


Inflection point in climatic suitability of insect pest species in Europe suggests non-linear responses to climate change

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Abstract

Climate change and globalization affect the suitable conditions for agricultural crops and insect pests, threatening future food security. It remains unknown whether shifts in species' climatic suitability will be linear or rather non-linear, with crop exposure to pests suddenly increasing when a critical temperature threshold is crossed. Moreover, uncertainty of forecasts can arise because of the modelling approach based either on species distribution data or on physiological measurements. Here, we compared the predictions of two modelling approaches (physiological models and species distribution models) for forecasting the potential distribution of agricultural insect pests in Europe. Despite conceptual differences, we found good agreement overall between the two approaches. We further identified a potential regime change in pest pressure along a temperature gradient. With both modelling approaches, we found an inflection point in the number of pest species with suitable climatic conditions around a minimum temperature of the coldest month of -3°C . Our results could help decision-makers anticipate the onset of rising pest pressure and provide support for intensifying surveillance measures, particularly in regions where temperatures are already beyond the inflection point.

KEYWORDS

agricultural crop, climate change, insect pest, physiological model, species distribution model, temperature threshold

1 | INTRODUCTION

Climate change is predicted to shift the distribution of agricultural crops and of the insect pest species feeding on them (Bebber, Holmes, & Gurr, 2014; Sloat et al., 2020; Tubiello, Soussana, & Howden, 2007). While changing climatic conditions might increase climatic stress factors and reduce resources for water irrigation of crops (Fader, Shi, Von Bloh, Bondeau, & Cramer, 2016), higher temperatures favour the expansion of cultivation and crop diversification at higher latitudes (Grünig, Mazzi, Calanca, Karger, & Pellissier, 2020; Tuck, Glendining, Smith, House, & Wattenbach, 2006; Walther et al., 2002). Climate change is however also associated with greater pest pressure (Deutsch et al., 2018). Further, trade flows and human travel help insect pests to overcome natural barriers, linking climate

change and globalization to pest invasions (Hulme, 2009; Paini et al., 2016; Robinet & Roques, 2010). Distribution ranges of pest species are expected to shift, to the detriment of cropping systems (Bebber, Ramotowski, & Gurr, 2013), and thus threaten food production (Schmidhuber & Tubiello, 2007) and undermine increasing consumer demands for local and more sustainably produced food (Feldmann & Hamm, 2015; Lamichhane, Dachbrodt-Saaydeh, Kudsk, & Messéan, 2016). Investigating the distribution of niches of pest species along climatic gradients can point to future opportunities and risks under climate change (Grünig et al., 2020) and help develop effective crop protection strategies.

The development of insects is a function of temperature over time (Jarošík, Honěk, Magarey, & Skuhrovec, 2011). Under climate change, temperatures in Europe, particularly at higher latitudes,

are expected to increase more than the global average warming (IPCC, 2007; MacDonald, 2010). Ongoing warming allows the cultivation of more crops (Maracchi, Sirotenko, & Bindi, 2005) but also favours insect pest survival in these regions (Bale & Hayward, 2010). Higher winter temperatures are crucial for the survival of insect pest species at higher latitudes (Bebber et al., 2013; Jarošík, Kenis, Honěk, Skuhrovec, & Pyšek, 2015), although in practice their realized distribution is restricted by additional factors, particularly biotic interactions (Hutchinson, 1957). To account for the multitude of factors that potentially define the climate suitability for insect pests, different modelling approaches have been developed, which should imply differences in predictions (Kearney, Wintle, & Porter, 2010; Newman, 2005; Robertson, Peter, Villet, & Ripley, 2003).

To model the climatic niche of pest species, deductive and inductive approaches have been developed (Tonnang et al., 2017; Venette et al., 2010). For the deductive approach adopted in physiological models, data from controlled experiments provide a basis to project the potential distribution of a species (Tonnang et al., 2017). Studies on the life history of species under different environmental conditions help define physiological thresholds for species survival, development and performance, which are often used to develop phenological models (e.g. Schaub, Breitenmoser, Derron, & Graf, 2017). By relating these thresholds to climatic variables in a spatial context (e.g. spatial raster layers of temperature), areas where species meet conditions that allow their development can be identified (Kearney & Porter, 2004, 2009). Inductive models use the occurrence records of a species and link them to climatic data to infer the conditions that are suitable for the species (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). Species distribution models (SDMs) implementing the inductive approach have been widely used to model climatic suitability of insect pests (e.g. Arthur, Morrison, & Morey, 2019). While deductive and inductive modelling approaches target similar goals of mapping suitable climatic conditions for a species in space, they differ in terms of the data used for model development. A better understanding of how systems can be expected to shift under climate change could potentially be achieved by comparing forecasts between those approaches.

The response of a biological system to climate change can be linear or non-linear. When the response is not linear, the ecosystem state typically shifts faster than what would be expected for a linear response (Dakos et al., 2019), eventually exhibiting discontinuities when critical thresholds in the driving variables are crossed (Lenton, 2011). Shifts in pest distributions under climate change may display discontinuous behaviour, implying a sudden change in the potential for colonization by pest species, including the invasion of non-native species, as a result of global warming (Paini et al., 2016). Invasive insects are likely to be introduced from geographic areas sharing similar climatic conditions (Brockhoff & Liebhold, 2017; Walther et al., 2009). With climate change, temperate regions will become warmer and therefore climatically more similar to regions where insect diversity is presently disproportionately higher. The study of pest species' climatic niches coupled with climate change scenarios help identify potential inflection points for pest suitability.

Here, we investigated the potential pest accumulation in Europe under climate change by comparing predictions obtained from deductive physiological models and inductive SDMs. We considered a comprehensive set of insect pests that includes a large number of quarantine insects. We evaluated whether climatic niches shift along a smooth gradient, or whether an inflection point exists, beyond which the increase in the number of potential niches accelerates.

