



Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models

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ABSTRACT

Aim Niche-based distribution models are often used to predict the spread of invasive species. These models assume niche conservatism during invasion, but invasive species can have different requirements from populations in their native range for many reasons, including niche evolution. I used distribution modelling to investigate niche conservatism for the Asian tiger mosquito (*Aedes albopictus* Skuse) during its invasion of three continents. I also used this approach to predict areas at risk of invasion from propagules originating from invasive populations.

Location Models were created for Southeast Asia, North and South America, and Europe.

Methods I used maximum entropy (MAXENT) to create distribution models using occurrence data and 18 environmental datasets. One native model was created for Southeast Asia; this model was projected onto North America, South America and Europe. Three models were created independently for the non-native ranges and projected onto the native range. Niche overlap between native and non-native predictions was evaluated by comparing probability surfaces between models using real data and random models generated using a permutation approach.

Results The native model failed to predict an entire region of occurrences in South America, approximately 20% of occurrences in North America and nearly all Italian occurrences of *A. albopictus*. Non-native models poorly predict the native range, but predict additional areas at risk for invasion globally. Niche overlap metrics indicate that non-native distributions are more similar to the native niche than a random prediction, but they are not equivalent. Multivariate analyses support modelled differences in niche characteristics among continents, and reveal important variables explaining these differences.

Main conclusions The niche of *A. albopictus* has shifted on invaded continents relative to its native range (Southeast Asia). Statistical comparisons reveal that the niche for introduced distributions is not equivalent to the native niche. Furthermore, reciprocal models highlight the importance of controlling bi-directional dispersal between native and non-native distributions.

Keywords

Aedes albopictus, niche-based distribution modelling, niche conservatism, niche shifts, reciprocal distribution modelling, species invasions.

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INTRODUCTION

Invasive species potentially threaten global biodiversity, cause economic loss and contribute to the spread of disease

(Lounibos, 2002; Lockwood *et al.*, 2007). Understanding the factors that make non-native species successful invaders is an important step to managing geographic spread. Niche-based models predict species distributions based on occurrence points

and climate and environmental datasets (Guisan & Thuiller, 2005; Phillips *et al.*, 2006) and have recently been extended to predict the geography of species invasions (Peterson, 2003; Reed *et al.*, 2008). A central assumption of such models is that a species' niche is conserved during invasion.

Niche conservatism is the tendency for a species to retain ancestral niche characteristics. This property is useful for understanding historical biogeography, patterns of species diversity, community ecology and speciation, and has been assumed when predicting the spread of invasive species (Wiens & Graham, 2005). While niche conservatism is probably the rule in several of these frameworks, the ability of non-native species to adapt to novel conditions could explain successful species invasion over modern time-scales. If this is the case, niche-based models will not accurately predict the spread of invasive species, and characteristics of the niche for non-native distributions will not accurately predict the native range. Indeed, this 'reciprocal distribution modelling' (RDM) approach revealed a niche shift for spotted knapweed and fire ant invasions in the United States (US; Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007). RDM proceeds by creating a model using native occurrences and projecting the model onto invaded regions to compare to the actual invasion. A second model using invasive occurrences is created and projected back onto the native distribution (Fitzpatrick *et al.*, 2007). If the native model accurately predicts the introduced distribution, and vice versa, the niche has been conserved. Discrepancies between models can facilitate hypothesis generation and the elucidation of processes influencing successful invasions (Fitzpatrick *et al.*, 2007).

One explanation for incongruence between model predictions is the 'enemy release hypothesis' (ERH). The ERH predicts that release from native biotic interactions could allow non-native species to colonize novel habitats, provided that the invader is already adapted to local abiotic conditions (Richardson *et al.*, 2000; MacIsaac *et al.*, 2001; Keane & Crawley, 2002). Thus, to best test ideas about niche conservation during invasion, species must be selected that minimize the likelihood of enemy release, such as a dominant competitor.

This study tests hypotheses using the invasion of the Asian tiger mosquito (*Aedes albopictus* Skuse). This species is native to Southeast Asia, and has invaded five continents in the last *c.* 25 years. Experiments evaluating competitive interactions between US populations of *A. albopictus* and the introduced *Aedes aegypti* have revealed *A. albopictus* consistently emerges as the superior competitor (Braks *et al.*, 2004; Juliano & Lounibos, 2005, and references therein). Furthermore, the native range of *A. albopictus* overlaps with other native and non-native mosquitoes in Southeast Asia. Thus, it is unlikely that competition constrains the extent of its native range.

In the current study, I used an RDM approach with maximum entropy models to test the null hypothesis that the niche for the Asian tiger mosquito (*A. albopictus*) has been conserved during its invasion of three continents. Niche conservation is indicated if the native model accurately predicts non-native distributions and non-native models accurately predict the native distribution. Alternatively, if reciprocal models poorly predict one

another, a niche shift is indicated. To support these reciprocal comparisons, I used two recently developed metrics of niche overlap (equivalency versus similarity; Warren *et al.*, 2008) to compare RDMs. I also applied multivariate analyses to visualize and evaluate statistical differences in multidimensional climate and environmental characteristics among continental distributions. Finally, I evaluated the risk of range expansion in Southeast Asia using non-native model predictions of the native range and highlight the potential for dispersal from invasive populations to other continents to increase the global invasiveness of the species.

