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The ongoing range expansion of the invasive oak lace bug across Europe: current occurrence and potential distribution under climate change

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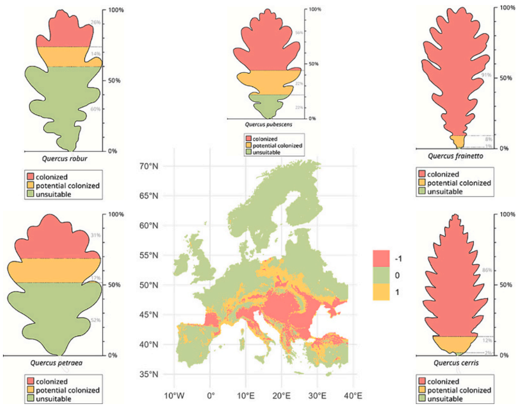
HIGHLIGHTS

- Oak lace bug occurrence data compiled from 21 countries.
- Realized niche and potential distribution was projected using an SDM ensemble model.
- The invasive species has not yet colonized all suitable areas.
- By 2100, >80 % of oak species distributions could be colonized.

GRAPHICAL ABSTRACT



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ABSTRACT

In recent years, the oak lace bug, *Corythucha arcuata*, has emerged as a significant threat to European oak forests. This species, native to North America, has in the last two decades rapidly extended its range in Europe, raising concerns about its potential impact on the continent's invaluable oak populations. To address this growing concern, we conducted an extensive study to assess the distribution, colonization patterns, and potential ecological niche of the oak lace bug in Europe.

We gathered 1792 unique presence coordinates from 21 Eurasian countries, utilizing diverse sources such as research observations, citizen science initiatives, GBIF database, and social media reports. To delineate the realized niche and future distribution, we employed an ensemble species distribution modelling (SDM) framework. Two future greenhouse gas scenarios (RCP 4.5 and RCP 8.5) were considered across three-time intervals (2021–2040, 2061–2080, and 2081–2100) to project and evaluate the species' potential distribution in the future.

Our analysis revealed that significant hotspots rich in host species occurrence for this invasive insect remain uninvaded so far, even within its suitable habitat. Furthermore, the native ranges of Turkey oak (*Quercus cerris* L.) and Hungarian oak (*Quercus frainetto* L.) species offer entirely suitable environments for the oak lace bug. In contrast, the pedunculate oak and sessile oak distribution ranges currently show only 40 % and 50 % suitability for colonization, respectively. However, our predictive models indicate a significant transformation in the habitat suitability of the oak lace bug, with suitability for these two oak species increasing by up to 90 %. This shift underlines an evolving landscape where the oak lace bug may exploit more of its available habitats than initially expected. It emphasises the pressing need for proactive measures to manage and stop its expanding presence, which may lead to a harmful impact on the oak population across the European landscape.

1. Introduction

In a European forest landscape, which is already experiencing severe and increasing disturbance regimes (Senf and Seidl, 2021a; Patacca et al., 2023), the populations of well-established pests have undergone significant upsurge over the past century (Santini et al., 2013). Bark beetle outbreaks in European forests have brought devastating consequences, leading to the loss of a staggering 30 million cubic metres of timber in 2017 alone (Hlásny et al., 2021). The expectation is that European native herbivorous insects will contribute to future outbreaks of increased severity. This is primarily due to climate change-induced alterations in flight and dispersal limits as well as changes in development and reproductive dynamics, diapause, and mortality (Netherer and Schopf, 2010).

Although oak species are generally considered to be resilient to disturbances related to climate change (Pretzsch et al., 2013; Ciceu et al., 2020), intensified drought episodes (Diffenbaugh et al., 2017) have led to increased outbreak intensities caused by widespread defoliators, such as spongy moth (*Lymantria dispar* L. (Lepidoptera: Erebidae)), and secondary insects, resulting in more pronounced damage to oak populations (Haavik et al., 2015). Furthermore, the global trade and unintended transfer of forest pests and diseases corroborated with a decline in forest ecosystem stability (Senf and Seidl, 2021b) has increased the risk posed by biological invasions worldwide. This heightened risk could potentially lead to significant negative consequences for native ecosystems and major ecosystem services (Seidl et al., 2018). Currently, Europe witnesses the identification of approximately 20 new alien insect species annually, a rate that is roughly double of what was observed four decades ago (Roques, 2010) and the accumulation curve is still increasing (Seebens et al., 2017; Pyšek et al., 2020). Recent studies have shown that the global costs of damage related to biological invasions rival those caused by natural hazards such as earthquakes or floods. Furthermore, the rate of increase in biological damage costs exceeds that of natural hazard damage costs (Turbelin et al., 2023).

In recent years, a particular species has shown the potential to exacerbate harm to oak forests health. The swift expansion of *Corythucha arcuata* (Say, 1832) (Hemiptera: Tingidae), commonly referred to as the oak lace bug (OLB), across Europe, has raised significant concerns (Bălăcenoiu et al., 2021a). Since its first detection in Italy in 2000 (Bernardinelli and Zandigiacomo, 2000), OLB has displayed invasive behaviour by rapidly colonizing new territories. Csóka et al. (2019)

reported that the OLB rapidly colonized the South Eastern part of Europe, and recent studies reported its presence in Portugal (Gil and Grosso-Silva, 2021), Spain (Riba-Flinch, 2022) and Germany (Zimmermann et al. in prep.), thus indicating that the expansion is still in progress. The OLB is an insect of North American origin with its natural range spreading across the southern part of Canada and several states in the eastern United States (Connell and Beacher, 1947; Drake and Ruhoff, 1965). According to studies conducted in the Nearctic region of North America (Connell and Beacher, 1947; Drake and Ruhoff, 1965), it develops on white oaks. However, in Europe, the OLB exhibits a broader host spectrum beyond white oaks, with various species identified as potential hosts (Csóka et al., 2019).

The impact of this species can be assessed by the feeding damage caused by both adults and nymphs. This damage is typically visible on the upper side of leaves where is characterized by yellowish spots (chlorotic discoloration), and the causality of OLB is ascertained by the presence of black spots on the underneath (Bernardinelli, 2006; Mutun et al., 2009). While the exact implications on growth remain unknown, the cumulative impact of this species' damage, combined with existing stressors, could potentially lead to decreased growth rates, reduced seed production, or even increased mortality rates in oak forests.

Several studies have provided insights into the occurrences and distribution of the invasive species at the national level (Mutun et al., 2009; Dobreva et al., 2013; Neimorovets et al., 2017; Tomescu et al., 2018; de Groot et al., 2022; Balacenoiu et al., 2024). Recent studies carried out in Slovenia and Austria showed that low altitude, high oak density, and proximity to highways and railways were the most explanatory factors of the distribution of the oak lace bug on a small scale (de Groot et al., 2022; Hoch et al., 2022). However, there exists a conspicuous research gap regarding the species' distribution at the macroecological level. In an effort to fill this gap, our study employs a species distribution modelling framework to offer a comprehensive overview of potentially suitable areas for the invasive species under current and future climate change scenarios. While acknowledging its limitations, such as a lack of functional understanding, the application of species distribution models (SDMs) for these purposes has been well-documented (Robinson et al., 2010; Sung et al., 2018; Rodríguez-Rey et al., 2019; Di Sora et al., 2023), demonstrating its reliability as a method for exploring a species' potential niche.

