Projection of climatic suitability for *Aedes albopictus* Skuse (Culicidae) in Europe under climate change conditions

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ABSTRACT

During the last decades the disease vector *Aedes albopictus* (*Ae. albopictus*) has rapidly spread around the globe. The spread of this species raises serious public health concerns. Here, we model the present distribution and the future climatic suitability of Europe for this vector in the face of climate change. In order to achieve the most realistic current prediction and future projection, we compare the performance of four different modelling approaches, differentiated by the selection of climate variables (based on expert knowledge vs. statistical criteria) and by the geographical range of presence records (native range vs. global range).

First, models of the native and global range were built with MaxEnt and were either based on (1) statistically selected climatic input variables or (2) input variables selected with expert knowledge from the literature. Native models show high model performance (AUC: 0.91–0.94) for the native range, but do not predict the European distribution well (AUC: 0.70–0.72). Models based on the global distribution of the species, however, were able to identify all regions where *Ae. albopictus* is currently established, including Europe (AUC: 0.89–0.91).

In a second step, the modelled bioclimatic envelope of the global range was projected to future climatic conditions in Europe using two emission scenarios implemented in the regional climate model COSMO-CLM for three time periods 2011–2040, 2041–2070, and 2071–2100. For both global-driven models, the results indicate that climatically suitable areas for the establishment of *Ae. albopictus* will increase in western and central Europe already in 2011–2040 and with a temporal delay in eastern Europe. On the other hand, a decline in climatically suitable areas in southern Europe is pronounced in the Expert knowledge based model. Our projections appear unaffected by non-analogue climate, as this is not detected by Multivariate Environmental Similarity Surface analysis.

The generated risk maps can aid in identifying suitable habitats for *Ae. albopictus* and hence support monitoring and control activities to avoid disease vector establishment.

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1. Introduction

The invasive disease vector *Aedes albopictus* (*Ae. albopictus*) has recently received much attention (e.g. Benedict et al., 2007; Enserink, 2008; Medley, 2010). The mosquito has been ranked among the first 100 of the Worlds´ worst invaders (Crans, 2008). It has spread from its original distribution area in South-east Asia (Hawley, 1988) to at least 38 countries in North and South America, Africa, Oceania and even Europe (Benedict et al., 2007), likely by global transport of goods (e.g. Lounibos, 2002; Tatem et al., 2006; Fischer et al., 2010a). The first European invasion of *Ae. albopictus* was reported in 1979 from Albania (Adhami and Reiter, 1998). Upon its second arrival in Europe in 1990 the mosquito managed to establish permanent populations in Italy (Sabatini et al., 1990) and is now found across the Mediterranean area (Spain, France, Slovenia, Croatia and Greece; see Suppl. Reference list).

The spread of *Ae. albopictus* raises serious public health concerns. Under experimental conditions *Ae. albopictus* is able to transmit 22 viruses (Gratz, 2004). In nature it is mainly known to be an important vector of dengue, chikungunya and West Nile. Also Yellow fever virus and eastern equine encephalitis virus (North America), Ross River virus (Australia), Usutu virus (Italy) and the heartworms *Diofilaria immitis* and *D. repens* (Italy) were isolated from specimens collected in the field (Mitchell et al., 1987; Cancrini et al., 2003a,b; Calzolari et al., 2010). Due to its rapid spread (Lounibos, 2002), broad ecological plasticity (Delatte et al., 2008b) and high population density, this species has the potential to serve as an epidemic vector. Furthermore, its capacity to vertically transmit dengue and La Crosse (Tesh and Gubler, 1975; Rosen et al., 1983) enhances the possibility of establishing diseases in new areas (Delatte et al., 2008a). In Europe, the medical relevance of *Ae. albopictus* was highlighted in 2007 when the occurrence of the species was related to a chikungunya-epidemic

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in northern Italy in the region of Ravenna (Rezza et al., 2007). Recently, autochthonous cases of dengue fever were diagnosed in southern France for the first time (La Ruche et al., 2010) where *Ae. albopictus* serves as vector. Furthermore, autochthonous dengue virus infections were reported from Croatia (Schmidt-Chanasit et al., 2010; Gjenero-Margan et al., 2011).

Even under conservative and optimistic scenarios, future climate change is likely to increase air temperatures. At the end of this century the number of hot days in central Europe is projected to reach conditions that are currently experienced in southern Europe. While heavy summer precipitation is expected to increase in north-eastern parts of Europe, it is likely to decrease in the south (Beniston et al., 2007). In addition, changes in annual cold extremes are projected, whereby the largest relative warming is expected for north-eastern Europe (Goubanova and Li, 2007). These climatic changes may support a range shift and further regional establishment of *Ae. albopictus*.

As an ectothermal arthropod, *Ae. albopictus* is unable to regulate its body temperature. Hence the species directly depends on the thermal conditions of its environment. Under laboratory conditions, changes in temperature and precipitation affect the population dynamics of *Ae. albopictus*, which suggests that climate change is likely to extend the limits of its northern distribution (Alto and Juliano, 2001). Regarding a northward shift, especially temperature constraints in the cold period and decreasing photoperiod are of outmost interest, because these factors determine diapause of eggs and thus the survival of the species. The 10 °C coldest-month isotherm coincides with the separation between continuously breeding populations and those that must undergo a period of dormancy to survive cold periods in winter (Mitchell, 1988). Larval surveillance in northern Japan shows that the mean temperature of the coldest month below −2 °C is potentially lethal there (Kobayashi et al., 2002). Nawrocki and Hawley (1987) state that the −5 °C coldest-month isotherm describes the maximum northward expansion of *Ae. albopictus* in continental Asia and, presumably, also in North America. A risk of establishment in Europe is considered for areas with 0 °C or higher as cold-month isotherm (Mitchell, 1995; Knudsen, 1995). But, it is not only the limitation by low temperatures that has to be considered; warm temperatures, too, play an important role for *Ae. albopictus*. Pumpuni et al. (1992) pointed out that higher temperatures greatly reduce or prevent diapause incidences in *Ae. albopictus* specimen that were exposed to critical photoperiods. Results from natural foci in southern Brazil demonstrate that diapause apparently evolved from non-diapause or non-photoperiodic ancestors, whereby in southern parts of USA a diapause reduction was observed presumably due to rapid local adaptation (Lounibos et al., 2003). Sufficient precipitation or perhaps more generally a suitable local moisture regime is an additional prerequisite for the occurrence of the species. Moisture directly controls the availability of breeding sites and the relative humidity is an important factor for egg survival (Juliano et al., 2002). Annual precipitation is reported to be higher than 500 mm in the species' habitats in the Mediterranean area (Mitchell, 1995).

