On the impact of re-mating and residual fertility on the Sterile Insect Technique efficacy: case study with the medfly *Ceratitis capitata*

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Abstract

Sterile insect techniques can be an efficient solution for reducing or eliminating certain insect pest populations. It is widely and efficiently used in agriculture against fruit flies, including the Mediterranean fly, *Ceratitis capitata*. The re-mating tendency of medfly females and the fact that sterile males are often released with slight residual fertility can at first sight appear to be detrimental for the successful implementation of SIT. Obtaining the right balance between sterility level and male quality is the key to a cost-efficient program. Since field experimental approaches can be impacted by many environmental variables, it is difficult to get a clear understanding on how some specific parameters can affect, alone or in combination, the efficacy of sterile males release. The use of models not only helps to gather knowledge, but it also helps simulating different situations scenarii and can be easily adapted to local values from the field population and sterile male production.

In this study, we consider how the minimal release ratio is affected by female re-mating rate (with an equal or higher tendency to re-mating after an insemination by a sterile male) and male residual fertility. Different scenarios were explored: continuous versus periodic releases, with and without ginger aromatherapy, which is known to enhance sterile male competitiveness. Parameters values were chosen from the literature on peach host fruit when available to reflect what could be expected in the Corsican context, for which SIT against the medfly is under consideration. Our results clearly show that low residual fertility is not necessarily detrimental to SIT performance. In contrast, re-mating of wild females provides contrasting results: when re-mating occurs without a change in the refractory period, it is beneficial because it requires the releases of less sterile males. On the other hand, if females mated with a sterile male have a faster re-mating, it is detrimental for the SIT program as the amount of sterile males to release can become too large. We also confirmed that the use of ginger aromatherapy is more than an essential step for SIT success against medfly. Our model can be easily adapted to different context and species, in order to help understanding release strategies and guiding decision making.

1 Introduction

The sterile Insect Technique (SIT) is an old autocidal control method used effectively against several agricultural pests in several countries worldwide. Some of the major operational programs include the Mediterranean fruit fly (Medfly) *Ceratis capitata*. SIT relies on a continuous mass production of the target insect, the sterilization of males (or both males and females, according to the species) as pupae or adults, using ionizing radiation, and their repeated and massive releases in the field that result in a progressive decay of the targeted pest population [17, 24].

For fruit flies, ionizing radiation is mostly used to sterilize males as part of the operational programs. However, a genetically engineered sterile strain of Medfly (*C. capitata*) has been developed and tested for population reduction on a small scale [6]. Other suppression approaches include the incompatible insect technique (IIT), which uses the bacterial endosymbiont Wolbachia [27], has been considered against Medflies [52]. In this study, we considered only the approach based on sterilization with irradiation.

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Conceptually, the Sterile Insect Technique appears to be very simple, but its efficient deployment requires understanding and tailoring several technical, logistical, ecological, and biological parameters, as well as socioeconomic elements [17]. Even if SIT against medflies is widespread (most of South and Central America, USA, Australia, South Africa, etc.), it is only operational in Spain and Croatia for Europe. France is developing an SIT research pilot project to determine the optimal conditions for the deployment of the SIT on Corsica Island to protect stone fruits and clementine production (CeraTIS Corse project). The Mediterranean fruit fly is the dominant fruit fly pest on citrus and deciduous fruit in Corsica; and nowadays treatments still rely mostly on the use of pesticides. The growing demand for more environmentally friendly approaches, together with the potential future unavailability of chemical substances, triggered a pilot research project to integrate SIT in the control strategies. Most Corsica crop fields appear to have challenging initial ecological conditions (high density of flies, crop areas surrounded by rural settings, and wild host plants for medflies). Designing an efficient and cost-effective suppression program will require a good understanding of the biological and technical parameters that can impact its success. As part of this effort, modeling the effect of sterile males' residual fertility, female re-mating and release frequency on release ratios is essential.

SIT impacts the reproduction of the targeted insect; therefore, its success depends on the ability of the released sterile males to find a lek, perform courtship, and attract wild females, successfully copulate and inseminate females with their sterile sperm, while eliciting effective female refractoriness to further re-mating by wild males. Medflies are considered to have a complex courtship behavior that could make SIT less efficient [46] however, the suppression of medflies using SIT is the most widely spread and has proven to be highly efficient and economically viable [18]. Modeling, model analysis, and simulations can be helpful in highlighting how specific parameters may positively or negatively impact the release strategy in the field.

SIT has been modeled since the early work by Knipling [24] in the fifties. Various discrete or continuous models have been developed that are more or less complex, considering different stages according to the pest/vector considered. Many SIT models consider sterile males to be fully sterilized, although this is rarely achieved. Indeed, reaching full sterility requires a very high dose of radiation, which often impairs the quality of males to a level that is not acceptable. However, if males are not fully sterile such that a small percentage of their sperm are still fertile, one could argue that releasing millions of almost-sterile males is equivalent to releasing a certain percentage of fertile males.

Residual fertility is easy to assess and is part of the quality control of every SIT program (interested readers are referred to the manual published by the International Atomic Energy Agency (IAEA) [19] for medfly SIT procedures). The level of sterility chosen during SIT programs is rarely 100% [37], such that a small number of sperm cells can still be fertile and those females can lay a small number of viable eggs. This is what we call residual fertility. For *C. capitata*, a dose of 140Gy is required to achieve full sterility, as in the medfly management program in Argentina [1]; however, this dosage can also negatively affect male performance and therefore be detrimental for SIT operations [44, 30]. On the other hand, in an ongoing operational SIT program against medflies in the region of Valencia, Spain, the induced average sterility reached $98.87 \pm 0.55\%$ with an irradiation dose of 100 Gy, leading to a residual fertility of $1.13 \pm 0.55\%$ [39].

Therefore, it is important to know the limit above which residual fertility can have a negative impact on SIT program performance and how to estimate this upper bound. In a recent study, on a different fruit fly species [5], we investigated this question using a very simple and minimalistic model. The result was straightforward: the percentage of residual fertility (RF), ε, must be lower than $\frac{1}{\mathcal{N}}$, where $\mathcal{N}$ is the basic offspring number, also called the basic reproduction number, which is related to the reproductive potential of the pest population. Clearly, for a wild population with a large $\mathcal{N}$, the constraint on RF can be strong, thereby significantly reducing its acceptable level for successful SIT. A similar result was obtained by Van den Driessche [49] using discrete models. In this study, we explored a more complex and generic model to verify these results, with a particular focus on medfly. Furthermore, we considered the important parameter of re-mating and whether there is a different response when wild females mate with sterile males as opposed to wild males.

Female medflies are facultative polyandrous [10, 12], and field estimations of wild female re-mating rates vary by up to 50% [10]. After mating, medfly females typically exhibit an average refractory period of two and a half days [33]. Their propensity to remate can be triggered by the courtship behavior of the male, sexual performance, and amount of ejaculate transferred [7, 21]. The likelihood of re-mating might (as evaluated under laboratory conditions) increase in situations of availability of oviposition substrate or highly male-biased sex ratios, which is the case of male-only release SIT programs [33, 50]. Medfly females possess 2 spermathecae, spherical organs that store sperm after insemination, and a fertilization chamber that serves as a functional third spermatheca [31]. Having more than one spermathecae could be seen as

advantageous in case of multiple inseminations; however, in most insects, the sperm from different males are mixed within the spermathecae, therefore not physically allowing for preferential selection during egg fertilization. However, the fertilization chamber in medflies allows a second male to remove sperm from the previous one [31]. Sperm precedence of the second male mating a female tends to win in fertilizing eggs (second male contribution greater than 0.5) [28, 10]. Lee et al [28] reported high individual variation in this pattern for medflies, as well as sperm mixing and no effect of the sterility status.

In the present study, we investigated how these two parameters (residual fertility and re-mating) can impact the required release ratios under different situations. Most medfly SIT programs involve biweekly releases, some with daily releases. Although release frequency has a direct impact on a program cost, it is useful to understand how it is affected by biological parameters. Moreover, as most programs have implemented the addition of ginger root oil (GRO) aromatherapy to enhance sterile male attractiveness [33], we also included a comparison of competitiveness parameters for males treated or not.

The paper is organized as follows: In Section 2, we build a continuous releases model. In Section 3, we derive theoretical results. In Section 4, we extend the SIT model to periodic releases. In Section 5, we provide numerical simulations related to continuous and periodic releases and discuss the results. Finally, in Section 6, we derive some conclusions and perspectives.

2 Material and methods

Previous models [49, 5], where residual fertility has been studied, appeared too simplistic for entomologists. We want to show that even if we consider a more complex model, where most of the stages, including also mating are taken into account, the relationship between the residual fertility and the parameters related to the reproductive potential of the pest population still holds.

On the basis of published models [2], we consider several compartments: non-adult individuals, A, gathering eggs, larvae and pupae; sexually mature females looking for matings, Y; fertile wild females, F_W; "almost" sterile females, F_S; almost sterile males, M_T; and also wild males, M. See the compartmental diagram 1, page 5. Contrary to [5, 16, 15], we model the residual fertility taking into account that young females that mate with sterile released males become "almost" sterile females, F_S. Indeed, we assume that females F_S have received a small proportion, ε, of fertile sperms, such that each female F_S is able to deposit εb hatched eggs per day, where b is the eggs daily deposit rate related to fertilized females, F_W. All variables and parameters are described in Table 1, page 4. As seen in diagram 1, the birth rate is impacted by $1-\dfrac{A}{K}$, where K is the carrying capacity (i.e. maximum number of larvae/pupae for all fruits) of the host(s). Since the average mating rate at first mating was shown to be similar for wild and V8 sterile males (0.67 and 0.64, respectively, [13]), we consider equal chance for wild and sterile males to mate.The impact of SIT is modeled by the term $\dfrac{M}{M+\gamma M_T}\left(\gamma\dfrac{M_T}{M+\gamma M_T}\right)$ which represents the probability for a sexually mature female to mate with a wild (sterile) male to enter the fertilized (almost sterile) female compartment, F_W (F_S). All linear terms represent either transfer rates, like ν_A and ν_Y, from one compartment to another, or death-rates, μ_A, μ_M, μ_F and μ_T: see Table 1, page 4. We now explain further the re-mating component that is also specifically investigated in this study.
Host fruit affect the rate and duration of development, in this study we considered values from stone fruits when available, as peaches, nectarines, and apricots are the most common fruits in Corsica, together with clementines. Peaches [20] and nectarines [38] appear to be very suitable fruits for the development of *C. capitata*, while clementine is less favorable for immature development [20] (see table (1) and (2) for the parameters used and their value). Developmental data also vary with season (temperature and fruit phenology), but those variables are not included in our model.

We take into consideration male and female's multiple mating capacity (re-mating). This parameter has been repeatedly studied in the laboratory with varying estimations. However, analysis of field-sampled females progeny showed less than 28% [11] or 50% [10] multiple mating. It is then possible to roughly estimate a percentage of female daily re-mating proportion: in average, between 7% and 12%. This is taken into account in our model by considering a linear flow from compartment F_W towards Y, through a parameter δ, where $1/\delta$ represents the average refractory period. For sake of simplicity we could assume that this probability is the same for wild and sterile females. However, some studies (for example [25]) showed that wild females that have mated ~~first~~ with sterile males, F_S, have a tendency to remate more often, such that the linear flow from F_S to Y is considered with a parameter $\delta_S \geq \delta$.

The addition of ginger root oil (GRO) to sterile adult males is now a common process that increases

Symbol	Description	Unit
A	Non-flying stages (larvae and pupae stages)	Individuals
Y	Sexually mature Female looking for matings	Individuals
M	Wild Males	Individuals
F_W	Mated and eggs-laying fertile females	Individuals
F_S	Mated and eggs-laying "almost" sterile females	Individuals
M_T	Sterile Males	Individuals
K	Larvae/pupae mean carrying capacity	Individuals
b	Mean number of viable/hatched eggs laid by female per day	days^{-1}
μ_A	Mortality rate of non-flying stages	days^{-1}
ν_A	Maturation rate from the non-flying stage to flying stages	days^{-1}
μ_Y	Mortality rate at the Y-stage	day^{-1}
ν_Y	Maturation rate from Y to mated females compartments	day^{-1}
r	Sex ratio	-
μ_M	Mortality rate of wild males	day^{-1}
μ_F	Mortality rate of mated females	day^{-1}
δ	Re-mating rate for the wild females	day^{-1}
δ_S	Re-mating rate for the sterile females	day^{-1}
μ_T	Mortality rate of sterile male	day^{-1}
Λ_T	Sterile male release rate	individuals $\times$ days^{-1}
γ	Competitivity parameter	-
ε	Proportion of fertile sperm - residual fertility	-

Table 1: Description of parameters and state variables of model (1)

the sterile males competitiveness. It has also been showed to reduces re-mating tendency, leading to similar percentages of re-mating whether females are mated first to wild or sterile males [35]. In this study we analyse the effect of GRO treatment on the release ratios.

