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Evolution of the recent habitat suitability area of *Aedes albopictus* in the extended Mediterranean area due to land-use and climate change

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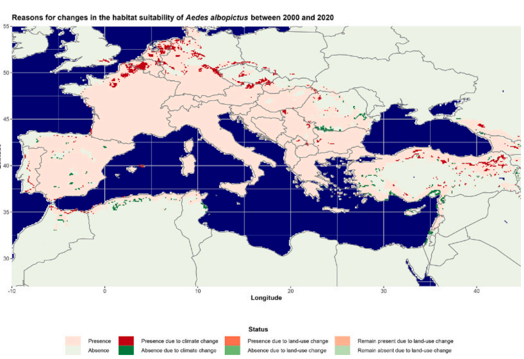
HIGHLIGHTS

- The habitat suitability of *Aedes albopictus* increased by 5 % between 2000 and 2020
- The applied method allows for identifying the reasons for change.
- On large scale, climate has a greater impact on changes in habitat suitability.
- Key drivers for change are temperature seasonality and precipitation intensity.
- Land-use factors for general habitat suitability differ from those driving changes.

GRAPHICAL ABSTRACT



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ABSTRACT

The Asian tiger mosquito, *Aedes albopictus*, is one of the world's most invasive species and is responsible for the transmission of several vector-borne diseases, including chikungunya, dengue, and Zika. *Aedes albopictus* has been established in southern Europe since the 1990s and has been spreading to other regions in recent years. The present study examines changes in the habitat suitability of *Aedes albopictus* over the period 2000–2020 using a multi-model ensemble (MME) of maximum entropy (MaxEnt) models.

An initial set of 38 climatic and 14 land-use predictors was considered for model setup. The model was built using *Aedes albopictus* distribution data for 2020. We included 19 bioclimatic variables, absolute humidity, and 18 extreme climate variables which are tailored to species specific thresholds based on expert knowledge. By means of statistical methods, predictor selection was performed. To assign changes to climate or land-use, we ran all habitat suitability models on varying climate with constant and varying land-use. Differences between both approaches indicate causes of change.

Land-use changes are an important factor until 2015, contributing at least as much as climate change to changes in the habitat suitability area of *Aedes albopictus* (HSA). In the following years, changes in the HSA are mainly shaped by climate change. In 2020, the MME shows an average 4.5 % increase in HSA compared to 2000, with decreasing habitat suitability in the south and increasing suitability in the north. Land use change accounts for 16–51 % of HSA change, but only 3.3 % of land use change is spatially consistent across the MME. In contrast, changes in the HSA due to climate change has a spatial consistency of 54.2 % across the MME. The overall

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increase in HSA between 2000 and 2020 also increases the risk of vector-borne disease infections, but land-use changes can counteract some of the climate-induced changes.

1. Introduction

Despite centuries of control efforts, the fight against mosquito-borne diseases (MBDs) is a challenge of huge public health importance (Tolle, 2009; Benelli and Mehlhorn, 2016). Although mosquitos and MBDs are commonly associated with tropical and subtropical regions, mosquitos are found beyond these regions and MBDs are flourishing worldwide (Tolle, 2009; Solomon et al., 2012). Thus, over 80 % of humanity are exposed to (Franklinos et al., 2019), and >700.000 deaths a year can be attributed to MBDs (Pan American Health Organization, 2020; Anoopkumar and Aneesh, 2022), making it the world's deadliest animal.

In the Mediterranean area, *Aedes* species are one of the most important transmitters of MBDs, causing, e.g., Chikungunya (CHIK), Dengue (DEN), Yellow Fever or Zika (Medlock et al., 2012; World Health Organization, 2020). The first records of *Aedes albopictus* date back to 1979 in Albania (Adhami and Reiter, 1998) and 1990 in northern Italy (Cunze et al., 2016b) and, thus, only allochthonous MBDs depending on this species were registered before. The second invasion led to a permanent establishment of *Aedes albopictus* in the northern and central parts of Italy (Dalla Pozza and Majori, 1992) and an ongoing spread can be observed across the Mediterranean (Fischer et al., 2011). This resulted in the first outbreak of CHIK within Europe in Italy 2007 (Rezza et al., 2007; Di Luca et al., 2017), followed by several isolated cases of DEN and CHIK in France and Croatia, where *Aedes albopictus* was proved to be the primary vector for transmission (La Ruche et al., 2010; Gjenero-Margan et al., 2011).

Globally, mosquitoes and MBDs are expected to increase in geographic distribution and abundance (Franklinos et al., 2019). There are several reasons for the invasion into new areas and the re-emergence of previously eradicated areas: mosquito dispersal depends mainly on high mobility, international trade, and globalization (Becker, 2008), while life cycle dynamics, survival and reproduction rates depend more on climate (Negev et al., 2015), land-use (Norris, 2004) and host availability (Cebrián-Camisón et al., 2020). Since we are interested in the long-term ecological habitat suitability rather than on the transient expansion of *Aedes albopictus* in the extended Mediterranean, we neglected dispersal factors and only analyzed factors that prevent or facilitate permanent establishment. In this study, the emphasis is placed on the climatological and land-use characteristics of the Mediterranean, while host availability is assumed to be sufficient throughout the study area. *Aedes albopictus* is an opportunistic forager with mainly anthropophilic feeding habits (Bertola et al., 2022). Therefore, a high population density, a high tourist attractiveness (Tovar-Sánchez et al., 2019), and an agricultural sector where livestock production is still an important factor (Bernués et al., 2011) should not pose limitations in terms of host availability across Europe. Thus, the habitat suitability of *Aedes albopictus* (HSA) represents the area, where climatic and land-use conditions are suitable for the establishment of the species. The HSA in our study does not represent the actual occupied habitat, but the potential habitat of the species within the extended Mediterranean area.

Mosquitoes are directly affected by weather and climate and therefore require temperature and precipitation above certain thresholds for adult activity and immature stage development (Waldock et al., 2013). Due to the strong ecological plasticity, *Aedes albopictus*, which originates from Southeast Asia, rapidly adapts to a very wide range of habitats (Paupy et al., 2009) and, thus, gets also used to the Mediterranean climate. Thresholds for different life cycle stages with respect to temperature and precipitation are mainly derived from climate chamber experiments (Cunze et al., 2016b). For example, Thomas et al. (2012) states that the eggs of *Aedes albopictus* survive temperatures of down to −12 °C for at least 1 h and temperatures of −10 °C for 12–24 h. In contrast, the critical upper threshold for survival is approximately 40 °C for adults (Brady et al., 2013) but only temperatures below 37 °C allow the development during the pupae stages (Waldock et al., 2013). For precipitation, a general threshold of at least 500 mm annual precipitation is accepted by many studies (e.g. Caminade et al., 2012; Medlock et al., 2015), but Waldock et al. (2013) point out that the survival of *Aedes albopictus* is also observed in regions with <300 mm annual precipitation. Therefore, the mean Mediterranean climate according to Koeppen-Geiger with minimum monthly mean temperatures >0 °C, >4 months with mean temperatures >10 °C (Alessandri et al., 2014) and annual precipitation amounts of 400–1500 mm in large parts of the Mediterranean provides a suitable environment for the further spread and establishment of *Aedes albopictus*.

However, mean changes are not the only important factor to determine impacts (Mearns and Washington, 2001). Franklin (2009) pointed out that the distribution of species depends more on climate variability and extremes than on annual mean values, and Bailey and van de Pol (2016) assume that changes to frequency and magnitude of extremes promote more drastic shifts in species distribution than changes in mean climate. Especially in the fringes of the distribution area, extremes provide significant additional improvements in model performance compared to the baseline climate alone (Stewart et al., 2021). Since the Mediterranean is a region, whose climate is particularly sensitive to global change, as evidenced by a strong decrease in mean annual precipitation and an increase in precipitation variability within the summer season (Giorgi, 2006), both means and extremes should be considered when assessing the spread of *Aedes albopictus*.

As mentioned above, thresholds are the result of climate chamber experiments and are biologically true (Waldock et al., 2013), but in anthropogenically influenced ecosystems these thresholds become blurred. In particular, land-use changes such as urbanization, irrigation, and deforestation have a major impact on MBD (Franklinos et al., 2019), causing changes that affect the niche, community composition, behavior/movement, and spatial distribution of vectors (Gottdenker et al., 2014). For example, in the absence of suitable climatic conditions, irrigation practices have been observed to increase the number of breeding sites (Patz et al., 2004) and extend the disease transmission season (Ijumba and Lindsay, 2001). Habitat suitability for mosquitoes, particularly reproduction, abundance, and species composition (Norris, 2004), is also affected by deforestation because it alters local environmental and climatic conditions (Gottwalt, 2013). In contrast, both retreat and spread of mosquitoes and MBDs can be observed due to urbanization (Franklinos et al., 2019). On the one hand, daily mean temperatures in urban areas are generally higher than in rural surroundings (Oke, 2002). Compared to natural environments, the so-called urban heat island effect smoothens the diurnal temperature range (LaDeau et al., 2015), which favors mosquito survival (Waldock et al., 2013). On the other hand, urbanization is also thought to reduce MBDs and the mosquito occurrence due to improved health care, education, and employment compared to rural areas (Wood et al., 2017). The same effect is assigned to the higher proportion of sealed areas and only little or no vegetation (Waldock et al., 2013). Kilpatrick and Randolph (2012) found that MBDs are highly sensitive to climate, but past and future changes in land-use are expected to affect MBDs more than climate change. This also includes indirect factors like the density, behavior and population dynamics of non-human hosts which are partially shaped by landscape features (Lambin et al., 2010). Therefore, to adequately assess the HSA, land-use categories should be considered in addition to climatic variables.

In the present study, we assessed the recent change in HSA for the extended Mediterranean area between 2000 and 2020 using a Maximum

Entropy Model (MaxEnt Version 3.4.3, Phillips et al., 2022) with climatological and fractional land cover variables. We checked different approaches for the background selection as well as different statistical predictor selection methods. Although some studies emphasize that machine learning tools can handle correlated predictors (e.g. Fourcade et al., 2018), we additionally follow the principle of Ockham's razor that enhances the probability of overfitting within future periods due to too many (correlated) predictors. By means of the time series and scenarios with fixed land-use, we were able to address the drivers of HSA changes. Many studies used machine learning tools such as Maximum Entropy (e.g. Fischer et al., 2011; Cunze et al., 2016b) or Random Forests (Ducheyne et al., 2018) as well as mechanistic models (e.g. Caminade et al., 2012) to assess the recent and future species distributions or HSA for Europe or subregions. However, all these studies are based on climatological variables only. Studies that include land-use variables as predictors for HSA either refer to regions outside of Europe (e.g. Hopperstad et al., 2021), use only one categorical land-use predictor (e.g. Khan et al., 2020), or assess only the recent distribution without considering changes over time (e.g. Medley, 2010).

The present study provides new insights into environmental dependencies and how climate and land-use changes affect the HSA. We present analyses that address changes in the HSA of *Aedes albopictus*, whether due to climate or land-use change, and identify the main drivers of these changes. In addition to the established bioclimatic variables, we also include a set of 18 extreme variables (EXVs) based on expert knowledge. A stepwise elimination of predictors by means of statistical methods is then used to identify significant climatological predictors. Identifying the interactions between climate and land-use and the main drivers helps to establish efficient monitoring programs and enables to locate regions where landscape shaping actions can reverse the establishment of *Aedes albopictus* to reduce the risk of MBDs. To our knowledge, the present study is the first that 1) includes EXVs based on expert knowledge, 2) addresses changes of the HSA to specific predictor groups (climate or land-use) and 3) identifies the most important predictors for the establishment/change within the larger European-Mediterranean area.

