



Climate change and the potential distribution of the glassy-winged sharpshooter (*Homalodisca vitripennis*), an insect vector of *Xylella fastidiosa*

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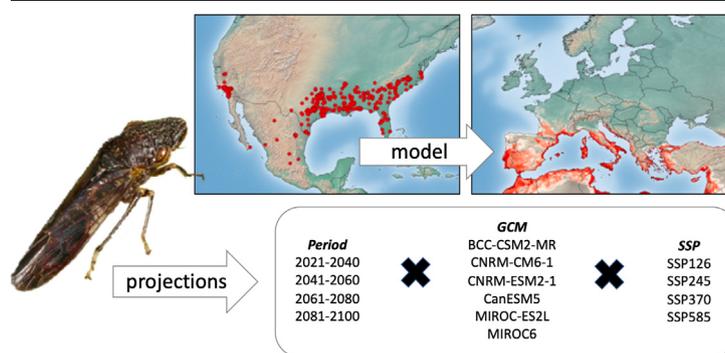
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HIGHLIGHTS

- We model the range of the invasive insect *Homalodisca vitripennis*.
- Current climate conditions allow potential geographical expansion.
- The effect of climate change varies according to the continent considered.
- Anticipating the risk of biological invasion is a key aspect of nations' biosecurity.

GRAPHICAL ABSTRACT



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ABSTRACT

Biological invasions represent a major threat for biodiversity and agriculture. Despite efforts to restrict the spread of alien species, preventing their introduction remains the best strategy for an efficient control. In that context preparedness of phytosanitary authorities is very important and estimating the geographical range of alien species becomes a key information. The present study investigates the potential geographical range of the glassy-winged sharpshooter (*Homalodisca vitripennis*), a very efficient insect vector of *Xylella fastidiosa*, one of the most dangerous plant-pathogenic bacteria worldwide. We use species distribution modeling (SDM) to analyse the climate factors driving the insect distribution and we evaluate its potential distribution in its native range (USA) and in Europe according to current climate and different scenarios of climate change: 6 General Circulation Models (GCM), 4 shared socioeconomic pathways of gas emission and 4 time periods (2030, 2050, 2070, 2090). The first result is that the climate conditions of the European continent are suitable to the glassy-winged sharpshooter, in particular around the Mediterranean basin where *X. fastidiosa* is present. Projections according to future climate conditions indicate displacement of climatically suitable areas towards the north in both North America and Europe. Globally, suitable areas will decrease in North America and increase in Europe in the coming decades. SDM outputs vary according to the GCM considered and this variability indicated areas of uncertainty in the species potential range. Both potential distribution and its uncertainty associated to future climate projections are important information for improved preparedness of phytosanitary authorities.

1. Introduction

Ongoing rapid climate change is a major driver of biodiversity reorganization and causes shifts of species distribution (Wallingford et al., 2020). As a consequence of an increasingly connected world, biological invasions are in parallel becoming a major environmental problem (Pyšek et al., 2020).

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The impact of climate change on bioinvasion dynamics and species range shifts is complex to anticipate. Indeed, climate warming induces contrasted effects depending on the taxonomical group concerned and the region considered (Bellard et al., 2013; Bradley et al., 2010; Diamond, 2018; McMahon et al., 2021). Many exotic species exhibit expanding distributions often leading to direct negative effects via mechanisms such as competition, predation or the alteration of certain ecosystem processes (Pyšek et al., 2020) or indirect effects (invasive species altering the interactions between 2 or more native of invasive species) (White et al., 2006). Biological invasions are also the cause of huge economic losses at a worldwide scale. For example, Diagne et al. (2021) estimated an annual mean cost of US\$ 26.8 billion over the past few decades (1970–2017). Despite efforts to restrict the spread of alien species, preventing their introduction remains the best strategy to efficiently control biological invasions. This highlights the importance of identifying potential invaders and areas at risk in order to establish a minimum level of emergency preparedness (Bradshaw et al., 2016; Fournier et al., 2019). Such *ex-ante* approach involves preplanned rapid-response capability, expert workforce and prior knowledge of the risk associated with potential invasive species under current and future climate conditions (Maino et al., 2021; Ricciardi et al., 2011).

Species Distribution Models (SDM) are well-known tools to model the climatic niche of species and to assess areas with suitable climatic conditions. They are therefore useful to identify areas where increasing surveillance and public information would be beneficial (Guisan et al., 2017). Furthermore, using SDM in conjunction with scenarios of climate change allows to estimate areas that would become suitable in the future i.e. areas at risk (Baquero et al., 2021; Godefroid et al., 2020; Hijmans and Graham, 2006; Urvois et al., 2021). However, the methodological decisions taken during the modeling process may lead to uncertainty in the prediction of future distributions (Bagchi et al., 2013; Buisson et al., 2010). The choice of the Global Circulation Models (GCM) accounts for a substantial proportion of this uncertainty (Buisson et al., 2010). Furthermore, the divergence between climate projections tends to increase when considering periods that are further in the future: atmospheric CO₂ concentrations are similar for the different shared socioeconomic pathways of gas emission until 2050 and then change (Kirtman et al., 2013; Lawrence et al., 2021). GCM mostly rely on similar assumptions but are parameterized with a slightly different set of conditions. This produces partially similar outputs with regionalized discrepancies (Shiogama et al., 2021). SDM fed with different GCM produce somewhat diverging outputs and this variability can be handled using ensemble models (Thuiller et al., 2019). Such differences contribute to the uncertainty associated with SDM outputs when assessing potential future species distribution. For that reason, it is recommended not to use a limited number of GCM (Thuiller et al., 2019) and a sensible choice could be guided by accounting for GCM interdependency (Anil et al., 2021; Sanderson et al., 2015; Shiogama et al., 2021; Whetton et al., 2012). SDM-related uncertainty should not be neglected and is a key aspect for preparedness and response to arrival of alien species.

Plant-vector-pathogen interactions are altered by environmental changes among which climate change and by the disruption of local communities that follows biological invasions (Chaloner et al., 2021; Islam et al., 2020). Hereafter we focus on the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar, 1821), a sap-sucking leafhopper that plays an important role in transmitting the endophytic bacterium *Xylella fastidiosa*. *Homalodisca* is a small genus of sharpshooters, that comprises 18 species mostly distributed in Central and South America. *H. vitripennis* is native to southeastern United States and northeastern Mexico (Sorensen and Gill, 1996). The species transmits the endophytic bacterium *X. fastidiosa* that causes tremendous economic losses associated with the Pierce's disease of grapevines (Tumber et al., 2014), the olive quick decline (Schneider et al., 2020), the bacterial leaf scorch (Hearon et al., 1980), the phony peach disease (Wells, 1983). Since its first detection in Europe (Italy) in 2013 (Saponari et al., 2013), *X. fastidiosa* has been detected in several European countries and is now considered a serious threat to numerous plants of economic importance (EFSA Panel on Plant Health et al., 2018) and to forests. In Europe, for example, Schneider et al. (2020) modelled

the economic impact of *X. fastidiosa* subspecies *pauca* on the Italian olive industry. In their worst-case scenario the potential economic impact over 50 y ranges from 1.9 billion to 5.2 billion Euros. Europe climate has been shown to be suitable for various subspecies of the bacterium (Godefroid et al., 2019) and the European fauna comprises native vectors of *X. fastidiosa* such as *Philaenus spumarius* (Cornara et al., 2016), *P. italoignus* and *Neophilaenus campestris* (Cavaliere et al., 2019) belonging to the Aphrophoridae.

