



Models for the practitioner: Predicting the efficient biocontrol of *Tuta absoluta* under different management scenarios

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ABSTRACT

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) is one of the most destructive pests of solanaceous crops. One possible biological control strategy is the augmentative release of parasitoids. However, parasitoid intervention efficacy is highly sensitive to the release timing and intensity. Virus-based biopesticides are additional control means since they are highly selective and can be combined with natural enemies. We developed a stage-structured population model, validated with results from a semi-field experiment, to investigate and predict the population dynamics of the pest *T. absoluta* and one of its parasitoids, *Necremnus tutae* Ribes & Bernardo (Hymenoptera: Eulophidae). The aim of the study was to assess the best release parameters of *N. tutae* to control the pest in four different management scenarios: without any other control method, with a biopesticide (PhopGV, Baculoviridae), with the natural presence of the parasitoid, and when combining the natural presence of the parasitoid with a biopesticide. Moreover, in each scenario, two growing seasons of different lengths were compared. To achieve the same control level, 3–45% fewer parasitoids are necessary in a long growing season than in a shorter one. Biopesticide applications reduce the number of required parasitoids by 66% and 78%, whereas the natural presence of parasitoids reduces it by 11% and 17% for short and long growing seasons, respectively. On average, with biopesticide application, the parasitoid intervention can be delayed by a month and remains efficient. These findings highlight the importance of mathematical models in applied pest management drawing precise predictions crucial for efficient control.

1. Introduction

To prevent harmful effects on the environment and human health, as well as the rise of pesticide resistance, agricultural systems must reduce their reliance on synthetic pesticides (Gould et al., 2018; Mahmood et al., 2016; Yadav and Devi, 2017). Moreover, to comply with the European pesticide regulation and to reach the goal of reducing the use of pesticides by 50% by 2030 (EC, 2020), alternative management options are required, which have to be reliable and efficient. An alternative to synthetic pesticides is the use of natural enemies to regulate pest populations. From microorganisms to insects, natural enemies are able to control pest outbreaks naturally and artificially as commercial solutions (van Lenteren et al., 2018).

Nevertheless, one single agent is frequently unable to control a pest sufficiently. Due to complementary resource use, multiple natural enemies instead of a single species often result in more efficient pest

suppression (Cardinale et al., 2003; Mody et al., 2017; Stiling and Cornelissen, 2005). As a viable agronomic solution, biocontrol must be efficient and reliable in many different scenarios. Hence, the main challenges for ecologists, agronomists and farmers are to predict the influence of natural enemies on the pest dynamics, to predict the effectiveness of the combined use of different biocontrol agents, and to optimize their effectiveness via precise dose and timing.

In order to provide better guidelines for biological control practitioners, the system of a worldwide, highly relevant invasive species was used to develop a framework for an optimal release strategy of natural enemies, i.e., the release of a parasitoid complemented with a biopesticide. *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), recently reclassified as "*Phtorimaea absoluta*" (Chang and Metz, 2021), is native to South America and causes catastrophic damage to tomato production in Europe, Africa, and Asia (Biondi et al., 2018; Aigbedion-Atalor et al., 2019; Han et al., 2019). The pest has a high reproductive potential and

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can cause complete crop failure if no control method is implemented (Desneux et al., 2010). In the most common European growing season (seven months), planting takes place from January to April (from south to north), and the crop is in production until July–October. The long seasons of continuous tomato crop (11 months) are present in northern countries, where glasshouses with heating systems are used (Arnó et al., 2009).

Numerous parasitoids have been found parasitizing *T. absoluta* in its invasive range, often colonizing the crop spontaneously (Arnó et al., 2021). Among them, the European larval parasitoid *Necremnus tutae* Ribes & Bernardo (Hymenoptera: Eulophidae), previously referred to as *N. artynes*, seems to be particularly efficient, reaching natural parasitism rates depending of the region ranging from 18% (Arnó et al., 2021) in N-E Spain to 73% (Crisol-Martínez and van der Blom, 2019) in S-E Spain. Also in augmentative release, the parasitoid significantly reduced *T. absoluta*'s pest density in greenhouse experiments (Calvo et al., 2016; de Campos et al., 2020). At least two European companies have produced the parasitoid for augmentative biological control, but its utilization is now shifting to conservation biological control due to an unfavorable cost–benefit ratio (Desneux et al., 2022). Therefore, reducing the number of parasitoids necessary by optimizing the timing of releases with a selective biopesticide could be a promising strategy. Recently, a microbial insecticide (biopesticide) based on Phthorimaea operculella granulovirus (PhopGV, Baculoviridae) was developed and tested to control *T. absoluta* (Tutavir®, Andermatt Biocontrol, Switzerland). The product is available in Brazil and has been granted emergency approval in different European countries. Tutavir® is recommended to be applied weekly upon the first detection of the pest. When ingested by neonate larvae of *T. absoluta*, PhopGV induces mortality and, in larger larvae, sublethal effects such as delayed development and pupation failure. Yet, very high doses (weekly application of the highest recommended concentration) are required to lethally infect the larger and most damaging larvae (Larem, 2019) thus complementary measures, such as *N. tutae* targeting the later larval instars of the pest (Calvo et al., 2013), are needed.

