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Modelling the potential range of *Agrilus planipennis* in Europe according to current and future climate conditions

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ABSTRACT

Agrilus planipennis, the emerald ash borer, is a species native to East Asia that was accidentally introduced to North America and Eastern Europe. In North America, it is responsible for tremendous damage. In Europe, its range has quickly expanded from the east where it was introduced in 2003, and it threatens the species of the genus *Fraxinus*. We developed an ensemble modelling approach to model the potential range of *A. planipennis* according to current climate conditions and four scenarios of climate change: SSP1–2.6, SSP2–4.5, SSP3–7.0 SSP5–8.5 in the period 2041–2060. We used three algorithms; random forest, boosted regression trees and Bayesian additive regression trees with occurrence data from both native and invaded ranges. The results indicate that most of the European continent is climatically suitable for *A. planipennis*. In Western Europe, the northern limit of the range is located in the British Isles and southern Scandinavia. The projection of the models according to estimates of future climate conditions shows that climate suitability would mostly remain unchanged in 2041–2060. During that period, the potential range is expected to slightly shrink in the south, around the Mediterranean Basin, and expand at its northern limit. Our results confirm that *A. planipennis* is, and will remain, a major threat to forest and ornamental ash tree health across Europe.

1. Introduction

Agrilus planipennis, the emerald ash borer is a species native to East Asia (China, the Russian Far East, the Korean Peninsula and Japan) that was accidentally introduced to North America and Eastern Europe. It was detected in 2002 in the United States of America in the state of Michigan and quickly spread across eastern and central North America. In its native range, *A. planipennis* only causes limited damage in natural forests where native ash trees are resistant (Rebek et al., 2008). On the contrary, in North America, it causes considerable damage to all species of American ash trees both in urban areas and in forests (Sun et al., 2024). Since its introduction to North America in the early 2000s, hundreds of millions of ash trees have been killed or felled, resulting in a cost exceeding ten billion dollars for tree protection, removal and replacement (Fantle-Lepczyk et al., 2022). In Europe, the emerald ash borer was reported for the first time in Moscow in 2003 (Orlova--Bienkowskaja, 2013) and has now spread over 600 km to the north and over 1000 km to the south (Orlova-Bienkowskaja and Bieńkowski, 2022a). The initial outbreaks of *A. planipennis* near Moscow were detected in the North American species *F. pennsylvanica*, which is commonly used as an ornamental in the cities of northeastern Europe. An outbreak was later recorded in the Moscow Region in 2014 (Musolin et al. 2017). The spread of the insect in Russia and Ukraine seems to be associated with the presence of these introduced species frequently planted along roads, but the European species *F. excelsior*, although rare in the region, has also been attacked (Meshkova et al., 2023). *Agrilus planipennis* host range is almost totally restricted to *Fraxinus* species: *Chionanthus virginicus* (Oleaceae), reported as an alternative host in the USA, is considered to be the only ascertained record in field conditions beyond that genus (Peterson and Cipollini, 2017).

The risk of expansion of *A. planipennis* from Eastern Europe westward, or an introduction from either native or invasive ranges strongly depends on climate suitability. Several studies based on species distribution or phenological models have been published (Barker et al., 2023; Dang et al., 2021; Flø et al., 2015; Meshkova et al., 2023). The MaxEnt models proposed by Flø et al. (2015), Dang et al. (2021) and Meshkova et al. (2023) indicate that climatically suitable areas are limited to the vicinity of the areas infested by the time of their study i.e. Russia and

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Ukraine, hence a fairly limited potential expansion. There is a strong contrast between these results and the consensual idea that *A. planipennis* threatens to spread largely in Europe (EFSA, 2020; Orlova-Bienkowskaja and Bieńkowski, 2022; Valenta et al., 2017) as well as with a recently published phenological model that indicates that large parts of Western Europe are highly climatically suitable for the emerald ash borer (Barker et al., 2023). The differences between these results can be explained in different ways, in particular by the use of different algorithms but also by the selection of different subsets of occurrence data during the calibration phase. There is no publication tackling the question of the impact of climate change on the potential distribution of *A. planipennis* in Europe, and this limits our capacity to improve our preparedness in important topics such as early warning capacity, management strategies, risk evaluation and tree species selection for urban forests and urban greenings.

Because of the contrasting results available in the literature and the absence of an evaluation of climate change impacts, we developed a set of Species Distribution Models (SDM) based on the most recent distributional data and three different algorithms. These models were used with projections from 11 global circulation models and four shared socio-economic scenarios to estimate the potential range of *A. planipennis* in Europe for the period 2041–2060.

2. Materials and methods

All statistical analyses, data management and graphics were done using the R environment for statistical computing and visualisation (R Core Team, 2023).

2.1. Occurrence data

We used the occurrences available from the GBIF database (GBIF.org, 2023 https://doi.org/10.15468/dl.y6yst6) and the datasets available from Orlova-Bienkowskaja and Volkovitsh (2018) and Dang et al. (2021).

2.2. Climate data

Climate data were downloaded from the Worldclim database (https://worldclim.org/) (Fick and Hijmans, 2017). We used climate data with a resolution of 2.5 min (≈22 km^2 at the equator). Data associated with *A. planipennis* occurrences were separated into two groups according to the date of observation: before and after 2001. For these periods, we used the data available for 1970–2000 in WorldClim version 2.1 (https://worldclim.org/data/worldclim21.html) and the historical monthly weather data for the period 2001–2018 (https://worldclim.org/data/monthlywth.html) respectively. In the latter case, we computed the average climate descriptors (hereafter referred to as bioclimatic variables) using the function “biovars” from the R package “dismo” (Hijmans et al., 2023). For future conditions, we considered the period 2041–2060 and used the datasets from 11 Global Circulation Models (hereafter GCM) listed in Table S1. Our analyses are based on the projections of these 11 GCM in the framework of 4 Shared Socioeconomic Pathways (SSPs) describing plausible greenhouse gas emissions scenarios according to different climate policies. These SSPs are referred to as sustainable development (SSP1), middle-of-the-road development (SSP2), regional rivalry (SSP3), and fossil-fuelled development (SSP5) (IPCC, 2023; Riahi et al., 2017). Details are provided in Table S2.