METHODS

Species occurrence data

All recorded occurrences of *A. albopictus* were compiled from the literature (Rossi *et al.*, 1999; Schaffner & Karch, 2000; Chadee *et al.*, 2003; Bennett *et al.*, 2005; Aranda *et al.*, 2006; Klobučar *et al.*, 2006; Benedict *et al.*, 2007; Krueger & Hagen, 2007). Occurrences were represented as points (latitude and longitude), except in the US where data were county-level. These data were converted to points by digitizing the centroid of each positive county in a GIS (ArcGIS, Environmental Systems Research Institute, Redlands, CA, USA). Literature reports of occurrence of *A. albopictus* without evidence of establishment were not included in the dataset. In total, 6599 occurrence points were compiled: 236 points for the native range (Asia, Indonesia and Japan), 73 points for Europe, 1052 points for North America and 5238 points for South America. To reduce sampling bias and autocorrelation of climatic data during model generation, I randomly selected 200 occurrence points from each of Asia, North America and South America using Hawth's Tools (<http://www.spatial ecology.com>). All 73 points were used for Europe because sample locations were not as clustered as for other continents, and to improve balance in the number of data points between continents for multivariate analyses (see 'Niche comparisons among continents' below). Comparable occurrence data were not available for Africa.

Climate layers

Climatic and environmental datasets were chosen based upon their ability to affect the physiological ecology of *A. albopictus* (Pumpuni *et al.*, 1992; Alto & Juliano, 2001; Lounibos *et al.*, 2002; e.g. Armbruster & Conn, 2006; Table 1). Variables that were highly correlated ($r \geq 0.70$) were excluded from the final models, resulting in seven variables representing temperature and precipitation from the WORLDCLIM database (Hijmans *et al.*, 2005), eight layers representing relative humidity and photoperiod from the IWMI database (<http://dw.iwmi.org>), land cover (Global Land Cover Facility) and mean frost days and mean wind speed obtained from the CRU CL 2.0 database (Table 1; New *et al.*, 2002). WORLDCLIM and land-cover data were obtained at 5-arcmin resolution and the remaining four layers were obtained at 10-arcmin resolution. To maintain the

Table 1 Climate and environmental layers used in models. Principal components analysis (PCA) eigenvalues are presented for all variables. Eigenvalues for the most important variables in the PCA are in bold. Additional source information and citations are provided in the text.

Data source	Variable	Description	PCA eigenvalues		
			Axis 1	Axis 2	Axis 3
WORLDCLIM	BIO1	Annual mean temperature	-0.77	-0.57	-0.14
	BIO5	Mean maximum temperature of the warmest month	-0.09	-0.72	0.25
	BIO6	Mean minimum temperature of the coldest month	-0.85	-0.39	-0.23
	BIO12	Annual precipitation	-0.77	0.19	0.10
	BIO13	Precipitation of the wettest month	-0.81	-0.16	0.00
	BIO14	Precipitation of the driest month	-0.07	0.55	0.22
IWM1	SUNFEB	Per cent maximum sunlight hours during February	-0.10	-0.63	0.49
	SUNJUN	Per cent maximum sunlight hours during June	0.50	-0.32	-0.49
	SUNAUG	Per cent maximum sunlight hours during August	0.53	-0.26	-0.57
	SUNNOV	Per cent maximum sunlight hours during November	-0.04	-0.78	0.25
	REHFEB	Per cent relative humidity during February	-0.57	0.36	-0.62
	REHMAY	Per cent relative humidity during May	-0.74	0.29	-0.21
	REHAUG	Per cent relative humidity during August	-0.47	0.38	0.66
	REHNOV	Per cent relative humidity during November	-0.57	0.50	0.02
CRU Cl 2.0	FRS	Days with ground frost per month	0.77	0.40	0.30
	WIND	Mean wind speed	0.54	0.02	0.18
GLCF	LANDCOV	Land cover	0.22	-0.16	0.33
Eigenvalue			5.53	3.34	2.19
Percentage variance			30.73	18.57	12.19
Cumulative percentage variance			30.73	49.3	61.49

highest data resolution, data at 10 arcmin were resampled to 5-arcmin resolution in ArcGIS using bilinear interpolation, and were clipped to the same extent as the WORLDCLIM layers. All layers were exported as ASCII grids. Although the datasets include both climate and local environmental data, the complete dataset will hereafter be referred to as 'environmental data' for simplicity.

Modelling approach

All models were developed using a maximum entropy algorithm implemented using MAXENT software (Phillips *et al.*, 2004, 2006). Maximum entropy is a machine-learning technique that predicts species distributions using detailed climatic and environmental datasets together with species occurrence data; it generally performs better than other algorithms in tests of model performance (Elith *et al.*, 2006; Phillips *et al.*, 2006; Ortega-Huerta & Peterson, 2008). Maximum entropy is more robust to spatial errors in occurrence data and uses presence-only datasets to predict the suitability of habitat (Phillips *et al.*, 2006; Graham *et al.*, 2008).

Reciprocal models

I generated reciprocal models by first creating a model for the native range and a model for each invasion (South America, North America and Europe) using occurrence points and environmental data clipped to the appropriate continent. I then

projected the native model onto each invasive distribution and compared it with the model generated using occurrences from each invaded range. I also projected each invasive distribution onto the native range and compared them with the distribution generated with native occurrences. Finally, to explore areas at risk of invasion globally from propagules originating from invasive distributions, I projected each invasive model onto all continents. To improve the transferability of models across space, I used a regularization modifier of 1 (Phillips & Dudík, 2008). Regularization reduces the likelihood of overfitting models, thus increasing the predictive ability of models beyond the training region (Phillips & Dudík, 2008).

