau_0) \in D_\alpha, \forall t \in [0, T_{BU}(\varphi, \tau_0)).$$

- (ii) *The semiflow \mathcal{U} restricted to D_α is a continuous semiflow when D_α is endowed with the metric d_{D_α} .*

Particularly, from (ii), we know that we can choose two different state spaces for A_t (Lip_α or BUC_α^1), but only in the case of BUC_α^1 can we get a continuous (in time) semiflow.

In system (3.1), we can see from the second equation that the delay $\tau(t, x)$ is a solution of an integral equation. In the following (Lemma 3.9) we will see that the delay $\tau(t, x)$ can be seen as the solution of a partial differential equation, too. In Lemma 3.13, we will see that the delay $\tau(t, x)$ can be also

regarded as a functional of A_t and (φ, τ_0) , which shows that this delay is actually a state-dependent delay. Specifically speaking, let $\delta_0 \in C_+(\Omega)$ be fixed, then we can define the map $\tau : D(\tau) \subset \text{Lip}_\alpha \rightarrow [0, +\infty)$ as the solution of

$$\int_{-\tau(\phi, x)}^0 f(\phi(s, \cdot))(x) ds = \delta_0(x) \quad (3.5)$$

with

$$D(\tau) = \left\{ \phi \in \text{Lip}_\alpha : \delta_0(x) < \int_{-\infty}^0 f(\phi(s, \cdot))(x) ds, \forall x \in \Omega \right\}.$$

Then we will see that

$$\tau(A_t, x) = \tau(t, x), \forall t \geq 0,$$

and the first equation in (3.1) can be rewritten as

$$\partial_t A(t, x) = F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(A_t, \cdot), \cdot))(x), \forall t \geq 0.$$

State-dependent delay differential equations have been used in the study of population dynamics of species [6, 7, 85, 104]. We refer in addition to [14, 80] and the references therein for a nice survey on this topic. Moreover, the semiflow properties of a general class of state-dependent delay differential equations have been recently studied by Walther [221] in D_α .

As an illustration, let us consider for example the following system

$$\begin{cases} \partial_t A(t, x) = F(A(t, \cdot))(x), \forall t \geq 0, \forall x \in \Omega, \\ \int_{-\tau(t, x)}^0 f(A(t + s, \cdot))(x) ds = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \forall t \geq 0, \forall x \in \Omega, \end{cases}$$

and the map $F : BUC_\alpha^1 \rightarrow \mathbb{R}$ is defined by

$$F(\phi) := \phi(-\tau(\phi))$$

where $\tau(\phi)$ is defined as above in (3.5). Assume in addition that f is continuously differentiable, then by Lemma 3.12, the state-dependent delay $\tau : BUC_\alpha \rightarrow C(\Omega)$ is C^1 . Then for $\phi_0 \in BUC_\alpha^1$, we have

$$\begin{aligned} F(\psi + \phi_0) - F(\phi_0) &= (\psi + \phi_0)(-\tau(\psi + \phi_0)) - \phi_0(-\tau(\phi_0)) \\ &= \psi(-\tau(\psi + \phi_0)) + \phi_0(-\tau(\psi + \phi_0)) - \phi_0(-\tau(\phi_0)), \end{aligned}$$

from which we deduce the derivative

$$DF(\phi_0)\psi = \psi(-\tau(\phi_0)) + \phi_0'(-\tau(\phi_0)) \cdot \partial_\phi \tau(\phi_0)\psi,$$

which satisfies the assumption (E) in Walther [221].

In this chapter, we consider the pair $(A_t, \tau(t, \cdot))$ as the state variable, and in this case we can also apply the result by Walther in [221] to the delay differential equation

$$\begin{cases} \partial_t A(t, x) = F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(t))(\cdot, \cdot))(x), \\ \partial_t \tau(t, x) = 1 - \frac{f(A(t, \cdot))(x)}{f(A(t - \tau(t, \cdot), \cdot))(x)}. \end{cases} \quad (3.6)$$

Nevertheless the existence of a maximal semiflow as well as the blow-up time has been considered by Walther [221].

This chapter is organized as follows. In section 2 we prove that D_α is dense in $BUC_\alpha \times C_+(\Omega)$. In section 3 we prove some results regarding the delay $\tau(t, x)$. In sections 4 and 5 we will investigate the uniqueness and local existence of solutions, and the properties of semiflows. In the last section of this chapter, we will illustrate our results by proving the global existence of solutions for a spatially structured forest model.

3.2 Density of the domain

In this preliminary section we will prove the first result of Theorem 3.7, namely the density of D_α in the space $BUC_\alpha \times C_+(\Omega)$.

Proof. Fix $\tau_0 \in C_+(\Omega)$. Consider the space

$$\mathcal{X} := C(\Omega) \times BUC_\alpha$$

which is a Banach space endowed with the usual product norm. Define the linear operator $\mathcal{A} : D(\mathcal{A}) \subset \mathcal{X} \rightarrow \mathcal{X}$ by

$$\mathcal{A} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} := \begin{pmatrix} -\partial_t \varphi(0, \cdot) \\ \partial_t \varphi \end{pmatrix}, \forall \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} \in D(\mathcal{A}),$$

with

$$D(\mathcal{A}) := \{0_{C(\Omega)}\} \times BUC_\alpha^1.$$

Then it is not difficult to prove that

$$\overline{D(\mathcal{A})} = \{0_{C(\Omega)}\} \times BUC_\alpha. \quad (3.7)$$

Moreover, the linear operator \mathcal{A} is a Hille-Yosida operator (see [127]). More precisely, we have $(0, \infty) \subset \rho(\mathcal{A})$ and for each $\lambda \in (0, \infty)$,

$$\begin{aligned} (\lambda I - \mathcal{A})^{-1} \begin{pmatrix} \alpha \\ \varphi \end{pmatrix} &= \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \\ \Leftrightarrow \psi(\theta, x) &= \frac{1}{\lambda} e^{\lambda\theta} [\alpha + \varphi(0, x)] + \int_\theta^0 e^{\lambda(\theta-l)} \varphi(l, x) dl. \end{aligned}$$

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The linear operator \mathcal{A} is Hille-Yosida since we have the following estimation from [127]

$$\|(\lambda I - \mathcal{A})^{-n}\|_{\mathcal{L}(\mathcal{X})} \leq \frac{1}{\lambda^n}, \forall n \geq 1, \forall \lambda > 0. \quad (3.8)$$

By using (3.7) and (3.8) and by the fact that

$$\lambda(\lambda I - \mathcal{A})^{-1} - I = \mathcal{A}(\lambda I - \mathcal{A})^{-1},$$

it follows that

$$\begin{aligned} & \lim_{\lambda \rightarrow +\infty} \left\| \lambda(\lambda I - \mathcal{A})^{-1} \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} - \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \right\|_{\mathcal{X}} \\ &= \lim_{\lambda \rightarrow +\infty} \left\| \mathcal{A}(\lambda I - \mathcal{A})^{-1} \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \right\|_{\mathcal{X}} \leq \lim_{\lambda \rightarrow +\infty} \frac{1}{\lambda} \|\mathcal{A}\|_{\mathcal{L}(\mathcal{X})} \left\| \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \right\|_{\mathcal{X}} \\ &= 0, \forall \psi \in BUC_\alpha. \end{aligned} \quad (3.9)$$

We define the nonlinear map $\mathcal{F} : \overline{D(\mathcal{A})} \rightarrow \mathcal{X}$,

$$\mathcal{F} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} := \begin{pmatrix} F(\varphi(0, \cdot), \tau_0(\cdot), \varphi(-\tau_0(\cdot), \cdot)) \\ 0_{BUC_\alpha} \end{pmatrix}, \forall \varphi \in BUC_\alpha.$$

We observe that

$$\begin{aligned} & (\varphi, \tau_0) \in D_\alpha \\ \Leftrightarrow & (\mathcal{A} + \mathcal{F}) \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} \in \overline{D(\mathcal{A})} \text{ with } \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} \in D(\mathcal{A}) \\ \Leftrightarrow & (I - \lambda\mathcal{A} - \lambda\mathcal{F}) \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} \in \overline{D(\mathcal{A})} \text{ with } \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} \in D(\mathcal{A}), \forall \lambda > 0. \end{aligned}$$

Let $\begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \in \{0_{C(\Omega)}\} \times BUC_\alpha$ be fixed. Then for each $\lambda > 0$, consider

$$(I - \lambda\mathcal{A} - \lambda\mathcal{F}) \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} = \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \text{ with } \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} \in D(\mathcal{A}),$$

which is equivalent to the fixed point problem

$$\begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} = \lambda^{-1} (\lambda^{-1}I - \mathcal{A})^{-1} \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} + (\lambda^{-1}I - \mathcal{A})^{-1} \mathcal{F} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix}.$$

Define the map

$$\Phi_\lambda \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix} := \lambda^{-1} (\lambda^{-1}I - \mathcal{A})^{-1} \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} + (\lambda^{-1}I - \mathcal{A})^{-1} \mathcal{F} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi \end{pmatrix}.$$

Then $r > 0$ being fixed, by using the fact that \mathcal{F} is Lipschitz on bounded sets and \mathcal{A} is a Hille-Yosida operator, one can prove that there exists $\eta = \eta(r) > 0$ such that

$$\Phi_\lambda(B_{\psi,r}) \subset B_{\psi,r}, \forall \lambda \in (0, \eta]$$

and Φ_λ is a strict contraction on $B_{\psi,r}$, where

$$B_{\psi,r} := B\left(\begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix}, r\right)$$

is the ball with center $\begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix}$ and radius r in $\overline{D(\mathcal{A})} = \{0_{C(\Omega)}\} \times BUC_\alpha$. Thus by the Banach fixed point theorem, $\forall \lambda \in (0, \eta]$, there exists $\begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} \in B_{\psi,r}$ satisfying

$$\Phi_\lambda\left(\begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix}\right) = \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix}.$$

Finally, since $\begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \in \overline{D(\mathcal{A})}$ and by using (3.8) and (3.9), we have

$$\begin{aligned} & \lim_{\lambda \rightarrow 0^+} \left\| \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} - \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \right\|_{\mathcal{X}} \\ &= \lim_{\lambda \rightarrow 0^+} \left\| (\lambda^{-1}(\lambda^{-1}I - \mathcal{A})^{-1} - I) \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} + (\lambda^{-1}I - \mathcal{A})^{-1} \mathcal{F} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} \right\|_{\mathcal{X}} \\ &= \lim_{\lambda \rightarrow 0^+} \left\| \mathcal{A}(\lambda^{-1}I - \mathcal{A})^{-1} \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} + (\lambda^{-1}I - \mathcal{A})^{-1} \mathcal{F} \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} \right\|_{\mathcal{X}} \\ &\leq \lim_{\lambda \rightarrow 0^+} \lambda \|\mathcal{A}\|_{\mathcal{L}(\mathcal{X})} \left\| \begin{pmatrix} 0_{C(\Omega)} \\ \psi \end{pmatrix} \right\|_{\mathcal{X}} + \lim_{\lambda \rightarrow 0^+} \lambda \|\mathcal{F}\|_{\mathcal{L}(\mathcal{X})} \left\| \begin{pmatrix} 0_{C(\Omega)} \\ \varphi_\lambda \end{pmatrix} \right\|_{\mathcal{X}} \\ &= 0, \end{aligned}$$

which completes the proof. \square

3.3 Properties of the integral equation for $\tau(t, x)$

In this section we will make the following assumption.

Assumption 3.8. Let $(\varphi, \tau_0) \in C((-\infty, 0], C(\Omega)) \times C_+(\Omega)$. Let $A \in C((-\infty, r), C(\Omega))$ (with $r \in (0, +\infty]$) be given and satisfy

$$A(t, \cdot) = \varphi(t, \cdot), \forall t \leq 0.$$

Lemma 3.9. *There exists a uniquely determined map $\tau : [0, r) \rightarrow C(\Omega)$ satisfying*

$$\int_{t-\tau(t,x)}^t f(A(s, \cdot))(x) ds = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \forall t \in [0, r), \forall x \in \Omega. \quad (3.10)$$

Moreover this uniquely determined map $t \mapsto \tau(t, x)$ is continuously differentiable and satisfies the following equation

$$\begin{cases} \partial_t \tau(t, x) = 1 - \frac{f(A(t, \cdot))(x)}{f(A(t - \tau(t, x), \cdot))(x)}, \forall t \in [0, r), \forall x \in \Omega, \\ \tau(0, x) = \tau_0(x). \end{cases} \quad (3.11)$$

Conversely if $t \mapsto \tau(t, x)$ is a C^1 map satisfying the above ordinary differential equation (3.11), then it also satisfies the above integral equation (3.10).

Remark 3.10. *By using equation (3.11), it is easy to check that*

$$\tau_0(x) > 0 \Rightarrow \tau(t, x) > 0, \forall t \in [0, r), \forall x \in \Omega,$$

and

$$\tau_0(x) = 0 \Rightarrow \tau(t, x) = 0, \forall t \in [0, r), \forall x \in \Omega.$$

Proof. Step 1 (Existence of $\tau(t, x)$): By Assumption 3.1, f is strictly positive, so fix $t \in [0, r)$ and $x \in \Omega$, and by considering the function $\tau \mapsto \int_{t-\tau}^t f(A(s, \cdot))(x) ds$ and observing that

$$\begin{aligned} \int_{t-0}^t f(A(s, \cdot))(x) ds &= 0 \leq \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \\ \int_{t-(t+\tau_0(x))}^t f(A(s, \cdot))(x) ds &\geq \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \end{aligned}$$

it follows by the intermediate value theorem that there exists a unique $\tau(t, x) \in [0, t + \tau_0(x)]$ satisfying (3.10).

Step 2 (The map $t \mapsto t - \tau(t, x)$ is increasing): First we prove that the function $t \mapsto t - \tau(t, x)$ is increasing. Indeed, assume by contradiction that $t_1 < t_2$ while $t_1 - \tau(t_1, x) \geq t_2 - \tau(t_2, x)$, $\forall x \in \Omega$, namely we have

$$t_2 - \tau(t_2, x) \leq t_1 - \tau(t_1, x) \leq t_1 < t_2.$$

Then by (3.10) we have

$$\int_{t_1 - \tau(t_1, x)}^{t_1} f(A(s, \cdot))(x) ds = \int_{t_2 - \tau(t_2, x)}^{t_2} f(A(s, \cdot))(x) ds$$

$$\begin{aligned}
 &= \int_{t_2 - \tau(t_2, x)}^{t_1 - \tau(t_1, x)} f(A(s, \cdot))(x) ds + \int_{t_1 - \tau(t_1, x)}^{t_1} f(A(s, \cdot))(x) ds \\
 &\quad + \int_{t_1}^{t_2} f(A(s, \cdot))(x) ds,
 \end{aligned}$$

thus

$$\int_{t_2 - \tau(t_2, x)}^{t_1 - \tau(t_1, x)} f(A(s, \cdot))(x) ds + \int_{t_1}^{t_2} f(A(s, \cdot))(x) ds = 0,$$

which is impossible since the function f is strictly positive.

Step 3 (The continuity of the map $x \mapsto \tau(t, x)$): Next we will prove the continuity of the map $x \mapsto \tau(t, x), \Omega \rightarrow C[0, r]$. By step 2 we have for each $t \in [0, r)$,

$$t - \tau(t, x) \leq -\tau_0(x) \Leftrightarrow 0 \leq \tau(t, x) \leq t - \tau_0(x), \forall x \in \Omega.$$

Now the boundness of the function $x \mapsto \tau(t, x)$ follows from the boundedness of $\tau_0(x)$. Then for any $t \in [0, r)$, we know that

$$\tau^\infty(t) := \sup_{x \in \Omega} \tau(x, t) < +\infty.$$

Let $\xi(x) := \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \forall x \in \Omega$. Then fix $x_0 \in \Omega$, for any $x \in \Omega$, we have

$$\begin{aligned}
 |\xi(x_0) - \xi(x)| &= \left| \int_{-\tau_0(x_0)}^0 f(\varphi(s, \cdot))(x_0) ds - \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds \right| \\
 &\leq \left| \int_{-\tau_0(x_0)}^{-\tau_0(x)} f(\varphi(s, \cdot))(x_0) ds \right| + \int_{-\tau_0(x)}^0 |f(\varphi(s, \cdot))(x_0) - f(\varphi(s, \cdot))(x)| ds \\
 &\leq |\tau_0(x_0) - \tau_0(x)| f(m_1)(x_0) + \tau_0^\infty \sup_{s \in [-\tau_0^\infty, 0]} |f(\varphi(s, \cdot))(x_0) - f(\varphi(s, \cdot))(x)|,
 \end{aligned}$$

where m_1 is the constant function defined with the constant value

$$m_1(x) = \inf_{s \in [-\tau_0^\infty, 0]} \|\varphi(s, \cdot)\|_\infty, \forall x \in \Omega$$

and $\tau_0^\infty := \sup_{x \in \Omega} \tau_0(x)$. Then the continuity of $\xi(x)$ in x follows from

$$\lim_{x \rightarrow x_0} |\xi(x_0) - \xi(x)| = 0$$

by the continuity of τ_0 and $f(\varphi)$. Now for each $t \in [0, r)$ fixed, by (3.10) we have

$$\xi(x_0) - \xi(x) = \int_{t - \tau(t, x_0)}^t f(A(s, \cdot))(x_0) ds - \int_{t - \tau(t, x)}^t f(A(s, \cdot))(x) ds$$

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$$= \int_{t-\tau(t,x_0)}^{t-\tau(t,x)} f(A(s, \cdot))(x_0) ds + \int_{t-\tau(t,x)}^t (f(A(s, \cdot))(x_0) - f(A(s, \cdot))(x)) ds,$$

thus

$$\int_{t-\tau(t,x_0)}^{t-\tau(t,x)} f(A(s, \cdot))(x_0) ds \leq |\xi(x_0) - \xi(x)| + \tau^\infty(t) \sup_{s \in [t-\tau^\infty(t), t]} |f(A(s, \cdot))(x_0) - f(A(s, \cdot))(x)|.$$

On the other hand, we have

$$\int_{t-\tau(t,x_0)}^{t-\tau(t,x)} f(A(s, \cdot))(x_0) ds \geq |\tau(t, x_0) - \tau(t, x)| f(M_1)(x_0)$$

where M_1 is the constant function defined by

$$M_1(x) := \sup_{s \in [-\tau_0^\infty, t]} \|A(s, \cdot)\|_\infty, \forall x \in \Omega.$$

Then there exists a constant $\eta := \eta(t, x_0)$ such that

$$|\tau(t, x_0) - \tau(t, x)| \leq \eta \left(|\xi(x_0) - \xi(x)| + \sup_{s \in [t-\tau^\infty(t), t]} |f(A(s, \cdot))(x_0) - f(A(s, \cdot))(x)| \right).$$

Then the continuity of $\tau(t, x)$ in x follows from

$$\lim_{x \rightarrow x_0} |\tau(t, x_0) - \tau(t, x)| = 0$$

by the continuity of ξ and $f(A)$.

Step 4 (Differentiability of the map $t \mapsto \tau(t, x)$): By applying the implicit function theorem to the map $\psi : (0, r) \times C(\Omega) \rightarrow C(\Omega)$ defined by

$$\psi(t, \gamma)(x) = \int_{\gamma(x)}^t f(A(s, \cdot))(x) ds - \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds$$

(which is possible since $\frac{\partial \psi(t, \gamma)}{\partial \gamma}(\hat{\gamma})(x) = -f(A(\gamma(x), \cdot))(x)\hat{\gamma}(x)$ and by Assumption 3.1, f is strictly positive), we deduce that $t \mapsto t - \tau(t, x)$ is continuously differentiable on $(0, r)$. Since the above formula of the derivative is also valid at $t = 0$ and $t = r$, the map $t \mapsto t - \tau(t, x)$ is continuously differentiable on $[0, r]$. By calculating the time derivative on both sides of (3.10), we get that $\tau(t, x)$ is a solution of (3.11).

Step 5 ((3.11) \Rightarrow (3.10)): Conversely, assume that $\tau(t, x)$ is a solution of (3.11). Then

$$f(A(t, \cdot))(x) = \left(1 - \frac{\partial \tau(t, x)}{\partial t} \right) f(A(t - \tau(t, x), \cdot))(x), \forall t \in [0, r], \forall x \in \Omega.$$

Integrating both sides with respect to t , we have

$$\int_0^t f(A(s, \cdot))(x) ds = \int_0^t f(A(s - \tau(s, x), \cdot))(x) \left(1 - \frac{\partial \tau(s, x)}{\partial s}\right) ds.$$

Make the change of variable $l = s - \tau(s, x)$, we have $\forall t \in [0, r), \forall x \in \Omega$,

$$\begin{aligned} \int_0^t f(A(s, \cdot))(x) ds &= \int_{-\tau_0(x)}^{t-\tau(t, x)} f(A(l, \cdot))(x) dl \\ \Leftrightarrow \int_{t-\tau(t, x)}^t f(A(s, \cdot))(x) ds + \int_0^{t-\tau(t, x)} f(A(s, \cdot))(x) ds &= \int_{-\tau_0(x)}^{t-\tau(t, x)} f(A(s, \cdot))(x) ds \\ \Leftrightarrow \int_{t-\tau(t, x)}^t f(A(s, \cdot))(x) ds &= \int_{-\tau_0(x)}^{t-\tau(t, x)} f(A(s, \cdot))(x) ds + \int_{t-\tau(t, x)}^0 f(A(s, \cdot))(x) ds \\ \Leftrightarrow \int_{t-\tau(t, x)}^t f(A(s, \cdot))(x) ds &= \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \end{aligned}$$

so $\tau(t, x)$ also satisfies the equation (3.10). \square

In order to see that the delay τ is also a functional of A_t and (φ, τ_0) , we define the following functional. We define the map $\hat{\tau} : D(\hat{\tau}) \subset BUC_\alpha \times C(\Omega) \rightarrow C(\Omega)$ as the solution of

$$\int_{-\hat{\tau}(\phi, \delta)(x)}^0 f(\bar{\phi}(s, \cdot))(x) ds = \delta(x) \quad (3.12)$$

where

$$\bar{\phi}(s, x) := \begin{cases} \phi(s, x), & \text{if } s \leq 0 \\ \phi(0, x), & \text{if } s \geq 0. \end{cases}$$

Since by Assumption 3.1 the map $f(\phi(0, \cdot))(x) > 0$, then if $\delta(x) \leq 0$ we have $\hat{\tau}(\phi, \delta)(x) \leq 0$ and

$$\int_{-\hat{\tau}(\phi, \delta)(x)}^0 f(\phi(0, \cdot))(x) ds = \delta(x) \Leftrightarrow \hat{\tau}(\phi, \delta)(x) = \frac{\delta(x)}{f(\phi(0, \cdot))(x)}.$$

We define the domain $D(\hat{\tau})$ by

$$D(\hat{\tau}) = \left\{ (\phi, \delta) \in BUC_\alpha \times C(\Omega) : \delta(x) < \int_{-\infty}^0 f(\phi(s, \cdot))(x) ds \text{ if } \delta(x) > 0 \right\}.$$

For clarity we prove the following lemma.

Lemma 3.11. *For each $(\phi, \delta) \in D(\hat{\tau})$ there exists $\hat{\tau}(\phi, \delta) \in C(\Omega)$.*

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Proof. Let $(\phi, \delta) \in D(\widehat{\tau})$ be fixed.

Step 1 (Existence of $\widehat{\tau}(\phi, \delta)(x)$): Let $x \in \Omega$ be fixed. If $\delta(x) \leq 0$, we have

$$\widehat{\tau}(\phi, \delta)(x) = \frac{\delta(x)}{f(\phi(0, \cdot))(x)}.$$

If $\delta(x) > 0$, by the definition of the domain $D(\widehat{\tau})$ we have

$$\delta(x) < \int_{-\infty}^0 f(\phi(s, \cdot))(x) ds,$$

therefore by the intermediate value theorem, we can find $\widehat{\tau}(\phi, \delta)(x) \in \mathbb{R}$ such that

$$\delta(x) = \int_{-\widehat{\tau}(\phi, \delta)(x)}^0 f(\phi(s, \cdot))(x) ds.$$

Step 2 (Boundedness of $\widehat{\tau}(\phi, \delta)(x)$): Assume by contradiction that $x \mapsto \widehat{\tau}(\phi, \delta)(x)$ is unbounded. Since Ω is compact, we can find a converging sequence $x_n \rightarrow \bar{x} \in \Omega$ as $n \rightarrow +\infty$ such that

$$\lim_{n \rightarrow +\infty} \widehat{\tau}(\phi, \delta)(x_n) = +\infty.$$

It is sufficient to consider the case $\delta(x_n) > 0$, since the case $\delta(x_n) \leq 0$ is explicit. By the continuity of the function δ we can assume that $\delta(\bar{x}) \geq 0$. By the definition of the domain $D(\widehat{\tau})$ we have

$$\delta(\bar{x}) < \int_{-\infty}^0 f(\phi(s, \cdot))(\bar{x}) ds.$$

So we can find a constant $M > 0$ such that

$$\delta(\bar{x}) < \int_{-M}^0 f(\phi(s, \cdot))(\bar{x}) ds,$$

and by continuity we can find a neighborhood U of \bar{x} such that

$$\delta(x) < \int_{-M}^0 f(\phi(s, \cdot))(x) ds, \forall x \in U.$$

It follows that for all integer n large enough,

$$\widehat{\tau}(\phi, \delta)(x_n) \leq M$$

a contradiction.

Step 3 (Continuity of the map $x \mapsto \widehat{\tau}(\phi, \delta)(x)$): From the previous part, we know that

$$\widehat{\tau}^\infty := \sup_{x \in \Omega} |\widehat{\tau}(\phi, \delta)(x)| < +\infty.$$

Fix $x_0 \in \Omega$. If $\delta(x_0) < 0$ there is nothing to prove. Let us assume that

$$\delta(x_0) \geq 0.$$

Let $x_n \rightarrow x_0$ be a converging sequence. If $\delta(x_0) = 0$ and there exists a subsequence $\{x_{n_k}\} \subset \{x_n\}$ satisfying $\delta(x_{n_k}) < 0, \forall k \in \mathbb{N}$, then it is clear that $\hat{\tau}(\phi, \delta)(x_{n_k}) \rightarrow \hat{\tau}(\phi, \delta)(x_0) = 0$. Assume that $\delta(x_n) \geq 0$ for each integer $n \geq 0$. By (3.12) we have

$$\begin{aligned} \delta(x_0) - \delta(x) &= \int_{-\hat{\tau}(\phi, \delta)(x_0)}^0 f(\bar{\phi}(s, \cdot))(x_0) ds - \int_{-\hat{\tau}(\phi, \delta)(x)}^0 f(\bar{\phi}(s, \cdot))(x) ds \\ &= \int_{-\hat{\tau}(\phi, \delta)(x_0)}^{-\hat{\tau}(\phi, \delta)(x)} f(\bar{\phi}(s, \cdot))(x_0) ds + \int_{-\hat{\tau}(\phi, \delta)(x)}^0 f(\bar{\phi}(s, \cdot))(x_0) ds \\ &\quad - \int_{-\hat{\tau}(\phi, \delta)(x)}^0 f(\bar{\phi}(s, \cdot))(x) ds. \end{aligned}$$

Assume without loss of generality that $\hat{\tau}(\phi, \delta)(x_0) > \hat{\tau}(\phi, \delta)(x)$, then we have

$$\begin{aligned} &\int_{-\hat{\tau}(\phi, \delta)(x_0)}^{-\hat{\tau}(\phi, \delta)(x)} f(\bar{\phi}(s, \cdot))(x_0) ds \\ &= (\delta(x_0) - \delta(x)) + \int_{-\hat{\tau}(\phi, \delta)(x)}^0 (f(\bar{\phi}(s, \cdot))(x) - f(\bar{\phi}(s, \cdot))(x_0)) ds \\ &\leq |\delta(x_0) - \delta(x)| + \hat{\tau}^\infty \sup_{s \in [-\hat{\tau}^\infty, 0]} |f(\bar{\phi}(s, \cdot))(x) - f(\bar{\phi}(s, \cdot))(x_0)|, \end{aligned}$$

and

$$\int_{-\hat{\tau}(\phi, \delta)(x_0)}^{-\hat{\tau}(\phi, \delta)(x)} f(\bar{\phi}(s, \cdot))(x_0) ds \geq |\hat{\tau}(\phi, \delta)(x_0) - \hat{\tau}(\phi, \delta)(x)| f(M_1)(x_0)$$

where M_1 is the constant function assigned with the single value $\sup_{s \in [-\hat{\tau}^\infty, 0]} \|\phi(s, \cdot)\|_\infty$.

Thus there exists a constant $\eta := \eta(x_0)$ such that

$$|\hat{\tau}(\phi, \delta)(x_0) - \hat{\tau}(\phi, \delta)(x)| \leq \eta \left(|\delta(x_0) - \delta(x)| + \sup_{s \in [-\hat{\tau}^\infty, 0]} |f(\bar{\phi}(s, \cdot))(x) - f(\bar{\phi}(s, \cdot))(x_0)| \right).$$

Then the result follows by the continuity of the functions δ and $f(\phi)$ in x . \square

Lemma 3.12. *Assume in addition that f is continuously differentiable. Then the domain $D(\hat{\tau})$ is an open subset of $BUC_\alpha \times C(\Omega)$ and the map $\hat{\tau} : D(\hat{\tau}) \subset BUC_\alpha \times C(\Omega) \rightarrow C(\Omega)$ is continuously differentiable.*

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Proof. Define the map $\Gamma : BUC_\alpha \times C(\Omega) \times C(\Omega) \rightarrow C(\Omega)$ by

$$\Gamma(\phi, \delta, \gamma)(x) := \int_{-\gamma(x)}^0 f(\bar{\phi}(s, \cdot))(x) ds - \delta(x).$$

Since by Assumption 3.1 the map f is C^1 , so is the map Γ . By (3.12), we have $\Gamma(\phi, \delta, \hat{\tau}(\phi, \delta))(x) = 0$ and

$$\partial_\gamma \Gamma(\phi, \delta, \gamma)(\hat{\gamma})(x) = f(\bar{\phi}(-\gamma(x), \cdot))\hat{\gamma}(x).$$

Since f is strictly positive, it follows that $\partial_\gamma \Gamma(\phi, \delta, \gamma)$ is invertible. The result follows by applying the implicit function theorem. \square

Lemma 3.13. *Set*

$$\delta_0(x) := \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds, \forall x \in \Omega.$$

Then we have the following equality

$$\hat{\tau}(A_t, \delta_0)(x) = \tau(t, x), \forall t \in [0, r),$$

where A is given by Assumption 3.8 and $\tau(t, x)$ is the solution of (3.10).

Proof. It is sufficient to observe that $\forall t \in [0, r)$ and $x \in \Omega$,

$$\begin{aligned} & \int_{-\hat{\tau}(A_t, \delta_0)(x)}^0 f(A_t(s, \cdot))(x) ds = \delta_0(x) = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds \\ & = \int_{-\tau(t, x)}^0 f(A(t + s, \cdot))(x) ds \end{aligned}$$

\square

For simplicity, we will write $\tau(\phi, x)$ instead of $\hat{\tau}(\phi, \delta_0)(x)$ if the function δ_0 is defined as in Lemma 3.13.

Lemma 3.14. *Let $\phi, \hat{\phi} \in BUC_\alpha$. If $\phi \leq \hat{\phi}$, namely $\phi(s, x) \leq \hat{\phi}(s, x), \forall s \leq 0, x \in \Omega$, then*

$$\tau(\phi, x) \leq \tau(\hat{\phi}, x), \forall x \in \Omega.$$

Proof. By (3.12) we have

$$\int_{-\tau(\phi, x)}^0 f(\phi(s, \cdot))(x) ds = \delta_0(x) = \int_{-\tau(\hat{\phi}, x)}^0 f(\hat{\phi}(s, \cdot))(x) ds.$$

Assume by contradiction that there exists $x \in \Omega$ such that $\tau(\phi, x) > \tau(\widehat{\phi}, x)$, then

$$\begin{aligned} 0 &= \int_{-\tau(\phi, x)}^0 f(\phi(s, \cdot))(x) ds - \int_{-\tau(\widehat{\phi}, x)}^0 f(\widehat{\phi}(s, \cdot))(x) ds \\ &= \int_{-\tau(\phi, x)}^{-\tau(\widehat{\phi}, x)} f(\phi(s, \cdot))(x) ds + \int_{-\tau(\widehat{\phi}, x)}^0 [f(\phi(s, \cdot)) - f(\widehat{\phi}(s, \cdot))](x) ds. \end{aligned}$$

Since by assumption $f(\phi(s, \cdot))(x) > 0$ and $\tau(\phi, x) > \tau(\widehat{\phi}, x)$, we have

$$\int_{-\tau(\phi, x)}^{-\tau(\widehat{\phi}, x)} f(\phi(s, \cdot))(x) ds > 0.$$

By assumption we also have $f(\phi(s, \cdot))(x) \geq f(\widehat{\phi}(s, \cdot))(x)$ when $\tau(\phi, x) > \tau(\widehat{\phi}, x)$, then

$$\int_{-\tau(\widehat{\phi}, x)}^0 [f(\phi(s, \cdot)) - f(\widehat{\phi}(s, \cdot))](x) ds \geq 0.$$

Then we have

$$0 = \int_{-\tau(\phi, x)}^{-\tau(\widehat{\phi}, x)} f(\phi(s, \cdot))(x) ds + \int_{-\tau(\widehat{\phi}, x)}^0 [f(\phi(s, \cdot)) - f(\widehat{\phi}(s, \cdot))](x) ds > 0 + 0 = 0,$$

which is a contradiction. \square

In the following lemma we obtain some a priori estimates for the delay.

