

1     The UK’s suitability for *Aedes albopictus* in current and future  
2   climates

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9   **Abstract**

10             The Asian tiger mosquito *Aedes albopictus* is able to transmit various pathogens to humans and  
11             animals and it has already caused minor outbreaks of dengue and chikungunya in southern Europe.  
12             Alarmingly, it is spreading northwards and its eggs have been found in the UK in 2016 and 2017. Climate-  
13             driven models can help to analyse whether this originally sub-tropical species could become established  
14             in northern Europe. But so far, these models have not considered the impact of the diurnal temperature  
15             range (DTR) experienced by mosquitoes in the field. Here, we describe a dynamical model for the  
16             life cycle of *Ae. albopictus*, taking into account the DTR, rainfall, photoperiod and human population  
17             density. We develop a new metric for habitat suitability and drive our model with different climate  
18             data sets to analyse the UK’s suitability for this species. For now, most of the UK seems to be rather  
19             unsuitable, except for some densely populated and high importation risk areas in south-east England.  
20             But this picture changes in the next 50 years: Future scenarios suggest that *Ae. albopictus* could become  
21             established over almost all of England and Wales, indicating the need for continued mosquito surveillance.

# 1 Introduction

About ten invasive species become established in Europe each year [1] and the UK alone spends about £1.7 billion annually to mitigate their impacts [2]. One of these species that has already invaded Europe and might now spread to the UK is the Asian tiger mosquito, *Ae. albopictus*. This mosquito spreads worldwide through its long-lasting and drought-resistant eggs that can be transported over long distances, for example in used vehicle tyres or lucky bamboo pot plants [3]. The eggs can also undergo a diapause to resist colder winter temperatures [4], allowing temperate regions significantly colder than its original niche in South East Asia to be colonised. In Europe, *Ae. albopictus* was introduced in the late 1970s to Albania [5], in 1990 to Italy [6] and more recently into greenhouses in the Netherlands [7]. Since its introduction into Italy, it has rapidly spread along the Mediterranean coast and is now expanding its northern range [8].

This is a major concern as *Ae. albopictus* is an effective disease vector. It can transmit a range of arboviruses affecting humans and animals, including chikungunya, dengue and Zika viruses [9], as well as filarial worms [10]. In Europe, it was responsible for two outbreaks of chikungunya in Italy and a few cases of dengue in Croatia and France in the last ten years [11, 12, 13]. In addition, it is a potent vector of zoonotic diseases because it feeds on mammals, birds, reptiles, and amphibians [14], although it feeds preferentially on humans in urban areas [15]. So whether or not *Ae. albopictus* will spread from continental Europe to the UK and subsequently become established is of significant public health interest. And there is evidence for recent introductions: in September 2016, eggs were found in Kent, the English county closest to France, by a surveillance team of Public Health England [16], followed by another finding of eggs and larvae in July 2017 at another site in the same county [17]. **Here, gravid females have probably been carried over in cars or lorries and subsequently laid eggs when released at motorway service points.**

Mechanistic and statistical niche models have been developed to analyse the UK's climatic suitability for *Ae. albopictus*, suggesting that large parts of southern England are already suitable [18, 19, 20]. Dynamical models, better suited to capture the non-linear behaviour of the mosquito's development, have been published more recently [21, 22, 23, 24]. While all of these models use seasonal or daily mean temperatures and rainfall as drivers, it has become clear that the diurnal temperature range (DTR) significantly affects the life cycle of insects too. The DTR is the difference between the maximum mid-day temperature and the minimum night-time temperature. Studies on *Aedes* mosquitoes show that rates for development and mortality differ substantially under constant temperature conditions compared with a realistic diurnal temperature cycle [25, 26, 27]. Models that already incorporate DTR have been developed for aphids [28], moths [29], generic insects [30] and its effect have been recently applied to a model for *Anopheles* mosquitoes [31].

Here, we describe the development of a novel dynamical model for *Ae. albopictus* that explicitly incorporates the effect of DTR on its life cycle. We use mosquito occurrence data and container index data to evaluate the model performance before analysing the suitability of the UK for this invasive mosquito under current climate conditions and under two climate projection scenarios for the future.

## 2 Model and methods

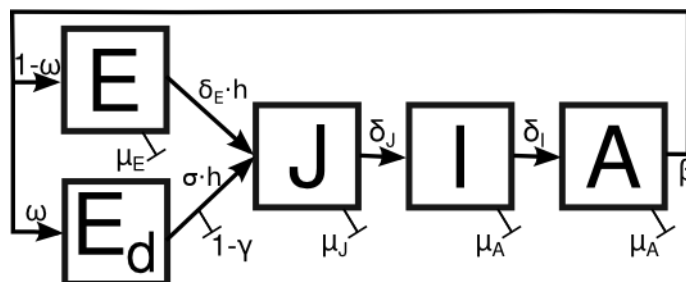
Based on previous studies, we chose a compartmental, climate-driven approach to model the life cycle of *Ae. albopictus* [21, 23, 24]. The model comprises five differential equations. Details on climate-dependent variables can be found in SI.1.

### 2.1 Dynamic life cycle model

The mosquito life cycle is described by five mosquito classes: normal, non-diapausing eggs  $E$ , juvenile aquatic stages  $J$ , immature female adults  $I$ , mature female adults  $A$ , and diapausing eggs  $E_d$  (Fig. 1). Normal, non-diapausing eggs are laid during summer by mature females. Larvae hatch after eggs complete a development period and are activated by rainfall. The four larval stages and the pupal stage are combined into a single aquatic juvenile class in the model. Assuming a sex ratio of 50:50, juveniles then develop into newly eclosed male and female adults. Newly eclosed female mosquitoes do not directly show host seeking behaviour. Instead, they first spend some time in a resting stage, only after which they take their first blood meal and start to lay eggs [32].