Our working hypotheses were as follows:

- (i) We expected congruent forecasts of suitable climate with the two modelling approaches. Under climate change, we expected a general pattern of increasing climatic suitability for insect pests across Europe, irrespective of the modelling approach applied.
- (ii) We expected non-linear responses to minimum temperatures for insect pests, involving thresholds beyond which the number of species with a suitable climate increases considerably.
- (iii) We expected to observe that temperatures in Southern Europe already exceed the threshold temperature identified under (ii). Hence, we expected to find that these regions already provide suitable climatic conditions for many insect pest species because temperatures rarely dip below freezing.

2 | MATERIALS AND METHODS

2.1 | Physiological data collection

For physiological data, we assembled insect developmental thresholds from the PRATIQUE database (Jarošík et al., 2011) and published literature. From the PRATIQUE database, we selected insect species classified as pests in the EPPO Global Database (www.eppo.org), which comprises information generated or assembled by the European and Mediterranean Plant Protection Organization. Further, we searched on Google Scholar for studies applying CLIMEX models for pest species (keyword combinations of "CLIMEX" + "insect" + "pest"). We obtained physiological parameters on the lower development threshold (LDT; minimum development threshold in CLIMEX studies) and the sum of effective temperatures (SET), that is, the number of growing degree days above the LDT required for the completion of a generation. LDTs and SETs reflect a linear relationship between developmental rate and temperature, and are calculated from the proportion of development occurring per unit of time (Jarošík et al., 2011). Where multiple entries per species were available, we used the average of the values. Further, we searched for lethal temperatures of all species. Whenever we did not find a lower lethal temperature ($T_{kill,min}$), we set it to 0°C for species not known to survive winter in a dormant stage and to -20°C for species with winter diapause. This implies that warm-adapted species are predicted to not occur in regions where the minimum temperature of the coldest month is below 0°C. We used 40°C as the upper lethal temperature ($T_{kill,max}$) for all species, as insects are known to have little variability in this regard, with values ranging from 40°C to 50°C

(Heinrich, 1981). We collected data on physiological parameters for 75 species (Table S1).

2.2 | Occurrence data collection

We compiled the distribution records of pest species in the published literature and the Global Biodiversity Information Facility (GBIF, www.gbif.org; Appendix S1 contains the list of datasets from which records were taken and download DOIs if available) for all pest species in the EPPO Global Database. We searched Google Scholar for the following keywords in various combinations: "Pest name", "distribution", "records", "occurrence", "sampling", "spatial" and "data". GBIF data were carefully checked for unreliable records. We classified the pest species into two categories: all species on the EPPO quarantine lists (A1, A2, Alert) were considered quarantine pests, and all others established pests. Species for which we could not obtain more than 20 occurrence records were dismissed (Wisiz et al., 2008). In total, we gathered occurrence data for 173 species (Table S2).

2.3 | Climate data and future scenarios

We acquired climate data from the CHELSA database (www.chelsa-climate.org). We used CHELSA V1.2 data for monthly minimum, maximum and mean temperatures, as well as bioclimatic variables, with a 2.5 arcmin (5 km) grid size resolution (Karger et al., 2017) to represent current climatic conditions. Further, we used climate change scenarios from the CMIP5 family representing two different scenarios (RCP 4.5, RCP 8.5) and four global circulation models (GCMs). We selected the following GCMs based on model interdependence to achieve a good representation of uncertainty in climate projections (Sanderson, Knutti, & Caldwell, 2015): CESM1-BGC (US National Center for Atmospheric Research, NCAR); CMCC-CM (Centro Euro-Mediterraneo per i Cambiamenti Climatici, CMCC); MIROC5 (University of Tokyo); and ACCESS1-3 (Commonwealth Scientific and Industrial Research Organization, CSIRO, and Bureau of Meteorology, BOM, Australia).

2.4 | Physiological models

We developed physiological models by coupling physiological data with monthly mean, minimum and maximum temperatures following FAO-ECOCROP (Hijmans, Guarino, Cruz, & Rojas, 2001; Ramirez-Villegas, Jarvis, & Läderach, 2013) and CLIMEX (Sutherst & Maywald, 1985) approaches. The output of the models is a suitability index (Si) calculated on cell basis of a spatial raster (5 km). As a global equation, we calculated Si as the product of a temperature index (Ti), a growing index (Gi) and a killing index (Ki; Equation 1).

$$Si = Ti * Gi * Ki. \quad (1)$$

Ti was calculated as the fraction of months in which the monthly mean temperature (T_k) exceeds LDT (Equation 2).

$$Ti = \frac{1}{12} \sum_{k=1}^{12} p_k, \quad (2)$$

with

$$p_k = \begin{cases} 1 & \text{if } \bar{T}_k > \text{LDT} \\ 0 & \text{otherwise} \end{cases}.$$

We evaluated Gi based on the growing degree days needed for completion of development (GDD_{req} ; Equation 3).

$$Gi = \begin{cases} 0 & \text{if } \sum_{k=1}^{12} (\bar{T}_k - \text{LDT}) < GDD_{req} \\ 1 & \text{otherwise} \end{cases}. \quad (3)$$

For Ki, we checked whether the monthly minimum temperature ($T_{min,k}$) fell below the lethal minimum temperature ($T_{kill,min}$) and whether the monthly maximum temperature ($T_{max,k}$) surpassed the lethal maximum temperature ($T_{kill,max}$; Equation 4).

$$Ki = \prod_{k=1}^{12} m_k \prod_{k=1}^{12} n_k,$$

with

$$m_k = \begin{cases} 1 & \text{if } \bar{T}_{min,k} > T_{kill,min} \\ 0 & \text{otherwise} \end{cases}, \quad (4)$$

$$n_k = \begin{cases} 1 & \text{if } \bar{T}_{max,k} < T_{kill,max} \\ 0 & \text{otherwise} \end{cases}.$$

We evaluated the physiological models using a maximum sensitivity approach based on occurrence data. To calculate the sensitivity of the model predictions, we projected the models to a global extent in order to include all available occurrence records for the evaluations. Models with a sensitivity score <0.5 were excluded from the analyses. The outputs were classified into binary predictions using the maximum sensitivity threshold calculated with the *optimal.thresholds* function in the 'PresenceAbsence' package (version 1.1.9; Freeman & Moisen, 2008).

