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Harnessing mosquito–*Wolbachia* symbiosis for vector and disease control

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ABSTRACT

Mosquito species, members of the genera *Aedes*, *Anopheles* and *Culex*, are the major vectors of human pathogens including protozoa (*Plasmodium* sp.), filariae and of a variety of viruses (causing dengue, chikungunya, yellow fever, West Nile). There is lack of efficient methods and tools to treat many of the diseases caused by these major human pathogens, since no efficient vaccines or drugs are available; even in malaria where insecticide use and drug therapies have reduced incidence, 219 million cases still occurred in 2010. Therefore efforts are currently focused on the control of vector populations. Insecticides alone are insufficient to control mosquito populations since reduced susceptibility and even resistance is being observed more and more frequently. There is also increased concern about the toxic effects of insecticides on non-target (even beneficial) insect populations, on humans and the environment. During recent years, the role of symbionts in the biology, ecology and evolution of insect species has been well-documented and has led to suggestions that they could potentially be used as tools to control pests and therefore diseases. *Wolbachia* is perhaps the most renowned insect symbiont, mainly due to its ability to manipulate insect reproduction and to interfere with major human pathogens thus providing new avenues for pest control. We herein present recent achievements in the field of mosquito–*Wolbachia* symbiosis with an emphasis on *Aedes albopictus*. We also discuss how *Wolbachia* symbiosis can be harnessed for vector control as well as the potential to combine the sterile insect technique and *Wolbachia*-based approaches for the enhancement of population suppression programs.

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1. Introduction

Mosquitoes represent the major vectors of many important human pathogens, transmitting diseases such as malaria, dengue, chikungunya, yellow fever, West Nile and filariasis (World Health Organisation, 2012). Vector mosquitoes mainly include species belonging to the *Aedes*, *Anopheles* and *Culex* genera. Anthropogenic factors as well as climate change have contributed to the spread of vector mosquito species along with human pathogens including arboviral threats like dengue, West Nile virus and chikungunya (Kilpatrick, 2011; World Health Organisation, 2012; Kyle and Harris, 2008; Weaver and Reisen, 2010; Tatem et al., 2006). The Asian Tiger mosquito *Aedes* (*Stegomyia*) *albopictus* (Skuse) is now considered to be the most invasive mosquito species in the world (ECDC, 2012). Indigenous to South East Asia (Smith, 1956), it has expanded its geographical distribution to almost all continents within the last couple of decades (Knudsen, 1995; Benedict et al.,

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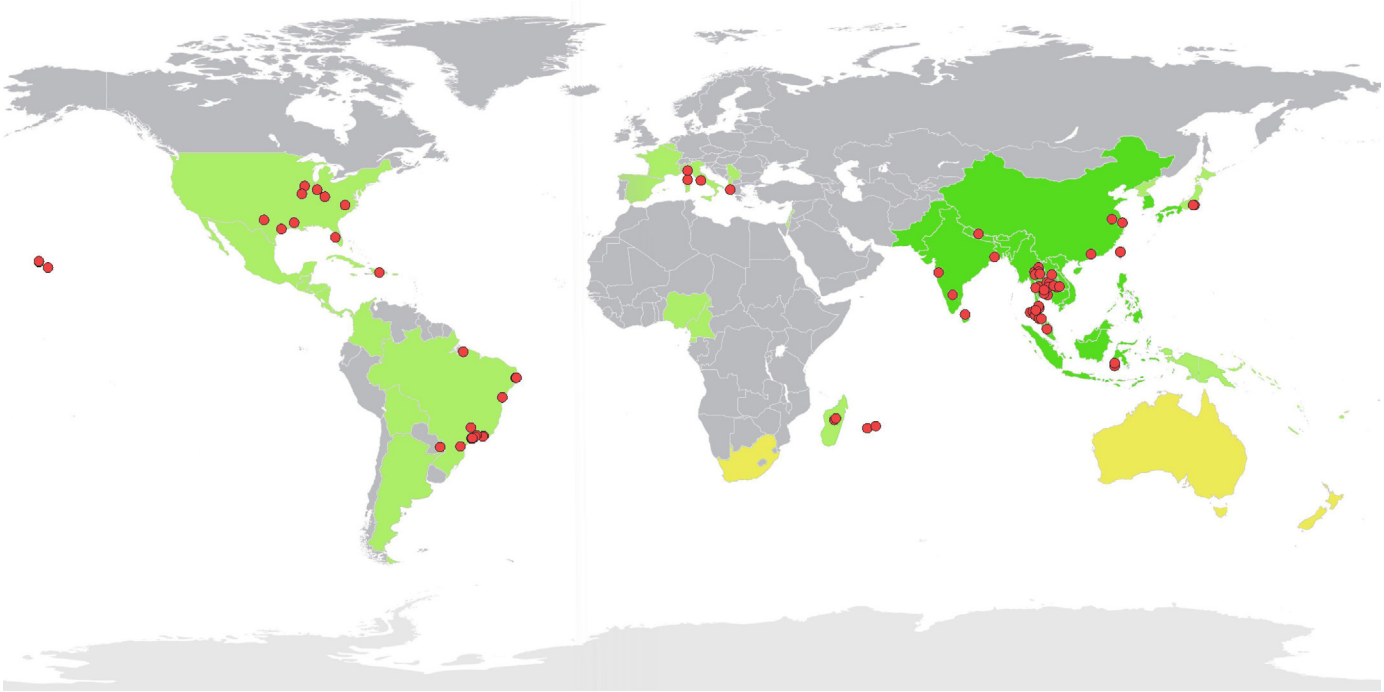

