

1 **Modeling the risk of invasion and spread of *Tuta absoluta* in Africa**

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21 **Abstract**

22 *Tuta absoluta* is an invasive insect that originated from South America and has spread to Europe
23 Africa and Asia. Since its detection in Spain in 2006, the pest is continuing to expand its
24 geographical range, including the recent detection in several Sub-Saharan African countries. The
25 present study proposed a model based on cellular automata to predict year-to-year the risk of the
26 invasion and spread of *T. absoluta* across Africa. Using, land vegetation cover, temperature,
27 relative humidity and yield of tomato production as key driving factors, we were able to mimic
28 the spreading behavior of the pest, and to understand the role that each of these factors in the
29 process of propagation of invasion. Simulations by inferring the pest natural ability to fly long
30 distance revealed that *T. absoluta* could reach the South of Africa ten years after being detected
31 in Spain (Europe). Findings also reveal that relative humidity and the presence of *T. absoluta*
32 host plants are important factors for improving the accuracy of the prediction. The study aims to
33 inform stakeholders in plant health, plant quarantine, and pest management on the risks that *T.*
34 *absoluta* may cause at local, regional and event global scales. It is suggested that adequate
35 measures should be put in place to stop, control and contain the process used by this pest to
36 expand its range.

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38 **Keyword:** *Tuta absoluta*, spatial spread, vegetation, climatic factor, Cellular automata,
39 prediction.

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42 **1. Introduction**

43 World-wide, among vegetables, tomato, *Solanum lycopersicum* L. (Solanaceae), ranks high as a
44 food as well as a cash crop (USAID, 2005). However, tomato production is constrained by
45 numerous factors. Some important factors are arthropod pests such as the red spider mite
46 (*Tetranychus evansi* Baker & Pritchard), African bollworm *Helicoverpa armigera* (Huebner),
47 leafminers (*Liriomyza* spp.) and thrips (*Frankliniella* spp.) (Varela *et al.*, 2003). The problem is
48 further compounded by the recent invasion by a micro-Lepidoptera moth, the tomato leafminer,
49 *Tuta absoluta* (Meyrick, 1997) (Lepidoptera: Gelechiidae), which is currently the dominant pest
50 of the crop devastating production in all the invaded regions, especially in Africa. *T. absoluta* has
51 high reproductive potential, capable of yielding up to 12 generations per year under optimal
52 condition. The optimal temperature for its development ranges from 21 to 30°C. Low
53 temperature is a limiting factor for its survival but high humidity is suitable for its development
54 and life span (Cuthbertson *et al.*, 2013; Erdogan, 2014; Khadidja and Salaheddine, 2014;
55 Miranda *et al.*, 1998; NAPPO, 2014). A mature female can lay up to 260 eggs. The live cycle of
56 this pest is comprised of four developments stage (egg, larva, pupa, adult); which are all harmful
57 and can attack different parts (leaves, stems and fruits) of the host plants (Cuthbertson *et al.*,
58 2013; Erdogan, 2014; Khadidja and Salaheddine, 2014; Miranda *et al.*, 1998; NAPPO, 2014).

59 Although tomato appears to be the primary host of the *T absoluta*, it has also been reported to
60 attack other cultivated solanaceous crops such as potato, (*Solanum tuberosum* L.) and
61 eggplant,(*Solanum melongena* L.) (Ferracini *et al.* 2012; Mohamed *et al.* 2015). Outside its
62 native home range the pest was detected for the first time in Spain in 2006, from where it has
63 spread to several European countries including Italy (2008), France (2008), Albania (2009),
64 Bulgaria (2009), Portugal (2009), the Netherlands (2009), United Kingdom (2009) and Serbia

65 (2011) (Desneux et al. 2011). The pest has further spread and has currently invaded and become
66 established in North Africa, the Middle East and several other Asian countries including India
67 (Abbes et al. 2012).

68 In African, the pest is swiftly moving southwards to invade several eastern and western sub-
69 countries (Pfeiffer et al. 2013; Brévault et al. 2014; Tonnang et al., 2015). In all the invaded
70 regions, the pest is threatening tomato production causing massive and sometimes completes loss
71 of tomato in both green houses and open fields (Abbes et al. 2012; Mohamed et al. 2015). The
72 pest continues to spread at an alarming rate across the continent as well as expanding its host
73 range by attacking other vegetables and staple crops (e.g. African night shade, potatoes) that are
74 important sources of food and income for millions of people, particularly in poor communities of
75 Africa.

76 The study of pest invasion and spread is governed by a sequence of complex interactions
77 between the invader and the recipient agro-ecological regions (Richardson & Pyšek 2006).
78 Physical and biological characteristics of landscapes contribute to the establishment of invaders
79 (Davies et al. 2005). Tropical regions such as the majority of Africa are highly vulnerable to
80 insect species invasions, nevertheless, only a few scientific investigations on the dynamics and
81 spread of invasive capability of alien species have been undertaken (Dangles et al. 2008; Crespo-
82 Pérez et al. 2011; Osawa et al. 2013). Considering the economic importance of *T. absoluta* , and
83 the threat it poses to the production and trade of its host plants, developing models to predict the
84 risk of invasion and spread to new localities is of paramount importance for early warning of
85 invasions and management of such colonization (Crespo-Pérez et al. 2011).

86 Many approaches for modeling species invasions and spreads have been documented (Balzter et
87 al., 1998; Colasanti et al., 2007; Farashi and Shariati Najafabadi, 2015; Morozov et al., 2008;

88 Simpson et al., 2013). Mechanistic models are often been applied and their developments are
89 based on the understanding of the studied system (Bullock et al., 2006; Nathan et al., 2003).
90 Such a modeling framework is very useful and plays an important role in providing solutions for
91 modeling phenomena that are difficult to measure in the field (Bullock et al., 2006; Nathan et al.,
92 2003). Cellular Automata (CA) are methods of developing mechanistic models using a discrete
93 representation of space, time, variables and local interaction between its elements. CA have been
94 successfully used for various applications such as vegetation dynamics (Balzter et al., 1998;
95 Colasanti et al., 2007), disease epidemics (Beauchemin et al., 2005; Rhodes and Anderson,
96 1996), microorganism growth and dispersal (Ferreira et al., 2013; Walters et al., 2006), urban
97 growth and dynamics (Al-Ahmadi et al., 2009; Syphard et al., 2005) and prey-predator systems
98 (Ferreri and Venturino, 2013). Moreover, CA has been intensively used for modeling the spread
99 of processes driven by climatic and environmental factors (Cabrera, 2014; Gage, 1999; Crespo-
100 Pérez et al., 2011; Zhang et al., 2008; Clarke et al., 1994). The temperature was coupled with CA
101 to study the dispersal of potato tuber moth (Crespo-Pérez et al., 2011). Relative humidity and
102 temperature within a CA framework were applied to study population dynamic of *aculops*
103 *lycopersici* (Zhang et al., 2008); and wildfire propagation (Clarke et al., 1994). Some studies also
104 investigated vegetation cover through a CA approach (Cabrera, 2014; Gage, 1999). The present
105 study combined normalized difference vegetation index (NDVI), temperature, relative humidity
106 and yield of tomato production within a CA conceptual framework to yield an integrated spatial
107 and temporal model for predicting *T. absoluta* invasion and spread in Africa taking as the origin
108 of spread Spain in Europe. The use of such an approach provides an early warning mechanism to
109 serve as a tool for phytosanitary officers and policy makers to make informed decisions in order

110 to safeguard against potential invasions, spread and establishment of *T. absoluta* and to prioritize
111 the management needs.

112

113 **2. Material and methods**

114 **2.1. Area of study and datasets used**

115 The area of interest for this study includes Spain, Portugal, and the entire African continent. The
116 datasets used are the following: *T. absoluta* occurrence data, normalized difference vegetation
117 index (NDVI), temperature, relative humidity and the yield of tomato production per country. *T.*
118 *absoluta* occurrences data were obtained from literature searches (Abbes et al., 2012; Anon.
119 2012; Desneux et al. 2010; Ouardi et al., 2012; Tonnang et al., 2015; USDA APHIS 2011).
120 They are georeferencing point representing the record of *T. absoluta* in a location. The NDVI is
121 obtained using the visible and near-infrared light reflected by vegetation. It is calculated using
122 near-infrared radiation (NIR) minus visible radiation (VIS) divided by near-infrared radiation
123 plus visible radiation ($NDVI = (NIR - VIS)/(NIR + VIS)$). Calculations of NDVI for a given
124 pixel always result in a number that ranges from minus one (-1) to plus one (+1) (Herring and
125 Weier, 2000). NDVI for Europe was downloaded from an open source website BOKU
126 (University of Natural Resources and Life Sciences, Vienna) (Vuolo et al., 2012) while NDVI
127 for Africa were obtained from the U.S. Geological Survey (USGS) web site
128 (<https://dds.cr.usgs.gov/emodis/Africa/historical/TERRA/>). Temperature values were retrieved
129 from the WorldClim database (<http://www.worldclim.org/current>) (Hijmans et al., 2005); relative
130 humidity datasets were obtained from the Surface meteorology and Solar Energy (SSE) website
131 (<http://eosweb.larc.nasa.gov/sse/>). Information on harvested production per unit of area for

132 tomato in Africa was retrieved from the “factfish” web site
133 (<http://www.factfish.com/statistic/tomatoes%2C%20yield>)

134

135 **2.2. Datasets transformation**

136 The NDVI datasets for Europe (year 2014) is produced at 16 days intervals. NDVI values for
137 Africa (year 2013) corresponding to satellite data are produced at 5-day intervals and the image
138 represents the mean value of every month. For standardization, the values of NDVI were divided
139 by 10,000 so that they range from -1 to 1. Temperature data were organized in monthly mean
140 values with a grid of 30 arc-seconds, corresponding to approximately 1 kilometer of resolution.
141 Using Geographic Information System (GIS) software Quantum GIS (QGIS) we extracted the
142 values of temperatures by overlaying the geographic coordinates of the area of study on
143 temperature files. Relative humidity data acquired were in text files and contained the
144 geographical coordinates of the Earth surface spaced by 1x1 degree. The Inverse Distance
145 Weighting method (IDW) (Roshan and Kang, 2011) was used to interpolate the relative humidity
146 values to obtain a map, which was then aligned to the geographical coordinates of the area of
147 study. This process was repeated for twelve months of the year. Tomato yield production of the
148 world per country ranged from 0.46 to 499.6 tons per hectare for the year 2013 (Factfish, 2013).
149 Information of 168 countries is available on the Internet; however, we only selected countries
150 that belong to Africa and subdivided them into three classes. The classification exercise is
151 performed to differentiate location with high production to those with low production of tomato.
152 Class 1 (very high producers), corresponds to countries with a production greater than 30 tons
153 per hectare. The second class (high producers), corresponds to areas with a production of 10 to

154 30 tons per hectare, and the third class (low producers), which corresponds to countries with
155 production less than 10 tons per hectare.

