

Natural enemies deployment in patchy environments for augmentative biological control

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21 1. Introduction

22 Pests are living organisms which cause harm to or damage animal livestock, crop plants
23 or stored products (Jain and Bhargava [1]); they impair ecosystem productivity, diversity
24 and stability. For instance, many different insect species like whiteflies, aphids, spider mites,
25 thrips, etc. are pests of horticultural crops like tomato, cucumber, pepper, etc. Early detec-
26 tion and identification of insect pests are necessary to take appropriate control actions before
27 the problem gets out of hand and farmers suffer economic losses. Insecticides are relatively
28 easy to use and have usually provided effective and immediate pest control. Unfortunately,
29 these chemicals also have some undesirable attributes as they usually cause some degree
30 of hazard to the applicators, other people associated with agricultural systems or even the
31 end consumers because of chemical residues on food. In addition to this, they can contam-
32 inate the area and induce harmful effects on pest natural enemies, reducing natural pest
33 suppression. Health issues related to pesticide use and its residues on food as well as the
34 emergence of resistant pests strains makes this an important issue for governments. In the
35 more economically developed countries, for instance in Europe, legal restrictions for the use
36 of chemical pesticides are gradually increasing. In consequence, there is a growing interest
37 among farmers, horticulturists, and gardeners to explore and adapt methods that achieve
38 pest control without the harmful impacts of pesticide use.

39 Biological control, in simple terms, is the reduction of pest populations by their natural
40 enemies (also referred to as beneficial species (Murdoch et al. [2])). For example, predators,
41 parasites, parasitoids and pathogens are some natural enemies of the pests. Biological control
42 can be implemented either through the long-term installation of natural enemies (inoculative
43 biological control) or by periodic releases of natural enemies (augmentative biological control)
44 in cropping systems. In highly damaged cropping systems, this control strategy may get more
45 efficient when coupled with other pest control tactics (like pesticide use) in an Integrated
46 Pest Management (IPM) program. Alternatively, reduction of pest/prey species can also be
47 achieved by the provision of alternative food to the predator species and the exploitation of
48 apparent competition effects between pests (Srinivasu et al. [3] and Kar and Ghosh [4]).
49 Indeed, Srinivasu et al. [3] concluded that pest species can be reduced at a desired level and
50 even eradicated by varying the quality and quantity of additional food.

51 The modeling and optimization of augmentative biological control has been the subject of
 52 many studies (from earlier works [5–7] to more recent ones [8, 9]) e.g. addressing the effects
 53 of inter- and intra-specific interactions on natural enemies. For instance, Liu et al. ([10–12])
 54 studied different pest-predator models with augmentative release strategies and derived the
 55 conditions for the system permanence as well as the existence and local stability of the unique
 56 pest-free solution. One of the key results in their contributions is that the pest eradication is
 57 possible only when the *period* between releases of fixed amount of predators is less than some
 58 critical value. On the other hand, Mailleret and Grogard ([13, 14]) established that pest can
 59 be eradicated (both locally and globally) when the *release rate*, i.e. the number of predators
 60 introduced *per* unit time, is higher than some threshold value, which is actually independent
 61 of the release period. This situation holds as long as predators do not interfere between
 62 each other. Actually, things change when density dependence comes into play. Nundloll et
 63 al. [15, 16] considered the influence of predator interference in pest-predator systems with
 64 augmentative biological control. They showed that the threshold release rate of predators
 65 ensuring pest eradication increases with the release period: for a specified release rate, a
 66 pest outbreak cannot be prevented if the release period is too large. When predators are
 67 marked by some form of fitness or efficiency decrease at small densities, i.e. a characteristic
 68 of obligate cooperation or Allee effects, the result is reversed: a given predator release rate
 69 is more likely to guarantee pest eradication when the release period is large (Bajeux et al.
 70 [17]).

71 These studies focused on biological control tactics in one-patch pest-predator models
 72 where spatial movement of the populations is neglected. However, space and population
 73 dispersal may also be important, for instance when two or more cropping fields are situated
 74 nearby; or when pest populations may move from a wasteland to a farmland. Therefore,
 75 dispersal has been shown to be a major driver of ecological dynamics in many empirical
 76 (Huffaker [18], Takafuji [19]) as well as theoretical (Levins [20], Hassell [21]) studies. Hence,
 77 seeking model based successful pest control tactics is an important issue Tang et al. [22]
 78 and Yang and Tang [23] investigated two-patch pest-predator models with non-interference
 79 interaction among predators and studied the impact of dispersal rates on the success of pest
 80 control programs. Their simulation results demonstrated that two isolated and identical

stable patches may not remain stable if predator populations start to disperse between patches with dissimilar dispersal rates. In the slightly different context of the release of diseased individuals to fight pests, two-patch SI epidemic models with dispersal of susceptible populations only (Georgescu and Zhang [24]) and dispersal of both classes of pest populations (Georgescu et al. [25]) have been studied. These Authors noted that susceptible pests can have large amplitude (see Fig. 5 in their paper) in the long-term if infected pest populations do not satisfy a specified balance equation.

We are mainly motivated by the successive developments of Tang et al. [22], Yang and Tang [23] and Georgescu et al. [25]. Yang and Tang [23] observed that in a spatially structured environment composed of two identical patches, a simple difference in the predator dispersal rate between the two patches may induce pest outbreaks when this difference is large enough. However, they did not determine accurately the conditions on predator releases leading to these outbreaks. Considering pest control based on the spread of a disease via the release of infected individuals, Georgescu et al. [25] computed the conditions ensuring pest eradication when infected pest populations in both patches satisfied a balanced equation. No information on the stability conditions was however given in the general case, when infected pests did not satisfy this equation. Actually, we are not aware of any study addressing the stability of pest eradication through biological control means in a spatially structured context in the general case. This prompted us to investigate further the influence of spatial structure on the efficiency of augmentative biological control. In particular, we aimed at identifying threshold predator release rates ensuring biological control success when heterogeneity comes from predators growth. In this context, we investigate whether the release period has an impact on this threshold, and also explore the effects of the spatio-temporal deployment of biocontrol agents into two patches.

This paper is organized as follows. In Section 2, we recall a result concerning the threshold predator release rate ensuring pest eradication in a simple one patch pest-predator model. In Section 3 we consider a two-patch pest-predator model: the continuous dynamics of pest and predator populations were already considered by Yang and Tang [23], but we introduce the release strategy of biocontrol agents in the framework developed by Mailleret and Grogard [13, 14]. In Section 4, we calculate the threshold predator release rate required for stability

of the pest-free periodic solution in a patchy environment. A detailed description of when the stability threshold depends only on the ecological parameters involved in the model and when it also depends on the release periods are given. We summarize our major results in Section 5 and detail some perspectives of the present work.

2. Stability threshold in a single patch model

A general augmentative biological control model has been proposed and investigated by Mailleret and Grogard [14]. The tri-trophic system (crop-pest-biocontrol agent) has been approximated by a bi-trophic interaction of the prey (pest) and predator (biocontrol agent) species; by assuming that the crop is not limiting for prey growth. Hence, Mailleret and Grogard [14] have proposed the pest-predator dynamic model as:

$$\begin{cases} \frac{dx(t)}{dt} = f(x) - g(x)y, \\ \frac{dy(t)}{dt} = h(x)y - my, \end{cases} \quad (2.1)$$

where x and y denote, respectively, the density of the pest (prey) and predator species. Here $f(x)$ denotes the prey growth rate in the absence of the predator species; $g(x)$ and $h(x)$ are respectively, the predator's functional response and numerical response. m is the specific natural mortality rate of the predator species. Actually, no competition between predator species is considered in the above modeling approach. Here, $f(\cdot)$, $g(\cdot)$ and $h(\cdot)$ are locally Lipschitz functions (Mailleret and Grogard [14]) on \mathbb{R}^+ such that:

- (i) $f(0) = 0$
- (ii) $g(0) = 0$, $g'(0) > 0$ and $\forall x > 0$, $g(x) > 0$
- (iii) the function $\frac{f(x)}{g(x)}$ is upper bounded for $x > 0$
- (iv) $h(0) = 0$ and $\forall x > 0$, $h(x) \geq 0$.

To eradicate the pest population, biocontrol agents are introduced into the pest-predator system at some discrete instants in time. If we now suppose that biocontrol agents are released at a constant release rate μ and that the release period is T then, at each time moment nT ($n \in \mathbb{N}$), the amount of natural enemies added to the predator population is μT (Mailleret and Grogard [13, 14], Mailleret and Lemesle [26]).

Therefore, the predator density at each time instant $t = nT^+$ reads

$$y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N}, \quad (2.2)$$

137 where nT^+ denotes the time just after $t = nT$.

138 Finally, the augmentative biological control model can be established by combining (2.1)
139 and (2.2) as:

$$\left\{ \begin{array}{l} \frac{dx(t)}{dt} = f(x) - g(x)y, \\ \frac{dy(t)}{dt} = h(x)y - my \end{array} \right\}, \quad t \neq nT, \quad (2.3)$$

$$y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N}.$$

140 The pest-free periodic solution of system (2.3) can be written as:

$$(x^T(t), y^T(t)) = \left(0, \frac{\mu e^{-mt}}{1 - e^{-mT}} \right), \quad nT < t \leq (n+1)T.$$

141 The condition for the stability of the pest-free periodic solution is given in the following
142 theorem.

143 **Theorem 1.** The pest-free periodic solution $(x^T(t), y^T(t))$ is locally asymptotically stable
144 (Mailleret and Grogard [13, 14]) if and only if

$$\mu > \hat{\mu} = \frac{mf'(0)}{g'(0)}.$$

145 As the right hand side of this inequation does not depend on the release period T , so
146 does the release threshold $\hat{\mu}$. Therefore, this theorem states that whatever the release period
147 may be (small or large), i.e. whatever the release strategy, small and frequent or large and
148 infrequent releases, the pest population can be eradicated if the release rate is larger than the
149 stability threshold. We now investigate whether the stability threshold stays independent of
150 the release period in a two-patch Lotka-Volterra type pest-predator model.

151 3. Two-patch biological control model

152 Here, we are interested in exploring the evolution of spatio-temporal dynamics of pest
153 and predator populations by adding biological control agents to the predator species. A

154 first step to gain insight on the effect of space on augmentative biological control is to
 155 consider a two-patch model. We consider a Lotka-Volterra type pest-predator model in a
 156 two-patch environment where species can disperse between patches (Yang and Tang [23]).
 157 The dynamics of both species in the presence of augmentative biological control is presented
 158 by:

$$\left\{ \begin{array}{l} \frac{dx_1(t)}{dt} = a_1x_1(t) - b_1x_1(t)y_1(t) - (d_{12}x_1(t) - d_{21}x_2(t)), \\ \frac{dx_2(t)}{dt} = a_2x_2(t) - b_2x_2(t)y_2(t) + (d_{12}x_1(t) - d_{21}x_2(t)), \\ \frac{dy_1(t)}{dt} = c_1x_1(t)y_1(t) - m_1y_1(t) - (D_{12}y_1(t) - D_{21}y_2(t)), \\ \frac{dy_2(t)}{dt} = c_2x_2(t)y_2(t) - m_2y_2(t) + (D_{12}y_1(t) - D_{21}y_2(t)) \end{array} \right\}, \quad t \neq nT, \quad (3.1)$$

$$y_i(nT^+) = y_i(nT) + \mu_i T, \quad \forall n \in \mathbb{N},$$

159 where $x_i(t)$ and $y_i(t)$ respectively, denote the density of the pest and the predator population
 160 in patch i , a_i is the growth rate of the pest population x_i , b_i is the predation rate of the
 161 predator population y_i on the pest population x_i and c_i is the corresponding increase in the
 162 predator population linked to the predation. m_i is the specific natural death rate of the
 163 predator population y_i . d_{ij} and D_{ij} ($i, j = 1, 2; \ i \neq j$) denote the dispersal rates of the
 164 pest and the predator population from patch i to patch j , respectively.

