

Review Articles

Mosquito vectors developing in atypical anthropogenic habitats: Global overview of recent observations, mechanisms and impact on disease transmission

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ABSTRACT

The major mosquito vectors of human diseases have co-evolved with humans over a long period of time. However, the rapid growth in human population and the associated expansion in agricultural activity and greater urbanisation have created ecological changes that have had a marked impact on biology of mosquito vectors. Adaptation of the vectors of malaria and important arboviral diseases over a much shorter time scale to the new types of preimaginal habitats recently created by human population growth and activity is highlighted here in the context of its potential for increasing disease transmission rates. Possible measures that can reduce the effects on the transmission of mosquito-borne diseases are also outlined.

Key words *Aedes aegypti*; *Ae. albopictus*; agricultural development; anthropogenic environmental changes; arboviral diseases; insecticide resistance; malaria; preimaginal habitats; salinity tolerance; urban pollution

INTRODUCTION

Many of the dominant mosquito vectors transmitting widely prevalent diseases like malaria¹ and dengue² are anthropophilic and, therefore, have physiological features that optimise their ability to blood-feed on humans. For example, an altered odorant receptor that specifically recognises the sulcatone produced by humans has been shown to be essential for the evolution of domestic forms of the arboviral vector *Aedes aegypti* from its sylvatic ancestors³. Anthropophilic mosquitoes have additionally evolved behavioural traits and ecological preferences that facilitate feeding on humans, *viz.* laying eggs and undergoing preimaginal development in habitats that readily permit emerging adult females to access humans. The two major *Aedes* vectors, *Ae. aegypti* and *Ae. albopictus* that transmit important human arboviral diseases like dengue, chikungunya and yellow fever, are notable examples of this process. Domestic *Ae. aegypti* develops in fresh water collections within houses (*e.g.* flower pot bases) and immediate surroundings (*e.g.* water storage tanks, phytotelmata)^{4–5}. *Aedes albopictus* develops in the peri-domestic environment, *e.g.* phytotelmata and discarded containers^{4–5}. Many freshwater anthropophilic human malaria vectors similarly develop in natural (*e.g.* rainwa-

ter pools) and artificial (*e.g.* water storage tanks) fresh water collections near human dwellings^{6–7}. Anthropophilic mosquito vectors have therefore, evolved over a very long-time period (hundreds or thousands of years) to take advantage of increasing human populations, their geographical expansion, and societal features such as agriculture and urbanisation.

The recent development and spread of insecticide resistance however shows that mosquito vectors have the capacity to evolve over a much shorter time span of years or decades in the face of human efforts at vector control^{8–9}. For example, after the first identification of resistance to dichlorodiphenyl-trichloroethane (DDT) in 1951 in malaria vectors from Greece, Iran and Turkey, resistance spread to Africa, America and Asia within two decades⁹. Resistance to dieldrin was first observed in 1956, but then quickly expanded widely enough to make it useless for malaria control in Africa⁹. Increasing and widespread resistance to the commonly used pyrethroid insecticides is now being documented^{8–9}.

Measures to control mosquito-borne diseases rely heavily on reducing vector populations. Such control methods include the indoor spraying of insecticides, minimising, eliminating and larviciding preimaginal habitats, and reducing human-vector contact through the use

of insecticide treated bednets that also kill host-seeking adult females^{1-2, 9}. In the case of many mosquito vectors that bite outdoor or during daytime, eliminating water collections, where eggs are laid and the preimaginal stages develop, are central approaches for controlling disease^{2, 9}. The article provides a global overview of recent observations that show the preimaginal development of major mosquito vectors of malaria and arboviral diseases in unusual man-made habitats that are not typically targeted in vector control programmes. The implications of the observations for disease transmission are discussed and the need to target such atypical preimaginal habitats in vector control programmes is also emphasised. It is suggested that other human diseases transmitted by mosquitoes, e.g. lymphatic filariasis, require analogous consideration.

Overview of the process of adaptation of mosquito vectors to new anthropogenic habitats

The availability of aqueous habitats where mosquitoes oviposit, the eggs hatch and then develop through various larval instars to pupae, strongly influence the density of the resulting adult mosquito populations. Such preimaginal habitats may have natural or anthropogenic origins. Their productivity is influenced by abiotic (hydrology, temperature, sunlight, pH, chemicals, salinity, nutrient availability, turbidity) and biotic (predation, competition) factors and the interactions between the different factors¹⁰. The selection of oviposition sites are influenced by the distance that adult females can fly after a blood meal. For example, *Ae. aegypti* and *Ae. albopictus*, the vectors of dengue and chikungunya, normally lay eggs within 1 km from the site of a blood meal¹¹⁻¹².

