

## 7. Consequences of deforestation and habitat degradation on wildlife mosquito-borne diseases

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### Abstract

Over the last several decades the rate of forest clearance has increased considerably. Millions of hectares of forests are lost every year for agricultural activities and timber extraction, which have significant consequences on atmospheric CO<sub>2</sub>, climate change and ecological interactions. Many studies carried out in perturbed habitats or areas that have gone through significant habitat loss have reported changes in vector-borne diseases dynamics, with an altered abundance of both the invertebrate and vertebrate hosts that has led to changes in pathogen prevalence. Following deforestation, altered microclimates with changes in temperatures, sunlight, and moisture and the addition of artificial breeding habitats tend to favour common vectors of disease, such as species of the mosquito genera *Anopheles*, *Aedes* and *Culex*. Land conversion for agricultural use also provides increased accessibility to blood meals with domesticated animals breeding in close quarters of humans. In fact, approximately three fourths of human emerging infectious diseases are caused by zoonotic pathogens due to the increasing contact among humans, domestic animal populations and wildlife hosts. The malaria parasite *Plasmodium knowlesi* and the Mayaro virus are examples of mosquito-borne zoonoses that jumped recently from wild hosts to humans following their encroachment into tropical forests. However, at the moment, it is simply unknown how many pathogens are transmitted to wildlife by mosquitoes and while many studies have shed light on the dynamics of avian malaria or the West Nile Virus, many other parasites and the likely multitude of undiscovered viruses are still poorly studied. The reality is that with rapid environmental change, without in-depth research on mosquitoes that feed on wildlife and the pathogens they harbour, we will not be able to predict why diseases emerge and what factors exacerbate their spread.

**Keywords:** *Aedes*, *Culex*, human land-use, malaria, arboviruses, zoonoses

### Introduction

In a very short time span, human-led changes, such as habitat destruction and climate change, have disturbed the natural stasis of most of the planet's ecosystems (Creutzig *et al.* 2019, He and Silliman 2019). In the last 40 years, natural vegetation, in tropical but also in the mid-latitudes, has been cleared at an arresting rate, millions of hectares per year, for agricultural activities such as support for livestock, monocultures and exotic tree plantations (Barlow *et al.* 2016, Tilman *et al.* 2001). Tropical forests, which account for one third of land-surface productivity and evapotranspiration (Malhi 2012), are estimated to host over half of all global terrestrial biodiversity (Pimm and Raven 2000) and are key to ensure many of the planet's vital functions. Since the second half of the past century, these ecosystems have been constantly shrinking. The latest data show that the tropics lost 11.9 million hectares of tree cover in 2019, with nearly a third of that loss, 3.8 million hectares, occurring within humid tropical primary forests (Global Forest Watch

2019). This habitat loss is the result of increasing impacts of multiple human activities, such as logging and other resource extraction (Malhi *et al.* 2014), livestock pastures (Almeida *et al.* 2016a) and conversion to agricultural use (Laurance *et al.* 2014). Among several crops, the cultivation of the oil palm *Elaeis guineensis* has been expanding at an annual rate of 9% worldwide (Vijay *et al.* 2016) and this rapid expansion has resulted in a significant loss of biodiversity and associated ecosystem services (Almeida *et al.* 2016b, Ganser *et al.* 2017, Savilaakso *et al.* 2014). In temperate areas, natural forests have also been intensively harvested and dramatically reduced, mainly due to overexploitation and conversion to farmland and tree plantations (Hannah *et al.* 1995, Teixido *et al.* 2010). As an example, the spread of the exotic tree species, *Eucalyptus globulus* has transformed the landscape of the Atlantic coast of Northern Iberia and is impoverishing regional avifauna and the communities of other taxonomic groups (Calviño-Cancela *et al.* 2012, Proença *et al.* 2010). In addition to solely habitat loss, habitat fragmentation is a consequential process that subdivides continuous habitats into smaller pieces and results in population isolation and a disruption in landscape connectivity (Fahrig 2003). Therefore, not only forests are under major threats, but also other biomes are in peril; e.g. the Cerrado in South America, which is considered one of the most important savanna biomes in the world, with a mixture of open grasslands, shrub lands, open woodland and closed canopy woodland (Bridgewater *et al.* 2004). This ecosystem is undergoing pervasive degradation because of agriculture expansion, with vast areas recently modified for soy cultivation (Lima *et al.* 2019), which has put wildlife populations at risk (Borges *et al.* 2019).

