



# *Spatially explicit economic effects of non-susceptible pests' invasion on Bt maize*

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1 Title: Spatially explicit economic effects of non-susceptible pests' invasion on *Bt* maize

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8 Running title: Spatial economics effects of pest invasion in *Bt*

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20

21        **Abstract**

22            Maize expressing the *Bacillus thuringiensis* Cry1Ab toxin (*Bt* maize) provides a more effective  
23 control of corn borers than the use of insecticides. Yet, the spatial expansion of *Bt* maize may offer ideal  
24 ecological conditions for the development and spread of secondary pests, i.e. pests not susceptible to the  
25 expressed toxin. This paper develops a bio-economic, spatially explicit population model to analyse the  
26 spread and economic consequences of a secondary pest outbreak. Results show that the present use and  
27 even an eventual expansion of *Bt* maize can be economically and environmentally advantageous, as it  
28 would decrease insecticide usage intensity. However, we show that caution is required when considering  
29 its widespread use. If a pest outbreak is not identified and dealt with at an early stage, it could lead to  
30 severe economic impacts even if insecticides are used in combination with the *Bt* maize. We further  
31 discuss potential policy and subsequent management strategies to address this issue.

32

33        **Keywords:** *Bacillus thuringiensis*; Spatially explicit; Bioeconomic model; *Bt* maize; Pest  
34 management; Population dynamics; Secondary pest.

35

36        **1. Introduction**

37            Commercialized genetically engineered insect resistant (GEIR) crops have provided economic  
38 and environmental benefits in relation to pest control (Areal et al., 2013; Areal and Riesgo, 2015).  
39 Presently, the only GEIR crop allowed for cultivation in the European Union (EU-28) is *Bt* (*Bacillus*  
40 *thuringiensis*) maize which contains the transformation event MON810 (Monsanto Company) and  
41 expresses *Bt* Cry1Ab toxin (Devos et al., 2014). The economic benefits associated with a significant  
42 decrease in insecticide application compared to the growth of conventional maize (Areal et al., 2013;  
43 Areal and Riesgo, 2015; Gómez-Barbero et al., 2008) are the main reason behind the rapid adoption of  
44 *Bt* maize among Spanish farmers (James, 2014). So far this technology has provided an efficient control  
45 of two primary pests, the Mediterranean Corn Borer, *Sesamia nonagrioides* Lefebvre (Lepidoptera:  
46 Noctuidae) and the European Corn Borer, *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae) (Farinos  
47 et al., 2011; González-Núñez et al., 2000). It was estimated that in European countries where *Bt* maize  
48 is not used yet (or where it is prohibited), farmers maybe foregoing benefits of between 157 to 334

49 million Euros per year (Park et al., 2011). Additionally, due to the high specificity and efficiency of *Bt*  
50 Cry toxins toward key target pest species, it is generally accepted that any eventual detrimental impact  
51 on non-target organisms is lower for *Bt* crops than for conventional crops treated with broad-spectrum  
52 insecticides (Meissle and Lang, 2005; Stephens et al., 2012). However, and regardless of their large-  
53 scale adoption (about 1% of the world's total maize hectareage (James, 2014)), GEIR crops remain a  
54 controversial technology dividing the scientific community (Kolseth et al., 2015; Lövei et al., 2009).  
55 This paper focuses on one aspect of the GEIR debate: regional economic impact (i.e. economic damage  
56 to the crop) of insect pests not susceptible to the expressed toxin of a genetically engineered (GE) crop,  
57 henceforth secondary pests, taking into account the landscape structure and farm pest management  
58 strategy.

59         The colonization of agro-ecological systems by pests is a well-established global issue that can  
60 lead to considerable economic and ecological damage (Pimentel et al., 2001). Pest species have diverse  
61 mechanisms of introduction and establishment within a new agroecosystem which are generally  
62 influenced by habitat suitability and anthropogenic activities (Liebhold et al., 2016). They may take  
63 opportunistic advantage of altered ecosystems and land-use patterns, such as the expansion of  
64 monocultures (Tilman, 1999). In this context, there are concerns that changes in cultural practices (e.g.  
65 conservation tillage and reduced insecticide use) due to the adoption of *Bt* maize might contribute to a  
66 change in species dynamics (Hutchison et al., 2010). For instance, insect species that are not susceptible  
67 to the expressed toxin can increase in number and develop into secondary pests, causing significant  
68 damage to the crop (Catarino et al., 2016, 2015). Two of the best-known cases related to GEIR maize  
69 cropping are the Western Bean Cutworm, *Striacosta albicosta* Smith (Lepidoptera: Noctuidae), a  
70 noctuid moth native to West and Central America (Eichenseer et al., 2008) and the Western Corn  
71 Rootworm, *Diabrotica virgifera* LeConte (Coleoptera: Chrysomelidae), native to South and Central  
72 America (He, 2002). These species are considered important secondary pests as they show low  
73 susceptibility to most transgenic maize events currently commercialized (Eichenseer et al., 2008). In the  
74 US and Canada the expansion of the western bean cutworm, which began in the mid 1990's, may be  
75 correlated with the introduction of transgenic maize (Dorhout and Rice, 2010; Lindroth et al., 2012).

76 Field trials have shown that transgenic crops expressing Cry1Ab and Cry9C toxins had larger  
77 populations of Western Bean Cutworm compared to conventional maize (Dorhout and Rice, 2010;  
78 Eichenseer et al., 2008; Lindroth et al., 2012). Researchers have recently suggested that a similar case  
79 could develop in Spain with an increase in True Armyworm populations, [*Mythimna (Pseudaletia)*  
80 *unipuncta* Haworth (Lepidoptera: Noctuidae)] (Pérez-Hedo et al., 2013, 2012), a pest capable of causing  
81 severe crop losses which is not susceptible to *Bt* Cry toxins. The increase of transgenic maize could  
82 affect the population dynamics of true armyworms due to the high efficiency of *Bt* maize against target  
83 pests (Eizaguirre et al., 2009; López et al., 2008).

84 Here we used a bio-economic spatially explicit population model to analyse the economic  
85 consequences of an outbreak of true armyworm, a possible secondary pest of maize in Spain. Dynamic  
86 bio-economic models that deal with the agro-economic impact of multiple insect pests (Aadland et al.,  
87 2014) or that estimate the removal costs of invasive species are not common in the literature (Jardine  
88 and Sanchirico, 2018). The research reported here builds on the model framework developed by Catarino  
89 et al (2016). Our analysis develops the existing bio-economic modelling literature by 1) incorporating  
90 spatial aspects (i.e. agricultural land use type); and 2) incorporating multi-pest species spatial interaction  
91 and spread. The flexible modelling approach presented here could be used for other pest species and in  
92 different regions. The methodology and results presented in the paper provide improved insights into  
93 pest spatial interrelations and their economic impact under different scenarios where *Bt* crops are grown.  
94 We provide recommendations for the development of policy/management strategies aimed at avoiding  
95 situations in which the eradication of the invading species is not feasible, as well as disclosing needs for  
96 further research.

97

## 98 **2. Methods**

99 The modelling framework from Catarino et al (2016) was adapted and expanded to incorporate  
100 spatial aspects, combining theories of movement ecology, population dynamics, statistics, and  
101 estimation of economic impacts and farmers' decisions. The model was used to analyse the economic  
102 impacts accrued from the spatial movement and spread of a primary pest, the Mediterranean corn borer,

103 and a secondary pest, the true armyworm, to maize farmers in Aragon, Spain. Both species are affected  
104 by abiotic, such as insecticides (Albajes et al., 2002), biotic factors, such as interspecific competition  
105 (Eizaguirre et al., 2009) and natural enemies (Alexandri and Tsitsipis, 1990; Eizaguirre and Pons, 2003),  
106 and the land-use effect (Eizaguirre and Fantinou, 2012; Menalled et al., 1999). The spatial model is  
107 developed in the context of the Aragon region in Spain using up-to-date landscape information, based  
108 on individually managed properties with a variety of uses. Each manager's control decisions (e.g.  
109 insecticide use and maize variety) indirectly impacts his/her neighbours' decisions, by affecting the  
110 spread of species across boundaries. It is assumed that farmers make control decisions based only on  
111 pest damage occurring on their own land (i.e. there is no publically or governmentally funded detection  
112 or control system) aiming to maximize their individual net present value (NPV) in the long-term (25  
113 years).

