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Acta Tropica

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Population genetics and ecological niche of invasive *Aedes albopictus* in Mexico



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ARTICLE INFO

Article history: Received 28 August 2015 Received in revised form 7 January 2016 Accepted 20 January 2016 Available online 24 January 2016

Keywords: Aedes albopictus Population genetics Ecological niche Mexico Climate change Invasive species

ABSTRACT

The Asian tiger mosquito Aedes albopictus (Skuse), is one of the most invasive mosquito species worldwide. In Mexico it is now recorded in 12 states and represents a serious public health problem, given the recent introduction of Chikungunya on the southern border. The aim of this study was to analyze the population genetics of A. albopictus from all major recorded foci, and model its ecological niche. Niche similarity with that from its autochthonous distribution in Asia and other invaded countries were analyzed and its potential future expansion and potential human exposure in climate change scenarios measured. We analyzed 125 sequences of a 317 bp fragment of the cyt b gene from seven A. albopictus populations across Mexico. The samples belong to 25 haplotypes with moderate population structuring (Fst = 0.081, p < 0.02) and population expansion. The most prevalent haplotype, found in all principal sites, was shared with the USA, Brazil, France, Madagascar, and Reunion Island. The ecological niche model using Mexican occurrence records covers 79.7% of the country, and has an 83% overlap with the Asian niche projected to Mexico. Both Neotropical and Nearctic regions are included in the Mexican niche model. Currently in Mexico, 38.6 million inhabitants are exposed to A. albopictus, which is expected to increase to 45.6 million by 2070. Genetic evidence supports collection information that A. albopictus was introduced to Mexico principally by land from the USA and Central and South America. Prevalent haplotypes from Mexico are shared with most invasive regions across the world, just as there was high niche similarity with both natural and invaded regions. The important overlap with the Asian niche model suggests a high potential for the species to disperse to sylvatic regions in Mexico.

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1. Introduction

Aedes albopictus (Skuse) (Diptera: Culicidae), better known as the "tiger mosquito", originated in Asia and is now distributed throughout tropical and temperate areas of all continents (Benedict et al., 2007). Its distribution has dramatically shifted as a result of introduction of the species from the Orient to the New World, Europe and Africa. One of the main dispersal mechanisms is via international trade and ground transport of used tires and lucky

bamboo (*Dracena sanderiana*) (Hawley et al., 1987; Craven et al., 1988; Fontenille and Toto, 2001; Scholte et al., 2008; Medlock et al., 2012). The species invasion of the American continent probably initiated in North America, first collected in the USA in 1985 (Sprenger and Wuithiranyagool, 1986). It has subsequently spread throughout the eastern and central US, as it has to South America (Brazil) (Forattini, 1986). Much later, in 1998, the species was identified in the Misiones province of northern Argentina, on the border with Brazil (Rossi et al., 1999).

A. albopictus was first collected in Mexico in the northern state of Coahuila in 1993, along the non-coastal region of the Mexico-USA border (Ibáñez-Bernal and Martínez-Campos, 1994). By a year later, it was also collected from the northeast Gulf of Mexico coast

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area, in and around Monterrey, Nuevo León (Ibáñez-Bernal and Martinez-Campos, 1994; Rodríguez-Tovar and Ortega-Martínez, 1994; Ibáñez-Bernal et al., 1997; Orta-Pesina et al., 2001). The species then dispersed progressively to other northern border states covering the northern width of Mexico from the Pacific coast, over the Neovolcanic Belt, and to the Gulf of Mexico in the span of a decade (Rodríguez-Tovar and Ortega-Martínez, 1994; Orta-Pesina et al., 2001, 2005; Reyes-Villanueva et al., 2013).

In 2002, specimens were collected close to the southern Mexico-Guatemala border although not in central Mexico, as would have been expected had there been natural north-south dispersal (Casas-Martínez and Torres-Estrada, 2003). The species was periodically reported after that year from other southern states by primary healthcare personnel, and finally in 2010 from the Neovolcanic high plains south of Mexico City, in Morelos (Villegas-Trejo et al., 2010). In 2012, a report confirmed the species from the northeast region of the Yucatan Peninsula, in Cancun (Salomón-Grajales et al., 2012). Currently, *A. albopictus* is recorded from 12 states in Mexico (Chiapas, Coahuila, Hidalgo, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Tamaulipas, and Veracruz) (CONABIO, 2013).

A wide range of amphibians, reptiles, birds, and mammals are natural hosts of A. albopictus in conserved, and anthropic environments, suggesting that the species can be a bridge vector of zoonotic pathogens for humans (Delatte et al., 2010). In human domestic habitats, it feeds and rests outdoors and on vegetation (Marquetti et al., 2000; Delatte et al., 2010), which implies that A. albopictus densities are usually highest in rural and suburban areas (Hawley, 1988). It is a confirmed secondary vector of dengue virus in the American continent (Serufo et al., 1993; Ibáñez-Bernal et al., 1997), even though vector competence and its specific role in maintenance and transmission of the virus is still being studied (Lourenco-de Oliveira et al., 2003; Lambrechts et al., 2010). Most notoriously, the species is a known vector of alphavirus such as Chikungunya, (recently introduced into southern Mexico in 2014), Eastern equine encephalitis virus and Venezuelan equine encephalitis virus; of Flavivirus such as Saint Louis encephalitis and West Nile virus, and Bunyavirus such as La Crosse encephalitis virus (Francy et al., 1990; Gratz 2004; Paupy et al., 2009; Paupy et al., 2010).

