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Mathematical modelling of a pest in an age-structured crop model: the coffee berry borer case *

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Abstract

Coffee production is an important agriculture activity which contributes significantly to the economic growth of many countries in the world. One of the major constraints to coffee production throughout the world is the damage caused by the coffee berry borer (CBB), *Hypothenemus hampei* (*Coleoptera: Scolytidae*). It is the most damaging insect pest to coffee production in the world. These insects infest coffee berries, preferably mature berries, and spend most of their life cycle inside the berries, which make them quite difficult to control. In this work, we introduce and analyse a berry age-structured model describing the infestation dynamics of coffee berries by CBB. Using the semigroup theory in the case of Lipschitz perturbation, we show that the model has a unique nonnegative and bounded solution. We derive an explicit formula of the basic reproduction number, $\mathcal{R}_0$, using the next generation approach and the biological interpretation of this threshold in a specific case. Numerical simulations are carried out to illustrate the theoretical results.

Keywords: Epidemiological model, plant-pest interaction, *Hypothenemus hampei*, semigroup theory, stability, numerical simulations

1 Introduction

The production of coffee plays an important role in the economic development of many countries. Native of Africa, two species of coffee, *Coffea arabica* and *Coffea canephora* (generally called robusta) are produced on over 10 million ha in more than 80 countries located in tropical and subtropical regions [26]. World coffee production for 2020–2021 is forecast to increase by 9.1 million bags (90 kg/bag) compared to the previous year, reaching 176.1 million bags [24]. However, coffee production is threatened by pests and diseases [17]. The most harmful pest is the coffee berry borer (CBB), *Hypothenemus hampei* (*Coleoptera: Scolytidae*), which is originated from Central Africa but now impacts most coffee-growing countries [6, 17, 26]. If no control

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measure is applied in the plantation, up to 100% of the berries can be attacked [11, 17]. The infestation levels in untreated plantations are estimated at 60% in Mexico, 60% in Colombia, 50–90% in Malaysia, 58–85% in Jamaica, 80% in Uganda and 90% in Tanzania [14]. CBB severely reduce the coffee production and alter its quality, thus impairing its commercial value. Economic losses are estimated at more than US$500 million annually, affecting a large proportion of more than 25 million rural households involved in coffee production worldwide [27]. These insects feed and spend most of their life inside coffee berries, preferably targeting ripe berries, although they may infest immature berries and cause them to fall prematurely. Due to their cryptic nature, they are difficult to control [4, 6, 26, 14].

Due to the seriousness of the damages caused by CBB in coffee plantations throughout the world, it is crucial to develop tools that help limiting CBB infestation. In this sense, mathematical modelling is relevant to understand the coffee berries–CBB interactions. We developed two pioneer tractable deterministic models describing the infestation dynamics of coffee berries by CBB during a cropping season [9, 10]. These models are based on the CBB life-cycle and take into account the coffee berry availability. They are both based on differential equations and in neither work did we integrate the CBB marked preference for mature berries, demonstrated in several field and laboratory studies [4, 11, 21, 26].

In this work, we develop an age-structured model describing the infestation dynamics of coffee berries by CBB that takes into account the preference of CBB for the mature berries. The model consists in two partial differential equations describing the age-structured dynamics of berries and two ordinary differential equations depicting the CBB life-cycle. We study the well-posedness of the model using the perturbation semigroup theory [19], which provides a flexible mathematical framework for determining the existence and uniqueness of a solution to age-structured models (see for instance [13, 16, 20, 29] and references cited therein). Considering that the production rate of new coffee berries is constant, we then compute the explicit expression of the basic reproduction number $\mathcal{R}_0$, which determines if the CBB population can vanish or persist in the plantation. Moreover, the biological interpretation of its expression is given.

The remaining sections of this paper are organised as follows. In Section 2, we introduce the age-structured model describing the infestation dynamics of coffee berries by CBB. In Section 3, the existence, uniqueness and boundedness of solutions are established. In Section 4, we compute the explicit formula of the basic reproduction number for a constant berry production rate. Numerical simulations are provided in Section 5 to illustrate the theoretical results and provide points for discussion.

2 Coffee berries–CBB interaction dynamics

2.1 Biological background

The coffee berry growth is divided into several stages that are characterised by the berry colour. After flowering, the berry successively goes through the green, yellow, red and black colours and becomes fully mature when it is red, after 6–9 months [2]. But on the same coffee tree, there are branches without flowers and branches with berries at all stages of maturation [2, 4]. Field and laboratory studies indicate that factors such as berry ripeness and colour play an important role on the susceptibility of coffee berries to CBB infestation, with a CBB preference for red and black berries [4, 26, 11, 21]. In addition, the CBB fertility rate is higher in mature than in young berries [18]. CBB can also attack small 2 to 3-months old green coffee berries that can be found on the branches up till the harvest time [3, 14].

The CBB life cycle is composed of four stages: egg, larva, nymph and adult (male and female) [6, 26]. All these stages take place inside the coffee berries, which provide food and shelter. The duration of development from egg to adult is positively correlated with temperature and may take 28 to 34 days at 27°C [6]. The CBB female feeds on and reproduces in the endosperm of the seed of the coffee berry, burrowing through exocarp, mesocarp and endocarp to reach it,

which may take up to 8 hours under optimum conditions. The female lays one to three eggs per day during approximately 20 days and remain inside the berry to take care of their offspring until they die [6]. There is a 10:1 female-to-male sex ratio [22, 6]. The larvae, nymphs, males and young females remain inside the coffee berry, together with the founder female. The males mate with the young females of their generation. A few days after fertilisation, females leave the berry to find other preferably uninfested berries for oviposition.

2.2 Model description

To take into account the CBB preference for mature berries, a berry age-structured model is formulated to study the infestation dynamics of coffee berries by CBB. The berry population density is subdivided into two compartments: the healthy berry density at time t and age a denoted by $s_b(t,a)$ and the infested berry density denoted by $i_b(t,a)$. The berry age being defined as a "classical" age, we have $da = dt$. We denote by $a_\dagger$ the maximal age of the coffee berries.

Since only fertilised females (also called colonising females) infest new hosts and considering that males are not limiting to fertilise young females in the berries, we only represent females in the model. At time t, we subdivide the female population into two compartments: the colonising females denoted by $y(t)$, which correspond to the flying females looking for new berries, and the infesting females denoted by $z(t)$, which correspond to the females that are laying eggs inside the berries. Figure 1 provides a schematic and simplified summary of the interactions between coffee berries and CBB.

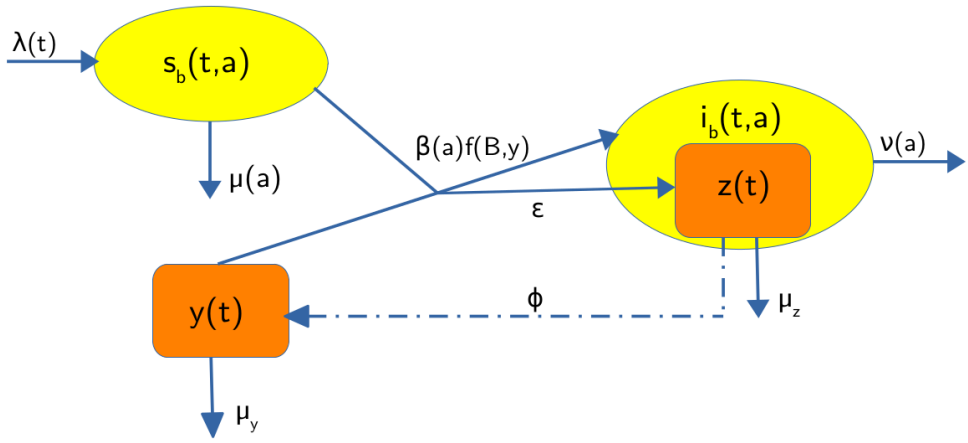

Figure 1: Schematic representation of the coffee berry–CBB interaction model. Healthy coffee berries $s_b(t,0)$ are produced at the time-dependent rate $\lambda(t)$. Colonising females $y(t)$ infest healthy coffee berries $s_b(t,a)$ at rate $\beta(a)f(B,y)$, where $B(t)$ represents the total number of healthy berries at time $t > 0$ and $f(.,.)$ the interaction function. This induces a transfer of berry densities, from healthy to infected berries $i_b(t,a)$, and its counterpart for CBB females, from colonising to infesting females $z(t)$. Infesting females lay eggs inside the coffee berries, which go through their development cycle until the emergence of new fertilised colonising females at rate ϕ. Colonising and infesting CBB females undergo mortality at rates μ_y and μ_z, healthy and infested coffee berries at rates $\mu(a)$ and $\nu(a)$.

