

Original Contribution

Macroclimate Determines the Global Range Limit of *Aedes aegypti*

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Abstract: *Aedes aegypti* is the main vector of dengue and a number of other diseases worldwide. Because of the domestic nature of this mosquito, the relative importance of macroclimate in shaping its distribution has been a controversial issue. We have captured here the worldwide macroclimatic conditions occupied by *A. aegypti* in the last century. We assessed the ability of this information to predict the species' observed distribution using supra-continental spatially-uncorrelated data. We further projected the distribution of the colonized climates in the near future (2010–2039) under two climate-change scenarios. Our results indicate that the macroclimate is largely responsible for setting the maximum range limit of *A. aegypti* worldwide and that in the near future, relatively wide areas beyond this limit will receive macroclimates previously occupied by the species. By comparing our projections, with those from a previous model based strictly on species-climate relationships (i.e., excluding human influence), we also found support for the hypothesis that much of the species' range in temperate and subtropical regions is being sustained by artificial environments. Altogether, these findings suggest that, if the domestic environments commonly exploited by this species are available in the newly suitable areas, its distribution may expand considerably in the near future.

Keywords: *Aedes aegypti*, Climate change, Dengue, Global distribution, Urban disease-vectors

INTRODUCTION AND PURPOSE

Aedes aegypti (L.) is the principal vector of dengue, yellow fever, and a number of other arboviruses worldwide. Believed to be originally from West Africa, this mosquito has

been dispersed by human agency since the fifteenth century and, ever since, it has invaded many tropical, subtropical, and mild temperate regions of the planet (Lounibos 2010). Because water-scarcity and thermal extremes are known constraints to its establishment, concerns exist that ongoing and future climatic change may alter its distribution and those of associated diseases (Shope 1991; Hales et al. 2002; Kearney et al. 2009; Lozano-Fuentes et al. 2012).

Ambient temperatures, as well as other climatic parameters, influence the developmental times and survival of *A. aegypti* in all life-stages (Focks et al. 1993). For in-

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stance, long-term exposures to temperatures below 0°C or above 34°C are commonly fatal to larvae (Christophers 1960). Likewise, water availability is a requisite for egg hatching and larval development (Hopp and Foley 2001; Kearney et al. 2009). Suitable conditions for the establishment of *A. aegypti* are thus unquestionably related to climate, but, as this species is almost exclusively associated with urban micro-environments (Christophers 1960) researchers have been questioning the influence of macroclimate alone as a determinant of the species distribution (Reiter 2001; Jansen and Beebe 2010). This is because in urban areas *A. aegypti* can exploit artificial thermal shelters and human-mediated water supply, which may allow it to overcome otherwise unsuitable macroclimatic conditions (e.g., Kearney et al. 2009; Williams et al. 2010). In addition, human eradication efforts and competitive exclusion can also be responsible for range contractions of this species (e.g., Omeara et al. 1995; Vasconcelos et al. 1999). The interacting role of these human and biotic factors challenges our current understanding about the relative importance of macroclimate in shaping the geographical range of *A. aegypti* and, consequently, our ability to predict the impact of climate change on its future distribution.

Because of the medical importance of *A. aegypti*, a number of studies have previously attempted to predict its observed distribution or potential range shifts under future conditions (e.g., Hopp and Foley 2001; Beebe et al. 2009; Kearney et al. 2009). These predictions aimed to inform decision makers of new areas under risk of arboviral disease, thus allowing a timely adoption of preventive measures. Two approaches can be adopted to achieve the predictions: (1) physiologically-based models and (2) correlative-based models (Buckley et al. 2010; Kearney et al. 2010). The former is explicitly based on the key mechanisms by which environmental factors determine population viability. Correlative models, on the other hand, rely on the association between the species distribution, and a set of potentially important environmental factors to deduce the drivers of distribution. Because the two approaches have limitations, there is an increasing recognition that a better reliability can be achieved if predictions are derived from both types of models (Hijmans and Graham 2006; Buckley et al. 2010; Kearney et al. 2010).

