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Modelling and control of a banana soilborne pest in a multi-seasonal framework

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Abstract

We study the infestation dynamics of banana or plantain plants by *Radopholus similis*, a plant-parasitic nematode that causes severe damages. Two control strategies are implemented in our model: pesticides, which are widely used, and fallows, which are more environmentally friendly. To represent the host-parasite dynamics, two semi-discrete models are proposed. During each cropping season, free nematodes enter the plant roots, on which they feed and reproduce. At the end of the cropping season, fruits are harvested. In the first model, the parent plant is cut down to be replaced by one of its suckers and pesticides are applied. In the second model, the parent plant is uprooted and a fallow period is introduced, inducing the decay of the free pest populations; at the beginning of the next cropping season, a pest-free vitroplant is planted. For both models, the effective reproduction number of pests is computed, assuming that the infestation dynamics are fast compared to the other processes, which leads to the model order reduction. Conditions on the pesticide load or the fallow duration are then derived to ensure the stability of the pest free equilibrium. Finally, numerical simulations illustrate these theoretical results.

Keywords: Epidemiological modelling, Semi-discrete model, Singular

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perturbation, Stability, Host-parasite interactions, Pest management

1. Introduction

Banana is the most popular fruit in the world and one of the most significant basic foods, along with rice, corn and wheat. In 2011, 107 million tons of banana were produced in more than 130 countries and out of 0.1 percent of the world agricultural surface [1] for a total commercial value of 9 billion dollars (FAO, 2013). In Cameroon, banana-plantain occupies the eighth rank in food productions (FAO, 2010), with an annual production of 1.4 million tons. This crop involves many stakeholders (more than 600 000 producers and around 40 000 tradesmen) and contributes to 2% of the gross domestic product [2].

Both banana and banana-plantain cultures are hampered by plant-parasitic nematodes, insect pests and soil-borne fungi, that seriously threaten the sustainability of these systems by decreasing yield, causing plant toppling or requiring intensive pesticide use. The burrowing nematode *Radopholus similis* is the most significant parasitic nematode of the banana and plantain plants in the world [3]. It is a phytophagous nematode that attacks the roots of host plants and causes damages, ranging from simple root lesions that reduce the production to the toppling of the plant. Hence, *R. similis* is one of the most regulated pests of banana plants [4]. To control this pest, nematicides can be applied. Their efficacy is sometimes limited. Moreover, the ecological impact of nematicides and their general toxicity have led to their prohibition in some countries [5]. Nevertheless, they are still frequently used, as they are very cost-effective and easy to implement [6, 7]. More sustainable and environmentally friendly banana cropping systems can be designed. Studying the hostless survival of *R. similis*, Chabrier noticed that nematode populations undergo a fast decay when hosts are lacking [8]. Previously, Loos had observed in Panama that after 5 months of submergence *R. similis* had disappeared from the soil [9]. This decay is essentially related to the absence of food resources and is also influenced by the soil temperature, moisture and oxygenation [10]. With this knowledge, an alternative cropping system has been developed in Martinique, based on the disinfestation of the land followed by the replanting of nematode-free banana vitroplants. Disinfestation is achieved either through a fallow period or a crop rotation with non-host plants, after obligatory destruction of the banana plants [11].

Mathematics is becoming a major tool for studying the evolution of plant epidemics and diseases (see [12] and references therein). For instance, several mathematical and computational models have been proposed for soilborne pests in the literature. Some crop rotation models have been proposed to control the dynamics of the root-knot nematode *Meloidogyne incognita* [13], the root-knot nematode *Meloidogyne arenaria* [14] and the root lesion nematode *Pratylenchus penetrans* [15]. Some reaction-diffusion models have also been proposed to link the temporal and spatial dynamics of soilborne pathogens [16]. However, to our knowledge, only one model has been proposed for *R. similis* [17]. The latter is a cohort-based model, is fairly complex and requires extensive data to be calibrated.

In the present work, we build on our previous modelling analysis [18]. We propose a multi-seasonal framework in which the dynamics of *R. similis* can be analysed and controlled either by chemical pesticides or by fallow, and we observe how effective both methods can be. The models we propose are based on a semi-discrete formalism. Such a formalism models continuous phenomena that are discretely perturbed. Some authors have already used this kind of model in the life sciences [19], and more precisely for plant-parasite interactions [20] or plant epidemics [21]. In this paper, we adopt the same framework as previous works [21, 22, 23] that we contextualize for the soilborne pest *R. similis*. This contextualization concerns some characteristics that are specific to both *R. similis* and its hosts studied here, namely banana and plantain. For example, the growth of banana and plantain roots stops at the flowering of the plant [24], which leads to a new hybridism in our models within continuous dynamics. Secondly, the cropping is made in non-arid tropical region, which implies that crops do not suffer harmful climatic disruptions like winter or hard summers and they can be grown any time during the year. This changes the perspective under which we calculate the effective reproduction number $\mathcal{R}$ which corresponds to the basic reproduction number under control measures such as fallow deployment. Also, the control strategies that are discussed in this paper are adapted to *R. similis* and its interaction with banana or plantain plants.

In the following, banana plants designate banana or plantain plants indifferently. The models on which this study is based are given in Section 2. We highlight results for both models in Section 3 : in Subsection 3.1 we investigate the action of nematicides, when banana suckers arise from lateral buds on the rhizome. We discuss the efficiency of this strategy. In Subsection 3.2, we analyse a more environmental-friendly model in which a fallow replaces nematicides at the end of each season. In Section 4, we discuss the relevance of our work compared to previous works.

2. Materials and Methods

2.1. Biological background and pathosystem

Banana cultivars are usually seedless and reproduce asexually by producing suckers, which are outgrows of vegetative buds. During their initial development, the suckers share their parent rhizome [25]. Hence, if the parent plant is infested, so are the suckers [25, 26]. In commercial plantations, one sucker is usually selected to grow out and regenerate the plant [27]. The banana plant produces roots continuously until the flowering [24]; then the plant growth concentrates on the shoots and fruits. At the end of the cropping season, the banana bunch is harvested and the plant is either cut down, or it dies naturally [27]. The roots that are not involved in the growth of the sucker quickly lose their freshness by senescence [28].

Like most nematodes in the *Pratylenchidae* family, *R. similis* is an obligate parasite which can only feed on fresh roots and induces root necrosis [29]. It is mainly found in roots and rhizomes, and rarely in the soil; the population density ratio in soil and roots is generally less than 1/100 [30]. When it infects functional roots, *R. similis* burrows the tissues while feeding. *R. similis* usually breeds by sexual reproduction. However, in the absence of males, unfertilized females can reproduce by parthenogenesis [31]. The females lay four to five eggs per day during two weeks in root necrotic areas [32]. Juveniles then either remain in the root and burrow to feed on fresh tissues, or they leave and migrate in the soil to find another root [29].

2.2. Core model

This work considers several cropping seasons and assumes a homogeneous repartition of nematodes in the roots. We therefore build a multi-seasonal compartmental model which represents the root growth, the pest dynamics and their interaction with the roots. Two cases are considered for banana plant reproduction. In the first case, a sucker of the parent plant is selected to form the new plant. Dying roots of the parent plant are assigned the term *old root pool* in our model. In the second case, a new nematode-free vitroplant is planted after the uprooting of the parent plant. Some root tips are then left in the soil, the uprooting being hardly perfect. These tips are also included in the *old root pool*.

We consider a single plant and make the following additional modelling assumptions:

1. The nematode population is divided into three compartments: free nematodes in the soil (P), infesting nematodes in the roots (X), infesting nematodes inside the old root pool (Y). Since the absence of males is not limiting because the females can reproduce by parthenogenesis, we do not pay attention to the sex of the pests.
2. There is one compartment for the biomass of functional roots (S).
3. During a cropping season, banana roots grow logistically [33] until the flowering at which moment root development stops. The duration of the growth period, *i.e.* the time elapsed between the start of the cropping season and the flowering of the plant, is termed d; the total duration of a

cropping season is termed D. We denote the starting point of the $(n+1)$-th season by t_n, and we set $t_0 = 0$ as the starting point of the first season. The logistic growth of the roots during a cropping season is therefore given by:

$$\frac{dS}{dt} = \rho(t) S\Big(1 - \frac{S}{K}\Big),$$

where

$$\rho(t) = \begin{cases} \rho & \text{for } t \in (t_n, t_n + d], \\ 0 & \text{for } t \in (t_n + d, t_n + D]. \end{cases}$$

4. Free pests (P) infest the plant roots (rate β). They undergo natural mortality (rate ω).
5. Infesting pests (X) feed on the plant roots with a Holling type II-like functional response $\frac{aSX}{S+\Delta}$ that is well-suited for invertebrates [34]. They undergo natural mortality (rate μ). This mortality rate differs from the mortality rate in the soil because the environments are different. The root, which serves both as host and food for the nematode, is more favourable to pest survival than the soil ($\mu < \omega$).
6. When infesting nematodes feed, the ingested root biomass is used for growth and for reproduction. Reproduction occurs inside (proportion γ) or outside (proportion $1 - \gamma$) the roots [29]. α is the conversion rate of ingested biomass into pests.
7. The old root pool quickly loses its freshness and degrades in the soil. The infesting pests in those roots are then free in the soil (rate δ). They also undergo natural mortality (rate μ).

Under the assumptions above, free nematodes (P), infesting nematodes (X), and infesting nematodes in the old root pool (Y) interact with the functional roots (S) during the cropping season, *i.e.* for $t \in (t_n, t_n + D]$, according to the following system:

$$\begin{cases} \dfrac{dP(t)}{dt} = \delta Y(t) - \beta P(t)S(t) + \alpha a(1-\gamma)\dfrac{S(t)X(t)}{S(t)+\Delta} - \omega P(t), \\ \dfrac{dS(t)}{dt} = \rho(t)S(t)\Big(1 - \dfrac{S(t)}{K}\Big) - a\dfrac{S(t)X(t)}{S(t)+\Delta}, \\ \dfrac{dX(t)}{dt} = \beta P(t)S(t) + \alpha a\gamma\dfrac{S(t)X(t)}{S(t)+\Delta} - \mu X(t), \\ \dfrac{dY(t)}{dt} = -(\delta+\mu)Y(t). \end{cases} \tag{1}$$

with the initial conditions at the beginning of the first season $P(0^+) = P_0$, $S(0^+) = S_0$, $X(0^+) = X_0$, $Y(0^+) = Y_0$; where 0^+ stands for the instant that directly follows the initial time 0.