Extending the baseline model found in [10] to incorporate the berry age, the diagram in Figure 1 can be translated into the following mathematical age-structured system:

$$\begin{cases} \partial_t s_b(t,a) + \partial_a s_b(t,a) = -f(B,y)\,\beta(a)\,s_b(t,a) - \mu(a)\,s_b(t,a), \\ \partial_t i_b(t,a) + \partial_a i_b(t,a) = +f(B,y)\,\beta(a)\,s_b(t,a) - \nu(a)\,i_b(t,a), \\ \dot{y}(t) = -\varepsilon\, f(B,y) \int_0^{a_\dagger} \beta(a)\,s_b(t,a)\,da - \mu_y\,y(t) + \phi\,z(t), \\ \dot{z}(t) = +\varepsilon\, f(B,y) \int_0^{a_\dagger} \beta(a)\,s_b(t,a)\,da - \mu_z\,z(t), \end{cases} \tag{1}$$

where $B(t) = \int_0^{a_\dagger} s_b(t,a)da$ represents the total number of healthy berries at time t. System (1) is supplemented by the following boundary and initial conditions:

$$\begin{gathered} s_b(t,0) = \lambda(t), \quad i_b(t,0) = 0, \\ s_b(0,a) = s_{b0}(a), \quad i_b(0,a) = i_{b0}(a), \quad y(0) = y_0, \quad y(0) = z_0. \end{gathered} \tag{2}$$

Model (1–2) relies on several assumptions listed below:

1. Many factors such as climatic and environmental conditions influence the development of the coffee crop. We do not explicitly represent these factors but we assume that healthy coffee berries are produced at time-dependent rate $\lambda(t)$.

2. We assume that there are enough males born in the berries to fertilise the young females.

3. In the force of infestation $\beta(a)f(B,y)$, $\beta(.)$ represents the age-specific infestation rate per unit of time, while the interaction between CBB and berries is described by function $f(.,.)$ which verifies the following hypotheses:

   - Function $f(.,.)$ is a bounded, C^1-Lipschitz function for both positive arguments, *i.e.* there exists a positive real number M such that:

     $$|f(B_1,y_1) - f(B_2,y_2)| \leq M\left(|B_1 - B_2| + |y_1 - y_2|\right),$$

     for all variables (B_1,y_1) and (B_2,y_2) in $\mathbb{R}_+^2$.
   - Moreover, $f(B,0) = 0$ and function $f(.,.)$ are non decreasing in y (for $B > 0$). Indeed, infestation can only occur when colonising females are present; furthermore, for a given number of berries, the more the colonising females, the more severe the infestation.
   - Finally, $f(.,.)$ is non increasing in B (for $y > 0$) and for all $y \in \mathbb{R}_+^*$, $\lim\limits_{B\to+\infty} Bf(B,y)$ is finite. The latter hypothesis means that infestation is limited by the number of colonising females. As a consequence, $\lim\limits_{B\to+\infty} f(B,y) = 0$.

   These hypotheses are compatible with density- or ratio-dependent interactions, as implemented in [10].

4. The females are able to differentiate infested from uninfested berries and choose healthy coffee berries. Indeed, super-parasitism is rarely observed in a plantation [11, 21]. Parameter ε is a scaling parameter that corresponds to the number of colonising females per infested berry. So usually, $\varepsilon = 1$ CBB/berry.

5. We assume that the number of colonising females emerging from the infested coffee berries per infesting female ϕ is constant.

6. The age-dependent mortality rates of healthy and infested coffee berries are respectively $\mu(a)$ and $\nu(a)$. We assume that $\nu(a) > \mu(a)$ since CBB infestation leads to the premature fall of coffee berries in the plantation [2, 6]. The parameters μ_y and μ_z represent the natural mortality rates for colonising and infesting females respectively. We assume that an infesting female may pursue its development if its berry falls down. In turn, even if an infesting female dies, its berry survives.

It is worth noticing that, if the age-dependent and time-dependent functions are chosen as positive constants, *i.e.* $\mu(a) = \mu$, $\beta(a) = \beta$, $\nu(a) = \nu$ and $\lambda(t) = \lambda$, then by integrating the first two equations of system (1) on $[0, a_\dagger]$, we obtain a nonlinear ordinary differential system similar to the models proposed in [9, 10].

As the age-dependent variable $i_b(t,a)$ does not appear in the equations of the other variables in system (1), one can ignore the dynamics of $i_b(t,a)$ and study the following reduced model given for $t \geq 0$ and $a \in [0, a_\dagger]$:

$$\begin{cases} \partial_t s_b(t,a) + \partial_a s_b(t,a) = -f(B,y)\,\beta(a)\,s_b(t,a) - \mu(a)\,s_b(t,a), \\ \dot{y}(t) = -\varepsilon f(B,y)\int_0^{a_\dagger} \beta(a)\,s_b(t,a)\,da - \mu_y\,y(t) + \phi z(t), \\ \dot{z}(t) = +\varepsilon\,f(B,y)\int_0^{a_\dagger} \beta(a)\,s_b(t,a)\,da - \mu_z\,z(t), \\ s_b(t,0) = \lambda(t), \quad s_b(0,a) = s_{b0}(a), \quad y(0) = y_0, \quad z(0) = z_0. \end{cases} \tag{3}$$

Let us denote by $(L^1_+(I), \|.\|)$ the space of nonnegative measurable functions equipped with the product norm and by $(L^\infty_+(I), \|.\|_\infty)$ the space of nonnegative and Lebesgue integrable functions over the set $I \subset \mathbb{R}$. We make the following realistic assumptions on the positivity and smoothness of the parameters and functions involved in model (3).

Assumption 1. *Throughout this manuscript, we assume that:*

1. *Parameters ϕ, ε, μ_y, μ_z and initial conditions y_0 and z_0 are nonnegative.*
2. *$\lambda(.) \in L^\infty_+(0,\infty)$, $\beta(.) \in L^\infty_+(0,a_\dagger)$; boundary conditions $s_{b0}(.)$, $i_{b0}(.) \in L^1_+(0,a_\dagger)$.*
3. *$\mu(.), \nu(.) \in L^\infty_+(0,a_\dagger)$ such that $\nu(a) \geq \mu(a)$ and there exists a real number $\widetilde{\mu} > 0$ satisfying : $\mu(a) \geq \widetilde{\mu}$ for almost every $a \in [0,a_\dagger]$.*

3 Well-posedness

In this section, we aim at proving the existence and uniqueness of a nonnegative solution for system (3). The preliminary step consists in finding the equivalent system with zero boundary conditions, using the ideas of [16, 20] and writing the new model as an abstract Cauchy problem, which is easier to handle. Then we prove the existence and uniqueness of a mild solution to this Cauchy problem in the nonnegative cone of a Banach space, by adapting the arguments of [19]. Finally, we deduce the existence and uniqueness of a mild solution for the initial system (3).

3.1 Abstract Cauchy problem

Let us define the survival probability of healthy coffee berries until age a by $\pi(a) = e^{-\int_0^a \mu(x)dx}$. For all $t \geq 0$, we introduce the new functional:

$$\Phi_t(.) : \xi \longrightarrow \Phi_t(\xi) := \begin{cases} \pi(\xi)\lambda(t-\xi) & \text{if } t \geq \xi \geq 0, \\ 0 & \text{otherwise.} \end{cases}$$

Based on these definitions and Assumption 1, we have the following instrumental lemma which can be easily established [16].

Lemma 1.

1. *The function $\pi(.) \in L^1_+(0,a_\dagger)$ and satisfies the differential equation: $\dot{\pi}(a) = -\mu(a)\pi(a)$. Moreover, for all $a \in [0,a_\dagger]$ and any $t \leq a$, $0 \leq \pi(a) \leq e^{-\widetilde{\mu}a}$ and $\frac{\pi(a)}{\pi(a-t)} \leq \pi(t)$.*
2. *The function $t \longmapsto \Phi_t(.)$ is in $\mathcal{C}(\mathbb{R}_+, L^1_+(0,a_\dagger))$. Moreover, for all $t \geq 0$, $\Phi_t(0) = \lambda(t)$ and $\Phi_t(.)$ satisfies the partial differential equation:*

$$\partial_t \Phi_t(a) + \partial_a \Phi_t(a) = -\mu(a)\Phi_t(a).$$

Considering the transformation $s_b(t,a) \longmapsto \widehat{s}(t,a) := s_b(t,a) - \Phi_t(a)$, then system (3) is equivalent to the following system with zero boundary conditions:

$$\begin{cases} \partial_t \widehat{s}(t,a) + \partial_a \widehat{s}(t,a) = -f(\widehat{B},y)\,\beta(a)[\widehat{s}(t,a) + \Phi_t(a)] - \mu\,\widehat{s}(t,a) \\ \dot{y}(t) = -\varepsilon\, f(\widehat{B},y)\|\beta(\widehat{s}(t,.) + \Phi_t)\| - \mu_y\, y(t) + \phi\, z(t) \\ \dot{z}(t) = +\varepsilon\, f(\widehat{B},y)\|\beta(\widehat{s}(t,.) + \Phi_t)\| - \mu_z\, z(t) \\ \widehat{s}(t,0) = 0, \quad \widehat{s}(0,a) = s_0(a) - \lambda(0), \quad y(0) = y_0, \quad z(0) = z_0. \end{cases} \tag{4}$$

where:

$$\widehat{B}(t) = \int_0^{a_\dagger} [\widehat{s}(t,a) + \Phi_t(a)]da,$$
$$\|\beta(\widehat{s}(t,.) + \Phi_t)\| = \int_0^{a_\dagger} [\beta(a)\widehat{s}(t,a) + \Phi_t(a)]da.$$