2.5 | Species distribution models

SDMs were calibrated using ensembles (unweighted averages) of generalized linear models (GLMs) and generalized additive models

(GAMs; Wood, 2006). For each species, we randomly sampled 5,000 pseudoabsences from the species biomes. We weighted presence records in order to balance their weights with the large number of pseudoabsence records. We assumed a binomial error distribution for both modelling techniques and used fourth-order polynomials to adjust the flexibility of the response curve. As predictor variables, we used growing degree days above 5°C and minimum temperature of the coldest month to reflect the variables used in the physiological models. We used a variable selection procedure to reach an acceptable model performance and projection for as many species as possible (see Note S1). Further, we followed the standards and guidelines for distribution modelling (Araújo et al., 2019). GLMs were fitted with the 'base' R-package, whereas GAMs were fitted with functions in the R-package 'gam' (version 1.16.1; Hastie, 2019). For the evaluation of model performance, we used a split sample approach (70% calibration data and 30% evaluation data) with 20 repetitions to calculate the area under the ROC-plot curve (AUC) and true skill statistics (TSS). We considered models to be reliable at $AUC > 0.7$ (Hosmer, Lemeshow, & Sturdivant, 2013) and $TSS > 0.4$ (Descombes et al., 2015) and discarded all others. Additionally, we inspected the quality of all model projections visually. For binary classifications of the model outputs, we used the optimal TSS threshold (Allouche, Tsoar, & Kadmon, 2006).

2.6 | Comparison of physiological models and SDMs

For each species with reliable projections in both modelling approaches, we calculated the Pearson correlation coefficient between the predicted suitability indices of the two model projections and the percentage of agreeing grid cells of the binary projections. Further, we calculated the Sørensen index for the community similarity between the modelling approaches. For this, we stacked together the predicted binary projections of all species for each timestep, resulting in species richness raster stacks for the different modelling approaches for each timestep. For these raster stacks we calculated the Sørensen dissimilarity index with the *beta.pair* function of the 'betapart' R-package (version 1.5.1; Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017), which we then subtracted from 1 to obtain a similarity index ranging from 0 to 1, where 1 indicates complete agreement for the exact same set of species and 0 no overlap between the predicted communities. To quantify differences between projections of the two modelling approaches (i.e. absolute model agreement), we subtracted the model projection of the SDM from the physiological model projection for each species and summed the resulting differences across all species. Positive values indicate overrepresentation by the physiological models, and negative values signify overrepresentation by the SDMs.

2.7 | Analysis of inflection points under climate change

Based on the predicted distribution in Europe for each species under current climatic conditions, we calculated the relationship between

the predicted occurrence and the minimum temperature of the coldest month by extracting values from all grid cells in the study area. Minimum temperature represents the most limiting factor for insect distributions (Jarošík et al., 2015). We calculated the average probability of occurrence for each temperature class (step of 0.1°C). We identified the turning-point temperature, marking the border of the climatic niche, for each species by fitting GAMs, using the R-package 'mgcv' (version 1.8-31; Wood, 2011), for the relationship between minimum temperature of the coldest month and average probability for the temperature class. For this, we extracted minimum temperatures, corresponding to occurrence probabilities in the range 0.4 to 0.6 (in steps of 0.05) from the fitted values of the GAM (Figure S1). We ordered species according to the turning-point temperature and then investigated the shape of the pattern of the number of species along the temperature gradient.

We used the 'segmented' R-package (version 1.1.0; Muggeo, 2003) to identify breakpoints, which mark a change in slope in the ordered sequence of turning-point temperatures. To find a suitable initial estimate of the number and location of the breakpoints, we used the final estimates of the breakpoints and the slopes of the linear regression models for the intervals between the breakpoints. We isolated the slopes of the two distinct clusters of niches and scaled them to the relative number of species used for each modelling approach. Finally, we mapped the breakpoint temperatures marking the end of the first cluster, the start of the second cluster and the end of the second cluster to highlight the areas that are likely to become climatically suitable for warm-adapted pests and potentially see a rapid accumulation of newly occurring pests. We used representative values of -6°C, 0°C and 6°C as limits for these domains, taking into account the good agreement between the breakpoints identified for the two different modelling approaches (Figure S2).

To determine the inflection point marking the transition between the first and the second cluster of pest species, we fitted a GAM to the ordered turning-points for each cut-off threshold (0.4–0.6) and identified the inflection point temperature with the function *ese* in the 'inflection' R-package (version 1.3.5; Christopoulos, 2016). We compared the AIC values of the GAMs with linear functions to check whether the data follows a non-linear distribution (Table S3). We calculated the mean and the confidence interval (0.95%) for the inflection zone from the inflection points of the different cut-off thresholds. All analyses were done in R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Model performance and niche limits

The development thresholds varied widely over the study species (Figure S3). LDTs were between 1.6°C and 15°C. Degree days required to complete development ranged from 148 to 1,800 and minimum killing temperature ranged from -40°C to 4.5°C. We

obtained acceptable model sensitivity (>0.5) for all 75 species, with a median of 0.97. We found lower niche limits between -19.3°C and 10.8°C , with a median over all species of -7.7°C . The upper niche limit was the same for all species (12.4°C) and the median niche breadth was 20.3°C . For SDMs, we gathered occurrence records for 173 pest species. We obtained satisfying model performance for 159 pest species, with a median model performance of 0.83 in terms of AUC score and 0.59 for TSS. We found lower niche limits between -22.8°C and 11.9°C , and upper limits between -4.4°C and 12.4°C . The median lower niche limit was 0.1, whereas the median upper niche limit was 12.4°C . We estimated a median niche breadth of 9.2°C .

