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Ecology of arboviruses and their potential mosquito vectors in Benin, Côte d'Ivoire and Gabon: a mini review

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Mosquito-borne arboviral zoonoses are an increasingly (re-)emerging threat for millions of people in endemic countries of Africa. *Aedes*-transmitted yellow fever (YF), dengue (DEN), chikungunya (CHIK), and Zika (ZIK) viruses, as well as *Aedes*- and *Culex* transmitted Rift Valley fever virus (RVFV) infections often go undiagnosed and as a result, accurate clinical reports for these viral diseases are lacking. The absence of evidence-based risk maps for arbovirus infections hinders the implementation of more suitable prevention/surveillance and control strategies in both non-endemic and endemic African countries. The vectorial capacity of arbovirus-transmitting vectors is highly complex mainly due to the interplay between biotic and abiotic factors that vary in time and space, explaining the differential patterns of arbovirus diseases between countries. Mapping the influential factors of arbovirus transmission, such as vector ecology, behavior, and biology in countries with different outcomes of arboviral diseases, will strongly help improve our understanding of local epidemiology and circulation of these diseases. Herein, we review up-to-date data on the distribution of arboviruses and their respective vectors from three sub-Saharan African countries (Benin, Côte d'Ivoire, and Gabon) presenting

different patterns of arbovirus diseases. We pinpointed major knowledge gaps and potential research interests to increase knowledge of the distribution of arboviral diseases and their vectors through African countries to improve the strategies to successfully prevent, monitor, and control the disease outbreak.

KEYWORDS

arbovirus, vector, Benin, Gabon, Côte d'Ivoire

1 Introduction

Globally, viruses transmitted by arthropod vectors (termed ‘arboviruses’) are one of the most persistent pathogens that cause life-threatening diseases in humans, infecting millions of people and imposing a considerable social and economic burden (1). Around 73% of current emerging and re-emerging pathogens are arboviruses (2) transmitted by mosquitoes, ticks, sandflies, and midges (1, 3–6). Mosquito-borne arboviruses have remained a (re)emerging threat to people’s well-being in Africa, with the potential to spread worldwide. *Aedes* and *Culex* species are the main vectors, which enable the transmission of arboviruses such as dengue virus (DENV), yellow fever virus (YFV), chikungunya virus (CHIKV), West Nile virus (WNV) and Rift Valley fever virus (RVFV) (7). Over the past five years, arbovirus infections have been responsible for a significant burden of vector-borne diseases with non-negligible public health and socio-economic impacts in Central and West African countries. Yellow fever (YF), dengue fever (DF), chikungunya (CHIK) and Zika (ZIK) threaten more than 831 million people in Africa, representing 70% of the continental population (8). The RVFV infections have led to increased abortions and stillbirths, as well as high mortality in newborns and young animals (sheep, cattle, goats, camels), with considerable economic losses to livestock, in addition to disease and mortality in humans (9).

Loss of biodiversity, climate change, consumption of wild animals, and population mobility are the main drivers of zoonosis (10). For instance, climate change may have a significant impact on human and animal movements due to changes in land use and housing design, which may further increase the complexity of arbovirus emergence (11). In addition, urban expansion has led to high concentrations of susceptible human hosts living in socio-economic conditions favourable to the expansion of vector populations. This facilitates arboviral transmission and the outbreak of epidemics (12). Success in arbovirus transmission depends on the vectorial competence of the infected vector and the infectivity of arbovirus strain (13), but other influential factors are vector population density, biting behavior, vector survival rate, and host availability. Thus, non-detection of arbovirus infection in humans in areas where potential vector species are found does not imply the absence of risk of arbovirus transmission but may depend on a wider range of factors, such as susceptibility of the vector or

host to certain viruses. For instance, *Aedes* species such as *Aedes (Ae.) aegypti formosus* and *Ae. aegypti aegypti* have demonstrated differential susceptibility to DENV (14). Even more complicated, some *Ae. aegypti* colonies (Rockefeller, Chetumal) have demonstrated in the laboratory, their susceptibility to dengue viruses, while colonies (Moyo-R, Cali) are refractory due to intrinsic factors (15). Here, we review up-to-date data on the distribution of arboviruses and their respective vectors in three sub-Saharan African countries: Benin, Côte d'Ivoire, and Gabon, which are of particular interest due to their widely divergent epidemiological status despite their geographical proximity. We identified key knowledge gaps and potential research interests to improve knowledge on the distribution of arboviral diseases.