156

157 **2.3. Cellular Automata (CA) model development and implementation**

158 The developed CA model is a spatially and temporally discrete system characterized by local
159 interactions and synchronous dynamical evolution. Overall, it consists of five main elements: (i)
160 a grid of cells, (ii) cell states, (iii) neighborhood, (iv) transition rules that determine how a cell
161 changes from one state to another, and (v) time step. The area of study was divided into square
162 regular lattices of 25x25 km to characterize an individual cell of the CA. Each cell can be in one
163 of the following three states: susceptible exposed and invaded. During the simulation, a
164 susceptible cell can either become exposed or invaded. The exposed state represents cells, which
165 *T. absoluta* may have crossed before reaching invaded cells. The invaded state corresponds to the
166 status of locations where the pest has a high risk of permanent establishment. Initially, all point
167 locations are susceptible to the invasion by *T. absoluta*. Only the point location in Spain, which
168 is the starting point of the simulation is considered invaded. The diagram in Fig. 2 is a schematic
169 representation, which outlines the model processes, algorithms, and state transitions.

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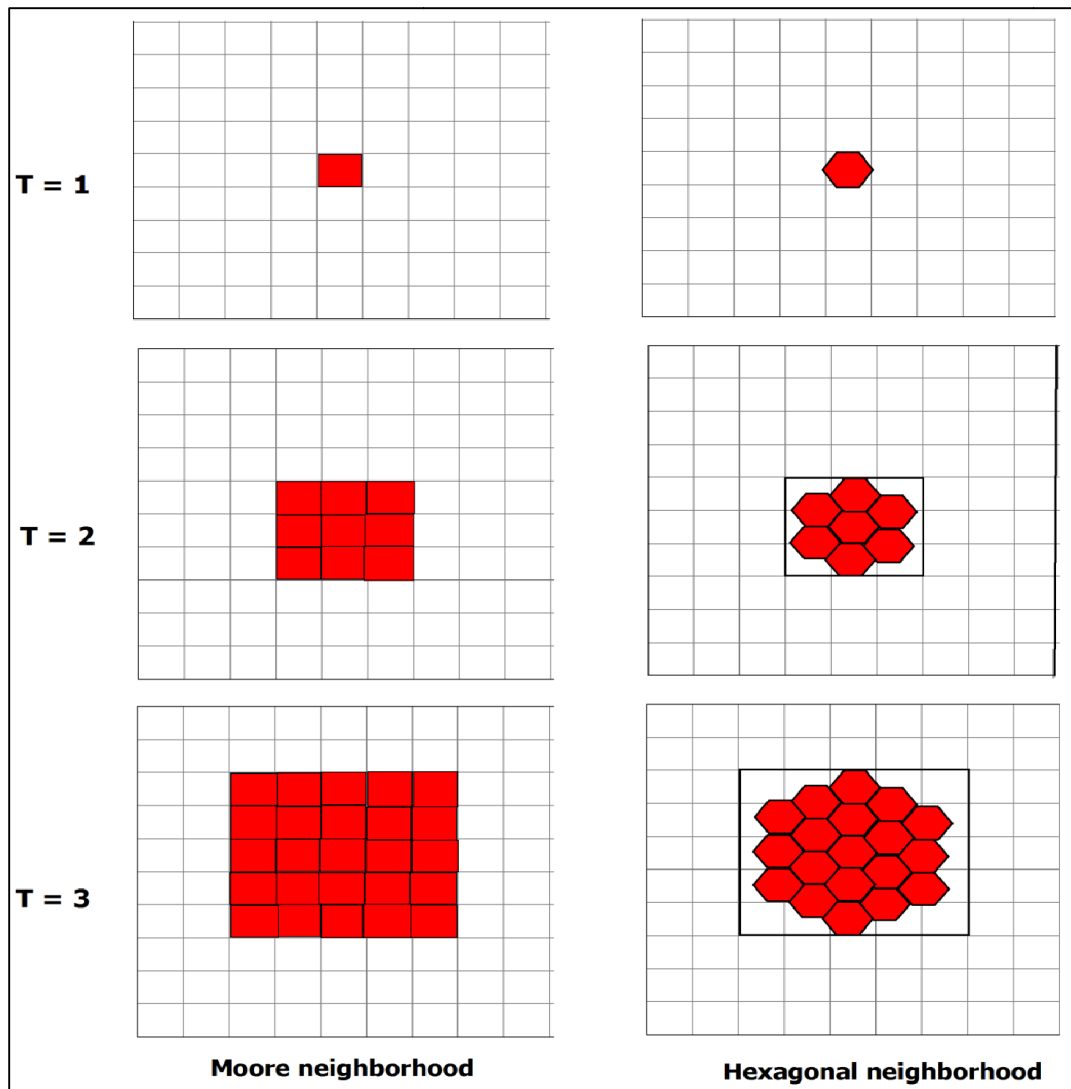
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172 **2.3.1. Cellular automata thresholds**

173 The rules of the CA model are defined with the aim to mimic the dispersion of *T. absoluta* in
174 Africa since its introduction in Europe. The optimum temperature threshold for its development
175 and dispersion range was used to define the rules. This information comes from laboratory and
176 field experiments on *T. absoluta*. Using the classification of NDVI developed by Badamasi et al.
177 (2012), we adopted two thresholds: The first value of NDVI threshold (threshold1 = 0.1) is

178 considered as the lower boundary to characterize the exposed zone; while the second threshold
179 (threshold2 = 0.3) is applied as the lower limit when the quantity of tomatoes production is
180 added as a variable for the selection of areas with risk of invasion and spread of the pest.
181 Temperature values for the development of immature life stages of *T. absoluta* range from 13°C
182 to 30°C and the complete developmental time of the pest is around 74 days at lower temperature
183 and shorter at higher temperature (Cuthbertson et al., 2013; Erdogan, 2014; Khadidja and
184 Salaheddine, 2014; Miranda et al., 1998). Between 21°C to 25°C the developmental time of *T.*
185 *absoluta* is approximately 30 days; therefore, it was found convenient to use a monthly time step
186 in the simulations, with a temperature threshold set at 22°C. Relative humidity for the
187 development of *T. absoluta* is suitable when it is greater than 50% (Brito et al., 2015; Cely et al.,
188 2011); for adequacy, it was set at 55%. Based on the classification on tomato yield production
189 presented above, we assigned zero (0) to locations with low production (class 3), one (1) to
190 locations of high production (class 2) and two (2) to locations of very high production (class 1).
191 In addition, because *T. absoluta* is reported to fly up to 100 Km (Government of Canada, 2012),
192 we opted for the Moore neighborhood (Moore, 1962) that covers an area of radius 100 km.
193 However, it was considered that the application of pheromone traps, insecticides, parasitoids or
194 any control and quarantine measures can contribute to reducing the population density and
195 dynamics of the pest. By doing so, *T. absoluta* ability to fly long distance may be affected and
196 the pest fly radius reduced. Under these assumptions, two simulations were carried out with
197 small values of the pest fly radius (75km and 50km). The choice of squared Moore neighborhood
198 provides a better coverage of space compared to the hexagonal neighborhood as shown Fig.
199 1(Langlois, 2013).

200



201

202 **Fig. 1.** Schematic representation of space coverage using squared Moore neighborhood and
 203 hexagonal neighborhood.

