UNIVERSITÀ DEGLI STUDI
DI MODENA E REGGIO EMILIA

Dottorato di ricerca in Scienze, Tecnologie e Biotecnologie Agro-alimentari

Ciclo XXXIII

Models supporting decision-making in pest management
The role of scales and contexts of application

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Ringraziamenti

Desidero ringraziare il mio Tutor, Prof. Gianni Gilioli per il suo continuo supporto e la sua disponibilità (24 ore su 24, 7 giorni su 7) durante l'intero periodo di Dottorato. La sua guida è stata fondamentale per crescere professionalmente (e non solo), per affrontare le sfide e per raggiungere i risultati che hanno caratterizzato il mio percorso.

Ringrazio la mia Co-Tutor, Prof.ssa Lara Maistrello e il Coordinatore del Corso di Dottorato, Prof. Alessandro Ulrici per il loro prezioso supporto e per aver risposto puntualmente alle mie mille domande e dubbi.

Ringrazio tutti i co-autori (sono tantissimi) che hanno contribuito allo sviluppo dei vari lavori pubblicati e in corso di finalizzazione. Il loro contributo è stato fondamentale per la realizzazione di questa Tesi.

Un ringraziamento speciale al Prof. Andrea Battisti e alla Dr.ssa Sara Pasquali per il loro fondamentale lavoro di revisione e valutazione della Tesi.

Ringrazio tutti gli amici, colleghi e docenti con i quali ho avuto il piacere di condividere fatiche e successi del nostro lavoro: Anna Simonetto, Michele Colturato, Prof.ssa Paola Gervasio, Matilde Zubani, Davide Bazzana, Francesca Orlando, Giacomo Santoiemma, Prof. Nicola Mori, Simone Parisi, Igor Valli, Isabella Ghiglieno, Valentina Caprarulo e Irene Tosato.

A tutti i miei amici più cari, per esserci sempre.

Grazie a tutti i miei familiari, ai miei genitori Ugo e Giulia, a mio fratello Damiano e mia sorella Lucia, agli zii e parenti per la loro vicinanza e per tutte le opportunità di crescere come persona espresse in un milione di modi diversi.

Alla mia compagna Valentina, per essermi vicina in ogni momento e per avermi sempre supportato (e sopportato) anche nei periodi più difficili.

Al piccolo Edoardo, mio figlio, che con un solo vagito mi ha fatto capire quali sono le cose veramente importanti della vita.

“In ogni secolo gli esseri umani hanno pensato di aver capito definitivamente l'Universo e, in ogni secolo, si è capito che avevano sbagliato. Da ciò segue che l'unica cosa certa che possiamo dire oggi sulle nostre attuali conoscenze è che sono sbagliate”.

Isaac Asimov

Contents

FOREWORD

The Thesis presented here deals with the development and the implementation of modelling tools supporting decision-making in the management of arthropod pests in agriculture. This was my main research topic during my doctoral period in which I had the opportunity to provide my contribution in the development of quantitative models and their application for pest management. Considering my background as biologist and ecologist, I have mainly worked on introducing relevant biological aspects within the modelling frameworks and the interpretation of model's outputs linked to the biological system under investigation and the related management issues. My contribution mainly refers to i) the development of the conceptual model representing the biological system, ii) the collection of data on the life-history strategies and dynamics of the species under investigation iii) the design of field sampling protocols for data collection, iv) the management and the analysis of weather and climatological data v) the design and the implementation of the model calibration and validation procedures. The majority of the work carried out during the doctoral period resulted in the chapters that constitute the conceptual framework presented in this Thesis. During the doctoral period, I have also produced other outputs dealing with the development of models and their application for supporting decision-making in various agro-ecological contexts.

Broadly speaking, considering the management issues under investigation, I have worked on three major areas of models' applications.

Models applied for the management of pests at the local level

In this Thesis is presented one work as a representative case study related to the development of a physiologically-based phenological model supporting the management of the Japanese beetle (*Popillia japonica*) presented in Chapter Three. Additionally, I have been involved in other projects in which I have collaborated on the development of models predicting the dynamics, the phenology and the potential impacts of relevant insect pests. Models have been developed and applied to the grape tortrix (*Argyrotaenia pulchellana*), the codling moth (*Cydia pomonella*), the oriental fruit moth (*Cydia molesta*), the corn earworm (*Helicoverpa armigera*), the barred fruit-tree tortrix (*Pandemis cerasana*), the grape berry moth (*Lobesia botrana*), the American grapevine leafhopper (*Scaphoideus titanus*), and the European corn borer (*Ostrinia nubilalis*). These models are under the process of development and/or calibration/validation and they will result in publications dealing with the simulation of various aspects related to the biology of the species and the provision of models' outputs supporting their management.

Models applied to the management of the risks linked to invasive alien species

In this Thesis, I have presented one work as a representative case study of a model applied to the assessment and the management of the risks related to invasive species. The model is presented in Chapter Five, and deals with the assessment of the distribution, abundance and activity of the Mediterranean fruit fly (*Ceratitis capitata*) under current and future climatic scenarios. I have also participated in other works related to invasive species, dealing with the assessment of the potential distribution and impacts of the tiger mosquito (*Aedes albopictus*) (Pasquali et al., 2020), the fall armyworm (*Spodoptera frugiperda*) partially presented in Chapter Four, and on the assessment of the habitat suitability and the potential diffusion of *P. japonica*.

Models applied to the assessment and management of the health status of honey bees

These works, not presented in the Thesis, have been published during my PhD. In particular I have worked on the conceptualisation of beekeeping management practices for their introduction within a mechanistic modelling framework (Sperandio et al., 2018), and on models for the assessment of the health status and productivity of honey bee colonies (Gilioli et al., 2018; 2019).

The full list of papers published during my doctoral period is presented in the following page.

List of publications

Gilioli, G., Orlando, F., Ghiglieno, I., Sperandio, G., & Simonetto, A. (2020). Biodiversità e agricoltura sostenibile. Equilibri, 24(1), 69-76.

Pasquali, S., Mariani, L., Calvitti, M., Moretti, R., Ponti, L., Chiari, M., Sperandio, G., & Gilioli, G. (2020). Development and calibration of a model for the potential establishment and impact of *Aedes albopictus* in Europe. Acta Tropica, 202, 105228.

Rossi, V., Sperandio, G., Caffi, T., Simonetto, A., & Gilioli, G. (2019). Critical success factors for the adoption of decision tools in IPM. Agronomy, 9(11), 710.

Sperandio, G., Simonetto, A., Carnesecchi, E., Costa, C., Hatjina, F., Tosi, S., & Gilioli, G. (2019). Beekeeping and honey bee colony health: A review and conceptualization of beekeeping management practices implemented in Europe. Science of the Total Environment, 133795.

Gilioli, G., Sperandio, G., Hatjina, F., & Simonetto, A. (2019). Towards the development of an index for the holistic assessment of the health status of a honey bee colony. Ecological Indicators, 101, 341-347.

Gilioli, G., Simonetto, A., Hatjina, F., Sperandio, G. (2018). Multi-dimensional modelling tools supporting decision-making for the beekeeping sector. IFAC-PapersOnLine, 51(5), 144-149.

ABSTRACT

Arthropod pests represent one of the major threats worldwide as they have an impact on agricultural and forestry production, and on the health of animals, humans and the environment. In particular, plant pests will play a prominent role in shaping the management practices and the technologies to be adopted in food production. With an increasing growth of human population and the consequent increase in food demand, a major challenge of the future will be to ensure safe and secure food. Decreasing crop losses due to pests and reducing both the direct and indirect costs linked to pest management is a fundamental aspect for ensuring global food security. The design and the implementation of rational and scientifically sound decisions in pest management can be supported by the use of models. In particular, physiologically-based models have proven to be useful tools able to provide quantitative information supporting decision-makers in the management of pests.

In this work, I present a general overview on the development and the application of models for pest management with particular emphasis on physiologically-based models applied at different contexts and at different spatial (from local to area-wide management) and temporal (from short to long term management) scales.

In Chapter One, I present an overview on the impacts of arthropod pests and the requirements to be satisfied when developing a model for pest management considering the spatio-temporal scale and the context of application. I discuss the different modelling approaches applied to pest ecology and the importance to realistically represent the biological system under investigation. In Chapter Two, I review the current state of the art on the development and the use of models supporting Integrated Pest Management. I discuss the modelling approaches, the fields of application, the benefits and the drivers influencing their adoption as tools for decision-making in crop protection. In Chapter Three, I present a physiologically-based model predicting the multi-annual phenology of the Japanese beetle (*Popillia japonica*). In particular, is introduced a realistic description of the overwintering process of the species and discussed the consequences on the predicted timing of emergence of the different life-stages. In Chapter Four, I present a physiologically-based model simulating the population dynamics of the fall armyworm (*Spodoptera frugiperda*). I discuss the implications linked to the introduction of a density-dependent control factor for the realistic simulation of intra-specific and inter-specific competition and the influence on the predicted dynamics of the species. In Chapter Five, I present a physiologically-based model simulating the potential distribution, abundance and activity of the Mediterranean fruitfly (*Ceratitis capitata*) in Europe under current and future climatic scenarios. In particular, I discuss the importance of capturing the non-linear relation between environmental drivers and the species' physiological responses as well as the consequences at the individual and at the population level. In Chapter Six, I briefly summarise the main results of the models presented and discuss their application for the assessment and the management of the risks linked to pests in different spatio-temporal scales and contexts of application. I also discuss how models for pest management might support decision-making in relation to the future global challenges we are called to face in the near future.

Keywords: pest management; invasive species; physiological models; agriculture; decision-making

RIASSUNTO

Gli artropodi parassiti rappresentano una delle principali minacce a livello globale a causa del loro impatto sulla produzione agricola e forestale e per gli effetti sulla salute degli animali, dell'uomo e dell'ambiente. In particolare, i parassiti delle piante influenzano le pratiche di gestione e lo sviluppo di tecnologie per assicurare la produzione alimentare. Con l'incremento della popolazione umana e del conseguente incremento della richiesta di cibo, un'importante sfida del futuro sarà quella di garantire la sicurezza e la disponibilità di risorse alimentari. Ridurre le perdite colturali causate dai parassiti e i costi diretti e indiretti legati alla loro gestione è un aspetto fondamentale per garantire la sicurezza alimentare globale. La pianificazione e l'implementazione di decisioni razionali e scientificamente valide per la gestione dei parassiti possono essere supportate dall'uso dei modelli. In particolare, i modelli a base fisiologica rappresentano utili strumenti in grado di fornire informazioni quantitative a supporto della loro gestione.

Nel presente lavoro, viene fornita una descrizione generale relativa allo sviluppo e all'applicazione di modelli per la gestione dei parassiti, ponendo l'accento sui modelli a base fisiologica e sulla loro applicazione a diversi contesti e su varie scale spaziali (dalla gestione locale a quella territoriale) e temporali (gestione a breve e a lungo termine).

Nel Capitolo Uno si descrivono gli impatti legati agli artropodi parassiti e si presentano i requisiti da rispettare per lo sviluppo di un modello applicato alla gestione dei parassiti, tenendo conto della scala spazio-temporale e del contesto di applicazione. Si discutono, inoltre, i diversi approcci modellistici applicati allo studio dell'ecologia dei parassiti e l'importanza di rappresentare in maniera realistica il sistema biologico investigato. Nel Capitolo Due si fornisce una revisione dello stato dell'arte legato all'uso di modelli per il supporto alla gestione integrata dei parassiti (*Integrated Pest Management*). Si discutono i diversi approcci, i campi di applicazione, i benefici ed i fattori che influenzano l'adozione di tali modelli per il supporto alle decisioni. Nel Capitolo Tre, viene presentato un modello a base fisiologica per prevedere la fenologia multi-annuale del coleottero Giapponese (*Popillia japonica*). Viene introdotto nel modello una descrizione realistica del processo di svernamento della specie e si discutono le conseguenze sulle tempistiche di emergenza predette per i diversi stadi di sviluppo. Nel Capitolo Quattro, viene presentato un modello a base fisiologica per la simulazione della dinamica di popolazione di *Spodoptera frugiperda*. Si discutono le implicazioni modellistiche legate all'introduzione di un termine densità-dipendente per la descrizione degli effetti della competizione intra- e inter-specifica sulla dinamica della specie. Nel Capitolo Cinque, viene presentato un modello a base fisiologica per simulare la distribuzione, l'abbondanza e l'attività della mosca mediterranea della frutta (*Ceratitis capitata*) in Europa, considerando diversi scenari climatici. In particolare, viene discussa l'importanza di descrivere le relazioni non-lineari esistenti tra le forzanti ambientali e le risposte a livello individuale e di popolazione. Nel Capitolo Sei viene fornito un breve riassunto dei risultati principali dei modelli presentati con riferimento alla loro applicazione per la stima e la gestione dei rischi legati ai parassiti in diversi contesti e scale di applicazione. Si discute, inoltre, il potenziale uso di tali modelli per rispondere alle sfide globali che saremo chiamati ad affrontare nel prossimo futuro.

Parole chiave: gestione parassiti; specie invasive; modelli fisiologici; agricoltura sostenibile; processo decisionale

CHAPTER 1 - Introduction

1. The importance of plant pests

One of the major challenges we are called to face in the near future is ensuring safe and secure food for a continuously increasing human population (Sharma et al. 2017). This means to produce more food, in a more sustainable way, and reducing pre- and post-harvest food losses due to pests. Plant pests are defined as any species, strain, or biotype of plant, animal, or pathogen injurious to plants or plant products. Their effective management represents a major challenge of our century (Kenis and Branco 2010). Pests have an impact on many human activities such as agriculture and forestry (Peshin et al. 2009; Pimentel et al. 2011). In addition, they negatively influence the provision of important ecosystem services (Kenis et al. 2012). Currently, the impacts of arthropod pests on global agricultural production worldwide has been estimated on around \$470 billion per year (Sharma et al. 2017). Direct costs to agriculture refer to direct yield losses or increased production costs. For instance, it has been estimated that between the 14% up to the 40% of global crop production is lost due to insect pests (Oerke 2006; Pimentel 2007). Among the direct costs, we find also the costs linked to pest management (e.g. through pesticides) that have been estimated at around €15 billion per year worldwide. Indirect costs refer to restriction to the trade of a certain product, influence on tourism, on public health, changes in land use, costs associated with research, education and training (Born et al. 2005). In addition to the impacts caused by established pests, the increasing rates of movement of humans and commodities worldwide are leading to an increased redistribution of thousands of species into new habitats. Eventually, some of these species might become invasive in the new habitat causing further impacts on crops, economic losses, biodiversity losses, and the disruption of habitats and ecosystems (Charles and Dukes 2008; Simberloff et al. 2013). For instance, it has been estimated that only in the United States, the costs linked to newly introduced arthropod pests reach \$20 billion yearly

(Pimentel et al. 2005). Climate change can also have a role on the invasiveness of pest species that are usually difficulty to quantify (Hellmann et al. 2008).

2. The two paradigms in the management of plant pests

Given the impacts that are caused by both established and invasive pest, it becomes fundamental to develop pest management strategies and control actions following precise and rational methodological and legislative frameworks. For instance, in Europe two are the main pillars dealing with the assessment of the risks and the control of pest populations: i) the EU Regulation 2016/2031, the so-called Plant Health Law, and ii) the Directive 2009/128/EC on the sustainable use of pesticides. The Plant Health Law sets up the rules for reducing the risks linked to the introduction, and the establishment of pests and the management of their outbreaks within the EU Territory. The assessment of the risks linked to pests is carried out through the Pest Risk Assessment (PRA) framework (EFSA PLH Panel 2018). The PRA relies on i) providing a scientifically sound and harmonised approach for the assessment of the risks linked to pests, ii) investigate the processes that caused a pest outbreak, and iii) apply quantitative methods for assessing the risks linked to pests. The PRA approach is based on the evaluation of the risks of entry, establishment, and spread of pests and on the assessment of their impacts in a certain area (Robinet et al. 2012). The results of the PRA is used for establishing the management measures to be applied in relation to the risks linked to the pest species (EFSA PLH Panel 2018). The PRA approach is particularly useful for: i) assessing the risks linked to the potential introduction and establishment of a pest, ii) assess the spread of an established pest, iii) assess the impacts from an economic, environmental, social and agricultural point of view.

The Directive 2009/128/EC provides the rules for ensuring the sustainable use of pesticides to reduce their impacts on the environment and on human health. The Directive requires the implementation of Integrated Pest Management (IPM) for controlling the diffusion and the impacts of pests (Caffi et al. 2017). Basically, the IPM approach aims at protecting plants against pests while reducing the impacts due to control interventions below levels that are considered ecologically and economically justifiable. The pillars of the IPM approach are i) ensure the routinely monitoring of pests, ii) use action threshold (i.e. the minimum population abundance that justifies the application of a pest control intervention), and iii) ensure the sustainable use of pesticides (Ehler 2006; Barzman et al. 2015).

3. The role and importance of models for pest management

The rational management of pests can be supported by models. A model can be considered as the representation of a portion of reality through considering the main elements involved and the interactions among them (Forrester 1994). If a model provides information and/or quantitative outputs that might be used for guiding the decision-making process it can be defined as a decision tool. The use of models can support decision-makers in solving complex issues while reducing the time and the efforts allocated to the analysis of a problem and the implementation of the best solution (Reddy 2018). Models can be used as a support to the decision-making process for both i) the assessment of the risks linked to pests within the PRA scheme and the comparative evaluation of risk management options, and ii) the design and the implementation of actions aimed at the control of pest populations within the IPM framework.

3.1. Models supporting PRA

Within the PRA scheme presented in EFSA PLH Panel (2018), the use of models allow the analysis of scenarios related to the status of the pest, the role of the drivers involved, and the evaluation of the effectiveness of the Risk Reduction Options (RROs) implemented. In each phase of the PRA procedure (assessment of entry, establishment, spread and impact of a pest), different modelling approaches can be implemented. For the assessment of the risks linked to the entry of a pest species, pathway modelling can be applied. These allow to quantify the risks of entry of a pest species through the assessment of the number of pest propagules that might be introduced in the risk assessment area (Douma et al. 2016). Basically, pathway models allow the estimation of the quantity of a pest entering a risk assessment area through the quantification of i) the trade flows, ii) the prevalence of the pest in a traded product, and iii) the effectiveness of pest removal due to the application of RROs. The assessment of pest establishment deals with the quantification of the number of pest populations that, once introduced in the risk assessment area, is able to persist in the future. Usually, spatial explicit models are used for the evaluation of the areas that are more suitable for the establishment of the species (Kearney et al. 2010; Kumar et al. 2014; Gilioli et al. 2014a; Ponti et al. 2015). The assessment of pest spread allow the quantification of the rate of diffusion and/or the population growth of the pest species within the infested area. Robinet et al. (2012) and Chapman et al. (2015) have provided a review on the different modelling approaches that can be applied for the assessment of pest spread. Some of the most used modelling approaches for assessing the potential diffusion of a pest are network models (Harwood et al. 2009; Koch et al. 2014), and reaction-diffusion models (Hancock and Godfray 2012; Kabir 2020). In the specific cases by which humans influence the diffusion of a pest, stratified dispersal models (Shaw 1995; Gilioli et al. 2013) are useful to simulate the natural dispersal of the species (e.g. flight activity, wind-mediated transportation) and the effects of human-mediated transportation (e.g. transport of infested materials or pest individuals). The assessment of pest impacts is generally carried out through models that provide a relation between pest population abundance and the impacts of the pest. Impacts can, for instance, be considered from an environmental (Kenis et al. 2012; Gilioli et al. 2014b) or an economic (Soliman et al. 2010; De Ros et al. 2015) point of view.

3.2. Models supporting IPM

Models have found their application also within the IPM framework. The decision-making process in IPM can be divided into three major levels: strategic (long-term), tactical (middle-term) and operational (short-term) decisions. At the strategic level, decision-making refers to the definition of the overall approach to be implemented against pests, and the major agronomic practices to be applied at both the farm level (e.g., crop rotation schemes) and at the field level (e.g., crop varieties to be planted etc.). Tactical decision-making refers to the definition of the methodologies to be applied for the implementation of the strategy, including the day-by-day decisions in response to the overall crop status (e.g., schedule monitoring and treatment campaigns). At the operational level, fast responses respect to crop conditions or to unpredictable events (e.g., unexpected rainfall event that delays the treatment of a pest) need to be defined and implemented. Models can support decision-making in IPM considering the three levels of implementation. At the strategic level, models can support decision-making on whether prevention and/or suppression measures are required. Prevention measures include strategies aimed at reducing the probability of pest occurrence and/or strategies aimed at reducing the crop's susceptibility to pest attack. Suppression measures refer to the application of cultural practices aimed at reducing pest's populations (Caffi et al. 2013). At the strategic level, models can support the definition of crop rotations schemes (Reichenbach et al. 2003; Dury et al. 2012), the assessment of the risks of crop diseases (Mahaman et al. 2003; Odile et al. 2010), the assessment of yield loss due to pests (Haverkort and Struik 2005), the definition of fertilisation plans (Radcliffe et al. 2009; MacCarthy et al. 2018), and support the implementation of suppression measures (Thysen 2007; Paolo et al. 2011). At the tactical level, models can support the optimisation of pest monitoring and protection interventions based on the concept of economic and ecological justification. The concept relies on the definition of pest abundance thresholds, above which a pest control application is economically and ecologically justified (Nutter et al. 1993). At the tactical level, models predicting the population dynamics (i.e. abundance) or the phenology (i.e. time of emergence) of a pest are useful for the scheduling and applying pest monitoring (Ravlin 1991), or control measures (Plant and Mangel 1987; Gilioli et al. 2016). At the operational level, models can provide relevant information on pesticides effectiveness, the physical-chemical characteristics of the pesticide and mode of action, the application rate and the means of pesticides distribution in the field (Bouma 2003; Barani et al. 2008; Gil 2009).

3.3. Developing and using a model: the modelling cycle

The development and the application of any model can be considered as a cycle in which a set of key steps must be followed and well documented (EFSA PLH Panel 2014). The cycle allows to iteratively reformulate parts of the model to increase model's performance and reliability. In this section, a general scheme of the modelling cycle for the development of models supporting the management of pests is provided. The modelling cycle is composed by the following steps: i) problem definition, ii) model conceptualisation, iii) model formalisation, iv) model calibration and v) model validation.

i) Problem definition: problem definition implies the identification of the main management issues related to the pest under investigation (e.g. control of local pest populations, assess the risk of establishment of a pest in a new area, etc.). This step sets the scene for the identification of the objectives of the model, the spatio-temporal scale, the scenarios of application, the type of outputs expected from the model, and how outputs can support the management of the pest.

ii) Model conceptualisation: a conceptual model provides a general and qualitative description of the system to be modelled. Model conceptualisation is based on the definition of the main objects (i.e., state variables) and processes characterising the biological system, as well as the main biotic or abiotic drivers influencing the processes. For instance, pest population dynamic models relies on the conceptualisation of the life cycle of the pest. Thus, a conceptual model can be represented by the definition of the state variables (i.e. population abundance in each developmental stage), the processes influencing the pest population dynamics (i.e., development, mortality and fertility), and the main drivers involved (i.e. temperature). Key information needed for model conceptualisation are related to i) the stage structure of the specie, ii) the number of generations per year (i.e., voltinism), iii) the main drivers influencing the stage-specific physiological responses, and iv) the physiological and behavioural adaptations to adverse conditions (diapause, developmental stages resistant to adverse climate, seek for refuge areas etc.).

iii) Model formalisation: the formalisation of a model consists on the representation of the conceptual model in terms of state variables, parameters and functions through mathematical equations and algorithms. The mathematical model can then be translated into a code useful to run simulations. Model formalisation consists of the definition and the quantification of state variables, forcing variables, model parameters and the equations describing the dynamics of the biological process. Quantitative values and functions representing processes can be obtained or estimated from existing literature, ad-hoc experiments or through expert knowledge. The availability and reliability of data are of paramount importance for ensuring model's performance and reducing uncertainty of the predicted outputs.

iv) Model calibration: model calibration is a procedure allowing the adjustment of some relevant model parameters to ensure a good fit between observed and simulated patterns. This procedure is fundamental when developing a model supporting decision-making. The calibration procedure must be well documented, thus listing the method used for calibrating model parameters, the patterns that are compared, the raw data used, the scenarios under which the model is calibrated, the parameters estimated, the biological relevance of the parameters, and the measure of the uncertainty linked with the estimation.

v) Model validation: model validation is a procedure that allows to evaluate the behaviour and the overall performance of the model. Models' performances can be evaluated through comparing model outputs with observed data. It is important to define the method used for validating the model, the patterns compared, the raw data used, and the scenarios under which the model is validated. Data used for model validation must not have been previously used for model calibration. The match between observed and simulated patterns cannot be "perfect", therefore the quality criteria to be met in this phase shall be defined before the implementation of the validation procedure. Once model validation proven satisfactory, the model can be applied in real contexts and used for management purposes, at least in areas that falls within the range of scenarios tested during model calibration and validation.

The modelling procedure described above, shall be considered as a cyclic and adaptive procedure. This means that, during each step of the modelling cycle, it is possible to re-define some or all of the modelling components according to new findings, the availability of new data, or until model outputs are considered reliable and robust enough to be used for pest management purposes (EFSA PLH Panel 2014).

4. Common modelling approaches applied to pest ecology, dynamics and control

Predictions on the potential pest population abundance, distribution and phenology represent key components for the application of models supporting decision-making in pest management. On this regard, empirical (i.e. statistical) and mechanistic (i.e. process-based) modelling are two of the most relevant modelling approaches for simulating pest ecology, distribution, abundance and applied to the management of pests (Rossi et al. 2012). Despite the fact that the distinction between empirical and mechanistic modelling approaches is being increasingly blurred (Madden and Ellis 1988), it is possible to highlight some general principles characterising the two modelling approaches.

Empirical models rely on the identification of the relationship between a response variable (e.g. pest distribution) and a set of independent variables (e.g. rainfall, temperature etc.) using mathematical or statistical approaches (Soberon and Nakamura 2009; Wiens et al. 2009; Warren 2012). Empirical models represent powerful tools for a first identification of the relationships existing within the biological system under investigation. Usually they are applied for the identification of the ecological niche of a pest and they provide information on the potential distribution of a pest species in the form of a habitat suitability index, through correlating species occurrence data and weather data (Peterson et al. 2012; Kumar et al. 2014). These indexes, however, do not provide information on the pest population dynamics and/or abundance, which are key elements in guiding decision-making in pest management (Abrol and Shankar 2012; Gilioli et al. 2017; EFSA PLH Panel 2018).

On the other hand, mechanistic modelling approaches are based on the explanation and the description through mathematical equations and functions of the main objects (i.e. pests' developmental stages) and processes (i.e. development, mortality and fertility) characterising the biological system under investigation (pest population). Mechanistic models are powerful tools for investigating and describing the influence of biotic and abiotic drivers on pest life-history traits (Kearney et al. 2010;

Wainwright and Mulligan 2013). In addition, mechanistic models can provide quantitative information on the pest population abundance allowing their application for the management of pests at both the local and the area-wide spatial scales (Gutierrez and Ponti 2013a; Pasquali et al. 2015; Ponti et al. 2015). The main key features that make mechanistic models particularly useful for supporting decision-making in pest management can be defined as follows:

i) Ensure the realistic representation of the main processes underlying the biological system. The mechanistic modelling approach relies on the representation of key biological responses to environmental drivers at both the individual and the population level (Gutierrez 1996; Ponti et al. 2015). This is ensured through simulation of the individual's physiological responses to the environment and their consequences on population dynamics (Régnière et al. 2012b; Gilioli et al. 2016). Temperature-dependent responses are the most important for poikilotherm populations (Régnière et al. 2012a; Rebaudo and Rabhi 2018). However mechanistic models can account for all kind of influences of abiotic (e.g., relative humidity, rainfall) and biotic (e.g., availability of resources, control due to natural or artificially introduce natural enemies) factors influencing pest population dynamics, both in space and time.

