

Potential areas of spread of *Trioza erytreae* over mainland Portugal and Spain

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Key Message

- The possible spread of *Trioza erytrae*, psyllid vector of HLB, throughout citrus areas in the Iberian Peninsula was assessed
- High spatial data resolution, a physical barrier, and long-distance dispersal events were used
- The obtained models for seven years overlapped the current spread of *T. erytrae*
- Two key areas for monitoring in Spain and one in Portugal were identified
- Further efforts in modeling are critical for pest management of *T. erytrae* and HLB

Abstract

Trioza erytrae is one natural psyllid vector of *Candidatus liberibacter*, the causal agent of the citrus greening disease (HLB). Since its introduction in 2014 into the Iberian Peninsula, *T. erytrae* was able to spread continuously toward southern coastal regions of Portugal and northern coastal regions of the Cantabric sea in Spain. Identifying key areas of potential colonization by the psyllid vector is crucial to anticipate derived problems of establishing the disease. This work aimed to find potential areas that could be colonized by *T. erytrae* throughout the Iberian Peninsula using 1 km spatial data resolution, a physical barrier, long-distance dispersal events (LDEs), and 30 years of simulation. The bioclimatic suitability of *Citrus* spp. was used as a surrogate of its spatial distribution and a measure of habitat invasibility. Two localities, one in Portugal and one in Spain, were considered as initial points of the spread of *T. erytrae*. Four spread scenarios were initially simulated, corresponding to very low, low, medium, and high spread. An altitude of 400 m was included in the model as a physical barrier, and cells up to 500 km apart were allowed to be colonized due to LDEs. In this work, three key risk areas were identified, the citrus growing areas of Setúbal (Portugal) and Huelva (Spain), and the potential corridors that may connect Guipúzcoa, where *T. erytrae* is already present, with the Ebro valley (Spain). Future modeling and simulation studies should include biological constraints such as the effect of parasitoids on the population of *T. erytrae* (e.g. *Tamarixia dryi*) and other barriers or corridors.

Keywords: monitoring, HLB, African citrus psyllid, MigClim, invasion, Europe.

Introduction

Citrus greening disease or huanglongbing (HLB) is caused by the Gram-negative bacterium *Candidatus liberibacter* spp. Worldwide, there is an increasing interest in modeling the current and future geographical distribution of the psyllid vectors of HLB due to the damage it causes on citrus crops. HLB symptoms encompass yellow shoots shown by young flushes on infected trees, leaves with blotchy mottle, and yellow veins, and fruits with color inversion (Bové 2006).

The Asian citrus psyllid, *Diaphorina citri* Kuwayama, 1908, and the African citrus psyllid, *Trioza erytreae* (del Guercio, 1918), are vectors of the putative causal agent of HLB. Both species have high spreadability, and once a new area is invaded and colonized, their eradication is costly or unsuccessful (Aubert and Quilici 1983; Gallien et al. 2010). Hence, efforts in predicting the current and future geographical distribution of HLB and its psyllid vectors have been made for the sake of developing and applying preventive measures and efficient control strategies (e.g. Narouei-khandan 2015; Aïdoz et al. 2019; Ajene et al. 2020; Benhadi-Marín et al. 2020; Urbaneja et al. 2020). Moreover, one of the psyllid vectors alone, *T. erytreae*, also reduces crop yield causing death in up to 90% of untreated young plants because of the formation of open gall-like structures and strong deformation of leaves (Caccarza et al. 2017). Together, the effects may lead to losses up to 74% in citrus crops (e.g. Singerman & Rogers 2020). In light of the destructive potential of both the disease and the psyllid vector, detection and monitoring for citrus psyllid vectors is a primary measure for a quick diagnosis and confirmation of HLB (Bové 2006).

Trioza erytreae is associated with plants of the Rutaceae family and shows a high preference for *Citrus limon* (L.) (Moran 1968; Benhadi-Marín et al. unpublished data). Therefore, studying and predicting the spatio-temporal dynamics of citrus psyllids as a proxy for HLB risk could be a tool for disease management (Bayles et al. 2017). The success of a biological invasion relies on key spatial and temporal processes. Accordingly, the causes and extent of the spread of HLB psyllid vectors have been studied from different points of view. For example, Zorzenon et al. (2020) investigated the climatic variables driving the movement patterns of *D. citri* and found that immigration was positively related to the new citrus flush production, which was, in turn, dependent on the maximum temperature and daily minimum temperature and rainfall during the previous weeks. Using artificial release experiments, Kobori et al. (2011) suggested that adults of *D. citri* moved little

after reaching a host plant. On the other hand, Sakamaki (2005) suggested that wind-assisted long-distance dispersal events (LDEs hereafter) may allow *D. citri* to travel up to 470 km in Japan and found that the flight capacity of *D. citri* is negatively affected above 30°C. Also, spatial drivers such as barriers raised interest, and Tomaseto et al. (2016) studied the effect of host and non-hosts plant barriers on the dispersal of *D. citri*. Unfortunately, little is known yet about the dispersal drivers and parameters of *T. erytrae*.

A wide range of core-modeling (*sensu* Di Cola et al. 2017) techniques and platforms based on the relationship of a species and the environment are available to make spatial predictions; however, predicting the potential geographic distribution of an invading species is challenging. For example, using environmental niche models based on the early occurrence of an invasive species may underestimate the potential future distribution since the spreading success may not be clear in the new landscape (Peterson 2005). Accordingly, further analyses to include processes such as dispersal can be useful to predict the actual distribution (Di Cola et al. 2017). In this context, different approaches are generally adopted for developing invasive species distribution models (iSDMs) such as predicting the potential distribution of a biological invasion by modeling the habitat requirements (e.g. climatic suitability) and estimating the actual distribution considering colonization time lag and dispersal limitations (e.g. barriers) (see Václavík 2010).

