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Climate and host plant availability are favorable to the establishment of *Lycorma delicatula* in Europe

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ABSTRACT

1. *Lycorma delicatula*, the spotted lanternfly, is a highly successful invasive phloem-feeding planthopper native to southern China. It has invaded South Korea, Japan, and the USA, where it is still geographically expanding but is absent from Europe. We examined two important ecological factors affecting the risk of establishment: climate suitability and the availability of compatible host plants.
2. We developed an ensemble species distribution model based on three algorithms to assess the potential geographical range of *L. delicatula* according to current and future climate conditions. We reviewed the literature to assess the host repertoire of *L. delicatula* and list host species present in Europe.
3. Current climate conditions appeared to be highly suitable for *L. delicatula* in much of Europe. Climate change will marginally alter climate suitability by 2060. Numerous known host plants are widely distributed in Europe.
4. We conclude that neither climate conditions nor the presence of compatible host plants constitutes an obstacle to the establishment of *L. delicatula* in Europe. Both current and future climate suitability and the list of potential hosts could be helpful to guide surveillance and improve the preparedness of phytosanitary authorities.

INTRODUCTION

Once established, eradicating invasive species is very difficult; thus, it is always best to avoid their establishment (Leung et al. 2002). Moreover, in the event of an incursion, the time between the arrival of the invasive organism and the start of the eradication campaign is crucial in determining the success of management measures (Hulme 2006). Monitoring is paramount here because it allows for the early detection of invasive species and reduces the time needed to implement management measures (Pluess et al. 2012). In this context, risk analysis is a vital element of pre-border actions as it helps direct surveillance, particularly by identifying *a priori* the most threatened geographical areas or entry routes for exotic species (Probert et al. 2020; Reaser et al. 2020). The first step in risk assessment involves distinguishing invasive from non-invasive alien species (Roy et al. 2019). Once a target species is identified, it becomes feasible to evaluate environmentally suitable areas where the potential economic or ecological impacts of invasion are significant. These regions could be the focus of regional monitoring efforts, where targeted public information campaigns can greatly enhance biological invasion management (Faulkner et al. 2020).

Climate plays a crucial role in shaping the distribution, survival, and reproduction of invasive species (Battisti et al. 2015). Environmental suitability also depends on biotic factors such as competition, predation, parasitism, and the availability of trophic resources, which are pivotal in the dynamics of biological invasions (Daly et al. 2023). For plant-feeding species, successful establishment often hinges on the presence of their preferred host plants or closely related species (Bacon et al. 2014; Bonnamour et al. 2023). While certain species may evolve rapidly to adapt to new environmental conditions or hosts (Pearman et al. 2008), the vulnerability of an ecosystem to a specific plant-feeding species largely depends on its fundamental host repertoire i.e. all compatible hosts of the species (Braga and Janz 2021). Therefore, assessing climate suitability, understanding the impact of global changes, and determining host range are central to pest risk analysis (Devorshak 2012).

Lycorma delicatula (White, 1845), the spotted lanternfly, is a phloem-feeding planthopper native to China. This species is highly polyphagous (Barringer and Ciafré 2020) and its dispersion is often passive, closely linked to human activities through human-mediated transport (Ladin et al. 2023; Montgomery et al. 2023). *L. delicatula* invaded South Korea in 2004, Japan in 2006, and finally Pennsylvania in the United States in 2014 (Barringer et al. 2015), from where it has significantly spread to adjacent states (Urban and Leach 2023). Local outbreaks of *L. delicatula* cause severe damage to a wide range of host plants, from herbaceous species (primarily as nymphs) to ornamental, woody, and fruit trees (Lee et al. 2019; Urban et al. 2021; Urban and Leach 2023). As of today, *L. delicatula* is not present in Europe. Host selection is highly dependent on available plants, but *L. delicatula* exhibits higher fitness when developing on the tree of heaven, *Ailanthus altissima* (Mill.) Swingle, 1916 (Uyi et al. 2021). *A. altissima* is present in Europe along with economically important host plant species such as grapes, fruit trees, woody trees, and ornamental trees, making *L. delicatula* a serious threat to European agriculture (Huron et al. 2022).

Several studies have assessed the potential distribution of *L. delicatula*, but they rely on different algorithms and offer contrasting results. Jung et al. (2017) reported low climate suitability in Europe using the “CLIMEX” model (“Compare Locations” option). In contrast, Wakie et al. (2020) and Huron et al. (2022) found high climate suitability in Europe using the Maxent algorithm. Namgung et al. (2020) also used the Maxent algorithm but focused their survey on South Korea. Given the conflicting results regarding Europe's climate suitability and the availability of more occurrence data since these studies were conducted, we aimed to develop a new model to assess the establishment potential of *L. delicatula* under current and future climate conditions. To achieve this, we used three different algorithms to minimize the uncertainty associated with the choice of modeling method. We also projected these models using a set of climate change scenarios, which, to our knowledge, has never been done for *L. delicatula*. Although we focus here on the climate suitability of the European continent, we provide worldwide assessments in the supplementary material. Our second objective was to list the known host plant species of *L. delicatula* to evaluate how many host species are present in Europe and in which countries. Combining climate suitability with host plant presence allowed us to assess the establishment potential of *L. delicatula* in Europe.

METHODS

All statistical analyses and data management were performed using the R environment for statistical computing and visualization (R Core Team 2023).

Species Distribution Model

Data collection and compilation

We collected occurrences of *L. delicatula* from the international database GBIF (Global Biodiversity Information Facility; dataset doi: https://doi.org/10.15468/dl.tfatn5; extracted the 08/02/2023), and from a literature review using the valid name *Lycorma delicatula* and its synonym *Aphaena delicatula*. Additionally, we included records from established populations in the United States, retrieved from the R package “LydemapR” (De Bona et al. 2023). “LydemapR” contains spatiotemporal data and mapping functions to visualize the current spread of *L. delicatula*. We compiled old publications to collect occurrences in the native range (published between 1906 and 2000) and recent publications tracking the progression of the invasion in the United States, Japan, and South Korea (see reference list in Appendix 1 and Appendix 2). When longitude-latitude coordinates were not available but the name of the observation site was provided, we assigned the coordinates of the locality's centroid using Google Maps. Occurrences retrieved from the literature without precise location information (only state or country mentioned) were discarded. The GBIF data were examined to exclude occurrences due to questionable identification (unknown basis of record) and missing geographic coordinates, as we considered these occurrences invalid.

