



# Simplified modelling enhances biocontrol decision making in tomato greenhouses for three important pest species

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## Abstract

Generalist and specialist predators are successfully used in biocontrol programs in greenhouse vegetable crops, like tomato. A greenhouse ecosystem is rather simple and provides an excellent opportunity for developing predator–prey decision models. Three systems were selected: (1) the generalist predatory bug *Macrolophus pygmaeus* and the greenhouse whitefly *Trialeurodes vaporariorum*, (2) the generalist predatory bug *Nesidiocoris tenuis* and the tobacco whitefly *Bemisia tabaci* and (3) the specialist predatory mite *Phytoseiulus persimilis* and the spider mite *Tetranychus urticae*. The study is based on an extensive field dataset. No complex mathematical predator–prey models were developed. A binomial variable was given the value of “0” for the period when the pest was not under control. As soon as the population declined after the peak density, this variable was given a value of “1”. The relationship between the densities of the prey and the predator was checked using a logistic regression model. The validated models do not calculate future pest densities but rather predict when pest control should be initiated, based on the number of pests and predators present at a certain time. Numerical simulation of the prey isoclines showed an L-shaped curve for the generalist predators and a linear curve for the specialist predators. Our simple, empirical modelling approach provides satisfactory models for biocontrol purposes. When combined with a standardized monitoring protocol, these models can be implemented in decision tools. In the future, more data will allow a machine learning approach, in which additional parameters like temperature, humidity, and time can be included.

**Keywords** *Bemisia tabaci* · Biocontrol · *Macrolophus pygmaeus* · *Nesidiocoris tenuis* · *Phytoseiulus persimilis* · *Tetranychus urticae* · *Trialeurodes vaporariorum*

## Key message

- Generalist and specialist beneficials are used in greenhouse crops to control pests.
- Predator–prey population models can be used to predict pest outbreaks and prevent pesticide applications. Currently, no such models are on the market for decision making.
- Simple, logistic regression models were built for three economic important pests and their predators in tomato crops.
- The predicted population dynamics are in line with generalist and specialist predator ecology.
- The models were validated and deemed satisfactory for practical guidance in biocontrol actions.

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## Introduction

The preventative release of generalist predators as biocontrol agents in IPM programs has become common practice in European greenhouse vegetable crops as they can develop and build up a strong standing army in the absence of the target pest (e.g. Nomikou et al. 2002; Messelink and Janssen 2014; Moerkens et al. 2017; Brenard et al. 2018). Specialist predators (or parasitoids) are released more curatively to target specific pests (e.g. Van Lenteren et al. 1996; Alatawi et al. 2011).

A big advantage of a greenhouse ecosystem compared to open, natural conditions is its simplicity. A Northwestern European greenhouse can be considered as a closed ecosystem with very few movements to the surrounding area (in comparison with open fields). The vegetation/crop is a monoculture, and the number of prey and predator species is small, during some periods even limited to one predator and one pest. Such one-to-one predator–prey interactions are rare in natural conditions. The simplicity of ecosystems in greenhouses allows more controlled ecological studies of a few species. Nevertheless, one or two pest species combined with one or more generalist or specialist predators can result in complex population dynamics. Greater insight into these dynamics would allow a better interpretation of the predator–prey interactions in the field and would improve biocontrol strategies.

The classic population model is a Lotka–Volterra predator–prey model (Gause et al. 1936). Models that are more complex have been proposed (e.g. Hanski et al. 1991; Turchin and Hanski 1997; Hanski et al. 2001; Mukhopadhyay and Bhattacharyya 2013). These models are very theoretical and try to convert several biological interactions in a mathematical formula. The drawback is their complexity when more parameters are included. Validation with extended field data on different locations is missing. A good example of this is the well-studied predatory mite *Phytoseiulus persimilis* (Athias-Henriot) (Acari: Phytoseiidae) and its prey, two-spotted spider mite *Tetranychus urticae* (Koch) (Acari: Tetranychidae). Several predator–prey models have been developed in the past (Bernstein 1985; Bancroft and Margolies 1999; Kozlova et al. 2005; Kuang et al. 2017), but validation in practical conditions is missing. For example, Kozlova et al. (2005) describes a deterministic model with diffusion and time delay, which gave a reasonably good fit to the field data. The goal of their study was not to describe the data but to determine the parameters and the type of behaviour that takes place in the particular system of prey and predator. For biocontrol purposes, it is sufficient to know the prey isocline (i.e. how many predators are needed to control the prey) in combination with the probability of a

pest population being under control or not at a given point in time, which is the scope of our study.