At the end of the season, the egg laying process depends on the photoperiod,  $P$ . When days are getting shorter, females start to lay diapausing eggs that do not hatch after a few days but overwinter. During the following spring, these eggs are ready to hatch when temperatures and photoperiod reach critical thresholds, and are eventually activated by rainfall.

All transitions from one class to another depend on temperature,  $T$ , and so do mortality rates. Because *Ae. albopictus*' water filled breeding sites are usually small [33], we use air temperature as a proxy for water temperature.



**Figure 1:** Life stages of *Ae. albopictus*. Eggs  $E$  hatch and become juveniles  $J$  (larvae and pupae). They develop to newly eclosed (immature) females  $I$  and finally to mature female adults. Adult female mosquitoes lay normal eggs  $E$  in the summer months or diapausing eggs  $E_d$  at the end of the season. Diapausing eggs overwinter and are activated by a combination of longer day lengths, warmer temperatures and rainfall in spring.

77 With parameter definitions given in Table 1, model equations are as follows:

$$\begin{aligned}
\frac{d}{dt}\mathbf{E}(t) &= \beta(1 - \omega)\mathbf{A}(t) - h\delta_E\mathbf{E}(t) - \mu_E\mathbf{E}(t) \\
\frac{d}{dt}\mathbf{J}(t) &= h\delta_E\mathbf{E}(t) + h\sigma\gamma\mathbf{E}_d(t) - \delta_J\mathbf{J}(t) - \mu_J\mathbf{J}(t) - \frac{\mathbf{J}(t)^2}{K} \\
\frac{d}{dt}\mathbf{I}(t) &= \frac{1}{2}\delta_J\mathbf{J}(t) - \delta_I\mathbf{I}(t) - \mu_A\mathbf{I}(t) \\
\frac{d}{dt}\mathbf{A}(t) &= \delta_I\mathbf{I}(t) - \mu_A\mathbf{A}(t) \\
\frac{d}{dt}\mathbf{E}_d(t) &= \beta\omega\mathbf{A}(t) - h\sigma\mathbf{E}_d(t)
\end{aligned}$$

**Table 1:** Parameter definitions and values used. Derivation and references of parameters are shown in **SI.1**. Environmental drivers are temperature,  $T$ , rainfall,  $R$ , photoperiod,  $P$ , latitude,  $L$  and human population density,  $H$ . **Please note that the egg activation by rainfall,  $h$ , and the environmental carrying capacity,  $K$ , are defined further down in the manuscript.**

	Parameter	Value/Formula
CTT <sub>S</sub>	Critical temperature over one week in spring (°C)	11.0*
CPP <sub>S</sub>	Critical photoperiod in spring (hours)	11.25*
$\sigma(T, P)$	Spring hatching rate (1/day)	$\begin{cases} 0 & \text{if } T_7 < \text{CTT}_S \text{ or } P < \text{CPP}_S \\ r_S = 0.1^\dagger & \text{if } T_7 \geq \text{CTT}_S \text{ and } P \geq \text{CPP}_S \end{cases}$
CPP <sub>A</sub> ( $L$ )	Critical photoperiod in autumn (hours)	10.058 + 0.08965 $L$
$\omega(P)$	<b>Fraction of eggs going into diapause</b>	$\begin{cases} 0 & \text{if } P > \text{CPP}_A \text{ or } t < \mathbf{183} \\ r_A = 0.5 & \text{if } P \leq \text{CPP}_A \text{ and } t \geq \mathbf{183} \end{cases}$
$\delta_E$	Normal egg development rate (1/day)	1/7.1
$\delta_J(T)$	Juvenile development rate (1/day)	1/(83.85 - 4.89 $T$ + 0.08 $T^2$ )
$\delta_I(T)$	First pre-blood meal rate (1/day)	1/(50.1 - 3.574 $T$ + 0.069 $T^2$ )
$\mu_E(T)$	Egg mortality rate (1/day)	$-\ln(0.955 \exp(-0.5 (\frac{T-18.8}{21.53})^6))$
$\mu_J(T)$	Juvenile mortality rate (1/day)	$-\ln(0.977 \exp(-0.5 (\frac{T-21.8}{16.6})^6))$
$\mu_A(T_{\text{mean}})$	Adult mortality rate (1/day)	$-\ln(0.677 \exp(-0.5 (\frac{T_{\text{mean}}-20.9}{13.2})^6) T_{\text{mean}}^{0.1})$
$\gamma(T_{\text{DJF}, \text{min}})$	Survival <b>probability</b> of diapausing eggs (1/winter)	$0.93 \exp(-0.5 (\frac{T_{\text{DJF}, \text{min}}-11.68}{15.67})^6)$
$\beta(T)$	Egg laying rate (1/day)	$\begin{cases} 33.2 \exp(-0.5 (\frac{T-70.3}{14.1})^2) (38.8 - T)^{1.5} & \text{if } T \leq 38.8 \\ 0 & \text{if } T > 38.8 \end{cases}$
$\lambda$	Carrying capacity parameter (larvae · days /hectare)	$10^6 \ddagger$

78 \* [34], † Best estimate, ‡ [22, 35]