If the senescence rate δ is very large, then the Y population is transferred into P very quickly with the old root pool disappearing. Hence, we assume that the transfer from Y to P is instantaneous and rewrite system (1) as follows:

$$\begin{cases} \dfrac{dP(t)}{dt} = -\beta P(t)S(t) + \alpha a(1-\gamma)\dfrac{S(t)X(t)}{S(t)+\Delta} - \omega P(t), \\ \dfrac{dS(t)}{dt} = \rho(t)S(t)\Big(1 - \dfrac{S(t)}{K}\Big) - a\dfrac{S(t)X(t)}{S(t)+\Delta}, \\ \dfrac{dX(t)}{dt} = \beta P(t)S(t) + \alpha a\gamma\dfrac{S(t)X(t)}{S(t)+\Delta} - \mu X(t). \end{cases} \tag{2}$$

with the initial conditions $P(0^+) = P_0 + Y_0$, $S(0^+) = S_0$, $X(0^+) = X_0$. To simplify the notation, we will assume in what follows that $Y_0 = 0$, which has no impact on the analysis as we could just change the value of the parameter P_0. By taking a larger value of parameter P_0, we compensate for what is lost when taking $Y_0 = 0$.

In this paper, the dynamics of (2) during the $(t_n, t_n + d]$ intervals will be called “the first subsystem of (2)”, while “the second subsystem of (2)” will concern interval $(t_n + d, t_n + D]$ with $\rho = 0$.

Figure 1 displays a diagram representing the parasitism process within the cropping season.

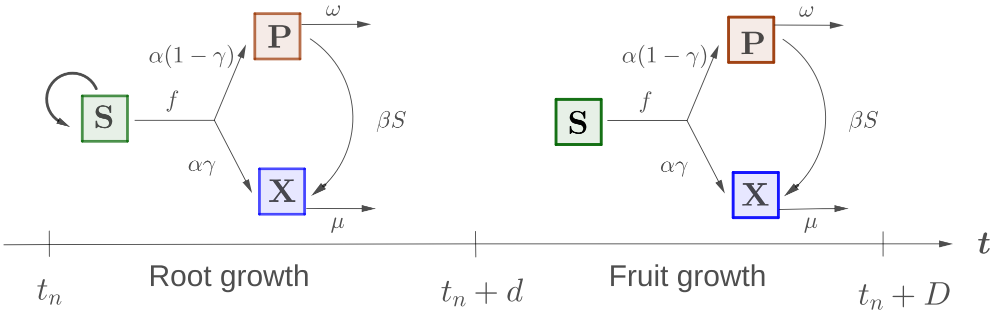


Figure 1: Schematic representation of the core model (2). P, S, and X denote the population of free nematodes, respectively. Function f is a Holling type II functional response, and constant α is the conversion rate of the ingested fresh roots that are used to reproduce inside the root with a proportion γ and outside with a proportion $(1-\gamma)$. The constants μ and γ are natural mortalities, and constant β is a rate of infection that depends on the biomass of available fresh roots. The arrow from S to S illustrates the root growth during the root growing period.

Switching from a cropping season to the following can be done in two different ways:

i) In the first case, the banana plant has a vegetative growth and a new sucker arises from the existing roots. Chemical nematicides are used at the beginning of each cropping season to control the pest.

ii) In the second case, a pest-free vitroplant is planted. A fallow is introduced between two cropping seasons to control the pest.

The following subsections describe both cases.

2.3. Chemical control model

In this case, since there is no fallow, each season is immediately followed by the next season, so $t_n = nD$.

R. similis can be controlled by nematicides. These have two means of action on nematodes: contact effect and systemic effect. Contact nematicides directly kill nematodes after contact, whereas systemic nematicides are absorbed by the plant roots and distributed throughout the organs where they act against pests [35]. Some nematicides present both effects. We assume that the nematicide is used at the begining of each season and presents both systemic and contact effects.

The switching between seasons is supported by the following assumptions:

- At the end of a season, a proportion q of the total biomass of the plant roots corresponds to the sucker that will grow during the next season. Assuming an homogeneous distribution of nematodes in the roots, the sucker bears the same proportion q of infesting nematodes. The sucker becoming the new parent plant, remaining roots of the previous parent plant are transferred to the old root pool. The old root pool therefore bears the proportion $(1-q)$ of infesting pests.

  This leads to the following switching rule at the beginning of the next season:

$$\begin{cases} P(t_n^+) = P(t_n), \\ S(t_n^+) = qS(t_n), \\ X(t_n^+) = qX(t_n), \\ Y(t_n^+) = (1-q)X(t_n), \qquad n \in \mathbb{N}^*. \end{cases} \tag{3}$$

  As we have assumed that the infesting pests in the old root pool (Y) instantaneously turn into free pests, we can write the previous switching rule (3) as follows:

$$\begin{cases} P(t_n^+) = P(t_n) + (1-q)X(t_n), \\ S(t_n^+) = qS(t_n), \\ X(t_n^+) = qX(t_n). \end{cases} \tag{4}$$

To add the action of the nematicide, we make the following assumptions:

- We assume that the natural clearance of the nematicide is very fast, so that the action of the nematicide is instantaneous on the pest population

[36, 37]. Hence, at time t_n^+, the nematicide contact action on free pests is given by:

$$P(t_n^+) = \lambda\big(P(t_n) + (1-q)X(t_n)\big), \tag{5}$$

with $0 \leq \lambda \leq 1$ the nematode survival rate on the application of the nematicide.

- We assume that the systemic and contact effects are equivalent, *i.e.* that their efficiency is the same for both free pests and infecting pests, so we obtain:

$$X(t_n^+) = \lambda q X(t_n), \qquad \text{with } 0 \leq \lambda \leq 1. \tag{6}$$

According to all the previous assumptions, the switching rule between seasons is given by:

$$\begin{cases} P(t_n^+) = \lambda\big(P(t_n) + (1-q)X(t_n)\big), \\ S(t_n^+) = qS(t_n), \\ X(t_n^+) = \lambda q X(t_n). \end{cases} \tag{7}$$

Systems (2) and (7) with $t_n = nD$ form our multi-seasonal model with the use of nematicide. A schematic is shown in Figure 2.

2.4. Fallow deployment model

In this case, banana crops are alternated with fallows or alternative non-host crops. Because of its mandatory parasitism, *R. similis* populations in the soil decline rapidly in the absence of hosts. In the following, we will term the period during which banana plants are not grown *fallow*, whether or not this is in fact due to fallowing or alternative non-hosts being deployed

We assume that all the fallow periods have the same duration designated by τ. A new season begins when both the cropping season and the fallow are

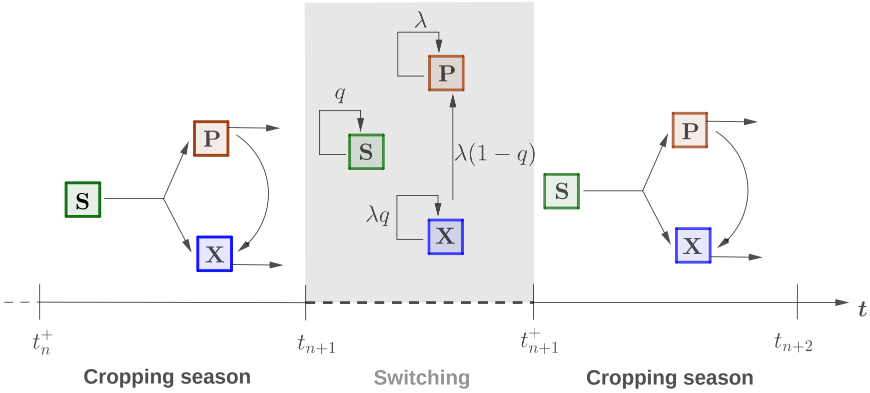


Figure 2: Schematic representation of the course of the plant-pest dynamics over two cropping seasons for the model (2)-(7). On the time axis, plain lines represent the continuous course of time whereas the dotted line represents a discrete time, when switching occurs. Interactions during continuous periods are based on the core model in Figure 1. At the switching, the fresh root biomass (S) is initialized as a fraction q of the biomass inherited from the preceding season, the free nematode population (P) is initialized as the population of free nematodes inherited from the preceding season plus a portion $(1 - q)$ of the infesting nematodes inherited from the preceding season, all with a survival rate λ to the instantaneous action of the nematicide. The infecting nematode population (X) is initialized as the fraction q of the population of infecting nematodes inherited from the preceding season, with a survival rate λ to the instantaneous action of the nematicide.

completed. The season duration is hence $D+\tau$ and the starting point of the (n+1)-th season $t_n = n(D+\tau)$.

