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# 16

## THE MOSQUITOME

### A new frontier for sustainable vector control

*Frederic Simard*

Invasive *Aedes* mosquitoes such as *Aedes aegypti* and *Ae. albopictus*, that support the bulk of inter-human arbovirus transmission causing dengue, chikungunya, Zika, yellow fever and others to come, are urban mosquitoes that have largely benefited and expanded from ongoing human settlement and development, such as deforestation, urbanization and increased global trade. In tropical areas, major human malaria vectors (*Anopheles* spp.) are also typically considered as highly anthropophilic mosquitoes, showing strong feeding preference for human blood over other vertebrate hosts, hence strongly contributing to inter-human transmission of life-threatening malaria parasites. All these major disease vectors are highly dependent upon humans, not only as a reliable source of blood for their hematophagous females, but also because human transformations to natural environments and ecosystems create numerous opportunities for these mosquitoes to breed and to rest, with low exposure to most of their natural enemies that do not develop in culturally modified areas. These major disease vectors represent only a small fraction of the more than 3,500 known mosquito species, but they have significantly diverged from their wild counterparts, both in their ecology (biting behaviour, host preference, reproductive dynamics, larval ecology, etc.) and their genetics (genetic diversity, gene duplications, insecticide resistance mutations, etc.) (Neafsey et al., 2015). As a matter of fact, we humans have been the major drivers of the recent evolutionary history of this group of highly synanthropic disease-vector mosquitoes, shaping what now appears to be a set of unintentionally domesticated animals that thrive where people live.

The emergence and rapid spread of resistance to artificial chemical insecticides in all major mosquito disease vectors over the last 30 years is an emblematic, ultimate evolutionary step in the adaptation of these mosquitoes to human environments. Indeed, insecticide resistance seriously jeopardizes recent public health success in the control of malaria in Africa, as well as significantly

hindering any preventive or reactive interventions against the highly invasive, virus-transmitting *Aedes* mosquitoes (Hemingway et al., 2016; Moyes et al., 2017). Is this another battle we are losing against our tenacious old foes? Is this the next step in our evolutionary arms race that is tightly linking us to this or that mosquito species, when we consider the pathogens they transmit? What happens next, and when and where will it end? In this chapter, I argue that it is time for a paradigm shift from aggressive “vector control” to biologically sensitive and evolutionarily lucid management of synanthropic mosquito vector populations, aiming at shrinking ecological niches of pathogen transmission in order to prevent their emergence and spread in human populations. Applying the principles of evolutionary biology to the control of mosquito-borne pathogens may suggest novel opportunities for sustainable control of diseases that result in mosquitoes helping us combat rather than propagate the diseases they transmit.

### Humans and their “Mosquitome”

Just as the “Microbiome” defines a community of bacteria, fungi, viruses and other microbes that inhabit a particular environment, be it the gut or skin of a human host, it is useful to introduce the term “Mosquitome” to describe the group of mosquitoes that thrive where people live, being composed of a handful of highly synanthropic mosquito species that have successfully adapted to humans and human-made environments. Species of the Mosquitome have come to closely depend on the presence of human beings for breeding and proliferating. Indeed, these mosquitoes have developed very specific and distinctive attributes when compared to their wild counterparts, resulting in them contributing to most of the world’s burden of mosquito-borne infectious diseases. Singling out the Mosquitome, rather than all mosquitoes, might help focus public and stakeholders’ attention on the accurate disease target while avoiding harm to the larger amalgam that includes other natural mosquito species of benefit to ecosystems. The scope of such a Mosquitome should include the African malarial mosquitoes, *Anopheles gambiae s.l.* complex (which includes *An. gambiae s.s.*, *An. coluzzii* and *An. arabiensis*) and *An. funestus*; the invasive Indian species, *An. stephensi*; and the highly invasive *Aedes aegypti* and *Ae. albopictus* that transmit such arboviruses as dengue, yellow fever, Zika and chikungunya. Although each mosquito species has its own evolutionary pathway, humans have played a key role in shaping the evolutionary trajectories of each and every species within the Mosquitome, serving to fine-tune this weapon of mass destruction that it has become.