79

80 Development rates,  $\delta$ , and mortality rates for eggs and juveniles,  $\mu_E$  and  $\mu_J$ , depend on the actual oscillating  
81 diurnal temperature  $T$ . **The development from juvenile to immature females is halved in the**  
82 **equation for  $\frac{d}{dt}I(t)$ ,  $\frac{1}{2}\delta_J$ , to account for the 50:50 sex ratio.** Only the mortality rate for adults is  
83 derived from field data that already include a DTR. Daily mean temperatures,  $T_{\text{mean}}$ , are therefore used for  
84  $\mu_A$ .  **$T_7$  is the average temperature over the recent seven days, used for the spring hatching**  
85 **rate.**

86 As there is no study investigating the survival rates of eggs over periods of several months, we assume a

87 survival **probability**  $\gamma$  of diapausing eggs that is dependent on the minimum winter temperature experi-  
 88 enced,  $T_{\text{DJF},\text{min}}$ . The survival **probability** is applied when eggs are activated in spring, see **SI.1** for details.  
 89 Remaining diapausing eggs that have not hatched until August are removed.  
 90 Larval mortality not only depends on temperature, but also on an environmental carrying capacity,  $K$ ,  
 91 representing juvenile competition and predation [36]. We use the model by White *et al.* [37] and its  
 92 extension by Erguler *et al.* [24] to calculate  $K$  from rainfall,  $R$ , and human population density,  $H$ :

$$K(R, H) = \lambda \frac{1 - \alpha_{\text{evap}}}{1 - \alpha_{\text{evap}}^t} \sum_{x=1}^t \alpha_{\text{evap}}^{+(t-x)} (\alpha_{\text{rain}} R(x) + \alpha_{\text{dens}} H(x)),$$

93 As we model mosquito abundance in individuals per hectare, we keep the parameters at  $\alpha_{\text{evap}} = 0.9$ ,  $\alpha_{\text{dens}} =$   
 94  $0.001 \text{ km}^2$ , and  $\alpha_{\text{rain}} = 0.00001 \text{ mm}^{-1}$  [24] but multiply by a scaling factor  $\lambda$  to reach a maximum carrying  
 95 capacity ranging between 500,000 and 800,000 individuals per hectare [22, 35].  
 96 Similar to the carrying capacity, we model the hatching of eggs depending on rainfall and human population  
 97 density. We use the rainfall-dependent approach by Abdelrazec and Gumel [38] and assume that up to  
 98  $\epsilon_{\text{rat}} = 20\%$  of eggs can hatch in densely populated areas regardless of rainfall conditions:

$$h(R, H) = (1 - \epsilon_{\text{rat}}) \frac{(1 + \epsilon_0) \exp(-\epsilon_{\text{var}} (R(t) - \epsilon_{\text{opt}})^2)}{\exp(-\epsilon_{\text{var}} (R(t) - \epsilon_{\text{opt}})^2) + \epsilon_0} + \epsilon_{\text{rat}} \frac{\epsilon_{\text{dens}}}{\epsilon_{\text{dens}} + \exp(-\epsilon_{\text{fac}} H(t))}.$$

99 We set the optimal amount of daily rainfall to  $\epsilon_{\text{opt}} = 8 \text{ mm}$ , and use  $\epsilon_0 = 1.5$  and  $\epsilon_{\text{var}} = 0.05 \text{ mm}^{-2}$  [38].  
 100 Density dependent parameters are  $\epsilon_{\text{dens}} = 0.1$  and  $\epsilon_{\text{fac}} = 0.01 \text{ km}^2$ , such that egg hatching is increased in  
 101 areas where  $H > 500$  people per  $\text{km}^2$ .

102 Note that other studies split the juvenile stage into larvae and pupae and some also split the mature female  
 103 stage into host seeking, gestating, and ovipositing stages [22, 24, 23]. We also simulated these scenarios but  
 104 they did not improve model fit to presence or container index data. As there was also more parametrisation  
 105 data available for a reduced model, we kept the model framework with a minimum number of equations. See  
 106 **SI.2** for further details.

107 The model is implemented in *Octave v4.2.1* and Runge-Kutta 4 is used to solve ODEs. All scripts and a  
 108 short example can be found in the electronic supplementary material.

## 109 Suitability index

110 We propose a suitability index  $E_0$  that relates to the basic reproduction number  $R_0$  in epidemiological studies.  
 111 In epidemiology,  $R_0$  is defined by the number of susceptibles infected by a single infectious individual in an  
 112 otherwise uninfected population. Accordingly, we define our suitability index by the number of eggs that  
 113 are produced at the end of a year, after placing a single (diapausing) egg at the beginning of the year into  
 114 an uncolonised location. The amount by which the number of eggs has increased (suitable) or decreased  
 115 (unsuitable) defines the suitability index  $E_i$  of that year  $i$ . Repeating this procedure for  $n$  consecutive  
 116 years and taking the geometric mean of the yearly suitability indices gives the suitability index,  $E_0$ , for the  
 117 according period,

$$E_0 = \sqrt[n]{\prod_{i=1}^n E_i},$$

118 with  $E_i = \frac{E_d(\text{day} = 365)}{E_d(\text{day} = 1)}$ . Note that the crucial scaling of  $E_0$  depends on the carrying capacity,  $K$ .  
 119 With our standard settings, the model predicts about 1,200 adult female *Ae. albopictus* per hectare for  
 120 August/September in Rome (Fig. 7). This is well in the range of mark-release-recapture data, with an  
 121 estimated 1,400 females per hectare [39]. **See SI.3 for further details.**

