



Identifying ecological factors mediating the spread of three invasive mosquito species: citizen science informed prediction

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Abstract

Due to their potential role in pathogen transmission, invasive mosquitoes pose considerable threats to human and animal health. Several studies have identified the most important ecological drivers mediating the establishment and spread of key mosquito species (e.g., *Aedes aegypti*, and *Ae. albopictus*), and made predictions for future distribution. We evaluated the effect of an exhaustive list of environmental predictors on the distribution of three invasive species in Hungary (*Ae. albopictus*, *Ae. japonicus*, and *Ae. koreicus*) by using the same standards for data collection based on citizen science observations. Current distribution maps of these species were generated from a 5-year survey, then were compared with various predictor maps reflecting climate, habitat type, food supply, traffic, and interspecific competition by using a boosted regression trees approach that resulted in a subset of variables with the strongest impact. The best predictor sets were used to predict the probability of occurrence of the focal species for the whole country, and these predictions based on citizen science were evaluated against the results of an independent recent field surveillance. We uncovered species-specific patterns and found that different predictor sets were selected for the three different species, and only predictions for *Ae. albopictus* could be validated with direct trapping data. Therefore, citizen science informed distribution maps can be used to identify ecological predictors that determine the spread of invasive mosquitoes, and to estimate risk based on the predicted distribution in the case of *Ae. albopictus*.

Keywords Alien species · Biological invasion · Emerging infectious diseases · Mobile application · Urbanization · Vector map

Key Message

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- Invasive mosquitoes are rapidly spreading and pose considerable threats to human and animal health
- We identified the key environmental factors that mediate the distribution of three species in Hungary
- Based on inputs from a citizen science surveillance, we made predictions for their future distribution
- Predictions for the tiger mosquito can be used to predict epidemiological risk
- Predicted distribution maps can be effectively used in disease and pest control.

Introduction

Enhanced by human movement and global climate change, invasive mosquito species from tropical regions, such as *Aedes aegypti* and *Ae. albopictus*, are rapidly expanding into temperate zones, where they establish reproducing populations (Garcia-Rejon et al. 2021; Kraemer et al. 2015; Medlock et al. 2015; Murray et al. 2013). These mosquitoes are significant global health concerns as they can transmit viruses like dengue, Zika, and chikungunya (Leta et al. 2018). By integrating into local ecosystems, they enhance the transmission of endemic pathogens and contribute to new disease outbreaks, creating ongoing infection risks in new areas (Mackenzie and Williams 2009; Martinet et al. 2019). To mitigate these risks, it is crucial to monitor how these mosquitoes spread, identify the ecological factors that mediate their distribution dynamics and predict future distribution.

Several attempts have been made to characterize the potential distribution of the most important invasive mosquitoes based on different environmental variables and species occurrence records by using species distribution modelling (Arnoldi et al. 2022; Barker and MacIsaac 2022; Kurucz et al. 2020; Marcantonio et al. 2016). These studies typically focus on climatic variables (e.g., temperature, precipitation, and humidity) or other potential predictors like vegetation cover, urbanization and human movement patterns (Cunze et al. 2016a), while data on the current distribution of mosquitoes originate from direct field surveillance and literature reviews. Studies vary in scope, but climatic variables appear to be of general importance in shaping the distribution of species as they influence mosquito development, survival, and reproduction (Da Re et al. 2022). Predictions often suggest an expansion of suitable habitats, potentially leading to increased disease transmission in new areas (Georgiades et al. 2023; Laporta et al. 2023; Wint et al. 2022). Regional studies providing more detailed insights on how distribution will continue to expand have suggested that local environmental drivers may be overlooked in global or continental-scale models (e.g. Liu et al. 2023; Moo-Llanes et al. 2021).

However, studies on invasive mosquito distribution face significant challenges due to several reasons. First, uncertainties in species occurrence data caused by incomplete mosquito surveillances (Barker and MacIsaac 2022; Carvalho et al. 2017) and inefficient sampling driving misleading conclusions about the absence of the species in areas (Gu and Swihart 2004) can both lead to inaccurate maps. Second, model outputs can be highly sensitive to the choice of environmental variables (Lim et al. 2023). Most studies typically focus on climate factors like temperature and precipitation, but these can overlook other

crucial determinants such as habitat, urbanization, human mobility, and interactions with other species (Kolimenakis et al. 2021; Westby et al. 2021; Yin et al. 2022). Based on a restricted set of predictors, models make simplifying assumptions about ecological processes. Third, a lack of independent validation datasets, especially in regions without comprehensive surveillance, undermines the reliability of these models (Lim et al. 2023; Yates et al. 2018). Without proper validation, model predictions will reflect habitat suitability but will not necessarily represent potential distribution. Fourth, most models concentrate on globally relevant species like *Ae. aegypti* and *Ae. albopictus* (Medlock et al. 2012), neglecting locally significant species such as *Ae. japonicus* and *Ae. koreicus* in Europe (<https://www.ecdc.europa.eu/en/publications-data/aedes-japonicus-current-known-distribution-october-2023> and <https://www.ecdc.europa.eu/en/publications-data/aedes-koreicus-current-known-distribution-october-2023>). Previous studies uncovered species-specific roles that preclude generalizations across species (Barker and MacIsaac 2022), thus it would be of higher practical importance to generate potential distribution maps for invasive species with local importance.

Citizen science is an effective alternative to direct field sampling for gathering species occurrence data, potentially useful in predicting the distribution and expansion of invasive mosquitoes (Dickinson et al. 2010). This indirect sampling method involves non-specialists submitting observations, often via mobile phones, which are then appropriately validated and used for scientific inference. Successful citizen science programs in countries like Spain, Germany, and Hungary have provided reliable data on mosquito distributions (Eritja et al. 2019; Garamszegi et al. 2023a; Walther and Kampen 2017), which can be used to uncover quantitative relationships with the environment (Garamszegi et al. 2023b). The main advantage of citizen science over direct surveillance methods is its relatively higher ability to cover broad areas with more consistent sampling over time, making it more cost-effective and logistically feasible than traditional trapping approaches (Eritja et al. 2019; Palmer et al. 2017). This benefit is particularly important when adaptation of sampling regimes is required to rapid distributional alterations. However, citizen science is also loaded with some limitations due to inherently uncontrollable sampling regime, which requires strict scientific standards for data validation, and interpretation to ensure accuracy (Aceves-Bueno et al. 2017).