In this study, three predator–prey systems (i.e. simplified systems with just one predator and only one of its prey species) which are common in tomato greenhouses were selected. The first predator–prey system is the predatory bug *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) and the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). *Macrolophus pygmaeus* is a zoophytophagous generalist predator, which is capable of controlling several pest species like whiteflies, aphids, mites, thrips and Lepidoptera (e.g. Enkegaard et al. 2001; Perdikis and Lykouressis 2002; Blaeser et al. 2004; Castañé et al. 2004; Alomar et al. 2006; Urbaneja et al. 2009). It can maintain its population by feeding on the plant while prey densities are low or absent (e.g. Perdikis and Lykouressis 2000; Ingegno et al. 2011). Population growth is accelerated when supplementary food is provided after inoculative release in the crop (Moerkens et al. 2017; Brenard et al. 2018, 2019).

The second predator–prey system is the predatory bug *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) and the tobacco whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), with a similar interaction as between *M. pygmaeus* and *T. vaporariorum*. *Nesidiocoris tenuis* is also a zoophytophagous generalist predator and is mostly released in South-European (Spain, Canary Islands, Sicily) tomato greenhouses as a biocontrol agent against *B. tabaci* (Carnero et al. 2000; Calvo et al. 2012a, b) and *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Urbaneja et al. 2009; Calvo et al. 2012b; Urbaneja et al. 2012).

The third predator–prey system is the predatory mite *P. persimilis* and the two-spotted spider mite, *T. urticae*. *Phytoseiulus persimilis* is a specialized feeder of spider mites and is commonly released as a biocontrol agent (e.g. Gough 1991; Drukker et al. 1997; Opit et al. 2004).

The population dynamics of these three predator–prey interactions in tomato greenhouses were simplified and simulated using a common logistic regression with the intention to predict a probability of control of the pest, based on the number of predators and prey at a certain time. The prey isoclines were computed numerically and compared between two generalist predators (*M. pygmaeus* and *N. tenuis*) and a specialist predator (*P. persimilis*).

## Materials and methods

### Data collection

#### Predator–prey model: *M. pygmaeus*–*T. vaporariorum*

Population dynamics were recorded in seven experimental greenhouse compartments (size between 500 and 1500 m<sup>2</sup>)

during several years (2016–2018) at Research Centre Hoogstraten (Belgium) and at eight commercial, Belgian tomato greenhouses with a minimum of four hectares per greenhouse. The different locations had a wide diversity of different tomato varieties (beef, cluster and specialty tomatoes) each with their own climate conditions. Tomato plants are cultivated year round in Belgium with artificially lit and non-lit crops (Moerkens et al. 2016a, b). More details on the different locations are described in Table 1.

The number of adult whiteflies and adult mirids were counted on yellow sticky traps (YSTs) (e.g. Bug-scan Dry, Biobest, Belgium), which is a common monitoring method in tomato greenhouses (Böckmann et al. 2015; Pinto-Zevallos 2013). These traps (25 × 10 cm) were hung just below the head of the plant on 185 fixed locations distributed throughout the different monitored greenhouses. Every week or maximum two weeks, the population densities of predator and prey were manually counted on all 185 YSTs. The YSTs were replaced during every sampling occasion. *Macrolophus pygmaeus* densities on YSTs are much lower compared to whiteflies and can vary a lot in time and between locations (unpublished observations). Therefore, mirid densities were counted on two sides of the YST (whiteflies only on one side) and were averaged over a minimum of four YST's. These four YSTs were located in the same plant row (at commercial greenhouses) or in the same greenhouse compartment (at Research Centre Hoogstraten). Thus, at each

time point, a minimum of four (eight sides) averaged YST counts were used for *M. pygmaeus*. This way variation in mirid counts was minimized. In total, 2730 unique predator–prey combinations were collected, divided over multiple greenhouses and time points. The total dataset contains a wide range of predator/prey ratios, including extreme values during pest outbreaks.

*Macrolophus pygmaeus* individuals were released at the start of each new crop cycle. The total number, the distribution and the feeding strategy differ between growers, as they work with different producers (e.g. Biobest Group N.V., Belgium and Koppert N.V., the Netherlands). A common release strategy is described by Moerkens et al. (2017). The whitefly populations naturally persist and disperse each cropping season, no extra releases were carried out. Periods when growers applied plant protection products or periods when secondary pests (e.g. *T. absoluta*, *A. lycopersici* and *T. urticae*) occurred were removed from the datasets in order to obtain one-to-one predator–prey interactions.

#### Predator–prey model: *N. tenuis*–*B. tabaci*

Population dynamics were recorded at four commercial tomato greenhouses in the Almeria province of Spain in 2018, each with a different climate condition. More details are presented in Table 1.