## 122 Diurnal temperature cycle

123 To incorporate the DTR, we use the model by DeWit [40], which is well suited to compute realistic temper-  
 124 atures throughout the day from maximum and minimum temperatures [41]. Time points for temperature  
 125 calculation are chosen according to the time steps for our explicit numerical solver, e.g. if  $k = \frac{1}{100}$ , we  
 126 calculate 100 actual temperatures throughout the day at 00:14, 00:19, ... 24:00. Temperatures during day  $i$   
 127 are calculated by

$$T_i(h) = \begin{cases} \frac{T_{i-1}^{\max} + T_i^{\min}}{2} + \frac{T_{i-1}^{\max} - T_i^{\min}}{2} \cos\left(\frac{h_t + 10}{10 + t_s} \pi\right) & \text{if } h_t < t_s \\ \frac{T_i^{\max} + T_i^{\min}}{2} - \frac{T_i^{\max} - T_i^{\min}}{2} \cos\left(\frac{h_t - t_s}{14 - t_s} \pi\right) & \text{if } t_s < h_t < 14 \\ \frac{T_i^{\max} + T_{i+1}^{\min}}{2} + \frac{T_i^{\max} - T_{i+1}^{\min}}{2} \cos\left(\frac{h_t - 14}{10 + t_s} \pi\right) & \text{else} \end{cases}$$

128 with  $T_i^{\max/\min}$  being the maximum or minimum temperature of day  $i$ . The model assumes  $T^{\min}$  at sunrise  
 129  $t_s$  and  $T^{\max}$  at 14:00 local time. The time of day in hours is given by  $h_t$ , and the time of sunrise,  $t_s$ , is  
 130 calculated using the daylight model by Forsythe *et al.* [42], depending on latitude,  $L$ , and the day of year.  
 131 See **SI.4** for daylight model equations.

## 132 Climate and population density data

133 We run our model with a range of different climate data sets from historical records and future climate pro-  
 134 jections. For mosquito suitability in the UK, we compare the observed gridded climate data sets from E-OBS  
 135 on a 25 km  $\times$  25 km spatial scale (<https://www.ecad.eu/download/ensembles/ensembles.php>) [43] and from  
 136 UKCP09 on a 5 km  $\times$  5 km scale ([https://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/](https://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html)  
 137 [download/index.html](https://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html)) [44]. **The E-OBS data set was also used for model validation over Europe**  
 138 **and the ERG5 Eraclito data set** ([https://www.arpae.it/dettaglio\\_documento.asp?id=6147&idlivello=1528](https://www.arpae.it/dettaglio_documento.asp?id=6147&idlivello=1528))  
 139 [45] is used for the model runs in the Emilia-Romagna region.

140 For future model runs across Europe, we used **25 km  $\times$  25 km spatial scale** climate projections from NEX  
 141 GDDP (<https://cds.nccs.nasa.gov/nex-gddp/>) [46] for two different emission scenarios, the median RCP4.5  
 142 and the extreme RCP8.5 scenario. A subset of five general circulation models from the full set of 21 was  
 143 chosen to represent the full range of uncertainty, see **SI.5** for details. For future changes, we focus on the  
 144 period 2060 – 2069, the 2060s hereafter.

145 Human population density is based on the GPWv4 data set ([http://sedac.ciesin.columbia.edu/data/collection/](http://sedac.ciesin.columbia.edu/data/collection/gpw-v4)  
 146 [gpw-v4](http://sedac.ciesin.columbia.edu/data/collection/gpw-v4)) [47]. For the 2060s projections, we assume the total UK population has increased from 65.5 million  
 147 to 75 million [48] but has not changed in its spatial distribution.

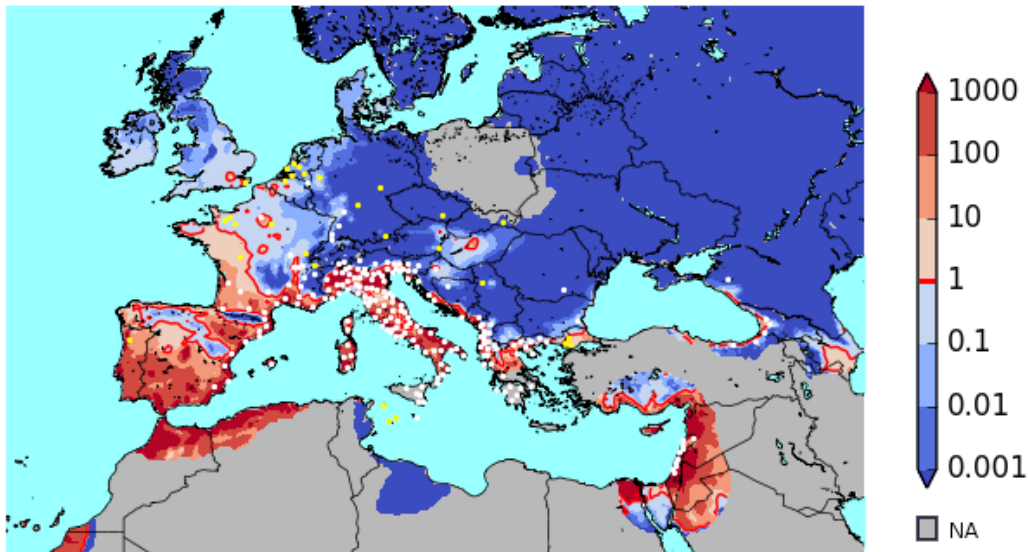
## 2.2 Validation

### Mosquito data

To validate the spatial distribution of suitability simulated by the model, we use *Ae. albopictus* occurrences [49], updated with data from recent literature [50, 51, 52, 16, 17, 53], and classified into established populations and one-time sightings according to the 2018 ECDC classification [8]. Occurrence points that were less than 25 km apart from one another were clustered together, resulting in a total of 234 out of 385 data points. We then checked whether each established occurrence point falls into a grid cell that is calculated to be suitable ( $E_0 > 1$ ).

