Pareto-efficient biological pest control enable high efficacy at small costs

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Abstract

Biological pest control is increasingly used in agriculture as a an alternative to traditional chemical pest control. In many cases, this involves a one-off or periodic release of entomopathogens. As the interaction between the entomopathogen and the pest is complex and the production of entomopathogens potentially expensive, it is not surprising that both the efficacy and economic viability of biological pest control are debated. Here, we investigate the performance of very simple control strategies. In particular, we show how Pareto-efficient one-off or periodic release strategies, which optimally trade off between efficacy and economic viability, can be devised and used to enable high efficacy for small economic costs. We demonstrate our method on a pest-pathogen-crop model with a tunable immigration rate of pests. By analyzing this model, we demonstrate that simple Pareto-efficient one-off release strategies are typically efficacious and simultaneously have average profits that are close to the theoretical maximum obtained by less efficacious and complicated profit-optimizing strategies. The only exception occurs for high pest-immigration rates, in which case periodic release is preferable. The methods presented here can be extended to more complex scenarios and thus be used to identify promising biological pest control strategies in many circumstances.

Keywords: Pareto frontier; pest management; optimization; dual target; Spodoptera litura

1. Introduction

Pests are a major concern in agriculture. Locally, outbreaks cause financial losses and regionally, outbreaks threaten the food security of entire populations. This is of particular concern in developing nations for which agriculture constitutes a larger share of the economy but agricultural practices have not yet reached the same technical and procedural standards as in developed nations. In India, for example, the "Army worm" *Spodoptera litura* (Fabr.) has defoliated many economically important crops including cotton, sunflower, and soybean (Dhaliwal et al. 2010). Farmers have traditionally resorted to pesticides to prevent and mitigate pest outbreaks, but their use may have unwanted consequences including insect resistance, resurgence, outbreak of secondary pests, and pesticide residues affecting human health and the environment. Heavy usage of synthetic pesticides have been linke to pest resistance, pest resurgence, health risks from exposure, and food contamination (Khooharo et al. 2008; Yadav 2010)

Biological pest control is an alternative to chemical pest control in which naturally occurring pathogens rather than pesticides are used to control the pests. The use of pathogens to suppress insect pests has several advantages over chemical pest control, in particular safety for farmers, consumers, and non-targeted organisms such as other natural enemies of the pest. Entomopathogens can potentially be efficacious at low cost and should not normally pose any danger for either farmers or consumers. They can be host-specific, they preserve natural enemies, and they may beneficially impact biodiversity (Lacey et al. 2001). Unlike the use of pesticides, there is little consensus on how to apply entomopathogens for maximal efficiency. This is not only because biological control agents have been introduced relatively recently, but it is also a consequence of a complex interplay of non-linear interactions between the crop, the pest, and the entomopathogen. The potential benefits of improved biological pest-control strategies are particularly large for inundative and augmentative control, in which large numbers of entomopathogens are released, as the timing of the release may significantly affect the total cost and efficacy.

A handful of studies have explored design of biological pest-control strategies from the perspective of mathematical analysis and/or optimal control theory. These studies have considered problems of bioeconomic equilibrium, demographic stability, and optimal release strategies (Getz and Gutierrez 1982; Grasman et al. 2001; Bhattacharyya and Bhattacharya 2006; Rafikov et al. 2008; Cardoso et al. 2009). While these studies have furthered our understanding of biological pest control, the proposed pest-control strategies cannot easily be communicated to agriculture professionals as they typically lack a regular pattern and often require continuous release of entomopathogens. Moreover, with Cardoso et al. (2009) as an important exception, only single-objective optimization is usually considered. Finally, to the authors knowledge, the studies to date have not explicitly modeled the crop, which as a third dynamic state variable could potentially impact the results. Developing simple but efficient rules for biological pest control in agricultural systems with crop-pest-pathogen interactions thus remains an important challenge from both a theoretical and applied perspective.

In this paper, we develop simple strategies for biological pest control that are easy to apply, efficacious, and simultaneously near optimal (85% of maximum) in terms of profit. The strategies are Pareto-efficient in that they offer an optimal trade off between profit and efficacy. We demonstrate how to use our methods on a dynamic model of the *Spodoptera litura* worm defoliating soybean crops while being controlled by a natural enemy, the *Spodoptera polyhedrosis* virus (Cherry et al. 1997; Fuxa 2004). Specifically, we investigate one-off control strategies and periodic control strategies. Using our measures of efficacy and profit, we find Pareto-efficient one-off and periodic control strategies that are close to optimal in the sense of profit and simultaneously not sensitive to perturbations. We show that one-off control strategies are preferable when immigration of pest is relatively low and intermediate. We also show that, for high immigration rates, one-off control can be replaced by simple periodic controls to achieve even better results.