Pre-processing and data preparation

At the time of the analyses (February 2023), a total of 15,211 occurrences of *L. delicatula* were retrieved from GBIF, 406 from the literature, and 1,970 from the R package “LydemapR”. Among the GBIF occurrences, 210 were discarded due to missing coordinates. From the literature occurrences (Appendix 2), 44 were excluded due to imprecise location data. Most of these imprecise occurrences pertained to the historical distribution of *L. delicatula* in its native range, where locations were often described only at the regional or provincial level. Finally, 17,333 occurrences were deemed valid and retained for further analyses. These 17,333 records included 121 occurrences with missing dates, which were excluded because it was impossible to associate them with the climate data corresponding to the period of observation.

One record predating 2001 was removed to ensure that all remaining data could be analyzed using the most recent climate data from the WorldClim database (see below). The spatial distribution of the remaining 17,211 records was compared with the resolution of the climate raster data used in the study (2.5 minutes, see below) to retain only one point per raster grid cell, thereby preventing over-representation of certain climate conditions (Elith et al. 2006). This process resulted in a total of 3,416 valid occurrence records. One record from India was discarded because the presence of viable populations in this country remains uncertain (Dara et al. 2015). The remaining 3,415 records are distributed across four countries as follows: China 295; South Korea 407; Japan 28; and USA 2,685.

We applied a geographical filtering procedure to the dataset to control for sampling bias (Aiello-Lammens et al. 2015). The distance threshold was arbitrarily set to 20 km, and computations were conducted using the R package "spThin" (Aiello-Lammens et al. 2015). The remaining records were distributed as follows: China 163; South Korea 114; Japan 8; and USA 275. Additionally, we performed environmental thinning following Varela et al. (2014), utilizing the original variables rather than outputs from a Principal Components Analysis (Velazco et al. 2022), as in Varela et al. (2014). We employed the function "occfilt_env" from the R package "flexsdm" (Velazco et al. 2022) and a set of eight bioclimatic variables available from the WorldClim database, representing average temperature and precipitation across the study area from 2001 to 2018 (see below): bio8 (mean temperature of the wettest quarter), bio9 (mean temperature of the driest quarter), bio10 (mean temperature of the warmest quarter), bio11 (mean temperature of the coldest quarter), bio16 (precipitation of the wettest quarter), bio17 (precipitation of the driest quarter), bio18 (precipitation of the warmest quarter), and bio19 (precipitation of the coldest quarter). This resulted in 362 remaining occurrence records distributed as follows: China 136; South Korea 80; Japan 8; and USA 138.

Climate datasets

The occurrence dataset used in this study is from 2001 onwards, and we utilized historical monthly weather data spanning from 2001 to 2018 (https://www.WorldClim.org, Fick and Hijmans 2017) to calibrate the models. Average climate descriptors for the period 2001–2018 (referred to as bioclimatic variables) were computed using the function "biovars" from the R package "dismo" (Hijmans et al. 2023). The resolution of the raster climate data is 2.5 minutes (≈22 km^2 at the equator). We projected the species distribution models for the period 2041–2060 using future climate data also available from WorldClim. For this purpose, we considered six Global Circulation Models (GCMs): BCC-CSM2-MR (Wu et al. 2019), CNRM-CM6-1 (Voldoire et al. 2019), CNRM-ESM2-1 (Séférian et al. 2019), CanESM5 (Swart et al. 2019), MIROC-ES2L (Hajima et al. 2020), and MIROC6 (Tatebe et al. 2019). Shared Socioeconomic Pathways (SSPs) describe plausible greenhouse gas emissions scenarios based on different climate policies (Riahi et al. 2017; Meinshausen et al. 2020). For each period and GCM, climate suitability was modeled using simulated climate data across four Shared Socioeconomic Pathways (SSPs): SSP5-8.5, SSP3-7.0, SSP2-4.5, and SSP1-2.6, representing high-end, medium-to-high-end, medium, and low-end greenhouse gas forcing pathways, respectively (Abram et al. 2019).

Our models were built using a set of 14 bioclimatic descriptors available from the WorldClim database (2001-2018), which encompass both temperature and precipitation-related environmental constraints: bio1 (annual mean temperature), bio5 (maximum temperature of the warmest month), bio6 (minimum temperature of the coldest month), bio8 (mean temperature of the wettest quarter), bio9 (mean temperature of the driest quarter), bio10 (mean temperature of the warmest quarter), bio11 (mean temperature of the coldest quarter), bio12 (annual precipitation), bio13 (precipitation of the wettest month), bio14 (precipitation of the driest month), bio16 (precipitation of the wettest quarter), bio17 (precipitation of the driest quarter), bio18 (precipitation of the warmest quarter), bio19 (precipitation of the coldest quarter) (Fick and Hijmans 2017).

Pre-processing and data preparation

One crucial aspect of species distribution modeling is the selection of predictors used in the model, which not only affects model performance but also its transferability (Petitpierre et al. 2017), particularly important when projecting processing, FOP analysis enabled us to discard variables displaying noisy or bimodal curves, retaining only predictor variables that yield ecologically realistic and meaningful response curves (Guevara et al. 2018; Vollering et al. 2019). FOPs were computed using the R package “MIAmaxent” (Vollering et al. 2019). This process led to the exclusion of the variables bio8, bio14, bio15, bio17, bio18, and bio19, while retaining bio1, bio5, bio6, bio9, bio10, bio11, bio12, bio13, and bio16 for model calibration. These variables describe different aspects of climate and their biological significance may vary for the species under study. Although no variables were objectively ruled out *a priori*, stepwise selection procedures implemented during model calibration ensured retention of those significantly contributing to the model (see below).

