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Improving the efficiency of augmentative biological control with arthropod natural enemies: A modeling approach

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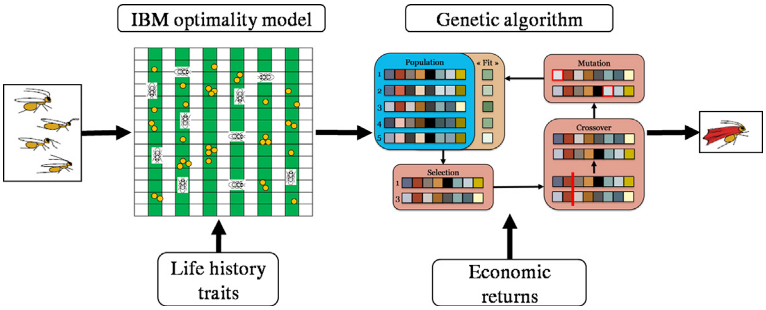
GRAPHICAL ABSTRACT



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ABSTRACT

A better understanding of the life-history traits of biocontrol agents and their effect on population dynamics is key to obtaining more efficient pest control and generating higher economic returns for biocontrol practitioners. To this end, we constructed an optimality simulation model based on principles of the behavioral ecology of natural enemies. This model allows for the identification of the most important life-history traits of natural enemies (*e.g.*, fecundity, longevity, attack rate, competition and dispersal), taking into account the costs and benefits for biocontrol practitioners. The model was kept general and was designed in such a way that it can be adapted to different target species and their specific ecology (natural enemy-pest-plant combination). Results indicate strong interactions between the optimized life-history traits of the biocontrol agents. Two different optimized life-history strategies for the agents were found with higher potential economic returns. These strategies differ most significantly in the plant-leaving decision and host handling time of the biocontrol agent, but also in their respective fecundity, longevity and dispersal ability. The preferred strategy depends on the number of agents released and the growth rate of the plant. Information from these optimality models can help to determine which agents should be released and how they should be released in a specific agro-ecological situation.

1. Introduction

Pest management has remained an important challenge over the last decades, leading to an increase in pesticide use in many parts of the world (Coll and Wajnberg, 2017). However, undesirable side effects of pesticides are causing growing consumer concerns, and have led to the

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introduction of increased legislative constraints on the use of chemicals for controlling pests in different countries (Bianchi et al., 2013). Due to these constraints, the use of biological control of arthropod pest populations by natural enemies has become a relevant and efficient strategy used worldwide (Mason et al., 2008). Today, biological control is a well-established methodology for the control of pest population levels by releasing predators, parasitoids, pathogens or antagonist populations into the field (Heimpel and Mills, 2017).

In this respect, there is a high demand for predictive, innovative, and inexpensive techniques to assess the efficiency of natural enemies as biocontrol agents, in order to envision in advance the expected pest control success of biocontrol agents, but also to find means for genetic improvement to increase agents' performance (Lommen et al., 2017).

Improved augmentative biological control depends on increasing the efficiency of the natural enemies, which is mostly determined by their behavioral features and their trophic interactions with the insect pests and the crop plants to be protected. A better understanding of these features and their effect on population dynamics is a critical step towards efficacious pest control. One way of determining the most important life-history traits of natural enemies is by using optimality models (Wajnberg et al., 2016). These models can fulfill a predictive role in the field of biocontrol and also contribute to a better understanding of success and failure in biological control releases (Mills and Kean, 2010).

Several mathematical models have been developed over the last decades to investigate host-natural enemy population dynamics (Hassell, 1978; Lima et al., 2009; Mills and Getz, 1996). More recently, there has been increasing interest in the effect of spatial and temporal heterogeneity in the distribution of natural enemy attacks, leading to an increase in the development of individual- or agent-based simulation models. These models can provide useful detailed insights into population dynamics that are often missing in classical mathematical models (Schofield et al., 2005). Individual-based simulation models allow for the analysis of population dynamics by scaling up from the interactions of species on an individual level (Judson, 1994). This proves to be very useful for the construction of optimality models, where the goal is to investigate effects of the behavioral traits of individual biocontrol agents (individual level) on the spatial processes and system perturbations at a population level (Wajnberg et al., 2016).

Previous individual-based models have focused on specific species (Pearce et al., 2006; Roitberg and Gillespie, 2014), or on two-trophic level interactions (Okuyama, 2015; Vinatier et al., 2009). Others focused on specific effects, such as the effect of landscape heterogeneity (Schofield et al., 2005; Wajnberg et al., 2012) or pesticide use (Bianchi et al., 2013; Stratonovitch et al., 2014) on the efficacy of natural enemies for classical biological control. The inclusion of stochasticity and spatial structure in individual-based models allows for better understanding of local interactions in pest management. For example, an individual-based model on the biocontrol efficacy of the parasitoid *Encarsia formosa*, found that variation in giving up time (GUT) of the parasitoids to be the strongest determinant for whitefly control efficacy (van Roermund et al., 1997). However, an aspect that has been overlooked is the divergence in interest between the biocontrol agent and the biocontrol practitioner (Wajnberg et al., 2016). For the biocontrol practitioner, it is of key importance that the method used to protect its crops is the most cost-effective. This perspective has not been incorporated into optimality models yet.

In the present work, we build a general individual-based model simulating the release of biocontrol agents for short term control (inundative releases), taking into account the revenues and costs for the biocontrol practitioner. By using a genetic algorithm, the model focuses on identifying the life-history traits of natural enemies that improve their performance as a biocontrol agent and thus the overall incomes for the biocontrol practitioner. Additionally, we aim at determining the release strategies that will lead to higher economic returns for the biocontrol practitioners.

2. Material and methods

We developed an individual-based, also called agent-based simulation model. The model is discrete in time and spatially explicit, which means that the spatial location of all components of the model is kept track of during the simulation. In order to keep the model as general as possible, we based it on basic principles in behavioral and population ecology of natural enemies. Space is represented as a two dimensional grid (23 cells × 23 cells) with cells in which plants are located and each cell in the grid is supposed to offer sufficient space for the plant to reach its maximum yield if not damaged by the pests (no space competition). In accordance with common practices in agriculture, the assumption was made that the plants are grown in rows in the grid, one every second row.