114

## 115 **2.1. Study context**

116 The only GE crop allowed for cultivation in Europe is *Bt* maize, which contains the transformation  
117 event MON810 (Monsanto Company), expressing Cry1Ab *Bt* toxin (Devos et al., 2014). Spain is by far  
118 the largest GE technology adopter, 92% of the total GE maize in the EU is grown there (James, 2014).  
119 Maize is the second most abundant crop in Spain on an area basis, exceeded only by wheat  
120 (MAGRAMA, 2013). In 2012, the areas of maize cultivated in the main maize-growing regions, Castile,  
121 Extremadura and Aragon were 105.061, 60.643 and 55.484 hectares respectively (MAGRAMA, 2013).  
122 In these areas, maize is almost entirely cropped in an intensive monoculture regime, which, allied with  
123 the Mediterranean climate conditions, favours the development of pests (Eizaguirre and Fantinou, 2012;  
124 Vasileiadis et al., 2011). The most worrying agents causing high control costs are corn borers and some  
125 secondary pests (Eizaguirre and Fantinou, 2012; Lopez et al., 2000). Traditionally these pests have been  
126 controlled by cultural practices and broad-spectrum insecticides (organophosphates and synthetic  
127 pyrethroids). The Aragon region is one of the 17 autonomous Spanish communities, is situated in the  
128 Ebro basin in north-eastern Spain with an area of 47.720 km<sup>2</sup>. Of the 55.484 hectares of maize planted  
129 in Aragon in 2012, 75% was *Bt* maize, representing a third of the total *Bt* maize produced in Spain

130 (James, 2014). The high adoption is likely to be due to the farmers' satisfaction with pest control and  
131 the general positive economic returns of the GE variety (Areal et al., 2013; Areal and Riesgo, 2015).

132

## 133 **2.2. The case study species**

134 There is broad consensus that the Mediterranean corn borer is one of the most important maize  
135 pest in countries around the Mediterranean basin, including Spain (Farinos et al., 2011; González-Núñez  
136 et al., 2000). In conventional maize cropping, Mediterranean corn borer control through the use of  
137 insecticides is only moderately effective since larval development occurs mainly inside the stalk  
138 (Albajes et al., 2002). Additionally, the expansion of maize production areas in monoculture system in  
139 the past decades (Eizaguirre and Fantinou, 2012) has also favoured its prevalence. In Spain, the true  
140 armyworm is considered to be an important secondary pest causing occasional but severe damage to  
141 maize (Eizaguirre et al., 2009; Pérez-Hedo et al., 2013, 2012). Attempts to analyse and predict true  
142 armyworm outbreaks have been constrained by the great capacity for flight of adults (moths), rapid  
143 reproduction rate, its explosive expansion and unpredictable behaviour (Hill and Atkins, 1982; Lopez et  
144 al., 2000). Additionally, under normal conditions the Mediterranean corn borer tends to outcompete the  
145 true armyworm (Eizaguirre et al., 2009). In this context, the increase of transgenic maize could affect  
146 the population dynamics of this secondary Lepidopteran pest due to the high efficiency of *Bt* maize  
147 against its target pests (López et al., 2008; Pérez-Hedo et al., 2012). True armyworms would be able to  
148 take advantage of the absence of major corn borers. These species are representative of the problem of  
149 secondary pest explored in this paper. Both species compete for the same food resource, maize, and the  
150 Mediterranean corn borer, although biologically more resilient than the true armyworm, is effectively  
151 controlled by *Bt* maize. For further information on both species description and relevance to maize  
152 production, the reader is directed to (Catarino et al., 2016).

153

## 154 **2.3. Modelling framework**

### 155 *2.3.1. Modelling scenarios*



156 The model developed requires knowledge of certain key economic and ecological parameters,  
157 namely flight and reproduction capacity parameters of pests, the geographic location and region of the  
158 maize fields and the economic maize production parameters for the base year of 2012 (Tables I and II).  
159 Five scenarios with different *Bt* maize adoption ratios are examined here. The first scenario (S1)  
160 represents the actual maize area for the year 2012. Scenario 1 is based on the actual proportions of areas  
161 of *Bt* and conventional maize and is evaluated under three different pest management strategies (PMS):  
162 PMS1, insecticides are used in both maize systems; PMS2, insecticides are only used in conventional  
163 maize, and; PMS3, no insecticides are used. The four other scenarios assume different *Bt*/conventional  
164 maize ratios to the areas recorded in 2012: S2, no *Bt* maize is cropped; S3, *Bt* maize area is reduced by  
165 50%; S4, *Bt* maize area is 50 % greater than recorded in 2012 and; S5, all cropped maize is *Bt* maize.  
166 Scenario 1 with PMS1 is used as the basis of comparison for the other scenarios.

167

### 168 2.3.2. Model simulations

169 The five different adoption scenarios were assessed in order to estimate the influence of *Bt* maize  
170 on the spread of a secondary pest and the consequent economic impacts for Aragon's maize farmers. A  
171 total of seven cases were analysed including the three PMSs of S1. To infer the influence of the  
172 landscape on the invasion process, each of the cases were simulated a 100 times. The simulations showed  
173 an acceptable convergence of the mean of the total producers' welfare losses and cumulative area  
174 invaded over 25 years (i.e. no significant difference was found in these values when the number of  
175 simulations was increased). The population of Mediterranean corn borers, as primary and endemic pest  
176 in Aragon, at  $T=0$  is considered to be 10% of its carrying capacity and present in all fields favourable to  
177 reproduction (Fig. 1a). It is assumed that true armyworms are introduced at a randomized location of  
178 favourable habitat, spreading to neighbouring cells. The initial population of the true armyworm  
179 population, i.e. at the moment of outbreak with  $T=0$ , is characterised by 2D 5x5 grid sized kernel (Fig.  
180 1b). The kernel represents the outbreak area: at the centre true armyworm's density is considered to be  
181 10% of its carrying capacity, and the surrounding cells follow a Cauchy distribution, usually used in the  
182 study of biological invasion (Kot et al., 1996), containing a proportion of individuals in relation to the

183 centre (Fig. 1b). After a local sensitivity analysis, no significance difference (using the Tukey HSD post-  
184 hoc test) was found between the different kernel sizes (3x3, 5x5, 7x7 and 9x9, simulated each case 25  
185 times for PMS1). Natural enemies for both species are present evenly throughout the landscape, being  
186 only affected by insecticide applications. In short, both species spread in all possible directions  
187 dependent on the local dynamics in each cell that are determined by the each species density, the  
188 landscape characteristics, natural enemies, pesticides applications and competition between and within  
189 species (see below local and spatial pest dynamics subheadings).

190 The parameters for the economic and ecological components of the model are presented in Table  
191 II. The model was written and numerically solved with R software (R Core Team, 2014) with support  
192 from the “deSolve” (Soetaert et al., 2015), “RcppDE” (Eddelbuettel, 2015), “Raster” (Hijmans, 2014)  
193 and “mgcv” packages (Simon Wood, 2016). The model was constructed as a reaction-diffusion system  
194 of two coupled partial differential equations, characterising the spatial population dynamics of the two  
195 pests. The reaction term describes the population growth and mortality at time  $t$ , and the diffusion term  
196 describes the spread of populations in space. The overall scheme use operator splitting between the  
197 reaction terms and the diffusion terms. The model was solved numerically by operator splitting, with  
198 the Runge-Kutta 4th order method solving the reaction term and the Alternating Direction Implicit  
199 scheme solving the diffusion term (as in Bourhis et al. (2015); see also Hundsdorfer and Verwer (2013)  
200 for details on those methods). The total area invaded (**TAI**) after  $T$  years represents the total colonized  
201 area at time  $T$ , i.e.  $TAI = \sum_{t=0}^T A_t$ . Where  $A_t$  is the colonized area at time  $t$ ,  $T$  is the length of the  
202 observation period.

203

### 204 2.3.3. *Aragon landscape*

205 The Aragon landscape is represented with a grid derived from an ASCII raster taken from the  
206 CORINE 2006 Land Cover dataset (Agency European Environment, 2010). Maize field data were  
207 directly obtained from the Aragon regional government statistics and explicitly incorporated in the  
208 CORINE map (Fig. 2a). The original regional landscape was aggregated for the relevant land cover  
209 types with a spatial resolution of  $500 \times 500$  m, i.e. 25 ha (Fig. 2b), composed of 11 different categories

210 (Table I). When aggregating the landscape fields, which was necessary for computation practicalities,  
 211 the total modelled maize area did not significantly differ from real data, only 4% of spatial maize  
 212 information was lost. The domain  $\Omega$  represents the whole simulation area,  $(\mathbf{x}, \mathbf{y}) \in \Omega$ , discretized as a  
 213  $483 \times 684$  ( $\Omega_x, \Omega_y$ ) matrix, from which 855 and 1279 cells are categorised as conventional ( $\Omega_{Conv}$ ) and *Bt*  
 214 maize ( $\Omega_{Bt}$ ), respectively. The effects of the spatial heterogeneity on each species influences survival  
 215 and movement. Based on expert knowledge and taking into consideration the resource availability, the  
 216 landscape was categorised into (see Table I): i) areas of favourable habitat, i.e. where the species can  
 217 reproduce, colonize and disperse; and ii) hostile habitat, where reproduction and dispersion are impeded.