Model algorithms

We employed three distinct algorithms for species distribution modeling: 1) Random Forests (RF), 2) Boosted Regression Trees (BRT), and 3) Bayesian Additive Regression Trees (BART). RF and BRT are widely utilized in species distribution modeling (Guisan et al., 2017), whereas BART was introduced more recently in ecology (Carlson, 2020). RF is a machine learning algorithm that combines outputs from multiple decision trees through bagging (Breiman, 2001; Guisan et al., 2017). We calibrated the model using the R package "randomForest" (Liaw and Wiener, 2002). Climate descriptors were selected via stepwise selection based on averaged variable importance (Li et al., 2016), implemented using the R package "steprf" (Li, 2022). Tuning of node size and the number of explanatory variables sampled at each split was achieved using the R package "randomForestSRC" (Ishwaran and Kogalur, 2007). We used a large (1000) but computationally feasible number of trees (Probst and Boulesteix, 2018).

BRT follows the same principle as RF by combining different decision trees, but it diverges in its sequential approach using a forward stagewise procedure. Elith et al. (2008) provided a practical guide to BRT for modeling species distribution. We calibrated our BRT model using the R package "dismo" (Hijmans et al., 2023). The model hyperparameters were set as follows: the tree complexity parameter was fixed at 5 to allow interactions between variables, the learning rate was set to 0.005, and the bag fraction (proportion of data selected at each step) was fixed at 0.5. We used the "gbm.simplify" function from the R package "dismo" to identify explanatory variables that could be removed for simplification. Additionally, we employed the "gbm.step" function to determine the optimal number of trees.

Similar to the previous methods, BART estimates the probability of presence or absence using a series of decision trees. It is characterized as a nonparametric Bayesian regression approach that incorporates priors on tree structure, resulting in a posterior distribution of estimated classification probabilities (Chipman et al., 2010). BART has recently been introduced in species distribution modeling (Carlson, 2020) and has shown considerable promise (Baquero et al., 2021; Strubbe et al., 2023; Rossi et al., 2024). For our analysis, we utilized the R package "embarcadero" (Carlson, 2020) and employed the variable selection procedure implemented in the function "bart.step" to identify the variables that significantly contributed to the model (details provided in Carlson, 2020). The model was run using 1000 trees.

Across all algorithms, we employed a number of pseudo-absences equal to our occurrence records (362) (Barbet-Massin et al., 2012), sampled from the initial 1000 points generated during the earlier stages of analysis (as described above).

We used the 14 climate descriptors previously mentioned (bio1, bio5, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio16, bio17, bio18, bio19) in our analysis. For each modeling approach—random forest (RF), boosted regression trees (BRT), and Bayesian additive regression trees (BART)—we utilized specific variable selection procedures to identify optimal subsets of these descriptors. Specifically, we used the "steprf" function for random forest, "gbm.step" for boosted regression trees, and "bart.step" for Bayesian additive regression trees. Each procedure determined a subset of variables that maximized model performance, which was then used to calibrate the respective model.

Pseudo-absences

True absence data *i.e.* localities where a species is absent because of unsuitable environmental conditions are often lacking particularly in the case of invasive organisms such as *L. delicatula*. Therefore, we employed pseudo-absences for model calibration (Lobo et al., 2010). Defining the geographical area for generating pseudo-absences is a critical step in species distribution modeling (Barbet-Massin et al., 2012). The native range of *L. delicatula* is well-known and we assumed absence in the northern and southern regions beyond its current range in China. Pseudo-absences were not generated to the east of its native range, as the species is currently expanding into this area, including Japan and Korea. To the west, the Tibetan Plateau acts as a natural barrier, limiting the species' dispersal and thereby complicating the sampling of pseudo-absences (the species may be absent from areas west of the Tibetan Plateau because this geographic feature is a dispersal barrier). The geographical area where pseudo-absences were sampled was thus defined as a surface extending 25 decimal degrees north and south of all documented species observations within its native range (see Appendix 3 for details). In North America, no pseudo-absences were generated for *L. delicatula* due to its ongoing expansion on the continent.

We generated a total of 1000 pseudo-absences using the function "sample_pseudoabs" from the R package "flexsdm" (Velazco et al., 2022). The allocation of these pseudo-absences was constrained by environmental suitability as determined by the bioclim model (Booth et al., 2014), focusing on four specific bioclimatic variables (bio5, bio6, bio13, and bio14) identified as climate limiting factors (Velazco et al., 2022). The probability of allocating a pseudo-absence point was higher in regions exhibiting lower climate suitability according to the results of the bioclim model.

Model performance

We evaluated the performance of our models using two metrics: the Area Under the Curve (AUC) of the receiver operating characteristic (ROC) plot (Fielding and Bell 1997), and the true skill statistic (TSS) (Allouche et al. 2006). These evaluations were conducted using a set of 3053 valid occurrences that were withheld from the raw dataset during thinning (geographical and environmental). An equal number of pseudo-absence points were generated, as described earlier, for model evaluation purposes. This approach allowed us to assess the models using independent data that were not used in their calibration process. The calculations of AUC and TSS were implemented using the R package "dismo" (Hijmans et al., 2023.

Estimation of climate suitability

We assessed the climate suitability under current and future climate scenarios using the R function "predict". Future climate projections were computed for the period 2041-2060 based on various General Circulation Models (GCMs) and Shared Socioeconomic Pathways (SSPs), as described previously.

