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Risk of establishment and potential impacts of transient populations of Spodoptera frugiperda in Europe

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1	Risk of establishment and potential impacts of transient populations of
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21 Abstract

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith), is an invasive pest threatening crop production and food security worldwide. High concerns are linked to the potential establishment of the species in Europe. The high migratory capacity of *S. frugiperda* cause concerns about the potential impacts of transient populations invading new areas from suitable hotspots. In the present work, we developed and used a physiologically-based demographic model to quantitatively assess the risks of *S. frugiperda* in Europe. The risks were assessed considering a best-, a median-, and a worst-case scenario. The Mediterranean coastal areas of Southern Europe resulted suitable for the establishment 29 of the species, with suitable areas reaching even higher latitudes, in the worst-case scenario. In 30 Europe, up to 4 generations per year were predicted. The predicted average yearly adult population 31 was 5 (\pm 4), 17 (\pm 5), and 139 (\pm 22) in the best, median-, and worst-case assessment scenario, 32 respectively. Model results showed that Southern and Central Europe might be exposed to the risk of 33 transient populations, at least up to the 48th parallel north, in the worst-case scenario. Depending on 34 the latitude and on the period of arrival of the propagule, transient populations might be able to 35 originate 1 or more generations per year. The model can be used to define strategies reducing the 36 risks of establishment of the pest at the country level. Predictions on the dynamics and phenology of 37 the pest can also be used to support its management at the local level.

38 Keywords: Fall armyworm; Invasive species; Pest risk assessment; Physiologically-based model;
39 Transient populations

40 Key message

- There are high concerns linked to the potential establishment and impacts of *Spodoptera frugiperda* in Europe
- We developed a physiologically-based model to quantitatively assess the risks linked to *S*.
 frugiperda
- Risk of establishment of *S. frugiperda* was predicted in the Mediterranean coastal areas of
 Southern Europe
- Risks linked to transient populations (i.e., populations migrating from suitable areas) were
 predicted in Southern and Central Europe
- 49 Statements and Declarations
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52 Authors' contribution. GG and GS conceptualised the work. GG, GS, AS, and PG performed 53 simulations. GG, GS, AS, and PG, interpreted outputs. GG, GS, and MC acquired and interpreted 54 data. All authors drafted the manuscript.

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56 Data availability. Raw data used in the present study are available upon request

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72 **1. Introduction**

73 The fall armyworm, Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) is a phytophagous 74 pest considered a major threat to agricultural production and food security (Early et al. 2018; Tambo 75 et al. 2021), especially in developing countries (Devi 2018; FAO 2020; Suby et al. 2020; Koffi et al. 76 2020). The species is known to feed on more than 350 host plants including economically valuable 77 crops such as maize, rice, soybean, sorghum, wheat, barley, and cotton (de Freitas Bueno et al. 2011; 78 Hardke et al. 2015; Montezano et al. 2018). Impacts on crops are caused mainly by late instar larvae 79 (Overton et al. 2021) feeding on stems, branches, leaves and reproductive structures of the host, and 80 causing direct yield loss, defoliation, and general weakness of the plant (Harrison 1984; Vilarinho et 81 al. 2011). The larval trophic activity might favour plant infection caused by fungi (Farias et al. 2014). 82 Yield loss to maize ranges from 11% to 67% (Hruska and Gould 1997; Day et al. 2017; Kumela et 83 al. 2019; Baudron et al. 2019). Reported average losses for other crops are 26% for sorghum, 24% 84 for sweet corn, 13% for bermudagrass, and for 5% rice. The control measures for protecting crops 85 affected by the species and restrictions on the trade of potentially infested products cause further economic and social costs (Overton et al. 2021). The species is native to tropical and subtropical 86 87 America where it is considered a prevalent pest for maize, soybean, cotton, and other major crops 88 (Nagoshi et al. 2007; Baudron et al. 2019; Koffi et al. 2020). Human-mediated transportation and 89 trades (Cock et al. 2017), the high migratory capacity (the species might fly up to 100 km per night) 90 (Rose et al. 1975; Westbrook et al. 2016), and the high prolificacy (more than 1500 eggs laid per 91 moth) (Luginbill, 1928) of the species facilitated the dispersal of the pest in non-native areas. In 2016, 92 the species was accidentally introduced in Central and Western Africa (Goergen et al. 2016) where it 93 was able to spread in vast areas of sub-Saharan and North Africa (Day et al. 2017; Cock et al. 2017; 94 EPPO 2020a). Since 2018, the species invaded vast areas of the Middle East (EPPO 2019a; EPPO 95 2020b,c,d), South Asia (EPPO 2018; Sharanabasappa et al. 2019), South-Eastern Asia (EPPO 96 2019b,c; EPPO 2020e; Sartiami et al. 2020; Zaimi et al. 2021), East Asia (EPPO 2019d; Suh et al. 97 2021), North-Eastern Asia (EPPO 2019e) and Oceania (EPPO 2020f). In Europe, the species is

98 currently (FAO 2021) present in the Canary Islands (EPPO 2021). S. frugiperda is on the EPPO A2 99 list of quarantine pests, and in the European Commission list of priority pests (EU 2019) due to the 100 risk of introduction, establishment and consequences of this pest to Europe. Fresh plant products 101 imported from Latin America represent the main pathway of entry of the species in the EU (EFSA 102 PLH Panel et al. 2017; 2018a; EFSA et al. 2020). Another pathway of introduction is represented by 103 the possibility of eggs and adults to entry as hitchhikers on international flights (Early et al. 2018). 104 The high migratory ability of the species causes concerns about the potential impacts of transient 105 populations moving from hotspots to new areas during the favourable season (EFSA PLH Panel et 106 al. 2018a; Timilsena et al. 2022). A realistic threat is the introduction of individuals from North Africa 107 to Europe due to natural or wind-mediated dispersal (Westbrook et al. 2016; Early et al. 2018).