2. Data and methods

2.1. Data

2.1.1. Study area

Since the HSA is assumed to expand northward under expected climate change, we have extended the Mediterranean region to the area from 10 W to 45E and 27 N to 55 N. With a spatial resolution of $0.1^\circ \times 0.1^\circ$ ($\sim$90 km^2 per grid box), the region comprises 154,000 grid boxes with 113,054 grid boxes over land areas. All data sets used in this study have been interpolated to the respective grid using the first-order conservative remapping algorithm of the Climate Data Operator (CDO, Schulzweida, 2022) where necessary.

The Mediterranean area is characterized by a warm climate with dry summer and humid winter seasons (Cs-climate according to the Köppen-Geiger classification). The adjacent regions to the north represent temperate oceanic climate (Cfb) in the western and warm-summer humid continental climate (Dfb) in the eastern parts of Europe. Overall, the Mediterranean area exhibits a high population density of 63.3 inhabitants per square kilometer but with much higher densities along the coasts. In addition, with over 300 million tourists per year (Tovar-Sánchez et al., 2019), the human density significantly increases especially along the coast during the summer season. Besides tourism, the agricultural sector is an important economic factor within the Mediterranean area. 237.6 million ha of the area of the Mediterranean countries is assigned as agricultural land (World Bank Group, 2023; Food and Agriculture Organization of the United Nations, 2021). A central feature of agriculture within the Mediterranean area is irrigation and all states have invested massively in large-scale dams, inter-basin transfers, and public irrigation schemes during the second half of the 20th century (Molle and Sanchis-Ibor, 2019). In the meantime, over 10 % of the agricultural areas are irrigated (World Bank Group, 2023; Food and Agriculture Organization of the United Nations, 2021). But also grazing-based livestock farming is still an important economic factor within the agricultural sector of the Mediterranean area (Bernués et al., 2011).

2.1.2. Observational dataset

Observations of *Aedes albopictus* are obtained from the European Centre for Disease Prevention and Control (ECDC, 2023) and the Global Biodiversity Information Facility (GBIF, 2022) for the period 2000–2020. Unless otherwise noted, all data with a status of ‘established’ or ‘introduced’ were reported as present, while data with a status of ‘absent’, ‘no data’ or ‘unknown’ were assumed to be absent.

2.1.3. Climatological dataset

Hourly climatological data were downloaded from the Copernicus Climate Data Store (CCDS). In this study, we used the ERA5-Land reanalysis dataset from 1970 to 2020 (Copernicus Climate Change Service, 2022; Muñoz Sabater, 2019). We calculated the first 19 bioclimatic variables (BIOs) according to the BIOCLIM program of Nix (1986). In the 1990s, the BIOs dataset was expanded to 35 variables (Booth et al., 2014; Xu and Hutchinson, 2011), but the most popular datasets only include the first 19 BIOs (e.g., WorldClim). Because *Aedes albopictus* is a mobile species that can hide in houses or barns and move to regions with moderate weather when local conditions are temporarily unsuitable, we calculated mean BIOs over 31-year periods (see the climatological approach in Merkenschlager et al., 2023) to represent long-term climatological conditions, as these are more important for the establishment of *Aedes albopictus* than annually aggregated values. The bioclimatic variables used in this study are listed in the Table 1.

In addition, based on expert knowledge, we aggregated 18 EXVs based on temperature and precipitation that represent thresholds of different life cycle stages of *Aedes albopictus*. Thus, we included the number of days (EXV-1) as well as the longest period (EXV-3) with minimum temperatures (TMIN) below $-10\ ^\circ$C, because *Aedes albopictus* eggs tolerate long-term exposure to $-2\ ^\circ$C and only temperatures below $-10\ ^\circ$C for 12 to 24 h ensure egg destruction (Thomas et al., 2012). In contrast, the upper threshold of the maximum temperature (TMAX) was set at 37 °C because this temperature represents the survival threshold for *Aedes albopictus* during the pupal stage (Waldock et al., 2013). However, we also included EXVs, which represent a comfort zone for *Aedes albopictus*. Delatte et al. (2009) found that optimal development of the immature stage of *Aedes albopictus* occurs at temperatures between

Table 1
Bioclimatic variables.

Variable	Definition
BIO-1	Annual TMEAN
BIO-2	Mean diurnal temperature range
BIO-3	Isothermality
BIO-4	Temperature seasonality
BIO-5	TMAX of the warmest month
BIO-6	TMIN of the coldest month
BIO-7	Temperature annual range
BIO-8	TMEAN of the wettest quarter
BIO-9	TMEAN of the driest quarter
BIO-10	TMEAN of the warmest quarter
BIO-11	TMEAN of the coldest quarter
BIO-12	Annual PRE
BIO-13	PRE of the wettest month
BIO-14	PRE of the driest month
BIO-15	PRE seasonality
BIO-16	PRE of the wettest quarter
BIO-17	PRE of the driest quarter
BIO-18	PRE of the warmest quarter
BIO-19	PRE of the coldest quarter

25 °C and 30 °C. Therefore, we also include the number of days (EXV-6) and the longest period (EXV-8) when the mean temperatures (TMEAN) are above 25 °C. In addition, we included climatological thresholds of 0 °C for all temperature variables and 20 °C for TMIN. The 0 °C threshold represents the threshold between frozen and liquid water that affects the aquatic stage of *Aedes albopictus*. The 20 °C threshold for TMIN defines tropical nights. Since *Aedes albopictus* is originally a subtropical species, a relationship between threshold and HSA may be possible. Regarding precipitation, there are no real thresholds based on expert knowledge. In general, extreme precipitation is thought to be more detrimental to the survival of *Aedes albopictus* than long periods of drought. Waldock et al. (2013) observed eggs surviving 243 days of desiccation and a loss of 2–10 % of immature stages of *Aedes albopictus* when exposed to light precipitation. In the absence of species-specific rainfall thresholds, we applied climatological thresholds of extreme rainfall and drought events (see Table 2). In accordance with the BIOs, the EXVs are calculated per year and averaged over a 31-year period.

The set of climatological variables is completed by absolute humidity (AHUM). AHUM is not directly downloadable from CCDS but can be approximated using TMEAN and dew point temperature, both of which are provided by CCDS. Fischer et al. (2011) state that moisture directly controls the availability of breeding sites, and that relative humidity is an important factor in egg survival. Since relative humidity is temperature dependent and therefore does not provide information on the true moisture content of the air, we used absolute humidity. According to Dickens et al. (2018), AHUM is one of the most important covariates for modeling the HSA, especially in arid areas and along the coast.

Overall, the set of climatological predictors consists of 38 variables, including 19 BIOs, 18EXVs and AHUM. In the following, we always used the last year of the specific periods as reference, i.e., when we assess the HSA of 2020, the model depends on the 31-year period from 1990 to 2020.

2.1.4. Land-use dataset

Historical land-use and land cover data sets for the period 2000–2020 were obtained from the Land Use and Coverage Area frame Survey (LUCAS) historical/future land-use and land cover change dataset, Version 1.0 (Hoffmann et al., 2021a, 2021b), provided by the World Data Center for Climate (WDCC) at the German Climate Computing Center (DKRZ). Annual values are provided for the period 1950–2015 (historical) and 2016–2100 of the shared socioeconomic pathways SSP119 (future) on a $0.1^\circ \times 0.1^\circ$ grid covering the area between 56 W to 84E and 16 N to 79 N. The dataset includes the fraction of 16 different land cover classes, but our study area contains only 14 classes because tropical classes do not occur in the extended Mediterranean area. In the following, we always consider the respective year for modeling, i.e., if we want to model the HSA of 2020, we only use the annual fractional land cover of 2020. All land-use variables used in this study are listed in Table 3.

Table 2
Extreme variables.

Variable	Definition
EXV-1	N days with TMIN < −10 °C
EXV-2	N days with TMIN >20 °C
EXV-3	Longest period with TMIN < −10 °C
EXV-4	Longest period with TMIN >20 °C
EXV-5	N days with TMEAN <0 °C
EXV-6	N days with TMEAN >25 °C
EXV-7	Longest period with TMEAN <0 °C
EXV-8	Longest period with TMEAN >25 °C
EXV-9	N days with TMAX <0 °C
EXV-10	N days with TMAX >37 °C
EXV-11	Longest period with TMAX <0 °C
EXV-12	Longest period with TMAX >37 °C
EXV-13	N days with PRE < 1 mm
EXV-14	N days with PRE > 20 mm
EXV-15	Longest period with PRE > 20 mm
EXV-16	Longest dry spell
EXV-17	Longest precipitation spell
EXV-18	Precipitation intensity (Annual precipitation amount / Number of rainy days per year)

2.2. Method

2.2.1. Maximum Entropy Model

Since *Aedes albopictus* is an invasive species in the Mediterranean area, not all climatological and ecological suitable regions are occupied. Consequently, presence and absence data do not represent the real potential distribution area. Therefore, we decided to use the Maximum Entropy Modeling of Species Geographic Distribution Version 3.4.3 (MaxEnt, Phillips et al., 2022) embedded in R version 4.3.2 (R Core Team, 2023) to assess the HSA since MaxEnt does not rely on real absence points.

The model setup for assessing the HSA was as follows: The models were established by means of the year 2020 as it is assumed to represent the HSA which is closest to the real potential distribution. We used 10,000 presence and 10,000 background points as sample data. For background selection we compared different selection methods: random and block selection as well as weighted, unweighted and hybrid selection methods. Results for the background point selection are given in S1. The block method divides the study area into four spatial blocks with an approximately equal number of presence points. From each block the same number of background points was selected. The random selection has no limitations. The weighted approach assesses the density of presence points by means of a two-dimensional kernel density estimation (kde2d) provided by the MASS R-package (Ripley et al., 2023). Densities were then used as weights for background point extraction, i.e., the closer an absence grid box is to a presence point, the higher the probability that the grid box will be selected as a background point. The hybrid model preferentially selects background points near and far from the known range of the species. Near points were included because they represent areas with species-specific thresholds between presence and absence. Additionally, these points represent suitable habitats that remain unoccupied due to the constraints of invasion speed. Distant background points were chosen because they are assumed to represent unsuitable conditions for the species and to encompass the entire climatology of the study area. The unweighted approach treats all grid boxes of our study area equally. For the establishment of the MaxEnt model we furthermore checked five different regularization modifiers (1 to 5) with six feature class combinations (**L**inear, L-**Q**uadratic, **H**inge, LQH, LQH-**P**roduct, LQHP-**T**hreshold). Finally, we evaluate all methods to define the best setup which was used in a 10-fold model calibration setup.

2.2.2. Model evaluation

To determine the best setup for the assessment of the HSA by means

Table 3
LUCAS Land-use classes.