Let $\mathcal{A}_s$ and $\mathcal{A}_I$ denote the differential operators defined by:

$$\begin{aligned} \mathcal{A}_s :\ D(\mathcal{A}_s) \subset L^1(0,a_\dagger) &\longrightarrow L^1(0,a_\dagger) \\ \Psi &\longmapsto \mathcal{A}_s\Psi(a) = -\Psi'(a) - \mu(a)\Psi(a), \\ \mathcal{A}_I :\ D(\mathcal{A}_I) \subset \mathbb{R}^2 &\longrightarrow \mathbb{R}^2 \\ \Psi &\longmapsto \mathcal{A}_I\Psi = \mathrm{diag}(-\mu_y, -\mu_z)\Psi, \end{aligned}$$

where: $D(\mathcal{A}_s) := \{\Psi \in W^{1,1}(0,a_\dagger) : \Psi(0) = 0\}$ and $D(\mathcal{A}_I) = \mathbb{R}^2$, with $W^{1,1}(0,a_\dagger)$ denoting the Sobolev space. Biologically speaking, the linear differential operators $\mathcal{A}_s$ and $\mathcal{A}_I$ represent the mortality processes related to the healthy coffee berries and females CBB respectively. Let us define the Banach space $\mathcal{X} = L^1(0,a_\dagger) \times \mathbb{R} \times \mathbb{R}$ equipped with the usual norm $\|.\|_{\mathcal{X}}$. The nonnegative cone of the Banach space $\mathcal{X}$ is $\mathcal{X}_+ = L^1_+(0,a_\dagger) \times \mathbb{R}_+ \times \mathbb{R}_+$. Let us define the linear differential operator $\mathcal{A} : D(\mathcal{A}) \subset \mathcal{X} \longrightarrow \mathcal{X}$ where $D(\mathcal{A}) = D(\mathcal{A}_s) \times D(\mathcal{A}_I)$ such that

$$\mathcal{A} := \mathrm{diag}(\mathcal{A}_s, \mathcal{A}_I). \tag{5}$$

Let $u(t) = (\widehat{s}(t,.), y(t), z(t))^\top$ denotes the solution of system (4) with $u(0) = (\widehat{s}_0(.), y_0, z_0)^\top$. We define a nonlinear perturbation map $\mathcal{H} : \mathbb{R}_+ \times \overline{D(\mathcal{A})} \subset \mathbb{R}_+ \times \mathcal{X} \longrightarrow \mathcal{X}$ as follows:

$$\mathcal{H}(t,u(t)) = \begin{pmatrix} -\beta(a)f(\widehat{B},y)[\widehat{s}(t,a) + \Phi_t(a)] \\ -\varepsilon f(\widehat{B},y)\|\beta(\widehat{s}(t,.) + \Phi_t)\| + \phi z(t) \\ \varepsilon f(\widehat{B},y)\|\beta(\widehat{s}(t,.) + \Phi_t)\| \end{pmatrix}. \tag{6}$$

Then, we can transform system (4) into the following abstract Cauchy problem in the Banach space $\mathcal{X}$:

$$\begin{cases} \dot{u}(t) = \mathcal{A}u(t) + \mathcal{H}(t,u(t)) \quad \text{for } t \geq 0 \\ u(0) = u_0 \in \overline{D(\mathcal{A})}. \end{cases} \tag{7}$$

To prove the existence and uniqueness of a solution to the abstract Cauchy problem (7), we begin by showing that the linear autonomous problem associated to system (7) has a unique solution. Then we prove the existence of a unique solution for the nonautonomous and nonlinear system (7) using the perturbation theory of linear evolution equations (see [19, 29] for more details).

3.2 The linear problem

This section is devoted to the definition of the semigroup generated by the differential operator $\mathcal{A}$ and the existence and uniqueness of a solution to the linear problem associated to the system (7). Let us define the resolvent set $\rho(\mathcal{A})$ of the linear operator $\mathcal{A}$ as the set of all complex number ζ for which $(\zeta I - \mathcal{A})$ is inversible, *i.e.* $(\zeta I - \mathcal{A})^{-1}$ is a bounded linear operator in $L^1(0,a_\dagger)$. Let Δ denotes the subset of the complex number defined by $\Delta := \{\zeta \in \mathbb{R} : \zeta > -\omega\}$ where $\omega = \min\{\widetilde{\mu}, \mu_y, \mu_z\}$.

Lemma 2. *The differential operator $\mathcal{A}$ is closed and the resolvent set $\rho(\mathcal{A}) \supset \Delta$. Moreover, the family of the bounded linear operators $(\zeta I - \mathcal{A})^{-1}$, called resolvent, satisfies $\|(\zeta I - \mathcal{A})^{-1}\| \leq \frac{1}{\zeta+\omega}$, $\forall \zeta \in \Delta$.*

Proof. We start by show that the differential operator $\mathcal{A}$ is closed. According to [5], it is sufficient to show that $D(\mathcal{A})$ with norm $\|x\|_{D(\mathcal{A})} = \|x\|_{\mathcal{X}} + \|\mathcal{A}x\|_{\mathcal{X}}$, $\forall x \in D(\mathcal{A})$ is a Banach space. It is easy to verify that $\|.\|_{D(\mathcal{A})}$ is a norm on $D(\mathcal{A})$. For show that $(\mathcal{A}, D(\mathcal{A}))$ is complete. we take (θ_n, y_n, z_n) to be a Cauchy sequence of points of $D(\mathcal{A})$. Thus $\theta_n \in W^{1,1}$ which is a Banach space (*i.e.* complete), so $\theta_n \xrightarrow[n\to\infty]{} \theta_\star$ in $W^{1,1}$, *i.e.* that $\theta_n \xrightarrow[n\to\infty]{} \theta_\star$ and $\theta'_n \xrightarrow[n\to\infty]{} \theta'_\star$ in L^1. Moreover, $y_n \xrightarrow[n\to\infty]{} y_\star \in \mathbb{R}$ and $z_n \xrightarrow[n\to\infty]{} z_\star \in \mathbb{R}$ since $\mathbb{R}$ is complete. Then $\|\mu\theta_n - \mu\theta_\star\| \leq \|\mu\|_\infty \|\theta_n - \theta_\star\| \xrightarrow[n\to\infty]{} 0$ since $\|\mu\|_\infty$ is finite. Therefore, $\mu\theta_n \xrightarrow[n\to\infty]{} \mu\theta_\star$ in L^1. We can thus see that the sequence (θ_n, y_n, z_n) converges in $D(\mathcal{A})$ to $(\theta_\star, y_\star, z_\star)$. In fact, $\|(\theta_n, y_n, z_n) - (\theta_\star, y_\star, z_\star)\|_{D(\mathcal{A})} \leq \|\theta_n - \theta_\star\| + \|y_n - y_\star| + \|z_n - z_\star| + \|\mu(\theta_n - \theta_\star) + (\theta'_n - \theta'_\star)\| + \mu_y\|y_n - y_\star| + \mu_z\|z_n - z_\star|$. Thus any Cauchy sequence is convergent and the space $D(\mathcal{A})$ with its norm $\|.\|_{D(\mathcal{A})}$ is complete. Hence the operator $\mathcal{A}$ is closed.

To check the estimation, Let $x \in \mathcal{X}$ with coordinates $x = (\psi, x_1, x_2)$ and $u = (\widehat{s}, y, z) \in D(\mathcal{A})$. We consider the equation $(\zeta I - \mathcal{A})u = x$ implies that $u = (\zeta I - \mathcal{A})^{-1}x$ that is $\widehat{s}(a) = \int_0^a e^{\zeta(\eta - a)} \frac{\pi(a)}{\pi(\eta)} \Psi(\eta) d\eta$, $\forall \psi \in L^1(0, a_\dagger)$, $y = \frac{1}{\zeta+\mu_y}$ and $z = \frac{1}{\zeta+\mu_z}$. Assuming $\zeta > -\omega$, then the direct calculation show that we have the estimate $\|(\zeta I - \mathcal{A})^{-1}\| \leq \frac{1}{\zeta+\omega}$. This achieves the proof. □

The properties of the linear operator $(\mathcal{A}, D(\mathcal{A}))$ are precised by the following proposition.