Lemma 3.15. *Let Assumption 3.8 be satisfied. Assume that there exists a constant $M > 0$ such that*

$$\sup_{t \in [0, r)} \|A(t, \cdot)\|_{\infty} \leq M. \quad (3.13)$$

Then

$$\tau_{\min} \leq \tau(A_t, x) \leq \tau_{\max}, \forall t \in [0, r), \forall x \in \Omega,$$

where the constants τ_{\min} and τ_{\max} are defined as follows:

$$0 \leq \tau_{\min} := \frac{\inf_{x \in \Omega} [\tau_0(x) f(\varphi_{\max})(x)]}{\sup_{x \in \Omega} f(-M_1)(x)} \leq \tau_{\max} := \frac{\sup_{x \in \Omega} [\tau_0(x) f(-\varphi_{\max})(x)]}{\inf_{x \in \Omega} f(M_1)(x)}$$

with M_1 and φ_{\max} being defined as constant functions as follows

$$M_1(x) := \max\{M, \varphi_{\max}\} \text{ and } \varphi_{\max}(x) := \sup_{t \in [-\tau_0^{\infty}, 0]} \|\varphi(t, \cdot)\|_{\infty}, \forall x \in \Omega \quad (3.14)$$

and

$$\tau_0^{\infty} := \sup_{x \in \Omega} \tau_0(x).$$

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Proof. For any $x \in \Omega$ and $t \in [0, r)$, since by Assumption 3.1 the map f is decreasing, it follows that

$$\begin{aligned} & \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds = \int_{-\tau(A_t, x)}^0 f(A(t+s, \cdot))(x) ds = \int_{t-\tau(A_t, x)}^t f(A(l, \cdot))(x) dl \\ & \leq \int_{t-\tau(A_t, x)}^t f(-M_1)(x) ds = \tau(A_t, x) \sup_{x \in \Omega} f(-M_1)(x). \end{aligned}$$

Then $\forall x \in \Omega, \forall t \in [0, r)$,

$$\tau(A_t, x) \geq \frac{\int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds}{\sup_{x \in \Omega} f(-M_1)(x)} \geq \frac{\inf_{x \in \Omega} [\tau_0(x) f(\varphi_{\max})(x)]}{\sup_{x \in \Omega} f(-M_1)(x)}.$$

The derivation of the estimation from above for $\tau(t, x)$ is similar. \square

Lemma 3.16. *Let $(\varphi, \tau_0), (\tilde{\varphi}, \tilde{\tau}_0), A, \tilde{A}$ satisfy Assumption 3.8. Assume that*

$$M := \max \left\{ \sup_{t \in [0, r)} \|A(t, \cdot)\|_{\infty}, \sup_{t \in [0, r)} \|\tilde{A}(t, \cdot)\|_{\infty} \right\} < +\infty.$$

Then there exists a constant $L_{\tau} > 0$ such that $\forall t \in [0, r), \forall x \in \Omega$,

$$|\hat{\tau}(A_t, \delta_0)(x) - \hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)| \leq L_{\tau} \left[\sup_{s \in [-\tilde{\tau}_0^{\infty}, r)} \|A(s, \cdot) - \tilde{A}(s, \cdot)\|_{\infty} + \|\delta_0 - \tilde{\delta}_0\|_{\infty} \right],$$

where δ_0 and $\tilde{\delta}_0$ are defined as in Lemma 3.13 respectively with (φ, τ_0) and $(\tilde{\varphi}, \tilde{\tau}_0)$ and

$$\tilde{\tau}_0^{\infty} := \max \left\{ \sup_{x \in \Omega} \tau_0(x), \sup_{x \in \Omega} \tilde{\tau}_0(x) \right\}.$$

Proof. Let $t \in [0, r)$ and $x \in \Omega$. Recall from Lemma 3.13 that

$$\delta_0(x) = \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds \text{ and } \tilde{\delta}_0(x) = \int_{-\tilde{\tau}_0(x)}^0 f(\tilde{\varphi}(s, \cdot))(x) ds, \forall x \in \Omega.$$

Without loss of generality we may assume that $\hat{\tau}(A_t, \delta_0)(x) \geq \hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x) > 0$. Then we have

$$\begin{aligned} \delta_0(x) - \tilde{\delta}_0(x) &= \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds - \int_{-\tilde{\tau}_0(x)}^0 f(\tilde{\varphi}(s, \cdot))(x) ds \\ &= \int_{t-\hat{\tau}(A_t, \delta_0)(x)}^t f(A(s, \cdot))(x) ds - \int_{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)}^t f(\tilde{A}(s, \cdot))(x) ds \end{aligned}$$

$$= \int_{t-\hat{\tau}(A_t, \delta_0)(x)}^{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)} f(A(s, \cdot))(x) ds + \int_{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)}^t \left[f(A(s, \cdot))(x) - f(\tilde{A}(s, \cdot))(x) \right] ds.$$

Since by Assumption 3.1, f is Lipschitz continuous, then

$$\begin{aligned} & \int_{t-\hat{\tau}(A_t, \delta_0)(x)}^{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)} f(A(s, \cdot))(x) ds \\ &= \int_{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)}^t \left[f(\tilde{A}(s, \cdot))(x) - f(A(s, \cdot))(x) \right] ds + (\delta_0(x) - \tilde{\delta}_0(x)) \\ &\leq \|f\|_{\text{Lip}} \int_{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)}^t \|\tilde{A}(s, \cdot) - A(s, \cdot)\|_{\infty} ds + \|\delta_0 - \tilde{\delta}_0\|_{\infty} \\ &\leq \bar{\tau}_{\max} \|f\|_{\text{Lip}} \sup_{s \in [-\bar{\tau}_0^{\infty}, r]} \|A(s, \cdot) - \tilde{A}(s, \cdot)\|_{\infty} + \|\delta_0 - \tilde{\delta}_0\|_{\infty} \end{aligned}$$

where $\bar{\tau}_{\max} := \max\{\tau_{\max}, \tilde{\tau}_{\max}\}$ and $\tau_{\max}, \tilde{\tau}_{\max}$ are obtained in Lemma 3.15. On the other hand, we have

$$\int_{t-\hat{\tau}(A_t, \delta_0)(x)}^{t-\hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x)} f(A(s, \cdot))(x) ds \geq \left(\hat{\tau}(A_t, \delta_0)(x) - \hat{\tau}(\tilde{A}_t, \tilde{\delta}_0)(x) \right) \inf_{x \in \Omega} f(M_1)(x)$$

where M_1 is the constant function defined with the single value $\max\{\varphi_{\max}, \tilde{\varphi}_{\max}, M\}$ and $\varphi_{\max}, \tilde{\varphi}_{\max}$ are defined in (3.14) respectively with $\varphi, \tilde{\varphi}$. The result follows. \square

3.4 Existence and uniqueness of solutions

We start this section with two technical lemmas.

Lemma 3.17. *Let $a < b$ be two real numbers. Let $\chi \in \text{Lip}([a, b], C(\Omega))$. Then for each $c \in (a, b)$ we have the following estimation*

$$\|\chi\|_{\text{Lip}([a, b], C(\Omega))} \leq \|\chi\|_{\text{Lip}([a, c], C(\Omega))} + \|\chi\|_{\text{Lip}([c, b], C(\Omega))}.$$

where

$$\|\chi\|_{\text{Lip}(I, C(\Omega))} := \sup_{t, s \in I: t \neq s} \frac{\|\chi(t, \cdot) - \chi(s, \cdot)\|_{\infty}}{|t - s|}.$$

Proof. Let $t, s \in [a, b]$ with $t > s$. Define the function $\rho : [0, 1] \rightarrow \mathbb{R}$ by

$$\rho(h) := \|\chi((t-s)h + s, \cdot) - \chi(s, \cdot)\|_{\infty}, \forall h \in [0, 1].$$

Then $\forall h, \hat{h} \in [0, 1]$ we have

$$|\rho(h) - \rho(\hat{h})|$$

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$$\begin{aligned}
&\leq \left| \|\chi((t-s)h + s, \cdot) - \chi(s, \cdot)\|_\infty - \|\chi((t-s)\hat{h} + s, \cdot) - \chi(s, \cdot)\|_\infty \right| \\
&\leq \|\chi((t-s)h + s, \cdot) - \chi((t-s)\hat{h} + s, \cdot)\|_\infty \\
&\leq \|\chi\|_{\text{Lip}([a,b], C(\Omega))} |t-s| |h - \hat{h}|,
\end{aligned}$$

thus ρ is Lipschitz continuous. Denote

$$\text{Lip}(\rho)(h) := \limsup_{\varepsilon \rightarrow 0^+} \frac{\rho(h + \varepsilon) - \rho(h)}{\varepsilon},$$

then

$$\text{Lip}(\rho)(h) \leq \begin{cases} \|\chi\|_{\text{Lip}([a,c], C(\Omega))} |t-s|, & \text{if } (t-s)h + s \in [a, c), \\ \|\chi\|_{\text{Lip}([c,b], C(\Omega))} |t-s|, & \text{if } (t-s)h + s \in [c, b]. \end{cases}$$

Since ρ is Lipschitz continuous, by using Theorem 8.17 in page 158 of Rudin [186], we deduce that ρ is differentiable everywhere on a subset of the form $[0, 1] \setminus N$ (where N has null Lebesgue measure) and

$$\rho(t) = \rho(0) + \int_0^t \rho'(l) dl, \forall t \in [0, 1].$$

By using the definition of $\text{Lip}(\rho)(t)$ we deduce that

$$\rho'(t) \leq \text{Lip}(\rho)(t) \leq C, \forall t \in [0, 1] \setminus N,$$

where $C := [\|\chi\|_{\text{Lip}([a,c], C(\Omega))} + \|\chi\|_{\text{Lip}([c,b], C(\Omega))}] |t-s|$. Therefore we obtain

$$\|\chi(t, \cdot) - \chi(s, \cdot)\|_\infty = \rho(1) - \rho(0) = \int_0^1 \rho'(l) dl \leq \int_0^1 C dl$$

which completes the proof. \square

Lemma 3.18. *Let $t \geq 0$. Assume that $A \in C((-\infty, t], C(\Omega))$ and $A_0 = \varphi$. Define for each $(\theta, x) \in (-\infty, 0] \times \Omega$,*

$$A_{t,\alpha}(\theta, x) := e^{-\alpha|\theta|} A_t(\theta, x) \text{ and } \varphi_\alpha(\theta, x) := e^{-\alpha|\theta|} \varphi(\theta, x).$$

Then we have the following estimations

$$\|A_{t,\alpha}\|_\infty \leq \sup_{\theta \in [0,t]} \|e^{\alpha(\theta-t)} A(\theta, \cdot)\|_\infty + e^{-\alpha t} \|\varphi_\alpha\|_\infty, \quad (3.15)$$

$$\|A_{t,\alpha}\|_{\text{Lip}((-\infty, 0], C(\Omega))} \leq \|A_{t,\alpha}\|_{\text{Lip}([-t, 0], C(\Omega))} + e^{-\alpha t} \|\varphi_\alpha\|_{\text{Lip}((-\infty, 0], C(\Omega))} \quad (3.16)$$

and

$$\|A_t\|_{\text{Lip}_\alpha} \leq \sup_{\theta \in [0,t]} \|e^{\alpha(\theta-t)} A(\theta, \cdot)\|_\infty + \|A_{t,\alpha}\|_{\text{Lip}([-t, 0], C(\Omega))} + e^{-\alpha t} \|\varphi\|_{\text{Lip}_\alpha}. \quad (3.17)$$

Proof. We have for the supremum norm

$$\begin{aligned} \|A_{t,\alpha}\|_\infty &= \sup_{\theta \leq 0} \|e^{\alpha\theta} A(t + \theta, \cdot)\|_\infty = e^{-\alpha t} \sup_{\theta \leq 0} \|e^{\alpha(t+\theta)} A(t + \theta, \cdot)\|_\infty \\ &\leq \sup_{s \in [0, t]} \|e^{\alpha(s-t)} A(s, \cdot)\|_\infty + e^{-\alpha t} \|\varphi_\alpha\|_\infty. \end{aligned}$$

The result follows by using similar arguments combined with Lemma 3.17 for the Lipschitz semi-norm. \square

Lemma 3.19 (Uniqueness of solutions). *Let $\varphi \in \text{Lip}_\alpha$ and $\tau_0 \in C_+(\Omega)$ satisfy*

$$\|\varphi\|_{\text{Lip}_\alpha} + \|\tau_0\|_\infty \leq M_0.$$

where $M_0 > 0$ is a given real number. Let $r \in (0, +\infty)$ be given. Then the equation (3.1) admits at most one solution $(A, \tau) \in C((-\infty, r], C(\Omega)) \times C([0, r], C(\Omega))$.

Proof. Suppose that there exist $(A^1, \tau^1), (A^2, \tau^2) \in C((-\infty, r], C(\Omega)) \times C([0, r], C(\Omega))$ two solutions of (3.1) on $(-\infty, r]$ with

$$(A_0^1, \tau^1(0, \cdot)) = (A_0^2, \tau^2(0, \cdot)) = (\varphi, \tau_0).$$

Define

$$t_0 = \sup \{t \in [0, r] : A^1(s, x) = A^2(s, x), \tau^1(s, x) = \tau^2(s, x), \forall s \in [0, t], \forall x \in \Omega\}.$$

Assume that $t_0 < r$. We first observe that since r is finite, we have

$$\tilde{K}_0 := \sup_{s \in [0, r]} \|A^1(s, \cdot)\|_\infty + \sup_{s \in [0, r]} \|A^2(s, \cdot)\|_\infty < +\infty.$$

By Lemma 3.15, $\tau^1(t, x)$ and $\tau^2(t, x)$ are also bounded from above (by τ_{\max}^1 and τ_{\max}^2 respectively) on $t \in [0, r]$. Since by Assumption 3.1, $F : C(\Omega)^2 \times C(\Omega^2) \rightarrow C(\Omega)$ is Lipschitz on bounded sets and for each $i = 1, 2$, each $t \in [0, r]$ and each $x \in \Omega$,

$$A^i(t, x) = \varphi(0, x) + \int_0^t F(A^i(l, \cdot), \tau^i(l, \cdot), A^i(l - \tau^i(l))(\cdot, \cdot))(x) dl,$$

it follows by using Lemma 3.15 that for each $i = 1, 2$,

$$\sup_{s \in [0, r]} \|F(A^i(s, \cdot), \tau^i(s, \cdot), A^i(s - \tau^i(s))(\cdot, \cdot))\|_\infty < +\infty,$$

and

$$K_L := \|A^1\|_{\text{Lip}([0, r], C(\Omega))} + \|A^2\|_{\text{Lip}([0, r], C(\Omega))} < +\infty.$$

Set

$$K_0 := 2(\tilde{K}_0 + \varphi_{\max}) + \tau_{\max}^1 + \tau_{\max}^2,$$

where φ_{\max} is defined in (3.14). For each $t \in [t_0, r]$ and each $x \in \Omega$ we have

$$A^1(t, x) - A^2(t, x) = \int_0^t [F(A^1(l, \cdot), \tau^1(l, \cdot), A^1(l - \tau^1(l))(\cdot, \cdot))(x) - F(A^2(l, \cdot), \tau^2(l, \cdot), A^2(l - \tau^2(l))(\cdot, \cdot))(x)] dl,$$

thus by using the fact that F is Lipschitz on bounded sets, we obtain

$$\begin{aligned} \|A^1(t, \cdot) - A^2(t, \cdot)\|_\infty &\leq (t - t_0)L(K_0) \sup_{s \in [t_0, t]} [\|A^1(s, \cdot) - A^2(s, \cdot)\|_\infty \\ &\quad + \|A^1(s - \tau^1(s))(\cdot, \cdot) - A^2(s - \tau^2(s))(\cdot, \cdot)\|_\infty \\ &\quad + \|\tau^1(s, \cdot) - \tau^2(s, \cdot)\|_\infty]. \end{aligned}$$

Define

$$\|A_t^1 - A_t^2\|_\infty := \sup_{s \leq 0} \|A^1(t + s, \cdot) - A^2(t + s, \cdot)\|_\infty.$$

By Lemma 3.16, for each $s \in [t_0, t]$ we have

$$\|\tau^1(s, \cdot) - \tau^2(s, \cdot)\|_\infty = \|\tau(A_s^1, \cdot) - \tau(A_s^2, \cdot)\|_\infty \leq L_\tau \|A_s^1 - A_s^2\|_\infty \leq L_\tau \|A_t^1 - A_t^2\|_\infty.$$

Thus

$$\begin{aligned} &\|A^1(s - \tau^1(s)) - A^2(s - \tau^2(s))\|_\infty \\ &\leq \|A^1(s - \tau^1(s)) - A^1(s - \tau^2(s))\|_\infty + \|A^1(s - \tau^2(s)) - A^2(s - \tau^2(s))\|_\infty \\ &\leq K_L \|\tau^1(s, \cdot) - \tau^2(s, \cdot)\|_\infty + \|A_t^1 - A_t^2\|_\infty, \end{aligned}$$

hence

$$\|A^1(s - \tau^1(s)) - A^2(s - \tau^2(s))\|_\infty \leq (K_L L_\tau + 1) \|A_t^1 - A_t^2\|_\infty.$$

So we obtain for each $t \in [t_0, r]$,

$$\|A_t^1 - A_t^2\|_\infty \leq (t - t_0)L(K_0)((K_L + 1)L_\tau + 2) \|A_t^1 - A_t^2\|_\infty.$$

It follows that we can find $\varepsilon \in (0, r - t_0)$ such that

$$\|A_t^1 - A_t^2\|_\infty = 0, \forall t \in [t_0, t_0 + \varepsilon],$$

which contradicts with the definition of t_0 . Thus $t_0 = r$. \square

Theorem 3.20 (Local existence of solutions). *Let $M_0 > 0$ be fixed. Then for $M > M_0$, there exists a time $r = r(M_0, M) > 0$ such that for each $(\varphi, \tau_0) \in \text{Lip}_\alpha \times C_+(\Omega)$ satisfying*

$$\|\varphi\|_{\text{Lip}_\alpha} + \|\tau_0\|_\infty \leq M_0,$$

system (3.1) admits a unique solution $(A, \tau) \in C((-\infty, r], C(\Omega)) \times C([0, r], C(\Omega))$. Moreover,

$$\|A(t, \cdot)\|_\infty \leq M, \forall t \in [0, r].$$

Proof. Step 1 (Fixed point problem): We start by defining the fixed point problem. Let $M_0 > 0$ be fixed. Let $\varphi \in \text{Lip}_\alpha$ and $\tau_0 \in C_+(\Omega)$ satisfy

$$\|\varphi\|_{\text{Lip}_\alpha} + \|\tau_0\|_\infty \leq M_0.$$

Let $M > M_0$ be fixed. Define

$$E_\varphi := \{A \in C((-\infty, r], C(\Omega)) : A_0 = \varphi \text{ and } \sup_{t \in [0, r]} \|A(t, \cdot)\|_\infty \leq M\}$$

where r will be determined later on.

Let $\Phi : E_\varphi \rightarrow C((-\infty, r], C(\Omega))$ be the map defined as follows: for each $t \in [0, r]$ and $x \in \Omega$,

$$\Phi(A)(t)(x) := \varphi(0, x) + \int_0^t F(A(l, \cdot), \tau(A_l, \cdot), A(l - \tau(A_l, \cdot), \cdot))(x) dl \quad (3.18)$$

where $\tau(A_t, x)$ is the unique solution of the integral equation (3.10), and for $t \leq 0$ and $x \in \Omega$,

$$\Phi(A)(t)(x) := \varphi(t, x).$$

Set

$$\widetilde{M} := \max\{M, \varphi_{\max}\} \quad (3.19)$$

where φ_{\max} is defined in (3.14). For any $A \in E_\varphi$ and $t \in [0, r]$, we have

$$\begin{aligned} & \|\Phi(A)(t)\|_\infty \\ & \leq \|\varphi(0, \cdot)\|_\infty + \int_0^t \|F(A(l, \cdot), \tau(A_l, \cdot), A(l - \tau(A_l, \cdot), \cdot))\|_\infty dl \\ & \leq M_0 + \int_0^t \|F(A(l, \cdot), \tau(A_l, \cdot), A(l - \tau(A_l, \cdot), \cdot)) - F(0, 0, 0)\|_\infty dl \\ & \quad + \int_0^t \|F(0, 0, 0)\|_\infty dl \\ & \leq M_0 + r[(2\widetilde{M} + \tau_{\max})L(2\widetilde{M} + \tau_{\max}) + \|F(0, 0, 0)\|_\infty]. \end{aligned}$$

Since $M > M_0$ we can find $r_1 > 0$ such that for each $r \in (0, r_1]$,

$$M_0 + r[(2\widetilde{M} + \tau_{\max})L(2\widetilde{M} + \tau_{\max}) + \|F(0, 0, 0)\|_\infty] \leq M,$$

and it follows that

$$\Phi(E_\varphi) \subset E_\varphi.$$

Step 2 (Lipschitz estimation): Set

$$M_L := \frac{M - M_0}{r} \geq (2\widetilde{M} + \tau_{\max})L(2\widetilde{M} + \tau_{\max}) + \|F(0, 0, 0)\|_\infty. \quad (3.20)$$

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For each $t, s \in [0, r]$ with $t \geq s$ and $A \in E_\varphi$ we have

$$\begin{aligned} & \frac{\|\Phi(A)(t) - \Phi(A)(s)\|_\infty}{|t - s|} \leq \frac{\int_s^t \|F(A(l, \cdot), \tau(A_l, \cdot), A(l - \tau(A_l, \cdot), \cdot))\|_\infty dl}{|t - s|} \\ & \leq \frac{\int_s^t \|F(A(l, \cdot), \tau(A_l, \cdot), A(l - \tau(A_l, \cdot), \cdot)) - F(0, 0, 0)\|_\infty dl}{|t - s|} \\ & \quad + \frac{\int_s^t \|F(0, 0, 0)\|_\infty dl}{|t - s|}, \end{aligned}$$

thus

$$\|\Phi(A)\|_{\text{Lip}([0, r], C(\Omega))} \leq M_L, \forall A \in E_\varphi.$$

Step 3 (Iteration procedure): Consider the sequence $\{A^n\}_{n \in \mathbb{N}} \subset E_\varphi$ defined by iteration as follows: for each $(t, x) \in (-\infty, r] \times \Omega$,

$$A^0(t, x) = \begin{cases} \varphi(0, x), & \text{if } t \in [0, r], \\ \varphi(t, x), & \text{if } t \leq 0, \end{cases}$$

and for each integer $n \geq 0$,

$$A^{n+1}(t, x) = \begin{cases} \Phi(A^n)(t)(x), & \text{if } t \in [0, r], \\ \varphi(t, x), & \text{if } t \leq 0. \end{cases}$$

From step 2 and the definition of A^0 , we know that for each integer $n \geq 0$,

$$A^n \in \text{Lip}([-\tau_0^\infty, r], C(\Omega)).$$

and

$$\|A^n\|_{\text{Lip}([-\tau_0^\infty, r], C(\Omega))} \leq \max\{M_L, \|\varphi\|_{\text{Lip}([-\tau_0^\infty, 0], C(\Omega))}\} =: \widehat{M}_L.$$

For each integer $n, p \geq 0$, the maps A^n and A^p coincide for negative time t , therefore we can define

$$\|A^n - A^p\|_\infty := \sup_{t \leq r} \|A^n(t, \cdot) - A^p(t, \cdot)\|_\infty.$$

Next, we have $\forall n \in \mathbb{N}$,

$$\begin{aligned} & \|A^{n+1} - A^n\|_\infty = \sup_{t \in [0, r]} \|\Phi(A^n)(t)(\cdot) - \Phi(A^{n-1})(t)(\cdot)\|_\infty \\ & \leq \int_0^r \|F(A^n(l, \cdot), \tau(A_l^n, \cdot), A^n(l - \tau(A_l^n, \cdot), \cdot)) \\ & \quad - F(A^{n-1}(l, \cdot), \tau(A_l^{n-1}, \cdot), A^{n-1}(l - \tau(A_l^{n-1}, \cdot), \cdot))\|_\infty dl \end{aligned}$$

$$\begin{aligned}
 &\leq rL(\widetilde{M} + \tau_{\max}) \left[\|A^n - A^{n-1}\|_\infty + \sup_{l \in [0, r]} \|\tau(A_l^n, \cdot) - \tau(A_l^{n-1}, \cdot)\|_\infty \right. \\
 &\quad \left. + \sup_{l \in [0, r]} \|A^n(l - \tau(A_l^n, \cdot), \cdot) - A^{n-1}(l - \tau(A_l^{n-1}, \cdot), \cdot)\|_\infty \right], \\
 &\leq rL(\widetilde{M} + \tau_{\max}) \left[\|A^n - A^{n-1}\|_\infty + (1 + \|A^n\|_{\text{Lip}([- \tau_0^\infty, r], C(\Omega))}) \right. \\
 &\quad \left. \sup_{l \in [0, r]} \|\tau(A_l^n, \cdot) - \tau(A_l^{n-1}, \cdot)\|_\infty \right].
 \end{aligned}$$

By Lemma 3.16, for each integer $n \geq 1$ we obtain

$$\|A^{n+1} - A^n\|_\infty \leq rC \|A^n - A^{n-1}\|_\infty$$

with $C := (2 + L_\tau(1 + \widehat{M}_L))L(\widetilde{M} + \tau_{\max})$.

Now we can find $r_2 \in (0, r_1]$ such that $r_2C < 1/2$, and for each $r \in (0, r_2]$ we have

$$\|A^{n+1} - A^n\|_\infty \leq \frac{1}{2^n} \|A^1 - A^0\|_\infty, \forall n \geq 1.$$

It follows that $\{A^n|_{[0, r]}\}$ is a Cauchy sequence in the space $C([0, r], C(\Omega))$ and $\{A^n\}$ coincides with φ for negative t . Define

$$A(t, x) := \begin{cases} \lim_{n \rightarrow +\infty} A^n(t, x), & \text{if } t \in [0, r], x \in \Omega, \\ \varphi(t, x), & \text{if } t \leq 0, x \in \Omega. \end{cases}$$

Then we have

$$\lim_{n \rightarrow +\infty} \|A^n - A\|_\infty = 0.$$

By using again Lemma 3.16, we have

$$\sup_{l \in [0, r]} \|\tau(A_l^n, \cdot) - \tau(A_l, \cdot)\|_\infty \leq L_\tau \|A^n - A\|_\infty, \forall n \geq 1.$$

Finally by taking the limit on both sides of the equation

$$A^{n+1}(t, x) = \varphi(0, x) + \int_0^t F(A^n(l, \cdot), \tau(A_l^n, \cdot), A^n(l - \tau(A_l^n, \cdot), \cdot))(x) dl,$$

we deduce that the couple $(A, \tau(A_t, \cdot))$ is a solution of equation (3.1).

Step 4: (Estimation of the solution) We observe that

$$\begin{aligned}
 \|A^{n+1} - A^0\|_\infty &\leq \|A^{n+1} - A^n\|_\infty + \|A^n - A^{n-1}\|_\infty + \dots + \|A^1 - A^0\|_\infty \\
 &\leq \sum_{k=0}^n \left(\frac{1}{2}\right)^k \|A^1 - A^0\|_\infty,
 \end{aligned}$$

therefore

$$\|A^{n+1} - A^0\|_\infty \leq 2\|A^1 - A^0\|_\infty,$$

and by taking the limit when n goes to infinity we obtain

$$\|A - A^0\|_\infty \leq 2\|A^1 - A^0\|_\infty.$$

From the definition of A^1 and A^0 we have

$$\|A^1 - A^0\|_\infty \leq \int_0^r \|F(A^0(l, \cdot), \tau(A_l^0, \cdot), A^0(l - \tau(A_l^0, \cdot), \cdot))\|_\infty dl,$$

so

$$\|A^1 - A^0\|_\infty \leq rC_1,$$

where $C_1 = \sup_{l \in [0, r]} \|F(A^0(l, \cdot), \tau(A_l^0, \cdot), A^0(l - \tau(A_l^0, \cdot), \cdot))\|_\infty$. It follows that for each $t \in [0, r]$,

$$\|A(t, \cdot)\|_\infty \leq \|A(t, \cdot) - \varphi(0, \cdot)\|_\infty + \|\varphi(0, \cdot)\|_\infty \leq \|A - A^0\|_\infty + M_0,$$

thus

$$\|A(t, \cdot)\|_\infty \leq M_0 + 2rC_1,$$

and by choosing r small enough we obtain $M_0 + 2rC_1 \leq M$. The proof is completed. \square

From step 2 in the above proof combined with Lemma 3.18, we have the following corollary.

Corollary 3.21. *With the same notation as in Theorem 3.20, we have*

$$A_t \in \text{Lip}_\alpha, \forall t \in [0, r],$$

and there exists $\widehat{M} := \widehat{M}(M, \tau_{\max}, \alpha) > M$ such that

$$\|A_t\|_{\text{Lip}_\alpha} \leq \widehat{M}, \forall t \in [0, r].$$

3.5 Properties of the semiflow

For each initial distribution $W_0 = \begin{pmatrix} \varphi \\ \tau_0 \end{pmatrix} \in \text{Lip}_\alpha \times C_+(\Omega)$, define

$$T_{BU}(W_0) = \sup\{t > 0 : \text{there exists a solution of (3.1) on the interval } [0, t] \text{ with the initial distribution } W_0\},$$

Observe by Theorem 3.20 that we must have $T_{BU}(W_0) > 0$.

In this section we investigate the semiflow properties of the map $W : D(W) \subset [0, +\infty) \times \text{Lip}_\alpha \times C(\Omega) \rightarrow \text{Lip}_\alpha \times C(\Omega)$ defined for each initial distribution W_0 as

$$W(t, W_0)(x) = \begin{pmatrix} A_t(\cdot, x) \\ \tau(t, x) \end{pmatrix}$$

where $\{(A(t, \cdot), \tau(t, \cdot))\}_{t \in [0, T_{BU}(W_0))}$ is the solution of (3.1) with initial distribution W_0 , which can be defined up to the maximal time of existence $T_{BU}(W_0)$. The domain is

$$D(W) = \bigcup_{W_0 \in \text{Lip}_\alpha \times C_+(\Omega)} [0, T_{BU}(W_0)) \times \{W_0\}.$$

Proof. (First part of Theorem 3.6) Suppose that $W_0 \in \text{Lip}_\alpha \times C_+(\Omega)$ satisfies $\|W_0\|_{\text{Lip}_\alpha \times C(\Omega)} \leq M_0$, where M_0 is a positive constant, and define \mathcal{U} by

$$\mathcal{U}(t)W_0(x) := \begin{pmatrix} A_t(\cdot, x) \\ \tau(t, x) \end{pmatrix}$$

where the map $t \mapsto (A(t, \cdot), \tau(t, \cdot))$ defined on $[0, T_{BU}(W_0))$ is the maximal solution of (3.1) with initial value W_0 . In this proof, we will verify that \mathcal{U} satisfies the properties (i)-(iv) of Definition 3.5.

The property (ii) of Definition 3.5 is trivially satisfied, since by construction $\mathcal{U}(0)W_0 = W_0$.