**Table 1** Model and validation dataset collection details for *M. pygmaeus*–*T. vaporariorum*, *N. tenuis*–*B. tabaci* and *P. persimilis*–*T. urticae* predator–prey interactions

Predator–prey	Year	Grower	Location (Belgium)	Lit/non-lit	# YST/plants	# assessments	Dataset
<i>M. pygmaeus</i> – <i>T. vaporariorum</i>	2016	Grower A	Hoogstraten	Lit	42	588	Model
	2017	PCH*	Hoogstraten	Lit	8	56	Model
	2018	PCH*	Hoogstraten	Non-lit	53	904	Model
	2018	PCH*	Hoogstraten	Lit	12	293	Model
	2018	Grower B	Putte	Lit	10	145	Validation
	2018	Grower C	Rijkevorsel	Lit	10	97	Validation
	2018	Grower D	Rijkevorsel	Non-lit	10	176	Validation
	2018	Grower E	Rijkevorsel	Non-lit	10	101	Validation
	2018	Grower F	Broechem	Lit	10	140	Validation
	2018	Grower F	Broechem	Non-lit	10	100	Validation
	2018	Grower B	Putte	Non-lit	10	130	Validation
<i>N. tenuis</i> – <i>B. tabaci</i>	2018	Grower G	La Venta Del Viso	Non-lit	20	320	Validation
	2018	Grower H	Vícar	Non-lit	20	320	Model
	2018	Grower I	Vícar	Non-lit	20	320	Validation
	2018	Grower J	La Cañada	Non-lit	20	260	Validation
<i>P. persimilis</i> – <i>T. urticae</i>	2016	PCH*	Hoogstraten	Non-lit	252	2016	Model
	2017	PCH*	Hoogstraten	Non-lit	476	5712	Validation

Different columns represent the predator–prey interaction, the year of sampling, the individual grower, the location (city) of the greenhouse, whether artificial light was used (lit/non-lit crops), the number of yellow sticky traps or plants that were sampled, the number of data assessments (#YST or plants multiplied by sampling occasions (time)) and whether the dataset was used for model input or validation

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The sampling method was identical to the one described above. Also for *N. tenuis* an average density for each sampled tomato row was calculated (10 YST sides). Every two weeks, the population densities were counted on 80 YSTs at fixed locations in the greenhouses. In total, 1220 unique YSTs were sampled. The total dataset contained a wide range of predator/prey ratios, including extreme values during pest outbreaks.

Like *M. pygmaeus*, *N. tenuis* individuals are released in a similar way at the start of each crop cycle and whitefly populations naturally persist and disperse each cropping season. Again, periods when growers applied plant protection products or periods when secondary pests occurred were omitted.

### Predator–prey model: *P. persimilis*–*T. urticae*

All data were obtained at Research Centre Hoogstraten, Hoogstraten, Belgium. During two subsequent cropping seasons in 2016 and 2017, tomatoes were planted in two different semi-commercial greenhouses of 200 m<sup>2</sup> in January 2016 and 2017 (Table 1). Crawling insects, like mites, require a different sampling approach compared to flying insects. Mites cannot be monitored using YSTs and require sampling on the plant. In 2016, 252 plants were monitored weekly between 11 May 2016 and 29 June 2016. In 2017, 476 plants were sampled weekly between 21 March 2017 and 6 June 2017. In total, there were 600 plants present in each greenhouse compartment. Every week, the number of adult *T. urticae* and *P. persimilis* were counted with the naked eye on the fourth leaf starting from the head of the plant. From previous experience, we know that the third to the fifth leaves hold the most spider mites (unpublished observations). Spider mites were released on 30 March in 2016 and 7 March in 2017. Tomato leaves infested with *T. urticae* were randomly distributed in the greenhouse, which resulted in hotspots of spider mites and plants with less spider mites. The predatory mite *P. persimilis* (Phytoseiulus-System, Biobest Group N.V., Westerlo, Belgium) was homogeneously released at a dose of 20 ind/m<sup>2</sup> in the head of each plant on 12 May in 2016 and 21 April 2017. The predatory bug *M. pygmaeus* was not released in these greenhouses. The number of whiteflies remained very low during the 8 and 11 week interval in 2016 and 2017, respectively. Only a few individuals were spotted by the end of the experiment. Therefore, spider mites and *P. persimilis* were the only pest and predator of significance present in the greenhouse.

### Logistic regression model

The population dynamics of the different predators and prey are typically characterized by a strong population growth of the prey, followed by that of the predator (Fig. 1). Sometimes, the pest outbreak was too severe and the grower