Information about the genetic structure and the molecular basis of the genomic background of specific vectors provides evidence of population diversity, an important parameter to evaluate control interventions (Ayres et al., 2002). Molecular genetic markers have been increasingly applied to assess genetic divergence or similarities among geographically isolated populations (Avise and Ball, 1990). Many authors have used one or several mtDNA markers to analyze the probable origin of this invasive species (Usmani-Brown et al., 2009; Porretta et al., 2012; Zhong et al., 2013). Phylogenetic data reported by Mousson et al. (2005), using cyt b, COI and ND5 genes, suggest that A. albopictus is part of a paraphyletic lineage with two major clades, an Asian lineage (Cambodia, Vietnam and Thailand) and another from South America (Brazil). A recent study has provided evidence for A. albopictus populations in Los Angeles (California) which had greater identity with Asian populations, as compared with those from the eastern and Southeastern USA (Zhong et al., 2013). Some studies comparing autochthonous populations (Asian region-Thailand, Cambodia, Vietnam, and Madagascar) versus invasive non-autochthonous populations (USA, Brazil, and Italy) indicate that population structure may be due to global mobility and gene flow (Usmani-Brown et al., 2009; Kamgang et al., 2011; Raharimalala et al., 2012). However, none of these studies have explored population structure or diversity and the speciesí or populationís geographic distribution.

Given the species' important invasive capacity, several studies have now attempted to develop ecological niche or environmental models in order to understand potential natural species distributions, to analyze disease transmission risk components, and to quantify dispersal potential (Benedict et al., 2007; Medley, 2010; Jacob et al., 2011; Ogden et al., 2014; Campbell et al., 2015). In a study focusing on Asian populations, Porretta et al. (2012) provide evidence that ancestral populations of A. albopictus did not experience a fragmentation phase (around the glacial period), but have undergone population growth in Asia as interconnected populations. In contrast, Medley (2010) has argued that the A. albopictus niche adapts along with its invasive capacity, although there is no attempt to adjust for realized niche restrictions, such as founder effects in domestic habitats (i.e., sympatric with Aedes aegypti). A recent study on the projected dispersal in climate change scenarios using niche models, suggests a doubling of the area with US populations to the northeast by the end of the century (Rochlin et al., 2013), and using climate indicators, another study predicted a general northward range expansion for the US (Ogden et al., 2014).

Global dispersal of A. albopictus has occurred via maritime and commercial air routes between continents (Reiter and Sprenger, 1987; Romi, 2001; Gratz, 2004). Similar to its delayed appearance on the west coast of the US, it is noteworthy that A. albopictus was not collected in Mexico prior to the 1990s, in either coastal areas or major maritime ports, and that a decade occurred between the first collection of A. albopictus along the US border in the northeast Gulf of Mexico region, and that from the southern border, nearest to the Pacific coast, where there is no major mercantile shipping. The question hence arises regarding what dispersal mechanisms and routes have been and may be most important for this invasive species within and to Mexico, and what is the potential for the species to invade sylvatic habitats in either Nearctic or Neotropical regions of the country. It is expected to disperse uniquely among anthropic habitats as it adapts to artificial containers, but it may not be restricted to these habitats if the predicted niche of the populations is similar to the original species iniche (Ali and Nayar, 1997). Global travel and sizeable international and intra-national population migrations represent unique challenges for zoonotic and vector-borne diseases. National and global surveillance systems will need timely and complete information in the future not only for vector susceptibility to population control strategies (WHO, 2012), but more specifically for disease transmission models. Vectorborne disease control programs need to understand a vector's ecological tolerance both on a macro-environmental (ecological niche), as well as a local landscape level (rural-urban gradient). The present study analyzes the current population genetics of A. albopictus from all major recorded foci and biogeographic regions and the ecological niche of this invasive species in Mexico. Possible future expansion and potential human exposure of A. albopictus has been projected in two future climate change scenarios.

2. Material and methods

2.1. Study area

Mexico has a highly diverse bio-geographical territory spanning both Nearctic and Neotropical regions, located between the coordinates 14°32′N, 32°43′N and 118°22′W, 86°42′W. The region was divided into 1, 732, 435 pixels at a resolution of 30 arc-s (0.008333° = 1 km) for latitude and longitude. The current Mexican population from the 2010 census is 112, 336, 537 inhabitants, divided into rural population (communities with < 10,000 inhabitants) (38, 491, 814) and urban population (73, 844, 723) (INEGI; www.censo2010.org.mx/; last accessed July 2014). Mexico has two principal mountain ranges along Pacific and Gulf of Mexico coasts: the Sierra Madre Occidental and the Sierra Madre Oriental, with the high plains of the Neovolcanic Belt in between.

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