Step 1 ((i) and (iii) of Definition 3.5): By Lemma 3.9, the map $t \mapsto (A(t, \cdot), \tau(t, \cdot))$ is the solution of (3.1) if and only if for each $t \in [0, T_{BU}(W_0))$ and each $x \in \Omega$ the equations

$$\begin{cases} A(t, x) = \varphi(0, x) + \int_0^t F(A(l, \cdot), \tau(l, \cdot), A(l - \tau(l))(\cdot, \cdot))(x) dl, \\ \tau(t, x) = \tau_0(x) + \int_0^t \left[1 - \frac{f(A(l, \cdot))(x)}{f(A(l - \tau(l))(\cdot, \cdot))(x)} \right] dl, \end{cases} \quad (3.21)$$

are satisfied together with the initial condition

$$(A_0, \tau(0, \cdot)) = W_0.$$

Let $s \in [0, T_{BU}(W_0))$. Let us prove that

$$s + T_{BU}(U(s)W_0) \leq T_{BU}(W_0)$$

and for each $t \in [0, T_{BU}(U(s)W_0))$,

$$\mathcal{U}(t + s)W_0 = \mathcal{U}(t)\mathcal{U}(s)W_0. \quad (3.22)$$

For each $t \in [0, T_{BU}(U(s)W_0))$,

$$\mathcal{U}(t)\mathcal{U}(s)(W_0) = \mathcal{U}(t) \begin{pmatrix} A_s \\ \tau(s, \cdot) \end{pmatrix} = \begin{pmatrix} \tilde{A}_t \\ \tilde{\tau}(t) \end{pmatrix}$$

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where $t \mapsto (A_t, \tau(t, \cdot))$ is the solution of (3.1) with initial condition W_0 and $t \mapsto (\tilde{A}_t, \tilde{\tau}(t, \cdot))$ is the solution of (3.1) with initial condition $\mathcal{U}(s)(W_0)$. Then we have for each $t \in [0, T_{BU}(U(s)W_0))$,

$$\begin{cases} \tilde{A}(t, x) = A(s, x) + \int_0^t F(\tilde{A}(l, \cdot), \tilde{\tau}(l, \cdot), \tilde{A}(l - \tilde{\tau}(l))(\cdot, \cdot))(x) dl \\ \tilde{\tau}(t, x) = \tau(s, x) + \int_0^t \left[1 - \frac{f(\tilde{A}(l, \cdot))(x)}{f(\tilde{A}(l - \tilde{\tau}(l))(\cdot, \cdot))(x)} \right] dl \end{cases} \quad (3.23)$$

with initial condition

$$\tilde{A}_0 = A_s, \tilde{\tau}(0, x) = \tau(s, x).$$

Now by setting

$$(\bar{A}_t, \bar{\tau}(t, \cdot)) := \begin{cases} (\tilde{A}_{t-s}, \tilde{\tau}(t-s, \cdot)), & \text{if } t \in [s, s + T_{BU}(U(s)W_0)), \\ (A_t, \tau(t, \cdot)), & \text{if } t \in [0, s], \end{cases}$$

then by using (3.21) and (3.23) we deduce that $t \mapsto (\bar{A}_t, \bar{\tau}(t, \cdot))$ is a solution of (3.1) on the time interval $[0, s + T_{BU}(U(s)W_0))$ with initial condition W_0 . It follows that

$$s + T_{BU}(U(s)W_0) \leq T_{BU}(W_0).$$

Now assume that $t \mapsto (A_t, \tau(t, \cdot))$ is a solution of (3.1) on the time interval $[0, T_{BU}(W_0))$ with initial condition W_0 . Let $s \in [0, T_{BU}(W_0))$. Then by using (3.21) it follows that $t \mapsto (A_{t+s}, \tau(t+s, \cdot))$ defined on $[0, T_{BU}(W_0) - s)$ is a solution of (3.1) with initial condition $U(s)W_0$. It follows that

$$T_{BU}(W_0) - s \leq T_{BU}(U(s)W_0)$$

and the properties (i) and (iii) of Definition 3.5 follow.

Step 2 ((iv) of Definition 3.5): Assume that $T_{BU}(W_0) < +\infty$. Suppose that $\|\mathcal{U}(t)W_0\|_{\text{Lip}_\alpha \times C(\Omega)}$ does not go to $+\infty$ when $t \nearrow T_{BU}(W_0)$. Then there exists a constant $M_0 > 0$ and a sequence $\{t_n\} \subset [0, T_{BU}(W_0))$ such that $\lim_{n \rightarrow +\infty} t_n = T_{BU}(W_0)$, and for any $n \in \mathbb{N}$,

$$\|\mathcal{U}(t_n)W_0\|_{\text{Lip}_\alpha \times C(\Omega)} = \left\| \begin{pmatrix} A_{t_n} \\ \tau(t_n, \cdot) \end{pmatrix} \right\|_{\text{Lip}_\alpha \times C(\Omega)} \leq M_0.$$

Let $W_{0,n} := \begin{pmatrix} A_{t_n} \\ \tau(t_n, \cdot) \end{pmatrix}$. Then by the local existence Theorem 3.20 and Corollary 3.21 we can find a constant $\widehat{M} > M_0$ and a time $r = r(M_0, \widehat{M}) > 0$ such that for any $n \in \mathbb{N}$,

$$T_{BU}(W_{0,n}) \geq r.$$

Moreover, from the previous part of the proof we have

$$T_{BU}(W_0) = t_n + T_{BU}(W_{0,n}) \geq t_n + r,$$

and when $n \rightarrow +\infty$ we obtain

$$T_{BU}(W_0) \geq T_{BU}(W_0) + r$$

a contradiction since $r > 0$. Thus we have

$$\lim_{t \nearrow T_{BU}(W_0)} \|\mathcal{U}(t)W_0\|_{\text{Lip}_\alpha \times C(\Omega)} = +\infty. \quad (3.24)$$

□

Proof. (Second part of Theorem 3.6) Let us prove that if $T_{BU}(W_0) < +\infty$ then

$$\limsup_{t \nearrow T_{BU}(W_0)} \|A(t, \cdot)\|_\infty = +\infty.$$

Assume that $T_{BU}(W_0) < +\infty$ and assume by contradiction that

$$\limsup_{t \nearrow T_{BU}(W_0)} \|A(t, \cdot)\|_\infty < +\infty.$$

Since the map $t \mapsto t - \tau(t, x)$ is increasing, we have

$$-\tau_0(x) \leq t - \tau(t, x) \leq t < T_{BU}(W_0), \forall x \in \Omega,$$

therefore

$$0 \leq \tau(t, x) \leq T_{BU}(W_0) + \tau_0(x).$$

And by assumption $T_{BU}(W_0) < +\infty$, then

$$\limsup_{t \nearrow T_{BU}(W_0)} \|\tau(t, \cdot)\|_\infty < +\infty.$$

Moreover, for each $t \in [0, T_{BU}(W_0))$,

$$\partial_t A(t, x) = F(A(t, \cdot), \tau(t, \cdot), A(t - \tau(t))(\cdot, \cdot))(x),$$

and since F is Lipschitz on bounded sets and by Lemma 3.18 we deduce that

$$\limsup_{t \nearrow T_{BU}(W_0)} \|e^{\alpha \cdot} A_t(\cdot)\|_{\text{Lip}} < +\infty,$$

which contradicts (3.24). □

Lemma 3.22. *We have the following results:*

- (i) *The map $W_0 \mapsto T_{BU}(W_0)$ is lower semi-continuous on $\text{Lip}_\alpha \times C_+(\Omega)$.*

3. Semiflow properties

(ii) For every $x \in \Omega$, for every $W_0 \in \text{Lip}_\alpha \times C_+(\Omega)$, $\widehat{T} \in (0, T_{BU}(W_0))$, and every sequence $\{W_0^{(n)}\}_{n \in \mathbb{N}} \subset \text{Lip}_\alpha \times C_+(\Omega)$ satisfying

$$\lim_{n \rightarrow +\infty} W_0^{(n)} = W_0 \text{ in } \text{Lip}_\alpha \times C_+(\Omega),$$

we have

$$\lim_{n \rightarrow +\infty} \sup_{t \in [0, \widehat{T}]} \left\| \mathcal{U}(t)W_0^{(n)} - \mathcal{U}(t)W_0 \right\|_{\text{Lip}_\alpha \times C(\Omega)} = 0. \quad (3.25)$$

Proof. Step 1 (Fixed point problem): Let $t \mapsto (\bar{A}(t, \cdot), \bar{\tau}(t, \cdot))$ be a solution of system (3.1) which exists up to the maximal time of existence $T_{BU}(\bar{W}_0)$ with the initial distribution $\bar{W}_0 = \begin{pmatrix} \bar{\varphi} \\ \bar{\tau}_0 \end{pmatrix} \in \text{Lip}_\alpha \times C_+(\Omega)$.

Let $t^* \in (0, T_{BU}(\bar{W}_0))$ be fixed. By construction the map $t \mapsto (\bar{A}_t, \bar{\tau}(t, \cdot))$ is continuous from $[0, T_{BU}(\bar{W}_0))$ to $BUC_\alpha \times C_+(\Omega)$. Therefore

$$\sup_{t \in [0, t^*]} [\|\bar{A}_t\|_{BUC_\alpha} + \|\bar{\tau}(t, \cdot)\|_\infty] < +\infty,$$

and since $\bar{A}(t, \cdot)$ satisfies the equation (3.1) for positive time t , it follows that

$$\widehat{M} := \sup_{t \in [0, t^*]} \|\bar{A}_t\|_{\text{Lip}_\alpha} < +\infty.$$

Let $t_0 \in [0, t^*]$ and $r > 0$ with $t_0 + r < t^*$ where r will be determined later on.

Let $\varepsilon > 0$ be fixed. Let $W_0 = \begin{pmatrix} \varphi \\ \tau_0 \end{pmatrix} \in \text{Lip}_\alpha \times C_+(\Omega)$ satisfy

$$\|\varphi - \bar{A}_{t_0}\|_{\text{Lip}_\alpha} \leq \varepsilon \text{ and } \|\tau_0 - \bar{\tau}(t_0, \cdot)\|_\infty \leq \varepsilon.$$

Let $M > \varepsilon$ be fixed. Define the space

$$E_{\varphi, t_0} := \left\{ A \in BUC_\alpha((-\infty, r], C(\Omega)) : A_0 = \varphi \text{ and } \sup_{t \in [0, r]} \|A(t, \cdot) - \bar{A}_{t_0}(t, \cdot)\|_\infty \leq M \right\}.$$

Let $\Phi : E_{\varphi, t_0} \rightarrow C((-\infty, r], C(\Omega))$ be the map defined by

$$\Phi(A)(t)(x) := \varphi(0, x) + \int_0^t F(A(l, \cdot), \widehat{\tau}(A_l, \delta_0), A(l - \widehat{\tau}(A_l, \delta_0), \cdot))(x) dl \quad (3.26)$$

whenever $t \in [0, r]$ and $x \in \Omega$, and

$$\Phi(A)(t)(x) := \bar{A}_{t_0}(t, x)$$

whenever $t \leq 0$ and $x \in \Omega$.

In the formula (3.26) the delay $\widehat{\tau}(A_t, \delta_0)(x)$ is the unique solution of

$$\int_{-\widehat{\tau}(A_t, \delta_0)(x)}^0 f(A(t+s, \cdot))(x) ds = \delta_0(x)$$

where

$$\delta_0(x) := \int_{-\tau_0(x)}^0 f(\varphi(s, \cdot))(x) ds.$$

For any $A \in E_{\varphi, t_0}$, $t \in [0, r]$ and $x \in \Omega$, we have

$$\begin{aligned} & |\Phi(A)(t)(x) - \bar{A}_{t_0}(t, x)| \\ = & \left| \varphi(0, x) + \int_0^t F(A(l, \cdot), \widehat{\tau}(A_l, \delta_0), A(l - \widehat{\tau}(A_l, \delta_0), \cdot))(x) dl \right. \\ & \left. - \bar{A}_{t_0}(0, x) - \int_0^t F(\bar{A}_{t_0}(l, \cdot), \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0), \bar{A}_{t_0}(l - \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0), \cdot))(x) dl \right| \\ \leq & \varepsilon + \int_0^t |F(A(l, \cdot), \widehat{\tau}(A_l, \delta_0), A(l - \widehat{\tau}(A_l, \delta_0), \cdot))(x) \\ & - F(\bar{A}_{t_0}(l, \cdot), \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0), \bar{A}_{t_0}(l - \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0), \cdot))(x)| dl, \end{aligned}$$

where

$$\bar{\delta}_0(x) = \int_{-\bar{\tau}(t_0, x)}^0 f(\bar{A}(t_0 + s, \cdot))(x) ds = \int_{-\bar{\tau}_0(x)}^0 f(\bar{\varphi}(s, \cdot))(x) ds.$$

By Lemma 3.16, we can find a constant $L_\tau > 0$ such that

$$\begin{aligned} & \|\widehat{\tau}(A_l, \delta_0) - \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0)\|_\infty \\ \leq & L_\tau \left[\sup_{s \in [-\max\{\tau_0^\infty, \bar{\tau}_0^\infty\}, r]} \|A(s, \cdot) - \bar{A}_{t_0}(s, \cdot)\|_\infty + \|\delta_0 - \bar{\delta}_0\|_\infty \right] \end{aligned}$$

where τ_0^∞ and $\bar{\tau}_0^\infty$ are defined as in Lemma 3.15.

By using the definition of δ_0 and $\bar{\delta}_0$ we have

$$\begin{aligned} \|\delta_0 - \bar{\delta}_0\|_\infty & \leq \sup_{x \in \Omega} \left| \int_{-\tau_0(x)}^{-\bar{\tau}(t_0, x)} f(\varphi(s, \cdot))(x) ds \right| \\ & \quad + \sup_{x \in \Omega} \left| \int_{-\bar{\tau}(t_0, x)}^0 [f(\varphi(s, \cdot))(x) - f(\bar{A}(t_0 + s, \cdot))(x)] ds \right| \\ & \leq \|\tau_0(\cdot) - \bar{\tau}(t_0, \cdot)\|_\infty \sup_{x \in \Omega} f(-\varphi_{\max})(x) \\ & \quad + \bar{\tau}_0^\infty \|f\|_{\text{Lip}} \sup_{s \in [-\bar{\tau}_0^\infty, 0]} \|\varphi(s, \cdot) - \bar{A}(t_0 + s, \cdot)\|_\infty \\ & \leq \varepsilon \left(\sup_{x \in \Omega} f(-\varphi_{\max})(x) + \bar{\tau}_0^\infty e^{\alpha \bar{\tau}_0^\infty} \|f\|_{\text{Lip}} \right) \end{aligned}$$

3. Semiflow properties

where φ_{\max} is defined as in Lemma 3.15.

From the above estimations, it follows that there exists a constant $M_1 > 0$ such that

$$\|\widehat{\tau}(A_l, \delta_0) - \widehat{\tau}(\bar{A}_{t_0+l}, \bar{\delta}_0)\|_\infty \leq M_1.$$

Now, similarly as in step 3 of the proof of Theorem 3.20 to evaluate $\|A^{n+1} - A^n\|_\infty$, we deduce that there exists a constant $r_1 > 0$ (independent of φ) such that for each $r \in (0, r_1]$, we have $\Phi(E_{\varphi, t_0}) \subset E_{\varphi, t_0}$.

Step 2 (Lipschitz estimation): Similarly as in step 2 of the proof of Theorem 3.20, we can deduce that there exists a constant $M_L > 0$ such that

$$\|\Phi(A)\|_{\text{Lip}([0, r], C(\Omega))} \leq M_L, \forall A \in E_{\varphi, t_0}.$$

Step 3 (Iteration procedure): Consider the sequence $\{A^n\}_{n \in \mathbb{N}} \subset E_{\varphi, t_0}$ defined by iteration as follows: for each $(t, x) \in (-\infty, r] \times \Omega$,

$$A^0(t, x) = \bar{A}_{t_0}(t, x),$$

and for each integer $n \geq 0$,

$$A^{n+1}(t, x) := \begin{cases} \Phi(A^n)(t)(x), & \text{if } t \in [0, r], \\ \varphi(t, x), & \text{if } t \leq 0. \end{cases}$$

From step 2, we deduce that there exists a constant $\widehat{M}_L > 0$ such that for each integer $n \geq 0$,

$$\|A^n\|_{\text{Lip}([-\tau_0^\infty, r], C(\Omega))} \leq \widehat{M}_L.$$

By using the same argument as in step 3 of the proof of Theorem 3.20, we can find a constant $r_2 \in (0, r_1]$ (independent of φ) such that $\forall r \in (0, r_2]$,

$$\|A^{n+1} - A^n\|_\infty \leq \frac{1}{2^n} \|A^1 - A^0\|_\infty, \forall n \geq 1.$$

It follows that $\{A^n|_{[0, r]}\}$ is a Cauchy sequence in the space $C([0, r], C(\Omega))$. Define

$$A(t, x) := \begin{cases} \lim_{n \rightarrow +\infty} A^n(t, x), & \text{if } t \in [0, r], x \in \Omega, \\ \varphi(t, x), & \text{if } t \leq 0, x \in \Omega. \end{cases}$$

Then we have

$$\lim_{n \rightarrow +\infty} \|A^n - A\|_\infty = 0,$$

and we deduce that $(A, \widehat{\tau}(A_l, \delta_0))$ is a solution of (3.1) with the initial distribution (φ, τ_0) .

Step 4 (Estimation of the solution): As in step 4 of the proof of Theorem 3.20, we also have

$$\|A - A^0\|_\infty \leq 2\|A^1 - A^0\|_\infty.$$

Since we have

$$\begin{aligned}
 & \|A^1 - A^0\|_\infty \\
 = & \sup_{t \in [0, r]} \sup_{x \in \Omega} \left| \varphi(0, x) + \int_0^t F(A^0(l, \cdot), \widehat{\tau}(A_l^0, \delta_0), A^0(l - \widehat{\tau}(A_l^0, \delta_0), \cdot))(x) dl \right. \\
 & \left. - \bar{A}_{t_0}(t, x) \right| \\
 \leq & \sup_{t \in [0, r]} \|\varphi(0, \cdot) - \bar{A}_{t_0}(0, \cdot)\|_\infty + \sup_{x \in \Omega} \left| \bar{A}_{t_0}(0, \cdot) + \right. \\
 & \left. \int_0^t F(A^0(l, \cdot), \widehat{\tau}(A_l^0, \delta_0), A^0(l - \widehat{\tau}(A_l^0, \delta_0), \cdot))(x) dl - \bar{A}_{t_0}(t, x) \right|
 \end{aligned}$$

and since $\bar{A}(t, x)$ is a solution, the second term in the above inequality is null. It follows that

$$\|A^1 - A^0\|_\infty \leq \varepsilon.$$

Then we obtain

$$\|A(t, \cdot) - \bar{A}_{t_0}(t, \cdot)\|_\infty \leq 2\varepsilon, \forall t \in [t_0, t_0 + r].$$

Step 5 (Convergence result): Fix $r = \frac{t^*}{n} \leq r_2$ for some integer $n \geq 1$. Choose an initial value satisfying

$$\|\varphi - \bar{A}_{t_0}\|_{\text{Lip}_\alpha} \leq \frac{\varepsilon}{2^{n+1}} \text{ and } \|\tau_0 - \bar{\tau}(t_0, \cdot)\|_\infty \leq \frac{\varepsilon}{2^{n+1}}.$$

By using the above result when $t_0 = 0$, we deduce that

$$\|A(t, \cdot) - \bar{A}(t, \cdot)\|_\infty \leq \frac{\varepsilon}{2^{n+1}}, \forall t \in [0, r].$$

and by induction $t_0 = kr$ for $k = 0, \dots, n$ we obtain

$$\|A(t, \cdot) - \bar{A}(t, \cdot)\|_\infty \leq \varepsilon, \forall t \in [0, t^*],$$

the result follows. \square

The part of Theorem 3.7: time continuity of the semiflow in BUC_α^1 is left to the reader.

3.6 Application to the forest model with space

For $x \in \Omega := [0, 1]$ and $t \geq 0$ we consider the forest spatial model with one species (parameter meanings as in Chapter 2)

$$\partial_t A(t, x) = e^{-\mu_J \tau(t, x)} \frac{f(A(t, x))}{f(A(t - \tau(t, x), x))} B(t - \tau(t, x), x) - \mu_A A(t, x), \quad (3.27)$$

where f is a continuously differentiable and decreasing function and the birth is defined by

$$B(t, x) := (I - \varepsilon\Delta)^{-1}[\beta A(t, \cdot)](x),$$

where Δ is the Laplacian operator on the domain Ω with periodic boundary conditions, and the state-dependent delay $\tau(t, x)$ is a continuous function satisfying

$$\int_{t-\tau(t,x)}^t f(A(\sigma, x))d\sigma = \int_{-\tau_0(x)}^0 f(\varphi(\sigma, x))d\sigma,$$

and $A(t, x)$ satisfies the initial condition

$$A(t, x) = \varphi(t, x), \forall t \leq 0,$$

with

$$\varphi \in \text{Lip}_\alpha \text{ and } \varphi \geq 0.$$

The solution of (3.27) is a continuous function A defined on $(-\infty, r] \times \Omega$ (r to be determined) satisfying

$$A(t, x) = \begin{cases} \varphi(0, x) + \int_0^t \left[e^{-\mu_J \tau(s,x)} \frac{f(A(s, x))}{f(A(s - \tau(s, x), x))} B(s - \tau(s, x), x) \right. \\ \left. - \mu_A A(s, x) \right] ds, t \geq 0, x \in \Omega, \\ \varphi(t, x), t \leq 0, x \in \Omega. \end{cases}$$

It is well known that $(I - \varepsilon\Delta)^{-1}$ is a positive operator, i.e.

$$(I - \varepsilon\Delta)^{-1}C_+(\Omega) \subset C_+(\Omega)$$

and

$$\|(I - \varepsilon\Delta)^{-1}\|_{\mathcal{L}(C(\Omega))} = 1.$$

3.6.1 Positivity

Assume that

$$\varphi(t, x) \geq 0, \forall (t, x) \in (-\infty, 0] \times \Omega.$$

Assume that the solution starting from this initial condition exists up to the time $T_{BU}(\varphi, \tau_0) > 0$. Then we have for each $t \in [0, T_{BU}(\varphi, \tau_0))$,

$$A(t, x) = e^{-\mu_A t} \varphi(0, x) + \int_0^t e^{-\mu_A(t-s)} e^{-\mu_J \tau(s,x)} \frac{f(A(s, x))}{f(A(s - \tau(s, x), x))} (I - \varepsilon\Delta)^{-1}[\beta A(s - \tau(s, x), \cdot)](x) ds.$$

Since the operator $(I - \varepsilon\Delta)^{-1}$ preserves the positivity of the condition and by Assumption 3.1, f is strictly positive, then the positivity of the solution follows by using fixed point arguments on $A(t, x)$ in the above integral equation.

3.6.2 Global existence

Consider the spatial density of juveniles

$$J(t, x) := \int_{t-\tau(t, x)}^t e^{-\mu_J(t-s)} \beta(I - \varepsilon\Delta)^{-1}(A(s, \cdot))(x) ds$$

for each $t \in [0, T_{BU}(\varphi, \tau_0))$. It is clear that

$$J(t, x) \geq 0, \forall t \in [0, T_{BU}(\varphi, \tau_0)). \quad (3.28)$$

Moreover we have

$$\begin{aligned} \partial_t J(t, x) = & \beta(I - \varepsilon\Delta)^{-1}(A(t, \cdot))(x) - e^{-\mu_J\tau(t, x)} \frac{f(A(t, x))}{f(A(t - \tau(t, x), x))} \\ & \beta(I - \varepsilon\Delta)^{-1}(A(t - \tau(t, x), \cdot))(x) - \mu_J J(t, x). \end{aligned}$$

By summing equation (3.27) and the above equation we obtain

$$\partial_t [A(t, x) + J(t, x)] = \beta(I - \varepsilon\Delta)^{-1}(A(t, \cdot))(x) - \mu_A A(t, x) - \mu_J J(t, x). \quad (3.29)$$

Set

$$U(t, x) := A(t, x) + J(t, x),$$

then we have

$$\partial_t U(t, x) \leq \beta(I - \varepsilon\Delta)^{-1}(U(t, \cdot))(x) - \mu U(t, x),$$

where $\mu := \min\{\mu_A, \mu_J\}$. By using a comparison argument we deduce that

$$U(t, x) \leq e^{[\beta(I - \varepsilon\Delta)^{-1} - \mu]t} (U(0, \cdot))(x), \forall t \in [0, T_{BU}(\varphi, \tau_0)).$$

Therefore by using (3.28), we deduce that

$$A(t, x) \leq e^{[\beta(I - \varepsilon\Delta)^{-1} - \mu]t} (U(0, \cdot))(x), \forall t \in [0, T_{BU}(\varphi, \tau_0)),$$

and by using Theorem 3.6, we must have $T_{BU}(\varphi, \tau_0) = +\infty$.

Chapter 4

Boundedness and dissipativity of a system of state-dependent delay differential equation

4.1 Introduction

In this chapter we are interested in a state-dependent delay differential equation modelling the growth of forest. Following Chapter 2, when the forest is composed of a single species of trees, we have the following system

$$\begin{cases} A'(t) = -\mu_A A(t) + \beta e^{-\mu_J \tau(t)} \frac{f(A(t))}{f(A(t - \tau(t)))} A(t - \tau(t)), \forall t \geq 0, \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = \int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma, \forall t \geq 0, \end{cases} \quad (4.1)$$

with the initial conditions

$$A(t) = \varphi(t) \geq 0, \forall t \leq 0 \text{ and } \tau(0) = \tau_0 \geq 0,$$

where φ belongs to

$$\text{Lip}_\alpha := \left\{ \phi \in C(-\infty, 0] : e^{-\alpha|\cdot|} \phi(\cdot) \in BUC(-\infty, 0] \cap \text{Lip}(-\infty, 0] \right\},$$

which is a Banach space endowed with the norm

$$\|\phi\|_{\text{Lip}_\alpha} := \|e^{-\alpha|\cdot|} \phi(\cdot)\|_{\infty, (-\infty, 0]} + \|e^{-\alpha|\cdot|} \phi(\cdot)\|_{\text{Lip}(-\infty, 0]},$$

where $\alpha \geq 0$, $BUC(-\infty, 0]$ denotes the space of bounded uniformly continuous functions from $(-\infty, 0]$ to \mathbb{R} , and $\text{Lip}(-\infty, 0]$ denotes the space of Lipschitz functions from $(-\infty, 0]$ to \mathbb{R} .

Equation (4.1) models the dynamics of the adult population of trees. Here $A(t)$ is the number of adult trees at time t , $\tau(t)$ is the time needed by newborns

to become adult at time t , $\mu_A > 0$ is the mortality rate of the adult trees, $\mu_J > 0$ is the mortality rate of the juvenile trees, $\beta > 0$ is the birth rate. In the context of forest modelling (see [139]), $f(A(t))$ describes the growth rate of juveniles, and the function f is capturing the effect of the competition for light between adults and juveniles. For mathematical convenience, we will make the following assumption.

Assumption 4.1. *We assume that*

- (i) *The coefficients $\mu_A > 0$, $\mu_J > 0$, $\beta > 0$;*
- (ii) *The function $f : \mathbb{R} \rightarrow (0, +\infty)$ is continuously differentiable and*

$$f(x) > 0, \lim_{x \rightarrow +\infty} f(x) = 0 \text{ and } f'(x) \leq 0, \forall x \in \mathbb{R}.$$

Actually system (4.1) has been first derived by Smith [193] from a size-structured model of the form

$$\begin{cases} A'(t) = -\mu_A A(t) + f(A(t))j(t, s^*), \forall t > 0, \\ \partial_t j(t, s) + f(A(t))\partial_s j(t, s) = -\mu_J j(t, s), \forall s \in [s_-, s^*], \forall t > 0, \\ f(A(t))j(t, s_-) = \beta A(t), \forall t > 0, \\ A(0) = A_0 \geq 0, \\ j(0, s) = j_0(s) \geq 0, \forall s \in [s_-, s^*], \end{cases}$$

where $0 \leq s_- < s^*$ are the minimal and maximal size of juveniles, and $j(t, s)$ is the density of juveniles with size s at time t . System (4.1) has also been extensively studied by Smith in [193, 194, 195, 196], where the author introduced a change of variable to transform this kind of state-dependent delay differential equation into a constant delay differential equation. The change of variable is given by

$$x = \int_0^t f(A(\sigma))d\sigma =: \Phi(t).$$

Set

$$\delta := \int_{-\tau_0}^0 f(\varphi(\sigma))d\sigma \geq 0,$$

then for $x \geq \delta$,

$$x - \delta = \int_0^t f(A(\sigma))d\sigma - \int_{t-\tau(t)}^t f(A(\sigma))d\sigma = \int_0^{t-\tau(t)} f(A(\sigma))d\sigma = \Phi(t - \tau(t)),$$

This means that $x - \delta$ corresponds to $t - \tau(t)$ under this change of variable. Moreover by setting $W(x) = A(t)$ and using the same arguments as in Smith [193], one also has

$$\tau(t) = \int_{-\delta}^0 f(W(x+r))^{-1}dr.$$

Therefore Smith [193] obtained the following constant delay differential equation

$$W'(x) = -\mu_A \frac{W(x)}{f(W(x))} + \beta e^{-\mu_J \int_{-\delta}^0 f(W(x+r))^{-1} dr} \frac{W(x-\delta)}{f(W(x-\delta))}, \forall x \geq 0. \quad (4.2)$$

Based on the analysis of this equation (4.2), Smith [193, 194, 195, 196] was able to prove the boundedness of solutions whenever $\delta > 0$. Along the same line, he was also able to analyse the uniform persistence and Hopf bifurcation around the positive equilibrium.

Let $A \in C((-\infty, r], \mathbb{R})$ (for some $r \geq 0$) be given. Then for each $t \leq r$, we will use the standard notation $A_t \in C((-\infty, 0], \mathbb{R})$, which is the map defined by

$$A_t(\theta) = A(t + \theta), \forall \theta \leq 0.$$

For clarity we will specify the notion of a solution.

Definition 4.2. *Let $r \in (0, +\infty]$. A solution of the system (4.1) on $[0, r)$ is a pair of continuous maps $A : (-\infty, r) \rightarrow \mathbb{R}$ and $\tau : [0, r) \rightarrow \mathbb{R}_+$ satisfying*

$$A(t) = \begin{cases} \varphi(0) + \int_0^t F(A(\sigma), \tau(\sigma), A(\sigma - \tau(\sigma))) d\sigma, \forall t \in [0, r), \\ \varphi(t), \forall t \leq 0, \end{cases}$$

and

$$\int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = \int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma, \forall t \in [0, r),$$

where

$$F(A, \tau, A_1) := -\mu_A A + \beta e^{-\mu_J \tau} \frac{f(A)}{f(A_1)} A_1.$$

In this problem the initial distribution is (φ, τ_0) . The semiflow generated by (4.1) is

$$\mathcal{U}(t)(\varphi(\cdot), \tau_0) := (A_t(\cdot), \tau(t)),$$

where $A(t)$ and $\tau(t)$ is the solution of (4.1) with the initial distribution (φ, τ_0) . The existence and uniqueness of a maximal semiflow on $\text{Lip}_\alpha \times [0, +\infty)$ (with blowup property when the time gets close to the maximal time of existence $T_{BU} = T_{BU}(\varphi, \tau_0)$) have been studied in the previous chapter.

In order to obtain a global existence result for the solution, we now focus on the positive solution. From the form of the equation we obtain

$$\varphi \geq 0 \Rightarrow A(t) \geq 0, \forall t \in [0, T_{BU}).$$

The number of juvenile individuals at time $t \in [0, T_{BU})$ is given by

$$J(t) := \int_{t-\tau(t)}^t e^{-\mu_J(t-\sigma)} \beta A(\sigma) d\sigma, \forall t \in [0, T_{BU}),$$

and $A \geq 0$ implies that

$$J(t) \geq 0, \forall t \in [0, T_{BU}).$$

Moreover we have

$$J'(t) = \beta A(t) - e^{-\mu_J \tau(t)} \frac{f(A(t))}{f(A(t - \tau(t)))} \beta A(t - \tau(t)) - \mu_J J(t).$$

By summing the A and J equations we obtain

$$[A(t) + J(t)]' = \beta A(t) - \mu_A A(t) - \mu_J J(t). \quad (4.3)$$

Set

$$U(t) := A(t) + J(t),$$

then since $A \geq 0$ we have

$$U'(t) \leq (\beta - \mu)U(t),$$

where $\mu := \min\{\mu_A, \mu_J\}$. By using a comparison argument we deduce that

$$U(t) \leq e^{(\beta - \mu)t} U(0), \forall t \in [0, T_{BU}),$$

and since $J \geq 0$ we deduce that

$$A(t) \leq e^{(\beta - \mu)t} U(0), \forall t \in [0, T_{BU}),$$

and by using Theorem 3.6 in the previous chapter, the maximal time of existence T_{BU} is equal to $+\infty$. Therefore the well-posedness and the global existence of solutions of system (4.1) is guaranteed on $M := (\text{Lip}_\alpha \times [0, +\infty)) \cap (C_+ \times [0, +\infty))$.