The aim of the present study is to identify the environmental factors that can mediate the distribution of the three locally important invasive *Aedes* species in Hungary, based on citizen science data, and use the set of the most influential factors to make predictions about their future distribution. To avoid sensitivity to the choice of environmental variables,

we considered an exhaustive list of potential predictors that can be hypothesized to influence the spread of these invasive mosquitoes within the country (Table 1). These predictors were incorporated into species distribution models (SDMs) to investigate their relative importance in mediating distribution patterns of the investigated species, as characterized by citizen science informed occurrence data. Then we made projections about the presence of species into the entire country including areas that had been uncovered by the citizen science sampling. We evaluated the correctness of these potential distribution maps based on an independent direct field sampling.

Materials and methods

Data from citizen science

Reports on the citizens' suspected encounters with *Ae. albopictus*, *Ae. koreicus*, and *Ae. japonicus* were submitted via email or the Mosquito Alert mobile application between 2019 and 2023 in Hungary (<http://www.mosquitosurveillance.hu/>). Physical specimens sent by post were also considered (number of reports that were submitted by different means: packages, $N=89$; e-mail, $N=3433$; application, $N=1458$; total: 4980, see also Table 2 that tabulates sample sizes by year). These observations were processed by expert dipterologists, who identified mosquito species (Garamszegi et al. 2023a). More details about the applied citizen science protocol (including the corresponding media campaign and the ethical aspects) can be found in Garamszegi et al. (2023a).

The validated reports were added to a core database with each row representing a record for a public observation and reflecting the validated taxonomic resolution. This database contains binary entries reflecting whether the citizen observation was true for any of the target species (that is, 0: if the taxonomic validation indicated that the given report was for none of the focal species, 1: if the taxonomic validation confirmed that the given report was a true observation for *Ae. albopictus*, *Ae. koreicus*, *Ae. japonicus*, respectively). These entries were created separately for the three species, if the species could be identified without any doubt by the experts. In some cases (see Table 2), based on the quality of the received material, it was not possible to unambiguously decide whether these reports corresponded to *Ae. koreicus* or *Ae. japonicus*, or the taxonomic identification could not go beyond the conclusion that the report is for one of the three invasive species. These uncertain cases could be handled in different ways (i.e., they could be excluded from the analyses, they could be randomly assigned to one of the target species,

and they could be used as positive evidence for all of the two or three species). We provide the results based on the most conservative approach, which considers that these are not true observations (0) for any of the focal species. However, if we used other approaches, we obtained very similar sample size and spatial distribution. Each entry in the database also received a temporal and a spatial tag (in the form of date and geographic coordinate, respectively), with the former reflecting the date of detection (i.e., the date of sample submission—if detection date was not specifically indicated otherwise).

We aggregated point observations into larger geographical units by tabulating raw reports into grids of quadrats covering $\sim 35 \text{ km}^2$ with the size of $5.5 \times 6.5 \text{ km}$ each (2827 non-overlapping spatial polygons can be defined for the territory of Hungary in this way). These units have originally been developed for grid-based vegetation mapping (Horváth et al. 2008), but the dimensions are comparable with the dispersion of adult mosquitoes (Tóth 2004), and with the dimensions of other data aggregation methods used in similar citizen science studies on invasive mosquitoes (Palmer et al. 2017). Based on the spatial tags of the public reports, we could unambiguously assign them into different quadrats, and determined if any of the investigated species were detected or not within these quadrats based on the 5-year citizen science surveillance period.

In each quadrat, for which at least one public observation was available, we could determine if the presence of *Ae. albopictus*, *Ae. japonicus*, or *Ae. koreicus* can be verified. Therefore, having at least one validated citizen science report for a focal species indicates true presence. However, cases in which citizens' reports were later validated to correspond to another, non-focal taxa can imply true absence for the focal species, or simply signal that the species is present but went unreported so far. Accordingly, quadrats, from which at least one citizen science report was received but these were not confirmed as true detections were considered as instances of pseudo-absence. Given that the number of observations largely varies among quadrats, any potential problem that is posed by pseudo-absence data depend on the underlying sampling effort. Therefore, we also calculated the number of total reports received irrespective of the species identity, which was used to reflect the underlying sampling effort to include in the statistical models.

In our analyses, we did not consider quadrats, for which there was no citizen science report (either true or mistaken observation) available for the five-year period. Accordingly, for *Ae. albopictus*, *Ae. japonicus*, and *Ae. koreicus* separately, we categorized quadrats with nonzero observation as being present ($N=132$, 185, and 106, respectively) or pseudo-absent ($N=527$, 474, and 553, respectively).

Table 1 Environmental and ecological factors that can be predicted to affect the occurrence and distribution of invasive *Aedes* species in their non-native range