218

### 219 2.3.4. The bio-economic spatially explicit population model

220 The final regional NPV after 25 years ( $NPV_{\Omega, T}$ ) accrued from maize production profits was  
 221 evaluated taking into consideration the implications of different pest management decisions over a time  
 222 interval  $[0, T]$ . We chose a long-term timeframe to allow pests to effectively disperse throughout the  
 223 space. The discount profit at time  $t$ , based on a discount rate of 5% ( $\delta$ ), results from the sum of the total  
 224 revenue ( $\Pi = pY(\mathbf{Z}, \mathbf{A})$ ) subject to the damage caused by both pests ( $\Lambda$ ), subtracting the costs of non-  
 225 insecticide inputs (i.e. labour, seeds, fertilizers etc.) and the insecticide costs, represented by  $p_m \mathbf{Z}$  and  
 226  $p_w \mathbf{W}$  respectively, per field. Thus, letting  $p_c$  denote output price,  $p_m$  the cost of conventional and of *Bt*  
 227 maize inputs unrelated to damage control ( $\mathbf{m} = \{\mathbf{Bt}, \mathbf{Conv}\}$ ),  $p_w$  the price of a unit of insecticide ( $\mathbf{w}$ ),  
 228 the bio-economic spatially explicit population model becomes:

229

$$NPV_{\Omega, T} = \left( \sum_{Conv=1}^{855} \Omega_{Conv} + \sum_{Bt=1}^{1279} \Omega_{Bt} \right) \int_0^T e^{-\delta t} \{p_c \Pi(\mathbf{Z}, \Lambda) - (p_m \mathbf{Z} + p_w \mathbf{W})\} dt \quad (1)$$

230

231 The damage-abating role of insecticide is taken into account explicitly in the production function,  
 232 through an asymmetric treatment of "productive" inputs ( $\mathbf{Z}$ ) and "damage-abating" insecticide ( $\mathbf{w}$ ),  $Y =$   
 233  $\Pi(\mathbf{Z}, \mathbf{A})$ , where  $Y$  is the actual output. The damage-abatement function,  $\mathbf{A}$ , represents the role of

234 insecticide in the model, which does not have the potential to increase the output but indirectly mitigates  
 235 yield losses through pest elimination.

236

### 237 *2.3.5. Local pest dynamics*

238 The local pest dynamics is based on a system of two first order differential equations that represent  
 239 the ecological interactions of both pests affected by the pest management practices and natural enemies:

$$\begin{cases} \frac{dN_1(t, x, y)}{dt} = r_1 N_1(t, x, y) \left[ 1 - b_{11} \frac{N_1(t, x, y)}{k_1} - b_{12} \frac{N_2(t, x, y)}{k_1} - e_1 - \delta q_1 - \phi h(w, t) \right] \\ \frac{dN_2(t, x, y)}{dt} = r_2 N_2(t, x, y) \left[ 1 - b_{22} \frac{N_2(t, x, y)}{k_2} - b_{21} \frac{N_1(t, x, y)}{k_2} - e_2 - \delta q_2 - \phi h(w, t) \right] \end{cases}$$

With:

(2)

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

$$\delta = \begin{cases} 0.8, & \text{Bt maize} \\ 0, & \text{Conventional maize} \end{cases}$$

240

241 The pest populations grow according to a classic logistical growth equation where population  
 242 dynamics are influenced by: the theoretical growth rate,  $r_i$ ; the species' intrinsic carrying capacity,  $k_i$ ;  
 243 intra-competition,  $b_{ii}$ ; inter-competition,  $b_{ij}$ ; mortality attributed to natural enemies,  $e_i$ ; the effectiveness  
 244 of *Bt* in controlling each pest population,  $q_i$ , and the application of insecticides,  $w$ . The dummy variable  
 245  $\phi$  assumes the value of one if either (or both) pest reaches its economic threshold, and zero otherwise.  
 246 The dummy variable  $\delta$  assumes the value of 0.8 if *Bt* maize is used, and zero otherwise. For further  
 247 information on both species description and relevance to maize production see Catarino et al (2016).

248

### 249 *2.3.6. Spatial pest dynamics*

250 Two sets of partial differential equation containing the dimensionless diffusion rate,  $D_i$  where  
 251  $i=1,2$ , were added to equation (2):

252

253

$$\left\{ \begin{array}{l}
\frac{\partial N_1(t, x, y)}{\partial t} = r_1 N_1(t, x, y) \left[ 1 - b_{11} \frac{N_1(t, x, y)}{k_1} - b_{12} \frac{N_2(t, x, y)}{k_1} - e_1 - \delta q_1 - \phi h(w, t) \right] + \\
\quad + \nabla_{x,y}(D_1(x, y) \nabla_{x,y} N_1(t, x, y)) \\
\frac{\partial N_2(t, x, y)}{\partial t} = r_2 N_2(t, x, y) \left[ 1 - b_{22} \frac{N_2(t, x, y)}{k_2} - b_{21} \frac{N_1(t, x, y)}{k_2} - e_2 - \delta q_2 - \phi h(w, t) \right] + \\
\quad + \nabla_{x,y}(D_2(x, y) \nabla_{x,y} N_2(t, x, y)) \\
\frac{\partial N_i(t, x, y)}{\partial \nu} \Big|_{\partial \Omega} = 0 \\
N_i(0, x, y) = N_i 0(x, y)
\end{array} \right. \quad (3)$$

254 with  $i \in \{1,2\}$ ,  $(x, y) \in \Omega$ ,  $t \geq 0$ ,  $\nabla_{x,y} = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ ,  $\Omega$  is the spatial domain,  $\nu$  is the normal unit

255 vector to the frontier of  $\Omega$  and  $D_i(x, y) = \begin{cases} D_i, & \text{if favourable habitat} \\ \frac{D_i}{1000}, & \text{otherwise} \end{cases}$ . Per time unit  $t$ , individuals

256 move randomly, i.e. they have equal probabilities of moving in any direction (left, right, up or down).

257 The diffusion rate for each species was derived, as in Shigesada and Kawasaki (1997), from the

258 theoretical maximum speed obtained in wind tunnels: for the Mediterranean corn borer is  $23.3 \text{ cm}\cdot\text{s}^{-1}$

259 (Bau et al., 1999) and  $135 \text{ cm}\cdot\text{s}^{-1}$  for the true armyworm (Luo et al., 2002, 1999). The dimensionless

260 diffusion rate was obtained by adjusting the spatial and temporal domain as in Gilligan (2008). It is

261 assumed that both species can disperse within the whole domain, with the exception of hostile habitat

262 that includes physical barriers, such as urban areas, mountain, sand, rocks and water. The boundaries

263 between spatial units are fixed during the course of the simulation. The homogeneous Neumann

264 boundary conditions (null derivative specified on the boundaries), were set for the spatial dimensions.

265

### 266 2.3.7. Pest control methods

267 Both pests are assumed to act simultaneously and the nature of the damage is species independent,

268 but with same negative impact upon yield. Farmers have two means of suppressing these pests, by using

269 *Bt* maize variety (pre-emptive action) and/or spraying insecticide when pest densities exceed an

270 economic threshold (**ET**). The two pests have different susceptibility to the *Bt* toxin. It is assumed that

271  $N_1$  is highly susceptible ( $q_1 = 0.99$ ) and that  $N_2$  is weakly susceptible ( $q_2 = 0.1$ ) to *Bt* toxins (Catarino et

272 al., 2016). We assumed that all *Bt* maize complied with the commonly advised 20% refuge of non-*Bt*

273 maize to promote survival of susceptible pests, thus avoiding resistance building to *Bt* toxin (Tabashnik  
274 et al., 2003).

