Global estimation of invasion risk zones for the western corn rootworm *Diabrotica virgifera virgifera*: integrating distribution models and physiological thresholds to assess climatic favourability

Pedro Aragón[1]*, Andrés Baselga[2] and Jorge M. Lobo[3]

[1]*Departamento Interuniversitario de Ecología, Facultad de Biología, Universidad Complutense de Madrid, José Antonio Novais, 2, 28040-Madrid, Spain;* [2]*Departamento de Zoología, Facultad de Biología, Universidad de Santiago de Compostela, Lope Gómez de Marzoa s/n, 15782-Santiago de Compostela, Spain; and* [3]*Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal, 2, 28006-Madrid, Spain*

Summary

1. Biological invasions represent a major threat to human health, ecosystem functioning and global biodiversity. Insect pests affecting agriculture and forestry are of special importance. Estimations of climatic similarity between a species' native range and potential zones of invasion can be useful for preventing new invasions, spreads and ulterior contacts among populations from multiple invasions.

2. We estimated areas climatically favourable for the establishment of the western corn rootworm (WCR), an insect pest of maize *Zea mays* in North America that has recently invaded Central Europe through multiple invasions, and it has the potential of invasion mainly in the Northern Hemisphere.

3. We used complementary techniques to assess the biological relevance of predictors and obtain areas of climatic favourability. The biological relevance of variables was first assessed accounting for two main components of the WCR's environmental niche (marginality and specialisation). Then, the most relevant predictors were used to obtain either climatic envelopes or environmental distances regarding the WCR's native range. Model outputs and predictor relevance were independently assessed in the currently invaded region of Europe and through the spatial projection of proposed physiological thresholds from previous empirical studies. Lastly, as examples of application for given time periods, we fed back results of environmental distances with maize data for a 10-year period in Europe, and refined global risk maps with the main maize zones for the year 2000.

4. We present global zones of climatic favourability and invasion risk for the WCR, with emphasis on the Northern Hemisphere. The northern and north-west range limits predicted by the climatic envelope in the WCR's native range mirrored the independently characterised physiological limits. Also, our model outputs explained some of the patterns observed in Europe supporting the validity of our procedures.

5. *Synthesis and applications.* Assessments of climatic favourability for the western corn rootworm can provide information on areas of invasion risk. Our study highlights the combination of holistic and reductionist approaches as a useful protocol to evaluate models and/or infer causality. Our methodology can be an efficient tool in combating future potential invasions, spreads and secondary contact zones of insect pests by reducing uncertainty regarding where to allocate prevention and/or eradication efforts.

Key-words: bioclim, biological invasion, climatic favourability, *Diabrotica virgifera virgifera*, Ecological Niche Factor Analyses, insect pest, Mahalanobis distances

*Correspondence author. Pedro Aragón, Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal, 2, 28006-Madrid, Spain. E-mail: paragon@mncn.csic.es

Introduction

Biological invasions have received a great deal of attention for decades because they can affect human health (Tatem, Hay & Rogers 2006), ecosystem functioning (Gewin 2005) and global biodiversity (Vidal, Khulmann & Edwards 2005; Borges *et al.* 2006). In recent decades, globalisation of transport networks has become an increasingly important human-mediated dispersal vector for species invasions far away from their native geographical range (Vidal, Khulmann & Edwards 2005; Tatem & Hay 2007; Kobel & Nentwig 2008; Hulme 2009; Wilson *et al.* 2009). Among biological invasions, insect pests have had some of the greatest ecologically and economically adverse impacts on agriculture and forestry (Vidal, Khulmann & Edwards 2005). Whereas pest eradication is indispensable when establishment has already occurred, there is consensus that prevention is the most cost-effective way to avoid conflicts with human interests and biodiversity conservation (Miller *et al.* 2005; Thuiller *et al.* 2005; Vidal, Khulmann & Edwards 2005).

Climatic similarity between the native range of invasive species and potential areas of invasion has been widely recognised as an important requirement for successful invasions (Tatem & Hay 2007; Kobel & Nentwig 2008). Therefore, techniques devoted to detecting areas of climatic favourability for the persistence of the subject organism's populations are considered useful approaches for preventing invasions (Thuiller *et al.* 2005; Tatem, Hay & Rogers 2006; López-Darias, Lobo & Gouat 2008). This is of special relevance in the case of insect pests, because climate is one of the most important environmental factors limiting, through their physiological dependence, the demography and colonisation ability of insect species (Chown & Terblanche 2007).

Niche modelling techniques have been widely used to predict the potential geographic range of species invasions (Peterson & Vieglais 2001; Peterson 2003; Thuiller *et al.* 2005; López-Darias, Lobo & Gouat 2008). These correlative techniques are based on the association between environmental factors and species geographical position, and they are designed to identify the environmental conditions in which species can maintain populations. Once these associations are modelled, the suitable conditions are projected into geographical space to derive spatial hypotheses on the species' potential distribution. Two limitations of these techniques are the difficulty of disentangling coincidence and true causation (Dormann 2007), and the fact that the observed species presence can only partially unveil its potential distribution. The realised species' distribution is the result of not only the abiotic factors but also the consequence of other historical, unique and contingent factors such as certain dispersal constraints, biotic interactions, anthropogenic effects and stochastic events (Dormann 2007; Jiménez-Valverde, Lobo & Hortal 2008), that might no longer be acting in the new area of invasion. Thus, when we are to elucidate the suitable environmental conditions regardless of the above-mentioned contingent factors, these factors may input noise in models because they may be different in the potential areas of invasions. More importantly, it follows that these model outputs cannot be fully evaluated with additional information on species' presence because it comes from its realised distribution (Jiménez-Valverde, Lobo & Hortal 2008). Therefore, complementary independent information should provide valuable insights.

