

# Past and future spread of the arbovirus vectors Aedes aegypti and Aedes albopictus

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#### 77 One Sentence Summary

Human mobility patterns and climate changes predict the spread of the arbovirus vectors *Aedes aegypti*and *Ae. albopictus*, which transmit viruses such as dengue, yellow fever, chikungunya, and Zika.

80 Abstract

81 The global population at risk from mosquito-borne diseases – including dengue, yellow fever, 82 chikungunya, and Zika – is expanding in concert with changes in the distribution of two key 83 vectors, Aedes aegypti and Ae. albopictus. The distribution of these species is largely driven by 84 both human movement and the presence of suitable climate. Using statistical mapping techniques, we show that human movement patterns explain the spread of both species in Europe and the 85 86 United States of America (USA) following their introduction. We find that the spread of Ae. 87 *aegypti* is characterised by long distance importations, whilst Ae. albopictus has expanded more 88 along the fringes of its current distribution. We describe these processes and predict the future 89 distributions of both species in response to accelerating urbanisation, connectivity, and climate change. Global surveillance and control efforts that aim to mitigate the spread of chikungunya, 90 91 dengue, yellow fever and Zika viruses must consider the so far unabated spread of these 92 mosquitos. Our maps and predictions offer an opportunity to strategically target surveillance and 93 control programs and thereby augment efforts to reduce arbovirus burden in human populations 94 globally.

95

#### 96 Main text

97 The geographical distributions of the arboviruses dengue, yellow fever, chikungunya, and Zika
98 have expanded, causing severe disease outbreaks in many urban populations.<sup>1–5</sup> Transmission of

99 these viruses depends, with few exceptions, on the presence of the competent mosquito vectors Aedes aegypti and Ae. albopictus<sup>6,7</sup>. Previous predictions of the future distributions of Aedes 100 101 aegypti [=Stegomyia aegypti] and Ae. albopictus [=Stegomyia albopicta] have focussed solely 102 on climate, despite the known importance of urbanisation and other socioeconomic factors in defining suitable habitat<sup>8</sup>. Moreover, those projections assumed that both species can fully infest 103 all areas of predicted newly suitable habitat<sup>4,9</sup>. Recent trends in the global spread of these species, 104 however, suggest that the process of expansion may be more complex and spatially structured 105 than previously acknowledged<sup>10</sup>. Expansion from the native ranges in *Ae. aegypti* (from African 106 107 forests) and Ae. albopictus (from Asia) was precipitated by a shift from zoophily to 108 anthropophily and by adaptation to container-breeding in domestic or peri-domestic environments<sup>11,12</sup>. Whilst their short flight ranges limit self-powered dispersal<sup>13</sup>. A century of 109 110 rapid human population growth and international trade has enabled their global spread. Trade in 111 items that provide potential larval development habitats such as tires and potted plants led to inter-continental dissemination of their desiccation-resistant eggs<sup>14–16</sup>. Moreover, the 112 113 establishment of Ae. albopictus in locations with cooler climates has been aided by its ecological plasticity, with eggs able to undergo diapause (dormancy) as one possible explanation for 114 populations persisting through winters too cold for adult survival<sup>17,18</sup>. 115

116 Whilst the various routes of inter-continental importation are well described<sup>11,19</sup>, the processes 117 underlying intra-continental spread of the species remain poorly quantified, preventing informed 118 prediction of future distributions. Modelling of human-mediated range expansion suggests that 119 quantitative models of human movement could, and should, be used to predict intra-continental 120 spread<sup>20–22</sup>. To address this, we developed predictive models of *Ae. aegypti* and *Ae. albopictus* 121 spread and combined these with forecasts of future climatic conditions and urban growth, to

predict the ranges of these medically important vectors from 2015 to 2080 (Extended Data Fig.1).

We collated spatially- and temporally-explicit data on the distributions of Ae. aegypti and Ae. 124 albopictus and their spread over time in the USA, and Ae. albopictus in Europe (Fig. 1, Extended 125 Data Figs. 2, 3). Extending a previous study<sup>4</sup>, we first mapped contemporary habitat suitability 126 127 for each species together with projected suitability in 2020, 2050, and 2080, under three different Representative Concentration Pathway (RCP) and 17 global climate models (GCMs), as well as 128 129 under projections of urban growth. We then parameterised quantitative models of human mobility using census data on migration and commuting patterns<sup>23,24</sup>, and general movement 130 patterns derived from mobile phone logs (call detail records) (Extended Data Fig. 1) $^{23-25}$ . The 131 132 combined predictions from these different mobility models and datasets capture different aspects of human travel and trade, and their ability to spread Aedes eggs and juveniles at different spatial 133 134 scales.

135 We tabulated annualised presence records which documented the first detection of each species 136 in 1,567 different locations over 38 years in Europe (225 / 1,588 districts, between 1979 - 2016) 137 and 32 years in the USA (1,342 / 3,134 counties, between 1985 and 2016) (Extended Data Fig. 138 2a, b, c). These data were used to parameterise statistical models of spatial spread for each 139 species. Detection within a given area was modelled as a function of i) the receptivity of the area 140 (as determined by the habitat suitability models), ii) long-distance importation pressure (from 141 multiple human movement models) and iii) short-distance importation pressure from adjacent 142 areas (to represent natural dispersal). Forward simulation of these fitted models of spatial spread 143 was then used to predict the future spread or recession of each species, considering climate 144 changes, urbanisation, and human-mediated importation. To account for potentially biased

sampling procedures we performed a comprehensive sensitivity analysis assuming different
levels of detection for both species (Supplementary Information).

147 Short-range importation between adjacent districts played a greater role in the inferred spread 148 process for Ae. albopictus (Fig. 1a, c, d, f) than for Ae. aegypti (Fig. 1b, e), which was more 149 frequently imported over longer distances. Historically, most of the observed range expansion of 150 Ae. aegypti in the USA originated from southern States (Fig. 1b, Extended Data Fig. 2b). Using 151 thin plate spline regression, we estimated the localised invasion velocity of Ae. aegypti spread in 152 the USA to be relatively homogeneous at ~250km per year (Fig. 1b, e). Aedes albopictus spread 153 in the USA was fastest between 1990 and 1995 (Fig. 1a, d) and has since slowed to about ~60km 154 per year. In contrast, the estimated rate of spread of Ae. albopictus in Europe is faster (~100km 155 per year) rising to ~150km per year over the last five years (Fig. 1c, f, Extended Data Fig. 2c, f, 156 i). The geographic origin of recent Ae. albopictus spread in Europe seems to be Italy, with the 157 Alps serving as a dispersal barrier that lowers rates of spread (Extended Data Fig. 2c, f). Once that barrier has been overcome, however, spread rates beyond the Alps are as high as in Italy. 158 159 This may explain the increased rate of spread in recent years, which also corresponds to the 160 detection of Ae. albopictus in areas north of the Alps (Extended Data Fig. 2c, f).

Using human-mobility-driven statistical models we can predict the past spread of both mosquito species with high reliability (Extended Data Fig. 6) and accuracy (out of sample area under the receiver operating characteristic curve [AUC]: 0.7-0.9, Extended Data Fig. 7). Only slight improvements are observed when including human mobility models over models that only included distance and adjacency metrics (Supplementary Information, Extended Data Fig. 12). Further, we evaluated our models' ability to predict the range expansion in Europe using a model fitted to US data (1,149 records) only. This test similarly documented a high degree of predictive

168 ability (out of sample AUC: 0.8-0.9, Extended Data Fig. 8). In addition, country borders seem 169 not to limit the spread of the mosquitoes (Extended Data Fig. 11) and our spread model is robust 170 even under different assumptions in mosquito sampling strategies but the underlying 171 observational data may impact our estimates of velocity of spread (Supplementary Information). 172 In contrast, the model fitted to only European data was unable to predict the spread in the USA, 173 presumably because of the relatively few Ae. albopictus records in Europe compared to the USA 174 (192 records). Therefore we used the model fitted to USA data to project the range of both 175 species into the future (Supplementary Information). Both Ae. aegypti and Ae. albopictus are 176 anticipated to continue expanding beyond their current distributions (Extended Data Figs. 4, 5). 177 For Ae. aegypti, predicted future spread is mostly concentrated within its tropical range and in 178 new temperate areas in the USA and China; reaching as far north as Chicago and Shanghai by 179 2050 (Figs. 2, 4, Extended Data Fig. 4). At the expansion front in the United States, our model 180 predicts the spread to occur mostly through long-distance introductions in large urban areas (Figs. 181 2a, b, Extended Data Fig. 10). Even under the most extreme scenarios (RCP8.5 in 2080), Ae. 182 *aegypti* is predicted to establish in Europe in only a few isolated regions of southern Italy and 183 Turkey (Extended Data Fig. 4). By 2080 we predict there will be 159 countries worldwide (range 156 - 162) reporting this species, of which three (range 0-6) will be reporting it for the first time 184 185 (Extended Data Tab. 8).

