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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*

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1 **1. Introduction**

2 The production of coffee plays an important role in the economic develop-
3 ment of many countries. Native of Africa, two species of coffee, *Coffea arabica*
4 and *Coffea canephora* (generally called robusta) are produced on over 10 mil-
5 lion ha in more than 80 countries located in tropical and subtropical regions
6 [1]. World coffee production for 2020–2021 is forecast to increase by 9.1 mil-
7 lion bags (90 kg/bag) compared to the previous year, reaching 176.1 million
8 bags [2]. However, coffee production is threatened by pests and diseases [3].
9 The most harmful pest is the coffee berry borer (CBB), *Hypothenemus hampei*
10 (*Coleoptera: Scolytidae*), which is originated from Central Africa but now im-
11 pacts most coffee-growing countries [4, 3, 1]. If no control measure is applied
12 in the plantation, up to 100% of the berries can be attacked [5, 3]. The in-
13 festation levels in untreated plantations are estimated at 60% in Mexico, 60%
14 in Colombia, 50–90% in Malaysia, 58–85% in Jamaica, 80% in Uganda and
15 90% in Tanzania [6]. CBB severely reduce the coffee production and alter its
16 quality, thus impairing its commercial value. Economic losses are estimated at
17 more than US\$500 million annually, affecting a large proportion of more than 25
18 million rural households involved in coffee production worldwide [7]. These in-
19 sects feed and spend most of their life inside coffee berries, preferably targeting
20 ripe berries, although they may infest immature berries and cause them to fall
21 prematurely. Due to their cryptic nature, they are difficult to control [8, 4, 1, 6].

22 Due to the seriousness of the damages caused by CBB in coffee plantations
23 throughout the world, it is crucial to develop tools that help limiting CBB in-
24 festation. In this sense, mathematical modelling is relevant to understand the
25 coffee berries–CBB interactions. We developed two pioneer tractable determin-
26 istic models describing the infestation dynamics of coffee berries by CBB during
27 a cropping season [9, 10]. These models are based on the CBB life-cycle and take

28 into account the coffee berry availability. They are both based on differential
29 equations and in neither work did we integrate the CBB marked preference for
30 mature berries, demonstrated in several field and laboratory studies [8, 5, 11, 1].

31 In this work, we develop an age-structured model describing the infestation
32 dynamics of coffee berries by CBB that takes into account the preference of CBB
33 for the mature berries. The model consists in two partial differential equations
34 describing the age-structured dynamics of berries and two ordinary differential
35 equations depicting the CBB life-cycle. We study the well-posedness of the
36 model using the perturbation semigroup theory [12], which provides a flexible
37 mathematical framework for determining the existence and uniqueness of a so-
38 lution to age-structured models (see for instance [13, 14, 15, 16] and references
39 cited therein). Considering that the production rate of new coffee berries is
40 constant, we then compute the explicit expression of the basic reproduction
41 number \mathcal{R}_0 , which determines if the CBB population can vanish or persist in
42 the plantation. Moreover, the biological interpretation of its expression is given.

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

50 **2. Coffee berries–CBB interaction dynamics**

51 *2.1. Biological background*

52 The coffee berry growth is divided into several stages that are characterised
53 by the berry colour. After flowering, the berry successively goes through the
54 green, yellow, red and black colours and becomes fully mature when it is red,
55 after 6–9 months [17]. But on the same coffee tree, there are branches without
56 flowers and branches with berries at all stages of maturation [17, 8]. Field and

57 laboratory studies indicate that factors such as berry ripeness and colour play
58 an important role on the susceptibility of coffee berries to CBB infestation, with
59 a CBB preference for red and black berries [8, 1, 5, 11]. In addition, the CBB
60 fertility rate is higher in mature than in young berries [18]. CBB can also attack
61 small 2 to 3-months old green coffee berries that can be found on the branches
62 up till the harvest time [19, 6].

63 The CBB life cycle is composed of four stages: egg, larva, nymph and adult
64 (male and female) [4, 1]. All these stages take place inside the coffee berries,
65 which provide food and shelter. The duration of development from egg to adult
66 is positively correlated with temperature and may take 28 to 34 days at 27°C
67 [4]. The CBB female feeds on and reproduces in the endosperm of the seed of
68 the coffee berry, burrowing through exocarp, mesocarp and endocarp to reach it,
69 which may take up to 8 hours under optimum conditions. The female lays one
70 to three eggs per day during approximately 20 days and remain inside the berry
71 to take care of their offspring until they die [4]. There is a 10:1 female-to-male
72 sex ratio [20, 4]. The larvae, nymphs, males and young females remain inside
73 the coffee berry, together with the founder female. The males mate with the
74 young females of their generation. A few days after fertilisation, females leave
75 the berry to find other preferably uninfested berries for oviposition.

76 2.2. Model description

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

84 Since only fertilised females (also called colonising females) infest new hosts
85 and considering that males are not limiting to fertilise young females in the
86 berries, we only represent females in the model. At time t , we subdivide the

87 female population into two compartments: the colonising females denoted by
 88 $y(t)$, which correspond to the flying females looking for new berries, and the
 89 infesting females denoted by $z(t)$, which correspond to the females that are
 90 laying eggs inside the berries. Figure 1 provides a schematic and simplified
 91 summary of the interactions between coffee berries and CBB.

