

Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia

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Summary

1. Climate change will alter the distribution and abundance of many species, including those of concern to human health. Accurate predictions of these impacts must be based on an understanding of the mechanistic links between climate and organisms, and a consideration of evolutionary responses.
2. Here we use biophysical models of energy and mass transfer to predict climatic impacts on the potential range of the dengue fever vector, *Aedes aegypti*, in Australia. We develop a first-principles approach to calculate water depth and daily temperature cycles in containers differing in size, catchment and degree of shading to assess habitat suitability for the aquatic life cycle phase. We also develop a method to predict potential climatic impacts on the evolutionary response of traits limiting distribution.
3. Our predictions show strong correspondence with the current and historical distribution and abundance of *Ae. aegypti* in Australia, suggesting that inland and northern limits are set by water availability and egg desiccation resistance, and southern limits by adult and larval cold tolerance.
4. While we predict that climate change will directly increase habitat suitability throughout much of Australia, the potential indirect impact of changed water storage practices by humans in response to drought may have a greater effect.
5. In northern Australia, we show that evolutionary changes in egg desiccation resistance could potentially increase the chances of establishment in a major centre (Darwin) under climate change.
6. Our study demonstrates how biophysical models of climate–animal interactions can be applied to make decisions about managing biotic responses to climate change. Mechanistic models of the kind we apply here can provide more robust and general predictions than correlative analyses. They can also explicitly incorporate evolutionary responses, the outcomes of which may significantly alter management decisions.

Key-words: climate change, human health, mechanistic model, biophysical ecology, evolution, species distribution, disease vector

Introduction

Human-induced climate change is forecasted to dramatically affect the distribution of species, including those transmitting human diseases (IPCC 2001). Efforts to predict the risk of disease spread under climate change thus depend critically on

predicting changes in the distribution and abundance of vector species. Mosquitoes are vectors for many human diseases including malaria, encephalitis-causing viruses, yellow fever, Chikungunya and dengue fever. Much is known about the dynamics of mosquito populations, and a number of models exist for predicting the spread of mosquito-borne disease (Focks *et al.* 1993b). Yet contention remains as to the potential impact of climate change on mosquitoes and diseases they carry (Hales *et al.* 2002; Hay *et al.* 2002; Reiter 2007).

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A limitation in previous studies is that they lack a mechanistic link between climate and microclimatic environments experienced by mosquitoes at different life stages (Focks *et al.* 1993a; Tong & Hu 2001; Hales *et al.* 2002; Hay *et al.* 2002; Hopp & Foley 2003; Thomas Davies & Dunn 2004; Martens & Thomas 2005; Reiter 2007). For example, Hales *et al.* (2002) predicted the global distribution of dengue fever under current and future climates based on regressions with macroclimatic data, whereas Peterson *et al.* (2005) used a machine-learning approach to describe patterns of mosquito occurrence through space and time. The container-inhabiting mosquito simulation model (CIMSIM) (Focks *et al.* 1993a,b; Focks *et al.* 1995; Hopp & Foley 2003; Williams *et al.* 2008), and that of Hoshen & Morse (2004), Pascual *et al.* (2006) and Martens *et al.* (1999), are more mechanistic, incorporating physiology and population dynamics. However, they assume that mosquitoes experience 'ambient' temperature, or are based on correlations between weather conditions and container environments. In addition, there is mounting evidence that species are evolving in response to climate change (Bradshaw & Holzapfel 2006; Parmesan 2006; Hoffmann & Daborn 2007). A complete analysis of climate change impact on a species must also incorporate evolutionary potential.

In this study we show how general models of energy and mass transfer for animals and their microclimates ('Niche MapperTM') can be used to assess mechanistically the role of climate in limiting the potential distribution and abundance of the dengue mosquito *Aedes aegypti* in Australia. These models (Porter *et al.* 1973, 2000; Porter 1989; Porter & Mitchell 2006; Natori & Porter 2007) combine information on the behaviour, physiology and morphology of an organism with environmental data to predict the climatic component of an organism's fundamental niche, that is, those combinations of

environmental conditions that allow survival and reproduction in the absence of biotic interactions. The niche can then be mapped to a landscape to predict geographical range (Kearney & Porter 2004; Kearney 2006; Kearney *et al.* 2008). Since the models are trait-based, as opposed to distribution-based, they also provide the opportunity to explicitly assess the impact of plastic or evolutionary changes in key limiting traits (e.g. Mitchell *et al.* 2008).

Here we apply Niche MapperTM to predict the current, historical and future geographical range of *Ae. aegypti* across Australia as a function of climatic impacts on the availability of breeding sites. This species' distribution in Australia is presently restricted to Queensland (Fig. 1a) (Sinclair 1992; P. Mottram, unpublished data), but it was considerably more widespread in the early 1900s (O'Gower 1956; Russell *et al.* 1984; Lee *et al.* 1987; Sinclair 1992). We use our analysis to assess the hypothesis that human-induced changes in water storage practices may have contributed to this range contraction, through changes in oviposition site availability (O'Gower 1956; Russell *et al.* 1984; Lee *et al.* 1987). We also demonstrate how a quantitative genetic model can be incorporated into biophysical analyses of range limits in a GIS framework, to assess the impact of evolutionary change in different contexts.

Methods

PHYSIOLOGICAL PARAMETERS

All physiological data used in our analyses was collated from previously published information. The thermal dependence of egg, larval and pupal development was taken from Focks *et al.* (1993a) as was thermal dependence of the completion of the gonotrophic (adult) cycle. The thermal dependence of development varies

