



OPEN The role of host plants, land cover and bioclimate in predicting the invasiveness of *Aromia bungii* on a global scale

Enrico Ruzzier^{1,4}✉, Seunghyun Lee^{2,3}, Pietro Tirozzi⁴, Valerio Orioli⁴, Andrea Di Giulio^{1,4}, Olivia Dondina^{4,5} & Luciano Bani^{4,5}

Aromia bungii is an invasive Cerambycidae of major concern at the global scale because of the damage caused to Rosaceae. Given the major phytosanitary relevance of *A. bungii*, predicting its spread in invaded areas and identifying possible new suitable regions worldwide remains a key action to develop appropriate management practices and optimise monitoring and early detection campaigns. To improve the predictive power of the modelling framework, a habitat suitability model (HSM), which includes host plants, was combined with a bioclimatic suitability model (BSM), both of which were calibrated on native occurrences. The range of *A. bungii* was substantially limited by the bioclimate, while habitat conditions acted as limiting factors in the species' distribution. Host plants were the most important variable that positively influenced habitat suitability. Bioclimatic suitability improved as rainfall in the warmest quarter and average temperatures in the wettest quarter increased and as isothermality decreased. According to the combination of HSM and BSM, Japan is the most suitable area outside the native range of the species. In Europe, despite its high habitat suitability, it is difficult to expect a species to expand its range except through a substantial change in its bioclimatic niche.

Keywords Cerambycidae, Coleoptera, Distribution, Invasive alien species (IAS), Pest, Spatial distribution model (SDM), Wood borer

The number of invasive wood-boring beetles is growing due to increasing global transportation and climate change^{1,2}. These beetles often spend their entire life cycle or at least their immature stages within plants, making them difficult to detect during quarantine inspections³. They cause direct damage to the flora of invaded regions, resulting in significant economic impacts on forestry, agriculture, and urban street trees⁴. Among these species, longhorn beetles (Coleoptera: Cerambycidae) include some of the most notorious invaders, such as *Anoplophora glabripennis* (Motschulsky, 1854) and *A. chinensis* (Forster, 1771)⁵. More recently, additional invasive or potentially invasive longhorn beetles, including *Aromia bungii* (Faldermann, 1835)⁶, *Psacotheta hillaris* (Pascoe, 1857)⁷, *Anoplophora horsfieldii* (Hope, 1843)⁸, *Chlorophorus annularis* (Fabricius, 1787)⁹, *Xylotrechus chinensis* (Chevrolat, 1852)^{10,11}, and *Olenecamptus bilobus* (Fabricius, 1801)¹², have been reported in the Northern Hemisphere.

Among them, *Aromia bungii* (Cerambycidae: Callichromatini Swainson, 1840), also known as the red-necked long-horned beetle, is a notable emerging invasive species that causes significant damage in invaded regions⁶. Native to Eastern Asia, including China, the Korean Peninsula, Mongolia, northern Vietnam, and the Russian Far East, *A. bungii* has established populations in Japan, Germany, and Italy and has been intercepted in shipments arriving in the UK, USA, and Australia⁶. While the extent of economic damage in both native and invaded regions has not been accurately estimated, it is clear that the agricultural (e.g., peach production) and cultural (e.g., cherry blossoming festivals in Korea and Japan) economies are experiencing significant impacts^{13,14}.

Understanding the history of past invasions and predicting future dispersal are crucial when dealing with emergent invasive species such as *A. bungii*. Past dispersal routes can be inferred through population genetics. For example, population genetics suggests that Japanese invasive populations are likely the result of multiple

¹Department of Science, Università Roma Tre, Rome, Italy. ²Department of Life Sciences, Natural History Museum, London, UK. ³Department of Life Sciences, Imperial College London, Ascot, UK. ⁴Department of Earth and Environmental Sciences, University of Milano-Bicocca, Milan, Italy. ⁵National Biodiversity Future Center (NBFC), Palermo, Italy. ✉email: enrico.ruzzier@uniroma3.it

independent introductions, with China being the most plausible source, despite the conclusions being limited due to insufficient genetic data and sample coverage^{13,14}. On the other hand, future distribution and dispersal paths can be estimated via species distribution modelling (SDM).

SDMs have been widely applied in invasion biology to assess the potential spread and risk posed by invasive species on the basis of records from their native areas^{15,16}. These models remain valuable tools for predicting areas that might be suitable for colonization by invasive species beyond their native ranges, particularly during the early stages of invasion or even before invasion occurs¹⁷.

Specifically, for phytophagous beetles, such as *A. bungii*, host plant availability significantly influences their future distribution¹⁸, and host plant abundance and diversity are crucial in enhancing their establishment and dispersal^{19,20}. Therefore, integrating host plants in modelling produces more reliable distribution predictions of potentially suitable areas outside the native range of a target species^{21,22}.

In this study, we conducted an SDM using host plants, land cover, and bioclimatic variables to predict the future distribution and potential invasiveness of *Aromia bungii* on a global scale.

Methods

Aromia bungii occurrence data

Occurrences of *Aromia bungii* in its native and invaded ranges were manually downloaded from the Global Biodiversity Information Facility (GBIF, 2024)²³ and iNaturalist (<https://www.inaturalist.org/>). The occurrence data used in the analyses are updated to December 16th, 2024. Only occurrences with coordinates in degrees with at least two decimal places of resolution were included in the analyses. This allowed us to associate each occurrence with habitat data derived from land cover cartography at a grid resolution of 0.04167° (see below), corresponding to approximately 5 km at the equator. Additionally, we checked for all potential issues (e.g., duplicate records, misidentifications, etc.). The dataset was further enhanced by incorporating species occurrences from S.L.'s field surveys conducted in South Korea.

We acknowledge that presence-only data derived from repositories are inherently incomplete. Furthermore, for many species, these data may be subject to certain forms of bias. However, these biases can be identified when the species' ecology is adequately documented. Consequently, the effect of bias can be mitigated to some extent, for example, by using background points allocations based on bias maps when modelling presence-only data.

The native range of *A. bungii* was retrieved from the Catalogue of Palaearctic Coleoptera, Chrysomeloidea I²⁴, and cross-checked with Horrocks et al.⁶. The countries where the species is native are the People's Republic of China, the Democratic People's Republic of Korea, the Republic of Korea, and Vietnam. Overall, 408 species occurrences were recovered from the native range (raw data used for model calibration on native range), and 39 were retrieved from the invaded areas. Due to the limited number of occurrences available for the species' native range and the fact that spatial thinning does not necessarily enhance model performance, we opted not to apply spatial thinning to the occurrence points in agreement with Ten Caten & Dallas²⁵.

Environmental data

Bioclimatic and land cover data

Bioclimatic (19 strata) and elevation (i.e., digital elevation model (DEM)) data were downloaded from WorldClim 2.1 (available at: <http://www.worldclim.com/version2>) and averaged for the years 1970–2000, with a grid resolution of 0.00833°.

For the land cover layers, we used the Global 1-km Consensus Land Cover, updated to 2006 (available at <http://www.earthenv.org>)²⁶. The dataset contains 12 layers (evergreen/deciduous needleleaf trees [EDNT], evergreen broadleaf trees [EBT], deciduous broadleaf trees [DBT], mixed/other trees [MOT], shrubs [SHR], herbaceous vegetation [HERB], cultivated and managed vegetation [CMV], regularly flooded vegetation [RFV], urban/built-up [BU], barren lands [BR], open waters [OW] and Snow/Ice [SI]), each of which provides consensus information on the prevalence of one land-cover class, expressed as a percentage in a pixel having a resolution of 30 arc-seconds (i.e., 0.00833° resolution).