165 The two-patch pest-predator continuous model (3.1) is the simplest model to investigate
 166 the impact of population dispersal in patchy environments. Indeed, variations of this model
 167 have recently been studied by Tang et al. [22], Yang and Tang [23], Georgescu and Zhang [24]
 168 and Georgescu et al. [25] in the context of pest control. However, the novelty of model (3.1)
 169 resides in the modelling of the discrete part, which allows to separately analyze the respective
 170 effect of predator release rate and release period. This was not possible in the formalism of
 171 Tang et al. [22], Yang and Tang [23], Georgescu and Zhang [24] and Georgescu et al. [25].
 172 Such a modelling of the releases has already been proposed by Grogard and Mailleret in
 173 ([13]-[17]), but never in a spatially explicit context, so that the interaction between threshold
 174 release rate/period and spatial structure has never been investigated before.

175 4. Pest eradication: Role of the release period

176 It is shown in Eq. (11) of Yang and Tang [23] that the system (3.1) has a single pest-free
 177 periodic solution $(0, 0, y_1^T(t), y_2^T(t))$ of the form

$$y_1^T(t) = \frac{n_1 e^{\lambda_2(t-nT)} - n_2 e^{\lambda_1(t-nT)}}{\lambda_1 - \lambda_2} y_1^* + \frac{D_{21}(e^{\lambda_1(t-nT)} - e^{\lambda_2(t-nT)})}{\lambda_1 - \lambda_2} y_2^*, \quad (4.1)$$

$$y_2^T(t) = \frac{n_1 n_2 (e^{\lambda_2(t-nT)} - e^{\lambda_1(t-nT)})}{D_{21}(\lambda_1 - \lambda_2)} y_1^* + \frac{n_1 e^{\lambda_1(t-nT)} - n_2 e^{\lambda_2(t-nT)}}{\lambda_1 - \lambda_2} y_1^*,$$

178 for some n_i, y_1^*, y_2^* in \mathbb{R} and $\lambda_i < 0$. Indeed, our calculations could be derived by plugging
 179 $\mu_i T$ in place of τ_i in Yang and Tang [23].

To establish the stability condition of the pest-free periodic solution $(0, 0, y_1^T(t), y_2^T(t))$, we follow Yang and Tang and set $x_i(t) = u_i(t)$ and $y_i(t) = y_i^T(t) + v_i(t)$ ($i = 1, 2$), where $u_i(t)$ and $v_i(t)$ are perturbations with small amplitude. The linearized system is then

$$\begin{pmatrix} \dot{u}_1(t) \\ \dot{u}_2(t) \\ \dot{v}_1(t) \\ \dot{v}_2(t) \end{pmatrix} = \begin{pmatrix} a_1 - d_{12} - b_1 y_1^T(t) & d_{21} & 0 & 0 \\ d_{12} & a_2 - d_{21} - b_2 y_2^T(t) & 0 & 0 \\ c_1 y_1^T(t) & 0 & -(d_1 + D_{12}) & D_{21} \\ 0 & c_2 y_2^T(t) & D_{12} & -(d_2 + D_{21}) \end{pmatrix} \begin{pmatrix} u_1(t) \\ u_2(t) \\ v_1(t) \\ v_2(t) \end{pmatrix} \\ \equiv \begin{pmatrix} B(t) & 0 \\ C(t) & A \end{pmatrix} \begin{pmatrix} u_1(t) \\ u_2(t) \\ v_1(t) \\ v_2(t) \end{pmatrix}, \quad (4.2)$$

180 which is T -periodic (where $A, B(t), C(t)$, and 0 are 2×2 matrices in the last expression).
 181 Note that the impulsive part disappears in these coordinates, since $v_i(nT^+) = y_i(nT^+) -$
 182 $y_i^T(nT^+) = y_i(nT) + \mu_i T - (y_i^T(nT) + \mu_i T) = v_i(nT)$. The solution of system (3.1) linearized
 183 around $(0, 0, y_1^T(t), y_2^T(t))$ can then be written as

$$\begin{pmatrix} u_1(t) \\ u_2(t) \\ v_1(t) \\ v_2(t) \end{pmatrix} = \Phi(t) \begin{pmatrix} u_1(0) \\ u_2(0) \\ v_1(0) \\ v_2(0) \end{pmatrix}, \quad 0 < t < T, \quad (4.3)$$

184 where $\Phi(t)$ is the fundamental matrix of the original system (3.1), which satisfies

$$\frac{d\Phi(t)}{dt} = \begin{pmatrix} B(t) & 0 \\ C(t) & A \end{pmatrix} \Phi(t), \quad (4.4)$$

185 with $\Phi(0) = I$, the identity matrix. Hence the linearized dynamics follow

$$\begin{pmatrix} u_1((n+1)T) \\ u_2((n+1)T) \\ v_1((n+1)T) \\ v_2((n+1)T) \end{pmatrix} = M \begin{pmatrix} u_1(nT) \\ u_2(nT) \\ v_1(nT) \\ v_2(nT) \end{pmatrix}$$

186 with $M = \phi(T)$ the monodromy matrix. **The local stability of the system (3.1) can then be**
 187 **analyzed by computing M .**

188 **If the matrices $B(t_1)$ and $B(t_2)$ commute for all t_1, t_2 in \mathbb{R} , then the fundamental solution**
 189 **matrix is given by:**

$$\Phi(t) = \begin{pmatrix} e^{\int_0^t B(s)ds} & 0 \\ \textcolor{red}{G}(t) & e^{At} \end{pmatrix}. \quad (4.5)$$

190 We do not need to specify the exact form of $G(t)$ in our analysis.

191 **Hence, if the Floquet multipliers (i.e., the eigenvalues) of the monodromy matrix M**
 192 **corresponding to $\Phi(T)$, which is given by**

$$M = \Phi(T) = \begin{pmatrix} e^{\int_0^T B(s)ds} & 0 \\ \textcolor{red}{G}(T) & e^{AT} \end{pmatrix} \quad (4.6)$$

193 have **modulus** less than unity, then the pest-free periodic solution would be locally asymp-
 194 totically stable. Since the block matrix A is Hurwitz **with real eigenvalues (the eigenvalues**
 195 **of A are in fact the aforementioned negative λ_1 and λ_2)**, it suffices to concentrate on the
 196 monodromy matrix generated by submatrix $B(t)$ to investigate the local stability of the
 197 pest-free solution.

198 As noted by Georgescu and Zhang [24] and Georgescu et al. [25], the fundamental matrix
 199 obtained by Yang and Tang [23] is only valid when $B(t_1)$ and $B(t_2)$ commute for all t_1, t_2
 200 in \mathbb{R} , which is not true in all generality. We start by identifying conditions ensuring this
 201 commutativity.

For some $t_1 \neq t_2$, we define $(\widehat{Z}_{ij}) = B(t_1)B(t_2)$ and $(\overline{Z}_{ij}) = B(t_2)B(t_1)$ ($i, j = 1, 2$).

Now it is easy to check (see **Appendix A**) that the diagonal elements of the matrices \widehat{Z} and \overline{Z} are always identical. However, the off-diagonal elements are only the same when one of the following conditions (commutativity conditions) are satisfied:

(i) $d_{12} = d_{21} = 0$ i.e., no pest dispersal

(ii) $b_1 = b_2$ and $y_1^T(t) = y_2^T(t)$, for all t in $(0, T]$, termed as balanced predator dynamics.

We say that predators in both patches have balanced dynamics if their time evolution in the absence of pests are the same and they have the same efficiency to attack pest populations, provided release rates in both patches are equal. This does not mean that predators in both patches have similar time response in the presence of pest populations. For instance, time response of balanced predators might be different if pests survive and their intrinsic growth rates in both patches are distinct.

In the following we consider three cases to examine whether the stability threshold is a function of the release period, and analyze the optimization of the total release rate. The three cases are:

(i) No pest dispersal

(ii) Balanced predator dynamics and pest dispersal

(iii) Unbalanced predator dynamics and pest dispersal.

4.1. No pest dispersal

In this problem, we suppose that pest populations do not disperse between patches (i.e., $d_{12} = d_{21} = 0$.) Therefore, matrix $B(t)$ satisfies the commutative condition and can be written as

$$\begin{pmatrix} a_1 - b_1 y_1^T(t) & 0 \\ 0 & a_2 - b_2 y_2^T(t) \end{pmatrix}. \quad (4.7)$$

The pest-free periodic solution is locally asymptotically stable when both eigenvalues of the matrix

$$B_1 = \int_0^T B(s)ds = T \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix},$$

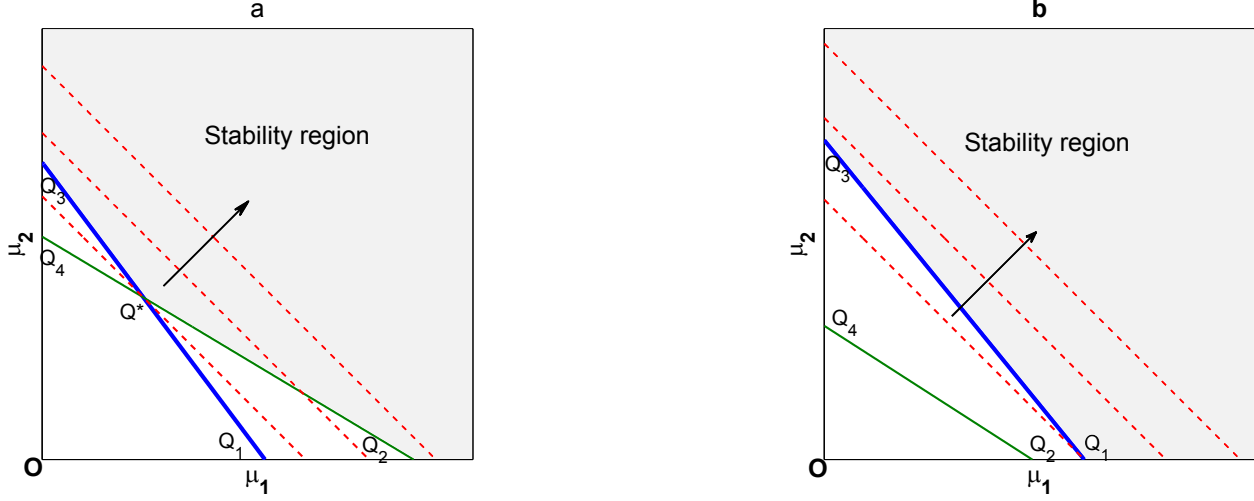


Figure 1: In both subfigures, the thick blue line represents $\alpha = 0$ and the thin green line is for $\beta = 0$. The dashed red lines are the level sets of the cost function $(\mu_1 + \mu_2)$, which are increasing as indicated by the arrows. (a) The curve $\widehat{Q_2 Q^* Q_3}$ is the stability threshold in the μ_1 - μ_2 plane. The minimum cost occurs at Q^* which is the optimal release threshold. (b) The blue curve $\alpha = 0$ solely represents the stability threshold line and Q_1 is the optimal threshold value. In both cases, predator introduction would be successful if the release pair (μ_1, μ_2) is chosen from the shaded region.

which are real, are negative, where

$$\alpha = a_1 - \frac{b_1}{\rho}(\mu_1 m_2 + (\mu_1 + \mu_2) D_{21}) \quad \text{and} \quad \beta = a_2 - \frac{b_2}{\rho}(\mu_2 m_1 + (\mu_1 + \mu_2) D_{12})$$

with $\rho = m_1 m_2 + m_1 D_{21} + m_2 D_{12}$.