Anthropogenic activities can create suitable new habitats within the natural range of the vectors. A combination of the new and pre-existing habitats can then lead to an increase in the vector population and, therefore, disease transmission. This process is illustrated in Fig. 1. Furthermore, anthropogenic activities that eliminate or greatly minimise the preimaginal habitats preferred by vector mosquitoes can be the driving force for their adaptation to less optimal and under-utilised habitats within their normal range close to human habitation. This process is illustrated in Fig. 2. In the second scenario in particular, the mosquitoes may undergo physiological and genetic changes to varying degrees that permit oviposition and preimaginal development in the new and less suitable habitats. Such adaptive changes can then predispose the vectors to extend their range to other areas in the country or indeed neighbouring countries where similar habitats are available. This ability has been termed

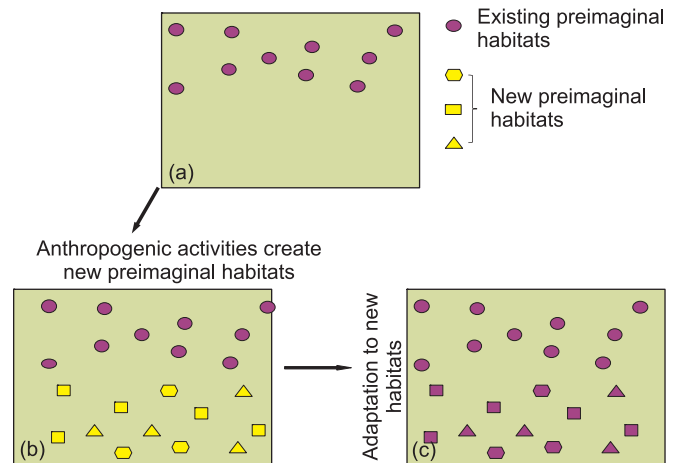


Fig. 1: Diagrammatic illustration of mosquito vectors expanding to new anthropogenic habitats within their natural range—(a): Existing natural habitats for preimaginal development; (b): Anthropogenic activities create new habitats for preimaginal development within the natural range of the mosquitoes; and (c): Mosquitoes developing in the newly created and pre-existing habitats.

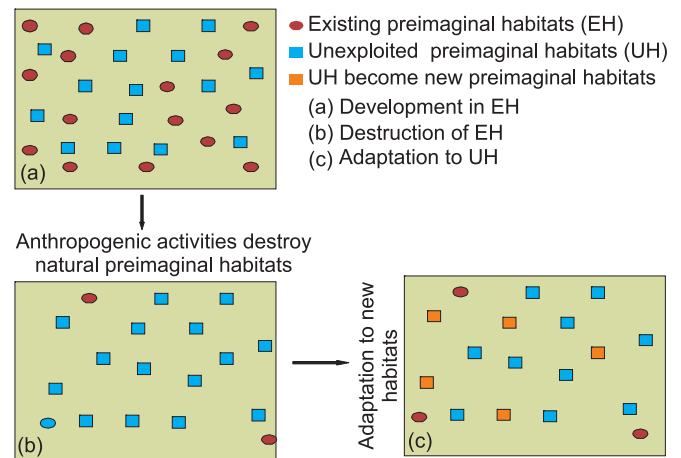


Fig. 2: Diagrammatic illustration of anthropogenic activities eliminating or minimising existing habitats in the natural range of mosquito vectors leading to their adaptation to other less desirable habitats within their range—(a) Existing natural habitats for preimaginal development; (b) Destruction of the existing habitats by anthropogenic activities; and (c) Mosquitoes adapting to other less desirable habitats in their natural range.

anthropogenically induced adaptation to invade, and supportive evidence for its occurrence has been reported in case of agricultural insect pests¹³.

Adaptation to occupy newly formed anthropogenic ecological niches has been postulated to be associated with recent speciation in major African vectors of the

Anopheles gambiae complex. The M molecular form now known as *An. coluzzi* and the S form now known as *An. gambiae* s.s. were shown to have adapted to more polluted urban habitats created after deforestation and less polluted rural habitats in the Cameroons respectively¹⁴. However in Burkino Faso, biogeographical factors such as humidity rather than anthropogenic changes appear to have influenced the differences in ecological niches occupied by the same two species¹⁵.

It is in this contextual framework that recent reports of mosquito vectors developing in a range of poorly described habitats created by human activity and the implications for controlling human diseases transmitted by them are discussed below.

A recent case study of a previously unreported adaptation of arboviral vectors associated with vector control measures to eliminate preimaginal habitats

Active source reduction, *i.e.* eliminating all possible breeding grounds for vector mosquitoes has an important role in the control of dengue. Dengue is the most common arboviral disease of humans, with at least 50–100 million annual cases in more than 100 countries (with recent local transmission in Western Europe and the USA), an increasing incidence and global spread, with a 2.5% fatality rate in severe dengue cases². Since, the two most important dengue vectors, *Ae. aegypti* and *Ae. albopictus*, develop in small water holding containers, active source reduction is carried out in almost all dengue affected countries to reduce vector populations and consequently disease transmission. However, it can be argued from an adaptive evolutionary point of view that the elimination of natural breeding grounds might have given opportunities to vector populations to exploit other unexploited and perhaps less desirable preimaginal habitats for survival (Fig. 2).