By contrast, *Ae. albopictus* is expected to spread broadly through Europe, ultimately reaching wide areas of France and Germany (Fig. 3b). Areas in northern USA and highland regions of South America and East Africa are also projected to see establishment of *Ae. albopictus* over the next 30 years (Figs. 2, 4). At the same time, some areas are predicted to become less suitable for the species, particularly locations in central southern USA (Fig. 2, Extended Data Fig. 5) and

191 Eastern Europe (Fig. 3) where climate models indicate aridity will increase. Due to Ae.

192 *albopictus* broader distribution in northern latitudes, as in the USA, the spread pressure follows a

193 clear front-like expansion (Figs. 2c, d). In total, 197 countries (range 181-209) are expected to

report *Ae. albopictus* by 2080, 20 (range 4-32) of those countries will be reporting its presence

195 for the first time (Extended Data Tab. 8).

196 Spread of both species over the next 5-15 years is predicted to occur independently of extensive 197 environmental changes as both species continue to expand into their anthropogenic ecological 198 niches through spatial dispersal. Aedes albopictus is anticipated to saturate its ecological niche 199 between 2030 and 2050 (Figs. 4d, f), and Ae. aegypti by 2020 (Figs. 4a,c). Beyond these dates 200 the predicted expansion of these species will be driven primarily by environmental changes that 201 create new habitat, including changes in climate, especially temperature (Extended Data Tab. 1, 202 2), as well as exploitation of the increased availability of large human urban environments. Thus 203 efforts to curb or reverse climate change are predicted to be insufficient to prevent fully the 204 expansion of these vector species; significantly greater expansion, however, is predicted, 205 especially between 2050 and 2080, if emissions are not reduced (Fig. 4). At the same time, future 206 human population growth is expected to be concentrated disproportionately within areas where 207 Ae. aegypti and Ae. albopictus already will be established, leading to large increases in the global 208 population at risk of diseases transmitted by these species.

209 Overall our predicted expansions will see *Ae. aegypti* invading an estimated 19.96 million km<sup>2</sup>

by  $2050 (19.91 - 23.45 \text{ million } \text{km}^2$ , depending on the climate and urbanisation scenarios),

211 placing an estimated 49.13% (48.23 – 58.10%) of the world's population at risk of arbovirus

transmission (Figs. 4c, f).

213 Few countries conduct routine, systematic surveillance for Ae. aegypti and Ae. albopictus. 214 Consequently our analysis relies on datasets from the USA and Europe that contain spatio-215 temporal biases in reporting (Extended Data Fig. 2), with an implicit assumption that the 216 processes driving spread in these regions apply elsewhere. These regions have (i) a 217 comparatively high capacity to track establishment and mitigate the spread of these species and (ii) openly available datasets on human movement $^{26}$ . Our modeled rate of spread is thus most 218 219 likely to be biased towards an underestimate of the global rate of spread (Supplementary 220 Information). We did not model potential changes in human mobility which could increase the 221 rate of spread of both species as population mobility increases. Competitive displacement may 222 occur between these two species but this possibility could not be included in this analysis due to a lack of available data<sup>27,28</sup>. However, current ecological literature and ecological theory suggests 223 224 interspecific competition occurs primarily at localized spatial scales and has not been found to 225 influence species' distributions at a coarser spatial resolution, such as the scale we consider here<sup>29–31</sup>. As both species are already established on every human-inhabited continent on the 226 227 planet, we did not model spread between continents.

In the context of predicting mosquito-borne viral transmission, *Aedes* distribution maps have already been shown to help predict the local<sup>32</sup>, regional<sup>33,34</sup>, and international<sup>1,2,6,7,35,36</sup> spread of chikungunya, dengue, yellow fever and Zika viruses. Moreover, local outbreaks of these arboviruses have typically followed within 5-15 years of infestation by *Ae. aegypti* and *Ae. albopictus*, emphasising the importance of vector spread importation as a key risk factor for arbovirus transmission.

There is significant uncertainty surrounding future predictions of changes in climatic conditions.
We used an ensemble approach to propagate the uncertainty from climate scenarios through our
predictions of both *Aedes* species (Figs. 2, 3, 4, Extended Data Figs. 4, 5).

Even under current climate conditions and population densities, both vector species will continue 237 238 to spread globally over the coming decades, filling unoccupied suitable habitats and posing a risk 239 to human health in the majority of locations where they survive and reproduce. Thus efforts to 240 prevent their global dissemination in the near future will be most effective if focussed on 241 preventing human-mediated spread and establishment. To prevent introductions, countries 242 should strengthen entomological surveillance, particularly around high-risk introduction routes 243 such as ports and highways and develop rapid response protocols for vector control to prevent introduced mosquitoes from establishing permanent populations<sup>37–41</sup>. We expect such efforts will 244 245 need to intensify over time as human populations become ever more connected and urban agglomerations grow further<sup>9</sup>. 246

247 Beyond 2030 and especially 2050, the distributions of both species will continue to expand, co-248 inciding with niche expansion into climatically suitable urban areas as opposed to the exploration 249 of the current niche. Increased urbanisation worldwide has already put great strains on our ability 250 to prevent the spread of certain disease vectors and has intensified endemic transmission of arboviruses<sup>42</sup>. Some areas may become less suitable for human habitation due to climate change 251 252 impacts, reducing the number of people living in areas at risk. In the longer term, reducing 253 emission of greenhouse gases would be desirable to limit the increase in Ae. aegypti and Ae. 254 albopictus suitable habitat. Every effort must be made to limit factors that contribute to the 255 global spread of Ae. aegypti and Ae. albopictus if we are to limit the future burden of the diseases 256 vectored by these mosquitoes.

### 259 Methods

260 We used a combination of two approaches to estimate the predicted future distribution of *Ae*.

261 *aegypti* and *Ae. albopictus:* (1) projecting the environmental suitability of both species using a

set of seven environmental covariates and (2) simulating the spread within each continent using

the species' past dispersal patterns, human movement data, and between region adjacency

264 matrices (Extended Data Fig. 1). Here we describe the models and data sources for both265 processes.

266 1. Data

#### 267 1.1. Global mosquito occurrence data

We used a previously collated database of 19,930 and 22,137 geopositioned occurrence records

for *Ae. aegypti* and *Ae. albopictus* respectively (Extended Data Fig. 3)<sup>43</sup>. Each of these records

270 corresponds to a unique detection of a mosquito population in a given location at a given point in

time, as described in detail elsewhere<sup>43</sup>. We excluded records that were classified as temporary

272 presence when such information was available.

273 1.2. Environmental and socio-economic covariates

Aedes survival is influenced by a variety of climatic and environmental factors such as long term
and inter-annual temperature<sup>44,45</sup>, water availability (described as relative humidity and
precipitation), and degree of urbanisation. We used projections from the "Representative
Concentration Pathways" (RCP) developed by the Intergovernmental Panel on Climate Change
(IPCC)<sup>46</sup> which represent different assumptions about emission scenarios that might result in a
variety of climatic changes over the next 65 years. Here we use RCPs 4.5, 6.0 and 8.5, which

assume emission peaks around 2040, 2080 and increases throughout the 21<sup>st</sup> century 280 respectively<sup>46</sup>. These time points were chosen because (i) 2020 represents the date when the 281 climate mitigating policies of the Paris Agreement within the United Nations Framework 282 Convention on Climate Change (UNFCCC) will come into action<sup>47</sup>, (ii) 2080 corresponds to the 283 284 date of the emission peaks modelled according to the RCP 6.0 scenario and (iii) 2050 represents 285 the midpoint between these dates. We use an ensemble of 17 GCMs and pattern scaling to 286 produce monthly mean values of maximum and minimum temperature and monthly totals of 287 rainfall as used in MarkSim. Humidity data were calculated from temperature estimates (see 288 details in section 3). To complement the changes in temperature, relative humidity, and 289 precipitation, we modelled a continued process of global urbanisation until 2080 using a probabilistic machine learning algorithm based on Linard et al<sup>48</sup>. Here we use urban growth rates 290 projected by the United Nations as a predictor variable<sup>49</sup> as well as a range of other critical 291 covariates, as described in van Vuuren et al<sup>48</sup>. 292

#### 293 1.3. Mosquito spatial spread data

A unique set of time-series occurrence records for both species were abstracted from Kraemer et al.<sup>4,43</sup>, and updated with records obtained from Hahn et al<sup>50</sup>. Records were available for *Ae*. *aegypti* in the United States from 1995 – 2016 with United States county-specific information regarding whether the species was present or absent; for *Ae*. *albopictus* information was available from the United States (1987 – 2013) and from Europe (1979 -2017) (Fig. 1, Extended Data Fig. 2). We considered these time periods because they show consistent expansion of the species distribution as described in Hahn et al<sup>50</sup>.