The result on boundedness of solutions for this case is as follows.

Theorem 4.3. *Let Assumption 4.1 be satisfied. Assume that $\tau_0 > 0$. Then for each $\varphi \geq 0$ with $\varphi \in \text{Lip}_\alpha$, the corresponding solution of system (4.1) is bounded.*

Remark 4.4. *One may observe that the boundedness of solutions might not be true when $\tau_0 = 0$. Indeed, by the second equation of (4.1),*

$$\tau_0 = 0 \Rightarrow \tau(t) = 0, \forall t \geq 0,$$

and in this special case the first equation of (4.1) becomes linear:

$$A'(t) = (\beta - \mu_A)A(t), \forall t \geq 0. \quad (4.4)$$

The solution of (4.4) exists but when $\beta - \mu_A > 0$, every strictly positive solution is unbounded.

In Chapter 2, we also constructed a mathematical model for a forest composed of two species of trees. And by comparing it with the forest model SORTIE, we find that it is capable of describing the dynamics of the two-species forest. Inspired by this, we now take a step forward and consider the following n -species model

$$\begin{cases} A_i'(t) = -\mu_{A_i}A_i(t) + \beta_i e^{-\mu_{J_i}\tau_i(t)} \frac{f_i(Z_i(t))}{f_i(Z_i(t - \tau_i(t)))} A_i(t - \tau_i(t)), \forall t \geq 0, \\ \int_{t-\tau_i(t)}^t f_i(Z_i(\sigma))d\sigma = \int_{-\tau_{i0}}^0 f_i(Z_{i\varphi}(\sigma))d\sigma, \forall t \geq 0, \end{cases} \quad (4.5)$$

with the initial conditions

$$A_i(t) = \varphi_i(t) \in \text{Lip}_\alpha, \varphi_i(t) \geq 0, \forall t \leq 0 \text{ and } \tau_i(0) = \tau_{i0} \geq 0,$$

where

$$Z_i(t) = \sum_{j=1}^n \zeta_{ij}A_j(t), Z_{i\varphi}(t) := \sum_{j=1}^n \zeta_{ij}\varphi_j(t)$$

with $\zeta_{ij} \geq 0$, $i = 1, \dots, n$. We will use the following assumptions.

Assumption 4.5. *We assume that $\forall i = 1, \dots, n$,*

- (i) *The coefficients $\mu_{A_i} > 0$, $\mu_{J_i} > 0$, $\beta_i > 0$ and $\zeta_{ii} > 0$;*
- (ii) *The function f_i satisfies Assumption 4.1-(ii) and*

$$\sup_{x \geq 0} \frac{f_i(x)}{f_i(cx)} < +\infty, \forall c \geq 1. \quad (4.6)$$

By using the same kind of notion of solutions as in the single species case (Definition 4.2) and by using the result in Chapter 3, the well-posedness of (4.5) and the global existence of positive solutions follow.

In this chapter, we will prove the following result for the n -species model (4.5).

Theorem 4.6. *Let Assumption 4.5 be satisfied. Then for each nonnegative initial values $\varphi_i \geq 0$ with $\varphi_i \in \text{Lip}_\alpha$ and each $\tau_{i0} > 0$, the corresponding solution of equation (4.5) is bounded.*

Remark 4.7. *The proof of Theorem 4.3 (single species case) uses a similar argument as the proof of Theorem 4.6 (n -species case), which will be presented in section 3. But for the single species case, the condition (4.6) in Assumption 4.5 is no longer needed.*

Remark 4.8. For the n -species case we can no longer use the change of variable employed by Smith in [193, 194] since the delays $\tau_i(t)$ are different in general. Nevertheless, in the following we show that the arguments employed to prove the boundedness of solutions and the dissipativity in [193, 194] can be adapted to the n -species case. The notion of dissipativity will be described in details in Theorem 4.16 and Theorem 4.21.

Remark 4.9. It is necessary to assume that $\tau_{i0} > 0$ because we possibly have

$$\zeta_{ij} = 0, \forall i \neq j.$$

Hence it is necessary to assume that in the case of species without coupling, the solution is bounded.

State-dependent delay differential equations have been used by several authors to describe the stage-structured population dynamics. We refer to [6, 7, 13, 80, 85, 104] for more results on this topic. We also refer to Walther [221] for a very general analysis of the semiflow generated by state-dependent delay differential equations.

This chapter is organized as follows. In section 2 we will present some results about the delay $\tau(t)$. Section 3 is devoted to the single species model (4.1). The goal is to clarify the arguments of proof that we will extend later in sections 4 and 5 to the n -species case. Section 4 is devoted to the proof the boundedness of solutions for the n -species model (4.5). In section 5, we prove a dissipativity result for such a system.

4.2 Properties of the integral equation for $\tau(t)$

For simplicity, we focus on the single species model (4.1) in this section. The same result can be similarly deduced for the n -species model (4.5). We have the following lemma of the equivalence of the integral equation for $\tau(t)$ and an ordinary differential equation.

Lemma 4.10. Let $A : (-\infty, r) \rightarrow \mathbb{R}$ be a given continuous function with $r > 0$ and $\varphi(t) = A(t)$, $\forall t \leq 0$. Then there exists a uniquely determined function $\tau : [0, r) \rightarrow [0, +\infty)$ satisfying

$$\int_{t-\tau(t)}^t f(A(\sigma))d\sigma = \int_{-\tau_0}^0 f(\varphi(\sigma))d\sigma, \forall t \in [0, r). \quad (4.7)$$

Moreover this uniquely determined function $t \mapsto \tau(t)$ is continuously differentiable and satisfies the ordinary differential equation

$$\tau'(t) = 1 - \frac{f(A(t))}{f(A(t - \tau(t)))}, \forall t \in [0, r), \text{ and } \tau(0) = \tau_0. \quad (4.8)$$

Conversely if $t \mapsto \tau(t)$ is a C^1 function satisfying the above ordinary differential equation (4.8), then it also satisfies the above integral equation (4.7).

Remark 4.11. By using equation (4.8), it is easy to check that

$$\tau_0 > 0 \Rightarrow \tau(t) > 0, \forall t \in [0, r)$$

and

$$\tau_0 = 0 \Rightarrow \tau(t) = 0, \forall t \in [0, r).$$

Proof. Assume $\tau_0 > 0$ (since by Remark 4.11 $\tau(t)$ exists for all $t \in [0, r)$ when $\tau_0 = 0$). Let $t \in [0, r]$. Since by Assumption 4.1, f is strictly positive, then by

considering the function $\tau \mapsto \int_{t-\tau}^t f(A(\sigma))d\sigma$, and observing that

$$\int_{t-0}^t f(A(\sigma))d\sigma = 0 < \int_{-\tau_0}^0 f(\varphi(\sigma))d\sigma$$

and

$$\int_{t-(t+\tau_0)}^t f(A(\sigma))d\sigma > \int_{-\tau_0}^0 f(\varphi(\sigma))d\sigma,$$

it follows by the intermediate value theorem that there exists a unique $\tau(t) \in [0, t + \tau_0]$.

By applying the implicit function theorem to the map

$$\psi : (t, \gamma) \mapsto \int_{\gamma}^t f(A(\sigma))d\sigma - \int_{-\tau_0}^0 f(\varphi(\sigma))d\sigma$$

(which is possible since $\frac{\partial \psi}{\partial \gamma} = -f(A(\gamma))$ and by Assumption 4.1, f is strictly positive), we deduce that $t \mapsto t - \tau(t)$ is continuously differentiable, and by computing the derivative with respect to t on both sides of (4.7), we deduce that $\tau(t)$ is a solution of (4.8).

Conversely, assume that $\tau(t)$ is a solution of (4.8). Then

$$f(A(t)) = (1 - \tau'(t))f(A(t - \tau(t))), \forall t \in [0, r).$$

Integrating both sides with respect to t , we have

$$\int_0^t f(A(\sigma))d\sigma = \int_0^t f(A(\sigma - \tau(\sigma))) (1 - \tau'(\sigma)) d\sigma.$$

Make the change of variable $l = \sigma - \tau(\sigma)$, we have $\forall t \in [0, r)$,

$$\begin{aligned} \int_0^t f(A(\sigma))d\sigma &= \int_{-\tau_0}^{t-\tau(t)} f(A(l))dl \\ \Leftrightarrow \int_{t-\tau(t)}^t f(A(\sigma))d\sigma + \int_0^{t-\tau(t)} f(A(\sigma))d\sigma &= \int_{-\tau_0}^{t-\tau(t)} f(A(l))dl \\ \Leftrightarrow \int_{t-\tau(t)}^t f(A(\sigma))d\sigma &= \int_{-\tau_0}^{t-\tau(t)} f(A(l))dl - \int_0^{t-\tau(t)} f(A(\sigma))d\sigma, \end{aligned}$$

this implies that $\tau(t)$ also satisfies the equation (4.7). \square

The delay $\tau(t)$ can be regarded as a functional of $A_t \in \text{Lip}_\alpha$. Indeed, given a constant $C > 0$, we can define the map $\hat{\tau} : D(\hat{\tau}) \subset C(-\infty, 0] \times [0, +\infty) \rightarrow [0, +\infty)$ as the solution of the integral equation

$$\int_{-\hat{\tau}(\phi, C)}^0 f(\phi(\sigma)) d\sigma = C \quad (4.9)$$

and the map $\hat{\tau}$ is defined on the domain

$$D(\hat{\tau}) = \left\{ (\phi, C) \in C((-\infty, 0]) \times [0, +\infty) : C < \int_{-\infty}^0 f(\phi(\sigma)) d\sigma \right\},$$

where the last integral is defined as the limit $\lim_{x \rightarrow -\infty} \int_x^0 f(\phi(\sigma)) d\sigma$ (which always exists since $f \geq 0$).

Lemma 4.12. *Set $C_0 := \int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma$, then we have the following relation*

$$\hat{\tau}(A_t, C_0) = \tau(t), \forall t \in (0, r),$$

where $\tau(t)$ is the solution of (4.7).

Proof. It is sufficient to observe that $\forall t \in (0, r)$,

$$\int_{-\hat{\tau}(A_t, C_0)}^0 f(A_t(\sigma)) d\sigma = \int_{t-\hat{\tau}(A_t, C_0)}^t f(A(\sigma)) d\sigma = C_0.$$

□

4.3 Boundedness and dissipativity in the single species case

Without loss of generality we assume in this section that

$$\int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma = 1.$$

The following property is fundamental in this problem (see Lemma 3.9 step 2 for a proof).

Lemma 4.13. *Let Assumption 4.1 be satisfied. Then the function $t - \tau(t)$ is strictly increasing with respect to t where $\tau(t)$ is the solution of (4.1).*

The first step to prove the boundedness is to prove that the map $t \mapsto t - \tau(t)$ crosses 0.

Lemma 4.14. *Let Assumption 4.1 be satisfied. Then there exists $t^* > 0$ such that $t^* - \tau(t^*) = 0$. Moreover, if $A(t)$ is a solution of system (4.1), $\forall t \geq 0$, then $A(t)$ is bounded on $[0, t^*]$.*

Proof. Rewrite the first equation of (4.1) as follows:

$$A'(t) = f(A(t))[-\mu_A \mathcal{B}(A(t)) + \beta e^{-\mu_A \tau(t)} \mathcal{B}(A(t - \tau(t)))], \quad \forall t \geq 0,$$

where

$$\mathcal{B}(x) = \frac{x}{f(x)}$$

is an increasing function and $\mathcal{B}(x) \nearrow +\infty$ as $x \rightarrow +\infty$, since we have

$$\mathcal{B}(x) \geq \frac{x}{f(0)} \quad \text{when } x \geq 0.$$

We define \hat{t} as

$$\hat{t} := \sup\{t \geq 0 : l - \tau(l) \leq 0, \forall l \in [0, t]\}.$$

This is well defined because the set on the right side contains at least one element 0. By Lemma 4.13, we know that the function $t - \tau(t)$ is strictly increasing, then we can assume by contradiction that $\hat{t} = +\infty$, which means that

$$t - \tau(t) < 0, \forall t \geq 0,$$

or more precisely,

$$t - \tau(t) \in [-\tau_0, 0), \quad \forall t \geq 0.$$

Then the equation at the beginning of this proof can be written as

$$A'(t) = f(A(t))[-\mu_A \mathcal{B}(A(t)) + \beta e^{-\mu_A \tau(t)} \mathcal{B}(\varphi(t - \tau(t)))], \quad \forall t \geq 0, \quad (4.10)$$

We define

$$\Gamma := \beta \mathcal{B} \left(\sup_{t \in [-\tau_0, 0]} \varphi(t) \right) \geq 0,$$

Then $A(t) \leq \hat{A}(t)$, $\forall t \geq 0$, where $\hat{A}(t)$ is the solution of

$$\begin{cases} \hat{A}'(t) = -\mu_A \hat{A}(t) + \Gamma f(\hat{A}(t)), \\ \hat{A}(0) = \varphi(0) \geq 0. \end{cases} \quad (4.11)$$

Define $g_\Gamma(\hat{A}(t)) := -\mu_A \hat{A}(t) + \Gamma f(\hat{A}(t))$, $\forall t \geq 0$. Apparently $g_\Gamma(\hat{A})$ is monotone decreasing with respect to \hat{A} and we have

$$g_\Gamma(0) = \Gamma f(0) \geq 0, \quad \lim_{\hat{A} \rightarrow +\infty} g_\Gamma(\hat{A}) = -\infty.$$

Fixing $\hat{A}^* \in [\varphi(0), +\infty)$ such that $g_{\Gamma}(\hat{A}^*) \leq 0$, we have

$$A(t) \leq \hat{A}(t) \leq \hat{A}^*, \forall t \geq 0.$$

Now

$$1 = \int_{t-\tau(t)}^t f(A(\sigma))d\sigma \geq \int_0^t f(A(\sigma))d\sigma \geq \int_0^t f(\hat{A}^*)d\sigma = tf(\hat{A}^*)$$

which is not possible for all $t \geq 0$ (since $f(\hat{A}^*) > 0$). By using the same comparison principle argument on $[0, t^*]$ we get the boundedness of $A(t)$ on $[0, t^*]$ (bounded above by \hat{A}^*). \square

Proof of Theorem 4.3. We have that $\forall t \geq 0$,

$$A'(t) = -\mu_A A(t) + \beta e^{-\mu_J \tau(t)} f(A(t)) \mathcal{B}(A(t - \tau(t))) \geq -\mu_A A(t),$$

where \mathcal{B} is defined in the same way as in the proof of Lemma 4.14 and that the solution of

$$z'(t) = -\mu_A z(t), \quad z(0) = m. \quad (4.12)$$

is

$$z(t) = z(t; m) = m e^{-\mu_A t}, \quad t \geq 0.$$

Step 1: For each $m \geq 0$, we define $\tau_m > 0$ as the unique solution of the integral equation

$$\int_0^{\tau_m} f(z(\sigma))d\sigma = 1,$$

which is equivalent to the integral equation

$$\int_0^{\tau_m} f(m e^{-\mu_A \sigma})d\sigma = 1.$$

The existence of τ_m and the fact that $\tau_m \rightarrow +\infty$ as $m \rightarrow +\infty$ can be proved in a similar way as in section 4 (see case 2 in the proof of Lemma 4.19 for a detailed proof).

Step 2: Let $m > 0$ large enough such that

$$\beta e^{-\mu_J \tau_m} < \mu_A. \quad (4.13)$$

Step 3: Due to the fact that the function \mathcal{B} is increasing and unbounded and $\mathcal{B}(0) = 0$, we can find $N > 0$, such that

$$\mathcal{B}(x) \geq \frac{\mu_A}{\beta} \mathcal{B}(N) \Rightarrow x \geq m.$$

Step 4: By Lemma 4.14, we can find $K \geq N$, such that

$$A(t) \leq K, \forall t \in [0, t^*].$$

Step 5: Next we will show that $\forall t > t^*$, $A(t) \leq K$. Define

$$t_K := \sup\{t \geq 0 : A(l) \leq K, \forall l \in [0, t]\},$$

and assume by contradiction that t_K is finite. Then $t_K \geq t^*$ and t_K satisfies the following properties

$$A(t) \leq K, \forall t \in [0, t_K); A(t_K) = K, A'(t_K) \geq 0. \quad (4.14)$$

Now by using (4.10) and the fact that $A'(t_K) \geq 0$, we obtain

$$\begin{aligned} \beta \mathcal{B}(A(t_K - \tau(t_K))) &\geq \beta e^{-\mu_J \tau(t_K)} \mathcal{B}(A(t_K - \tau(t_K))) \\ &\geq \mu_A \mathcal{B}(A(t_K)) = \mu_A \mathcal{B}(K) \geq \mu_A \mathcal{B}(N), \end{aligned}$$

and by using step 3 we deduce that

$$A(t_K - \tau(t_K)) \geq m.$$

By using a comparison principle on

$$A'(t) \geq -\mu_A A(t), \forall t \geq t_K - \tau(t_K), A(t_K - \tau(t_K)) \geq m$$

and the equation (4.12), we have

$$A(t) \geq z(t - t_K + \tau(t_K)), \forall t \geq t_K - \tau(t_K).$$

Now since $x \mapsto f(x)$ is decreasing we deduce that

$$1 = \int_{t_K - \tau(t_K)}^{t_K} f(A(\sigma)) d\sigma \leq \int_{t_K - \tau(t_K)}^{t_K} f(z(\sigma - t_K + \tau(t_K))) d\sigma = \int_0^{\tau(t_K)} f(z(\sigma)) d\sigma.$$

By the definition of τ_m , we must have

$$\tau(t_K) \geq \tau_m. \quad (4.15)$$

By using (4.13)-(4.15), we obtain

$$\begin{aligned} 0 &\leq A'(t_K) = f(A(t_K)) [-\mu_A \mathcal{B}(A(t_K)) + \beta e^{-\mu_J \tau(t_K)} \mathcal{B}(A(t_K - \tau(t_K)))] \\ &= f(K) [-\mu_A \mathcal{B}(K) + \beta e^{-\mu_J \tau(t_K)} \mathcal{B}(A(t_K - \tau(t_K)))] \\ &\leq f(K) [-\mu_A \mathcal{B}(K) + \beta e^{-\mu_J \tau_m} \mathcal{B}(A(t_K - \tau(t_K)))] \\ &\leq f(K) (-\mu_A \mathcal{B}(K) + \beta e^{-\mu_J \tau_m} \mathcal{B}(K)) \\ &= K (-\mu_A + \beta e^{-\mu_J \tau_m}) < 0. \end{aligned} \quad (4.16)$$

This contradiction shows that t_K cannot be finite. By using the definition of t_K we deduce that $A(t) \leq K, \forall t > t^*$. \square

In the rest of this section we study the dissipativity of the system, namely we look for an asymptotic uniform bound for solutions starting in some bounded sets. In order to study this property we need the following lemma.

Lemma 4.15. *Let Assumptions 4.1 be satisfied. Suppose that $(A(t), \tau(t))$ is the solution of system (4.1), then*

$$\lim_{t \rightarrow +\infty} [t - \tau(t)] = +\infty.$$

Proof. If $\tau_0 = 0$, then $\tau(t) = 0, \forall t \geq 0$ and there is nothing to prove. If $\tau_0 > 0$, then by Theorem 4.3 we know that $t \mapsto A(t)$ is bounded from above by a certain constant $K > 0$. Since $\tau(t)$ is the unique solution of the integral equation

$$\int_{-\tau(t)}^0 f(A(t + \sigma)) d\sigma = \delta, \forall t \geq 0$$

where

$$\delta := \int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma > 0,$$

by using the fact that $x \mapsto f(x)$ is decreasing we deduce that $\tau(t)f(K) \leq \delta, \forall t \geq 0$, and it follows that $t \mapsto \tau(t)$ is bounded by $f(K)^{-1}\delta$. This completes the proof. \square

Theorem 4.16 (Dissipativity). *Let $\alpha > 0$ and $\tau_0 > 0$. Let Assumption 4.1 be satisfied. Let $B \subset \text{Lip}_\alpha$ be a bounded subset and $[\tau_{\min}, \tau_{\max}] \subset (0, +\infty)$ be a fixed interval. Denote*

$$\delta_{\min} := \inf_{(\varphi, \tau_0) \in B \times [\tau_{\min}, \tau_{\max}]} \int_{-\tau_0}^0 f(\varphi(\sigma)) d\sigma > 0.$$

Then for each initial condition $(\varphi, \tau_0) \in B \times [\tau_{\min}, \tau_{\max}]$, there exists a constant $M^ = M^*(\delta_{\min}) > 0$ (independent of the initial condition) such that*

$$\limsup_{t \rightarrow +\infty} A(t) \leq M^*.$$

Proof. Similarly as in step 1 of the proof of Theorem 4.3, we consider τ_m the unique solution of the integral equation

$$\int_0^{\tau_m} f(me^{-\mu_A \sigma}) d\sigma = \delta_{\min}.$$

Then we can find $M^* > 0$ (large enough) such that for each $M \geq M^*$, the two following inequalities

$$-\mu_A + \beta e^{-\mu_A \tau_m} < 0 \text{ with } m := \frac{\mu_A M}{\beta} \tag{4.17}$$

and

$$-\mu_A + \beta e^{-\mu_J \frac{\delta_{\min}}{f(M)}} < 0 \quad (4.18)$$

are satisfied.

Now suppose that we can find $t \mapsto (A(t), \tau(t))$ the solution of system (4.1) with the initial condition $(\varphi, \tau_0) \in B \times [\tau_{\min}, \tau_{\max}]$ satisfying

$$M := \limsup_{t \rightarrow +\infty} A(t) \geq M^*.$$

Then we have the following alternative:

Case 1: There exists a sequence $\{t_n\}_{n \in \mathbb{N}}$ which satisfies $\lim_{n \rightarrow +\infty} t_n = +\infty$ and for any t_n ,

$$A'(t_n) = 0,$$

and

$$A(t_n) \rightarrow M \text{ as } n \rightarrow +\infty.$$

Then we have

$$0 = A'(t_n) = -\mu_A A(t_n) + \beta e^{-\mu_J \tau(t_n)} \frac{f(A(t_n))}{f(A(t_n - \tau(t_n)))} A(t_n - \tau(t_n)).$$

By taking the supremum limit on both sides when $n \rightarrow +\infty$ and notice that $e^{-\mu_J \tau(t_n)} \leq 1$, we have

$$0 \leq -\mu_A M + \beta f(M) \limsup_{n \rightarrow +\infty} \frac{A(t_n - \tau(t_n))}{f(A(t_n - \tau(t_n)))},$$

and since the map $x \mapsto \frac{1}{f(x)}$ is increasing, we deduce that

$$0 \leq -\mu_A M + \beta \frac{f(M)}{f(M)} \limsup_{n \rightarrow +\infty} A(t_n - \tau(t_n)).$$

Hence

$$\limsup_{n \rightarrow +\infty} A(t_n - \tau(t_n)) \geq \frac{\mu_A M}{\beta} = m. \quad (4.19)$$

Now we replace in (4.12) $z(t)$ and m by $z_n(t)$ and m_n where $m_n \rightarrow m$ as $n \rightarrow +\infty$, then we can repeat the steps of the proof of Theorem 4.3 and notice that

$$\delta_{\min} \leq \int_{t_n - \tau(t_n)}^{t_n} f(A(\sigma)) d\sigma \leq \int_{t_n - \tau(t_n)}^{t_n} f(z(\sigma - t_n + \tau(t_n))) d\sigma = \int_0^{\tau(t_n)} f(z(\sigma)) d\sigma,$$

we get $\tau(t_n) \geq \tau_m$. Thus we can repeat the procedure in (4.16) and get a contradiction

$$0 = \lim_{n \rightarrow +\infty} A'(t_n) \leq M (-\mu_A + \beta e^{-\mu_J \tau_m}) < 0.$$

Case 2: The solution $A(t)$ is eventually monotone. So we can assume that there exists a time $\bar{t} > 0$ such that

$$A'(t) \geq 0, \forall t \geq \bar{t}$$

(the case $A'(t) \leq 0, \forall t \geq \bar{t}$ being similar). Since $A(t)$ is eventually increasing, we deduce that

$$\lim_{t \rightarrow +\infty} A_t = M \text{ in } C_\alpha := \{\phi \in C(-\infty, 0] : e^{-\alpha|\cdot|}\phi(\cdot) \text{ is bounded}\}$$

where C_α is the Banach space endowed with the norm $\|\phi\|_{C_\alpha} := \|e^{-\alpha|\cdot|}\phi(\cdot)\|_\infty$.

As $A(t)$ is bounded, $\{A'_t\}_{t \geq 0}$ is relatively compact in Lip_α (since $\alpha > 0$, $A(t)$ satisfies system (4.1) and by applying the Arzelà-Ascoli theorem locally on the bounded interval $[-\theta^*, 0]$ for each $\theta^* > 0$ and by using the step method to extend to $(-\infty, 0]$), we get

$$\lim_{t \rightarrow +\infty} A'_t = 0 \text{ in } L_\alpha^\infty := \{\phi : e^{-\alpha|\cdot|}\phi(\cdot) \in L^\infty(-\infty, 0]\}$$

where L_α^∞ is the Banach space endowed with the norm $\|\phi\|_{L_\alpha^\infty} := \|e^{-\alpha|\cdot|}\phi(\cdot)\|_{L^\infty}$.

Moreover, we have

$$\delta_{\min} \leq \int_{t-\tau(t)}^t f(A(\sigma))d\sigma =: \delta,$$

and by taking the limit when $t \rightarrow +\infty$ (and since by Lemma 4.15 $t - \tau(t) \rightarrow +\infty$) we obtain

$$\lim_{t \rightarrow +\infty} \tau(t) = \frac{\delta}{f(M)} \geq \frac{\delta_{\min}}{f(M)}.$$

By taking the limit when $t \rightarrow +\infty$ in the first equation of system (4.1) we obtain the following contradiction

$$0 = \lim_{t \rightarrow +\infty} A'_t \leq -\mu_A M + \beta e^{-\mu_J \frac{\delta_{\min}}{f(M)}} \frac{f(M)}{f(M)} M < 0.$$

Both cases lead to a contradiction, which implies that

$$\limsup_{t \rightarrow +\infty} A(t) \leq M^*.$$

□

4.4 Boundedness of solutions in n -species case

In this section we will investigate the boundedness of a trajectory of system (4.5) with the initial conditions satisfying

$$\int_{-\tau_{i0}}^0 f_i(Z_{i\varphi}(\sigma))d\sigma > 0, \forall i = 1, \dots, n.$$

Multiplying each of the above integrals by a positive constant, in this section we can assume without loss of generality that

Assumption 4.17.

$$\int_{-\tau_{i0}}^0 f_i(Z_{i\varphi}(\sigma))d\sigma = 1, \forall i = 1, \dots, n.$$

We also have the following lemma from Lemma 3.9 step 2.

Lemma 4.18. *Let Assumptions 4.5 be satisfied. Then the functions $t - \tau_i(t)$ are strictly increasing with respect to t , $\forall i = 1, \dots, n$.*

Next we will prove the following result.

Lemma 4.19. *Let Assumptions 4.5 and 4.17 be satisfied. Then for each $i = 1, \dots, n$ there exists $t_i^* > 0$ such that $t_i^* - \tau_i(t_i^*) = 0$.*

Proof. For each $i = 1, \dots, n$ we define

$$t_i^* := \sup\{t \geq 0 : s - \tau_i(s) \leq 0, \forall s \in [0, t]\}.$$

Case 1: We assume that all the elements of $\{t_i^*\}_{i=1}^n$ are infinite, and we will prove that this is not possible. By the above definition of t_i^* , we have $\forall t \geq 0$, $t - \tau_i(t) \leq 0$, or precisely,

$$t - \tau_i(t) \in [-\tau_{i0}, 0].$$

Then the equation for $A_i(t)$ becomes

$$A_i'(t) = -\mu_{A_i}A_i(t) + \beta_i e^{-\mu_{A_i}\tau_i(t)} \frac{f_i(Z_i(t))}{f_i(Z_{i\varphi}(t - \tau_i(t)))} \varphi_i(t - \tau_i(t)), \forall t \geq 0.$$

We set

$$\Gamma_i := \beta_i \sup_{t \in [-\tau_{i0}, 0]} \frac{\varphi_i(t)}{f_i(Z_{i\varphi}(t))} \geq 0.$$

Since $f_i(Z_i(t)) \leq f_i(\zeta_{ii}A_i(t))$, $\forall t \geq 0$, then we have $A_i(t) \leq \hat{A}_i(t)$, $\forall t \geq 0$, where $\hat{A}_i(t)$ is the solution of

$$\begin{cases} \hat{A}_i'(t) = -\mu_{A_i}\hat{A}_i(t) + \Gamma_i f_i(\zeta_{ii}\hat{A}_i(t)), \forall t \geq 0, \\ \hat{A}_i(0) = \varphi_i(0) \geq 0. \end{cases}$$

Define $g_{\Gamma_i}(\hat{A}_i(t)) := -\mu_{A_i}\hat{A}_i(t) + \Gamma_i f_i(\zeta_{ii}\hat{A}_i(t))$, $\forall t \geq 0$, $i = 1, \dots, n$. As $g_{\Gamma_i}(\hat{A}_i)$ is decreasing with \hat{A}_i and we have

$$g_{\Gamma_i}(0) = \Gamma_i f_i(0) \geq 0, \quad \lim_{\hat{A}_i \rightarrow +\infty} g_{\Gamma_i}(\hat{A}_i) = -\infty,$$

so fixing $\hat{A}_i^* \in [\varphi_i(0), +\infty)$ such that $g_{\Gamma_i}(\hat{A}_i^*) \leq 0$, we have

$$A_i(t) \leq \hat{A}_i(t) \leq \hat{A}_i^*, \forall t \geq 0.$$

Now since by assumption $t - \tau_i(t) \leq 0, \forall t \geq 0$, we obtain for each $t \geq 0$

$$1 = \int_{t-\tau_i(t)}^t f_i(Z_i(\sigma))d\sigma \geq \int_0^t f_i(Z_i(\sigma))d\sigma \geq t f_i \left(\sum_{j=1}^n \zeta_{ij} \hat{A}_j^* \right) \quad (4.20)$$

which is impossible.

Case 2: We assume that exactly j elements of $\{t_i^*\}_{i=1}^n$ are finite, where $1 \leq j < n$, and we will prove that this is not possible, either. Without loss of generality we might assume that t_1^*, \dots, t_j^* are finite and t_{j+1}^*, \dots, t_n^* are infinite. Firstly we prove that $A_1(t), \dots, A_n(t)$ are bounded on $[0, +\infty)$.

Following a similar argument as in case 1, for each $i = j+1, \dots, n$, as t_i^* is infinite, we can find $\hat{A}_i^* \in [\varphi_i(0), +\infty)$ such that

$$A_i(t) \leq \hat{A}_i^*, \forall t \geq 0.$$

For each $k = 1, \dots, j$, consider

$$z_k(t) = z_k(t; m_k) = m_k e^{-\mu_{A_k} t}, t \geq 0$$

where $m_k > 0$ will be fixed later on and as before $z_k(t)$ is a solution of the following ordinary differential equation

$$z_k'(t) = -\mu_{A_k} z_k(t), z_k(0) = m_k. \quad (4.21)$$

We define $\tau_{k, m_k} > 0$ as the unique solution of the integral equation

$$\int_0^{\tau_{k, m_k}} f_k(\zeta_{kk} z_k(\sigma))d\sigma = 1. \quad (4.22)$$

By Assumption 4.5-(i), we have $\zeta_{kk} > 0$ and

$$\int_0^{\tau} f_k(\zeta_{kk} z_k(\sigma))d\sigma \geq \int_0^{\tau} f_k(\zeta_{kk} m_k)d\sigma = \tau f_k(\zeta_{kk} m_k) > 0 \text{ when } \tau > 0,$$

therefore $\tau_{k, m_k} > 0$ exists and is finite. Next we observe that we have

$$\tau_{k, m_k} \rightarrow +\infty \text{ as } m_k \rightarrow +\infty. \quad (4.23)$$

Indeed, assume by contradiction that there exists a subsequence $\{m_{k, l}\}_{l \geq 0} \rightarrow +\infty$ and a sequence $\{\tau_{k, m_{k, l}}\}_{l \geq 0}$ bounded by $\tau^* > 0$. Then we have

$$1 = \int_0^{\tau_{k, m_{k, l}}} f_k(\zeta_{kk} z_k(\sigma))d\sigma \leq \int_0^{\tau^*} f_k(\zeta_{kk} z_k(\sigma))d\sigma \rightarrow 0 \text{ as } l \rightarrow +\infty$$

which is impossible.