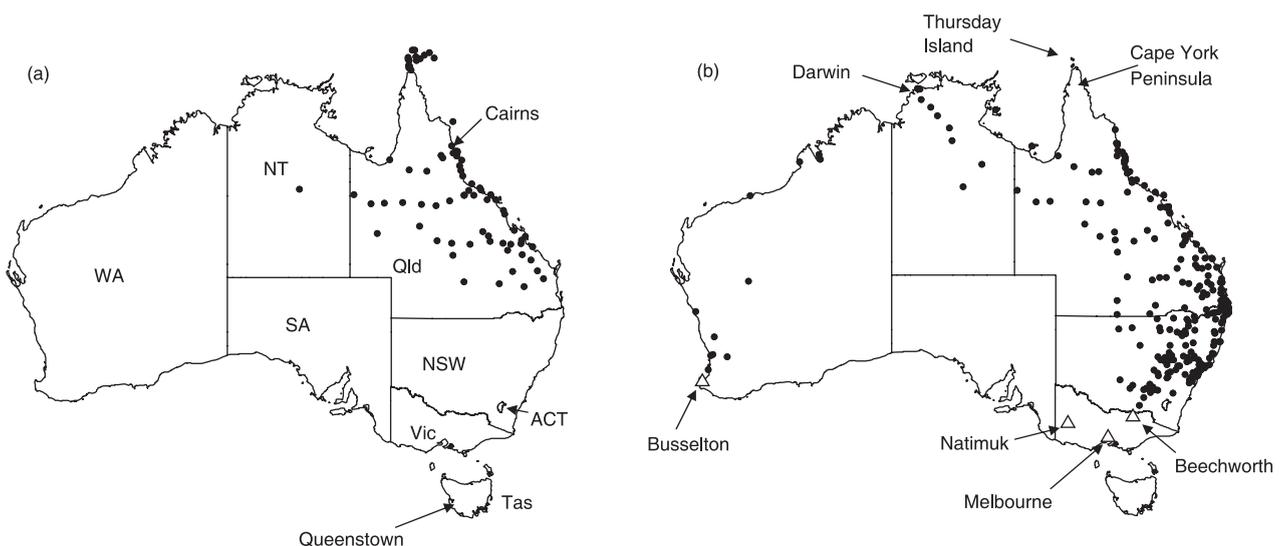


Fig. 1. The current (a) and early 1900s (b) range of *Ae. aegypti* in Australia, based on multiple sources (O'Gower 1956; Russell *et al.* 1984; Lee *et al.* 1987; Sinclair 1992; S. Ritchie, pers. obs, P. Mottram, unpublished data). The states and territories of Australia are indicated in Fig. 1a (WA, Western Australia; NT, Northern Territory; SA, South Australia; Qld, Queensland; NSW, New South Wales; ACT, Australian Capital Territory; Vic, Victoria; Tas, Tasmania). Sites indicated with a triangle in Fig. 1b are unconfirmed. Fig. 1a also indicates the locations of the two sites used in Fig. 4 (Cairns and Queenstown).

geographically in *Ae. aegypti* (Bar-Zeev 1958; Reuda *et al.* 1990; Tun-Lin *et al.* 2000). While data are available for one Australian population (Thursday Island, Tun-Lin *et al.* 2000), we used the equations from Focks *et al.* (1993a) because they involve all life stages (Sharpe & DeMichele 1977). The larval and pupal equations of Tun-Lin *et al.* (2000) and Focks *et al.* (1993a) predict similar rates across the thermal range considered by Tun-Lin *et al.* (2000) although the Tun-Lin *et al.* equation predicts slower larval development at some temperatures (see Fig. S1 in Supporting Information). We estimated egg survivorship during periods when containers were dry (< 1 cm water depth) using the logistic regression equation of Juliano *et al.* (2002) for *Ae. aegypti*, which incorporates the effect of temperature, humidity and time on survivorship of eggs out of water.

BIOPHYSICAL MODELING AND BREEDING CONTAINER PROPERTIES

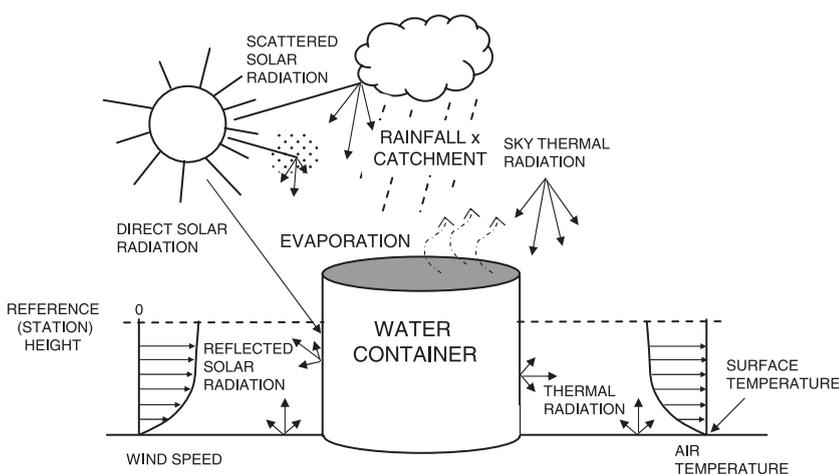
We modelled the availability and temperature of water in two types of cylindrical breeding containers representing ground containers and rainwater tanks. We recognize that other container types, such as subterranean communication pits (Kay *et al.* 2000) and artificially flooded garden accoutrements (e.g. potplant bases, birdbaths) (Barker-Hudson *et al.* 1988) are a significant source of *Ae. aegypti* in north Queensland. We focused on ground containers and rainwater tanks as they represent potential habitats common in human settlements across the entire continent, and closely tied to climatic change since they are not manually filled. Finally, we briefly considered the significance of subterranean environments.

To predict water temperatures, we solved coupled transient-state energy and mass balance equations for each container under different microclimatic conditions, including terms for short- and long-wave radiation exchange, convection, conduction and evaporation (Fig. 2). We then calculated the consequences for survival and development of immature stages based on published data described above. The process is represented as a flow diagram in Fig. 3 and described in more detail below. We emphasize that we have only considered

thermal constraints on development, whereas in nature other factors such as organic load in containers, and host availability, affect survival and development. Our predictions thus represent the maximum possible numbers of life-cycle completions – actual numbers would usually be lower.

The container properties were taken directly from Focks *et al.* (1993a); we modelled a 19 L bucket 36 × 30 cm (height × diameter) and a 3600 L rainwater tank (cistern) 150 × 175 cm (height × diameter). Each container type received the mean monthly rainfall, spread evenly across each day of the month, with the rainwater tank receiving additional runoff (10 × monthly rainfall) as well as a daily 20 L drawdown. The top of the bucket was assumed to be uncovered while the top of the rainwater tank was 90% covered.

