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2 **Natural enemies deployment in patchy environments**  
3 **for augmentative biological control**

4 Bapan Ghosh<sup>1,2</sup>, Frédéric Grognard<sup>2\*</sup>, and Ludovic Mailleret<sup>3,4,5,2</sup>

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6 <sup>1</sup> Department of Mathematics, National Institute of Technology Meghalaya, Bijni Complex,  
7 Shillong-793003, Meghalaya, India

8 <sup>2</sup> INRIA BIOCORE, 2004 route des Lucioles, Sophia-Antipolis, France

9 <sup>3</sup> INRA, UMR 1355 Institut Sophia Agrobiotech, 06903, Sophia Antipolis, France

10 <sup>4</sup> Université Nice Sophia Antipolis, UMR 7254 Institut Sophia Agrobiotech, 06903, Sophia  
11 Antipolis, France

12 <sup>5</sup> CNRS, UMR 7254 Institut Sophia Agrobiotech, 06903, Sophia Antipolis, France

13

14 E-mails:

15 keshab\_bg@yahoo.in (Bapan Ghosh)

16 frederic.grognard@inria.fr (Frederic Grognard)

17 ludovic.mailleret@sophia.inra.fr (Ludovic Mailleret)

18 \*Corresponding author

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20 predator-prey model, populations dynamics, two-patch model, dispersal, stability.

## 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 pest 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

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

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

105 This paper is organized as follows. In Section 2, we recall a result concerning the threshold  
106 predator release rate ensuring pest eradication in a simple one patch pest-predator model. In  
107 Section 3 we consider a two-patch pest-predator model: the continuous dynamics of pest and  
108 predator populations were already considered by Yang and Tang [23], but we introduce the  
109 release strategy of biocontrol agents in the framework developed by Mailleret and Grognard  
110 [13, 14]. In Section 4, we calculate the threshold predator release rate required for stability

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

## 115 2. Stability threshold in a single patch model

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

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

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

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

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

136 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 Grognard [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  $\tau_i$  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

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

180 which is  $T$ -periodic (where  $A, B(t), C(t)$ , and  $0$  are  $2 \times 2$  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

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

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:**

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

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**

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

193 have **modulus** less than unity, then the pest-free periodic solution would be locally asymptotically stable. Since the block matrix  $A$  is Hurwitz **with real eigenvalues (the eigenvalues of  $A$  are in fact the aforementioned negative  $\lambda_1$  and  $\lambda_2$ )**, it suffices to concentrate on the monodromy matrix generated by submatrix  $B(t)$  to investigate the local stability of the 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.

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

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

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

207 (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.

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

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

217 (i) No pest dispersal

218 (ii) Balanced predator dynamics and pest dispersal

219 (iii) Unbalanced predator dynamics and pest dispersal.

#### 220 4.1. No pest dispersal

221 In this problem, we suppose that pest populations do not disperse between patches (i.e.,  
 222  $d_{12} = d_{21} = 0$ .) Therefore, matrix  $B(t)$  satisfies the commutative condition and can be  
 223 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

