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The dengue vector *Aedes aegypti*: what comes next

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Abstract

Aedes aegypti is the urban vector of dengue viruses worldwide. While climate influences the geographical distribution of this mosquito species, other factors also determine the suitability of the physical environment. Importantly, the close association of *A. aegypti* with humans and the domestic environment allows this species to persist in regions that may otherwise be unsuitable based on climatic factors alone. We highlight the need to incorporate the impact of the urban environment in attempts to model the potential distribution of *A. aegypti* and we briefly discuss the potential for future technology to aid management and control of this widespread vector species.

Keywords: Aedes aegypti; Dengue; Climate change; Distribution

1. Introduction

Aedes (*Stegomyia*) *aegypti* (Linneaus) is the major urban vector of dengue viruses worldwide. Over the last 25 years, there has been a global increase in both the distribution of *A. aegypti* and epidemic dengue virus activity [1]. The emergence and re-emergence of epidemic dengue activity has prompted much debate regarding the potential role of climate and climatic changes in the changing epidemiology of the disease. Likewise, the role of climate (average weather pattern in a locality or region over time) and weather (local daily events in the atmosphere) in determining the potential future geographical distribution of *A. aegytpi* is a highly topical subject. However, the domestic nature of this species probably exerts more influence on its distribution than either climate or climatic variables. Although *A. aegypti* is considered a tropical mosquito [2] and its distribution does appear to be influenced by climate in some temperate regions of the world, contemporary and historical records document persistence outside these regions.

A. aegypti is closely associated with human habitation and readily enters buildings to feed and to rest [2]. Adult females preferentially feed on humans: other vertebrate species constitute only a small proportion of their bloodmeals [3,4]. Unlike many other mosquito species, *A. aegypti* is a day-biting mosquito, and often feeds on multiple hosts during a single gonotrophic cycle. Females preferentially lay eggs in man-made or artificial containers including water tanks, flower vases, pot plant bases, discarded tyres, buckets or other containers typically found around or inside the home [2]. Eggs are laid on or near the water surface in containers and, once embryonated, can withstand desiccation for up to one year [5].

Juliano and Lounibos [6] determined that the occupancy of human-dominated habitats is significantly associated with the invasive status of a mosquito species. This association is certainly evident for *A. aegypti* which readily exploits the domestic environment, and which is still establishing in new regions, despite adult *A. aegypti* mosquitoes demonstrating very limited dispersal capability [7,8]. Indeed, the peri-domestic behaviour of *A. aegypti* and its desiccation-resistant eggs afford this species an alternative mode of long-distance