Proposition 1. *The linear operator $(\mathcal{A}, D(\mathcal{A}))$ is an infinitesimal generator of a strongly positive C_0-semigroup of contraction $T_{\mathcal{A}}(t) = diag\,(T_{\mathcal{A}_s}(t), T_{\mathcal{A}_I}(t))$ such that for every $t \geq 0$ and $\Psi \in L^1(0, a_\dagger)$:*

$$T_{\mathcal{A}_s}(t)\Psi(a) = \begin{cases} \dfrac{\pi(a)}{\pi(a-t)}\Psi(a-t) & \text{if } t \leq a \leq a_\dagger, \\ 0 & \text{otherwise}, \end{cases} \tag{8}$$

and for every $(x, y) \in \mathbb{R}^2$:

$$T_{\mathcal{A}_I}(t)(x, y) = diag\left(e^{-\mu_y t}, e^{-\mu_z t}\right)(x, y) = (xe^{-\mu_y t}, ye^{-\mu_z t}). \tag{9}$$

Moreover, the semigroup $\{T_{\mathcal{A}}(t)\}_{t\geq 0}$ is exponentially stable.

Proof. From Lemma 2 and according to the Hille–Yosida Theorem [19], the linear differential operator $(\mathcal{A}, D(\mathcal{A}))$ is an infinitesimal generator of a C_0-semigroup of contraction $T_{\mathcal{A}}(t)$. Moreover, its resolvent is positive on $\mathcal{X}$, then the C_0-semigroup of contraction $T_{\mathcal{A}}(t)$ is positive [19, 29]. Hence, performing a change of variable $\xi = a - \eta$ in the resolvent equation $\widehat{s}(a) = \int_0^a e^{\zeta(\eta - a)} \frac{\pi(a)}{\pi(\eta)} \Psi(\eta) d\eta$, $\forall \Psi \in L^1(0, a_\dagger)$ and computing the exponential of the operator $\mathcal{A}_I$, we obtain the desired expressions for the semigroup $T_{\mathcal{A}}(t)$. Finally, the estimation is a direct consequence of Lemma 1 which implies that $\|T_{\mathcal{A}}(t)\| = \sup\{\|T_{\mathcal{A}_s}(t)\|, \|T_{\mathcal{A}_I}(t)\|\} \leq \max\{\pi(t), e^{-\mu_y t}, e^{-\mu_z t}\} \leq e^{-\omega t}$, with $\omega = \min\{\widetilde{\mu}, \mu_y, \mu_z\}$ for all $t > 0$. Then, the operator $\|T_{\mathcal{A}}(t)\|$ converges towards zero when $t \to +\infty$. Therefore, the semigroup $\{T_{\mathcal{A}}(t)\}_{t\geq 0}$ is positive and exponentially stable. □

As a consequence of Proposition 1 and according to [13, 19], we obtain the following result regarding the existence of a solution to the linear abstract Cauchy problem.

Theorem 1. *For the given initial condition $u(0) \in D(\mathcal{A})$, $u(t) = T_{\mathcal{A}}(t)u_0$ for all $t \geq 0$ is a unique classical solution of the linear abstract Cauchy system $\dot{u}(t) = \mathcal{A}u(t)$ in $\mathcal{X}$.*

3.3 Existence and uniqueness of the solution for the nonlinear system

Having established the existence and uniqueness of a solution to the linear problem given by Theorem 1, we are now interested in establishing the existence and uniqueness of a solution to the nonlinear evolution problem (7). To do so, we opt for the Lipschitz perturbation approach for a semigroup. The map $\mathcal{H}(., u(.))$ in the abstract system (7) is considered as a perturbation of the semigroup generated by the linear differential operator $\mathcal{A}$. For every constant $\delta > 0$, $\mathcal{B}_\delta$ denotes the ball of centre 0 and radius δ in space $\mathcal{X}$, $\mathcal{B}_\delta := \{x \in \mathcal{X} : \|x\|_\mathcal{X} \leq \delta\}$. We show that the nonautonomous map $\mathcal{H}(., u(.))$ is a Lipschitzian perturbation of the continuous semigroup $\{T_\mathcal{A}(t)\}_{t\geq 0}$. We begin with the following lemma.

Lemma 3. *The perturbation map $\mathcal{H}$ is a locally Lipschitz continuous function in $u(.)$, uniformly in $t \geq 0$: for all $\delta > 0$, there exists a constant depending on δ denoted by M_δ such that:*

$$\|\mathcal{H}(t, u_1) - \mathcal{H}(t, u_2)\|_\mathcal{X} \leq M_\delta \|u_1 - u_2\|_\mathcal{X}, \quad \forall (u_1, u_2) \in (\mathcal{B}_\delta)^2.$$

Proof. See A. □

We establish the existence of the solution of system (7) in the following theorem.

Theorem 2. *For any initial condition in $\mathcal{X}$, there exists an interval of time $[0, t_{max})$ in which the abstract Cauchy problem (7) has a unique mild solution.*

Proof. We use a fixed point method by adapting the ideas of [16, 19, 20]. Let $\tau > 0$ and $\widehat{\delta} > 0$ such that:

$$\widehat{\delta} := 2\|u_0\|_\mathcal{X} \sup_{t\in[0.1]} \|T_\mathcal{A}(t)\|_\mathcal{X}, \ \tau := \min\left\{1, \frac{\|u_0\|_\mathcal{X}}{\widehat{\delta} M_{\widehat{\delta}}}\right\}, \tag{10}$$

where the $M_{\widehat{\delta}}$ is the local Lipschitz constant for the map $\mathcal{H}(.,.)$ defined in Lemma 3. Let us consider the ball defined by:

$$\mathcal{B}^c_{\widehat{\delta}} := \left\{u \in \mathcal{C}([0, \tau], \mathcal{X}) : \ \|u(t)\|_\mathcal{X} \leq \widehat{\delta} \text{ for all } t \in [0, \tau]\right\}.$$

Next, consider the nonlinear mapping:

$$\begin{aligned} \mathbb{G} : \ & \mathcal{C}([0, \tau], \mathcal{X}) \longrightarrow \mathcal{C}([0, \tau], \mathcal{X}) \\ & u(.) \longmapsto \mathbb{G}(u(t)) = T_\mathcal{A}(t)u_0 + \int_0^t T_\mathcal{A}(t - \varsigma)\mathcal{H}(\varsigma, u(\varsigma))d\varsigma. \end{aligned}$$

Standard boundedness techniques, as performed in [19, page 187], prove that $\mathbb{G}$ maps the ball $\mathcal{B}^c_{\widehat{\delta}}$ into itself and is a contraction mapping of $\mathcal{B}^c_{\widehat{\delta}}$ with Lispschitz constant 1/2. Consequently, the Banach fixed point theorem implies that map $\mathbb{G}$ possesses a unique fixed point $u \in \mathcal{B}^c_{\widehat{\delta}}$. This fixed point is the desired mild solution on interval $[0, \tau]$ of the evolution system (7). We repeat all previous arguments, but now with initial condition $u(\tau)$ instead of $u(0)$, $\tau_1 = \tau + \gamma$ with $\gamma > 0$, together with space $\mathcal{C}([\tau, \tau_1], \mathcal{X})$ and mapping $\mathbb{G}_1$ defined in a similar way to $\mathbb{G}$. The same arguments applied to the latter case also show that $\mathbb{G}_1$ is a strict contraction with Lipschitz constant 1/2. This gives once more a unique fixed point which extends the previous solution on interval $[0, \tau_1]$. By proceeding successively, we can extend the solution on $[0, t_{max})$, so that $u \in \mathcal{C}([0, t_{max}), \mathcal{X})$ is a mild solution of system (7). □

Since we have shown that the abstract Cauchy problem (7) has a unique mild solution $u \in \mathcal{C}([0, t_{max}), \mathcal{X})$, the transformation $u(t) \longmapsto u(t) + (\Phi_t(.), 0, 0) := (s_b(t, .), y(t), z(t))$ leads to the existence and uniqueness of a mild solution $(s_b, y, z) \in \mathcal{C}([0, t_{max}), \mathcal{X})$ of system (3). We only obtain a local solution, so it is important to show that this solution is actually global by showing that the solution is bounded. This is provided by the following lemma.