108 Given the potential threats of S. frugiperda to European agriculture, it is fundamental to quantitatively 109 estimate the risk of establishment and the potential impacts linked to the species. This information is 110 fundamental for planning and implementing surveillance and inspections to reduce the likelihood of 111 introduction and establishment of the pest in Europe (EFSA PLH Panel et al. 2018a; EFSA et al. 112 2020). So far, many species distribution models have been developed for predicting the potential 113 habitat suitability for S. frugiperda (Ramirez-Cabral et al. 2017; Du Plessis et al. 2018; Early et al. 114 2018; Liu et al. 2020; Baloch et al. 2020; Fan et al. 2020; Zacarias 2020; Huang et al. 2020; Tepa-115 Yotto et al. 2021; Ramasamy et al. 2021). However, there is high uncertainty on the risks linked to 116 the establishment of this pest in Europe. For instance, no risk of establishment but only risk linked to 117 transient populations was predicted by Du Plessis et al. (2018). On the contrary, suitable areas in 118 Southern Europe were identified by Early et al. (2018) and EFSA PLH Panel et al. (2018a). Other 119 authors identified risks in areas of the Central Europe (Zacarias 2020) or further north, up to Ireland 120 (Liu et al. 2020; Ramasamy et al. 2021) and Southern Norway (Tepa-Yotto et al. 2021), although with low habitat suitability indices. This high uncertainty reflects the need to establish sound criteria 121 122 and reliable models for obtaining a realistic assessment of the risk linked to a pest (Ponti et al. 2015).

123 In this work, we aimed at providing a solid and quantitative assessment of the risks linked to S. 124 frugiperda in Europe through the application of a physiologically-based (i.e., mechanistic) modelling 125 approach. This approach allows to faithfully describe important aspects of the biology of the species 126 (Sparks 1979), such as the non-linear responses to temperature and the influence of relevant abiotic drivers (density-dependent factors, mortality due to biotic agents) on the individual physiology, 127 128 population distribution and dynamics (Régnière et al. 2012a; Gutierrez and Ponti 2013). The model 129 was used to respond to the following Assessment Questions (AQ), which are highly relevant for 130 estimating the risks linked to S. frugiperda in Europe (EFSA PLH Panel et al. 2018b). AQ 1 - Is the 131 model able to predict the pattern of population dynamics and the limits of establishment in the area 132 of current distribution? (current distribution and dynamics); AQ 2 - Can the species establish in 133 Europe? If yes, what is the area of potential establishment of the species? (establishment in Europe); 134 AQ 3 - What is the population dynamics of the species in the areas of potential distribution in Europe? 135 (population dynamics in Europe); AQ 4 - Can the species originate transient populations in Europe? 136 If yes, can population abundance in transient populations represent a risk for cultivated plants? 137 (dynamics of transient populations)

138 **2. Materials and methods**

139 **2.1. The model**

140 In this work, we developed a physiologically-based model using a system of Kolmogorov partial 141 differential equations to simulate the stage-specific population dynamics of S. frugiperda considering 142 the two dimensions of time t and physiological age x (Buffoni and Pasquali 2007; Rafikov et al. 143 2008; Solari and Natiello 2014; Lanzarone et al. 2017) (full mathematical details of the model are 144 present in Section S1 of supplementary material 1). We assumed a population of S. frugiperda being 145 composed of four stages i, namely egg (i = 1), larva (i = 2), pupa (i = 3) and adult (i = 4). Physiological age in the *i*-th stage, $x^i \in [0,1]$, represents the level of development of an individual in 146 the stage *i* (Buffoni and Pasquali 2007). With $x^i = 0$ we represent an individual at the beginning of 147 *i*-th stage, while with $x^i = 1$ we represent an individual at the end of the *i*-th stage. The term $\phi^i(t, x)$ 148

149 represents the number of individuals in stage i at time t with physiological age [x, x + dx]. The overall number of individuals in stage i at time t is calculated as $N^{i}(t) = \int_{0}^{1} \phi^{i}(t, x) dx$. The 150 population abundance in the stage i, $N^{i}(t)$, is defined by the number of individuals in a spatial unit 151 152 as defined in Section 2.5.2. In the present work, we assumed population abundance as a descriptor of 153 the potential impacts of S. frugiperda. The simulations were performed using MATLAB version 154 R2018a (MATLAB, R2018a, The MathWorks, Inc., MA, USA). We assumed the population dynamics of S. frugiperda was dependent on the species' life-history strategies. These were described 155 156 at the individual level by stage-specific development, mortality and fecundity rate functions. Since 157 temperature is considered one of the main variables influencing the physiology of poikilotherms 158 (Gutierrez 1996; Régnière et al. 2012b; Gilioli et al. 2021a), the effects of the time-dependent 159 temperature profile T(t) affecting the species' life-history strategies were considered in the model 160 (Barfield et al. 1978a; Silva et al. 2017; Du Plessis et al. 2020).