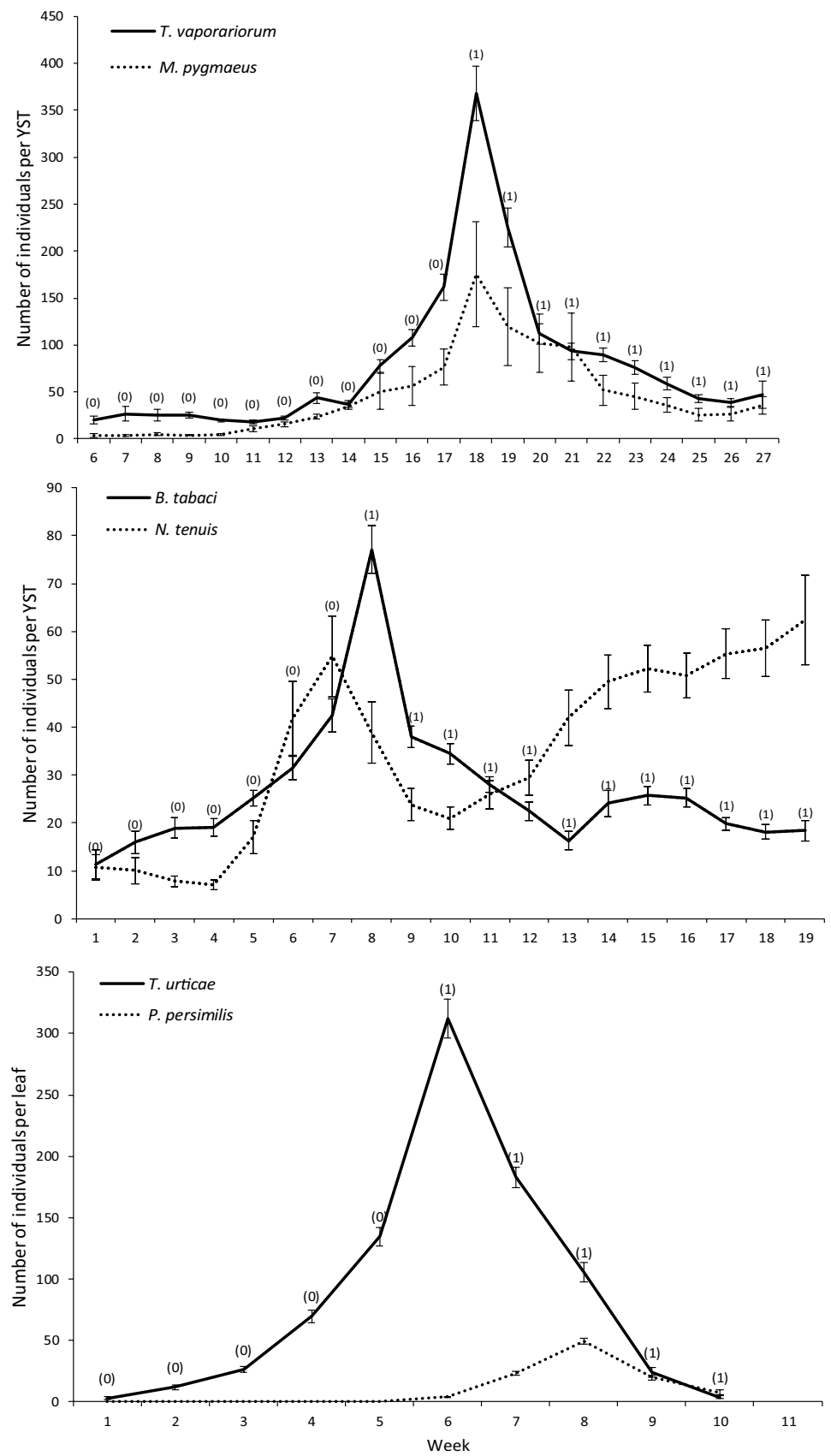
decided to use a chemical plant protection product. As mentioned earlier, the data were cut off at these moments and not considered for further analysis. For the logistic models, a variable “pest control” was created. This binomial variable was given the value of “0” for the period when the pest densities were increasing. As soon as the population declined after the peak density, the pest control variable was given a value of “1”. This variable was created manually for each YST (flying insects) or plant (crawling insects) time series. If population densities were very low or confusing and no clear “0” or “1” value could be given, the data were omitted from the dataset. All datasets are independent between years and growers (Table 1.).

We quantified through a generalized linear model (glm) how the variable pest control yes (1) or no (0) changed in relation to the previous densities of the predator and the pest. This logistic regression was built with a binomial distribution and logit link function. The number of insects on the YSTs and the number of mites on the leaves were log transformed (log + 1) prior to the regression analyses. The statistical analysis started with a saturated model and interactions, and non-significant main factors were dropped at a significance level of 0.05. Predicted probabilities from this logistic regression model were converted to their original state using the inverse logit formulae ( $\exp^{\text{model parameters}} / (1 + \exp^{\text{model parameters}})$ ). All statistics were carried out in R v.3.5.1 (R Core Team 2018). The used model input datasets are indicated in Table 1.

### Model validation

The logistic regression model enables us to predict the probability of biocontrol at given pest and predator densities. In order to validate the model, the predictions of the model were compared to the observations of an independent dataset. The datasets used for model validation are marked in Table 1. The output of the model is a probability (between 0 and 1), while the observed data consist of values of either 0 or 1 (no/yes control). Therefore, the model output probability was rounded to 0.10 and grouped together according to the following categories: (0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, 0.90, and 1.00). For each category, the proportion of samples with actual, observed biocontrol (value 1) was determined. This way, we can compare the model output, which is a chance of biocontrol with the actual, observed proportion of biocontrol. Frans et al. (2018) describe a similar method for internal fruit rot in bell pepper. The slope and intercept of the regressions lines between observed and estimated proportions were checked whether they differed from unity and zero, respectively. All statistics were carried out in R v.3.5.1 (R Core Team 2018).

