Unveiling human-assisted dispersal mechanisms in invasive alien insects: Integration of spatial stochastic simulation and phenology models

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ABSTRACT

Capturing the spread of biological invasions in heterogeneous landscapes is a complex modelling task where information on both dispersal and population dynamics needs to be integrated. Spatial stochastic simulation and phenology models have rarely been combined to assist in the study of human-assisted long-distance dispersal events.

Here we develop a process-based spatially explicit landscape-extent simulation model that considers the spread and detection of invasive insects. Natural and human-assisted dispersal mechanisms are modelled with an individual-based approach using negative exponential and negative power law dispersal kernels and gravity models. The model incorporates a phenology sub-model that uses daily temperature grids for the prediction and timing of the population dynamics in each habitat patch. The model was applied to the study of the invasion by the important maize pest western corn rootworm (WCR) *Diabrotica virgifera* ssp. *virgifera* in Europe. We parameterized and validated the model using maximum likelihood and simulation methods from the historical invasion of WCR in Austria.

WCR was found to follow stratified dispersal where international transport networks in the Danube basin played a key role in the occurrence of long-distance dispersal events. Detection measures were found to be effective and altitude had a significant effect on limiting the spread of WCR. Spatial stochastic simulation combined with phenology models, maximum likelihood methods and predicted versus observed regression showed a high degree of flexibility that captured the salient features of WCR spread in Austria. This modelling approach is useful because it allows to fully exploit and the often limited and heterogeneous information available regarding the population dynamics and dispersal of alien invasive insects.

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1. Introduction

Harmful non-indigenous species (NIS) lead to the extinction of vulnerable native species and to severe alterations of ecosystems and agroecosystems (Hulme, 2006). NIS impacts and their management entail considerable economic costs. For instance, the annual costs of control and yield losses due to the invasive pest western corn rootworm (WCR) (*Diabrotica virgifera virgifera*) and other related rootworm species in the world have been estimated to greatly exceed $1 billion (Gray et al., 2009).

Understanding the mechanisms underlying the spread of a certain NIS is of great value for decision-makers to identify the most adequate management strategy. Among dispersal mechanisms, long-distance dispersal events have been shown to be highly influential on the spread velocity of NIS (Neubert and Caswell, 2000). Due to the spatial and temporal magnitude of biological invasions, experimental approaches to study long-distance dispersal events at the landscape-scale are unfeasible, rendering modelling and empirical analysis of historical invasions as the most suitable methodologies.

A very insightful approach for the study of NIS spreading by human-assisted dispersal when spatial time series of data on the invasion are available is the use of empirical methods to fit spatially explicit spread models. These approaches have been used to detect long-distance dispersal mechanisms at the landscape-scale by studying the association of human population density and transport networks with the spatial patterns of observed spread.

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Using this approach, the emerald ash borer (*Agrilus planipennis*), the leaf-miner moth *Cameraria ohridella* and the pinewood nematode (*Bursaphelenchus xylophilus*) were found to perform long-distance dispersal events caused by human-assistance (Gilbert et al., 2004; Muirhead et al., 2006; Robinet et al., 2009). These models, however, rarely consider explicitly the variation of the population dynamics and the phenology of the NIS through the landscape; thus not fully exploiting all the available information regarding the NIS.

Prediction of the population dynamics and timing of invasive insects development can be obtained using spatial phenology models (Gray, 2004). Phenology models are suitable to estimate the timing and number of individuals in the different development stages of poikilothermic organisms because their ontogeny is controlled mainly by temperature. Some examples are GEO-BUG for the study of the development of agricultural pests in the UK using daily temperature grids (Jarvis, 2001) and ECAMON that intended to assess changes in the distribution of the European corn borer (*Ostrinia nubilalis*) under climate change scenarios (Trnka et al., 2007). Phenology models, however, seldom consider either dispersal or landscape connectivity.

An ideal invasive insect invasion modelling framework would incorporate features from spatial simulation spread models fitted to historical invasion data using empirical approaches and spatial phenology models. Despite their potential, both approaches are rarely integrated. A flexible modelling alternative to integrate dispersal and landscape heterogeneity with the phenology of the invasive insect are spatially explicit simulation models. These models are dynamic and can incorporate the heterogeneities of the landscape, especially regarding climatic variability (Higgins et al., 2000; Lurz et al., 2001). They have been combined with decision-making modules to manage plant invasions (Higgins et al., 2000) and to assess the effect of control activities on the population dynamics and consequently on the spread of invasive weeds (Grevstad, 2005; Wadsworth et al., 2000) and diseases (Keeling et al., 2001).