161 *Development rate function*. We defined $v^i(T(t))$ as the temperature-dependent development rate 162 function of individuals in stage *i* as a function of temperature T(t). For the stages i = 1,2,3 we used 163 the development rate functions that are defined in Gilioli et al. (2021b). For the stage i = 4, respect 164 to Gilioli et al. (2021b), we increased the life-span of the adults by reducing the development rate 165 function $v^4(T(t))$ by a fixed factor of 2.5 to obtain more realistic adult survival curves (He et al. 166 2021a; Zhang et al. 2021). The methodology used for estimating parameters of the development rate 167 function $v^i(T(t))$, is presented in Section S1.1 of supplementary material 1.

168 *Mortality rate function*. As in Gilioli et al. (2021b), we assumed the mortality rate function $m^{i}(t)$ 169 for the stages i = 1, 3, 4 depending on temperature according to the following law

170
$$m^{i}(t) = \mu^{i}(T(t)), \quad i = 1, 3, 4$$

171 with $\mu^i(T(t))$ being the temperature-dependent instantaneous mortality acting on individuals within 172 each stage at time *t* (see Section S1.2 of supplementary material 1). The mortality of larvae is affected 173 by multiple factors, such as weather conditions (Varella et al. 2015), the attack of biotic agents (e.g., predators, parasites and pathogens) (Escribano et al. 2000; Zanuncio et al. 2008) and densitydependent factors, (e.g., cannibalistic behaviour) (Chapman 1999; Chapman et al. 2000; Andow et al. 2015; He et al. 2021b). To account for these factors, in the present work, the mortality rate function for the larval stage $m^2(t)$ is expressed as follows

178
$$m^{2}(t) = \mu^{2} \left(T(t) \right) \left(1 + \alpha \left(\frac{N^{2}(t)}{\gamma} \right)^{2} \right) + \beta$$

179 with $\left(1 + \alpha \left(\frac{N^2(t)}{\gamma}\right)^2\right)$ representing a density-dependent component simulating the intraspecific 180 competition (e.g., cannibalistic behaviour), $\alpha > 0$ representing a multiplicative term and $\beta > 0$ 181 representing a biotic component simulating the role of predators, parasites and pathogens.

The parameter $\gamma > 0$ represents the larval carrying capacity based on resources availability. The parameter γ was set to 3000 which corresponds to the larval abundance at the carrying capacity in the spatial unit considered in the present study (see Section 2.5.2 for details). The methodology used for estimating the temperature-dependent component of the mortality rate function $\mu^i(T(t))$ is presented in Section S1.2 of supplementary material 1. Parameters α and β were estimated through the calibration procedure (Section 2.2).

188 *Fecundity rate function*. For the adult stage, we defined the fecundity rate function $F^{1}(t)$ 189 representing the production of eggs by adult females (Johnson 1987). As in Gilioli et al. (2021b), the 190 fecundity rate function depends on female age and temperature. In the present work, we further 191 introduced a density-dependent regulation term to account for the role of intraspecific competition on 192 egg production due to limitations in the per-capita food supply (Leather 2018). The fecundity rate 193 used in the present study is

194
$$F^{1}(t) = g(T(t)) \left(1 - \frac{N^{4}(t)}{S + N^{4}(t)}\right) \int_{0}^{1} \phi^{4}(t, x) h(x) dx$$

195 with g(T(t)) describing the temperature-dependent component, $\left(1 - \frac{N^4(t)}{S + N^4(t)}\right)$ describing the 196 density-dependent component, $\phi^4(t, x)$ being the number of adult individuals at time t and

197 physiological age x, and h(x) describing the physiological age-dependent component. The terms g(T(t)) and h(x) were taken from Gilioli et al. (2021b) (see Section S1.3 of supplementary material 198 199 1 for details). The term S is a half-saturation term in the density-dependent regulation of female 200 fecundity. Based on the assumption that the adult abundance at the carrying capacity in the spatial unit is $N_K^4 = 320$ adult individuals per week (see Section 2.5.2 for details), we set $S = 0.5 N_K^4 = 160$. 201 With this set up, the density-dependent term $\left(1 - \frac{N^4(t)}{S + N^4(t)}\right)$ is almost 1.00 (negligible density-202 dependent effects) for adult population abundances lower than 10 individuals, and almost 0.35 203 204 (relevant density-dependent effects) for adult population abundances higher than 300 individuals per 205 trap per week.

206 **2.2. Model calibration**

The calibration procedure consisted in estimating the parameter α_j and β_j that will be used for the definition of the parameters α of the density-dependent mortality term and the biotic mortality term β included in the mortality rate function of the larval stage $m^2(t)$. Parameters α_j and β_j were estimated by minimising the mean squared distance between the simulated and the observed adult abundance for each of the 21 observation datasets *j* representing the calibration dataset (see Section 2.5.1). The minimisation was performed for each of the 21 observation datasets *j* through solving the following function

214
$$Q_j(\alpha_j, \beta_j) = \sum_{j=1}^{21} \frac{1}{R_j} \sum_{i=1}^{R_j} \left| N_j^4(t_i; \alpha_j, \beta_j) - A_j(t_i) \right|^2$$

The term $A_j(t_i)$ represents the observed adult abundance in the dataset j at the time t_i corresponding to the time at which adult abundance was sampled. The term R_j represents the number of sampled data available for each dataset j. With $N_j^4(t_i; \alpha_j, \beta_j)$ we define the adult abundance at in the dataset j at time t_i , obtained by solving the Kolmogorov equations with the parameters $\alpha = \alpha_j$ and $\beta = \beta_j$ keeping fixed the other parameters. The optimal parameters $\hat{\alpha}_j$ and $\hat{\beta}_j$ were the minimisers of the Q_j , i.e., they allow for the minimum difference between simulated and observed adult populationabundance

222
$$Q_j(\widehat{\alpha}_j, \widehat{\beta}_j) = \min_{\alpha_j, \beta_j} Q_j(\alpha_j, \beta_j)$$

For the minimisation procedure, we used the MATLAB function fmincon with step tolerance equal to 10⁻⁵ for the stopping test.