Variable	Definition
TBET	Temperate broadleaf evergreen trees
TDT	Temperate deciduous trees
ECT	Evergreen coniferous trees
DCT	Deciduous coniferous trees
CS	Coniferous shrubs
DS	Deciduous shrubs
C3	C3 grass
C4	C4 grass
T	Tundra
S	Swamp
NIC	Non-irrigated crops
IC	Irrigated crops
U	Urban
B	Bare

of MaxEnt, we use different skills with respect to model quality and transferability to new times and spaces. As *Aedes albopictus* is an invasive species and the actual distribution does not represent the potential distribution, the skill of the models can hardly be estimated. Thus, we evaluate the quality of the setup by using three different measures of skill and one for applicability to new times and spaces. The three skills are targeting three different aspects of the MaxEnt model. The size-corrected Akaike Information Criterion (AICc) obtained by the ENMevaluate function of the ENMeval R package (Kass et al., 2023) was used to assess the regularization modifiers and best feature class combinations. The model with delta-AICc = 0 is assumed to represent the best setup for modeling the ENAA. The True Skill Statistics (TSS) was used to determine the threshold between presence and absence of *Aedes albopictus* within the study area. The threshold used was the probability with the highest TSS. A weighted Brier Skill Score (wBSS) was used to assess the quality of the assessments. The BSS is a common measure used to assess the ability of dichotomous variables. As different thresholds were obtained for the different model setups, we do not use the probabilities to calculate the wBSS since the same probability may be present in one model and absent in another. Instead, we used the presence (1) absence (0) output of the models. To consider the characteristics of invasive species, weights have been included that reduce the impact of points close to presences in favor of presence points and points far away that are assumed to be definitely absent. Since all skills address different aspects of the model setup, we average and adjust all skills into an overall skill score, with 1 representing a perfect model and negative values or values near 0 representing low performing models.

The dissimilarity index (DI) and the area of applicability (AoA) of Meyer and Pebesma (2021) were used to assess the transferability of the models to new time and space constellations. The DI is based on the distances of the standardized predictors weighted by their importance within the model. The threshold of the DI is calculated using the nearest training data point that is not in the same fold. The outlier-removed maximum represents the threshold for AoA, i.e., if a new data point is below the threshold, the model is transferable to new times or spaces. Finally, the overall skill is calculated by taking the mean of the normalized AICc, the weighted BSS and the TSS and adding the AoA to calculate the overall score.

2.2.3. Predictor selection

Selecting the right set of predictors is a challenging task. On the one hand, developers of species distribution or ecological niche models recommend that predictors should be selected using expert knowledge (if available) and statistical methods (e.g. Bradie and Leung, 2017; Porfirio et al., 2014; Synes and Osborne, 2011), as arbitrary choices can affect assessments and introduce uncertainty (Synes and Osborne, 2011). On the other hand, a larger set of predictors also increases the likelihood of detecting predictors that are critical for the presence or absence of species (Title and Bemmels, 2018; Braunisch et al., 2013). Fourcade et al. (2018) suggest a relatively relaxed selection of predictors when the goal of the study is to model ecological niches or habitat suitability, rather than the real distribution of the species. However, MaxEnt is well suited to handle many predictors, and the inclusion of a larger number of variables improves MaxEnt's ability to accurately estimate variable importance (Bradie and Leung, 2017). Therefore, we decided to include a large number of climatological predictors, some of which are based on expert knowledge (e.g., EXVs), and to eliminate predictors using statistical methods. In total, the initial model includes 52 predictors, 38 (bio)climatological variables and the fraction of 14 land-use classes. In the following, we describe the elimination of predictors using statistical methods. As we are also interested in how land-use changes affect the HSA, land-use classes are excluded from the elimination.

We first run the initial model with all predictors and then eliminate predictors based on their contribution and importance. Because MaxEnt considers all predictors separately during the model-building process, it provides a stable ranking of the importance and contribution of variables (Bradie and Leung, 2017). Therefore, the average contribution and importance over all realizations were considered as well as the contribution and importance per realization. Three different selection criteria were applied to the predictor set: the loose and moderate selections are based on the mean of all model runs, while the strict selection considers each realization separately. The loose selection retains all predictors with a mean contribution OR mean importance >1 %. The moderate selection retains all predictors with a mean contribution AND mean importance >1 %. The 1 % threshold is in line with Tran et al. (2013), who also only retain parameters that contribute to >1 % of the output variance. The strict selection eliminates all predictors that have a contribution or importance of 0 % in any of the realizations.

A second selection step is included to address collinearity and correlation issues. Correlation and collinearity are not the same, but a high correlation coefficient also indicates a higher linear relationship between variables (Dormann et al., 2013). Especially when models are transferred to new space or time, it can be problematic if correlation patterns change (Braunisch et al., 2013). Title and Bemmels (2018) point out that there is a high degree of collinearity when all predictors are considered, but Bradie and Leung (2017) emphasize that important predictors may be missed when predictors will be eliminated due to correlation issues. Therefore, Dormann et al. (2013) suggest excluding one of the correlated predictors when the correlation coefficient $|r| > 0.7$. Under consideration of the rankings with respect to importance or contribution, we eliminate these predictors which exhibit a correlation coefficient $|r| > 0.7$ with a higher ranked predictor. Since machine learning algorithms consider correlated variables separately and in interaction (Araujo et al., 2005), and the inclusion of multiple climate variables in ambiguous situations may even outweigh possible collinearity problems (Braunisch et al., 2013), we also evaluate models without selection by correlations.

In total, we use 10 different model configurations to estimate the HSA, each applied to 10 realizations, resulting in total of 100 model runs. These result from three selection options based on importance and contribution (loose – moderate -strict), three selection options considering correlations (importance – contribution – none) and one model considering the entire predictor set. All predictor selection methods were tested under consideration of the six different setups for selecting presence and background points. Results for the different models are given in the Tables S2.1–S2.3.

2.2.4. Identification of drivers of habitat suitability area shifts

To determine whether climate or land-use changes are responsible for the changes within the HSA, we run each established model twice, one with constant (CLU, 2000 land-use), one with varying land-use (VLU). The results of both time series are compared to the ones of the reference year 2000 (REF). For example, if all the three REF, CLU and VLU show presence (1), *Aedes albopictus* is considered established (see Table 4). If REF and CLU show absence, but VLU shows presence, changes in climate are not sufficient to change the status from absence to presence and changes in the HSA are attributed to land-use changes (0|0|1). The status of "remains present due to land-use change" (1|0|1) is represented by presence within the reference period, but absence in the

Table 4
Categories of changes for the habitat suitability. 1 = presence; 0 = absence.

N	REF	CLU	VLU	Category
1	1	1	1	Present
2	0	0	0	Absent
3	0	1	1	Change to Present due to Climate Change
4	1	0	0	Change to Absent due to Climate Change
5	0	0	1	Change to Present due to Land-Use Change
6	1	1	0	Change to Absent due to Land-Use Change
7	1	0	1	Remain Present due to Land-Use Change
8	0	1	0	Remain Absent due to Land-Use Change

CLU model. Thus, if land-use were unchanged, climate change would change the status from present to absent. But land-use changes have a stronger signal compared to climate change, so the status remains present. We are aware that in some cases both effects lead to status changes, and changes in only climate or land-use alone would not lead to status changes. However, in these cases, we assume land-use changes as the trigger for status changes. Since climate is a global issue and mitigation efforts will only be successful if the entire global community pulls together, our analysis focuses on land-use changes as triggers because they can be implemented regionally and the effects of changes can be seen relatively quickly.

The results of each model setup and run are first evaluated separately, and finally aggregated to obtain a Multi-Model-Ensemble (MME). In some cases, when we want to show effects of different model setups, the aggregation of results is restricted to the respective setup. All results are related to the assessed HSA of the reference year 2000 (R-HSA; not the study domain or the land area), i.e., the habitat of the reference always represents 100 %. Results separated by model run as well as for the MME are given in Table S2.4.

2.2.5. Identification of the most important predictor (MIP)

The identification of the MIP is based on three different factors: importance, contribution, and range of response. Contribution and importance are extracted from the model output statistics, and the range of response is determined from the response curves of each predictor, i.e., we check what changes could be observed in the predictor variable between the beginning of the time series and the year of interest and whether the model responses to these changes. All factors are then normalized and averaged across all models. The product of these variables is the index used to identify the MIP. The higher the index, the more important is the predictor for changes in the status of *Aedes albopictus*. The product of the factors ensures that it is zero if there are no observed changes, or the predictor is not important. The analysis of the MIP is performed separately for the climate and land-use variables.

3. Results

The results reported here are based on a random selection of background points without further constraints, as it guarantees the transferability of the established models into new times and spaces without losing skill. Furthermore, analyses are restricted to the random k-fold selection for model establishment, where nine folds were used for training and one for validation. With respect to model skill and transferability, all results of the evaluation of different background selection methods and a comparison of random k-fold versus block method are presented in S1. In the following, we use the term “model” to refer to the assessment of the parameters and “habitat suitability model (HSM)” when we want to refer explicitly to the assessment of the HSA.

3.1. Model evaluation

In addition to the models that consider all predictors, the other models based on different selection methods consider 4–17 BIOs and 3–13 EXVs climatic predictor variables. Due to correlation issues, 11.1 % of the combinations of BIOs and 20.9 % of the combinations of EXVs cannot be considered when correlation is a selection criterion, and additional combinations can be eliminated when correlations between BIOs and EXVs are considered (not shown). Only 4 BIOs are included in all models: Mean diurnal temperature range (BIO-2), Isothermality (BIO-3), temperature seasonality (BIO-4) and temperature annual range (BIO-7; Table S2.1). For EXV, only two predictors are taken into account in each model: Longest period with TMAX <0 °C (EXV-11) and precipitation intensity (EXV-18). In terms of importance and contribution, BIO-4 is the predictor that represents the BIO with the highest values, followed by BIO-2. The main EXV in any model setup is EXV-18 (Table S2.2). When considering the combined set of climate predictor variables, BIO-4 represents the most important predictor, while EXV-18 represents the predictor with the highest contribution. In terms of land-use, Bare represents in 99 % of all cases the land-use category with the highest values for importance and contribution and only one run is represented by NIC (Table S2.3). Therefore, whether or not *Aedes albopictus* becomes established mainly depends on the Bare fraction.

According to the overall skill score, the model ensemble based on the loose first order selection criteria are better than the moderate and strict criteria (Fig. S2.1). With respect to the second order selection criteria, no further selection is better than eliminating predictors by correlations under consideration of importance or contribution rankings (Fig. S2.2). Overall, the single model with strict selection and without further selection (strict-none) achieves the highest skills and scores, followed by the model which considers all predictors (Table S2.4). It represents the model with the largest number of predictors after selection (only 7 climatological variables excluded) and correlated variables are included. In terms of transferability, all models achieve an AoA of over 99 %, i.e. all models are transferable to new times and spaces as the climatological predictors used for model calibration cover most of the climatic conditions of the study area.