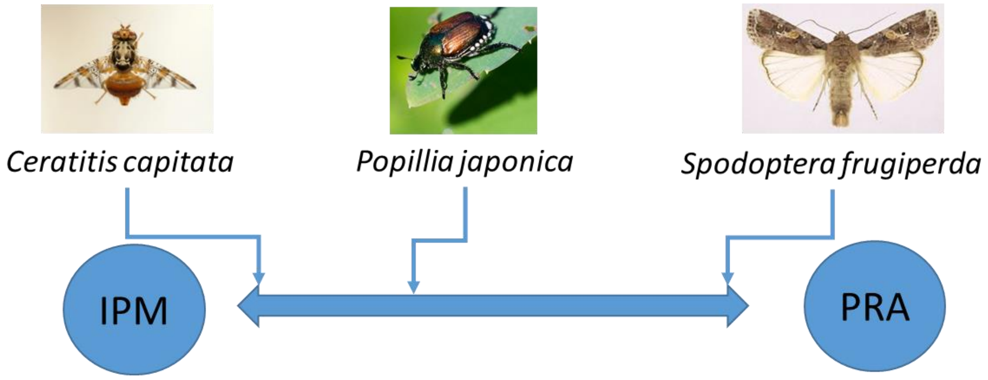
ii) Provide biologically sound and quantitative outputs. A fundamental aspect linked to mechanistic models is their capacity to provide biologically relevant and quantitative outputs. For instance, a common output provided by a mechanistic model applied for pest management is the abundance of individuals per area unit. This type of output benefits decision-makers as they are able to directly link model outputs to the potential impacts/risks linked to the pest species and to plan actions accordingly (Gutierrez and Ponti 2013b; Pasquali et al. 2015). In addition, modellers can easily evaluate model's performance through comparing model outputs against observed patterns (Gilioli et al. 2014a). Quantitative outputs allow also to increase model's transparency and provide an objective evaluation of the risks or the population pressure linked to the pest (EFSA PLH Panel 2018).

iii) Flexibility respect to the scale and context of application. The capacity of mechanistic models to represent the main processes influencing biological responses at both the individual and the population level, is at the basis of their flexibility in relation to their application under various scales and contexts. For instance, predictions on the daily (or sub-daily) pest population abundance in a certain location is fundamental for guiding the implementation of operational measures at the local level (e.g. IPM application). On the other hand, predictions on the potential distribution and abundance of the species (calculated as yearly average abundance) is a key element for guiding the assessment of the risks linked to an invasive species (e.g. PRA application). This flexibility allows mechanistic models to be applied to both IPM and PRA issues and to fine-tune the developmental procedure as well as the model's outputs according to model's purpose.

5. Aims of the Thesis

The overall objective of this Thesis is to present and apply a mechanistic modelling framework for the management of pests considering different contexts (from IPM to PRA) and scales (from local to area-wide pest management) of applications (Figure 1).

In Chapter Two, is presented a review on the benefits and the drivers linked with the application of models as decision tools in pest management, with particular emphasis on their application for IPM purposes. From Chapter Three to Chapter Five a set of case-studies related to the application of mechanistic models for pest management are presented. In each chapter, critical aspects of the pest's biology are considered, as well as the potential application of the model based on the spatial scale and the context of application. In Chapter Three, is presented a model predicting the phenology of the Japanese beetle (*Popillia japonica*) applied for the local management of the species. The model includes the simulation of the diapause termination process and its influence on the overall phenology of the species. In Chapter Four, is presented a model predicting the population dynamics of the fall armyworm (*Spodoptera frugiperda*) applied at the local level. The model includes the introduction of a density-dependent mortality term accounting for the realistic representation of intra-specific competition influencing the population dynamics of the species. In Chapter Five, is presented a model predicting the potential distribution and abundance of the Mediterranean fruitfly (*Ceratitis capitata*) applied at the continental level (Europe), with particular emphasis on the investigation of the potential role of temperature in ruling the physiology and the population dynamics of the species. In Chapter Six, I provide a general overview of the main results obtained and concluding remarks.



Integrated Pest Management (IPM)

- Applied to well established organisms
- Pest management mainly by private sector
- Prevention and mitigation of the impacts through the implementation of monitoring and pest control actions

Pest Risk Assessment (PRA)

- Applied to quarantine organisms
- Managed by public bodies
- Assessment of the risks of entry, establishment, spread and impact

Fig.1 Schematic representation of the two main contexts of intervention in pest management (PRA and IPM). The two contexts can be regarded as the extremes along a gradient in which pest species can be assigned based on its current status in a given region (e.g. from pests that are not introduced to pests that are well established in a certain area). The position of the three species along the gradient is purely indicative and it refers to the current status of the species in Italy. The three species reported represent the three case-studies considered in this Thesis.

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CHAPTER 2 - Critical Success Factors for the Adoption of Decision Tools in IPM

This Manuscript has been published in Agronomy

Rossi, V., Sperandio, G., Caffi, T., Simonetto, A., & Gilioli, G. (2019). Critical success factors for the adoption of decision tools in IPM. Agronomy, 9(11), 710. https://doi.org/10.3390/agronomy9110710

The author of the present Thesis has been involved in the conceptualisation and the design of the work, in performing literature review, and in drafting the manuscript.

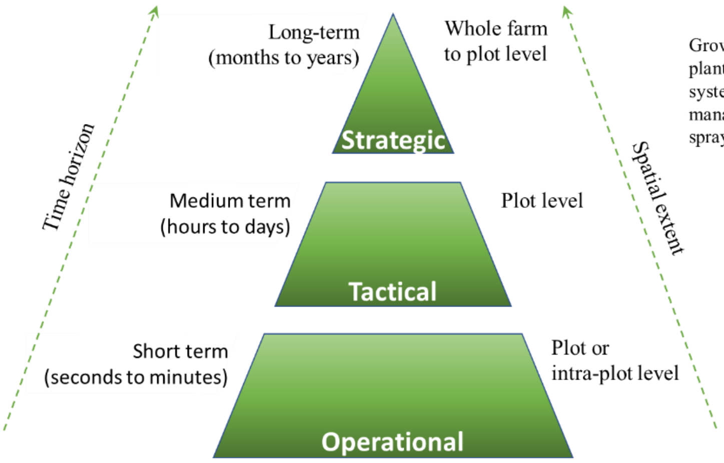
Abstract: The rational control of harmful organisms for plants (pests) forms the basis of the integrated pest management (IPM), and is fundamental for ensuring agricultural productivity while maintaining economic and environmental sustainability. The high level of complexity of the decision processes linked to IPM requires careful evaluations, both economic and environmental, considering benefits and costs associated with a management action. Plant protection models and other decision tools (DTs) have assumed a key role in supporting decision-making process in pest management. The advantages of using DTs in IPM are linked to their capacity to process and analyze complex information and to provide outputs supporting the decision-making process. Nowadays, several DTs have been developed, tackling different issues, and have been applied in different climatic conditions and agricultural contexts. However, their use in crop management is restricted to only certain areas and/or to a limited group of users. In this paper, we review the current state-of-the-art related to DTs for IPM, investigate the main modelling approaches used, and the different fields of application. We also identify key drivers influencing their adoption and provide a set of critical success factors to guide the development and facilitate the adoption of DTs in crop protection.

Keywords: decision tools; integrated pest management; decision support systems; pest management; crop protection

1. Integrated Pest Management: principles, barriers and benefits

Integrated pest management (IPM) aims at protecting crops against pests (i.e., any species, strain, or biotype of plant, animal, or pathogen injurious to plants or plant products [1]) keeping pesticides and other interventions to levels that are economically and ecologically justified, thus reducing or minimizing the risks for humans and the environment [2,3]. This concept was used for the first time by Smith and van den Bosch in 1967 [4] and nowadays, several policies and extension strategies linked to crop protection are inspired by IPM principles all over the world [5–7]. IPM relies on an integrated evaluation of the dynamic processes characterising the agricultural ecosystems and their components (e.g., plants, animals, environment, human intervention) towards a long-term sustainability of crop production and pest control [3,8,9]. Ensuring the routine monitoring of pests, the use of action thresholds (i.e., the minimum pest population abundance that justifies the application of a treatment [10]), and the rational and sustainable use of pesticides [11] are the pillars of IPM. According to Barzman and colleagues [3], IPM is based on eight principles: (1) Prevention of pest occurrence and suppression of pest populations; (2) monitoring of harmful pests; (3) informed decision-making; (4) priority to non-chemical methods; (5) multi-criteria selection of pesticides; (6) pesticide use reduction; (7) avoidance of pests resistance to pesticides; and (8) evaluation.

The application of IPM concepts and practices might lead to an increased profit for farmers while ensuring the successful management of pests [12–16]. Beyond successful control of pests, IPM might increase the overall farm resilience and contribute to increasing the natural capital and to preserve and/or foster the provision of ecosystem services [17]. Despite the potential benefits, IPM did not have the success expected and its application is still partial and jeopardized [18–20]. Farmers perceive IPM as complex, time- and labour-consuming, difficult to implement, and linked to lower or to unpredictable economic advantages with respect to conventional or organic farming [2,16,20,21]. Indeed, IPM may be knowledge-intensive and requires time and resources for planning activities, and integrating various sources of information for informed decision-making under uncertain conditions [22–25]. Complexity of decision-making is another important limiting factor preventing a wider implementation of IPM worldwide. The decision making in IPM concerns the complexity of the processes relating to the three levels involved (strategic, tactical, and operational) [26,27] (Figure 1). At the strategic level, the overall approach implemented against pests and the long-term decision-making at both the farm level (e.g., crop rotation) and at the field level (e.g., the plant variety to be grown) need to be defined. At the tactical level, the different methodologies that can be used to implement a strategy are considered, and it requires day-by-day decision-making in response to the crop overall status (e.g., treatment against a disease outbreak). At the operational level, fast responses with respect to the crop or within the crop conditions (e.g., treatment to be adapted to the size of the canopy) or unpredictable events (e.g., rainfall that delays the treatment of a pest) are selected and implemented.



Growing system (e.g., IPM vs organic); crop rotation; plants (species and varieties) to be grown; planting system and density; soil tillage; crop residue management; sanitation interventions; machinery (e.g., sprayer's type)

Scheduling of a crop protection action; crop protection measures to be applied; pesticide/s dosage for the specific intervention; micro-environment modifiers (e.g., agronomic interventions of fertilisation, irrigation, canopy management, etc.)

Setting of the sprayer; reaction to an accidental pesticide spill; reaction to changing weather conditions during a pesticide application

Fig.1 Relationship between the decision-making process and the type of operation in integrated pest management (IPM) at various spatio-temporal scales

Adequate pest monitoring, using suitable methods and tools, including field observations, use of insect/spore traps, and forecasting systems, are essential for guiding decision-making in IPM. From the end-users' perspective, access to up-to-date information related to crops and pests, and to the available scientific and technical innovations, is required. Furthermore, decision-making in IPM should consider the specific local conditions related to environmental variables, land-use schemes, farmers' socio-economic conditions, and other relevant information in order to make IPM programs flexible and adaptable to the specific needs [18,28]. To support decision-making (at strategic, tactical, and operational levels) in crop protection, a large number of tools predicting the dynamics of organisms harmful to crops and guiding their management have been developed, including population dynamics and epidemiological models, risk algorithms, intervention thresholds, decision rules, and decision support systems (DSSs). All these tools are collectively named decision tools (DTs) in this review. The overall scope of DTs for IPM is to support knowledge-based management of harmful organisms in agriculture. DTs help decision-makers in solving complex problems while reducing the time and the resources allocated for analyzing the available information and selecting the best solution [29]. Here, we provide a short review of the current knowledge and state-of-the-art related to the types of DTs supporting strategic, tactical, and operational decision-making for the management of crop pests. The aim is to investigate and define the combination of important factors required in order to reach the goal of effective DTs implementation, i.e., the so-called 'critical success factors' in IPM programs [30].

2. Decision Tools for IPM

Since 1980, an increasing number of DTs were developed for supporting farmers, practitioners, and farm managers in their decision-making at various spatio-temporal scales [31,32]. Thanks to the increasing availability of personal computers and modems at farm level, many government-funded programs were created worldwide with the aim to boost the introduction of these new technologies, enhancing the use of computers on farms, the development of pest and disease models, and the exchange of information [33]. In the European Union (EU), for example, some concerted actions (e.g., the European network for operational and tactical DSS on crop protection (EU.NET.DSS) and European cooperation in science and technology (EU-COST) actions were specifically supported for encouraging both the development and introduction of this new information technology as a common initiative). The epidemic prevention (EPIPRE) system for supervised integrated control of wheat diseases [34] represented one of the earliest experience of a computer-based advisory systems in Europe. These DTs have been developed and/or adapted by: (i) Public research and extension services; (ii) plant protection organizations; (iii) private companies/groups marketing products or services or providing consultancy to farmers. The number of DTs available for crop protection rapidly increased worldwide. In Europe, for example, the EU-funded project ENDURE reviewed 70 systems implemented in the EU in 2008 [35] while this number increased up to more than 200 in 2018, covering 32 crops, as result of the inventory performed by the SHARE4IPM (see Supplementary materials). DTs currently applied in pest management vary in terms of structure, complexity, and type of output provided. The most advanced DTs used in IPM programs are represented by the DSSs as they comprise an interconnected technological infrastructure including: (i) Sensors and tools for data collection; (ii) databases for data storage and management; (iii) tools for data analysis; (iv) automatic procedures for data interpretation; and (v) a user-friendly interface [27,36]. Currently, the access to DTs by users (e.g., farmers, agricultural advisers, policymakers) is uneven and restricted to particular areas and/or groups of users because of the diversity of the systems and the crops to be managed. However, DTs might be potentially used at a wider scale and applied to different agro-climatic conditions.

2.1 Benefits of Decision Tools in IPM

The main advantage of using DTs is linked to their capacity of processing, analyzing, and summarising relevant input data, making them available to the end-users in a suitable form (e.g., graphs, tables, etc.) for decision-support purposes [25,37]. DTs used in pest management provide several types of information as, for instance, predictions of the timing of pest potential emergence, pest abundance, and impacts as influenced by biotic and abiotic driving variables and the effects of management practices [25]. The main outputs of DTs are accessible to the end-user throughout a web-based user-friendly interface or by other means of communication (e.g., phone SMS, e-mails, newsletters, etc.) and targeted to their specific needs [27,32,38]. DTs can be fine-tuned for providing information that falls within the IPM framework (e.g., by providing text advices or suggesting best practices) and supporting the users in implementing the best strategies, tactics, and operations based on the available information [27]. Therefore, DTs represent a valuable contribution for the implementation of IPM at the field level as well as for supporting the implementation of large-scale crop protection policies.

2.2 Modelling approaches used in DTs

Mathematical and/or statistical models for pest population dynamics and disease epidemiology represent the basis of the vast majority of DTs applied in IPM and broadly, in agriculture [27]. A model can be defined as a simplified representation of a part of reality (e.g., an object, a process, etc.) based on the current available knowledge [39]. Empiric and mechanistic models are the most relevant categories of models in supporting decision-making in IPM:

- Empiric (data-based) models organizing data and standardising their relationship in terms of mathematical or statistical representations (e.g., correlation between pest abundance and air temperature). Empiric models provide useful insight to explore the relationships within a system that are unknown or poorly known;

- Mechanistic or process-based models describing a process (e.g., pest population dynamics/epidemics) based on the underlying functional mechanisms of the process. Mechanistic models are crucial to evaluate the biological responses as function of one or more environmental independent variables (e.g., air temperature, relative humidity, etc.).

The decision about the type of modelling approach to implement is fundamental when developing a DT. Data-based models were the most frequently used in the past. The first approaches based on empiric models were limited in providing explicit information on the underlying processes linking pest population distribution, abundance, and impacts with the environmental driving variables. Mechanistic models are highly reliable in investigating how biotic and abiotic drivers influence individual's life-history and, in turn, the overall population dynamics/epidemics. Furthermore, mechanistic models seek the dynamical description of the biological and physiological responses in relation to the population dynamics and epidemics, both in space and time, of the environmental drivers [40]. The bottom-up approach used in mechanistic models requires that the underlying mechanisms of the processes involved (population dynamics/epidemics) are previously known in detail [40]. Despite the need for detailed knowledge about the processes involved, the amount of data needed for the development of mechanistic models is usually lower relative to the data required for the development of empiric models that have been proposed more recently in agriculture [27]. Table1 shows a schematic representation of the main characteristics of data models and mechanistic models.

Table 1 Main characteristics of empiric and mechanistic models

Characteristics	Mechanistic Models	Empiric Models
Data Requirements	Data on biological response to external drivers are needed	Wide and representative field data are required for developing the model
Knowledge on the organism to be modelled	Detailed knowledge on biological processes is required	A specific knowledge on the pest is not needed
Explanatory ability	Seek for a mechanistic exploration of biological processes	Do not provide an explanation of the biological mechanisms underlying a process
Predictive ability	Prediction is possible in a wide range of agricultural contexts	No prediction is possible outside the range of input data

		(extrapolation) and under different agricultural contexts

However, the distinction between empiric and mechanistic models is becoming increasingly blurred. Several authors highlighted a continuum across empiric and mechanistic models, with mechanistic models including some data-driven components and empiric models containing mechanistic parts [41]. In addition to this, the capacity of empiric models in including causal processes among variables is increasing and, currently, their capacity of integrating the biology of the species to be modelled is approaching that of mechanistic models (e.g., machine learning). Thus, the choice of the modelling approach to be implemented in developing a DT can take advantage of a wide range of possibilities to be adapted in relation to knowledge and data availability, the level of complexity to be represented, and the type of output required.

Other tools that are implemented in IPM refer to optimization models and expert systems [31,40]. Optimization models focus on supporting the optimization of a process respect to some variables (e.g., keep crop losses due to pest below a certain threshold) while satisfying the constraints existing on some process components (e.g., economic and environmental sustainability). For example, these types of models are used in supporting economic decisions related to land use changes in a way that a certain field yields the highest rent [40] or for optimizing the management of pests [42]. Expert systems simulates human decision-making to solve complex problems in a very specific domain. They are computer systems reasoning through bodies of knowledge based on a set of defined rules. Expert systems are used, for instance, to support the identification of pests and suggest appropriate treatments [43] or for supporting the development of cropping plans and crop rotation schemes [44].

2.3 Intended use of DTs

The definition of the specific issues to be solved is of paramount importance when developing a DT. This requires a continuous interaction between modellers and users (e.g., farmers, consultants, technicians) in order to develop tools that might resolve specific agricultural or pest management problems. Nowadays, various types of DTs have been developed to respond to various issues related to pest management and crop protection [45]. Some of the most important issues currently addressed by DTs are discussed below. Some of these DTs address strategic decision-making (as in 2.3.1); others support tactic (as in 2.3.2 and 2.3.3) or operational (as in 2.3.4) decisions.

2.3.1 Decision on whether prevention and/or suppression measures are needed

The decision on whether to apply measures for prevention and/or suppression is important for the rational management of a pest. Prevention aims at reducing the probability that a pest develops populations that require control interventions by applying agronomic measures that make the environment less conducive for the pest and/or the plant less susceptible to pest attack. These measures include the use of resistant cultivars, the selection of the crop to be grown based on soil characteristics and land use, the regulation of soil drainage, etc. Suppression measures refers to the application of cultural practices (e.g., seed-bed sanitation, management of crop residue, soil tillage, application of chemical treatments) aimed at reducing the pest population during winter or in the inter-crop period, so that the pest development in the following season is delayed [46]. In this regard, DTs are developed to support strategic decisions to develop cropping plans, schedule planting and crop rotation schemes [47,48], assess the risks of crop diseases [43,49], simulate yield loss as a result of pest impacts [50], provide early warnings based on cultivar resistance [44], and support fertilization plans [51–54]. The information provided by DTs might also support the application of suppression measures, for instance, on whether to intervene based on the estimation of the pest population as influenced by environmental (e.g., temperature or rain) and agricultural (e.g., previous crop or soil type) drivers [55–58]. DTs might also be used for interpreting crop protection scenarios, including the potential influence of pests and providing management guidelines to farmers [59].

2.3.2 Decision on scheduling crop protection interventions

In IPM, crop protection interventions might be applied following specific rules (see for example Annex III of the EU Directive 128/2009). Methods for deciding whether and when an intervention is needed include the definition of thresholds for arthropod pests’ abundance and the estimation of the level of risk that a crop develops a disease, based on the concept of ecological and economic justification [10]. There are several examples of models developed for supporting the definition of best timing and frequency for the implementation of pest control measures on different crops, in relation to key environmental drivers. For instance, models are available in grapevine for European berry moth [60,61], vine mealybug, and American leafhopper [62], as well as for some diseases like downy mildew [63,64], powdery mildew [65], black rot [66], and botrytis [67]. These DTs allows to predict the insect phenology (e.g., time of emergence) and population dynamics (i.e., pest population abundance) as well as the time of disease outbreak, the infection risk, and the epidemic development. These tools allow the user to identify the optimal timing and frequency for the implementation of pest control measures according to the emergence of the stage to be treated and avoiding major impacts on the crop [68]. Similarly, DTs might also support the definition of thresholds to be used in IPM [69,70]. To increase model reliability and accuracy, DTs can include details related to pest biology (e.g., voltinism, overwintering strategies, stage of the pathogen), the role of biotic/abiotic drivers such as competition for space, photoperiod, temperature and humidity, seasonality, and host susceptibility [71,72], as well as information on the host plant physiology and phenology [60]. Inclusion of crop responses in the DT supports the assessment of potential impacts (in terms of crop yield and crop quality) due to pests [73–75]. For instance, a model simulating crop losses caused by pests developed through reverse mechanistic modelling [76] may support the implementation of management options and strategies, as well as quantify the gains that could be expected from management. This approach enables addressing individual pathogens/pests in a given crop, as well as combined pests.

2.3.3 Optimization of pest monitoring program

Crop pest monitoring is a pillar of IPM in order to minimize crop losses, optimize pest control, and reduce costs [77]. It mainly involves scouting for pests to determine if, when, and how intervention should occur. Given their costs and time requirements, crop pest monitoring activities must be planned in order to maximize the data gathered per unit of monitoring cost (e.g., visit the crop only when the likelihood of pests to emerge is high). DTs are useful for providing relevant information supporting pests' monitoring programs [78]. Seasonal temperature and rainfall patterns are major factors in ruling pest phenology, emergence, and incidence [79]; DTs supporting pest monitoring must take into account these environmental factors to provide early warnings on the likely onset of a pest or the emergence of the damaging stage of the pest, so that scouting can be organized accordingly [80,81]. Biology and ecology of the pest under investigation and the interaction with the physiology and phenology of the host plant are also important factors to be considered in pest monitoring programs and tools [60]. Examples of information provided by these DTs are the time for first occurrence of a certain pest [82], the estimate of immigrant pests from neighboring areas [83], and the onset of plant diseases such as Cercospora leaf spot of sugar beet, or leaf rust of wheat [84].

2.3.4 Supporting decision on pesticide use

In IPM, decisions about the use of pesticides should consider both the potential effectiveness of a pesticide to the specific pest to be managed and its specificity for the pest, to minimize the possible effects on non-target organisms, including humans. Chemical inputs shall be kept as low as possible while ensuring efficient pest control and the prevention of the development of resistant pest populations. DTs have been developed to support optimization of pesticide use. These include, among others: (i) tools for the selection of the pesticides based on multiple and combined factors such as the target organism/s, its/their developmental stage, the pesticide movement on plant surfaces and/or inside the plant tissues, etc. [85]; (ii) pesticide efficacy models [86]; (iii) tools for defining the application rate of pesticides like the tree row volume and leaf wall area calculators [87,88]; and (iv) tools for calibration and setting of sprayers to optimize pesticide distribution on crops [89].

Models simulating the potential effect of plant protection products on pest populations can provide useful insights on pesticide-induced mortality and effectiveness in reducing pest population pressure below a 'safe' threshold [90–92]. Pesticide effectiveness can be assessed under laboratory conditions by exposing the pest to several concentrations of an active substance and/or for different periods of exposure. For insecticides, the effectiveness can be evaluated considering both the instantaneous effects on pest survival or more complex effects involving pest life-history traits (e.g., pesticide effects on development or fertility) [90]. For fungicides, the effectiveness is linked to the physical mode of action (PMoA) of the product. PMoA can be evaluated under environmental controlled conditions with artificial inoculations to investigate the intensity and duration of pre- and post-infection activity, as well as pre- and post-symptom activity, rain fastness, and tenacity of the fungicide under investigation [85]. Recently, a new process-based model, which included functions' parametrization through experimental studies, experts' judgment, and technical advice, was elaborated to predict fungicide efficacy dynamics [85]. In order to develop more reliable and realistic DTs, data on pesticide effectiveness must be coupled with other relevant data related to: (i) Pesticide application (e.g., pesticide volume rate, pesticide application frequency); (ii) environmental degradation; (iii) pesticide intake rate; and (iv) chemical degradation/elimination rate in the body organism [93].

2.3.5 Estimate the environmental fate of pesticides

Informing decision-makers on pesticide fate can support the optimization of pesticide use in agriculture and also promote a reduction of their use. For this purpose, DTs can provide reliable information on pesticide fate, mobility, persistence, and risks to the environment based on relevant abiotic drivers [94]. To address these aspects, the contribution of environmental components should be considered, including the physical and hydrological characteristics of the soils (e.g., porosity, presence of water), the uptake from vegetation and the environmental drivers (e.g., temperature). For instance, relevant information on the composition of pesticides, their residues, and the formulation of mixtures are provided by the Danish Plantenet system [95]. Moreover, in UK a DT was developed in order to support government stakeholders in the optimization of agricultural pesticide-use policies [96], while in Germany, a DT was developed for assessing the risks to the environment caused by the use of plant protection products [97].

3 Drivers influencing the adoption of DTs for IPM

Even though many tools supporting decision making have been developed for crop protection, their use in IPM is still jeopardized and restricted to certain areas and/or to a limited group of users [22,98–100]; therefore, the impact of DTs on agricultural practices is still limited [32]. Frequently, the main use of DTs is indirect, via the activities performed by the agricultural advisors that are in charge of running the models in different areas and then distributing model outputs or model-based advices to the final users [25,101]. DTs faced, and are still facing [102,103], the so-called 'problem of implementation' that is defined as the 'lack of sustained use in a way that influence practice' [22]. Various authors have analysed the main factors influencing the adoption of DTs in agriculture [23,37,102]. These include their soundness, user-friendliness, ease of use, flexibility, frequency of update, as well as the real and/or perceived benefits envisaged and the previous knowledge of the user [104]. To summarize, under-utilization has been ascribed to two sets of reasons: (i) Technological limitations of decision-support tools and (ii) socio-economic constraints [23,25].

3.1 Technological constraints

Most of the technological constraints identified in the 1990s as potential obstacles to the adoption of DTs in agriculture have been solved by technological progress (i.e., wider access to personal computers, internet and web-based services) [101]. However, despite the widespread advancement and spread of ICT (information and communication technologies) that has occurred in recent years and the increased rate of adoption of these new technologies by farmers [105], some constraints still exist. In the last decade, attention has been directed to investigating the user's perception linked to the role of DTs in the decision-making process [22,102]. In agreement with Matthews and colleagues [102], it is observed that DT developers have focused too much of their attention on implementing advanced technological features, while lower priority was given to ensuring DT's credibility and their capacity to be integrated within the decision-making process.

3.2 Socio-economic constraints

Socio-economic constraints mostly refer to the real and/or perceived economic advantages that the adoption of a new technology (in our case, a new DT) can bring to the end-user. Kuehne and colleagues [106] developed a quantitative model to define 22 factors influencing adoption of innovations in agriculture, which can be useful for addressing the implementation problem. These factors are related to: (i) The ease and speed of learning to use the new tool and (ii) the role of end-users in increasing the perception of the relative advantage of adopting it. Other factors influencing the adoption of innovative DTs were investigated by Rose and colleagues [107] who highlighted the role of easiness to use, cost-effectiveness, efficiency, relevance to the user, and agreement with conformity demands. These factors have been confirmed in other studies [25,102,104,108]. Additional constraints refer to the type of user and its ability and willingness to invest time and efforts in learning and using the DT [23,109].

4 Towards wider adoption of DTs in IPM

Even though there are factors limiting the adoption of DTs for IPM, examples of their successful application with positive results on crops exist [108,110–112]. Below, we provide a set of critical success factors guiding developers in efficiently conceptualising and implementing DTs, and users selecting DTs to be implemented in practical IPM.

