

1 **The African mosquito-borne diseasesome: Geographical patterns and range expansion**

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13

14 **Abstract** Mosquito-borne diseases (MBDs) such as malaria, dengue, and Rift Valley fever
15 threaten public health and food security globally. Despite their cohesive nature, they are
16 typically treated as distinct entities. Applying biological system analysis to the African MBDs
17 from a One Health perspective, we provide the first biogeographic description of the African
18 mosquito fauna corresponding with the pathogens they transmit. After compiling records
19 accumulated over a century, we find that there are 677 mosquito species in Africa, representing
20 16 genera, and 151 mosquito-borne pathogens (MBPs) circulating primarily among wild
21 tetrapods, dominated by viruses (95) and protozoans (47). We estimate that reported MBPs
22 represent ~1% of the actual number. Unlike mosquitoes, African arboviruses and mammalian
23 plasmodia represent a higher share of the World's total based on the area – species richness
24 relationship ($P < 0.0001$), explaining the disproportional large share of global MBPs that
25 originated from Africa. Species richness of African mosquitoes and MBPs are similarly
26 concentrated along the equator, peaking in central Africa, with a secondary “ridge” along
27 eastern Africa. Moderate diversity and low endemicity in mosquitoes across the Sahel reveals a
28 fauna with high propensity for long-range migration. Regional differences in species richness,
29 endemicity, and composition agreed with country-based results. The composition of mosquitoes
30 and MBPs separates sub-Saharan Africa from north Africa, in accordance with the Palearctic
31 and Afrotropical faunal realms, and west and central Africa are clustered together distinctly from
32 the cluster of eastern and southern Africa. With ~25% of the species occupying a single country,
33 ~50% in 1–3 countries and <5% found in >25 countries, the typical ranges of both mosquitoes
34 and MBPs are surprisingly small. The striking similarity in diversity and especially in range
35 distributions of mosquitoes and MBPs suggest that most MBPs are transmitted by one or few
36 narrow-range mosquito vectors. Exceptionally widespread mosquito species (e.g., *Ae. aegypti*,
37 *Cx. quinquefasciatus*, and 10 *Anopheles* species) feed preferentially on people and domestic
38 animals, and nearly half are windborne migrants. Likewise, exceptionally widespread MBPs are
39 transmitted between people or domestic animals and are vectored by one or more of the
40 aforementioned widespread mosquitoes. Our results suggest that few MBPs have undergone a
41 dramatic range expansion, after adapting to people or domestic animals as well as to

42 exceptionally-widespread mosquitoes. During the intermediate phase of range expansion,
43 MBPs extend their vector and vertebrate host ranges with a concomitant gradual increase in
44 geographical range. Because range size may serve as a marker of the phase of range
45 expansion, ranking the African MBPs according to range, we identified several MBPs that pose
46 elevated risk for disease emergence (e.g., Wesselsbron virus). Taken together, our database,
47 approach, and results can help improve MBD surveillance and lead to a better understanding of
48 disease emergence. This knowledge has the potential to improve capacity to prevent and
49 mitigate new and emerging MBD threats.

50 Introduction

51 Africa carries the heaviest global burden of mosquito borne diseases (MBDs), with more than
52 400,000 deaths attributable to malaria of the 700,000 caused by vector-borne diseases annually
53 (WHO, 2020). At least eight of the 11 topmost impactful global mosquito-borne pathogens
54 (MBPs) originated in Africa—namely Yellow Fever virus (YFV), West Nile virus (WNV),
55 Chikungunya virus (CHIKV), Rift Valley fever virus (RVFV), Zika virus (ZIKV) and three human
56 *Plasmodium* species (*falciparum*, *malariae*, *ovale*) (WHO, 2020). Excluding its islands, Africa
57 comprises only 20% of the earth's land surface, but is the origin of 73% (8 of 11) of these global
58 MBPs. Based on the species richness – area relationship (Lomolino, 2020), this excess is highly
59 significant ($P < 0.001$, exact binomial test), corroborating a recent literature review that has
60 reached a similar conclusion using different data (Swei *et al.*, 2020). The reasons for Africa's
61 disproportional role as the origin of so many global MBPs may include being the only continent
62 that extends from the northern to southern temperate zones, covering $>70^\circ$ of latitudes (37°N –
63 34°S), and straddling several biomes including the outstandingly diverse equatorial forest
64 (Burgess *et al.*, 2004; Guernier *et al.*, 2004; Lomolino, 2020). As the homeland of the hominids
65 and extant apes, we expected that Africa would contain most human MBPs (Wolfe *et al.*, 2007),
66 yet, five of the eight global MBDs are zoonotic (YF, WN, RVF, CHIK, and ZIK), leading to a new
67 hypothesis that Africa has more MBDs in total, not only those affecting humans. Africa is also
68 home to the largest number of megafauna species, and thus it poses a greater risk to many
69 phylogenetically related domestic animals. Understanding the MBDs of Africa, therefore, would
70 be valuable for global health and food security. As Africa undergoes dramatic perturbations due
71 to deforestation and global climate change (e.g., desertification), coupled with food and water
72 scarcity, the risk for the emergence/re-emergence of MBDs should be closely monitored.
73 Baseline knowledge is a prerequisite to successful mitigation of MBDs, however— as we have
74 found—this vital information is scarce and not readily accessible.

75 The study of MBDs has traditionally been fragmented into separate fields: virology, parasitology,
76 entomology, etc. Most studies have focused on one or a few related pathogens, and/or their
77 vectors in a limited region. Excepting a few reviews of certain MBDs (Weaver *et al.*, 2012;
78 Braack *et al.*, 2018), the ensemble of MBDs as a biological system composed of mosquitoes
79 and pathogens has never before been holistically studied to our knowledge. On the other hand,
80 the increasing frequency of disease emergence in humans has deservedly been the focus of
81 extensive study (Burke, 1998; Binder *et al.*, 1999; Taylor *et al.*, 2001; Woolhouse & Gowtage-
82 Sequeria, 2005; Jones *et al.*, 2008; Morse *et al.*, 2012; Rosenberg, 2015), yet their broad scope
83 may have precluded inferences into commonalities shared among certain groups of diseases.
84 Here, focusing on the MBDs in continental Africa from a One Health perspective, we include all
85 known pathogens transmitted by mosquitoes to terrestrial tetrapods, and compare
86 biogeographical features of this disease system after constructing a dedicated database, based
87 on a comprehensive literature search (Supp. Materials). We describe the composition and
88 geographical organization of the mosquito species and the MBPs in Africa to better understand
89 the process of MBD range expansion. Specifically, we evaluate the hypothesis that Africa has

90 exceptionally high mosquito and MBP diversities, and map the landscapes of their species
91 richness, endemism, and composition. The results lead to insights into the role of mosquito and
92 MBP dispersal, the nature of barriers to their spread, and the future of MBD surveillance in
93 Africa. Evaluating variation in range size of mosquito and MBP species and attributes of
94 extremely widespread species, we propose a process for range expansion of MBDs and
95 accordingly rank the African MBDs as to their present phase of range expansion as a marker of
96 risk for disease emergence.