We now calculate the stability threshold by setting $\alpha = 0$ and $\beta = 0$, which respectively yield

$$\mu_2^\alpha(\mu_1) = \frac{a_1 \rho}{b_1 D_{21}} - \frac{(m_2 + D_{21}) \mu_1}{D_{21}}$$

intersecting the axes at $Q_1 = \left(\frac{a_1 \rho}{b_1(m_2 + D_{21})}, 0 \right)$ and $Q_3 = \left(0, \frac{a_1 \rho}{b_1 D_{21}} \right)$, and

$$\mu_2^\beta(\mu_1) = \frac{a_2 \rho}{b_2(m_1 + D_{12})} - \frac{D_{12} \mu_1}{(m_1 + D_{12})}$$

intersecting the axes at $Q_2 = \left(\frac{a_2 \rho}{b_2 D_{12}}, 0 \right)$ and $Q_4 = \left(0, \frac{a_2 \rho}{b_2(m_1 + D_{12})} \right)$. Note that stability is not achieved on the threshold since one of the eigenvalues is equal to 0 there. However, it is achieved as soon as $\mu_2 > \max(\mu_2^\alpha(\mu_1), \mu_2^\beta(\mu_1))$.

Since the slope of μ_2^α with respect to μ_1 is smaller than -1 and the one of μ_2^β is large than -1, the only way both could intersect in the positive orthant is illustrated in Fig. 1a. The

intersection takes place at

$$Q^* = (\mu_1^*, \mu_2^*) = \left(\frac{a_1 m_1}{b_1} + \frac{a_1 D_{12}}{b_1} - \frac{a_2 D_{21}}{b_2}, \quad \frac{a_2 m_2}{b_2} - \frac{a_1 D_{12}}{b_1} + \frac{a_2 D_{21}}{b_2} \right),$$

228 which is in the positive orthant if

$$\frac{a_1}{b_1 D_{21}} > \frac{a_2}{b_2 (m_1 + D_{12})} \quad (4.8)$$

229 and

$$\frac{a_2}{b_2 D_{12}} > \frac{a_1}{b_1 (m_2 + D_{21})}. \quad (4.9)$$

230 We now wish to solve the minimum effort problem that can be reformulated as

$$\begin{aligned} & \min(\mu_1 + \mu_2) \\ & \text{such that } \mu_2 \geq \mu_2^\alpha \text{ and } \mu_2 \geq \mu_2^\beta. \end{aligned} \quad (4.10)$$

231 As a linear programming problem, if it has a solution, there necessarily exists a solution
232 at a vertex of the set of constraints. In our case, unbounded μ_1 or μ_2 yield infinite cost,
233 so that the problem necessarily has a finite solution. We then just have to check which of
234 Q_2, Q_3 or Q^* has the smallest cost.

The cost corresponding to Q^* is

$$\mu_1^* + \mu_2^* = \frac{a_1 m_1}{b_1} + \frac{a_2 m_2}{b_2}.$$

On the other hand, the cost at Q_2 is

$$\begin{aligned} \mu_2^0 &= \frac{a_2 \rho}{b_2 D_{12}} = \frac{a_2 m_2}{b_2} + m_1 \frac{a_2 (m_2 + D_{21})}{b_2 D_{12}} && \text{(Plugging the value of } \rho) \\ &> \frac{a_2 m_2}{b_2} + \frac{a_1 m_1}{b_1} = \mu_1^* + \mu_2^* && \text{(Using inequality (4.9)).} \end{aligned}$$

235 Hence, the cost at Q_2 is higher than that corresponding to Q^* . Similarly we can show
236 that the cost at Q_3 is also higher than that corresponding to Q^* . Consequently, the minimum
237 cost occurs at Q^* , as also illustrated in Fig. 1a.

238 This reveals that releasing biocontrol agents in both patches is the best control policy to
239 minimize the release rate.

240 Next we consider that $\alpha = 0$ and $\beta = 0$ do not intersect in the positive orthant of the
241 μ_1 - μ_2 plane. This results in Fig. 1b, where stability is solely determined by $\alpha \geq 0$, or its
242 dual, where $\beta \geq 0$ ensures stability.

Fig. 1b is characterized by the intersections of $\alpha = 0$ with the axes being at larger values than those of $\beta = 0$. This yields

$$\frac{a_2}{b_2 D_{12}} < \frac{a_1}{b_1(m_2 + D_{21})} \quad (4.11)$$

and

$$\frac{a_1}{b_1 D_{21}} > \frac{a_2}{b_2(m_1 + D_{12})}, \quad (4.12)$$

where (4.12) can directly be seen as a consequence of (4.11). The solution of the minimization problem (4.10) is then at Q_1 or Q_3 where $(\mu_1 + \mu_2)$ equals $a_1 \rho / (b_1(m_2 + D_{21}))$ and $a_1 \rho / (b_1 D_{21})$ respectively. The latter being larger than the former, the solution of problem (4.10) is given by Q_1 , so that it has $\mu_2 = 0$. All the releases only take place in the first patch. We can now give some insight into why releases should be made in both patches or in one patch by recalling the previous pest-predator model (3.1). In the absence of pest dispersal and releases, the equilibrium of the continuous pest-predator model (3.1) is

$$E^*(x_1^e, x_2^e, y_1^e, y_2^e) = \left(\frac{a_1 b_2 m_1 + a_1 b_2 D_{12} - a_2 b_1 D_{21}}{a_1 b_2 c_1}, \frac{a_2 b_1 m_2 + a_2 b_1 D_{21} - a_1 b_2 D_{12}}{a_2 b_1 c_2}, \frac{a_1}{b_1}, \frac{a_2}{b_2} \right).$$

In view of (4.8) and (4.9) we observe that pest populations survive (all components of E^* are positive) in both patches before releases, therefore releases should be conducted in both patches.

On the contrary, x_2^e becomes negative due to (4.11) and hence the biologically meaningful equilibrium in the absence of release becomes

$$E \left(\frac{m_1 m_2 + m_1 D_{21} + m_2 D_{12}}{(m_2 + D_{21}) c_1}, 0, \frac{a_1}{b_1}, \frac{a_1 D_{12}}{(m_2 + D_{21}) b_1} \right).$$

As pest populations cannot survive in the second patch of the natural system (before releases), it makes sense that biocontrol agents should only be released into the first patch.

One simple way to understand the above two scenarios is to consider homogeneous patches except for the predator dispersal rates. We define the degree of dissymmetry in the predator dispersal rate between patches as $|D_{12} - D_{21}|$. If the degree of dissymmetry is smaller, one can observe the situation as shown in Fig. 1a. On the other hand, the second situation arises (see Fig. 1b) when the degree of dissymmetry is larger. Suppose $D_{12} \gg D_{21}$, then most of the predator populations move to the second patch and few predators come to the

first patch. In consequence, higher predator density in the second patch drives the pest populations to extinction before releases and this imposes a biological control tactics in the first patch only.

Finally, we note that the stability threshold in either case (one patch release case or two patch release case) does not depend on the release period. It is also noted that the minimum effort, while releasing natural enemies into both patches, is independent of the predator dispersal rates. However, in the one patch release case, the release threshold also depends on the predator dispersal rate. To sum up this optimality approach, we recall that stability is not achieved for (μ_1, μ_2) on the stability threshold as stated earlier; the solution of the present minimization problem then gives an infimum to the total release rates that can be used to achieve stability of the pest-free solution.

4.2. *Balanced predator dynamics and pest dispersal*

In this case, we consider that both pest and predator populations disperse between patches and we release natural enemies with the same rates $\mu_1 = \mu_2 = \mu$ in each patch. In the absence of pest populations, we assume that predators in both patches evolve through the same dynamics, which allows us to write: $y_1^T(t) = y_2^T(t) (= y^T(t))$. The explicit parametric condition for which $y_1^T(t) = y_2^T(t)$ is described below (see also Georgescu et al. [25]).

We write

$$\left. \begin{aligned} \frac{dy_1^T(t)}{dt} &= -(m_1 + D_{12})y^T(t) + D_{21}y^T(t), \\ \frac{dy_2^T(t)}{dt} &= D_{12}y^T(t) - (m_2 + D_{21})y^T(t). \end{aligned} \right\} \quad (4.13)$$

Since $\frac{dy_1^T(t)}{dt} = \frac{dy_2^T(t)}{dt}$, we have

$$-(m_1 + D_{12}) + D_{21} = D_{12} - (m_2 + D_{21}).$$

Hence, a necessary condition to balanced predator dynamics is:

$$(m_1 - m_2) = 2(D_{21} - D_{12}). \quad (4.14)$$

If we consider the above balance equation together with $b_1 = b_2 = b$ and $\mu_1 = \mu_2 = \mu$ then matrix $B(t)$ can be written as

$$\begin{pmatrix} a_1 - d_{12} - by^T(t) & d_{21} \\ d_{12} & a_2 - d_{21} - by^T(t) \end{pmatrix}. \quad (4.15)$$

Thus matrix $B(t)$ now satisfies the commutativity condition and hence matrix B_1 takes the form:

$$B_1 = \int_0^T B(s)ds = T \begin{pmatrix} \alpha_1 & d_{21} \\ d_{12} & \beta_1 \end{pmatrix},$$

where $\alpha_1 = L_1 - A\mu$, $\beta_1 = L_2 - A\mu$ with $L_1 = a_1 - d_{12}$, $L_2 = a_2 - d_{21}$, $A = b(m_1 + 2D_{12})/\rho = b(m_2 + 2D_{21})/\rho$ (using the balance equation).

The eigenvalues of B_1 are:

$$\lambda_3 = \left(\frac{\alpha_1 + \beta_1 + \sqrt{(\alpha_1 - \beta_1)^2 + d_{12}d_{21}}}{2} \right) T \text{ and } \lambda_4 = \left(\frac{\alpha_1 + \beta_1 - \sqrt{(\alpha_1 - \beta_1)^2 + d_{12}d_{21}}}{2} \right) T.$$

As $\lambda_4 < \lambda_3$, we need $\lambda_3 = 0$ to calculate the stability threshold μ for the pest-free periodic solution.

$$\lambda_3 = 0 \Rightarrow (\alpha_1 + \beta_1)^2 = (\alpha_1 - \beta_1)^2 + 4d_{12}d_{21},$$

which yields

$$4A^2\mu^2 - 4A(L_1 + L_2)\mu + (4L_1L_2 - d_{12}d_{21}) = 0.$$

The solutions of the above equation are

$$\mu = \frac{L_1 + L_2 \pm \sqrt{(L_1 - L_2)^2 + 4d_{12}d_{21}}}{2A}.$$

Only the largest root corresponds to $\alpha_1 + \beta_1 < 0$ so that $\lambda_3 = 0$ and it produces the stability threshold (can also be viewed as the optimal threshold). Explicitly we write

$$\mu = \frac{(a_1 + a_2) - (d_{12} + d_{21}) + \sqrt{(a_1 - a_2)^2 + (d_{12} + d_{21})^2 - 2(a_1 - a_2)(d_{12} - d_{21})}}{2A}.$$

The main observation is that the stability threshold is independent of release period.

Another information can be drawn, that if the natural growth rates of the pest populations in both patches are the same (i.e., $a_1 = a_2 = a$), the threshold becomes

$$\begin{aligned} \mu &= \frac{a(m_1m_2 + m_1D_{21} + m_2D_{12})}{b(m_1 + 2D_{12})}, \\ &= \frac{a}{b} \left(\frac{\frac{1}{2}m_1m_2 + m_1D_{21}}{m_1 + 2D_{12}} + \frac{\frac{1}{2}m_1m_2 + m_2D_{12}}{m_1 + 2D_{12}} \right) \\ &= \frac{a}{b} \frac{m_1 + m_2}{2}. \end{aligned}$$

The last equality has been obtained by calling upon the balance equation (4.14) to replace the denominator of the first term. This expression is independent of the dispersal rates

(symmetric, dissymmetric, unidirectional, large or small dispersal) and is equal to the one that would have been obtained in the absence of dispersal. Note also that, since $\mu_1 = \mu_2 = \mu$, the stability threshold also gives information on the infimum effort as defined in the previous section (under the constraint of identical release rates), which is then twice the threshold μ .

