

A one-dimensional map to study multi-seasonal coffee infestation by the coffee berry borer*

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Abstract

The coffee berry borer (CBB, *Hypothenemus hampei*) is the most serious insect pest of coffee worldwide; understanding the dynamics of its reproduction is essential for pest management. The female CBB penetrates the coffee berry, eats the seed, and reproduces inside it. A mathematical model of the infestation progress of the coffee berry by the CBB during several coffee seasons is formulated. The model represents the interaction among five populations: uninfested, slightly infested, and severely infested coffee berries, and free and encapsulated CBBs. Coffee harvesting is also included in the model. A one-dimensional map is derived for tracking the population dynamics subject to certain coffee harvesting percentages over several seasons. Stability analysis of the map's fixed points shows that CBB infestation could be eliminated or controlled to a specific level over multiple seasons of coffee harvesting. However, the percent of coffee harvesting required is determined by the level of CBB infestation at the beginning of the first season and in some cases it is impossible to achieve that percentage.

Keywords:

Biological control, *Hypothenemus hampei*, Mathematical modeling,

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1. Introduction

Coffee exports worldwide are worth around \$24 billion, and coffee is a key part of the economies and cultures of many of the more than 80 countries that produce it [1]. Infestation of coffee by the coffee berry borer (CBB, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae)) causes about \$500 million in losses each year [2]. The CBB is now found in almost all coffee-producing countries and is very difficult to control. Since its detection in Puerto Rico in 2007, the CBB has colonized the entire coffee-growing region. Infestation reaches to 95% in some farms, but varies greatly from year to year [3]. Therefore, there is a great need for, and interest in, new tools for CBB infestation prediction and management.

The CBB is a very small beetle of ~ 1.5 mm in length [4]. The female CBB flies to a coffee fruit, bores a hole to the seed, and lays eggs. The larvae eat the developing seed, reducing its weight and quality [5–7]. When female offspring mature they leave and search for a new fruit to colonize. Male offspring fertilize their sisters but never leave the fruit.

The whole life cycle of the CBB passes within the coffee fruit, except when females emerge to colonize new fruits. The fruit thus protects the CBB from control measures. For example, insecticides will only be effective if they make contact with female CBBs in their brief trip outside the fruit. Integrated pest management (IPM) seeks to control pests to manageable levels by combining several approaches: monitoring, the use of resistant crop varieties, chemical control, biological control, and management of how the crop is grown, referred as cultural control (management that is location or country specific that reduces exposure or susceptibility to the pathogen) [8]. Because there are no resistant varieties of coffee and chemical and biological control are difficult when the CBB is inside the fruit, cultural control is very important for management. After harvest, all remaining fruits must be removed because they are a reservoir where the CBB can live until the next coffee crop is mature enough to infest [9, 10]. Similarly, fallen coffee fruits on the ground are a reservoir for the CBB and must be collected [3]. These control measures are effective but labor-intensive. Many growers say they cannot afford to implement them, especially in Hawaii and Puerto Rico where labor costs are higher than in other coffee-producing countries [11].

The cultural practice of collection and removal of all ripe and overripe berries has been documented and recommended in the literature [3, 11–13]. The purpose of this study is to provide qualitative and quantitative explanations for this practice and its observed effects in Puerto Rican coffee farms.

Mathematical models of the interactions between coffee fruits and CBB could be useful for understanding when cultural and biological control measures would be most effective. The models reveal both qualitative and quantitative features of CBB population when tracked over many seasons. Previous quantitative studies includes models of the growth and development of coffee plants [14], CBB and its interaction with the coffee berry, including traps as a method of cultural control [15], and parasitoids of the CBB [16]. These models include physiological and environmental factors that affect the reproduction rates of the populations, using data from Colombia. Previously a similar model was used with data from Brazil [17]. The authors used the age-structured approach, which is needed in these sites because there are at least two flowering periods per year and thus there may be fruits in different stages on the same plant at the same time.

In this study, we formulate a multi-season model of the coffee berry infestation by the CBB, which includes fruit harvesting, using data from Puerto Rico where there is only one flowering period per year. The populations are assumed homogeneous. A one-dimensional map is derived for tracking the population dynamics subject to certain annual coffee harvesting percentages over several seasons. We will show that over a wide set of parameters the map possesses two stable fixed points and one unstable fixed point. The stable fixed points correspond to either complete eradication of the CBB or total infestation by the CBB. The unstable fixed point is a threshold that separates initial CBB population values that get attracted to one of these two stable solutions. The ability to determine the threshold value is the primary advantage of using a map-based approach. Further, if immigration of CBBs is added at the beginning of each season, then the stable fixed point corresponding to extinction of CBBs moves to a positive value, which implies that infestation can be controlled but not eradicated. In short, the map determines whether or not a CBB infestation can be eliminated or controlled with an appropriate harvesting strategy over several coffee seasons. Our aim is to provide tools that help coffee growers to manage such practices of pest control by providing quantitative criteria for applying the measures.

2. Mathematical model

Assumptions are based on the literature (e.g., [6, 18]) and on our data from Puerto Rico [3, 19]. We first model the coffee berry¹ infestation by the CBB. To determine the infestation progress, the model tracks the dynamics of interactions among five populations. Each population is represented in a single and well-mixed compartment. Thus, we are assuming that the infestation progress is not affected by the spatial dimension. The span of each season is a year running from May 1st ($t = 0$), when the berries are sufficiently developed to be susceptible to infestation by the CBB, to April 30th ($t = 364$) of the next calendar year.

Then we incorporate the effect of coffee harvesting within a single season. In every season, the coffee is harvested at day $t = t_h$. This can easily be extended to allow harvesting the total amount in steps over several days. Because this model assumes homogeneity in space, by harvesting we mean picking the coffee from the tree and cleaning the ground of coffee fruits. Removing fallen coffee fruits from the ground is essential for control of the CBB [9], but it is often overlooked in Puerto Rico and Hawaii [11].

Finally, to model several coffee seasons, we concatenate the seasons by taking the number of CBBs at the start of each season equal to their number at the end of the previous season.

2.1. Model assumptions for the annual infestation process

To formulate the model equations we used a population dynamics approach in which the populations interact as shown in Figure 1. The model consists of five state variables that are meant to model distinct categories within two different populations: coffee berries per tree and CBB per tree. The state variables are: uninfested coffee berries (c_u), slightly infested coffee berries (c_{i_1}), severely infested coffee berries (c_{i_2}), free CBBs (b_o), and encapsulated CBBs (b_e). The characteristics of each variable are the following (Fig. 1 and Table 1).

1. *Uninfested coffee.* The uninfested coffee berry population decreases when it is infested by the CBB at a rate $\varepsilon_c c_u b_o$, where ε_c is the coffee berry infestation rate constant.

¹We refer to the fruits as “berries” to be consistent with the literature, even though the term is technically incorrect.

2. *Slightly infested coffee.* Once a coffee berry is infested by the CBB, it passes to the infested state and cannot return to the uninfested state. In this category we include the coffee that is infested with a single CBB; the CBB may be laying eggs, but the weight of the seed is close to that of uninfested coffee. The CBBs reproduce inside the seed and the seed may become severely infested. The slightly infested coffee becomes severely infested at a rate $\varepsilon_{c_1} c_{i_1}$, where ε_{c_1} is the coffee berry severe infestation rate constant.
3. *Severely infested coffee.* Once a coffee berry becomes severely infested, it contains several CBBs (usually progeny of the colonizing female), has lost weight and cannot return to the slightly infested state. From these berries the CBBs can exit to infest other berries. Because of its light weight, we assume that the coffee in this category is discarded after harvest (though this is not always the case). Severely infested berries may be dropped by the plant [20]; this does not affect the model, because they continue to be severely infested and a source of CBBs on the ground. It is uncommon for a CBB to attack a coffee fruit already attacked by another [18]. Given that we see very little evidence of more than one CBB attacking a single fruit in the field, we have neglected this aspect in our model.
4. *Free CBB.* When the insects are outside of coffee berries they don't reproduce; their goal is to infest a coffee berry at a rate $\varepsilon_{b_o} c_u b_o$. The free CBB population increases when encapsulated CBBs exit the severely infested berries at a rate $\varepsilon_{b_e} b_e c_{i_2}$. Here ε_{b_o} and ε_{b_e} are the CBB entering and exiting rate constants, respectively. They can die by natural death or human intervention at a rate $\delta_b b_o$, where δ_b is the CBB death rate constant.
5. *Encapsulated CBB.* Once the insects are inside of coffee berries, they can reproduce by following a logistic-type model in which the carrying capacity is limited by the available space inside the severely infested berry. Thus the reproduction rate is given by $\rho_b b_e ((\kappa_{b,t} - b_e) / \kappa_b)$, where ρ_b is the CBB reproduction rate constant, $\kappa_{b,t}$ is the CBB carrying capacity of severely infested coffee (this varies with time as it is a function of c_{i_2}), and κ_b is the CBB carrying capacity of total coffee (this is kept fixed to the total amount of coffee). Letting α_b be the CBB carrying capacity of an individual coffee berry, the variable carrying capacity can be defined by $\kappa_{b,t} = \alpha_b c_{i_2}$. Note that, by conservation, the total amount of coffee is equal to the sum of uninfested and infested