2 Methodology

The data presented in this review were collected through a web-based search for original articles published using PubMed, Web of Science databases, and Google Scholar web. Our search included all articles published in the study areas up to October 2023. Search terms used in all databases were “Arbovirus in Africa”, “Arbovirus in Gabon”, “Arbovirus in Benin”, “Arbovirus in Ivory Coast”, “Mosquito species in Gabon”, “Mosquito species in Ivory Coast”, “Mosquito species in Benin”, “Mosquito-borne viral diseases in Benin, Ivory Coast and Gabon”. Out of a total of 819 articles identified, 127 were deemed relevant, of which only 55 were selected and examined as part of this study.

3 Arboviruses and vectors

3.1 Mosquito vectors of arboviruses

Several mosquito species serve as vectors of arboviruses in the wild, and many others are competent vectors in laboratory settings. Nowadays, *Aedes* and *Culex* spp. are the main vectors of medically important arboviral diseases in humans (16). In this review, 30 mosquito species belonging to the genera *Aedes* and *Culex* were reported in Gabon, Côte d'Ivoire, and Benin (Table 1). Mosquito species diversity was highest in Côte d'Ivoire, with *Ae. aegypti* being the predominant species. More so, the population of adult *Aedes*

TABLE 1 Mosquito species abundance in Gabon, Benin, and Côte d'Ivoire with special emphasis on arbovirus-transmitting species.

Country	Mosquito species	Abundance	Collection methods	Sites
Gabon	<i>Ae. aegypti</i>	4050 (17–24)	Ovitrap, HLC, BG Sentinel trap	Lopé, Franceville, Ndangui, Libreville, Lastourville, Oyem
	<i>Ae. africanus</i>	23 (21)	Ovitrap, HLC, BG Sentinel trap	Lopé
	<i>Ae. albopictus</i>	10688 (17–22, 24)	Ovitrap, HLC, BG Sentinel trap	Lopé, Franceville, Ndangui, Libreville, Lastourville, Oyem
	<i>Ae. apicoargenteus</i>	11 (21)	Ovitrap, HLC, BG Sentinel trap	Lopé
	<i>Ae. dendrophilus</i>	31 (21)	Ovitrap, HLC, BG Sentinel trap	Lopé
	<i>Ae. fraseri</i>	15 (21)	Ovitrap, HLC, BG Sentinel trap	Lopé
	<i>Ae. simpsoni</i>	198 (18, 19, 23, 24)	HLC	Franceville, Ndangui, Libreville
	<i>Aedes</i> sp.	775 (21, 25)	Larva dipper, Ovitrap, HLC, BG Sentinel trap	Lopé, Akanda
	<i>Culex quinquefasciatus</i>	1676 (17, 19, 23)	HLC	Franceville, Libreville
	<i>Culex</i> sp.	513 (19, 23, 25)	Larva dipper, HLC	Franceville, Libreville
Benin	<i>Ae. aegypti</i>	33156 (26–31)	Larva dipper, HLC, BG Sentinel trap	Atakora, Abomey-Calavi, Porto Novo, Ouesse, Allada, Adjara, Sakété, Ifangni, Kétou
	<i>Ae. albopictus</i>	2400 (31)	Ovitrap, HLC	Ifangni, Kétou, Porto Novo, Abomey-Calavi, Adjara, Sakété
	<i>Ae. circumluteolus</i>	108 (27)	HLC, BG Sentinel trap	Ouesse, Allada
	<i>Ae. gr. Palpalis</i>	15 (26)	HLC	Atakora
	<i>Ae. gr. tarsalis</i>	30 (26)	HLC	Atakora
	<i>Ae. longipalpis</i>	26 (26)	HLC	Atakora
	<i>Ae. luteocephalus</i>	155 (26–28)	Larva dipper, HLC, BG Sentinel trap	Atakora, Abomey-Calavi, Ouesse, Allada
	<i>Ae. quinquefasciatus</i>	753 (32)	HLC	Porto Novo
	<i>Ae. vitattus</i>	115 (26–28)	Larva dipper, HLC, BG Sentinel trap	Atakora, Abomey-Calavi, Ouesse, Allada
	<i>Culex fatigans</i>	100 (27)	HLC, BG Sentinel trap	Ouesse, Allada
	<i>Culex quinquefasciatus</i>	735 (33)	BG Sentinel trap	Cotonou
	<i>Culex tigripes</i>	465 (27)	HLC, BG Sentinel trap	Ouesse, Allada
Côte d'Ivoire	<i>Ae. aegypti</i>	92998 (34–41)	WHO layer-traps, larval dipper, Ovitrap, HLC	Bouake, Abidjan, Korhogo, Ehania-V1, Blockhauss, Treichville, Port of San-Pedro
	<i>Ae. africanus</i>	423 (34–36)	HLC, Ovitrap	Korhogo, Ehania-V1, Blockhauss, Treichville
	<i>Ae. albopictus</i>	54 (38)	Ovitrap	Abidjan
	<i>Ae. angustus</i>	6 (38)	Ovitrap	Abidjan
	<i>Ae. apicoargenteus</i>	14 (38)	Ovitrap	Abidjan
	<i>Ae. dendrophilus</i>	503 (34, 35)	Ovitrap	Ehania-V1, Blockhauss, Treichville
	<i>Ae. fraseri</i>	17 (34)	Ovitrap	Ehania-V1, Blockhauss, Treichville
	<i>Ae. furcifer</i>	322 (34–36)	HLC, Ovitrap	Korhogo, Ehania-V1, Blockhauss, Treichville
	<i>Ae. luteocephalus</i>	146 (34–37)	HLC, Ovitrap, WHO layer-traps	Bouake, Korhogo, Ehania-V1, Blockhauss, Treichville
	<i>Ae. metallicus</i>	68 (34)	Ovitrap	Ehania-V1, Blockhauss, Treichville
	<i>Ae. palpalis</i>	244 (35)	Ovitrap	Ehania-V1, Blockhauss, Treichville
	<i>Ae. unilineatus</i>	2 (37)	WHO layer-traps	Bouake