The Jaffna peninsula in northern Sri Lanka might provide a good example of such an occurrence. The Jaffna peninsula is highly populated and almost all households have artesian domestic well, used for various purposes including drinking, washing and irrigation. However, due to its limestone geology, low rainfall and the unsustainable use of ground water, increasing salinization is an emerging problem in the Jaffna peninsula^{16–17}. On the other hand dengue is a major public health problem in the region and an active source reduction campaign is implemented and enforced in law. It has been recently observed that the normally fresh water *Aedes* vectors are exploiting brackish water habitats in the Jaffna peninsula and elsewhere in coastal Sri Lanka¹⁸. Six per cent of food and beverage containers in beaches, and 25% of house-

hold wells along the Jaffna City coast had *Ae. aegypti* larvae in brackish water of up to 1.5% salt^{18–19}. The high larval positivity rates in brackish water habitats were associated with a high incidence of dengue¹⁸. *Aedes albopictus* was also observed to undergo development in brackish water habitats in the Jaffna peninsula and along the eastern coast of Sri Lanka¹⁸. However, larval development times are prolonged when *Ae. aegypti* larvae develop in brackish water, showing that brackish water habitats might be less optimal for their development than fresh water habitats²⁰. These observations in the Jaffna peninsula are a likely example of the process where elimination of the natural habitats of *Aedes* vector mosquitoes by human activity has led the vectors to adapt in less desirable new habitats within their natural range as illustrated in Fig. 2.

It has also been suggested that the use of insecticides for controlling agricultural pests in inland areas of the Jaffna peninsula and indoor residual spraying of insecticides to control malaria, could have additionally contributed to the adaptation of *Ae. aegypti* and *Ae. albopictus* to coastal brackish water habitats in Sri Lanka^{18, 21–22}. This is supported by the greater susceptibility of coastal *Ae. aegypti* to the organophosphate insecticide malathion compared with inland *Ae. aegypti* in the Jaffna peninsula¹⁸.

Furthermore, brackish water *Ae. aegypti* in the Jaffna peninsula were shown to have significantly adapted to laying eggs in brackish water and their larvae were able to tolerate salinity to a greater extent than fresh water *Ae. aegypti*²⁰. These findings suggest that there are genetic differences between brackish and fresh water *Ae. aegypti* in the Jaffna peninsula. Although brackish and fresh water *Ae. aegypti* in Sri Lanka have been shown to interbreed²⁰, the findings demonstrate a potential for speciation in *Ae. aegypti* that may result from continuing efforts to eliminate their freshwater preimaginal habitats and reproductive isolation between brackish and fresh water populations in the long run.

The vertical or transovarial transmission of dengue virus in brackish water *Ae. aegypti* and *Ae. albopictus* has also been documented and it was proposed that brackish water *Aedes* vectors might constitute a perennial reservoir of the virus in coastal areas of the Jaffna peninsula that could be the origin of dengue epidemics that occur with the advent of monsoonal rains²³.

Many tropical and temperate countries where the *Aedes* vectors are found, have extensive coastal areas and/or a high coastline to land mass ratio²². We have hypothesised that the development of *Aedes* vectors in brackish water habitats is a globally widespread phenomenon favoured wholly or partly by the exclusive focus of dengue control

measures on fresh water habitats^{16–18, 21–22}. It has been suggested that this adaptability of *Aedes* vectors may have unknowingly contributed to the persistence or recent emergence of dengue and chikungunya in Sri Lanka, chikungunya in Réunion Island, and dengue, despite intensive control programmes, in countries like Cuba, Singapore and Brunei^{18, 21–23}. It has been also speculated that the more recent epidemics of dengue and chikungunya in small islands and coastal areas in the western hemisphere^{2, 23–24} might have been partly caused because of the neglect of brackish water habitats in vector control programmes.

Impact of habitat changes caused by deforestation and reforestation

Deforestation resulting from expanding agriculture and housing, logging, *etc.*, contributes in a major way to changing local ecosystems that affect local flora and fauna including disease vectors¹⁰. Ecological divergence resulting from the deforestation creates novel habitats and ecological heterogeneities that provide new adaptive opportunities to mosquito vectors that are in turn capable of influencing disease transmission¹⁰. In this process some vector species may be favoured and others replaced¹⁰. Malaria transmission in parts of the Peruvian Amazon was increased due to deforestation that favoured the breeding of *An. darlingi*²⁵. In contrast, environmental changes due to deforestation in Macapa in the northeastern Amazon resulted in the replacement of *An. darlingi* by *An. marajoara*, as the primary vector²⁶. Deforestation in Central Africa has been shown to contribute to the ecological segregation of the closely related *An. gambiae* s.s. and *An. coluzzi* within the *An. gambiae* complex¹⁴. Deforestation associated changes in malaria vectors resulting in alterations in malaria transmission has also been well documented in Asia, for example in Thailand²⁷. Disease transmission intensity changes in many situations have been directly related to variations in vector densities accompanying alterations in forestry cover²⁸. However, forests continue to be sources of malaria transmission in India²⁹ (both human to human and zoonotic malaria transmission) and elsewhere in the world³⁰. The effects of alterations in forest cover therefore have to be examined in detail for each particular case for its impact on the development of mosquito vectors and the diseases that they transmit.

Impact of habitat changes due to agricultural development

Agricultural development involving the creation of large plantations with or without deforestation, and the

building of necessary infrastructure and irrigation facilities, leads to ecological changes that alter the habitats of many mosquito vectors. New habitats are created within the natural range as illustrated in Figs. 1 and 2. Specific vectors respond to the newly created habitats in different ways to cause an increase or decrease in disease transmission rates and this has been extensively reviewed with many examples elsewhere²⁸. Therefore, only some other pertinent examples, where an association between agricultural development and disease transmission has been made, are presented here. A high prevalence of malaria in the vicinity of newly constructed irrigation canals in northcentral Sri Lanka was attributed to a high density of *An. annularis* s.l. (a minor freshwater malaria vector that usually develops in rain-fed forest pools) through its rapid adaptation to oviposit and undergo preimaginal development in such canals³¹. It was also suggested that the very high entomological inoculation rates observed in the vicinity of the canals might have acted as a nucleus for precipitating the island wide epidemics of malaria that were common in the 1990s in Sri Lanka³¹. *Anopheles annularis* was reported, in an analogous manner, to have become the predominant species in a new irrigation project area in central India³². Swift adaptation to habitats made available by irrigation development has also been documented elsewhere with other malaria vectors, *e.g.* *An. arabiensis* in Ethiopian sugar plantations³³.