Since habitat niche models may not capture *sensu stricto* the dynamics of invasions, other procedures such as curve fitting models, matrix population models, metapopulation models, landscape models, individual-based models, mechanistic niche models and cellular automata arose (see Gallien et al. 2010). For example, modeling platforms such as MigClim (Engler and Guisan 2009) allow the coupling of predictive distribution maps (habitat suitability of the species of interest) with a cellular automaton that simulates dispersal, colonization, growth, and extinction of the species in the landscape.

In the Iberian Peninsula, *D. citri* is not yet present but *T. erytrae* was first reported in 2014 from Vila Nova de Arousa (northwestern Spain), although it was detected shortly after in Porto (northwest Portugal) (Pérez-Otero et al. 2015). Using a series of PRA (pest risk analysis) models (i.e. models to support the quantitative assessment of spread in pest risk analysis), Benhadi-Marín et al. (2020) suggested that the observed distribution of *T. erytrae* during the first five years of spread throughout the Iberian Peninsula (i.e. years 2014–2019) was best fitted by a kernel dispersal model with two simultaneous entry points (Vila Nova de Arousa and Porto, respectively) instead of considering only the first one. However, since the model did not

include any physical constraint to predict the spread (beyond the bioclimatic suitability of the host) nor long-distance dispersal events (LDEs), the simulated occupied area after five years of spread greatly extended beyond the observed area toward inner mainland territory. To the best of our knowledge, no attempts have been made yet to model the potential risk areas of colonization by *T. erythrae* using a spread-based approach considering barriers and LDEs. Hence, in this work we aimed to refine the approach followed by Benhadi-Marín et al. (2020) in three ways: (1) improving the spatial data resolution, (2) including a physical barrier and LDEs for modeling purposes, (3) extending the prediction to 30 years after the introduction of *T. erythrae* in the Iberian Peninsula, and (4) simulating different scenarios of spread.

Material and methods

Data inputs

The occurrence dataset of *T. erythrae* was an update of the one used in Benhadi-Marín et al. (2020), i.e. the pool of records provided by the Spanish and Portuguese government technical reports for the period 2014–2021 (Xunta de Galicia. 2017, 2019; DGAV 2016–2021) plus recent reports of presence throughout the northernmost area of Spain, i.e. Asturias, Cantabria, and Basque Country (BOC 2020; Eppo 2020). The occurrence data set of the host was obtained by combining the available data of the Global Biodiversity Information Facility online database (GBIF 2020) for the whole genera *Citrus* (GBIF.org 2020), the Information System on Land Occupation of Spain (SIOSE 2020), and the occurrence data of *T. erythrae*. The citrus occurrence dataset was filtered to minimize overfitting so that only presence locations interspaced at least 30 km were retained for modeling.

Modeling platform and tools

The spread model was fed using the bioclimatic suitability of the host (*Citrus* spp.) as a surrogate of its spatial distribution and a measure of habitat invasibility throughout the Iberian Peninsula, and the two entry points of *T. erythrae* in the Iberian Peninsula suggested by Benhadi-Marín et al. (2020). The bioclimatic suitability of *Citrus* was estimated using the R implementation of the machine-learning method Maxent (Phillips et al. 2006). The MigClim R package (Engler et al. 2012) was used to predict the dispersal of *T. erythrae* after 30

years since the introduction in the Iberian Peninsula. The MigClim R package was used to implement species-specific dispersal constraints into the projection of the *Citrus* distribution model. The spread model uses a cellular automaton procedure in which the basic modeling unit is a cell that can be inhabited or not. According to our geographical knowledge on the region, the altitude was selected as a potential physical barrier. The gridded altitudinal data was obtained from a digital elevation model (Reuter et al. 2007). The whole modeling process was conducted in R (R Core Team 2019).

Model development

The bioclimatic suitability of *Citrus* was estimated using the maxent function of {dismo} package (Hijmans et al. 2017). Although colinearity among drivers has little effect on Maxent (Feng et al. 2019), we used the four most contributing bioclimatic variables (i.e. percentage of contribution > 10%) found by Benhadi-Marín et al. (2020) for the Iberian Peninsula. The selected bioclimatic variables were obtained from the WorldClim (Fick and Hijmans 2017) database at 30 seconds spatial resolution ($\approx 1 \text{ km}^2$ at the equator) (Online Resource: Table S1). Model selection followed Muscarella et al. (2014). The best model was selected as the one with the lowest AIC (Akaike Information Criterion) across the combinations of feature classes and regularization multipliers using the {ENMeval} package (Muscarella et al. 2014). The feature classes (i.e. the transformations of the original covariates) used were linear, product, quadratic, and hinge combined with eight regularization multipliers (for model smoothing purposes) ($\beta = 0.5, 1, 1.5, \text{ and } 2$) and the “checkerboard1” method for partitioning occurrence. After model tuning, the AUC (area under the receiver operating characteristic curve) was calculated for the optimal model as an independent measure of predictive accuracy based on the ranking of locations (Merow et al. 2013). Finally, the ROC curve (receiver operating characteristic, a graphical representation of sensitivity versus specificity) was calculated following Steven and Phillips (2009) using the {ROCR} package (Sing et al. 2005) and the response curves for each bioclimatic variable were drawn using the {dismo} package.