To evaluate model accuracy, I randomly selected 40% of occurrence points (from the set of 200 points selected for Asia, North America and South America and from the full set of 73 points for Europe) to train each model and used the remainder to test each model using both binary tests of omission and analysis of the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips *et al.*, 2006). I calculated binary omission rates as the proportion of test points that were not predicted at a threshold probability that equalled the minimum probability of any pixel containing an occurrence point. AUC is a composite measure of model performance, and provides a global comparison of model fit to that of a random prediction. AUC values range from 0 to 1, where 1 is a perfect fit. Useful models produce AUC values of 0.7–0.9, and excellent models produce AUC values above 0.9 (Swets, 1988).

Niche comparisons among continents

I used principal components analysis (PCA) to compare environmental data among distributions using PC-ORD 5 (MjM Software, Gleneden Beach, OR, USA). I extracted environmental data at each occurrence point in a GIS (ARCGIS). To conform to the assumption of normality, I log-transformed Bio 3 and Bio 4 WORLDCLIM data and all relative humidity data from IWMI, and square-root transformed the mean number of frost days. To assess significance, I compared variation explained by each PCA axis to that obtained from 1000 PCAs conducted on matrices containing random values. A significant result indicates that PCA axes are significantly better than a random configuration (McCune & Grace, 2002). I used multi-response permutation procedures (MRPP) in PC-ORD 5 to test the null hypothesis that environmental data at occurrence points in the native range for *A. albopictus* were no different from those data at occurrence points on other continents. MRPP is a non-parametric procedure that tests differences between groups, and is conceptually similar to ANOVA in that it assesses within-group similarity compared with among-group similarity (McCune & Grace, 2002). Finally, I correlated each environmental variable with scores from the most important PCA axes to evaluate the most important variable(s) in the PCA.

In addition to evaluating environmental differences among continents at occurrence points, I used two new approaches to evaluate niche characteristics between modelled distributions (Warren *et al.*, 2008). Evaluating differences only at known occurrences biases environmental values towards sampling locations. Comparisons between entire distributions provide a broader estimate of the niche for each distribution, including potential occurrences within distributions. I used a permutation-based approach to evaluate niche similarity and niche equivalency between distributions. Both values compare niche overlap between a pair of real models with niche overlap between a real model and a model generated using either randomly generated occurrence points (niche similarity) or a randomly selected subset of the pooled occurrences for both distributions in the comparison (niche equivalency). For both comparisons, I calculated niche overlap between pairs of models using the metric *I* (Warren *et al.*, 2008), which ranges from 0 (no overlap) to 1 (identical). The metric compares probability values for individual pixels between two distributions. Thus, *I* evaluates differences in potential occupancy predictions between two models. I provide specific methods for niche similarity and niche equivalency below.

Niche similarity

Niche similarity compares models created with real occurrences with models created with randomly generated occurrences over the same geographic area (Warren *et al.*, 2008). To evaluate niche similarity, I calculated *I* between two models based upon real occurrences: one (focal) distribution generated with occurrences in that range (e.g. the native model) and another model generated with occurrences in another range (e.g. the South

American model) that was projected onto the geographic space of the focal distribution. Then I created models with 200 randomly generated points in each distribution and replicated this 100 times in a script written in R 2.8.1 using the *sp* package. I calculated *I* between each random model and the focal model, and compared the *I*-value calculated between real models with a histogram of *I*-values between the focal model and random models. A significant (one-tailed) test indicates niche overlap between real models is higher than niche overlap between real and random models.

Niche equivalency

Niche equivalency compares models created with real occurrences with models created with occurrences randomly selected from real occurrences (Warren *et al.*, 2008). For this study, the geographic extent of each distribution in the comparison was the combined size of two distributions. The metric *I* was calculated in the same way as for niche similarity, except that permutations used a random subset of 200 of the *actual* pooled occurrence points for both distributions included in each calculation. The probability that distributions are significantly different is indicated by the calculated *I* relative to a histogram of *I*-values calculated from random distributions. A significant (two-tailed) test indicates that niche overlap between real models is not equivalent to niche overlap between real and random models.

RESULTS

Models for individual distributions were all significantly better than random and predicted occurrences within the training region with low omission and high AUC values, indicating excellent model performance (Table 2). However, modelled distributions for one continent did not accurately predict the distributions for other continents. The native model (Fig. 1a) predicted a broad distribution for South America with high-risk areas in the south-east and north-west of the continent, and

Table 2 Model accuracy results using area under the curve (AUC) and binary tests of omission. AUC is a global assessment of model performance and values range from 0–1, where 1 is a perfect fit. A binomial omission test evaluated the rate of failure for test point prediction for each model. A significant binomial test indicates that the predicted omission rate was less than a random prediction. *P*-values for all omission tests were less than 0.001.