4.1 The DTs considers crop protection as part of a multicomponent system

DTs often concentrate on a single problem (e.g., a single pest or saving an individual spray), while farmers need to cope with a broad range of multiple issues all along the production system (e.g., multiple pests and their interaction with cropping practices) [23,113]. The cooperation between farmers and DT developers through participatory educational approaches [114] might be the best solution towards the development of DTs capable of supporting broad issues in IPM and to fine-tune DT's features to stakeholders' needs [115]. In the words of Wearin [115], 'Indeed, lack of education of IPM developers about the perceptions of farmers is probably a much greater obstacle to implementation than the reverse.’ The capacity of DTs to respond to specific stakeholders’ requirements is then of paramount importance towards the adoption of these tools within IPM schemes. The DTs for IPM must be able to tackle the issues of multiple stakeholders’ categories (e.g., single farmers, farmer cooperatives, big farming companies, advisors, consultants, policy-makers, etc.); this requires the consideration of the appropriate spatial (from local to area-wide) and temporal (from short- to mid-term decisions) scale in relation to the type of problem and the type of stakeholder. The lack of adoption of a DT is often the result of a failure in responding and tackling real farmers’ problems [27,32]. Therefore, involving end-users during the various developmental phases of the DTs might be a solution for solving the implementation problem and increasing the rate of adoption of DTs [103,116,117]. For instance, Oliver and colleagues [116] provided a protocol that included the involvement of UK farmers during the development of a DT within a participatory educational scheme.

4.2 The DT has been calibrated and validated

A key aspect to be considered when selecting a DT is whether the models implemented have been calibrated and validated. With calibration, we refer to the practice of estimating a model’s parameters by solving the model’s equations using observational data for both dependent and independent variables; the aim is to minimize the deviation between predicted and observed data. Once the calibration procedure proves satisfactory, the model must be evaluated in its capacity to provide reliable predictions of the biological processes it addresses. This procedure is called model validation and consists of comparing model outputs against field data (data must be different from those used in model calibration). Validation aims to demonstrate that the model is able to replicate real observations under different biotic and/or abiotic conditions (with respect to those used for model calibration) and guarantees the reliability of the model, as well as the possibility to generalize the model’s outputs under different contexts (also called robustness of the model). For providing valuable information to final users and facilitating the selection of a DT, validation should also include a comparison of different models simulating the same process, when available [118]. The validation process is often performed by the model's developers because it requires thorough knowledge about the model including the modelling approach implemented, the equations used, and the biological processes represented. Calibration and validation might be time-consuming and difficult to perform, especially when the DT accounts for multiple variables. Techniques of parameters' estimation (based on stochastic approaches and Bayesian methods) might facilitate the process of DT's calibration and validation [119]. Lack of extensive validation affects model's usefulness, limits its potential use, and it is questionable from an economic and ethical standpoint. Errors might be not only related to inaccurate estimation of pest's presence and abundance, but also linked to misdiagnosis of pests. Unfortunately, models may be published and released to the market without a proper validation, essentially because there are no shared 'minimum requirements' to be satisfied in order to consider a model as correctly validated [23].

4.3 The DT is open and transparent

When selecting a DT for its use in IPM, a careful evaluation of the model's algorithms and computer codes is important. This evaluation is sometimes difficult as computer codes are often not available for one of the following reasons: (i) The code is unknown to the end-user and not published; (ii) the code is published but only partially described; and (iii) the models are tweaked but without documentation of the improvements made. The lack of transparency relating to the computer code might cause difficulties during model calibration and validation by third persons (i.e., different from the developer) and contributes to the lack of adoption of DTs. Even though end-users are mainly interested on the accuracy and the reliability of the outputs provided, increasing the code's transparency (especially among modellers that might replicate and test the codes) might increase DT's trustfulness and thus the rate of adoption. Efforts in increasing the transparency of DT algorithms include the open-source and the knowledge-sharing approaches. The open-source approach implies that the DT and the related codes are: (i) Released and publicly available in open-source platforms and (ii) licensed under a general public license ensuring that users have the right to consult, modify, enhance, and redistribute the code.

The knowledge-sharing approach implies that technical and practical knowledge on the uses of the DTs are made available and exchanged between the developers, the final users, and the other interested parties [120]. This requires that: (i) Information linked to DTs and the code is provided to the end-users; (ii) final users are kept informed about the availability of knowledge; (iii) ensure that end-users have access to knowledge; and (iv) foster the access and the use of knowledge.

4.4 The DT is user-friendly

User-friendliness means the DT is simple for people to use [22,121]. The following is a list of some of the most important requirements a DT software should satisfy to guarantee user-friendliness:

- Learning time. Clarity of the instruction manual and limitation of the time requirements for learning how to use the DT. The organization of training, seminars, workshops, and continuous support to users (e.g., through extension services and experts) may facilitate the long-term adoption of DTs;
- Time spent for navigating in the DT to obtain the information. Some DTs are time consuming because of tedious input requirements or delays in data processing. The time demand on the user has been recognized as a paramount element in determining the adoption of DTs [22,98]. The time needed for inputting, processing, and analyzing data is often a shortcoming for several DTs, discouraging their use within the IPM schemes. For example, the users of the GPFARM (https://www.ars.usda.gov/plains-area/fort-collins-co/center-for-agricultural-resources- research/rangeland-resources-systems-research/docs/system/gpfarm/), a DT for strategic planning of the whole farm, declared not to have enough time to provide inordinate information requested as input by the system; moreover, the excessive run-time required discouraged adoption by producers and consultants;
- Timely information. The information should be provided in a timely manner in order to be effective within the decision-making process. For example, decisions about the control of grape downy mildew (*Plasmopara viticola*) are taken every 12 h during the most critical

periods of the season, and thus information supporting decision-making should be delivered by a DT considering this time interval;

- Time spent for input requirements. Relevant data supplying inputs to DTs are often related to: (i) Agro-meteorology; (ii) crop production and phenology; and (iii) pest presence and abundance. DTs must be supported by monitoring activities and sensors' networks timely supplying up-to-date data that are needed to run models and generate outputs. Difficulties in rapidly updating the databases (e.g., weather data) reduce the usefulness of the system to the growers;
- Clarity of the output. This is a crucial point for the adoption of a DT [22,121]. Nowadays, most of the DTs are delivered through web-platforms or applications integrating a user-friendly graphical user interface (GUI) allowing the user to navigate within the DT, and consult the main outputs and recommendations. Therefore, accessibility to the use of DTs can be highly increased by the development of easy-to-use GUIs, which can be evaluated following structured methodologies [22,121]. Furthermore, the information provided should not be redundant, difficult to read, or irrelevant to the end-user. Regarding this, Worm and colleagues [122] investigated the direct link between the rate of acceptance of a DT and the overall design of the system. For example, presenting the outputs of a DT in quantitative terms, might lead to difficulties in the interpretation of the information. In some cases, a graphic representation, indicating for instance the overall risks linked to a consequent management action, might be more informative for the end-user [23].

4.5 The DT is regularly maintained and updated

DTs require regular maintenance and updating. Providing periodic software updates and related users' guides and training has a positive influence on the adoption rate of a DT [24]. As for the DTs development, also updating DTs requires a multi-actor approach that involves multiple expertise ranging from Information Technology (IT) developers, modellers, ecologists, and agronomists. It also benefits from the direct involvement of end-users, especially for the definition of model outputs (in relation to their needs), the type of access required, and the communication means (e.g., through web-based applications, phone SMS, emails). The development of a DT needs adequate time and financial resources. This is frequently covered by ad-hoc research projects that should include the costs for maintaining the system after the end of the project and ensuring periodic update. When maintenance and updating costs are not provided by the specific project, these costs must be provided by end-users in the form of fees. For instance, Jones and colleagues [101] estimated the value of the fee to be paid for a DT supporting IPM in tree fruit by calculating the costs needed for the maintenance of the DT (including the training activities) and the number of users.

4.6 The DT supports and does not replace the farmer as decision-maker

An important aspect to consider when developing a DT is the definition of the role of the different actors (the DT itself, the service provider, the end-user, etc.) in the decision-making process. For example, the unsuccessful adoption of some DTs aimed at simulating human decision-making processes (e.g., expert systems) was attributed to the fact that the end-user felt left out of the decision-making process [22]. Indeed, the aim of a DT should be not to replace humans, but to provide a support to the end-users in making a rational decision based on the available information (and possibly the potential uncertainties) [22,37]. Therefore, the users should be considered as the main actors in the decision-making process, while the DT should provide relevant, suitable, and accessible information targeted to their own needs and integrated in their own decisional process [22,123]. The rate of acceptance and adoption of DTs aimed at supporting human decision making was higher when compared to DTs used as a proxy of human decision process [24].

4.7 The DT provides benefits to users

Once a DT has been calibrated and validated against real data, it is important to evaluate whether its use leads to real benefits in IPM programs. According to the food and agriculture organization of the United Nations (FAO), the adoption of any DT is highly correlated to the economic advantages (real or perceived) that it might bring [22]. To this aim, it is important to carry out observations in order to prove and possibly quantify, the advantages in terms of pest control, rational use of chemicals, increased crop yield, and crop quality. For example, the DT named vite.net (https://www.horta-srl.it/sito/en/portfolio-item/vite-net/), implemented for sustainable vineyard protection, provided a saving of 195 €/ha/year by reducing the amount of fungicides by an average of 24%, when compared to the standard practice in organic farming across Italy [32]. The same DT was tested across Europe and facilitated the same quality as the standard practice with a fungicide savings of 31.5% in IPM and 43.7% in organic farming, respectively, leading to an overall decrease of the costs linked to disease management of approximately 200 €/ha/year [124]. Farmers seem to be more prone to adopt (and thus trust) DTs for low-to mid-income crops (i.e., extensive or semi-intensive cropping systems). For intensive crops, farmers are more prone to increase the number of treatments in order to minimize the risk of yield loss (and thus income) [24]. However, exceptions exist as in the case of previously cited viticulture [32,125].

Frequently, users are sceptical about the real contribution of DTs to better decision-making for IPM. Therefore, the establishment of the practical impact and market credentials of a DT is really important [123], and evidence of the relevance the DT can have on the activities of potential users and the resulting benefits must be carefully demonstrated. For instance, Caffi and colleagues [126,127] demonstrated that the use of DTs for the management of powdery and downy mildews in viticulture led to a reduction on the application of pesticides by 30%. Considering that the costs of pesticide treatments against these diseases might reach 500 €/ha per year, a DT is able to decrease these costs by 150 €/ha per year. Unfortunately, demonstration of the real benefits generated by the DT are available only in a few cases. In these cases, a DT can gain farmers' trust if it is adopted by users that are considered as expert and trustworthy, or if it is widely used in the same or similar crop-growing area of the adopter. The introduction of a new technology (such as a DT) in the context of pest management represents a 'sustaining innovation' that needs to be supported by significant changes of approach and practices [128]. The introduction of a DT can be considered as a discontinuous technological advancement, as it requires the complete redesign of the working procedures within the farming system as, for example, a regular field monitoring or consultation of the DT. Therefore, the adoption of a DT requires, in addition to the evaluation of the potential benefits that might bring, the recognition of the influence that this tool might have on the overall organization of the farming system [128]. However, demonstration that the DT provides economic benefits does not ensure its wide adoption [116,129]. Kuhlmann [130] offered an economic explanation: A more effective reduction of agricultural costs can be reached by reducing farming inputs, investing in low-priced inputs, and reducing farm operations in respect to the adoption of a DT. However, also considering the potential benefit that a DT can bring in terms of long-term economic, social, and environmental sustainability may support its acceptability. From this viewpoint, the advantages of using a DT include also the support at: (i) Preserving the status of the agroecosystem; (ii) reducing the use of external inputs (e.g., plant protection products); (iii) enhancing crop yield and quality; (iv) meeting government and community expectations about landscape management; and (v) ensuring access to markets characterized by high standards related to environmental safety and product quality. Quantifying these not strictly economic benefits requires the adoption of multi-criteria approaches [118].

5 Concluding remarks

The efficient and rational control of pests, while ensuring agricultural productivity and economic and environmental sustainability, is at the basis of the IPM approach. The successful implementation of IPM requires proper incentives to farmers [131] and that information and tools for pest monitoring and for supporting decision-making are made available to professional users. These tools are designed to support the end-users by providing early warnings, facilitating pest monitoring, early diagnosis, forecasts about pest dynamics, and providing sound thresholds for the application of pesticides. In the framework of implementation of IPM, it becomes of paramount importance to provide to the end-users reliable, user-friendly, accessible, and up-to-date DTs while, if needed, adapting their outputs according to specific stakeholders' needs and/or to specific local conditions. In this paper, we reviewed the main factors influencing the adoption of DTs in IPM, which are related, among others, to technical constraints, farmers' attitude towards the adoption of new technologies and tools, the capacity of the DTs to solve farmers' real problems, reliability, and user-friendliness. We also provide and discuss the critical factors that should be considered by: (i) DTs developers for providing efficient tools, and by (ii) multiple users' types for selecting the DTs to be implemented in practical IPM at various spatio-temporal scales. These factors should be considered in the frame of developing reliable DTs for pest management and able to support decisional processes within IPM schemes implemented in diverse agricultural, geographical, and socio-economic contexts. Increasing the adoption of DTs in IPM by a wider public and facilitating their use under diverse contexts requires careful investments and the capacity to create synergies among stakeholders (DTs producers, policy-makers, farmers, etc.) and different expertise (modellers, agronomists, pathologists, entomologists, etc.) within a multi-actor approach. These expertise are also important for the continuous software maintenance and the periodic updates that are essential requirements for effective use of DTs in IPM. Knowledge sharing is a key principle for ensuring DTs openness and transparency. However, this is only possible if all the stakeholders' categories involved can envisage benefits. Finally, the organization of training, seminars, workshops, and continuous support to farmers (e.g., through extension services and experts) must be provided in order to sustain the long-term adoption of DTs in IPM.

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Supplementary materials

Table S1. List of decision tools implemented in the EU.

Crop	N. of pests	N. of DTs[1]	Pest/mycotoxin names
Almond	7	7	*Alternaria alternata, Eurytoma amygdali, Monilinia fructicola, Myzus persicae, Taphrina deformans, Tetranychus urticae, Wilsonomyces carpophilus*
Apples	5	9	*Argyrotaenia pulchellana, Cydia pomonella, Erwinia amylovora, Pandemis cerasana, Venturia inaequalis*
Asparagus	1	1	*Stemphylium vesicarium*
Barley	12	17	*Blumeria graminis, Deoxynivalenol (DON), Drechslera teres, Fusarium avenaceum, F. culmorum, F. graminearum, F. langhsetiae, F. poae, F. sporotrichoides, Microdochium nivale, Puccinia hordei, Rhynchosporium secalis*
Blackberries	1	1	*Drosophila suzukii*
Cherries	2	2	*Drosophila suzukii, Monilinia fructicola*
Cucurbits	3	4	*Golovinomyces orontii, Podosphaera xanthii, Pseudoperonospora cubensis*
Eldberry	1	1	*Drosophila suzukii*
Flowers (cut)	1	1	*Botrytis cinerea*
Grapes	10	19	*Aspergillus carbonarius, Botrytis cinerea, Drosophila suzukii, Erysiphe necator, Guignardia bidwellii, Lobesia botrana, Ochratoxin A, Planococcus ficus, Plasmopara viticola, Scaphoidues titanus*
Kiwifruit	1	1	*Pseudomonas syringae* pv. *actinidiae*
Legumes	10	10	*Ascochyta rabiei, A. pinodes, Alternaria alternata, Bruchus rufimanus, Colletotrichum lindemuthianum, C. lupini, Cydia nigrana, Helicoverpa (=Heliothis) armigera, Sitona sp., Uromyces phaseoli*
Loquat	1	1	*Fusicladium eriobotryae*
Maize	16	19	Larvae and adults of *Agriotes lineatus, A. obscurus, A. sordidus, A. sputator, Aspegillus flavus, Chaetocnema*

			pulicaria, Diabrotica virgifera, Fusarium graminearum, F. langsethiae, F. verticillioides, Ostrinia nubilalis, Peniciullium spp., Aflatoxins, Fumonisins, DON, T2/HT2
Oats	1	1	DON
Oilseed rape	5	5	*Brassicogethes aeneus, Ceutorhynchus napi, C. pallidactylus, Psylliodes chrysocephalus, Sclerotinia sclerotiorum*
Olives	2	6	*Fusicladium oleaginum, Bactrocera oleae*
Onions	1	2	*Peronospora desctructor*
Peaches	9	13	*Adoxophyes orana, Anarsia lineatella, Cydia molesta, Monilinia fructicola, Monilinia* spp., *Sphaerotheca pannosa, Taphrina deformans, Wilsonomyces carpophilus, Xanthomonas arboricola*
Pears	6	8	*Argyrotaenia pulchellana, Cydia pomonella, Erwinia amylovora, Pandemis cerasana, Stemphylium vesicarium, Venturia pirina*
Pistachio	1	1	*Septoria* spp.
Plums	2	2	*Cydia funebrana, Drosophila suzukii*
Potatoes	9	18	Larvae and adults of *Agriotes lineatus, A. obscurus, A. sordidus, A. sputator, Alternaria alternata, A. solani, Leptinotarsa decemlineata, Phthorimaea operculella, Phytophthora infestans*
Raspberries	1	1	*Drosophila suzukii*
Rice	5	5	*Cochliobolus miyabeanus, Pyricularia oryzae, Rhizoctonia solani*, Rice Tungro S and B viruses, *Xanthomonas campestris* pv. *oryzae*
Rye	3	3	*Puccinia recondita, Blumeria graminis, Rhynchosporium secalis*
Strawberry	1	2	*Botrytis cinerea*
Sugar beet	2	8	*Erysipahe betae, Cercospora beticola*
Tobacco	1	1	*Peronospora tabacina*
Tomatoes	7	11	*Alternaria solani, Helicoverpa (=Heliothis) armigera, Oidium lycopersici, Phthorimaea operculella,*

			Phytopthora infestans, Pseudomonas syringae, Xanthomonas campestris pv. vesicatoria
Triticale	6	6	*Puccinia triticina, P. striiformis, Blumeria graminis, Rhynchosporium secalis, Parastagonospora nodorum, Zymoseptoria tritici*
Wheat	22	31	*Blumeria graminis*, BYDV, *Fusarium avenaceum, F. culmorum, F. graminearum, F. langhsetiae, F. poae, F. sporotrichoides, Microdochium nivale, Parastagonospora nodorum, Puccinia recondita, P. striiformis, P. triticina, Pyrenophora tritici-repentis, Rhopalosiphum maidis, R. padi, Sitobion avenae, Zymoseptoria tritici*, DON, Nivalenol (NIV), T2-HT2, Zearalenon (ZEA)
TOTAL	155	217	

CHAPTER 3 - Modelling diapause and phenology of the Japanese beetle, *Popillia japonica*

The author of the present Thesis has been involved in the conceptualisation and the design of the work, in the management and analysis of both biological and temperature data, in the application of the model, in the biological interpretation of the results and in drafting the manuscript.

Abstract: We have developed a mechanistic, stage-structured model simulating the phenology of *Popillia japonica*. The model simulates the influence of soil temperature on the larval diapause termination and on the development rate function of post-overwintering larvae and pupae. Data used for the calibration and validation procedure refer to time-series adult trap catches collected by the Phytosanitary Service of Lombardy Region within the infested area of Lombardy (Italy). Data refer to 24 different locations (equally distributed in a calibration and in a validation dataset), and cover five sampling years from 2015 to 2019. The calibration procedure allowed to obtain biologically realistic parameters related to the sub-model simulating the diapause termination and to the development rate function of post-overwintering larvae. The model performed well in simulating the overall phenology of the adult stage and the beginning of adult emergence (calculated at the 2nd, at the 5th and at the 10th percentile of emergence) in nine out of twelve different locations in Italy, along five sampling years (from 2015 to 2019) and four ages since first infestation (from one to four years since first infestation). The model presented can support the definition of the best timing for the implementation of monitoring and treatment activities for the local and the area-wide management of *P. japonica*.

Keywords: *Popillia japonica*; pest phenology; pest management; pest control; mechanistic model

1. Introduction

The Japanese beetle (*Popillia japonica*) is an invasive and highly polyphagous pest belonging to the family of Scarabaeidae. The species has been reported on more than 300 host plants, including economic valuable crops and wild plants such as *Acer* spp., *Glyicine max, Prunus* spp., *Rosa* spp., *Vitis* spp., and *Zea mays* (Fleming 1972; Gyeltshen and Hodges 2005; Vittum 2020). Larvae grow beneath the soil at 15-20 cm depth and feed on the radical systems of many crops and weeds (Klein 2008). Adult individuals feed on the flowers and fruits of host plants. The species originated from North-Eastern Asia where it is native in Northern China and in Japan. In 1916 the species was introduced in North America (Fleming 1976) where it became invasive and a serious pest for turf grass (Potter and Held 2002). In the 1970s the species was found in Europe in Terceira island (Portugal) where it was able to establish and spread on other Azorean islands (Vieira 2008). In 2014 the species was first found in mainland Europe, in Italy on the Ticino Valley along the border between Lombardy and Piedmont Regions (Pavesi 2014). The species was also reported in Switzerland since 2017 (EPPO 2017; EPPO 2020). Although control measures were immediate, in Italy the species is now considered not eradicable.

Currently, the management of the species in Italy is under the official control of the National Phytosanitary Service and involves the Regional Phytosanitary Organisations which seek to contain pest populations and prevent the spread of the species. The control of *Popillia japonica* populations might benefit from the use of phenological models predicting the emergence of susceptible life-stages (e.g. pre- and post-diapause larvae and adults), thus allowing to schedule monitoring and treatment actions accordingly (Ascerno 1991; Samietz et al. 2007; Pasquali et al. 2019). On this regard, temperature-driven mechanistic models represent valuable tools for simulating the life-history strategies of *P. japonica* and for supporting the management of the species (Régnière et al. 1981). These models are able to simulate the life-history strategies of the species and how they are influenced by relevant environmental drivers (e.g. temperature, relative humidity etc.). In this work, we present a temperature-driven, mechanistic model predicting the diapause termination and the adult phenology of *Popillia japonica*. The model accounts for the realistic representation of the role of soil temperature influencing the life-history strategies of the species (Ludwig 1928, 1930; Fleming 1972; Gutierrez 1996; Régnière et al. 2012). The life-cycle of the species is modelled by means of development rate functions simulating the non-linear influence of soil temperature on the duration in days of each developmental stage. The model presented includes a sub-model simulating the role of soil temperature on the larval diapause termination and the potential impact on the overall species' phenology. Data used for calibrating and validating the model refer to time-series adult trap catches collected by the Regional Phytosanitary Service of the Lombardy Region (Italy) within the infested area in Lombardy. Through the calibration procedure we aim at estimating relevant parameters related to diapause termination and to the development of post-overwintering larvae. Through the validation procedure we test model's performance to predict the overall observed adult emergence and the beginning of the first flight calculated at the 2nd, at the 5th and at the 10th percentile of adult emergence. These two different aspects related to the phenology of the species are of fundamental importance for supporting the management of the species. Predictions on the overall adult phenology allows to determine the whole period of emergence of the adult stage and to estimate periods of major increase in population abundance. This is basically is done through measuring the slope of the cumulated emergence curve. Predictions on the beginning of the first flight allow to timely schedule and implement monitoring and control measures for the management of the species. Finally, we discuss model's performances in relation to the biological relevance of parameters obtained, and propose directions for future research.

2. Materials and Methods

2.1 Model development

2.1.1 Conceptual model and model assumptions

The model presented simulates the phenology of post-overwintering larvae, pupae and adults of *P. japonica*. The model includes two sub-models: i) a sub-model (M1) simulating the role of temperature on the termination of the diapause period of the larval stage, allowing the development of post-overwintering larvae, and ii) a sub-model (M2) simulating the development of post-overwintering larvae and pupae, and the emergence of the adult stage. The model requires setting the initial conditions expressed as the initial age distribution of diapausing larvae. In all the simulations, the model initiates with 100 larvae at the beginning of their development. This allows to include the time required to complete the development of post-overwintering larvae during winter and spring. This is in line with current knowledge on the life cycle of the pest, where it is reported post-overwintering larval development may end from May to July depending on local weather conditions (Potter and Held 2002; Marianelli et al. 2018; Shanovich et al. 2019). We assume the development rate function of larvae during the diapause period being equal to zero. This is in line with the results of Ludwig (1928) that reported a complete inhibition of larval development, at least during the winter period. Soil temperature is one of the main drivers influencing the species' diapause induction and termination as well (Ludwig 1932, 1939). Thus, in the sub-model M1 we simulate the process of diapause termination triggered when the average soil temperature of the last 15 days is above a soil temperature threshold T_{La}. The control period of 15 days is introduced to simulate a period of latency between the occurrence of favourable weather conditions and activation of physiological responses among larval individuals. Once the diapause termination occurred, individuals within the larval stage begin with their development process as post-overwintering larvae. The sub-model M2 simulates the development processes of post-overwintering larvae and pupae, and the transfer of individuals among stages. The output of M2 is represented by the cumulated percentage of emergence of adult individuals, ranging from 0% (no adult emergence occurred) to 100% (all adults are emerged). During the calibration procedure we estimate the soil temperature threshold triggering diapause termination T_{La} and the parameters related to the development rate function of post-overwintering larvae. We introduce the condition that T_{La} and the minimum temperature threshold allowing the development of post-overwintering larvae must be equal.

2.1.2 Mathematical model

The yearly phenology of *P. japonica* is simulated through a mechanistic, stage-structured demographic model based on the Kolmogorov equation (Gardiner 1985; Buffoni and Pasquali 2010). The model allows to simulate the influence of soil temperature on individuals along three developmental stages i, larvae ($i = 1$), pupae ($i = 2$) and adults ($i = 3$). The physiological age x of an individual is defined as the proportion of individual development within a stage (Buffoni and Pasquali 2007, 2010), with $x = 0$ representing beginning of the development and $x = 1$ refers to the age at the completion of the development within a stage. In a stage *i* the individual physiological age varies according to a stage-specific development rate function $v^i(t)$ (see section 2.3). A description of the Kolmogorov equation used for simulating pest population dynamics and phenology is presented in (Gilioli et al. 2016; Pasquali et al. 2019, 2020). The full mathematical description of the model presented here can be found in the Supplementary materials.

2.2 Data

2.2.1 Data on adult emergence

Time-series monitoring data used for model calibration and validation are collected by the Regional Phytosanitary Service of the Lombardy Region (Italy) carried out from 2015 to 2019. A hexagonal mesh has been superimposed on the area potentially interested by the presence of the species. Each hexagon has a surface of 5.42 km^2 and it represents the spatial unit considered in our study (hereinafter, cell). In each cell, the adult monitoring activity is performed using pheromone-baited Trecè traps. Traps have been inspected, emptied and individuals have been counted on a weekly or bi-weekly basis. Within each cell we have calculated the cumulated percentage of emergence of the adult stage, as the relative cumulated adult abundance in each sampling period respect to the total amount of adults collected in the whole flight period (from 0% to 100%). For the purpose of our study, we have selected a subset of data covering the whole flight period of the adult stage (i.e. approximately from May to October).

2.2.2 Environmental drivers

Yearly soil temperature (depth 10 cm) at an hourly temporal resolution are used as input data in both M1 and M2. Being aware about the vertical movement performed by *P. japonica* larvae within the soil during the season (Hawley 1944), we use soil temperature data at 10 cm depth as a rough approximation of the overall vertical distribution of larvae and pupae during the whole period of presence of the stages (e.g. from January to May) considered in the model (Fleming 1972). Temperature datasets from the first two soil layers available (depth 3.5 cm and depth 17.5 cm) are extracted from the ERA5 land hourly data (Muñoz Sabater, 2019). Temperature data are vertically interpolated using inverse weighting distance in order to obtain soil temperature at a soil depth of 10 cm. Horizontal interpolation using inverse weighting distance is used to obtain soil data at the centroid of each cell considered in the present study.

2.3 Development rate functions estimation

The development rate functions $v^i(T)$ are defined for post-overwintering larvae and the pupal stage. The development rate functions are defined by the Brière function (Briere et al. 1999).

$$v^i(T) = \begin{cases} r^i T\left(T - {T^i}_{inf}\right)\sqrt{{T^i}_{sup} - T} & {T^i}_{inf} \leq T \leq {T^i}_{sup} \\ 0 & otherwise \end{cases} \tag{5}$$

where r^i is an empirical constant, ${T^i}_{inf}$ and ${T^i}_{sup}$ are the lower and the upper developmental temperature thresholds respectively. Data related to the duration (in days) of the pupal stage are collected from Ludwig (1928) that tested the duration in days of pupae in laboratory studies conducted in climate chambers under different constant temperature conditions. We used these data for estimating parameters r^i, ${T^i}_{inf}$ and ${T^i}_{sup}$ of the temperature-dependent development rate function of pupae using least square method through the function `lsqcurvefit` in MATLAB Version R2018a. The termination tolerance on the first-order optimality is set at 10^{-6}. The development rate function of larvae during diapause is set equal to zero. Parameters of the Brière function for post-overwintering larvae are estimated during the calibration phase, following the procedure explained in Section 2.4.1. Parameters of the estimated development rate functions used in this study are presented in Table 3.