2.3. Species distribution modelling

2.3.1. Model algorithms

We choose machine learning methods because of their ability to handle potentially complex linear and nonlinear connections between species distributional data and environmental descriptors (Hastie et al., 2009; Merow et al., 2014), their tolerance to collinearity (Dormann et al., 2013) and their very good predictive performance (Elith et al., 2006). Elith (2019) provided an overview of machine learning methods in the field of species distribution modelling. We used 3 different modelling algorithms: Random Forests (hereafter RF), Boosted Regression Trees (hereafter BRT) and Bayesian Additive Regression Trees (hereafter BART). RF and BRT are frequently used in the field of SDM and are fully documented in Guisan et al. (2017) and Elith et al. (2008) while BART was introduced in ecology more recently and is presented in Carlson (2020). The RF model was calibrated using the R package “randomForest” (Liaw and Wiener, 2002). We used the step-wise selection method based on the averaged variable importance (Li et al., 2016) to identify the most relevant climate descriptors to be included in the model using the R package “steprf” (Li, 2022). The node size and the number of explanatory variables sampled at each split were optimized using the R package “randomForestSRC” (Ishwaran and Kogalur, 2007). RF was calibrated using 1000 trees. We calibrated BRT following the working guide provided by Elith et al. (2008) and the R package “dismo” (Hijmans et al., 2023). The climate descriptors to be included in the model were selected using a step-wise procedure implemented in the function “gbm.simplify” (R package “dismo”) while the optimal number of trees to use was determined by the function “gbm.step” (package “dismo”). The BART model was calibrated using the R package “embarcadero” (Carlson, 2020). The package provides a step-wise variable section procedure (function ”bart.step”) and we used 1000 trees (details in Carlson 2020). In each case, we used a number of pseudo-absences equal to the number of presence points (see below for details about the pseudo-absences creation).

2.3.2. Candidate variable selection

Temperature range and degree-day accumulation are considered to be the most important climate factors constraining *A. planipennis* geographic distribution (Valenta et al., 2017). We thus retained the following variables: the maximum temperature of the warmest month (referred to as bio5 in the Worldclim database), the minimum temperature of the coldest month (bio6), the mean temperature of the warmest quarter (bio10) and the mean temperature of the coldest quarter (bio11). These climate descriptors are correlated but the machine learning methods we used are relatively immune to collinearity (Dormann et al., 2013). The importance of the amount of heat (degree days) as a constraint shaping the distribution of insects, particularly in cold and temperate regions is well-known (Bale, 2002) and has been highlighted in the case of the emerald ash borer (Orlova-Bienkowskaja and Bieńkowski, 2022b; Webb et al., 2021). We accounted for this important climatic constraint by adding the number of accumulated growing degree days in our set of predictive variables and we used a base temperature of 10 °C following Orlova-Bienkowskaja and Bieńkowski (2022b). The variable is hereafter referred to as GDD10. GDD10 was computed using the function “growingDegDays” of the R package “envirem” (Title and Bemmels, 2018). We computed the frequency of observed presences (FOPs; Halvorsen, 2013) or each candidate variable (bio5, bio6, bio10, bio11 and GDD10). FOPs depict the rate of observed occurrence in the function of the environmental descriptors. This graphic representation allowed us to discard variables displaying noisy or bimodal curves and thus ensures that only explanatory variables that could lead to ecologically realistic and meaningful response curves are retained. FOPs were computed using the R “MIAmaxent” (Vollering et al., 2019).

2.3.3. Preprocessing of occurrence data

We only considered the GBIF occurrence data points that were associated with valid spatial coordinates. The points associated with the following issues, “RECORDED_DATE_INVALID”, “IDENTIFIED_DATE_INVALID”, “MODIFIED_DATE_INVALID” and “RECORDED_DATE_UNLIKELY” were discarded. This process led to 3090 occurrence points. We additionally used the occurrence data available from Orlova-Bienkowskaja and Volkovitsh (2018) (108 points) and

Dang et al. (2021) (43 points). The date of observation spanned from 1800 to 2023. 25 occurrences had no date and were discarded. The point associated with an observation dating back to 1800 was discarded because no climate data was available for that period. We subdivided the observation points into two groups based on the date of observation: before 2001 (35 observations) and after 2000 (3180 observations).

The valid occurrences were thinned to a single point per unique 2.5 min cell (Boria et al., 2014). We also removed the points falling outside the land surface. This number depends on the resolution of the climate data. This led to a total of 25 and 1888 occurrence data for the periods before and after 2001 respectively. The resulting dataset was submitted to geographical filtering to control for the possible sampling bias (Aiello-Lammens et al., 2015) using an arbitrary threshold of 10 km and the R package "spThin" (Aiello-Lammens et al., 2015). This led to 25 and 1125 occurrence points for the periods before and after 2001 respectively.

We extracted the climate data corresponding to the occurrence points of each period and built a unique dataset which was analysed by a principal component analysis to perform environmental filtering and remove environmental redundancy between data points (Varela et al., 2014). This led to a total of 924 occurrences representing 28.8 % of the initial pool of valid records.