Spatial stochastic simulation models and phenology models together would provide for an ideal mechanistic modelling framework to be empirically fitted to observed invasion patterns. In addition, because the data related to NIS are scarce and fragmented, a mechanistic modelling framework where knowledge about spread and spatial phenology can be integrated would be very beneficial.

In this paper, we attempt to advance the area of modelling of NIS spread pursuing two aims: (i) integrate phenology models with spatial stochastic simulation models of invasive insects spread at the landscape-scale and (ii) parameterize the model to spatiotemporal invasion data of WCR in Austria in such a way that heterogeneous sources of information (previous studies, field trials and observed spread) can be fully exploited. To achieve these aims, we develop, parameterise and validate a process-based landscape extent spatially explicit simulation model that incorporates natural and human-assisted long-distance dispersal of a spreading invasive insect. The model combines modelling concepts from spatial simulation models of NIS spread (Higgins et al., 2000; Le Maitre et al., 2008), empirical approaches that study historical long-distance spread (Gilbert et al., 2004) and spatial phenology models for insect development (Jarvis, 2001). We apply the model to the case of the invasion by the western corn rootworm (WCR) *Diabrotica virgifera* ssp. *virgifera* LeConte (Coleoptera: Chrysomelidae), an important pest of maize, in Austria. In addition we aim to answer the specific questions: which were the most relevant mechanisms of spread that explained the observed pattern of spread of the WCR invasion in Austria? And how effective were the detection measures of the surveillance programmes?

1.1. Case study: western corn rootworm invasion in Europe

The model was applied to the current invasion of western corn rootworm (WCR), *Diabrotica virgifera* ssp. *virgifera* LeConte (Coleoptera: Chrysomelidae) in Europe. WCR is a univoltine insect that overwinters in the egg stage and is one of the most destructive pests of maize (*Zea mays* L.) in the USA. WCR larvae attack the roots of maize leading to a decrease of nutrient intake, reduced growth of the plant and a higher risk of lodging (Gavloski et al., 1992). WCR larvae can only develop on maize and a few alternative hosts (Moeser and Vidal, 2005). WCR adults are extremely mobile. For instance, half of the adults performing trivial flights can disperse between 117 and 425 m in 1 day (Carrasco et al., 2010) and some young mated females are capable of making unassisted migratory flights of up to 24 km (Coats et al., 1986).

WCR was first detected in Europe in Serbia in 1992 and subsequently WCR has spread rapidly through central and south-eastern Europe (a map describing the range of WCR in Europe can be accessed at http://www.entm.purdue.edu/wcr/). The European Commission (EC) has implemented measures aimed at preventing the spread of WCR in Europe. In 2003, eradication and detection measures were required by EC Decision 2003/766/EC (Anonymous, 2003). Measures to prevent the spread of WCR include EU Member States conducting official pheromone trap surveys for the presence of WCR in their territories in areas where maize is grown (Anonymous, 2003). When the presence of WCR is detected in a previously uninfested field, management measures are applied within radial zones (buffer zones) around each infested field (Anonymous, 2003). In this paper we will refer to buffer zones as the areas where maize is forced to rotate twice in three consecutive years.

WCR was first detected in Austria in the eastern and south-eastern regions in 2002 and 2003 respectively (Fig. 2A). WCR is likely to have entered Austria from adjacent infested regions in Hungary, Slovenia and the Slovak Republic. A management approach that focused exclusively on the eradication of new isolated colonies was adopted. Buffer zones were enforced on those newly infested fields that occurred over 40 km away from the fields infested the previous year. Nevertheless, WCR continued to spread in Austria between 2002 and 2008 (Fig. 2B–D).

The main human-assisted dispersal vectors that WCR might have encountered in Austria are motorways, railways and inland-water transport networks. The Danube basin is especially relevant since most of the international transport networks connecting Germany with south-eastern Europe run through it. Furthermore, farmers tend to grow continuous maize along the river banks because maize is more likely to survive in case of flood compared to other crops. This would facilitate the establishment of new colonies on the river bank. The occurrence of human-assisted dispersal of WCR has been hypothesized in Austria. For instance, isolated outbreaks beyond the main body of the invasion occurred in maize fields near important Danube harbours and near the last petrol station before the border with Germany where many trucks stop to refuel because petrol is more expensive in Germany than in Austria. Similar detection patterns have been observed in the south of Germany from roads connecting to the infested regions of the north of Italy (Wudtke et al., 2005).