H. vitripennis is a very efficient vector of *X. fastidiosa* because it has a large host range, has the ability to feed on woody tissue (Redak et al., 2004) and can have 2 to 3 distinct generations annually (Hummel et al., 2006). *H. vitripennis* is absent from Europe but has successfully established in California before 1990 (Sorensen and Gill, 1996). The species also colonized various part of the world outside Northern and Central America (French Polynesia, Hawaii and Easter Island, as well as the Cook Islands) (Grandgirard et al., 2006; Petit et al., 2008) which highlights its invasive potential (Rathé et al., 2015). Many studies have been undertaken to model different aspects of *H. vitripennis* population dynamics and its impact on the epidemiology of *X. fastidiosa* (reviewed in Lessio and Alma, 2021). Hoddle (2004) modelled the current geographical range using the CLIMEX model and showed that most grape production areas worldwide show favorable climate conditions. European preparedness towards *X. fastidiosa* threat should account for the bacterium vectors and alien vectors not already present should be carefully considered. The objectives of the present study are two-fold. First, we aimed at assessing the potential distribution of *H. vitripennis* in Europe according to current climate conditions and forecasting its potential range shifts in the future according to a large set of climate projections i.e. 6 General Circulation Model, 4 shared socioeconomic pathways of gas emission (SSP) and 4 time periods to evaluate the risk of establishment in case of introduction. The second aim was to explore GCM-induced variability of SDM outputs to identify geographical regions where models may disagree, which models would lead to dissimilar SDM outputs and how such variation change according to the periods considered. These results were intended to feed the discussion on the use of future climate projection of agricultural pests in a context of preparedness of sanitary crises.

2. Material and methods

All data analyses, calculations and graphs were made using the R language for statistical computing (R Core Team, 2021).

2.1. Occurrence datasets

Occurrence data were retrieved from the GBIF database (GBIF.org, 2021) and additional points were gathered from literature (Supplementary material Table S1). We considered all available occurrences (both native and invasive range). We examined the issues associated to each record retrieved from the GBIF database. Four issues were considered as problematic regarding occurrence validity: *txmatfuz* (TAXON_MATCH_FUZZY), *gdativ* (GEODETTIC_DATUM_INVALID) and *rdativ* (RECORDED_DATE_INVALID). All points associated to one of these labels were excluded from further analysis. Points were associated to different climate data according to the date of observation. Two periods were considered: 2001–2018 and before 2001. Observations dating before 2001 were associated to the climate data covering the period 1970–2000 while a climate dataset was generated for more recent observations (see below). Occurrence points are depicted in supplementary Fig. S1A.

A total of 1594 occurrences were retrieved from the GBIF database of which 1591 were retained after removing the problematic records to which 21 occurrences points collected from the literature were added leading to a final dataset comprising 1612 occurrence records. In 9 cases, no observation date was available, 15 records predated 1970, 10 records occurred between 1971 and 2000, and 1578 were posterior to 2000. Data with missing date were removed while points predating 1970 were gathered with points dating from the 1970–2000 period. We ended with 2

groups of occurrences representing 25 and 1578 occurrences associated with 1970–2000 and 2001–2018 periods respectively. Only one point per raster grid cell (see below) was retained to prevent over-representation of certain climate conditions (Elith et al., 2006). This led to retain 19 and 703 occurrences records for 1970–2000 and 2001–2018 periods respectively. Subsequent analyses were thus based on a set of $19 + 703 = 722$ occurrences. The environmental filtering (see below Section 2.4) led to retaining 537 occurrence records (74.37 % of the initial dataset).

2.2. Climate datasets

2.2.1. Current conditions

We used the climate dataset available from the worldclim database v2.1 (<https://www.worldclim.org>) (Fick and Hijmans, 2017). The database provides a set of average climate values for the period 1970–2000 considered to be representative of near present historical climate data. However, because of climatic change, these historical climate descriptors may be inappropriate when dealing with recent observations of *H. vitripennis*. For that reason, we retrieved a second type of dataset from worldclim: the historical monthly weather data. We used these datasets to compute the average climate descriptors for the period 2001–2018 using the function `biovars` from the R package `dismo` (Hijmans et al., 2021). This allowed us to attribute our occurrences of *H. vitripennis* to two sets of climate descriptors (1970–2000 and 2001–2018) according to the date when the species record was made (dynamic SDM sensu Milanese et al., 2020). The resolution of the data is 2.5 min ($\approx 21 \text{ km}^2$).

2.2.2. Future climate

We used future climate projections for four periods (CMIP6: Eyring et al., 2016) spanning from 2020 to 2100 (2021–2040, 2041–2060, 2061–2080 and 2081–2100). In each case we considered 6 Global Circulation Models (GCM): BCC-CSM2-MR (Wu et al., 2019), CNRM-CM6-1 (Voltaire et al., 2019), CNRM-ESM2-1 (Séférian et al., 2019), CanESM5 (Swart et al., 2019), MIROC-ES2L (Hajima et al., 2020), MIROC6 (Tatebe et al., 2019). For each period and GCM we assessed climate suitability according to four Shared Socioeconomic Pathways. Shared Socioeconomic Pathways (SSPs) are reference pathways describing plausible alternative scenarios of the evolution of society and ecosystems (Meinshausen et al., 2020). They are used to infer greenhouse gas emissions scenarios according to different climate policies (Riahi et al., 2017). We used SSP585, SSP370, SS245 and SSP126 that represent the high end, the medium to high end, medium part and the low end of the range of future forcing pathways respectively (Abram et al., 2019). This led to $4 \times 6 \times 4 = 96$ climate suitability estimations. Future climate data have the same resolution as the current climate data.

2.3. Climate descriptors

Choosing the predictors used in a SDM has a profound effect upon the transferability of the resulting model (Petitpierre et al., 2017). The climate datasets considered for modeling *H. vitripennis* included 11 climate descriptors representing both temperature and water constraints. Three variables described temperature variability: mean diurnal temperature range (referred to as `bio2` in the worldclim database), isothermality (`bio3`) and temperature seasonality (`bio4`). Four variables depicted acute temperature or water stress: maximum temperature of warmest month (`bio5`), minimum temperature of coldest month (`bio6`), precipitation of the wettest month (`bio13`) and precipitation of the driest month (`bio14`). Four variables represented average temperature or precipitation over 3 months periods: mean temperature of warmest quarter (`bio10`), mean temperature of coldest quarter (`bio11`), precipitation of the wettest quarter (`bio16`) and the precipitation of the driest quarter (`bio17`). For each variable we realized an initial examination of the patterns in occurrence by means of the frequency of observed presences (FOP) as described in Vollering et al. (2019) (supplementary Fig. S2). FOP consists of a plot of the observed occurrence rates against intervals of the climate descriptors. It shows how commonly the species

occurs across the range of the climate descriptors (Halvorsen, 2013). Variables associated to very noisy or bimodal FOP were discarded from further analyses to ensure that the model produces ecologically realistic and meaningful response curves (Guevara et al., 2018). This initial data preparation step led to retain 7 variables: `bio4`, `bio5`, `bio6`, `bio10`, `bio11`, `bio13` and `bio16`. Some explanatory variables may be collinear with possible effects upon species distribution models (but see Feng et al., 2019). This point is discussed below.

2.4. Model algorithm and calibration

We modelled the distribution of *H. vitripennis* with the Maxent algorithm (Phillips and Dudík, 2008) because it does not require absence data *stricto sensu* but rather background points and is considered to perform well when to assess climate suitability in future climate conditions (Elith et al., 2006). Maxent is a general-purpose machine learning method relying on presence points and a set of background locations. Background points are not interpreted as absence data but rather provide a description of the range of climate conditions across the study area (Elith et al., 2010). We used the implementation of the Maxent algorithm proposed by Vollering et al. (2019) in the R package `MIAMaxent`. The advantage of that approach is that it implements a forward stepwise selection procedure allowing to select a subset of transformed explanatory variables in the model calibration. As a consequence, the resulting model is less complex which improves its generalizability (Mazzoni et al., 2015) hence our ability to use the model outside of the spatial or temporal context of the data.