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

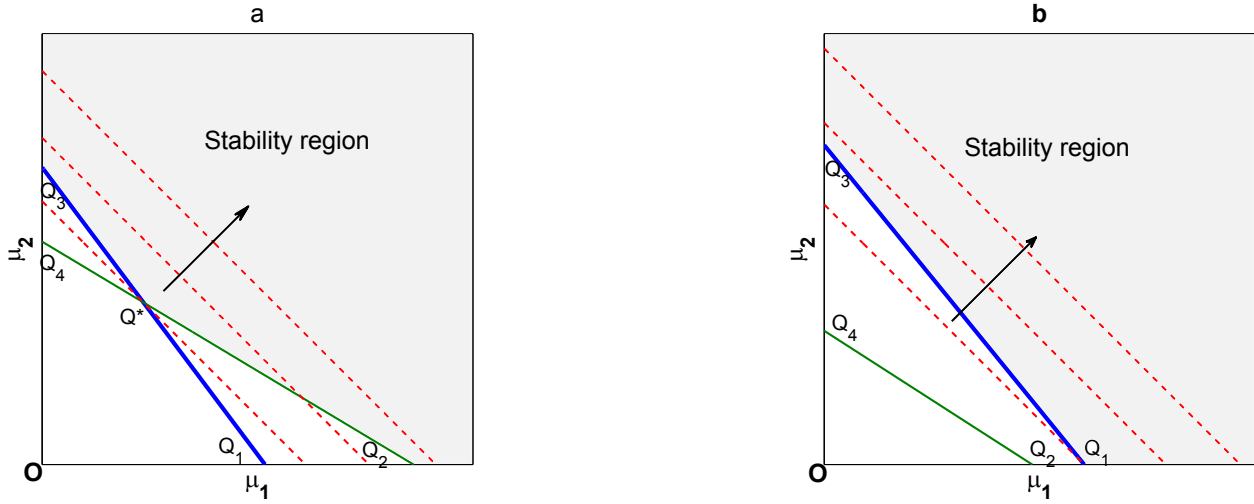


Figure 1: In both subfigures, the thick blue line represents  $\alpha = 0$  and the thin green line is for  $\beta = 0$ . The dashed red lines are the level sets of the cost function  $(\mu_1 + \mu_2)$ , which are increasing as indicated by the arrows. (a) The curve  $\widehat{Q_2Q^*Q_3}$  is the stability threshold in the  $\mu_1$ - $\mu_2$  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  $(\mu_1, \mu_2)$  is chosen from the shaded region.

which are real, are negative, where

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

224 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

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

225 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  
 226 is not achieved on the threshold since one of the eigenvalues is equal to 0 there. However, it  
 227 is achieved as soon as  $\mu_2 > \max(\mu_2^\alpha(\mu_1), \mu_2^\beta(\mu_1))$ .

Since the slope of  $\mu_2^\alpha$  with respect to  $\mu_1$  is smaller than -1 and the one of  $\mu_2^\beta$  is large than -1, the only way both could intersect in the positive orthant is illustrated in Fig. 1a. The

intersection takes place at

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

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  $\mu_1$  or  $\mu_2$  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  $\mu_1$ - $\mu_2$  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.

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

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

245 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

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

246 In view of (4.8) and (4.9) we observe that pest populations survive (all components  
 247 of  $E^*$  are positive) in both patches before releases, therefore releases should be conducted in  
 248 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

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

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

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

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

260 Finally, we note that the stability threshold in either case (one patch release case or two  
 261 patch release case) does not depend on the release period. It is also noted that the minimum  
 262 effort, while releasing natural enemies into both patches, is independent of the predator  
 263 dispersal rates. However, in the one patch release case, the release threshold also depends  
 264 on the predator dispersal rate. To sum up this optimality approach, we recall that stability  
 265 is not achieved for  $(\mu_1, \mu_2)$  on the stability threshold as stated earlier; the solution of the  
 266 present minimization problem then gives an infimum to the total release rates that can be  
 267 used to achieve stability of the pest-free solution.

#### 268 *4.2. Balanced predator dynamics and pest dispersal*

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

274 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

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

275 Hence, a necessary condition to balanced predator dynamics is:

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

276 If we consider the above balance equation together with  $b_1 = b_2 = b$  and  $\mu_1 = \mu_2 = \mu$   
 277 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  $\mu$  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



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

### 288 *4.3. Unbalanced predator dynamics and pest dispersal*

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

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

#### 307 *4.3.1. Simple model*

308 As a first step in the analysis, we concentrate on the simplest case for which balanced  
309 dynamics conditions do not hold. We consider a simple model, which yields  $y_1^T(t) = y_2^T(t)$ ,  
310 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  
311 assume the following parameter simplification:  $a_1 = a_2 = m, m_1 = m_2 = m, d_{12} = d_{21} = m$

312 and  $D_{12} = D_{21} = m$  which allows for analytic computations without altering the main  
 313 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

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

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

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

315 Suppose  $\Phi_1(0)$  and  $\Phi_2(0)$  are the initial state, then the solution of the above linear system  
 316 (4.16) at the terminal time  $T$  can be written as:

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

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

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

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

320 then the pest-free periodic solution is asymptotically stable.

