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PAPERS

Modelling the evolutionary dynamics of insecticide quantitative resistance in mosquito populations

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Abstract

Malaria remains a significant global health challenge, with sub-Saharan Africa bearing the majority of the burden. While vector control measures such as pyrethroid-based insecticidal nets and indoor residual spraying have significantly reduced malaria incidence, the emergence of insecticide resistance in *Anopheles* mosquito populations threatens these gains. Resistance develops through genetic mutations under prolonged selection pressure, complicating control efforts and necessitating a deeper understanding of its evolutionary dynamics. This study introduces a novel mathematical framework to investigate the emergence and spread of insecticide resistance in mosquito populations. By modelling insecticide resistance as a continuous (quantitative) trait influenced by multiple genes, we capture its variability and evolutionary transient dynamics. We propose an age-structured mosquito population model using integro-differential equations, where the resistance trait influences life-history parameters such as mortality and reproduction. Our approach provides new insights into how resistance emerges and spreads within mosquito populations over time. We analyse the model's properties, including the existence of a unique maximal bounded semiflow, and derive conditions for the existence and stability of steady states. Through parameterization and simulations, we explore the transient and long-term dynamics of resistance evolution under different scenarios. The results offer valuable insights into the evolutionary mechanisms driving insecticide resistance and inform the design of sustainable vector control strategies.

1. Introduction

Malaria, a vector-borne disease transmitted to humans through the bite of an infected female Anopheles mosquito, remains a significant public health challenge, affecting nearly half of the global population. In 2022, malaria caused 249 million infections and 608,000 deaths worldwide, with 95% of the burden concentrated in sub-Saharan Africa [37]. To mitigate the impact of malaria, global initiatives have focused on vector control measures, which significantly reduced the disease burden in Africa between 2005 and 2015 [7, 44]. This success was largely driven by widespread use of pyrethroid-based insecticides and indoor residual spraying (IRS), with pyrethroid-treated nets (ITNs) playing a pivotal role due to their low toxicity to mammals and strong irritant effects on mosquitoes [2, 44].

However, these gains are now under threat due to the rapid emergence of insecticide resistance in mosquito populations. Prolonged insecticide use exerts selection pressure, allowing mosquitoes to survive and reproduce despite exposure to chemical agents such as pyrethroids [2, 21, 36]. Since long-lasting insecticidal nets (LLINs) form the cornerstone of malaria eradication strategies, resistance in Anopheles mosquitoes presents a critical challenge to public health efforts in sub-Saharan Africa [35]. Resistance arises as exposure to insecticides selects genetic mutations that confer survival advantages, enabling the spread of resistance genes in mosquito populations (e.g. [1, 19, 26]). Understanding the evolutionary dynamics underlying the emergence and spread of mosquito insecticide resistance is therefore essential for developing sustainable management strategies.

Mathematical modelling has long been a valuable tool for understanding the complex dynamics of biological systems with nonlocal terms and structured populations, particularly in epidemiology (e.g. [5, 6, 13, 38]). In the context of vector-borne diseases, mathematical models have played a key role in elucidating how mosquito population dynamics influence disease transmission. More recently, models incorporating population genetics have been developed to investigate the community-level consequences of insecticide resistance in mosquito populations [3, 4, 8, 22, 24, 25, 27, 33, 34, 40]. These models typically address qualitative resistance by examining the dynamics of specific resistance alleles – homozygous sensitive (SS), heterozygous (RS) and homozygous resistant (RR) – and their interactions within the population. While these approaches provide valuable insights into the genetic basis and spread of resistance, they often overlook the transient evolutionary dynamics that contribute to its emergence.

In cases where resistance is driven by point mutations, mosquito insecticide resistance can be viewed as a continuous trait, referred to as quantitative insecticide resistance. This form of resistance arises from the combined effects of multiple genes, each contributing incrementally to the overall resistance phenotype [20, 39]. Unlike qualitative resistance, which is typically governed by one or a few major genes, quantitative resistance varies continuously within a population. This variability highlights the need for a deeper understanding of the evolutionary mechanisms that drive the emergence of resistance.

In this study, we introduce a continuous phenotypic trait, x taking values in the open set Ω and representing the level of mosquito insecticide resistance. This framework enables the simultaneous study of mosquito population dynamics and the evolutionary dynamics of resistance. This trait influences various aspects of the mosquito life cycle, including egg laying and mortality rates. We propose an age-structured mosquito model that treats insecticide resistance as a continuous trait. Insecticide resistance selection is influenced not only by vector control activities; mosquitoes may also be exposed to agricultural or household insecticides during their aquatic or adult stages [16]. Therefore, our model considers both eggs and adult female mosquitoes (AFMs), regardless of their exposure to insecticides. By capturing the transient evolutionary dynamics underlying resistance emergence, our model offers a novel approach to studying this phenomenon. To our knowledge, this is the first framework to address the continuous nature of insecticide resistance in mosquito populations using an age-structured approach. Employing this quantitative framework, we develop a system of integro-differential and age-structured equations to investigate the emergence and spread of insecticide resistance.

The remainder of the paper is organized as follows: Section 2 presents the model description. In Section 3, we establish some main properties of the model, including the existence of the unique maximal bounded semiflow. We also give necessary and sufficient conditions for the existence of steady states of the model proposed. The asymptotic behaviour and uniform persistence of the semiflow are detailed in Section 4. Section 5 presents the model's parameterization and the simulated dynamics. Finally, the overall findings of the manuscript are discussed in Section 6.

2. The model formulation

The proposed model tracks the evolutionary dynamics of a mosquito population, distinguishing between individuals unexposed to insecticides (subscript 0) and those exposed to insecticides (subscript 1). At any time t, let $E_0(t, x)$ and $E_1(t, x)$ denote the total number of eggs with insecticide resistance level x laid by the unexposed and exposed AFMs, respectively. The variable $x \in \Omega$ represents the level of insecticide resistance (IR) in AFMs where Ω is an open subset of $\mathbb{R}$. Similarly, we denote $A_0(t, a, x)$ and $A_1(t, a, x)$ the population sizes of AFMs of age a, unexposed and exposed to insecticides, respectively. The larvae and pupae stages of the mosquito development are not explicitly taken into account.

Let us introduce the quantity:

$$E(t) = \int_{\Omega} (E_0(t, x) + E_1(t, x))\,\mathrm{d}x, \tag{2.1}$$

which represents the total number of eggs at time t. We assume that both insecticide-exposed and unexposed AFMs oviposit within the same restricted environment, therefore intraspecific competition arises due to limited resource availability. We model this competitive interaction using the function H, depending on the quantity $E(t)$, which captures the decline in egg survival or development as density increases and is defined as follows:

$$H(E(t)) = (1 + E(t))^{-\kappa}, \tag{2.2}$$

where κ is a scaling positive constant modulating the intensity of density dependence. Larger positive values of κ indicate stronger competition among eggs.

Eggs laid by AFMs A_j with an insecticide resistance (IR) level x die at a rate $\mu_j(x)$ and hatch at a rate $\gamma_j(x)$. Among the hatched eggs, only a proportion $\tau(x)$ successfully emerge and reach adulthood as females. At time t, a proportion $c(t)$ of mosquitoes emerging from the hatched eggs E_0 that have not yet encountered insecticides is exposed to the insecticide and subsequently transitions to the exposed AFM compartment (A_1). Conversely, a proportion $(1 - c(t))$ of these mosquitoes escape exposure and progress to the unexposed AFM compartment (A_0). Furthermore, mosquitoes emerging from the hatched eggs E_1 transition to the exposed AFM compartment at a rate $\tau(x)$. Therefore, the numbers of newly emerged AFMs at time t are given by:

$$\begin{cases} A_0(t, a = 0, x) = (1 - c(t))\tau(x)\gamma_0(x)E_0(t, x), \\ A_1(t, a = 0, x) = c(t)\tau(x)\gamma_0(x)E_0(t, x) + \tau(x)\gamma_1(x)E_1(t, x). \end{cases} \tag{2.3}$$

With the above notations, we can derive the following age-structured and integro-differential equations, which describe the spread of insecticide resistance within a mosquito population:

$$\begin{cases} \partial_t E_0(t, x) = H(E(t)) \displaystyle\int_{\Omega} \int_0^{\infty} m_0(x, y) r_0(a, y) A_0(t, a, y)\mathrm{d}a\mathrm{d}y - (\mu_0(x) + \gamma_0(x))E_0(t, x), \\ \partial_t E_1(t, x) = H(E(t)) \displaystyle\int_{\Omega} \int_0^{\infty} m_1(x, y) r_1(a, y) A_1(t, a, y)\mathrm{d}a\mathrm{d}y - (\mu_1(x) + \gamma_1(x))E_1(t, x), \\ (\partial_t + \partial_a)\, A_0(t, a, x) = -d_0(a, x)A_0(t, a, x), \\ (\partial_t + \partial_a)\, A_1(t, a, x) = -d_1(a, x)A_1(t, a, x), \end{cases} \tag{2.4}$$

with $E(t)$ and $H(E(t))$, respectively, defined in (2.1) and (2.2). AFMs A_j of age a, with insecticide resistance level x, die at rate $d_j(a, x)$, $j = 0, 1$. The number of new eggs with insecticide resistance level x produced at time t by AFMs (A_j) is quantified by $H(E(t)) \int_{\Omega} \int_0^{\infty} m_j(x, y) r_j(a, y) A_j(t, a, y)\mathrm{d}a\mathrm{d}y$, where $m_j(x, y)$ is the probability for AFMs with insecticide resistance level y to produce eggs with resistance level x and $r_j(a, y)$ is the egg-laying rate. The above system is coupled with the following initial conditions:

$$\begin{cases} E_0(0, x) = E_{0,0}(x) \quad ; \quad A_0(0, a, x) = A_{0,0}(a, x), \\ E_1(0, x) = E_{1,0}(x) \quad ; \quad A_1(0, a, x) = A_{1,0}(a, x). \end{cases}$$

Finally, Model (2.3)–(2.4) is summarized in Figure 1, and all model variables and parameters are listed in Table 1.

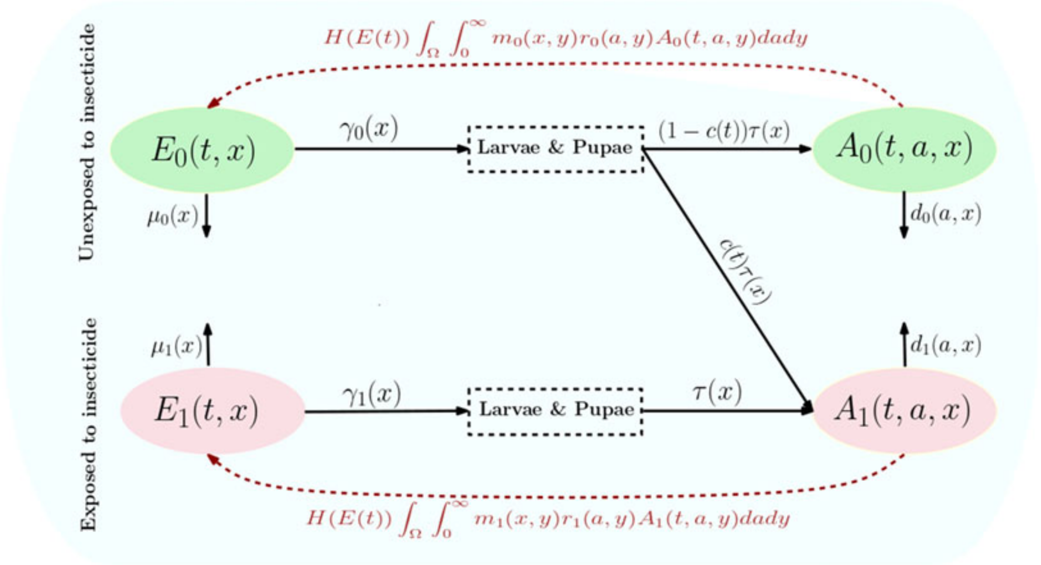

Figure 1. *Flow diagram of the mosquito model. E_j denotes the number of eggs laid by adult female mosquitoes A_j, $j = 0, 1$.* ***Unexposed to insecticide:*** *the number of new eggs with insecticide resistance level x produced at time t by unexposed AFMs (A_0) is $H(E(t))\int_\Omega\int_0^\infty m_0(x,y)r_0(a,y)A_0(t,a,y)\mathrm{d}a\mathrm{d}y$, where $m_0(x,y)$ is the probability for unexposed AFMs with insecticide resistance level y to produce eggs with resistance level x, $r_0(a,y)$ is the egg-laying rate depending on the age a and $H(E(t)$ is the function that regulates the growth of eggs. Eggs laid by unexposed AFMs (E_0) die at rate $\mu_0(x)$ and hatch at rate $\gamma_0(x)$. Hatched eggs laid by AFMs emerge at rate $\tau(x)$. A proportion $c(t)$ of mosquitoes emerging from the hatched eggs E_0 that have not yet encountered insecticides is exposed to the insecticide and subsequently transitions to the exposed AFM compartment (A_1). Conversely, a proportion $(1-c(t))$ of these mosquitoes escape exposure and progress to the unexposed AFM compartment (A_0). Unexposed AFMs die at rate $d_0(a,x)$.* ***Exposed to insecticide:*** *Similarly to the unexposed group, the number of new eggs with insecticide resistance level x produced at time t by exposed female mosquitoes (A_1) is given by $H(E(t))\int_\Omega\int_0^\infty m_1(x,y)r_1(a,y)A_1(t,a,y)\mathrm{d}a\mathrm{d}y$, where $m_1(x,y)$ is the probability for exposed female mosquitoes with insecticide resistance level y to produce eggs with resistance level x and $r_1(a,y)$ is the egg-laying rate. Eggs laid by exposed female mosquitoes (E_1) die at rate $\mu_1(x)$ and hatch at rate $\gamma_1(x)$. Mosquitoes emerging from the hatched eggs E_1 transition to the exposed AFM compartment (A_1) at a rate $\tau(x)$.*

Model (2.3)–(2.4) will be considered under the following assumptions:

Assumption 2.1. *For $i \in \{0, 1\}$:*

1. *τ, μ_i and γ_i are positive, continuous and bounded functions on Ω.*
2. *The functions r_i and d_i are positive, continuous and bounded on $(0,\infty)\times\Omega$.*
3. *The mutation kernel m_i is strictly positive almost everywhere, Lipschitz continuous, integrable, bounded on Ω and has a unit mass, i.e. $\int_\Omega\int_\Omega m_i(x,y)\mathrm{d}x\mathrm{d}y = 1$.*

Assumption 2.2. *Furthermore, the mutation kernel m_i, $\quad i \in \{0, 1\}$.*

1. *is symmetric on Ω,* ie. *$m_i(x,y) = m_i(y,x)$.*
2. *decays rather rapidly towards infinity in the sense that $\lim_{|x|\to\infty}|x|^n m(x,\cdot) = 0$, for all $n \in \mathbb{N}$.*

Table 1. *Notations, state variables and parameters used in the model*

Notations	Meaning	
t	Chronological time	
a	Age of adult female mosquito	
x	Level of mosquito insecticide resistance	
State variables	**Description**	
$E_0(t, x)$	Number of eggs laid by AFM* unexposed to insecticide at time t with resistance level x	
$E_1(t, x)$	Number of eggs laid by AFM* exposed to insecticide at time t with resistance level x	
$A_0(t, a, x)$	Number of AFM unexposed to insecticide aged a at time t with resistance level x	
$A_1(t, a, x)$	Number of AFM exposed to insecticide aged a at time t with resistance level x	
Functional parameters	**Biological meaning (unit)**	
$c(t)$	Exposure rate to insecticide at time t (dimensionless)	
$m_0(x, y)$	Probability of mutation from IR level y to IR level x for unexposed AFM (dimensionless)	[5.1]
$m_1(x, y)$	Probability of mutation from IR level y to IR level x for exposed AFM (dimensionless)	[5.2]
$r_0(a, x)$	Egg-laying rate for an AFM unexposed to insecticide (number/day)	[5.3]
$r_1(a, x)$	Egg-laying rate for an AFM exposed to insecticide (number/day)	[5.3]
$d_0(a, x)$	Natural mortality rate of AFM unexposed to insecticide (percentage/day)	[5.4]
$d_1(a, x)$	Natural death rate of AFM exposed to insecticide (percentage/day)	[5.5]
$\gamma_0(x)$	Proportion of eggs laid by AFM unexposed to insecticide that hatch (percentage/day)	
$\gamma_1(x)$	Proportion of eggs laid by AFM exposed to insecticide that hatch (percentage/day)	
$\tau(x)$	Proportion of hatched eggs laid by AFM that reach adulthood (percentage/day)	
$\mu_0(x)$	Natural death rate of eggs laid by AFM unexposed to insecticide (percentage/day)	
$\mu_1(x)$	Natural death rate of eggs laid by AFM exposed to insecticide (percentage/day)	

Table 1. Continued

Notations	Meaning	
Fixed parameters	**Biological meaning**	**Value, [Ref.]**
A	AFM age limit (in days)	30, [10]
a_L	Average age at which AFMs start laying eggs (in days)	3, [10]
a_{LS}	Average lifespan of AFMs (in days)	21, [10]
r_m	Maximum number of eggs laid by the reference sensitive strain	200, [11]
r_0	Average number of eggs laid by the reference sensitive strain	$0.875 \times r_m$, [Assumed]
r_1	Average number of eggs laid by the reference resistant strain	$0.750 \times r_m$, [Assumed]
Variable parameters	**Biological meaning**	**Range**
p_S	Probability of surviving insecticide exposure during one day	(0,1)
$\bar{d}_0$	Death rate of reference sensitive strain due to insecticide	$-\log(p_S)$
$\bar{d}_1$	Death rate of reference resistant strain due to insecticide	$-\log(1-p_S)$
κ	Scaling positive constant	(0,1)

[*] AFM = adult female mosquitoes.