Previous approaches to map suitable climatic conditions for the establishment of *Ae. albopictus* in Europe mostly focused on the risk of invasion under current climatic conditions. Considering rainfall beside other factors (photoperiod, temperature and humidity), Mitchell (1995) developed a risk map for the Mediterranean Basin by comparing the climatic conditions of the region with the estimated climatic envelope of *Ae. albopictus*. Knudsen et al. (1996) investigated the distribution of *Ae. albopictus* in Italy and projected the risk for a broader distribution throughout Europe. This projection is based on climatic criteria identified by Nawrocki and Hawley (1987) including winter mean temperature, mean annual rainfall, and mean summer temperature. Eritja et al. (2005) used the same climatic limits as Mitchell (1995) and generated a detailed risk map for Spain, which considered regional climatic conditions. For the United Kingdom,

Medlock et al. (2006) developed a GIS based model using mean monthly temperature, annual rainfall and photoperiod to assess the overwintering survival, spring hatching and production of over-wintering eggs in autumn. The European Centre for Disease Prevention and Control (ECDC) produced risk maps that are aiming to predict climatic suitability of *Ae. albopictus* for the years 2010 and 2030 (ECDC, 2009). On a global scale, Benedict et al. (2007) investigated the regional risk of invasion by *Ae. albopictus*. Their analysis was carried out using eleven environmental data layers of the present climate. Recently, Medley (2010) investigated environmental (including climatic) niche shifts during the global invasion of the species, by modelling niches separately for each continent. Notably, most of the relevant literature is concerned with the present distribution and risk of invasion by *Ae. albopictus* under current climatic conditions. However, the predicted increase in temperature that is based on climate change scenarios will probably extend the spatial availability of breeding sites and also enhance mosquito survival (Woodward et al., 2001).

Our analysis starts from the assumption that *Ae. albopictus* will colonise climatically suitable niches around the world. We want to identify areas that could serve as potential habitat for the species today and in the future. Here, we assess the potential of *Ae. albopictus* to establish in Europe under projected climatic trends in the 21st century. In order to account for uncertainty in the selection of presence records and environmental variables, we (1) compare projections based on the species' former native range to those based on its recent entire global range, and (2) apply variable selection by expert knowledge as well as variable selection by an automated statistical procedure.

2. Material and methods

We created distribution models with MaxEnt, using species occurrences of the native range and of the entire range across the globe. For both training areas (global and native) two sets of bioclimatic data were prepared as input variables. One set was selected using expert knowledge on species climatic constraints. The second set was selected using solely statistical criteria. The future climatic suitability of *Ae. albopictus* in Europe was projected for two climate change scenarios. In addition, niche similarity between global and native regions and climatic similarity between projections was analysed.

2.1. Spatial distribution and presence records of Aedes albopictus

Presence records of *Ae. albopictus* at the global scale were taken from Benedict et al. (2007). Additionally, a literature search of scientific articles and reports of mosquito surveillance was conducted for the years 2003 onwards to consider additional infestations (see Supplemental Reference list). Reported occurrences of *Ae. albopictus* without evident establishment were excluded from the dataset. This resulted in a global dataset that consists of 6347 occurrence points with 4683 occurrence points just for Brazil, due to a detailed monitoring system in South America. Presence records for the United States are available on county level but not as precise geographical coordinates. Therefore the 1033 counties with documented presence records were converted to points by digitising the centroids for each of the counties.

Considering that worldwide, apart from the USA and Brazil, less than 1000 coordinate pairs were available, a random set of ten percent of the data were extracted for Brazil and the USA. Hence, the density of presence records for Brazil and the USA was reduced to levels that correspond to the density of documented presence points in other regions with maybe less intensified mosquito monitoring systems. Without this stratified subsampling, the results would have been biassed towards the climatic conditions of South and North America

(Medley, 2010). Additionally, duplicate species records within one raster cell of the training area (described in Section 2.2) were removed. The total global number of presence records used for modelling was 1199 (including 241 records in the native range).

2.2. Selection and pre-processing of climatic data

Current bioclimatic data (19 bioclimatic variables) were taken at a spatial resolution of 5 arcmin (http://www.worldclim.com). These bioclimatic variables are derived from monthly temperature and rainfall values in order to generate more biologically meaningful variables, which are recommended to use in ecological niche modelling (Hijmans et al., 2005). Higher spatial resolution would not correspond to the spatial accuracy of occurrence data for *Ae. albopictus*.

Two climatic datasets with different spatial extent were generated. The global climatic conditions of the land surfaces were used to model the global distribution. For the definition of the "native range" models, each native presence record was buffered with a circle of 1000 km radius. The native range then included all areas which were located in at least one of the circles. Hence, this range included a climatic gradient within Asia, in order to yield a clear delineation of the species' climate niche, but excluded areas that may be too far from the realised distribution, such that geographical factors rather than climate are dominant in limiting the species' distribution.

We used two sets of variables as input for global and native models. The first set is based on expert knowledge on the climatic requirements of the target species (e.g. Mitchell, 1995). Those variables are the same for the native and for the global range. Most variables represent thermal constraints (Table 1). In this model, some variables show substantial collinearity: Annual mean temperature (Bio1) is correlated with mean temperature of the warmest and coldest quarter (Bio10 and Bio11) in the native and the global range higher than $r = 0.7$ (Pearson correlation coefficient). Nevertheless, as a pre-selection of variables based on expertise is often useful (Elith and Leathwick, 2009), we kept these variables in our analyses, and chose a modelling approach that is known to be robust against collinearity (see Section 2.3). Hereafter, we will refer to this set as the expert knowledge based model (EKBM).

The second set of variables was selected by using a statistical procedure for native and global range separately. First, the importance of each variable was quantified with a Jackknife test implemented in MaxEnt (Elith et al., 2011). Variable importance is calculated in a twofold manner based on the training gain for all variables in isolation and for the remaining set of variables when the isolated variable is dropped from the set (Yost et al., 2008). To reduce collinearity in the set of statistically selected variables (Dormann et al., 2008) variables were removed that had a Pearson correlation coefficient $r > 0.7$ with any other higher-ranking variable in the results of the Jackknife test. We applied the variable selection procedure separately for the native and global range. The statistically derived sets of variables consist mainly of variables that represent the precipitation regime for the global range and identical number of temperature and precipitation variables for native range (Table 1). Models based on this set of variables are henceforth called statistic based model (SBM).