In complete genericity, it could be possible to expect the releases numbers of sterile males to vary in time. Thus, we consider a release rate $u(t) \geq 0$, with a death-rate μ_T. However, for sake of simplicity, we will consider two constant cases: continuous (daily) releases, $u(t) \equiv \Lambda_S$, and periodic impulsive releases, i.e.

$$u(t) = \begin{cases} 0, & t \neq n\tau \\ \tau\Lambda_{S,per} & t = n\tau, \qquad n = 1, 2, ... \end{cases}$$

The system is summarized in the compartmental diagram 1, page 5 and the mathematical model becomes

$$\begin{cases} \dfrac{dA}{dt} = b\left(F_W + \varepsilon F_S\right)\left(1 - \dfrac{A}{K}\right) - \left(\nu_A + \mu_A\right)A \\ \dfrac{dY}{dt} = r\nu_A A + \delta F_W + \delta_S F_S - \left(\nu_Y + \mu_Y\right)Y \\ \dfrac{dM}{dt} = \left(1 - r\right)\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M + \gamma M_T} Y - \left(\delta + \mu_F\right)F_W, \\ \dfrac{dF_S}{dt} = \nu_Y \dfrac{\gamma M_T}{M + \gamma M_T} Y - \left(\delta_S + \mu_F\right)F_S, \\ \dfrac{dM_T}{dt} = \Lambda - \mu_T M_T. \end{cases} \tag{1}$$

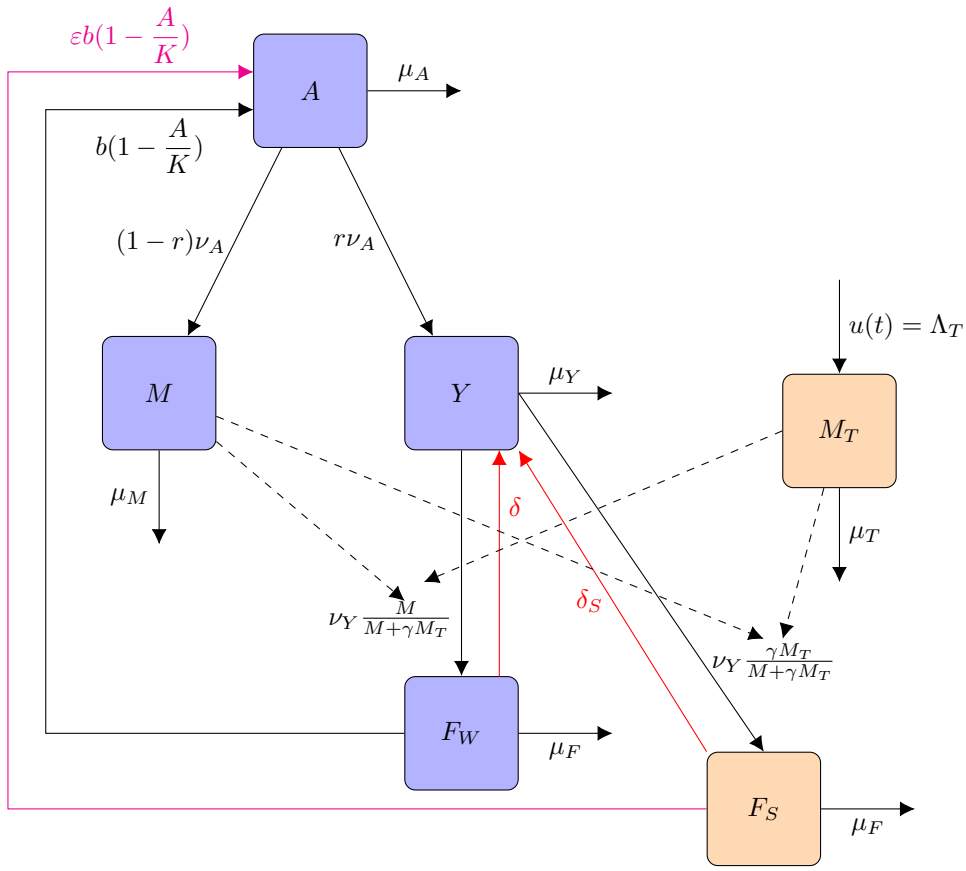

Figure 1: Flow diagram of model (3)

The M_T-equation $(1)_6$ being independent, it is equivalent to study the following system

$$\begin{cases} \dfrac{dA}{dt} = b\left(F_W + \varepsilon F_S\right)\left(1-\dfrac{A}{K}\right) - \left(\nu_A + \mu_A\right)A \\ \dfrac{dY}{dt} = r\nu_A A + \delta F_W + \delta_S F_S - \left(\nu_Y + \mu_Y\right)Y \\ \dfrac{dM}{dt} = \left(1-r\right)\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M+\gamma M_T} Y - \left(\delta + \mu_F\right)F_W, \\ \dfrac{dF_S}{dt} = \nu_Y \dfrac{\gamma M_T}{M+\gamma M_T} Y - \left(\delta_S + \mu_F\right)F_S, \end{cases} \tag{2}$$

However, setting $F_T = F_W + F_S$, and summing $(2)_4$ and $(1)_5$, we have

$$\frac{dF_T}{dt} = p_i \nu_Y Y + \left(\delta_S - \delta\right)F_W - \left(\delta_S + \mu_F\right)F_T,$$

such that system (2) can be rewritten as follows the previous system is equivalent to the following ones

$$\begin{cases} \dfrac{dA}{dt} = b\left((1-\varepsilon)F_W + \varepsilon F_T\right)\left(1-\dfrac{A}{K}\right) - \left(\nu_A + \mu_A\right)A \\ \dfrac{dY}{dt} = r\nu_A A + \delta_S F_T - \left(\delta_S - \delta\right)F_W - \left(\nu_Y + \mu_Y\right)Y \\ \dfrac{dM}{dt} = \left(1-r\right)\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M+\gamma M_T} Y - \left(\delta + \mu_F\right)F_W, \\ \dfrac{dF_T}{dt} = \nu_Y Y + \left(\delta_S - \delta\right)F_W - \left(\delta_S + \mu_F\right)F_T. \end{cases} \tag{3}$$

with $\delta_S \geq \delta$ and

$$r\nu_A A + \delta F_W - (\nu_Y + \mu_Y) Y \leq \frac{dY}{dt} \leq r\nu_A A + \delta_S F_T - (\nu_Y + \mu_Y) Y.$$

Thus, system (3) is lower and upper bounded by two monotone cooperative auxiliary systems [47]. Thus even if system (3) is not cooperative, it can be studied using the monotone theory approach [47].

The following lemmas show that system (3) is mathematically and biologically well posed: it remains positive and bounded.

Lemma 1 *Let M_T be a non-negative, piecewise continuous function on $\mathbb{R}_+$ and assume non-negative initial data. The solution to the Cauchy problem associated with (3) exists on $\mathbb{R}_+^5$, is unique, continuous and piecewise continuously differentiable. This solution is also forward-bounded and remains non-negative. It is positive for all positive times if $F(0)$, $Y(0)$ or $F(0)$ is positive.*

It is also straightforward to show that the set $\mathcal{E}_5 := \{A \leq K\} \subset \mathbb{R}_+^5$ is forward invariant for (2), and any trajectory enters it in finite time.

3 Some theoretical results

3.1 Qualitative analysis without SIT releases

We recover the equations that drive the dynamics of the pest/vector population

$$\begin{cases} \dfrac{dA}{dt} = bF_W \left(1 - \dfrac{A}{K}\right) - (\nu_A + \mu_A) A \\ \dfrac{dY}{dt} = r\nu_A A + \delta F_W - (\nu_Y + \mu_Y) Y \\ \dfrac{dM}{dt} = (1 - r) \nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y Y - (\delta + \mu_F) F_W, \end{cases} \tag{4}$$

Model (4) is similar to one the sub-model studied by the author in [2].

We define the basic offspring number related to model (4) as follows

$$\mathcal{N} = \mathcal{N}(\delta) = \frac{br\nu_A\nu_Y}{(\nu_A + \mu_A)\left((\mu_Y + \nu_Y)\mu_F + \mu_Y\delta\right)} \tag{5}$$

Through straightforward calculations and using the theory of monotone cooperative system [47], we show

Theorem 1 ([2]) *System (4) defines a forward dynamical system in $\mathcal{E}_4 := \{A \leq K\} \subset \mathbb{R}_+^4$. In addition*

- *if $\mathcal{N} < 1$, then $\mathbf{0}_{\mathbb{R}^4} = (0, 0, 0, 0)^T$ is globally asymptotically stable on $\mathcal{E}_4$.*
- *if $\mathcal{N} > 1$, then a positive equilibrium $\mathbf{E}$ exists where*

$$A_0^* = \left(1 - \frac{1}{\mathcal{N}}\right) K, \tag{6}$$

$$Y_0^* = \frac{r\nu_A(\delta + \mu_F)}{\nu_Y\mu_F + \mu_Y(\delta + \mu_F)} \left(1 - \frac{1}{\mathcal{N}}\right) K, \tag{7}$$

$$F_{0,W}^* = \frac{r\nu_A\nu_Y}{\nu_Y\mu_F + \mu_Y(\delta + \mu_F)} \left(1 - \frac{1}{\mathcal{N}}\right) K, \tag{8}$$

$$M_0^* = \frac{(1 - r)\nu_A}{\mu_M} \left(1 - \frac{1}{\mathcal{N}}\right) K. \tag{9}$$

Furthermore, $\mathbf{E}$ is globally asymptotically stable on $\mathcal{E}_4 \setminus \{\mathbf{0}_{\mathbb{R}^4}]\}$.

Proof. The proof of the local stability was not provided in [2, Theorem 9]. However, in appendix A, we derive additional computations that will be useful in the next sections. □

However, we can go further and show that System (4) defines a forward dynamical system in

$$\mathcal{E}_{4,b} := \{A \leq A_0^*, Y \leq Y_0^*, F_W \leq F_{0,W}^*, M \leq M_0^*\} \subset \mathbb{R}_+^4.$$

3.2 Qualitative analysis for constant continuous SIT releases

For the rest of the paper, we assume $\mathcal{N} > 1$. SIT induces a strong Allee effect [4] by reducing mate finding probabilities such that a population level extinction threshold exists and such that we get bi-stability between $\mathbf{0}$ and a positive equilibrium, $E^*_{\varepsilon,+}$, when sterile males releases are not too large. This effect is particularly useful when the pest population is either (very) small or invading the domain, or to consider a long term SIT strategy using first massive releases, and then small releases, as explained in [4, 5]. Indeed, massive releases will drive the pest population into a subset that belongs to the basin of attraction of $\mathbf{0}$, related to a given size for the small releases, such that we can switch from massive to small releases to keep the pest population as small as needed and also to drive it slowly, but surely, towards elimination. In contrary, it shows that once used, sterile males releases have to be maintained: if, for any reason, SIT is stopped, then the Allee effect is lost, even under isolated geographies.

System (3), being (almost) monotone, has useful properties, such that it suffices to study their equilibria. Obviously, system (3) always admits a trivial equilibrium or steady state, $\mathbf{0}$.

We first derive results on the existence or not of positive equilibria. We set

$$\mathcal{N}_S = \mathcal{N}(\delta_S) = \frac{br\nu_A\nu_Y}{(\nu_A+\mu_A)\left((\mu_Y+\nu_Y)\mu_F+\mu_Y\delta_S\right)}. \tag{10}$$

This is the basic offspring number related to the SIT model.

Since

$$\mathcal{N}_S = \frac{\nu_Y\mu_F+\mu_Y(\delta+\mu_F)}{\nu_Y\mu_F+\mu_Y(\delta_S+\mu_F)}\mathcal{N},$$

we deduce that $\mathcal{N}_S \leq \mathcal{N}$ when $\delta_S \leq \delta$. Thus the SIT impacts the dynamic of the wild population.

We show the following results

Lemma 2 *When $\varepsilon\mathcal{N}_S < 1$, then $\mathbf{0}_{\mathbb{R}^5}$ is always Locally Asymptotically Stable (LAS) for system (2) and thus for system (3). It is unstable, otherwise.*

Proof. See appendix 9, page 28. □

This result implies several remarks. First, if residual fertility is sufficiently small, then SIT introduces, as expected, a strong Allee effect, meaning that if the wild population is sufficiently small, then it can be driven to elimination by SIT, considering an isolated landscape. Let us set

$$\mathcal{R}_\delta = \frac{br\nu_A\nu_Y}{(\nu_A+\mu_A)(\mu_Y+\nu_Y)(\delta+\mu_F)}. \tag{11}$$

$\mathcal{R}_0$ is the basic offspring number without re-mating, $\delta = 0$. Using the definition of $\mathcal{N}$, $\mathcal{N}_S$ and $\mathcal{R}$, and using the fact that $0 \leq \delta \leq \delta_S$, we deduce that

$$\mathcal{N}_S \leq \mathcal{N} \leq \mathcal{R}_0. \tag{12}$$

Remark 1 *Without re-mating, i.e. $\delta = \delta_S = 0$, we recover the condition on ε, namely $\varepsilon\mathcal{R} < 1$, like in [5, 49].*

Proposition 1 *Assume $\mathcal{N}_S > 1$ then we following results hold true for system (2):*

- *Assume $\varepsilon > \dfrac{1}{\mathcal{N}_S}$, then there always exists one positive steady state $\mathbf{E}^* >> 0$, such that A^* is always bounded from below by*

$$A^*_0\sqrt{\frac{\mathcal{N}}{\mathcal{N}-1}\left(1-\frac{1}{\varepsilon\mathcal{N}_S}\right)}, \tag{13}$$

  whatever the size of the sterile males releases.