97 Despite being studied for over a century, the main vector species of MBPs of vertebrates remain
98 largely unknown, including many sylvatic vectors (transmitting among wild animals) of the most
99 well-studied pathogens (Karabatsos, 1985; Service, 2001; Njabo *et al.*, 2009; Diallo *et al.*, 2012;
100 Perkins, 2014; Kyalo *et al.*, 2017; Villinger *et al.*, 2017; Nanfack Minkeu & Vernick, 2018;
101 Weaver *et al.*, 2020; Wilkerson *et al.*, 2021). This is also the case for many MBP species of
102 vertebrates (Karabatsos, 1985; Njabo *et al.*, 2009; Weaver *et al.*, 2012; Perkins, 2014, 2018).
103 Therefore, it is most likely that the role of many mosquito species as vectors of known and
104 unknown pathogens is yet to be discovered. Accordingly, we included all known African
105 mosquitoes as the basis for describing and understanding patterns that we expect would also
106 apply to as yet unrecognized mosquito vector species. In this exploratory analysis, we
107 summarize trends based on knowledge that has been accumulated over at least 120 years.
108 With the expected growth in this domain due to the renewed recognition of the value of disease
109 surveillance brought about by the ongoing COVID-19 pandemic, as well as the advance in
110 methodologies such as metagenomics, it would be valuable to revisit these trends every decade
111 and assess the changes in the patterns described herein.

112 RESULTS

113 As many of the records on mosquito and MBP distribution were collected before 1980, reliable
114 localization of a large portion of these records is only available at the country level (Karabatsos,
115 1985; Fontenille *et al.*, 1998; Foley *et al.*, 2007; Kyalo *et al.*, 2017; Braack *et al.*, 2018; CDC,
116 2019; Irish *et al.*, 2020; Wilkerson *et al.*, 2021). Because many African countries cover multiple
117 ecozones (Burgess *et al.*, 2004) and biogeographic regions as defined for various animal
118 classes (Linder *et al.*, 2012), and vary in size, our analysis addresses fuzzy eco-geographic
119 units.

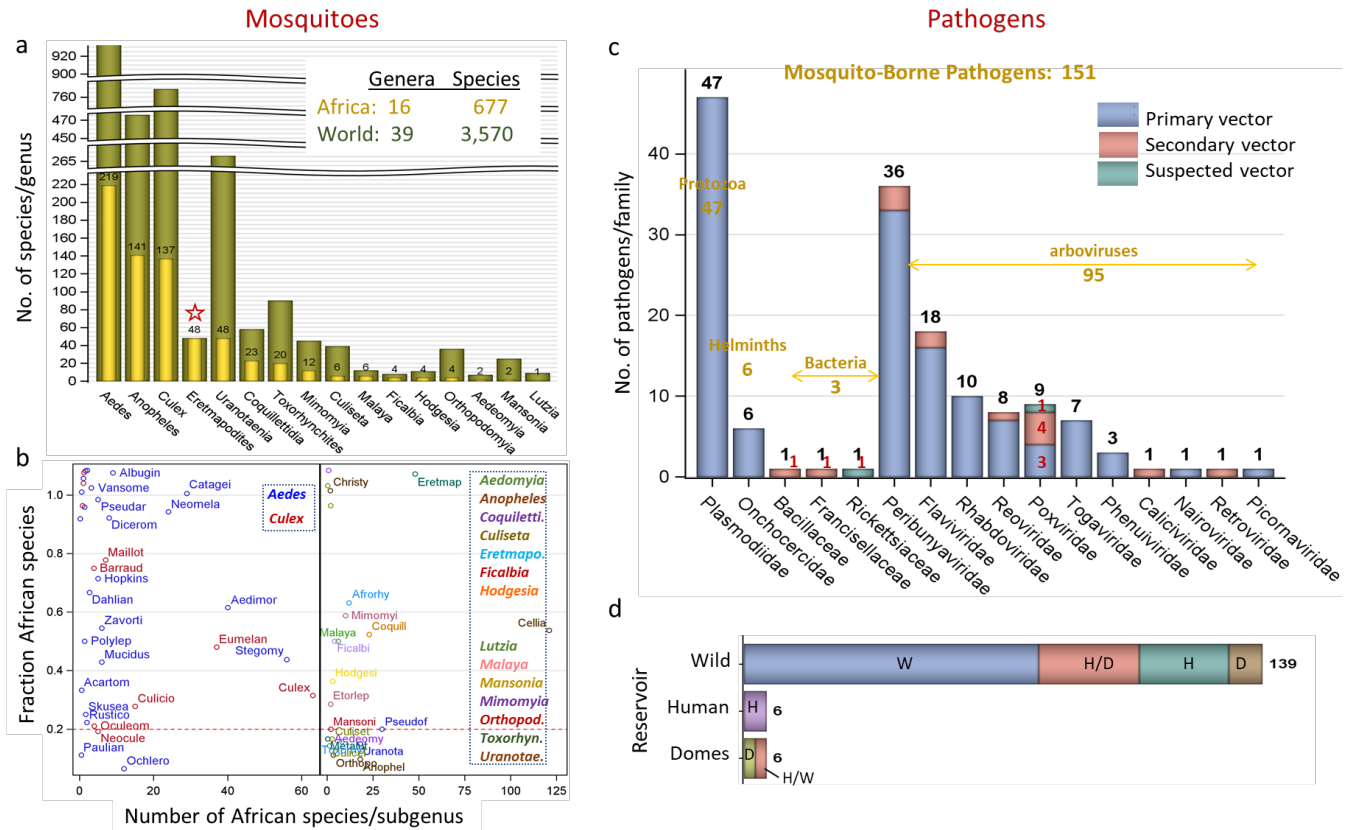
120 Composition of African mosquitoes and mosquito-borne pathogens

121 Continental Africa, which comprises 20% of the World's land surface, supports 19% of all known
122 global mosquito species ($N = 3,570$, see Methods) (Wilkerson *et al.*, 2021). The African
123 mosquito fauna is represented by 677 species spanning 16 genera and 53 subgenera, with
124 *Aedes* comprising the largest number of species, followed by *Anopheles* and *Culex* (Fig. 1a).
125 Goodness of fit tests of 20% across the 16 represented genera where $N > 15$ species/genus
126 revealed higher fractions of African species in *Aedes* (23%, $P < 0.01$, $X^2_1 = 6.9$), in *Anopheles*
127 (30%, $P < 0.0001$, $X^2_1 = 27.5$), and in *Coquillettidia* (40%, $P < 0.0002$, $X^2_1 = 14.0$), but was
128 insignificant in the other genera. The highest fraction of African species (100%) is found in the
129 genus *Eretmapodites* ($n = 48$), which is endemic to Africa (Fig. 1a). Fractions $> 20\%$ were found
130 in several genera, indicating local speciation on the continent. Among the 53 mosquito
131 subgenera in Africa, *Anopheles* subgenus *Cellia* is by far the most speciose ($n = 121$, Fig. 1b,
132 Table S1). Several subgenera have a high proportion of African species (Fig. 1b), although most
133 of these have a small number of species in total, e.g., *Anopheles* subgenus *Christya* ($n = 2$).
134 Nonetheless, the 29 *Aedes* species in the subgenus *Catageomyia* are exclusively African
135 species and 24 of the 28 species of the *Aedes* subgenus *Neomelanicion* are African (Fig. 1b,

136 Table S1). While not precluding that some of the species also occur outside Africa, a high
137 fraction of species found in Africa, especially in taxa with large number of species, highlights the
138 fauna's unique elements.