275 Insecticides are applied throughout the cropping season according to the ET and subject to the  
276 pest dynamics. The parameters *a*, *b*, *c* and *d* in Equation 4, i.e. the optimal amount of insecticides applied,  
277 referent to the best possible farmers' NPV regarding the trade-off between the reduction of the pest  
278 density and the cost of the insecticide, throughout the cropping season (*w*), were estimated as in Catarino  
279 et al (2016). For conventional maize farmers, the optimal insecticide application takes the set of values  
280 {*a*=2.877152; *b*=-0.08932803; *c*=0.004002907; *d*=-0.00003733741} and for *Bt* maize farmers: {*a*=  
281 1.9946108422; *b*=-0.1508647313; *c*=0.0060110437; *d*=-0.0000316881}.

$$w(t) = a + bt + ct^2 + dt^3 \quad (4)$$

282

283 The ET was set as 25% of the economic injury level (**EIL**) as suggested by Pedigo et al (1986).  
284 In Equation 5a, *p<sub>w</sub>* is the cost of management per unit (€/ha); *p<sub>w</sub>*, the product market value per ton  
285 (€/ton); *L<sub>y</sub>*, yield lost per larvae (tons/ha); and *s*, the proportion of larvae killed (%):

$$ET = \frac{EIL}{4} \quad (5)$$

With:

$$EIL = \frac{p_w}{p_w L_y s} \quad (5a)$$

286

### 287 2.3.8. Model validation

288 Model validation was undertaken under the scenario S1 with PMS1, which showed that economic  
289 outcome are in line with published data. In 2012, the Aragon government reported an average maize  
290 yield of approximately of around 12 tons/ha (Lopez et al., 2000). Taking into account the impact of  
291 pests, the average yield predicted by the model when farmers apply insecticides in both maize systems  
292 is relatively close to the real value, 10.9 tons/ha. In 2012 the Aragon maize (combining conventional  
293 and *Bt* maize) producers obtained an average profit of 499 €/ha (López, 2014), the model predicted an  
294 average profit per hectare of 670 ± 0.04 €/ha for the first simulation year. The difference in the economic

295 returns of the first year may be due to two factors: 1) it is assumed that all farmers act optimally which  
296 is not always the case in reality; and, 2) no other pests were taken into consideration, hence insecticide  
297 expenditures may have been higher than we have accounted for in the total costs. Similarly, in terms of  
298 insecticide expenditure, our model predictions ( $48.6 \pm 0.0$  €/ha for conventional and  $11.0 \pm 2.3$  €/ha for  
299 *Bt* farmers in Zaragoza, a region characterized by the high pest level incidence) are also in line with the  
300 results reported by (Gómez-Barbero et al (2008)).

301 Numerous studies in Spain (Lopez et al., 2000), Canada (Fields and McNeil, 1984), the US  
302 (Willson and Eisley, 1992) and Mexico (Ramírez and Higuera, 2013) have reported on the true  
303 armyworm's destructive potential and sporadic population outbreaks with larvae marching *en masse*  
304 across the landscape. Attempts to analyse and predict outbreaks have been constrained by their great  
305 flying capacity and high reproduction rate of true armyworm, and its gregarious, explosive and  
306 unpredictable behaviour. Armyworms frequently disappear almost as suddenly as they appear, either  
307 burrowing into the ground to pupate or migrating to further fields in search of food. Additionally, there  
308 is a close link to temperature as this species does not have a diapause and cannot survive prolonged  
309 temperatures below freezing (Bues et al., 1986; Fields and McNeil, 1984). This has a major influence  
310 on the erratic nature of true armyworm's outbreaks and invasions. Thus, there may be an extended period  
311 of farmers not noticing the pest. In this work, the best knowledge reported in literature was used to  
312 evaluate the possible spread pattern of true armyworm in Aragon.

313

### 314 **3. Results and discussion**

#### 315 **3.1. Modelling overview**

316 The model analysis focused on the economic impact of the spread of true armyworm on maize  
317 farmers' gains under three different pest management strategies (PMS) based on optimal insecticide  
318 applications (see Catarino et al (2016) for details on the methodology) and five different *Bt* maize  
319 adoption scenarios. The true armyworm's spread is influenced by the landscape and competition with  
320 the main or primary pest, Mediterranean corn borer. In general terms, the overall control success, i.e.  
321 regional or farmers' economic returns, is defined in terms of achieving the highest NPV after a given

322 time span, 25 years in this case (Equation 1). Using a spatially explicit landscape model we aim to  
323 answer two specific questions: 1) What is the influence of landscape characteristics and Mediterranean  
324 corn borer competition on true armyworm's spread and the consequent economic impact; and, 2) what  
325 is the influence of the regional area in which *Bt* maize is grown on true armyworm's spread and the  
326 consequent economic impact? We discuss potential policy and subsequent management strategies to  
327 address these issues. In this study, geographic information data on real landscapes were used as it was  
328 critical to assess the feasibility of a spatial *Bt* maize expansion under realistic constraints.

329

### 330 **3.2. True armyworm spread is influenced by landscape characteristics**

331 When evaluating spatial distributions and the establishment of invasive species in new niches it  
332 is important to consider the area under management as well as the ecological and economic impacts  
333 associated with the management control options (Keller et al., 2007). The spatial structure, i.e. the  
334 connectivity of favourable fields for dispersion and reproduction (Jager et al., 2005), is another  
335 important factor which could have a strong influence on the dynamics and control of invasive species  
336 (Epanchin-Niell and Wilen, 2012). Here, two perspectives are considered in order to label an area as  
337 effectively invaded: 1) an agronomic perspective, i.e. when true armyworm density is above the ET per  
338 hectare, and 2) an ecological perspective, i.e. when at least one individual can be found per hectare.

339 From an agronomic perspective, about half of the Aragon area was invaded by true armyworm in  
340 our simulations:  $47.3 \pm 8.6\%$ ,  $47.9 \pm 6.9\%$  and  $49.7 \pm 6.7\%$  for PMS1, PMS2 and PMS3 respectively  
341 (Table III). The model results suggest that the variance in total invaded area (TAI) could be explained  
342 by the initial introduction area (or outbreak point) of true armyworm (Fig. 3). Depending on the starting  
343 point, the total invaded maize area varied from a minimum of 92 km<sup>2</sup> to a maximum of 298 km<sup>2</sup> (17 and  
344 56% of total maize area) in PMS1, and 310 km<sup>2</sup> (58% of total maize area) in PMS2 (Table III).  
345 Insecticide applications did not stop or meaningfully alter true armyworm's invasion. Using insecticides  
346 in both cropping systems (PMS1) reduced the TAI by only c. 3.5%, when compared to no insecticide  
347 use in the *Bt* maize strategy (PMS3). Figs. 4a and 4b shows the invasion patterns from two distinct initial  
348 points, illustrating how the invaded area is highly dependent on the place in which the outbreak occurs.



349 This suggests that only controlling the invasive species in maize fields is not an efficient management  
350 strategy. As outlined by Catarino et al (2015), the use a specific pest control strategy, such as *Bt* maize,  
351 may cause highly complex changes in the agro ecosystems. *Bt* maize could create a mechanism for the  
352 spread of secondary pest species that are not susceptible to a particular *Bt* toxin. The model results  
353 suggest that after 25 years virtually the whole region would be populated by at least one true armyworm  
354 per ha, regardless of the PMS adopted (Table III). Thus, it can be expected that the growth and spread  
355 will continue until suitable habitats and resources become scarce, which may cause serious constraints  
356 to farmers. Extending the geographic range of the secondary pest brings additional potential risks.  
357 Notably, if a mutation appears to be linked to some form of partial resistance to current insecticides, it  
358 could spread quicker throughout the geographic range, with no means of immediate control.

359 Even though our results suggest that most suppressive effect on the pest is achieved by having  
360 every farmer spraying pesticides in their fields, further efficient control measures should be looked for  
361 at other scales, which might be calling for regional coordination. The model assumes that no  
362 communication exists between farmers (i.e. farmers are not aware of what occurs in areas neighbouring  
363 their fields). However, in reality, farmers' decision to control or not a pest is frequently grounded on the  
364 perceived threat of the pest in the vicinity of their fields and the guidance of governmental entities or  
365 commercial advisors (Larson et al., 2011). Furthermore, farmers in the same region are often influenced  
366 by similar circumstances. Therefore if an active communication system is in place, it could create a  
367 coordinated response for pest control that is effective at a landscape scale (Diekert, 2012; Larson et al.,  
368 2011). From an economic perspective, a cost effective strategy (that we deemed beyond the scope of  
369 our study) would likely require efficient collaboration by all farmers. An extension of the model could  
370 include direct and/or indirect communications between farmers as observed in real life (Larson et al.,  
371 2011) in which cooperation could arrive as an opportunity for a new maxima of this bioeconomic  
372 problem.

373

374 **3.3. The use of *Bt* maize improves farmers' economic returns while reducing chemical input**

375 The use of *Bt* maize can be economically advantageous at both the individual farmer level and  
376 the regional level while decreasing insecticide use by eliminating the target pest (Areal et al., 2013;  
377 Areal and Riesgo, 2015; Gómez-Barbero et al., 2008). However, recent literature suggests that the  
378 outbreak of secondary pests previously suppressed could reduce the economic advantages of *Bt*  
379 technology (Catarino et al., 2015). Our results show that after 25 years with PMS1, *Bt* farmers realize  
380 higher profits per hectare, ~ 74% more, than conventional maize farmers while decreasing insecticides  
381 applications by about 68% (Table IV). The difference in insecticide expenditure per hectare after 25  
382 years between both maize systems is relatively large, with conventional maize farmers spending an  
383 average of €645 per hectare and *Bt* farmers spending only €50. The use of insecticides by conventional  
384 farmers is a necessity. Not using insecticides (PMS3) would lower the NPV after 25 years by ~ 77%.  
385 Whereas for *Bt* maize farmers, during the same period, not applying insecticides (PMS3) would have  
386 just a residual effect on the NPV, ~2% lower (Table IV).