2. Methods

We first model a pest-pathogen-crop system in which pest is controlled biologically through the release of individuals that are infected with a virus. The infection spread into the susceptible pest population and thus control the growth of pest biomass in the field. Second, we give a precise definition of the control strategies that we consider for the release of infective individuals. This class of control strategies is chosen for conceptual simplicity, though as we will show these strategies are capable of achieving near-optimal profits. Third, we define our measures of profit and efficacy, after which we describe the concept of Pareto efficiency used for dual-objective optimization. Finally, we list the software packages used for numerical analysis.

2.1. Crop-pest-pathogen system

We model a crop-pest-pathogen system inspired by soybeans devoured by the "army worm" *Spodoptera litura* (Komatsu et al. 2004). The army worm is being controlled biologically through the release of individuals that are infected with *Spodoptera polyhedrosis* virus (O'Reilly and Miller 2006). The biomass of soybean is denoted $C = C(t)$, while the density of infected and susceptible pest are respectively denoted $P_I = P_I(t)$ and $P_S = P_S(t)$. Disease transmission between susceptible and infective pests follow the law of mass action with a constant transmission coefficient β (McCallum et al. 2001). An overview of model variables and parameters is given in Table 1.

To arrive at a tractable model that nonetheless incorporate the essential features of the crop-pest-pathogen system, we integrate two influentaional and established models in theoretical biology, the Rosenzweig-MacArthur predator-prey model (Rosenzweig and MacArthur 1963) and the classical SI-compartment model in epidemiology (Hethcote 2000). On this basis, we assume that the dynamics of the crop are given by the following ordinary differential equation:

$$\frac{\mathrm{d}C}{\mathrm{d}t} = rC\left(1 - \frac{C}{K}\right) - \frac{a_S C P_S}{b_S + C} - \frac{a_I C P_I}{b_I + C}, \tag{2.1}$$

where the terms on the right hand side represent logistic growth in the absence of consumption by the pest, and consumption of susceptible and infected pests respectively. The dynamics of susceptible and infective pests are respectively given by:

$$\frac{\mathrm{d}P_S}{\mathrm{d}t} = c_S \frac{a_S C P_S}{b_S + C} - \beta P_S P_I - d_S P_S + A, \tag{2.2}$$

$$\frac{\mathrm{d}P_I}{\mathrm{d}t} = c_I \frac{a_I C P_I}{b_I + C} + \beta P_S P_I - d_I P_I. \tag{2.3}$$

From left to right, the terms represent reproduction of pests, disease transmission and mortality. Susceptible pests are assumed to immigrate from neighboring fields at a constant rate $A \geq 0$. Both susceptible and infective pests are capable of crop consumption and reproduction, but virulence is assumed to affect infected pests, through reduced fecundity, reduced crop consumption rate, and increased mortality. These assumptions are reflected in the following conditions in the parameters, $a_S \gg a_I$, $c_I \gg c_S$, $d_I > d_S$, and $b_S > b_I$. In Table 1 we state units and numerical values for all model parameters.

Before discussing some basic dynamic properties of system (2.1)–(2.3), we note that slightly similar mathematical systems have been used by e.g. Li et al. (2010) when studying a predator-prey system with group defense and impulsive control strategies, and by Zhang and Georgescu (2015) when studiying the influence of the multiplicity of infection upon the dynamics of a crop-pest-pathogen model with defence mechanisms.

Table 1: State variables and parameters of the crop-pest-pathogen model. In the table "-" represents that the impact of the parameter value will be explored later, or that the parameter will be explained later in the paper. *Sources*: (1) Ball et al. (2000); (2) Ruis-Nogueira etal. (2001); (3) Xiao and Van Den Bosch (2003); (4) Dale (2006); (5) U.S. Department of Agriculture's National Agricultural Statistics Service.

Quantity	Symbol	Default value	Unit	Sources
Biomass of the soybean crop population	C	variable	gram m^{-2}	
Density of the susceptible pest population	P_S	variable	m^{-2}	
Density of the infected pest population	P_I	variable	m^{-2}	
Crop intrinsic growth rate	r	0.45	day^{-1}	(1)
Carrying capacity of the soybean crop	K	500	gram m^{-2}	(2)
Consumption rate of susceptible pests	a_S	0.8	gram day^{-1}	
Consumption rate of infected pests	a_I	0.01	gram day^{-1}	
Half saturation constant of susceptible pests	b_S	200	gram m^{-2}	
Half saturation constant of infected pests	b_I	50	gram m^{-2}	
Reproductive rate of susceptible pests	c_S	0.5	$gram^{-1}$	
Reproductive rate of infected pests	c_I	0.01	$gram^{-1}$	
Mortality rate of susceptible pests	d_S	0.1	day^{-1}	(3)
Mortality rate of infective pests	d_I	0.8	day^{-1}	
Contact rate	β	0.008	m^2 day^{-1}	
Immigration rate of susceptible pests	A	-	m^{-2} day^{-1}	
Release rate of infected pests	U	-	m^{-2} day^{-1}	
Duration of the total growth period	$t_{final} - t_0$	140	day	(4)
Initial biomass of soybeans	C_0	5	gram m^{-2}	
Initial amount of susceptible pests	$P_S(0)$	0	m^{-2}	
Initial amount of infected pests	$P_I(0)$	-	m^{-2}	
Price of soybeans	p_{crop}	4.5×10^{-4}	\$ $gram^{-1}$	(5)
Fixed other costs	p_{fixed}	0.01	\$ m^{-2}	
Price per infective pests	p_{infected}	2×10^{-5}	\$	
Price of placing infective pest in the field	p_{labour}	5×10^{-3}	\$ m^{-2}	

We next briefly consider some dynamic properties of system (2.1)–(2.3). Typically, trajectories behave as shown in Fig. 1. The crop population will start growing slowly, followed by a rapid increase due to the logistic growth assumption.