Figure 2 shows the suitability index for the period 2006 – 2016, which is highly consistent with occurrence data: 83% of the established populations fall into a suitable grid cell, 17% into unsuitable ones (excluding grid cells that are not covered by climate data). However, the model misses some points in the southern Alps, possibly because occurrences fall into warmer valleys with microclimate conditions that are not captured by the coarser climate data. Other areas that should be suitable are parts of southern Germany and the Bulgarian/Romanian Black Sea coast. The model predicts suitable conditions for these areas in most years but specific years with a very cold winter or dry summer lower the 10-year suitability index (compare Figure S7). **Also, (semi-)urban areas such as southern German cities with their microclimate will slip through the coarser resolution of the climate data used.**

**Bigger** densely populated areas, such as Madrid, Paris and London **show up as suitable though**; they act as heat islands further increasing mosquito development [54], and they supply mosquito breeding sites by man-made containers and irrigation.



**Figure 2: Spatial validation** White dots show established *Ae. albopictus* populations, **yellow** dots show one-time sightings. Background colours show the simulated suitability index of the period 2006 to 2016. Red contour distinguishes suitable ( $E_0 > 1$ ) from unsuitable areas ( $E_0 < 1$ ). In the grey area, climate data from the E-OBS data set was incomplete for all years of the according period.

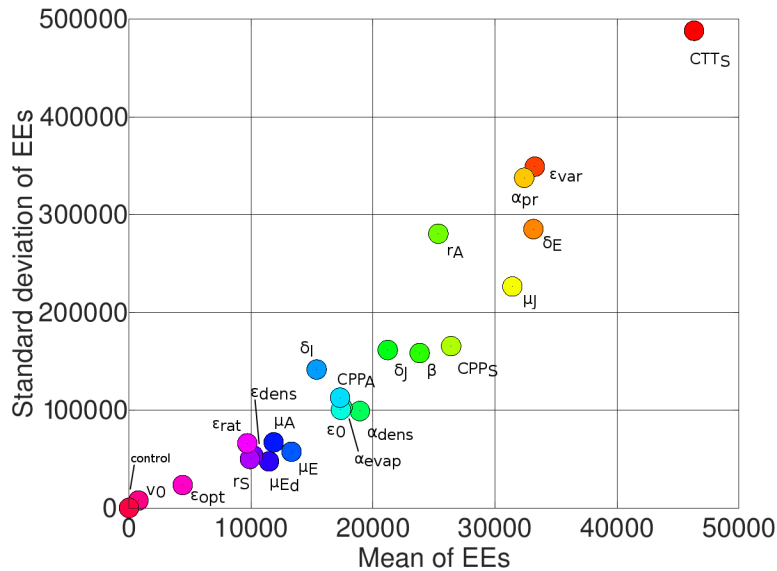
We also used observed container index (CI) data that is available for northern Italy to validate our model not

170 only in space but in time, see **SI.7**. While the onset and end of the yearly mosquito season is well captured  
 171 by the model, it sometimes over- or underestimates peak mosquito numbers at interannual time scale. The  
 172 Pearson correlation between observed and simulated egg data is  $r = 0.70$  (95% CI:  $0.67 \leq r \leq 0.73$ ,  $N=996$ ).

173 **Sensitivity analysis**

174 To investigate the influence of each parameter on the final model output,  $E_0$ , we perform the elementary  
 175 effects test (EET) [55]. The EET measures the influence of single input parameters on model outputs, as well  
 176 as their degree of interaction with other parameters. Latin Hypercube Sampling is used to vary parameters  
 177 in the range of  $\pm 10\%$  of the standard setting [56]. The model is then run with the Italian climate data until  
 178 convergence and the total egg number after five years is taken as reference. *Octave* scripts for these methods  
 179 come from the SAFE toolbox [57].

180 The critical temperature threshold in spring,  $CTT_S$ , has the biggest effect on  $E_0$ , followed by parameters  
 181 determining rainfall-dependencies,  $\epsilon_{var}$  and  $\alpha_{rain}$ , and egg development,  $\delta_E$  (Fig. 3). Other mosquito specific  
 182 parameters range in the middle. Parameters such as initial egg numbers,  $v_0$ , or other hatching rate param-  
 183 eters,  $\epsilon_{dens}$ ,  $\epsilon_{rat}$  and  $\epsilon_{opt}$ , have only limited impact on the model output for the Italian climate settings. The  
 184 distributions for mean and standard deviation of EEs indicate that parameters with a bigger effect on other  
 185 parameters also have a bigger effect on the model output.



**Figure 3:** Elementary effects test. The higher the mean EEs, the more influential the parameter on model outcome. The higher the standard deviation of the EEs, the larger its degree of interactions with other parameters.