4.3. Unbalanced predator dynamics and pest dispersal

In the previous two scenarios, either the pest populations were not mobile between patches or the predator populations presented balanced dynamics, for which matrix $B(t)$ satisfied the commutative property. In consequence, we have obtained that the stability threshold of the release rates stays independent of the release period T . Georgescu et al. [25] have investigated a similar situation through simulations in a two patch environment where predator populations do not satisfy the balanced equation, but we are not aware of any systematic study focusing on unbalanced predator dynamics and how it affects the efficiency of biocontrol agents releases against pests. In this contribution, we calculate the stability thresholds of release rates to eliminate pest populations through augmentative biocontrol agents and we show that the mathematical property linked to the unbalanced character of the predator dynamics has important consequences on the stability properties of the pest-free solution. In particular, it makes the threshold release rate dependent upon the release period T .

Actually, if either predator dispersal rates, specific mortality rates of predators, predation rates or release rates are distinct in both patches, unbalanced predator dynamics occurs. We first consider a very simple model, where dissimilar dynamics are linked to the predation rate, to show that the stability threshold depends upon the release period. Later, we study the complete model with dissimilar dispersal rates through numerical simulations to investigate the question of how the stability threshold is influenced by the release period.

4.3.1. Simple model

As a first step in the analysis, we concentrate on the simplest case for which balanced dynamics conditions do not hold. We consider a simple model, which yields $y_1^T(t) = y_2^T(t)$, but $b_1 \neq b_2$. Here, $\mu_1 = \mu_2 = \mu$ is necessary to satisfy $y_1^T(t) = y_2^T(t)$. In addition, we assume the following parameter simplification: $a_1 = a_2 = m, m_1 = m_2 = m, d_{12} = d_{21} = m$

and $D_{12} = D_{21} = m$ which allows for analytic computations without altering the main non-commutativity property.

The pest-free periodic solution under such parameter selection is the T -periodic repeat of

$$\left(0, 0, \frac{\mu T e^{-mt}}{(1-e^{-mT})}, \frac{\mu T e^{-mt}}{(1-e^{-mT})} \right), 0 < t \leq T.$$

For the stability analysis around the pest-free periodic solution, we use the same tools as in (4.4). As the matrix

$$B(t) = \begin{pmatrix} -\frac{b_1 \mu T e^{-mt}}{1-e^{-mT}} & m \\ m & -\frac{b_2 \mu T e^{-mt}}{1-e^{-mT}} \end{pmatrix}$$

is such that the matrices $B(t_1)$ and $B(t_2)$ do not commute, we explicitly solve the system:

$$\begin{pmatrix} \frac{d\Phi_1(t)}{dt} \\ \frac{d\Phi_2(t)}{dt} \end{pmatrix} = B(t) \begin{pmatrix} \Phi_1(t) \\ \Phi_2(t) \end{pmatrix}, \quad 0 < t \leq T. \quad (4.16)$$

Suppose $\Phi_1(0)$ and $\Phi_2(0)$ are the initial state, then the solution of the above linear system (4.16) at the terminal time T can be written as:

$$\begin{pmatrix} \Phi_1(T) \\ \Phi_2(T) \end{pmatrix} = \begin{pmatrix} M_{11}(T, \mu) & M_{12}(T, \mu) \\ M_{21}(T, \mu) & M_{22}(T, \mu) \end{pmatrix} \begin{pmatrix} \Phi_1(0) \\ \Phi_2(0) \end{pmatrix}, \quad (4.17)$$

where the elements of the monodromy matrix $M(T, \mu) = (M_{ij}(T, \mu))$ ($i, j = 1, 2$) are given in **Appendix B**.

If $M(T, \mu)$ satisfies the following Jury conditions (Wang [27]):

$$\begin{aligned} \text{Cond 1: } \quad & \psi_1(T, \mu) \equiv 1 - \text{tr}M + \det M > 0, \\ \text{Cond 2: } \quad & \psi_2(T, \mu) \equiv 1 + \text{tr}M + \det M > 0, \\ \text{Cond 3: } \quad & \psi_3(T, \mu) \equiv 1 - \det M > 0, \end{aligned} \quad (4.18)$$

then the pest-free periodic solution is asymptotically stable.

We have proved (see **Appendix C**) that Jury Conditions 2 and 3 trivially hold. However, the satisfaction of Condition 1 depends on both the release rate and the release period, the two control parameters. Here, we establish a relationship between T and μ for the stability threshold and define a region in the T - μ plane where all Jury conditions are satisfied.

In **Appendix C** we have analytically shown that the release rate must be larger than $\hat{\mu} = m^2/\sqrt{b_1 b_2}$ for pest eradication when releases are very frequent ($T \rightarrow 0$). We have also computed a stability threshold $\bar{\mu} = \max(m^2/b_1, m^2/b_2)$ ($> \hat{\mu}$ since $b_1 \neq b_2$) for very infrequent releases ($T \rightarrow +\infty$). Consequently, we have that the threshold release rate evolves with the release period and that, for release rates between $\hat{\mu}$ and $\bar{\mu}$, the pest-free periodic solution will be stable for some release periods and unstable for others. However, it seems difficult to explicitly compute the critical release period at which stability is lost. Hence, simulation results are helpful to understand how stability changes with the release period. We are interested in understanding the qualitative information of the model rather than quantitative results. Thus, in simulations, we use hypothetical values for the ecological parameters, that are illustrative of the different qualitative outcomes and of the changes in stability.

For illustration, we chose $m = 0.7$, $b_1 = 0.6$ and $b_2 = 0.1$. Then the lower and upper release thresholds are $\hat{\mu} = 2.0005$ and $\bar{\mu} = 4.9$ respectively. In Fig. 2 we represent the variations of $\psi_1(T, \mu)$ for increasing release period when $\mu = 1.8$, 3 and 5.5 respectively. The top subplot always has $\psi_1 < 0$, which indicates that pest populations cannot be eradicated if the release rate is less than the threshold $\hat{\mu}$. The bottom subplot indicates that when the release rate is high enough, pest suppression is effective whatever the release period. From the middle subplot we can infer that pest populations from both patches can be eradicated for small release periods when the release rate is between $\hat{\mu}$ and $\bar{\mu}$; however, instability occurs for larger release periods. In that intermediate release rate case, small and frequent releases yield successful biological control while it will fail with large and infrequent ones. This observation is very important since it indicates how, with a given biological control agent budget, a farmer should deploy control over time.

We also represented different level curves of ψ_1 in the T - μ plane (see Fig. 3) in order to identify the stability region of the pest-free periodic solution. The zero level curve of ψ_1 is the threshold curve which creates two subregions: the upper one is the stable region and the lower one is the unstable one; it is an increasing function of T whose value is $\hat{\mu}$ in zero and converges to $\bar{\mu}$ as T becomes large. For any pair of (T, μ) below the zero level curve, establishment of biological control agents cannot drive the pest population to extinction

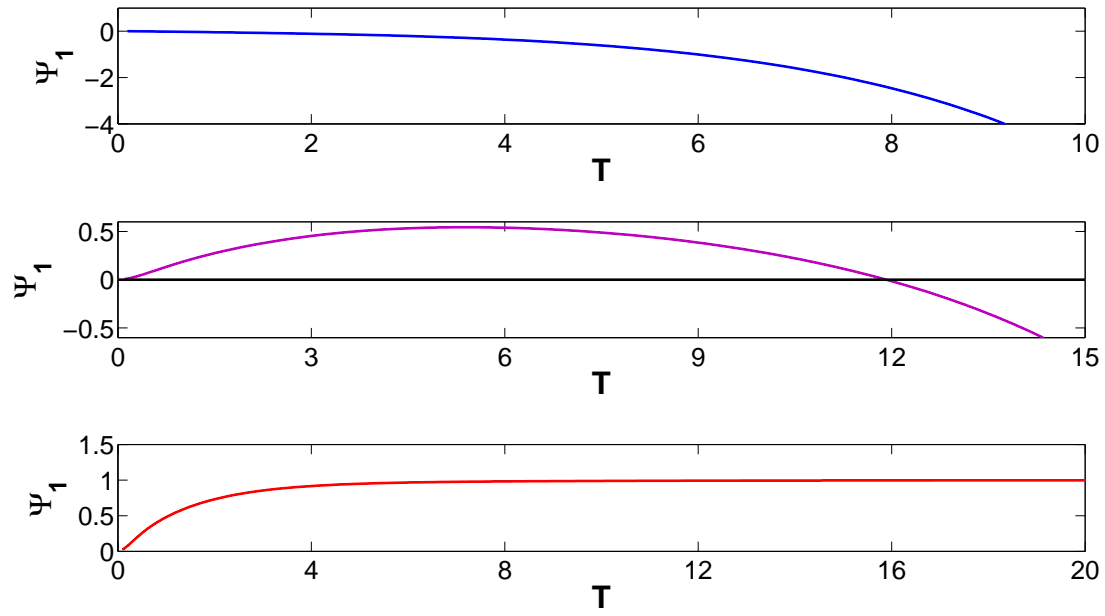


Figure 2: When $\mu = 1.8 < \hat{\mu}$, then $\psi_1(T)$ is negative and decreases with respect to T (top subplot). When $\hat{\mu} < \mu = 3 < \bar{\mu}$, then $\psi_1(T)$ is positive and increases for smaller values of T , but decreases as T crosses 5.6. $\psi_1(T)$ becomes negative for $T > 11.9$ and fails to satisfy Jury condition 1 (middle subplot). If $\mu = 5.5 > \bar{\mu}$, then $\psi_1(T)$ increases and approaches unity as T increases (lower subplot).

while pest eradication would be achieved above the level curve $\psi_1 = 0$. In this case, for a fixed value of T , ψ_1 increases with μ and this indicates that the pest-free periodic solution would be asymptotically stable with higher release rate. On the other hand, for a fixed value of $\mu < \bar{\mu}$, the value of ψ_1 eventually decreases as the release period increases and the pest-free solution may lose its stability as shown in Fig. 2 and in **Appendix C**. From the zero level curve, we can conclude that the stability threshold depends on the release period when predator populations follow unbalanced dynamics. In fact, pest eradication is more easily obtained for large release rates and small release periods.

Finally, the stability threshold again yields the infimum effort capable of achieving pest eradication under the constraint that $\mu_1 = \mu_2$.