Fig. 1 shows the results of the MME for the year 2020, where the HSMs were trained and validated. The upper left Fig. (A) represents the observations from CEG dataset with a total of four categories with “No Data” summarizing the ECDC categories “No Data”, “Unknown” and “Outside Scope”. The upper right Fig. (B) shows the agreement of the MME with respect to the presence status of *Aedes albopictus*. Dark red colors indicate that all HSMs agree with the presence status of *Aedes albopictus*, while dark green colors indicate exclusive absence. At the bottom of Fig. 1, we highlight these areas where *Aedes albopictus* is established or introduced (C), is not established or introduced (D), and where it is observed absent (E). It shows that all HSMs are generally able to reproduce the areas where *Aedes albopictus* is present, but with some limitations for areas with the introduced status. Especially in the northeastern edge between central Germany and Slovakia, and in some areas of Spain and Turkey, the HSMs mainly show an absence for areas where *Aedes albopictus* has been introduced (C). With respect to the regions where no observational data are available, along the coastlines between Morocco and Tunisia, south and east of the Black Sea, and the Levant the HSMs generally agree that these areas are suitable for the establishment of *Aedes albopictus* (D). In addition, the HSA is also given in the border area between Portugal and Spain, the Basque province, Northern France, Switzerland, Austria, Southern and Western Germany, Southeastern Europe and the coastal areas of the Turkish Mediterranean (E), although the status of these regions is observed absence.

3.2. Changes in habitat suitability area for Aedes albopictus between 2000 and 2020

Overall, all HSMs predict an increase of the HSA between 2000 and 2020, but the magnitude of changes vary considerably (Fig. 2A). The most defensive HSM shows an increase of the HSA of 1.87 % in 2020, while the most offensive HSM assesses an increase of 12.35 %. The median of the MME is 3.87 % and the interquartile range comprises the range between 2.96 % - 5.42 % increase of the HSA. Large areas where the HSMs show changes from absence to presence can be found in the north like France, the Benelux countries, Germany, and the Czech Republic. Also, Portugal, Turkey and the coast of Morocco in the south have large areas where many HSMs show an expansion of the HSA (Fig. 2B). In contrast, some parts of Central Spain, Austria, Romania, Western Turkey and the coasts of Algeria and Tunisia show a decrease of the HSA.

In terms of first order predictor selection, the moderate selection represents the most defensive HSMs with its maximum increase around +2.6 %, while the strict selection is the most offensive approach (MAX: +3.7 %). In addition, the moderate selection shows a narrower range of estimated increase in HSA with values consistently below 10 % (Fig. 2C).

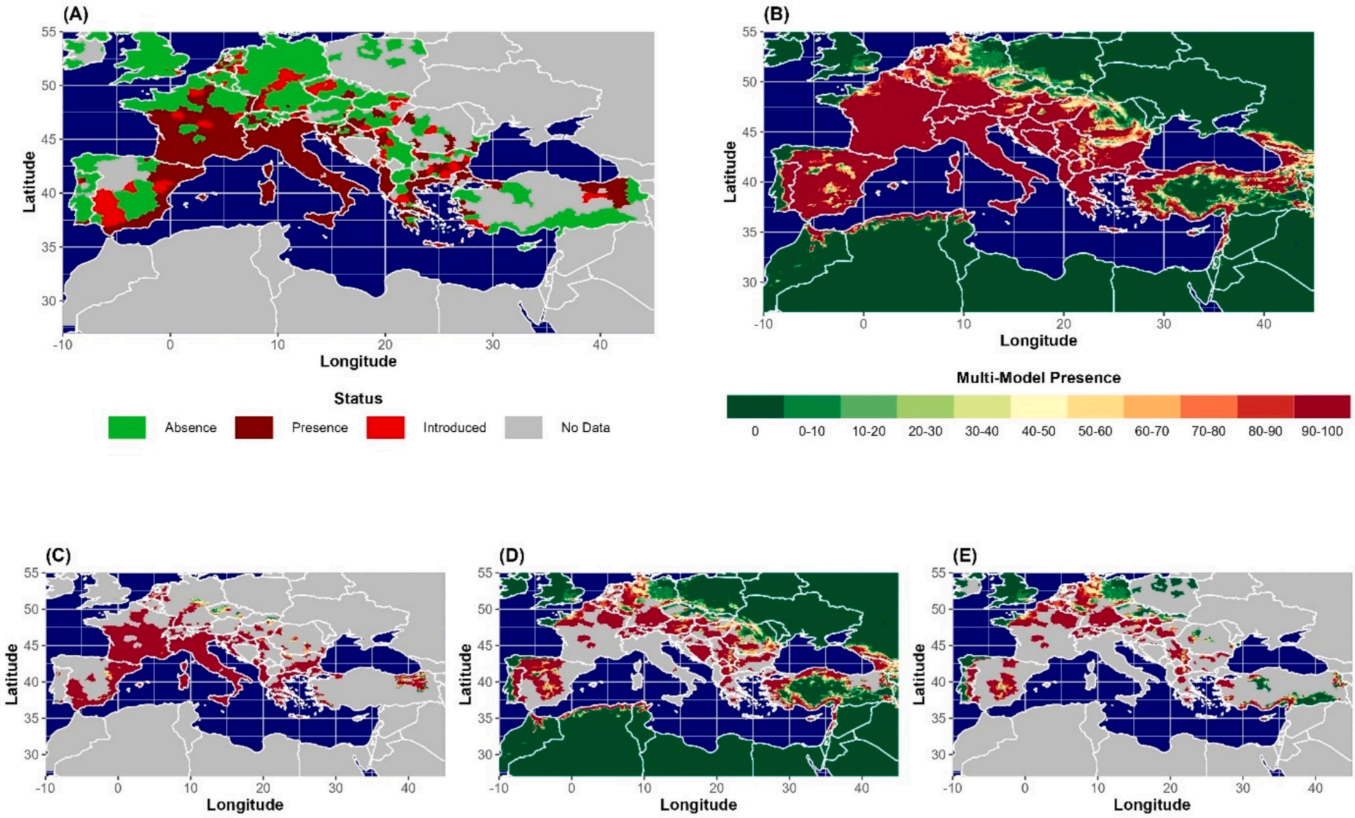

Fig. 1. Spatial distribution of Aedes albopictus: (A) Observation, (B) multi-model presence in terms of the HSA, both for the year 2020. The figures at the bottom highlight the multi-model presence for (C) regions of observed presences, (D) regions with no observed presences, and (E) regions with observed absences.

With respect to the second order predictor selection, the most conservative changes in the HSA are obtained when no further selection is performed (+2.4 %), and the greatest changes are observed with fine selection is based on contribution (+4.0 %). In comparison to the second order selection based on importance or contribution, the larger number of predictors, when no further selection is performed, provides a more consistent assessment of the HSA change (Fig. 2D).

3.3. *Drivers responsible for habitat suitability area shifts of Aedes albopictus*

Fig. 3 shows that both climate and land-use changes contribute to the spread of *Aedes albopictus* in the wider Mediterranean region. The mean expansion of the HSA due to climate change is 3.4 % (Fig. 3B), while the mean expansion due to land-use change is 1.3 % (Fig. 3C). 3.8 % of the R-HSA is climatologically unsuitable in 2020, but the HSA of 2020 also gains 7.2 % of the area that was considered unsuitable in the reference (Fig. 3A). With respect to land-use changes, a loss of 0.4 % of the HSA is compensated by a gain of 1.7 %. It also shows that the net land-use changes have a greater impact on the expansion of the HSA by 2014 than climate change, although the share of present or absent due to climate change is larger than that due to land-use changes. In the following years, the overall share of land-use changes stagnates, while the share of climate changes increases because of smaller changes in areas absent due to climate change. Looking at changes of the HSA due to climate and land-use separately, the MME estimates changes due to climate in the range of +1.3 % to +8.8 % and those due to land-use in the range of +0.4 % to +3.2 % by 2020. By 2015, some HSMs of the MME even predict a decrease in HSA due to climate change (Fig. 3B), while land-use change consistently promotes an increase in HSA (Fig. 3C).

The maps in Fig. 4 show the agreement of the MME with respect to changes in the status of *Aedes albopictus* due to climate and land-use change for the year 2020. The agreement between the HSMs is generally higher for climate than for land-use change. Up to 100 % of the HSMs show a high agreement that the former climatologically suitable conditions in the central parts of Spain, along the coastal region between Turkey and Israel, along the coastal region of Algeria and in the southern parts of Romania became unfavorable in 2020. In contrast, the region between northern France and the Czech Republic in the north and Portugal, the coastal regions of the Straits of Gibraltar and the eastern parts of Turkey in the south turn into climatologically suitable areas (maximum agreement: 97 %). Overall, most HSMs agree on the presence or absence due to climate change. On average, 60.8 % (44.2 %) of the grid boxes assigned to presence (absence) due to climate change by each model run are also represented by the MME. Much less agreement is observed for changes in status due to land-use change. Higher agreements with respect to presence due to land-use change (maximum agreement 48 %) is observed in Spain, the eastern parts of Turkey, southern Romania, the border area of Romania, Hungary, and Ukraine and in southern parts of Poland. All HSMs show the greatest disagreement in terms of absence due to land-use change. Only in Germany, the Czech Republic, Great Britain, and Romania an agreement of up to 36 % can be observed. Overall, the MME agrees for only 17 grid boxes (3.3 %) with the status presence due to land-use change in 2020, but none with the status absence due to land-use change.

3.4. *Evaluation of the most important predictors*

Fig. 5 shows the MIPs for the status of *Aedes albopictus* for the climate (top) and land-use (bottom) predictors. The most important climate predictors are temperature seasonality (BIO-4, 23.6 %) and precipitation intensity (EXV-18, 68.5 %), followed by mean diurnal temperature range (BIO-2, 2.7 %) and isothermality (BIO-3, 2.5 %). EXV-18 is