225 **2.3. Simulation design**

The population dynamics model of *S. frugiperda* was used to explore the four Assessment Questions reported in Section 1. To account for the uncertainty linked to the estimates of parameters α and β , the model was implemented considering three assessment scenarios (see Section 2.4).

229 Assessment Question 1 - Current distribution and dynamics

230 The capacity of the model to predict the local population dynamics of S. frugiperda was tested 231 comparing simulated results with observed adult abundance data obtained in three locations selected 232 along a latitudinal gradient in the area of current distribution in North America (see Section 2.5.1). 233 From south to north, we considered a highly suitable location (Miami Dade County, Florida), a 234 location at the edge of the area of establishment (Alachua County, Florida), and a location which is 235 currently known to be reached only by migrating populations (Tift County, Georgia) (Westbrook et 236 al. 2016; Garcia et al. 2018). The population dynamics were simulated using the temperature profile 237 of the current climate in the tested locations as input data (see Section 2.5.4). Initial conditions were 238 set to 5 pupae uniformly distributed in their physiological age (from 0 to 1) on the 1st of January. The 239 model was implemented for four consecutive years, repeating the same yearly temperature profile, to 240 obtain stable population dynamic patterns and model outputs that were independent of the initial 241 conditions. We assumed that no migration of individuals was possible from and to each location in 242 which the model was implemented. The assessing variables considered were the average yearly adult abundance, the number of generations per year, and the maximum adult population abundance 243 244 reached over the last year of simulation.

245 Assessment Question 2 - Establishment in Europe

246 For assessing the potential distribution and abundance of S. frugiperda in Europe, we implemented 247 the model in a spatial grid of $0.1^{\circ} \times 0.1^{\circ}$ representing the European territory (see Section 2.5.4). In 248 each node of the grid, the population dynamics was assessed using the same initial conditions defined 249 in AQ 1 and the temperature profile of that specific node (Gilioli et al. 2014, 2021c; Pasquali et al. 250 2020). The species was considered established in a node if, at the first time-step of January 1st of the 251 last year of simulation, the adult abundance was higher than an adult abundance threshold 252 $(A_0 = 0.01)$. The threshold A_0 was set by considering the average of the minimum population abundance reached by the species at the northernmost edge of the area of establishment in a set of 253 254 locations in North America, including the location of Alachua County (Florida) tested in AQ 1. 255 Species' potential distribution was estimated over the last year of simulation. The area of potential 256 establishment of S. frugiperda in Europe was given by the set of grid nodes where the species was 257 considered established.

258 Assessment Question 3 - Population dynamics in Europe

The local population dynamics of *S. frugiperda* in Europe were assessed by implementing the model in 3 locations using the initial conditions explained in AQ 1. Locations were chosen based on the simulated *S. frugiperda* potential dynamics in Europe obtained by answering AQ 2. Based on the model's result, a highly suitable location was selected in Cyprus, and two less suitable locations were selected, in Southern France and on the Atlantic coast of Portugal. We considered the same assessing variables presented in AQ 1.

265 Assessment Question 4 - Dynamics of transient populations

Transient populations are supposed to originate from migrating adults arriving in a location where temporary suitable conditions may occur, but no establishment is possible due to unsuitable conditions in other periods of the year. The population dynamics of transient populations was assessed by simulating an inoculum of 5 adults, uniformly distributed in their physiological age (from 0 to 1), on three different Days of the Year (DOY): April 1st (90th DOY), June 1st (150th DOY), and August 271 1st (210th DOY). The model was implemented from the date of inoculum to the end of the year, using 272 as temperature profile the current climate of the tested location (see Section 2.5.4). The assessing 273 variables considered were the average adult abundance, the number of generations, and the maximum 274 adult population abundance over the simulation period. We assumed that the inoculum was not able 275 to originate a transient population if the predicted adult population abundance reached values below 276 or equal to the adult abundance threshold A_0 during the simulation period. The predicted dynamics 277 of transient populations were evaluated in four maize production areas in Europe, outside the area of 278 potential establishment: Rădoiești (Romania, 44th parallel north), Ghedi (Italy, 45th parallel north), 279 Ouarville (France, 48th parallel north), and Engelsberg (Germany, 48th parallel north).

280 **2.4. Generation of assessment scenarios**

281 Considering the range of distribution of the parameters α_i and β_i estimated through the calibration 282 procedure (see Section 2.2), we calculated the 10th, the 50th and the 90th quantiles of the distributions 283 for the definition of parameters α and β . To account for variability in the population dynamics, we 284 generated 9 different assessment scenarios, combining the quantiles of α and β . In the present study, 285 we consider the worst-case assessment scenario where the species has lower mortality ($\alpha = 10th$; $\beta = 10th$), The median-case assessment scenario, obtained considering the medians of parameters 286 287 distribution ($\alpha = 50th$; $\beta = 50th$), and the best-case assessment scenario, where S. frugiperda 288 mortality is high ($\alpha = 90th$; $\beta = 90th$). The values of parameters related to the three investigated 289 scenarios are reported in Table 1. The population dynamics of S. frugiperda in the current area of 290 establishment in North America (AQ 1) and the dynamics of transient populations in Europe (AQ 4) 291 were predicted considering the median-case assessment scenario. The best-case, the median-case and 292 the worst-case assessment scenarios were considered for predicting the potential distribution of S. 293 frugiperda in Europe (AQ 2) and the population dynamics of the pest within the predicted area of 294 establishment (AQ 3).