Most previous studies explicitly attempting to predict the potential distribution of *A. aegypti*, were confined to regional scales (e.g., Beebe et al. 2009; Kearney et al. 2009). A notable exception was provided by Hopp and Foley (2001), which used known physiological relationships between

population dynamics and coarse climatic patterns to predict the species distribution and abundance at the global scale. However, up-to-date, global scale correlative models for *A. aegypti* remain absent. Accordingly, it is our aim to provide such an assessment here. We use alpha-shapes to delimit the worldwide climatic conditions occupied by *A. aegypti* based on its known distribution from 1901 to 2000—which closely depicts its maximum range limits. Distinctively from Hopp and Foley (2001), our model captures all macroclimatic conditions under which *A. aegypti* was able to establish (hereafter referred to as “macroclimatic envelope”). This will also include those macroclimates that the species was able to endure due to human activity. We then test if the captured macroclimates alone are able to predict the species’ observed range. In addition, we also assess how global climatic suitability for this mosquito may change in the near future (2010–2039) under two future climate scenarios. By using a distinct modeling approach, we expect that our results will complement previous insights from physiologically-based predictions concerning (1) the relative importance of macroclimate in shaping the global distribution of *A. aegypti* and (2) the impact of global climate change on its future distribution.

METHODS

Species Distribution Data

We compiled a dataset of worldwide occurrence records of *A. aegypti* from a large number of sources including the Global Biodiversity Information Facility, (GBIF; <http://www.gbif.org>), VectorMap (<http://www.vectormap.org/>), scientific papers, monographs, and gray literature (full list is available from the lead author upon request). We only retained occurrences referring to persisting populations recorded from 1901 to 2000. Population persistence was assessed either directly—i.e., from information contained in the source of the record—or deduced from other works describing the species’ regional distribution. Records for which long-term population stability could not be confirmed were ignored. All records consisting only of place names were translated into geographical coordinates using Google Earth.

We followed the previous protocol for compiling a second dataset describing the distribution of *A. aegypti* along the Americas. This dataset was used for validation purposes (see below) and contained the presence or ab-

sence (i.e., the nonexistence of occurrence records from 1901 to 2000) of *A. aegypti* in all of the Americas' country capitals and capitals of first-level administrative subdivisions of countries with an area greater than 500,000 km². We selected the Americas as validation region for 3 main theoretical and practical reasons: (1) it has a wide latitudinal range which enables projecting the model over a wide diversity of climatic combinations; (2) propagules of *A. aegypti* had likely been dispersed over most of its extent—considering its long invasion history and wide range in this region—and (3) there was an adequate information regarding the presence or absence of this mosquito for most targeted cities.

The worldwide occurrence dataset was composed by a total of 1,136 records. In order to match with the temporal resolution of our climatic data (see below), this information was divided into two sets: historical occurrences (1901–1949; $n = 377$) and current occurrences (1950–2000; $n = 759$). The locations in which the species was found in both time periods contributed one record for each set. When combined, the occurrence records collected provide a comprehensive representation of the maximum range of *A. aegypti* worldwide, as described by Christophers (1960) (Fig. 1 in Appendix A). The validation dataset was composed of 147 cities having the species occurrence and 100 cities where it was absent. A small number of cities were excluded ($n = 47$; $\approx 16\%$) because it was not possible to determine the presence or absence of the mosquito from the literature (Fig. 2 in Appendix A).

Climate Data

We used seven climatic variables to characterize global climates. These represented seasonal and extreme temperatures (mean temperature of the warmest quarter; mean temperature of the coldest quarter; maximum temperature of the warmest month; and minimum temperature of the coldest month) and water availability (annual precipitation; precipitation of the wettest quarter; and precipitation of the driest quarter). We extracted these data directly from Worldclim (Hijmans et al. 2005) for the period 1950–2000 at a 2.5 arc minutes resolution (ca. 4.6 km at the equator). This resolution agrees well with the spatial precision of our occurrence data since urban areas rarely exceeded such extent.

Climatic data at a comparable level of detail were not available for the period 1901–1949. To overcome this limitation we downscaled historical climate data using a

change-factor approach following Ramirez-Villegas and Jarvis (2010). Accordingly, we used the 0.5° resolution CRU TS 3.1 dataset (Harris et al. 2013) to calculate monthly averages of mean minimum temperature, mean maximum temperature, and monthly total precipitation from 1901 to 1949. As a climate baseline, we used the monthly averages (1950–2000) of minimum temperature, maximum temperature, and total precipitation available at the Worldclim database at a resolution of 2.5 arc minutes. Finally, we used the “biovars” function within package “dismo” for R to transform the downscaled monthly data into the seven variables representing global climates for the historical period.