The climate descriptors (explanatory variables) used in the present study are continuous and were transformed according to five types of transformation: linear, monotonous, deviation, forward hinge, reverse hinge and threshold (Halvorsen, 2013; Phillips and Dudík, 2008). An infinity of transformations is possible for spline-type transformations (i.e. forward hinge, reverse hinge and threshold) and the R package `MIAMaxent` allows to automatically identify the ones that best explain the variation in the data (see package documentation and Vollering et al., 2019). The transformed variables were submitted to the forward stepwise selection as described in Vollering et al. (2019) and Halvorsen (2013). At the end of the procedure, the climate descriptors represented by the transformed variables explaining a significant amount of variation in the response variable i.e. species presence-absence data are identified. A very interesting aspect of this procedure is that it accounts for collinearity between explanatory variables during the selection procedure (Vollering et al., 2019) hence relaxing the well-known problem associated to collinearity in model calibration (Dormann et al., 2013). We used significance threshold $\alpha = 0.01$ during the selection procedure. Once the final model was established, we estimated the contribution of the explanatory variables to the model as the fraction of total variation they accounted for (Halvorsen et al., 2015) using the `MIAMaxent` function `calculateFTVA`.

Occurrence data originate from heterogeneous sources and are subject to possible bias which may alter model performances (Kramer-Schadt et al., 2013). We dealt with that difficulty by using an environmental filtering approach (Varela et al., 2014). We performed a Principal Component Analysis (PCA) (Legendre and Legendre, 2012) on the dataset formed by the different climate descriptors documented at each occurrence location. The range of the occurrence scores upon the first axis of the PCA was divided in 150 bins. Bins of similar amplitude were used to divide the second axis of the PCA leading to a square grid. Occurrence thinning was realized using the following rule: when several occurrence points fell in the same grid cell, one point was randomly selected and retained to calibrate the model while the other occurrences would be used for model evaluation (see below).

2.5. Background points

Background points were randomly distributed within a large area comprising the occurrences (longitude ranging from -170 to -70 decimal degrees and latitude ranging from 15 to 40 dd). Two sets of 10,000

background points were generated (Phillips and Dudík, 2008). One was used for model calibration and the remaining was used for model evaluation using AUC (see below). Background points are depicted in supplementary Fig. S1B. The ratio between the number of presence points and the number of background points was $537/10000 = 5.37\%$.

2.6. Model evaluation

We computed the Area Under the Curve (AUC) of the receiver operating characteristic plot to evaluate the performance of the model (Fielding and Bell, 1997) which is a very common practice in species distribution modeling. However, it relies both on true and false absences which information is lacking in presence-only studies like ours. In that case background data are treated as absence data and this is problematic (Yackulic et al., 2013). The AUC value reported herein is thus provided for comparative purpose only. Computation was realized using the R package MIAMaxent (Vollering et al., 2019) and we used the occurrence records removed from the raw dataset during the environmental thinning phase hence not used for model calibration.

We additionally evaluated the performance of the model using the Continuous Boyce Index (CBI) specifically developed with the aim of evaluating presence-only models (Boyce et al., 2002; Hirzel et al., 2006). The method operates as follows: the model is used to estimate climate suitability (CS) across the geographical area under study. The range of CS values is divided in N classes and P , the frequency of occurrences falling into each class, is computed. We additionally compute E , the expected frequency of points randomly falling into each class given the total number of points available in the study. The shape of the plot of P/E against the CS classes provides precious information on the performances of the model (Hirzel et al., 2006). Good models exhibit monotonically increasing P/E with increasing CS classes. The CBI is defined as the Spearman-rank correlation between P/E and CS values. It varies from $+1$ for perfect prediction to 0 (randomness) and -1 for counter-prediction. The CBI was computed using the R package *ecospat* (Broennimann et al., 2020).

Beyond model evaluation, the shape of the P/E vs. CS plot provides interesting hints at CS thresholds useful to reclassify CS maps into a limited number of meaningful categories (Hirzel et al., 2006). CS values below the threshold at which $P/E < 1$ are associated to fewer presences than expected by chance and the corresponding geographical areas are to be considered as unsuitable environments. On the contrary, CS values above that threshold point towards suitable areas. In certain cases, other thresholds can be identified and indicate extremely favorable environments (Hirzel et al., 2006; see an example in Streito et al., 2021).

One should ideally use new or independent data i.e. not involved in model fitting to assess model performance (Barry and Elith, 2006) although such data are not often available. Here we used the occurrence data that were removed from the raw dataset during the environmental thinning phase. The dataset was submitted to a spatial thinning procedure (threshold of 50 km) to avoid possible sampling bias (Aiello-Lammens et al., 2015). A set of 100 different thinned datasets were generated and used to compute the P/E curve (Hirzel et al., 2006). We computed a statistical envelop for the median of these values using the quantiles for $p = 0.025$ and $p = 0.975$. The median was used to compute the CBI.

2.7. Forecasting future distribution of *H. vitripennis*

We projected the model using the different datasets depicting possible future climate conditions listed above using the R package MIAMaxent. The CS derived from the models were reclassified using the thresholds obtained with the CBI approach. We additionally computed presence-absence maps by solely using the threshold at which $P/E < 1$. We computed the proportion of land corresponding to suitable climate conditions in Europe (-12.5 dd $<$ longitude $<$ 46.5 dd and 31 dd $<$ latitude $<$ 72 dd) and North America + Pacific (-170 dd $<$ -longitude $<$ -70 dd and 15 dd $<$ latitude $<$ 40 dd), all SSPs and all periods considered.

The inter-GCM variations lead to some variability in the SDM estimate of CS. We assessed this variability in two manners:

First, we computed an ensemble forecast representing agreements between model predictions after transformation into binary data (i.e. presence and absence) using the threshold at which $P/E < 1$. This ensemble forecast, referred to as committee averaging, depicts the likelihood of being present given the data (Guisan et al., 2017; Marmion et al., 2009). When expressed in relative terms (%) the committee averaging shows agreement between predictions (values close to 0 % (absence) or 100 % (presence)) and disagreement (uncertainty). The maximum uncertainty is reached when the committee averaging is 50 % which means that half projections suggest presence and the other half absence of the species.

Second, we compared the CS estimated by projecting the model using the different GCM for a given SSP at a given date using pair-wise comparisons based on the I similarity index proposed by Warren et al. (2008). This index is the sum of the pair-wise differences between two predictions and thus quantifies similarity of the two distributions in a single value. Computations were done using the R package SDMTTools (VanDerWal et al., 2014).

We additionally computed the consensus models summarizing the model projection associated to each GCM for a given date and a given SSP on the basis of the median (less sensitive to extreme values than the mean). The results are shown in the supplementary material.

3. Results

3.1. Variable selection and model calibration

The 7 climate variables (bio4, bio5, bio6, bio10, bio11, bio13 and bio16) referred to as EVs were transformed into 61 derived variables (referred to as DVs, function *deriveVars* in MIAMaxent). Of these DVs, 17 were selected using the forward procedure implemented in the function *selectDVforEV* of MIAMaxent under the specified significance threshold of 0.01. Two EVs (bio4 and bio16) were dropped during the selection procedure because associated to insignificant DVs and the remaining 5 initial EVs were kept in the form of the 17 DVs. The trail of forward selection of individual EVs is shown in supplementary Table S2. We retained the 3 EVs that were selected at round 3 and significantly explained 10.7 % of the null deviance. Adding supplementary EVs only slightly increased the explanatory power of the model (up to 11.6 % of null deviance for 5 EVs) (supplementary Fig. S3) while increasing model complexity and potentially jeopardizing model transferability. The retained EVs were bio5 (maximum temperature of warmest month), bio10 (mean temperature of warmest quarter) and bio11 (mean temperature of coldest quarter). The associated DVs are given in supplementary Table S3. The fraction of total variation accounted for the variables bio11, bio10 and bio5 was 64.5, 19.6 and 15.9 % respectively. The response curves are given in supplementary Fig. S4.