3.2 | Agreement between modelling approaches

Generally, we observed good agreement between the two modelling approaches regarding pest species distributions, despite large variation among species and regions. Comparing the pair of model projections for all species, we found a median Pearson correlation coefficient between the occurrence probability predictions of the two modelling approaches of 0.68 under current climatic conditions, ranging from -0.8 to 0.88 and with a standard deviation of 0.31. For binary projections, this corresponded to agreement of predictions in

85% of the grid cells. For future climate change scenarios, the pairwise model agreement decreased until 2100, where we found a median Pearson correlation of 0.46 with higher uncertainty (standard deviation 0.48), corresponding to agreement in 70% of the grid cells (Figures S4 and S5). Concerning the spatial model agreement, we observed differences in the community similarity predicted by the two modelling approaches. Disagreement arose mainly in Northern and Northeastern Europe, as well as in mountain ranges (Figure 1). Under future projections, the community similarity increased towards Northeastern Europe, but decreased in southern regions. The cumulated model disagreement showed that SDMs were responsible for the discrepancies in southern regions, because they were more restricted at southern range borders (Figures S6 and S7). When comparing the niche breadth predicted by the two modelling approaches, we observed much broader niches predicted by physiological models than by SDMs. The median of the pairwise niche breadth difference was 3.8°C .

3.3 | Shift in modelled pest distribution

Regarding changes in pest species richness over time, agreement between the modelling approaches was good over Central Europe and the United Kingdom (Figure 2), while in marginal areas

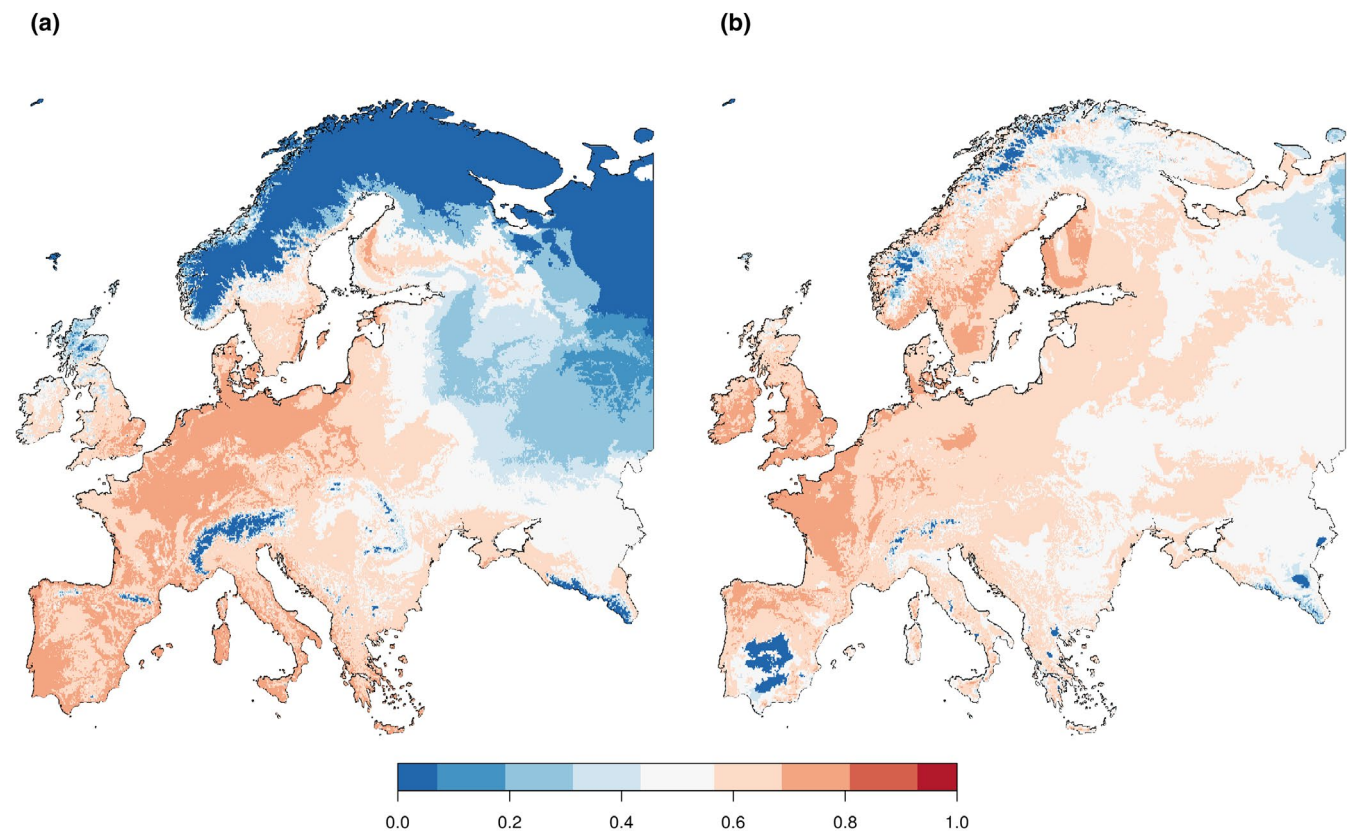


FIGURE 1 Maps of model agreement (Sørensen similarity index) for 2010 (a) and 2100 (b). Blue/red colours indicate lower/higher community similarity of predicted species. Results in (b) are based on the RCP8.5 climate change scenario (for results based on the RCP4.5 scenario, see Figure S8)

