

Climatic suitability of *Aedes albopictus* in Europe referring to climate change projections: comparison of mechanistic and correlative niche modelling approaches

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The Asian tiger mosquito, *Aedes albopictus*, is capable of transmitting a broad range of viruses to humans. Since its introduction at the end of the 20th century, it has become well established in large parts of southern Europe. As future expansion as a result of climate change can be expected, determining the current and projected future climatic suitability of this invasive mosquito in Europe is of interest. Several studies have tried to detect the potential habitats for this species, but differing data sources and modelling approaches must be considered when interpreting the findings. Here, various modelling methodologies are compared with special emphasis on model set-up and study design. Basic approaches and model algorithms for the projection of spatio-temporal trends within the 21st century differ substantially. Applied methods range from mechanistic models (e.g. overlay of climatic constraints based on geographic information systems or rather process-based approaches) to correlative niche models. We conclude that spatial characteristics such as introduction gateways and dispersal pathways need to be considered. Laboratory experiments addressing the climatic constraints of the mosquito are required for improved modelling results. However, the main source of uncertainty remains the insufficient knowledge about the species' ability to adapt to novel environments.

Background

In recent years, European awareness concerning the introduction and establishment of invasive mosquitoes has increased, most notably due to the incursion of the Asian tiger mosquito, *Aedes albopictus* – the most invasive disease vector globally [1,2]. This mosquito has spread from its original distribution area in south-east Asia [3] to all continents via shipping of goods [4]. After its initial introduction to Europe at the end of the 20th century, *A. albopictus* became well established in southern Europe [2]. Recent observations hint towards a spread of this vector to the continental interior of

Europe [5]. This mosquito is capable of transmitting several viruses that are pathogenic to humans [1,6]. Most strikingly, *A. albopictus* was the vector that caused the first autochthonous transmission of chikungunya virus [7,8] and dengue virus [9-11] in the Mediterranean area. More recently, a dengue outbreak occurred in the autonomous region of Madeira, Portugal. In this case, *A. aegypti*, the yellow fever mosquito, acted as the vector [12].

Several studies have aimed to determine the climatic suitability of *A. albopictus* at the end of 20th and the beginning 21st century [13-15], as well as the expected future tendencies in Europe [16-19]. Most recently, Caminade et al. [19] implemented three established modelling approaches [14,16,20], making use of new observations, climate data and a report on model quality. However, a comparative methodological evaluation of the different approaches was still missing. Here, we provide a comprehensive comparison of studies assessing the climatic suitability of European regions for *A. albopictus* as a result of a rapidly changing climate during the 21st century. General information as well as limitations in study design and data quality is highlighted. Uncertainties related to climate change and insect vectors are identified. In so doing, we aim to provide guidance for future research.

Review of distribution models for *Aedes albopictus*

In order to assess knowledge about the responses of *A. albopictus* to climate change in Europe, we conducted a literature search, using the Thomson Reuters Web of Knowledge research portal (which includes the databases Web of Science, BIOSIS, Current Contents Connect, MEDLINE and Journal Citation Reports) as well as Google Scholar. Search terms were built from all possible combinations of the keywords '*Aedes albopictus*', '*Stegomyia albopicta*' or 'Asian tiger mosquito' in combination with 'climat* change', 'climat* warming'

or ‘global warming’. We considered only those research studies with a detailed analysis of methodological tasks and comparison of results, in which distribution modelling approaches were applied to European regions.

Our search identified six studies (up to November 2012) that aimed to determine the distribution of *A. albopictus* in Europe [14-19]. Methodological details and study design are described (Tables 1 and 2). Four of them analysed changing spatial patterns of *A. albopictus* in Europe by using climate change scenarios [16-19]. The studies with projections were used to derive general trends concerning the future development arising from a comparison of the resulting projections. In this review, we bring these specific studies for Europe into a wider context, as we account for the (methodological) development in the creation of risk maps of *A. albopictus* in order to understand the philosophy behind the work more intuitively.

Generally, two methodological approaches seem to be appropriate for the projection of climatic suitability of European habitats for *A. albopictus*: mechanistic models and correlative niche models. Mechanistic models do not require geographical occurrence data for species. They are either based on the construction of overlay functions for climatic constraints in geographic information system (GIS) environments or process-based models with mechanistic principles. The aim of such models is to simulate and project the response of an individual organism or a population by explicitly incorporating biological processes calibrated with observations on individuals in natural populations and controlled field or laboratory studies [21]. Thus, mechanistic models rely on the implicit assumption that the model structure and process formulations are correct [22].

A second, rather statistical approach is the use of correlative environmental niche models. Here, species presence and, in some approaches, also absence locations are related to environmental or climatic variables with the aim of determining the species-specific niche (synonymously used: ‘envelope’) that is defined by the parameter values – including the multivariate combinations – from the known occurrences. This niche can be interpolated or extrapolated to infer species’ geographical distribution. Advanced modelling techniques offer novel opportunities for the determination of species changing spatial distribution patterns as a response to environmental and climatic changes [23]. The main issue with correlative models is their dependence on the amount, quality and relevance of the data used [22]. Commonly, niche-modelling algorithms require presence as well as absence records. However, some models make use of pseudo-absence data or even presence-only data, as in many cases, absence data are not available. The lack of absence data may also suggest that areas where the species is missing might be suitable, but the insect may simply not

be present yet. Consequently, presence-only models are appropriate to handle most of the data for mobile and invasive insects in the course of climate impact research.

Distribution models devoid of climate change projections

Several studies identified the past or current climatic suitability for *A. albopictus*, based either on mechanistic [13,14,20] or correlative [15,16,24,25] distribution modelling approaches for specific regions or globally. Here, we highlight studies with relevance for Europe.

Mechanistic approaches

Kobayashi et al. identified a close connection with the annual and January mean temperature for the distribution of *A. albopictus* in northern Japan [20]. In addition, a period with daily temperature continuing above at least 11 °C during summer months (more than 186 days per year) was observed and interpreted as a requirement for larval development.