In the past, baculoviruses have been used successfully (Beas-Catena et al., 2014) and may replace broad-spectrum synthetic insecticides in the future. Baculoviruses are selective and pose no direct threat to parasitoids (Cory, 2003). Recent laboratory experiments have shown that PhopGV poses no risk for *N. tutae* (Gonthier et al., 2023). Although complementarity and intraguild predation in biocontrol application has been well-studied between parasitoids and predators in tomato (Chailleux et al., 2013; Malo et al., 2012; Moreno-Ripoll et al., 2014; Müller and Brodeur, 2002), few studies have evaluated the efficiency of combining parasitoids with biopesticides such as baculoviruses (Cossetine, 2009). Moreover, no study has ever assessed the impact of parasitoids with biopesticide application on pest population dynamics over an entire growing season. In this study, to understand the range of possible ecological interactions between the pest and the two antagonists, an exploration of the theoretical dynamics of the parasitoid-pest-baculovirus system was conducted.

A stage-structured dynamic population model has been developed to simulate the interaction between antagonists and the pest. The model was calibrated with life table parameters from the published literature and later corrected and validated with data from a large-scale semi-field trial (Koller et al., 2023). The model was developed to respond to the following research objectives: To assess the best timing and intensity of parasitoid intervention for successful augmentative biocontrol of *T. absoluta* with *N. tutae*: **A** as a single control agent (reference scenario, *T. absoluta* + augmentative release); **B** in combination with natural parasitism, the situation in Southern Europe where *N. tutae* is naturally present (*T. absoluta* + augmentative release + natural parasitism); **C** in combination with a biopesticide (*T. absoluta* + augmentative release + PhopGV); and **D** where the biopesticide application is made in areas with *N. tutae* naturally present (*T. absoluta* + augmentative release + natural parasitism + PhopGV). The release parameters and control

effectiveness for a short (seven months) and a long growing season (11 months) were compared for all four scenarios.

2. Material and methods

2.1. The stage-structured population model

The stage-structured population model used to describe the population dynamics of *T. absoluta* and its parasitoid *N. tutae* is based on Nisbet & Gurney formulations of delay-differential equations for a continuous-time population dynamics model (Nisbet and Gurney, 1983). These equations are implemented in the R package StagePop (Kettle and Nutter, 2015). The model assumes that an organism begins its life as an egg and progresses through different stages (larvae, pupae, and adult) if it survives long enough. The assumption is that individuals within each stage have identical vital rates, such as death rates and stage duration. Two equations can describe the model:

One equation tracks the change in the number of individuals in each stage over time, accounting for recruitment, development (maturation), and per capita loss rate where the change of the stage variable, i.e., the number of individuals N_i in stage i over time t , is described as:

$$1) \quad dN_i(t)/dt = R_i(t) - D_i(t) - \delta_i(t)N_i(t)$$

Where $R_i(t)$ corresponds to the recruitment into stage i , $D_i(t)$ describes the development from stage i , and $\delta_i(t)$ is the per capita loss rate of individuals in stage i .

The second equation accounts for the stage development or maturation, which is determined by recruitment, survival rate, and a time delay factor. Recruitment into the first stage is based on the reproduction rate in the adult stage. The development rate, $D_i(t)$, is given by:

$$2) \quad D_i(t) = R_i(t - \tau_i(t))P_i(t)(1 - d\tau_i(t)/dt),$$

where $R_i(t)$ corresponds to the recruitment into stage i , $P_i(t)$ denotes at time t the fraction of individuals entering stage $i - \tau_i(t)$ that has survived to time t . Development from one stage corresponds to recruitment into the next stage.