The spread models were developed using the MigClim.migrate function of the MigClim package and parameterized as follows (see the comprehensive user guide for details using the function MigClim.userGuide): The input habitat suitability data (*Citrus* spp.) was used in continuous mode so that the values of habitat suitability were used as the conditional probability that a cell becomes colonized. Only cells

with an associated climatic suitability $P > 0.5$ were considered as suitable to be colonized by *T. erythrae*. The initial distribution of *T. erythrae* in the Iberian Peninsula was set at Vilanova de Arousa (Spain) (42.562, -8.823) and Porto (Portugal) (38.596, -9.168) (Benhadi-Marín et al. 2020). Since no environmental change was taken into account, the number of environmental change steps was set to one. The number of dispersal steps was initially 7 years (corresponding to the spread from 2014 to 2021). Short distance dispersal followed a dispersal kernel considering the maximum distance of potential dispersal estimated by Benhadi-Marín et al. (2020) so that:

$$\text{kernel} = k^x$$

where x represents the sequence from 1 to 130 km/year (Online Resource: Figure S1), and k stands for different scenarios of ability to spread. In this work we used $k = 0.25, 0.50, 0.75,$ and 0.99 , representing very low, low, medium, and high spread, respectively (hereafter models 1, 2, 3, and 4, respectively). The altitudinal barrier dataset was considered of type “strong” and according to our geographical knowledge of the region (geographical extent of plantations and climate) was set at 400 m. Furthermore, an exploratory analysis using 300 and 500 m respectively was conducted, dismissing these values due to lack of visual fitting with the predicted bioclimatic suitability of *Citrus*. The cell “age” at which it starts to produce propagules was set at one and the vector for probabilities associated to each cell age, from its initial maturity age to one year before full maturity was established as [0.6, 0.7, 0.8, and 0.9].

Different drivers are known to facilitate long-range dispersal such as low-level jet winds (Irwin and Thresh 1988). Thus, among the first set of four models, the one that best fitted the current observed spread (i.e. the k that best approximated the occurrence) was refitted as an extra scenario (model 5 hereafter) considering LDEs. LDEs were implemented by parameterizing the frequency of the events and the minimum and maximum distance at which the events should occur. The frequency of LDEs was established at 0.01 so that, on average, 1 occupied cell in 100 with full propagule production potential will generate a LDE. The minimum and maximum distance were set at 131 km (since this value must be larger than the largest distance of the dispersal kernel) and 500 km (approximately the radius of the Iberian peninsula), respectively. Finally, using the selected best k , two more runs were conducted for 30 years without LDEs (model 6) and considering LDEs (model 7).

Results

The best maxent model for the climatic suitability of *Citrus* resulted from the combination of the linear, quadratic, hinge, and product feature classes and $\beta = 1$ with an estimated AUC = 0.81 ± 0.03 resulting in 16 parameters (Online Resource: Table S2). Following Swets (1988), a model with an AUC > 0.8 provides good model performance. The sensitivity versus specificity curve (ROC) for the optimal model is provided at the supplementary material (Online Resource: Figure S1). The most contributing bioclimatic variable was the minimum temperature of the coldest month (Table 1) (Online Resource: Figure S2). The best climatic suitability for *Citrus* spp. was found to follow the circumpeninsular areas of the whole Iberian Peninsula, especially the eastern coastal area of Spain, entering into inner areas throughout the southern half of Portugal (Figure 1). Also, the whole Balearic islands (Spain) were found as optimal areas (Figure 1).

The first four developed spread models performed differently according to the k parameter of the kernel (Figure 2). Regarding the number of occupied cells, a full sigmoid growth was only detected in the case of model 4 (Figure 3). At the end of the simulation (i.e. 7 time steps), only 3.34 % of suitable cells were colonized using model 1, models 2 and 3 predicted 22.00 and 41.10 % of suitable cells colonized, respectively, whereas model 4 predicted 71.57 % of suitable cells colonized (Figure 3). The area colonized after seven time steps predicted by model 1 barely extended up to ~100 kilometers beyond the entry points (Figure 4a). Model 2 predicted a spread that reached the northernmost region of Galicia (northwestern Spain) to the north and the district Setúbal to the south throughout Portugal (Figure 4b). Model 3 performed similarly to model 2, although the predicted spread reached even the southernmost areas of Portugal up to the Algarve region (district of Faro) (Figure 4c). Model 4 showed clear waves and significantly extended the predicted spread compared to the latter. The front wave reached the province of Málaga (southern Spain), entering relevant citrus cultivation areas in Andalusia following the valley of the river Guadalquivir (Figure 4d). In northern Spain, model 4 predicted almost a complete spread over the coastal areas of Spain, reaching the Basque Country (close to the frontier with France) (Figure 4d).

Among models 1, 2, 3, and 4, the one that best approached the observed distribution of *T. erythrae* was model 2 ($k = 0.50$) (see Figure 1) so that model 5 was fitted using the same parameters plus LDEs. Model 5 performed similarly that model 2 (22.37 % of suitable cells occupied), thus also providing a good overlap

with the observed distribution of *T.erythrae*. However, a pool of colonized cells throughout the southwestern region of Portugal fell out of the occurrence area of *T. erythrae* (Figure 5a). On the other hand, model 5 was able to predict isolated patches across the northern region of Spain and inner territories of Portugal (Figure 5b).

Models 2 and 5 were then run for 30 years becoming models 6 and 7, respectively. After the first 7 years, models 6 and 7 consistently differed predicting 72.41 and 83.93 % of suitable cells occupied at the end of the simulation, respectively (Figure 6a). In the absence of LDEs, model 6 predicted an area similar to model 4 (Figure 6b), whereas model 7 extended the spread up to mid-eastern regions of Spain reaching the province of Alicante and entering the citrus cultivation areas of Valencia (eastern Spain). Following the Mediterranean coastal line, the northernmost colonized cells appeared in the surrounding area of Barcelona (northeastern Spain). Among the Balearic Islands, the southern half of Ibiza also was predicted to be colonized. Regarding the northern region, model 7 extended the distribution of *T. erythrae* to the easternmost suitable areas reaching the Spanish frontier with France (Figure 6c).