To synthesize the outputs from our three models (RF, BRT, and BART), we employed a consensus approach known as committee averaging (Guisan et al., 2017, Araújo and New, 2007). This method involves two main steps: 1) transforming model outputs into binary (presence/absence) values using a threshold and 2) averaging the binary projections from RF, BRT, and BART to compute the committee averaging score. This score ranges from 0 (indicating all models predict absence) to 100 (indicating all models predict presence), providing an intuitive assessment of the likelihood of species presence We used the threshold that optimized the TSS statistics computed with the function “threshold” from the R package “dismo”.

For future climate projections (2041-2060) under each SSP, the committee averaging process described above was repeated using projections of all considered GCMs (6 in total). This resulted in 18 projections (3 models x 6 GCMs) per SSP.

Model extrapolation

To address potential issues of model extrapolation when projecting under non-analogous environmental conditions, we employed the multivariate environmental similarity surface (MESS) index, as introduced by Elith et al. (2010). This index quantifies how similar a point is to the training dataset based on a specified set of reference explanatory variables. A negative MESS value indicates that at least one of these explanatory variables falls outside the range of the reference dataset, suggesting potential extrapolation. We computed the MESS index for the climate descriptors used to calibrate the models (current climate conditions, 2001-2018) and for the different climate change scenarios. For each SSP, the minimum value of the MESS index computed for the 6 GCM was retained. Computations were done using the function “mess” from the package “dismo”.

***Lycorma delicatula* host plant dataset**

In our assessment of the risk of *L. delicatula* establishment in Europe, the presence of compatible host plants plays a crucial role. We compiled a comprehensive list of host plants based on various sources including reviews, research articles, theses, and pest risk analysis reports (refer to Appendices 4 and 5). To differentiate host plants, we categorized them based on whether feeding events were observed or if *L. delicatula* was merely observed resting or egg-laying. Our analysis focused on reports where explicit feeding or damage by *L. delicatula* was documented. For taxonomic classification, we updated the plant names according to the Plant of the World Online (POWO) classification system (https://powo.science.kew.org). We examined the origin of each feeding host plant and its distribution in native and invaded areas, as well as its status (introduced, native, or cultivated) in Europe.

The geographical distribution (presence or absence) and status of each feeding host plant in European countries were compiled from several authoritative databases: 1) Plant of the World Online (POWO) and GRIN (Germplasm Resources Information Network) for native and invaded areas worldwide (https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch) 2) Euro+Med PlantBase for European countries (https://www.emplantbase.org/home.html).

We defined Europe according to administrative boundaries and included the following countries: Albania, Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Kosovo, Latvia, Liechtenstein, Lithuania, Luxembourg, Macedonia, Malta, Moldova, Monaco, Montenegro, Netherlands, Norway, Poland, Portugal, Romania, San Marino, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, and United Kingdom.

RESULTS

Calibration and evaluation of the models

The variables retained by the selection procedures in BART and BRT were similar: bio1, bio5, bio6, bio9, bio11, bio12, and bio16. The selection procedure in RF yielded a slightly different set: bio1, bio6, bio9, bio10, bio11, bio12, and bio16, where bio5 was replaced by bio10. The AUC was respectively 0.999, 0.998 and 0.999 for RF, BRT and BART. The TSS was respectively 0.994, 0.996 and 0.994 for RF, BRT and BART. These results indicated a very good performance of the 3 models. The suitability thresholds that maximized the TSS were 0.623, 0.362 and 0.540 respectively for RF, BRT and BART.

Current climate suitability (2001-2018)

Figures 1A-C depict climate suitability for the period 2001-2018 according to each model (RF, BRT, BART), showing very high suitability in western Europe with a northern boundary through England and Scandinavia (Sweden, Finland) and Russia. Southern Europe also exhibited suitability extending into northern Morocco, Algeria, and northeastern Tunisia. Figure 1D illustrates committee averaging of RF, BRT, and BART model outputs, highlighting areas of consensus and divergence, particularly around the Mediterranean basin and northern Europe. The MESS index map (Figure 1E) indicates minimal model extrapolation in western Europe (positive values), contrasting with increased extrapolation in North Africa, the Middle East, and northern Europe's Novaya Zemlya region (negative values).

Climate suitability in 2041-2060

The committee averaging of projections across the four SSPs is depicted in Figures 2A, 2C, 2E, and 2G. In the period 2041-2060, suitable areas expanded slightly northward, particularly under scenarios with high greenhouse gas emissions, notably affecting northern Scandinavia and the north-western Ural Plain in Russia (Figure 2G). Conversely, there was a decrease in suitability observed in the southern Iberian Peninsula (southern Spain and Portugal) and North Africa (Morocco). Figures 2B, 2D, 2F, and 2H display maps of the MESS index, which showed a similar spatial pattern compared to the period 2001-2018. However, the MESS index increased across all considered SSPs in central Spain, the Middle East, southern Kazakhstan, Uzbekistan, and Turkmenistan. These findings underscore the need for caution when interpreting projections in these regions, due to potential extrapolation beyond the range of environmental conditions corresponding to the dataset used for models' calibration.

Host plants

A total of 104 taxa were identified as feeding host plants of *L. delicatula*, comprising 103 species and 1 subspecies (*Betula pendula* subsp. *mandshurica*), distributed across 65 genera and 39 botanical families (see Appendix 5). Additionally, *L. delicatula* was associated with 72 plant species and 11 botanical families where feeding observations were absent. Among these, 12 species were noted with observations of both eggs and nymphs/adults, 33 species with only observations of nymphs/adults, and 17 species solely reported as egg supports. The number of host plants varied significantly by country (Appendix 7).

During the invasion of Japan, South Korea, and the USA, *L. delicatula* acquired 68 new host species, with specific host plant numbers for these countries being 1, 28, and 33, respectively. Only 22 host species were exclusively reported from China, while one feeding host species (*Ailanthus altissima*) was common across China, Japan, South Korea, and the USA (see Appendix 8).