139 A total of 151 known mosquito-borne-pathogen species (MBPs) affecting vertebrates have been
140 reported from continental Africa (Fig. 1c). These include 95 viruses, 47 protozoans, six
141 helminths, and three bacteria, comprising a total of 16 families and 30 genera (Fig. 1c, including
142 3 unclassified genera). These 95 arboviruses represent a significantly higher share than
143 expected from the known global total based on the surface land area of Africa (32% vs. 20%,
144 $P < 0.0001$, $X^2_1 = 25.5$). The fraction of MB arboviruses is likely even higher because among the
145 total of 300 arboviruses that have been isolated from mosquito pools worldwide (Wilkerson *et*
146 *al.*, 2021), some are probably not vectored by mosquitoes. Likewise, of the 60 mammalian
147 plasmodia (Perkins 2014), 27 species (40%) are reported from Africa, which is a larger than
148 expected based on the continental/global land mass area ($P < 0.0001$, $X^2_1 = 23.4$). Plasmodia of
149 birds were not considered here because recent molecular analyses revealed many lineages that
150 likely represent yet-to-be named species (Bensch *et al.*, 2009; Njabo *et al.*, 2009; Perkins,
151 2014). Additionally, many trans-continental migrant birds may be exposed to plasmodia only in
152 Europe and Asia (Hellgren *et al.*, 2007) and thus should not be considered African — a problem
153 that may apply to other avian pathogens.

154 Fig. 1: Taxonomical composition of African mosquitoes and MBPs. a) Number of African species/genus (gold and
155 numerals) compared to the total number worldwide (green). Star denotes entirely African genus. Note: breaks in the
156 Y-axis. b) The fraction of African mosquito species per subgenus (Y-axis) of their worldwide total in relation to their
157 number in Africa (X-axis). To minimize label overlap, values near 1 were jittered. Subgenera labels (abbreviated to
158 the first 7 letters) are shown if they have two or more species. Where no subgenera are known, e.g., *Ficalbia* (Table
159 S1), genus names were used. Corresponding genera (bold italics font) of the same color are listed in dotted frame.
160 Red line marks expected 20% based on African share of land surface (text and Suppl. Table 1). c) Taxonomic
161 composition of African mosquito borne pathogens affecting vertebrates by family and importance of mosquito-borne
162 transmission (legend). Suspected mosquito transmission reflects compelling, yet non-definitive evidence (Supp. Mat).
163 The number of pathogens in each family is shown above bars (black) and the total by taxonomic group shown across
164 (gold). The number of pathogens transmitted mechanically are listed (red). d) Division of MBPs by group of
165 vertebrate host acting as reservoir (Y-axis) and by the host group impacted by the pathogen (subgroups in color).
166 Key: W, H, and D denote wild, human, and domestic animal (those raised by people, Domes), respectively and H/D
167 denotes that humans and domestic animals are impacted by MBPs whose reservoir are wild animals.

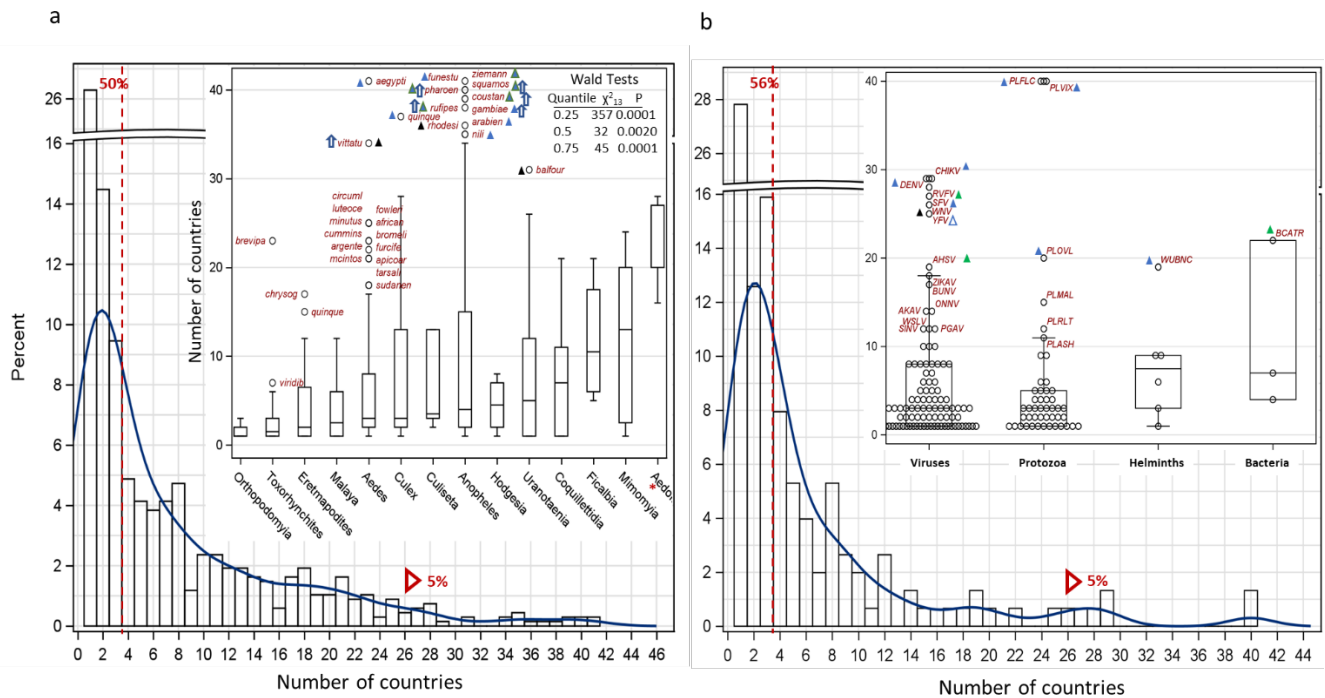


169 The vast majority of MBPs are maintained in wild hosts reservoirs (Fig. 1d), although a few can
 170 be transmitted for short periods between humans, e.g., YFV, O'nyong'nyong virus (ONNV) or
 171 domestic animals e.g., RVFV. Mosquito transmission is the primary route of vertebrate infection
 172 in the majority of the MBPs (Fig. 1c), whereas 16 pathogens rely on other arthropods or on
 173 direct transmission as their primary mode of transmission and use mosquitoes as a secondary
 174 route (Fig 1c). At least 8 of the 9 poxviruses are transmitted mechanically by mosquitoes as are
 175 the three bacteria (Turell & Knudson, 1987) (Fig.1c, Supp. File 2). Mechanical transmission
 176 appears to be linked to secondary transmission (Fig. 1c, Supp. File 2), although certain
 177 poxviruses can be transmitted several weeks post exposure (Kligler *et al.*, 1928; DaMassa,
 178 1966).