296 **2.5.1. Data on pest population dynamics**

297 Data on pest population dynamics were used for estimating parameters in the function describing the 298 larval mortality (see Section 2.2) and to test the model's capacity to predict the population dynamics 299 patterns and the establishment of S. frugiperda in North America (AQ 1). Population dynamics data 300 used for calibration purposes (hereinafter, calibration dataset) refer to 21 time-series adult trap catches 301 data collected in the area of establishment in Central and North America from 1982 to 2019, selected 302 for their quality in terms of completeness of the time-series and realism of population trends (see 303 supplementary material 2) (Silvain and Ti-A-Hing 1985; Pair et al. 1986; Nagoshi and Meagher 2004; 304 Meagher and Nagoshi 2004; Rojas et al. 2004; Salas-Araiza 2018; Salazar-Blanco et al. 2020). The 305 calibration dataset covers latitudes between 4.85 and 28.76 parallel north and it includes, 1 time-series 306 data collected in French Guyana (Matoury), 1 in Costa Rica (Guanacaste), 3 in Mexico (Manzano 307 and Irapuato) and 16 the United States (from Southern to Northern Florida). Additional population 308 dynamics data were used for answering the AQ 1 and refer to time-series adult trap catches collected 309 in three locations: Miami Dade County (Florida, 25th parallel north), Alachua County (Florida, 29th 310 parallel north), and Tift County (Georgia, 31st parallel north) (Pair et al. 1986; Meagher and Nagoshi 311 2004; Garcia et al. 2019).

312 **2.5.2. Definition of the spatial unit**

The simulated adult abundance variable used in our model $N^4(t)$ refers to the number of individuals 313 314 caught in a trap per week. To allow the comparison between observed and simulated adult abundance, 315 the temporal unit of the population dynamics data used in the present study was referring to weekly 316 adult trap catches. Since a pheromone-baited trap can effectively catch insects within a range of two 317 hectares (Tingle and Mitchell 1979), the spatial unit for the definition of the population abundance 318 was considered two hectares in the present study. Our model required the estimation of the larval 319 carrying capacity γ . Considering the calibration dataset we first calculated, the average maximum 320 observed adult abundance (284 individuals). Based on this result we assumed a conservative value representing the adult carrying capacity $N_K^4 = 320$ in the spatial unit. The relation between the seasonal fluctuation of adults (captured using pheromone-baited traps) and larvae (captured using sweep nets) of *S. frugiperda* was investigated for three consecutive years (1981-1983) by Silvain and Ti-A-Hing (1985). From their work, we extracted 10 datasets and calculated the average amount of larvae produced by a single adult (i.e., the ratio between larval and adult abundance at the peaks of the population) P = 9.34. Based on this result, we calculated the carrying capacity of larvae $\gamma =$ $N_K^4P = 2989$ which was rounded to $\gamma = 3000$ in the present study.

328 **2.5.3. Data on species physiology**

The development $v^i(T(t))$, mortality $m^i(t)$ and fecundity $F^1(t)$ rate functions were estimated 329 330 considering data available in the literature on stage-specific responses of S. frugiperda exposed to 331 different constant temperature conditions. Data referring to the average stage-specific duration in days were used for estimating the development rate function $v^i(T(t))$ (Barfield et al. 1978b; 332 333 Simmons 1993; Oeh et al. 2001; Busato et al. 2005; Milano et al. 2008; Barros et al. 2010; Ríos-Díez 334 and Saldamando-Benjumea 2011; Garcia et al. 2018). Data referring to the stage-specific percentage survival were used for estimating the temperature-dependent component $\mu^i(T(t))$ of the mortality 335 rate function $m^{i}(t)$ (Barfield et al. 1978b; Pashley et al. 1995; Murúa and Virla 2004; Busato et al. 336 2005; Milano et al. 2008; Barros et al. 2010; Garcia et al. 2018). Data referring to the temperature-337 338 dependent average total fecundity, average daily fecundity, and average duration in days of the oviposition period were used for estimating the temperature- g(T(t)) and the physiological age-339 dependent h(x) components of the fecundity rate function $F^{1}(t)$ (Barfield et al. 1978b; Pashley et al. 340 341 1995; Oeh et al. 2001; Milano et al. 2008; Barros et al. 2010; Garcia et al. 2018).

342 **2.5.4. Temperature data**

Yearly temperature data used as inputs during model calibration refer to the 5th generation of
European ReAnalisys (ERA5-Land), reporting hourly air temperature data at a 0.1° x 0.1 spatial
resolution (Muñoz Sabater 2019). Bilinear interpolation was used to obtain temperature data for each

346 location of the calibration dataset. The current climatic scenario used to respond to the Assessment 347 Questions was extracted from the Coordinated Regional Downscaling Experiment (CORDEX) (Jacob 348 et al. 2014) and refers to the Coupled Model Intercomparison Project Phase 5 (CMIP5). The scenario 349 is based on Representative Concentration Pathways (RCPs) which consider the greenhouse gases 350 emissions up to the year 2100 (van Vuuren et al. 2011). The climatic scenario provides tri-hourly 351 temperature data on 0.11° x 0.11° spatial resolution for the European domain over a period ranging 352 between 2016 and 2025. Temperature data were regridded through bilinear interpolation to a regular 353 0.1° x 0.1° grid using Climate Data Operators command lines (Schulzweida 2019). We then averaged tri-hourly data over the whole decade (2016-2025) of the scenario to obtain an annual average 354 355 temperature profile, which was assumed as the current climate (see Section S2 of supplementary 356 material 1).