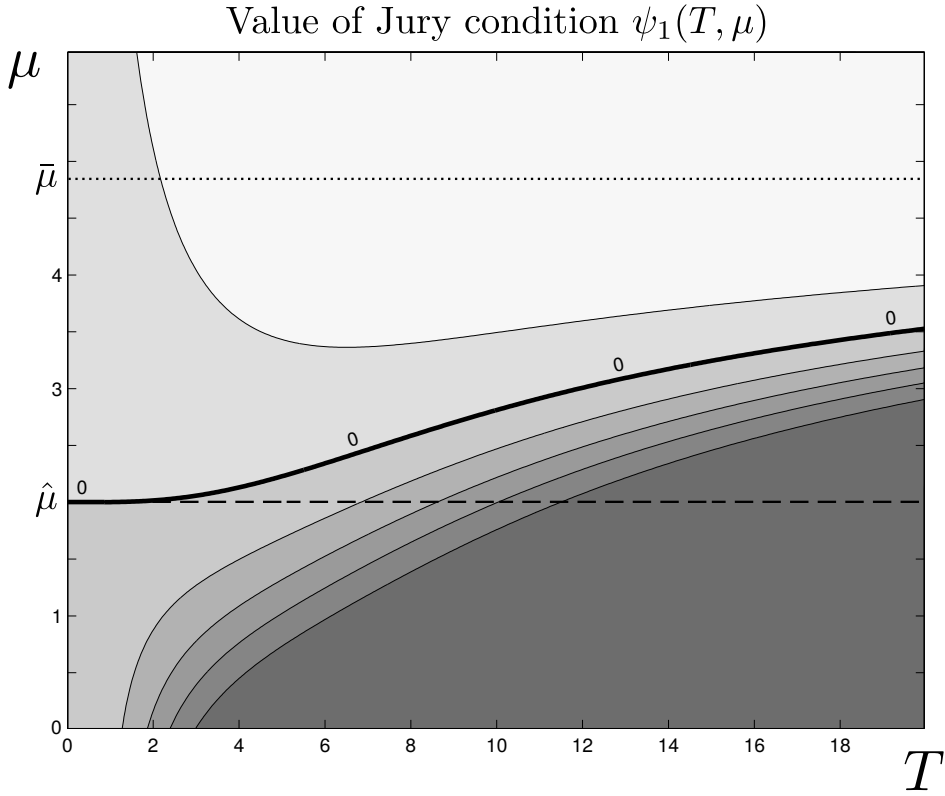


Figure 3: Contour plot of the first Jury condition ψ_1 in the (T, μ) plane. Darker areas correspond to smaller values of ψ_1 . The zero level curve of ψ_1 is displayed as a thick curve: it corresponds to a threshold release rate which increases with the release period. Positive (resp. negative) values of ψ_1 , above (resp. below) the threshold level curve correspond to stable (resp. unstable) situations. $\bar{\mu}$ and $\hat{\mu}$ defined in the main text are also displayed.

366 4.3.2. Analysis of the full model

367 To keep developments simple, we assume that both patches are identical (similar pest
368 and predator growth in both patches) except regarding predator dispersal, which leads to
369 dissimilar predator dynamics. In such situation, unequal predator releases in both patches
370 cannot make $y_1^T = y_2^T$. Thus, because of these dissymetries, predator dynamics are unbal-
371 anced, and, as in the previous section, the simple computations linked to the commutativity
372 property cannot be used.

373 In particular, through these investigations, we are interested by the following questions
374 concerning the stability threshold.

- 375 (i) Do the properties of the pest-free stability thresholds identified in the previous subsec-
376 tion transfer to this model? Specifically, are the stability thresholds T -dependent?
- 377 (ii) What is the influence of the level of pest dispersal on the pest-free stability thresholds?

378 In order to analyze these stability properties, we need to numerically compute the mon-
379 odromy matrix M . This is done by following equation (4.4) which gives us $\Phi(t)$ and subse-
380 quently $M = \Phi(T)$. Concentrating on the u equations, we just have to twice integrate system
381 $\dot{u} = B(t)u$ numerically with $u(0) = (1 \ 0)'$ and then $u(0) = (0 \ 1)'$ as initial conditions, and
382 then put the obtained solutions evaluated in T together in a matrix in order to obtain M
383 (see also Teschl [28]).

384 Issues (i) and (ii) are addressed by considering simulations with $a_1 = a_2 = 3$, $b_1 = b_2 =$
385 0.4 , $m_1 = m_2 = 0.3$, $D_{12} = 0.3$ and $D_{21} = 0.1$. In these developments, we consider $d_{12} = d_{21}$,
386 for various values of d_{ij} , and pick $\mu_1 = 3.75$. We then compute, for increasing values of T ,
387 the value of μ_2 corresponding to the stability threshold, that is the one such that, for a given
388 T , if μ_2 is larger than this value, the pest-free solution is stable and otherwise it is unstable.
389 This threshold can be obtained by evaluating the Jury conditions (4.18) and finding the
390 μ_2 value that either imposes ψ_1, ψ_2 , or ψ_3 to be equal to zero while the remaining two are
391 positive. In our particular case, this always corresponds to $\psi_1 = 0, \psi_2 > 0$ and $\psi_3 > 0$. These
392 releases generate the threshold curve $\mu_2(T)$ for stability. We will not detail why here, but a
393 first observation that we made in this particular case is that, independently of the value of
394 $d_{12} = d_{21}$, we found that, as $T \rightarrow 0$, the μ_2 threshold value tends to 0.75.

395 Considering first that pest dispersal rates are very low and given by $d_{12} = d_{21} = 0.01$, we
396 see that, for the fixed $\mu_1 = 3.75$, the stability threshold $\mu_2(T)$ is an increasing function of
397 the release period T from $\mu_2(0) = 0.75$ (see Fig. 4a). Likewise, by considering the converse
398 problem and fixing the release rate $\mu_2 = 0.75$ independently of T , we observe that the $\mu_1(T)$
399 threshold release rate increases with T (see Fig. 4b). Therefore, the stability threshold is
400 period dependent and an increasing function of T as we noticed in the "simple model" case.
401 As we observe below, this qualitative property is not affected by the level of pest dispersal
402 (Fig. 4). These observations confirm the results of the previous section and give a positive
403 answer to question (i) above.

404 We now focus on the second issue (ii). Having already studied the $d_{12} = d_{21} = 0.01$
405 case, we now consider the pest dispersal rates as $d_{12} = d_{21} = 0.3$. Fixing $\mu_1 = 3.75$, the
406 threshold $\mu_2(T)$ is illustrated in Fig. 4c while the case where μ_2 is fixed at 0.75 yields the
407 $\mu_1(T)$ threshold given in Fig. 4d. Here, we again observe that the stability threshold of the
408 release rate in either patch increases with the release periods when the release rate is fixed
409 in the other patch, but we also notice that the rate of increase of the threshold with respect
410 to the release period in Fig. 4c (respectively, Fig. 4d) is larger compared to that in Fig.
411 4a (respectively, Fig. 4b). This intuitively reveals that, for a fixed release period, higher
412 release rates would be required to reach stability if pest populations disperse more. Now if
413 we increase the pest dispersal rate further by choosing $d_{12} = d_{21} = 3$, the stability threshold
414 in either patch also increases with the release period (see Figs. 4e and 4f). However, the
415 rate of increase of the threshold in Fig. 4e (respectively, Fig. 4f) is lower compared to
416 that in Fig. 4c (respectively, Fig. 4d). This contradicts our previous statement that for
417 a fixed release period, higher release rates would be required to reach stability when pest
418 populations disperse more. This apparent paradox is explained below.

419 From Fig. 4a (respectively, Fig. 4b) we observe that the rate of increase of the stability
420 threshold is low; strikingly when the release period is less than 5 units of time, the stability
421 threshold is a horizontal line. As pest dispersal rates are very low, pest populations do not
422 disperse much between patches. This situation could in fact be approximated by the "no
423 pest dispersal" case (See Subsection 4.1) and consequently matrix $B(t)$ (see Eqn. (4.4))
424 would almost satisfy the commutativity property for small release periods, hence have a

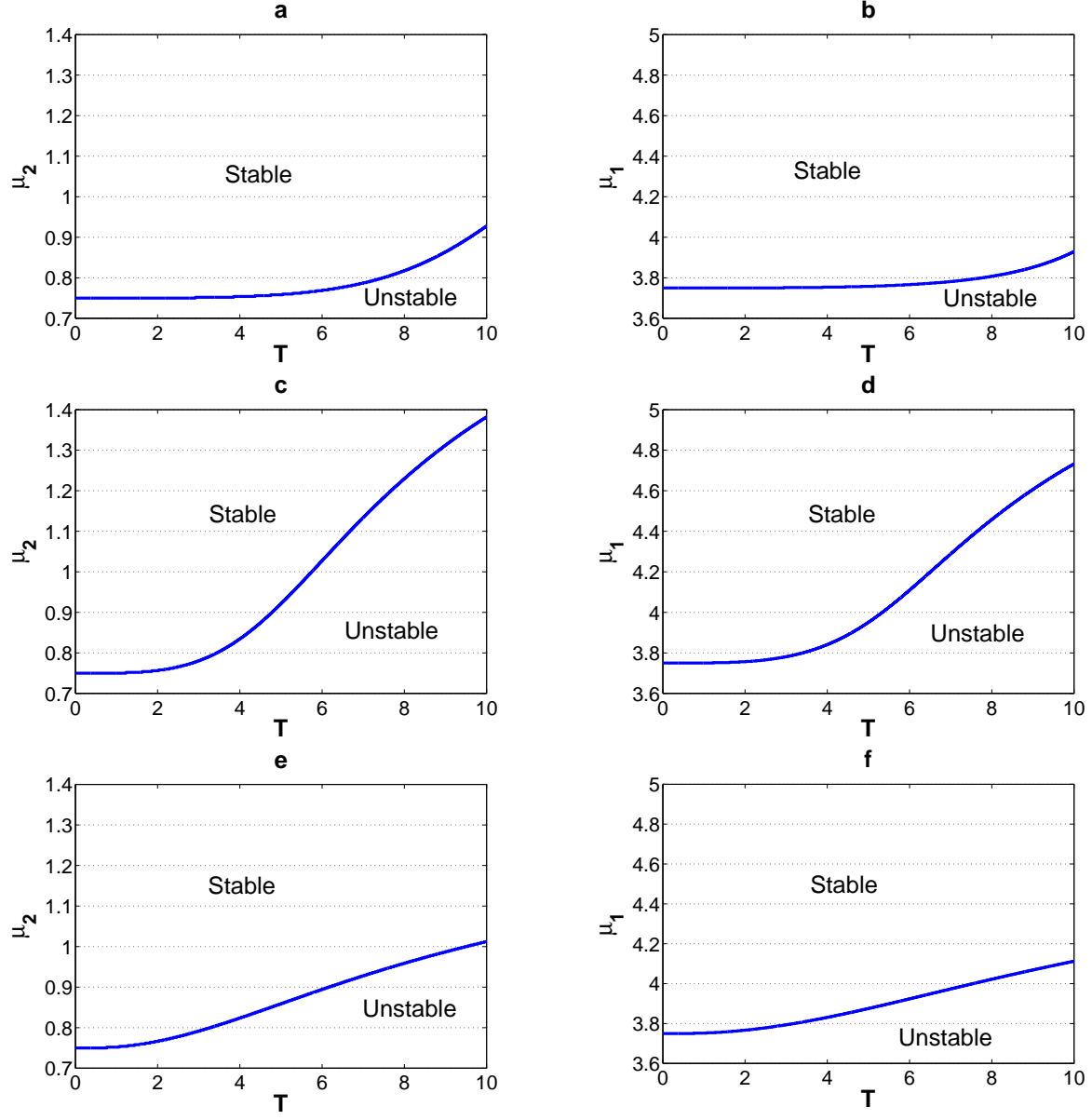


Figure 4: In each sub-figure we plotted the stability threshold which creates two regions: a region ensuring stability of the pest-free solution, and one for instability. In each case, the stability threshold is an increasing function of the release period. All the threshold curves are drawn in the same scale to compare the variation of thresholds with each other. Pest free-periodic solutions are stable if the release rate is larger than the stability threshold. We assume $a_1 = a_2 = 3$, $b_1 = b_2 = 0.4$, $m_1 = m_2 = 0.3$, $D_{12} = 0.3$ and $D_{21} = 0.1$ for all subplots with $\mu_1 = 3.75$ for subplots a, c and e and $\mu_2 = 0.75$ for subplots b, d and f. $d_{12} = d_{21} = 0.01$ (sedentary pest species) holds for subplots a and b, $d_{12} = d_{21} = 0.3$ (moderate pest dispersal) for subplots c and d and $d_{12} = d_{21} = 3$ (fast pest dispersal) for subplots e and f.