Plant characteristics are kept as simple as possible, with the only modeled parameter being its biomass (translated into yield). Plants grow according to the Von Bertalanffy curve, an equation commonly used for describing the growth pattern of living organisms (von Bertalanffy, 1938). The size of a plant, in this case its biomass or yield (B_t), increases at each time step t, dependent on its maximal size/biomass/yield (B_{max}: arbitrarily fixed to 100) and a growth rate k_t which is dependent on the number of pests present on the plant at this time step.

$$B_t = B_{max}\left(1 - e^{-k_t}\right) \tag{1}$$

In order to reduce the complexity of the model and to allow for investigation of competition between natural enemies, the model considered that pests are arriving at a single time only in the crop development process. This time of arrival of the pests is a preset parameter and is set for all simulations at time step 5. The number of pests that arrive to a single plant was drawn from a Poisson distribution with a parameter λ (arbitrarily fixed to 7), that defines the average number of pests attacking the entire crop. Pests reduce each plants growth rate k_t according to a negative linear relationship ($k_t = k_{max} - S_t/150$), where k_{max} is the maximum growth rate of the plant without any pest present (see Table 2) and S_t is the number of pests attacking the plant at time step t. A high number of pests results in a negative growth rate for the plant and ultimately its death, with no possibility to recover. In this case, all pests die with the plant since pests are unable to disperse in the model. Pests also do not reproduce and generate offspring, because the timeframe of the release of natural enemies was too short to allow for pest reproduction.

Pests can be attacked by natural enemies, resulting in their immediate death. Since the term "natural enemy" can entail a lot of different species, from predatory mites to parasitic wasps, it was important to keep the agents' behavioral parameters as general as possible. However, the model was initially targeted towards pro-ovigenic natural enemies. We focused on the most important life-history traits for biocontrol agents and decided to consider eight life-history parameters (Table 1), that affected their longevity, attack rate, competition and dispersal capability. Natural enemies have to optimize their lifetime reproductive success by maximizing their breeding attempts during

Table 1
Life-history parameters of the natural enemies used in the model with their initial range.

	Parameter	Range
x	Lifetime of agent (time steps)	[1–200]
Q	Maximum attack rate (number of pests/time step)	[0–40]
m	Interference coefficient (competition between natural enemies)	[0–1]
T_h	Host handling time (time steps)	[0–1]
β_c	Exponent for the effect of competition with other agents on dispersal	[0–8]
β_h	Exponent for the effect of the presence of hosts/pest on dispersal	[0–8]
μ_d	Mean dispersal distance (cells)	[0–32.5]
σ_d	Standard deviation of dispersal distance (cells)	[0–3.25]

Table 2
Biocontrol practice parameters with values used in the model.

Parameter	Values
Number of releases in the field	1 *vs.* 2
Number of overall agents released	10 *vs.* 20
Time of release (time steps)	6 *vs.* 10
Maximum growth rate of plant without any pest present (k_{max})	0.05 *vs.* 0.06
Cost of a single agent (yield, arbitrary unit)	200 *vs.* 300

their lifetime (Wajnberg et al., 2012). An ideal natural enemy would have both high fecundity and longevity to maximize its breeding attempts during its lifetime. However, natural enemies have limited energy reserves, forcing them to choose an energy allocation strategy. The result is an inter-individual trade-off between fecundity and longevity, as has been experimentally observed (Ellers et al., 2000; Tatar et al., 1993). For this, a genetically determined trade-off between fecundity and longevity was considered according to the following equation:

$$F = F_{max}(1-\frac{x}{L}) \tag{2}$$

in which F is the number of eggs available during lifetime, F_{max} the maximum fecundity (arbitrarily fixed to 50), x the longevity of the agent, and L its maximum longevity (arbitrarily fixed to 200). The arbitrary values have been chosen according to the set up for the simulations (size of the grid, number of agents released, etc.).

Released biocontrol agents have the ability to attack pests at each time step, but solely on the plants on which they are present at that time, and if they still have enough eggs remaining to be laid. The biocontrol agent reduces its number of eggs by attacking pests, losing a single egg per attacked pest. An agent that runs out of eggs is considered dead, since it no longer has the ability to reduce the pest level. Other parameters that can limit biocontrol agents' ability to attack pests on a given plant are their attack rate per time step, their host handling time and the intra-specific competition. Such intra-specific competition is managed by an interference coefficient, and assumes that the search efficiency of biocontrol agents declines with competitor density on the crop. The attack rate a of an agent at each time step was computed following the equation of Hassell and Varley (1969):

$$a = QP_t^{-m} \tag{3}$$

In which Q is the maximum attack rate, m the interference coefficient, and P_t the number of competitors present on the plant with the agent at that time step.

The attack rate a is then used in a Holling (1959) Type II functional response to calculate the number of pests an agent is able to attack (N_t) at time step t:

$$N_t = \frac{aS_t}{1 + aT_hS_t} \tag{4}$$

in which T_h is the host handling time by the natural enemies and S_t is the pest density on the plant. We assume that the attack of a biocontrol agent results in the immediate death of the pest, rendering them unable to cause any further damage to the plant. This assumption, for example, corresponds to a predator species attacking prey or a parasitoid species paralyzing its hosts. Since the death of a single pest is immediate, it can never be attacked by more than one agent. Whenever there are multiple agents present on the same plant, they will share the number of pests randomly amongst them. Should the number of possible attacks exceed the number of pests, then all pests are killed and the egg load is reduced by the number of pests killed only.

Natural enemies have the ability to disperse at each time step, and such a dispersal decision depends on two life-history parameters, according to the following equation:

$$PR_{disp} = (1-e^{-\beta_c P_t}) + e^{-\beta_h S_t} - ((1-e^{-\beta_c P_t}) \times e^{-\beta_h S_t}) \tag{5}$$

in which PR_{disp} is the probability to leave the plant on which they are located, β_c and β_h are respectively the coefficients determining the strength of the effect of the number of competitors P_t and hosts s_t present on that plant, to trigger the dispersing decision of the agents.