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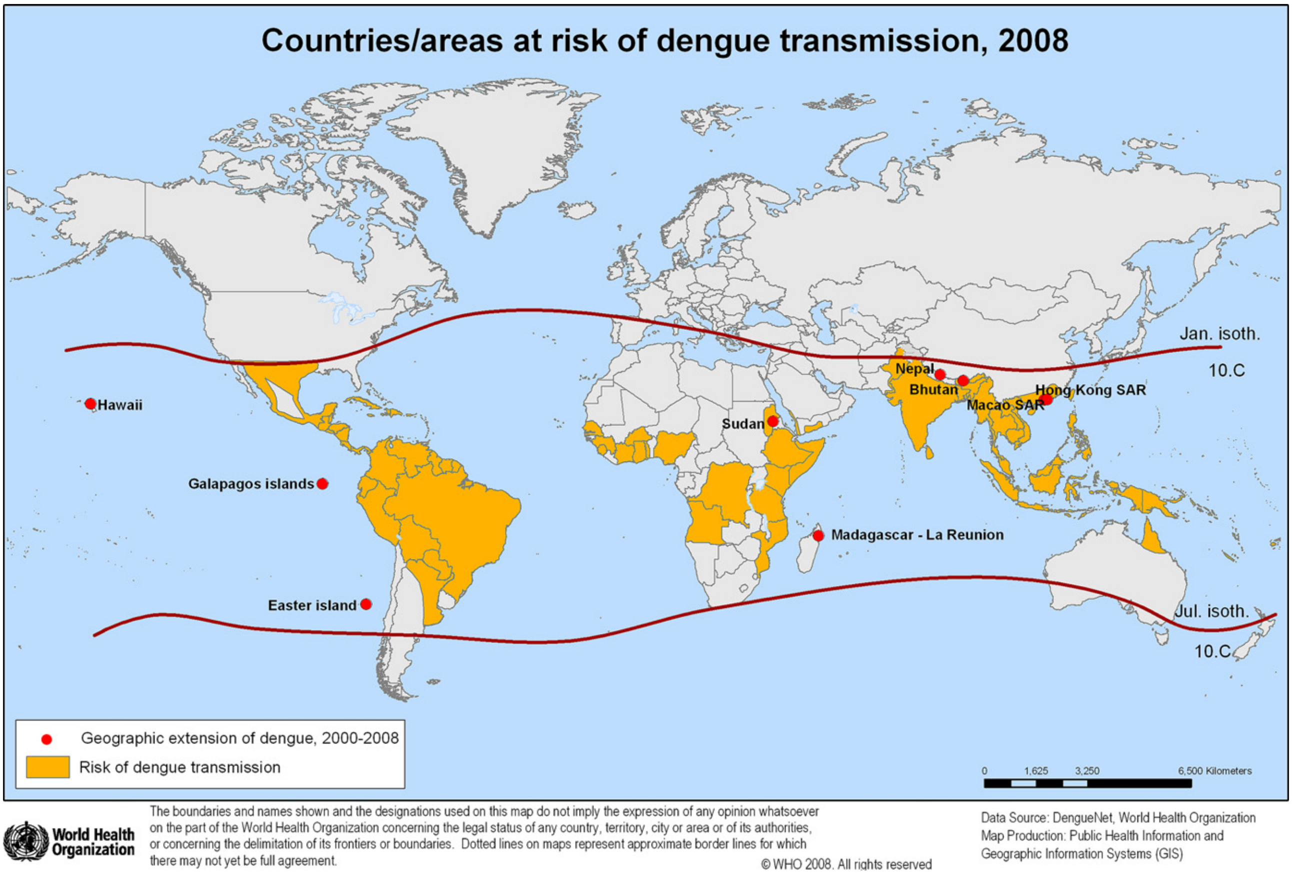
dispersal via human-mediated transportation within and between continents.

While the distribution of *A. aegypti* is dependent on climate to some extent, critical scrutiny must be applied to the oversimplified assumption that climate change will independently lead to an increased range for this species and a concomitant expansion of the risk of dengue infections around the world. Rather, as demonstrated below, a range of dynamic factors must be considered when predicting future global distribution trends. We show that several modelling attempts fail to adequately address the implications of a domestic lifestyle on the distribution of this species. However, constraining the focus of models to a local and/or regional scale rather than aspiring for global models may increase their predictive capacity. In light of climate change, the major drivers of future dengue will likely include – unprecedented population growth, particularly in urban areas of the tropics; an increase in the movement of both vectors and viruses reservoir via modern transport; and a lack of effective mosquito management [1]. Despite the ability of *A. aegypti* to persist in a range of urban localities and facilitate dengue epidemics in many countries, population suppression or even eradication of this species is possible – albeit that it requires both coordinated efforts and a sustained commitment to vector management [9,10].

2. Global distribution of *A. aegypti*

Historically, *A. aegypti* has been able to establish in regions between the northern January and southern July 10 °C isotherms [2] (Fig. 1). Originating in Africa, *A. aegypti* probably invaded other continents via trading and transport ships that resupplied in African ports during the fifteenth through seventeenth centuries [2,11]. These ships carried freshwater reservoirs on board and could maintain breeding colonies of *A. aegypti* [2], and it is probable that *A. aegypti* was introduced into the rest of the world on a number of occasions via this means [12].

Given the occurrence of concurrent outbreaks of dengue in Asia, Africa and North America in the late 1700s, it is probable that dengue vectors (predominantly *A. aegypti*, although there are others) have had a wide a distribution throughout the world's tropics for the last two centuries [13]. However, the introduction of *A. aegypti* into Asia appears relatively recent, as endemic dengue fever in urban areas was not recorded in this region until the late nineteenth century [14], and low genetic diversity across tropical Asian populations suggests recent dispersal [12]. South-east Asia experienced much epidemic dengue activity following 1945 [15] and *A. aegypti* is currently widespread in Asia [16].



The boundaries and names shown and the designations used on this map do not imply the expression of any opinion whatsoever on the part of the World Health Organization concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. Dotted lines on maps represent approximate border lines for which there may not yet be full agreement.