We were also interested in projecting the distribution of *A. aegypti* under future climatic conditions. Accordingly, we collected mean global projections of the seven climatic variables described above for the period 2010–2039. These variables were downloaded from the CCAFS-CGIAR database (Ramirez-Villegas and Jarvis 2010) for two distinct greenhouse gas emissions scenarios: A2a and B2a. The A2a scenario projects medium to high emissions of greenhouse gases resulting from a highly heterogeneous future world having a continuously increasing global population, uneven economic growth, and the usage of fossil fuels primarily determined by regional availability. The B2a scenario projects low to medium emissions, resulting from a future world that is also heterogeneous, but one which has increased environmental and social sustainability and a slower rate of population growth than in A2a. In order to account for variability among future climate projections, each variable corresponded to the average of the predictions of four distinct General Circulation Models (GCMs) used in the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report: CCCma-CGCM2, CSIRO-MK2, NIES99, and UKMO-HadCM3.

Modeling of the Macroclimatic Niche

In recent years, several techniques have been applied for delimiting occupied climates based on species distribution data (see Jeschke and Strayer 2008, for a review). In this study we use alpha-shapes (Edelsbrunner et al. 1983; Edelsbrunner and Mücke 1994), a method that has been successfully applied for boundary delimitation problems (e.g., Albou et al. 2009). Alpha-shapes are a generalization of the convex hull. They correspond to a geometric object (not necessarily convex) that represents the broad “shape” of a set of points. The level of adjustment of this geometric

object to the individual points is controlled by the parameter alpha (α). This parameter can range from 0 to infinity and as it increases, the alpha-shape will increasingly approach the convex hull of that set of points. However, as α reduces, the alpha-shape shrinks through the development of cavities which may join forming holes in the shape. We selected this method because of two main reasons. First, alpha-shapes do not rely on absence-records. Because the absence of mosquitoes can be caused by factors other than climate (see “Introduction”), the use of such data could originate underestimated projections of its macroclimatic envelope (Jiménez-Valverde et al. 2011). Second, unlike most methods that use only occurrence data, alpha-shapes make no *a priori* assumption about the shape of the species’ climatic niche. In the Appendix B, we provide a detailed description of the advantages and limitations of this method.

We applied alpha-shapes to delimit the macroclimatic envelope of *A. aegypti* in a three-dimensional space. For that purpose we used a Principal Components Analysis (PCA) to reduce the dimensionality of the climatic variables. Because we were interested in combining both current and historical occurrences into the same three-dimensional space, we reduced the dimensionality of each climatic set using the mean correlation matrix of the two sets. For each set, we retained the three main components which, in both cases, explained $\approx 96\%$ of the total variation of the mean climatic conditions (Appendix C). Next, for each climatic period, we projected these components into the geographic space. We overlaid the corresponding set of species occurrences and extracted the climatic conditions occupied by each record. Finally, we projected all occurrences into a three-dimensional space and delimited the macroclimatic envelope of *A. aegypti* using the R package “alphashape3d.” To select the value of α , we calculated multiple alpha-shapes each resulting from an increment of this parameter at steps of 0.05. From these, we then selected the one resulting from the smallest value of α encompassing all species occurrences without forming holes or voids (Fig. 3 in Appendix A). This criterion is appropriate for the purpose of species’ climate envelope delimitation because it diminishes the chance of overestimating encompassed macroclimates—since the alpha-shape is tightly adjusted to the conditions occupied by the species—while all inner conditions are maintained, which is an ecologically realistic assumption (Webber et al. 2012; Guisan et al. 2012).

We used the delimited alpha-shape to project the macroclimatic envelope of *A. aegypti* into the geographic

space. For that purpose, we initially projected all existing climatic combinations from 1901 to 2000 into the three-dimensional space of the alpha-shape (i.e., macroclimatic envelope). Any area having a climatic combination falling inside the alpha-shape was classified as within the species’ macroclimatic envelope; all other areas were classified as outside. We also performed this classification for each future climatic scenario (A2a and B2b) after reducing the dimensionality of each set through a PCA. A necessary assumption of this, or any other correlative model predicting for new time periods, is that the correlation structure among variables is maintained (Jiménez-Valverde et al. 2011).