The first GIS-based risk maps were developed by Mitchell [13] for the Mediterranean Basin. Expert knowledge on temperature, rainfall and humidity as well as the photoperiod was applied in order to frame climatic constraints. For the United Kingdom, Medlock et al. [14] used temperature and daylight thresholds to simulate life cycle dynamics via overlay functions in GIS. Furthermore, they created different scenarios by altering the diurnal length of the photoperiod. This was done to assess the ability of eggs to survive in winter and predict the hatching in spring and the subsequent production of diapausing eggs in autumn. Consequently, the potential responses to these alterations in mosquito life cycle can be determined. It should be noted that the scenarios of Medlock et al. [14] do not refer to scenarios announced in the special report on emissions scenarios (SRES) [26] from the Intergovernmental Panel on Climate Change (IPCC). In the technical report of the European Centre for Disease Prevention and Control (ECDC), *Development of Aedes albopictus risk maps* [16], the approach from Medlock [14] is adapted, but was expanded to cover Europe. In this ECDC report [16], two further modelling approaches were used: one further mechanistic and one correlative approach, which are described below.

Correlative approaches

Presence/absence models

Many niche modelling algorithms require both documented presence, as well as absence localities in order to build statistical relationships. In its report, ECDC deployed random forest models (based on regression trees) in order to estimate the current climatic suitability for *A. albopictus* in Europe [16]. In short, random forest is an ensemble classifier that consists of combined decision trees and gives the class that is the mode of the classes by individual trees as an output. Centroids (geometric centres) of the European municipalities

TABLE 1
Studies addressing current and projected climatic suitability of *Aedes albopictus* in Europe

Study	Region	Model	Input data: climate/ environmental	Validation or data/ model predictive power	Climate projection or climate model	Scenario	Time step
Medlock et al. 2006 [14]	UK	GIS overlay (MA)	<ul style="list-style-type: none"> Climate data: annual mean rainfall and monthly mean temperature from 1971 to 2000 provided by the UK Meteorological Office (1 km) Weekly weather data: derived from monthly temperature data using a continuous piecewise quadratic function 	–	Own alteration	Own scenarios	–
ECDC 2009 [16]	Europe	Random forest (CA)	<ul style="list-style-type: none"> World climatic zones Temperature data archive at the University of Daytona, US: daily mean temperatures (1995–2007) MODIS: day- and night-time LST (1 km) CRU: monthly mean temperatures and rainfall variables averaged from 1961 to 1990 (5 km) NDVI and EVI (1 km) 	<ul style="list-style-type: none"> n=1,525 (presences and absences, due to centroids of municipalities) training sample (n=300), divided over both the presence (n=165) and absence (n=135) AUC 	No projection	–	–
	Europe	GIS overlay (CA) sensu Medlock et al. [14]	<ul style="list-style-type: none"> Same climate data source as for the random forest (CA) 	–	No projection	–	–
	Europe	MCDA (CA)	<ul style="list-style-type: none"> Same climate data source as for the random forest (CA) 	–	According to IPCC (no further details)	Minimal and maximum impact scenarios	2010, 2030
Fischer et al. 2011 [17]	Europe	MaxEnt (CA)	<ul style="list-style-type: none"> Worldclim: 19 bioclimatic variables derived from monthly temperature, rainfall values and altitude (10 km) 	<ul style="list-style-type: none"> Presence point data worldwide (n=1,199) Randomly selected test (30%) and training (70%) data; the split into training and test data was replicated 100 times AUC 	Regional climate model COSMO-CLM rescaled to 10 km	A1B ^a B1 ^a	2011–2040, 2041–2070, 2071–2100
Roiz et al. 2011 [18]	Trentino (north-east Italy)	GLM (CA)	<ul style="list-style-type: none"> Daily LST (MODIS Terra and Aqua satellites), reprojected to 200 m Human population data from official population census (2001) and from Landsat Global Population Database 	<ul style="list-style-type: none"> Absence and presence point data at 145 sample stations AIC 	No specific climate model: increase in mean January temperature (1.5 °C) and mean annual temperature (1 °C) with respect to reference period 1961–1990	A2 ^a	2040–2050
Caminade et al. 2012 [19]	Europe	GIS overlay (MA) sensu Kobayashi et al. [20] and Medlock et al. [14], MCDA sensu ECDC [16]	<ul style="list-style-type: none"> Gridded climate dataset based on station measurements at daily and monthly temporal resolution (25 km²) 	<ul style="list-style-type: none"> Absence and presence data at the regional administrative level of the European Union AUC 	10 selected regional climate models (ensembles), 0.25 ° step: C4IRCA3, CNRM-RM4.5, DMI-HIRAM5, ETHZ-CLM, ICTP-RegCM3, KNMI-RACMO2, METO-HC-HadRM3.0, MPI-M-REMO, OURANOSMRCC4.2.1, SMHIRCA	A1B ^a	2030–2050
ECDC 2012 [15]	Europe	Non-linear discriminant analysis (CA)	<ul style="list-style-type: none"> Fourier transformation of MODIS temperature (Terra satellite) and elevation data Worldclim data Human population density from Global Rural-Urban Mapping Project 	<ul style="list-style-type: none"> Thousands of occurrence records via existing databases and own literature search (for <i>A. albopictus</i> and <i>A. aegypti</i>) Generation of pseudo-absences via environmental (MD) and geographical distance measure 	No projection	–	–

AIC: Akaike's Information Criterion; AUC: area under the receiver operator characteristic curve; CA: correlative approach; CRU: Climate Research Unit; ECDC: European Centre for Disease Prevention and Control; EVI: enhanced vegetation index; GIS: geographic information system; IPCC: Intergovernmental Panel on Climate Change; LST: land surface temperature; MA: mechanistic approach; MCDA: multi criteria decision analyses; MD: Mahalanobis distance; MODIS: Moderate Resolution Imaging Spectroradiometer; NDVI: normalised difference vegetation index UK: United Kingdom; US: United States.