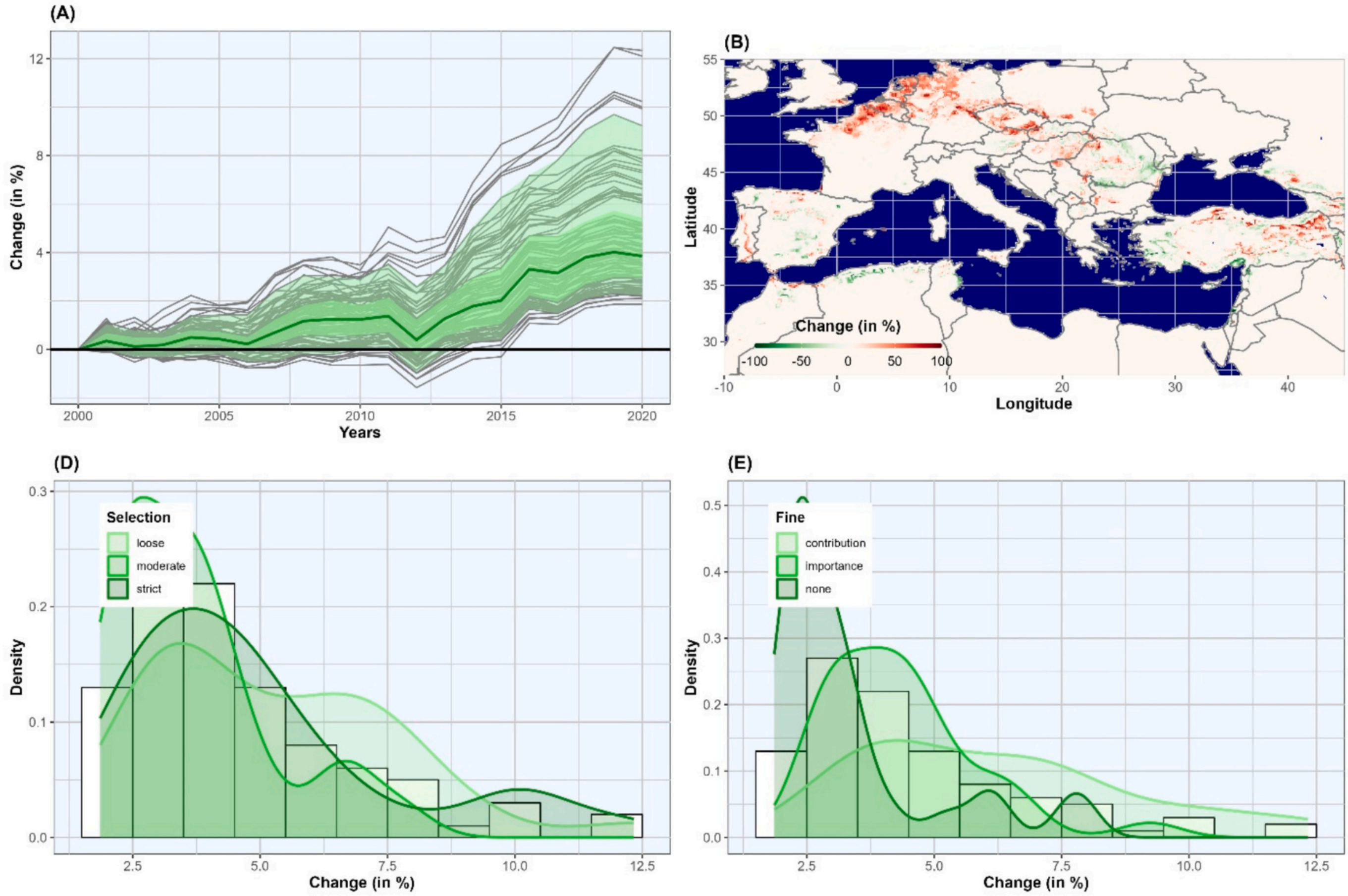

Fig. 2. Changes in the habitat suitability of *Aedes albopictus* between 2000 and 2020. The time series (A) show the results of all model runs (gray lines), the median of change for the MME (dark green line), the interquartile range (green shaded area) and the range between the 5th and 95th percentiles (light green shaded area). The map (B) shows the proportion of HSMs that show a change in the status of *Aedes albopictus* between 2000 and 2020. Dark red (green) colors indicate that most HSMs changed status from absent (present) to present (absent), and beige colors indicate no status change. The figures at the bottom show the density of projected change by different model configurations. The bars always represent the entire MME, and the shaded areas represent the respective setup. Results are shown for the first (C) and second (D) order predictor selection.

widespread throughout the study area, but mountainous regions (e.g., Alps, the Dinaric Alps, the Carpathians) and western coasts (e.g., Morocco, Portugal, Spain, France, United Kingdom) are dominated by BIO-4. The response curves show that EXV-18 is positively correlated with the HSA while BIO-4 has a plateau between 500 and 750 °C*100 where suitability is most pronounced. BIO-2 is assigned as the main predictor in parts of France, Morocco, along the Libyan/Egyptian coast and in the Levant region. South of 39° latitude, the longest period with TMEAN >25 °C (EXV-8) is also substantial for the establishment of *Aedes albopictus*. Both, BIO-2 and EXV-8 are negatively correlated with HSA.

Deciduous shrubs are the main land-use predictor for 38.8 % of the study area, followed by non-irrigated crops (22.9 %). In general, the further north, the more important deciduous shrubs are for the establishment of *Aedes albopictus*, while non-irrigated crops are more important along the Mediterranean coast, in the Alpine region and in Ireland. A higher fraction of deciduous shrubs promotes the spread of *Aedes albopictus* whereas a small fraction of <5 % of non-irrigated crops is more favorable than higher fractions. In Algeria, Slovenia, southeastern France and southern Belgium, urban structures (2.3 % of the study area, positively correlated to the HSA) favor the establishment of *Aedes albopictus*, and evergreen coniferous trees are relevant (9.1 %, negatively correlated to HSA when fraction >1 %) in central Portugal, France, the western parts of the United Kingdom, Romania and Slovakia, and the eastern parts of the Ukraine. However, 26.3 % do not show any substantial changes (NSC) in the response of the predictors. These regions are exclusively located in the arid regions of North Africa and the Levant, away from the coast.

3.4.1. MIPs for regions with status changes

We analyzed separately the regions where the MME shows high concordance with respect to absence or presence due to climate change and presence due to land-use change. For areas with the status presence due to climate change (Fig. 6 top) 81.5 % have EXV-18 as MIP, followed by BIO-4 with 16.4 %. The figure on the left shows all grid boxes with the status present due to climate change and EXV-18 as MIP (dark red) and with other MIPs (red). Especially in the northern regions of the study area EXV-18 is responsible for status changes. The middle figure shows the absolute change of EXV-18 over the period 2000–2020 for grid boxes assigned presence due to climate change. Precipitation intensity increases slightly on average from 5.33 mm to 5.46 mm precipitation per rainy day (Fig. 6 top middle) which increases the probability of presence by 2 %. In terms of climate-induced absence (Fig. 6 middle), 30.9 % of the area has EXV-18 as MIP, followed by BIO-4 with 29.9 %. In particular, Romania and the southwestern coast of Turkey have BIO-4 as MIP (Fig. 6 middle left), while EXV-18 is the MIP along the coastal regions of Tunisia and Algeria and Spain (not shown). The increase of BIO-4 from 760.3 to 780.2 °C*100 (Fig. 6 center) results in a 2 % decrease in probability (Fig. 6 center right).

With respect to land-use change, we only analyzed the grid boxes with the status present due to land-use change (Fig. 6 bottom), as the

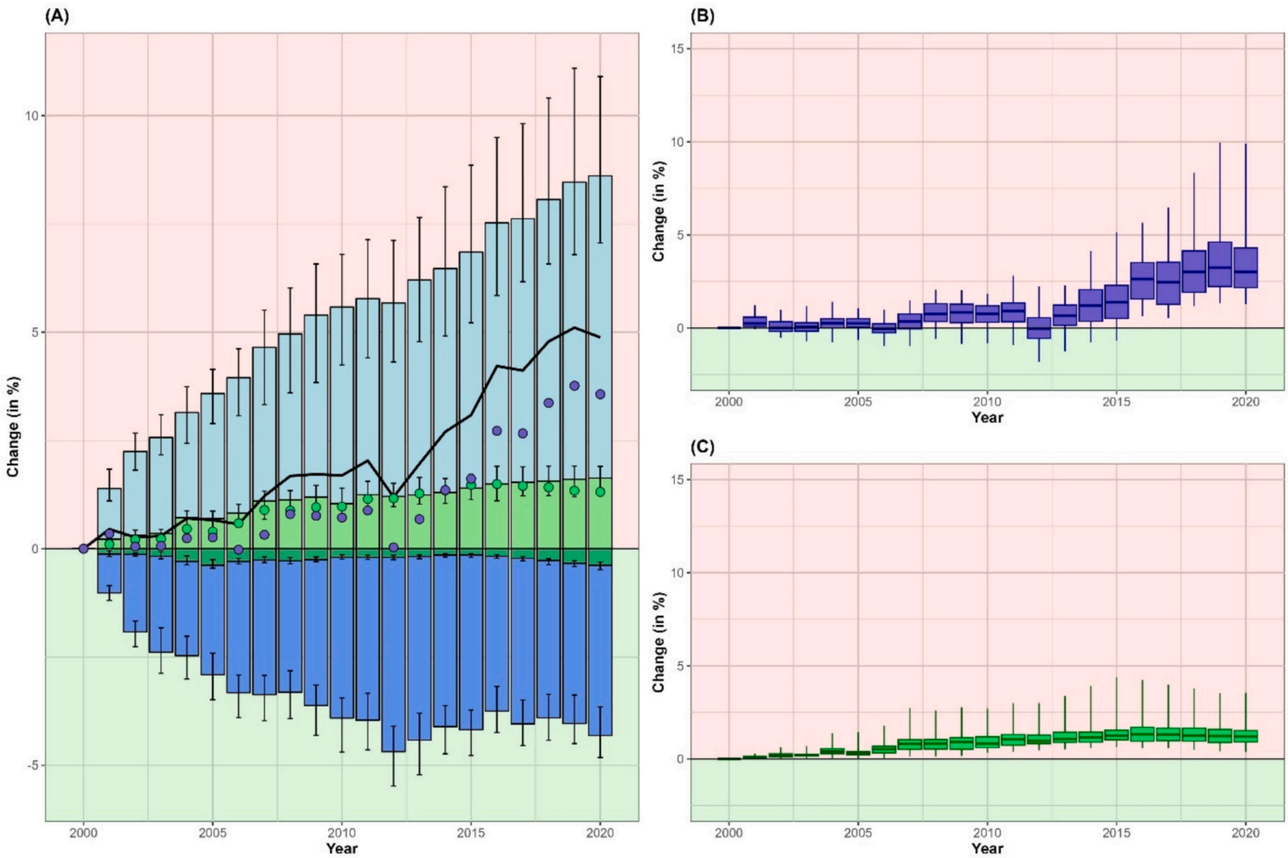

Fig. 3. Time series of MME changes categorized by their attribution to land-use change (present: light green, absent: dark green) and climate change (present: light blue, absent: dark blue) between 2000 and 2020 (A). Areas with expanding *Aedes albopictus* have a red background, while those with retreating population are green. Bars represent the median change within each category with error bars showing the interquartile range of the MME. Colored dots represent the mean change due solely to land-use (green) or climate (blue) change, and the black line represents the overall mean change. The Box-Whisker plots on the right (B: climate, C: land-use) represent aggregated changes over time. The box represents the interquartile range, and the whiskers the range between the minimum and maximum.

MME shows only little agreement across the other land-use categories. The region where an increase of evergreen coniferous trees from 0 to 0.5 % promotes the establishment of *Aedes albopictus* is in Romania and the Hungarian/Ukrainian border area. An increase of only 0.5 % has the same effect on the suitability of the ENAA as the changes observed within the climatic predictor variables.

3.4.2. Changes in the most suitable areas with respect to the main climatic predictors between 2000 and 2020

The change in response of the main climate predictors and the climatologically most suitable areas are shown in Fig. 7. As the responses of the predictors are not linear, we do not consider absolute changes in the predictor variables, but changes in the response. The range of response is divided into ten classes with equal spacing from unsuitable (blue, 0–10) to suitable (red 90–100; Fig. 7, left). With respect to BIO-4, large parts of the study area are at least suitable (50+) for the establishment of *Aedes albopictus*, with only Ireland, the west coast of the United Kingdom, northwestern Spain and the eastern parts of the study area which are away from the coast providing mainly unsuitable conditions. Overall, suitable conditions decreased between 2000 and 2020, especially north of the Black Sea and in some parts of Algeria, the United Kingdom, Spain, and Turkey. Changes favoring the establishment of *Aedes albopictus* are observed only along the Atlantic coasts of Morocco, Portugal, and Spain and, at a lower level, in the easternmost parts of the study area as well as in Belarus and Russia.

With respect to EXV-18, only the central parts of the study area have large areas of suitable conditions while areas north and south have lower precipitation intensities and thus smaller responses. The greatest increase in suitability is observed in the border area of Morocco and Algeria and in Iraq, but slight increases are also observed in the northern parts of the study area.