2.2. Assigning life history parameters

The life stage durations of *T. absoluta* eggs, larvae, and pupae were based on de Campos et al. (2020). The mortality parameters were then adapted to field-realistic values. To do so, the initial model of unconstrained *T. absoluta* population growth was fitted with step-wise increasing the natural mortality from de Campos et al. (2020) until the modeled dynamic matched with data from semi-field trials (Koller et al., 2023, see SI first section and Fig. S1). For the adults, the reproductive stage duration from Krechmer and Foerster (2015) was used instead of the total lifespan since only reproductive adults should be considered in the model dynamic. The time unit of the model is the day; therefore, the published rate (such as oviposition or mortality), usually determined for an entire stage, had to be adapted to a daily rate. The entire adult lifespan was used for the *N. tutae* adult stage duration since female wasps almost do not cease oviposition during their lifetime (Calvo et al., 2013). *N. tutae* lays more than one egg onto a host larva, on average 1.41 per host (Chailleux et al., 2014). Therefore, to model the number of offspring emerging from a parasitized host larvae, each host parasitized was multiplied by the average number of eggs laid per host so that a single host parasitized produces more than one parasitoid offspring. Previous laboratory experiments at 25°C showed that two PhopGV applications after the emergence of the neonate increased the natural mortality of *T. absoluta* larvae from 24% in the control to 53% in the treated group (Gonthier et al., 2023). Therefore, to simulate the *T. absoluta* population with PhopGV, the natural mortality of *T. absoluta* larvae was increased two-fold. All other parameters were taken at 25°C

Table 1

Life table parameters used in the model for the pest *Tuta absoluta* and the parasitoid *Necremnus tutae*, with a description of each parameter, the time unit, the absolute value, and the literature reference.

Parameter	Unit	Value	Reference
Stage duration of <i>T. absoluta</i> (egg, larvae, pupae, adult)	d	4.8, 12.3, 7.4, 13.9	de Campos et al., (2020); Krechemer and Foerster (2015)
Stage duration of <i>N. tutae</i> (egg, larvae pupae, adult)	d	1.6, 4, 5.3, 16	Calvo et al., (2013)
Number of eggs laid by female <i>T. absoluta</i>	eggs/d	10.71	Krechemer and Foerster (2015)
Number of eggs laid by female <i>N. tutae</i>	egg/d	2.68	Chailleux et al., (2014)
Number of eggs laid by female <i>N. tutae</i> per host larvae	egg/host larvae	1.41	Chailleux et al., (2014)
Number of host larvae parasitized by female <i>N. tutae</i>	host larvae/d	1.9	Chailleux et al., 2014
Number of host larvae killed by parasitism and host feeding by female <i>N. tutae</i>	host larvae/d	3.6	Chailleux et al., 2014
Death rate of <i>T. absoluta</i> per stage (egg, larvae, pupae, adult)	individual rate/d	0.078, 0.036, 0.06, 0.021	de Campos et al., (2020); Krechemer and Foerster (2015); Mohamed et al., (2022)
Death rate of <i>N. tutae</i> per stage (egg, larvae, pupae, adult)	individual rate/d	0.15, 0.05, 0.007, 0.06	Calvo et al., (2013)
Mortality of <i>T. absoluta</i> caused by PhopGV biopesticide	individual rate/d	0.072	Gonthier et al., (2023)

without modification from the references and are summarized in Table 1.

2.3. Modeling parasitoid population and host-interaction

The host species *T. absoluta* (T) has four life stages (eggs, Te; larvae, Tl; pupae, Tp; adult, Ta). Reproduction of *T. absoluta* is given by $Ta(t)^*$

Table 2

Parameters for each scenario. Four scenarios were modeled to address the outlined objectives and assess the optimal parameters of augmentative release of the parasitoid *Necremnus tutae* against the pest *Tuta absoluta*: A reference scenario; B natural parasitism level of about 18%; C Biopesticide application at the recommended dose and D combination of natural parasitism and biopesticide application. Each scenario was compared between a short growing season of 7 months and a long growing season of 11 months.

Scenarios (management strategies)	Length of growing season	
	Short (7 months)	Long (11 months)
A) Reference (pest + augmentative release)	210 days 10 adult pests on day 1 No natural parasitoids on day 1 Mortality of pest larvae = 0.036	330 days 10 adult pests on day 1 No natural parasitoids on day 1 Mortality of pest larvae = 0.036
B) Natural parasitism (pest + augmentative release + natural parasitism)	210 days 10 adult pests on day 1 Ratio of 0.15 parasitoid/pest on day 1 Mortality of pest larvae = 0.036	330 days 10 adult pests on day 1 Ratio of 0.15 parasitoid/pest on day 1 Mortality of pest larvae = 0.036
C) Biopesticide (pest + augmentative release + PhopGV)	210 days 10 adult pests on day 1 No natural parasitoids on day 1 Mortality of pest larvae = 0.072	330 days 10 adult pests on day 1 No natural parasitoids on day 1 Mortality of pest larvae = 0.072
D) Natural parasitism & biopesticide (pest + augmentative release + natural parasitism + PhopGV)	210 days 10 adult pests on day 1 Ratio of 0.15 parasitoid/pest on day 1 Mortality of pest larvae = 0.072	330 days 10 adult pests on day 1 Ratio of 0.15 parasitoid/pest on day 1 Mortality of pest larvae = 0.072

the daily number of eggs laid by a single female. *T. absoluta*, the host, is attacked by the parasitoid *N. tutae* (N). *N. tutae* also has four life stages (eggs, Ne; larvae, Nl; pupae Np; adult, Na).