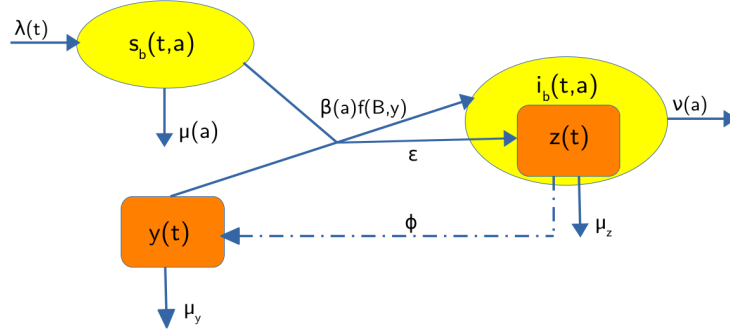


Figure 1: Schematic representation of the coffee berry–CBB interaction model. Healthy coffee berries $s_b(t, 0)$ are produced at the time-dependent rate $\lambda(t)$. Colonising females $y(t)$ infest healthy coffee berries $s_b(t, a)$ at rate $\beta(a)f(B, y)$, where $B(t)$ represents the total number of healthy berries at time $t > 0$ and $f(\cdot, \cdot)$ the interaction function. This induces a transfer of berry densities, from healthy to infested 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 $\nu(a)$.

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

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

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

97 ditions:

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

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

- 99 1. Many factors such as climatic and environmental conditions influence the
100 development of the coffee crop. We do not explicitly represent these factors
101 but we assume that healthy coffee berries are produced at time-dependent
102 rate $\lambda(t)$.
- 103 2. We assume that there are enough males born in the berries to fertilise the
104 young females.
- 105 3. In the force of infestation $\beta(a)f(B, y)$, $\beta(\cdot)$ represents the age-specific
106 infestation rate per unit of time, while the interaction between CBB and
107 berries is described by function $f(\cdot, \cdot)$ which verifies the following hypothe-
108 ses:

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

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

111 for all variables (B_1, y_1) and (B_2, y_2) in \mathbb{R}_+^2 .

- 112 • Moreover, $f(B, 0) = 0$ and function $f(\cdot, \cdot)$ are non decreasing in y (for
113 $B > 0$). Indeed, infestation can only occur when colonising females
114 are present; furthermore, for a given number of berries, the more the
115 colonising females, the more severe the infestation.

- 116 • Finally, $f(\cdot, \cdot)$ is non increasing in B (for $y > 0$) and for all $y \in \mathbb{R}_+^*$,

117 $\lim_{B \rightarrow +\infty} Bf(B, y)$ is finite. The latter hypothesis means that infesta-
118 tion is limited by the number of colonising females. As a consequence,

119 $\lim_{B \rightarrow +\infty} f(B, y) = 0.$

120 These hypotheses are compatible with density- or ratio-dependent inter-
121 actions, as implemented in [10].

- 122 4. The females are able to differentiate infested from uninfested berries and
123 choose healthy coffee berries. Indeed, super-parasitism is rarely observed
124 in a plantation [5, 11]. Parameter ε is a scaling parameter that corresponds
125 to the number of colonising females per infested berry. So usually, $\varepsilon = 1$
126 CBB/berry.
- 127 5. We assume that the number of colonising females emerging from the in-
128 fested coffee berries per infesting female ϕ is constant.
- 129 6. The age-dependent mortality rates of healthy and infested coffee berries
130 are respectively $\mu(a)$ and $\nu(a)$. We assume that $\nu(a) > \mu(a)$ since CBB
131 infestation leads to the premature fall of coffee berries in the plantation
132 [17, 4]. The parameters μ_y and μ_z represent the natural mortality rates for
133 colonising and infesting females respectively. We assume that an infesting
134 female may pursue its development if its berry falls down. In turn, even
135 if an infesting female dies, its berry survives.

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

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

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

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

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

- 149 1. *Parameters $\phi, \varepsilon, \mu_y, \mu_z$ and initial conditions y_0 and z_0 are nonnegative.*
 150 2. *$\lambda(\cdot) \in L_+^\infty(0, \infty)$, $\beta(\cdot) \in L_+^\infty(0, a_+)$; boundary conditions $s_{b0}(\cdot), i_{b0}(\cdot) \in$
 151 $L_+^1(0, a_+)$.*
 152 3. *$\mu(\cdot), \nu(\cdot) \in L_+^\infty(0, a_+)$ such that $\nu(a) \geq \mu(a)$ and there exists a real number
 153 $\tilde{\mu} > 0$ satisfying : $\mu(a) \geq \tilde{\mu}$ for almost every $a \in [0, a_+]$.*

154 3. Well-posedness

155 In this section, we aim at proving the existence and uniqueness of a non-
 156 negative solution for system (3). The preliminary step consists in finding the
 157 equivalent system with zero boundary conditions, using the ideas of [14, 15] and
 158 writing the new model as an abstract Cauchy problem, which is easier to handle.
 159 Then we prove the existence and uniqueness of a mild solution to this Cauchy
 160 problem in the nonnegative cone of a Banach space, by adapting the arguments
 161 of [12]. Finally, we deduce the existence and uniqueness of a mild solution for
 162 the initial system (3).

163 3.1. Abstract Cauchy problem

164 Let us define the survival probability of healthy coffee berries until age a by
 165 $\pi(a) = e^{-\int_0^a \mu(x) dx}$. For all $t \geq 0$, we introduce the new functional:

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

166 Based on these definitions and Assumption 1, we have the following instrumental
 167 lemma which can be easily established [14].