Released natural enemies are assumed to perceive their surrounding environment, leading them to orient towards locations containing higher pest densities. For this, it is assumed that natural enemies are able, *e.g.*, to respond to chemical cues coming from both their hosts and the plants that they are damaging, for example by mean of host-induced plant volatiles cues (Wajnberg and Colazza, 2013). In our model, natural enemies thus dispersed in a non-random manner, weighted by the pest density on the plants. For this, at each time step, dispersal distance for each simulated animal was drawn using the following method: each cell within the two-dimensional grid was assigned a value corresponding to a probability given by a Gaussian distribution with a given mean and standard deviation (dependent on the life-history parameters), multiplied by the number of pests present. Cells with a higher number of pests and closer within the radius of search (*i.e.*, closer to the mean of the Gaussian distribution) will thus be allocated a higher value. Dividing the obtained value in each cell by the sum of all values in the two-dimensional grid provides a 2D probability density function, that allows to randomly draw the new position for the moving agent. In the model, dispersal ability was entailing some risk of dying (R_{mort}) which was dependent on the distance D that an agent moves and the maximal possible dispersal distance D_{max} (equal to the length of the diagonal of the grid) following the equation (Johnson et al., 2009):

$$R_{mort} = \frac{D}{D_{max}} \tag{6}$$

The simulation model starts with the sowing of the plants at time step 0, followed by the arrival of all pests at time step 5 and the release of natural enemies, dependent on the biocontrol practice parameters, either at time step 6 or 10. Then, at each time step, three different processes happen in successive order. First, plants grow according to their growth rate, eventually affected by the number of pests present. Then, natural enemies attack the pests depending on their life-history parameters. Finally, natural enemies may have the ability to disperse to a new plant, entailing then a mortality risk during dispersal. Biocontrol agents thus perform two major processes every time step: oviposition and dispersal (Fig. 1). The order in which agents are iterated is randomized at each time step.

The economic returns for the biocontrol practitioner are defined as the combined yield of all plants at the end of the simulation, reduced by the total costs of releasing natural enemies. The simulation model is repeated for 32 different combinations of the five biocontrol practice parameters defining the conditions of release of natural enemies (Table 2). When a single release of biocontrol agent was done in the field, it was located in the middle, while two release points were decided to be in two predefined spots equally distanced from the middle of the field.

The optimized life-history parameters in the different simulated situations of biocontrol practice were identified by mean of a genetic algorithm, a form of evolutionary computing used to find solutions to optimization problems by making use of bio-inspired operators (Hamblin, 2013, Hoffmeister and Wajnberg, 2008; Mitchell, 2009; Ruxton and Beauchamp, 2008). A random population of 150 chromosomes was initialized, each having exactly eight genes coding for the eight life-history traits (see Table 1). The values for these eight life-history traits were randomly drawn from initial ranges (see Table 1), which were selected after multiple preliminary studies. For each chromosome, a fitness value was generated from the average economic returns (crop yield - cost) of 100 independent simulations of the simulation model described above. Then, at the next generation, a new population of chromosomes was created from the current population using bio-inspired operators: elitism, selection, cross-over (60%) and mutation (2.5%). The mutation rate allows a change in the value of the