The life cycle of the parasitoid summarizes as follows: the female lays its eggs on the larvae of *T. absoluta*, then the eggs emerge, and the larvae feed on the host until pupation. Therefore, the reproduction into the parasitoid egg class (parasitism rate) was $Na(t)^*$ the daily egg rate of *N. tutae* female. The daily parasitoid reproduction was limited to the number of available host larvae in the system. Only females lay eggs, and since the sex ratio of *T. absoluta* is about 0.5 (Leite et al., 1999) and that of *N. tutae* ranges between 0.2 and 0.7 depending on the host larval instar (Gonthier et al., 2023), the outcome of the reproduction function for the pest and the parasitoid was divided by two. Not each killed host larvae results in a parasitoid offspring because the parasitoid also performs non-reproductive host killing, mainly via host feeding (Chailleux et al., 2014). Therefore, the daily death rates of *T. absoluta* larvae due to parasitoids were $(\text{host-feeding rate} + \text{parasitism rate}) * Na(t)$ for each host larvae divided by the number of host larvae present at that moment in the system $Nl(t)$.

2.4. Simulating management scenarios

Four different management scenarios against *T. absoluta* were considered (Table 2). Scenario A (reference scenario) involves using only one control agent, which is the augmentative release of *N. tutae*. Scenario B combines augmentative release with the natural presence of the parasitoid. Scenario C combines augmentative release with the application of the biopesticide PhopGV. Lastly, scenario D involves applying the biopesticide PhopGV in areas where *N. tutae* is naturally present, while also conducting augmentative release.

In all management scenarios, the colonization of ten adult *T. absoluta* was simulated on day one to mimic the natural colonization of a closed environment (greenhouse) by the pest. The food resource for *T. absoluta* (tomato plants) was assumed to be unlimited. The natural parasitism rate of 18% found by Arnó et al. (2021) was simulated by releasing 1.5 individuals simultaneously with the pest on day one (see Fig. S2 for estimation). All initial scenario parameters can be found in Table 2. To calculate the best timing and number of parasitoids necessary for the effective control of *T. absoluta* in each scenario, all possible

combinations for the four different scenarios were run for the following release parameters: a) day of release of *N. tutae* (0–90) and b) an increasing number of released parasitoids (0–500 by groups of 10). Each scenario was then compared between a short and a long growing season.

Short growing seasons for tomatoes typically last six or seven months, from spring to fall, as seen in Europe's most common growing regions. In contrast, long growing seasons can last up to 11 months and are mostly present in France and Germany. These longer growing seasons are made possible through glasshouses with heating systems, allowing for transplants in fall or winter and a harvest that lasts until October or November (Arnó et al., 2009).

The mean runtime of the models was below 3 s. Models with extreme parameter values did not converge within a reasonable time (model running for longer than 300 s); those were interrupted automatically. The code can be found in the Supplementary Information, including all functions to reproduce the presented results. The Supplementary Information also describes the large-scale semi-field assay from Koller et al. (2023) and the model validation (Fig. S3).

2.5. Determining control effectiveness

The density over time of *T. absoluta* adults was used as an indicator for control success. Adult density over time is a good proxy for the pest pressure because the simulations with positive slopes resulted in a high density of larvae far beyond any economic threshold. For each model output, the slope of the *T. absoluta* adult density over the entire period was calculated. When the net slope of the adult population (over the total observation time) was negative or neutral, the pest population was defined as under control, and the augmentative release was considered effective (Fig. 1A+B). Conversely, the pest was not under control when the slope was positive, and thus the augmentative release was insufficient (Fig. 1C). All the simulations simplified into binary positive-negative results were plotted for the parasitoid release day and the number of parasitoids released.

3. Results

Running the model for the different scenarios with the different

release parameters provided 18'564 model outputs. Three are shown in Fig. 1 as examples of situations in which control is achieved (Fig. 1A and B) or not (Fig. 1C) for the reference scenario when the only control method is the release of the parasitoid. When the parasitoids are released into the system early on day 30 (Fig. 1A), a small intervention of 50 *N. tutae* (five times more than the initial inoculum of *T. absoluta*) is sufficient to control the pest in the third generation. If the parasitoid is released later on day 50 (Fig. 1B), the intervention with the parasitoids must be tripled (150 *N. tutae*) to be successful. However, if released later on day 70 (Fig. 1C), even 300 *N. tutae* cannot control the pest, and the number of *T. absoluta* grows exponentially. For a better understanding, the arbitrarily chosen examples from Fig. 1 are also marked in Fig. 2A, where all model outputs are represented.