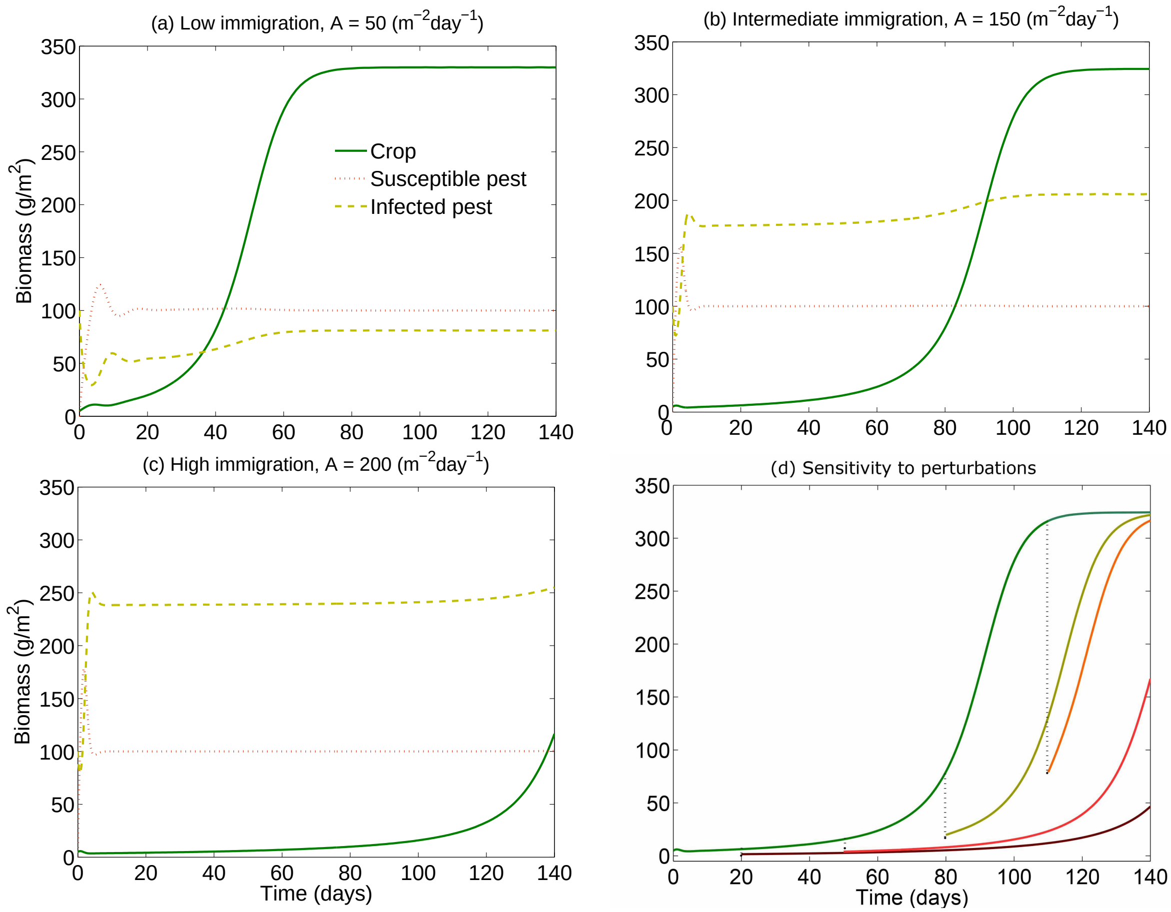

Figure 1: (a)-(c): Trajectories of crop (green, solid), susceptible pest (red, dotted) and infected pest (yellow, dashed). The soybean crop biomass increases rapidly at near half its equilibrium value. As immigration rate of susceptible pest increases, the rapid increase comes later in the season. In panel (c) it is delayed beyond the end of the season. Initial amount of infected pest was set to $P_I(0) = 100$ g/m^2. (d): The final crop biomass is sensitive to perturbations in the beginning of the season when the crop biomass is small and grows slowly. Trajectory of crop biomass without perturbation (green). Trajectories of crop biomass with a sudden reduction to 1/4 of its amount at time 110 (yellow), 80 (orange), 50 (red) and 20 (dark red). Initial amount of infected pest was set to $P_I(0) = 100$ g/m^2.