- At the beginning of each cropping season, a pest-free vitroplant is planted [11]. The initial condition $X(0^+)$ of system (2) becomes $X_0 = 0$. Moreover, $S(t_n^+) = S_0$ and $X(t_n^+) = 0$.
- At the end of a cropping season, *i.e.* at $t = t_n + D$, the plant is uprooted. Since uprooting is imperfect, so we assume that a fraction r of the roots remains in the soil and constitutes the old root pool, in which the nematodes Y are uniformly distributed. This leads to the following switching rule for $n \in \mathbb{N}^*$:

$$\begin{cases} P(t_{n-1}+D^+) = P(t_{n-1}+D), \\ S(t_{n-1}+D^+) = 0, \\ X(t_{n-1}+D^+) = 0, \\ Y(t_{n-1}+D^+) = rX(t_{n-1}+D). \end{cases} \tag{8}$$

  As we have assumed that the infesting pests (Y) in the old root pool instantaneously turn into free pests (P), we can rewrite the previous switching rule (8) as follows:

$$\begin{cases} P(t_{n-1}+D^+) = P(t_{n-1}+D) + rX(t_{n-1}+D), \\ S(t_{n-1}+D^+) = 0, \\ X(t_{n-1}+D^+) = 0. \end{cases} \tag{9}$$

- In the absence of hosts, during the fallow, free pests undergo an exponential decay [8]:

$$\frac{dP(t)}{dt} = -\omega P(t) \quad \text{for } t \in (t_{n-1}+D, t_n]. \tag{10}$$

Solving equation (10) with the initial condition given by (9) leads to the following transition rule:

$$\begin{cases} P(t_n^+) = \Big(P(t_{n-1}+D) + rX(t_{n-1}+D)\Big)e^{-\omega\tau}, \\ S(t_n^+) = S_0, \\ X(t_n^+) = 0, \end{cases} \tag{11}$$

where S_0 is the size of newly planted pest-free vitro-plant.

The system formed by equations (2) and (11) form the multi-seasonal model with fallow. This is schematically displayed in Figure 3.

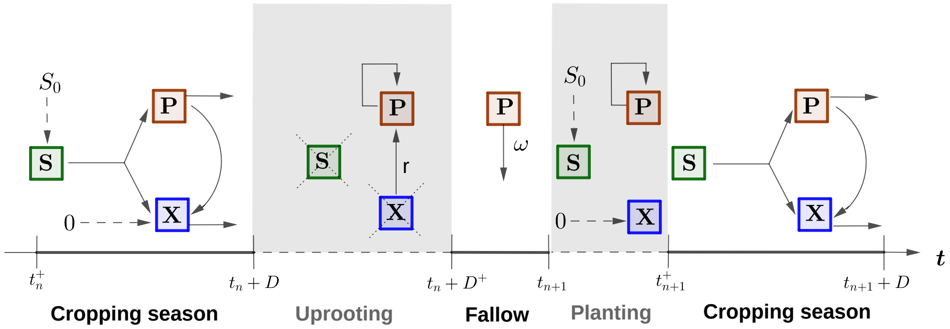


Figure 3: Schematic representation of the course of the plant-pest dynamics from one cropping season to the next. On the time axis, plain lines represent the continuous course of time whereas dotted lines represents discrete instants, where discrete phenomena occur (uprooting, planting). Interactions during cropping seasons are based on the core model in Figure 1. When switching from a cropping season to a fallow period, infecting nematodes convert into free nematodes with a conversion faction r. Crossed-out boxes represent the uprooting, i.e. the fresh root removal. When switching from a fallow period to a cropping season, i.e. planting a new sucker, the fresh root biomass is initialized at S_0 and infesting pest at 0 whereas free pest population stays the same.

2.5. Well-posedness of the problem

Considering system (2) with either the switching rule (7) or (11), the problem is well-posed.

Indeed, each subsystem of system (2) is a well-posed Cauchy problem. The first subsystem has $P = P_0$, $S = S_0$, $X = X_0$ as the initial conditions when

$n = 0$ and the initial conditions are given by (7) or (11) when $n \geq 1$. The second subsystem of system (2) has the value of the solution of its first subsystem as the initial condition. Therefore, since S is bounded and the (P, X) dynamics are linearly bounded, system (2) admits a unique continuous solution on $(t_n, t_n + D]$.

The non-negativity of the trajectories is straightforward and given in Appendix A.

3. Results

The analysis of the two models in the previous section turns out to be very different from the analysis of similar models in the literature [22, 23]. This is because these models are more complex, their non-linearities are stronger and more numerous than those of the models in the literature, and the form of the growth function of the roots brings an additional hybridism to the models. We will reduce the models, at least on the intervals on which the Tychonov theorem holds, in order to obtain local stability results and some thresholds related to this stability.

3.1. Chemical control

In this subsection we consider the system formed by equations (2) and (7) with $t_n = nD$.

Solving the root equation in the absence of pests leads to the following solution:

$$S(t) = \begin{cases} \dfrac{S(t_n^+)K}{S(t_n^+) + (K - S(t_n^+))e^{-\rho(t-t_n)}} & \text{if } \ t \in (t_n, t_n + d], \\ \dfrac{S(t_n^+)K}{S(t_n^+) + (K - S(t_n^+))e^{-\rho d}} & \text{if } \ t \in (t_n + d, t_{n+1}] \end{cases} \tag{12}$$

such that:

$$S(t_{n+1}^+) = q \frac{S(t_n^+)K}{S(t_n^+) + \big(K - S(t_n^+)\big)e^{-\rho d}}. \tag{13}$$

If $S(t_{n+1}^+) < S(t_n^+)$ then the root biomass will decrease over time even if there is no pest. In order to avoid such unrealistic scenario, for small $S(t_n^+)$, we want $S(t_{n+1}^+) > S(t_n^+)$, that is:

$$q > e^{-\rho d} + \frac{S(t_n^+)}{K}\big(1 - e^{-\rho d}\big),$$

which is satisfied for small enough $S(t_n^+)$ when:

$$q > e^{-\rho d}. \tag{14}$$

Under condition (14), the discrete system (13) will be stabilized around the equilibrium S_0^* whose expression is given by:

$$S_0^* = \frac{K(q - e^{-\rho d})}{1 - e^{-\rho d}}$$

and upon which a periodic Pest Free Solution (PFS) of system (2,7) is built.

Generally, in the presence of host plants, the size of the *R. similis* population is very small [38, 39, 40, 41]. In this modelling, this can be interpreted as a high infestation rate, leading to the fast convergence of the free pest level to zero.

The following proposition allows us to reduce the order of the first subsystem of (2) by assuming that the infestation rate β is large and by using singular perturbation theory for the slow-fast dynamics [42].

Proposition 3.1. *Assuming that the primary infestation β is large and considering the state variable $N = P + X$, the first subsystem of (2) can be approximated by the following Rosenzweig-MacArthur model [43] on the $(t_n, t_n + d]$ intervals:*

$$\begin{cases} \dfrac{dS}{dt} = \rho S\Big(1 - \dfrac{S}{K}\Big) - a\dfrac{SN}{S+\Delta}, \\ \dfrac{dN}{dt} = \alpha a\dfrac{SN}{S+\Delta} - \mu N, \end{cases} \tag{15}$$

with initial conditions $S(0^+) = S_0$, $N(0^+) = P_0 + X_0$, $S(t_n^+) = S_0$ and $N(t_n^+) = P(t_n^+) + X(t_n^+)$.

The proof is given in Appendix B.

Remark 3.1. *According to this proposition, the number of free pests is null in the reduced first subsystem. This is a good approximation when β has a high value. Thus, we are going to consider that the second second subsystem of (2)* *starts with a free pest population* $P = P(t_n + d) = 0$ *and an infesting pest population* $X = N(t_n + d)$.

Figure 4 illustrates the dynamics of the reduced system (15) over the root 245 growing period, and how it initializes the full model on the fruit growing period.

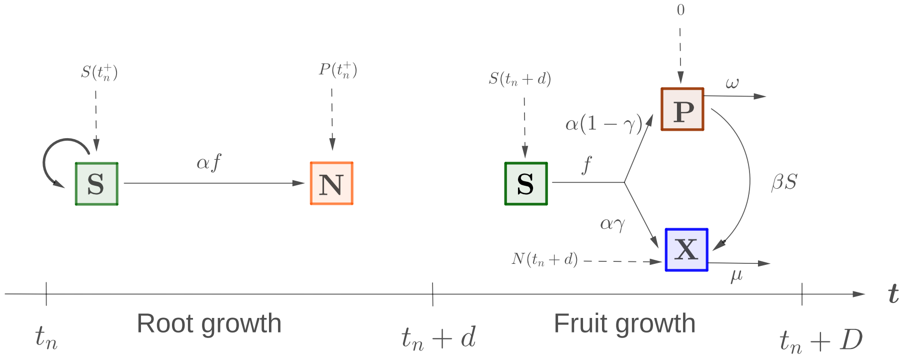


Figure 4: Schematic representation of the reduced model, with first subsystem of model (2) reduced into model (15). During the root growing period, the system is reduced to a Rosenzweig-MacArthur model where the population of free nematodes is null, and the state variable N represents the sum of nematodes populations that stands for the population of infesting nematodes.At the flowering $t_n + d$, the nematode population from the end of the root growing period becomes the pest population at the start of fruit growing period, whereas the population of free nematodes is initialized as zero. The circled arrow represents the growth of fresh roots (S) that is effective before the flowering and null after, during the fruit growing period.

We can obtain the analytical solution of the reduced system (15) linearised around the pest free solution thanks to the following proposition.

Proposition 3.2. *For* $q > e^{-\rho d}$*, the periodic pest free solution of system (2,7) is:*

$$S^*(t) = \begin{cases} \dfrac{S_0^* K}{S_0^* + (K - S_0^*)e^{-\rho(t-t_n)}} & \textit{if} \;\; t \in (t_n, t_n + d], \\ \dfrac{S_0^* K}{S_0^* + (K - S_0^*)e^{-\rho d}} & \textit{if} \;\; t \in (t_n + d, t_{n+1}]. \end{cases} \tag{16}$$

Moreover, the following results hold:

- *For all $n \in \mathbb{N}$, the solution of equations (15) linearised around the pest-free solution for $t \in (t_n, t_n + d]$ is given by:*

$$N(t) = \big(P(t_n^+) + X(t_n^+)\big)\ \exp\left(-\mu(t \bmod D) + \int_{t_n}^{t} \frac{\alpha a S^*(\tau)}{S^*(\tau) + \Delta} d\tau\right), \quad (17)$$

$$\begin{aligned} S(t) = S^*(t) + &\left[\int_{t_n}^{t} -F(\xi) \exp\left(-\int_{t_n}^{\xi} \rho\Big(1 - \frac{2S^*(\tau)}{K}\Big) d\tau\right) d\xi + \tilde{S}(t_n^+)\right] \\ &\times \exp\left(\int_{t_n}^{t} \rho\Big(1 - \frac{2S^*(\tau)}{K}\Big) d\tau\right), \end{aligned} \quad (18)$$

where $F(t) := \frac{aS^*(t)}{S^*(t)+\Delta}\tilde{N}(t)$ and $\tilde{S}(t_n^+) = S(t_n^+) - S_0^*$.