coffee. Thus as the amount of severely infested coffee increases, the uninfested coffee decreases. In turn, this implies that the available resources for CBBs to reproduce are larger but the amount of coffee that can be infested is smaller. If c_T is the total amount of coffee berries in the season, then the global carrying capacity is $\kappa_b = \alpha_b c_T$. In the event of all coffee becoming severely infested, the reproduction rate limits to the standard logistic growth equation $\rho_b b_e (1 - b_e / \kappa_b)$. Also the encapsulated CBB population increases when free CBBs infest a coffee fruit at a rate $\varepsilon_{b_o} c_u b_o$. The encapsulated CBB can exit the berry to infest another berry² at a rate $\varepsilon_{b_e} b_e c_{i_2}$.

6. At the harvesting time t_h , we assume that the three coffee populations are reduced by the same fraction ϕ . Since encapsulated CBBs reside in the infested coffee, we assume their population is also reduced by the fraction ϕ .

Because the female CBB is the one that exits the coffee berry to infest another berry, the model only represents the female CBB population.

2.2. Model equations

Based on the assumptions in Section 2.1 and the diagram in Fig. 1 we obtain the following system of equations for the rate of change of each population:

$$\frac{dc_u}{dt} = -\varepsilon_c c_u b_o \quad (1)$$

$$\frac{dc_{i_1}}{dt} = \varepsilon_c c_u b_o - \varepsilon_{c_i} c_{i_1} \quad (2)$$

$$\frac{dc_{i_2}}{dt} = \varepsilon_{c_i} c_{i_1} \quad (3)$$

$$\frac{db_o}{dt} = \varepsilon_{b_e} b_e c_{i_2} - \varepsilon_{b_o} c_u b_o - \delta_b b_o \quad (4)$$

$$\frac{db_e}{dt} = \rho_b b_e \left(\frac{c_{i_2}}{c_T} - \frac{b_e}{\kappa_b} \right) + \varepsilon_{b_o} c_u b_o - \varepsilon_{b_e} b_e c_{i_2} \quad (5)$$

²Several stimuli may cause a CBB to leave a coffee fruit to colonize a new fruit. Once a CBB leaves the coffee berry other CBBs and other generations could remain inside the coffee continuing to reproduce. The carrying capacity of a coffee berry refers to the maximum number of CBBs that can share the space at a specific moment.

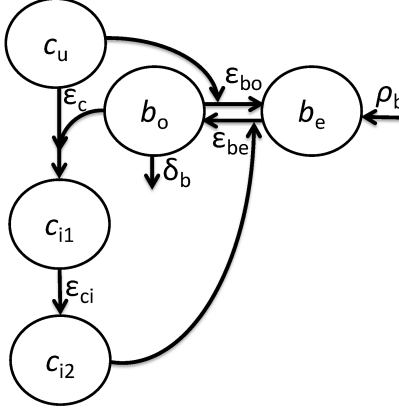


Figure 1: Diagram of interaction between coffee berry (c_u , uninfested; c_{i1} , slightly infested; c_{i2} , severely infested) and CBB (b_o , free; b_e , encapsulated). ρ_b , CBB reproduction rate constant; ε_c , coffee berry infestation rate constant; ε_{ci} , coffee berry severe infestation rate constant; ε_{be} , CBB exiting rate constant; ε_{bo} , CBB entering rate constant; δ_b , free CBB death rate constant

with the following prescribed initial values at $t = 0$:

$$c_u(0) = c_T, \quad c_{i1}(0) = 0, \quad c_{i2}(0) = 0, \quad b_o(0) = b_o^0, \quad \text{and} \quad b_e(0) = 0, \quad (6)$$

where b_o^0 is the initial amount of CBBs in the season.

2.2.1. Equation normalization

We normalize the dependent variables and parameters such that each population is measured as a proportion and each term of the equations is in units 1/day. By introducing the following change of variable in the dependent variables

$$\tilde{c}_u = \frac{c_u}{c_T}, \quad \tilde{c}_{i1} = \frac{c_{i1}}{c_T}, \quad \tilde{c}_{i2} = \frac{c_{i2}}{c_T}, \quad \tilde{b}_o = \frac{b_o}{\kappa_b}, \quad \tilde{b}_e = \frac{b_e}{\kappa_b}, \quad (7)$$

and the parameters

$$\tilde{\varepsilon}_c = \varepsilon_c \kappa_b, \quad \tilde{\varepsilon}_{be} = \varepsilon_{be} c_T, \quad \tilde{\varepsilon}_{bo} = \varepsilon_{bo} c_T, \quad (8)$$

the model equations become

$$\frac{d\tilde{c}_u}{dt} = -\tilde{\varepsilon}_c \tilde{c}_u \tilde{b}_o \quad (9)$$

$$\frac{d\tilde{c}_{i_1}}{dt} = \tilde{\varepsilon}_c \tilde{c}_u \tilde{b}_o - \varepsilon_{c_i} \tilde{c}_{i_1} \quad (10)$$

$$\frac{d\tilde{c}_{i_2}}{dt} = \varepsilon_{c_i} \tilde{c}_{i_1} \quad (11)$$

$$\frac{d\tilde{b}_o}{dt} = \tilde{\varepsilon}_{b_e} \tilde{b}_e \tilde{c}_{i_2} - \tilde{\varepsilon}_{b_o} \tilde{c}_u \tilde{b}_o - \delta_b \tilde{b}_o \quad (12)$$

$$\frac{d\tilde{b}_e}{dt} = \rho_b \tilde{b}_e (\tilde{c}_{i_2} - \tilde{b}_e) + \tilde{\varepsilon}_{b_o} \tilde{c}_u \tilde{b}_o - \tilde{\varepsilon}_{b_e} \tilde{b}_e \tilde{c}_{i_2} \quad (13)$$

By adding Equations (9) to (11), one finds that $\tilde{c}_u + \tilde{c}_{i_1} + \tilde{c}_{i_2} = 1$, and, by using that $\tilde{c}_{i_2} = (1 - \tilde{c}_u - \tilde{c}_{i_1})$, the model equations reduce to

$$\frac{d\tilde{c}_u}{dt} = -\tilde{\varepsilon}_c \tilde{c}_u \tilde{b}_o \quad (14)$$

$$\frac{d\tilde{c}_{i_1}}{dt} = \tilde{\varepsilon}_c \tilde{c}_u \tilde{b}_o - \varepsilon_{c_i} \tilde{c}_{i_1} \quad (15)$$

$$\frac{d\tilde{b}_o}{dt} = \tilde{\varepsilon}_{b_e} \tilde{b}_e (1 - \tilde{c}_u - \tilde{c}_{i_1}) - \tilde{\varepsilon}_{b_o} \tilde{c}_u \tilde{b}_o - \delta_b \tilde{b}_o \quad (16)$$

$$\frac{d\tilde{b}_e}{dt} = \rho_b \tilde{b}_e (1 - \tilde{c}_u - \tilde{c}_{i_1} - \tilde{b}_e) + \tilde{\varepsilon}_{b_o} \tilde{c}_u \tilde{b}_o - \tilde{\varepsilon}_{b_e} \tilde{b}_e (1 - \tilde{c}_u - \tilde{c}_{i_1}) \quad (17)$$

with normalized initial values

$$\tilde{c}_u(0) = 1, \quad \tilde{c}_{i_1}(0) = 0, \quad \tilde{b}_o(0) = \tilde{b}_o^0, \quad \text{and} \quad \tilde{b}_e(0) = 0. \quad (18)$$