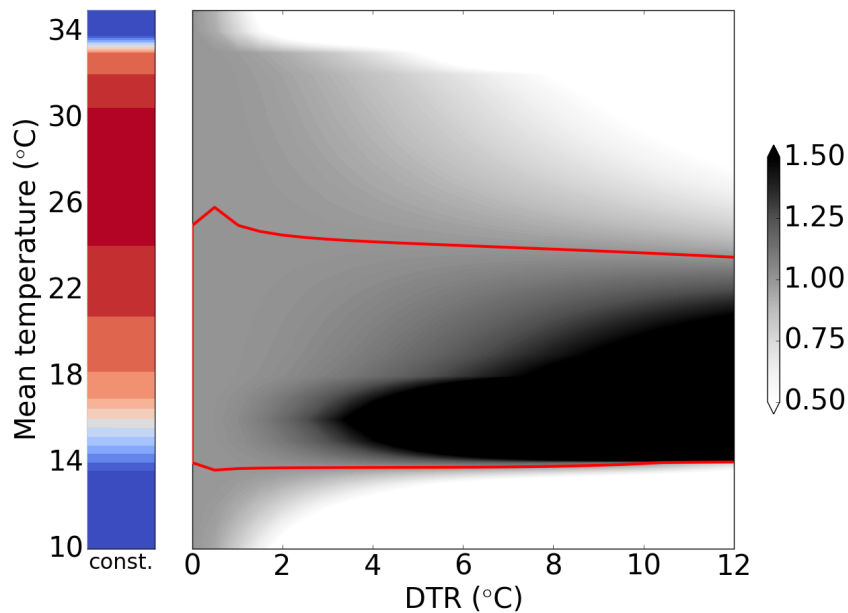


### 186 3 Results

#### 187 3.1 Diurnal temperature range

188 To analyse the effect of the DTR on mosquito population size, we run the model for a range of temperatures  
189 ( $10^{\circ}\text{C} \leq T_{\text{mean}} \leq 35^{\circ}\text{C}$ ), first with constant mean temperatures (DTR =  $0^{\circ}\text{C}$ ) and afterwards with oscil-  
190 lating temperatures ( $0^{\circ}\text{C} < \text{DTR} \leq 12^{\circ}\text{C}$ ), simulating the diurnal temperature cycle. We then compare  
191 absolute mosquito numbers after 365 simulated days.

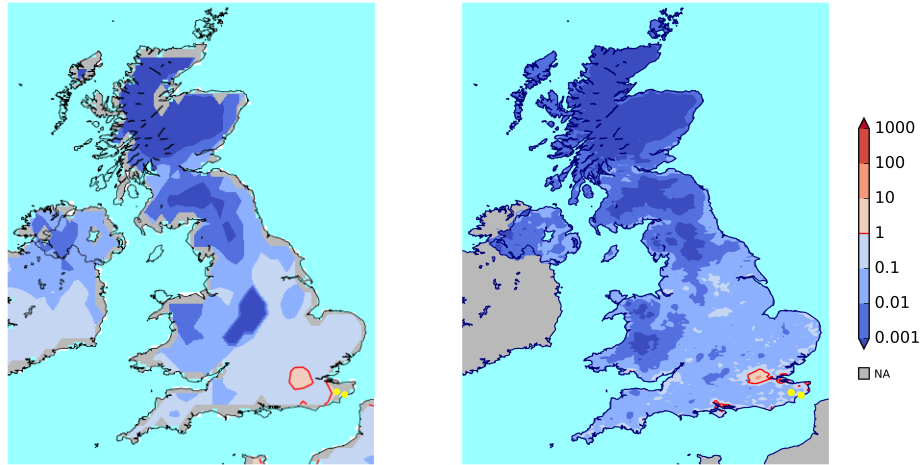
192 Figure 4 shows that oscillating temperatures have a positive effect on the population size at lower mean  
193 temperatures, roughly for  $14^{\circ}\text{C} < T_{\text{mean}} < 24^{\circ}\text{C}$ . This is actually the lower bound of the mosquito’s suit-  
194 able temperature niche. Equilibria and stability analyses show that mosquito populations could survive at  
195 constant temperatures between approx.  $13^{\circ}\text{C}$  and  $32^{\circ}\text{C}$ , see **SI.9**. Only when temperatures are very low  
196 ( $T < 13^{\circ}\text{C}$ ), we see a sharp decrease in numbers as mosquitoes experience high mortalities at these low  
197 temperatures. **See Figure S12 for population growth over time, used to create Figure 4.** DTR  
198 increases the suitability especially in northern regions compared with model runs that only use daily mean  
199 temperatures (Figure S11).



**Figure 4: Influence of the diurnal temperature range on mosquito numbers** Left panel: Population size of *Ae. albopictus* at constant temperature, with color coding as in Figure 2. Right panel: Relative population size after 365 days with diurnal temperature cycle compared to the population size experiencing constant temperatures (left panel). Values above 1 (within the red contour line) indicate where oscillating temperatures increase the population size. Mean temperature is given on the y-axis and the DTR is given on the x-axis.