It can be useful to rewrite Model (2.3)–(2.4) into a compact form. For this purpose, let us set $\boldsymbol{u}(t,x)=(E_0(t,x),E_1(t,x))^T$, $\boldsymbol{v}(t,a,x)=(A_0(t,a,x),A_1(t,a,x))^T$, $\mathbf{1}_2=(1,1)^T$ and $\boldsymbol{\mathcal{T}}=\left(\frac{1}{\tau(\cdot)},\frac{1}{\tau(\cdot)}\right)^T$ where $(\cdot)^T$ is the transpose vector. Then, Model (2.3)–(2.4) becomes:

$$\begin{cases}\partial_t\boldsymbol{u}(t,x)=h(\boldsymbol{u})(t)\displaystyle\int_0^\infty\mathcal{B}[\boldsymbol{v}(t,\cdot,\cdot)](a,x)\mathrm{d}a-\mathcal{N}(x)\boldsymbol{u}(t,x),\\ \boldsymbol{v}(t,0,x)=\mathcal{C}(x)\boldsymbol{u}(t,x),\\ (\partial_t+\partial_a)\boldsymbol{v}(t,a,x)=-\mathcal{D}(a,x)\boldsymbol{v}(t,a,x),\end{cases}\tag{2.5}$$

with, $h(\boldsymbol{u})(t)=H(E(t))=\left(1+\bar{h}(\boldsymbol{u})(t)\right)^{-\kappa}$, where $\bar{h}(\boldsymbol{u})(t)=E(t)$, and

$$\boldsymbol{m}(x,y)=\mathrm{diag}(m_0(x,y),m_1(x,y)),\quad \boldsymbol{r}(a,x)=\mathrm{diag}(r_0(a,x),r_1(a,x)),$$
$$\mathcal{D}(a,x)=\mathrm{diag}(d_0(a,x),d_1(a,x)),\quad \mathcal{N}(x)=\mathrm{diag}(\mu_0(x)+\gamma_0(x),\mu_1(x)+\gamma_1(x)),$$
$$\mathcal{B}[\boldsymbol{v}(t,\cdot,\cdot)](a,x)=\int_\Omega\boldsymbol{m}(x,y)\boldsymbol{r}(a,y)\boldsymbol{v}(t,a,y)\mathrm{d}y,\quad \mathcal{C}(x)=\begin{pmatrix}(1-c)\tau(x)\gamma_0(x) & 0\\ c\tau(x)\gamma_0(x) & \tau(x)\gamma_1(x)\end{pmatrix}.$$

Moreover, we set

$$\boldsymbol{\Pi}(\tau_1,\tau_2,x)=\exp\left(-\int_{\tau_1}^{\tau_2}\mathcal{D}(\sigma,x)\mathrm{d}\sigma\right),\ \text{with } 0\le\tau_1\le\tau_2,$$

the diagonal matrix whose diagonal components, denoted

$$\pi_i(\tau_1,\tau_2,x)=e^{-\int_{\tau_1}^{\tau_2}d_i(\sigma,x)\mathrm{d}\sigma},\quad i\in\{0,1\},\tag{2.6}$$

are finite constants under Assumption 2.1.

3. Main results

In this section, we establish the main results of the model (2.5). Such results include the existence of the unique maximal bounded semiflow. We also give necessary and sufficient conditions for the existence of steady states of the aforementioned model when parameter c is a constant function.

To establish the global well-posedness, positivity and dissipativity of the solutions of system (2.5), we formulate it as an abstract Cauchy problem. Let us introduce the Banach space $X=L^1(\Omega,\mathbb{R}^2)\times L^1(\Omega,\mathbb{R}^2)\times L^1((0,\infty)\times\Omega,\mathbb{R}^2)$, endowed with the usual product norm $\|\cdot\|_X$, as well as its positive cone $X_+=L^1_+(\Omega,\mathbb{R}^2)\times L^1_+(\Omega,\mathbb{R}^2)\times L^1_+((0,\infty)\times\Omega,\mathbb{R}^2)$. Consider the linear operator $\mathcal{A}:D(\mathcal{A})\subset X\to X$ be defined by $D(\mathcal{A})=W^{1,1}(\Omega,\mathbb{R}^2)\times\{0_{L^1(\Omega,\mathbb{R}^2)}\}\times W^{1,1}((0,\infty)\times\Omega,\mathbb{R}^2)$ and

$$\mathcal{A}\begin{pmatrix}\boldsymbol{u}\\ \mathbf{0}_{L^1}\\ \boldsymbol{v}\end{pmatrix}=\begin{pmatrix}-\mathcal{N}\boldsymbol{u}\\ -\boldsymbol{v}(0,\cdot)\\ -\partial_a\boldsymbol{v}-\mathcal{D}\boldsymbol{v}\end{pmatrix}.$$

Note that $\mathcal{A}$ is not densely defined in X as $\overline{D(\mathcal{A})}=X_0\subset X$. We note $X_{0+}=X_0\cap X_+$ the positive cone of X_0. Let $F:X_0\to X$ be the non-linear map defined by:

$$F\begin{pmatrix}\boldsymbol{u}\\ \mathbf{0}_{L^1}\\ \boldsymbol{v}\end{pmatrix}=\begin{pmatrix}h(\boldsymbol{u})\displaystyle\int_0^\infty\mathcal{B}[\boldsymbol{v}](a,\cdot)\mathrm{d}a\\ \mathcal{C}\boldsymbol{u}\\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R}^2)}\end{pmatrix}.\tag{3.1}$$

By setting $\boldsymbol{w}(t)=(\boldsymbol{u}(t,\cdot),0_{L^1},\boldsymbol{v}(t,\cdot,\cdot))^T$ and $\boldsymbol{w}_0=(\boldsymbol{u}_0,0_{L^1},\boldsymbol{v}_0)^T$ the associated initial condition, System (2.5) rewrites as the following abstract Cauchy problem:

$$\begin{cases}\dfrac{\mathrm{d}\boldsymbol{w}(t)}{\mathrm{d}t}=\mathcal{A}\boldsymbol{w}(t)+F(\boldsymbol{w}(t)),\quad t>0,\\ \boldsymbol{w}(0)=\boldsymbol{w}_0.\end{cases}\tag{3.2}$$

We have the following result.

Theorem 3.1. *Let Assumption 2.1 be satisfied. There exists a unique strongly continuous semiflow* $\{\Phi(t,\cdot): X_0 \to X_0\}_{t\geq 0}$ *such that, for each* $\boldsymbol{w}_0 \in X_{0+}$*, the map* $\boldsymbol{w} \in \mathcal{C}((0,\infty), X_{0+})$ *defined by* $\boldsymbol{w} = \Phi(\cdot, \boldsymbol{w}_0)$ *is a mild solution of (3.2), i.e.* $\int_0^t \boldsymbol{w}(s)\mathrm{d}s \in X_0$ *and* $\boldsymbol{w}(t) = \boldsymbol{w}_0 + \mathcal{A}\int_0^t \boldsymbol{w}(\sigma)\mathrm{d}\sigma + \int_0^t F(\boldsymbol{w}(\sigma))\mathrm{d}\sigma$ *for all* $t \geq 0$*. Moreover, the semiflow* $\{\Phi(t,\cdot)\}_{t\geq 0}$ *satisfies the following properties:*

1. *Let* $\Phi(t, \boldsymbol{w}_0) = (\boldsymbol{u}(t,\cdot), 0_{L^1}, \boldsymbol{v}(t,\cdot,\cdot))^T$*, then the following Volterra formulation holds true*
$$\boldsymbol{v}(t,a,x) = \begin{cases} \boldsymbol{\Pi}(a-t,a,x)\,\boldsymbol{v}_0(a-t,x) & \text{if } t \leq a, \\ \boldsymbol{\Pi}(0,a,x)\,\mathcal{C}(x)\,\boldsymbol{u}(t-a,x) & \text{if } t > a, \end{cases}$$
coupled with the $\boldsymbol{u}$*-equation of (2.5).*
2. *For all* $\boldsymbol{w}_0 \in X_0$*, we have*
$$E(t) \leq H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right), \quad \forall t > 0$$
and
$$\int_\Omega \int_0^\infty \frac{1}{\tau(x)}(A_0(t,a,x) + A_1(t,a,x))\mathrm{d}a\mathrm{d}x \leq z_0 e^{-t\beta} + \frac{\alpha}{\beta}H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right)\left(1 - e^{-t\beta}\right), \quad \forall t > 0,$$
where $z_0 = \int_\Omega \int_0^\infty \frac{1}{\tau(x)}(A_{0,0}(a,x) + A_{1,0}(a,x))\mathrm{d}a\mathrm{d}x$, $\nu = \|r\|_\infty \max\left\{\int_\Omega \sup_y m_0(x,y)\mathrm{d}x, \int_\Omega \sup_y m_1(x,y)\mathrm{d}x\right\}$ *and* $\alpha = \max\{\|\gamma_0\|_\infty, \|\gamma_1\|_\infty\}$, $\beta = \min\left\{\inf_{(a,x)\in(0,\infty)+\times\Omega} d_0, \inf_{(a,x)\in(0,\infty)+\times\Omega} d_1\right\}$*. The constant* $\bar{c}$ *satisfies:* $0 < \bar{c} < \min\left(\frac{\min\{\underline{\mu_0} + \underline{\gamma_0}, \underline{\mu_1} + \underline{\gamma_1}\}}{\alpha}, \frac{\nu}{\beta}\right)$*. Here,* $\underline{f} := \inf_{x\in\Omega} f$*.*
3. *The semi-flow* $\{\Phi(t,\cdot): X_0 \to X_0\}_{t\geq 0}$ *is bounded dissipative, that is, there exists a bounded set* $\mathcal{K} \subset X_0$ *such that for any bounded set* $\mathcal{Q} \subset X_0$*, there exists* $\tau = \tau(\mathcal{Q}, \mathcal{K}) \geq 0$ *such that* $\Phi(t, \mathcal{Q}) \subset \mathcal{K}$ *for* $t \geq \tau$*.*
4. *The semi-flow* $\{\Phi(t,\cdot)\}_t$ *is asymptotically smooth in* X_+*, i.e. for any nonempty, closed, bounded and positively invariant set* $B \subset X_+$*, there exists a compact set* $\mathcal{K} \subset X_+$ *such that* $\lim_{t\to\infty} d_H(\Phi_t(B), K) = 0$*, where* d_H *is the Hausdorff semi-distance [18] defined as* $d_H(B, \mathcal{K}) = \sup_{w\in B}\inf_{v\in\mathcal{K}} \|w - v\|_X$*.*

Remark that item 1 of Assumption 2.2 is not required for the results stated in Theorem 3.1 (item 4).

3.1. Proof of Theorem 3.1

3.1.1. Proof of Theorem 3.1: Items 1, 2 and 3

We can easily check that the operator $\mathcal{A}$ is a Hille–Yosida operator and the nonlinear map F defined in (3.1) is positive, continuous and locally Lipschitz on X_0. Then, standard results can be applied to provide the existence and uniqueness of a mild solution to (3.2) (see [29, 41, 43]). The Volterra formulation is also well known (see [23, 45] for more details).

For the boundedness, let us set
$$E(t) = \int_\Omega (E_0(t,x) + E_1(t,x))\mathrm{d}x, \quad A(t) = \int_\Omega \int_0^\infty \frac{1}{\tau(x)}(A_0(t,a,x) + A_1(t,a,x))\mathrm{d}a\mathrm{d}x.$$

Then, by (2.3)–(2.4), it comes
$$\begin{aligned} \dot{E}(t) =& H(E(t))\int_\Omega\int_\Omega\int_0^\infty (m_0(x,y)r_0(a,y)A_0(t,a,y) + m_1(x,y)r_1(a,y)A_1(t,a,y))\mathrm{d}a\mathrm{d}y\mathrm{d}x \\ &- \int_\Omega (\mu_0(x) + \gamma_0(x))E_0(t,x)\mathrm{d}x - \int_\Omega (\mu_1(x) + \gamma_1(x))E_1(t,x)\mathrm{d}x, \\ \dot{A}(t) =& \int_\Omega (\gamma_0(x)E_0(t,x) + \gamma_1(x)E_1(t,x))\mathrm{d}x - \int_\Omega\int_0^\infty \frac{1}{\tau(x)}(d_0(a,x)A_0(t,a,x) + d_1(a,x)A_1(t,a,x))\mathrm{d}a\mathrm{d}x. \end{aligned}$$

By Assumption 2.1, we find that

$$\begin{aligned}\dot{E}(t) &\leq \nu H(E(t))A(t) - \zeta E(t),\\ \dot{A}(t) &\leq \alpha E(t) - \beta A(t),\end{aligned} \tag{3.3}$$

where $\nu = \|\tau\|_\infty \max\left\{\|r_0\|_\infty \int_\Omega \sup_y m_0(x,y)\mathrm{d}x, \|r_1\|_\infty \int_\Omega \sup_y m_1(x,y)\mathrm{d}x\right\}$, $\zeta = \min\left(\underline{\mu}_0 + \underline{\gamma}_0, \underline{\mu}_1 + \underline{\gamma}_1\right)$, $\alpha = \max\{\|\gamma_0\|_\infty, \|\gamma_1\|_\infty\}$ and $\beta = \min\left\{\inf_{(a,x)\in(0,\infty)+\times\Omega} d_0, \inf_{(a,x)\in(0,\infty)+\times\Omega} d_1\right\}$. Here, $\underline{f} := \inf\limits_{x\in\Omega} f$.

Let $\bar{c} > 0$, and set $W = E + \bar{c}A$. Estimates (3.3) give

$$\dot{W}(t) \leq (\bar{c}\alpha - \zeta)\, E(t) + (\nu H\,(E(t)) - \bar{c}\beta)\, A(t). \tag{3.4}$$

Since the function H, introduced in (2.2), is decreasing and takes values in (0, 1), we have

$$\nu H\,(E(t)) - \bar{c}\beta < 0 \quad \text{iff} \quad E(t) > H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right),$$

where, of course, the above estimate holds on the necessary condition $\frac{\bar{c}\beta}{\nu} \in (0,1)$. Thus, by choosing $\bar{c}$, such that

$$0 < \bar{c} < \min\left(\frac{\zeta}{\alpha}, \frac{\nu}{\beta}\right), \tag{3.5}$$

estimate (3.4) leads to $\dot{W}(t) < 0$ as soon as $E(t) > H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right)$. From where we find that E is ultimately bounded and for all t,

$$E(t) \leq H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right),$$

with $\bar{c}$ satisfying (3.5).

Finally, by (3.3), we find for all $t \geq 0$:

$$A(t) \leq A(0)e^{-t\beta} + \frac{\alpha}{\beta}H^{-1}\left(\frac{\bar{c}\beta}{\nu}\right)\left(1 - e^{-t\beta}\right).$$

This ends the proof of items 1, 2 and 3 of Theorem 3.1.

3.1.2. Proof of Theorem 3.1: Item 4

We first introduce the following proposition:

Proposition 3.1. *Let Assumptions 2.1 and 2.2 hold. Then, the semiflow $\{\Phi(t)\}_{t\geq 0}$ induced by the Cauchy problem (3.2) satisfies, $\Phi = \Phi_1 + \Phi_2$, such that*

1. *For each $t > 0$, $\Phi_1(t) : X_{0+} \to X$, maps bounded sets of X_{0+} into relatively compact sets of X;*
2. *There exists $\zeta : [0, +\infty) \times [0, +\infty) \to [0, +\infty)$ such that for each $\epsilon > 0$, $\lim\limits_{t\to+\infty} \zeta(t,\epsilon) \to 0$ and, if $\boldsymbol{w}_0 \in X_{0+}$ with $\|\boldsymbol{w}_0\|_X \leq \epsilon$, then $\|\Phi_2(t)\boldsymbol{w}_0\|_X \leq \zeta(t,\epsilon)$ for all $t \geq 0$.*

Before providing the proof of Proposition 3.1, note that, by [18, Lemma 3.2.3], this proposition concludes the proof of Theorem 3.1, item 4.