The transient-state energy and water balance was modelled hourly for the middle day of each month, subject to the environmental conditions at the height of the midpoint of the container, either under low (25%) or high (75%) shade. A stable daily periodic in container temperature was obtained after three iterations of each day. The transient-state energy balance subroutines solved a standard energy balance equation that included a storage term, using an Adams–Moulton predictor–corrector numerical integrator with a Runge–Kutta starting algorithm (Forsythe *et al.* 1977, Mathews & Fink 2004). Intermediate derivatives were computed using a four point Lagrangian interpolation scheme. Convective heat and mass transfer calculations for the ground surface were computed using a turbulent velocity profile approximately logarithmic in shape to calculate air temperatures, wind speeds and humidity between the 2 m reference height and ground (Porter *et al.* 1973). A constant mass of water per unit volume in the air was assumed to correct for temperature-dependent relative humidity change between the 2 m input data and the surface over 24 h. The mass of water evaporated from the opening of the container each month was subtracted from the total volume and depth re-calculated accordingly, before adding rainfall for the subsequent month. Initial container depth was determined by the January rainfall entering the container. Rainfall was assumed to be evenly distributed across the month (adding the



Energy Balance

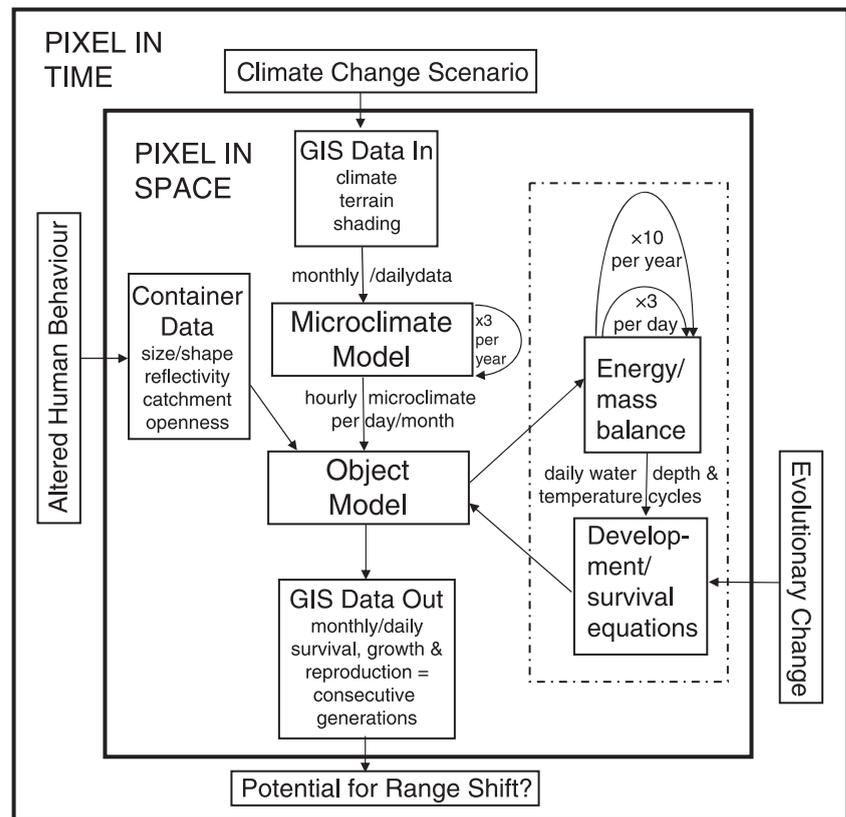
$$Q_{\text{SOL}} + Q_{\text{IR}} + Q_{\text{ST}} = Q_{\text{IR}} + Q_{\text{CONV}} + Q_{\text{COND}} + Q/M_{\text{EVAP}}$$

$$M_{\text{RAIN}} = M_{\text{USED}} + M_{\text{ST}}$$

Mass Balance

Fig. 2. Diagrammatic representation of microclimatic conditions relevant to the solution of the coupled transient-state energy (Q) and mass (M) balance equations for a rainwater-filled container. The energy balance equation includes terms for solar (SOL) and infra-red (IR) radiation, convection (CONV), conduction (COND) and evaporation (EVAP) as well as storage (ST). The mass balance equation includes terms for rainfall (RAIN), storage, evaporation and ‘drawdown’ (USED).

Fig. 3. Flow diagram depicting how Niche Mapper™ is used in a GIS context to predict habitat suitability for the immature phases of the life cycle of *Aedes aegypti*. The program consists of two modules, a microclimate and an object module. The object module may be used for calculating energy and mass balance of an organism or, in this case, an inanimate object (a potential breeding container). Calculations and program flow are depicted per pixel across space and time, illustrating how climate change, evolutionary change and changes in human behaviour can be incorporated to predict range shifts. Note that each day was run three times to obtain a stable daily periodic in container temperature, and the entire year was run ten times to obtain a stable annual periodic in container depths. Further details are provided in the text.



rainfall in weekly or monthly intervals made only subtle differences to the predictions). We ran 10 iterations of each year to ensure a stable periodic annual cycle in container depth.

Solution of the transient-state energy balance equation for the container provides an estimate of the hourly container 'core temperature' throughout the year (Fig. 4). This temperature was used to calculate the fraction of total development per month for eggs, larvae and pupae potentially inhabiting the container. The rate of completion of the gonotrophic life cycle assumed that mosquito body temperature was equal to the shaded air temperature at 2 m height. Adult activity was modelled to occur between 15 and 32 °C (Rowley & Graham 1967). The number of consecutive completions of the life cycle was summed for each locality across the year for each site and used to represent site suitability. This summed value was reduced by the fraction of eggs that would have died if at any time the container had < 1 cm of water, based on empirical data (Juliano *et al.* 2002).

MODELING EVOLUTIONARY RESPONSES TO CLIMATE CHANGE

We found egg desiccation to be a key limiting trait in regions of northern Australia subject to monsoonal wet and dry seasons (see results). To investigate the evolutionary potential of this trait, we computed desiccation mortality as described above and then treated this as a threshold trait with an underlying liability distribution following standard quantitative genetic models (Falconer & Mackay 1996). Under this model, a trait is expressed when it crosses a threshold value of another underlying trait (like the level of a hormone or activity of an enzyme). The underlying trait is assumed to have a normal distribution and produces a liability of the threshold being expressed. This approach ignores potential tradeoffs that might limit

selection responses, and thus provides an upper bound on the potential response. We used the mortality level to compute the intensity of selection (i) and then computed the response to selection ($R = ih^2V_p$) under low and high heritability values (0.15, 0.5) for a standardized trait with a phenotypic variance (V_p) of one. We appreciate that heritabilities may change; for instance genetic variance is depleted by directional selection, although gene flow might introduce new genetic variants that help maintain high levels of heritability (Pigliucci & Schlichting 1997). An empirical relationship was used to approximate the selection intensity from the mortality data ($i = 2.2014 - 0.04884s + 0.000558s^2 - 0.0000029s^3$ where s is survival as a percentage) based on the association in Falconer and Mackay (1996). The response to selection measures the difference between the starting and selected populations defined in this case in terms of liability standard deviation. By summing R and the initial liability, a new survival value for the evolving population was computed based on the cumulative normal distribution. We tested the ability of this approach to predict empirical observations of evolutionary change in desiccation resistance, using selection experiments from *Drosophila* literature (e.g. Hoffmann & Parsons 1993). The response to selection on *Drosophila melanogaster* and *D. simulans* produces a liability change of 0.2–0.5 standard deviations per generation if selection is on both sexes, heritabilities are in the range 0.2–0.6, and tradeoffs do not constrain selection responses. This is sufficient to increase survival 5–20% across a generation when the initial survival is 50%, in agreement with the empirical data.