2.4 Model calibration and validation procedure

A subset of 12 locations are randomly selected and used for model calibration (calibration dataset) and a subset of 12 locations are randomly selected and used for model validation (validation dataset). In both the calibration and the validation datasets we have ensured that cell selection includes five different years (years 2015, 2016, 2017, 2018 and 2019) and four different ages since the first infestation of the species (from one to four years since the first infestation of the cell). Note that the same cell can be selected multiple times within both the calibration and the validation dataset. If this happens, the sampling year (and thus the age of first infestation) are obviously different. This procedure allowed to calibrate the model's parameters and test model's performances considering the role of different spatial contexts, weather conditions and ages since first infestation. The result of the random cell selection is presented in Table 1.

Table 1 Results of the random selection of locations for the calibration dataset and the validation dataset.

Calibration dataset					
Id location	**Cell**	**Lon**	**Lat**	**Sampling year**	**Year since first infestation**
1	1	8.710	45.526	2017	1
2	2	8.960	45.537	2019	3
3	3	8.737	45.694	2017	2
4	4	8.710	45.616	2015	1
5	5	8.821	45.458	2016	1
6	6	8.738	45.514	2016	2
7	7	8.625	45.762	2019	4

8	8	8.765	45.593	2017	3
9	9	8.821	45.346	2018	2
10	10	8.792	45.717	2018	3
11	4	8.710	45.616	2018	4
12	11	8.821	45.368	2019	4
Validation dataset					
13	5	8.821	45.458	2019	4
14	12	8.821	45.526	2018	3
15	13	8.793	45.604	2017	2
16	14	8.821	45.503	2016	1
17	15	8.737	45.604	2015	1
18	16	8.682	45.627	2016	2
19	4	8.710	45.616	2017	3
20	17	8.794	45.357	2018	2
21	12	8.821	45.526	2019	4
22	18	8.960	45.627	2019	3
23	19	8.820	45.728	2019	2
24	20	8.765	45.548	2016	1

2.4.1 Calibration procedure

The model calibration procedure consists in the estimation of the soil temperature threshold T_{La} that triggers the termination of the diapause period in M1 and the parameters r^1, $T^1{}_{inf}$ and $T^1{}_{sup}$ of the development rate function of post-overwintering larvae used in M2. Parameters are estimated through the minimisation of the squared distance between the estimated and the observed cumulated adult emergence of *P. japonica* (least square method) using time series data of the calibration dataset. The minimizations are performed using the MATLAB function `fmincon`, with the function tolerance set at 10^{-12} and the step tolerance set at 10^{-30}. In Table 2 are presented the lower and the upper bounds used for the exploration of the parameters. Bounds are chosen in order to obtain biologically realistic parameters based on the available knowledge on the life-history strategies of the species (Ludwig 1928; Fleming 1972; Régnière et al. 1981; Potter and Held 2002). Beyond the bounds, another condition that must be respected during the calibration procedure is that the values of parameters T_{La} and $T^1{}_{inf}$ must be equal. This in order to link the temperature related to diapause termination to the minimum temperature requirements allowing the development of post-overwintering larvae.

Table 2 Lower and upper bounds related to the parameters to be estimated during the calibration procedure.

	$\hat{r}^1$	$\hat{T}_{inf}{}^1$	$\hat{T}_{sup}{}^1$	T_{La}
Lower bound	$1.00 \cdot 10^{-5}$	11	32	11
Upper bound	$6.00 \cdot 10^{-5}$	16	38	16

Full mathematical details on the procedure used for model calibration is presented in Supplementary materials. The resulting parameters (presented in Table 3) will be used during the validation procedure.

2.4.2 Validation procedure

Model validation consists of testing the model's capacity to simulate two fundamental aspects of the phenology of the species. These are the cumulated emergence of the adult stage and the beginning of adult first flight. The model is validated using adult trap catches data of the validation dataset. The indexes used for testing model's performances are the mean squared distance between simulated and observed phenological curves (obtained as the average of the mean quadratic distances over the cells considered), and the difference between the simulated and the observed beginning of adult first flight measured at the 2nd, at the 5th and at the 10th percentile of adult emergence. Data related to the phenology of *P. japonica* are discrete in time as they have been collected on a weeky or bi-weekly basis. In order to allow fine comparisons between the simulated and the observed beginning of adult emergence, it is important to obtain a continuous adult cumulated emergence curve. The latter is realistically obtained through fitting cumulative Erlang distribution functions on emergence data (Curry and Feldman 1987). In Supplementary materials we report the results of the Erlang function fitting on the time-series data of the validation dataset. This allowed to make comparisons between the observed and the simulated beginning of adult emergence.

3. Results

The model calibration procedure allowed to obtain T_{La} and the parameters of the development rate functions of post-overwintering larvae that ensure the best fit between simulated and the observed emergence of the calibration dataset. A summary table showing the parameters resulting from the calibration procedure and the parameters of the development rate function of pupae fitted from the data presented in Ludwig (1928) is presented in Table 3. The mean squared between simulated and observed cumulated adult emergence of the validation dataset is $4.35 \cdot 10^{2}$. The graphical results are reported in Supplementary materials.

Table 3 Summary table showing the parameters used in the present study and the results obtained during the calibration procedure.

Stage	$\hat{r}^{i}$	$\hat{T}_{inf}{}^{i}$	$\hat{T}_{sup}{}^{i}$	T_{La}
Post-overwintering larvae	$4.96 \cdot 10^{-5}$ [a]	15.8 [a]	32.0 [a]	15.8 [a]
Pupae	$8.36 \cdot 10^{-5}$ [b]	11.4 [b]	39.1 [b]	N.A.

[a] Parameter estimated during the calibration procedure.

[b] Parameter estimated from laboratory data collected from Ludwig (1928).

The model validation procedure allowed to make comparisons between the observed and the simulated adult phenology. The graphical results of the model validation procedure is showed in Figure 1. The mean (± 95 C.I.) squared distance between observed and simulated adult phenology is

$6.04 \cdot 10^{2}$ (± $3.07 \cdot 10^{2}$). The mean (± 95 C.I.) difference in days between the simulated and the observed beginning of adult emergence is -5.49 (± 4.09), -5.10 (± 3.64) and -4.06 (± 3.30) for the 2nd, the 5th and the 10th percentile, respectively. The model performed particularly well in predicting the observed beginning of adult emergence in nine out of 12 locations with absolute differences in days between the simulated and the observed beginning of adult emergence less than 6.94, 7.61 and 8.00 on the 2nd the 5th and the 10th percentile, respectively. High discrepancy between the simulated and the observed beginning of adult emergence is found in three out of 12 locations with absolute differences in days up to 19.10, 17.07 and 13.50 on the 2nd the 5th and the 10th percentile, respectively. In general model's predictions are anticipated respect to the observed beginning of adult emergence. This is particularly relevant on the 2nd percentile where the simulated emergence is anticipated from 0.00 to 19.10 days respect to the observed emergence. The degree of anticipation reduces as we move to the 5th (from 1.28 to 17.07 days) and to the 10th (from 1.77 to 13.50 days) percentile. Only in three out of 12 locations the simulated emergence is delayed respect to the observed emergence. The delay in the simulated beginning of the first flight respect to observations is up to 1.78, 2.28 and 4.58 days in the 2nd, the 5th and the 10th percentile, respectively.

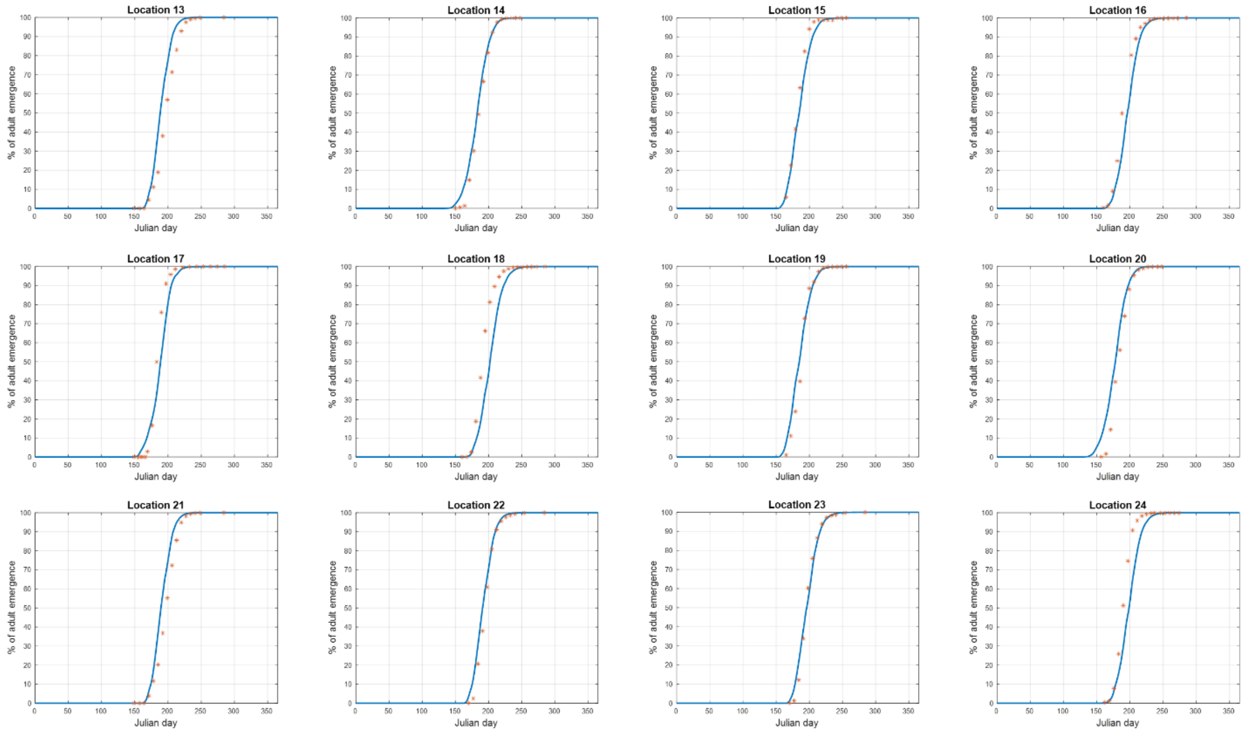

Fig.1 Graphical results of the validation procedure implemented in the 12 locations of the validation dataset. Asterisks represent observed adult cumulated emergence and the full line represents simulated adult emergence.

4. Discussion

In this paper, we present the first mechanistic stage-structured model simulating the potential role of soil temperature on the phenology of *P. japonica* that includes the description of the overwintering process of the species. The calibration procedure allowed to obtain biologically realistic parameters for the representation of the potential role of soil temperature in ruling the life-history strategies of the species. In particular the estimated parameters of the development rate functions of post-overwintering larvae $\hat{T}_{inf}{}^{1} = 15.8$ and $\hat{T}_{sup}{}^{1} = 32.0$ are within the lower and the upper mortality thresholds (15 °C and 35 °C, respectively) reported in Ludwig (1928) and in Fleming (1972). This suggests that post-overwintering larvae might be able to develop within these temperature extremes even though the development will be a lengthy process (e.g. we estimate 138 days at 31.9 °C) and probably resulting with the death of individuals. The parameter $\hat{T}_{inf}{}^{1}$ is higher than the lower developmental threshold of third instar larvae (10 °C) estimated by Régnière et al. (1981). However, it should be noted that Régnière et al. (1981) recorded slow developmental times at 14 °C, with pupation occurring only in the 10% of individuals after 220 days. This suggests that development is highly reduced at temperatures below 14 °C. The optimal temperature for the development of post-overwintering larvae is 27.8 °C with pupation occurring in 29 days at constant temperature. Both the optimal temperature and the related development rate are in line with what is reported in Régnière et al. (1981). The estimated temperature threshold triggering diapause termination $T_{La} = 15.8$ is higher than the temperature threshold of 10 °C proposed in the available literature (Hawley 1944; Potter and Held 2002). However as already discussed, development of third instar larvae at temperatures below 14 °C might be considered negligible (Régnière et al. 1981) while Ludwig (1928) reported no development of third instar larvae at temperatures below 20 °C. Therefore it is reasonable to consider

10 °C as a temperature threshold triggering larval movement upwards in the soil during the spring season looking for warmer temperatures and food, while the consistent development of third instar larvae starts at temperatures higher than 15 °C (Ludwig 1928; Fleming 1972). The 15 days period introduced as latency period for the termination of the diapause seems reasonable considering the delayed response of biological systems to environmental changes, especially when considering diapause and post-diapause processes (Koštál 2006).

Parameters estimated allowed to obtain good modelling performances in predicting the overall adult phenology and the beginning of the adult emergence in at least nine out of 12 locations used in the validation dataset. In the remaining three locations model's outputs are highly anticipated respect to the observed phenology of the species. Broadly speaking, model's predictions anticipate the observed phenology (nine out of 12 locations), in three locations model's outputs are delayed respect to observations. The overall advance of model's outputs respect to the observations can be reduced through the inclusion within the modelling framework of other drivers that might have an impact on the penology of the species. For instance soil moisture or larval feeding rate (Ludwig 1953), might play a role in larval development and overwintering period. Additionally, the variability in the vertical distribution of larvae and their movement in soil during the pre- and post-diapause period (Fleming 1972; Villani and Nyrop 1991; Potter and Held 2002) might have an influence on individual physiology and thus on the overall phenology of the species.

Further studies investigating the influence of relevant environmental drivers on the life-history strategies of *P. japonica* would be particularly important for a finer parameterisation and for increasing the accuracy of the model presented. This includes, for instance, setting up ad-hoc mesocosm experiments in order to quantify the role environmental drivers in ruling larval diapause and post-diapause period under environmental or controlled laboratory conditions (Ludwig 1953). However, working with larvae might be complex due to difficulties linked to sampling larvae in their natural environment and to rearing larvae and observing their physiological changes under natural or semi-natural conditions.

The quantitative outputs provided by the phenological model presented can be valuably used for supporting the management of the species *P. japonica*. The application of the model at the local level (i.e. point-based simulations) provide relevant information on the potential phenology of the species based on local temperature conditions. This might support decision-makers acting at the local level (farmers, farming cooperatives, private individuals etc.) in the timely implementation of pest monitoring and/or control activities based on the estimate emergence of the adults. The model can be also used for monitoring and control post-overwintering larvae populations. The model can be applied at the regional scale (i.e. area-wide simulations) in order to obtain maps of the phenology of the species. This might support decision-makers acting at the Regional level (e.g. National and Regional Phytosanitary Services) in the prioritisation of the areas of intervention, in the implementation of early-warning systems, and in planning actions aimed at the wider management of *P. japonica* populations. Further model's expansions will aim at simulating larval emergence in spring and the factors triggering larval dormancy period, in order to obtain a model covering the entire life-cycle of the species.

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Supplementary materials

Mathematical description of the model

Assuming the population of *P. japonica* being composed by three stages i, namely larvae ($i = 1$), pupae ($i = 2$), and adults ($i = 3$), the model is described by a system of partial differential equations

$$\frac{\partial \phi^i}{\partial t} + \frac{\partial}{\partial x}\left[v^i(t)\phi^i - \sigma^i \frac{\partial \phi^i}{\partial x}\right] = 0, \quad t > 0,\ x \in (0,1), \tag{1}$$

$$\left[v^i(t)\phi^i(t,x) - \sigma^i \frac{\partial \phi^i}{\partial x}\right]_{x=0} = F^i(t), \tag{2}$$

$$\left[-\sigma^i \frac{\partial \phi^i}{\partial x}\right]_{x=1} = 0, \tag{3}$$

$$\phi^i(0,x) = \hat{\phi}^i(x), \tag{4}$$

The function $\phi^i(t,x)$ is the number of individuals in stage i at time t with physiological age x. The term $v^i(t)$ represents the stage-specific development rate function. The functions $\hat{\phi}^i(x)$ represent the initial conditions of the model in terms of individual abundance within a stage. In all the simulations, the initial conditions are set to 100 overwintering larvae at the 1st of January. All simulations end at the 31st of December of the same year. The term σ^i is a diffusion coefficient, introduced to include the effects of stochasticity on the stage-specific development process.

The flux of individuals from stage i to stage $i + 1$ is represented by the functions $F^i(t)$.

$$F^i(t) = v^{i-1}(t)\, \phi^{i-1}(t,1), \qquad i = 2, 3.$$

The cumulated adult emergence is defined by the following non-decreasing function

$$Z^3(t) = Z^3(t - dt) + F^3(t), \qquad \text{with} \qquad Z^3(0) = 0.$$

Procedure of model calibration

Denoting by $N_j^3(t_i,\ r^1,\ T_{inf}{}^1,\ T_{sup}{}^1, T_{La})$ the adult abundance at location j at time t_i, for parameters r^1, $T_{inf}{}^1$, $T_{sup}{}^1, T_{La}$ of post-overwintering larvae we define the functional

$$Q\left(r^1,\ T_{inf}{}^1,\ T_{sup}{}^1, T_{La}\right) = \sum_{j=1}^{3} \frac{1}{R_j} \sum_{i=1}^{R_j} \left| N_j^3\left(t_i;\ r^1,\ T_{inf}{}^1,\ T_{sup}{}^1, T_{La}\right) - A^j(t_i) \right|^2$$

where $A^j(t_i)$ is the observed adult abundance at location j at time t_i and R_j is the number of available data for location j. Then, we find the optimal parameters $\left(\hat{r}^1,\ \hat{T}_{inf}{}^1,\ \hat{T}_{sup}{}^1,\ \hat{T}_{La}\right)$ looking for the minimum of Q, namely

$$\left(\hat{r}^1,\ \hat{T}_{inf}{}^1,\ \hat{T}_{sup}{}^1, \hat{T}_{La}\right) = \min_{r^1, T_{inf}{}^1, T_{sup}{}^1.\ T_{La}} Q\left(r^1,\ T_{inf}{}^1,\ T_{sup}{}^1, T_{La}\right)$$

Results of the calibration procedure

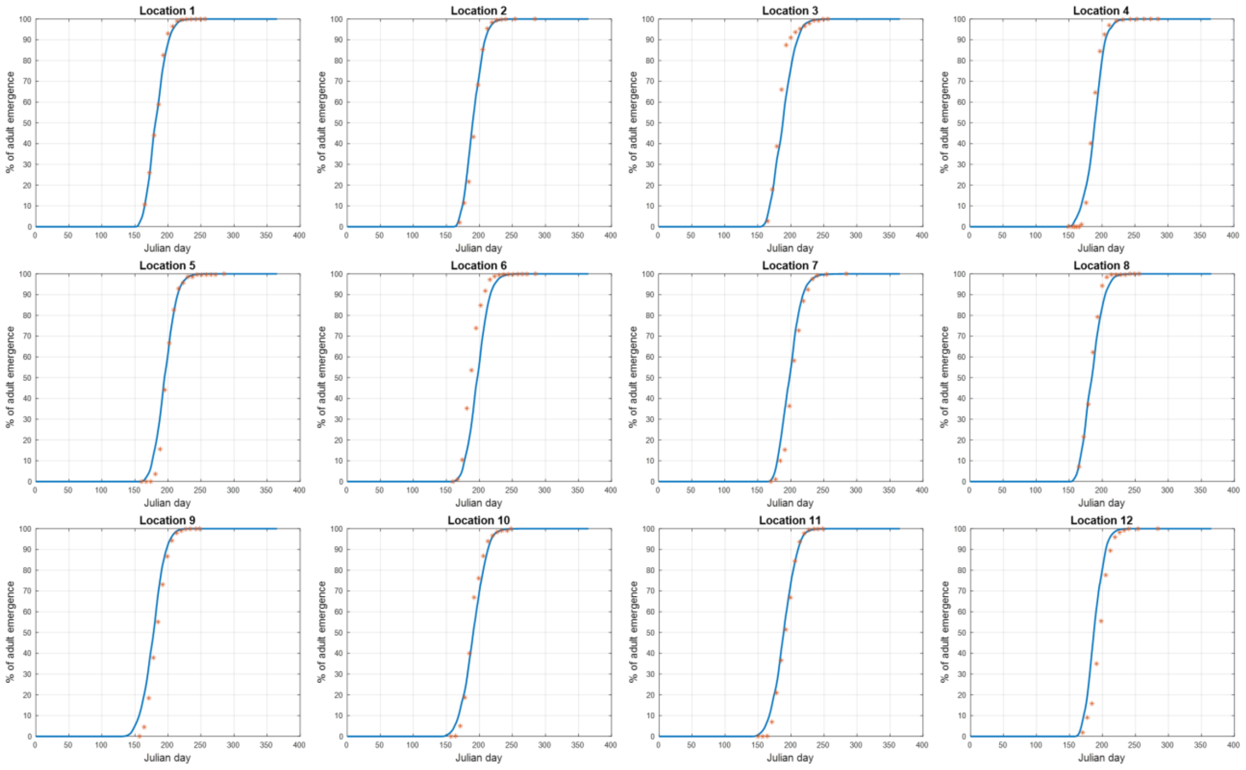


Fig.S1 Graphical results of the calibration procedure implemented in the 12 locations of the calibration dataset. Asterisks represent observed adult cumulated emergence and the full line represents simulated adult emergence.

Erlang distribution curve fitting on adult cumulated emergence data

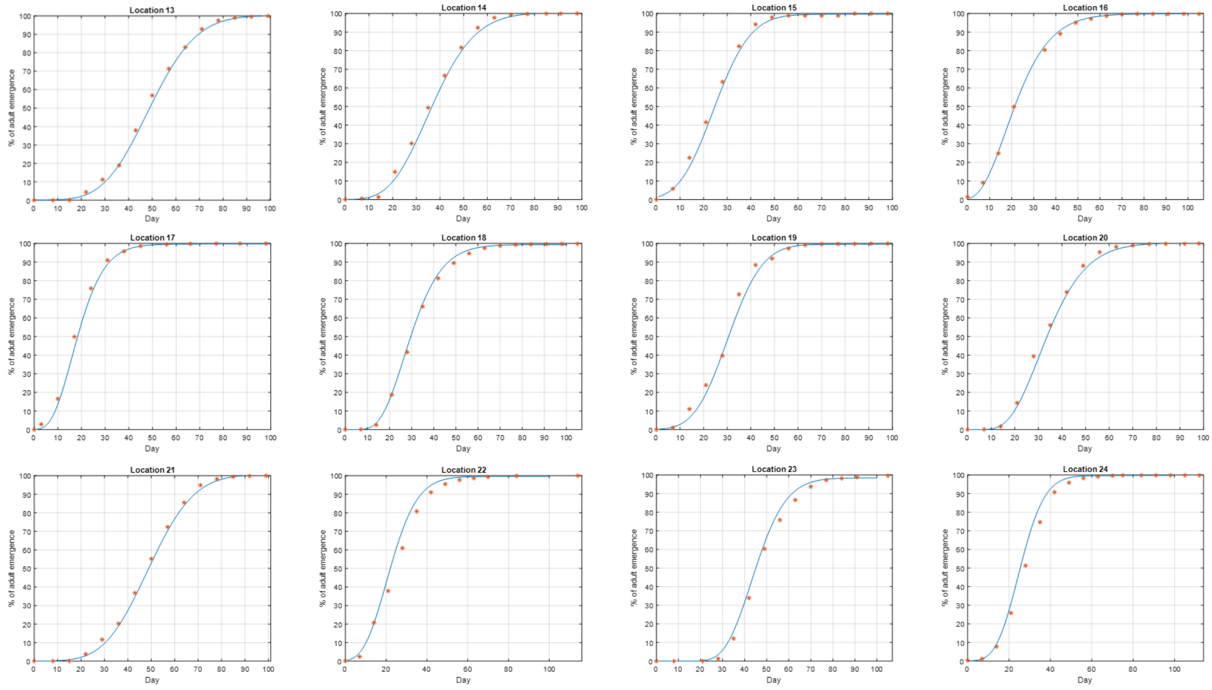


Fig.S2 Cumulative Erlang distribution functions fitted on adult emergence data of the 12 locations of the validation dataset. Asterisks represent observed adult cumulated emergence starting from the first day of sampling and the full line represents the estimated function.

CHAPTER 4 - A nonlinear model for stage-structured population dynamics with nonlocal density-dependent regulation: an application to the fall armyworm moth

The author of the present Thesis has been involved in the conceptualisation and the design of the work, in the management and analysis of both biological and temperature data, in the application of the model, in the biological interpretation of the results and in drafting the manuscript.

Abstract: The assessment and the management of the risks linked to insect pests can be supported by the use of physiologically-based demographic models. These models are useful in population ecology to simulate the dynamics of stage structured populations, by means of functions (e.g., development, mortality and fecundity rate functions) realistically representing the nonlinear individuals physiological responses to environmental forcing variables. Modeling population dynamics considering only the role of environmental variables might lead to populations that grow indefinitely depending only on the persistence over time of favorable environmental conditions. Since density-dependent responses are important regulating factors in population dynamics, we propose a nonlinear physiologically-based model describing the dynamics of a structured population in which a time-dependent mortality rate is coupled with a nonlocal density dependent term. The model is applied for simulating the population dynamics of the fall armyworm moth (*Spodoptera frugiperda*), a highly invasive pest threatening agriculture worldwide.

Keywords: Physiologically-based models; Pest management; Invasive species; Solvability of nonlinear PDEs; Numerical simulation; *Spodoptera frugiperda*

1. Introduction

Insect pests represent an important threat for agriculture and environment and pose serious issues linked to human health (Charles and Dukes 2014; Mazza et al. 2014; Paini et al. 2016). Among the most dangerous pests, the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) represents one of the main threats for agriculture worldwide (Day et al. 2017; Early et al. 2018). The species is known for its great migratory capacity that facilitates the spread of the species along wide areas (Kumela et al. 2019). It feeds on more than 180 host plant species including economic valuable crops such as maize, sorghum, rice and millets (Hogg et al. 1982; Oeh et al. 2001; Murúa and Virla 2004; Busato et al. 2005; Milano et al. 2008; Baudron et al. 2019; Wang et al. 2020). The species is native to the tropical and sub-tropical areas of South and North America. Since 2016, it has been reported in the African continent (Nigeria, Sao Tomè, Benin and Togo) where it became invasive (Goergen et al. 2016; FAO 2018). More recently, the species has been reported in India (Ganiger et al. 2018), Bangladesh (FAO 2019a), China (FAO 2019b), Myanmar (FAO 2019c), Sri Lanka (FAO 2019d), Thailand (IPPC 2018) and Korea Republic (IPPC 2019).

The high migratory capacity of the species and the risks to import infested plant products from countries with established population of *S. frugiperda* raise concerns for the potential introduction and establishment of the species in Europe (Early et al. 2018; EFSA PLH Panel 2018a). Various modelling approaches have been applied for the assessment and the management of the risks linked to *S. frugiperda* (Farias et al. 2008; Valdez-Torres et al. 2012; Rios et al. 2014; Prasanna et al. 2018; Early et al. 2018; EFSA PLH Panel 2018b; Garcia et al. 2019; Liu et al. 2020; Wang et al. 2020; FAO 2020). Physiologically-Based Demographic Models (PBDMs) are particularly useful to investigate the population dynamics of stage-structured populations (Gurtin and Maccamy 1974; Gyori 1990; Gyllenberg and Hanski 1992; Diekmann et al. 2001; Allen 2009; Ponosov et al. 2020). PBDMs account for the realistic representation of pests' physiological responses driven by environmental variables (Barfield et al. 1978; Gutierrez 1996; Garcia et al. 2019) at different spatial (from local to regional) and temporal (short to mid- long terms) levels (Di Cola et al. 1990; Gilioli et al. 2016; Rossi et al. 2019). In the present contribution we present a PBDM based on the Kolmogorov equation describing the population dynamics of the *S. frugiperda*. To our knowledge, this is the first PBDM describing the population dynamics of the species. In PBDMs, the physiological responses of individuals to environmental drivers are commonly modeled through functions (i.e,. development, mortality and fertility rate functions). The model presented here takes into account the nonlinear stage-specific responses of individuals to air temperature (Gutierrez 1996; Regniere et al. 2012; Ponti et al. 2015), and the effects on stochasticity of the development process of the individuals (Dautray and Lions 1988; Cushing 1992; Dautray and Lions 1992; Huffaker and Gutierrez 1999; Batchelder et al. 2002).