For the United States, counties were identified as reporting presence of either species in a given
year if at least one specimen of any life stage of the mosquito was collected, using any collection

method<sup>50</sup>. Sampling efforts, techniques and temporal resolution were heterogeneous across 303 counties and states in the United States. Therefore, the baseline presence datasets may classify 304 some areas as absent where either of the two Aedes species considered may be present. 305 For Europe, Administrative/Statistical units (NUTS3) were identified as reporting establishment 306 307 of either species in a given year if immature stages and overwintering were observed, using any 308 collection method. Sampling efforts, techniques, and temporal resolution were heterogeneous 309 across countries and either species may have been absent before investigations were triggered by 310 citizen complaint. Therefore, dates correspond to published reports or expert-shared data 311 (VBORNET, VectorNet), and a species could have established earlier in some locations where 312 regular surveillance had not been implemented. Because we were not able to quantify the 313 sampling biases, we instead employed a sensitivity analysis to account for potential under- or 314 over-reporting (see section 2.4).

#### 315 1.4. Human mobility datasets

Overland human movements are known to drive the importation of both species<sup>38,39,41</sup>. Therefore we used human movement data to infer the connectivity between regions as a proxy for

318 importation risk of *Ae. aegypti* and *Ae. albopictus*.

319 US commuting data: For the United States, where both species have been spreading successfully,

we obtained data on workforce commuting flows from county to county between 2009 - 2013,

321 conducted by the American Community Survey (ACS). Data are freely available at

322 <u>http://www.census.gov/hhes/commuting/</u>. Here, commuting was defined as a worker's travel

between home and workplace, where the latter refers to the geographical location of the worker's

job. Daytime population refers to the estimated number of people who are residing and working

in an area during "daytime working hours". The data represent 3,134 counties including 50 states

326 and the District of Columbia (DC) but excluding Puerto Rico. The generalisability of this data 327 has been demonstrated in studies that have successfully approximated human movements derived from mobile phone data and predicted the spread of infectious diseases<sup>24</sup>. As described 328 329 below in section 2.3 in detail, we considered gravity and radiation movement models as well as nearest neighbour-type movements for human movement. We used the fitted models from the 330 USA to extrapolate to all other regions in the Americas using the movement package in R<sup>51</sup>. 331 332 European mobile phone data: For Europe, we obtained mobile phone data (or call detail records, 333 or CDRs) from three different countries where Ae. albopictus is present or has recently been detected: France<sup>43</sup>, Portugal<sup>52</sup>, and Spain<sup>43</sup>. CDR data contain the time at which a call was made 334 335 or a text message was sent, the duration of the call, and the code of the cell in which 336 communication started. The cell corresponds to an area covered by a specific mobile phone 337 tower that serves a particular area. This means that the spatial resolution is restricted to the tower 338 area, the specific location of each individual in the dataset cannot be ascertained. As our analysis 339 was performed at the district level, all users' activity profiles were aggregated up to the district 340 level, which is generally larger than cell tower areas. We thereby obtained a connectivity matrix 341 that shows the connections made between each district *i* to each district *j* within each respective 342 country.

For Portugal, data were available from over one million mobile phone users between April 2006 and March 2007 (12 months). In Spain, CDRs were extracted from 1,034,430 users over three months between November 2007 and January 2008. In France we had the largest sample of 5,695,974 users, collected between September 2007 and mid-October 2007 covering the entire country. Other aspects of the collection and processing methods have been described in detail

elsewhere<sup>23</sup>. We used the fitted models from Europe to extrapolate to all other regions in Europe,
using the movement package in R<sup>51</sup>.

350 Human movement data for Asia: Mobility matrices for Asia are inferred from data from Chinese 351 users of Baidu, the largest location-based service (LBS) in China. Baidu offers a large variety of 352 apps and software for mobile devices and personal computers, mostly for online searching. We extracted GPS data from 23 April 2013 to 30 April 2014 (about 400 million users in China). The 353 354 raw data was collected at the county level (n = 2,959) and aggregated to the prefecture level (345) 355 prefectures). We then estimated daily flows of people between each pair of counties and aggregated this information per year. Movement is recorded in the Baidu data such that on each 356 day if a user was observed at locations A->B->C, then A->B and A->C are counted which may 357 358 produce biased population flow estimates. To explore potential bias in the data we compared the 359 data derived from Baidu to a complete dataset of taxi-based GPS locations in the capital city of 360 Hunan province, covering a one week period (full details below). The correlation of origin-to-361 destination flows in the city between the Baidu data and the complete taxi GPS data was very 362 high (R2 = 0.99).

Baidu data validation: To verify the validity of the Baidu LBS data, we obtained a complete 363 364 dataset of GPS locations for all taxis in Changsha city (capital of Hunan Province, population: 7 365 million) in 2014. The location of each taxi is recorded for regulatory reasons using a GPS device 366 in each taxi. The location is updated every 30 seconds. There were approximately 7,000 taxis in Changsha resulting in 20.16 million records (7000\*24\*60\*2) on a daily basis. The status of the 367 368 cab was also recorded, such as the locations where passengers get on and off. These data are then 369 used to extract the movements between the five districts in the main area of Changsha: Kaifu 370 district, Furong district, Yuhua district, Tianxin district, and Yuelu district. For the purpose of

comparison, one week's data (April 4 to April 17, 2016) were extracted and analysed. The
movements were normalized and then compared with the same week in 2014 from the Baidu
LBS data. The correlation between the mobility estimates extracted from the Baidu LBS data and
from the taxi's GPS data for Changsha city is presented in Extended Data Fig. 9. There is a high
level of similarity between the two datasets, with a correlation coefficient of 0.99 (p=0.001). We
subsequently used the fitted models from China to extrapolate to other regions in Asia and
Oceania again using the movement package in R51.

378 Human movement data for Africa: To calibrate the gravity and radiation models for Africa, we 379 used aggregated and de-identified mobile phone-derived mobility estimates at the constituency 380 level from Namibia between 1 October 2010 and 30 September 2011. These data represent the 381 proportion of time that unique subscriber identity module (SIM) cards in each constituency 382 spend in all other constituencies, as described in detail in Jones & Thornton (2000)53. We used 383 this data set from Namibia because it was openly available and because it offered the best spatial 384 and temporal resolution compared to census-derived data. We then used the fitted models to 385 extrapolate to all other regions in Africa using the movement package in R51. Systematic 386 surveys of cross-border human movements were not available at the time of the study and for the study regions. 387

It is possible that there are significant differences between regions in terms of mobility, but unfortunately no sufficiently widespread and well-resolved data source was available to test this. Our model captured the spread process of *Aedes* mosquitoes using a variety of human movement data, including both CDR data and commuting data. To assess the generalizability of our results we applied the model fitted to commuting data in the USA to the range expansion process observed in Europe. The predictive ability of this cross-continental validation indicates that the

394 mobility data used are sufficiently robust in the context of this study (Extended Data Fig. 8). 395 However, we note there may be several limitations to using commuting data to infer vector 396 introductions as they overly emphasize work-related movements. To test whether our model 397 would perform well even in the absence of human movement data, we performed a cross validation that uses only distance and adjacency matrices which only marginally reduces 398 399 predictability (Extended Data Fig. 12). Despite this, such data has indeed been used in the United 400 States to successfully predict the long distance spread of infectious diseases. We are therefore 401 confident that such data can be applied to predict both short and long distance spread in the USA<sup>54</sup>. Similarly, CDR data has been used to describe the spread of pathogens such as influenza 402 in  $Europe^{23}$ . As new data become available, our model is flexible enough to incorporate them 403 404 and estimates of the predicted range expansion of Ae. aegypti and Ae. albopictus can be updated. 405 There was also no suitable data available on cross border movements that could improve 406 estimates of between-country spread (see section 2.4. for a sensitivity analysis).

