

Predicting the spread of *Aedes albopictus* in Australia under current and future climates: Multiple approaches and datasets to incorporate potential evolutionary divergence

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Abstract When predicting the potential and future invasive range of a species, there is a growing appreciation that insights about factors limiting distributions can be provided by using multiple modelling approaches and by incorporating information from different parts of a species range. Here we apply this strategy to build on previous CLIMEX models to predict the invasion potential of *Aedes albopictus*, the Asian tiger mosquito, in mainland Australia. A combination of CLIMEX and MAXENT modelling indicated that the mosquito was expected to become widespread along the eastern seaboard and extend into northern Tasmania, but to remain restricted to the coastal fringe, a pattern which is not expected to shift much under climate change. However, a recent expansion of *A. albopictus* in North America points to evolutionary changes affecting the distribution of this species; when the North American range is included in models, *A. albopictus* is predicted to become much more widespread and extend inland and into Western Australia. These patterns highlight the potential impact of evolution on species distributions arising from multiple introductions or *in situ* evolution. By considering future climate scenarios, we demonstrate that there is likely to be a persistent public health threat associated with invasion by this species.

Key words: *Aedes albopictus*, CLIMEX, environmental niche model, invasion biology, species distribution model.

INTRODUCTION

Pre-emptive action in the form of species distribution modelling may aid in identifying the potential spread of invasive organisms into novel environments. Ecological niche models (ENMs) have been shown to have high predictive power in determining the point of invasion for species, though they may under-predict the entire invasive range for a species (Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007; Hill *et al.* 2012). This discrepancy is thought to be because of a number of factors, one of which is niche shift in the invasive range (Hill *et al.* 2012). For invasive species that have established across a range of environments globally, models based on both native and invasive distributions may lead to a more complete understanding of the range of species–environment relationships (Mau-Crimmins *et al.* 2006; Beaumont *et al.* 2009; Petersen 2013). Similarly, partitioning of occurrence data based on populations may reveal species–environment relationships that are divergent and thus informative for predicting potential distributions (Pearman *et al.* 2010).

By characterizing a broad range of these relationships, including apparent niche shifts, more accurate assessments of invasion risk for new areas can be made (Broennimann & Guisan 2008).

While correlative ENMs are able to indirectly incorporate adaptive shifts into predictions, rarely do they explicitly consider evolutionary processes that allow species to extend their range outside of distribution limits determined from historical data (Kearney & Porter 2009). Trait-based, or mechanistic models, can allow for evolutionary adaptation to be incorporated into models (Kearney *et al.* 2009). CLIMEX (Sutherst *et al.* 2007) is a semi-mechanistic modelling method that examines relationships between climate, species distributions and patterns of growth (Macfadyen & Kriticos 2012). Models can be fitted using a combination of empirically measured parameters and point distribution records. As CLIMEX incorporates generalized ecophysiological parameters, it is also possible to investigate simple trait evolution by changing model parameters to match observations. For example, Lozier and Mills (2011) incorporated adjustments to cold stress parameters into an existing CLIMEX model for *Epiphyas postvittana* moths which resulted in model predictions matching distribution data for colder regions.

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Here we consider ways of including evolutionary processes in predicting the spread of *Aedes albopictus*, the Asian tiger mosquito, into Australia. This disease vector has spread globally in the last few decades through human migration and activity, exemplified by the used tyre trade into the USA (Reiter & Sprenger 1987; Gratz 2004). Currently *A. albopictus* has not established invasive colonies in Australia, most likely because of quarantine in seaports and eradication programmes, but populations exist in the Torres Strait islands just north of the mainland (Ritchie *et al.* 2006; Williams 2012). However, it seems likely that *A. albopictus* will eventually establish and spread on the mainland. Eradication campaigns require persistent financial investment and community will to prevent invasions or reinvasions of pest mosquitoes, and are prone to failure (Gratz 2004). The closely related yellow fever mosquito, *A. aegypti*, remains the primary vector for the dengue virus (DENV) in north Queensland and this species has a highly domestic and anthropophilic habit. Because *A. albopictus* prefers undisturbed, vegetated landscapes and has zoophilic feeding habits, control mechanisms aimed at *A. aegypti* may be less effective against *A. albopictus* (Ritchie *et al.* 2006; Lounibos *et al.* 2010).

Historically, *A. albopictus* has been responsible for several outbreaks of dengue and chikungunya within multiple countries and is capable of disseminating a range of other arboviruses (Gratz 2004; Paupy *et al.* 2009). During periods between epidemics, vertical transmission and maintenance of DENV may play an important role within endemic zones. In Australia *A. aegypti* is not known to transmit DENV transovarially, but *A. albopictus* may be more capable of transmitting DENV through this route (Martins *et al.* 2012). While dengue is currently not endemic in Australia, the potential presence of widespread populations of *A. albopictus* with a higher rate of viral transmission might therefore increase the risk of endemicity developing. It is therefore important to identify high-risk areas for invasion around Australia and predict the likely status of these areas into the future.