Both the bioclimatic data and land cover layers were rescaled to a 0.04167° resolution via the “aggregate” function included in the *terrapackge*²⁷ in R version 4.3.1²⁸.

To avoid collinearity issues, a preselection of bioclimatic covariates (removing those strongly correlated, i.e., those with an absolute value of Pearson's correlation coefficient higher than 0.7²⁹) was performed via the “vifcor” function of the *usdmR* package³⁰.

Host plant taxa

Aromia bungii host plants were obtained from Horrocks et al.⁶. If more than one species belonging to the same genus was known as a host plant or if congeneric species could be used as vicariant host plant species in areas potentially exposed to invasion risk, we used the genus as the host taxon. Otherwise, we used a single species as the host plant. The host taxa were *Prunus* spp., *Malus* spp., *Pyrus* spp., *Eriobotrya japonica* (Thunb.) (Rosaceae), *Populus* spp. (Salicaceae), *Albizia julibrissin* Durazz. (Fabaceae), *Camellia sinensis* (L.) Kuntze (Theaceae), *Castanea* spp. Blume (Fagaceae), *Diospyros kaki* Thunb. (Ebenaceae), *Ilex* spp. Sims (Aquifoliaceae), *Juglans* spp. L. (Juglandaceae), *Morus* spp. L. (Moraceae), and *Punica granatum* L. (Lythraceae).

For host plants at the genus level, data for all occurrences of each single species pertaining to the genus were downloaded from GBIF via the “occ_data” function available from the *rgbifR* package³¹. The same procedure was adopted for host plants at the species level.

The data for each host plant taxon were then combined into a single layer of georeferenced points (through the “as.ppp” function from the *spatstat* package^{32,33}) to produce a density map with a kernel interpolation procedure via the “density.ppp” function from *spatstat*. The kernel interpolation radius of the points was estimated via the “bw.ppl” function from *spatstat*. We used the logarithm of the kernel density maps (i.e., the quantitative range

map of each host plant taxon) to reduce possible bias in the host sampling effort. To avoid overestimating the distribution of each host taxon, the logarithm of their density layer was subsequently multiplied for the land cover type associated with the taxon habit (e.g., deciduous broadleaf trees) and/or the land cover type in which the taxon can be found if of economic interest (e.g., cultivated and managed vegetation); see Table 1 for the associations between the host plant taxon and land cover. This approach allows for the generation of a proxy for the quantitative distribution map of each host plant. Finally, as the last step, we produced the overall host plant layer, extracting the maximum density value retrieved in each grid cell among those of all the host plant layers. Since host plants can replace each other on a local scale, to avoid possible overestimation of the host plant density, we used the maximum density value instead of calculating the sum among all density layers.

Data on host plant taxa were downloaded from the GBIF on June 30, 2024 (range maps for all host taxa are available in the “.tiff” format in the supplementary materials).

Species distribution modelling

The modelling procedure was based on the ensemble modelling approach^{34,35} since the combined output derived from an ensemble model should tendentially have higher explanatory and predictive performances than a model obtained from a single algorithm^{36–40}.

To better evaluate the contribution of environmental variables in explaining the spatial distribution of the species, bioclimatic and habitat variables were modelled into two separate ensemble models, and their respective output maps were combined in their spatial product, following the framework given in Ruzzier et al.²². This choice stems from the evidence that combining scenopoetic (bioclimatic; *sensu* Hortal et al.⁴¹) variables with those of a local character (habitat) would result in an underestimation of variables' importance (see Ruzzier et al.²² for further details).

SDMs based on presence-only data rely directly on pseudoabsence (PA) or background data⁴². Therefore, PA selection was performed separately for the bioclimatic and habitat modelling procedures, given their different requirements in terms of PA allocation for the HSM with respect to the bioclimatic suitability model (BSM)²².

To assess the effects of habitat covariates on HSM, PAs should be identified strictly within known native species ranges^{22,43–45}. Starting from this consideration, the HSM was developed over a narrow geographic area around occurrence data (narrow native calibration range; Fig. S1 in Sup. Mat. 1; for more details, refer to the PA selection for the HSM in the Methods section). Japan and Taiwan were excluded from the HSM calibration area (i.e., countries excluded from PA allocation) because they are outside the putative native range of the species; in these countries, *A. bungii* is naturally absent, presumably because of the existence of a major biogeographic barrier (ocean) that the species is unable to overcome, whereas present occurrences are the result of human introduction¹³. For BSM, we assessed the effects of bioclimatic variables over a wider geographic area centred on *A. bungii* occurrences (wide calibration range, between 0° and 70° N and 70° E and 160°E; Fig. S2 in Sup. Mat. 1); in this case, we considered all areas geographically contiguous with *A. bungii* occurrences (i.e., mainland Central

Host plant taxon	Land cover					
	DBT	MOT	SHR	CMV	EBT	BU
<i>Albizia julibrissin</i>	x		x	x		x
<i>Camellia sinensis</i>				x	x	x
<i>Castanea</i> spp.	x	x		x		
<i>Diospyros kaki</i>	x			x		
<i>Eriobotrya japonica</i>	x			x		x
<i>Ilex</i> spp.		x	x		x	
<i>Juglans</i> spp.	x			x		
<i>Koelreuteria</i> spp.	x		x	x		x
<i>Malus</i> spp.	x			x		
<i>Morus</i> spp.	x		x	x		x
<i>Populus</i> spp.	x			x		x
<i>Prunus</i> spp.	x		x	x		x
<i>Punica granatum</i>	x			x		x
<i>Pyrus</i> spp.	x			x		
<i>Robinia</i> spp.	x		x	x		x
<i>Rubus</i> spp.	x	x	x	x	x	x
<i>Salix</i> spp.	x			x		x
<i>Xylosma racemosus</i>			x	x	x	x
<i>Zanthoxylum bungeanum</i>	x		x	x		x

Table 1. Schematic associations between the host plant taxon and land cover (DBT: deciduous broadleaf trees; MOT: mixed/other trees; SHR: shrubs; CMV: cultivated and managed vegetation; EBT: evergreen broadleaf trees; BU: urban/built-up).

and East Asia), removing islands belonging to the Indomalayan bioregion due to biogeographic discontinuity rather than the actual lack of suitable bioclimatic conditions.

The HSM and BSM were developed via a use-vs-availability approach³⁵, and both models return a map of suitability in terms of species presence probability. From the spatial product of the two maps of species presence probabilities, we obtained an overall suitability map, which returns the probability of finding the species in a given location on the basis of both habitat and bioclimatic covariates (see Ruzzier et al.²² for details).

The modelling procedure was performed via the *biomod2* package version 4.2–6-2⁴⁶. In order to have just one occurrence per grid cell, we set the option “filter.raster=T” in the formatting data step (“BIOMOD_FormatingData” function).

The generalized additive model (GAM), generalized boosting model (GBM), random forest (RF), and maximum entropy (MAXNET) were used as modelling algorithms. The number of PAs was set to 4 times the number of occurrences, and the sets of PAs used were 20 for the HSM and 5 for the BSM^{22,47}; the models were tested via 5-fold cross-validation runs²².