407 2. Model fitting to data

408 2.1 Description of speed of dispersal:

409 To understand the past range expansion of both species and to provide basic summary statistics of the speed of dispersal over time in areas where sufficient observations were available, we use 410 the methods of spread rate measurements employed by Tisseuil et al<sup>55</sup>. For each species and 411 412 study area, the centroids of the spatial units where the species were observed were re-projected in 413 a metric system (epsg 102003 in the US, and epsg 3035 in Europe) and the first date of detection 414 in each centroid was interpolated on a 10 km resolution grid using thin plate spline regression (TPSR). The local slope of the surface was measured by a 3 x 3 moving windows filter, and the 415 resulting friction surface (time / distance) was smoothed by an average 11 x 11 cell filter to 416

417 prevent local null frictions values. The local spread rate was then obtained by taking the inverse 418 of the friction. This measure was computed within a mask, which was obtained by kernel density 419 smoothing of the centroids of spatial units where the species were observed. We used the method of Berman and Diggle<sup>56</sup> to determine the optimal bandwidth for the US and EU invasions. In 420 order to have a similar bandwidth for all masks, we used the maximum of the three estimated 421 422 optimal bandwidths, which was found to be 73.2 km. A density threshold of 2.9 points per 10,000 km<sup>2</sup> was chosen to delineate the mask, which was the maximum threshold value allowing 423 424 the inclusions of all observation points in the mask in both the US and EU.

#### 425 2.2. Mosquito environmental niche modelling

To predict the likely future distributions of both species independently (in years 2020, 2050 and 426 427 2080), we first fitted species distribution models to data from the present day. This approach built on previous work<sup>4</sup> using the boosted regression tree (BRT) models fit to mosquito 428 429 occurrence data (section 1.1.). BRTs combine strengths from regression trees and machine 430 learning (gradient boosting) and are able to accommodate non-linear relationships to identify the 431 environmental niche in which the environment is suitable for the species in question. After an initial regression tree is fitted and iteratively improved upon in a forward stepwise manner 432 433 (boosting) by minimising the variation in the response variable not explained by the model at each iteration. This approach has been shown to simultaneously fit complex non-linear 434 response functions efficiently while guarding against over-fitting. 435

We first developed a baseline scenario for the year 2015, using the global dataset of Ae. aegypti

437 and *Ae. albopictus* occurrence (section 1.1)<sup>43,57</sup> and a set of environmental and socioeconomic

438 predictors (section 1.2). In a BRT modelling framework pseudo-absences need to be generated to

439 allow for discrimination between areas where the mosquitoes can persist, and to identify biases

in reporting<sup>58</sup>. We used the approach previously described in and applied by Kraemer et al<sup>4</sup> using
background points from the Global Biodiversity Information Facility (GBIF) and the inverse of
an *Aedes* temperature suitability mask<sup>45</sup> with equal ratio between presence and absence points
and no threshold being applied. From that we constructed 100 sub-models to derive the mean
prediction map and model-fitting uncertainty using the SEEG-SDM package in R<sup>59,60</sup>.

#### 445 2.3. Human mobility modelling

Given the heterogeneous abundance of both species<sup>61</sup> as well as the low probability of their
surviving slower and longer transits, the chance of a species being introduced following any
single translocation event is low. Hence we used relatively long time steps (yearly) and
generalized human movement models fitted to a variety of data sources to understand the spatial
spread patterns of *Ae. aegypti* and *Ae. albopictus*.

We incorporated three distinct human movement models that act at different scales, since we are 451 452 uncertain *a priori* which type of human movement will be most associated with mosquito spread. 453 We considered (i) a gravity model, (ii) a radiation model, (iii) an adjacency network model and (iv) un-transformed great-circle distance. Each of these models have been shown to be useful 454 455 depending on the local context to infer regular daily commuting patterns, longer-term movements, and as general descriptions of human mobility<sup>24,62,63</sup>. First, the gravity model, 456 assumes that fluxes between two areas *i* and *j* are  $T_{i,j} = k \frac{N_i^{\alpha} N_j^{\beta}}{d_{i,j}^{\gamma}}$ , where *N* represents human 457 population size and d is great circle distance between two locations, and k,  $\alpha$ ,  $\beta$ , and  $\gamma$  are 458 parameters to be fit<sup>64,65</sup>. The gravity model emphasises the attractive power of large population 459 centres. Second, the radiation model assumes fluxes to be  $T_{i,j} = T_i \frac{N_i N_j}{(N_i + S_{i,j})(N_i + N_j + S_{i,j})}$ , where  $T_i$ 460 is the number of individuals leaving area i and  $s_{ii}$  is the total population in the circle centered at 461

462	<i>i</i> with radius $d_{i,j}$ excluding the population of the two areas <i>i</i> and <i>j</i> . The radiation model
463	considers not only distance and population sizes at origin and destination but also the cumulative
464	population at a lesser distance from the origin than the destination <sup>24</sup> . Consequently, this model
465	considers not only the origin and destination but also the landscape of 'intervening opportunities'
466	between them. Third, adjacency networks encode the number of district borders an individual
467	would need to cross to move from one district to another. Thus, this metric reflects the
468	neighbourhood effect. Finally, we computed the great-circle distance between each pair of
469	locations and used that as a metric of mobility in and of itself <sup>32,66</sup> .
470	For each second Administrative unit (county/municipality) in the world, we determined the total
471	human population size using gridded population estimates and calculated the great-circle
472	distance between the centroids of each pair of districts within each continent <sup>67</sup> . Gravity and
473	radiation model parameters were fitted by maximum likelihood methods to the empirical data
474	described above using the movement R package <sup>51</sup> . National adjacency networks were computed
475	using administrative boundary data from the GADM dataset ( <u>http://www.gadm.org</u> ). To account
476	for neighbourhood effects of spread and for the potential importance of within-country and
477	between-country movements, we constructed adjacency matrices that were disaggregated into
478	three binary connectivity matrices with connectivity degrees of one ( <i>i.e.</i> , districts share a border).
479	two ( <i>i.e.</i> , districts share a common neighbour), and three ( <i>i.e.</i> , more than two degrees away).

480 2.4. Mosquito spread modelling

481 Let  $x_i(t)$  be the *Aedes* population status of district *i* at time *t* (*i.e.*, a binary variable takes the

482 value 1 if there were *Aedes* mosquitoes that time, and 0 otherwise). Given the nature of the

- 483 dataset collected, we assumed that all data points represented detection of established
- 484 populations and thus assumed continuous presence of the species for the first and last reported

485 occurrences. We used a standard logistic model to characterize the probability that some district j486 will become occupied at time t:

$$logit \left( P(x_j(t) = 1 | x_j(t-1) = 0) \right) = \beta_0 + \sum_{k=1}^n \beta_k Y_{j,t}^{(k)}$$

where  $Y_{j,t}^{(k)}$  corresponds to the value of explanatory variable k in district j at time t. Explanatory 487 488 variables included in this analysis were the predicted vector habitat suitability (i.e. suitability for 489 establishment of an introduced vector, 2.1.) and connectivity between infested and non-infested districts (*i.e.* probability of introduction of a vector). Separate metrics of connectivity were 490 defined for each human movement model (2.2.). From each human movement model, a 491 connectivity matrix  $A_{ij}^{(k)}$  was calculated for each location *i* and *j*. A corresponding covariate for 492 the occupation model was then computed to represent the global force of importation, exerted 493 from all other infested districts to *j*:  $Y_{i,t}^{(k)} = \sum_i A_{ii}^{(k)} x_i(t-1)$ . 494

495 These models were re-fit in each successive year separately for the North American and 496 European datasets, and for each vector species, using all available data up to that year. Model selection was done through backward selection using Akaike Information Criterion (AIC).<sup>68</sup> The 497 498 fitted model was then evaluated prospectively over the next year by comparing predicted 499 presence or absence with observations, thereby allowing us to evaluate and validate model 500 performance over time. For model evaluation we considered all locations (*i.e.* 3,134 counties in 501 the USA, 1,587 NUTS in Europe). This model evaluation was used to identify the best 502 explanatory variables to include in the Aedes spread model. Model evaluation was performed 503 using receiver operating characteristic curves (ROC curves) (Extended Data Fig. 7) and model 504 accuracy was characterized comparing the predicted probabilities of first detection vs the

505 response (Extended Data Fig. 6). We calculated the probability of first detection  $p_w$  predicted by 506 the model for each district-year that had not yet reported mosquitoes. We then partitioned district-years into eight groups with predicted probability in the range of 0-1%, 1-5%, 5-10%, 507 10-15%, 15-20%, 20-25%, 25-35%, and 35-100%. For each group, we calculated the mean 508 509 predicted probability and compared it with the proportion of district-years in the group in which 510 range expansion was observed. Our model assumes that each mosquito species will persist in an 511 area once detected, whilst there are some examples of incursions apparently having been 512 successfully eradicated or died out. It is possible that this assumption could result in inflated 513 predictions of the rate of spread, due to an overestimated number of source populations for each 514 potential invasion event. However, it should be noted that this overestimate of the number of 515 source populations would also be present in the training data, and would be at least partially 516 absorbed into estimates of the probabilities of importation. Insufficient data were available to test 517 or account for this potential bias, but based on additional experiments, we do not anticipate our 518 estimates to greatly overpredict *Aedes* presence (see section: sensitivity analyses and sampling 519 bias).