We used this approach to generate a coarse model of the potential for evolutionary change in egg desiccation resistance to influence the occurrence and spread rate of *Ae. aegypti* in northern Australia, with and without concurrent climate change. For a given year we used the 'buffer' function in ArcGIS to define a region of spread based on the

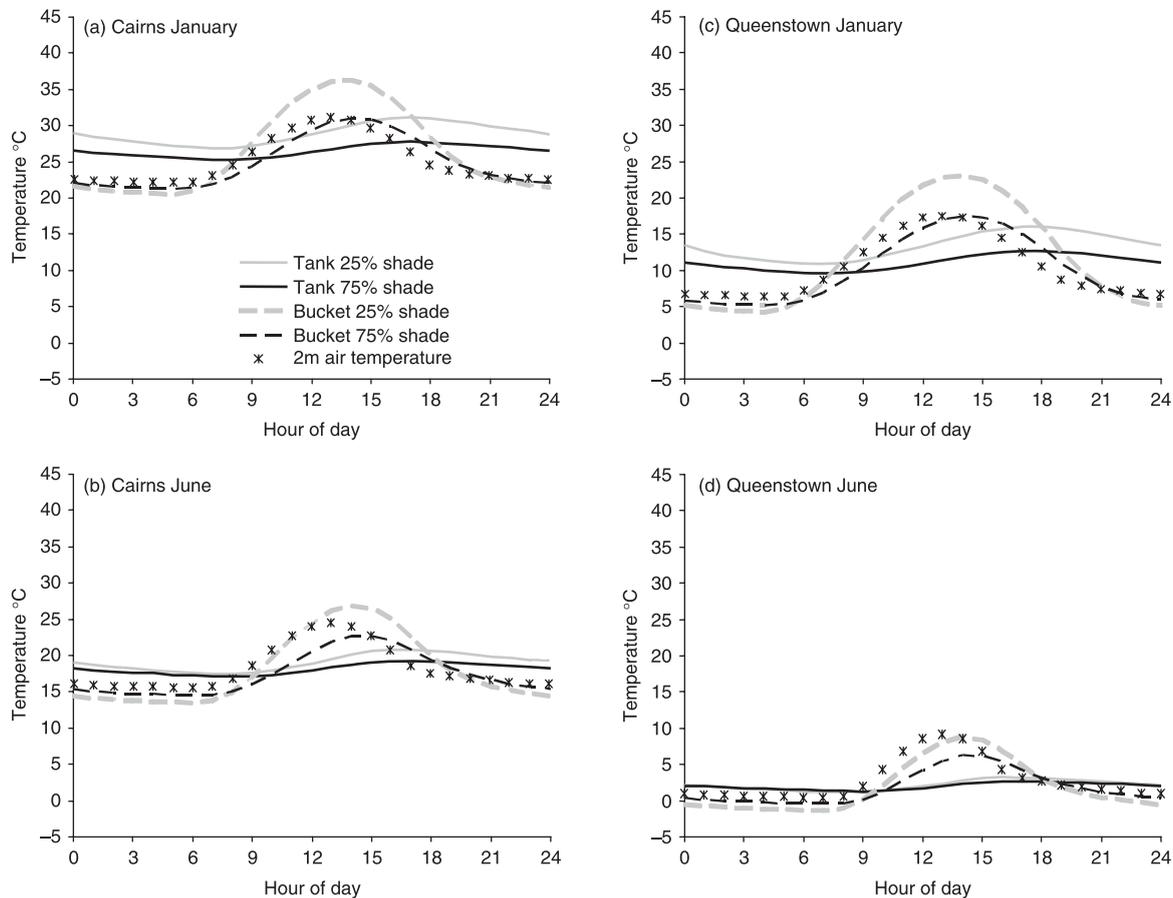


Fig. 4 Predicted daily thermal cycles of full water containers (buckets or rainwater tanks) in shade or sun for Cairns during January (a) and June (b) and for Queenstown, Tasmania during January (c) and June (d). See Fig. 1a for locations.

number of potential life-cycle completions for each habitable region for that year. *Aedes aegypti* is relatively sedentary (Muir & Kay 1998; Russell *et al.* 2005) but dispersing individuals can move up to 800 m (Honório *et al.* 2003). As an upper bound to dispersal rate, we buffered 1 km per generation around each habitat pixel. Selection was then implemented as above, using the map calculator function, and the buffer region was assessed for suitable sites (potential life-cycle completions greater than 1 per year) into which we allowed range expansion. The process was repeated each year, using a linear interpolation from the current climate scenario to the 2050 climate change scenario to determine yearly changes in environmental layers (duration of dry period, mean humidity and mean temperature during dry period), and in the potential annual life-cycle completions before any desiccation mortality.

SPATIAL DATA SETS AND CLIMATE CHANGE SCENARIO

We based our analyses on monthly maximum and minimum values of air temperature, humidity and wind speed, as well as mean monthly rainfall and cloud cover, averaged over 30 years (Kearney & Porter 2004). Elevation was based on a 9'' Digital Elevation Model (DEM) for Australia (Hutchinson 2000). Temperatures (initially 0.05° resolution) were corrected to the fine-resolution DEM using an adiabatic lapse rate of $-5.5\text{ }^{\circ}\text{C km}^{-1}$ elevation increase. Coarse-scale analyses were based on queries to these layers for a grid of 17 417 points approximately 0.2° apart, whereas fine-scale analyses were based on a grid of 20 682 points approximately 0.02° apart.