A challenge in modelling the invasive distribution of *A. albopictus* is that this species appears to have exhibited niche shifts in terms of climatic relationships in novel environments outside its native range of south-east Asia (Benedict *et al.* 2007; Medley 2010). These shifts are most likely to include the evolution of diapause characteristics that show clinal patterns, and appear to have developed since the invasion of this species into North America (Urbanski *et al.* 2012). As in the case of *A. aegypti* in Australia (Kearney *et al.* 2009), evolutionary changes need to be considered in making predictions of likely shifts in distribution and abundance particularly under future climates.

Previous distribution models for *A. albopictus* have been based on ENM approaches (Benedict *et al.* 2007;

Medley 2010) and CLIMEX (Russell *et al.* 2005; Sutherst *et al.* 2007). These models do not yet incorporate projections into future climate change scenarios and they also have not considered evolutionary capacity within *A. albopictus*. An additional study by Rochlin *et al.* (2013) examined climate change impacts, but only for north-eastern USA. By using correlative ENMs in conjunction with semi-mechanistic approaches, such as CLIMEX, it should be possible to compare modelling methods, incorporate some level of niche-shift and evolution, and then identify areas that show model congruence and that are highly susceptible to invasion risk (Lozier & Mills 2011; Webber *et al.* 2011).

We aimed to determine potential establishment points for an *A. albopictus* invasion into Australia under both present and future climate conditions. We evaluated this through predictive modelling of the species range of *A. albopictus* applied to mainland Australia. We used both correlative models and the semi-mechanistic CLIMEX model, but refocused them to an Australian-specific context to consider two main questions. (i) Do the native and invasive ranges of *A. albopictus* pose geographically different invasion risks? (ii) Will these change with future climate change? These approaches should aid in reducing uncertainty in model predictions and provide better estimates of invasion risk.

METHODS

Distribution data

Species locality data were obtained from published (Benedict *et al.* 2007; Medley 2010; Rochlin *et al.* 2013) and online database sources: Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed 10/03/2011) and MosquitoMap (<http://www.mosquitomap.org>, accessed 28/02/2011). The records from the USA that represented positive occurrences in counties (Benedict *et al.* 2007; Medley 2010) were converted to a single point by calculating centroids in ArcMap 10 (ESRI, Redlands, CA, USA). In an attempt to account for error in taking US county centroids for *A. albopictus* locations, we selected counties that had positive records and then created a random point in each of those counties. We produced 10 replicates of these randomized county localities of the North American county centroids. We added the Rochlin *et al.* (2013) data to each of these datasets to use as 10 separate North American randomized datasets.

Environmental data

We obtained environmental data from CliMond (Kriticos *et al.* 2012), which provides data suitable for both correlative ENMs and CLIMEX models (e.g. Webber *et al.* 2011). For ENM construction, CliMond provides 35 bioclimatic

variables describing means, seasonality and trends for temperature, precipitation, solar radiation and soil moisture. Many of these variables (or ones closely associated with them) were employed in both the Benedict *et al.* (2007) and Medley (2010) ENMs. However, for comparison with CLIMEX models, we focused solely on using the CliMond dataset and subsequently did not incorporate variables describing topography, wind speed or frost days into our ENMs. We used a grid cell resolution of 10', which is roughly 20 × 20 km at the equator.

ENM construction

We chose to model two geographic regions to investigate differences in invasion potential from the native range (Asia), or established invasive populations (North America) that have also demonstrated recent evolutionary adaptation and subsequent range expansion (Urbanski *et al.* 2012). While *A. albopictus* is found in other regions such as South America, these environments represent niche-space that is found within the native Asian range (Medley 2010). We did combine all available data into a single dataset to include in analysis, however. Using these two distinct regions should provide a better measure of *A. albopictus* invasion potential into Australia. We defined the modelling background for each of these regions in terms of accessible area for *A. albopictus*. Accessible area was chosen based on occupied bioclimatic regions (Soberon 2010; Barve *et al.* 2011) using Köppen–Geiger classifications, following the rules defined in Kriticos *et al.* (2012) as applied to the 5' resolution WorldClim global climatology (<http://www.worldclim.org>; Version 1.4, release 3; Hijmans *et al.* 2005). This provides a broad geographic area to account for data availability and occurrence record biases, but omits large geographic areas that are not relevant to modelling the species distribution. Wide backgrounds may give false impressions of model validity when assessed through means such as AUC (area under the curve of the receiver operator characteristic), but restricted backgrounds may not reflect access opportunity to all environment types for a species, leading to reduced discriminatory power (VanDerWal *et al.* 2009; Giovanelli *et al.* 2010).