204 **2.3.2. Rules of the CA**

205 Cells in the neighborhood of infected area are updated deterministically according to the
 206 following rules:

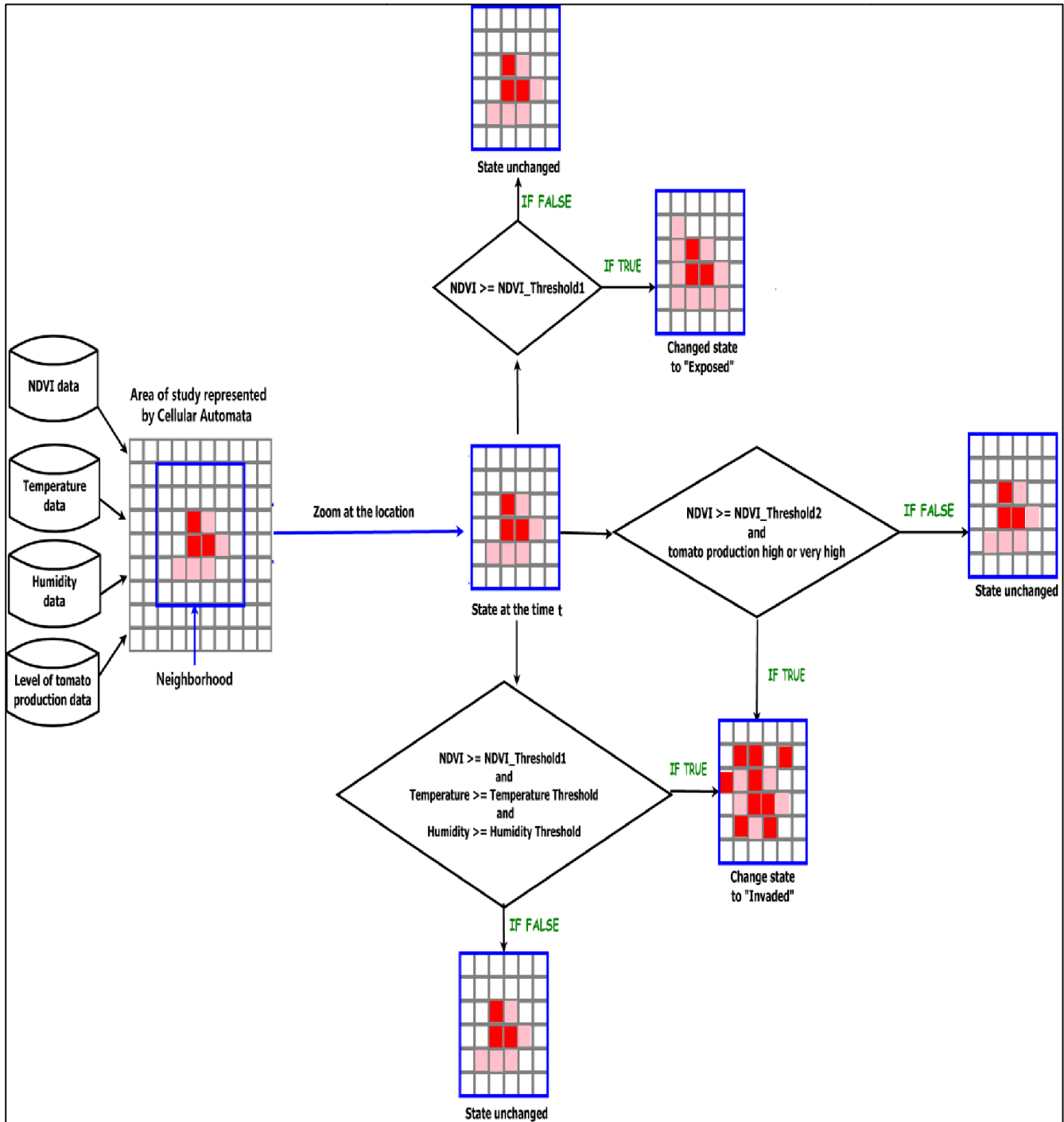
207 Susceptible cell (S): A susceptible cell can become exposed (E), invaded (I) or still susceptible
 208 (S) depending on the state of the parameters. The following conditions allow a susceptible
 209 cell(S) to remain or change state. i) If the value of NDVI is lower than the NDVI threshold

210 (NDVI < threshold1), meaning that there is no reasonable environmental condition in the
211 location to allow the change of state. The susceptible cell remains susceptible (S to S). ii) If the
212 value of NDVI is greater than or equal to the NDVI threshold (NDVI \geq threshold1); this means
213 that the insect may be there but without clear damages to crops, probably because the climatic
214 conditions are not favorable for its development and reproduction, the susceptible cell turns
215 exposed (S to E). iii) A susceptible cell change state and becomes infected (S to I) when either
216 one of the following conditions is satisfied: 1) If the value of NDVI, temperature, and relative
217 humidity are greater than the value of their corresponding threshold (NDVI \geq threshold1,
218 temperature \geq temperature threshold and relative humidity \geq relative humidity threshold); or 2) if
219 regardless of the value of relative humidity and temperature, the NDVI is greater than the NDVI
220 threshold (threshold2) and the location belongs to an area of the first and second classes using
221 the classification based on the quantity of tomatoes production (NDVI \geq threshold_2 and tomato
222 production=1or2).

223 An exposed location can become invaded (E to I) if environmental conditions change and
224 become suitable for the establishment of *T. absoluta*, meaning that one of the rules for the
225 infestation described above is satisfied otherwise, it does not change its state. An invaded
226 location cannot change its state during the simulations if no quarantine and control measures
227 against *T. absoluta* are applied.

228

229



230

231 **Fig. 2.** Schematic representation of the modeling approach for the invasion and spread of *T.*
 232 *absoluta*. The approach is based on cellular automata and the grid represents the cells of our area
 233 of study. The rules of the cellular automata are defined using NDVI, temperature, relative
 234 humidity and yield of tomato production.

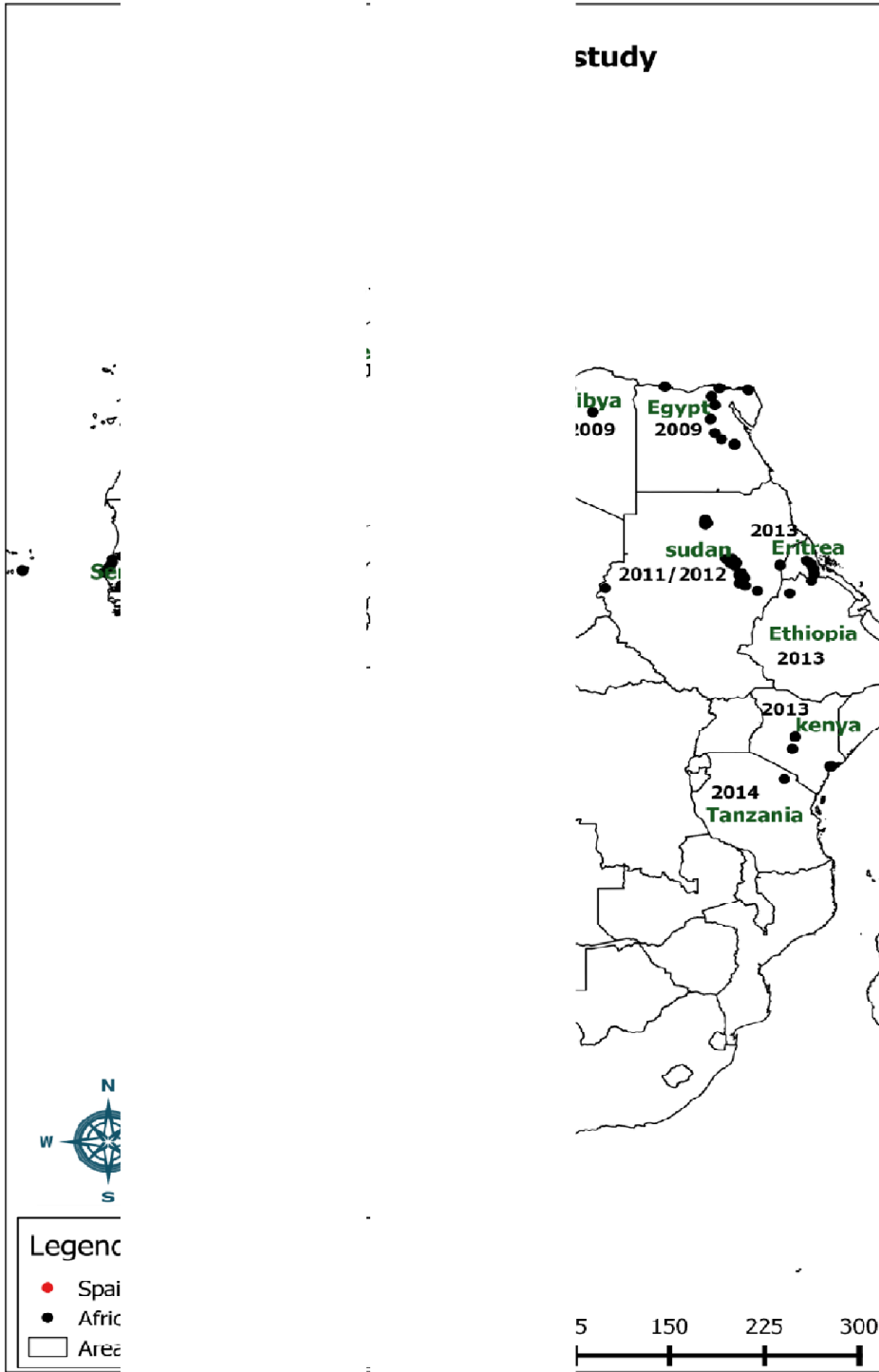
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239 **2.4. Model implementation and simulation processes**

240 The model was implemented in MATLAB (R2010a, The MathWorks). Starting from the
241 knowing infected locations in Spain, the temporal and spatial spreading of the insect-pest was
242 observed considering different scenarios. It permits to evaluate the sensitivity of the model
243 parameters (temperature, vegetation index and others) and to enhance the understanding of the
244 invasion process of *T. absoluta*. We begin the simulations by taking in consideration only
245 vegetation (NDVI) data as an input parameter; thereafter we progressively introduced
246 temperature, relative humidity and the yield of tomatoes per region. Fig. 3 displays the overall
247 studied areas and the initial geographical location of the simulations.

study



248

249 **Fig. 3.** Studied area where the spread of *T. absoluta* occurs. The geo-referenced points in black
250 represent known locations of occurrence of *T. absoluta* and the red spot in Spain is considered as
251 the initial point of invasion from where *T. absoluta* has spread in Africa.

252 **2.5. Model validation**

253 The validation of the model is done using pattern-oriented modeling strategy (Grimm, 2005;
254 Grimm et al., 1996). With this approach, we have to assess the model ability to reproduce the
255 time period that past events have occurred and to predict the timing of future advents. The
256 Validation required that after 7 years *T. absoluta* should have reached Kenya. Further
257 verification of the accuracy rests on the fact that, by reaching Kenya, the pest might have
258 progressively infested other areas in the northern, western and eastern parts of the African
259 continent. So far *T. absoluta* has been confirmed in the following countries: Morocco in
260 2007/2008; Algeria and North of Sahel in 2008; Tunisia in 2008/2009; Egypt and Libya in 2009;
261 Ethiopia, Niger, Senegal, Sudan in 2011/ 2012; and Kenya in 2013 (Abbes et al., 2012; Desneux
262 et al., 2010; Anon. 2012; Mohamed et al., 2012; Ouardi et al., 2012; Pfeiffer et al., 2013; USDA
263 APHIS 2011). After several calibrations, once the developed model reasonably satisfied the
264 evaluation criteria by correctly reproducing the timing known events described above, it was
265 then used to predict the time *T. absoluta* is likely to take in order to reach the South of Africa.