Model	Omission rate (% of test points not predicted)	AUC
Native (Southeast Asia)	4.9	0.989
South America	0.2	0.985
North America	0.5	0.993
Europe	0.0	0.998

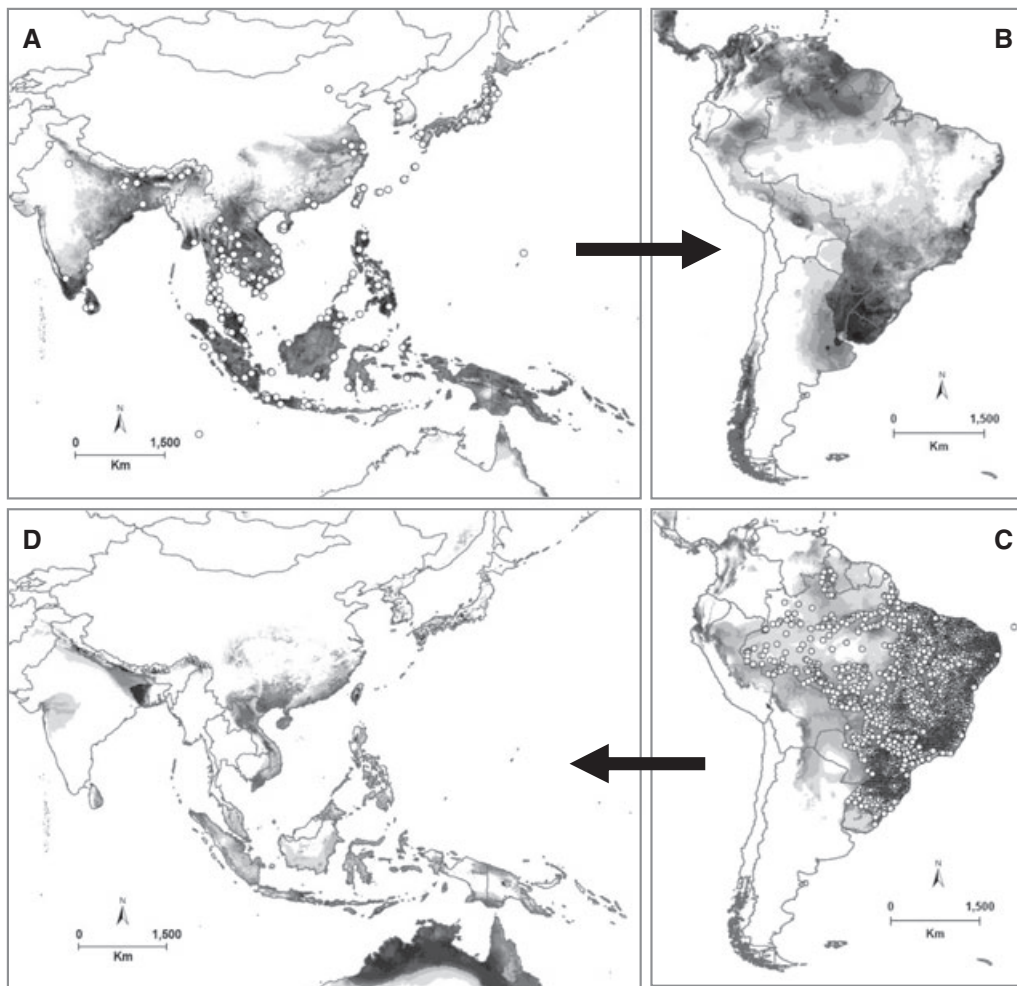


Figure 1 Distributions based upon maximum entropy niche models using environmental data and point occurrences for *Aedes albopictus*. Colour darkens on a ramp from low to high probability of occurrence (0–100%). White dots represent occurrences for *A. albopictus*. (A) Native model generated with occurrences in the native range (Asia, Japan, Indonesia). (B) Native model (Asia, Japan, Indonesia) projected onto South America. (C) Model generated with occurrences in South America. (D) South American model projected onto the native range. Arrows indicate the direction of model projections.

failed to predict many occurrences along the north-east coastal region and Amazon Basin (Fig. 1b). Reciprocally, the South American model (Fig. 1c) predicted a portion of the native distribution, but also predicted high-risk areas in eastern India and northern Australia (Fig. 1d). For North America, the native model (Fig. 2a) predicted a large portion of actual occurrences (c. 80%, Fig. 2b), but failed to predict its northward and westward expansion (Fig. 2c). Rather, the native model shifted high-risk areas into Mexico and the Caribbean islands (Fig. 2b). Reciprocally, the North American model (Fig. 2c) predicted a very small native distribution (Fig. 2d) that was a subset of the actual native distribution and extended slightly north-east beyond the distribution predicted with the native model. Finally, the native model (Fig. 3a) predicted a European distribution along the border between Italy and France, Switzerland and Germany, and areas along the eastern Adriatic coast (Fig. 3b), but failed to predict nearly all actual occurrences in Italy. The European model predicted much higher local probabilities of

occurrence in Italy (Fig. 3c). When projected onto the native range, the European model predicted a wide band of high risk near the northern border of the native distribution (south-central China), and failed to accurately predict the distribution in Southeast Asia (Fig. 3d).

Statistical comparisons between continents supported differences among modelled distributions. PCA ordination revealed three axes that were significantly different from random ($P < 0.001$), and indicated clear shifts in the niche space at occurrence points in the four distributions (Fig. 4). Variables that were strongly correlated ($r > 0.70$) with the first axis were annual mean temperature, mean minimum temperature for the coldest month, annual precipitation, precipitation of the wettest month, relative humidity during May and number of frost days (Table 1). Mean maximum temperature for the warmest month and November photoperiod correlated most with the second axis (Table 1). MRPP analyses revealed that environmental characteristics at occurrence points were significantly different