(Continued)

TABLE 1 Continued

Country	Mosquito species	Abundance	Collection methods	Sites
	<i>Ae. unnilioris</i>	1 (40)	Larva dipper	Abidjan
	<i>Ae. usambara</i>	32 (34)	Ovitrap	Ehania-V1, Blockhauss, Treichville
	<i>Ae. vitattus</i>	292 (34–36)	HLC, Ovitrap	Korhogo, Ehania-V1, Blockhauss, Treichville
	<i>Culex Antennatus</i>	108 (36)	HLC	Korhogo
	<i>Culex cinereus</i>	126 (36, 40)	Larva dipper, HLC	Korhogo, Abidjan
	<i>Culex fraseri</i>	20 (41)	Larval collection	Ehania-V1, Blockhauss, Treichville, Port of San-Pedro
	<i>Culex nebulosus</i>	221 (36, 38, 41)	HLC, Ovitrap	Korhogo, Port of San-Pedro, Abidjan
	<i>Culex Poicilipes</i>	263 (35)	Larval collection (WHO)	Ehania-V1, Blockhauss, Treichville
	<i>Culex quinquefasciatus</i>	7442 (35, 36, 40, 41)	Larva dipper, HLC	Korhogo, Abidjan, Ehania-V1, Blockhauss, Treichville, Port of San-Pedro
	<i>Culex rima</i>	12 (41)	Larval collection	Port of San-Pedro
	<i>Culex</i> sp.	1004 (39)	Larva dipper	Abidjan
	<i>Culex tigripes</i>	171 (35, 36)	HLC	Korhogo, Ehania-V1, Blockhauss, Treichville

Trap types used in the presented studies were: egg collection via Ovitrap; larval collection via Larva dipper or Larval collection; Adult female collection via BG sentinel trap, HLC (human landing catch) or double layer trap. The superscript number in the abundance column refers to the reference used to calculate the abundance numbers