As already pointed out by Gurtin and Maccamy (1974) and Diekmann et al. (2001), there are some implicit difficulties linked to using temperature as the only driver ruling the dynamics of a population. The main shortcoming is represented by the fact that the solution of the model is unbounded and thus a population might potentially grow indefinitely depending on the persistence over time of favorable environmental conditions. Since the population growth is ruled not only by abiotic drivers (e.g. temperature, presence and availability of resources etc.) but also by biotic drivers (e.g. competition for resources and the effects of crowding) acting as density-dependent regulating factors, an indefinite population growth is biologically unrealistic (Sinclair and Pech 1996; Tamburini et al. 2013). In particular, the population dynamics of several insect species is regulated also by density-dependent factors acting on the survival of the species (Deangelis et al. 1980; Clother and Brindley 2000).This is also the case of *S. frugiperda*. Indeed, the species is known for the role of density-dependent factors, including larval cannibalistic behavior, in ruling the species' overall population dynamics (Barfield et al. 1978; Andow et al. 2015; Varella et al. 2015; Garcia et al. 2018).

In order to provide a realistic description of the population dynamics of the species under investigation, we consider a Kolmogorov equation perturbed by a temperature-dependent mortality rate coupled with a nonlinear and non-local density-dependent term. Many stage-structured population models with density-dependent mortality terms and nonlocal factors have been proposed in the last decades (let us quote, without any sake of completeness, e.g., Gyori (1990), Gyllenberg and Hanski (1992), Diekmann et al. (2001), Allen (2009) Robertson et al. (2018). However, on the basis of our knowledge, the Kolmogorov equation with a nonlinear and nonlocal density-dependent mortality term has not yet been addressed nor has its mathematical analysis been discussed.

The Kolmogorov equation with nonlinear and nonlocal density-dependent mortality term is highly nonlinear and faithfully embody three crucial biological aspects:

1. the simulation of the dynamics of a stage-structured population;
2. the representation of the stage-specific and nonlinear response of individid- uals to environmental drivers (i.e., air temperature);
3. the introduction of a density dependent control factor influencing the pop- ulation dynamics of the species;

Let us stress that some existing models can be recovered as special cases of the model considered in this paper (a detailed comparison can be found in Section 2).

The paper is organized as follows. Section 2 is devoted to the derivation of the model. In order to support with empirical evidence the introduction of the density-dependent mortality term, in Section 4 we apply the model to a case study by describing the population dynamics of the fall armyworm *Spodoptera frugiperda* and show that this new approach plays a crucial role in the description of the population dynamics. Numerical results are shown in Section 5, while in Section 6 we suggest future perspectives.

2. Model derivation

The fall armyworm *Spodoptera frugiperda* can be considered as a stage structured population (eggs, larvae, pupae and adults) with discontinuous stage structure(see, e.g., Kelpin et al. (2000), Buffoni and Cappelletti (2000), Abia et al. (2004), Angulo and López-Marcos (2004), Buffoni et al. (2004), Buffoni and Pasquali (2007)). The individual growth in a single stage is described by the physiological age $x \in [0,1]$ evolving along time $t \in [0,T]$, with $T > 0$. We denote by

$$\phi_s(t,x)\,dx$$

the average number of individuals at stage $s = 1, \dots, \mathcal{S}$, at time t with physiological age between x and $x + dx$, where dx indicates an infinitesimal variation of age. The strictly positive value $\mathcal{S} \in \mathbb{N}$ stands for the total number of growth stages: stages from 1 to $\mathcal{S} - 1$ are the immature ones (e.g., eggs, larvae, pupae) while stage S is the reproductive one.

The seminal von Foerster equation describes the population dynamic at stage s as

$$\partial_t \phi^s(t,x) + \partial_x \phi^s(t,x) = -M^s \phi^s(t,x), \qquad (t,x) \in (0,T) \times (0,1), \tag{1}$$

with boundary condition

$$\phi^s(t,0) = \int_0^1 G^s(y)\phi^s(t,y)dy, \tag{2}$$

and initial condition

$$\phi^s(0,x) = \phi_0^s(x), \tag{3}$$

where M^s and G^s denote the stage-specific mortality and fecundity rate, respectively, while the nonnegative function ϕ_0^s represents the initial abundance of each stage. In the last decades, several authors consider the von Foerster equation, suitably modified both by the introduction of time-dependent rate functions and density-dependent mortality term. We refer, e.g., to Gyori (1990), Gyllenberg and Hanski (1992), Diekmann et al. (2001), Allen (2009), Robertson et al. (2018).

Since the development rate among individuals may depend on environmental conditions, food, assimilation and genetic characteristics, Kolmogorov adopted a stochastic approach and modified the von Foerster equation (1)–(3) by taking into account the stage-specific development rate S^s, the diffusion parameters b^s, and by replacing the term $\partial_x \phi^s(t,x)$ with $\partial_x H^s(t,x)$, where

$$H^s(t,x) = S^s \phi^s(t,x) - b^s \partial_x \phi^s(t,x). \tag{4}$$

The so-called forward Kolmogorov equation is derived from the balance equation for the density function $\phi^s(t,x)$, it is an advection-diffusion equation with elimination, namely

$$\partial_t \phi^s(t,x) + \partial_x\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big) = -M^s\phi^s(t,x). \tag{5}$$

$$\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big)_{x=0} = F^s\int_0^1 G^s(y)\phi^s(t,y)\,dy, \tag{6}$$

$$\big(-b^s\partial_x\phi^s(t,x)\big)_{x=1} = 0, \tag{7}$$

$$\phi^s(0,x) = \phi_0^s(x). \tag{8}$$

The previous system (5)–(8) can be also interpreted as a one-dimensional Fokker-Planck equation. Denoting by F^s a stage-specific positive parameter, the boundary condition (6) models the reproduction process as an input condition at the beginning of the stage, i.e., at $x = 0$. On the other hand, the boundary condition (7) states that $H^s(t,x)$ equals the number of individuals at the end of the stage itself, i.e., at $x = 1$.Finally, (8) prescribes the initial conditions of the system. The system (5)–(8) has been widely employed in literature. We refer, e.g., to Lee et al. (1976), Plant and Wilson (1986), Bergh and Getz (1988), Iannelli (1994). Let also quote Mazzocchi et al. (2006), where an individual-based model of copepod populations is considered, and Buffoni and Pasquali (2010). In particular, Buffoni and Pasquali (2010) considers the following system: for $s = 1,\dots,\mathcal{S}$

$$\partial_t \phi^s(t,x) + \partial_x\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big) = -M^s\phi^s(t,x). \tag{9}$$

$$\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big)_{x=0} = \mathcal{F}^s(t), \tag{10}$$

$$\big(-b^s\partial_x\phi^s(t,x)\big)_{x=1} = 0, \tag{11}$$

$$\phi^s(0,x) = \phi_0^s(x). \tag{12}$$

where the terms

$$\mathcal{F}^1(t) = F\int_0^1 G(y)\phi^{\mathcal{S}}(t,y)\,dy, \tag{13}$$

$$\mathcal{F}^s(t) = S^{s-1}\phi^{s-1}(t,1), \qquad s = 2,\dots,\mathcal{S} \tag{14}$$

represent the input flux into stage s.

Since the mortality rate M^s of several insects species is related to the abundance of individuals themselves, in the line of Gyori (1990), Diekmann et al. (2001) we consider a time-dependent mortality rate $M^s : [0,T] \mapsto [0,1]$ and the nonlocal and nonlinear density-dependent function

$$\mathcal{M}^s(t) = M^s(t)\left(1 + a^s\left(\int_0^1 \phi^s(t,y)dy\right)^2\right)^{d^s}, \qquad a^s, d^s \in (0,+\infty), \tag{15}$$

which will yield the nonlinear reaction term in the model. We observe that the integral term appearing on the right hand side of (15) represents the abundance of individuals at stage s at time t, namely

$$N^s(t) = \int_0^1 \phi^s(t,y)dy.$$

By replacing M^s in (9) with the density-dependent mortality term $\mathcal{M}^s$, we are led to

$$\partial_t\phi^s(t,x) + \partial_x\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big) = -\phi^s(t,x)\mathcal{M}^s(t), \tag{16}$$

for $s = 1,\dots,\mathcal{S}$.

Finally, we replace the classical development and reproduction rates appearing in (9)–(12) with time-dependent ones, i.e., S^s, F^s: $[0,T] \mapsto [0,1]$. Then, from (16) and (6)–(8) we obtain the *Kolmogorov equation with nonlinear and nonlocal density-dependent mortality term*, which is

$$\partial_t\phi^s(t,x) + \partial_x\big(S^s(t)\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big) = -\phi^s(t,x)\mathcal{M}^s(t), \tag{17}$$

$$\big(S^s\phi^s(t,x) - b^s\partial_x\phi^s(t,x)\big)_{x=0} = \mathcal{F}^s(t), \tag{18}$$

$$\left(-b^s \partial_x \phi^s(t,x)\right)_{x=1} = 0, \tag{19}$$

$$\phi^s(0,x) = \phi_0^s(x). \tag{20}$$

where

$$\mathcal{F}^1(t) = F(t) \int_0^1 G(y) \phi^{\mathcal{S}}(t,y)\, dy, \tag{21}$$

$$\mathcal{F}^s(t) = S^{s-1}(t) \phi^{s-1}(t,1), \qquad s = 2, \dots, \mathcal{S} \tag{22}$$

Let us stress that some existing models can be recovered as special cases of (17)–(20): the classical Kolmogorov equation (see (5)–(8)) is obtained by setting $a^s = 0$ in (15); a class of von Foerster equations perturbed by a nonlinear and nonlocal density dependent term is obtained by choosing $a^s \neq 0$ and $b^s = 0$ in (15). The von Foerster equation considered in Gyori (1990) can be obtained as particular case by choosing $a^s = 1$, $b^s = 0$ and $d = 1$ in (15).

3. Application to the case study of *Spodoptera frugiperda*

The model presented is applied for simulating the population dynamics of *S. frugiperda*. We consider the stage-structured model (17)–(20) and specify the development, mortality and fertility rate functions for each stage $s = 1, \dots, 4$. According to Buffoni and Pasquali (2010), we fix the diffusion coefficient $b^s = 0.001$ for every $s = 1, \dots, 4$ and assume that development, mortality and fertility rate functions M, S and F depend on time only through the temperature $\vartheta(t), \vartheta \in C^1([0,T])$, then we define $\tilde{S}$, $\widetilde{M}$ and $\tilde{F}$ such that

$$\tilde{S}\left(\vartheta(t)\right) = S(t), \qquad \widetilde{M}\left(\vartheta(t)\right) = M(t), \qquad \tilde{F}\left(\vartheta(t)\right) = F(t). \tag{23}$$

3.1 Data

The stage-specific development, mortality and fertility rate functions of *S. frugiperda* are estimated with the following procedure. Temperature-dependent responses of the rate functions are estimated from laboratory experiments conducted in climate chambers under different constant temperature conditions collected at the individual level. For estimating the development rate function (see section 3.2) we have used data from Barfield et al. (1978), Hogg et al. (1982), Simmons (1993), Busato et al. (2005), Milano et al. (2008), Barros et al. (2010a), Rìos-Dìez and Saldamando-Benjumea (2011), Garcia et al. (2019). For estimating the mortality rate function (see section 3.3) we have used data from Barfield et al. (1978), Simmons (1993), Murúa and Virla (2004), Busato et al. (2005), Milano et al. (2008) and Garcia et al. (2019). For estimating the fertility rate function (see section 3.4) we have used data from Barfield et al. (1978), Pashley et al. (1995), Oeh et al. (2001), Milano et al. (2008), Barros et al. (2010b), Garcia et al. (2018) and Garcia et al. (2019). Data refer to the temperature-dependent average total fecundity $[eggs \cdot days^{-1}]$, the average daily fecundity $[eggs \cdot female^{-1} \cdot days^{-1}]$ and the average duration $[days]$ of the oviposition period. Data used for estimating the oviposition profile G refer to the age-dependent amount of eggs laid by a female (Murúa and Virla 2004) tested under controlled laboratory conditions.

For estimating the density-dependent component, we use data related to *S. frugiperda* adult trap catches. We consider two datasets. The first refer to adult trap catches collected in Irapuato (Guanajuato, Mexico) in 2015 (Salas-Araiza et al. 2018) and it is used for calibrating the density-dependent mortality rate function. The second dataset refer to adult trap catches collected in Gainesville (Florida, US) in 2013 (Garcia et al. 2018) and it is used for model validation purposes. Time-series temperature data used in our model have been obtained considering daily minimum and maximum air temperature from the NASA Power Global Meteorology, Surface Solar Energy and Climatology Data Client (https://power.larc.nasa.gov/, accessed: 15 May 2019). Hourly temperature data are then calculated using the algorithm described in Gilioli et al. (2014).

3.2 Development rate function

Since the development rate S is null for temperatures under a lower threshold $\vartheta_{\vee}^{s}$ and above a upper threshold $\vartheta_{\wedge}^{s}$, it is reasonable to consider the temperature-dependent development Briere rate proposed in Briere et al. (1999), namely

$$S^{s}(t) = \tilde{S}s(\vartheta) = max\left(p^{s}\vartheta\left(\vartheta - \vartheta_{\vee}^{s}\right)\chi(\vartheta)\sqrt{\vartheta_{\wedge}^{s} - \vartheta}, 1\right), \; s = 1, \dots ,4, \qquad (24)$$

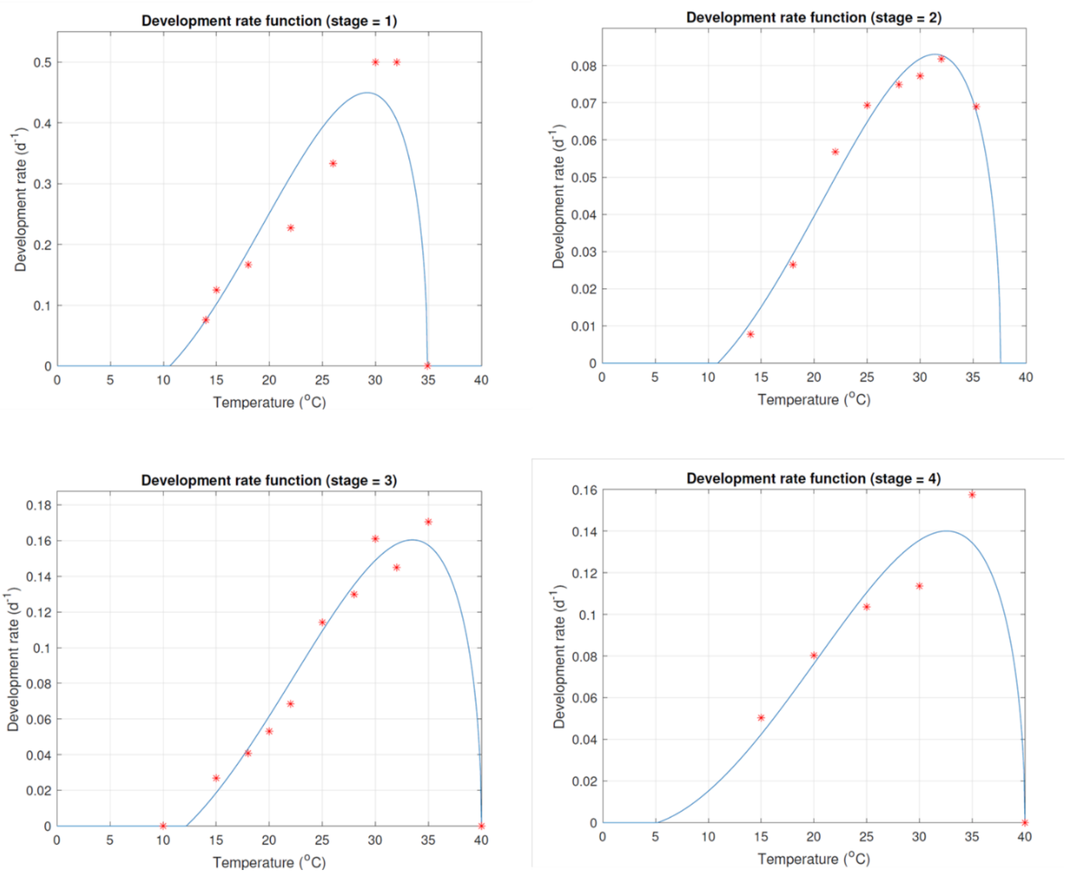
where p^{s} is a positive stretching parameter and χ is the characteristic function of the interval $[\vartheta_{\vee}^{s}, \vartheta_{\wedge}^{s}]$. The parameters p^{s}, $\vartheta_{\vee}^{s}$ and $\vartheta_{\wedge}^{s}$ are computed by the `lsqcurvefit` function of MATLAB© which finds the coefficients of (24) with the purpose to best fit the nonlinear function $\tilde{S}$ to the data (see Section 3.1) in the least-square sense. It is straightforward to prove that the optimum development temperature $\hat{\vartheta}^{s}$ does not depend on the parameter p^{s}. Indeed, we have that

$$\hat{\vartheta}^{s} = \frac{4\vartheta_{\wedge}^{s}+3\vartheta_{\vee}^{s}+\sqrt{16{\vartheta_{\wedge}^{s}}^{2}+9\vartheta_{\vee}^{s}-16\vartheta_{\wedge}^{s}\vartheta_{\vee}^{s}}}{10}, \qquad s = 1, \dots ,4. \qquad (25)$$

In table 1 we list the parameters of the function S^{s}, $s = 1, \dots ,4$ defined in (24), while the corresponding graphs are shown in Figure 1.

Table 1. The parameters used to model the functions $S^{s}(t)$ defined in (24).

	$\boldsymbol{s = 1}$	$\boldsymbol{s = 2}$	$\boldsymbol{s = 3}$	$\boldsymbol{s = 4}$
$\boldsymbol{p^{s}}$	3.47·10–2	$5.18 \cdot 10^{-3}$	$8.81 \cdot 10^{-3}$	$5.76 \cdot 10^{-3}$
$\boldsymbol{\vartheta_{\vee}^{s}}$	10.60	10.90	12.17	5.174
$\boldsymbol{\vartheta_{\wedge}^{s}}$	34.90	37.59	40.00	40.00


Development rate function (stage = 1)

Development rate function (stage = 2)

Development rate function (stage = 3)

Development rate function (stage = 4)

Fig.1 Development rate functions $S^s, s = 1, \dots, 4$.

3.3 Mortality rate function

For each stage $s = 1, \dots, 4$, we define the average stage proportional mortality μ^s, modeled with a convex and continuous function, namely $\mu^s(\vartheta) = \max(\tilde{\mu}^s(\vartheta), 0$ with

$$\tilde{\mu}^s(\vartheta) = \begin{cases} k^s, & \vartheta < \vartheta_{k^s}^{inf}, \\ A^s + B^s\vartheta + C^s, & \vartheta_{k^s}^{inf} \leq \vartheta \leq \vartheta_{k^s}^{sup}, \\ k^s, & \vartheta > \vartheta_{k^s}^{sup}, \end{cases} \tag{26}$$

where $k^s \in [0,1]$ and $A^s > 0$. The coefficients A^s, B^s, C^s are obtained by linear least-square fitting of the mortality data. Then, fixing a cut-off threshold k^s, we find $\vartheta_{k^s}^{sup}$ and $\vartheta_{k^s}^{inf}$ in order to guarantee that μ^s is globally continuous. In Table 2 we list the parameters used to define μ^s, while the corresponding graphs are shown in Figure 2.

Table 2. The parameters used to model the functions $\tilde{\mu}^s(t)$ defined in (26).

	$s = 1$	$s = 2$	$s = 3$	$s = 4$
k^s	0.9	0.9	0.9	0.9
$\vartheta_{k^s}^{sup}$	36.41	37.32	40.91	40.91
$\vartheta_{k^s}^{inf}$	9.22	14.60	11.31	11.31
A^s	4.89·10−3	5.41·10−3	3.70 ·10−3	3.70 ·10−3
B^s	−2.23 ·10−1	−2.80 ·10−3	−1.93 ·10−1	−1.93 ·10−1
C^s	2.56	3.84	2.62	2.62

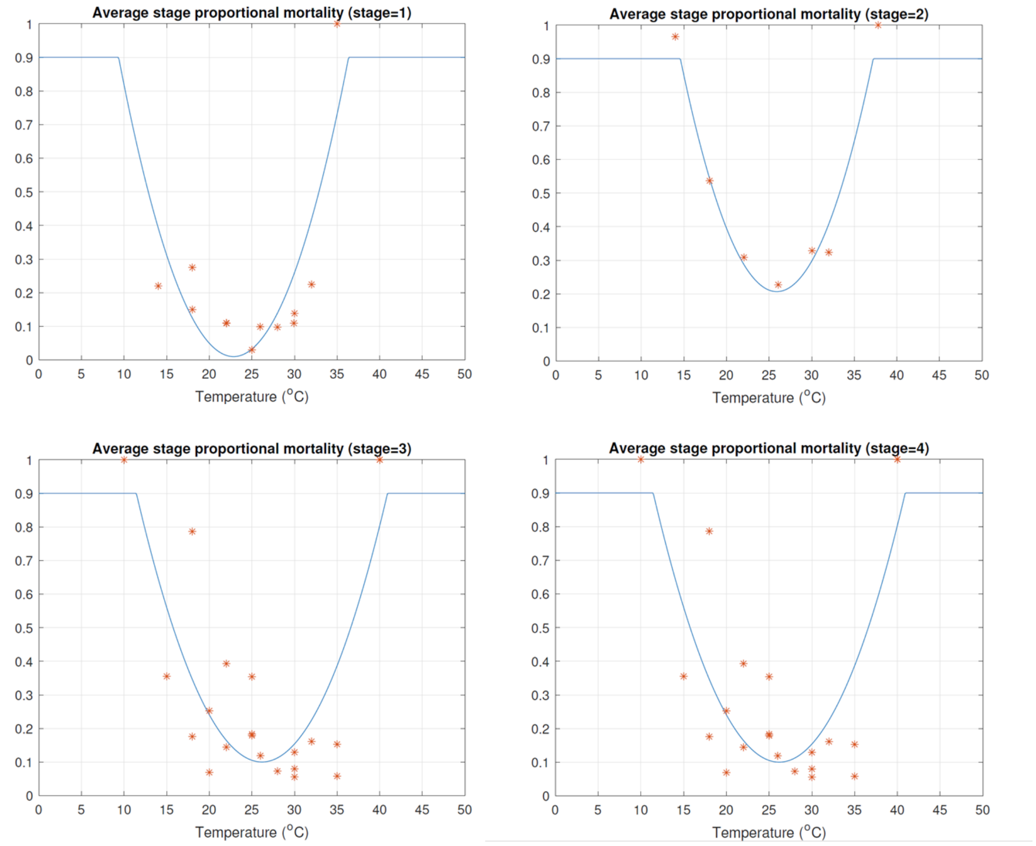


Fig.2 Average stage proportional mortality $\mu^s, s = 1, \dots, 4$.

Then, we consider the function

$$
\mathrm{m}^s(\vartheta) = \begin{cases} c_{1l}^s\left(\vartheta - \vartheta_{k^s}^{inf}\right)^2 + c_{2l}^s\left(\vartheta - \vartheta_{k^s}^{sup}\right) + c_{3l}^s, & \vartheta < \vartheta_{\vee}^s, \\ -S^s(\vartheta)\ln\left(1 - \mu^s(\vartheta)\right), & \vartheta_{k^s}^{inf} \le \vartheta \le \vartheta_{k^s}^{sup}, \\ c_{1r}^s\left(\vartheta - \vartheta_{k^s}^{sup}\right)^2 + c_{2r}^s\left(\vartheta - \vartheta_{k^s}^{sup}\right) + c_{3r}^s & \vartheta > \vartheta_{\wedge}^s, \end{cases} \tag{27}
$$

where the parameters c^s_{il} and c^s_{ir}, $i = 1{,}2{,}3$, of the outer branches of m^s are inferred from the constraints on sign, slope and concavity of the middle branch in order to guarantee that m^s is globally C^1. According to Wagner et al. (1984), we define the mortality rate

$$M^s(t) = \widetilde{M}^s(\vartheta) = min(\mathrm{m}^s(\vartheta), 1) \tag{28}$$

and list the parameters of m^sin Table 3 and the corresponding graphs in Figure 3, respectively.

Table 3. The parameters used to model the functions $\mathrm{m}^s(t)$ defined in (27).