168 **Lemma 1.**

- 169 1. *The function $\pi(\cdot) \in L_+^1(0, a_+)$ and satisfies the differential equation: $\dot{\pi}(a) =$
 170 $-\mu(a)\pi(a)$. Moreover, for all $a \in [0, a_+]$ and any $t \leq a$, $0 \leq \pi(a) \leq e^{-\tilde{\mu}a}$
 171 and $\frac{\pi(a)}{\pi(a-t)} \leq \pi(t)$.*

2. The function $t \mapsto \Phi_t(\cdot)$ is in $\mathcal{C}(\mathbb{R}_+, L_+^1(0, a_\dagger))$. Moreover, for all $t \geq 0$, $\Phi_t(0) = \lambda(t)$ and $\Phi_t(\cdot)$ satisfies the partial differential equation:

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

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

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

where:

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

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

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

174 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 $W^{1,1}(0, a_\dagger)$
 175 denoting the Sobolev space. Biologically speaking, the linear differential op-
 176 erators \mathcal{A}_s and \mathcal{A}_I represent the mortality processes related to the healthy
 177 coffee berries and females CBB respectively. Let us define the Banach space
 178 $\mathcal{X} = L^1(0, a_\dagger) \times \mathbb{R} \times \mathbb{R}$ equipped with the usual norm $\|\cdot\|_{\mathcal{X}}$. The nonnegative
 179 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
 180 linear differential operator $\mathcal{A} : D(\mathcal{A}) \subset \mathcal{X} \longrightarrow \mathcal{X}$ where $D(\mathcal{A}) = D(\mathcal{A}_s) \times D(\mathcal{A}_I)$
 181 such that

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

182 Let $u(t) = (\widehat{s}(t, \cdot), y(t), z(t))^\top$ denotes the solution of system (4) with $u(0) =$
183 $(\widehat{s}_0(\cdot), y_0, z_0)^\top$. We define a nonlinear perturbation map $\mathcal{H} : \mathbb{R}_+ \times \overline{D(\mathcal{A})} \subset$
184 $\mathbb{R}_+ \times \mathcal{X} \longrightarrow \mathcal{X}$ as follows:

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

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

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

187 To prove the existence and uniqueness of a solution to the abstract Cauchy
188 problem (7), we begin by showing that the linear autonomous problem asso-
189 ciated to system (7) has a unique solution. Then we prove the existence of
190 a unique solution for the nonautonomous and nonlinear system (7) using the
191 perturbation theory of linear evolution equations (see [12, 16] for more details).

192 3.2. The linear problem

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

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

203 *Proof.* We start by show that the differential operator \mathcal{A} is closed. According
204 to [21], it is sufficient to show that $D(\mathcal{A})$ with norm $\|x\|_{D(\mathcal{A})} = \|x\|_{\mathcal{X}} + \|\mathcal{A}x\|_{\mathcal{X}}$,

205 $\forall x \in D(\mathcal{A})$ is a Banach space. It is easy to verify that $\|\cdot\|_{D(\mathcal{A})}$ is a norm
 206 on $D(\mathcal{A})$. For show that $(\mathcal{A}, D(\mathcal{A}))$ is complete. we take (θ_n, y_n, z_n) to be
 207 a Cauchy sequence of points of $D(\mathcal{A})$. Thus $\theta_n \in W^{1,1}$ which is a Banach
 208 space (*i.e.* complete), so $\theta_n \xrightarrow[n \rightarrow \infty]{} \theta_*$ in $W^{1,1}$, *i.e.* that $\theta_n \xrightarrow[n \rightarrow \infty]{} \theta_*$ and
 209 $\theta'_n \xrightarrow[n \rightarrow \infty]{} \theta'_*$ in L^1 . Moreover, $y_n \xrightarrow[n \rightarrow \infty]{} y_* \in \mathbb{R}$ and $z_n \xrightarrow[n \rightarrow \infty]{} z_* \in \mathbb{R}$ since \mathbb{R}
 210 is complete. Then $\|\mu\theta_n - \mu\theta_*\| \leq \|\mu\|_\infty \|\theta_n - \theta_*\| \xrightarrow[n \rightarrow \infty]{} 0$ since $\|\mu\|_\infty$ is finite.
 211 Therefore, $\mu\theta_n \xrightarrow[n \rightarrow \infty]{} \mu\theta_*$ in L^1 . We can thus see that the sequence (θ_n, y_n, z_n)
 212 converges in $D(\mathcal{A})$ to (θ_*, y_*, z_*) . In fact, $\|(\theta_n, y_n, z_n) - (\theta_*, y_*, z_*)\|_{D(\mathcal{A})} \leq$
 213 $\|\theta_n - \theta_*\| + \|y_n - y_*\| + \|z_n - z_*\| + \|\mu(\theta_n - \theta_*) + (\theta'_n - \theta'_*)\| + \mu_y \|y_n - y_*\| + \mu_z \|z_n - z_*\|$.
 214 Thus any Cauchy sequence is convergent and the space $D(\mathcal{A})$ with its norm
 215 $\|\cdot\|_{D(\mathcal{A})}$ is complete. Hence the operator \mathcal{A} is closed.