**Fig. 1** Averaged ( $\pm$ SE) population densities of all datasets combined for three different predator–prey interactions, namely *M. pygmaeus*–*T. vaporariorum*, *N. tenuis*–*B. tabaci*, *P. persimilis*–*T. urticae*. The binomial classification for periods when the prey population increases (0) or decreases (1) is indicated between brackets for each time point



## Calculation of prey isoclines

Simulation of prey isoclines requires calculation of a curve, along which the prey population neither grows nor declines as a function of the predator population. These are the points in time series of pest/prey densities where this series reaches its maximum. In order to use a logistic regression model, we have categorized the increasing phase of the pest densities as “0” and the decreasing phase, including the maximum, as “1” as illustrated in Fig. 1. Therefore, the model will predict whether the pest population will increase (0) or decrease (1). The output of this model is not “0” or “1” but a probability between “0” and “1”. To determine the point of maximum pest density (i.e. data point on the pest isocline), we need to determine the required density of predators. This was achieved by numerically changing the predator density values for a range of prey densities until the model output reached a chance of 50%. The prey isocline was defined as a curve where the prey population had 50% chance of increasing or decreasing, which is similar to the classic definition of a curve along which the prey population neither grows nor declines. Above this curve, the pest population has a higher chance to decrease and below this curve the pest population has a higher chance to increase. In addition, curves that mark when the pest population has a 25% and 75% chance of increasing were added to the plots.

## Results

### Data collection

As an illustration of the datasets, the total averaged population densities of predator and prey are given in Fig. 1. After removing zero values (prey) and unusable data (unclear “0” and “1” values), 1829 and 967 data points were usable for the *M. pygmaeus*–*T. vaporariorum* model for the model input and validation, respectively. For the *N. tenuis*–*B.*

*tabaci* model 319 and 527 data points remained and for *P. persimilis*–*T. urticae* 2016 and 1832 data points.

### Logistic regression model

The interaction effect between the densities of the predator and prey was dropped from the model for both *M. pygmaeus*–*T. vaporariorum* (glm:  $z = -0.283$ ;  $p = 0.777$ ) and *N. tenuis*–*B. tabaci* (glm:  $z = -0.366$ ;  $P = 0.714$ ). The additive effect of the predator and the prey was highly significant for both predator–prey models ( $P < 0.05$ ). For *P. persimilis*–*T. urticae*, the saturated model was significantly better than simplified ones. All statistical details can be found in Table 2.

### Model validation

The relations between the observed and estimated chances of biocontrol were checked with a linear regression. The slope and the intercept of this regression for the *M. pygmaeus*–*T. vaporariorum* model tested not significantly different from unity ( $t = -0.926$ ;  $P = 0.090$ ) and zero ( $t = -0.539$ ;  $P = 0.605$ ), respectively (Fig. 2). Likewise, the slope and the intercept for the *N. tenuis*–*B. tabaci* model tested not significantly different from unity ( $t = -0.131$ ;  $P = 0.899$ ) and zero ( $t = 0.965$ ;  $P = 0.363$ ), respectively (Fig. 2). Similar results were found for the *P. persimilis*–*T. urticae* model for the slope ( $t = -0.592$ ;  $P = 0.580$ ) and the intercept ( $t = -0.233$ ;  $P = 0.825$ ) (Fig. 2). One outlier was removed from the dataset at the estimated chance for biocontrol of 0.60 because of low sample size ( $n = 23$ ). Overall, the values on the  $x$ -axis (observed) are equal to the values on the  $y$ -axis (estimated) for all three predator–prey models.

### Calculation of prey isoclines

The prey isoclines of the whiteflies have an L shape in relation to their generalist predators (Fig. 3). At low prey densities (for *T. vaporariorum*  $< 100$  and *B. tabaci*  $< 30$ ), more

**Table 2** Parameter estimates and statistics of the logistic regression models for each predator–prey interaction

Predator–prey	Parameter	Estimate	SE	Statistics
<i>M. pygmaeus</i> – <i>T. vaporariorum</i>	Intercept	– 5.218	0.271	$z = -19.25$ ; $P < 0.0001$
	Predator	1.677	0.155	$z = 10.82$ ; $P < 0.0001$
	Prey	1.518	0.131	$z = 11.62$ ; $P < 0.0001$
<i>N. tenuis</i> – <i>B. tabaci</i>	Intercept	– 4.233	0.870	$z = -4.87$ ; $P < 0.0001$
	Predator	2.395	0.387	$z = 6.19$ ; $P < 0.0001$
	Prey	1.510	0.496	$z = 3.04$ ; $P = 0.0023$
<i>P. persimilis</i> – <i>T. urticae</i>	Intercept	– 3.135	0.288	$z = -10.88$ ; $P < 0.0001$
	Predator	12.025	0.986	$z = 12.20$ ; $P < 0.0001$
	Prey	0.728	0.135	$z = 5.39$ ; $P < 0.0001$
	Predator $\times$ Prey	– 3.040	0.406	$z = -7.50$ ; $P < 0.0001$