Crucially, mosquitoes need blood to reproduce; specifically, female mosquitoes need blood to mature and then to lay their eggs. Strong, anthropophilic preferences for human blood over other vertebrate blood have been shown to be a heritable, genetically encoded phenotype that has arisen and disappeared at multiple occasions in the course of mosquito evolution (Besansky, Hill & Costantini, 2004; Neafsey et al., 2015). Indeed, specializing in human ecosystems

has provided the Mosquitome with one of the most widespread and reliable sources of blood on Earth. Humans are gregarious animals that live in groups making them easy to locate. Moreover, humans shape their own environments wherever they settle, often removing many natural enemies of the mosquito, be they competitors or predators, such as insects, birds, bats and fish. Changes in land use through deforestation, agriculture and urbanization provide further opportunities for mosquito breeding and resting. In fact, beyond being a nearly inexhaustible source of blood, humans also provide mosquitoes with reliable and permanent access to water surfaces crucial to developing larvae.

The major human malaria vector in Africa, *An. gambiae*, lays its eggs in temporary water pounds with no vegetation, producing larvae that are highly “heliophilic,” or requiring direct exposure to sunlight to develop. Such surface-water collections are widespread during the rainy season throughout sub-Saharan Africa. And in areas where the rainy season is short, human environmental modifications for water management and irrigation, such as dams and rice fields, offer good breeding opportunities that expand mosquito presence and density in both space and time (Gimonneau et al., 2012). In equatorial areas with dense vegetation that blocks direct sunlight, deforestation and urbanization can expand suitable environments for *An. gambiae* that seek breeding habitats. As a result of these mosquito habitat preferences, there is a strong correlation observed between the presence of people, villages, roads and agricultural areas, and the presence of the *An. gambiae* complex in areas of sub-Saharan Africa (Costantini et al., 2009; Simard et al., 2009). In this respect, it has been hypothesized that the *An. gambiae*’s preference for feeding on humans over other vertebrates resulted from the colonization of suitable larval development sites by ancestral populations of the mosquito in Central Africa some 5,000 years ago, when Bantu agriculturalists adopted “slash and burn” agricultural techniques to open up the forest canopy and favour the breeding of larvae in the vicinity of humans (Ayala & Coluzzi, 2005).

In the same way, recent findings based on genomic, ecological and behavioural data obtained from various populations of *Ae. aegypti* strongly suggest that its preference for human-biting originally evolved as a by-product of breeding in human water containers, such as tanks and jars, in areas where doing so was the only way to survive the long and harsh Sahelian dry season (Rose et al., 2020). Here again, humans have been a reliable source of both water and blood, becoming a host of choice for those mosquitoes that have been able to adapt and continue to adapt to this human environment. In this way, *Ae. aegypti*, the “yellow fever mosquito” of African origin, was able to take hold and become the human nemesis that it is.

It is therefore fair to claim that tight relationships and intense long-lasting interactions between humans and their Mosquitome have long been driving mosquito-borne disease evolution. A recent and emblematic example of this evolution is the rapid rise of resistance in all major human disease-vector mosquitoes to all insecticidal compounds that have been used to control them

(Hemingway et al., 2016; Moyes et al., 2017). Some of the mechanisms used by mosquitoes to resist insecticides have been thoroughly described and can be monitored in wild mosquito populations. Longitudinal studies in the field as well as molecular, physiological and genomic studies have described the origin and spread of these resistances in vector populations, unraveling their extraordinary evolutionary potential, which is driven by short generation times and high levels of fecundity. Other studies have suggested that insecticide resistance may arm the mosquito with a non-specific detoxifying enzymatic capability that enables cross-resistance to other kinds of human-linked xenobiotics and pollutants, thereby further promoting mosquito colonization of areas with high human densities (Chouaibou et al., 2008).

Humans have therefore not only facilitated the instalment of their Mosquitome across the planet, but they have been a key contributor to the movement and dispersal of this group of highly anthropophilic mosquito species. This is especially the case for both *Aedes* species which have spread across the world by human transportation. In this way, *Ae. aegypti* originated in Africa and populated the Americas and Europe during the slave trade, while adapting to breeding conditions onboard ships (Powell & Tabachnick, 2013). More recently, the Asian tiger mosquito (*Ae. albopictus*) has also benefited by increased globalization and international trade, to spread from Southeast Asia to North America and the rest of the world within decades (Hawley, 1988; Paupy et al., 2009). Their physiological and behavioural traits have facilitated unintentional transportation of their eggs and mated females across long distances (Hawley, 1988; Eritja et al., 2017). Both *Ae. albopictus* and *Ae. aegypti* produce eggs that resist desiccation for several months; both prefer day-time host-seeking and biting activities; and both have a marked preference for breeding in small temporary water collections, such as tree holes, rock pools and other artificial water holders, leading to their nickname as “container mosquitoes.”