Lemma 4. *Under Assumption 1, the solution of system (3) remains nonnegative and bounded for all time $t > 0$. Moreover, the domain:*

$$\Sigma := \left\{ (s_b, y, z) \in \mathcal{X}_+ : \ \varepsilon \|s_b(t,.)\| + z \leq \frac{\varepsilon \|\lambda\|_\infty}{\xi}, \ y \leq \frac{\varepsilon \phi \|\lambda\|_\infty}{\mu_y \xi} \right\},$$

where $\xi := \min\{\widehat{\mu}, \mu_z\}$, is positively invariant under the flow of system (3).

Proof. See B. □

A direct consequence of Lemma 4 is that $\|(s_b(t,.), y(t), z(t))\|_{\mathcal{X}}$ is bounded for all time $t > 0$ in bounded intervals, which means that $t_{max} = +\infty$. Therefore, we have the following result.

Corollary 1. *Let Assumption 1 be satisfied. Then for every nonnegative initial condition, there exists a unique mild solution $(s_b(t,.), y(t), z(t)) \in \mathcal{C}([0, +\infty), \mathcal{X}_+)$ for system (3).*

Let us introduce the total CBB population $w(t) = y(t) + z(t)$. By adding the second and third equations of system (3), we obtain the total population dynamics $\dot{w}(t) = -\mu_z(1-\mathcal{R})z(t) - \mu_y y(t)$, where $\mathcal{R} = \frac{\phi}{\mu_z}$ corresponds to the average number of emerging colonising females produced by a single infesting female during its lifespan. If $\mathcal{R} < 1$, the total population $w(t) \leq w(0)e^{-\zeta t}$ with $\zeta = \min\{\mu_z(1-\mathcal{R}), \mu_y\}$, so the CBB population disappears in the plantation. However, as previously stated, with realistic parameter values $\mathcal{R} \gg 1$.

4 Asymptotic behaviour for constant berry production

In this section, we study the existence and stability of the pest-free equilibrium point for a constant berry production rate $\lambda(t) = \lambda$ and determine the basic reproduction number.

System (3) always has a pest-free steady state $\mathcal{E}(a) = (s_b^0(a), 0, 0)$, where $s_b^0(a) = \lambda\pi(a)$, corresponding to the equilibrium without CBB. We now compute the basic reproduction number, $\mathcal{R}_0$, using the next generation operator approach [13, 7]. Linearising the system around the pest-free steady state with $x(t,a)$, $v(t)$ and $w(t)$ being the perturbations, that is $x(t,a) = s_b(t,a) - s_b^0(a)$, $v(t) = y(t)$ and $w(t) = z(t)$, we obtain the following linear system written in the abstract form:

$$\dot{\psi}(t) = \mathcal{A}\psi(t) + D\mathcal{H}(\mathcal{E}(a))(\psi(t)), \quad \psi(0) = 0 \in D(\mathcal{A}). \tag{11}$$

where $\psi(t) = (x(t,.), v(t), w(t))^\top$, $B^0 = \int_0^{a_\dagger} s_b^0(a)da$ and the linear operator $D\mathcal{H}(\mathcal{E}(a)) : \mathcal{X} \longrightarrow \mathcal{X}$ is defined by:

$$D\mathcal{H}(\mathcal{E}(a))(\psi(t)) = \begin{pmatrix} -f_y(B^0, 0)[\beta s_b^0]v \\ \phi w - \varepsilon f_y(B^0, 0)\|\beta s_b^0\|v \\ \varepsilon f_y(B^0, 0)\|\beta s_b^0\|v \end{pmatrix}.$$

The next generation operator is defined by $\mathcal{B}(-\mathcal{A})^{-1}$, where the operator $\mathcal{B} := D\mathcal{H}(\mathcal{E}(a))$. Consider the vectors $(z_1, z_2, z_3)^\top \in \mathcal{X}_0$ and $(\Phi, y, z)^\top \in \mathcal{X}$, then we have $(-\mathcal{A})^{-1}(z_1, z_2, z_3)^\top = (\Phi, y, z)^\top$ which implies that

$$z_1(a) = z_1(0)e^{-\int_0^a \mu(\sigma)d\sigma} - \int_0^a \Phi(\sigma)e^{-\int_\sigma^a \mu(l)dl}d\sigma, \quad y = -\frac{1}{\mu_y}z_2, \quad z = -\frac{1}{\mu_z}z_3.$$

Therefore, we get by direct calculation:

$$\mathcal{B}(-\mathcal{A})^{-1} = \begin{pmatrix} 0 & -\frac{1}{\mu_y}f_y(B^0, 0)[\beta s_b^0] & 0 \\ 0 & -\frac{\varepsilon}{\mu_y}f_y(B^0, 0)\|\beta s_b^0\| & \frac{\phi}{\mu_z} \\ 0 & \frac{\varepsilon}{\mu_y}f_y(B^0, 0)\|\beta s_b^0\| & 0 \end{pmatrix}.$$

Based on [13, 7], the basic reproduction number is defined as the spectral radius of the next generation operator $\mathcal{B}(-\mathcal{A})^{-1}$, that is:

$$\mathcal{R}_0 = \frac{1}{2}\left(-\mathcal{T} + \left(\mathcal{T}^2 + 4\mathcal{R}\mathcal{T}\right)^{\frac{1}{2}}\right),$$

where $\mathcal{T} = \frac{\varepsilon}{\mu_y} f(B^0, 0)\|\beta s_b^0\|$.

Remark 1.

1. *Using the computation approach proposed in [25], we obtain the following basic reproduction number:*
$$\widetilde{\mathcal{R}_0} = \mathcal{R}\frac{\varepsilon f_y(B^0, 0)\|\beta s_b^0\|}{\varepsilon f_y(B^0, 0)\|\beta s_b^0\| + \mu_y}. \tag{12}$$

2. *We have the relation $\widetilde{\mathcal{R}_0} = \frac{\mathcal{R}_0(\mathcal{T}+\mathcal{R}_0)}{\mathcal{T}+1}$. Simple calculations show that $\mathcal{R}_0 < 1 (= 1, > 1)$ is equivalent to $\widetilde{\mathcal{R}_0} < 1 (= 1, > 1)$.*

3. *Threshold $\mathcal{R}_0$ is difficult to interpret biologically. The biological interpretation of threshold $\widetilde{\mathcal{R}_0}$ is more straightforward:*

   - *The term $\frac{\varepsilon f_y(B^0,0)\|\beta s^0\|}{\varepsilon f_y(B^0,0)\|\beta s_b^0\|+\mu_y}$ represents the average number of infesting females produced by a colonising female.*
   - *So $\mathcal{R}_0$ can be defined as the average number of new infesting females originated from a single infesting female in the coffee plantation during its lifespan.*

4. *If $\mathcal{R} = \frac{\phi}{\mu_z} < 1$, which corresponds to unrealistic parameter values leading to the extinction of the CBB population, then $\widetilde{\mathcal{R}_0} < 1$.*

Before establishing some results about stability, let us recall the notion of spectrum, growth bound and essential growth bound in spectral theory and some of their properties.

Let K be the infinitesimal generator of the strongly continuous semigroup $\{T_K(t)\}_{t\geq 0}$ on a Banach space X. The spectrum of K denoted by $\sigma(K)$ and the spectral bound denoted by $\mathfrak{s}(B)$ are defined by $\sigma(K) = \mathbb{C} \setminus \rho(K)$ and $\mathfrak{s}(K) = \sup\{Re\zeta, \zeta \in \sigma(K)\}$ respectively. Let $\omega_0(K)$ be the growth bound of a semigroup $\{T_K(t)\}_{t\geq 0}$ defined by $\omega_0(K) := \lim\limits_{t\to+\infty} t^{-1}\ln\left(\|T_K(t)\|\right)$. Then it is proved in [8] that:

$$\omega_0(K) = \max\{\omega_{ess}(K), \mathfrak{s}(K)\},$$

with the essential growth bound $\omega_{ess}(K) := \lim\limits_{t\to+\infty} t^{-1}\ln\left(\alpha[T_K]\right)$, where $\alpha[T]$ is the measure of noncompactness of a bounded linear operator T. If C is a bounded linear operator in X, then $K + C$ is the infinitesimal generator of a strongly semigroup. Moreover, if C is also compact, then:

$$\omega_{ess}(K) = \omega_{ess}(K + C).$$

Theorem 3. *If $\widetilde{\mathcal{R}_0} < 1$, then the pest-free steady state $\mathcal{E}(a)$ is locally asymptotically stable and is unstable whenever $\widetilde{\mathcal{R}_0} > 1$.*

Proof. According to [28], the steady state $\mathcal{E}(a)$ is locally asymptotically stable if $\omega_0(\mathcal{A}+D\mathcal{H}(\mathcal{E})) < 0$ and becomes unstable when $\omega_0(B + D\mathcal{H}(\mathcal{E})) > 0$ and $\omega_{ess}(B + D\mathcal{H}(\mathcal{E})) < 0$.