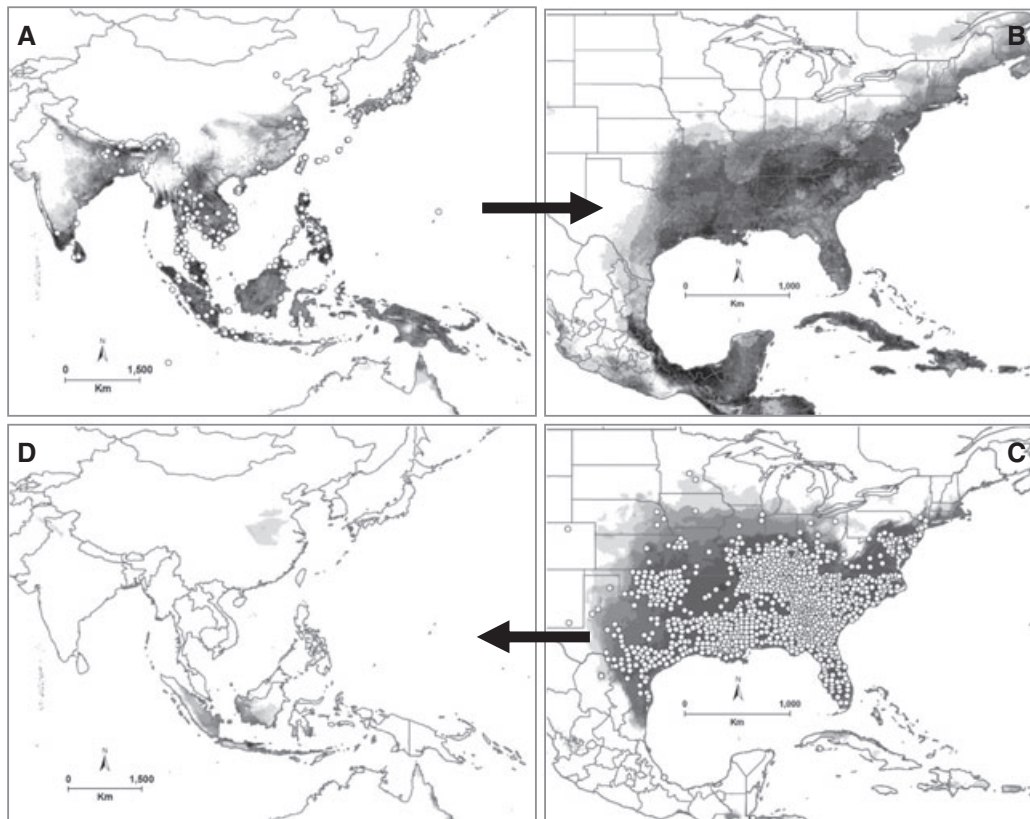


Figure 2 Distributions based upon maximum entropy niche models using environmental data and point occurrences for *Aedes albopictus*. Colour darkens on a ramp from low to high probability of occurrence (0–100%). White dots represent occurrences for *A. albopictus*. (A) Native model generated with occurrences in the native range (Asia, Japan, Indonesia). (B) Native model (Asia, Japan, Indonesia) projected onto North America. (C) Model generated with occurrences in North America. (D) North American model projected onto the native range. Arrows indicate the direction of model projections.

between all pairs of continents. Tests for niche similarity revealed that all native and introduced distributions were more similar than random (Table 3). However, for all comparisons, the niche for introduced distributions was not equivalent to the native niche (Table 3).

Projecting invasive distributions onto all continents revealed areas at risk of invasion and/or further spread (Fig. 5). In addition to predicting high-risk areas in north Australia, the South American model predicted a broad area of high risk in Africa (Fig. 5a). The North American model predicts a high-risk area along the north-east coast of South America (Fig. 5b), and the European model predicts high-risk areas in north-western South America where populations have not yet established (Fig. 5c).

DISCUSSION

Niche shifts are apparent for three invasions (North and South American, Europe) of *A. albopictus*, based upon reciprocal niche-based distribution models, ordination and measures of niche similarity and equivalency. Ordination techniques such as PCA are commonly employed to evaluate niche differences between distributions, but because this approach only considers

the environment at sampling points, information from other areas where populations probably exist (but aren't sampled) is lost. In the current study, some error could have been introduced into the ordination (PCA) by extracting environmental data from the centroid of US counties, but a more comprehensive comparison of the niche was possible by using newly developed permutation-based niche overlap statistics (Warren *et al.*, 2008). These statistics revealed that the niche for introduced distributions was more similar than expected by chance, but the niche for invasive distributions was not equivalent to the native niche. The niche between populations of the same species and even closely related species is expected to be similar (Wiens & Graham, 2005), so the result that native and invasive populations of *A. albopictus* were more similar than random is not surprising. Niche divergence between native and introduced distributions revealed by niche equivalence statistics, however, leads to hypotheses explaining mechanisms for divergence during invasion.

Differences in niche characteristics among all current distributions of *A. albopictus* could result from a shift in the fundamental or realized niche, where the realized niche is a subset of the fundamental niche because of biotic interactions (Hutchinson, 1957). By definition, occurrence points used to