Alternatively, other techniques are based on physiological information of the species used to translate it to the geographical space (e.g. Battisti *et al.* 2005; Deutsch *et al.* 2008; Kearney & Porter 2009). While these approaches may allow more accurate exploration of mechanistic processes, it is exceedingly difficult to catch all of the relevant biological information. In other words, whereas correlative approaches, such as niche modelling techniques, encompass too much information to give accurate interpretations of causality, mechanistic models use more directed information but derive overly reductive spatial hypotheses on only one or few aspects of the species' biology. Therefore, because different sources of information may carry different sources of limitations, it can be argued that the combination of different types of information can be complementary to each other.

The western corn rootworm (WCR), *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), is one of the most severe pests of cultivated maize *Zea mays*. Damage due to larvae feeding on maize roots causes important economic costs in terms of maize yield and management efforts. For this reason, the biology, physiology and ecology of the WCR have been the subject of study for decades in the USA (Krysan & Miller 1986), and are receiving increasing attention because of recent invasion events outside the USA (Miller *et al.* 2005; Vidal, Khulmann & Edwards 2005; Ciosi *et al.* 2009). In recent years, this pest has invaded and spread in Europe (http://www.eppo.org), and multiple invasions independent in time and location have been detected near European airports (Ciosi *et al.* 2008, http://www.eppo.org), thus representing a problem of global importance. Prevention and eradication of this pest is a challenge because some populations have been confirmed to be resistant to management techniques like crop rotation (Levine *et al.* 2002) and some insecticides (Meinke *et al.* 1998; Ciosi *et al.* 2009). Furthermore, the expansion of the host spectrum of WCR from maize to other crops, such as soybean, oil pumpkin and *Miscanthus* grass, has been suggested or confirmed (Meinke *et al.* 2009; Spencer & Raghu 2009).

The aim of this study was to define areas in Europe and worldwide with climatic conditions similar to that of the recorded WCR native range in North America. We focused on the WCR subspecies because it is both an invasive and pest organism. The other subspecies (*D. v. zeae*), although it is a pest, is not invasive and has not invaded Europe (EPPO 2004). Another important key difference is that *D. virgifera virgifera* is adapted to temperate climates through diapause, while *D. virgifera zeae* is adapted to warm climates (without diapause) (EPPO Standards. 2004). We sought to contrast the results of correlative models with physiological information from previous studies on this subspecies. We used different complementary modelling techniques to select biologically relevant predictors and to determine areas of climatic similarity. First, estimation of the biological relevance of potential

predictors was grounded on niche theory. Then, climatic similarity was obtained using envelope models and environmental distances. The relevance of predictors and predictive capacity of the models were then independently assessed in two ways, comparing predictions: (i) with the current European area of invasion and (ii) with the spatial projection of physiological thresholds obtained from previous empirical studies. Finally, model predictions and maize cultivation areas were jointly examined in order to provide invasiveness risk maps at a global extent.

Materials and methods

MODELLING CLIMATIC FAVOURABILITY

The recorded presence of the WCR in the native region (northern Mexico, USA and southeastern Canada) was digitised and geo-referenced from available sources (Krysan & Smith 1987) at a 5-km resolution. The current area of influence in the invaded Europe (as of 2008) was digitised from Edward & Kiss (2008). Environmental variables at the same resolution were obtained from the WorldClim source (Hijmans *et al.* 2005). To detect the key bioclimatic variables, we used the Ecological Niche Factor Analysis (ENFA) implemented in the GIS-statistical tool Biomapper (Hirzel *et al.* 2002). ENFA is analogous to principal component analysis with the difference that it is grounded in the niche concepts of the organism's marginality and specialisation (see Appendix S1 in Supporting information for a full description of this procedure). Then, we estimated the climatic niche using the WCR's presences in North America.

We used two complementary modelling techniques to delimit risk areas of invasion regarding departures from the WCR's climate optimum as characterised by the most relevant predictors assessed by ENFA. Considering a potential-realised distribution gradient, Jiménez-Valverde, Lobo & Hortal (2008) recommended the use of simple presence-only methods, such as environmental envelopes, when the purpose is to obtain predictions more related to the species' potential distribution. Our delimitation of climatic favourability areas for an invasive organism should be closer to the prediction of its potential distribution along the above-mentioned distribution gradient. Therefore, we used a Multidimensional Envelope modelling procedure (MDE), which estimates the climatic species range regarding its recorded presences (Busby 1991). We first used the simplest procedure to generate a Boolean map of risk areas obtained from the climatic hypervolume encompassed by the minima and maxima of climatic variables within the WCR's native range.

As a complementary approach, to obtain continuous risk areas, we calculated Mahalanobis distances (MD) from each cell to the mean of the hypervolume of the selected variables, with reference to WCR's presence records, a procedure widely used in studies of spatial ecology (e.g. Corsi, Duprè & Boitani 1999; Farber & Kadmon 2003; Etherington *et al.* 2009). Specifically, the use of predictors selected by ENFA, or analogous techniques, to then obtain MD has been previously proposed as a useful tool to estimate area favourability for a species (e.g. Calenge *et al.* 2008).

MDE and MD are complementary to each other in potential shortages specific to each technique. Whereas the environmental mean used to obtain MD is more susceptible to the unavoidable error arising when realised distributions are used to predict potential distributions, MDE is less susceptible to this noise as it considers only the environmental extremes (*sensu lato* Jiménez-Valverde, Lobo & Hortal 2008). On the other hand, whereas MDE might extend the organism

niche to environmental combinations where the organism would not persist, the MD takes into account the associations and interactions among predictors (Farber & Kadmon 2003).

Finally, we also geographically projected physiological temperature thresholds regarding key WCR's fitness components (oviposition, hatching and immature development) obtained from empirical data (see Appendix S2, Supporting information for a full description of the methodology used). Then, the geographical representation of these physiological thresholds was compared with the outputs from the above-mentioned models.