425 stability threshold independent of the release period. In that case, pest disperse so little
 426 that the influence of the spatial structure of the environment vanishes. In the case of Fig.
 427 4c (respectively, Fig. 4d), pest populations move between patches with higher rate. Hence,
 428 matrix $B(t)$ no longer satisfies the commutativity condition. When pest disperse even more
 429 ($d_{12} = d_{21} = 3$; Fig. 4e and f), the pest population becomes homogenized between the two
 430 patches and the influence of the spatial structure of the environment decreases again, making
 431 the stability thresholds less sensitive to the release period. This can also be observed from
 432 the commutativity point of view; indeed, the off-diagonal terms in the \hat{Z} and \bar{Z} matrices
 433 (defined in Appendix A) become dominated by the pest-dispersal terms when dispersal rates
 434 are large. Since these terms are identical between the two matrices, commutativity almost
 435 holds.

436 We also investigate some other cases in which the predator dispersal rates are different,
 437 but the degree of dissymmetry of the predator dispersal rates, $|D_{12} - D_{21}|$, is invariant. We
 438 suppose the pest dispersal rates as $d_{12} = d_{21} = 0.3$ and examine three cases: (i) $D_{12} = 0.21$
 439 and $D_{21} = 0.01$, (can be viewed as unidirectional movement of the predator populations from
 440 the first patch to the second patch), (ii) $D_{12} = 0.6$ and $D_{21} = 0.4$ (bidirectional movement)
 441 and (iii) $D_{12} = 1$ and $D_{21} = 0.8$. In each case, we can choose $\mu_1 = 3.75$ and $\mu_2 = 0.75$ as
 442 stability thresholds for $T \rightarrow 0$. We fix $\mu_1 = 3.75$ for all T and observe that the stability
 443 threshold μ_2 is an increasing function of the release period in all three cases (see Fig. 5).
 444 Similar trends are also found when $\mu_2 = 0.75$ is kept fixed. These figures indicate that large
 445 individual predator dispersals reduce the influence of the degree of dissymmetry and the
 446 predator dynamics in both patches become very similar. Therefore, comparatively smaller
 447 releases can prevent pest outbreak if predator populations disperse very fast.

448 We now formulate a third question with respect to this general case:

449 (iii) How can we spread predators between the two patches to ensure efficient pest control?

450 In order to give an answer to that question, we consider the parameter setting corre-
 451 sponding to Fig. 4c and d. The minimal threshold release rate that we have identified in
 452 that case corresponds to $T = 0$ with $\mu_1 = 3.75$ and $\mu_2 = 0.75$ so that the total release rate
 453 is $\mu = (3.75 + 0.75) = 4.5$ and the ratio $\mu_1/\mu_2 = 83/17$: 83% of the predators are released
 454 in patch 1. Indeed, since we have noticed that $\mu_2(T)$ and $\mu_1(T)$ are increasing with T in

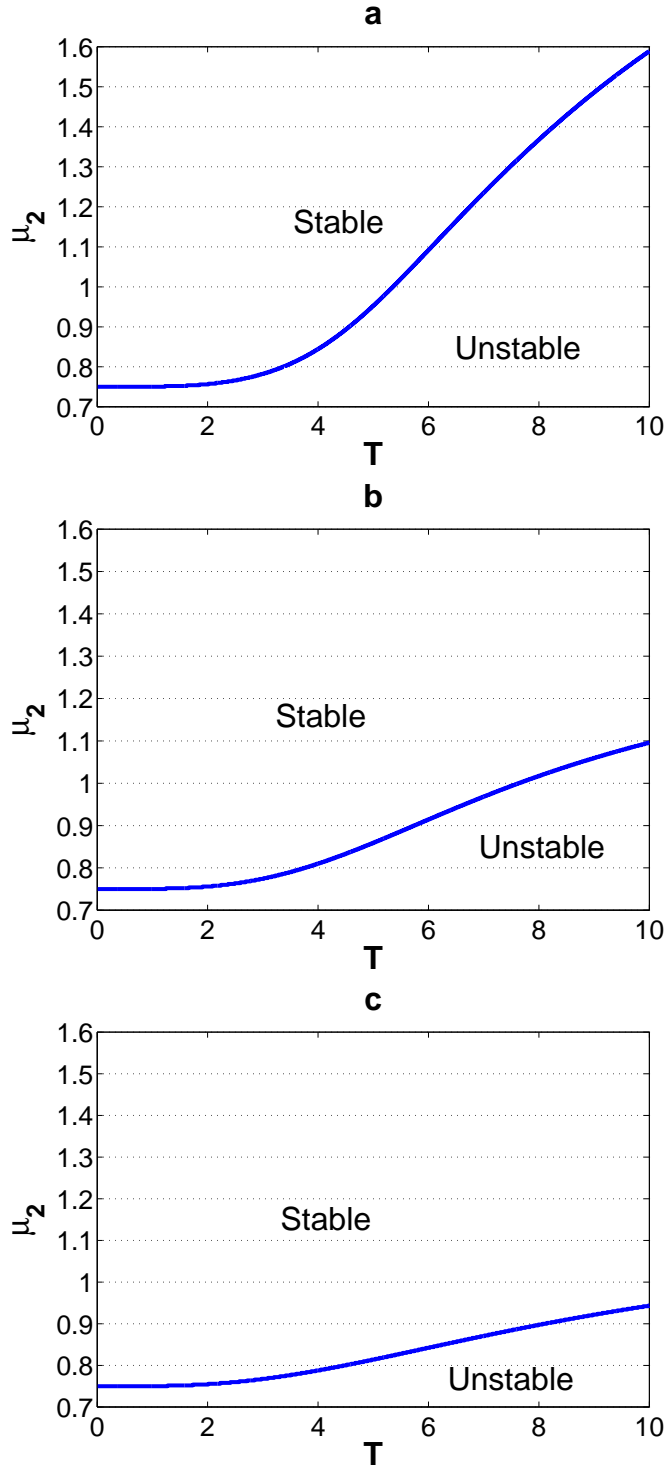


Figure 5: Stability threshold μ_2 is plotted for different predator dispersal rates. We select $D_{12} = 0.21$ and $D_{21} = 0.01$ for subplot a, $D_{12} = 0.6$ and $D_{21} = 0.4$ for subplot b and $D_{12} = 1$ and $D_{21} = 0.8$ for subplot c.

Fig. 4c and d, a larger total release rate would be necessary for larger T -values; otherwise, no biological control strategy could work for $T > 0$. To cover positive T -values it is then necessary to consider total release rates μ larger than 4.5 to be spread between the two patches. We assume that a spatio-temporal biological control strategy is then defined by the pair (T, p) , with T the release period and $p \in [0, 1]$ the proportion of the total release rate put in the first patch, so that we have $\mu_1 = p\mu$ and $\mu_2 = (1 - p)\mu$.

We formulate a first problem, illustrated in Fig. 6a, as follows: with μ fixed at a given value $\bar{\mu}(> 4.5)$, which biological control strategies (T, p) do yield asymptotic stability of the pest-free solution? By computing numerically the monodromy matrix and its eigenvalues for this $\bar{\mu}$ value on a (T, p) grid, we were able to compute the stability region, that contains the (T, p) values where all the eigenvalues of M lie within the unit-circle. The stability region lies on the left of the $\mu = \bar{\mu}$ curve in Fig. 6a, so that it is enclosed by that curve, the p -axis, and potentially the $p = 0$ and $p = 1$ levels. This computation is achieved in Fig. 6a for different values of $\bar{\mu}$ ranging from 4.6 to 14; it identifies, for a given $\bar{\mu}$, the (T, p) values for which pests can be eradicated from both patches.

From this figure, it is clear that, for $\mu \leq 4.8$, only releasing all biocontrol agents in the first or second patch cannot eradicate pest populations as the stability region does not touch either the $p = 1$ or $p = 0$ level. As can be seen in Fig. 6a, different deployments of biological control agents can however succeed in controlling the pests. For instance, for $\mu = 4.8$, when $T < 3$, both 70% of the releases in the first patch (30% in the second) and 95% in the first patch (5% in the second) are efficient. For this same $\mu = 4.8$, when the release period increases, the size of the p -interval corresponding to successful biological control decreases with T . In particular, 76% should be distributed in the first patch (i.e., $\mu_1/\mu_2 = 76/24$) when the release period $T = 6.25$ (approximately); beyond $T = 6.25$, no biological control built by spreading the total release rate $\mu = 4.8$ between the two patches can succeed as the p -interval vanishes. This is a companion property of the dependency in T : a given release rate does not determine per se the stability; the way biological control agents are deployed over the two patches matters.

Extending on these two properties observed for $\mu = 4.8$, we first see that, for larger μ values, the stability region reaches the $p = 1$ and then $p = 0$ levels. On the one hand, for

$\mu \geq 5$, $p = 1$ can achieve pest eradication as long as T is taken small. This means that pest eradication can be achieved by only releasing predators in the first patch for these T -values. On the other hand, stability of the pest-free periodic solution only occurs with $p = 0$ when $\mu > 14$. This dissymmetry in the μ value at which pest eradication can be achieved in the whole system by only putting predators in one patch is linked to the connectivity of the patches for the predators: with $D_{12} = 0.3$ and $D_{21} = 0.1$, predators flow more easily from the first patch to the second than the other way around. Predators put in the first patch can then help eradicating pests in the second, but it is much less true in the other direction: in order for predators put only in the second patch to eradicate pests in the first patch, they need to be put in very large number.

The second observation that we made concerned the right tip of the stability region: for a given μ , pest eradication can only be achieved over a limited interval of T values and fails if T is too large. We notice for $\mu = 4.6, 4.8$, and 5 that the right tip of the stability region takes place for increasing values of T as μ increases, so that efficient biological control is possible for larger release periods when μ is larger. It is also true beyond these μ values, though not illustrated because the regions corresponding to $\mu = 6, 8, 10, 12$ and 14 are larger in size and extend beyond $T > 10$.

In a more general sense, the stability region for a given μ is strictly included in the ones defined for larger μ values; this is quite natural since, for a given strategy (T, p) , having μ larger means that more predators are introduced in both patches, which should facilitate pest suppression. Finally, this also gives us some optimality information: for all the (T, p) pairs on the boundary of the stability region, the μ value used for the computation of this graph is the infimum of the values that ensure pest-eradication with those (T, p) strategies.

From the last discussion, we have seen that there are many choices of (T, p) in the stability region, for a given μ , which ensure pest eradication from both patches. Therefore, it is important to investigate which strategy (T, p) would yield faster convergence rate of the pest population to zero. As shown in [16], this can however not be achieved by simply comparing the largest modulus $\lambda(T, p)$ of the eigenvalues of M , which yield the slowest dynamics of the discrete system, in order to evaluate the convergence rate of the semi-discrete system. Indeed, when comparing two strategies with identical λ , the one with a

smaller T will converge faster to pest eradication in actual time than the one with a larger one. In order to alleviate this problem, we define $W = (u_1, u_2, v_1, v_2)$ from (4.2) and, with $W(0^+)$ an eigenvector corresponding to the eigenvalue η_i whose modulus is $\lambda(T, p)$, we have

$$W(kT^+) = M^k W(0^+) = \eta_i^k W(0^+)$$

so that

$$\|W(kT^+)\| = \lambda(T, p)^k \|W(0^+)\|$$

In order to check what this represents in actual time, we identify these dynamics to those of a linear system $\frac{d}{dt}\|W(t)\| = \theta(T, p)\|W(t)\|$, with $\theta(T, p)$ the evolution rate of the system. The latter dynamics are defined in the actual time t so that various values of $\theta(T, p)$ can be compared between them. This gives

$$\|W(kT^+)\| = e^{\theta(T, p)kT} \|W(0^+)\|$$

Identifying the $\|W(kT^+)\|$ expressions, we obtain

$$\theta(T, p) = \frac{\ln \lambda(T, p)}{T}$$

Hence, the pest free solution is asymptotically stable if and only if $\theta(T, p)$ is negative and the smaller $\theta(T, p)$ the faster the convergence.