We projected the best models (determined by AUC-value, Section 2.3) to the future European climate. Projections of climate change in the 21st century refer to the scenarios for greenhouse gas emissions implemented within global or regional climate models. A1B and B1 scenario, which were considered as marker scenarios that best illustrate the respective storyline (IPCC, 2007), were applied for our projections of the future climate suitability for *Ae. albopictus* in Europe. In short, the A1B scenario is characterised by rapid global oriented economic growth and technological change towards the balanced use of fossil and non-fossil energy resources. The B1 scenario projects a more rapid change towards a service information economy with the introduction of resource efficient technologies while assuming a similar economic growth. It matches well with the European Union target of keeping global anthropogenic warming below two Kelvin above the pre-industrial level (Jacob and Podzun, 2010). Hence warming tendencies are projected to be stronger in the A1B scenario.

On http://www.worldclim.com data of the projected climate change are provided for the global climate models CCCMA and HADCM, which originally have very coarse spatial resolution (about 250 km). Climatic changes were interpolated to the high grid resolution of the current climatic conditions. As a consequence, this simple downscaling procedure does not account for climatic changes at small scales. In order to achieve more realistic projections of future climatic suitability for *Ae. albopictus* in Europe, we instead used data of climate change provided from the regional climate model COSMO-CLM (CCLM). Near-scale physical processes integrated in CCLM (spatial resolution about 18 km) are fitted at the boundaries with large-scale conditions given by the global model ECHAM5 (Rockel et al., 2008). Such a dynamical downscaling procedure enhances the quality of climate impact studies on vector-borne diseases due to integrated small-scale specifics such as topography or further landscape features (Jacob, 2008).

Table 1

Selected bioclimatic variables of native and global models, referring either to expert knowledge based or statistic based model. Listed are the training gains for the selected bioclimatic variables measured by Jackknife test. Variables without mentioned training gain were not part of the selected data set. Training gains were calculated for a single variable if used solely for the modelling procedure and additionally for the remaining dataset if this variable has been dropped from the set. Both aspects must be considered for a statistical selection of variables. For instance, altitude as variable achieved comparatively low values for the training gain is used as the single variable for modelling procedure, but training gain of the dataset decreases remarkable, if altitude is removed. Therefore it is advisable to keep this variable within the set. After selection of the variables, training gain was calculated for modelling with all selected variables. Training gain for the complete selected dataset is highest for the native datasets (expert knowledge based: 1.67, statistic based: 1.69). Training gain of the global dataset is 1.42 for the expert knowledge based selection and 1.34 for the statistic based selection.

Training gain of selected bioclimatic variables and altitude		Expert knowledge based				Statistic based			
		Global		Native		Global		Native	
		Without variable	With only variable	Without variable	With only variable	Without variable	With only variable	Without variable	With only variable
Bio1	Annual mean temperature	1.35	0.67	1.42	0.80	0.99	0.66	–	–
Bio4	Temperature seasonality	–	–	–	–	–	–	1.43	0.84
Bio10	Mean temperature of the warmest quarter	1.27	0.70	1.42	0.72	–	–	–	–
Bio11	Mean temperature of the coldest quarter	1.33	0.64	1.42	0.90	–	–	1.50	0.91
BIO12	Annual precipitation	1.20	0.71	1.35	1.00	1.17	0.72	1.51	1.00
Bio17	Precipitation of the driest quarter	–	–	–	–	–	–	1.42	0.66
Bio18	Precipitation of the warmest quarter	–	–	–	–	1.23	0.31	–	–
Bio19	Precipitation of the coldest quarter	–	–	–	–	1.21	0.48	–	–
Alt	Altitude	1.16	0.16	1.24	0.74	1.18	0.16	1.36	0.75

Climatic data were separately averaged over time periods 2011–2040, 2041–2070 and 2071–2100 for each scenario. Bioclimatic variables for modelling future climate projections were calculated in the same way as the original variables for current conditions. The spatial resolution of CCLM was resampled to the 5 arcminutes used for the current conditions. The pre-processing of the CCLM data was done via climate data operator codes (Schulzweida et al., 2009). The spatial extension of Europe for the current and future projections is adjusted to the defined space of the CCLM data.

2.3. Species distribution models

Species distribution models were built with MaxEnt. MaxEnt is a machine-learning technique combining species occurrence data with detailed climatic and environmental datasets in order to predict species distribution (Phillips et al., 2006; Phillips and Dudik, 2008). MaxEnt is favoured among other (pseudo) presence-only species distribution models due to high predictive power across all sample sizes (Elith et al., 2006; Wisz et al., 2008). In addition, variable selection in MaxEnt is less affected by correlated variables than e.g. stepwise regression, so there is less need to remove such correlated variables or, for instance, pre-process covariates by calculating principal components (Elith et al., 2011). Model residuals were tested for spatial autocorrelation using Morans I (Dormann et al., 2007).

Several parameter settings affect MaxEnt performance: Regularisation modifiers, which reduce the likelihood of overfitting and thus increase the predictive ability of modes beyond the training region (Phillips and Dudik, 2008), were set to 1. Increasing the number of model training iterations beyond the default value of 500 enhanced model performances, and the maximum number of iterations was therefore set on 2000 for all models. Furthermore, models were run with following settings: feature types were automatically selected depending on the training sample size (auto feature), convergence thresholds were 0.00001, maximum number of background points were 10000 as more background points do generally not enhance model quality criteria, but extend running time (Phillips and Dudik, 2008).

The model performance was quantified using the area under the receiver operator characteristic curve (AUC), a threshold-independent quality criterion (e.g. Elith et al., 2006). AUC-values can be interpreted as the probability that the model assigns a higher occurrence probability to a randomly selected presence location than to a randomly selected absence location. In order to yield unbiased estimates of model performance, we employed a standard split-sample strategy. Models were trained using a random subset (70%) of occurrence data and then tested on the remaining 30% (see also Araujo et al., 2005). This procedure was replicated 100 times and finally averaged. Both native models were additionally projected onto current climatic conditions of Europe.

Those models were further analysed that yielded high model quality criteria when tested with European presence records (Table 2). Additionally, prediction quality was visualised with maps of current climatic suitability for the entire range, for the native range, and for Europe (Figs. 2–3). Climate change projections were made for three time periods at high spatial resolution for Europe in order to identify regions with future climatic suitability for the mosquito.

2.4. Niche similarity and climatic similarity

We tested for differences in environmental conditions at the occurrence points using Multiresponse Permutation Procedure (MRPP) with 999 replicates. Occurrence points were assigned to one of three groups: the native range, the invasive non-European range, or the invasive European range. The MRPP was repeated for all three sets of environmental variables that were used in the modelling, i.e. those of the EKBM, the native SBM, and the global SBM. Additionally, we tested for niche differences between models trained on the native or on the global range, using a randomization test based on a method by Warren et al. (2008). Niche overlap between two model predictions is quantified with the I statistic (Table 3). Since our main regional interest is Europe, we evaluated niche similarity for Europe only. The test compares the niche overlap of the original data with the niche overlap of randomised data, where we randomised the assignments to the regions (native and global), for both occurrence and background points. In order to keep the number of presence records constant in both regions, we separately randomised the region assignments for occurrence points and for background points. We used a one-sided test, with the null hypothesis that niche similarity is smaller or equal in the randomised data than in the original data; 199 randomisations were performed.

