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Spread of the Tiger: Global Risk of Invasion by the Mosquito *Aedes albopictus*

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Abstract

Aedes albopictus, commonly known as the Asian tiger mosquito, is currently the most invasive mosquito in the world. It is of medical importance due to its aggressive daytime human-biting behavior and ability to vector many viruses, including dengue, LaCrosse, and West Nile. Invasions into new areas of its potential range are often initiated through the transportation of eggs via the international trade in used tires. We use a genetic algorithm, Genetic Algorithm for Rule Set Production (GARP), to determine the ecological niche of *Ae. albopictus* and predict a global ecological risk map for the continued spread of the species. We combine this analysis with risk due to importation of tires from infested countries and their proximity to countries that have already been invaded to develop a list of countries most at risk for future introductions and establishments. Methods used here have potential for predicting risks of future invasions of vectors or pathogens.

Keywords

Insect vectors; Biodiversity; Public health; Forecasting; Risk factors; Computer simulation

INTRODUCTION

Aedes albopictus, a mosquito native to Asia, has been one of the fastest spreading animal species over the past two decades. In addition to the ecological problems inherent in rapid spread of any species, of particular importance are the serious public health risks posed by the introduction and establishment of an aggressive pest and efficient disease vector.

Ae. albopictus has spread from its native range to at least 28 other countries around the globe, largely through the international trade in used tires (Table 1 and Reiter and Sprenger 1987). These recent invasions by *Ae. albopictus* are modern analogues to the cosmopolitan spread of *Ae. aegypti* on sailing vessels, a process documented by Tabachnick (1991). As an inhabitant of artificial and natural containers, *Ae. albopictus* is especially prone to inadvertent transport of its relatively cold-hardy and long-lived eggs, and to live in close affiliation with humans and their dwellings and refuse (see reviews by Hawley [1988] and Estrada-Franco [1995]). Such specific biologic characteristics of *Ae. albopictus* that are relevant to the invasiveness and ability to displace other species have been reviewed elsewhere (Juliano and Lounibos 2005).

Upon establishment, *Ae. albopictus* may become merely a pest, but its potential to vector a wide range of human pathogens causes the most concern. It ranks second only to *Ae. aegypti* in importance as a vector of dengue virus, and it is a laboratory-competent vector of seven alphaviruses (e.g., Eastern Equine encephalitis and Ross River viruses) and eight bunyaviruses (e.g., LaCrosse and Rift Valley fever viruses). *Ae. albopictus* is also competent to develop three flaviviruses (Japanese encephalitis, West Nile, and yellow fever) to humans (Mitchell 1995, Shroyer 1986), and these, as well as dengue virus, transovarially to its offspring (Estrada-Franco 1995). Here, we model the global spread of *Ae. albopictus* based on its native Asian range using ecological niche modeling. We compare its predicted potential range to those of others made using environmental-limit models. We then compare our results to the locations of documented establishments and spread over the last 20 years. Finally, we list the countries most at risk for future introduction and establishment of *Ae. albopictus*.

MATERIALS AND METHODS

Data

Mosquito occurrence—A database consisting of 206 occurrence points of *Ae. albopictus* in Asia was created by combining 164 records from literature and 42 original points from collections performed in 1989 by W. Hawley and L. Munstermann (personal communication). Four of these could not be used because they fell in coastal fringes outside of the climate layer coverages used. The remaining points were used to develop the species distribution map for its native Asian range. These points are spatially accurate to the minute and to the second in many cases where more precise data were available.

We collected additional information on exotic (i.e., non-Asian) arrivals or establishments of the species in the past 20 years by a literature search and personal communication with public health officials. This consists of 181 unique points distributed worldwide, 5574 in Brazil, and 1033 counties in the United States where *Ae. albopictus* has been collected and recorded. U.S. data were converted from county name to its centroid latitude and longitude. All data are available upon request from the authors.

Environmental—Eleven environmental data layers were selected for model inclusion based on error patterns in preliminary analyses. Ten layers were obtained from the Intergovernmental Panel on Climate Change (IPCC, Anonymous 1989) for the years 1961–1990: annual mean temperature, annual mean maximum temperature, annual mean minimum temperature, average daily temperature range, frost days per annum, topographic aspect (direction of pixel slope), flow accumulation (number of pixels in watershed), topographic index (USGS-Hydro1k, an index combining slope and flow accumulation), annual mean precipitation, and wet days per annum. Land-use/land-cover data were from the University of Maryland, Department of Geography, 1961–1990. Resolution (pixel size) of each environmental layer was 0.1 degrees.