In combination of the main climate predictors, most of the areas provide suitable conditions (70+) in 2000 and 2020. Only the northeastern parts of Turkey away from the coast have values below 40. Thus, other factors not included in the two main climatic predictors play a critical role in the establishment of *Aedes albopictus*. In contrast, the study area also contains regions where both predictors show a high suitability but *Aedes albopictus* is absent. In particular, Morocco and Tunisia, as well as the adjacent regions northeast of the HSA, have values of 80+, but other factors still prevent further spread.

4. Discussion

4.1. Background selection

Regarding the selection of background points, the use of the random selection method outperforms the block selection method. In particular, the overall model skill score (OMSS) for random selection is much higher than for block selection, while the block selection models have slightly higher AoA values on average. Title and Bemmels (2018) argue that the block selection method leads to a more realistic and less biased assessment of the ecological niches, especially when the model is transferred to new spaces or times. However, in our analysis, both methods have high AoA values, but the OMSS of random selection (on average: 0.76) outweighs block selection (0.60) so that random selection is preferred. In terms of introducing a weighting scheme on the

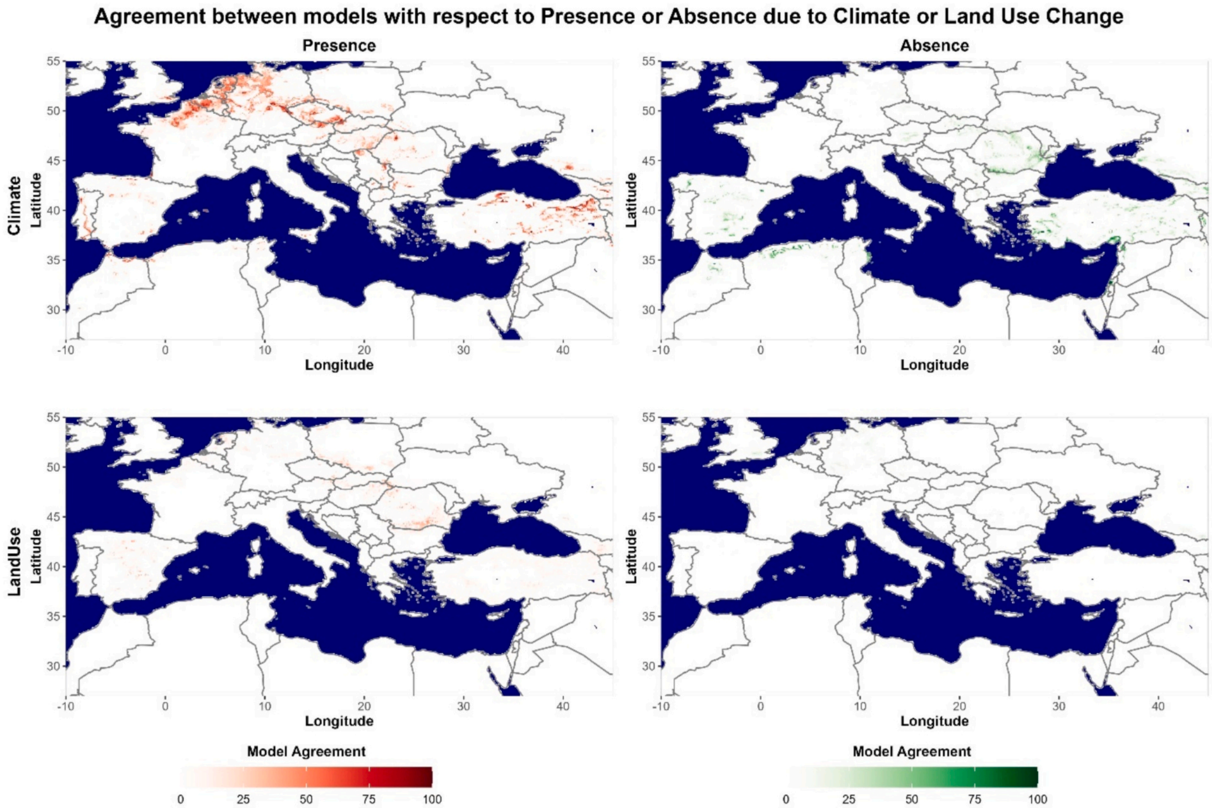

Fig. 4. Multi-Model-Ensemble agreement with respect to absence of *Aedes albopictus* due to climate change (top left), presence due to climate change (top right), absence due to land-use change (bottom left) and presence due to land-use change (bottom right) for the year 2020.

background data, the best results are obtained with an unweighted background selection. Both OMSS and AoA are significantly higher for random and hybrid background selection than for weighted background selection. Furthermore, OMSS is significantly higher for random selection than for hybrid selection, while AoA is only slightly improved for random selection. We think that weighting in favor of points close to presence could improve OMSS when species reach their ecological equilibrium, but for invasive species, random selection is more promising. With respect to the AoA, we assume that weighting reduces transferability, especially when the study area is much larger than the presence area.

4.2. Predictor selection

The temperature related bioclimatic variables that are most important for the modeling of the HSA in the extended Mediterranean area all describe diurnal or seasonal variations (BIO-2, BIO-3, BIO-4, BIO-7) which supports the theory of Franklin (2009) that the distribution of species depends more on variability and extremes than on annual means. However, this contrasts with many studies that have modeled the habitat suitability for *Aedes albopictus* in Europe or parts of Europe (e.g. Cunze et al., 2016a, 2016b; Koch et al., 2016; Ibáñez-Justicia et al., 2020; Roiz et al., 2011). Only Cunze et al. (2018) highlight BIO-4 which is the main bioclimatic variable in our study. All authors refer to the selection of predictors based on expert knowledge, which is perfectly understandable since we know that life cycle stages of *Aedes albopictus* are linked to specific temperature thresholds. It is a logical conclusion to include minimum temperature of the coldest month (BIO-6) or mean temperature of the coldest quarter (BIO-11) when it is known that cold temperatures prevent the development of *Aedes albopictus*. In this study, BIO-6 and/or BIO-11 are replaced by the longest period with TMAX below 0 °C (EXV-11), which supports the findings of Stewart et al. (2021) that extremes provide significant additional improvements in model performance compared to baseline climate. Furthermore, Bailey and van de Pol (2016) assume that changes to frequency and magnitude of extremes promote more drastic shifts in species distribution than changes in mean climate. In addition, the temperature threshold of 25 °C for TMEAN seems to be substantial for the modeling of the HSA. Based on the second selection criteria, either the longest period with TMEAN >25 °C (EXV-8, Importance) or the number of days with TMEAN >25 °C (EXV-6, Contribution) was considered. Like the temperature related variables, the two main precipitation predictors (EXV-18 and BIO-15) represent measures of precipitation variability. In comparison to the other studies, only Cunze et al. (2016a) include precipitation seasonality while most studies include annual precipitation or precipitation of the warmest quarter (BIO-18). It is interesting to note that both Waldock et al. (2013) as well as Dieng et al. (2012) have shown in experiments that flushing from aquatic environments by heavy precipitation negatively affects the survival of *Aedes albopictus*. Here, the number of days and the longest period with precipitation >20 mm is not an inhibiting factor, and the probability of establishment increases with higher values of EXV-18, since water availability seems to play a more important role than flood risk.

The number of temperature and precipitation related predictors, their contribution and importance support findings of other studies that highlight the greater importance of temperature related predictors for modeling of the HSA (e.g. Cunze et al., 2016a, 2016b; Tran et al., 2013). On the one hand, this can be attributed to the sufficient water supply within the study area. Although experts recommend a threshold of 500 mm for annual mean precipitation, Kuhlisch et al. (2018) state that 250-500 mm is enough for the establishment of *Aedes albopictus* in Europe and Koch et al. (2016) modeled presences even for areas with 160 mm. Ducheyne et al. (2018) assume that precipitation predictors are more important in arid areas with shortages in water supply. In our study area, only parts of Africa and the Arabian Peninsula away from the coast have <160 mm of annual precipitation, and only a few areas within Europe

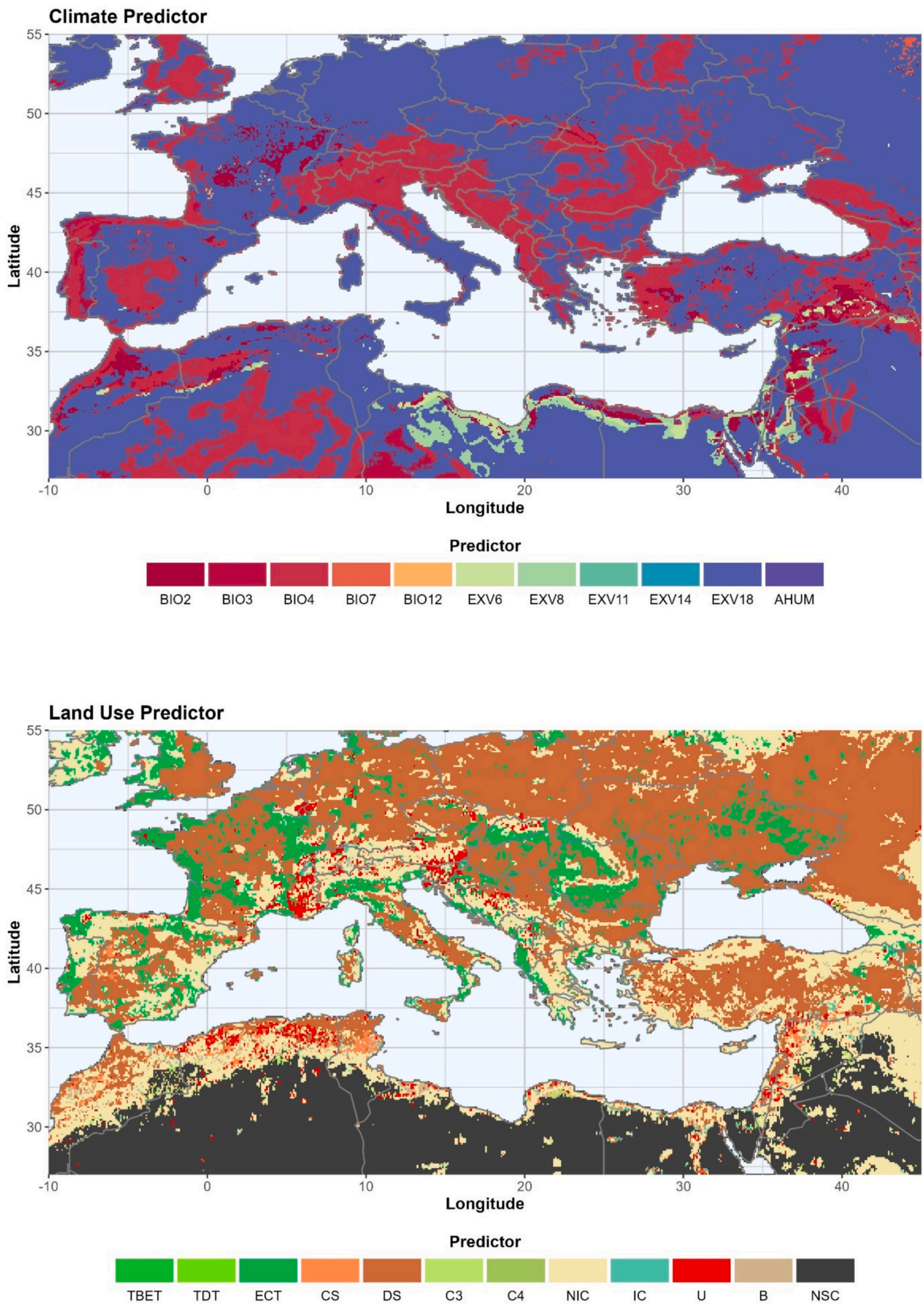

Fig. 5. The most important predictor with respect to climate (top) and land-use (bottom) change. No changes (NSC) are displayed in black.