2.3.4. *Pseudo-absences*

Because absence data were lacking, we calibrated our models using pseudo-absences (VanDerWal et al., 2009). Since the native range of *A. planipennis* is well known we could safely assume that the species is absent at the north and south of that area (Supplementary figure S1). In the Russian Far East, the species has been recorded in the southern part of the Khabarovsk Krai while its presence in Mongolia is doubtful (EPPO website https://gd.eppo.int/reporting/article-6465) but data are lacking (Orlova-Bienkowskaja and Volkovitsh, 2018).

2.3.5. *Model performance*

We computed the Area Under the Curve (AUC) of the receiver operating characteristic plot (Fielding and Bell, 1997) and the true skill statistic (TSS) (Allouche et al., 2006) using the valid occurrences that were discarded from the analysis at the step of geographic and environmental filtering ($n = 989$) and an equal number of pseudo-absences generated as explained above. In doing so we evaluated the performance of the models based on data that were not used in the calibration phase. The computation was done using the R package "dismo".

2.3.7. *Ensemble modelling and committee averaging*

Each algorithm led to one projection of climate suitability for each climate dataset. For a given period (current or future) and in the case of future, for each SSP and GCM considered, we thus had 3 projections (one for each algorithm). Averaging model outputs in the form of probabilities might cause problems since these values are not always comparable (Guisan et al., 2017). We therefore combined the outputs of BART, BRT and RF by computing the community averaging (Guisan et al., 2017 p. 336). The first step consisted of transforming the model outputs into binary (presence/absence) projections using the threshold that optimized the TSS statistics. We used the function "threshold" from the R package "dismo". The resulting binary outputs were then averaged. The resulting committee averaging ranges from 0 % (all the models predict absence) to 100 % (all the models predict presence). It depicts the climate suitability and provides a picture of the agreement between models. In the case of projection according to one SSP, the average was computed for the 11 projections (one for each GCM) associated with each algorithm (11 x 3 = 33 projections).

2.4. *Assessing possible environmental novelty*

Caution is needed when interpreting the results of models projected in environmental conditions non-analogue to those used for the calibration because the results might be biologically meaningless (Elith et al., 2010). The Multivariate Environmental Similarity Surface (MESS) index has been introduced by Elith et al. (2010) to quantify environmental novelty. Areas, where at least one climate descriptor lies outside the range of the reference dataset, are associated with a negative MESS index value. Conversely, positive MESS index values indicate the absence of environmental novelty (extrapolation). We computed the MESS index for current and future climate conditions. For each SSP, we retained the minimum value amongst the MESS estimates corresponding to the 11 GCM. The computations were done using the function "mess" of the R package "dismo".

3. Results

3.1. *Climate variable selection*

The candidate climate variable (bio5, bio6, bio10, bio11 and GDD10) exhibited a bell-shaped FOP curve and were thus used in the step-wise selection procedure of each algorithm (Supplementary Figure S2). The step-wise variable selection procedure retained bio5, bio6, bio10, bio11 and gdd10 in the case of BART and bio6, bio10, bio11 and gdd10 for both BRT and RF.

3.2. *Evaluation metrics*

The AUC and TSS values were >0.99 for all algorithms indicating very good performances.

3.3. *Current climate suitability and committee averaging*

The committee averaging for the models' projections according to the current climate conditions (2001–2018) is shown in Fig. 1-A. The corresponding maps of raw and reclassified climate suitability stemming from each algorithm are given in Supplementary Figures S3 and S4. Most parts of Western Europe were climatically suitable for *A. planipennis*. The northern margins of that potential range corresponded to northern England, Denmark, Southern Sweden, and Southern Finland. In the south, the limit corresponds to hot and dry climates mostly located in Southern Portugal and Spain. The committee averaging revealed some discrepancies between the projections of the 3 algorithms (Fig. 1A, Supplementary Figures S3 and S4). These disagreements occurred in the northern part of the potential range and illustrated the fact that each algorithm slightly differed in their consideration of the way the climate constraints the margin of the range. On the contrary, there was a very good agreement between the three models concerning climate suitability across most of the European continent. Interestingly, the MESS index indicated the absence of possible problems linked to environmental novelty i.e. extrapolation in Europe (Fig. 2) where the index was > 0. Fig. 2 shows that areas where the index was < 0 occurred in northern Russia in the region of Novaya Zemlya (Russia), in Iraq and southern Algeria (Sahara). The worldwide assessment is given in Supplementary Figure S5.

3.4. *Projection according to future climate scenarios*

The northern limit of the potential distribution shifted norward for the period 2041–2060 according to the results obtained for the different SSPs (Fig. 1 B-E). For example, the southern half of Finland became more suitable when the models were projected using data for SSP1–2.6 and the suitable area was larger when we considered scenarios leading to higher temperature increases (SSP5–8.5>SSP3–7.0>SSP2–4.5>SSP1–2.6). The southern limit changed according to currently suitable regions becoming unsuitable due to temperature increase. This is the case of Southern Portugal and Spain as well as the Balearic Islands (Spain), Sardinia and Sicilia (Italy) and some coastal regions around the Mediterranean basin such as the Southeastern part of the Apulia region in

