Modelling the effect of *Bt* maize introduction on pest dynamics, insecticide use and economic returns to farmers

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Thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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May, 2016

Declaration of Authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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May, 2016

ABSTRACT

The use of genetically engineered (GE) crops promises to deliver remarkable results from an environmental, economic and human health point of view. Presently, the world area planted with GE crops is devoted mainly to three sorts of genetic alteration, herbicide tolerance, insect resistance (IR) or a combination of both. In this thesis, the discussion focuses on genetically engineered insect resistant (GEIR) crops expressing toxins from the soil bacteria *Bacillus thuringiensis* (*Bt*) producing Crystalline (Cry). The prevailing scientific opinion is that although GEIR crops carry a certain degree of uncertainty, the potential risks are not considerably different to those associated with insecticides. Given the current understanding, the actual dispute about the risks is based mainly on the potential long-term effects, including gene slipover, development of pest resistance and the impact on non-target organisms. A further concern is that insect species that are not susceptible to the expressed toxin will develop into secondary pests and cause significant damage to the crop.

In this thesis, the causes and impact of secondary pest outbreak are reviewed, analysed and incorporated within a novel bio-economic modelling framework. The bio-economic model takes into consideration the dynamics of two pest insects competing for the same resource and the resultant impact on maize farmers' net returns. The modelling developed culminates with the inclusion of spatial features explicitly represented. The resulting bio-economic spatially explicit population model evaluates the development and impact of an invasive species that is not susceptible to the insecticide toxin expressed by the transgenic crop. This work provides insights and future recommendations for academic research, policy makers and farmers regarding the control and management of a new incursion of hazard (non-native) species. The research undertaken in this thesis aims to fill an important research gap on the impact of secondary pests GEIR crops, in particularly *Bt* maize. Overall, the results show that the use of *Bt* maize could indeed bring economic benefits to farmers while decreasing the burden of insecticides. It is also demonstrated that farmers need to be conscious of the possibility of an outbreak of a secondary pest and the consequences of this on yields and farm profits. Depending on several factors, it may take a number of years for secondary pests to proliferate to relevant levels of importance, thus the need to understand pest dynamics.

OUTLINE OF PUBLICATIONS

Manuscript 1

Catarino, R., Ceddia, G., Areal, F. J. and Park, J. (2015) *The impact of secondary pests on Bacillus thuringiensis (Bt) crops*. Plant Biotechnology Journal, 13 (5). pp. 601-612. ISSN 1467-7652 doi: 10.1111/pbi.12363

Manuscript 2

*C*atarino, R., Ceddia, G., Areal, F., Parisey, N. and Park, J. (2016) *Managing maize under pest species competition: is Bt (Bacillus thuringiensis) maize the solution?* Ecosphere. ISSN 2150-8925 (In Press)

Manuscript 3

*C*atarino, R., Areal, F., Parisey, N. and Park, J. (2016) *Predicting the patterns and effects of non-susceptible pests' invasion on Bt maize: a bio-economic spatially explicit population perspective.* PlosONE. Under review

ACKNOWLEDGMENTS

This thesis is not merely an exercise of scientific knowledge pursue, ultimately it is the culmination of an extraordinary three years' journey. I have been provided with a life lesson that I will carry forever. I have certainly endured some stressful, exhausting and hectic moments over this period. Yet no comparison can be made with the numerous joyful experiences shared with new and old colleagues and friends within and outside Reading. I recognize, with an immense gratitude, the scholarship provided by the AMIGA project. Certainly I would not have been able to realise the fulfilment of my research without this support.

First and foremost I would like to express my sincere gratitude to Professor Julian Park, Dr. Francisco Areal and Dr. Graziano Ceddia, my PhD supervisors, for their support, guidance, useful criticism, enormous encouragement and patience over these years. A great thanks also goes to Dr. Nicolas Parisey for all the insights and valuable technical support along these years. A special word of appreciation goes to Professor Nikos Georgantzis and Dr Nick Bardsley for their support and illuminating scientific (and other!) discussions. Many thanks as well to Dr Alice Mauchline, my academic tutor, for providing support when needed. Lastly, I would like to extend my special appreciation to all staff members of the School of Agriculture, Policy and Development and of the MODUL University for their support and compelling discussions.

Over these years, I have crossed paths with many peoples, with whom I have shared the most bitter as well as the most thrilling moments. My Portuguese manos e manas, who were and always will be there: Ritinha, Naza, André, Duda, Xibo, Palma, Joaninha, Sary and Catarina; Kawaii, a full life will not be sufficient! An exceptional thank you to my colleagues, Jose (oh well!), Moon, Dr. Mark Hirons, Dr. Alex Arnall, Dr. Yiorgos Gadanakis, Toju and Tuyo; my housemates: Nico, Nenia, Aldo and Silvia (□□□); to those that will stay for life and beyond: Dr. Eddie, Manuela, Edd, Mr. Taylor, Cal and Francesco; to my whole Global family; and to my Karate club colleagues.

Finally, I would like to dedicate this thesis to my family, especially to my grandparents. Avô, nunca esquecerei as tua lições e ... Avó, não existem palavras para expressar o meu agradecimento por tudo o que fizeste por mim. Mãe obrigado por estares sempre ao meu lado, Pai the greatest man I have ever met!, Americo, sem a tua ajuda há muitos anos, nada disto seria possivel, my sisters, Tania, Anita e Carol, Pimona … love you all deeply, and my godson…padineee ☺

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LIST OF ACRONYMS

ASCII:	American Standard Code for Information Interchange
Bt:	*Bacillus Thuringiensis*
CEW:	Corn Earworm
Cry:	Crystalline
DAISIE:	Delivering Alien Invasive Species Inventories For Europe
DE:	Differential Equations
DEA:	Differential Evolution Algorithm
ECB:	European Corn Borer
EIL:	Economic Injury Level
ESEB:	European Socio-Economic Bureau
ET:	Economic Threshold
EU:	European Union
FIFRA:	Federal Insecticide, Fungicide and Rodenticide Act
GA:	Genetic Algorithms
GE:	Genetically Modified
GEIR:	Genetically Engineered Insect Resistant
GSA:	Global Sensitivity Analysis
HT:	Herbicide Tolerant
IR:	Insect Resistance
LCM:	Land Cover Map
LV:	Lotka-Volterra
LZ:	Lichtenberg And Zilberman
MAGRAMA **:**	Ministerio De Agricultura, Alimentación Y Medio Ambiente
MCB:	Mediterranean Corn Borer
MS:	Member State
NPV:	Net Present Value
NTO:	Non-Target Organisms
ODE:	Ordinary Differential Equations
PDE:	Partial Differential Equations
RD:	Reaction-Diffusion
RK4:	Runge–Kutta 4th Order
SP:	Secondary Pest
TAW:	True Armyworm
WCB:	Western Bean Cutworm
WCR:	Western Corn Rootworm

CHAPTER 1. GENERAL INTRODUCTION

1.1 Contextualizing biotechnology, agriculture and the present research

The application of biotechnology in agriculture, sometimes referred to as gene revolution (Raney 2007), can potentially mitigate some of the backlashes caused by agriculture intensification in the 20th century (Tilman 1999). The potential wide benefits include a decrease in pesticide burden, reduction of water requirements, enhanced crop capacities in less viable soil conditions and nutritional enhancement of essential crops (Gura 1999, Wolfenbarger and Phifer 2000). Presently, the world area planted with GE crops, 179.7 million hectares, is mainly devoted to three sorts of genetic alteration: herbicide tolerance[1] (53% of the global GE area), insect resistance (IR) (14%) or a combination of both (33%) (James 2015). In this thesis, the discussion will focus on genetically engineered insect resistant (GEIR) crops expressing toxins from the soil bacteria *Bacillus thuringiensis* (*Bt*) producing Crystalline (Cry).

Given the current level of understanding, the actual dispute of risks and benefits is mainly based on the potential long-term effects, such as gene slipover, development of pest resistance and the impact on non-target organisms (NTOs) (Garcia and Altieri 2005, Smale 2006, Lövei et al. 2009). It has been argued that ecological shifts may take several years to manifest (Ho et al. 2009), and that the dispersion GEIR crops' contents vary temporally and spatially on a case-by-case basis, which may not reflect the results obtained in laboratory studies (Andow et al. 2006, Lövei et al. 2009). A further concern is that other insect species that are not susceptible to the expressed toxin will develop into secondary pests and cause significant damage to the crop (Sharma and Ortiz 2000, Wu and Guo 2005). The consummation of these concerns will certainly affect other trophic chains which, depending on the magnitude of the impact, could become of high economic and ultimately of ecological relevance.

Understanding the spatial patterns of landscape processes and the driving forces that affect flora and fauna dynamics and persistence is essential to effective pest management (Lawler et al. 2006, Melbourne and Hastings 2008). The incorporation of these dynamics into economic models is an effective way to evaluate optimal control strategies. Several models have been developed to provide management solutions combining economics and ecology (Keller 2009). These models contribute to a reduction in control or eradication costs by recommending cost-effective management procedures. The spatial dimension of bio-economic spatially explicit models provides not just new insights into biological processes. But also, by predicting the potential distributions and establishment ecological niches, the area upon control should focus is significantly lessened (Mack et al. 2000).

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[1] For further insights on genetically engineered herbicide tolerant crops, the reader is directed to Mazur and Falco (1989), Firbank et al. (2003) and Ammann (2005)

The thesis is structured as follows: in this first chapter, a brief introduction to the topic is given, and the objectives and research questions are outlined. Chapter two provides an overview of the relevant literature concerning secondary pests in the context of GEIR crops. Chapter three introduces the study context giving brief background information on the maize sector in Spain, and describing the surrogate species used in the modelling work. Chapter four provides a comprehensive study of the main causes and consequences of secondary pests in the context of GEIR crops, which serves as the basis for the work undertaken in the rest of the thesis. Chapter five develops a bio-economic model to analyse interactions between primary and secondary insect populations and the impact of different management strategies on insecticide use and economic impact over time. Chapter six expands the previous model to integrate spatial dynamics of both species using Aragon as a case study, in which the spatial characteristics of the region are explicitly incorporated. In particular, this chapter focuses on economic impact for the farmers, as accrued from the spread of an invasive species under different control strategies. Lastly, chapter seven summarizes and discusses the overall results including the implications for famers, stakeholders and policy makers. Recommendations for future research are also provided based on the findings of this thesis.

1.2 AMIGA project

This research is part of, and was funded by, the EU FP7 “Assessing and Monitoring the Impacts of Genetically Modified Plants on Agro-ecosystems” (AMIGA) project. AMIGA’s main objective is to develop a framework that establishes protection goals and baselines for European agro-ecosystems, and to improve understanding and awareness of the potential long term environmental effects of genetically engineered plants. This thesis forms part of the working pack number 10, “Economic and financial assessment of transgenic crops in the EU”, contributing in specific to task 10.3, “To estimate potential “external” economic impacts at the farm level in relation to wider agroecosystem function”.

1.3 Research objective and research questions

This thesis aims to provide a better understanding of the secondary effects of genetically engineered insect resistant (GEIR) crops, namely *Bt* maize, on the agroecosystem and economic returns to farmers. Spain has been chosen as study region because it is the leading transgenic adopter in Europe. The spatial model is applied to the Aragon since, within Spain, it is the region with the greatest *Bt* maize hectarage. Furthermore, due to the prevailing edaphoclimatic conditions maize farmers are confronted with serious pest problems, mainly from corn borers. Paradoxically, it is the high specificity and efficiency of *Bt* Cry toxins against corn borers that may offer ideal ecological conditions for the outbreak of secondary pests. There is the possibility that non-susceptible pests will take advantage of the expansion of GEIR crops and resultant absence of the primary pests (Eizaguirre et al. 2010). The modelling work presented in this thesis follows an ex-ant assessment perspective. The importance of predicting the biological behaviour of a primary and secondary pest, to provide the best management strategy, is stressed. The optimal pest control strategy depending on several ecological and economic specifications is explored.

Specifically, the thesis addresses the following research questions:

1) What are the main causes of a secondary pest outbreak in the context of GEIR crops?
2) What are the implications on insecticide use and related economic returns to famers when *Bt* maize is adopted?
3) What is the impact of a number of pest management options on primary and secondary pest populations?
4) What are the regional economic implications for maize farmers in Aragon if the secondary pest is an invasive species, considering the actual and different conventional/*Bt* maize proportion?
5) To what extent does non-spatial insecticide optimization provide a robust method for considering pests' spatial dynamics control?

To address the questions outlined above, the thesis is divided into four main research parts. Firstly, chapter two and three review the general literature and provide a contextualization of the study. Next, chapter four provides an extensive and specific literature review on the mechanisms that may be responsible for a secondary pest outbreak the context of GEIR. Three main conjectural causes are raised and discussed: i) a reduction in broad-spectrum insecticide applications; ii) reduction of natural enemies, and iii) niche replacement. The lessons learned in this chapter are used through the remaining thesis, i.e. they form the basis for the mathematical modelling formulation developed further.

In the third part of the thesis, chapter five, a bio-economic model is developed to analyse the interactions between primary and secondary insect populations and the impact of different management options on insecticide use and economic returns over time. The farmers' economic decision model component determines the future insecticide intensity as a function of fixed economic inputs, crop yields and pest dynamics. The final farmers' goal is to optimize the insecticide intensity with respect to an objective function criterion, the net present value (NPV), after 25 years. This methodology allows for the incorporation of several control techniques simultaneously (e.g. insecticides and *Bt* maize). By changing the relevant parameters (e.g. prices or control thresholds) numerous scenarios are analysed through sensitivity analysis. This model is applied to an agricultural landscape (whose area is normalized to one hectare) populated by a profit maximizing farmer.

The fourth part, chapter six, expands the bio-economic model to include a variety of spatial features, using a coupled reaction-diffusion system. Specifically this chapter focuses on the maize farmers' economic impact due to the spread of an invasive species under different control strategies based on the application of insecticides in the region of Aragon, Spain. This work provides a robust tool prepared to receive and incorporate pests' specific ecological spatial data to predict its impact on farmers' future net returns in a given area. Thus, chapter six not only provides new insights to understanding pest specific biological processes, but also attempts to predict the potential invasion distributions and the resultant establishment of ecological niches, i.e. the area upon pest control should focus.

1.4 Summary

GEIR crops, like other technical innovations in agriculture, may bring a range of effects on the agroecosystem which in turn have a range of secondary impacts. The aim of this thesis is to fill an important gap in the assessment of GEIR crops: the outbreak of pests that are not susceptible to the toxin expressed by the plant. Particular attention is given to the case of *Bt* maize in Spain. Using data from various sources, a spatially explicit bio-economic population model is developed to account for dynamic feedbacks between economic decisions and agro-ecological conditions to support farmers' management decisions. The final goal of the research is to provide insights into the effects of alternative control strategies on pest population dynamics and farmers' economic returns, and the impacts of such alternative pest management strategies.

CHAPTER 2. LITERATURE REVIEW

2.1 Chapter introduction

The intensification of agriculture and development of synthetic insecticides in the mid-twentieth century more than doubled worldwide grain production in the last third of the 20th century (Krebs et al. 1999). Conversely, heavy dependence on and overuse of insecticides has had many unintended consequences. Insecticides have been responsible for millions of cases of poisoning including several hundred fatalities across the globe (Ecobichon 2001). Negative environmental and ecological impacts have also been attributed to the use of insecticides, such as a reduction in biodiversity, insect resistance, negative effects on non-target species (e.g. natural enemies) and the development of secondary pests (Hardin et al. 1995, Matson et al. 1997, Vitousek et al. 1997). In spite of this, in 2011, around 1.3 thousand tons of insecticidal active ingredients were used around the world (FAOSTAT data 2011). Genetically engineered insect resistant (GEIR) crops could effectively offer a viable alternative to mitigate many of the major negative side effects and limitations of insecticides. This would support an agricultural revolution that is more productive (Conway and Toenniessen 1999) and which maintains healthy and functional ecosystems for future generations (Tilman et al. 2001, Poppy and Sutherland 2004). This chapter provides an overview of the underlying theory, principles and literature that support this research. Additionally, it introduces the general modelling approach that will be used in chapter five and six.

2.2 *Bacillus thuringiensis*

GEIR crops have been designed to control infestations of primary target pests in fields, through the insertion of the soil bacterium *Bacillus thuringiensis* (*Bt*) in the plant tissues. *Bt* is a gram-positive bacterium, common in soil, characterised by its ability to produce insecticidal crystal (Cry) proteins (Broderick et al. 2006). These Cry proteins have a specific toxic activity against larvae of some Lepidoptera, Diptera and Coleoptera (Broderick et al. 2006). It has been proposed that larvae exposure to the toxin causes a prolonged cessation of feeding and eventual death by starvation[2]. The high expressed concentration of *Bt* toxin and susceptibility of specific species delivers an almost perfect control during the whole growing season, protecting the plant during the vegetation period as well as the eventual yield (González-Núñez et al. 2000).

2.3 The uncertainties of GEIR cropping

Overall, the existing literature suggests that the benefits of commercialized GEIR crops have exceeded the expectations of field pest control failures based on worst-case scenarios so far (Tabashnik et al. 2008, Carrière et al. 2010). Additionally, due to the high specificity and efficiency of *Bt* Cry toxins toward key target pest species, it is generally accepted that any eventual detrimental impact on non-target organisms (NTO) is lower for *Bt* crops than for broad-spectrum insecticides (Cattaneo et al. 2006, Marvier et al. 2007). In theory, GEIR crops reduce the reliance on insecticides thereby enabling a reduction in farm operations, leading to possible economic, environmental and social benefits (Wolfenbarger and Phifer 2000). The reduced use of insecticides may allow higher diversity and density of beneficial arthropods (Naranjo 2005a, Lu et al. 2012). Still, regardless of fast adoption worldwide, GEIR crops remain a controversial technology surrounded by uncertainty and dividing the scientific community (e.g. the following debate: Andow et al. 2009, Lövei et al. 2009, Shelton et al. 2009).

The doubts about the sustainability of GEIR crops are mainly based on alleged methodological research faults concerning the potential long-term impacts of GEIR crops, such as the development of insect resistance and the impact on NTOs (Garcia and Altieri 2005, Smale 2006, Lövei et al. 2009). Two key arguments are used to claim that these long-term impacts will be realised: i) ecological shifts can take several years to manifest (Ho et al. 2009), and ii) the impact of *Bt* crops and/or the dispersion of its contents vary temporally and spatially on a case-by-case basis, which may not reflect the results obtained in laboratory studies (Andow et al. 2006, Lövei et al. 2009). A further concern is that other insect species that are not susceptible to the expressed toxin will develop into secondary pests and cause significant damage to the crop (Sharma and Ortiz 2000, Wu and Guo 2005). If these impacts materialise it will certainly affect other trophic

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[2] For further information on the action mechanisms of Cry toxin in the larvae midgut, the reader is directed to Broderick et al. (2006), González-Cabrera et al. (2013), Pérez-Hedo et al. (2013) and Muñoz et al. (2014)

chains which, depending on the magnitude of the impact, could become of high economic and ultimately of ecological relevance.

2.4 Secondary pest in the context of GEIR

There are two phenomena in agricultural systems that are considered as ecological backlash events that are of relevance to this concept: firstly “resurgence of insect pests” and secondly “outbreaks of secondary pests”. The former refers to a situation in which a suppressed pest population unexpectedly rebounds to greater numbers following a pest control action, exceeding the economic injury level (Hardin et al., 1995). The latter refers to the emergence of a pest other than that originally targeted by an agricultural intervention, and can be seen as “replacement” for the primary pest (Hardin et al., 1995; Metcalf, 1980). The causes responsible for both phenomena are relatively similar and include reduction in the number of natural enemies and removal of competitors (Hardin et al., 1995; Ripper, 1956). To further understand the concept of secondary pests, it is necessary to define the concept of a primary pest as the "targeted" pest for which a *Bt* crop is planted. According to FIFRA Scientific Advisory Panel (1998), a secondary pest is a "non-targeted" pest that has historically posed a small or non-existent economic threat, but which could be affected directly, by a low to high dose expressed in a *Bt* crop, or indirectly through changes in insecticide use patterns. Metcalf (1986) defined secondary pest outbreaks as a “type II resurgence”, which occurs when the primary pest is strongly affected by a pest management strategy, yet is replaced by another pest not affected by this pest management strategy. While Berryman et al. (1987, p.3) define this event as ‘an explosive increase in the abundance of a particular species that occurs over a relatively short period of time’. As a result of a secondary pest outbreak, additional pest management tactics are required. In most cases due to its swift and unexpected appearance these events will lead to spraying with broad-spectrum insecticides (Gross and Rosenheim, 2011).

2.5 The opportunistic invasive behaviour of secondary pests

The colonization of agro-ecological systems by invasive species[3], also known as biological invasions, is a growing global issue that can inflict considerable economic and ecological damage (Liebhold et al. 2015). Invasive pest species have diverse means of introduction, establishment and spatial-dynamics patterns, generally influenced by habitat suitability and anthropogenic activities (Byers 2002). They may take opportunistic advantage of altered ecosystems and land-use patterns, such as the expansion of monocultures (Tilman 1999, Byers 2002), rather than being the drivers of disturbance themselves (Didham et al. 2005).

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[3] Several other terms have also been used to coin “invasive” species, including “non-indigenous”, “non-native”, “exotic”, “noxious” and “alien”. However, according to National Invasive Species Council (2006) only the terms “invasive” or “noxious species” should be applied to “non-native” species whose introduction will likely cause a “negative impact on economic, environmental, human or animal health”.

Conceivably the two most well-known cases with major impact on GEIR maize cropping are the western bean cutworm (WBC) (*Striacosta albicosta* (Smith)) a noctuid moth native to West and Central America (Douglass et al. 1957) and the western corn rootworm (WCR), *Diabrotica virgifera virgifera LeConte* (Coleoptera: Chrysomelidae). Both these species are considered important secondary pests, since they show low susceptibility to most transgenic maize events currently commercialized (Wilson et al. 2005, Eichenseer et al. 2008). In the mid 1990s, the WBC began a well-documented expansion of population range size in correlation with the introduction of transgenic maize. It has now effectively established itself as a major Lepidopteran pest of maize crops in some areas of the Corn Belt in the USA and Canada (Dorhout and Rice 2010, Michel et al. 2010, Lindroth et al. 2012).

Field trials have shown that transgenic crops expressing Cry1Ab and Cry9C toxins had larger populations of WBC compared to conventional maize (Catangui and Berg 2006, Dorhout and Rice 2010). It is possible that changes in cultural practices (e.g. conservation tillage and reduced insecticide use) due to the widespread adoption of *Bt* maize across these areas might have contributed to the WBC's rapid expansion (Hutchison et al. 2011). The WCR, native to South and Central America, where it was in biological equilibrium with its natural enemies, has spread to North America likely due to the intensification of maize production (Hummel 2002). While in Europe it was thought to have been introduced via international shipments in the 1990s (Kiss et al. 2005), it has since become one of the major pests in maize throughout central Europe and its eradication has become impossible (Kiss et al. 2005).

Nowadays, invasive weeds cause the greatest direct economic losses with substantive control costs in crop production followed by pathogens, which affect mainly plants and livestock (Pimentel et al. 2001). Invasive insects, although less damaging than the other two groups are still economically important; approximately 40% of all insects present in agricultural crops are invasive species (Pimentel et al. 2001, Pimentel et al. 2005). Worldwide the costs of control and damage associated with invasive species were estimated by Pimentel et al. (2001) to be more than US $1 trillion annually, or 5% of the global economy. In Europe, the number of non-native species established has increased exponentially in the past few decades (Butchart et al. 2010). Based on the increasing annual trend in international trade (Levine and D'Antonio 2003), the prospects of reducing this rate are small. More than 3000 new invertebrate species have already breached European borders (Hulme et al. 2009), and 11 of these insect species with agricultural interest are included in the 100 worst invasive species present in Europe (DAISIE 2016). According to Kettunen et al. (2009), the monetary impact of invasive species present in the European continent is estimated to be around €12 billion per annum over the last 20 years.

2.6 Bio-economic modelling perspective

In recent years researchers have acknowledged that only a multidisciplinary approach could respond to the variety of objectives and challenges faced by various fields, including biological conservation, natural resource management and agriculture (Schmolke et al. 2010). Agricultural systems evolve according to a variety of global and local driving forces, be they of ecological, economic or political nature. The latest development of bio-economic models has aimed to efficiently integrate these viewpoints into a unique flexible tool (Carrasco et al. 2010c, Marten and Moore 2011, Atallah et al. 2015).

Bio-economic models are tools to evaluate ex-post or to estimate ex-ante impact of farm management and policy and/or technology change on agriculture, economics and environment. The integration of biophysical models and economic mathematical programming models has proven to deliver important, multi-scaled and multi-disciplinary answers to a wide range of farming systems under various agro-ecological scenarios (Janssen and Van Ittersum 2007, Groot et al. 2012). Specifically, in agriculture, a bio-economic model relates a system describing farmers' management decisions to a system that illustrates current and/or alternative production inputs (e.g. fertilizers) or pest control choices (e.g. insecticides) in order to obtain an optimal output and associated externalities (Janssen and Van Ittersum 2007, Catarino et al. 2015).

Realism (to a certain extent) is assured with the inclusion of several constraints in the optimization procedures: i) farm limitations (e.g. restricted resources); ii) policy constraints (e.g. maximum allowed input use); and iii) biological constraints (e.g. pest damage). The model developed in this thesis is based on a mechanistic normative modelling approach, which optimizes the decision variables while maximizing the objective set. In contrast to empirical models, which try to find relationships in the observed data, mechanistic models rely on existing knowledge and theory (Colbach 2010).

Normative mathematical optimization approaches have the advantage that calibrations with historical data are not strictly required, meaning that a sound knowledge of the system is sufficient to construct the model (Buysse et al. 2007). Lack of calibration with real data brings a consequent drawback, the resulting outcomes do not necessarily guarantee that practical model replications are efficiently reproduced (Buysse et al. 2007). However, acknowledging this limitation, the use of mechanistic modelling approach assumes high importance in going beyond the collected data. A sound mechanistic framework allows the extrapolation of situations (e.g. from one surrogate species to another, changes in production parameters, etc.) including the assessment of extreme scenarios, or simply hypotheses of the relationship between model variables.

This thesis has built on the pioneering work of Lichtenberg and Zilberman (1986)[4], in which the a damage control model considered pesticides as a damage abatement input that has an indirect effect on output. In previous studies, pesticides were modelled as a yield-increasing input (Headley 1968, Hall and Norgaard 1973). In the LZ approach, damage control inputs do not increase potential output, their influence on production is realized by reducing the direct damage, either by humans or in this case by pests. Hence, a distinction is made between control methods and other factors of production like land, capital, and labour,

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[4] For a detailed review on the Lichtenberg and Zilberman (1986) damage control approach see Sexton et al. (2007).

which also have the capacity to increase the final output. Furthermore, this approach allows for changes in the damage control agent productivity over time, i.e. it makes possible the integration of biological dynamic systems such as pest population dynamics or resistance building models (Chambers 1988, Babcock et al. 1992, Carrasco-Tauber and Moffitt 1992). The specifications of this approach are developed further in chapter four.

2.7 The integration of space in bio-economic models

It has been recognized that incorporating economics into invasive models is an effective way to assess control strategies (Finnoff et al. 2009, Epanchin-Niell and Hastings 2010, McDermott et al. 2013). Numerous models have been developed to provide management solutions that combine economics and ecology (Keller 2009). These models can reduce control or eradication costs by recommending cost-effective management procedures. However, much of the economic literature on biological invasions regarding pest management has not focused on the spatial features of the problem. Biological invasions are by nature related to spatial-dynamic processes. The spatial dimension of bio-economic spatially explicit models provides not just new insights to understanding biological processes, but by predicting potential distributions and establishment of ecological niches, the area upon which control should focus is significantly lessened (Mack et al. 2000). Although the recent advancement in modelling development has increased our ability to better estimate species behaviour, the lack of data is still a limiting factor (Getz and Saltz 2008). This has engendered great challenges due to large uncertainty in the model components (Epanchin-Niell and Hastings 2010).

Spatial heterogeneity is an important factor to consider in the study of populations, ecosystems and landscapes (Shaver 2005). Understanding the spatial patterns of landscape processes and the driving forces that affect flora and fauna dynamics and persistence is essential to effective pest management (Lawler et al. 2006). In the case of invasive species it is of primary importance to link spatial patterns and economic aspects to ecological processes, such as resources distribution (Tscharntke et al. 2002), competition with other species (Hastings et al. 2005) , exposure to predation (Fenichel et al. 2010) and movement patterns of organisms (Mazzi and Dorn 2012). However, incorporating spatial aspects into bio-economic analysis is not trivial (Seppelt and Voinov 2002, Vinatier et al. 2011).

There are essentially two different approaches to modelling a population over time and space: individual (or agent) based models (IBM) and population based models. The latter has been applied in several fields (Bonabeau 2002, Evans and Kelley 2004, Railsback et al. 2006, Matthews et al. 2007), including the management of invasive species (Grimm et al. 2005, Epanchin-Niell and Hastings 2010). IBM are exclusively computer systems composed of autonomous entities, such as animals, plants or humans, capable of taking decisions and interacting with the environment and other individuals (Huston et al. 1988, Rebaudo and Dangles 2013). Each individual is explicitly modelled as unique and discrete entity, acting according to a set of rules, that may change along its life cycle (Grimm et al. 2006). If their biological features are common and well known (Bousquet and Le Page 2004), for example in a colony of insects, it is possible to construct the dynamics of the entire population or group (Jongejans et al. 2008) by tracking and aggregating the individual's behaviour, mobility, reproduction, growth and mortality.

In chapter six, building on the bio-economic model developed in chapter five, the spatial dynamics between two competing pest species are modelled based on a reaction-diffusion (RD) system (Okubo 1980). In population based models, the movement of a group of organisms is frequently treated as a diffusion process using a partial differential equation (PDE) (Okubo and Levin 2013). The intuition behind using PDEs is that patterns resulting from the average movement at a population level are not dependent on the individual behaviours of organisms (Okubo and Levin 2013). Spread in this methodology is treated as continuous and constant (Hastings et al. 2005). This modelling framework requires a robust analytical structure so control strategies can be prioritized and directed appropriately (Finnoff et al. 2009). Due to their inherent complexity, numerical experiments and simulations are generally required to solve these models (Morozov and Poggiale 2012). Research models based on a realistic landscape, such as the one here developed, can be used to predict species spread behaviour and the associated economic effects.

2.8 Summary

In this chapter, the underlying theory, principles and literature that support this research have been outlined. It was shown that although GEIR technology may offer benefits to agriculture, it also raises several concerns. One of these concerns is the focus of this research; the outbreak of secondary pests in GEIR crops. Intensive agriculture and the employment of GEIR crops brings ecological disturbances which secondary pests may take advantage of, as they would any other insecticidal control technique. This aspect will be discussed in detail in chapter four. Finally the general modelling approach that will be used in chapter five and six was reviewed. The following chapter introduces the study region as well as the surrogate species, and demonstrates the reasoning behind these choices.

CHAPTER 3. STUDY CONTEXT

3.1 Chapter Introduction

Despite the fact that the global area planted with genetically engineered (GE) crops has increased substantially, the European Union (EU) case is rather different. Due to the strict regulations on transgenic plants, the cropping area and the number of adopting member states, countries have oscillated considerable. Nowadays only Spain is growing significant amounts of the only GE crop allowed, *Bt* maize. This chapter provides a general view on transgenic crop adoption in Europe and it introduces the motives behind choosing Spain as the study context and the surrogate species used.

3.2 European Union context

While the world experiences a considerable increase in the number of adopting countries as well as in the GE cropping area, in the EU the case is different. The EU has moved towards GM crop biotechnology with scepticism, mainly due to the continuing debate among political, scientific and consumer communities. In 2015, 19 EU member states (MS) requested a complete ban on GEIR production in all or part of their territories. Furthermore, European legislation on transgenic plants requires the completion of extensive studies to determine that their release does not pose any risk to human health or the environment. Consequently, the national regulatory approaches taken by most EU member states reflect the inclination to adopt a highly precautionary[5] approach given the alleged scientific uncertainties associated with GM use (Levidow et al. 2005, Masip et al. 2013). However, by and large economists have argued that this policy framework hinders competitiveness in international markets (Masip et al. 2013). The lower yields accrued from pest damage and lower prices caused by decrease in product quality may disadvantage maize famers in the world market (Gomez-Barbero et al. 2008). Scientific and policy debates on GE crops in the EU have focused more on hypothetical environmental health and safety and less on the possible agronomic and economic impact on farmers (Ortego et al. 2009, EFSA 2010b, a).

Due to legislative barriers, since its first introduction in 1998, the cropping area and the number of countries adopting GE crops has oscillated (figure 3.1). Nowadays, although several other events are under evaluation by the European Food Safety Authority (EFSA), the only GE crop allowed for cultivation in the EU is the maize expressing the insecticidal protein Cry1Ab from *Bacillus thuringiensis* (*Bt* maize) (EFSA 2010a). This GE maize presents a high level of resistance to the main corn borers present in the EU (González-Núñez et al. 2000). In 2012[6], *Bt* maize was cultivated over 116 thousand hectares, in differing proportions, in Spain, Portugal, Czech Republic, Romania and Slovakia countries (James 2013). However, Spain is the only EU member state growing significant amounts of *Bt* maize.

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[5] The precautionary principle states that in areas where science is limited and outcomes are unpredictable, regulatory authorities are justified in taking action to avoid possible negative outcomes (Levidow et al. 2005)

[6] The agro-economic description made through the thesis concerns the year of 2012 as a matter of coherence, in line with the maize spatial data used.

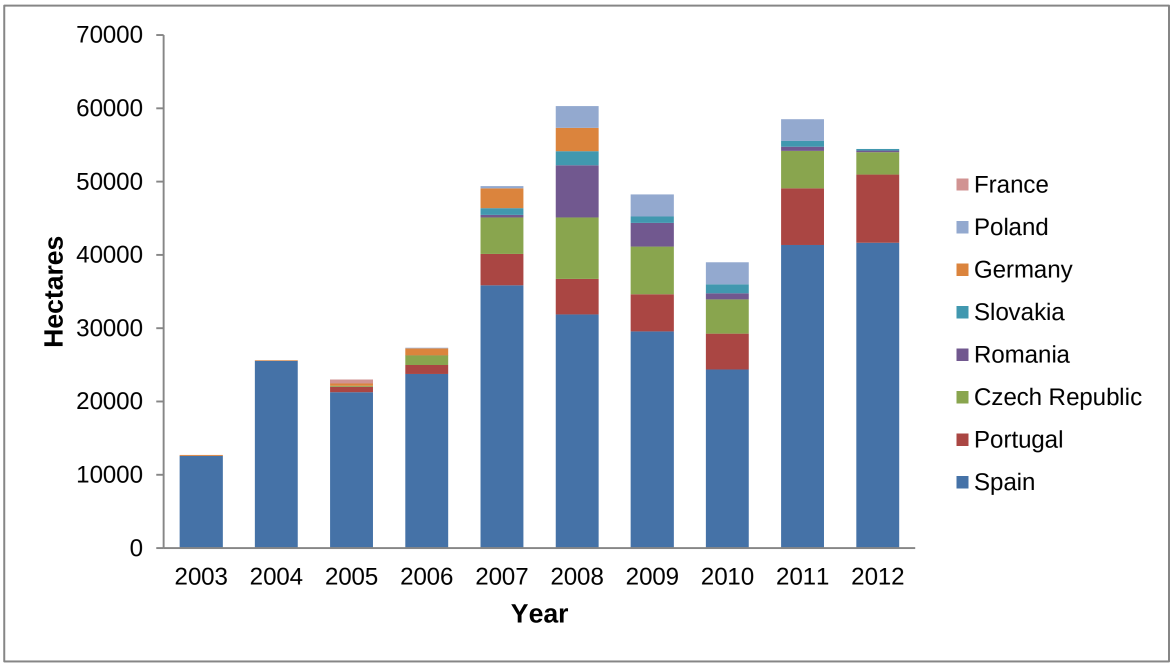

Figure 3.1 - Hectares of *Bt* Maize planted from 2003 to 2012 in EU countries (James 2004, 2006, James 2009, James 2011, James 2013).

3.3 Area of study

3.3.1 Spain

Maize is cultivated widely in Spain. The regions with the largest maize-growing areas are Castile, Estremadura and Aragon (105,061, 60,643 and 57,496 hectares respectively in 2012 (figure 3.2), which crops more than half of the total Spanish maize area. The production is located almost entirely in irrigated areas and fertile land with a high productive potential (MAGRAMA 2015). Average maize yields per hectare from irrigated land in Spain are clearly higher than from non-irrigated land (10.4 vs 4.5 tonnes/hectare) (MAGRAMA 2015). These yields are usually obtained with reasonable production costs, hence the interest of Spanish farmers in producing maize. The most significant inputs are the sowing, fertilization, irrigation and plant health checks. Ex post economic analysis of the performance of *Bt* maize shows that Spanish adopters have obtained higher yields, higher gross margins and better quality of harvested product, along with a significant decrease in insecticide applications compared with conventional farmers (Gomez-Barbero et al. 2008, Riesgo et al. 2012).