266 **2.6. Keys assumptions of the model**

267 The model we designed and implemented is based on following assumptions: (i)The type of
268 vegetation is not taking into consideration, meaning that in any location where there is
269 vegetation, it was assumed that the area is suitable for the growth of any host plant of *T.*
270 *absoluta*. (ii)Altitude is neglected because the current distribution of *T. absoluta* suggests that it
271 can survive at both low and high altitude(BIOCOMES, 2015; Hardy and International Potato
272 Center, 1996; Povolny, 1975). (iii) The values of NDVI are considered to be identical for the
273 whole simulation period. No distinction was made on the fact that NDVI of Europe was
274 produced in 16 days interval (Vuolo et al., 2012) whereas in Africa it was produced at 5 days

275 interval (<https://dds.cr.usgs.gov/emodis/Africa/historical/TERRA/>). (iv)For every cellular
276 automata (CA) cell, a barycenter was estimated and the closest georeference point location to
277 this barycenter was considered as the center of the cell.

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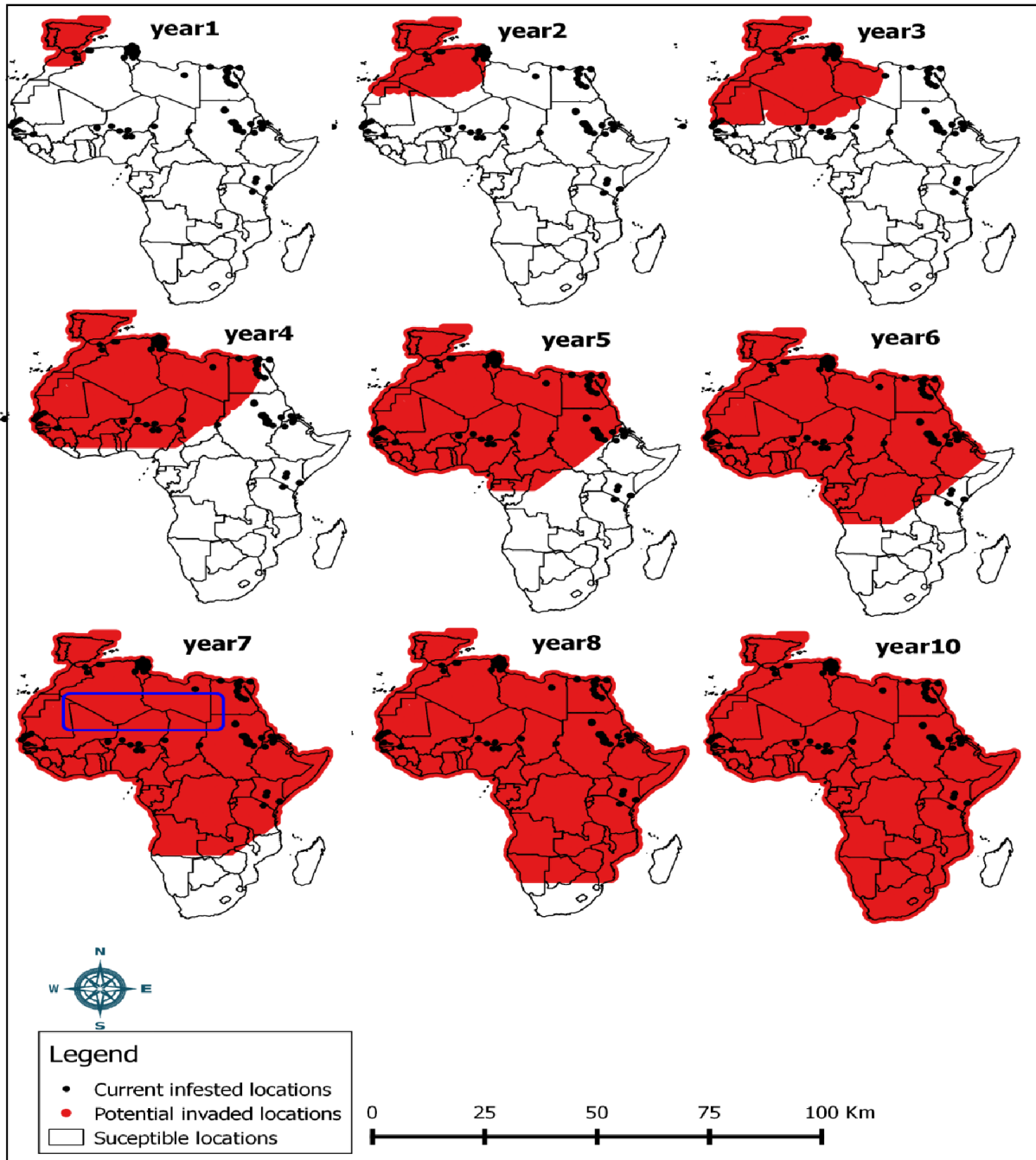
279 **3. Results**

280 The predictions of the risk of invasion and spread of *T. absoluta* in Africa considering Spain as
281 the initial posit of the pest dispersal are presented in different maps. Fig. 4 displays the results of
282 the simulation when only the vegetation parameter is taken into account. A similar trend is
283 observed with the combined effects of both vegetation and temperature (Fig. 5). When the
284 vegetation and relative humidity are both considered (Fig .6), it is observed that although *T.*
285 *absoluta* has the ability to fly for long distances, its spread across the Sahara desert and its
286 invasion into the sub-Sahara region could not have been via natural means, but rather through
287 human-mediated activities such as trade. Taking into account relative humidity and temperature
288 (Fig. 7) we obtained maps almost identical to the scenario, which only account for vegetation
289 and relative humidity. The combined effects of vegetation, relative humidity and temperature
290 (Fig. 8) did not show major changes from previous scenarios that include relative humidity. Fig.
291 9 shows 10 years of simulation of *T. absoluta* spread with the collective effects of vegetation,
292 relative humidity, temperature and yield of tomato production per area. The introduction of the
293 yield of tomato production allows the detection of some areas, which were not well captured in
294 previous cases when only climatic factors were considered as main variables in the simulations.
295 As shown in Fig. 6 and 7, relative humidity seems to be an important parameter for predicting
296 the risk of invasion and spread of *T. absoluta*. In all simulations when this parameter is included,
297 the pest invasion and spread evolution is the closest to the boundaries of natural observations.

298 Changes in the values of the relative humidity threshold from 50% to 60% gave good results;
299 below 50% the spread and invasion observed is similar to Figures 5 and 6; while above 65% we
300 observed a lot of discontinuity in the spread, which did not reflect the observed occurrence of the
301 pest.