Proof of Proposition 3.1. The nonlinear map F, given by (3.1), is such that $F = F_1 + F_2$, with

$$F_1\begin{pmatrix}\boldsymbol{u}\\ \boldsymbol{0}_{L^1}\\ \boldsymbol{v}\end{pmatrix} = \begin{pmatrix} h(\boldsymbol{u})\displaystyle\int_0^\infty \mathcal{B}[\boldsymbol{v}](a,\cdot)\mathrm{d}a\\ \boldsymbol{0}_{L^1}\\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R}^2)}\end{pmatrix}, \text{ and } \quad F_2\begin{pmatrix}\boldsymbol{u}\\ \boldsymbol{0}_{L^1}\\ \boldsymbol{v}\end{pmatrix} = \begin{pmatrix}\boldsymbol{0}_{L^1}\\ \mathcal{C}\boldsymbol{u}\\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R}^2)}\end{pmatrix}. \tag{3.6}$$

By Assumptions 2.1 and 2.2, F_1 maps bounded sets of X_{0+} into a relatively compact set of X_0 (e.g. see [13]). Let $B \subseteq X_{0+}$ be a bounded subset of X_{0+}. Note that for any $\boldsymbol{w}_0 \in B$, the integrated solution $t \in [0, +\infty) \mapsto \Phi(t)\boldsymbol{w}_0$ of the Cauchy problem (3.2) writes, for all $t \geq 0$:

$$\Phi(t)\boldsymbol{w}_0 = T_{\mathcal{A}_0}(t)\boldsymbol{w}_0 + \lim_{\lambda \to +\infty} \int_0^t T_{\mathcal{A}_0}(t-s)\lambda(\lambda - \mathcal{A})^{-1}F(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s, \tag{3.7}$$

where $\mathcal{A}_0 : \mathcal{D}(\mathcal{A}_0) \subset X_0 \to X$ is the part of $\mathcal{A}$ on X_0, defined by

$$\mathcal{A}_0\boldsymbol{w} := \mathcal{A}\boldsymbol{w}, \ \forall \boldsymbol{w} \in \mathcal{D}(\mathcal{A}_0) = \{\boldsymbol{w} \in \mathcal{D}(A) : \mathcal{A}\boldsymbol{w} \in X_0\},$$

and $\{T_{\mathcal{A}_0}(t)\}_t$ is the C_0-semigroup generated by $\mathcal{A}_0$.

By [42, Theorem 3.14] and [28, Lemma 2.1], note that $\mathsf{s}(\mathcal{A}_0) = \mathsf{s}(\mathcal{A}) < 0$, where $\mathsf{s}(G)$ is the spectral bound of G defined by:

$$\mathsf{s}(G) := \sup\{\Re(\lambda) : \lambda \text{ is in the spectral set of } G\}.$$

Consequently, if $\omega_{\mathcal{A}} \in (-\mathsf{s}(\mathcal{A}_0), 0)$, there exists a constant $M_{\mathcal{A}} \geq 1$ such that:

$$\|T_{\mathcal{A}_0}(t)\|_{\mathcal{L}(X_0)} \leq M_{\mathcal{A}}e^{-\omega_{\mathcal{A}}t}, \ \forall t \geq 0. \tag{3.8}$$

Define, for each $\boldsymbol{w}_0 \in B$, the maps $t \mapsto \hat{\Phi}(t)\boldsymbol{w}_0$, $t \mapsto \tilde{\Phi}(t)\boldsymbol{w}_0$ and $t \mapsto \check{\Phi}(t)\boldsymbol{w}_0$ by:

$$\hat{\Phi}(t)\boldsymbol{w}_0 = \lim_{\lambda \to +\infty} \int_0^t T_{\mathcal{A}_0}(t-s)\lambda(\lambda - \mathcal{A})^{-1}F_1(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s, \tag{3.9}$$

$$\tilde{\Phi}(t)\boldsymbol{w}_0 = \lim_{\lambda \to +\infty} \int_0^t T_{\mathcal{A}_0}(t-s)\lambda(\lambda - \mathcal{A})^{-1}F_2(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s, \tag{3.10}$$

$$\check{\Phi}(t)\boldsymbol{w}_0 = T_{\mathcal{A}_0}\Phi(t)\boldsymbol{w}_0. \tag{3.11}$$

The uniqueness of the integrated solution (3.7) and (3.9)–(3.11) gives: for each $\boldsymbol{w}_0 \in B$,

$$\Phi(t)\boldsymbol{w}_0 = \hat{\Phi}(t)\boldsymbol{w}_0 + \check{\Phi}(t)\boldsymbol{w}_0 + \tilde{\Phi}(t)\boldsymbol{w}_0, \ \forall t \geq 0.$$

By items 1, 2 and 3 of Theorem 3.1, we can find a positive constant $\ell_0 := \ell_0(B) > 0$ such that

$$\sup_{t \geq 0, \boldsymbol{w}_0 \in B} \|\Phi(t)\boldsymbol{w}_0\|_X \leq \ell_0. \tag{3.12}$$

Furthermore, by estimate (3.8), the equality (3.11) and the boundedness of B, we can find a positive constant $\ell_1 := \ell_1(B) > 0$ such that

$$\sup_{\boldsymbol{w}_0 \in B} \|\check{\Phi}(t)\boldsymbol{w}_0\|_X \leq \ell_1 e^{-\omega_{\mathcal{A}}t}, \ \forall t \geq 0. \tag{3.13}$$

□

Proposition 3.1 is direct consequence of the following lemma:

Lemma 3.1. *Let Assumptions 2.1 and 2.2 be satisfied. Then,*

1. *For each $T > 0$, the set $S_B = \{\hat{\Phi}(\cdot)\boldsymbol{w}_0 \in C([0, T], X_0) : \boldsymbol{w}_0 \in B\}$ is relatively compact in $C([0, T], X_0)$.*
2. *The nonlinear maps $\{\tilde{\Phi}(t)\}_{t \geq 0}$ defined in (3.10) has the form $\tilde{\Phi} = \tilde{\Phi}_1 + \tilde{\Phi}_2$, such that*
   - *(i) For each $t > 0$, $\tilde{\Phi}_1(t) : X_{0+} \to X$, maps B into relatively compact sets of X;*
   - *(ii) There exists a constant $\ell = \ell(B) > 0$ such that $\|\tilde{\Phi}_2(t)\boldsymbol{w}_0\|_X \leq \ell e^{-\omega_{\mathcal{A}}t}$, for all $t \geq 0$ and $\boldsymbol{w}_0 \in B$; with $\omega_{\mathcal{A}} \in (-\mathsf{s}(\mathcal{A}_0), 0)$.*

Therefore, to conclude the proof of Proposition 3.1, and consequently, the proof of Theorem 3.1 (item 4), we will provide additional details on the proof of Lemma 3.1.

Proof of Lemma 3.1: item 1. Our aim is to prove that for all $t \geq 0$, the set $S_B(t)$ defined by $S_B(t) = \{\hat{\Phi}(t)\boldsymbol{w}_0 : \boldsymbol{w}_0 \in B\}$ is compact in X_0 and S_B is an equicontinuous family. Because $F_1(\Phi(s)\boldsymbol{w}_0) \in X_0$ for all $s \geq 0$, $\boldsymbol{w}_0 \in B$, (3.9) rewrites

$$\hat{\Phi}(t)\boldsymbol{w}_0 = \int_0^t T_{\mathcal{A}_0}(t-s)F_1(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s,$$

and by (3.12), we introduce the bounded set $B_0 = \{\Phi(t)\boldsymbol{w}_0 : t \geq 0, \boldsymbol{w}_0 \in B\}$. Thus, the compactness of F_1 gives that $F_1(B_0)$ is relatively compact. Since $(s, y) \mapsto T_{\mathcal{A}_0}(s)y$ is continuous, it comes that

$$\{T_{\mathcal{A}_0}(t-s)F_1(\Phi(s)\boldsymbol{w}_0) : s \in [0, t], \boldsymbol{w}_0 \in B\} \subset \{T_{\mathcal{A}_0}(t-s)F_1(y) : s \in [0, t], y \in B_0\}$$

is relatively compact. Consequently, Mazur's theorem (see, e.g. [9, Corollary 3.8] or the original paper by Mazur [31]) implies that for all $t > 0$, the set $S_B(t)$ is relatively compact.

It remains to prove that S_B is equicontinuous. Let $0 \leq t_0 \leq t \leq T$, then

$$\begin{aligned}\hat{\Phi}(t)\boldsymbol{w}_0 - \hat{\Phi}(t_0)\boldsymbol{w}_0 &= \textstyle\int_{t_0}^{t} T_{\mathcal{A}_0}(t-s)F_1(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s + \int_0^{t_0} [T_{\mathcal{A}_0}(t-s) - T_{\mathcal{A}_0}(t_0-s)]F_1(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s \\ &= \textstyle\int_{t_0}^{t} T_{\mathcal{A}_0}(t-s)F_1(\Phi(s)\boldsymbol{w}_0)\mathrm{d}s + \int_0^{t_0} [T_{\mathcal{A}_0}(t-t_0+s) - T_{\mathcal{A}_0}(s)]F_1(\Phi(t_0-s)\boldsymbol{w}_0)\mathrm{d}s.\end{aligned}$$

The above equality leads to

$$\|\hat{\Phi}(t)\boldsymbol{w}_0 - \hat{\Phi}(t_0)\boldsymbol{w}_0\|_X \leq \sup_{y \in B_0} \|F_1(y)\|_X \int_{t_0}^{t} M_{\mathcal{A}} e^{-\omega_{\mathcal{A}}(t-s)}\mathrm{d}s + t_0 \sup_{s \in [0,t_0], y \in F_1(B_0)} \|T_{\mathcal{A}_0}(t-t_0+s)y - T_{\mathcal{A}_0}(s)y\|_X.$$

The equicontinuity of S_B holds from the above estimate and the relative compactness of $F_1(B_0)$. □

Proof of Lemma 3.1: item 2. For $t \geq 0$ and $\boldsymbol{w}_0 \in B$, set $\Phi(t)\boldsymbol{w}_0 = (\boldsymbol{u}(t,\cdot), 0_{L^1}, \boldsymbol{v}(t,\cdot,\cdot))$, as well as $\hat{\Phi}(t)\boldsymbol{w}_0 = (\hat{\boldsymbol{u}}(t,\cdot), 0_{L^1}, \hat{\boldsymbol{v}}(t,\cdot,\cdot))$, $\tilde{\Phi}(t)\boldsymbol{w}_0 = (\tilde{\boldsymbol{u}}(t,\cdot), 0_{L^1}, \tilde{\boldsymbol{v}}(t,\cdot,\cdot))$ and $\check{\Phi}(t)\boldsymbol{w}_0 = (\check{\boldsymbol{u}}(t,\cdot), 0_{L^1}, \check{\boldsymbol{v}}(t,\cdot,\cdot))$. Therefore,

$$\boldsymbol{f} = \hat{\boldsymbol{f}} + \tilde{\boldsymbol{f}} + \check{\boldsymbol{f}}, \text{ for } \quad \boldsymbol{f} \in \{\boldsymbol{u}, \boldsymbol{v}\}. \tag{3.14}$$

By estimates (3.12) and (3.13), we, respectively, have, $\forall t \geq 0$:

$$\begin{cases}\sup_{\boldsymbol{w}_0 \in B} \|\boldsymbol{u}(t,\cdot)\|_{L^1} \leq \ell_0, \\ \sup_{\boldsymbol{w}_0 \in B} \|\check{\boldsymbol{u}}(t,\cdot)\|_{L^1} \leq \ell_1 e^{-\omega_{\mathcal{A}} t}.\end{cases} \tag{3.15}$$

By (3.6) and (3.10), we have

$$\begin{cases}\partial_t \tilde{\boldsymbol{u}}(t,\cdot) = -\mathcal{N}\tilde{\boldsymbol{u}}(t,\cdot), \\ \tilde{\boldsymbol{v}}(t,0,\cdot) = \mathcal{C}\boldsymbol{u}(t,\cdot), \\ (\partial_t + \partial_a)\tilde{\boldsymbol{v}}(t,\cdot,\cdot) = -\mathcal{D}\tilde{\boldsymbol{v}},\end{cases}$$

with the initial condition $\tilde{\boldsymbol{u}}(0,\cdot) = \boldsymbol{0}_{L^1}$, and $\tilde{\boldsymbol{v}}(0,\cdot,\cdot) = \boldsymbol{0}_{L^1}$. It then comes, for all $t \geq 0$:

$$\tilde{\boldsymbol{u}}(t,\cdot) \equiv \boldsymbol{0}_{L^1}, \text{ and } \quad \tilde{\boldsymbol{v}}(t,a,\cdot) = \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\,\boldsymbol{u}(t-a,\cdot). \tag{3.16}$$

Thus, by (3.14) and (3.16), we find

$$\boldsymbol{u} = \hat{\boldsymbol{u}} + \check{\boldsymbol{u}}.$$

Therefore, (3.16) gives

$$\tilde{\boldsymbol{v}}(t,a,\cdot) = \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\left(\hat{\boldsymbol{u}}(t-a,\cdot) + \check{\boldsymbol{u}}(t-a,\cdot)\right) := \tilde{\boldsymbol{v}}_1[\boldsymbol{w}_0](t,a,\cdot) + \tilde{\boldsymbol{v}}_2[\boldsymbol{w}_0](t,a,\cdot),$$

with $\tilde{\boldsymbol{v}}_1[\boldsymbol{w}_0](t,a,\cdot) = \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\hat{\boldsymbol{u}}(t-a,\cdot)$, and $\tilde{\boldsymbol{v}}_2[\boldsymbol{w}_0](t,a,\cdot) = \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\check{\boldsymbol{u}}(t-a,\cdot)$.

We now show that the set $\{\tilde{\boldsymbol{v}}_1[\boldsymbol{w}_0](t,\cdot,\cdot)\}_{\boldsymbol{w}_0 \in B}$ is relatively compact in $L^1((0,\infty) \times \Omega)$. Let $\{\tilde{\boldsymbol{v}}_{1,n}(t,a,\cdot) = \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\hat{\boldsymbol{u}}_n(t-a,\cdot)\}_{n \in \mathbb{N}}$ a bounded sequence in $\left\{\tilde{\boldsymbol{v}}_1[\boldsymbol{w}_0](t,\cdot,\cdot)\right\}_{\boldsymbol{w}_0 \in B}$. By Lemma 3.1 (item 1.), the set $\{\hat{\boldsymbol{u}}_n(t,\cdot)\}_{n \in \mathbb{N}}$ is compact in $C\left([0,t], L^1(\mathbb{R})\right)$. As a result, we can find $\bar{\hat{\boldsymbol{u}}} \in C\left([0,t], L^1(\mathbb{R})\right)$, such that $\hat{\boldsymbol{u}}_n \to \bar{\hat{\boldsymbol{u}}}$ in $C\left([0,t], L^1(\mathbb{R})\right)$, as $n \to \infty$. Thus, $\tilde{\boldsymbol{v}}_{1,n}(t,a,\cdot) \to \boldsymbol{1}_{[0,t]}(a)\boldsymbol{\Pi}(0,a,\cdot)\,\mathcal{C}(\cdot)\bar{\hat{\boldsymbol{u}}}(t-a,\cdot)$, in $L^1((0,\infty) \times \Omega)$, as $n \to \infty$.

Finally, by (3.15), we can find a positive constant $\ell = \ell(B)$, such that $\|\tilde{\boldsymbol{v}}_2[\boldsymbol{w}_0](t,\cdot,\cdot)\|_{L^1} \leq \ell e^{-\omega_{\mathcal{A}} t}$, for all $t \geq 0$. This ends the proof of Lemma 3.1. □

3.2. The steady states

The next results are concerned with the existence of the steady states of the system (3.2), which always exhibits a mosquito-free steady state given by $\mathcal{E}^0 = (0, 0, 0, 0)^T$.

The existence of fully-exposed and co-existence steady states of System (3.2) is strongly related to the linear operator $\boldsymbol{\mathcal{L}}$ defined by:

$$\boldsymbol{\mathcal{L}} : (L^1(\Omega))^2 \ni \boldsymbol{\varphi}(\cdot) \longmapsto \int_{\Omega} \boldsymbol{m}(\cdot, y)\boldsymbol{\theta}(y)\boldsymbol{\varphi}(y)\mathrm{d}y \in (L^1(\Omega))^2, \tag{3.17}$$

where $\boldsymbol{\theta} : \Omega \to \mathbb{R}^2_+$:

$$\boldsymbol{\theta}(x) = \left(\int_0^{\infty} \boldsymbol{r}(a, x)\boldsymbol{\Pi}(0, a, x)\mathrm{d}a\right)\mathcal{C}(x)\mathcal{N}^{-1}(x). \tag{3.18}$$

Note that

$$\boldsymbol{\mathcal{L}} = \begin{pmatrix} (1-c)\mathcal{L}_0 & 0 \\ c\mathcal{L}_0 & \mathcal{L}_1 \end{pmatrix},$$

with $\mathcal{L}_j$,s the linear operators defined by:

$$\mathcal{L}_j : L^1(\Omega) \ni \varphi(\cdot) \longmapsto \int_{\Omega} m_j(\cdot, y)\theta_j(y)\varphi(y)\mathrm{d}y \in L^1(\Omega), \quad \text{for} \quad j \in \{0, 1\}, \tag{3.19}$$

with

$$\theta_j(x) = \frac{\tau(x)\gamma_j(x)}{\mu_j(x) + \gamma_j(x)} \int_0^{\infty} r_j(a, x)\pi_j(0, a, x)\mathrm{d}a, \quad j \in \{0, 1\}. \tag{3.20}$$

The quantity $\theta_j(x)$ can be interpreted as the reproductive number (or fitness) of an AFM with the insecticide resistance level x in insecticide state j. Note that $\theta_j(x)$ – hereafter referred to as the *fitness function* – represents the fitness of an AFM with insecticide resistance level x within the j – insecticide state. In the above expression, the survival probability $\pi_j(0, a, x) = e^{-\int_0^a d_j(\sigma,x),d\sigma}$ of an AFM with IR level x up to age a, multiplied by $r_j(a, x)$, represents the contribution of the AFM to egg production at age a. Integrating this product over all ages a gives the total number of eggs effectively produced by the AFM during its lifetime. Note that under Assumption 2.1, the positive functions $\theta_j : \Omega \mapsto \mathbb{R}_+$ are continuous. The vector-valued fitness function $\boldsymbol{\theta}(x)$ then represents the overall fitness of AFMs with insecticide resistance level x. Finally, note that here, θ_j is not derived directly from the next-generation operator approach, but it can be shown that this corresponds to the basic reproduction number when applying the next-generation operator approach [13, 38].