To determine key variables for model inclusion, we applied Ecological Niche Factor Analysis for each dataset across the respective background using the adehabitat package (Calenge 2006) in R (R Core Team 2013; version 3.0.0). This method provides two uncorrelated axes, marginality and specialization (Hirzel *et al.* 2002). Variables were ranked on marginality (0–1), with the top 10 variables for each dataset then checked for spatial autocorrelation. Values for 10 000 random points were extracted across each background and we performed pairwise correlation tests across all variables. We considered any pair with a correlation of >0.75 as highly correlated and removed a variable from the pair based on a lower marginality score. By removing variables in this manner, we hoped to reduce issues that may arise from multicollinearity (Heikkinen *et al.* 2006), and its effects on models projected to new geographical regions (Rodder & Lotters 2009).

We examined how differences in environmental conditions across our backgrounds may effect predictions of invasion potential in Australia. We sampled 10 000 random points

across the bioclimatic regions in Australia that matched the respective regions for the Asian and North American backgrounds. We then conducted principal components analysis (PCA) for the variables chosen in the respective train datasets across the paired backgrounds to examine overlap between locality datasets, the calibration background and the area of model projection (Australia). We also coupled each projection with a multivariate similarity surface (MESS, Elith *et al.* 2010 (Appendix S2)) to examine each predictor variable between ranges and determine if the test, or projected range layers held values outside those of the training range (extrapolation). Areas that are outside of training range for a given variable may lead to erroneous extrapolation and should be interpreted with caution.

To build correlative ENMs, we used the presence-background algorithm, MAXENT (Phillips *et al.* 2006; Phillips & Dudik 2008) (Version 3.3.3i), as it has been applied widely to model invasive species distributions (Ficetola *et al.* 2007; Giovanelli *et al.* 2008; Hill *et al.* 2012) and as it was recently used to identify suggested niche shift for the global distribution of *A. albopictus* (Medley 2010). Each grid cell was limited to one occurrence point. To enforce smooth response curves and explore the effects of model complexity, we only enabled hinge features (see Elith *et al.* 2010) and increased regularization (β) from 1–5. We then used corrected Akaike information criterion (AIC_c) to examine effects of changes in β (Warren & Seifert 2011). All other MAXENT parameters were left at default. Models were then run across 10 cross-validation replicates, taking the average of all replicates for spatial predictions. For North America we included all 10 datasets of randomized localities as separate replicates, combining model output to form single consensus layers. The respective predictor variable sets were then examined using the jackknife feature of MAXENT together with percent contribution to model, and the removal of variables having less than 5% contribution was examined.

CLIMEX modelling

CLIMEX (described above) processes a series of weekly growth and stress indices that are combined to produce an Ecoclimatic Index (EI). The EI describes regions that are unsuitable for the species to persist, through to those that provide a 'perfect' environment for the species. This is interpreted within a scale of 0–100 (Olfert *et al.* 2011), with values over 30 considered to convey ideal conditions (Sutherst *et al.* 2007), and below 10 an unfavourable environment, though rating interpretations will be species-specific to some extent.

CLIMEX has been used to predict new geographical regions for invasive invertebrate species, and also responses to climate change (e.g. Mika & Newman 2010; Lozier & Mills 2011; Macfadyen & Kriticos 2012) including *A. albopictus* (Sutherst *et al.* 2007). After *A. albopictus* was reported in the Torres Strait Islands, the model of Sutherst (1993) was revised slightly for a tropical strain (Russell *et al.* 2005). This involved widening the temperature response curve at the higher end, allowing for the upper optimal temperature for population growth (DV2) extended to 30°C and the highest temperature threshold for population growth (DV3) to be extended to 37°C (Russell *et al.* 2005).

To allow for adaptation in North America to be considered, we constructed a modified 'adapt' model by lowering

the DV0 (lowest temperature threshold for population growth) and DV1 (lower threshold for optimal population growth) parameters to account for populations that now persist in colder climatic regions (Urbanski *et al.* 2012). As CLIMEX considers a 'generalized' species without explicit life stages, we lowered these parameters with respect also to egg development rates at lower temperatures (5°C for DV0, though no data were available for temperatures below this value, and 12°C for DV1) (Delatte *et al.* 2009). The other parameters were unchanged from Russell *et al.* (2005). We compared the model using these lowered DV0 and DV1 parameters to the Russell *et al.* (2005) model.