- *Assume $\varepsilon = \dfrac{1}{\mathcal{N}_S}$, then, setting $\gamma\Lambda^{crit,*}_{cont,\varepsilon} = \mu_T\dfrac{\delta_S+\mu_F}{\delta+\mu_F}\mathcal{N}_S M^*_0$, we deduce that*
  - *If $\Lambda \geq \Lambda^{crit,*}_{cont,\varepsilon}$, there is no positive steady state.*
  - *If $0 \leq \Lambda < \Lambda^{crit,*}_{cont,\varepsilon}$, there is one positive steady state $\mathbf{E}_*$.*

- *Assume* $0 \leq \varepsilon < \dfrac{1}{\mathcal{N}_S}$*, then, setting*

$$\gamma\Lambda^{crit}_{cont,\varepsilon} = \mu_T \frac{(\delta_S + \mu_F)}{(\delta + \mu_F)} \frac{\left(1 - \dfrac{1}{\mathcal{N}}\right)}{\dfrac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \dfrac{1}{\mathcal{N}}\right) + 2\sqrt{\left(\dfrac{1}{\mathcal{N}_S} - \varepsilon\right)\left(\dfrac{1}{\mathcal{N}_S} - \dfrac{\varepsilon}{\mathcal{N}}\right)}} M_0^*. \tag{14}$$

  we deduce that

  - *If* $\Lambda > \Lambda^{crit}_{cont,\varepsilon}$*, there is no positive steady state.*
  - *If* $\Lambda = \Lambda^{crit,}_{cont,\varepsilon}$*, there is one positive steady state* E^*_ε*.*
  - *If* $0 < \Lambda < \Lambda^{crit}_{cont,\varepsilon}$*, then there are two positive steady states* $E_{\varepsilon,-}$ *and* $E_{\varepsilon,+}$*, such that*

$$\mathbf{0}_{\mathbb{R}^5} < E^*_{\varepsilon,-} < E^*_{\varepsilon,+}.$$

Proof. See appendix 8, page 24. □

Remark 2 *Inequality* (13) *is of utmost importance, because it clearly states that if the residual fertility is large, then the impact of SIT will be very limited. For instance, for a pest, like C. capitata, assume that* $\mathcal{N}_S = \mathcal{N} = 100$ *(it can be greater than* 100*), and assume a residual fertility of* 2%*, then, the previous result gives that* $\dfrac{A^*}{A_0^*} > \sqrt{\dfrac{100}{2 * 99}} = 0.7107$*: the non-flying stage cannot become lower than* 71% *of the initial equilibrium, whatever the size of the releases!*

Remark 3 *According to* (12)*, and thanks to Lemma 2, when re-mating occurs, i.e* $\delta > 0$*, the constraint on the residual fertility is relaxed because* $\dfrac{1}{\mathcal{R}_0} < \dfrac{1}{\mathcal{N}}$*.*

Remark 4 *Even better: if re-mating for sterile female (mated with sterile males), is more frequent , i.e.* $\delta_S > \delta$*, then, again, the constraint on the residual fertility is relaxed because* $\dfrac{1}{\mathcal{N}} < \dfrac{1}{\mathcal{N}_S}$

Finally, we have the following result

Theorem 2 *Assume* $\varepsilon\mathcal{N}_S < 1$ *and* $\Lambda > \Lambda^{crit}_{cont,\varepsilon}$*, then* $\mathbf{0}_{\mathbb{R}^5}$ *is GAS for the upper monotone system related to system* (3) *and thus GAS for system* (2)*.*

Proof. See appendix 9.1, page 29. □

Remark 5 *According to Theorem 2, provided that* ε *is sufficiently small, it is possible to reach (asymptotically) elimination when* Λ *is large enough.*

According to Proposition 1 and Theorem 2, we can deduce that the residual fertility, ε, is an essential parameter to take into account when designing SIT programs. If ε is too large, then SIT can become less efficient, and eventually fail.

The precision and homogeneity of the sterilization step is very important. Although the irradiation process is very well mastered, the level of residual fertility will depend on the homogeneity of the dose delivered to the fly pupae, which may be affected by container volume, irradiation equipment and source. The classical recommendation is to have the lowest residual fertility as possible, but here we provide first insights on the impact of RF on the release success.

Technical and production improvements in medfly SIT have been obtained using genetic sex strains [32] in which males also have a naturally reduced fertility level (49.29%).The residual fertility of the VIENNA-8 GSS strain was reported to $0.84\% \pm 0.08\%$ ($0.6\% \pm 0.13\%$) at $100Gy$ ($120Gy$) [32][Table 3] on average. However, a higher residual fertility was observed for a similar strain (VIENNA-8 GSS strain with a Valencian background) irradiated at the same dose but with an electron beam accelerator [39], i.e.$1.13\% \pm 0.55\%$ for 100Gy.

Another important element is the re-mating of females: we showed theoretically that it is important to have a good knowledge on this phenomenon because it really relaxes the constraint on the residual fertility, ε. We will illustrate this in the numerical section. Even if from time to time the constraint $\varepsilon\mathcal{N}_S < 1$ is not verified, it seems preferable to release sterile males with a residual fertility that verifies $\varepsilon\mathcal{N}_S < 1$, along the year, in order to be efficient.

However, it is important to have in mind that targeted crops may also affect the effectiveness of a SIT program. Indeed, Ceratitis capitata's basic reproduction numbers depends on their main fruit hosts and, thus, can take a large range of values. For instance, according to [38], estimates of $\mathcal{R}_0$ on deciduous fruits, like Nectarine (or Plum), derive $\mathcal{R}_0 \approx 227.28 \pm 89.1$ ($\mathcal{R}_0 \approx 276.59 \pm 54.15$), at 25^oC, whereas $\mathcal{R}_0 \approx 27.05$ on citrus, at 24^oC [34]. Thus clearly the constraint on ε will not be the same when the main targeted host crop is Citrus or Nectarine: for instance, a residual fertility of 2% might be acceptable for Citrus but not necessarily acceptable for Nectarine or Plum: compare $1/27.05 \approx 0.037$ and $1/227.05 \approx 0.0044$. In the application, we will consider medflies data related to Peach, obtained in Tunisia [20], as this shows greater similarities to the agricultural context of Corsica.

Remark 6 *Obtaining theoretically the stability properties of the positive equilibria, when they exists, $E^*_{\varepsilon,-}$ and $E^*_{\varepsilon,+}$ is not easy considering the complexity of the system. The numerical simulations indicate that $E^*_{\varepsilon,-}$ is unstable while $E^*_{\varepsilon,+}$ is asymptotically stable, and that the equilibria are the only invariant set of the system on $\mathbb{R}^+_5$. However, we provide in appendix C, conditions to verify to check, at least numerically, if they are unstable or not.*

4 Periodic impulsive SIT releases

We assume now that sterile males are released periodically, every τ days. Assuming each release as an instantaneous event, this can be modeled using a semi-discrete approach, like in [4, 5, 9]. Thus, model (3) becomes

$$\begin{cases} \dfrac{dA}{dt} = b\left((1-\varepsilon)F_W + \varepsilon F_T\right)\left(1 - \dfrac{A}{K}\right) - (\nu_A + \mu_A)\,A, \\ \dfrac{dY}{dt} = r\nu_A A + \delta_S F_T - (\delta_S - \delta)\,F_W - (\nu_Y + \mu_Y)\,Y, \\ \dfrac{dM}{dt} = (1-r)\,\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M + \gamma M_T} Y - (\delta + \mu_F)\,F_W, \\ \dfrac{dF_T}{dt} = \nu_Y Y + (\delta_S - \delta)\,F_W - (\delta_S + \mu_F)\,F_T, \\ \dfrac{dM_T}{dt} = -\mu_T M_T. \end{cases} \tag{15}$$

with

$$\begin{cases} A(n\tau_+) = S_h(n\tau), \\ Y(n\tau_+) = I_h(n\tau), \\ M(n\tau_+) = R_h(n\tau), \\ F_W(n\tau_+) = A(n\tau), \\ F_T(n\tau_+) = F_T(n\tau), \\ M_T(n\tau_+) = M_T(n\tau) + \tau\Lambda_{per}. \end{cases} \tag{16}$$

It is straightforward to show that, as $t \to +\infty$, M_T converge toward the periodic solution

$$M_{T,per}(t) = \frac{\tau\Lambda_{per}}{1 - e^{-\mu_T \tau}} e^{-\mu_T (t - \lfloor t/\tau \rfloor \tau)},$$

such that system (15)-(16) can be reduced to

$$\begin{cases} \dfrac{dA}{dt} = b\left((1-\varepsilon)F_W + \varepsilon F_T\right)\left(1-\dfrac{A}{K}\right) - (\nu_A + \mu_A)\,A, \\ \dfrac{dY}{dt} = r\nu_A A + \delta_S F_T - (\delta_S - \delta)\,F_W - (\nu_Y + \mu_Y)\,Y, \\ \dfrac{dM}{dt} = (1-r)\,\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = p_i \nu_Y \dfrac{M}{M + \gamma M_{T,per}(t)} Y - (\delta + \mu_F)\,F_W, \\ \dfrac{dF_T}{dt} = p_i \nu_Y Y + (\delta_S - \delta)\,F_W - (\delta_S + \mu_F)\,F_T. \end{cases} \tag{17}$$

Setting

$$\begin{cases} \underline{M}_T = \min\limits_{t\in[0,\tau]} M_T^{per}(t) = \dfrac{\tau\Lambda_{per}}{1-e^{-\mu_T\tau}} e^{-\mu_T\tau}, \\ \overline{M}_T = \max\limits_{t\in[0,\tau]} M_T^{per}(t) = \dfrac{\tau\Lambda_{per}}{1-e^{-\mu_T\tau}}, \end{cases}$$

it is obvious to deduce that, for t sufficiently large, system (17) is lower and upper bounded by the following two monotone systems

$$(L)\begin{cases} \dfrac{dA}{dt} = b\left((1-\varepsilon)F_W + \varepsilon F_T\right)\left(1-\dfrac{A}{K}\right) - (\nu_A + \mu_A)\,A, \\ \dfrac{dY}{dt} = r\nu_A A + \delta F_W - (\nu_Y + \mu_Y)\,Y \\ \dfrac{dM}{dt} = (1-r)\,\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M + \gamma \overline{M}_T} Y - (\delta + \mu_F)\,F_W, \\ \dfrac{dF_T}{dt} = p_i \nu_Y Y + (\delta_S - \delta)\,F_W - (\delta_S + \mu_F)\,F_T, \end{cases}$$

$$(U)\begin{cases} \dfrac{dA}{dt} = b\left((1-\varepsilon)F_W + \varepsilon F_T\right)\left(1-\dfrac{A}{K}\right) - (\nu_A + \mu_A)\,A, \\ \dfrac{dY}{dt} = r\nu_A A + \delta_S F_T - (\nu_Y + \mu_Y)\,Y \\ \dfrac{dM}{dt} = (1-r)\,\nu_A A - \mu_M M, \\ \dfrac{dF_W}{dt} = \nu_Y \dfrac{M}{M + \gamma \underline{M}_T} Y - (\delta + \mu_F)\,F_W, \\ \dfrac{dF_T}{dt} = \nu_Y Y + (\delta_S - \delta)\,F_W - (\delta_S + \mu_F)\,F_T. \end{cases}$$

Using (14), and applying Proposition 1 to system (L) or system (U), we obtain

Proposition 2 *Assume $\mathcal{N}_S > 1$ and $\varepsilon\mathcal{N}_S < 1$.*

- *When $\underline{M}_T > \dfrac{\Lambda_{cont,\varepsilon}^{crit}}{\mu_T}$, the trivial equilibrium $\mathbf{0}_{\mathbb{R}^5}$ is Globally asymptotically stable for system (U)*
- *When $0 < \overline{M}_T \leq \dfrac{\Lambda_{cont,\varepsilon}^{crit}}{\mu_T}$, system (L) admits one or two positive equilibria $\overline{E}_{1,5D} \leq \overline{E}_{2,5D}$. In addition, if the initial data of (L) is greater than or equal to $E_{1,5D}$, then the corresponding solution is also greater than or equal to $E_{1,5D}$. Similarly, since $0 < \underline{M}_T < \overline{M}_T \leq \dfrac{\Lambda_{cont,\varepsilon}^{crit}}{\mu_T}$, then system (U) admits one or two positive equilibria $\underline{E}_{1,5D} \leq \underline{E}_{2,5D}$. Finally, the set $\{(A,Y,M,F_w,F_T)^T \in \mathbb{R}_+^5 : (A,Y,M,F_w,F_T) \leq \underline{E}_{1,5D}\}$ belongs to the basin of attraction of $\mathbf{0}_{\mathbb{R}^5}$ for system (U), hence by comparison, it belongs to the basin of attraction of $\mathbf{0}_{\mathbb{R}^5}$ for system (17).*

From the previous remarks, we can deduce

Proposition 3 *Assume $\mathcal{N}_S > 1$, $\varepsilon\mathcal{N}_S < 1$ and $\overline{M}_T \leq \dfrac{\Lambda^{crit}_{cont,\varepsilon}}{\mu_T}$, the set*

$$\Omega_5 = \{(A, Y, M, F_w, F_T)^T \in \mathbb{R}^5_+ : \overline{E}_{1,5D} \leq (A, Y, M, F_w, F_T) \leq \mathbf{E}\}$$

is positively invariant by system (17), where $\mathbf{E}$, the initial wild equilibrium, is defined in Theorem 1.

Finally, using the previous result and Brouwer fixed point theorem, with comparison arguments, it is possible to show

Theorem 3 *Assume $\mathcal{N}_S > 1$, $\varepsilon\mathcal{N}_S < 1$ and $\overline{M}_T \leq \dfrac{\Lambda^{crit}_{cont,\varepsilon}}{\mu_T}$. Then, for each initial condition in Ω_5, system (17) has at least one positive τ-periodic solution $\mathbf{E}_{per}$ such that $\mathbf{E}_{per} \in \Omega_5$.*

The previous results are obtained by comparison arguments using monotone Lower- and Upper-systems of system (17). While they insure the existence of periodic critical release rate, $\Lambda^{crit}_{per,\varepsilon}$, it is not possible to find an analytical formula, like for the continuous case. However, it is possible to estimate $\Lambda^{crit}_{per,\varepsilon}$ numerically.