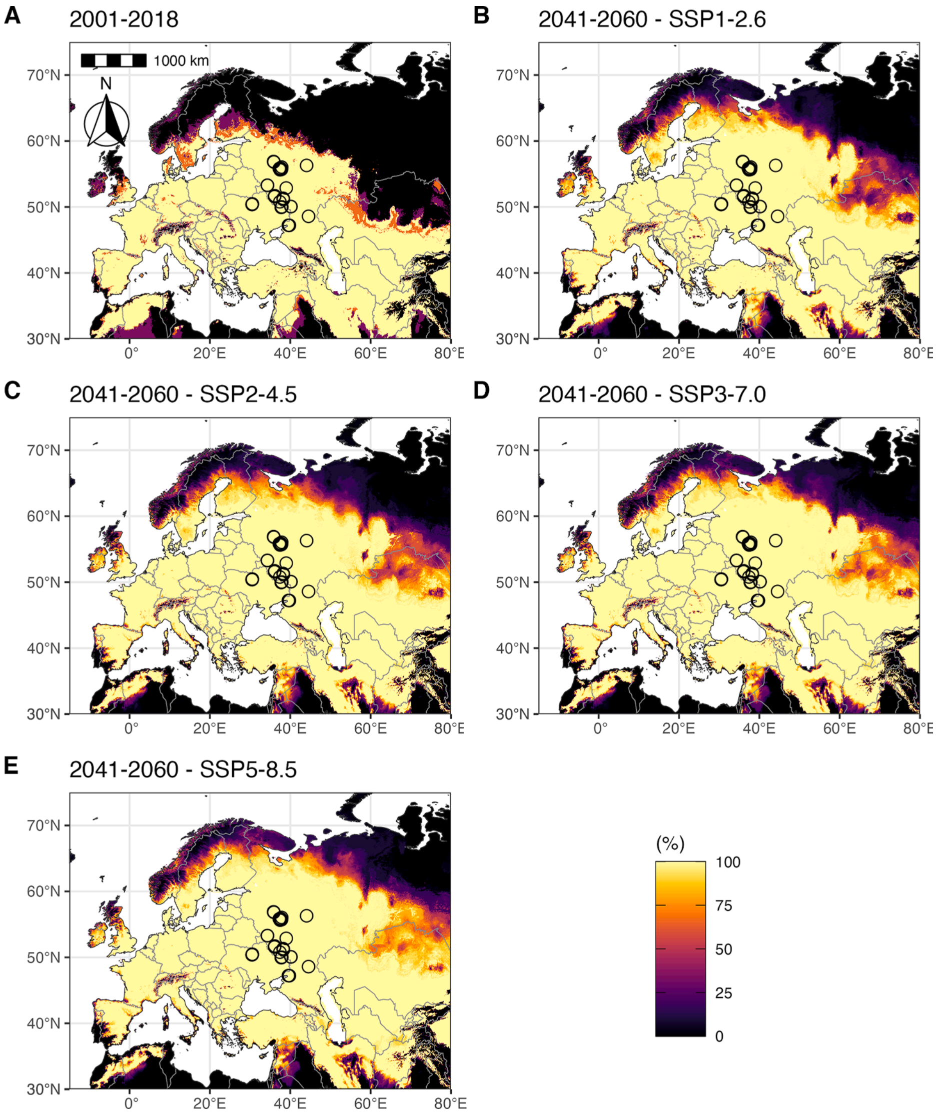


Fig. 1. Climate suitability for *Agrilus planipennis*. A. Climate suitability according to current climate conditions (2001–2018). B. Climate suitability according to the shared socioeconomic pathways SSP1–2.6 for the period 2041–2060. C. Climate suitability according to the shared socioeconomic pathways SSP2–4.5 for the period 2041–2060. D. Climate suitability according to the shared socioeconomic pathways SSP3–7.0 for the period 2041–2060. E. Climate suitability according to the shared socioeconomic pathways SSP5–8.5 for the period 2041–2060. The maps depict the committee averaging expressed as the percentage of projections indicating suitable climate conditions (see text for details). Open circles indicate presence points. Projection: EPSG 4326.

Italy. Apart from the Atlas Mountains, North Africa was unsuitable according to current conditions and this remained the case according to the 4 scenarios. The MESS index was positive everywhere in Europe as shown in Supplementary Figure 6.

4. Discussion

Our models provided estimates of the potential distribution of *A. planipennis* that differed from certain previously published models. For example, Flø et al. (2015) found that European climate suitability was restricted to an area centred around the infested areas in Russia at the time of the model calibration. Similarly, Dang et al. (2021) and Meshkova et al. (2023) reported limited suitable areas in Europe. Such discrepancies are not rare. For example, some models established by different authors for the spotted lanternfly *Lycorma delicatula* are very different (Jung et al., 2017; Wakie et al., 2020). The sources of divergences are multiple. The nature of the algorithm used to calibrate the models is very important and for *A. planipennis*, this has been highlighted by Sobek-Swant et al. (2012) who reported diverging results for the models MaxEnt and GARP. For that reason, it is generally advised to use different modelling algorithms and build ensemble models (Araujo and New, 2007). In the present study, we used three machine learning algorithms well-known for their good performances which provided consistent although not identical projections. The between-model differences provided a straightforward picture of uncertainty that occurred at the margin of the potential range which is areas of transition between suitable and unsuitable climates. These marginally suitable areas are differently accounted for by the three methods but the models were otherwise in very good accordance. Other differences with published models were that some models were calibrated with the native occurrences only (Dang et al., 2021) or the occurrence from newly invaded areas in central Europe (Flø et al., 2015; Meshkova et al., 2023 but see Barker et al., 2023). To fully capture the species' climatic niche, it is better not to restrict the amount of data used to calibrate the model. First, the native range might not be sampled with sufficient density and some features of the climate niche could be missed. In that case, datasets collected from invaded range(s) could provide this information. Although it has been advocated that most invasive species conserve their