All these human activities and habitat degradation are expected to disrupt ecological interactions, notably relationships between hosts, vectors and pathogens, and to influence the dynamics of transmission of infectious diseases (Faust *et al.* 2018, Sehgal 2010, Walsh *et al.* 1993; Figure 1). There have been many examples of direct effects of deforestation on human pathogens (e.g. malaria: Burkett-Cadena and Vittor 2018, Yanoviak *et al.* 2006, Yasuoka and Levins 2007). Increased levels of sunlight, associated with open spaces, have been correlated with increased mosquito densities and feeding rates of mosquitoes on humans and increased parasite transmission (Vittor *et al.* 2006, 2009). However, some studies have also reported no obvious link between deforestation and the prevalence of vector-borne diseases (see examples in review Tucker Lima *et al.* 2017). These conflicting findings are likely attributable to the complexity of vector-borne disease systems, and depend on the study region and associated socio-ecological factors (MacDonald and Mordecai 2019). As with infectious diseases in humans, numerous studies focusing on avian malaria have found conflicting results on the impacts of deforestation and fragmentation (Chasar *et al.* 2009, Loiseau *et al.* 2010, Rivero de Aguilar *et al.* 2018, Tchoumbou *et al.* 2020). Interestingly, although the diversity of mosquitoes that feed on birds can be higher in degraded environments, some studies also found a lower abundance in urban habitats (Abella-Medrano *et al.* 2015, 2018) or fragmented forests (Tchoumbou *et al.* 2020) compared to well-preserved forests.

Environmental changes are therefore modifying transmission dynamics of pathogens specific to humans or to wildlife, but another consequence of deforestation and encroachment into wildlife habitat, and associated activities such as hunting, wildlife trade, live animal and bushmeat markets (Symes *et al.* 2018), is the risk of the emergence of zoonoses (Jones *et al.* 2013). A zoonosis is any bacterial, viral or parasitic disease that is naturally transmissible from animals to humans. Approximately three fourths of human emerging infectious diseases are caused by zoonotic pathogens (Taylor *et al.* 2001) and because humans and domestic animal populations come into increasing contact with wildlife hosts harbouring potentially zoonotic pathogens, a large increase of zoonotic pathogens emergence has been reported in the last decades (Swei *et al.* 2020). Zoonoses can be transmitted directly from animals to humans, such as Ebola (Buceta and Johnson 2017), Nipah virus (Gurley *et al.* 2017), or the novel SARS-CoV-2 (Andersen *et al.* 2020),

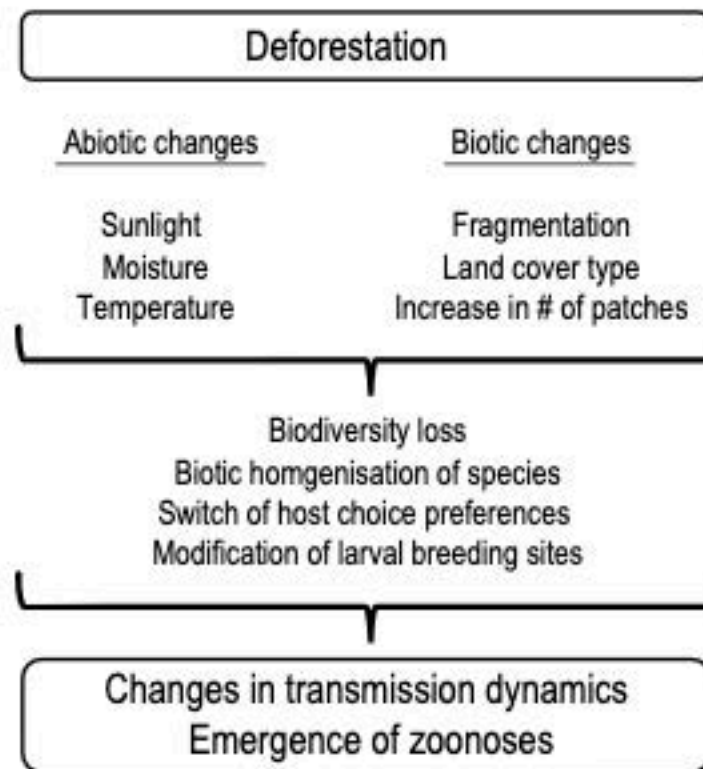


Figure 1. Diagram of deforestation consequences on mosquito-borne diseases.