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Data Source: DengueNet, World Health Organization
Map Production: Public Health Information and Geographic Information Systems (GIS)

Fig. 1. Current global dengue transmission risk map (yellow) also showing the hypothetical 10 °C global winter isotherm distribution limits of *A. aegypti* proposed originally by Christophers in 1960 [2]. Map courtesy of WHO [24].

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In the Americas, large and coordinated yellow fever eradication efforts initiated by the Pan American Health Organisation (PAHO) in the 1950s and 1960s saw a marked decline in *A. aegypti* populations in that part of the world and the subsequent successful eradication of the species in much of Central and South America by the 1970s [17]. However, a reduction in control efforts in the early 1970s saw the reinfestation of *A. aegypti* in most regions of both north and south America, followed by subsequent epidemics of dengue and the emergence of dengue hemorrhagic fever in some areas [18].

Although *A. aegypti* was common in the Mediterranean region prior to World War II [19], it also disappeared from southern Europe and North Africa following this period. The reason for this is unclear, although it is probably attributable to malaria eradication efforts and widespread use of DDT [16].

While *A. aegypti* currently has a wide distribution in most tropical and subtropical areas, the present distribution does not reflect the maximum range of its potential distribution as defined by historical records. This is particularly evident in parts of Europe, in North America and in Australia where the species has previously displayed a much larger geographical distribution [19]. Overall, the geographical distribution of *A. aegypti* is not static, and appears to have undergone significant changes in a number of continents over time.

3. Climate distribution and abundance

Climatic factors alone do not determine the geographical distribution of *A. aegypti*, principally because the close association of *A. aegypti* with domestic environments affords this species microenvironments which are highly moderated by human behaviour and this in turn gives the mosquito the ability to avoid the effects of transient weather to some measure. For example, its use of manually filled water receptacles obviates the mosquitoes' reliance on rainfall to flood suitable oviposition sites, and the tendency for adults to rest indoors provides shelter and protection from external environmental conditions.

While ostensibly a tropical mosquito, *A. aegypti* is remarkable in its ability to accommodate adverse environmental conditions. At one temperature extreme, laboratory experiments show that *A. aegypti* larvae perish when the water temperature exceeds 34 °C while adults start to die as the air temperature exceeds 40 °C [2]. Yet observations from the field reveal *A. aegypti* existing and transmitting dengue in India's Thar desert townships in north-western Rajasthan, where the mosquito avoids very hot ambient temperatures – often rising above 40 °C in summer – by exploiting household pitchers and underground cement water tanks [20]. Conversely, while larvae can be susceptible to extreme conditions such as freezing in laboratory experiments [21], observations from the field have recorded viable *A. aegypti* larvae in ice-encrusted water [2,22]. Additionally, populations of *A. aegypti* have historically persisted in Memphis (USA) where minimum winter temperatures commonly fall below 0 °C [16], and in Australia, historical collections have revealed the mosquitoes' existence in towns with winter mean temperatures of 5–6 °C [23] – well below the hypothetical 10 °C winter isotherm limit displayed in Fig. 1 [2,24].

So while temperature does influence larval development time and survival rate [2,25,26], temperature alone is generally not a useful predictor for larval abundance [27]. In Australia, the current geographical range of *A. aegytpi* is not predicated by climate, and an increase in mean temperatures on the east coast of the continent over the past 60 years has not been accompanied by an apparent southward increase of this vector's distribution [28]. Indeed, the distribution of *A. aegypti* in Australia has retreated to Queensland since the mid-1900s, despite historical distributions that reached at least as far south as Culcairn in New South Wales (36°S; [29]).

In some regions, rainfall is positively correlated with larval abundance, especially where rain-filled containers appear to be the primary larval sites [27]. While *A. aegypti* larvae require water for survival, they readily utilise human-filled containers and thus are not totally dependent on rainfall to flood their container habitats. For example, in one north-eastern city of Brazil, Pontes et al. [30] found *A. aegypti* abundance (indicated using the House Index) to be independent of rainfall. Rather, high vector abundance was correlated with increased household storage of water during a period of local drought and a simultaneous reduction of vector control activities. In summary, the association between rainfall and *A. aegypti* abundance will almost certainly vary between localities due to both the range of container types that are available as larval habitats and differences in the water storage practices of the local population.