One realizes that humans have indeed shaped the evolutionary history of a handful of highly synanthropic mosquitoes that take advantage of human-modified environments to thrive and spread. In other words, we humans are a major evolutionary driver of the Mosquitome. The good news is that basic knowledge of medical entomology and mosquito physiology combined with recent advances in mosquito genomics, ecological modelling and evolutionary biology should now allow us to modify the evolution of the Mosquitome for preventing, rather than promoting, the transmission of mosquito-borne human diseases.

## The Mosquitome and disease transmission

One must remember that mosquitoes are not the problem; rather, the diseases they transmit are the problem. By applying evolutionary principles, mosquitoes can become part of the solution to limit mosquito-borne diseases. To date, synanthropic mosquitoes have been considered as pests that need to be

fought and ultimately eliminated for the sake of public health. And to date, only transient successes have been achieved in controlling the diseases they transmit, with many regions seeing more mosquitoes flying than ever before. Adopting the Mosquitome approach may help identify novel opportunities to tackle the challenge of sustainably controlling diseases in a changing world.

There are at least three biological tenets relevant to the status of major human disease vectors that are characteristic of the Mosquitome species (Cohuet et al., 2010): (1) a high level of contact with humans, especially by preferring to bite humans over other vertebrates; (2) genetic compatibility with the pathogen for sustaining pathogen development; and (3) unusual mosquito longevity for allowing this vector to bite susceptible hosts after the pathogen has reached the salivary glands. All these specificities result from well-adapted, co-evolutionary processes between mosquitoes and their human hosts, and between the transmitted pathogen(s) and vector-specific assemblages (see Duvallet et al., 2017 and references therein).

Existing data suggest that there is a correlation between a mosquito species' level of anthropophily (measured as the level of preference for human blood), and its longevity (measured as daily survival), with mosquitoes from the Mosquitome being champions in both categories (Figure 16.1). Greater longevity is a key parameter to vector capacity because it enables the female mosquito to survive long enough for the pathogen to develop in her body, infest her salivary glands and be transmitted through subsequent biting (Garrett-Jones, 1964; Cohuet et al., 2010). Longer lifetimes are a remarkable trait of synanthropic mosquitoes, reflecting their divergence from their wild counterparts in the course of their adapting to domestic habitats, and facilitating pathogen transmission. Thus, a key strategy for disease control is to curb the extraordinary longevity of Mosquitome species, thereby diminishing pathogen transmission intensity, while preserving mosquito biodiversity as a whole.

Longevity is correlated not only with anthropophily in mosquitoes. Indeed, as is true for all living species, longevity and fecundity are major traits of a species' fitness that appear to suffer "antagonistic pleiotropy" or genetic expressions that offer beneficial as well as detrimental effects. Conflicts in resource allocation result in an evolutionary trade-off between survival and early life fecundity that is an important basis of an organism's life-history strategy. This trade-off has long been recognized and studied in a number of organisms, from insects to plants and mammals. Long-lived organisms tend to invest less in early-life reproduction, often spreading out their offspring in time and space, compared to short-lived organisms that may rely on a single, massive reproductive event during their adult life. Most mosquitoes tend to follow the strategy of massive early reproduction, and here again Mosquitome mosquitoes stand out; as compared with non-vector species of *Culex* and *Mansonia* genera, major human malaria mosquitoes typically lay their eggs in successive batches across their lifespan, investing less in early-life fecundity (Clements, 1992). This continuous fecundity may indeed benefit such mosquitoes since the *An.*



Mosquitoes from the Mosquitome therefore present very peculiar biological traits that most likely evolved through intense, ancient and ongoing contact with humans. Many human pathogens, including some of the historically most deadly ones such as the malaria parasite or the amaril virus, have taken advantage of this intimate human–mosquito relationship for their own, widely successful inter–human transmission. By recognizing this relationship, it might now be in our hands to drive the Mosquitome’s evolutionary trajectory back to a situation where mosquitoes do not transmit diseases, rather than continuing to naively try to eliminate this group of highly adaptive organisms with enormous evolutionary potential.