The potential niche is defined as the segment of the fundamental niche space that could be accessible to the species across the studied area (Hutchinson, 1957; Jackson and Overpeck, 2000). However, as the oak lace bug is still in the establishment and dispersal phases, covering the entire suitable range based on current occurrences allows us to establish only the realized niche. Although in many studies the realized niche and realized distribution are used interchangeably we separate them in this study. We define the realized niche as the environmental space where the species could exist due to its similarity to the areas already occupied, while the realized distribution indicates the specific areas where the species has already been observed.

In this study, we aim to develop two sets of models—one delineating the current realized niche and another predicting the potential distribution of the invasive species. We employ a two-step approach to correct dispersal-limited absences and identify environmentally unsuitable conditions for predicting the potential distribution (Engler et al., 2004; Mainali et al., 2015; Hattab et al., 2017). To achieve this, we utilize a comprehensive dataset of species occurrences and implement a multi-model ensemble species distribution modelling framework. We examined the link between the invasive species and the main host by incorporating them into the model, anticipating that this relationship will have a significant impact on the species' future colonization pathways and speed. Furthermore, our last objective is to explore the potential spread of the invasive species under future climate change scenarios.

2. Methods

2.1. Area description

European forests are home to a diverse array of oak species with distinct traits. These oaks inhabit various ecosystems from semi-arid Mediterranean shrublands covered by holm oak (*Quercus ilex* L.), Kermes oak (*Q. coccifera* L.), Pyrenean oak (*Q. pyrenaica* Willd.), or cork oak (*Q. suber* L.) to cool temperate and transitional boreal forests adorned with pedunculate oak (*Q. robur* L.), and sessile oak (*Q. petraea* (Matt.) Liebl.).

Since its initial occurrence in Europe, OLB has primarily been observed on oak species, displaying a clear preference for them; however, multiple deciduous species have been reported as secondary host species (refer to Fig. 1b for the spatial distribution of host density for the oak lace bug).

Although its colonization extends to Asia, our study predominantly focuses on the European continent, even though presence data has been collected beyond its boundaries.

2.2. OLB presence data

Presence data for OLB was obtained using a multi-step approach involving international databases and expert inputs. The first step involved downloading data from the Global Biodiversity Information Facility (GBIF) on March 13, 2023, using the species name as a search parameter. The downloaded data was then processed using the CoordinateCleaner package (Zizka et al., 2019) in the statistical program R (R Core Team, 2022), to remove duplicates, occurrences within a 1 km radius of capital cities (considered biased occurrences), coordinates that matched country centroids, locations associated with institutions, and coordinates with identical absolute values. Records with low coordinate precision (< 1 km) were also removed.

Subsequently, specialists from each country were asked to assess the remaining coordinates for their validity using their expert judgement and knowledge of the species' presence in their respective countries. Only 40 occurrences from the GBIF dataset remained unvalidated by the experts. The subsequent analysis was exclusively conducted with occurrences that had been validated.

In addition to GBIF, presence data collected directly by experts from survey plots and research projects, and provided by national experts and research institutions, were compiled. The two datasets were then merged, resulting in the collection of presence covering a broad range of geographic locations and environmental conditions (Fig. 1a). To ensure comprehensive coverage, all countries that reported the presence of the species on the European and Mediterranean Plant Protection Organization platform were contacted.

Ultimately, 21 Eurasian countries contributed to the database, resulting in 1792 unique presence coordinates. However, multiple sample points were revisited over several years or each host species was registered separately, contributing to a combined observation count of 2626 within the dataset. This comprehensive approach not only encompasses the spatial distribution of the species, but also captures its temporal variation since its outburst 2001 to 2023.

Most of the data providers contributed data from their research projects or literature reported in their countries, classified under the label "Research obs." These occurrences were collected by experts and hold the highest confidence level. Additionally, one country that conducted a citizen science projects provided citizen science data (classified under the label "Citizen science.") (de Groot et al., 2024), which were also the subject of a validation protocol. A very few contributors provided data reported in national open science databases as social media. We ensured that there is no redundancy between the data extracted from GBIF and the data from other Citizen Science sources. We eliminated all GBIF records that were identical to citizen science data provided by experts. It's important to note that we exclusively collected presence