System (2.1)–(2.3) has a bistable phenomenon when immigration rate of susceptible pest A is relatively large. In particular, simulations indicate the existence of only one attractor, which is a positive globally stable equilibrium, when the immigration rate is low, $A \in (0, 210.2]$. For higher immigration rates, $210.25 \leq A \leq 1417.03$, the system has also, in addition to the positive equilibrium, an extinction equilibrium (a crop free state). Simulations of the basins of attraction for both equilibria has been performed, indicating that the above mentioned equilibria are the only existing attractors in the system. If the initial biomass of soybeans is small while immigration is high, then the extinction equilibrium is the attractor which lead to the crop-free state.

2.2. *Control strategies*

We first consider the case of releasing infected pests only once, in particular, in the beginning of the season. We call this strategy *one-off control*. This simple strategy has one control variable, the total amount of released infected pests $\widetilde{P}_I$.

We next consider periodic control in which we assume that the same amount of infected pests is released the first day of each week throughout the growing season. Since the growth of the crop biomass is most sensitive to perturbations in the beginning of the season, we always assume that the first release happens at the first day of the season. Then the same amount of infected pest is released the first day of any following week, ending with week N, where $N = 1, 2, 3, \ldots$. This periodic control strategy involves two control variables, the number of weeks N where an impulse of infected pest is released, and the total amount of released infected pests $\widetilde{P}_I$.

2.3. *Dual-objective approach*

Besides trying to optimize profit we also consider maximizing efficacy (minimizing sensitivity to perturbations on the profit). We will now define our profit function, our measure of efficacy (half-biomass time) and also recall the economic concept Pareto-efficiency, which we will use to trade-off between the two objectives profit and efficacy.

Profit measure. To determine a profit function, we first assume that yield is proportional to crop biomass and, without loss of generality, that the constant of proportionality is 1. If p_{crop} is the market price for the crop, then the revenue is given by $p_{\text{crop}}\, C(t_{\text{final}})$ where t_{final} is the time at the end of the growth season. We also assume that the total cost is given by $p_{\text{fixed}} + p_{\text{infected}}\, \widetilde{P}_I + p_{\text{labour}}\, N$, where p_{fixed} represent annually-recurring costs for seed, sowing, fertilizer, irrigation, pest monitoring, taxes, etc. that remain fixed within a single growth season; p_{infected} is the price of infected pests; and p_{labour} is cost for work needed to place a burst of infected pests in the field. Hence, the profit is given by

$$\text{Profit} = p_{\text{crop}}\, C(t_{\text{final}}) - p_{\text{fixed}} - p_{\text{infected}}\, \widetilde{P}_I - p_{\text{labour}}\, N.$$

Efficacy measure. To construct a measure of efficacy on the crop biomass we consider the typical behavior of trajectories. Figure 1 shows that, starting from a small initial crop biomass of 5 g/m^2, then crop grows slowly in the beginning of the season followed by a rapid increase starting at approximately 50 g/m^2. In particular, when crop biomass is small, then from (2.1) we see that $\partial C/\partial t \approx rC$ and so the relative (to biomass) growth rate is constant. Low profit results when the rapid increase in crop biomass takes place too late in the season. Hence, it is important that the period of fast growing crop biomass is within the growth season, as it is in Figs. 1a and b, but not in c. As Fig. 1d shows, the location of the rapid increase, and hence the final crop biomass, is sensitive to perturbations in the beginning of the season when the crop biomass is small and grows slowly. Based on these observations, we chose to measure efficacy with *half-biomass time*, which we define as the time needed for the crop biomass to grow from its initial state to half of the equilibrium crop biomass. This equilibrium may be thought of as an expected value of the final crop biomass. The higher the half-biomass time is, the larger is the risk for the farmer to obtain a small final crop biomass and hence a bad profit.

Pareto efficiency. A control strategy is said to be Pareto efficient if any change in the control strategy will make either the profit or the efficacy worse. The Pareto front is defined as the set of all Pareto-efficient strategies. Hence, the Pareto front consist of the "best" strategies and the choice of strategy on this front depends on the desired trade-off between the two objectives. For further information on Pareto efficiency and dual-objective optimization, we recommend an introductory textbook such as Karpagam 1999.

2.4. Numerical analysis

We implemented the crop-pest-pathogen system in MATLAB R2014b using the ODE-solver ode45. To compare the profit achieved within our class of contral strategies with the best achievable from arbitrary continuous-release control, we employed the optimal-control software TOMLAB (Holmstrom 1999) to identify the optimal control.

3. Results

In this section, we show how to find preferable control strategies. First, we conclude that only a small reduction in profit allows for efficacious control strategies. Second, we show that one-off control strategies are sufficient when immigration rates of susceptible pest are low to intermediate, while periodic control strategies are recommended for high immigration rates. Finally, we conclude that the determined control strategies are not far from optimal in terms of profit, despite their simplicity.