For illustration, we consider the case for $\mu = 5$ in Fig. 6 and draw several θ -level curves. It is observed that, for a fixed release period, many (T, p) strategies ensure the same evolution rate (e.g., see the level curve $\theta = -0.15$). If the biological control problem is given in terms of ensuring a given evolution rate θ for a given release rate μ , the solution is not unique and this degree of liberty can be used for secondary optimization purpose: for instance, as there may be a cost for doing frequent releases, it might be best to take T as large as possible and choose the (T, p) value corresponding to the right tip of the θ level curve. Also, if relasing in both patches is more costly than in a single patch $p = 0$ or $p = 1$ strategies might be favored (a $p = 1$ choice could be made in the present case if $\theta = -0.05$ was imposed). If the biological control problem is given in terms of obtaining the best evolution rate for a given release rate, we should then pick the (T, p) strategy corresponding to the "*" point in the Figure. This optimal solution is on the $T = 0$ axis and is coherent with all previous results that showed that increasing T was here detrimental for biological control.

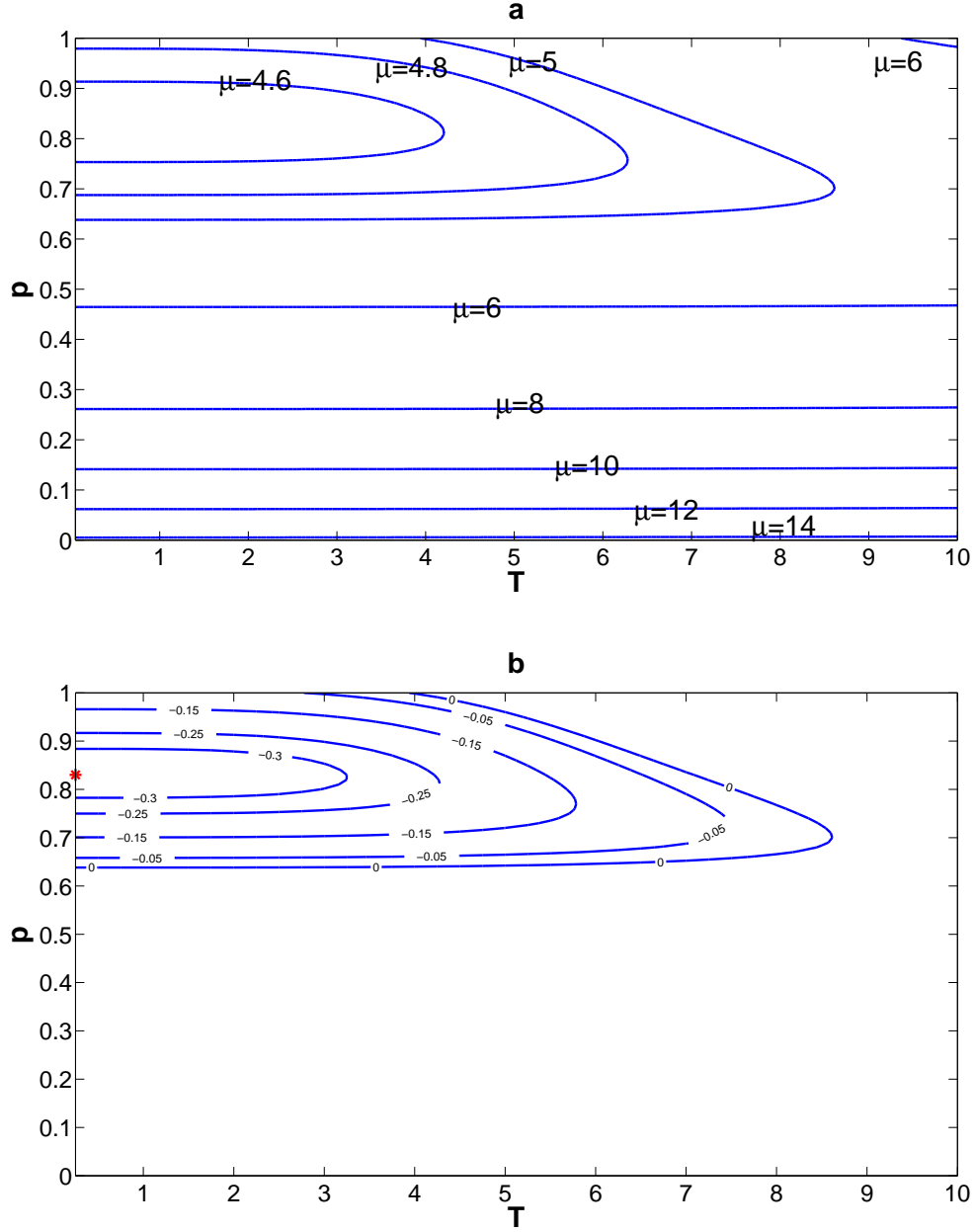


Figure 6: (a) Numerical investigation of the efficacy of the spatio-temporal deployment of biological control agents in the (T, p) plane, with T the release period and p the fraction of the releases deployed in patch 1. The biological parameters correspond to those of Fig. 4c and d. (a) Stability regions correspond to all (T, p) pair which can eradicate pest population from both patches are shown for different release rates μ ; they are on the left of the illustrated level curves. (b) The level curves of mean evolution rate θ of the pest-free solution are given for $\mu = 5$. The mean convergence rate is maximal at "*" where $p = 0.83$ and $T \rightarrow 0$.

539 5. Discussion and Conclusion

540 In this study, we have considered a spatially structured pest-predator system coupled to
541 releases of predators with applications to augmentative biological control. We modeled such
542 a system using a continuous-time two-patch Lotka-Volterra pest-predator model coupled
543 with periodic additions to the predator population at discrete moments in time. Our main
544 purpose was to investigate how biological control efficiency, as measured via the stability of
545 the pest-free solution, was affected by the predator release rate, i.e. the number of predators
546 introduced per unit time, and by the period of time between predator releases, i.e. the release
547 period. In comparable spatially unstructured pest-predator models, Mailleret and Grognaud
548 [13, 14] have shown that the threshold release rate required for stability of the pest-free
549 solution is independent of the release period, and that it depends only on the ecological
550 parameters of the pest-predator model. Here, we have shown that this result does not hold
551 anymore when space and species dispersal are explicitly taken into account.

552 Our major contributions can be summarized as follows. Firstly, when pest populations
553 do not disperse the threshold release rate required for stability of the pest-free solution is
554 independent of the release period, just as when spatial structure is neglected. That is, a
555 preassigned release rate larger than the fixed stability threshold guarantees the eradication
556 of pest populations from both patches, whatever the value of the release period. In this
557 regard, the introduction of natural enemies into both patches helps to minimize the total
558 release rate if pest populations can survive in both patches in the absence of introductions.
559 If pest populations die out from either patch due to natural pest-predator interaction, one
560 must release natural enemies in the single patch where pest populations are present.

561 Secondly, the stability threshold also stays independent of the release period if both pest
562 and predator populations disperse, but predator populations follow balanced dynamics, i.e.
563 follow similar asymptotic dynamics in the absence of pest species. Moreover, we have shown
564 that in such situations, the stability threshold is independent of both predator and pest
565 dispersal rates (symmetric, dissymmetric, unidirectional, etc.) when intrinsic growth rates
566 of pest populations in both patches are the same.

567 Our most important contribution is that the stability threshold predator release rate is
568 release period dependent in the general case, when predator populations do not satisfy the

balanced equation. Actually, when the release rate is fixed in one patch, the threshold release rate in the other patch ensuring the stability of the pest free solution in both patches is an increasing function of the release period (Fig. 4 and 5). In addition, we have also shown that a given biocontrol agents release rate spread between the two patches may be not efficient for pest control when the release period exceeds some critical value (Fig. 6a). Hence, we conclude that frequent releases of small amounts of predators can more readily guarantee the pest eradication that infrequent releases of large amounts in environments where spatial structure matters. This modeling study is to our knowledge the first to report such an effect of space on biological control strategies.

Finally, a companion property of the release period dependency of the threshold release rate is that the way predators are deployed over space also determines whether pests can be suppressed or not (Fig. 6a). Moreover, smaller release periods appear to guarantee pest suppression over larger ranges of spatial predator deployment (Fig. 6a). Overall, this study shows that not only the spatial nor the temporal component of predator introductions is important: it is the complete spatio-temporal pattern of deployment of biocontrol agents that actually determines augmentative biological control efficacy. Such results are particularly important since most agricultural landscapes are characterized by a strong spatial structure determined by the different habitat characteristics of fields carrying different crops and uncultivated areas. Our results show that the design of augmentative biological control programs should not overlook spatial heterogeneity. This advocates for a landscape-scale approach to augmentative biological control, which would rely on coordinated actions of neighbouring farmers. That being said, small and frequent predator releases are overall expected to be more efficient than rare and infrequent ones since such strategies (i) yield pest eradication with smaller release rates, (ii) are more robust to inaccuracies in the spatial deployment of predators, and (iii) yield faster pest eradication for a given release rate.

In previous studies, Nundloll et al. [15, 16] considered augmentative biological control in spatially implicit pest-predator models in which predators suffer from negative density dependence. As in the present study, they have shown that the threshold predator release rate ensuring the stability of the pest-free solution was an increasing function of the release period and that pest eradication was faster for smaller values of the release period. Here,

599 the spatial structure of the environment seems thus to have the very same effects as direct
600 inter-predator competition in Nundloll et al. [15, 16].

601 Our results in spatially structured environments nicely complement those of Yang and
602 Tang [23] and of Georgescu et al. [25]. Indeed both studies report results that mostly
603 apply to balanced predator dynamics. The most novel part of our work is the analysis of
604 the full model when predators follow unbalanced dynamics. It has been achieved through
605 an analytico-numerical study of the eigenvalues of the monodromy matrix and provides a
606 comprehensive picture of the impact of spatial structure of the environment on augmentative
607 biological control. Moreover, the studies [23] and [25] were conducted in a framework which
608 does not put the emphasis on the time-dependence of the stability threshold. Terry [29]
609 also considered the issue of pest control in a two-patch context, but through impulsive pest
610 culling rather than through biological control. Some of his results are comparable to ours,
611 like the fact that the way culls are deployed over space has an influence on the control of
612 pests. He also showed that more frequent culls allow to control pests more easily. This
613 result is in fact quite different from ours since the per unit time control effort also increases
614 with the decrease of the period, while it stays constant in our framework. Actually, the fair
615 comparison of taking regimes occurring at different frequencies (e.g. culls) is complicated,
616 and the theory is still in its early developments (Mailleret et al. [30]).

617 The next step of research concerning augmentative biological control in spatially struc-
618 tured environments will be to confirm our results in the very general cases. At this stage,
619 even in the more general model investigated in Section 4.3.2, we indeed imposed some simpli-
620 fications on the within patch dynamics. Other developments should consider alternatives to
621 the very basic Lotka Volterra dynamics we considered here, and evaluate how such formula-
622 tions would modify our results. For instance, Bajeux et al. [17] recently considered spatially
623 implicit augmentative biological control models in which predators were affected by positive
624 density dependence, i.e. Allee effects. They have shown that in this case, the threshold
625 predator release rate is a decreasing, not increasing, function of the release period. We be-
626 lieve that the consideration of the combined effects of space and positive density dependence
627 is an important avenue for future research, which may well lead to unveil a non-monotonic
628 relationship between biological control efficiency and natural enemies release frequency.