### **Mosquitome management for sustainable disease prevention**

Until now, all strategies for mosquito vector control have relied on the assumption that any method of decreasing vector fitness is the best way to control disease. However, as demonstrated by the widespread use of synthetic insecticides, aggressive control tools will invariably result in selection for resistance. Furthermore, elimination of mosquitoes is not, and should not, be a requirement for interrupting disease transmission. An alternative and more effective approach to disease and vector control may well rely on strategies to create evolutionary incentives to the Mosquitome that will restore its former life history traits of epidemiological importance, especially longevity and anthropophily, to ranges typically observed in non-vector species. In other words, we must utilize evolutionary processes to drive the Mosquitome back to its natural, pre-human condition, rather than constantly attempting to counteract the effects of such processes. Countering Mosquitome longevity and anthropophily is likely the only way to achieve sustainable mosquito-borne disease prevention and vector risk-mitigation.

Opportunities exist to disentangle vector fitness from pathogen transmission (Michalakis & Renaud, 2009). Because only old female mosquitoes are actively involved in transmitting pathogens, strategies aimed at reducing their lifespans by killing them late in life, after they have reproduced but before they are able to transmit pathogens, would diminish natural selection of resistance. Biological agents such as fungi in the genus *Beauveria* and bacteria in the genus *Wolbachia* have been considered good candidates for late-life control. By developing slowly in infected mosquitoes, the fungus allows the female to mate and lay several batches of eggs before it eventually dies from infection. For their part, strains of *Wolbachia* serve to speed up senescence in dengue-transmitting mosquitoes, shortening their lifespan and reducing the efficiency of viral transmission. Exposing the Mosquitome to this kind of innovative, late-life vector control, the theory and development of which is still being worked out, may therefore provide significant control of disease transmission, with fewer impacts on mosquito populations.



From an evolutionary perspective, a shift towards relying on late-life-acting control strategies—while reducing selection for resistance—may also promote selection of more subtle life-history adaptations in the mosquito by reallocating resources towards short-term reproduction from longer-term survival. Indeed, experimental evolution experiments conducted with the model fly *Drosophila* have shown that exposing flies to different extrinsic mortality regimes over 50–90 generations resulted in shifts towards higher fecundity and reduced lifespan even in the absence of selection (Stearns et al., 2000). Such investigations corroborate the claim that insects are able to quickly adapt their life-history strategies to changes in their environment, as by balancing fecundity and longevity to optimize reproductive outputs. Just as mosquitoes of the Mosquitome increased their lifespan when adapting to novel, low-risk human environments, the *drosophila* study shows that it may be possible to reverse this trend and decrease the lifespan of anthropophilic mosquitoes. Indeed, extrapolating the *drosophila* experiment results to mosquitoes and malaria transmission, Ferguson and colleagues (2012) demonstrated that a similar drop in mean longevity (7.7% over 90 generations in the *drosophila* study) would result in more than 80% reduction in malaria transmission due to the non-linear relationship between vector longevity and vector capacity. These authors propose that a similar evolutionary shift may be induced in malaria-vector mosquitoes through enforced vector-control interventions, and that this shift can act as a hidden weapon that eventually eliminates malaria transmission when the vector's lifespan drops below the parasite's development time. Other evolutionary outcomes that include selection for parasites developing faster in their vector mosquito, or increased innate vector competence in mosquito progenies, may further interfere, and so need to be monitored in the frame of scaling-up vector-control interventions.

Opportunities also exist to manipulate host preference in mosquitoes, with existing genetic variation in the Mosquitome allowing for natural selection to drive mosquitoes away from human scent when it becomes associated with higher fitness cost. Although host-preference in mosquitoes is influenced by environmental factors such as host availability, there is also a genetic basis to this preference. Ecological and ethological studies conducted in the field and lab have documented plasticity and strong shifts in host choice in response to divergent selection pressures, while genome-wide investigations have shown that the genetic basis to host preference in mosquitoes is as complex as it is evolutionarily labile (Besansky et al., 2004; Lyimo & Ferguson, 2009; Neafsey et al., 2015). Anthropophily therefore might not only be subdued, but also eliminated when the Mosquitome finds a fitness incentive for switching hosts. We should hence develop these fitness incentives in the Mosquitome for alternative host-choice by better protecting humans from aggressive bites and, at the same time, by offering other possible prey or artificial blood sources for the Mosquitome in our cities. The development of novel personal protection tools, including improved repellents and attractants to manipulate vector behaviour, next-generation mosquito nets and screens to protect homes from vector intrusion, and replenished urban

biodiversity to dilute mosquito-biting pressure on humans, will be an integral part of such an endeavour.