3.1. Optimizing the parasitoid release

Polynomial regression analysis estimated well the border relationships between areas with effective control (green, Fig. 2) and areas where the pest is out of control (red, Fig. 2). The best release parameters for parasitoid intervention vary sensibly depending on the simulated scenarios. Overall, few parasitoids (less than 25) are sufficient to keep the pest population under control until the beginning of the second pest generation around day 25 (Table 3). Later, the curves become steeper, and on day 50, when the third generation starts in the reference (scenario A), more than 400 parasitoids must be released for effective control of the initial pest infestation of ten individuals (Table 3). After day 75, the polynomial function reaches a steep slope with no control possible anymore (Fig. 2).

3.2. The length of the growing season matters

A difference in the number of parasitoids necessary between the short and long growing seasons was only visible in the scenarios with the biopesticide C and D. More parasitoids were necessary to control the pest in the short growing season than in the long one. On day 75 (the start of the fourth pest generation), in scenarios with biopesticide applications C and D, up to 33% and 45% fewer parasitoids were necessary, respectively, for efficient control in the long than in the short

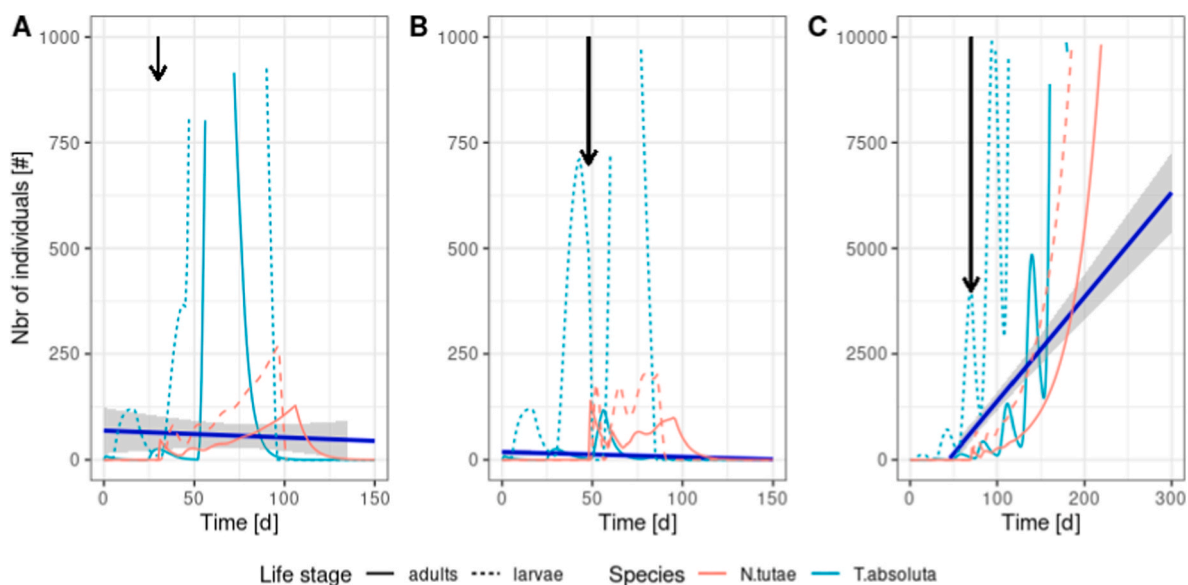


Fig. 1. Population dynamic of *Tuta absoluta* (light blue) and its parasitoid *Necremnus tutae* (red) under different release parameters. The black arrows show the parasitoid release timing (arrow length is proportional to intervention intensity), and the dark blue line represents the linear slope of the adult pest density over time. **A** Release of 50 parasitoids on day 30 - the pest is under control (neutral or negative slope for the solid blue line); **B** Release of 150 parasitoids on day 50 - the pest is under control; **C** Release of 300 parasitoids on day 70 - the pest is not under control (positive slope for the solid blue line). NB axis limit of **A** and **B** = 150 d and 1'000 individuals whereas **C** runs up to 300 d and 10'000 individuals.