We then have the following result.

Theorem 3.2. *Let Assumption 2.1 be satisfied. Let $r(\mathcal{L}_j)$ for $j \in \{0, 1\}$ and $r(\boldsymbol{\mathcal{L}})$ denote the spectral radii of the operators $\mathcal{L}_j$ and $\boldsymbol{\mathcal{L}}$, respectively. Additionally, let ϕ_j^* and $\boldsymbol{\psi}^*$ be their associated positive eigenfunctions, which are normalized such that $\|\phi_j^*\|_{L^1} = 1$ and $\|\boldsymbol{\psi}^*\|_{L^1 \times L^1} = 1$.*

1. *When $r(\mathcal{L}_j) < 1$ for all $j \in \{0, 1\}$, the mosquito-free steady state $\mathcal{E}^0 = (0, 0, 0, 0)^T$ is the unique steady state of system (3.2).*
2. *When $r(\mathcal{L}_1) > 1$ and $c = 1$, in addition to $\mathcal{E}^0$, system (3.2) has a fully-exposed steady state $\mathcal{E}^R = (0, 0, E_1^R(x), A_1^R(a, x))^T$ such that:*

$$E_1^R(x) = p[\mathcal{E}^R]\frac{\phi_1^*(x)}{\mu_1(x) + \gamma_1(x)} \quad \textit{and} \quad A_1^R(a, x) = p[\mathcal{E}^R]\frac{\tau(x)\gamma_1(x)\phi_1^*(x)}{\mu_1(x) + \gamma_1(x)}\pi_1(0, a, x),$$

with

$$p[\mathcal{E}^R] = \left(r(\mathcal{L}_1)^{\frac{1}{K}} - 1\right)\left(\int_{\Omega} \frac{\phi_1(x)}{\mu_1(x) + \gamma_1(x)}\mathrm{d}x\right)^{-1}.$$

3. *When* $r(\boldsymbol{\mathcal{L}}) = \max\left((1-c)r(\mathcal{L}_0), r(\mathcal{L}_1)\right) > 1$, *system* (3.2) *has a positive steady state* $\mathcal{E}^* = (u^*(x), v^*(a,x))$ *with* $u^*(x) = (E_0^*(x), E_1^*(x))$ *and* $v^*(a,x) = (A_0^*(a,x), A_1^*(a,x))$ *such that*

$$u^*(x) = p\,[\mathcal{E}^*]\,\mathcal{N}^{-1}(x)\boldsymbol{\psi}^*(x) \quad \text{and} \quad v^*(a,x) = p\,[\mathcal{E}^*]\,\boldsymbol{\Pi}(0,a,x)\mathcal{C}(x)\mathcal{N}^{-1}(x)\boldsymbol{\psi}^*(x),$$

where

$$p\,[\mathcal{E}^*] = \left(r(\boldsymbol{\mathcal{L}})^{\frac{1}{\kappa}} - 1\right)\bar{h}\left(\mathcal{N}^{-1}(\cdot)\boldsymbol{\psi}^*(\cdot)\right)^{-1}.$$

Furthermore, at the positive steady state $\mathcal{E}^*$, *the total number of AFM unexposed to insecticide* A_0^* *and exposed to insecticide* A_1^* *is such that*

$$A_0^* = p\,[\mathcal{E}^*]\,(1-c)\int_\Omega \frac{\tau(x)\gamma_0(x)\bar{\pi}_0(x)}{\mu_0(x)+\gamma_0(x)}\psi_0^*(x)\mathrm{d}x, \tag{3.21}$$

$$A_1^* = p\,[\mathcal{E}^*]\,c\int_\Omega \frac{\tau(x)\gamma_0(x)\bar{\pi}_1(x)}{\mu_1(x)+\gamma_1(x)}\psi_0^*(x)\mathrm{d}x + p\,[\mathcal{E}^*]\int_\Omega \frac{\tau(x)\gamma_1(x)\bar{\pi}_1(x)}{\mu_1(x)+\gamma_1(x)}\psi_1^*(x)\mathrm{d}x, \tag{3.22}$$

where $\boldsymbol{\psi}^* = (\psi_0^*, \psi_1^*)$, *and* $\bar{\pi}_j(x) = \int_0^\infty \pi_j(0,a,x)\mathrm{d}a$ *is the average lifespan of AFM with the IR level* x.

Before going through the proof of Theorem 3.2, observe that the positive steady state $\mathcal{E}^*$ is closely related to the principal eigenfunction of the linear operators $\mathcal{L}$ for any given probability kernel m satisfying Assumptions 2.1 and 2.2. The profile of the steady state $\mathcal{E}^*$ with respect to $x \in \Omega$ can be explicitly characterized when mutation kernels m_j depends on a small positive parameter ε (with $\varepsilon \ll 1$) using the scaling form:

$$m_j^\varepsilon(x) = \varepsilon^{-1}m_j\left(\varepsilon^{-1}x\right),$$

where $\varepsilon > 0$ represents the mutation variance in the phenotypic space. Specifically, for small ε, the eigenfunction ψ_j concentrates on the set $\mathcal{M}_j$ defined by:

$$\mathcal{M}_j = \left\{x \in \Omega : \theta_j(x) = \|\theta_j\|_\infty\right\}.$$

This set, $\mathcal{M}_j$, is known as the set of evolutionary attractors (or dominant strains) in the classical adaptive dynamics framework (e.g. [17, 32]). Moreover, when θ_j is at least $\mathcal{C}^1$ with a finite number of maxima, it has been shown in [13] that these dominant strains coincide with the set $\mathcal{M}_j$.

Denoting by $\mathcal{L}_j^\varepsilon$ the operator $\mathcal{L}_j$ modified by replacing the kernel m_j with m_j^ε, it follows from Theorem 2.2 in [13] that the spectral radius $r\left(\mathcal{L}_j^\varepsilon\right)$ satisfies, for sufficiently small ε:

$$r\left(\mathcal{L}_j^\varepsilon\right) = \left(\theta_j(x^*)\right)^2 + \mathcal{O}(\varepsilon), \quad \text{for all } x^* \in \mathcal{M}_j.$$

From this estimate, we deduce that $\operatorname{sign}\left[r(\boldsymbol{\mathcal{L}}) - 1\right] = \operatorname{sign}\left[\max\left((1-c)\theta_0^2(x^*), \theta_1^2(x^*)\right) - 1\right]$, for all $x^* \in \mathcal{M}_j$ and sufficiently small ε. Furthermore, if $\varepsilon \ll 1$, $\mathcal{M}_j = \{x_j^*\}$ and $\max\left((1-c)\theta_0^2(x_j^*), \theta_1^2(x_j^*)\right) > 1$, then the eigenfunction ψ_j^* is concentrated around the evolutionary attractor x_j^* in the IR space Ω and $\lim_{\varepsilon\to 0}\int_\Omega w(x)\psi_j^*(x)\mathrm{d}x = w\left(x_j^*\right)$ for any continuous function $w \in \mathcal{C}\left(\Omega\right)$. For a detailed analysis of this concentration phenomenon, see Theorem 2.3 in [13].

Consequently, for sufficiently small ε, by (3.21)–(3.22), the total number of FM exposed and unexposed at the positive steady state $\mathcal{E}^*$ rewrite

$$A_0^* = p\,[\mathcal{E}^*]\,(1-c)\frac{\tau(x_0^*)\gamma_0(x_0^*)\bar{\pi}_0(x_0^*)}{\mu_0(x_0^*)+\gamma_0(x_0^*)},$$

$$A_1^* = p\,[\mathcal{E}^*]\,c\frac{\tau(x_0^*)\gamma_0(x_0^*)\bar{\pi}_1(x_0^*)}{\mu_1(x_0^*)+\gamma_1(x_0^*)} + p\,[\mathcal{E}^*]\,\frac{\tau(x_1^*)\gamma_1(x_1^*)\bar{\pi}_1(x_1^*)}{\mu_1(x_1^*)+\gamma_1(x_1^*)}.$$

3.2.1. Proof of Theorem 3.2

Recall that in this section, we assume that c is a constant function. The steady states of system (2.5) are obtained by solving the following system:

$$\begin{cases} H\left(E^*\right)\displaystyle\int_\Omega\int_0^\infty m_0(x,y)r_0(a,y)A_0^*(a,y)\mathrm{d}a\mathrm{d}y-\left(\mu_0(x)+\gamma_0(x)\right)E_0^*(x)=0,\\ A_0^*(0,x)=(1-c)\tau(x)\gamma_0(x)E_0^*(x),\\ \partial_aA_0^*(a,x)=-d_0(a,x)A_0^*(a,x),\\ H\left(E^*\right)\displaystyle\int_\Omega\int_0^\infty m_1(x,y)r_1(a,y)A_1^*(a,y)\mathrm{d}a\mathrm{d}y-\left(\mu_1(x)+\gamma_1(x)\right)E_1^*(x)=0,\\ A_1^*(0,x)=c\tau(x)\gamma_0(x)E_0^*(x)+\tau(x)\gamma_1(x)E_1^*(x),\\ \partial_aA_1^*(a,x)=-d_1(a,x)A_1^*(a,x), \end{cases} \tag{3.23}$$

where

$$E^*=\int_\Omega\left(E_0^*(x)+E_1^*(x)\right)\mathrm{d}x,$$

and

$$H(E^*)=(1+E^*)^{-\kappa},\kappa>0. \tag{3.24}$$

1. It is obvious that $\mathcal{E}^0=(0,0,0,0)^T$ is a trivial solution of (3.23) without any condition.
2. In an environment where all mosquitoes are exposed to the insecticide (i.e. $c=1$), system (3.23) becomes

$$\begin{cases} H\left(E^*\right)\displaystyle\int_\Omega\int_0^\infty m_0(x,y)r_0(a,y)A_0^*(a,y)\mathrm{d}a\mathrm{d}y-\left(\mu_0(x)+\gamma_0(x)\right)E_0^*(x)=0,\\ A_0^*(0,x)=0,\\ \partial_aA_0^*(a,x)=-d_0(a,x)A_0^*(a,x),\\ H\left(E^*\right)\displaystyle\int_\Omega\int_0^\infty m_1(x,y)r_1(a,y)A_1^*(a,y)\mathrm{d}a\mathrm{d}y-\left(\mu_1(x)+\gamma_1(x)\right)E_1^*(x)=0,\\ A_1^*(0,x)=\tau(x)\gamma_0(x)E_0^*(x)+\tau(x)\gamma_1(x)E_1^*(x),\\ \partial_aA_1^*(a,x)=-d_1(a,x)A_1^*(a,x). \end{cases} \tag{3.25}$$

Solving (3.25) for A_0^* yields $A_0^*\equiv0$, which in turn implies that $E_0^*\equiv0$. Thus, system (3.25) rewrites as:

$$\begin{cases} H\left(E^*\right)\displaystyle\int_\Omega\int_0^\infty m_1(x,y)r_1(a,y)A_1^*(a,y)\mathrm{d}a\mathrm{d}y-\left(\mu_1(x)+\gamma_1(x)\right)E_1^*(x)=0,\\ A_1^*(0,x)=\tau(x)\gamma_1(x)E_1^*(x),\\ \partial_aA_1^*(a,x)=-d_1(a,x)A_1^*(a,x), \end{cases} \tag{3.26}$$

where

$$E^*=\int_\Omega E_1^*(x)\mathrm{d}x. \tag{3.27}$$

Solving (3.26) for A_1^* gives

$$A_1^*(a,x)=\tau(x)\gamma_1(x)\pi_1(0,a,x)E_1^*(x). \tag{3.28}$$

Replacing (3.28) in the first equation of (3.26) yields

$$H\left(E^*\right)\int_\Omega\int_0^\infty m_1(x,y)r_1(a,y)\tau(y)\gamma_1(y)\pi_1(0,a,y)E_1^*(y)\mathrm{d}a\mathrm{d}y=\left(\mu_1(x)+\gamma_1(x)\right)E_1^*(x). \tag{3.29}$$

By setting $\bar{E}_1^*(x) = (\mu_1(x) + \gamma_1(x))\, E_1^*(x)$, (3.29) becomes

$$\int_\Omega \int_0^\infty m_1(x,y)\frac{\tau(y)\gamma_1(y)}{\mu_1(y)+\gamma_1(y)} r_1(a,y)\pi_1(0,a,y)\bar{E}_1^*(y)\mathrm{d}a\mathrm{d}y = \frac{1}{H(E^*)}\bar{E}_1^*(x),$$

which leads to

$$\int_\Omega m_1(x,y)\theta_1(y)\bar{E}_1^*(y)\mathrm{d}y = \frac{1}{H(E^*)}\bar{E}_1^*(x), \tag{3.30}$$

where θ_1 is given by

$$\theta_1(y) = \frac{\tau(y)\gamma_1(y)}{\mu_1(y)+\gamma_1(y)} \int_0^\infty r_1(a,y)\pi_1(0,a,y)\mathrm{d}a.$$

Equality (3.30) rewrites as

$$\mathcal{L}_1[\bar{E}_1^*](x) = \frac{1}{H(E^*)}\bar{E}_1^*(x),$$

where $\mathcal{L}_1$ is the linear operator given by (3.19). Thus, the existence of $E_1^* > 0$ is strongly related to the spectral property of operator $\mathcal{L}_1$. Since operator $\mathcal{L}_j$, for $j \in \{0,1\}$, is positive, bounded, irreducible and compact, then Frobenius theorem applies (e.g. see [13]), and there exists an eigenfunction $\phi_j \in L^1_+(\Omega)$ normalized by $\|\phi\|_{L^1} = 1$ such that

$$\mathcal{L}_j[\phi_j] = r\left(\mathcal{L}_j\right)\phi_j.$$

From (3.30), we find that

$$r(\mathcal{L}_j) = \frac{1}{H(E^*)}\ , E_1^*(x) = p[\mathcal{E}^R]\frac{\phi_1(x)}{\mu_1(x)+\gamma_1(x)}, \text{ and } A_1^*(a,x) = p[\mathcal{E}^R]\frac{\tau(x)\gamma_1(x)\phi_1(x)}{\mu_1(x)+\gamma_1(x)}\pi_1(0,a,x), \tag{3.31}$$

for some constant $p[\mathcal{E}^R]$ that we compute as follows:

from (3.31) and (3.24), one has $\dfrac{1}{r(\mathcal{L}_1)} = H(E^*) = (1+E^*)^{-\kappa}$.

On the other hand, (3.27) leads to $E^* = p[\mathcal{E}^R]\displaystyle\int_\Omega \frac{\phi_1(x)}{\mu_1(x)+\gamma_1(x)}\mathrm{d}x$,

from which we obtain:

$$p[\mathcal{E}^R] = \left(r(\mathcal{L}_1)^{\frac{1}{\kappa}} - 1\right)\left(\int_\Omega \frac{\phi_1(x)}{\mu_1(x)+\gamma_1(x)}\mathrm{d}x\right)^{-1}.$$

It follows that $p[\mathcal{E}^R] > 0$ if and only if $r(\mathcal{L}_1) > 1$.