2.2.2. Steady-state solutions of the model

There exist two steady-state solutions of Equations (14)-(17) of biological interest, the infestation-free steady-state solution characterized by $\tilde{b}_o = 0$ and the infestation steady-state solution by $\tilde{b}_o \neq 0$. To find these solutions, we set the right-hand side of Equation (14)-(17) equal to zero and solve. By doing so, we obtain the infestation-free steady-state solution as

$$\tilde{c}_u = 1, \quad \tilde{c}_{i_1} = 0, \quad \tilde{c}_{i_2} = 0, \quad \tilde{b}_o = 0, \quad \text{and} \quad \tilde{b}_e = 0. \quad (19)$$

And the infestation steady-state solution is

$$\tilde{c}_u = 0, \quad \tilde{c}_{i_1} = 0, \quad \tilde{c}_{i_2} = 1, \quad \tilde{b}_o = \frac{\tilde{\varepsilon}_{b_e} (\rho_b - \tilde{\varepsilon}_{b_e})}{\rho_b \delta_b}, \quad \text{and} \quad \tilde{b}_e = \frac{\rho_b - \tilde{\varepsilon}_{b_e}}{\rho_b}, \quad (20)$$

which is biologically feasible only if

$$\rho_b > \tilde{\varepsilon}_{b_e} \geq 0, \quad \text{and} \quad \delta_b > 0. \quad (21)$$

2.3. Harvesting effect on the dynamics of a single season

We use the assumption that harvesting occurs at $t = t_h$ to remove a uniform fraction ϕ from the coffee populations as well as the encapsulated CBB population. Mathematically, we solve Equations (14)-(17) with initial conditions given by Equation (18) until $t = t_h$. We then impose the harvesting condition,

$$\begin{aligned} \tilde{c}_u(t_h^+) &= (1 - \phi)\tilde{c}_u(t_h^-), & \tilde{c}_{i_1}(t_h^+) &= (1 - \phi)\tilde{c}_{i_1}(t_h^-), \\ \text{and } \tilde{b}_e(t_h^+) &= (1 - \phi)\tilde{b}_e(t_h^-). \end{aligned} \quad (22)$$

Here the superscripts \pm on the harvest time t_h indicate the limit from above and below. We then solve Equations (14)-(17) with new initial conditions given by Equation (22) from $t = t_h$ until $t = 364$. Note that the harvesting condition produces a discontinuity in the graph of the variables \tilde{c}_u , \tilde{c}_{i_1} and \tilde{b}_e , but not in \tilde{b}_o , as the latter population is not harvested. After harvesting, the conservation equation becomes $\tilde{c}_u + \tilde{c}_{i_1} + \tilde{c}_{i_2} = 1 - \phi$.

2.4. Population dynamics over multiple seasons

We now describe how to track the coffee berry and CBB populations over multiple seasons. This will involve the derivation of a one-dimensional map that determines the free CBB population at the start of each season based on the previous season's population dynamics. The first step is to consider the dynamics over one season. This amounts to solving Equations (14)-(17) with initial conditions given by Equation (18) until $t = t_h$. Then continuing to solve Equations (14)-(17) with initial conditions given by Equation (22). Note that in (18), \tilde{b}_o^0 appears as a free parameter. Thus the values of the variables $\tilde{c}_u(364)$, $\tilde{c}_{i_1}(364)$, $\tilde{b}_o(364)$ and $\tilde{b}_e(364)$ will depend on this initial choice, as described in Section 3, the Results.

To link the CBB populations from year to year, we set the total CBB population (free plus encapsulated) at the end of one season to be the free CBB population at the start of the subsequent season. This assumes that there is no remaining infested or severely infested coffee at the start of a

season and only uninfested coffee berries exist³. In other words, at the start of each season, we assume $\tilde{c}_u = 1$, $\tilde{c}_{i1} = 0$ and $\tilde{b}_e = 0$. To make this mathematically precise, define s_n to be the free CBB population at the start of the n^{th} season. Thus $s_1 = \tilde{b}_o(0) + \tilde{b}_e(0)$, which because of Equation (18) implies that $s_1 = \tilde{b}_o^0$. At the start of the next season $s_2 = \tilde{b}_o(364) + \tilde{b}_e(364)$, where these values are computed from the single season dynamics that include harvesting. We then compute the second season population dynamics by solving Equations (14)-(17) with the free CBB population starting with the value of s_2 , uninfested coffee starting at one, the other variables starting at zero, and with harvesting at $t = t_h$. The new value s_3 is determined and so on. This yields a one-dimensional map, $s_{n+1} = f(s_n)$, where the function f utilizes Equations (14)-(17) as well as the harvesting condition (22) at $t = t_h$. A fixed point s^* of the map satisfies the equation $s^* = f(s^*)$. This represents the case where the free CBB population at the beginning of a season is exactly equal to the free plus encapsulated CBB population at the end of that season. The value $s^* = 0$ is always a fixed point of this scheme because if there are no free CBBs at the start of a season there is no way for the CBB population to grow. This will correspond to the infestation-free steady-state solution (19). Total extinction of the CBB population is also represented by the condition $s^* = 0$. We will show that another stable fixed point exists which corresponds to the multi-season with harvesting infestation solution. Further, we show that an unstable fixed point exists that provides a threshold between the infestation-free and infestation fixed points. Doing so will allow us to determine what initial values s_1 lead to sequences s_n that converge to $s^* = 0$. As we will show in Section 3, understanding how the stable and unstable fixed points of the one-dimensional map depend on parameters will help determine conditions which lead to either an extinction or explosion of the free CBB population.

³This assumption is true if all infested coffee is harvested or falls off the plants, and if infested berries on the ground decompose before the next season, as has been reported in Puerto Rico [3, 21]. It is not completely understood how or where the free CBBs survive between the coffee harvest and the start of the next season; some studies have proposed alternative hosts as a place of refuge [2, 22], and [23], but since this is not certain they are not considered here.

2.5. Model parameters

We use parameter values that are typical for a coffee tree on a farm in the island of Puerto Rico. A set of parameter values was chosen or estimated from the literature; another set of parameters was estimated by solving a least-squares problem to fit the model Equations (14)-(17) to field data.

2.5.1. Parameter values

In Table 1, we show the values of the parameters. The basic unit of measurement is a tree. We assume that there are 1,000 coffee berries per tree [20]. The CBB carrying capacity of a berry is 20 CBBs per berry (though occasionally this carrying capacity may be exceeded, [19]), which under our assumptions results in a CBB carrying capacity per tree of 20,000. In this model the coffee is harvested at day (t_h) 184, i.e., November 1st of each year, [12].

The study of Jaramillo et al. [24] suggests that the CBB reproduction rate ρ_b is temperature dependent. For the sake of simplicity, we initially assume a constant reproduction rate corresponding to an average temperature of 24°C. We chose as reproduction rate the developmental rate of egg to adult reported in Fig. 3 in [24]. In Section 3.5, we will consider temperature dependence by allowing the reproduction rate to depend on it. It is difficult to estimate mortality rate in the field because infestation is asynchronous and sampling is destructive. In the study of Johnson et al. [13], the authors measured mortality of borers inside dry coffee and found values that ranged approximately from 7×10^{-4} to 4×10^{-3} per day. Here we assume a death rate δ_b of 1×10^{-3} per day. The CBB exiting rate constant $\tilde{\varepsilon}_{b_e}$ was chosen to satisfy the solution feasibility condition (21), here taken to be $\tilde{\varepsilon}_{b_e} = 0.75\rho_b$.

2.5.2. Parameter estimation

There are still three parameter values to estimate. These are the berry infestation rate constant $\tilde{\varepsilon}_c$, the berry severe infestation rate constant ε_{c_i} , and the CBB entering rate constant $\tilde{\varepsilon}_{b_o}$. To compute these parameter values we used unpublished field data from Bayman's laboratory (see Table 2a). They collected samples of coffee berries in June (the early stage of the coffee season) and September, October, and November (late stage) in different years and counted the number of infested fruits, i.e., fruits with a CBB entry hole. To compute the parameter values we fitted the model equations (14)-(17), running from $t = 0$ to $t = 184$ days (May 1 to November 1), to the data on Table 2a by solving a least-squares problem. Specifically, we minimized the

Table 1: Model parameters

Parameter	Description	Value	Reference
t_h (day)	harvesting time	184	[12]
c_T (berry/tree)	total number of coffee berries in the season	1,000	[20]
α_b (CBB/berry)	CBB carrying capacity per berry	20	[19]
κ_b (CBB/tree)	CBB carrying capacity per tree	20,000	
ρ_b (day ⁻¹)	CBB reproduction rate constant	0.0345	[24]
$\tilde{\varepsilon}_c$ (day ⁻¹)	coffee berry infestation rate constant	0.742	computed, see text
ε_{ci} (day ⁻¹)	coffee berry severe infestation rate constant	0.0230	computed, see text
$\tilde{\varepsilon}_{b_o}$ (day ⁻¹)	CBB entering rate constant	0.0334	computed, see text
$\tilde{\varepsilon}_{b_e}$ (day ⁻¹)	CBB exiting rate constant	0.0259	chosen, see text
δ_b (day ⁻¹)	CBB death rate constant	0.001	chosen, see text