Main environmental driving factors	Predicted effect	References	Particular predictors tested in this study
Climate	Climatic conditions that favour successful overwintering, faster larval development or reproductive rate positively associate with mosquito occurrence; increased precipitation leads to new breeding habitats thus facilitates mosquito reproduction	(Baldacchino et al. 2017; Cunze et al. 2016a; Cunze et al. 2020; Cunze et al. 2016b; Hira et al. 2018; Kache et al. 2020; Komagata et al. 2017; Kurucz et al. 2020; Manica et al. 2016; Marini et al. 2020; Ravasi et al. 2022; Reiskind and Lounibos 2013; Tran et al. 2013; Versteirt et al. 2014; Wieser et al. 2019)	Spring mean temperature Winter mean temperature Maximum temperature of warmest month Precipitation seasonality (coefficient of variation) Precipitation of warmest quarter
Habitat characteristics (breeding ecology)	Increased number of suitable breeding sites or factors generating ideal environmental conditions for breeding and overwintering enhance the establishment of invasive species	(Bevins 2007; Čabanová et al. 2021; Champion and Vitek 2014; Kaufman et al. 2014; Klobučar et al. 2019; Li et al. 2014; McClure et al. 2018; Müller et al. 2016; Säringer-Kenyeres et al. 2020; Vezzani 2007; Westby et al. 2021)	Corine Land Cover variables Distance from rivers Distance from lakes Human population density (reflecting the level of urbanization) Distance from cemeteries
Feeding ecology	Higher abundance of the main food sources enhances the establishment and reproduction of invasive species	(Garamszegi et al. 2023b; Manica et al. 2016; Zahouli et al. 2017)	Human population density (reflecting the density of main food sources)
Human transportation	Increased levels of transportation (ground, aerial, water), or closeness to traffic hubs facilitate migration and lead to higher chances of introduction causing greater frequency of invasive species occurrences (traffic-mediated migration)	(Egizi et al. 2016; Eritja et al. 2017; Montarsi et al. 2015; Müller et al. 2020; Rasheed et al. 2013; Shabani et al. 2018; Wang et al. 2023)	Distance from paved (asphalt) roads Total length of paved (asphalt) roads Distance from highways Total length of highways Distance from traffic hubs (airports and ports) Distance from rivers
Mosquito control	Higher levels of human intervention cause a decline in the mosquito abundance	(Baldacchino et al. 2015; Bengoa et al. 2013; Boubidi et al. 2016; Senmartin et al. 2015)	Volume of chemical control of mosquito
Interspecific competition	Competition between native and invasive species decreases the probability of establishment and the occurrence of invasive mosquitoes	(Carrieri et al. 2003; Costanzo et al. 2014; Yee and Skiff 2014)	Occurrence of <i>Aedes geniculatus</i> Occurrence of <i>Aedes pulcritarsis</i> Occurrence of <i>Anopheles plumbeus</i> Occurrence of <i>Orthopodomyia pulcripalpis</i> Occurrence of <i>Culex pipiens pipiens</i> Occurrence of <i>Culex pipiens molestus</i> Occurrence of <i>Culex hortensis</i> Occurrence of <i>Culex torrentium</i>

Table 2 Summary of reports from a citizen science campaign targeting invasive mosquito species in Hungary. Numbers show the number of reports that the public considered as observation for an invasive species, but were then categorized by taxonomic experts into the appropriate taxonomical category (total number of reports received: 2019, $N=394$; 2020, $N=1315$; 2021, $N=1140$, 2022, $N=1075$, 2023, $N=1056$)

	2019	2020	2021	2022	2023
<i>Aedes albopictus</i>	49	245	403	327	502
<i>Aedes japonicus</i>	52	233	85	74	28
<i>Aedes koreicus</i>	6	54	51	89	60
Invasive mosquito species (any of the above, but cannot be identified)	0	55	71	26	25
Native mosquito species	233	467	206	125	129
Other dipteran family	44	148	105	148	110
Other insect order	10	16	12	16	14
Cannot be categorized	0	97	207	270	188

Data from field sampling

In 2023, we organized a direct field sampling to obtain independent observations that can be used to validate predictions from models relying on the citizen science data. To achieve homogeneous sampling, we randomly chose 7–8 quadrats from each county (the territory of Hungary can be divided into 20 large administrative regions). Altogether, as the logistic constraints allowed, we successfully collected adult mosquito samples via direct trapping in pre-defined 131 different localities during the most active mosquito breeding season (between 15/07/2023 and 15/09/2023). On these localities, we followed a standard trapping regime, by which two BG-Sentinel mosquito traps (supplied with CO₂ and lure as attractants) were positioned for two nights. The content of the traps was collected and stored in a freezer until further examination, upon which all specimens were identified at the species level under a microscope by taxonomists based on morphological characteristics (Medlock et al. 2018). From these assignments, we determined whether any of the invasive mosquito species were present or not in the given quadrat (*Ae. albopictus*, *Ae. japonicus*, *Ae. koreicus*, respectively: present, $N=13$, $N=11$, $N=34$; absent, $N=118$, $N=120$, $N=97$, see also Fig. 1), and we considered this dataset as an evaluation dataset in the SDM (see below).

Environmental predictors

Review of the literature revealed the most important environmental factors presumably or provenly affecting the distribution of invasive *Aedes* species (Table 1). We attempted to obtain spatial datasets to cover all the relevant factors. Overall, 69 environmental predictors reflecting climate, habitat type, feeding preference, human intervention, traffic and

interspecific competition were calculated for the ~35 km² quadrats based on various raster and vector data sources including WorldClim 2.1 (Fick and Hijmans 2017), Corine Land Cover 2018 (Copernicus 2023), EuroGlobalMap (EuroGlobalMap 2023), OpenStreetMap (OpenStreetMap contributors 2015) and the Hungarian mosquito fauna (Tóth et al. 2022) databases. The full reference list of the datasets and the main geoprocessing steps resulting in the predictors are provided in the supplementary material (Table S1).

First, the environmental predictors were visually checked for their spatial distribution, variance and missing values. Then, following suggestions from Dormann et al. (2013), we screened the list of predictors to create a predictor subset that fulfils our multicollinearity criteria: pairwise Pearson's correlation coefficients were limited to $|r| < 0.8$, Variance Inflation Factor (VIF) of the predictors were maximized at 10, and Condition Number (CN) of the subset was maximized at 10. The correlation matrix of the initial predictor set is provided as supplementary material (Table S2). We excluded the following variables: distance from parking lots (because it strongly correlated with distance from highways), land cover fraction of discontinuous urban fabric (because it strongly correlated with population density), altitude (because it strongly correlated with land cover fraction of broad-leaved forest), maximum temperature of the wettest month (because it strongly correlated with average spring temperature and altitude), and land cover fraction of non-irrigated arable land (because it had high VIF value). Also, to ensure that environmental predictors have variation across quadrats, we removed 14 constant predictors from the dataset (land cover fractions of land cover types not present at the studied quadrats). Multicollinearity of the resulting predictor subset that contained 50 predictors was 6.67 according to the Condition Number, while the maximum of VIF values was 5.81 (human population density) and the maximum of pairwise correlations was 0.67 (population density versus land cover fraction of industrial or commercial units).