321  
 322 We have proved (see **Appendix C**) that Jury Conditions 2 and 3 trivially hold. However,  
 323 the satisfaction of Condition 1 depends on both the release rate and the release period, the  
 324 two control parameters. Here, we establish a relationship between  $T$  and  $\mu$  for the stability  
 325 threshold and define a region in the  $T$ - $\mu$  plane where all Jury conditions are satisfied.

326 In **Appendix C** we have analytically shown that the release rate must be larger than  
 327  $\hat{\mu} = m^2/\sqrt{b_1 b_2}$  for pest eradication when releases are very frequent ( $T \rightarrow 0$ ). We have  
 328 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  
 329 infrequent releases ( $T \rightarrow +\infty$ ). Consequently, we have that the threshold release rate evolves  
 330 with the release period and that, for release rates between  $\hat{\mu}$  and  $\bar{\mu}$ , the pest-free periodic  
 331 solution will be stable for some release periods and unstable for others. However, it seems  
 332 difficult to explicitly compute the critical release period at which stability is lost. Hence,  
 333 simulation results are helpful to understand how stability changes with the release period.  
 334 **We are interested in understanding the qualitative information of the model rather than**  
 335 **quantitative results. Thus, in simulations, we use hypothetical values for the ecological**  
 336 **parameters, that are illustrative of the different qualitative outcomes and of the changes in**  
 337 **stability.**

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

350 We also represented different level curves of  $\psi_1$  in the  $T$ - $\mu$  plane (see Fig. 3) in order  
 351 to identify the stability region of the pest-free periodic solution. The zero level curve of  $\psi_1$   
 352 is the threshold curve which creates two subregions: the upper one is the stable region and  
 353 the lower one is the unstable one; ; it is an increasing function of  $T$  whose value is  $\hat{\mu}$  in zero  
 354 and converges to  $\bar{\mu}$  as  $T$  becomes large. For any pair of  $(T, \mu)$  below the zero level curve,  
 355 establishment of biological control agents cannot drive the pest population to extinction