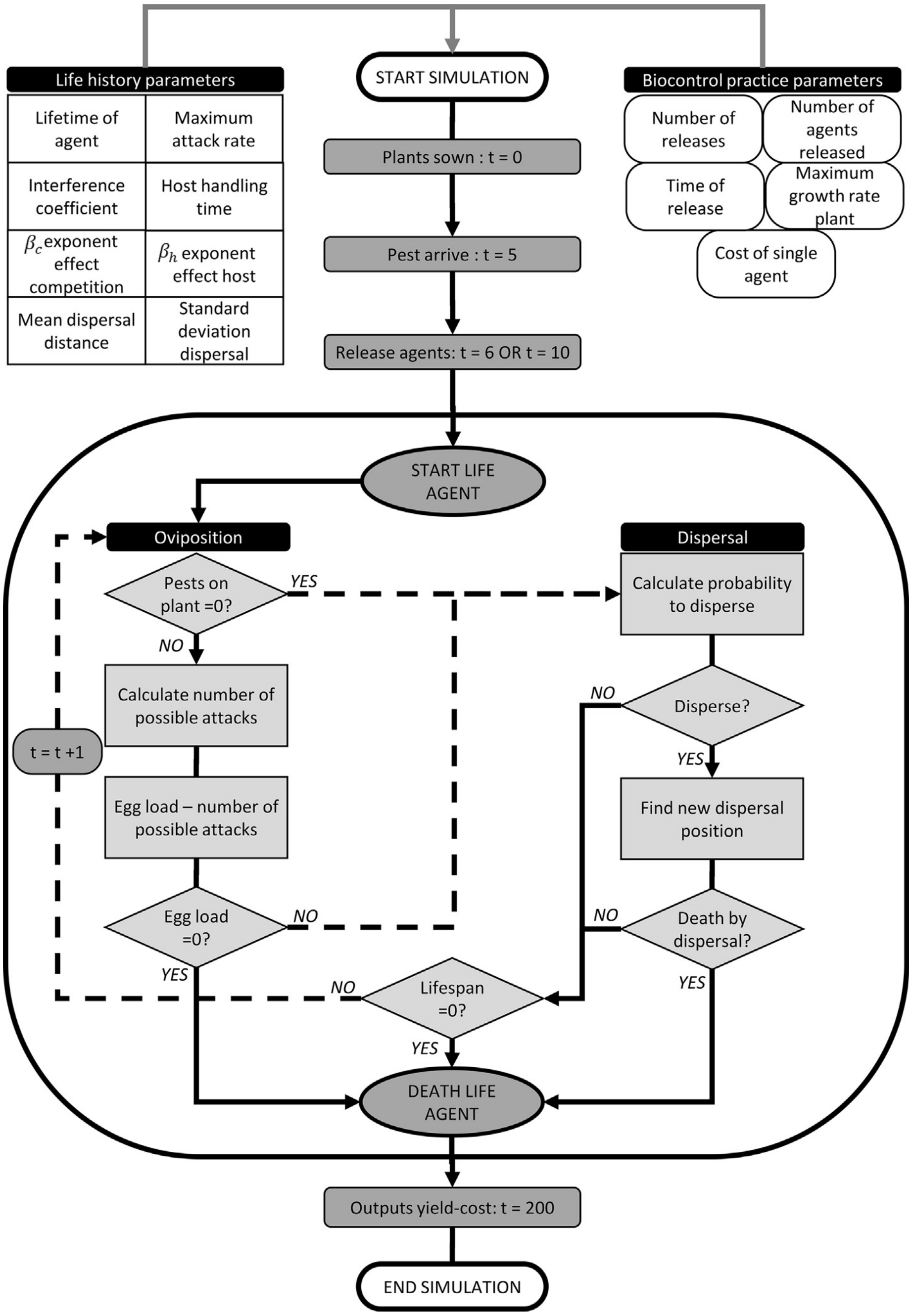


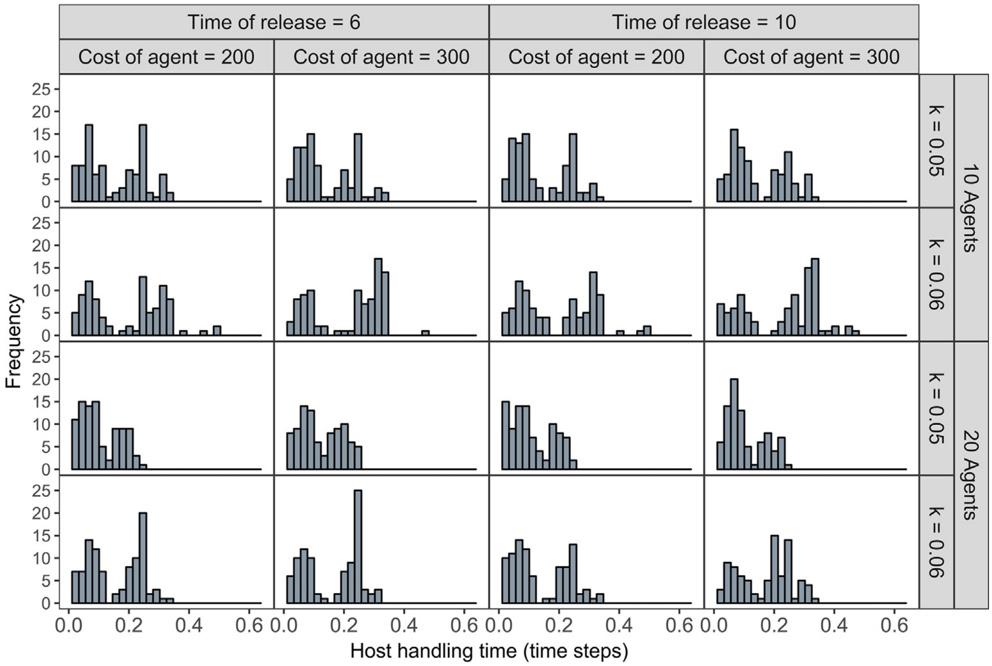
Fig. 1. Model flow chart of the individual-based model that simulates the release of natural enemies for short term control. Both life-history parameters and biocontrol practice parameters are inputted before the start of the simulation. The big round rectangle corresponds to the life span of the biocontrol agents, and involves the two major processes in the biocontrol agent life (oviposition and dispersal). Dashed lines represent the transition between the two processes. At every time step, the biocontrol agent undergoes all steps in both major life processes, until its egg load/life span reaches zero or it dies through dispersal.

life-history trait, allowing the value to go beyond its initial range. Several preliminary studies indicated that the crossing-over and mutation rates used led to rapid evolutionary stable solutions in less than 300 generations. We thus decided that the genetic algorithm should be run for 300 generations. The entire computation process was repeated 100 times for each different situation of biocontrol practice, leading to a total of $100 \times 32 \times 300 \times 150 \times 100 = 14{,}400{,}000{,}000$ simulations. The output from this entire computation process was the frequency distribution of optimal values for the eight life-history traits from the 100 repetitions in each different situation of biocontrol practice.

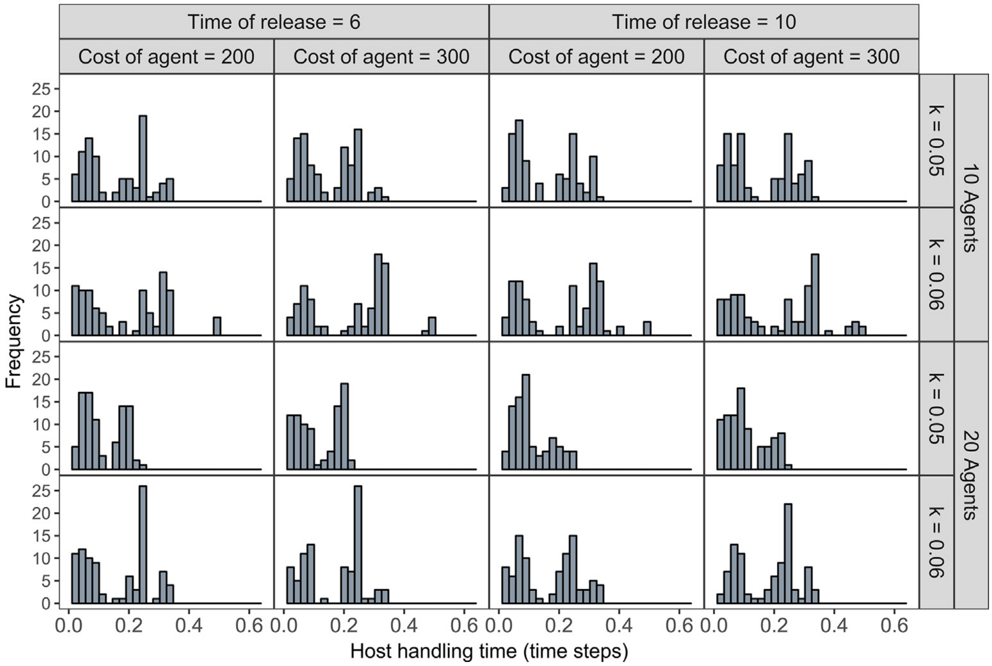
After computing the optimized parameter values in all situations, a sensitivity analysis was conducted to further investigate the influence of the biocontrol practice parameters that affect the release of natural enemies. Simulations were repeated with larger ranges for the two biocontrol practice parameters which had been shown to significantly affect the optimization of life-history parameters: the number of agents released [10, 20, 30, 40, 50] and the growth rate of the plant [0.03, 0.04, 0.05, 0.06, 0.07]. The other three biocontrol practice parameters were kept fixed (number of release = 1, time of release = 10, cost of agents = 100).