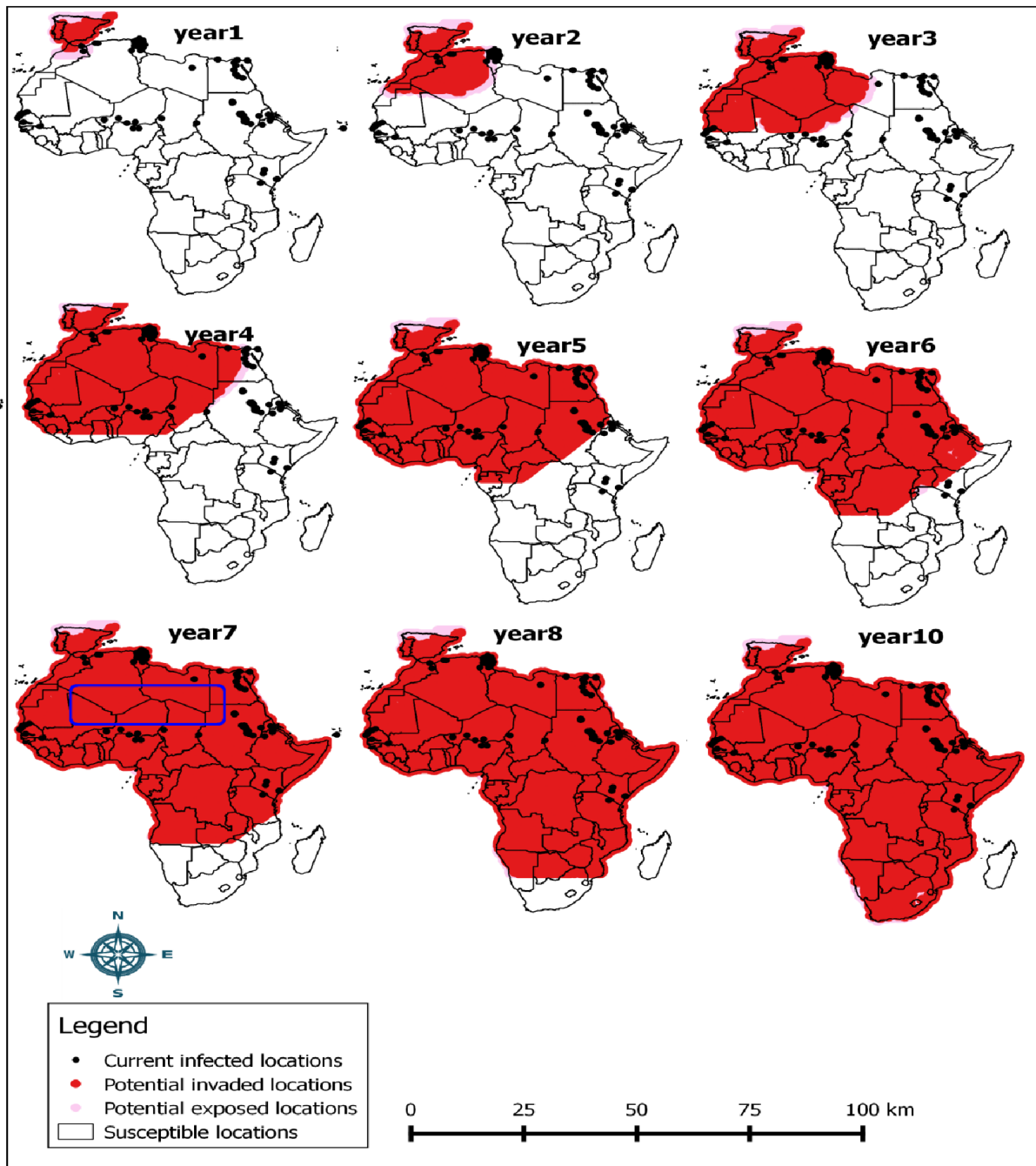
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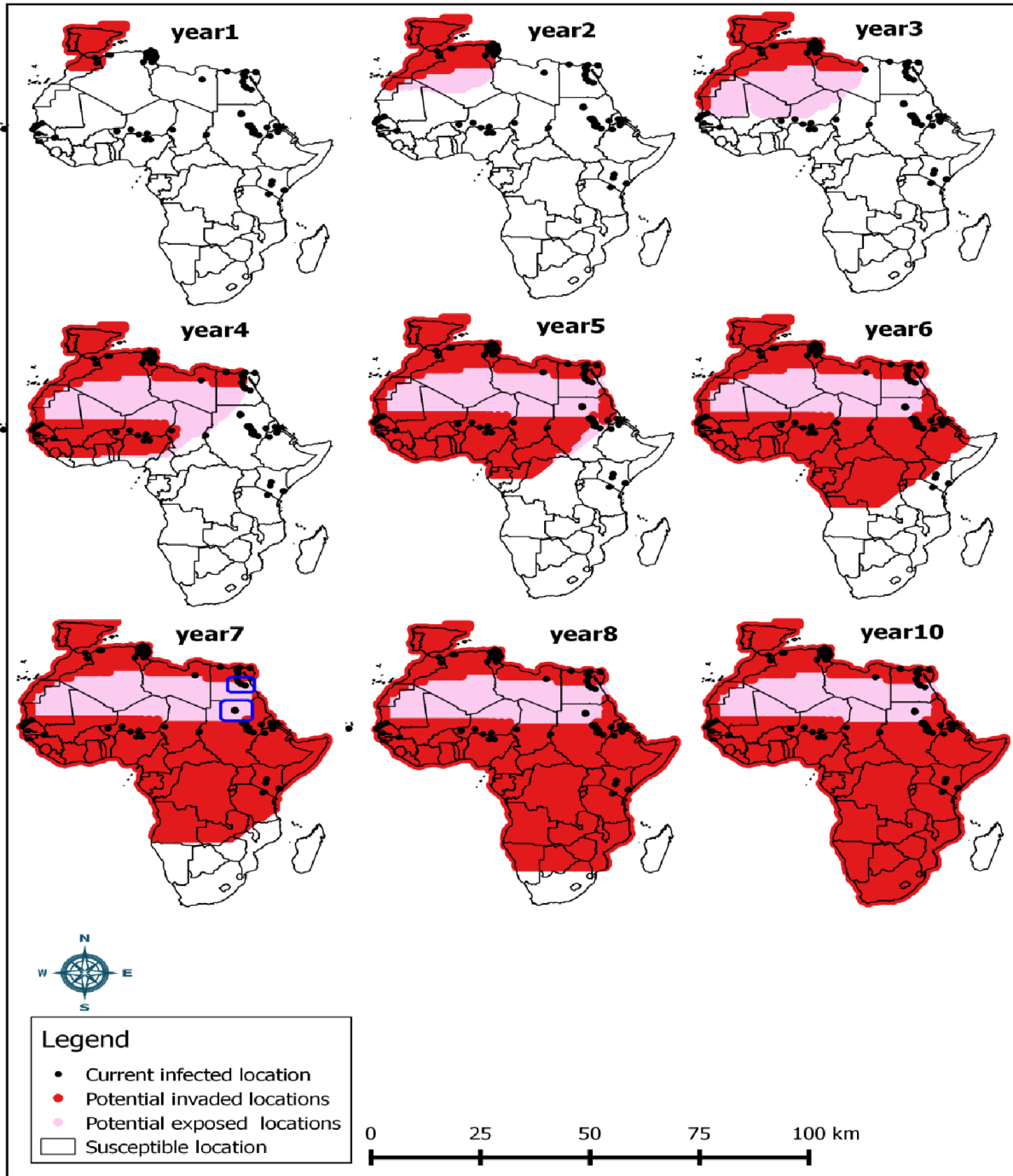
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305 **Fig. 4.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 306 account only vegetation as a parameter for the pest propagation. The geo-referenced points in
 307 black represent locations of occurrence of *T. absoluta* and the areas in white are susceptible
 308 locations. Zones in red represent zones at high risk of invasion and spread of the pest. The
 309 simulations are carried out within the 10-year period from 2008 to 2018. Areas in blue color in
 310 year 7, represents zone of mismatch requesting an improvement of the model.



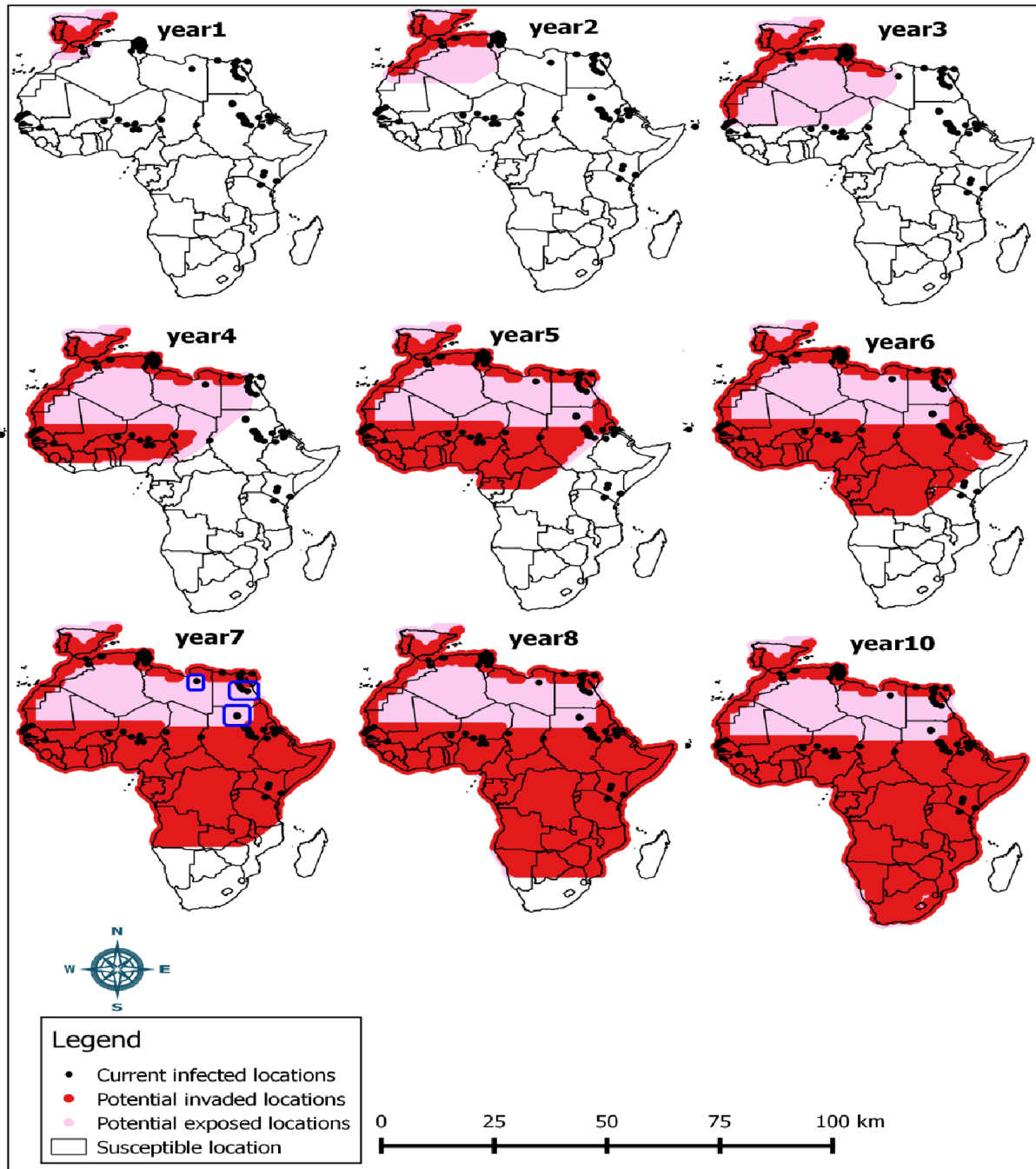
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312 **Fig. 5.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 313 account vegetation and temperature as parameters for the pest propagation. The geo-referenced
 314 points in black represent locations of occurrence of *T. absoluta* and the areas in white are
 315 susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 316 Zones in red represent zones at high risk of invasion and spread of the pest. The simulations are
 317 carried out within the 10-year period from 2008 to 2018. Areas in blue color in year 7, represents
 318 the zone of mismatch requesting an improvement of the model.