357 **3. Results**

Below, are presented the answers to the four Assessment Questions, based on the results of the model.

AQ 1 - Predicted population dynamics and limits of establishment of Spodoptera frugiperda in areas of current distribution

361 The graphical results of the model implemented along a south-north latitudinal gradient under the 362 median-case assessment scenario are presented in Figure 1. In the area of Miami Dade (Florida), the 363 model predicted 7 peaks (i.e. generations) per year; the average yearly adult abundance was around 364 64 individuals and the maximum adult population abundance was around 165 individuals reached 365 during the 6th generation. In the area of Alachua (Florida) the model predicted 2 generations per year; 366 the average yearly adult abundance was around 17 individuals, and the maximum adult population 367 abundance was around 98 individuals reached during the 2nd generation. Adult population abundance 368 reached values lower than the adult population threshold A_0 over the simulation period in the area of 369 Tift (Georgia). Thus, the potential establishment of the pest was considered not possible in the above-370 mentioned area.

371 AQ 2 - Risk of establishment and potential distribution of Spodoptera frugiperda in Europe

372 Figures 2 and 3 show the risks linked to the establishment of S. frugiperda in Europe under the three 373 assessment scenarios. In the median-case scenario, risk of establishment was predicted on the 374 southern coastal areas of the Mediterranean basin (Cyprus, Syria, Lebanon, Southern Turkey, 375 Southern Italy, Southern and Western Spain). Lower risk of establishment was expected in the Atlantic coasts of Portugal, and sporadic locations on the west coast of Sardinia. In the median case 376 377 assessment scenario, the measured area of potential establishment was 0.26% of the whole area under 378 assessment. The area of establishment decreased by 89% (0.03% of the total assessed area) in the 379 best-case assessment scenario and increased by 116% (0.57% of the total assessed area) in the worst-380 case assessment scenario. The northernmost latitudinal limit marking the presence of S. frugiperda 381 populations was the 38th parallel north (Eastern Spain), the 43rd parallel north (Southern France) and 382 the 44th parallel north (Northern Italy) in the best-case, median-case and worst-case assessment 383 scenarios, respectively.

AQ 3 - Predicted population dynamics of Spodoptera frugiperda in areas of potential distribution in Europe

386 Estimated population abundance within the area of potential establishment in Europe was highly 387 variable depending on the assessment scenarios. The average yearly adult abundance in the spatial 388 unit (\pm standard deviation) was 5 (\pm 4) in the best-case, 17 (\pm 5) in the median-case, and 139 (\pm 22) 389 in the worst-case assessment scenario. More details on the yearly population dynamic patterns of S. 390 frugiperda are provided by the results of the local implementation of the model in areas with different 391 suitability for the species in Europe (Figure 4). The results of the model implemented in a highly 392 suitable area (Cyprus), showed low population abundances at the beginning of the year due to low 393 temperatures. Approaching the spring season, a rise in the adult population abundance was predicted 394 according to temperature increase. Four adult population peaks (i.e., generations) were predicted 395 around the 186th, 225th, 264th and 314th DOY with the maximum adult population abundance 396 reached on the third generation. Predicted adult population abundances during the peaks ranged 397 between 90 and 130 individuals. After the fourth generation, a decline in the abundance of adults was 398 observed, due to temperature drops in fall. The model implemented in the northernmost edge of the 399 predicted establishment area in Europe (La Seyne-sur-Mer, Southern France) resulted in a single 400 generation at around the 250th DOY. Adult abundance reached 90 individuals and then a sharp drop 401 in population abundance was observed due to cold temperatures in fall. The model implemented in 402 the Atlantic coast of Portugal (Alchochete) showed that a single generation at around the 297 DOY 403 with low adult population abundance during the peak (18 individuals).

404 AQ 4 - Risks linked to transient populations of Spodoptera frugiperda in Europe

405 Simulations of the inoculum in different periods of the year (considering the median-case assessment 406 scenario) clearly showed that the species might be able to originate transient populations in areas 407 outside the predicted establishment in Europe (Figure 5). The results of the model implemented in 408 Rădoiești (Southern Romania, 44th parallel north) and Ghedi (Northern Italy, 45th parallel north) 409 showed risks linked to transient populations in all three introduction periods. A single generation was 410 predicted for introductions at the 90th DOY, and at the 210th DOY and two generations were 411 expected for introductions at the 150th DOY when weather conditions can be particularly suitable for 412 the species. The yearly average abundance ranged between 19-20 adults with peaks at around 70 413 individuals (introduction at the 90th DOY) to 43-52 individuals (introductions at the 150th and 210th 414 DOY). The model was implemented in areas further north in Europe (48th parallel north) in Ouarville 415 (Northern France) and Engelsberg (Southern Germany). Introductions at the 90th DOY did not represent a risk of transient populations ($N^4 < A_0$ during the simulation period) due to the unsuitable 416 417 environmental conditions affecting species' survival. Introductions occurring during warmer periods 418 in late spring (150th DOY) and summer (210th DOY) allowed the species to originate transient 419 populations. However, only low yearly average adult population abundances (1-2 individuals) were 420 predicted, thus representing a low risk linked to transient populations.