3.2. Model performance

The AUC and the Boyce indices were respectively 0.877 and 0.984, and indicated very good performances. The plot of P/E against the classes of climate suitability is shown in supplementary Fig. S5. The shape of the curve allowed to identify 2 thresholds. The first threshold ($th1 = 0.211$) corresponded to the CS values for which the predicted/expected ratio confidence interval is lower than 1 i.e. the model is predicting less presences than expected by chance. An additional threshold was placed at the step of the curve for CS value of 0.4906 from which the predicted/expected ratio highly increased. The threshold allowed to distinguish between unsuitable ($<th1$), suitable ($>th1$ and $<th2$) and optimal ($>th2$) climate suitability values. The climate suitability maps were reclassified using these thresholds leading to the maps shown in Figs. 1 and 2. Not surprisingly, large parts of North America appeared to be climatically suitable to *H. vitripennis*. Suitable areas occurred around the Mediterranean region in Europe and North Africa.

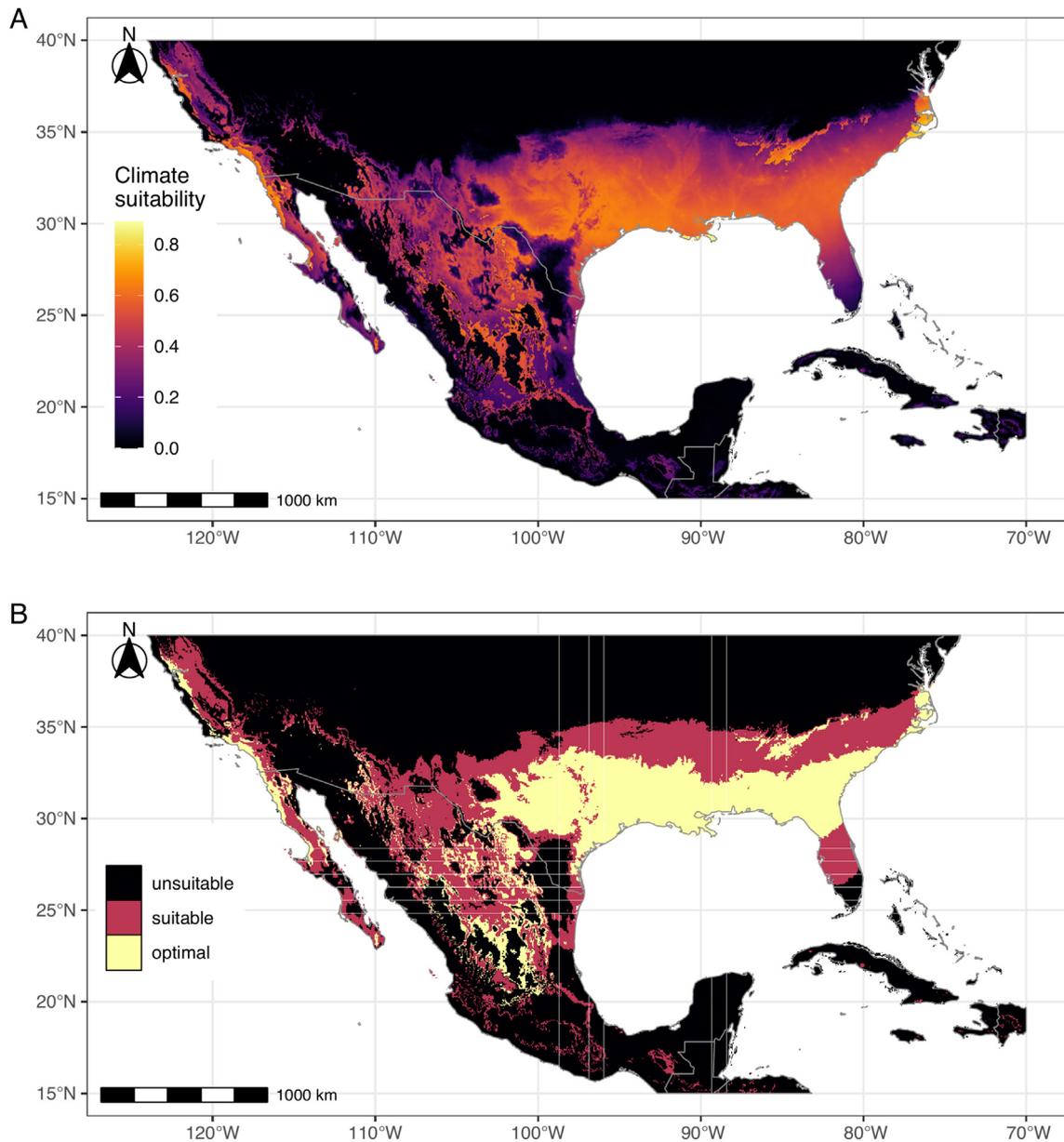


Fig. 1. Current climate suitability for the glassy-winged sharpshooter *Homalodisca vitripennis* in North America. A Climate suitability quantified by the logistic output of a Maxent model. B Climate suitability reclassified into unsuitable, suitable and optimal classes (see text for details). Projection: EPSG 4326.

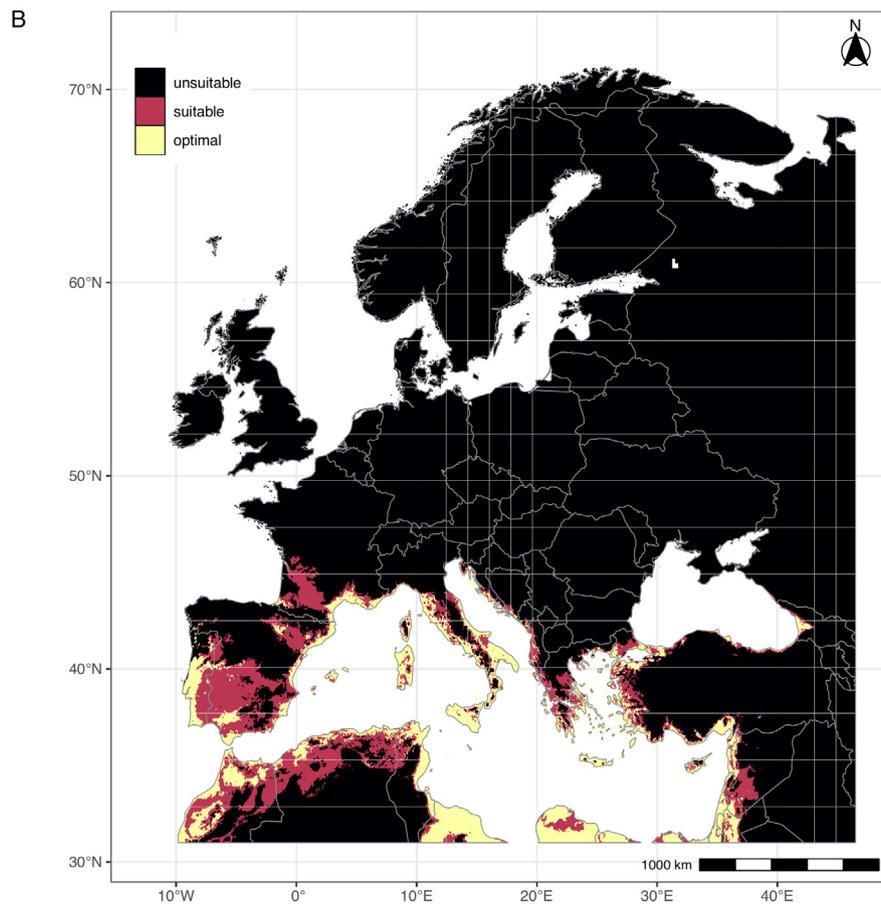
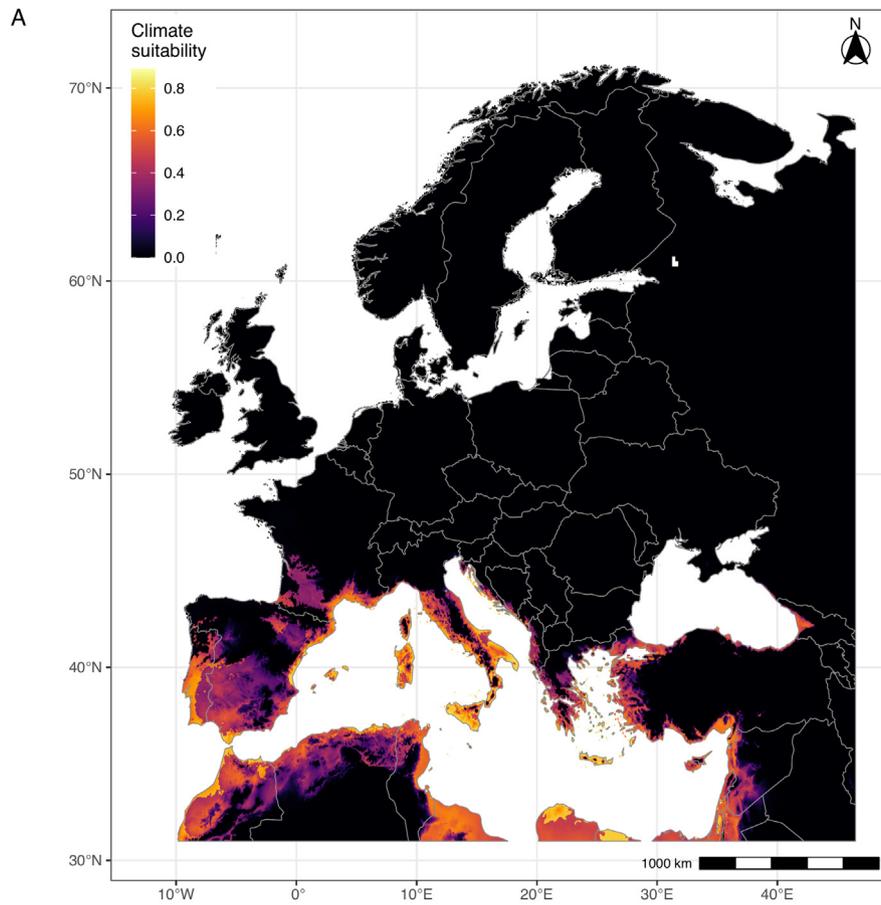
3.3. Forecasting future climate suitability