An issue of fundamental importance when predicting the suitability of climatic conditions for new time periods is the potential presence of non-analog climates—i.e., climatic combinations that do not occur in the datasets used for model calibration (Fitzpatrick and Hargrove 2009). Species distribution data alone provides no information on how a species will respond to new climatic combinations and, thus, correlative predictions should be avoided for non-analog climates (Fitzpatrick and Hargrove 2009; Capinha et al. 2012). Moreover, because of the geometric nature of alpha-shapes, the new climatic combinations are likely to fall outside the species niche. This happens because these conditions are not found in the sampled data and not necessarily because they are unsuitable to the species. To overcome this difficulty, we spatially delimited all areas where future climates have no analogs in our current or historical climate sets. This was made also using an alpha-shape based on the full array of current and historical climatic conditions.

Evaluation of Predictive Ability

In order to avoid pervasive effects of spatial autocorrelation, species distribution models should be evaluated with data spatially independent from the calibration dataset (Araújo et al. 2005). Accordingly, we evaluated how well our model predicted the distribution of *A. aegypti* in the Americas based on the macroclimates the species occupied on the rest of the world. For that purpose, we built the smallest alpha-shape without holes or voids based on current and historical occurrences of *A. aegypti* outside the Americas. We then classified each historical or current climatic combination of the Americas as “inside” or “outside” the species envelope. We also removed from the analysis any climatic combination found only in the vali-

dition region. We compared the predictions against our validation set containing information about the presence or absence of *A. aegypti* in American country capitals and capitals of first-level administrative subdivisions. Finally, we measured the ability of the model in correctly predicting the species' presence and absence using the true skill statistic (TSS; Allouche et al. 2006). TSS ranges from -1 to 1 and values >0.6 indicate good predictive accuracy, $0.2-0.6$ fair to moderate, and <0.2 poor (Jones et al. 2010).

RESULTS

Model Performance

We evaluated the performance of our predictive approach using 221 spatially-uncorrelated records of the species presence ($n = 133$) and absence ($n = 88$) in American cities (26 cities of the original dataset overlaid non-analog climates and were excluded) (Fig. 2 in Appendix A). When compared against these data, our model showed a marginally good predictive ability (TSS = 0.61).

Current Climatic Space and Predicted Changes Under Future Climates

Overall, the projected macroclimates encompassed by *A. aegypti* agree well with its observed distribution during the last century (Figs. 1a, 2 in Appendix A). The climatic conditions found at latitudes higher than $\approx 45^\circ\text{N}$ or $\approx 35^\circ\text{S}$ remained almost unanimously unoccupied by the species. Below these extremes, the species encompassed mainly climatic combinations typical of tropical areas, but also some warm temperate climates such as those found in South-west and South-east United States, Uruguay, North-east Argentina, the Mediterranean basin, Northern India, East China, and East Australia. The inclusion of some semi-arid to arid macroclimates within the species envelope is also noticeable. These have their geographic correspondence mainly in Australia and the Somali Peninsula, as well as in the coastal areas of the Arabian Peninsula and Pakistan. Nonetheless, the majority of hot arid climates remained unoccupied (e.g., the Sahara, Arabian, Kalahari and Thar deserts, and inner Australia), as well as the climates found in areas at higher altitudes (e.g., in the mountain ranges of México, Central and South America, South Africa, or New Guinea).

Regardless of the future climate scenario, for the period 2010–2039, the species macroclimatic envelope will also

encompass relatively wide new areas (Fig. 1bc). In the Northern Hemisphere, these areas are largely concentrated in the European and North-central and North-eastern United States regions between $\approx 36^\circ\text{N}$ and $\approx 48^\circ\text{N}$ (Figs. 1b, c, 2a, b) while in the Southern Hemisphere these are, overall, predicted to emerge between $\approx 12^\circ\text{S}$ and $\approx 36^\circ\text{S}$ encompassing wide regions in the west of Southern Africa and Central Australia. The high variability regarding the altitude at which these new areas will emerge is also noticeable (Fig. 2a, b). Although some differences can be found between the two climatic scenarios, most of the new areas at high altitude ($\geq 1,000$ m) are predicted to occur between $\approx 21^\circ\text{S}$ to $\approx 9^\circ\text{S}$, $\approx 6^\circ\text{N}$ to $\approx 9^\circ\text{N}$ and at $\approx 33^\circ\text{N}$. On the other hand, at latitudinal extremes these are predicted exclusively for low altitudes.