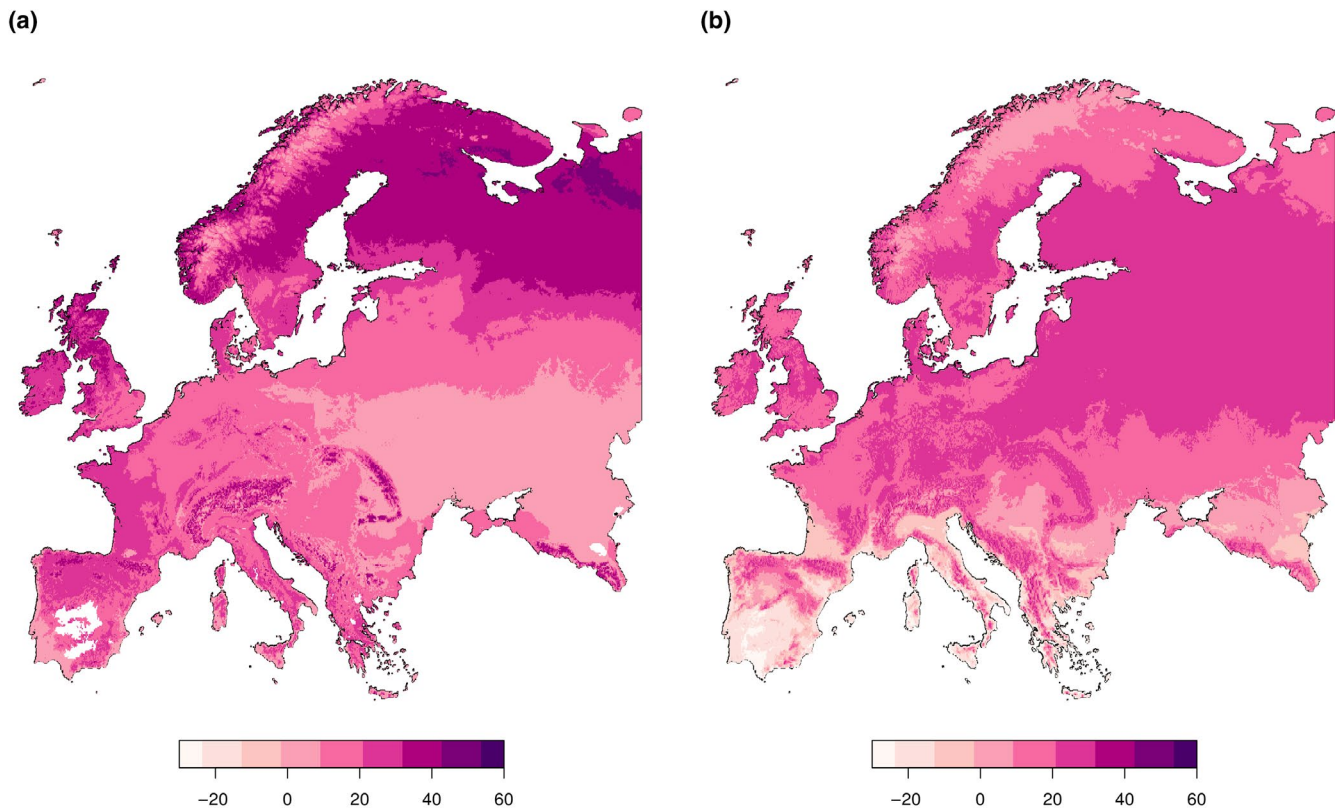


FIGURE 2 Change in the number of species between 2010 and 2100, as predicted by (a) physiological models and (b) species distribution models (SDMs). The number of modelled pest species was higher for the SDMs (159) than for the physiological models (75), and we therefore scaled the changes to 100 species to enable model comparison despite this difference. The white area in central Spain marks the region where maximum monthly temperatures above the assumed upper lethal temperature of 40°C in 2100 prevented species occurrence. Results shown here are based on the RCP8.5 climate change scenario (for results based on the RCP4.5 scenario, see Figure S9)

(Eastern Europe, in particular Belarus and the Ukraine) changes were predicted differently by the two modelling approaches. We observed an increase in Northeastern Europe and mountainous regions of up to 30 species with physiological model projections and up to around 70 species with SDM projections. This corresponds to about 50% of species for physiological models and 40% for SDMs. When comparing the results of the different RCP scenarios, we found a greater increase in the number of species with a suitable climate under RCP8.5 than under RCP4.5. In particular, physiological models showed a much greater increase in northern regions by 2100. For SDMs, the increase across Europe was very similar under the two scenarios, but differences arose in southern regions (e.g. Iberian Peninsula), where fewer species with suitable climatic conditions were predicted for the year 2100 under RCP8.5.

3.4 | Relationship between predicted niche distribution and temperature

We observed a non-linear relationship between species richness and temperature with the physiological models and SDMs (Figure 3). Temperature niches showed two distinct groups with both modelling approaches. The first group included cold-adapted

species, predicted to occur in regions that experience minimum temperatures of the coldest month below the breakpoint temperature of -6°C . The second group consisted of warm-adapted species, existing only in regions where minimum temperatures of the coldest month never fall below the breakpoint temperature of 0°C . For both modelling approaches, there was only a partial overlap between cold-adapted and established species, and between warm-adapted and quarantine pests. In the warm-adapted group, quarantine species were overrepresented (Figure S10). The inflection point, marking the switch between the two groups, corresponded to a minimum temperature of the coldest month of -3.0°C for physiological model predictions and -3.1°C for SDM predictions. Additionally, we calculated inflection points for the subset of species for which we generated physiological models and SDMs (53 species). Including only these species, we observed inflection points at -3.0°C (physiological models; $\pm 1.5^{\circ}\text{C}$) and -1.7°C (SDMs; $\pm 1.5^{\circ}\text{C}$).