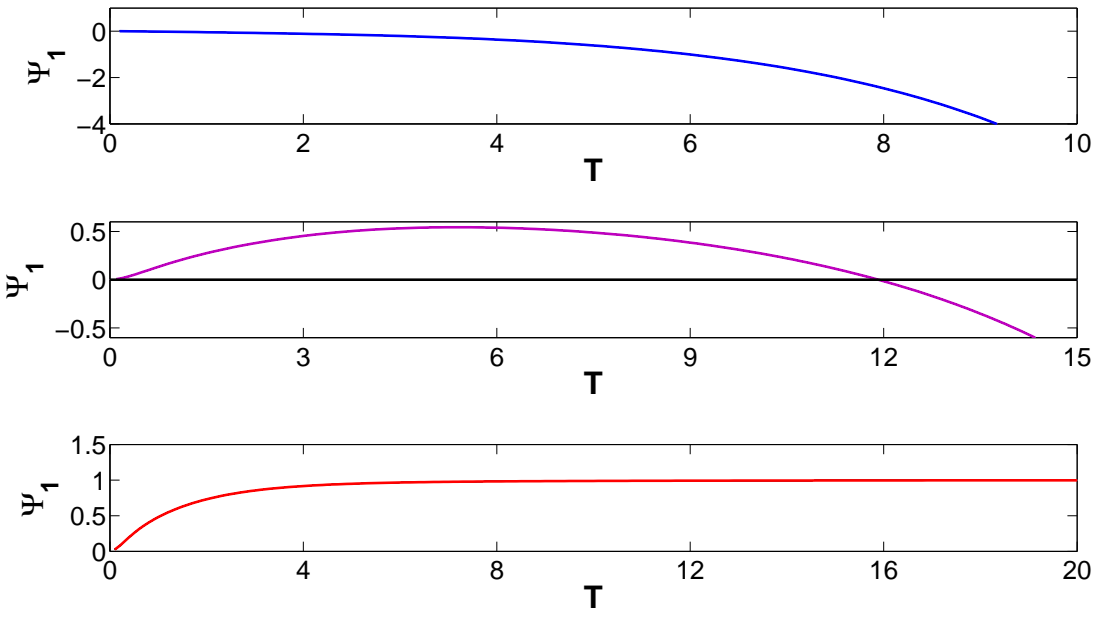


Figure 2: When  $\mu = 1.8 < \hat{\mu}$ , then  $\psi_1(T)$  is negative and decreases with respect to  $T$  (top subplot). When  $\hat{\mu} < \mu = 3 < \bar{\mu}$ , then  $\psi_1(T)$  is positive and increases for smaller values of  $T$ , but decreases as  $T$  crosses 5.6.  $\psi_1(T)$  becomes negative 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).

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

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

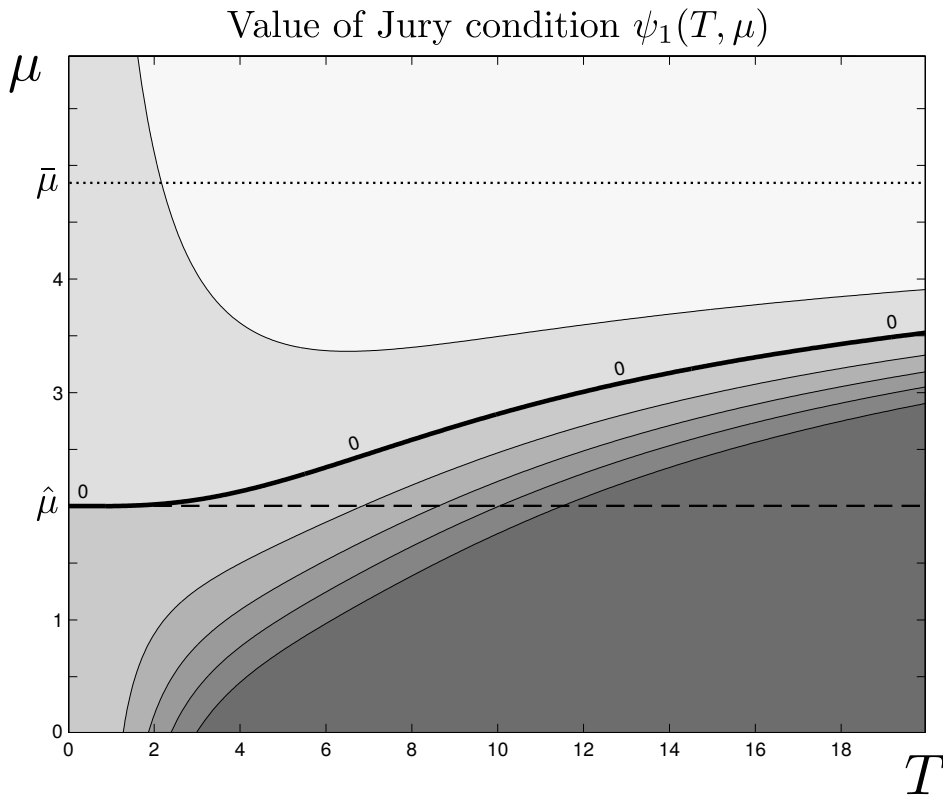


Figure 3: Contour plot of the first Jury condition  $\psi_1$  in the  $(T, \mu)$  plane. Darker areas correspond to smaller values of  $\psi_1$ . The zero level curve of  $\psi_1$  is displayed as a thick curve: it corresponds to a threshold release rate which increases with the release period. Positive (resp. negative) values of  $\psi_1$ , 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  $\mu_2$  corresponding to the stability threshold, that is the one such that, for a given  
388  $T$ , if  $\mu_2$  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  $\mu_2$  value that either imposes  $\psi_1, \psi_2$ , or  $\psi_3$  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  $\mu_2$  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  $\mu_2$  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