2. Methods

2.1. Model description

We developed a process-based landscape extent spatially explicit stochastic simulation model. The model integrated population dynamics, spread, government detection campaigns, landscape connectivity and climate for the study of biological inva-
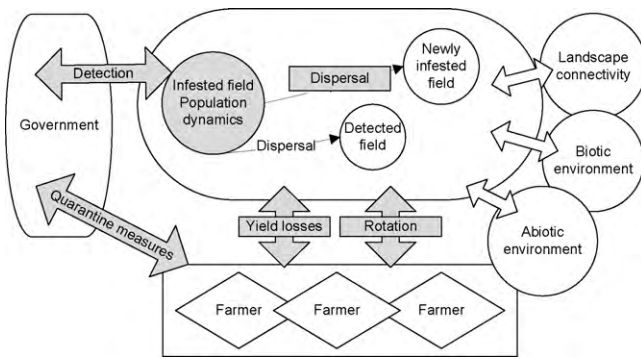
Fig. 1. Conceptual framework of the model.

sions (see Fig. 1 that represents the conceptual framework of the model). The model was programmed in Java and linked to a geographic information system (GIS). The model simulates the population dynamics of WCR in each field following the object oriented programming paradigm. Dispersal was modelled following an individual-based model approach (a description of the sub-models, scheduling and structure of the model is available in Appendices S1 and S3 in the supplementary data).

2.1.1. Population dynamics

A phenology model driven by temperature grids was employed to simulate WCR population dynamics and maize phenology (see Table S1 for a description of the sub-models used and Appendix S2 for the temperature interpolation methods used). The susceptible fields each year (fields where WCR could complete its life cycle) were calculated using a cumulative degree-day threshold over a temperature of 11 °C (see Fig. 2) (Baker et al., 2003).

The sub-processes considered were immature and mature phenological stages, extended diapause eggs, proportion of eggs developing on alternative hosts, egg laying and adult mortalities (see Table S1). The difficulty to find a mating partner when population density is low was included using a probabilistic mathematical model (Kuno, 1978) (see equation in Table S1 of the supplementary information). A model of emergence that used degree-day budgets over 11 °C and below 18 °C (Davis, 1996) was fitted to existing data to predict the dates of adult emergence in Austria from 2002 to 2005, Fig. 4):

$$p_{\text{emerg}} = \frac{1}{\exp(-a_1 + b\,\text{DD})}$$

where p_{emerg} is the probability of emergence; DD is the accumulated degree-days over 11 °C and below 18 °C; a_1 and b are parameter to be estimated.

2.1.2. Dispersal

WCR can disperse by several mechanisms: (i) natural dispersal, where most of WCR adults disperse by short trivial flights and a small proportion of young mated females can perform long-distance dispersal events by means of migratory sustained flights (Coats et al., 1986) and (ii) human-assisted dispersal via airplanes (Miller et al., 2005) and hypothetically via terrestrial and inland-water transport networks (Wudtke, 2005).

2.1.3. Natural dispersal

We modelled dispersal using spatial stochastic simulation. The approach was based around spatially explicit metapopulation models where the populations are considered within discrete patchy habitats. The habitat patches were maize fields (from the official pheromone traps survey) and "macro-fields" where the area of maize grown in each municipality was represented as a single field.

We considered two types of dispersal kernels representative of the two main generic models used to study dispersal: the negative exponential, with a rapidly declining probability after a certain distance, and the negative power law, which has a fatter tail allowing for more frequent long-distance dispersal events. We used specifically a negative exponential distribution:

$$p(r|\theta) = \frac{\Phi}{\lambda(\exp(r/\lambda))} \tag{1}$$

and a half Cauchy distribution:

$$p(r|\theta) = \frac{2\Phi}{\pi\lambda(1 + (r/\lambda)^2)} \tag{2}$$

where $p(r|\theta)$ is the probability of a dispersal event to radial distance r along a bearing θ, λ is the distance that half of the WCR adults travelling along a given bearing θ are expected to reach (we will call it "median scale") and Φ is the reduction of dispersal probability due to altitude; where Φ is (Cook et al., 2007):
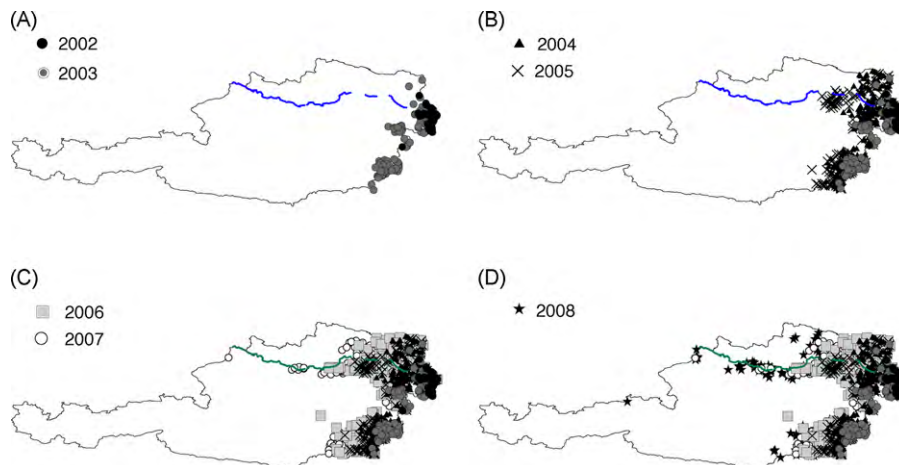
$$\Phi = \exp(-a(A_j - A_i))$$