The spatial dynamics of the inflection point indicated clear shifts towards the northeast (Figure 4). The breakpoints (-6°C , 0°C , 6°C) are predicted to be dislocated at different rates. While the area above the -6°C isoline, marking the border of suitability for all cold-adapted species, almost covered the entire European continent, the other two isolines, marking the start and the end of the cluster

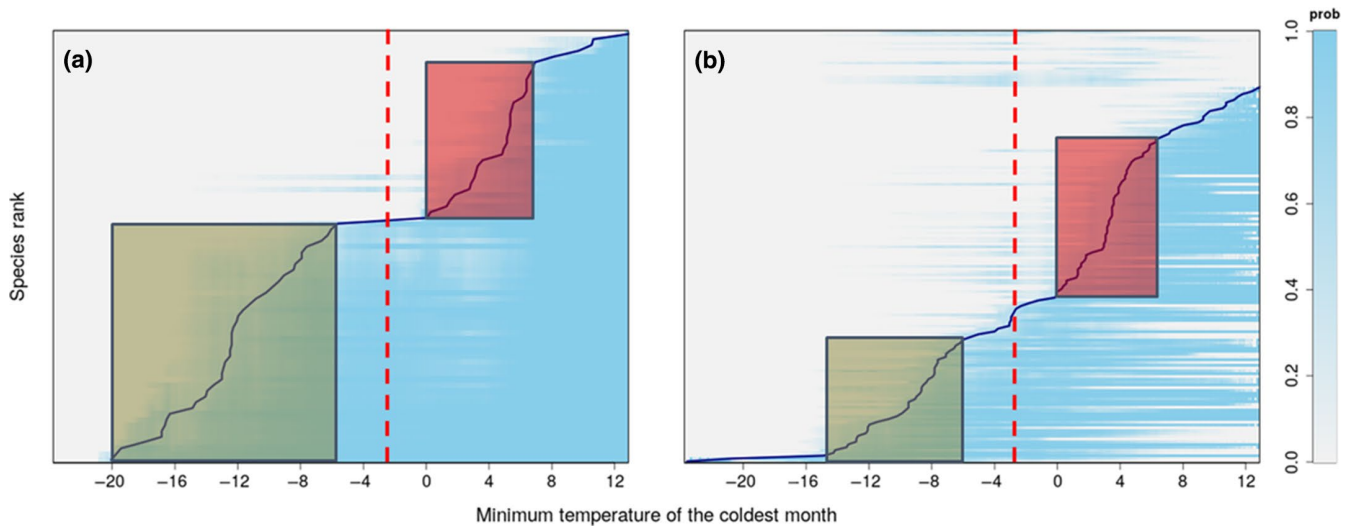


FIGURE 3 Climatic niches of pest species along a gradient of the minimum temperature of the coldest month. Light blue areas show the range in the climatic niche predicted by the physiological models (a) and species distribution models (SDMs; b) for each species, sorted by the turning-point temperature obtained with a cut-off threshold of 0.5. Denser blue areas correspond to a higher proportion of grid cells with this temperature predicted to be suitable for the species (prob). The dark blue lines show the distribution of turning-point temperatures. Inflection points were identified at -3.0°C for physiological model predictions and -3.1°C for SDMs (indicated by the red dashed lines). Yellow boxes indicate the group of cold-adapted species (up to the breakpoint of -6°C) and red boxes the group of warm-adapted species (between the breakpoints of 0°C and 6°C). For the subset with 53 species, see Figure S11