216 To check the estimation, Let $x \in \mathcal{X}$ with coordinates $x = (\psi, x_1, x_2)$ and
 217 $u = (\widehat{s}, y, z) \in D(\mathcal{A})$. We consider the equation $(\zeta I - \mathcal{A})u = x$ implies that
 218 $u = (\zeta I - \mathcal{A})^{-1}x$ that is $\widehat{s}(a) = \int_0^a e^{\zeta(\eta-a)} \frac{\pi(a)}{\pi(\eta)} \Psi(\eta) d\eta$, $\forall \psi \in L^1(0, a_\dagger)$, $y = \frac{1}{\zeta + \mu_y}$
 219 and $z = \frac{1}{\zeta + \mu_z}$. Assuming $\zeta > -\omega$, then the direct calculation show that we have
 220 the estimate $\|(\zeta I - \mathcal{A})^{-1}\| \leq \frac{1}{\zeta + \omega}$. This achieves the proof. \square

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

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

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

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

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

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

228 *Proof.* From Lemma 2 and according to the Hille–Yosida Theorem [12], the
 229 linear differential operator $(\mathcal{A}, D(\mathcal{A}))$ is an infinitesimal generator of a C_0 -

230 semigroup of contraction $T_{\mathcal{A}}(t)$. Moreover, its resolvent is positive on \mathcal{X} , then
 231 the C_0 -semigroup of contraction $T_{\mathcal{A}}(t)$ is positive [12, 16]. Hence, performing a
 232 change of variable $\xi = a - \eta$ in the resolvent equation $\widehat{s}(a) = \int_0^a e^{\zeta(\eta-a)} \frac{\pi(a)}{\pi(\eta)} \Psi(\eta) d\eta$,
 233 $\forall \Psi \in L^1(0, a_{\dagger})$ and computing the exponential of the operator \mathcal{A}_I , we obtain the
 234 desired expressions for the semigroup $T_{\mathcal{A}}(t)$. Finally, the estimation is a direct
 235 consequence of Lemma 1 which implies that $\|T_{\mathcal{A}}(t)\| = \sup\{\|T_{\mathcal{A}_s}(t)\|, \|T_{\mathcal{A}_I}(t)\|\} \leq$
 236 $\max\{\pi(t), e^{-\mu_y t}, e^{-\mu_z t}\} \leq e^{-\omega t}$, with $\omega = \min\{\widetilde{\mu}, \mu_y, \mu_z\}$ for all $t > 0$. Then,
 237 the operator $\|T_{\mathcal{A}}(t)\|$ converges towards zero when $t \rightarrow +\infty$. Therefore, the
 238 semigroup $\{T_{\mathcal{A}}(t)\}_{t \geq 0}$ is positive and exponentially stable. \square

239 As a consequence of Proposition 1 and according to [13, 12], we obtain
 240 the following result regarding the existence of a solution to the linear abstract
 241 Cauchy problem.

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

245 3.3. Existence and uniqueness of the solution for the nonlinear system

246 Having established the existence and uniqueness of a solution to the linear
 247 problem given by Theorem 1, we are now interested in establishing the existence
 248 and uniqueness of a solution to the nonlinear evolution problem (7). To do so, we
 249 opt for the Lipschitz perturbation approach for a semigroup. The map $\mathcal{H}(\cdot, u(\cdot))$
 250 in the abstract system (7) is considered as a perturbation of the semigroup
 251 generated by the linear differential operator \mathcal{A} . For every constant $\delta > 0$, \mathcal{B}_δ
 252 denotes the ball of centre 0 and radius δ in space \mathcal{X} , $\mathcal{B}_\delta := \{x \in \mathcal{X} : \|x\|_{\mathcal{X}} \leq \delta\}$.
 253 We show that the nonautonomous map $\mathcal{H}(\cdot, u(\cdot))$ is a Lipschitzian perturbation
 254 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 $u(\cdot)$, uniformly in $t \geq 0$: for all $\delta > 0$, there exists a constant depending on
 δ denoted by M_δ such that:

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

255 *Proof.* See Appendix A. □

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

258 **Theorem 2.** *For any initial condition in \mathcal{X} , there exists an interval of time*
259 *$[0, t_{max})$ in which the abstract Cauchy problem (7) has a unique mild solution.*

260 *Proof.* We use a fixed point method by adapting the ideas of [14, 12, 15]. Let
261 $\tau > 0$ and $\widehat{\delta} > 0$ such that:

$$\widehat{\delta} := 2\|u_0\|_{\mathcal{X}} \sup_{t \in [0,1]} \|T_{\mathcal{A}}(t)\|_{\mathcal{X}}, \quad \tau := \min \left\{ 1, \frac{\|u_0\|_{\mathcal{X}}}{\widehat{\delta} M_{\widehat{\delta}}} \right\}, \quad (10)$$

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

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

Next, consider the nonlinear mapping:

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

262 Standard boundedness techniques, as performed in [12, page 187], prove that \mathbb{G}
263 maps the ball $\mathcal{B}_{\widehat{\delta}}^c$ into itself and is a contraction mapping of $\mathcal{B}_{\widehat{\delta}}^c$ with Lipschitz
264 constant 1/2. Consequently, the Banach fixed point theorem implies that map
265 \mathbb{G} possesses a unique fixed point $u \in \mathcal{B}_{\widehat{\delta}}^c$. This fixed point is the desired mild
266 solution on interval $[0, \tau]$ of the evolution system (7). We repeat all previous
267 arguments, but now with initial condition $u(\tau)$ instead of $u(0)$, $\tau_1 = \tau + \gamma$ with
268 $\gamma > 0$, together with space $\mathcal{C}([\tau, \tau_1], \mathcal{X})$ and mapping \mathbb{G}_1 defined in a similar
269 way to \mathbb{G} . The same arguments applied to the latter case also show that \mathbb{G}_1 is
270 a strict contraction with Lipschitz constant 1/2. This gives once more a unique
271 fixed point which extends the previous solution on interval $[0, \tau_1]$. By proceeding
272 successively, we can extend the solution on $[0, t_{max})$, so that $u \in \mathcal{C}([0, t_{max}), \mathcal{X})$
273 is a mild solution of system (7). □