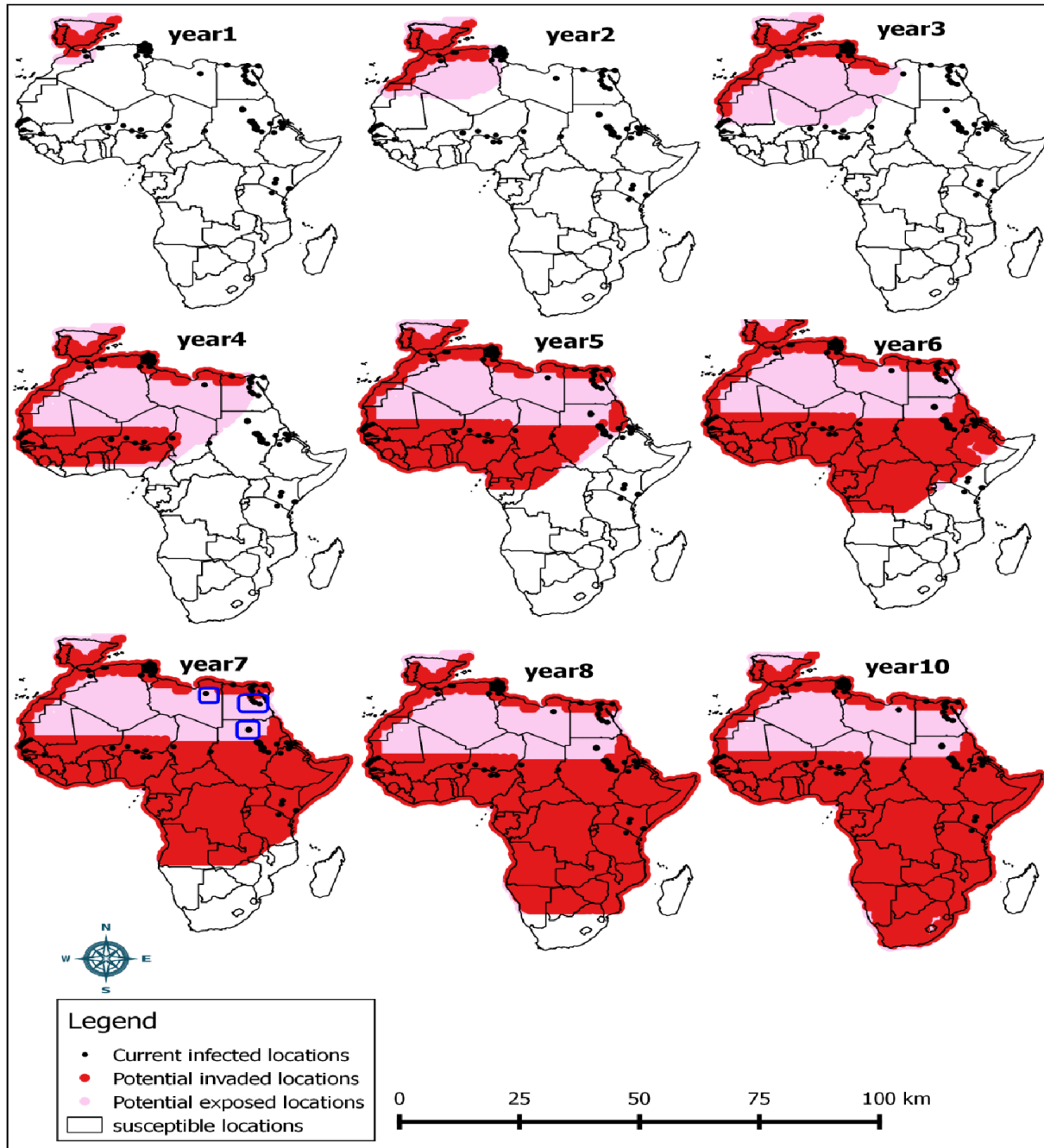
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320 **Fig. 6.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 321 account vegetation and humidity as parameters for the pest propagation. The geo-referenced
 322 points in black represent locations of occurrence of *T. absoluta* and the areas in white are
 323 susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 324 Zones in red represent zones at high risk of invasion and spread of the pest. The simulations are
 325 carried out within the 10-year period from 2008 to 2018. Areas in blue color in year 7, represents
 326 zones of mismatch requesting an improvement of the model.



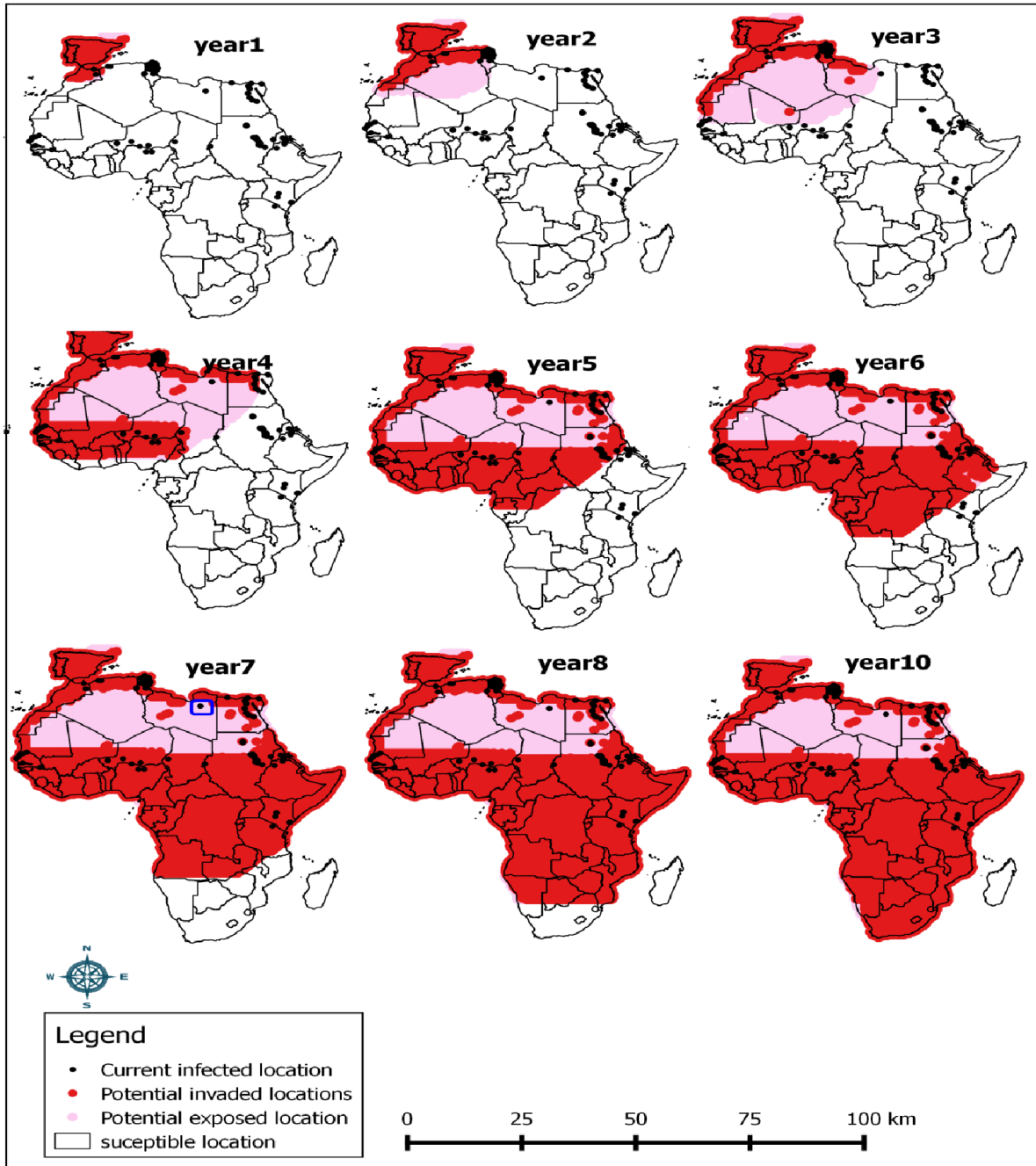
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328 **Fig. 7.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 329 account humidity and temperature as parameters for the pest propagation. The geo-referenced
 330 points in black represent locations of occurrence of *T. absoluta* and the areas in white are
 331 susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 332 Zones in red represent zones at high risk of invasion and spread of the pest. The simulations are
 333 carried out within the 10-year period from 2008 to 2018. Areas in blue color in year 7, represents
 334 zones of mismatch requesting an improvement of the model.



335

336 **Fig. 8.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 337 account vegetation, humidity, and temperature as parameters for the pest propagation. The geo-
 338 referenced points in black represent locations of occurrence of *T. absoluta* and the areas in white
 339 are susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 340 Zones in red represent zones at high risk of invasion and spread of the pest. The simulations are
 341 carried out within the 10 year period from 2008 to 2018. Areas in blue color in year 7, represents
 342 zones of mismatch requesting an improvement of the model.



343

344 **Fig. 9.** The spread of *T. absoluta* in Africa obtained through a 10 years simulation taking into
 345 account vegetation, humidity, temperature and yield of tomatoes production as parameters for the
 346 pest propagation. The geo-referenced points in black represent locations of occurrence of *T.*
 347 *absoluta* and the areas in white are susceptible locations. Zones in pink are zone at low risk of
 348 invasion and spread of the pest. Zones in red represent zones at high risk of invasion and spread
 349 of the pest. The simulations are carried out within the 10-year period from 2008 to 2018. Areas
 350 in blue color in year 7, represents zones of mismatch requesting an improvement of the model.

351 The following table summarizes and compares simulation according to different parameters used
 352 and provides justification on why additional inputs were included to improve the model outputs.