Fig. 2. Historical spread of WCR in Austria from pheromone traps surveys. Only the traps with WCR adults are displayed. For confidentiality reasons the latitude and longitude of the fields were modified at the second level in the maps.

Table 1
Parameters estimated by maximum likelihood – simulation and model cross-validation using predicted versus observed regression.

Parameter	Uncertainty distribution	ML Model 1		ML Model 2		ML Model 3	
		NE	NPL	NE	NPL	NE	NPL
λ_{NAT} (m)	Uniform (0, 50,000)	6030	2562	5729	2462	3568	352
$p_{findHost}$	Uniform (10^{-9}, 10^{-2})	0.090	0.065	0.326	0.100	0.573	0.095
a	Uniform (0, 0.1)	0.006	0.004	0.002	0.008	0.003	0.002
p_{detect}	Uniform (0, 1)	0.001	0.001	0.001	0.002	0.004	0.004
$\lambda_{GRAV\text{-}LDDE}$ (m)	Uniform (0, 50,000)	–	–	6784	2161	–	–
Θ	Uniform (10^{-16}, 10^{-12})	–	–	4.87×10^{-13}	7.24×10^{-12}	–	–
γ	Uniform (1.5, 2.5)	–	–	1.605	1.877	–	–
β	Uniform (0.5, 1.5)	–	–	0.530	0.520	–	–
$\lambda_{INTER\text{-}LDDE}$ (m)	Uniform (0, 10,000)	–	–	–	–	4422	9095
p_{INTER}	Uniform (10^{-9}, 10^{-2})	–	–	–	–	5.03×10^{-8}	2.36×10^{-6}
Slope	–	0.39[***]	0.43[***]	0.53[***]	0.54[***]	0.85[***]	0.95[***]
AIC	–	97.43	93.76	96.79	97.99	68.3	80.4

Θ, constant of proportionality of the gravity model; γ and β, effect of distance between cities and cities sizes respectively on the proportion of adults performing human-assisted long-distance dispersal (LDD) events; λ_{NAT}, $\lambda_{GRAV\text{-}LDDE}$ and $\lambda_{INTER\text{-}LDDE}$, median scaled of the dispersal kernel of the adults performing natural, terrestrial transport (modelled with a gravity model) and river transport human-assisted LDD respectively; a, effect of altitude on dispersal; p_{detect}, daily probability of detection of a WCR adult in an infested field; ML, maximum likelihood; Model 1, "*natural spread model*"; Model 2, "*domestic spread model*"; Model 3, "*international spread Danube model*"; NE and NPL negative exponential and negative power law dispersal kernels. The ML estimates were obtained using the historical spread of WCR in Austria from 2002 to 2004. The predictions of the model refer to the invasion from 2005 to 2008. Slope: estimate of the slope coefficient of the regression of predicted against observed first date of invasion detection in the Austrian districts. AIC: Akaike Information Criterion of the regression. The regression was forced through the origin.

[***] Significance level at $p < 0.001$; p, probability ($> |t\text{-statistic}|$).

a is the parameter representing the effect of altitude on dispersal; A_j and A_i are the altitudes of the uninfested potential sink field and infested source field respectively (see supplementary data S4 for a detailed description of the dispersal model).

2.1.4. Human-assisted long-distance dispersal

We considered two types of human-assisted dispersal: *domestic* and *international*. In the case of domestic-assisted dispersal, the probability of an adult performing human-assisted long-distance dispersal ($p_{i \to j}$) was modelled using a gravity model that related the interaction strength between two cites m and n, weighted by the distance between them analogously to Newton's Law of Gravitation. Human population of cities (P) were used as surrogates of the transport networks:

$$p_{i \to j} = \frac{\vartheta(P_m^\beta P_n^\beta)}{d_{m \to n}^\gamma}$$

where θ is a constant of proportionality and the exponents β and γ tune the dependence of $p_{i \to j}$ with the distance between two cities ($d_{m \to n}$). WCR adults within 1 day flying distance to the lines connecting the 10 most populated cities in Austria (see Fig. S2B in the supplementary data) could perform long-distance dispersal with probability $p_{i \to j}$. The distance travelled followed a negative power law dispersal kernel of median $\lambda_{GRAV\text{-}LDDE}$.