274 Since we have shown that the abstract Cauchy problem (7) has a unique mild
 275 solution $u \in \mathcal{C}([0, t_{max}), \mathcal{X})$, the transformation $u(t) \mapsto u(t) + (\Phi_t(\cdot), 0, 0) :=$
 276 $(s_b(t, \cdot), y(t), z(t))$ leads to the existence and uniqueness of a mild solution
 277 $(s_b, y, z) \in \mathcal{C}([0, t_{max}), \mathcal{X})$ of system (3). We only obtain a local solution, so
 278 it is important to show that this solution is actually global by showing that the
 279 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:*

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

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

281 *Proof.* See Appendix B. □

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

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

288 Let us introduce the total CBB population $w(t) = y(t) + z(t)$. By adding
 289 the second and third equations of system (3), we obtain the total population
 290 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
 291 average number of emerging colonising females produced by a single infesting
 292 female during its lifespan. If $\mathcal{R} < 1$, the total population $w(t) \leq w(0)e^{-\zeta t}$ with
 293 $\zeta = \min\{\mu_z(1 - \mathcal{R}), \mu_y\}$, so the CBB population disappears in the plantation.
 294 However, as previously stated, with realistic parameter values $\mathcal{R} \gg 1$.

295 4. Asymptotic behaviour for constant berry production

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

299 System (3) always has a pest-free steady state $\mathcal{E}(a) = (s_b^0(a), 0, 0)$, where
 300 $s_b^0(a) = \lambda\pi(a)$, corresponding to the equilibrium without CBB. We now compute
 301 the basic reproduction number, \mathcal{R}_0 , using the next generation operator approach
 302 [13, 22]. Linearising the system around the pest-free steady state with $x(t, a)$,
 303 $v(t)$ and $w(t)$ being the perturbations, that is $x(t, a) = s_b(t, a) - s_b^0(a)$, $v(t) =$
 304 $y(t)$ and $w(t) = z(t)$, we obtain the following linear system written in the
 305 abstract form:

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

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

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

306 The next generation operator is defined by $\mathcal{B}(-\mathcal{A})^{-1}$, where the operator
 307 $\mathcal{B} := D\mathcal{H}(\mathcal{E}(a))$. Consider the vectors $(z_1, z_2, z_3)^\top \in \mathcal{X}_0$ and $(\Phi, y, z)^\top \in \mathcal{X}$,
 308 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, 22], the basic reproduction number is defined as the spectral radius of the next generation operator $\mathcal{B}(-\mathcal{A})^{-1}$, that is:

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

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

310 **Remark 1.**

311 1. Using the computation approach proposed in [23], we obtain the following
 312 basic reproduction number:

$$\widetilde{\mathcal{R}}_0 = \mathcal{R} \frac{\varepsilon f_y(B^0, 0) \|\beta s_b^0\|}{\varepsilon f_y(B^0, 0) \|\beta s_b^0\| + \mu_y}. \quad (12)$$

313 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
 314 $\mathcal{R}_0 < 1 (= 1, > 1)$ is equivalent to $\widetilde{\mathcal{R}}_0 < 1 (= 1, > 1)$.

315 3. Threshold \mathcal{R}_0 is difficult to interpret biologically. The biological interpre-
 316 tation of threshold $\widetilde{\mathcal{R}}_0$ is more straightforward:

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

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

324 Before establishing some results about stability, let us recall the notion of
 325 spectrum, growth bound and essential growth bound in spectral theory and
 326 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 $\mathfrak{s}(K)$ are defined by $\sigma(K) = \mathbb{C} \setminus \rho(K)$ and $\mathfrak{s}(K) = \sup\{\operatorname{Re} \zeta, \zeta \in \sigma(K)\}$ respectively. Let $\omega_0(K)$ be the growth bound of a semigroup $\{T_K(t)\}_{t \geq 0}$ defined by $\omega_0(K) := \lim_{t \rightarrow +\infty} t^{-1} \ln(\|T_K(t)\|)$. Then it is proved in [24] that:

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

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

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

331 **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 $\widetilde{\mathcal{R}}_0 > 1$.*

332
 333 *Proof.* According to [25], the steady state $\mathcal{E}(a)$ is locally asymptotically stable
 334 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
 335 $\omega_{ess}(B + D\mathcal{H}(\mathcal{E})) < 0$.

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:

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

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:

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

336 Hence, $\mathfrak{s}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$ if and only if all roots $\zeta \in \mathbb{C}$ of the characteristic
 337 equation $\det(\zeta I - \chi) = 0$ have a negative real part. The trace $Tr(\chi) =$
 338 $-\varepsilon f_y(B^0, 0) \|\beta s_b^0\| - \mu_y - \mu_z$ is negative. When $\widetilde{\mathcal{R}}_0 < 1$, the determinant
 339 $\det(\chi) = \varepsilon \phi f_y(B^0, 0) \|\beta s_b^0\| \left(\frac{1}{\widetilde{\mathcal{R}}_0} - 1\right)$ is positive and it becomes negative when
 340 $\widetilde{\mathcal{R}}_0 > 1$. Then all the roots ζ of the characteristic equation associated with
 341 matrix χ have a negative real part if $\widetilde{\mathcal{R}}_0 < 1$. Therefore, if $\widetilde{\mathcal{R}}_0 < 1$, then
 342 $\mathfrak{s}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$ and $\omega_{ess}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$, hence $\omega_0(\mathcal{A} + D\mathcal{H}(\mathcal{E})) < 0$.
 343 Thus, the pest-free steady state is locally asymptotically stable if $\widetilde{\mathcal{R}}_0 < 1$.