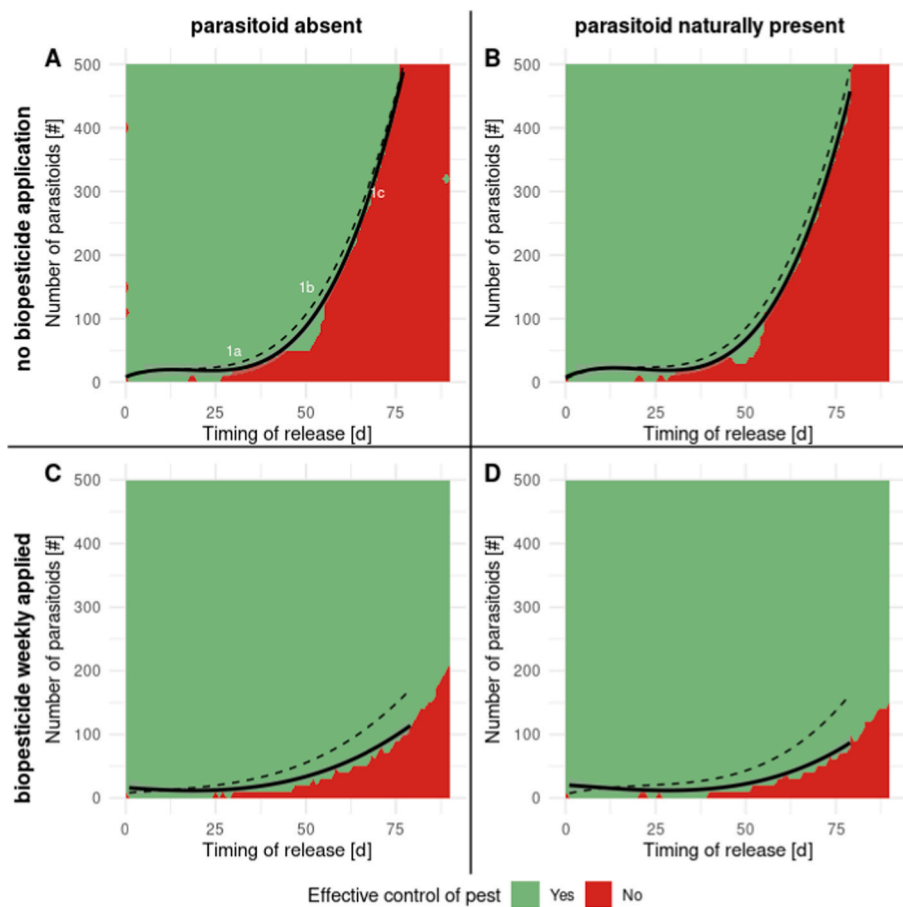


Fig. 2. The outcome of pest control: successful (green: negative or neutral slope of *Tuta absoluta* adults over the growing season) or pest outbreak (red: positive slope of adults over the growing season, the exponential growth of the pest) in relationship with the intervention parameters of the parasitoid *Necremnus tutae* (intensity, i.e., number on the Y-axis) and timing of the intervention (ranging from 0 to 90 days on the X-axis). The solid line shows the polynomial regression of the threshold line (separation of green and red) for the long growing season and the dashed line for the short growing season. **A** Reference scenario with no intervention other than the parasitoid release, when no parasitoids are released (no control method), is displayed at 0 on the Y-axis. **B** Situation with the parasitoid being naturally present (southern Europe). **C** Combination of the intervention with PhopGV biopesticide and **D** PhopGV biopesticide applications in locations where the parasitoid is naturally present.

season (Table 3). In scenarios A and B, similar quantities of parasitoids achieve control in the short and long seasons (reduction of 3% and 9%, respectively; Table 3, Fig. 2).

3.3. Natural parasitism and biopesticide effectiveness

The presence of natural parasitism in scenario **B** slightly reduces the number of parasitoids necessary for efficient control compared to the reference scenario **A** (Table 3). In the short growing season 89%, and in the long one 83% of parasitoids are necessary for efficient control at day 75. Compared to the reference scenario, scenario **C** with biopesticide substantially reduces the number of parasitoids necessary to 33% and 22%, respectively. Adding the natural presence of parasitoids to the biopesticide in scenario **D** reduces the number of parasitoids necessary for efficient augmentative release to only 31% and 17%, respectively, compared to the reference scenario.

4. Discussion

Mathematical models for population dynamics can help to determine the optimal timing and dosage for augmentative releases of natural enemies (Pfab et al., 2018; Rubio et al., 2022; Shea and Possingham, 2000). The work presented here complements this research and compares diverse scenarios such as different lengths of the growing season for the first time and the combination with a virus-based biopesticide. It also considers the parasitoid population naturally present in the field. The findings suggest that the efficiency of a biological control strategy against *T. absoluta* by augmentation of the larval parasitoid *N. tutae* strongly depends on the timing of the release. According to the models, the optimal release time lies during the first pest generation. Applying the PhopGV biopesticide strongly reduces the number of parasitoids

necessary for efficient augmentative release and permits to delay the parasitoid intervention. The following sections discuss some fundamental assumptions and their possible implications.