Temporal changes in the proportion of emerged land associated to suitable and optimal conditions (referred as suitable for simplification) are shown in Fig. 3 for three GCM (see supplementary Figs. S6 and S7 for all available GCM and worldwide estimates). The climate suitability of lands in North America tended to decrease from 2021–2040 to 2080–2100. A contrasted situation is observed in Europe where surfaces associated to suitable climate increased or remained stable. When present, trends were generally more clearly marked for ssp585 and ssp370. Worldwide estimates (supplementary Fig. S7) showed a global decrease of suitability irrespective of the GCM and SSP considered.

Figs. 4 and 5 (see also supplementary Figs. S8 to S15) show the ensemble forecast referred to as committee averaging. Comparing current distribution and the period covering 2021–2040 for ssp245 shows a fragmentation of suitable areas in Mexico and a shift from favorable conditions to unfavorable conditions in California. In several states in the USA, the climatic conditions are globally less favorable and an increase in

uncertainty is observed, i.e. certain projections indicate the presence of the species while others indicate the opposite. This is, for example, what is observed in Texas, Louisiana and Arkansas (Figs. 1, 4). If we examine the projections for the period 2081–2100 (ssp245), the favorable zones shift towards the northeast and Texas becomes completely unfavorable while the proportion of projections indicating a favorable climate decreases sharply for states like Texas, Louisiana and Arkansas. On the contrary, Tennessee, Kentucky and Virginia offer favorable conditions for *H. vitripennis*. On the west coast, climate suitability increases in Oregon.

In Europe (Fig. 5), a shift in favorable areas towards the north by the 2021–2040 period is observed. In some regions of Spain (Ciudad Real, Jaén, Albacete) the conditions are evolving towards a decrease in suitability. In North Africa, this trend takes the form of a reduction in the southern fringe of currently suitable areas (Fig. 5). The projections according to the different GCMs are consistent except for central France where the uncertainty is higher. This trend continues in the period 2081–2100 (ssp245): France and northern Spain (Coruña, Lugo, Asturias, Cantabria, Alaya) will become favorable while and unfavorable areas of the center of the Iberian



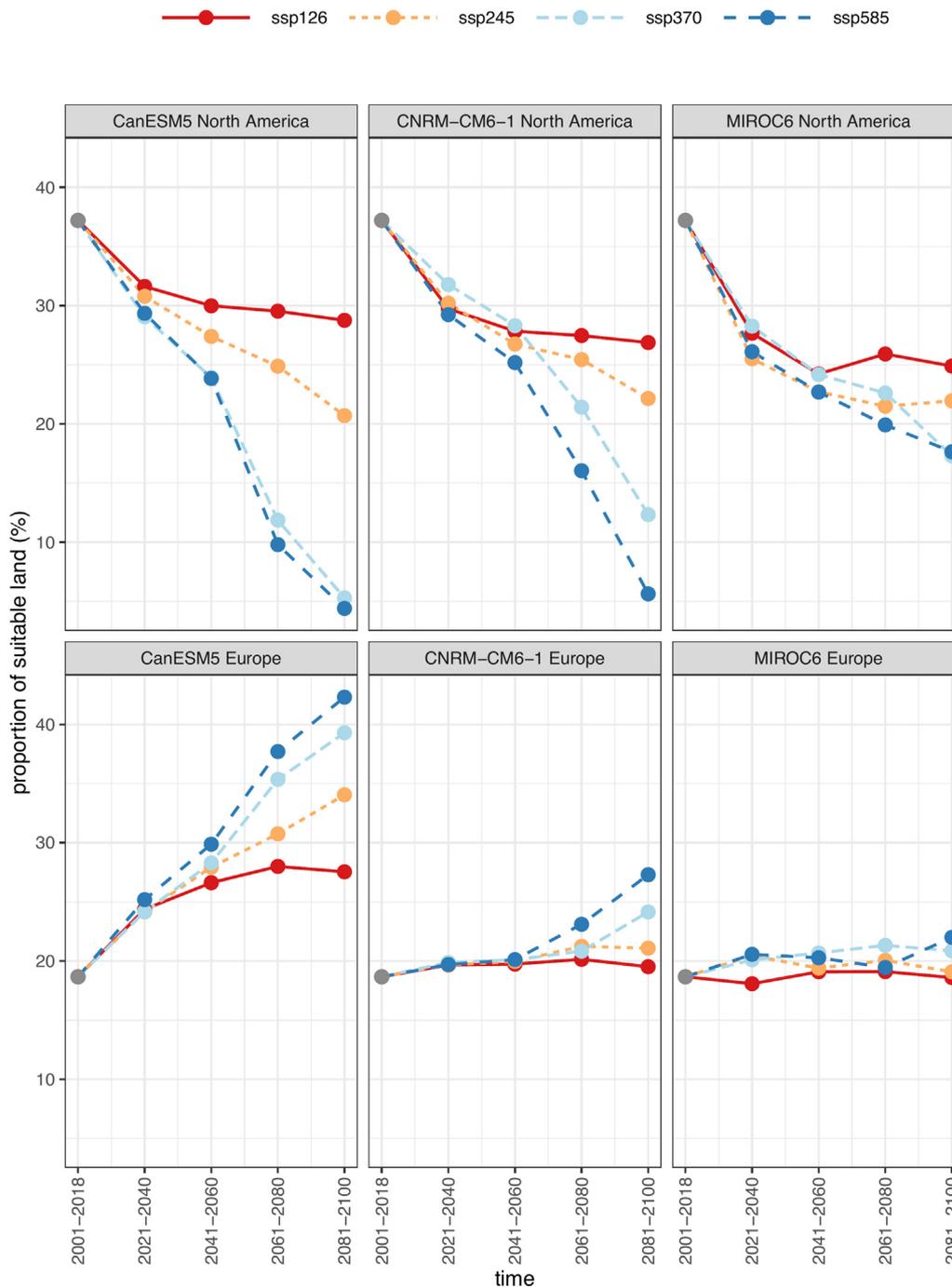


Fig. 3. Changes in the proportion of emerged lands associated to suitable conditions (the sum of suitable or optimal classes shown in Figs. 1 and 2). The surfaces associated to suitable climate are decreasing in North America while they increase or remain stable in Europe.