Table 2: Early and late coffee infestation

Percent of infested coffee per month					
year	June	September	October	November	b_o^{0a}
<i>a: Data values</i>					
2010	1.67	5.62	7.34	12.41	
2011	15.98	46.43	51.37	58.37	
2015	5.58	6.21	9.16	11.02	
2018	21.22	25.35	32.31	44.05	
<i>b: Predicted values</i>					
~ 2010	4.53	7.27	7.65	8.05	65
~ 2011	21.60	41.81	49.60	60.16	330
~ 2015	6.24	10.25	10.94	11.74	90
~ 2018	16.21	29.96	34.58	40.90	242

^aInitial amount of free CBB/tree.

sum of the squares of the differences between the data values and the model infested coffee $\tilde{c}_{i_1}(t) + \tilde{c}_{i_2}(t)$ at $t_1 = 31$, $t_2 = 123$, $t_3 = 153$, and $t_4 = 184$ for each year. The parameters allowed to vary in the least-squares problem were the three parameters mentioned above ($\tilde{\varepsilon}_c$, ε_{c_i} , and $\tilde{\varepsilon}_{b_o}$) and the initial values of free CBB, b_o^0 in (6), for each year. The resulting parameter values are reported in Table 1. Model outcomes are reported in Table 2b and the comparison of these results with field data are shown in Fig. 2. The sum of the squares of the differences between the data values and the model infested coffee at the least-squares solution is equal to 2%. The initial values b_o^0 obtained by solving the least-squares problem are not used in the subsequent computations since they were obtained for model calibration purpose only.

2.6. Model programs

Programs to solve the model equations were written in MATLAB (R2020a), MathWorks[®]. Programs are provided in the Supplementary Material. To solve the initial value problem we use the function `ode45`, which is a Runge-Kutta method. The nonlinear least-squares problem, to fit the model parameters to the data, was solved with the function `lsqnonlin` (from the MATLAB Optimization Toolbox[™]), which uses a trust-region reflective method to compute a minimum.

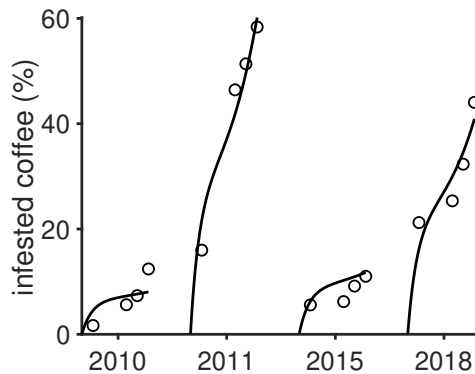


Figure 2: Model fitting to field data, which account for percent of infested coffee in June, September, October, and November. Open circle, data; black curve, model results

3. Results

The goal of our analysis is to show that with an appropriate harvesting strategy, the coffee berry borer (CBB) population can be eliminated or controlled over several seasons. This strategy is determined through the analysis of our mathematical model and will proceed over several steps. We have already analyzed the model Equations (14)-(17) without regard to the season length. This provided us with relationships on parameters that fall within a biologically meaningful range, leading to the infestation-free and infestation steady-state solutions. In this section, we begin by studying the dynamics of coffee and CBB populations within a single season to understand the effects of harvesting. This is followed by tracking these populations over multiple seasons using the one-dimensional map. We will show that the percentage of harvesting per season affects an unstable fixed point of the map, which in turn provides information about what amount of initial free CBB can be eradicated. Then, by introducing immigration of CBBs at the beginning of each coffee season, we will see that the value of the stable and unstable fixed points come closer together. Thus, the effect of immigration narrows the interval of initial free CBB for which the infestation can be controlled, and owing to the constant immigration the infestation cannot be eliminated. The section concludes with a few different examples of strategies for control of the CBB population leading to an infestation-free solution.

3.1. Model dynamics for one coffee season

We begin by studying the population dynamics and the amount of available coffee for consumption by solving the model Equations (14)-(17) for a single season (365 days) without harvesting ($\phi = 0$ in (22)) for different initial values of free CBB, b_o^0 in (6). In Fig. 3 we show the population dynamics over this coffee season. The values of b_o^0 are 100, 150, and 200 CBB/tree in Figs. 3a, 3b, and 3c, respectively. At the harvest day (184), the percentages of consumable coffee (i.e., uninfested plus slightly infested coffee) are 88%, 81%, and 74% for the initial CBB values of 100, 150, and 200 CBB/tree, respectively. At the end of the season, if the coffee is not harvested, the percentages of consumable coffee would be 79%, 54%, and 25% for the initial CBB values of 100, 150, and 200 CBB/tree, respectively. When starting with 100, 150, and 200 CBB/tree, the amount of CBB/tree at the end of the season increases to 311, 936, and 2,291, respectively.

Now we solve the model equations (14)-(17) for one coffee season for different percentages of coffee harvesting, ϕ in Equation (22), but keeping fixed the initial value of free CBBs, b_o^0 , equal to 200 CBB/tree in (6). In our model each population is represented in a single and well-mixed compartment. Thus, by harvesting percentage, we mean the percentage of coffee berries that are picked from the tree and/or up from the ground. In Fig. 4, we show the population dynamics over one coffee season. In the three cases, the percentage of consumable coffee at the harvesting day (184) is 74%. However, the amount of available CBBs for the next season decreases as the percent of harvesting increases, with 473 CBB/tree for 50% harvesting (Fig. 4a), 184 CBB/tree for 75% harvesting (Fig. 4b), and 91 CBB/tree for 90% harvesting (Fig. 4c). Clearly, increased harvesting is beneficial for control of the CBB population.

3.2. One-dimensional map for the discrete dynamics of multiple coffee seasons

The season-to-season population dynamics can be predicted by using the one-dimensional map $s_{n+1} = f(s_n)$ that takes the free CBB population at the beginning of a season, and predicts what the population will be at the start of the next season. The function $f(x)$ is computed using Equations (14)-(17) with harvesting at $t = t_h$ (here we use x as the independent variable for explanatory purposes). While we cannot explicitly express $f(x)$ with an analytic formula, we can describe several of its properties. First, by letting $\tilde{b}_o^0 = 0$ in (18) (which means $s_n = 0$), the solution given in (19) implies that

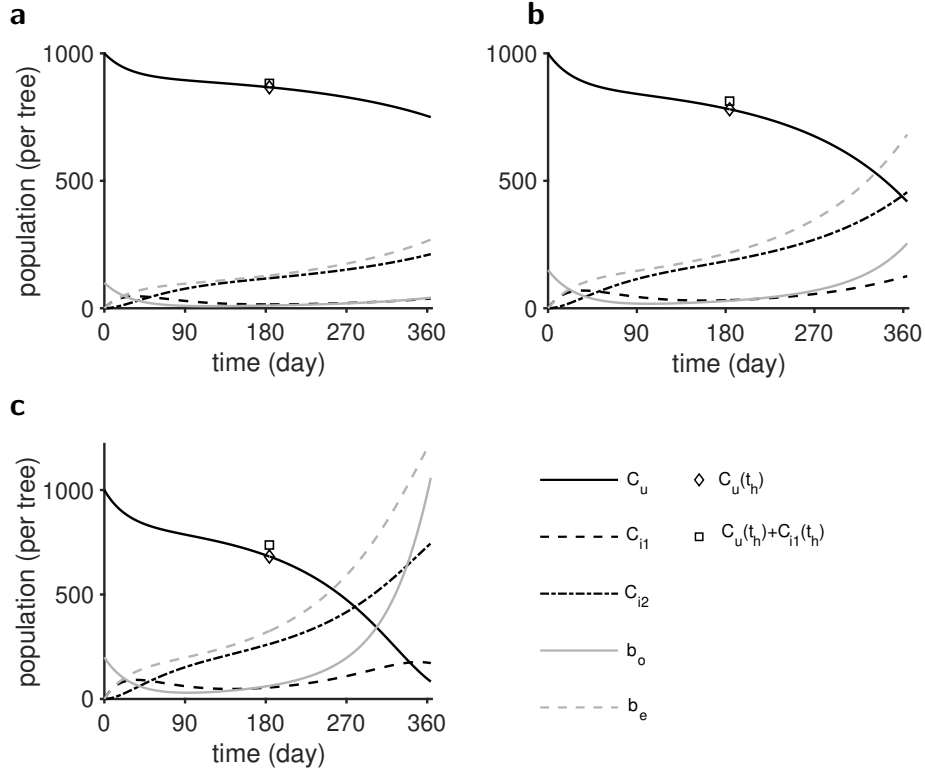


Figure 3: Population dynamics over a coffee season for different initial values of free CBB, b_o^0 ; the initial values for the rest of variables are shown in Equation (18). In panel **a** $b_o^0 = 100$ CBB/tree, in **b** $b_o^0 = 150$ CBB/tree, and in **c** $b_o^0 = 200$ CBB/tree. Black solid line, uninfested coffee c_u ; black dashed line, slightly infested coffee c_{i1} ; black dotted-dashed line, severely infested coffee c_{i2} ; grey solid line, free CBB b_o ; grey dashed line, encapsulated CBB b_e ; diamond, amount of uninfested coffee per tree at the harvesting day; square, amount of consumable coffee at the harvesting day, that is, the sum of uninfested coffee and slightly infested coffee