520 Cross-validation: To test whether the spread between countries is different to the spread within 521 countries, we used the multi-country dataset from *Ae. albopictus* in Europe and varied the 522 relative frequency of within- and between-country mobility by decreasing movement between 523 countries by 20%, 50%, and 70%. The results were then compared with a baseline, in which 524 predicted within-country movement is the same as between-country movement (Extended Data 525 Fig. 11). We also performed sensitivity analyses to evaluate how a model including human 526 movements compares to single variable models that have objective measurements such as great

527 circle distance and adjacency. A model that includes human movements only slightly increased528 predictive performance (Extended Data Fig. 12).

529 Sensitivity analyses and sampling bias: Surveillance efforts to detect Ae. aegypti and Ae. 530 albopictus may vary in time and space due to gradual progressive improvements as a result of 531 technology trapping technology, general expertise, or in response to specific events. Three types 532 of possible changes in surveillance could bias the estimates of our spread model: (1) spatial 533 expansion of surveillance system coverage to new areas; (2) intensification of sampling effort 534 within areas where the surveillance system already operates; and (3) changes in sampling 535 methods within areas where the surveillance system already operates that make it more or less 536 likely to detect either Ae. aegypti or Ae. albopictus. To address each of these, we completed 537 sensitivity analyses to understand how possible changes in surveillance may affect the inference about spread in the future. 538

Expansions of the surveillance system can be definitively distinguished from true known
expansions of the vectors by comparing the state transitions of areas in longitudinal datasets,
such as our *Ae. albopictus* dataset in Europe between the years of 2013 and 2017. Areas that first
report absence of the species (often for multiple years) and later report presence are as close to a
clear example of introduction as possible and give a reasonable estimate of the arrival date.
Conversely, if an area's first report is presence of the species, the species' arrival date may have
been estimated later than it truly occurred.

546 Firstly, the existence of such longitudinal records in the *Ae. albopictus* database in Europe is 547 strong evidence that the distribution of the species is expanding, however to test if expanding 548 surveillance efforts is a contributing factor to the observed rate of spread we compared our 549 original model fit to the full *Ae. albopictus* in Europe dataset, as used in our main analysis

550 (model 1), with a model fit only to the data points that have strong evidence for a specific 551 introduction date (i.e., report absence before presence; model 2). We tabulated data from Ae. 552 *albopictus* in Europe where information was available whether there was ongoing surveillance 553 prior to the reporting of the species (transition from absence to presence). Such data was available for 179 out of 600 observations between 2013 – 2018, a time period where 400 new 554 regions reported the presence of the species making our sub-sample about 50% of all new 555 556 invasions. This data was available at higher spatial resolution that the full Ae. albopictus dataset 557 for Europe. 75% of these records are from locations of most recent spread in France and 558 Germany. Finally, as model 2 was fit to data from a narrower date range we also consider a third 559 model (model 3) which was fit to both occurrence and longitudinal data but only from the more 560 recent date range (Extended Data Tab. 3). If expansion of surveillance efforts is a contributing 561 factor to the observed rate of spread in the data, then we would expect Model 2 to predict a significantly lower rate of spread than Models 1 or 3 (our null hypothesis). 562 563 Each of these models were fit to the above datasets, then used to simulate Ae. albopictus spread 564 from a common baseline (based on occurrence and longitudinal data at the end of 2012) for five 565 years between 2013 and 2017 as described previously. The predicted total number of new districts infested of this period was calculated and is shown in Extended Data Tab. 4. Note that 566 comparison of goodness of fit metrics for these models was not possible since the models were 567

568 fit to different datasets.

569 Contrary to the expectation that more precise dates of invasion would lead to conclusions of 570 slower rates of spread, this sensitivity exercise found that restricting the model to just areas 571 where the date of introduction is known significantly increases the predicted rate of spread. Thus, 572 this exercise rejects our above null hypothesis. This effect was also independent of the time

period of the fitting data (similar results for Model 1 and Model 3). These results suggest that it
is more likely that true spread of *Ae. albopictus* is outpacing expansion of mosquito surveillance,
and if longitudinal surveillance was in place everywhere, the observed rates of spread would be
greater.

We therefore believe that the currently implemented model is a conservative estimate of spread of these species that is not highly affected by changes in spatial coverage of surveillance systems and provides the most robust estimates of spread over these time periods given the available data. Given the limited number of years of data available to fit Model 2, we believe that Model 1 provides the most reliable estimates of future spread.

582 Intensification in sampling effort and technological advancements in collection methods may 583 affect the probability of detection of a species in earlier in their invasion process vs today. Here we test both hypotheses through inclusion of different terms in our spread model regression and 584 585 compare such models to the null of no changes in surveillance intensity over time (as currently 586 implemented in our main analysis). To represent increases or decreases in surveillance over time, 587 we include the spline-smoothed year of detection as a variable in the regression analysis. To 588 represent step changes in surveillance efforts in response to specific events we include a factor 589 variable; either before the 2003 peak in West Nile Virus cases in the USA, or after 2003 (only 590 for models in USA). Internal cross validation was then used to compare the predictive 591 performance of these three models with evaluation on three-year-lookahead holdout sets, subject 592 to a minimum of 10 consecutive years of data to fit the models. Model predictive performance 593 was then compared using deviance from observed values in the holdout set. 594 This showed that for all species in all continents, the inclusion of a temporal (Year) term reduced

595 predictive accuracy (increased deviance). This was the case for both gradual change over time

(s(Year)) and for breakpoint changes in response to specific events (Year > 2003). As a result,
we conclude that there is no evidence for temporal changes in sampling effort in any of the
datasets concerned and therefore do not include such terms in our final predictions (Extended
Data Tab. 5).

600 Finally, there is a possibility that changes in general vector surveillance strategies could have led 601 to changes that affected the probability of detection of one species more than the other. Such 602 differential biases could undermine our inter-species spread rate comparison. One key period of 603 concern is around the 2003 West Nile Virus (WNV) outbreak in the US where vector 604 surveillance may have prioritized trapping in more rural environments to optimize detection of 605 various *Culex* species. Such a focus on rural environments may have led to relative increases in 606 sampling intensity of Ae. albopictus and relative reductions in sampling intensities for Ae. 607 aegypti.

To test this hypothesis, we follow a similar approach to the above analysis, where covariates for "before" and "after" the 2003 WNV outbreak are included in the USA spread model for each species. If the above hypothesis is true, such terms should i) have larger "after" values than "before" values in the *Ae. albopictus* model and vice versa in the *Ae. aegypti* model, and ii) improve model prediction accuracy.

The best fits from the *Ae. aegypti* and *Ae. albopictus* spread models in the USA show that
detection of *Ae. aegypti* marginally increased relative to *Ae. albopictus* (positive model
coefficients for post-2003 term in *Ae. aegypti*, negative in *Ae. albopictus*) (Extended Data Tab.
6). However, as previously stated, inclusion of such changes in surveillance quality over time
reduces the model predictive performance (increase in deviance for both species) and therefore
may not provide a better time period to mirror the spread of the species in the United States.

#### 619 2.5. Classifying the ranges of each mosquito species and incorporating uncertainty

620 Current reported distributions of Ae. aegypti and Ae. albopictus are unlikely to be fully representative of their actual distributions because of logistical and financial constraints on 621 vector surveillance.<sup>37</sup> Therefore we used the following method to estimate the current-day global 622 623 distribution (realised niche) of each mosquito species by comparing environmental suitability maps with occurrence data. We extracted the predicted environmental suitability value at each of 624 625 the locations where the mosquito species has been reported, and the value of environmental 626 suitability that encompassed 90% of these reported locations was chosen as the range threshold. 627 Every value above or equal to this threshold was defined as within the range of the mosquito 628 species (Extended Data Fig. 13). This approach assumes that the 10% of occurrences outside of 629 the predicted range represent temporary introductions that do not persist longer than one year and 630 are not representative of the long-term distribution of the species. As there is uncertainty in what 631 proportion of the data are representative of these transient identifications (given that the majority 632 of the data are cross-sectional not longitudinal), we undertook a sensitivity analysis that varied 633 this threshold from 85% to 95%, thereby creating 96 different possible range maps that represent 634 different realisations of the current distribution of each species. In doing so, we capture locations that have the conditions for mosquito presence and where there is potential for onward spread. 635 636 We did not include international shipping as a contributor to infrequent long-distance 637 importation events between continents since both species are already well established on each 638 continent and therefore new occurrences are more likely to be driven by intra-continental 639 importation pressure.