And while temperature, humidity and rainfall have overt impacts on mosquito survival and ecology, other climatic factors such as photoperiod and wind velocity may also be influential. Importantly, it is necessary to consider that these meteorological conditions have a combined effect on the survival and development of mosquitoes and that it is difficult to examine the potential impact of these factors independently as a consequence. Also, general climatic observations may not reflect the local microclimate experienced by individual mosquitoes throughout their life stages.

4. Other factors driving geographical distribution

In most cases, it appears that the highly domestic nature of *A. aegypti* means that humans, rather than climate, drive the distribution of this species. While local weather may explain the abundance of *A. aegypti* in a particular location at a given time, other factors may be more predictive for the presence of this species. Particular features that have been observed as associated with *A. aegypti*'s presence include urbanisation, socioeconomic factors, building design and construction features, the quality of water supply and management, and the quality of other public health infrastructure services [16,31]

Increases in the size and population density of major cities place increasing demands on infrastructure and essential services, particularly in developing countries. The response to these demands may dramatically alter the suitability of

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a locality for urban mosquito breeding. An absence or irregularity of water supply will lead to an increase in domestic water storage practices which, in turn, will alter the landscape of potential *A. aegypti* habitat – perhaps providing a far more regular or numerous supply of larval sites. For example, the potential increased risk of dengue re-emerging in Australia is attributable to human adaptation to the current and projected climate change scenarios which suggest the drying of southern Australia, rather than directly to changes in the climate [23]. Indeed, it is the widespread installation of government subsidised rainwater tanks intended to drought-proof urban areas that may facilitate the re-appearance of *A. aegypti* in these regions.

The degree of public health infrastructure in a community can also influence the abundance of *A. aegypti*. For example, poor sanitation standards which result in the accumulation of debris and other material that collect rainwater can facilitate major expansion of this mosquito's populations [31]. Conversely, *A. aegypti* can be very sensitive to well-implemented control initiatives. As demonstrated by the widespread PAHO mosquito control effort in the Americas, effective *A. aegypti* population suppression and/or eradication is possible, although maintenance of this control requires a long-term commitment to urban vector management to prevent recolonisation. Thus, governments with a robust public health strategy may be better equipped to manage *A. aegypti* populations and provide sustained vector control.

Biological interactions between species occupying similar niches may also influence the distribution and abundance of *A. aegypti*. For example, marked declines in both the abundance and range of *A. aegypti* have been observed in association with the invasion and geographic range expansion of the Asian tiger mosquito, *A. albopictus*, particularly in some south-eastern regions of the United States [32–34]. Whilst a number of underlying processes including interspecific larval resource competition have been suggested to explain this observed trend [6,35], it is most likely that multiple factors determine the current distributions of each species. Examples of these interconnected factors include the potentially asymmetrical effects of abiotic factors (including climate) on different life cycle stages, apparent competition induced by parasites, mating interference and variation between the microclimates in given locations [6,35].

5. Climate, *A. aegypti* and dengue

As outbreaks of urban dengue are governed largely by the simultaneous availability of the virus and containers for *A. aegypti* oviposition and larval development, climatic variables may play a less critical role in dengue transmission than is the case with other arboviruses [36]. The distribution of urban dengue is limited by the distribution of *A. aegypti*, but the presence of the vector alone does not assure dengue transmission, even if it is imported to a non-endemic region [16]. Rather, the pattern of dengue transmission depends on the interaction of numerous transmission parameters including virus multiplication dynamics, the ecology and behaviour of its vectors, and the ecology, behaviour and immunity of its human hosts. Importantly, however, climate and weather may influence a number of these parameters (for more detail see [31]).

First, the period of time before a mosquito is able to transmit virus following an infectious bloodmeal (extrinsic incubation period; EIP) is often temperature-dependant. Indeed, the EIP of dengue virus in *A. aegypti* decreases with increasing temperature [37,38]. Conversely, lower ambient temperatures may lengthen the EIP, which may in turn decrease dengue transmission as fewer mosquitoes live long enough to transmit the virus.

In addition to influencing the duration of the EIP in the mosquito, climatic factors may also influence its capacity to transmit virus due to resultant changes in mosquito abundance and survival. Low humidity can negatively affect adult survival [2] and may decrease the proportion of the vector population that survive the EIP and thus becomes infectious by bite.