Finally, opportunities also exist for increasing resilience of the domestic environment to mosquito breeding and spreading. Rational use and storage of water is becoming a pressing need stemming from climate change, and the way we address this urgent challenge will have a dramatic impact on the Mosquitome's ecology, and associated risks of disease transmission. Limiting surface water is key to reducing mosquito habitat suitability, and diminishing mosquito presence, density and viability. It should also be recognized that given the Mosquitome's adaptability to human-shaped environments and its extraordinary evolutionary potential, we may be doomed to share some of our space with these mosquitoes. Thus, just as we are learning how to manage our microbiome so that it can help us minimize infections and other detrimental impacts to our bodily ecosystem, we can also learn how to manage our Mosquitome so that it can help us develop more harmonious public health. Monitoring and managing our Mosquitome in a way that limits mosquito breeding in and around human dwellings will serve to limit transmission of diseases. Moreover, maintaining a resilient Mosquitome should, by occupying suitable habitats, hinder invasion by external mosquito populations with greater vector competence. Reducing vector capacity of the Mosquitome will require increasing extrinsic mortality for reducing life expectancies in resident mosquito populations. One way of decreasing mosquito longevity is by increasing natural mosquito enemies in cities and agricultural settings, which will produce novel equilibria in the Mosquitome life-history traits. Some mosquito threats in human settlements can be countered by such novel tools as mosquitoes controlling other mosquitoes. Additional mosquito-control techniques such as female-driven delivery of specific insect growth regulators, application of mosquito-specific pathogens to larval development sites, sterile-insect techniques or genetically modified mosquitoes that contain altered vector competence and/or altered vector reproduction (see also Moyes et al., 2017; Roiz et al., 2019) may all contribute to selecting for reduced longevity in the Mosquitome. The challenge now resides in our ability to carry out a gradual implementation of these complementary tools within the framework of concerted, locally designed and inclusive Mosquitome management strategies. Such a challenge will come at the cost of accepting to live with our Mosquitome. By willingly coinhabiting our Mosquitome, we may finally be achieving a Mosquitopia: that state in which mosquitoes and people can harmoniously coexist.

This scenario thus offers a paradigm shift in the way we set out to control mosquito vectors and the diseases they transmit by relying on long-term risk-mitigation of pathogen transmission, rather than short-term mosquito elimination. It is time to take care of our Mosquitome and recognize our duties in husbanding this highly specific evolutionary branch of biodiversity (Martin et al., 2015; Johnson & Munshi-South, 2017). We should strive to increase extrinsic vector mortality in cities through every means, work to (re)install mosquito

biological enemies such as predators, competitors and pathogens, design effective late-life-acting control tools and chemicals that shorten mosquito lifespan while preserving lifelong fecundity, and monitor the infrastructure of our neighbourhoods and water-management systems in order to limit breeding opportunities. Recent advances in evolutionary biology and emerging frameworks of urban ecology and commensalism in anthropogenic environments should help identify opportunities for translating theory into action (Roche et al., 2018; Hulme-Beaman et al., 2016). We must also build upon recommendations from the World Health Organization for tackling research gaps and fostering intra- and inter-sectoral collaboration for implementing the Global Vector Control Response (WHO, 2017; Roiz et al., 2019).

### Concluding remarks

The spring of 2020 was indeed silent. But this silence was due not to the reasons outlined in Rachel Carson's book. A sky without planes, traffic without motion and the general economic shutdown were due to a pandemic. The dramatic experience of COVID-19 highlighted the novel fate of infectious diseases in our globalized world and called for integrating preventive measures for sustainable disease mitigation. Mosquito-borne diseases are a prime public health threat for the next global emergency. They require the utmost attention. At the same time, the preservation of biodiversity has become a major societal and ecological challenge requiring immediate action, with one of the most pressing moves being an escape from our insecticide era to protect our food and health.

In this world view, I propose the Mosquitome as a concept like that of the microbiome to emphasize: (1), that when dealing with major human disease-vector mosquitoes, one deals with a very tiny fraction of the overall mosquito biodiversity and one that relies on very specific ecological attributes; (2), that this specific assemblage of mosquito species is tightly associated with and dependent upon humans; and (3), that we have long lived with these creatures and should now learn to benefit from that close association. In this view, mosquito elimination is no longer an expected or even a desirable outcome. Rather, acknowledging the Mosquitome as an integral part of our immediate environment prompts our long-term commitment to its management. Vector control programmes need to be transformed into Mosquitome management strategies to achieve sustainability in disease risk-mitigation while helping preserve biodiversity and improving ecosystem functioning, locally and globally.

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