EVALUATION OF PREDICTORS AND MODELS

To examine the adequacy of the selected variables, we compared among the predictions obtained from three sets of outputs: (i) those obtained when using the seven most relevant ENFA variables, (ii) those obtained when using the seven less relevant ENFA variables and (iii) those obtained when using all variables. Prediction errors in the MDE outputs were assessed by calculating the proportions of wrongly predicted WCR absences (omission errors) and wrongly predicted presences (commission errors) (Fielding & Bell 1997) regarding the observed presences and the area encompassed by the estimated physiological thresholds respectively. We calculated the omission errors as the percentage of 5-km cells with wrongly predicted absences (i.e. wrongly predicted as climatically unfavourable) within the area of invasion in Europe in 2008. Because the MDE models were built using the extremes of the environmental predictors regarding presence records in America, there were no omission errors in the WCR's native continent. On the other hand, invasive organisms are not necessary at equilibrium with the environment in the invaded area because the invasion process might be not yet finished. Thus, model outputs can predict areas of climatic favourability where the WCR is currently absent but has the potential to colonize that area. Therefore, commission errors cannot be fully assessed using the invaded area. We performed an alternative partial approximation using the area delimited by the physiological thresholds. As a partial estimation of the commission error, we calculated for each set of predictors the percentage of cells in America, Europe and worldwide predicted as climatically favourable that were actually beyond the considered physiological thresholds.

On the other hand, MD outputs were compared both for the presence records in America used for model building and for the current area of invasion in Europe. These analyses were performed using repeated measures ANOVAS with the MD as the dependent variable, and the set of predictors regarding relevance as a three level within-subject factor. Pairwise *post hoc* comparisons were performed using Tukey tests. Additionally, we plotted histograms for the WCR records in America and for the region of the European invasion along the MD corresponding to each set of predictors. Thus, the set of predictors reflecting the stronger constraints should show the highest percentage of records toward the smaller distances in an exponential manner.

Once the most relevant predictors were confirmed, we further independently evaluated our MD output. We obtained a threshold value from the histogram of the WCR presences in America along the corresponding MD, and then applied it in Europe. The threshold value *a priori* proposed was set at the first distance corresponding to only 1% of presences, which encompassed 93% of all presences (Fig. S1 in Appendix S3, Supporting Information). This threshold proposes a division at a MD value of 4. Areas beyond this value might be considered as less favourable with respect to the bioclimatic predictors used, though this does not necessary imply that the WCR would

not occur beyond this value. Finally, we examined the extent to which the pattern obtained through this threshold matched with the invaded region. That is, even if the organism is not at its climatic equilibrium in Europe, we could examine whether the MD was lower in the regions where populations persist (potentially secondary source populations) than in those where they do not remain stable (potentially sink populations).

COMBINING CLIMATIC FAVOURABILITY AND MAIZE DATA

The variables designated most relevant according to ENFA were shown to be the best predictors to map favourable climate areas beyond the native region (see Results). Therefore, we present maps of the MDE and MD predictions in Europe, superimposed on the digitised region of invasion, as well as a global map to detect potential areas of future invasion. To gain in precision, the MD for the global map was restricted to the physiological temperature limits previously calculated.

To refine our maps of invasion risk, and as an example of application, we fed back our model outputs with both information on available maize statistics of most European countries, and geo-referenced data of a worldwide maize map. Since maize is not the only host plant for WCR, and as invasive organisms are not necessarily at equilibrium, we firstly performed an additional analysis to test to what extent maize, climatic favourability and their interaction can predict the current invasion in Europe. We generated three variables for each country: the proportion of maize area (area of production in a given country/country area), the proportion of area with high climatic favourability (area with MD ≤ 4 in a given country/country area), and the proportion of invaded area (area invaded in a given country/country area). We performed an ANCOVA where the response variable was the proportion of invaded area per country, and the predictor covariables were the proportion of area covered with maize, the proportion with high climatic favourability and their interaction. The proportion of maize area were obtained from Eurostat (http://epp.eurostat.ec.europa.eu) and averaged for the years 1999–2009. The simultaneous effect of both covariables was plotted as the isopleths generated by distance-weighted least squares regression connecting conditions of equal expected proportion of invasion, and the situation of each country in the plot.

Then, we elaborated a refined risk map combining our model outputs with the available spatial data on maize over the world for the year 2000 (Monfreda, Ramankutty & Foley 2008; http://www.geog.mcgill.ca). We focused on the zones were the percentage of maize area per grid cell was higher than 0·1, and where our models predicted climatic favourability.

Results

EVALUATION OF PREDICTORS AND MODELS

Seven predictors were estimated by ENFA as the most relevant: the mean temperatures of the wettest and warmest quarters, minimum temperature of the coldest month, temperature annual range, maximum temperature of the warmest month, isothermality and precipitation of the warmest quarter (Appendix S1, Supporting information). The predictions of the MDE models revealed that the proportion of omission errors in the European invaded region was the lowest when the most relevant predictors were used, and the highest when all

fourteen bioclimatic variables were used (Table 1). In fact, only the MDE prediction using the most relevant predictors was able to predict subtle patterns such as the dispersal corridor recently observed between the populations of Italy and those of the Hungarian–Serbian core (Fig. 1a and Appendix S4, Supporting information).

The proportion of commission errors, with regard to the physiological thresholds, was the highest when the less relevant variables were used, either for America, Europe and worldwide, and was similar when either the most relevant or all variables were used (Table 1). When the most relevant predictors were included in the MDE models, the northern and north-west limits of the predictions mirrored the independently characterised physiological limits (Appendix S4). In contrast, when using the less relevant predictors, the MDE output in America extended northward far beyond the limits of both the physiological threshold and the observed presences (Appendix S4). On the other hand, the considered physiological thresholds seemed to be unable to offer a reasonable limit under tropical or subtropical conditions when compared with MDE models regardless of the set of predictors used (Appendix S4).

Regarding the MD in the locations where the WCR is present in America, there were significant differences among the different sets of predictors (repeated measures ANOVA: $F_{2,2056} = 2543·46$, $P < 0·0001$; Fig. 2). The MD outputs were smallest when calculated using the most relevant predictors and the largest when calculated with the less relevant variables (Tukey tests: $P < 0·0001$ in all cases). Comparison of the MD in the European region of invasion also showed significant differences ($F_{2,105414} = 561054·58$, $P < 0·0001$; Fig. 2), and were likewise smallest when calculated using the most relevant predictors and the largest for the less relevant variables ($P < 0·0001$ in all cases).