Furthermore, potential non-analogue climatic conditions between all projections in space and time were calculated. If non-analogue climate is detected, this requires caution in the interpretation of the results (Fitzpatrick and Hargrove, 2009). We determined potential non-analogue climate by using Multivariate Environmental Similarity Surface (MESS) analysis (Elith et al., 2010) for all of our projections in space and time. The MESS analysis measures the similarity between those environments used to train the model and the new projected environments for any grid cell (Elith et al., 2011). Regions with dissimilar values of the used variables, representing values that are outside the range of environmental training area, can be detected (Elith et al., 2010).

Preparation of presence records, current and projected climatic data was executed in ArcGIS 9.3.1 and R 2.11.0 (R Development Core Team, 2010). Correlation analysis of bioclimatic variables and Moran's I test were done in R. This software was also used to perform MRPP using the package "vegan" (Oksanen et al., 2011), while the package "phyloclim" (Heibl, 2011) was used for calculating I statistics (Warren et al., 2008). Species distribution models and MESS as well as calculation of variables contribution and Jackknife tests were carried out in MaxEnt 3.3.3e.

3. Results

3.1. Bioclimatic envelope and current distribution

Regarding the bioclimatic envelope, the occurrence of the mosquito mainly refers to regions that exhibit more than 500 mm of average annual precipitation and annual mean temperatures above

Table 2
Evaluation of model performance based on the area under the curve for the receiver–operator characteristic (AUC). AUC-values range from 0 to 1 (perfect discrimination); useful models have AUC-values above 0.7, excellent models achieve AUC-scores above 0.9. AUC values were calculated on randomly selected test and training data; the split into training and test data was replicated 100 times, reported are mean and, in brackets, standard deviation. Both global models performed best and were used for further analysis.

| Evaluation of model quality via AUC-scores	Native model (trained and tested in native range)		Native model (trained in native range, tested in European range)		Global model (trained and tested in global range)	
	Expert knowledge based	Statistic based	Expert knowledge based	Statistic based	Expert knowledge based	Statistic based
Training data	0.93 ($\pm$0.01)	0.94 ($\pm$0.01)	0.94 ($\pm$0.01)	0.94 ($\pm$0.01)	0.91 ($\pm$0.01)	0.90 ($\pm$0.01)
Test data	0.91 ($\pm$0.01)	0.91 ($\pm$0.01)	0.72 ($\pm$0.02)	0.70 ($\pm$0.02)	0.90 ($\pm$0.02)	0.89 ($\pm$0.01)

Table 3
Niche similarity based on I statistic (Warren et al., 2008) for the different models, evaluated for the regional example of Europe. In all comparisons, a randomisation test indicates significant differences in the pairs of modelled niches (p<0.05).

Model comparison	Niche similarity
Global expert knowledge based vs. global statistic based model	0.91
Native expert knowledge based vs. native statistic based model	0.85
Global expert knowledge based vs. native expert knowledge based model	0.72
Global expert knowledge based vs. native statistic based model	0.65
Global statistic based vs. native expert knowledge based model	0.74
Global statistic based vs. native statistic based model	0.66

10 °C (Fig. 1). This is found to be true for both, the native and the invasive range. Within its invasive distribution the mosquito established in areas with annual mean temperatures between 10 and 25 °C and annual precipitation that ranges from 500 mm up to 2000 mm. The native range of *Ae. albopictus* is characterised by slightly higher temperatures and rainfall compared to the invasive range. Notably, the invaded range in Europe achieved the lowest values of annual mean temperature and annual precipitation.

The EKBMs were mainly built on temperature variables. Results of the Jackknife test for the selection of meaningful variables for the SBM differ for the global and the native range: While the global-driven SBM mainly includes hydrological variables, the native-driven SBM reflects equally thermal and hydrological constraints. Altitude and annual precipitation were the only variables used in both EKBMs and SBMs, regardless of the chosen training region (Table 1). Both native and both global models showed high model performance for their respective training region (Table 2). The global EKBM and SBM
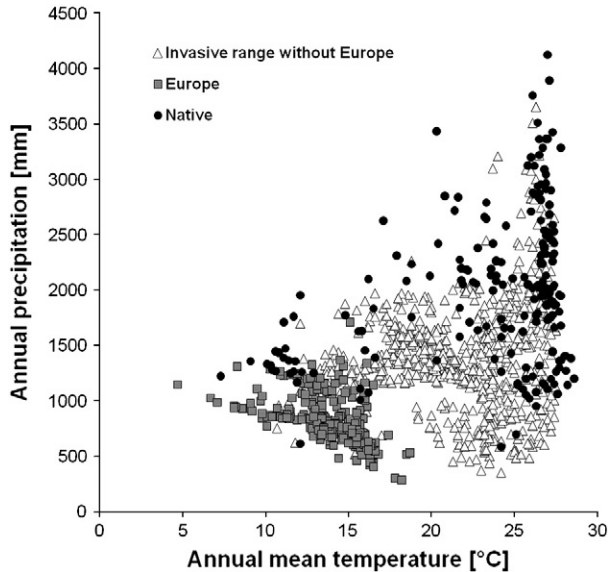
Fig. 1. Bioclimatic envelope for *Aedes albopictus* (native and invasive range), derived by geographically explicit overlay of presence records with annual bioclimatic variables. Annual mean temperature is highest in the native range (South-east Asia) with an average value of 23.7 °C (±5.1 standard deviation) and the invasive range excluding Europe with 21.7 °C (±3.7), but lowest in Europe with 13.8 °C (±2.2). High values of annual precipitation are characteristic for the native range (2028 mm ±691) and for the invasive range without Europe (1392 mm ±496). Invaded European regions obtain an average of 831 mm (±218) of annual precipitation. Globally, the averaged annual mean temperature for regions with occurrence of the species is 20.3 °C (±5.2) and averaged annual precipitation is 1392 mm (±632). The climatic conditions at the occurrence points differ significantly between the native range, the invaded European range, and the invaded non-European range (significance level of 0.001, Multiresponse Permutation Procedure with 999 replicates; the result holds for all three sets of environmental variables used in this study).

delivered a realistic representation of the global range (Fig. 2). Interestingly, large parts of the continental west coasts of South America (Chile), Mexico and the United States (California, Oregon and Washington) as well as Europe (France, Portugal) are determined as climatically suitable, although there are currently no presence records. Furthermore the eastern side of Australia has been predicted as climatically suitable in both global models where the species is not established. The SBM made better predictions of the distribution of the mosquito in India. European areas with current distributions are successfully predicted with both global models (Figs. 2,4,5).