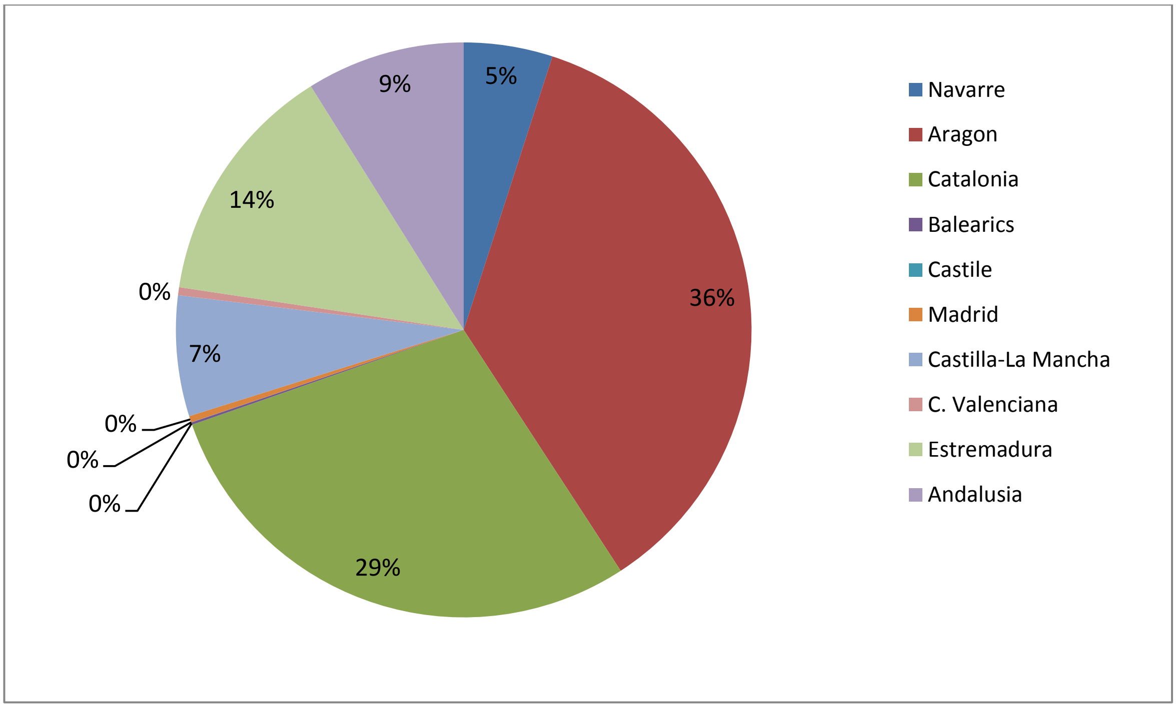

Figure 3.2 – Proportion of total maize planted within the Spanish region in 2012 in Spain (MAGRAMA 2013). The "other regions" (C. Valenciana, Madrid, Balearics and Castile) share among them 1105 hectares.

Maize is almost entirely cropped in a monoculture intensive regime, which, allied with Mediterranean climate conditions, favours the development of pests and diseases (Vasileiadis et al. 2011). The most troublesome agents that cause high control costs are corn borers, soil insects, some secondary pests and, very sparsely, mites and aphids (Gil and Castro 2015). Traditionally, pests have been controlled by cultural practices and chemicals, such as seed treatments to control soil worms and broad-spectrum insecticides (organophosphates and synthetic pyrethroids) against corn borers and the sporadic appearance of other pests (Gil and Castro 2015). Nonetheless, farmers continue to face numerous pest management problems. Cultural practices are not efficient and the range of active substances available has decreased over time due to environmental protection measures and pest resistance (Maiorano et al. 2009). A further issue, as it will be shown in section 3.4, is the problematic case of corn borer control based on insecticide applications. Hence it is not surprising that Spanish farmers, especially in regions where corn borer pressure is high such as Catalonia and Aragon, have quickly adopted *Bt* maize.

In Spain, *Bt* maize cultivation began in 1998 after the approval of the variety *Bt*-176 by the company Syngenta. In 2003 the EU approved cultivation of new *Bt* maize (MON-810 by Monsanto), leading to a substantial increase in the cultivated area (figure 3.1). In 2012, two out of the 11 regions where *Bt* maize was grown accounted for about 65% of the total planted area (López 2013). These were Aragon in the first place (41669 hectares, 75 % adoption rate) and Catalonia in second (33531 hectares, 93% adoption rate) (figure 3.3).

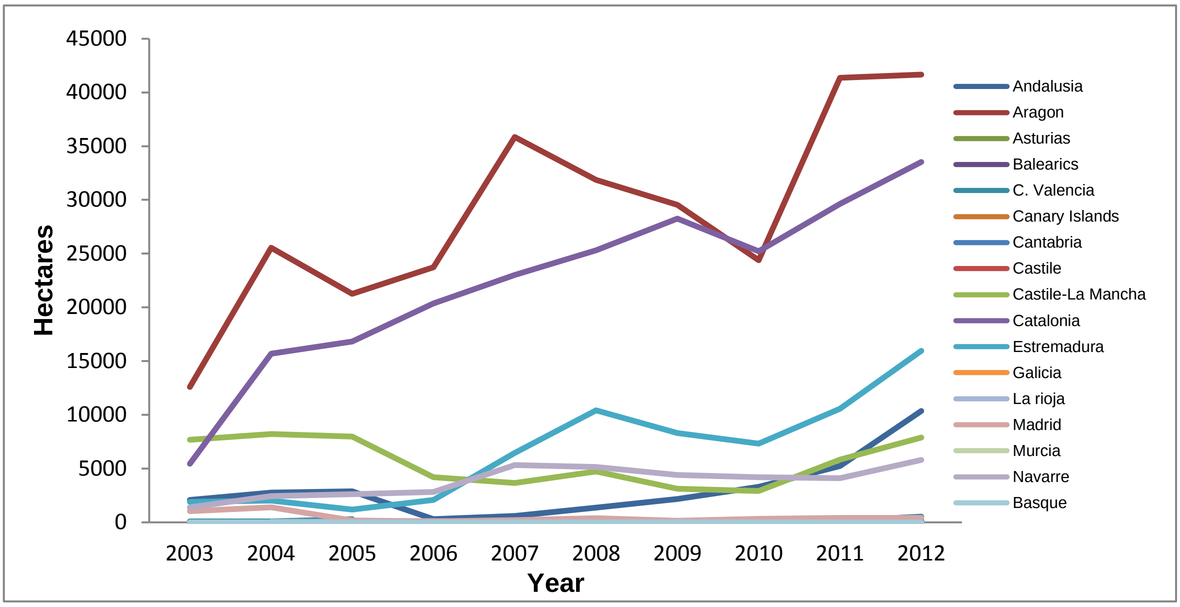

Figure 3.3 – Evolution, from 2003 to 2012, of *Bt* maize hectarage within the Spanish autonomous regions (MAGRAMA 2013). Each line represents a different Spanish autonomous region.

3.3.2 Aragon

Aragon is one of 17 Spanish autonomous communities, situated in the Ebro basin in north-eastern Spain with an area of 47.720 km^2. Within the 2.345 km^2 of Aragon's UAA (in 2012), after barley and wheat, maize was the most important cereal, and being within the Ebro basin the most important maize area in the region. The total cultivated area of maize has fluctuated over the last ten years without a growth or decline trend. However, it is clearly noted in figure 3.4 that the area cultivated with *Bt* maize has increased substantially since 2003. From the 55.484 hectares planted with maize in 2012, 75% was *Bt* maize, contributing with 1/3 of the total *Bt* maize produced in Spain (López 2013). The high adoption likely mirrors the farmers' satisfaction with pest control and the general positive economic returns of the GE variety (Gomez-Barbero et al. 2008).

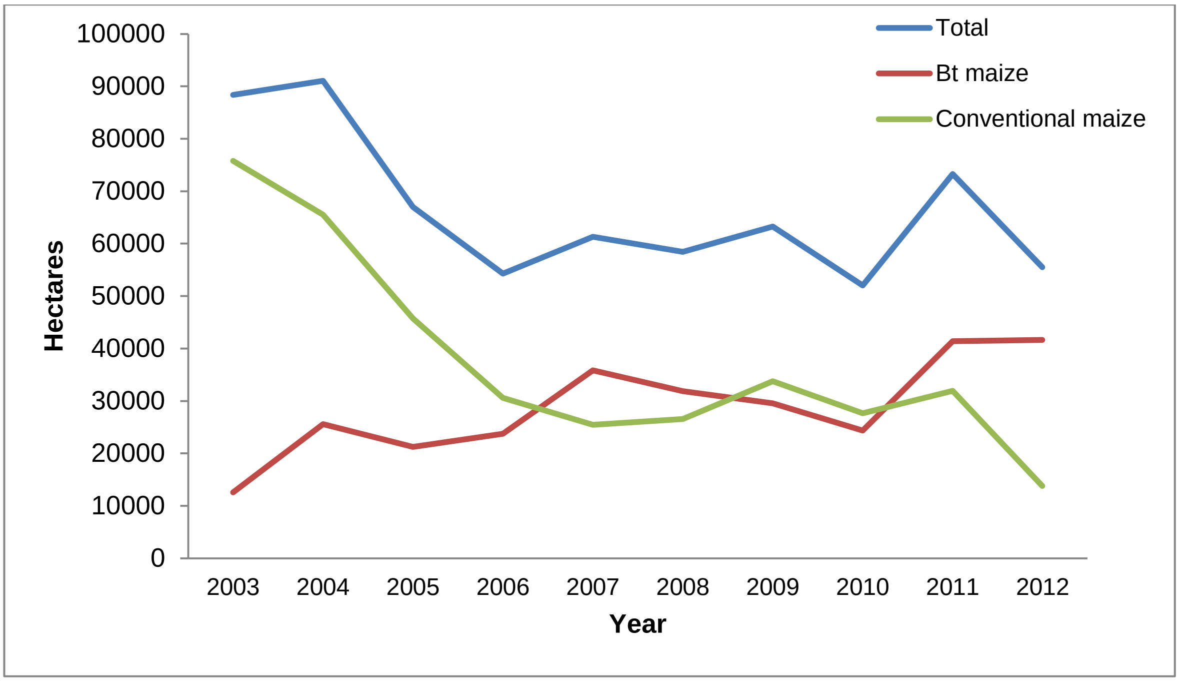

Figure 3.4 – Evolution, from 2003 to 2012, of *Bt* (red line*)*, conventional (green line) and total maize (blue line) hectarage in Aragon, Spain (López 2013, MAGRAMA 2013).

Aragon regional edaphoclimatic conditions are ideal for corn borers and other pests to develop, causing recurrent production losses. As will be shown in the following section, control of pests, especially corn borers, is very difficult. Hence, severe crop losses are not unusual within conventional maize farming systems.

3.4 The surrogate species

There is broad consensus that the Mediterranean corn borer (MCB), *Sesamia nonagrioides* (Lefebvre) (Lepidoptera: Noctuidae) and the European corn borer (ECB), *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae) are the most economically important maize pests in Spain and in other countries around the Mediterranean basin (Cordero et al. 1998, Malvar et al. 2002). Unlike insecticides, *Bt* maize provides an effective control of these two major lepidopteran pests (González-Núñez et al. 2000, Farinós et al. 2011). However, in Spain, two other Lepidoptera, the true armyworm (TAW), [*Mythimna (Pseudaletia) unipuncta* (Haworth) (Lepidoptera: Noctuidae)], and the corn earworm, *Helicoverpa armigera* (Hübner), are considered to be important secondary pests causing occasional but severe damage to maize (Eizaguirre et al. 2010, Pérez-Hedo et al. 2012). Attempts to analyse and predict TAW's outbreaks have been constrained by its high flying capacity and reproduction rate, and its expansive and unpredictable behaviour. Additionally, under normal conditions, the MCB tends to outcompete the TAW (Eizaguirre et al. (2009). In this context, it has been suggested that the increase of transgenic maize could affect the population dynamics of this secondary Lepidopteran pests due to the high efficiency of *Bt* maize against its target pests (López et al. 2000, López et al. 2008, Eizaguirre et al. 2010). This would arise if TAW takes advantage of the absence of the major corn borers (Eizaguirre et al. 2010). These species are representative of the problem of secondary pests explored in this thesis, as both species compete for the same food resource – maize – and the MCB, although biologically stronger than the TAW, is effectively controlled by *Bt* maize.

3.4.1 The primary pest – Mediterranean corn borer

The MCB is here used as an example of a primary pest due to its historical importance and present susceptibility – 99% – to the Cry1Ab toxin (González-Núñez et al. 2000, Farinós et al. 2011). The MCB is a cosmopolitan multivoltine species with a wide range of host plants, including maize and rice (Kfir et al. 2002, Eizaguirre and Fantinou 2012). Where maize production areas have increased in these areas in the past, the pest has expanded as a consequence (Eizaguirre and Fantinou 2012). However, its distribution and population levels are mainly driven by its sensitivity to sub-zero winter temperatures (Gillyboeuf et al. 1994).

Temperature is central to the number of MCB generations per year, ranging from one or two generations on the Atlantic coasts, up to four generation in the coastal regions of the Mediterranean basin (Gillyboeuf et al. 1994, Eizaguirre and Fantinou 2012). The influence of local climatic conditions and planting times will influence MCB's incidence and consequent impacts (Eizaguirre et al. 2002). Cold winters help reduce the over-wintering population and can contribute to reduced pest pressure in the following growing season. Also, advancing maize cropping period, where field conditions allow, tends to provide better protection compared with attacks on later plantings (Eizaguirre et al. 2002). MCB development includes four stages: egg, larvae, pupae, and adult, and it overwinters as a diapausing larva in maize stalks and roots (Gillyboeuf et al. 1994). The effect of photoperiod and temperature on MCB diapause induction and development has been extensively studied (e.g. Eizaguirre et al. 1994, Fantinou et al. 1995). In the study area, this species usually achieves two complete generations and one incomplete generation per year (Eizaguirre et al. 2002, Eizaguirre et al. 2008). According to Gillyboeuf et al. (1994), only about 5 to 25% of the overwintering larvae survive to pupate in spring, with the minimum threshold temperature for the pest being around 10ºC (Eizaguirre et al. 2008). These factors were used to calculate the species' intrinsic annual growth rate (see appendix 1).

Both the ECB and the MCB have a similar behaviour within the plant. Larvae cause damage by tunnelling into stems or the ear until pupation, weakening the plants and consequently reducing yield (Malvar et al. 1993). Additionally, it facilitates the appearance of fungi (e.g. fusarium) and other pathogens through the pest feeding wounds, which decrease the product quality (Folcher et al. 2009). Although uncommon, the weakened plant could fail, resulting in a total production loss, especially in cases with severe weather situations such as stronger winds and more frequent pelting rains or hail (Gil and Castro 2015). Economic losses accrued to MCB in Spain have not been fully quantified, since the injury is indistinguishable from that caused by ECB (Eizaguirre and Fantinou 2012). The damage caused by MCB can reach 30% of the maize yield, depending on the date of sowing and on the plant development stage when attacked (Butrón et al. 1999, Malvar et al. 2004, Velasco et al. 2004, Butrón et al. 2009).

Endophyte larval behaviour critically limits the efficiency of biological and chemical control. In conventional maize cropping, MCB control through the use of insecticides is only moderately effective since larval development occurs mainly inside the stalk (Albajes et al. 2002). Application timing is crucial for control success with insecticides, hence it is not unusual that repeated applications are often necessary (Velasco *et al.*, 1999). When considering an efficient scouting and timing, Clark et al. (2000) report an insecticide efficacy of between 67 and 80% per application.

Conversely, farmers recognize that over applying insecticides may kill certain beneficial natural predators of MCB and other maize pests, such as spider mites, requiring additional use of other chemicals (for a detailed discussion on farmers perspective on insecticide applications to control MCB, see Gómez-Barbero et al. 2008). Natural enemies, such as ground beetles, spiders, *T. busseolae* (Hymenoptera: *Scelionidae*), and parasitoids of MCB play an important role in the control of this pest (Alexandri and Tsitsipis 1990, Eizaguirre and Pons 2003, Farinós et al. 2008). Predation pressure comes mainly from egg parasitoids which may be responsible for up to 65% of egg mortality, depending on natural environmental conditions (Alexandri and Tsitsipis 1990, Figueiredo and Araujo 1996, Monetti et al. 2003). Several other management strategies, besides insecticides and the use of *Bt* maize, have been suggested for the control of the MCB populations, such as the uprooting and exposure of the diapausing larvae to the winter cold temperatures and mating disruption techniques using sex pheromones (Aguilar et al. 1992, Gillyboeuf et al. 1994, Albajes et al. 2002).

3.4.2 The secondary pest – True Armyworm

The TAW is an important cosmopolitan secondary pest of the Noctuidae family in Europe and North America (Bues et al. 1986, McNeil 1987). It is an invasive species that was first noticed in Europe in the 19th century (Bues et al. 1986). The TAW feeds on the leaves of several non-agricultural and cultivated gramineous plants, including maize (Guppy 1961). Sporadic outbreaks, where large numbers of larvae march across the landscape causing devastating economic impact, have been reported in Spain (López et al. 2000), Canada (McNeil 1987), the US (Willson and Eisley 1992), Mexico (Ramírez Dávila and Esquivel Higuera 2013), among others. In Europe, it is most prevalent in the Mediterranean basin due to the larvae's low ability to survive prolonged temperatures below freezing (Bues et al. 1987). In Spanish climatic conditions this species typically completes four generations per year (López et al. 2000). Despite favourable climatic conditions and their high mobility capacity[7], the inconsistency of TAW prevalence is related to a combination of two other factors. Firstly, the existence of natural enemies, and secondly, the implementation of tillage practices and regular weed control (Willson and Eisley 1992, Clark et al. 1994). Contrary to MCB, this species is highly susceptible to natural enemies, Menalled et al. (1999) note 80% mortality in field experiments. It is not uncommon to observe parasitism and other sorts of predation at rates capable of maintaining the population below endemic levels (Guppy 1967, Kaya 1985, Laub and Luna 1992).

Although the devastating effects of Armyworm larvae have been commonly documented, the impact on maize yields specifically is not clear due to the erratic nature of outbreaks (Douglas et al. 1981, Hill and Atkins 1982, Buntin 1986). The larvae often move from other adjacent weeds or crops to the maize fields when food is limited. They seek refuge at the bottom of plants during the day, making visualization rather difficult. TAW's activity usually starts at dusk and goes on for several hours. In the case of maize, the larvae chew the leaves and the damage can be serious when populations enter the gregarious phase. Musick (1973) reported that six larvae were enough to destroy one plant, while Harrison et al. (1980) noted that an infestation level of one larva per plant was sufficient to cause a significant yield impact. Presently the TAW's management recommendations focus on preventive measures such as the constant crop monitoring, bait traps and weeding in the surrounding areas of the crop field (Gil and Castro 2015). Crop monitoring is especially relevant in dry winters due to a shortage of gramineous weeds. This situation it is likely to create favourable conditions for crop invasion. It is recommended that insecticides are used as soon as individuals are spotted. The optimal timing of treatment is when the caterpillars are small, a state in which they are more voracious and vulnerable to insecticides.

Several studies have evaluated the efficacy of different *Bt* maize transgenic lines against the TAW, reporting substantial plant damage on the varieties assessed (e.g. Pilcher et al. 1997, Schaafsma et al. 2007, Eizaguirre et al. 2010, González-Cabrera et al. 2013, Pérez-Hedo et al. 2013). Eizaguirre et al. (2010) found no difference in the number of TAW larvae per plant between *Bt* and isogenic varieties in the majority of field trials. Pérez-Hedo et al. (2013) noted that larvae complete their development, presenting similar growth rates, regardless of whether they are fed on a *Bt* or non-*Bt* diet. In laboratory experiments González-Cabrera et al. (2013) found TAW survival rates of approximately 80% when fed on a diet of *Bt* maize Cry1Ab. It is therefore possible that the increasing use of transgenic maize expressing Cry1Ab toxin might amplify TAW's economic importance (Eizaguirre et al. 2010).

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[7] Hendrix and Showers (1992) showed that TAW could travel at least 1,300 km from Texas to Iowa during northward migration in spring.

3.5 Summary

In this chapter the regional study context as well as the surrogate species were introduced. Low transgenic crop adoption in Europe compared with the rest of the world was discussed briefly. However due to more flexible laws and agronomic need, Spanish farmers have quickly adopted *Bt* maize, which has proved to be economically beneficial, mainly due to the efficient control of the primary pests MCB and ECB. However other secondary pests which are not susceptible to the toxin, such as TAW, may become more predominant with the expansion of *Bt* maize. The following chapter introduces the core of the thesis with an extensive and specific literature review of the mechanisms that may be responsible for a secondary pest outbreak the context of GEIR.

CHAPTER 4. THE IMPACT OF SECONDARY PESTS ON GENETICALLY ENGINEERED INSECT RESISTANT CROPS

4.1 Chapter Introduction

The intensification of agriculture and the development of synthetic insecticides in the mid-20th century enabled worldwide grain production to more than double in the last third of the century. However, heavy dependence on and, in some cases, overuse of insecticides has been responsible for negative environmental and ecological impacts across the globe, such as a reduction in biodiversity, insect resistance to pesticides, negative effects on non-target species (e.g. natural enemies) and the development of secondary pests. Genetically engineered insect resistant (GEIR) technology could offer a viable alternative, mitigating many of the major negative side effects and limitations of pesticides. Nevertheless, despite the widespread adoption and continued increase in the area of GEIR crops grown across the globe, there are still a range of questions concerning longer term agro-ecosystem interactions that remain unanswered. For instance, insect species that are not susceptible to the expressed toxin can develop into secondary pests and cause significant damage to the crop. In this chapter the main causes surrounding secondary pest dynamics in GEIR crops and the impact of such an outbreak are reviewed. Regardless of the causes, if non-susceptible secondary pest populations exceed economic thresholds the sustainable use of the technology may be in jeopardy. Consequently, insecticide spraying will become the only immediate solution at farmers' disposal, which per se will disrupt the agro-ecosystem even further. Based on the literature review, five recommendations for future research are outlined that will help to improve knowledge of the possible long-term ecological trophic interactions of employing this technology.

4.2 Secondary pests in GEIR crops

The development of synthetic insecticides in the mid-twentieth century has enabled worldwide grain production to more than double in the last third of the 20th century (Krebs et al. 1999). However, the overuse of insecticides has been accountable for numerous environmentally and ecologically negative impacts, such as decline in biodiversity, pest resistance and the development of secondary pests (Hardin et al. 1995, Matson et al. 1997, Vitousek et al. 1997). It is expected that genetically engineered insect resistant (GEIR) crops expressing toxins from the soil bacteria *Bacillus thuringiensis* (*Bt*) producing Crystalline (Cry) proteins could effectively offer a viable alternative or partially alleviate the major limitations of insecticides. Unlike other agricultural technological advances, GE crops have been subject to serious and extensive discussion regarding their potential long-term negative impacts (e.g. the following debate: Andow et al. 2009, Lövei et al. 2009, Shelton et al. 2009). A large share of the scientific findings and the majority of adopting farmers suggest that when compared with insecticides, the ecological and economic benefits of GEIR crops are substantial. On the other hand, some scientists supported by evidence from some countries, such as China, claim that the potential long-term impact of GEIR crops could bring irreversible effects and adoption should only be undertaken with great caution (Garcia and Altieri 2005, Smale 2006, Lövei et al. 2009). One of these concerns relates to insect species that are not susceptible to the expressed toxin developing into secondary pests and causing significant damage to the crop (Sharma and Ortiz 2000, Wu and Guo 2005). Such an event could have further negative effects of economic and ultimately of ecological relevance.

The concept of secondary pests is intrinsically linked with that of non-target organisms (NTOs). According to Arpaia (2010, p.14), in the context of GEIR, NTOs are "all living organisms that are not meant to be affected by newly expressed compounds in GEIR crops, and that can be potentially exposed, directly or indirectly, to the GEIR plant and/or its products in the agro-ecosystem where GEIR crops will be released or in adjacent habitats". Although food webs in agro-ecosystems are typically simplified compared to natural habitats, they still present complex multi-trophic relationships (Altieri 1999, Arpaia 2010). In any given cropping system, numerous species and scores of ecosystem functions can be found with different features and ecological functioning (Matson et al. 1997, Hooper et al. 2005), although only a few are capable of inducing major losses in crop yield or quality (Price et al. 2011). A lethal or sub-lethal effect of a GEIR crop upon one or a group of NTOs might occur through direct exposure (to the *Bt* toxin) or indirectly due to changes in the ecosystem on which that species depends (Snow et al. 2005). In order to assess the impact of GEIR crops on NTOs at different trophic levels, ideally scientists would need to be acquainted with the majority of arthropod species prevalent in a given agro-ecosystem (Meissle et al. 2010). Lövei et al. (2009), in summarising the published literature, concluded that stating that GEIR crops will pose "no harm" to NTOs is still a premature conclusion due to the limited number of non-target (beneficial) species currently studied.

There are two phenomena in agricultural systems that are considered as ecological backlash events that are of relevance to this concept: firstly ''resurgence of insect pests'' and secondly "outbreaks of secondary pests". The former refers to a situation in which a suppressed pest population unexpectedly rebounds to greater numbers following a pest control action, exceeding the economic injury level (Hardin et al. 1995). The latter, and the focus of this paper, refers to the emergence of a pest other than that originally targeted by an agricultural intervention, and can be seen as "replacement" for the primary pest (Metcalf 1980, Hardin et al. 1995). The causes responsible for both phenomena are relatively similar and include reduction in the number of natural enemies and removal of competitors (Ripper 1956, Hardin et al. 1995). To further understand the concept of secondary pests, it is necessary to define the concept of a primary pest as the "targeted" pest for which a *Bt* crop is planted. According to FIFRA Scientific Advisory Panel (1998), a secondary pest is a "non-targeted" pest that has historically posed small or even no economic threat, but which could be affected directly by a low to high dose expressed in a *Bt* crop, or indirectly through changes in insecticide use patterns. Metcalf (1986), defined secondary pest outbreaks as a "type II resurgence", which occur when the primary pest is strongly affected by a pest management strategy, yet is replaced by another pest not affected by this pest management strategy. Berryman et al. (1987, p.3), meanwhile, define this event as 'an explosive increase in the abundance of a particular species that occurs over a relatively short period of time'. In the event of a secondary pest outbreak, additional pest management tactics are required. In most cases, due to their swift and unexpected appearance, these events will lead to crop spraying with a broad-spectrum insecticide (Gross and Rosenheim 2011). As a result of a secondary pest outbreak, additional pest management tactics are required. In most cases, due to swift and unexpected pest appearance, these events will lead to spraying with broad-spectrum insecticides (Gross and Rosenheim 2011).

This chapter focuses on the development and effects of secondary pests on GEIR crops. This issue, although of high importance, has received only limited attention to date. Only a few studies have addressed the impact of controlling one pest on the population of a second pest, and consequent ensuing implications. Citing Harper (1991, p.22), "ignoring secondary pests can lead to devastating crop damage that may continue over a considerable period of time". This chapter has three main goals: i) to assess the main causes of a secondary pest outbreak in the context of GEIR crops; ii) to review the current impact of a secondary pest outbreak due to the use of GEIR crops; and iii) to provide recommendations for future research.

4.3 Causes for secondary pest outbreaks in GEIR crops

The employment of *Bt* crops may carry non-intuitive negative effects on agricultural ecosystem interactions and even on farm profits (Sharma and Ortiz 2000, Wolfenbarger and Phifer 2000). *Bt* toxins have a narrow spectrum aimed to control and kill only the target pest and thus are meant to indirectly provide a safe environment for the growth of non-target pests (Sharma and Ortiz 2000, Lu et al. 2010). Hence, secondary pests, which before were of minor relevance, might now find favourable conditions to develop and themselves become major pests. In the spectrum of GEIR crops, three main drivers that may trigger an outbreak of secondary pest species were found: i) reduction in broad-spectrum insecticide applications; ii) reduction in natural enemy populations; or iii) decrease in inter-specific competition with the target pest.

i) Reduction in broad-spectrum insecticide applications

The introduction of GEIR technology, at least in the early years, brought significant decreases in insecticide application among adopters, considerably alleviating the negative impacts associated with such insecticides (Meissle et al. 2010, Kouser and Qaim 2011, Krishna and Qaim 2012). Despite warnings from several authors (e.g. Sharma and Ortiz 2000, Wu and Guo 2005) that some NTOs could appear in such number that they become key insect pests in *Bt* crop fields, specific measures to combat their population increases were not taken. Consequently there have been outbreaks of secondary pests (that are not affected by the specific *Bt* toxin) which were previously controlled by the insecticide applications originally targeting the primary pest (Lu et al. 2010, Pemsl et al. 2011). This situation has been particularly evident in *Bt* cotton production in China. Less than 3 years after GEIR introduction in 1998, several pest groups including sucking insects like whiteflies, plant hoppers, aphids, mirids and mealy bugs increased in number (Men et al. 2004 , Yang et al. 2005a). These insects are not affected by the *Bt* toxin since they feed not on plant cells but on sap, resulting in levels of toxin ingestion which are insufficient to cause harmful effects (Romeis and

Meissle 2011). Similarly in *Bt* maize, there is evidence that several secondary pests have acquired higher levels of agronomic importance (Gray et al. 2009, Eizaguirre et al. 2010, Erasmus et al. 2010, Pérez-Hedo et al. 2012). This has meant that in some cases farmers have had to re-commence insecticide applications because GEIR cropping systems have failed to control the insect pest populations.

ii) Reduction in natural enemy populations

Agro-ecosystem biodiversity is important not only because of its fundamental ecological, environmental and anthropocentric value but also because it is vital to a healthy and sustainable agriculture (Matson et al. 1997, Hooper et al. 2005). The employment of *Bt* crops and the consequent reduction in insecticide usage further increases the importance of natural enemies to control secondary pests (Naranjo 2005a). Natural enemies include predatory insects, such as Coleoptera, Heteroptera and Neuroptera, parasitic insects such as Hymenopteran parasitoids and pathogens such as fungi and bacteria. Natural enemies are critical to ecosystem functioning because they inhibit the excessive multiplication of several potential pests in agricultural systems through 'biological control' (Lang et al. 1999, Romeis et al. 2006, Meissle and Romeis 2009). Natural enemies alone may be sufficient in some cases to keep secondary pest populations under economic injury thresholds (Romeis et al. 2006, Snyder et al. 2006). Hence, a major concern related to the growing of *Bt* crops is their potential impact on the abundance of natural enemies (Marvier et al. 2007). The selectivity of Cry toxins in some cases is not entirely known, leading eventually to unintended effects on beneficial species which may influence other non-susceptible pests (Lövei et al. 2009). Interactions between prey and natural enemies are extremely complex; not all herbivores that feed on *Bt* plants uptake the toxin, nor will all natural enemies be negatively affected by prey that have ingested the toxin (Dutton et al. 2002).

Due to these complex uncertainties regarding ecological risks, many laboratory and field research studies have been conducted in order to evaluate the impact of *Bt* toxins on natural enemies. While several laboratory studies reported no significant effects on natural enemies (e.g. Dutton et al. 2002, Meissle and Romeis 2009, Li and Romeis 2010), others have indicated negative effects (e.g. Hilbeck et al. 1998, González-Zamora et al. 2007, García et al. 2012). Results from studies performed at a field level are similar; some found no significant impacts (e.g. Pons et al. 2005, Chen et al. 2006, Eckert et al. 2006), while other studies reported negative effects (e.g. Meissle et al. 2005, Obrist et al. 2006, Stephens et al. 2012). The overall disparity of results across the literature is striking (see Lövei and Arpaia 2005, Marvier et al. 2007, Wolfenbarger et al. 2008 for detailed reviews, Lövei et al. 2009, Lang and Otto 2010). The uncertainties are mainly focused on the degree of relevance of laboratory studies to the complexity of field-scale agro-ecosystems (Lövei and Arpaia 2005, Lövei et al. 2009). While natural enemies are present in higher numbers in insecticide-free conventional fields compared to *Bt* fields (Marvier et al. 2007, Naranjo 2009), it is nonetheless widely accepted that the use of insecticide applications has substantially larger negative direct effects on natural enemies than does the use of *Bt* crops (Cattaneo et al. 2006, Wolfenbarger et al. 2008, Romeis et al. 2009).

Natural enemies are affected either directly or indirectly by *Bt* toxins (Romeis et al. 2006). Direct impacts occur through the ingestion of the insecticidal protein (Meissle et al. 2005, Obrist et al. 2006, Stephens et al. 2012) however, the mechanism of action of several available *Bt* toxins is still unknown or inconclusive (Lövei and Arpaia 2005, Lövei et al. 2009). Thus, it is conceivable that *Bt* toxins may cause similar negative effects on predators as they do on herbivores (Andow et al. 2006). A recent study, (2012) found that *Bt* proteins were passed from the Cry3Bb *Bt*-maize plant to the predator (*Harmonia axyridis*, a common coccinellid) via prey consumption (*Rhopalosiphum maidis*, the corn leaf aphid and *Rhopalosiphum padi*, the bird cherry-oat aphid), which significantly reduced their life span. Furthermore, although not yet demonstrated in the context of GEIR, there is some concern regarding toxin bioaccumulation through the food chain, possibly driving cascade effects within the ecosystem (Chen et al. 2009). Indirect effects might arrive through reductions in prey/host populations or in the nutritional quality of the prey item. Many herbivores may also suffer the consequences of uptake of the toxin at a sub-lethal level which can affect life parameters such as lifespan and fecundity (Romeis et al. 2004, Meissle and Romeis 2009).

There is evidence of a significant impact on the performance, development and even survival of natural enemies due to the low nutritional quality of prey items after they have ingested *Bt* proteins (Dutton et al. 2002, Obrist et al. 2006, Stephens et al. 2012). Moreover, high mortality rates in the target species may cause a reduction in specialized predators, which are important prey for generalist natural enemies (Stephens et al. 2012). Additionally, prey species might migrate to non-*Bt* fields in search of preferable food resources (Daly and Buntin 2005, Naranjo 2005a). Thus, if the prey availability for predators in *Bt* fields is scarce, predators might be encouraged to “migrate” to adjacent conventional crops, negatively affecting their abundance within *Bt* fields (Sisterson et al. 2007, Razze and Mason 2012). As a result, any lethal or sub-lethal impacts on pest predators will disproportionally affect insect population dynamics. Hence, it may be possible that these negative impacts will permit the development of secondary pests in the crop itself or even in neighbouring crops (Gutierrez et al. 2006, Gross and Rosenheim 2011). Understanding the direct and indirect effects of GEIR cultivars on natural enemies is central for the management of insect pests since undoubtedly these insects play a major role in biological control of primary and secondary pests (Snyder et al. 2006, Naranjo 2009, 2011).

iii) Decrease in inter-specific competition with the target pest

Competition certainly plays an important role in regulating the dynamics of herbivorous insects (Kaplan and Denno 2007). However, the importance of niche replacement through competition between primary and secondary pests has been generally ignored in conventional agriculture (Denno et al. 1995, Hardin et al. 1995), and especially in GEIR cropping. GEIR crops, as insecticides, artificially impose a disturbance on the ecosystem, hence it is not surprising that niche rearrangement may occur (Catangui and Berg 2006). It is possible that when a primary pest is successfully controlled by a *Bt* toxin, a non-susceptible species fills the newly available ecological niche (Hardin et al. 1995, Gross and Rosenheim 2011). This situation occurs in cases where, prior to the pest management treatment, the primary pest is a dominant competitor species and the secondary pest is a weak competitor (Shivankar et al. 2007).

A notorious example of niche replacement is the western bean cutworm (WBC) (*Striacosta albicosta* (Smith)), a noctuid moth native to West and Central America (Douglass et al. 1957). Since the widespread planting of *Bt* maize hybrids has effectively eliminated the intra-guild competition with the European corn borer (ECB) (*Ostrinia nubilalis*), and the corn earworm (CEW) (*Helicoverpa zea*) (Catangui and Berg 2006, Dorhout and Rice 2010) it is possible that a niche was opened for WBC, creating an exclusive habitat for its settlement (Catangui and Berg 2006, Dorhout and Rice 2010). To date only one study appears to have been specifically conducted to assess the interaction between WBC and other species. Dorhout and Rice (2010) assessed several hypothetical intra-guild competition scenarios involving the highly aggressive CEW, the ECB and the WBC. It was noted that CEW had a significant negative impact on WBC survival when both were fed on a meridic or isoline maize silk diet. However, when both pests where fed a transgenic silk diet, WBC presented high survival rates. CEWs are extremely aggressive by nature, compared with the WBC (Douglass et al. 1957) and Dorhout and Rice (2010) observed that CEW larvae often killed the WBC larvae even when it was present in larger numbers. Competition with the ECB exists because of their similar feeding behaviour on the kernels in corn ears (Catangui and Berg 2006). Hence, along with the high flight capacity of WBC (Michel et al. 2010), the reduction in direct competition certainly played a fundamental part in its territorial expansion.