However more complicated habitat interactions can also occur when forests are cleared to make way for plantations. The replacement of forests for the cultivation of oil palm in North Sarawak was reported to result in a decrease in malaria vector and an increase in dengue vector densities³⁴.

In a different type of example, the prolific development of *Ae. albopictus* in latex-collecting containers attached to rubber tree-trunks in rubber plantations has been proposed to have given rise to the periodic chikungunya epidemics in Kerala, India. Preventive measures effectively employed in this situation include inverting the cups during the rainy season when latex is not collected or covering the cups with plastic^{35–36}.

Another example described in the 1960s refers to the recurrence of an outbreak of malaria in 1961 in the Demerara river estuary in Guyana in South America. This was partly attributed to rice cultivation, displacing livestock from pasture land causing the salinity tolerant and relatively exophilic and zoophilic *An. aquasalis* to adapt to become endophilic and anthropophilic³⁷. Although, no preimaginal habitat changes were described in *An. aquasalis* developing in the brackish estuarine water, the observation demonstrated the com-

plex effects that changing agriculture can have on disease transmission.

The presently available data, therefore, emphasise the need to carefully examine the likely impact of changes in land use associated with agriculture on vector habitats and therefore disease transmission.

Impact of other human activities on habitat adaptation and range expansion

From a sylvatic and zoophagic origin in sub-Saharan Africa, *Ae. aegypti* evolved into a domestic anthropogenic vector that has spread to America, Asia, Australia and parts of Europe³⁸. *Aedes albopictus* has similarly expanded from its origin in tropical Asia to Africa, America and Europe³⁹. The tolerance of their eggs to desiccation, the global trade in used tyres and the ability of *Ae. albopictus* eggs to tolerate cold through a diapause mechanism helped extend the range of the vectors^{38–39} and consequently the areas afflicted by dengue, yellow fever and chikungunya.

Aedes aegypti and *Ae. albopictus* are well adapted to oviposit and undergo preimaginal development in fresh water collections in small discarded plastic and rubber containers^{2,7}. However, several unusual or atypical habitats have been recently reported, providing examples of the processes illustrated in Figs. 1 and 2. These include the water bowl of an encaged bird and flush tank of a toilet in urban Malaysia⁴⁰. Both vector species have been recently shown to develop in fresh water domestic wells in south India⁴¹ while *Ae. aegypti* has been earlier shown to develop in domestic wells that do not contain fish in Sri Lanka¹⁹. The preimaginal development of *Ae. aegypti* was lately documented in highly polluted water in domestic septic tanks in Puerto Rico⁴² and Nigeria⁴³. Vertical dispersal of *Aedes* mosquitoes where there is extensive construction of high rise buildings has been reported to occur up to 120 ft above ground level in the city of Colombo in Sri Lanka⁴⁴ and Putrajaya in Malaysia⁴⁵.

Furthermore, another ongoing study also demonstrated the ability of *Ae. aegypti* to undergo preimaginal development in polluted drain water and oil-contaminated water in the Jaffna peninsula of Sri Lanka (Surendran SN, Sivapalakrishnan K and Ramasamy R, unpublished observations).

Anopheles culicifacies, a dominant South Asian malaria vector, has been long regarded to develop only in clear, sunlit and unpolluted, fresh water collections with high dissolved oxygen content^{7,46}. But its larvae were recently found developing in polluted water in blocked urban drains in north eastern Sri Lanka⁴⁷. *Anopheles gambiae*, also nor-

mally considered to develop in clean fresh water pools has recently been reported to develop in polluted drains in metropolitan Lagos⁴⁸ and elsewhere in Africa⁴⁹, and in water contaminated with spilled oil in Nigeria⁵⁰.

Since, Australia has experienced prolonged droughts, European colonists developed a tradition of harvesting rain water in their homes. As a result, tanks that store rainwater have become suitable habitats in the suburbs of Brisbane for the small container developing *Ae. notoscriptus*, a vector of Ross River and Barmah forest viruses⁵¹.

These recent observations show the need for vector control programmes to be cognisant of likely new and unusual habitats created by human activity to which mosquito vectors can readily adapt.

Climate change, rising sea levels and expansion of coastal brackish water habitats

Anthropogenic global warming, caused mainly by the unregulated burning of fossil and wood fuels by expanding populations, is expected to increase the sea level and this will result in the expansion of saline (>3% salt) and brackish (0.05–3% salt) water bodies along coastal areas^{16–17, 21–22}. While the expansion of brackish water bodies will increase the densities of salinity-tolerant vector mosquitoes such as *An. sundaicus*, it can also lead to adaptation of fresh water mosquitoes to undergo preimaginal development in saline and brackish water bodies^{16–17, 21–22}. We recently observed the development of *An. culicifacies*, the major vector of malaria in South Asia, in brackish water of up to 0.4% salt in coastal areas of eastern Sri Lanka⁵². In a major paradigm shift, *Ae. aegypti* and *Ae. albopictus*, widely acknowledged to be fresh water developing mosquitoes were recently shown to develop in brackish water of up to 1.5 and 1.4% salt respectively in discarded food and beverage containers, and wells in coastal Sri Lanka and Brunei Darussalam, with this property being associated in both countries with dengue transmission^{18–20, 52}.