^a Emissions scenarios are based on the IPCC special report on emissions scenarios (SRES), where different storylines describe the relationships between the driving forces of climate change. The A1B scenario describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter and the rapid introduction of new and more efficient technologies. The A2 scenario assumes a continuously increasing global population, the economic development is primarily regionally oriented and per capita, economic growth and technological changes are more fragmented and slower than in other storylines. The B1 scenario is based on the assumption that economic structures will change rapidly towards a service and information economy and resource-efficient technologies will be introduced [26].

were used as presence or absence localities [27]. It should be noted that these municipalities differ in their spatial extent. The average area calculated from the political boundaries of the municipalities in southern Europe (e.g. Italy or Spain) may be up to three times bigger than in those in central Europe (e.g. Germany), which limits the ability to account for landscape heterogeneity. The centroids indicating species presences or absences are correlated with 57 (standardised) climate data layers, from which four variables are chosen as predictors via a backward stepwise procedure. All selected predictors are related to temperature.

Another approach recently published in a later ECDC technical report, The climatic suitability for dengue transmission in continental Europe, is based on multivariate discriminant analyses [15]. Again, this approach concentrates on modelling the current climatic suitability for *A. albopictus*. Here, global occurrence of this species was used as a model input. Accounting for the global dimension offers the opportunity to include the entire environmental space occupied by the species. However, this neglects the role of adaptation in regional populations. As discriminant analyses require absence records, (global) pseudo-absences were generated by evaluating localities that were geographically and environmentally dissimilar to presences. The models aim to discriminate between these two categories using the predictor variables available. The final risk maps were produced by averaging over 100 bootstrap samples [15].

Presence-only models

Many insect databases rely on documented presence localities, especially if a species is globally distributed. As the generation of pseudo-absences is ambitious (see [15]), novel ways to cope with presence-only data have been developed. In presence-only models, relationships are based on comparison of a species presence with the environmental background. Within this environmental background, the species were not recorded, which could also mean that data collection was not attempted in the respective region. Thus, at those sites, no information on the suitability of the environment or climate exists.

Employing the correlative environmental niche model Genetic Algorithm for Rule-set Prediction (GARP), Benedict et al. determined the global risk of invasion by *A. albopictus* [24]. A model built with GARP is iteratively chosen from non-random correlations between environmental and occurrence data. The non-random correlations describe environmental thresholds, depending on the chosen type of mathematical rule. Apparently, *A. albopictus* occupies different environmental niches on the invaded continents, which is revealed by Medley by applying correlative niche models for isolated geographical occurrence localities from the native and invaded range [25]. For all comparisons, the niche for introduced distributions was not equivalent to the native niche. For this purpose, Medley [25]

applied the Maximum Entropy approach (implemented in MaxEnt software) [28]. MaxEnt has replaced GARP as a preferred modelling algorithm for presence-only data during the past years, due to improved model performance [23]. The idea behind MaxEnt is to find the probability distribution of maximum entropy (most spread out) that is subject to constraints imposed by information available on the species presence and the environmental conditions across the study area [28,29].

Distribution models that consider climate change projections

Until November 2012, there were four studies that aimed to determine potential future climatic suitability of *A. albopictus* in Europe (summarised in Table 1 and 2) [16-19]. In two studies [16,19], climatic suitability was projected via mechanistic models, while the results of the two other studies [17,18] were based on correlative approaches. One study [18] was applied to a limited study region, while the other three [16,17,19] cover the entire European continent. In order to detect methodological qualities and constraints, these studies are compared in detail.

Information concerning input data is given including: climate variables, model validation and source and steps, e.g. of climate data for the respective emission scenario as well as addressed future time steps.

Mechanistic approaches

Within the technical report of the ECDC, a mechanistic multi criteria decision analysis (MCDA) was performed [16]. In contrast to the correlative approaches of this report, the results of the MCDA were projected to future conditions. An MCDA is a structured tool within a decision support framework. This enables evaluation of multiple decision constraints based on previously defined estimation criteria. The exploration of such decision alternatives for complex problem settings was recently developed within GIS frameworks in order to achieve accurate spatial risk assessment of vectors and vector-borne diseases [30]. In order to detect climatic suitability for *A. albopictus*, sigmoidal or symmetric sigmoidal membership functions were generated for the standardised variables and combined linearly with equal weight [16]. This was done based on expert advice. Generally, MCDA applications for spatial pattern analysis offer an opportunity to identify gaps and limits in knowledge; however, they are limited in determining causality [30]. Projections were applied for the MCDA approach and applied to the expected situation in 2010 and 2030, using SRES-scenarios with minimal or maximal impact [25]. Detailed information concerning the climate model and scenario characteristics was not given.

The mechanistic approaches used by Kobayashi et al. [20], Medlock [14] and the MCDA by ECDC [16] were adapted by Caminade et al. [19]. In contrast to previous approaches, Caminade et al. evaluated model performance via the area under the receiver operator

TABLE 2A

 Variables and model set-up in studies addressing current and projected climatic suitability of *Aedes albopictus* in Europe