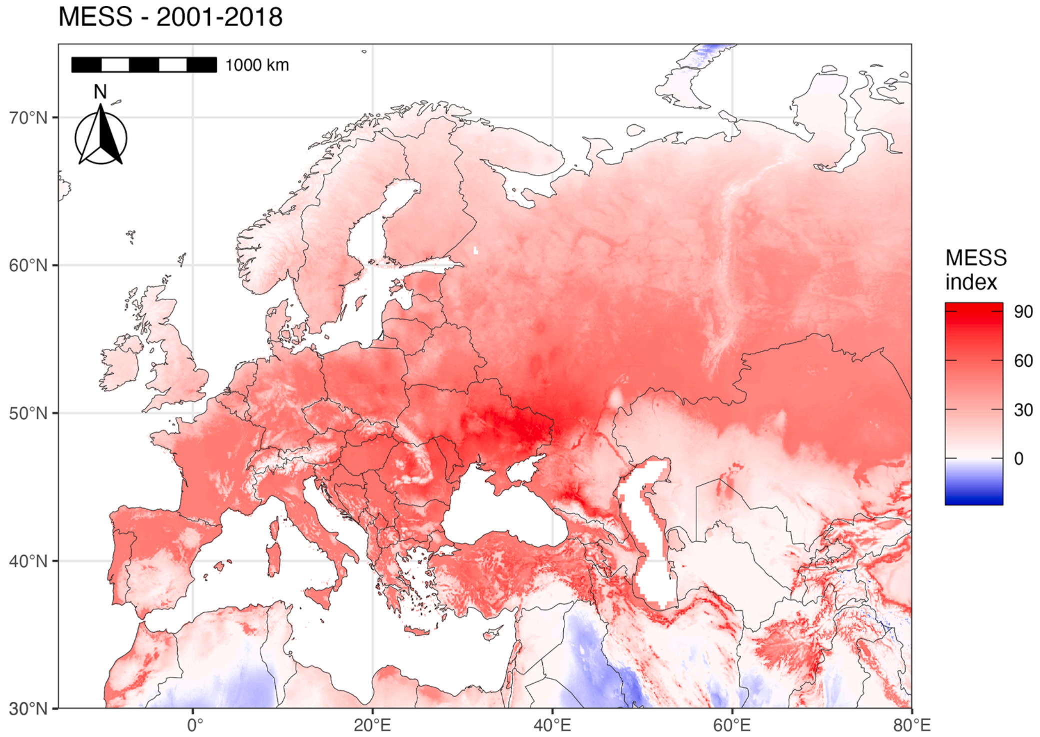
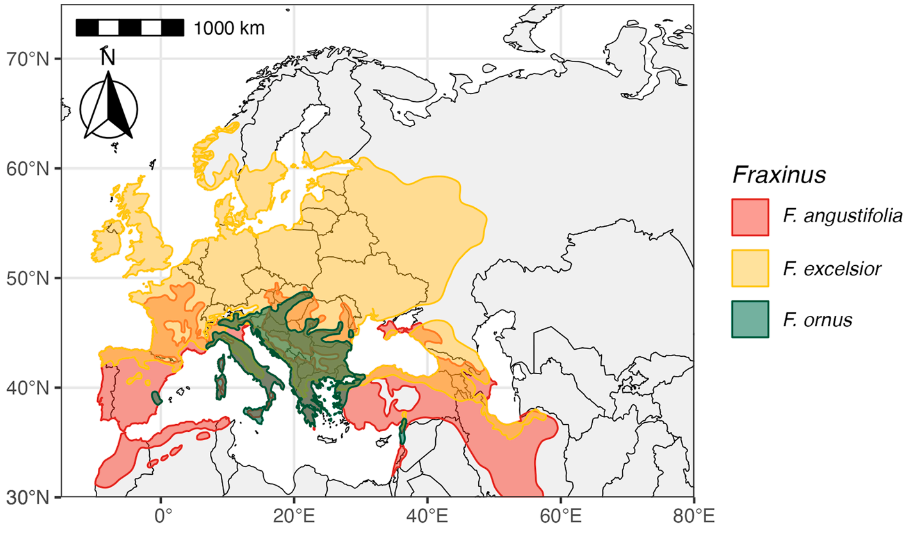


Fig. 2. Model extrapolation. The map depicts the Multivariate Environmental Similarity Surfaces (MESS) comparing current climate conditions in Europe to reference points used for model calibration. Analogous environments are shown in red (positive values) and novel environments are shown in blue (negative values). Projection EPSG 4326.

climatic niche (Liu et al., 2020), niche shift can occur quickly (Wiens et al., 2019) and local adaptation should not be dismissed because accounting for such features could valuably improve the models (DeMarche et al., 2019; Hällfors et al., 2016). Although it is not possible to determine if niche shifts occurring during biological invasions are affecting the fundamental niche or simply convey differences in realized niches, they generate climate-related information that should be incorporated into species distribution models (Broennimann and Guisan, 2008). Accounting for invaded ranges is important because native areas are not always well-documented (Hierro et al., 2005). This is the case for *A. planipennis* (Orlova-Bienkowskaja and Volkovitsh, 2018) as it is for pests that remain discrete in their native range and are thus not intensively studied. When considering species distribution modelling of invasive species, certain native populations at the margin of the core range might be pre-adapted to peculiar climate or environmental conditions making them more prone to invasive success. Rey et al. (2012) provide a good example with the little fire ant *Wasmannia auropunctata*. It is obvious that if such populations were undersampled in the native range, not using the data from the invaded areas amounts to possibly missing important information and decreases the models' ability to properly assess the potential range. Available models for *A. planipennis* also differ in their handling of climate descriptors which, as far as



data from Caudullo et al. (2017)

Fig. 3. Distribution of *Fraxinus* species in Europe (data from Caudullo et al. 2017). Projection: EPSG 4326.

possible, should convey direct ecological constraints. In the present study, we limited the climate descriptors to variables with known direct impact on the emerald ash borer distribution e.g. minimum temperatures (Crosthwaite et al., 2011) or accumulated degree days (Orlova-Bienkowskaja and Bieńkowski, 2022b).