Discussion

We used a cell automaton-based model to predict the potential areas occupied by *T. erythrae* throughout the Iberian Peninsula. A previous study by Benhadi-Marín et al. (2020) suggested that physical barriers may be involved in the ability of *T. erythrae* to colonize new suitable areas beyond the habitat suitability of the host. Hence, here we coupled the altitude and LDEs as a new drivers for modeling.

Here we found that the variable that contributed the most to the climatic suitability of *Citrus* was the minimum temperature of the coldest month. The modeled bioclimatic suitability of the host mostly overlapped with the favorable areas found by Benhadi-Marín et al. (2020), although the new data and resolution allowed to uncover a new fringe of the suitable area extending all over northern Spain covering the north of the Cantabrian mountain range till the coastal line. Furthermore, evergreen *Citrus* trees depend on soil temperature and variations in light exposure (see Vincent et al. 2020) corresponding to sunny areas of the Iberian Peninsula where chilling and frost events are infrequent and mild such as the Mediterranean coastal line. However, using the bioclimatic suitability of the host as a surrogate for the underlying occurrence data of

a pest could not be strong enough to predict actual spread patterns accurately. For instance, how the crop landscapes are spatially connected, the chemical control treatments applied, and the effect of natural enemies such as the parasitoid *Tamarixia dryi* (Waterson, 1922; Hymenoptera: Eulophidae) (Cocuzza et al. 2017) is crucial to derive accurate predictions on the dynamics (i.e. restrictions and corridors) of the populations of *T. erytrae*.

The first set of developed models were parameterized to resemble four scenarios of spread velocity considering high values in terms of the probability of a cell to produce propagules, i.e. the species starts to develop propagule production after the first time step when the cell is colonized. The ability of a cell to produce propagules increases linearly to its maximum at the age of five time steps, then it remains at its maximum potential till the end of the simulation. In this work, we did not focus on the habitat requirements of *T. erytrae* beyond the habitat suitability of the host, a physical barrier, and the probability of long-distance dispersal events. Among the four scenarios regarding the spread velocity (i.e. increasing values of k), the model that best predicted the current spread of *T. erytrae* throughout the Iberian Peninsula was $k = 0.5$ plus LDEs. This scenario was able to predict the extended population in Asturias (northern Spain) and explains isolated populations such as the one observed in Chaves (northern Portugal). Using this parameterization, a simulation of 30 years of spread predicted a potential favorable bioclimatic corridor in southernmost areas of Portugal (region of Algarve) regardless of LDEs. These areas could represent a way of entry of *T. erytrae* into southern Spanish citrus production areas. However, Paiva et al. (2020) suggested that water vapor pressure could drive the habitat suitability of *T. erytrae*. Since this area (Algarve) was found to encompass highly unfavorable water vapor pressure conditions for *T. erytrae*, its spread toward southwestern Spain may be at some extent delayed or even stopped.

Notwithstanding, LDEs may allow *T. erytrae* to reach suitable areas beyond the latter and continue expanding its distribution, reaching the Mediterranean coastal line toward Valencia and the Balearic Islands. Long-distance dispersal by psyllids has been reported, for example, Lewis-Rosenblum et al. (2015) studied the long-range dispersal capacity of *D. citri* and found that the Asian citrus psyllid was able to disperse a minimum of 2 km in a time-lapse of 12 days in the absence of severe weather events. Gottwald et al. (2007) suggested that wind-assisted dispersal of *D. citri* could reach up to 145 km in the USA, whereas *T. erytrae* can disperse up to 1.52 km within 7 days (Van Den Berg and Deacon, 1988).

In light of our results, we recommend careful and permanent monitoring in key areas in Portugal, such as the Setúbal district. Moreover, the presence of *T. erytrae* has been recently detected in the provinces of Asturias, Cantabria, and the Basque Country in 2020 in northern Spain in lemon (*Citrus limon*) and orange trees (*Citrus sinensis*) (EPPO 2020). This suggests a potential risk of spread toward eastern provinces such as Navarra, Huesca, and Lérida (Figure 6c), although the altitudinal physical barrier could prevent this expansion to the Mediterranean areas following the Ebro river valley. Although it has been suggested that spread throughout the Mediterranean coast could be slow (see Cocuzza et al. 2017), these areas, such as the Levante region, could be reached by the advance by the south, so that the province of Huelva (southwestern Andalusia) also deserves a strong monitoring effort. Finally, the Balearic islands encompass a lot of lemon trees in parks and especially in private gardens. In addition, the great amount of import of plant material for hotels and apartments, and a suitable climate may facilitate the entering and settlement of *T. erytrae*.