increases with urbanization due to more breeding sites such as used tires, disposable containers, and water storage receptacles in urban areas (34). Similarly, *Ae. aegypti* was predominant in Benin, while in Gabon *Ae. albopictus*, identified for the first time in 2007 (17), was predominant, followed by a fairly significant presence of *Ae. aegypti*. However, the mosquito species *Ae. albopictus* has become the most dominant and widespread arbovirus vector in Gabon (18). This occurred at the same time as the emergence and epidemic of CHIKV in the country (19), indicating that, *Ae. albopictus* is an efficient vector for CHIKV in Gabon. Altogether, there is a high discrepancy in the distribution of *Aedes* species between Gabon, Côte d'Ivoire, and Benin, specifically concerning the presence and absence of *Ae. aegypti* and *Ae. albopictus*. Furthermore, an absence of *Ae. vitattus* and *Ae. luteocephalus* was observed in Gabon, even though these species of mosquito are present in West Africa (26–28, 34–37). This absence might be attributed to the extensive forested areas in Gabon, where over 88% of its total surface is covered by rainforests, making it one of the most forested countries globally. However, the highest prevalence of *Ae. vitattus* was observed in savannahs and barren land covers (42). Furthermore, collecting bias could cause the lack of *Ae. luteocephalus*, which most frequently bites in in the forest canopy as compared to the ground (were most trapping occurred) in arboreal environments. *Culex* (*Cx.*) *quinquefasciatus* appears to be the most abundant *Culex* species in all three countries (Table 1).

3.2 Distribution of arboviruses in the three African countries

3.2.1 Arboviruses detected in mosquitoes

The majority of previous studies were focussed on the detection of arboviruses in humans and very few works have analyzed the

presence of arboviruses in mosquitoes in Africa. For instance, only one study from Benin screened arboviruses in mosquitoes and reported dengue virus type 3 (DENV-3) for the first time in a pool of *Ae. aegypti* mosquitoes (29). This is also the case for the Ivory Coast, where only one study has been carried out on the infection of mosquitoes with arboviruses, reporting a case of DENV-2 in a pool of *Ae. aegypti* mosquitoes (43). In contrast, data from Gabon are much more numerous, for example, *Ae. albopictus* specimens positive for CHIKV, DENV and ZIKV were reported (18, 20, 22–24), while only CHIKV was also found in *Ae. aegypti* (18, 24). Besides mono-infection, a case of CHIKV-DENV coinfection was detected for *Ae. albopictus* (24) in the country.

3.2.2 Arboviruses in the human population

Considering the human cases of arbovirus disease, both prevalence and the active foci differ greatly in the three countries (Table 2): In Gabon, a variety of arboviruses such as CHIKV, DENV (DENV-1, DENV-2, and DENV-3), ZIKV, YFV and WNV were detected as active infection events (19, 24, 44, 49, 53). Especially from 2007–2010, a significant number of active cases of CHIKV and DENV-2 have been observed in Gabon (19, 24, 44, 49). Furthermore, serological data indicate a high number of past infections with ZIKV, WNV and RVFV in Gabon (4, 49). In Côte d'Ivoire active cases of DENV (DENV-1 and DENV-3), as well as YFV, were found, however, reported case numbers were lower than in Gabon (54, 56, 57, 63, 64, 67). In contrast, Benin only reported two active DENV cases (one DENV-1 and one DENV-3) and no CHIKV cases (56, 57). Serological evidence indicates low prevalence of DENV (DENV-1 and DENV-2) and circulation of CHIKV in Benin but no circulation of YFV (54, 67). Furthermore, some cases of exported infections were reported. For example, five cases of export of arboviruses DENV-1, DENV-2 and DENV-3 from Côte d'Ivoire to France, Japan and Senegal, respectively (60, 62–64, 68)

TABLE 2 Summary of arbovirus cases in human patients reported in Gabon, Benin, and Côte d'Ivoire from 1982 to 2021.

Country	Site	Arbovirus	Detection method	Number of cases
Gabon	LBV, FCV, Oyem, Minvoul, Ntoum, Kango, Mintzic, Kyé-ossi, LBN, KLT, Djole, Ndakaba, LTV	CHIKV	P, S	3110 (19, 24, 44–47), 122 (45, 48)
	LBN, LBV	DENV	P, S	1 (45), 87 (3, 45)
	LBN	DENV-1	P	22 (49, 50)
	LBV, Cocobeach, Oyem, Minvoul	DENV-2	P	448 (19, 49)
	LBN	DENV-3	P	35 (3, 49, 51)
	LBN, LBV	ZIKV	P, S	6 (23, 50), 156 (3)
	LBN, all regions	WNV	P, S	3 (3), 98 (3)
	LBN	RVFV	P, S	0 (3), 200 (3, 52)
		YFV	P	10 (53)
Benin	Cotonou	CHIKV	S	141 (54, 55)
	Ouesse	DENV	S	15 (27, 55)
	Not specified	DENV-1	P	1 (56)
		DENV-2	NA	NA
	Not specified	DENV-3	P	1 (57)
		ZIKV	NA	NA
		WNV	NA	NA
		RVFV	NA	NA
		YFV	NA	NA
Côte d'Ivoire		CHIKV	NA	NA
	Abidjan	DENV	P, S	1 (58), 5 (58, 59)
	Abidjan	DENV-1	P	2 (60, 61)
	Abidjan	DENV-2	P	2 (62)
	Abidjan	DENV-3	P	9 (59, 63–65)
		ZIKV	NA	NA
		WNV	NA	NA
		RVFV	NA	NA
	Ouassadouyou, Dézidouyou, Kouakoudouyou	YFV	P, S	27 (66), 65 (66)