We used the package Ozclim v2 (CSIRO, Australia) to derive predictions for changes in monthly maximum and minimum air temperature and relative humidity, as well as mean monthly rainfall by 2050 under a moderate scenario of climate change (SRES marker scenario B1 mid, CSIRO mk2, 0.8–1.5 °C increase in mean annual temperature).

Results

The thermal constraints on adult activity precluded the occurrence of *Ae. aegypti* from small high-altitude regions in the south-east of the continent (see supplementary figures for monthly maps of potential adult activity time, container water depths and number of life-cycles completed for different container types). Breeding container type had a more dramatic influence on the potential range; predictions based on rainwater tanks corresponded with the historical distribution of *Ae. aegypti* (Fig. 5a,b), while predictions based on buckets corresponded with the region within the current range where most dengue outbreaks occur (Fig. 5c,d).

Rainwater tanks contained at least 1 cm of water for part of the year throughout much of northern, eastern and southern Australia, but remained dry throughout the year in the arid centre of Australia (supplementary figures). Under the rainwater tank scenario, successful completion of at least one generation per year was predicted at most sites where water

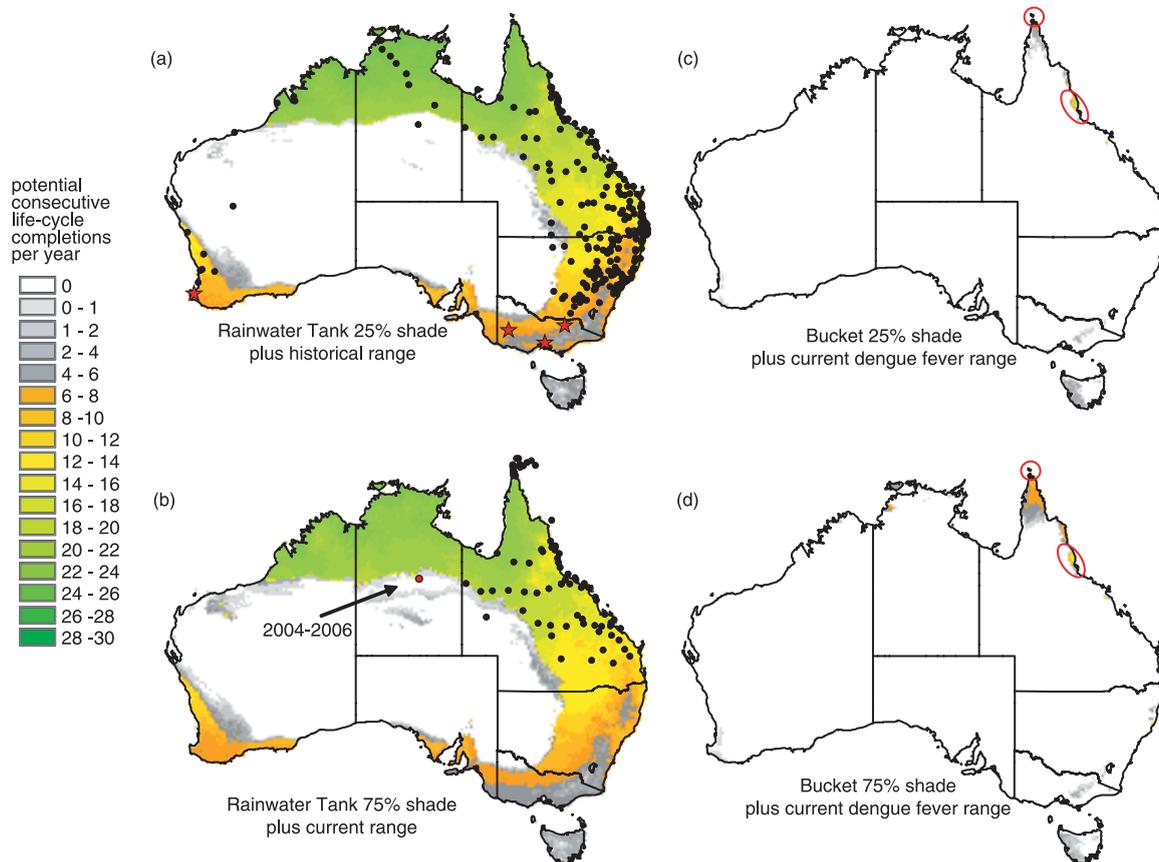


Fig. 5. Predictions of the number of consecutive life-cycle completions per year that could emerge from two simulated breeding containers (rainwater tanks, buckets) under different levels of shade. The model assumes that urbanized areas with containers that could sustain *Ae. aegypti* are present. (a) The historical distribution is imposed, (b) the present distribution is imposed; and (c) and (d) the locations of recent (since 1990) dengue outbreaks are imposed.

was available for at least part of the year (Fig. 5a,b); the only exceptions were high altitude areas in the south-east, where chronic low-water temperature (and reduced adult activity) prevented successful development (supplementary figures). The low-shade simulations predicted more life-cycle completions per year than did the high shade simulations, due to increased water temperatures in unshaded tanks (Figs 4 and 5c,d). Up to 30 consecutive life-cycle completions per year were possible (from a thermal perspective) in unshaded rainwater tanks in the most northern parts of Australia. The southern historical limit to *Ae. aegypti* in Australia corresponds closely with the region where at least 6–10 life-cycle completions per year are possible in rainwater tanks. This region encompasses the three historical (but unconfirmed) reports of *Ae. aegypti* for the southern state of Victoria (Natimuk, Beechworth and Melbourne), and the most southern (but unconfirmed) record for the south-west of Western Australia (Busselton).

Simulations using buckets predicted a much narrower and more fragmented potential range (Fig. 5c,d), mostly due to an absence of water in the containers across most of the continent throughout the year (supplementary figures). The predicted potential range includes the high rainfall area between Mossman and Ingham, where persistent populations of *Ae. aegypti* are presently found and where dengue fever

outbreaks occur regularly (Ritchie *et al.* 2002; Ritchie 2005; Hanna *et al.* 2006). Other suitable areas include Cape York Peninsula, the north west of the Northern Territory, patches on the northern NSW coast, the south-eastern highlands of Victoria, and the south-west regions of Western Australia and Tasmania (Fig. 5c,d). Shaded buckets were more suitable than unshaded buckets, largely because of reduced evaporation (although thermal extremes were also reduced; Fig. 4). The maximum number of consecutive life-cycle completions from shaded buckets was predicted to be no more than 18, consistent with the observed maximum number of generations per year at Cairns of around 15 (S. Ritchie, pers. obs.).