Finally, the histograms showing the number of presences in America along the MD revealed that the majority of presences (71%) were associated with the smallest class of MD (MD < 0·5) when using the most relevant predictors. However, the peak of the distribution was displaced to the right when using the less relevant predictors (29%) or all variables

Table 1. Prediction errors for the MDE output using the most relevant predictors, the less relevant predictors and all predictors according to ENFA. Omission errors in the European area of invasion (% wrongly predicted absences) and commission errors (% potentially wrongly predicted presences) regarding physiological temperature thresholds (see 'Materials and methods') in America, Europe and worldwide

|	Omission error (%)	Physiological commission error (%)		
	Invaded Europe	America	Europe	Global
Most relevant ENFA vars.	33	1·71	0·02	1·23
Less relevant ENFA vars.	41	25·18	3·74	12·13
All vars.	47	1·47	0·02	0·82
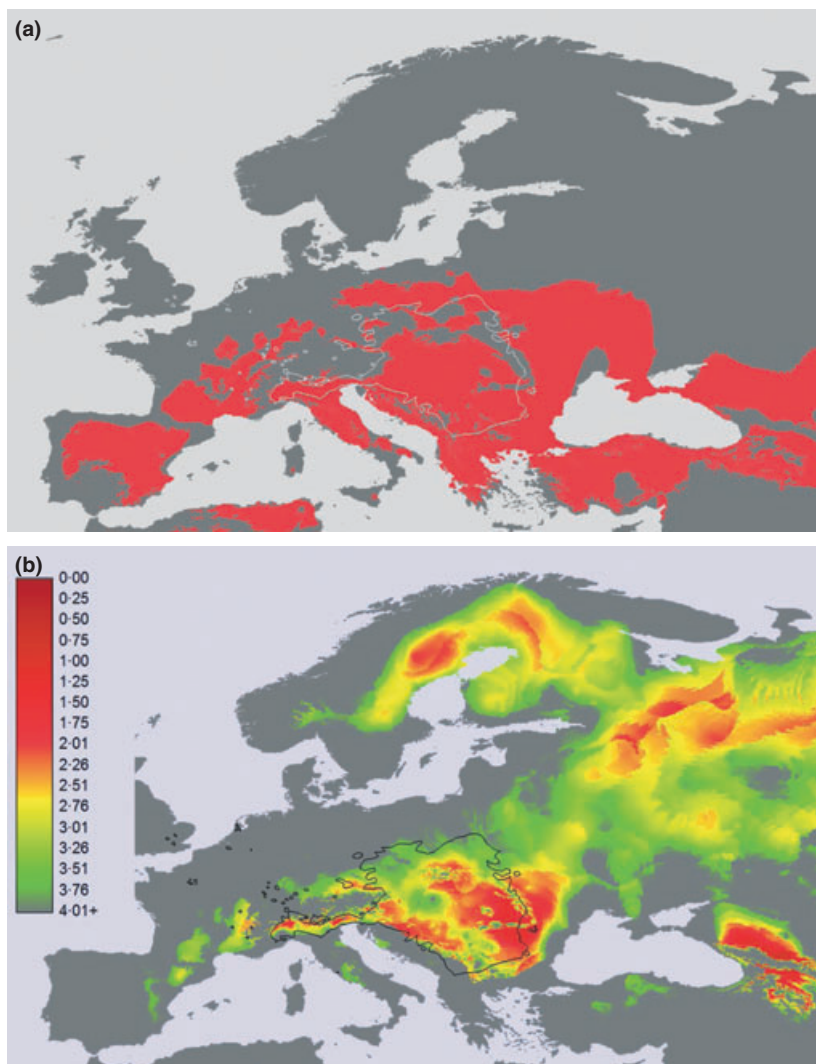
Fig. 1. Areas of climate similarity in Europe regarding presence records of *Diabrotica virgifera virgifera* in America. (a) Climatic range obtained from the MDE technique (red area) together with the observed area of invasion (white contour). (b) Increasing Mahalanobis distances (from red to grey) together with the observed area of invasion (black contour). Larger distances were grouped (grey) beyond an estimated threshold (Appendix S3). Outputs of both techniques were obtained using the most relevant ENFA predictors (Appendix S1).

(28%), and was wider in both cases (Fig. S1 in Appendix S3). Thus, when fitting each model to an exponential function, the MD calculated with the most relevant predictors showed the greatest slope, and those calculated with all variables showed the smallest slope (Fig. S3a in Appendix S3). For the invaded region of Europe, we found an analogous trend. The peak of the distribution was more skewed to the right of the distribution for MD calculated with the less relevant predictors or with all variables (Fig. S2 in Appendix S3). Fitting these histograms to the exponential function gave the greatest slope for the most relevant predictors and the smallest slope for all variables (Fig. S3b in Appendix S3).

COMBINING CLIMATIC FAVOURABILITY AND MAIZE DATA

The ANCOVA showed that the proportion of maize area alone cannot predict the invasion probability for each country in Europe ($F_{1,31} = 0.79$, $P = 0.779$), and that the proportion of area with high climatic favourability for the WCR was close to significance ($F_{1,31} = 3.20$, $P = 0.083$). However, the interac-
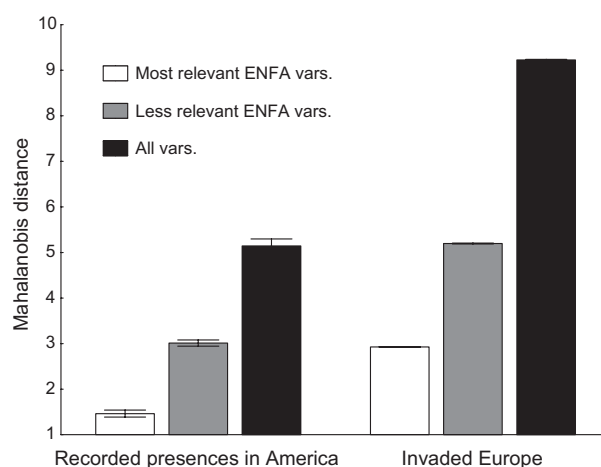
Fig. 2. Mean ± SE Mahalanobis distances (MD) for the recorded presences of *Diabrotica virgifera virgifera* in America, and in the European area of invasion when using (a) the most relevant ENFA predictors, (b) the less relevant ENFA predictors and (c) all predictors (see 'Materials and methods'). Higher MD values denote higher departures from the species' environmental mean in America.

tion effect between maize area and climatic favourability on the invasion rate was significant ($F_{1,31} = 6.86$, $P = 0.013$; Fig. 4). In the light of these results we generated maps of the main areas of maize cultivation in the world combined with both the MDE outputs and the MD denoting high climatic favourability (Fig. 5).