Study	Variables	Method
Medlock et al. 2006 [14]	Overwintering criteria <ul style="list-style-type: none"> - Mean January temperature >0 °C - Annual mean rainfall >500 mm Spatio-temporal activity Scenario 1 Low risk <ul style="list-style-type: none"> - Spring mean temperature $10-10.5$ °C - Spring photoperiod $11-11.25$ h (daylight) - Temperature for cessation of egg/larval activity <9.5 °C - Critical photoperiod for autumn diapause $13-13.25$ h Medium risk <ul style="list-style-type: none"> - Spring mean temperature $10.5-11$ °C - Spring photoperiod $11.25-11.5$ h - Temperature for cessation of egg/larval activity $9.5-10$ °C - Critical photoperiod for autumn diapause $13.5-14$ h High risk <ul style="list-style-type: none"> - Spring mean temperature >11 °C - Spring photoperiod >11.5 h - Temperature for cessation of egg/larval activity >10 °C - Critical photoperiod for autumn diapause >14 h Scenario 2 <ul style="list-style-type: none"> - Critical photoperiod for autumn diapause 11 h, 11.5 h and 12 h for high, medium and low risk, respectively. The other three parameters stay the same. Photoperiod is based on astronomical equations of sunrise and sunset. 	GIS-based overlay Assessing the potential for survival and spatio-temporal activity dynamics (number of weeks between the first hatching of overwintered eggs in spring and the production of diapausing eggs)
ECDC 2009 [16] GIS overlay	Adapted by Medlock et al. [14] but no overwintering criteria <ul style="list-style-type: none"> - Critical photoperiod for autumn diapause 13.5 h - Spring photoperiod $11-11.5$ h - Spring mean temperature $10-11$ °C 	GIS-based overlay sensu Medlock et al. [14]
ECDC 2009 [16] Random forest	Four predictor variables chosen from 57 data layers <ul style="list-style-type: none"> - Maximum night-time LST - Mean annual daytime LST - Minimum daytime LST - Second amplitude of daytime LST 	Random forest <ul style="list-style-type: none"> - 200 aggregated classification trees for classification - Stepwise backward reduction of the number of variables until accuracy dropped below 90%.
ECDC 2009 [16] MCDA	Annual mean rainfall <ul style="list-style-type: none"> - No suitability <450 mm - Maximum suitability >800 mm Summer temperature (June–August) <ul style="list-style-type: none"> - No suitability <15 °C or >30 °C - Maximum suitability $20-25$ °C Mean January temperature <ul style="list-style-type: none"> - No suitability <-1 °C - Maximum suitability >3 °C 	MCDA <ul style="list-style-type: none"> - Sigmoidal transformation of mean annual rainfall and temperature in January - Symmetrical sigmoidal transformation of summer temperatures - Linear combination for suitability data layers, whereby each factor was assigned with equal weight
Fischer et al. 2011 [17] Expert knowledge-based model	Selection from 20 bioclimatic variables <ul style="list-style-type: none"> - Annual mean temperature - Mean temperature of the warmest quarter - Mean temperature of the coldest quarter - Annual precipitation - Altitude 	MaxEnt <ul style="list-style-type: none"> - Selection of variables based on expert knowledge
Fischer et al. 2011 [17] Statistic based model	Selection from 20 bioclimatic variables <ul style="list-style-type: none"> - Annual mean temperature - Annual precipitation - Precipitation of the warmest quarter - Precipitation of the coldest quarter - Altitude 	MaxEnt <ul style="list-style-type: none"> - Jackknife test to measure variables' importance - Calculations of models' training gains for variables' in isolation and for remaining dataset if this variable is dropped
Roiz et al. 2011 [18]	Survival of overwintering eggs <ul style="list-style-type: none"> January mean temperature >0 °C Annual mean temperature >11 °C Highly suitable: <ul style="list-style-type: none"> January mean temperature ($JanT_{mean}$) >0 °C and Annual mean temperature ($AnnT_{mean}$) >11 °C Moderately suitable: <ul style="list-style-type: none"> $JanT_{mean} >0$ °C and $AnnT_{mean} <11$ °C or $JanT_{mean} <0$ °C and $AnnT_{mean} >11$ °C Unsuitable: <ul style="list-style-type: none"> $JanT_{mean} <0$ °C and $AnnT_{mean} <11$ °C Human population data <ul style="list-style-type: none"> - Human population density - Distance to human settlements 	GLM with binomial distribution (multiple logistic regression) <ul style="list-style-type: none"> - Relating species' presences/ absences to variables

TABLE 2B

 Variables and model set-up in studies addressing current and projected climatic suitability of *Aedes albopictus* in Europe

Study	Variables	Method
Caminade et al. 2012 [19] Model 1	Annual mean temperature <ul style="list-style-type: none"> - Totally suitable >12 °C - High risk 11–12 °C - Moderate risk 10–11 °C - Low risk 9–10 °C Overwintering criterion <ul style="list-style-type: none"> Highly unsuitable <ul style="list-style-type: none"> - Mean January temperature <0 °C - Annual mean rainfall <500 mm Medium unsuitable <ul style="list-style-type: none"> - Mean January temperature 0–1 °C - Annual mean rainfall 500–600 mm Low unsuitable <ul style="list-style-type: none"> - Mean January temperature 1–2 °C - Annual mean rainfall 600–700 mm Suitable <ul style="list-style-type: none"> - Mean January temperature >2 °C - Annual mean rainfall >700 mm 	GIS-based overlay sensu Kobayashi et al. [20]
Caminade et al. 2012 [19] Model 2	See ECDC [16] (MCDA)	MCDA sensu ECDC [16]
Caminade et al. 2012 [19] Model 3	Overwintering criterion (see model 1) <ul style="list-style-type: none"> Weeks of activity <ul style="list-style-type: none"> - Mean weekly temperatures - Mean weekly photoperiods Hatching onset (medium scenario) <ul style="list-style-type: none"> - Spring temperature >10.5 °C - Photoperiod >11.25 h Autumn diapause <ul style="list-style-type: none"> - Temperature >9.5 °C - Photoperiod >13.5 h 	GIS-based seasonal activity model sensu Medlock et al. [14] <ul style="list-style-type: none"> - Overwintering criterion to mask the areas where the mosquito would not be able to survive - Photoperiod calculation as the period between sunrise and sunset - Computation of the start of spring hatching and autumn egg diapause is based on medium scenario
ECDC 2012 [15]	Clear documentation of pre-processing MODIS data; no further information about the chosen variables	Non-linear discriminant analysis <ul style="list-style-type: none"> - Preliminary k-means cluster analysis to analyse outliers in training set for exclusion in modelling process - 100 random bootstrap samples with equal number of presences and absences - Stepwise inclusion of 10 environmental variables - 100 results were averaged to produce the final risk maps

GIS: geographic information system; GLM: generalised linear model; LST: land surface temperature; MCDA: multi criteria decision analyses; MODIS: Moderate Resolution Imaging Spectroradiometer.

characteristic curve (AUC) [19]. AUC is based on signal detection theory and illustrates the performance of a binary classifier system when the discrimination threshold varies. Hence, it is typically used to determine performance of correlative niche models. Although it is a mechanistic approach, presence and absence localities based on centroids created from administrative level are generated [27]. These data were used as an evaluation of their results of the mechanistic classification in order to measure model performance. A novel feature was that Caminade et al. considered the role of climate change in Europe in past years (1960–1989, 1990–2009, 2005–2009) in the spread of the mosquito [19]. Furthermore, ensemble data of climate change projections were used, which were given by 10 regional climate models. Regional climate models are driven, at their boundaries, by global climate models. Employing

ensemble data enables variations of future projections to be assessed and, consequently, reduces uncertainty [31]. Usually, projections based on ensemble data include a multitude of potential variations by averaging over all possible developments. In the study of Caminade et al., projections were solely based on the A1B emission scenario [19]. The A1 storyline describes a future world with very rapid economic growth and a rapid introduction of new and more efficient technologies. Thereby, the global population peaks mid-century and declines thereafter. In the A1B scenario, a balanced use across all energy resources is expected [26].