or transmitted via an arthropod-vector, such as Zika virus (Saiz *et al.* 2016) and West Nile virus (Tolsá *et al.* 2018) among others. Here, we will attempt to evaluate and give an overview of the impacts of deforestation, habitat fragmentation and degradation (1) on mosquito communities (i.e. diversity, abundance, and assemblage), (2) the consequences on mosquito-borne disease specific to animals, and (3) the consequences on mosquito-borne zoonotic diseases. Finally, we address potential challenges working with mosquito-borne diseases and recommend future lines of research.

### How are mosquito communities affected by environmental degradation?

Given the unprecedented global effects on the environment and biodiversity worldwide, distributions of vector-borne diseases are similarly changing radically. For mosquitoes, important components for their survival are temperature, the availability of water and plant resources, plus the necessity of blood meals for females. With global climate change, deforestation, urbanisation, and other changes in land use by humans, mosquito populations and the pathogens they transmit are undergoing shifts that may have long-term effects on wildlife and humans. As with biodiversity worldwide, we can expect a homogenisation of niches (Clavel *et al.* 2011), resulting in a loss of habitat specialist mosquitoes and the global proliferation of generalists and invasive ones, such as *Aedes albopictus* (Niebylski *et al.* 1994), which is a major human disease vector.

Globally, with more than 3,500 species, mosquitoes are among the most successful insect groups on the planet, with their richness increasing along a gradient from the higher latitudes toward the equator (Foley *et al.* 2007). About 50% of the species are endemic, but only 3% or about hundred species actually feed on humans (Foster and Walker 2019). With global climate change, the general expectation is that mosquitoes will move into the higher latitudes, following rising temperatures. With deforestation, urbanisation, and loss of wetlands and other habitats, we expect an overall reduction in mosquito species diversity, and a general trend towards the spread

of invasive mosquitoes and the loss of endemics (Brady and Hay 2020, Manguin and Boëte 2011). This will be most apparent on islands, and is punctuated by the classic example of the invasion of the Hawaiian Islands by mosquitoes in the 19<sup>th</sup> century (Keyghobadi *et al.* 2006). One important understudied aspect of mosquito entomology is how the loss of many endemic mosquito species will shape ecosystem services, such as plant pollination (Lahondère *et al.* 2020), the filtering of water by consuming microorganisms and detritus (Merritt *et al.* 1992) or the survival of other threatened species that could be dependent on them as a food resource (Blaustein and Chase 2007, Poulin *et al.* 2010). The loss of endemic species could in turn lead to an increase in the invasive mosquitoes that may replace them (Johnson and Sukhdea 2013). Since there is a general disdain for mosquitoes by humans, as they are certainly not charismatic megafauna, mosquito conservation biology has not been a very active area of research. However, it is likely that the loss of many endemic mosquito species will lead to ecosystem deficits, and perhaps the loss of other dependent organisms (Fang 2010).

With the demise of such a substantial portion of the planet's native habitats due to human encroachment, habitat generalist mosquitoes are increasingly spreading across the planet. With the mosquitoes, pathogens will follow. It has been shown that several invasive mosquitoes have recently moved into habitats that were once dominated by endemics. The yellow fever mosquito, *Aedes aegypti*, is one of the most dangerous mosquitoes to humans due to its capacity to transmit several debilitating viruses, such as the Dengue, Chikungunya as well as Zika and Yellow fever, among others. It is believed that this mosquito species, up until as recently as 500 years ago was entirely a forest-dwelling mosquito that fed on non-human mammals (Powell *et al.* 2018). As humans moved into its native habitat, it quickly adapted to using human water containers for its larval stages, and began to preferentially feed on humans (Brady and Hay 2020). It began to spread worldwide with the movement of ocean-going ships. In particular, it most likely arrived in the New World with the slave trade (Powell *et al.* 2018) and is now spreading worldwide (Akiner *et al.* 2016, Liu-Helmersson *et al.* 2019). With its capacity to transmit dangerous flaviviruses and alphaviruses, it already has killed untold numbers of humans (Brady and Hay 2020) and has also affected wildlife (e.g. West Nile, Rift Valley, Usutu viruses; Bird *et al.* 2009, McLean *et al.* 2002, Roesch *et al.* 2019). Similarly, *Anopheles stephensi*, which transmits human malaria in Asia has expanded its range recently, and was discovered in Sri Lanka for the first time in 2017, most likely arriving with humans from India (Sinnathamby *et al.* 2019). These are just two of the numerous documented cases of mosquito vectors expanding their ranges with human populations.