After all, we considered the selected 50 environmental predictors that were available for 2827 quadrats and used in the subsequent analyses by combining with the presence/pseudo-absence data for the three mosquito species across 659 quadrats. Predictor calculation and selection was conducted in R statistical software (R Core Team 2023) using its packages "areal" (Prenner and Revord 2019), "car" (Fox and Weisberg 2019), "corrplot" (Wei and Simko 2021), "extractr" (Baston 2022), "Hmisc" (Harrell 2022), "raster" (Hijmans 2023), "sf" (Pebesma 2018) and "xlsx" (Dragulescu and Arendt 2020).

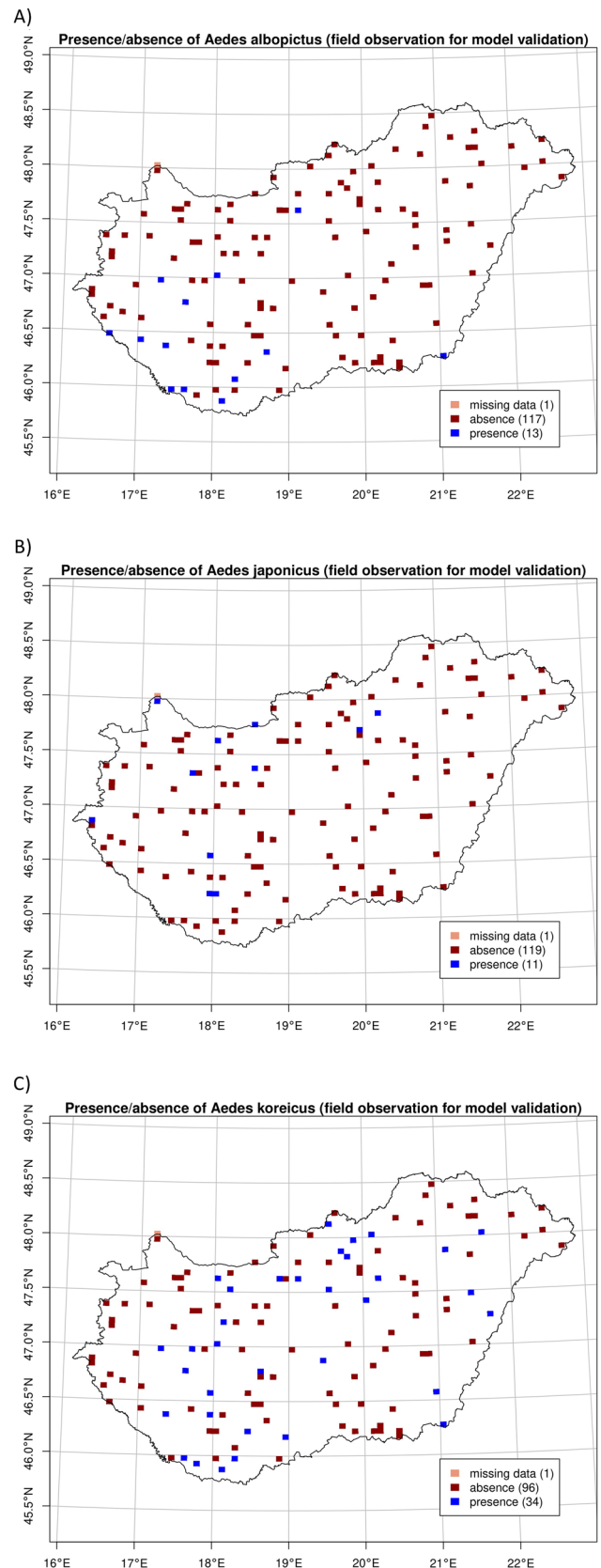
Species distribution modelling

For the three studied *Aedes* species, independent SDMs were trained and later used to predict the probability of potential

Fig. 1 The localities, where at least 1 day of trapping efforts were performed in the field in 2023 with the aim of catching one of the three invasive *Aedes* mosquitoes in Hungary. Colours reflect whether these efforts were successful for the given species or not (blue: at least one individual was detected in the trap, red: none of the individuals caught corresponded to the target species). Squares indicate the sampling units of the study (35 km² quadrats, see text), for which the investigated environmental variables (Table 1) were also available, and for which predictions for species' distribution could be generated (in one quadrat—marked with pink colour—, trapping in the field was performed but predictions could not be generated due to missing data for some predictors). **A** *Aedes albopictus*, **B** *Aedes japonicus*, *Aedes koreicus*

occurrence. From the several alternative SDM methods, boosted regression trees (BRT; a.k.a. gradient boosting model, GBM; Friedman et al. 2000; Friedman 2002; Schapire 2003) was selected. BRT is a robust but flexible SDM method with excellent predictive power (Bühlmann and Hothorn 2007; Elith et al. 2006; Velásquez-Tibatá et al. 2016). For each model, the whole presence/pseudo-absence dataset on the quadrat-level was used for training. Model parameters "bag fraction" and "tree complexity" were fixed at 50% and 3, respectively. We followed the guidelines of Elith et al. (2008) on the iterative learning rate selection to ensure that the trained models consist of 1000–10,000 trees. Initial models were simplified with backward selection by removing each of those predictors whose drop reduces the model's deviance less than the standard error of the deviance of the original model (i.e., the model that contained all the predictors) (Elith et al. 2008). The relative importance of the retained predictors (i.e., predictor contribution) was estimated by the formula of Friedman (Friedman 2001) that is based on the number of times a predictor was selected for splitting, weighted by the squared improvement to the model as a result of each split, averaged over all trees, and, finally, rescaled so that the sum of all predictor contributions adds to 100 (Elith et al. 2008; Friedman and Meulman 2003). In the supplementary material (Figures S1–3), we present how the retained environmental variables after the backward selection relate to the presence of the focal mosquito species by using density plots that depict the density of occurrences versus background points.