GARP modeling

All models were created using the Genetic Algorithm for Rule Set Production (GARP), which is an implementation of a genetic algorithm designed for predicting and modeling the ecological niches of species (Stockwell and Peters 1999) and is available at www.lifemapper.org/desktopgarp. The GARP modeling system is a simulation of genetic processes of mutation, recombination, and selection operating as a nonrandom search for a solution consisting of an optimized rule set describing the niche. The data set consists of a series of environmental grids and species point occurrence data which are geo-referenced collection sites for a particular species but which do not consider abundance. GARP analyzes distribution information to relate specific ecological characteristics to known occurrences. GARP models have been shown to have predictive value for mosquitoes that is statistically

significant by both stringent intrinsic tests performed on a subset of the data during development and by extrinsic tests of models using data not included in model development (Peterson 2001, Levine et al. 2004). We created 10 GARP models and summed them using ArcView GIS 3.3 for each of the final prediction maps. Therefore, individual pixels of all maps were assigned values of 0–10 representing the number of models that predicted occurrence, i.e., ecological suitability in that pixel. In the results, we refer to the number of models in a particular prediction map that agree on ecological suitability merely to describe the distribution of points and not as a statistical test. Such tests are described separately. All models were created using a maximum of 100,000 iterations and a convergence criterion of 0.0001. The latter criterion determines the degree of change between subsequent models created during each model development that is required to continue the iteration process.

We projected the ecological niche characteristics developed from the mosquito's native range separately onto five other geographic zones: (1) North America and Central America, (2) South America, (3) Europe and the Middle East, (4) Australia and the Pacific Islands, and (5) Africa. These projections are produced by mapping areas of each region that are similar to those determined for the native range predictions using the GARP software. Maps created for each of the five zones were joined together to show a world prediction map for *Ae. albopictus* establishment.

Subsequent to creating the GARP prediction maps based only on ecological suitability, risk of establishment was determined by considering other factors in a stepwise manner. As a precondition for risk, countries in which ecological conditions similar to those in the native range were selected. We observed that all countries in which establishment has occurred have some areas in which there was at least weak prediction map agreement, therefore we excluded countries not having any models agreeing on establishment from further consideration. (Some islands below the resolution of the model climate layers are excluded in this analysis.) We included as infested all countries that have been reported (Table 1) and five more that—although unreported—are likely to be imminently infested due to the proximity of geo-referenced collections near or on the country border: Peru, Uruguay, Venezuela, Guyana, and French Guiana.

Among the remaining ecologically suitable countries, three risk factors were considered: (1) the extent of favorable area for establishment, (2) probable means of introduction via used tire shipments, and (3) shared borders with infested countries. Tire exports from infested countries to uninfested countries for 2002–2004 were obtained from the UN Statistics Division COM-TRADE database under the classification HS02-401220. Most data were provided as kilogram per annum, but where data were presented in number of units, we used the Rubber Manufacturers Association's data to produce a conversion factor of 18.337 kg per tire. Data from all reporters were included, and per annum import averages were calculated. Cluster analysis was performed on the point occurrence precipitation and temperature variables by multiple regression considering two classes: above and below 30 degrees north latitude.

RESULTS AND DISCUSSION

The predicted Asian range map included 202 occurrence points of which two fell completely outside of the predicted range (Fig. 1): one on the Island of Hokkaido, Japan, and the other on the eastern coast of India. Of the remainder, 175 data points (87 %) were within pixels on which a majority of models (i.e., 6 or more) predicted presence.

A χ^2 test was performed to determine whether the distribution of observed occurrences was random relative to the predicted distribution. Of the terrestrial pixels used to create the Asia prediction (Fig. 1), 72.8% (367,740) of the pixels corresponded to those with model agreement

of one or greater. Therefore, a random distribution of points would predict that on average, 147 of the occurrence points would fall within the predicted range by chance. In fact, 200 of 202 fell within the predicted range (χ^2 19.1, 1 *df*, $p < 0.0001$) confirming that the GARP predictions were not random. Potential ranges of *Ae. albopictus* were projected elsewhere using the rules and niche developed in this analysis (Fig. 2) (Peterson and Vieglais 2001).