344 When $\widetilde{\mathcal{R}}_0 > 1$, then there exists at least one root ζ_0 with a positive real part.
 345 This implies that $\mathfrak{s}(\mathcal{A} + D\mathcal{H}(\mathcal{E})) = \mathcal{R}e\zeta_0 > 0$. Therefore, $\omega_0(\mathcal{A} + D\mathcal{H}(\mathcal{E})) > 0$
 346 and it follows that $\mathcal{E}(\cdot)$ is unstable. This achieves the proof. \square

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

351 5. Numerical results

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

357 5.1. Numerical scheme

This scheme is based on semi-implicit finite differential equations for the vari-
 ables $y(t)$ and $z(t)$ and on the hyperbolic partial differential equation verified
 by $s_b(t, a)$ [26]. The integral terms are discretised using an explicit composite
 trapezoidal rule. Let $\Delta a > 0$ be the discretisation step for the interval $[0, a_+]$,
 with $N = \frac{a_+}{\Delta a}$ the number of age sub-intervals, and let $\Delta t > 0$ be the discretisa-
 tion 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:

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

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

360 Since berry age evolves at the same speed as chronological time, choosing
 361 $\Delta a = \Delta t$ ensures that the necessary CFL (Courant–Freidriche–Lewy) stability
 362 condition, *i.e.* $\frac{\Delta t}{\Delta a} \leq 1$, holds [27, 26].

363 5.2. Parameter values

364 In the numerical simulations, we assume that flowering occurs in the planta-
 365 tion throughout the cropping season, so that we can consider a constant berry
 366 production rate $\lambda(t) \equiv \lambda$. Since coffee berries become fully mature after 6–9
 367 months [17], the maximum berry age of is set at $a_{\dagger} = 250$ days. We found no
 368 data on age-dependent mortality for uninfested berries, so we apply a constant
 369 rate μ to all berries up to the berry maximum age a_{\dagger} . CBB colonising females
 370 infest healthy berries of all ages, but with a preference for more mature berries
 371 [5, 11]. According to [19], the infestation of berries younger than 90 days is
 372 very low. So we represent the infestation rate as a constant function for berry
 373 ages lower than a_{β} and an increasing function for older ages, according to the
 374 following function:

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

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

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

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

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

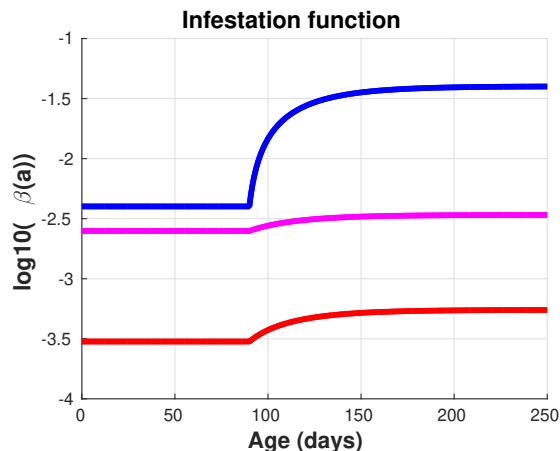


Figure 2: Infestation function β , defined in equation (13) as a function of berry age, for the three parameter sets selected in Table 1: $(\beta_{\min}, \beta_a) = (3 \cdot 10^{-4}, 2.5 \cdot 10^{-4}) \text{ day}^{-1}$ corresponding to $\widetilde{\mathcal{R}}_0 = 0.64$ (red curve), $(\beta_{\min},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

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

386 Moreover, we use the following initial conditions. At the beginning of the
 387 cropping season, flowering has not started yet. We also assume that there are
 388 only colonising females, as infesting females were eliminated from the plantation
 389 when berries were picked during the preceding harvest. So there are initially
 390 neither coffee berries nor infesting females, *i.e.* $s_{b0}(a) = 0$ for all $a \in [0, a_+]$ and
 391 $z(0) = 0$. The number of initial colonising females is set at $y(0) = 10^4$ females.

392 5.3. Simulations

393 Using the parameters given in Table 1 and the initial conditions described
 394 above, we numerically solved system (3). Results are illustrated in Figure 3, for
 395 three set of parameters of the infestation function, leading to three contrasted
 396 values of the basic reproduction number $\widetilde{\mathcal{R}}_0$ defined in equation (12). Panels (a–
 397 c) represent the dynamics of the (integrated) state variables, *i.e.* the colonising
 398 y in panel (a) and infesting z CBB females in panel (b), and the total healthy
 399 coffee berries B in panel (c). Panel (d) depicts the final healthy berries density

Table 1: Model parameter values, based on biological data collected in the literature [17]; 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
β_{\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

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

400 at the end of cropping season, which gives a proxy of the yield, as berries are
401 picked at that time. Only healthy mature berries, *i.e.* older than 120 days, have
402 a significant market value.