179 *Range size occupied by the African mosquitoes and MBPs*

180 Crude range approximations defined by the number of African countries occupied by mosquito
 181 species revealed that 26% of all African mosquito species are endemic (known only within a
 182 single country), and that over 50% are restricted to only 1–3 countries (median= 3.0, Fig. 2a).
 183 The L-shape distribution reveals that only 5% of the total number of species are widespread
 184 across over half the continent (i.e., occupying 26 or more countries, Fig. 2a). The Pearson
 185 correlation coefficient between the number of countries and total area (sum over countries
 186 areas) occupied by each species is 0.966 (N= 677, P<0.0001), indicating that the number of
 187 countries approximates range size reasonably well. The median area occupied by a mosquito
 188 species is $3.09 \times 10^6 \text{ km}^2$ (95% CI: $2.72\text{--}3.42 \text{ km}^2$). Range size varies among genera (P<0.05,
 189 quantile regression, Fig. 2a: inset).

190 Figure 2. Mosquito (a) and MBPs (b) geographic range based on the number of countries per species overall and by
 191 taxonomical groups (Insets). Note the break in the Y-axis. The fraction of species occupying 1–3 countries and over
 192 25 countries are shown to the left of the red broken line and red triangle, respectively. Insets: Number of countries per
 193 species across mosquito genera (a) and taxonomic group of MBPs (b). Genera represented by <3 species (*Lutzia*
 194 (*N*=1), *Mansonia* (*N*=2), and *Aedeomyia* (*N*=2)) were pooled (red asterisk). The box shows the 25th, 50th, and 75th
 195 quantiles of the distribution and the whiskers extends to the more extreme observations up to 1.5 x the interquartile
 196 range (75th – 25th quantiles). Outliers exceeding the whiskers are shown by abbreviated species name (a) and
 197 acronym (b) in red; triangles indicate preference to blood feeding on (a) and transmission between (b) humans (blue)
 198 domestic animals (green) and wild hosts (black). Empty triangle (b) indicate transmission to humans but no persistent
 199 transmission from humans. Table (a) summarizes results of the quantile regression (see text).



201 Species of *Lutzia*, *Mansonia*, *Aedeomyia*, *Mimomiya*, *Ficalbia*, and *Coquillettidia* have the
 202 largest ranges (Fig. 2a). However, the most widespread mosquito species that are found in 30
 203 or more countries (14 of 677 species, Fig. 2) include *An. gambiae*, *An. arabiensis*, *An. funestus*,
 204 *Ae. aegypti* and *Cx. quinquefasciatus*, as well as *An. pharoensis*, *An. squamosus*, *An. coustani*,
 205 *An. ziemanni* and *Ae. vitattus*. With ten of the 14 species, *Anopheles* predominates this group of
 206 exceptionally widespread species. Eleven of these 14 species thrive in domestic environments
 207 and blood-feed on people or domestic animals (Fig. 2a), whereas at least six engage in high
 208 altitudes wind-borne migration based on recent studies in Mali (Huestis *et al.*, 2019).

209 The distribution of African MBPs is remarkably similar to that of the mosquitoes (Fig. 2b), with
 210 28% being single country-endemic, 56% found in 1–3 countries (median= 3.0), and 5% found in
 211 26 or more countries (i.e., over approximately half the continent). The Pearson correlation
 212 coefficient between the number of countries and total area occupied by each MBP species is
 213 0.967 (*N* = 151, *P*<0.0001), corroborating the suitability of the number of countries as an index of
 214 total area. The median area occupied by a MBP is 2.15 x10⁶ km² (95% CI: 1.64-2.65 x10⁶ km²).
 215 The most widespread MBPs (40 countries) are *Pl. falciparum* and *Pl. vivax* (PLFLC, PLVIX) with
 216 only nine MBPs being reported in 20 or more countries (Fig. 2b). Except West Nile virus (WNV),
 217 which is primarily transmitted among birds (including migratory birds), all of these exceptionally
 218 widespread MBPs are transmitted among humans (6) or domestic animals (2), and without

219 exception, all are vectored by at least one of the most widespread mosquito species mentioned
220 above (Fig. 2a). For example, PLFLC, PLVIX, and *Pl. ovale* (PLOVL) are transmitted by all, or
221 some of the above *Anopheles* species, and DENV, CHIKV, and YFV are transmitted by *Ae.*
222 *aegypti* in urban and semi-urban settings (Jupp & McIntosh, 1990; Collins & Jeffery, 2005; Diallo
223 *et al.*, 2014; Faye *et al.*, 2014; Kyalo *et al.*, 2017; Braack *et al.*, 2018; Twohig *et al.*, 2019).
224 Similarly, WNV is transmitted by *Cx. quinquefasciatus* and YFV and ZIKV are transmitted by *Ae.*
225 *vittatus* (Faulde *et al.*, 2012; Epelboin *et al.*, 2017; Braack *et al.*, 2018; Diagne *et al.*, 2021).