To explore the significance of subterranean breeding sites, we simulated larval survival and development rates across Australia at 60 cm depth below ground, assuming permanent water (Supporting Information). From a thermal perspective, between 11 and 22 life-cycle completions per year could occur in underground water bodies in northern Queensland where *Ae. aegypti* presently occurs, with only a small region in Tasmania dropping below one generation per year.

The climate change scenario we considered had only moderate impacts on the predicted range of *Ae. aegypti* when using rainwater tanks (Fig. 6a,b). Minor range contractions occurred at the inland border, whereas the number of potential

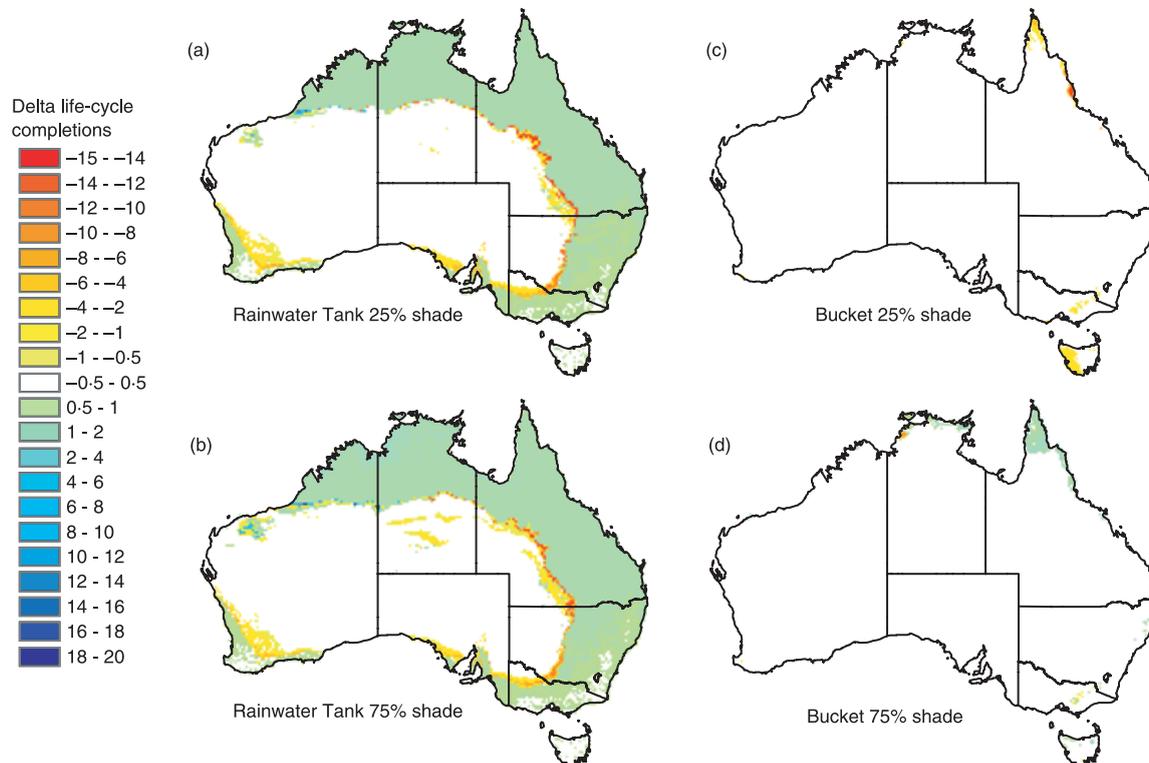


Fig. 6 The change in the number of potential life-cycle completions per year that could emerge from two simulated breeding containers (rainwater tanks, buckets) under different levels of shade and a climate change scenario for Australia in 2050 (SRES marker scenario B1 mid, CSIRO mk2).

life-cycle completions increased by 1–2 across much of the region predicted as suitable under current climate. The largest changes occurred in the northern interior range borders, where a large number of annual life-cycle completions are possible from a thermal perspective contingent on the presence of water in containers. The least change occurred in the cool southeast and southwest, where the number of potential life-cycle completions shifted by < 50%.

When buckets were used for breeding, the effect of climate change on the potential range of *Ae. aegypti* depended strongly on whether containers were shaded. Low-shade containers all reduced in suitability, with only a very small area in the wet-tropics region permitting > 1 generation per year due to perennially dry containers (Fig. 6c). In contrast, high-shade containers almost always increased in suitability, permitting 1–2 extra life-cycle completions to occur per year, and potential range expansions in the northern extremes (Fig. 6d).

Mortality data (Table 1) indicates that trait heritability had large effects on rate of approach to < 5% mortality, with an increase in heritability from 0.15 to 0.50 reducing time to 5% mortality by roughly two-thirds. Climate change had smaller effects. The closest seed population to reach Darwin was that from Litchfield National Park. Spread was fastest under climate change with high heritability (19 years) and slowest under climate change with low heritability (29 years) unless evolution was absent. Climate change increased the rate of spread by several years.

Table 1. The simulated impact of heritable variation and climate change on the number of years for the potential population to reach 5% desiccation mortality during the dry season and for the closest initial population to reach the township of Darwin. Note that once desiccation mortality has reached minimal levels (5% or lower), the rate of spread is then limited only by dispersal rate

Heritability	Climate change?	Time 0.05 mortality (year)	Time to Darwin (year)
0	No	–	–
	Yes	–	–
0.15	No	15	29
	Yes	17	23
0.50	No	5	24
	Yes	5	19

A detailed analysis of changes in the distribution and development of *Ae. aegypti* in the Northern Territory was undertaken at high and low heritability values, with and without climate change (Fig. 7). When the predicted effects of climate change were tested in the absence of evolution, the potential distribution of *Ae. aegypti* did not extend to Darwin after 10 years. However with evolution and a heritability of 0.5, *Ae. aegypti* was predicted in Darwin after 10 years even without climate change. The combined effects of climate change and evolution were predicted to have the greatest impact on range expansion. These analyses highlight the substantial impact that evolution might have on the spread of *Ae. aegypti*.