According to the present study, the European continent is clearly at risk of being widely invaded by *A. planipennis*, which confirms the results of several previous studies (EFSA, 2020; Valenta et al., 2017). The climate is suitable for *A. planipennis* and the potential hosts are widely distributed across the continent, either North American *Fraxinus* species (such as *F. pennsylvanica*) used for ornamental purposes (Orlova-Bienkowskaja, 2014) or native species that are considered suitable hosts for *A. planipennis* (Caudullo et al., 2017; Meshkova et al., 2023) (Fig. 3). Although modelling studies yielded contrasted results (as discussed above), our conclusions are not surprising since *A. planipennis* is tolerant to very low winter temperatures (Crosthwaite et al., 2011) and is also distributed in temperate regions according to the Köppen-Geiger classification (Beck et al. 2023) in North America and well as in China (Supplementary Figure 1 and 6). Since its first record in Moscow in 2003, *A. planipennis* has quickly spread at an average speed of 50 km per year to the north and the south and its distribution has now exceeded the estimates of previously published models (Orlova-Bienkowskaja and Bieńkowski, 2022a) but other studies yielded lower dispersal rates ranging from 6.5 to 20 km (Musolin et al. 2017). Host connectivity and the highly suitable climate conditions indicated by our models are expected to ease emerald ash borer spread across Europe. Our models indicated lower climate suitability in Northern England, Wales, Ireland, Scotland and some parts of Scandinavia, which is in line with the findings of Webb et al. (2021) and Orlova-Bienkowskaja and Bieńkowski (2022b). Because *F. excelsior* stands are present in these regions, they could become refugia if the emerald ash borer reached Western Europe. In that case, *F. excelsior* could nevertheless remain threatened by the ash dieback which is present in these regions (Carroll and Boa, 2024). Interestingly, Liang and Fei (2014) highlighted that a similar divergence between the invasive ranges of *A. planipennis* and the native ash species could increase due to climate change in North America. In the case of Western Europe, our results indicate that the current potential distribution of *A. planipennis* would not change markedly by 2041–2060. Suitable areas would expand in the north and shrink in the south but these changes are expected to remain limited. The larger the greenhouse gas emission and thus the increase of surface temperature, the larger the northern (southern) increase (decrease) in climate suitability. These results indicate that climatic conditions are, and will likely remain, suitable for *A. planipennis* across Europe in the coming decades, resulting in a significant risk of ecological and economic impacts.

Although species distribution models depict the potential range of a species, they provide no information about the spatial dynamics of the possible expansion. For this purpose, various modelling approaches can be used such as spatially explicit mechanistic models (Lustig et al., 2017). One very important question is to estimate the species spread. In the case of *A. planipennis*, the natural spread is limited to a few kilometres (Orlova-Bienkowskaja and Bieńkowski, 2018) but human-aided, long-distance dispersal can be much higher. Because it results from human transportation of infested ash material, a modelling approach such as the flexible spatiotemporal stochastic network model PoPS (Montgomery et al., 2023) could be very useful as it couples international trade network and ecological drivers of invasions such as climate suitability, host availability as well as propagule pressure. In a recent study, Barker et al. (2023) proposed a very promising approach to coupling phenology and climate suitability. The authors provide a model predicting the phenology of *A. planipennis* across the invaded and the native range. Such a tool is very interesting in terms of management because it indicates when and where actions could be realized. It should be noted that their model, like ours, predicts that most of western Europe is climatically suitable for *A. planipennis*.

CRediT authorship contribution statement

Jean-Pierre Rossi: Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Raphaëlle Mouttet:** Writing – review & editing, Validation, Conceptualization. **Pascal Rousse:** Writing – review & editing, Validation, Conceptualization. **Jean-Claude Streito:** Writing – review & editing, Validation, Conceptualization.

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

Raw data are available from references and links provided in the text. The outputs of the models are available in the form of raster source files (GeoTIFF format) at https://doi.org/10.5281/zenodo.10955964.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2024.100559.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS): assessing the accuracy of distribution models. J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Araujo, M., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. (Amst.) 22, 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Bale, J.S., 2002. Insects and low temperatures: from molecular biology to distributions and abundance. Phil. Trans. R. Soc. Lond. B 357, 849–862. https://doi.org/10.1098/rstb.2002.1074.

Barker, B.S., Coop, L., Duan, J.J., Petrice, T.R., 2023. An integrative phenology and climatic suitability model for emerald ash borer. Frontiers in Insect Science 3, 1239173. https://doi.org/10.3389/finsc.2023.1239173.

Beck, H.E., McVicar, T.R., Vergopolan, N., Berg, A., Lutsko, N.J., Dufour, A., Zeng, Z., Jiang, X., Van Dijk, A.I.J.M., Miralles, D.G., 2023. High-resolution (1 km) Köppen-Geiger maps for 1901–2099 based on constrained CMIP6 projections. Sci. Data 10, 724. https://doi.org/10.1038/s41597-023-02549-6.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol. Modell. 275, 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012.

Broennimann, O., Guisan, A., 2008. Predicting current and future biological invasions: both native and invaded ranges matter. Biol. Lett. 4, 585–589. https://doi.org/10.1098/rsbl.2008.0254.

Carlson, C.J., 2020. embarcadero: species distribution modelling with Bayesian additive regression trees in R. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.13389.

Carroll, D., Boa, E., 2024. Ash dieback: from Asia to Europe. Plant Pathol. 00, 1–19. https://doi.org/10.1111/ppa.13859. Available from.

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Brief 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007.

Crosthwaite, J.C., Sobek, S., Lyons, D.B., Bernards, M.A., Sinclair, B.J., 2011. The overwintering physiology of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: buprestidae). J. Insect Physiol. 57, 166–173. https://doi.org/10.1016/j.jinsphys.2010.11.003.