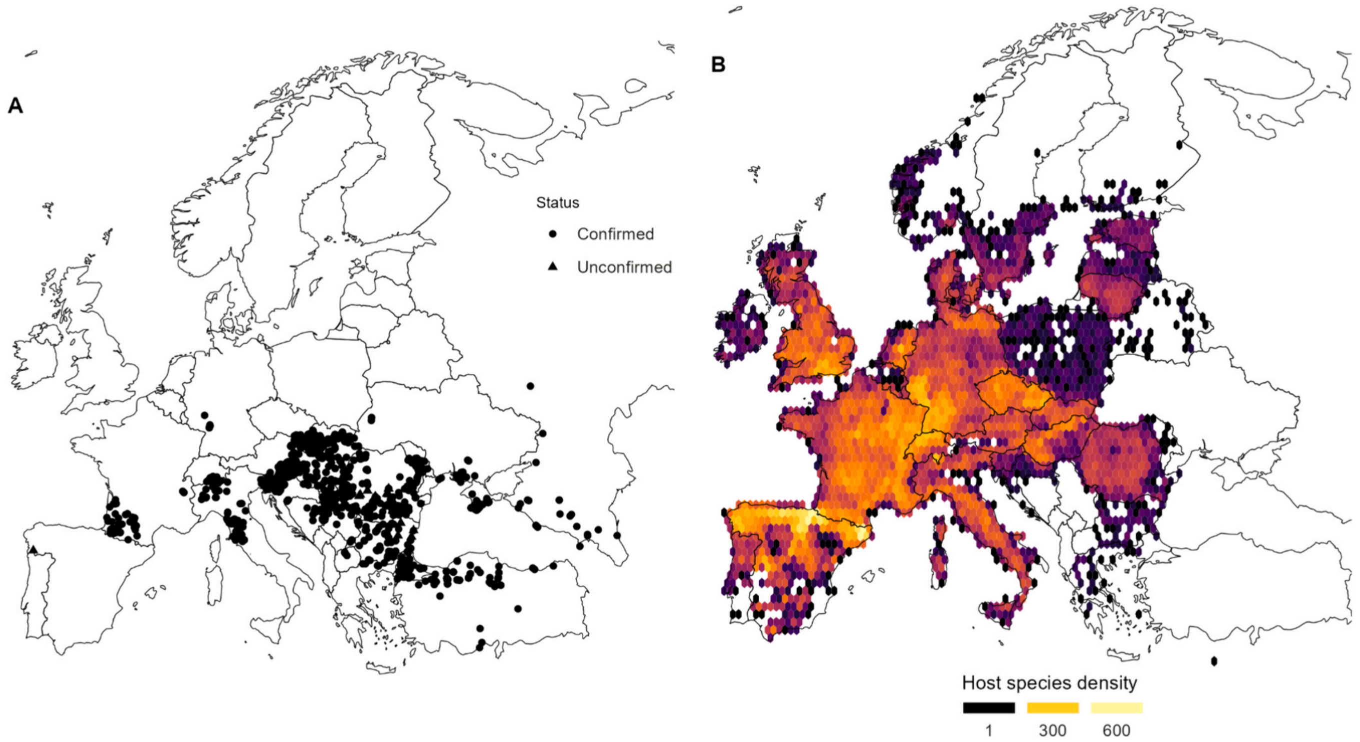

Fig. 1. OLB presence records (a) and the heatmap of the number of host species (b) The host species heatmap is derived from tree species presence records within a European collection of national forest inventory data (Mauri et al., 2017), with each hexagon representing the count of distinct locations where at least one host species, as documented in various studies (Bernardinelli, 2006; Csóka et al., 2019), was identified within that particular hexagonal area.

data.

The full dataset is available in Annex 1 of this article, and details regarding column explanations can be found in Annex 2, Table S3, within the data section.

2.3. Climate

The modelling framework used in this study relied on climate data sourced from the European Climate Index Projections (ECLIPS 2.0) (Chakraborty et al., 2021a, 2021b). This dataset contains gridded data for 82 climate variables, including annual, seasonal, and monthly variables, for two past time frames and five future time frames (the list of variables tested can be found in Annex 2 Table S2). The future data were generated using five RCMs driven by two greenhouse gas concentration scenarios, RCP 4.5 and RCP 8.5. The ECLIPS 2.0 dataset has a high spatial resolution of 30 arcsec, equivalent to approximately 1 km^2. A list with the full description of the climate data used and the five RCM can be found in Annex 2 (Table S1 and Table S2).

To project the current and future potential distribution of the OLB, climatic variables associated with specific time frames were used. The climate data for the time frame of 1991–2010 was used to project the current potential distribution, while the climate data for the time frames of 2021–2040, 2061–2080, and 2081–2100 were used to project the future potential distribution of the species. The climatic dataset utilized covers the period from 2000 to 2100, divided into 20-years climatic average periods. However, the host species projections are structured in 30-year intervals for the same duration. This misalignment resulted in the exclusion of the climate projection for the 2041–2060 time frame as it did not align with the species projection.

2.4. Host species suitability as additional predictors

We considered the OLB dependency on its host by including a selection of oak species that play a significant role in driving its expansion and distribution. We achieved this by utilizing a database that covers both present and projected distributions of tree species across Europe (Mauri et al., 2022). Within this database, we deliberately selected five oak species that proved to be the most frequently attacked oak species in the introduced range of the OLB: Turkey oak (*Q. cerris* L.), Hungarian oak (*Q. frainetto* L.), pedunculate oak (*Q. robur* L.), sessile oak (*Q. petraea* (Matt.) Liebl.) and downy oak (*Q. pubescens* (Willd.)) in which OLB outbreak populations are most commonly found (Csóka et al., 2019). The distributions of these species show significant overlap with those of the majority of other oak species such that this choice is unlikely to have biased our understanding of the current distribution of the OLB. The host species projections encompass two distinct emission scenarios (RCP 4.5 and RCP 8.5) and span various timeframes, including the current conditions centred around 2005, as well as future projections centred around 2035, 2065, and 2095. This suitability was assessed at a scale that spans from 0 (unsuitable) to 1000 (highly suitable). The initial projections were adjusted to exclude regions where future climatic conditions were considered improbable using a multivariate environmental approach (Mauri et al., 2022). To ensure consistency in the format of explanatory variables, these areas were filled with a suitability value of 0 in our analysis.

Based on the individual projections of the suitability for the five oak species, we generated a layer corresponding to the maximum suitability of these species for each location in Europe. This layer was then utilized as an additional predictor alongside the climatic predictors.

The spatial resolution of the distribution data was transformed from 5 arc-minutes (~10 km) to that of the climate data.

2.5. Pseudo-absence selection

OLB is a relatively recent arrival in Europe and its distribution has not yet attained a state of equilibrium with the environment. As we exclusively gathered presence data, we employed two distinct approaches to generate pseudo-absence instances that aligned with our objectives. Our primary goal was twofold: i. to delineate the current realized niche of the species and ii. to outline its potential distribution.

The initial pseudo-absence approach involved randomly selecting pseudo-absences. We initiated the process by establishing a 50 km buffer around each confirmed presence point. This step aids in correcting for undetected presence data, reducing the likelihood of erroneously assigning false absence data points. Subsequently, we conducted randomised sampling across Europe outside the 50 km buffer. This approach allowed us to define the current realized niche, projecting the species' suitability on a scale from 0 (unsuitable) to 1000 (highly suitable). For delineating the potential distribution, we adopted a strategy similar to that of Engler et al. (2004). We first pinpointed areas with the lowest suitability values (〈100) as projected by the realized niche, as these locations showcased the most substantial environmental contrast between presence data and the environmental space. Subsequently, in order to sample from different environmental profiles these coordinates were organized into 12 distinct clusters similar to Senay et al. (2013). The number of clusters was determined based on the "elbow" of the total within-cluster sum of squares and the number of clusters plot. Each of these clusters was then randomly sampled to match the total count of true presence data, generating pseudo-absences.

2.6. Feature selection

Since our features dataset encompassed 83 variables (82 climatic variables +1 hosts species maximum suitability map), our initial step involved reducing the dimensionality of these features. To achieve this, we employed a two-step "embedded" covariate selection procedure utilizing the *covsel* R package (Adde et al., 2023). In the first phase of this procedure, the algorithm reduced the dimensionality of potential features by excluding the less informative ones from collinear pairs. This was accomplished by excluding collinear feature pairs that exhibited a Pearson correlation coefficient greater than the $|0.7|$ (Brun et al., 2020). In the second step, the features that passed the filtering process were used to train models using the generalized linear model, generalized additive model, and random forest, all of which include embedded selection procedures. These procedures incorporate techniques for feature selection directly into the algorithm's framework. This means that the process of feature selection is seamlessly integrated into the model construction, rather than being a separate preprocessing stage. The final feature selection is determined by how frequently each feature was chosen by each respective algorithm.

The algorithm was iterated 10 times to accommodate the randomness in pseudo-absences for both the realized niche and potential distribution models. The most important feature dataset was identified for both models, and the chosen number of features was calculated as the mean number of features selected in each run, with the selected features being the most frequently occurring ones.