387 At a regional level, when farmers apply insecticides in both *Bt* and conventional fields, the region  
388 of Aragon would obtain a total NPV of €294.3M ( $\pm 5.5$ ) after 25 years, of which 72% is attributable to  
389 *Bt* maize production. The sum of the total regional losses in maize due to true armyworm determines  
390 the benefit value of an effective control strategy. During the 25 year period the amount lost in this  
391 scenario, even when using insecticides, to both true armyworm and Mediterranean corn borer would be  
392 15.3 M EUR ( $\pm 3.4$ ), c. 5% of the total NPV, of which 69% is directly linked to true armyworm. When  
393 direct losses to pests are taken into account together with the total insecticide expenditure, approximately  
394 €31M is lost in 25 years in Aragon (Table IV). Results at both farmer and regional level show the high  
395 efficiency of *Bt* maize usage towards the primary pest. Since we have assumed that there was no  
396 communication within farmers and insecticides were only applied in maize fields, the NPV per hectare  
397 according to the initial outbreak field was identified to infer its influence on the final maize farmers'  
398 average NPV (Table V). When the outbreak originated outside of the maize fields, the farmers' NPV  
399 was c. 2% lower. This small variation suggests that the final NPV is not dependent on the type of field  
400 in which the outbreak occurs.

401

402 **3.4. Promoting use of *Bt* maize may increase regional economic and environmental benefits but**  
403 **also the geographic range of secondary pests**

404 The Aragon's regional ratio of conventional/*Bt* maize has a preponderant effect on the true  
405 armyworm's economic impact (Table VI). The economic and environmental (by reducing the necessity  
406 of insecticide) benefit of expanding *Bt* maize in Aragon are evident. The higher the area planted with *Bt*  
407 maize, the higher the aggregated regional profits. Intensifying the *Bt* cropping area by 50%, would bring  
408 an extra 16% to Aragon's maize economic revenues. Most importantly, it would reduce insecticide  
409 expenditure by an average of 51%. Interestingly, by increasing *Bt* hectareage, conventional farmers would  
410 also be c. 2% better off economically, while decreasing their insecticide expenditure by c. 55%. These  
411 results suggest that as in Hutchison et al (2010), the use of *Bt* maize may provide economic benefits for  
412 farmers who plant conventional maize in nearby fields. Thus, it is possible that shrinking the area of  
413 Mediterranean corn borer action, i.e. source fields, makes the pests' general control more efficient.  
414 Conversely, if farmers ceased to grow *Bt* maize, the economic losses could increase by 32% of the  
415 current losses in 25 years whilst at the same time more than doubling insecticide expenditure.

416 Regarding the true armyworm spread process, the results suggest that the invaded area and the  
417 ratio between the two maize varieties seem to be positively related, i.e. the higher the *Bt* area, the more  
418 the true armyworm area expands over the 25 year period. Thus, although the economic benefits of using  
419 *Bt* maize at a local level appear clear, it should be noted that the introduction of GEIR maize mono-  
420 cropping into an agricultural landscape might lead to wider issues. The simplification of cropping  
421 systems would lead to an increase in genetic uniformity of agroecosystems with subsequent negative  
422 ecological implications, such as an increase in vulnerability to pathogens or pests (Woltz et al., 2012).  
423 Hence, research on GEIR crops must consider the wider environmental impacts in order to avoid the  
424 same problems that agriculture faces with overuse of and resistance to some pesticides.

425

426 **4. Conclusion**

427 The results of this research are important to the European Union agriculture sector since maize is  
428 the second most important crop in EU agriculture. The Mediterranean corn borer is one of the principal

429 maize borers in Europe (Eizaguirre and Fantinou, 2012), especially in areas below the 45th parallel  
430 (Eizaguirre and Fantinou, 2012), since its distribution and population levels are mainly determined by  
431 its sensitivity to negative winter temperatures (Gillyboeuf et al., 1994). Yet, future climate projections  
432 suggest that an overall temperature increase will bring suitable conditions for the Mediterranean corn  
433 borer to proliferate in higher latitudes (Maiorano et al., 2014). Thus, in such a scenario the expansion of  
434 *Bt* maize would bring financial benefits to farmers and wider society in general by alleviating the need  
435 for using insecticides. According to our model results, the use of *Bt* maize together with insecticides (at  
436 a lower rate) yields lower crop losses and higher gross margins, in line with data reported in recent  
437 studies (Areal et al., 2013; Gómez-Barbero et al., 2008; Meissle et al., 2010). However, farmers adopting  
438 *Bt* maize need to be aware of future potential invasion of (new) pests that are not susceptible to the toxin.

439         If the occurrence of secondary pests is not identified and dealt with at an early stage it is possible  
440 that population numbers will establish and expand beyond the ET and spread throughout an entire  
441 region. This research suggests that the establishment of a secondary pest leads to severe economic  
442 impacts even if insecticides are applied in combination with the *Bt* maize. The results also suggest that  
443 damage to crops from secondary pests can increase with the expansion of *Bt* maize if no additional  
444 measures are used, such as additional insecticide applications or the use of stacked traits. It is important  
445 to note that in addition to the economic impacts and increase in insecticide applications, the secondary  
446 pest might cause several other negative effects with possible trophic cascading effects, e.g. by having a  
447 negative influence on other species (natural enemies), or being a vector of diseases. Therefore, the  
448 situation at hand remains sensitive and is surrounded by a high level of uncertainty regarding the  
449 expected magnitude of impacts, as the latent effects of *Bt* maize expansion cannot be completely  
450 predicted.

451         It is also important to note the implication of any potential time lags between the arrival of a  
452 secondary pest species in an area and its detection (Solow and Costello, 2004). This is of particular  
453 importance in GEIR cropping since *Bt* maize farmers are usually less active in scouting their maize  
454 fields for the presence of pests (Wilson et al., 2005). If *Bt* maize farmers fail to rapidly identify a pest  
455 that is not susceptible to the toxin expressed by the GE maize, it will allow a window of time large

456 enough for population numbers to increase and for the pest to spread throughout the region. Successful  
457 pest management programs are clearly subject to the capacity of farmers, stakeholders and agencies to  
458 recognise, detect and report new incursions (Macfadyen et al., 2018). We suggest that governments  
459 require land managers to adopt quarantine measures or carry out detection campaigns and legislative  
460 control measures. Although prevention is cost intensive, its benefits are likely to outweigh its costs,  
461 particularly for highly mobile and resource generalist species such as true armyworm. Lastly, we  
462 recommend that further modelling investigations should be done with regard to seasonal temperature  
463 constraints on insect development. Phase shifts in occurrence might be a constraint not completely  
464 covered here, that may have implications on the competition between and within two species, hence on  
465 secondary pest expansion.

466

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472

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729           **Code availability.** The computer code used for this study is available from the corresponding  
730 author upon request.

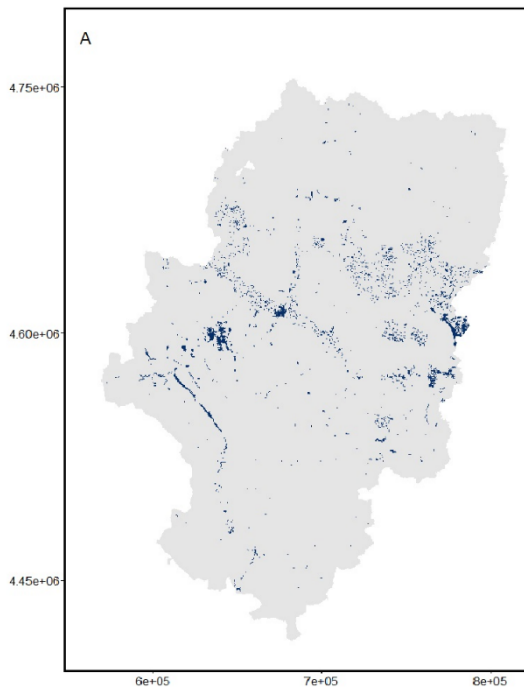
731           **Data availability.** The datasets analysed during the study are available from the corresponding  
732 author upon request.