While developing the HSM, the “disk” strategy was adopted to randomly select PAs within a buffer ranging from 2.5 to 500 km to species occurrence. The lower limit of 2.5 km was established to prevent PAs from being placed too close to occurrence points, thereby minimizing the likelihood of locating PAs within suitable habitats. The upper limit of 500 km was set to avoid placing PAs in regions where differences are predominantly influenced by variations in bioclimatic conditions²².

For the BSM, a random selection of PAs was adopted in the entire selected area (other than the ocean). This approach of PAs allocation allows for a more consistent evaluation of the effect of bioclimatic covariates through the ratio created between presences and PAs along the latitudinal gradient²².

Models were calibrated using the settings included in the “bigboss” strategy, in accordance with the recommendations provided by the *biomod2* developers⁴⁶. As an alternative, we conducted a tuning process for the algorithms (GAM, GB, and RF; not for MAXNET, as the “bm_tuning” function cannot be applied in the *biomod2* package). However, this approach proved to be less effective compared to the “bigboss” strategy. This conclusion was based on our empirical evidence. Specifically, in the tuning process, all sets of PAs are used to optimize the algorithms. Conversely, when using the “bigboss” strategy, the sets of PAs that are ineffective at distinguishing differences in environmental composition between occurrence points and background points are discarded.

Given the lack of external data to evaluate the models’ accuracy, a 5 cross-validations data-splitting procedure was performed using 80% of the data as the training set with the remaining 20% as the validation set. Each of the models obtained from both the HSM and BSM was validated via three validation metrics: the area under the receiver operating characteristic (ROC) curve (AUC⁴⁸), the true skill statistic (TSS⁴⁹), and Cohen’s kappa⁵⁰, with thresholds of 0.9, 0.7, and 0.65, respectively^{49,51,52}.

Habitat (HSM) and bioclimatic (BSM) ensemble models were calculated via the “EMwmean” function. To account for the performance of each individual model used in building the ensemble model, we weighted its contribution by setting a “proportional” option decay⁴⁶. A three-run permutation procedure was used to assess the importance of each variable included in the ensemble model. The same ensemble model framework was adopted for both the HSM and the BSM.

The HSM and BSM were projected to the following four extents: (a) native countries only; (b) global, (c) Eastern and Southeast Asia (ESA), and (d) Western Palearctic (WP; excluding Fennoscandia). The ESA projection provides a detailed map of the native range and the closely invaded area. The WP projection provides a map of where adventive populations were found.

The Boyce index^{53,54} was used to evaluate the modelling performance and was applied to the HSM, BSM, and overall suitability map for the narrow native calibration range (*modEvA* package⁵³).

As the final step, the multivariate environmental similarity surface index (MESS¹⁵), implemented in the *dismo* package⁵⁶, was used to detect possible extrapolation effects of the HSM and BSM at the global scale.

Results

Assessment of the performance of species distribution models and determination of influential variables

Overall, we used 202 occurrences to calibrate HSM and BSM in the *A. bungii* native range. Among the 12 land use layers, we excluded a priori from the HSM procedures of the SI and OW. None of the remaining land use covariates were pairwise correlated. After the VIF analysis, six of the 19 bioclimatic variables were retained for the BSM procedure (Bio2, Bio3, Bio8, Bio15, Bio18, and Bio19).

Overall, we developed 1200 models for the HSM (4 modelling algorithms × 20 sets of PAs × 5 cross-validation runs × 3 validation metrics) and 300 models for the BSM (4 modelling algorithms × 5 sets of PAs × 5 cross-validation runs × 3 validation metrics).

For the HSM, according to the ROC curve, 250 out of 400 (62.5%) models were outstanding (ROC > 0.9); following the TSS, 66 out of 400 (16.5%) models exhibited excellent performance (TSS > 0.7), and according to the KAPPA, 140 out of 400 (35.0%) models exhibited substantial performance (KAPPA > 0.6). Nevertheless, according to the three metrics of validation, virtually all the models were adequate since they exceeded the critical thresholds that define a successful model (ROC > 0.7, TSS > 0.5, KAPPA > 0.4). For the BSM, according to the ROC curve, all the models were outstanding (ROC > 0.9). Following the TSS, 97 out of 100 achieved excellent performance (TSS > 0.7), and according to the KAPPA, 97 out of 100 achieved substantial performance (KAPPA > 0.6). Additionally, for the BSM, all the models were found to be adequate, exceeding the critical thresholds for the three validation metrics (see Tables S1 and S2 in Sup. Mat. 2 for the validation metrics obtained for the HSM and BSM).

The best-performing models (456 out of 1200 for the HSM and 294 out of 300 for the BSM) were retained to realize the HSM and BSM ensemble models projected for the four extents. The ensemble model process allowed us to obtain the importance of covariates (Tables S3 and S4 in Sup. Mat. 2) and the corresponding response curves for the HSM and BSM; to obtain each single variable effect, we set all other variables to their median value (Figs. S3 and S4 in Sup. Mat. 1). Since all three HSM maps obtained via the ROC, TSS, and KAPPA metrics were highly correlated (pairwise Pearson's correlation > 0.997), we decided to use the HSM built after ROC model selection. The same applied to the BSM maps, for which the pairwise Pearson's correlation was greater than 0.996. Habitat suitability was affected mostly by host plants (variable importance HP.max: 0.504), followed by evergreen broadleaf trees (EBT: 0.149), cultivated and managed vegetation (CMV: 0.144), built-up areas (BU: 0.124), and herbaceous vegetation (0.104). Host plants and built-up areas had positive effects on the probability of species presence, whereas we found negative effects for evergreen broadleaf trees, cultivated and managed vegetation and herbaceous vegetation. Bioclimatic suitability was substantially and positively affected by the mean temperature of the wettest quarter (BIO8: 0.431) and the precipitation of the warmest quarter (variable importance BIO18: 0.277) and; in contrast, isothermality (BIO3: 0.360) was found to negatively influence the probability of species presence.

The Boyce indices used for the validation of both the HSM map (habitat suitability map and its 95% confidence intervals; Fig. S5 in Sup. Mat. 1) and the BSM map (bioclimatic suitability map and its 95% confidence intervals; Fig. S6 in Sup. Mat. 1) projected on their calibration ranges returned 0.983 and 0.997, respectively (see Figs. S7 and S8 in Sup. Mat. 1 for the Boyce graphs).

The overall suitability map (Fig. S9 in Sup. Mat. 1), which was calculated as the spatial product of the habitat suitability and bioclimatic suitability maps for the narrow native calibration range, yielded a Boyce index of 0.988 (see Fig. S10 in Sup. Mat. 1 for the Boyce graph). The good modelling performance can also be observed in the overall suitability map, where the presence points of *A. bungii* clustered within areas with a high probability of occurrence of the species (Fig. S9 in Sup. Mat. 1).

MESS analyses of habitat and bioclimatic variables revealed that projections were not substantially subject to extrapolation (Figs. S11 a and b in Sup. Mat. 1).

SDM projections at the global, ESA, and WP levels

The projections of HSM and BSM at the global, ESA, and WP scales allowed us to obtain habitat, bioclimatic, and overall species suitability maps at the three mentioned geographic extents (see Figs. 1 and 2, and 3, respectively).