Correlative approaches

Previous findings hint towards niche shifts of *A. albopictus* during the global invasion process [25]. In order to account for this, Fischer et al. applied two models

built on presence-only data beyond the European distribution with MaxEnt [17]. Firstly, global occurrence was used for training. Secondly, the native (Asian) distribution served as a training region. Both models were tested for the current European climatic conditions. The database contains more than 6,000 occurrence records of which 1,200 were selected as model input. The initial database was reduced by using geographically weighted correction to minimise spatial bias and autocorrelation in data. Geographically explicit point localities were taken from the literature and completed with presences reported on county level from the United States for the generation of the global database. The problematic issue with political or administrative borders in datasets was mentioned before. While the native range models, containing the Asian distribution and environments, fail to predict the current distribution in Europe, the global-trained model predicts the current European distribution with highly satisfactory quality. This suggests the use of the entire 'climatic niche' for projections. Two sets of bioclimatic variables provided by WorldClim (global climate data) [32] were used as model input. The first set was based on expert knowledge on species' ecology. The second set was chosen via statistical tests to determine the highest explanatory power of the model. All models were validated with AUC values. As both the expert knowledge- and statistical-based models of the global range yield high AUC values, they were both projected to future climate conditions in Europe. The training region seemed to be more important than the chosen set of climatic variables. Projections were based on data given by the regional climate model COSMO-CLM, applying the two scenarios A1B and B1. The A1B scenario has been described above. The B1 storyline describes the same development of the global populations in a globalised world, as in the A1B scenario, but with a rapid change in economic structures towards a service- and information-oriented economy with environmental sustainability [26]. The B1 scenario is a rather moderate scenario and corresponds to the aim of the European Union of keeping anthropogenic warming below 2 Kelvin in comparison to the pre-industrial level [33]. Non-analogue climate is a problematic issue in species distribution modelling, as the observed distribution of a species provides no information about species response under novel climates, e.g. [22,34,35]. Hence, projections (in space and/or time) to regions with non-analogue climate are biased and require caution in interpretation. In the study of Fischer et al. [17], however, non-analogue climate in projections were excluded via multivariate environmental similarity surface analysis as state-of-the-art evaluation (see [36]).

Roiz et al. focused on the potential spread of *A. albopictus* to higher altitudes in the Alps of northern Italy using binomial generalised linear model (GLM) as a logistic regression [18]. They related presences and absences of *A. albopictus* in ovitraps to land surface temperature (LST) data from satellite and human population data. Multiple years of daily LST data from

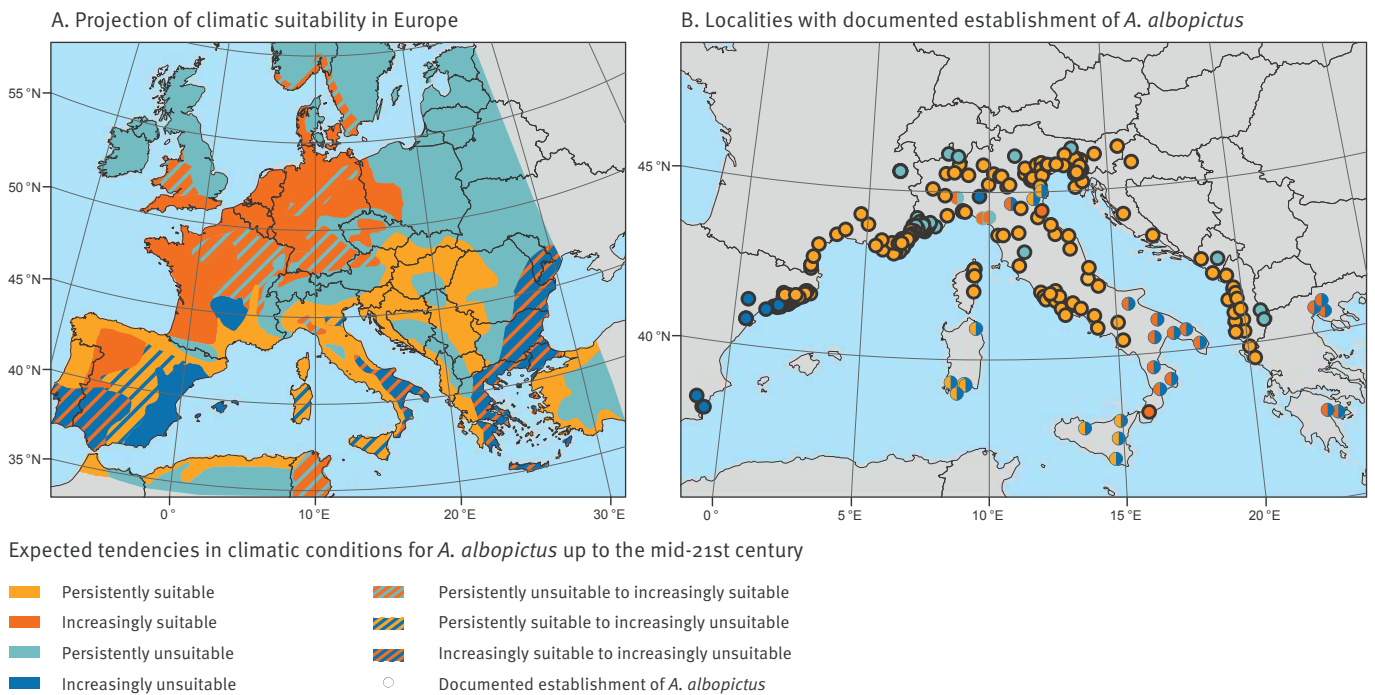
the Moderate Resolution Imaging Spectroradiometer (MODIS) were reprocessed at increased spatial resolution of 200 m pixels. The geographically explicit presence/absence data offers the opportunity to correlate them with the background data at this high spatial resolution. A temperature-gradient-based model was used to fill no-data areas from more than 11,000 daily MODIS LST scenes from 2000 to 2009. On the basis of this, threshold conditions for the survival of eggs in the winter, alongside the survival of the adults, were determined. The best models were selected via Akaike's Information Criterion (AIC). AIC is grounded on the concept of information entropy and evaluates the information loss, when a given model should describe reality. It can be interpreted as a trade-off between model accuracy and complexity. In concurrence with previous results [20], Roiz et al. identified annual mean temperature (11 °C) and January mean temperature (0 °C) as best predictors for identifying areas suitable for *A. albopictus* establishment [18]. Applying the A2 scenario, they considered an increase of the annual mean temperature of 1 and 1.5 Kelvin in winter in order to simulate the expected climatic conditions in 2050. Using data obtained directly from regional climate models would be inappropriate as these data are given in a resolution of 10–20 km. The A2 storyline describes a heterogeneous regionally oriented world and economy with a continuously increasing global population. Warming tendencies are more pronounced than in the previously described A1B and B1 scenarios [26].