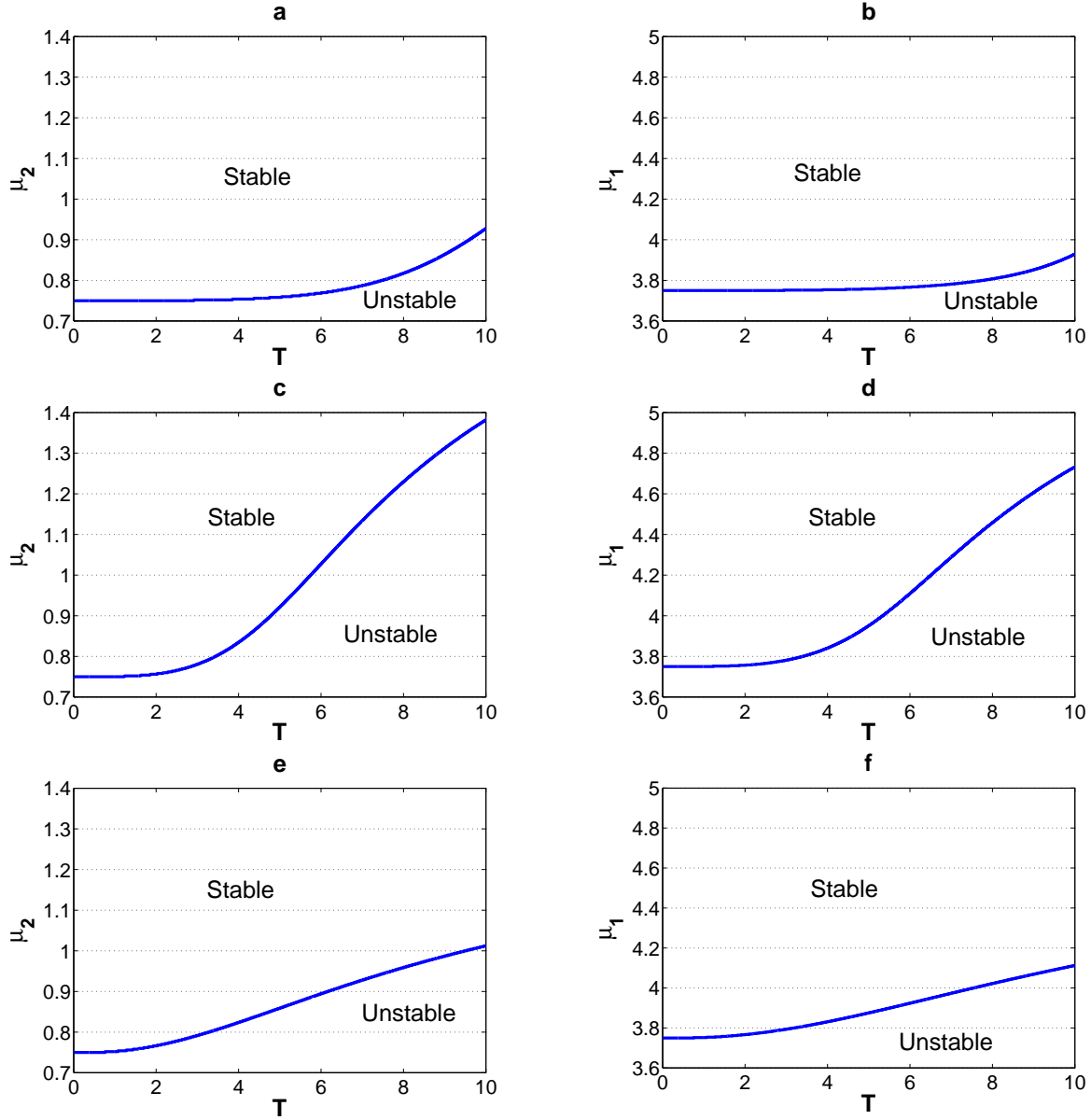


Figure 4: In each sub-figure we plotted the stability threshold which creates two regions: a region ensuring stability of the pest-free solution, and one for instability. In each case, the stability threshold is an increasing function of the release period. All the threshold curves are drawn in the same 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  $\mu_2$  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