Finally, system (2.5) has a fully-exposed steady state when $r(\mathcal{L}_1) > 1$ such that $\mathcal{E}^R = (0, 0, E_1^R(x), A_1^R(a,x))^T$ with

$$E_1^R(x) = p[\mathcal{E}^R]\frac{\phi_1(x)}{\mu_1(x)+\gamma_1(x)} \quad \text{and} \quad A_1^R(a,x) = p[\mathcal{E}^R]\frac{\tau(x)\gamma_1(x)\phi_1(x)}{\mu_1(x)+\gamma_1(x)}\pi_1(0,a,x).$$

3. Here, we assume that E_i^* and A_i^* are nonzero functions, for $i \in \{0,1\}$.
   By setting $u^*(x) = \left(E_0^*(x), E_1^*(x)\right)^T$ and $v^*(a,x) = \left(A_0^*(a,x), A_1^*(a,x)\right)^T$, system (3.23) rewrites as:

$$\begin{cases} h(u^*)\int_0^\infty \mathcal{B}[v^*](a,x)\mathrm{d}a - \mathcal{N}(x)u^*(x) = 0, \\ v^*(0,x) = \mathcal{C}(x)u^*(x), \\ \partial_a v^*(a,x) = -\mathcal{D}(a,x)v^*(a,x). \end{cases} \tag{3.32}$$

Solving (3.32) for v^* yields

$$v^*(a,x) = \mathbf{\Pi}(0,a,x)\mathcal{C}(x)u^*(x). \tag{3.33}$$

Replacing (3.33) in (3.32) gives

$$h(u^*)\int_\Omega\int_0^\infty \boldsymbol{m}(x,y)\boldsymbol{\Pi}(0,a,y)\mathcal{C}(y)u^*(y)\mathrm{d}a\mathrm{d}y=\mathcal{N}(x)u^*(x). \tag{3.34}$$

Define $\bar{u}^*(x)=\mathcal{N}(x)u^*(x)$. Then, (3.34) becomes

$$\int_\Omega\int_0^\infty \boldsymbol{m}(x,y)\boldsymbol{\Pi}(0,a,y)\mathcal{C}(y)\mathcal{N}^{-1}(y)\bar{u}^*(y)\mathrm{d}a\mathrm{d}y=\frac{1}{h(u^*)}\bar{u}^*(x).$$

Consequently, we obtain

$$\int_\Omega \boldsymbol{m}(x,y)\boldsymbol{\theta}(y)\bar{u}^*(y)\mathrm{d}y=\frac{1}{h(u^*)}\bar{u}^*(x), \tag{3.35}$$

where $\boldsymbol{\theta}(x)$ is given by

$$\boldsymbol{\theta}(x)=\left(\int_0^\infty \boldsymbol{r}(a,x)\boldsymbol{\Pi}(0,a,x)\mathrm{d}a\right)\mathcal{C}(x)\mathcal{N}^{-1}(x).$$

Equality (3.35) rewrites as:

$$\boldsymbol{\mathcal{L}}[\bar{u}^*](x)=\frac{1}{h(u^*)}\bar{u}^*(x), \tag{3.36}$$

with $\boldsymbol{\mathcal{L}}$ the linear operator given by (3.17). Therefore, the existence of $\bar{u}^*>0$ is strongly related to the spectral property of operator $\boldsymbol{\mathcal{L}}$. Since operator $\boldsymbol{\mathcal{L}}$ is positive, compact and irreducible, then Krein-Rutman theorem applies (see [15]) and ensures the existence of an eigenfunction $\boldsymbol{\psi}^*\in L^1(\Omega,\mathbb{R}^2)$, $\boldsymbol{\psi}^*>0$ and normalized (*ie.* $\|\boldsymbol{\psi}^*\|_{L^1\times L^1}=1$) such that:

$$\boldsymbol{\mathcal{L}}\left[\boldsymbol{\psi}^*\right](x)=r(\boldsymbol{\mathcal{L}})\boldsymbol{\psi}^*(x).$$

We deduce from (3.36) that

$$r(\boldsymbol{\mathcal{L}})=\frac{1}{h(u^*)}=\left(1+\bar{h}(u^*)\right)^\kappa; \tag{3.37}$$

$$u^*(x)=p\left[\mathcal{E}^*\right]\mathcal{N}^{-1}(x)\boldsymbol{\psi}^*(x); \tag{3.38}$$

and

$$v^*(a,x)=p\left[\mathcal{E}^*\right]\boldsymbol{\Pi}(0,a,x)\mathcal{C}(x)\mathcal{N}^{-1}(x)\boldsymbol{\psi}^*(x), \tag{3.39}$$

for some constant $p\left[\mathcal{E}^*\right]$. Equality (3.37) leads to $\bar{h}(u^*)=r(\boldsymbol{\mathcal{L}})^{\frac{1}{\kappa}}-1$. Furthermore, from (3.38), one has:

$$\bar{h}(u^*)=p\left[\mathcal{E}^*\right]\bar{h}\left(\mathcal{N}^{-1}(\cdot)\boldsymbol{\psi}^*(\cdot)\right).$$

Finally, we obtain:

$$p\left[\mathcal{E}^*\right]=\left(r(\boldsymbol{\mathcal{L}})^{\frac{1}{\kappa}}-1\right)\bar{h}\left(\mathcal{N}^{-1}(\cdot)\boldsymbol{\psi}^*(\cdot)\right)^{-1},$$

with $p\left[\mathcal{E}^*\right]>0$ if and only if $r(\boldsymbol{\mathcal{L}})>1$.

Notice that $\boldsymbol{\mathcal{L}}=\begin{pmatrix}(1-c)\mathcal{L}_0 & 0\\ c\mathcal{L}_0 & \mathcal{L}_1\end{pmatrix}$. Thus, it follows that $r(\boldsymbol{\mathcal{L}})=\max\left((1-c)r(\mathcal{L}_0),r(\mathcal{L}_1)\right)$.

4. Asymptotic behaviour and uniform persistence

In this section, we first present some technical details regarding the linearized system around a given steady state $\overline{\mathcal{E}}$ of System (2.3)–(2.4). This includes results concerning the spectral bound of the linearized system. Additionally, we provide the asymptotic behaviour and the uniform persistence result for System (2.3)–(2.4), considering an appropriate non-negative and continuous mapping.

More precisely, let $\overline{\mathcal{E}} = (\bar{u}, \bar{v})$ be a steady state of System (2.3)–(2.4) or equivalently System of (3.2). Then, linearizing (3.2) around $\overline{\mathcal{E}}$ leads to

$$\begin{cases} \partial_t u(x) = -\kappa \times Dh(\bar{u})(u) \int_0^\infty \mathcal{B}[\bar{v}](a,x)\mathrm{d}a + h(\bar{u}) \int_0^\infty \mathcal{B}[v](a,x)\mathrm{d}a - \mathcal{N}(x)u(x), \\ v(a=0,x) = \mathcal{C}(x)u(x), \\ \partial_t v(a,x) = -\partial_a v(a,x) - \mathcal{D}(a,x)v(a,x), \end{cases} \tag{4.1}$$

where $Dh(\bar{u})(u) = h^{1+\frac{1}{\kappa}}(\bar{u})\bar{h}(u)$.

By setting $w(t) = (u(t,\cdot), 0_{L^1(\Omega,\mathbb{R}^2)}, v(t,\cdot,\cdot))^T$, System (4.1) rewrites as

$$\frac{\mathrm{d}w(t)}{\mathrm{d}t} = \left(\mathcal{V}[\overline{\mathcal{E}}] + \mathcal{G}[\overline{\mathcal{E}}]\right) w(t),$$

where

$$\mathcal{V}[\overline{\mathcal{E}}] \begin{pmatrix} u(x) \\ 0_{L^1} \\ v(a,x) \end{pmatrix} = \begin{pmatrix} -\mathcal{N}(x)u(x) - \kappa Dh(\bar{u})(u) \int_0^\infty \mathcal{B}[\bar{v}](\sigma,x)\mathrm{d}\sigma \\ -v(0,x) \\ -\partial_a v(a,x) - \mathcal{D}(a,x)v(a,x) \end{pmatrix},$$

and

$$\mathcal{G}[\overline{\mathcal{E}}]w(t) = \begin{pmatrix} h(\bar{u}) \int_0^\infty \mathcal{B}[v](a,x)\mathrm{d}a \\ \mathcal{C}(x)u(x) \\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R}^2)} \end{pmatrix}. \tag{4.2}$$

4.1. Technical materials

The first technical result reads as:

Lemma 4.1. *Let Assumption 2.1 be satisfied. Let $\overline{\mathcal{E}} = (\bar{u}, \bar{v})$ be a steady state of System (3.2) such that $\bar{v} \equiv 0$. Then, the spectral bound $\mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}])$ of $\mathcal{V}[\overline{\mathcal{E}}]$ is such that $\mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}]) < 0$. Furthermore, the linear operator $\mathcal{V}[\overline{\mathcal{E}}]$ is resolvent positive, i.e. for each $\lambda > \mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}])$, the operator $\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}]$ is invertible and $(\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}])^{-1} X_{0+} \subset X_{0+}$.*

Proof of Lemma 4.1. To prove that $\mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}]) < 0$, it is sufficient to prove that $\mathcal{V}[\overline{\mathcal{E}}]$ is resolvent positive.

Let $\lambda \in \mathbb{C}$, $(u, 0_{L^1}, v)^T \in X_0$ and $(\varphi, \phi, \psi)^T \in X$ such that $\left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right) \begin{pmatrix} u \\ 0_{L^1} \\ v \end{pmatrix} = \begin{pmatrix} \varphi \\ \phi \\ \psi \end{pmatrix}$. One has:

$$\begin{cases} (\lambda \mathrm{I_d} + \mathcal{N}(x))\, u(x) + \kappa Dh(\bar{u})(u) \int_0^\infty \mathcal{B}[\bar{v}](a,x)\mathrm{d}a = \varphi(x), \\ v(0,x) = \phi(x), \\ \partial_a v(a,x) + (\lambda \mathrm{I_d} + \mathcal{D}(a,x))\, v(a,x) = \psi(a,x). \end{cases} \tag{4.3}$$

Solving (4.3) for v yields

$$v(a,x) = e^{-\lambda a}\mathbf{\Pi}(0,a,x)\phi(x) + \int_0^a e^{-\lambda(a-s)}\mathbf{\Pi}(s,a,x)\psi(s,x)\mathrm{d}s, \tag{4.4}$$

for $\Re(\lambda) > -\min\left\{\inf_{(0,\infty)\times\Omega} d_0(\cdot,\cdot), \inf_{(0,\infty)\times\Omega} d_1(\cdot,\cdot)\right\}$.

Replacing (4.4) in (4.3) leads to

$$\begin{aligned} &u(x) + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \left(\int_\Omega \mathbf{1}_2 u(y)\mathrm{d}y \right) b(\lambda, \bar{v})(x) + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) f(\lambda, \bar{u}, \bar{v}, \phi, \psi) b(\lambda, \bar{v})(x) \\ &\quad = (\lambda \mathrm{I_d} + \mathcal{N}(x))^{-1} \varphi(x), \text{ for } \Re(\lambda) > -\min\left\{ \sup_{x\in\Omega}\{\mu_0(x) + \gamma_0(x)\}, \sup_{x\in\Omega}\{\mu_1(x) + \gamma_1(x)\} \right\}, \end{aligned} \tag{4.5}$$

wherein we have set

$$b(\lambda, \bar{v})(x) = (\lambda \mathrm{I_d} + \mathcal{N}(x))^{-1} \left(\int_0^\infty \mathcal{B}[\bar{v}](a, x)\mathrm{d}a \right),$$

$$f(\lambda, \bar{u}, \bar{v}, \phi, \psi) = \int_0^\infty \int_\Omega \mathcal{T}(y) \left(e^{-\lambda a} \mathbf{\Pi}(0, a, y)\phi(y) + \int_0^a e^{-\lambda(a-s)} \mathbf{\Pi}(s, a, y)\psi(s, y)\mathrm{d}s \right) \mathrm{d}y\mathrm{d}a.$$

Therefore, by (4.5), we find that

$$\int_\Omega \mathbf{1}_2 u(y)\mathrm{d}y = \left(1 + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \int_\Omega b(\lambda, \bar{v})(x)\mathrm{d}x \right)^{-1} \int_\Omega \mathbf{1}_2 f(\lambda, \bar{u}, \bar{v})(x)\mathrm{d}x,$$

with

$$f(\lambda, \bar{u}, \bar{v})(x) = (\lambda \mathrm{I_d} + \mathcal{N}(x))^{-1} \varphi(x) - \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) f(\lambda, \bar{u}, \bar{v}, \phi, \psi) b(\lambda, \bar{v})(x).$$

We then find that

$$\begin{aligned} u(x) &= (\lambda \mathrm{I_d} + \mathcal{N}(x))^{-1} \varphi(x) - \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) f(\lambda, \bar{u}, \bar{v}, \phi, \psi) b(\lambda, \bar{v})(x) \\ &\quad - \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \left[\left(1 + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \int_\Omega b(\lambda, \bar{v})(y)\mathrm{d}y \right)^{-1} \int_\Omega \mathbf{1}_2 f(\lambda, \bar{u}, \bar{v})(y)\mathrm{d}y \right] b(\lambda, \bar{v})(x). \end{aligned}$$

Finally, we have

$$\left(\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}]\right)^{-1} \begin{pmatrix} \varphi \\ \phi \\ \psi \end{pmatrix} = \begin{pmatrix} (\lambda \mathrm{I_d} + \mathcal{N}(x))^{-1} \varphi(x) - h(\lambda, a, \bar{u}, \bar{v}, \phi, \psi) \\ 0_{L^1(\Omega, \mathbb{R}^2)} \\ e^{-\lambda a} \mathbf{\Pi}(0, a, x)\phi(x) + \int_0^a e^{-\lambda(a-s)} \mathbf{\Pi}(s, a, x)\psi_i(s, x)\mathrm{d}s \end{pmatrix}, \text{ for } \lambda > -\lambda_0, \tag{4.6}$$

where

$$\begin{aligned} h(\lambda, a, \bar{u}, \bar{v}, \phi, \psi) &= \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) f(\lambda, \bar{u}, \bar{v}, \phi, \psi) b(\lambda, \bar{v})(x) \\ &\quad + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \left[\left(1 + \kappa h^{1+\frac{1}{\kappa}}(\bar{u}) \int_\Omega b(\lambda, \bar{v})(y)\mathrm{d}y \right)^{-1} \int_\Omega \mathbf{1}_2 f(\lambda, \bar{u}, \bar{v})(y)\mathrm{d}y \right] b(\lambda, \bar{v})(x), \end{aligned}$$

and $\lambda_0 = \min \left\{ \inf_{(0,\infty)\times\Omega} d_0(\cdot, \cdot), \inf_{(0,\infty)\times\Omega} d_1(\cdot, \cdot), \sup_{x\in\Omega}\{\mu_0(x) + \gamma_0(x)\}, \sup_{x\in\Omega}\{\mu_1(x) + \gamma_1(x)\} \right\}$.

For $\bar{v} = 0$, it is straight forward to show that $(\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}])^{-1}(\varphi, \phi, \psi)^T \in X_{0,+}$ for any $(\varphi, \phi, \psi)^T \in X_+$. It follows that $\mathcal{V}[\overline{\mathcal{E}}]$ is resolvent positive for $\bar{v} = 0$ and $\lambda > -\lambda_0$. □

We now set

$$\mathcal{S}_\lambda = \mathsf{r}(\mathcal{G}[\overline{\mathcal{E}}](\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}])^{-1}), \quad \forall \lambda > \mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}]). \tag{4.7}$$

Thanks to [42, Theorem 3.4], we have

$$\mathsf{sgn}(\mathcal{S}_\lambda - 1) = \mathsf{sgn}(\lambda + \mathsf{s}(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])), \quad \forall \lambda > \mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}]).$$

Since $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])$ and $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0$, the part of $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])$ in X_0 has the same spectral set [28, Lemma 2.1], we have

$$\mathsf{sgn}(\mathcal{S}_\lambda - 1) = \mathsf{sgn}(\lambda + \mathsf{s}(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])) = \mathsf{sgn}(\lambda + \mathsf{s}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0)), \quad \forall \lambda > \mathsf{s}(\mathcal{V}[\overline{\mathcal{E}}]).$$

Let us go through more explicit characterization of $\mathcal{S}_\lambda$. For that ends, let us introduce the Banach space

$$X_1 = L^1(\Omega, \mathbb{R}^2) \times L^1(\Omega, \mathbb{R}^2) \times 0_{L^1((0,\infty)\times\Omega, \mathbb{R}^2)}.$$

Notice that $\mathcal{G}[\overline{\mathcal{E}}](\lambda \mathrm{I_d} - \mathcal{V}[\overline{\mathcal{E}}])^{-1}$ has the same spectral radius as its restriction on X_1 [14, Lemma 2.2]. We then introduce the linear operator $\mathcal{M}_\lambda : X_1 \to X_1$ by

$$\mathcal{M}_\lambda(\varphi, \phi, 0) = \mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1} (\varphi, \phi, 0).$$

For $\lambda > \mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}])$ and $(\varphi, \phi, 0) \in X_1$, we have, from (4.2) and (4.6):

$$\mathcal{M}_\lambda(\varphi, \phi, 0) = \mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1} \begin{pmatrix} \varphi \\ \phi \\ 0 \end{pmatrix} = \begin{pmatrix} \mathcal{F}_\lambda[\phi] \\ \mathcal{H}_\lambda[\varphi] \\ 0 \end{pmatrix}, \tag{4.8}$$

with

$$\mathcal{F}_\lambda[\phi](x) = h(\bar{u}) \int_0^\infty \mathcal{B}\left[e^{-\lambda a} \mathbf{\Pi}(0, a, x)\phi(x)\right] \mathrm{d}a,$$
$$\mathcal{H}_\lambda[\varphi](x) = \mathcal{C}(x) \left(\lambda \mathrm{I_d} + \mathcal{N}(x)\right)^{-1} \varphi(x).$$

By (4.8), it comes

$$\left(\mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1}\right)^2 \begin{pmatrix} \varphi \\ \phi \\ 0 \end{pmatrix} = \begin{pmatrix} \mathcal{F}_\lambda \circ \mathcal{H}_\lambda[\varphi] \\ \mathcal{H}_\lambda \circ \mathcal{F}_\lambda[\phi] \\ 0 \end{pmatrix}. \tag{4.9}$$

Because $\mathsf{r}(\mathcal{H}_\lambda \circ \mathcal{F}_\lambda) = \mathsf{r}(\mathcal{F}_\lambda \circ \mathcal{H}_\lambda)$ and $\mathsf{r}\left(\left(\mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1}\right)^2\right) = \mathsf{r}\left(\mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1}\right)^2$, it follows from (4.7) and (4.9) that

$$\mathcal{S}_\lambda = \sqrt{\mathsf{r}\left(\mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1}\right)^2} = \sqrt{\mathsf{r}(\mathcal{H}_\lambda \circ \mathcal{F}_\lambda)}.$$

From the above discussion, we have the following results.