Peninsula will increase. The reduction of favorable areas in North Africa continues. The projections corresponding to different SSP and time periods show that the trend described below is stronger for increasing SSP and time periods (supplementary Figs. S8 to S15).

3.4. Variability of climate suitability according to GCM

As indicated by the ensemble models described above, some discrepancies between CS estimated using the model and various GCM/SSP could be

important in a few areas such as the Mississippi state during 2081–2080 or the center of France in 2021–40 for ssp245. Fig. 6 depicts the similarity between the CS estimated according to the different GCM at all periods and all SSP considered for Europe. The corresponding plot for North-America is shown in supplementary Fig. S16. Both plots showed similar trends. The variability between CS based on the different GCM tends to increase through time (larger in the future), with increasing SSP. This conveys the divergence between future climate projections expressed through GCM. Interestingly, larger dissimilarity (lower similarity) does not imply the same

Fig. 2. Current climate suitability for the glassy-winged sharpshooter *Homalodisca vitripennis* in Europe. A Climate suitability quantified by the logistic output of a Maxent model. B Climate suitability reclassified into unsuitable, suitable and optimal classes (see text for details). Projection: EPSG 4326.

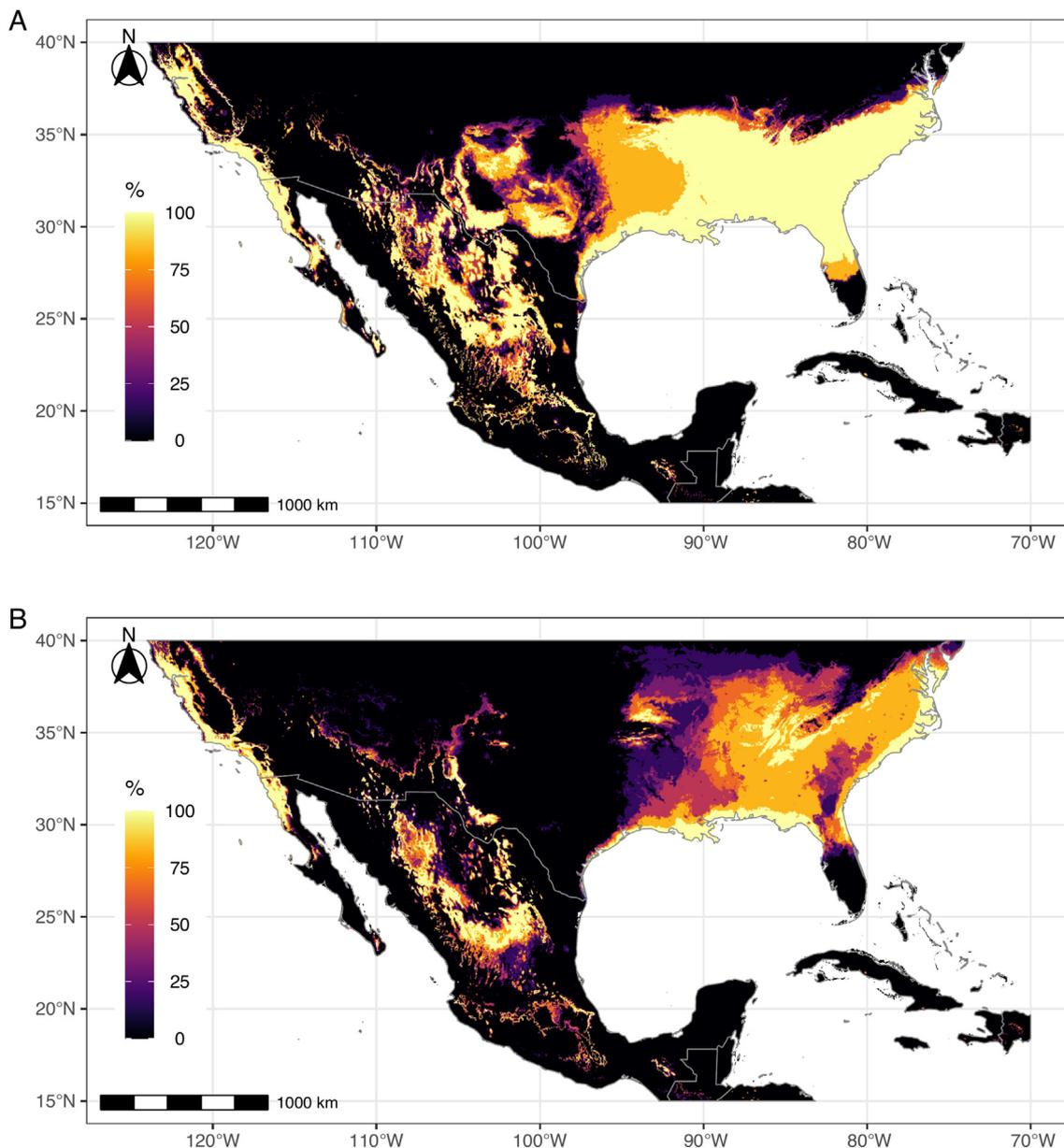


Fig. 4. Committee averaging depicting the proportion of future climate projections indicating suitable conditions in the periods 2021–2040 (A) and 2081–2100 (B) for ssp245 in North America. Mapped values range from 0 % (all projections indicate unsuitable climate conditions) to 100 % (all projections indicate suitable climate conditions). Projection: EPSG 4326.

couple of GCM across time or SSP. The most different pairs of GCM that are most often found are CanESM5 - BCC.CSM2.MR and CanESM5 - CNRM. CM6.1.