421 **4. Discussion**

The lack of suitable data forced us to make reasonable assumptions for the estimates of the values of the half-saturation term S = 160 and the larval carrying capacity $\gamma = 3000$. Based on these assumptions, we generated the three assessment scenarios used in the present study, to account for the uncertainty linked to the estimates of parameters α , simulating the density-dependent component of larval mortality and β , simulating the effects of biotic agents on larval mortality.

427 The model presented was able to satisfactorily predict the population dynamics, the variability in the 428 number of generations and the limits in the area of establishment of S. frugiperda along a latitudinal 429 gradient within the area of current distribution in North America. The model implemented under the 430 median-case assessment scenario predicted up to 7 generations per year in an area where the species 431 is well established (Florida, Miami Dade County) and only 2 generations per year in a location 432 situated at the northernmost edge of the establishment for the species (Florida, Alachua County). This 433 result is in agreement with the available observations reporting a high number of generations in areas 434 characterised by warmer temperature conditions (Sparks 1979; Busato et al. 2005) and around six 435 generations in warm areas of North America (Luginbill 1928). According to the results of the model, 436 the number of generations progressively decreases at the extreme southern and northern areas of 437 distribution of the species (Johnson 1987; Ramirez-Cabral et al. 2017; Schlemmer 2018). Correctly, 438 the model predicted no establishment in an area (Tift County, Georgia) that is considered reached 439 only by migratory populations. These results highlight the prominent role of climate in influencing 440 the distribution and the dynamics of S. frugiperda (Capinera 2002; Garcia et al. 2018, 2019).

Predicted distribution and dynamics of *S. frugiperda* in Europe, clearly highlighted risks of establishment of the species, especially in the coastal areas of the Mediterranean basin due to more favourable climatic conditions. In particular, higher population abundances were predicted in the coastal areas of Southern Spain, Southern Italy, Greece, Cyprus, Southern Turkey and Lebanon. Our results are in partial disagreement with the work of Du Plessis et al. (2018), which reported low risk of establishment, but mainly risk linked to transient populations, associated to the pest in Europe. In agreement with our results, suitable areas for the establishment of *S. frugiperda* in the Mediterranean 448 coasts of Europe have been reported in EFSA PLH Panel et al. (2018a), Early et al. (2018), Liu et al. 449 (2020), Baloch et al. (2020), Zacarias (2020), and Tepa-Yotto et al. (2021). The predicted 450 northernmost limit that might be reached by *S. frugiperda* was between the 38th and the 44th parallel 451 north based on the different scenarios under assessment. These results are in partial disagreement with Liu et al. (2020), Baloch et al. (2020), Fan et al. (2020), and Tepa-Yotto et al. (2021). These 452 453 authors reported areas potentially suitable for the establishment of the species further north, reaching 454 United Kingdoms and Southern Sweden (although with low habitat suitability indices). Current 455 knowledge on the biology of S. frugiperda seems justifying our predictions, especially in the light of 456 the prominent role of climate in shaping the area of distribution of the species (Early et al. 2018). In 457 particular, it is reported that the species does not enter diapause and suffers from cold weather 458 conditions (Capinera 2002; Nagoshi et al. 2012). This might prevent the establishment of S. 459 frugiperda in cold areas (EFSA PLH Panel et al. 2018a).

The population dynamics pattern of *S. frugiperda* predicted by the model in a highly suitable location in Europe showed that a rise in population abundance (up to 90-130 adult individuals) may occur during the early summer period, with up to four generations per year. A single generation per year and lower population abundances (around 18-90 adult individuals) were predicted in less suitable locations in Europe. This result is in agreement with EFSA PLH Panel et al. (2018a) that reported up to four generations per year in the most suitable areas in Southern Europe. The population pressure expected in a suitable European location might represent a risk for local crop production.

Given the high migratory ability of the species, transient populations might represent a threat in areas outside the area of potential establishment of the species. The results of the model showed that in Europe, high risk due to transient populations can be expected in areas up to the 45th parallel north, with population abundances (20-70 adult individuals) that might cause impacts on local crop production. Lower risks due to transient populations in Europe can be expected in areas up to the 48th parallel north, where unsuitable climatic conditions hinder the survival of the inoculum.

473 **5. Conclusion**

474 In this work, we presented the results of a physiologically-based model applied to S. frugiperda to i) 475 predict the species' population dynamics and abundance, ii) assess the risk of establishment of the 476 species in Europe, and iii) predict the risk linked to transient populations in Europe. To the best of our knowledge, this is the first physiologically-based model simulating the life-history of S. 477 478 frugiperda used for investigating the potential dynamics and distribution of the species. The 479 physiologically-based modelling approach allows simulating the influence of biotic (density-480 dependent effects and mortality due to biotic agents) and abiotic (e.g., temperature) variables on the 481 life-history strategies of a pest (Soberon and Nakamura 2009; Gutierrez and Ponti 2013). This 482 approach allows obtaining realistic predictions, that are independent of data on the current distribution 483 of the species, that might be uncomplete and/or biased (Wiens et al. 2009). The model can provide 484 fundamental elements for supporting the management of the pest considering different spatio-485 temporal scales and management contexts (Sperandio 2021). For instance, the development of 486 strategies to reduce the risks associated to S. frugiperda can be supported by coupling risk maps on 487 the potential establishment of the pest and information on trade routes and movement of people 488 (EFSA PLH Panel et al. 2018b; FAO 2021). The model also provides relevant information on the 489 potential impacts caused by transient populations that might represent a risk for local crop production. 490 In case the species becomes established in mainland Europe, predictions on the population phenology 491 and dynamics of S. frugiperda can be used for the timely implementation of control actions aimed at 492 reducing pest population pressure and thus reducing the impacts on local crops (Rossi et al. 2019).