Parameter	**Value used in the model(s)**	**Based on values from the literature**	
		Wild Males and Females (virgin or mated with Wild males)	Sterile males (Tsl-Vienna 8 GSS)
Number of viable eggs per day	$b = 12.13$ day^{-1}	Average values of 13 eggs per day and an egg eclosion rate of 92% for flies grown in peach [20].	no difference)
Maturation rate from non-flying stage to flying stage	$\nu_A = 0.027$ day^{-1}	Average of 20 days from eggs to adult emergence in peach (at 25°C) [20]	NA
Mortality rate non-flying stages	$\mu_A = 0.0227 day^{-1}$	Average survival of 82.5% eggs to adult emergence on peach (at 25°C) [20].	NA
Average Time needed for a sexually mature female to mate and be fertilized	$\frac{1}{\nu_Y} = 1$ day^{-1}	Estimate based on [29]	NA
Average sex ratio	$r = 0.53$	Based on development on peach [20]	NA
Adult death rate	$\mu_Y = \mu_F = 1/42.66$ day^{-1} $\mu_M = 1/50.33$ day^{-1} $\mu_T = 0.23$ day^{-1}	Males: average lifespan of 50 days for flies grown in peach (at 25°C) [20]. Females: average lifespan of 43 days for flies grown in peach (at 25°C) [20].	Up to 50% sterile males survived over 3 days [40]; 90% of the sterile males released (exposed or not to GRO) were recaptured within 5 days [36]
Competitiveness (without GRO treatment)	$\gamma = 0.6129$	NA	RSI $= 0.34 \pm 0.004$ [36]
Competitiveness (with GRO treatment)	$\gamma = 2.03$	NA	RSI $= 0.67$ [36]

Table 2: *C. capitata* entomological parameter values used in this model (literature selected for demographic parameters were studies using host fruits rather than artificial diet, and field studies when available). The parameters values for δ and δ_S are given below in Table 3

5 Application and discussion

We now apply the previous theoretical result to the Medfly *Ceratis capitata*. We summarize in table 2, page 12, the values estimated for some biological parameters obtained from the litterature on medfly developed on peach (when available) and on sterile males from the V8 GSS.

5.1 Parameterization and simulations

The difficulty of using modeling to understand biological phenomenon lies in the estimation of the values of the biological parameters. Most behavioral or biological studies are made in a laboratory settings and under controlled conditions; they do not necessarily reflect a behavior in the field. On the other hand, reports from field studies may cover only a small portion of the diversity of behaviors or physiology of wild populations. Most of the parameters values here were estimated directly or indirectly from the literature, selecting studies that brought the closest estimates to what may occur in the field.

We estimated ν_A and μ_A from the data provided on peach development [20] as follows. Since $\dfrac{1}{\nu_A+\mu_A} = 20.1$ such that $\nu_A + \mu_A \approx 0.0497$ such that since $\nu_A = 0.027$, we deduce that $\mu_A = 0.0227$. Then, the proportion of non-adult individuals that become adults is given by 0.6609 [20][Table 3]. Thus only 66.03% of the hatched eggs become adults, that is $\dfrac{\nu_A}{\nu_A+\mu_A} = 0.6609$, that is $\nu_A = 0.0328$ and $\mu_A = 0.0169$. Little literature exist on development parameters from fruit host rather than artificial diet. Big variations can occur according to the host, citrus or clementine having lower developmental rate and longer duration but a higher adult lifespan, as compared to peach hosts [20].

The model from Plant & Cunningham [40] predicted that 50% of the released sterile males were dead after 3 days; assuming that the population size is given by $P(t) = P(0)e^{-\mu_T t}$ we derive that $\mu_T = \dfrac{\ln 2}{3} = 0.2310$.

The estimation of the sterile males' competitiveness index is based on the Relative Sterility Index (RSI), through cages experiments. Without GRO treatment, the mean RSI is low, around 0.38, but still greater than the threshold 0.2, leading to a competitiveness parameter $\gamma = 0.61$ [35]. When sterile males are treated with an optimal dose of ginger root oil (GRO) [35], then the mean RSI becomes 0.67 which implies a competitive parameter $\gamma = 2.03$. Note that sterile male and wild males are equally competitive when $RSI = 0.5$, for a $1:1:1$ density. The parameters values are summarized in Table 2, page 12.

Some field studies reported percentages of double mating in wild females: up to 50% [10]; $< 28\%$ [12]; 4 to 28% [26]. Laboratory tests reported by Abraham et al [1] indicated 20% re-mating for females mated with 100Gy-irradiated males. Recently, Pogue et al (2022)have shown that female mating propensity reduces over time [41]: with an average of 75% females C.capitata re-mating a second time but only less than 25% performing successive re-mating. Here, we've chosen to estimate the parameters δ and δ_S based on the values reported from laboratory experiments by [33, Table 1]. From competing scenarios with wild and sterile males, we could estimate that the re-mating rate was equal to the proportion of re-mating, (40% when females are mated first with a wild male), divided by the mean Refractory period (RFP), (i.e. 2.5 days), such that we get $\delta = \dfrac{0.4}{2.5} = 0.16$ day^{-1} for females exposed to sterile males not treated with GRO. Using the same reasoning we derive also δ_S with and without GRO-treatment:

	δ	δ_S
SM	$0.4/2.5 = 0.16$	$0.64/2.02 = 0.3161$
SM-GRO	$0.2/2 = 0.1$	$0.34/1.44 = 0.2361$

Table 3: Re-mating rates with and without GRO treatment [33]

The lifespan of sterile males was reported not to be impacted by the GRO treatment (see [36]).

	$\mathcal{N}_S$	$\mathcal{N}$	$\mathcal{R}_0$
SM	111.2725	125.9497	145.6401
SM-GR0	118.34	132.6764	145.6401

Table 4: Basic Offspring numbers with and without GRO treatment according to Tables 2 and 3

Using Table 3, we derive Table 4, page 13, where the values for the basic offspring number are computed according to the different sub-cases: with and without re-mating, with and without GRO-treatment. As shown, the impact of re-mating is not negligible on the basic offspring number: the smaller the refractory period the larger the basic offspring number. Despite the fact that GRO-treatment increases the basic offspring numbers $\mathcal{N}$ and $\mathcal{N}_S$, which could render SIT control more difficult, the results are clearly better than without GRO-treatment because the competition parameter γ_{GRO} is larger than γ. Clearly, with or without GRO-treatment, mating and re-mating have to be studied deeply for females that mated either with wild males or sterile males.

Thanks to Table 4 we derive the maximal tolerable values for the residual fertility: see Table 5, page 14. It is interesting to note that $\varepsilon_{\max,GRO} < \varepsilon_{\max}$ when $\delta_S \geq \delta > 0$. This comes from the fact that δ and δ_S are smaller for the GRO-treatment (see Table 3).

	$\delta_S > \delta > 0$	$\delta_S = \delta > 0$	$\delta = 0$
$\varepsilon_{\max}$	0.0090	0.0079	0.0069
$\varepsilon_{\max,GRO}$	0.0085	0.0075	0.0069

Table 5: Upper bound for the residual fertility - with and without GRO treatment

Remark 7 *It is interesting to compare the bounds given in Table 5 with real values. For instance, in [32][Table 3], the sterility induced by* $100GY$ *(*$120GY$*) sterilized males was* $99,42\% \pm 0.1$ *(*$99.72\% \pm 0.15$*), that is an average residual fertility of* 0.58% *(*0.28%*), when considering the percentage of pupae surviving from progeny of females mated by sterilized males. This is below the upper bounds given in Table 5, whatever re-mating occurs or not. On the other hand, in [39], the sterility induced by* $100GY$ *sterilized males was* $98.87\% \pm 0.55$ *providing an average residual fertility of* 1.13%*, that is* $\varepsilon = 0.0113$*. This value is much larger than the values given in Table 5. Following our theoretical results, this means that the the sterile males released under the conditions of [39] could only induce a reduction of the wild population, but not an elimination.*

The tolerable value for residual fertility is very low according to the chosen parameters values. This would give reason to SIT implementation programs that choose a fully sterilizing dose, such as [1]. In the following simulations, we consider RF values varying from 0 to 0.9%.

We now derive some simulations in order to highlight the issues of residual fertility and re-mating in SIT control treatment. In the forthcoming simulations we will consider three cases: (a) without re-mating; (b) when equal re-mating occurs, i.e. $\delta_S = \delta$; (c) when re-mating occurs with $\delta_S > \delta$.

First, using formula (14), we show the evolution of the ratio between $\Lambda^{crit}_{cont,\varepsilon,}$ and the wild male population at equilibrium, M_0^*, before the SIT treatment begins, as shown in Figs. 2, page 16. We derive simulations with and without GRO-treatment. As shown theoretically, re-mating (blue dotted line and red circles in Figs. 2) helps when the residual fertility becomes large: the constraint on residual fertility is relaxed when re-mating is considered. However, with and without residual fertility, only equal re-mating is beneficial; the critical release rate values are smaller than those obtained without re-mating. When RF is small (less than 0.6%), re-mating with $\delta_S > \delta$ is problematic because the release rate has to be larger than for the other cases. It is interesting to note that there exists a value ε^* such that for $\varepsilon \in [0, \varepsilon^*)$, we have $\Lambda^{crit}_{\Lambda_{cont,\varepsilon,}}(\delta) < \Lambda^{crit}_{\Lambda_{cont,\varepsilon,}}(\delta_S)$. Numerically, it is clear that when ε is large, i.e. close from $\varepsilon_{\max}$, then the release rate has to be very large, making the SIT control almost inefficient.

When GRO-treatment is considered, it clearly reduces the release ratio necessary for daily release, as expected (see Fig. 2(b)). This is because GRO-treated sterile males are very competitive, that is, $\gamma = 2.03$. For both treatments, equal re-mating ($\delta_S = \delta$), decreases the release ratio and increases $\varepsilon_{\max}$. However, for non-equal re-mating, that is, $\delta_S > \delta$, the release ratio increases drastically, regardless of the residual fertility.

Note that $\Lambda^{crit}_{cont,\varepsilon}$ is a critical value such that the wild population can be eliminated in the long term. If we consider larger release rate values, that is, $\Lambda_{cont} >> \Lambda^{crit}_{cont,\varepsilon}$, then elimination, or at least a strong reduction (say 90%) can be reached more rapidly.

In both simulations the release ratios seem to be large, but these values are in good agreement with the ratios recommended by IAEA in [43][Table 3], at least when RF is supposed to be 0. When RF is close to its limit-value, then the ratio can be very large and above the ratio given in [43]. This indicates that SIT cannot be recommended.

In Fig. 3, page 17, we consider periodic releases without and with GRO-treatment. As in Fig. 2, we show the ratio between the critical periodic release rates, $\tau\Lambda^{crit}_{\varepsilon,per}$, and M_0^*, when $\tau = 7$ days. Clearly, as

in the continuous release case, only the equal re-mating case is beneficial; see the blue dotted curve in Fig. 3). However, due to the short lifespan of sterile males, the control effort becomes very heavy once residual fertility occurs. This indicates that the periodicity of the release must be lower. The same simulations were performed considering the GRO treatment in Fig. 3(b), page 17. Even if there is a clear benefit of the GRO treatment, the amount of sterile males released is still large when the residual fertility is above 0.5%. Except for the GRO treatment, we are above the release ratios recommended by [43][Table 3]. In fact, the 7-day treatment is particularly bad, in terms of ratio between sterile males and wild males, because μ_S is too large.

For this reason, we also provided 3-day periodic releases, taking into account the short lifespan of sterile males (see Figs. 4, page 18, without and with GRO-treatment. Clearly, these results are better than those shown in Fig. 3(a), page 17. In particular, with the GRO treatment, the ratio between the amount of sterile males and wild males, at equilibrium, to release, is much more reasonable, even if the residual fertility increases (see Figs. 4(b), page 18. However, it seems that a ratio between 1:22 and 1:11 is more appropriate when the residual fertility is between 0% and 0.6%.

5.2 Discussion

The overall success of an SIT program relies on (1) the field efficacy of sterile males in securing matings and sterile progeny and (2) reasonable production costs. The former is affected mainly by the radiation dose (and therefore both sterility level and competitiveness of males) and by re-mating proportions biased towards wild males. The latter can be affected by the release ratio among other factors.

Releasing males 100% sterile is rarely achieved in SIT programs. Indeed, the dose-response curves for sterility to reach, asymptotically, complete sterility, and the elimination of the last 1% residual fertility may require too high doses [8]. Thus, the balance between acceptable residual fertility and quality (that is, competitiveness and average lifespan) must be determined as highlighted by our simulations showing that the necessary release ratio increases drastically as residual fertility increases. Moreover, when residual fertility is above a certain threshold, determined by $1/\mathcal{N}$, where $\mathcal{N}$ is the basic offspring number, SIT may not be efficient.

It is sometimes recommended to prefer more competitive males over full sterility, at the beginning of the SIT deployment to ensure that most females would mate with the released males, and then switch to fully sterile males once the wild population density had decreased to a level where less competitive males would be highly outnumbering the wild males, compensating for their lower mating success [37]. Use of this model could help operators better plan the use of such a strategy according to the tolerable limit for residual fertility. Although more work would be needed to understand what is the population reduction target that would trigger the change to releases of fully sterile males.