By Assumption 4.5-(ii), for each $c \geq 1$,

$$M_{f_k}(c) := \sup_{x \geq 0} \frac{f_k(x)}{f_k(cx)} < +\infty.$$

By using (4.23) we can fix m_k (large enough) such that

$$-\mu_{A_k} + \beta_k e^{-\mu_{J_k} \tau_{k,m_k}} M_{f_k} \left(\frac{\zeta_{k1} + \cdots + \zeta_{kn}}{\zeta_{kk}} \right) < 0. \quad (4.24)$$

For a constant $K > 0$, define

$$t_K := \sup\{t \geq 0 : \max\{A_1(s), \dots, A_j(s)\} \leq K, \forall s \in [0, t]\}.$$

Let us now prove that $A_1(t), \dots, A_j(t)$ are bounded on $[0, +\infty)$. Assume by contradiction that t_K is finite for each $K > 0$ large enough. Then at least one of $A_k(t), k = 1, \dots, j$ reaches K at t_K . Assume that $A_{i(K)}(t_K) = K$. Firstly we prove that

$$t_K - \tau_{i(K)}(t_K) \geq 0 \quad (4.25)$$

for each $K > 0$ large enough. Otherwise $\exists K$ large enough such that $t_K - \tau_{i(K)}(t_K) < 0$. Assume without loss of generality that $i(K) = 1$. We know that t_K must be smaller than t_1^* , then we can use the same comparison principle arguments as in case 1 on the interval of time $[0, t_1^*]$, and we can find $\hat{A}_1^* > 0$ (independent of K) such that

$$K = A_1(t_K) \leq \hat{A}_1^*,$$

which becomes impossible whenever K becomes large enough. We deduce that (4.25) holds true.

Now we will prove $A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \rightarrow +\infty$ when $K \rightarrow +\infty$. By assumption t_K is finite, and by definition of t_K we have

$$A_{i(K)}(t) \leq K, \forall t \in [0, t_K]$$

and we must have

$$A'_{i(K)}(t_K) \geq 0.$$

Then

$$\begin{aligned} 0 &\leq A'_{i(K)}(t_K) = -\mu_{A_{i(K)}} A_{i(K)}(t_K) \\ &\quad + \beta_1 e^{-\mu_{J_{i(K)}} \tau_{i(K)}(t_K)} \frac{f_{i(K)}(Z_{i(K)}(t_K))}{f_{i(K)}(Z_{i(K)}(t_K - \tau_{i(K)}(t_K)))} A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \\ &\leq -\mu_{A_{i(K)}} K + \beta_{i(K)} \frac{f_{i(K)}(\zeta_{i(K),i(K)} K)}{f_{i(K)}((\zeta_{i(K),1} + \cdots + \zeta_{i(K),n}) \hat{K})} A_{i(K)}(t_K - \tau_{i(K)}(t_K)), \end{aligned}$$

where

$$\hat{K} := \max \left\{ K, \hat{A}_{j+1}^*, \dots, \hat{A}_n^*, \max_{t \in [-\tau_{10}, 0]} \varphi_1(t), \dots, \max_{t \in [-\tau_{n0}, 0]} \varphi_n(t) \right\}.$$

Notice that $\frac{(\zeta_{i(K),1} + \dots + \zeta_{i(K),n})\hat{K}}{\zeta_{i(K),i(K)}K} \geq 1$, we have

$$\begin{aligned} A_{i(K)}(t_K - \tau_{i(K)}(t_K)) &\geq \frac{\mu_{A_{i(K)}}K}{\beta_{i(K)}} \cdot \frac{f_{i(K)}((\zeta_{i(K),1} + \dots + \zeta_{i(K),n})\hat{K})}{f_{i(K)}(\zeta_{i(K),i(K)}K)} \\ &\geq \frac{\mu_{A_{i(K)}}K}{\beta_{i(K)}} \cdot \frac{1}{M_{f_{i(K)}} \left(\frac{(\zeta_{i(K),1} + \dots + \zeta_{i(K),n})\hat{K}}{\zeta_{i(K),i(K)}K} \right)}. \end{aligned}$$

Now since for all $K > 0$ large enough $\hat{K} = K$, we deduce that

$$A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \rightarrow +\infty \text{ as } K \rightarrow +\infty.$$

By using (4.25), we can fix K large enough such that

$$A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \geq m_{i(K)} \text{ and } t_K - \tau_{i(K)}(t_K) \geq 0.$$

By using the comparison principle on equation (4.21) and

$$A'_{i(K)}(t) \geq -\mu_{A_{i(K)}}A_{i(K)}(t), \forall t \geq t_K - \tau_{i(K)}(t_K)$$

with

$$A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \geq m_{i(K)},$$

we have

$$A_{i(K)}(t) \geq z_{i(K)}(t - t_K + \tau_{i(K)}(t_K)), \forall t \geq t_K - \tau_{i(K)}(t_K).$$

An integration shows that

$$\begin{aligned} 1 &= \int_{t_K - \tau_{i(K)}(t_K)}^{t_K} f_{i(K)}(Z_{i(K)}(\sigma))d\sigma \leq \int_{t_K - \tau_{i(K)}(t_K)}^{t_K} f_{i(K)}(\zeta_{i(K),i(K)}A_{i(K)}(\sigma))d\sigma \\ &\leq \int_{t_K - \tau_{i(K)}(t_K)}^{t_K} f_{i(K)}(\zeta_{i(K),i(K)}z_{i(K)}(\sigma - t_K + \tau_{i(K)}(t_K)))d\sigma \\ &= \int_0^{\tau_{i(K)}(t_K)} f_{i(K)}(\zeta_{i(K),i(K)}z_{i(K)}(\sigma))d\sigma. \end{aligned}$$

By the definition of $\tau_{i(K),m_{i(K)}} > 0$ (defined as the solution of (4.22)), we have

$$\tau_{i(K)}(t_K) \geq \tau_{i(K),m_{i(K)}}.$$

Now by using (4.24), we have

$$\begin{aligned}
0 &\leq A'_{i(K)}(t_K) = -\mu_{A_{i(K)}} A_{i(K)}(t_K) \\
&\quad + \beta_{i(K)} e^{-\mu_{J_{i(K)}} \tau_{i(K)}(t_K)} \frac{f_{i(K)}(Z_{i(K)}(t_K))}{f_{i(K)}(Z_{i(K)}(t_K - \tau_{i(K)}(t_K)))} A_{i(K)}(t_K - \tau_{i(K)}(t_K)) \\
&= f_{i(K)}(Z_{i(K)}(t_K)) \left[-\mu_{A_{i(K)}} \frac{A_{i(K)}(t_K)}{f_{i(K)}(Z_{i(K)}(t_K))} \right. \\
&\quad \left. + \beta_{i(K)} e^{-\mu_{J_{i(K)}} \tau_{i(K)}(t_K)} \frac{A_{i(K)}(t_K - \tau_{i(K)}(t_K))}{f_{i(K)}(Z_{i(K)}(t_K - \tau_{i(K)}(t_K)))} \right] \\
&\leq f_{i(K)}(Z_{i(K)}(t_K)) \left[-\mu_{A_{i(K)}} \frac{K}{f_{i(K)}(\zeta_{i(K),i(K)} K)} \right. \\
&\quad \left. + \beta_{i(K)} e^{-\mu_{J_{i(K)}} \tau_{i(K),m_i(K)}} \frac{K}{f_{i(K)}((\zeta_{i(K),1} + \dots + \zeta_{i(K),n}) K)} \right] \\
&= \frac{f_{i(K)}(Z_{i(K)}(t_K)) K}{f_{i(K)}(\zeta_{i(K),i(K)} K)} \left[-\mu_{A_{i(K)}} \right. \\
&\quad \left. + \beta_{i(K)} e^{-\mu_{J_{i(K)}} \tau_{i(K),m_i(K)}} \frac{f_{i(K)}(\zeta_{i(K),i(K)} K)}{f_{i(K)}((\zeta_{i(K),1} + \dots + \zeta_{i(K),n}) K)} \right] \\
&\leq \frac{f_{i(K)}(Z_{i(K)}(t_K)) K}{f_{i(K)}(\zeta_{i(K),i(K)} K)} \left[-\mu_{A_{i(K)}} \right. \\
&\quad \left. + \beta_{i(K)} e^{-\mu_{J_{i(K)}} \tau_{i(K),m_i(K)}} M_{f_{i(K)}} \left(\frac{\zeta_{i(K),1} + \dots + \zeta_{i(K),n}}{\zeta_{i(K),i(K)}} \right) \right] \\
&< 0, \tag{4.26}
\end{aligned}$$

which leads to a contradiction. Thus for $K > 0$ large enough t_K is infinite, namely

$$A_k(t) \leq K, \forall t \geq 0, \forall k = 1, \dots, j.$$

Observe that by assumption t_{j+1}^*, \dots, t_n^* are infinite, which means that $t - \tau_i(t) \leq 0, \forall t \geq 0, \forall i = j+1, \dots, n$, therefore we deduce that for all $t \geq 0$,

$$\begin{aligned}
1 &= \int_{t-\tau_i(t)}^t f_i(Z_i(\sigma)) d\sigma \geq \int_0^t f_i(Z_i(\sigma)) d\sigma \\
&\geq \int_0^t f_i((\zeta_{i1} + \dots + \zeta_{ij}) K + \zeta_{i,j+1} \hat{A}_{j+1}^* + \dots + \zeta_{in} \hat{A}_n^*) d\sigma \\
&= t f_i((\zeta_{i1} + \dots + \zeta_{ij}) K + \zeta_{i,j+1} \hat{A}_{j+1}^* + \dots + \zeta_{in} \hat{A}_n^*)
\end{aligned}$$

which is impossible when t is large enough. The proof is completed. \square

Proof of Theorem 4.6. For each $i = 1, \dots, n$, we define τ_{i,m_i} satisfying

$$\int_0^{\tau_{i,m_i}} f_i(\zeta_{ii} z_i(\sigma)) d\sigma = 1,$$

where $z_i(t) = m_i e^{-\mu_{A_i} t}$, $t \geq 0$. Like the (4.24) in case 2 of Lemma 4.19, we can similarly fix m_i large enough such that

$$\beta_i e^{-\mu_{J_i} \tau_i, m_i} M_{f_i} \left(\frac{\zeta_{i1} + \dots + \zeta_{in}}{\zeta_{ii}} \right) < \mu_{A_i}.$$

For a constant $K > 0$, we define

$$t_K := \sup\{t > 0 : \max\{A_1(s), \dots, A_n(s)\} \leq K, \forall s \in [0, t]\}.$$

Then similar to the procedure of case 2 in the proof of Lemma 4.19, we can get a K large enough and we can deduce that $t_K = +\infty$. Thus $A_i(t)$ is bounded for all $t \geq 0$. \square

4.5 Dissipativity result in n -species case

In this section we will investigate the dissipativity of system (4.5). First, we have the following lemma similar to Lemma 4.15.

Lemma 4.20. *Let Assumptions 4.5 be satisfied. Suppose that $(A_i(t), \tau_i(t))$ is the solution of system (4.5), then*

$$\lim_{t \rightarrow +\infty} [t - \tau_i(t)] = +\infty.$$

Proof. If $\tau_{i0} = 0$, then again there is nothing to prove. When $\tau_{i0} > 0$, by Theorem 4.6 we know that $t \mapsto A_i(t)$ is bounded from above by a certain constant $K > 0$. Since $\tau_i(t)$ is the unique solution of the integral equation

$$\int_{t-\tau_i(t)}^t f_i(Z_i(\sigma)) d\sigma = \hat{\delta}, \forall t \geq 0$$

where $\hat{\delta} := \int_{-\tau_{i0}}^0 f_i(Z_{i\varphi}(\sigma)) d\sigma > 0$, then similar as the proof of Lemma 4.15, we deduce that $t \mapsto \tau_i(t)$ is bounded by $f_i((\zeta_{i1} + \dots + \zeta_{in})K)^{-1} \hat{\delta}$. This completes the proof. \square

Theorem 4.21 (Dissipativity). *Let Assumption 4.5 be satisfied. Let $B_i \subset \text{Lip}_\alpha$ be a bounded subset and $[\tau_{i,\min}, \tau_{i,\max}] \subset (0, +\infty)$ be a fixed interval, $i = 1, \dots, n$. Let*

$$B := \prod_{i=1}^n B_i \text{ and } I_\tau := \prod_{i=1}^n [\tau_{i,\min}, \tau_{i,\max}].$$

Denote

$$\hat{\delta}_{\min} := \inf_i \inf_{(\varphi_i, \tau_{i0}) \in B_i \times [\tau_{i,\min}, \tau_{i,\max}]} \int_{-\tau_{i0}}^0 f_i(Z_{i\varphi}(\sigma)) d\sigma.$$

4. Boundedness and dissipativity

Then for each initial condition $(\varphi, \tau_0) \in B \times I_\tau$ where $\varphi := (\varphi_1, \dots, \varphi_n)$ and $\tau_0 = (\tau_{10}, \dots, \tau_{n0})$, there exists a constant $M^* = M^*(\hat{\delta}_{\min}) > 0$ (independent of the initial condition) such that

$$\limsup_{t \rightarrow +\infty} \max_{i=1, \dots, n} \{A_i(t)\} \leq M^*.$$

Proof. Similarly as in case 2 of the proof of Lemma 4.19, for each i we consider τ_{i, m_i} the unique solution of the integral equation

$$\int_0^{\tau_{i, m_i}} f_i(\zeta_{ii} z_i(\sigma)) d\sigma = \hat{\delta}_{\min}.$$

Then we can find $M^* > 0$ (large enough) such that for each $M \geq M^*$, the two following inequalities

$$-\mu_{A_i} + \beta_i e^{-\mu_{J_i} \tau_{i, m_i}} M_{f_i} \left(\frac{\zeta_{i1} + \dots + \zeta_{in}}{\zeta_{ii}} \right) < 0 \quad (4.27)$$

with $m_i := \frac{\mu_{A_i} M}{\beta_i} \cdot \frac{1}{M_{f_i} \left(\frac{\zeta_{i1} + \dots + \zeta_{in}}{\zeta_{ii}} \right)}$ and

$$-\mu_{A_i} + \beta_i e^{-\mu_{J_i} \frac{\hat{\delta}_{\min}}{F_i(\zeta_{ii} M)}} M_{f_i} \left(\frac{\zeta_{i1} + \dots + \zeta_{in}}{\zeta_{ii}} \right) < 0 \quad (4.28)$$

are satisfied for any $i = 1, \dots, n$.

Now suppose that we can find $t \mapsto (A(t), \tau(t))$ the solution of system (4.5) with the initial condition $(\varphi, \tau_0) \in B \times I_\tau$ satisfying

$$M := \limsup_{t \rightarrow +\infty} \max_{i=1, \dots, n} \{A_i(t)\} \geq M^*.$$

Without loss of generality we might assume that $M = \limsup_{t \rightarrow +\infty} A_1(t)$. Then we

have the following alternative:

Case 1: There exists a sequence $\{t_n\}_{n \in \mathbb{N}}$ which satisfies $\lim_{n \rightarrow +\infty} t_n = +\infty$ and for any t_n ,

$$A_1'(t_n) = 0,$$

and

$$A_1(t_n) \rightarrow M \text{ as } n \rightarrow +\infty.$$

Then we have

$$0 = A_1'(t_n) = -\mu_{A_1} A_1(t_n) + \beta_1 e^{-\mu_{J_1} \tau_1(t_n)} \frac{f_1(Z_1(t_n))}{f_1(Z_1(t_n - \tau_1(t_n)))} A_1(t_n - \tau_1(t_n)).$$

By taking the supremum limit on both sides when $n \rightarrow +\infty$ and notice that $e^{-\mu_{J_1}\tau_1(t_n)} \leq 1$, we have

$$0 \leq -\mu_{A_1}M + \beta_1 f_1(\zeta_{11}M) \limsup_{n \rightarrow +\infty} \frac{A_1(t_n - \tau_1(t_n))}{f_1(Z_1(t_n - \tau_1(t_n)))},$$

and since the map $x \mapsto \frac{1}{f(x)}$ is increasing, we deduce that

$$0 \leq -\mu_{A_1}M + \beta_1 \frac{f_1(\zeta_{11}M)}{f_1((\zeta_{11} + \dots + \zeta_{1n})M)} \limsup_{n \rightarrow +\infty} A_1(t_n - \tau_1(t_n)).$$

Hence

$$\limsup_{n \rightarrow +\infty} A_1(t_n - \tau_1(t_n)) \geq \frac{\mu_{A_1}M}{\beta_1} \cdot \frac{1}{M_{f_1} \left(\frac{\zeta_{11} + \dots + \zeta_{1n}}{\zeta_{11}} \right)} = m_1. \quad (4.29)$$

Now by using the similar idea in case 1 of the proof of Theorem 4.16 and by using a similar method as in case 2 of the proof of Lemma 4.19 and by noticing that

$$\begin{aligned} \hat{\delta}_{\min} &\leq \int_{t_n - \tau_1(t_n)}^{t_n} f_1(Z_1(\sigma)) d\sigma \leq \int_{t_n - \tau_1(t_n)}^{t_n} f_1(\zeta_{11}A_1(\sigma)) d\sigma \\ &\leq \int_{t_n - \tau_1(t_n)}^{t_n} f_1(\zeta_{11}z_1(\sigma - t_n + \tau_1(t_n))) d\sigma = \int_0^{\tau_1(t_n)} f_1(\zeta_{11}z_1(\sigma)) d\sigma, \end{aligned}$$

we get $\tau_1(t_n) \geq \tau_{1,m_1}$. Thus we can repeat the procedure in (4.26) and get a contradiction

$$0 = \lim_{n \rightarrow +\infty} A'_1(t_n) \leq M \left(-\mu_{A_1} + \beta_1 e^{-\mu_{J_1}\tau_{1,m_1}} M_{f_1} \left(\frac{\zeta_{11} + \dots + \zeta_{1n}}{\zeta_{11}} \right) \right) < 0.$$

Case 2: The solution $A_1(t)$ is eventually monotone. So we can assume that there exists a time $\bar{t} > 0$ such that

$$A'_1(t) \geq 0, \forall t \geq \bar{t}$$

(the case $A'_1(t) \leq 0, \forall t \geq \bar{t}$ being similar). Since $A_1(t)$ is eventually increasing, we deduce that

$$\lim_{t \rightarrow +\infty} A_{1,t} = M \text{ in } C_\alpha := \{ \phi \in C(-\infty, 0] : e^{-\alpha|\cdot|}\phi(\cdot) \text{ is bounded} \}$$

where C_α is the Banach space endowed with the norm $\|\phi\|_{C_\alpha} := \|e^{-\alpha|\cdot|}\phi(\cdot)\|_\infty$.

As $A_1(t)$ is bounded, $\{A'_{1,t}\}_{t \geq 1}$ is relatively compact in Lip_α (since $\alpha > 0$, $A_i(t), i = 1, \dots, n$ satisfy the system (4.5) and by applying Arzelà-Ascoli

theorem locally on the bounded interval $[-\theta^*, 0]$ for each $\theta^* > 0$ and by using the step method to extend to $(-\infty, 0]$, we get

$$\lim_{t \rightarrow +\infty} A'_{1,t} = 0 \text{ in } L_\alpha^\infty := \{\phi : e^{-\alpha|\cdot|}\phi(\cdot) \in L^\infty(-\infty, 0]\}$$

where L_α^∞ is the Banach space endowed with the norm $\|\phi\|_{L_\alpha^\infty} := \|e^{-\alpha|\cdot|}\phi(\cdot)\|_{L^\infty}$. Moreover, we have

$$\hat{\delta}_{\min} \leq \int_{t-\tau_1(t)}^t f_1(Z_1(\sigma)) d\sigma =: \delta_1,$$

and by taking the limit when $t \rightarrow +\infty$ (and since by Lemma 4.20 $t - \tau_1(t) \rightarrow +\infty$) we obtain

$$\lim_{t \rightarrow +\infty} \tau_1(t) = \frac{\delta_1}{f((\zeta_{11} + \dots + \zeta_{1n})M)} \geq \frac{\hat{\delta}_{\min}}{f(\zeta_{11}M)}.$$

By taking the limit when $t \rightarrow +\infty$ in the first equation of system (4.5) we obtain the following contradiction

$$0 = \lim_{t \rightarrow +\infty} A'_{1,t} \leq -\mu_{A_1}M + \beta_1 e^{-\mu_{J_1} \frac{\hat{\delta}_{\min}}{f(\zeta_{11}M)}} \frac{f_1(\zeta_{11}M)}{f_1((\zeta_{11} + \dots + \zeta_{1n})M)} M < 0.$$

Both cases lead to a contradiction, which proves that

$$\limsup_{t \rightarrow +\infty} \max_{i=1, \dots, n} \{A_i(t)\} \leq M^*.$$

□

Chapter 5

Numerical simulations of a forest and parasite prey-predator model

5.1 Introduction

Pine wilt disease (PWD) is one of the most serious disease of pine species in all over the world. The pine wood nematode (PWN) *Bursaphelenchus xylophilus*, the pathogenic agent of PWD, is a native nematode species in north America. This kind of parasite is transmitted from tree to tree by a species of insect *Monochamus*. It was first introduced in Japan in the early 20th century and spreaded into other Asian countries (China, Korea, etc.) in the 1980s. In 1999, it was first detected in Portugal [155] and the only insect vector is *Monochamus galloprovincialis* [198, 199]. Till 2008, with the detection of this PWN in other areas of Portugal and even on the Island of Madeira, the entire territory of Portugal was affected [182]. PWD also spreads into other European countries due to the wood transportation. For more information about the spread of PWD in Europe and in the world, we refer in addition to [156, 157, 206] and the references therein.

In this paper we consider the population of nematode, which is a parasite spreading into a wild pine tree forest. This means that we totally neglect the way the nematode spreads in between the pine trees, namely the insect vector *Monochamus galloprovincialis*. The life cycle of nematode is very short (around 4 days). In comparison, the pine tree's life cycle is rather slow. Therefore it makes sense to use instantenous production of new nematodes while pine trees are degraded by nematodes and pine trees serve as a resource to produce new nematodes. We refer to [115] for more information about the biology of nematode.

There have been some attempts to build a model to describe the dynamics in the pine-nematode community ([71] and the references therein). In this paper, in order to describe the relationship between pine trees and nematodes, we will use a predator-prey system which goes back to Lotka [129] and Volterra

[211, 213] in the early 20th century. More generally speaking, the class of system we have in mind is the so-called consumer-resource model which attracts a lot of interests in ecology during the last four decades. We refer to [87, 88, 122, 134, 149, 184] and the references therein for a nice overview on this subject. Let $A(t)$ be the number of adult pine trees, and $I(t)$ be the number of nematodes. We consider a simplified model for the population dynamic of pine trees and nematodes

$$\begin{cases} \frac{dA(t)}{dt} = (\beta - \mu_A)A(t) - \underbrace{\frac{\gamma_A I(t)A(t)}{1 + \kappa A(t)}}_{\text{pine tree destruction}}, \\ \frac{dI(t)}{dt} = \left(\underbrace{\frac{\varepsilon \chi \gamma_A A(t)}{1 + \kappa A(t)}}_{\text{production of new nematodes}} - \mu_I \right) I(t), \end{cases} \quad (5.1)$$

where $\beta > 0$ is the birth rate of trees, $\mu_A > 0$ is the natural mortality of adult trees, $\gamma_A > 0$ is the number of adult trees consumed per nematode per unit time, $\kappa \geq 0$ is interpreted as a constant handling time for each prey captured [1, 49, 102], $\varepsilon > 0$ is the conversion efficiency from tree biomass to nematode biomass, $\chi > 0$ is the birth rate of nematodes, $\mu_I > 0$ is the natural mortality of nematodes.

One may observe that the special case $\kappa = 0$ of system (5.1) corresponds to the classical Lotka-Volterra model, while the case $\kappa > 0$ corresponds to the Holling's type II functional response [89, 90]. In the article we will investigate both cases for κ .

In order to incorporate the vital dynamic of the population of trees, we need to add a limitation of the growth of trees due to the competition for light. This can be achieved by using the so-called size-structured models. We refer to [138, 193, 194, 227] for a nice survey on this topic. In [138] a comparison of size-structured model with a forest computer simulator has been successfully done, and the model considered takes the following form

$$\begin{cases} \partial_t u(t, s) + f(A(t)) \partial_s u(t, s) = -\mu(s)u(t, s), \text{ for } t \geq 0, s \geq s_-, \\ f(A(t))u(t, s_-) = \beta A(t), \text{ for } t \geq 0 \end{cases} \quad (5.2)$$

with the initial distribution of trees

$$u(0, \cdot) = u_0(\cdot) \in L_+^1(0, +\infty),$$

where $s_- > 0$ is the minimal size of juvenile trees and $s \mapsto u(t, s)$ is the density of population of trees of size s at time t , which means that for each $s_2 \geq s_1 \geq s_-$,

$$\int_{s_1}^{s_2} u(t, s) ds$$

is the number of trees of size in between s_1 and s_2 at time t . Therefore the total number of trees in the population is

$$U(t) = \int_{s_-}^{+\infty} u(t, s) ds.$$

We assume that the number of adult and juvenile trees are respectively given by

$$A(t) := \int_{s^*}^{+\infty} u(t, s) ds \text{ and } J(t) := \int_{s_-}^{s^*} u(t, s) ds$$

where $s^* > s_-$ is the size of maturity for trees, namely the minimal size of adult trees.

Moreover, to describe the fact that the more adult trees there are, the less light is left to juvenile trees to grow, we assume that the growth speed depends on the number of adults, namely

$$f(A(t)) := \frac{\alpha}{1 + \delta A(t)},$$

where $\alpha > 0$ and $\delta > 0$ are parameters that will be determined later on.

The full model combining both the parasite destruction and the vital dynamic of the population of tree is the following

$$\begin{cases} \partial_t u(t, s) + f(A(t)) \partial_s u(t, s) = - \left[\mu(s) + \frac{\gamma(s) I(t)}{1 + \kappa A(t)} \right] u(t, s), \text{ for } s \geq s_-, t \geq 0, \\ f(A(t)) u(t, s_-) = \beta A(t), \text{ for } t \geq 0, \\ \frac{dI(t)}{dt} = \frac{\varepsilon \chi}{1 + \kappa A(t)} \int_{s_-}^{+\infty} \gamma(s) u(t, s) ds I(t) - \mu_I I(t), \text{ for } t \geq 0, \end{cases} \quad (5.3)$$

with the initial distributions

$$u(0, \cdot) = u_0(\cdot) \in L^1_+(0, +\infty); \quad I(0) = I_0 \geq 0.$$

In system (5.3) $\mu(s) > 0$ is the mortality of trees of size s and $\gamma(s) \geq 0$ is the number of trees of size s consumed per nematode per unit time. We assume for simplicity that

$$\mu(s) = \begin{cases} \mu_A > 0, & \text{if } s \geq s^*, \\ \mu_J > 0, & \text{if } s < s^*, \end{cases} \quad \gamma(s) = \begin{cases} \gamma_A \geq 0, & \text{if } s \geq s^*, \\ \gamma_J \geq 0, & \text{if } s < s^*. \end{cases}$$

As is described in Appendix D (see also in Chapter 2 and [193, 194]), we can transform system (5.3) into the following state-dependent delay differential

equations

$$\left\{ \begin{array}{l} \frac{dA(t)}{dt} = f(A(t)) \frac{\beta A(t - \tau(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t) - \gamma_J \int_{t-\tau(t)}^t \frac{I(l)}{1 + \kappa A(l)} dl} - \mu_A A(t) - \frac{\gamma_A I(t) A(t)}{1 + \kappa A(t)}, \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_-, \\ \frac{dI(t)}{dt} = \left[\frac{\varepsilon \chi}{1 + \kappa A(t)} (\gamma_A A(t) + \gamma_J J(t)) - \mu_I \right] I(t), \end{array} \right. \quad (5.4)$$

with the initial distributions

$$A(t) = A_0(t) \geq 0, \forall t \in (-\infty, 0]; \quad \tau(0) = \tau_0 \geq 0; \quad I(0) = I_0 \geq 0.$$

In system (5.4), the function $\tau(t)$ describes the time needed by a tree to grow to the maturity size s^* at time t from the minimal size s_- , namely $\tau(t)$ is the time needed for a tree to become mature at time t . A detailed explanation will also be found in Appendix D.

In the following we will assume for simplicity that $\gamma_A > 0$ and $\gamma_J = 0$. Therefore in this article we consider the following model

$$\left\{ \begin{array}{l} \frac{dA(t)}{dt} = f(A(t)) \frac{\beta A(t - \tau(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t)} - \mu_A A(t) - \frac{\gamma_A I(t) A(t)}{1 + \kappa A(t)}, \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_-, \\ \frac{dI(t)}{dt} = \left(\frac{\varepsilon \chi \gamma_A A(t)}{1 + \kappa A(t)} - \mu_I \right) I(t) \end{array} \right. \quad (5.5)$$

with the initial distributions

$$A(t) = A_0(t) \geq 0, \forall t \in (-\infty, 0]; \quad \tau(0) = \tau_0 \geq 0; \quad I(0) = I_0 \geq 0.$$

The first basic fact about system (5.5) is that when $I_0 = 0$ then

$$I(t) = 0, \forall t \geq 0.$$

Therefore $I_0 = 0$ corresponds to the model without parasite, namely equation (2.5).

One can also prove that (see in Chapter 3, Remark 3.10) when $\tau_0 = 0$ then

$$\tau(t) = 0, \forall t \geq 0.$$

This means that when $\tau_0 = 0$, the system (5.5) becomes (5.1).

The goal of this article is to investigate the influence of introducing nematode into a pine tree forest population. This can be regarded as a predator-prey

system where the prey has (possibly) a complex dynamics describing a state-dependent delay differential equations. We will investigate some scenarios of the tree population and add the parasite into such a population.

This chapter is organized as follows. In section 2 we compute the positive interior equilibrium. In section 3, we will conduct the numerical simulations of system (5.5). We will start by reviewing some "classical" results about the predator-prey model in ODE case (5.1). Then we will conduct some simulations of system (5.5) in several cases and scenarios (see Table 1). We conclude the paper by discussing the numerical results to see what influence the maturation delay and the introduction of nematodes bring to the solutions.

5.2 Positive interior equilibrium

The system (5.5) has a unique interior equilibrium

$$\bar{A} := \frac{\mu_I}{\varepsilon\chi\gamma_A - \mu_I\kappa}, \bar{\tau} := \frac{s^* - s_-}{f(\bar{A})} \text{ and } \bar{I} := (\beta e^{-\mu_J\bar{\tau}} - \mu_A) \frac{1 + \kappa\bar{A}}{\gamma_A}.$$

Therefore system (1.5) will have a unique positive interior equilibrium if and only if

$$\varepsilon\chi\gamma_A - \mu_I\kappa > 0 \text{ and } \beta e^{-\mu_J\bar{\tau}} - \mu_A > 0. \quad (5.6)$$

In particular if we assume that $\bar{\tau} = 0$ (i.e. $s^* - s_- = 0$), we obtain a unique positive interior equilibrium for system (5.1) if and only if

$$\varepsilon\chi\gamma_A - \mu_I\kappa > 0 \text{ and } \beta - \mu_A > 0. \quad (5.7)$$

Remark 5.1. *Even though we don't know how to investigate analytically the uniform persistence for system (5.5), we strongly suspect that the parasite will persist if and only if the condition (5.6) is satisfied. Therefore one may compare conditions (5.6) and (5.7) to see the effect of the vital dynamic of the tree population on the persistence of parasite.*

5.3 Numerical simulations

In this section we will conduct numerical simulations of system (5.5). According to the analysis in Chapter 2, we have two scenarios of population dynamics of adult trees population $A(t)$ without nematodes (namely when $I_0 = 0$): a steady solution (Scenario 1), a damped oscillating solution (Scenario 2). And by changing one parameter μ_J in Scenario 1, we will get a third scenario: a periodic solution (Scenario 3). We list all the parameters used in the numerical simulations for the three scenarios in Table 1 and calculate the positive interior equilibrium in Table 2.