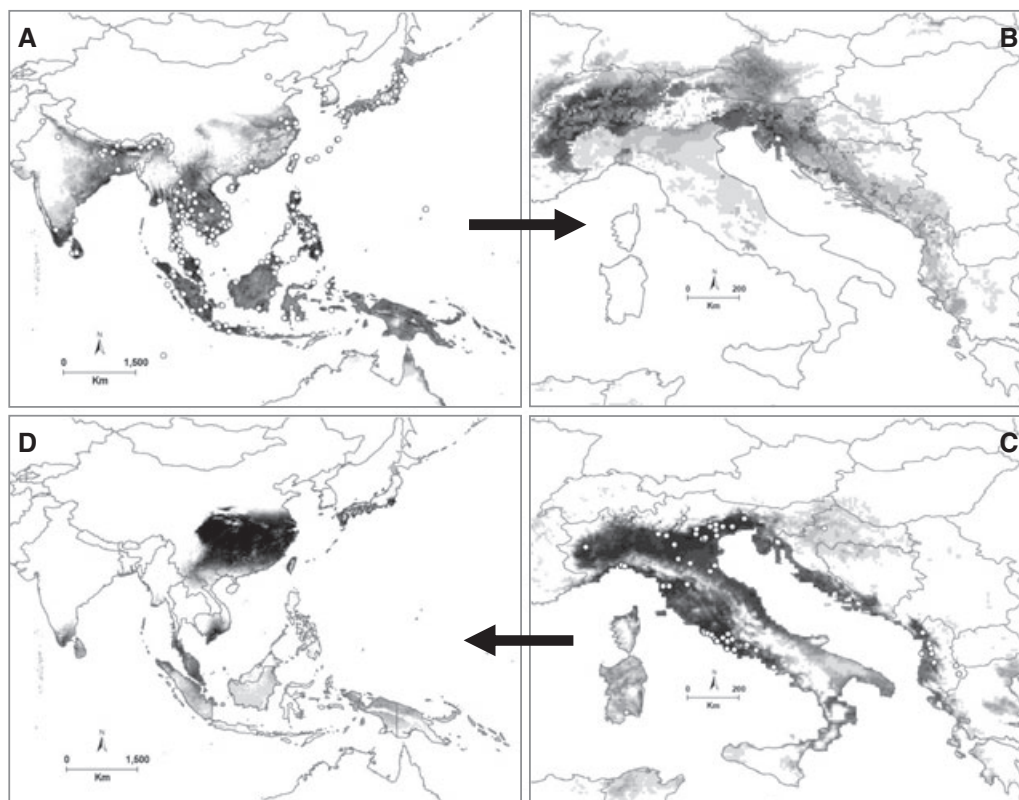


Figure 3 Distributions based upon maximum entropy niche models using environmental data and point occurrences for *Aedes albopictus*. Colour darkens on a ramp from low to high probability of occurrence (0–100%). White dots represent occurrences for *A. albopictus*. (A) Native model generated with occurrences in the native range (Asia, Japan, Indonesia). (B) Native model (Asia, Japan, Indonesia) projected onto Europe. (C) Model generated with occurrences in Europe. (D) European model projected onto the native range. Arrows indicate the direction of model projections.

generate niche-based distribution models represent the realized niche (Phillips *et al.*, 2006), but sampling efforts can incorporate a broad range of environmental heterogeneity. Phillips *et al.* (2006) recommend that models be calibrated with occurrence data from a broad geographic extent so that they approximate the fundamental niche as much as possible. Because the native range for *A. albopictus* is quite broad, it should encompass sufficient environmental variation to predict invasive ranges well. However, patterns of biotic interactions that could constrict the niche throughout the native range are not known, although ecological experiments suggest limited effects of biotic interactions on *A. albopictus*. For instance, recent experiments reveal *A. albopictus* as a consistently dominant competitor, providing evidence that *A. albopictus* is probably not constrained by competition from other mosquitoes (Braks *et al.*, 2004; Juliano & Lounibos, 2005, and references therein). In addition, invasive populations of *A. aegypti* in the US have contracted their range since the invasion of *A. albopictus* and now occur primarily in urban areas in the south-east US (Juliano & Lounibos, 2005). This pattern suggests competitive exclusion of *A. aegypti* by *A. albopictus*, though *A. aegypti* may exclude *A. albopictus* from heavily urban areas. Despite this latter possibility, exclusion from habitat patches does not constrain the extent of the US distribution of *A. albopictus*. Therefore, enemy release seems

unlikely for *A. albopictus*, and niche shifts appear to be in the fundamental niche rather than the realized niche, although verifying this hypothesis requires direct empirical evaluation.

Potential explanations for niche shifts include adaptive evolutionary changes or sampling of genetic material due to founder events. Several cases of adaptive evolution during species invasions have been recently documented. The cane toad invasion of Australia corresponded with greater hind leg length for toads at the invasion front, suggesting an adaptive advantage to colonizing new habitats (Phillips *et al.*, 2006). In England, climate change resulted in range expansion and increased niche breadth for two butterfly species, and selected for flight in a dimorphic cricket (Thomas *et al.*, 2001). Other explanations for apparent niche shifts result from founder events. Founding populations are a genetic subset of the source population, which probably results in a loss of genetic diversity (Holgate, 1966). This should result in lower fitness, but some alleles that are lost during founder events could have previously masked the expression of other alleles (i.e. epistasis). Thus, founder events during invasion could allow expression of beneficial fitness-related alleles in novel environments (Blows & Hoffmann, 2005). Furthermore, multiple introductions could result in novel genetic combinations and allow invasive species to rapidly adapt to different conditions (Kolbe *et al.*, 2004).