#### 640 3. Future projections

#### 641 3.1. Projecting environmental and socioeconomic covariates

642 We used 17 GCMs to estimate 30 arc-sec images for monthly mean climate data. Extended Data 643 Table 7 provides the designation, origin, references and number of replicate runs for each model. The procedures are described in detail in MarkSim documentation<sup>65</sup>. For each GCM the baseline 644 monthly climate was derived from the historic runs for temperatures and rainfall, the monthly 645 646 means were calculated for each GCM for the years 2000 to 2095, and the difference 'delta' for 647 each month was calculated by subtracting the specific GCM baseline. The deltas were 648 interpolated from the native GCM pixel (Extended Data Tab. 7) to a one degree by one degree pixel for the globe. The data were pattern scaled to WorldClim 1.03<sup>64</sup> for each one degree pixel, 649 RCP, and month. For each variant a fourth order polynomial regression was fitted over the 96 650 years of data and through the origin at 1985 (1985 being the mean midpoint of the data used in 651 652 the WorldClim construction) to calculate one output per model per year per scenario. 653 Humidity data were estimated directly at the 30 arc-sec level from dewpoint calculated by the tabular method of Linacre<sup>69</sup> and the mean temperature. To fully propagate the variation between 654 655 the climate models through our predictions we used the outputs of 17 GCM, for all 3 years, and 3 656 scenarios.

Global temperature estimates were converted into temperature suitability for mosquito
population persistence (separate metrics for each vector species), hereafter referred to as
temperature suitability, using temperature-based mathematical models from Riahi et al<sup>44</sup> and
Fujino et al<sup>45</sup>. These show the effects of diurnal and seasonal changes in temperatures on the
generation time of the mosquito and its resultant effects on the persistence of a population.

As a highly anthropophilic mosquito species, the future distribution of the *Aedes* is likely to depend critically on both environmental and human socioeconomic factors that modify the availability of its habitat<sup>8</sup>. To incorporate these features, we also modelled the continued process of global urbanisation until 2080 using a probabilistic machine learning algorithm based on the work of Linard et al<sup>48</sup>. Here we use urban growth rates predicted by the United Nations as a predictor variable<sup>49</sup> as well as a range of other covariates as previously described in van Vuuren et al<sup>48</sup>.

#### 669 3.2. Projecting future niche of Ae. aegypti and Ae. albopictus

Although niche shifts might occur over long time-periods, the future effects remains unclear for *Ae. aegypti* and *Ae. albopictus* since their expansion from their native range<sup>70</sup>. Therefore, we assume niche conservatism, implying that the mosquitoes tend to establish and survive under similar environmental conditions in native and invaded ranges in the future<sup>4,71,72</sup>.

Our final aim was to produce 18 maps predicting *Ae*. aegypti and *Ae*. *albopictus* suitability in the years 2020, 2050 and 2080 under three different emissions scenarios (RCPs). Each of these 18 maps were composed of 100 ensemble predictions that randomly sampled (with replacement) the following aspects of the analysis:

1. The fitted *Aedes* BRT model (from a choice of 100 BRT models fitted to 2015 data)

- 679 2. The predicted temperature suitability for *Aedes* survival (from a choice of 17 GCMs)
- 680 *3.* The predicted minimum precipitation (from a choice of 17 GCMs)
- 681 *4.* The predicted relative humidity (from a choice of 17 GCMs)
- 5. The predicted minimum precipitation (from a choice of 17 GCMs)
- 683 *6.* The predicted geographic expansion via land from the spread models (section 3.3).

This approach sought to fully propagate the uncertainty in the climate, *Aedes* temperature suitability and *Aedes* models through to the final prediction. These 100 predictions were then summarised by mean and 95% credible intervals to give the final prediction for each year RCP combination. Uncertainties are shown in all maps along the X-axes.

Our baseline map modelling is different from previously published maps in so far that it uses only projectable environmental and socio-demographic variables and does not use the Enhanced Vegetation Index (EVI), as the EVI is a direct empirical measure of the Earth's current greenness<sup>4</sup>. To minimise potential reduction in the predictive ability of the model by omitting this covariate, we include precipitation and relative humidity as predictors for suitability for green vegetation growth in both the present day and future models.

#### 694 3.3. Projecting mosquito spread

695 To derive yearly model-based estimates of the possible expansion of both species by 2080 we 696 forward-simulated the geographic spread model based on the equation in 2.4. To account for the 697 spatio-temporal dependence in first detection probabilities (each district's probability is a 698 function of every other district that was infested the year before), we run 1,000 simulations 699 forward in time. Within each simulation we estimate the probability of infestation to each district 700 that had yet to detect the species. We then drew a Bernoulli random variable with that probability 701 of '1' (i.e., invasion) and imputed those results for each potential detection. Using these imputed 702 invasions as well as all districts that had previously been infested, we repeat the estimation of 703 range expansion for the next year. This process is repeated up to the desired forecast horizon. 704 This represents a single simulation. It is important to note that we did not allow for the situation where an already infested district will 'lose' its infection status (*i.e.*, if  $x_i(t-1) = 1$  for district 705

*i*, we force  $x_i(t) = 1$ ). We then combine the results of the 1,000 simulations to identify which districts were most likely to have a positive species presence at any point.

#### 708 3.4. Calculating population at risk and area expansion

709 To classify areas as at risk or not at risk of Ae. aegypti and Ae. albopictus a threshold was 710 defined for the continuous Aedes suitability maps by the value that maximised sensitivity and 711 specificity when classifying the occurrence and background data using the 2015 map. This value 712 was found to be 0.47 and 0.51 for Ae. aegypti and Ae. albopictus respectively. Any pixel with a predicted suitability value above that was considered at risk and the same threshold was applied 713 714 to each time point and scenario to calculate the population and area at risk in each global region. 715 The final maps for 2020, 2050, 2080 are then overlaid with contemporary estimates of human 716 populations at 5 km resolution and extracted the relevant population at risk was estimated using 717 the raster package in R. We paired the climatic scenarios based on Shared Socioeconomic Pathways (SSPs) that were defined by O'Neill *et al.* in 2014<sup>73</sup>. They represent reference 718 719 pathways that describe plausible alternate trends in the evolution of society and ecosystems over 720 a century, in the absence of climate change or climate policies. SSPs are predicated on possible 721 outcomes that would make it more or less difficult to respond to climate change challenges. Each 722 SSP consists of quantified population and Gross Domestic Product (GDP) trajectories, serving as 723 the starting points for various organisations to model these factors and to provide projections for 724 demographic and economic development variables. The Integrated Assessment Modelling 725 Consortium (IAMC) made available certain peer-reviewed projections via the International Institute for Applied Systems Analysis (IIASA, http://www.iiasa.ac.at), whereby the SSP 726 storylines were converted into population and GDP projections for 195 countries<sup>74</sup> for every 727 728 decade between the years 2010 and 2100.