Because three qualities of data were available, we discuss three non-Australasian areas, United States, and Brazil, individually. Data for Central America (including Mexico), Africa, and Europe and the Middle East were analyzed to determine how many models predicted the occurrence points. The results for Central America and Africa were similar: 92% and 86% of the points, respectively, fell within pixels predicted by a majority of the models, and by far most were within pixels predicted by 9 or 10 models. In contrast, because few pixels in Europe were predicted for presence by a majority of models, only 17 % fell in this range, and 10% fell within pixels for which no models predicted presence, many of these in northern Italy.

For the United States, less precise, but more abundant, occurrence information is available. Two GARP prediction maps (as described above), respectively predicted presence in all but two or 14 of 1011 counties in the United States in which *Ae. albopictus* has been reported (Fig. 3). The exceptions were mainly on the western fringe of the major predicted distribution. In some cases, lack of sampling and/or reporting appear to be responsible for the presumed over-prediction: it is highly likely that Arkansas, Mississippi, Alabama, and Virginia have been extensively colonized by *Ae. albopictus*. Areas that are in fact suitable for *Ae. albopictus* may or may not in fact be occupied either because of lack of an introduction resulting in establishment, model error, and microclimates that support establishment yet fail to be represented by the relatively coarse resolutions used in making predictions.

We predict extensive suitable range on the west coast of the United States that is unoccupied. Three possibilities explain this: (1) over-prediction, (2) introductions resulting in establishment have not yet occurred, or (3) inhospitable seasonal conditions with rainy periods corresponding to cool periods, and warm periods usually being dry. Various authors have previously noted this as a potential obstacle to west coast establishment of *Ae. albopictus* (Nawrocki and Hawley 1987). Egg diapause in the winter, characteristic of temperate *Ae. albopictus* (Lounibos et al. 2003) would limit hibernal development on the West Coast, unless introduced populations were of tropical origin, as observed in southern California in 2001 (Madon et al. 2002). While it is within the capabilities of GARP to account for such variables, this was not done in the current analysis.

An extensive geo-referenced dataset for establishment of *Ae. albopictus* in Brazil was available. It is generally consistent with the GARP predictions (Fig. 4), but because we predict almost all of Brazil is suitable for *Ae. albopictus*, over-prediction is not useful to determine the utility of GARP. Of all points, 4334 of 5501 fell within pixels in which a majority of models agreed on presence.

Two approaches have been used to estimate the potential range of *Ae. albopictus*: field distribution information and laboratory observations of the effects of environment on development and survival. Most emphasis has been placed on winter survivorship of temperate populations which may be protected by egg diapause (Hawley 1988, Kobayashi et al. 2002, Nawrocki and Hawley 1987). However, these provided little detail except for limited areas of Europe (Knudsen 1996, Mitchell 1995), Japan (Kobayashi et al. 2002), and, to a lesser extent, North America (Nawrocki and Hawley 1987). These utilized average January temperatures, degree-days, average annual temperature and precipitation to circumscribe the potential range. The -5°C January isotherm, which Nawrocki and Hawley (1987) considered a liberal estimate of the northern distribution limit, is similar to that which we predict using GARP, though the

latter method resulted in more detail and added a prediction of the western limit of potential habitat in the Midwest. Mitchell (1995) suggested that the maximum distribution of *Ae. albopictus* included limited parts of Spain, Portugal, France, Italy, Greece, Albania, Macedonia, Bulgaria, and Turkey. However, this model did not predict occupied habitat in both northern Italy and France predicted by GARP. Knudsen et al. (1996) used a number of climate factors to develop a risk map for European countries including areas where the monthly mean temperature is 0°C or less in winter and 20°C or more in summer and with at least 50 cm of mean annual rainfall. While ascertaining that the maximum range of *Ae. albopictus* was necessarily more extensive than the location of the 10°C isotherm, the resulting risk map classified the nations of Europe into three categories of high, medium, and low risk and did not attempt to illustrate spatial variation of habitat within each country. Their resulting highest risk countries were ultimately the same ones presented by Mitchell.