2.7. Ensemble model

We applied a well-established ensemble species distribution modelling platform, BIOMOD2, to delineate both the realized niche and potential distribution. Operating within this framework, we harnessed six distinct modelling algorithms: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Generalized Boosting Models (GBM), Multiple Adaptive Regression Splines (MARS), Classification Tree Analysis (CTA), and Random Forest (RF). These algorithms are extensively utilized (Chakraborty et al., 2021a, 2021b; Bonannella et al., 2022; Mauri et al., 2022) for such purposes and encompass various fitting procedures, ranging from regression to decision trees. Due to the divergence in sampling strategies and data sources, a thinning process became necessary. Notably, citizen science data exhibited higher densities, especially along transportation routes, while research observations displayed lower densities and random spatial coverage. To address this disparity, we introduced a tile-based thinning approach with a 5 km resolution. Consequently, each 5 km tile retained solely one presence or absence point.

To validate the models, we employed a cross-validation selection strategy with 10 repetitions. Each cross-validation dataset was randomly split into 80 % training and 20 % validation observations. The Receiver Operating Characteristic curve (ROC), Area Under the Curve (AUC), and True Skill Statistic (TSS) were employed to assess the performance of the models.

Finally, based on predictions from each algorithm, a consensus model was computed by taking the median of probabilities from the selected individual models. Only models with a TSS higher than 0.7 were considered.

Probabilistic ensemble forecasts were then converted into binary maps (presence-absence) using the true skill statistic (TSS). Subsequently, the potential distribution models, previously calibrated for present conditions, were projected into the future, utilizing two emission scenarios (RCP 4.5 and RCP 8.5) across three distinct time intervals: 2021–2060, 2061–2080, and 2081–2100.

Model uncertainty was assessed using the coefficient of variation (CV) among the individual algorithms. The CV reflects the consensus among the individual algorithm predictions: the grater the CV, the higher the uncertainty. Maps for each timeframe and climate change scenario were employed to visualise model uncertainty.

More detailed information on the ODMAP (Overview, Data, Model, Assessment, Prediction) is provided in Annex 2 (Table S3).

3. Results

3.1. Feature selected

The dimensionality of the potential predictors underwent a substantial reduction after the initial stage of the *covsel* package algorithm, which incorporated a collinearity-filtering procedure. Out of the initial 83 candidate features, only 7 were identified as common covariates by the three distinct model-specific embedded regularization techniques for the realized niche model, and 6 for the potential distribution model. These sets of covariates were subsequently ranked differently by each of the models. Among the top-ranked features identified by both the realized niche and potential distribution models, the variable number of degree days above 5 °C (DDabove5) emerged as the first-ranked variable (Fig. 2). Other variables such as the number of degree days below 0 °C (DDbelow0), continentality (TD), the mean coldest month temperature (MCMT), the summer heat: moisture index (SHM), the average monthly precipitation of the second month (PPT02) and the average monthly precipitation of the sixth month (PPT06) were consistently selected as features. The maximum suitability of the 5 oak species (*Quercus* spp.) was also consistently selected as a predictor thus included in the models.

3.2. Model performance

Among the six algorithms employed for constructing the ensemble models, the random forest algorithm consistently outperformed others in both the realized niche and potential distribution models (Fig. 3). The two-step pseudo-absence selection enhanced the performance of all models. The potential distribution ensemble model exhibited higher accuracy, as indicated by both AUC and TSS accuracy statistics although a lower number of features were selected as important. The TSS values for the calibration dataset in the realized niche model varied among the six algorithms, ranging from 0.778 to 0.993, with a mean value of 0.872. Meanwhile, for the potential niche model, the TSS values ranged from 0.955 to 1, with a mean value of 0.980. On average, based on the TSS, the realized niche model performed 6.4 % worse on the validation dataset than on the calibration dataset. In comparison, the potential distribution model exhibited only a 2.6 % decrease in performance on the validation dataset compared to the calibration dataset.

The coefficient of variation in our predictions displays significant

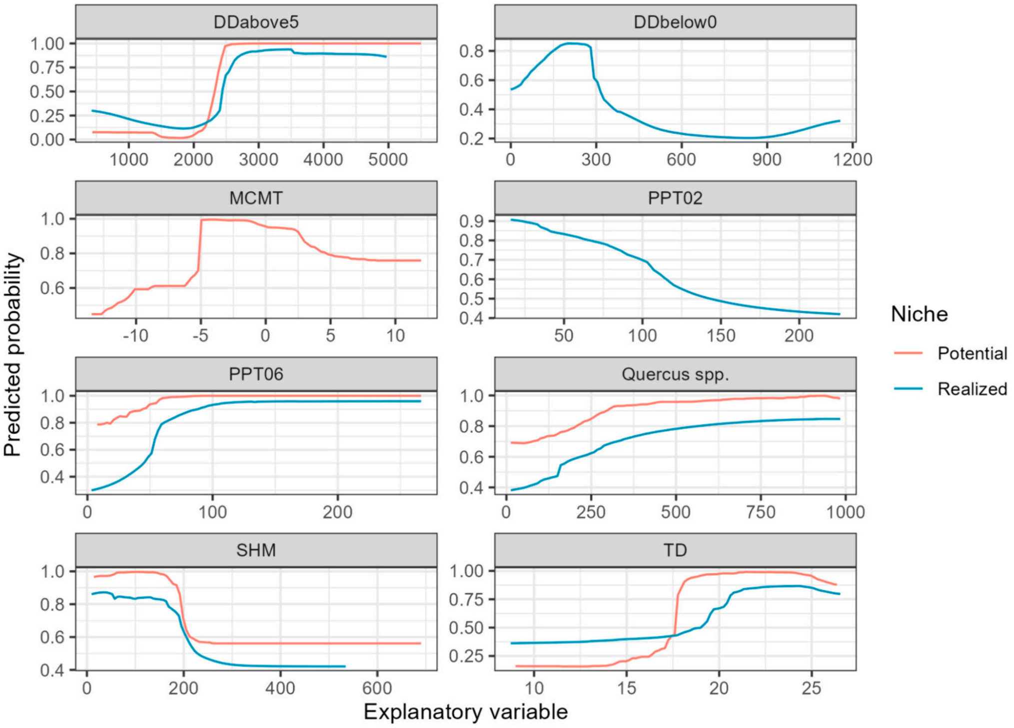

Fig. 2. Response curves of the realized niche and potential distribution models. Where DDabove5 is the number of degree days above 5 °C; DDbelow0 - number of degree days above 0 °C; MCMT - mean coldest month temperature (°C); PPT02 - average monthly precipitation of the second month (mm); PPT06 - the average monthly precipitation of the sixth month (mm); TD - continentality (°C); SHM - the summer heat:moisture index (°C/mm); Quercus spp. - maximum suitability derived from the individual species distribution models of pedunculate, sessile, Turkey, Hungarian and downy oaks (0 - not suitable; 1000 suitable).