Parameter	Holling's type I functional response			Holling's type II functional response		
	Scenario 1	Scenario 2	Scenario 3	Scenario 1	Scenario 2	Scenario 3
μ_J	0.03	0.031	0.0036	0.03	0.031	0.03
μ_A	0.001	0.0037	0.001	0.001	0.0037	0.06
β	2	4	2	2	4	2
δ	0.1	0.1	0.1	0.1	0.1	0.1
α	0.1709	0.249	0.1709	0.1709	0.249	0.1709
τ_0	121	127	121	121	127	121
s_-	0	0	0	0	0	0
s^*	0.5318	0.4164	0.5318	0.5318	0.4164	0.5318
γ_A	0.001	0.001	0.001	0.001	0.001	0.001
κ	0	0	0	0.0001	0.0001	0.0001
ε	1	1	1	0.68/1/10	0.68/1/10	0.68/1/10
χ	0.1	0.1	0.1	0.1	0.1	0.1
μ_I	0.05	0.05	0.05	0.05	0.05	0.05

Table 1: We show in this table the parameter values used in the numerical simulations of system (5.5). The first six parameter values come from Chapter 2 Table 1-3. We set $s_- = 0$ for simplicity and we use the formula $\int_{-\tau_0}^0 f(A(s))ds = s^* - s_-$ to calculate s^* . Notice also that with Holling's type II functional response, we will investigate three cases regarding different values of the conversion efficiency $\varepsilon = 0.68$, $\varepsilon = 1$ and $\varepsilon = 10$ for each scenario. Scenario 1-3 correspond to three different dynamics of adult tree population. This will serve to investigate the effect of the introduction of nematodes depending on the type of dynamics of adult tree population.

Equilibrium	Holling's type I functional response		
	Scenario 1	Scenario 2	Scenario 3
\bar{A}	500	500	500
$\bar{\tau}$	158.6998	85.2867	158.6998
\bar{I}	16.1142	280.6375	1128.56

Equilibrium	Holling's type II functional response, Scenario 1		
	$\varepsilon = 0.68$	$\varepsilon = 1$	$\varepsilon = 10$
\bar{A}	793.6508	526.3158	50.2513
$\bar{\tau}$	250.0769	166.8887	18.7488
\bar{I}	0.1118	13.0384	1144.3

Table 2: This table gives the values of positive interior equilibria of system (5.5) with the parameter values given in Table 1 for Scenario 1-3 with Holling's type I functional response and for Scenario 1 with Holling's type II functional response.

5.3.1 Model without maturation period - case $\tau = 0$

In this subsection we will review some results about the classical predator-prey ODE system (5.1).

Holling's type I functional response - case $\kappa = 0$

Set $\kappa = 0$, then system (5.1) becomes the classical Lotka-Volterra model

$$\begin{cases} \frac{dA(t)}{dt} = (\beta - \mu_A)A(t) - \gamma_A I(t)A(t), \\ \frac{dI(t)}{dt} = (\varepsilon\chi\gamma_A A(t) - \mu_I)I(t). \end{cases} \quad (5.8)$$

We use the parameter values of Scenario 1 with Holling's type I functional response in Table 1 for the numerical simulations in Figure 5.1.

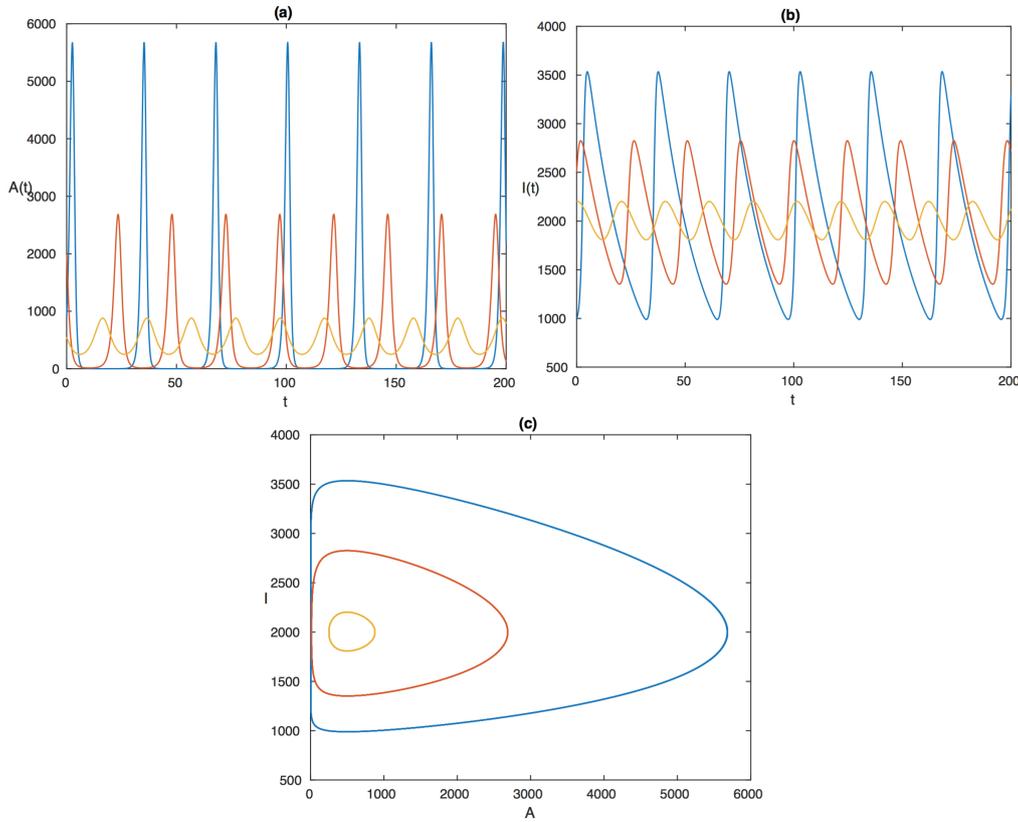


Figure 5.1: We plot the simulation of system (5.8) with parameters of Scenario 1 with Holling's type I functional response in Table 1: $\beta = 2$, $\mu_A = 0.001$, $\gamma_A = 0.001$, $\varepsilon = 1$, $\chi = 0.1$, $\mu_I = 0.05$. The initial values (A_0, I_0) are $(550, 2200)$ (yellow curve), $(2000, 2500)$ (orange curve) and $(901.3603, 1000)$ (blue curve). Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the trajectory on the phase plane. The positive interior equilibrium is $(500, 1999)$.

For the parameter values of the other two scenarios with Holling's type

I functional response, the behaviours are similar (periodic solutions) and we omit those figures here.

Holling's type II functional response - case $\kappa > 0$

We use the parameter values of Scenario 2 with Holling's type II functional response in Table 1 for the numerical simulations of system (5.1) and we get the following trajectory spiraling around the positive interior equilibrium on the phase plane.

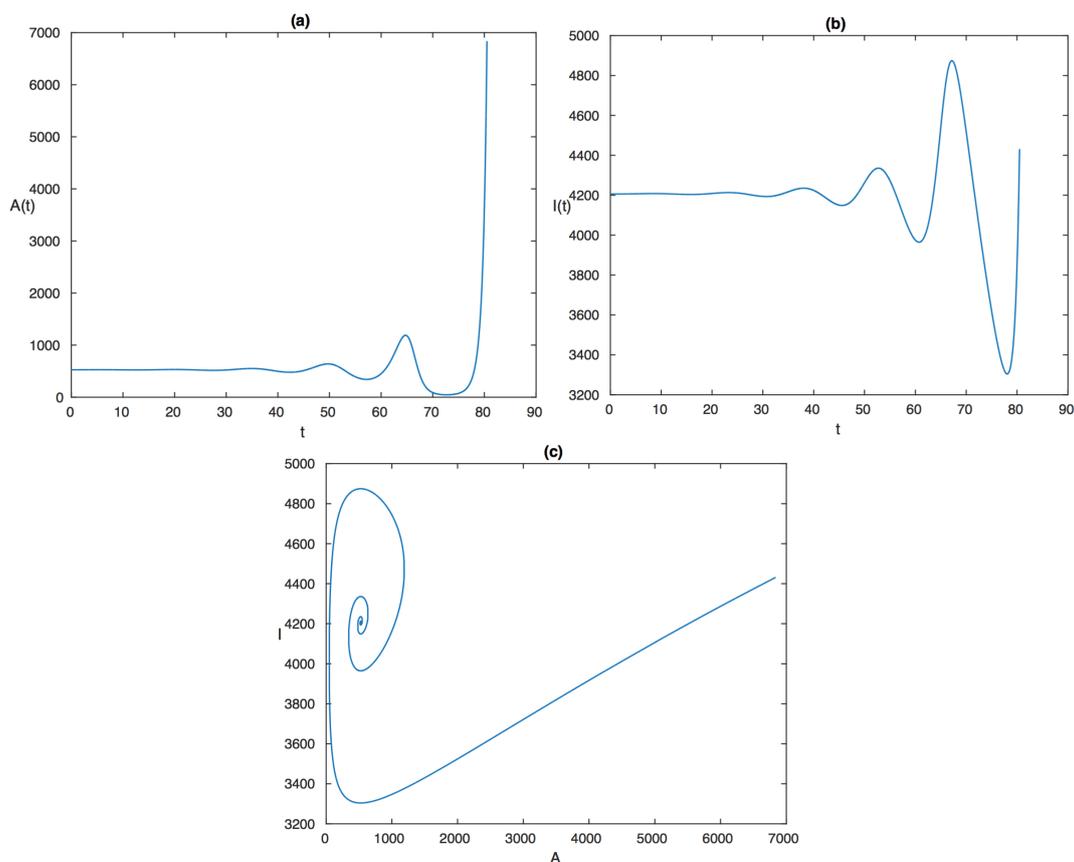


Figure 5.2: We plot the simulation of system (5.1) with parameters of Scenario 2 with Holling's type II functional response in Table 1: $\beta = 4$, $\mu_A = 0.0037$, $\gamma_A = 0.001$, $\varepsilon = 1$, $\chi = 0.1$, $\mu_I = 0.05$, $\kappa = 0.0001$. The initial values are $A_0 = 526$, $I_0 = 4206$. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the trajectory on the phase plane. A simple calculation shows that the positive interior equilibrium is $(526.3158, 4206.6)$.

We can see from Figure 5.2 that after spiraling around the positive equilibrium, the solutions follow a line and blow up when the time t goes to infinity.

For the remaining sets of parameters corresponding to the other two scenarios in Table 1, similar behaviours happen.

5.3.2 Simulation with maturation period - case $\tau > 0$

In this section we conduct numerical simulations of the system (5.5) with parameter values given in Table 1.

Holling's type I functional response - case $\kappa = 0$

We set $\kappa = 0$ in this part to see the behaviours of the system (5.5) with the Holling's type I functional response.

Scenario 1 (no oscillations): In this part, the parameters of the system are chosen such that in absence of parasite (i.e. when $I_0 = 0$), the number of adult trees $A(t)$ has no oscillations around the positive equilibrium \bar{A} (see Figure 5.3).

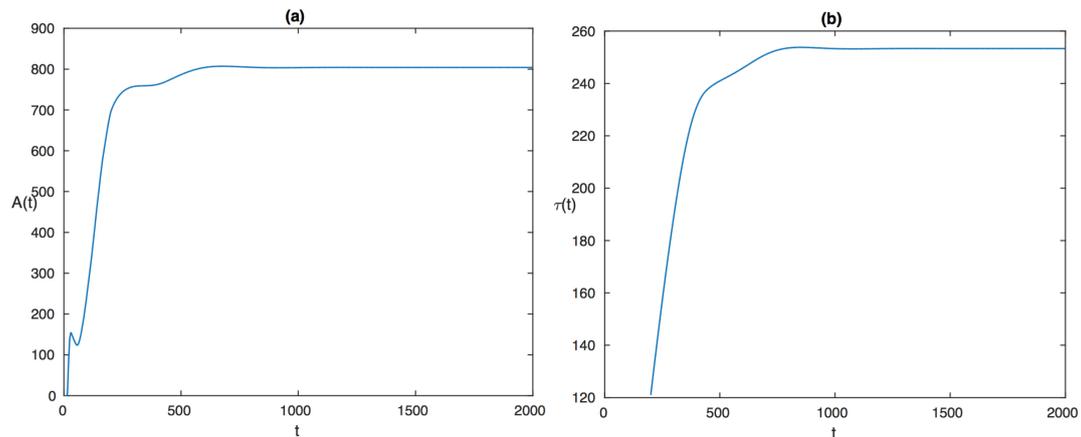


Figure 5.3: We plot the simulation of forest model (5.5) with parameters of Scenario 1 with Holling's type I functional response in Table 1: $\mu_A = 0.001$, $\mu_J = 0.03$, $\beta = 2$, $\delta = 0.1$, $\gamma_A = 0.001$, $\kappa = 0$, $\varepsilon = 1$, $\chi = 0.1$, $\mu_I = 0.05$. We take the distribution of $A(t)$ on the time interval $[0, 200]$ (which comes from the data in Chapter 2) and $\tau_0 = 121$ as the initial distribution and at the time $t = 200$ we introduce the nematodes with the initial value $I_0 = 0$. Figure (a) shows the adult tree population number $A(t)$ and Figure (b) shows the corresponding time delay $\tau(t)$.

Now we introduce the nematodes, namely we set $I_0 = 1000$, and we have the following figures.

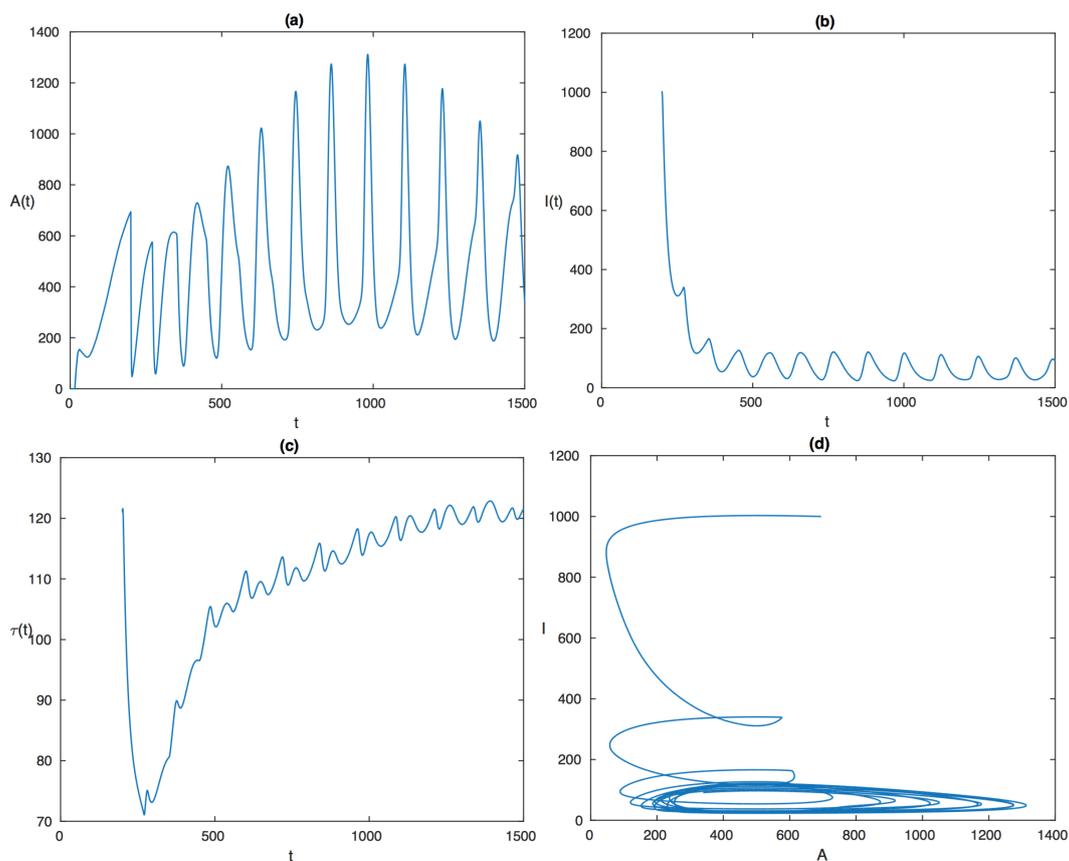


Figure 5.4: We plot the simulation of the system (5.5) for Scenario 1 with Holling's type I functional response in this figure. The parameters and the initial distributions are the same as in Figure 5.3 except that at the time $t = 200$ we introduce the nematodes with the initial value $I_0 = 1000$. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the corresponding time delay $\tau(t)$ and Figure (d) shows the behaviour on the phase plane.

We find that after the introduction of nematodes, the steady solution $A(t)$ becomes oscillated with a varying amplitude and the maturation period $\tau(t)$ of trees is decreased. But after conducting a longtime simulation, we see that the amplitude of $A(t)$ is gradually stabilized and the trajectory converges to what seems to be a limit cycle (see Figure 5.5). This seems to be related to the periodic solution of the Lotka-Volterra model. Moreover, the maximal value of $A(t)$ is also increased after we introduce the nematodes. However, compared with the Lotka-Volterra model (the blue curve in Figure 5.1), the amplitudes of oscillations of both $A(t)$ and $I(t)$ are reduced here.

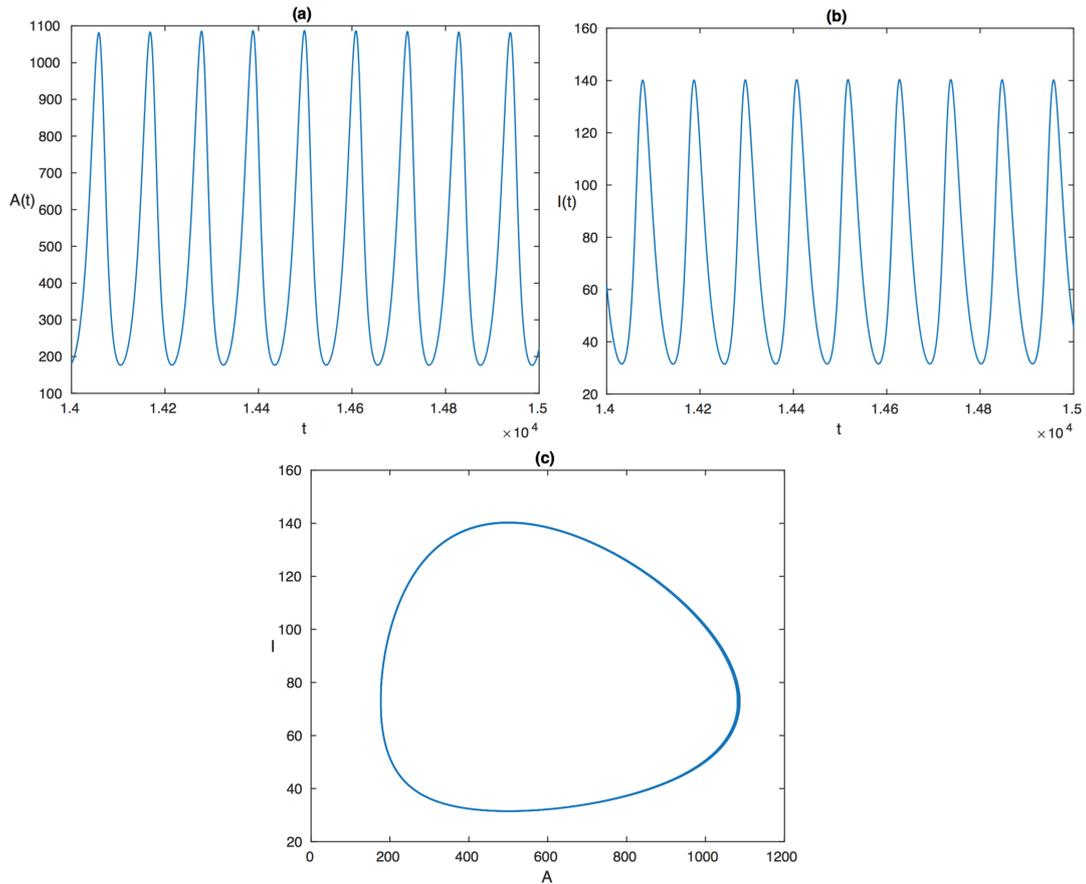


Figure 5.5: We plot the longtime behaviour of the simulation in Figure 5.4 in the time interval $[14000, 15000]$. The parameters and the initial distribution are the same as in Figure 5.4. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the trajectory on the phase plane.

Scenario 2 (damped oscillations): In this part, the parameters of the system are chosen such that in absence of parasite (i.e. when $I_0 = 0$), the number of adult trees $A(t)$ has some damped oscillations around the positive equilibrium \bar{A} (see Figure 5.6).

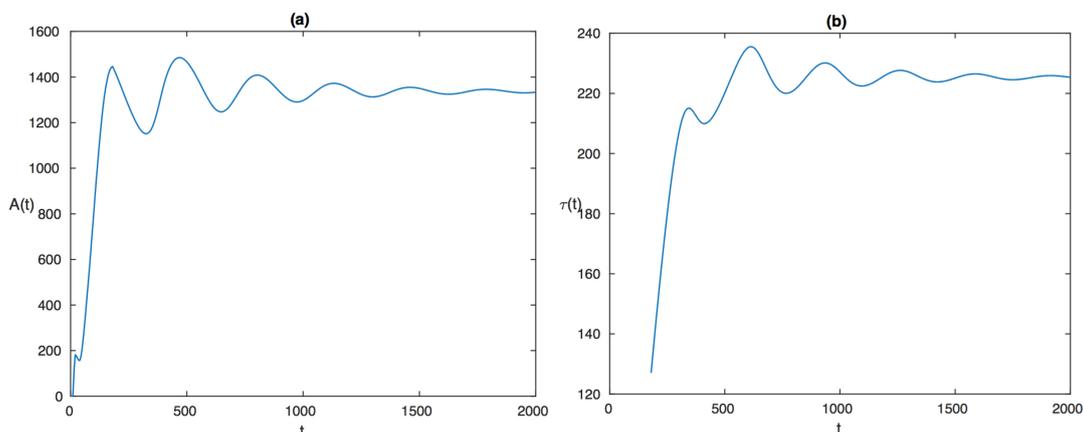


Figure 5.6: We plot the simulation of forest model (5.5) with parameters of Scenario 2 with Holling's type I functional response in Table 1: $\mu_A = 0.0037$, $\mu_J = 0.031$, $\beta = 4$, $\delta = 0.1$, $\gamma_A = 0.001$, $\kappa = 0$, $\varepsilon = 1$, $\chi = 0.1$, $\mu_I = 0.05$. We take the distribution of $A(t)$ on the time interval $[0, 180]$ (which comes from the data in Chapter 2) and $\tau_0 = 127$ as the initial distribution and at the time $t = 180$ we introduce the nematodes with the initial value $I_0 = 0$. Figure (a) shows the adult tree population number $A(t)$ and Figure (b) shows the corresponding time delay $\tau(t)$.

Now if we introduce the nematodes and fix $I_0 = 1000$, we obtain Figure 5.7. We can see that the damped oscillating solution $A(t)$ becomes undamped and the amplitude is varying more significantly and more rapidly after we introduce the nematodes. However, the maximal value of $A(t)$ is decreased instead and the maturation period $\tau(t)$ of the trees is also decreased. Compared with the Lotka-Volterra model (the blue curve in Figure 5.1), the amplitudes of oscillations of both $A(t)$ and $I(t)$ are also reduced here. On the other hand, compared with Scenario 1, the longtime behaviour is different. The solutions $A(t)$ and $I(t)$ are still oscillating but they exhibit some kind of superposition of periodic orbits (see Figure 5.8). The nematode population number $I(t)$ is also increased and the maturation period $\tau(t)$ is decreased compared with Scenario 1.

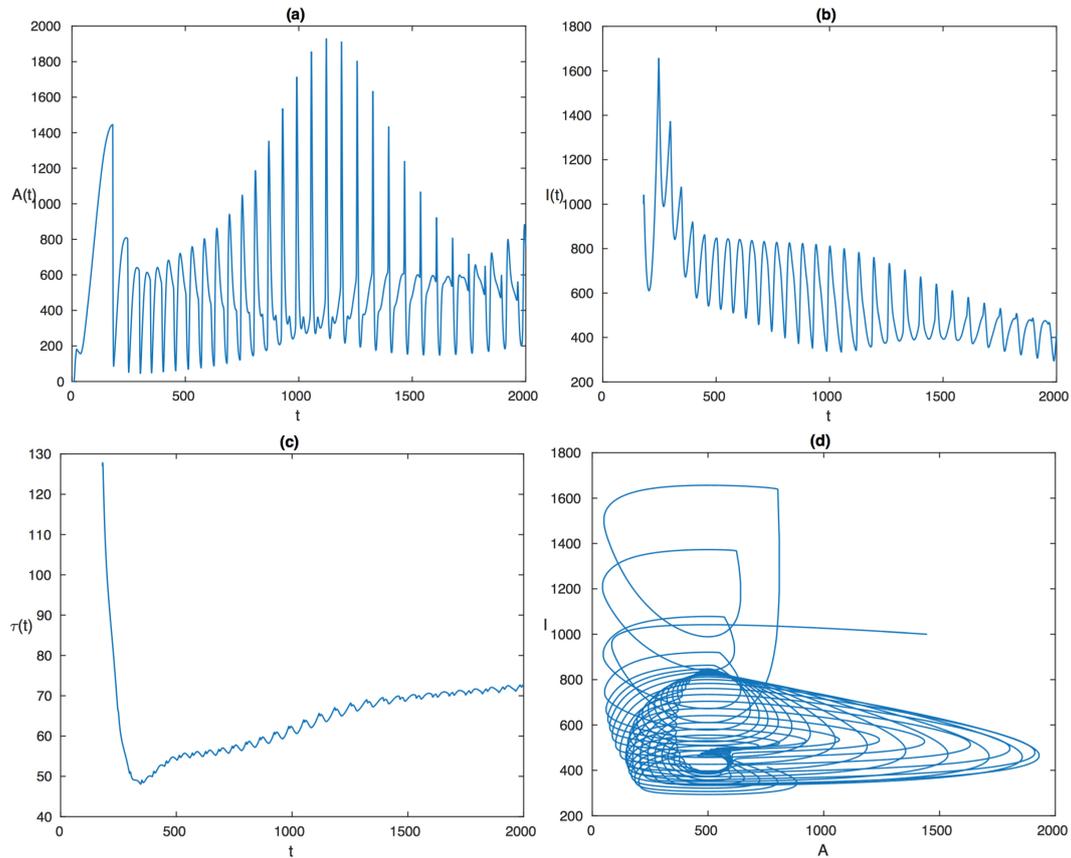


Figure 5.7: We plot the simulation of the system (5.5) for Scenario 2 with Holling's type I functional response in this figure. The parameters and the initial distributions are the same as in Figure 5.6 except that at the time $t = 180$ we introduce the nematodes with the initial value $I_0 = 1000$. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the corresponding time delay $\tau(t)$ and figure (d) shows the behaviour on the phase plane.

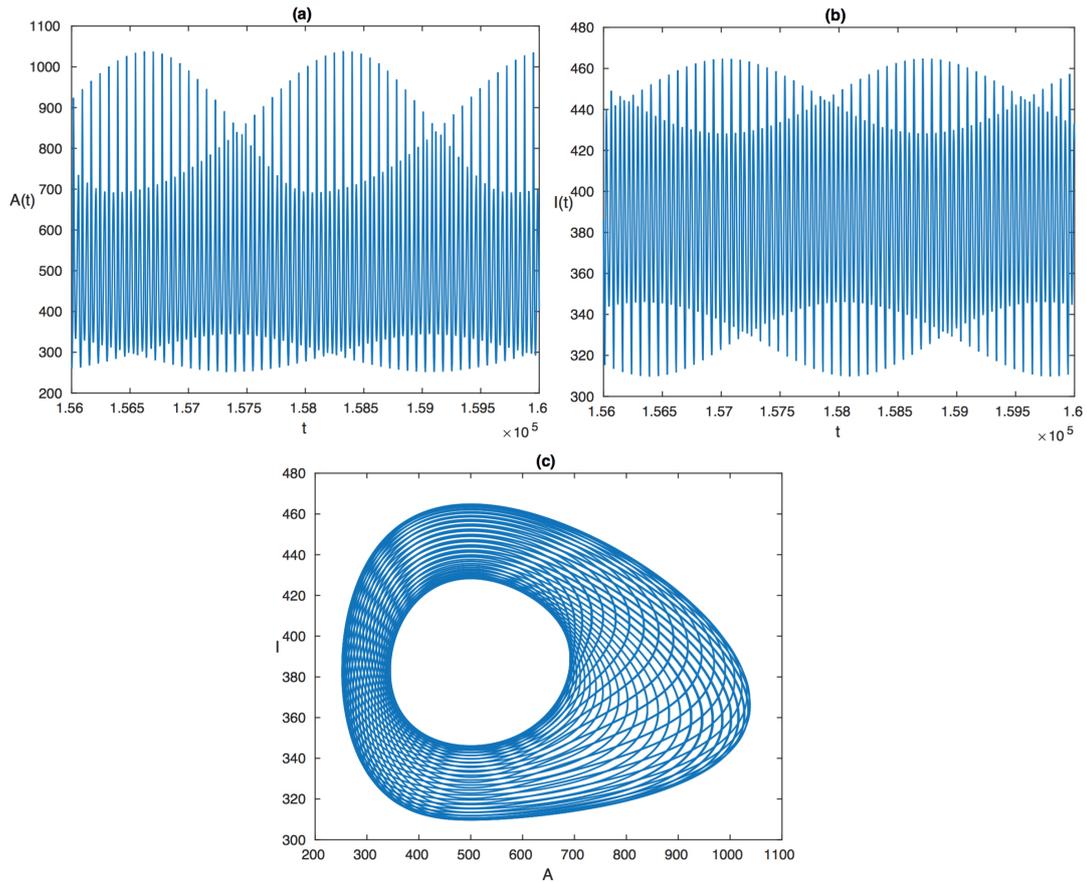


Figure 5.8: We plot the longtime behaviour of the simulation in Figure 5.7 in the time interval $[156000, 160000]$. The parameters and the initial distribution are the same as in Figure 5.7. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the trajectory on the phase plane. The solutions look like some kind of superposition of periodic orbits.

Scenario 3 (undamped oscillations): In Scenario 3, the only change is the parameter μ_J , which passes from 0.03 in Scenario 1 to 0.0036 in Scenario 3. As a consequence, in absence of parasite (i.e. when $I_0 = 0$), the number of adult trees $A(t)$ has some undamped oscillations around the positive equilibrium \bar{A} (see Figure 5.9).

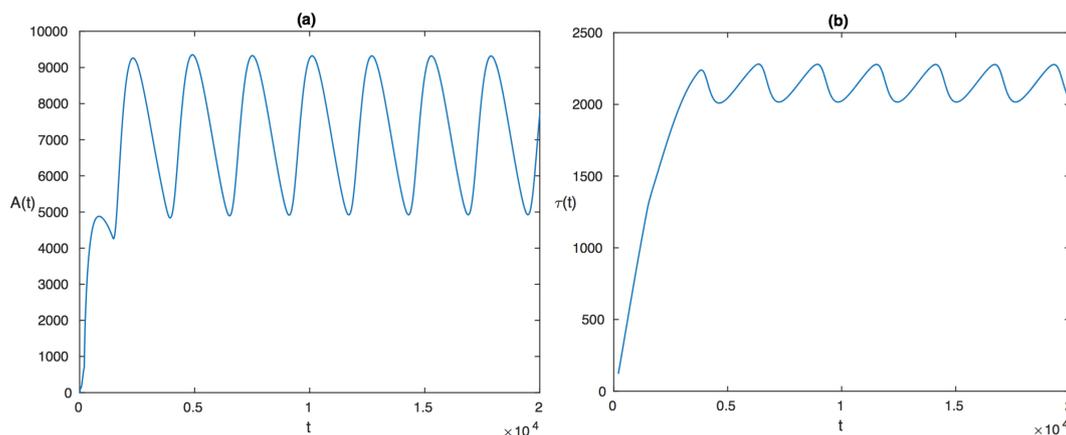


Figure 5.9: We plot the simulation of forest model (5.5) with parameters of Scenario 3 with Holling's type I functional response in Table 1: $\mu_A = 0.001$, $\mu_J = 0.0036$, $\beta = 2$, $\delta = 0.1$, $\gamma_A = 0.001$, $\kappa = 0$, $\varepsilon = 1$, $\chi = 0.1$, $\mu_I = 0.05$. We take the distribution of $A(t)$ on the time interval $[0, 200]$ (which comes from the data in Chapter 2) and $\tau_0 = 121$ as the initial distribution and at the time $t = 200$ we introduce the nematodes with the initial value $I_0 = 0$. Figure (a) shows the adult tree population number $A(t)$ and Figure (b) shows the corresponding time delay $\tau(t)$.