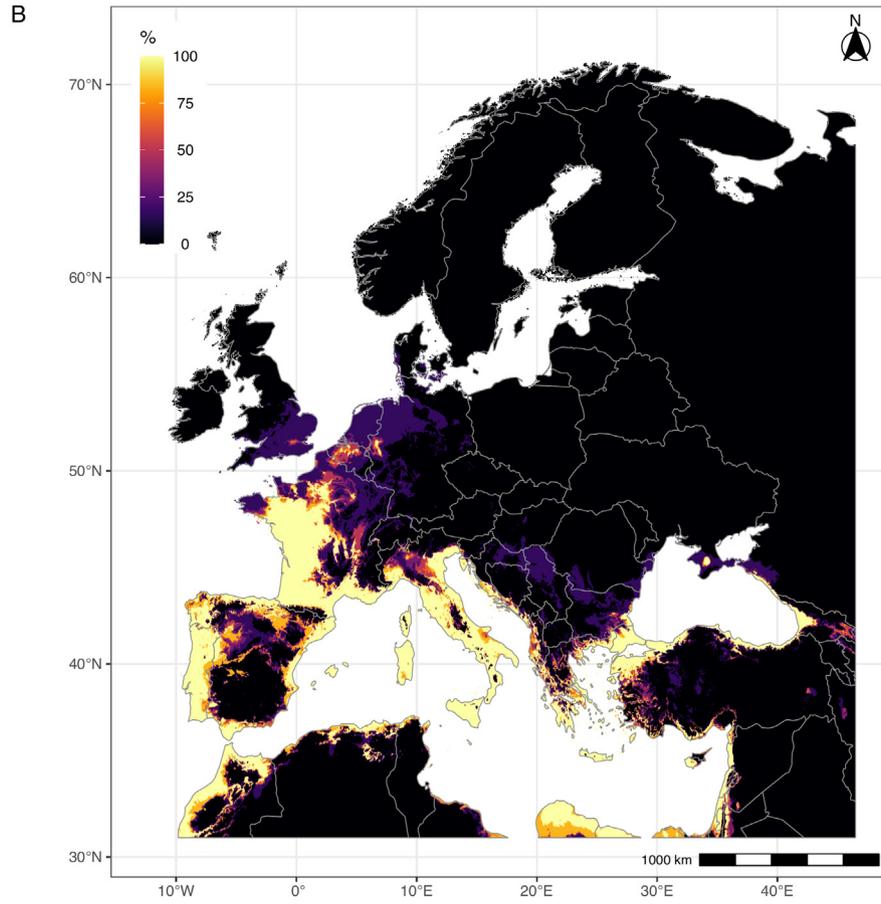
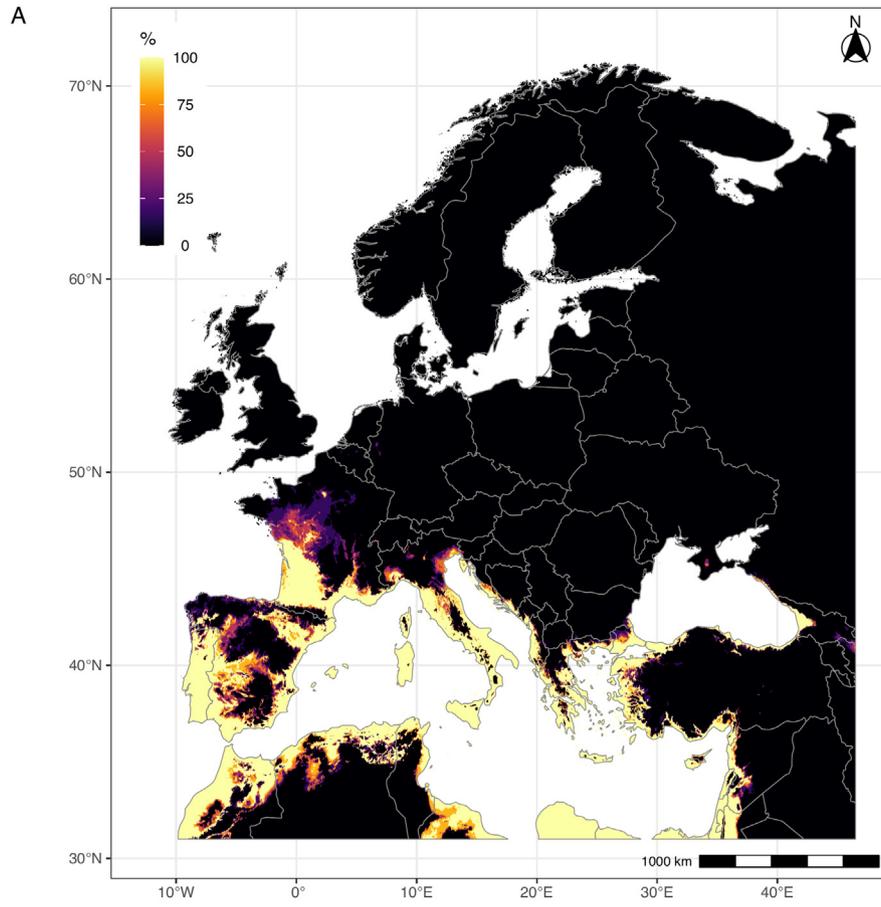
3.5. Worldwide maps

Worldwide maps are available in supplementary material S17 to S35 (consensus maps based on the median) and S36 to S51 (maps of the committee averaging). The raster source files (geotiff format) are available from Recherche Data Gouv at doi:10.57745/ABP160

4. Discussion

Homalodisca vitripennis is one of the greatest threats for countries where climate conditions allow the species to complete its natural-life cycle and where *X. fastidiosa* is present (Rathé et al., 2012). Hoddle (2004) used the CLIMEX model to show that in addition to its North-American range, climatically suitable areas for *H. vitripennis* comprised numerous grape production areas worldwide as well as large tropical and semi-tropical regions in Africa, America, Asia and Australia. Our results, based on up-to-date occurrence datasets and a different modeling approach led to

Fig. 5. Committee averaging depicting the proportion of future climate projections indicating suitable conditions in the periods 2021–2040 (A) and 2081–2100 (B) for ssp245 in Europe. Mapped values range from 0 % (all projections indicate unsuitable climate conditions) to 100 % (all projections indicate suitable climate conditions). Projection: EPSG 4326.



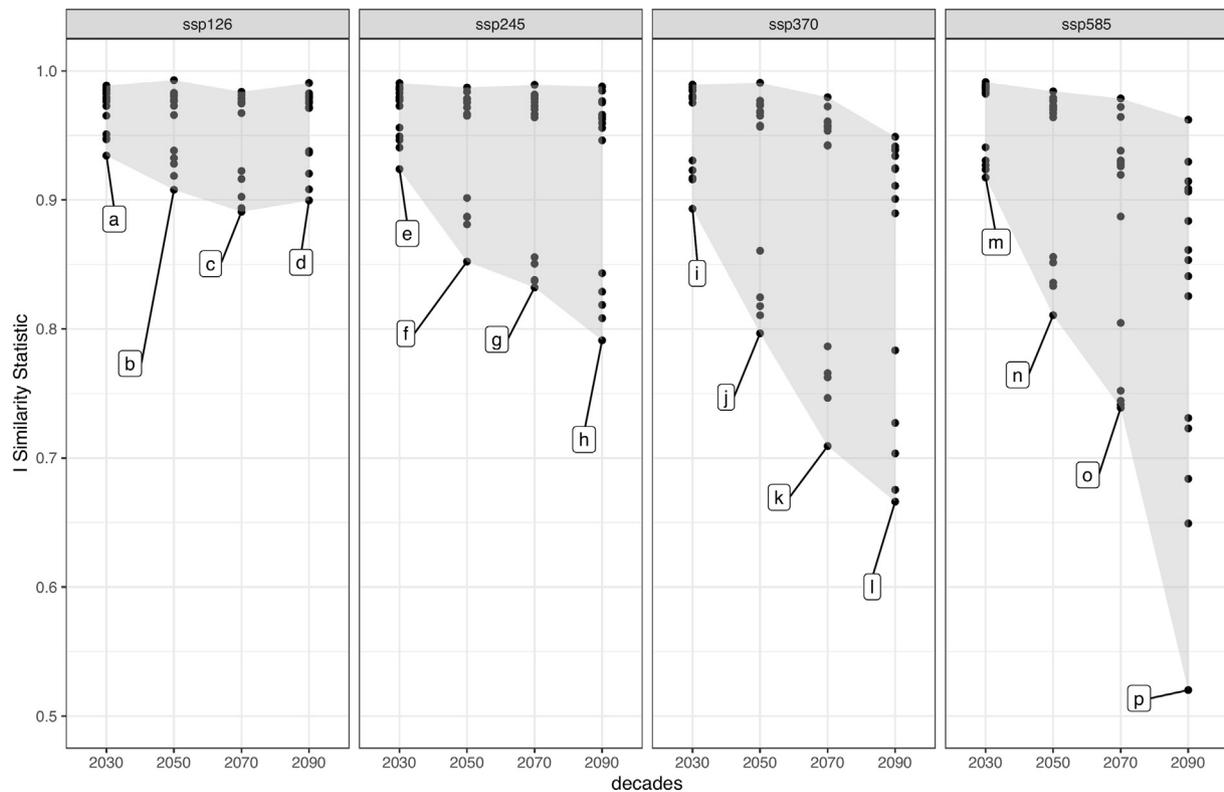


Fig. 6. Changes in the similarity between model projections according to six GCM and four shared socio-economic pathways in Europe. The output of 6 GCM form a set of $(6 \times 6 - 6) / 3 = 15$ pairs of GCM. Pairs of GCM are compared using the I similarity index Warren et al. (2008). Letters indicates the couples of GCM exhibiting the lower similarity: a) BCC.CSM2.MR vs. CanESM5 b) BCC.CSM2.MR vs. CanESM5 c) CanESM5 vs. CNRM.CM6.1 d) BCC.CSM2.MR vs. CanESM5 e) CanESM5 vs. CNRM.CM6.1 f) CanESM5 vs. CNRM.CM6.1 g) CanESM5 vs. CNRM.CM6.1 h) CanESM5 vs. MIROC6 i) CanESM5 vs. CNRM.CM6.1 j) CanESM5 vs. CNRM.CM6.1 k) CanESM5 vs. CNRM.CM6.1 l) CanESM5 vs. MIROC6 m) CanESM5 vs. CNRM.CM6.1 n) CanESM5 vs. CNRM.CM6.1 o) CanESM5 vs. CNRM.CM6.1 p) BCC.CSM2.MR vs. CanESM5.

similar yet not identical conclusions. Our model excludes tropical regions from suitable areas. This contrast could be related to available occurrences or climate data but an important difference between the studies lies with the algorithm employed to model the insect distribution. CLIMEX and Maxent are different approaches that may lead to partly divergent results (Early et al., 2021). As in the case of the present study, Jung et al. (2017) developed a CLIMEX model for the spotted lanternfly *Lycorma delicatula* predicting large favorable areas including tropical regions while for the same species but with maxent, Wakie et al. (2020) obtained a model excluding tropical regions from suitable areas. However, the results of this study are in agreement with those of Hoddle (2004) about Europe that appears to offer suitable conditions throughout areas bordering the Mediterranean Sea, but not in territories further north due to colder conditions (variable bio11).