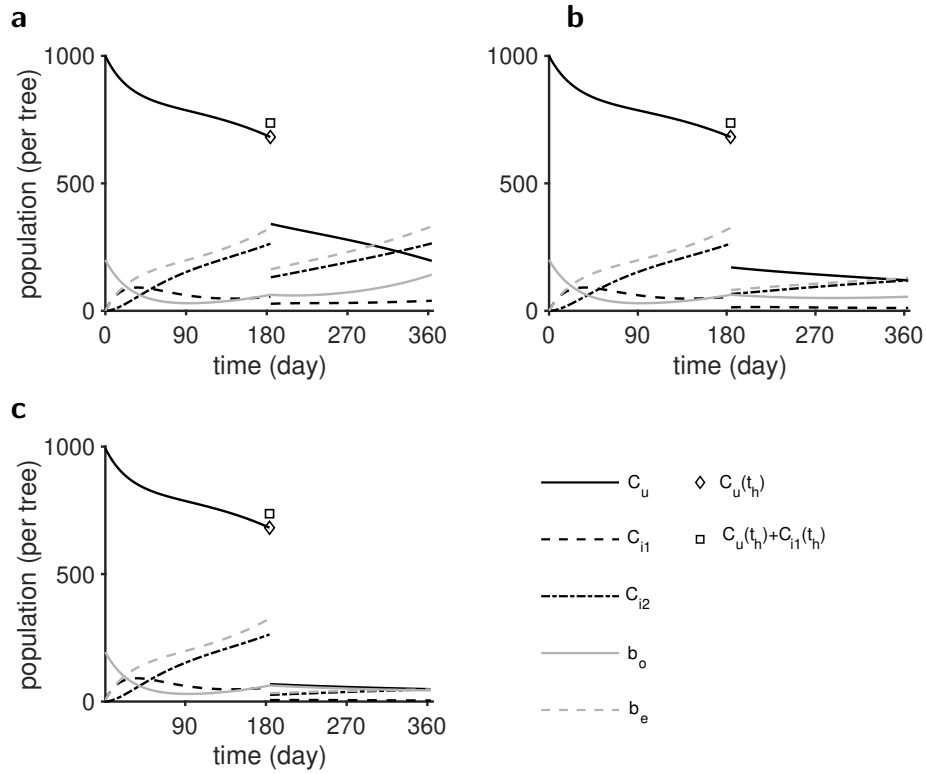


Figure 4: Population dynamics over a coffee season for different percentages of coffee harvesting (ϕ) at day 184; the initial value of free CBBs (b_o^0) is kept fixed to 200 CBB/tree. In panel **a** $\phi = 50\%$, in **b** $\phi = 75\%$, and in **c** $\phi = 90\%$. Black solid line, uninfested coffee c_u ; black dashed line, slightly infested coffee c_{i_1} ; black dotted-dashed line, severely infested coffee c_{i_2} ; grey solid line, free CBB b_o ; grey dashed line, encapsulated CBB b_e ; diamond, amount of uninfested coffee per tree at the harvesting day; square, amount of consumable coffee at the harvesting day, that is, the sum of uninfested coffee and slightly infested coffee

$s_{n+1} = 0$, and thus $f(0) = 0$. This means that if the free CBB population is zero at the start of a season, it will also be zero at the start of the next season. This is a condition for CBB extinction. Second, $f(x)$ is a continuous, monotone increasing function with regard to the value x . We can graph the function $y = f(x)$ together with the diagonal identity line $y = x$. Any point at which these two graphs intersect is a fixed point of the one-dimensional map. Further, since the slope of the identity line is always one, we can easily determine if the derivative of the function $f(x)$ at a fixed point is less than (stable) or greater than one (unstable). Third, for a wide range of parameters, the map will possess three fixed points. In addition to the $s = 0$ extinction fixed point, there exists another stable fixed point at large values of CBB called the map's infestation solution. In between the extinction and infestation fixed points lies an unstable fixed point which is the threshold that separates solutions that get attracted to either of these two. Finally, the graph of the map $f(x)$ depends on parameter values, which in turn changes the value of the unstable threshold as well as the stable infestation fixed point.

Fig. 5a shows an example of the graphical representation of the map with 80% harvesting. The grey diagonal line represents the identity and the black curve depicts the function $f(x)$. Note that these two curves intersect at two points (one filled and one open circle). The slope at the filled circle ($x = 0$) is less than one as the function emerges below the diagonal. Thus this fixed point is stable and any nearby values will be iterated towards it. The slope at the open circle ($x = 256$) is larger than one as the curve passes from below to above the diagonal. This fixed point is therefore unstable and nearby initial conditions iterate away from it.

In Fig. 5b, we show the same map for 80% harvesting in the zoomed out interval $[0, 13000]$ CBB/tree to illustrate the third fixed point of the map at $x = 12,680$. The slope at the third fixed point is less than one as the curve crosses the diagonal from above to below it and thus that point is stable. Fig. 5c shows the map for 90% harvesting. Note how the unstable fixed point has shifted to a higher value of 352. All of these figure panels also show a cobweb diagram. In Fig. 5a with 80% harvesting, if an initial free CBB population of 246 CBB/tree (cobweb on the left) is chosen, the iterates of the map predict that the free CBB population decreases year by year until extinction after roughly 7 years (numbers next to each iterate indicate the corresponding year). Alternatively, if the initial CBB population is taken to be equal to 266 CBB/tree (cobweb on the right), then the CBB

population increases each year leading to complete infestation (cobweb from Panel a continued in Panel b). From this example, we see that if the initial CBB population has a value that is smaller than the unstable fixed point, eradication is possible. If not, total infestation occurs.

Fig. 5c shows the cobweb diagram with 90% harvesting. Since the unstable fixed point of the map has shifted to the larger value of 352, an initially larger value of the CBB population can still be eliminated. For example, an initial CBB population of $s_1 = 342$ leads to extinction after roughly 6 years. Note that this initial condition under 80% harvesting would lead instead to infestation (see Fig. 5a). Also observe the increased concavity of the map for 90%. This leads to faster convergence towards extinction compared to the 80% harvesting case. Indeed, starting with an initial CBB population of $s_1 = 246$ with 90% harvesting would lead to extinction in just three years (grey dashed cobweb) instead of seven years (cobweb on the left of the unstable fixed point in Fig. 5a).

Although 90% harvesting leads to extinction of larger initial CBB population, it may not be feasible to maintain that level of harvesting over a large number of years. Our results suggest that a higher harvesting rate can be reduced in subsequent years and still obtain extinction. For example, in Fig. 5d, we superimpose the maps for both 80 and 90% harvesting. We choose an initial value of $s_1 = 342$ and harvest at 90% for 4 years. The value $s_4 = 228$ (diamond) is less than $x = 256$, which is the value of the unstable fixed point for the 80% map (open circle). We can then switch to 80% harvesting and still achieve eradication. Note that it takes two years longer than if we had continued at the 90% rate.

The one-dimensional map above predicts that for 80% and 90% of coffee harvesting it will take about seven years to eliminate the CBB population. We solved the model Equations (14)-(17) for eight consecutive years for the two different percentages of harvesting. It is assumed that each year the same percentage of harvesting is carried out in each case. In the first year, the free CBB/tree initial values are 246 and 342 for 80% and 90% of coffee harvesting, respectively. After the first year, the free CBB initial value is taken equal to the summation of the free and encapsulated CBB at the end of the previous season. Results are shown in Fig. 6 for uninfested coffee and free and encapsulated CBB, showing eradication of the CBB population in eight years to four digits of accuracy, i.e., when the number of free plus encapsulated CBBs per tree at the end of the n^{th} year is less than 0.5×10^{-4} . This result is consistent with the prediction of the map.