Temperature and humidity values at *Ae. albopictus* occurrence points demonstrate an ability to inhabit either relatively cold and dry or warm and wet climates (Fig. 5, Table 2), therefore risk of establishment depends to some extent on the origin of the mosquitoes. Genetic analyses have corroborated that *Ae. albopictus* that colonized the United States were from temperate Japan, but colonizing populations of the same species in Brazil were of tropical origin (Birungi and Munstermann 2002). In its native range, the distribution of *Ae. albopictus* extends from Japan and China to tropical countries such as Malaysia and Singapore (Fig. 1; Hawley 1988). Establishment of temperate latitudes by this species has been facilitated by an egg diapause which confers cold-hardiness but which is absent in tropical populations of *Ae. albopictus* (Hawley et al. 1987, 1989). However, over time, the incidence of egg diapause has decreased as *Ae. albopictus* has spread into warmer climates of the southern United States (Lounibos 2002). By contrast, in Brazil, where *Ae. albopictus* invaders had no diapause in the 1980s (Hawley et al. 1987), this trait was detected in a small percentage of populations that had spread into southern, temperate regions of that country by 2001 (Lounibos 2002).

The egg stage of *Ae. albopictus* suffers high mortality in conditions of low humidity and high temperature, and the known interaction between these mortality factors (Juliano et al. 2002) may account in part for the distribution of U.S. populations of the species in relation to rainfall and temperature (Fig. 1) and the large gap in the midcontinental range (Fig. 3). Although egg diapause confers some resistance to desiccation (Sota and Mogi 1992), most U.S. populations retain a high diapause incidence (Lounibos 2002). Superior tolerance of *Ae. aegypti* eggs to humidity and temperature extremes allows this inferior larval competitor to coexist with *Ae. albopictus* or occupy habitats environmentally unfavorable to the Asian tiger mosquito (Braks et al. 2003).

The approach we have taken of lumping diapausing and non-diapausing types means that our models predict potential distribution *in toto* rather than that of one type or the other. Moreover, because we determined potential distribution based on annual climate values, prediction of habitat whose seasonal suitability would not be reflected in annual averages would be underpredicted or overpredicted. Even with this caveat, previous estimates of risk underestimate the potential distribution in part because annual temperature and rainfall limit values were more restrictive than the range of values observed for the actual distribution of the species. Environmental data for *Ae. albopictus* occurrence demonstrate that it can establish in areas with much lower annual mean temperatures (5°C–28.5°C) and less rainfall (as low as 29 cm annually) than has been suspected.

Establishment risk from a combination of tire import introductions and the extent of suitable habitat was determined. Suitable data were available for 31 unfested countries (Fig. 6): Mainland Australia, New Zealand, and South Africa are clearly most at risk. Two other high tire import countries—The Netherlands and Canada—have an additional risk factor of

bordering on infested countries but are sufficiently cold that disease risk is low. Of the African countries examined, Guinea, Kenya, Tanzania, Uganda, and Zambia are at greatest risk. Additional countries for which no tire data were available also contain extensive areas of suitable niche: Democratic Republic of Congo, Mozambique, Angola, the Central African Republic, Ethiopia, Congo, Côte d' Voire, and Gabon. Regardless of whether tires will be the mode of introduction, *Ae. albopictus* dispersion across the entire continent from the three infested countries (Nigeria, Cameroon, and Equatorial Guinea) could occur toward both the east and west. Only Ethiopia is sufficiently isolated that introduction may not occur via either dispersion or tire imports.

The most suitable large areas in Europe occur in France and may be already infested. However, Portugal, the eastern Adriatic coast, eastern Turkey, and the Caspian Sea coast of Russia are also at risk from both dispersion and tire imports. In the Caribbean and Central America, Belize, Costa Rica, and Haiti have not reported *Aedes albopictus* yet all are surrounded by, or adjacent to, infested countries and they themselves provide suitable niche. Establishment seems highly probable if it has not occurred already. However, the Bahamas and Jamaica may yet escape establishment because both are isolated, but no tire importation data were available.

South America appears to be close to the end of the initial phase of colonization by *Ae. albopictus*. If our presumption of the imminent or actual infestation of five countries bordering Brazil is correct, only three remain uninfested, and all have large areas of suitable niche: Suriname, Ecuador, and Chile. Only Chile differs and may yet escape invasion because the suitable area is isolated from dispersion from neighboring countries. Furthermore, Chile, like some other countries, has banned the importation of used tires, a measure that will provide some protection. However, free trade considerations may win the day over public health concerns (www.trade-environment.org/page/theme/tewto/tyrescase.htm).

There are numerous ways in which risk could be estimated, therefore we present our method as one of many reasonable approaches. By analogy to a forest fire, we based risk on initial introduction—the spark—occurring in favorable ecological habitat—the fuel—with subsequent spread dependent upon the proximity and suitability of additional favorable habitat.