Discussion

We used biologically relevant climatic predictors of the WCR's native range (North America) to estimate the degree of climatic favourability in Europe, where an invasion is taking place, and globally. Climatic similarity was represented by combining outputs of two complementary techniques (Boolean MDE and continuous MD). Our procedure followed several steps to generate risk maps. First, relevance of predictors was grounded on the niche concepts of marginality and specialisation to estimate which factors may constrain the WCR's climatic range, and, therefore, better forecast potential areas of future invasions. Then, we tested our procedure of variable selection by comparing the predictive power of models when using different sets of predictors (most relevant, less relevant and all predictors). Further, both modelling techniques were evaluated independently in two ways: (i) by examining to what extent the contour limits of the model outputs match the spatial projection of physiological temperature thresholds based on key fitness components of the WCR's life cycle and (ii) by cross-validating our model outputs in the European area of invasion. Finally, as an example of how the proposed protocol can be refined for specific time windows, we fed back our model outputs with available data on the areas covered with maize. Thus, we tested for a 10-year period of maize data the extent to which maize, WCR's climatic favourability or their simultaneous action can predict the invasion probability for most of the European countries. Furthermore, we generated refined risk maps at a global scale combining our model outputs with the main maize cultivation zones for the year 2000.

The proportion of omission errors with respect to climatic favourability, tested in the invaded area of Europe, and commission errors, beyond the proposed physiological thresholds, confirmed that the selection of the most relevant predictors was adequate for MDE. In the same way, MD calculated with these predictors showed the highest climatic similarity both for the recorded presences in the native range and within the area of invasion. Taken together, the predictors used in both techniques to estimate areas of climatic favourability in Europe and worldwide are indeed biologically relevant. These results agree with previous studies encouraging the identification of a minimum set of biologically relevant environmental predictors (Beaumont, Hughes & Poulsen 2005), preferably with regard to environmental availability (Hirzel *et al.* 2002; Calenge *et al.* 2008), in order to improve predictive capabilities.