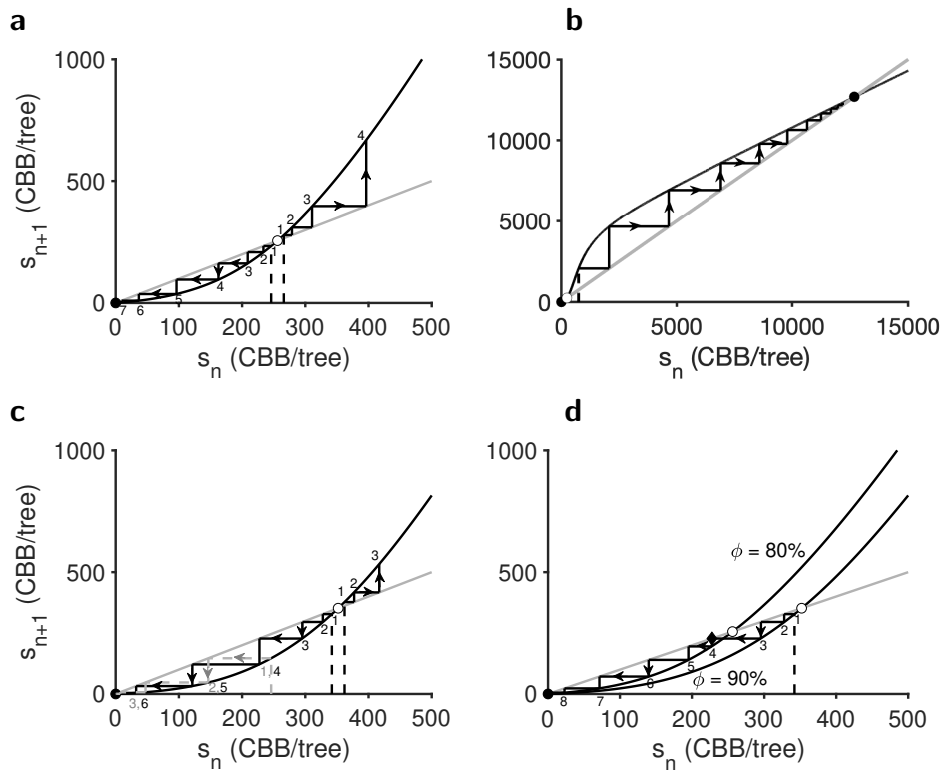


Figure 5: Map of the discrete dynamics over multiple seasons. Panel **a**, map shown in the interval $[0, 500]$ for 80% harvesting, $\phi = 80\%$; panel **b**, zoom out of the map in panel **a** to complete the entire map for 80% harvesting and show three fixed points; in panels **c** and **d** relevant maps are shown in the interval $[0, 500]$; panel **c**, 90% harvesting, $\phi = 90\%$; panel **d**, comparison of the numbers of years it will take to eliminate the CBB by harvesting 90% of the coffee and then switching to harvesting 80% after passing the unstable point versus staying with 90% harvesting as in panel **c**. Grey line, the identity; black curve, the map s_{n+1} ; filled circle, stable fixed point of the map; open circle, unstable fixed point of the map; vertical and horizontal lines with arrows, cobweb diagram; numbers close to a curve, season sequence; arrows, direction of a stable point; diamond, season at which the harvesting percentage changes

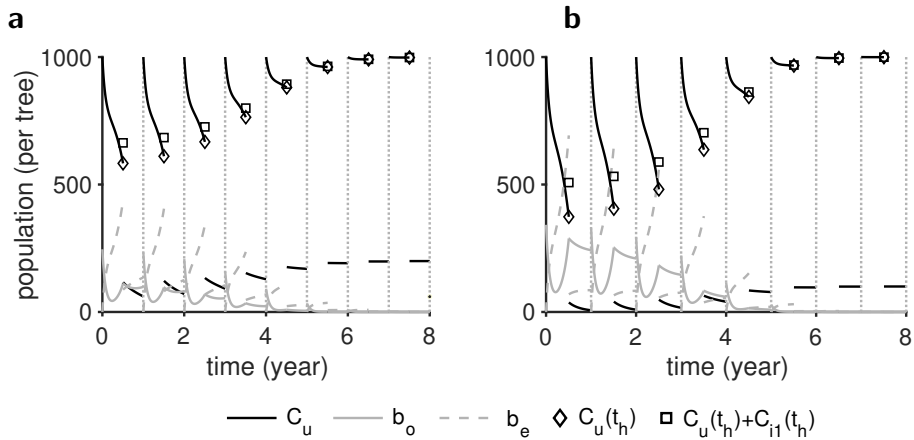


Figure 6: Population dynamics over eight coffee seasons for two different percentages of coffee harvesting (ϕ) at day 184 and a free CBB initial value (b_o^0) that is smaller than the unstable fixed point corresponding to the harvesting percentage used. After the first year the free CBB initial value is chosen equal to the summation of the free and encapsulated CBB at the end of the previous season. Panel **a**, $\phi = 80\%$ and $b_o^0 = 246$ CBB/tree; panel **b**, $\phi = 90\%$ and $b_o^0 = 342$ CBB/tree. Black solid line, uninfested coffee c_u ; grey solid line, free CBB b_o ; grey dashed line, encapsulated CBB b_e ; diamond, amount of uninfested coffee at the harvesting day; square, amount of consumable coffee at the harvesting day, that is, the sum of uninfested coffee and slightly infested coffee (not shown)

3.3. Immigration effect at the start of each season

In the results we have obtained thus far, zero is a stable fixed point of the one-dimensional map, which means that under certain conditions the CBB can be eradicated. However, to the best of our knowledge, in the literature there is not any evidence that suggests the extinction of the CBB is possible once they have invaded a site. Perhaps this is due to arrival of new CBBs each season, i.e., immigration of the CBB. Hence, we studied the effects on the existence and stability of the map fixed points due to introduction of a constant amount of CBB/tree at the beginning of the coffee season and keeping that amount constant in subsequent seasons. Immigration, for all other parameters fixed, has the effect of increasing the value of $f(s)$; that is the map moves up in the s_n - s_{n+1} plane. As a result, the stable fixed point at $s = 0$ will shift to a non-zero positive value of s and the value of the unstable fixed point will decrease.

Figure 7 displays results of the map over multiple seasons assuming different amounts of CBB immigration at the beginning of each coffee season. In the computations 80% harvesting in each season is assumed. When the initial addition is 10 CBB/tree, the stable and unstable fixed points move to 12 and 248 from 0 and 256 CBB/tree without immigration, respectively (Fig. 7a). Note that the stable fixed point (12 CBB/tree) is larger than the amount of CBB immigrating (10 CBB/tree), to reduce the stable fixed point to 10 CBB/tree, one needs to harvest 91% of the berries each season. If 25 CBB/tree are immigrating, then the stable fixed point increases to 32 CBB/tree and the unstable fixed point decreases to 235 CBB/tree (Fig. 7b). For an immigration of 50 CBB/tree, the stable fixed point is 73 CBB/tree and the unstable fixed point is 205 CBB/tree (Fig. 7c). When immigration is 70 CBB/tree the stable and unstable fixed points collide at a saddle-node bifurcation (143 CBB/tree, see Fig. 7d). As a result, whenever there is an immigration of 70 or more CBB/tree 80% harvesting is not enough to control the CBB infestation and the percentage of harvesting must be increased.