Finally, of course, humans also respond to meteorological conditions. Thus, climate and weather may induce behavioural changes in humans which in turn influence the transmission dynamics of arboviral disease. As the larval habitat of *A. aegypti* is largely comprised of artificial containers, domestic water storage practices can directly influence the availability of larval rearing sites. For example, increased urban water hoarding in response to drought or decreased rainfall can increase the number of productive larval sites if provisions are not made to eliminate this risk – and thus too little rain may lead to elevated *A. aegypti* densities.

In this way, human behaviour in response to climatic variables can determine the extent to which individuals are exposed to the bite of mosquitoes – as can accompanying economic factors. For example, the installation of air conditioning systems in conjunction with closed and/or screened windows reduces exposure to adult *A. aegypti*, which readily feed and rest indoors – but the adoption of these protective measures can be driven more by economic than climatic factors. In a study which compared serological survey results between the two adjoining cities of Nuevo Laredo, Tamaulipas (Mexico) and Laredo, Texas (USA), Reiter et al. [39] found that the incidence of dengue cases was higher in Nuevo Laredo, despite a higher abundance of *A. aegypti* across the border in Laredo. The authors attributed the lower incidence of dengue in Laredo primarily to characteristics of the houses including the presence of air conditioning and screens on windows, in addition to a lifestyle spent mainly inside sealed buildings. These housing and lifestyle characteristics are not popular in Nuevo Laredo, where income is much lower. Thus, the authors suggest that the higher prevalence of dengue in Mexico is chiefly due to economic rather than climatic factors.

Overall, when considering the effect of climate on the transmission dynamics of mosquito-borne pathogens, it is necessary to acknowledge the enormous complexity of the vector–pathogen–host system. Fundamental climatic variables such as temperature, rainfall and humidity cannot be considered independently as these factors usually provide

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a cumulative influence upon disease transmission. Furthermore, short-term patterns of local weather, which may be most important for dengue transmission, can be overlooked if analysis is limited to the consideration of climate trends in terms of longer term means and averages.

6. What about climate change?

While evidence continues to grow that future climates will be affected by human-induced change [40], there is still great uncertainty surrounding exactly what will happen in relation to regional climates and weather and how this will play on each landscape as more energy accumulates in the system due to global warming.

6.1. Global scale models

In attempting to better understand and even forecast the potential distribution of *A. aegypti* and the associated risk of dengue transmission today and under future climate change scenarios, global models have produced mixed results [41–43]. Below, we give three examples – which vary in their complexity – of attempts to develop global models of potential dengue activity. Importantly, these global models often do not resolve or consider patterns of historical dengue activity [29].

The first of these global models involves the relatively complex vectorial capacity and mosquito life-table models of Jetten and Focks [41] and was used to project potential changes in dengue transmission under current and future climate warming scenarios. The authors modified the typical vectorial capacity equation to develop an equation that describes a critical density threshold – an estimate of the number of adult female vectors required to maintain the virus in a human population. The critical parameter of temperature was used to make projections for 2 °C and 4 °C increases in the current climate. Temperature alone was used because it influences adult survival, the lengths of time between obtaining a bloodmeal to developing an egg batch, the EIP of the virus in the vector, and the vector's size – a factor that also indirectly influences the biting rate. The model described the current dengue activity with an associated increase in transmission and a possible expansion of potential dengue activity through latitude and altitude under warming temperatures. However while this model was validated using current patterns of dengue activity, it acknowledges that it was limited by not taking account of historical dengue activity in some regions that are now dengue-free.

A second global model [42] is based on CIMSiM, a mosquito life-table model that incorporates elements of stochasticity, such as daily meteorological data with its inherent variations and the daily changeability of larval food delivery – which in this case was not limiting. Again, results agreed with current observed global distributions of *A. aegypti* with an increased latitudinal distribution in the warmer summer months. Acknowledged issues with this model included the very coarse resolution of 1° (~100 km grid), its lack of focus on local weather, and a failure to incorporate human-mediated environmental modifications.