Competitiveness of sterile males against their wild counterparts is important for the success of SIT programs. The use of GRO treatment to enhance the attractiveness of sterile males is now common in SIT programs against medflies. Our simulations clearly shows the positive impact of higher competitiveness value on the success of the release campaign. Even with daily releases, the necessary ratios were almost two to three times higher for untreated sterile males.

Our numerical outputs show how the occurrence of equal re-mating in medfly females can positively affect the success of SIT: in all simulations the "equal re-mating" case needs a lower release ratio than without re-mating. In contrary, if wild females tend to remate more often after mating with sterile males, then the release ratio needs to be increased drastically, as expected, in order to ensure that most re-mating will be performed by another sterile male. In addition, thanks to (12), re-mating relaxes the constraint on the residual fertility threshold. These results clearly show how re-mating is an important parameter but it does not necessarily have a negative impact on SIT success. However, more field studies of the remating behavior would be necessary to optimize the SIT success.

Daily versus periodic releases will have a considerable impact on the cost of an operational program. It is important to analyse if continuous releases would benefit the efficiency on the releases. Because of the short average lifespan of sterile males considered in the simulations (see Table 2, page 12), a 7 days periodic releases do not appear suitable. Although lifespan is difficult to estimate in the field, one can consider that sterile males are only useful as long as they can inseminate wild females.

Three days periodic releases (of GRO-treated males) would require ratios of under 20 sterile males to one wild male for up to approximately 0.5% residual fertility. Whereas a ratio of almost 50 to 1 would be necessary for a 7-days release frequency, and only approximately 26 to 1 male for continuous releases. Continuous releases are rarely being performed due to production and operational costs, and a three-day

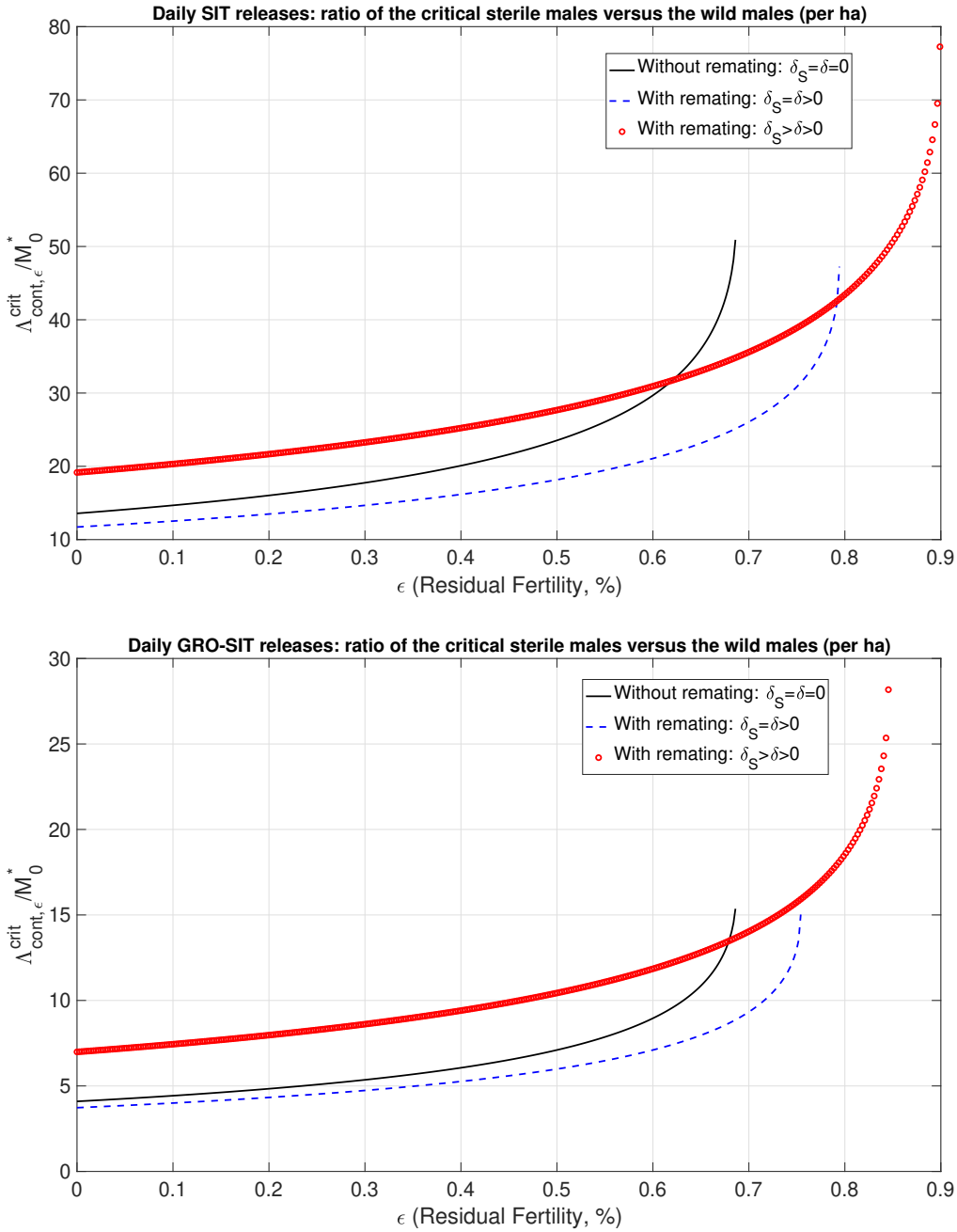

Figure 2: Critical continuous releases values when equal and non-equal re-mating is considered or not: (a) without GRO-treatment; (b) with GRO-treatment

release frequency appears as a good compromise between cost and efficiency.

This model could benefit from understanding some additional elements of wild medflies biology and sterile male flies capacity. This work shows that it would be important to know what proportion of females from the Y compartment never get to the Fw or Fs compartments, in order to be more accurate. For instance, Field trapping studies reported that an average of 41% of the wild females captured in traps were mated [45]. This proportion varied with the season and spatially with the ripening of fruits. Juan-Blasco et al [23] reported 48.9% of inseminated females in traps. However, information on the age of those unmated flies would be important to understand if they remain unmated all their life. It would be also interesting to study the behavior of females mated with sterile males to understand if their egg laying behavior is changed and

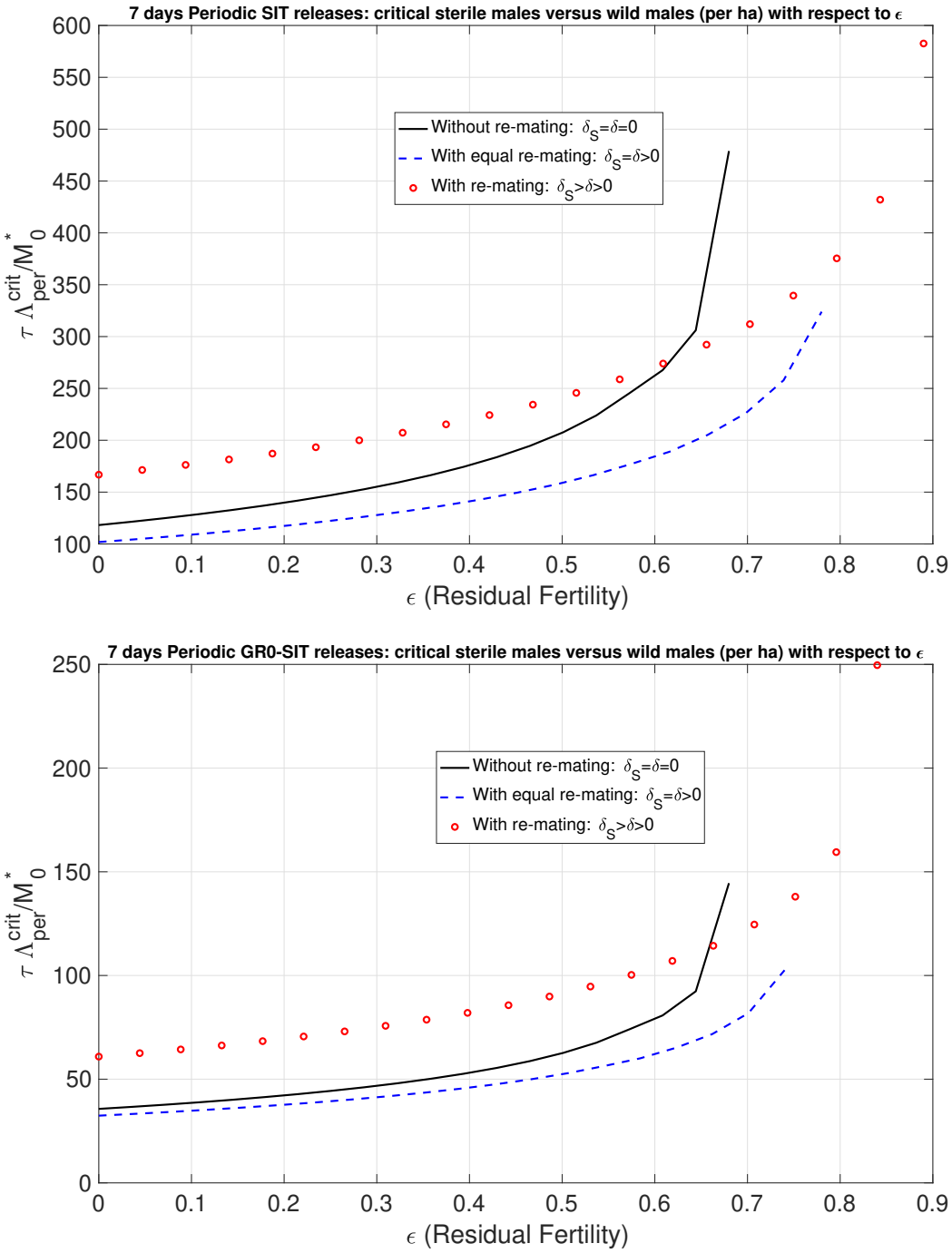

Figure 3: $\tau = 7$ days - Critical periodic releases value estimates when equal and non-equal re-mating is considered or not: (a) without GRO-treatment; (b) with GRO-treatment

if this would impact their likelihood to encounter males around host fruits, and thus to remate. Further improvements in the model could be considered, in particular the fact that wild and sterile males may not have the same capacity to inseminate females. Costa et al. [14] showed that a (wild) male would use most of its sperm contained in the testes to inseminate one female and a 24h period appears sufficient to replenish the testes with mature sperm [51]. Wild males can inseminate females every day. On the other hand, a sterile male loses the capacity to mature new sperm as the immature cells would have been damaged by the irradiation process; Catala-Oltra et al. [13] showed that 70% of sterile (irradiated at 100 Gy) males

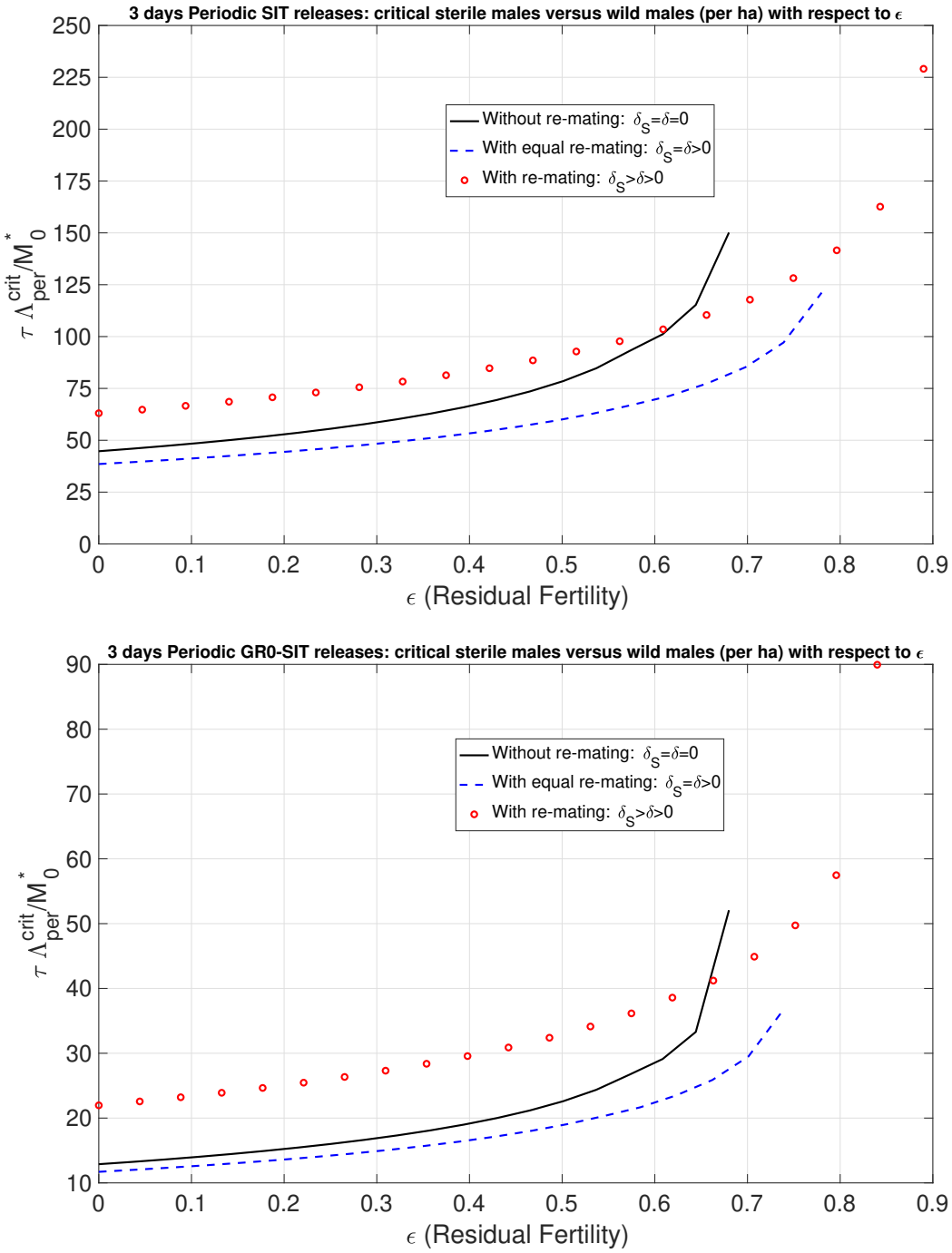

Figure 4: $\tau = 3$ days - Critical periodic releases value estimates when equal and non-equal re-mating is considered or not: (a) without GRO-treatment; (b) with GRO-treatment

mated again 24h after their first mating, and 25% of males mated up to five times. Sterile Queensland flies were reported to have a maximum of 2 or 3 mating capacity [42]; however, even depleted, they were able to copulate and to induce refractoriness in females. Studies have shown that the injection of male accessory gland substances was able to induce refractoriness in Queensland flies, but also in medflies [1, 22]. Costa et al. [14] showed that a lower quantity of sperm transferred would increase the chances of re-mating in females. A more precise understanding of sterile male reproductive capacity could allow optimization of release frequency, ensuring that mating sterile males always saturates the field.