In addition to the native range of *A. bungii*, according to the global habitat suitability map, the most favourable areas for the species were in Japan, different parts of northern and southern Australia, the Cape Region in South Africa, from the lower to high latitudes of the Western Palaearctic, central parts of European Russia and the Caucasus, eastern North America from the Gulf of Mexico to the Great Lakes Region, Pacific Southwest North America, including Texas and Baja California, central Mexico, Southeast Brazil, and multiple areas in central Argentina (Fig. 1a). Notably, although many areas appear potentially suitable due to the availability of habitats, ecological knowledge regarding *A. bungii* has led to the exclusion of areas located at relatively high latitudes that may be suitable for the species due to bioclimatic constraints. In contrast, the global bioclimatic suitability map highlights suitable areas only in Japan. However, moderate suitability was observed from the area south of the Great Lakes region towards the east. Slightly suitable areas appeared in central and eastern Europe and southern territories of European Russia (Fig. 1b). The overall suitability map, in addition to the native area, revealed three areas with different levels of suitability at the global scale (Fig. 1c): (a) Japan was the area with the highest suitability, except for the island of Hokkaido; (b) the southern area of the Great Lakes Region was moderately suitable, whereas other areas in eastern North America were only slightly suitable; and (c) central and eastern Europe up to the southern territories of European Russia appeared suitable, although to a very limited extent.

The habitat suitability map of the ESA extent revealed a large availability of suitable areas (Fig. 2a), although in the native range, the habitat availability was rather limited to some areas along the coasts of the East China Sea and the Republic of Korea. Outside the native range of *A. bungii*, suitable areas were identified (a) along the land strip from Tyumen Oblast to Prymorsky Krai (Russia), which was found to be moderately to highly suitable; (b) in the Indian Peninsula, which was extensively but only moderately suitable; (c) in Japan, which was highly suitable overall; and (d) on the western coasts of Taiwan, which was highly suitable. The bioclimatic suitability map (Fig. 2b) highlights a wide and continuous suitable area but is limited to eastern China, the Democratic People's Republic of Korea, and the Republic of Korea. A separate highly favourable bioclimatic area corresponds to Japan (Hokkaido excluded). Considering the overall suitability map for SE (Fig. 2c), the most suitable areas were limited to the Republic of Korea and coastal areas of China, where the species is native. In addition, highly suitable areas were also found in the invaded range of Japan, particularly on Honshu, Shikoku, and Kyushu Islands.

The habitat suitability map of the Western Palaearctic (excluding Fennoscandia), the only area outside Asia where *A. bungii* presented adventive populations, appeared highly suitable to a large extent, except for Ireland and the western parts of Great Britain and central and Eastern Turkey. All desertic as well as alpine habitats were not suitable (Fig. 3a). However, the area was poorly suitable from a bioclimatic perspective (Fig. 3b). The overall suitability map of the western Palaearctic (Fig. 3c) displayed generally scarce suitability for the entire geographic extent, with the probability of species presence rarely exceeding 0.10.

Discussion

It is important to highlight that the species suitability must be interpreted according to the overall suitability map, which is defined by the combination of the HSM and BSM maps.

Based on the bioclimatic suitability map derived for the native range, the overall distribution of *A. bungii* appears to be largely constrained by bioclimatic conditions. However, within the bioclimatically suitable areas,

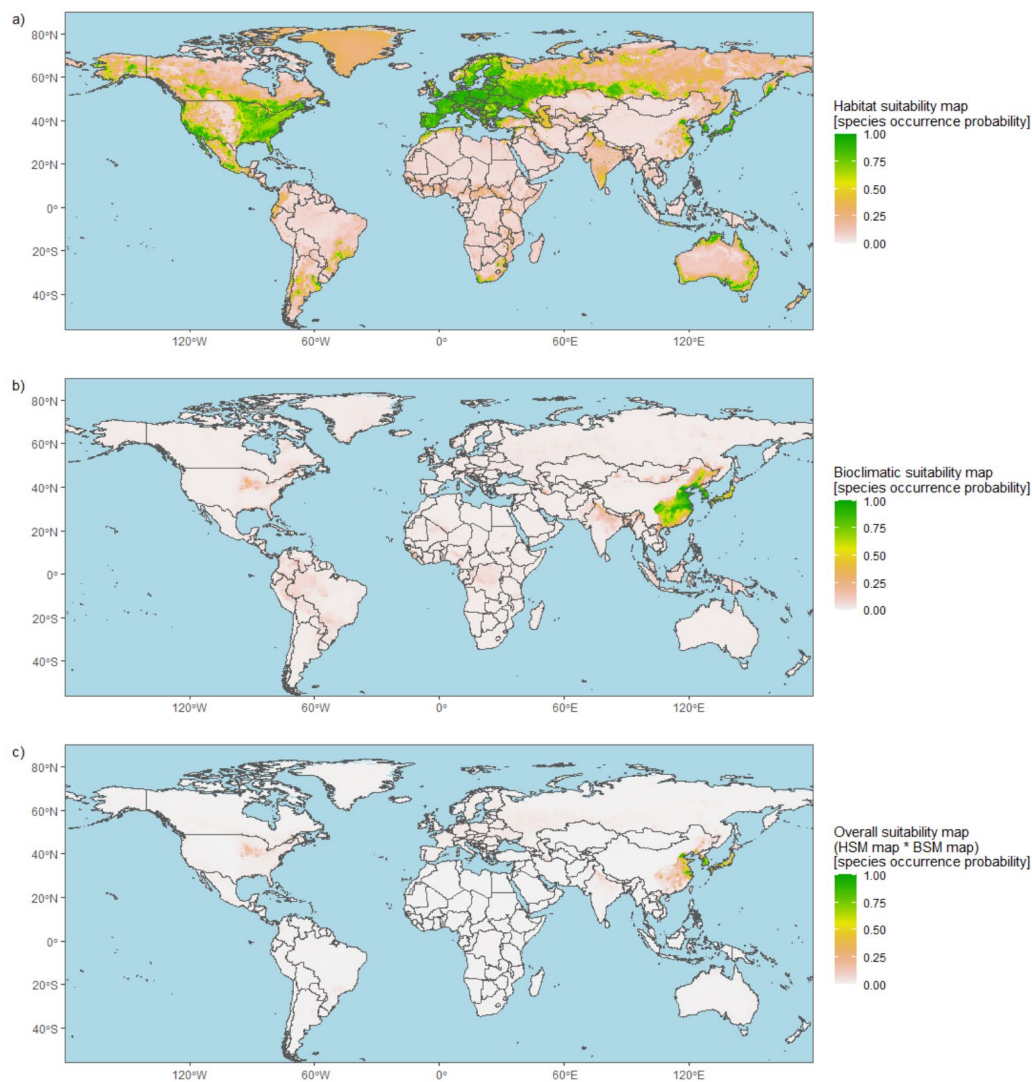


Fig. 1. World projections of *A. bungii* suitability maps; (a) habitat suitability map; (b) bioclimatic suitability map; (c) overall suitability map (maps were created using the libraries *sj*^{57,58}, *rnatuarearth*⁵⁹ and *ggplot2*⁶⁰ in R).

habitat emerged as a limiting factor in the species distribution pattern, as shown by the habitat suitability map. When considering the overall suitability map, the combined influence of bioclimatic and habitat covariates on the species' distribution pattern becomes even more apparent.