**Fig. 2** Validation of the logistic regression models for all three predator–prey systems. Estimated probability of biocontrol from the logistic regression models, and observed chance of biocontrol by manual counting of 0 and 1's. Numbers in brackets indicate the number of data points for each category (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1)

mirids are needed to control the pest population. *N. tenuis* is able to control *B. tabaci* at lower densities on the yellow sticky trap compared to *M. pygmaeus* and *T. vaporariorum*. However, the catch rate on the yellow sticky trap can be different for the different species. Therefore, the densities can be biased, which makes comparison between species difficult.

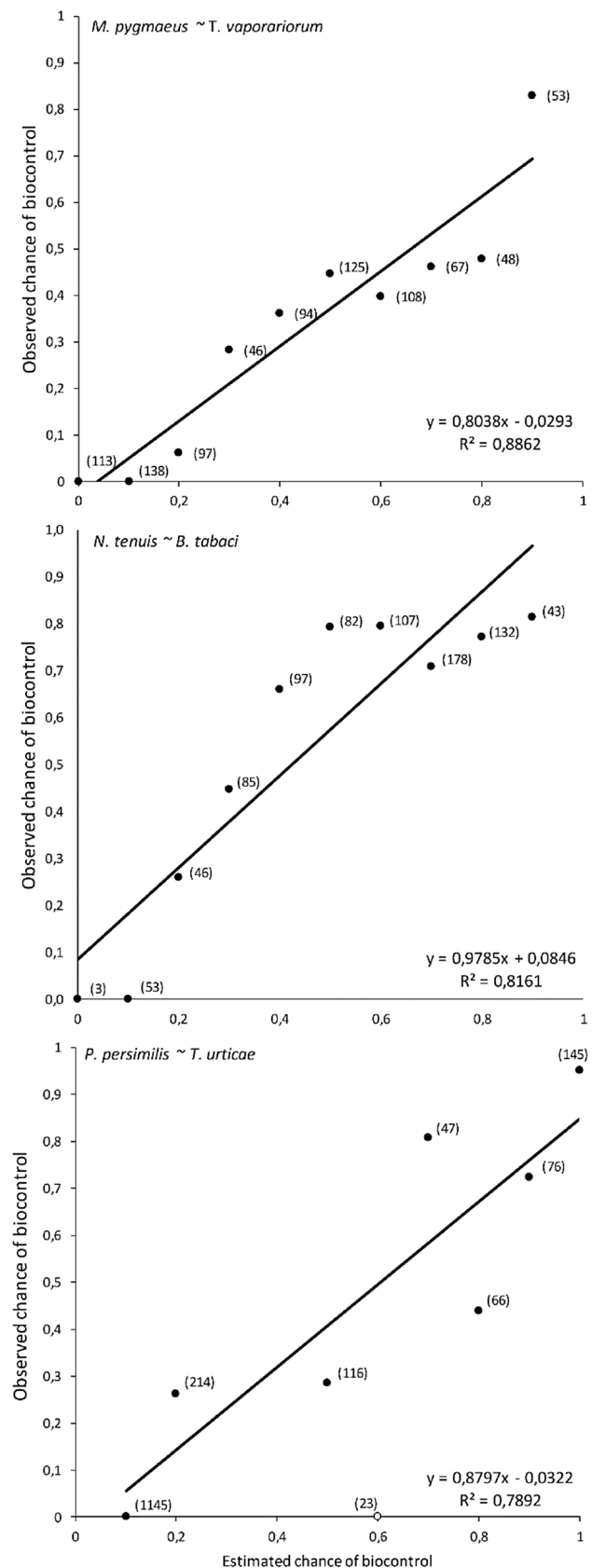
The specialist *P. persimilis* has a more linear/horizontal relationship with his prey (Fig. 3). More *P. persimilis* is needed at increasing spider mite densities. An observation of only one adult *P. persimilis* per leaf is sufficient to reduce the spider mite population almost independent of the pest density.

Prey isoclines with a probability of 0.25 and 0.75 are shown in Fig. 3. Above the prey isocline, the prey population has a higher tendency to decrease. Below the prey isocline, the pest population will most likely increase.