3.1. A small reduction in profit allows efficacious control strategies

Figure 2a-c shows different one-off and periodic control strategies for low, intermediate and high immigration of susceptible pest. In each panel, different curves correspond to different N, starting with one-off control, i.e. $N = 1$, (green) and continuing with periodic controls for $N = 2, 3, 4, \ldots$ (black). Each curve is produced by varying the released infected pest $\widetilde{P}_I$ over all possible values. Using Fig. 2a-c, we can find control strategies that give a profit close to optimal, in the sense of one-off and periodic control strategies, and which are simultaneously efficacious in the sense of having a short half-biomass time. This is possible since the slope of the Pareto-front (light green curve) is small near the maximum profit of the front, in particular for low to intermediate immigration rates. We recommend such Pareto-efficient strategies in place of optimizing only profit, to obtain more stable outcomes.

In Table 2, we specify in detail four representative strategies on the Pareto front. These stategies are marked with circles in Fig. 2a-c. All four strategies have a half-biomass time of less than 80 and profit not far from the highest that can be achieved for any strategy of the same type. Depending on how one wishes to trade off between profit and efficacy, other strategies on the Pareto front with higher or lower efficacy can naturally also be considered.

3.2. One-off control strategies are sufficient for low and intermediate immigration

From Fig. 2a-c we conclude that one-off control strategies are preferable for low to intermediate immigration rates. For high immigration rates, we recommend periodic control with either two or three ($N = 2$ or $N = 3$) releases of infected pest. In particular, in a field with high immigration, using periodic control in place of one-off control can result in the half-biomass time being reduced by 25% without reducing the profit.

Table 2: Representative pest-control strategies.

Immigration (m^{-2})	Profit (\$ m^{-2})	Half-biomass time (days)	Released infected pest (m^{-2})	Number of pest bursts
50	0.132	53	64	1 (one-off)
150	0.126	72	256	1 (one-off)
250	0.089	79	1700	2 (periodic)
250	0.089	79	1450	3 (periodic)

3.3. The determined control strategies are not far from optimal in terms of profit

To compare the representative control strategies in Table 2 to the optimal profit, when considering profit as the only target under optimization, we determined the best possible continuous-release control strategy using the software TOMLAB (Holmstrom 1999). Unlike the control strategies we have considered, this optimal control strategy can take any form and may be very hard to implement in practice. To compare the profit achieved through applying this optimal control strategy with those of our representative control strategies, we assume in this section that the labour cost for placing infective pest in the field is zero, i.e. $p_{\text{labour}} = 0$. This assumption is necessitated by the fact that the determined optimal control strategy requires continuous release of infective individuals. By making this assumption, we thus achive a situation in which the difference in profit between the two strategies should be largest.

Figure 2 (d) shows the profit of the representative control strategies given in Tables 2 (with $p_{\text{labour}} = 0$) together with the optimal profit obtained by TOMLAB. We conclude that the profit of the representative control strategies are not far from the optimal profit in the whole range of immigration rate. In particular, the representative control strategies yield more than 85% of the optimal profit. We remark that the gap between the optimal profit and the representative control strategies would decrease further when adding any reasonable cost for work to both controls. We have also observed, not surprisingly, that the trajectories for crop resulting from the optimal control strategies obtained by simulations in TOMLAB have a large half-biomass time. Therefore, they are sensitive to perturbations which in turn clearly yields an additional cost.