The BRT modelling framework allows varying weighting for sites (Elith et al. 2008), which we exploited to account for heterogeneity in sampling effort affecting the interpretation of observed zero occurrence (Eritja et al. 2019; Palmer et al. 2017). Given that that meaning of validated presence of an invasive mosquito species in a quadrat is obvious irrespective to the underlying sampling effort, quadrats with positive evidence were handled with maximum weight. On the other hand, for quadrats with unconfirmed presence (pseudo-absence), we introduced a weight factor depending on the underlying sample size (the number of total reports received within the quadrats). In a previous study (Garamszegi et al. 2023a), for each of the



three target species, we have determined the minimum sample size that is required to confirm the presence of the species with 95% confidence in a quadrat where it is truly present. Therefore, pseudo-absence data quadrats, in which the underlying sample size reached the target-specific criterion (*Ae. albopictus*: $N=7$, *Ae. japonicus*: $N=20$, *Ae. koreicus*: $N=10$), were also considered with full weight. If sample size was lower than the determined critical value, quadrats with zero observation were handled with weights proportional to the logarithm of the underlying sample size. Accordingly, the range of weight factor varies from the potential minimum value (0) reflecting the situation with zero sample size to the potential maximum value (1) when the sample size is equal or higher than the species-specific minimum sample size criteria, while values between these boundaries gradually downweighed pseudo-absence based on the underlying sampling effort.

We predicted the probability of potential occurrence on the continuous scale by the trained models (relying on the citizen science data) for each of the 2827 quadrats, and used these estimates to statistically compare with the evaluation dataset (relying on the direct field sampling at 130 quadrats). This evaluation was done by three goodness-of-fit measures: the Area Under the ROC Curve (AUC; Hanley and McNeil 1982), the maximum of the True Skill Statistics (maxTSS; Allouche et al. 2006) along the binarization cutoff gradient, and the Boyce index (Boyce et al. 2002; Hirzel et al. 2006). We also investigated the relationship between the predicted values of the probability of occurrence and the observed detections from the field surveillance by using a generalized linear model with binomial error structure and logit link function (i.e., logistic regression). To establish the significance of the full model we used a likelihood ratio test, comparing its deviance with that of the null model comprising only the intercept. For better visualization, continuous predictions falling within the [0; 1] interval were rescaled to a five-level ordinal scale (from 'not probable' to 'highly probable') using specific thresholds that account for observed presences (Somodi et al. 2017). Rescaling enhances interpretability and allows comparability of the predictions across different species (Somodi et al. 2017).

Model training, evaluation and prediction was done in R statistical software (R Core Team 2023) using its packages "dismo" (Hijmans et al. 2020), "ecospat" (Broennimann et al. 2023), "gbm" (Greenwell et al. 2020), "ICEbox" (Goldstein et al. 2015), "ROCR" (Sing et al. 2005), and "sf" (Pebesma 2018).

Results

Aedes albopictus

Learning rate for models for the tiger mosquito was 0.0016 resulting in 1400 trees. The algorithm retained two

predictors: human population density (predictor contribution: 34.85) and winter mean temperature (predictor contribution: 65.15). The density plots showed that increasing human population density up to c.a. 2000 individual/km² positively enhances the probability of detection of *Ae. albopictus*, while higher winter temperature is also positively associated with the presence of the species (Figure S1).

The predicted distributions from the trained models are shown in Fig. 2A. The predicted distributions suggest that the most suitable habitats for the species are in the southern-west part of the country and around the capital. The occurrence of the tiger mosquito is unlikely in the north-eastern part of the country, at least based on the considered predictors. In this region, citizen science detected some incidences despite the generally low predicted probability of occurrence based on habitat suitability. The independent trap sampling revealed similar patterns, as the presence of the species was confirmed in mostly the same regions (Fig. 1A). The goodness-of-fit measures of the training (citizen science) dataset against the evaluation (trap) dataset showed the following statistics: AUC: 0.878, maxTSS: 0.643, Boyce index: 0.767. Furthermore, we also fit a logistic regression line between the predicted (continuous) and observed values for quadrats that were sampled in 2023 directly in the field, which also indicated a good match between the two independent estimates (likelihood ratio test: $\chi^2=24.56$, $df=1$, $P<0.001$, Fig. 2B).

Aedes japonicus

For the Asian bush mosquito, models trained 2650 trees with a learning rate of 0.0016, and selected the following predictors: total length of paved roads (predictor contribution: 5.68), distance from traffic hubs (predictor contribution: 6.05), distance from lakes (predictor contribution: 7.65), volume of chemical control of mosquito (predictor contribution: 16.27), human population density (predictor contribution: 10.90), sport and leisure facilities (class 11 in Corine Land Cover 2018, predictor contribution: 7.58), complex cultivation patterns (class 20 in Corine Land Cover 2018, predictor contribution: 7.46), broad-leaved forest (class 23 in Corine Land Cover 2018, predictor contribution: 4.51), mixed forest (class 25 in Corine Land Cover 2018, predictor contribution: 4.87), transitional woodland-shrub (class 29 in Corine Land Cover 2018, predictor contribution: 5.50), water bodies (class 41 in Corine Land Cover 2018, predictor contribution: 5.31), precipitation seasonality (BIO15 in WorldClim 2.1, predictor contribution: 7.42), winter mean temperature (predictor contribution: 10.80). The relationships of these environmental predictors with the detection probability of the species are shown in Figure S2.

The predicted distributions (Fig. 3A) revealed a more uniform picture for the whole country indicating mostly