## Discussion

Monocultures in greenhouse crops provide a perfect semi-natural environment for studying population dynamics of different predators and their prey. In comparison with natural ecosystems with a multitude of variables, greenhouses are simple, semi-enclosed ecosystems, wherein even climate conditions are standardized within specific boundaries for crop cultivation. Data collection of one-to-one predator–prey systems in tomato greenhouses provided a large database of three study systems: *M. pygmaeus*–*T. vaporariorum*, *N. tenuis*–*B. tabaci* and *P. persimilis*–*T. urticae*. For each predator–prey system a logistic regression model was fitted and validated based on field data collected at semi-commercial and commercial companies. We do not predict population densities, but the probability of being in the increase or decrease phase of the pest population, given the population sizes of prey and predators.

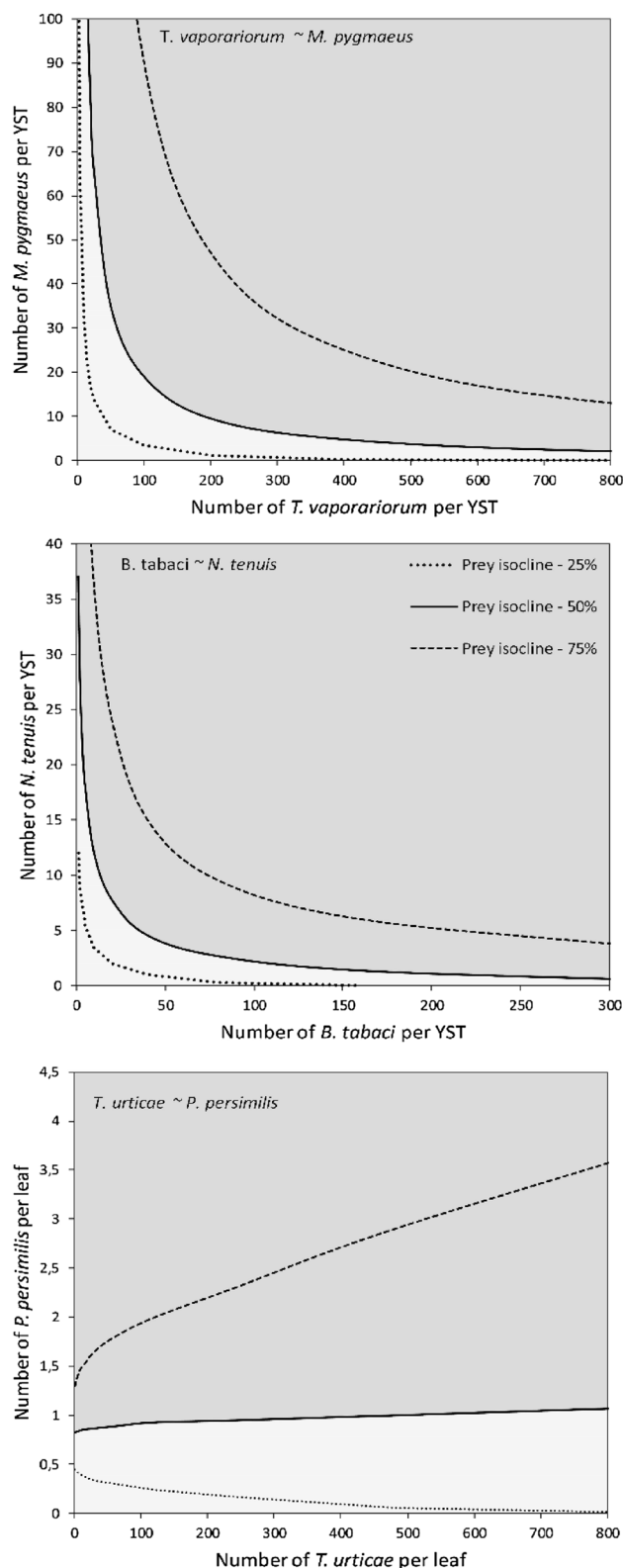
Generalist and specialist predators interact in a different way with their prey. When prey is scarce, a generalist predator will add alternative prey or food sources to their diet (Křivan 1996; Turchin and Hanski 1997; Hanski et al. 2001; van Baalen et al. 2001; Symondson et al. 2002; Mukhopadhyay and Bhattacharyya 2013). For both *M. pygmaeus* and *N. tenuis* and their prey, an L-shaped prey isocline was simulated based on our rather simple logistic regression model (Fig. 3). Such an L-shaped isocline was previously