Among the 103 feeding host taxa of *L. delicatula*, 57 species were identified in Europe (see Figure 3, Appendix 9). Some species had wide geographic distributions (Eurasiatic) and were native to both China or Europe (e.g., *Arctium lappa*, *Betula pendula*, *Rosa pendulina*, *Vitis vinifera*), or were invasive (e.g., *A. altissima*, *Celastrus orbiculatus*), cultivated (e.g., apricot: *Prunus armeniaca*, kaki persimmon:

Diospyros kaki), and/or ornamental (e.g., honeysuckle: *Lonicera maackii*, *Melia azedarach*, weeping willow: *Salix babylonica*). Certain American hosts introduced to Europe as ornamental or cultivated species include *Quercus rubra*, *Juglans cinerea*, and *Acer rubrum*, some of which have become invasive like *Prunus serotina*. Two American hosts, *Acer platanoides* and *Acer pseudoplatanus*, are native to Europe. Countries with the highest risk of *L. delicatula* establishment, based on the availability of host plants, include Ukraine, France, and Germany, each hosting more than 40 host species (see Figure 3).

Worldwide distributions

The worldwide projections for current climate conditions are detailed in Appendix 10, highlighting regions of high climate suitability in both the native range and invaded areas (South Korea, Japan, and extensive parts of the USA). The MESS index provided in Appendix 11 shows positive values in these regions, indicating minimal issues with extrapolation. Additionally, certain regions of South America (Chile, Argentina), South Africa, and Australia (specifically Victoria, New South Wales, and Queensland) exhibited high climate suitability according to all three models. Appendices 12 to 19 present worldwide projections for the period 2041-2060 under different Shared Socioeconomic Pathways (SSPs), along with corresponding MESS maps. These projections indicated an increase in climate suitability towards the north and a decrease towards the south relative to the current potential range.

DISCUSSION

The three algorithms employed in this study demonstrated strong performance and provided consistent projections for Europe. While some discrepancies were noted in Southern Finland and Western Russia, the majority of Western Europe exhibited current climate conditions that are deemed suitable for *L. delicatula*. This finding aligns with the conclusions drawn by Wakie et al. (2020), although our models indicated higher and more uniform climate suitability across the European continent. Both Wakie et al. (2020) and our study suggest that *L. delicatula* would struggle to establish in tropical zones, contrasting with the findings of Jung et al. (2017). This disparity could stem from differences in the algorithm used or variations in available data during the respective analyses. Beyond Europe, regions with climatically favourable conditions extend to North America (Mexico, USA), South America (Argentina, Chile), Africa (South Africa), Asia (China, Korea, Japan), Southeast Australia, and the North Island of New Zealand (Appendix 10).

Numerous known host plants are already established in Europe, with countries like Germany, France, and Ukraine hosting more than 40 identified host species. In addition, European host species that *L. delicatula* could potentially acquire upon establishment should also be considered. The insect's ability to adapt to new hosts is evident from its acquisition of numerous American species during the invasion of the USA (Barringer and Ciafré 2020). Our findings also reveal minimal overlap among host plant species across the three Asian countries where *L. delicatula* is present. While this could partly be due to gaps in literature information, it's important to note that China, Japan, and Korea naturally exhibit relatively low overlap in plant species (Guowen 1997; Wang et al. 2023).

L. delicatula is a notable invasive species, particularly because its preferred host, *Ailanthus altissima*, is itself a highly successful invasive plant with a global distribution (Park et al. 2009). *A. altissima* is recognized as one of the most pervasive invasive plants (Sladonja et al. 2015), and despite regulatory efforts within the European Union (Regulation 1143/2014), its spread continues. This situation could potentially facilitate the establishment of *L. delicatula* if introduced, presenting a scenario akin to invasional meltdown (Simberloff and von Holle 1999). Although *L. delicatula* reduces the annual growth of *A. altissima* (Dechaine et al. 2023), its non-specific feeding behavior typically excludes it from consideration as a suitable biocontrol agent (Ding et al. 2006), though Brooks et al. (2020) explored its potential role in vectoring plant pathogens.

Climate change is anticipated to have diverse impacts on both crop species and pest organisms, such as range shifts (Bebber et al. 2013; Battisti and Larsson 2015) and potentially heightened crop losses (Deutsch et al. 2018). While the specific impact on crop losses due to *L. delicatula* in Europe remains uncertain, our findings suggest that its potential range by 2060 is not likely to undergo significant changes. There may be a slight contraction in southern Europe, particularly in regions of South Portugal and Spain, but this effect is expected to be limited. Conversely, there could be a modest northward expansion of suitable climate conditions, particularly in Scandinavia and Russia. It is important to note that model extrapolation increases in regions where climate suitability is projected to decrease, indicating that these results should be interpreted cautiously. On a global scale, there is an anticipated increase in climate suitability in the southwest of Australia and New Zealand.

The risk associated with the spread of *L. delicatula* in Europe encompasses both environmental and economic dimensions, as framed by the hazard-exposure-vulnerability model widely used in risk analysis (Field et al. 2015). The hazard, characterized by the probability of introduction and establishment, is deemed high due to substantial trade connections between Europe and regions where the insect is native or has invaded (Huron et al. 2022). Should L*. delicatula* be introduced, favourable climatic conditions and abundant host plants would likely facilitate its widespread dispersal across Europe, aided either by human transport or natural means. The exposure component of the risk is significant given the diverse range of plant species that could potentially be impacted, many of which hold considerable agricultural (e.g., *Vitis*, *Prunus*, *Malus*, *Juglans*) or forestry (e.g., *Populus*, *Acer*, *Fraxinus*) value. Previous research indicates that *L. delicatula* can complete its lifecycle on multiple hosts beyond *A. altissima*, including *Acer saccharinum*, *Salix babylonica*, *Humulus lupulus*, *Juglans* species, *Liriodendron tulipifera*, *Melia azedarach*, and *Quercus acutissima* (Uyi et al. 2020, 2021; Murman et al. 2020). A recent study by Huron et al. (2022) underscored the potential for global disruption in the wine market if *L. delicatula* were to establish in viticultural regions. Finally, the vulnerability term of the risk encompasses the propensity to be adversely affected and the lack of capacity to cope and adapt. Preparedness measures are crucial, including rapid response capabilities, expert workforce readiness, and informed public awareness aligned with current and projected climate conditions (Ricciardi et al. 2021). Strengthening pest surveillance programs and enhancing international information exchange are also pivotal (Giovani et al. 2020) regarding vulnerability.