The majority of habitats on the planet are experiencing rapid environmental changes, where some of the major contributing processes can be classified by deforestation, urbanisation, agricultural development and at the larger scale, global climate change (Franklinos *et al.* 2019). It is clear that biodiversity is rapidly lost with forest clearance (Newbold *et al.* 2015), and can result in the emergence of mosquito-transmitted diseases. Following deforestation, changes in microclimates (temperatures, sunlight, and moisture) and the addition of artificial breeding habitats tend to favour vectors of disease, such as species of *Anopheles*, *Aedes* and *Culex* (Burkett-Cadena and Vittor 2018, Mayi *et al.* 2019). Similarly, land conversion for agricultural use, in addition to providing more suitable habitats for human disease-carrying mosquitoes, may also provide increased accessibility to blood meals with domesticated animals breeding in close quarters (Service 1991). Most humans now live in urban environments, and this results in altered climates through the creation of urban heat islands, which again favour the urban vectors of the genus *Aedes* (Murdock *et al.* 2017), but may hinder the development of *Anopheles* species, which transmit malaria (Qi *et al.* 2012).

The effects of global climate change on mosquito populations are complex, and there is no general consensus regarding how changes in climatic conditions will impact the risk of mosquito-borne diseases (Franklinos *et al.* 2019). Some climate scenarios will result in better habitats for mosquitoes, and others will hinder their survival. The effects of increasing temperatures on insects are expected to be non-linear, where some mosquito populations will benefit and others may suffer from reduced fitness, such that certain areas of the planet may actually see reduced numbers of mosquito-borne disease cases (Mordecai *et al.* 2017). It is most straightforward to surmise that climate change will have unpredictable effects on mosquitoes, since they are so closely tied to the often capricious behaviours of humans (Bartlow *et al.* 2019). We can be certain however that environmental change will alter the patterns of transmission, in humans, domestic animals and wildlife.

### **How does environmental degradation alter infectious disease dynamics in wildlife?**

As stated earlier, deforestation and habitat fragmentation affect the diversity and abundance of mosquitoes. Mosquitoes are known vectors for many pathogens, and while they are well known to transmit human diseases such as dengue, Zika, malaria, lymphatic filariasis and others, it must be remembered that in studying the ecology of disease, research on human diseases can be confounded by human socioeconomic conditions and health interventions (MacDonald and Mordecai 2019, Tucker Lima *et al.* 2017). For example, human malaria was at one time prevalent in many parts of the world, including North America, but was eradicated with the advent of pesticides, and improvements in anti-malarial drugs (Andrews 1948, Carter and Mendis 2002). Thus, studying the ecology of mosquito-borne diseases of wildlife can give a better indication of the true effects of rapid environmental changes and deforestation on disease transmission.

Over the last decades, avian malaria has become a trenchant model system to research how habitat changes can affect the prevalence and diversity of vector-borne pathogens in wildlife (Ferraguti *et al.* 2020, Sehgal 2015). We have learned that pathogen dynamics are highly complex. First, the prevalence of avian malaria (of the genus *Plasmodium*), and other related haemosporidian parasites, varies tremendously with habitat and bird communities. In terms of deforestation, studies have reported contrasting results for *Plasmodium* parasites, with either an increase in prevalence in disturbed habitats (Chasar *et al.* 2009, Hernández-Lara *et al.* 2017, Reis *et al.* 2020, Tchoumbou *et al.* 2020), a higher prevalence in forests (Bonneaud *et al.* 2009, Loiseau *et al.* 2010) or no impact of the land use type (Rivero de Aguilar *et al.* 2018, Sebaio *et al.* 2012). Recently further work has shown that the prevalence of avian malaria is significantly and positively correlated with mosquito abundance in a fragmented African rainforest (Tchoumbou *et al.* 2019; Figure 2), although it is apparent that this type of association can be readily affected by the seasonality and again the species, or lineage, of the parasite (Fecchio *et al.* 2017, Lalubin *et al.* 2013). Similarly, the diversity of the parasites varies with changes of habitat. As is typical with biodiversity in general, deforestation and loss of rich diverse habitats result in a decreased diversity of avian malaria parasites, and this can be expected due to the loss of locally endemic bird species and mosquito vectors (Sehgal 2015). Moreover, we hypothesise that with deforestation and habitat loss, there will be a loss of specialist parasites, and generalists will prevail. This could eventually lead to the dominance of generalists such as the parasite *Plasmodium relictum*, which caused the large-scale deaths of birds when it invaded the Hawaiian Islands (LaPointe *et al.* 2012). In effect, we can expect more generalist malaria parasites to emerge with associated rapid environmental change, which may contribute to the loss of many endemic or immunological naïve bird species.