3.2. Projected climatic suitability for Aedes albopictus in Europe

The modelled niches for Europe differed significantly between models based on native and global occurrence records (Table 3). Both native models that are based on records of South-east Asia do not predict the recent distribution of *Ae. albopictus* in Europe well (Table 2, Fig. 3). While the native-driven EKBM projected the north-western part of Europe (British Isles and north-west of France) as a preferable region for mosquito establishment, the SBM additionally detected Denmark and the northern part of Germany as climatically suitable. Only the northeast of Italy and some eastern coastal Mediterranean regions are correctly predicted as climatically suitable in both native-driven models. As a consequence, European climatic suitability of *Ae. albopictus* in the 21st century was projected using the current global range of distribution as training region.

Italy provides highest climatic suitability under current climatic conditions in both global models. The western Atlantic coast of Portugal, Spain and France are pointed out as climatically suitable as well, though records from these regions are still missing. Both models already project a slight decrease of climatic suitable areas in southern Europe for 2011–2040 (Figs. 4–5). The decrease is more pronounced in south-western parts of Europe. However, Italy and south-eastern parts of Europe will still provide suitable climatic conditions for the mosquito. Passing the mid-century the Mediterranean coast of Spain seems to become unfavourable for *Ae. albopictus*. On the other hand, climatic suitability in western Europe is projected to increase considerably. France can be expected to become the country with the best climatic suitability, regardless of the applied model or scenario. At the end of the century, our results suggest that especially some western parts of the Mediterranean such as Spain seem to develop towards a climatically unsuitable direction for the species. Today's temperate regions of Europe will be characterised by a continental gradient of climatic suitability, with central Europe becoming a more and more suitable habitat. The United Kingdom will be exposed to the establishment and spread of *Ae. albopictus* as well. Scandinavia is projected to remain outside of the bioclimatic niche, with the exception of Denmark, where a limited suitability is indicated at the end of the century.

3.3. Comparison of model results

Even though the decreasing climatic suitability in the south and the increasing suitability in central Europe are highlighted by both scenarios and models, this tendency is more pronounced in the EKBM. Notably, this model tends to attribute central and eastern Europe with substantially higher values of suitability throughout the 21st century than the SBM (Suppl. Fig. 1). The SBM, however, pointed out better habitat conditions for the south-west, south and south-east of Europe and additionally for the United Kingdom than the EKBM. This is true for both scenarios.

Differences between climate change scenarios are worth mentioning (see also Suppl. Fig. 2). Generally, higher values of climatic suitability for *Ae. albopictus* in both models refer to the A1B scenario. This becomes especially apparent in the SBM for central Europe, eastern Europe, and for the British Isles (time periods 2011–2040 and
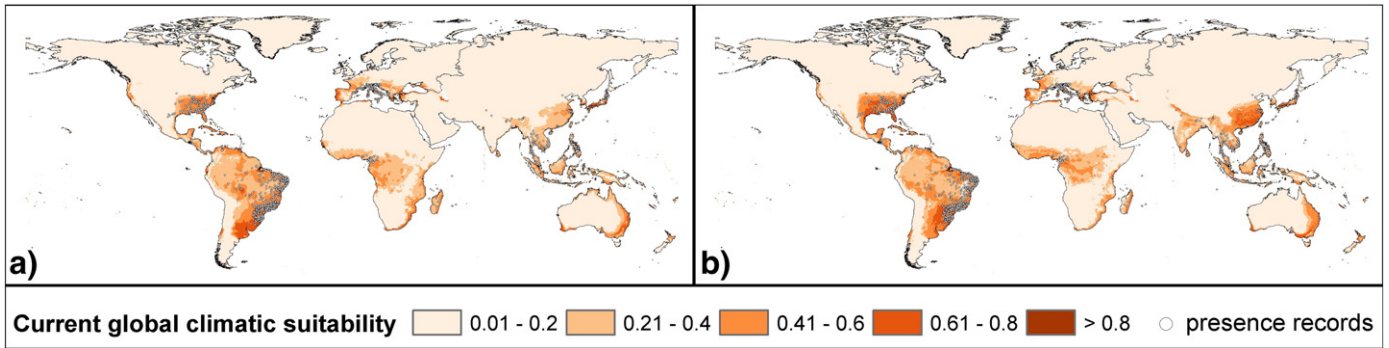
Fig. 2. Global climatic suitability, modelled based on global occurrence data under current conditions. MaxEnt suitability values range from zero to one. High values represent favourable climatic conditions for the species; values close to zero indicate unfavourable climatic conditions. Results are mapped for the global-driven: a) expert knowledge based model and b) statistic based model.

2041–2070) and in the EKBM in the later period (2071–2100). Regionally limited areas of the Iberian Peninsula and France are detected to be more suited following the B1 scenario.

Regarding the changing climatic suitability we compare trends across different time periods. Clear temporal trends of the changing climatic suitability in projections of the EKBM exist, with a stronger emphasis in the A1B scenario (Suppl. Fig. 3). Western, central and eastern Europe are characterised by an increase in climatic suitability throughout the 21st century, while climatic suitability decreases in the south from one period to the following. Nevertheless, projections of the SBM do not show such a clear tendency (Suppl. Fig. 4). Although suitability also decreases generally in southern Europe, some spatially limited regions in central Spain and northern Italy show increasing climatic suitability, when the time period 2011–40 is compared with current conditions. For the southern parts of Europe generally only

small changes in climatic suitability are projected from the time period 2011–40 to 2041–70 in both scenarios. Instead, increasing suitability at higher latitudes is projected for the end of the century.