Now we set $I_0 = 1000$, and we have the following figures. We can see that after we introduce the nematodes, the periodic solution of $A(t)$ is no longer periodic but with complex oscillations around the positive equilibrium (500, 1128.56) (see Figure 5.11 for a detailed view). Compared with the Lotka-Volterra model (the blue curve in Figure 5.1), the range of oscillations of both $A(t)$ and $I(t)$ is also reduced, as the previous two scenarios do. Compared with the previous two scenarios, the range of the oscillation of $A(t)$ is reduced, while the number of nematodes $I(t)$ is largely increased. The maturation delay of the tree population is also increased, which might be the consequence of the large quantity of nematodes slowing down the growth of trees.

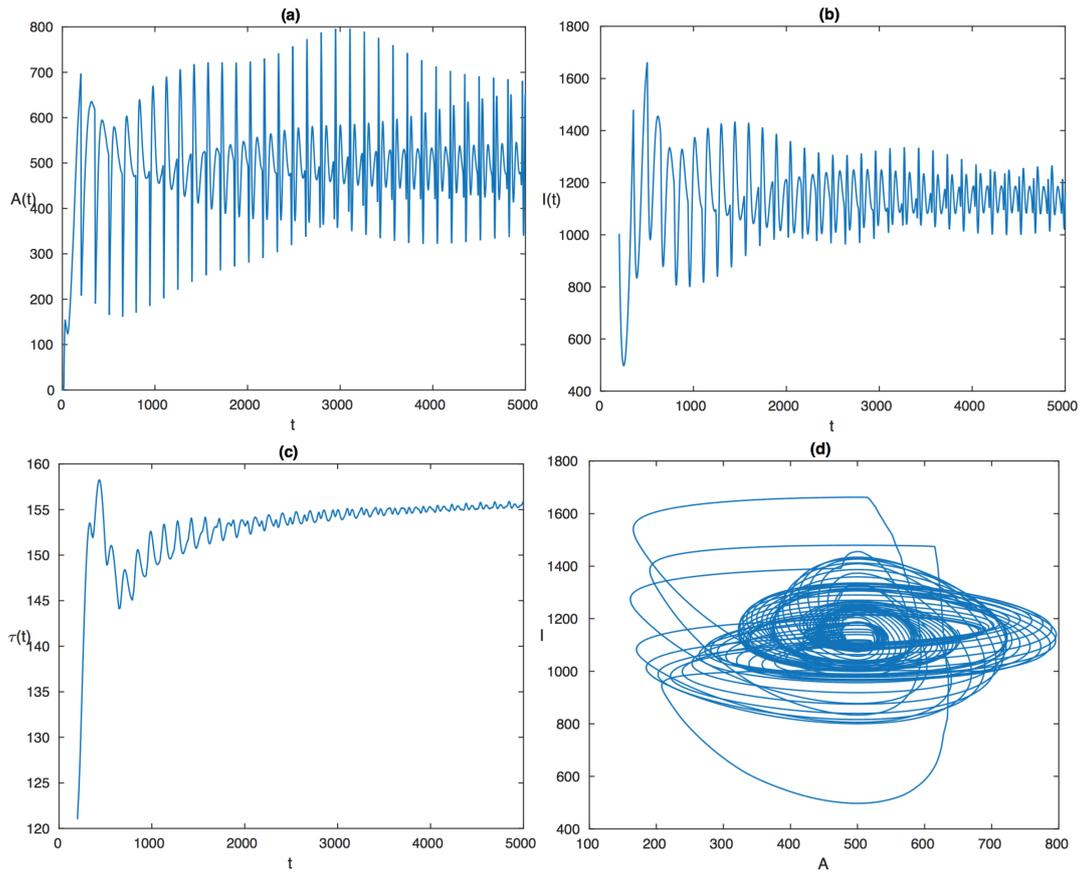


Figure 5.10: We plot the simulation of the system (5.5) for Scenario 3 in this figure. The parameters and the initial distributions are the same as in Figure 5.9 except that at the time $t = 200$ we introduce the nematodes with the initial value $I_0 = 1000$. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the corresponding time delay $\tau(t)$ and Figure (d) shows the behaviour on the phase plane.

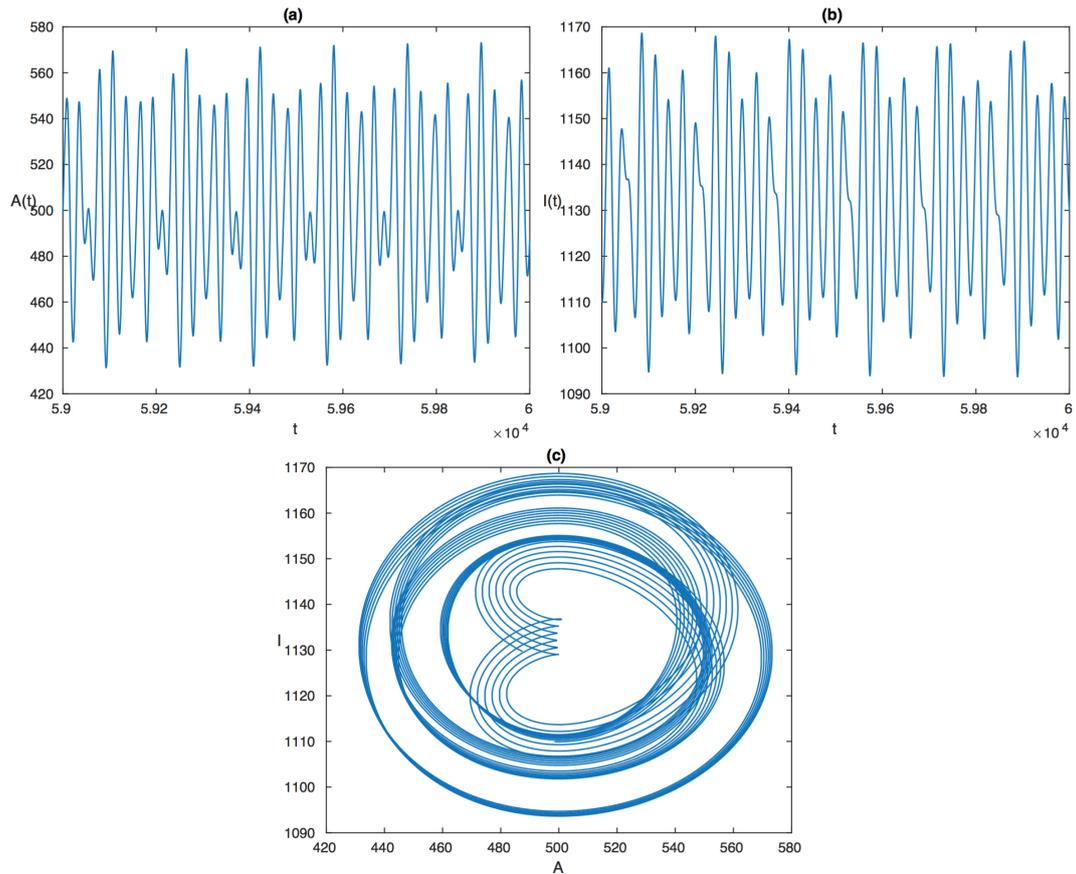


Figure 5.11: We plot the longtime behaviour of the simulation in Figure 5.10 in the time interval $[19000, 20000]$. The parameters and the initial distribution are the same as in Figure 5.10. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. The solutions oscillate around the positive equilibrium $(500, 1128.56)$.

Holling’s type II functional response - case $\kappa > 0$

Now we turn to the Holling’s type II functional response. We will set $\kappa = 0.0001$ in this part.

We start with the numerical simulation of Scenario 1. When $I_0 = 0$, this will be the same result as in Figure 5.3, namely the forest model without nematode will have no oscillations. Now we set $I_0 = 1000$ and $\varepsilon = 0.68$, and we get the following results.

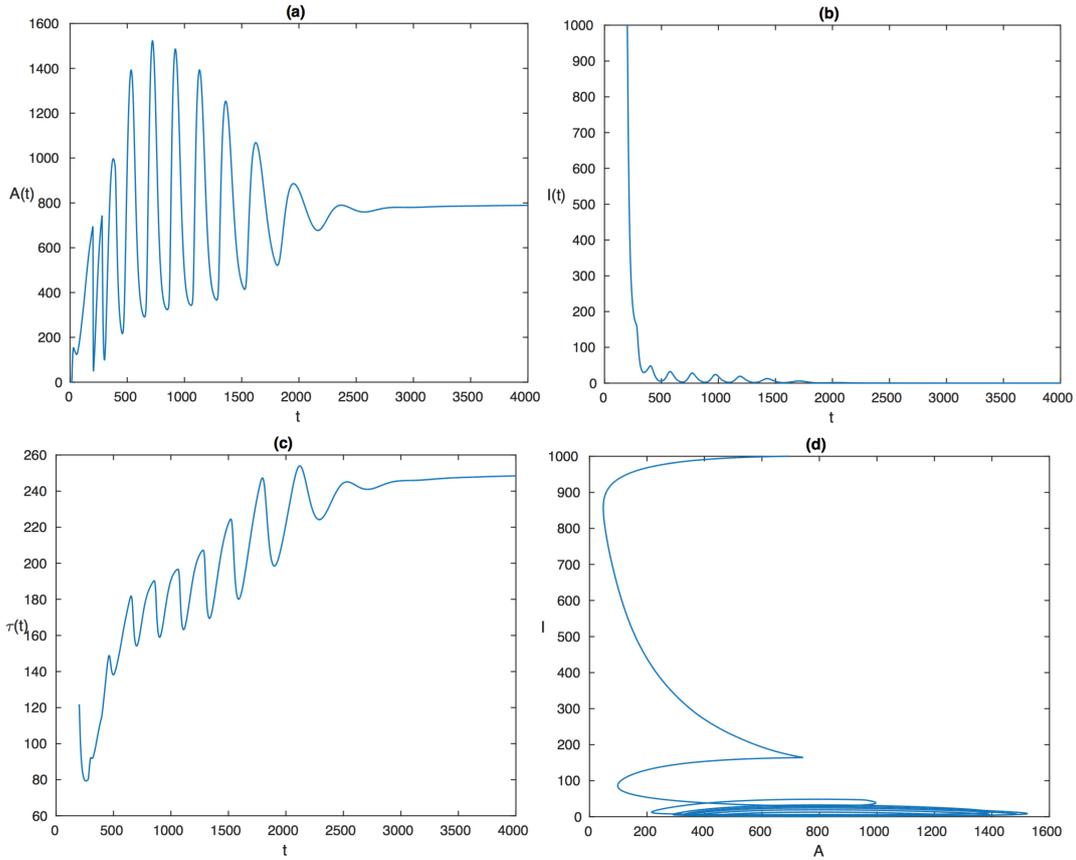


Figure 5.12: We plot the simulation of the system (5.5) with parameters of Scenario 1 with Holling’s type II functional response in Table 1: $\mu_A = 0.001$, $\mu_J = 0.03$, $\beta = 2$, $\delta = 0.1$, $\gamma_A = 0.001$, $\kappa = 0.0001$, $\varepsilon = 0.68$, $\chi = 0.1$, $\mu_I = 0.05$. We take the distribution of $A(t)$ on the time interval $[0, 200]$ and $\tau_0 = 121$ as the initial distribution and at the time $t = 200$ we introduce the nematodes with the initial value $I_0 = 1000$. Figure (a) and (b) show the adult tree population number $A(t)$ and the nematode population number $I(t)$ respectively. Figure (c) shows the corresponding time delay $\tau(t)$ and Figure (d) shows the behaviour on the phase plane. The solutions $A(t)$ and $I(t)$ converge to the positive interior equilibrium $(793.6508, 0.1118)$ (calculated in Table 2).

5. Forest and parasite model

We can see that after the introduction of nematodes, the solution $A(t)$ is oscillating and both solutions $A(t)$ and $I(t)$ converge to the positive interior equilibrium $(793.6508, 0.1118)$, and as the equilibrium of $I(t)$ is very small (0.1118), the longtime behaviour is actually still similar to the system without nematode, namely Figure 5.3. This is probably due to the small value of the conversion efficiency ε and thus the biomass transformed from trees to nematodes is rather little, which is a disadvantage for the nematodes to persist in a large quantity. Something else happens if we set ε larger.

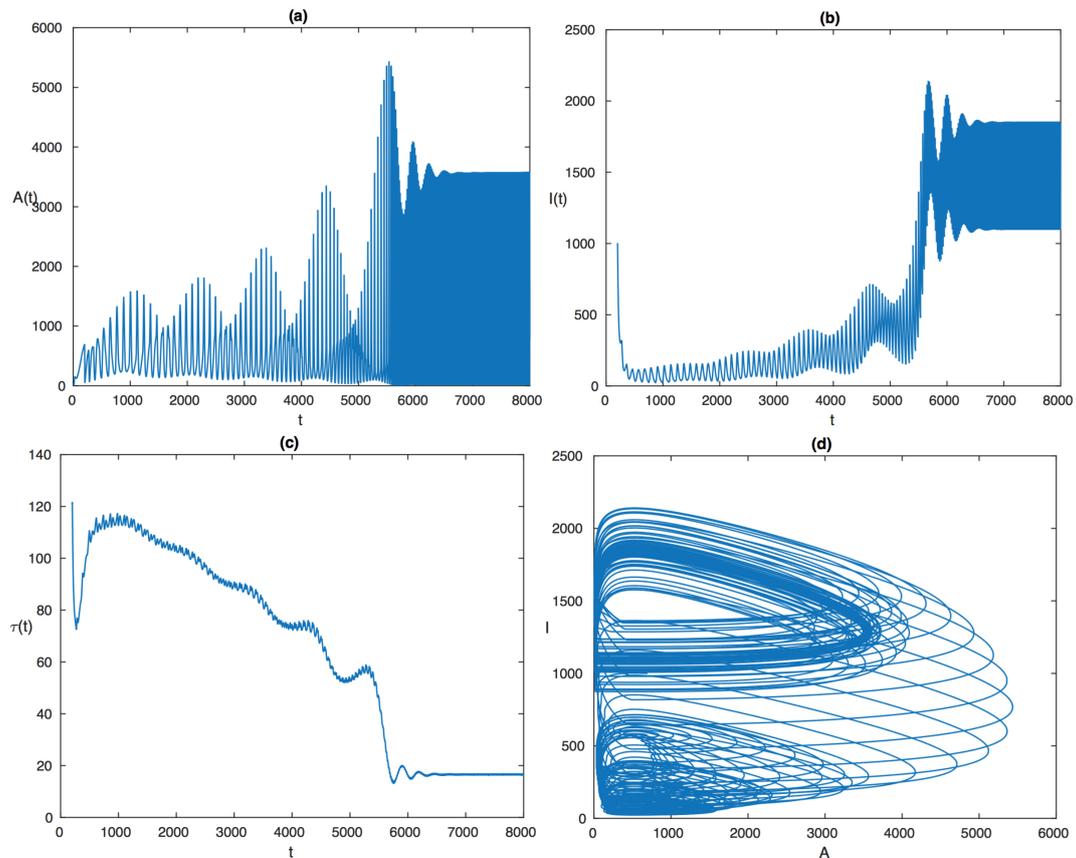


Figure 5.13: We plot the simulation of the system (5.5) for Scenario 1 with Holling's type II functional response in this figure. The parameters and initial distributions and the meaning of each figure are the same as in Figure 5.12 except that $\varepsilon = 1$. We get oscillating solutions.

With the increase of the conversion efficiency $\varepsilon = 1$, which creates some benefits for the nematode at some level, we get the uniform persistence for both solutions $A(t)$ and $I(t)$, and both solutions exhibit largely perturbed oscillations and the amplitude is largely varying at the beginning and then become stable (actually a long time simulation shows that the "stable" ampli-

tude is still increasing very slowly). This also shows that the positive equilibrium (526.3158, 13.0384) (calculated in Table 2) is not stable. Moreover, the maximal value of $A(t)$ is increased and the maturation period $\tau(t)$ of trees is decreased compared with both the case $\varepsilon = 0.68$ (Figure 5.12) and the case $I_0 = 0$ (Figure 5.3).

We increase ε again to see what happens next.

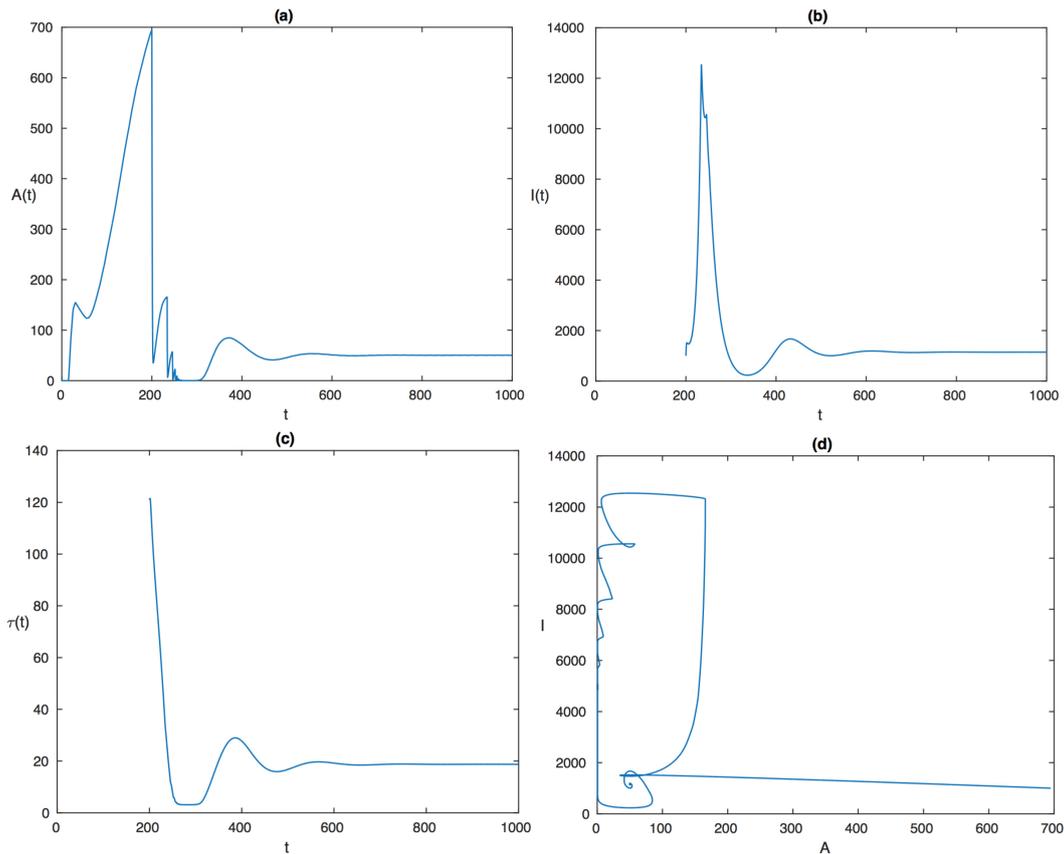


Figure 5.14: We plot the simulation of the system (5.5) for Scenario 1 with Holling's type II functional response in this figure. The parameters and initial distributions and the meaning of each figure are the same as in Figure 5.12 except that $\varepsilon = 10$. We get slightly oscillating solutions.

When we set $\varepsilon = 10$, no complex oscillations are occurring as in the case $\varepsilon = 1$. The nematode population $I(t)$ reaches a large quantity quickly after it is introduced, due to the high conversion efficiency, and thus the tree population is decreased quickly. After this the tree population oscillates to almost an extinction state but they persist again. This is possibly because the decrease of the tree population leads to the decrease of the nematode population, which creates again a favorable environment for the trees to survive. The solutions

both persist in the end and are continuously oscillating with small amplitudes (see Figure 5.15).

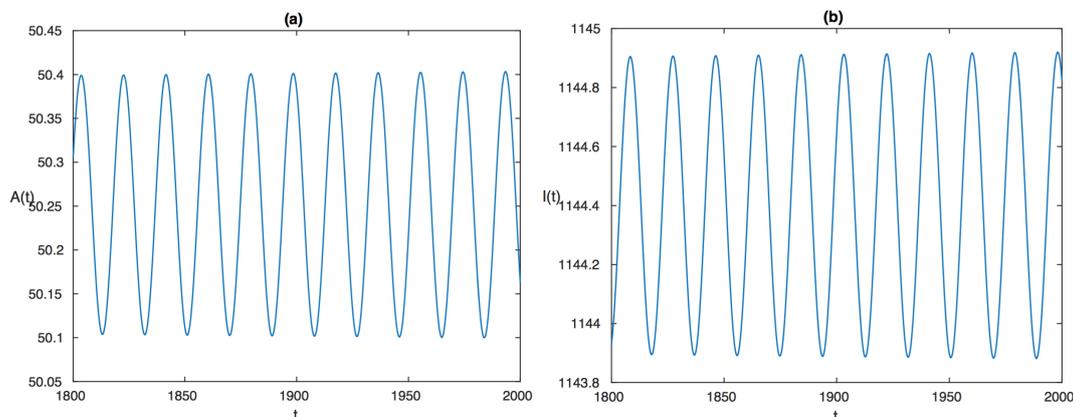


Figure 5.15: We plot the simulation of the solution $A(t)$ and $I(t)$ in Figure 5.14 in the time interval $[1800, 2000]$ in this figure. The solutions are oscillating with small amplitude.

Remark 5.2. We have run some simulations for the other two scenarios with different values of ε and we find that the system exhibits similar behaviors than Scenario 1. We have also run some simulations for the system with Holling's type III functional response, namely the following system

$$\begin{cases} \frac{dA(t)}{dt} = f(A(t)) \frac{\beta A(t - \tau(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t)} - \mu_A A(t) - \frac{\gamma_A I(t) A^2(t)}{1 + \kappa A^2(t)}, \\ \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_-, \\ \frac{dI(t)}{dt} = \left(\frac{\varepsilon \chi \gamma_A A^2(t)}{1 + \kappa A^2(t)} - \mu_I \right) I(t). \end{cases}$$

We also have similar simulations as in the case of Holling's type II functional response.

5.4 Discussion

Predator and prey systems, or more generally, consumer and resource, is playing a fundamental role in ecology. Different mechanisms between predator and prey will lead to different models with different functional responses [1, 175]. In this paper, we build a predator-prey model with Holling's type I and II functional response and with a state-dependent maturation delay for the prey population. This is based on a forest model, which is constructed in [138]

and in general leads to three scenarios of forest population dynamics (no oscillations, damped oscillations, undamped oscillations), and we incorporate the nematode population into this forest model.

We conduct numerical simulations for the three scenarios and two types of functional responses. First, with Holling's type I functional response, after we introduce a non-null state-dependent delay to describe the maturation period of the tree population, the solutions start with complex oscillations and then become regular, that is to say, the solutions converge to a limit cycle again in Scenario 1 and undergoes some superposition of two oscillations in Scenario 2 and 3. Moreover, for all the three scenarios, the two solutions still persist, only with a reduced amplitude of oscillations compared with the corresponding system without the maturation delay (system (5.8)).

With Holling's type II functional response, the system is perturbed vastly after the introduction of the maturation delay, and the previous unbounded solution becomes bounded. But this also depends on the rate of conversion efficiency of the energy from prey to predator. When this rate is too low, the predator can't persist, and thus the system has similar behaviours as when there is no predator. If this rate of conversion efficiency is rather high, the system risks of going to extinction for both predator and prey but it adapts itself to a persisting state again.

Now, from another point of view, after we introduce the nematodes into the forest, no matter which type of functional response it is, we see that the solution $A(t)$ which doesn't oscillate before (Scenario 1) starts to oscillate, and which has oscillations (damped or periodic) before (Scenario 2 and 3) undergoes undamped oscillation after the introduction of nematodes.

We might also notice that after the introduction of nematodes, the maturation delay $\tau(t)$ is also reduced for all three scenarios and two types of functional responses. That is because with the introduction of nematodes $I(t)$, the adult tree population number $A(t)$ is affected, then by the second equation of system (5.5), which is used to solve $\tau(t)$, this maturation delay will also be affected. Moreover, we need to point out that the unit of the solution $\tau(t)$ is "year". Then there seems to be something unrealistic here in that in some cases, the equilibrium of $\tau(t)$ is more than 100, which means that it needs more than 100 years for a tree to grow mature. Actually, the delay $\tau(t)$ is used to describe the time needed for the trees to grow to be adults, and also, to be able to produce new generations in the middle of a forest. This means that the trees can be affected by the other surrounding trees, then not so many trees can survive to be able to produce an adult tree and thus on average it takes a longer time for them to grow.

Appendix A

Derivation of the state-dependent FDE (2.6)

The single species model (2.1) we consider here is very similar with the one considered by H. Smith in [193]. Nevertheless, our mortality rate $\mu(s)$ is dependent on the size s , so we will re-derive the state dependent FDE for completeness. Differentiating (2.4) with respect to t , we have

$$\begin{aligned}\frac{dA(t)}{dt} &= \int_{s^*}^{+\infty} \partial_t u(t, s) ds = -f(A(t)) \int_{s^*}^{+\infty} \partial_s u(t, s) ds - \int_{s^*}^{+\infty} \mu(s) u(t, s) ds \\ &= f(A(t)) u(t, s^*) - \int_{s^*}^{+\infty} \mu(s) u(t, s) ds.\end{aligned}\tag{A.1}$$

Next we deal with the term $u(t, s^*)$. The characteristic curves for the first equation in (2.1) are (shown in Figure A.1)

$$\frac{ds(t)}{dt} = f(A(t)).\tag{A.2}$$

Then we have the following representation of s

$$C + \int_0^t f(A(\sigma)) d\sigma = s(t).\tag{A.3}$$

Suppose t^* is the time when juveniles present at time 0 become adults, namely

$$\int_0^{t^*} f(A(\sigma)) d\sigma = s^* - s_-.\tag{A.4}$$

We can see that the curve

$$S = \left\{ (t, s) : 0 \leq t \leq t^*, s = s_- + \int_0^t f(A(\sigma)) d\sigma \right\}$$

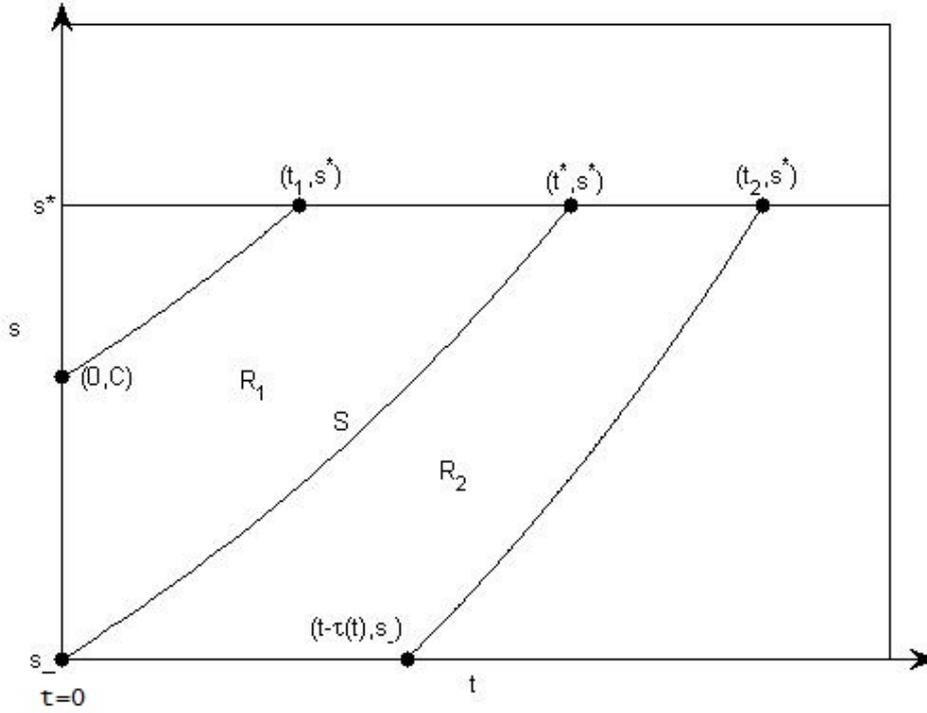


Figure A.1: In this figure we present the characteristic curves (A.2).

divides the strip $[0, +\infty) \times [s_-, s^*]$ into two parts R_1 and R_2 . Assuming that $s - s_- \leq \int_0^t f(A(\sigma))d\sigma$, then we can find $T(t, s) \geq 0$ such that

$$\int_{t-T(t,s)}^t f(A(\sigma))d\sigma = s - s_- \quad (\text{A.5})$$

in the region R_2 , so it denotes the time it takes for a juvenile to grow to size s at time t from the minimal size s_- . Replacing s in $u(t, s)$ with (A.3), we can compute formally as follows, assuming that u is a C^1 -function

$$\begin{aligned} & \frac{d}{dt} u \left(t, C + \int_0^t f(A(\sigma))d\sigma \right) \\ &= \partial_t u \left(t, C + \int_0^t f(A(\sigma))d\sigma \right) + f(A(t)) \partial_s u \left(t, C + \int_0^t f(A(\sigma))d\sigma \right) \\ &= -\mu \left(C + \int_0^t f(A(\sigma))d\sigma \right) u \left(t, C + \int_0^t f(A(\sigma))d\sigma \right). \end{aligned}$$

This is a separable ODE with respect to t . Integration of this equation, and by using the initial distribution and the boundary condition, we obtain the

following expression of $u(t, s)$

$$u(t, s) = \begin{cases} u_0 \left(s - \int_0^t f(A(\sigma)) d\sigma \right) e^{-\int_0^t \mu(s - \int_0^l f(A(\sigma)) d\sigma + \int_0^l f(A(\sigma)) d\sigma) dl}, & \text{if } s \geq s_- + \int_0^t f(A(\sigma)) d\sigma, \\ \frac{\beta b(A(t - T(t, s)))}{f(A(t - T(t, s)))} e^{-\int_{t-T(t, s)}^t \mu(s_- + \int_{t-T(t, s)}^l f(A(\sigma)) d\sigma) dl}, & \text{if } s \leq s_- + \int_0^t f(A(\sigma)) d\sigma. \end{cases} \quad (\text{A.6})$$

Whenever $s^* - s_- \leq \int_0^t f(A(\sigma)) d\sigma$, we can specifically define $\tau(t) := T(t, s^*)$ as the solution of

$$\int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = s^* - s_-. \quad (\text{A.7})$$

Actually the term $\tau(t) = T(t, s^*)$ represents the time spent by a newborn becoming an adult.

We now assume the mortality function as follows

$$\mu(s) = \begin{cases} \mu_A > 0, & \text{if } s \geq s^*, \\ \mu_J > 0, & \text{if } s \in [s_-, s^*]. \end{cases}$$

Then when $s = s^*$, we have for $t \in [0, t^*]$,

$$u(t, s^*) = u_0 \left(s^* - \int_0^t f(A(\sigma)) d\sigma \right) e^{-\mu_J t},$$

and for $t > t^*$,

$$u(t, s^*) = \frac{\beta b(A(t - \tau(t)))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t)}.$$

Replacing $u(t, s^*)$ back in (A.1), we get the model (2.5).

By differentiating the second equation of (2.5) in time, we obtain

$$\frac{d}{dt} \int_{t-\tau(t)}^t f(A(\sigma)) d\sigma = 0 \Leftrightarrow f(A(t)) - f(A(t - \tau(t))) (1 - \tau'(t)) = 0.$$

Therefore the state-dependent delay differential equation (2.6) is derived.

Remark A.1. Note that the function $t \rightarrow t - \tau(t)$ is strictly increasing because

$$\frac{d}{dt} (t - \tau(t)) = \frac{f(A(t))}{f(A(t - \tau(t)))} > 0.$$

Remark A.2. Notice that system (2.5) is valid when $t > t^*$. However, as this system is autonomous, we can make a translation so that the initial time of the system will become $t = 0$. But the numerical simulations are still conducted with the initial time $t = t^*$ for the sake of simplicity.