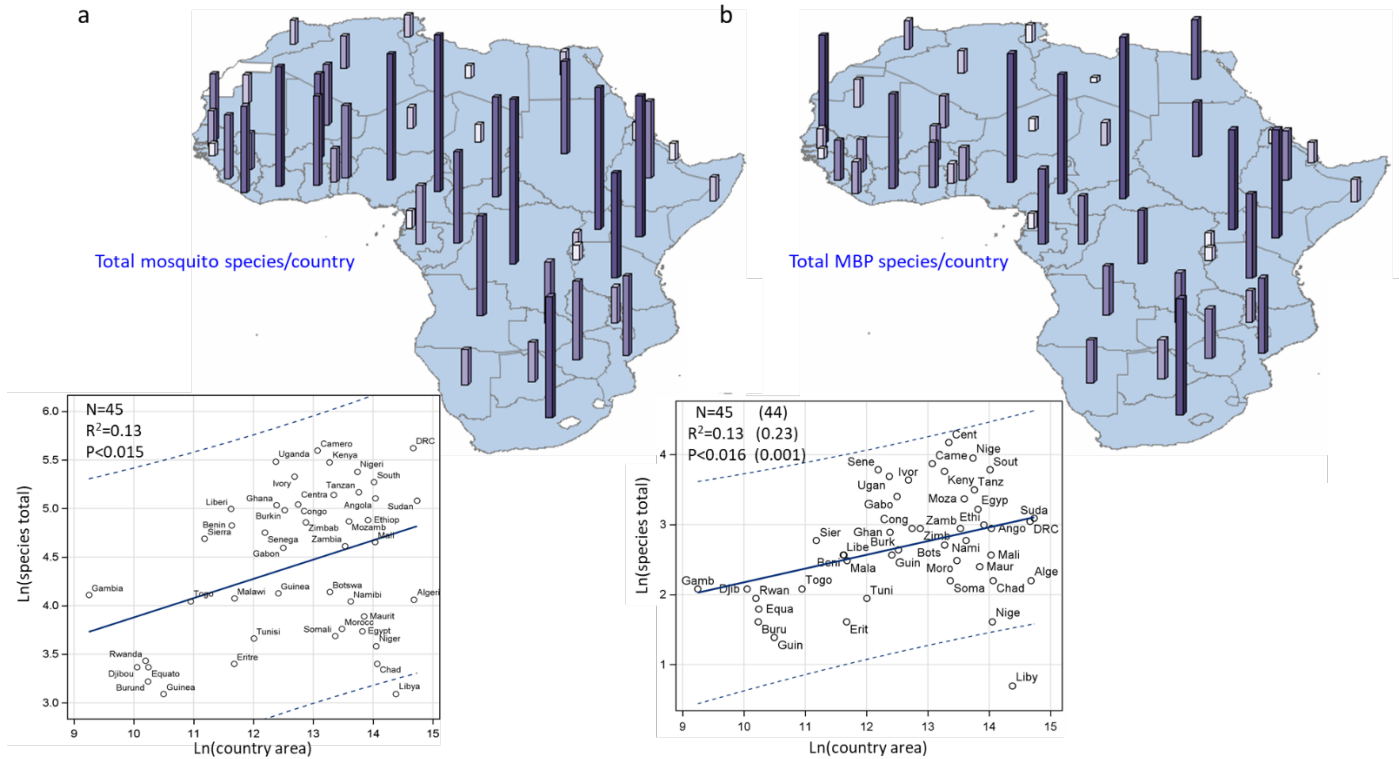
226 *Diversity and endemism across the continent:*

227 According to the area - species richness principle (Lomolino, 2020), mosquito species richness
228 has been found to increase with a country's area in a worldwide analysis (Foley *et al.*, 2007). In
229 Africa, this relationship accounted for only 13% of the variance compared to 42% worldwide,
230 highlighting the importance of other factors (Fig. 3a). The regions of highest species richness
231 include a belt along the equatorial forest, which appears widest in central Africa (Fig. 3a). The
232 countries with highest species richness include DRC, Cameroon, Uganda, Kenya, Nigeria, and
233 Ivory Coast. Adjusting for area minimally changes these countries' ranking (Fig. 3a). North Africa
234 represents a uniform belt of lowest mosquito diversity (Figs. 3a) with Libya being an extreme
235 outlier that exceeds the 95% CL, given its area (Fig. 3a). A corridor of modest diversity along
236 the Sahel (from Mauritania to Chad), and possibly another corridor between central and East
237 Africa includes countries from Namibia and Botswana to Rwanda, which remains stable after
238 accommodating country area (Fig. 3a).

239 Similar to mosquitoes, species richness of African MBPs is highest in Central Africa, followed by
240 an East African zone stretching from Kenya to South Africa (Fig. 3b). Except Senegal and the
241 Ivory Coast, West Africa exhibits lower diversity of MBPs than East Africa. Sahelian countries
242 and those between Central and East Africa exhibit lower MBP richness than the surrounding
243 regions, whereas North Africa exhibits the lowest MBP richness (Fig. 3b). Species richness
244 increased with country's size, but this relationship accounted for only 13% of the variance
245 among countries (excluding outliers: Libya, increased R^2 to 23%, Fig. 3b).

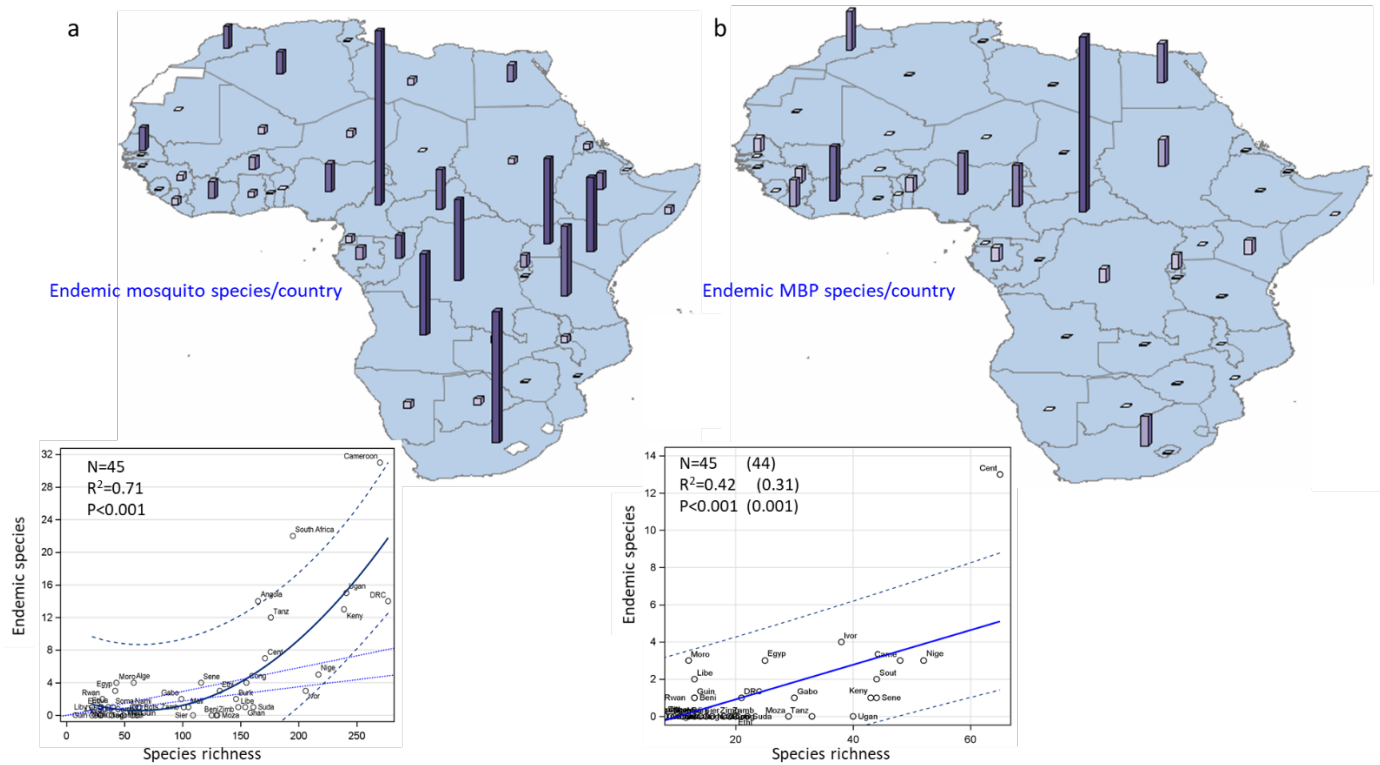
246 The distribution of country endemic mosquito species reveals greater heterogeneity than
247 species richness, with highest endemism in Equatorial Central Africa, especially Cameroon
248 (31), followed by South Africa and Angola (22, Fig. 4a). These three countries represent outliers
249 after accommodating species richness and, indirectly, country area (captured by species
250 richness, Fig. 3a). Unlike species richness, lowest mosquito endemism is found across the
251 Sahel from Mauritania to Somalia and, notably, extending to equatorial West Africa. Additionally,
252 the secondary "corridor" of low species richness separating South Africa from Central and East
253 Africa (Fig. 3a) appears wider for endemism. Countries without known endemic mosquito
254 species included Chad and Mozambique (Fig. 4a). The number of endemic species per country
255 is correlated with the total species richness ($r= 0.7$, $N= 45$, $P< 0.001$, Fig. 4a), but the
256 relationship was not monotonic, and visual inspection suggests a higher slope after species
257 richness exceeds ~100 species per country (Figs. 3a and 4a).