On the one hand, the differential operator $(\mathcal{A}, D(\mathcal{A}))$ is an infinitesimal generator of a strongly continuous semigroup $\{T_{\mathcal{A}}(t)\}_{t\geq 0}$ in $\mathcal{X}$ satisfying $\|T_{\mathcal{A}}(t)\| \leq e^{-\omega t}$, $\forall t \geq 0$ and, on the other hand, we see that $D\mathcal{H}(\mathcal{E})$ is finite dimensional, so $D\mathcal{H}(\mathcal{E})$ is a compact bounded operator. It follows that:

$$\omega_{ess}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) \leq \omega_{ess}(\mathcal{A}) \leq \omega_0(\mathcal{A}) = \lim_{t\to+\infty} t^{-1}\ln(e^{-\omega t}) = -\omega.$$

We can observe that the variable $x(t,a)$ has no impact on the dynamics of the two remaining variables in system (11). Then it suffices to use the second and third equations of (11) to determine the stability criterion of system (3) around the pest-free steady state. To this end, we seek solutions with an exponential form, setting $v(t) = \tilde{v}e^{\zeta t}$ and $w(t) = \tilde{w}e^{\zeta t}$, where $\tilde{v}$ and $\tilde{w}$ are real numbers which can be estimated and ζ is either a real or a complex number. Substituting these exponential forms in system (11), we obtain the linear homogeneous system $(\zeta I - \chi)\tilde{g} = 0$, where $\tilde{g} = (\tilde{v}, \tilde{w})^\top$, I is identity matrix and:

$$\chi = \begin{pmatrix} -\varepsilon f_y(B^0,0)\|\beta s_b^0\| - \mu_y & \phi \\ \\ \varepsilon f_y(B^0,0)\|\beta s_b^0\| & -\mu_z \end{pmatrix}.$$

Hence, $\mathfrak{s}(\mathcal{A}+D\mathcal{H}(\mathcal{E})) < 0$ if and only if all roots $\zeta \in \mathbb{C}$ of the characteristic equation $\det(\zeta I - \chi) = 0$ have a negative real part. The trace $Tr(\chi) = -\varepsilon f_y(B^0,0)\|\beta s_b^0\| - \mu_y - \mu_z$ is negative. When $\widetilde{\mathcal{R}_0} < 1$, the determinant $\det(\chi) = \varepsilon\phi f_y(B^0,0)\|\beta s_b^0\| \left(\frac{1}{\widetilde{\mathcal{R}_0}} - 1\right)$ is positive and it becomes negative when $\widetilde{\mathcal{R}_0} > 1$. Then all the roots ζ of the characteristic equation associated with matrix χ have a negative real part if $\widetilde{\mathcal{R}_0} < 1$. Therefore, if $\widetilde{\mathcal{R}_0} < 1$, then $\mathfrak{s}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$ and $\omega_{ess}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$, hence $\omega_0(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$. Thus, the pest-free steady state is locally asymptotically stable if $\widetilde{\mathcal{R}_0} < 1$. When $\widetilde{\mathcal{R}_0} > 1$, then there exists at least one root ζ_0 with a positive real part. This implies that $\mathfrak{s}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) = \mathcal{R}e\zeta_0 > 0$. Therefore, $\omega_0(\mathcal{A} + D\mathcal{H}(\mathcal{E})) > 0$ and it follows that $\mathcal{E}(.)$ is unstable. This achieves the proof. □

Theorem 3 means that the CBB population could disappear from the coffee plantation if $\widetilde{\mathcal{R}_0} < 1$ and if the initial CBB population is in the basin of attraction of the pest-free steady state. In this case, it would not be necessary to control CBB.

5 Numerical results

To illustrate the theoretical results contained in previous sections, we begin by giving a brief description of the numerical scheme used to plot the state variables of system (3). We then present the model parameters and simulations of system (3) with constant berry production λ, as in Section 4, for various values of the basic reproduction number $\widetilde{\mathcal{R}_0}$ defined in equation (12).

5.1 Numerical scheme

This scheme is based on semi-implicit finite differential equations for the variables $y(t)$ and $z(t)$ and on the hyperbolic partial differential equation verified by $s_b(t,a)$ [23]. The integral terms are discretised using an explicit composite trapezoidal rule. Let $\Delta a > 0$ be the discretisation step for the interval $[0, a_\dagger]$, with $N = \frac{a_\dagger}{\Delta a}$ the number of age sub-intervals, and let $\Delta t > 0$ be the discretisation step for the interval $[0, t_f]$, with $K = \frac{t_f}{\Delta t}$ the number of time sub-intervals. Replacing the derivative in time with a backward difference and the derivative in age with a forward difference, $\partial_t x(t,a)$ and $\partial_a x(t,a)$ are evaluated at time t_n and age a_j by:

$$\partial_t x(t_n, a_j) \simeq \frac{x_{j+1}^{n+1} - x_{j+1}^n}{\Delta t} \quad \text{and} \quad \partial_a x(t_n, a_j) \simeq \frac{x_{j+1}^n - x_j^n}{\Delta a},$$

where n and j denote the time and age index, respectively, and x_j^n denotes the solution approximation at time $t_n := n\Delta t$ and age $a_j := j\Delta a$.

Since berry age evolves at the same speed as chronological time, choosing $\Delta a = \Delta t$ ensures that the necessary CFL (Courant–Freidriche–Lewy) stability condition, *i.e.* $\frac{\Delta t}{\Delta a} \leq 1$, holds [1, 23].

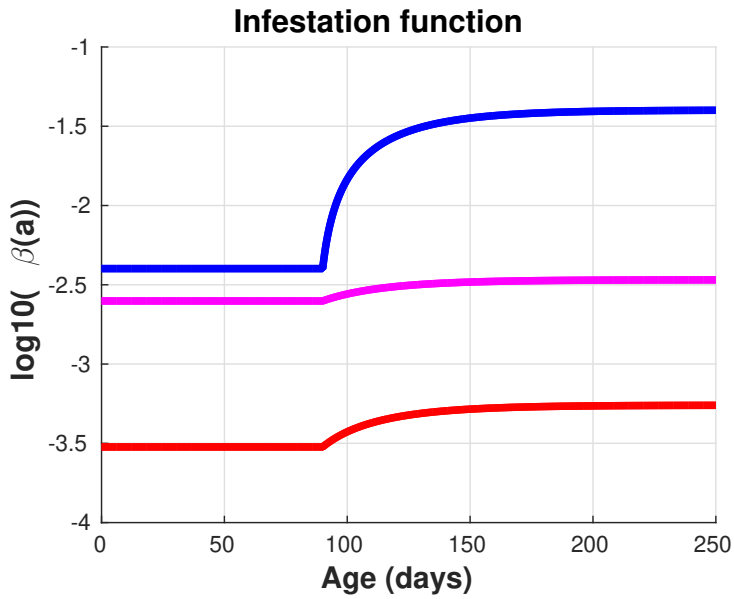

Figure 2: Infestation function β, defined in equation (13) as a function of berry age, for the three parameter sets selected in Table 1: $(\beta_{\min}, \beta_a) = (3\,10^{-4}, 2.5\,10^{-4})$ day^{-1} corresponding to $\widetilde{\mathcal{R}_0} = 0.64$ (red curve), $(\beta_{\min}, \beta_a) = (2.5\,10^{-3}, 9\,10^{-4})$ day^{-1} corresponding to $\widetilde{\mathcal{R}_0} = 4.2$ (magenta curve) and $(\beta_{\min}, \beta_a) = (4\,10^{-3}, 3.6\,10^{-2})$ day^{-1} corresponding to $\widetilde{\mathcal{R}_0} = 20.1$ (blue curve). Note that a semilog scale is used.

5.2 Parameter values

In the numerical simulations, we assume that flowering occurs in the plantation throughout the cropping season, so that we can consider a constant berry production rate $\lambda(t) \equiv \lambda$. Since coffee berries become fully mature after 6–9 months [2], the maximum berry age of is set at $a_\dagger = 250$ days. We found no data on age-dependent mortality for uninfested berries, so we apply a constant rate μ to all berries up to the berry maximum age $a_\dagger$. CBB colonising females infest healthy berries of all ages, but with a preference for more mature berries [11, 21]. According to [3], the infestation of berries younger than 90 days is very low. So we represent the infestation rate as a constant function for berry ages lower than a_β and an increasing function for older ages, according to the following function:

$$\beta(a) = \begin{cases} \beta_{\min} & 0 \le a < a_\beta, \\ \beta_{\min} + \beta_a(1 - e^{-k_\beta(a-a_\beta)}), & a_\beta \le a \le a_\dagger. \end{cases} \tag{13}$$

In the simulations below, we varied parameters $\beta_{\min}$ and β_a to obtain different values of the basic reproduction number $\widetilde{\mathcal{R}_0}$ defined in equation (12) (see Table 1). The three functions hence obtained are depicted in Figure 2. They have the same shape: a plateau followed by a sharp increase from the age of 90 days, the infestation almost reaching its maximum value $\beta_{\min} + \beta_a$ for berries aged more than 200 days. The plateau and maximum values, however, differ among the functions, both increasing with the $\widetilde{\mathcal{R}_0}$ value.