730	References		
731 732	1.	Nsoesie, E. O. <i>et al.</i> Global distribution and environmental suitability for chikungunya virus, 1952 to 2015. <i>Eurosurveillance</i> <b>21</b> , pii=30234 (2015).	
733 734	2.	Messina, J. P. <i>et al.</i> Mapping global environmental suitability for Zika virus. <i>Elife</i> <b>5</b> , e15272 (2016).	
735	3.	Bhatt, S. et al. The global distribution and burden of dengue. Nature 496, 504–7 (2013).	
736 737	4.	Kraemer, M. U. G. <i>et al.</i> The global distribution of the arbovirus vectors Aedes aegypti and Ae. albopictus. <i>Elife</i> <b>4</b> , e08347 (2015).	
738	5.	Lessler, J. et al. Assessing the global threat from Zika virus. Science 353, aaf8160 (2016).	
739 740	6.	Faria, N. R. <i>et al.</i> Epidemic establishment and cryptic transmission of Zika virus in Brazil and the Americas. <i>Nature</i> <b>546</b> , 406–10 (2017).	
741 742 743	7.	Grubaugh, N. D., Ladner, J. T., Kraemer, M. U. G., Dudas, G. & Tan, A. L. Genomic epidemiology reveals multiple introductions of Zika virus into the United States. <i>Nature</i> <b>546</b> , 401–5 (2017).	
744 745	8.	Messina, J. P. <i>et al.</i> The many projected futures of dengue. <i>Nat. Rev. Microbiol.</i> <b>13</b> , 230–9 (2015).	
746 747	9.	Kraemer, M. U. G. <i>et al.</i> Progress and challenges in infectious disease cartography. <i>Trends Parasitol.</i> <b>32</b> , 19–29 (2016).	
748	10.	Powell, J. R. Mosquitoes on the move. Science 354, 971–972 (2016).	
749 750	11.	Powell, J. R. & Tabachnick, W. J. History of domestication and spread of Aedes aegypti - a review. <i>Mem. Inst. Oswaldo Cruz</i> <b>108 Suppl,</b> 11–7 (2013).	
751 752	12.	Scott, T. W. <i>et al.</i> Longitudinal Studies of Aedes aegypti (Diptera: Culicidae) in Thailand and Puerto Rico: Blood Feeding Frequency. <i>J. Med. Entomol.</i> <b>37</b> , 89–101 (2000).	
753 754 755	13.	Guerra, C. A. <i>et al.</i> A global assembly of adult female mosquito mark-release-recapture data to inform the control of mosquito-borne pathogens. <i>Parasites and Vectors</i> <b>7</b> , 276 (2014).	
756 757 758	14.	Hawley, W. A., Pumpuni, C. B., Brady, R. H. & Craig, G. B. Overwintering survival of Aedes albopictus (Diptera, Culicidae) eggs in Indiana. <i>J. Med. Entomol.</i> <b>26</b> , 122–129 (1989).	
759 760 761	15.	Maynard, A. J. <i>et al.</i> Tiger on the prowl: Invasion history and spatio-temporal genetic structure of the Asian tiger mosquito Aedes albopictus (Skuse 1894) in the Indo-Pacific. <i>PLoS Negl Trop Dis</i> <b>11</b> , e (2017).	
762 763 764	16.	Benedict, M. Q., Levine, R. S., Hawley, W. a & Lounibos, L. P. Spread of the tiger: global risk of invasion by the mosquito Aedes albopictus. <i>Vector borne zoonotic Dis.</i> <b>7</b> , 76–85 (2007).	
765 766	17.	Armbruster, P. A. Review Photoperiodic Diapause and the Establishment of Aedes albopictus (Diptera: Culicidae) in North America. <i>J. Med. Entomol.</i> <b>53</b> , 1013–1023 (2016).	
767	18.	Vega-rua, A. et al. High Efficiency of Temperate Aedes albopictus to Transmit	

768		Chikungunya and Dengue Viruses in the Southeast of France. PLoS One 8, e59716 (2013).
769 770	19.	Gloria-soria, A. <i>et al.</i> Global genetic diversity of Aedes aegypti. <i>Mol. Ecol.</i> <b>25</b> , 5377–5395 (2016).
771 772 773	20.	Padilla, D. K., Chotkowski, M. A. & Buchan, L. A. J. Predicting the Spread of Zebra Mussels (Dreissena polymorpha) to Inland Waters Using Boater Movement Patterns. <i>Glob. Ecol. Biogeogr. Lett.</i> <b>5</b> , 353–359 (1996).
774 775 776	21.	Roche, B. <i>et al.</i> The Spread of Aedes albopictus in Metropolitan France: Contribution of Environmental Drivers and Human Activities and Predictions for a Near Future. <i>PLoS One</i> <b>10</b> , e0125600 (2015).
777 778 779 780	22.	Moore, C. G., Medicine, V., Sciences, B. & State, C. Using Geographic Information Systems to Analyze the Distribution and Abundance of Aedes aegypti in Africa : The Potential Role of Human Travel in Determining the Intensity of Mosquito Infestation. <i>Int.</i> <i>J. Appl. Geospatial Res.</i> <b>4</b> , 9–38 (2013).
781 782	23.	Tizzoni, M. <i>et al.</i> On the use of human mobility proxies for modeling epidemics. <i>PLoS Comput. Biol.</i> <b>10</b> , e1003716 (2014).
783 784	24.	Simini, F., González, M. C., Maritan, A. & Barabási, AL. A universal model for mobility and migration patterns. <i>Nature</i> <b>484</b> , 96–100 (2012).
785 786	25.	Simini, F., Maritan, A. & Néda, Z. Human mobility in a continuum approach. <i>PLoS One</i> <b>8</b> , e60069 (2013).
787 788 789	26.	Canali, M., Rivas-Morales, S., Beutels, P. & Venturelli, C. The Cost of Arbovirus Disease Prevention in Europe: Area-Wide Integrated Control of Tiger Mosquito, Aedes albopictus, in Emilia-Romagna, Northern Italy. <i>Int. J. Environ. Res. Public Health</i> <b>14</b> , 444 (2017).
790 791 792	27.	Leishnam, P. T., Lounibos, L. P., O'Meara, G. F. & Juliano, S. A. Interpopulation divergence in competitive interactions of the mosquito Aedes albopictus. <i>Ecology</i> <b>90</b> , 2405–13 (2009).
793 794 795	28.	Camara, D. C. P. <i>et al.</i> Seasonal differences in density but similar competitive impact of Ae. albopictus (Skuse) and Aedes aegypti (L.) in Rio de Janeiro, Brazil. <i>PLoS One</i> <b>11</b> , e0157120 (2016).
796 797	29.	Lounibos, L. P. <i>et al.</i> Does temperature affect the outcome of larval competition between Aedes aegypti and Aedes albopictus? <i>J. Vector Ecol.</i> <b>27</b> , 86–95 (2002).
798 799 800	30.	Prinzing, A., Durka, W., Klotz, S. & Brandl, R. Geographic variability of ecological niches of plant species: Are competition and stress relevant? <i>Ecography (Cop.).</i> <b>25,</b> 721–729 (2002).
801 802	31.	Soberón, J. Grinnellian and Eltonian niches and geographic distributions of species. <i>Ecol. Lett.</i> <b>10,</b> 1115–1123 (2007).
803 804	32.	Kraemer, M. U. G. <i>et al.</i> Big city, small world: density, contact rates, and transmission of dengue across Pakistan. <i>J. R. Soc. Interface</i> <b>12</b> , 20150468 (2015).
805 806	33.	Kraemer, M. U. G. <i>et al.</i> Spread of yellow fever virus outbreak in Angola and the Democratic Republic of the Congo 2015–16; a modelling study. <i>Lancet Infect. Dis.</i> <b>17.</b>

807 330–338 (2017).

- 808 34. Perkins, T. A., Siraj, A. S., Ruktanonchai, C. W., Kraemer, M. U. G. & Tatem, A. J.
  809 Model-based projections of Zika virus infections in childbearing women in the Americas.
  810 Nat. Microbiol. 16126, (2016).
- Bogoch, I. I. *et al.* Potential for Zika virus introduction and transmission in resource
  limited countries in Africa and Asia-Pacific. *Lancet Infect. Dis.* 16, 1237–45 (2016).
- 813 36. Bogoch, I. I. *et al.* Anticipating the international spread of Zika virus from Brazil. *Lancet*814 387, 335–336 (2016).
- Schaffner, F. *et al.* Development of guidelines for the surveillance of invasive mosquitoes
  in Europe. *Parasit. Vectors* 6, 209 (2013).
- 817 38. Moore, C. G. & Mitchell, C. J. Aedes albopictus in the United States: ten-year presence
  818 and public health implications. *Emerg. Infect. Dis.* 3, 329–34 (1997).
- 819 39. Flacio, E., Engeler, L., Tonolla, M., Lüthy, P. & Patocchi, N. Strategies of a thirteen year
  820 surveillance programme on Aedes albopictus (Stegomyia albopicta) in southern
  821 Switzerland. *Parasites and Vectors* 8, (2015).
- 40. Collantes, F. *et al.* Review of ten-years presence of Aedes albopictu s in Spain 2004 –
  2014 : known distribution and public health concerns. *Parasit. Vectors* 8, (2015).
- 41. Eritja, R., Palmer, J. R. B., Roiz, D., Sanpera-calbet, I. & Bartumeus, F. Direct Evidence
  of Adult Aedes albopictus Dispersal by Car. *Sci. Rep.* 7, 14399 (2017).
- 42. Salje, H. *et al.* Dengue diversity across spatial and temporal scales: Local structure and the effect of host population size. *Science* 355, 1302–1306 (2017).
- Kraemer, M. U. G. *et al.* The global compendium of Aedes aegypti and Ae . albopictus
  occurrence. *Sci. Data* 2, 150035 (2015).
- Brady, O. J. *et al.* Global temperature constraints on Aedes aegypti and Ae. albopictus
  persistence and competence for dengue virus transmission. *Parasit. Vectors* 7, 338 (2014).
- Brady, O. J. *et al.* Modelling adult Aedes aegypti and Aedes albopictus survival at
  different temperatures in laboratory and field settings. *Parasit. Vectors* 6, 351 (2013).
- 46. IPCC. Climate Change 2013: the physical science basis: contribution of working group I
  to the Fifth Assessment Report on The Intergovernmental Panel on Climate Change, IPCC
  Fifth Assessment Report: Climate Change 2013 (AR5). (Cambridge University Press,
  2013).
- 47. UNFCCC (United Nations Framework Convention on Climate Change). Adoption of the
  Paris Agreement. 21st Conf. Parties (2015).
- 48. Linard, C., Tatem, A. J. & Gilbert, M. Modelling spatial patterns of urban growth in
  Africa. *Appl. Geogr.* 44, 23–32 (2013).
- 49. United Nations Population Division. World Urbanization Prospects: The 2014 Revision.
  43. (United Nations, 2014).
- 844 50. Hahn, M. B. et al. Reported Distribution of Aedes (Stegomyia) aegypti and Aedes