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780 Figures captions

- Fig.1 Observed (red asterisks) and simulated (blue line) adult population dynamics of *Spodoptera frugiperda* within the area of current distribution in North America: (left) Southern Florida, Miami
- 783 Dade County, and (right) Northern Florida, Alachua County
- **Fig.2** Heat map showing the predicted distribution and the average weekly abundance of adult
- 785 individuals of Spodoptera frugiperda under the median-case assessment scenario
- 786 Fig.3 Heat maps showing the predicted distribution and the average weekly abundance of adult
- 787 individuals of Spodoptera frugiperda under the best-case (A) and worst-case (B) assessment scenarios
- 788 Fig.4 Simulated (blue line) population dynamics of adults of Spodoptera frugiperda along a south-
- north latitudinal gradient within the area of potential establishment in Europe, in (A) Cyprus, (B)
- 790 Southern France, and (C) Atlantic coast of Portugal
- 791 Fig.5 Population dynamics of adults of Spodoptera frugiperda simulating an inoculum of 5 adults at
- the 90th, (green line), 150th (blue line), and 210th (red line) day of the year in (upper left corner)
- 793 Ghedi (Southern Italy), (upper right corner) Rădoiești (Southern Romania), (lower left corner)
- 794 Ouarville (Northern France) and (lower right corner) Engelsberg (Germany)
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796 **Tables captions**

- 797 **Table 1** Estimates of parameters $\alpha \beta$ linked to larval mortality for the best-case, the median-case,
- and the worst-case assessment scenario discussed in the present study
- 799
- 800 Supplementary materials captions
- 801 Supplementary material 1.
- 802 S1. Full mathematical details of the model based on the Kolmogorov equation and temperature- and
- 803 age-dependent parameters estimation
- 804 S2. Correlation test between simulated and measured air temperature data
- 805 S3. Parameters estimates for each location of the calibration dataset

- 806 Supplementary material 2. List of the locations from which time-series adult trap catches data were
 807 collected (calibration dataset)
- 808

809 Supplementary figures captions

- 810 **Fig.S1** Fitted development rate functions v(T(t)) (blue lines) on temperature for eggs, larvae, pupae,
- 811 and adults of *Spodoptera frugiperda*. Red asterisks refer to data on *S. frugiperda* development rates
- 812 calculated at different constant temperatures
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- 814 pupae, and adults of Spodoptera frugiperda. Red asterisks refer to data on S. frugiperda survival at
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- 817 larvae, pupae, and adults of Spodoptera frugiperda
- 818 Fig.S4 Graph showing the temperature-dependent component g(T(t)) and the physiological age-
- 819 dependent component h(x) of the fecundity rate function $F^{1}(t)$ for the adult stage of Spodoptera
- 820 frugiperda
- **Fig.S5** Scatter-plot showing the monthly-wise correlations between air temperature data related to the current climatic scenario (monthly averages on the 2016-2025 period) and observed air temperature data (monthly averages on the 2010-2019 period)
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825 Supplementary tables captions

- 826 **Table S1** Estimated parameters r, T_{inf} and T_{sup} of the temperature-dependent development rate
- function v(T(t)) for eggs, larvae, pupae, and adults of *Spodoptera frugiperda*
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- 829 M(T(t)) for eggs, larvae, pupae, and adults of *Spodoptera frugiperda*

830 **Table S3** Estimated parameters c_{L1} , c_{L2} , c_{L3} , c_{R1} , c_{R2} , c_{R3} , T_{inf}^{μ} and T_{sup}^{μ} of the temperature-831 dependent instantaneous mortality $\mu(T(t))$ for eggs, larvae, pupae, and adults of *Spodoptera* 832 *frugiperda*

- 833 Table S4 Results of the monthly-wise Pearson correlation test between air temperature data related 834 to the current climatic scenario (monthly averages on the 2016-2025 period) and observed air 835 temperature data (monthly averages on the 2010-2019 period)
- 836 **Table S5** Estimates of parameters α and β of the mortality rate function for larvae $m^2(t)$ of
- 837 Spodoptera frugiperda and Mean Squared Error (MSE) resulting from the calibration procedure
- 838 implemented in each location of the calibration dataset

Figures

Figure 1

Observed (red asterisks) and simulated (blue line) adult population dynamics of *Spodoptera frugiperda* within the area of current distribution in North America: (left) Southern Florida, Miami Dade County, and (right) Northern Florida, Alachua County

Figure 2

Heat map showing the predicted distribution and the average weekly abundance of adult individuals *of Spodoptera frugiperda* under the median-case assessment scenario

Figure 3

Heat maps showing the predicted distribution and the average weekly abundance of adult individuals *of Spodoptera frugiperda* under the best-case (A) and worst-case (B) assessment scenarios

Figure 4

Simulated (blue line) population dynamics of adults of *Spodoptera frugiperda* along a south-north latitudinal gradient within the area of potential establishment in Europe, in (A) Cyprus, (B) Southern France, and (C) Atlantic coast of Portugal

Figure 5

Population dynamics of adults of *Spodoptera frugiperda* simulating an inoculum of 5 adults at the 90th, (green line), 150th (blue line), and 210th (red line) day of the year in (upper left corner) Ghedi (Southern Italy), (upper right corner) Rădoiești (Southern Romania), (lower left corner) Ouarville (Northern France) and (lower right corner) Engelsberg (Germany)

Supplementary Files

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