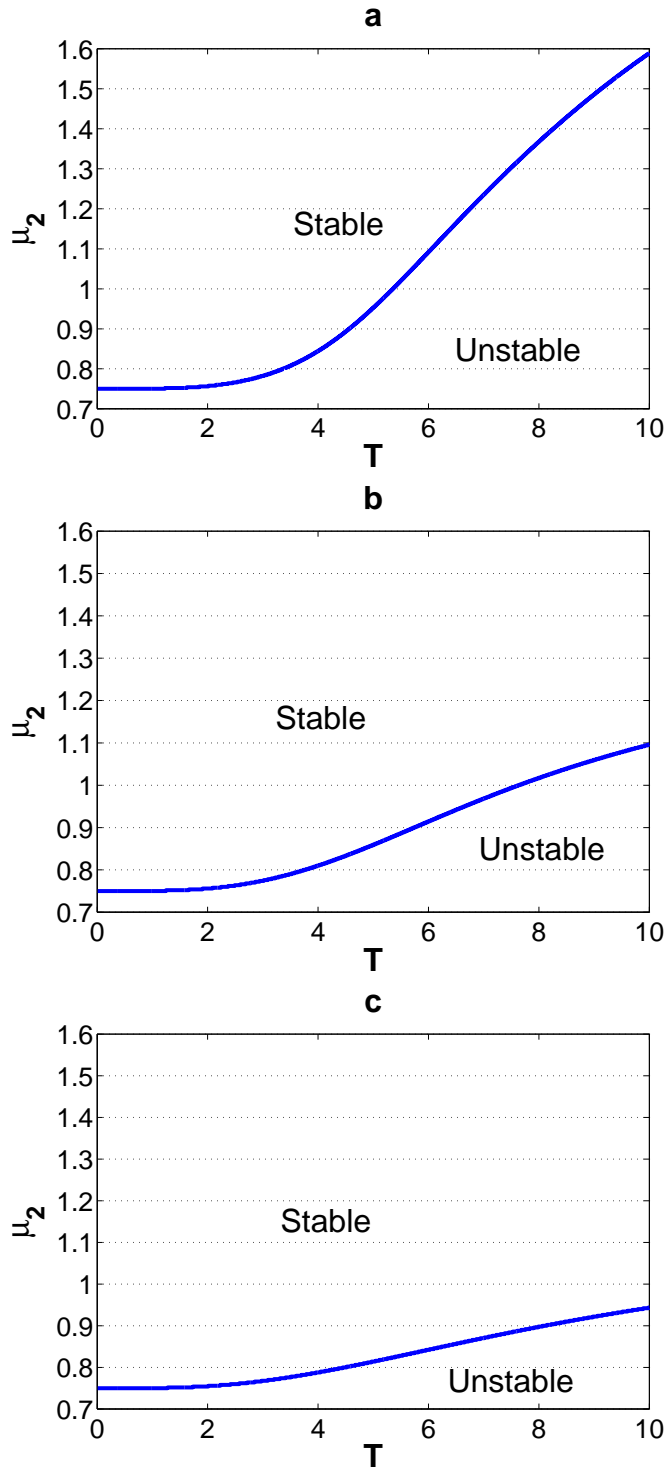


Figure 5: Stability threshold  $\mu_2$  is plotted for different predator dispersal rates. We select  $D_{12} = 0.21$  and  $D_{21} = 0.01$  for subplot a,  $D_{12} = 0.6$  and  $D_{21} = 0.4$  for subplot b and  $D_{12} = 1$  and  $D_{21} = 0.8$  for subplot c.