403 As predicted, we observe that for a low CBB infestation capacity, corre-
404 sponding to $\widetilde{\mathcal{R}}_0 = 0.64 < 1$ (Figure 3, red curves), the trajectories of the model
405 converge to the pest-free steady state and are very close to the berry dynamics
406 without CBB (Figure 3, panel (c), dashed black curve). The CBB disappear
407 from the plantation and the berry harvest is not affected (Figure 3, panel (d),
408 red and dashed black curves). Assuming a constant berry price of 0.025 US\$ per
409 mature healthy berry, *i.e.* for healthy berries older than 120 days, the yield is
410 2705 US\$ without CBB and 2703 US\$ with CBB in the plantation. In addition,
411 as the season starts with no berries, which are then produced at a constant rate,
412 we note that there are less mature than young berries at the end of the cropping
413 season.

414 In contrast, CBB persist in the plantation when threshold $\widetilde{\mathcal{R}}_0 \in \{4.2, 20.1\} >$
415 1 (Figure 3, magenta and blue curves, respectively). These values correspond to
416 higher and more realistic CBB infestation capacities. In both cases, the infesting
417 and colonising CBB (Figure 3, panels (a) and (b)) rapidly increase after a few
418 weeks and reach very high levels at the end of the cropping season. Moreover,
419 they have an impact on the harvest (Figure 3, panel (d)).

420 When $\widetilde{\mathcal{R}}_0 = 4.2$ (Figure 3, magenta curves), despite the CBB population in-
421 crease, the number of healthy berries and their final density remain close to the
422 number and density observed without CBB (dashed black curves). The CBB im-
423 pact on the yield remains limited: 2347 US\$ instead of 2705 US\$ without CBB.
424 Furthermore, age preference is not apparent in these simulations (panel (d)) be-
425 cause the infestation function is still relatively low for all berries age (Figure 2,
426 magenta curve).

427 When $\widetilde{\mathcal{R}}_0 = 20.1$ (Figure 3, blue curves), the CBB population has a notable
428 impact on coffee berries. When the first berries produced at the beginning of
429 the cropping season become more attractive to CBB, after *ca.* 90 days (Figure 2,
430 blue curve), the healthy coffee berries stagnate and then decrease. The CBB

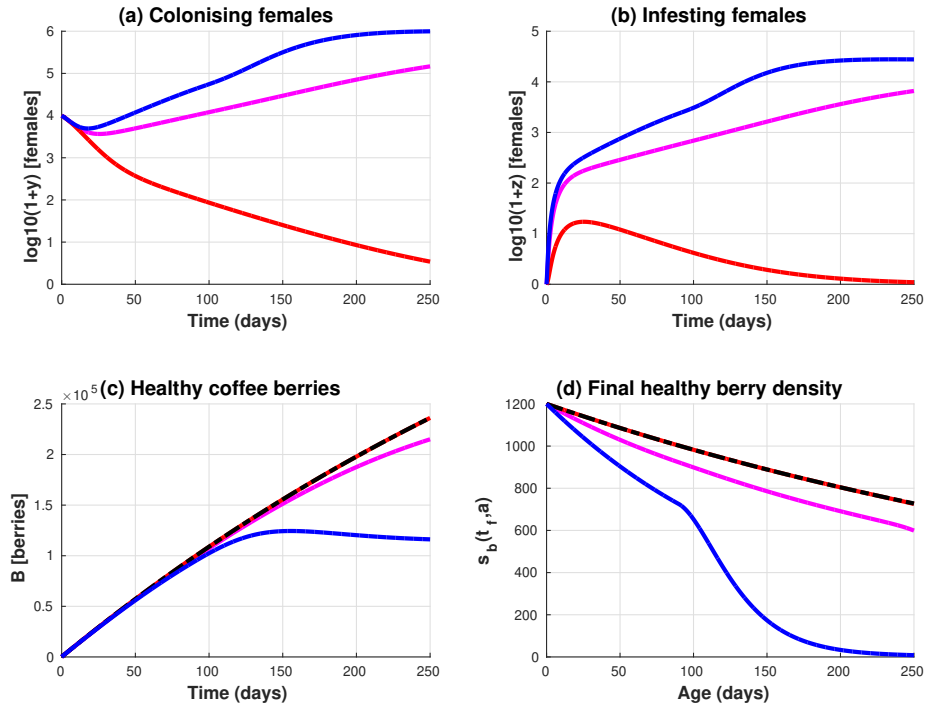


Figure 3: (a, b, c) Simulation of system (3) and (d) Age distribution of healthy coffee berries at the end of cropping season. Parameter values are given in Table 1. According to the values selected for the infestation function, the values of the basic reproduction number defined in equation (12) are $\widetilde{\mathcal{R}}_0 = \{0.64, 4.2, 20.1\}$, 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.

431 preference for mature berries is also reflected in the density of healthy berries
432 at the end of the cropping season (Figure 3, panel (d)), with a sharp decrease in
433 berries older than 90 days. As a consequence, the yield is drastically reduced:
434 343 US\$ instead of 2705 US\$ without CBB.