	$\boldsymbol{s = 1}$	$\boldsymbol{s = 2}$	$\boldsymbol{s = 3}$	$\boldsymbol{s = 4}$
$\boldsymbol{\vartheta^s_\wedge}$	28.08	28.52	21.61	15.78
$\boldsymbol{\vartheta^s_\vee}$	22.38	15.00	15.00	15.00
$\boldsymbol{c^s_{1l}}$	2.88·10−3	7.70 ·10−3	8.4 ·10−3	1.55 ·10−2
$\boldsymbol{c^s_{2l}}$	−1.30 ·10−2	−2.35 ·10−1	−2.49 ·10−1	−3.67· 10−1
$\boldsymbol{c^s_{3l}}$	1.46	1.82	1.86	2.22
$\boldsymbol{c^s_{1r}}$	4.21·10−3	7.10·10−3	1.22·10−2	1.02·10−2
$\boldsymbol{c^s_{2r}}$	−2.09 ·10−1	−4.01 ·10−2	−7.59 ·10−1	−6.175 ·10−1
$\boldsymbol{c^s_{3r}}$	2.61	5.59	11.84	9.36 ·10−1

In order to model the larval competition and cannibalism, following Pasquali et al. (2020), we consider a density-dependent mortality term

$$\mathcal{M}^s = \widetilde{M}^s(t)\left(1 + a^s\left(\int_0^1 \phi^s(t,y)dy\right)^2\right)^{d^s}, \tag{29}$$

applied only in stage $s = 2$. The estimation of the coefficients a^s and d^s $(s = 2)$ is of fundamental importance to define the mortality function (29).To this aim, we have computed a^s and d^s $(s = 2)$ as the minimisers of the root mean square error

$$RMSE(\hat{a}, \hat{d}) = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(N^4(t_i, \hat{a}, \hat{d}) - \bar{N}^4_i\right)^2}, \tag{30}$$

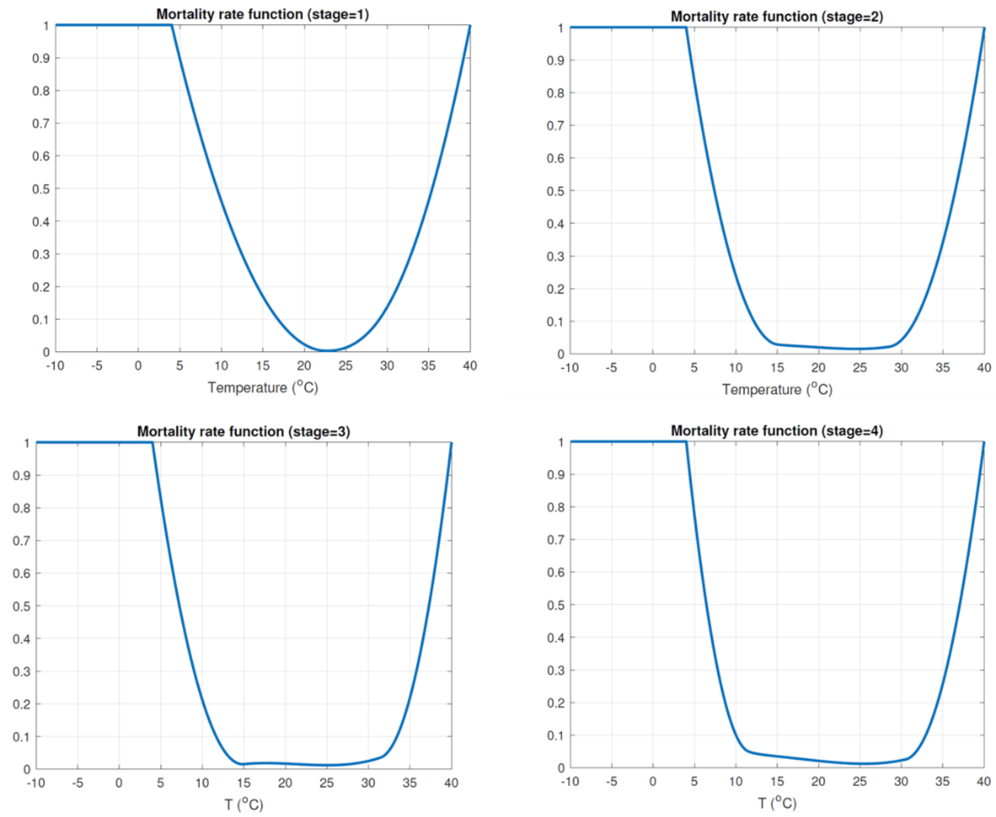


Fig.3 Mortality rate functions $\mathrm{M}^s, s = 1, \ldots, 4$.

in which $\overline{N}_i^4$ (for $i = 1, \ldots, n$) are the measured abundances of the 4th stage at certain times t_i in Irapuato (Guanajuato, Mexico), while $N^4\left(t_i, \hat{a}, \hat{d}\right)$ are the abundances computed with our model with a^2 and d^2 in (29) replaced by $\hat{a}$ and $\hat{d}$ respectively. The minimisers of RMSE have been computed by the interior-point method (see, e.g., Pólik and Terlaky (2010)) implemented in the `fmincon` of MATLAB©. The parameters obtained are

$$a^2 = 49.92 \qquad \text{and} \qquad d = 0.267. \tag{31}$$

3.4 Fertility rate function

The input flux of eggs in stage $s = 1$ is defined by

$$\mathcal{F}^1(t) = \int_0^1 F(t) G(x) \phi^4(t, x)\, dx, \tag{32}$$

where $D(t,x) = F(t)G(x)$ is the temperature- and age-dependent fertility rate function, with $F(t)$ being the temperature-dependent fertility rate and $G(x)$ being the reproductive profile which depends on adult female age. Since experimental data suggest that F is concave in a specific temperature range $[\vartheta_m^E, \vartheta_M^E]$ with a peak at the optimal temperature $\hat{\vartheta}^E$, the temperature-dependent fertility rate is defined by the following analytic expression (see, e.g. Royer et al. (1999))

$$F(t) = \tilde{\mathrm{F}}(\vartheta) = k^E \vartheta \chi(\vartheta)(\vartheta - \vartheta_m^E)\sqrt{\vartheta_M^E - \vartheta}, \qquad k^E > 0, \tag{33}$$

where χ is the characteristic function of the interval $[\vartheta_m^E, \vartheta_M^E]$. The coefficients k^E, ϑ_m^E and ϑ_M^E are computed by the `lsqcurvefit` function of MATLAB©, fitting (in the least-square sense) the nonlinear function (33) to the data. We find

$$k^E = 0.111, \qquad \vartheta_m^E = 11.442, \qquad \vartheta_M^E = 35.576. \tag{34}$$

For estimating the age-dependent fertility rate function G we refer to the data reported in Murúa and Virla (2004) which provide data that have been interpolated with the normalized Gamma distribution (see Sporleder et al. (2004)). Based on Murúa and Virla (2004), we assume that, the maximum value of eggs occurs at the optimal age $x_{opt} = 0.23$, and then declines up to a final age $x_{end} = 0.92$. Then, we consider the normalized Gamma distribution

$$G(x) = \frac{x^{\alpha-1}e^{-\beta x}}{\|x^{\alpha-1}e^{-\beta x}\|_{L^1(0,1)}}, \tag{35}$$

where $\alpha$and β are positive are positive parameters obtained in order to guarantee that the maximum age-dependent fertility rate occurs at physiological $x_{opt} = 0.23$,

i.e.,

$$x_{opt} = \frac{\alpha-1}{\beta} = 0.23 \tag{36}$$

and that

$$\int_0^{x_{end}} x^{\alpha-1}e^{-\beta x}dx = \frac{99}{100}\int_0^1 x^{\alpha-1}e^{-\beta x}dx. \tag{37}$$

Applying (36)-(37) we find

$$\alpha = 0.318 \cdot 10^1, \qquad \beta = 0.948 \cdot 10^1. \tag{38}$$

The plots of F and G (see (33) and (35) are shown in Figure 4.

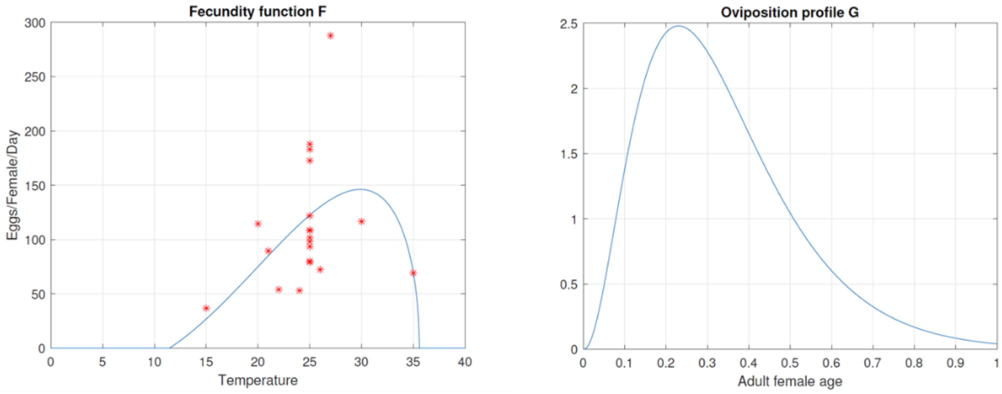


Fig.4 Functions F and G.

4 Numerical results

The numerical solution of the first year is affected by the initial conditions, but during the successive years the solution is periodic without blow-ups nor damping effects (see Figure 5).

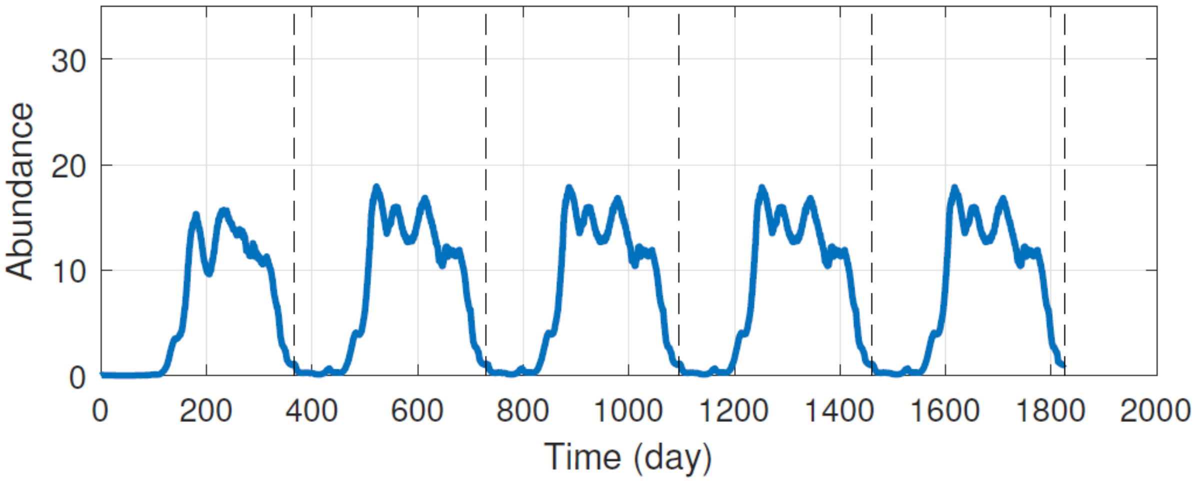


Fig.5 Numerical solutions for the stage $s = 4$ (Irapuato, Guanajuato, Mexico) with $a^s = 49.92$ and $d^s = 0.267$, for $s = 2$.

Therefore, we run the model for three years and we compare the simulated adult population dynamics of the third year with the adult monitoring data. In Figure 6a the simulated adult population dynamics is compared with the adult monitoring data extracted from Salas-Araiza et al. (2018) referring to adult catches through a pheromone-baited trap located in Irapuato (Guanajuato, Mexico) in the year 2015. In Figure 6b the simulated adult population dynamics is compared with the adult monitoring data extracted from Garcia et al. (2018) referring to adult catches in Gainesville (Florida, US) in the year 2013.

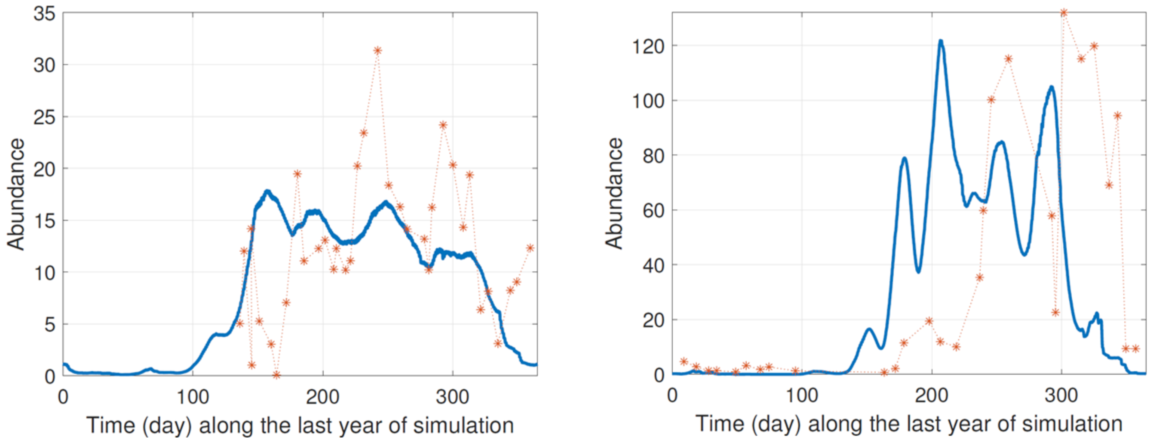


Fig.7 On the left (Fig.7a) numerical solution for the stage $s = 4$ (continuous blue line) and experimental data (colored asterisks) (Irapuato, Guanajuato, Mexico). On the right (Fig.7b) numerical solution for the stage $s = 4$ (continuous blue line) and experimental data (colored asterisks) (Gainesville, Florida, US). Parameters $a = 49.92$ and $d = 0.267$, for $s = 2$.

From the numerical results shown in Figure 5 and Figure 6 we evince that the model proposed in this paper provides a first reasonable interpretation of the phenology and the population dynamics of the species. If the density-dependent mortality term is nullified, we obtain an unlimited (and thus unrealistic) growth of the simulated population abundance. This is a confirmation that the regulation due to abiotic factors is not sufficient to model the population dynamics of the species. Although two extra parameters appear in the equation of our model, the benefits of our approach are considerable because the density dependent mortality term ensures a realistic limitation of the population abundance.

5 Conclusions and future perspectives

The model presented is characterised by a high degree of biological realism since it represents the temperature-dependent responses of the life-history strategies and it includes density-dependent control factors influencing the survival of the larval stage.

The model is able to predict the high variability in the overall abundance of adult individuals among the calibration and the validation dataset. The model is also able to realistically simulate reduced population abundances during the unfavourable seasons (late autumn and winter). As in relation to the time of emergence and the peaks of adult individuals there is a considerable discrepancy between observations and simulation results. However, the present work is mainly focussed on exploring the consequences of the introduction of a density-dependent control term on the overall population dynamics of the species under investigation. It is not surprising that, using a single dataset for model calibration, the performances of the model might not be optimal. We do expect that, increasing the number of population dynamics datasets used in the calibration procedure would improve the predictive performances of the model. This will allow to calibrate the model's parameters under different contexts, thus allowing to evaluate model's performances and investigate species' physiological responses to different environmental conditions. These aspects will be addressed in a subsequent work.

The quantitative outputs (i.e., population abundance) provided by the model is particularly useful for setting knowledge-based management strategies of the pest species at various spatial-temporal scales. For instance, at the farm level, predictions on the time of emergence and the species’ population abundance can be used for planning and implementing pest monitoring and pest control activities

(Rossi et al. 2019). The model presented can also be applied at the regional level (e.g., at country or continental level) for the development of risk maps showing the potential distribution and abundance of the species under different climatic and risk management scenarios. These information are fundamental for guiding the categorization and prioritization of pest species and for assessing the potential risks of entry, establishment and impacts of the species (EFSA PLH Panel 2017; EFSA PLH Panel 2018a; EFSA PLH Panel 2018b; EFSA PLH Panel 2020).

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CHAPTER 5 - Non-linear physiological responses affecting *Ceratitis capitata* distribution and abundance under climate change

The author of the present Thesis has been involved in the conceptualisation and the design of the work, in the management and analysis of both biological and temperature data, in the application of the model, in the biological interpretation of the results and in drafting the manuscript.

Abstract: Understanding how climate change might influence distribution and abundance of crop pests is fundamental for the development and the implementation of pest management strategies. Here we present and apply a modelling framework assessing the non-linear physiological responses of the Mediterranean fruit fly (*Ceratitis capitata*, Wiedemann) life-history strategies to temperature. The model is used to explore how climate change might influence the distribution and abundance of the pest in Europe. We investigate the change in the distribution, abundance and activity of the species under current (year 2020) and future (years 2030 and 2050) climatic scenarios. The model predicts a northward expansion in the area of distribution of *C. capitata* due to climate change. With respect to the distribution reported in 2020, the model predicts an increase in population abundance in 62% of the area (adults) and 64% of the area (larvae) in 2030, and 79% (adults) and 86% (larvae) in 2050. A decrease in population abundance is expected in 17% of the area (adults) and 23% (larvae) in 2030 to 14% (adults) and 10% (larvae) in 2050. A relative stability is predicted in the remaining areas. The effects of climate change on the distribution, abundance, and activity of *C. capitata* are heterogeneous both in time and in space. This heterogeneity reflects the contribution of both the spatial variability in the predicted climatic patterns and the non-linearity in the responses of pests' life-history strategies to temperature.

Keywords: Climate change; *Ceratitis capitata*; Invasive species; Process-based model; Pest risk assessment; Pest management

1. Introduction

The Mediterranean fruit fly (or medfly), *Ceratitis capitata* Wiedemann (Diptera: Teprhitidae) is a phytophagous invasive insect considered one of the most important threat for horticulture and fruit-growing (Liquido et al. 1990; Papadopoulos et al. 2001; De Meyer et al. 2002; Weldon et al. 2018). The medfly has been reported on more than 300 host plants including citrus, stone fruits, pome fruits, tomatoes, figs and others (Morales et al. 2004; Meats and Smallridge 2007). The damage on fruit is caused by adult oviposition, which also facilitates the transmission of bacteria and fungi, and by the larval trophic activity (Cayol et al. 1994). The economic impact is related to the need of applying pre- and post-harvest control measures and the limitations to export products from infested areas to medfly-free areas (Hulme 2009). The medfly has been classified as an EPPO A2 quarantine pest (Rossler and Chen 1994). The species originated from south-eastern Africa (White 1992; Gasperi et al. 2002; Malacrida et al. 2007). Facilitated by human-mediated transportation and trade (De Meyer et al. 2002; Bonizzoni et al. 2004; Malacrida et al. 2007), the medfly colonised the whole African country, the Mediterranean Basin (Robinson and Hooper 1989), the Middle East, western Australia (Bonizzoni et al. 2004), Latin America (Harris and Lee 1989) and Central America (Headrick and Goeden 1996; Vera et al. 2002). The biological traits of *C. capitata* explaining its successful invasion and establishment in new areas are related to the high polyphagy (Malacrida et al. 2007), the short generation times (Duyck and Quilici 2002; Grout and Stoltz 2007), the capacity of long distance flights (Meats and Smallridge 2007), and the adaptability to different climatic conditions (Nyamukondiwa et al. 2010). Responses of *C. capitata* to climate are of particular importance. Recent research demonstrated the capacity of *C. capitata* to tolerate a wide range of temperature conditions both in laboratory (Nyamukondiwa et al. 2010; Weldon et al. 2011, 2018) and in semi-field tests (Nyamukondiwa et al. 2013) and thus to increase its success in colonising temperate areas (Malacrida et al. 1992; De Meyer et al. 2002). Furthermore, transient populations might survive in refuge areas, allowing *C. capitata* to reinvade new regions as soon as the seasonal weather conditions become suitable for the species (Carey 1991). An example of the species' adaptability is the expansion of the northern limit of its distribution in Europe. The species was traditionally considered limited to the 41st parallel north (Robinson and Hooper 1989; Israely et al. 2004) and to habitats where temperatures are persistently below 10 °C (Mwatawala et al. 2015). However, Papadopoulos et al. (1996, 1998, 2001) reported the capacity of the species to overwinter as larva under cold winter conditions and survive under subfreezing temperature. Stable *C. capitata* populations have been reported in southern France (Cayol and Causse 1993), northern Italy (Rigamonti et al. 2002; Rigamonti 2004, 2005; Zanoni 2018; Zanoni et al. 2019), and Austria (Egartner et al. 2017) suggesting the capacity of the species to complete its life-cycle in areas far above its traditional northward distribution limit. Climate change is expected to play a primary role in altering the potential distribution and performance of the species worldwide (Gutierrez and Ponti, 2011; Sultana et al. 2020), and in the species' capacity to reinvade new areas by local transient populations (Gutierrez and Ponti).

Given the severe impacts on plant health and the high invasive capacities shown by *C. capitata,* it is fundamental to produce reliable risk scenarios, accounting for an appropriate spatial and temporal resolution in relation to the scale of management. Models are appropriate tools for exploring how the main drivers of risk (i.e., pest species distribution and abundance) (EFSA PLH Panel 2018) are affected by climate variability and change both in time and space (Hill et al. 2016b). Here we propose a modelling framework to improve the reliability of *C. capitata* risk scenarios in Europe considering the effects of climate change. The modelling framework is based on four key methodological elements briefly presented below.

1 – *Use of reliable climatic scenarios with appropriate spatial and temporal resolution*. Scenarios that provide a reliable representation of temperature variations at high spatial resolution are required in any exploration of future pest risk scenarios at the regional level (Kriticos et al. 2015; EFSA PLH

Panel 2018). At the local level, projections at a high temporal resolution is also required to accurately describe and explain the duration of the favourable period for reproduction, the effects of winter temperatures on overwintering and also the effects of sub-optimal warm temperatures in summer (Logan et al. 2003; David Logan et al. 2005; Tamburini et al. 2013). This is often obtained for relatively short time horizons (Kriticos et al. 2012; Sultana et al. 2017). The climate scenarios used in this work were obtained from the Coordinated Regional climate Downscaling Experiment (CORDEX) based on Regional Climate Model (RCM) simulations for the European domain (Jacob et al. 2014).

2 – *Consideration of non-linearity in the responses of the pests' physiology to the environmental drivers*. Several models have been proposed to estimate the risk of establishment of *C. capitata*. The vast majority are correlative models, investigating the correlation existing between the current distribution (i.e. presence/absence) of the pest and relevant driving variables (i.e., temperature, rainfall, land use etc.) (Vera et al. 2002; Gevrey and Worner 2006; De Meyer et al. 2007; Li et al. 2009; Szyniszewska and Tatem 2014; Karsten et al. 2015; Godefroid et al. 2015; Kaya et al. 2017). In most of the published models, relations existing between the pests' life-history strategies and the environmental drivers are not explicitly considered. Here we propose a process-based (i.e. mechanistic) modelling approach allowing the exploration of the non-linear effects of environmental drives on species physiological responses and population dynamics (Gutierrez and Ponti 2011; Régnière et al. 2012b; Gilioli et al. 2016). By comparing the pattern of population response to that of climate change, we investigate how future climate scenario could affect the risks associated with *C. capitata*.

3 – *Provide biologically relevant and quantitative outputs*. Most of the correlative models are powerful tools that, under specific assumptions (Soberon and Nakamura 2009; Wiens et al. 2009; Warren 2012) represent an optimal compromise between data and time required for model development and the capacity to describe the current and the projected distribution of a species.

However, they provide information in the form of habitat suitability indices. No information is provided on the potential population abundance, which is one of the most important driving forces of the impacts of a pest in a certain area (Gilioli et al. 2017c; EFSA PLH Panel 2018). Despite the intensive efforts required for model development (Kriticos et al. 2012), process-based models can provide quantitative information on the local abundance, that is the number of individuals per habitat unit (e.g., a host plant) or effort unit (e.g., a trap) under the influence of biotic and/or abiotic conditions (Gutierrez and Ponti 2013; Ponti et al. 2015; Pasquali et al. 2015). The model presented in this study provides population projections in terms of stage-specific pest distribution, abundance and activity.

4 - *Thorough model calibration and validation*. A complete and well-documented procedure for model calibration and validation is fundamental to guarantee the reliability of model projections used to generate pest risk scenarios (Venette et al. 2010; Venette 2015). We first calibrate the model using data on the temperature-dependent individual physiological responses under experimental conditions. Model's parameters are then refined using pest population dynamics datasets from five different locations in the Mediterranean Basin (Italy, Spain, Portugal, Croatia and Israel) in order to account for population variability of physiological responses under different environmental conditions. We then validate the model in its capacity to correctly predict both the northernmost distribution of the pest in Europe and the altitudinal limit of the species using independent datasets on pest abundance and distribution.

The paper is organised as follows. In Section 2 we present the model's overall structure and assumptions, the scheme of the simulations, the data and the scenarios used, and the methodology for parameter estimation, calibration and validation. In Section 3 we present the results. In Section 4 we discuss the results obtained. In Section 5 we provide conclusions and future research perspectives.

2. Materials and methods

2.1. Model assumptions

The population dynamics model for *C. capitata* is based on the following assumptions:

- *C. capitata* populations are structured in four developmental stages i, namely eggs ($i = 1$), larvae ($i = 2$), pupae ($i = 3$) and adults ($i = 4$).
- Individual life history strategies are represented by development, mortality and fecundity stage-specific rate functions. These functions depend on temperature, which is the main environmental driving force influencing poikilotherm population dynamics (Gutierrez 1996; Régnière et al. 2012a; Rebaudo and Rabhi 2018). Individual physiological responses to temperature are non-linear.
- Fecundity rate function has a component related to adult physiological age.
- In addition to temperature, the mortality rate function has two more components. We include a mortality term to account for density-dependent responses simulating the intra-specific competition, and a mortality term accounting for an extrinsic control due to inter-specific interactions (with competitors and predators) both acting on the trophic stages (i.e. larvae and adults) (Carey et al. 1995; Dukas et al. 2001; Diamantidis et al. 2020).
- The model simulates the local population dynamics in each node of a regular grid 0.1° x 0.1° (lattice model) covering the European continent. Population dynamics in the node are influenced only by conditions in the node (temperature, population abundance and structure). The nodes are assumed to be isolated from the others (no flux of individuals among the nodes) and identical in terms of resources for the pest and biotic control agents.

We denote by $x \in [0,1]$ the individual physiological age, defined as the proportion of the individual development within a stage. With $x = 0$ we denote individuals at the beginning of the development within a certain stage, while $x = 1$ refers to individuals that have completed the development within that stage. Let $\phi^i\,(t, x)$ be the population abundance of individuals in stage i at time t, with physiological age in $[x, x + dx]$, where dx stands for an infinitesimal age increment. Hence, the number of individuals in stage i at time t is

$$N^i(t) = \int_0^1 \phi^i(t,x)\, dx.$$

We describe the population dynamics of *C. capitata* through a process-based model based on the Kolmogorov equation (Lee et al. 1976; Weiss 1986; Bergh and Getz 1988; Iannelli 1995; Buffoni and Pasquali 2007). This approach has been already applied to other insect species in Rafikov et al. (2008), Solari and Natiello (2014), Gilioli et al. (2014, 2016, 2017a,b,c), Lanzarone et al. (2017) and Pasquali et al. (2019). The model is described by a system of partial differential equations

$$\frac{\partial \phi^i}{\partial t} + \frac{\partial}{\partial x}\left[v^i(t)\phi^i - \sigma^i \frac{\partial \phi^i}{\partial x}\right] + m^i(t)\phi^i = 0, \quad t > 0,\ x \in (0,1), \tag{1}$$

$$\left[v^i(t)\phi^i(t,x) - \sigma^i \frac{\partial \phi^i}{\partial x}\right]_{x=0} = F^i(t), \tag{2}$$

$$\left[-\sigma^i \frac{\partial \phi^i}{\partial x}\right]_{x=1} = 0, \tag{3}$$

$$\phi^i(0,x) = \hat{\phi}^i(x), \tag{4}$$

with $i = 1, \dots, 4$ where $m^i(t)$ and $v^i(t)$ are the stage-specific mortality and development rates, respectively. The functions $\hat{\phi}^i(x)$ represent the initial conditions of the model in terms of individual abundance in a certain stage, while the term σ^i is a diffusion coefficient, introduced to include the effects of stochasticity on the stage-specific development process. The functions $F^i(t)$ represent the fluxes of individuals from stage i to stage $i+1$. For the egg stage, the flux F^1 represents the production of eggs by adult individuals (adult fecundity) and is defined as

$$F^1(t) = \int_0^1 g(t)\, h(x)\, \phi^4(t,x)\, dx$$

where $g(t)$ and $h(x)$ represent the temperature-dependent and the physiological age-dependent fertility functions, respectively. For $i > 1$ the flux of individuals is represented by

$$F^i(t) = v^{i-1}(t)\, \phi^{i-1}(t,1), \qquad i = 2, 3, 4.$$

2.2. Model rate functions estimation

The development and the mortality rate functions are defined for each developmental stage. The fertility rate function is defined for the adult stage. The parameters of the rate functions are estimated through least square method using the `lsqcurvefit` function in MATLAB version R2018a setting the termination tolerance on the first-order optimality at 10^{-6}. In the following, we will omit for brevity the dependence on the stage $i = 1, \dots, 4$, specifying in the corresponding tables the stage-specific parameters of each function.

2.2.1. Development rate function

The stage-specific temperature-dependent development rate function $v(T)$ is described by the Brière function (Briere et al. 1999)

$$v(T) = \begin{cases} rT\left(T - T_{inf}\right)\sqrt{T_{sup} - T} & T_{inf} \leq T \leq T_{sup} \\ 0 & otherwise \end{cases} \qquad (5)$$

where $T = T(t)$ is the air temperature at time t, r is a scaling parameter, T_{inf} and T_{sup} represent the stage-specific minimum and maximum temperature at which the development occurs, respectively. The parameters of function (5) are estimated from experimental data on the temperature-dependent development times (in days) of *C. capitata* exposed to different temperatures. The parameters of function (5) are estimated using a least square method based on data from Carey (2011), Diamantidis et al. (2011), Duyck and Quilici (2002), Grout and Stoltz (2007), Gutierrez and Ponti (2011), Muñiz and Mariano (1986), Ricalde et al. (2012), Rössler (1975), Shoukry and Hafez (1979) and Vargas et al. (1997, 2000). Parameters of the development rate functions are reported in Table 1.

Table 1. Estimates of parameters of the temperature-dependent, stage-specific development rate function (5)

	r	T_{inf} (ºC)	T_{sup} (ºC)
Eggs	$0.2984 \,.\, 10^{-3}$	9.3864	39.3708
Larvae	$0.0754 \,.\, 10^{-3}$	6.6406	38.7532

Pupae	$0.0874 . 10^{-3}$	9.8996	35.3521
Adults	$0.0121 . 10^{-3}$	11.1493	37.8964

2.2.2. Mortality rate function

The stage-specific temperature-dependent finite mortality rate *M(T)* (percentage of mortality in a stage at a given temperature T) is expressed by

$$M(T) = \begin{cases} k & T < T_{inf}^{\mu} \\ p_1T^2 + p_2T + p_3 & T_{inf}^{\mu} \leq T \leq T_{sup}^{\mu} \\ k & T > T_{sup}^{\mu} \end{cases} \quad (6)$$

where T_{inf}^{μ} and T_{sup}^{μ} are the abscissa of the intersections among the polynomial function defined in (6) and the constant function $k = 0.9$ representing the hypothesised maximum stage-specific mortality. The parameters of function (6) are estimated from experimental data on *C. capitata* survival at different temperatures using a least square method based on data from Diamantidis et al. (2011), Duyck and Quilici (2002), Gutierrez and Ponti (2011) and Vargas et al. (2000). As no data are available on the stage-specific mortality of the adult stage, we assume it being equal to the stage-specific proportional mortality of pupae. The parameters of function (6) are reported in Table 2.