3.4. Niche overlap, climatic similarity and non-analogue climate

Climatic similarity between regions was determined by MESS analysis (Elith et al., 2010) ranging theoretically from 100 (maximum similarity) to zero (minimal similarity). Negative values represent non-analogue climatic conditions. Non-analogy may be caused either by e.g. completely divergent relationships between the chosen climatic variables in training and projected area or by completely novel relationships of the variables in the projections across space and/or time (Fitzpatrick and Hargrove, 2009). Projections of a species' climatic suitability must then be expected to be biassed.
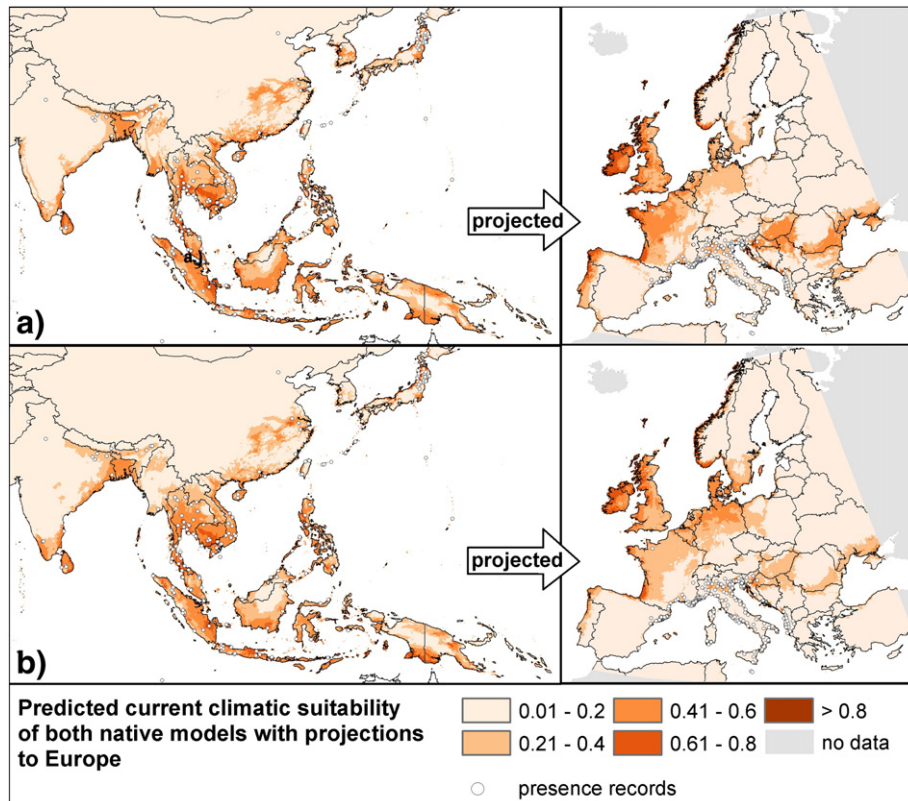
Fig. 3. Current climatic suitability modelled based on the species' occurrences in the native range and projected to the European continent. Results are mapped for the global-driven a) expert knowledge based model and b) statistic based model. Both native models failed to predict the current distribution of *Aedes albopictus* in Europe.
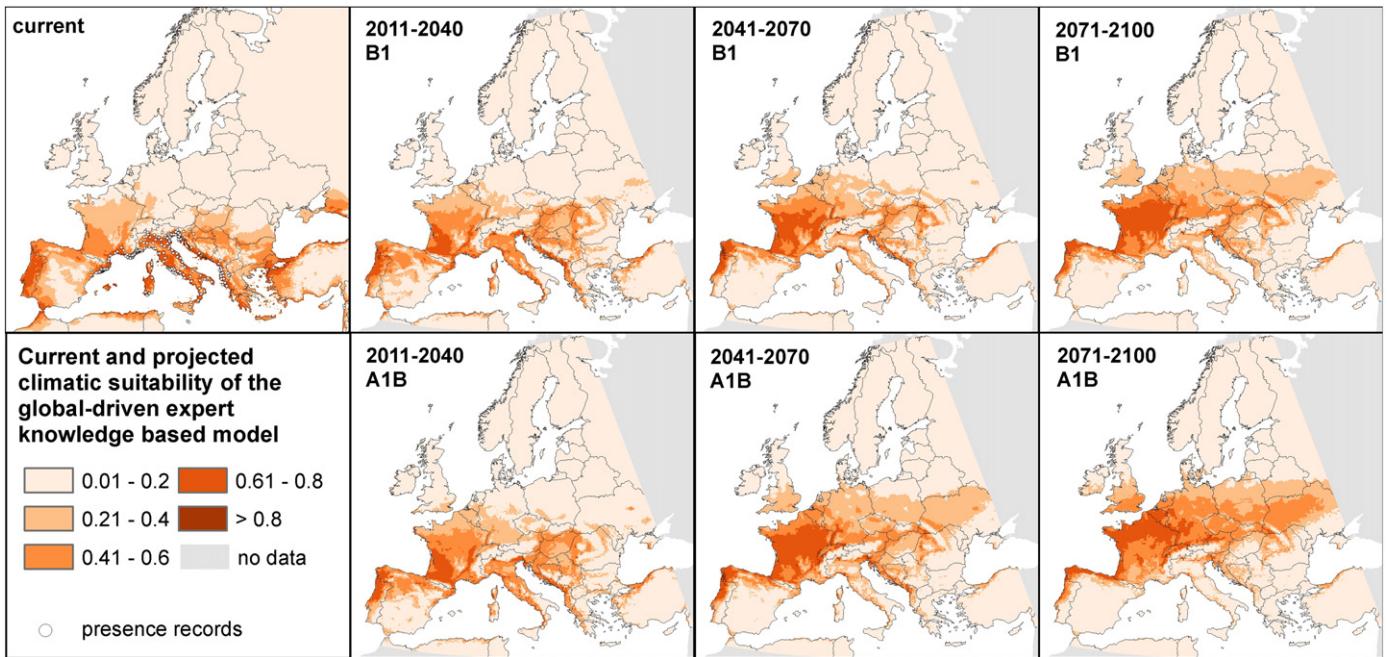
Fig. 4. Current and projected climatic suitability for *Aedes albopictus* in Europe derived from the global-driven expert knowledge based model.

In none of our projections non-analogue climate can be identified (Suppl. Figs. 5–7). For projections of the native models to current European climate (Suppl. Fig. 5), the climatic variables selected of the EKBM show higher similarity. Regions with lowest similarity in both projections are the northeast of Italy, the coastal areas of Belgium, the Netherlands, the north-west of Germany and parts of Scandinavia as well as mountainous regions in general.