- *For all $n \in \mathbb{N}$ and $t \in (t_n + d, t_n + D]$, there exists a matrix $\Pi(t)$, detailed in Appendix C, such that:*

$$\begin{pmatrix} P(t) \\ X(t) \end{pmatrix} = \Pi(t \pmod D) - d). \begin{pmatrix} 0 \\ N(t_n + d) \end{pmatrix}$$

and

$$S(t) = S^*(t) - a\frac{S(t_n + d)}{S(t_n + d) + \Delta} \int_{t_n+d}^{t} X(\tau) d\tau + \big[S(t_n + d) - S^*(t_n + d)\big],$$

where $S(t_n + d)$ is obtained from (18).

The proof is given in Appendix C.

We can finally use Proposition 3.2 to study the discrete dynamics of the total pest population $N(t_n^+)$ in the neighbourhood of the pest free solution. This leads to the computation of the seasonal effective reproduction number $\mathcal{R}$, which corresponds to the quantity of free pest at the beginning of a season produced by a single free pest at the beginning of the previous season, in a pest-free context under control measures [22, 44] . If this number is larger than 1, pests tend to persist over time. If it is smaller, pests tend to decline. These results are given in the following proposition whose proof appears in Appendix D.

Proposition 3.3. *Pest persistence and effective reproduction number* $\mathcal{R}$

1. *For all* $n \in \mathbb{N}$*, the discrete pest dynamics in the neighbourhood of the pest free solution are defined by:*

$$N(t_n^+) = (\lambda\theta)^n N_0, \tag{19}$$

where:

$$\theta = \big(\Pi_{1,2}(D-d) + \Pi_{2,2}(D-d)\big)e^{-\mu d + \displaystyle\int_0^d \frac{\alpha a S^*(\tau)}{S^*(\tau)+\Delta}d\tau},$$

$N_0 = P_0 + X_0$*,* S^* *is given by equation 16, and the* $\Pi_{i,j}$ *are the inputs of the matrix* Π *defined in Appendix C.*

2. *The effective reproduction number is given by:*

$$\mathcal{R} = \lambda\theta. \tag{20}$$

3. *The pest free solution is locally asymptotically stable for nematode survival rate to pesticide load* $\lambda < \lambda_0$*, with:*

$$\lambda_0 = \frac{1}{\theta} \tag{21}$$

Proposition 3.3 shows that the effective reproduction number depends on the nematode survival rate to pesticide load λ. Thereby, if this number is greater than the threshold λ_0, the effective reproduction number will be greater than 1 and the population or *R. similis* will persist over time; otherwise this population undergoes a decline. We are going to illustrate this numerically.

Numerical simulations

In these simulations, we first show how well the reduced system (15) approximates the first subsystem of equation (2). Then, we illustrate the pest behaviour in the reduced model, in terms of persistence or decline, according to the values taken by λ and $\mathcal{R}$ on both sides of their critical values.

Most parameters were set to realistic values obtained from experimental studies in the literature and are given in Table 1. However, some parameters cannot be easily measured and were estimated indirectly:

- The consumption rate a of *Radopholus similis* is evaluated from the size, and therefore the mass, of a single pest [45]. Given the value of this consumption rate, the consumption efficiency α and the half-saturation constant Δ are evaluated in order to keep an appropriate range of pest population over the time.
- The growth rate of roots ρ is chosen such that, when there is no pest, the roots almost reach their maximum biomass at the end of their growing period.

Generally, infestation is about $[400, 51400]$ nematodes per 100 g of roots [50]. However in this work, in order to compare the two strategies exposed, we consider that both studies begin with a pest-free sucker $X_0 = 0$ and a rather large value of nematodes in the soil $P_0 = 100$.

In Figure 5, we first compare, over a single cropping season, the full model described by equation (2) and the reduced model defined by equation (15) combined to the second subsystem of (2), according to several values of parameter β ranging from 0.001 to 1. As expected, the reduced system approximates the full model better when β gets larger. $\beta = 0.1$ leads to a very good approximation.

We hence set $\beta = 0.1$ for the remaining simulations. With this parameter value and the other parameter values given in Table 1, the critical threshold for the nematode survival rate to pesticide load is $\lambda_0 = 0.01$. Figure 6 illustrates the pest dynamics when the λ survival rate λ varies:

(a) A small value of the effective reproduction number $\mathcal{R} = 0.1$ is obtained when $\lambda = 0.001 \ll \lambda_0$. It leads to a very fast decline of the pests since $\mathcal{R} \ll 1$.

(b) A value $\mathcal{R} = 0.9$ close to but less than 1 is obtained when $\lambda = 0.009 < \lambda_0$. It leads to a slower decline of the pests.

(c) A value $\mathcal{R} = 1.1$, obtained when $\lambda = 0.011 > \lambda_0$, induces pest persistence. Nematodes first steadily decrease and then persist with small oscillations. No nematode eradication is achieved.

Param.	Description	Literature values	Value (s)
d	Duration of the roots growth	210-240 days (Berangan), 180-210 days (Cavendish) [46]	210 days
D	Duration of the cropping season	$300-360$ days [46]	330 days
β	Infestation rate	\	1, 10^{-1}, 10^{-2}, 10^{-3}
K	Maximum roots biomass	≥ 143 g [47]	150 g
ρ	Roots growth rate	\	0.025 day^{-1} (1)
ω	Mortality rate of free pests	0.0495 day^{-1} [48]	0.0495 day^{-1}
μ	Mortality rate of infested pests	$0.05-0.04$ day^{-1} [49]	0.045
a	Consumption rate	magnitude 10^{-4} g (2) [45]	2.10^{-4} g.day^{-1}
α	Conversion rate of ingested roots	\	400 g^{-1} (3)
Δ	Half-saturation constant	\	60 g (3)
γ	Proportion of pests laid inside	\	0.5
q	Proportion of roots forming the new sucker	\	1/3 (4)
r	Proportion of roots forming the old pool after uprooting	\	5% (5)
S_0	Initial root biomass	60 g [47]	60 g (6)
P_0	Initial soil infestation	small [39, 41, 40, 38]	100
X_0	Initial roots infestation	0 [11]	0

(1) ρ is estimated such that $S(d) \simeq K$.

(2) The magnitude of a is evaluated from the size of *R. similis*.

(3) α and Δ are estimated to maintain a sensible population size.

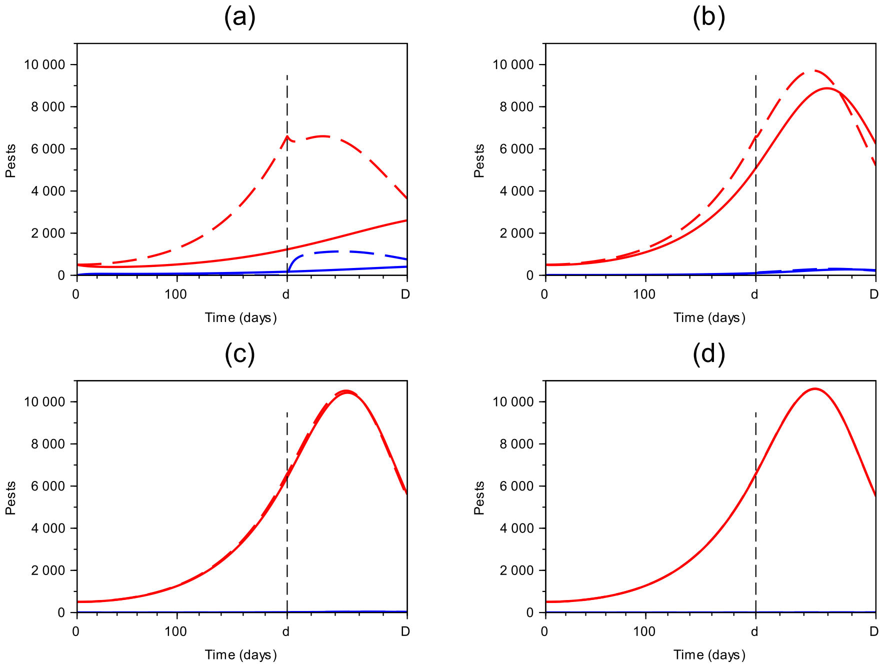
(4) The proportion q of the maximum biomass is close to the pest survival critical level;

(5) We assume that the uprooting is carefully done.

(6) The initial root biomass corresponds to the sucker survival critical level.

\ No data available in the literature.