Finally, a third attempt [43] estimated potential dengue activity using vapour pressure and dengue distribution records between 1975 and 1996 as its basis. This measure of humidity was found to be the most important individual predictor of dengue activity and a correlation between humidity and current global dengue activity was presented in this work, while projected warming through climate change scenarios again suggested a potential latitudinal expansion beyond present dengue activity. Authors limited their dengue activity input data to exclude past dengue activity in some regions including south-east Australia, and this resulted in projections that could not accurately incorporate past dengue activity.

Any model of dengue risk is implicitly modelling the potential distribution of the vector *A. aegypti*. As discussed earlier, the historical distribution of this vector can be mostly captured within a global winter isotherm of 10 °C (Fig. 1) that was first described by Christophers in 1960 [2] and is still used today by the World Health Organisation to describe the species' potential geographic limits [24]. It is interesting that the projections described above do not account for historical dengue activity in places like Australia where, in first half of the 20th century, dengue epidemics in southern Queensland swept south into New South Wales reaching a town at 35° latitude [29,44] – well beyond the limits projected by these models. Indeed, some of these epidemics only stopped their southern movement as winter encroached [45].

Environment can modify local microclimates in ways that cannot be extrapolated from meteorological stations which are usually positioned above the ground and away from vegetation to restrict ground effects that can affect climate data. Weather stations collect temperature, humidity, rainfall, pressure, sunshine, wind, cloud and visibility data. However, natural and artificial or human-modified ground features, vegetation and ultimately human action and its attendant behaviours can all modify these variables. These local conditions not only produce microclimates that may be exploited as suitable niches for mosquitoes, but they also render extrapolations made from meteorological station data precarious as these could generate inappropriate conclusions. Thus, for the reasons discussed above, attempts to generate global models of dengue risk are at best unhelpful and risk itself is unlikely to be accurately captured in models that utilise parameters based on means and averages.

The intricate dynamics of dengue activity are driven more by human-induced microgeographic factors including the local landscape dynamics that link mosquito larval habitat [46], water storage and water use behaviour as well as local climate [47]. Local mosquito infection dynamics and microepidemiological factors such as herd immunity are also important factors in understanding transmission (see [48] for more detail). And what about evolution? Can models account for genetic factors such as the virus and vector genotype heterogeneity that will always exist in genetically diverse natural populations [49]? A focus on smaller scale models that use local climate characteristics to modify local short-term associations may be more valuable, as

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this may prove more informative in terms of understanding disease epidemiology [50].

6.2. Climate envelope and mechanistic modelling

Given the potential of more intimate life process models focusing on *A. aegypti* we describe below two independent approaches that try to elucidate the historical and current distribution of *A. aegypti* in Australia.

Throughout the 20th century, *A. aegypti* has occurred in pockets of urban settlement across much of Australia's continent with a distribution both inside and outside the 10 °C winter isotherm [23]. Human behavioural changes in water storage practices (particularly a move from rainwater tanks to reticulated water supplies) probably assisted in the regression of *A. aegypti* north into the warmer and more tropical regions of Queensland [51]. However when Australia's historical continental distribution of *A. aegypti* was assessed using a climate envelope modelling methodology (i.e. statistical/correlative climate matching) in an attempt to project the mosquitoes' potential Australian distribution, a reasonable distribution could not be realised, and the models wrongly suggested that this species could exist in colder climates than had been observed. This inappropriate result highlighted the fact that the biology and ecology and thus the distribution of this mosquito itself are more strongly influenced by human activity than by climate, which essentially buffers the mosquito from the external environment [23]. For example, large domestic rainwater tanks common throughout Australia in the early 20th century probably presented stable larval microclimates permitting populations to exist in colder temperate regions of Australia. Indeed the re-adoption of rainwater tanks in southern Australia as an adaptation to climate change may see the re-emergence of this vector further south once again.

A more successful approach in terms of indirectly accounting for human behaviour traits was to construct a mechanistic model around the organism or its key microhabitat – in this case, the water containers where eggs are placed and larvae develop [52]. This mechanistic or process modelling approach is based around the mass energy transfer kinetics of the larval container – a vital part of the life cycle – and was superior in terms of resolving the historical and current distribution of *A. aegypti* in Australia. It also provided a much better understanding of *A. aegypti*'s historical persistence in container habitats as well as its potential to adapt through evolution.

Perhaps next generation modelling of *A. aegypti* distribution (and, in turn, of dengue activity) will be able to better incorporate other important influential factors such as socioeconomic conditions, housing design, and water storage practices and management.