In an example not related to human activity, *An. stephensi*, a vector of urban malaria in India, was observed to develop in pools of brackish water left behind in southern India after the great Asian tsunami of 2004⁵³. The density of *An. sundaicus* s.l., a well-known but as yet inadequately characterised salinity-tolerant malaria vector in coastal Asia^{55–56}, increased in the Andaman and Nicobar Islands after the 2004 tsunami due to new and temporary habitats created by the intrusion of sea water into inland areas of the islands⁵⁷. This was associated with an increased incidence of *P. falciparum* malaria in the islands⁵⁷. Such findings portend the likely impact of rising sea levels on mosquito-borne disease

Table 1. Examples of anthropogenic changes in vector habitats associated with altered incidence of mosquito-borne diseases

Vector species	Disease	Anthropogenic change	Country (Reference)
<i>Anopheles annularis</i>	Malaria	New irrigation canals	Sri Lanka ³¹ , India ³²
<i>Aedes albopictus</i>	Chikungunya	Rubber plantations	India ³⁵⁻³⁶
<i>An. sundaicus</i>	Malaria	Shrimp farming	Vietnam ⁵⁸
Many <i>Anopheles</i> species	Malaria	A range of other changes associated with agriculture	Many countries ²⁸ , Ethiopia ³³ ; Malaysia ³⁴
<i>Ae. gambiae</i>	Malaria	Urban pollution and oil contamination	Benin, Nigeria ⁵⁹
<i>Ae. aegypti</i> and <i>Ae. albopictus</i>	Dengue	Beach litter and coastal domestic wells	Sri Lanka ¹⁸⁻¹⁹ ; Brunei ⁵³

transmission in coastal areas and in situations where new brackish water habitats can be unwittingly created by human activities.

Aquaculture is a widespread activity in tropical coasts. Shrimp farming involves the creation of brackish water ponds, and in the Mekong delta of Vietnam this has been shown to locally increase the density of the salinity tolerant malaria vector *An. sundaicus* s.l.⁵⁸.

Implications for disease transmission and vector control

Key data on the adaptation of mosquito vectors to human-induced environmental changes creating new habitats for them and thereby likely impacting on the incidence of mosquito-borne diseases are summarized in Table 1. It is possible that intrinsic plasticity in their physiology allows mosquitoes to develop in some of these atypical habitats and this aspect had previously gone unnoticed. However, the evidence suggests that genetic changes, including changes in resistance to insecticides used for disease control, contribute to adaptation to salinity in *Ae. aegypti*²⁰ and oil pollution in *An. gambiae*⁵⁹. A possibility that requires further investigation is that resistance to pollutants and insecticides are linked to the same genetic changes, e.g. greater cuticular resistance to absorbing chemicals and more active detoxification mechanisms^{6, 60}. This has implications for the worldwide occurrence of vector mosquitoes adapting to develop in polluted waters and therefore the control of mosquito-borne diseases in many countries.

Increase in urban pollution due to population growth and greater availability of brackish water collections in coastal areas due to global warming^{17, 20} are worldwide phenomena. Mosquito vectors adapted to the new habitats therefore have the potential to extend their range to similar habitats in other areas, constituting new invasive species in this manner¹³. For example, it is not inconceivable that brackish water-adapted *Ae. aegypti* and *Ae. albopictus* in Sri Lanka and Brunei can invade neighbouring countries to develop in similar coastal brackish water habitats. Similarly, pollutant-adapted *An. gambiae* from Lagos has the potential to spread to de-

velop in comparable habitats in nearby cities. This would be consistent with the anthropogenically induced adaptation to invade hypothesis discussed previously¹³. The rate of spread of salinity or pollution-adapted mosquito vectors will depend on the selective forces in play in different areas. However the recent rapid spread of insecticide resistance⁸⁻⁹, where the selective forces are very strong, has to be kept in mind.

The adaptations described make current larval control practices less effective as these are directed towards typical fresh water habitats of the vectors. Disease transmission rates can therefore increase. Adaptation-associated physiological changes can influence the infectivity of pathogens to mosquitoes and this needs further investigation, e.g. it is not known whether anopheline vectors developing in polluted water have the same vectorial capacity as other members of the same species developing in fresh water. Pathogens can also rapidly co-evolve to adapt to any genetic changes in vector populations. Further research on the highlighted aspects of mosquito vector ecology and evolution in the context of vectorial capacity are therefore needed to more effectively control mosquito-borne human diseases in the future.

Hence, it is suggested that the available data warrant (i) more detailed scrutiny of the potential for creating unusual man-made habitats for mosquito vector development, during environmental impact assessments of new development projects in coastal, urban and rural areas; (ii) a broader view on potential preimaginal habitats to be taken by vector-borne disease control programmes with appropriate revision of the guidelines for control; and (iii) more resources to be allocated for research on vector biology and for monitoring vector populations in potentially changing habitats.