353 **Table 1: summary effects of inputs parameters on simulations results**

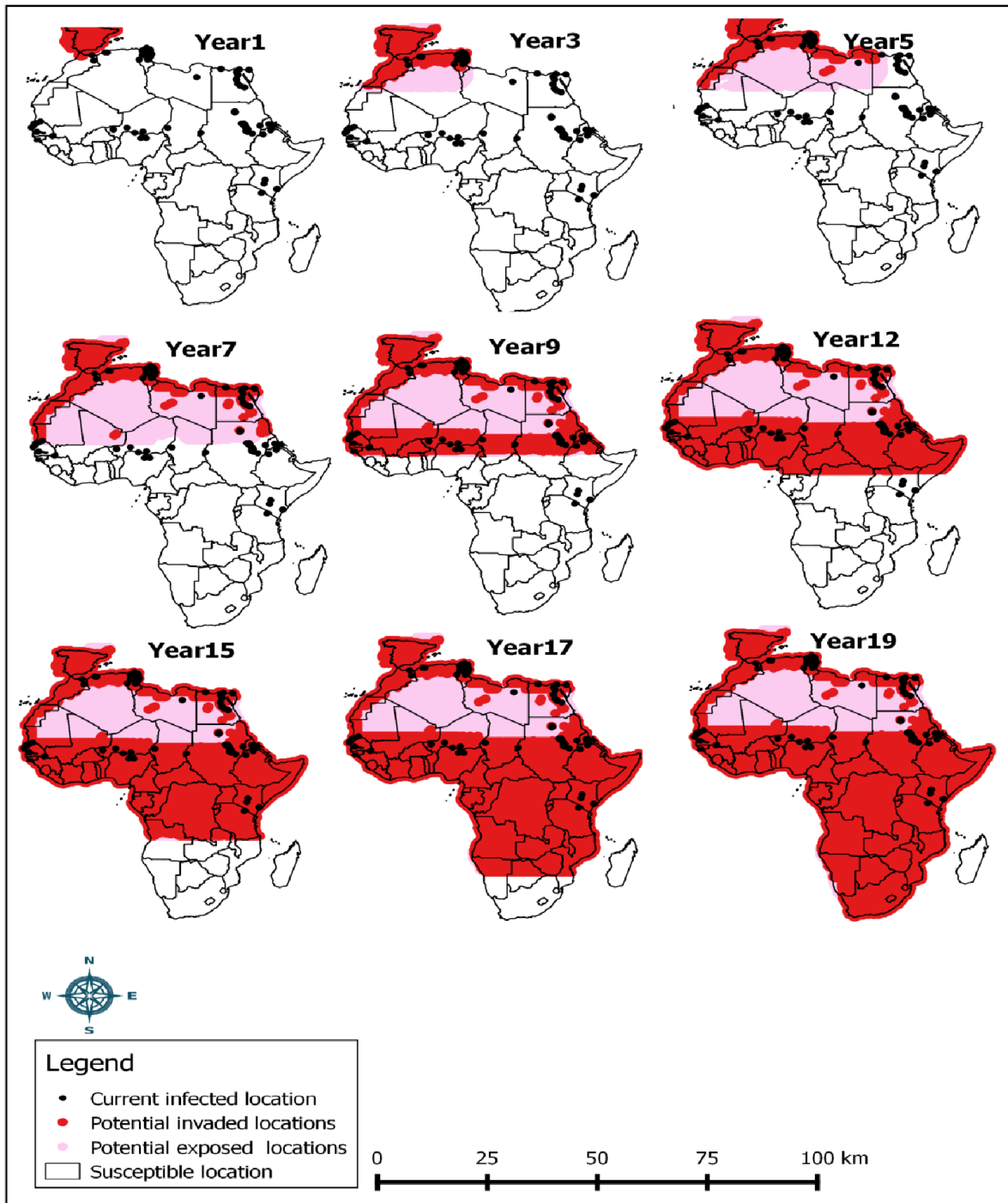
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	Parameter used				Observation
	NDVI	Temperature	Relative humidity	Tomato Production	
Fig. 4	✓				The model invaded Kenya after seven years but included the Sahara desert (graphical zone depiction in blue) as potentially invaded location, which in reality may not be the case
Fig. 5	✓	✓			No improvement in the model output as the Sahara desert is still included as potentially invaded location by the pest.
Fig. 6	✓		✓		An improvement in the model output was observed because the Sahara desert is no more captured as potentially invaded locations. Nevertheless, some known invaded locations in Egypt and Sudan (graphical depiction in blue) are not captured
Fig. 7		✓	✓		Locations in Egypt, Sudan, and Libya (see the graphical areas depiction in blue) are not captured; as potentially invaded zone
Fig. 8	✓	✓	✓		No improvement as locations in Egypt, Sudan and Libya are still not identified as invaded
Fig. 9	✓	✓	✓	✓	The adding of tomato production improved the model output and more areas of Egypt and Sudan are captured.

355

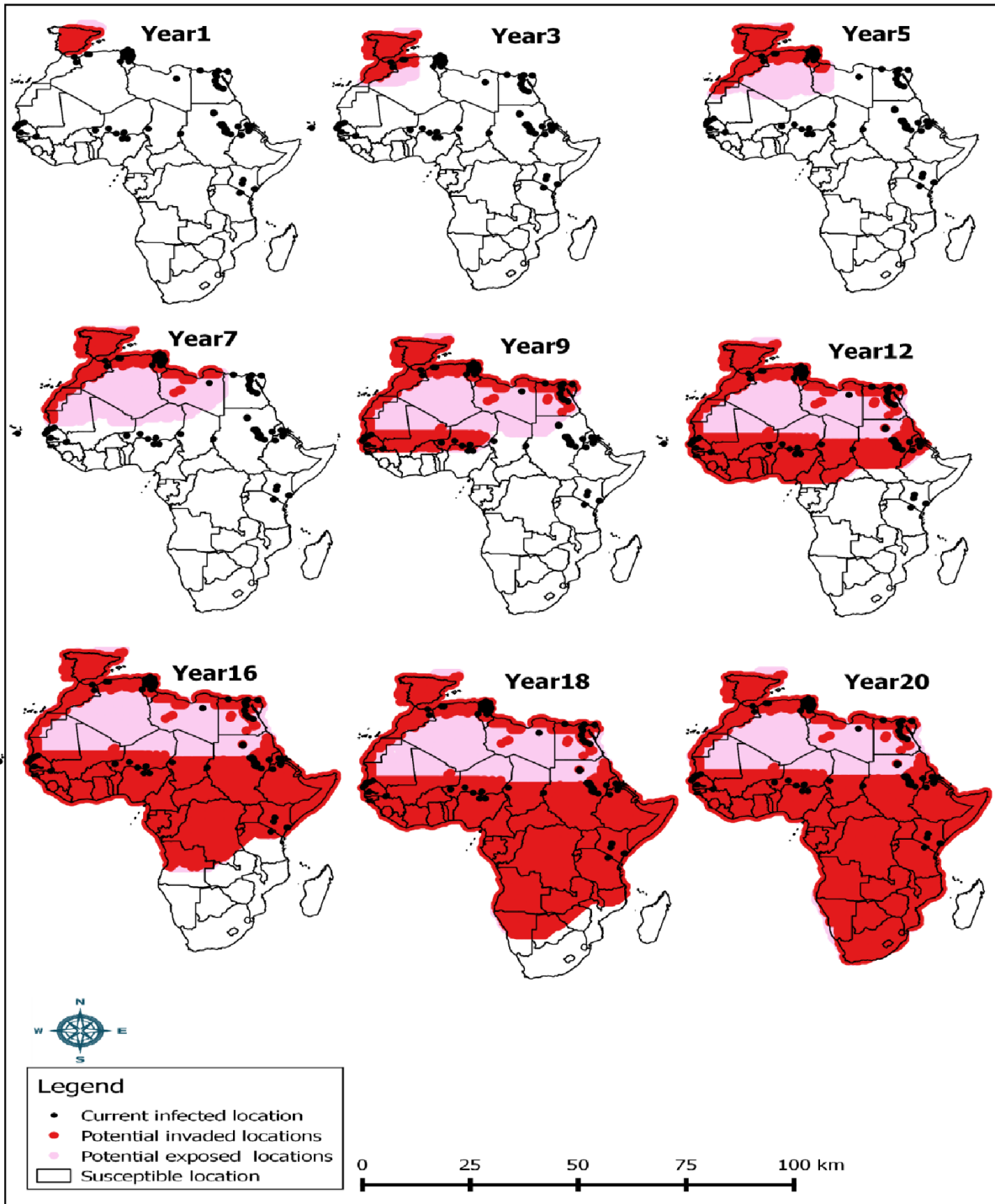
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357



358

359 **Fig. 10.** The spread of *T. absoluta* in Africa at a flying radius of 75km. The result is obtained
 360 after 19 years of simulation (from 2008 to 2027) taking into account vegetation, humidity,
 361 temperature and yield of tomatoes production as parameters for the pest propagation. The geo-
 362 referenced points in black represent locations of occurrence of *T. absoluta* and the areas in white
 363 are susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 364 Zones in red represent zones at high risk of invasion and spread of the pest.



365

366 **Fig. 11.** The spread of *T. absoluta* in Africa at a flying radius of 50 km. The result is obtained
 367 after 20 years of simulation (from 2008 to 2028) taking into account vegetation, humidity,
 368 temperature and yield of tomatoes production as parameters for the pest propagation. The geo-
 369 referenced points in black represent locations of occurrence of *T. absoluta* and the areas in white
 370 are susceptible locations. Zones in pink are zone at low risk of invasion and spread of the pest.
 371 Zones in red represent zones at high risk of invasion and spread of the pest.

372 Overall, the simulations demonstrate that the entire continent is at high risk of invasion and
373 spread of *T. absoluta*. The pest reaches Morocco after 1 year, Algeria and North of Sahel after 2
374 years, Tunisia after 3 years, Senegal in West Africa after 4 years, Sudan and Ethiopia after five
375 years and Kenya after 7 years. These sequences of events confirm the reported dates of detection
376 of the pest in these countries. Given the model adequacy in reproducing past and current events
377 of *T. absoluta* invasion and spread, we found it adequate to use for predicting the time period
378 when *T. absoluta* will reach the southern part of Africa if nothing is done to contain the pest and
379 curb its southward movements. Based on our model predictions *T. absoluta* will reach South
380 Africa 10 years after its presence was declared in Spain. Another important result showed by the
381 simulations suggested that relative humidity is the environmental factor, which has the greatest
382 influence on the suitability of the location for the establishment of *T. absoluta*. Moreover for
383 locations where environmental factors are not suitable the presence of *T. absoluta* host plants
384 such as tomato highly increases the pest risk of invasion and spread.

385 Results accounting on the application of some control measures that impact *T. absoluta*
386 population density and dynamics are shown in Fig 10 - 11. These Figures display the outputs of
387 the model simulations with the pest-flying radius of 75km (Fig. 10) and 50km (Fig. 11)
388 respectively. With *T. absoluta* flying radius of 75km it takes 19years for the pest to reach the
389 South of Africa and only Morocco, Algeria and Tunisia were invaded at the recorded time period
390 of three years. When 50 km was considered as the flying radius, it takes 20 years for the pest to
391 reach the South of Africa and none of the known areas of occurrence of *T. absoluta* within Africa
392 were captured at the exact time period. Under these scenarios of varying the pest population
393 density and dynamics by changing the values of the flying radius, we observed that *T. absoluta*
394 would have taken at least 12 to reach Kenya. This outcome suggests that if adequate quarantine

395 and control measures were introduced since the pest occurrence in Spain it should have taken
396 several years (> 20) for the pest to be found under natural invasion and spread mechanism in
397 South Africa.

398 **4. Discussion**

399 Developing dynamic models for invasive species such as *T. absoluta* spread in mixed
400 environments is a challenging task that necessitates a robust conceptual framework, capable of
401 exploring population dynamics both temporally and spatially as well as capturing the biology,
402 life history, host plants and other biotic and abiotic factors (Sebert-Cuvillier *et al.*, 2008). Herein,
403 we proposed a model based on cellular automata to predict the potential invasion of *T. absoluta*.
404 The pest spread was sensitive to changes made on the thresholds values of some keys parameters
405 that are related to the species life history and bioecology. Although this modeling framework
406 uses simulations, it provides prediction of the timing and record dates that are compared to
407 known time periods of the occurrence of *T. absoluta* in the regions of interest (Russell IPM,
408 2015).