Model projections

For climate change projections, we used both the CSIRO Mk. 3.0 and Miroc-H models (available from CliMond) for the time periods 2030 and 2050 under the A2 SRES for future climate change. The A2 SRES represents one of the higher rates, though not the highest, of warming in the Fourth Assessment Report (AR4; IPCC 2007).

For the ENMs, we set a least training presence threshold on the projected output, allowing for 5% of training records to be in error (LTP-E (Donalisio & Peterson 2011)). In this sense, error allows for distribution data that may have been collected from microclimates or observations of populations that would not normally persist where recorded. For climate change scenarios, we repeated this process and averaged model predictions for each timeframe/training background (10 replicates of two climate models, for North America this was taken for 10 replicates of each of the 10 randomized locality datasets as well).

Because of their weekly growth and stress indices, CLIMEX models can be run on climate change data independently of current climate information, avoiding issues like extrapolation in correlative ENMs. We ran the CLIMEX

models on the same climate change scenarios and time frames in Australia, and then averaged the EI across the CSIRO and Miroc-H models for each time frame.

RESULTS

The global distribution of *A. albopictus* and the two backgrounds used in ENM construction are shown in Figure 1. In total 1641 georeferenced *A. albopictus* points were included, 263 for native populations across South-East Asia and the Malay Archipelago and 1378 across invasive populations in North & South America, Europe and Africa. Our background selection method meant that some Köppen–Geiger climate zones in North America were only included in the background considering all available data as these zones were only occupied elsewhere in the global range of *A. albopictus* (Fig. 1). The Brazilian distribution is underrepresented in this figure because of lack of data availability – see Medley (2010) for more complete information on this issue. Each model had differing final variables and all variables included in final models and their respective model contributions for each of the datasets are shown in Table 1.

For each of the final variable sets used in the ENMs, the PCs give visual representations of the environmental space occupied by the training points, the available environmental space to *A. albopictus* for the respective datasets and how this overlaps with environmental space within Australia (Fig. 2). The highest overlap in environmental space between backgrounds and training points is seen for the dataset comprising all available points. For the regional data subsets, there

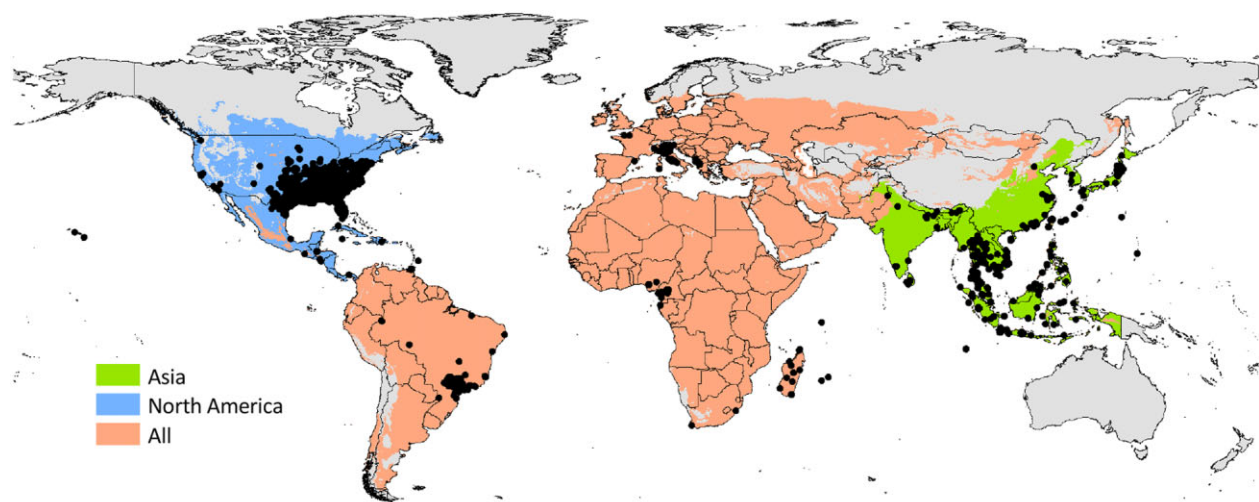


Fig. 1. Global distribution of *Aedes albopictus*. Black dots represent occurrence/detection points. Shaded areas represent backgrounds used in Environmental Niche Model (ENM) construction based on Köppen–Geiger classifications (green = Asia-trained model; blue = North America-trained model; orange = other areas used for 'all available data'). Note, the 'All' background includes all areas in the Asia and North America backgrounds too.