6 Conclusion

The aim of this study was to investigate the role of (equal and non-equal) re-mating and residual fertility on sterile insect technique efficiency. We confirm the constraint found in [5] to be able to reach elimination: residual fertility is constrained by the basic offspring number of the targeted population, i.e. $\varepsilon\mathcal{N} < 1$. In other words, the larger the basic offspring number, the lower the tolerance that can be allowed on residual fertility. Our theoretical and numerical results also show that equal re-mating may be a benefit, even when residual fertility occurs. As the level of residual fertility is related to the radiation dose, our results indicate that a small percentage of residual fertility is not necessarily detrimental to SIT. This is important because the radiation dose has an impact on the lifespan and competitiveness of sterile males. However, it remains a parameter that has to be controlled very carefully, as the tolerable limit is below 1%. When re-mating is not equal, that is, re-mating is faster after mating with a sterile male, it is necessary to drastically increase the release ratios. In this case, re-mating can be detrimental to SIT release and, thus, SIT success. Our results also show that GRO-treatment is very important to enhance the competitiveness of sterile males and allows reducing the release ratios.

This study was performed within the framework of an SIT feasibility project, CeraTIS-Corse in Corsica on a 400 ha area of citrus and stone fruits. The Corsican agricultural context is a mosaic of small plots with different cultivars that span the harvest over several months. The climate is particularly suitable for medflies, which are found in traps from May to December, with low adult levels potentially hibernating and reproducing in pomelos as early as February. Medfly life parameters are known to vary according to the host fruit species, and models can consider this variability according to fruit phenology and temperature variation, when available, over the year to obtain a picture of the natural evolution of the population, as in [15] for *Aedes albopictus* in Réunion island. SIT models consider more simplistic population dynamics with averaged parameters over the year; however, it would be interesting to understand whether variation of released male numbers over the year brings a better or similar control while reducing the program costs.

Last but not least, it would be interesting to study another SIT control objective, like reducing the wild population below a given economic threshold, like in [15] where decaying the epidemiological risk was possible even if $\varepsilon\mathcal{N} > 1$.

No operational SIT program exists in France yet; however, there is growing interest in making this tool available for farmers as a response to environmental requirements and to the removal of chemical pesticides. The cost-efficiency of SIT will be a crucial element in growers' adoption of the technique. Therefore, understanding the optimal release strategy that will reduce production costs while ensuring high field efficacy is key. To date, there is no sterile flies production capacity in France, therefore SIT implementation would rely on import from a producing country. It is therefore crucial to determine the limiting factors that may affect release success. This study has shown that field operators should try to gather a better understanding of re-mating occurrence in the field, but should also carefully specify or control the accuracy of the sterilizing dose and level of residual fertility of the imported sterile flies. Due to its genericity, our model can be applied to other fruit flies, and even to mosquitoes.

Acknowledgements The authors acknowledge the financial support of the CeraTIS - Corse project, within the framework of ECOPHYTO 2019, "Leviers territoriaux pour réduire l'utilisation et les risques liés aux produits phytopharmaceutiques (2020 - 2023)". YD is also co-funded by the European Union: Agricultural Fund for Rural Development (EAFRD), by the Departmental council of La Réunion and by the Regional council of la Réunion. YD acknowledges the support of the DST/NRF SARChI Chair, South Africa M3B2 in Mathematical Models and Methods in Biosciences and Bioengineering at the University of Pretoria, South Africa (grant 82770).

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7 Appendix A: Stability/unstability of the model without SIT

7.1 Stability of the non-SIT model

We compute

$$J(X) = \begin{pmatrix} -\frac{b}{K}F_W - (\nu_A + \mu_A) & 0 & 0 & b\left(1 - \frac{A}{K}\right) \\ r\nu_A & -(\nu_Y + \mu_Y) & 0 & \delta \\ (1-r)\,\nu_A & 0 & -\mu_M & 0 \\ 0 & p_Y\nu_Y & 0 & -(\delta + \mu_F) \end{pmatrix},$$

then we consider

$$N = \begin{pmatrix} -\frac{b}{K}F_W - (\nu_A + \mu_A) & 0 & 0 & b\left(1 - \frac{A}{K}\right) \\ 0 & -(\nu_Y + \mu_Y) & 0 & \delta \\ 0 & 0 & -\mu_M & 0 \\ 0 & 0 & 0 & -(\delta + \mu_F) \end{pmatrix}, \qquad M = \begin{pmatrix} 0 & 0 & 0 & 0 \\ r\nu_A & 0 & 0 & 0 \\ (1-r)\,\nu_A & 0 & 0 & 0 \\ 0 & p_Y\nu_Y & 0 & 0 \end{pmatrix}$$

Matrix N is Metzler stable and M a nonnegative matrix, such that $M + N$ is a regular splitting. Then

$$-N^{-1} = \begin{pmatrix} \frac{1}{\frac{b}{K}F_W + (\nu_A + \mu_A)} & 0 & 0 & \frac{b}{(\delta + \mu_F)\left(\frac{b}{K}F_W + (\nu_A + \mu_A)\right)}\left(1 - \frac{A}{K}\right) \\ 0 & \frac{1}{(\nu_Y + \mu_Y)} & 0 & \frac{\delta}{(\delta + \mu_F)(\nu_Y + \mu_Y)} \\ 0 & 0 & \frac{1}{\mu_M} & 0 \\ 0 & 0 & 0 & \frac{1}{(\delta + \mu_F)} \end{pmatrix},$$

such that

$$-N^{-1}M = \begin{pmatrix} 0 & \frac{bp_Y\nu_Y}{(\delta + \mu_F)\left(\frac{b}{K}F_W + (\nu_A + \mu_A)\right)}\left(1 - \frac{A}{K}\right) & 0 & 0 \\ \frac{r\nu_A}{(\nu_Y + \mu_Y)} & \frac{\delta p_Y\nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)} & 0 & 0 \\ \frac{(1-r)\,\nu_A}{\mu_M} & 0 & 0 & 0 \\ 0 & \frac{p_Y\nu_Y}{\delta + \mu_F} & 0 & 0 \end{pmatrix}.$$

Thus, we have

$$p(z) = z^2 \begin{vmatrix} -z & \frac{bp_Y\nu_Y}{(\delta + \mu_F)\left(\frac{b}{K}F_W + (\nu_A + \mu_A)\right)}\left(1 - \frac{A}{K}\right) \\ \frac{r\nu_A}{(\nu_Y + \mu_Y)} & \frac{\delta p_Y\nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)} - z \end{vmatrix},$$

that is

$$p(z) = z^2 q(z) = z^2\left(z^2 - \frac{\delta p_Y\nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)}z - \frac{r\nu_A}{(\nu_Y + \mu_Y)}\frac{bp_Y\nu_Y}{(\delta + \mu_F)\left(\frac{b}{K}F_W + (\nu_A + \mu_A)\right)}\left(1 - \frac{A}{K}\right)\right),$$

with

$$q(z) = z^2 - \frac{\delta p_Y\nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)}z - \mathcal{R}_\delta\frac{\nu_A + \mu_A}{\left(\frac{b}{K}F_W + (\nu_A + \mu_A)\right)}\left(1 - \frac{A}{K}\right),$$

Thus, for a second order polynomial $q(z) = z^2 + a_1 z + a_2$, Jury criterion leads to the following necessary conditions

$$\begin{cases} q(1) > 0, \\ q(-1) > 0, \end{cases}$$

and a sufficient condition

$$|a_2| < 1.$$

- When $E = \mathbf{0}$, then

$$q(z) = z^2 - \frac{\delta p_Y \nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)} z - \mathcal{R}_\delta,$$

  Then, $|a_2| < 1$ iff $\mathcal{R}_\delta < 1$. Then $q(-1) > 0$ and

$$q(1) = 1 - \frac{\delta p_Y \nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)} - \mathcal{R}_\delta = \mathcal{R}_\delta \left(\frac{1}{\mathcal{N}} - 1 \right) > 0,$$

  iff $\mathcal{N} < 1$. Thus, $\mathbf{0}$ is LAS iff $\mathcal{R}_\delta < 1$ and $\mathcal{N} < 1$, that is iff $\mathcal{N} < 1$, because $\mathcal{R}_\delta \leq \mathcal{N}$.

- When $E = E^*$, we have

$$A^* = \left(1 - \frac{1}{\mathcal{N}}\right) K,$$

  and

$$F_W^* = \frac{r \nu_A p_Y \nu_Y}{(\nu_Y \mu_F + \mu_Y (\delta + \mu_F))} \left(1 - \frac{1}{\mathcal{N}}\right) K = \frac{\nu_A + \mu_A}{b} (\mathcal{N} - 1) K.$$

  Thus

$$\mathcal{R}_\delta \frac{\nu_A + \mu_A}{\left(\frac{b}{K} F_W + (\nu_A + \mu_A)\right)} \left(1 - \frac{A}{K}\right) = \frac{\mathcal{R}_\delta}{\mathcal{N}^2}.$$

$$q(1) = 1 - \frac{\delta p_Y \nu_Y}{(\delta + \mu_F)(\nu_Y + \mu_Y)} - \frac{\mathcal{R}_\delta}{\mathcal{N}^2} = \frac{\mathcal{R}_\delta}{\mathcal{N}} \left(1 - \frac{1}{\mathcal{N}}\right) > 0,$$

  iff $\mathcal{N} > 1$. Obviously, under the same condition we have $q(-1) > 0$ and since $\frac{\mathcal{R}_\delta}{\mathcal{N}^2} < 1$ we have $|a_2| < 1$. Thus E^* is LAS iff $\mathcal{N} > 1$.

8 Existence of Equilibria

Looking for equilibria, from the right-hand side of system (1), we derive the following equations We have

$$\nu_Y Y = (\delta + \mu_F) F_W + (\delta_S + \mu_F) F_S,$$

$$r \nu_A A^* = \mu_F F_W + \mu_F F_S + \mu_Y Y = \left(\mu_F + \frac{\mu_Y}{\nu_Y} (\delta + \mu_F)\right) F_W + \left(\mu_F + \frac{\mu_Y}{\nu_Y} (\delta_S + \mu_F)\right) F_S.$$

Thus

$$A^* = \frac{1}{r \nu_A} \left(\left(\mu_F + \frac{\mu_Y}{\nu_Y} (\delta + \mu_F)\right) F_W + \left(\mu_F + \frac{\mu_Y}{\nu_Y} (\delta_S + \mu_F)\right) F_S \right).$$

Since $\mu_M M^* = (1 - r) \nu_A A^*$, we have

$$\frac{M^*}{M^* + \gamma M_T} = \frac{(1 - r) \nu_A}{(1 - r) \nu_A A^* + \mu_M \gamma M_T} A^*.$$

Similarly, we have

$$\frac{\mu_M \gamma M_T}{(1 - r) \nu_A A^* + \mu_M \gamma M_T} (\delta + \mu_F) F_W = (\delta_S + \mu_F) F_S \left(1 - \frac{\mu_M \gamma M_T}{(1 - r) \nu_A A^* + \mu_M \gamma M_T}\right),$$

that is

$$\mu_M \gamma M_T (\delta + \mu_F) F_W = (1 - r) \nu_A A^* (\delta_S + \mu_F) F_S.$$

Assuming $M_T > 0$, then

$$\begin{aligned} A^* &= \frac{1}{r\nu_A}\left(\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)F_W + \left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)F_S\right) \\ &= \frac{1}{r\nu_E}\left(\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)(1-r)\nu_A A^* \frac{(\delta_S+\mu_F)}{\mu_M\gamma M_T(\delta+\mu_F)} + \left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)\right)F_S. \end{aligned}$$