Figure 2. Picture of a CDC light trap installed in a palm oil plantation to collect vectors and identify their associated diseases in highly disturbed habitat after deforestation. © Rafael Gutiérrez-López.

It is likely that deforestation and land use changes will affect the prevalence of malaria in many other animals besides birds. It is now known that malignant human malaria (*Plasmodium falciparum*) originated in gorillas (Liu *et al.* 2010), and many primates are frequently infected with various species of primate malaria (Prugnolle *et al.* 2010). With the persistent human encroachment into areas frequented by primates, it is likely that human *Plasmodium* parasites may more readily be transmitted between humans and non-human primates (Duval *et al.* 2010, Liu *et al.* 2010, Loy *et al.* 2017). Primates are threatened more now than ever in their long history because of the extensive habitat loss, increased bushmeat hunting and illegal trade (Estrada *et al.* 2017). With altered mosquito communities, deforestation will also make them more susceptible to human mosquito-borne pathogens. As we now know, many human pathogens have a sylvatic cycle, and mosquito populations with access to both primate and human communities will undoubtedly contribute to more disease in both wildlife and humans (Valentine *et al.* 2019). For example, the Yellow Fever virus is greatly impacting primate populations in South America (Holzmann *et al.* 2010). New World monkeys suffer habitat destruction and hunting pressure, which fragments populations. They are in addition highly vulnerable to this virus, which is almost always fatal, and therefore, outbreak events of yellow fever are another major threat to their survival (Agostini *et al.* 2015). Interestingly the humans and monkeys are probably only temporary amplifiers of yellow fever, since studies showed that mosquitoes could be the primary reservoirs, as they are infected throughout their lives, with maternal transmission from adults to eggs (Tomori 2004).

Today, it is simply unknown how many pathogens are transmitted to wildlife by mosquitoes. Certainly, many studies have shed light on the dynamics of avian malaria, the West Nile Virus (Blitvich 2008, Morin and Comrie 2013), and to a lesser extent avian pox (Atkinson and LaPointe 2009), but many other parasitic pathogens, such as nematodes and trypanosomes and the likely multitude of undiscovered viruses are relatively unstudied. Thus, the reality is that with rapid environmental change, without in-depth research on mosquitoes that feed on wildlife and the

pathogens they harbour, we will not be able to predict why diseases emerge and what factors exacerbate their spread.

### **What are the consequences of deforestation on zoonotic diseases dynamics?**

Vector-borne zoonoses represent today a problem of increasing importance since they are almost impossible to eliminate. Indeed, there is no way to control all the natural reservoir hosts (wild birds and mammals) that are part of sylvatic cycle of numerous viruses and eukaryote parasites that infect humans. However, the risks of an infectious disease jumping from wildlife to humans can be reduced by investigating and knowing: (1) the diversity of wildlife pathogens in a region, which is considerably more important in the tropics than in temperate regions, (2) the effects of environmental changes on wild populations and on the distribution of vectors and (3) the frequency of contacts between humans and wildlife (Wolfe *et al.* 2005).

In 1993, Walsh *et al.* wrote one of the first reviews about the effects of deforestation on vector-borne diseases. The authors described the discovery of a tick-borne zoonosis in the tropics: Kyasanur Forest Disease (KFD). At first, in South India, languor monkeys, *Semnopithecus entellus*, and macaque monkeys, *Macaca radiata*, were found dead in a forested area, infested with ticks. Not long after, researchers identified a new virus, and then, on a quite small geographical scale, every year, new cases were reported as well as the deaths of people in the nearby villages. Monkeys, small mammals such as rats, mice and shrews, as well as birds were found to act as amplifier hosts, and to carry infected ticks in villages (Hoogstraal 1966). The KFD is one of the examples of diseases that came into contact with human population following ecological changes, namely deforestation and wildlife habitat perturbation. There are many additional examples in the literature of the effects of deforestation, habitat fragmentation and global changes on a wide array of vectors and their associated pathogens (Colwell *et al.* 2011). Here, we choose to focus on zoonotic mosquito-borne diseases caused by two different pathogens: *Plasmodium knowlesi* and the Mayaro virus, found in Southeast Asia and the Americas respectively. These two pathogens are still restricted to their original regions, as opposed to others such as the West Nile or Dengue viruses that are now cosmopolitan, and therefore they require heightened vigilance to avoid uncontrolled spread.