Other examples of niche replacement range expansion of secondary pests include: the corn leafhopper (*Dalbulus maidis*) in maize in the absence of the target pest *Spodoptera frugiperda* in Argentina (Virla et al. (2010), in Spain the true armyworm *Mythimna unipuncta* could have competitive advantage in the absence of both the Mediterranean and European corn borer (Malvar et al. 2004, Eizaguirre et al. 2010), in *Bt* cotton in the USA stink bug pests have recently become a severe problem in the absence of target pests *H. zea* and *Heliothis virescens* (Zeilinger et al. 2011) and lastly, in South Africa Van Wyk et al. (2007) noted that *Helicoverpa armigera*, *Acantholeucania loreyi* and *Eublemma gayneri* could also gain competitive advantage following the displacement of *Busseola fusca* from *Bt* Maize. The niche replacement hypothesis, although seeming to make sense from an ecological point of view, still needs to be evaluated in more detail (Hutchison et al. 2011). As GEIR cropping expands worldwide it is of high importance to determine the key species, of susceptible and non-susceptible pests, which might compete for resources within the same transgenic crop.

4.4 Impact of secondary pests on *Bt* crops

In the early years of GEIR cropping, there were reports of increased efficiency in overall production due to reductions of insecticide applications ranging from 40-60% alongside increasing crop yields as compared with non-adopters (e.g. Fitt 2000, Huang et al. 2002b, Pray et al. 2002, Qaim and Zilberman 2003, Thirtle et al. 2003, Bennett et al. 2004, Gomez-Barbero et al. 2008, Naranjo 2011). This was mirrored by a reduction in human insecticide poisoning along with several positive environmental impacts (Huang et al. 2002b, Pray et al. 2002, Bennett et al. 2003). Nonetheless, there were early concerns about the potential for secondary pest outbreaks due to decrease in insecticide applications (Wu et al. 2002, Qaim 2003, Morse et al. 2005). This chapter focuses on the development of secondary pests in two of the most important GEIR crops, *Bt* maize and *Bt* cotton.

Cotton

Of the 24.3 million hectares cropped with *Bt* cotton worldwide in 2012, India, China and USA accounted for 11.0, 4.2 and 4.1 million hectares respectively (James 2013), with the adoption rate varying between 90 and 95% (James 2013). The *Bt* cotton hectarage in Africa is increasing, for instance, Burkina Faso and Sudan cropped 50% (in ha) and 300% (in ha) more *Bt* cotton, respectively, compared with 2012 (James 2013). In China, in some areas where the bollworm incidence is higher, the adoption is close to 100% (Xu et al. 2008), and undoubtedly *Bt* cotton has reinvigorated Chinese cotton production. Historically, cotton along with rice crops have required the largest number of insecticide applications in the world (Deguine et al. 2008). Until the end of the 20th century, insecticides were intensively applied to control the cotton bollworm (Wu and Guo 2005). However in the early 1990s effective control of this pest became problematic, the cotton bollworm became resistant to most insecticides due to overuse (Wu and Guo 2005, Deguine et al. 2008). Following the introduction of GEIR technology in 1999, insecticide applications in *Bt* cotton fields dropped from about 61 kg/ha (20 applications), to approximately per year 12kg/ha (6.6 applications) (Huang et al. 2002b). By 2002 this figure starting creeping up; farmers applied on average 15.6 kg/ha (10.7 applications) of insecticides, of which 4.7kg were used against the cotton bollworm, and the remaining against the *lygus* bug and other pests (Pemsl et al. 2011). By 2005, farmers applied roughly the same amount against the cotton bollworm, but the amount sprayed against secondary pests had increased by 20%, to a total of 18.6 kg/ha (14.2 applications) (Pemsl et al. 2011). Within the space of approximately 10 years, the initial advantage of *Bt* crops had gone; Zhao et al. (2011) reported that *Bt* adopters were using on average between 16 and 22 insecticide applications, while conventional cotton farmers were using only 11 to 17 applications on average per year. Hence, nowadays those insects once considered of minor relevance are actually the main concern of farmers (Pemsl and Waibel 2007). The drop in insecticide use and the ineffectiveness of *Bt* cotton against these secondary pests has led to a reversal of the ecological role of cotton (Lu et al. 2010, Li et al. 2011). While before, the main sink for the mirid bug secondary pest was the conventional cotton system, nowadays *Bt* cotton fields are an actual source for these pests (Lu et al. 2010). This has led to a situation where there are no major differences in the total quantity and expenditure in insecticide application between *Bt* and conventional cotton farmers (Yang et al. 2005b, Zhao et al. 2011). However, in comparison with the period prior to *Bt* adoption, farmers are generally not worse off. Cotton production is still effective and farmers are applying fewer sprayings in early season, consequently with lower instance of human poisoning (Huang et al. 2014). Moreover, a higher survival of generalist arthropod predators has been recorded (ladybirds, lacewings and spiders), providing additional biocontrol to neighbouring crops, such as maize and soybean (Lu et al. 2012, Huang et al. 2014).

Cotton farming in India is comparable with that of China, in both there are numerous small scale farmers (Huang et al. 2002b, Qaim et al. 2009). Recent evidence shows that secondary pests now pose a major problem (Nagrare et al. 2009), with farmers battling against non-target insects (Stone 2011). Ramaswami et al. (2012) found no significant difference between adopters and non-adopters in terms of insecticide use and this is consistent with *Bt* farmers' perceptions, who have attributed a total of 77% of cotton damage to aphids and other sucking pests and only 23% to the primary Lepidopteran pests (Stone 2011). According to the same author 99% of the famers did use spray against secondary pests. However, it is important to note that until now, according to the studies mentioned earlier, the impact of *Bt* cotton on farm profits is clearly superior to conventional cotton.

Elsewhere in the world similar issues as in the Chinese and Indian cases have been reported in cotton. Adopting farmers are either still using significant numbers of insecticide applications in order to control secondary pests, or the damage caused by these pests has increased. Some examples include: South Africa (Hofs et al. 2006, Schnurr 2012), Burkina Faso (Dowd-Uribe 2014), Pakistan (Jaleel et al.), Australia (Wilson et al. 2013), Brazil (Sujii et al. 2013) and Mexico (Traxler and Godoy-Avila 2004).

In the USA for example, in the mid-southern and south-eastern cotton-producing regions, there has been a significant increase in the number of insects considered as secondary cotton pests, such as aphids, leafhoppers, mirid plant bugs and stinkbugs (Naranjo 2011). The same author analysed the National Cotton Council data, reporting that before *Bt* cotton adoption, farmers were applying an average of 17 applications per hectare, and this figure dropped post-adoption to 5 applications (a 71% reduction). Additionally, *Bt* cotton losses due to pest damage are around 5.4%, a decrease of 27% as compared with pre-1996 levels. Nonetheless, while insecticide use to control primary pests has decreased, insecticide applications used to control secondary pests such as plant bugs have nearly doubled to approximately four applications per hectare in order to achieve adequate control (Naranjo 2011). Importantly, in contrast with the Chinese and the other cases around the world previously mentioned, most of the secondary pests in the US are being effectively managed with sensible use of insecticides and other IPM tactics (Naranjo and Ellsworth 2009).

Maize

The economic benefit of *Bt* maize associated with the regional suppression of specific pest populations is significant (Carpenter 2010, Areal et al. 2013). Hutchison et al. (2010) estimated the cumulative benefits of controlling ECB with *Bt* maize over the last 14 years at $6.8 billion for maize growers in the US Midwest, with more than 60% of this total – $4.3 billion – accruing to non-*Bt* maize growers due to savings in insecticide applications because of overall suppression of ECB populations. Presently, in the USA the most problematic secondary pest in *Bt* maize is the WBC. Catangui and Berg (2006) reported that yield losses caused by the WBC on transgenic Cry1Ab *Bt* maize reached 70% in 2003 in South Dakota. This value is not surprising, since only one WBC larvae per maize plant at dent stage can reduce yields by 232 kg/ha (Appel et al. 1993). The CEW and the fall armyworm, are considered important secondary pests. Their moderate survival rates in *Bt* maize expressing Cry1Ab and Cry1F makes them economically important (Archer et al. 2001, Storer et al. 2001, Hardke et al. 2011). According to Speese III et al. (2005), the net profit for *Bt* cultivars is about 13% higher when compared with conventional non-*Bt* cultivars with five applications of insecticides. The same author noted that the overall net profit would about 32% higher if two insecticide applications were used with *Bt* cultivars in order to reduce damage caused by the CEW and sap beetles.

Currently, the only *Bt* maize allowed for cultivation in Europe contains the transformation event MON810 (Monsanto Company) expressing Cry1Ab *Bt* toxin (EFSA 2010a) although several other events are under evaluation by the European Food Safety Authority (EFSA). This transgenic maize presents a highly efficient level of resistance to the two primary maize lepidopteran borers present in the EU, the Mediterranean and the European corn borer (González-Núñez et al. 2000, Eizaguirre et al. 2010). In European conditions, *Bt* Cry1Ab is not efficient against several secondary pests, such as the western corn rootworm and the true armyworm (Gray et al. 2009, Pérez-Hedo et al. 2012). The western corn rootworm was first noticed in Europe in the mid-1980s (Bača 1994, Miller et al. 2005) and it has been spreading through maize fields across the continent at an average rate of 33 to 40 km per year, depending on climatic conditions (Gray et al. 2009, Meinke et al. 2009). Its presence is more common in central, eastern European countries and in the Po Valley in Italy where attributable yield losses of about 2–3% have been reported (Meissle et al. 2010). According to Wesseler and Fall (2010), the economic benefits of employing an event capable of controlling the Western corn rootworm is 472 million euros per year. Several other arthropod pests of maize are also present in Europe, although they tend to be more regional and usually less damaging to the crop (see Meissle et al. 2010 for an exhaustive list). Field research concerning secondary pests has mainly been conducted in Spain. Recent studies have revealed that the true armyworm is only mildly susceptible to *Bt* maize expressing the Cry1Ab toxin (Pilcher et al. 1997, González-Cabrera et al. 2013) and field trials found no substantial differences in the number of *M. unipuncta* larvae per plant nor in the larvae development between *Bt* and isogenic varieties (Eizaguirre et al. 2010, Pérez-Hedo et al. 2012). Hence, it is possible that the increased use of transgenic maize expressing Cry1Ab toxin will further amplify its importance due to decreasing conventional insecticide applications, which could in time mean it becomes a major pest (Pérez-Hedo et al. 2012, González-Cabrera et al. 2013).

In South Africa, the first African country to commercially produce *Bt* crops, some studies have been conducted in order to scrutinize the impact of *Bt* maize on secondary pests (Van den Berg et al. 2013). It was noticed that GEIR maize has the potential, when well-managed, to effectively control primary lepidopteran pests, such as *B. fusca*, *S. calamistis* and *C. partellus* (Van den Berg and Van Wyk 2007, Van Wyk et al. 2009, Kruger et al. 2012). However, several important secondary pests are also present in the ecosystem including *A. segetum*, *H. armigera* and *A. loreyi* (Van Wyk et al. 2008, Van Wyk et al. 2009, Erasmus et al. 2010). Although these secondary pests may show some degree of susceptibility to Cry proteins (their densities are usually lower in *Bt*-maize fields compared to non-*Bt* fields) their ability to seriously damage the crop under field condition is well recognized (Van Wyk et al. 2007, Van Wyk et al. 2008). Similar importance is now given to *H. armigera* in other countries, for example in China, Australia and South Africa (Tabashnik et al. 2003, Van Wyk et al. 2008) and to the corn leafhopper, an efficient vector of several plant pathogens, in Argentina (Bastos et al. 2007). Ecological explanations for higher attraction to *Bt* maize in some pest species have been found; for example chemical and/or morphological characteristics expressed by the *Bt* maize make it especially attractive to the corn leafhopper secondary pest (Bastos et al. 2007).

This review suggests that *Bt* hybrids do not effectively control all Noctuidae pests under field conditions due to the emergence of secondary pest species. Further, in both *Bt* maize and *Bt* cotton, the increased significance of secondary pests is intrinsically linked with insecticide use. On the one hand, as previously shown, decreases in insecticide applications can allow non-*Bt* susceptible insects to increase in numbers within the *Bt* crop. On the other hand, broad-spectrum insecticide spraying is the cheapest and most efficient solution for farmers to avoid severe crop damage due to a sudden pest outbreak of a non-target pest species. Several other issues are also linked to insecticide use in GEIR crops; such as pest resistance caused mainly by a lack of refuge strategies, weak institutional structures, poor education and a lack of understanding of the technology (Yang et al. 2005a, Morse et al. 2007, Dowd-Uribe 2014).

4.5 Outstanding issues

Regardless of the outbreak cause, if non-susceptible secondary pest populations exceed economic thresholds the sustainability of the technology may be in jeopardy. If natural enemies are incidentally affected by *Bt* toxins an ecological opportunity may appear for the emergence of a new pest species which had previously been controlled through predation or parasitism. Consequently, insecticide spraying is the only immediate solution at farmers’ disposal, which is inherently even more disruptive to the natural enemies’ complex. If a secondary pest outbreak occurs due to an unexpected niche replacement, the same immediate solution will be used with equivalent impacts. Hence, farmers growing *Bt* crops will potentially re-embark the “insecticide treadmill” as in the 20th century (van den Bosch 1978), leading back to the negative impact of insecticides on the environment that GEIR crops were hoped to reduce (Krebs et al. 1999, Pemsl et al. 2011).There are serious disadvantages associated with overuse of pesticides, for instance, human poisonings, pest resistance and natural enemy mortality (Metcalf 1987, Jeyaratnam 1990, Hardin et al. 1995, Graff Zivin and Sunding 2000, Kouser and Qaim 2011). Additionally, pests tend to increase their reproductive rate when stressed by sub-lethal quantities of a control agent; a phenomenon known as ‘‘hormoligosis’’ (Luckey 1968, Morse 1998). It appears that to date ‘‘hormoligosis’’ has not been studied within the GEIR crops context, however it is understood to be partly responsible for past outbreaks of secondary pests related to the misuse of insecticides (Gross and Rosenheim 2011, Cordeiro et al. 2013, Guedes and Cutler 2014). Research presented in this review suggests that secondary pests are eroding some of the economic and ecological benefits of *Bt* crops. Chinese cotton production is a clear example. In fact it was shown that, even in successful GEIR cropping systems (such as *Bt* cotton in USA), insecticide applications remain a strategically important method of controlling secondary pest outbreaks.

New stacked events expressing several *Bt* toxins may overcome some of the drawbacks associated with secondary pests. Scientists are hopeful that these stacked crops will mitigate some of the concerns raised so far for single traits and increase yields still further (e.g. Shi et al. 2013). From an ecological perspective, such expectations have yet to be proven, as stacked events may equally cause faster changes in ecosystem processes, affecting the resilience of the systems as a whole to adapt efficiently. Furthermore, some agro-ecosystem responses may occur over a long timeframe, so that only long-term studies could effectively detect any effects (see Symstad et al. 2003 for a detailed discussion). For example, continuous exposure to a range of *Bt* toxins throughout the full season may affect prey species and food chains (Groot and Dicke 2002) and the occurrence of resistance may be increased in pests with low susceptibility to *Bt* toxins over time (Brévault et al. 2013). This lack of certainty regarding ecological impacts and the complexity of agro-ecosystems has led to questions about the conclusions of several studies assessing the impacts of transgenic crops due to their simplistic methodological approaches (e.g. Andow et al. 2006, Smale 2006, Lövei et al. 2009, Glover 2010a, b, Stone 2011, Kruger et al. 2012, Dowd-Uribe 2014). There is a risk that interactions evaluated over a short period are failing to observe potential longer-term impacts (Kouser and Qaim 2011, Pemsl et al. 2011). The occurrence of secondary pests is clearly linked with profitability, which in turn is affected by other important factors, such as the variability of toxin expression, quality of seeds, development of resistance, environment, farm size, regional, social and institution variability, along with farmers' knowledge/education, skills and wealth (Yang et al. 2005a, Smale 2006, Shantharam et al. 2008, Xu et al. 2008, Kruger et al. 2011, Stone 2011, Kruger et al. 2012, Dowd-Uribe 2014). For example, making an assumption that early adopters are similar in terms of performance to late adopters or small-scale farmers may introduce a bias to the results (Crost et al. 2007, Ismael et al. 2007, Morse et al. 2007, Stone 2011). Similarly, differences in agricultural systems are important factors that are often omitted (Stone 2011); such as irrigated versus non-irrigated fields in India (Qaim and Zilberman 2003) and it is likely that such systems have differences in pest abundance and insecticide use (Stone 2011)[8].

Nor are studies assessing the impact of GEIR crops on NTOs free from criticism over the methodological approaches used. Ecological criticisms are mainly based on the reliability of data, poorly replicability, low numbers of possible response variables, short temporal frame and failure to take into consideration environmental variability across regions (Marvier 2002, Lövei and Arpaia 2005, Andow et al.

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[8] For a detailed discussion concerning the general inconsistencies of socio-economic studies around transgenic crop adoption see Smale (2006).

2006, Shantharam et al. 2008). Undoubtedly laboratory studies are essential in the assessment of the effects of *Bt* crops on NTOs, provided that they are assessed across the full variety of relevant ecological contexts (Lövei and Arpaia 2005). In the laboratory or in controlled field cages, most non-field scale studies have assessed the impact that the toxin has directly on the predator, on the prey or on the impact of a predator through prey consumption (see for example Marvier et al. 2007, Wolfenbarger et al. 2008, Lövei et al. 2009, Lang and Otto 2010). However, the relevance of these findings within the field agro-ecosystem is uncertain (Andow and Hilbeck 2004, Lövei and Arpaia 2005) and such studies often fail to account for indirect spatial and temporal effects on tritrophic population dynamics (Andow et al. 2006). Further, the occurrence and distribution of insect pests in crops are non-uniform, depending instead on factors such as the agro-climate conditions, agro-ecology, anthropogenic interventions, introduction of new crops, pest control management techniques, and other hard to define random factors (Baker et al. 2000, Sisterson et al. 2005, Velasco et al. 2007).

4.6 Conclusions

Like insecticides, GEIR crops alter agro-ecosystem processes and functioning. In some cases this may lead to large and complex landscape-level effects on pest dynamics, a rearrangement of niches, and thus a possible outbreak of secondary pests. This review has explored the reasons for, and the results of, secondary pest outbreaks in GEIR crops, with a focus on *Bt* Maize and *Bt* cotton. Undoubtedly, GEIR crops have led to several economic and environmental advantages, but many claim that those gains, although real, have been overemphasized (Smale 2006, Stone 2011). Although secondary pest outbreaks are a well-known phenomenon in agriculture, this phenomenon has generally been overlooked in transgenic cropping research. While GEIR crops are highly efficient at controlling target pest levels, they may not be as effective at controlling other pests that have historically posed less or even no threat (Sharma and Ortiz 2000). Here the three potential mechanisms related to secondary pests were reviewed: i) a reduction in broad-spectrum insecticide applications; ii) a reduction in control by natural enemies; and iii) a decrease in inter-specific competition with the target pest.

It is evident from the literature that, owing to lower insecticide applications, secondary pests that are not susceptible to the expressed toxin are becoming an increasing concern in some agro-ecosystems where GEIR crops are grown. The potentially negative influence of GEIR crops on natural enemies has generated considerable debate among scientists, although there appears to be agreement that a negative impact is conceivable (e.g. Andow et al. 2009, Lövei et al. 2009, Shelton et al. 2009). This impact can be direct; through the ingestion of the toxin, or indirect; due to changes in the agro-ecosystem on which that species depends, such as reduced prey density (Snow et al. 2005, Andow et al. 2006). Less attention has been given to niche replacement, notable exceptions are the studies conducted by Dorhout and Rice (2010) and Virla et al. (2010). These authors have proposed that direct competition between susceptible and non-susceptible species is one explanation for secondary pest outbreaks. However, secondary pests may take several years to develop to a point where they actually become a major concern (Ho et al. 2009). Hence, it has been suggested that additional research is needed to evaluate the potential long-term effects of the wide scale adoption of new GEIR events and their impact on the ecosystem (Krishna and Qaim 2012). It is important that the ecological relevance of such studies is properly addressed (Gatehouse et al. 2011), especially regarding the impact on ecological services across the agricultural landscape (Scherr and McNeely 2008) and on the resilience of agro-ecosystems on a regional scale (Tscharntke et al. 2005). Based on this review of the literature, the chapter concludes with five major issues that require further exploration:

I. Large-scale, multi-trophic and multi-species field studies should be encouraged in order to reveal the potential impacts on ecosystems and their extent (Lang and Otto 2010) since: i) *Bt* toxin concentrations vary throughout the season depending on expressed toxin and the cultivar (Nguyen and Jehle 2009, Showalter et al. 2009); ii) Interactions between GEIR fields and adjacent ecosystems will surely occur (e.g. natural enemy migration or niche replacement) (Dorhout and Rice 2010, Razze and Mason 2012), which might carry direct and/or indirect biotic impacts across the landscape (Lundgren et al. 2009); iii) In the case of stacked GEIR crops, potential interactions between the expressed events may occur (Zhao et al. 2005) and resistance may be increased in pests with low susceptibility to *Bt* toxins (Brévault et al. 2013). Hence, laboratory and/or single species studies may fail to capture wider trophic impacts as a result of high field environmental variability (Lövei et al. 2009) and only a holistic knowledge of pests and the behaviour of natural enemies will enable the formulation of a sustainable IPM framework capable of effectively supressing secondary pest outbreaks (Sisterson et al. 2007, Lundgren et al. 2009).

II. The baseline for risk analysis studies should be adjusted. Until now studies have used conventional cropping with insecticide treatments as the main basis for comparison of risk of GEIR crops (Sisterson et al. 2007, Meissle et al. 2011). However, this comparison should be broadened to include other scenarios, such as organic or untreated cropping systems (Andow et al. 2006). The assessment of GEIR cropping with other IPM strategies, such as crop rotation, tillage, selective insecticides and biological control (Musser and Shelton 2003, Deguine et al. 2008, Vasileiadis et al. 2011) would be useful, especially taking into consideration the forecasted world food demand (Park et al. 2011b). Failure to take this aspect into consideration might lead farmers to neglect other good farming practices (Bergé and Ricroch 2010);

III. Economic studies should move towards a wider approach, taking into consideration farmers' heterogeneity (Glover 2010a, b). Assessing the mean yield/profits of a crop within an entire country/region will likely be biased towards wealthier and better informed/educated farmers (Sanglestsawai et al. 2014). Although not directly mentioned in economic studies, it is believed that the issue of secondary pests is invariably connected with farm profits. This is especially relevant in developing countries, where institutional networks are weak, making the enforcement of laws, policies and agricultural recommendations less effective (Shantharam et al. 2008, Xu et al. 2008, Kruger et al. 2011, Stone 2011, Kruger et al. 2012, Dowd-Uribe 2014). As Stone (2011, page 395) states, "longitudinal, multi-village, multi-ethnic, probabilistically selected, ethnographically grounded studies that avoid bias are helpful".

IV. In order to identify possible secondary pests and non-target effects of GEIR crops with insecticidal properties, knowledge is required on which arthropod species occur in a given agro-ecosystem (Truter et al. 2014). Presently, several million hectares of crops with GEIR traits are being grown, hence researchers should take advantage of such “large-scale field research” opportunities. Continuous, post-market, spatiotemporal monitoring is critical for rapid identification of the development of ecological problems. This could lead to timely regulatory decisions and the efficient deployment of mitigation measures (Waage and Mumford 2008, Sanvido et al. 2009, Smale 2012). Furthermore, it is suggested that post-market monitoring could help build a robust spatiotemporal database of insect species according to their ecological functions and occurrence in the specific receiving environments. Such a methodical process would also help to select a number of relevant and practical surrogate species for detailed laboratory or field tests (Hilbeck et al. 2014)

V. The importance of spatially-dynamic, bio-mathematical and -economic multi-species models in pre and post GEIR crops risk assessment research has been recognized for some time (Chatterjee 1973, Gutierrez and Wilson 1989, Harper and Zilberman 1989, Marino and Landis 1996, Sanchirico and Wilen 1999). Rigorous assessments of the present and future economic impacts, based on ecological constraints are required to provide sound information to policy makers (Keller et al. 2007, Ascough II et al. 2008, Holmes et al. 2010, McDermott et al. 2013). It has been suggested that these models combined with empirical investigations can provide important insights into the impact of IPM tactics on the behaviour of target and non-target organisms (Yang et al. 2009, Vinatier et al. 2011). By allowing the manipulation of key biological parameters with economic production and damage functions, it will be possible to analyse potential solutions under different IPM scenarios, real or hypothesised (Carrasco et al. 2010c, DeJonge et al. 2012, Liang et al. 2012). Additionally a robust assessment of the effects of agro-ecosystem heterogeneity on pest population dynamics might be obtained when a geographic information system (GIS) approach is added to the model (Carrière et al. 2006). From these models it will be possible to assess which insects are most likely to be susceptible to landscape or environmental changes (Maiorano et al. 2014, Petrovskii et al. 2014). Hence it is important to foster research collaborations between the fields of ecology, mathematics and economics (Codling 2014, Crowder and Jabbour 2014).

4.7 Summary

In summary, despite the widespread adoption of GEIR and a continued increase in the area grown of these crops internationally, there are still a range of questions associated with longer term agro-ecosystem interactions that remain unanswered, for instance in relation to secondary pests. These may not be serious enough to undermine the use of the technology but do require further exploration so that practical and economically viable advice can be given to farmers and so that regulators are aware of potential issues and risks during the approval phase. The next chapter develops a bio-economic model to analyse the interactions between primary and secondary insect populations and the impact of different management options on insecticide use and economic impact over time.

CHAPTER 5. MANAGING MAIZE UNDER PEST SPECIES COMPETITION: IS *BT* (*BACILLUS THURINGIENSIS*) MAIZE THE SOLUTION?

5.1 Chapter introduction

Transgenic crops that contain Cry genes from *Bacillus thuringiensis* (*Bt*) have been adopted by farmers over the last 17 years. Unlike traditional broad spectrum chemical insecticides, *Bt*'s toxicity spectrum is relatively narrow and selective, which may indirectly benefit secondary insects that may become important pests. The economic damage caused by the rise of secondary pests could offset some or all of the benefits associated with the use of *Bt* varieties. This chapter develops a bio-economic model to analyse the interactions between primary and secondary insect populations and the impact of different management options on insecticide use and economic impact over time. Results indicate that some of the benefits associated with the adoption of genetically engineered insect resistant crops may be eroded ecological dynamics are taken into account. It is suggested that secondary pests could easily become key insect pests requiring additional measures - such as insecticide applications or stacked traits – to keep their populations under the economic threshold.

5.2 The economic sustainability of GEIR' cropping

In 1996, the first generation of genetically engineered insect resistant (GEIR) crops expressing toxins (crystalline (Cry) proteins) from the soil bacterium *Bacillus thuringiensis* (*Bt*) were made commercially available. Since then they have been used worldwide for controlling insect pests of major crops such as maize and cotton (James 2013). So far, the benefits of commercialized GEIR crops have exceeded expectations (Carrière et al. 2010). It is now broadly accepted that any eventual detrimental impact on non-target organisms (NTO) is lower for *Bt* crops than for conventional crops requiring broad-spectrum insecticides (Cattaneo et al. 2006). There is evidence from the use of a number of environmental impact indicators that GEIR crops have reduced (or at least have not increased) the impact of agriculture on biodiversity through selective targeting and associated reductions in the use of broad-spectrum insecticides (Carpenter 2010, Areal and Riesgo 2015). Furthermore, the economic benefit of *Bt* crops associated with the regional suppression of specific pest populations appear to be significant (Gomez-Barbero et al. 2008, Carpenter 2010, Hutchison et al. 2010, Areal et al. 2013). The damage caused by stalk-boring feeding insects, such as the European corn borer (ECB) [*Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae)], is enough to cause a significant reduction in maize yields (Malvar et al. 1993, Bohn et al. 1999). Hutchison et al. (2010) estimated the cumulative benefits of controlling ECB with *Bt* maize over the last 14 years at $6.8 billion for maize growers in the US Midwest, with more than 60% of this total accruing to non-*Bt* maize growers. On the other hand, in European countries where *Bt* maize has still not been employed, yield losses without control may reach 30%

in areas highly infested with stalk-borer feeding insects (Meissle et al. 2010). According to Park et al. (2011a) this represents a loss to farmers of between 157 million and 334 million Euros each year.

Despite its wide adoption, the sustainability of *Bt* crops is still a controversial topic among the scientific community. Two concerns are usually raised: i) ecological shifts may take several years to manifest (Ho et al. 2009), hence, it is important to understand the long term ecological interactions around GEIR crops (Snow et al. 2005) and ii) the impact of *Bt* crops on NTOs in field conditions may not reflect the results obtained in laboratory studies (Andow et al. 2006, Lövei et al. 2009). In particular, researchers have predicted that NTOs could appear in such numbers that they may become key secondary insect pests[9] in *Bt* crop fields (Andow and Zwahlen 2006). Citing Harper (1991, p.22), “ignoring secondary pests can lead to devastating crop damage that may continue over a considerable period of time”. Such occurrence of secondary pests would require additional spraying with conventional broad-spectrum insecticides, which may erode (at least) some of the benefits of GEIR crop technology (Pemsl et al. 2011).

This chapter develops a bio-economic model to evaluate the impact of a number of pest management options on primary and secondary pest populations, as well as on insecticide use and related economic outcomes. It uses a production function based on a system of two first order differential equations that represent the ecological interactions of the primary and secondary pests with the pest management practices. As far as the author is aware, such an approach has not yet been considered in the literature. The model takes into consideration the dynamics of two surrogate pest species, the Mediterranean corn borer (MCB) [*Sesamia nonagrioides* (Lefebvre) (Lepidoptera: Noctuidae)], a target pest, and the true armyworm (TAW), [*Mythimna (Pseudaletia) unipuncta* (Haworth) (Lepidoptera: Noctuidae)], a secondary pest. Their effects on the production function are used to predict pest control decisions. Optimal insecticide applications under deterministic conditions are calculated through a Differential Evolution dynamic nonlinear optimization technique[10] (Storn and Price 1997, Mullen et al. 2011). Furthermore, numerical simulations of various scenarios arising from different hypotheses are developed and analysed. In particular, this focuses on farmers’ net returns due to the changes in insecticide use and the development of secondary pests on *Bt* maize. The chapter concludes by considering the management implications of the results as well as suggesting future research directions.

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[9] A secondary pest is a "non-targeted" pest that has historically posed small or no economic threat, but which could be directly or indirectly affected by changes in insecticide use patterns, such as those caused by *Bt* cropping, associated with the management of a primary pest (FIFRA Scientific Advisory Panel 1998).

[10] Differential Evolution (DE) is a simple yet powerful global optimization method which belongs to the class of Evolutionary Algorithms (EA) (Storn and Price 1997, Price 1999). This metaheuristic method attempts to find the optimum of the problem by iteratively refining the candidate solution with respect to the objective function (function to be optimized) value (Storn and Price 1997, Price et al. 2005). Due to its convergence speed, accuracy, and robustness, it is often preferred to other optimization methods (e.g. genetic algorithm and evolutionary programming) in order to solve real-world problems over continuous domains (Vesterstrom and Thomsen 2004).

5.3 Secondary pest outbreaks in the context of GEIR crops

Bt toxins have a narrow efficacy spectrum aimed at controlling only the target pest. This offers a safe environment for the development of non-target pests (Sharma and Ortiz 2000, Lu et al. 2010), which may lead to crop damage (Sharma and Ortiz 2000, Wu and Guo 2005). Depending on the magnitude of the impact, the adoption of *Bt* crops might convey unexpected negative effects on agricultural ecosystem interactions and consequently on farm profits (Wolfenbarger and Phifer 2000, Catarino et al. 2015, Catarino et al. 2016). In the context of GEIR crops, three main causes may trigger an outbreak of secondary pest species: i) a reduction in broad-spectrum insecticide applications (Lu et al. 2010, Pemsl et al. 2011, Stone 2011); ii) a sufficient reduction in pests' natural enemies (Naranjo 2005b, a, Marvier et al. 2007); or iii) a decrease in inter-specific competition with the lowering of target pest numbers (Catangui and Berg 2006, Dorhout and Rice 2010, Virla et al. 2010). These causes are not necessarily independent.

It is postulated that, whatever the cause of the rise in secondary pest numbers, insecticide spraying would be the only immediate solution at a farmers' disposal. The most notorious case concerns sap-feeding bugs on *Bt* cotton plants in China. Presently, in order to control these secondary pests, Chinese *Bt* cotton farmers are applying about 20 sprayings per season (for more details see Lu et al. 2010, Pemsl et al. 2011). Such application rates are similar to those before *Bt* cotton adoption when insecticides were used mainly to control cotton bollworm (Wu and Guo 2005). Insecticide spraying on *Bt* crops may convey ecological disturbances with knock-on consequences, such as the destruction of the primary and/or secondary pest's natural enemies' complex. Hence, if non-susceptible secondary pest populations exceed economic thresholds, the sustainability of *Bt* technology may be put in jeopardy. The bio-economic model developed in the following section demonstrates the interaction and economic impact of such an event.

5.4 Methodology

This chapter follows the pioneering work of Lichtenberg and Zilberman (1986)[11], in which a damage control model considered pesticides as a damage abatement input that has an indirect effect on output. In previous studies, pesticides were modelled as a yield-increasing input (Headley 1968, Hall and Norgaard 1973). This approach allows for changes in the damage control agent productivity over time, including the integration of pest population (see section 2.6 for further details).

Mathematical modelling plays an integral part in attempts to understand the dynamics of two species. In general, competition can be defined as an interaction in which the survival and reproduction of individuals is negatively affected by the interaction with other individuals, from the same or different species. The

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[11] For a detailed review on the Lichtenberg and Zilberman (1986) damage control approach see Sexton et al. (2007).

classical theory of ecological competition between two species is usually modelled by a system of nonlinear ordinary differential equations (ODE) of first order which is associated with Volterra (Volterra 1928) and Lotka (Lotka 1925). The Lotka-Volterra (LV) system models species growth where intra- and inter-specific interaction coefficients are introduced into the dynamics. The LV system of equations is usually described by a set of deterministic equations involving a small number of variables. In this thesis, it is considered that the pest population growth rate is negatively affected by the intra- and inter-specific competition, natural enemies and the control parameters, insecticides and *Bt* toxin. For each species, their specific parameters values were obtained from literature (table 5.2).

5.4.1 Bio-economic model

Following Lichtenberg and Zilberman (1986), a bio-economic model is designed where pest interactions are incorporated into a production function. The damage-abating role of insecticide is taken into account explicitly in the production function through an asymmetric treatment of "productive" inputs (z) and "damage-abating" insecticide ***(x): y = F(x, D(z))***. ***D(x)*** is the so called damage-abatement function, representing the role of insecticide in the model, which do not have the potential to increase the output but indirectly mitigate yield loss through pest elimination. The effect of pest impact on the output is based on the Lotka-Volterra model which defines the population dynamics of two species competing for the same resource. Although the Lichtenberg and Zilberman (1986) damage control approach is not free from criticism (Lansink and Carpentier 2001, Zhengfei et al. 2006), it has been successfully used in other bio-economic models of GEIR crops (Huang et al. 2002a, Pemsl et al. 2008, Qaim 2009) and to model the management of invasive alien species (Ceddia et al. 2009).

The initial model assumptions are as follows. The agricultural product is attacked by two rather different pests: the MCB – primary pest (N_1) – is a highly competitive pest that is also highly susceptible to *Bt* toxin; and the TAW – secondary pest (N_2) – is negatively affected by the first species, but has a higher tolerance to the *Bt* toxin. Both have the same negative impact upon the yield. The dynamic behaviour of both species, with and without pest control, is analysed below. It is assumed that the farmer has only two means to suppress pests, by adopting *Bt* varieties and by spraying insecticide when pest densities exceed an economic threshold (ET[12]).

Actual output

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[12] Economic threshold is defined as the "density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level". The economic injury level was defined by these authors as the "lowest population that will cause economic damage" (Stern et al. 1959).

Let ***G(Z)*** denote the aggregate potential maize output over a landscape, which includes both conventional maize ***(G_c)*** and GEIR maize ***(G_{Bt})***, where ***Z*** represents a vector of non-insecticide inputs (i.e., labour, seeds, fertilizers etc.). The damage control framework models the actual output, ***Y***, as a function of potential output, ***G(Z)***, damage, ***D(N_1,N_2)***, and proportion of the total landscape planted with *Bt* maize (***Ω***). The actual output is given by:

$$Y = G(Z)[1 - D\,(N_1, N_2)]$$

With:

$$G(Z) = (1 - \Omega)G_c(Z) + \Omega G_{bt}(Z) \tag{5.1}$$

$$G' > 0, G'' < 0$$

Damage is a function of the density of both pest populations – ***N_1*** and ***N_2*** – and expresses the fraction of yield lost (***D_y***) due to the sum of damage caused per each species (***I***). It is assumed that both pests can act simultaneously and the nature of the damage is species independent:

$$D = D_{N_1} + D_{N_2} \tag{5.2}$$

With:

$$D_{N_1} = \frac{IN_1}{Plant\ density} \tag{5.2a}$$

$$D_{N_2} = \frac{IN_2}{Plant\ density} \tag{5.2b}$$

Economic Threshold

The ET is a practical operational rule difficult to access theoretically, hence the ET was set at a fixed level – 25% – below the economic injury level (EIL), as suggested by Pedigo et al. (1986). Following the same author, the EIL is composed of four primary variables: ***w***, the cost of management per unit (€/ha); ***p***, the product market value per ton (€/ton); ***D_y***, yield lost per larvae (tons/ha); and ***s***, the proportion of larvae killed (%).

$$ET = \frac{EIL}{4} \tag{5.3}$$

With:

$$EIL = \frac{w}{pD_ys} \tag{5.3a}$$

Population dynamics

Applying the LV methodology, equation 5.4 demonstrates the case of two species competing for the same resource, where $\boldsymbol{N_i}$ indicates the population density of species $(\boldsymbol{i = 1, 2};\ \boldsymbol{i \neq j})$. The parameter $\boldsymbol{r_i}$ the intrinsic growth rate, i.e. the net *per capita* growth rate at low populations densities when competition is negligible; the intra-specific competition coefficient $\boldsymbol{a_{ii}}$ measures the effect of species $\mathbf{i}$ on itself; the inter-specific competition coefficient $\boldsymbol{a_{ij}}$ *meas*ures the effect of species $\boldsymbol{i = 1}$ on species $\boldsymbol{j = 2}$; $\boldsymbol{k_i}$ represents the maximum population the involved environment can hold, i.e. the carrying capacity; and $\boldsymbol{m_i}$ the mortality attributed to natural enemies.