258 Figure 3. Maps showing mosquito (a) and MBP (b) country diversity (top) and the country's area – species richness
259 relationship (bottom). Bar height and color shows total endemic species per country (top). Linear regression (solid
260 line) shows the increase in expected number of species per country given its area with 95% confidence limit for
261 individual countries (broken lines). Values in parenthesis (b) show the change in the regression's summary statistics
262 after exclusion of outliers. Abbreviated country names are used. Note: Countries with insufficient information are
263 excluded (e.g., Eswatini), or pooled together (e.g., South and North Sudan) to reflect available information (Methods).



265 Country-endemic MBPs comprised 25 arboviruses, 11 plasmodia, and 1 nematode, reflecting
 266 similar proportion of endemicity across taxa: 27.5%, 25.6%, and 16.7%, respectively. Endemic
 267 MBPs showed an extreme hotspot in Central African Republic, moderate endemicism in Ivory
 268 coast, followed by Nigeria and Cameroon, Egypt, and Morocco (Fig. 4b). Endemic MBP species
 269 per country also increased with species richness and indirectly with species area, which was a
 270 determinant of the latter (Fig. 3b). After accounting for species richness, the Central African
 271 Republic remains an outlier endemic hotspot, towering over all other countries.

272 Figure 4. Maps showing endemic species of mosquito (a) and MBP (b) per country (top) and the relationship between
 273 species endemicity and richness (bottom). Bar height and color shows total endemic species per country (top).
 274 Quadratic (a, bottom) and linear regression (b, bottom) solid lines show the increase in expected mean number of
 275 endemic species given species richness with 95% confidence limits for individual countries (broken lines). Dotted
 276 lines show expected linear trends assuming monotonic increase predicted by the mean (higher) and median (lower)
 277 ratio of endemics to total species. Values in parenthesis (b) show the regression summary statistics after exclusion of
 278 outliers. Abbreviated country names are used.



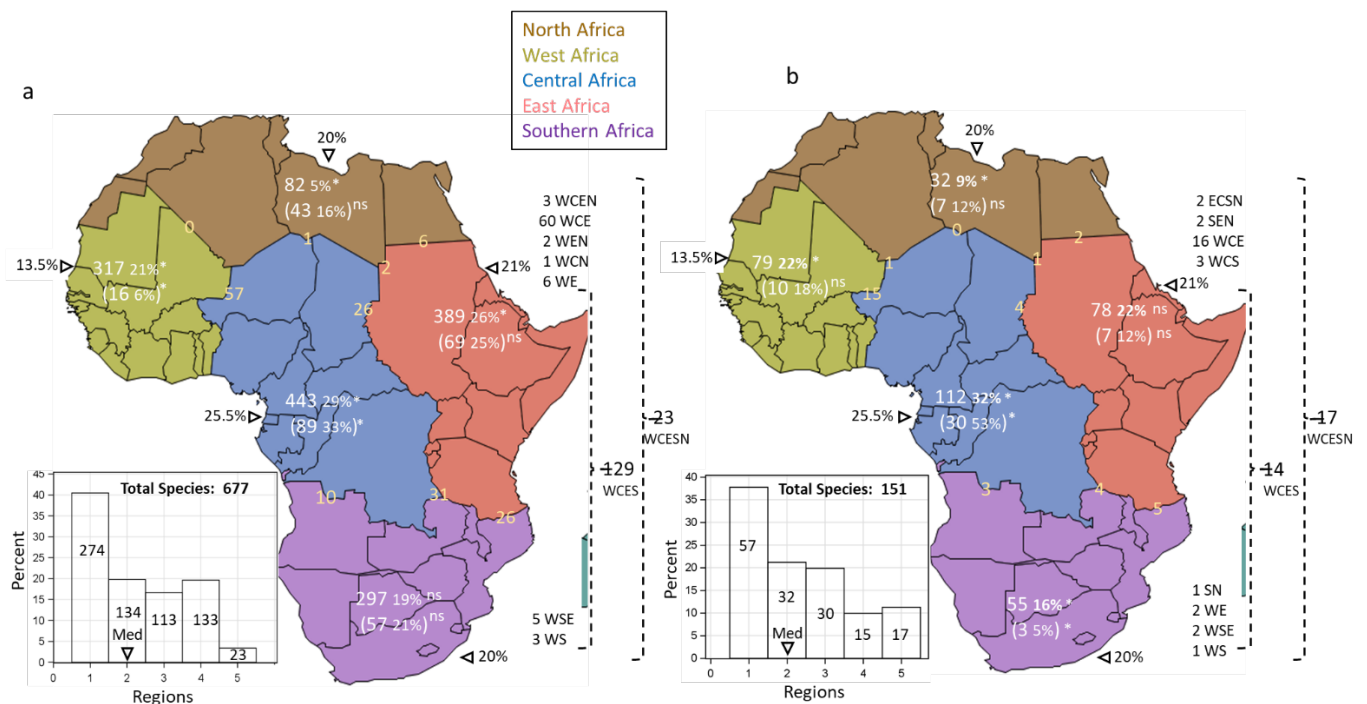
280 Heterogeneity in species composition across regional and country scales