While climate suitability maps and host analyses indicate widespread threat across Europe, they provide no clues toward the spatio-temporal dynamics of a potential invasion. For that, population dynamics models (Smyers et al. 2021; Lewkiewicz et al. 2022) or phenology models (Maino et al. 2023, Barker et al. 2023) could be developed. Early warning systems could benefit from targeted monitoring of *A. altissima* and other potential sentinel plants, as recommended by the European Food Safety Authority (EFSA et al. 2023). Promoting preemptive biocontrol programs, i.e. biocontrol developed prior to the arrival of invasive pests, has proven effective and could mitigate European vulnerability to *L. delicatula* (Avila et al. 2023; Gómez Marco et al. 2023). Implementing such strategies is important to protect European biodiversity and agricultural sectors from the potential impacts of this invasive insect.

CONCLUSION

Neither the climate conditions nor the presence of compatible host plants constitutes an obstacle to the establishment of *L. delicatula* in Europe. Climate assessments under different scenarios suggest that conditions will remain favorable for *L. delicatula* in the coming decades across much of Europe.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Host plant datasets are available from the supplementary files associated with this article. *L. delicatula* occurrence datasets are available from the gbif database, the R package “LydemapR” and the supplementary files associated with the article. Model projections, the corresponding committee averaging and the MESS index for current and future climate conditions are available from the repository: https://doi.org/10.57745/U1YKUR.

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FIGURES

Fig. 1 Potential geographical distribution of *Lycorma delicatula* in Europe under current climate conditions (2001-2018). A. Climate suitability according to the random forest model (RF), B. Climate suitability according to the boosted regression trees model (BRT), C. Climate suitability according to the Bayesian additive regression trees model (BART), D. Committee averaging F. Multivariate environmental similarity surfaces (MESS) comparing current climate conditions in Europe to reference points used for model calibration. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).

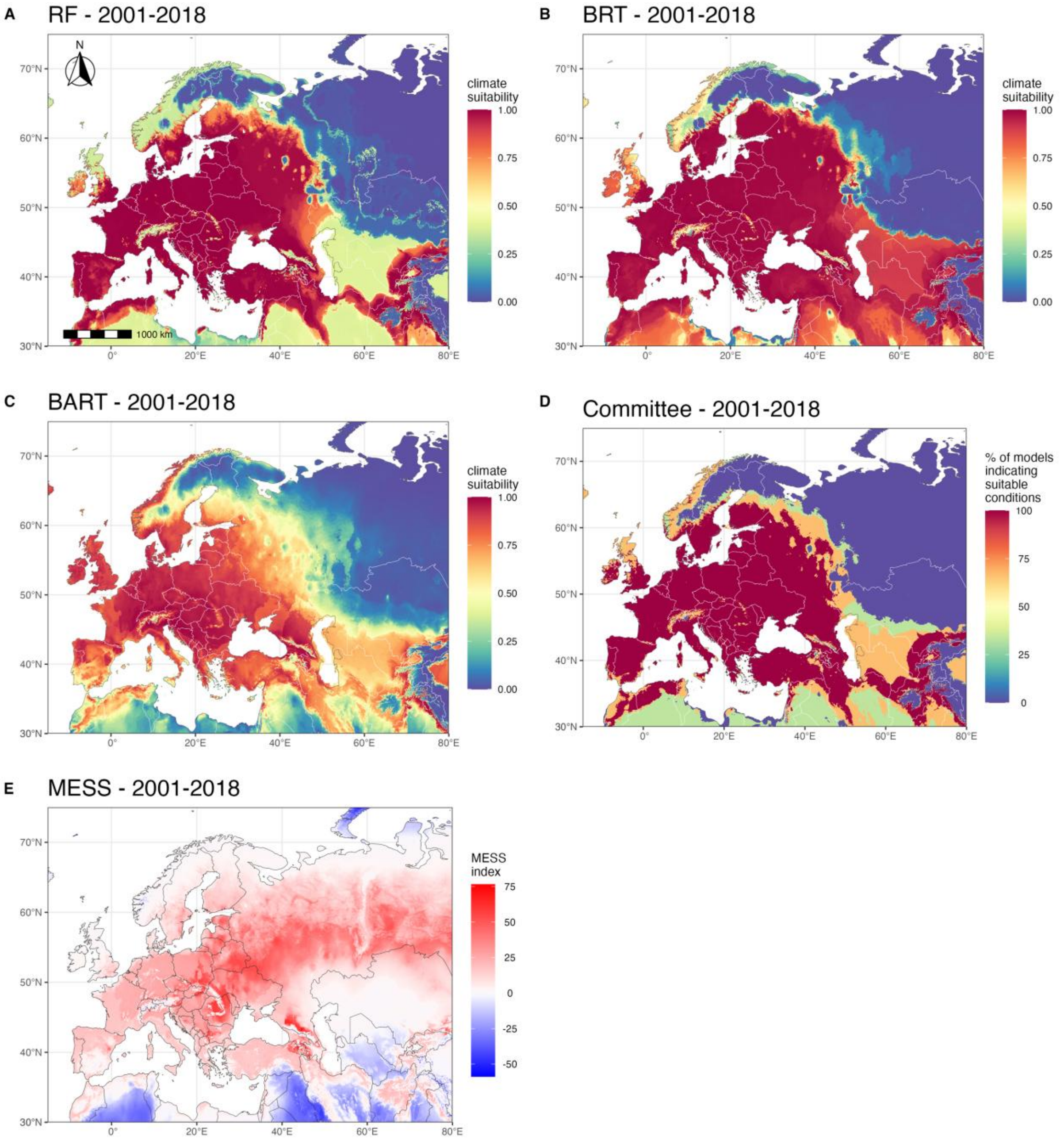


Fig. 2 Climate suitability and MESS index for the period 2041-2060. A. Climate suitability for SSP1-2.6, B. MESS index for SSP1-2.6, C. Climate suitability for SSP2-4.5, D. MESS index for SSP2-4.5, E. Climate suitability for SSP3-7.0, F. MESS index for SSP3-7.0, G. Climate suitability for SSP5-8.5, H. MESS index for SSP5-8.5. For a given SSP, the climate suitability map depicts the committee averaging of values obtained for 3 model algorithms and 6 global circulation models (see text for details).