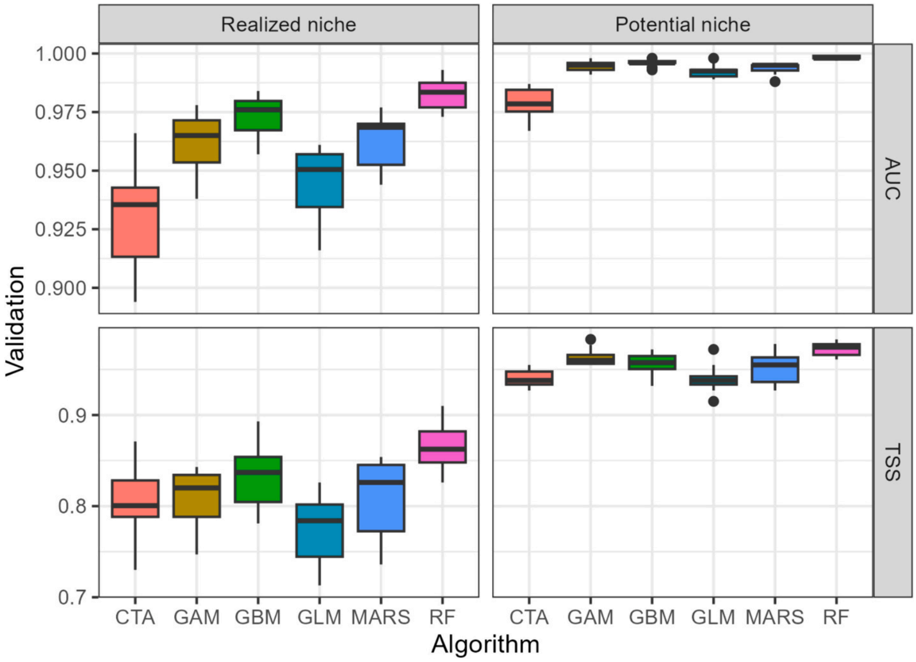

Fig. 3. Individual algorithm performance on the validation dataset.

heterogeneity attributed to the individual algorithms performances. The mean coefficient of variation for the realized niche across the entire study area is 9.9 %, while for the potential distribution, it stands at 10.6 %. Notably, the coefficient of variation values declined to 7.6 % during the 2081–2100 timeframe in the RCP 8.5 scenario. This reduction can be attributed to a larger geographic area becoming more climatically similar to the one associated with the current presence data used in model training, a change driven by climate change. This increased similarity enhances the predictive capabilities of the individual algorithms, particularly in identifying areas where species are likely to be found. Maps depicting the coefficient of variation for each climatic scenario and timeframe are presented in Annex 2 (Fig. S1 and S2).

3.3. Realized niche and potential distribution

The predictions for both realized and potential niches indicate that the invasive species has considerable suitable space for further expansion. (Fig. 4). Presently, it is widely distributed in southeastern Europe. The models suggest that further spread might occur in central and western Europe, particularly in the Iberian Peninsula, France, and Germany. In the northern region, the suitable area is somewhat reduced, mainly due to climatic constraints associated with colder temperatures.

Interestingly, the realized niche covers areas where the presence of the species has not yet been reported.

When overlaying the species prediction onto the natural distribution maps of the five most important oak species serving as OLB hosts in Europe, we observed that the insect had colonized areas ranging from 26 % to 91 %, while the suitable areas could potentially increase by 8 % to 22 %. Although sessile and pedunculate oak were both found to be the most frequent host species, large parts of their distribution ranges are not suitable for OLB at present, due to their extensive distribution in the northern part of the continent. Regarding the two southeastern oak species, namely Turkey and Hungarian oak, their entire natural ranges fall within the realized niche and potential distribution of OLB, something that has already been observed in large parts of their ranges. Finally, only 50 % of the downy oak distribution is suitable for the species according to the current realized niche mostly because its distribution stretches far more to the west than the previously two mentioned species. However, an additional approximately 20 % could be suitable for the areas according to the potential distribution model.

3.4. Future potential distribution

The future potential distribution maps reveal a significant increase in suitability for the OLB in northern Europe as a consequence of climate change. For the scenario RCP4.5, the model suggests that the southern part of the Iberian Peninsula and the island of Great Britain will remain unsuitable for the OLB. However, for the scenario RCP8.5 the model suggests that the species might also colonize the southern parts of the Scandinavian Peninsula and Great Britain (Fig. 5).

When analysing the distribution of the OLB in relation to its main host species, we observed that the distribution areas of Turkey oak and Hungarian oak may already be completely covered by the invasive species (Fig. 6). However, by the end of the century, their areas become climatically less suitable for OLB, and they are expected to become less affected over time. In contrast, the ranges of pedunculate oak and sessile oak could be entirely colonized by the OLB, particularly during the last decades of the century. By the end of this century, the areas with non-suitable climatic conditions occupied with sessile oak are predicted to be <25 % in the case of the RCP4.5 scenario and <15 % in the case of the RCP8.5 scenario.