REFERENCES

1. *Malaria: Fact sheet*. Geneva: World Health Organization 2015. Available from: <http://www.who.int/mediacentre/factsheets/fs094/en> (Accessed on July 30, 2015).
2. *Dengue and severe dengue: Fact sheet*. Geneva: World Health Organization 2015. Available from: <http://www.who.int/>

- mediacentrefactsheets/fs117/en* (Accessed on July 30, 2015).
3. McBride CS, Baier F, Omondi AB, Spitzer SA, Lutomia J, Sang R, *et al.* Evolution of mosquito preference for humans linked to an odorant receptor. *Nature* 2014; 515(7526): 222–7.
 4. Juliano SA, Lounibos LP. Ecology of invasive mosquitoes: Effects on resident species and on human health. *Ecol Lett* 2005; 8(5): 558–74.
 5. Chan KL, Ho BC, Chan YC. *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) in Singapore City 2. Larval habitats. *Bull World Health Organ* 1971; 44(5): 629–33.
 6. Surendran SN, Ramasamy R. The *Anopheles culicifacies* and *An. subpictus* species complexes in Sri Lanka and their implications for malaria control in the country. *Trop Med Health* 2010; 38(1): 1–11.
 7. Barraud PJ. *The fauna of British India, including Ceylon and Burma*. Diptera Culicidae, Tribe: Megarhinini-and Culicini v V. In: Sewell RBS, Edwards PW, editors. London: Taylor and Francis 1934; p. 28–426.
 8. Liu N. Insecticide resistance in mosquitoes: impact, mechanisms, and research directions. *Annu Rev Entomol* 2015; 60: 537–59.
 9. *Global plan for insecticide resistance management in malaria vectors*. Geneva: World Health Organisation 2012. Available from: <http://www.who.int/malaria/publications/atoz/gpirm/en/> (Accessed on October 14, 2015).
 10. Rejmánková E, Grieco J, Achee N, Roberts DR. Ecology of larval habitats. In: Manguin S, editor. *Anopheles mosquitoes—New insights into malaria vectors*. *InTech* 2013; p. 397–446. DOI: 10.5772/55229.
 11. Hono'rio NH, Silva Wda C, Leite PJ, Gonçalves JM, Lounibos LP, Lourenço-de-Oliveira R, *et al.* Dispersal of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in an urban endemic dengue area in the state of Rio de Janeiro, Brazil. *Mem Inst Oswaldo Cruz* 2003; 98(2): 191–8.
 12. Harrington LC, Scott TW, Lerdthusnee K, Coleman RC, Costero A, Clark GG, *et al.* Dispersal of the dengue vector *Aedes aegypti* within and between rural communities. *Am J Trop Med Hyg* 2005; 72(2): 209–20.
 13. Hufbauer RA, Facon B, Ravigné V, Turgeon J, Foucaud J, Lee CE, *et al.* Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evol Appl* 2012; 5(1): 89–101.
 14. Kamdem C, Fossog BT, Simard F, Etoua J, Ndo C, Kengne P, *et al.* Anthropogenic habitat disturbance and ecological divergence between incipient species of the malaria mosquito *Anopheles gambiae*. *PLoS One* 2012; 7(6): e39453.
 15. Costantini C, Ayala D, Guelbeogo WM, Pombi M, Some CY, Bassole IH, *et al.* Living at the edge: Biogeographic patterns of habitat segregation conform to speciation by niche expansion in *Anopheles gambiae*. *BMC Ecol* 2009; 9: 16.
 16. Ramasamy R, Surendran SN. Global climate change and its potential impact on disease transmission by salinity-tolerant mosquito vectors in coastal zones. *Front Physiol* 2012; 3: 198.
 17. Ramasamy R, Surendran SN. Possible impact of rising sea levels on vector-borne infectious diseases. *BMC Infect Dis* 2011; 11: 18.
 18. Ramasamy R, Surendran SN, Jude PJ, Dharshini S, Vinobaba M. Larval development of *Aedes aegypti* and *Aedes albopictus* in peri-urban brackish water and its implications for transmission of arboviral diseases. *PLoS Negl Trop Dis* 2011; 5(11): e1369.