4.1. Determining the optimal timing of a biocontrol intervention

A crop protection intervention's timing is crucial, particularly when working with natural enemies. The release should be early enough for parasitoids to build up a considerable population and keep up with the pest but also late enough to ensure the presence of a minimum number of hosts in suitable stages for parasitoid establishment. The models show that during the first pest generation, the number of parasitoids necessary for efficient control was low and relatively constant, making it the best window of opportunity. Early detection is crucial, mainly if no other control method is applied. In the case of late detection, even a strong parasitoid intervention cannot help reducing the pest population. For example, when waiting with an intervention up to the fourth generation, even the highest effort cannot save the crop (Fig. 2A). Yet releasing parasitoids too early when no hosts are present is counterproductive. Studies have shown that preventative parasitoid releases are less effective than curative ones (Lopes et al., 2009). Theoretically, the parasitoid *N. tutae* should be released six days after crop invasion by its host since they do not accept first-instar larvae (Calvo et al., 2013), and the time to develop from an egg into second-instar larvae of *T. absoluta* at 25 °C takes approximately six days (de Campos et al., 2020). The first small red marks on day one in Fig. 2 show that slightly more parasitoids are necessary in the first days for effective control than a few days later because no host larvae are present. Nevertheless, experience shows that detection in practice is imperfect and that detection one week after the arrival of the first adult pest, the parasitoid will likely find enough host larvae

Table 3
The minimum number of parasitoids necessary for efficient augmentative release in each scenario at day 25 (start of the second pest generation) and 75 (start of the fourth pest generation). Polynomial functions are shown with the correlation coefficient (r). Intervention strength shows, on day 75, the percentage of parasitoids necessary for efficient control in each scenario relative to the reference scenario. Reduction long vs. short shows for each scenario how much fewer parasitoids are necessary for the long growing season on day 75.

Scenarios (management strategies)	Growing season	Function	r	Minimum number		Intervention strength ^a	Reduction long vs. short
				Day 75			
				Day 25	Day 75		
A) Reference	Short	$8.33 + 1.88x - 0.102x^2 + 0.00208x^3$	0.98	24.1	453.1	100%	3%
	Long	$8.22 + 2.21x - 0.132x^2 + 0.00239x^3$	0.99	18.3	439.7	100%	
B) Natural parasitism	Short	$5.07 + 2.80x - 0.139x^2 + 0.00230x^3$	0.98	24.1	403.5	89%	9%
	Long	$7.77 + 2.67x - 0.147x^2 + 0.00234x^3$	0.99	19.2	368.3	83%	
C) Biopesticide	Short	$8.78 + 0.650x - 0.0129x^2 + 0.000394x^3$	0.90	23.1	151.2	33%	33%
	Long	$15.8 - 0.0922x - 0.00235x^2 + 0.00025x^3$	0.93	15.9	101.1	22%	
D) Natural parasitism & Biopesticide	Short	$7.46 + 1.42x - 0.0486x^2 + 0.000710x^3$	0.87	23.7	140.1	31%	45%
	Long	$19.2 - 0.00894x - 0.0131x^2 + 0.000312x^3$	0.86	15.6	76.5	17%	

^a Relative percentage of the effort in comparison to the reference scenario on day 75.

already.

In this context, biopesticide application and natural parasitism allow more time before parasitoid intervention (Fig. 2). For the same release rate still being efficient - the intervention with *N. tutae* can be delayed, strongly with biopesticide application and slightly with natural parasitism. The biopesticide slows down the pest population build-up by killing some of the larvae. Although the biopesticide alone cannot control the pest population completely, it can be combined with natural enemies. Therefore, applying the biopesticide might be a good strategy when the initial detection probability of the pest is low.

Even though it is generally recommended that parasitoids be released multiple times during the crop season for optimal synchronization with the pest, here we show that one single, well-placed intervention with the parasitoid *N. tutae* can effectively control *T. absoluta*. Since the larval stage of *T. absoluta* is long (about 12 days at 25°C, de Campos et al., 2020), the egg and pupal stages are short; there are only a few days without hosts available for the parasitoids. The first red peaks of Fig. 2 around day 18 show that slightly more parasitoids are necessary for effective control when the host larvae of the second generation are not present. However, releasing a few more individuals can compensate for this incorrect synchronization with the pest. A single, well-placed release of parasitoids reduces efforts for the growers compared to multiple releases.