Table 2. Estimates of parameters related to the temperature-dependent, stage-specific average stage proportional mortality presented in equation (6)

	p_1	p_2	p_3
Eggs	0.0047	-0.1988	2.1074
Larvae	0.0053	-0.2361	2.5511
Pupae	0.0049	-0.2081	2.2152
Adults	0.0049	-0.2081	2.2152

Following the method proposed in Gilioli et al. (2016) and Pasquali et al. (2020) we derive the temperature-dependent instantaneous mortality rate $\mu(T)$ from the finite mortality rate in (6)

$$\mu(T) = \begin{cases} c_{L1}\,(T - T^{\mu}_{inf}\,)^2 \; + \; c_{L2}(T - T^{\mu}_{sup}\,) \; + \; c_{L3} & T < \; T_{inf} \\ -v(T)\log(1 - M(T)) & T_{inf} \leq T \leq T_{inf} \\ c_{R1}\,(T - T^{\mu}_{inf}\,)^2 \; + \; c_{R2}(T - T^{\mu}_{sup}\,) \; + \; c_{R3} & T > T_{sup} \end{cases} \qquad (7)$$

where the parameters c_{Lj} and c_{Rj}, $j = 1, 2, 3$ of the outer branches of μ are inferred to obtain the desired slope of the curve and a sufficiently regular connection with the middle branch (μ of class C^1). The stage-specific parameters of the functions (7) are listed in Table 3.

Table 3. Estimates of parameters of the temperature-dependent mortality rate function (7)

	c_{L1}	c_{L2}	c_{L3}	c_{R1}	c_{R2}	c_{R3}	T^{μ}_{inf} (°C)	T^{μ}_{sup} (°C)
Eggs	0.0006	-0.0212	0.2084	0.0016	-0.0046	1.0244	15.00	30.55
Larvae	0.0013	-0.0231	0.1205	-0.0001	0.0236	-0.6114	8.71	30.27
Pupae	0.0005	-0.0209	0.2210	-0.0001	0.0169	-0.3615	20.75	28.05
Adults	0.0021	-0.0878	0.9110	0.0021	-0.1197	1.7522	20.75	29.81

For the egg and pupal stages ($i = 1, 3$) the stage-specific mortality rate $m^i(T)$ appearing in (1) is defined as

$$m^i(T) = \mu^i(T)$$

For the larval and the adult stages ($i = 2, 4$) we also consider a density-dependent mortality term (intra-specific competition) and a mortality term due to inter-specific interactions (competition and predation). For these two stages the mortality rate function is modified as follows

$$m^i(t) = \mu^i\big(T(t)\big) + \delta^i + \left(\frac{N^i(t)}{N^i_{max}}\right)^2 \qquad (8)$$

where N^i_{max} refers to the maximum stage-specific abundance that might be sustained with respect to the available trophic resources while the term δ^i is an extrinsic biotic mortality due to the effects of competitors and natural enemies. The parameters in (8) are estimated from population dynamics data following the procedure presented in Section 2.4.1.

2.2.3. Fecundity rate function

The fecundity rate function includes two components, $g(T)$ describing the temperature-dependent term and $h(x)$ describing the adults' physiological age-dependent term as follows

$$g(T) = \max(aT^2 + bT + c, 0)$$

$$h(x) = \max\left(\alpha x^{\beta}(1-x)^{\gamma}, 0\right)$$

Following Gutierrez et al. (2012) and Gilioli et al. (2014) the parameters $a = -18.44$, $b = 952.76$, $c = -9444.21$, $\alpha = 0.13$, $\beta = 0.545$ and $\gamma = 3$ are estimated through least square method from experimental data on temperature-dependent adult fecundity (eggs/female per day), total fecundity (eggs/female) and physiological age-dependent fecundity. The data were collected from Carey (2011), Chang et al. (2007), Muñiz and Mariano (1986), Rössler (1975), Shoukry and Hafez (1979) and Vargas et al. (1997, 2000).

2.3. Model simulations and climate scenarios

Model simulations provide the current and the future distribution, abundance and activity of *C. capitata*. Simulation results are obtained by solving the model (1-4) numerically in each point of the 0.1° x 0.1° grid covering the European territory. The simulations are performed using the scientific software MATLAB by employing second-order Finite Volumes in space and first-order Finite Differences in times. The climate scenarios are described in Section 2.5.2.

The model outputs presented in this study are: (i) the yearly mean adult and larval abundance considering only the abundances higher or equal to a stage-specific abundance threshold, and (ii) the yearly adult and larval activity calculated as the number of days when the adult and the larval abundance is higher or equal to a stage-specific abundance threshold. The stage-specific abundance threshold is set to one individual for the adult stage and to 30 individuals for the larval stage. The points of the grid in which the yearly mean adult and larval abundance is higher or equal to the stage-specific abundance threshold define the area of potential distribution of adults and larvae, respectively. For each node of the grid, the calculated yearly mean adult and larval population abundance refers to a unit area A_0 assumed as the range of attractiveness covered by a single trap for *C. capitata* adults baited with trimedlure. Based on the work of Manoukis et al. (2015) we assume A_0 being approximately 7-14 meters. For any area of size A, the abundance varies linearly with the ratio A/A_0. For all the simulations, the initial condition on the 1st of January is set to five larvae uniformly distributed within their physiological age interval [0,1]. In order to obtain stable population dynamics and let the model outputs be independent from the initial conditions, we run the model for ten consecutive years. Model outputs are calculated in the last year of simulation. Model outputs obtained for the current climate scenario (2020) are then compared with that obtained for 2030 and 2050 scenarios (Section 3.3.).

2.4. Model calibration and model validation

2.4.1. Model calibration

The model calibration procedure consists in the estimation of the two biotic mortality terms in the mortality rate function (8) applied to larvae and adults. Parameters of the biotic mortality terms in function (8) are obtained through the minimisation of the squared distance between the estimated and the observed abundances of *C. capitata* adults (least square method) considering time series data of *C. capitata* abundance collected in five different locations (see Section 2.5.3 for further details on the datasets). Yearly temperature datasets at hourly time resolution are used as input data for model calibration (Section 2.5.1).

Denoting by $N_j^4(t_i,\ \delta^2,\ \delta^4, N_{max}^2, N_{max}^4)$ the adult abundance at location j at time t_i obtained by integrating the solution to system (1)-(4) respect to physiological age, for parameters $\delta^2,\ \delta^4, N_{max}^2, N_{max}^4$ (see (8)), we define the functional

$$Q(\delta^2,\ \delta^4, N_{max}^2, N_{max}^4) = \sum_{j=1}^{5} \frac{1}{R_j} \sum_{i=1}^{R_j} \left| N_j^4(t_i;\ \delta^2, \delta^4, N_{max}^2, N_{max}^4\ ) - A^j(t_i) \right|^2$$

where $A^j(t_i)$ is the observed adult abundance at location j at time t_i and R_j is the number of available data for location j. Then, we find the optimal parameters $\bar{\delta}^2,\ \bar{\delta}^4, \bar{N}^2_{max}, \bar{N}^4_{max}$ looking for the minimum of Q, namely

$$(\bar{\delta}^2,\ \bar{\delta}^4, \bar{N}^2_{max}, \bar{N}^4_{max}) = \min_{\delta^2,\ \delta^4, N^2_{max}, N^4_{max}} Q\left(\delta^2,\ \delta^4, N^2_{max}, N^4_{max}\right)$$

The minimization is performed using the MATLAB function `fmincon`, with the default tolerance of 10^{-5}.

2.4.2. Model validation

Model validation is based on testing the model’s capacity to predict i) the altitudinal limit of the species distribution in a transect crossing the Alps in northern Italy, and ii) the northernmost distribution limit of *C. capitata* in Europe considering the countries where the species is considered established. For the altitudinal limit, we test the model in predicting the establishment in Riva del Garda, Bressanone and Bolzano (Trentino Alto Adige, Italy) in 2016 (Zanoni 2018) using local yearly temperature datasets at hourly time resolution (Section 2.5.1). The model’s ability to predict the current distribution of *C. capitata* is tested by superimposing data on *C. capitata* occurrence in Europe onto the map of the predicted distribution of the species obtained by model simulation under the current climate scenario.

2.5. Data

2.5.1. Point-based temperature data

Temperature data used for model calibration and validation are obtained from the Global Surface Summary of Day Product elaborated by the US National Climatic Data Centre (https://www.ncdc.noaa.gov/). Daily minimum and maximum air temperatures are extracted from the nearest station to each location where the model is calibrated or validated. Hourly temperature data are then calculated from daily maximum and minimum air temperature using the algorithm described in Woodhead (1979) and applied in Gilioli et al. (2014).

2.5.2. Climate scenarios

Climate scenarios are obtained from the Coordinated Regional Downscaling Experiment (CORDEX) and refer to Regional Climate Model (RCM) simulations for the European Domain (from 27th to 72th parallel north and from the 22th meridian west to -45th meridian east) (Jacob et al. 2014). Scenarios provide tri-hourly bias-adjusted air temperature at a 0.11° x 0.11° spatial resolution. The scenarios refer to the Coupled Model Intercomparison Project Phase 5 (CMIP5) and are based on Representative Concentration Pathways (RCPs) (Van Vuuren et al. 2011), i.e., the greenhouse gases emission scenarios corresponding to a determined radiative forcing up to the year 2100. We have used two RCPs available for the European domain: the RCP4.5 (referring to a stabilization of radiative forcing from 2150 onwards at 4.5 W/m²) and the RCP8.5 (referring to rising radiative forcing crossing 8.5 W/m² at the end of 21st century). Temperature data are re-gridded to a regular 0.1° x 0.1° grid through bilinear interpolation using Climatic Data Operators (Schulzweida 2019) and averaged over a period of 10 years in order to avoid extreme climatic variations. The climatic scenarios used in the present study refer to 2020 RCP4.5 (average for the years 2016-2025) assumed as the current climate (see Supplementary materials for details), 2030 RCP8.5 (average for the years 2026-2035) and 2050 RCP8.5 (average for the years 2046-2055).

2.5.3. Data on population abundance and distribution

Time series data related to *C. capitata* adult trap catches collected from five independent studies are used for model calibration (Figure 1). Studies were conducted on fruit orchards or on wild plants in Latium in 2007 (Sciarretta and Trematerra 2011), in Tarragona in 2007 (Martínez-Ferrer et al. 2010), in Thessaloniki in 1991,(Papadopoulos et al. 2001) in Dubrovnik in 2002,(Bjeliš et al. 2007), and in Kibbutz Zova between 1994 and 2001 (Israely et al. 2004).

Information on the occurrence of the species from the Trentino Alto Adige/Südtirol describing its northern limit of distribution in Italy are used for model validation along an altitudinal gradient. In the area of Riva del Garda, at the foothills of the Alps the species has been sporadically reported since 1990 with only marginal impacts on fruit orchards. However, in 2016, the area was characterized by high presence of the species showing a transition towards more stable populations (Zanoni 2018). In other two locations, Bressanone and Bolzano from the same region, further up north from Riva del Garda and into the Alps, the species is not reported to occur, therefore they can be considered outside the species' potential capacity for establishment. Data on the occurrence of *C. capitata* in Europe collected from de Meyer and Heughebaert (http://www.biodiversity.be), Szyniszewska and Tatem (2014) and from the Global Biodiversity Information Facility dataset (https://www.gbif.org/) are used for validating the model in its capacity to predict the current distribution of the species. The occurrence data presented in Figure 1 refer to the countries where the species is considered present, based on the information reported from the European and Mediterranean Plant Protection Organization (EPPO) Global database (https://gd.eppo.int/).

3. Results

3.1. Model calibration and validation

The mean quadratic distance between observed and simulated adult abundance of *C. capitata* in the five tested locations using the parameters minimising the functional Q is reported in Table 4.

Table 4. Results of model calibration obtained comparing observed and simulated within-year population dynamics data. Mean quadratic distance between observed and simulated adult abundance is used as criterion for best fitting procedure (general minimisation default tolerance of 10^{-5})

Area	Location	Mean quadratic distance between observed and simulated adult abundance
Central Italy	Latium	46.22
North-eastern Spain	Tarragona	24.86
Central Greece	Thessalonikki	50.94
Southern Croatia	Dubrovnik	40.17
Central Israel	Kibbutz Zova	14.67

The parameters obtained representing the biotic components of the mortality function (8) $\delta^{i}$and N_{max}^{i} are used in the present study (Table 5). The validation procedure reveals that the model is able to interpret the altitudinal limit of the distribution in a transect crossing the Alps in northern Italy. The model successfully predicts the presence of stable populations in Riva del Garda (Trento, Italy) (Zanoni 2018), and a sharp drop to zero in the population abundance along the altitudinal gradient in Bolzano and Bressanone (Bolzano province, Italy). In these two locations, stable populations of *C. capitata* are not reported as the weather conditions do not allow the species to survive in winter. The vast majority of the occurrence data for *C. capitata* falls within the area of distribution predicted by the model (see Figure 1) confirming the model's capacity to accurately predict the northernmost distribution limit in Europe.

Table 5. Estimated parameters of the density-dependent mortality rate function (8) that minimize functional *Q*

Stage	$\boldsymbol{\delta}$	$\boldsymbol{N_{max}}$
Larvae ($i = 2$)	4.5459 . 10-2	1.5361 . 104
Adults ($i = 4$)	2.5579 . 10-1	1.5677 . 101

3.2. Distribution, abundance and activity of C. capitata under current climate scenario

The simulated distribution and the yearly mean abundance of *C. capitata* adult and larvae in Europe for 2020 is reported in Figure 1 and in Figure 2 respectively.

The predicted current distribution of *C. capitata* covers the Iberian Peninsula, Morocco, Algeria, Tunisia, Greece, part of Turkey, Syria, the coastal area of the Balkans, the Danube area of Romania and Bulgaria, Italy and the south-western France. The mountainous areas are not suitable for the species, as it is clearly showed in Spain, Italy and the Balkans. Established populations of *C. capitata* can potentially reach the 48th parallel north in France with some sporadic populations in the central part of the country where climatic conditions are more suitable. In the southern France and the northern Italy, the distribution is limited to the 46th parallel north. This latitude marks the distribution limit also in the eastern Europe where the distribution is not continuous over the Balkan area but is influenced by the local climatic conditions. The yearly average number of adult ranges between 1 (the threshold set for defining the possibility of establishment) and 30 (the maximum level of abundance reported in southern Italy). Yearly mean larval abundance ranges between 30 (the threshold set for defining the possibility of establishment) and the maximum value of 2545 individuals per unit area reported in Morocco. In Europe, the higher average number of adults (30 individuals) and larvae (above 2500 individuals) are reported in Andalucía (southern Spain), Sicily (southern Italy) and Cyprus. The yearly mean population abundance decreases along a south-north gradient.

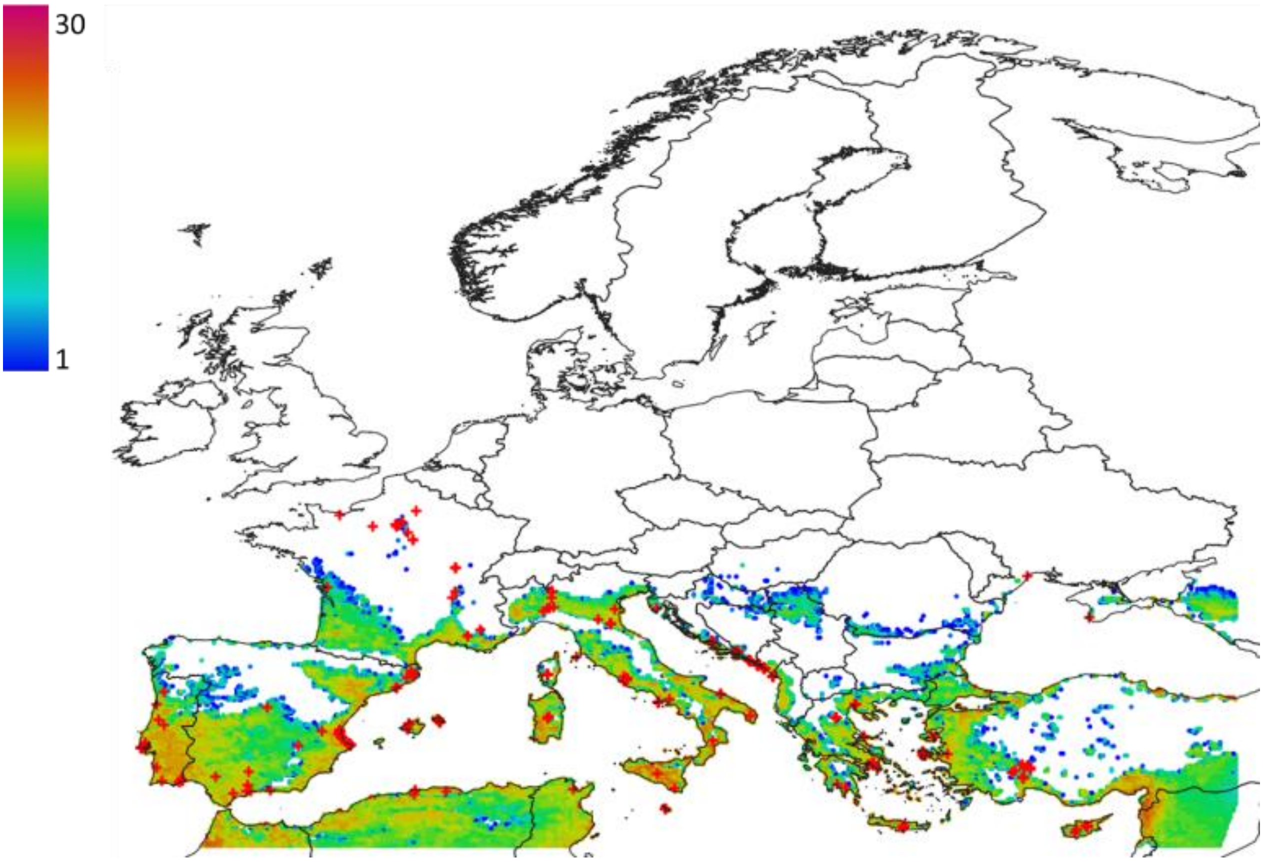

Fig.1 Heat map showing the predicted distribution and the yearly mean adult abundance of *C. capitata* in Europe (expressed as number of adults per unit area) under current climate scenario (year 2020). Red crosses represent the occurrence data of *C. capitata* in the countries where the species is considered established, as reported in the EPPO Global database (https://gd.eppo.int/)

Higher population abundance is predicted in the warmer areas of southern Europe and in the eastern coasts of the Mediterranean Basin (Turkey and the Near East). Population abundance drops down towards the northernmost distribution limits of the species or towards the mountainous areas. Figure 3 shows the relation between the average yearly temperature and the average yearly adult and larval abundance under current (2020) climatic scenario. Model's outputs suggest that populations of *C. capitata* are not able to establish in the areas characterised by a yearly average temperature below 12.4 °C. Above this threshold, population abundance clearly increases with temperature. The rate of increase progressively diminishes for temperatures higher than 15-16 °C. The graph highlights the non-linear response of population abundance to the yearly average temperature.

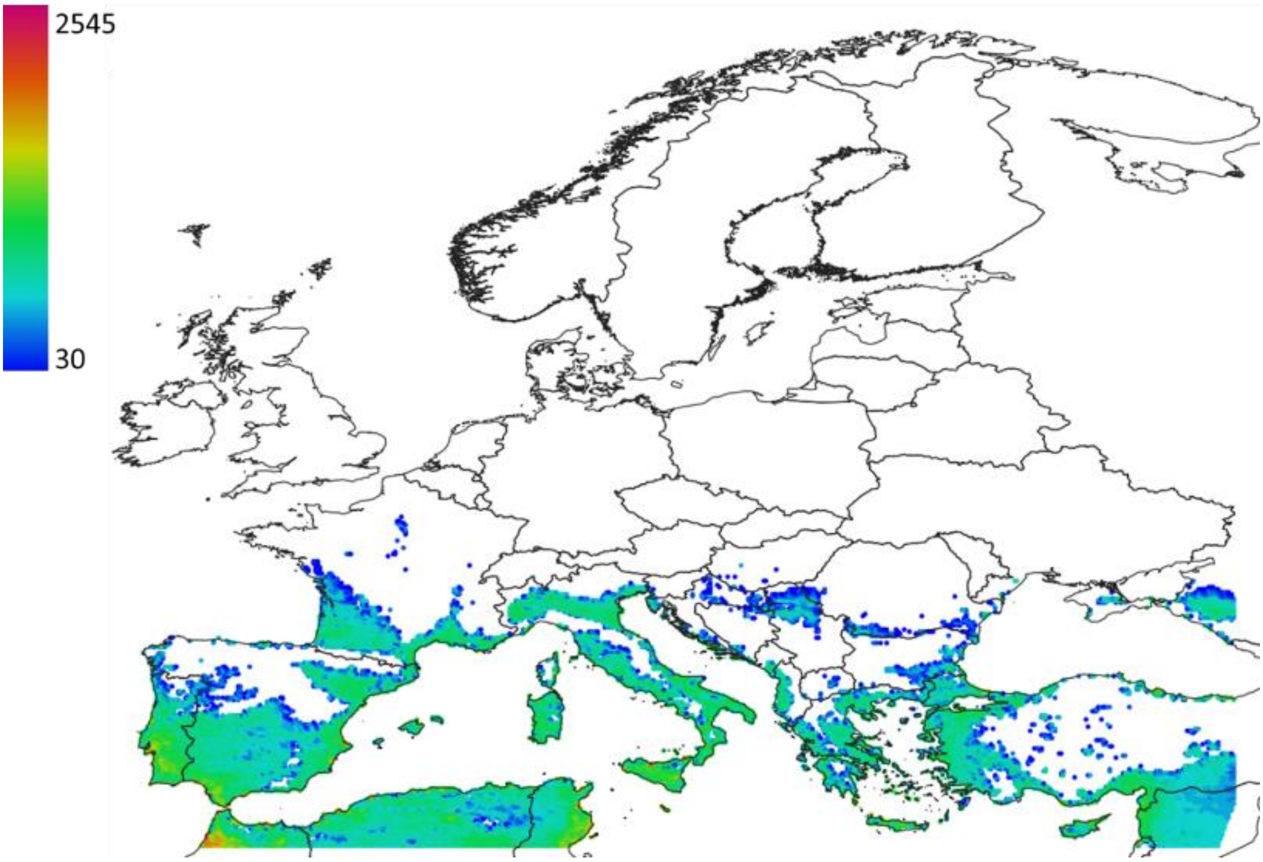

Fig.2 Heat map showing the predicted distribution and the yearly mean larval abundance of *C. capitata* in Europe (expressed in terms of number of larvae per unit area) under current climate scenario (year 2020)

The simulated adult and the larval activity of *C. capitata* adult and larvae in Europe for 2020 is presented in Figure 4. Low activity is recorded towards the northern distribution limit of the species or in the inland areas, while moving south and along the Mediterranean coast, an increased activity of both adults and larvae is observed. The model predicts a continuous activity of adults in the coastal and in the inland areas of Morocco, Algeria, and Tunisia, and the southern coastal areas of Spain, Portugal, Italy, Greece, Turkey, Cyprus and Near East. The area characterized by the presence of larval populations for the entire year is more extended, and covers the Mediterranean coasts of southern Europe, the inland areas of Spain, Portugal, Turkey, and the Near East.

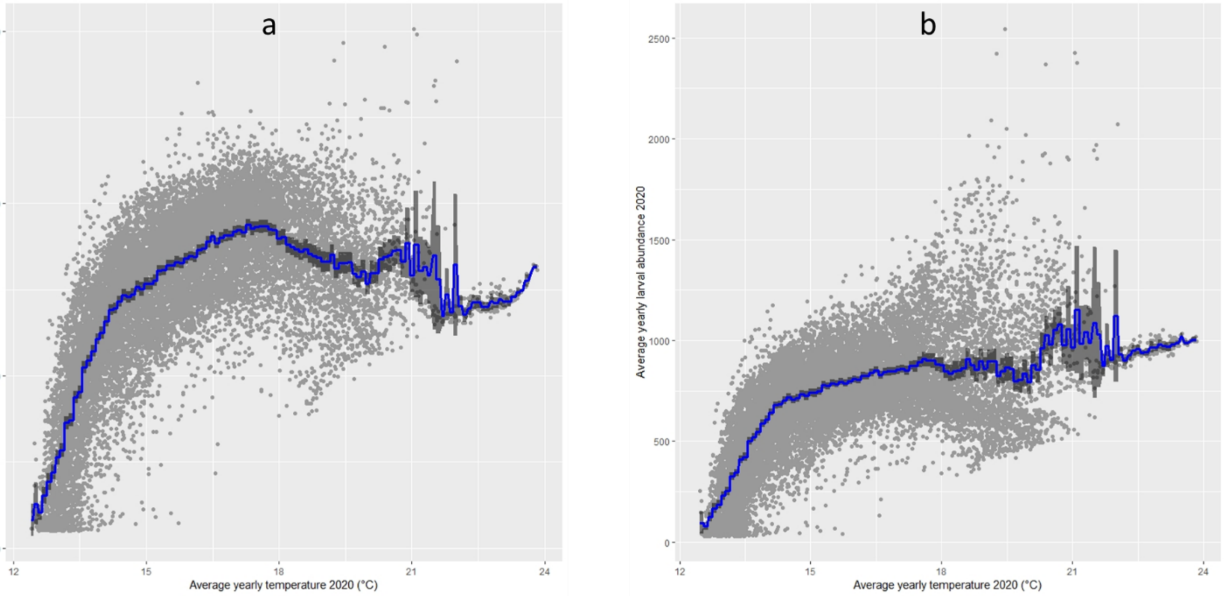

Fig.3 Scatter-plot with mean and 95% confidence interval representing the relation between the average yearly temperature and the average yearly abundance of adult (a) and larval (b) individuals of *C. capitata* under current (2020) scenario.

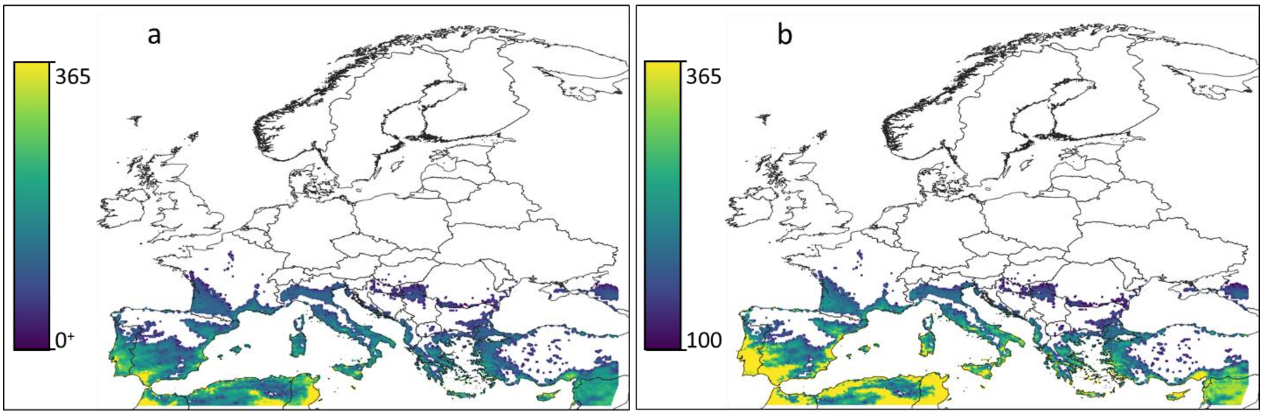

Fig.4 Heat map showing the predicted adult (a) and larval (b) activity (expressed as number of days in which the population abundance is equal or greater than one adult individual or 30 larval individuals per unit area) under current climate scenario (year 2020)

3.3. Distribution, abundance and activity of C. capitata under climate change scenarios

We run the model using the 2030 and 2050 climate scenarios and compare the results with the 2020 scenario. The results (Figures 5-8) are presented in term of variation of the output variables (populations abundance and activity *of C. capitata*) with respect to the 2020 scenario. A positive variation means an increase in the output variable (higher abundance or longer period of activity with respect to the 2020 scenario); a negative variation shows a decrease in the output variable (lower abundance or shorter period of activity with respect to the 2020 scenario).