Thus we can deduce

$$F_S^* = \frac{r\nu_A A^*}{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)(1-r)\nu_A A^* \frac{(\delta_S+\mu_F)}{\mu_M\gamma M_T(\delta+\mu_F)} + \left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)}$$

and

$$F_W^* = \frac{(1-r)r}{\mu_M\gamma M_T(\delta+\mu_F)} \frac{(\delta_S+\mu_F)(\nu_A A^*)^2}{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)(1-r)\nu_A A^* \frac{(\delta_S+\mu_F)}{\mu_M\gamma M_T(\delta+\mu_F)} + \left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)}.$$

such that replacing F_W^* and F_S^* into $b(F_W + \epsilon F_S)\left(1 - \frac{A^*}{K}\right) = (\nu_A + \mu_A)A^*$, leads to

$$\begin{aligned} &br\nu_E\left(\frac{(1-r)(\delta_S+\mu_F)}{\mu_M\gamma M_T(\delta+\mu_F)}\nu_A A^* + \epsilon\right)\left(1 - \frac{A^*}{K}\right) = \\ &= (\nu_A+\mu_A)\left(\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)\frac{(1-r)(\delta_S+\mu_F)}{\mu_M\gamma M_T(\delta+\mu_F)}\nu_A A^* + \left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)\right) \end{aligned}$$

If $\delta_S = \delta$, then

$$((1-r)\nu_A A^* + \epsilon\mu_M\gamma M_T)\left(1 - \frac{A^*}{K}\right) = = \frac{1}{\mathcal{N}}((1-r)\nu_A A^* + \mu_M\gamma M_T).$$

Otherwise

$$\begin{aligned} &br\nu_A((1-r)(\delta_S+\mu_F)\nu_A A^* + \epsilon\mu_M\gamma M_T(\delta+\mu_F))\left(1 - \frac{A^*}{K}\right) = \\ &= (\nu_A+\mu_A)\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)\left((1-r)(\delta_S+\mu_F)\nu_A A^* + \frac{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)}{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)}\mu_M\gamma M_T(\delta+\mu_F)\right), \end{aligned}$$

that is

$$\begin{aligned} &((1-r)(\delta_S+\mu_F)\nu_A A^* + \epsilon\mu_M\gamma M_T(\delta+\mu_F))\left(1 - \frac{A^*}{K}\right) = \\ &= \frac{1}{\mathcal{N}}\left((1-r)(\delta_S+\mu_F)\nu_A A^* + \frac{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta_S+\mu_F)\right)}{\left(\mu_F + \frac{\mu_Y}{\nu_Y}(\delta+\mu_F)\right)}\mu_M\gamma M_T(\delta+\mu_F)\right), \end{aligned}$$

leading to the second order equation

$$\begin{aligned} &\frac{(1-r)(\delta_S+\mu_F)\nu_A}{K}(A^*)^2 - \left((1-r)(\delta_S+\mu_F)\nu_A\left(1 - \frac{1}{\mathcal{N}}\right) - \frac{\epsilon\mu_M\gamma M_T(\delta+\mu_F)}{K}\right)A^* + \\ &+ \left(\frac{1}{\mathcal{N}}\frac{(\mu_F\nu_Y + \mu_Y(\delta_S+\mu_F))}{(\mu_F\nu_Y + \mu_Y(\delta+\mu_F))} - \varepsilon\right)\mu_M\gamma M_T(\delta+\mu_F) = 0. \end{aligned}$$

That is

$$\begin{aligned} &\frac{(1-r)(\delta_S+\mu_F)\nu_A}{K}(A^*)^2 - \left((1-r)(\delta_S+\mu_F)\nu_A\left(1 - \frac{1}{\mathcal{N}}\right) - \frac{\epsilon\mu_M\gamma M_T(\delta+\mu_F)}{K}\right)A^* + \\ &\qquad + \left(\frac{1}{\mathcal{N}_S} - \varepsilon\right)\mu_M\gamma M_T(\delta+\mu_F) = 0, \end{aligned}$$

where $\mathcal{N}_S$ is defined in (10). We compute the discriminant

$$\Delta(\varepsilon) = \left((1-r)(\delta_S+\mu_F)\nu_A\left(1 - \frac{1}{\mathcal{N}}\right) - \frac{\epsilon\mu_M\gamma M_T(\delta+\mu_F)}{K}\right)^2 - 4\left(\frac{1}{\mathcal{N}_S} - \varepsilon\right)(1-r)(\delta_S+\mu_F)\nu_A(\delta+\mu_F)\mu_M\frac{\gamma M_T}{K}.$$

- Assume $\epsilon = 0$, then

$$\Delta(0) = \left((1-r)(\delta_S+\mu_F)\nu_A\left(1-\frac{1}{\mathcal{N}}\right)\right)^2 - \frac{4}{\mathcal{N}_S}(1-r)(\delta_S+\mu_F)\nu_A(\delta+\mu_F)\mu_M\frac{\gamma M_T}{K}.$$

Setting

$$\Lambda_{cont}^{crit} = \frac{\mu_T(\delta_S+\mu_F)(1-r)\nu_A\left(1-\frac{1}{\mathcal{N}}\right)^2}{(\delta+\mu_F)\mu_M}\frac{\mathcal{N}_S}{4\gamma}K = \mu_T\frac{(\delta_S+\mu_F)}{(\delta+\mu_F)}\left(1-\frac{1}{\mathcal{N}}\right)\frac{\mathcal{N}_S}{4\gamma}M_0^*, \tag{18}$$

we deduce that when $\Lambda > \Lambda_{cont}^{crit}$, then $\Delta(0) < 0$, such that there is no positive equilibrium. Only the trivial equilibrium, $\mathbf{0}$, exists. Based on previous results, we know that in that case, the population can be driven to elimination.

Remark 8 *It is interesting to notice that the threshold value M_{T_1} is a multiple of the wild males at equilibrium, M_0^*. Thus, if the sterile males are fully competitive, i.e. $\gamma = 1$, then it suffices to release at least $\frac{(\delta_S+\mu_F)}{(\delta+\mu_F)}\left(1-\frac{1}{\mathcal{N}}\right)\frac{\mathcal{N}_S}{4}$ times the amount of wild male mosquitoes at equilibrium. When $\delta_S = \delta$, we recover the result, i.e. $\frac{\mathcal{N}-1}{4\gamma}M_0^*$, obtained in [48], and also in [49], where discrete SIT models have been considered.*

When $M_T \in [0, M_{T_1})$, then, using (9), we show that two positive equilibria exist $E_{0,-}^*$ and $E_{0,+}^*$ such that

$$A_{0,-}^* = \frac{\mu_M}{2(1-r)\nu_A}\left(M_0^* - \sqrt{(M_0^*)^2 - \frac{\mathcal{N}}{\mathcal{N}_S}\frac{4}{\mathcal{N}-1}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}M_0^*\gamma M_T}\right)$$

that is

$$A_{0,-}^* = \frac{1}{2}A_0^*\left(1-\sqrt{1-\frac{\mathcal{N}}{\mathcal{N}_S}\frac{4}{\mathcal{N}-1}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\frac{\gamma M_T}{M_0^*}}\right),$$

and

$$A_{0,+}^* = \frac{1}{2}A_0^*\left(1+\sqrt{1-\frac{\mathcal{N}}{\mathcal{N}_S}\frac{4}{\mathcal{N}-1}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\frac{\gamma M_T}{M_0^*}}\right)$$

Note carefully that $A_{0,+}^* \in \left(\frac{A_0^*}{2}, A_0^*\right)$. Last but not least, for a given value of $A_{0,-}^*$ we can estimate the minimal amount of sterile males to release. This will be useful later.

- Assume now that $\varepsilon > 0$.
  - When $\frac{1}{\mathcal{N}_S} < \varepsilon$, then $\Delta_\varepsilon > 0$: there exists only one positive equilibrium

$$A^* = \frac{\mu_M}{2(1-r)\nu_A}\left(M_0^* - \epsilon\gamma M_T\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)} + \right.$$
$$\left. + \sqrt{\left(M_0^* - \epsilon\gamma M_T\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\right)^2 + \frac{4\mathcal{N}}{\mathcal{N}-1}\left(\varepsilon - \frac{1}{\mathcal{N}_S}\right)\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\gamma M_T M_0^*}\right)$$

    A straightforward analysis shows that $A^*(M_T)$ is bounded from below by

$$A_0^*\sqrt{\frac{\mathcal{N}}{\mathcal{N}-1}\left(1-\frac{1}{\varepsilon\mathcal{N}_S}\right)},$$

    where A_0^* is defined in (6). Thus, whatever the size of the release, the wild equilibrium will always be bounded from below by a positive equilibrium, depending on the value taken by ε.

– When $\varepsilon = \dfrac{1}{\mathcal{N}_S}$, then $\Delta(\varepsilon) = 0$, iff

$$\gamma M_{T_*} = \frac{\delta_S + \mu_F}{\delta + \mu_F} \mathcal{N}_S M_0^*. \tag{19}$$

When $M_T \geq M_{T_*}$, then there exists no positive equilibrium, while when $0 \leq M_T < M_{T_*}$, there exists one positive equilibrium, E_*, such that

$$A^* = A_0^* - \frac{1}{\mathcal{N}_S}\left(1 - \frac{1}{\mathcal{N}}\right)\frac{(\delta + \mu_F)}{(\delta_S + \mu_F)}\frac{\gamma M_T}{M_0^*}K.$$

Remark 9 *Result (19) is very interesting and shows that if the residual fertility is large, and at least greater than or equal to $1/\mathcal{N}_S$, then the proportion of sterile males to release is at least equal to $\mathcal{N}_S$. For a pest, like C. capitata, $\mathcal{N}_S$ can be greater than 100. Thus, it is necessary to release at least, 100 times more sterile males than wild males!*

– When $\varepsilon < \dfrac{1}{\mathcal{N}_S}$, then

$$\begin{aligned}\Delta(M_T) = \quad & \left((1-r)(\delta_S + \mu_F)\nu_E\left(1 - \frac{1}{\mathcal{N}}\right)\right)^2 + \left(\frac{\epsilon\mu_M\gamma M_T(\delta + \mu_F)}{K}\right)^2 \\ & -2(1-r)(\delta_S + \mu_F)\nu_A\left(\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right)\right)(\delta + \mu_F)\mu_M\frac{\gamma M_T}{K}.\end{aligned}$$

Setting $x = (\delta + \mu_F)\mu_M\dfrac{\gamma M_T}{K}$, we have a second-order polynomial in x to solve

$$(\varepsilon x)^2 - 2(1-r)(\delta_S + \mu_F)\nu_E\left(\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right)\right)x + \left((1-r)(\delta_S + \mu_F)\nu_A\left(1 - \frac{1}{\mathcal{N}}\right)\right)^2 = 0,$$

such that

$$\Delta_{M_T} = 4\left((1-r)(\delta_S + \mu_F)\nu_A\left(\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right)\right)\right)^2 - 4\varepsilon^2\left((1-r)(\delta_S + \mu_F)\nu_A\left(1 - \frac{1}{\mathcal{N}}\right)\right)^2$$

$$\Delta_{M_T} = 4\left((1-r)(\delta_S + \mu_F)\nu_A\right)^2\left[\left(\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right)\right)^2 - \varepsilon^2\left(1 - \frac{1}{\mathcal{N}}\right)^2\right]$$

$$\Delta_{M_T} = 4\left((1-r)(\delta_S + \mu_F)\nu_A\right)^2\left[\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right) - \varepsilon\left(1 - \frac{1}{\mathcal{N}}\right)\right]\left[\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right) + \varepsilon\left(1 - \frac{1}{\mathcal{N}}\right)\right],$$

that is

$$\Delta_{M_T} = 16\left((1-r)(\delta_S + \mu_F)\nu_A\right)^2\left[\left(\frac{1}{\mathcal{N}_S} - \varepsilon\right)\right]\left[\frac{1}{\mathcal{N}_S} - \frac{\varepsilon}{\mathcal{N}}\right].$$

We deduce that $\Delta_{M_T} > 0$ iff $\varepsilon < \dfrac{1}{\mathcal{N}_S}$, such that

$$\gamma M_{T_1,s}^{\varepsilon} = \frac{(1-r)(\delta_S + \mu_F)\nu_A}{(\delta + \mu_F)\mu_M}\frac{\dfrac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \dfrac{1}{\mathcal{N}}\right) - 2\sqrt{\left(\dfrac{1}{\mathcal{N}_S} - \varepsilon\right)\left(\dfrac{1}{\mathcal{N}_S} - \dfrac{\varepsilon}{\mathcal{N}}\right)}}{\varepsilon^2}K$$

$$\gamma M_{T_1,s}^{\varepsilon} = \frac{(1-r)(\delta_S + \mu_F)\nu_A}{(\delta + \mu_F)\mu_M}\frac{\left(\dfrac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \dfrac{1}{\mathcal{N}}\right)\right)^2 - 4\left(\dfrac{1}{\mathcal{N}_S} - \varepsilon\right)\left(\dfrac{1}{\mathcal{N}_S} - \dfrac{\varepsilon}{\mathcal{N}}\right)}{\varepsilon^2\left(\dfrac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \dfrac{1}{\mathcal{N}}\right) + 2\sqrt{\left(\dfrac{1}{\mathcal{N}_S} - \varepsilon\right)\left(\dfrac{1}{\mathcal{N}_S} - \dfrac{\varepsilon}{\mathcal{N}}\right)}\right)}K.$$

However, the numerator can be simplified

$$\left(\frac{2}{\mathcal{N}_S} - \varepsilon\left(1 + \frac{1}{\mathcal{N}}\right)\right)^2 - 4\left(\frac{1}{\mathcal{N}_S} - \varepsilon\right)\left(\frac{1}{\mathcal{N}_S} - \frac{\varepsilon}{\mathcal{N}}\right) = \varepsilon^2\left(1 - \frac{1}{\mathcal{N}}\right)^2.$$

Thus

$$\gamma M^{\varepsilon}_{T_1,s} = \frac{(\delta_S+\mu_F)}{(\delta+\mu_F)} \frac{\left(1-\frac{1}{\mathcal{N}}\right)}{\frac{2}{\mathcal{N}_S} - \varepsilon\left(1+\frac{1}{\mathcal{N}}\right) + 2\sqrt{\left(\frac{1}{\mathcal{N}_S}-\varepsilon\right)\left(\frac{1}{\mathcal{N}_S}-\frac{\varepsilon}{\mathcal{N}}\right)}} M_0^*, \tag{20}$$

When $\varepsilon = 0$, we recover (18), and when $\varepsilon = \frac{1}{\mathcal{N}_S}$, we recover (19).