3.4. Harvesting as an infestation control practice

Based on the model assumptions and parameter values in Table 1, we now obtain the relation between CBB infestation and the percentage of coffee harvesting that should be applied to eliminate or control the CBB (see Table 3). We compare two cases: neglecting CBB migration at the beginning of each coffee season (second column of Table 3) and introducing 10 CBB/tree in each season to account for borer immigration (third column of

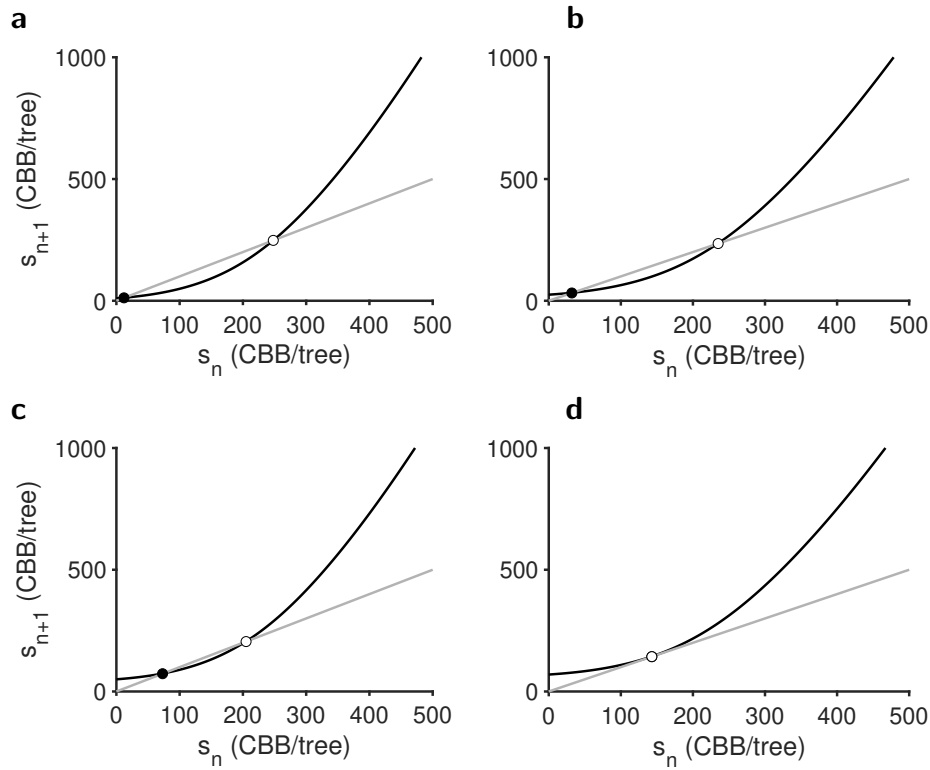


Figure 7: Map of the discrete dynamics over multiple seasons with CBB immigration. In each season a fixed amount of CBB/tree is added from outside to account for immigration: Panel **a**, 10 CBB/tree are added; panel **b**, 25 CBB/tree; **c**, 50 CBB/tree; panel **d**, 70 CBB/tree. 80% harvesting is assumed. Grey line, the identity; black curve, the map s_{n+1} ; filled circle, stable fixed point of the map; open circle, unstable fixed point of the map. Note that the stable and unstable fixed points collided for an immigration of 70 CBB/tree

Table 3). The value of the unstable fixed point is labeled as the threshold value such that the initial free CBB/tree in the first season must be less than this value to be able to control the infestation after several subsequent years of this practice. We computed this threshold value for different harvesting percentages for the cases of no migration or immigration of 10 CBB/tree. The results shown on Table 3 suggest that to control the CBB one must estimate the number of CBB at the beginning of the season when berries are formed and, at harvesting time, harvest at least the percentage of coffee indicated in the table for several years. For example, if one estimates 100 CBB/tree at the beginning of a season, one must harvest at least 60% of the coffee for multiple years. Further, whenever the initial amount of free CBB is greater than 413 CBB/tree without immigration or 408 with 10 CBB/tree added from the outside, even 100% coffee harvesting will lead to total infestation. The reason is that at harvest time t_h the amount of free CBB will be larger than the initial value. In view of the small death rate there will be enough free CBB to increase the infestation in the next season. In the fourth column of Table 3 we show the number of years it would take to control the number of CBB/tree for each percent of harvesting, starting with 50 CBB/tree in the first year. Computations are carried out to four digits of accuracy. Note that the value used in Figure 6 for the initial number of CBB/tree (246 CBB/tree for 80% harvesting) is too high and we chose it simply to illustrate the capacity of this practice. However, 50 CBB/tree is a more typical value. As can be seen in Table 3, by applying 80% harvesting for three consecutive years without immigration it is possible to eliminate the CBB.

We computed bifurcation diagrams which clearly show the threshold effect of the unstable fixed point. Figure 8a plots the values of the stable and unstable fixed points of the map in the absence of immigration for different levels of harvesting. Filled circles denote stable fixed points and open circles are unstable fixed points. For this case, for any level of harvesting (x -axis), there is a fixed point at 0 indicating complete eradication. However, as the harvesting percentage decreases, the value of the unstable fixed points decreases (see Table 3 middle column for exact values), lowering the threshold value that separates the two stable solutions, which in turn shrinks the basin of attraction of the infestation-free solution. In other words, as the harvesting percentage decreases, the initial value of CBBs per tree must also be smaller in order to ensure eradication. Note that the scale on the vertical y -axis is split, with the lower values 0 to 500 corresponding to the unstable and lower

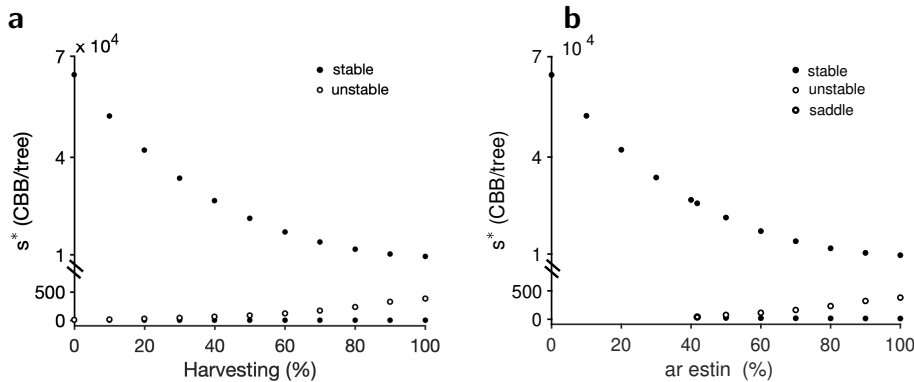


Figure 8: Bifurcation diagram for different harvesting percent. Each diagram shows three sets of the map’s fixed points, two stable (filled circles) and one unstable (open circles). Panel **a**, no immigration is considered; panel **b**, immigration of 10 CBB/tree is included in each season. A saddle-node bifurcation occurs at harvesting percentage 42% (bold open circle). Note that the vertical scale in each panel has two distinct parts separated by the double backslash marks. Values for the unstable fixed points correspond to those shown in Table 3.

stable branch and the higher values 1 to 7×10^4 corresponding to the upper branch of stable points. Figure 8b shows the bifurcation diagram when 10 CBBs per tree are allowed to immigrate per year. Now the merging of the unstable and lower stable branch at a saddle-node bifurcation point is evident (bold open circle) at 42% harvesting (see also Caption of Table 3). Thus for any harvesting percentage less than 42% only the infestation solution remains and is the attracting solution.

3.5. Temperature Dependence of CBB reproduction rate

We studied how seasonal changes in the temperature will affect our results. While the temperatures in the coffee-growing region in Puerto Rico may range from 8-34°C [3], we note that the extremes of these temperatures in the hills does not last for the entire day. According to Figure 3 (Egg-Adult) in [24], borers reproduce when the temperature is roughly in the range of 15-32°C. Thus, in our model we use the range of temperatures 15-30°C and incorporate its effect on the encapsulated borer population reproduction rate ρ_b , which in turn affects the encapsulated borer exit rate $\tilde{\epsilon}_{b_e}$ (21). In particular, we replace the constant value of ρ_b used earlier with the expression [24]

$$\rho_b(T) = e^{aT} - e^{(aT_{\max} - (T_{\max} - T)/b)} + c, \quad (23)$$

Table 3: Coffee harvesting needed to control CBB depending on initial levels of CBB infestation

Harvesting (%)	Threshold value ^a		Years to control infestation starting with 50 CBB/tree w/o immigration
	w/o immigration	immigration of 10 CBB/tree	
100	413	408	2
90	352	345	2
80	256	248	3
70	181	172	4
60	130	119	5
50	94	78	7
40	67	–	11
30	47	–	–
20	31	–	–
10	19	–	–
0	11	–	–

^aNumber of CBB/tree. The initial free CBB/tree in the first season must be less than this value. For 42% of harvesting with immigration the stable and unstable fixed points collided at 38 CBB/tree, for smaller harvesting fractions there were no fixed points.

where the parameters a , b , c , and T_{\max} are taken from Table 3 in [24] and the temperature function is taken as

$$T(t) = 15 + (30 - 15) \sin((t + 90 \bmod 365)\pi/365) \quad (24)$$

Because a coffee season in the model starts on May 1st, the sin function is shifted by 90 days to reflect that the coolest temperature is at the end of January and the hottest day is at the beginning of August. The value of the encapsulated borer exit rate remains at the same ratio as in the constant temperature case, $\tilde{\varepsilon}_{b_e} = 0.75\rho_b$.