As expected, as an obligate endophytophagous and xylophagous species, *A. bungii* responds primarily to the presence of its host plants when bioclimatic needs are satisfied. Indeed, the importance of the host plant covariate is slightly more than four times greater than that of the only other covariate with positive effect, the built-up area (BU). A possible bias in species data collection may also contribute to the positive relationship between *Aromia bungii* and BU; occurrences of *A. bungii* might be more easily recorded in areas frequently visited by humans, who are therefore more likely to provide records associated with urban contexts. Notably, the species' native area has been densely inhabited by humans since historical times; therefore, progressive anthropisation may also have affected its distribution. Indeed, it is possible that, at least in some areas, *A. bungii* might behave as a synanthropic species since the distribution of its host plants has been widely modified because of economic interest in gardening or agriculture. However, the importance of BU is substantially lower than that of host plants. The effect of evergreen-broadleaf trees (EBT) is negative, as most of the host species of *A. bungii* are deciduous broadleaf trees; this could be linked to the negative effects of these areas located outside the host plant range. Furthermore, cultivated and managed areas (CMV) negatively influence the presence of *A. bungii*. This could be linked to the negative effects of these areas located outside the host plants range. The effect of habitat management, together with the connectivity between suitable areas as factors influencing the probability of species presence, is consistent with the findings of Zhang et al.⁶¹ for a native context, and Osawa et al.⁶² for an invaded area.

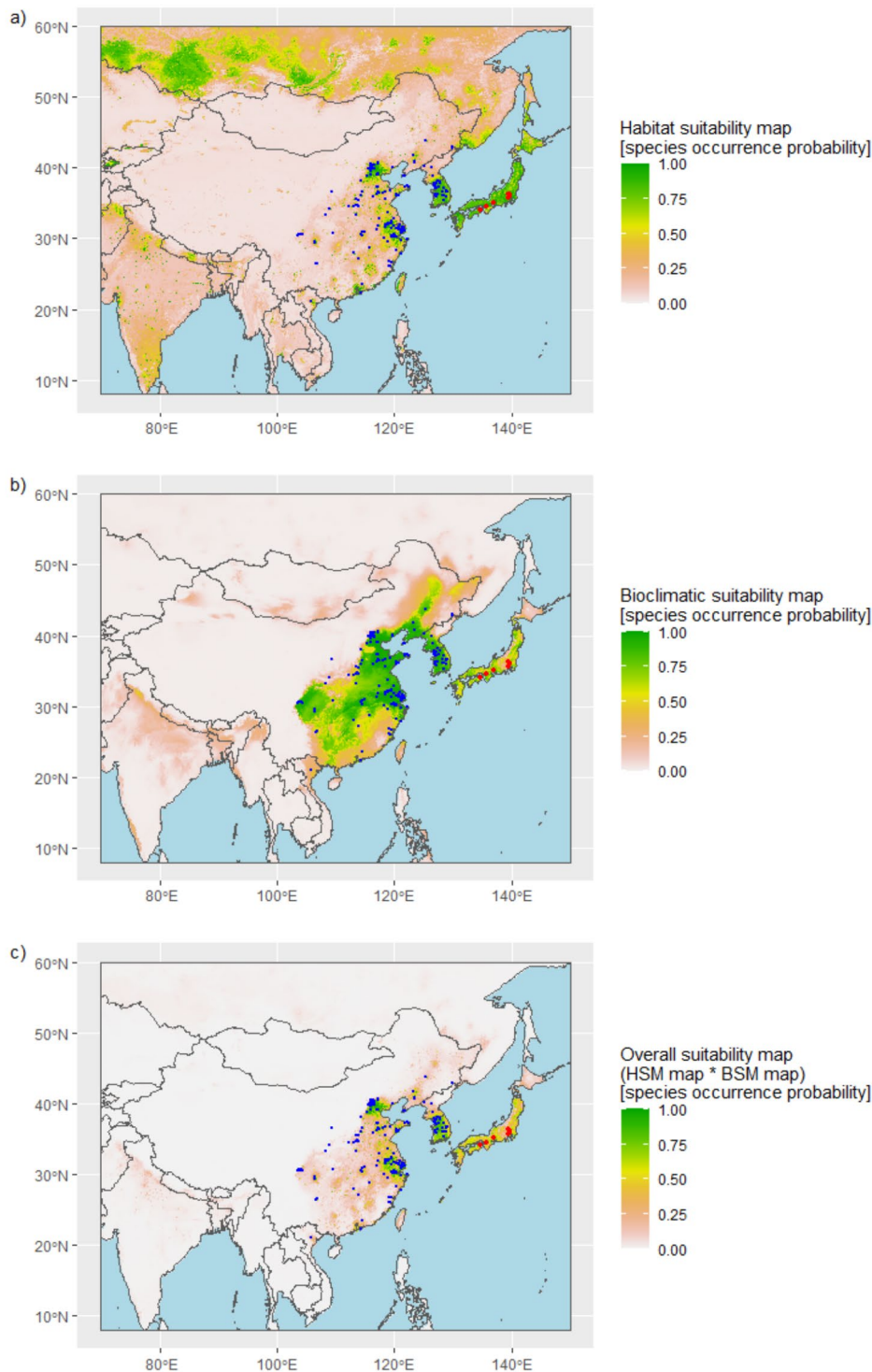


Fig. 2. Eastern and Southeast Asia (ESA) projections of *A. bungii* suitability maps; **(a)** habitat suitability map; **(b)** bioclimatic suitability map; **(c)** overall suitability map (maps were created using the libraries *sf*^{57,58}, *rnaturlaearth*⁵⁹ and *ggplot2*⁶⁰ in R).

Aromia bungii was positively influenced by warm temperatures, requiring 25–30 °C degrees during the warmest quarter of the year (Bio8), in areas with a marked seasonality (i.e., low isothermality index; Bio3 < 25), and with cumulative precipitation above 600 mm in the warmest quarter (Bio18). This result is partially in agreement with that of Horrocks et al.⁶. Indeed, in both our and Horrocks et al. studies, Bio18 was the most important variable defining the bioclimatic suitability for the species. However, discrepancies in the importance of other bioclimatic variables could derive from the different criteria used for the identification of the calibration