3. Results

The economic returns for the biocontrol practitioner appear highest when the biocontrol agents have a considerably short lifespan, very low host handling time, low β_h exponent value for the effect of the presence



a) 1 Release point of agents



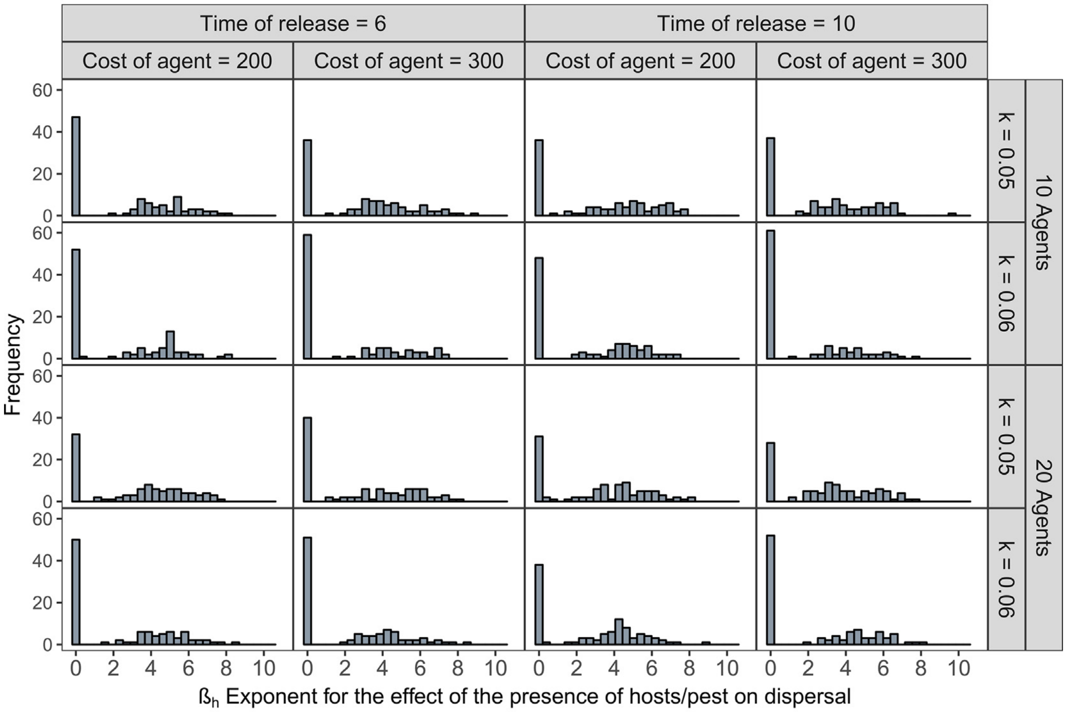
b) 2 Release points of agents

Fig. 2. Distribution of optimized values of the host handling time for all of the 32 different biocontrol practice situations tested: (a) one or (b) two release points of natural enemy in the field, and with different times of release, cost of a single agent, numbers of overall agents released and the maximum plant growth rate.

of pests on the dispersal decision and limited dispersal capacities (Figs. 2, 3 and S1, S5 & S6). The frequency distribution of the optimal values for three life-history parameters (maximum attack rate, interference coefficient, β_c exponent for the effect of competition with other agents on dispersal) corresponds to normal distributions with ranges very similar to their initial ranges (Figs. S2, S3, S4). When comparing the optimal values for each life-history parameter, we noticed that these three life-history parameters did not correlate with the optimal values of the other life-history parameters. This was in contrast to the other life-history parameters that did correlate strongly with one another: lifetime of the agent, host handling time, β_h exponent for the effect of the presence of pests on the dispersal decision, the mean and standard deviation of dispersal distance.

Most noteworthy was the negative correlation between host handling time and the β_h exponent value for the effect of the presence of pests on the dispersal decision of the biocontrol agents (Spearman rank correlation $\rho = -0.74$). A bimodal distribution was observed for the optimized values of the host handling time (Figs. 2 & 3, respectively) with considerable differences between the values of the two peaks of the distributions. The distribution of the β_h exponent value for the effect of the presence of pests on the dispersal decision of the biocontrol agents is characterized by a high frequency of zeros at the one end and a low frequency of values higher than 2 at the other end (Fig. 3). Additionally, both life-history parameters seem to be correlated with the

a) 1 Release point of agents



b) 2 Release points of agents

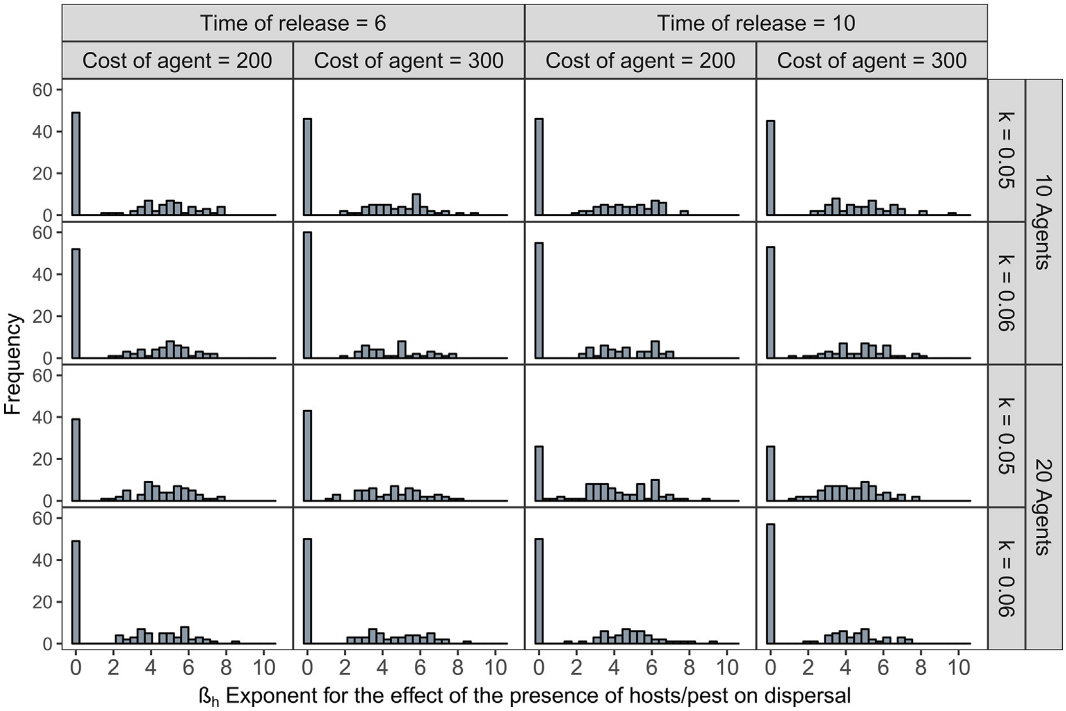


Fig. 3. Distribution of optimized values of the β_h exponent for the effect of the presence of pests on the dispersal decision of the biocontrol agents for all 32 different biocontrol practice situations tested: (a) one or (b) two release points of natural enemy in the field in the field, and with different times of release, cost of a single agent, numbers of overall agents released and the maximum growth plant rate.

lifetime of the agent (ρ = 0.74 and ρ = −0.65, respectively) and the mean dispersal distance (ρ = 0.33 and ρ = −0.35, respectively), the level of correlation depending on the situation of biocontrol practice. Finally, there is a strong negative correlation between the mean dispersal distance and the standard deviation of dispersal distance (ρ = −0.67). The bimodality in the distribution of the host handling time and the correlation with other life-history parameters, most noteworthy the β_h exponent value for the effect of the presence of pests on the dispersal decision of the biocontrol agents, might indicate the existence of multiple life-history strategies for the biocontrol agents that optimize the economic returns for the biocontrol practitioner.