Table 1. Final variables[†] and contributions as assessed through MAXENT selected for the three Ecological Niche Models

Variable	Model					
	Asia		N. America		All	
	PC	PI	PC	PI	PC	PI
Bio07	26.5	34.5				
Bio10			32.7	52.6		
Bio12	39.4	18.8				
Bio14					76.1	68.4
Bio15	34.1	46.7	5.7	23.5	4.9	6.1
Bio17			59	20		
Bio18			2.6	4		
Bio28					10.5	13.7
Bio31					4.1	5.9
Bio34					4.1	5.9

[†]Bio07 = Temperature annual range (Bio05–Bio06) (°C); Bio10 = Mean temperature of warmest quarter (°C); Bio12 = Annual precipitation (mm); Bio14 = Precipitation of driest week (mm); Bio15 = Precipitation seasonality (coefficient of variation); Bio17 = Precipitation of driest quarter (mm); Bio18 = Precipitation of warmest quarter (mm); Bio28 = Annual mean moisture index; Bio31 = Moisture index seasonality (coefficient of variation); Bio34 = Mean moisture index of warmest quarter. PC, percent contribution; PI, permutation importance.

is less overlap between the training points and the Australian background – Australia holds regions of non-analogue environmental space from both Asia and North America as measured by the first two principal components of the respective variable sets (Fig. 2). The environmental space of the *A. albopictus* localities used in the Asia-trained models only occupies a portion of the available environmental space across the Asia background (Fig. 2). The locality points in North America are also largely non-overlapping with the Australian background points, though they overlap highly with the North American background (Fig. 2).

The best performing ENMs as assessed through lowest AIC_c score in terms of complexity were $\beta = 1$ for all data points, $\beta = 4$ for the Asia dataset and $\beta = 1$ for the North American dataset. Coupled with lowest AIC_c scores, the mean AUC_{TEST} value across the cross-validated replicates for the Asia-trained model was moderately high (0.769) and high for the North America-trained (0.877) model and combined dataset model (0.849), indicating good model performance in relation to the backgrounds chosen. As another form of validation, we examined the global projection of these models built on our backgrounds against the known distribution of *A. albopictus*. The Asia-trained ENM was successful in projecting to nearly all global points, whereas the North American-trained ENM severely under-predicted the global distribution of

A. albopictus (Appendix S1). When projected to Australia, the Asia-trained ENM displays the east coast of Australia as climatically suitable (Fig. 3a). This extends from northern Queensland down to Tasmania in the south. The south-east corner of Western Australia is also shown to be suitable under current climate conditions, as are some restricted regions at the top of the Northern Territory. No inland regions are suitable based on the Asia-projected model. The North America-trained ENM shows only congruence in the southern parts of the eastern Australian projection (Fig. 3a). However, this projection does extend further inland in eastern Australia than the Asia-trained ENM and ENM based on all available data. The projections of the all available dataset to Australia are congruent with the Asia-trained ENM, though they extend further inland. Under the climate change scenarios investigated here, suitable climate space retracts coastward around Australia (Fig. 3b,c) and is reduced to a narrow region in Western Australia. The MESS analyses revealed no single predictor variable for the respective ENMs outside their training range in Australia (Appendix S2).

The ‘original’ Sutherst (1993)/Russell *et al.* (2005) models and the modified ‘adapt’ CLIMEX models are markedly different (Fig. 4a,b). Parameters for these models are shown in Table 2. The original model predicts that climate along the coast of northern and north-eastern Australia is suitable (where EI > 30). There is also suitable area in the south-eastern corner of Western Australia. Climatically suitable area extends down the east coast to Victoria, but there is little suitable climate space for *A. albopictus* in the south-eastern corner of Australia. In contrast, the lowered DV0 and DV1 values for the ‘adapt’ model allow for suitable climate space to extend further into Victoria and northern Tasmania. The ‘adapt’ CLIMEX model shows high congruence with the Asia-trained correlative ENM. Under the climate change scenarios investigated here, there appears to be little-to-no change in suitable climate for *A. albopictus* in 2030 or 2050 for either ‘original’ or ‘adapt’ CLIMEX models (Fig. 4c–f). While overall model congruence is high between methods, the ENM and CLIMEX models disagree about the likely occurrence of *A. albopictus* inland along the east coast of Australia, the ENMs predicting a much larger suitable habitat. Another major difference is that for Tasmania the ENMs predict a more southerly distribution.