Fig. 1. *The global distribution of Wolbachia infection in Aedes albopictus.* Red circles indicate populations of *A. albopictus* that have been screened for *Wolbachia* infection using various methodologies. All such populations have been shown to be infected with *Wolbachia*, but because of methodological limitations only a subset has been shown to be superinfected with both the strains *w*AlbA and *w*AlbB. The data on *Wolbachia* infection were collated from the published literature (Baton and Moreira, in preparation). Countries shaded in dark green indicate the ancestral distribution of *A. albopictus*. Countries shaded in light green indicate the invasion and expansion of *A. albopictus* into new territories within the last 40 years. Countries shaded in yellow indicate locations where *A. albopictus* has been intercepted at ports before colonization could be established. Data on the distribution of *A. albopictus* were taken from Tatem et al. (2006) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

2007) (Fig. 1). This mosquito species is a competent vector of numerous arboviruses such as Dengue (DENV) and Chikungunya (Mitchell, 1995; Paupy et al., 2010; Schroyer, 1986; Reiter et al., 2006; Gratz, 2004; Delatte et al., 2005) even in temperate regions (Angelini et al., 2007; Grandadam et al., 2011; Vega-Rua et al., 2013). *Aedes albopictus* was first discovered in Asia but is now also present in North, Central and South America, the Middle East, Africa, Europe and Northern Australia (Reiter and Sprenger, 1987; Benedict et al., 2007; Scholte and Schaffner, 2007). Within North America, *A. albopictus* was first discovered in Houston (Texas) in 1965 (Sprenger and Wuithiranyagool, 1986) and is now present in 26 states of the USA. Independently introduced into Brazil in 1986, it now occurs in seven Brazilian states, and between 1993 and 1997 was detected in the Dominican Republic, Mexico, Guatemala, Cuba, Bolivia, El Salvador, Columbia and Cayman Islands (CDC, 2011). In 1979, Albania was the first country in Europe where *A. albopictus* was recorded (Adhami and Murati, 1987) followed by Italy in 1990 (Romi et al., 2008). Since then, it has become established in more than 15 European countries including Spain (Aranda et al., 2010) and France (Schaffner and Karch, 2000) and has also been reported in Belgium, Germany, Greece and the Netherlands (Schaffner et al., 2004; Scholte et al., 2007; ECDC, 2012). *A. albopictus* is continuously expanding its geographical distribution in the Pacific (Guillaumot et al., 2012) (established in New Zealand and the northern Australian border), in Africa from Central African Republic to Nigeria, Gabon, Cameroon, and in the Middle East, in Syria and Lebanon (Savage et al., 1992; Coffinet et al., 2007; Haddad et al., 2007; Diallo et al., 2010; Paupy et al., 2010). Globalisation and the increase of travel and trade between the continents facilitated the spread of *A. albopictus*, most likely as eggs which are able to resist desiccation for several months (Tatem et al., 2006; Focks et al., 1994).

In contrast to the 1980s, recent reports showed that *A. albopictus* outcompetes its sister taxon *Aedes aegypti* in insular regions of Madagascar and La Réunion (Delatte et al., 2011; Raharimalala et al., 2012). There is no doubt that *A. albopictus* is probably one of the most robust and invasive mosquito species. Its ability to adapt to various environmental conditions, to compete for breeding sites and to invade new ones, confer to this species unique advantages compared with other species (Romi et al., 2006; Benedict et al., 2007; Juliano and Lounibos, 2005) rendering its effective control by existing means very difficult (Gratz, 2004; La Ruche et al., 2010; Talbalaghi et al., 2010). The current conventional control methods for *A. albopictus* mostly rely on insecticides and community participation. However, decreasing susceptibility and the establishment of strains resistant to insecticides are now being reported (Ponlawat et al., 2005; Kamgang et al., 2011). In addition, insecticides have negative effects on non-target insect populations and a toxicological impact on humans and the environment. Moreover, community participation in programs to mechanically reduce mosquito breeding sites is very difficult to achieve and sustain in the long term. Consequently, implementation of alternative methods to control mosquitoes is sought worldwide.

Wolbachia pipientis is a monophyletic group of bacterial strains, closely related to the *Ehrlichia*, *Anaplasma* and *Neorickettsia* genera, all being members of *Alphaproteobacteria* (O'Neill et al., 1992; Rousset et al., 1992; Lo et al., 2007). This bacterial group is widespread and abundant among insect species and has been associated with the induction of a number of reproductive manipulations including male killing, feminization, parthenogenesis and, most commonly, cytoplasmic incompatibility (CI) (Bourtzis and Miller, 2003, 2006; O'Neill et al., 1997). During the last few years, a significant amount of evidence has been accumulated that shows *Wolbachia* infections to affect several aspects of host biology, physiology, immunity, ecology and evolution and reproduction (Werren et al., 2008; Serbus et al., 2008; Saridaki and Bourtzis, 2010). The ability of *Wolbachia* to manipulate diverse functional systems of

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