Evaluation of climate change effects on the habitat suitability

Evidently, several distribution modelling efforts have been used to project the future climatic suitability of *A. albopictus* in Europe, which differ in model algorithm, climate data and scenarios. Here, we generated a simple GIS overlay (Figure 1A) to compare the risk map from the technical report of ECDC [16] with the results from Fischer et al. [17] and Caminade et al. [19]. However, an accurate comparison concerning the results of future projections cannot be presented, for several reasons. Firstly, there were clear differences regarding the chosen time-steps, emission scenarios and spatial resolution (Tables 1 and 2). Secondly, both, geographical and projected coordinate systems were used in the different studies. Hence, the comparison must be considered as a schematic and qualitative generalisation rather than a quantitative detailed compilation. Furthermore, we labelled localities with documented establishments of *A. albopictus* with the colour of the local climatic suitability (Figure 1B), to indicate how accurate the models reflect these occurrences. In general, the models under investigation were capable of predicting well the current localities of *A. albopictus* in Europe (Figure 1B). Only a few presences were observed in regions with rather unsuitable conditions.

FIGURE 1

Projections of climatic suitability of *Aedes albopictus* in Europe (A) and in European localities with documented establishment of *A. albopictus* (B)



A. Evaluation of projections of climatic suitability of *A. albopictus* within the first half of the 21st century in Europe in comparison with the situation at the end of the 20th century. Results of the mechanistic models based on multi criteria decision analyses of ECDC [16] and Caminade et al. [19] were compared with the statistical-based correlative niche model of Fischer et al. [17]. This is simply a schematic and qualitative generalisation, due to differences in time periods, scenarios and spatial resolution.

B. The records are coloured according to the evaluation of the changing climatic suitability of *A. albopictus* (ranging from the end of the 20th century up to the first half of the 21st century) presented in panel A.

General trends arising from comparison of the studies

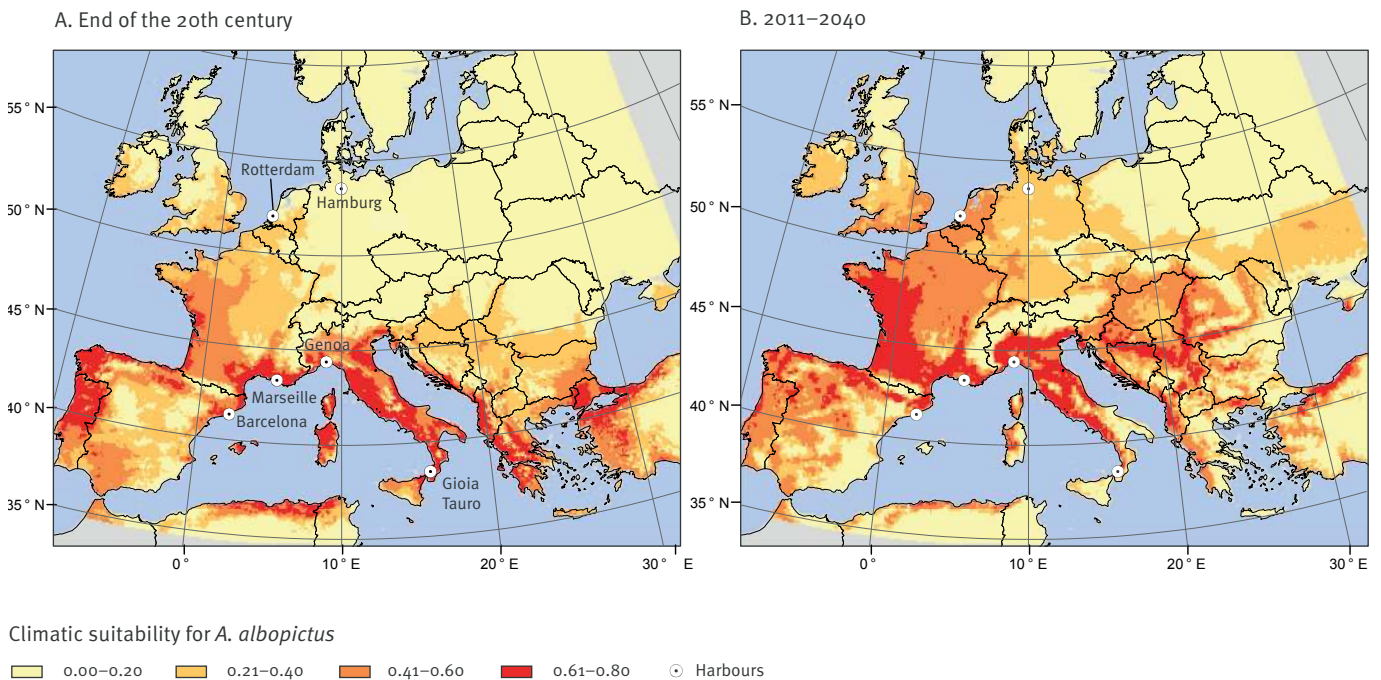
Regardless of the above-mentioned differences and obstacles for comparisons, some general tendencies concerning the evolving climatic suitability for *A. albopictus* in Europe within the first half of the 21st century can be derived. Projections indicate that climatic suitability will especially increase in many regions where the species is not yet established. Regions that are currently characterised by a rather low or moderate suitability have the potential for invasion by mid-century, due to increasing climatic suitability (Figure 1A). As a general tendency of all studies at the continental scale [16,17,19] it can be inferred that especially western Europe (Belgium, France, Luxembourg and the Netherlands) will provide favourable climatic conditions within the next decades. Furthermore, climatic suitability can be expected to increase in central Europe (e.g. parts of Germany) and the southernmost parts of the United Kingdom. Climatic conditions will continue to be suitable in southern France, as well as most parts of Italy and Mediterranean coastal regions in south-eastern Europe. Astonishingly, decreasing

suitability for *A. albopictus* is projected for the western Mediterranean coast of Spain. This is very likely a consequence of an increased expectancy of drier conditions during the summer months.