In conclusion, models including LDEs predicted similar percentages of spread than models without LDEs, although LDEs generated different spatial patterns, further extending the colonized areas and explaining better the current distribution of *T. erytrae*. Our approach suggests that at least two key areas in the Iberian Peninsula deserve special monitoring efforts, the citrus growing areas of Setubal (Portugal) and Huelva (Spain) and the potential corridors that could connect Guipúzcoa with the Ebro valley (Spain). Nevertheless, continuous monitoring in citrus orchards currently not invaded by *T. erytrae* is also mandatory to prevent or manage accidental long-distance introduction events. Future spread-based models should consider information related to accurate data on the bioecology of *T. erytrae* such as potential spread limitations derived from unfavorable water vapor pressure areas and consider the effect of predators, parasitoids, fungi, and chemical control. For example, biological control measures such as the mass release of the specific parasitoid *T. dryi* (Cocuzza et al. 2017) and the natural limitation derived from predators such as spiders, chrysopids, coccinellids, and syrphids (van der Berg et al. 1987) could reduce or even stop the development of *T. erytrae*. On the other hand, anthropogenic drivers such as terrestrial communication nets including highways and major plant trade nodes, may play a role favoring accidental human-based long-distance dispersal events. In addition, there is no information available on the ability of *T. erytrae* to move passively long distances through the planetary boundary layer of the atmosphere with the help of low-level jet winds. This long distance dispersal has been reported several times for aphids (Parry, 2013) and could also facilitate

the spread of *T. erytrae* across the Iberian Peninsula. We hope the parameters and simulation information derived from this work encourage further modeling efforts to allow making efficient pest management recommendations toward monitoring and prevention of crop losses due to *T. erytrae* and HLB.

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Table 1 Percent of contribution of each selected bioclimatic driver used to model the climatic suitability of citrus in the Iberian Peninsula

Variable	Percent contribution
Minimum temperature of the coldest month	53.8
Temperature seasonality (standard deviation \times 100)	30.2
Mean temperature of the wettest quarter	9.9
Precipitation seasonality (coefficient of variation)	6.1

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Figure captions

Fig. 1 Maxent prediction for the climatic suitability of citrus in the Iberian peninsula. Red areas and dots encompass areas of occurrence of *Trioza erytreae*. Colors represent the gradient of climatic suitability (P)

Fig. 2 Dispersal kernels used to parameterize the spread models. a: $k = 0.25$; b: $k = 0.50$; c: $k = 0.75$; d: $k = 0.99$

Fig. 3 Performance of the five developed models for the first seven years of spread according to different scenarios of spread velocity ($k = 0.25$, $k = 0.50$, $k = 0.75$, $k = 0.99$) (models 1, 2, 3, and 4, respectively) and a scenario including long-distance dispersal events (LDEs) ($k = 0.50$; frequency of LDEs = 0.01; maximum distance for LDEs = 500 km) (model 5)

Fig. 4 Simulated spatio-temporal evolution during the first seven years of the spread of *Trioza erytreae* since its introduction in 2014 in the Iberian peninsula according to different scenarios of spread velocity. a: $k = 0.25$ (model 1). b: $k = 0.50$ (model 2). c: $k = 0.75$ (model 3). d: $k = 0.99$ (model 4). Blue dots represent the two initial entry points.

Fig. 5 a: Simulation of the spatio-temporal evolution during the first seven years of the spread of *Trioza erytreae* since its introduction in 2014 in the Iberian Peninsula considering long-distance dispersal events (LDEs), $k = 0.50$; frequency of LDEs = 0.01; maximum distance for LDEs = 500 km (model 5). b: Detail of long dispersal events throughout the northwestern region of the Iberian peninsula using model 5. In a and b, blue dots represent the two initial entry points. In a, the red polygons and red dots encompass current areas of occurrence of *Trioza erytreae*. In b, red arrows indicate LDEs

Fig. 6 Performance of the two developed models for 30 years of spread ($k = 0.50$) with and without long-distance dispersal events (LDEs) ($k = 0.50$; frequency of LDEs = 0.01; maximum distance for LDEs = 500 km). a: Percentage of suitable cells occupied along time. b: Predicted spread of *Trioza erytreae* throughout the

Iberian peninsula without LDEs (model 6). c: Predicted spread of *T. erythrae* throughout the Iberian peninsula considering LDEs (model 7). Blue dots represent the two initial entry points. Red circles indicates the key suggested areas encompassing Setúbal (Portugal) (dotted line), the Ebro river valley (Spain) (continuous line), and Huelva (Spain) (dashed line)

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Figure 1.