Dang, Y.-Q., Zhang, Y.-L., Wang, X.-Y., Xin, B., Quinn, N.F., Duan, J.J., 2021. Retrospective analysis of factors affecting the distribution of an invasive wood-boring insect using native range data: the importance of host plants. J Pest Sci (2004) 94, 981–990. https://doi.org/10.1007/s10340-020-01308-5.

DeMarche, M.L., Doak, D.F., Morris, W.F., 2019. Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. Glob Chang Biol. https://doi.org/10.1111/gcb.14562.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Garcia Marquez, J. R., Gruber, B., Lafourcade, B., Leitao, P.J., Muenkemueller, T., McClean, C., Osborne, P.E., Reineking, B., Schroeder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

EFSA (European Food Safety Authority), Schans, J., Schrader, G., Delbianco, A., Graziosi, I., Vos, S., 2020. Pest Survey Card On *Agrilus planipennis*. EFSA Support. Publ. 17, 1945E.

Elith, J., 2019. Machine Learning, Random Forests, and Boosted Regression Trees, in: Quantitative Analyses in Wildlife Science. Johns Hopkins University Press.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC, M., Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M., E. Zimmermann, N., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Fantle-Lepczyk, J.E., Haubrock, P.J., Kramer, A.M., Cuthbert, R.N., Turbelin, A.J., Crystal-Ornelas, R., Diagne, C., Courchamp, F., 2022. Economic costs of biological invasions in the United States. Sci. Total Environ. 806, 151318 https://doi.org/10.1016/j.scitotenv.2021.151318.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

Flø, D., Krokene, P., Økland, B., 2015. Invasion potential of *Agrilus planipennis* and other *Agrilus* beetles in Europe: import pathways of deciduous wood chips and MaxEnt analyses of potential distribution areas. EPPO Bulletin 45, 259–268. https://doi.org/10.1111/epp.12223.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models With Applications in R, Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge; New York, NY, United Kingdom.

Hällfors, M.H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G.C., Hellmann, J.J., 2016. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecol. Appl. 26, 1154–1169. https://doi.org/10.1890/15-0926.

Halvorsen, R., 2013. A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. Sommerfeltia 36, 1–132. https://doi.org/10.2478/v10208-011-0016-2.

Hastie, T., Tibshirani, R., Friedman, J.H., Friedman, J.H., 2009. The Elements of Statistical learning: Data mining, inference, and Prediction. Springer, New-York.

Hierro, J.L., Maron, J.L., Callaway, R.M., 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J. Ecol. 93, 5–15. https://doi.org/10.1111/j.0022-0477.2004.00953.x.

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2023. dismo: Species Distribution Modeling. R package Version 1.3-14. https://CRAN.R-project.org/package=dismo.

IPCC (Intergovernmental Panel on Climate Change), 2023. Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel On Climate Change, 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009157896.

Ishwaran, H., Kogalur, U.B., 2007. Random Survival Forests For R. R News, 7, pp. 25–31.

Jung, J.-M., Jung, S., Byeon, D., Lee, W.-H., 2017. Model-based prediction of potential distribution of the invasive insect pest, spotted lanternfly Lycorma delicatula (Hemiptera: fulgoridae), by using CLIMEX. J Asia Pac Biodivers.

Li, J., 2022. steprf: Stepwise Predictive Variable Selection For Random Forest. R package Version 1.0.2. https://CRAN.R-project.org/package=steprf.

Li, J., Tran, M., Siwabessy, J., 2016. Selecting optimal random forest predictive models: a case study on predicting the spatial distribution of seabed hardness. PLoS One 11, e0149089. https://doi.org/10.1371/journal.pone.0149089.

Liang, L., Fei, S., 2014. Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change. Clim. Change 122, 735–746. https://doi.org/10.1007/s10584-013-1024-9.

Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. R News 2, 18–22.

Liu, C., Wolter, C., Xian, W., Jeschke, J.M., 2020. Most invasive species largely conserve their climatic niche. Proc. Natl. Acad. Sci. U.S.A. 117, 23643–23651. https://doi.org/10.1073/pnas.2004289117.

Lustig, A., Worner, S.P., Pitt, J.P.W., Doscher, C., Stouffer, D.B., Senay, S.D., 2017. A modeling framework for the establishment and spread of invasive species in heterogeneous environments. Ecol. Evol. 7, 8338–8348. https://doi.org/10.1002/ece3.2915.

Merow, C., Smith, M.J., Edwards, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E., Elith, J., 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography 37, 1267–1281. https://doi.org/10.1111/ecog.00845.

Meshkova, V., Borysenko, O., Kucheryavenko, T., Skrylnyk, Y., Davydenko, K., Holusa, J., 2023. Potential Westward Spread of Emerald Ash Borer, *Agrilus planipennis* Fairmaire, 1888 (Coleoptera: buprestidae) from Eastern Ukraine. Forests 14, 736. https://doi.org/10.3390/f14040736.

Montgomery, K., Walden-Schreiner, C., Saffer, A., Jones, C., Seliger, B.J., Worm, T., Tateosian, L., Shukunobe, M., Kumar, S., Meentemeyer, R.K., 2023. Forecasting global spread of invasive pests and pathogens through international trade. Ecosphere 14, e4740. https://doi.org/10.1002/ecs2.4740.

Musolin, D.L., Selikhovkin, A.V., Shabunin, D.A., Zviagintsev, V.B., Baranchikov, Y.N., 2017. Between ash dieback and emerald ash borer: two Asian invaders in Russia and the future of ash in Europe. Balt For 23, 316–333.

Orlova-Bienkowskaja, M.J., 2014. Ashes in Europe are in danger: the invasive range of *Agrilus planipennis* in European Russia is expanding. Biol. Invasions 16, 1345–1349. https://doi.org/10.1007/s10530-013-0579-8.