Proposition 4.1. *Let Assumption 2.1 be satisfied. Let* $\bar{\mathcal{E}} = (\bar{u}, \bar{v})$ *be a steady state of System (3.2) such that* $\bar{v} \equiv 0$. *Then,* $\mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}]) < 0$, *and we have:*

1. $\mathsf{sgn}(\mathcal{S}_\lambda - 1) = \mathsf{sgn}(\lambda + \mathsf{s}(\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])) = \mathsf{sgn}(\lambda + \mathsf{s}((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0)), \quad \forall \lambda > \mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}])$.
2. *For all* $\lambda > \mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}])$, *the linear operator* $\left(\mathcal{G}[\bar{\mathcal{E}}] \left(\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}]\right)^{-1}\right)^2 : X_1 \to X_1$ *is compact and positive.*
3. *For all* $\lambda > \mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}])$, *the spectral radius* $\mathcal{S}_\lambda$ *of* $\mathcal{G}[\bar{\mathcal{E}}](\lambda \mathrm{I_d} - \mathcal{V}[\bar{\mathcal{E}}])^{-1}$ *is such that* $\mathcal{S}_\lambda = \mathsf{r}(\mathcal{M}_\lambda) = \sqrt{\mathsf{r}(\mathcal{H}_\lambda \circ \mathcal{F}_\lambda)}$.

Note that, since

$$\mathcal{F}_0 \circ \mathcal{H}_0[\varphi](x) = \mathcal{F}_0\left[\mathcal{C}(\cdot)\mathcal{N}^{-1}(\cdot)\varphi\right](x) = h(\bar{u})\boldsymbol{\mathcal{L}}[\varphi](x),$$

it comes

$$\mathcal{S}_0 = \sqrt{\mathsf{r}(\mathcal{H}_0 \circ \mathcal{F}_0)} = \sqrt{h(\bar{u})\mathsf{r}(\boldsymbol{\mathcal{L}})} = \sqrt{h(\bar{u}) \max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\}}.$$

Lemma 4.2. *We have*

1. $\mathsf{s}((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0) = \omega((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0)$, *where* $\omega((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0)$ *is the growth bound of the semigroup generated by* $(\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0$, *the part of* $(\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])$ *on* X_0.
2. $\mathsf{sgn}(\mathcal{S}_0 - 1) = \mathsf{sgn}(\mathsf{s}((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0)) = \mathsf{sgn}(\omega((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0))$.
3. *If* $\mathcal{S}_0 > 1$, *then* $\mathsf{s}((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0) = \omega((\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])_0) > 0$ *is an eigenvalue of* $(\mathcal{G}[\bar{\mathcal{E}}] + \mathcal{V}[\bar{\mathcal{E}}])$ *with eigenvector* $\bar{w} \in X_{0+} \cap D(\mathcal{V}[\bar{\mathcal{E}}])$.

Proof of Lemma 4.2. The first item of Lemma 4.2 is a direct consequence of the fact that X is an abstract L space (see [42, Theorem 3.14]). The second item is a consequence of Proposition 4.1, item 1.

We still need to prove item 3 of the lemma. Assume $\mathcal{S}_0 > 1$. Since $\mathcal{V}[\bar{\mathcal{E}}]$ is a Hille–Yosida operator, the map $\lambda \in (\mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}]), \infty) \to \mathcal{M}_\lambda \in \mathcal{L}(X_1)$ is continuous. Recalling that $\mathcal{M}_\lambda^2$ is a compact operator for all $\lambda > \mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}])$, we find that $\lambda \in (\mathsf{s}(\mathcal{V}[\bar{\mathcal{E}}]), \infty) \to \mathsf{r}\left(\mathcal{M}_\lambda^2\right)$ is continuous (e.g. see [12, Theorem 2.1]). Furthermore, since $\mathcal{V}[\bar{\mathcal{E}}]$ is a Hille–Yosida linear operator, one has $\mathcal{M}_\lambda^2 \to 0_{\mathcal{L}(X_1)}$ when $\lambda \to \infty$. This implies that $\mathcal{S}_\lambda = \sqrt{\mathsf{r}\left(\mathcal{M}_\lambda^2\right)} \to 0$ when $\lambda \to \infty$. Since $\mathcal{S}_0 > 1$, we infer from the intermediate values theorem that there exists $\lambda > 0$ such that

$$\mathcal{S}_\lambda = 1 \Longleftrightarrow \mathsf{r}\left(\mathcal{M}_\lambda^2\right) = 1.$$

By Proposition 4.1, item 1, it comes

$$\lambda = \mathsf{s}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0) = \mathsf{s}(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}]) > 0.$$

With similar arguments as in the proof of Theorem 3.1 (item 4), we can find that the part $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0$ of $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])$ in X_0 generated a C_0-semigroup $\{T_{(\mathcal{G}[\overline{\mathcal{E}}]+\mathcal{V}[\overline{\mathcal{E}}])_0}(t)\}_{t\geq 0}$ such that

$$T_{(\mathcal{G}[\overline{\mathcal{E}}]+\mathcal{V}[\overline{\mathcal{E}}])_0}(t) = W_1(t) + W_2(t),$$

where $W_1(t)$ is a compact linear operator for all $t > 0$, and $W_2(t)$ verified

$$\|W_2(t)\|_{\mathcal{L}(X_0)} \leq \ell e^{-\eta t}, \quad \forall t \geq 0,$$

with ℓ and η, two positive constants. Consequently, by the same arguments as in [46, Proposition 2.4], it comes

$$\omega_{0,ess}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0) \leq \limsup_{t\to+\infty} \frac{\ln(\|W_2(t)\|_{\mathcal{L}(X_0)})}{t} \leq -\eta,$$

with $\omega_{0,ess}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0)$ the essential growth bound of $(\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0$.

Finally, since $\lambda = \omega((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0) > 0$, Proposition 4.1 (item 1) gives that $\omega_{0,ess}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0) < \omega((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0) = \lambda = \mathsf{s}((\mathcal{G}[\overline{\mathcal{E}}] + \mathcal{V}[\overline{\mathcal{E}}])_0)$. The result follows directly from [46, Proposition 2.5] or [29, Proposition 4.6.5]. ☐

4.2. Asymptotic behaviour

In this section, we present results concerning the asymptotic behaviour of System (2.3)–(2.4). These results include the non-persistence of both exposed and unexposed mosquito populations when $\max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\} < 1$, as well as the non-persistence of the unexposed mosquito population when $(1-c)r(\mathcal{L}_0) < 1$.

Theorem 4.1. *Let Assumptions 2.1 and 2.2 be satisfied.*

1. *If* $\max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\} < 1$, *then the steady state* $\mathcal{E}^0$ *of System (2.3)–(2.4) is globally exponentially stable in* X_+, *i.e. for each initial condition* $\boldsymbol{w}_0 \in X_+$, *the semiflow* $\Phi(t, \boldsymbol{w}_0) = (E_0, E_1, A_0, A_1)$ *is such that*
$$\lim_{t\to+\infty}\left(\int_\Omega (E_0(t,x) + E_1(t,x))\,\mathrm{d}x + \int_\Omega\int_0^\infty (A_0(t,a,x) + A_1(t,a,x))\,\mathrm{d}a\mathrm{d}x\right) = 0.$$
2. *If* $(1-c)r(\mathcal{L}_0) < 1$, *then unexposed mosquitoes population goes to extinction, i.e. for each initial condition* $\boldsymbol{w}_0 \in X_+$, *the semiflow* $\Phi(t, \boldsymbol{w}_0) = (E_0, E_1, A_0, A_1)$ *is such that*
$$\lim_{t\to+\infty}\left(\int_\Omega E_0(t,x)\mathrm{d}x + \int_\Omega\int_0^\infty A_0(t,a,x)\mathrm{d}a\mathrm{d}x\right) = 0.$$

Proof of Theorem 4.1. By Lemma 4.2, we have

$$\mathsf{sgn}(\mathcal{S}_0 - 1) = \mathsf{sgn}(\mathsf{s}(G[\mathcal{E}^0])_0) = \mathsf{sgn}(\omega(G[\mathcal{E}^0])_0),$$

with $\mathcal{S}_0 = \sqrt{\max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\}}$, $\mathcal{E}^0$ the mosquito-free steady state and $G[\mathcal{E}^0] = \mathcal{G}[\mathcal{E}^0] + \mathcal{V}[\mathcal{E}^0]$ the linear operator associated to the linearization of System (3.2) around $\mathcal{E}^0$. From where item 1 of Theorem 4.1 directly follows.

For item 2, let $\boldsymbol{w}_0 \in X_+$ be an initial condition, and $\Phi(t, \boldsymbol{w}_0) = (E_0, E_1, A_0, A_1)$ the associated semiflow. Since $H(E(t)) \leq 1$, for all $t \geq 0$, it comes

$$\begin{cases} \partial_t E_0(t,x) \leq \int_\Omega \int_0^\infty m_0(x,y) r_0(a,y) A_0(t,a,y)\mathrm{d}a\mathrm{d}y - (\mu_0(x) + \gamma_0(x))E_0(t,x), \\ \partial_t E_1(t,x) \leq \int_\Omega \int_0^\infty m_1(x,y) r_1(a,y) A_1(t,a,y)\mathrm{d}a\mathrm{d}y - (\mu_1(x) + \gamma_1(x))E_1(t,x), \\ (\partial_t + \partial_a)\, A_0(t,a,x) = -d_0(a,x)A_0(t,a,x), \\ (\partial_t + \partial_a)\, A_1(t,a,x) = -d_1(a,x)A_1(t,a,x). \end{cases}$$

Therefore, by the comparison theorem in [30], it follows that for all $t \geq 0$:

$$\begin{cases} 0_{L^1} \leq E_0(t,\cdot) \leq Z(t,\cdot), \\ 0_{L^1} \leq A_0(t,\cdot,\cdot) \leq J(t,\cdot,\cdot), \end{cases} \tag{4.10}$$

where $t \mapsto (Z(t,\cdot), J(t,\cdot,\cdot))$ is the mild solution of the following system:

$$\begin{cases} \partial_t Z(t,x) = \int_\Omega \int_0^\infty m_0(x,y) r_0(a,y) J(t,a,y) \mathrm{d}a\mathrm{d}y - (\mu_0(x) + \gamma_0(x)) Z(t,x), \\ J(t, a=0, x) = (1-c)\tau(x)\gamma_0(x) Z(t,x), \\ (\partial_t + \partial_a)\, J(t,a,x) = -d_0(a,x) J(t,a,x), \end{cases} \tag{4.11}$$

with the initial condition $Z_0(\cdot) = E_0(0,\cdot)$, and $J_0(\cdot,\cdot) = A_0(0,\cdot,\cdot)$ at time $t=0$.

Note that $O = (0,0)$ is always a stationary state of System (4.11). By setting $w(t) = (Z(t,\cdot), 0_{L^1(\Omega,\mathbb{R})}, J(t,\cdot,\cdot))$, System (4.11) rewrites as

$$\frac{\mathrm{d}w(t)}{\mathrm{d}t} = (\mathcal{V} + \mathcal{G})\, w(t),$$

where

$$\mathcal{V}\begin{pmatrix} Z(x) \\ 0_{L^1} \\ J(a,x) \end{pmatrix} = \begin{pmatrix} -(\mu_0(x) + \gamma_0(x)) Z(x) \\ -J(0,x) \\ -\partial_a J(a,x) - d_0(a,x) J(a,x) \end{pmatrix},$$

and

$$\mathcal{G}\begin{pmatrix} Z(x) \\ 0_{L^1} \\ J(a,x) \end{pmatrix} = \begin{pmatrix} \int_\Omega \int_0^\infty m_0(x,y) r_0(a,y) J(t,a,y) \mathrm{d}a\mathrm{d}y \\ (1-c)\tau(x)\gamma_0(x) Z(x) \\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R})} \end{pmatrix}.$$

Therefore, by similar arguments as for the proof of Lemma 4.2, we find that

$$\lim_{t\to+\infty} \left(\int_\Omega Z(t,x)\mathrm{d}x + \int_\Omega \int_0^\infty J(t,a,x)\mathrm{d}a\mathrm{d}x \right) = 0.$$

Item 3 then holds from (4.10). □

4.3. Uniform persistence

Assume that $r(\boldsymbol{\mathcal{L}}) = \max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\} > 1$. Let the non-negative and continuous map $\rho : X_+ \to \mathbb{R}_+$, such that, for all $(\boldsymbol{u}_0, 0_{L^1}, \boldsymbol{v}_0) \in X_+$:

$$\rho(\boldsymbol{u}_0, 0_{L^1}, \boldsymbol{v}_0) = \int_\Omega (E_0(x) + E_1(x))\, \mathrm{d}x + \int_\Omega \int_0^\infty (A_0(a,x) + A_1(a,x))\, \mathrm{d}a\mathrm{d}x,$$

where $\boldsymbol{u}_0(x) = (E_0(x), E_1(x))^T$ and $\boldsymbol{v}_0(a,x) = (A_0(a,x), A_1(a,x))^T$.

Next, we set

$$M_0 := \{\boldsymbol{w}_0 = (\boldsymbol{u}_0, 0_{L^1}, \boldsymbol{v}_0) \in X_+ : \rho(\boldsymbol{w}_0) > 0\},$$

and

$$\partial M_0 := \{\boldsymbol{w}_0 = (\boldsymbol{u}_0, 0_{L^1}, \boldsymbol{v}_0) \in X_+ : \rho(\boldsymbol{w}_0) = 0\}.$$

Note that $X_+ = M_0 \cup \partial M_0$.

Lemma 4.3. *Let Assumptions 2.1 and 2.2 be satisfied. Further assume that* $\max\{(1-c)\mathsf{r}(\mathcal{L}_0), \mathsf{r}(\mathcal{L}_1)\} > 1$. *We have*

$$\forall t \geq 0, \quad \Phi(t, \partial M_0) \subset \partial M_0, \quad \textit{and} \quad \Phi(t, M_0) \subset M_0.$$

where $\{\Phi(t, \boldsymbol{w}_0) = (\boldsymbol{u}(t,\cdot), 0_{L^1}, \boldsymbol{v}(t,\cdot,\cdot))\}_t$ *is the associated semiflow.*

Proof of Lemma 4.3. Let $\boldsymbol{w}_0=(\boldsymbol{u}_0,0_{L^1},\boldsymbol{v}_0)\in X_+$ and $\{\Phi(t,\boldsymbol{w}_0)=(\boldsymbol{u}(t,\cdot),0_{L^1},\boldsymbol{v}(t,\cdot,\cdot))\}_t$ the associated semiflow. The Volterra formulation of System (2.5) leads to

$$\boldsymbol{v}(t,a,x)=\begin{cases}\boldsymbol{\Pi}(a-t,a,x)\,\boldsymbol{v}_0(a-t,x) & \text{if } t\le a,\\ \boldsymbol{\Pi}(0,a,x)\,\mathcal{C}(x)\,\boldsymbol{u}(t-a,x) & \text{if } t>a,\end{cases}\tag{4.12}$$

and

$$\begin{aligned}\partial_t\boldsymbol{u}(t,x)=h(\boldsymbol{u})(t)&\int_0^t\int_\Omega \boldsymbol{m}(x,y)\boldsymbol{r}(a,y)\boldsymbol{\Pi}(0,a,y)\,\mathcal{C}(y)\,\boldsymbol{u}(t-a,y)\mathrm{d}y\mathrm{d}a\\ &+h(\boldsymbol{u})(t)\int_t^\infty\int_\Omega \boldsymbol{m}(x,y)\boldsymbol{r}(a,y)\boldsymbol{\Pi}(a-t,a,y)\,\boldsymbol{v}_0(a-t,y)\mathrm{d}y\mathrm{d}a-\mathcal{N}(x)\boldsymbol{u}(t,x).\end{aligned}\tag{4.13}$$

Let $\boldsymbol{w}_0=(\boldsymbol{u}_0,0_{L^1},\boldsymbol{v}_0)\in\partial M_0$, *i.e.* $\int_\Omega \boldsymbol{u}_0(x)\mathrm{d}x=0$ and $\int_\Omega\int_0^\infty \boldsymbol{v}_0(a,x)\mathrm{d}a\mathrm{d}x=0$. Note that

$$\int_t^\infty\int_\Omega \boldsymbol{m}(x,y)\boldsymbol{r}(a,y)\boldsymbol{\Pi}(a-t,a,y)\,\boldsymbol{v}_0(a-t,y)\mathrm{d}y\mathrm{d}a\le\|\boldsymbol{m}\|_\infty\|\boldsymbol{r}\|_\infty\int_\Omega\int_0^\infty \boldsymbol{v}_0(a,x)\mathrm{d}a\mathrm{d}x=0.$$

From where (4.13) becomes

$$\partial_t\boldsymbol{u}(t,x)=h(\boldsymbol{u})(t)\int_0^t\int_\Omega \boldsymbol{m}(x,y)\boldsymbol{r}(a,y)\boldsymbol{\Pi}(0,a,y)\,\mathcal{C}(y)\,\boldsymbol{u}(t-a,y)\mathrm{d}y\mathrm{d}a-\mathcal{N}(x)\boldsymbol{u}(t,x),$$

i.e. $\int_\Omega \boldsymbol{u}(t,x)\mathrm{d}x=0$, for all $t>0$, as soon as $\int_\Omega \boldsymbol{u}_0(x)\mathrm{d}x=0$. Moreover, estimate (4.12) then gives $\int_\Omega\int_0^\infty \boldsymbol{v}(t,a,x)\mathrm{d}a\mathrm{d}x=0$, for all $t>0$. Consequently, $\Phi(t,\partial M_0)\subset\partial M_0$, for all $t\ge0$.