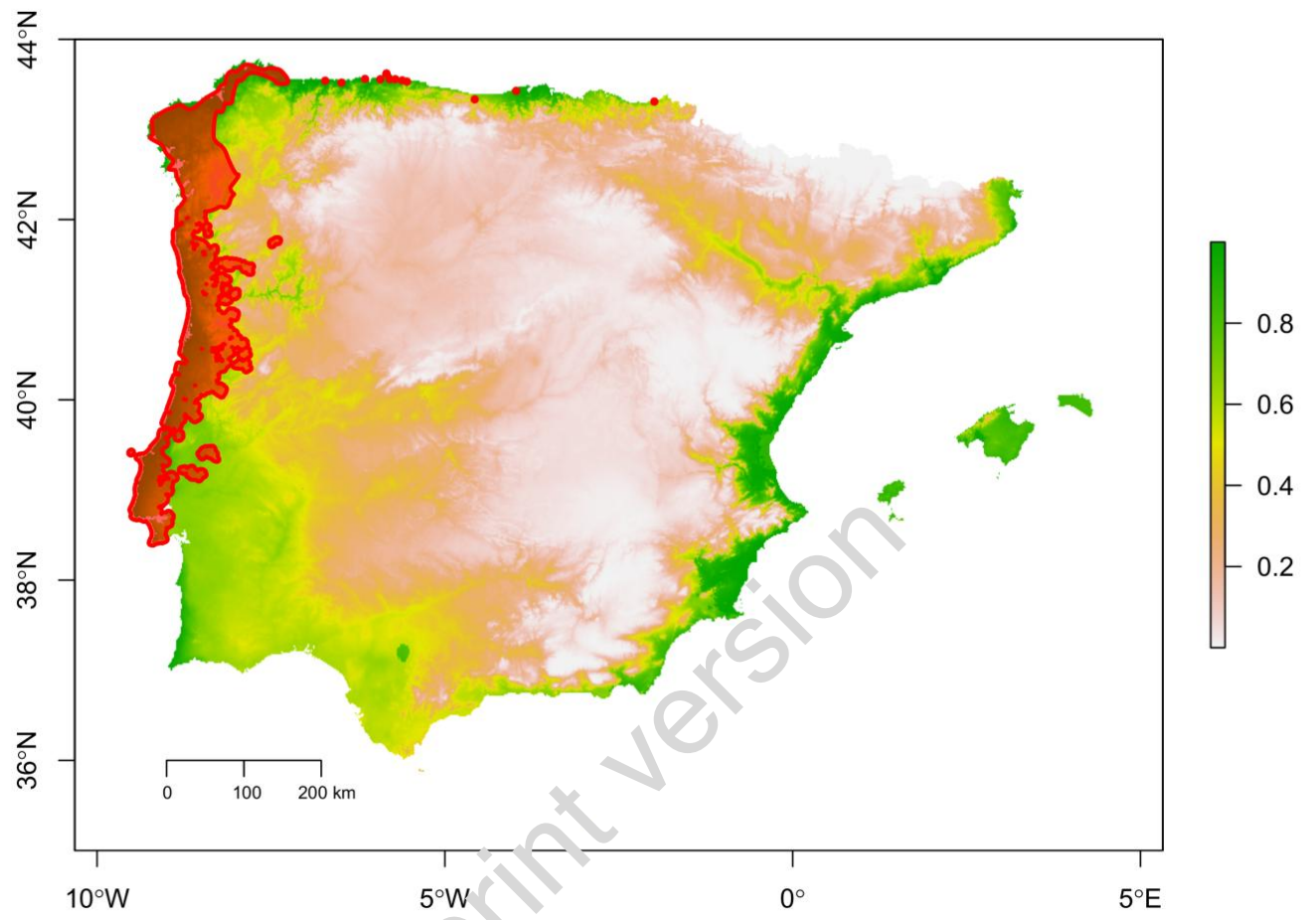


Figure 2.

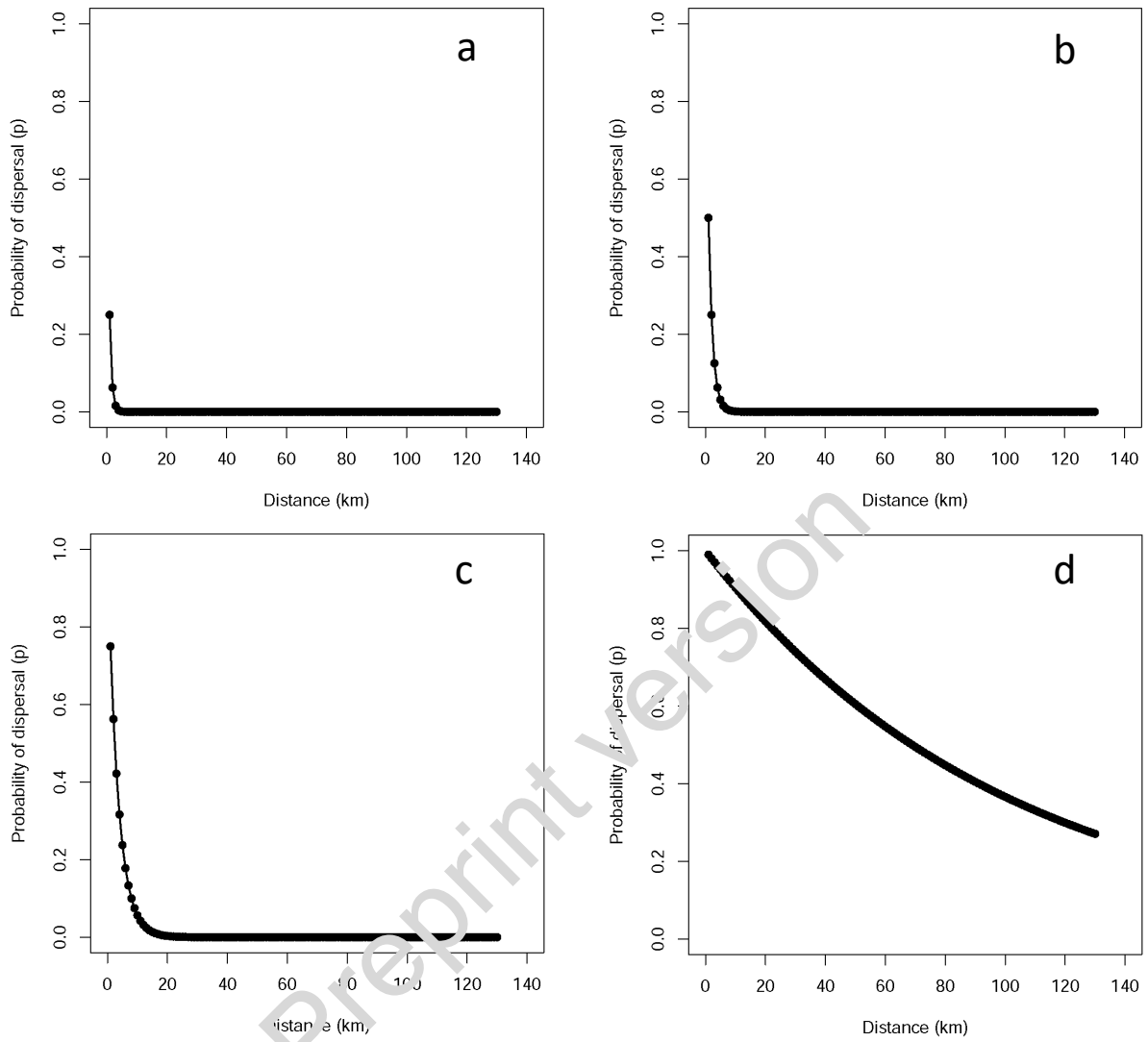


Figure 3.