*P. knowlesi* malaria is a mosquito-borne zoonosis present in Southeast Asia, which infects primarily long-tailed, *Macaca fascicularis*, and pig-tailed macaques, *Macaca nemestrina* (Eyles *et al.* 1962) and was identified as an emergent public health threat only recently in 2004 (Cox-Singh and Singh 2008, Singh *et al.* 2004). This simian *Plasmodium* is transmitted by various forest-dwelling mosquitoes such as *Anopheles balabacensis*, which is considered the primary vector in Sabah (Wong *et al.* 2015) but also *Anopheles cracens* (= *An. balabacensis balabacensis*) in Peninsular Malaysia (Vythilingam *et al.* 2008), *Anopheles hackeri* (Wharton and Eyles 1961) and *Anopheles latens* in Sarawak, Malaysia (Vythilingam *et al.* 2006). Several studies have shown that changes in forest cover have impacted vector abundance and assemblages, as well as disease prevalence in humans (Brock *et al.* 2019, Hawkes *et al.* 2019, Wong *et al.* 2015) but very few have investigated the effects of deforestation and habitat fragmentation on macaque populations and their movement and distribution. It was suggested that deforestation may cause macaques to crowd into the remaining forest patches, spend more time on the ground (Riley 2008, Singh *et al.* 2001) and seek crops and food around human settlements (Hambali *et al.* 2012). These behavioural changes, subsequent to habitat perturbation, are resulting in an increased contact rate between macaques, humans and *Anopheles* mosquitoes, and therefore an increase in spillover events from macaques to humans is expected. In fact, experimental work in the laboratory has shown that *P. knowlesi* could be transmitted via mosquito bites from monkey to monkey, from monkey to humans, from

humans to humans and from humans back to monkeys (Chin *et al.* 1968). In addition, *Anopheles* mosquitoes that feed on both macaques and humans have been found to harbour several other simian parasites (e.g. *Plasmodium cynomolgi*, *Plasmodium coatneyi* and *Plasmodium inui*; Wong *et al.* 2015), which might be of concern to humans in the near future (Raja *et al.* 2020). Taking into account the ecological requirements of each host through an integrative approach, at both the small and large-scale, is necessary to define areas at risk for this zoonotic mosquito-borne disease (Brock *et al.* 2016, Davidson *et al.* 2019).

The Mayaro virus is an Alphavirus of the family *Togaviridae*, such as Chikungunya and Sindbis viruses (Lavergne *et al.* 2006). This virus circulates in Central and South America in humans and causes acute febrile illness (Anderson *et al.* 1957), which is difficult to differentiate clinically from Chikungunya or Dengue (Tesh *et al.* 1999). It was first isolated from sick forest workers in Trinidad and Tobago in 1954, then in Colombia, Brazil, Suriname, Guyana, Peru, Bolivia (see references in Tesh *et al.* 1999), French Guiana (Talarmin *et al.* 1998) and Venezuela (Torres *et al.* 2004). Interestingly, a very diverse group of wild vertebrates have been found with anti-Mayaro virus antibodies: lizards (Taylor 1967), birds (Calisher *et al.* 1974), several primate species (Hoch *et al.* 1981, Seymour *et al.* 1983, Talarmin *et al.* 1998), but also marsupials, sloths, rodents and carnivores (De Thoisy *et al.* 2003). Studies found that, in general, animals that are diurnal and live in the canopy tend to have a higher prevalence of the virus than others (De Thoisy *et al.* 2003, Talarmin *et al.* 1998), which corresponds to the niche of the mosquito genus *Haemagogus*; the main vectors of the Mayaro virus. These diurnal mosquitoes are tree-dwellers, very common in rainforests (Hoch *et al.* 1981), and are rather opportunistic feeders, which can explain the large variety of vertebrate hosts infected, including humans (Alencar *et al.* 2005).