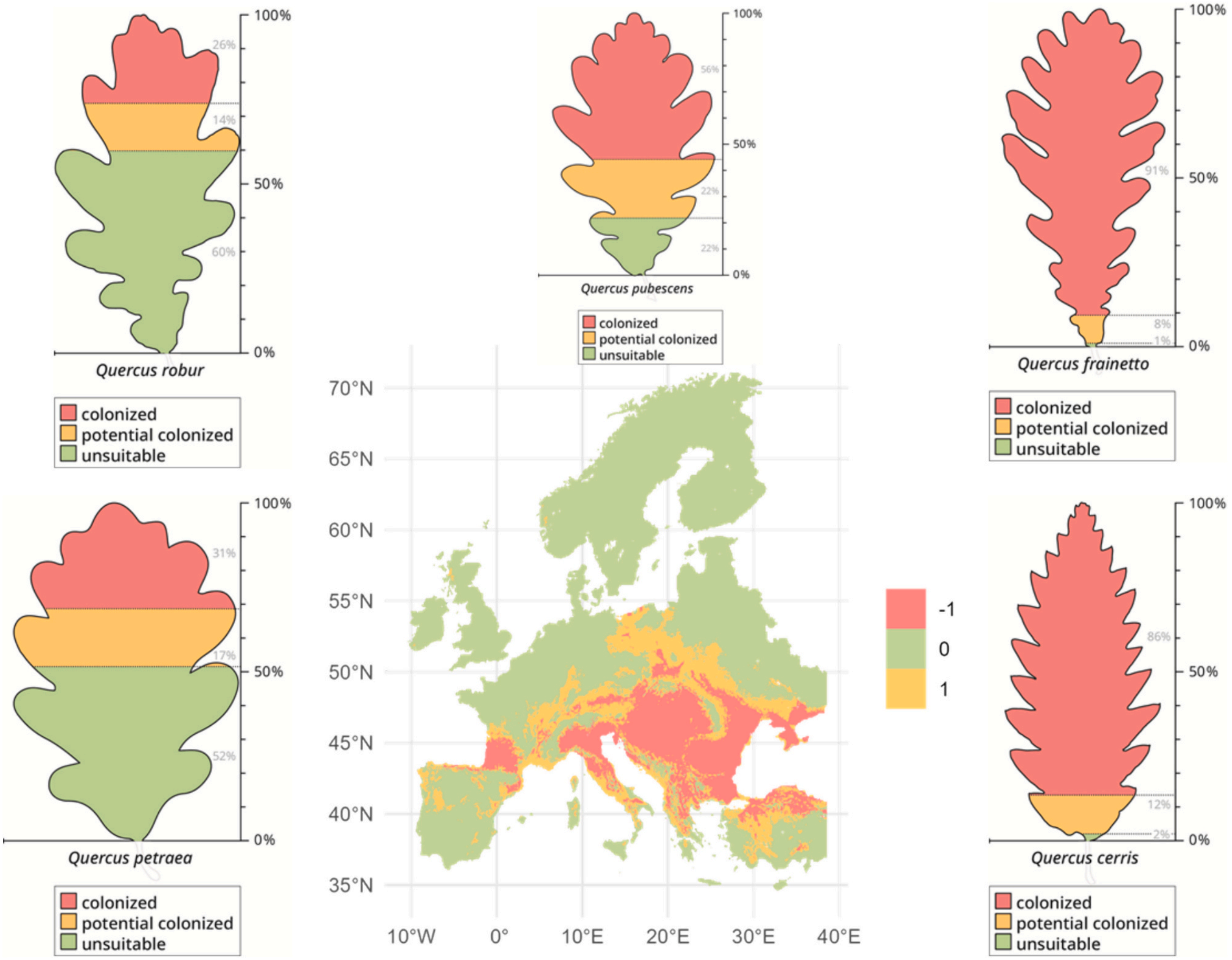

Fig. 4. Current realized niche and potential distributions of OLB as predicted by the ensemble models. The map on the centre displays the realized niche and potential distributions at the European level. On the right and left-hand side, we can see the areas of host species that are predicted to be potentially colonized, colonized, and currently not suitable.

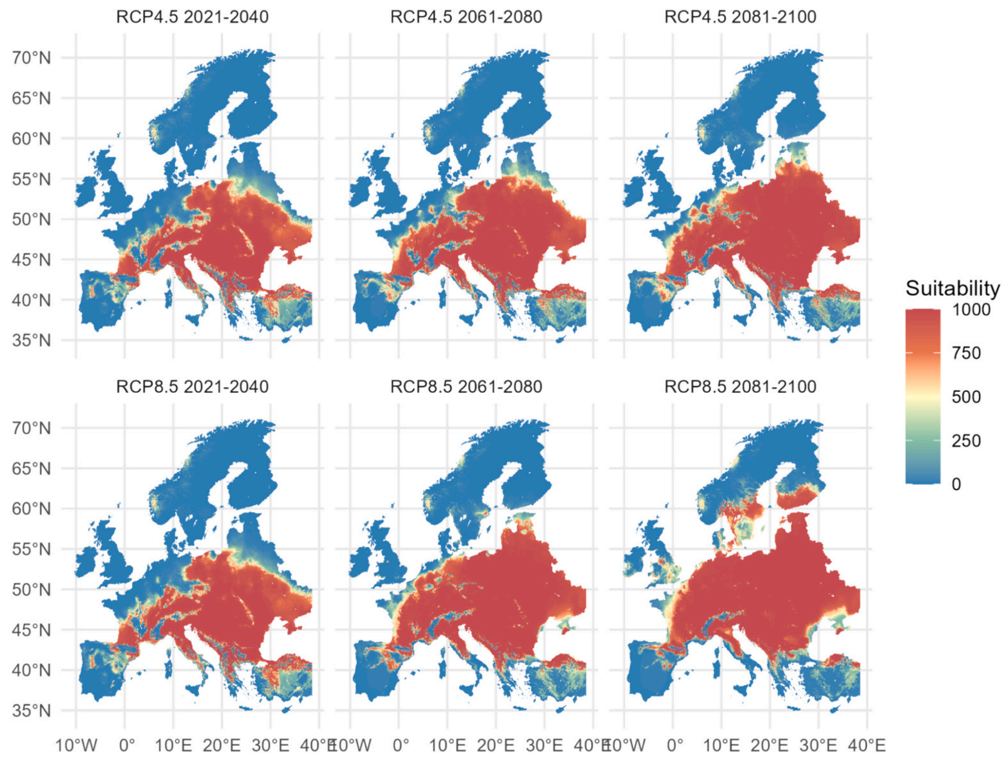

Fig. 5. Suitability maps for OLB under two climate change scenarios and three time steps. The scale represents a habitat suitability gradient from 0 (unsuitable) to 1000 (highly suitable).

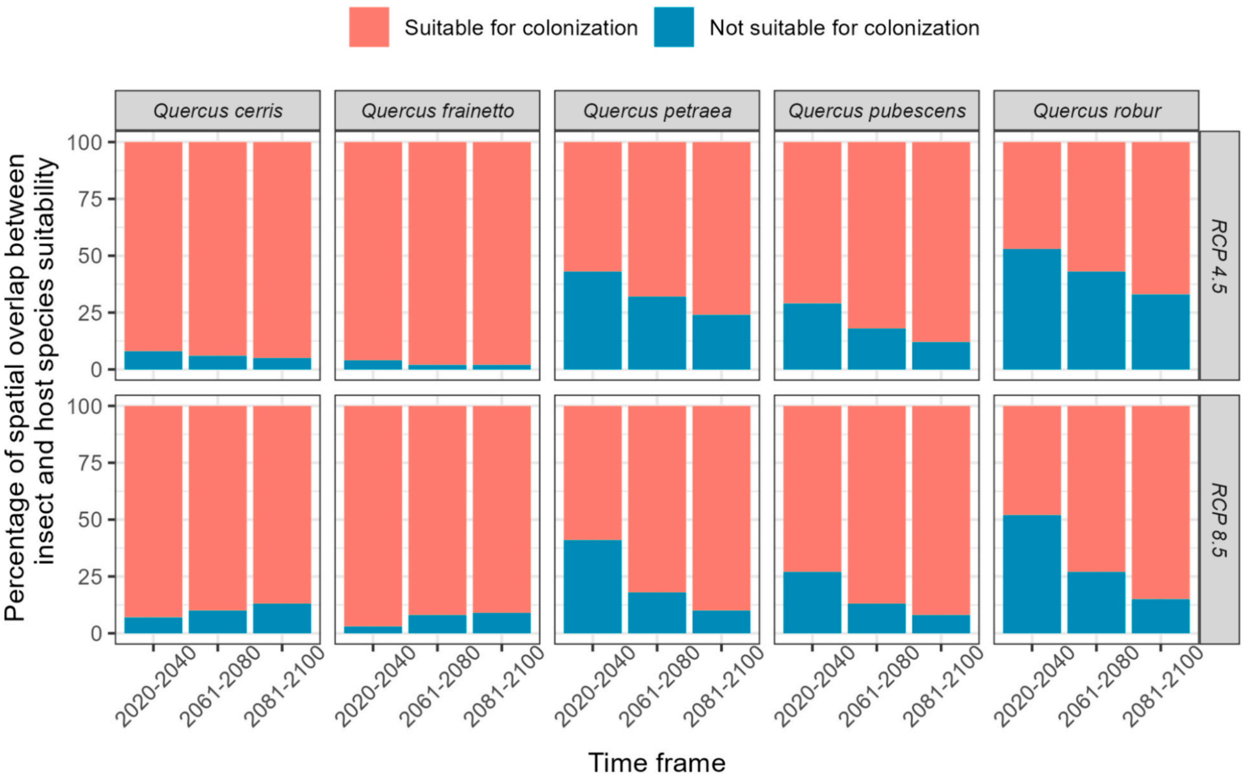

Fig. 6. Extent of spatial overlap between suitability for the insect species and suitability for the host species, expressed as a percentage of the total area under different climate change scenarios and time-frames.