However, some uncertainties in projections of the different studies are worth mentioning (see Figure 1A): differences between projections are evident in France, Germany, and western parts of the United Kingdom (Wales), where projections range from persistently unsuitable to increasingly suitable. In central parts of the Iberian Peninsula, Sardinia and Sicily, it is uncertain whether climatic conditions will continue to be suitable or will become less suitable in the future. Deviations between projections are most pronounced in the south-western parts of the Iberian Peninsula, south-eastern Italy and parts of eastern parts of Greece including also the west coast of the Black Sea. In these regions, uncertainties in model outputs vary strongly in projections: climatic suitability is expected to persist or increase in the projections of ECDC [16] and Caminade et al. [19], while Fischer et al. [17] identified decreasing climatic suitability. Generally, projections are more sensitive to uncertainties for precipitation

FIGURE 2

End of the 20th century (A) and projected (2011–2040) (B) climatic suitability of *Aedes albopictus* in Europe, with locations of important harbours



Data concerning the current and projected climatic suitability (A1B scenario) for *A. albopictus* refer to results of the statistical-based niche model of Fischer et al. [17]. Values for establishment theoretically range from 0 (completely unfavourable) to 1 (extremely favourable). Additionally, the changes in climatic suitability for 2011 to 2040 become obvious. Suitability will increase for the biggest European harbours of Rotterdam and Hamburg, which marks these as potential gateways for unintended mosquito introduction. In order to account for areas involved in cargo transport on a regional scale, we created buffer zones with different radii around the harbours of Rotterdam, the Netherlands, and Hamburg, Germany. This was done in order to detect examples of climatic suitability of the regions surrounding harbours with expected container transport. Climatic suitability was averaged for each buffer zone. Currently, climatic suitability is rather low for regions around Hamburg (radius (r) 50 km = 0.12 ± 0.01 ; r 100 km = 0.12 ± 0.02 ; r 200 km = 0.11 ± 0.03), while moderate suitability can be found for areas around Rotterdam (r 50 km = 0.21 ± 0.02 ; r 100 km = 0.23 ± 0.05 ; r 200 km = 0.23 ± 0.07). For 2011 to 2040, suitability of both regions of interest will increase remarkably. Regions around Hamburg will provide moderate suitability (r 50 km = 0.27 ± 0.03 ; r 100 km = 0.28 ± 0.05 ; r 200 km = 0.29 ± 0.06), while climatic suitability will even favour establishment of *A. Albopictus* in zones around Rotterdam (r 50 km = 0.50 ± 0.03 ; r 100 km = 0.51 ± 0.03 ; r 200km = 0.48 ± 0.05).

than for temperature, which is particularly evident in southern Europe. Compared with the studies of ECDC [16] and Caminade et al. [19], the influence of precipitation in climatic suitability is more pronounced within the statistical-based model of Fischer et al. [17] (see also Table 2).

Further trends to be expected

The general trend of increasing climatic suitability in regions that are currently rather unfavourable for *A. albopictus* establishment leads to the assumption of a northward spread in western but also central Europe up to the middle of the century. This is the time frame of results published by ECDC [16] and Caminade et al. [19]. From then on, trends can only be obtained by accounting solely for the study of Fischer et al. [17]. According to their projections, climatic suitability will further increase in central Europe and climate will become suitable for mosquito establishment in eastern Europe during the second half of the century [17].

Besides the continental dimension, potential range expansions on a local scale become crucial for the spread of *A. albopictus* in Europe as well. For instance, increasing temperatures may facilitate an upward spread in alpine regions, which has been demonstrated in northern Italy (Trentino) [18].

Future research avenues

In a warmer world, invasion processes of species may exhibit novel dynamics [37,38]. Thus, new challenges arise concerning the surveillance of invasive mosquitoes in Europe with high ability to colonise new territories as it is the case with *A. albopictus* [39]. Future research addressing invasive species that are of societal importance (e.g. regarding health issues) requires a comprehensive strategy for embedding climatic risk analyses in a broader scientific context. The main issues, such as transport mechanisms, alterations of habitats due to climatic extremes and biotic interactions, are highlighted below, as they are the most challenging tasks in modelling.

Continental dispersal pathways

None of the studies on potential future European occurrence of *A. albopictus* explicitly addresses processes such as the introduction and dispersal of the species. The introduction of this mosquito in Europe can be attributed to the global shipping of goods, especially by the world trade of used tyres or the import of tropical plants such as ‘Lucky Bamboo’ (*Dracaena braunii*) [1,2]. Undoubtedly, shipping is extremely effective in overcoming long-distance oceanic barriers [2,40,41]. Thus, the intercontinental range expansions of *A. albopictus* proved to be predictable using this combination of frequencies and traffic volumes of shipping lines in combination with climatic data at the target region around harbours [35]. The establishment of *A. albopictus* evidently took place around Mediterranean harbours, e.g. around the seaports of Genoa, La Spezia and Gioia Tauro in Italy as well as Barcelona, Spain – regions that are considered to be climatically suitable for the species today (Figure 2).