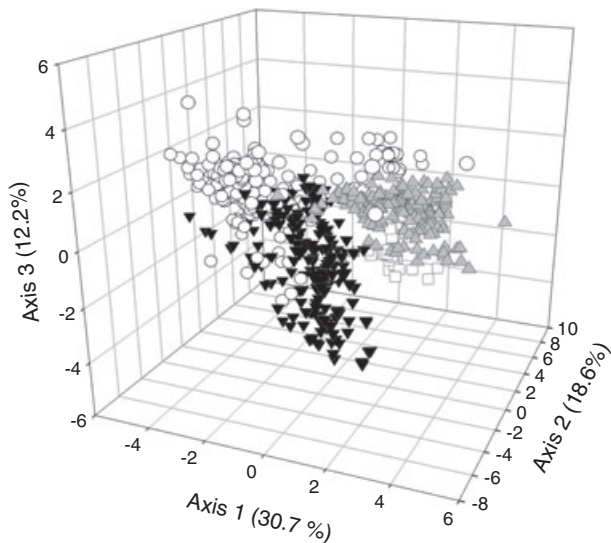


Figure 4 Principal components analysis (PCA) ordination of 18 environmental characteristics at known occurrences for *Aedes albopictus*. Symbols represent continents: black triangle, South America; grey triangle, North America; hollow circle, Asia; square, Europe. The three axes shown explain 62% of the variance for the PCA (axis 1 = 31%, axis 2 = 19%, axis 3 = 12%). Multi-response permutation procedures revealed that all paired comparisons were significantly different ($P < 0.001$).

Table 3 Values for niche overlap (I) and statistics evaluating niche similarity and niche equivalency between distribution models. Significant values for niche similarity indicate that the two distributions are more similar than random. For niche equivalency, significant values indicate that the two distributions are not equivalent. All comparisons reveal that niche is more similar between native and introduced distributions than expected by chance, but they are not equivalent. For niche similarity, the first I -value reported in the pair represents the comparison between the native and introduced model projected onto the introduced distribution. The second value represents the comparison between the native and introduced model projected onto the native range.

Comparison	I	P
Niche similarity		
Europe and Asia	0.50, 0.59	< 0.01
North America and Asia	0.66, 0.62	< 0.01
South America and Asia	0.72, 0.54	< 0.01
Niche equivalency		
North America and Asia	0.39	< 0.01
South America and Asia	0.39	< 0.01
Europe and Asia	0.48	< 0.01

Experimental and observational studies with *A. albopictus* support evolutionary changes in the fundamental niche. In the US, northern populations of *A. albopictus* have refined the ability to diapause and can withstand periods of severe cold and desiccation (Focks *et al.*, 1994; Hanson & Craig, 1995). This is

expected because evidence suggests northern Asian populations to be the source of the US invasion and these populations are more likely to need diapause to persist in the temperate climate (Hawley *et al.*, 1987). However, populations in south Florida have recently reduced the expression of diapause (Lounibos *et al.*, 2003). Armbruster & Conn (2006) detected geographic differences in larval growth rate partially due to temperature on the northern edge of the US range. In South America, genetic evidence points to non-diapausing populations in Southeast Asia as the source of introduction (Kambhampati *et al.*, 1991). Interestingly, the southernmost populations of *A. albopictus* in South America have now developed diapause (Lounibos *et al.*, 2003). It is unclear whether this is due to local adaptive divergence or the introduction of propagules from source populations that express diapause (as discussed above).

A mechanistic understanding of the apparent niche shifts observed here for *A. albopictus* requires empirical evaluation. For example, range margins can expand as a result of local adaptation by sink populations. Dispersal and gene flow may influence this process, though this relationship is equivocal (Garant *et al.*, 2007). Experiments designed to detect adaptation over modern time-scales are challenging, and understanding evolution in sink populations is difficult given the transient nature of such populations. Thus, much work in this area has involved simulation modelling (Holt *et al.*, 2003, 2004), which provides a sound foundation for experimental tests of niche shifts.

If niche conservatism doesn't apply to the spread of invasive species, niche conservatism remains useful to predict the location of introduction. A study examining niche shifts in spotted knapweed in the western US showed that models poorly predicted spread in the invasive range, but accurately predicted sites of introduction (Broennimann *et al.*, 2007). The current study showed a similar result. The first recorded occurrence of *A. albopictus* in the US was in Houston, Texas, in 1985 (Hawley *et al.*, 1987). This area was predicted by the native model, but the species has since spread into areas not predicted by this model. The first occurrence of *A. albopictus* in Europe was recorded in Albania in 1979, and was predicted by the native model (Adhami & Reiter, 1998). Subsequent spread into Italy in 1990 (Sabatini *et al.*, 1990), however, was not predicted by the native model. In South America, Rio de Janeiro was probably the first location of establishment for *A. albopictus* (Lounibos, 2002). Again, this location was predicted by the native model, but the subsequent northward spread of the invasion was not well predicted.

The poor ability of niche-based distribution models to predict invasive distributions is probably not due to insufficiencies in the MAXENT algorithm. This algorithm predicted the native range with high accuracy using native occurrences (Table 2), and many studies comparing this algorithm with others consistently show MAXENT is the most accurate (Hernandez *et al.*, 2006; Phillips *et al.*, 2006; Graham *et al.*, 2008; Ortega-Huerta & Peterson, 2008). Rather, such reciprocal comparisons can be used to understand the process of invasion and broader questions about biogeography.