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - b_{11}\dfrac{N_1}{k_1} - b_{12}\dfrac{N_2}{k_1} - m_1\right) \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - b_{22}\dfrac{N_2}{k_2} - b_{21}\dfrac{N_1}{k_2} - m_2\right) \end{cases} \tag{5.4}$$

In the absence of the competitor, the dynamics of both species follow a logistic model. In this case, as the population density increases, the effect of intra-specific competition effectively slows down the rate of growth until equilibrium is reached at the environment carrying capacity. In the presence of other species, the growth rate also decreases due to interspecific competition. The pressure of the competitor is proportional to specific densities and is influenced by the *competition coefficient*.

Within this basic framework, two forms of pest control are introduced: the adoption of *Bt* seeds ($\boldsymbol{\Omega}$) and the application of broad-spectrum insecticide ($\boldsymbol{x}$). The parameter q_i ($\boldsymbol{i=1,2}$) indicates the effectiveness of *Bt* in controlling each pest population. The pest dynamics become:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 (1 - b_{11}\dfrac{N_1}{k_1} - b_{12}\dfrac{N_2}{k_1} - \phi u(x) m_1 - q_1 \Omega - \phi h(x)) \\ \dfrac{dN_2}{dt} = r_2 N_2 (1 - b_{22}\dfrac{N_2}{k_2} - b_{21}\dfrac{N_1}{k_2} - \phi u(x) m_2 - q_2 \Omega - \phi h(x)) \end{cases} \tag{5.5}$$

Farmers' adoption of *Bt* technology is assumed to be exogenous and develops according to the following logistic function:

$$\Omega = \frac{\lambda_f \lambda_i e^{r_\Omega t}}{\lambda_f + \lambda_i (e^{r_\Omega t} - 1)} \tag{5.6}$$

The insecticide's effectiveness is specified by ***h(x)*** which is a function of the number of insecticide applications ($\boldsymbol{x}$), and by ϕ, a dummy variable, assuming the value of one if $\boldsymbol{N_1 \geq ET_{N_1}}$ or $\boldsymbol{N_2 \geq} \mathbf{ET}_{\boldsymbol{N_2}}$, and zero otherwise. Both pests are equally affected by the insecticide. It is important to note the insertion of the new component into the natural enemies' variability parameters $\phi\boldsymbol{u}(\boldsymbol{x})$ which reflects the negative impact of insecticide applications on natural enemies (Equation 5.8).

Following Shoemaker (1973) and Bor (1995), mortality rate is an exponential function of insecticide dosage because high insect mortality requires a large dosage of insecticide. Consequently, the following kill efficiency function is:

$$h(x) = (1 - e^{-x(t)s_p}) \tag{5.7}$$

$$x(t) = a + bt + ct^2 + dt^3 \tag{5.7a}$$

$$u(x) = (1 - e^{-x(t)s_{ne}}) \tag{5.8}$$

h(x) is assumed to be monotonically increasing in *x(t)*, which represents the application of insecticide at time t, and satisfies $\boldsymbol{h\,(0) = 0, lim_{X\to\infty}\,h(x) \leq 0.}$ It is assumed the farmer applies insecticide as a preventative measure (Sexton et al. 2007). Using this approach, the farmer can make an accurate estimation concerning the possibility of pests occurring. The parameters a, b, c and d in this expression are estimated though the maximization of the farmer's net present value as specified below. Insecticide applications assume a cubic form in order to provide a higher degree of freedom when carrying out the optimization process.

Net present value

An agricultural landscape (whose area is normalized to one ha) populated by a profit maximizing farmer is used to explore the economic implications of different pest management decisions. The problem is formulated in terms of the maximization of NPV after 25 years of aggregate landscape profits, subject to the pest management problem over a time interval ***[0, T]***. This is accomplished by choosing the appropriate amount of insecticide to apply throughout the cropping season according to the economic threshold given in the above pest dynamic scenario. The farmer determines his optimal insecticide application at the beginning of the planning horizon by choosing the values of parameters ***a***, ***b***, ***c*** and ***d*** in expression (***7a***) so as to maximize his NPV over the given time horizon. To make the problem more treatable, it is also assumed that all other inputs (***Z***) in the equation below are applied in fixed proportions.

Letting $\boldsymbol{\delta}$ denote the discount factor, $\boldsymbol{p}$ the output price, $\boldsymbol{u_c}$ and $\boldsymbol{u_{Bt}}$ the prices of conventional and GEIR maize inputs unrelated to damage control, $\boldsymbol{w}$ the price of a unit of insecticide ***(x)***, then the problem is:

$$\max_{\{a,b,c,d\}} \int_0^T e^{-\delta t}\ \{pg(Z)[1 - D(h(N_1, N_2, q, X))] - Z[(1-\Omega)u_c + \Omega u_{bt}] - \phi w x\}\, dt$$

s.t.

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 (1 - b_{11}\frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1} - (1-\phi)m_1 - \Omega q_1 - \phi h(x))) \\ \frac{dN_2}{dt} &= r_2 N_2 (1 - b_{22}\frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2} - (1-\phi)m_2 - \Omega q_2 - \phi h(x))) \end{aligned} \tag{5.9}$$

With

$$\phi = \begin{cases} 1, N_1 \geq ET_{N_1} \\ 1, N_2 \geq ET_{N_2} \\ 0, otherwise \end{cases}$$

The model therefore computes aggregate maize output as the potential yield minus the fraction of the crop that is lost due to the damage caused by both pest species. The model excludes external social and environmental costs of insecticide use for both society and the farmer. Two different scenarios are analysed – before and after *Bt* maize adoption. Each scenario includes the two cases: a) the use of insecticides and b) the non-use of insecticides.

5.4.2 Model parameterization

Population growth rates for the pests were derived from laboratory data given in peer-reviewed scientific publications (see appendix 1 and 2). The laboratory conditions in these experiments represent the typical temperature and photoperiod conditions of the Mediterranean basin area. In Spanish conditions, researchers have found not more than five larvae of MCB and TAW larvae per plant (Velasco et al. 2004, Velasco et al. 2007, López et al. 2008, Eizaguirre et al. 2010). Hence this value was assumed as the maximum larvae number, for each species, per maize plant. Consequently the carrying capacity ($\boldsymbol{K_1}$ and $\boldsymbol{K_2}$) is equal to the maximum possible density of larvae within the cropped field, assuming a plant density of 90,000 per ha. Due to the large available habitat the intraspecific competition parameter was included within the carrying capacity, $\boldsymbol{b_{ii}}$=1. Considering a maximum carrying capacity of five larvae per plant and a maximum damage of 30 % (as indicated above), it is assumed that each MCB and TAW larvae is able to reduce yields by 6% per plant. It has been suggested that due to behavioural characteristics, MCB may negatively influence the TAW, however until now this effect has not been quantified (López et al. 2003, Eizaguirre et al. 2009). The chapter evaluates the case in which MCB has a strong negative effect on TAW ($\boldsymbol{b_{21}}$=0.9), while the reciprocal effect is relatively small ($\boldsymbol{b_{12}}$=0.1).

The parameters $\boldsymbol{m_1}$ and $\boldsymbol{m_2}$ take into account the impact of natural enemies on MCB and TAW populations respectively and the random effect of variable external factors that can affect predatory activity, such as temperature, humidity or agricultural practices (Kaya and Tanada 1969). Since little information is available about these, it was assumed that m_1 and m_2 follow random uniform distributions with m_1 varying between 0.1 and 0.65 and m_2 between 0.1 and 0.9. The difference between the ranges of $\boldsymbol{m_1}$ and $\boldsymbol{m_2}$ is explained by the cryptic nature of the MCB larvae which reduces its vulnerability to predation (see section 3.4.1 for further details). Small values of $\boldsymbol{m_i}$ reflect a bad year for the occurrence, abundance and subsequent predatory activity of natural enemies; high values of $\boldsymbol{m_i}$ reflect high levels of pressure by natural enemies and efficiency in capturing the pest. The parameter $\boldsymbol{q_i}$ $\boldsymbol{(i=1,2)}$ which indicates the effectiveness of *Bt* in controlling each pest population takes values $\boldsymbol{q1}$=0.99 and $\boldsymbol{q2}$=0.2. These values indicate different pest susceptibility to the *Bt* toxin. It is assumed that $\boldsymbol{N_1}$ is highly susceptible and that $\boldsymbol{N_2}$ is weakly susceptible to *Bt* technology. It is hypothesized that full adoption of the *Bt* variety happens within 10 years ($\boldsymbol{r}_\Omega = 0.8$). Initial adoption is set as 10% ($\boldsymbol{\lambda_i} = 0.1$) and the maximum adoption is 80% ($\boldsymbol{\lambda_f} = 0.8$) reflecting the minimum 20% refuge commonly advised. When adoption reaches a plateau, it means that 100% of the agricultural land is under a GEIR crop scheme.

In this study, although potentially very important, any eventual impact of *Bt* toxin on the natural enemies of the case study pests is not taken into account. Nonetheless it should be noted that, at least for Cry1Ab, no significant impacts have been reported especially when compared with insecticides (Naranjo 2005a, Cornell 2010). It is assumed that the farmer applies insecticide with optimal timing, obtaining an 80% ($\boldsymbol{s_{ne}}$) pest control efficiency per application (Hyde et al. 1999, Folcher et al. 2009). It is further assumed that insecticides have a 100% efficiency on the natural enemies' complex $\left(\boldsymbol{s_p} = 1\right)$ since it has been reported that the effect of insecticides on natural enemies is greater than the effect on pests (Longley and Jepson 1996, Van Emden 2014). Insecticide applications change over time according to the expression (*7a*).

The parameters for the economic and ecological components of the model are presented in table 5.1 and table 5.2 respectively. The time horizon considered in the analysis extends over 25 years after the initial (hypothetical) adoption of *Bt* varieties (so T=25). The model is numerically solved with R software (R-Core-Team 2012) with support from the packages "deSolve" and "RcppDE" (Soetaert et al. 2010, Eddelbuettel 2015, Soetaert et al. 2015). After calibration, the numerical results appear consistent with data reported in recent studies (e.g. Gomez-Barbero et al. 2008, Meissle et al. 2010, Areal et al. 2013). The model sensitivity analysis is presented in the following section.

Table 5.1 - Economic parameters used in the bio-economic model.

Parameters	Value	Units
Plant density per hectare	90000[a]	Plants/ha
Potential conventional maize yield (Yc)	11.30[b]	T/ha
Potential *Bt* maize yield (Y*Bt*)	11.80[b]	T/ha
Price maize (p)	248.70[a]	€/T
Conventional seed price (Sc)	253.80[a]	€/ha
Bt seed price (S*Bt*)	284.40[a]	€/ha
Fixed costs (uc)	1797.88[a]	€/ha
Fixed costs (u*Bt*)	1815.88[a]	€/ha
Insecticide cost per application (w)	18[a]	€/ha/application
Discount rate (δ)	0.05 [d]	
Initial adoption (λ_i)	0.10[d]	
Full adoption (λ_f)	0.80 [d]	

[a] (AGPME 2012); [b](Gomez-Barbero et al. 2008); [c] (MAGRAMA 2014); [d] assumption; [e] (Maund 2002)

Table 5.2 - Biological parameters for MCB and TAW used in the bio-economic model.

Parameters	N_1 (MCB)	N_2 (TAW)
Growth rate (r_i)	2.02 [a]	3.13 [a]
Intraspecific competition (b_{ii})	1[b]	1 [b]
Interspecific competition (b_{ij})	0.10[b]	0.90[b]
Susceptibility to *Bt* toxin (q_i)	0.99[c]	0.20[d]
Susceptibility to insecticide (s)	0.80[e]	0.80[e]
Minimum natural enemies impact	0.1[b]	0.1[b]
Maximum natural enemies impact	0.65[b,f]	0.90[b,g]
Maximum larvae per plant	5[h]	5[h]
Initial population	9×10^4 [b]	9×10^4 [b]
Damage per larvae (I)	0.06[b]	0.06[b]

[a] appendix 1 and 2; [b] assumption; [c] (Hellmich et al. 2008); [d] (González-Cabrera et al. 2013); [e] (Hyde et al. 1999, Folcher et al. 2009); [f] (Alexandri and Tsitsipis 1990, Figueiredo and Araujo 1996, Monetti et al. 2003); [g] (Guppy 1967, Kaya 1985, Laub and Luna 1992, Menalled et al. 1999, Costamagna et al. 2004); [h] (Butrón et al. 1999, Malvar et al. 2004, Velasco et al. 2004, Butrón et al. 2009)

5.4.3 Model integration procedure - Runge–Kutta 4th order

Most often, as in the case of this thesis, DE systems cannot be solved analytically. Algorithms based on numerical methods are therefore needed. In order to solve the ODE system, the Runge–Kutta 4th order (RK4) method was applied (Boyce and Prima 2009). The RK4 is one of several techniques used for estimating solutions of DEs based on numerical approximations. In brief, the numeral integration computes from an initial condition, $\boldsymbol{N(t_0) = N_0}$, numerous successive points that satisfy the evolution equation $\frac{\boldsymbol{dN_i}}{\boldsymbol{dt}} = \boldsymbol{f(t, N_i)}$. Using the same notation as in the foregoing, the summary of the steps of RK4 method are the following:

1) For two general 1st order ODE's:

$$\begin{cases} \dfrac{dN_1}{dt} = \mathrm{f}(N_1, N_2, t) \\ \dfrac{dN_2}{dt} = \mathrm{g}(N_1, N_2, t) \end{cases} \tag{5.10}$$

With $N_\mathrm{i}(0) = N_{\mathrm{i}_0}$

2) The 4th order Runge-Kutta[13] formula's for a system of 2 ODE's are:

$$\begin{cases} N_{1_{\mathrm{i}+1}} = N_{1_\mathrm{i}} + \dfrac{1}{6}(s_0 + 2s_1 + \ 2s_2 + s_3) \\ N_{2_{\mathrm{i}+1}} = N_{2_\mathrm{i}} + \dfrac{1}{6}(l_0 + 2l_1 + \ 2l_2 + l_3) \end{cases} \tag{5.11}$$

Where

$$\begin{cases} s_0 = \mathrm{f}(N_{1_\mathrm{i}}, N_{2_\mathrm{i}}, t_i) \\ s_1 = hf\left(t_i + \dfrac{1}{2}h, N_{1_\mathrm{i}} + \dfrac{1}{2}s_0, N_{2_\mathrm{i}} + \dfrac{1}{2}l_0\right) \\ s_2 = \ hf\left(t_i + \dfrac{1}{2}h, N_{1_\mathrm{i}} + \dfrac{1}{2}s_1, N_{2_\mathrm{i}} + \dfrac{1}{2}l_1\right) \\ s_3 = \ hf\left(t_i + h, N_{1_\mathrm{i}} + s_2, N_{2_\mathrm{i}} + \dfrac{1}{2}l_2\right) \end{cases}$$

And

$$\begin{cases} l_0 = \mathrm{f}(N_{1_\mathrm{i}}, N_{2_\mathrm{i}}, t_i) \\ l_1 = hg\left(t_i + \dfrac{1}{2}h, N_{1_\mathrm{i}} + \dfrac{1}{2}s_0, N_{2_\mathrm{i}} + \dfrac{1}{2}l_0\right) \\ l_2 = \ hg\left(t_i + \dfrac{1}{2}h, N_{1_\mathrm{i}} + \dfrac{1}{2}s_1, N_{2_\mathrm{i}} + \dfrac{1}{2}l_1\right) \\ sl_3 = \ hg\left(t_i + h, N_{1_\mathrm{i}} + s_2, N_{2_\mathrm{i}} + \dfrac{1}{2}l_2\right) \end{cases}$$

5.4.4 Model optimization procedure - Differential evolution algorithm

A differential evolution algorithm (DEA)[14] is used as the optimization technique (Storn and Price 1997). DEAs are a direct and heuristic optimization technique belonging to the class of genetic algorithms

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[13] The parameters "$\boldsymbol{s}$" and "$\boldsymbol{l}$" are not related to future parameters in the thesis, this notation was used merely for explanatory purposes.

(GAs[15]). In contrast with linear optimization techniques[16], DEAs can handle any category of objective function or constraint defined in discrete, continuous or mixed search space (Mayer et al. 2005). The incorporation of stochastic variables (such as the impact of natural enemies), into the optimization model is possible using this process. DEAs have been used extensively in the fields of agriculture economics and ecology (Taylor and Hastings 2004, Mayer et al. 2005, Groot et al. 2007, Carrasco et al. 2010c). It makes the assumption that farmers act optimally, i.e. that they have perfect knowledge of the problem in the given time-frame. In brief, as every direct search, the DEA generates variations of the parameter vectors, after which a decision is made whether or not to accept the newly derived parameters. Under this principle[17], the new vector is accepted if, and only if, it reduces the value of the objective function. In this thesis case, the model is run for each possible combination of the parameters to be optimized (equation 5.9) using Monte Carlo simulation with Latin Hypercube sampling[18] until convergence to those that led to the highest mean NPV of total costs is achieved.

5.4.5 Sensitivity analysis

To assess the influence and importance of the biological parameters $\{\boldsymbol{r_1}, \boldsymbol{r_2}, \boldsymbol{m_1}, \boldsymbol{m_2}, \boldsymbol{b_{12}}, \boldsymbol{b_{21}}, \boldsymbol{b_{11}}, \boldsymbol{b_{22}}\}$ on the model results, a global sensitivity analysis (GSA) is conducted using the Morris (1991) method[19] (Saltelli et al. 2000b). The Morris method has been used in several dynamic agroecosystem modelling projects (e.g. Confalonieri et al. 2010, DeJonge et al. 2012, Ben Touhami et al. 2013). Use of this method of sensitivity analysis aids the selection of parameters which have greater influence on the model final output variability. The parameter's uncertainty distribution values are shown in table 5.3.

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[14] Other direct search algorithms that could be used to optimize the non-line and non-differentiable objective function include Nelder-Mead and Hooke-Jeeves methods (Price et al. 2006)

[15] As the name indicates, genetic algorithms are based on the biological concept of genetic reproduction by mimicking the natural selection processes of evolution. For further insights please see Davis (1991); And Gen and Cheng (2000)

[16] Usually bio-economic model in agricultural problems are based on linear programming techniques (see Janssen and Van Ittersum 2007, for an overview). The main limitation behind this approach is the necessity to use only linear functions of the variables on the objective and constraints systems.

[17] All basic direct search methods use the greedy criterion to make this decision (Storn and Price 1997)

[18] Latin hypercube sampling is a method of sampling that can be used to produce input values for estimation of expectations of functions of output variables (Stein 1987 , McKay et al. 2000)

[19] The GSA was conducted in R software using the 'sensitivity package' (Pujol et al. 2015).

Table 5.3 – Uncertainty distribution of parameter values used in the global sensitivity analysis, Morris method.

Parameter	Nominal Value	Uncertainty interval
r_1	2.02	1.01-3.03
r_2	3.13	1.57-4.70
b_{11}	1	0.5-1
b_{22}	1	0.5-1
b_{12}	0.1	0.05-0.15
b_{21}	0.9	0.45-1
m_1	0.1-0.65	0.05-0.75
m_2	0.1-0.9	0.1-1

The Morris analysis has been used in several dynamic agroecosystem modelling projects (e.g. Confalonieri et al. 2010, DeJonge et al. 2012, Ben Touhami et al. 2013). The results generated give two measures of sensitivity, firstly the final output mean variation ($\boldsymbol{\mu*}$) in relation to the computed values (horizontal axis), and secondly the correspondent effect standard deviation ($\boldsymbol{\sigma}$) (vertical axis). Parameters with higher $\boldsymbol{\mu*}$ will have a stronger influence on the final output, while parameters with a high σ implies dependency through nonlinear responses and/or interactions with other parameters (Saltelli et al. 2000a, Saltelli et al. 2004). The sensitivity analysis using the Morris method showed that interspecific competition between primary and secondary pests ($\boldsymbol{b_{11}}$) is the most influential parameter (figure 5.1). Four other parameters: natural enemies on secondary pest ($\boldsymbol{m_2}$), primary and secondary pest intraspecific competition ($\boldsymbol{b_{11}}, \boldsymbol{b_{22}}$), and the effect of the primary pest on secondary pest {b_{21}} are also noticeably influential, while the remaining parameters have a sensitivity about threefold lower (figure 5.1).

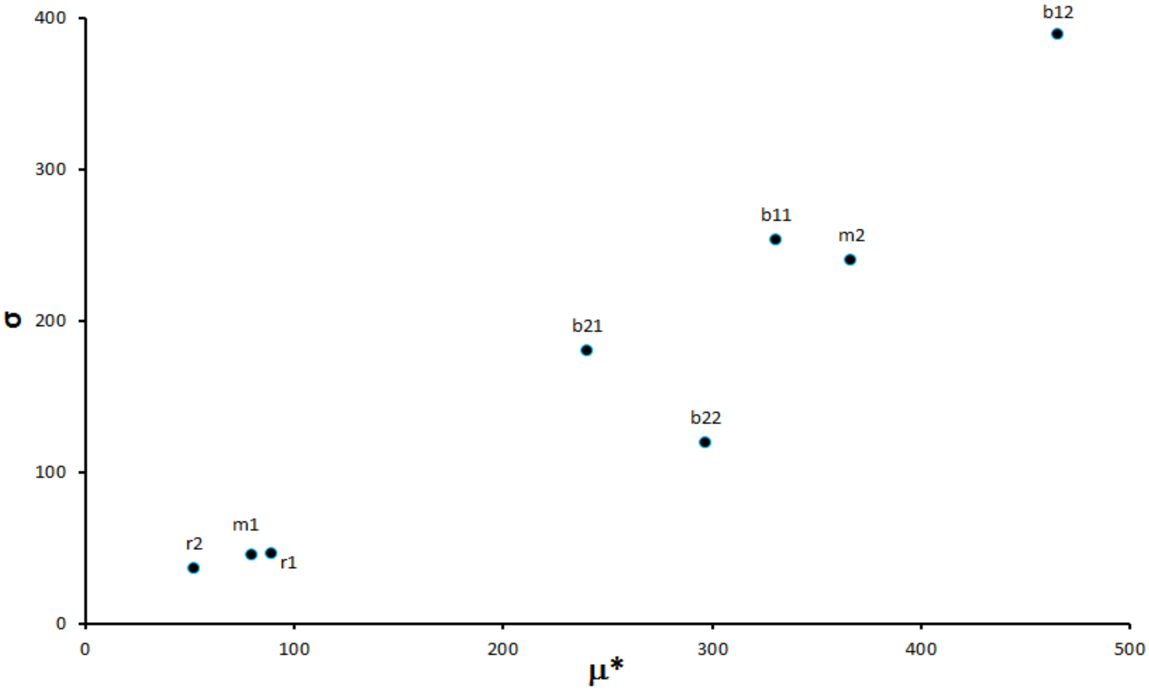

Figure 5.1 - Results of the Morris method (across 30 trajectories, 16 levels and 8 grid jumps) on mean (μ*) and standard deviation (σ) associated with the NPV after 25 years. Parameters were automatically scaled before computing the elementary effects so that all factors would vary within the range [0,1]. It was implicitly assumed here that the uncertain model parameters were uniformly distributed. For each parameter, the tested range before scaling is shown in table 5.3

5.5 Results and Discussion

The NPV maximization over 25 years (Equation 5.9) is solved numerically using the following postulated pest management option scenarios. In the first assessed scenario (section 5.5.1), the pest dynamics and NPV after 25 years are modelled, with and without insecticide control, assuming that the farmer did not have access to *Bt* maize seeds. In the second scenario (section 5.5.2), a new control technology – *Bt* maize expressing Cry1Ab toxin – becomes available. The adoption rate is not linear (Equation 5.6). It is assumed that at time T=0, 10% of the area is covered with *Bt* maize, reaching an 80% plateau after approximately 11 years. Assuming that the farmer may lack a full understanding of the capacity and limitations of *Bt* technology, two different cases are tested: the first assumes that the farmer will rely on GEIR technology completely and all insecticide applications are stopped; the second assumes the farmer utilizes both of the pest control means at his/her disposal, with the *Bt* maize adopted at the projected rate and insecticide applications used whenever pest numbers exceed the ET. The results obtained are also compared with a conjectural case where both pests are highly susceptible to *Bt* toxin. In section 5.5.3, two additional scenarios are explored: 1) a +/- 25% variation of the seven parameters shown to influence pest dynamics $\{\boldsymbol{r_1}, \boldsymbol{r_2}, \boldsymbol{b_{12}}, \boldsymbol{b_{21}}, \boldsymbol{q_{11}}, \boldsymbol{q_2}, \boldsymbol{\lambda_i}\}$; and 2) due to the importance of natural enemies, five additional cases of different natural enemies' densities (representing different levels of ecosystem disruption) are assessed with the assumption that the farmer uses a selective insecticide harmless to these enemies. In both additional scenarios, a comparison is made between the resulting NPV after 25 years and the number of insecticide applications with the results obtained in the optimal pest management control strategy (when insecticide is used along with *Bt* maize).

5.5.1 Scenario 1: Prior to *Bt* maize adoption

This scenario reflects a situation in which conventional maize is grown and *Bt* maize is not adopted (e.g. technology is not accessible), and primary and secondary pests are present in the agro-ecological system. Results under this scenario show the evolution of the population dynamics during a period of 25 years for the primary (MCB) and secondary (TAW) pest without (figure 5.2) and with (figure 5.3) pest control (i.e. insecticides). Without pest control the TAW density passes unnoticed for most of the period due to strong competition from the MCB and pressure from natural enemies (figure 5.2). This leads to high crop damage and a low NPV after 25 years, and is therefore not desirable to the farmer (table 5.4). Figure 5.3 shows the results under a conventional maize cropping system with the farmer applying insecticide. In this case, over 25 years, an average of 3.55 insecticide applications per ha are made (s.d.= 0.61), obtaining a total NPV of 8563 €/ha (table 5.4).

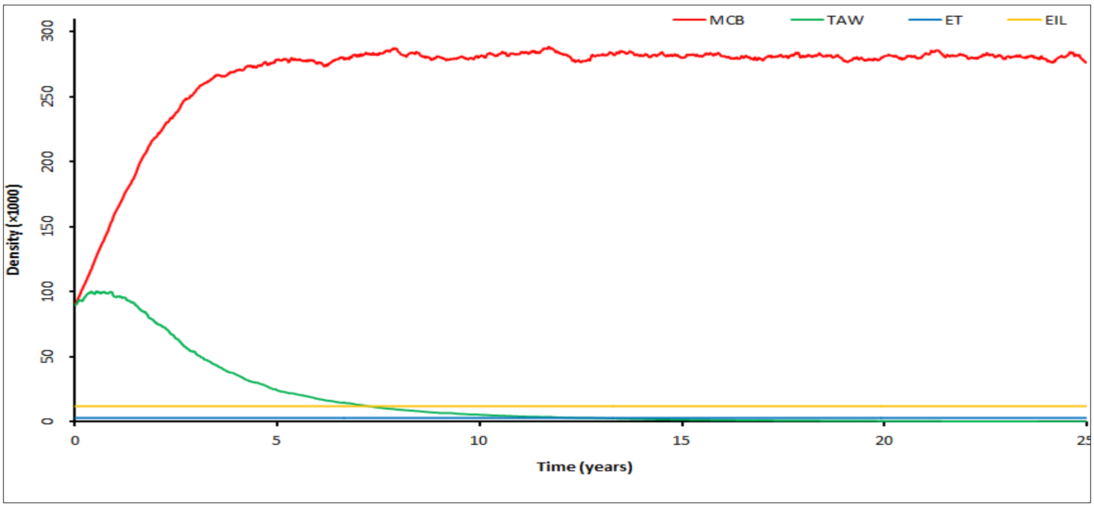

Figure 5.2 - Pest dynamics, prior to Bt adoption without insecticides applications, during a period of 25 years for the primary and dominant pest, the MCB (red line), and the secondary pest, TAW (green line). The blue line represents the economic threshold and the yellow line the economic injury level (point at which pest cause economic impact on the culture).

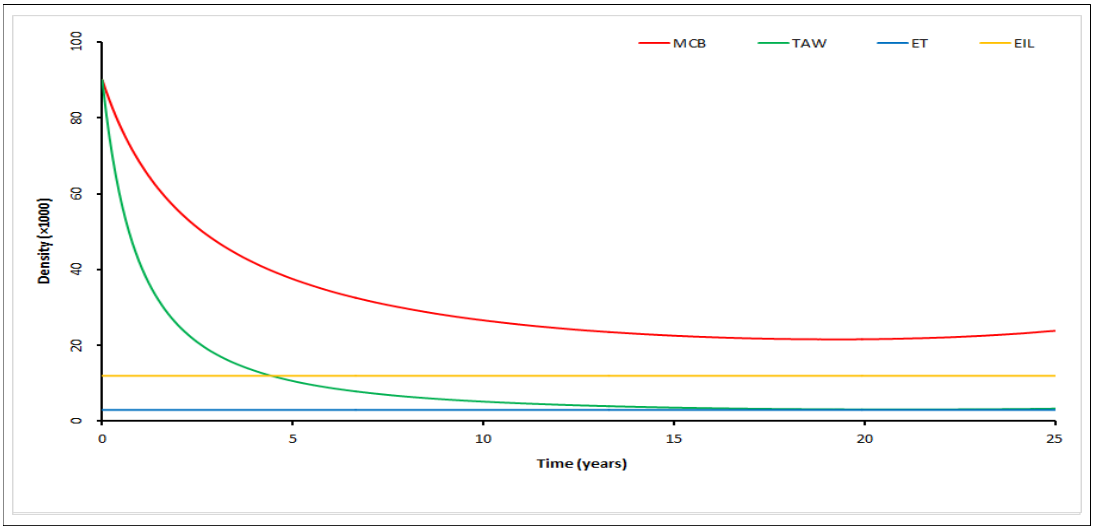

Figure 5.3 - Pest dynamics, prior to Bt adoption with insecticides applications, during a period of 25 years for the primary (MCB) and secondary (TAW) pest. The blue line represents the economic threshold, point at which farmer initiates insecticides application to prevent an increasing pest population from reaching the economic injury level (yellow line).

The small variability in the amount of insecticide used occurs because the farmer is not able (and not economically willing) to completely eradicate the pest, but seeks to keep it under the EIL. Having the latter goal in mind, the farmer only reacts when a pest reaches the ET. Because the MCB's proliferation capacity is high, its density will always rebound above the EIL obliging the farmer to keep constant attention on the fields. Assuming that resistance factors are constant, pest populations will then oscillate in line with population numbers in previous years. Accordingly, it is expected that this insecticide application pattern continues with (brief) periods in which no applications are needed, as seen in figure 5.4. The drops to zero insecticides applications observed in figure 5.4 reflect a brief drop in insect population levels under the ET caused by this pest management strategy.

Table 5.4 – NPV, insecticides applications (mean ± SE) and damage (mean ± SE) results accrued from the 4 different scenarios.

Scenario	NPV (€/ha)	Insecticide applications	Damage (%)
No pest control	3202		19.00 ± 1.06
Only insecticide[1]	8563	3.54 ± 0.61	2.80 ± 1.71
Only *Bt*	7052		10.58 ± 1.61
Bt + insecticide`	10353	2.01 ± 0.68	1.06 ± 1.94

[1] with: a=4.080582e+00; b=1.918453e-02; c=-2.830495e-03; d=-4.804419e-05

[2] with: a=3.576192e+00; b=-1.986176e-01; c=4.870921e-03; d=-2.525556e-05

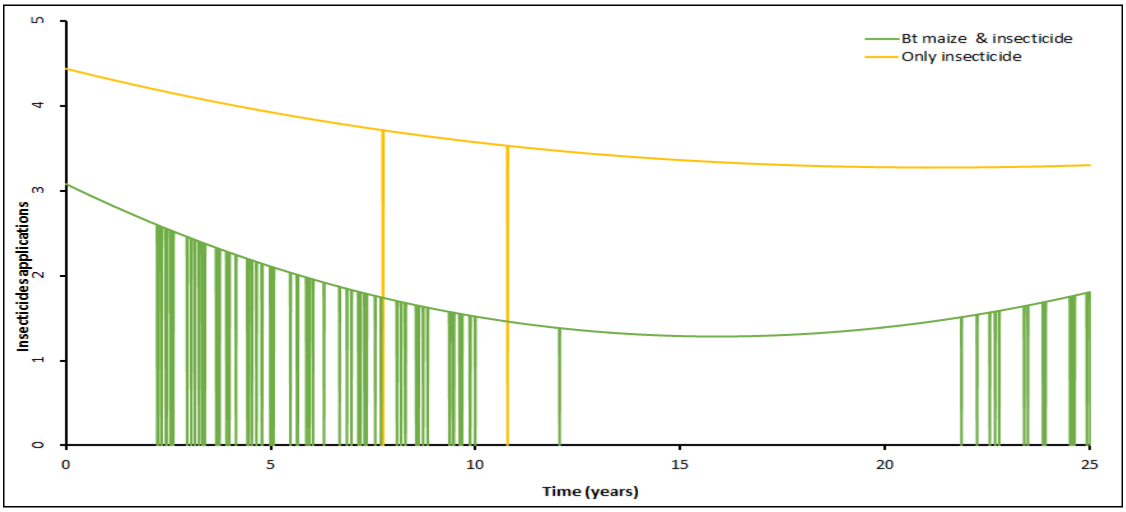

Figure 5.4 – Insecticides applications over time prior to *Bt* maize adoption (yellow line) and when *Bt* maize is used (green line). The drops to 0 (zero) insecticides applications reflect an instant drop in insect population's level under the ET. Being the economic threshold the point at which farmer will reinitiates insecticides application to prevent the pest population from reaching the economic injury level.

5.5.2 Scenario 2: *Bt* maize adoption

In the first case, the farmer relies solely on the efficiency of *Bt* maize, putting aside insecticides (figure 5.5). After an initial rise in both pest densities, the TAW population is slightly suppressed by the MCB. However due to the increasing presence of *Bt* toxin, after the MCB population peaks, its density steadily declines. MCB population levels below the EIL are reached after the 9th year of adoption. The ET is reached around the 12th year of adoption and with 80% of the maize area planted with *Bt* varieties. This translates into a decrease in the MCB's competition capacity and with a corresponding ascension in TAW numbers. In this case, the TAW population becomes the main pest that is always above the EIL, and causes serious damage to the crop. The oscillation in TAW numbers is due to the variable pressure of environmental factors and natural enemies affecting it. After 25 years, MCB population is marginal and its complete eradication is never achieved. However, a quick recovery of the population will occur in the case that *Bt* seeds stop being used. In this case, where *Bt* maize is used without insecticide, the farmer obtains an NPV of just 7052 €/ha after 25 years, which is about 82% of what was achieved when relying solely on insecticide (table 5.4). This scenario is slightly unrealistic as it fails to take into consideration the insecticide applications of non-adopting farmers. Nonetheless, it clearly demonstrates the problem of relying on a single pest control technique and illustrates what happens when a farmer is not aware of the secondary pest problem.

More realistically, farmers can be expected to utilize both of the pest control means at their disposal (figure 5.5), with the *Bt* seeds adopted at the projected rate (as in equation 6) and insecticide applications used whenever pest numbers exceed the ET. In this case, due to the rapid insecticide action, both pest populations suffer an immediate decrease. Competition pressure is evident during the first three years when TAW's population surpasses MCB population. TAW's population is kept below the EIL but above the ET until the end of the time period under consideration. MCB population reaches the EIL after 3 years of adoption, and the ET 1 year later, with 54% and 69% of maize area planted with *Bt* maize respectively. At this point due to both control measure pressures, the MCB density steadily falls below the ET until it is entirely eradicated after approximately 12 years. It is the MCB decline, hence the lack of competition, that causes a plateauing of TAW within the ET and EIL. Here, the farmer continues to apply insecticides, but now in order to control TAW (figure 5.6). The insecticide application frequency falls to an average of 2.01 applications per ha (s.d.= 0.68) (table 5.4). This amount represents a reduction of about 43% in the number of insecticide applications compared to conventional maize use. This noteworthy decline can be attributed to the use of *Bt* and its efficiency in controlling MCB, and its provision of a safer environment for the natural enemies of TAW. In section 5.5.3, the impact of natural enemies is discussed. The reduction in insecticide applications found here is sufficient to compensate the farmer for the extra cost of *Bt* seeds (roughly 10% more expensive than conventional seeds). After 25 years the farmer would realize an NPV of 10353 €/ha (table 5.4), which is higher than what is realized with both conventional seeds and using only *Bt* maize (table 5.5).