Table 1: Parameter values used in model simulations

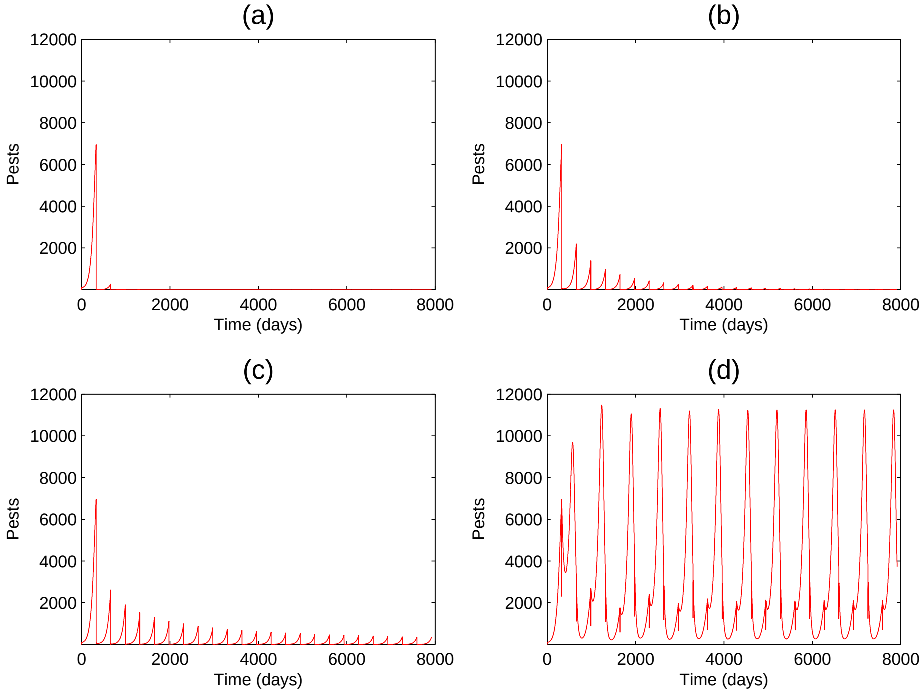


(a) $\beta = 0.001$; **(b)** $\beta = 0.01$; **(c)** $\beta = 0.1$; **(d)** $\beta = 1$.

Figure 5: Pest population evolution over a single cropping season for different values of the infestation rate β. The infesting pests (red lines) and the free pests (blue lines) are represented for the full model (2) (plain lines) and the reduced model (15) (dashed lines). Paramater values are given in Table 1.

(d) When the nematicide is not applied $\lambda = 1 \gg \lambda_0$. The effective reproduction number takes its larger possible value $\mathcal{R} = \mathcal{R}_0 = 97.7 \gg 1$. This value of $\mathcal{R}$ is realistic in this multi-seasonal formalism, as it measures the average number of pests that a single pest, introduced at the beginning of a season in a pest-free context, produces for the following season. Indeed, a nematode of the species *R. similis* has a life cycle of 21 days and a single female produces about 18 larvae (hatched eggs) during its life cycle [51]. Throughout a cropping season that lasts until 330 days, several generations of descendants follow each other, and surviving descendants produce each about 18 larvae. Without control, a single original pest can therefore produce a huge number of pests. The saturation of resources (roots) is the reason why exponentially high numbers are not reached. The pests persist with large oscillations and a doubled periodicity that we analyse in Figure 7. A periodicity over two periods arises. A first season starts with a large root biomass (t_5), which allows an explosion of pests that ravage the root in the second half of the season. A second season (t_6) therefore starts with a much lower root biomass, which prevents the quick development of nematodes during the first part of the season and therefore gives a large root in the second half of the season; which in turn will favour the explosion of nematodes. And so on.

These simulations show that the nematicide needs to destroy more than 99% of the pests at the beginning of each season to lead to their disappearance over time. Besides the fact that nematicides are harmful for the environment, studies show that most nematicides cannot reach such an efficacy. While a very efficient nematicide like tannic acid can have an efficient mortality rate that goes up to 94% in a "kind" soil like fine sand [52], Fenamiphos can only reach a mortality of 77% in *in vitro* tests, and high dosages of the biological nematicide "ABG-9008" barely reach a mortality of 70% [53]. It therefore appears that, in case of a single application per season, nematicides can only provide a partial remedy in terms of nematode control but cannot result in complete pest eradication.



(a) $\lambda = 0.001$ and $\mathcal{R} = 0.1$; **(b)** $\lambda = 0.009$ and $\mathcal{R} = 0.9$; **(c)** $\lambda = 0.011$ and $\mathcal{R} = 1.1$; **(d)** $\lambda = 1$ and $\mathcal{R} = 97.7$.

Figure 6: Infesting pest dynamics of model (2) - (7) over several cropping seasons for different values of λ. The infestation rate is $\beta = 0.1$, so that the reduced model approximates the full model well. Remaining parameter values are given in Table 1, leading to the threshold value $\lambda_0 = 0.010$ defined in equation (21).

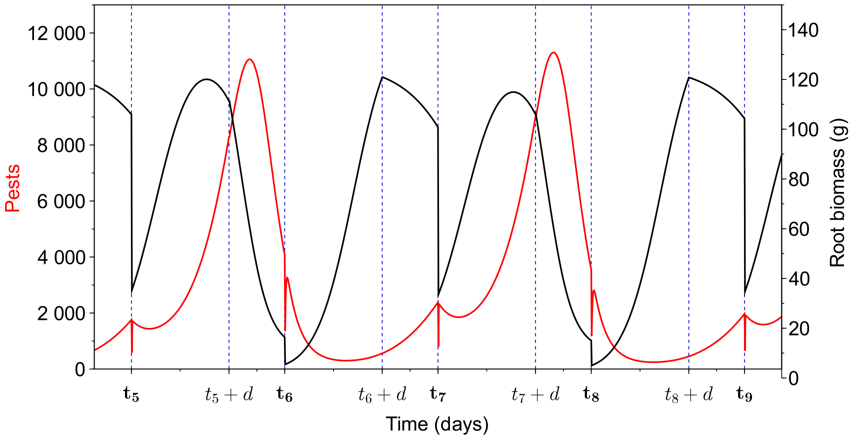


Figure 7: Pest-root dynamics over four seasons without chemical control ($\lambda = 1$) of model (2) - (7). At the beginning t_i of each season, root biomass grows until either the growth stops (at $t_i + d$) or the pest populations are so high that they overeat the roots. The jumps in the root dynamics at t_i are due to the switch (7), where a portion of the root pool of the parent plant turns into a pool of old roots that die quickly by senescence. The remaining portion represents the root pool of the sucker from which the new plant grows. The jumps in the pest dynamics are also due to the switch (7), with in particular a proportion of the infesting pests which become free pests because of the senescence of the part of the roots they are in. The level of infesting pests goes up very quickly because the free pests return quickly in the fresh roots, since β is high.

In case of multiple applications, plant growth is strongly impacted. Indeed, pesticides reduce the symbiotic efficiency of nitrogen-fixing bacteria and host plants [54] and plants use fixed nitrogen (ammonia) to synthesize proteins. It is therefore necessary to study a more environment-friendly and possibly more efficient mean of control.

In the next section, we replace the pesticide by crop rotation with non-host plants or fallows.

3.2. Sufficient fallow deployment

In this subsection we study the system formed by equations (2) and (11). We remind that t_n, the starting point of the $(n+1)$-th season, here has the value $t_n = n(D+\tau)$; where τ stands for the duration of the fallow. Since the new-planted suckers are assumed to be pest-free, it seems coherent that here $X(0^+) = 0$.

Through this section, we are going to present significant results that will bring us to the computation of a threshold duration τ_0 of the fallow. The tropical character of the banana cultures gives us an important freedom for this fallow duration as synchronization with seasonality is not required.

The system (2,11) admits the following periodic pest free solution:

$$\bar{S}(t) = \begin{cases} \dfrac{S_0 K}{S_0 + (K - S_0)e^{-\rho(t-t_n)}} & \text{if } \ t \in (t_n, t_n + d] \\ \dfrac{S_0 K}{S_0 + (K - S_0)e^{-\rho d}} & \text{if } \ t \in (t_n + d, t_n + D] \\ 0 & \text{if } \ t \in (t_n + D, t_{n+1}] \end{cases} \tag{22}$$

As in subection 3.1, we reduce the first subsystem of equation (2) to a Rosenzweig-MacArthur model, by introducing a new state variable $N = P + X$ that represents the total number of nematodes and using the singular perturbation theory, to obtain equation (15) on $(t_n, t_n + d]$ intervals with this time the initial conditions $S(t_n^+) = S(0^+) = S_0, \ N(t_n^+) = P(t_n^+), \ N(0^+) = P_0$.

The reduced system admits the same pest free solution. With this knowledge, we can obtain the solutions of the reduced system of (2) - (11) on $(t_n, t_n+d]$

intervals, linearised around the pest free solution. The following proposition gives such result:

Proposition 3.4.

- *For all $n \in \mathbb{N}$, the reduced equation (15), with initial conditions $S(t_n^+) = S(0) = S_0$, $N(t_n^+) = P(t_n)$, $N(0^+) = P_0$, linearised around the pest free solution (22), admits for $t \in (t_n, t_n + d]$ the solution:*

$$N(t) = P(t_n^+) \exp\left(-\mu(t \bmod (D+\tau)) + \int_{t_n}^{t} \frac{\alpha a \bar{S}(\tau)}{\bar{S}(\tau) + \Delta} d\tau\right) \tag{23}$$

$$\begin{aligned} S(t) = {} & \bar{S}(t) - \int_{t_n}^{t} F(\xi) \exp\left(-\int_{t_n}^{\xi} \rho\left(1 - \frac{2\bar{S}(\tau)}{K}\right) d\tau\right) d\xi \\ & \times \exp\left(\int_{t_n}^{t} \rho\left(1 - \frac{\bar{S}(\tau)}{K}\right) d\tau\right). \end{aligned} \tag{24}$$

- *For all $n \in \mathbb{N}$ and $t \in (t_n + d, t_n + D]$.*

  There exists a matrix $\Pi(t)$ detailed in Appendix C such that:

$$\begin{pmatrix} P(t) \\ X(t) \end{pmatrix} = \Pi\big(t \pmod{D+\tau} - d\big) . \begin{pmatrix} 0 \\ N(t_n + d) \end{pmatrix} \tag{25}$$

  and

$$S(t) = \bar{S}(t) - a \frac{S(t_n + d)}{S(t_n + d) + \Delta} \int_{t_n + d}^{t} X(\tau) d\tau + \big[S(t_n + d) - \bar{S}(t_n + d)\big], \tag{26}$$

  Where $S(t_n + d)$ is obtained from (24).

Proof.

The proof is the same as for Proposition 3.2, setting initial conditions X^+ to 0 and $\tilde{S}(t_n^+) = S_0 - S_0 = 0$.