Projecting non-native models onto the native distribution provides information about independent invasions and

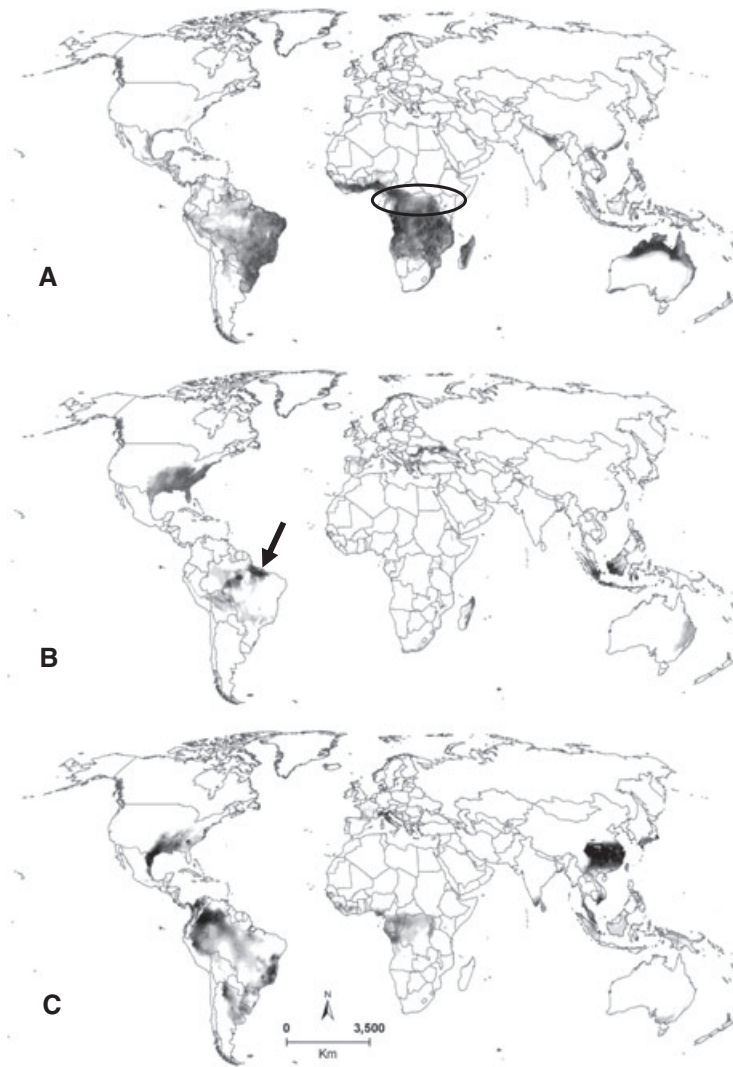


Figure 5 Models from non-native distributions projected across the globe: South American (A), North American (B) and European (C). The darkest shading shows areas at risk of invasion from propagules originating from non-native distributions. The ellipse in (A) shows the approximate distribution for *Aedes albopictus* in Africa. The arrow in (B) shows a population postulated to have been founded from a temperate source (Lounibos *et al.*, 2003). Maps are projected using the Robinson projection.

indicates risk for expansion of the native range. Projecting the South American model onto the native range suggests that initial propagules probably originated from Taiwan or north-east India and Burma/Myanmar. Based on model results, North American propagules probably originated from Indonesia, northern China or Japan. Japan or northern China had previously been considered sources for the initial introduction into Houston based on incidence of egg diapause in colonists (Hawley *et al.*, 1987). Interestingly, high-probability areas predicted in Indonesia by the North American model suggest that Indonesian populations may also have been a viable source of founding propagules. Projecting the European model onto Asia reveals a wide, high-probability band on the northern edge of the native distribution, suggesting that dispersal from Europe into Asia could cause a northward and westward expansion of the native range.

Projecting invasive models onto all continents reveals areas at risk of further expansion and alternate explanations for sources of invasions. High-risk areas predicted in Australia suggest that propagules from South America could establish in Australia. The South American model also predicts a large area of suitability

from the centre of the African continent southward. The current known extent of African populations of *A. albopictus* is rather narrow (Fig. 5a, circle), so it appears that propagules originating from South America could contribute to a southern expansion in Africa. To evaluate invasion into South America, Lounibos *et al.* (2003) examined diapause incidence in South American populations of *A. albopictus*. They found that populations in São Luis on the north-east coast of Brazil had an unusually high diapause response compared with other South American populations, and pointed to an independent invasion from a temperate source. Interestingly, the North American model predicts a high-probability area near São Luis, suggesting that North America could have been the source of this local invasion (Fig. 5b, arrow). Finally, the high-risk area predicted in north-western South America by the European model is currently unoccupied by *A. albopictus* (Fig. 5c). These comparisons collectively reveal that dispersal from native to non-native areas, subsequent niche shifts and dispersal from invasive distributions could serve as an 'invasion ratchet' that broadens the overall niche and the potential for propagules to invade new areas globally. In support of this hypothesis, recent work has shown

that models using both native and invasive occurrence points together to predict invasive species spread are generally more accurate at predicting the extent of spread and the pattern of risk for invasive distributions (Mau-Crimmens *et al.*, 2006; Broennimann & Guisan, 2008).

These results show that successful invasions might best be explained by a combination of ecology (initial establishment) and evolutionary changes (spread) allowing species to occupy novel habitats and spread into new regions. Furthermore, these models illustrate the importance of monitoring both export of propagules from the native range and then from introduced ranges to prevent further expansion in the native range and globally.

CONCLUSIONS

The analyses herein resulted in two important conclusions: the niche for invasive populations of *A. albopictus* has shifted from its native state during invasion of North and South America and Europe, and propagules dispersing from invasive populations have the potential to increase the extent of global spread. These results are important in the broader context of predicting the spread of invasive species because niche-based distribution models may not be an appropriate tool for predicting patterns of spread. However, because the locations of introduction appear to be predicted accurately, niche-based models can be used to focus eradication efforts at ports of entry. Furthermore, these results highlight the importance of controlling transport of invasive species from non-native areas into other areas, as niche shifts in invasive areas and subsequent spread may lead to 'invasion ratcheting', a process that increases the global invasive potential for the species.

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BIOSKETCH

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