Table 5.5 - NPV difference between optimal control strategy and the remaining 3 cases: no control, only insecticide used and only *Bt* maize used (percentage in brackets).

	No control	Only insecticide	Only *Bt*
Bt + insecticides	7151€ (+223%)	1790€ (+21%)	3301 € (+32%)

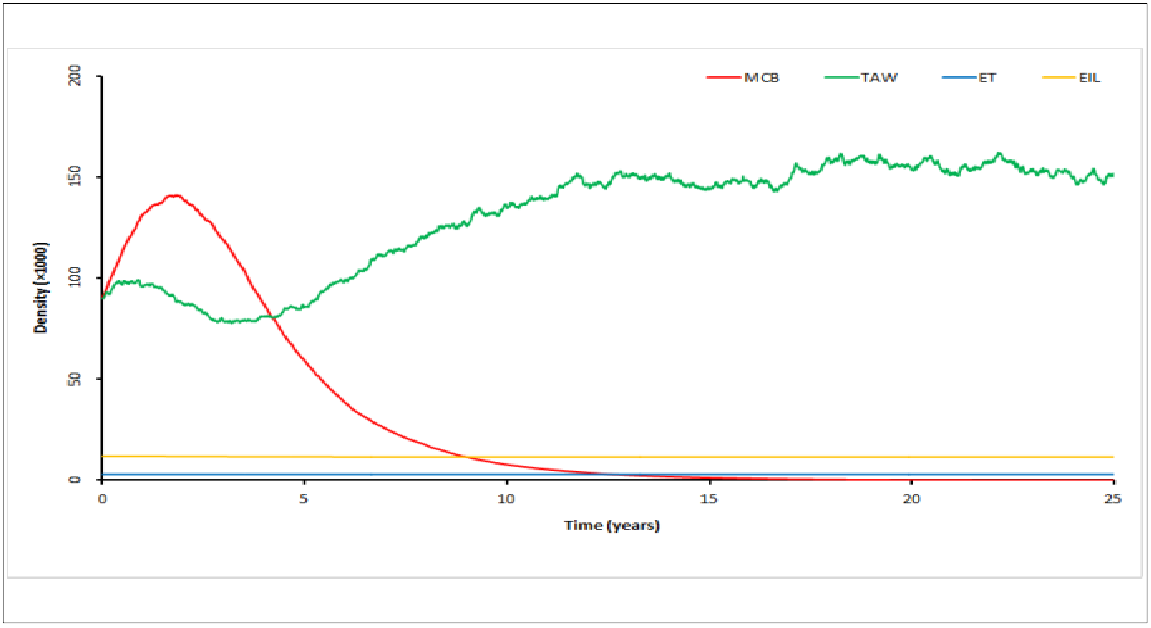

Figure 5.5 - Pest dynamics subsequent to Bt adoption without insecticides applications during a period of 25 years period. The MCB (red line) density suffers a substantial decline and it is substituted as the main pest by TAW (green line). The blue line represents the economic threshold, point at which farmer initiates insecticides application to prevent an increasing pest population from reaching the economic injury level (yellow line).

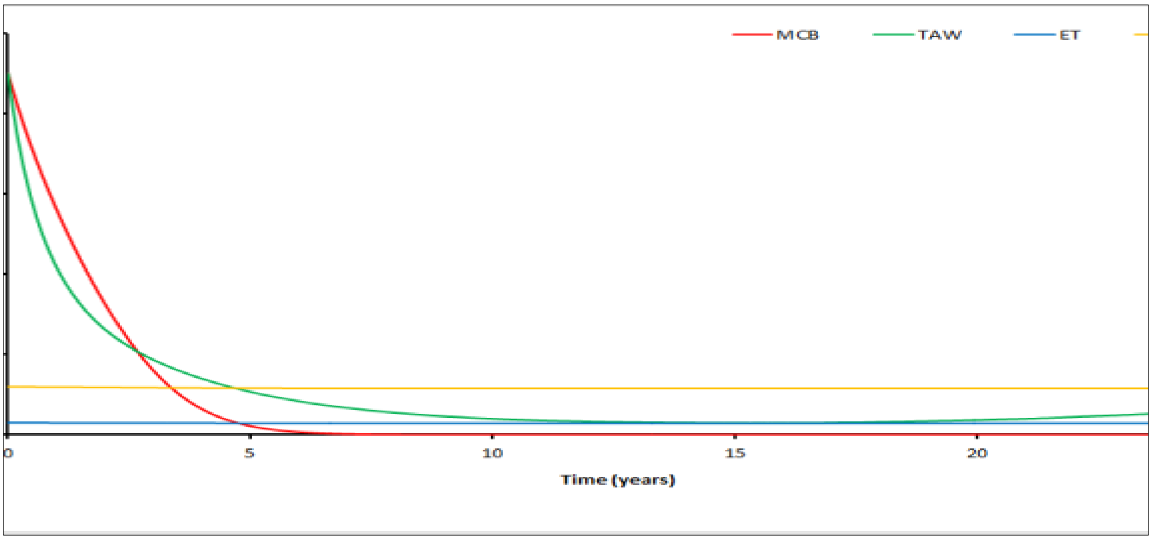

Figure 5.6 - Pest dynamics, prior to Bt adoption with insecticides applications, during a period of 25 years for the primary (MCB) and secondary (TAW) pest. Both pests are efficiently controlled below the economic injury level (yellow line). Farmer (re)initiates insecticides application whenever either pest reached the economic threshold (blue line).

For comparison, in the case of *Bt* maize with stacked traits[20] conferring a perfect control to MCB and TAW, insecticide applications steadily decrease until the farmer stops applying insecticide altogether after the 5th year of adoption (at which point 70% of the total maize cropping area is planted with stacked *Bt* maize). The farmer achieves the goal of entirely eradicating both pests and, logically, realizes a higher NPV of 10906 €/ha after 25 years (see stacked traits line in figure 5.7). Realistically however, this situation is unlikely for two reasons: firstly, agriculture is not a closed system, migration into crop fields by either known or unknown pests must be taken into consideration; secondly, as happened in the current assessment, a species whose population is significantly subdued so as to in effect be 'concealed' by the present insecticide or by the effect of a strong competitor, could unexpectedly reappear.

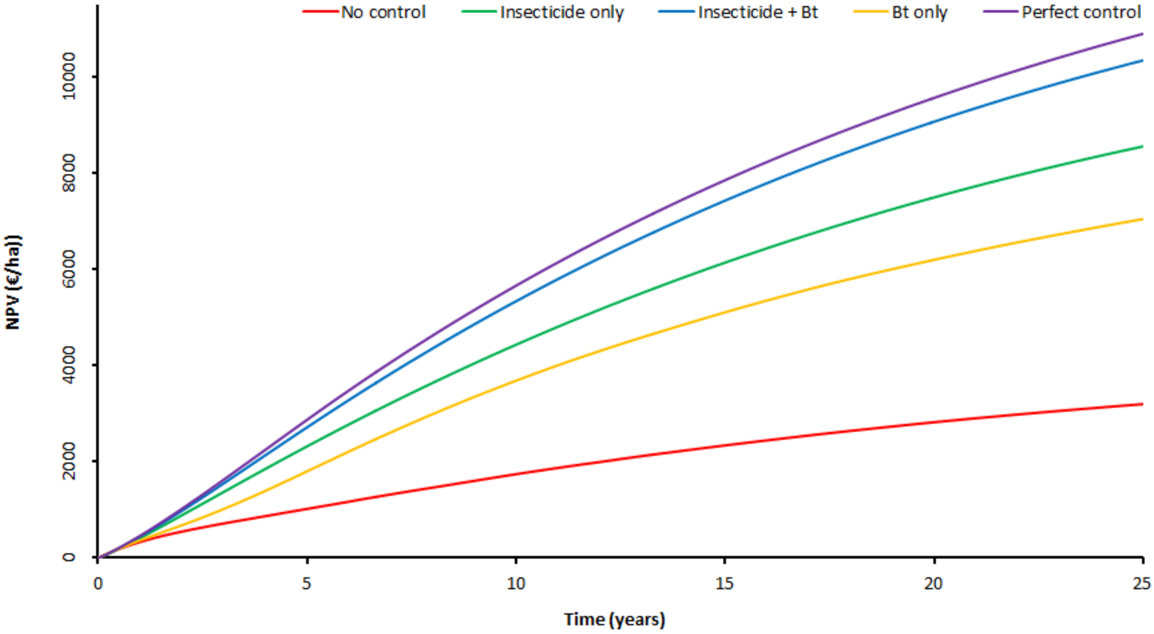

Figure 5.7 - Optimized NPV after 25 years for the 5 cases (no control; only insecticide is used; only *Bt* maize is used; insecticide and *Bt* maize are used; stacked *Bt* maize conferring perfect control to both pests is used).

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[20] Gene 'stacking' or 'pyramiding' refers to the process of combining two or more genes of interest into a single plant (Halpin 2005). The combined traits resulting from this process are called stacked traits. A stacked GE crop contains at least two novel genes, having different modes of action. Hence, by definition, crops with stacked traits are more effective than mono-trait varieties due to their wider range of action (Edgerton et al. 2012).

5.5.3 Further scenarios

In this section, two further scenarios are explored in which the five key parameters implicated in pest dynamics are varied – growth rate $(\boldsymbol{r_i})$, interspecific competition $(\boldsymbol{b_{ij}})$, susceptibility to *Bt* toxin $(\mathbf{q_i})$**,** initial *Bt* adoption $(\boldsymbol{\lambda_i})$ and natural enemies $(\boldsymbol{m_i})$. The full results are presented in table 5.6 and 5.7. When decreasing the parameters $\{\boldsymbol{b_{ij}}, \boldsymbol{q_i}, \boldsymbol{\lambda_i}\}$ by 25%, the NPV is expected to decrease and insecticide applications to increase. Similarly, when increasing these parameters by 25%, the NPV is expected to increase and insecticide applications to decrease. It is also expected that $\boldsymbol{r_i}$ would respond in the opposite direction to its counterparts. From the 16 results obtained, 14 have expected outcomes. The two unexpected outcomes have relatively small deviation values (see values marked with * in table 5.6); although the mean insecticide applications varied as expected, the NPV varied in the opposite direction. These unexpected outcomes are believed to represent an active response from the farmer to lower/higher pest density in the initial cropping period, initiating insecticide applications accordingly.

Table 5.6 – Difference between the NPV and insecticide applications (mean) obtained in the optimal control strategies and those accrued from the ±25 % variation in four parameters $\{\mathbf{r_i}, \mathbf{b_{ij}}, \mathbf{q_i}, \boldsymbol{\lambda_i}\}$ implicated in pest dynamics.

	Parameters	NPV (€)	Insecticide applications
-25% deviation	Growth rate (r_i)[1]	-131.36*	-0.01
	Interspecific competition (b_{ij})[2]	-7.75	0.01
	Bt susceptibility (q_i)[3]	-131.19	0.30
	Initial *Bt* adoption (λ_i) [4]	-48.50	0.03
+25% deviation	Growth rate (r_i)[5]	86.64*	0.02
	Interspecific competition (b_{ij})[6]	2.02	-0.01
	Bt susceptibility (q_i)[7]	89.16	-0.27
	Initial *Bt* adoption (λ_i)[8]	42.61	-0.06

[1] with: a=3.590208e+00; b=-1.723988e-01; c=3.611697e-03; d=-4.817101e-05

[2] with: a=3.693049e+00; b=-2.168674e-01; c=5.774393e-03; d=-4.310029e-05

[3] with: a=3.666050e+00; b=-1.317110e-01; c=1.864184e-03; d=-2.431446e-05

[4] with: a=3.699506e+00; b=-2.285133e-01; c=7.556475e-03; d=-9.728075e-05

[5] with: a=3.645738e+00; b=-0.254399e-01; c=0.009034e-03; d=-0.000082e-05

[6] with: a=3.646094e+00; b=-2.011897e-01; c=4.619282e-03; d=-2.463909e-05

[7] with: a=3.591855e+00; b=-2.828358e-01; c=8.857541e-03; d=-4.278481e-05

[8] with: a=3.489076e+00; b=-0.185497e-01; c= 0.005118e-03; d=-0.000073e-05

*not expected

Due to the high importance of natural enemies, the individual impact of this parameter is assessed in model uncertainty. Five cases were explored representing various levels of disturbance in the ecosystem, assuming that the farmer uses a selective insecticide which does not causes harm to natural enemies (table 5.7). In the first, the impact of natural enemies on pest dynamics varies randomly as in the baseline cases in sections 5.5.1 and 5.5.2; in the second, there are no natural enemies present; and in the third, fourth and fifth, the impact of natural enemies is low, medium and high respectively. All results are as expected, the higher the natural enemies' impact the lower the need for insecticide applications, yielding a higher NPV. It is interesting to note that the previous optimal outcome in terms of NPV (derived from the use of *Bt* maize with a broad-spectrum insecticide) lies between a scenario in which natural enemies are absent, and one where the impact of natural enemies on pest populations is low. This result suggests that boosting the population of natural enemies through selective use of insecticide, rather than broad-spectrum, has a knock on positive impact on NPV. Assuming the utopia around the last scenario, the scenario where mi=0.8 should be pointed out, as it reflects a substantial and constant presence of natural enemies. Here, the farmer would ultimately cease the insecticide applications, while increasing the NPV by 9% after 25 years. These results indicate that pest populations are highly sensitive to natural means of control, and that pest populations could be managed with a relatively small increase in natural enemy numbers.

Table 5.7 – NPV and insecticides applications (mean ± SE) accrued from the five different levels of natural enemies impact when selective insecticide is used.

Scenario	NPV(€)	Insecticide applications
NE base variation[2]	10991	0.78 ± 0.64
No NEs (m_i=0)[2]	10231	2.56 ± 0.62
Low NEs density (m_i=0.2)[3]	10680	1.66± 0.49
Medium NEs density (mi=0.5)[4]	11021	0.91 ± 0.56
High NEs density (m_i=0.8)[5]	11240	0.19 ± 0.58

[1] with: a=2.532052e+00; b=-2.756687e-01; c=9.790500e-03; d=-2.912951e-05

[2] with: a=4.027806e+00; b=-1.970536e-01; c=5.689231e-03; d=-4.987196e-05

[3] with: a=3.091811e+00; b=-2.637044e-01; c=9.885022e-03; d=-4.993487e-05

[4] with: a=2.510126e+00; b=-2.842099e-01; c=1.072332e-02; d=-4.985597e-05

[5] with: a=2.398763e+00; b=-3.420088e-01; c=1.310324e-02; d=-4.992738e-05

5.6 Conclusions

The work performed in this chapter corroborates the hypothesis that secondary pests might emerge due to a significant reduction in insecticide applications (Lu et al. 2010, Pemsl et al. 2011, Catarino et al. 2015). The general results suggest that a) a secondary pest can become the key insect pest in unsprayed *Bt* maize compared with sprayed *Bt* fields, due to the high specificity of Cry1Ab toxin; and b) the damage to crops from secondary pests can increase with the expansion of *Bt* technology if no additional measures –

such as insecticide applications or stacked traits – are taken. One of the claimed benefits of *Bt* crops is that they decrease the need to use insecticides, in turn diminishing contamination of food and the environment, as well as increasing farm profits. Indeed, the use of *Bt* maize has a has a knock on positive impact on NPV, as well as in the environment by decreasing the need for insecticides. Furthermore, the farmer would accomplish the goal of entirely eradicating the MCB after 14 years. Nonetheless, insecticide applications would not cease due to the outbreak of TAW, the secondary pest.

Results from the sensitivity analysis showed that when holding prices, costs and other input parameters constant, the results suggest that the parameters related to the secondary pest influence the final output more than those related to the primary pest. The uncertainty in the results arises from two main areas: a) it is unlikely that available data and model parameters are error-free; and b) no simulation model is an entirely true reflection of the physical process being modelled. Results show the need to be conscious of the possibility of an outbreak from a secondary pest and the consequences of such an event upon yields and farm profits. The results suggest that it may take several years for secondary pests to proliferate to relevant levels of importance, thus the need to understand pest dynamics (Ho et al. 2009). The model demonstrates a case where the outbreak of a secondary pest in *Bt* fields is not a random event. It can arise as a natural result of the use of *Bt* technology, and may be predicted with access to accurate data. The model shows that insecticide applications and the presence of natural enemies contribute most to achieving a higher NPV. The presence of natural enemies is intrinsically related to environmental conditions, and agricultural procedures, which in turn will certainly influence the number of insecticide applications needed each year. This is an important insight to take into consideration, given that future climate shifts are expected. Hence, alongside the deployment of GEIR crops, it is therefore highly advisable to also promote agricultural practices that could enhance the presence of natural enemies. When farmers effectively comply with certain procedures, such as having a refuge strategy and using extra selective insecticide applications (Meissle et al. 2011), the economic, environmental and social benefits can be substantial (Wesseler et al. 2007, Skevas et al. 2010).

Models of pest dynamics are a valuable tool, especially in a world affected by strong environmental and agricultural shifts. For example, forecasted global warming and increases in GEIR cropping could enable insect pests to spread into new habitats (Maiorano et al. 2014). A more profound knowledge of how agro-ecological systems work is needed to evaluate the full benefits of *Bt* crops. If new agricultural technologies are to be used as a viable IPM solution, understanding insect dynamics is vital, and requires an integration of ecosystem services into management decisions. For that, further research should accurately estimate, either in field trials or in the laboratory, the nature of intra- and inter-specific pest competition.

5.7 Summary

In this chapter, a bio-economic model was used to analyse different pest control approaches – *Bt* technology and insecticides – on secondary pest outbreaks. This is a problem that has been largely ignored until now, along with subsequent effects on farm profits. Optimized insecticide applications under deterministic conditions were achieved through a dynamic nonlinear optimization technique. The model developed in this study is capable of effectively evaluating the impact of GEIR crops on two pest species that compete for the same resource. As shown in section 5.5.3, the model enables the incorporation of different scenarios, such as insecticide restrictions, new transgenic traits and other means of pest control. The general results suggest that although *Bt* maize can increase economic benefits while decreasing insecticide applications, there is a risk that secondary pests might emerge due to a significant reduction in insecticides applications (Lu et al. 2010, Pemsl et al. 2011, Catarino et al. 2015). In the following chapter, the model developed here will be expanded by incorporating a reaction-diffusion system. This development will allow the assessment of the impact on maize resulting from TAW invasion throughout Aragon.

CHAPTER 6. PREDICTING THE PATTERNS AND EFFECTS OF NON-SUSCEPTIBLE PESTS' INVASION ON *BT* MAIZE: A BIO-ECONOMIC SPATIALLY EXPLICIT POPULATION PERSPECTIVE

6.1 Chapter Introduction

The previous two chapters have explored the concept and economic implications of a secondary pest outbreak[21] in *Bt* (*Bacillus thuringiensis*) maize expressing Cry1Ab *Bt* toxin[22]. It was found that the economic damage caused by the rise of secondary pests could offset some of the benefits associated with the use of *Bt* varieties. This issue is of special relevance to the largest *Bt* maize adopter region in Spain, Aragon. Spanish researchers (e.g. Eizaguirre et al. 2010) have highlighted their concerns in relation to the possibility of invasions of the true armyworm (TAW), *Mynthimna unipuncta*, becoming more frequent. In chapter five it was demonstrated that TAW could gain ecological advantage over *Bt* maize due to the absence of the Mediterranean Corn Borer (MCB), *Sesamia nonagrioides*, and the low susceptibility of TAW to the Cry1Ab toxin. This chapter develops a bio-economic spatially explicit population (BeSEP) model that integrates species spatial dynamics with the bio-economic model developed in chapter five. Particularly, this chapter focuses on the maize farmers' economic impact of the spread of an invasive species under different control strategies based on insecticide application in the Aragon region, Spain. As in chapter five, a situation where the species considered is not susceptible to Cry1Ab toxin, and hence has the potential to become a secondary pest in *Bt* maize, is considered. The chapter has three main objectives:

i) To develop the BeSEP model that allows the incorporation of spatial dynamics into the bio-economic modelling developed in chapter five;
ii) To assess the economic impact on farmer's profit of various *Bt* and insecticide application regimes in Aragon, considering the following three scenarios:
    a. Spread of TAW from an invasion hotspot area assuming the actual conventional/*Bt* maize proportion of 2012 in Aragon;

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[21] A secondary pest is a "non-targeted" pest that has historically posed small or no economic threat, but which could be directly or indirectly affected by changes in insecticide use patterns, such as those caused by *Bt* cropping, associated with the management of a primary pest (FIFRA Scientific Advisory Panel 1998).

[22] Although several other events are under evaluation by the European Food Safety Authority (EFSA), the only *Bt* maize currently allowed for cultivation in Europe contains the transformation event MON810 (Monsanto Company), expressing Cry1Ab *Bt* toxin (EFSA 2010a). This transgenic maize presents a high level of resistance to its primary pests – the two main maize borers present in the EU, the MCB and the ECB (González-Núñez et al. 2000).

   b. Spread of TAW from an invasion hotspot area assuming different conventional/*Bt* maize proportions[23] from above; and,
   c. TAW is endemic throughout the region, although initially suppressed by the prevailing pesticide regime.

iii) To discuss the wider implications of the model output for both Aragon and other regions where *Bt* crops are grown, and to outline management recommendations and future path research in order to improve predictions.

Results indicate that if an invasion is effectively controlled, the use of *Bt* maize could bring regional economic and environmental benefits. Conversely, if the TAW is not detected early the invasive species may become so abundant and widespread that containment and eradication will no longer be possible. Under this situation farmers would need to adopt additional pest control measures – such as adopting new GE crops or increasing insecticide applications. Furthermore, it has been suggested that landscape structure is a critical feature affecting population spread. Future research should pay particular attention to the spatial effects of invasion, specifically the connectivity between favourable habitats.

6.2 Biological invasions

The success of biological invasions depends on environmental and anthropogenic factors. Within the environmental factors, climate change (Diez et al. 2012), habitat disturbance – such as storms and fires (Didham et al. 2005) – and a lack of natural predators and/or competition in the new habitat (Wilby and Thomas 2002) are common pathways that facilitate the movement of species within regions. On the anthropogenic side, an increase in international movement of humans and goods (Levine and D'Antonio 2003), and the quick transformation of landscapes in agricultural land-use patterns (Hobbs 2000), has progressively enhanced the importance of the issue of invasive species' colonisation. The spatial and temporal uniformity of landscapes increases habitat connectivity and may benefit the spread process (Tilman 1999, Byers 2002).

Although other factors (e.g. decline of native biodiversity (Sala et al. 2000)) may impact management decisions, the economic value of an agricultural good is a major argument in the context of a political decision as to when and how to act upon biological invasions (Leung et al. 2002). The strategic control decisions associated with an invasion are therefore reliant on an awareness of whether and how the invasive species is likely to impact on the economics of production. Hence, it is essential to predict as accurately as possible a bio-invasion, particularly one causing undesirable effects on marketable commodities (e.g.

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[23] The assessed conventional/*Bt* maize proportions are the following: i) no adoption, i.e. only conventional maize is cropped in the region, ii) 50% of the *Bt* maize famers move to conventional maize faming, iii) 50% of the conventional farmers adopt *Bt* maize, and iv) total adoption, i.e. all farmed maize is *Bt*.

agricultural or silvicultural crops). This can only be achieved with an understanding of the factors linked to species invasion that lead to actual establishment, whether anthropogenic factors (Levine and D'Antonio 2003), biological processes (Mack et al. 2000) or climate change (Diez et al. 2012). In agro-economic assessments of biological invasions, a distinction is usually made between two different types of costs and benefits: ex-post and ex-ante assessments (Born et al. 2005).

In ex-post assessment, the evaluation of the success (or failure) of already implemented measures is conducted by allocating monetary values to recorded effects such as yield losses and impacts on health and on biodiversity (e.g. Pimentel et al. 2001, Pimentel et al. 2005). In ex-ante assessment, which is the approach followed in this chapter, an evaluation of possible measures is conducted in order to prioritize where and which control strategies are desirable (Epanchin-Niell et al. 2014, Epanchin-Niell and Liebhold 2015). However there is a clear imbalance between these two methodologies in favour of ex-post studies (Marbuah et al. 2014), although anticipation of the spread behaviour to provide the best management strategy is of clear importance. The optimal control approach depends not only on the phase of the invasion process but also on the likely introduction zones, or “hotspots” (Mack et al. 2000). The major caveat in forecasting the impact of an invasion process lies in availability of data in a system in which the invasion has not occurred yet (Parry et al. 2013, Groom et al. 2015) . This barrier may explain why work that explicitly represents space using real landscapes in spatial-dynamic bio-economic modelling is scarce; the few examples include Cacho et al. (2010) and Carrasco et al. (2012).

Spatial heterogeneity is an important aspect to consider in the study of populations, ecosystems and landscapes (Shaver 2005). Understanding the spatial patterns of landscape processes and the driving forces that affect flora and fauna dynamics and persistence is essential to effective pest management (Lawler et al. 2006). This chapter contributes to the development of spatially explicit bio-economic models with multiple insect pests by describing dynamics of two pests in space according to two systems of partial differential equations of type “reaction-diffusion”. This work is thought to be unique as no bio-economic modelling work has yet spatially explicitly approached the problem of invasive species taking into consideration competition between two species in the GM crops context. The main focus is an ex-ante assessment of the economic consequences for maize farmers in Aragon relating to a secondary pest outbreak. It takes into consideration the direct income effects, specifically the spraying of insecticides and the use of *Bt* maize, connecting the interaction of an invasive and a native species as well as different mitigation control strategies. Both costs and benefits caused by the impact of the invasive species are calculated in market price terms. Only direct use-values are considered. The wider, and important, scope of the social and ecosystem impact of biological invasions are not considered. Numerical simulations of three scenarios are conducted and analyzed. In particular, the work focusses on farmers’ net returns due to changes in insecticide use and the impact of pests. The chapter concludes by considering the management implications of the results as well as suggesting future research directions.

6.3 The arrival, establishment and spread of invasive species

Non-native species must pass through a number of steps in order to become invasive. Biological invasions are divided into three main phases: arrival, establishment and spread (Andow et al. 1990, Hastings 1996). The first phase is characterized by the arrival of a few individuals in a single area of the new habitat (Andow et al. 1990). These pioneers need to reach a certain level in order to sustain a local population (Grevstad 1999). The initial population may pass undetected due to their small numbers and consequent effects. Many invasions do not reach the sufficient density to propagate, failing to become established because of inadaptability to the local environment (Kolar and Lodge 2001) and Allee effects[24] (Blackwood et al. 2012). Assuming that the non-native population survives the initial introductory period, it will likely grow in numbers, initiating the establishment period. A time-lag is common between initial introduction and subsequent population growth (Kowarik 1995, Solow and Costello 2004). The time-lag period can last from several decades to just some weeks or months as in the case of the western corn rootworm (WCR), *Diabrotica virgifera virgifera LeConte* (Coleoptera: Chrysomelidae). This species was introduced via international shipment in the 1990's (Kiss et al. 2005), since then it has become one of the major pests in maize throughout central Europe, its eradication impossible (Kiss et al. 2005). Several factors are preponderant on the establishment stage length, such as temporary unfavourable environmental conditions, interaction with native species, size of introductions or more complex indirect dynamical effects (Kolar and Lodge 2001, Lockwood et al. 2005). In the final stage, the invasive species spreads across the landscape from the invasion origin. At this stage the invasion is easily noticeable and identifiable by farmers or environmental managers (Liebhold et al. 2015). The growth and spread continues until suitable habitat and resources become scarce.

The intrinsic dispersal capacity (or speed), population growth rate and the type of spread process the invader follows determines its rate of invasion (Clark et al. 2001). Several different approaches have been adopted for estimating spread rates (Okubo and Levin 2013). Here, spread is evaluated in terms of the radial rate of invasion (RRI), by averaging the RRI from all simulations, ***sim*** (equation 6.1 and 6.2).

$$\text{RRI} = \frac{\left(\sqrt{\frac{A_{t+n}}{\pi}} - \sqrt{\frac{A_t}{\pi}}\right)}{n} \qquad (6.1)$$

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[24] Allee effects are defined as a decline in individual fitness at low population size or density, which may lead to critical population thresholds below which populations crash to extinction (Lewis and Kareiva 1993, Blackwood et al. 2012)

$$\overline{RRI} = \sum_{i=1}^{sim=100} \frac{RRI_i}{sim} \tag{6.2}$$

Where $\boldsymbol{A_t}$ is the colony area at time $\boldsymbol{t}$, $\boldsymbol{n}$ is the length of the observation period, $\boldsymbol{\pi}$ is the numerical constant that represents the ratio of a circle's circumference to its diameter on a flat plane surface, and $\boldsymbol{sim}$ is the number of simulations performed. Invading organisms may spread through stratified (or jump) dispersal or through diffusion-like processes. In short, in stratified dispersal, species spread from the establishment point as a continuous process coupled with discontinuous spread where populations jump ahead and form isolated populations which may merge in due course (Liebhold and Tobin 2008). Stratified dispersal is related to a rare event, where individuals travel long distances over what may be considered an inhospitable habitat (Liebhold and Tobin 2008). In the vast majority of the cases, stratified dispersal is closely related to human activity such as the WCR case (Vitousek et al. 1997, Kiss et al. 2005). If some pioneers disperse according to jump processes, temporarily establishing themselves ahead of the main invasion front, the three biological invasions could occur simultaneously (Shigesada et al. 1995). Diffusion relates to the gradual population spread, across a suitable environment, resulting from the average movement of all individuals as they strive into a new habitat (Okubo and Levin 2013). Insect diffusion is often associated with random movement, i.e., each individual is uninfluenced by other individuals and has an equal chance of moving from one unit to an adjacent one (Okubo and Levin 2013). The diffusion process is modelled as a reaction-diffusion (RD) system using partial differential equations (PDE) (Okubo 1980), in which spread is treated as continuous and constant (Hastings et al. 2005). Assuming a two-dimensional space, the RD model[25] is expressed as it follows:

$$\frac{\partial N_i(x,y,t)}{\partial t} = r_i N_i \left(1 - \frac{b_i N_i}{K_i}\right) + D_i \left(\frac{\partial^2 N_i}{\partial x^2} + \frac{\partial^2 N_i}{\partial y^2}\right) \tag{6.3}$$

In equation (6.3), the reaction term representing the population dynamics comprises the population growth formulated by a logistic growth function, where N is the local population density as a function of both time and spatial location, $\boldsymbol{r}$ is intrinsic optimal growth rate with, $\boldsymbol{b}$ represents the effect of intraspecific competition, and **K** the carrying capacity. The diffusion is expressed by the diffusion coefficient term **(D)**, and by the sum of the second partial derivatives of $\boldsymbol{N_i}$ with respect to each of the spatial coordinates $(\boldsymbol{x}, \boldsymbol{y})$. The RD systems have been widely used in theoretical biology and ecology since the remarkable pioneer

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[25] See Okubo and Levin (2013) and Shigesada and Kawasaki (1997) for further applications of the Fisher model

work, describing diffusive spread for one species in one-dimensional environment, performed by Kolmogorov et al. (1937), Fisher (1937), Skellam (1951) and more recently by Okubo (1980). The use of PDEs allows a complete combination of analytical and simulation approaches (Kareiva et al. 1990, Holmes et al. 1994). The intuition behind using PDEs is that patterns at a population level are not dependent on the individual behaviours of organisms.

6.4 Economic impacts and management of biological invasions

Undoubtedly the impacts of invasive pests are becoming a major economic problem in agriculture. The world is getting “smaller”, globalization and especially international trade (Hulme 2009) are linking ecological systems daily, hence increasing the prospects for invasion-style processes to thrive (Vitousek et al. 1997). Fortunately not all exotic species have the ability to successfully establish new communities, to spread much further than the original incursion site or to have significant impact (Williamson and Fitter 1996). However, for those that cause harm, their impact can be tremendous. In the United States alone, Pimentel et al. (2005) estimated that at least 50,000 species have entered the country, causing losses above 100 billion dollars per year resulting from agricultural damage. In Europe, according to Kettunen et al. (2009) the monetary impact of invasive species is estimated to be around €12 billion per annum over the last 20 years. Although these figures include costs of damage and costs of control/management/restoration, it can still be said that the costs are underestimated, since they do not account for negative socio-economic or ecosystem services (Pimentel et al. 2005, Kettunen et al. 2009). For example, the losses caused by WCR are estimated to surpass $1 billion in the US and □500 million in Europe per year (Wesseler and Fall 2010).

In recent years research has focused on assessing the economic impact of invasive species. When evaluating the economic impact of invasive species it is important to distinguish between ex-ante and ex-post assessments. In ex-post assessment, an evaluation of the success (or failure) of implemented measures is conducted. Here, monetary values are allocated to impacts such as yield losses and effects on health and biodiversity (Turner et al. 2003). A typical example is the work performed by Pimentel et al. (2001) and Pimentel (2005), which included in the assessment the costs of a range of implemented strategies along with the economic damage caused by biological invasions. In ex-ante assessment, the approach used in this research, an evaluation of the economic effect of possible pest control measures is conducted. This type of analysis can identify the most cost efficient control strategy. For instance, Cook et al. (2007) developed a stochastic bio-economic model that estimated the economic impact over 30 years of an invasive pest, the varroa bee mite, before its arrival. These authors estimated that the economic costs avoided would be of US$16.4–38.8 million per year. Depending on which stage an invasion is at (section 6.3), different management decisions can be taken by government agencies responsible for managing invasive species. Decisions can be designed to prevent, eradicate, contain, slow down and/or accept the invasion (Liebhold et al. 2015).

The question of "where" to allocate control receives little attention, most literature focuses rather on "when" and "how" (Epanchin-Niell and Wilen 2012). In predicting the potential spatial distributions and establishment of invasion niches, i.e. the hotspots, it is important to rationalise the area under management (Mack et al. 2000), hence the costs associated with control. Furthermore, the costs of control (including eradication) of invasive species are likely to increase as they become better established (Finnoff et al. 2007). Due to the inherent uncertainty of the species invasion and establishment, prevention – even though in some cases very costly – is often the most effective management approach, through for example border security scrutiny and quarantine (Leung et al. 2002). A surveillance effort should be carried out when long-term costs of damage and/or control exceed short-term costs of successful policy (Liebhold et al. 2015). If the invasive species achieves a certain population threshold, eradication is often not feasible, as happened in the case of the WCR in the US (Gray et al. 2009) and Europe (Carrasco et al. 2010c), the gypsy moth (*Lepidoptera: Lymantriidae*) (Sharov and Liebhold 1998) and the true armyworm in the US and Canada (Guppy 1961, McNeil 1987).

6.5 Bio-economic spatially explicit modelling overview

Spatially explicit models are classified according to diverse criteria. They can be classified based on the way that individual(s), space and time are considered (e.g. whether space and time are discrete or continuous) (Berec 2002, Hui et al. 2011). Spatially explicit population models in invasion ecology are individual or population based, involving complex rules with often intractable analytical solutions (Hui et al. 2011). They can be empirical or process-based, static or dynamic, simple or complex, and utilise low or high spatial and temporal resolution (Costanza and Voinov 2004). Individual-based models (IBM), are computer systems composed of autonomous entities, such as animals, plants or humans, capable of making decisions and interacting with the environment and other individuals (Grimm et al. 2005). Each individual is explicitly modelled as a unique and discrete entity, acting according to a set of rules, that may change along its life cycle (Grimm et al. 2006). On the other hand, Andow et al. (1990) showed that even when individual behaviour is put to one side, population level patterns can be explained by reaction-diffusion (RD) models.

The model developed here is based on RD as opposed to a stratified dispersal approach (section 6.3). The outcomes accrued from RD models provide outcomes relatively close to reality for some species, such as the muskrat and small cabbage white butterfly (Andow et al. 1990). Species, such as the cereal leaf beetle, whose spread does not fit the reaction-diffusion model, may spread driven by a range of modes of dispersal, as seen above (Andow et al. 1990). In the past few years, RD systems have been extensively used to model population dynamics and biological invasions (Cantrell and Cosner 2003), especially when the movement of individual organisms cannot be followed independently (Shigesada and Kawasaki 1997). The large majority of RD systems have considered space as a homogeneous entity (Carrasco et al. 2010a). Due to the absence of spatially specific records to populate and validate such models (Cantrell and Cosner 2003), RD models in which space is conceived as heterogeneous have rarely been used in applied population biology (Roques et al. 2008).