Of course, $\gamma M^{\varepsilon}_{T_1}$ is increasing according to ε, the larger the residual fertility the larger the releases. When $\varepsilon = 0$, we recover (18), and when $\varepsilon = \frac{1}{\mathcal{N}_S}$, we recover (19).

Thus, we can deduce that if $M_T > M^{\varepsilon}_{T_1}$, then there is no positive equilibrium, only the trivial ones, $\mathbf{0}$. When $0 < M_T < M^{\varepsilon}_{T_1}$, then the system admits two positive equilibria, $E^*_{\varepsilon,-}$ and $E^*_{\varepsilon,+}$, such that

$$A^*_{\varepsilon,-} = \frac{A_0^*}{2}\left(1-\epsilon\frac{\gamma M_T}{M_0^*}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)} - \sqrt{\left(1-\epsilon\frac{\gamma M_T}{M_0^*}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\right)^2 - \frac{4\mathcal{N}}{\mathcal{N}-1}\left(\frac{1}{\mathcal{N}_S}-\varepsilon\right)\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\frac{\gamma M_T}{M_0^*}}\right).$$

and

$$A^*_{\varepsilon,+} = \frac{A_0^*}{2}\left(1-\epsilon\frac{\gamma M_T}{M_0^*}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)} + \sqrt{\left(1-\epsilon\frac{\gamma M_T}{M_0^*}\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\right)^2 - \frac{4\mathcal{N}}{\mathcal{N}-1}\left(\frac{1}{\mathcal{N}_S}-\varepsilon\right)\frac{(\delta+\mu_F)}{(\delta_S+\mu_F)}\frac{\gamma M_T}{M_0^*}}\right).$$

9 Appendix: SIT model - Stability analysis of Equilibrium 0

We compute the Jacobian related to system (2)

$$J(X) = \begin{pmatrix} -\frac{b}{K}(F_W+\varepsilon F_S) - (\nu_A+\mu_A) & 0 & 0 & b\left(1-\frac{A}{K}\right) & \varepsilon b\left(1-\frac{A}{K}\right) \\ r\nu_A & -(\nu_Y+\mu_Y) & 0 & \delta & \delta_S \\ (1-r)\nu_A & 0 & -\mu_M & 0 & 0 \\ 0 & p_Y\nu_Y\frac{M}{M+\gamma M_T} & p_Y\nu_Y\frac{\gamma M_T}{(M+\gamma M_T)^2}Y & -(\delta+\mu_F) & 0 \\ 0 & p_Y\nu_Y\frac{\gamma M_T}{M+\gamma M_T} & -p_Y\nu_Y\frac{\gamma M_T}{(M+\gamma M_T)^2}Y & 0 & -(\delta_S+\mu_F) \end{pmatrix},$$

from which we deduce

$$J(\mathbf{0}) = \begin{pmatrix} -(\nu_A+\mu_A) & 0 & 0 & b & \varepsilon b \\ r\nu_A & -(\nu_Y+\mu_Y) & 0 & \delta & \delta_S \\ (1-r)\nu_A & 0 & -\mu_M & 0 & 0 \\ 0 & 0 & 0 & -(\delta+\mu_F) & 0 \\ 0 & p_Y\nu_Y & 0 & 0 & -(\delta_S+\mu_F) \end{pmatrix}.$$

Thus the characteristic polynomial is given by

$$q(z) = -(z+\mu_M))(z+\delta+\mu_F)p(z),$$

with

$$p(z) = -\begin{vmatrix} -(\delta_S+\mu_F)-z & 0 & p_Y\nu_Y \\ \varepsilon b & -(\nu_A+\mu_A)-z & 0 \\ \delta_S & r\nu_A & -(\nu_Y+\mu_Y)-z \end{vmatrix}.$$

Thus

$$p(z) = ((\nu_Y+\mu_Y)+z)((\nu_A+\mu_A)+z)((\delta_S+\mu_F)+z) - p_Y\nu_Y(\varepsilon b r\nu_A + \delta_S((\nu_A+\mu_A)+z))$$

$$p(z) = ((\nu_A+\mu_A)+z)[((\nu_Y+\mu_Y)+z)((\delta_S+\mu_F)+z) - p_Y\nu_Y\delta_S] - \varepsilon b r\nu_A p_Y\nu_Y$$

$$p(z) = ((\nu_A + \mu_A) + z)\left[(\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y + ((\nu_Y + \mu_Y) + (\delta_S + \mu_F))\, z + z^2\right] - \varepsilon b r \nu_A p_Y \nu_Y$$

Expanding $q(z)$, we deduce

$$\begin{aligned} p(z) = \quad & z^3 + ((\nu_A + \mu_A) + (\nu_Y + \mu_Y) + (\delta_S + \mu_F))\, z^2 + ((\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y)\, z + \\ & + ((\nu_A + \mu_A)\left[(\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y\right] - \varepsilon b r \nu_A p_Y \nu_Y) \end{aligned}$$

$$\begin{aligned} p(z) = \quad & z^3 + ((\nu_A + \mu_A) + (\nu_Y + \mu_Y) + (\delta_S + \mu_F))\, z^2 + ((\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y)\, z + \\ & + (\nu_A + \mu_A)\left[(\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y\right](1 - \varepsilon \mathcal{R}_S) \end{aligned}$$

Thus, setting we have

$$p(z) = z^3 + a_2 z^2 + a_2 z + a_0,$$

with

$$\begin{aligned} a_2 &= (\nu_A + \mu_A) + (\nu_Y + \mu_Y) + (\delta_S + \mu_F), \\ a_1 &= (\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y, \\ a_0 &= (\nu_A + \mu_A)\left[(\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S p_Y \nu_Y\right](1 - \varepsilon \mathcal{R}_S). \end{aligned}$$

All coefficients are positive provided that $\varepsilon \mathcal{R}_S < 1$. In addition

$$a_2 a_1 - a_0 = ((\nu_Y + \mu_Y) + (\delta_S + \mu_F) + (\nu_A + \mu_A)\,\varepsilon \mathcal{R}_S)\left[(\nu_Y + \mu_Y)(\delta_S + \mu_F) - \delta_S \nu_Y\right] > 0.$$

Thus we deduce that $\mathbf{0}$ is LAS when $\varepsilon \mathcal{R}_S < 1$, and unstable, otherwise.

9.1 Appendix C: Stability analysis of the SIT Upper-system

The Jacobian related to system (3) leads to

$$J(X) = \begin{pmatrix} -\frac{b}{K}((1-\epsilon)F_W + \epsilon F_T) - (\nu_A + \mu_A) & 0 & 0 & b(1-\epsilon)\left(1 - \frac{A}{K}\right) & b\epsilon\left(1 - \frac{A}{K}\right) \\ r\nu_A & -(\nu_Y + \mu_Y) & 0 & 0 & \delta_S \\ (1-r)\,\nu_A & 0 & -\mu_M & 0 & 0 \\ 0 & \nu_Y \frac{M}{M + \gamma M_T} & \nu_Y \frac{\gamma M_T}{(M + \gamma M_T)^2} Y & -(\delta + \mu_F) & 0 \\ 0 & \nu_Y & 0 & (\delta_S - \delta) & -(\delta_S + \mu_F) \end{pmatrix}.$$

Thus

$$J(\mathbf{0}) = \begin{pmatrix} -(\nu_A + \mu_A) & 0 & 0 & b(1-\epsilon) & b\epsilon \\ r\nu_A & -(\nu_Y + \mu_Y) & 0 & 0 & \delta_S \\ (1-r)\,\nu_A & 0 & -\mu_M & 0 & 0 \\ 0 & 0 & 0 & -(\delta + \mu_F) & 0 \\ 0 & \nu_Y & 0 & (\delta_S - \delta) & -(\delta_S + \mu_F) \end{pmatrix}.$$

We consider the following decomposition $J = N + M$,with

$$N = \begin{pmatrix} -(\nu_A + \mu_A) & 0 & 0 & b(1-\epsilon) & b\epsilon \\ 0 & -(\nu_Y + \mu_Y) & 0 & 0 & \delta_S \\ 0 & 0 & -\mu_M & 0 & 0 \\ 0 & 0 & 0 & -(\delta + \mu_F) & 0 \\ 0 & 0 & 0 & 0 & -(\delta_S + \mu_F) \end{pmatrix},$$

and

$$M = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ r\nu_A & 0 & 0 & 0 & 0 \\ (1-r)\,\nu_A & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & \nu_Y & 0 & (\delta_S - \delta) & 0 \end{pmatrix},$$

such that N is Metzler stable and M a non-negative matrix.]We have

$$-N^{-1} = \begin{pmatrix} \frac{1}{\nu_A+\mu_A} & 0 & 0 & \frac{b(1-\epsilon)}{(\nu_A+\mu_A)(\delta+\mu_F)} & \frac{b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)} \\ 0 & \frac{1}{(\nu_Y+\mu_Y)} & 0 & 0 & \frac{\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} \\ 0 & 0 & \frac{1}{\mu_M} & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{(\delta+\mu_F)} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{(\delta_S+\mu_F)} \end{pmatrix},$$

such that

$$-N^{-1}M = \begin{pmatrix} 0 & \frac{\nu_Y b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)} & 0 & \frac{(\delta_S-\delta)b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)} & 0 \\ \frac{r\nu_A}{(\nu_Y+\mu_Y)} & \frac{\nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} & 0 & \frac{\delta_S(\delta_S-\delta)}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} & 0 \\ \frac{(1-r)\nu_A}{\mu_M} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{\nu_Y}{(\delta_S+\mu_F)} & 0 & \frac{(\delta_S-\delta)}{(\delta_S+\mu_F)} & 0 \end{pmatrix}$$

Thus the characteristic polynomial becomes

$$p(\lambda) = \lambda^2 \begin{vmatrix} -\lambda & 0 & 0 \\ \frac{(\delta_S-\delta)b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)} & -\lambda & \frac{\nu_Y b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)} \\ \frac{\delta_S(\delta_S-\delta)}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} & \frac{r\nu_A}{(\nu_Y+\mu_Y)} & \frac{\nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} - \lambda \end{vmatrix}$$

$$p(\lambda) = -\lambda^3\left(\lambda^2 + \frac{\nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)}\lambda - \frac{\nu_Y b\epsilon}{(\nu_A+\mu_A)(\delta_S+\mu_F)}\frac{r\nu_A}{(\nu_Y+\mu_Y)}\right) = -\lambda^3 q(\lambda),$$

with

$$q(\lambda) = \lambda^2 + \frac{\nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)}\lambda - \varepsilon\mathcal{R}_{\delta_S},$$

and

$$\mathcal{R}_{\delta_S} = \frac{br\nu_A\nu_Y}{(\delta_S+\mu_F)(\nu_Y+\mu_Y)(\nu_A+\mu_A)},$$

Following Jury's criterion, we needs $\varepsilon\mathcal{R}_{\delta_S} < 1$, $q(1) > 0$ and $q(-1) > 0$. In particular

$$\begin{aligned} q(-1) &= 1 - \frac{\nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} - \varepsilon\mathcal{R}_S \\ &= \frac{(\nu_Y+\mu_Y)(\delta_S+\mu_F) - \nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)} - \varepsilon\mathcal{R}_S \\ &= \frac{(\nu_Y+\mu_Y)(\delta_S+\mu_F) - \nu_Y\delta_S}{(\nu_Y+\mu_Y)(\delta_S+\mu_F)}(1-\varepsilon\mathcal{N}_S) > 0 \end{aligned}$$

when $\varepsilon\mathcal{N}_S < 1$. Since $\mathcal{N}_S > \mathcal{R}_{\delta_S S}$, we deduce that $\varepsilon\mathcal{R}_{\delta_S} < 1$, which also implies that $q(1) > 0$. Thus, when $\varepsilon\mathcal{N}_S < 1$, $\mathbf{0}$ is LAS for the Upper monotone system related to system (3).

Assume now that Λ, the release rate, is large enough, at least greater than $\Lambda^{crit}_{cont,\varepsilon}$, then according to Proposition 1, page 7, only one equilibrium exists, $\mathbf{0}$, and it is LAS when $\varepsilon\mathcal{N}_S < 1$. Thanks to the Theory of Monotone Cooperative system [47], and following [3, Theorem 6] or [4, Theorem 1], it is straightforward to deduce that $\mathbf{0}$ is not only LAS but it is GAS when $\varepsilon\mathcal{N}_S < 1$. The equilibrium $\mathbf{0}$ being GAS for the Upper Monotone system related to system (3), it is also GAS for system (3) and thus for system (2).