 19. Surendran SN, Jude PJ, Thabothiny V, Raveendran S, Ramasamy R. Pre-imaginal development of *Aedes aegypti* in brackish and fresh water urban domestic wells in Sri Lanka. *J Vector Ecol* 2012; 37(2): 471–3.
 20. Ramasamy R, Jude PJ, Veluppillai T, Eswaramohan T, Surendran SN. Biological differences between brackish and fresh water-derived *Aedes aegypti* from two locations in the Jaffna peninsula of Sri Lanka and the implications for arboviral disease transmission. *PLoS One* 2014; 9(8): e104977.
 21. Ramasamy R. Adaptation of fresh water mosquito vectors to salinity increases arboviral disease transmission risk in the context of anthropogenic environmental changes. In: Shapshak P, Sinnott JT, Somboonwit C, Kuhn JH, editors. *Global virology I- Identifying and investigating viral diseases*. New York: Springer International Publishing AG 2015; p. 45–54.
 22. Ramasamy R, Surendran SN, Jude PJ, Dharshini S, Vinobaba M. Adaptation of mosquito vectors to salinity and its impact on mosquito-borne disease transmission in the South and Southeast Asian tropics. In: Morand M, Dujardin J-P, Lefait-Robin R, Apiwathnasorn C, editors. *Socio-ecological dimensions of infectious diseases in Southeast Asia 2015*. Singapore: Springer 2015; p. 107–22.
 23. Ramasamy R, Surendran SN. *Global environment changes and salinity adaptation in mosquito vectors*. Saarbrücken, Germany: Lap Lambert Academic Publishing 2013; p. 1–100.
 24. *Chikungunya: Fact sheet* No. 327. Geneva: World Health Organization 2015. Available from: <http://www.who.int/mediacentre/factsheets/fs327/en/> (Accessed on October 19, 2015).
 25. Vittor AY, Pan W, Gilman RH, Tielsch J, Glass G, Shields T, *et al.* Linking deforestation to malaria in the Amazon: Characterization of the breeding habitat of the principal malaria vector, *Anopheles darlingi*. *Am J Trop Med Hyg* 2009; 81(1): 5–12.
 26. Conn JE, Wilkerson RC, Segura MNO, De Souza RTL, Schlichting CD, Wirtz RA, *et al.* Emergence of a new neotropical malaria vector facilitated by human migration and changes in landuse. *Am J Trop Med Hyg* 2002; 66(1): 18–22.
 27. Overgaard HJ, Suwonkerd W, Hii J. The malaria landscape: Mosquitoes, transmission, landscape, insecticide resistance, and integrated control in Thailand. In: Morand S, Dujardin J-P, Lefait-Robin R, Apiwathnasorn C, editors. *Socio-ecological dimensions of infectious diseases in Southeast Asia*. Singapore: Springer 2015; p. 123–53.
 28. Yasuoka J, Levins R. Impact of deforestation and agricultural development on anopheline ecology and malaria epidemiology. *Am J Trop Med Hyg* 2007; 76(3): 450–60.
 29. Kar NP, Kumar A, Singh OP, Carlton JM, Nanda N. A review of malaria transmission dynamics in forest ecosystems. *Parasit Vectors* 2014; 7: 265.
 30. Ramasamy R. Zoonotic malaria – Global overview and research and policy needs. *Front Pub Health* 2014; 2: 123.
 31. Ramasamy R, De Alwis R, Wijesundera A, Ramasamy MS. Malaria transmission in a new irrigation scheme in Sri Lanka: The emergence of *Anopheles annularis* as a major vector. *Am J Trop Med Hyg* 1992; 47(5): 547–53.
 32. Singh N, Mishra AK. Anopheline ecology and malaria transmission at a new irrigation project area (Bargi dam) in Jabalpur (Central India). *J Am Mosq Control Assoc* 2000; 16(4): 279–87.
 33. Jaleta KT, Hill SR, Seyoum E, Balkew M, Gebre-Michael T, Ignell R, *et al.* Agro-ecosystems impact malaria prevalence: Large-scale irrigation drives vector population in western Ethiopia. *Malar J* 2013; 12: 350.
 34. Chang MS, Hii J, Buttner P, Mansoor F. Changes in abundance and behaviour of vector mosquitoes induced by landuse during