As previously mentioned, dynamic BeSEP models that include farmer behaviour are rare, which is especially relevant in the case of biological invasions modelling (Carrasco et al. 2010b). Also rare are those that deal with the agro-economic impact of multiple insect pests. Hence, two extra dimensions of complexity are necessary to provide sound invasion pattern predictions and to enable efficient control measures to be taken. Firstly, economic models of human-behaviour are essential in order to fit control into the real actors' necessities and behaviours, be they farmers or stakeholders (Carrasco et al. 2010b). Secondly, multi-species models, although more complex, are important for understanding the impact of invasive species on other organisms (Tilman 2004). The model developed here is flexible enough to consider the most relevant ecological processes, whilst being underpinned by empirical data in relation to the way processes are formalized. In reality, the description of individual processes in all models is in some way a balance between the process-based paradigm and empirical relationships (Costanza and Voinov 2004). Such an aspect allows the model to remain within a sensible range of complexity, hence of computational requirements. The next section presents the modelling framework conceptualized here, giving particular relevance to reaction-diffusion dispersal modelling.

6.6 Materials and Methods

The general purpose of the BeSEP model is to provide pest risk analysts and invasion managers with a tool that allows them to link invasion dispersal models with economic impact estimation and spatial management strategies. The modelling framework was adapted and further expanded to incorporate spatial aspects from Catarino et al. (2016). This combined theories for dispersal, population dynamics, statistics, estimation of economic impact and farmers' decisions. This research centres on a real landscape, Aragon, composed by many individually managed properties with a variety of uses. Each manager's control decisions (e.g. the use of insecticides and *Bt* maize) indirectly impacts his/her neighbours' decisions, by affecting the spread of species across boundaries. It is assumed that farmers make control decisions based only on pest damage occurring on their own land (i.e. there is no public or government funded control) with the aim of maximizing their individual net present value (NPV) in the long-term (25 years). Although the model focusses on the landscape properties of Aragon, the model framework is flexible, so it could be adapted and used for any other species, cropping system and/or region, by changing the relevant parameters. The model is constructed as a reaction-diffusion system through two coupled partial differential equations, characterising the spatial population dynamics of two pests: a primary pest, the Mediterranean corn borer (MCB) [*Sesamia nonagrioides* (Lefebvre) (Lepidoptera: Noctuidae)] and an invasive pest, the true armyworm (TAW), [*Mythimna* (*Pseudaletia*) *unipuncta* (Haworth) (Lepidoptera: Noctuidae)]. The model was written and numerically solved with R software (R-Core-Team 2012)[26].

6.6.1 Study perspective

The only GE crop allowed for cultivation in Europe is the *Bt* maize variation containing the transformation event MON810 (Monsanto Company), expressing Cry1Ab *Bt* toxin (EFSA 2010a). Spain is by far the largest GE technology adopter, growing 92% of the total GE maize in the EU (James 2014). In 2014, Spanish farmers sowed more than 130,000 hectares of GE maize, representing 32% of the total country's surface sowed with maize (James 2014). In the Aragon region, situated in the Ebro basin in north-eastern Spain with an area of 47.720 km^2, after barley and wheat, maize is the most important cereal. In 2012, the year for which maize data were obtain for this study, 55,484 hectares were cropped in Aragon, of which 75% was *Bt* maize. This represented 2/3 of the total *Bt* maize produced in Spain (López 2013). Maize farmers have obtained an average profit of 499€/ha, value in line with previous years (López 2014). Due to the edaphoclimatic conditions, maize production faces high pressure from several pests. In particular from the MCB and the European corn borer (ECB) [*Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae)], causing frequent phytosanitary problems and consequent economic damage (Meissle et al. 2010). Hence, it is not surprising that farmers in Aragon, as explained in sections 3.3 and 3.4, were quick to adopt *Bt* maize. Of the other maize pests, farmers show particular concern about TAW[27] (López et al. 2000). On the European continent, TAW is an invasive species, first noticed in Europe in the 19th century (Bues et al. 1986). The bio-economic Spatially Explicit Population (BeSEP) model developed allows the demonstration, across a 25 years period, of the dynamics and economic impacts of a potential invasion from TAW on the regional maize production in Aragon.

6.6.2 Modelling development

Step 1) Mapping the Aragon landscape

The Aragon landscape is represented explicitly with a grid derived from an ASCII raster taken from the CORINE 2006 Land Cover dataset (EEA 2006)[28]. Maize field data[29] were directly obtained from the Aragon regional government statistics and explicitly incorporated in the CORINE map (figure 6.1). The

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[26] Following a list of tasks and respective used R packages: "Raster" (Hijmans and Van Etten 2013) to create raster objects and "mgcv" (Wood and Wood 2015) for the GAM model

[27] See chapter three, section 3.3.2 for a description of this pest

[28] http://uls.eionet.europa.eu/CLC2006

[29] Year 2012

original landscape was aggregated for the relevant land cover types, ϑ_{land} , with a spatial resolution of 500×50 0m, i.e. 25ha (figure 6.2). ϑ_{land} is composed of 11 different fields as described in table 6.1. When aggregating the landscape fields, which was compulsory for computation feasibility, the total maize area did not differ significantly from real data, only 4% of spatial maize information was lost (table 6.1). The domain ϑ represents the whole simulation area, $(\mathbf{x}, \mathbf{y}) \in \vartheta$, formed by a 483×684 $(\boldsymbol{\vartheta}_x, \boldsymbol{\vartheta}_y)$ matrix, from which 855 and 1279 cells are categorised conventional and *Bt* maize, respectively. The effects of the spatial heterogeneity on each species influences survival and movement. Informed by expert knowledge, and taking into consideration the resource availability, the landscape was categorised into areas of favourable habitat, i.e. where the species can reproduce and can disperse normally; and unfavourable habitat, i.e. where reproduction is not viable and dispersion is lower (table 6.1).

Table 6.1 – Description of the Aragon land use. The table shows the area, the ratio in relation to the total area and the respective habitat quality for each different land us. For MCB and TAW, the landscape was categorised into areas of favourable habitat, i.e. where the species can reproduce and can disperse normally; and unfavourable habitat, i.e. where reproduction is not viable and dispersion is lower

Fields	Area (Km^2)	Ratio (%)	Habitat quality	
			MCB	TAW
Bt Maize	320	0,7%	Favourable[30]	
Conventional Maize	214	0,4%	Favourable	
Farmland	8641	18,1%	Unfavourable	
Rice	421	0,9%	Favourable	
Vineyards, fruit trees & forest	6397	13,4%	Unfavourable	
Pastures	2958	6,2%	Unfavourable	Favourable
Natural grassland	11850	24,8%	Unfavourable	Favourable
Urban areas	225	0,5%	Unfavourable	
Non-agricultural vegetated areas	15568	32,6%	Unfavourable	
Sand, rocks, etc ...	859	1,8%	Unfavourable	
Water	280	0,6%	Unfavourable	
Total	47732	100		

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[30] The effect of the *Bt* toxin on dispersion and survival rate was considered to be external to the landscape effect.

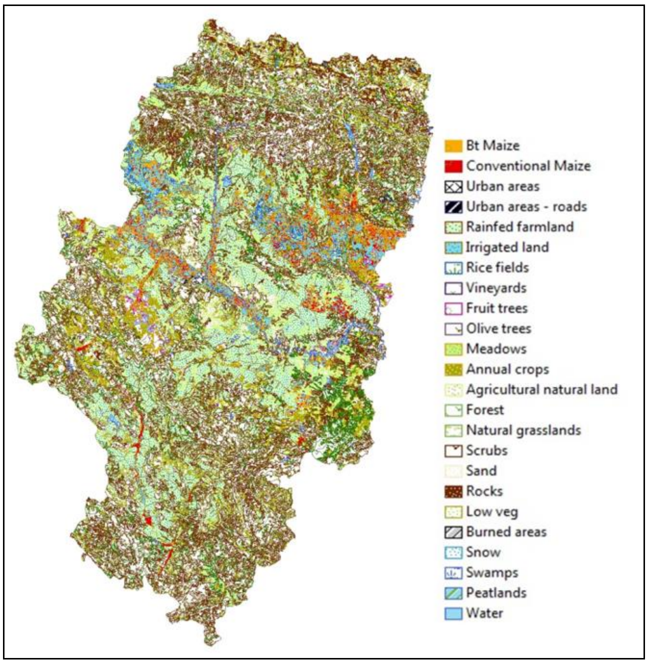

Figure 6.1 - CORINE geographical land use map encompassing the main land cover categories. The resolution of the data is 100 x 100m (adapted from LCM (2006)).

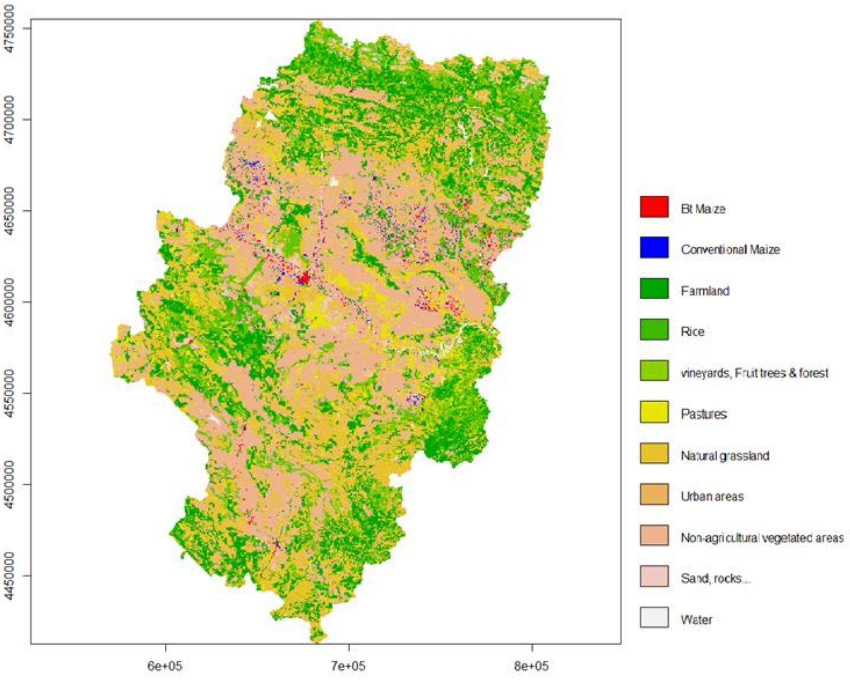

Figure 6.2 - Map of the aggregated land-use, from LCM (2006), for the Aragon region used in this study. The map shows the location of Bt (blue) and conventional (blue) maize. The resolution of the

map is 500 x 500m.

Step 2) Valuing pest control methods – Optimal individual farmer insecticide use and Bt maize

As in chapter five, maize is assumed to be vulnerable to attack by two different pests: the MCB – primary pest (N1) – is a highly competitive pest that is also highly susceptible to *Bt* toxin; and the TAW – an invasive species with the capacity to become a secondary pest (N2) – is negatively affected by the first species, but has a higher tolerance to the *Bt* toxin (chapter five, table 5.2). It is assumed that the farmer has only two means to suppress pests[31], by using *Bt* maize variety and/or spraying insecticide when pest densities exceed an economic threshold (ET[32]). Pest susceptibility to both *Bt* and insecticide is assumed to be as in chapter five. *Bt* maize fields have, from the beginning of the analysis, the commonly advised 20% refuge of non-*Bt* maize to promote survival of susceptible pests, thus avoiding resistance building to *Bt* toxin (Tabashnik et al. 2003). This adjustment, as compared with chapter five where *Bt* adoption reached its maximum after 10 years, has a consequent impact on the number of insecticide applications. Hence a new optimal insecticide path for *Bt* maize adopters' NPV maximization after 25 years was calculated using the same methodology, but now assuming a constant adoption of 80%[33]. Each individual, conventional and *Bt* adopter maize farmer applies insecticides according to the optimum 25 years' optimal insecticide path[34] at time $\mathbf{t}$ defined by the parameters a, b, c and d (equation 6.4). In another words, farmers make a long-term educated guess about the possibility of pests occurring according to their knowledge of biological dynamics, optimizing the application of insecticides in order to maximize their NPV. Following Shoemaker (1973) and Bor (1995), mortality rate is an exponential function of insecticide dosage. Hence, the insecticide impact upon the pest[35] $\boldsymbol{h}(\boldsymbol{w})$ and the insecticide impact on natural enemies by $\boldsymbol{u(\rho)}$ are a function of the number of insecticide applications $(\mathbf{w})$ and bounded by the maximum effectiveness for the pest $(\boldsymbol{s_p})$ and/or natural enemies $(\boldsymbol{s_{ne}})$.

$$w(t) = a + bt + ct^2 + dt^3 \tag{6.4}$$

---

[31] Other pest control strategies could include for example biological control and crop rotation (see for further details *Control of pests and weeds by natural enemies: an introduction to biological control*)

[32] Economic threshold is defined as the "density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level".

[33] Equivalent to saying that 100% of the field is under a GEIR crop scheme

[34] For conventional maize farmers, the optimal insecticide application takes the set of values {a=4.080582e+00; b=1.918453e-02; c=-2.830495e-03; d=-4.804419e-05} and for *Bt* maize farmers {a=2.430850e+00; b=-2.942969 e-01; c=2.358879 -02; d=5.998633 -05}

[35] Both pests are equally affected by the insecticide

$$h(w) = (1 - e^{-\mathrm{w}(t)s_p}) \tag{6.5}$$

$$u(w) = (1 - e^{-\mathrm{w}(t)s_{ne}}) \tag{6.6}$$

The ET (equation 6.7) was set as 25% of the economic injury level (**EIL**[36]) as suggested by Pedigo et al. (1986).

$$ET = \frac{EIL}{4} \tag{6.7}$$

With:

$$EIL = \frac{u_w}{p_m L_y s} \tag{6.7a}$$

$\boldsymbol{u_w}$ being the cost of management per unit (€/ha); $\boldsymbol{p_m}$, the product market value per ton (€/ton); $\boldsymbol{L_y}$, yield lost per larva (tons/ha); and $\boldsymbol{s}$, the proportion of larvae killed (%). It is assumed that both species have the same negative impact upon yield.

Step 3) Developing the population dynamics (reaction) term

In a biological sense, the reaction term of the RD model (section 6.3) describes the population dynamics (growth and mortality) at time **t**. The population dynamics are based on a system of two first order differential equations that represent the ecological interactions of both pests with the pest management practices and natural enemies:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left[1 - b_{11}\dfrac{N_1}{K_1} - b_{12}\dfrac{N_2}{K_1} - (1-\Omega)m_1 - \delta q_1 - \phi h(w)\right] \\ \dfrac{dN_2}{dt} = r_2 N_2 \left[1 - b_{22}\dfrac{N_2}{K_2} - b_{21}\dfrac{N_1}{K_2} - (1-\Omega)m_2 - \delta q_2 - \phi h(\mathrm{w})\right] \end{cases} \tag{6.8}$$

With:

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[36] The economic injury level was defined by these authors as the "lowest population that will cause economic damage" " (Stern et al. 1959).

$$\phi = \begin{cases} 1, & N_1 \geq ET_{N_1} \\ 1, & N_2 \geq ET_{N_2} \\ 0, & Otherwise \end{cases}$$

$$\Omega = \begin{cases} 0.8, & Bt\ maize \\ 0, & Connventional\ maize \end{cases}$$

The pest populations grow according to a classical logistic growth equation where population dynamics are influenced by: the theoretical growth rate, $\boldsymbol{r_i}$, the species' intrinsic carrying capacity, $\boldsymbol{k}_i$; intra-competition, $\boldsymbol{b_{ii}}$; inter-competition, $\boldsymbol{b_{ij}}$; mortality attributed to natural enemies, $\boldsymbol{m_i}$ (*i=1,2; i≠j*); the effectiveness of *Bt* in controlling each pest population,$\boldsymbol{q_i}$; and the application of insecticides, **w**. The parameter ϕ, a dummy variable, assumes the value of one if $N_1 \geq ET_{N_1}$ or $N_2 \geq \mathrm{ET}_{N_2}$, and zero otherwise; and the parameter Ω, assumes the value of 0.8 if *Bt* maize is used, and zero otherwise. For further information on both species' characteristics and relevance to maize production, the reader is directed to chapter three.

Step 4) Developing the spread (diffusion) term

The diffusion term, $\boldsymbol{D_i}\left(\frac{\partial^2 N_i}{\partial x_i^2} + \frac{\partial^2 N_i}{\partial y_i^2}\right)$, describes the spread of populations in space (section 6.3). Besides space, the main component of the diffusion term is the dispersal rate. Per time unit **t**, the individuals move randomly, i.e., there is an equal probability of them moving in any direction (left, right, up or down). The dispersal rate for each species was derived from the theoretical speed obtained in wind tunnel, as follows: the theoretical maximum possible speed for MCB ($\boldsymbol{v_{MCB}}$) is 23.3 cm.s^{-1} (Bau et al. 1999) and 0.081 Km.m^{-1} for TAW ($\boldsymbol{v_{TAW}}$) (Luo et al. 1999, Luo et al. 2002). Both species can disperse within the whole domain, however the dispersal rate changes depending if dispersal occurs in favourable or unfavourable fields. After calibration it was assumed that the dispersal rate in unfavourable fields for both species has a value of 1% of the actual dispersal rate[37].

The dimensionless disperse rate, $\boldsymbol{D_i} = \frac{\vartheta_i^{\ 2}}{\pi T_i}$ where ***i***=MCB;TAW, was obtained by adjusting the spatial and temporal domain as in Gilligan (2008), taking into consideration the maximum domain size (ϑ_y)[38] in meters and the units in which theoretical speed was reported[39]. For MCB: since the theoretical speed (given in cm.s^{-1}), the maximum domain size was converted into centimetres: $\vartheta_{MCB} = \frac{v_{MCB}}{\vartheta_y \times 100cm}$, and the yearly

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[37] i.e. resource availability is a determinant of pest mobility (Barbosa et al. 2012, Cho and Kim 2013)

[38] $\vartheta_y = 684 \times 500 = 342000$ meters

[39] Otherwise, the dimensionless dispersal rate would have been improperly estimated (see Gilligan (2008) for further details)

timeframe ($\boldsymbol{Ty}$) in seconds: $\boldsymbol{t_{MCB}} = \frac{\boldsymbol{Ty}}{\boldsymbol{Ts}}$. For TAW, the speed was given in Km.m^{-1}, hence the maximum domain size was in kilometres: $\vartheta_{\boldsymbol{TAW}} = \frac{\mathbf{1000}\boldsymbol{m}\times\boldsymbol{v_{TAW}}}{\vartheta_{\boldsymbol{y}}}$, and the yearly timeframe into minutes: $\boldsymbol{t_{MCB}} = \frac{\mathbf{Ty}}{\mathbf{Tm}}$. Where $\mathbf{v_i}$ is the species theoretical speed (in reported units), $\mathbf{T_y}$ represents a period of one year, $\mathbf{T_s}$ and $\mathbf{T_m}$ the number of seconds and minutes in one year respectively. The boundaries between spatial units are fixed during the course of the simulation. Homogeneous Neumann boundary conditions (null derivative specified on the boundaries), were set for the spatial dimensions:

$$\begin{cases} \frac{\partial N_1}{\partial\vartheta}\ (t,x,y,N_1,N_2)|_{\partial_\vartheta} = 0 \\ \frac{\partial N_2}{\partial\vartheta}\ (t,x,y,N_1,N_2)|_{\partial_\vartheta}\ = 0 \end{cases} \tag{6.9}$$

Step 5) Evaluating the regional net present value

Chapter five developed a bio-economic model based on that of Lichtenberg and Zilberman (1986)[40], in which the interactions of two pests are incorporated into a production function. In order to reflect spatial movement of both species, this model was expanded by introducing a two-dimensional diffusion term. The simulations are performed within the landscape explicitly represented and described above, which is populated by profit maximizing maize farmers. The final NPV after 25 years of aggregate landscape profits is evaluated taking into consideration the implications of different pest management decisions over a time interval [0, T]. The conventional fields are represented by $\boldsymbol{\vartheta_{\mathrm{Conv}}}$, and *Bt* maize fields by $\boldsymbol{\vartheta_{Bt}}$. This is accomplished using the optimal amount of insecticides applied throughout the cropping season according to the economic threshold subject to pest dynamics. Letting **p** denote output price, $\boldsymbol{u_c}$ and $\boldsymbol{u_{Bt}}$ the prices of conventional and of *Bt* maize inputs unrelated to damage control and $\boldsymbol{u_w}$ the price of a unit of insecticide (**w**), the BeSEP model becomes:

$$\sum_{i=1}^{\vartheta}(\vartheta_{\mathrm{Conv}} + \vartheta_{Bt}) \int_0^T e^{-\delta t}\ \{\boldsymbol{p_m}g(Z)\big[1\ -\ D\big(h(N_1,N_2,q,\mathrm{W})\big)\big] - Z[(1-\Omega)u_c + \Omega u_{bt}] \\ -\ \phi\boldsymbol{u_w}w\}\ dt \tag{6.10}$$

s.t.

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[40] For a detailed review on the Lichtenberg and Zilberman (1986) damage control approach, see Sexton et al. (2007).

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left[1 - b_{11}\dfrac{N_1}{K_1} - b_{12}\dfrac{N_2}{K_1} - (1-\Omega)m_1 - \delta q_1 - \phi h(w)\right] + \\ \qquad\qquad + D_{N_1}\left(\dfrac{\partial^2 N_1}{\partial x^2} + \dfrac{\partial^2 N_1}{\partial y^2}\right) \\ \dfrac{dN_2}{dt} = r_2 N_2 \left[1 - b_{22}\dfrac{N_2}{K_2} - b_{21}\dfrac{N_1}{K_2} - (1-\Omega)m_2 - \delta q_2 - \phi h(\mathrm{w})\right] + \\ \qquad\qquad + D_{N_2}\left(\dfrac{\partial^2 N_2}{\partial x^2} + \dfrac{\partial^2 N_2}{\partial y^2}\right) \end{cases}$$

With:

$$\phi = \begin{cases} 1, & N_1 \geq ET_{N_1} \\ 1, & N_2 \geq ET_{N_2} \\ 0, & Otherwise \end{cases}$$

$$\Omega = \begin{cases} 0.8, & Bt\ maize \\ 0, & Connventional\ maize \end{cases}$$

The damage-abating role of insecticides is taken into account explicitly in the production function through an asymmetric treatment of "productive" inputs (Z) and "damage-abating" insecticide (w)**:** Y = F(w, D(Z)). The aggregated potential maize output over the landscape, which includes both conventional maize ***(G_c)*** and GEIR maize ***(G_{Bt})***, is denoted by ***G(Z)***. ***Z*** represents a vector of non-insecticide inputs (i.e., labor, seeds, fertilizers etc.). The damage control framework models the actual output, ***Y***, as a function of potential output, ***G(Z)***, damage, ***D(N_1,N_2)***, and proportion of the total landscape planted with *Bt* maize (*Ω*). Both pests act simultaneously and the nature of the damage is species independent. The damage function is represented as a function of the density of both pest populations – ***N_1*** and ***N_2*** – and expresses the fraction of yield lost (**I**) due to the sum of the damage caused. The model therefore computes aggregate regional maize output as the potential yield minus the fraction of the crop that is lost due to the damage caused by both pest species. The model does not take into account the external social and environmental costs of insecticide use for both society and the farmer.

6.6.3 Scenarios explored

In order to assess the aggregated regional NPV after 25 years accrued from maize production considering the expected damage from spatial interactions between the invasive species (TAW), abiotic (insecticides) and biotic factors (MCB and natural enemies interactions), and the effect of the landscape, three scenarios are investigated[41]: 1) Spread of TAW from an invasion hotspot area with the actual

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[41] The first and second phases of the invasion process were “effective”, the analysis focuses exclusively on the third invasion phase process, i.e. the spread.

conventional/*Bt* maize proportion; 2) Spread of TAW from an invasion hotspot area altering the conventional/*Bt* maize proportion, and 3) TAW spread was not effectively controlled in time. The model was solved with operator-splitting. A landscape is considered in which farmers do not interact with one another nor have knowledge of the behaviour of others. They act according to their own interests and pest density in their fields. For the three scenarios the cases in which: i) insecticides are applied in both conventional and *Bt* maize fields; ii) only in conventional fields, and iii) no insecticides are used are evaluated. Additionally, it is assumed that the initial population of MCB is 10% of its carrying capacity, and present in all fields favourable to reproduction. Natural enemies are present evenly throughout the landscape, being negatively affected by insecticide applications. The reaction terms were solved following the fourth order explicit Runge–Kutta (section 5.4.1). The diffusion term was solved with a second order semi-implicit scheme called Alternating Direction Implicit (ADI)[42]. The model parameters were obtained in chapter five, tables 5.1 and 5.2. In the following, a description of the three scenarios is presented.

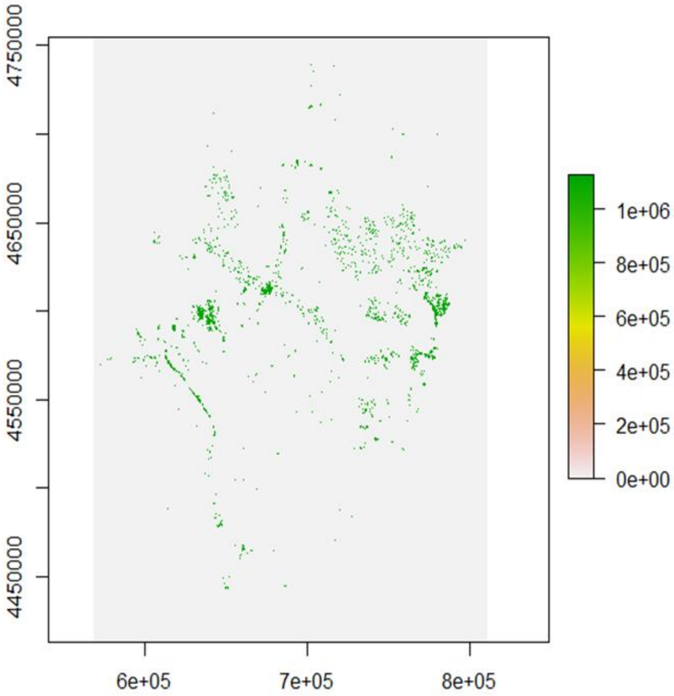

Figure 6.3 MCB initial population (green). It is assumed that MCB is present in all fields favourable to reproduction with a density equivalent to 10% of its carrying capacity. The resolution of the map is 500 x 500m.

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[42] Operator splitting is a powerful method to numerically solve complex models, by splitting a complex problem into a sequence of simpler tasks, called split sub-problems (accuracy of operator splitting for advection-dispersion-reaction problems) (ADI schemes for higher-order nonlinear diffusion equations) The reader is directed to Press (2007) and Bourhis et al. (2015) for a detailed description of the ADI method.

Scenario 1) Spread of TAW from an invasion hotspot area with the actual conventional/Bt maize proportion

In the first scenario the spatial economic impacts, patterns and the radial rate of invasion (equation 6.1) accrued from a physical spread of TAW from an invasion hotspot are assessed. To infer the influence of the starting point location on the invasion process a Monte Carlo simulation technique for 100 simulations[43] is used. For each simulation, TAW is introduced in a randomized location of favourable habitat, spreading to neighbouring cells[44]. The TAW population at the centre of the invasion is considered to have a density of 10% of its carrying capacity outside maize fields (figure 6.4b). Figure 4a shows an example of an area that received the initial introduction.

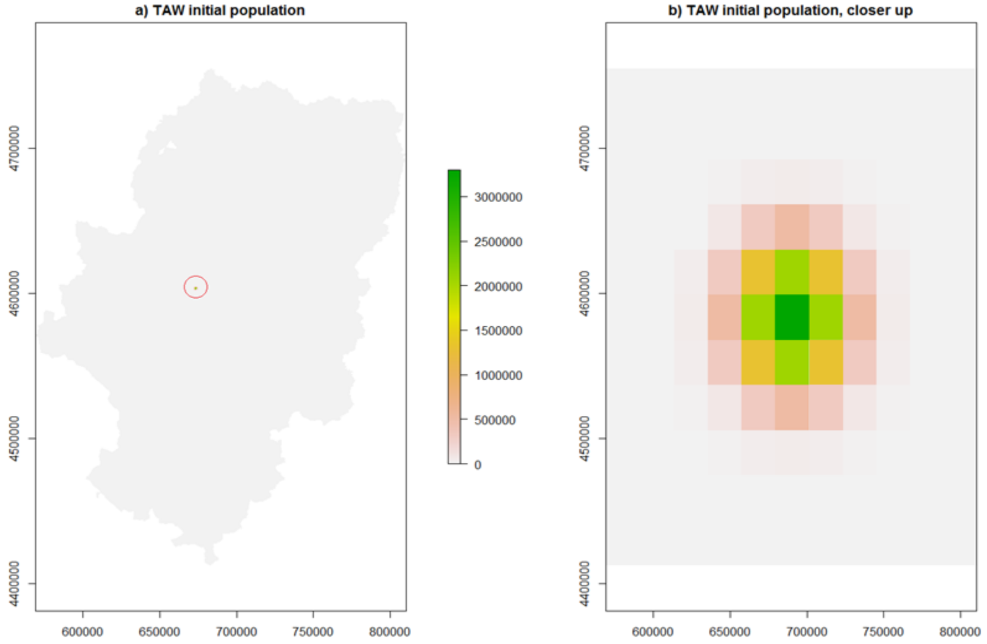

Figure 6.4 a) Example of a TAW initial population from one randomized simulation, whole region view; b) Cauchy kernel closer up evidencing the proportion of individuals in relation to the initial population shown in Figure 4a.

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[43] 100 simulations show an acceptable convergence of the mean of the total producers' welfare losses and cumulative area invaded over 25 years. No significant difference was found in these values when the number of simulations was increased.

[44] A Cauchy kernel is assumed, because it is easy to compute and has a long history in the study of biological invasion (Kot et al. 1996).

To predict the possible hotspots of invasion, i.e. where a pest outbreak or introduction area would have higher economic impact for Aragon maize producers, each cell from the domain is spatially interpolated using Generalized Additive Models (GAM[45]). This method overcomes the issue of individually evaluating the invasion effects on every possible introduction field. The GAM modelling methodology has been extensively applied in spatial ecology (e.g. Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Beale et al. 2010, Miller et al. 2013). A GAM class of equations called "smoothers" or "scatterplot smoothers" was used that generalizes data into smooth curves by local fitting to subsections of the data. Considering a nonparametric smoothing function in which $\boldsymbol{\Gamma}$ represents the interception parameter, $\boldsymbol{s}$ the "smoothers" as a function of the initial coordinates, $\boldsymbol{\vartheta}_{\boldsymbol{i,j}}$, at the centre of the invasion introduction, and the log of the NPV after 25 years as the independent variable, the GAM model becomes:

$$\log(NPV_i) = \Gamma + \sum_{\boldsymbol{i,j=1}}^{\vartheta} s\left(\vartheta_{\boldsymbol{i,j}}\right) + \boldsymbol{\varepsilon_i} \tag{11}$$

The approach employed with GAMs using "smoothers", is the division of the data into a number of segments, using "knots" at the ends of each segment. After this a low order polynomial or spline function is fitted to the data in each of the segments. The best fitting model[46] was determined using a step-wise GAM based on the Akaike Information Criterion (AIC) test statistic. The lowest AIC statistic gave the best combination of parameters for the final model. This methodology allowed prediction of invasion "hotspots", i.e. the primary areas where control efforts should be considered due to the economic consequences associated with their spread across landscape.

Scenario 2) Spread of TAW from an invasion hotspot area altering the conventional/Bt maize proportion

To assess the influence and importance of spatial distribution and ratio of *Bt*/conventional maize on the spread process, insecticide use and the subsequent economic impact, the original maize cropping area is altered to four different conventional/*Bt* maize proportions: i) only conventional maize is cropped in the

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[45] In brief, GAMs are a flexible extension of the generalized linear models (GLMs) (McCullagh and Nelder 1989) which allow the inclusion of multiple linear and non-linear relationships between coordinates by identifying the appropriate non-linear function (Simpson and Walsh 2004). GAMs are parameterized just like GLMs, except that some predictors can be modelled non-parametrically in addition to linear and polynomial terms for other predictors (Guisan et al. 2002). However a complete overview is beyond the scope of this work, and readers are referred to more specialized literature on GAM models (Hastie and Tibshirani 1986, Guisan et al. 2002).

[46] Several models were tested, for example not logging the independent variable, logging the explanatory variable or using the field type as an additional explanatory variable.

region, ii) 50% of the *Bt* maize famers move to conventional maize faming, iii) 50% of the conventional farmers adopt *Bt* maize, and iv) all farmed maize is *Bt*. In this scenario, it is assumed that insecticides are applied in all maize fields, according to the respective (*Bt* and conventional maize) optimal insecticide path, whenever the pests reach the ET. For each assessment, a Monte Carlo simulation technique is applied for 100 simulations.

Scenario 3) TAW spread is endemic throughout the region

The challenge of detecting a recently established invasive pest is central to efficient control. There are numerous examples of invasive species that escaped early detection and became so abundant and widespread that containment and eradication were no longer possible (Myers et al. 1998). This scenario evaluates the economics of not effectively controlling the spread of TAW in time, i.e. if TAW becomes endemic in the region. It is assumed that at time zero, TAW is present in all fields where its reproduction is possible with density per hectare equivalent to its ET in maize (figure 6.5).

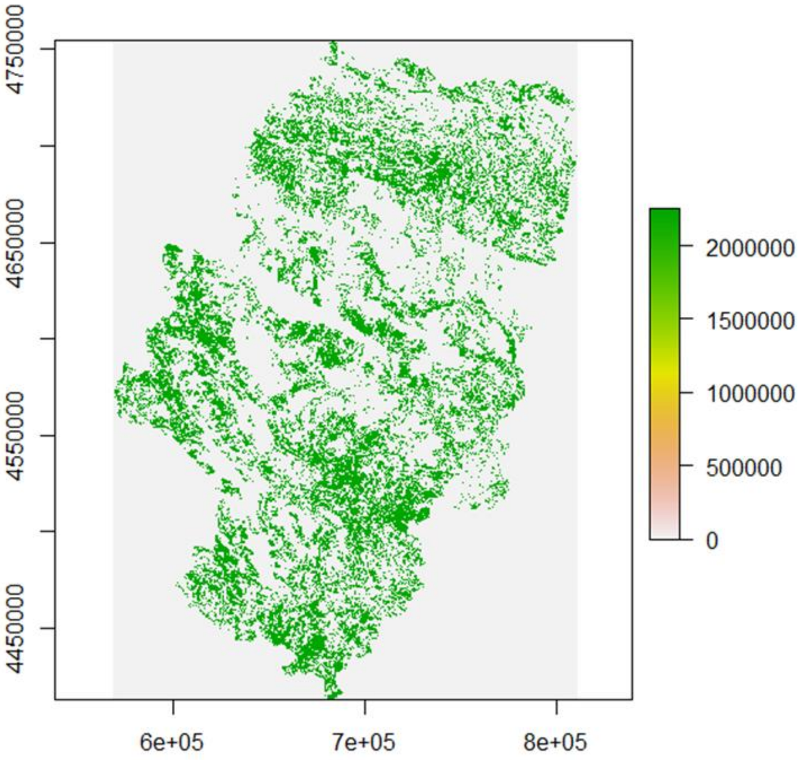

Figure 6.5 - TAW initial population (green). It is assumed that TAW is present in all fields favourable to reproduction with a density equivalent to 10% of its carrying capacity. The resolution of the map is 500 x 500m.

6.7 Model validation

Model validation has been undertaken, showing that economic outcomes are in line with published data. In 2012, the Aragon government reported an average maize production of around 12 tons/ha (López 2013). Including the impact of pests, when farmers apply insecticides in both maize systems, the average yield computed by the model is relatively close to the real value, 10.9 tons/ha. However, there is a substantial deviation from the average profit per hectare. While in 2012 the Aragon maize producers obtained an average profit of 499€/ha (López 2014), this study reports a profit average of 725€/ha. This difference may be due to the conjunction of two factors: i) in this research it is assumed that all farmers act optimally, which in reality does not happen; and, ii) it is possible that the total costs were not properly estimated due to the complexity of maize production, for example no other pests were taken into consideration, hence insecticide expenditures may have been higher.

Numerous studies of Spain (López et al. 2000), Canada (Fields and McNeil 1984), the US (Willson and Eisley 1992) and Mexico (Ramírez Dávila and Esquivel Higuera 2013) have reported on the TAW's destructive potential and sporadic population outbreaks with larvae marching *en masse* across the landscape. Attempts to analyse and predict outbreaks have been constrained by the high flying capacity and reproduction rate of TAW, and its gregarious, explosive and unpredictable behaviour. Armyworms frequently disappear almost as suddenly as they appear, either burrowing into the ground to pupate or migrating to further fields in search of food.

Finally, there is a close link with temperature as this species does not have a diapause and cannot survive prolonged temperatures below freezing (Fields and McNeil 1984, Bues et al. 1986). This has a major influence on the erratic nature of TAW's outbreaks and invasions. Thus there may be an extended period without farmers noticing the pest. To the best knowledge of the author, the spatial identification of TAW's range of action, evaluation of the TAW spread patterns, possible effects of clustering and its influence in neighbouring areas has not been conducted. In this work, the best knowledge reported in literature was used to evaluate the possible spread pattern of TAW in Aragon. The author is aware that several parameters could be more accurately estimated, however the density map patterns appear to be in line with the only spatial model known by the authors for TAW (Ramírez Dávila and Esquivel Higuera 2013).