For the second part of the lemma, assume that $\boldsymbol{w}_0=(\boldsymbol{u}_0,0_{L^1},\boldsymbol{v}_0)\in M_0$, *i.e.* $\int_\Omega \boldsymbol{u}_0(x)\mathrm{d}x+\int_\Omega\int_0^\infty \boldsymbol{v}_0(a,x)\mathrm{d}a\mathrm{d}x>0$. If $\int_\Omega \boldsymbol{u}_0(x)\mathrm{d}x>0$, then (4.13) gives $\int_\omega \boldsymbol{u}(t,x)\mathrm{d}x>0$, for all $t>0$. From where, $\Phi(t,M_0)\subset M_0$, for all $t\ge0$. If $\int_\Omega\int_0^\infty \boldsymbol{v}_0(a,x)\mathrm{d}a\mathrm{d}x>0$, then (4.12) gives $\int_\Omega\int_0^\infty \boldsymbol{v}(t,a,x)\mathrm{d}a\mathrm{d}x>0$, for all $t>0$. From where, $\Phi(t,M_0)\subset M_0$, for all $t\ge0$. ☐

Lemma 4.4. *Let Assumptions 2.1 and 2.2 be satisfied. Further assume that* $\max\{(1-c)\mathsf{r}(\mathcal{L}_0),\mathsf{r}(\mathcal{L}_1)\}>1$. *Let* $\boldsymbol{w}_0\in M_0$. *Then, there exists a constant* $\eta>0$ *such that*

$$\limsup_{t\to\infty}\rho(\Phi(t,\boldsymbol{w}_0))>\eta.$$

Proof of Lemma 4.4. Set $\Phi(t,\boldsymbol{w}_0)=(\boldsymbol{u}(t,\cdot),0_{L^1},\boldsymbol{v}(t,\cdot,\cdot))$. We argue by contradiction, *i.e.* let $\zeta>0$ and small enough such that,

$$\limsup_{t\to\infty}\rho(\Phi(t,\boldsymbol{w}_0))=\limsup_{t\to\infty}\left(\int_\Omega \boldsymbol{u}(t,x)\mathrm{d}x+\int_\Omega\int_0^\infty \boldsymbol{v}(t,a,x)\mathrm{d}a\mathrm{d}x\right)\le\zeta.\tag{4.14}$$

Therefore, we can find $t_0\ge0$ such that, $\rho(\Phi(t,\boldsymbol{w}_0))\le\zeta$, for all $t\ge t_0$. Consequently, for all $t\ge t_0$,

$$\int_\Omega\langle\mathbf{1}_2,\boldsymbol{u}(t,x)\rangle\mathrm{d}x+\int_\Omega\int_0^\infty\langle\boldsymbol{\mathcal{T}},\boldsymbol{v}(t,a,x)\rangle\mathrm{d}a\mathrm{d}x\le\max\,(1,\sup_x\tau^{-1})\rho(\Phi(t,\boldsymbol{w}_0))=\zeta\,\max\,(1,\sup_x\tau^{-1}).$$

It then comes,

$$h(\boldsymbol{u})(t)\ge(1+\zeta\,\max\,(1,\sup_x\tau^{-1}))^{-\kappa},\quad\forall t\ge t_0.$$

By this latter inequality, System (2.5) becomes

$$\begin{cases} \partial_t \boldsymbol{u}(t,x) \geq \bar{h}(\zeta) \displaystyle\int_0^\infty \mathcal{B}[\boldsymbol{v}(t,\cdot,\cdot)](a,x)\mathrm{d}a - \mathcal{N}(x)\boldsymbol{u}(t,x), \\ \boldsymbol{v}(t,0,x) = \mathcal{C}(x)\boldsymbol{u}(t,x), \\ (\partial_t + \partial_a)\boldsymbol{v}(t,a,x) = -\mathcal{D}(a,x)\boldsymbol{v}(t,a,x), \end{cases}$$

where $\bar{h}(\zeta) = \left(1 + \zeta \max\left(1, \sup_x \tau^{-1}\right)\right)^{-\kappa}$. By the comparison principles (e.g. [30]), it comes

$$0 \leq \boldsymbol{u}_\zeta(t,\cdot) \leq \boldsymbol{u}(t+t_0,\cdot), \quad \text{and} \quad 0 \leq \boldsymbol{v}_\zeta(t,\cdot,\cdot) \leq \boldsymbol{v}(t+t_0,\cdot,\cdot),$$

for all $t \geq 0$, and where $\left(\boldsymbol{u}_\zeta(t,\cdot), \boldsymbol{v}_\zeta(t,\cdot,\cdot)\right)_t$ is the mild solution of the following system

$$\begin{cases} \partial_t \boldsymbol{u}_\zeta(t,x) = \bar{h}(\zeta) \displaystyle\int_0^\infty \mathcal{B}[\boldsymbol{v}_\zeta(t,\cdot,\cdot)](a,x)\mathrm{d}a - \mathcal{N}(x)\boldsymbol{u}_\zeta(t,x), \\ \boldsymbol{v}_\zeta(t,0,x) = \mathcal{C}(x)\boldsymbol{u}_\zeta(t,x), \\ (\partial_t + \partial_a)\boldsymbol{v}_\zeta(t,a,x) = -\mathcal{D}(a,x)\boldsymbol{v}_\zeta(t,a,x), \\ \boldsymbol{u}_\zeta(0,x) = \boldsymbol{u}(t_0,x), \quad \boldsymbol{v}_\zeta(0,a,x) = \boldsymbol{v}(t_0,a,x). \end{cases} \tag{4.15}$$

By setting, $w_\zeta(t) = (\boldsymbol{u}_\zeta(t,\cdot), 0_{L^1}, \boldsymbol{v}_\zeta(t,\cdot,\cdot))$, System (4.15) writes

$$\frac{\mathrm{d}w_\zeta(t)}{\mathrm{d}t} = (\mathcal{G}_\zeta + \mathcal{V})w_\zeta(t), \tag{4.16}$$

with

$$\mathcal{G}_\zeta \begin{pmatrix} u(x) \\ 0_{L^1} \\ v(a,x) \end{pmatrix} = \begin{pmatrix} \bar{h}(\zeta) \int_0^\infty \mathcal{B}[v(t,\cdot,\cdot)](a,x)\mathrm{d}a \\ \mathcal{C}(x)u(t,x) \\ 0_{L^1((0,\infty)\times\Omega,\mathbb{R}^2)} \end{pmatrix},$$

and

$$\mathcal{V} \begin{pmatrix} u(x) \\ 0_{L^1} \\ v(a,x) \end{pmatrix} = \begin{pmatrix} -\mathcal{N}(x)u(x) \\ -v(0,x) \\ -\partial_a v(a,x) - \mathcal{D}(a,x)v(a,x) \end{pmatrix}.$$

Similarly, as in Lemma 4.1, we find that the spectral bound $\mathsf{s}(\mathcal{V})$ of $\mathcal{V}$ satisfies $\mathsf{s}(\mathcal{V}) < 0$, and the linear operator $\mathcal{V}$ is resolvent positive. Let us set

$$\mathcal{S}_\lambda^\zeta = \mathsf{r}(\mathcal{G}_\zeta(\lambda \mathrm{I_d} - \mathcal{V})^{-1}), \quad \forall \lambda > \mathsf{s}(\mathcal{V}).$$

We claim that

Claim 4.1. *Let Assumptions 2.1 and 2.2 be satisfied. Let* $\mathcal{S}_0 > 1$.

1. *If* $\mathcal{S}_0^0 > 1$, *then* $\mathsf{s}((\mathcal{G}_\zeta + \mathcal{V})_0) = \omega((\mathcal{G}_\zeta + \mathcal{V})_0) > 0$ *is an eigenvalue of* $(\mathcal{G}_\zeta + \mathcal{V})$ *with eigenvector* $\bar{w}_\zeta \in X_{0+} \cap D(\mathcal{V})$; *with* $\omega((\mathcal{G}_\zeta + \mathcal{V})_0)$ *the growth bound of* $(\mathcal{G}_\zeta + \mathcal{V})_0$, *the part of* $(\mathcal{G}_\zeta + \mathcal{V})$ *in* X_0.
2. *We can define a rank one projector* $\mathcal{P}_\zeta : X_0 \to X_0$ *such that*

$$\mathcal{P}_\zeta T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t) = T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t)\mathcal{P}_\zeta = e^{\lambda_\zeta t}\mathcal{P}_\zeta, \ \forall t \geq 0, \ \textit{where} \ \lambda_\zeta = \mathsf{s}((\mathcal{G}_\zeta + \mathcal{V})_0) > 0$$

and for each $w_0 \in X_{0+} \setminus \{0_{X_0}\}$, *we have* $\|\mathcal{P}_\zeta w_0\|_X > 0$. *Furthermore,* $e^{-\lambda_\zeta t}T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t) \to \mathcal{P}_\zeta$, *as* $t \to +\infty$, *for the operator norm topology.*

Before dealing with the proof of Claim 4.1, we first end with the proof of Lemma 4.4. Let $w_\zeta^0 = (\boldsymbol{u}_\zeta(t_0,\cdot), 0_{L^1}, \boldsymbol{v}_\zeta(t_0,\cdot,\cdot)) \in X_0$, then by (4.16), we have $w_\zeta(t) = T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t)w_\zeta^0$ for all $t \geq 0$. Since $\mathcal{S}_0 > 1$, item 2 of Claim 4.1 leads to

$$e^{-\lambda_\zeta t}\left\|T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t)w_\zeta^0\right\| \to \left\|\mathcal{P}_\zeta w_\zeta^0\right\|, \text{ as } t \to \infty. \tag{4.17}$$

Moreover, since $\left\|w_\zeta^0\right\| = \int_\Omega \boldsymbol{u}_\zeta(t_0, x)\mathrm{d}x + \int_\Omega \int_0^\infty \boldsymbol{v}_\zeta(t_0, a, x)\mathrm{d}a\mathrm{d}x > 0$, by item 2 of Claim 4.1, we also have $\left\|\mathcal{P}_\zeta w_\zeta^0\right\| > 0$. Therefore, by (4.17), it comes

$$\left\|T_{(\mathcal{G}_\zeta+\mathcal{V})_0}(t)w_\zeta^0\right\| = \int_\Omega \boldsymbol{u}(t, x)\mathrm{d}x + \int_\Omega \int_0^\infty \boldsymbol{v}(t, a, x)\mathrm{d}a\mathrm{d}x \to \infty, \text{ as }, t \to \infty.$$

A contradiction holds with (4.14). This ends the proof of Lemma 4.4. ☐

Proof of Claim 4.1. The item 1 is similar to the proof of Lemma 4.2.
For the proof of item 2, we refer to [38, Proposition 5.4]. ☐

5. Model parameters and simulated dynamics

This section outlines how our general analysis can be applied for a sustainable reduction of mosquito populations through insecticide pressure.

5.1. Model parameters

The probability of mutation of unexposed AFM from IR level y to level x is assumed to follow a Gaussian distribution with mean 0 and variance varJ0 $= 10^{-2}$. Specifically,

$$m_0(x, y) = \frac{1}{\sqrt{0.02\pi}} e^{-\frac{1}{0.02}(y-x)^2}. \tag{5.1}$$

Similarly, the probability of mutation of exposed AFM from IR level y to level x follows a Gaussian distribution with 0 and variance varJ1 $= 2\times$varJ0 (due to high selection pressure from insecticide exposure). Thus,

$$m_1(x, y) = \frac{1}{\sqrt{0.04\pi}} e^{-\frac{1}{0.04}(y-x)^2}. \tag{5.2}$$

The egg-laying rate for an AFM depends on the age a of the mosquito and its resistance level x. As in the framework introduced by [14], we assume that

$$r_0(a, x) \equiv r_1(a, x) = r_m \left[1 + \left(\frac{r_m - r_0}{r_0}\right)\left(\frac{r_0}{r_1} \cdot \frac{r_m - r_1}{r_m - r_0}\right)^x\right]^{-1} \times \mathbf{1}_{a > a_\mathrm{L}}, \tag{5.3}$$

where $r_m := r(-\infty, \cdot) < \infty$ is a constant due to physiological constraints and a_L is the average age at which AFMs start laying eggs. The constants r_0 and r_1 are egg-laying rates of the reference 'sensitive' and 'resistant' mosquitoes $x_0 = 0$ and $x_1 = 1$, with $0 < r_1 < r_0 < r_m$ given in Table 1.

The death rate $d_0(a, x)$ of unexposed AFMs aged a with resistant level x is such that

$$d_0(a, x) = \kappa_0 \mathbf{1}_{a > a_\mathrm{LS}}, \tag{5.4}$$

where a_LS is the average lifespan of mosquitoes, and κ_0 is a positive constant. With this formulation, the average lifespan of mosquitoes is approximately a_LS days. Indeed, setting $D_0(a, x) = \exp\left(-\int_0^a d_0(s, x)\mathrm{d}s\right)$ as the probability that a mosquito remains alive after a days, the average lifespan is given by $\int_0^\infty D_0(a, x)\mathrm{d}a = a_\mathrm{LS} + \frac{1}{\kappa_0}$. Here, we fix, e.g. $\kappa_0 = 10$, such that $\int_0^\infty D_0(a, x)\mathrm{d}a \approx a_\mathrm{LS}$. Thus, the exact value of κ_0 is not critical as long as this approximation holds.

For AFMs exposed to the insecticide, their death rate $d_1(a, x)$ accounts for the insecticide pressure such that

$$d_1(a, x) = \kappa_0 \mathbf{1}_{a > a_\mathrm{LS}} + \bar{d}_0 \left(\frac{\bar{d}_1}{\bar{d}_0}\right)^x, \tag{5.5}$$

where $\bar{d}_0$ and $\bar{d}_1$ represent the insecticide activity experienced by the reference sensitive mosquito x_0 and resistant mosquito x_1, respectively, and are given in Table 1. The survival probabilities of unexposed and

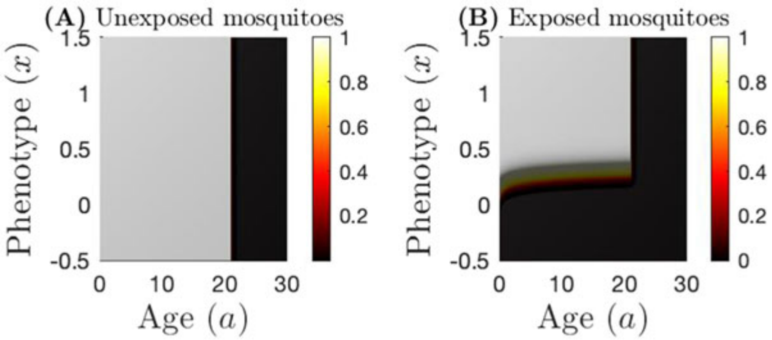

Figure 2. The survival probability of mosquitoes population as a function of their age a and resistance level x. ***(A)*** *For mosquitoes unexposed to insecticide.* ***(B)*** *For mosquitoes exposed to insecticide. Here, the probability of surviving insecticide exposure during one day is* $p_S = 10^{-10}$.

exposed mosquitoes are illustrated in Figure 2, and all other model parameters are assumed to be constant and are provided in Table 1.