Wide extents currently encompassed by the species macroclimate envelope are also predicted to receive non-analog climates in the nearby future (Fig. 1b, c). These areas are mainly expected for the north of South America, the Indian Peninsula, Indonesia, and the North-west of the Gulf of Mexico. Finally, relatively broad areas encompassed by the species macroclimatic envelope are also expected to receive non-currently occupied macroclimates. These areas are predicted to be mainly located in the range margins of hot arid regions such as the Sahara, Arabian or Thar deserts, as well as in the contiguity of most areas receiving novel climatic conditions.

DISCUSSION

The model we used in this study captured the worldwide macroclimatic conditions under which *A. aegypti* established persisting populations during the twentieth Century. The projection of these conditions into the geographical space shows a relatively close agreement with the maximum range limit known for the species. Moreover, we also verified a marginally good predictive ability of our model in predicting the species' American distribution based solely on the macroclimates occupied elsewhere. These results suggest that macroclimate is indeed an important range determinant and should be considered when attempting to predict the broad range boundaries of *A. aegypti*.

It is not unexpected that macroclimate variables alone are informative in predicting the long-term distribution of this mosquito at the global scale. Human factors can undoubtedly assist *A. aegypti* in circumventing macroclimatic adversities, however, given the long invasion history

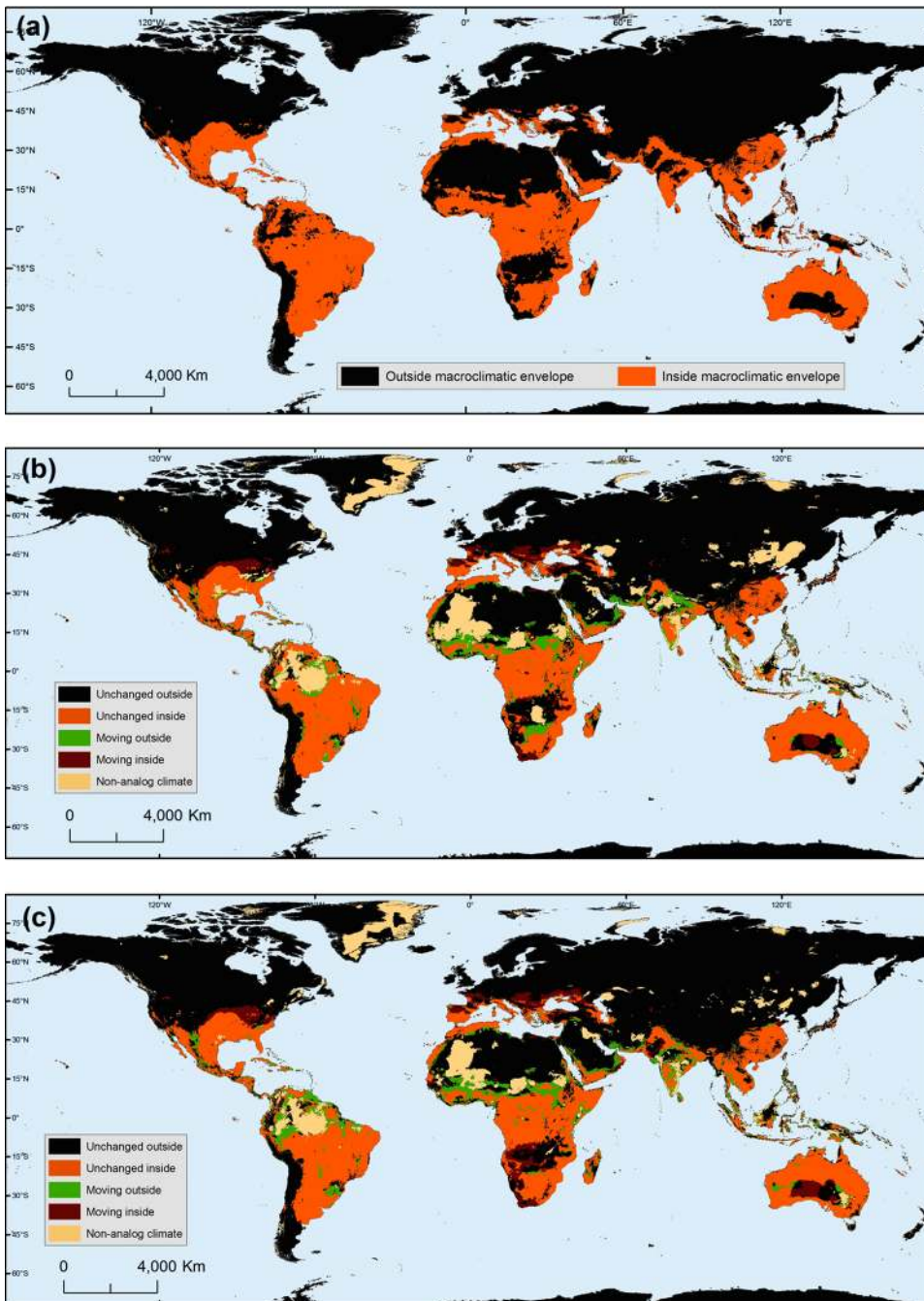


Figure 1. Worldwide projection of areas falling inside or outside the macroclimatic envelope of *Aedes aegypti*. Projections were made for the climatic conditions of **a** the previous century and for nearby future conditions (2010–2039) under, **b** the B2a and **c** the A2a climate-change scenarios

of the species worldwide (ca. 500 years; Lounibos 2010), it is plausible to expect that the spatial expression of this assistance is already fully realized. In other words, beyond its observed maximum range, artificial environments are not sufficient for the species to overcome unsuitable macroclimates. In support of this interpretation is the relatively stable altitudinal and latitudinal maximums of the species during the last century (Christophers 1960; Wertheim et al. 2012), regardless of the availability of man-made habitats

and the supply of propagules above those limits (e.g., in Central Mexico Mountains; Lozano-Fuentes et al. 2012) while, on the other hand, large-scale distributional fluctuations below these maximums were very common (Soper 1967; Wertheim et al. 2012).

The facilitating role of humans appears, nonetheless, to be essential for the species to realize its maximum geographical range. The model of Hopp and Foley (2001), which was strictly based on the physiological response of

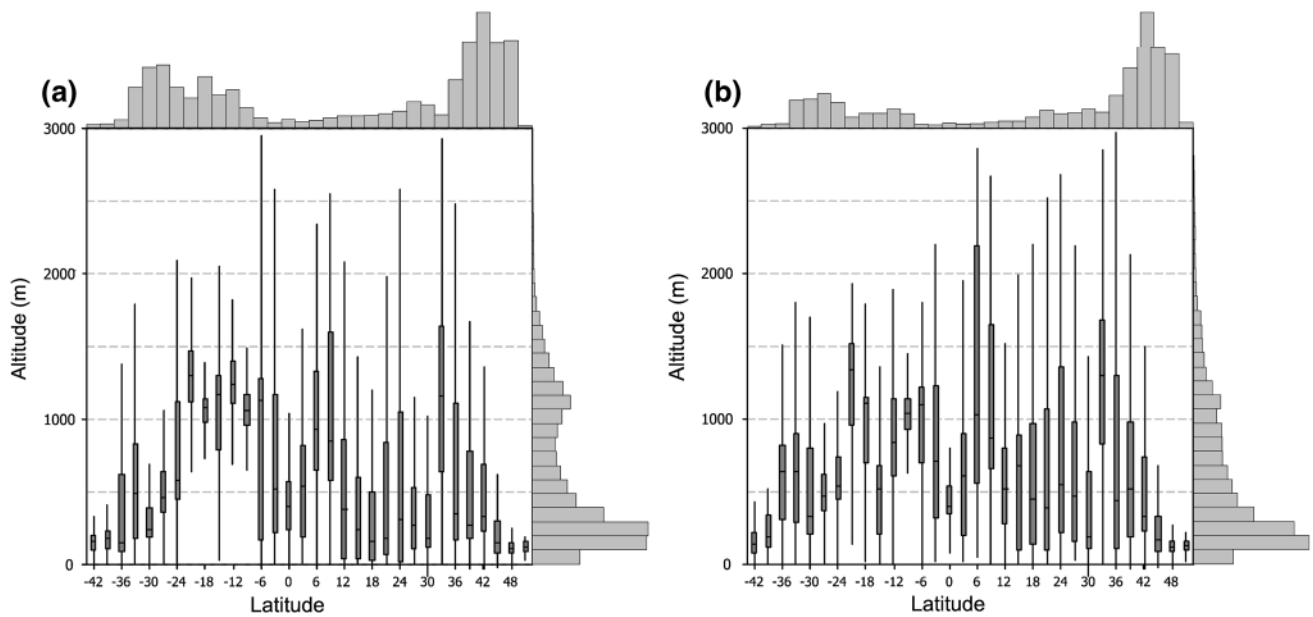


Figure 2. Latitudinal and elevational characterisation of the new areas predicted to receive macroclimatic conditions occupied by *Aedes aegypti* under **a** the B2a and **b** the A2a climate-change scenarios