435 **6. Conclusion**

436 In this study, we formulate and analyse an original PDE model describing
437 the infestation dynamics of coffee berries by CBB during a cropping season. It
438 is an extension of the model studied in [9, 10], taking into account the important
439 role played by the coffee berry age in the CBB infestation process. Indeed, CBB
440 colonising females preferably infest mature coffee berries and we show that this
441 preference has an impact on the coffee berry yield at harvest. The existence and
442 uniqueness of a solution is established via the semigroup perturbation theory.
443 The basic reproduction number and its biological interpretation are investigated
444 when the production rate is constant, which is not unrealistic as one can observe
445 berries at different stages on coffee tree branches in a plantation [17]. We then
446 show that CBB vanish from the plantation when the basic reproduction number
447 is less than one.

448 However, more realistic parameter values should lead to notably higher val-
449 ues of the basic reproduction number, as CBB are able to colonise a plantation.
450 In the numerical simulations presented to illustrate our analytical results, we
451 varied the parameters of the infestation function, which cannot be easily mea-
452 sured or estimated, leading to three contrasted values of the basic reproduction
453 number. The lower value, less than one, is not realistic. With the intermediate
454 value, the impact of CBB on the berry production is fairly limited, which is
455 not consistent with the patterns observed in plantations worldwide [28]. Hence,
456 the higher value is probably closer to the CBB capacity to infest berries and
457 colonise a plantation.

458 The next step would be to introduce control methods to limit CBB infes-
459 tation in the plantation. As chemical pesticides are costly and have a negative

460 impact on the environment, control should rather be based on environmentally
461 friendly methods, such as bio-insecticide to reduce berry infestation, or traps
462 to capture the colonising CBB. The ultimate goal of coffee farmers being the
463 production of high quality coffee at the best market price and the lowest cost,
464 it would be appropriate to design an optimal control problem to maximise the
465 profit. This approach was carried out on a simpler ODE model, without berry
466 structure, in previous works [9, 10] and could be extended to the model pre-
467 sented and analysed in this study.

468 **Appendix A. Proof of Lemma 3**

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

$$\begin{aligned}
\beta(a)f(\hat{B}_1, y_1)(\hat{s}_1 + \Phi_t) &- \beta(a)f(\hat{B}_2, y_2)(\hat{s}_2 + \Phi_t) \\
&= \beta(a)(f(\hat{B}_1, y_1) - f(\hat{B}_2, y_2))(\hat{s}_2 + \Phi_t) \\
&+ \beta(a)f(\hat{B}_1, y_1)(\hat{s}_1 - \hat{s}_2). \tag{A.1}
\end{aligned}$$

472 Using the fact that the function $f(.,.)$ is bounded and Lipschitz continuous
473 with respect to its arguments, a straightforward computation using relation
474 (A.1) shows that there is a constant $K_1 > 0$ which depends on constants $M, \tilde{\mu}$,
475 $\|\beta\|_\infty, \|\lambda\|_\infty$ and δ such that:

$$\|\beta f(\hat{B}_1, y_1)(\hat{s}_1 + \Phi_t) - \beta f(\hat{B}_2, y_2)(\hat{s}_2 + \Phi_t)\| \leq K_1 (\|\hat{s}_1 - \hat{s}_2\| + |y_1 - y_2|), \tag{A.2}$$

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

$$|f(\hat{B}_1, y_1)\|\beta(\hat{s}_1 + \Phi_t)\| - f(\hat{B}_2, y_2)\|\beta(\hat{s}_2 + \Phi_t)\|| \leq K_2 (\|\hat{s}_1 - \hat{s}_2\| + |y_1 - y_2|). \tag{A.3}$$

478 Hence, from (A.2,A.3), it follows by direct computation that there exists a
479 $M_\delta > 0$ depending on K_1, K_2, ϕ and δ such that the following inequality holds:
480 $\|\mathcal{H}(t, u_1) - \mathcal{H}(t, u_2)\|_{\mathcal{X}} \leq M_\delta \|u_1 - u_2\|_{\mathcal{X}}$. This achieves the proof.

481 **Appendix 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 [29, 25] solves the $s_b(t, a)$ -equation in system (3) along the characteristic $t - a = \text{constant}$ as follows:

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

482 It is clear that $s_b(t, a)$ remains nonnegative for nonnegative initial conditions.
 483 Moreover, since $\dot{y} = \phi z \geq 0$ when $y = 0$ and $\dot{z} = \varepsilon f(B, y) \|\beta s_b(t, \cdot)\| \geq 0$ when
 484 $z = 0$, the state variables $y(t)$ and $z(t)$ are nonnegative for nonnegative initial
 485 conditions. Then the first quadrant of \mathbb{R}_+^2 is positively invariant and the solution
 486 of system (3) remains nonnegative at any time $t > 0$.

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

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

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

$$\varepsilon \|s_b(t, \cdot)\| + z(t) \leq \frac{\varepsilon \|\lambda\|_\infty}{\xi} + \left(\varepsilon \|s_{b0}\| + z(0) - \frac{\varepsilon \|\lambda\|_\infty}{\xi} \right) e^{-\xi t}. \quad (\text{B.1})$$

Thus, for all $t \geq 0$:

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

The colonising female population can be bounded similarly, since:

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

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

$$y(t) \leq \frac{\phi D}{\mu_y} + \left(y(0) - \frac{\phi D}{\mu_y} \right) e^{-\mu_y t}, \quad (\text{B.2})$$

489 Hence, for all $t \geq 0$:

$$y(t) \leq \max \left(y(0), \frac{\phi D}{\mu_y} \right). \quad (\text{B.3})$$

490 Therefore, the solutions of system (3) are bounded. Furthermore, inequalities
 491 (B.1) and (B.2) show that the set Σ is positively invariant under the flow of
 492 system (3).

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