In summary, few suitable countries considered have a reasonable prospect of excluding *Ae. albopictus*. Mainland Australia, New Zealand, the Bahamas, Jamaica, Chile and Ethiopia are most isolated, but thorough inspections and control will be necessary to prevent infestation.

This study predicts the potential global distribution and risk map for the establishment of *Ae. albopictus*. Globalization of cargo trade and increasing air travel means that opportunities for introductions of exotic organisms including pathogens and their hosts are abundant. Methods used in this analysis have potential for predicting risk from future invasions of vectors or pathogens.

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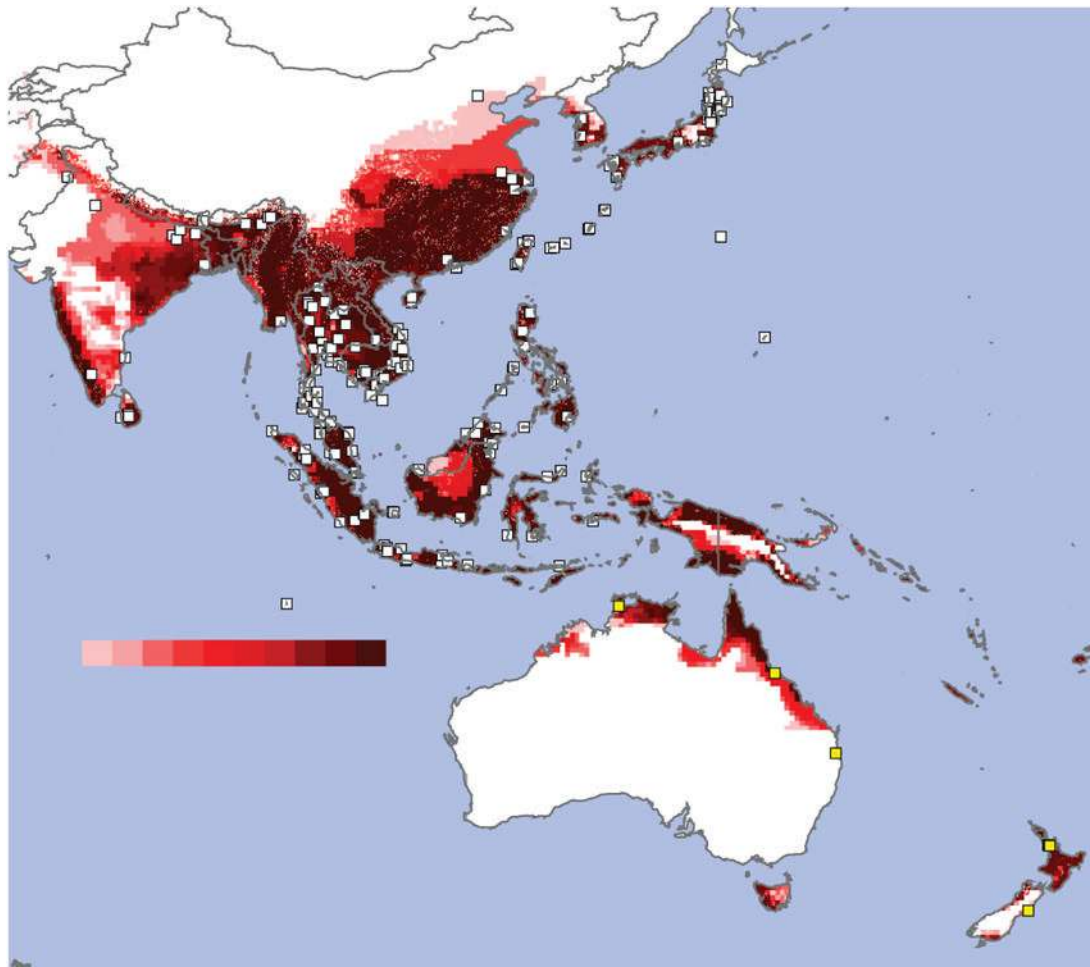


FIG. 1.

Predicted Australasian range map of *Ae. albopictus*. Darker shades indicate pixels for which higher numbers of models predicted potential suitable niches with the darkest shades signifying 10 models. The legend bar shows the 10 colors used. White squares represent the known occurrence points used to create the models. Yellow squares are known introduction sites outside of the native range.