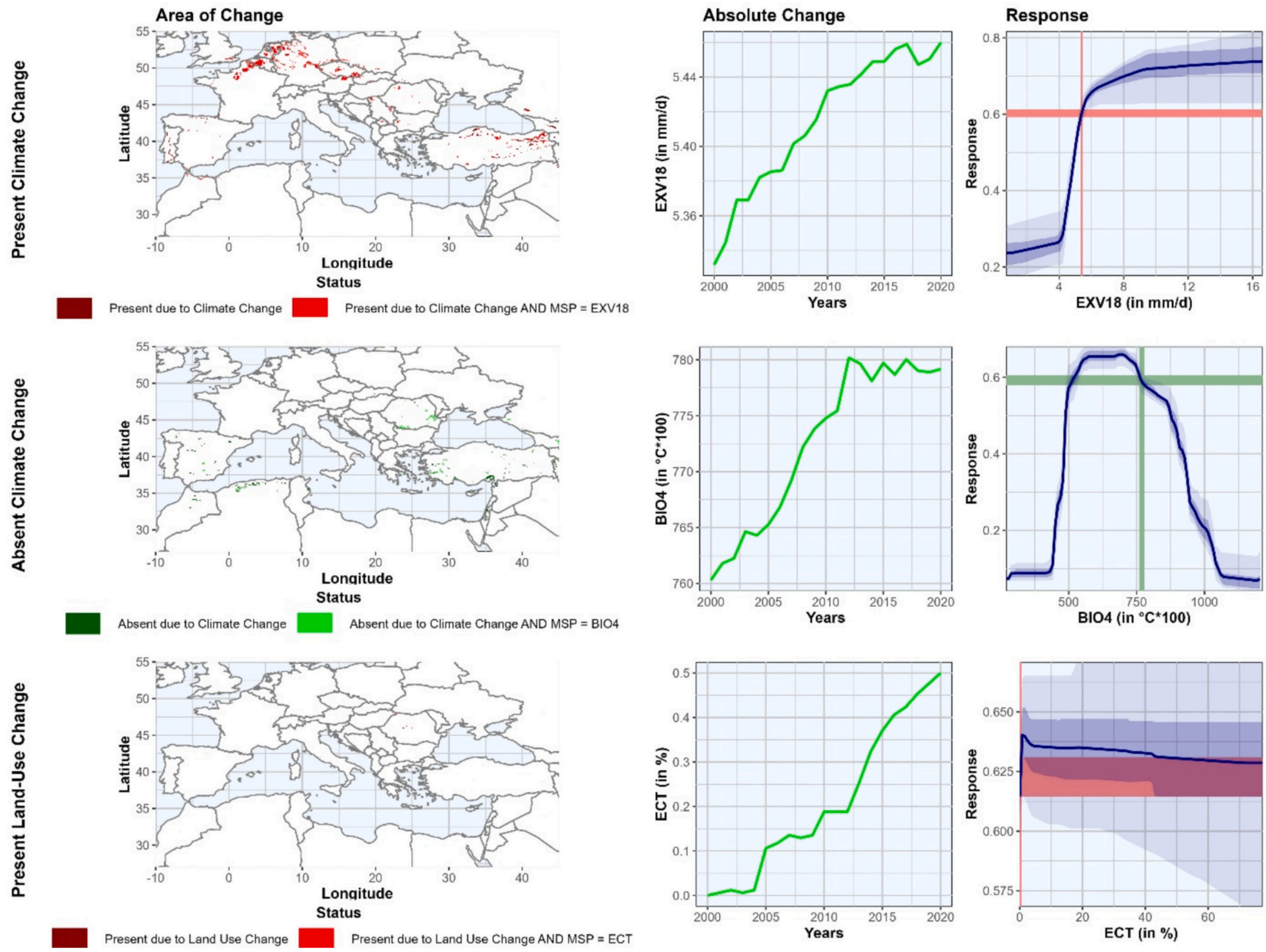

Fig. 6. Area of change (left), time series of absolute predictor variables (middle), and model response (right) for the predictors primarily responsible for status changes: presence due to climate change (top), absence due to climate change (middle), and presence due to land-use change (bottom).

have <250 mm. Thus, the annual rainfall in the Mediterranean and Europe does not limit the establishment of *Aedes albopictus*. On the other hand, some authors assume that human water supply and artificial containers independent of rainfall are even more important for the population dynamics of *Aedes albopictus* than precipitation (e.g. Roiz et al., 2011; Cunze et al., 2016b; Waldock et al., 2013).

4.3. HSA modeling

The results of the HSMs show great agreement with other studies. The main HSA represents the Mediterranean countries, but there is already a further spread to northern countries. Depending on the year of publication and the reference period, the studies observed a more or less pronounced northward expansion. In general, the earlier the study or reference, the more the HSA is restricted to the coastal regions of the Mediterranean (c.f. Caminade et al., 2012). More recent studies have observed the spread of the HSA in northern and eastern direction as confirmed in our study (c.f. Oliveira et al., 2021; Pasquali et al., 2020). The main reason for these differences could be the underlying observed presences for model training. The Alps have long served as a dispersal barrier between the established populations of the Mediterranean and the northern neighbors (Kraemer et al., 2019). Until the middle of the last decade, only few observations of *Aedes albopictus* were made north of the Alps (ECDC, 2023; GBIF, 2022). Kuhlisch et al. (2018) mention that in the second half of the last decade, *Aedes albopictus* was able to reproduce and overwinter for the first time. Kraemer et al. (2019) found that the barrier effect of the Alps had reduced the rate of spread of *Aedes albopictus* in Europe by this time. Once the barrier has been overcome, the authors noticed an increased rate of spread. Thus, the more time that has elapsed since the barrier was crossed, the more time *Aedes albopictus* has had to expand into its habitat north of the Alps. Since our model was calibrated to the 2020 distribution, the HSA already shows a northward and eastward expansion compared to the HSA of previous studies. With respect to regional studies, our MME is also able to cover most of the suitable habitats on the fringes of the HSA. The MME covers the presences of Kuhlisch et al. (2018) in the German federal state of Thuringia, but with a lower agreement. The suitable habitat of Kozynenko and Tytar (2020) in the southern and western parts of the Ukraine is also well represented, but to a lesser extent, whereas the HSA in the Netherlands described by Ibáñez-Justicia et al. (2020) is over-represented. The predicted probability of *Aedes albopictus* matches the occurrence of Ducheyne et al. (2018) in the eastern parts of the Mediterranean and along the North African coast, but with some limitations in the Nile Delta. Furthermore, our HSMs also represents the HSA in the southeastern parts of the United Kingdom which is described in several studies (e.g. Oliveira et al., 2021; Fischer et al., 2014; Caminade et al., 2012). Only in mountainous regions like the Alps and the Pyrenees our HSMs show high agreements with respect to the HSA while other studies exclude these regions (e.g. Oliveira et al., 2021). However, Roiz et al. (2011) mention that there is an ongoing spread of *Aedes albopictus* in the valleys of the Italian Alps since 1996. Under the assumption that this spread is not limited to the Italian Alps, the coarser resolution of our study region, and the fact that presences are assigned to territorial units rather than coordinates, it is understandable that these regions were

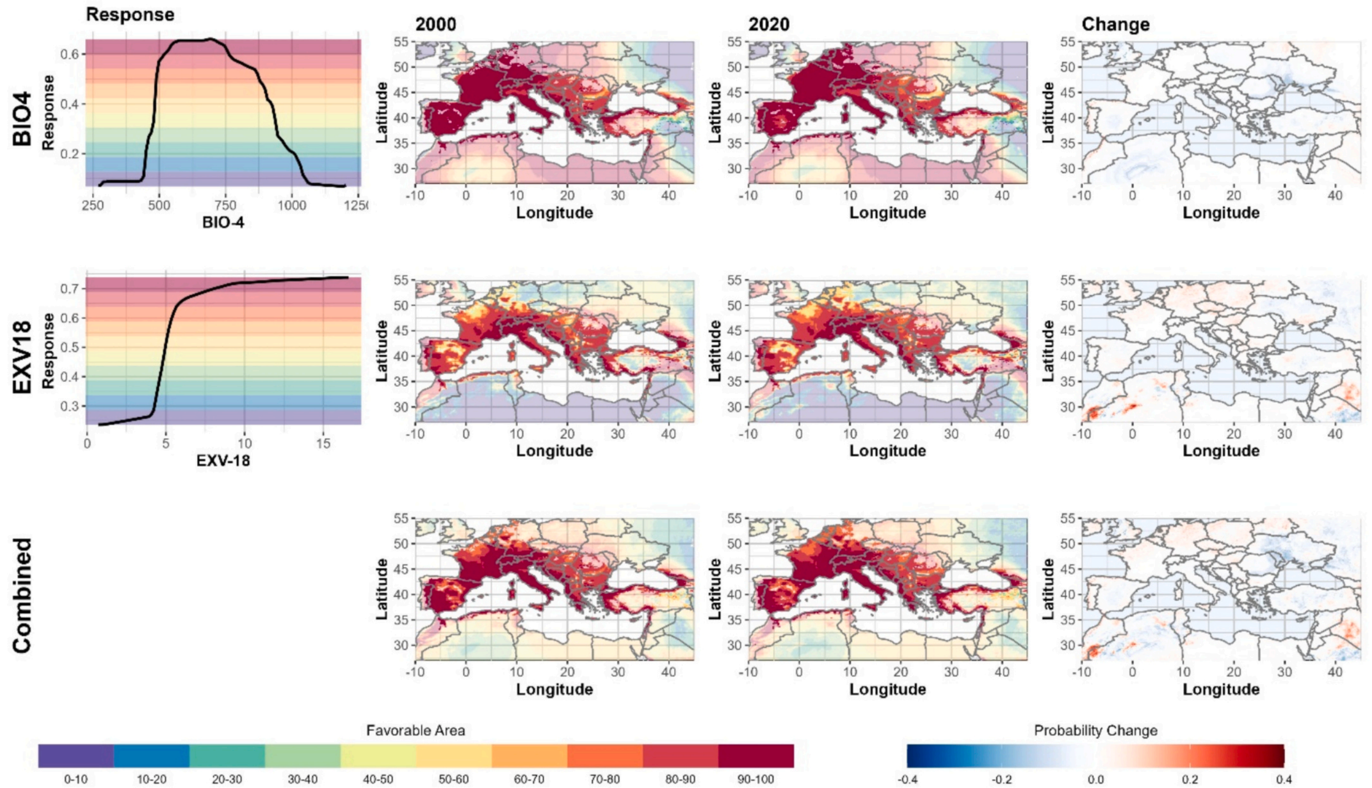

Fig. 7. Changes in the most suitable areas for *Aedes albopictus* between 2000 and 2020 with respect to the response of the two main climatic predictors. The response curves (left) are classified into 10 categories (unsuitable (0–10) – suitable (90–100)). The regional classification for 2000 and 2020 is shown in the middle for BIO4 (top), EXV18 (middle) and for the combined predictors (bottom). Full colors represent the suitable habitat of *Aedes albopictus*, transparent colors represent areas where *Aedes albopictus* is not established. Response changes of the predictor variables are shown on the right.

considered suitable for the establishment of *Aedes albopictus*. Thus, our MME works well for both the main region and the edges of the habitat suitability.