Human-assisted long-distance dispersal related to international transport through the Danube basin (inland-waters transport, international motorways and railways) was modelled considering that adults within 1 day flying distance of the Danube river could perform long-distance dispersal with probability p_{INTER}. The distance dispersed was modelled with a negative power law dispersal kernel of parameter $\lambda_{INTER\text{-}LDDE}$.

2.1.5. Control measures

The model reproduced current EC eradication policies as they were applied in Austria with respect to the use of buffer zones around newly infested fields (Anonymous, 2003). Once a field was detected as infested and beyond 40 km of previously infested fields, the fields within the buffer zone are set to change rotation patterns. Rotation is assumed to inflict mortality to all of the eggs in the rotated field with exception of extended diapause eggs and eggs developing on alternative hosts.

2.1.6. Detection measures

The allocation of pheromone traps by the model reproduced the official surveys in Austria from 2002 to 2008. We model the number of adults captured per field by the official pheromone trap survey as a binomial stochastic process $B_{in}(p_{detect}, n)$. Where p_{detect} is the daily probability of capturing each adult male per ha of maize field and n is the density of adult males per ha in a field on a given day.

2.2. Model specifications considered

Because of the uncertainty on the prevailing dispersal mechanisms of WCR in Europe, we consider three main models: "*natural spread model*" where we only consider natural short and long-distance dispersal of WCR; "*domestic spread model*" where both natural spread mechanisms and long-distance dispersal due to terrestrial transport networks were considered; and "*international spread Danube model*", with consideration of both natural dispersal and dispersal through the Danube basin via international boats, trains and motorways transport. Each main model is divided in two sub-models depending on the type of dispersal kernel used to model natural dispersal: negative exponential or negative power law.

2.3. Model parameterization

Parameterization of large process-based models is a complex problem. We employed a maximum likelihood parameterization method combined with spatial stochastic simulation (Keeling et al., 2001) to compare model predictions and observed data of the historical invasion from 2002 to 2004 (see the supplementary information S4 for the details of the parameterization process). This approach was used to parameterise the three models considered using both the negative power law and the negative exponential kernel (see results in Table 1).

2.3.1. Model cross-validation

We tested the three models (with both types of dispersal kernel each) by evaluating their capacity to reproduce the observed spread of WCR in Austria from 2005 to 2008 (the observed data from 2005 to 2008 were not used to parameterise the model) using the maximum likelihood parameter sets obtained. We carried out a predicted versus observed regression which is a simple and effective approach to evaluate model performance (Piñeiro et al., 2008).
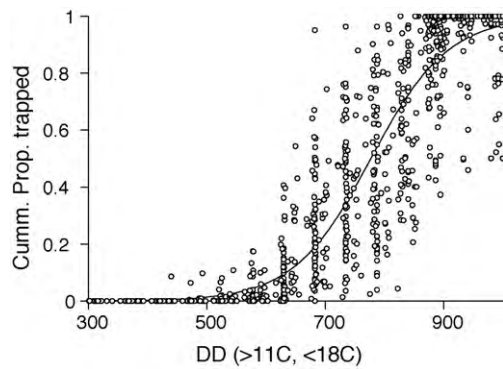
Fig. 3. Davis (1996) model of WCR emergence fitted to the cumulative proportion of trapped adult WCR males (Cumm. Prop. Trapped) data in Austria from 2002 to 2004. The explanatory variable was degree-days accumulation above 11 °C and below 18 °C (DD).

We performed a linear regression of the observed date of first detection against the predicted mean date in each of the 84 Austrian districts (Gilbert et al., 2004).

3. Results

The maximum likelihood estimates of the median scale of the dispersal kernels of the "natural spread model" were relatively low. Higher median scales were discarded by the parameterization process because they led to a high number of fields wrongly predicted as infested at the north of the Danube River and to the west of the south-eastern outbreak. The parameters representing long-distance dispersal by terrestrial transport networks in the "domestic spread model" also presented low values. The reason was that models that relied heavily on this mechanism to predict dispersal were penalised because of overestimation of the infested areas.