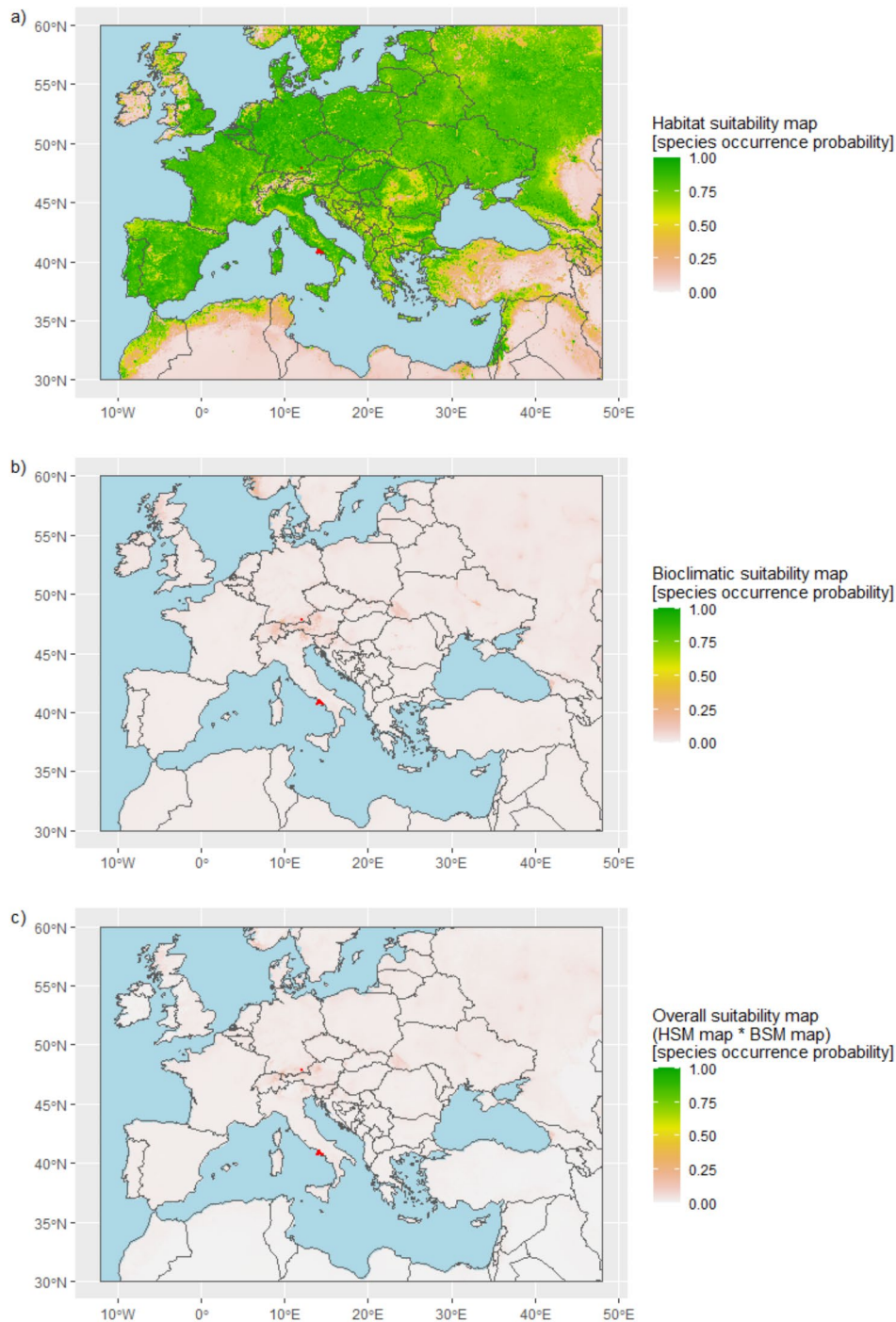


Fig. 3. Western Palaearctic (WP) projections of *A. bungii* suitability maps; **(a)** habitat suitability map; **(b)** bioclimatic suitability map; **(c)** overall suitability map (maps were created using the libraries *sf*^{57,58}, *rnatuarearth*⁵⁹ and *ggplot2*⁶⁰ in R).

area (calibration area identified within the bioregion of the species native range, in the present study, vs. worldwide, in Horrocks et al.⁶), which in turn may have influenced both the set of bioclimatic variables used in the modelling framework and the allocation of PAs; furthermore, the different algorithms may have produced appreciable differences between the two studies (ensemble model based on four algorithms, present study, vs. single algorithm, Horrocks et al.⁶). Some discrepancies in the variables used in the model developed by Zhang et al.⁶¹ and that of our study can be attributed to the two different calibration areas. Furthermore, the algorithms employed also differ between the two studies. Nonetheless, the suitable areas for *A. bungii* in China are essentially equivalent.

However, it should be highlighted how our and Horrocks et al.⁶ studies, even though one is calibrated in an area only slightly larger than the native range (i.e., within the biogeographical region of the species) and the other on a global scale, have produced similar bioclimatic suitability maps. These maps indicated that there were no highly bioclimatic suitable areas (e.g., probability of occurrence > 0.20) outside the native range that invaded Japan. The similarity of the results could be because, although Horrocks et al.⁶ allocated PAs on a global scale, PAs were never located in areas bioclimatically similar to those found in the native range and Japan, as such conditions strictly occur only there.

The global-scale habitat suitability map revealed large areas of potentially favourable establishment of *A. bungii* in various biogeographic areas of the world. This aspect has been analysed by us for the first time, and therefore it is not possible to compare it with other studies. This is probably due to the wide native distribution of host plants, combined with the fact that these plants have expanded in range and are largely modified by humans due to their economic interests. Conversely, the global-scale bioclimatic suitability map highlighted generally poor favourable conditions for *A. bungii* establishment, except for a few areas in East and Southeast Asia. The availability of suitable areas, according to habitat and bioclimatic conditions, highlights that favourable areas for *A. bungii* globally are restricted to some coastal areas of China towards the Yellow Sea, the Korean Peninsula, and Japan.

The predicted habitat suitability map for the ESA revealed multiple favourable areas for *A. bungii*. These areas encompass southern parts of eastern Siberia, the Indian subcontinent, coastal areas of China, and Japan. This pattern of suitability differed completely from that of the bioclimate, where the most suitable areas were strictly limited to the central and coastal areas of China, the Korean peninsula, and Japan. This highlights how bioclimatic conditions are an ecological forcing driver of particular importance in shaping the *A. bungii* range. This can be appreciated by observing the distribution of occurrences, both native and invasive, that fell right within the most suitable bioclimatic areas in the ESA. However, within this bioclimatically suitable area, habitat conditions play an important role in defining areas that are truly suitable for *A. bungii*. When the bioclimatic requirements were met, the species was detected only in areas with suitable habitats. The presence of *A. bungii* in Japan, with introduced and stable populations, is linked to the overall high suitability of this territory for the species in terms of both habitat and climate. The natural absence of *A. bungii* in the area is most likely attributable to the presence of the sea, which acts as an important biogeographic barrier and separates Japan from the native range of the species. The role of the sea as a barrier is consistent with genetic data obtained for native Korean populations and invasive populations in Japan^{13,14}.

The WP is the only area on a global scale where two adventive populations have been detected: Rosenheim (Germany⁶³) and the Gulf of Naples (Italy⁶⁴). The habitat suitability map revealed that the populations were in highly potentially favourable areas, likely due to the high availability of host plants within the wide anthropised landscapes in Europe. Given the nature of the host plants, which are of ornamental and fruit-growing interest, their abundance could be favoured even more by anthropised areas, as evidenced by the positive effects of land use, built-up areas and cultivated and managed vegetation. Conversely, the bioclimatic suitability map in the WP showed how the adventive populations were in poor to unfavourable areas. The very low bioclimatic suitability in the Mediterranean area is probably due mostly to the scarcity of rainfall during the warm period of the year, contrary to the requirements of the ecology of the species.

Conclusions

To properly assess the effects of covariates acting at local scales compared to those operating at broader scales, a two-step modeling approach is required. This ensures that the two types of variables do not obscure each other's effects. Our approach has thus enabled a more effective evaluation of the impact of host plants and habitat context (included in the HSM), independently from bioclimatic variables (included in the BSM). The latter are, in fact, the variables most used to assess the invasiveness of non-native species at a global scale. However, this approach allows for the definition of suitable ranges but does not identify the specific areas within them that are invadable by a non-native species. By combining the two models (HSM x BSM), the two-step approach provides a way to assess, on a global scale, the areas that are truly invadable by *A. bungii* within bioclimatically favourable ranges.