281 Because countries differ considerably in surveillance effort, a regional analysis, whereby each
 282 region consists of multiple countries, exhibits less variability in surveillance effort and can be
 283 used to ascertain the patterns noted at the country level. Five regions were defined to group
 284 neighboring countries together and maximize distances among regions, accommodate
 285 latitudinal variation, and minimize inter-region enclaves (without regard to political regions,
 286 specific ecological, or species distributional data, Methods). Over 40% of the mosquito species
 287 are region-endemic and 60% of the mosquito species are found in 1-2 regions. Only 19% are
 288 found across sub-Saharan Africa and merely 3% are distributed across the five regions (Fig. 5a:
 289 histogram). Consistent with country results (Fig. 4a), the highest mosquito richness and
 290 endemicity are found in Central Africa and the lowest species richness is in North Africa.
 291 Notably, endemicity is lowest in West Africa (Fig. 5a). Significant excesses of species richness
 292 based on the region size were found in West and Central Africa, whereas a significant deficit
 293 was found in North Africa ($P<0.01$, $Z> 3.1$, Exact Binomial tests, Fig. 6a). Significant excess of
 294 endemic species was detected in Central Africa, whereas West Africa exhibits the lowest
 295 endemicity and largest deficit of endemic species based on its size, reflecting the large number
 296 of species it shares with Central Africa ($N= 57$), as well as with both East and Central Africa ($N=$
 297 60, Fig. 5a).

298 Similar to trends seen for mosquitoes, 38% of the MBP species are region-endemic, 60% are
 299 found in 1–2 regions, only 10% are found across sub-Saharan Africa, and an additional 11% are
 300 found across the continent (Fig. 5b: histogram). MBP richness is highest in Central Africa and
 301 lowest in North Africa, whereas West and East Africa have similar MBP richness which appear
 302 higher than that of Southern Africa (Fig. 5b). Considering the region's area, excess of MBPs
 303 was detected in Central Africa and West Africa, whereas a deficit was detected in North Africa
 304 (Fig. 5b, $P<0.01$, $|Z|> 2.6$, Binomial test). MBP endemicity is also highest in Central Africa, but

305 lowest in Southern Africa, showing corresponding sharp departures from expectations based on
 306 the region's area (Fig. 5b, $P < 0.01$, $|Z| > 2.5$, Binomial test). Similar numbers of region-endemic
 307 MBPs are found in West, North, and East Africa in accord with expectations based on area (Fig.
 308 5b, $P > 0.05$). West and Central Africa share more MBPs than other region pairs, whereas North
 309 Africa shares the fewest MBPs with all adjoining regions (Fig. 5b). Overlapping MBPs between
 310 three regions was especially high between West, Central, and East Africa ($N = 16$) compared to
 311 other combinations (1–4, Fig. 5).

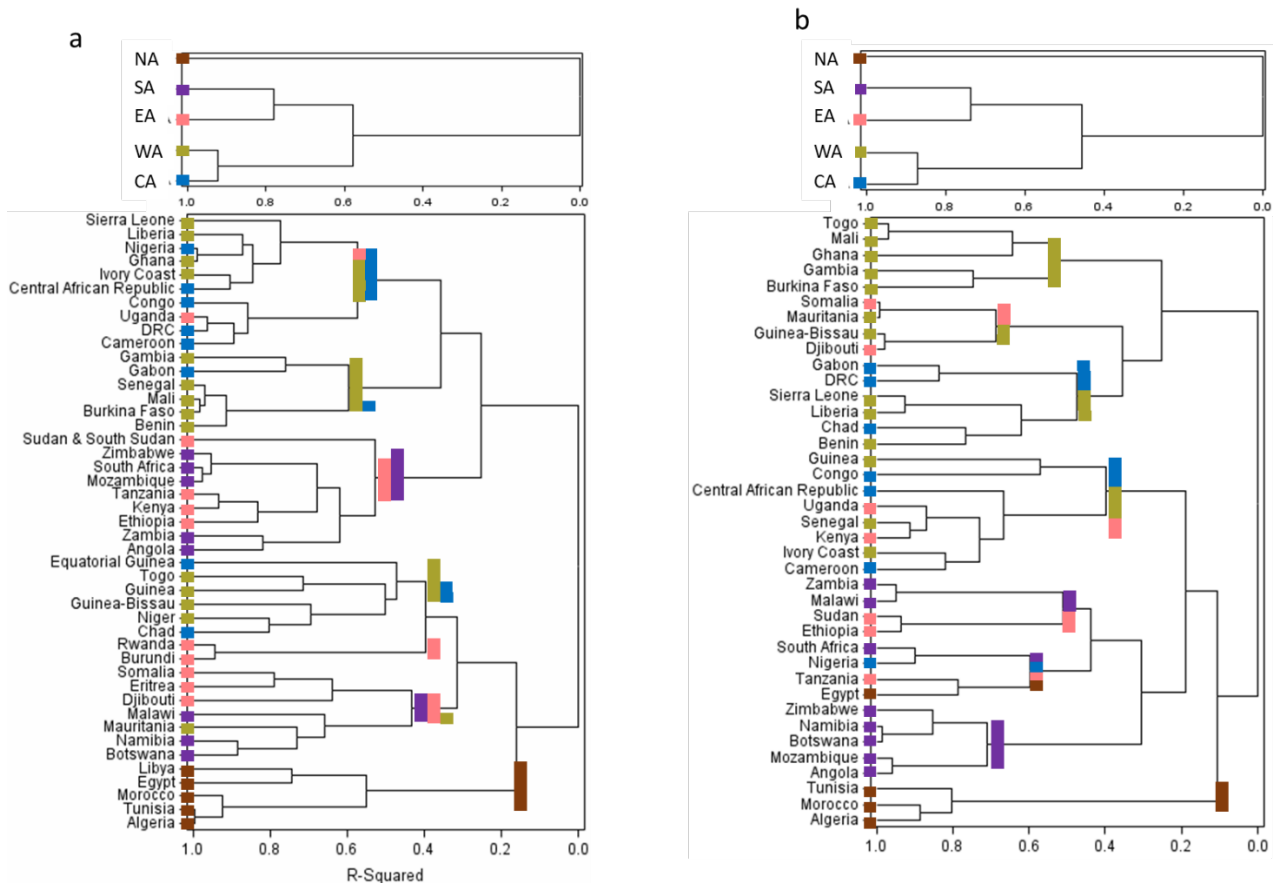
312 Figure 5. Composition of mosquitoes (a) and MBP species (b) across 5 regions in Africa (North, West, Central, East
 313 and Southern Africa). Regional species richness and (region-endemic) in absolute and percentage numbers (white
 314 font) against each region's relative landmass in percent (black font behind triangles). Statistically significant
 315 departures ($P < 0.05$) of the actual species richness or endemicity from expectations based on the region area is
 316 marked by '*', 'ns' denotes insignificant departure. The number of species between two and three adjacent regions
 317 are shown at the border between regions (yellow font). Number of species shared between disjointed regions are
 318 shown on the right (black) before the regions' acronym. Histogram showing the number of species occupying different
 319 number of regions (median = 2, marked by a black triangle, mean = 2.25).