The daily probability of detection was relatively high (0.001–0.04, Table 1) in all models. This implied that even new established colonies at low population densities might be detected if intensive trapping is used (1 male with an average lifespan of 42 days in a field with 1 trap per ha is detected in a season with probability of 0.165 and a field with 10 adults and one trap per ha will be detected with probability of 0.84). In reality, however, the density of traps per ha is much lower than, reducing the probability of detection.

The emergence of WCR adults was estimated to begin for 500 degree-days (above 11 °C and below 18 °C) and peak emergence was estimated to occur between 700 and 900 degree-days (Fig. 3). The parameter estimations were significantly different from zero (Akaike Information Criterion = −1321.9; t-statistic for a and b in Eq. (1) was −35.15 and −35.99 respectively) and very similar to those estimated for WCR emergence in the US (a = 11.11; b = 0.0216 (Davis, 1996) compared to a = 11.9; b = 0.0153 in our case).

The regression of the observed versus predicted date of infestation of the Austrian districts showed high differences in the performance of the models. The "international spread Danube model" with a negative power law dispersal kernel was clearly the model that reproduced the spatial and temporal dimension of the invasion (slope of the regression close to 1 indicating the high similarity between predicted and observed dates of first invasion of the Austrian districts, Table 1 and Fig. 4). Whereas the "natural spread model" and the "domestic spread model" were able to reproduce the diffusive spread of WCR, they severely underestimated the long-distance dispersal events through the Danube basin in the northeast outbreak (for those districts that were not infested before 2008, the average predicted spread velocity was used to esti-
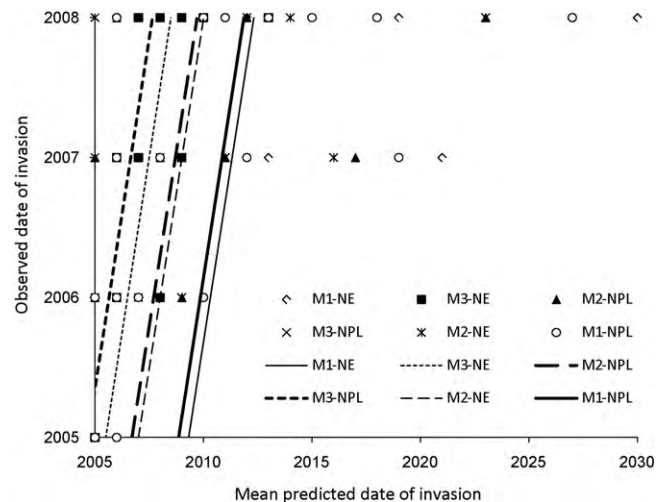

Fig. 4. Observed versus simulated date of the first detection of WCR in the Austrian districts. Line segments indicate the linear regression fit of survey observed data versus model estimates without a constant term. M1: Model 1 "*natural spread model*"; M2: Model 2 "*domestic spread model*"; M3: Model 3 "*international spread Danube model*"; NE and NPL: negative exponential and negative power law dispersal kernels respectively used to model natural spread. M3-NPL presented an slope of 0.95 (see Table 1 for the fitting results).

mate the date of infestation). Therefore, the spatial pattern of the invasion could not be explained by natural spread and/or human-assisted domestic transport networks long-distance dispersal but by a combination of natural spread and human-assisted international transport through the Danube basin (boats, railways and motorways connecting south-eastern Europe and Germany).

The invasion by WCR according to the "international spread Danube model" with a negative power law dispersal kernel of 352 m presented several phases. First, population density in the infested regions in the east of Austria built up in the first 2–3 years of the invasion and spread followed a diffusive pattern through natural dispersal (natural spread continued for the rest of the years). Second, once the population density of these regions was high, the number of WCR adults likely to perform long-distance dispersal by means of international transport running through the Danube basin was also high. This led to a high propagule pressure causing several long-distance dispersal events every year infesting fields along the banks of the Danube. Many of the newly infested fields presented low population densities and were not detected for 2–3 years of their initial colonization. Third, in 2008, the populations of the isolated colonies were dense enough to start spreading by natural means to nearby fields.

With the intention of assessing the influence of the phenology sub-model on the parameterization and prediction of the invasion, we constructed two new versions of the "international spread Danube model" (Model 3) with a negative power law dispersal kernel (which was the model that reproduced the observed pattern of the invasion). The new versions implied an increasing loss of spatial phenological information; in Model 4 we averaged monthly temperatures across fields to obtain a national monthly temperature common in all fields, that is spatial differences in degree-day accumulation were not accounted for; in Model 5 we deactivated the phenology model. We assumed that a newly infested field would be able to infest neighbouring fields a year after its infestation, i.e. that spread was governed only by the dispersal model.