In conclusion, based on the modelling findings, *A. bungii* would appear to lack the adaptive plasticity to become a particularly invasive species in contexts other than Southeast Asia. This limitation is inferred from the fact that in native areas, the species remains confined to bioclimatically favourable regions and does not spread outside them despite the wide availability of suitable habitats.

The fact that *A. bungii* is widely invasive in Japan is explained by the simultaneous natural presence of both bioclimatic and habitat conditions favourable to the species. Therefore, although Japan is geographically close to the mainland range of the species, the sea acted as an important geographic barrier that prevented island natural colonization.

It is therefore highly probable that the invasive populations of *A. bungii* in Japan, unlike those observed with other invasive species, did not undergo any ecological niche shift having already found in the invaded area all the conditions most favourable to them and not having been subjected to any selection events during the invasion process.

At present, there do not seem to be any ideal areas for the species globally outside of those identified in Southeast Asia. *Aromia bungii* appears to have very little ability to spread naturally in the Western Palaearctic. In fact, it seems improbable that introduced populations of Europe, despite the large availability of suitable habitat, could significantly expand their range because of inadequate bioclimatic conditions. However, it will be necessary to consider the areas of North America south of the Great Lakes, where models indicate areas whose suitability, though almost negligible, should not be ignored.

In general, introduced populations of *A. bungii* could hardly be expected to expand their range, except through a change in their bioclimatic niche, a process that, however, would seem unlikely based on the model calibrated on the native area and its projection on Southeast Asia.

Data availability

The datasets and the R code used during the current study available from the corresponding author on reasonable request.

Received: 26 September 2024; Accepted: 13 January 2025

Published online: 17 January 2025

References

- Haack, R. A. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Can. J. Res.* **36**, 269–288 (2006).
- Wu, Y. et al. Identification of wood-boring beetles (Cerambycidae and Buprestidae) intercepted in trade-associated solid wood packaging material using DNA barcoding and morphology. *Sci. Rep.* **7**, 40316. <https://doi.org/10.1038/srep40316> (2017).
- Eyre, D. & Haack, R. A. Invasive cerambycid pests and biosecurity measures in Cerambycidae of the World (ed. Wang, Q) 577–632. (CRC, (2017).
- Aukema, J. et al. Economic impacts of nonnative forest insects in the United States. *PLoS ONE*. **6**, e24587. <https://doi.org/10.1371/journal.pone.0024587> (2011).
- Haack, R. A., Hérard, F., Sun, J. & Turgeon, J. J. Managing invasive populations of Asian longhorn beetle and citrus longhorn beetle: a worldwide perspective. *Annu. Rev. Entomol.* **55**, 521–546. <https://doi.org/10.1146/annurev-ento-112408-085427> (2010).
- Horrocks, K. J. et al. Biology, impact, management and potential distribution of *Aromia bungii*, a major threat to fruit crops around the world. *J. Pest. Sci.* **97**, 1725–1747; (2024). <https://doi.org/10.1007/s10340-024-01767-0> (2024).
- Lupi, D. et al. Exploring the range expansion of the yellow-spotted longhorn beetle *Psacotha hilaris* in northern Italy. *Agric. Entomol.* **25**, 511–521. <https://doi.org/10.1111/afe.12570> (2023).
- Lee, S. et al. Establishment of nonnative *Anoplophora horsfieldii* (Coleoptera: Cerambycidae) in South Korea. *J. Integr. Pest Manag.* **14** <https://doi.org/10.1093/jipm/pmad008> (2023).
- Seidel, M. et al. Citizen scientists significantly improve our knowledge on the nonnative longhorn beetle *Chlorophorus annularis* (Fabricius, 1787)(Coleoptera, Cerambycidae) in Europe. *BioRisk* **16**, 1–13. <https://doi.org/10.3897/biorisk.16.61099> (2021).
- Sarto i Monteys, V. Torras i Tutusaus, G. A new alien invasive longhorn beetle, *Xylotrechus chinensis* (Cerambycidae), is infesting mulberries in Catalonia (Spain). *Insects* **9**, 52. <https://doi.org/10.3390/insects9020052> (2018).
- Ruzzier, E. et al. New records of non-native Coleoptera in Italy. *Biodivers. Data J.* **11**, e111487. <https://doi.org/10.3897/BDJ.11.e111487> (2023a).
- Ruzzier, E., de Queros, C. R., Mas, H. & Di Giulio, A. Simultaneous detections of *Olenecamptus Bilobus* (Fabricius, 1801) (Cerambycidae, Dorcaschematini) in Europe. *Biodivers. Data J.* **11**, e114432. <https://doi.org/10.3897/BDJ.11.e114432> (2023b).
- Lee, S., Cha, D., Nam, Y. & Jung, J. Genetic diversity of a rising invasive pest in the native range: Population genetic structure of *Aromia Bungii* (Coleoptera: Cerambycidae) in South Korea. *Diversity* **13**, 582. <https://doi.org/10.3390/d13110582> (2021).
- Tamura, S. & Shoda-Kagaya, E. Genetic differences among established populations of *Aromia Bungii* (Faldermann, 1835)(Coleoptera: Cerambycidae) in Japan: suggestion of multiple introductions. *Insects* **13**, 217. <https://doi.org/10.3390/insects13020217> (2022).
- Elith, J., Kearney, M. & Phillips, S. The art of modelling range-shifting species. *Methods Ecol. Evol.* **1**, 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x> (2010).
- Mainali, K. P. et al. Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Glob Change Biol.* **21**, 4464–4480. <https://doi.org/10.1111/gcb.13038> (2015).
- Srivastava, V., Roe, A. D., Keena, M. A., Hamelin, R. C. & Griess, V. C. Oh the places they'll go: improving species distribution modelling for invasive forest pests in an uncertain world. *Biol. Invasions.* **23**, 297–349. <https://doi.org/10.1007/s10530-020-02372-9> (2021).
- Berzitis, E. A., Minigan, J. N., Hallett, R. H. & Newman, J. A. Climate and host plant availability impact the future distribution of the bean leaf beetle (*Cerotoma trifurcata*). *Glob Change Biol.* **20**, 2778–2792. <https://doi.org/10.1111/gcb.12557> (2014).
- Dethier, V. G. Food-plant distribution and density and larval dispersal as factors affecting insect populations. *Can. Entomol.* **91**, 581–596 (1959).
- Harrison, S. Resources and dispersal as factors limiting a population of the tussock moth (*Orgyia vetusta*), a flightless defoliator. *Oecologia* **99**, 27–34 (1994).
- Dang, Y. Q. et al. 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.* **94**, 981–990. <https://doi.org/10.1007/s10340-020-01308-5> (2021).
- Ruzzier, E. et al. A two-step species distribution modelling to disentangle the effect of habitat and bioclimatic covariates on *Psacotha Hilaris*, a potentially invasive species. *Biol. Invasions.* **26**, 1861–1881. <https://doi.org/10.1007/s10530-024-03283-9> (2024).
- GBIF.org. *Aromia bungii* GBIF Occurrence Download (2024). <https://doi.org/10.15468/dl.tqvvgp>
- Danilevsky, M. L. *Catalogue of Palaearctic Coleoptera, Chrysomeloidea I (Vesperiidae, Disteniidae, Cerambycidae)* Brill, (2020).
- Ten Caten, C. & Dallas, T. Thinning occurrence points does not improve species distribution model performance. *Ecosphere* **14**, e4703. <https://doi.org/10.1002/ecs2.4703> (2023).
- Tuanmu, M. N. & Jetz, W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Glob Ecol. Biogeogr.* **23**, 1031–1045. <https://doi.org/10.1111/gcb.12182> (2014).
- Hijmans, R. *terra: Spatial Data Analysis*. R package version 1.7–78 (2024). <https://CRAN.R-project.org/package=terra>
- R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (2023). <https://www.R-project.org>
- Dormann, C. F. et al. 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> (2013).
- Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K. & Toxopeus, A. G. Where is positional uncertainty a problem for species distribution modelling? *Ecography* **37**, 191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x> (2014).
- Chamberlain, S. et al. *rgbif: Interface to the global biodiversity information facility*. R package version 3.7.9; (2024). <https://CRAN.R-project.org/package=rgbif>
- Baddeley, A., Turner, R. & spatstat An R package for analysing spatial point patterns. *J. Stat. Softw.* **12**, 1–42. <https://doi.org/10.18637/jss.v012.i06> (2005).
- Baddeley, A., Rubak, E. & Turner, R. *Spatial Point Patterns: Methodology and Applications with R* (CRC, 2005).
- Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47. <https://doi.org/10.1016/j.tree.2006.09.010> (2007).