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

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

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

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

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

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

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

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

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

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

518 so that

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

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

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

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

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

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

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

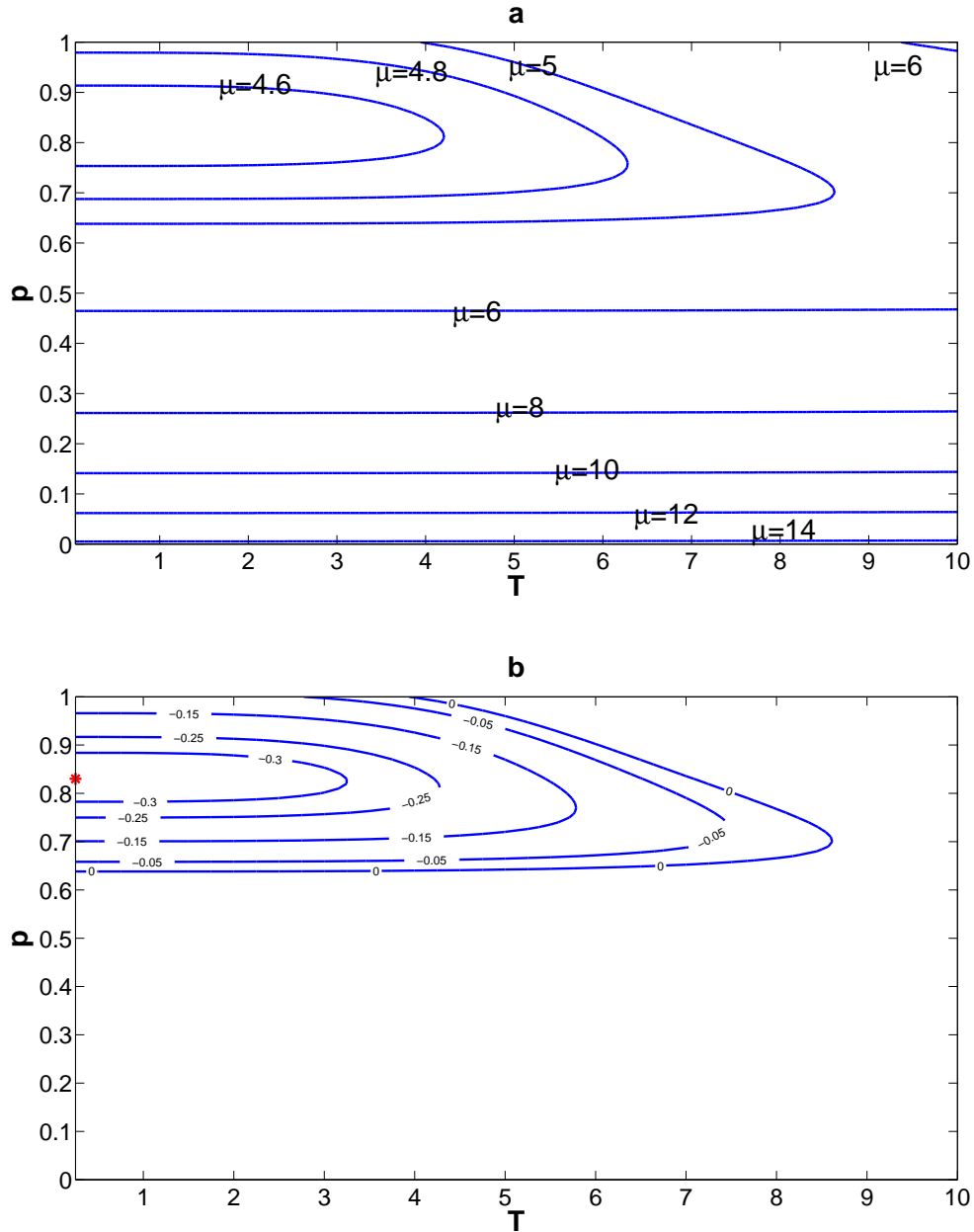


Figure 6: (a) Numerical investigation of the efficacy of the spatio-temporal deployment of biological control agents in the  $(T, p)$  plane, with  $T$  the release period and  $p$  the fraction of the releases deployed in patch 1. The biological parameters correspond to those of Fig. 4c and d. (a) Stability regions correspond to all  $(T, p)$  pair which can eradicate pest population form both patches are shown for different release rates  $\mu$ ; they are on the left of the illustrated level curves. (b) The level curves of mean evolution rate  $\theta$  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