6.8 Results and discussion

This section shows how spatial dynamics patterns of MCB and TAW affects the economic performance of maize farmers in Aragon according to three pest control regimes: 1) insecticides are applied in both conventional and *Bt* maize fields; 2) only in conventional fields; and, 3) no insecticides are used. The overall success is defined in terms of achieving the highest NPV after a given time span of 25 years (equation 6.10). Firstly, the results from the first scenario are analysed and discussed, i.e. the case in which TAW is introduced or breaks out from a hotspot area with the actual conventional/*Bt* maize proportion. The results of scenario one are divided into three parts: i) evaluation of the physical spread characteristics of TAW, ii) evaluation of the invasion economic impact and consequent implications, and iii) a prediction of the possible hotspots of invasion, i.e. where a pest outbreak or introduction area would have higher impact for Aragon maize producers. Secondly, the influence and importance of spatial distribution and ratio of *Bt*/conventional maize on the spread process (scenario two) is assessed. This section ends with the results from the third scenario; the economic implications of not effectively controlling the spread of TAW in time are discussed.

6.8.1 Scenario 1) Spread of TAW from an invasion hotspot area with the actual conventional/*Bt* maize proportion

Evaluation of the physical spread characteristics of TAW

The TAW's annual radial rate of invasion (RRI) and total area invaded (TAI) after 25 years were calculated according to equations 6.1 and 6.2. To illustrate variation in the spatial range of biological invasions, two different 'invasion levels' for a field to be considered successfully invaded were evaluated: i) at least one individual is present per hectare, ii) when TAW population reaches the ET numbers per hectare in maize, i.e. when the farmer "spots" the pest (table 6.4).

Table 6.2 – Annual radial rate of invasion (RRI) and total area of invasion (TAI) results considering the three pest management regimes (PMR), and the two invasion levels for a field to be considered successfully invaded.

	> 1 TAW larvae per ha			
	units	PMR 1*	PMR 2**	PMR 3***
		Mean	Mean	Mean
Annual RRI	km.year^{-1}	4.89±0.02	4.89±0.02	4.89±0.02
TAI	km2	46999±351	47026±377	47025±341
	TAW population > ET			
		Mean	Mean	Mean
Annual RRI	km.year^{-1}	3.55±0.25	3.49±0.23	3.58±0.24
TAI	km2	24744±3216	24754±3177	25333±3394

* Insecticides in both *Bt* and Conventional maize

** Insecticides only Conventional maize

*** No insecticides applications

TAW effectively invaded almost the whole region regardless of whether insecticides were used or not, based on the assumption that a field is considered successfully invaded when at least one individual is found per hectare, with a mean radial rate of invasion of 4.7 – 4.9 km.year^{-1}. The growth and spread continues until suitable habitat and resources become scarce. Recalling that each simulation had a different geographical starting point, it is possible to infer the existence of a strong correlation between the TAI and the initial introduction area. Figure 6.6 shows the total invaded area, over the 25 years simulation period, where TAW has surpassed the ET level for the scenario in which insecticides are used in both *Bt* and conventional maize. Each line in the figure represents one model simulation. Additionally, figures 6.7 and 6.8 exhibit the invasion patterns from two distinct initial points, clearly showing how the invaded area is highly dependent on the starting point, also noted in the high variance in the TAI mean (table 6.2). In this case, regardless of whether insecticides are used or not, the final average TAI is 25.000 km^2 (52% of the total area of Aragon).

Turning to consideration of the invaded maize itself, the outcomes are in line with previous results. The total maize area in which TAW surpasses the economic threshold ranges from a minimum of 103 km^2 to a maximum of 311 km^2 (table 6.3). The average TAW numbers in conventional fields do not vary within the three pest control regimes. In *Bt* maize fields the prevalence of TAW is always higher when compared with conventional fields. This indicates that the TAW population in conventional fields will remain low either due to insecticide use or competition pressure from the MCB. The results also reflect the TAW's ecological advantage in the absence of MCB and reduced insecticide intensity (Catarino et al. 2016). This finding suggests that controlling the invasive species only in maize fields is not an efficient management strategy. Furthermore, the spatial structure, i.e. the connectivity of favourable fields for dispersion and reproduction (Jager et al. 2005), assumes a critically important feature which can have a strong influence on the dynamics of invasive species. Scenario two evaluates whether the ratio and localization of conventional/*Bt* maize fields influences the spread of TAW.

Table 6.3 – Invasion results (scenario 1) in maize fields in which TAW surpasses the economic threshold in the final year considering the three pest management regimes (PMR).

		units	Min	Max	Mean
PMR 1*	Maize invaded area	km^2	103	311	218±54
	Conv maize invaded area	km^2	39	126	83±27
	Bt maize invaded area	km^2	63	194	136±31
	Total TAW average density	Insect/plant	0.16	1.12	0.65±0.19
	Conventional field TAW average	Insect/plant	0.06	1.23	0.57±0.23
	Bt fields TAW average density	Insect/plant	0.13	1.13	0.67±0.20
PMR 2*	Maize invaded area	km^2	133	303	226±57
	Conv maize invaded area	km^2	50	123	89±26
	Bt maize invaded area	km^2	83	182	137±33
	Total average TAW density per plant	Insect/plant	0.11	1.09	0.59±0.22
	Conv average TAW density per plant	Insect/plant	0.11	1.18	0.51±0.26
	Bt average TAW density per plant	Insect/plant	0.11	1.10	0.63±0.22
PMR 3*	Maize invaded area	km^2	126	310	210±53
	Conv maize invaded area	km^2	42	131	80±27
	Bt maize invaded area	km^2	81	195	130±30
	Total average TAW density per plant	Insect/plant	0.12	1.1	0.67±0.25
	Conv average TAW density per plant	Insect/plant	0.12	1.20	0.58±0.27
	Bt average TAW density per plant	Insect/plant	0.12	1.19	0.72±0.26

* Insecticides in both *Bt* and Conventional maize

** Insecticides only Conventional maize

*** No insecticide applications

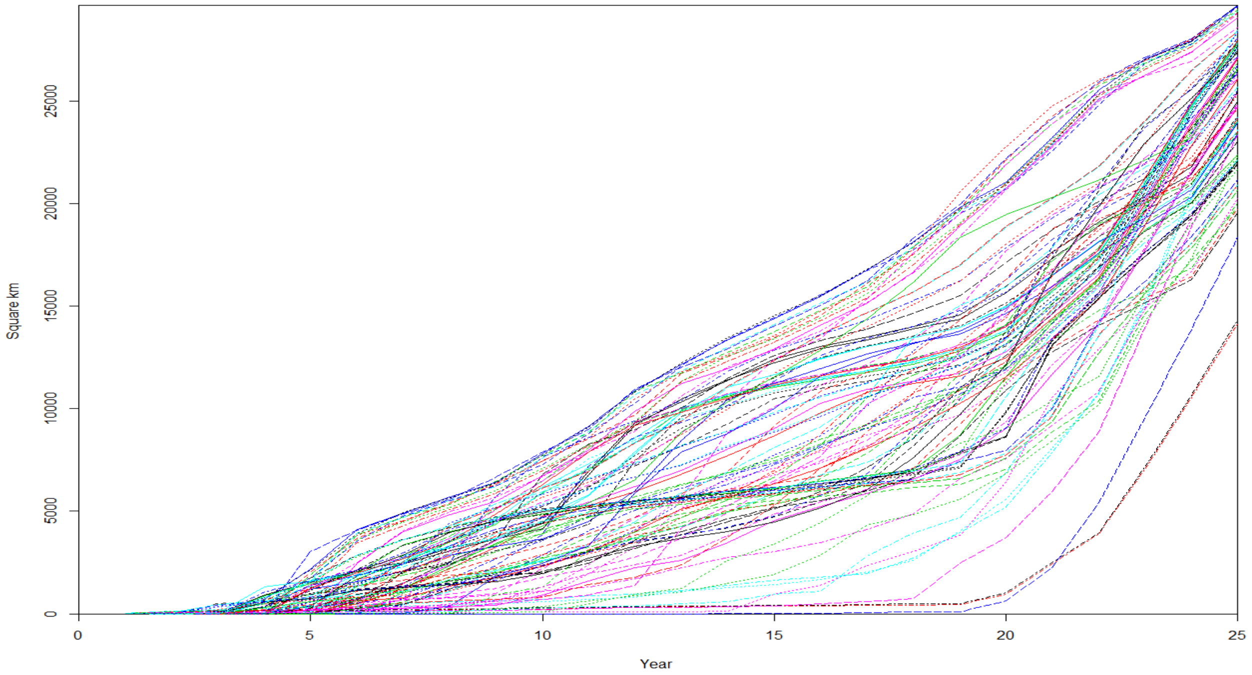

Figure 6.6 – Total invaded area, over the 25 years simulation period, where TAW has surpassed the ET level for the scenario in which insecticides are used in both Bt and conventional maize. Each line in the figure represents one model simulation

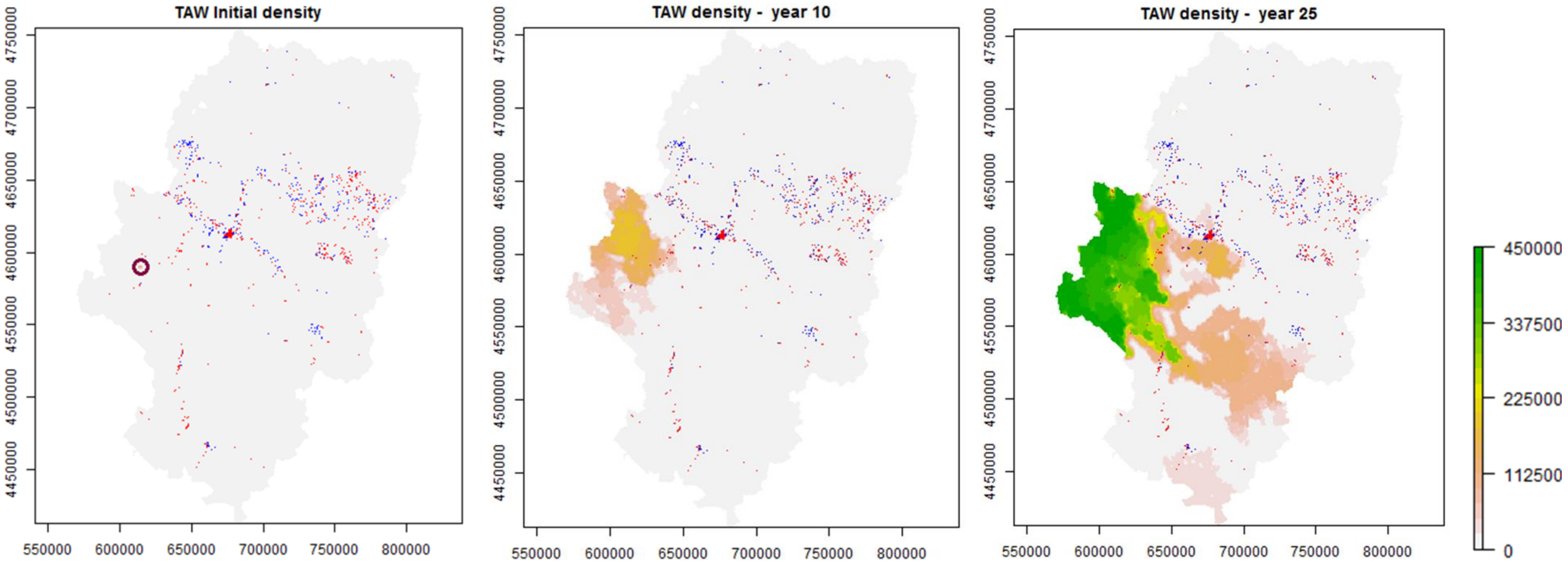

Figure 6.7 – Example 1 of the TAW invasion process over 25 years when insecticides are used in both *Bt* and conventional maize. The first image shows the initial outbreak area, occurring in the west of Aragon. The last image shows the final spread accrued from this simulation. The red cells represent *Bt* maize fields, while blue cells represent conventional maize. The resolution of the map is 500 x 500m.

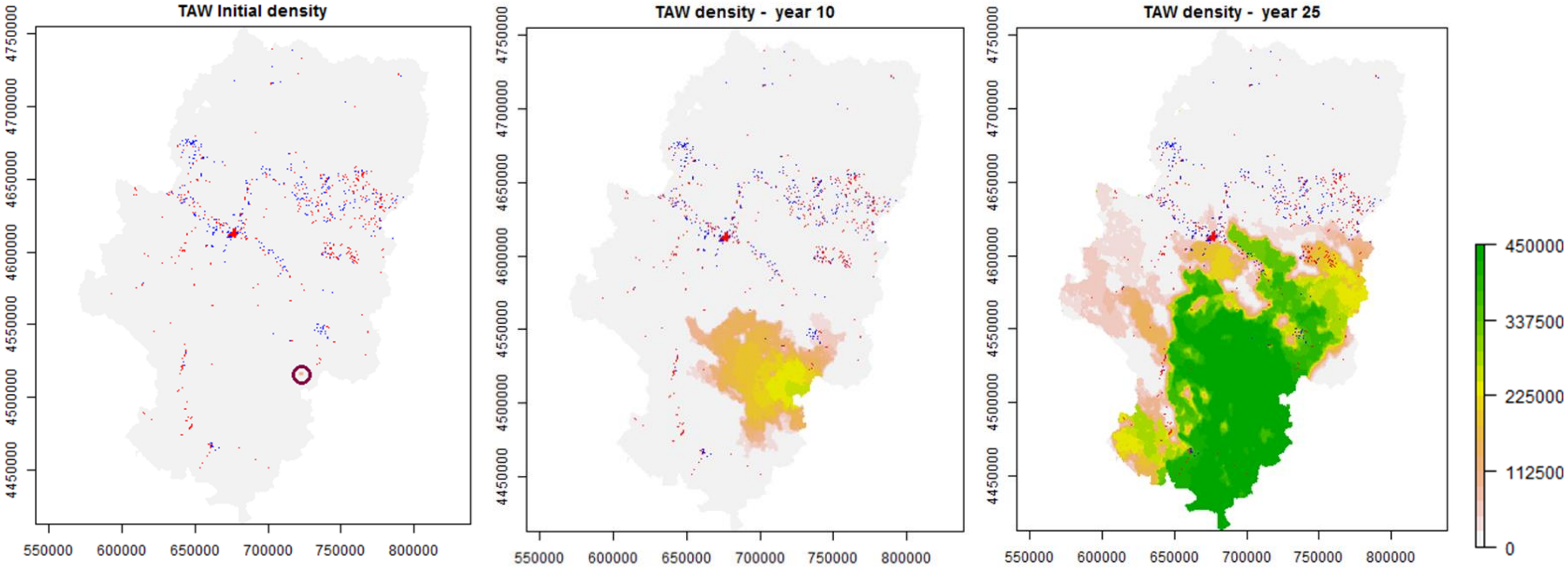

Figure 6.8 – Example 2 of the TAW invasion process over 25 years when insecticides are used in both *Bt* and conventional maize. The first image shows the initial outbreak area, occurring in the south east of Aragon. The last image shows the final spread accrued from this simulation. The red cells represent *Bt* maize fields, while blue cells represent conventional maize.

Invasion impact and consequent economic implications

The aggregated discounted average revenue for maize is computed for the whole region in combination with pest damage to calculate the potential damage costs and the NPV after 25 years. The total pest damage results from both MCB and TAW. The sum of the total regional losses in maize accrued from TAW determines the benefit value of an invasion control program. Subsequently, the economic results from the three pest management cases that have been considered are presented and discussed. Table 6.4 shows the NPV results per hectare after 25 years according to the initial outbreak field. The initial outbreak field was identified (first column, table 6.4) to infer its influence on the final NPV. However, no significant difference was found, i.e. the NPV variation is not dependent on the type of field in which the outbreak occurs. Taking the invasion process into consideration, the results are as expected; *Bt* farmers realize higher profits, approximately 18% more than conventional maize farmers, while decreasing insecticide use per year by more than 90%.

The results obtained when no insecticides are used in *Bt* maize were not as predicted. In this situation famers are practically as well off as if they used insecticides. As seen above, although TAW invasion is not efficiently controlled, not all maize fields are invaded at a level sufficient to inflict significant economic impact on farmers' NPV, at least for the 25 year period. Considering the high efficiency of *Bt* maize towards MCB, for adopting farmers the insecticide expenditure targeted at controlling TAW in this case is approximately the same as the damage imposed by this pest. On the other hand, insecticides are used in all conventional maize fields at a maximum level, suggesting that MCB would cause severe damage if neither *Bt* nor insecticides were used.

For conventional maize farmers, insecticide use brings an average 46% increase in the NPV, while for *Bt* farmers only 0.5%. Additionally, the use of insecticides on *Bt* fields brings an average 1% increase in the final NPV of conventional farmers. As Hutchison et al. (2010) found, *Bt* maize provides economic benefits for farmers who plant conventional maize in nearby fields. These results suggest that by shrinking the area of MCB infection general control is made more efficient. As noted before, the population growth rate, which is intrinsically linked to population numbers, is a major factor in the species' invasion capacity.

The summary for the final regional aggregated costs and benefits is shown in table 6.5. When farmers apply insecticides in both *Bt* and conventional fields, the region of Aragon would obtain a total NPV of €559M (±3.7) after 25 years, of which 65% is attributable to *Bt* maize production. During the same period the amount lost, even using insecticides, to just these two insects equalled €43M (approximately 7.7% of the total NPV), from which 22% is directly linked to the invasive species. The difference in insecticide expenditure amongst both maize systems is relatively large, with conventional maize farmers spending €18M and *Bt* famers spending only €1M. When direct losses to pests are taken into account together with the total insecticide expenditure, around €61M is lost in 25 years in Aragon alone.

Table 6.4 – NPV after 25 years according to the initial outbreak field for the first scenario, i.e. spread of TAW from an invasion hotspot area with the actual conventional/*Bt* maize proportion, considering the three pest management regimes (PMR).

	PMR 1*			
Fields	N. simulations	Conv	*Bt*	Total
Maize	3	9272±77	11376±85	10523±61
Rice	4	9311±91	11280±74	10397±112
Pastures	21	9194±127	11247±109	10411±110
Grassland	72	9213±86	11252±81	10434±84
Mean NPV		9248±73	11289±70	10471±69

	PMR 2*			
Fields	N. simulations	Conv	*Bt*	Total
Maize	2	9201±68	11329±23	10516±99
Rice	5	9138±91	11319±116	10485±107
Pastures	16	9116±128	11199±103	10364±158
Grassland	77	9198±89	11233±124	10413±109
Mean NPV		9161±104	11232±102	10409±99

	PMR 3*			
Fields	N. simulations	Conv	*Bt*	Total
Maize	1	4951±129	11071±91	8613±109
Rice	6	4953±132	11061±93	8613±102
Pastures	36	4935±113	11104±134	8632±123
Grassland	70	4949±68	11088±76	8628±69
Mean NPV		4945±104	11084±101	8625±100

* Insecticides in both *Bt* and Conventional maize

** Insecticides only Conventional maize

*** No insecticide applications

The total direct loss represents 44% of the agricultural component of Aragon's GDP[47] and 8% of the total Aragonese GDP[48], using the same discount rate used in this study (5% per year). Both the results at the individual farm and regional level show the high efficiency of *Bt* maize towards the primary pest. Additionally, the use of insecticides could be ceased in *Bt* fields since the insecticide expenditure and the monetary damage caused by the invasive pests is basically the same.

Table 6.5 – Regional statistics based on the regional optimal profit of €225.7M for conventional maize farmers and of €375.6M for *Bt* maize farmers.

	PMR 1*			
	Units	Conv	*Bt*	Total
Actual NPV Aragon	Million €	198±1.6	361.0±2.2	558.7±3.7
Aragon pest total loss	Million €	28.0	14.6	42.6
Insecticide applications	$ha.year^{-1}$	3.42±0.00	0.24±0.04	1.39±0.02
Aragon insecticide total cost	Million €	18.3	1.3	19.6

	PMR 2*			
	Units	Conv	*Bt*	Total
Actual NPV Aragon	Million €	195.8±2.1	359.1±4.0	555.0±6.5
Aragon pest total loss	Million €	29.8	16.5	46.3
Insecticide applications	$ha.year^{-1}$	3.42±0.0		
Aragon insecticide total cost	Million €	18.3		18.3

	PMR 3*			
	Units	Conv	*Bt*	Total
Actual NPV Aragon	Million €	105.7±2.2	354.4±3.2	460.1±5.4
Aragon pest total loss	Million €	119.9	21.2	141.1
Insecticide applications	$ha.year^{-1}$			
Aragon insecticide total cost	Million €	119.9	21.2	141.1

* Insecticides in both *Bt* and Conventional maize

** Insecticides only Conventional maize

*** No insecticide applications

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[47] https://ec.europa.eu/growth/tools-databases/regional-innovation-monitor/base-profile/aragon

[48] http://www.datosmacro.com/pib/espana-comunidades-autonomas

Prediction of possible TAW's invasion 'hotspots'

The results above outline the challenge of detecting and confirming the presence of invasive species. Predicting and quantifying the potential distribution and rate of invasion of invasive species is a critical step in evaluating their ecological and economic impacts, and management control options (Keller et al. 2008, Beale et al. 2010). Biological invasions are complex dynamic systems with several sources of uncertainty and generally exhibit strong geographical variation. Cacho et al. (2010) showed that the probability of eradication can increase and total costs of managing an invasion can be reduced considerably if surveillance efforts are effectively allocated across a landscape.

A step-wise GAM is used to determine the best fitting model based on the Akaike Information Criterion (AIC) test statistic. The lowest AIC statistic gave the best final model. The response variable logged, while the independent variables are composed by a spline smoothing function, **s** which assesses the shape of the response variable as a function of the predictor (table 6.6). To see the predicted values on the probability scale the values were unlogged and fitted into the Aragon map. The GAM model indicated that the NPV strongly depended on the initial coordinates, latitude and longitude, in which the outbreak occurs, corroborating the inferences made above. For the three pest control regimes, the initial coordinates alone explain 79.8 – 88.4% of the variation in TAW impact. The GAM plots of how the outbreak point would impact final NPV indicate the invasion 'hotspots', i.e. areas where surveillance is essential in the detection and control of invasions, and show that the centre of the region is the most sensitive area (figure 6.9). This is valid for both *Bt* and conventional farmers, whereas the borders are the less sensitive areas. The results for the GAM model are shown in table 6.6.

Table 6.6 – GAM results for the hot-spot map for actual Aragonese land use, when insecticides are used in both *Bt* and conventional maize.

Model: $\boldsymbol{log}\ (\boldsymbol{NPV.ha^{-1}}) = \boldsymbol{s(x,y)}$ Family: gaussian ; Link function: identity

Parametric coefficients:

	estimate	Std. Error	T value	Pr(>|t|)
(Intercept)	9.2504616	0.0003385	27324	<2e-16 ***

Approximate significance of smooth terms:

	Edf	Red.df	F	p-value
$\boldsymbol{s(x,y)}$	27.24	28.81	24.17	<2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj): 0.876 ; Deviance explained: 91.1%

GCV score: 1.5778e-05; Scale est. = 1.1232e-05 ; n = 100

Invasive species are particularly difficult and expensive to control or eradicate, hence the importance of evaluating the most efficient management strategies. As discussed previously, prevention is usually more cost-effective than post-entry eradication or containment. It is also very important to avoid the dispersal and settlement of invasive species, which could bring devastating and irreversible consequences. A model that can predict the rate and direction of spread and its economic impacts, such as the one developed here, may assist government agencies and environmental authorities to design effective monitoring and control measures. In situ investments to limit the size and spread of the invasive population could be activated and efficiently directed taking the predicted spread into consideration. A surveillance effort, focussing on the area highlighted in figure 6.9, should be carried out when long-term costs of damage and/or control exceed short-term costs of successful policy. Although it is difficult to quantify how much the government should invest, recommendations could be based on the difference between the total loss results of scenario 1 and 2. If the spread is not efficiently controlled, the whole region would lose about €255M in 25 years, not considering the environmental damage accrued from increased spraying frequency.

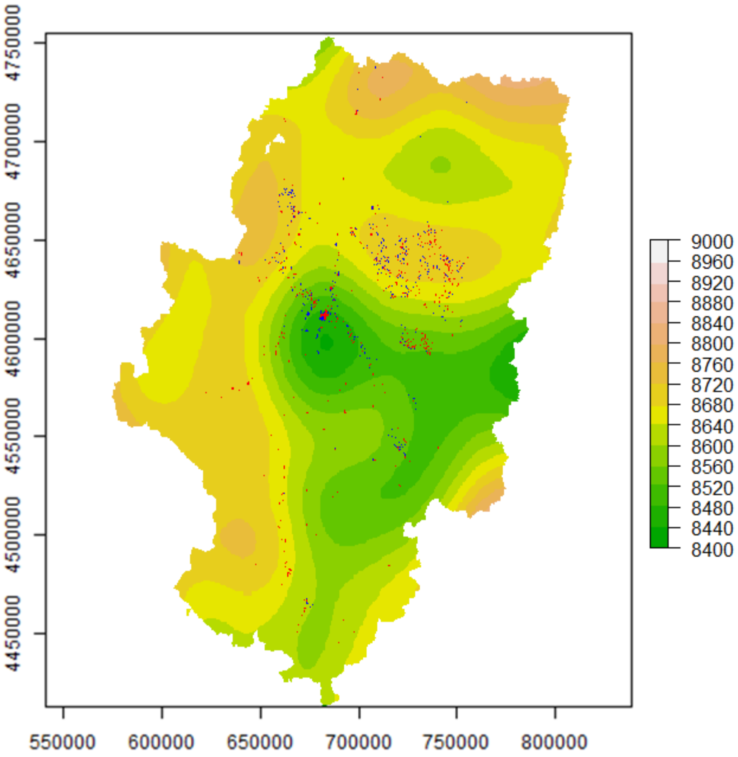

Figure 6.9 – Hot-spot map for the NPV after 25 years indicating the most sensitive areas, when insecticides are used in both *Bt* and conventional maize. The red and blue colours indicate the location of *Bt* and conventional fields, respectively. The resolution of the map is 500 x 500m.

6.8.2 Scenario 2) Spread of TAW from an invasion hot-spot area altering the conventional/*Bt* maize proportion

Four different conventional/*Bt* maize proportions were modelled in order to assess the influence and importance of spatial distribution and ratio of *Bt*/conventional maize to spread process, insecticide use and subsequent economic impact. The results are compared with the original maize spatial distribution when insecticides are applied in both *Bt* and conventional maize fields whenever the pests reach the ET[49]. These four additional cases complement the spatial economic analysis of TAW invasion. The results are shown in table 6.7.

The ratio conventional/*Bt* maize has a preponderant effect on the results. The economic and environmental (by reducing the necessity of insecticide) benefits of expanding *Bt* maize in Aragon are evident. The higher the area with *Bt* farming, the higher the profits. Intensifying the *Bt* cropping area by 50% would bring an extra €36M to the region after 25 years. Most importantly, it would on average reduce insecticide application by 64.5%. If farmers ceased to grow *Bt* maize, the whole region would lose approximately €109M in 25 years while increasing insecticide expenditure by more than double. Regarding the spread process, no major correlation was found between the invaded area (or the RRI) and the ratioes of the two maize varieties.

Although the economic benefits of using *Bt* maize are clear, it should be noted that planting the agricultural landscape with GEIR maize monocultures should be undertaken with caution. The simplification of cropping systems would lead to an increase in genetic uniformity of agroecosystems with subsequent negative ecological implications, such as an increase in vulnerability to pathogens or pests (Altieri 1999). Recent literature highlights that the widespread use of GEIR crops could generate great environmental changes, such as the appearance of new pests or the outbreak of pests previously controlled (Catarino et al. 2015). Hence, research on GEIR crops must take a steps to avoid the same problems that agriculture faces with the use of pesticides.

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[49] The optimal pest control regime, i.e. where famers' obtain a higher NPV

Table 6.7 – Comparison (in %) between the results accrued from TAW invasion with real Aragon land-use and four different conventional/*Bt* proportions.

	RRI (km.year^{-2})	Total area invaded (km^2)	NPV (M euros)			Economic loss to pests (M euros)			Expenditure in insecticides (M euros)			Total loss (M euros)		
			Conv	*Bt*	Total	Conv	*Bt*	Total	Conv	*Bt*	Total	Conv	*Bt*	Total
Real	3,6	24939	9214	11256	10437	28	14	42,6	18,3	1,3	19,6	46,3	15,9	62,2
100% conv	-4,7%	-8,9%			-19,5%			170,5%			122,0%			154,7%
- 50% *Bt*	6.6%	21,8%	-0,6%	-0,5%	-6,4%	86,5%	-40,3%	43,0%	65,8%	8,9%	62,3%	78,0%	-36,3%	49,3%
+ 50% *Bt*	-5,4%	-10,6%	0,6%	0,5%	6,4%	-75,2%	43,0%	-34,7%	-76,2%	110,1%	-64,5%	-75,6%	48,4%	-44,4%
100% *Bt*	-5,3%	-10,2%			8,3%			-45,2%			-91,3%			-60,2%

6.8.3 Scenario 3) TAW spread is endemic throughout the region

This scenario evaluated the economic implications of an extreme but possible situation, i.e. TAW becoming endemic throughout the region. This scenario may arise either from a different dispersal mechanism as shown before (section 6.3), or due to failure in controlling the invasive pest spread. It is assumed that at time zero, TAW is present in all fields where its reproduction is possible with density per hectare equivalent to its ET in maize (figure 6.5). The challenge of detecting a recently established invasive pest is central to efficient control. There are numerous examples of invasive species that escaped early detection and became so abundant and widespread that containment and eradication were no longer possible (Myers et al. 1998). As seen in the first scenario, after 25 years it is possible to find at least one individual per hectare throughout the region. Hence it is to be expected that if a longer timeframe were considered, the TAW's regional population density would be higher. Lastly, in the other scenarios only one point of introduction was considered, but it is reasonable to expect that several entry points may exist within a given period. In any situation, the outcomes would be utterly different, as shown below.

The results comparing the impact of TAW invasion and TAW being a widespread species in Aragon are presented in table 4.10. Clearly, if TAW becomes widespread throughout the region, the environmental and economic impacts will be severe. In this situation, *Bt* farmers increase their insecticide application more than fivefold. However even doing so, in line with the aggregated total NPV for Aragon, *Bt* farmers' NPV after 25 years is reduced by more than a third. Actually, the loss percentage on *Bt* maize is greater than on conventional maize (table 6.8). It is evident that the optimal insecticide path calculated in chapter five should be taken with care.

As seen in figure 6.10 the number of optimal annual insecticide applications, for both *Bt* and conventional maize systems, is not sufficient to control the invasive species. Since TAW is not susceptible to the Cry1Ab toxin, the use of this maize variety would become less effective as a pest control management practice in this region. This situation is a result of TAW's high flying capacity. Hendrix and Showers (1992) showed that TAW could travel at least 1300 km from Texas to Iowa during northward migration in spring. The surrounding fields act as a constant source of this pest, making its control difficult. *Bt* farmers would need to either increase their insecticide applications once again or adopt another GEIR maize variety capable of controlling the invasive species. Not considering public and political aspects of *Bt* adoption[50], the latter solution remains highly debatable.

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[50] Presently, only *Bt* maize Cry1Ab is allowed in Europe (see Meissle et al. 2011, Masip et al. 2013 for a general discussion)

Table 6.8 – Comparison (in %) between the impact of TAW invasion and TAW being a settled species in Aragon, considering the three pest management regimes (PMR).

	PMR 1*		
	Conv	*Bt*	Total
Actual NPV Aragon	-31,2%	-34,9%	-33,6%
Aragon pest total loss	320,1%	963,3%	540,5%
Insecticide application per ha	0,0%	501,5%	150,5%
Aragon insecticide total cost	0,0%	495,7%	126,3%
Aragon total losses	233,1%	923,8%	409,8%
	PMR 2**		
	Conv	*Bt*	Total
Actual NPV Aragon	-33,2%	-36,9%	-35,6%
Aragon pest total loss	318,5%	902,0%	526,4%
Insecticide application per ha	0,0%		0,0%
Aragon insecticide total cost	0,0%		0,0%
Aragon total losses	235,1%	904,4%	405,6%
	PMR 3***		
	Conv	*Bt*	Total
Actual NPV Aragon	-58,4%	-37,4%	-42,2%
Aragon pest total loss	151,5%	725,3%	237,8%
Insecticide application per ha	0,0%		0,0%
Aragon insecticide total cost	0,0%		0,0%
Aragon total losses	151,5%	726,4%	237,7%

* Insecticides in both *Bt* and Conventional maize

** Insecticides only Conventional maize

*** No insecticide applications

As outlined by Catarino et al. (2015), the use of such a specific pest control strategy may bring highly complex changes to agro ecosystems. *Bt* maize could open a route for the spread of new species that are not susceptible to a particular *Bt* toxin. It should be noted that this “new species” may be introduced from the exterior, as a typical invasive species; or a native species that, prior to *Bt* adoption, was effectively controlled by either competition from other species or by a large amount of insecticide use. As seen in section 6.3, Allee effects play a preponderant role in species spread, hence allowing pest that is not susceptible to increase their density to numbers large enough to sustain an efficient spread, which could have devastating results. In fact, the employment of *Bt* maize is only advantageous if the invasion is controlled in time. Otherwise, the benefits of using *Bt* maize, namely the high reduction in insecticide use, could be eroded.

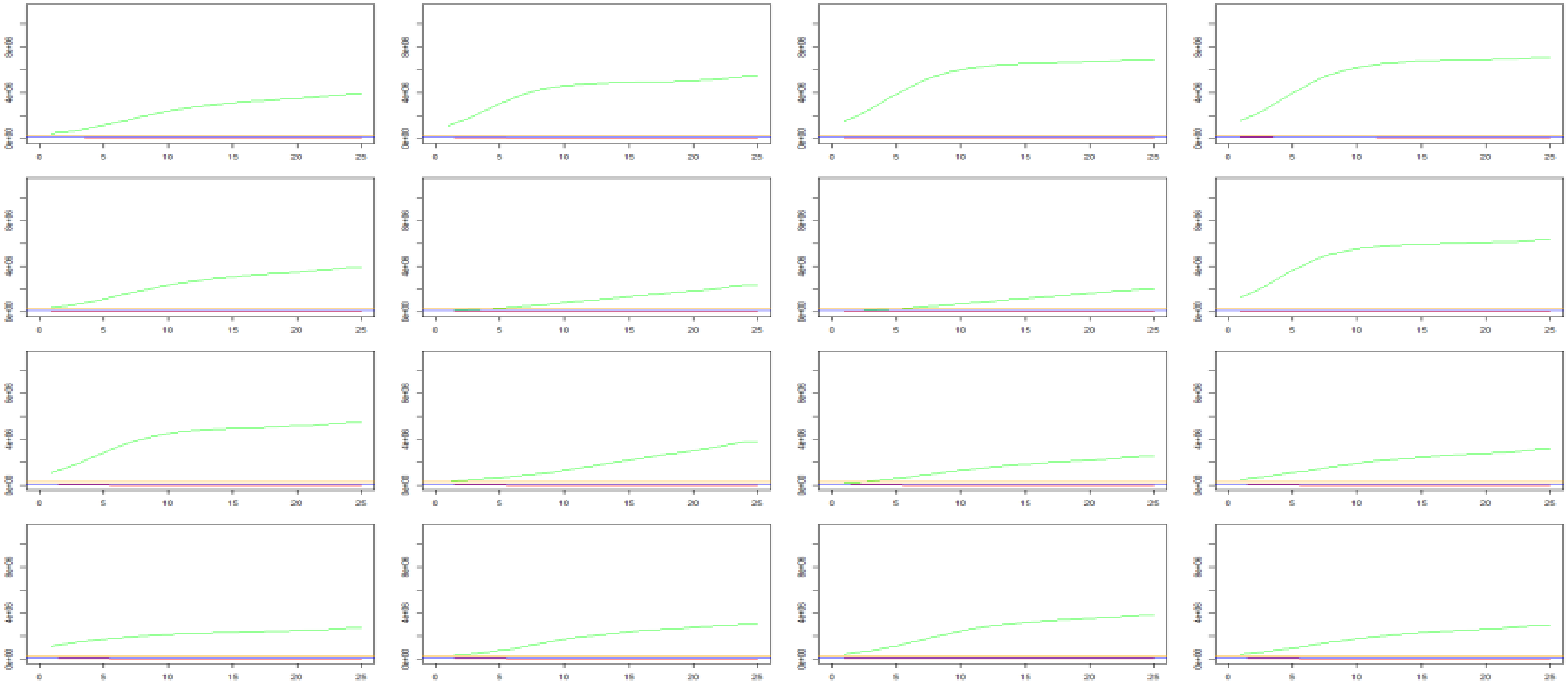

Figure 6.10 – 12 examples of the dynamics along 25 years of MCB (in red) and TAW (in green) in the case that TAW became a settled species in Aragon, when insecticides are used in both *Bt* and conventional maize. Each image represents one *Bt* field.