4. Discussion

In this study, using a comprehensive compiled dataset and a species distribution modelling framework, we developed predictive models to estimate both the realized niche and potential distributions of the species. These models were then utilized to project the behaviour of the species into the future. Our study reveals that, under current climate change scenarios, there is still potential for the invasive species to colonize new areas. Furthermore, it highlights that areas rich in host presence have not yet been exploited. Hungarian oak and Turkey oak natural distributions are entirely suitable for the species; however, for the two oak species with a wider distribution, only half of their range is currently suitable for colonization by OLB. Nonetheless, with possible host species migration, the area suitable for colonization is expected to increase by up to 30 % in the RCP 8.5 scenario. Similar to our study, Paulin et al. (2020) estimated that at least 30 million hectares of oak forests could become suitable hosts in Europe in the future.

Incorporating the interaction between host species and their pests into a model predicting potential distribution is crucial for improving accuracy and ensuring that the model mirrors the biological behaviour of the pest. To address this, we calculated a maximum suitability variable based on the potential distribution of five oak species. These oak species collectively cover the entire extent of Europe, overlapping with the distribution of the remaining oak species for which we lacked potential distribution projections. We chose to create a unified genus layer as the OLB currently demonstrates no distinct preference among oak species in its food selection (Csóka et al., 2019).

During the feature selection process, Turkey oak and sessile oak emerged as significant predictors when their individual distributions were introduced as potential predictors. However, their selection as important predictors is primarily attributed to the fact that OLB occurrences in the southeastern part of the continent align perfectly with the entire environmental niche of Turkey oak. Conversely, occurrences in the central and western parts of Europe mainly coincide with the widespread distribution of sessile oak and pedunculate oak. Since sessile oak is less prevalent in the northern part of the continent compared to pedunculated oak, occurrences were primarily associated with sessile oak, indicating a high suitability for the latter. Meanwhile, a larger number of pseudo-absences were linked to pedunculated oak distribution. Therefore, introducing individual species distributions separately in the model posed the risk of biasing the model towards the distribution of a specific oak species. Consequently, we concluded that a genus predictor would better reflect the species' behaviour in the model.

Besides the host species, we identified several climatic predictors, with some acting as limiting factors. Two of the most significant factors are the number of degree days above 5 °C and number of degree days below 0 °C, highlighting the role of cold temperatures as a limiting factor. When annual degree sums above 5 °C are below 2500 degree days, the model predicts suitability near 0, while at the same time low suitability occurs for areas where annual degrees sums below 0 are higher than 300 degree days. It is worth noting that recent research on the cold tolerance of the oak lace bug has revealed its potential to withstand temperatures as low as approximately −20 °C before lethal freezing occurs and continuous exposure to −5 °C over a 3-week period (Paulin et al., 2023). Consistent with this finding, our model reflects a similar trend, indicating low values for the probability of occurrence in areas where the mean temperature of the coldest month drops below 5 °C.

Additionally, our study found that precipitation in the second and sixth months of the year plays a significant role in predicting the species' behaviour. These factors have contrasting effects on the species. On one hand, the suitability of the species is linked to drier winters, while on the other hand, it is associated with wetter springs/summers. This pattern can be explained by the species' life cycle. In April/May, the insects become active after overwintering and start searching for high-quality food sources. This behaviour suggests a preference for regions with abundant precipitation during this period, likely because it results in a more favourable sap supply, which aligns with their feeding needs. It also implies a preference for areas where their host species thrive, providing an ample food source at the beginning of the growing season. However, heavy rains during the period when the overwintered adult emerge, may lead to severe mortality.

In line with our findings, but at a local level Bălăcenoiu et al. (2021b) demonstrated that air temperature and humidity can influence both diurnal and seasonal population dynamics of the OLB. Their study revealed that the flight activity of OLB adults exhibited a rising trend during the vegetation season, corresponding to increased air temperatures and decreased air humidity. When investigating the ecology of a closely related insect, *Corythucha ciliata* (Say, 1832) (Hemiptera, Tingidae), Ju et al. (2011) also observed that the development of this species is positively affected by air temperature. Furthermore, Lu et al. (2019) conducted a study on the same insect, *C. ciliata*, and found that its flight activity was significantly faster, more sustained over time, and covered longer distances within a specific temperature range of 20–30 °C.

However, it is important to note that limited existing research investigates the relationship between this species and environmental factors. In comparison to the aforementioned studies, our research takes a macroecological approach, providing new insights into the species at the population level. Consequently, benchmark results for comparison are scarce, making it challenging to directly compare our findings with previous research. One study similar to ours (Sarıkaya et al., 2023), but concentrating on the eastern part of OLB distribution, found that temperature-related variables held greater importance than precipitation-related variables. However, they did not consider the host species as a potential predictor.

Determining whether climatic variables are the sole limiting factors for the species' distribution, or if other elements such as natural enemies are at play, remains a complex question. While the host species are limited in the natural range of invasive species, our gathered observations indicate a higher level of damage to hosts within the species' introduced range compared to its original range. This severe damage can likely be attributed to the absence of natural enemies and competitors (Csóka et al., 2019).

With the invasion of the insect into Europe, several studies have explored the potential of entomopathogenic fungal species in influencing the development of oak lace bug populations. For example, in Hungary, the OLB mortality rate caused by a *Beauveria* fungus was quite low, standing at only 0.1 % (Paulin et al., 2020), while results from Turkey (Sönmez et al., 2016) and Croatia (Kovač et al., 2020, 2021) have provided hope for a potential future biological control program for the oak lace bug, with *Beauveria* fungi species demonstrating exceptionally high efficiency in nymph and adult mortality. These results, however, were obtained in laboratory conditions and still need to be replicated in the field for confirmation. Although a considerable number of native natural enemies have been documented in Europe, including coccinellids, lacewings, predatory bugs, velvet mites, and spiders, none have been observed to significantly regulate the populations (Paulin et al., 2020).

It might be the case that the expansion in Europe is actively controlled by natural predators that have not yet been detected or studied or competition with another pest. Hence, it is evident that further research is required to gain a comprehensive understanding of all aspects of this issue and to model the behaviour of the species within a broader biocenosis.