We repeated the parameterization process for Models 4 and 5. Averaging monthly temperatures at a national scale (Model 4) led to all the fields accumulating enough degree-days for WCR development. Under these favourable conditions for colony development, the parameters estimated by maximum likelihood for Model 3
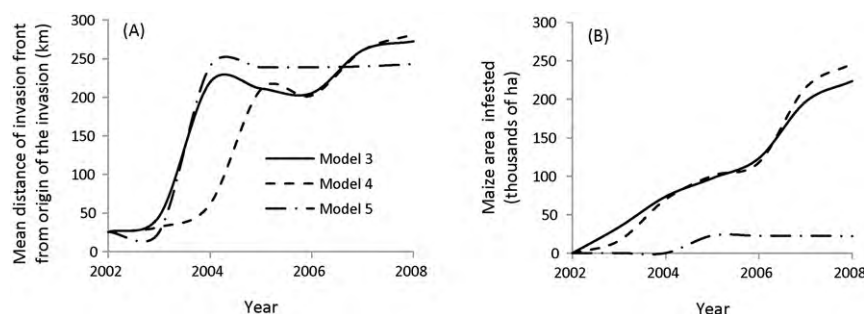
Fig. 5. Comparison of the predictions of Model 3 "*international spread Danube model*" (Model 3) regarding mean distance of invasion front from the origin of the invasion (A) and area infested (B) with simplifications of the model where: (a) monthly temperatures are averaged at national level (Model 4); (b) phenology sub-model is deactivated such that newly infested fields can immediately infest neighbouring fields the next season (Model5).

were no longer adequate for Model 4 because they tended to overestimate the number of fields infested and led to a premature colonization of the Danube basin. The parameterization process of Model 4 corrected this overestimation by reducing the median scale parameter of the dispersal kernel governing human-assisted long-distance dispersal events (a reduction of $\lambda_{\text{INTER-LDDE}}$ from 9095 to 4020 m. See Table S6 of the supplementary data).

In the case of Model 5, the parameter estimates of Model 3 were no longer the best fitting ones because they led to an overestimation of the number of infested fields. The parameterization process of Model 5 had to counter this overly optimistic consideration of the population dynamics by reducing the median scale of the dispersal kernel governing natural spread to the point that the model that best fitted the data was one without natural spread (Table S6 with a reduction of λ_{NAT} from 352 to 0 m).

We compared the predictions of the new Models 4 and 5, with Model 3 regarding: (i) the mean distance of the invasion front from the origin of the invasion; and (ii) the host area infested each year. Model 4, as a consequence of the reduction of the long-distance dispersal capabilities of WCR to compensate for the overly favourable degree-day accumulation, underestimated the mean distance of invasion front from the origin of the invasion (Fig. 5A) by 1 year with respect to Model 3. In terms of area infested, Model 4 produced relatively similar estimations to Model 3, however underestimating the area infested in the initial years of the invasion and then overestimating it in the latter years of the invasion (Fig. 5B). Model 5 predicted a relatively similar invasion velocity in the Danube basin to Model 3 although it predicted the invasion to peak and stabilise more abruptly; suddenly changing from a small localised invasion to the occurrence of colonies at far distances (Fig. 5A). In terms of area, Model 5 severely underestimated the area infested and thus failed to reproduce the spatial pattern of the invasion. The reason was the non-inclusion of the natural dispersal of WCR (Fig. 5B).

4. Discussion

Here we developed and parameterized a process-based landscape-extent spatial stochastic simulation model that integrated the spread and phenology of invasive insects for the study of biological invasions. The model was adapted to the important case of the invasive alien western corn rootworm that is threatening maize production in Europe.

WCR was found to spread following stratified dispersal where its two main mechanisms of spread were natural dispersal and human-assisted dispersal via international inland-water, motorways and railways transport in the Danube basin. Maximum likelihood methods and predicted versus observed regression allowed us to unveil human-assisted long-distance dispersal events in the Danube basin that could not be explained only by domestic transport within Austria or by natural dispersal. Insights on the

effect of the mountains on spread and the effectiveness of detection could also be inferred.