In correlative studies, it is always challenging to disentangle which specific mechanisms limit a species' geographical range. For instance, it is known that climatic factors play an important role in the life cycle of both *D. v. virgifera* (Meinke *et al.* 2009) and maize (Payero *et al.* 2006), but causality often can only be speculated upon. Nevertheless, we aimed to go further inferring potential mechanisms in two ways: (i) with the proposed physiological thresholds and (ii) examining the predictive capacity of maize and the WCR's climatic favourability either separately or jointly. The north and north-west contour limits of the MDE output for its native range in America, where the WCR should be closer to the equilibrium, mirrored the spatial projection of physiological temperature thresholds. This matching strongly suggests that the predictors estimated as most relevant and subsequently used for model-building are linked, at least in part, with physiological constraints of the WCR. In concordance with the physiological information, the overall specialisation value obtained from distributional data revealed the WCR as quite restrictive, especially regarding minimum temperatures (Appendix S1). On the other hand, the fact that our proposed physiological temperature thresholds did not match the southern and eastern limits of the WCR's
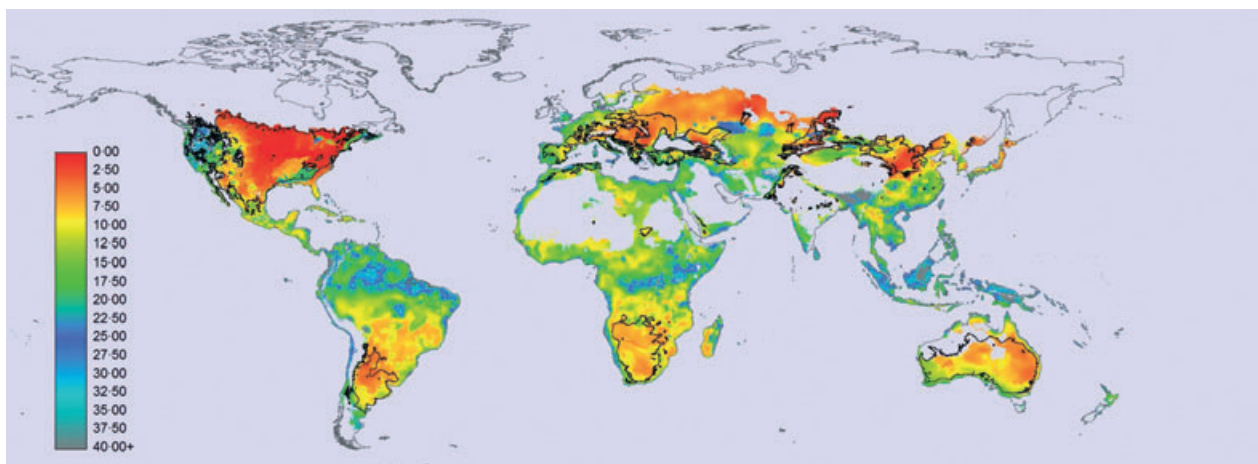
Fig. 3. Global map showing the areas of climate similarity based on presence records of *Diabrotica virgifera virgifera* in America. The output combined Mahalanobis distances (MD) and Multidimensional Envelope techniques (MDE, black contours), and an estimated partial physiological threshold. MD were restricted within an independently estimated partial physiological range (see 'Materials and methods'). Increasing MD (from red to grey) denote increasing departures from the environmental mean of the species in America.
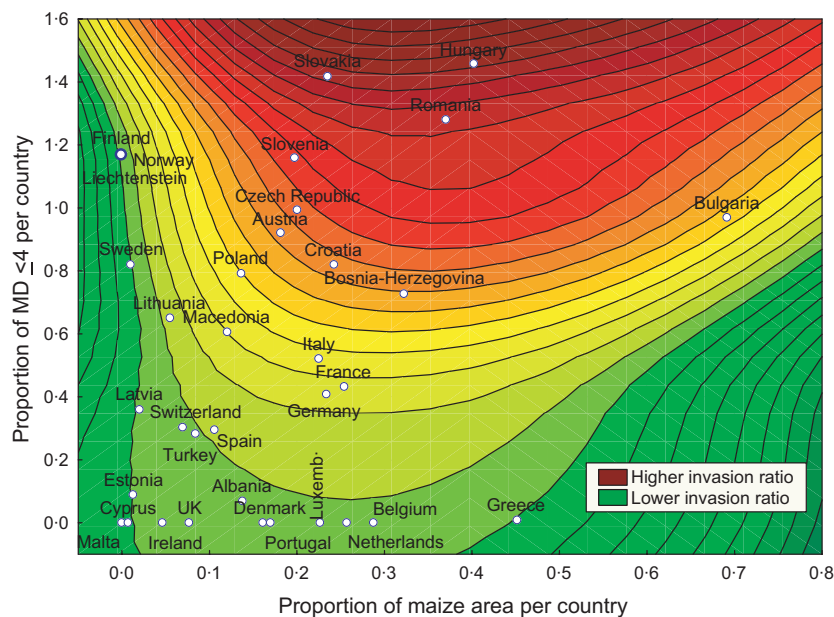
Fig. 4. Proportion of invaded area for each country in Europe as a function of their proportion of maize and high climatic favourability areas. Climatic favourability was estimated by the Mahalanobis distances. Isopleths were generated by distance-weighted least squares regression connecting conditions of equal expected proportion of invasion. All variables were angular-transformed. Maize data for Serbia-Motenegro, Moldova, Ukraine and Belarus not available.
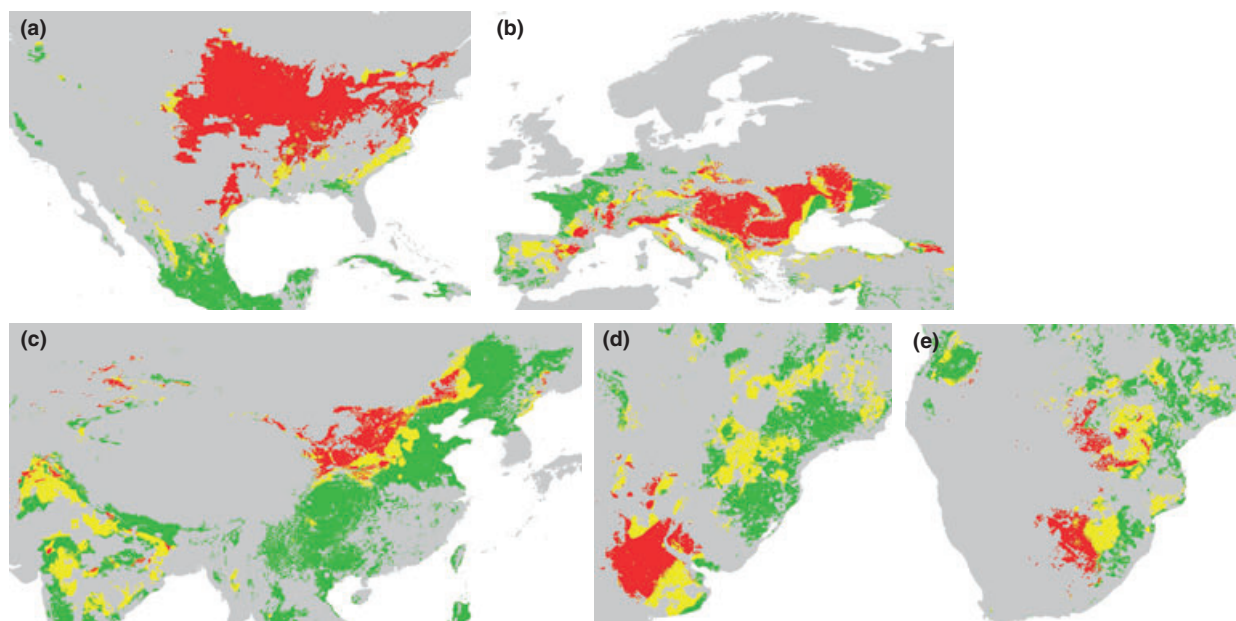
Fig. 5. Risk maps of invasion by *Diadrotica virgifera virgifera* combining main maize zones and climatic favourability estimated by the two model outputs. Increasing risk is categorized as no current risk (area without maize, grey), moderate risk (with maize but without climatic favourability, green), medium risk (with maize and predicted climatic favourability by one model, yellow) and high risk (with maize and predicted climatic favourability by both models, red). (a) North America, (b) Europe, (c) Asia, (d) South America and (e) South Africa.

native range suggests that other factors, either abiotic or biotic, constrain these flanks. For instance, water availability also plays an important role in the biology of both *D. virgifera* (Krysan 1978; Ellsbury & Lee 2004) and maize (Payero *et al.* 2006). Thus, while our proposed physiological thresholds did not include moisture thresholds, our procedure to select

relevant predictors for model building did include precipitation of the warmest quarter. Whatever the processes involved in shaping the southern range limits of the WCR, it is unlikely that maize as the main host plant is constraining these limits. This can be argued because there are important extents of maize beyond the southern limits of the WCR in Mexico (Fig. 5a). In

agreement, a simple linear model to predict the proportion of invasion area for each European country revealed that maize alone cannot predict it, while the joint effect of maize and climatic favourability was the best predictor.