### 200 3.2 Current suitability of the UK

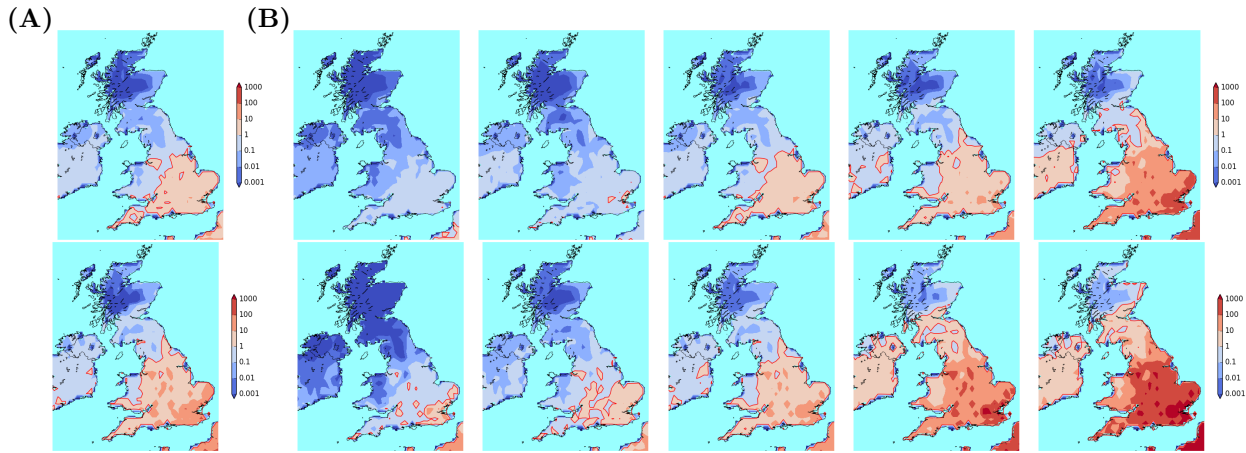
201 To analyse the UK’s suitability for this mosquito, we run our model with two climate data sets for the  
202 recent period 2006 – 2016. Figure 5 shows that simulations driven by climate data sets with high and low  
203 spatial resolution agree in that the London area, the Thames estuary and parts of the southern coast are  
204 already suitable for the mosquito. Other warmer areas around the Severn estuary or in East Anglia, as well  
205 as populated northern regions such as Merseyside or around Sheffield are close to but not yet suitable. The  
206 Scottish Highlands, the Pennines and the Welsh mountains are unsuitable. Note that we are looking at a  
207 10-year period to analyse the suitability for long-term establishment. We can also look at individual years,  
208 finding especially the most recent years more suitable already (compare Fig. S7).



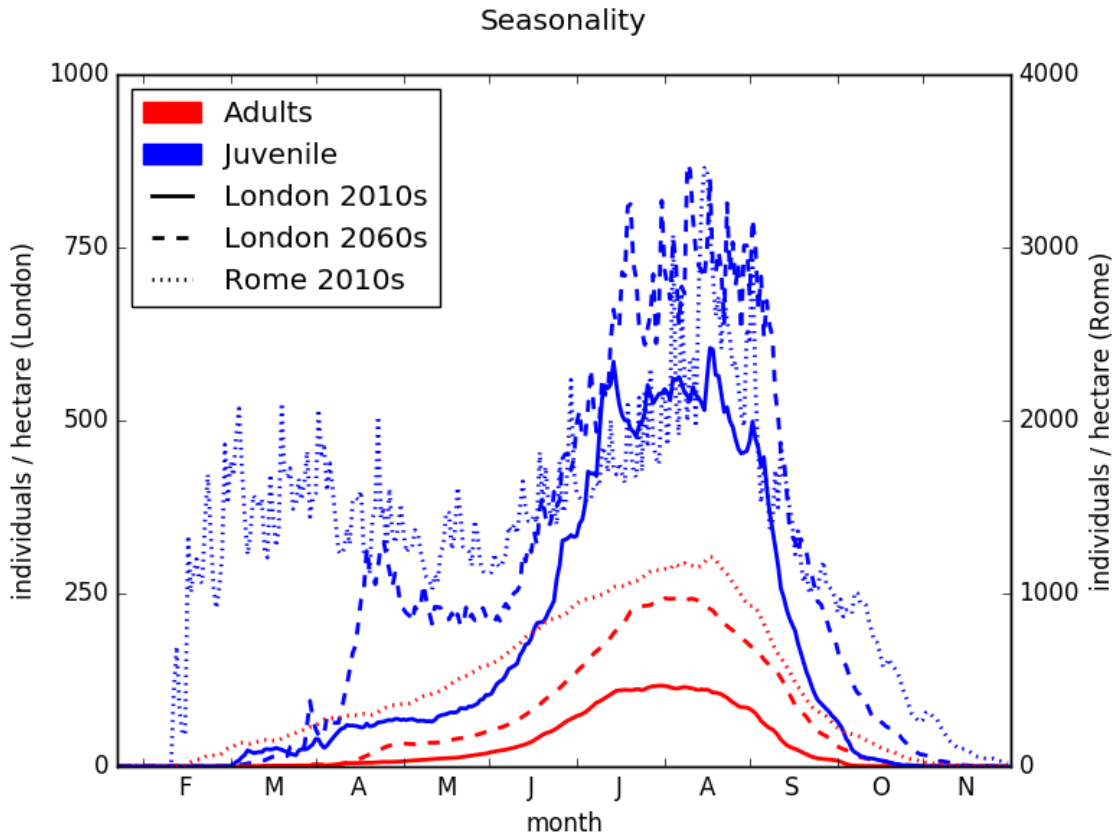
**Figure 5: Suitability of the UK** Comparison of UK mosquito suitability for different resolutions for the years 2006 until 2016, using E-OBS (left) and UKCP09 (right) climate data. Yellow points show spots where *Ae. albopictus* has been found in 2016 and 2017.