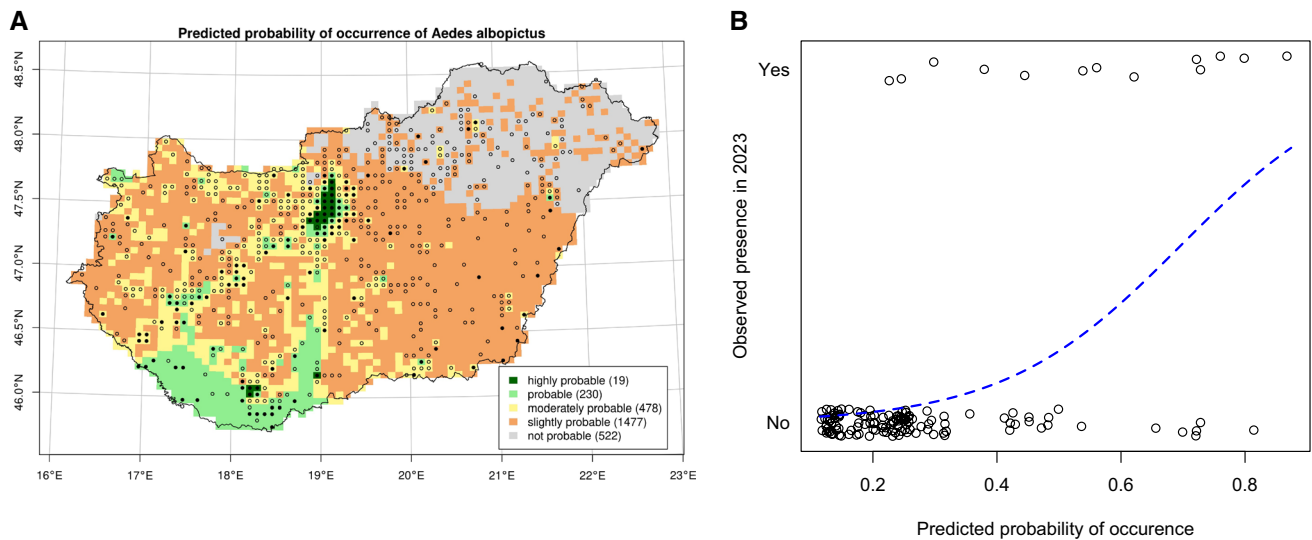


Fig. 2 **A** The predicted probabilities of occurrence for *Aedes albopictus* resulting from a species distribution modelling by Boosted Regression Trees that relied on citizen science data covering a 5-year survey in Hungary and that included various environmental variables reflecting climate, habitat type, food supply, traffic, and interspecific competition (Tables 1 and S1). Observed presences are displayed

above the predictions with filled circles and observed pseudo-absences with empty circles. **B** The relationship between the predicted probabilities of occurrence from the model and the observed presence of the species based on an independent trapping effort performed in the field in 2023 (Fig. 1)

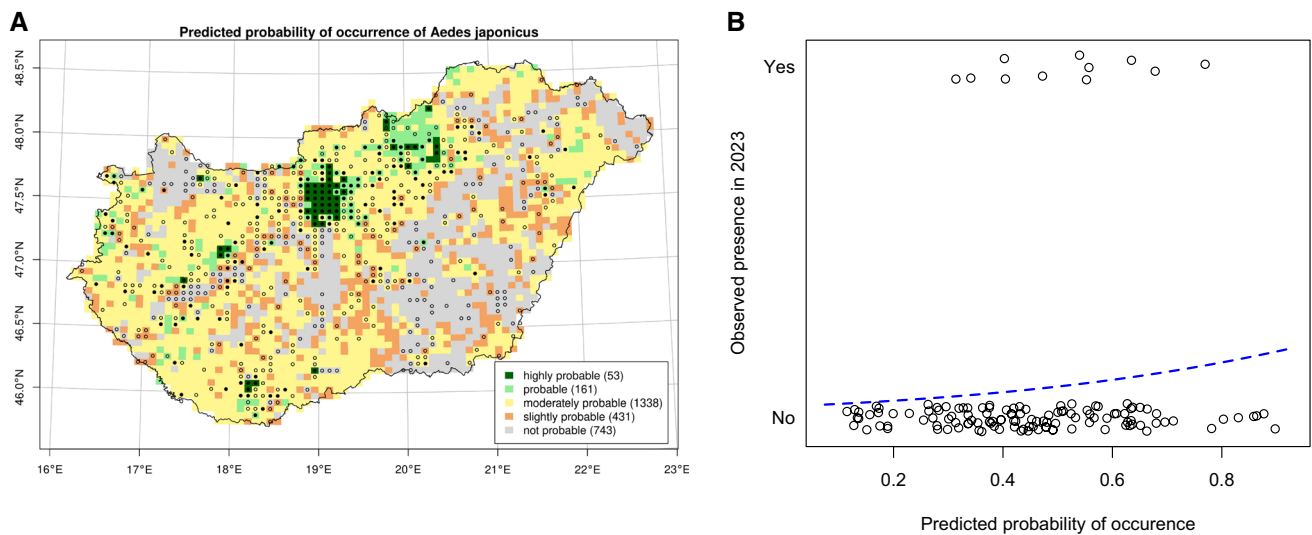


Fig. 3 **A** The predicted probabilities of occurrence for *Aedes japonicus* resulting from a species distribution modelling by Boosted Regression Trees that relied on citizen science data covering a 5-year survey in Hungary and that included various environmental variables reflecting climate, habitat type, food supply, traffic, and interspecific competition (Tables 1 and S1). Observed presences are displayed

above the predictions with filled circles and observed pseudo-absences with empty circles. **B** The relationship between the predicted probabilities of occurrence from the model and the observed presence of the species based on an independent trapping effort performed in the field in 2023 (Fig. 1)

some moderate chances of detection on a large part of the country but with large areas where the occurrence of the species in not probable based on habitat suitability. The only exception was around the capital, where the probability of occurrence is very high. In some areas in different

parts of the country, the probability of occurrence exceeds moderate levels. The citizen science detected incidences for *Ae. japonicus* in various point locations that were more evenly distributed on the map of Hungary than for *Ae. albopictus*.

However, the validation against detections from the independent monitoring implied that the presence of the species could not be confirmed by trap sampling in many regions that came out with relatively high habitat suitability from the above modelling (goodness-of-fit statistics: AUC: 0.625, maxTSS: 0.262, Boyce index: 0.421). The logistic regression also suggested that there was a poor match between the predicted values resulting from the training dataset and observed values from evaluation (trap) dataset (likelihood ratio test: $\chi^2 = 1.583$, $df = 1$, $P = 0.208$, Fig. 3B).

Aedes koreicus

Models for this species could be characterized by a learning rate of 0.0016 and 1850 resulting trees, and retained the following predictors: distance from cemeteries (predictor contribution: 17.13), volume of chemical control of mosquito (predictor contribution: 17.54), human population density (predictor contribution: 34.65), transitional woodland-shrub (class 29 in Corine Land Cover 2018, predictor contribution: 14.51), precipitation of warmest quarter (BIO18 in WorldClim 2.1, predictor contribution: 16.16). The relationships of these environmental predictors with the detection probability of the species are shown in Figure S3.