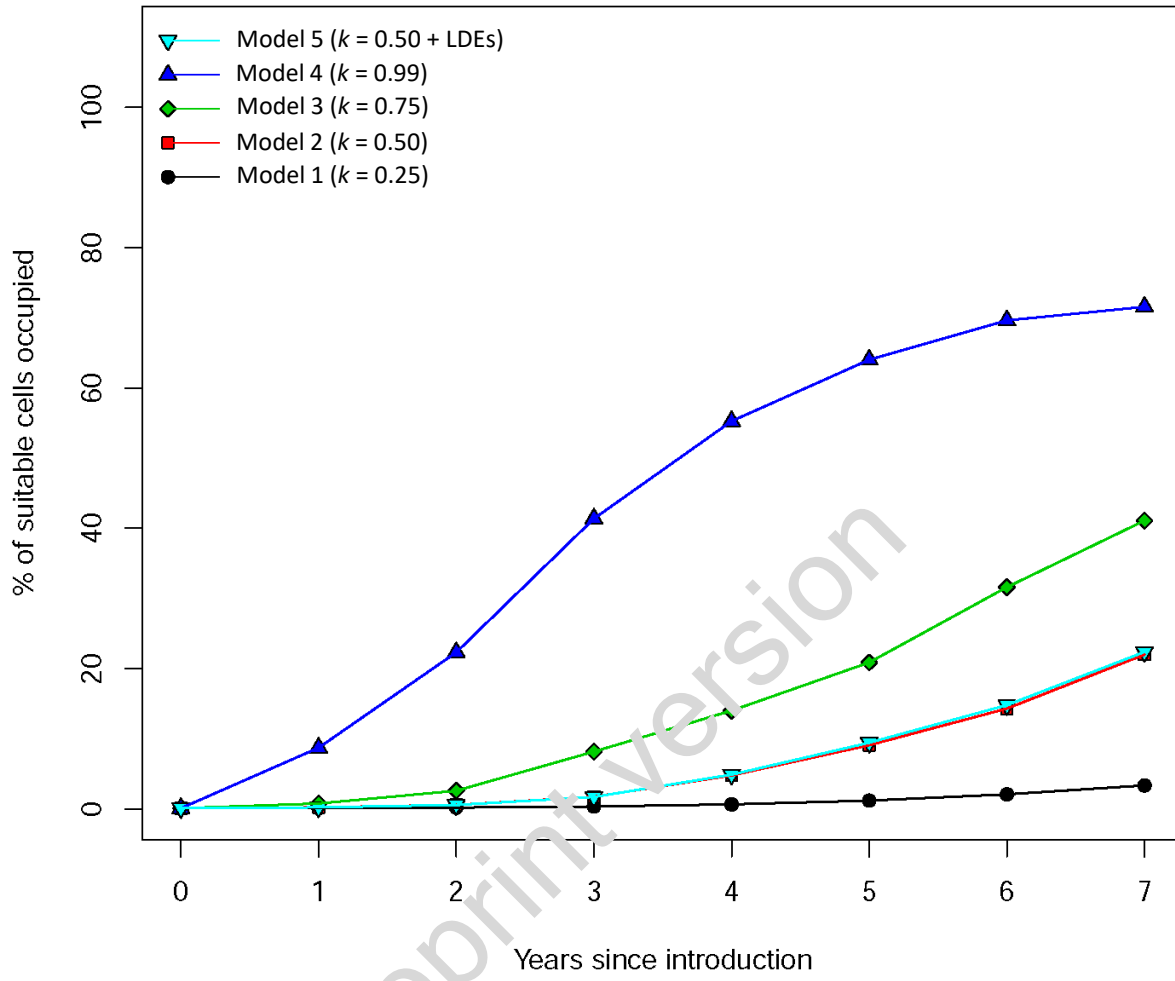


Figure 4.