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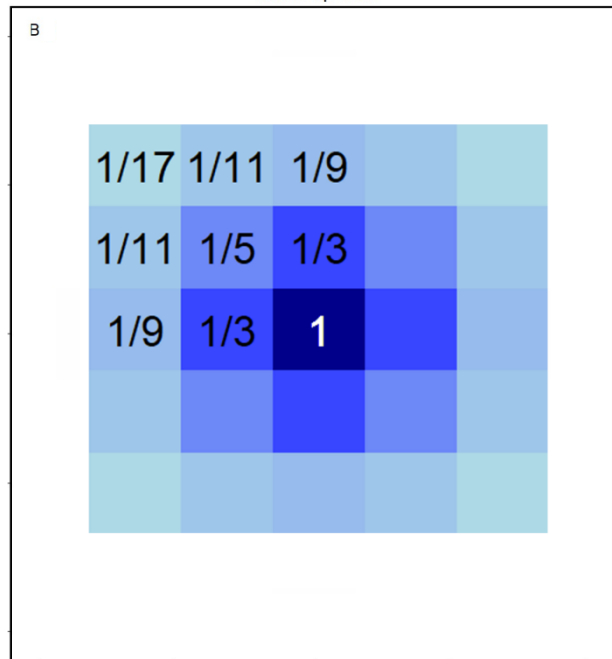
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735 **6. Figures**

Primary pest, Mediterranean corn borer (MCB), initial population



Secondary pest, true armyworm (TAW), initial population  
closer up view



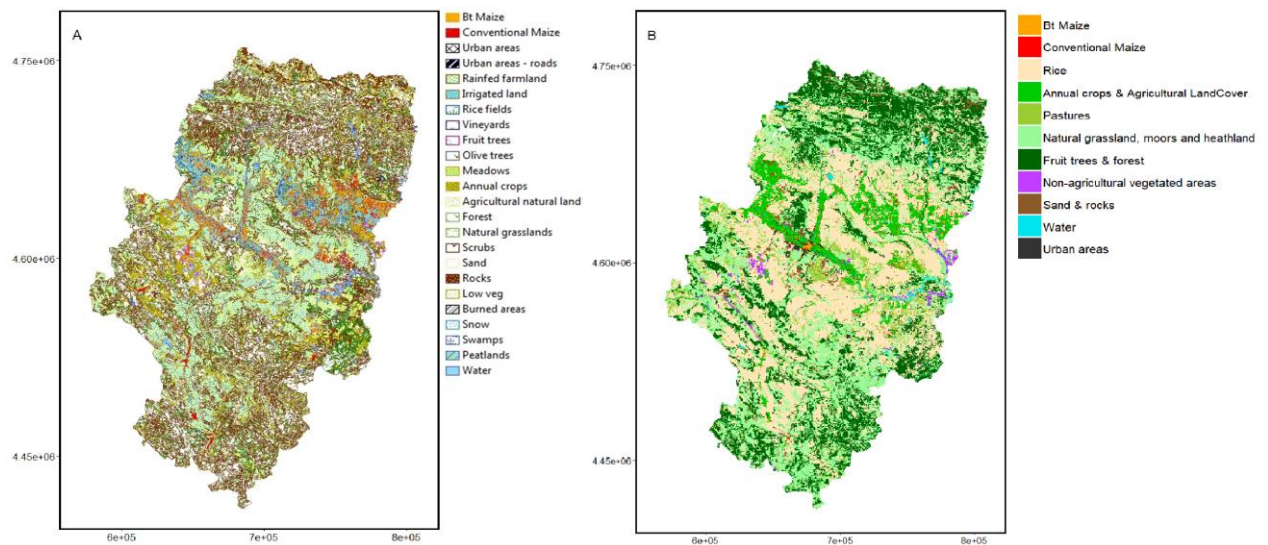
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737 **Fig. 1.** Initial population of both pests, Mediterranean corn borer (MCB) and true armyworm (TAW).

738 Fig. a) shows the initial population of MCB. It is assumed that MCB is present in all fields favourable  
 739 to reproduction at a density equivalent to 10% of its carrying capacity on maize ( $1.125 \times 10^6$  individuals  
 740 per cell =  $4.5 \times 10^4$  individuals per hectare = 0.5 individuals per maize plant). Fig. b) shows the initial  
 741 population of secondary pest, true army worm (TAW), close up in the form of a Cauchy kernel,  
 742 evidencing the respective proportion of individuals in relation to the population density at the centre.  
 743 TAW initial population density has also a density equivalent to 10% of its carrying capacity on maize  
 744 ( $2.25 \times 10^6$  individuals per cell =  $9 \times 10^4$  individuals per hectare = 1 individuals per maize plant). Each cell  
 745 represents 25 hectares.

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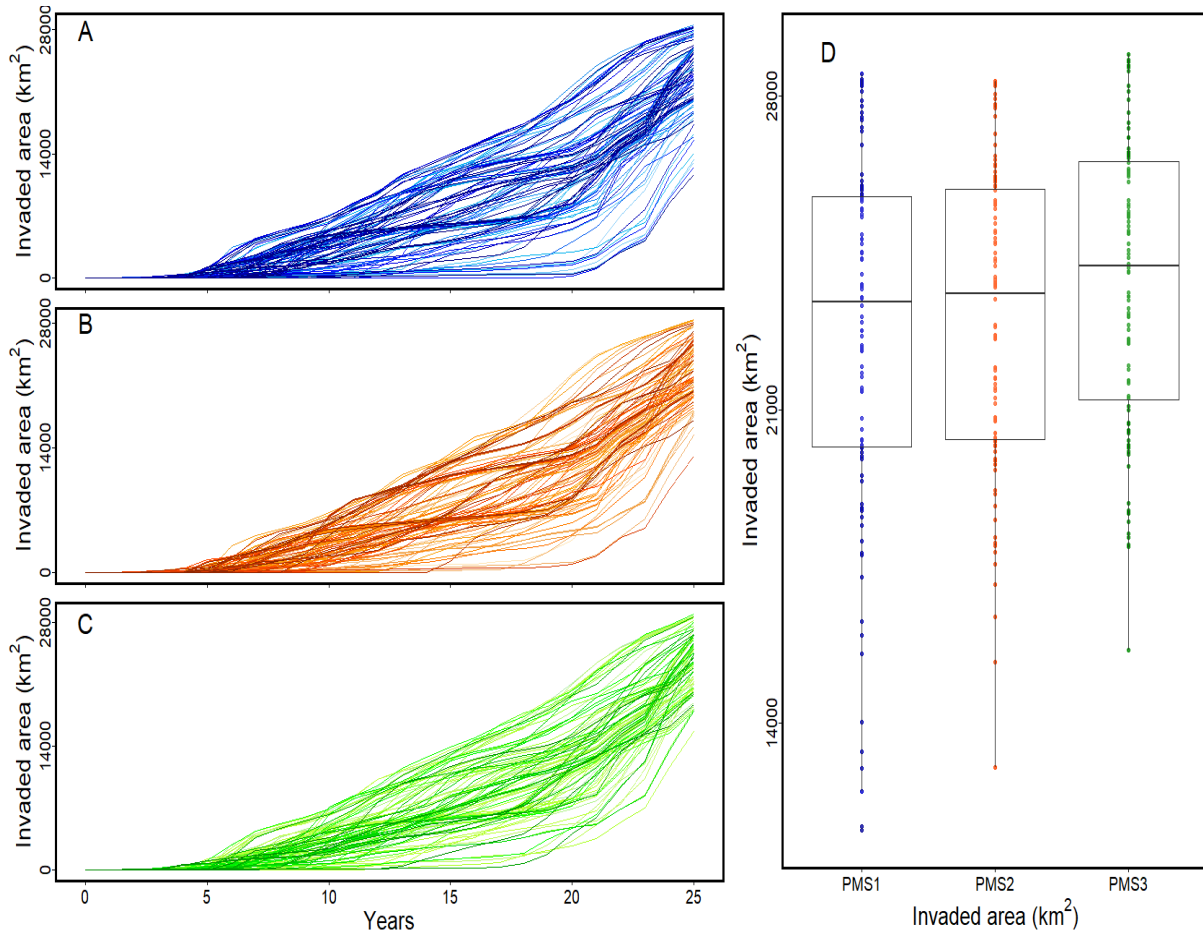
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749 **Fig. 2.** Aragon land use maps. a) CORINE geographic land use map encompassing the main land cover  
 750 categories, represented explicitly with a grid derived from an ASCII raster adapted from the CORINE  
 751 2006 Land Cover. The resolution of the data is 100x100 m. b) The original landscape aggregated for the  
 752 relevant land cover types with a spatial resolution of 500x500 m, i.e. 25 ha.