The solution given by Proposition 3.4 is used to initialise the second subsystem of equation (2), from which we compute the effective reproduction number of the pest and the minimal duration τ_0 of fallow that leads to the decline of pests. That is the aim of the following proposition whose proof is given in Appendix E.

Proposition 3.5. *(Pest eradication)*

We have the following results:

1. *For all $n \in \mathbb{N}$, the discrete pest dynamics in the neighbourhood of the pest free solution is defined by:*

$$P(t_n^+) = P_0 e^{-n\omega\tau} \theta^n \big[\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big]^n, \tag{27}$$

where

$$\theta = \exp\left(-\mu d + \int_0^d \frac{\alpha a \bar{S}(\tau)}{\bar{S}(\tau)+\Delta} d\tau\right).$$

2. *The effective reproduction number is given by:*

$$\mathcal{R} = e^{-\omega\tau}\theta\big[\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big]. \tag{28}$$

3. *The pest free solution is locally asymptotically stable for fallow durations $\tau > \tau_0$, with:*

$$\tau_0 = \frac{ln\Big(\big[\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big]\theta\Big)}{\omega}. \tag{29}$$

In Proposition 3.5, equation (28) shows that the effective reproduction number $\mathcal{R}$ depends exponentially negatively on the duration τ of the fallow periods. Thereby, the larger the value of τ, the smaller the value of $\mathcal{R}$. When τ is greater than the threshold τ_0 given by equation (29), $\mathcal{R}$ will be smaller than 1 and the pests will decline. Whereas when τ is below the threshold τ_0, $\mathcal{R}$ will be greater than 1 and the pest will persist. We are going to illustrate this numerically.

Numerical simulations

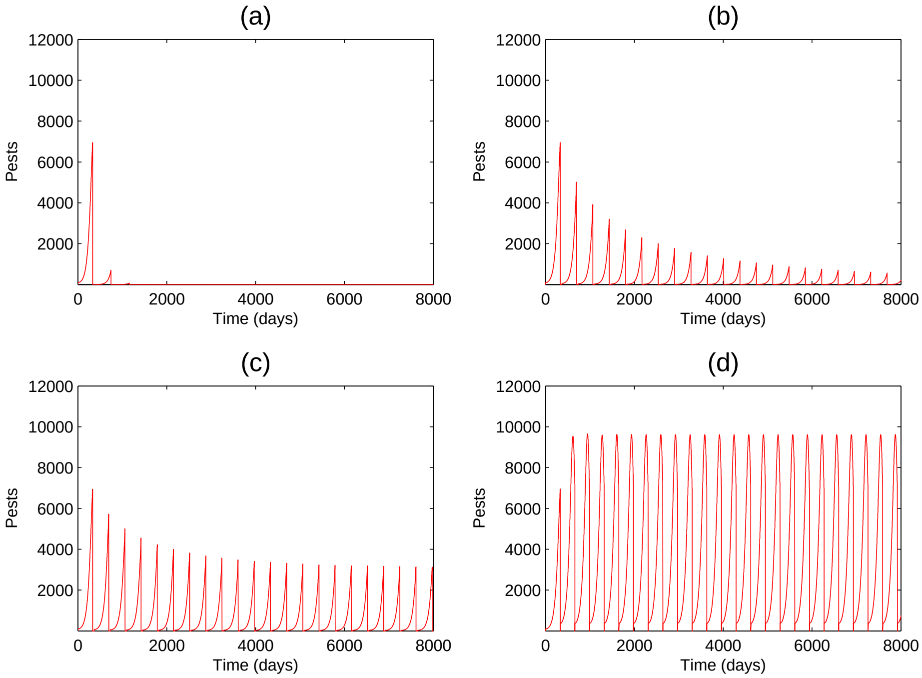
As in Subsection 3.1 $\beta = 0.1$, so that the reduced system (15) approximates well the first subsystem of (2) such that the results of Proposition 3.5 are accurate for both. We consider the system (2,11).

We illustrate the behaviour of the population of nematodes, in terms of persistence or decline, according to the values taken by τ and $\mathcal{R}$ on both sides of the critical values $\tau = \tau_0$ and $\mathcal{R} = 1$.

The parameter values are given in Table 1. With these parameters, the critical duration of fallow is $\tau_0 = 36.79$ days. In Figure 8, four results are illustrated: (a) A high duration of fallow $\tau = 83.3$ days leads to a small effective reproduction number $\mathcal{R} = 0.1 \ll 1$. The pests therefore decline rapidly. (b) When the fallow period is set to $\tau = 38.92$ that remains higher than the threshold τ_0, the effective reproduction number $\mathcal{R} = 0.9$ is larger but remains less than 1. The pests decline more slowly. (c) When $\tau = 34.86$ days $< \tau_0$, the effective reproduction number takes the value $\mathcal{R} = 1.1 > 1$ that leads to the persistence of pests. (d) The highest value of the effective reproduction number, that is the basic reproduction number $\mathcal{R} = \mathcal{R}_0 = 6.18$, is obtained when there is no fallow ($\tau = 0$) and leads to the persistence of the pests with regular oscillation of their population.

It is well known that semi-discrete equations can give rise to periodic or oscillating solutions when modelling epidemics [55, 56]. Oscillations in Figure 8 can find a biological meaning since populations of *R. similis* also show oscillating behaviour in empirical studies. Indeed, some authors have shown that *R. similis* nematode populations on a banana plant can vary over time in line with banana root dynamics and the stage of the parent plant; nematode populations grow until banana flowering, are constant during inflorescence development, and are stable after bunch harvest [57, 58, 59, 60]. We would have preferred to find, in the simulations, intervals during which the populations are more or less constant, but it is not a feature of our model.

These simulations and the computed value of τ_0 show that for a reasonable 37 fallow days after each cropping season, the tendency of the pest population is the decline. In addition to being more environmental-friendly, controlling *R. similis* by deploying fallows also seems easier to implement than chemical control. Indeed, the latter requires the eradication of more than 99% of the nematodes each time the nematicide is used. Moreover, the use of fallow leads to a smaller highest possible value $\mathcal{R} = 6.18$ of the effective reproduction number, compared to the value $\mathcal{R} = 97.7$ obtained with chemical control. This huge difference can be easily explained by the size of pests reservoir. Indeed, in



(a) $\tau = 83.3$ and $\mathcal{R} = 0.1$; **(b)** $\tau = 38.92$ and $\mathcal{R} = 0.9$; **(c)** $\tau = 34.86$ and $\mathcal{R} = 1.1$; **(d)** $\tau = 0$ and $\mathcal{R} = 6.18$.

Figure 8: Infesting pest dynamics of model(2)-(11) over several cropping seasons for different values of τ. The infestation rate is $\beta = 0.1$, so that the reduced model approximates the full model well. Remaining parameter values are given in Table 1, leading to the threshold value $\tau_0 = 36.79$ defined in equation (29).

the case of deployment of fallow, only a few root tips constitute the reservoir of pests (portion $r = 5\%$) between cropping seasons, whereas a whole pool of roots inherited from the parent plant constitutes the reservoir of pests when there is no fallow (portion $1 - q = 2/3$).

4. Discussion

We found in the literature only one study of *R. similis* populations with or without the use of nematicide [17]. The model has been named SIMBA-NEM, and showed that population-related parameters (limit capacities, growth rates) have a large impact on the population of *R. similis*, while in contrary, the parameters related to the use of pesticides had a little impact. This remark does not contradict our conclusion of Subsection 3.1, where it has been noted that large quantities of nematicide were needed to significantly reduce the infestation. SIMBA-NEM is a population model based on the cohort structure, which describes different stages of the nematode life cycle. As a result, it is a discrete and computational model that pioneers pest dynamics in cropping system models.

However, SIMBA-NEM being computational, it has no analytic result or qualitative description and its outputs and conclusions strongly depend on the value of the parameters and precision in their estimation, which often requires extensive data [61]. But we have not found in the literature quantitative studies that count nematodes by sorting them by age, stage or cohort; possibly because it is difficult to set up this type of experiment for microscopic worms. Also, the model does not allow fallowing or crop rotation with non-host plants, whereas it has been shown empirically that these are effective strategies to fight the spread of R. similis [11, 6, 8].

The crop rotation models presented in our introduction [13, 14, 15] are not adapted to the dynamics of *R. similis* because the studied pests have different life cycles and sometimes different hosts that have different symptoms of the infestation. Also, since *R. similis* does not have a large diffusive spread in the soil [62], a spatially explicit model is not necessary when studying its dynamics. However, knowing that the spread of *R. similis* is mainly by water [62, 63], it might be interesting to study its spatial dynamics in highly irrigated environments. In this case, we can rely on excellent preliminary work found in reference [16].

The analysis of plant-pest dynamics subjected to interruptions is not new. Gubbins and Gilligan have studied the persistence of continuous plant-parasite systems in discrete disturbed environments [20]. The semi-discrete formalism has also been studied for SEIR models [21] and many other plant epidemic or more general dynamics including seasonality (see [19]). More precisely, a general framework for soilborne parasite models has been given by Mailleret et al. [22] and Hamelin et al. [23].

But those models remains general frameworks not precisely related to the dynamics of *R. similis*. For instance, they do not interrupt root growth after the flowering of the plant, giving rise to an additionnal switching within the continuous dynamics of the cropping season. Moreover, in such models, the specific off-season (e.g. winter) during which hosts lack has a fixed size that cannot be manipulated in order to control the pest. As the geographical area we analyse in Subsection 3.2 of this paper has a tropical climate that is well-suited for banana growing all year long, it does not suffer fixed-sized and fixed-distributed off-season. We can handle the size of such off-season that correspond here to a fallow. In this way, we differentiate from previous works, and therefore can see the effective reproduction number $\mathcal{R}$ under a new perspective. Indeed, it is now correlated with a threshold size τ_0 of the off-season, around which the pest dynamics show different behaviours.