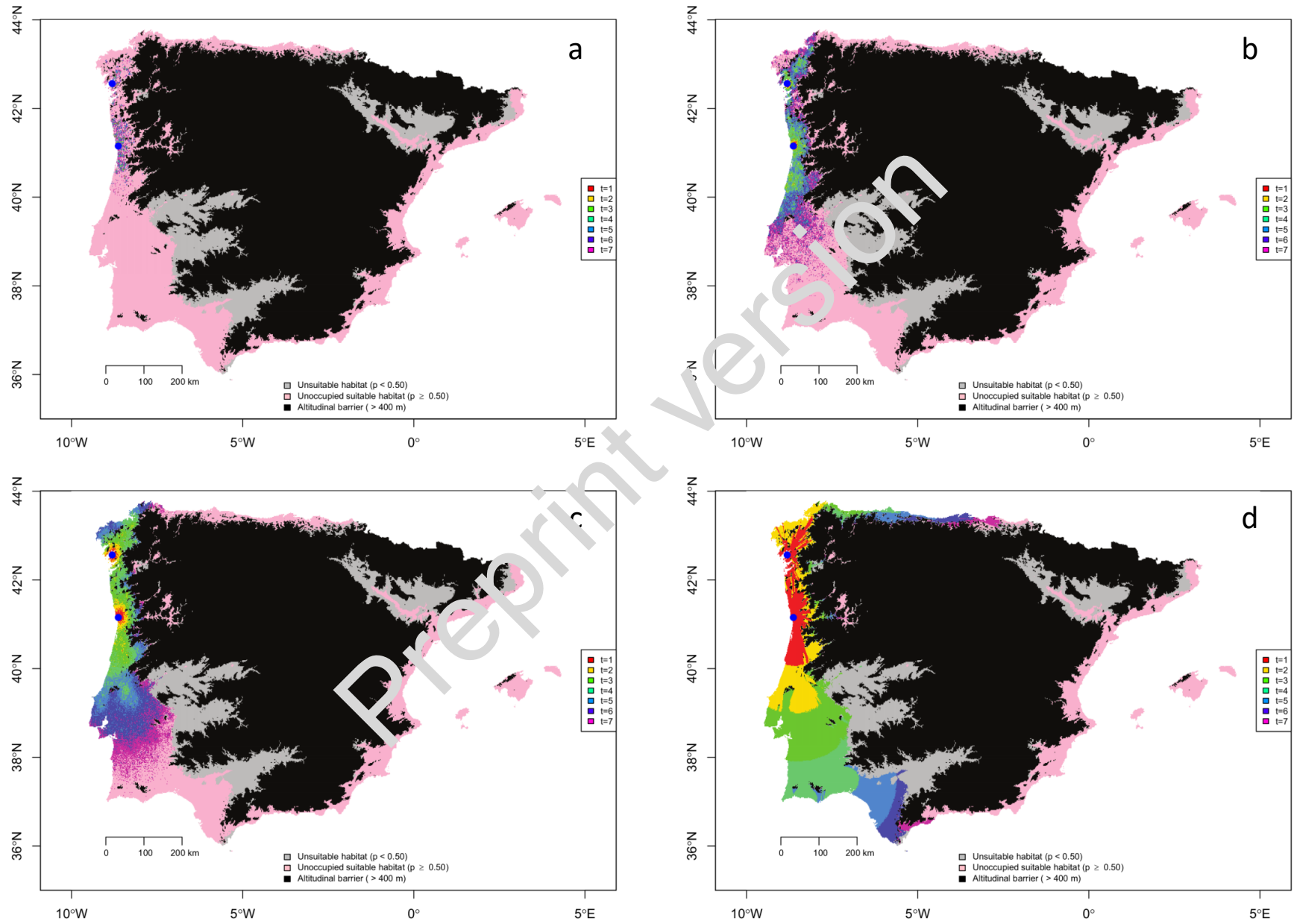


Figure 5.

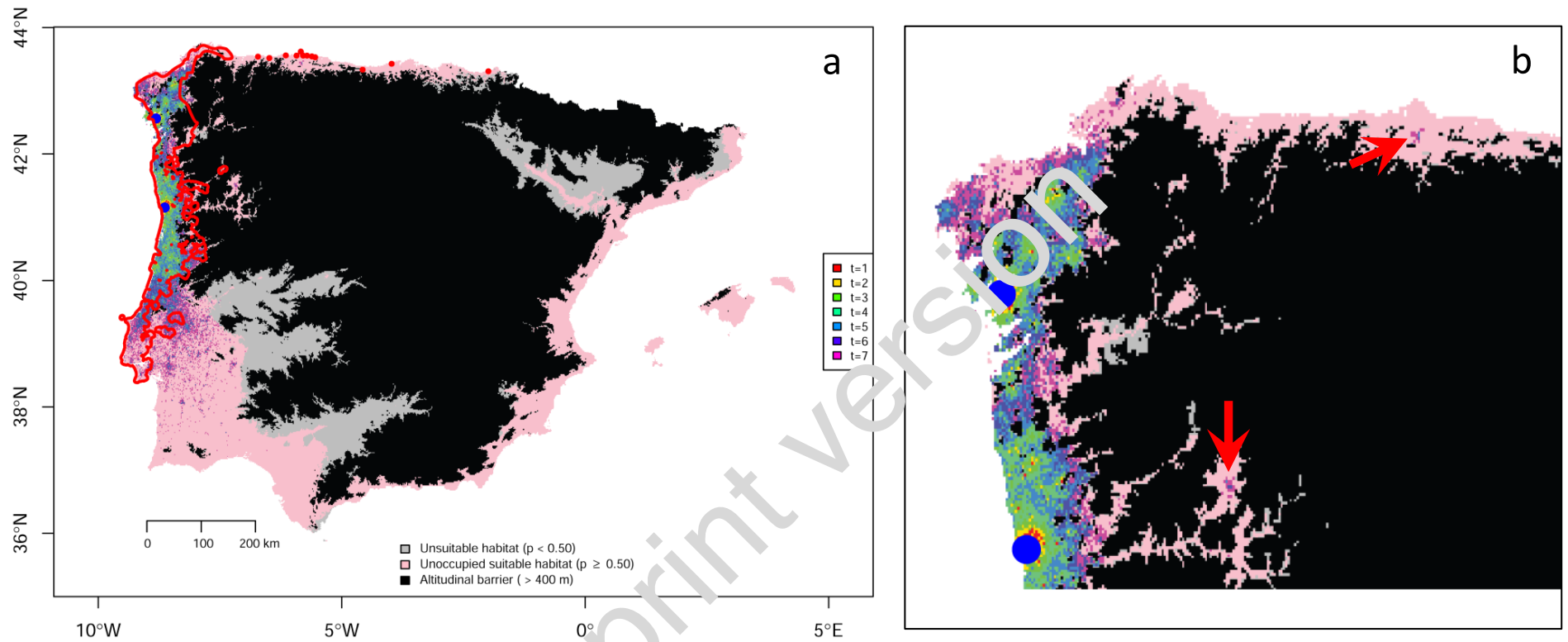


Figure 6.