The CBB–berry interaction function $f(.,.)$ is modelled by:

$$f(B, y) = \frac{y}{y + \alpha B + 1},$$

in order to ensure that both coffee berries and colonising females are limiting variables for the infestation process. As generally $y \gg 1$, $f(.,.)$ introduces a ratio-dependent-like interaction between CBB and coffee berries.

All parameter values used in the simulations are given in Table 1.

Table 1: Model parameter values, based on biological data collected in the literature [2]; more information is available in [10]. Parameters of the infestation function $\beta(a)$ vary to obtain different values of the basic reproduction number $\widetilde{\mathcal{R}_0}$ defined in equation (12).

Symbol	Description	Value(s)
t_f	Duration of a cropping season	250 days
$a_\dagger$	maximum age of coffee berry	250 days
λ	Production rate of new coffee berries	1200 berries.day^{-1}
μ	Natural mortality rate of healthy coffee berries	0.002 day^{-1}
ε	Colonising CBB per berry (scaling factor)	1 female.berry^{-1}
$\beta(a)$	Infestation function (13):	day^{-1}
$\beta_{\min}$	minimum infestation rate	$\{0.3, 2.5, 4\}\,10^{-3}$ * day^{-1}
β_a	age-dependent extra infestation rate	$\{2.5, 9, 360\}\,10^{-4}$ * day^{-1}
k_β	infestation coefficient	0.035 day^{-1}
a_β	infestation threshold age	90 days
α	CBB–berry interaction constant	0.7 female.berry^{-1}
ϕ	Emergence rate of new colonising females	2 day^{-1}
μ_y	Natural mortality rate of colonising females	1/20 day^{-1}
μ_z	Natural mortality rate of infesting females	1/27 day^{-1}

* $\beta_{\min}$ and β_a values respectively lead to the following $\widetilde{\mathcal{R}_0}$ values: $\{0.64, 4.2, 20.1\}$

Moreover, we use the following initial conditions. At the beginning of the cropping season, flowering has not started yet. We also assume that there are only colonising females, as infesting females were eliminated from the plantation when berries were picked during the preceding harvest. So there are initially neither coffee berries nor infesting females, *i.e.* $s_{b0}(a) = 0$ for all $a \in [0, a_\dagger]$ and $z(0) = 0$. The number of initial colonising females is set at $y(0) = 10^4$ females.

5.3 Simulations

Using the parameters given in Table 1 and the initial conditions described above, we numerically solved system (3). Results are illustrated in Figure 3, for three set of parameters of the infestation function, leading to three contrasted values of the basic reproduction number $\widetilde{\mathcal{R}_0}$ defined in equation (12). Panels (a–c) represent the dynamics of the (integrated) state variables, *i.e.* the colonising y in panel (a) and infesting z CBB females in panel (b), and the total healthy coffee berries B in panel (c). Panel (d) depicts the final healthy berries density at the end of cropping season, which gives a proxy of the yield, as berries are picked at that time. Only healthy mature berries, *i.e.* older than 120 days, have a significant market value.

As predicted, we observe that for a low CBB infestation capacity, corresponding to $\widetilde{\mathcal{R}_0} = 0.64 < 1$ (Figure 3, red curves), the trajectories of the model converge to the pest-free steady state and are very close to the berry dynamics without CBB (Figure 3, panel (c), dashed black curve). The CBB disappear from the plantation and the berry harvest is not affected (Figure 3, panel (d), red and dashed black curves). Assuming a constant berry price of 0.025 US$ per mature healthy berry, *i.e.* for healthy berries older than 120 days, the yield is 2705 US$ without CBB and 2703 US$ with CBB in the plantation. In addition, as the season starts with no berries, which are then produced at a constant rate, we note that there are less mature than young berries at the end of the cropping season.

In contrast, CBB persist in the plantation when threshold $\widetilde{\mathcal{R}_0} \in \{4.2, 20.1\} > 1$ (Figure 3, magenta and blue curves, respectively). These values correspond to higher and more realistic CBB infestation capacities. In both cases, the infesting and colonising CBB (Figure 3, panels (a) and (b)) rapidly increase after a few weeks and reach very high levels at the end of the cropping season. Moreover, they have an impact on the harvest (Figure 3, panel (d)).

When $\widetilde{\mathcal{R}_0} = 4.2$ (Figure 3, magenta curves), despite the CBB population increase, the number of healthy berries and their final density remain close to the number and density observed without

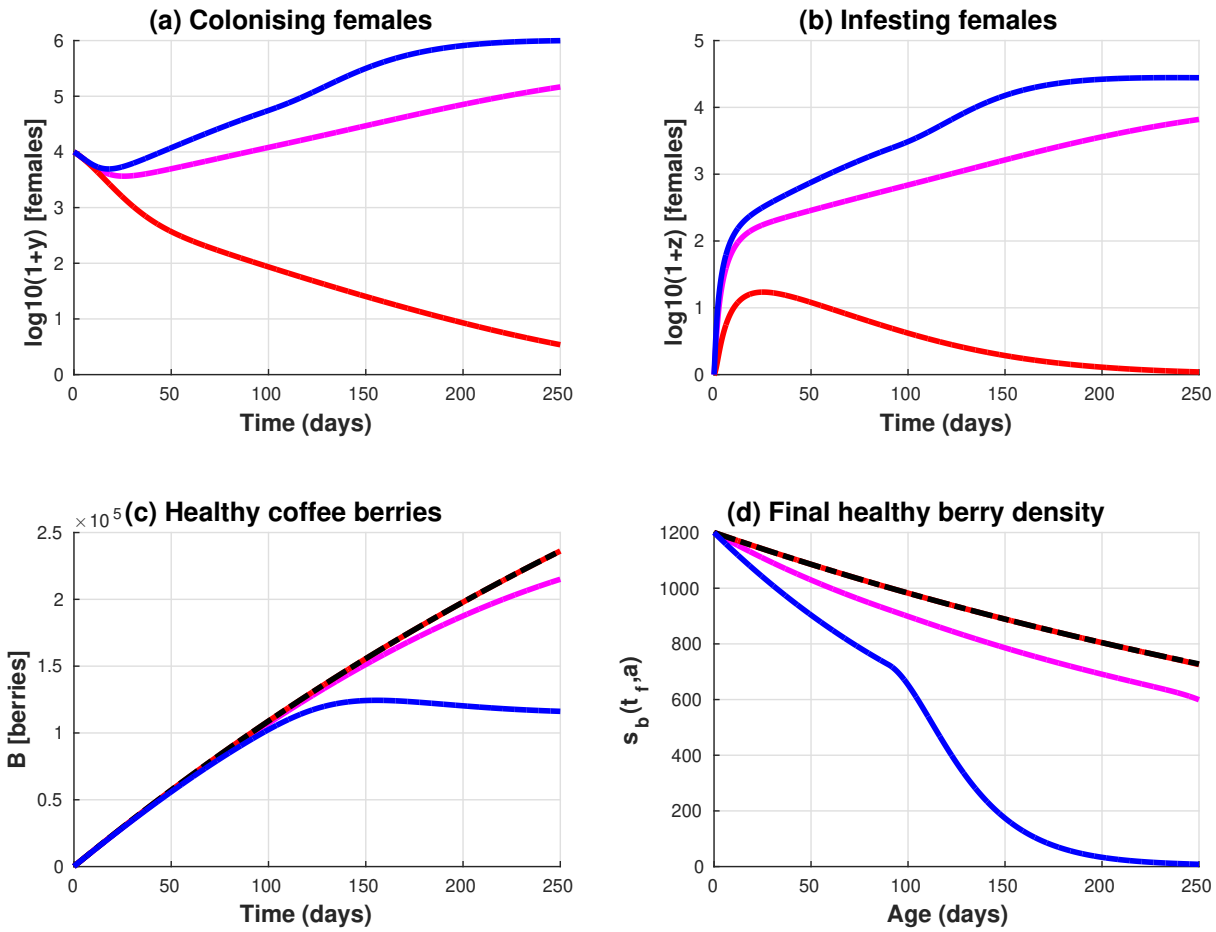

Figure 3: (a, b, c) Simulation of system (3) and (d) Age distribution of healthy coffee berries at the end of cropping season. Parameter values are given in Table 1. According to the values selected for the infestation function, the values of the basic reproduction number defined in equation (12) are $\widetilde{\mathcal{R}_0} = \{0.64, 4.2, 20.1\}$, corresponding to the red, magenta and blue curves respectively. The dashed black curve corresponds to the case without CBB. Zero initial conditions are set, including (dashed black curve) or except for colonising CBB: $y(0) = 10^4$ females (red, magenta and blue curves). Note that in panels (a) and (b), semilog scales are used.