Climate change may affect the biosecurity of Europe by facilitating the establishment of pest that nowadays occur in warmer climates. Therefore, predicting areas at risk for some quarantine vectors of *X. fastidiosa* is a step towards the development of a more efficient biosecurity network. Modeling the potential geographical range of agricultural pests faces the problem that available climate datasets (e.g. the worldclim database in the present study) provide large-scale precipitation and temperature data that cannot account for localized spatial features. In the case of *H. vitripennis*, as for other species of vectors such as *Philaenus spumarius* (Godefroid et al., 2021), this translates into the difficulty of incorporating the effects of irrigation or localized heat islands. Irrigation modifies local conditions and allows species such as *H. vitripennis* to survive in dry and hot areas such as the Californian desert (Hoddle, 2004). As a consequence, the range of the species might be underestimated. Our model indicates that regions bordering the Mediterranean Sea are climatically suitable for *H. vitripennis*. Since its first detection in Europe in 2013 (Italy) (Saponari et al., 2013), different sub-species of *X. fastidiosa* have been identified

from various European countries and it has been shown that parts of southern Europe exhibit suitable climate conditions for the bacterium (Godefroid et al., 2022, 2019). Therefore, an introduction of *H. vitripennis* in Europe may pose a significant plant health problem, mostly around the Mediterranean basin since these areas have suitable climate conditions for both the disease and this highly efficient vector.

However, climate suitability is only one of the factors at play in the risk of invasion by *H. vitripennis* which also depends on the pathways of entry, the way propagules are transported (e.g. ornamental plants), the number of individuals and their survival during the travel (Petit et al., 2008; Rathé et al., 2015). *H. vitripennis* may be introduced either as egg masses laid on plants or immature and adults (motiles) (Rathé et al., 2012; Sorensen and Gill, 1996). Air transport is likely to be the way it has been introduced from French Polynesia to Easter Island and the Cook Islands. Rathé et al. (2015) showed that motiles could survive to the conditions of humidity and temperature prevailing in cargo holds of aircraft during 24 h therefore illustrating how much air transport could be suitable to the species. The recent detection of *Draeculocephala robinsoni* another American insect vector of *X. fastidiosa*, in France and Spain (Rösch et al., 2022) points out how much long-distance introduction of such Cicadellidae species is plausible. Since *H. vitripennis* is a polyphagous species, the availability of trophic resources is not likely to be a limiting factor of its establishment in case of introduction in the Mediterranean basin. We therefore conclude that the risk is high that *H. vitripennis* would establish if it were introduced and that introduction is a genuine possibility albeit difficult to estimate. It should be noted that once introduced, organisms can evolve in situ and adapt locally to new environmental conditions (Pearman et al., 2008) that cannot be accounted for by SDM calibrated using source populations data. This limitation should be remembered since it is well-recognized that contemporary evolution does strongly shape phenotypic changes accompanying invasion events (Lee, 2002; Westley, 2011). Furthermore,

climate change might also impact the prevalence of the disease inside the vector. Such a phenomenon has recently been discussed in the case of *X. fastidiosa* and its vector *Philaenus spumarius* in France (Farigoule et al., 2022) but very little is known for other species.

Preparedness benefits from the knowledge of regions at risk but it is also useful to assess how these exposed areas would change in the coming decades under the effect of climate change. Our results highlight the uncertainty of the SDM outputs with regards to both GCM and SSP (see below) but some general trends emerge. The climate suitability is expected to increase in Europe and decrease in North America in the between 2030 and 2090. The trend is more acute for increasing shared socioeconomic pathways i.e. ssp126 < ssp245 < ssp370 < ssp585 which observation conveys the impact of the magnitude of climate change in our species distribution model. The changes we found are important and could lead to a dramatic range shift in North-America. In Europe, the pattern is a decrease of climate suitability in the areas currently suitable (i.e. around the Mediterranean basin, south Spain, North Africa) with northern region becoming suitable. Climate change will relax cold stress in northern regions while high temperatures (variable bio5 and bio10) may cause heat stress in the south. While the areas currently at risk will remain largely exposed, the surveillance will have to be implemented in more countries and larger regions. As a consequence, the number of climatically suitable hubs for *H. vitripennis* introduction will probably increase hence the economic cost of surveillance. Anticipating the change in distribution area is a way to guide surveillance and improve introduction prevention. This type of information could be shared between phytosanitary authorities for an improved international coordination of early-warning systems (Carvajal-Yepes et al., 2019; Giovani et al., 2020; Reaser et al., 2020). With changing climate suitability, new areas at risk could be identified and phytosanitary services could optimize the surveillance networks accordingly. Such information could also improve the future pest risk analyses and help authorities when making policies about trapping for early detection.

In the present study, we used the Maxent algorithm in association with a forward stepwise selection procedure allowing to select a subset of transformed explanatory variables. This approach is appealing because it yields models that are simpler than those produced by the standard procedure implemented in Maxent (Vollering et al., 2019). As a consequence the risk of overfitting is lower and the model transferability is better which is important in the context of forecasting future potential distributions (Jiménez-Valverde et al., 2011; Mazzoni et al., 2015). Regardless of the model intrinsic features, the uncertainties regarding the evolution of the climate in the future limit our capacity to forecast species range (Beaumont et al., 2008; Koo et al., 2017). Here, we report increasing variability between the climate suitability stemming from our model through time. Such a trend was reported by e.g. Buisson et al. (2010) and conveys the increasing discrepancies between GCM with time. Interestingly, we also report higher variability in SDM predictions with increasing SSP. Again, this conveys the increasing dissimilarity between GCM according to SSP corresponding to increasing emissions (Fig. 6). Another source of variability is that the most dissimilar predictions are associated with different GCM according to the time period and SSP considered. The main consequence of these substantial sources of variability is not new and implies that environmental scientists should use multiple GCM when their objective is to assess the impact of future climate upon species potential distribution (Beaumont et al., 2008; Hannah, 2015). In the present study we used all the GCM projections available from the worldclim database for the four SSPs and the different time periods under investigation (Fick and Hijmans, 2017). However, this strategy may not always be optimal because GCM projections might not be fully independent in the statistical sense (Sanderson et al., 2015). The problem of GCM interdependency has been recently discussed by Shigama et al. (2021) who proposed a method allowing to select a subset of GCM representative of the uncertainty range of available models. Such approach is promising and should be tested for GCM selection prior to SDM projection. Daron et al. (2021) highlighted the importance of providing a picture of the range of uncertainty and avoiding to solely focus on the mean or the median of estimates when communicating about climate change manifestations. A

similar principle could be applied to species potential distribution and phytosanitary risk.

CRedit authorship contribution statement

Jean-Pierre Rossi: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing – original draft. **Jean-Yves Rasplus:** Conceptualization, Data curation, Writing – original draft.

Data availability

Part of the dataset is provided in the supplementary material; the rest comes from GBIF and can be downloaded by readers. A DOI is provided in the references section.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.160375>.

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