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Appendix A: Commutativity condition

Suppose $B(t_1)B(t_2) = (\widehat{Z}_{ij})$ ($i, j = 1, 2$), then

$$\widehat{Z}_{11} = (a_1 - d_{12} - b_1 y_1^T(t_1)) (a_1 - d_{12} - b_1 y_1^T(t_2)) + d_{12} d_{21},$$

$$\widehat{Z}_{12} = d_{21} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_1) - b_2 y_2^T(t_2)) ,$$

$$\widehat{Z}_{21} = d_{12} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_2) - b_2 y_2^T(t_1)) ,$$

$$\widehat{Z}_{22} = d_{12} d_{21} + (a_2 - d_{21} - b_2 y_2^T(t_1)) (a_2 - d_{21} - b_2 y_2^T(t_2)).$$

Again suppose $B(t_2)B(t_1) = (\overline{Z}_{ij})$ ($i, j = 1, 2$), then

$$\overline{Z}_{11} = (a_1 - d_{12} - b_1 y_1^T(t_2)) (a_1 - d_{12} - b_1 y_1^T(t_1)) + d_{12} d_{21},$$

$$\overline{Z}_{12} = d_{21} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_2) - b_2 y_2^T(t_1)) ,$$

$$\overline{Z}_{21} = d_{12} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_1) - b_2 y_2^T(t_2)) ,$$

$$\overline{Z}_{22} = d_{12} d_{21} + (a_2 - d_{21} - b_2 y_2^T(t_2)) (a_2 - d_{21} - b_2 y_2^T(t_1)).$$

It is clear that $\overline{Z}_{11} = \widehat{Z}_{11}$ and $\overline{Z}_{22} = \widehat{Z}_{22}$ for all t_1 and t_2 in $(0, T]$.

Now

$$\overline{Z}_{12} - \widehat{Z}_{12} = d_{12} (b_1(y_1^T(t_2) - y_1^T(t_1)) - b_2(y_2^T(t_2) - y_2^T(t_1))) ,$$

and

$$\overline{Z}_{21} - \widehat{Z}_{21} = -d_{21} \begin{pmatrix} b_1(y_1^T(t_2) - y_1^T(t_1)) - b_2(y_2^T(t_2) - y_2^T(t_1)) \\ \end{pmatrix}.$$

Therefore, $B(t_1)$ and $B(t_2)$ would commute for all t_1 and t_2 in $(0, T]$ if and only if

$$\overline{Z}_{12} - \widehat{Z}_{12} = \overline{Z}_{21} - \widehat{Z}_{21} = 0.$$

Appendix B: Matrix element of (M_{ij})

As linear system (4.16) is difficult to solve analytically by hand, we use Maple software, which gives the following elements of the monodromy matrix.

$$M_{11} = \frac{e^{-mT}}{(b_1 - b_2)^2 \mu^2 T^2} \begin{pmatrix} m^2 e^{-\frac{b_2 \mu T}{m}} (e^{mT} - 1)^2 \\ -e^{-\frac{b_1 \mu T}{m}} \left(m(e^{mT} - 1) - (b_1 - b_2) \mu T \right) \left(m(e^{mT} - 1) + (b_1 - b_2) e^{mT} \mu T \right) \end{pmatrix},$$

$$M_{12} = \frac{m(e^{mT} - 1) e^{-\frac{T(m^2(e^{mT} - 1) + (b_1 - b_2)e^{mT} \mu)}{m(e^{mT} - 1)}}}{(b_1 - b_2)^2 \mu^2 T^2} \begin{pmatrix} m \left(e^{\frac{(e^{mT} b_1 + b_2) \mu T}{m(e^{mT} - 1)}} \right. \\ \left. - e^{\frac{(e^{mT} b_2 + b_1) \mu T}{m(e^{mT} - 1)}} - e^{\frac{T(m^2 + b_1 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} + e^{\frac{T(m^2 + b_2 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} \right) \\ \left. - \left(e^{\frac{(e^{mT} b_2 + b_1) \mu T}{m(e^{mT} - 1)}} - e^{\frac{T(m^2 + b_1 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} \right) (b_1 - b_2) \mu T \right),$$

$$M_{21} = \frac{m(e^{mT} - 1) e^{-\frac{T(m^2(e^{mT} - 1) + (b_1 - b_2)e^{mT} \mu)}{m(e^{mT} - 1)}}}{(b_1 - b_2)^2 \mu^2 T^2} \begin{pmatrix} m \left(-e^{\frac{(e^{mT} b_1 + b_2) \mu T}{m(e^{mT} - 1)}} \right. \\ \left. + e^{\frac{(e^{mT} b_2 + b_1) \mu T}{m(e^{mT} - 1)}} + e^{\frac{T(m^2 + b_1 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} - e^{\frac{T(m^2 + b_2 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} \right) \\ \left. + \left(e^{\frac{(e^{mT} b_1 + b_2) \mu T}{m(e^{mT} - 1)}} - e^{\frac{T(m^2 + b_2 \mu)(e^{mT} - 1) + (b_1 + b_2) \mu}{m(e^{mT} - 1)}} \right) (b_1 - b_2) \mu T \right),$$

$$M_{22} = \frac{e^{-mT}}{(b_1 - b_2)^2 \mu^2 T^2} \begin{pmatrix} m^2 e^{-\frac{b_1 \mu T}{m}} (e^{mT} - 1)^2 \\ -e^{-\frac{b_2 \mu T}{m}} \left(m(e^{mT} - 1) + (b_1 - b_2) \mu T \right) \left(m(e^{mT} - 1) - (b_1 - b_2) e^{mT} \mu T \right) \end{pmatrix}.$$

742 Appendix C: Stability threshold in simple model

We obtain

$$\det M = e^{-\frac{(b_1+b_2)\mu T}{m}} < 1$$

743 for all T and μ . Therefore, Jury condition 3 is satisfied.

744 The trace is given as

$$\text{tr} M = \frac{me^{-mT}(e^{mT} - 1)^2 \left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}} \right)}{(b_1 - b_2)\mu T} + \frac{\left(e^{-\frac{b_2\mu T}{m}} + e^{-\frac{b_1\mu T}{m}} \right) (b_1 - b_2)\mu T}{(b_1 - b_2)\mu T}.$$

745 The value of the trace is always positive for $b_1 \neq b_2$. Hence, Jury condition 2 is satisfied.

746

747 Since the form of ψ_1 is complex, it is difficult to test Jury condition 1 for arbitrary μ
748 and T . In this regard, we calculate the values of ψ_1 for sufficiently small and large release
749 periods and indicate if there is a stability switching for varying T by keeping μ fixed.

750 Taking second order approximation of ψ_1 (by neglecting the third and higher order terms
751 in T) near $T = 0$, we have

$$\begin{aligned} \det M &= e^{-\frac{(b_1+b_2)\mu T}{m}} \approx 1 - \frac{(b_1 + b_2)\mu T}{m} + \frac{(b_1 + b_2)^2\mu^2 T^2}{2m^2} \\ &= 1 - \frac{(b_1 + b_2)\mu T}{m} + \frac{b_1^2\mu^2 T^2}{2m^2} + \frac{b_2^2\mu^2 T^2}{2m^2} + \frac{b_1 b_2 \mu^2 T^2}{m^2}. \end{aligned}$$

752 The first term of $\text{tr} M$ is

$$\begin{aligned} &\frac{me^{-mT}(e^{mT} - 1)^2 \left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}} \right)}{(b_1 - b_2)\mu T} \\ &\approx \frac{m \left(1 - mT + \frac{m^2 T^2}{2} \right) \left(mT + \frac{m^2 T^2}{2} \right)^2 \left(\left(1 - \frac{b_2\mu T}{m} + \frac{b_2^2\mu^2 T^2}{2m^2} \right) - \left(1 - \frac{b_1\mu T}{m} + \frac{b_1^2\mu^2 T^2}{2m^2} \right) \right)}{(b_1 - b_2)\mu T} \\ &\approx \frac{m(mT)^2 \left(\frac{b_1\mu T}{m} - \frac{b_2\mu T}{m} \right)}{(b_1 - b_2)\mu T}, \quad (\text{by neglecting } T^3 \text{ and higher order terms}) \\ &\approx m^2 T^2. \end{aligned}$$

Similarly, the second term of $\text{tr}M$ is

$$\frac{\left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}}\right)(b_1 - b_2)\mu T}{(b_1 - b_2)\mu T}$$

$$\approx 1 - \frac{b_2\mu T}{m} + \frac{b_2^2\mu^2 T^2}{2m^2} + 1 - \frac{b_1\mu T}{m} + \frac{b_1^2\mu^2 T^2}{2m^2}.$$

By approximation, we can write

$$\psi_1(T) \approx -m^2 T^2 + \frac{b_1 b_2 \mu^2 T^2}{m^2}.$$

Therefore, $\psi_1(T) \rightarrow 0^+$ as $T \rightarrow 0$ iff $\mu > m^2/\sqrt{b_1 b_2}$.

Thus Jury condition 1 would be satisfied for $\mu > \hat{\mu} = m^2/\sqrt{b_1 b_2}$. Hence, pest populations can be eradicated from both patches when releases are very frequent and release rates are greater than $\hat{\mu}$.

For smaller value of T , $\psi_1(T)$ increases (respectively, decreases) with respect to release period for $\mu > \hat{\mu}$ (respectively, for $\mu < \hat{\mu}$) along a parabolic path. However, it seems difficult to compute $\psi_1(T)$ analytically for any other finite value of T .

We now examine the stability behaviour when the release period is very large.

Here

$$\lim_{T \rightarrow \infty} \det M = 0.$$

$$\begin{aligned} \lim_{T \rightarrow \infty} \text{tr} M &= \lim_{T \rightarrow \infty} \left(\frac{me^{-mT}(e^{mT} - 1)^2 \left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}}\right)}{(b_1 - b_2)\mu T} + \frac{\left(e^{-\frac{b_2\mu T}{m}} + e^{-\frac{b_1\mu T}{m}}\right)(b_1 - b_2)\mu T}{(b_1 - b_2)\mu T} \right) \\ &= \lim_{T \rightarrow \infty} \left(\frac{me^{-mT}(e^{mT} - 1)^2 \left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}}\right)}{(b_1 - b_2)\mu T} + e^{-\frac{b_2\mu T}{m}} + e^{-\frac{b_1\mu T}{m}} \right) \\ &= \lim_{T \rightarrow \infty} \frac{m(e^{mT} - 2 + e^{-mT}) \left(e^{-\frac{b_2\mu T}{m}} - e^{-\frac{b_1\mu T}{m}}\right)}{(b_1 - b_2)\mu T} \end{aligned}$$

$$= \lim_{T \rightarrow \infty} \frac{m \left(e^{(m - \frac{b_2 \mu}{m})T} - e^{(m - \frac{b_1 \mu}{m})T} \right)}{(b_1 - b_2)\mu T}.$$

766 We define $\bar{\mu} = \max(m^2/b_1, m^2/b_2)$, then $\hat{\mu} < \bar{\mu}$. If the release rate μ satisfies
 767 $\hat{\mu} < \mu < \bar{\mu}$, both $(m - b_1\mu/m)$ and $(m - b_2\mu/m)$ have opposite sign. Hence,

$$\lim_{T \rightarrow \infty} \text{tr} M = \infty.$$

768 Ultimately, we have

$$\lim_{T \rightarrow \infty} \psi_1(T) = -\infty.$$

769 Thus Jury condition 1 is no longer satisfied for large release periods. This reveals that
 770 predator establishment would be successful for very frequent releases, but fail to do so for
 771 very infrequent releases even when release rates are simply larger than $\hat{\mu}$. This is the first
 772 observation where stability switches for larger release periods.

773 If the release rate is increased beyond $\bar{\mu}$, both $(m - b_1\mu/m)$ and $(m - b_2\mu/m)$ become
 774 positive. Therefore,

$$\lim_{T \rightarrow \infty} \text{tr} M = 0$$

775 and consequently

$$\lim_{T \rightarrow \infty} \psi_1(T) = 1.$$

776 In this case, Jury condition 1 is satisfied even for very large release periods. Therefore, we
 777 can state that pest populations can be eradicated for very frequent and infrequent releases
 778 if the release rate is larger than $\bar{\mu}$.