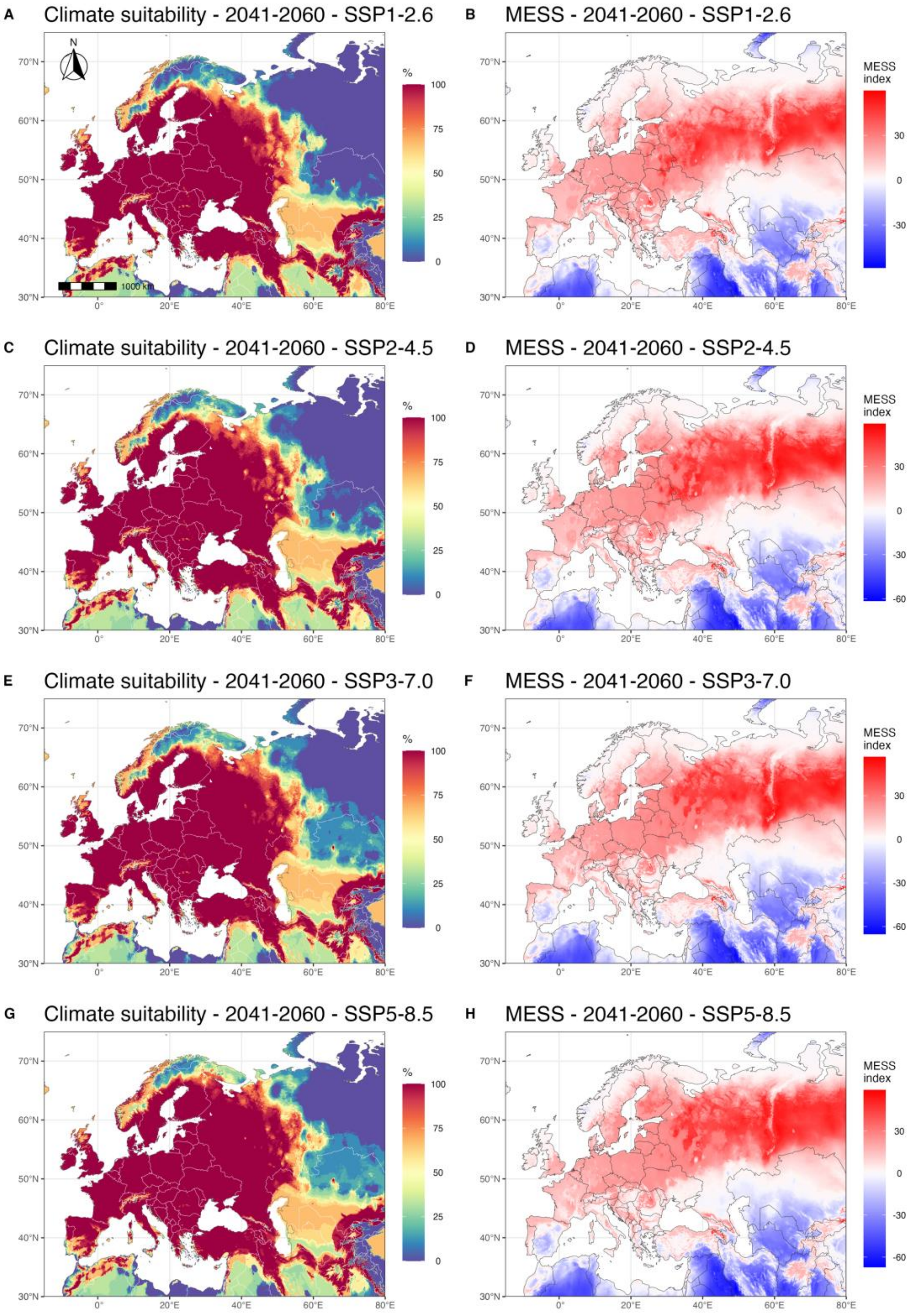
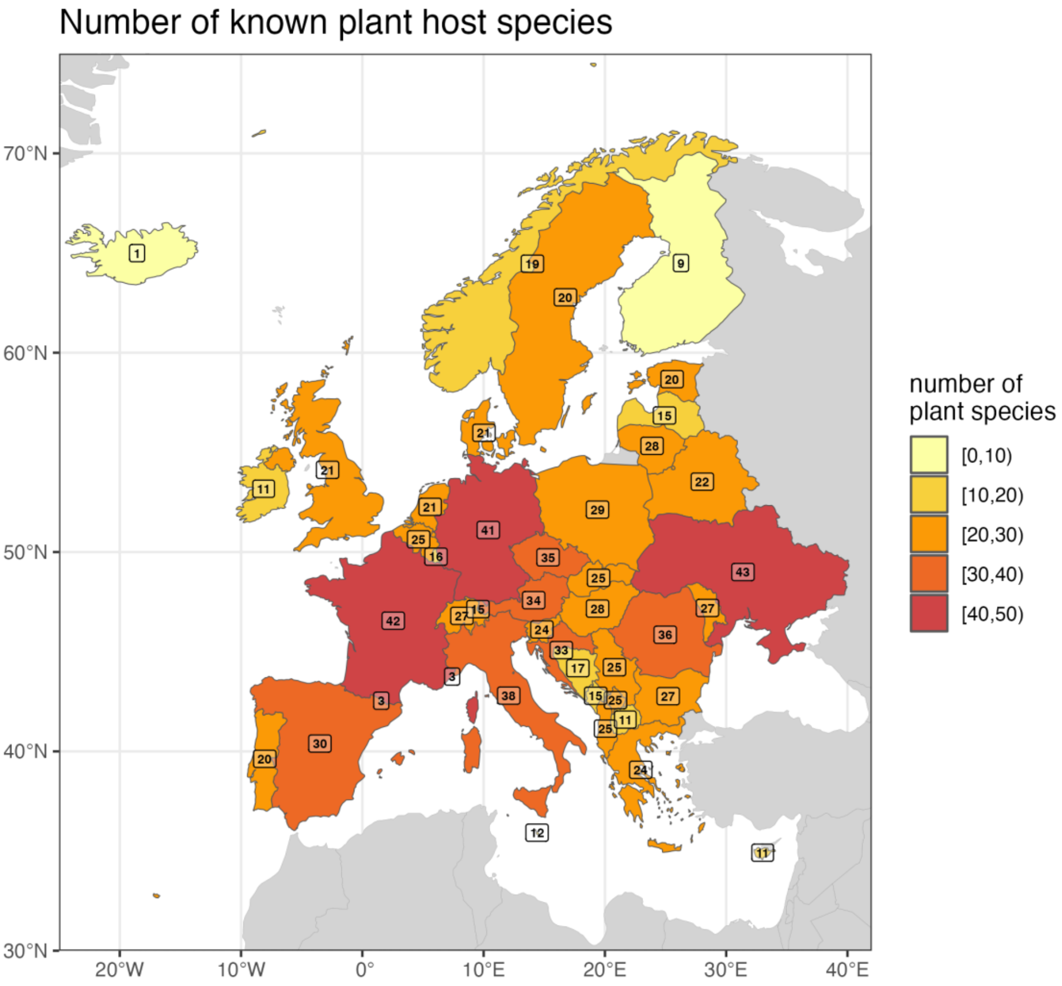