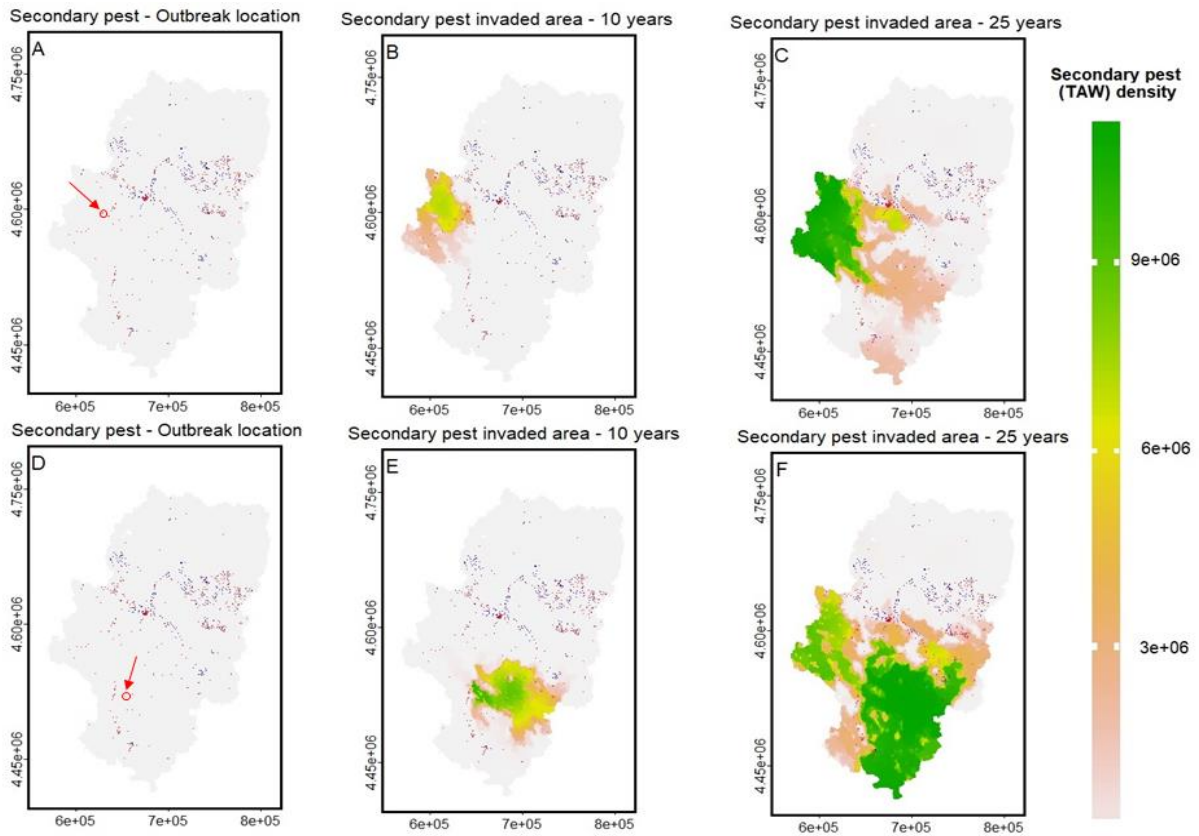
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756  
 757 **Fig. 3.** Total area invaded per year throughout the 25 years when TAW surpassed the economic  
 758 threshold (ET) level for the pest management strategies (PMS): insecticides are used in both *Bt* and  
 759 conventional maize (A, PMS1); insecticides are used only in conventional maize (B, PMS2);  
 760 insecticides are not used in neither *Bt* nor conventional maize (C, PMS3). Each line, in figs. A, B and  
 761 C, represents one model simulation. Depending on the starting point, the total invaded maize area after  
 762 25 years ranges from a minimum of 11615, 13022 and 15636 km<sup>2</sup> to a maximum of 28506, 28332 and  
 763 28939 km<sup>2</sup> (51.4%, 51.1% and 52.2% of the total Aragon area) on PMS1, PMS2 and PMS3 respectively.  
 764 The boxplots on D show the invaded area at the end of the 25 years period for the three PMSs.  
 765



766

767 **Fig. 4.** Two examples of the secondary pest, true armyworm (TAW), invasion process over 25 years  
 768 when insecticides are used in both *Bt* and conventional maize from two randomized simulations. Images  
 769 A) and D) show the initial outbreak area, occurring in west and south west of Aragon (highlighted with  
 770 red circle and arrow), respectively; B) and E) show the invasion area after 10 years; and C) and F) show  
 771 the final spread accrued from these two simulations. The red cells represent *Bt* maize fields, while blue  
 772 cells represent conventional maize. Values are given per cell. Each cell represents 25 hectares with  
 773  $9.0 \times 10^4$  maize plants each.

774

775

776 **7. Tables**

777

778 **Table I.** Aragon aggregated land use and habitat quality for both pests, Mediterranean corn borer (MCB)  
 779 and true armyworm (TAW). The landscape is categorised into: i) areas of favourable habitat, i.e. where  
 780 the species can reproduce, colonize and disperse; and ii) hostile habitat, where reproduction and  
 781 dispersion are impeded.

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

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783

784 **Table II.** Economic and biologic parameters used in the bio-economic model and respective sources.

785

	Value	Units	Source
Economic parameters	Plant density per hectare	90000	Plants/ha (AGPME, 2012)
	Potential conventional maize yield ( $Y_c$ )	11.30	T/ha (AGPME, 2012)
	Potential <i>Bt</i> maize yield ( $Y_{Bt}$ )	11.80	T/ha (AGPME, 2012)
	Price maize ( $p$ )	212.3	€/T (MAGRAMA, 2018)
	Conventional seed price ( $S_c$ )	253.80	€/ha (AGPME, 2012)
	<i>Bt</i> seed price ( $S_{Bt}$ )	284.40	€/ha (AGPME, 2012)
	Fixed costs ( $u_c$ )	1797.88	€/ha (AGPME, 2012)
	Fixed costs ( $u_{Bt}$ )	1815.88	€/ha (AGPME, 2012)
	Insecticide cost per application ( $w$ )	18	€/ha/app (AGPME, 2012)
	Discount rate ( $\delta$ )	0.05	Assumption
	$N_1$ (MCB)	$N_2$ (TAW)	
Biologic parameters	Growth rate ( $r_i$ )	2.02	3.13 (Catarino et al., 2016)
	Diffusion rate ( $D_i$ )	$4.659 \times 10^{-6}$	$9.538 \times 10^{-3}$ See spatial pest dynamics
	Intraspecific competition ( $b_{ii}$ )	1	1 (Catarino et al., 2016)
	Interspecific competition ( $b_{ij}$ )	0.10	0.90 (Catarino et al., 2016)
	Susceptibility to <i>Bt</i> toxin ( $q_i$ )	0.99	0.20 MCB: (Hellmich et al., 2008) TAW: (González-Cabrera et al., 2013)
	Susceptibility to insecticide ( $s$ )	0.80	0.80 (Folcher et al., 2009; Hyde et al., 1999)
	Minimum natural enemies impact	0.1	0.1 (Catarino et al., 2016)
	Maximum natural enemies impact	0.65	0.90 MCB: (Alexandri and Tsitsipis, 1990; Figueiredo and Araujo, 1996; Monetti et al., 2003) TAW: (Costamagna et al., 2004; Guppy, 1967; Kaya, 1985; Laub and Luna, 1992; Malvar et al., 2004)
	Maximum larvae per plant	5	10 (Butrón et al., 2009, 1999; Malvar et al., 2004; Velasco et al., 2004)
	Initial population (larvae per plant)	5	5 (Catarino et al., 2016)
Damage per larvae ( $I$ )	0.06	0.06 (Butrón et al., 2009, 1999; Malvar et al., 2004; Velasco et al., 2004)	

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787

788 **Table III.** True armyworm (TAW) invasion simulation results (scenario 1) after 25 years. Except when  
789 mentioned, the results refer to the case in which TAW surpasses the economic threshold (ET) in maize  
790 fields. It is showed detailed information on the predicted total area of invasion (TAI) by TAW and the  
791 density of individuals per plant for the three pest management regimes (PMR): PMS 1, insecticides are  
792 applied in both *Bt* and conventional maize; PMS 2, insecticides are only applied in conventional maize,  
793 and; PMS 3: no insecticides are applied.