4.4. Changes in the HSA and the drivers of the shifts

The greatest changes of the HSA between 2000 and 2020 can be observed in the northern parts of the study area. Since we include different predictors, a comparison with other studies can rather be made. In terms of climate change, EXV-18 is the main predictor favoring northward expansion, especially since 2015. Most of the areas that are assigned to presence due to climate change show an increasing precipitation intensity between 2000 and 2020, but not necessarily an increase of annual precipitation. Only 49 % of the respective grid boxes show an increase in both EXV-18 and BIO-12. Especially the northernmost areas (Netherlands, northern Germany) and the border triangle of Austria, Czech Republic and Slovakia show an increase of both variables, while Spain, northern France, central Germany, and Romania show an opposite development. In Turkey, only the northeastern parts show an increase of both variables, but mainly an opposite development can be observed. This suggests that it is not necessarily the annual rainfall that is a limiting factor for *Aedes albopictus* in Europe, but the amount of rainfall per rain event. Increasing EXV-18, combined with decreasing BIO-12, favors more intense precipitation events that sufficiently fill natural or artificial reservoirs. Subsequently, longer dry spells and, due to the lack of clouds, higher incoming solar radiation and thus solar heating of the reservoirs lead to perfect environmental conditions for the immature stages of *Aedes albopictus*. The higher initial rainfall is sufficient to maintain the aquatic habitat during the immature stages. In contrast, in retreat areas where EXV-18 is the main predictor, 77 % of the cases show decreasing precipitation intensities. In areas with increasing precipitation intensity and EXV-18 as the main predictor, it is predominantly associated with decreasing annual precipitation amounts (BIO-12). Here, BIO-12 is either below the 500 mm threshold recommended by experts (58 %), or far above the threshold. If EXV-18 increases and BIO-12 is below the threshold, we assume that either the dry periods between rain events may be too long to ensure a permanent life cycle dynamic, or that the reservoirs are not fully filled during the entire aquatic phase. If EXV-18 increases and BIO-12 is far above the threshold, occasional heavy rainfall events can flush out the reservoirs, hindering the development of *Aedes albopictus* during the immature stages (Waldock et al., 2013; Dieng et al., 2012).

The optimal range of the standard deviation of the monthly mean temperature (BIO-4) is between 5.5 °C and 7.5 °C. This range covers much of Western and Central Europe and the European Mediterranean coastlines. The European Atlantic coasts and the northern coast of Africa are below the optimal range, while central Spain, the Po Valley, Eastern Europe, Turkey, the Levant, and much of the Maghreb region are above the optimal range. Unfavorable conditions with respect to BIO-4 are found only in the northwesternmost parts of Spain and France, Ireland, the west coast of the UK and in the easternmost parts of the study area. Partly, these findings agree with other studies. Fischer et al. (2011) assume a continental gradient of habitat suitability and Pasquali et al. (2020) assume that habitat suitability is positively influenced by the proximity of the Atlantic. This is also supported by the findings that the impact of BIO-7 on the HSA is less pronounced compared to BIO-4, although it carries similar information. In contrast to BIO-4 that represents a degree of continentality, BIO-7 is more of a latitudinal gradient. For Western and Central Europe, the differences are rather small, but for Eastern Europe (BIO-4 maximum) and North Africa (BIO-7 maximum) the differences are substantial. The increasing continental gradient leads to higher temperature seasonality with temperatures well below zero during the winter month. Cold winter temperatures have been identified as the most limiting factor within Eastern Europe by Cunze et al. (2016b). Furthermore, Kraemer et al. (2019) observed an increasing trend of aridity in Eastern Europe. The combination of both effects can explain habitat unsuitability in Eastern Europe. In contrast, the proximity to the Atlantic should favor habitat suitability, but the response of BIO-4 decreases with decreasing temperature seasonality. This contradicts Oliveira et al. (2021), who found a high consensus of habitat suitability for the northwestern Iberian Peninsula. Other studies also highlight the suitability of the western parts of the Iberian Peninsula (e.g. Caminade et al., 2012; Fischer et al., 2011; Kraemer et al., 2015). Our HSMs also predict habitat suitability for the French Atlantic coasts, but not for the Atlantic coasts of the Iberian Peninsula. We hypothesize that either other confounding factors prevent the expansion of the HSA in these regions or the model cannot assign these environmental conditions to the HSA due to lack of presences in these regions. However, with respect to a decrease in HSA due to climate change, over 98 % are above the optimal range and 96 % show increasing values for BIO-4. Thus, a logical connection between the retreat of the HSA and increasing BIO-4 can be observed.

Regarding land-use, it is difficult to draw conclusions. On the one hand, we have strong indications that land-use has a significant impact on the HSA. The HSM with the largest changes due to land-use shows an increase in the HSA by 4.4 %, and a decrease by 1.2 %. Overall, land-use accounts for 16.1–51.9 % of changes in the HSA, but in contrast to climate change, we only have little spatial agreement. Only 19 grid boxes of the MME indicate changes due to land-use change. At first sight, these results contradict Lambin et al. (2010) who postulate that land-use change may be the most important driver of the recent global spread of mosquitoes and MBDs. However, if we compare the maximum flight distance of the species (Verdonschot and Besse-Lototskaya, 2014) with the spatial resolution of our data, we see that the maximum flight distance is substantially lower than the grid resolution. Thus, with the current spatial resolution, we are not able to adequately resolve land-use changes that are important for the establishment of the species. We can only assume that the overall composition of the grid boxes is favorable or unfavorable, always considering that within each grid box there are favorable and unfavorable biotopes for the establishment of *Aedes albopictus*. When we evaluate the studies that postulate that land-use is the crucial factor for establishment, we see that they all provide a higher spatial resolution (e.g. Lambin et al., 2010; Rakotoarinia et al., 2022, 2023). Thus, we conclude that the importance of land-use depends on the spatial resolution. The higher the resolution, the more important characteristics of the species' habitat can be captured.

The most important land-use category is represented by Bare that has the highest model importance and contribution. The MME response curves (Supplementary S3) show that the higher the Bare fraction, the lower the suitability of the HSA. This represents a logical relationship since the higher the Bare fraction, the lower the fraction of vegetation and, thus, the lower the fraction of hosts. In addition, Bare mainly represents regions with low precipitation. However, with respect to changes due to land-use change, Bare represents only a subordinate variable. Considering the response range in combination with model importance and contribution, deciduous shrubs (39 % of the study area) and non-irrigated crops (23 % of the study area) are the most important land use variables for changes in the HSA. On average, deciduous shrubs increase by 0.4 % while non-irrigated crops decrease by 2.6 %. Both changes mainly occur in the range where the response of the model is greatest and favor the establishment of *Aedes albopictus*. Deciduous shrubs are often associated with gardening and thus with host availability and water supply. A fraction of 15 % is sufficient to reach a comfortable level of habitat suitability. A further increase in the proportion of deciduous shrubs has little effect on the HSA. A possible explanation could be that 15 % represents a kind of threshold between wild-growing and managed cultivation. With respect to Non-irrigated Crops (NIC), the maximum response is reached at 4 %, followed by a steady decrease. We assume that an increasing fraction of NIC is associated with an increasing use of insecticides that has direct effects on *Aedes albopictus* as well as indirect effects on host availability. In interaction with a lack of water supply, a high proportion of NIC has negative impacts on the HSA.

5. Conclusions

The present study makes an important contribution to the understanding of habitat suitability area for *Aedes albopictus* and provides the basis for investigating the spread of vector-borne diseases in Europe under climate and land-use change. For the first time, climate and land-use changes have been analyzed separately over the Mediterranean and Central Europe, in order to attribute changes in suitability to either climate or land-use changes. However, the suitability of the habitat of the vector does not necessarily mean that viruses or the mosquito will arrive or become established in the concerned areas (Santos and Meneses, 2017; Messina et al., 2016), but the possibility for vector establishment within these regions certainly increases the probability for infections. Further investigations are necessary to investigate the suitability for respective viruses.

Although land-use has a lower impact on the HSA than climate, we identified land-use categories that at least hamper the establishment of *Aedes albopictus*. These findings are very interesting especially with respect to landscaping. For example, the transition from irrigated to non-irrigated crops provides less breeding sites for mosquitoes and, thus, reduces the HSA and the risk for MBDs. However, the ongoing transition from non-irrigated to irrigated crops between 2000 and 2020 favors the establishment of *Aedes albopictus*, especially in Euro-Mediterranean countries and in northern parts of Iraq. Here, a return to non-irrigated crops or the use of modern irrigation techniques such as drip irrigation, which avoids puddles of standing water, can reduce the HSA. Targeted irrigation systems also reduce water wastage, which will become increasingly important as climate change is expected to reduce water availability in the Mediterranean region. Changes in the Evergreen Coniferous Trees within the range where the response is greatest can be found, for example, in the northern parts of Italy, Romania and in some regions of the Iberian Peninsula. It is therefore not surprising that Northern Italy is the origin of the European spread of *Aedes albopictus*, as it offers perfect climatic and land use conditions. The Po Valley, with extensive areas of IC and the establishment of ECT on the neighboring hillsides, corresponds to the land use conditions preferred by *Aedes albopictus*. With respect to deciduous shrubs, the most important land-use predictor in the northern parts of the study area, changes favor the establishment of *Aedes albopictus* especially in eastern Europe. The identified regions are those regions where countermeasures should be considered to reduce the HSA. However, countermeasures should be carefully evaluated, as in some cases they may counteract efforts to reduce climate change. Thus, countermeasures that reduce the HSA due to land-use may lead to more favorable conditions due to climate. Since climate has the greater impact on HSA, these countermeasures may be counterproductive. Further research should also be conducted on these positive and negative feedbacks between climate and land-use in both directions.

Our results identify unfavorable land-use class compositions and provide an opportunity to establish countermeasures within the affected regions. Preparations, monitoring programs and, if necessary, countermeasures can also be implemented in regions where *Aedes albopictus* recently finds suitable habitats, but the species has not yet been reported. Kraemer et al. (2019) assume that the potential habitat of *Aedes albopictus* will be saturated between 2030 and 2050. In some regions, there is hence enough time to act.

CRediT authorship contribution statement

Christian Merkenschlager: Writing – review & editing, Writing –

original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Freddy Bangelesa:** Writing – review & editing, Conceptualization. **Heiko Paeth:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Elke Hertig:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christian Merkenschlager reports financial support was provided by German Research Foundation. Freddy Bangelesa reports financial support was provided by German Research Foundation. Heiko Paeth reports financial support was provided by German Research Foundation. Elke Hertig reports financial support was provided by German Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179202.

Data availability

All data utilized in this study are publicly accessible via the Internet. The respective organizations and owners of the data are acknowledged in the text. The code will be made available on request.

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