Table 2 lists the number of human patients per collection area. LBN, Lambaréné; LBV, Libreville; LTV, Lastourville; KLT, Koulamoutou; FCV, Franceville. The detection method for arboviruses was either nucleic acid detection (P) or serology(S); cases are separated by comma according to the detection method. If no respective data on a virus were reported from a sampling area NA: No data available is given in the number of cases column. The superscript number in the abundance column refers to the reference used to calculate the case numbers.

and one DENV-3 infection in a Japanese traveller returning from Benin (57).

4 Discussion and conclusion

For this review, we choose three geographically representative countries in West and Central Africa: Benin, Gabon, and Côte d'Ivoire. Research institutions from these three countries have also recently formed a network for the study of arbovirus infection and

transmission (EcoVir). The literature examined within this review demonstrates that even though mosquito-borne arboviruses such as YFV, DENV, CHIKV, RVFV, and WNV affecting human health have long been reported, there is only limited information on the occurrence and impact of these diseases in these three countries. This may be due to misdiagnosis, poor awareness, or inadequate surveillance (68). This review aims to generate an overview of the occurrence of arboviruses in the three countries by summarizing publicly available information on active human cases, serological human screenings as well as on the vectors present. Since there are

only a few ongoing surveillance programs, the distribution of arboviruses in vectors is still largely unknown (54). Comparing the reporting frequencies of arbovirus infections in humans and reports of mosquito surveys in these countries a misbalance becomes apparent:

In Gabon, compared to the two other countries many reports on arbovirus cases including CHIKV, DENV, WNV, RVFV, YFV and ZIKV (3, 18–20, 23, 44, 48, 51, 53) have been published leading to a comprehensive picture of the current arbovirus situation in this country. Many mosquito surveillance studies have also been conducted showing a strongly established and widespread invasive mosquito species *Ae. albopictus* (18) which was first discovered in 2007 in this country (17, 69). It appears that this new invasive species displacing the native *Ae. aegypti*, which until recently was the dominant *Aedes* species and an important vector for arboviruses. The discovery of this species coincided with the description of several severe arbovirus outbreaks of CHIKV and DENV (19), which means that the altered vector population must probably have a strong influence on the transmission of arboviruses to humans.

In Benin, reports on arbovirus cases are sparse. Thus far, there are no reports on current outbreaks of arboviruses although the DENV seems to be endemic with two reported human cases (56, 57) and CHIKV seem to circulate as suggested by a couple of studies (54, 55). The low numbers of arbovirus cases in Benin might be due to under-diagnosed or under-reported cases, as DENV for example has similar symptoms to malaria (27). In contrast to Gabon, mosquito surveillance studies revealed the dominance of *Ae. aegypti* mosquitoes although *Ae. albopictus* is also present there (first described in 2021 (23)). In this country, only one study screened mosquitoes for arboviruses and thereby identified dengue virus in a pool of *Ae. aegypti* mosquitoes (29). No further data on mosquito arbovirus infection-studies could be found. Moreover, the few studies available from Benin on arboviruses and their vectors, focus on the southern part of the country such as Abomey, Porto Novo, and Cotonou (26–30, 33, 54, 56, 57, 70). This pronounced regional focus may partly explain the lack of nationwide arbovirus outbreak reports, as well as the absence of comprehensive data regarding arbovirus prevalence in northern or other regions of the country. The factors contributing to the lower incidence of arbovirus cases in Benin are likely multifaceted. They may encompass various ecological, environmental, and human-related elements, including climatic conditions, vector competence, immunity, mosquito control measures, and local public health interventions. Understanding these factors is crucial to maintaining the current low arbovirus prevalence and to guide future efforts in arbovirus surveillance and prevention in Benin.