Intensified monitoring systems are installed in harbour regions at higher latitudes. After introduction, *A. albopictus* populations were found in glasshouses in the Netherlands used by Lucky Bamboo importers [42]. Such unintended import of the mosquito to the Netherlands seems to be a repeated phenomenon [43], although no evidence consists concerning the establishment of *A. albopictus* in Dutch landscapes. This is probably related to their low climatic suitability. This is also still true for other regions around the most important European harbours of Rotterdam, the Netherlands, and Hamburg, Germany,) that are characterised by the highest number of import containers, coming from endemic regions. Obviously, the harbours are not the final destination of the containers, as they are transported to the continental interior. We calculated the averaged climatic suitability within buffer zones of different radii (50–200 km) around the harbours of Rotterdam based on the results of Fischer et al. [17]. Increasing climatic suitability within these buffer zones around the introduction gateways may become crucial for future *A. albopictus* spread (Figure 2).

Once *A. albopictus* has been introduced and established, the question arises how to determine the risk of the mosquitoes spreading to further potentially climatically suitable habitats. Using the example of sandflies, it has been demonstrated that the dispersal of disease vectors on the continental scale can be evaluated by creating artificial cost surfaces that include several landscape features that are attributed with cost factors [44]. Consequently, the pathway with least costs for a species’ dispersal can be considered as the most likely path of the species to move across landscapes. However, in contrast to sandflies, the dispersal of *A. albopictus* is mainly driven by unintended human transport through trade and traffic as opposed to natural dispersal. Hence, accounting anthropogenic factors in dispersal analyses is ambitious and acquires attribution of (rail-) roads and resting places

in analyses. Consideration of these dispersal mechanisms, combined with current risk mapping and climate change assessments, suggests that further expansion across much of Europe is probable [2]. The necessity of dispersal analyses on the continental scale is highlighted by the recent incursion of *A. albopictus* in south-westernmost parts of Germany [45]. Thus, it has been concluded that *A. albopictus* crossed the Alps via transportation on motorways [46]. Another striking example is the recent importation of the mosquito to southernmost parts of the Czech Republic due to transit traffic [47]. Further spreading pathways need to be identified, as invasive mosquitoes may also be adaptable to new environments in a target region [2,36,48,49]. Without human transportation, the spreading potential of *A. albopictus* is limited to the local scale. In Italy, a flight range up to 300 m around their breeding containers has been observed [50]. This short-distance natural dispersal can be only assessed with high-resolution (250 m pixel resolution), gap-filled daily LST satellite data to predict areas that are potentially affected by infestation of *A. albopictus* [51,52].

Climatic constraints and novel scenarios

Integration of expert knowledge in modelling approaches demands detailed information on mosquitoes’ ecology. In temperate regions, diapausing is a strategy to maintain species’ typical life cycle traits, as diapausing eggs show remarkable desiccation resistance aside from increased cold tolerance [53]. In Italy, either favourable microclimates or cold acclimation may play a decisive role in the context of overwintering [54]. Likewise overwintering was identified as a constraint also in Switzerland [52]. Under laboratory conditions, the low-temperature thresholds for the survival of eggs of European populations of *A. albopictus* have been identified [55]. Such experiments help to detect potential regions, capable of overwintering populations. To date, information is mostly obtained by field observations; however, the thresholds for survival can be derived by simulating extremes that then can be transferred to climate change scenarios.

Currently, the development of the next generation of IPCC climate change scenarios is under way. Until now, a sequential approach has been used for scenario development [56]. These scenarios depict a linear chain of causes and consequences of anthropogenic climate change, handed from one research community to the next in a lengthy process, leading to inconsistencies. The new parallel process begins with the identification of radiative forcing characteristics that support modelling a wide range of possible future climates. In parallel, new socio-economic scenarios will be developed to explore important socio-economic uncertainties affecting both adaptation and mitigation. This is directly linked to, and integrated within, the new climate scenarios [5,57]. The extensive exchange between scientific disciplines acquired a more sophisticated design matching. Then, projections based on climatic extremes and their ecological consequences

will be improved. To date, projections concerning future climatic suitability of *A. albopictus* in Europe are based on long-term changes and do not consider the decisive role of rather short-term extremes. Modified climatic variability and associated sporadic extreme conditions are likely to create windows of opportunity for the establishment and reproduction of disease vectors such as *A. albopictus*, even if this is not reflected in trends of long-term average values [58].

Projections for the climatic suitability of *A. albopictus* can be combined, for instance, with the temperature-dependent extrinsic incubation period of an arbovirus, the time between pathogen infection of the insect vector and the vector's ability to infect the next vertebrate host. An accurate risk assessment of a climate-driven shift or spread of a vector-borne disease can then be obtained by combining risk maps of vector and transferred pathogen amplification in the light of a rapidly changing European climate for dengue [15,59,60] or chikungunya [61,62].

Further challenges for risk assessment

Aside from the above-mentioned novel opportunities, some challenges pertaining to future developments and their analyses need to be mentioned. A combination of phylogenetic analyses with distribution models was used to reconstruct the spatial occurrence of *A. albopictus* during the Pleistocene [63]. Such combined approaches seem to be a promising effort to support future projections. However, mutations and rapid adaptations of short-lived species to changing environment must be expected. Furthermore, outside of its native range *A. albopictus* acts as a strong competitor to local mosquitoes [49]. This not only affects the vectors' occurrence, but also the activity phase and population dynamics [64].

As *A. albopictus* prefers anthropogenic habitats, modified human behaviour is also a source of uncertainty. For instance, humans provide breeding sites for this container-breeder that enable survival in dry regions due to water storage [40]. Thus, changes in human behaviour or more general in human societies demand a comprehensive philosophy that must be implemented in risk assessments of climate change effects on emerging diseases. Estimating climatic suitability should be considered as a first step in risk assessment. Once future climatic suitability is detected for specific regions, societal and demographic aspects must be considered and regional specifics of health-care systems can then be designed in a more specific and efficient way [65-67]. Such hierarchical and logical strategies may contribute to lowering the risks of vector spread and pathogen transmission. Recently, ECDC has launched the E3 Geoportal as a (spatial) data dissemination platform to facilitate data sharing and usability [68]. In order to guarantee accuracy for environmental risk mapping of *A. albopictus*, a proof of concept was given [69]. Furthermore, ECDC initiated research

activities on assessing the related risk of chikungunya [62] and dengue virus transmission in Europe [70].

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