**Fig. 3** Numerical simulations of the logistic regression models. Prey isoclines were calculated at a probability of achieving biological control of 0.5. Prey isocline boundaries at 25 and 75% were included. The light grey areas represent situations where the pest population will increase because not enough predators are present (possibly extra control measurements are required). Similarly, the dark grey areas represent situations where the pest population will decrease (no further control actions needed)

described as a prey refuge (Křivan 2011; Křivan and Priyadarshi 2015). This means that a part of the prey population was inaccessible for the predator. Such an L shape is not illogical for a generalist predator as they will add alternative prey or food sources (i.e. tomato fruit/leaves) to their diet when the prey becomes scarce. Thus, at low prey densities, much higher predator densities are required to control the pest. Mirids, like *M. pygmaeus* and *N. tenuis*, always require plant food in their diet for water and nutrient uptake (Moerkens et al. 2016; Urbaneja-Bernat et al. 2019). They can also survive on the plant when prey is absent or scarce (e.g. Perdakis and Lykouressis 2000; Ingegno et al. 2011). In fact, the L shape can be considered as a lack of encounter rates between predator and prey and/or limited searching efficiency of the predator. A prey would not go extinct very quickly in combination with a generalist predator, as they ideally reach a stable equilibrium point. Our model does not allow prediction of the predator isocline or calculations of equilibrium points. However, Fig. 1 illustrates that both predator and prey densities remain within an acceptable range (based on personal communication with the growers) after the pest population peak for both *M. pygmaeus* and *N. tenuis*. At very high prey densities the carrying capacity of the environment/crop will theoretically limit the reproduction of the prey and less predators will be required to reduce the pest population. Such prey isoclines are characterized by a “hump”. The classic example of such a model is the Rosenzweig–MacArthur model (Rosenzweig and MacArthur 1963). The combination of such a model with a “prey refuge” was described by Křivan (2011) and Křivan and Priyadarshi (2015). Such a “hump” was not detected in the data, although the prey isocline has a slow decline at high prey densities. In other words, at increasing pest densities, less predators are required to achieve control of the population. We expect that the logistic regression model is not complex enough to show the expected “hump” in our data.

Specialist predators only feed on one prey type. Even at low prey densities, they will keep searching for this prey or they die. Therefore, specialist predator–prey systems are characterized by large oscillations through time (Turchin and Hanski 1997; Hanski et al. 2001; Symondson et al. 2002; Mukhopadhyay and Bhattacharyya 2013). A linear prey isocline is expected, as more predators are required when prey densities increase. Indeed, the prey isocline of the *P. persimilis*–*T. urticae* predator–prey system appeared to be



a linear curve. When more spider mites are present, more predatory mites are required. The slope of this curve is not steep and becomes almost horizontal, which resembles the classic Lotka–Volterra model (Gause et al. 1936). The trial



did not last long enough to detect population oscillation in time. Figure 1 clearly shows a dramatic drop of both predator and prey on all plants, causing local extinctions of spider mites and/or predatory mites. In addition, the “hump” caused by the carrying capacity of the crop was expected (Rosenzweig and MacArthur 1963), as it was included in other spider mite models (Kozlova et al. 2005; Kuang et al. 2017), but was not observed. Again, we expect that the logistic regression model is not complex enough to show these dynamics.

To conclude, this study provides actual, realistic generalist and specialist predator–prey dynamics based on real field data. In order to model the essential parameters (i.e. prey isoclines and the chance of biocontrol), the available data were simplified and complex mathematical modelling was avoided. The validated models are easy to interpret. We acknowledge the fact that more complex dynamics, like the lack of a carrying capacity, are masked in our modelling approach. However, for biocontrol purposes these models are easy to implement as a decision tool in the near future. Many Northwestern European tomato growers are monitoring their crop using yellow sticky traps (Böckmann et al. 2015; Pinto-Zevallos 2013). This way, they obtain quantitative data of both the pest and the predator (e.g. whiteflies and mirids). Unfortunately, most growers focus on the densities of the pest and not the predators. Tools for more efficient monitoring, like automatic counting of pests and predators on yellow sticky traps, are under active development and will encourage growers to monitor in a standardized way (Moerkens et al. 2019). In the near future, growers will be able to automatically count insects on yellow sticky traps using smartphone images. As these data are fed into the presented population models, a decision support system will increase the efficiency of biocontrol actions, like the release of additional biocontrol agents or spot treatments with selective pesticides. Currently the tools presented require some form of interpretation, as a greenhouse in which plant protection products has been used, or in which alternative predator or pest species are present can alter the associations between pest control and prey and predator densities. Therefore, we recommend the use of this decision support system in collaboration with a biological crop advisor. In the future, more data will allow comparable analysis using machine learning techniques, which will hopefully be able to forecast densities of predator and prey. Additional parameters like temperature, humidity, growing stage of the plant, time (week, month), etc., can be added in order to increase the predictive power of the models and reduce variation.

Monitoring quantitative spider mite and predatory mite densities on leaves is more labour intensive. It is unlikely growers will start counting all these mites. New automatic approaches with standardized images of leaves are required.

Only then, will the above described model be applicable on a large scale in greenhouses.

## Author contributions

RM, NB, HL and VS conceived the ideas and designed methodology; RM, DJ, MMT, ER, RE and LB collected the data; RM and VS analysed the data; RM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Compliance with ethical standards

**Conflict of interest** All authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with human participants performed by any of the authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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