4.2. The length of the growing season matters

A long growing season generally has a higher pest increase potential than shorter ones because if no control measures are applied, pest populations can have more generations and, thus, eventually reach the economic threshold. Here, the models show that when combined with biopesticide applications, fewer parasitoids could achieve the same control in the long versus short growing season if release is scheduled correctly and controls the first generation. By increasing the natural mortality of the pest larvae, the biopesticide allows the parasitoid population to keep up and eventually control it in the long growing season. In the short growing season, this seems to play out less likely, because the parasitoids do not have enough time to reach a sufficient density for pest control. However, it is important to note that in some cases, control happens late, and even though the pest population eventually comes under control, the damage might already be too severe for the growers.

4.3. Model limitations

The models are highly suitable for detecting long-term changes in populations, nevertheless, several important limitations need to be considered. The current model only examines the dynamics at a fixed temperature of 25°C. This temperature was selected because most published life cycle data are available at this temperature and it is very close to the average greenhouse temperature in Koller et al. (2023). In all cases, laboratory growth experiments conducted over different but constant temperatures suggest that higher or lower temperatures would similarly accelerate or slow down the dynamics of the pest and the parasitoid. For instance, to complete its entire life cycle, *N. tutae* needs twice as many days at 20°C than at 30°C (25 vs. 12.75 days, Calvo et al., 2013). Similarly, *T. absoluta* needs about double the time at 20°C compared to 30°C (34.8 vs. 18.3 days, Krechmer and Foerster, 2015). Fluctuating temperatures could be integrated into future studies, which would imply defining a function involving time-varying stage durations.

The model simulated colonization by a small pest inoculum early in the season. Yet, it did not include immigration and the emigration of pests or parasitoids. Nevertheless, as both species' populations increase rapidly after colonization, immigration of a few individuals later in the season will likely have a weak effect on the already large population. Moreover, greenhouses limit the number of individuals migrating and, thus, are less sensitive to dispersion than open fields. As a consequence,

it is possible that the findings would be slightly different in open-field production systems. The model was based on and validated with data from protected crops, and future work should assess if the findings also apply to field conditions.

One goal of the study was to estimate the density that the pest can reach when not under control. Therefore, the model did not consider a carrying capacity for the pest. Greenhouses can span up to several hectares with two to three plants per m². Thus, the enormous quantity of food can be considered ad libitum, to some extent.

For reasons of simplicity, the environment was assumed to be homogeneous and affect all individuals in the same way. The model neglected the complex ecological web in which both species are embedded. Often, tomato greenhouses harbour polyphagous predators and other pests, such as whiteflies (Moreno-Ripoll et al., 2014). Such a multi-species system can have numerous effects on the populations and possible control efforts. A natural progression of this work would be the integration of mirid predators into the equation since they play a significant role in controlling *T. absoluta* (Desneux et al., 2022).

4.4. Extension of the model framework to other pests and biocontrol agents

Besides *N. tutae*, other parasitoids are known to attack *T. absoluta*, including *Dolichogenidae gelichiivivoris* Marsh (Hymenoptera: Braconidae), which is newly present in the invaded areas and originates from the same area as *T. absoluta* (Denis et al., 2022; Krache et al., 2021; Salas Gervasio et al., 2019). Traditional approaches such as life table assessment remain fundamental for model developments. If the life table parameters are known, the modeling framework could be easily adapted to other larval parasitoids, as long as they have similar environmental needs. Host searching behavior varies greatly between species and would be a key parameter to integrate into future parasitoid-host interaction models via the functional response. For instance, the *N. tutae* host searching capacity is higher at low host density (type two functional response; Bodino et al., 2019) than the capacity of *D. gelichiivivoris* (type three functional response; Mama Sambo et al., 2022).

Likewise, the findings can be transferred directly to other microbial insecticides, such as *Bacillus thuringiensis* (Bt), as long as they do not affect parasitoid fitness, or if they do, their effect could be included in the model, for example, as higher parasitoid mortality or lower fertility.

5. Conclusions

This applied study can promote sustainable agriculture and reduce pesticide use by improving the efficiency of a biocontrol strategy. Models can help to predict the outcomes of new biocontrol combinations precisely. We showed here that the timing of intervention is crucial; therefore, investing in monitoring to find the right moment for intervention is key to combining both agents efficiently. Based on the model predictions, a tool could be developed to offer practical advice and assist greenhouse tomato producers, such as proposed by Rincon et al. (2023). Finally, the models could be easily adapted to other pest and parasitoid species - for example, to tackle new challenges like the brown marmorated stink bug *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) and *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae) in greenhouse vegetable production or well-known pest problems like whiteflies and *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae). Including the relative costs of each strategy to choose the best alternative in terms of cost-efficacy would be the next logical step.

Authors' contributions

J.G., J.C. and L.S. designed the research. J.G. and L.S. developed the model and interpreted the data. J.G. and L.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final

approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The R code used to generate the data is given in the Supplementary Material as well as the link to the dryad repository with the dataset used for model validation

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Appendix A. Supplementary data

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