COMBINING CLIMATIC FAVOURABILITY AND MAIZE DATA

After refining model outputs through the main maize areas for the year 2000 the main patterns remain similar in Europe (Figs 1 and 5; see Appendix S5, Supporting information, for a full description and discussion on the climatic favourability maps). Thus, both model outputs and maize areas converged in the core areas of the current area invaded by the WCR. Also, models and maize data converged revealing Bulgaria, Romania, Moldova, Ukraine and Azerbaijan as areas of potential future invasions and/or new spread directions. On the other hand, higher latitudes in Russia and Scandinavia are no longer at high risk once the main maize areas were included (Figs 1, 3 and 5b). In agreement, the invasion risk areas predicted in Scandinavia can also be ruled out once MD outputs were analysed jointly with maize data for a 10-years period (Fig. 4).

Once the climatic favourability map for Asia was combined with the maize areas, China was revealed as the zone with larger continuous extents of concordance between the two models (Fig. 5c), this denoting a higher risk of spread in the case of invasion. After refining with maize data in the Southern Hemisphere, the areas of model convergence remained compact in Argentina and in the so-called maize triangle (South Africa and Lesotho), and scattered in Zimbabwe and Zambia (Fig. 5d and e), whereas in Australia the maize areas were very small in comparison. It is important to highlight that the probability of colonisation success in the Southern Hemisphere should be substantially lower than in the Northern Hemisphere, as this is a univoltine species (see Appendix S5 for further discussion).

MANAGEMENT IMPLICATIONS

Obviously, there are other environmental conditions that would also be necessary for the WCR's colonisation success and spread. Therefore, similar climatic conditions can be argued as necessary but not sufficient conditions for successful invasions. The most evident factor is the maize planting distribution. However, human-mediated land uses, including cropland areas, are not static (Foley *et al.* 2005). Thus, our predictions can be used as a more dynamic tool for managers, organisations and policymakers to decide where it is necessary to concentrate monitoring and economic efforts to prevent the pest in zones where there are maize plantings (as in our examples of application for given periods) or where its cultivation is planned or recommended, as well as to decide where to cultivate it.

As in other invasive species (Wilson *et al.* 2009), one of the biggest challenges to prevent and monitor the WCR colonisation success and spread is that it is necessary to cope with two types of dispersal: (i) human-mediated dispersal by air transport, which can be considered as almost a universal dispersal capacity and (ii) the natural dispersal capacity inherent to the WCR. A previous study revealed that there are considerable numbers of airports that, although geographically distant, they have similar climatic conditions, representing potential links between native and invasion areas. Moreover, this climate similarity among airports is the highest in the June–August period, which matches the annual peak in air traffic (Tatem & Hay 2007) and with the oviposition period of the WRC (Meinke *et al.* 2009). Therefore, our maps can be used to detect those airports located within zones of high climatic favourability for the WCR to detect potential foci of invasion. Among those countries with predicted areas of continuous climatic favourability, China has undergone a rapid increment of airport traffic, which is partially responsible of the concomitant recent increase of biological invasions there (Ding *et al.* 2008). Our results can also be useful in detecting the direction of potential spreads in zones where invasion is taking place since the WCR is not yet at equilibrium with its bioclimatic niche. Thus, our estimations of climatic favourability suggest that the WCR might spread from the Hungarian–Serbian core toward Eastern Europe.

On the other hand, of special importance is the detection of potential secondary contact zones between genetically differentiated populations coming from independent transatlantic introductions (Prentis *et al.* 2008). A previous study revealed genetic differences between the populations of northwestern Italy and the Hungarian–Serbian core before the connection occurred between them (Ciosi *et al.* 2008). Ulterior contacts between populations might result in an increment of genetic variability, thus increasing the adaptive potential of an organism in the invaded zone (Ellstrand & Schierenbeck 2000). Using presence records of the native continent our models converged to detect the dispersal corridor connecting the Italian and Hungarian–Serbian core. Therefore, our model outputs might be useful for detecting other potential contact zones among currently invaded areas and/or potential areas of invasion.

To conclude, while climatic similarity may not be sufficient, it can be implemented in integrated pest management together with other techniques to prevent successful invasions. Our procedures to obtain areas of climatic favourability were able to reflect at least part of the patterns observed in the European area of invasion. Our results advocate for the complementary use of physiological information and bioclimatic models to build more reliable predictions and evaluate distributional-based estimations. Although it is always necessary to consider that distributional data might provide a partial picture of climatic suitability (Jiménez-Valverde, Lobo & Hortal 2008), our results provide basic information for the design of management strategies devoted to preventing potential future invasions of the WCR, at least in the Northern Hemisphere. For instance, it is worthy the regular monitoring around potential colonization localities via human-mediated dispersal (e.g. airports) that are in turn climatically favourable for the persistence of the WCR. Also, the direction of future spreads can be assessed regarding dispersal corridors of climatic favourability and maize cultivations.

Acknowledgements

References

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. & Larsson, S. (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications*, **15**, 2084–2096.

Beaumont, L.J., Hughes, L. & Poulsen, M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling*, **186**, 250–269.

Borges, P.A.V., Lobo, J.M., De Azevedo, E.B., Gaspar, C.S., Melo, C. & Nunes, L.V. (2006) Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. *Journal of Biogeography*, **33**, 169–187.

Busby, J.R. (1991) BIOCLIM – a bioclimate analysis and prediction system. *Nature Conservation: Cost effective Biological Surveys and Data Analysis* (eds C.R. Margules & M.P. Austin), pp. 64–68. CSIRO, Melbourne.

Calenge, C., Darmon, G., Basille, M., Loison, A. & Jullien, J.-M. (2008) The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology*, **89**, 555–566.

Chown, S.L. & Terblanche, J.S. (2007) Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology*, **33**, 50–152.

Ciosi, M., Miller, N.J., Kim, K.S., Giordano, R., Estoup, A. & Guillemaud, T. (2008) Invasion of Europe by the western corn rootworm, *Diabrotica virgifera virgifera*: multiple transatlantic introductions with various reductions of genetic diversity. *Molecular Ecology*, **17**, 3614–3627.