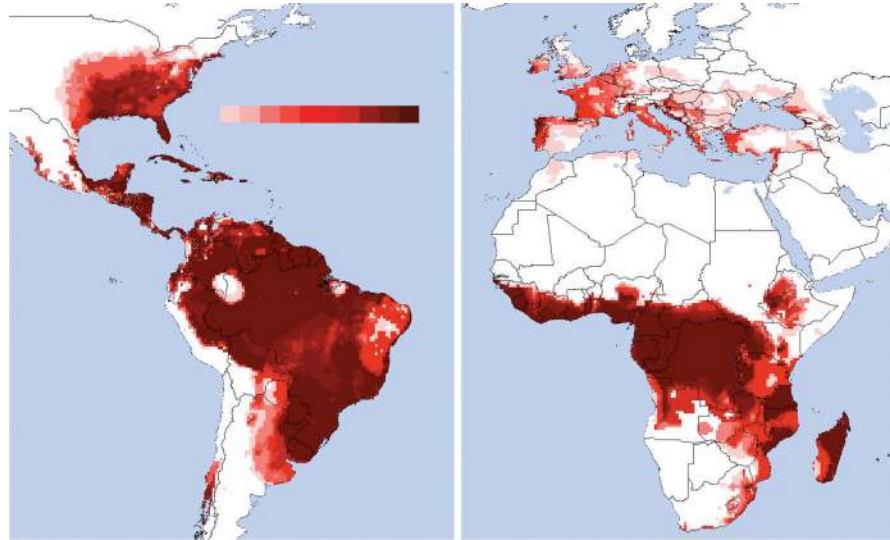


FIG. 2. Predicted non-Australasian potential distribution of *Ae. albopictus*. Darker shades indicate greater numbers of models in agreement for suitable habitat with the darkest shades signifying 10 models with the legend showing each. The predicted distribution in western North America is shown in Figure 3.

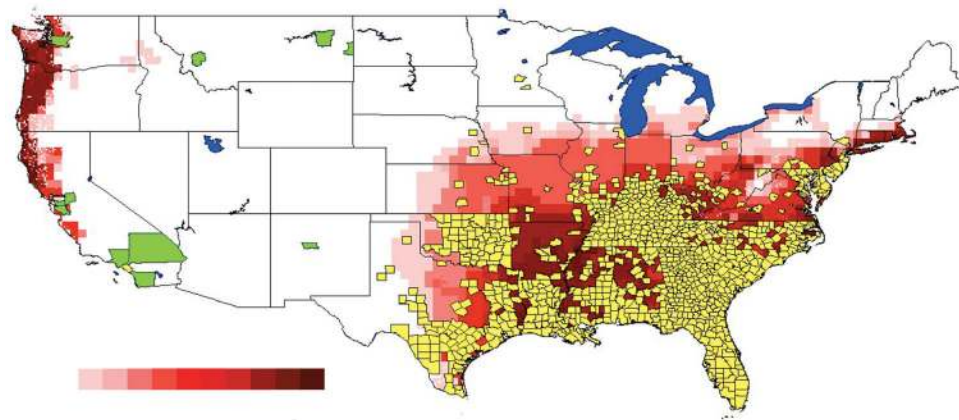


FIG. 3.

Predicted distribution maps and actual spread of *Ae. albopictus* in the lower 48 states. The predicted distribution areas (red) and the documented spread (yellow) of *Ae. albopictus* through the year 2001 are shown. One of the two prediction maps for the US is shown. Differences between the two consisted largely of one of the ten models used to create the prediction map that predicted a broader Texas distribution. Counties colored green are those in which introduction has occurred but not establishment.