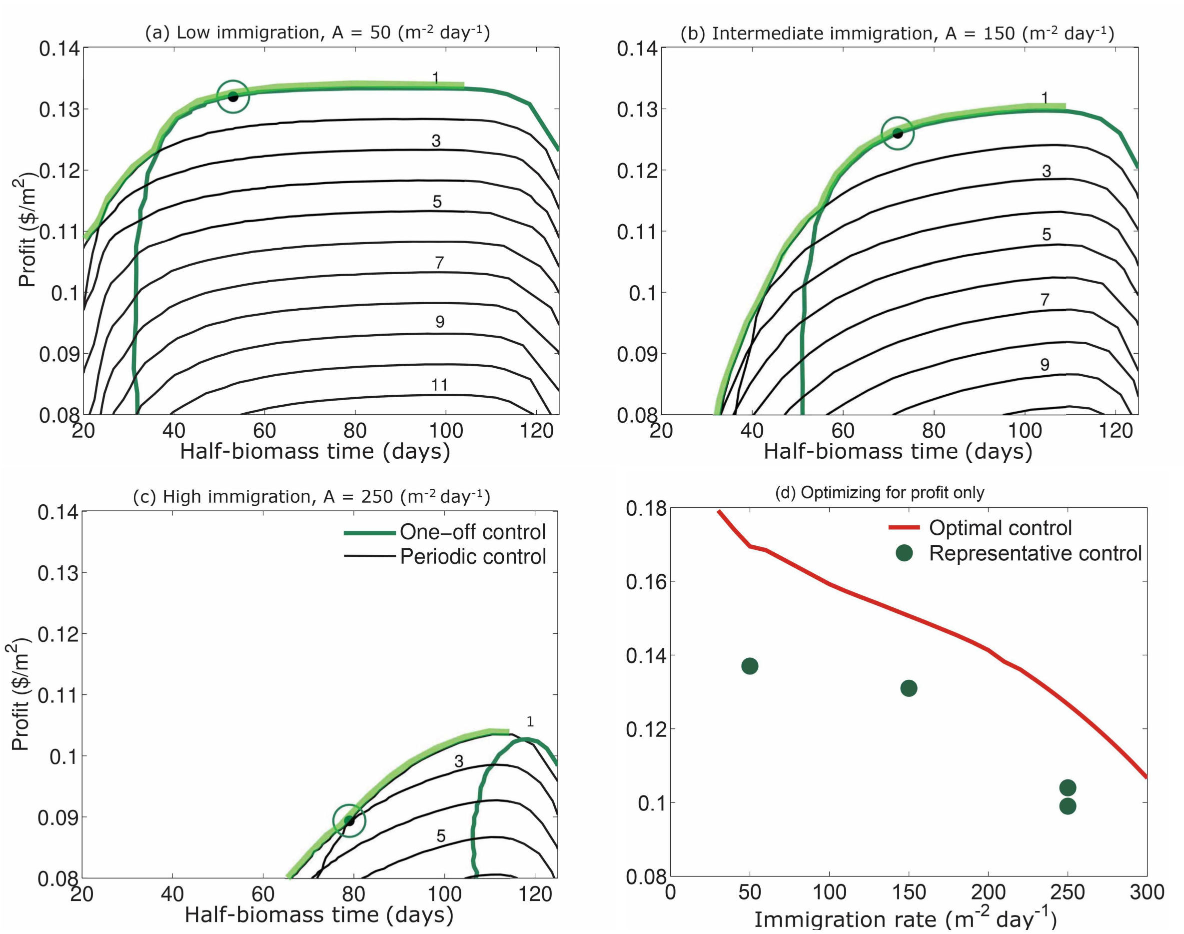

Figure 2: Pareto-efficient control strategies allow safe controls to a small cost in profit. The circles indicate representative control strategies on the Pareto-front (light green curve). In each subfigure, different curves correspond to different N, starting with one-off control (green) and continuing with periodic controls for $N = 2, 3, 4, \ldots$ (black). Each curve is produced by varying the released infected pest $\widetilde{P}_I$ over all possible values. The Pareto-front is given by the light green curve. Panels (a) and (b): For low and intermediate immigration, we recommend the farmers to use one-off controls, while for high immigration (c) periodic control is better and we recommend either two or three bursts ($N = 2$ or $N = 3$). (d): The representative control strategies are not far from optimal in the sense of profit. The optimal profit obtained by running the software TOMLAB, maximizing only profit, is given by the red curve. The profit of the representative control strategies is marked with green balls. In panel (d), all results are without cost for labour, i.e. $p_{\text{labour}} = 0$.

3.4. Robustness

In this section we investigate robustness of our results by varying values of crop intrinsic growth rate r, contact rate β as well as immigration of susceptible pest A. Figures 3a-c show regions where the recommended control is one-off control, periodic control and where it is impossible to obtain a positive profit. To find a border between recommending one-off or periodic control, we use here the following rule of thumb: We recommend to use periodic control, in place of one-off control, if the returntime thereby can be reduced by at least 20% without loosing more than 20% of the best profit resulting from the one-off controls. Figures 3a-b are produced by examination of numerous figures of the same type as Fig 2a-c. Besides results illustrated in Figures 3a-c, we concluded from these simulations that the structure of the curves seems to be rather stable. This means that our conclusions that a small reduction in profit allows efficacious control strategies seems robust. Moreover, our conclusion that one-off control strategies are sufficient for (relatively) low and intermediate immigration holds whenever $r > 0.4$ and $\beta > 0.007$. In addition, the later conclusion can be extended as: one-off control strategies are sufficient for relatively low and intermediate immigration, as well as for relatively high contact rate and relatively high crop intrinsic growth rate.

The simulations in this section also verifies the natural facts that crop growth will increase in r, β and decrease in A.

4. Discussion

We have considered biological control of agricultural pests. Using a dual-objective approach and the economic concept of Pareto-efficiency, we have determined one-off and periodic control strategies which are stable to perturbations and simultaneously nearly optimal in terms of profit. Depending on the immigration rate of pests from nearby fields, we recommend either one-off control, with entomopathogens released only once in the beginning of the growing season, or periodic control, with entomopathogens released at periodic intervals. Surprisingly, as we showed in Sect. 3.3, these two conceptually simple pest-control strategies come close to the best that can be achieved, even when allowing for complicated continuous-release strategies.

The exact threshold for the immigration rate at which one should switch from one-off control to periodic control as well as the other control parameters can be determined from our model after it has been parameterized for the system of interest. We also believe that it should be possible to determine reasonable values for the control parameters through controlled field experiments, or even individual experimentation. Future work may aim to overcome the problem of parametrization by deriving even more general insights, such as adaptive rules which relate the timing of release or the released quantity to observed changes in the crop and pest population.