7. Population suppression and eradication: looking forward

The domestic nature of *A. aegypti* can make it very sensitive to control initiatives. As previously mentioned, effective *A. aegypti* vector control is certainly possible, although maintenance of population suppression requires a long-term commitment to urban vector management [18]. Control or eradication of established *A. aegypti* populations from an urban landscape is an undertaking that demands large resources and requires considerable public education and the subsequent modification of human behaviour – each of these components are essential for the sustainability of any vector control method [10]. Consequently, governments with a robust and economically sustainable public health infrastructure may be better placed to manage *A. aegypti* populations and provide sustained vector control initiatives, given their capacity for integrated vector management and public engagement over time.

Contemporary eradication and control methods are not so dissimilar to those employed over half a century ago – principally top-down integrated vector management programs that implement larval source reduction and are complemented by modern insecticides and chemical larvicides. In Singapore, elevated dengue activity in the 1960s saw the genesis of a top-down vector control program that also utilised law enforcement with a subsequent and dramatic reduction in both vector abundance and dengue activity. Although dengue activity increased a decade later, this was not due to an increase in vector density but rather to a lowering in herd immunity of the population (see [53] for more detail).

Biological interventions have shown some success in mosquito control through approaches such as the use of endemic copepods which eat mosquito larvae in Vietnam [54] – the sustainability of which requires vigorous community engagement to maintain copepod populations in water containers. A question remains whether such approaches could be effective in regions without similar social or institutional structures in place.

While the tools described above have proven effective in attempts to control *A. aegypti* in the highly urban regions where it is now endemic, new *A. aegypti* population suppression and replacement tools may open a next chapter in our battle against this vector. The Sterile Insect Technique (SIT) is not a new approach for insect population control and has already been successfully implemented against a range of agricultural pest insects (reviewed in [55]). But the recently developed RIDL® system (Release of Insects Carrying a Dominant Lethal) incorporates a novel genetic sexing system for the mass rearing of male mosquitoes using a repressible female specific lethal gene that permits the production of male-only *A. aegypti* populations [56]. This genetically modified *A. aegypti* sterile male release technology creates a species-specific population control method that relies primarily on the mass rearing and release of sterile males only [55], and provides a technology that appears to present an exciting alternative to traditional *A. aegypti* population suppression methods in that it makes use of species-specific mate seeking behaviour to locate conspecific females and thus generate no effect on non-target insects.

The second and equally exciting development in terms of novel control strategies is the discovery that strains of the naturally occurring endosymbiotic bacterium *Wolbachia* – commonly present in insect populations – can inhibit

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replication of the dengue virus in *A. aegypti* [57]. Introducing these strains of *Wolbachia* into wild populations of *A. aegypti* could potentially underpin a population replacement strategy that could suppress or perhaps even eliminate dengue transmission in affected areas.

While neither of these novel tools is likely to be used alone, they would perhaps rather be adopted as part of an integrated vector management program. In light of the continuing global expansion of dengue epidemic activity, consideration of novel technologies such as these should be encouraged and embraced when designing future vector control initiatives.

8. Concluding remarks

Meteorological variables alone cannot account for the geographical distribution of *A. aegypti*. Patterns observed in the historical distribution of this species also reflect global trends in urbanisation, infrastructure development, socioeconomic conditions and control efforts. The majority of attempts to model the potential distribution of this species in relation to climate have to date failed to adequately incorporate these factors and now face the challenging task of incorporating and addressing the important role that humans and the domestic environment play in the local presence and abundance of *A. aegypti*.

A. aegypti stands as a classic example of an invasive species − and its close association with the human environment affords it the ability to persist in locations that may otherwise be unsuitable in terms of climatic conditions alone. Given this, and even in light of all the evidence of current and continuing anthropogenic climate change, the major drivers of past and most likely future dengue growth appear to remain the same. These include i) unprecedented population growth, particularly in urban areas of the tropics; ii) an increase in the movement of both vectors and viruses in human hosts via modern transport; and iii) a lack of effective mosquito management in terms of government policy and public health [1]. Changes in climate will impact on various aspects of these factors, but human behaviour and the conditions of the domestic environment remain far more influential in terms of the distribution of *A. aegypti* and the epidemiology of dengue under any projected climate scenario.

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