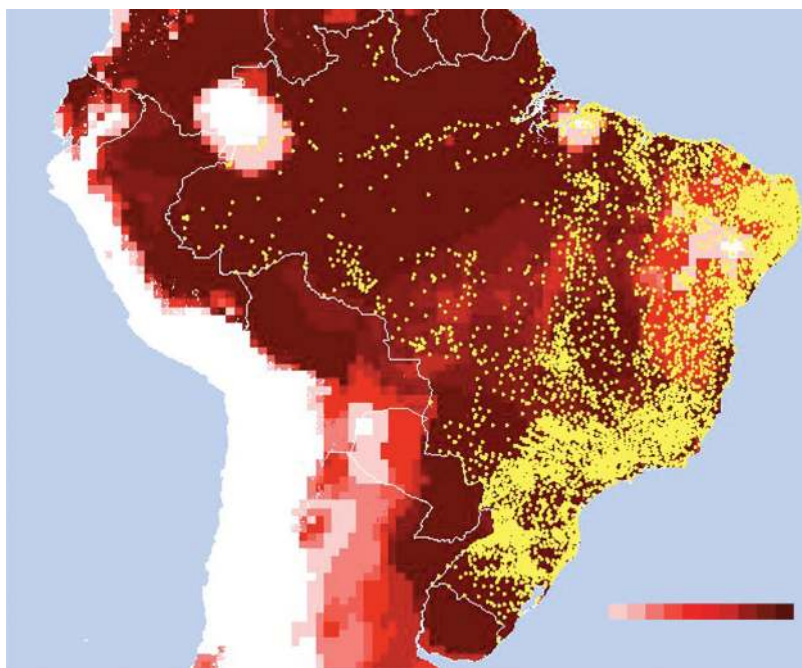
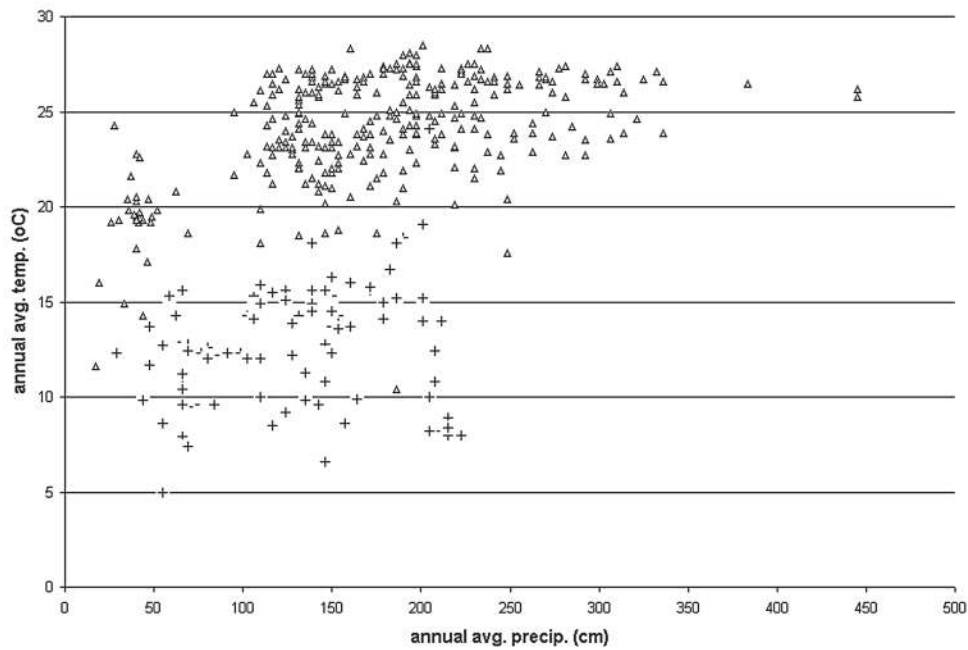


FIG. 4. Predicted distribution and actual spread of *Ae. albopictus* in Brazil as of 2004. Both the predicted distribution (shades of red) and the documented spread (yellow points) of *Ae. albopictus* are displayed.

**FIG. 5.**

Relationship of average annual precipitation and temperature for a subset of global sites of *Ae. albopictus* establishments. Note that the data points fall into two clusters of temperature and precipitation ($p < 0.0001$). Those in the quadrant beneath approximately 18°C and 225 cm precipitation are located above 30 degrees north latitude (Δ). For this analysis, all worldwide points plus a subsample of 10 random U.S. counties and 67 early references to occurrence from Brazil were selected. These are the same points whose values are presented in Table 2.