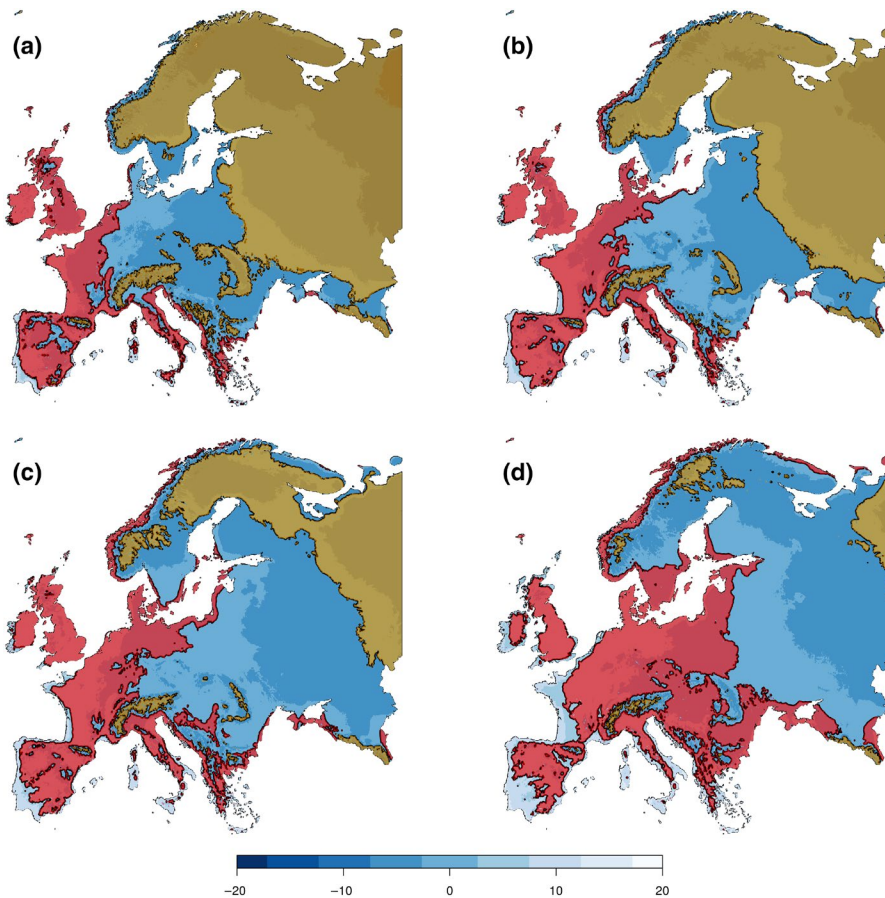


FIGURE 4 Spatial analysis of the inflection point across Europe. The maps show the minimum temperature of the coldest month across Europe in 2010 (a), 2040 (b), 2070 (c) and 2100 (d) under the RCP8.5 scenario. The yellow shaded area marks the region where minimum temperatures of the coldest month are below the -6°C breakpoint. The red shaded area marks the region between the 0°C and the 6°C breakpoints, where a strong acceleration of pest climatic suitability is expected. Figure S12 shows the results for the RCP4.5 scenario

of warm-adapted pests, were more stable. The area between 0°C and 6°C in Figure 4 corresponds to where warm-adapted species were predicted to encounter suitable climatic conditions. This area

increased mainly in Western and Central Europe, but was predicted to reach the Atlantic coast of Norway in the North, as well as Poland and the coast of the Baltic Sea in the East, by 2100. Slopes of the

increasing number of pests with suitable climatic conditions varied between the two groups. With physiological models we found an increase of about five species per degree for cold-adapted species and seven species per degree for warm-adapted species, and SDMs predicted four (cold-adapted) and seven (warm-adapted) species per degree.

4 | DISCUSSION

In this study, we compared predictions of species distributions by physiological models and SDMs to investigate climatic niches of a comprehensive set of insect pest species of agricultural crops. Employing both physiological (deductive) and statistical (inductive) models entails robustness in cases of agreement and prompts interesting hypotheses when differences arise (Hijmans & Graham, 2006). We show general agreement in the predicted species distribution between the two modelling approaches. Moreover, with both modelling approaches, we found inflection points around -3°C in the minimum temperature of the coldest month, indicating increasing pest pressure after this threshold temperature is crossed.

Physiological and statistical models provide coherent results despite conceptual differences. Model projections for current climatic conditions showed good agreement for pairwise suitability index predictions (0.68), corresponding to 85% of the grid cells for binary projections. We found the highest model agreement in areas where both approaches predicted similar pest community composition to encounter suitable climatic conditions. We found lower similarity in Northern Europe (i.e. Scandinavia and the European part of Russia), as well as in high mountain ranges (Pyrenees, Alps and Carpathian Mountains), mainly because few insect pest species were predicted to occur in those regions. Furthermore, the niche breadth obtained from models reflects differences between the fundamental and the realized niche. We expected niches modelled based on physiological limits to be broader than realized niches (Soberón & Arroyo-Peña, 2017; Venette et al., 2010). The results confirmed this expectation, with realized pest niches predicted by SDMs (median niche breadth 9.2°C) much lower than fundamental climatic niches predicted by physiological models (17.1°C). Pairwise comparisons likewise suggested narrower climatic niches predicted with SDMs than with physiological models. The broader climatic niches predicted with physiological models indicates that SDMs may underestimate the climatically suitable area, implying that the regions of potential invasions could be larger than estimated based on SDMs alone. Yet, physiological models have also a methodological limitation regarding upper development thresholds, because data are not available for most species. Available data for 31 species indicated an average of 34.4°C , with only two species having their upper development thresholds below 30°C . Monthly mean temperatures above 34°C do not occur in Europe under the current climate and are unlikely to occur during this century (Figure S13) and thus it is unlikely that including upper development thresholds would have altered our predictions for pest species.

Forecasts of species distributions under climate change have been reported to be congruent for deductive and inductive models (Kearney et al., 2010), although inductive models have also been reported to produce more pessimistic predictions than deductive models (Lobell & Asseng, 2017). Here, we found a decline in model agreement for future projections, with a decrease in median correlation from 0.68 in 2010 to 0.46 in 2100, although the latter value still represents relatively good agreement for binary projections (70%). We observed that the southern range borders modelled with physiological models remained mostly in the same locations, while SDM borders moved towards higher latitudes, resulting in lower community similarity in Southern Europe and decreasing model agreement. SDMs for future projections are more prone to extrapolation errors in areas where new climatic conditions will occur, which is not the case for physiological models (Kearney & Porter, 2009). This problem is particularly important for invasive species because the distribution is often projected to new environmental conditions (Elith, 2017), which could explain the decreasing model agreement and increasing differences in pairwise comparisons as time progresses.

On the individual species level, we observed differences between modelling approaches in the predictions of the area with suitable climatic conditions for a few species (e.g. *Dendroctonus ponderosae*; Pearson correlation of -0.8). For these species, the occurrence records used for the SDMs may not reflect the climatic niche represented by the physiological thresholds obtained from laboratory studies. For other species, we observed a good spatial match between the two approaches regarding distribution ranges (e.g. *Spodoptera litura*; Pearson correlation of 0.88), suggesting that the occurrence records for these species well represent their fundamental climatic niche, giving additional robustness to the prediction (Hijmans & Graham, 2006). For future investigations, we suggest using ensemble approaches of physiological models and SDMs for a proper understanding of the modelled system, as proposed in previous studies (Overmars, de Groot, & Huigen, 2007). One approach could be to restrict the predicted distribution from correlative SDMs with the fundamental niche produced by physiological models (Kearney & Porter, 2009). Physiological models alone are too general, predicting only the fundamental climatic niche, while SDMs may be too restricting, capturing non-accountable factors (e.g. restriction through competition), which distort model projections to future conditions (Sinclair, White, & Newell, 2010). However, physiological models give a more direct biological understanding than statistical models, which can be more valuable than exact prediction (Lobell & Asseng, 2017).