When defining the periodic control strategies in Sect. 2.2, we assumed that the same amount of pest is released once a week. This assumption should be considered more as an example than a rule. In fact, the efficacy of the periodic control will only be marginally affected by smaller changes in the length of this time interval. The costs associated with the periodic control does, however, strongly depend on the price of placing the infected pests in the field (p_{labour}). A lower price will make the controls that releases more often (higher N) better. Moreover, a natural extension of the periodic controls tested here would be to allow for the combination of one-off control and periodic control. We have seen that one-off control performs well in most tested cases, and therefore we believe in releasing larger amounts of pest at impulses in the beginning

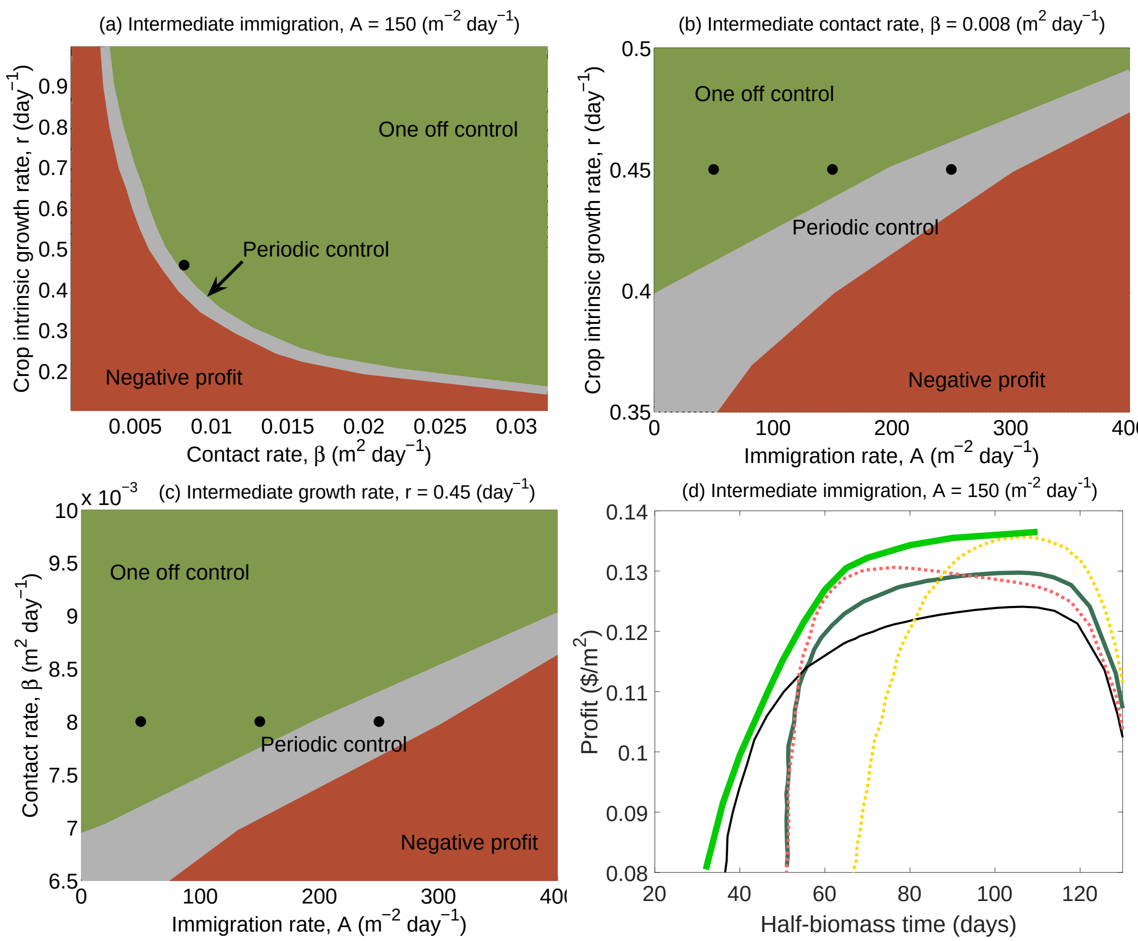

Figure 3: (a)-(c) Regions where the recommended control is one-off control (green), periodic control (grey) and where it is impossible to obtain a positive profit (red). The black dots represent parameter values used in Figures 1 and 2. (a) Imigration rate $A = 150$ is fixed while crop intrinsic growth rate r and contact rate β are varied. (b) Contact rate $\beta = 0.008$ is fixed while crop intrinsic growth rate r and immigration rate A are varied. (c) Crop intrinsic growth rate $r = 0.45$ is fixed while contact rate β and immigration rate A are varied. (d) Profit and half-biomass time when allowing for combinations of periodic controls and one-off controls in the setting of intermediate immigration $A = 150$. The light green curve represents the Pareto-front. One-off control (green), periodic control with $N = 2$ and $\tau = 7$ (black), periodic control with $N = 2$ and $\tau = 137$ (red, dotted), and combined one-off and periodic control with two impulses satisfying $\widetilde{P}_{\text{one-off}} = 0.1\widetilde{P}_{\text{periodic}}$ (yellow, dotted).

of the growth season, and smaller amounts later during the season. We will further discuss this below.