	units	Mean	Min	Max
<b>PMS 1</b>				
Aragon invasion area (>1 larvae ha <sup>-1</sup> )	km <sup>2</sup>	47043 ± 337	46275	47527
Aragon invasion area	km <sup>2</sup>	22685 ± 4130	11632	28515
Maize invaded area	km <sup>2</sup>	200 ± 57	92	298
Conv maize invaded area	km <sup>2</sup>	76 ± 26	37	123
<i>Bt</i> maize invaded area	km <sup>2</sup>	124 ± 35	55	189
Total TAW average density	Insect/plant	0.5 ± 0.26	0.08	1.21
Conventional field TAW density	Insect/plant	0.44 ± 0.26	0.08	1.17
<i>Bt</i> fields TAW average density	Insect/plant	0.55 ± 0.27	0.07	1.23
<b>PMS 2</b>				
Aragon invasion area (>1 larvae ha <sup>-1</sup> )	km <sup>2</sup>	47080 ± 330	46343	47567
Aragon invasion area	km <sup>2</sup>	23012 ± 3330	13042	28340
Maize invaded area	km <sup>2</sup>	213 ± 53	99	310
Conv maize invaded area	km <sup>2</sup>	81 ± 25	38	130
<i>Bt</i> maize invaded area	km <sup>2</sup>	132 ± 31	60	192
Total average TAW density per plant	Insect/plant	0.61 ± 0.27	0.09	1.3
Conv average TAW density per plant	Insect/plant	0.53 ± 0.27	0.1	1.22
<i>Bt</i> average TAW density per plant	Insect/plant	0.67 ± 0.28	0.09	1.35
<b>PMS 3</b>				
Aragon invasion area (>1 larvae ha <sup>-1</sup> )	km <sup>2</sup>	47233 ± 260	46712	47620
Aragon invasion area	km <sup>2</sup>	23867 ± 3221	15658	28950
Maize invaded area	km <sup>2</sup>	218 ± 53	128	317
Conv maize invaded area	km <sup>2</sup>	84 ± 25	41	135
<i>Bt</i> maize invaded area	km <sup>2</sup>	134 ± 32	80	194
Total average TAW density per plant	Insect/plant	0.63 ± 0.27	0.13	1.32
Conv average TAW density per plant	Insect/plant	0.56 ± 0.27	0.14	1.23
<i>Bt</i> average TAW density per plant	Insect/plant	0.68 ± 0.28	0.13	1.38

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796 **Table IV.** The economic implications of predicated invasions, after 25 years, at regional and field level  
797 for conventional and *Bt* maize for each of the pest management strategies (PMS). The regional economic  
798 losses to pest are based on the regional optimal profit (i.e. zero losses to pests) of € 122.4 M for  
799 conventional maize farmers and € 221.6 M for *Bt* maize farmers. Field losses to pests were determined  
800 by averaging the former values for the total hectareage.  
801

		PMS 1			
	Units	Conv		<i>Bt</i>	
NPV (regional level)	Million €	81.6 ± 2.3		212.7 ± 3.2	
NPV (field level)	€·ha <sup>-1</sup>	3817.2 ± 106.3		6651.7 ± 101.6	
Insecticide cost (regional level)	Million €	13.8 ± 3.1		1.7 ± 0.4	
Insecticide cost (field level)	€·ha <sup>-1</sup>	643.68 ± 143.76		49.45 ± 12.2	
Insecticide applications	app·ha <sup>-1</sup> ·year <sup>-1</sup>	2.51 ± 0.3		0.81 ± 0.16	
		MCB	TAW	MCB	TAW
Pest loss (regional level)	Million €	4.2 ± 2.4	3.2 ± 1.9	0.6 ± 0.1	7.3 ± 3.6
Pest loss (field level)	€·ha <sup>-1</sup>	196.4 ± 110.6	150.7 ± 88	17.2 ± 2.7	227.7 ± 111.5
		PMS 2			
	Units	Conv		<i>Bt</i>	
NPV (regional level)	Million €	81.3 ± 2.1		213.7 ± 3	
NPV (field level)	€·ha <sup>-1</sup>	3804.4 ± 98.8		6683.1 ± 94.5	
Insecticide cost (regional level)	Million €	15.3 ± 0		0 ± 0	
Insecticide cost (field level)	€·ha <sup>-1</sup>	715.2 ± 0		0 ± 0	
Insecticide applications	app·ha <sup>-1</sup> ·year <sup>-1</sup>	2.56 ± 0		0 ± 0	
		MCB	TAW	MCB	TAW
Pest loss (regional level)	Million €	3 ± 0.1	3.9 ± 2	0.7 ± 0	8.8 ± 3.7
Pest loss (field level)	€·ha <sup>-1</sup>	142.6 ± 3.8	180.5 ± 93.7	21.9 ± 0.5	276.7 ± 115.7
		PMS 3			
	Units	Conv		<i>Bt</i>	
NPV (regional level)	Million €	18.9 ± 2.2		209.5 ± 3.5	
NPV (field level)	€·ha <sup>-1</sup>	885.8 ± 100.9		6551.7 ± 108.3	
Insecticide cost (regional level)	Million €	0 ± 0		0 ± 0	
Insecticide cost (field level)	€·ha <sup>-1</sup>	0 ± 0		0 ± 0	
Insecticide applications	app·ha <sup>-1</sup> ·year <sup>-1</sup>	0 ± 0		0 ± 0	
		MCB	TAW	MCB	TAW
Pest loss (regional level)	Million €	20.9 ± 0.2	4.1 ± 2	2.1 ± 0	9 ± 3.7
Pest loss (field level)	€·ha <sup>-1</sup>	978.5 ± 8.1	190.7 ± 92.4	64.3 ± 1.1	282.4 ± 115.4

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805 **Table V.** Farmers' net present value (NPV) per hectare depending on the initial field of outbreak of  
 806 true armyworm (TAW). Results are shown for the first pest management strategy, i.e. insecticides used  
 807 in both conventional and *Bt* maize, in five different conventional/*Bt* proportions (means per Agricultural  
 808 System). It is assumed that TAW are introduced at a randomized location of favourable habitat. Nb field  
 809 indicates the number of outbreaks in the respective field.

Fields	Nb fields	NPV (mean±sd)
PMR 1 - Scenario 1 (actual maize area)		
<i>Bt</i> Maize	3	5634.7 ± 45
Conv Maize	4	5503.7 ± 110
Annual Crops	23	5484.2 ± 109
Rice	70	5520.4 ± 89.6
PMR 1 - Scenario 2 (no <i>Bt</i> maize)		
Conv Maize	3	3837.7 ± 102.3
Annual Crops	20	3717.1 ± 81.9
Rice	77	3749.7 ± 78.3
PMR 1 - Scenario 3 ( <i>Bt</i> maize area reduced by 50%)		
<i>Bt</i> Maize	3	4753.9 ± 14.4
Conv Maize	3	4681.8 ± 19.8
Annual Crops	27	4593.1 ± 94.8
Rice	67	4623 ± 93.3
PMR 1 - Scenario 4 ( <i>Bt</i> maize area increased by 50%)		
<i>Bt</i> Maize	5	6450.7 ± 120.6
Conv Maize	1	6441.3 ± NA
Annual Crops	17	6328.4 ± 118.4
Rice	77	6384.5 ± 223.7
PMR 1 - Scenario 5 (no conventional maize)		
<i>Bt</i> Maize	5	6722.1 ± 196.6
Annual Crops	19	6627 ± 112.6
Rice	76	6721.7 ± 98.1

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**Table VI.** Comparison of the results for five different *Bt* maize adoption cases. Simulation results are shown as a percentage, considering of the actual Aragon land-use areas in PMS 1 (S1), insecticide used in both systems, using four different conventional/*Bt* proportions (means per Agricultural System). Comparisons for the total area invaded (TAI) by true armyworm (TAW), and the economic implications of predicated pest dynamics, after 25 years at field level, are shown. Table entries show the comparison (in %) between the baseline scenario (S1) that represents the actual maize area for the year 2012 under the baseline pest management regime (PMS 1), i.e. with insecticides are used in both maize systems, and four other scenarios with different conventional/*Bt* maize proportions per agricultural system: S2, no *Bt* maize is cropped; S3, *Bt* maize area is reduced by 50%; S4, *Bt* maize area is increased by 50% and; S5, all cropped maize is *Bt* maize. If the value equals zero, no change was noted.

	TAI (km <sup>2</sup> )	NPV (€·ha <sup>-1</sup> )			Economic loss to Pest (€·ha <sup>-1</sup> )						Insecticide expenditure (€·ha <sup>-1</sup> )		
		Conv	<i>Bt</i>	Mean	Conv		<i>Bt</i>		Mean		Conv	<i>Bt</i>	Mean
					MCB	TAW	MCB	TAW	MCB	TAW			
S1: PMS1	22685	3817.2	6651.7	5516.0	196.4	150.7	17.2	227.7	89.0	196.8	643.7	49.5	287.5
S2: 100% Conv	-1.49%	-1.88%		-32.10%	6.92%	-1.79%			135.96%	-24.82%	0.00%		68.33%
S3: -50% <i>Bt</i>	-0.96%	-0.48%	-1.64%	-16.21%	2.34%	-1.13%	16.28%	-7.77%	64.86%	-15.01%	0.00%	13.58%	36.35%
S4: +50% <i>Bt</i>	1.89%	2.04%	0.15%	15.69%	-3.26%	0.86%	-33.14%	5.40%	-66.78%	17.40%	-55.38%	-16.05%	-51.41%
S5: 100% <i>Bt</i>	4.24%		0.54%	21.24%			-40.12%	14.19%	-88.43%	32.08%		-28.40%	-61.10%