Non-analogue climate must not only be a phenomenon occurring between regions but also between time periods. But again, no

European region was found to exhibit non-analogue climatic conditions in temporal projections of the two global models. The lowest values of similarity are detected in the highest mountainous regions (Alps and Pyrenees), the north-eastern parts of Italy, the coastal areas of the North Sea and the coast of Norway. Projections of the EKBM (Suppl. Fig. 6) generally result in higher values of similarity. However, these projections tend to perform dispersed spatial patterns of similarity. Using the SBM projection (Suppl. Fig. 7) France, the Iberian Peninsula and Turkey reach considerably
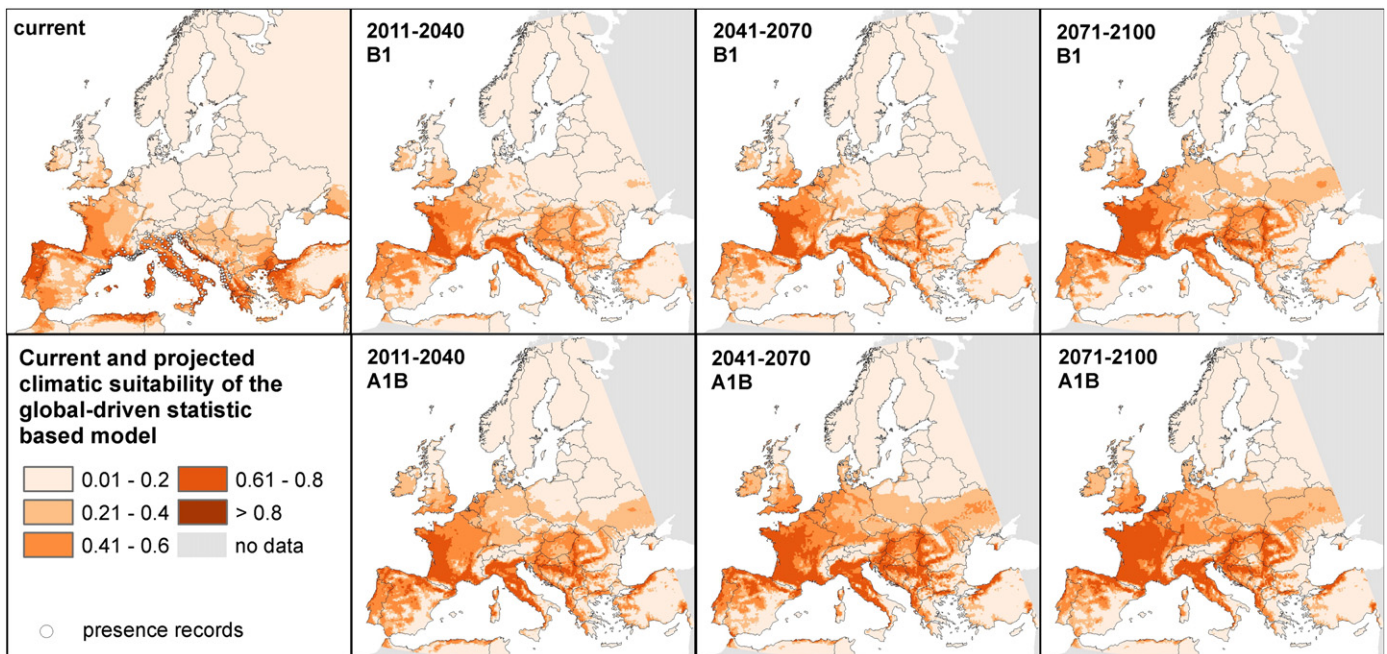

Fig. 5. Current and projected climatic suitability for *Aedes albopictus* in Europe derived from the global-driven statistic based model.

lower values of similarity compared to the EKBM projection. Only slight deviations between scenarios and time periods were found in the results for both global climatic datasets that were used for projection.

4. Discussion

4.1. Reflection of the results and comparison to previous studies

Our aim was to identify areas that can serve as a potential habitat for *Ae. Albopictus*, today and under future climate change. Two sets of bioclimatic variables were used to detect the influence of variable selections on spatio-temporal patterns of model output. In addition, we tested if records of occurrence of the former native or of the recent global range are more appropriate for predicting the current distribution in Europe.

Particularly in early stages of the invasion process, niche models are usually trained with data from the native range and applied to areas that are novel for the potentially invasive species (Mau-Crimmins et al., 2006). As invasive species are known to be adaptive (Eritja et al., 2005; Juliano and Lounibos, 2005), the habitat preferences of the species may change during the invasion process (e.g. Pearman et al., 2008; Medley, 2010). In that case, the ecology of the species in its native range cannot be directly transferred to the invaded area. On the other hand, the native range may not necessarily cover a species' entire fundamental niche (Broennimann et al., 2007).

Modelling potential spread and range dynamics based on the native habitats of a species alone has limits that can be overcome when additional data from recently occupied locations are integrated into the analyses (Broennimann and Guisan, 2008). Hence, we built native and global models in order to assess the influence on the estimated environmental niches of the invasive species. Since the global models use presence records of Europe, it was expected that they showed good results concerning the current European distribution. *Ae. albopictus* has the potential to adapt to local conditions during or after the invasion process (Medley, 2010). Hence, even using all existing species occurrence data does not guarantee per se accurate predictions of species current distribution.

We applied the regional climate model CCLM for climate projections of Europe. CCLM projects Europe to experience only a moderate warming during the first half of the century (annual mean temperature and mean winter temperatures). As mean temperature is projected to increase significantly from the mid-century onwards, certain regions reach the temperature threshold found by the global climatic envelope of the species. Precipitation, however, may be overestimated during all seasons and therefore the largest number of consecutive dry days may be higher than projected (Roesch et al., 2008), resulting in reduced habitat availability and survival rates.

An expansion of climatically suitable habitats over time could be observed in both model projections. The results raise concerns of a serious risk for the establishment of *Ae. albopictus* in western and central Europe. Once the species arrives there, it will be able to survive and establish permanent populations (Takumi et al., 2009). Annual mean temperature and annual precipitation are the only climatic variables that are applied in both global-driven models. Nevertheless, annual mean values should be considered as proxy-values, because the species is not active throughout the whole year in all established regions.

The risk of invasion of *Ae. albopictus* under current climatic conditions was examined in previous approaches for European countries (Knudsen et al., 1996), the Mediterranean Basin (Mitchell, 1995), and Spain (Eritja et al., 2005). In comparison to the previously hypothesised suitable areas for establishment of *Ae. albopictus* in Spain (Eritja et al., 2005), we found a greater extent of suitable climatic conditions in the north-west (Galicia) and south-west of

Spain (western Andalucía). The European risk map of Knudsen et al. (1996) is categorised in three classes at country level: high, moderate and low risk. This does not enable for a detailed detection of suitable areas. Benedict et al. (2007) present a global risk map for the establishment of *Ae. albopictus* under current climatic conditions. When focusing on the European part of this global map it is noticeable, that the south-western areas of the United Kingdom and Ireland show a higher climatic suitability than we found in our investigation. We observe a "coast phenomenon" beyond the one described in Benedict et al. (2007): The coastal areas of invaded continents seem to be climatically suitable for *Ae. albopictus*. This is especially true for the Americas (Pacific coastline of Washington, Oregon, California, Mexico and Chile), Europe (Atlantic coastline of Portugal, Spain and France), Africa (Atlantic coastline of Ghana, Cote d'Ivoire and for the Indian Ocean coastline of Mozambique), and for Australia (southern and western coastline). But no occurrences have yet been documented in these areas.