DISCUSSION

Aedes albopictus is expected to invade mainland Australia and the current models provide an indication of invasion potential under current and future climatic conditions. By modelling both native and invasive

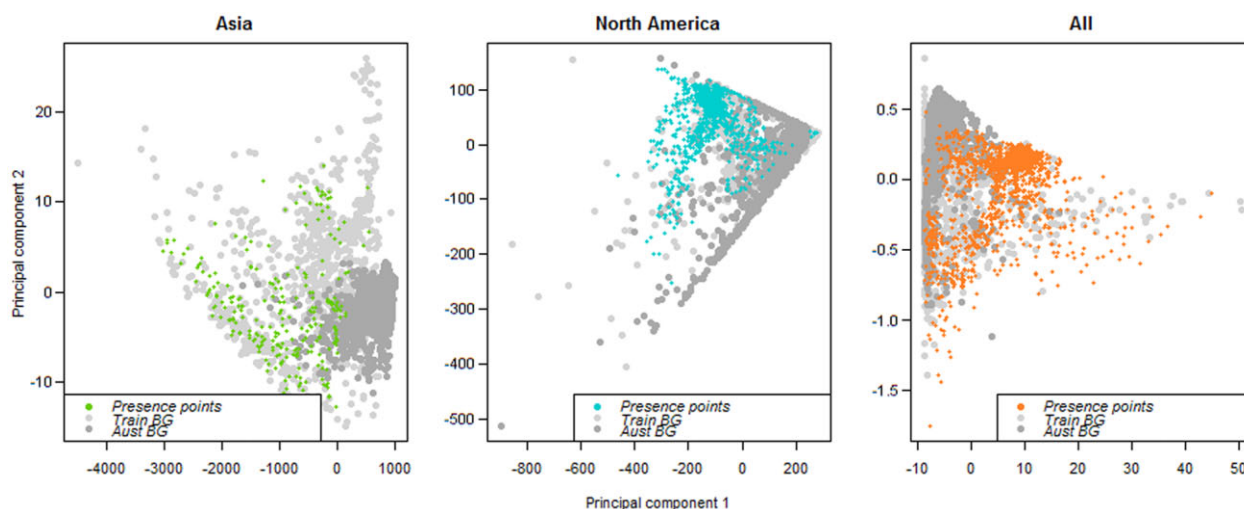


Fig. 2. Principal components analysis (PCA) of the three final predictor variable sets for the respective datasets. The first two principal component axes are shown, giving a summary of the environmental space available in the training background (light grey), the environmental space in Australia (dark grey) and the environmental space of the training points (respective colours).

ranges in our ENMs, we show that different environments can lead to changes in the importance of predictor variables and different geographical projections. Through simple parameter adjustments to allow for evolution in our CLIMEX models, we show that shifts in traits such as cold tolerance can allow for large range expansions. The models predict an invasion potential that is much wider than seen in earlier models, particularly when the expanded North American distribution of this species is taken into account through both modelling methods. Our results support the use of ENMs and CLIMEX together to investigate evolutionary processes that may facilitate establishment and spread of an invasive species.

The invasion potential predicted by the Asian distribution of *A. albopictus* is similar to that presented by Russell *et al.* (2005), with the distribution of this species expected to be closely tied to coastal regions with only a low likelihood of occurrence away from the coast and in southern Victoria and Tasmania. When the invasive distribution in North America or the combined dataset of all available localities are considered, the species is expected to occur in areas with colder extremes (e.g. inland eastern Australia) than indicated by Russell *et al.* (2005) and the risk in Western Australia is also increased. Both models (and predictions based on both ranges) suggest that the species, if established, could persist under climate change with an expanded distribution, particularly by 2050.

The different predictions from the 'original' and 'adapt' CLIMEX models, and the Asia and North American-trained ENMs, highlight the importance of considering evolutionary changes, whether directly or indirectly, when making predictions about species ranges. Previously it has been shown in *A. aegypti* that

evolutionary changes in pupal diapause characteristics may allow this species to persist in Darwin in northern Australia under climate change predictions, whereas this is unlikely without evolution (Kearney *et al.* 2009). This conclusion was based on a model that allows pupal survival under dry conditions to evolve as a threshold trait with an underlying continuous distribution. The current paper follows a different approach, in that the invasive range is used to establish changes in parameters as a consequence of evolutionary shifts, on the assumption that the evolved changes in diapause in North America (Urbanski *et al.* 2012) as well as changes in other traits affecting invasive distributions could also occur in Australia. The likelihood of such evolutionary changes in response to climate will depend partly on levels of genetic variation within Australian populations, as well as other factors influencing rates of evolutionary adaptation under climate variability (Hoffmann & Sgrò 2011).