People living within or in close proximity to forests appear to be the most affected by the disease (Black *et al.* 1970, Talarmin *et al.* 1998) and an increasing number of human cases in the Amazon basin seem to be due to ecosystem disturbances. Since the 1950's, regular outbreaks have occurred in Brazil but not only in the northern region where the disease is endemic: this raises concerns about the spread and transmission of the virus to areas outside of the Amazon basin (Esposito and Fonseca 2017). Several monkey species are quite common near villages and cities, and could act as reservoirs to an urban transmission cycle, in addition to the birds that may also have a role in the natural transmission of the virus (Hoch *et al.* 1981). Today, of primary concern are the peri-urban mosquito species that have been found naturally infected with Mayaro virus (*Mansonia venezuelensis*, Aitken *et al.* 1960; *Culex vomerifer*, Galindo and Srohongse 1967) and others that have been found as competent vectors in the laboratory such as *Ae. aegypti* and *Ae. albopictus* (Smith and Francy 1991, Long *et al.* 2011). The extensive deforestation in South America and urbanisation, coupled with the colonisation of this expanding habitat by the anthropophilic mosquitoes, *Ae. aegypti* and *Ae. albopictus* will probably lead to movement of the Mayaro virus outside the sylvatic cycle, as did Chikungunya or Dengue (Mackay and Arden 2016, Weaver and Reisen 2010). These two viruses lost the requirement for wildlife amplification and have now an efficient human-mosquito-human transmission. When and where this could happen with Mayaro virus remains difficult to predict.

## Challenges and future research

Researchers studying mosquito-borne diseases in wildlife face several challenges. First, in tropical regions, there is an overwhelming diversity of mosquito species with complexes of species often extremely difficult to identify. The description of new species requires advanced entomological expertise and today there are very few researchers that have practice identifying mosquitoes of



little medical or veterinary importance. One avenue to enhance the knowledge of the diversity of mosquitoes in remote regions, especially in tropical rainforests, is through the use of new methodological tools, such as metabarcoding of eDNA samples (Ji *et al.* 2013, Ruppert *et al.* 2019). In fact, collecting water where larvae grow is relatively straightforward and this technique has shown promising results (Boerlijst *et al.* 2019, Krol *et al.* 2019). However, the issue remains that database references are incomplete and that in depth taxonomy work is still necessary to match DNA sequences to species identifications.

In addition, researchers often lack information about the feeding habits of mosquitoes, which is essential to understand the transmission dynamics of diseases. To evaluate how disturbances will influence the host choice of vectors and eventually the switch of pathogens from one host species to the other, the analysis of blood meals is critical (Stephenson *et al.* 2019). However, sampling blood-fed mosquitoes is a challenge in itself, even for medical entomologists. Blood-fed females, depending on the species, rest on the vegetation, near the ground or in the canopy and therefore canopy-dwelling mosquito species are nearly impossible to catch. Still, improved rope-climbing methods (Picart *et al.* 2014), cranes (Nakamura *et al.* 2017) or original airborne devices and canopy rafts have been created (Charron *et al.* 2020, Gottsberger 2017) to allow scientists to access forest canopies and unravel their amazing biodiversity; richer than in all the other forest strata.

Encouraging collaborations among researchers with complementary expertise is essential. Since many pathogens infect wildlife and humans, entomologists, ecologists, wildlife conservationists, parasitologists and sociologists should work together to better understand how deforestation and habitat disturbances affect the diversity of mosquito species and the dynamics of their associated diseases. In the early years of the 21<sup>st</sup> century, 'One Health' was proposed as a concept to foster interdisciplinary collaborations. This approach promotes integrative studies to tackle complex, interconnected human – animal – ecosystem disease problems (Gibbs 2014). Multi and transdisciplinarity between life sciences, social sciences and the humanities is required, but researchers, human and animal health organisations are sometimes facing institutional and logistical barriers to achieve such an approach (Waltner-Toews 2017). Although predictive maps of infectious disease emergence are regularly produced (Allen *et al.* 2017, Messina *et al.* 2019, Wilkinson *et al.* 2018), who knows how many zoonoses the world will face in the next decades. In the meantime, mosquitoes keep swarming and spreading while sadly humans keep destroying forests.

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