Certainly, some of these regions have implemented pronounced mosquito monitoring and control programmes. On the one hand, these findings may indicate that introduction of the species has not yet occurred or has been avoided. On the other hand, further climate factors could play a role under oceanic climatic conditions, which contribute to suppress the mosquito populations, such as wind, sea salt aerosols, or humidity.

ECDC (2009) practised ensemble forecasting for specific years (2010 and 2030) by embedding different scenarios to detect future possible risk areas for the establishment of *Ae. albopictus* in Europe. In contrast, we used climatic averages over longer time periods, which handicap the direct comparability of the results. Nevertheless, under current conditions our global-driven models seem to project higher climatic suitability for the south-west of France and Portugal and lower suitability for Spain compared to the ECDC statistical model. Even the minimal impact scenario of the ECDC-projections (2030) determines more European regions to be climatically suitable, especially France, Belgium, Luxembourg, the Netherlands, Germany and Greece. The tendencies of the projected eastward expansion in climatic suitability in this study are in agreement with our findings.

4.2. Limitations

As with all climate impact studies, uncertainties connected to future climate projections must be taken into account (Beaumont et al., 2008). To minimise this limitation we applied two scenarios that document the respective storyline best: A1B and B1 (IPCC, 2007). Apart from overall climatic conditions, microclimate and habitat availability will strongly influence the success of *Ae. albopictus* (Romi et al., 2006; Lounibos et al., 2010). Regions that display unsuitable annual rainfall in general might nevertheless supply the mosquito with hydroponic facilities when ambient conditions are dry (Romi et al., 2006). In the same way indoor hibernation could protect the mosquito from cold extremes. Such aspects are difficult to account for on the regional scale (Kysely and Beranova, 2009). The short-term availability of suitable conditions at small scales can be responsible for local establishment events under very special conditions. In the Netherlands, *Ae. albopictus* was monitored in greenhouses of companies that imported "Lucky Bamboo" (*Dracaena sanderiana*) (Scholte et al., 2007). However, such anthropogenic factors cannot be covered with our analysis. Nevertheless, the number of records used in this study as well as the large geographical extent of data provides a sound basis for the detection of robust large scale patterns.

In addition to spatial aspects of uncertainty, temporal variability is relevant. Besides changes in climatic trends, extreme weather events are also expected to increase in magnitude and frequency (Semmler and Jacob, 2004; Jentsch and Beierkuhnlein, 2008), so that a temporal window of opportunity for an invasive vector could arise. Up to now,

both aspects can hardly be reflected and projected accurately in climate models (Beniston et al., 2007).

Using only climatic variables as explanatory variables for scenarios may be problematic (Dormann, 2007; Wiens et al., 2009): Land use and land cover can modify the realised ecological niche in a certain region, but become more important for modelling species distribution on smaller spatial scales (Pearson and Dawson, 2003). Knowledge on interspecific competition, predation as well as quantitative life history traits may improve the understanding of the invasion processes (Juliano et al., 2004; Juliano and Lounibos, 2005; Armbruster and Conn, 2006; Armistead et al., 2008; Juliano, 2009) and could provide input data for process-based models of invader spread. As the mosquito adapts rapidly to its environment the ecological niche models will have to be updated iteratively. Mutations and even epigenetic responses have to be considered. However, this kind of knowledge is not available yet.

On a more technical level, a further source of uncertainty stems from spatial autocorrelation, which MaxEnt – at least currently – cannot take into account. Spatial autocorrelation in the residuals may for example bias parameter estimates, and lead to optimistic estimates of model performance. Based on Moran's I, we detected statistically significant spatial autocorrelation in the residuals for all models. However, estimates of AUC using 32-fold spatially structured cross-validation (e.g. Reineking et al., 2010), which is expected to be less affected by spatial autocorrelation, were only slightly lower than those by the 70/30 splitting approach. This indicates limited bias in our estimates of model performance.

4.3. Relevance

Even when considering the limits of extrapolative niche modelling, environmental envelope models remain a powerful tool to envisage potential responses in species distribution to climate change (Wiens et al., 2009).

Our projections refer to the regional model CCLM, which is integrated into the well established global simulations of ECHAM5 (Rockel et al., 2008). In comparison to their driving models, regional models project patterns of climate change at a higher spatial resolution. This is especially relevant in climate impact studies on human health, where precise geographical information is needed (Giorgi and Diffenbaugh, 2008). In particular, small-scale heterogeneity has to be considered in studies on vector-borne diseases (Jacob, 2008; Fischer et al., 2010b). We detected those regions of Europe that are especially endangered regarding a potential establishment of *Ae. albopictus* under current conditions. Subsequently, we projected for the first time geographic patterns of climatic suitability for the mosquito that can be expected to develop during the entire 21st century. These risk maps of potentially suitable areas for the establishment may serve as a valuable support for the design of monitoring and control activities. These can contribute to avoid the further spread of the disease vector and prevent the human population from unexpected disease outbreaks. Knowledge of potential future occurrences of the vector Ae. albopictus becomes especially relevant regarding the increasing European areas that are expected to provide suitable temperatures for dengue-virus amplification in the 21st century (Thomas et al., 2011).

Projections of species distribution in regions of non-analogue climate are a common, but still a rarely addressed problem in species distribution modelling. The consequences can be ecologically and statistically invalid studies (Fitzpatrick and Hargrove, 2009). To assess the problem of non-analogue climate, we re-analysed our dataset using the MESS analysis (Elith et al., 2010). No regions with non-analogue climate were detected.

5. Conclusions

Our findings indicate an increasing risk of establishment by *Ae. albopictus* especially for the Atlantic Coast of the Iberian Peninsula and

for the south-west of France. In addition to the detection of already potentially appropriate areas, we find additional areas of potential future establishment of *Ae. albopictus*. It is possible that the mosquito has already colonised larger areas than noticed. Large areas of western and central Europe that are inappropriate for the species today are projected to change during the 21st century towards a climate that can support the survival of the species. Once the species is established, it is very difficult to control.

However, unintended anthropogenic introduction (e.g. by shipping goods) can be expected as a constant source of insecurity and will very likely contribute consistently to the introduction of mosquito populations especially close to the hubs of infrastructure (harbours and large railroad terminals). Therefore, we believe in efficiency of monitoring schemes for Europe, in order to be able to limit the spread of *Ae. albopictus* and the diseases that can be transmitted by this vector.

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