In 2030, the potential distribution of the species increases in the inland areas of France, and reaches southern Germany, Switzerland, Austria, and Hungary. In 2030 It is observed a range of variation of -4 (-13%) and +14 (+47%) for adult individuals and -234 (-9%) and +700 (+27%) for larval individuals respect to 2020 (Figure 5).

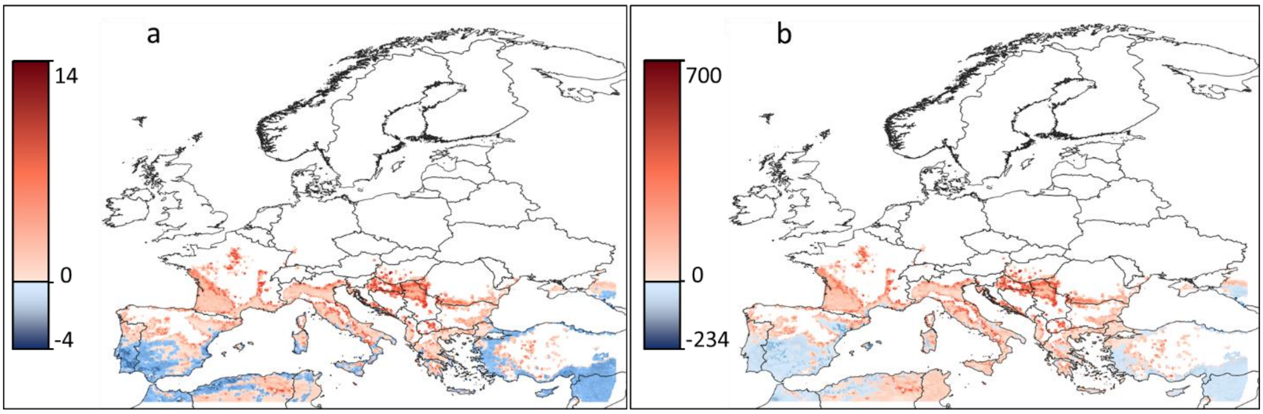

Fig.5 Heat map showing the predicted variation in the average adult (a) and larval (b) abundance between scenario 2030 and current (2020) scenario

The variation of population activity (Figure 6) ranges between -64 and +110 days for adults and between -152 and +220 days for larvae. In 2050, the model predicts established populations reaching northern France, central Germany, Poland, and the Netherlands (Figure 7). The comparison between the 2020 and 2050 scenarios shows variation of population abundance ranging between -4 (-13%) and +18 (+60%) for adults and between -129 (-5%) and +888 (+35%) for larvae (Figure 7).

The variation of population activity ranges between and -50 and +173 days for adults and -28 and +279 days for larvae (Figure 8).

Overall, scenario comparisons show both an increased population abundance and activity towards the species' northern distribution limit and towards the inner areas of the Mediterranean basin. The decrease in population abundance is particularly evident in continental Turkey, the Iberian Peninsula, Morocco, Tunisia and Algeria. The decrease in population activity is more pronounced in 2030 (especially, in central Spain and Portugal).

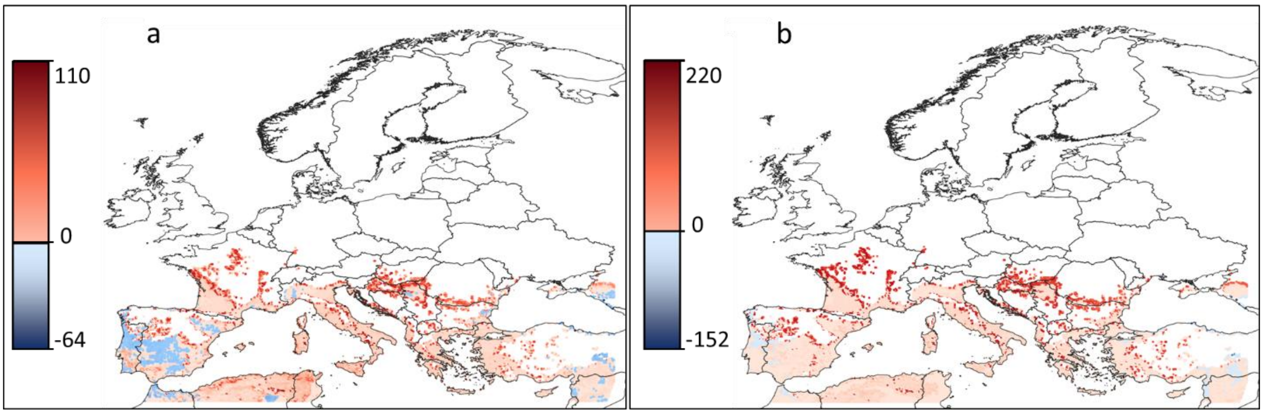

Fig.6 Heat map showing the predicted variation in the adult (a) and larval (b) activity (expressed as number of days in which the adult population abundance is equal or greater than one individual and the larval population abundance is equal or greater than 30 individuals) between scenario 2030 and current (2020) scenario

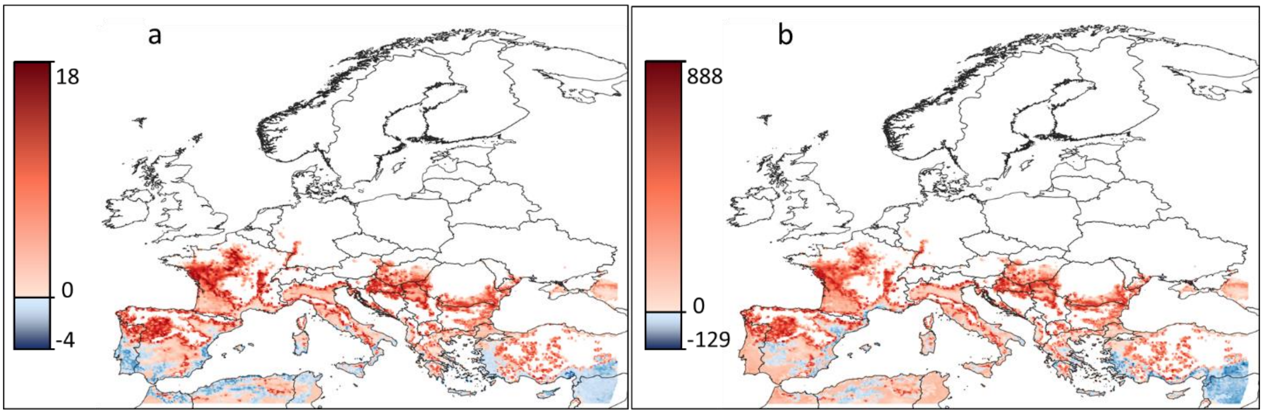

Fig.7 Heat map showing the predicted variation in the average adult (a) and larval (b) abundance between scenario 2050 and current (2020) scenario

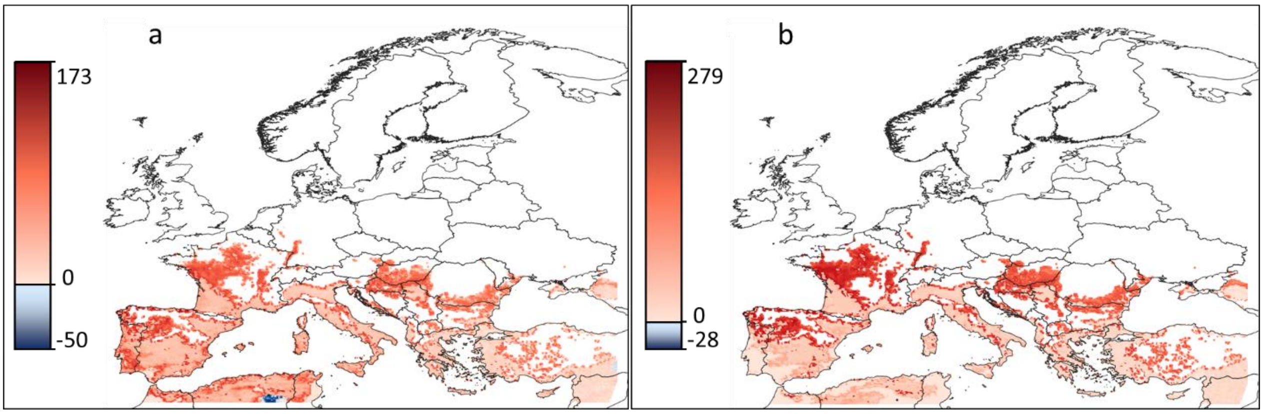

Fig.8 Heat map showing the predicted variation in the adult (a) and larval (b) activity (expressed as number of days in which the adult population abundance is equal or greater than one) between scenario 2050 and current (2020) scenario

4. Discussion

Model simulations show that the current northernmost distribution limits of *C. capitata* reaches the 46th parallel north in Italy and in the eastern Europe while sporadic populations are able to reach the 48th parallel north in France. The predicted current distribution of *C. capitata* complies with the most updated data related to the occurrence of the species in Europe (http://www.biodiversity.be; https://www.gbif.org/; Szyniszewska and Tatem 2014). This as indications about the validity of the predictions of the model presented. Local climatic conditions is a key factor for defining the area of potential distribution of *C. capitata* as for distribution and dynamics of poikilotherms (Walther et al. 2002; Svobodová et al. 2014; Battisti and Larsson 2015; Merrill and Peairs 2017). Areas above the predicted current distribution limits shall be considered as climatically unsuitable for the establishment of *C. capitata* even though an accidental introduction of the species might result in the local presence of transient populations surviving in refuge areas or under particularly warm winter conditions. Overall, the model predicts a south-north gradient in relation to the population abundance and activity of *C. capitata* with higher populations observed in southern Europe and along the Mediterranean coastal areas. Within the area of potential establishment also the altitudinal limit, influenced by climate is an important factor limiting the distribution of the species towards mountainous areas. The continuous presence of adult individuals within the year is predicted for the southern Mediterranean coasts and the Near East while the area interested by the continuous presence of larvae is more extended and reaches the southern coasts of France. This result suggests the capacity of *C. capitata* to overwinter as larva especially in Mediterranean areas while adults are not able to survive cold winter conditions (Papadopoulos et al. 1996; Peñarrubia-María et al. 2012). Even if this hypothesis is still under debate (Israely et al. 2004), results from other studies suggest that the species might be able to overwinter in areas characterised by temperate winters or under sub-freezing temperatures (Papadopoulos et al. 1996, 1998, 2001; Rigamonti 200; Escudero-Colomar et al. 2008). Projections on the potential activity of the species should be carefully considered and supported by further ad-hoc studies.

The effects of climate change on model outputs, namely species distribution, abundance and activity, are not homogeneous in the whole territory under investigation and no simple trends or gradients can be derived. Model projection allows identifying patterns of variation in Europe that describe the joint effects of the spatial heterogeneity in the expected change in temperature and the non-linear temperature-dependent response of the species' life-history traits. The results of our scenario comparison show five different patterns in the investigated area:

- A northward expansion of the area of potential distribution of the species. The area of distribution increases of +12% in 2030 and +42% in 2050 respect to the 2020 scenario. The northward expansion of the species is evident in central Europe. Therefore, areas that are currently not suitable for the establishment of the species due to low temperatures might become more suitable under a changing climate.
- A rise in the altitudinal limit marking the presence of established populations. This is particularly evident along the border between Spain and France (Pyrenees), in Italy (Apennines) and along the borders between Italy, France, Switzerland, and Austria (Alps).
- Increase in population abundance of *C. capitata*. The percent area interested by this phenomenon is 62% (adults) and 64% (larvae) in 2030, and 79% (adults) and 86% (larvae) in 2050. The increase in the abundance and activity is prominent towards the northward distribution limit and along the altitudinal limit of distribution of the species. The increase can be explained in terms of species physiological responses to temperature variation. In these areas, temperature variations act to the almost linear and positive (slope > 0) area of the rate functions expressing the species' life history traits (development, fecundity and survival).

- Stability in the population abundance of *C. capitata*. The percent area of potential distribution in which the population abundance is stable is 21% (adults) and 13% (larvae) in 2030, and 7% (adults) and 4% (larvae) in 2050. Stability of the populations is evident in southern Portugal, the coastal areas of Italy and Greece, limited areas of the Near East, Morocco and Algeria. The temperature variations in these areas are in the range where the rate functions are non-linear and close to the maximum values. In this range, positive and negative life-history traits responses to temperature compensate.
- A decrease of population abundance of *C. capitata*. The percent area interested by this phenomenon is 17% (adults) and 23% (larvae) in 2030, and 14% (adults) and 10% (larvae) in 2050. This pattern is particularly relevant in vast areas of Morocco, Algeria and Tunisia, the Near East, Turkey, southern Spain and limited areas in southern Italy. This decrease in population performance is probably due to the effects of the increase of temperature acting to the range where the rate functions are non-linear and negative (slope < 0).

The non-linearity of population responses to climate change derives from the interaction between individual's physiological responses, spatial and temporal heterogeneity of current and future climate. The complexity and the non-linearity of population responses to temperature is highlighted in Figure 9 where we represent the changes in the average population abundance of adult individuals of *C. capitata* with respect to the average yearly current temperature and the temperature variation under climate change (yearly average variation between 2020 and 2050).

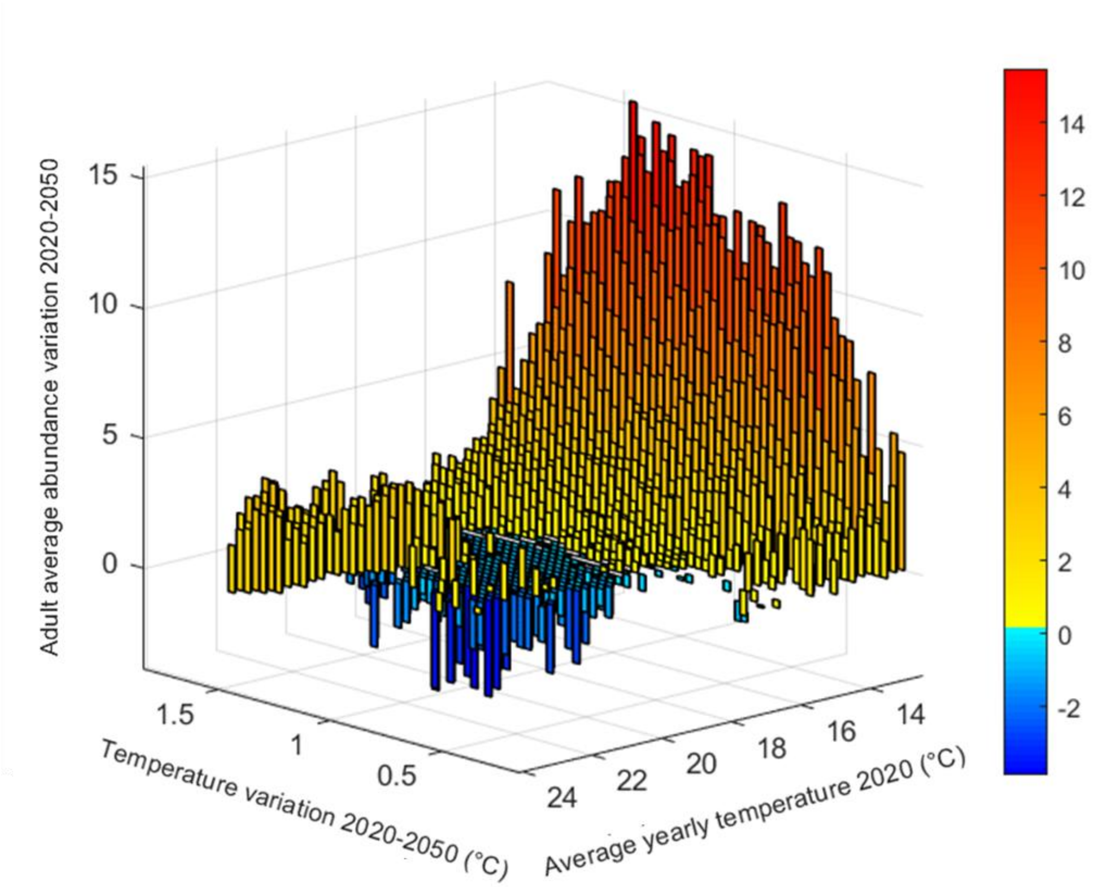

Fig.9 Bar-plot showing the predicted changes in the adult population abundance of *C. capitata* (comparing 2020 and 2050 temperature scenarios) respect to the current temperature and the yearly temperature variation in the two climatic scenarios. The graph considers only the area where the species is established in 2020 according to model's results

Model's output allow the identification of the following:

- The higher positive variation in the average adult population abundance is reported for the areas characterised by lower yearly average current temperature and where higher positive temperature variations are expected in 2050.
- The adult population abundance variation shows a non-linear decrease as the yearly average current temperature rises.
- In the areas characterised by yearly average current temperature approximately above 17 °C and a temperature variation below 1.5 °C the variation in the abundance of *C. capitata* might even be negative.

- In the areas characterised by temperature higher than 22 °C, and with positive temperature variations above 1.5 °C due to climate change we observe a positive and mild increase in the abundance of *C. capitata*.

5. Conclusions

In this paper, we present the results of a process-based, stage-structured model providing quantitative information on distribution, abundance and activity of *C. capitata* under current climate and future climatic scenarios. The model presented provides future pest projections that can inform decision-makers in the allocation of efforts and resources for the management of the pest in the areas considered at major risk of invasion of *C. capitata* (Hill et al. 2016a; Weldon et al. 2018). The model allows the investigation of the non-linear physiological responses to environmental forcing drivers (and their variations both in time and in space) at the individual and at the population level. The capacity to describe and interpret the heterogeneity in the population responses to climate change are fundamental elements in guiding the assessment and the management of future risks linked to *C. capitata* at both the regional and the local spatial scale (Hill et al. 2016a; Weldon et al. 2018). The model can also be applied at the local scale for estimating high temporal and spatial resolution outputs in terms of within-year pest population dynamics and phenology. This output can be used for supporting the definition of the optimal timing for the implementation of monitoring or pest treatment activities at the local scale (Manoukis and Hoffman 2014; Kean and Stringer 2019; Rossi et al. 2019). Simulations at high spatial and temporal resolution are valid support for pest management in areas where the species is well established, but they might also be applied for investigating transient populations of *C. capitata* and assessing the risks of establishment of the species in new areas (Papadopoulos et al. 2013; Kean and Stringer 2019).

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Supplementary materials

Results of monthly-wise Pearson correlation test between scenario (scn) and observed (obs) temperature data. Scenario data refer to bias-adjusted, 2-meters air temperature (2016-2025) data generated by CNRM-CERFACS within the CMIP5 (Coupled Model Intercomparison Project Phase 5) Project. Observed air temperature (2010-2019) data are extracted from the E-OBS 21.0e Dataset (Cornes et al. 2018). The correlation test was performed on a subset of 10% of randomly selected grid cells.

Table S1. Results of the monthly-wise Pearson correlation test between scenario and observed temperature data

Month	**rho**	**p value**
Jan	0.948	0
Feb	0.956	0
Mar	0.959	0
Apr	0.973	0
May	0.968	0
Jun	0.963	0
Jul	0.970	0
Aug	0.977	0
Sep	0.976	0
Oct	0.972	0
Nov	0.975	0
Dec	0.952	0

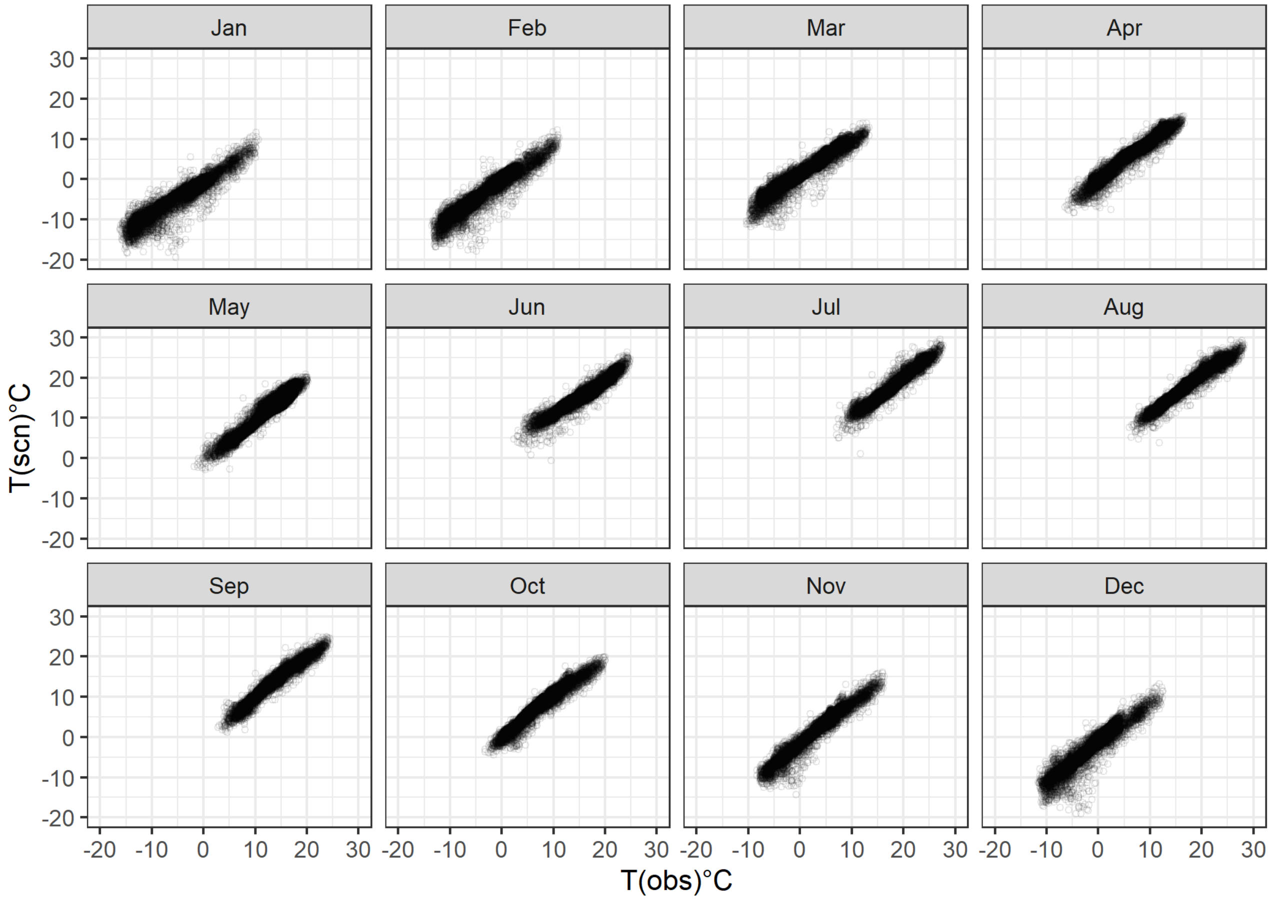

Fig.S1 Scatter-plot showing the monthly-wise correlations between scenario and observed temperature data

CHAPTER 6 - Concluding remarks

The present Thesis focuses on the definition and the application of a mechanistic modelling framework supporting decision-making in pest management considering different contexts (from IPM to PRA) and spatial scales (from local to area-wide management) of application. These concepts are thoroughly discussed in Chapter One.

In Chapter Two, a review is provided on the benefits, the barriers and the critical success factors linked to the use of models as decision tools for pest management. In this chapter are discussed factors determining the success and the usefulness of models as tools supporting decision-making in pest management with particular emphasis on IPM. Among them, importance is given to a thorough model calibration and validation phase, model's transparency, user-friendliness, precision and reliability of model outputs.

Chapters Three to Five, present a set of case studies of application of a mechanistic (i.e., process-based) modelling approach supporting the management of several pest species. In these chapters are explored the requirements and the implications for model development and implementation considering the management context and the scale of application. For a process-based modelling approach the key issues emerging from this exploration are: i) the realistic representation of the biological system under investigation, ii) the mathematical representation of the influence of environmental drivers on the pests' physiological responses and life-history strategies, iii) a thorough model calibration and validation phase taking into account independent field datasets, and iv) the provision of relevant and quantitative outputs, useful in pest management.

Chapter Three shows the results of a phenological model simulating the diapause and the phenology of the Japanese beetle (*Popillia japonica*). The phenological model realistically represents the role of soil temperature on the life-history strategies of the species, including diapause termination. This is the first time that the diapause termination process is simulated in a model predicting the phenology of *P. japonica*. The phenological model is designed to support the management of pest populations at the local level. Predictions on the time of emergence of the adult stage allow to schedule and implement monitoring and treatment activities. This type of output is particularly relevant in IPM, where it is expected to monitor the presence of the pest and to target pesticides treatments only when susceptible life-stages are present. Additionally, the model can be applied at a wider spatial scale for the development of high-resolution maps showing the pattern of emergence of the species based on local weather conditions.

Chapter Four presents the results of the first physiologically-based model developed for interpreting and describing the fall armyworm moth (*Spodoptera frugiperda*) population dynamics. The model introduces an important novelty for stage-structured population models that are described by the Kolmogorov equation: a density-dependent control term that accounts for the intraspecific competition on species population dynamics. Intraspecific competition is simulated through a density-dependent mortality influencing larval survival. The quantitative output provided by the model is the stage-specific population abundance at the local level. This output is of particular importance for the local management of the pest since it is the most important driver of the pest's potential impact on the host plants and it can be used for guiding control interventions. Within the IPM framework, the availability of information on population abundance is crucial, since decisions are taken comparing the actual abundance value with thresholds defining conditions when the economic and ecological costs due to the implementation of a phytosanitary measure are lower than the expected impacts caused by the pest. The model on *S. frugiperda* can be also applied at a wider spatial scale (e.g., at National or at Continental spatial scale) for the development of maps supporting the risk assessment (area of potential establishment and evaluation of the potential impact based on local weather and climate information) and risk management (including surveillance) of the species within the PRA framework. Outside the area of potential establishment, the model can also support the assessment of the risk due to the transient populations. This information is of particular importance, for instance in Europe where the species is not present so far, but the risks of introduction and establishment of the species are high, especially in the Mediterranean region.

In Chapter Five, are presented the results of a physiologically-based population dynamics model investigating the potential impacts of climate change on the distribution, the period of activity and the abundance of *Ceratitis capitata* in Europe. The species is well established in Europe, and it has been reported an expansion of the distribution in recent years due to climate change. The model developed is used to investigate the possibility of a further increase in the area of distribution and a change in abundance and impact of the pest in future climatic scenario. The model performs a high spatial resolution analysis on the changes in the distribution, the activity and abundance of the species under current (year 2020) and future (year 2050) climate. Particular attention is given to the non-linear effects of temperature variations on species' responses at both individual and population levels. The results of the model presented are particularly relevant for the assessment and the management of the risks linked to the species within the PRA framework. In particular, the model allows to investigate the joint effects of spatial heterogeneity in the temperature changes and the non-linear responses of the species to temperature. Model outputs clearly shows that no simple trends can be drawn when assessing the future risks linked to pests in relation to climate change scenarios. For instance, higher risks are expected in those areas where positive temperature variations due to climate change positively influence species life-history (e.g. increased development and fertility and reduced mortality). On the contrary, lower risks are expected in those areas where positive temperature variations negatively influence species life-history traits (e.g. reduced development and fertility and increased mortality). The quantitative evaluation of these trends are particularly relevant in PRA for understanding the potential role of climate in ruling pests distribution and impacts.

Given the role of pests in shaping food security in a changing world and the multiple drivers influencing pests' distribution and impacts, tools for defining and implementing rational pest management schemes are of primary importance. Due to the complexity related to pest-plant-environment interaction and the requirements of decision-making process, mechanistic models might represent important tools in supporting rational, scientifically-sound and cost-efficient pest management. The modelling framework presented in this Thesis is a valid candidate for providing key elements for supporting decision-making in pest management. The case studies presented represent successful examples of application of the methodological framework which led to the development of reliable models supporting the management of pests under different contexts of management (from IPM to PRA) and at different spatial scales (from local to area-wide management).