Confidence placed on ENM predictions of invasion potential should increase by incorporating distribution points as they become available from regions such as South America and Europe. Medley (2010) examined these environments, in addition to Asia and North America, using PCA. This analysis suggested niche divergence between all of these environments (Medley 2010). While populations in North America have adapted to cold conditions (Urbanski *et al.* 2012), for South America and Europe mechanisms behind niche divergence remain speculative (Medley 2010). In the present study we therefore focussed on a contrast between modelling the native range and a range that has undergone recent adaptive shifts, as well as on all available data. The Asia-trained ENM successfully projected to the global range of *A. albopictus*, whereas

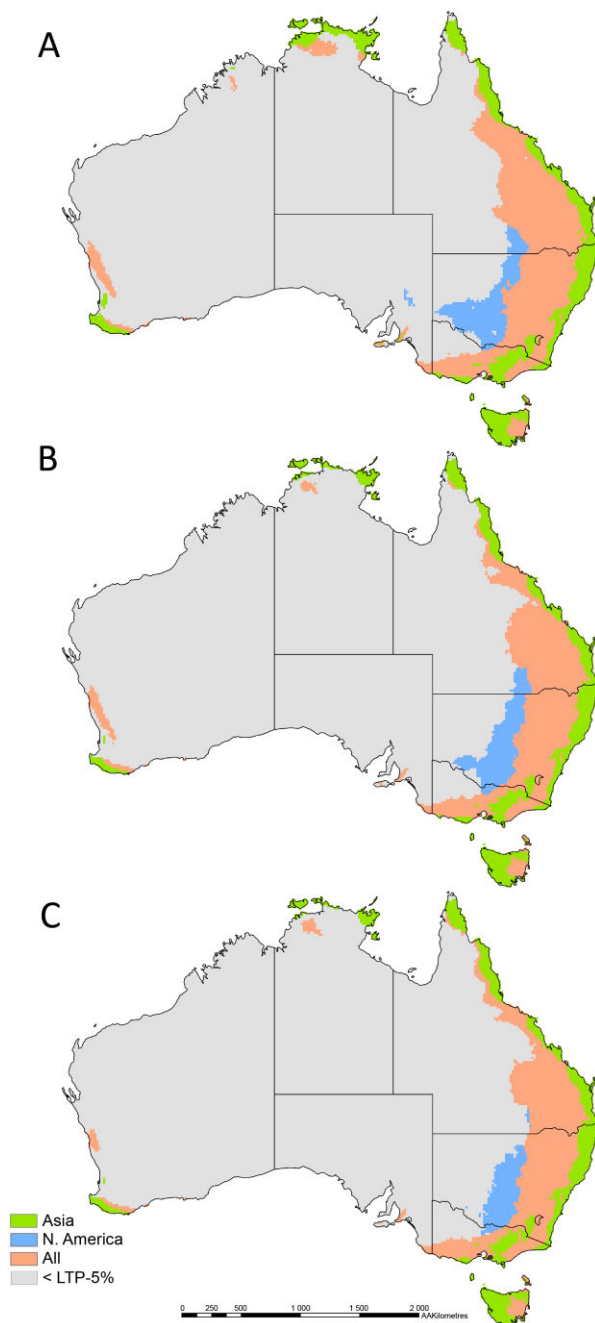


Fig. 3. Environmental Niche Model projections to Australia from native (Asia) and invasive (North America) ranges. Each projection is set at a threshold of least training presence – 5%, allowing for the lower 5% of training record model values to be omitted (LTP-E). Grey represents where ENMs have not projected to Australia above this threshold. A = projection under current climatic conditions. Projections for future time series (B = 2030, C = 2050) are average of CSIRO and Miroc-H A2 SRES projections

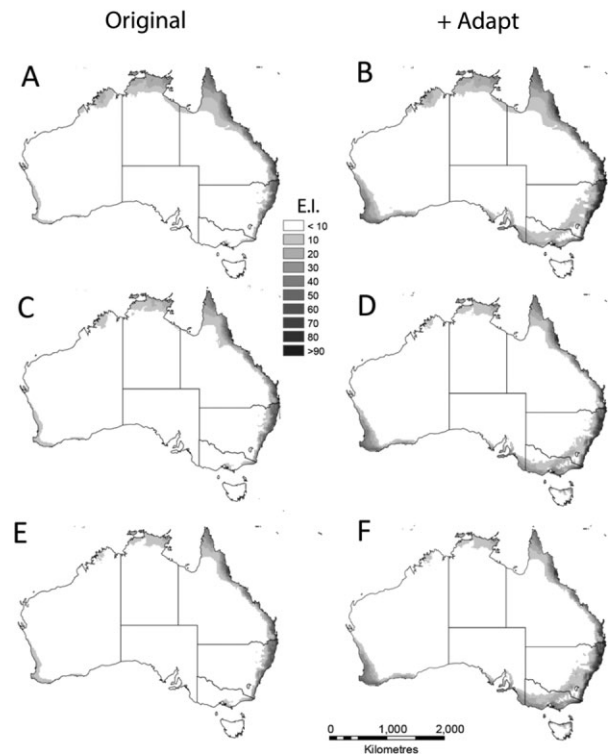


Fig. 4. CLIMEX output for 'original' (Sutherst 1993; Russell *et al.* 2005) and 'adapt' models (lowered DV0 and DV1 parameters). Shading reflects Ecoclimatic Index (EI). A & B = current climate conditions. Projections for future time series are average of CSIRO and Miroc-H A2 SRES projections (C & D = 2030; E & F = 2050).