845 (Stegomyia) albopictus in the United States, 1995-2016 (Diptera: Culicidae). J. Med. Entomol. 1-7 (2016). doi:10.1093/jme/tjw072 846 51. 847 Golding, N., Schofield, A. & Kraemer, M. U. G. Movement: Functions for the analysis of movement data in disease modelling and mapping. *R Packag. version 0.2* (2015). 848 849 52. Osório, H. et al. Detection of the Invasive Mosquito Species Aedes (Stegomyia) albopictus (Diptera: Culicidae) in Portugal. Int. J. Environ. Res. Public Heal. 2018, Vol. 850 851 15, Page 820 15, 820 (2018). 53. Ruktanonchai, N. W. et al. Identifying Malaria Transmission Foci for Elimination Using 852 853 Human Mobility Data. PLOS Comput. Biol. 12, e1004846 (2016). Viboud, C. et al. Synchrony, waves, and spatial hierarchies in the spread of influenza. 854 54. Science 312, 447-51 (2006). 855 55. Tisseuil, C. et al. Evaluating methods to quantify spatial variation in the velocity of 856 biological invasions. Ecography (Cop.). 39, 409-418 (2015). 857 858 56. Berman, M. & Diggle, P. Estimating weighted integrals of the second-order intensity of a spatial point process. J. R. Stat. Soc. Ser. B 51, 81–92 (1989). 859 57. 860 Kraemer, M. U. G. et al. Data from: the global compendium of Aedes aegypti and Ae. albopictus occurrence. Dryad Digit. Repositry (2015). doi:dx.doi.org/10.5061/dryad.47v3c 861 58. Phillips, S. J. et al. Sample selection bias and presence-only distribution model: 862 implications for background and pseudo-absence data. Ecol. Appl. 19, 181–97 (2009). 863 R Core Team. R: A language and environment for computing. Vienna, Austria. R Found. 864 59. 865 Stat. Comput. (2016). 866 60. Golding, N. Streamlined functions for species distribution modelling in the seeg research group. R Packag. version 0.1-3 (2014). 867 868 61. Perkins, T. A., Scott, T. W., Le Menach, A. & Smith, D. L. Heterogeneity, mixing, and the spatial scales of mosquito-borne Ppathogen transmission. PLoS Comput. Biol. 9, 869 870 e1003327 (2013). 871 62. Brockmann, D. & Helbing, D. The hidden geometry of complex, network-driven contagion phenomena. Science 342, 1337-42 (2013). 872 873 Jongejans, E. et al. A unifying gravity framework for dispersal. Theor. Ecol. 8, 207–223 63. 874 (2015). Wesolowski, A., O'Meara, W. P., Eagle, N., Tatem, A. J. & Buckee, C. O. Evaluating 875 64. 876 Spatial Interaction Models for Regional Mobility in Sub-Saharan Africa. PLOS Comput. *Biol.* **11**, e1004267 (2015). 877 878 65. Wesolowski, A. et al. Commentary: Containing the Ebola outbreak - the potential and 879 challenge of mobile network data. PLOS Curr. Outbreaks Sep 29, (2014). Tatem, A. J., Hemelaar, J., Gray, R. R. & Salemi, M. Spatial accessibility and the spread 880 66. of HIV-1 subtypes and recombinants. AIDS 26, 2351-60 (2012). 881 882 67. WorldPop project. WorldPop. Available at: http://worldpop.org.uk/.

- 883 68. Hastie, T. J. & Tibshirani, R. J. Generalized additive models. (CRC Press, 1990).
- 69. Linacre, E. T. A simple formula for estimating evaporation rates in various climates, using
  temperature data alone. *Agric. Meteorol.* 18, 409–424 (1977).
- Medley, K. A. Niche shifts during the global invasion of the Asian tiger mosquito, Aedes
  albopictus Skuse (Culicidae), revealed by reciprocal distribution models. *Glob. Ecol. Biogeogr.* 19, 122–33 (2010).
- Wiens, J. J. & Graham, C. H. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36, 519–39 (2005).
- 891 72. Petitpierre, B. *et al.* Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders.
  892 Science 338, 1344–8 (2012).
- 893 73. O'Neill, B. C.*et al.* A new scenario framework for climate change research : the concept of
  894 shared socioeconomic pathways. *Clim. Change* 122, 387–400 (2014).
- Kc, S. & Lutz, W. Demographic scenarios by age, sex and education. *Popul. Environ.* 35, 243–260 (2014).
- 897 75. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–13 (2008).
- Rochlin, I., Ninivaggi, D. V, Hutchinson, M. L. & Farajollahi, A. Climate Change and
  Range Expansion of the Asian Tiger Mosquito (Aedes albopictus) in Northeastern USA:
  Implications for Public Health Practitioners. *PLoS One* 8, e60874 (2013).
- 902 77. Ogden, N. H., Milka, R., Caminade, C. & Gachon, P. Recent and projected future climatic
  903 suitability of North America for the Asian tiger mosquito Aedes albopictus. *Parasit.*904 *Vectors* 7, in press (2014).
- 905 78. Butterworth, M. K., Morin, C. W. & Comrie, A. C. An Analysis of the Potential Impact of
  906 Climate Change on Dengue Transmission in the Southeastern United States. *Environ.*907 *Health Perspect.* 125, 579–585 (2017).

#### 909 Figures











930 **Fig. 3:** Predicted future spread of *Aedes albopictus* in Europe. Panel a shows the expansion (red) and

931 contraction (blue) of Ae. albopictus between 2020 and 2050 under the medium climate scenario RCP6.0

- 932 with emissions peaking in 2080. Panel b shows the predicted distribution of Ae. albopictus. Panel b
- 933 shows the predicted suitability of presence of *Ae. albopictus* in 2050. Pixels with no predicted
- 934 suitability are coloured in grey.



935

936 Fig. 4: Predicted global geographic distribution of Ae. aegypti (a) and Ae. albopictus (c) in 2050 under the 937 medium climatic scenario RCP6.0 and uncertainty for Ae. aegypti (b) and Ae. albopictus (e). Predicted 938 suitability of Ae. *aegypti* quantile cutoff points were 0.24, 0.66, 0.88. Relative uncertainty was 939 computed as the ratio of the 95% uncertainty intervals and predicted *Ae. aegypti* suitability for each 940 pixel. Cutoff points for uncertainty were 0.08, 0.18, 0.31. The lowest quantile of predicted suitability 941 is shown in white, and the highest in dark pink. The lowest quantile for uncertainty is white and the 942 highest is blue. The colours overlap such that areas coloured purple have both high predicted 943 suitability of *Ae. aegypti* and high relative uncertainty. Pixels with no predicted suitability are 944 coloured in grey. Panel c show the corresponding results for Ae. albopictus. Predicted suitability of 945 Ae. *albopictus* quantile cutoff points were 0.13, 0.41, 0.70. Cutoff points for uncertainty for Ae. 946 *albopictus* were 0.16, 0.36, 0.53. The global population predicted to live in areas suitable for *Ae*. 947 *aegypti* (b) and *Ae. albopictus* (c) under the conservative (RCP4.5), medium (RCP6.0), and worst-948 case scenario (RCP8.5) using the binary cutoff values of suitability of 0.46 and 0.51 for both species 949 respectively.

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