5.2. Typical simulated dynamics

For all simulated dynamics, we assume that the mosquito population unexposed to insecticide has reached the equilibrium before the insecticide is introduced at time $t = 0$. The insecticide pressure is then maintained on the mosquito population for a period denoted as n_y years. Furthermore, we also assume that unexposed and exposed mosquitoes population have a sufficient growing capability captures by $r(\mathcal{L}_0)$ and $r(\mathcal{L}_1)$ such that $r(\mathcal{L}_0) > r(\mathcal{L}_1) > 1$. The inequality $r(\mathcal{L}_0) > r(\mathcal{L}_1)$ assumes a global fitness cost within the population of exposed mosquitoes that are evading the insecticide activity.

The proposed model captures evolutionary outcomes, such as the time of resistance emergence ($\mathrm{T}_{\mathrm{emg}}$), and epidemiological outcomes, such as the relative gain from introducing the insecticide ($\mathrm{r}_{\mathrm{gain}}$). More specifically, $\mathrm{T}_{\mathrm{emg}}$ represents the time at which the initially rare population exposed to insecticide reaches 10% of the total AFMs. Note that $\mathrm{T}_{\mathrm{emg}} = \mathrm{T}_{\mathrm{emg}}(c)$ depends on the insecticide exposure strategy c. Additionally, $\mathrm{r}_{\mathrm{gain}} = \mathrm{r}_{\mathrm{gain}}(c)$ is calculated as the number of AFMs alive during the insecticide usage period T relative to the number of AFMs alive in the absence of insecticide pressure, i.e.

$$\mathrm{r}_{\mathrm{gain}}(c) = 1 - \frac{\int_0^{n_y} \int_{\mathbb{R}} \int_0^{\infty} \left(A_0(t,a,x) + A_1(t,a,x)\right) \mathrm{d}a\mathrm{d}x\mathrm{d}t\Big|_{c\neq 0}}{\int_0^{n_y} \int_{\mathbb{R}} \int_0^{\infty} \left(A_0(t,a,x) + A_1(t,a,x)\right) \mathrm{d}a\mathrm{d}x\mathrm{d}t\Big|_{c\equiv 0}}.$$

We defined the difference in performance $D(c_1, c_2)$ between two insecticide exposure strategies, c_1 and c_2, as $D(c_1, c_2) = \mathrm{r}_{\mathrm{gain}}(c_1) - \mathrm{r}_{\mathrm{gain}}(c_2)$, which corresponds to the percentage difference in effectiveness between the two strategies. For instance, a positive value of 5% indicates that strategy c_1 is 5% more beneficial than strategy c_2, while negative values indicate that c_2 outperforms c_1.

Consider the scenario where the fitness functions Θ_0 and Θ_1 for unexposed and exposed mosquito populations are illustrated in Figure 3A. In such a scenario, while the optimal phenotype for unexposed mosquitoes corresponds to the one with minimal resistance, insecticide pressure shifts the optimal phenotype of exposed mosquitoes to a higher resistance level (Figure 3A).

When a constant insecticide exposure is maintained within the mosquito population for $n_y = 10$ years, this corresponds to approximately 150 mosquito generations, assuming mosquitoes complete 15 generations per year. When insecticide exposure is maintained at a relatively low rate with $c = 0.2$ (Figure 3), the durability of insecticide efficacy is about $\mathrm{T}_{\mathrm{emg}} = 3.1$ years. This insecticide durability is associated with a moderate gain from introducing the insecticide, with a relative gain $\mathrm{r}_{\mathrm{gain}} \approx 23\%$ (Figure 3B). Therefore, compared to taking no action, a constant and relatively low rate of insecticide exposure results

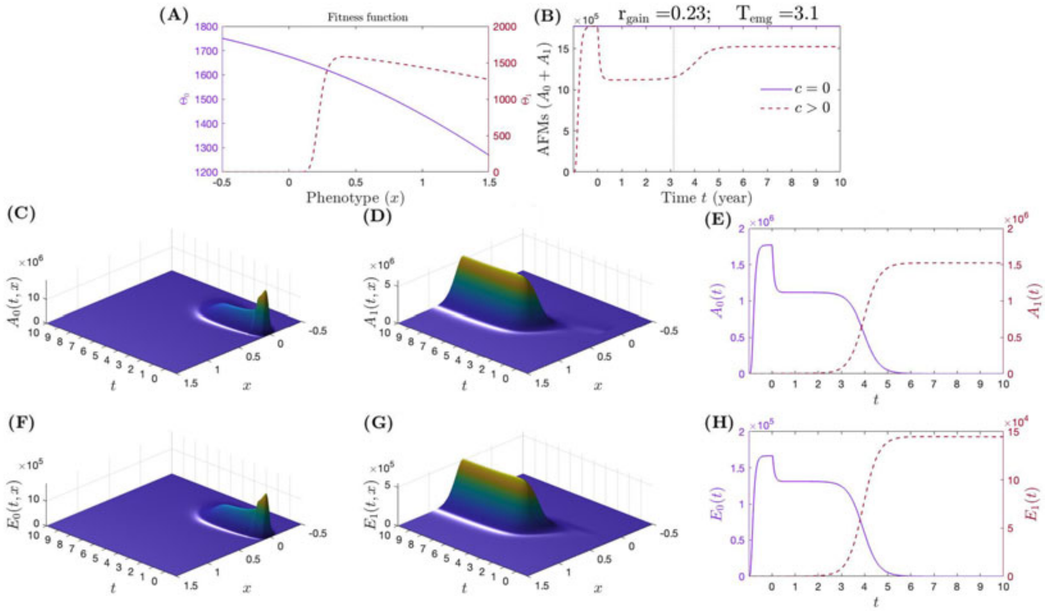

__Figure 3.__ Evolutionary dynamics with a constant and low insecticide exposure rate $c = 0.2$. ***(A)*** *The fitness functions.* ***(B)*** *The dynamics of AFMs.* ***(C–E)*** *The dynamics of AFMs for exposed and unexposed populations.* ***(F–H)*** *The dynamics of eggs laid by AFMs for exposed and unexposed populations. Here, the probability of surviving insecticide exposure during one day* $p_S = 10^{-10}$ *and other parameters are given by Table 1.*

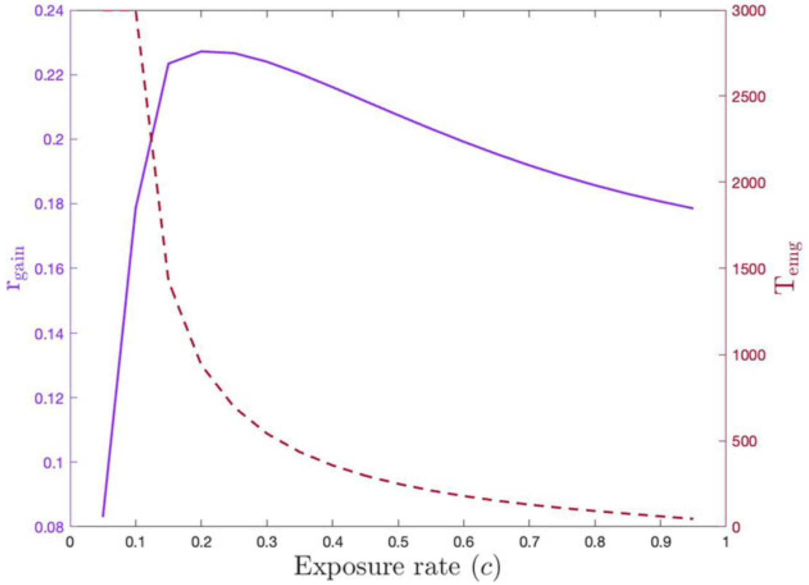

__Figure 4.__ Effect of the insecticide exposure rate c on the relative gain from introducing the insecticide $\mathrm{r_{gain}}$*, and the time of resistance emergence* $\mathrm{T_{emg}}$*. Here,* $p_S = 10^{-10}$ *and other parameters are given by Table 1.*

in a moderate gain from introducing the insecticide. This is explained by the relatively short durability period of such a strategy. However, increasing the insecticide exposure rate does not provide significant advantages in either the long term, quantified by $\mathrm{T_{emg}}$, or the short term, quantified by $\mathrm{r_{gain}}$ (Figure 4).

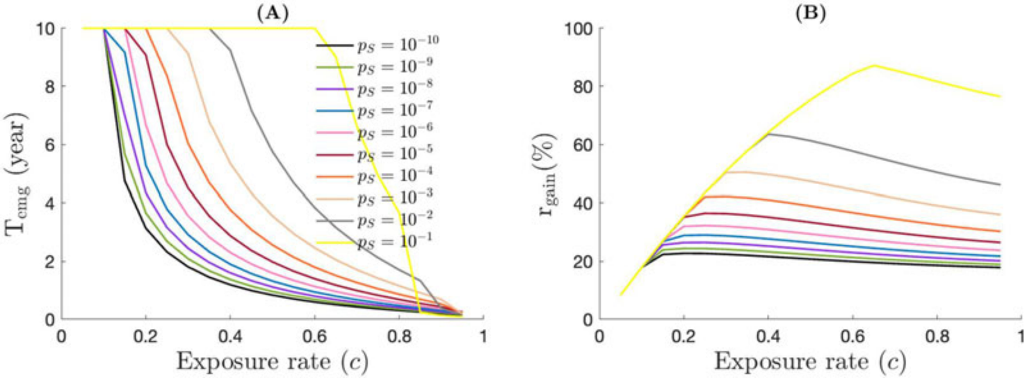

Figure 5. *Rgain and Temg.*

6. Discussion

Vector control interventions, particularly the use of pyrethroid-based insecticides in ITNs and IRS, have played a pivotal role in reducing malaria prevalence. Notably, the extensive deployment of pyrethroid-only ITNs between 2005 and 2015 significantly contributed to a substantial decline in the malaria burden across Africa. This study presents a novel mathematical framework to examine the emergence and spread of insecticide resistance in mosquito populations. By modelling insecticide resistance as a continuous (or quantitative) trait influenced by multiple genes, the framework captures variability and evolutionary transient dynamics. We propose an age-structured mosquito population model based on integro-differential equations, where the resistance trait affects life-history parameters such as mortality and reproduction. This approach offers fresh insights into the processes driving the emergence and spread of resistance within mosquito populations over time.

We investigate the model's properties, including the existence of a unique maximal bounded semi-flow, and establish conditions for the existence and stability of steady states. Through parameterization and simulations, we examine both transient dynamics (captured by the relative gain from introducing the insecticide) and long-term dynamics (measured by the time of resistance emergence). The findings shed light on the evolutionary mechanisms behind insecticide resistance and provide guidance for designing sustainable vector control strategies.

In this context, the type of insecticide in use is characterized by the probability of surviving insecticide exposure in a single day, denoted as p_S. The parameter p_S plays a fundamental role on both the time of resistance emergence (T_{emg}) and the relative gain from introducing the insecticide (r_{gain}). Indeed, a strong insecticidal effect, corresponding to a very low daily survival probability (p_S), is associated with the rapid emergence of resistance in the mosquito population, even under scenarios of moderate exposure rates (Figure 5A). The corresponding relative gain is limited, showing rapid saturation as the intensity of insecticide application increases (Figure 5B). In contrast, a moderate insecticidal effect – corresponding to a low but not extremely low daily survival probability (p_S) – is associated with more sustainable insecticide efficacy (Figure 5A) and a higher relative gain (Figure 5B). Importantly, the optimal constant exposure rate that maximizes T_{emg} and r_{gain} decreases significantly as the daily survival probability (p_S) decreases (Figure 5).

For example, consider a scenario where the daily survival probability is $p_S = 0.1$. According to Figure 5, the optimal insecticide exposure rate is achieved at approximately $c \approx 0.6$. In this configuration, the insecticide remains effective for a relatively long duration, with $T_{emg} \approx 10$ years. Additionally, the relative gain from using the insecticide during the deployment period is substantial, with $r_{gain} \approx 84\%$ (Figure 6).

Although the theoretical results presented in Section 3 are based on the assumption of a constant insecticide exposure rate, this strategy is not only demonstrating a moderate gain in reducing the AFM population but also a quite short durability of the insecticide efficiency, as illustrated by the results

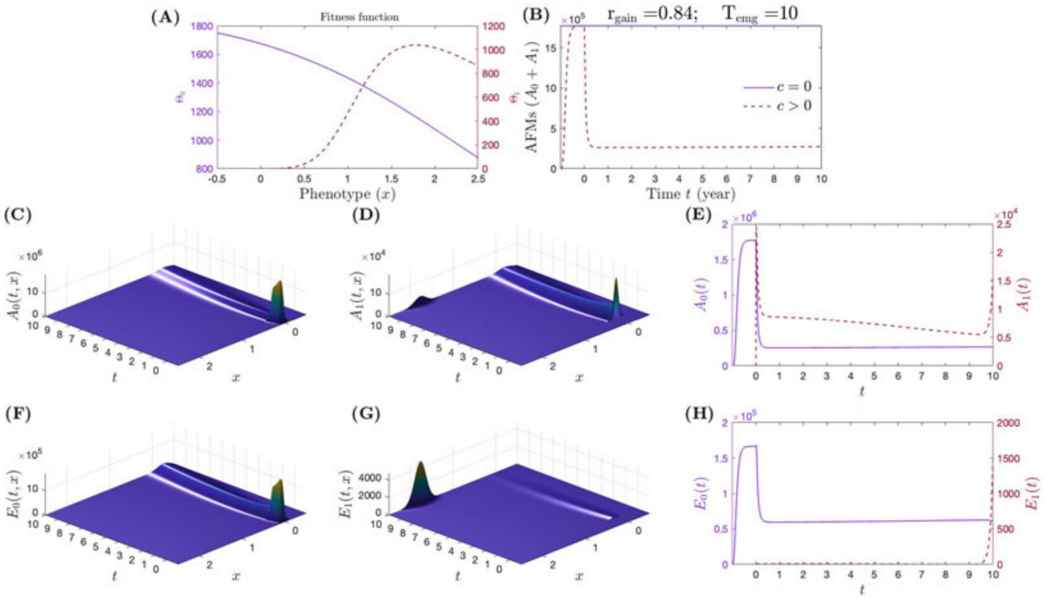

Figure 6. *Evolutionary dynamics with a constant exposure rate* $c = 0.6$ *and* $p_S = 0.1$. ***(A)*** *The fitness functions.* ***(B)*** *The dynamics of AFMs.* ***(C–E)*** *The dynamics of AFMs for exposed and unexposed populations.* ***(F–H)*** *The dynamics of eggs laid by AFMs for exposed and unexposed populations.*

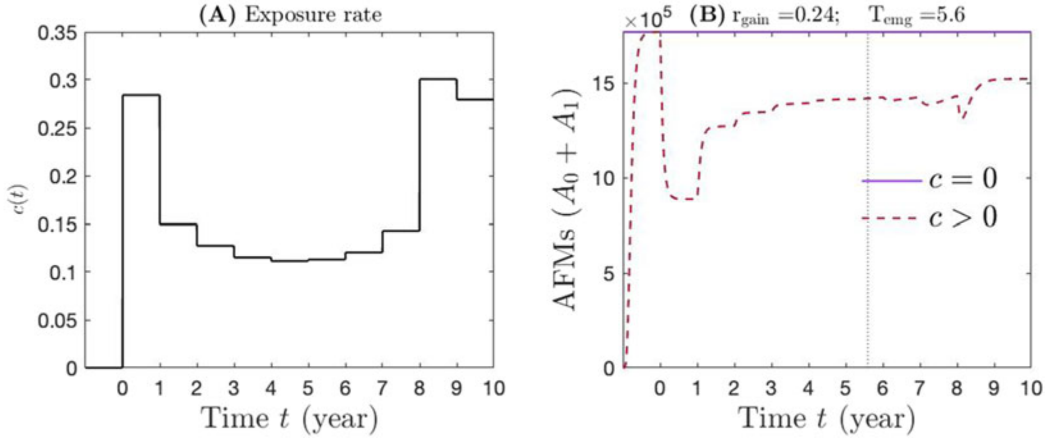

Figure 7. *The dynamics with the optimal exposure rate in a configuration of strong insecticidal effect with the probability of surviving insecticide exposure in a single day* $p_S = 10^{-10}$. ***(A)*** *The optimal exposure rate.* ***(B)*** *The dynamics of AFMs.*

above. However, we can derive optimal step functions leading to sustainable usage of the insecticide. We assume that the optimal strategy is updated every period of one year by keeping a constant exposure during each year. The insecticide deployment strategy over a period of n_y years consists of defining the exposure rate as a steps function $c(t) = \sum_{n=0}^{n_y-1} \bar{c}_n \mathbf{1}_{[n,n+1)}(t)$, where the constants $\bar{c}_n$,s are determined such that

$$\mathrm{r_{gain}}(\bar{c}_0, \ldots, \bar{c}_{n_y-1}) = \max_{0 \le c_n \le 1} \mathrm{r_{gain}}(c_0, \ldots, c_{n_y-1}).$$

With a strong insecticidal effect, i.e. when the probability of surviving insecticide exposure in a single day is very low $p_S = 10^{-10}$, while the relative gain remains approximately the same between the maximal constant exposure strategy (Figure 3B) and the optimal exposure strategy (Figure 7), the time to resistance emergence significantly increases, from 3.1 years under the maximal constant exposure strategy (Figure 3B) to 5.6 years under an optimal exposure strategy (Figure 7).

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