The model advanced the literature of biological invasions modelling by combining, in a spatially stochastic modelling framework (Higgins et al., 2000; Lurz et al., 2001), elements of spread and phenology of the NIS. This novel approach was useful because it allowed the incorporation of heterogeneous existing information regarding the population dynamics driven by temperature and the dispersal of WCR. This integration permitted a greater mechanistic understanding of the progression of the invasion. Understanding the mechanisms of an invasion is an intricate problem that involves, in many cases, the reconstruction of observed historical invasions in the context of data and model structural uncertainty. The quest for finding the model that can explain the invasion is daunting given the innumerable model options to choose from. By incorporating many times experimentally well tested, phenology data we can observe a drastic reduction in the set of models that could possibly explain the mechanism of an invasion. For example, lower winter temperatures in some regions and years will lead to lower population densities in those regions conditioning the pattern of the progression of the invasion. Predicting those variations in population dynamics through the landscape would reduce the number of combinations of mechanisms that can reproduce the invasion history.

To further attempt to evaluate the relevance of the integration of phenology models with spatial stochastic simulation spread models, we compared the model that best reproduced the invasion with two new versions of it that incorporated an increasing loss of information about spatial phenology. The reduction of information about spatial phenology and deactivation of the phenology sub-model led to new parameter estimates and subsequently, different invasion predictions. The non-inclusion of spatial phenology considerations, despite the necessary time lags for population densities to build up before new propagules could be generated, introduced a bias in the phenology sub-model. This bias was countered in the dispersal sub-model by reducing the median scales of the parameters of the dispersal kernels. This underestimation of dispersal would compensate for the lag in the building up of the population.

Biological invasion modellers have to decide on a model structure according to specific research questions. They face a daunting trade-off between model complexity (represented by the explicit consideration of more spread mechanisms and subsequently more model parameters) and feasibility of model parameterization and validation. Considering spatial phenology processes in invasion models increases our confidence in the estimation of the dispersal parameters but involves an increase in modelling, parameterization and data demands. Not considering spatial phenology information might not necessarily prevent the invasive insect modeller from detecting human-assisted dispersal events, however, the obtained dispersal parameters might need to be treated with caution in

these cases. We need to ask ourselves certain questions to find out whether the dispersal parameters of a model without information about spatial phenology are countering phenological dynamics biases: (1) will the population dynamics and timing of phenological events of the invasive insect differ clearly in different spatial regions of the landscape considered? and (2) does the invasive insect need time to build up its population in newly infested patches? If the answers are yes, our model will benefit from the use of a phenology sub-model. Alternatively, if only the second question is answered with yes, a compromise could be the integration of simple population dynamics sub-models with the dispersal sub-models.

The model presented some caveats: (a) even though we could identify international transport as responsible for long-distance dispersal events, discriminating between the types of transport was not possible because motorways, boats and railways trajectories shared a common space in the river Danube basin; (b) WCR immature stages occur inside the soil. Soil temperatures are different to air temperatures and depend on the deepness, soil type and the humidity, making their spatial modelling extremely complicated. Immature mortalities in the model are a source of uncertainty that could only be approximated; (c) monthly temperature data were used instead of daily temperature grids because the latter were lacking. This could have affected the accuracy of the predictions regarding population dynamics, however, similar parameters fit were obtained for the Davis' emergence model (1996) (original fit done using daily temperature) using monthly temperature data. The results gave us confidence that the deviation in prediction accuracy because of using monthly temperature data was not relevant; and (d) more informed estimation of detection effectiveness could have been obtained by using prior information regarding the effectiveness of pheromone traps to detect WCR in the field, however this information was lacking. Further experimental research at the field scale would be beneficial.

The model can be applied to other invasive insects and be used as a "virtual laboratory" to test the effect of spread mechanisms on spread velocity. One advantage of the model is its process-based nature embedded in a maximum likelihood parameterization framework. Thus, existing information on the spread of the NIS can be fully combined from different sources (e.g. historical spread, field trials and literature). When information is lacking, the model can still be run and the range of potential outcomes regarding the existent uncertainty can be explored. This is one advantage of process-based models over phenomenological models because they do not rely on extensive historical spread data (Higgins and Richardson, 1996), which are scarce or lacking for most NIS. In addition, linking population dynamics to climate data provides for a ready modelling framework to test the effect of climate change on the spread and eventual distributions of NIS.

Spatial stochastic models fitted to observed biological invasions to study human-assisted long-distance dispersal events presents a great advance of the study of biological invasions (e.g. Gilbert et al., 2004; Muirhead et al., 2006; Robinet et al., 2009). The incorporation of the phenology of the invasive insect adds an extra layer of mechanistic accuracy to the modelling framework. The usefulness of adding the phenology of the invasive insect will become more apparent when data on phenology are available and data on dispersal are missing. Landscape-extent spatial stochastic models putting together dispersal and phenology will contribute to the understanding of insect biological invasions dynamics and the unveiling of human-assisted dispersal mechanisms.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.05.012.

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