6.9 Conclusion

According to the results, from an economic and environmental perspective, the use of *Bt* maize can be advantageous at both an individual and regional level. The use of *Bt* maize, which expresses the toxin throughout the whole plant and across the cropping season is directly responsible for the decrease in insecticide use by efficiently eliminating MCB[51]. Furthermore, it was showed that the use *Bt* maize may reduce the presence of MCB not only in *Bt* maize fields but also in conventional maize fields. This extrinsic positive effect was not quantified here, but it is important to draw comprehensive picture regarding the cost-benefits assessment *Bt* maize production. Several studies have already shown this positive feedback mechanism on the control of the target pest (Wu et al. 2008, Hutchison et al. 2010). Reducing insecticide applications will consequently reduce the chemical drift onto other crops, environmentally sensitive areas and impact on non-target organisms. Yet, these benefits will only be fully realised if TAW, i.e. the non-susceptible pest, is prevented from reaching endemic status. Early detection and prompt control are vital in avoiding this scenario, and hence to gain all the benefits of planting *Bt* maize.

However, as Wilson et al. (2005) showed, *Bt* maize farmers are usually significantly less active in scouting their maize fields for the presence of pests. If *Bt* maize farmers are not prepared to foresee an eventual appearance of a (new) pest that is not susceptible to the toxin, simply because the fields were not scouted as regularly as pre *Bt*-adoption (Wilson et al. 2005), it could create a temporal frame large enough to let populations number to increase and spread throughout the region. The large majority of invasive insect pests, even those that are already established in a particular area, continue to spread actively into new areas exhibiting non-equilibrium population dynamics (Paini et al. 2010).

Analysis of the RRI should be taken with caution, since there may exist a time lag between the arrival of the species to the field and the actual detection (Kowarik 1995, Solow and Costello 2004). As emphasized by many researchers (Liebhold and Tobin 2008, Jarrad et al. 2011), here it is shown that surveillance and early detection play a critical role in the management of biological invasions. If they escape early detection, or if early detection mechanisms are not in place, the invasive species may continue to thrive, becoming so abundant and widespread that containment and eradication may no longer be possible. This situation would bring a loss of about €255M in 25 years, this value is the equivalent of 31% component of Aragon GDP[52].

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[51] Chemical control of MCB and other borers is made difficult for two reasons: firstly the larvae feeds deep inside plant whorls and stalks where they are protected from insecticides; and secondly, farmers are not concerned with overlapping of pest generations, which usually require the need to have specialised spraying equipment to enter into fields, particularly when conditions (weather or crop stage) are unsuitable for aerial application. See section 3.3.1 for further insights

[52] taking in consideration an annual discount rate of 5%

Hence, in a case such as the one presented in this research, it is suggested that a surveillance effort policy, focusing on the area highlighted in figure 6.9, should be carried out in order to avoid these long-term costs.

In this modelling exercise it was assumed that no communication existed between farmers. Farmers are not aware of what occurs in their neighbouring area outside their fields. In other words, farmers have no perception on how likely or how close their fields are to be invaded until they are effectively invaded. In reality, farmers' decision on whether to control a pest is frequently grounded on the perceived threat of the pest in the vicinity of their fields and the guidance of governmental entities or commercial advisors (Milne et al. 2015). Farmers in the same region are often influenced by similar circumstances, hence if an active communication system is in place, it could create a coordinated response for pest control that is effective at a landscape scale (Röling 1994, Larson et al. 2011). That is, if one farmer notices the problem, other farmers near by could start preventive measures.

Successful invasive species management programs are clearly subject to the capacity of farmers, stakeholders and agencies to recognise, detect and report new incursions (Maguire 2004). This can be achieved by putting in place or enhancing the existing community surveillance networks (Callaham Jr et al. 2006, Lodge et al. 2006). The government itself could ask land managers to adopt quarantine measures or to carry out detection campaigns and legislated control measures. Although prevention may be cost intensive, the benefits are likely to outweigh the costs, particularly for highly mobile and resource generalist species such as TAW.

It is important to note that besides the economic impact and increase in insecticide applications, the invasive species might have several other negative effects with possible trophic cascading effects, such as their influence on other species (natural enemies) or as a vector of new diseases. As these effects cannot be adequately predicted, this is a very sensitive situation surrounded by a high level of uncertainty regarding the expected magnitude of impact. It ought to be particularly stressed that further research using the methodology developed here should address the following three points:

i) to perform a spatial NPV optimization taking in consideration insecticide application for each cell where maize is cultivated;

ii) to find the best integration of control methods, such as biological (e.g. natural enemies), cultural (e.g. barrier zones) and chemical (insecticides), in order to stop, slow, or reverse spread;

iii) to include weather data in the model, which will certainly influence insect growth, hence the spread rate; and,

iv) since spread is a species-specific phenomenon, optimal management of bio-invasion strategies are likely to vary among different species, the model should be calibrated and used for other cases in which data is available, including situations with long-distance dispersal events

6.10 Summary

This chapter provided a general review of economic assessment and modelling of biological invasions. Building on the information gathered, a BeSEP model based on a reaction-diffusion system was developed. The BeSEP model integrates species' spatial dynamics with the bio-economic model developed in chapter five. The analysis focused on the economic impact for maize farmers' of the spread of an invasive species under different control strategies based on optimal insecticide applications, as estimated in chapter five. The general results suggest that, from an economic and environmental viewpoint, the use of *Bt* maize can be beneficial. However, these benefits will only be fully attained if the non-susceptible pest does not reach endemic status. It was showed that particular attention should be given to the connectivity of favourable habitats, i.e. landscape structure, which critically affects population spread magnitude. Successful invasive species management programs, such as an efficient community surveillance networks, early detection and prompt control are highlighted as crucial in avoiding a situation in which containment and/or eradication is no longer possible. The following and final chapter critically discusses the findings of the thesis including the implications for famers, stakeholders and policy makers. Recommendations for technology companies, research institutes, farmers and policy makers are provided based on the thesis' findings.

CHAPTER 7. FINAL DISCUSSION AND CONCLUSION

7.1 Chapter introduction

The goal of this last chapter is to discuss the findings of the thesis critically with respect to the thesis' research questions. This thesis builds on and extends a topic that has, until now, received only limited attention: the secondary impacts of genetically engineered insect resistant (GEIR) crops on the agroecosystem, economic returns to farmers and insecticide use. The main aim of this research was to provide further insights into the debate and to deliver a tool that can help policy makers and researchers to evaluate the economics of GEIR crops deployment effectively, while taking the ecological side of the problem into consideration. The case study focuses on the evaluation of the adoption impact of *Bt* maize containing the transformation event expressing Cry1Ab *Bt* toxin in Spain. The motivation behind this choice is straightforward: *Bt* Cry1Ab maize is the only event which is allowed to be cropped within the European Union (EU) (EFSA 2010c), and Spain is by far the largest adopter.

The chapter is structured as follows: in section 7.2, the main findings of the thesis are summarised; section 7.3 specifically answers the research questions as outlined in section 1.3; section 7.4 outlines the main noteworthy recommendations for the relevant players in pest management; and section 7.5 finishes the chapter and thesis with the principal outstanding question to be investigated in future research as well as the limitations of the current thesis.

7.2 Summary of research activities

The core of the thesis is divided into four main research components. The first component, comprising chapters two and three, reviews the general literature and provides a contextualization of the study. In chapter two, the underlying theory, principles and literature that support this research are described. Special importance is given to the issue of secondary pests in the context of GEIR crops. In chapter three, the regional study context as well as the surrogate species are introduced. Here, the reasons behind the low transgenic crop adoption in Europe when compared with the rest of the world are also explicated, and the reasons that Spanish farmers have quickly adopted *Bt* maize.

The second component, chapter four, introduces the issues that form part of the controversy behind the adoption of GEIR crops and provides an extensive literature review on the mechanisms that may be responsible for a secondary pest outbreak in the context of GEIR. The following three main causes were raised and discussed: i) a reduction in broad-spectrum insecticide applications; ii) reduction of natural enemies, and iii) niche replacement. The lessons learned in this chapter were used to aid the development of the mathematical models in the following chapters.

In the third component, chapter five, a bio-economic model was developed to evaluate the interactions between primary and secondary insect populations and the impact of different management strategies on insecticide use and economic returns over time. The model follows the Lichtenberg and Zilberman (1986) approach in which pest interactions are incorporated into a production function and the damage-abating role of insecticide is taken into account explicitly in the production function. The farmers' net present value (NPV) after 25 years, in the various assessed scenarios, was determined considering the optimal insecticide intensity as a function of fix economic inputs, crop yields and pest dynamics.

The fourth and final research component, chapter six, expanded the bio-economic model previously developed to include the spatial features of the Aragon region, Spain, and of both species. The insect spatial dynamics element was modelled using a coupled reaction-diffusion system. This chapter evaluated the economic impact on maize farmers due to the spread of an invasive species according to different hypothesis and under different control strategies in the region of Aragon. Additionally, a number of insights into the pest's physical spread and advances in methods of predicting the invasive species' potential distributions and the area upon which pest control should focus were put forward. These three main chapters were formulated to provide the relevant answers to the research question, which will be answered in the following section.

7.3 Consideration of the research questions

1) *<u>What are the main causes involved in a secondary pest outbreak in the context of GEIR crops?</u>*

The first research question concerned the understanding of the main causes involved in a secondary pest outbreak (SPO) in the context of GEIR crops, the core of chapter four. To contextualize, SPO refers to the emergence of a pest other than that originally targeted by an agricultural intervention, in this case the toxin expressed by *Bt* maize, and can be seen as "replacement" for the primary pest (Metcalf 1980, Hardin et al. 1995). It was hypothesised here that the secondary pest problem may become more relevant within the context of GEIR due to the high specificity and constant spatial and temporal toxicity expressed throughout the cropping season. Three main drivers for this event were identified and can be summarised as:

i. a reduction in broad-spectrum insecticide applications. The alleviation in insecticide applications could result in an uprising of pests that are immune to the expressed toxin. In such a situation further (insecticide) treatments would be necessary in *Bt* crop fields. As an example, following the introduction of *Bt* cotton, farmers' in China reported increased economic returns due to reductions of insecticides applications, ranging from 40-60% as compared with non-adopters. However, within the space of approximately ten years the insects once considered of minor relevance became a major concern for farmer;
ii. A decline in natural enemy populations. Although it is generally accepted that GEIR crops cause less impact on NE compared with insecticides (Cattaneo et al. 2006, Marvier et al. 2007), some studies show a contrary effect (Lövei and Arpaia 2005, Lövei et al. 2009, Lang and Otto 2010). The

impact of *Bt* toxins on natural enemies can have direct effects, due to the ingestion of the toxin, and/or indirect effects, due to reductions in prey/host population numbers or nutritional quality;

iii. The niche replacement hypothesis, while ostensibly making sense from an ecological point of view, still needs to be evaluated in more detail. Until now only a few studies have focussed on this problem (Catangui and Berg 2006, Dorhout and Rice 2010, Zeilinger et al. 2011). This situation could occur in cases where, prior to the pest management treatment, the primary pest is a dominant competitor species and the secondary pest is a weak competitor (Shivankar et al. 2007) and tolerant to the expressed toxin. Elimination of the primary pest would create a space for the outcompeted species to flourish. In chapter three it was demonstrated that this hypothesis is indeed likely to happen when two species with different susceptibility to the toxin are competing for the same resource.

2) *<u>What are the implications on insecticide use and related economic returns to farmers when Bt maize is adopted?</u>*

Overall, as shown in chapters five and six, the use of *Bt* maize is likely to provide higher returns to farmers while decreasing the burden of insecticide use. Optimizing the farmers' NPV after 25 years (chapter five), in conventional maize systems yielded to an average of 3.5 applications/year^{-1}/ha^{-1} to obtain a total NPV of 8500 €/ha. On the other hand, when *Bt* maize was used at the proposed adoption rate, the average optimal insecticide applications dropped by almost half while the final NPV increased by more than 20%. Similar results were reported by Carpenter (2010) and Areal et al. (2013). This substantive decline in insecticides and increase in profits is associated with the use of *Bt* and its efficiency in controlling MCB. Based on the indications of the non-spatial model results in chapter five, the primary pest would be eradicated after 14 years. This corresponds to the information reported by the Spanish government regarding the minimal presence of corn borers in *Bt* maize fields in Spain after a similar cultivation period (López 2014).

The average profit obtained by maize farmers is approximately 700€/ha, which is approximately the double of what was reported by the Aragon government for 2012 (López 2014). Hence it is possible that the economic return calculated has been overestimated. This difference may be due to two factors: i) in this study it is assumed that all farmers act optimally, which in reality does not happen; and ii) it is possible that the total costs were not properly estimated due to the complexity of maize production, for example no other pests were taken into consideration, hence insecticide expenditures may be higher.

3) *<u>What is the impact of a number of pest management options on primary and secondary pest populations?</u>*

The results from this thesis corroborate the hypothesis that although that *Bt* maize is a better option than conventional maize, with time the initial advantage of *Bt* technology may diminish due to the rise of secondary pests. Prior to *Bt* maize adoption the major concern, and the reason behind insecticide application, was the primary pest. After *Bt* adoption, the rise of the secondary pest lead farmers to return to insecticide applications. In chapter five it was shown that when insecticides are not applied in conventional maize, the farmer has no "knowledge" of the presence of the secondary pest since it is kept at low population levels by the effect of MCB competition pressure.

When no insecticides are re-applied, as is often the case with *Bt* maize, the secondary pest takes (in this study the TAW) advantage of its immunity to the expressed toxin and lack of competition from the primary pest (in this study the MCB) to become the main pest. In chapter six, the same situation is noted, while the average TAW numbers in conventional fields do not vary within the three pest control regimes, in *Bt* maize fields the prevalence of TAW is always higher when compared with conventional fields. Additionally it was shown that the reduction in insecticide use provides a safer environment for NEs to act upon pests, with positive impact on the farmers' final NPV.

4) <u>What are the regional economic implications for maize farmers in Aragon if the secondary pest (TAW) is an invasive species, considering the actual and different conventional/Bt maize proportion?</u>

In chapter six it was shown that, based on the invasion characteristics of TAW, the regional economic impact of TAW's invasion are not substantial, which is reflected in the famers' final insecticide expenditure and NPV after 25 years. This happens because not all maize fields are invaded in the course of the simulation period. Thus, allied with the efficient control of *Bt* maize against the primary pest, *Bt* farmers realise more than 2/3 of the total aggregated regional final NPV, €559M. Interestingly, the use of insecticides on *Bt* fields brings an extra 1% increase in the final conventional farmers' NPV. As Hutchison et al. (2010) found, *Bt* maize provides economic benefits for farmers who plant conventional maize in nearby fields. Since the overall population growth rate is intrinsically linked with population numbers, these results suggest that lessening the favourable area for a pest, i.e. decreasing the possible source of new individuals, makes general control more efficient.

The use of insecticides does not have a preponderant or sizeable effect on the adopters' economic returns. The high efficiency of *Bt* maize, even considering the primary pest dynamics at a spatial scale, is further noted in the total insecticide expenditure, while conventional maize farmers spend an average of €18M, *Bt* farmers spend only €1M over 25 years. However, it should be noted that pests still have a sizeable effect on farmers' net return. Farmers apply insecticides whenever pests reach the ET, i.e. to avoid reaching the level in which the marginal revenue of applying insecticides is null, the EIL. Even doing so, the average economic loss when combining pest damage with insecticide expenditure, is €63M (3/4 supported by farmers cropping conventional maize). This figure represents approximately 11% of the aggregated maize regional NPV.

The economic impact of promoting the adoption of *Bt* technology is evident. Promoting *Bt* maize adoption would increase the regional NPV after 25 years while reducing the need for insecticide applications. As before, these results are linked to the high efficiency of the *Bt* toxin towards MCB and the lower densities of the invasive pest. Intensifying the *Bt* cropping area by 50% would bring an extra €36M to maize farmers in Aragon, while reducing insecticide applications by 64.5%. Conversely, if farmers were to cease growing *Bt* maize, the whole region would lose approximately €109M in 25 years whilst more than doubling insecticide expenditure. However, it should be noted an agricultural landscape dominated by GEIR maize monocultures may itself be problematic for two reasons. Firstly, the simplification of cropping systems would lead to an increase in genetic uniformity of agroecosystems with subsequent negative ecological implications, such as an increase in vulnerability to pathogens or pests (Altieri 1999). Furthermore, the widespread of GEIR crops could generate great environmental changes, such as the appearance of new pests or the outbreak of pests previously under control.

5) *To what extent does non-spatial insecticide optimization provide a robust method for considering pests spatial dynamics?*

Considering the invasion scenario in Aragon, as outlined in chapter six, the results indicate that the insecticide path estimated in the optimization process is sufficient to control both pests. However, if TAW is endemic throughout the region the optimal insecticide regime is clearly not sufficient to control TAW, especially in *Bt* fields. The results suggest that adopting farmers would in this case return to insecticide applications at least at the level used in conventional maize systems. This happens because the secondary pest reaches such a density that the landscape surrounding maize fields acts as a continuous pest source. In such situations, secondary pest control is made difficult if not impossible. Since TAW can survive in a wide range of host plants and has a high flying capacity, this allows the species to easily prosper outside maize fields. This scenario is comparable with some secondary pest problems faced by countries such as China and India (Catarino et al. 2015). For example, in Chinese cotton production, insecticide applications dropped from about 20 applications per year to seven after *Bt* cotton was adopted (Huang et al. 2002b). However after just ten years, insecticide applications used to control the rise of secondary pests led to a situation where no major differences in the total quantity of insecticide applications are found between adopters and non-adopters (Lu et al. 2010, Zhao et al. 2011).

7.4 Model limitations

To sharpen the analysis and discussion of secondary pests in GEIR crops, the model assumptions were kept fairly simple and context specific. The model developed in this thesis has some limitations but is also capable of accommodating further extensions, discussed below, which could improve its performance and enable further investigations:

i) Life-stages: Discretizing the insect life cycle would better reflect different behaviours and environmental/resource dependence within each age class. For example, the damage and dispersal capacity of a larva is utterly distinct from that of a moth, while both are highly significant pests. This would also allow a distinction to be made between the different impacts of insecticides, Bt toxin and natural enemies throughout the pest life cycle. A further advantage of this approach is that it can easily be related to field or laboratory data.

ii) Temperature: The geographical distribution and lifecycle of insects (including risk of invasion) is affected by various factors, amongst which climate plays a significant role. Following the points raised in i), the effect of temperature on each age class would add further insights into winter survival, fecundity, number of generations annually and, ultimately, changes in crop/pest synchrony (Maiorano et al. 2014). Furthermore, this parameter would play an important role in assessing the effect of climate change on pests' temporal and spatial dynamics. The inclusion of temperature in the pest life-stages would be crucial in allowing exploration into the reasons why TAW or other secondary pest outbreaks are so unsystematic and spontaneous.

iii) Resistance: In this thesis, it is assumed that farmers follow the recommended 20% refuge area of conventional maize thus that pest resistance is managed efficiently. However, Tabashnik et al. (2013) recently noted an increase in documented cases of pest resistance across the world. Hence the inclusion of a genetic resistance model within population dynamics would be of great interest and importance (Gassmann et al. 2014).

iv) Time-scale and key economic parameters: In this study, only a long-run approach was considered, i.e. 25 years, in order to demonstrate clearly the dynamics of both species (especially relevant in the BeSEP model). From the farmer's perspective the expectation that a pest control strategy spanning 25 years will be implemented is highly unrealistic, while a time frame of three to five years is far more achievable. It is important to note that some parameters are likely to change over time, such as prices, and these changes could be endogenous. Lastly, in this study, a discount rate of 5% per year was assumed, which may indeed be a small value compared with reality. It is possible that due to the typical risk averseness' of farmers, the discount rate could be higher. Hence, a systematic sensitivity analysis of these key parameters would bring further important insights into farmers' optimal pest management strategy.

Bt maize and other GE crops are cropped in varied geographic locations across the globe. For example, South Africa planted 2.7 million hectares of GE maize, soybean, and cotton in 2014. Differences in location will present complex systems with different biological characteristics (such as pest species, landscape, climate conditions and management). Incorporation of the variables described above will allow the circumstances under which secondary pests occur to be explored effectively for a wider range of taxa and locations, to ensure that effective pest management protocols are designed and implemented. Therefore, this model is put forward as a prototype and a guide for the development of more specific models for the management of particular pest populations in specific edaphoclimatic conditions.

7.5 Concluding Remarks

The results of this research are of major importance for the European Union agricultural sector. Maize is, after wheat, the second most important crop in EU agriculture. In 2014, the EU-28 grew more than 15 million hectares[53], less than 1% of which is *Bt* maize (EUROSTAT 2015). The future possibilities for the expansion for *Bt* maize (and/or other GE crops) are considerable. It is likely that wider adoption would, according to the results of this thesis, bring financial benefits to farmers and potentially to society in general by alleviating the pressure of insecticides. Given a typical profit maximizing farmer, the use of *Bt* maize together with insecticides (at a lower rate) leads to lower crop losses and higher gross profit, in line with data reported in recent studies (e.g. Gomez-Barbero et al. 2008, Meissle et al. 2010, Areal et al. 2013). However, adopting farmers need to be aware of the possible eventual invasion of (new) pests that are not susceptible to the toxin. If such rises in secondary pests are not identified and dealt with at an early stage, then populations of secondary pests could become established and expand beyond the ET and spread throughout the region. This research suggests that this would have a severe economic impact even if insecticides are applied. The results also suggest that damage to crops from SPs can increase with the expansion of *Bt* technology if no additional measures – such as insecticide applications or stacked traits – are taken.

The interdisciplinary nature of this research in linking three important research fields, economics, new technologies in agriculture and ecology, has been challenging. As far as the author is aware the model developed here is unique in scientific literature. A new bio-economic spatially explicit population model based on reaction-diffusion theory was successfully developed. It allows for the investigation of the spatial population dynamics of two pests at landscape level taking biological factors into account (e.g. natural enemies and pest competition) and agricultural landscape structure with an integrated pest. The BeSEP model is highly flexible and generic, so it could be adapted and used for other species, cropping systems and/or regions, simply by changing the relevant parameters. The outputs from the model can assist not only the

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[53] 60% (9.4 million ha) is harvested as grain and 40% (5.9 million ha) as silage

bodies responsible for pest management, including the spread of invasive species, but also the future assessment of GE crops viability. Furthermore, by incorporating temperature (as recommended above), it can assist climate change studies by projecting the movement of pests into previously climatically hostile areas as climate and weather patterns change.

The methodology developed here offers a basis for continued research into dispersal simulation across heterogeneous landscapes. The research illustrates the usefulness of applying BeSEP models in agricultural assessments, particularly in the case of insect pest management strategies. The model code was written in an open source software (R-Core-Team 2012), so future work can be easily performed with researchers from diverse disciplinary fields collaborating. Based on the research undertaken here several recommendations for the relevant stakeholders involved in the pest management are made in the next section.

7.6 Recommendations

This subsection provides some of the most relevant recommendations for technology companies, research institutes, farmers and policy makers. Effective assessment of the secondary impacts of GEIR crops will require answers to a number of outstanding questions. Empirical research should investigate the circumstances under which secondary pests occur for a wide range of taxa, so that effective pest management protocols are designed. Furthermore, cooperation between all bodies involved in this issue is essential to the effective preservation of beneficial populations, ecosystem services and processes within (agro-)ecosystems. Hence, the following recommendations are given:

For technology companies and research institutions:

1) Consider the implementation of large-scale, multi-trophic and multi-species field studies in order to reveal potential impacts on ecosystems and their extent, i.e. in relation to Post Market Environmental Monitoring (PMEM). Additionally, such monitoring should now consider stacked events expressing several *Bt* toxins. Although these crop varieties could temporarily mitigate the issue of secondary pests, they may potentially bring faster changes in ecosystems processes, affecting the resilience of the systems;
2) A change in the baseline studies, i.e. the vast majority of the research conducted here assessing the impact of GEIR in comparison with broad-spectrum insecticides applications. Moving forward, the focus should be on comparing GEIR cropping systems not only with conventional systems but also with (for example) organic farming. Additionally research should move towards a wider approach, taking into consideration farmers' heterogeneity, i.e. including important social aspects such as education, institutional roles, etc; The importance of this has been recognised by the recent establishment of the European Socio-Economic Bureau (ESEB) (Devos et al. 2014);

3) Build on the work of AMIGA to provide a robust spatiotemporal database of insect species according to their ecological functions and occurrence in specific receiving environments;

4) To further validate and use the BeSEP model, taking in consideration the following points:

  a. Discretization of insect life-stages;
  b. Inclusion of a population genetics model which embodies the factors affecting pest resistance evolution management;
  c. Insertion of temperature within the insect life-stages;
  d. Carrying out spatial optimization insecticide applications at a regional and/or farmer level.

For farmers and land managers:

1) Constant field surveillance is essential to minimize the costs of both the production damage associated with implementing a secondary pest control tactic. Without effective surveillance, pests can reach such numbers that their control and/or eradication will become simply unviable;

2) Implementation of general surveillance networks within the most susceptible areas. For such cooperation between the relevant national agricultural authorities, risk assessors, regulators and famers is essential. Sustainable and efficient management of secondary pests must a collective objective and not an individual one; and,

3) Diffusion of information and strategic communication with and within the farming community. This will allow the identification of the invasive pathways at an early stage of introduction/outbreak of secondary pests and implementing, hence farmers' preventive control can be effectively undertaken. Certainly the quality, relevance and accessibility of information would play a key factor in assisting the rapid control of a new pest incursion.

For policy makers:

1) Increase the capacity of farmers and stakeholders to recognise, detect and report new incursions. This could be achieved with the enforcement of an effective educational system;

2) Ensure that a surveillance network is implemented and actively maintained for high risk areas and species. The implementation of a clear and comprehensible platform of communication between the scientific communities, farmers and the general public is indispensible;

3) Based on the information gathered, develop and implement appropriate surveillance, eradication or containment programs for new incursions;

4) Review the legal restrictions for long-term field studies for research purposes. The only way for pest management strategies to thrive, with a technology that can offer so many benefits, is to provide clear-cut evidence of how to achieve these advantages and to mitigate its alleged limitations. Hence, it

is essential that field experiments over prolonged periods of time (within a reasonable scope) are conducted.

7.7 Outstanding questions

The model developed in this thesis has some limitations but also is capable of accommodating further extensions which could improve its performance qualities and enable further investigations, as briefly mentioned in the previous section. At the landscape level, several other questions arise. It would be very interesting to validate and test the present model with accurate field data. In other words, here the model was used as an ex-ante assessment. The question posed now is whether the model can be further strengthened by use in ex-post analysis of an invasive species in the context of GEIR crops? If the model results differ substantially, this could be the first step in understanding the reasoning behind TAW's dynamics. Time and space have not permitted the investigation of certain pertinent questions. Here is a list of four future research questions arising from this research that may be worthy of further investigation:

i) How would the insecticide applications vary when optimizing the final NPV at a spatial level?
ii) Is it more profitable/efficient to optimize insecticide applications at a regional, provincial or farm level?
iii) What is the specific influence of landscape structure on pest dispersal? Should *Bt* maize be clustered in a specific area? How would the landscape look if it was optimized to avoid a spread of a pest invasion?
iv) How important is the coordination of farmers' efforts regarding pest management in avoiding the costs associated with pest control? And,
v) How would the pest management strategies of other cropping systems influence maize farmers?

A range of other methodologies could be used when conducting spatial optimization, for example Bayesian network models (Hof and Bevers 2002, Guisan and Thuiller 2005). It has to be noted that investigation of each of these further recommendations will increase the complexity of the model, but will surely bring better insights into, and understanding of, the complex issues surrounding secondary pests in GEIR crops. Overall the thesis has flagged the growing importance of secondary pests in GE systems and provided a number of tools to investigate both the ecological dynamics of pest interactions in the context of GE and has given insights into the longer term implications of using *Bt* as a pest control mechanism.

CHAPTER 8. REFERENCES

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CHAPTER 9. APPENDIX 1 - MCB GROWTH RATE

Figure A1 - Scheme representing the MCB annual life cycle used to calculate the Mediterranean corn borer annual growth rate.

Table A1: Biological parameters used to calculate the Mediterranean corn borer annual growth rate.

	Coefficients	Values	References
1st generation	Larvae winter mortality	0.9	(Gillyboeuf et al. 1994)
	Larvae survival (L1)	0.74	(Fantinou et al. 1996)
	Pupae survival (P1)	0.8135	(Fantinou et al. 2003)
	Oviposition per moth (O1)	550	(Fantinou et al. 2004)
	Eggs hatch (E1)	0.6	(Gillyboeuf et al. 1994)
2nd generation	Larvae survival (L2)	0.74	(Fantinou et al. 1996)
	Pupae survival (P2)	0.88	(Fantinou et al. 2003)
	Oviposition per moth (O2)	375	(Fantinou et al. 2004)
	Eggs hatch (E2)	0.4	(Gillyboeuf et al. 1994)

9.1 MCB Annual growth rate:

Initial population (IL_0): 9×10^4 larvae

Year 1: $\mathrm{MCB}_{1,1} = \mathrm{IL}_0 \times \mathrm{L}_1 \times \mathrm{P}_1 \times \mathrm{O}_1 \times \mathrm{E}_1$

$\mathrm{MCB}_{1,2} = \mathrm{MCB}_{1,1} \times \mathrm{L}_2 \times \mathrm{P}_2 \times \mathrm{O}_2 \times \mathrm{E}_2 \times \mathrm{W}$

Year 2: $\mathrm{MCB}_{2,1} = \mathrm{MCB}_{1,4} \times \mathrm{L}_1 \times \mathrm{P}_1 \times \mathrm{O}_1 \times \mathrm{E}_1$

$\mathrm{MCB}_{2,2} = \mathrm{MCB}_{2,1} \times \mathrm{L}_2 \times \mathrm{P}_2 \times \mathrm{O}_2 \times \mathrm{E}_2 \times \mathrm{W}$

$$Annual\ growth\ rate = Log\left(\frac{MCB_{2,4}}{MCB_{1,4}}\right) = 2.024284$$

CHAPTER 10. APPENDIX – TAW GROWTH RATE

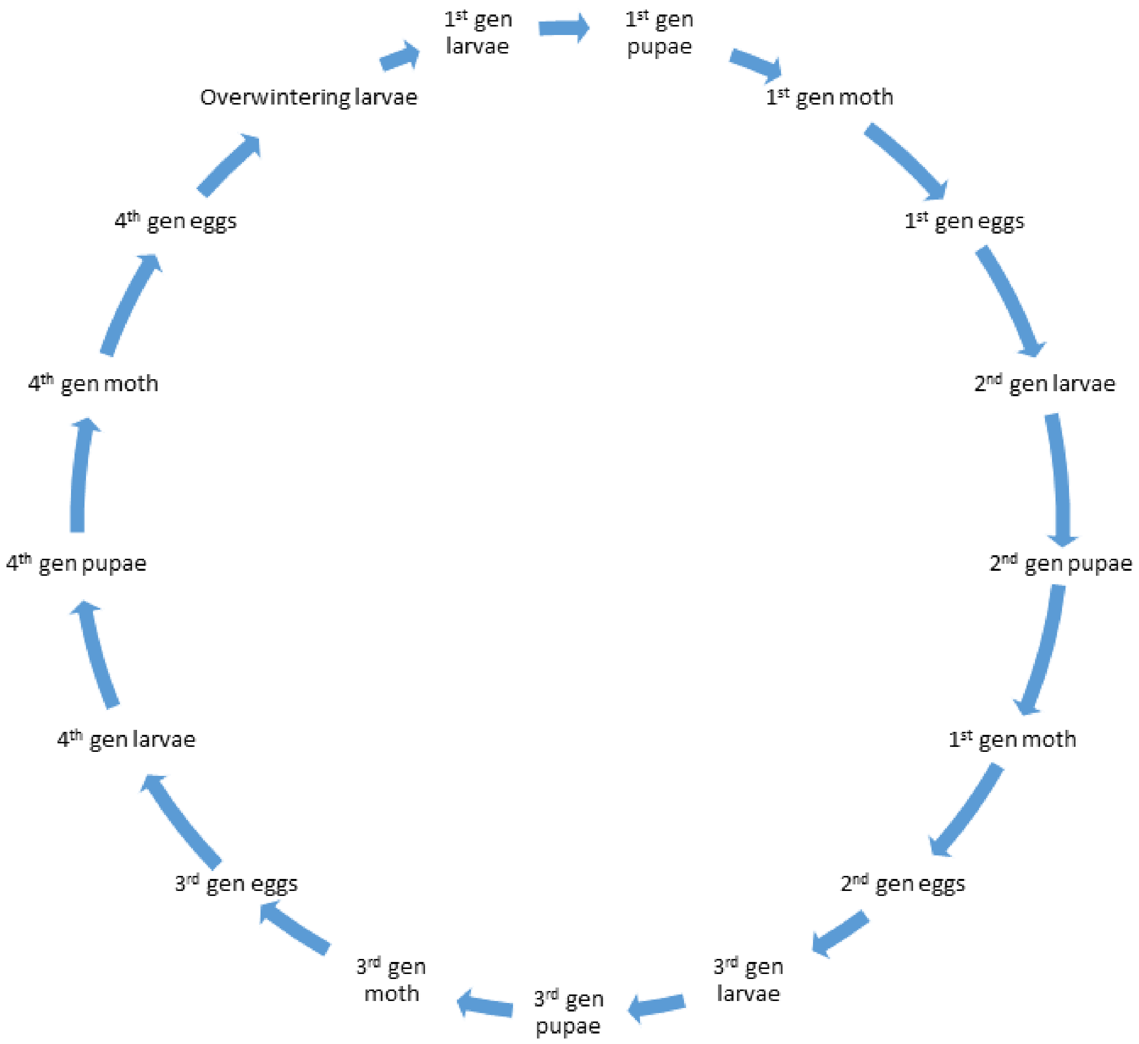

Figure A2 - Scheme representing the TAW annual life cycle used to calculate the Mediterranean corn borer annual growth rate.

Table A1: Biological parameters used to calculate the true armyworm annual growth rate.

	Coefficients	Values	References
1st generation	Larvae winter mortality (W)	0.9	(Naibo 1984)
	Larvae survival (L1)	0.66	(McDonald 1990)
	Pupae survival (P1)	0.93	(McDonald 1990)
	Oviposition per moth (O1)	1302	(Smith 1986)
	Eggs hatch (E1)	0.563	(Smith 1986)
2nd generation	Larvae survival (L2)	0.31	(McDonald 1990)
	Pupae survival (P2)	0.7	(McDonald 1990)
	Oviposition per moth (O2)	1393	(Smith 1986)
	Eggs hatch (E2)	0.953	(Smith 1986)
3rd generation	Larvae survival (L3)	0.93	(McDonald 1990)
	Pupae survival (P3)	0.78	(McDonald 1990)
	Oviposition per moth (O3)	1470	(Smith 1986)
	Eggs hatch (E3)	0.967	(Smith 1986)
4th generation	Larvae survival (L4)	0.53	(McDonald 1990)
	Pupae survival (P4)	0.89	(McDonald 1990)
	Oviposition per moth (O4)	1656	(Smith 1986)
	Eggs hatch (E4)	0.892	(Smith 1986)

10.1 TAW Annual growth rate:

Initial population (IL_0): 9×10^4 larvae

Year 1:

$$\begin{aligned}
\mathrm{TAW}_{1,1} &= \mathrm{IL}_0 \times \mathrm{L}_1 \times \mathrm{P}_1 \times \mathrm{O}_1 \times \mathrm{E}_1 \\
\mathrm{TAW}_{1,2} &= \mathrm{TAW}_{1,1} \times \mathrm{L}_2 \times \mathrm{P}_2 \times \mathrm{O}_2 \times \mathrm{E}_2 \\
\mathrm{TAW}_{1,3} &= \mathrm{TAW}_{1,2} \times \mathrm{L}_3 \times \mathrm{P}_3 \times \mathrm{O}_3 \times \mathrm{E}_3 \\
\mathrm{TAW}_{1,4} &= \mathrm{TAW}_{1,3} \times \mathrm{L}_4 \times \mathrm{P}_4 \times \mathrm{O}_4 \times \mathrm{E}_4 \times \mathrm{W}
\end{aligned}$$

Year 2:

$$\begin{aligned}
\mathrm{TAW}_{2,1} &= \mathrm{TAW}_{1,4} \times \mathrm{L}_1 \times \mathrm{P}_1 \times \mathrm{O}_1 \times \mathrm{E}_1 \\
\mathrm{TAW}_{2,2} &= \mathrm{TAW}_{2,1} \times \mathrm{L}_2 \times \mathrm{P}_2 \times \mathrm{O}_2 \times \mathrm{E}_2 \\
\mathrm{TAW}_{2,3} &= \mathrm{TAW}_{2,2} \times \mathrm{L}_3 \times \mathrm{P}_3 \times \mathrm{O}_3 \times \mathrm{E}_3 \\
\mathrm{TAW}_{2,4} &= \mathrm{TAW}_{2,3} \times \mathrm{L}_4 \times \mathrm{P}_4 \times \mathrm{O}_4 \times \mathrm{E}_4 \times \mathrm{W}
\end{aligned}$$

$$Annual\ growth\ rate = Log\left(\frac{TAW_{2,4}}{\mathrm{TAW}_{1,4}}\right) = 3.133519$$