Fig. 3 Number of host plants in European countries where climate conditions are suitable for *Lycorma delicatula.*



SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix 1: References for occurrences of *Lycorma delicatula*.

Appendix 2: Occurrences of *Lycorma delicatula* collected from the literature. Status indicates if the occurrence is valid. References are given in Appendix 1.

Appendix 3: Maps of the occurrence points and areas where pseudo-absence points were randomly generated for the species distribution modelling of the *Lycorma delicatula*.

Appendix 4: References for host plants of *Lycorma delicatula*.

Appendix 5: List of host plants of *Lycorma delicatula*. References are given in Appendix 4.

Appendix 6: Reclassified maps of the climate suitability for *Lycorma delicatula* according to 3 algorithms. A Random forests (RF) B. Boosted regression trees (BRT) C. Bayesian additive regression trees (BART). The climate conditions represent the period 2001-2018.

Appendix 7. List of feeding host species and the country of observation.

Appendix 8. Venn diagram showing the number of feeding host plants of *Lycorma delicatula* by country. Shape overlaps contain the number of species shared by countries. All countries: N=104 feeding species.

Appendix 9. Number of known feeding hosts and non-feeding plant species present in European countries. Feeding host species include all plant species on which *L. delicatula* feeding events have been explicitly reported in the literature. Non-feeding species include plant species on which *L. delicatula* has been observed but on which no explicit feeding event was reported (e.g. resting, egg laying).

Appendix 10. Potential geographical distribution of *Lycorma delicatula* under current climate conditions (2001-2018). The map depicts the committee averaging of values obtained for three algorithms (see text for details).

Appendix 11. Multivariate environmental similarity surfaces (MESS) comparing current climate conditions (2001-2018) for the world to reference points used for model calibration. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).

Appendix 12. Potential geographical distribution of *Lycorma delicatula* under future climate conditions (2041-2060, SSP1-2.6). The map depicts the committee averaging of values obtained by projecting the data of 6 GCM using 3 species distribution models (see text for details).

Appendix 13. Multivariate environmental similarity surfaces (MESS) comparing future climate conditions (2041-2060, SSP1-2.6) for the world to reference points used for model calibration. At each pixel, the map shows the lower value of the index computed for the projections of 3 models according to the climate conditions associated with 6 GCM. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).

Appendix 14. Potential geographical distribution of *Lycorma delicatula* under future climate conditions (2041-2060, SSP2-4.5). The map depicts the committee averaging of values obtained by projecting the data of 6 GCM using 3 species distribution models (see text for details).

Appendix 15. Multivariate environmental similarity surfaces (MESS) comparing future climate conditions (2041-2060, SSP2-4.5) for the world to reference points used for model calibration. At each pixel, the map shows the lower value of the index computed for the projections of 3 models according to the climate conditions associated with 6 GCM. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).

Appendix 16. Potential geographical distribution of *Lycorma delicatula* under future climate conditions (2041-2060, SSP3-7.0). The map depicts the committee averaging of values obtained by projecting the data of 6 GCM using 3 species distribution models (see text for details).

Appendix 17. Multivariate environmental similarity surfaces (MESS) comparing future climate conditions (2041-2060, SSP3-7.0) for the world to reference points used for model calibration. At each pixel, the map shows the lower value of the index computed for the projections of 3 models according to the climate conditions associated with 6 GCM. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).

Appendix 18. Potential geographical distribution of *Lycorma delicatula* under future climate conditions (2041-2060, SSP5-8.5). The map depicts the committee averaging of values obtained by projecting the data of 6 GCM using 3 species distribution models (see text for details).

Appendix 19. Multivariate environmental similarity surfaces (MESS) comparing future climate conditions (2041-2060, SSP5-8.5) for the world to reference points used for model calibration. At each pixel, the map shows the lower value of the index computed for the projections of 3 models according to the climate conditions associated with 6 GCM. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values).