This work was done after having reduced the model using singular perturbations, by considering that the infestation rate was markedly high, which satisfies biological observations [38, 39, 40, 41]. We then compared the pest population dynamics for different values of the infestation rate (Figure 5). For high enough values, the reduced model is an excellent approximation of the full model, as shown for instance in Figure 5 (c) for $\beta = 0.1$. However, for lower values such as $\beta = 0.001$ illustrated in Figure 5 (a), the approximation does not hold and the full model should be used.

5. Conclusion and future work

Our work proposes a multi-seasonal framework which describes the infestation of banana (or plantain) roots by the burrowing nematode *R. similis*. In this work, we have studied two semi-discrete models based on impulsive ordinary differential equations, where the feeding of the pests has a saturated response. In both models, pests have two living stages: a free stage in the soil and an infesting stage in the roots. The difference between the two models lies in their control method: the first one includes the use of pesticides while the second one relies on fallow periods between seasons. We were able to provide local stability results for these new models, to compute effective reproduction numbers and link them to biological thresholds, while managing well the difficulties related to a step root growth function.

The two models bring out an obvious similarity: whether we use pesticides or fallows, the infestation can be reduced by playing on the thresholds that are related to the effective reproduction number. In the first model, it relies on the increase of the pesticide dosage, while in the second model it requires the increase of the duration of the fallows between cropping seasons. However, we have shown that chemical control is not very effective. Indeed, the required pesticide efficiency which results from our computations and the value of our parameters is barely achieved in realistic environments, and would require large amounts of pesticide. The fallow deployment model has also allowed us to find an oscillation behaviour of nematode populations as found in the literature.

However, the two models showing similarities in study and pest management, both of them present implementation issues due to different factors:

(i) The first model implies the use of pesticides which have harmful ecological impact [5] and the nematode can evolve to develop resistance to their application. Besides, the effect of phytotoxicity of such pesticides has been identified in practice [64], but has not been included in our model yet. Such an effect would certainly eliminate the linearity in the basic pest reproduction number and induce the existence of an intermediate value of λ that minimizes the effective pest reproduction number, with no guarantee that the latter would be smaller than 1. Consideration of phytotoxicity could therefore change the control strategy. Also, nematicides have a cost and increasing the dosage also mean to increase the expense of chemical control.

(ii) The reproduction of the plant in the second model comes exclusively from the use of healthy vitro-plants which each have a financial cost. Hence, the cost of this strategy could be prohibitive for small farmers, while the natural asexual reproduction of the plants by lateral shot is free of cost. Besides, we have shown that long fallow periods reduce significantly the infestation; but long fallow periods can also decrease the number of cropping seasons over a fixed time horizon. The legitimate question is how far the duration of the fallow can be extended and still be accepted by planters? It appears that the development of sustainable strategies for the management and control of plant diseases, in general, requires an understanding of economic and social constraints that influence the deployment of control [65].

(iii) Although our second model has been able to highlight the population oscillations described in the literature, we were not able to obtain a simulation in which the population of *R. similis* seems to be constant during a certain period as observed by some authors [60, 57, 58, 59].

In order to solve issues (i) and (ii), we can think about linking fallow durations to an economical yield to identify optimal fallow deployments. An interest in linking epidemiological with economic modelling arises when there are constraints over the amount of control that can be applied, whether it is chemical, cultural, genetical or biological [65]. Concerning fallow deployment, the control is cultural and is related to the duration of fallow periods between cropping seasons. A constraint arises naturally from this control, since one cannot deploy too large fallow periods in order to maintain a reasonable yield.

The control relies on planting healthy vitro-plant at the beginning of each cropping season. Therefore, finding the optimal control strategy requires estimates for the cost of a healthy vitro-plant and crop yield losses induced by the infestation. An interesting metric to capture the yield of crops in compartmental models has been proposed in the literature [66]. In this metric, the yield depends on the biomass of healthy tissues and a weighting function over the time.

Finally, in order for optimal control strategies to be implemented, the parameters must be well-known. Poorly understood parameters can lead to systematic biases in decision-making and distort control. Unfortunately, we see in Table 1 that many parameters are poorly known, which could question the future results of the optimization described above. To overcome such biases, we can rely on parameter estimation and sensitivity analysis. In case real-time data measurements are possible, we could use a Control Smart Algorithm (CSA) to know whether to wait to collect the data or to implement the control directly with the data as it is available [67]. This may improve the efficiency of our future optimal control models.

Acknowledgement

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Appendix A. Non-negativity of trajectories of models (2)-(7) and (2)-(11)

Lemma 1. *The state variables of system (2) with either switching rule (7) or (11) remain non-negative.*

Proof.

We first consider $n = 0$ and denote by $W = (P, S, X)$ the state vector and by $W(0^+)$ the initial condition. As these state variables represent biological quantities, we set $W(0^+) \geq 0$. The structure of the model then ensures that the state variables remain non-negative in the course of time. Besides, the discrete rules (7) and (11) ensure that if the non-negative orthant is positively invariant for season n, then the initial condition for season $n + 1$ will be positive. Hence, the same conclusion holds for $n \geq 1$.

Appendix B. Proof of Proposition 3.1

Let's consider the first subsystem of equation (1), i.e. $t \in (t_n, t_n + d[$. Let $N = P + X$ and consider the system in (P, S, N).

Assuming that β is large, let $\beta = \frac{\beta'}{\varepsilon}$, $0 < \varepsilon \ll 1$ and $\zeta = \frac{t}{\varepsilon}$. The new time ζ is called *fast time*. The system with derivatives according to ζ is written:

$$\begin{cases} \dfrac{dP}{d\zeta} = -\beta' PS + \varepsilon\alpha a(1-\gamma)\dfrac{S(N-P)}{S+\Delta} - \varepsilon\omega P, \\ \dfrac{dS}{d\zeta} = \varepsilon\rho S\Big(1 - \dfrac{S}{K}\Big) - \varepsilon a\dfrac{S(N-P)}{S+\Delta}, \\ \dfrac{dN}{d\zeta} = \varepsilon\alpha a\gamma\dfrac{S(N-P)}{S+\Delta} + \varepsilon(\mu-\omega)P - \varepsilon\mu N, \end{cases} \tag{B.1}$$

When $\varepsilon = 0$, we then define the *fast equation* by

$$\frac{dP}{d\zeta} = -\beta' PS$$

Which admits an equilibrium $\bar{P} = 0$ that is asymptotically stable because $S > 0$ according to Lemma 1 in Appendix A.

The *slow equation* is written as:

$$\begin{cases} \dot{S} = \rho S\Big(1 - \dfrac{S}{K}\Big) - a\dfrac{SN}{S+\Delta}, \\ \dot{N} = \alpha a \gamma \dfrac{SN}{S+\Delta} - \mu N, \end{cases} \tag{B.2}$$

Which corresponds to a Rosenzweig-MacArthur model. The Tychonov theorem ensures that

$$\lim_{\varepsilon \to 0} P(t,\varepsilon) = 0, \quad t \in (t_n, t_n + d[$$

$$\lim_{\varepsilon \to 0} (S(t,\varepsilon), N(t,\varepsilon)) = (\bar{S}(t), \bar{N}(t)), \quad t \in (t_n, t_n + d[$$

Where $(\bar{S}, \bar{N})$ is the solution of equation (B.2) and $(P(t,\varepsilon), S(t,\varepsilon), N(t,\varepsilon))$ is the solution of the perturbed system:

$$\begin{cases} \varepsilon \dot{P} = -\beta' PS + \varepsilon \alpha a (1-\gamma) \dfrac{S(N-P)}{S+\Delta} - \varepsilon \omega P, \\ \dot{S} = \rho S\Big(1 - \dfrac{S}{K}\Big) - a\dfrac{S(N-P)}{S+\Delta}, \\ \dot{N} = \alpha a \dfrac{S(N-P)}{S+\Delta} + (\mu - \omega) P - \mu N. \end{cases}$$

Appendix C. Proof of Proposition 3.2

- First, in absence of pest, the periodic solution occurs and we have $S(t_n^+) = S_0^*$. The Pest Free Solution is written for all $t \in [0, d]$, $\begin{pmatrix} S^*(t) \\ N^*(t) \end{pmatrix} = \begin{pmatrix} \frac{S_0^* K}{S_0^* + (K - S_0^*)e^{-\rho t}} \\ 0 \end{pmatrix}$,
  with $S_0^* = \frac{K(q - e^{-\rho d})}{1 - e^{-\rho d}}$.

  Considering the deviation variables $\tilde{S} = S(t) - S^*(t)$ and $\tilde{N} = N(t) - N^*(t) = N(t)$, one can write the deviation system as:

$$\begin{cases} \dot{\tilde{S}} = \rho(\tilde{S} + S^*(t))\Big(1 - \dfrac{\tilde{S} + S^*(t)}{K}\Big) - \dfrac{a(\tilde{S} + S^*(t))\tilde{N}}{\tilde{S} + S^* + \Delta} - \rho S^*(t)\Big(1 - \dfrac{S^*(t)}{K}\Big), \\ \dot{\tilde{N}} = \dfrac{\alpha a (\tilde{S} + S^*(t))\tilde{N}}{\tilde{S} + S^* + \Delta} - \mu \tilde{N}, \\ \tilde{S}(0^+) = q\tilde{S}_0, \ \tilde{N}(0^+) = N(0^+) = P_0 + X_0. \end{cases} \tag{C.1}$$

In a neighbourhood of the PFS, the system is equivalent to

$$\begin{pmatrix} \dot{\tilde{S}} \\ \dot{\tilde{N}} \end{pmatrix} = \begin{pmatrix} \rho\Big(1-\dfrac{2S^*(t)}{K}\Big) & -\dfrac{aS^*(t)}{S^*(t)+\Delta} \\ 0 & -\mu+\dfrac{\alpha a S^*(t)}{S^*(t)+\Delta} \end{pmatrix} \cdot \begin{pmatrix} \tilde{S} \\ \tilde{N} \end{pmatrix} \tag{C.2}$$