Inputting the optimized values of these life-history parameters in the simulation model for the different biological control situations compared did indeed reveal the existence of two optimized life-history

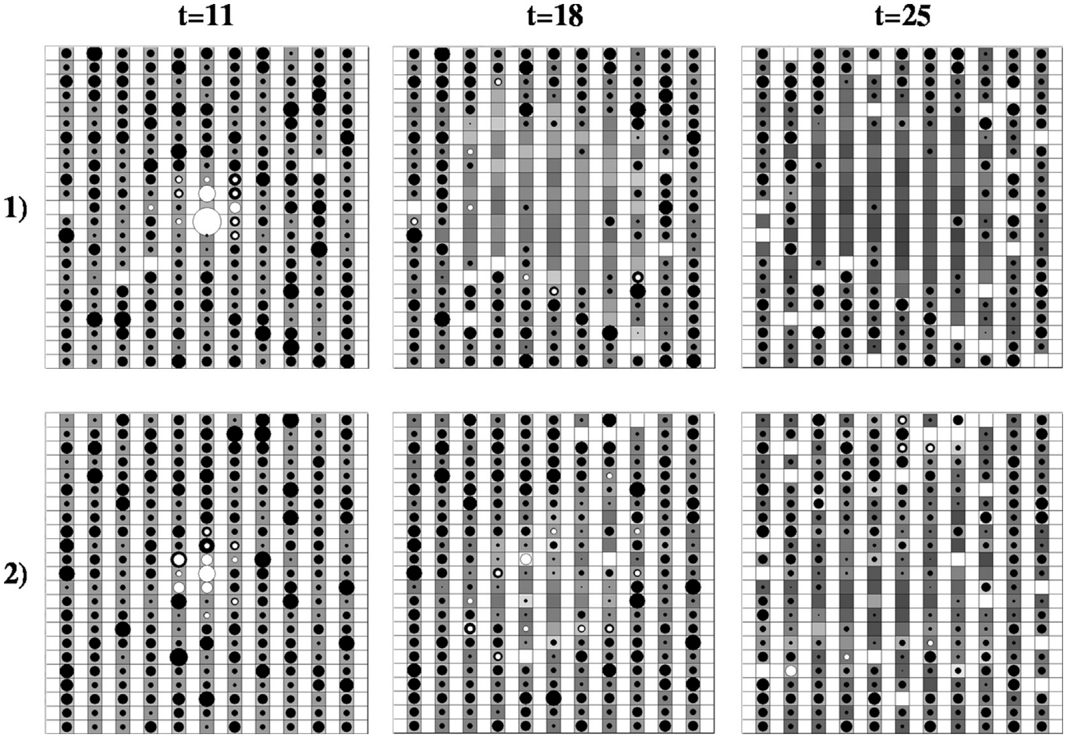


Fig. 4. Examples of the simulation model outputs showing the two different optimized strategies that the agents can follow to generate maximal economic returns/profit in a biological control program. The first line shows the strategy in which the agents clear the entire plant of pests before leaving (incremental), the second line the other strategy in which agents disperse irrespective of the number of pest present (decremental). Each graph represents the crop field with plants growing in rows. White cells represent empty cells; grey patches represent cells with plants. An increase in biomass of the plant results in a darker grey cell. Pests and agents are represented by black and white circles respectively, with the radius of the circle relating to their respective density. The three different panels for each strategy represent three different time steps in the simulation: (A) directly after the release of agents, (B) distribution of agents and (C) death of majority of agents. All graphs are built with 1 release of 20 agents at time step 10, on plants having a maximal growth rate of 0.06 and with a cost of 200 for the agents. Agents have a maximum attack rate of 20 pests per time step, with an interference coefficient of 0.5, a β_c value of 4, and a standard deviation of dispersal distance of 1.2 cells. In the first row, agents lifetime and host handling time were of 14 and 0.05 time steps, respectively, β_h was 4, and the mean dispersal distance was 0.5 cells. In the second row, these values were 20, 0.25, 0 and 1, respectively,

strategies corresponding to the bimodal distribution of the handling time shown in Figs. 2 and 3 (see examples in Fig. 4). The first optimized life-history strategy is characterized by biocontrol agents with a low handling time (and a higher than zero β_h value), thus increasing the overall number of pests attacked locally and lowering the decision to disperse. The biocontrol agents only move to the next plant when the plant on which they are located is cleared from pests. On the contrary, in the second optimized life-history strategy, biocontrol agents are characterized by a higher handling time (and a β_h value of zero), which means that they move between plants at each time step irrespective of the number of pests present on which they are located. This somewhat higher handling time reduces the number of pests that are attacked locally, hence allowing the agents to save some eggs for later opportunities after dispersal. Combined with a higher incentive to disperse, this allows pests to be attacked over a bigger surface than for the first optimized strategy.

Additionally, two biocontrol practice parameters (*i.e.*, number of overall agents released and maximum growth rate of plant without any pest present) seem to affect the shape of the bimodal distribution of the optimized host handling time (Fig. 2), suggesting a preference for one strategy of the biocontrol agents in certain situations. Figs. 5 and S7 show the results of the sensitivity analysis that was performed to further look into the effects of these two biocontrol practice parameters. The emphasis was put on the five life-history parameters (lifetime of agent, host handling time, β_h value for the effect of the presence of pests on the dispersal decision of the biocontrol agents, mean and standard deviation of dispersal distance) that were significantly affected (Fig. 5).

The interaction between both biocontrol practice parameters seems to heavily affects the optimal lifetime of the released agents (Fig. 5a), which is by definition negatively linked to the number of eggs that agents can lay during their lifetime. On slow growing plants, the difference in optimal lifetime of the agents depends heavily on the number of agents that are released. Agents released in high numbers benefit from having a long lifespan, as the higher collective eggs of the group does not require them to have such a high fecundity. However, lowering the number of agents released in the same situation will lead to a stronger selection of reduced lifetime. This difference is not observed for agents released on fast growing plants, and in this situation high fecundity is always preferred over high longevity. Fast growing plants are less susceptible to attacks from pests, which leads to less strong selection on life history traits of the biocontrol agents.