- the development of an oil palm plantation in Sarawak. *Trans R Soc Trop Med Hyg* 1997; 91(4): 382–6.
35. Sumodan PK. Species diversity of mosquito breeding in rubber plantations of Kerala, India. *J Am Mosq Control Assoc* 2012; 28(2): 114–5.
 36. Sumodan PK, Vargas RM, Pothikasikorn J, Sumanrote A, Lefait-Robin R, Dujardin J-P. Rubber plantations as a mosquito box amplification in South and Southeast Asia. In: Morand M, Dujardin J-P, Lefait-Robin R, Apiwathnasorn C, editors. *Socio-ecological dimensions of infectious diseases in Asia*. Singapore : Springer 2015; p. 155–67.
 37. Giglioli G. Ecological change as a factor in renewed malaria transmission in an eradicated area. A localized outbreak of *An. aquasalis*-transmitted malaria on the Demerara River estuary, British Guiana, in the fifteenth year of *An. darlingi* and malaria eradication. *Bull World Health Org* 1963; 29: 131–45.
 38. Powell JR, Tabachnik WJ. History of domestication and spread of *Aedes aegypti*—A review. *Mem Inst Oswaldo Cruz* 2013; 108(Suppl 1): 11–7.
 39. Benedict MQ, Levine RS, Hawley WA, Lounibos LP. Spread of the tiger: Global risk of invasion by the mosquito *Aedes albopictus*. *Vector Borne Zoonotic Dis* 2007; 7(1): 76–85.
 40. Dieng H, Saifur RG, Ahmad AH, Salmah MRC, Asiz AT, Satho T, *et al.* Unusual developing sites of dengue vectors and potential epidemiological implications. *Asia Pac J Trop Biomed* 2012; 2(3): 228–32.
 41. Mariappan T, Thenmozhi V, Udayakumar P, Bhavaniumadevi V, Tyagi BK. An observation on breeding behaviour of three different vector species (*Aedes aegypti* Linnaeus 1762, *Anopheles stephensi* Liston 1901 and *Culex quinquefasciatus* Say 1823) in wells in the coastal region of Ramanathapuram district, Tamil Nadu, India. *Int J Mosq Res* 2015; 2(2): 42–4.
 42. Burke R, Barrera R, Lewis M, Kluchinsky T, Claborn D. Septic tanks as larval habitats for the mosquitoes *Aedes aegypti* and *Culex quinquefasciatus* in Playa-Playita. Puerto Rico. *Med Vet Entomol.* 2010; 24: 117–23.
 43. Nwoke BE, Nduka FO, Okereke OM, Ehighibe OC. Sustainable urban development and human health: Septic tank as a major breeding habitat of mosquito vectors of human diseases in south-eastern Nigeria. *Appl Parasitol* 1993; 34(1): 1–10.
 44. Jayathilake TA, Wickramasinghe MB, de Silva BG. Oviposition and vertical dispersal of *Aedes* mosquitoes in multiple storey buildings in Colombo district, Sri Lanka. *J Vector Borne Dis* 2015; 52(3): 245–51.
 45. Wan-Norafikah O, Nazni WA, Noramiza S, Shafa'ar-Ko'ohar S, Azirol-Hisham A, Nor-Hafizah R, *et al.* Vertical dispersal of *Aedes* (Stegomyia) spp in high rise apartments in Putrajaya, Malaysia. *Trop Biomed.* 2010; 27(3): 662–7.
 46. Surendran SN, Ramasamy R. Some characteristics of the larval breeding sites of *Anopheles culicifacies* species B and E in Sri Lanka. *J Vector Borne Dis* 2005; 42(2): 39–44.
 47. Gunathilaka N, Fernando T, Hapugoda M, Wickremasinghe R, Wijeyerathne P, Abeyewickreme W. *Anopheles culicifacies* breeding in polluted water bodies in Trincomalee district of Sri Lanka. *Malar J* 2013; 12: 285.
 48. Awolola TS, Oduola AO, Obansa JB, Chukwurar NJ, Unyimadu JP. *Anopheles gambiae* s.s. breeding in polluted water bodies in urban Lagos, southwestern Nigeria. *J Vector Borne Dis* 2007; 44(4): 241–4.
 49. Kasili S, Odemba N, Ngere FG, Kamanza JB, Muema AM, Kutima HL. Entomological assessment of the potential for malaria transmission in Kibera slum of Nairobi, Kenya. *J Vector Borne Dis* 2009; 46(4): 273–9.
 50. Djouaka RF, Bakare AA, Bankole HS, Doannio JM, Coulibaly ON, Kossou H, *et al.* Does the spillage of petroleum products in *Anopheles* breeding sites have an impact on the pyrethroid resistance? *Malar J* 2007; 6: 159.
 51. Trewin BJ, Kay BH, Darbo JM, Hurst TP. Increased container-breeding mosquito risk owing to drought-induced changes in water harvesting and storage in Brisbane, Australia. *Int Health* 2013; 5(4): 251–8.
 52. Jude PJ, Tharmasegaram T, Sivasubramaniam G, Senthilnathanan M, Kannathasan S, Raveendran S, *et al.* Salinity-tolerant larvae of mosquito vectors in the tropical coast of Jaffna, Sri Lanka and the effect of salinity on the toxicity of *Bacillus thuringiensis* to *Aedes aegypti* larvae. *Parasit Vectors* 2012; 5: 269.
 53. Idris FH, Usman A, Surendran SN, Ramasamy R. Detection of *Aedes albopictus* preimaginal stages in brackish water habitats in Brunei Darussalam. *J Vector Ecol* 2013; 38(1): 197–9.
 54. Gunasekaran K, Jambulingam P, Srinivasan R, Sadanandane C, Doss PB, Sabesan S, *et al.* Malaria receptivity in the tsunami-hit coastal villages of southern India. *Lancet Infect Dis* 2005; 5(9): 531–2.
 55. Surendran SN, Singh, OP, Jude, PJ, Ramasamy R. Genetic evidence for malaria vectors of the *Anopheles sondaicus* complex in Sri Lanka with morphological characteristics attributed to *Anopheles subpictus* species B. *Malar J* 2010; 9: 343.
 56. Sinka ME, Bangs MJ, Manguin S, Chareonviriyaphap T, Patil AP, Temperley WH, *et al.* The dominant *Anopheles* vectors of human malaria in the Asia-Pacific region: Occurrence data, distribution maps and bionomics. *Parasit Vectors* 2011; 4: 89.
 57. Krishnamoorthy K, Jambulingam P, Natarajan R, Shriram AN, Das PK, Sehgal SC. Altered environment and risk of malaria outbreak in South Andaman, Andaman & Nicobar Islands, India affected by the tsunami disaster. *Malar J* 2005; 4: 32.
 58. Trung HD, Van Bortel W, Sochantha T, Keokenchanh K, Quang NT, Cong LD, *et al.* Malaria transmission and major malaria vectors in different geographic areas of Southeast Asia. *Trop Med Int Health* 2004; 9(2): 230–7.
 59. Djouaka RF, Bakare AA, Coulibaly ON, Akogbeto MC, Ranson H, Hemingway J, *et al.* Expression of the cytochrome P450s, CYP6P3 and CYP6M2 are significantly elevated in multiple pyrethroid resistant populations of *Anopheles gambiae* s.s. from Southern Benin and Nigeria. *BMC Genomics* 2008; 9: 538.
 60. Hemingway J, Hawkes NJ, McCarroll L, Ranson H. The molecular basis of insecticide resistance in mosquitoes. *Insect Biochem Mol Biol* 2004; 34(7): 653–65.

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