This leads to the equation in $\tilde{N}$

$$\dot{\tilde{N}} = \Big(-\mu+\frac{\alpha a S^*(t)}{S^*(t)+\Delta}\Big)\tilde{N},$$

whose solution is given by

$$\tilde{N}(t) = \big(P(0^+)+X(0^+)\big)e^{-\mu t+\displaystyle\int_0^t \frac{\alpha a S^*(\tau)}{S^*(\tau)+\Delta}d\tau}.$$

One can now replace this expression in (C.2) and let $F(t) := \frac{aS^*(t)}{S^*(t)+\Delta}\tilde{N}(t)$ to obtain the equation in $\tilde{S}$:

$$\dot{\tilde{S}} = \rho\Big(1-\frac{2S^*(t)}{K}\Big)\tilde{S}(t) - F(t), \qquad \tilde{S}^+(0) = q\tilde{S}(0).$$

This leads to the solution

$$\tilde{S}(t) = \Big[\int_0^t -F(\xi)\exp\Big(-\int_0^\xi \rho\big(1-\frac{2S^*(\tau)}{K}\big)d\tau\Big)d\xi + q\tilde{S}(0)\Big]\times\exp\Big(\int_0^t \rho\Big(1-\frac{2S^*(\tau)}{K}\Big)d\tau\Big)$$

- On $(t_n+d, t_n+D]$, the second subsystem of equation (2) is written:

$$\begin{cases} \dot{P}(t) = -\beta P(t)S(t) + \alpha a(1-\gamma)\dfrac{S(t)X(t)}{S(t)+\Delta} - \omega P(t), \\ \dot{S}(t) = -a\dfrac{S(t)X(t)}{S(t)+\Delta}, \\ \dot{X}(t) = \beta P(t)S(t) + \alpha a\gamma\dfrac{S(t)X(t)}{S(t)+\Delta} - \mu X(t). \end{cases} \tag{C.3}$$

With initial conditions $P(t_n+d^+) = 0$, $X(t_n+d^+) = N(t_n+d)$ and $S(t_n+d^+) = S(t_n+d)$ from the system (15).

The pest free equilibrium (PFE) can be written $Y_P(t) = \begin{pmatrix} P_p(t) \\ S_p(t) \\ X_p(t) \end{pmatrix} = \begin{pmatrix} 0 \\ S^*(d) \\ 0 \end{pmatrix}$. Considering the deviation variables $\tilde{P}(t) = P(t) - P_p(t) =$

$P(t), \tilde{S}(t) = S(t) - S_p(t), \tilde{X}(t) = X(t) - X_p(t) = X(t)$, one can write the equation in the new variables as:

$$\begin{cases} \dot{\tilde{P}} = -\beta \tilde{P}(\tilde{S} + S^*(d)) + \alpha a(1-\gamma)\dfrac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta} - \omega \tilde{P}, \\ \dot{\tilde{S}} = -a\dfrac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta}, \\ \dot{\tilde{X}} = \beta \tilde{P}(\tilde{S} + S^*(d)) + \alpha a\gamma \dfrac{(\tilde{S} + S^*(d))\tilde{X}}{\tilde{S} + S^*(d) + \Delta} - \mu \tilde{X} \end{cases} \tag{C.4}$$

And the Jacobian matrix $J = \begin{bmatrix} -\beta S^*(d) - \omega & 0 & \alpha a(1-\gamma)\frac{S^*(d)}{S^*(d)+\Delta} \\ 0 & 0 & -a\frac{S^*(d)}{S^*(d)+\Delta} \\ \beta S^*(d) & 0 & -\mu + \alpha a\gamma\frac{S^*(d)}{S^*(d)+\Delta} \end{bmatrix}$.

In the neighbourhood of the PFE, system (C.4) is then equivalent to the linearised system

$$\dot{\tilde{Y}} = J.\tilde{Y}, \quad \tilde{Y} = (\tilde{P}, \tilde{S}, \tilde{X}). \tag{C.5}$$

Since the second column of J is null, one just has to compute the exponential of At that will generate a local solution for $\tilde{P}$ and $\tilde{X}$, where $A := \begin{bmatrix} -\beta S^*(d) - \omega & \alpha a(1-\gamma)\frac{S^*(d)}{S^*(d)+\Delta} \\ \beta S^*(d) & -\mu + \alpha a\gamma\frac{S^*(d)}{S^*(d)+\Delta} \end{bmatrix}$.

We deduce $\tilde{S}$ from $\dot{\tilde{S}} = -a\frac{S^*(d)}{S^*(d)+\Delta}\tilde{X}$, i.e.

$$\tilde{S}(t) \quad = \quad -a\tfrac{S^*(d)}{S^*(d)+\Delta}\int_0^d \tilde{X}(\tau)d\tau + \tilde{S}(d).$$

And so one for each season, assuming the trajectories remain close enough to the PFS. Since A is a Metzler matrix, it admits two distinct real eigenvalues $\lambda_{1,2} = \frac{tr(A)}{2} \pm \frac{1}{2}\sqrt{tr^2(A) - 4det(A)}$ and we have $\Pi(t) = \begin{pmatrix} \Pi_{1,1}(t) & \Pi_{1,2}(t) \\ \Pi_{2,1}(t) & \Pi_{2,2}(t) \end{pmatrix}$, where

$$\Pi_{1,1}(t) = \frac{1}{\lambda_2 - \lambda_1}\Big(e^{\lambda_1 t}(\lambda_2 + \beta S^*(d) + \omega) - e^{\lambda_2 t}(\lambda_1 + \beta S^*(d) + \omega)\Big)$$

$$\Pi_{1,2}(t) = -\frac{1}{\lambda_2 - \lambda_1}\Big(\frac{\alpha a(1-\gamma)}{S^*(d) + \Delta}(e^{\lambda_1 t} - e^{\lambda_2 t})\Big)$$

$$\Pi_{2,1}(t) = -\frac{1}{\lambda_2 - \lambda_1}\Big(\beta S^*(d)(e^{\lambda_1 t} - e^{\lambda_2 t})\Big)$$

$$\Pi_{2,2}(t) = \frac{1}{\lambda_2 - \lambda_1}\Big(e^{\lambda_1 t}(\lambda_2 + \mu - \frac{\alpha a S^*(d)}{S^*(d) + \Delta}) - e^{\lambda_2 t}(\lambda_1 + \mu - \frac{\alpha a S^*(d)}{S^*(d) + \Delta})\Big)$$

Appendix D. Proof of Proposition 3.3

1. From Proposition 3.2, when the pests remain in a neighbourhood of the PFS,
$$\begin{pmatrix} P(t) \\ X(t) \end{pmatrix} = \Pi\big(t-(t_n+d)\big).\begin{pmatrix} 0 \\ N(t_n+d) \end{pmatrix}$$
Hence,
$$\begin{array}{rcl} N\big(t_{n+1}\big) & = & P\big(t_{n+1}\big)+X\big(t_{n+1}\big) \\ & = & \big(\Pi_{1,2}(D-d)+\Pi_{2,2}(D-d)\big)N(t_n+d) \\ & = & \big(\Pi_{1,2}(D-d)+\Pi_{2,2}(D-d)\big)N(t_n^+)e^{-\mu d+\displaystyle\int_0^d \frac{\alpha a S^*(\tau)}{S^*(\tau)+\Delta}d\tau} \\ & & (from \;\; equation(17)) \\ & = & \theta N(t_n^+). \end{array}$$
Thus, $N\big(t_{n+1}^+\big)=\lambda\theta N(t_n^+)$
Therefore, $\forall n\in\mathbb{N}$,
$$\begin{array}{rcl} N(t_n^+) & = & (\lambda\theta)^n N(0^+) \\ & = & (\lambda\theta)^n\big(P_0+X_0\big). \end{array}$$
2. Since for $(P_0+X_0)\neq 0$, $N(t_n^+)\longrightarrow 0$ iff $(\lambda\theta)<1$, we deduce $\mathcal{R}=\lambda\theta$.

Appendix E. Proof of Proposition 3.5

1. From equation (23), we have
$$N(t_n+d)=P(t_n^+)e^{-\mu d+\displaystyle\int_0^d \frac{\alpha a\bar{S}(\tau)}{\bar{S}(\tau)+\Delta}d\tau}.$$
Hence, $N(t_n+d)=P(t_n^+)\theta$.

Equation (25) therefore involves
$$\begin{pmatrix} P(t_n+tf) \\ \\ X(t_n+D) \end{pmatrix} = \begin{pmatrix} \Pi_{1,1}(D-d) & \Pi_{1,2}(D-d) \\ \\ \Pi_{2,1}(D-d) & \Pi_{2,2}(D-d) \end{pmatrix}\begin{pmatrix} 0 \\ \\ \theta P(t_n^+) \end{pmatrix}$$
Hence,
$$\left\{\begin{array}{rcl} P(t_n+D) & = & \Pi_{1,2}(D-d).P(t_n^+)\theta \\ \\ X(t_n+D) & = & \Pi_{2,2}(D-d).P(t_n^+)\theta \end{array}\right.$$

So, according to the switching rule (11),

$$P(t_{n+1}^+) = \Big[\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\Big] P(t_n^+)\theta e^{-\omega\tau}$$

From where we deduce

$$P(t_n^+) = P_0 e^{-n\omega\tau}\theta^n \big[\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big]^n.$$

2. Since $P(t_n^+) \to 0$ iff

$$\big(\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big)\theta e^{-\omega\tau} < 1, \tag{E.1}$$

   We deduce $\mathcal{R} = \big(\Pi_{1,2}(D-d) + q\Pi_{2,2}(D-d)\big)\theta e^{-\omega\tau}$.

3. We deduce τ_0 from the condition (E.1) above, by rearranging as $\tau > \frac{ln\Big(\big[\Pi_{1,2}(D-d)+q\Pi_{2,2}(D-d)\big]\theta\Big)}{\omega} \equiv \tau_0$.

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