409 NDVI dynamics have been reported as a good predictor for animal presence/absence (Pettorelli,
410 2013). The NDVI was used to study the change in the geographic distribution of black cutworm,
411 *Agrotis ipsilon* (Hufnagel) (Insecta: Lepidoptera: Noctuidae) in the United States (Showers,
412 1997). However, it is important to note that there are two contradictory schools of thought that
413 relate to the influence of NDVI for predicting species spread and distribution. The first highlights
414 the influence of land cover on species distribution (Blake *et al.*, 2013; Cornélis *et al.*, 2011; Ito *et*
415 *al.*, 2006), especially when the study is conducted on a small scale, whereas the second school of
416 thought supports the idea that there is no influence of land cover on the spread of species
417 (Thuiller *et al.*, 2004; Wilson *et al.*, 2013). Indeed, our results, which are in agreement with

418 previous studies on species invasion and spread conducted at large scales (Thuiller et al., 2004;
419 Wilson et al., 2013), revealed that the spread of *T. absoluta* is not significantly influenced by
420 NDVI.

421 Evidence of the direct and indirect effect of climatic factors on the spread of organisms has been
422 broadly illustrated (Travis et al., 2013). Temperature is reported as one of the most important
423 factors influencing the development and behavior of insects (Chapman et al., 2013). The use of
424 temperature in a CA modeling framework for the spread of potato tuber moth was presented by
425 Crespo-Pérez et al. (2011). The authors captured the variable temperature of a cell with a linear
426 function. In the present study, although we selected temperature within the optimum threshold
427 for *T. absoluta* development (Cuthbertson et al., 2013; Erdogan, 2014; Khadidja and
428 Salaheddine, 2014; Miranda et al., 1998; NAPPO, 2014), it was found that temperature was not a
429 key parameter in predicting the risk of invasion and spread of the pest.

430 High humidity is crucial for the growth of the solanaceae host (Bakker, 1991; Schwarz et al.,
431 2014). It is also reported that high humidity is suitable for the development of *T. absoluta*
432 (Cuthbertson et al., 2013; Erdogan, 2014; Khadidja and Salaheddine, 2014; Miranda et al.,
433 1998). A review of the literature (Brito et al., 2015; Cely et al., 2011; Cuthbertson et al., 2013;
434 Erdogan, 2014), permits the precise choice of the threshold of relative humidity. These values
435 provide a good trend for the invasion and spread of *T. absoluta*. The inclusion of relative
436 humidity as a variable in our simulation allows better predictions leading to the hypothesis that
437 this variable might be an important climatic factor determining the choice of a location during
438 the invasion and spread of *T. absoluta*.

439 One of the most important ecological causes of pest problems is the practice of monoculture
440 (Pimentel, 2009, 1997). Current agricultural systems are characterized by the growing of one
441 species of plant in large areas (Matson et al., 1997); such practice highly increases the
442 probability of invasion and establishment of insect pests because it offers in permanence food
443 (host plants). These findings are further confirmed by our results. Firstly, by comparing a recent
444 map of the distribution of *T. absoluta* (Russell IPM, 2015) with the map of climatic suitability of
445 Tonnang et al (2015), we observe that many of the current known occurrence locations belong to
446 areas identified as not suitable or with moderate level of suitability for the establishment of *T.*
447 *absoluta*. When the yields of tomatoes production per area were inputted into the simulations, we
448 found a considerable improvement in the results by capturing more invaded locations in the
449 Eastern part of Africa, which were not reflected when using only climatic factors. These results
450 support the assertion that intensification of agriculture production widely increases the risk of
451 invasion and spread as well as the density of pest damage in crops (Bianchi et al., 2006; Matson
452 et al., 1997; Segoli and Rosenheim, 2012).

453 The model predicts that the invasion by *T. absoluta* could reach South Africa 10 (ten years) after
454 its detection in Spain. An interesting feature is that the progress of the pest through simulation
455 year-to- year is quite similar to the observed dates of progression of *T. absoluta* in Africa (
456 Abbes et al., 2012; Anon. 2012; Desneux et al. 2010; Ouardi et al., 2012; Tonnang et al., 2015;
457 USDA APHIS 2011). Madagascar, though it enjoys climatic conditions, which are conducive for
458 establishment of *T. absoluta*, might not be invaded due to its geographical location as an isolated
459 island except by accidental introduction. In this context, our results suggest that adequate
460 measures should be put in place to stop, control and contain the process this pest is using to
461 expand its range from the geographical areas it currently occupies into new zones. The

462 effectiveness of such approach has been proved to be successful to slow down the spread and the
463 crop production loss due to the pest (Adams and Lee, 2011). In regions already invaded by the
464 pest, efficient control approaches within Integrated Pest Management (IPM) strategies should be
465 introduced. This especially true knows that resistance of *T. absoluta* to insecticide has been
466 reported (Gontijo et al., 2013; Silva et al., 2011). All locations predicted to be at risk of invasion
467 belong to areas identified as potentially suitable for a long-term establishment of the *T. absoluta*
468 (Tonnang et al., 2015). Moreover, the designing of this model is not based on presence/absence
469 data such as that used for CLIMEX modeling approach by Tonnang et al. (2015), rather; time
470 period of record data was used only for the model validation. Another peculiarity of the
471 modeling approach used in this study is that the prediction is made on the annual basis, which
472 allows predicting when *T. absoluta* might spread in time and space and invade new areas.

473 The studies of insects physiology and behaviors (Chapman et al., 2013; Wigglesworth, 2012)
474 reported that, after reaching mature stages, these animals initiate the process of flight migration
475 (Wigglesworth, 2012), looking for suitable environment to feed, mate and reproduce (Alyokhin
476 and Ferro, 1999; Prasad, 1985). It is during these processes that agricultural crops are damaged
477 by insects' herbivores. The goal of control measures is to maintain pest damage at economically
478 acceptable levels (University of Minnesota, 2012) and direct impact of a good application of a
479 control measure is to slow down the level of damage caused by pest. Current, strategies used to
480 control *T. absoluta* are garden sanitation, destruction of alternative host and the use of mass
481 trapping with sex pheromone. The majority of these methods aim to reduce the pest population
482 density and dynamics. In this study, an attempt of introducing control measures was applied by
483 varying *T. absoluta* flying radius ability. The findings suggest that efficient control measures
484 would considerably slow down the progression of spread *T. absoluta* and if such measures were

485 introduced since the pest detection in Spain in 2006 it should have taken more than 7 years to
486 reach Kenya.

487 The spatial heterogeneity of the environment of study is one the key factor which greatly
488 influences the invasion process; given that unsuitable locations will have the effect of slowing
489 down the spread (Hastings et al., 2005). Indeed, CA by its definition offers the possibility to take
490 into account this heterogeneity by applying rules on each cell of the area of study with a fixed
491 time step for the pest progression. Reaction-diffusion, gravity, and individual-based models are
492 also proposed as approaches which could handle spatial heterogeneity for modeling the complex
493 process of insect invasion and spread (Hastings et al., 2005). However, some form of diffusion
494 model based on partial differential equations sometimes ignores the underlying variation of the
495 environment and assumes that movement is essentially the result of a very large number of steps
496 of arbitrarily small size (Hastings et al., 2005). In the gravity model, the heterogeneity of the
497 surrounding environment is used to estimate and determine the attractiveness of the given
498 destination (Bossenbroek et al., 2001; Hastings et al., 2005). Individual-based models represent
499 the best approach to incorporate all detailed information like fecundity, phenology and landscape
500 structure in the process of invasion (Hastings et al., 2005). Another alternative to CA could have
501 been the use of reaction-diffusion model, which is also suitable to study and understand the
502 generality driving the process of invasion (Hastings et al., 2005). Moreover, it has been shown
503 that CA can be used as an alternative to differential equations that are forms of reaction-diffusion
504 model (Toffoli, 1984).

505 Although the time periods predict by our model to invade a location are not fully in-line with
506 those obtained from the dates of occurrence, they give general insights on how and when *T.*
507 *absoluta* could spread within Africa. Reasons for the discrepancies can be explained by the

508 following arguments. 1) Data on NDVI, temperature and relative humidity used for every
509 simulation are not those of the actually observed information corresponding to each specific
510 year. The values of one year were assumed to represent all the years of the simulations. It is
511 expected that the model predictions should have improved if during the simulation we used
512 datasets corresponding to each year. 2) Insects behavior in nature is complex and random, thus,
513 we cannot really predict with high accuracy their exact attitude but only identify areas with high
514 suitability for its establishment. 3) Human-assisted invasion and spreading pathways were not
515 included into the model (Crespo-perez et al., 2011; Gagnon et al., 2015; Koch et al., 2014). 4)
516 There are also many other elements such as the phenology of *T. absoluta*, the speed and direction
517 of the wind, the flux on exchange of host plants among different countries and regions that may
518 greatly influence the spread of this pest. Nevertheless, the ability of the model to predict with
519 certainty the exact year that *T. absoluta* was reported in Kenya and other countries provides
520 some level of assurance to trust that the pest could reach South Africa if no control measures are
521 applied ten years after been reported in Spain. Indeed, the present model can serve as an early
522 warning tool for phytosanitary officers and policy makers to take appropriate decisions in order
523 to safeguard against further invasion and establishments of *T. absoluta*. This calls to put in place
524 adequate quarantine measures to counteract the pest invasion and spread.

525 **5. Conclusion**

526 The proposed model for the spread pattern of *T. absoluta* aimed to predict its timing of invasion
527 across Africa. We were able to annually mimic and predict the spreading behavior and pattern of
528 *T. absoluta* that lead us to estimate the time this pest will take to invade the whole Africa. We
529 were able to understand among factors such vegetation, temperature, relative humidity, and
530 tomato production per area, which one has a major influence in facilitating the spread of the pest.

531 When only considering the climatic factor, relative humidity seems to have the strongest
532 influence in enhancing the spread of *T. absoluta*. In addition, taking into account areas with a
533 high production of the pest host plant improved the model predictions. Including the life
534 histories, biology, and ecology of *T. absoluta* could help extend this study. Simulations could
535 also target the whole terrestrial planet.

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