Orlova-Bienkowskaja, M.J., Bieńkowski, A.O., 2022a. Low heat availability could limit the potential spread of the emerald ash borer to Northern Europe (prognosis based on growing degree days per year). Insects 13, 52. https://doi.org/10.3390/insects13010052.

Orlova-Bienkowskaja, M.J., Bieńkowski, A.O., 2022b. Southern range expansion of the emerald ash borer, *Agrilus planipennis*, in Russia threatens ash and olive trees in the Middle East and Southern Europe. Forests 13, 541. https://doi.org/10.3390/f13040541.

Orlova-Bienkowskaja, M.J., Bieńkowski, A.O., 2018. Modeling long-distance dispersal of emerald ash borer in European Russia and prognosis of spread of this pest to neighboring countries within next 5 years. Ecol. Evol. 8, 9295–9304. https://doi.org/10.1002/ece3.4437.

Orlova-Bienkowskaja, M.J., Volkovitsh, M.G., 2018. Are native ranges of the most destructive invasive pests well known? A case study of the native range of the emerald ash borer, *Agrilus planipennis* (Coleoptera: buprestidae). Biol. Invasions 20, 1275–1286. https://doi.org/10.1007/s10530-017-1626-7.

Orlova-Bienkowskaja, M.Ja., 2013. Dramatic expansion of the range of the invasive ash pest, buprestid beetle *Agrilus planipennis* Fairmaire, 1888 (Coleoptera, Buprestidae) in European Russia. Entomological Review 93, 1121–1128. https://doi.org/10.1134/S0013873813090042.

Peterson, D.L., Cipollini, D., 2017. Distribution, predictors, and impacts of emerald ash borer (*Agrilus planipennis*) (Coleoptera: buprestidae) Infestation of white fringetree (*Chionanthus virginicus*). Environ. Entomol. 46, 50–57. https://doi.org/10.1093/ee/nvw148.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation For Statistical Computing.

Rebek, E.J., Herms, D.A., Smitley, D.R., 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: buprestidae) among North American and Asian ash (*Fraxinus* spp.). Environ. Entomol. 37, 242–246. https://doi.org/10.1603/0046-225X(2008)37[242:IVIRTE]2.0.CO;2.

Rey, O., Estoup, A., Vonshak, M., Loiseau, A., Blanchet, S., Calcaterra, L., Chifflet, L., Rossi, J.-P., Kergoat, G.J., Foucaud, J., Orivel, J., Leponce, M., Schultz, T., Facon, B., 2012. Where do adaptive shifts occur during invasion? A multidisciplinary approach to unravelling cold adaptation in a tropical ant species invading the Mediterranean area. Ecol. Lett. 15, 1266–1275. https://doi.org/10.1111/j.1461-0248.2012.01849.x.

Riahi, K., van Vuuren, D.P., Kriegler, E., Edmonds, J., O'Neill, B.C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J.C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., Ebi, K., Hasegawa, T., Havlik, P., Humpenöder, F., Da Silva, L.A., Smith, S., Stehfest, E., Bosetti, V., Eom, J., Gernaat, D., Masui, T., Rogelj, J., Strefler, J., Drouet, L., Krey, V., Luderer, G., Harmsen, M., Takahashi, K., Baumstark, L., Doelman, J.C., Kainuma, M., Klimont, Z., Marangoni, G., Lotze-Campen, H., Obersteiner, M., Tabeau, A., Tavoni, M., 2017. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: an overview. Glob. Environ. Chang. 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009.

Sobek-Swant, S., Kluza, D.A., Cuddington, K., Lyons, D.B., 2012. Potential distribution of emerald ash borer: what can we learn from ecological niche models using Maxent and GARP? For. Ecol. Manage. 281, 23–31. https://doi.org/10.1016/j.foreco.2012.06.017.

Sun, J., Koski, T.-M., Wickham, J.D., Baranchikov, Y.N., Bushley, K.E., 2024. Emerald ash borer management and research: decades of damage and still expanding. Annu. Rev. Entomol. 69, 239–258. https://doi.org/10.1146/annurev-ento-012323-032231.

Title, P.O., Bemmels, J.B., 2018. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography 41, 291–307. https://doi.org/10.1111/ecog.02880.

Valenta, V., Moser, D., Kapeller, S., Essl, F., 2017. A new forest pest in Europe: a review of Emerald ash borer (*Agrilus planipennis*) invasion. J. Appl. Entomol. 141, 507–526. https://doi.org/10.1111/jen.12369.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecol. Modell. 220, 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010.

Varela, S., Anderson, R.P., García-Valdés, R., Fernández-González, F., 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37, 1084–1091. https://doi.org/10.1111/j.1600-0587.2013.00441.x.

Vollering, J., Halvorsen, R., Mazzoni, S., 2019. The MIAmaxent R package: variable transformation and model selection for species distribution models. Ecol. Evol. 9, 12051–12068. https://doi.org/10.1002/ece3.5654.

Wakie, T.T., Neven, L.G., Yee, W.L., Lu, Z., 2020. The establishment risk of *Lycorma delicatula* (Hemiptera: fulgoridae) in the United States and globally. J. Econ. Entomol. 113, 306–314. https://doi.org/10.1093/jee/toz259.

Webb, C.R., Mona, T., Gilligan, C.A., 2021. Predicting the potential for spread of emerald ash borer (*Agrilus planipennis*) in Great Britain: what can we learn from other affected areas? Plants People Planet 3, 402–413. https://doi.org/10.1002/ppp3.10195.

Wiens, J.J., Litvinenko, Y., Harris, L., Jezkova, T., 2019. Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. J. Biogeogr. 46, 2115–2125. https://doi.org/10.1111/jbi.13649.