Species distribution models have received both criticism and praise for their utility in modelling invasive species ecological niche (Gallien et al., 2012; Mainali et al., 2015; Barbet-Massin et al., 2018; Liu et al., 2020). A primary concern relates to the equilibrium between environment and species occurrence, which, in turn, restricts the model's transferability across different spatial and temporal dimensions. We addressed this concern by implementing a two-step pseudo-absence sampling procedure (Engler et al., 2004). Random pseudo-absence selection, while suitable when comprehensive presence data is available, may not be apt for relatively new invasive species such as the OLB which we can reasonably assume has not fully colonized all suitable areas. This assumption gains support from the most recent documented colonization in 2021, as reported by Gil and Grosso-Silva (2021). With this perspective, we adopted a random sampling approach across Europe to predict the present realized distribution, distinguishing areas that are suitable and unsuitable for the species based on available data. In the second step, within the pool of predicted absent locations, we excluded those that were environmentally similar but geographically distant from true presence sites. These refined absences were then utilized to predict the potential distribution. Similar approaches could be found in Thuiller et al. (2016) or Hattab et al. (2017).

Models calibrated during the initial phases of an invasion often fall short in predicting the full extent of the species' ecological range (Václavík and Meentemeyer, 2012). However, it has been >20 years since the OLB first colonized European territory. The presence data reveal clustered occurrences in the southern part of Europe, characterized by a combination of central European and Mediterranean climates. While the invasive species continues to colonize new areas, its preference for Eastern-continental and Mediterranean climates remains consistent. We believe that the present dataset and the chosen modelling framework have allowed us to reduce uncertainty related to the non-equilibrium effect and have enabled us to build a robust model.

Another substantial criticism, especially pertinent when dealing with invasive species that strongly depend on host species, is that climate alone cannot be the exclusive driver of the species' expansion. By incorporating the potential distribution of the host species as an additional predictor, we ensure that there is a link between the invasive species and its habitat both for the present and future predictions.

However, caution is needed when interpreting the maps, as predictions may vary depending on different modelling assumptions (Qiao et al., 2015, 2019). Furthermore, the unavailability of data on certain host species further constrains the model. Despite incorporating five host species, we overlooked additional potential hosts that could act as expansion corridors in different regions, thereby introducing uncertainty into the model's predictions. Additionally, due to the limited spatial extent of the projected distribution of host species, we could not utilize all possible occurrences. Assuming those locations differ from those used to calibrate the model, inaccuracies may arise in estimating the potential niche.

Another significant limitation arises from the lack of information on the long-distance flight capacity of OLB under various climatic conditions. While studies offer insights into the flight capacity of *Corythucha ciliata* (Lu et al., 2019), no comparable information exists for OLB. Consequently, the model's predictions neglect the species' spreading capacity, representing only its maximum potential spread. Even if an area becomes climatically and environmentally suitable, the time required for the insect to reach there may be considerably longer.

Interestingly, oaks are considered primary beneficiaries in the context of climate change. They are projected to expand their distribution, occupying land previously unsuitable for drought-intolerant species (Hanewinkel et al., 2013). Furthermore, with an increase in spring temperatures, seed production in oaks is expected to rise (Caignard et al., 2017). However, there are numerous reports indicating oak forest decline in Europe (Thomas et al., 2002; Denman et al., 2014; Haavik et al., 2015) with defoliating insects and climatic extreme events being contributing factors. Given that the oak lace bug can precipitate a substantial reduction in photosynthetic rates, reaching up to 50 % (Nikolić et al., 2019), the outlook for the future of oak forests appears increasingly threatened. Currently, there is no implemented control strategy in forest management practices to regulate the expansion of species or alleviate its impact on oak forest ecosystems. However, our research could provide valuable insights for forest managers and policymakers. Primarily, the study raises awareness of the significant threat posed by the OLB in Europe, offering risk maps to identify potential hotspots for species expansion. These identified areas deserve heightened attention, alerting forest managers to the increased risk of OLB invasion. In regions already affected by drought, the compounded impact of OLB further stresses oak stands, potentially leading to increased mortality.

Furthermore, in areas designated as high-risk zones, careful consideration is crucial in the selection of species for reforestation and afforestation programs, with an emphasis on avoiding the promotion of oak species beyond their natural range. Introducing a mix of other tree species in these regions could serve as a strategic measure to decelerate the expansion of the OLB.

An additional management strategy could involve adopting local restrictions on the trade of wood harvested from heavily infested OLB areas, as they facilitate species spread. This restriction could apply to regions identified as suitable by our projection but where the species has not yet been detected, with the recommendation to implement quarantine measures until a viable solution for OLB population control is identified.

Furthermore, a prospective management direction, contingent on the development of a viable control method, faces challenges due to the substantial investment required for large-scale coverage. However, leveraging the risk maps presented in our paper enables strategic resource allocation, directing efforts towards the primary hotspots for potential future expansion of the species.

5. Conclusion

The oak lace bug is part of a large number of invasive species infiltrating Europe annually, with significant repercussions evident in its impact on oak populations. What is particularly disconcerting is the rapid pace of its invasion since its arrival. It could be safely stated that it is the most threatening invasive arthropod in European oak ecosystems, exerting multiple negative effects not only on oaks themselves but also on the oak food webs. In this study, through collaborative efforts, we compiled an extensive presence dataset, incorporating various sources. However, better monitoring of the species spread is needed, and integrating citizens in the early detection of the species could be the answer (de Groot et al., 2023). Citizen science not only empowers the wider community, but also exponentially amplifies our capability for early detection and swift response. Furthermore, in the context of biological invasions, a more comprehensive and inclusive perspective is needed. As climate change continues to reshape ecosystems, comprehending the intricate interplay between invasive species, host species, and climatic variables becomes ever more critical for informed conservation and management endeavours. Rather than addressing invasive species in isolation, a broader multi-species approach is warranted. Future models should consider the interconnected relationships between various species and ecosystems, recognizing the intricate web of dependencies. Finally, to mitigate biological invasion, a crucial line of defence against the inadvertent dissemination of invasive species should involve strengthening and enforcing biosecurity protocols worldwide.

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CRediT authorship contribution statement

Albert Ciceu: Writing – original draft, Visualization, Software, Methodology, Data curation, Conceptualization. **Flavius Bălăcenoiu:** Writing – original draft, Methodology, Data curation, Conceptualization. **Maarten de Groot:** Writing – review & editing, Methodology, Data curation. **Debojyoti Chakraborty:** Writing – review & editing, Methodology. **Dimitrios Avtzis:** Writing – review & editing, Data curation. **Marek Barta:** Writing – review & editing, Data curation. **Simon Blaser:** Writing – review & editing, Data curation. **Matteo Bracalini:** Writing – review & editing, Data curation. **Bastien Castagneyrol:** Writing – review & editing, Data curation. **Ulyana A. Chernova:** Writing – review & editing, Data curation. **Ejup Çota:** Writing – review & editing, Data curation. **György Csóka:** Writing – review & editing, Data curation. **Mirza Dautbasic:** Writing – review & editing, Data curation. **Milka Glavendekic:** Writing – review & editing, Data curation. **Yuri I. Gninenko:** Writing – review & editing, Data curation. **Gernot Hoch:** Writing – review & editing, Data curation. **Karel Hradil:** Writing –

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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.

Data availability

The occurrence dataset used to calibrate the species distribution models is presented in Annex 1 of this paper.

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