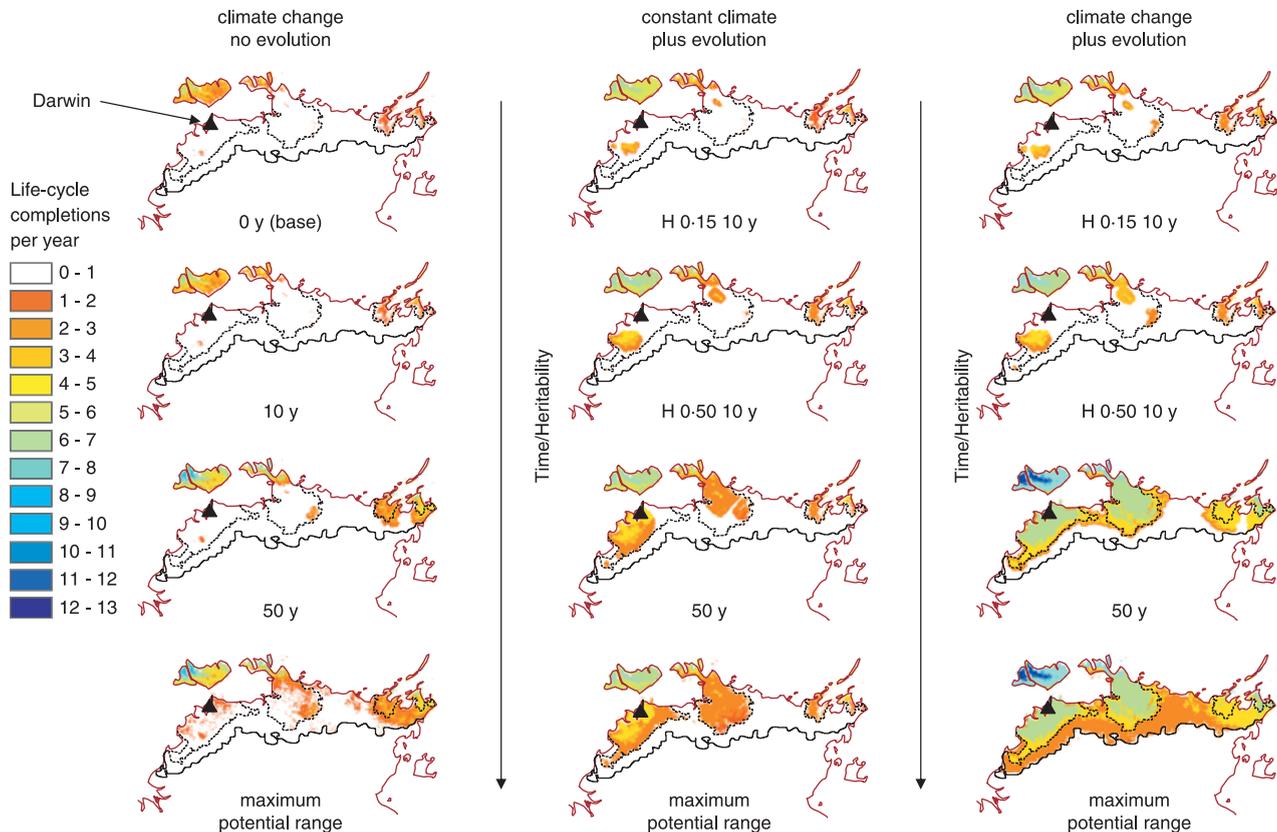


Fig. 7 The potential number of life-cycle completions per year of *Aedes aegypti* in the Northern Territory as a function of climate under different evolutionary and climate change scenarios. The base prediction for current levels of egg desiccation resistance, under long-term average climate, is top left. Predictions after 10 years, 50 years and at maximum extent of change are also shown. For predictions involving evolutionary change, scenarios under low (0.15) and high (0.50) heritabilities (h^2) are indicated. The evolutionary predictions after 50 years are virtually identical for different heritabilities, hence no value is specified. The dotted and solid lines represent the maximum possible range if egg desiccation survival was 100% under current climate, and under the 2050 climate change scenario, respectively (two right-most figures in the bottom row).

Discussion

Our analysis of the potential range of *Ae. aegypti* in Australia builds on previous approaches in two ways. First, it provides mechanistic links between climatic data, microclimates and the environmental conditions within user-specified breeding containers. Second, it provides a framework for incorporating evolutionary change into GIS-based predictions of the potential future range. We discuss each issue in turn.

BREEDING CONTAINER ENVIRONMENTS AND RANGE LIMITS

We are yet to incorporate a full population dynamics model with host-interactions into our analysis, as done in previous approaches (Focks *et al.* 1993a,b; Hoshen & Morse 2004). However, we were able to make inference on the potential range of *Ae. aegypti* by assigning regions as either inside or outside the fundamental niche due to one or more factors (Kearney 2006; Kearney *et al.* 2008). The most potent influence in this respect was climatic limitations on immature stages of the life cycle, specifically the availability of suitable

breeding sites. However, our conclusions depended strongly on container type.

Small rainwater-catching containers receiving minimal runoff, such as rain-filled buckets, are probably dry throughout a typical year, rendering them unsuitable across most of the Australian continent (Fig. 5 & supplementary figures). Only in scattered regions of northern Australia, particular in the wet-tropics region, would small containers provide a thermal and hydric niche for *Ae. aegypti*. Indeed, the wet tropics of north Queensland have persistent populations of *Ae. aegypti*, and recent dengue fever outbreaks (Figs 4 and 5c,d). Small containers in the top of the Northern Territory, and parts of Cape York, would be seasonally dry (supplementary figures), and we predict that a key trait limiting population persistence is egg desiccation resistance over this dry period.

In contrast, for predictions based on large rainwater tanks with runoff, water availability was only limiting in the arid centre, even when containers were unshaded (Fig. 5a,b see also supplementary figures). While we used the runoff factor of 10 specified for the cistern in the CIMSIM package (Focks *et al.* 1993a), a value of 50 would render water available throughout the year at all sites (simulations not shown). Thus

egg desiccation resistance would not be limiting where large water-storage containers are available for breeding, and instead only the cold tolerance of larvae becomes limiting. We note that our simulations assumed that food was not limiting, and in nature the relative suitability of containers will also reflect in part the associations between container types and organic load (Tun-Lin *et al.* 2000).

Our predicted distributions indirectly support the contention that reductions in the availability of large water storage containers may have been important in the historical contraction of *Ae. aegypti* (O'Gower 1956; Russell *et al.* 1984; Lee *et al.* 1987). For instance, the abundance of *Ae. aegypti* was once very high in Darwin but declined to extinction after the introduction of reticulated water supply following WWII (O'Gower 1956). In addition to the range of possible human-induced changes, range contraction may have been influenced by competitive interactions with other mosquitoes, particularly *Ae. notoscriptus* (Russell *et al.* 1984; Russell 1986; Tun-Lin *et al.* 1999; Kay *et al.* 2000).