Looking at the situation in Côte d'Ivoire, the most prevalent arboviral diseases are dengue and yellow fever with single or combined outbreaks since 2008 (37). Thus far, the published data showed that similar to the situation in Benin, *Ae. aegypti* dominate the catches and only a very low number of specimens of *Ae. albopictus* were reported (38). To investigate the spread of *Ae. albopictus* in Benin and Côte d'Ivoire, longitudinal monitoring is required (33).

Considering these three geographically very close countries and their drastically different arbovirus prevalence and human active cases, the question arises as to how these differences can be explained. On the one hand, the vector distribution of the main arbovirus vectors suggests a change in vector competence, but some differences, such as the CHIKV cases, cannot be conclusively explained by vector distribution, since both *Ae. aegypti* and *Ae. albopictus* can transmit it (20, 71, 72).

The detection of viral activity generally serves as a warning system to initiate appropriate measures to contain outbreaks (73). So far, this warning system in these countries (especially Benin and Côte d'Ivoire) is almost based exclusively on active cases and serological detection in humans. The detection of viruses in mosquito pools has so far been poorly developed in these countries. This leads to a delayed disease transmission risk warning. Furthermore, these methods are prone to errors: due to the need for a cold chain for sample transport, but also the cross-reactivity between related viruses in serological tests, as well as the need for special equipment and infrastructure, for example for molecular biological tests, and ultimately the overall costs (73–75).

Detecting arboviruses is not only challenging when using advanced tests (antibody determination or molecular biological methods). The clinic of arboviral human diseases is also difficult to differentiate from other diseases such as the frequently occurring malaria (28). Furthermore, such studies often only capture severe cases, as factors such as poor access to affordable health care, primary health education that is not always culturally sensitive and evidence-based, as well as the availability and use of medicines, are likely to result in mild to moderate cases being missed since such patients do not consult a doctor (76–79). The medical care and the population's attitude toward medicine appear to be very similar in the three countries at first glance. Therefore, the question arises as to whether additional socio-ecological differences or discrepancies in arbovirus detection may explain the phenomenon of differing arbovirus prevalence in the three countries.

New diagnostic tools, such as the use of NGS, have the potential to expand the genetic information obtained from samples which not only allows the detection of new arboviruses but also reveals information about the vector (in the case of a vector sample) (80, 81). Such tools will be indispensable in the future, as changes like international travel and trade, population increase, the importation of used tires, or the abundance of non-degradable disposable containers serving as breeding sites for vectors, the establishment of large agricultural scheme of crops like Hevea contribute to the spread of arboviruses. NGS enables the improved monitoring of both the genetic background of vector populations and viruses, which could potentially help explain the phenomenon of differing arbovirus prevalence in the three countries, including factors like vector competence, virus mutations, and more. To determine the effect of population flows on the circulation of arboviruses between countries and continents, it is important to carry out surveillance using molecular tools, to define the epidemiology of arboviruses of serious health concerns. Most investigations are carried out only during noticeable outbreaks due to inadequate diagnoses. Hence,

there is the need for surveillance for the prevention and control of mosquito-borne arboviruses (56).

In summary, there is an urgent need for research to better understand the current situation of arbovirus distribution and prevalence in these three countries and help predict future outbreaks. Potential explanations may include shifts in vector populations (displacement of native mosquito species by invasive species or the non-establishment of invasive species), socio-ecological differences, as well as variations in virus detection methods and procedures. Standardizing vector trapping methods, and technology transfer specifically the establishment of state-of-the-art methods to harmonize and simplify arbovirus detection, in these three countries could aid in making rapid advances.

Author contributions

GPM: Writing – original draft. E-MS-M: Writing – original draft. FH: Writing – original draft. JZBZ: Writing – review & editing. ASBT: Writing – review & editing. YNB: Writing – review & editing. J-DKD: Writing – review & editing. EHG: Writing – review & editing. GDM: Writing – review & editing. JPK: Writing – review & editing. JZ: Writing – review & editing. GCO-M: Writing – review & editing. TSB-S: Writing – review & editing. LSD: Writing – review & editing. AM: Writing – review & editing. OD: Writing – review & editing. JFM: Writing – review & editing. RM-G: Writing – review & editing. AAA: Writing – review & editing. SCB: Writing – review & editing. SB: Writing – original draft.

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