The negative correlation between the host handling time and the β_h value, describing the effect of the presence of pests on the dispersal decision of the agents, outlined above appears to be confirmed by the sensitivity analysis (Fig. 5b and c). In most situations, agents with a low host handling time and a high β_h value are favored for generating the highest economic returns for the biocontrol practitioner. When the number of overall agents released is reduced in a field with fast growing crops, both an increase in the host handling time and a reduction in the β_h value for the agents prove to be more optimal for the biocontrol practitioner.

Finally, the mean and standard deviation of dispersal distance are significantly influenced by the biocontrol practice parameters (Fig. 5d and e). In most situations, the optimal mean dispersal distance for a biocontrol agent should be very low. The only exception is for biocontrol agents released in high numbers on slow growing plants. The

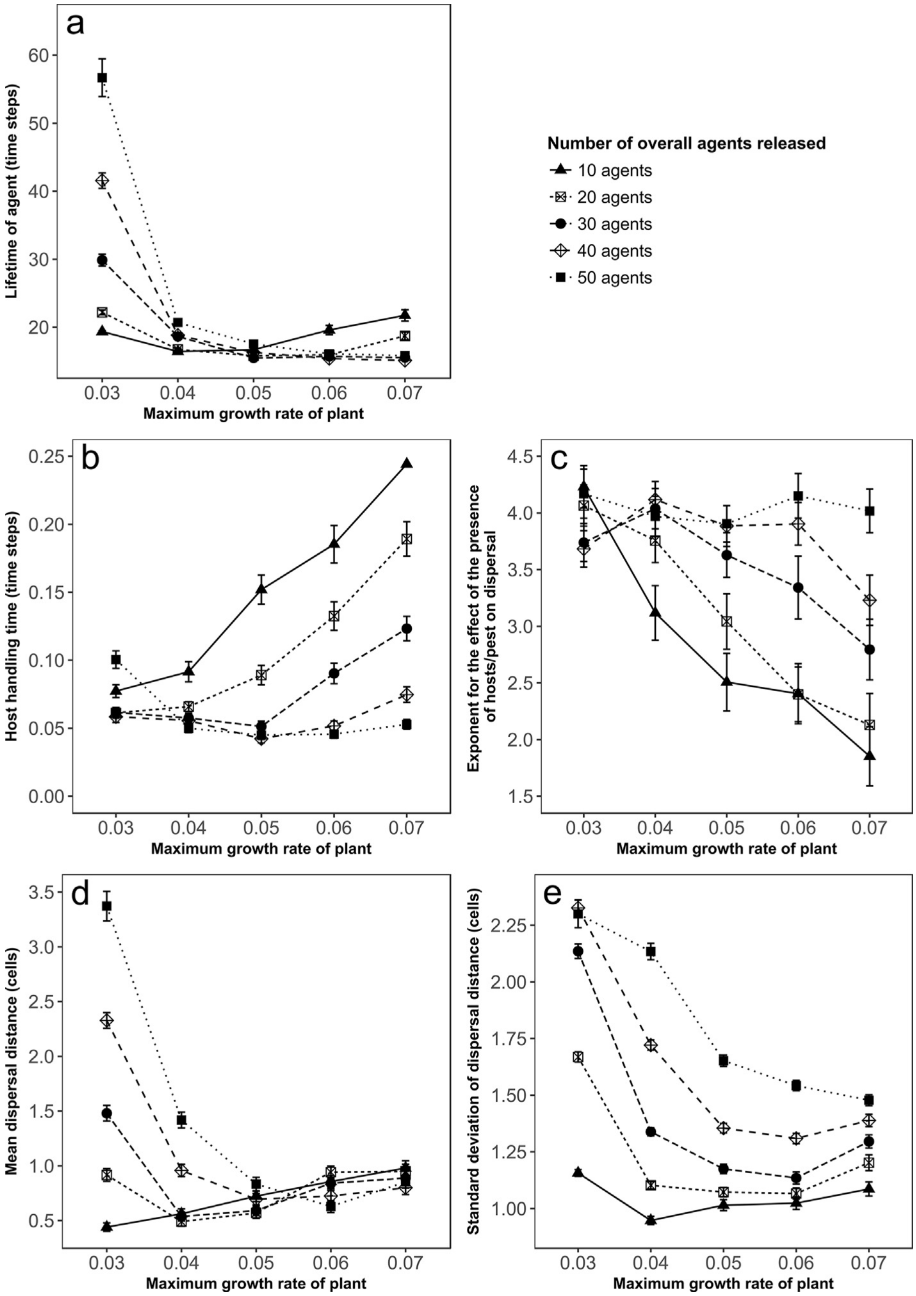


Fig. 5. Average (± SE) effect of two biocontrol practice parameters, *i.e.*, number of overall agents released and maximum growth rate of plant without any pest present on the optimized values of the five most affected life-history parameters: a) lifetime of agents, b) host handling time, c) β_h exponent for the effect of the presence of pests on the dispersal decision of the agents, d) mean dispersal distance and e) standard deviation of dispersal distance.

standard deviation correlates positively with the number of agents released, and negatively with the plant growth rate.

4. Discussion

The results obtained in this work indicate that studying the effects of life-history traits of biocontrol agents through optimality models can provide insights on improving biocontrol programs for biocontrol practitioners. We found that some life-history traits affect the overall outcome of augmentative biological control programs more than others. It appears that the optimal life-history traits of the agents from an economic perspective depend on the specific agro-ecological situation that the biocontrol practitioner must manage.

Our model indicates that, from an economic perspective, agents with a high fecundity might be more efficient to control pests. Considering the trade-off between longevity and fecundity, efficacious biocontrol agents should thus favor immediate reproduction (eggs) over future survival and reproduction. A review on the life-history traits of different parasitoids species by Mayhew (2016) shed more light on this trade-off between longevity and fecundity. The trade-off between immediate and future reproduction seems to be resolved in favor of immediate reproduction for most parasitoids, all other factors being equal (Mayhew, 2016). Secondly, the optimal dispersal capacity of efficient biocontrol agents seems to remain quite low. This does not coincide with the optimal intermediate dispersal rate from the Goldilocks hypothesis of Heimpel and Asplen (2011), but this could be due to high risk of mortality and a high availability of pests remaining in our model. Lastly, parameters related to competition had considerable less effect than other parameters on the efficacy of biocontrol agents in biological control programs. These results are in contrast with the findings on the parasitoid *Hyposoter horticola*, where the avoidance of competitors has a strong effect on the exploitation of available hosts (Montovan et al., 2015). However, that study focuses on the individual parasitoid fitness, while we focus on the economic benefits for the biocontrol practitioner.