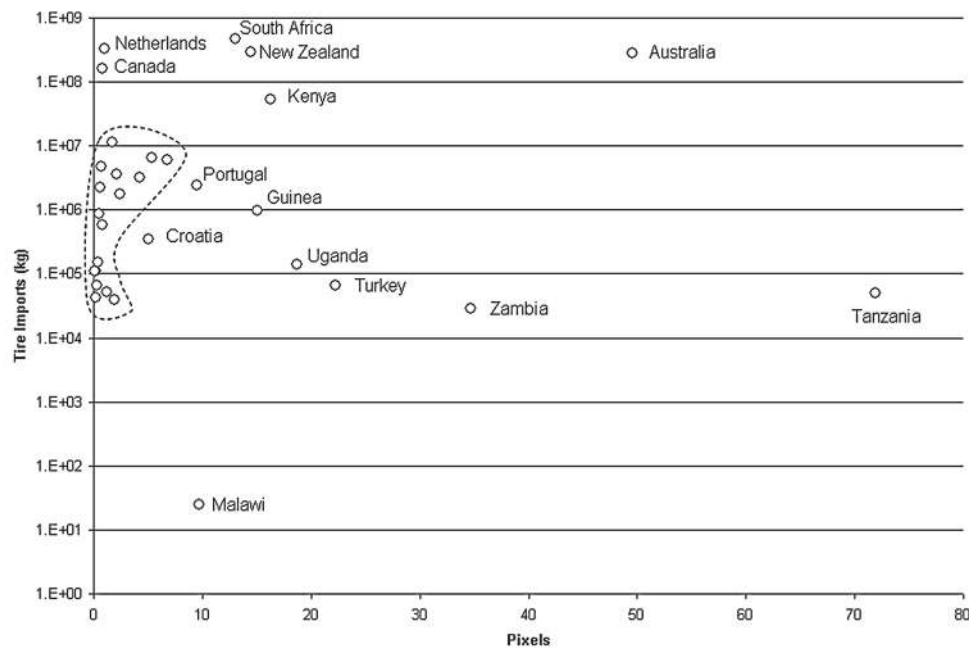


FIG. 6. Comparison of tire imports from infested countries and extent of suitable habitat. Tire imports from infested countries compared to extent of niche in the 4–10 model agreement range. Not labeled individually within the cluster of points in the dotted shape are Germany, Russia, Nepal, Romania, United Kingdom, Benin, Senegal, Pakistan, Guinea, Switzerland, Slovenia, Croatia, Bulgaria, Uganda, Luxembourg, Austria, Macedonia, Hungary, Burkina Faso, Ireland, Zambia, and Malawi.

Table 1
Countries in which *Ae. Albopictus* was Established Between 1979–2004

Invasion year	Country	Reference
1979	Albania ^a	Adhami and Reiter 1998
1983	Trinidad	Le Maitre and Chade 1983
1985	United States	Sprenger and Wuithiranyagool 1986
1986	Brazil	Forattini 1986
1988	Mexico	Anonymous 1989
1990	Italy	Sabatini et al. 1990
1991	Nigeria	Savage et al. 1992
	South Africa ^b	Cornel and Hunt 1991
1993	Barbados	Reiter 1998
	Dominican Republic	Peña 1993
1995	Cuba	Broche and Borja 1999
	Guatemala	Ogata and Samayoa 1996
	Honduras	
	El Salvador	M. Suarez, personal communication
1997	Bolivia	M. Suarez, personal communication
	Cayman Islands	D. Malone, personal communication
		Lounibos et al. 2003
1998	Argentina	Rossi et al. 1999
	Colombia	Velez et al. 1998
	Paraguay	B. Cousinho, personal communication
1999	France	Schaffner and Karch 2000
2000	Cameroon	Fontenille and Toto 2001
2001	Equatorial Guinea	Toto et al. 2003
2002	Panama	
2003	Nicaragua	Lugo et al. 2005
	Greece	Y-M. Linton, personal communication
	Israel	L. Blaustein, personal communication
	Switzerland	Flacio et al. 2004
2004	Belgium	Schaffner et al. 2004
	Spain	Nart 2004

^aInfestations were detected as early as 1979.

^bIntroduction but not establishment was reported.

Table 2

Annual Values for Climatic Environmental Variables at 408 Random Geo-Referenced Points where *Ae. albopictus* Occurs Worldwide

Environmental characteristic	Range	Mean	Median
Mean annual temperature (°C)	5.0–28.5	21.5	23.4
Mean maximum annual temperature (°C)	8.2–33.4	26.3	28.55
Mean annual minimum temperature (°C)	–1.8–24.4	16.7	18.3
Mean annual precipitation (cm)	29.2–445.3	169.0	157.0
Mean annual wet days (<i>n</i>)	30.0–280.8	167.6	169.2
Ground-frost days/month (<i>n</i>)	0–138	14.9	0