With these changes the results are qualitatively similar to the ones obtained with constant CBB reproduction rate. The parameter values and results of the model fitting to the data are shown in the Supplementary Material in two tables analogous to Tables 1 and 2. Interestingly, for an infestation that in the first year begins with 50 CBB/tree, both models, constant and temperature dependent CBB reproduction rate, require the same number of years to control the infestation for 50% or more harvesting (fourth column in Tables 3 and 4). The main difference between the two models is that the one with variable CBB reproduction rate is able to control the infestation (in 19 years) applying 30% harvesting whereas the model with constant reproduction rate is unable to control the infestation with that percentage of harvesting because its threshold is below the initial number of CBB/tree. We also compared the number of years that it takes to control the CBB for the constant and variable CBB reproduction rate for different initial numbers of CBB/tree in the first year by varying that value from 50 to 225 CBB/tree in increments of 25 CBB/tree (not shown). The results were similar to the ones shown in the fourth column of Tables 3 and 4. Note that for an initial value of 225 CBB/tree 80% harvesting is required (second column, Tables 3 and 4). As the starting amount of CBB/tree increases from 50 to 225, the control time increases linearly from 3 to 8 years (fourth column, Tables 3 and 4 and Figure 6).

4. Discussion

We have developed a quantitative model for applying CBB control management in an infested coffee site in Puerto Rico. The procedure is based on the cultural practice of harvesting and picking up fallen coffee fruits from the ground. The model provides a threshold for identifying whether an infestation can be controlled and, if that is possible, it estimates the minimal

Table 4: Coffee harvesting needed to control CBB depending on initial levels of CBB infestation, variable CBB reproduction rate

Harvesting (%)	Threshold value ^a		Years to control infestation starting with 50 CBB/tree w/o immigration
	w/o immigration	immigration of 10 CBB/tree	
100	361	355	2
90	311	304	2
80	243	235	3
70	183	174	4
60	138	126	5
50	104	88	7
40	77	–	10
30	55	–	19
20	37	–	–
10	23	–	–
0	13	–	–

^aNumber of CBB/tree. The initial free CBB/tree in the first season must be less than this value. For 40% of harvesting with immigration the stable and unstable fixed points collided at 40 CBB/tree, for smaller harvesting fractions there were no fixed points.

percentage of harvesting that must be applied during a number of subsequent coffee seasons to eliminate or reduce the infestation. Further, the model can estimate the number of years that it may take to control the CBB infestation based on an initial number of CBB/tree.

The main findings of this paper involved analyzing a coupled set of nonlinear differential equations that modeled the population levels of free and encapsulated CBBs and of coffee berries (uninfested and slightly and severely infested). Instead of relying on simulations of a five-dimensional system, we derived a novel one-dimensional map that tracks the free borer population from season to season. During a single season, defined here as May 1 to April 30 of the next year, the dynamics of all five populations were computed using the five-dimensional system which also included the percentage of harvesting at roughly halfway through the season. At the end of the season, we simply used the remaining CBBs to serve as the initial free CBBs for the next season. There are several advantages to using this map-based approach compared to running simulations of the nonlinear equations. First, the map reveals the existence of a harvesting percentage dependent threshold (the map's unstable fixed point) that separates out initial CBB population values that can be regulated versus those that lead to total infestation. Thus, the map provides a quantifiable and useful prediction of the level of harvesting needed in order to control the CBB population. Second, the map makes a prediction of how many seasons a particular harvesting strategy must be followed in order to eradicate the CBB. Third, it is straightforward to understand how the map depends on relevant parameters, for example, the harvesting percentage or the death rate of the CBB. Changes in parameters typically change the value of the threshold in a systematic way, e.g., an increase in the harvest percentage increases the threshold to more CBBs/tree. Simulations alone do not reveal the existence of the threshold or its dependence on parameters, nor do they predict the number of seasons to eradication. Discrete maps similar to the one-dimensional map described here have long been used to understand biological processes. Often these take the form of a Poincaré map to study general biological oscillators [25] or neuronal dynamics [26]. In other circumstances, the one-dimensional map can be derived by using important observable quantities from the underlying nonlinear equations. For example, phase response curves (see [27] for a review) which track the change in phase of an oscillator due to a perturbation can be formulated in the context of one-dimensional maps. One- and two-dimensional maps also have a long history in deriving error-correction schemes which govern synchronization of an

oscillator with an external periodic signal [28–30]. In all of the above cases, the map-based approach revealed information and mechanisms that governed the underlying dynamics of the nonlinear system that were not immediately evident from simulations alone.

Our results provide theoretical support to earlier observations that removing infested fruits is key to reducing CBB infestation in subsequent years [9, 11, 17, 21]. However, as noted in Fig. 6, a successful management strategy may not produce noticeable results for the first four or five years. The squares in the graphs in Fig. 6 indicate the amount of coffee available for harvesting. However, from that amount, we only harvest a fraction. For example, during the first three years of harvesting 90% the coffee yield is less than 529 fruits per tree. This is counterintuitive because it may appear that the strategy is not working for the first few years. This situation is something that could discourage coffee farmers from pursuing this strategy. However, our model simulations show that after four years of this practice a dramatic increase in consumable coffee is achievable. Coffee farmers base decisions about harvesting on various factors: the size of the crop, the price they will receive for their coffee, the availability and price of labor, among others. The model results also suggest a note of caution if the harvesting percentage drops too significantly in any given year. Namely, if the number of CBB/tree lies above the value of the unstable fixed point of the map corresponding to that harvest percentage, then the CBB population would increase during that year. Our results suggest that the effect of harvesting on future CBB infestations should also be a consideration, and this model can help inform decisions about how important the effect of harvesting will be.

The difficulty of the first years exhibited by the harvesting strategy (Fig. 6) could be overcome by combining this practice with other methods of cultural, chemical or biological control. These include traps to catch free CBBs, application of the entomopathogenic fungus *Beauveria bassiana*, release of parasitoid wasps that attack the CBB, and pruning of coffee plants to reduce reservoirs of CBBs [11, 12]. As we have seen with the cultural practice of harvesting, none of these control measures by itself might be sufficient to eliminate the CBB from coffee farms, but in combination they could reduce it to manageable levels.

Harvest levels vary greatly, depending on the price of coffee, the cost and availability of labor, and quality of the crop. In Puerto Rico the harvesting levels discussed in this paper (80-90%) are realistic. Many coffee farms are

harvested in a single pass, and a lot of fruits are missed. This may be because the pickers have more incentive to pick as much as they can in a given period of time instead of harvesting all fruits. In years when the crop is bad or labor is scarce, harvesting percentages may drop below this 80-90% estimate.

In countries where labor is cheaper and more readily available, harvest levels tend to be higher. But even so, the harvesting levels here are relevant. Much of the literature on this subject makes the point that more complete harvesting is essential for controlling the CBB [4, 5, 11, 12], so the conclusion here is consistent with the literature as well as with harvesting levels.

Our model assumes that fruits that fall on the ground are removed from the system, and are the same as harvested fruits. This may be an oversimplification in some contexts. In fact, fallen fruits may be an important source of CBBs that attack new fruits; several studies have shown that they can contain substantial numbers of CBBs [3, 12, 13]. However, in Puerto Rico and other humid climates these fruits degrade quickly, so they are not a long-term source of CBBs [3, 21]. For a more comprehensive study on the effect of removing ground berries, future modeling studies will need to split each coffee state into two new state variables: tree and ground coffee for each category.

The model equations (14)–(17) of interaction between coffee berries and CBBs assume a constant amount of coffee berries at the beginning of each season and population interaction rates that are time independent. However, the initial amount of coffee berries depends on several factors such as weather (e.g., amount of rainfall in the previous year) and physiology [14, 17]. Further, the CBB emergence and death rates may be affected by environmental conditions such as temperature and rainfall [15, 17]. Our choice of these parameters are based on average values, which exhibit small variability in Puerto Rico’s coffee farms.

In conclusion, in this paper we have introduced a new management strategy based on the cultural practices of coffee farmers for control of CBB infestation. We have demonstrated through mathematical modeling that there exists a critical threshold that can be potentially identified and used by farmers to develop multi-season harvesting practices. Our work shows that modeling the infestation can be a key tool for efficient and successful CBB infestation management.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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