the North America-trained ENM highlighted unique inland areas in Australia that could also be susceptible to invasion and establishment of *A. albopictus*. These results support the importance of modelling both native and invasive range data (Mau-Crimmins *et al.* 2006; Beaumont *et al.* 2009; Petersen 2013) and also considering sub-taxon subsets (Pearman *et al.* 2010). A trait-based model incorporating cold adaptation may provide a further test of these predicted patterns, especially as the CLIMEX model is more congruent with the Asia-trained projections than with projections based on North America.

There are issues of model transferability when ENMs are extrapolated to novel conditions in either time or space (Jimenez-Valverde *et al.* 2011; Webber *et al.* 2011), as novel combinations of environmental predictors in the projected region may result in either under- or over-prediction of suitability. For instance, the wide predictions given by the North America ENM may be because of the large degree of non-overlap in environmental space between the training data and Australia as seen by the PCA. That is, whilst the MESS analysis revealed no single variable outside of its training range, the combination of variables in

Table 2. CLIMEX parameters for the ‘original’ *Aedes albopictus* model of Sutherst (1993)/Russell *et al.* (2005) and the ‘adapt’ model (this study)

Variable	Description	Sutherst (1993)	Russell <i>et al.</i> (2005)	This study
DV0	Temperature response parameters	12		<u>5</u>
DV1		20		<u>12</u>
DV2		27	30	
DV3		30	37	
SM0	Moisture response parameters	0.2		
SM1		0.7		
SM2		2		
SM3		3		
	Degree days per generation	0		
	Daylength at no growth	0		
	Daylength at maximum growth	0.01		
TTCS	Cold stress temp threshold	0		
THCS	Cold stress Temperature rate	0		
	Cold Stress degree-day threshold	15		
	Cold stress degree-day rate	–0.00015		
TTHS	Heat stress temperature threshold	36		
THHS	Heat stress temperature rate	0		
	Heat stress degree-day threshold	200		
	Heat stress degree-day rate	–0.001		
SMDS	Dry stress threshold	0.2		
HDS	Dry stress rate	0.001		
SMWS	Wet stress threshold	3		
HWS	Wet stress rate	0		
	Day-degree accumulation above DV3	100		

Different values are underlined and in bold.

environmental space is different. Further, by reducing complexity for our correlative ENMs and using simple environmental predictors, we may be over-predicting the invasion potential of *A. albopictus* into Australia. However, a greater risk is that the ENMs are overly complex or over-fitted and then under-predict the invasion potential for Australia (Jimenez-Valverde *et al.* 2011). Other studies have examined how correlative methods (and CLIMEX) behave during extrapolation (Webber *et al.* 2011), the effect of different predictor variable sets on ENMs (Ficetola *et al.* 2007; Peterson & Nakazawa 2008; Rodder & Lotters 2009), and how ENMs can be used to elicit ecological processes that change during invasion (Broennimann *et al.* 2007; Hill *et al.* 2012). As we could compare our predictions with an existing CLIMEX model, reduced-complexity ENMs provide a comparatively broad assessment of invasion potential for *A. albopictus* into Australia. Our Asia-trained ENM displayed high congruence with the CLIMEX ‘adapt’ model, providing a baseline for evaluating invasion risk for *A. albopictus* in Australia; other model-generated hypotheses can then be tested through empirical means (e.g. the North America-trained ENM projections).

In summary, it appears likely that *A. albopictus* will have a broad geographic distribution in Australia and

that this distribution is likely to persist across future decades under climate change. The distribution will be influenced by evolutionary shifts within mosquito populations and/or introductions from different geographical regions. These types of results serve as an important risk assessment for *A. albopictus* invasion into Australia (Williams 2012) and also as a comparison to future trait-based models built on the life-history of this species. The approaches we used also illustrate more generally how *in situ* evolutionary processes and/or multiple introductions might be incorporated into distribution models to predict areas likely to be occupied by invasive species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Global projections of *Aedes albopictus* ecological niche models.

Appendix S2. Multivariate environmental similarity surface layers for global projections of *Aedes albopictus* ecological niche models.