A. aegypti to macroclimates, predicted an appreciably narrower range of suitable climates than what was predicted by our occurrence-based approach—in which the potential role of artificial environments is included. Most omissions refer to temperate and arid climates, namely those found in North-western Mexico, the Mediterranean basin, most of South Africa and Botswana, coastal areas of the Arabian Peninsula, and non-tropical Australia. While some of these discrepancies can be due to the temporal mismatch of the climate data used for the projections—1901–2000 in our approach and during 1931–1997 (but varying among variables) in the model of Hopp and Foley (2001)—it is likely that they also reflect the role of human activity on the ability of this mosquito to overcome unsuitable macroclimates. If this is the case, it suggests that the persistence of most mosquito populations close to maximum range limits may be entirely dependent on artificial conditions, such as human-mediated water supply or shelter from thermal extremes. A congruent explanation was recently supplied for the disappearance of *A. aegypti* from Southern Australia, where changes in human water-storage practices appear to have driven the large-scale extinction (Williams et al. 2010). Accordingly, and despite further studies evaluating the spatial expression of the prevailing role of man-made environments over macroclimate are clearly necessary, our results seem supportive of Williams et al. (2010) assertion that the natural extinction

of *A. aegypti* may be attainable in subtropical and temperate regions. For that purpose, vector control efforts should focus on the identification and posterior elimination of the artificial environments allowing *A. aegypti* to overcome its macroclimatic vulnerabilities.

Our results also show that climate change may indeed promote relevant modifications on the species' global distribution. Particularly important is the finding that, over the next decades, wide areas beyond the species' maximum range will present potentially suitable macroclimates. The colonization of these areas will still depend on the ability of *A. aegypti* to reach them, on the absence of competitive exclusion and, eventually, on the availability of favorable artificial environments. The latter factor may be even crucial because most of these peripheral areas will have new macroclimates that are only endured by *A. aegypti* because of human assistance (e.g., the water-storage practices in Southern Australia; Williams et al. 2010; see above). Thus, the species capacity to colonize this sort of climates in new areas will also depend on the availability of human aid. Nonetheless, in the absence of preventive vector control measures, poleward and upward range shifts of *A. aegypti* seem likely to occur in the nearby future—and may even already be noticeable (e.g., Lozano-Fuentes et al. 2012). Conversely, some areas are also predicted to receive macroclimates that were not occupied during the twentieth century. Although suggestive of the inability of the species to maintain populations in these regions, this result

should, however, be interpreted with caution. Many of these areas have emerged in the contiguity of non-analog climates. This indicates that despite existing between 1901 and 2000, most of these unoccupied macroclimates were “uncommon”—i.e., located at the edges of the existing climatic combinations. Consequently, the absence of the species under these macroclimates may have been solely driven by this uncommonness. A large uncertainty also surrounds the response of *A. aegypti* to non-analog climates. In the nearby future, novel climatic combinations are expected for relatively wide extents of the species range. Because these conditions cause correlative approaches to extrapolate, we greatly encourage the future assessment of their impacts using other approaches.

CONCLUSION

Although multiple factors interact to shape the distribution of *A. aegypti*, our results show that macroclimate is responsible for the delimitation of its long-term range limits at the global scale. In addition, we also found support to the hypothesis that much of the species range between tropical regions and these limits is maintained by man-made environments. These findings are important for predicting future range changes of this disease-vector. Our forecasts identified that, in the forthcoming decades, a particularly relevant poleward displacement of macroclimatic barriers will take place in Europe, the United States, Southern Africa, and Central Australia. The release from macroclimatic constraints in these areas will clearly increase their vulnerability to colonisation by *A. aegypti* as it will, thereafter, depend mainly on the species being introduced and on the availability of favourable domestic environments. In conclusion, our results support the view that macroclimate is of major importance in determining the long-term global distribution of *A. aegypti* and that climate change will likely promote profound modifications on its future range limits. While, we show that correlative models may be able to anticipate some of these modifications, we encourage further investigations based on distinct modelling approaches and application over a wider array of future climate conditions.

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