35. Guisan, A., Thuiller, W. & Zimmermann, N. E. *Habitat Suitability and Distribution Models: With Applications in R* (Cambridge University Press, 2017).
36. Breiner, F. T., Guisan, A., Bergamini, A. & Nobis, M. P. Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol. Evol.* **6**, 1210–1218. <https://doi.org/10.1111/2041-210X.12403> (2015).
37. Hao, T., Elith, J., Guillera-Arroita, G. & Lahoz-Monfort, J. J. A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Divers. Distrib.* **25**, 839–852. <https://doi.org/10.1111/ddi.12892> (2019).
38. Früh, L. et al. Modelling the potential distribution of an invasive mosquito species: comparative evaluation of four machine learning methods and their combinations. *Ecol. Model.* **388**, 136–144. <https://doi.org/10.1016/j.ecolmodel.2018.08.011> (2018).
39. Hao, T., Elith, J., Lahoz-Monfort, J. J. & Guillera-Arroita, G. Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography* **43**, 549–558. <https://doi.org/10.1111/ecog.04890> (2020).
40. Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J. & Elith, J. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecol. Monogr.* **92**, e01486. <https://doi.org/10.1002/ecm.1486> (2022).
41. Hortal, J., Roura-Pascual, N., Sanders, N. J. & Rahbek, C. Understanding (insect) species distributions across spatial scales. *Ecography* **33**, 51–53. <https://doi.org/10.1111/j.1600-0587.2009.06428.x> (2010).
42. Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. Selecting pseudoabsences for species distribution models: how, where and how many? *Methods Ecol. Evol.* **3**, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x> (2012).
43. Fournier, A., Barbet-Massin, M., Rome, Q. & Courchamp, F. Predicting species distribution combining multiscale drivers. *Glob. Ecol. Conserv.* **12**, 215–226 (2017).
44. Mateo, R. G. et al. Hierarchical species distribution models in support of vegetation conservation at the landscape scale. *J. Veg. Sci.* **30**, 386–396. <https://doi.org/10.1111/jvs.12726> (2019).
45. Adde, A. et al. N-SDM: a high-performance computing pipeline for nested species distribution modelling. *Ecography* e06540; (2023). <https://doi.org/10.1111/ecog.06540> (2023).
46. Thuiller, W. et al. biomod2: ensemble platform for species distribution modeling. R package version 4.2-6-2; (2024). <https://biomodhub.github.io/biomod2/>
47. Steen, B., Broennimann, O., Maiorano, L. & Guisan, A. How sensitive are species distribution models to different background point selection strategies? A test with species at various equilibrium levels. *Ecol. Model.* **493**, 110754. <https://doi.org/10.1016/j.ecolmodel.2024.110754> (2024).
48. Hanley, J. A. & McNeil, B. J. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**, 29–36. <https://doi.org/10.1148/radiology.143.1.7063747> (1982).
49. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x> (2006).
50. Cohen, J. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* **20**, 37–46. <https://doi.org/10.1177/001316446002000104> (1960).
51. Landis, J. R. & Koch, G. G. An application of hierarchical kappa-type statistics in the assessment of majority agreement among multiple observers. *Biometrics* **33**, 363–374 (1977).
52. Mandrekar, J. N. Receiver operating characteristic curve in diagnostic test assessment. *J. Thorac. Oncol.* **5**, 1315–1316. <https://doi.org/10.1097/JTO.0b013e3181ec173d> (2010).
53. Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. A. Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300;10.1016/S0304-3800(02)00200-4 (2002).
54. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. A. & Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152. <https://doi.org/10.1016/j.ecolmodel.2006.05.017> (2006).
55. Barbosa, A. M., Real, R., Munoz, A. R. & Brown, J. A. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Divers. Distrib.* **19**, 1333–1338. <https://doi.org/10.1111/ddi.12100> (2013).
56. Hijmans, R. J., Phillips, S., Leathwick, J. & Elith, J. *dismo: Species Distribution Modelling*. R package version 1.3–14 (2023). <https://CRAN.R-project.org/package=dismo>
57. Pebesma, E. Simple features for R: standardized support for spatial Vector Data. *R J.* **10**, 439–446. <https://doi.org/10.32614/RJ-2018-009> (2018).
58. Pebesma, E. & Bivand, R. *Spatial Data Science: with Applications in R; 10.1201/9780429459016* (Chapman and Hall/CRC, 2023).
59. Massicotte, P., South, A. & `_rnatuarearth` World Map Data from Natural Earth. R package version 1.0.1, (2023). <https://CRAN.R-project.org/package=rnatuarearth>
60. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, 2016).
61. Zhang, L., Wang, P., Xie, G. & Wang, W. Spatial distribution pattern of *Aromia bungii* within China and its potential distribution under climate change and human activity. *Ecol. Evol.* **14**, e70520. <https://doi.org/10.1002/ece3.70520> (2024).
62. Osawa, T., Tsunoda, H., Shimada, T. & Miwa, M. Establishment of an expansion-predicting model for invasive alien cerambycid beetle *Aromia Bungii* based on a virtual ecology approach. *Manag Biol. Invasion.* **13**, 24–44. <https://doi.org/10.3391/mbi.2022.13.1.02> (2022).
63. EPPO Update on the situation of *Aromia Bungii* in Germany. *EPPO Report. Service.* **2023/110** <https://gd.eppo.int/reporting/article-e-7592> (2023).
64. EPPO Update on the situation of *Aromia Bungii* in Italy and record of *Prunus laurocerasus* as a new host plant. *EPPO Report. Service.* **2022/210** <https://gd.eppo.int/reporting/article-7441> (2022).

Acknowledgements

Funder: Project funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of the Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP F83C22000730006 / CUP H43C22000530001, Project title “National Biodiversity Future Center - NBFC”.

Author contributions

Conceptualization, E.R. and L.B.; methodology and formal analysis, E.R., P.T. and L.B.; data curation and validation, E.R. and S.L.; writing—original draft preparation, E.R. S.L., P.T. and L.B.; writing—review and editing, E.R., P.T., O.D., V.O., A.G., S.L. and L.B.; supervision, E.R. and L.B.; Funding acquisition: E.R., A.G., O.D. and L.B. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-86616-5>.

Correspondence and requests for materials should be addressed to E.R.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025