Correlations between life-history traits contribute to indicate the existence of two very different optimal life-history strategies for the biocontrol agents. The differences between the two strategies can be phrased in terms of plant-leaving decision rules (β_h value for the effect of the presence of pests on the dispersal decision of the agents) in combination with the number of pests that the agent can attack during a single time step (host handling time). Both strategies have their merit for the biocontrol practitioner. The strategy in which the agents clear the entire plant of pests before leaving, generates higher economic returns from the plants around the points of release while sacrificing border plants. The other strategy, for which agents move between plants at each time step irrespective of the number of pests present, allows for border plants to better survive, but comes with the cost of lower economic returns from the plants around the points of release. This partial resource exploitation has been documented in different parasitoid species (Montovan et al., 2015; Outreman et al., 1999).

The differentiation into two optimal strategies is not novel in behavioral ecology and has been discussed multiple times in terms of incremental *vs.* decremental patch-leaving strategy (van Alphen et al., 2003; Wajnberg, 2006). There exists empirical evidence for parasitoid species with either incremental, decremental or both mechanisms used for foraging (Driessen and Bernstein, 1999; van Alphen et al., 2003; Wajnberg, 2006). A similar relationship between patch-leaving strategy and dispersal capacities was encountered, more precisely a negative correlation between time spent per host patch and dispersal (Wajnberg, 2006).

We show that the optimal strategy for biological control practitioners actually depends on the particular agro-ecological situation to address. In most agro-ecological situations, the incremental strategy (clearing the plant of pests before dispersing) seems to be the optimal life-history strategy of the biocontrol agent for the biocontrol practitioner. The decremental strategy (dispersing irrespective of the number of pest present) only becomes beneficial when biocontrol agents are released in small numbers in a field with fast-growing plants. Another modeling approach showed similarly that the incremental strategy was favored at high densities of biocontrol agents, as host patches have a higher chance of already being exploited by competitors (Spataro and Bernstein, 2000). From an economic perspective, since the biocontrol agents in our model have a limited cumulative attack possibility, attacks have to be optimally distributed over diverse plants, deeming it beneficial to move before clearing the entire plant. This way, the small groups of agents have the opportunity to reach the plants at the borders of the field before they are completely deemed unworthy for consumption.

Overall, the optimal dispersal capacity of a biocontrol agent should remain low, but depends heavily on the number of agents that are released. Considering the high associated risk of mortality, dispersal is always very risky, but especially if there is just a small number of individuals released. However, having a large range to find the best plants with highest number of pests is beneficial and this proves to be even more beneficial when released in large quantities. There seems to be a strong trade-off in dispersal capacity between risk of mortality and dispersal range. A similar trade-off was already proposed for the optimal dispersal rate of biocontrol agents by the Goldilocks hypothesis, but neglected the factor of mortality risk in the trade-off for dispersal (Heimpel and Asplen, 2011). Instead, the emphasis is on the risk of emigration out of the field by biocontrol agents at high dispersal rates (Heimpel and Asplen, 2011).

Finally, the release of a high number of biocontrol agents in a field with slow-growing plants is a special situation. This agro-ecological situation of biocontrol practice is characterized by a high cost (number of agents) and a low yield (slow growth rate leads to plants that are very susceptible to pest attacks). In this case, the biocontrol agents would optimally disperse much further to find pest-infected plants, thereby greatly risking their life. However, given the large number of agents and the high susceptibility of plants to pest attacks, the benefit of 'saving' these plants outweighs the cost of losing a single biocontrol agent. In contrast, the outcome of the rather high optimal lifetime of the agent in this situation is not that straightforward. One hypothesis is that an increase in number of released biocontrol agents lowers the requirement for high fecundity. The additional lifespan could give the agents that manage to get to the borders of the field more time to attack pests, thereby targeting the benefit of a few biocontrol agents over the collective benefit. However, there is high variation in the optimized values for these two life-history parameters, making it hard to identify their influence on the economic returns.

This situation demonstrates the limits in optimizing the biological control practice with one single type of biocontrol agent and inspires research into the effects of the release of multiple types of biocontrol agents simultaneously. An interesting question might be to test whether the simultaneous release of biocontrol agents with both optimal strategies would be cumulative for the economic returns of the biocontrol practitioners under certain agro-ecological situations of biocontrol practice.

In this study, we focused on methods to increase the efficacy of biocontrol agents. We noticed that attaining more efficacious biocontrol could be accomplished either via direct changes to life-history traits of the biocontrol agents themselves, or indirectly through modifications to the release environment. Modification of the biocontrol agents have already been accomplished by changes in the rearing conditions, as has been shown for biocontrol agent *Mastrus ribendus* that decreased its dispersal rate when reared with continuous food access (Hougardy and Mills, 2006) or through alternative release methods, as for the aphid parasitoid *Aphelinus asychis* that increased its dispersal rate when released in large quantities (Fauvergue and Hopper, 2009). Genetic improvement could provide a new method for the modification of biocontrol agents, especially considering the increased availability of genetic information on non-model species (Lommen et al., 2017). In genetic improvement, the genetic variation in natural populations of biocontrol agents is exploited to optimize them for augmentative releases through breeding selection programs (Wajnberg, 2004).

5. Conclusion

Our model suggests that improving the efficacy of biocontrol agents should be done by essentially focusing on a couple of key life-history traits, such as longevity, fecundity, host handling time and dispersal capacity. Also, the agro-ecological situation faced by the biocontrol practitioners plays an important role in determining what behavioral characteristics of natural enemies should be optimized to increase their efficacy as biological control agents. It seems of utmost importance to take into account the characteristics of the plant, more specifically their growth rate while subjected to pest damages. The insights from this model can determine the best release environment for the biocontrol agent, and help improving biocontrol agents through different release strategies, rearing conditions and genetic improvement methods. However, the current results depend heavily on general assumptions, so there is a need for information on the ecology and behavior of biocontrol agents to validate the assumptions made in this model. The next step would thus be to parameterize the model, using real estimated values from a specific natural enemy. Unfortunately, there is a relative paucity of information on many life-history traits of biocontrol agents (Heimpel and Asplen, 2011; Mayhew, 2016). An increase in collaborations and communication between theoreticians and experimentalists could help in alleviating this problem and lead to more efficient biocontrol.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.biocontrol.2018.05.010.

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