Our model also elucidates the key role that artificially flooded containers play in the biology and distribution of *Ae. aegypti* in Australia. Garden accoutrements such as pot plant bases and bird baths are artificially flooded by residents, and a common source of *Ae. aegypti* year round in Cairns and Townsville (S. Ritchie, pers. obs.). Subterranean service pits and sump pits often maintain water throughout the dry season, and are responsible for significant production of *Ae. aegypti* in dry areas even during the dry season (Kay *et al.* 2000; Russell *et al.* 2005).

How is climate change likely to affect the current distribution of *Ae. aegypti* in Australia? Under the global warming scenario predicted for Australia by 2050, assuming a moderate mitigation of CO₂ production, our simulations predict overall increases in the number of potential generations per year across most of the range if breeding were to occur in rainwater tanks, particularly in the north (Fig. 6a,b). If mosquitoes were restricted to small, rain-filled containers such as buckets for breeding, the impact of climate change depends critically on shading. If shade is low, increased evaporation under climate change reduces the number of potential life-cycle completions across the previously habitable range (Fig. 6c), with persistence only possible in the wet-tropics. In contrast, if shading is high, there is an increase in the potential number of life-cycle completions and geographic range, when compared with current climate (Fig. 6d).

Some authors have emphasized that land-use and other human behavioural changes often have more dramatic effects on disease spread than changes in climate (e.g. Patz & Olson 2006). The potential direct impact of climate on the distribution and abundance of *Ae. aegypti* is minor when compared to the potential effect of changed water-storage behaviour. In many Australian cities and towns, a major impact of climate change is reduced rainfall (Holper *et al.* 2007), resulting in a dramatic increase in domestic rainwater storage and other forms of water-hoarding. Without due caution with water storage hygiene, this indirect effect of climate change via human adaptation could dramatically re-expand the current range of *Ae. aegypti*.

INCORPORATING EVOLUTIONARY CHANGE

Our approach was adapted to incorporate assessments of evolutionary potential in range-limiting traits. It is important to consider evolutionary potential when assessing potential shifts in range and abundance, since a species distribution limit is as much an evolutionary constraint as it is an ecological one (Hoffmann & Blows 1994; Holt & Keitt 2005). An advantage of trait-based approaches to predicting species' distribution limits over more correlative approaches is that they identify key limiting traits that alter a species' range through evolutionary change. Our analysis indicates that two key traits underlying the distribution limits of *Ae. aegypti* are resistance to cold and egg desiccation resistance for large and small containers, respectively. This leads to the hypothesis that *Ae. aegypti* would be more capable of establishing in Darwin, particularly under climate change, if it shifted its resistance to desiccation to 100% survival under the environments of northern Australia (Fig. 7). We have demonstrated a simple way of including evolution into range predictions by using a threshold model of desiccation resistance where an underlying and normally distributed liability dictates whether eggs are resistant. This approach allowed us to model changes in mortality levels due to evolution for increased levels of desiccation resistance. Although there are no direct estimates of the heritability of egg desiccation resistance for *Ae. aegypti*, and tradeoffs might limit selection responses, the estimates we used and rates of response to selection are consistent with the range of estimates obtained for *Drosophila* species (Hoffmann & Harshman 1999; Hoffmann 2000) and consistent with the rate of change of mortality seen in selection experiments (Hoffmann & Parsons 1993). Evolutionary changes in response to desiccation stress have also been detected in *Ae. aegypti* adults (Machado-Allison & Craig 1972), demonstrating that mosquitoes are capable of adapting to aridity gradients.

More complex evolutionary models could be developed within a mechanistic framework. Higher levels of gene flow could be incorporated by averaging mortality levels and selection across different spatial scales. Gene flow from large central populations to smaller marginal populations can limit species distributions (Kirkpatrick & Barton 1997). Potential costs of high levels of resistance to desiccation and other stresses that might limit evolutionary responses could also be included in models, by modelling multivariate selection responses in response to different environmental variables (Blows & Hoffmann 2005).

LIMITATIONS AND EXTENSIONS

While our analysis provides insights into the distribution and abundance of *Ae. aegypti* in Australia, it could be extended to include fine-scale population dynamics and disease transmission. An ability to predict the population dynamics of *Ae. aegypti* in a given location is critical for successful predictions of the risk of dengue transmission. Our approach provides a way to drive the already very sophisticated models of dengue

transmission (Focks *et al.* 1993a,b; Focks *et al.* 1995) with an equally sophisticated mechanistic link between climate and mosquito population dynamics. The egg and larval phases appear most important in constraining the overall potential distribution and abundance of *Ae. aegypti* in Australia and presumably other parts of its range. Yet the adult phase and its thermal response will be critical to dengue infection dynamics, since dengue incubation time within the host, as well as the biting frequency of the adult phase, vary with temperature (Focks *et al.* 1995). A mechanistic approach to incorporating climate impacts on the dynamics of *Ae. aegypti* and dengue fever will allow better risk assessments of invasion potential and infection frequencies. Ongoing efforts to produce biological controls for *Ae. aegypti*, including the introduction of *Wolbachia* strains (Ruang-areerate & Kittayapong 2006), will also require information on these processes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Developmental equations used in CIMSIM (Focks *et al.* 1993a) and in the present study, compared to those derived for pupae and larvae by Tun-Lin *et al.* (2000). The low-temperature threshold for development is 13.4 °C, while the upper lethal limit is 44 °C.

Fig. S2 Monthly predictions of daily activity time for adult *Aedes aegypti* assuming diurnal activity in the shade between body temperatures of 15–32 °C.

Fig. S3 Monthly predictions of mean monthly water depths in rainwater tanks assuming 25% shade.

Fig. S4 Monthly predictions of mean monthly water depths in buckets assuming 75% shade.

Fig. S5 Monthly predictions of site suitability (life-cycle completions penalized by egg desiccation during dry periods) for water tanks in 25% shade.

Fig. S6 Monthly predictions of site suitability (life-cycle completions penalized by egg desiccation during dry periods) buckets in 75% shade.

Fig. S7 Numbers of months that water tanks and buckets were predicted to hold more than 1 cm depth of water under different scenarios of shade and climate change.

Fig. S8 Suitability of subterranean sites for *Aedes aegypti* assuming a depth of 60 cm and permanent water.

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