CBB (dashed black curves). The CBB impact on the yield remains limited: 2347 US$ instead of 2705 US$ without CBB. Furthermore, age preference is not apparent in these simulations (panel (d)) because the infestation function is still relatively low for all berries age (Figure 2, magenta curve).

When $\widetilde{\mathcal{R}_0} = 20.1$ (Figure 3, blue curves), the CBB population has a notable impact on coffee berries. When the first berries produced at the beginning of the cropping season become more attractive to CBB, after *ca.* 90 days (Figure 2, blue curve), the healthy coffee berries stagnate and then decrease. The CBB preference for mature berries is also reflected in the density of healthy berries at the end of the cropping season (Figure 3, panel (d)), with a sharp decrease in berries older than 90 days. As a consequence, the yield is drastically reduced: 343 US$ instead of 2705 US$ without CBB.

6 Conclusion

In this study, we formulate and analyse an original PDE model describing the infestation dynamics of coffee berries by CBB during a cropping season. It is an extension of the model studied in [9, 10], taking into account the important role played by the coffee berry age in the CBB infestation process. Indeed, CBB colonising females preferably infest mature coffee berries and we show that this preference has an impact on the coffee berry yield at harvest. The existence and uniqueness of a solution is established via the semigroup perturbation theory. The basic reproduction number and its biological interpretation are investigated when the production rate is constant, which is not unrealistic as one can observe berries at different stages on coffee tree branches in a plantation [2]. We then show that CBB vanish from the plantation when the basic reproduction number is less than one.

However, more realistic parameter values should lead to notably higher values of the basic reproduction number, as CBB are able to colonise a plantation. In the numerical simulations presented to illustrate our analytical results, we varied the parameters of the infestation function, which cannot be easily measured or estimated, leading to three contrasted values of the basic reproduction number. The lower value, less than one, is not realistic. With the intermediate value, the impact of CBB on the berry production is fairly limited, which is not consistent with the patterns observed in plantations worldwide [15]. Hence, the higher value is probably closer to the CBB capacity to infest berries and colonise a plantation.

The next step would be to introduce control methods to limit CBB infestation in the plantation. As chemical pesticides are costly and have a negative impact on the environment, control should rather be based on environmentally friendly methods, such as bio-insecticide to reduce berry infestation, or traps to capture the colonising CBB. The ultimate goal of coffee farmers being the production of high quality coffee at the best market price and the lowest cost, it would be appropriate to design an optimal control problem to maximise the profit. This approach was carried out on a simpler ODE model, without berry structure, in previous works [9, 10] and could be extended to the model presented and analysed in this study.

A Proof of Lemma 3

It is easy to verify that under the Assumption 1, we have $\|\Phi_t\| \leq \frac{1}{\widetilde{\mu}}\|\lambda\|_\infty$. Let $\delta > 0$ and for any $u_1 = (\widehat{s}_1, y_1, z_1)$, $u_2 = (\widehat{s}_2, y_2, z_2) \in \mathbb{B}_\delta$, then we get the relation:

$$\begin{aligned} \beta(a)f(\widehat{B}_1, y_1)(\widehat{s}_1 + \Phi_t) &- \beta(a)f(\widehat{B}_2, y_2)(\widehat{s}_2 + \Phi_t) \\ &= \beta(a)(f(\widehat{B}_1, y_1) - f(\widehat{B}_2, y_2))(\widehat{s}_2 + \Phi_t) \\ &+ \beta(a)f(\widehat{B}_1, y_1)(\widehat{s}_1 - \widehat{s}_2). \end{aligned} \tag{14}$$

Using the fact that the function $f(.,.)$ is bounded and Lipschitz continuous with respect to its arguments, a straightforward computation using relation (14) shows that there is a constant $K_1 > 0$ which depends on constants M, $\widetilde{\mu}$, $\|\beta\|_\infty$, $\|\lambda\|_\infty$ and δ such that:

$$\|\beta f(\widehat{B}_1, y_1)(\widehat{s}_1 + \Phi_t) - \beta f(\widehat{B}_2, y_2)(\widehat{s}_2 + \Phi_t)\| \leq K_1 \left(\|\widehat{s}_1 - \widehat{s}_2\| + |y_1 - y_2|\right), \tag{15}$$

Proceeding similarly, we can show that there is a positive constant K_2, which also depends on constants M, $\widetilde{\mu}$, $\|\beta\|_\infty$, $\|\lambda\|_\infty$ and δ, such that:

$$|f(\widehat{B}_1, y_1)\|\beta(\widehat{s}_1 + \Phi_t)\| - f(\widehat{B}_2, y_2)\|\beta(\widehat{s}_2 + \Phi_t)\|| \leq K_2 \left(\|\widehat{s}_1 - \widehat{s}_2\| + |y_1 - y_2|\right). \tag{16}$$

Hence, from (15,16), it follows by direct computation that there exists a $M_\delta > 0$ depending on K_1, K_2, ϕ and δ such that the following inequality holds: $\|\mathcal{H}(t, u_1) - \mathcal{H}(t, u_2)\|_{\mathcal{X}} \leq M_\delta \|u_1 - u_2\|_{\mathcal{X}}$. This achieves the proof.

B Proof of Lemma 4

Let $n(t,r) = \mu(r) + \beta(r) f(B(t), y(t))$ and $\eta(t,r) = e^{-\int_0^a n(t,r)dr}$. The application of Volterra formulation [12, 28] solves the $s_b(t,a)$-equation in system (3) along the characteristic $t - a =$ constant as follows:

$$s_b(t,a) = \begin{cases} s_{b0}(a-t)e^{-\int_{a-t}^{a} n(t,r)dr} = s_{b0}(a-t)\frac{\eta(t,a)}{\eta(t,a-t)} & \text{if } a > t \\ \lambda(t-a)e^{-\int_0^a n(t,r)dr} = \lambda(t-a)\eta(t,a) & \text{if } a \leq t. \end{cases}$$

It is clear that $s_b(t,a)$ remains nonnegative for nonnegative initial conditions. Moreover, since $\dot{y} = \phi z \geq 0$ when $y = 0$ and $\dot{z} = \varepsilon f(B,y)\|\beta s_b(t,.)\| \geq 0$ when $z = 0$, the state variables $y(t)$ and $z(t)$ are nonnegative for nonnegative initial conditions. Then the first quadrant of $\mathbb{R}^2_+$ is positively invariant and the solution of system (3) remains nonnegative at any time $t > 0$.

Let $(s_b(t,.), y(t), z(t)) \in \mathcal{X}$ denote a solution of system (3). Adding the integral of first equation and the third equation of system (3) yields:

$$\frac{d}{dt}\left(\varepsilon\|s_b(t,.)\| + z(t)\right) \leq \varepsilon\|\lambda\|_\infty - \xi\left(\varepsilon\|s_b(t,.)\| + z(t)\right),$$

where $\xi = \min\{\tilde{\mu}, \mu_z\}$. Hence, using the Gronwall inequality, we have:

$$\varepsilon\|s_b(t,.)\| + z(t) \leq \frac{\varepsilon\|\lambda\|_\infty}{\xi} + \left(\varepsilon\|s_{b0}\| + z(0) - \frac{\varepsilon\|\lambda\|_\infty}{\xi}\right)e^{-\xi t}. \tag{17}$$

Thus, for all $t \geq 0$:

$$\varepsilon\|s_b(t,.)\| + z(t) \leq \max\left(\varepsilon\|s_{b0}\| + z(0), \frac{\varepsilon\|\lambda\|_\infty}{\xi}\right) =: D.$$

The colonising female population can be bounded similarly, since:

$$\dot{y}(t) \leq \phi z(t) - \mu_y y(t) \leq \phi D - \mu_y y(t).$$

Thus, using the Gronwall inequality once more, we obtain:

$$y(t) \leq \frac{\phi D}{\mu_y} + \left(y(0) - \frac{\phi D}{\mu_y}\right)e^{-\mu_y t}, \tag{18}$$

Hence, for all $t \geq 0$:

$$y(t) \leq \max\left(y(0), \frac{\phi D}{\mu_y}\right). \tag{19}$$

Therefore, the solutions of system (3) are bounded. Furthermore, inequalities (17) and (18) show that the set Σ is positively invariant under the flow of system (3).

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