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

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

594 In previous studies, Nundloll et al. [15, 16] considered augmentative biological control  
595 in spatially implicit pest-predator models in which predators suffer from negative density  
596 dependence. As in the present study, they have shown that the threshold predator release  
597 rate ensuring the stability of the pest-free solution was an increasing function of the release  
598 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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## 708 **Appendix A: Commutativity condition**

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

710

$$711 \widehat{Z}_{11} = (a_1 - d_{12} - b_1 y_1^T(t_1)) (a_1 - d_{12} - b_1 y_1^T(t_2)) + d_{12} d_{21},$$

712

$$713 \widehat{Z}_{12} = d_{21} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_1) - b_2 y_2^T(t_2) ),$$

714

$$715 \widehat{Z}_{21} = d_{12} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_2) - b_2 y_2^T(t_1) ),$$

716

$$717 \widehat{Z}_{22} = d_{12} d_{21} + (a_2 - d_{21} - b_2 y_2^T(t_1)) (a_2 - d_{21} - b_2 y_2^T(t_2)).$$

718

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

720

$$721 \overline{Z}_{11} = (a_1 - d_{12} - b_1 y_1^T(t_2)) (a_1 - d_{12} - b_1 y_1^T(t_1)) + d_{12} d_{21},$$

722

$$723 \overline{Z}_{12} = d_{21} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_2) - b_2 y_2^T(t_1) ),$$

724

$$725 \overline{Z}_{21} = d_{12} (a_1 + a_2 - d_{12} - d_{21} - b_1 y_1^T(t_1) - b_2 y_2^T(t_2) ),$$

726

$$727 \overline{Z}_{22} = d_{12} d_{21} + (a_2 - d_{21} - b_2 y_2^T(t_2)) (a_2 - d_{21} - b_2 y_2^T(t_1)).$$

728

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

730 Now

731

$$732 \overline{Z}_{12} - \widehat{Z}_{12} = d_{12} ( b_1 (y_1^T(t_2) - y_1^T(t_1)) - b_2 (y_2^T(t_2) - y_2^T(t_1)) ),$$

733

734 and

735

$$736 \quad \overline{Z}_{21} - \widehat{Z}_{21} = -d_{21} \left( b_1(y_1^T(t_2) - y_1^T(t_1)) - b_2(y_2^T(t_2) - y_2^T(t_1)) \right).$$

737

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

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

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

740 As linear system (4.16) is difficult to solve analytically by hand, we use Maple software,

741 which gives the following elements of the monodromy matrix.

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

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

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

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

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  $\mu$ . 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  $\psi_1$  is complex, it is difficult to test Jury condition 1 for arbitrary  $\mu$   
748 and  $T$ . In this regard, we calculate the values of  $\psi_1$  for sufficiently small and large release  
749 periods and indicate if there is a stability switching for varying  $T$  by keeping  $\mu$  fixed.

750 Taking second order approximation of  $\psi_1$  (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

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

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

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

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

754 By approximation, we can write

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

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

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

759  
760 For smaller value of  $T$ ,  $\psi_1(T)$  increases (respectively, decreases) with respect to release  
761 period for  $\mu > \hat{\mu}$  (respectively, for  $\mu < \hat{\mu}$ ) along a parabolic path. However, it seems difficult  
762 to compute  $\psi_1(T)$  analytically for any other finite value of  $T$ .

763  
764 We now examine the stability behaviour when the release period is very large.

765 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  $\mu$  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  $\bar{\mu}$ .