We have considered dual-objective optimization which accounts for both efficacy and profit. The fundamental drawback with optimizing profit alone is that the resulting crop trajectory may behave similar to the trajectory for crop biomass given in Fig. 1b. Even worse, the increase in crop abundance may come closer to the end of the season so that a small perturbation during the growth season may pass it beyond the end of the season, as the trajectories of crop in Fig. 1c and d. Hence, instead of optimizing only profit, farmers should consider a trade-off between profit and some measure of efficacy (sensitivity to perturbations). To exclude growth patterns which are very sensitive to perturbations and hence implies a high risk for farmers, we introduced in Sect. 2 a measure of efficacy, the half-biomass time, and applied a dual-objective approach through Pareto-efficiency.

Our measure of efficacy, half-biomass time, is related to resilience, which is nowadays frequently used in ecology (Pimm and Lawton 1977; Loreau and Behera 1999; Petchey et al. 2002; Montoya et al. 2006; Loeuille 2010; Valdovinos *et al.* 2010). In essence, short half-biomass time corresponds to high resilience as it means that the crop is quickly able to approach an equilibrium state. In ecology, resilience is usually defined as the reciprocal of the return time to a stable equilibrium of a trajectory, perturbed from the same equilibrium. Therefore, a high resilience relates to a short half-biomass time. We define half-biomass time based on typical growth patterns for crops in our model. However, a similar definition will apply to other models showing similar growth patterns, involving models where biomass is assumed to grow logistic. It is worth noting that the measure half-biomass time may be replaced by any other suitable measure which can be defined for the model in question.

The study closest to ours is the impressive effort by Cardoso et al. (2009) in understanding biological of caterpillar (*Anticarsia gematalis*) by natural enemies such as wasps and spiders. Similar to us, these authors use a dual-objective approach and use the economic concept of Pareto-efficiency. In their case, the two objectives are measures of the number of prey (the pest) and the number of predators (the natural enemy of the pest) which are released. Like us, these authors aim to derive more practical pest-control strategies by moving away from continuous-release strategies towards release at specified time points, so-called impulsive release (Tang et al. 2005; Zhang et al. 2007). Apart from the different choice of study system, a few differences are worth noting: First, Cardoso et al. (2009) do not compare the impulsive-control strategies that they derive with simple one-off control and periodic-control strategies as considered here. Second, whereas we develop and motivate a non-linear measure of pest-control efficacy, Cardoso et al. (2009) uses a measure of the number of released natural enemies as the second objective. Third, we explicitly consider the dynamics of the crop and move beyond the traditional Lotka-Volterra framework by incorporating realistic functional responses. Interestingly, the optimal strategies presented in Figs. 3-5 of Cardoso et al. (2009) have a clear resemblance to a periodic control except at the beginning and the end of season. Based on this observation and our own results, we conjecture that effective strategies of biological pest control can be obtained by combining one-off control and periodic control. Figure 3d shows the Pareto-front for profit and half-biomass time when allowing for such combinations in the setting of intermediate immigration $A = 150$. In particular, the combined control has four control variables; the amount of released pest in the beginning of the season ($\widetilde{P}_{\text{one-off}}$), the total amount of released pest during the following periodic control ($\widetilde{P}_{\text{periodic}}$), the number of days between pest impulses (τ) and the total number of impulses (N). By comparing Figure 2b with Figure 3d we conclude that the Pareto-front is slightly higher in Figure 3d. Thus, allowing for combinations of periodic controls and one-off controls opens for slightly more efficient control strategies. Moreover, the dotted curves in Figure 3d, which reaches near Pareto optimality, consists of strategies with only two impulses ($N = 2$), the first at the beginning of the season and the second near the end of the season. Hence, simple strategis performs well also when allowing for combinations of one-off control and periodic control.

As noted in this paper, several studies in applied mathematics have aimed to determine optimal strategies of biological pest control. These studies draw upon and synthesize a rich scientific heritage of mathematical modeling in ecology, dynamical systems theory, and optimal control theory. The crowning achievement is the ability to determine the optimal timing for releasing entomopathogens across a range of pest-pathogen systems. This accomplishment of modern science will, however, be almost for nothing if insights are not distilled and the results disseminated in a form that is useful for the agricultural community. Our aim with this paper has been to demonstrate how practically useful pest-control strategies can be determined from mathematical models of crop-pest-pathogen interactions. While we have arguably not succeeded in bridging the full width of the gulf that currently exist between mathematical theory and practical applications, we expect the width of that gulf to shrink as future authors continue the effort to uncover practically useful strategies of biological pest control.

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