Ciosi, M., Toepfer, S., Li, H., Haye, T., Kuhlmann, U., Wang, H., Siegfried, B. & Guillemaud, T. (2009) European populations of *Diabrotica virgifera virgifera* are resistant to aldrin, but not to methyl-parathion. *Journal of Applied Entomology*, **133**, 307–314.

Corsi, F., Duprè, E. & Boitani, L. (1999) A large scale model of wolf distribution in Italy for conservation planning. *Conservation Biology*, **13**, 150–159.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.

Ding, J.Q., Mack, R.N., Lu, P., Ren, M.X. & Huang, H.W. (2008) China's booming economy is sparking and accelerating biological invasions. *BioScience*, **58**, 317–324.

Dormann, C.F. (2007) Promising the future? Global change projections of species distributions *Basic and Applied Ecology*, **8**, 387–397.

Edward, C.R. & Kiss, J. (2008) *Diabrotica virgifera virgifera* LeConte in Europe 2008. Available at http://www.eppo.org.

Ellsbury, M.M. & Lee Jr, R.E. (2004) Supercooling and cold-hardiness in eggs of western and northern corn rootworms. *Entomologia Experimentalis et Applicata*, **111**, 159–163.

Ellstrand, N.C. & Schierenbeck, K. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 7043–7050.

EPPO Standards. (2004) Diagnostic protocols for regulated pests. *EPPO Bulletin*, **34**, 155–157.

Etherington, T.R., Ward, A.I., Smith, G.C., Pietravalle, S. & Wilson, G.J. (2009) Using the Mahalanobis distance statistic with unplanned presence-only survey data for biogeographical models of species distribution and abundance: a case study of badger setts. *Journal of Biogeography*, **36**, 845–853.

Farber, O. & Kadmon, R. (2003) Assessment of alternative approaches for bioclimatic modelling with special emphasis on the Mahalanobis distance. *Ecological Modelling*, **160**, 115–130.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

Gewin, V. (2005) Eco-defense against invasions. *PLoS Biology*, **3**, 2066–2071.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: how to compute habitat suitability maps without absence data? *Ecology*, **83**, 2027–2036.

Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10–18.

Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance in concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.

Kearney, M. & Porter, W.P. (2009) Mechanistic niche modeling: combining physiological and spatial data to predict species ranges. *Ecology Letters*, **12**, 334–350.

Kobel, M. & Nentwig, W. (2008) Alien spider introductions to Europe supported by global trade. *Diversity and Distributions*, **14**, 273–280.

Krysan, J.L. (1978) Diapause, quiescence, and moisture in the egg of the western corn rootworm, *Diabrotica virgifera*. *Journal of Insect Physiology*, **24**, 535–540.

Krysan, J.L. & Miller, T.A. (1986) *Methods for the Study of Pest Diabrotica*. Springer-Verlag, New York.

Krysan, J.L. & Smith, R.F. (1987) Systematics of the *virgifera* species group of *Diabrotica* (Coleoptera: Chrysomelidae: Galerucinae). *Entomography*, **5**, 375–484.

Levine, E., Spencer, J.L., Isard, S.A., Onstad, D.W. & Gray, M.E. (2002) Adaptation of the western corn rootworm to crop rotation: evolution of a new strain in response to a management practice. *American Entomologist*, **48**, 94–107.

López-Darias, M., Lobo, J.M. & Gouat, P. (2008) Predicting invasive species potential distribution: the exotic Barbary ground squirrel in the Canarian Archipelago and west Mediterranean region. *Biological Invasions*, **10**, 1027–1040.

Meinke, L.J., Siegfried, B.D., Wright, R.J. & Chandler, L.D. (1998) Adult susceptibility of Nebraska western corn rootworm (Coleoptera: Chrysomelidae) populations to selected insecticides. *Journal of Economic Entomology*, **91**, 594–600.

Meinke, L.J., Sappington, T.W., Onstad, D.W., Guillemaud, T., Miller, N.J., Komáromi, J., Levay, N., Furlan, L., Kiss, J. & Toth, F. (2009) Western corn rootworm (*Diabrotica virgifera virgifera* LeConte) population dynamics. *Agricultural and Forest Entomology*, **11**, 29–46.

Miller, N., Estoup, A., Toepfer, S., Bourguet, D., Lapchin, L., Derridj, S., Kim, K.S., Reynaud, P., Furlan, L. & Guillemaud, T. (2005) Multiple transatlantic introductions of the western corn rootworm. *Science*, **310**, 992.

Monfreda, C., Ramankutty, N. & Foley, J.A. (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles*, **22**, GB1022.

Payero, J.O., Melvin, S.R., Irmak, S. & Tarkalson, D. (2006) Yield response of corn to deficit irrigation in a semiarid climate. *Agricultural Water Management*, **84**, 101–112.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology*, **78**, 419–433.

Peterson, A.T. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience*, **51**, 363–371.

Prentis, P.J., Wilson, J.R.U., Dormontt, E.E., Richardson, D.M. & Lowe, A.J. (2008) Adaptive evolution in invasive species. *Trends in Plant Science*, **13**, 288–294.

Spencer, J.L. & Raghu, S. (2009) Refuge or Reservoir? The potential impacts of the biofuel crop Miscanthus × giganteus on a major pest of maize *PLoS ONE*, **4**, e8336.

Tatem, A.J. & Hay, S.I. (2007) Climatic similarity and biological exchange in the worldwide airline transportation network. *Proceedings of the Royal Society of London B*, **274**, 1489–1496.

Tatem, A.J., Hay, S.I. & Rogers, D.J. (2006) Global traffic and disease vector dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 6242–6247.

Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.

Vidal, S., Khulmann, S. & Edwards, C.R. (2005) *Western Corn Rootworm Ecology and Management*. CABI Publishing, CAB International, Oxfordshire, UK.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, **24**, 136–144.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Assessing variable importance through ENFA factors.

Appendix S2. Estimation of physiological temperature thresholds.

Appendix S3. Number of presence records along the Mahalanobis distances.

Appendix S4. Global maps of climatic envelopes with different sets of predictors and a physiological range.

Appendix S5. Description of climatic favourability maps.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.