We conduct a comparison between the growth function (2.2) and the intrinsic function of the growth submodel in the simulator SORTIE. From the model (2.3), we only care about the growth of juveniles, so first we assume the radius function of a juvenile

$$r(t) = \frac{\text{diam}_{10}(t)}{2}$$

where diam_{10} represents the diameter at 10cm height. We use the following change of variable to define the size s which we are using in the model (2.1)

$$s(t) := \ln \frac{r(t)}{r_-}, \quad (\text{A.8})$$

where r_- is the minimal radius of the juvenile. We will have

$$s'(t) = \frac{r'(t)}{r(t)} = f(A(t)).$$

Then the approximation of the derivative of $r(t)$, which describes the growth of the radius, is

$$\frac{r(t + \Delta t) - r(t)}{\Delta t} = r(t) \cdot \frac{\alpha}{1 + \delta A(t)} = r(t) \cdot \frac{\alpha A(t)^{-1}}{\delta + A(t)^{-1}}. \quad (\text{A.9})$$

Take $\Delta t = 1$ (one year), then (A.9) shows the increase of the radius in one year.

On the other hand, we have the following formula for growth in SORTIE from [106, 169, 170]

$$\text{Annual Radius Increase} = \text{Radius} \cdot \frac{G_1 \cdot \text{GLI}}{\frac{G_1}{G_2} + \text{GLI}}, \quad (\text{A.10})$$

where G_1 is the asymptotic growth rate at high light and G_2 is the slope at 0 or low light. The term GLI (global light index) describes the percentage of light transmitted through tree gaps and perceived by trees, thus is a measure for light. Comparing the two formulas (A.9) and A.10, we find that they have the same form, and the parameters $A(t)^{-1}, \alpha, \delta$ correspond to $\text{GLI}, G_1, G_1/G_2$ respectively. So the choice of the growth function (2.2) is reasonable. Plus, this also explains what is size s in our model (2.1). By this definition of $s(t)$, we have the minimal size of juveniles $s_- = 0$ (as $r(t) = r_-$), and the minimal size of adults $s_* = \ln(r^*/r_-)$, where r^* is the minimal radius of adults.

Appendix B

Positive equilibrium for two-species model (2.9)

We compute the positive equilibrium for the system (2.9), which is, we compute the solution for the following equations

$$\begin{cases} 0 = e^{-\mu_{J_1}\tau_1}\beta_1 A_1 - \mu_{A_1} A_1, \\ \int_{t-\tau_1}^t \frac{\alpha_1}{1 + \delta_1(\zeta_{11}A_1 + \zeta_{12}A_2)} d\sigma = s^* - s_-, \end{cases} \quad (\text{B.1})$$

and

$$\begin{cases} 0 = e^{-\mu_{J_2}\tau_2}\beta_2 A_2 - \mu_{A_2} A_2, \\ \int_{t-\tau_2}^t \frac{\alpha_2}{1 + \delta_2(\zeta_{21}A_1 + \zeta_{22}A_2)} d\sigma = s^* - s_-, \end{cases} \quad (\text{B.2})$$

Obviously, $A_1 = 0, A_2 = 0$ is a trivial equilibrium for the species, in which case we have

$$\tau_1 = \frac{s^* - s_-}{\alpha_1}, \quad \tau_2 = \frac{s^* - s_-}{\alpha_2}.$$

Moreover, we have two "boundary" equilibrium $(\bar{A}_1, 0)$ and $(0, \tilde{A}_2)$, where

$$\bar{A}_1 = \frac{1}{\delta_1 \zeta_{11}} \left(\frac{\alpha_1}{\mu_{J_1}(s^* - s_-)} \ln \frac{\beta_1}{\mu_{A_1}} - 1 \right),$$

$$\bar{\tau}_1 = \frac{1}{\mu_{J_1}} \ln \frac{\beta_1}{\mu_{A_1}}, \quad \bar{\tau}_2 = \frac{(s^* - s_-)(1 + \delta_2 \zeta_{21} \bar{A}_1)}{\alpha_2},$$

and

$$\tilde{A}_2 = \frac{1}{\delta_2 \zeta_{22}} \left(\frac{\alpha_2}{\mu_{J_2}(s^* - s_-)} \ln \frac{\beta_2}{\mu_{A_2}} - 1 \right),$$

$$\tilde{\tau}_1 = \frac{(s^* - s_-)(1 + \delta_1 \zeta_{12} \tilde{A}_2)}{\alpha_1}, \quad \tilde{\tau}_2 = \frac{1}{\mu_{J_2}} \ln \frac{\beta_2}{\mu_{A_2}}.$$

Now we turn to the positive equilibrium. As $A_1, A_2 \neq 0$, we solve the first equation in (B.1) and (B.2) and get

$$\tau_1 = \frac{1}{\mu_{J_1}} \ln \frac{\beta_1}{\mu_{A_1}}, \quad \tau_2 = \frac{1}{\mu_{J_2}} \ln \frac{\beta_2}{\mu_{A_2}} \quad (\text{B.3})$$

By the second equation of (B.1) and (B.2), we have

$$\begin{cases} \zeta_{11}A_1 + \zeta_{12}A_2 = \frac{1}{\delta_1} \left(\frac{\alpha_1 \tau_1}{s^* - s_-} - 1 \right), \\ \zeta_{21}A_1 + \zeta_{22}A_2 = \frac{1}{\delta_2} \left(\frac{\alpha_2 \tau_2}{s^* - s_-} - 1 \right) \end{cases} \quad (\text{B.4})$$

We replace τ_1 and τ_2 in (B.4) by (B.3), and we get the following linear equations

$$\begin{cases} \zeta_{11}A_1 + \zeta_{12}A_2 = \Phi_1, \\ \zeta_{21}A_1 + \zeta_{22}A_2 = \Phi_2, \end{cases} \quad (\text{B.5})$$

where

$$\Phi_1 := \frac{1}{\delta_1} \left[\frac{\alpha_1}{\mu_{J_1}(s^* - s_-)} \ln \frac{\beta_1}{\mu_{A_1}} - 1 \right], \quad \Phi_2 := \frac{1}{\delta_2} \left[\frac{\alpha_2}{\mu_{J_2}(s^* - s_-)} \ln \frac{\beta_2}{\mu_{A_2}} - 1 \right].$$

First, as we want a positive solution, we need the following conditions

$$\Phi_1 \geq 0, \quad \Phi_2 \geq 0. \quad (\text{B.6})$$

We solve the equation (B.5) directly without considering its solvability

$$A_1 = \frac{\zeta_{22}\Phi_1 - \zeta_{12}\Phi_2}{\zeta_{11}\zeta_{22} - \zeta_{12}\zeta_{21}}, \quad A_2 = \frac{\zeta_{11}\Phi_2 - \zeta_{21}\Phi_1}{\zeta_{11}\zeta_{22} - \zeta_{12}\zeta_{21}}. \quad (\text{B.7})$$

In order to have a positive solution, we need the following conditions

$$\begin{cases} \zeta_{11}\zeta_{22} - \zeta_{12}\zeta_{21} > 0, \\ \zeta_{22}\Phi_1 - \zeta_{12}\Phi_2 > 0, \\ \zeta_{11}\Phi_2 - \zeta_{21}\Phi_1 > 0, \end{cases} \quad \text{or} \quad \begin{cases} \zeta_{11}\zeta_{22} - \zeta_{12}\zeta_{21} < 0, \\ \zeta_{22}\Phi_1 - \zeta_{12}\Phi_2 < 0, \\ \zeta_{11}\Phi_2 - \zeta_{21}\Phi_1 < 0, \end{cases} \quad (\text{B.8})$$

or in another simplified form

$$\frac{\zeta_{12}}{\zeta_{22}} < \frac{\Phi_1}{\Phi_2} < \frac{\zeta_{11}}{\zeta_{21}}, \quad \text{or} \quad \frac{\zeta_{11}}{\zeta_{21}} < \frac{\Phi_1}{\Phi_2} < \frac{\zeta_{12}}{\zeta_{22}}, \quad (\text{B.9})$$

So we have

Lemma B.1. *Under the condition (B.6) and (B.9), the equations (B.1) and (B.2) have a positive equilibrium as in (B.7).*

B. Positive equilibrium

We check the conditions (B.6) and (B.9) for our previous results in Table 1-3, and we have

$$\Phi_1 = 100.6839 > 0, \quad \Psi_2 = 133.4324 > 0,$$

$$\frac{\zeta_{12}}{\zeta_{22}} = 0.6, \quad \frac{\Phi_1}{\Phi_2} = 0.7546, \quad \frac{\zeta_{11}}{\zeta_{21}} = 0.625,$$

which does not satisfy the condition (B.9), so there is no positive equilibrium in our previous simulation, and eastern hemlock is disappearing. In order to have a positive equilibrium, we reduce the influence of American beech towards eastern hemlock, namely we lower ζ_{21} from 1.6 to 1. Then we have

$$\frac{\zeta_{11}}{\zeta_{21}} = 1,$$

which satisfies the condition (B.9). And we have the coexistence of both species as is shown in Figure 2.9 and Figure 2.13.

Appendix C

Resolvent of the Laplacian operator Δ in (2.11)

Assume that $\psi(x, y) : [0, x_{\max}] \times [0, y_{\max}] \rightarrow \mathbb{R}$ is a function. The resolvent of the Laplacian operator Δ with periodic boundary condition is given for $(x, y) \in [0, x_{\max}] \times [0, y_{\max}]$ by

$$(\lambda I - \varepsilon \Delta)^{-1}(\psi)(x, y) = \int_0^{+\infty} e^{-\lambda t} T_{\Delta}(\varepsilon t)(\widehat{\psi})(x, y) dt, \quad (\text{C.1})$$

where $\widehat{\psi}$ extends ψ periodically on $\mathbb{R} \times \mathbb{R}$, that is to say

$$\widehat{\psi}(x, y) = \psi(x, y), \forall (x, y) \in [0, x_{\max}] \times [0, y_{\max}]$$

and

$$\begin{cases} \widehat{\psi}(x + x_{\max}, y) = \widehat{\psi}(x, y), \forall x, y \in \mathbb{R}, \\ \widehat{\psi}(x, y + y_{\max}) = \widehat{\psi}(x, y), \forall x, y \in \mathbb{R}. \end{cases}$$

Moreover $T_{\Delta}(t)$ is the semigroup generated by the Laplacian operator Δ . A result in Engel and Nagel [61, p. 69] shows that

$$T_{\Delta}(t)(\widehat{\psi})(x, y) = \frac{1}{4\pi t} \iint_{\mathbb{R}^2} e^{-\frac{(x-\widehat{x})^2 + (y-\widehat{y})^2}{4t}} \widehat{\psi}(\widehat{x}, \widehat{y}) d\widehat{x} d\widehat{y}. \quad (\text{C.2})$$

The numerical approximation of $(I - \varepsilon_i \Delta)^{-1}$ is given by the matrix $(I + \varepsilon_i \mathbf{A})^{-1}$ where

$$\mathbf{A} = \begin{pmatrix} \mathbf{B} & \mathbf{C} & 0 & \dots & \mathbf{C} \\ \mathbf{C} & \mathbf{B} & \ddots & \ddots & \vdots \\ 0 & \ddots & \ddots & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & \mathbf{C} \\ \mathbf{C} & \dots & 0 & \mathbf{C} & \mathbf{B} \end{pmatrix},$$

where

$$\mathbf{B} = \begin{pmatrix} \frac{2}{dx^2} + \frac{2}{dy^2} & -\frac{1}{dx^2} & 0 & \dots & \dots & -\frac{1}{dx^2} \\ -\frac{1}{dx^2} & \frac{2}{dx^2} + \frac{2}{dy^2} & -\frac{1}{dx^2} & \ddots & & \vdots \\ 0 & \ddots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & 0 \\ \vdots & & \ddots & \ddots & \ddots & -\frac{1}{dx^2} \\ -\frac{1}{dx^2} & \dots & \dots & 0 & -\frac{1}{dx^2} & \frac{2}{dx^2} + \frac{2}{dy^2} \end{pmatrix}$$

and

$$\mathbf{C} = \begin{pmatrix} -\frac{1}{dy^2} & 0 & \dots & 0 \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & -\frac{1}{dy^2} \end{pmatrix}.$$

Appendix D

Derivation of the state-dependent delay differential equation (5.4)

We can transform the system (5.3) into a state-dependent delay differential equation using the method in Appendix A and [193, 194]. Differentiating the following formula

$$A(t) = \int_{s^*}^{+\infty} u(t, s) ds$$

with respect to t , we have

$$\begin{aligned} \frac{dA(t)}{dt} &= \int_{s^*}^{+\infty} \partial_t u(t, s) ds \\ &= -f(A(t)) \int_{s^*}^{+\infty} \partial_s u(t, s) ds - \int_{s^*}^{+\infty} \left[\mu(s) + \frac{\gamma(s)I(t)}{1 + \kappa A(t)} \right] u(t, s) ds \\ &= f(A(t))u(t, s^*) - \int_{s^*}^{+\infty} \left[\mu(s) + \frac{\gamma(s)I(t)}{1 + \kappa A(t)} \right] u(t, s) ds. \end{aligned} \quad (\text{D.1})$$

Next we deal with the term $u(t, s^*)$. The characteristic curves for the first equation in (5.3) are (shown in Figure D.1)

$$\frac{ds(t)}{dt} = f(A(t)). \quad (\text{D.2})$$

Then we will have the following representation of s

$$s(t) = C + \int_0^t f(A(\sigma)) d\sigma. \quad (\text{D.3})$$

Suppose t^* is the time when juveniles present at time 0 become adults, namely

$$\int_0^{t^*} f(A(\sigma)) d\sigma = s^* - s_-.$$

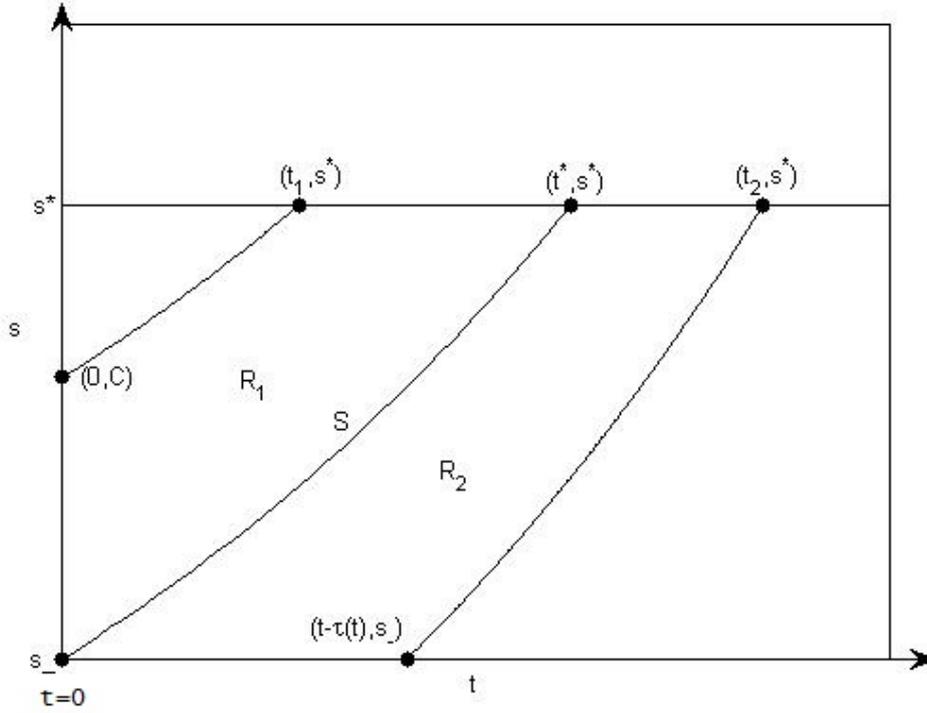


Figure D.1: In this figure we present the characteristic curves (D.2).

We can see that the curve

$$S = \left\{ (t, s) : 0 \leq t \leq t^*, s = s_- + \int_0^t f(A(\sigma)) d\sigma \right\}$$

divides the strip $[0, +\infty) \times [s_-, s^*]$ into two parts R_1 and R_2 . Assuming that $s - s_- \leq \int_0^t f(A(\sigma)) d\sigma$, then we can find $T(t, s) \geq 0$ such that

$$\int_{t-T(t,s)}^t f(A(\sigma)) d\sigma = s - s_-$$

in the region R_2 , so it denotes the time it takes for a juvenile to grow to size s at time t from the minimal size s_- . Replacing s in $u(t, s)$ with (D.3), we can compute formally as follows, assuming that u is a C^1 -function:

$$\begin{aligned} & \frac{d}{dt} u \left(t, C + \int_0^t f(A(\sigma)) d\sigma \right) \\ &= \partial_t u \left(t, C + \int_0^t f(A(\sigma)) d\sigma \right) + f(A(t)) \partial_s u \left(t, C + \int_0^t f(A(\sigma)) d\sigma \right) \\ &= - \left[\mu \left(C + \int_0^t f(A(\sigma)) d\sigma \right) + \frac{\gamma \left(C + \int_0^t f(A(\sigma)) d\sigma \right) I(t)}{1 + \kappa A(t)} \right] u \left(t, C + \int_0^t f(A(\sigma)) d\sigma \right) \end{aligned}$$

$$\int_0^t f(A(\sigma))d\sigma \Big).$$

This is a separable ODE with respect to t . Integration of this equation, and by using the initial distribution and the boundary condition, we obtain the following expression of $u(t, s)$

$$u(t, s) = \begin{cases} u_0 \left(s - \int_0^t f(A(\sigma))d\sigma \right) \exp \left\{ - \int_0^t \left[\mu \left(s - \int_0^t f(A(\sigma))d\sigma + \int_0^l f(A(\sigma))d\sigma \right) + \frac{\gamma \left(s - \int_0^t f(A(\sigma))d\sigma + \int_0^l f(A(\sigma))d\sigma \right) I(l)}{1 + \kappa A(l)} \right] dl \right\}, & \text{if } s \geq s_- + \int_0^t f(A(\sigma))d\sigma, \\ \frac{\beta A(t - T(t, s))}{f(A(t - T(t, s)))} \exp \left\{ - \int_{t-T(t, s)}^t \left[\mu \left(s_- + \int_{t-T(t, s)}^l f(A(\sigma))d\sigma \right) + \frac{\gamma \left(s_- + \int_{t-T(t, s)}^l f(A(\sigma))d\sigma \right) I(l)}{1 + \kappa A(l)} \right] dl \right\}, & \text{if } s \leq s_- + \int_0^t f(A(\sigma))d\sigma. \end{cases} \quad (\text{D.4})$$

Whenever $s^* - s_- \leq \int_0^t f(A(\sigma))d\sigma$, we can specifically define $\tau(t) := T(t, s^*)$ as the solution of

$$\int_{t-\tau(t)}^t f(A(\sigma))d\sigma = s^* - s_-. \quad (\text{D.5})$$

Actually the term $\tau(t) = T(t, s^*)$ represents the maturation period of one individual.

We now assume

$$\mu(s) = \begin{cases} \mu_A > 0, & \text{if } s \geq s^*, \\ \mu_J > 0, & \text{if } s < s^*, \end{cases} \quad \gamma(s) = \begin{cases} \gamma_A \geq 0, & \text{if } s \geq s^*, \\ \gamma_J \geq 0, & \text{if } s < s^*. \end{cases}$$

Then the third equation of (5.3) becomes

$$\frac{dI(t)}{dt} = \left[\frac{\varepsilon \chi}{1 + \kappa A(t)} (\gamma_A A(t) + \gamma_J J(t)) - \mu_I \right] I(t). \quad (\text{D.6})$$

When $s = s^*$, we have for $t \in [0, t^*]$,

$$u(t, s^*) = u_0 \left(s^* - \int_0^t f(A(\sigma))d\sigma \right) e^{-\mu_J t - \gamma_J \int_0^t \frac{I(l)}{1 + \kappa A(l)} dl},$$

and for $t > t^*$,

$$u(t, s^*) = \frac{\beta A(t - \tau(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t) - \gamma_J \int_{t-\tau(t)}^t \frac{I(l)}{1 + \kappa A(l)} dl}.$$

Replacing $u(t, s^*)$ back in (D.1) for $t > t^*$, we get the equation of $A(t)$ in (5.4):

$$\begin{aligned} \frac{dA(t)}{dt} &= \frac{f(A(t))}{f(A(t - \tau(t)))} e^{-\mu_J \tau(t) - \gamma_J \int_{t-\tau(t)}^t \frac{I(l)}{1 + \kappa A(l)} dl} \beta A(t - \tau(t)) \\ &\quad - \mu_A A(t) - \gamma_A \frac{A(t)}{1 + \kappa A(t)} I(t). \end{aligned} \quad (\text{D.7})$$

Set $\gamma_J = 0$. Then when $t > t^*$, system (5.3) is transformed into system (5.5).

Appendix E

Derivation of the numerical scheme of (5.5)

We will give the numerical scheme in this appendix for the system (5.5). First we can rewrite system (5.5) in the following form:

$$\begin{cases} A'(t) = F(A(t), I(t), \tau(t), A(t - \tau(t))), \\ \int_{t-\tau(t)}^t f(A(\sigma))d\sigma = s^* - s_-, \\ I'(t) = G(A(t), I(t)). \end{cases} \quad (\text{E.1})$$

where

$$F(A_0, I, \tau, A_{-\tau}) := \frac{f(A_0)}{f(A_{-\tau})} e^{-\mu_J \tau} \beta A_{-\tau} - \mu_A A_0 - \gamma_A \frac{A_0}{1 + \kappa A_0} I$$

and

$$G(A, I) := \left(\frac{\varepsilon \chi \gamma_A A}{1 + \kappa A} - \mu_I \right) I.$$

First we give a derivation of the numerical scheme of the computation of $\tau(t)$. From the second equation of (E.1) we have

$$\int_{t-\tau(t)}^t f(A(\sigma))d\sigma = \int_{t+\Delta t-\tau(t+\Delta t)}^{t+\Delta t} f(A(\sigma))d\sigma,$$

which is equivalent to

$$\int_{t-\tau(t)}^{t+\Delta t} f(A(\sigma))d\sigma + \int_{t+\Delta t}^t f(A(\sigma))d\sigma = \int_{t+\Delta t-\tau(t+\Delta t)}^{t-\tau(t)} f(A(\sigma))d\sigma + \int_{t-\tau(t)}^{t+\Delta t} f(A(\sigma))d\sigma.$$

So

$$\int_{t+\Delta t}^t f(A(\sigma))d\sigma = \int_{t+\Delta t-\tau(t+\Delta t)}^{t-\tau(t)} f(A(\sigma))d\sigma. \quad (\text{E.2})$$

Assume Δt is small enough, then $f(A(\sigma))$ can be seen as a constant function on the interval $[t, t + \Delta t]$ and $[t - \tau(t), t + \Delta t - \tau(t + \Delta t)]$. Thus we approximate $f(A(\sigma))$ by $f(A(t))$ in the first integral and by $f(A(t - \tau(t)))$ in the second integral in (E.2), and we have the following approximation

$$\Delta t f(A(t)) = (\Delta t - \tau(t + \Delta t) + \tau(t)) f(A(t - \tau(t))),$$

and

$$\tau(t + \Delta t) = \tau(t) + \Delta t \left(1 - \frac{f(A(t))}{f(A(t - \tau(t)))} \right).$$

Then the numerical scheme used in this article will be

$$\begin{cases} A(t + \Delta t) = \Delta t F(A(t), I(t), \tau(t), A(t - \tau(t))) + A(t), \\ \tau(t + \Delta t) = \Delta t \left(1 - \frac{f(A(t))}{f(A(t - \tau(t)))} \right) + \tau(t), \\ I(t + \Delta t) = \Delta t G(A(t), I(t)) + I(t). \end{cases} \quad (\text{E.3})$$

It remains to find a numerical approximation to calculate $A(t - \tau(t))$, namely the past value of A at time $t - \tau(t)$ in the above approximation, which might not be given in the previous calculation because $t - \tau(t)$ might not be in our discretized sequence of time for the simulation. In order to determine this value, we use the method of linear interpolation. First we determine the time interval $[t_n, t_{n+1}]$ (with $t_n := n\Delta t$ for some integer $n \in \mathbb{Z}$) to which the time $t - \tau(t)$ belongs, then we use the following linear interpolation

$$A(t - \tau(t)) \approx A(t_n) + (t - \tau(t) - t_n) \frac{A(t_{n+1}) - A(t_n)}{t_{n+1} - t_n} \quad (\text{E.4})$$

to get the approximation of the value $A(t - \tau(t))$. This will be more accurate than the rough approximation of using just $A(t_n)$ or $A(t_{n+1})$.

Appendix F

MATLAB codes

In this section I present one MATLAB code of the numerical simulations in this thesis. Due to the length of various MATLAB codes built for this thesis, I will present only one code here. I refer to [235] for the numerical simulations of two-species case in Chapter 2, [236] for the numerical simulations of two-species case with spatial structure in Chapter 2, and [237] for the numerical simulations of forest-parasite model in Chapter 5.

The following MATLAB code corresponds to Figure 2.6, the parameter fitting for the first species FAGR in the single species case in Chapter 2. This code goes together with the file *DATAoldtime.dat* corresponding to the simulation for SORTIE, which can be downloaded from [233]. For the second species in the single species case, the code is similar, available on [234], with a change of original data and parameter range.

```
function compaFAGR

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% load the data of 50 runs and compute the average
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

DATAold=load('DATAoldtime.dat','-ascii');
DATAold(2:51,:)=9*DATAold(2:51,:);

dto=5;
oldtime=DATAold(1,:);
Not=size(oldtime);
not=Not(2);
dtn=1;
newtime=0:dtn:2000;
Nnt=size(newtime);
nnt=Nnt(2);

DATAnew=zeros(50,nnt);

for i=1:50
    DATAnew(i,1)=DATAold(i+1,1);
    for j=2:nnt
        j1=ceil(newtime(j)/5); % decide in which interval of the original timescale
        DATAnew(i,j)=(newtime(j)-oldtime(j1))*(DATAold(i+1,j1+1)-DATAold(i+1,j1))/5+DATAold(i+1,j1);
    end
end

DATAnewave=mean(DATAnew);

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% compute the best fit of the parameters
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

s2=log(50);
s1=0;
```

```

Ddelta=0.1;
Dxi=1;
Dtau0=1;
DMuJ=0.01;
DMuA=0.001;
Dbeta=0.5;

deltamax=0.1;
ximax=0;
tau0max=200;
MuJmax=0.03;
MuAmax=0.001;
betamax=2;

delta=0:Ddelta:deltamax;
xi=0:Dxi:ximax;
tau0=0:Dtau0:tau0max;
MuJ=0.03:DMuJ:MuJmax;
MuA=0.001:DMuA:MuAmax;
beta=0:Dbeta:betamax;

Ndelta=size(delta);
ndelta=Ndelta(2);
Nxi=size(xi);
nxi=Nxi(2);
Ntau0=size(tau0);
ntau0=Ntau0(2);
NMuJ=size(MuJ);
nMuJ=NMuJ(2);
NMuA=size(MuA);
nMuA=NMuA(2);
Nbeta=size(beta);
nbeta=Nbeta(2);

Dt=1;
tmax=2000;

Timen=0:Dt:tau0max;
Ntn=size(Timen);
ntn=Ntn(2);
Timep=tau0max+Dt:Dt:tmax;
Ntp=size(Timep);
ntp=Ntp(2);

for iTimen=1:ntn
    A(iTimen)=DATAnewave(iTimen);
end

iLS=1;

tic
for idelta=1:ndelta
    for ixi=1:nxi
        for itau0=1:ntau0
            for iMuJ=1:nMuJ
                for iMuA=1:nMuA
                    for ibeta=1:nbeta
                        tau(1)=(1-(1+delta(idelta))*A(1))/(1+delta(idelta))*A(ntn))*Dt+tau0(itau0);
                        A(ntn+1)=(beta(ibeta)*exp(-MuJ(iMuJ)*tau0(itau0)-xi(ixi)*A(1))*A(1)*(1+delta(idelta))*
                        A(1))/(1+delta(idelta))*A(ntn))-MuA(iMuA)*A(ntn))*Dt+A(ntn);
                        for i=2:ntp
                            %j=min(ceil((i*Dt+tau0max+Dt-tau(i-1))/Dt)+ntn-2,i+ntn-2);
                            %j=min(ceil((t-tau(1,i))/Dt)+n1,i+n1);
                            j=max(1,min(i-1-ceil((tau(i-1)-tau0max)/Dt),ntn+i-2));
                            A1=A(j+1);
                            tau(i)=(1-(1+delta(idelta))*A1)/(1+delta(idelta))*A(ntn+i-1))*Dt+tau(i-1);
                            A(ntn+i)=(beta(ibeta)*exp(-MuJ(iMuJ)*tau(i-1)-xi(ixi)*A1)*A1*(1+delta(idelta))*A1)/(1+
                            delta(idelta))*A(ntn+i-1))-MuA(iMuA)*A(ntn+i-1))*Dt+A(ntn+i-1);
                        end
                        LS(iLS)=sum((DATAnewave(ntn:1:ntn+ntp)-A(ntn:1:ntn+ntp)).*(DATAnewave(ntn:1:ntn+ntp)-
                        A(ntn:1:ntn+ntp)));
                        Fdelta(iLS)=delta(idelta);
                        Fxi(iLS)=xi(ixi);
                        Ftau0(iLS)=tau0(itau0);
                        FMuJ(iLS)=MuJ(iMuJ);
                        FMuA(iLS)=MuA(iMuA);
                        Fbeta(iLS)=beta(ibeta);
                        iLS=iLS+1;
                    end
                end
            end
        end
    end
end
end
end
toc

[C,I]=min(LS)
fdelta=Fdelta(I)

```

F. MATLAB codes

```

fxi=Fxi(I)
ftau0=Ftau0(I)
fMuJ=FMuJ(I)
fMuA=FMuA(I)
fbeta=Fbeta(I)

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%% compute alpha using simpson method %%%%%%%%%%%%%%%

tminsimp=-ftau0;
tmaxsimp=0;
Dtsimp=Dt;
Timesimp=tminsimp:Dtsimp:tmaxsimp;

ntsimp=size(Timesimp);
auxsimp=round(ntsimp(2)/2);
if(2*auxsimp>ntsimp(2))
    Timesimp=(tminsimp-Dtsimp):Dtsimp:0;
end
ntsimp=size(Timesimp);
nsimp=ntsimp(2);

Asimp=A(1:nsimp);
Isimp=1./(1+fdelta*Asimp);

% C means the sum
nlsimp=nsimp/2-1;
I1simp=zeros(1,nlsimp);
Csimp=0;
for i=1:nlsimp
    Csimp=Csimp+Isimp(2*i);
    I1simp(1,i)=Csimp;
end

I2simp=zeros(1,nlsimp+1);
Csimp=0;
for i=1:nlsimp+1
    Csimp=Csimp+Isimp(1,2*i-1);
    I2simp(1,i)=Csimp;
end

Xsimp=Dtsimp/3*(Isimp(1)+2*I1simp(1,nlsimp)+4*I2simp(1,nlsimp+1)+Isimp(2*(nlsimp+1)))

falpha=(s2-s1)/Xsimp

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%% alpha end %%%%%%%%%%%%%%%

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% plot the best fit and the data
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

tau(1)=(1-(1+fdelta*A(1))/(1+fdelta*A(ntn)))*Dt+ftau0;
A(ntn+1)=(fbeta*exp(-fMuJ*tau0-fxi*A(1))*A(1)*(1+fdelta*A(1))/(1+fdelta*A(ntn))-fMuA*A(ntn))
*Dt+A(ntn);
Timep1(1)=tau0max+Dt;
for i=2:ntp
    %j=min(ceil((i*Dt+tau0max+Dt-tau(i-1))/Dt)+ntn-2,i+ntn-2);
    j=max(1,min(i-1-ceil((tau(i-1)-tau0max)/Dt),ntn+i));
    A1=A(j);
    tau(i)=(1-(1+fdelta*A1)/(1+fdelta*A(ntn+i-1)))*Dt+tau(i-1);
    A(ntn+i)=(fbeta*exp(-fMuJ*tau(i-1)-fxi*A1)*A1*(1+fdelta*A1)/(1+fdelta*A(ntn+i-1))-fMuA
    *A(ntn+i-1))*Dt+A(ntn+i-1);
    Timep1(i)=Timep1(i-1)+Dt;
end

Timep2=[Timen,Timep1];

subplot(1,2,1)
plot(Timep2,A(1:ntn+ntp),'-','Timep2,DATANewave','LineWidth',2)
legend('simulation','data','Location','best')
xlabel('t');
ylabel('A(t)');
set(yl,'Rotation',0);
title('a')

subplot(1,2,2)
plot(Timep1,tau,'LineWidth',2)
xlabel('t');
ylabel('\tau(t)');
set(yl,'Rotation',0);
title('b')

saveas(gcf,'1','fig')
end

```

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