### 209 3.3 Future suitability of the UK

210 Figure 6 shows the UK’s future mosquito suitability for two emission scenarios, RCP4.5 and RCP8.5.  
211 Compared with recent UK suitability (Fig. 5), most of England will have become suitable for the establish-  
212 ment of *Ae. albopictus* populations in about 50 years. Parts of Wales might become suitable, depending on  
213 the emission scenario. Scotland and Northern Ireland remain mostly unaffected.  
214 Looking at a whole year, simulations indicate that in current London, *Ae. albopictus* population sizes would  
215 be small in early summer and reach relative high number in July and August (Fig. 7). Future scenarios  
216 show an expansion of this peak into September and an overall increase in numbers. However, the length of  
217 the peak mosquito season would be short and population sizes remain low with respect to simulated values  
218 in Rome for recent climate conditions. Simulations for Figure 7 were started one year ahead of the analysed  
219 period and mosquito numbers transferred from the end of a year into the next.



**Figure 6: Future suitability of the UK** Suitability index for 2060–2069. **(A)** Geometric mean over all five model outputs for RCP4.5 (top) and RCP8.5 (bottom). **(B)** Suitability index shown for each climate model individually for RCP4.5 (top) and RCP8.5 (bottom). Left to right: Minimum, 25<sup>th</sup> quantile, median, 75<sup>th</sup> quantile, maximum temperature increase for the British Isles. Climate models in order from the coldest to warmest are innmcm4, MRI-CGCM3, NorESM1-M, CanESM2, MIROC-ESM-CHEM for RCP4.5, and innmcm4, CESM1-BGC, NorESM1-M, CanESM2, MIROC-ESM-CHEM for RCP8.5.



**Figure 7: Mosquito season** Comparing the simulated length of the mosquito season in London in the 2010s and 2060s and with Rome in the 2010s. Means of 10 years for London and Rome 2010s data, based on E-OBS climate data. Future estimates are based on the ensemble mean of five RCP4.5 projection runs for 2060s. Note the different scales for London and Rome.

## 4 Discussion

Numerous studies investigating the climatic dependencies of *Ae. albopictus* have been published in recent years [58, 59, 60, 61, 4, 62, 63]. Taking these new findings into account and building on other modelling studies [21, 23, 24], we developed a dynamical model for *Ae. albopictus* that explicitly simulates the effects of rainfall for egg hatching and larval development, photoperiod for diapause induction and ending, and minimum and maximum temperatures that shape mortality and development rates of aquatic and adult stages.

The full temperature range experienced by mosquitoes in the field tend to increase model development rates throughout all stages. Mosquito populations at the lower temperature range (14 °C to 24 °C) develop better with oscillating temperatures. Here, night-time temperatures do not affect the development rates that are quite low anyway, while higher temperatures during the day significantly increase them [31]. Conversely, when mean temperatures are already high, lower night-time temperatures decrease development rates, while even higher temperatures during the day tend to increase mortality rather than development rates [27]. Thus, the DTR can be crucial for suitability analyses and should be considered for modelling the life cycle of mosquitoes and other insects [30, 31], as it has already been done for the modelling of temperature-dependent viruses or malaria protozoans that mosquitoes can transmit [64, 65, 66].

Looking at the UK climate conditions for the past 10 years, we find large parts of the UK rather unsuitable for *Ae. albopictus*, except for some warmer and densely populated areas in the south-east of England. This suggests the mosquito has to be introduced into specific areas to enable a long-term establishment, contrary to what other modelling studies have found that predict a **medium to high suitability** [19, 20, 67, 24] of larger parts of England with up to five months adult mosquito activity in certain areas [18].

Our results are a bit more conservative because we included a rainfall-dependent mechanisms for egg hatching and larval mortalities in the model. Instead of constant egg hatching, we assumed that rainfall events lead to eggs being submerged under water and subsequent hatching. Similar to the finding of Tran *et al.* [22], the introduction of a rainfall-dependent egg hatching rate does not improve the model output fit to empirical abundance or ovitrap data. However, we found it enhances model performance in arid and unpopulated areas such as central Spain and Turkey.

We further assumed that a high human population density positively influences both the hatching of eggs and the survival of larvae because it has been shown that the mosquito is able to develop indoors [68], but also in arid but densely populated areas, where water storage and sprinkling create breeding habitats [69].

While large parts of England might not yet be suitable for a long-term establishment of this mosquito, individual years (especially the warmer recent ones) already show a higher suitability which will continue to increase in the future [70]. Looking 50 year ahead, our projections suggest that *Ae. albopictus*, if introduced, could establish itself over most of England and southern Wales during the 2060s. The mosquito could become abundant in London over future summers; but even the most catastrophic scenario suggest that population sizes would still remain small with respect to current conditions in Rome, Italy. Large uncertainties related to the selected climate model and the emission scenario are related to the large variability of rainfall and temperature projections in the multi-model ensemble.

The question whether *Ae. albopictus* is able to spread from continental Europe to England is of great importance for public health and veterinary services. This mosquito is a vector that can transmit pathogens that are present or constantly introduced into the UK, such as several arboviruses [71] and the canine

261 heartworm *Dirofilaria immitis* [72]. Moreover, it is a very competitive species that could replace endemic  
262 mosquito species and become a biting nuisance to the local population [73]. Finding parts of south-east  
263 England already suitable and predicting a strong increase in suitability for most of England in the future,  
264 we highly recommend stringent vector surveillance in southern UK ports and high importation risk areas  
265 along motorways [3, 74]. In addition, human and veterinary health services should get prepared to deal  
266 with pathogens transmitted by *Ae. albopictus* in warm summers [75], as it is recently happening in southern  
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