The predicted distributions from the trained models (Fig. 4A) indicated that the area around the capital has the highest probability of occurrence for the species, while the remaining part of the country can be characterized by very low to slightly moderate probability. Citizen science

detections between 2019 and 2023 indicated sporadic incidences in several parts of the country.

The trap sampling in 2023 showed that the species is present in various localities (Fig. 1C), and these detections were inconsistent with the predictions of the model that was trained based on the citizen science data (goodness-of-fit statistics: AUC: 0.592, maxTSS: 0.235, Boyce index: 0.521). There was no significant association between the predicted values that had been trained by the citizen science dataset and the observed values relying on the independent trap sampling (likelihood ratio test: $\chi^2 = 1.225$, $df = 1$, $P = 0.268$, Fig. 4B).

Discussion

We considered a large number of predictors describing climate, human transportation, habitat characteristics, feeding preference, the intensity of mosquito control and interspecific competition (Tables 1 and S1) to predict the potential distribution of three invasive mosquitoes in Hungary. We applied species distribution models to select the most important variables that explain the detected distributions reconstructed from citizen science observations (Figures S1–3, the potential effect of particular predictors on the probability of detection of invasive mosquito species are discussed in the supplementary material). Both detected and predicted distribution maps indicated that all invasive species are highly likely to occur around the capital. The predicted probability

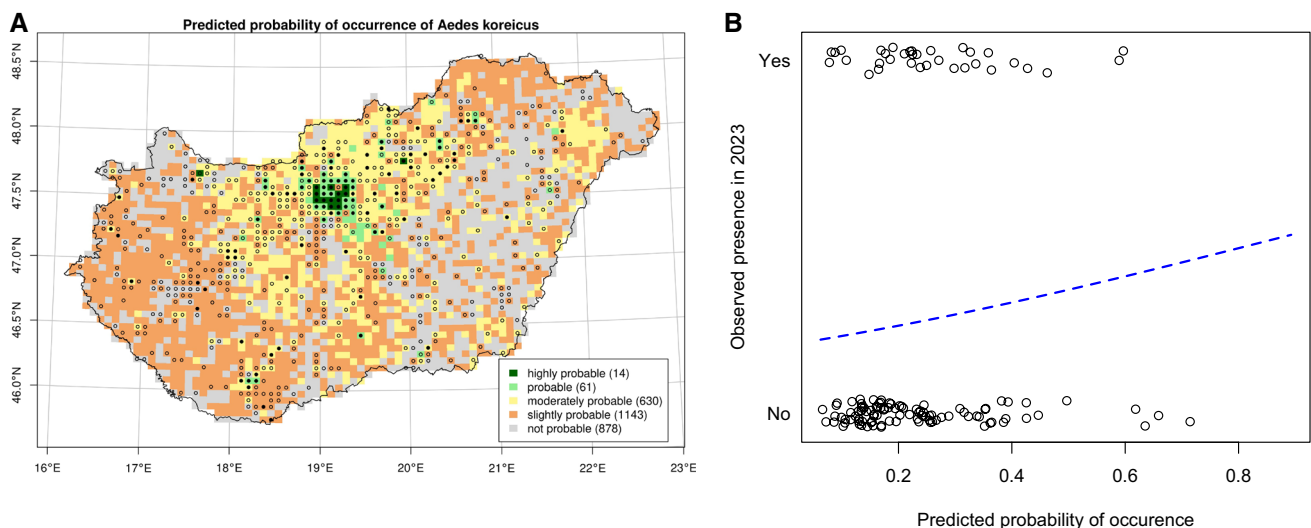


Fig. 4 **A** The predicted probabilities of occurrence for *Aedes koreicus* resulting from a species distribution modelling by boosted regression trees that relied on citizen science data covering a 5-year survey in Hungary and that included various environmental variables reflecting climate, habitat type, food supply, traffic, and interspecific competition (Tables 1 and S1). Observed presences are displayed above the

predictions with filled circles and observed pseudo-absences with empty circles. **B** The relationship between the predicted probabilities of occurrence from the model and the observed presence of the species based on an independent trapping effort performed in the field in 2023 (Fig. 1)

of occurrence for *Ae. albopictus* in other large regions of the country show relatively high spatial variance (i.e., there are extended regions where the species is very likely, but in other regions it is unlikely). However, the picture for the other two species is more even (systematically small or moderate probabilities across the whole country). Validations of the predicted distributions against surveillance data from an independent trap sampling suggested that the generated probabilities of occurrence on the spatial scale can be trustfully extended to previously unsampled areas for *Ae. albopictus*, but these cannot be considered as reliable predictions for *Ae. japonicus* and *Ae. koreicus*.

These differences suggest that habitat suitability primarily dictates the distribution of *Ae. albopictus*, whereas other unmeasured or unpredictable environmental factors may exert greater influence on the spread of *Ae. japonicus* and *Ae. koreicus* from year to year. Despite their introduction to Hungary probably around the same period (between 2012 and 2016) (Sáring-Kenyeres et al. 2018), the expansion dynamics of the populations displayed divergent trajectories among the three species. The prevalence of *Ae. albopictus*, as assessed through citizen science, exhibited high repeatability between years, in contrast to the other two species (Garamszegi et al. 2023a). Consequently, one may infer that *Ae. albopictus* exhibits a more consistent distribution compared to the other species, potentially explaining why predictions for its occurrence are more reliable than for the other two species. One of the assumptions behind species distribution models, which is rarely fulfilled by invasive species (Elith et al. 2010; Jiménez-Valverde et al. 2011), is the equilibrium between the species' distribution and the environment (Araújo and Pearson 2005; Pearson and Dawson 2003; Velazco et al. 2024). Good predictability of *Ae. albopictus* suggests that the species is close to reaching its equilibrium. However, we cannot exclude the simple explanation that the citizen science data for *Ae. koreicus* and *Ae. japonicus* are insufficient or not ecologically robust enough to fit a predictive model.