Our results suggest that climate change will lead to an accelerated increase in pest pressure over large parts of Europe in the near future. We observed a non-linear relationship between niche limit positions and the prevalence of insect pest species. Crossing the inflection point implies a transition from cold- to warm-adapted species, and crossing the breakpoint temperature of 0°C of minimum temperature of the coldest month implies an abrupt increase in the number of pests with suitable climatic conditions and therefore in the number of pest species that may threaten European crop

production. Previous studies have shown that climate change will entail northward movement of insect pest species in the near future (Bebber et al., 2013; Grünig et al., 2020). Here, we identified an inflection point around -3°C in the minimum temperature of the coldest month, beyond which the number of pest species with suitable climatic conditions in Europe accelerates.

Finding an inflection point for the minimum temperature of the coldest month below 0°C would be reasonable, given the physiology of insects and their reaction to freezing. Cold tolerance limits the distribution of many insects that do not go through winter diapause (Bale & Hayward, 2010). As we considered only monthly mean temperatures, the temperatures actually experienced by insects are likely to be more extreme than those reported here. For a monthly minimum temperature around -3°C , freezing events are very likely to occur, even in microhabitats that potentially buffer air temperature fluctuations and provide shelter to insects for overwintering (Danks, 1978). Minimum temperature and freezing events are known to act as limiting factors for insect spreading and protect many regions from invasions (Jarošik et al., 2015; Maxmen, 2013), underlining the importance of the inflection point.

Based on the non-linear response of pest niche distributions along a temperature gradient, we investigated the temporal and spatial dynamics of inflection points under climate change. We showed that the presence of two groups of species, warm-adapted and cold-adapted, could lead to two waves of increasing pest pressure. While northern regions are currently facing the first wave of insect pest invasion, with the cluster of cold-adapted species, Southern and Central European regions have already passed the inflection point temperatures, and are therefore expected to face the second wave, with the cluster of warm-adapted species, in the near future. The expected timing of the arrival of the second wave in these regions depends on the RCP scenario. Our results support the findings of previous studies, showing that abating CO_2 emissions could be crucial in preventing the impact of pests on crop yields (Deutsch et al., 2018), as we find a greater number of species with suitable climatic conditions under the RCP8.5 scenario than under RCP4.5. Moreover, our results show that some areas are already confronted with increased pest pressure, including most parts of Southern Europe, the British Isles and Western Europe. Indeed, these regions serve regularly as entry gates to Europe for invasive crop pests, such as *Drosophila suzukii* (Calabria, Máca, Bächli, Serra, & Pascual, 2012) and *Tuta absoluta* (Desneux et al., 2010). France and Italy have the highest recorded numbers of established alien invertebrates in Europe (Roques et al., 2009). While these countries are part of the major pathways of global trade and entry gates to Europe for international shipping traffic, the Mediterranean climate has mild winters, supporting the establishment of more species than in northern regions. These findings support the importance of border control and improved inspection capacity with increasing trading volume (Poland & Rassati, 2019).

The analyses applied in our study have limitations arising from data availability and differences in the total number of species for which suitable models could be developed depending on the

modelling approach. Including data on more detailed requirements for insect development (e.g. on diapause initiation and termination) would improve the individual physiological models, however such data is scarce and not available for a broad range of species. Further, the size of the sample influences the outcome of the general response of species prevalence with respect to temperature. We tried to circumvent this problem by including data for a wide range of pests, including both cold- and warm-adapted species, but our list of pests is not complete. In addition, the global species pool for invasive insects shows no sign of saturation (Seebens et al., 2017). Indeed, quarantine (i.e. potentially invasive) species were underrepresented in this study, suggesting an even stronger acceleration of pest pressure after the inflection point is crossed. We observed that the inferred inflection zones for pests are very similar, irrespective of the chosen modelling approach and despite the fact that different sets of species were included in the analysis (75 species with physiological models and 159 with SDMs). We checked whether the same pattern occurs with only a subset of the species by only using the 53 species for which we could develop models for both the deductive and the inductive approach. The results confirmed the existence of an inflection point around -3°C . Within the warm-adapted cluster, the majority are quarantine species, implying a high invasion risk in new areas if minimum temperatures exceed the inflection point in these regions. Established pest species, for which we also predicted range shifts towards higher latitudes and expanding areas with suitable climatic conditions within Europe, heighten pest pressure in these regions. Increasing temperatures will not only promote more invasions of quarantine pests, but also increase the spread of established pests, threatening agricultural cropping areas that are expanding to more northern latitudes in response to global warming.

5 | CONCLUSIONS

We used deductive and inductive models to highlight trends of increasing climate suitability for insect pest species across Europe and a non-linear distribution of their climatic niches along a minimum temperature gradient. We found good model agreement between physiological models and SDMs under current climatic conditions. Forecasts under climate change showed diverging model agreement for pest species over time, indicating increasing uncertainty. Further, investigating the non-linear relationship between pest prevalence and minimum temperature made it possible to identify an inflection point beyond which the number of pest species with suitable climatic conditions increases rapidly. By mapping the inflection temperature spatially, we showed temporal and spatial dynamics of potential pest pressure under future climate change. Such information can inform policy-makers and stakeholders on where and when climatic conditions approach the transition point for the onset of accelerated pest invasions. New insights are necessary for planning crop protection strategies that can

effectively help control the new threats. Ultimately, with expanding areas in Europe becoming susceptible to pest pressure in the near future, we advise a strengthening of surveillance measures in general and border control in particular, and for an improvement in inspection capacity.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

M.G. contributed to conceiving ideas, gathering distribution data, establishing and running models, performing analysis and writing the manuscript; D.M. contributed to conceiving ideas and writing; P.C. contributed to conceiving ideas, performing analysis and writing; L.P. contributed to conceiving ideas, establishing models and writing. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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