False negatives in the observations, i.e., labelling a site as not occupied by the studied species, whereas the species is actually present, could impact the accuracy of species distribution models trained on these observations (Barnes et al. 2021). Accordingly, our study acknowledges limitations stemming from the potential presence of false negatives within both the citizen science (training) and trap (validation) datasets. False negatives in citizen science data may arise when the species is present but remains undetected due to erroneous reports by participants, leading to an underestimation of species occurrence (Cruickshank et al. 2019). However, the SDM approach relied on weighting observations based on the underlying sample size, which balances the effect of uneven sampling effort to some degree (Barbet-Massin et al. 2012; Guisan et al. 2017; King and Zeng 2001).

We also appreciate that trapping efforts conducted over relatively short durations may also be susceptible to false negatives, mistakenly indicating species absence in areas where they are present but went undetected (Garamszegi et al. 2023a). If limitations caused by false negatives both in the citizen science and trapping data were substantial, they would likely manifest as a complete mismatch between predicted and detected distributions. However, in the case of *Ae. albopictus*, the reasonable correspondence between predicted and observed occurrences suggested a reliable level of robustness in the model's predictions. Improved trapping efficiency in regions where the predicted probability of occurrence is high, but where species were not captured during the trapping regime applied in this study, may enhance the detection of true positive occurrences in the future, and may thus actually lead to a stronger prediction power.

Class imbalance in the response variable can also be considered as a shortcoming as it may negatively affect the performance of classification algorithms (Galar et al. 2012; Valavi et al. 2021). We infer that class imbalance is not heavily present in our data (presence:absence ratios are 1:3.99, 1:2.56, 1:5.22 for *Ae. albopictus*, *Ae. japonicus* and *Ae. koreicus*, respectively; see also Čengić et al. (2020)), while we also implemented a weighting method within the BRT framework that downscales quadrats with low sampling effort, which reduces any confounding effect (e.g., Barbet-Massin et al. 2012).

Another source of flaw can be that the scale at which mosquitoes interact with their environment may be different than what the chosen 35 km² resolution implies. Unfortunately, it was impractical to apply finer scales for our mapping unit, but we can argue that if this problem was so influential, we would not expect to find any biologically relevant pattern. This was obviously not the case (Figures S1–3) suggesting that some environmental factors are in effect at a larger scale, even if individuals move less than 1 km (Vavassori et al. 2019). This is because the spread and establishment (and not the local interaction with the environment) are shaped by these environmental factors.

Sampling location bias is an additional issue that deserves special attention when using SDM approaches in the field of ecology and nature conservation. In particular, citizen science data on mosquito occurrence can be heavily biased over time and space due to the unequal engagement of users (Albert et al. 2010; Austin 2007; Bazzichetto et al. 2023; Hortal et al. 2008). This effect can cause that most citizen science detections are concentrated in urban and highly populated areas (Virgillito et al. 2024), which may partially explain why population density was a retained predictor for each species in the current study. However, variation due to habitat effects may exist even within the biased citizen science data, as a previous study indicated that the level of urbanization within citizen science reports predicts the

probability of detection, at least for *Ae. albopictus* (Garamszegi et al. 2023b).

In general, we highlight that in spite of the potential shortcomings caused by uneven sampling, class imbalance, the mismatch between the resolution of environmental maps and mosquito movement and spatial bias we have shown with an independent dataset based on direct field trapping that the predictions based on our approach are reliable and robust for at least one species. The presented analyses exhibit several strengths, distinguishing it from traditional approaches to species distribution modelling, particularly in the context of invasive mosquito species. Unlike many existing models that predominantly rely on climatic variables (e.g., Cunze et al. 2016b; Hussain and Dhiman 2022; Koch et al. 2016; Peach et al. 2019), we used an extensive array of predictors encompassing a broad spectrum of ecological mechanisms. By employing this comprehensive approach across three different invasive mosquito species, the research was able to discern the species-specific probabilities of occurrence and uncover substantial variations in distribution dynamics among them. Notably, this study represents one of the recent efforts that integrate validated citizen science data into species distribution models (Graba-Landry et al. 2023; Matutini et al. 2021; O'Neill et al. 2023), thereby generating predicted distribution maps. According to our knowledge, such an approach was not performed for invasive *Aedes* species previously. Despite the caveat of potential false negatives within the data, the easily adaptable nature of citizen science protocols suggests promising avenues for model improvement as datasets expand (see Južnič-Zonta et al. 2022). This adaptability allows for the generation of continuously updated predictions, facilitating real-time adjustments to distribution maps based on evolving data trends.

The predicted distribution for *Ae. albopictus* can inform further researches with practical importance. These distribution maps can serve as valuable tools for identifying regions where the likelihood of detecting *Ae. albopictus* is high, allowing for targeted sampling. Therefore, in these designated high-probability areas a more focused mosquito surveillance, including screening for pathogens transmitted by invasive species, could be effectively applied. Conversely, in areas with a low probability of occurrence, allocating resources to intensive surveillance programs may not be warranted.

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distribution of native species. Two anonymous reviewers provided valuable comments during the evaluation process. Map data copyrighted OpenStreetMap contributors and available from <https://www.openstreetmap.org>. EuroGlobalMap dataset includes Intellectual Property from European National Mapping and Cadastral Authorities and is licensed on behalf of these by EuroGeographics. Corine Land Cover data were produced with funding by the European Union.

Author contribution L.Z.G. and Á.B.-F. conceived the main ideas, L.Z.G., T. S. and Z.S. performed literature review, L.Z.G., K.K. and Z.S. designed methodology for sampling, K.K., Z.S. and G. N. collected the data, the data analysis was led by Á.B.-F. with conceptual inputs from L.Z.G., L.Z.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Upon acceptance data will be made available in a registered open-access repository of research data and via www.mosquitosurveillance.hu.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval This study does not have ethical considerations regarding the subject animals (mosquitoes). The authors fully adhered to the appropriate ethical guidelines for citizen science (Groot & Abma, 2022; Rasmussen & Cooper, 2019; <https://osf.io/xpr2n/wiki/home/>; <https://www.bto.org/our-science/bto-approach-science/citizen-science-research-ethics>). We took the maximum care to secure the anonymity of the citizen participants.

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