321 The regional mosquito fauna is split into sub-Saharan and North Africa – the most distinct
 322 divisions in term of mosquito species composition, followed by further split of sub-Saharan
 323 Africa between the West - Central and the East - Southern fauna (Fig. 6a: top). A country-based
 324 dendrogram reveals a more complex picture (Fig. 6a: bottom). Most countries from West and
 325 Central Africa are grouped together, as are countries from East and Southern Africa (Fig. 6a).
 326 Nine of the twelve high similarity clusters ($R^2 > 0.9$) group countries from the same region, with
 327 only three exceptions (Nigeria–Ghana, Ivory Coast–Central African Republic, and DRC–
 328 Uganda, Fig. 6a), which share ecological similarity if not geographic continuity. The country
 329 dendrogram suggests substantive differences in mosquito faunas between Sahelian and
 330 equatorial West Africa countries, which is further supported by the grouping of Chad with Niger,
 331 as well as Nigeria with Liberia. Assemblages of mosquitoes defined by their significant co-
 332 occurrence in particular areas, independently from the regions defined above are illustrated in
 333 Fig. S1a (Supplementary Results and Discussion).

334 The composition of the MBPs at the regional scale follows almost exactly that of the
335 mosquitoes, showing a deep split into sub-Saharan and North African fauna, followed by a further
336 split of sub-Saharan Africa into the West-Central Africa and the East-Southern African fauna
337 (Fig. 6b, top). The MBP composition of West and Central Africa are most similar. The country-
338 based dendrogram based on MBP composition reveals more pervasive cross-regional and
339 cross sub-divisions clusters. For example, North African countries are clustered together, but
340 Egypt is clustered with Tanzania (Fig. 6b). Nonetheless, most countries are grouped by their
341 region or sub-division, i.e., West and Central African countries as well as East and Southern
342 African countries (Fig. 6b). Departures from regional clustering often follows ecological similarity
343 between countries in the equatorial forests, (e.g., Cameroon and Ivory Coast). Assemblages of
344 MBPs defined by their significant co-occurrence in particular areas, independently from the
345 regions defined above are illustrated in Fig. S1b (Supp. Results and Discussion).

346 Figure 6. Dendrograms showing clustering of regions (above) and countries (below) based on species composition
347 of mosquitoes (a) and MBPs (b). Region and country color follows color of the regions in Figure 5 (North Africa
348 (brown), West Africa (green), Central Africa (blue), East Africa (pink), Southern Africa (purple)).



350 DISCUSSION

351 Africa is undergoing explosive growth in human population density, deforestation,
352 desertification, and urbanization – processes that are projected to significantly impact disease
353 dynamics as they increase exposure of humans and domestic animals to diseases of wildlife
354 and generate conditions favoring rapid disease spread (Taylor *et al.*, 2001; Guernier *et al.*,
355 2004; Jones *et al.*, 2008; Fenollar & Mediannikov, 2018). Given Africa's high burden of MBDs

356 and the disproportionately high number of global MBDs that originated from the continent, a
357 better knowledge of the African mosquito borne diseasesome, as a biological system, is
358 essential to improve local and global health and food security. To our knowledge, this study
359 provides the first holistic description of the biodiversity of mosquitoes and MBPs in any
360 continent. Despite scarce/incomplete information and historical unbalanced sampling efforts of
361 these taxa across Africa and the globe (below), the data recovered herein summarizes more
362 than a century of bio-surveillance efforts and is worthy of compilation and exploration to guide
363 future surveillance efforts by recognizing key knowledge gaps. Our results identify regions
364 expected to contain more sylvatic vectors of known and yet-to-be discovered MBPs and
365 advance understanding of the factors that have shaped the diversity of the African MBDs. Here,
366 we examine the process of range expansion of these diseases, as a key element of disease
367 emergence and interpret our results by addressing the following key questions: (i) Does
368 exceptional biodiversity of mosquitoes and MBPs in Africa account for its disproportionately larger
369 share as the origin of global MBDs and how likely is this trend to continue? (ii) What is the
370 geographical organization of mosquitoes and MBPs in Africa and has the former structured the
371 latter? and, (iii) What are the roles of domestication, dispersal, and adaptation to new vectors
372 and hosts as drivers of MBD range expansion?

373 A caveat of our analysis is the low resolution of the country-based distributional data. As
374 explained above, a substantial part of the records on mosquito and MBP distribution is only
375 available at the country level. Because many African countries cover multiple ecozones
376 (Burgess *et al.*, 2004) and biogeographic regions (Linder *et al.*, 2012), our geographical analysis
377 is coarse, addressing fuzzy geographic-ecological units. Although well-defined geographic-
378 ecological units based on new high-resolution data will improve future biogeographical
379 investigation of the African mosquito-borne diseasesome, our analysis and interpretation of the
380 results accommodate these limitations.

381 **Global MBDs that originated from Africa: past and future**

382 The disproportional larger share of global MBDs originating from Africa (Swei *et al.*, 2020) along
383 with the zoonotic nature of most of these diseases (Introduction), led to our hypothesis that the
384 African mosquito and/or MBP faunas are especially diverse. Our results reveal that the share of
385 the African mosquito fauna (677 species) in the global culicid diversity closely agrees with
386 expectation based on the continental land area (19% vs. 20%). Moreover, it is dominated by
387 cosmopolitan genera, such as *Aedes*, *Culex*, and *Anopheles* (Fig. 1a), indicating no markedly
388 distinct fauna based on genera composition; yet, it has a distinct assemblage of subgenera (Fig.
389 1b). Unlike mosquito diversity, the biodiversity of African arboviruses and (mammalian)
390 plasmodia—the largest taxonomic groups of MBPs (Fig. 1c)—are considerably greater than
391 expected by land mass at 30% and 40%, respectively ($P < 0.0001$). These data support a
392 disproportionately higher diversity of MBPs in Africa than in any other continent. Avian plasmodia
393 could not be evaluated as explained above. The higher diversity of African MBPs (but not of
394 African mosquitoes) may account for the higher share of global MBDs originating in Africa and
395 in part for its disproportionately heavy burden of MBDs. While, we cannot rule out the possible
396 effect of greater sampling effort of MBPs in Africa compared with other continents. Yet, a recent
397 study reveals that sampling effort of emergent vector borne diseases has been lower in Africa
398 compared with other continents (Swei *et al.*, 2020). If the excess diversity of MBPs reported
399 here is correct, new global MBPs will continue to emerge from Africa at a higher rate than from
400 other continents, making Africa a prime target for future disease surveillance and control.

401 Unlike the mosquito fauna, which is mostly well described, the African MBPs remain poorly
402 known, given that 47% of the MBPs have been found in humans and domestic animals

403 whereas, at least 92% are maintained in wild species reservoirs (Fig. 1c). A conservative
404 estimate of the African MBPs of vertebrates can be derived assuming that humans represent a
405 typical host for vertebrate-specific MBPs of African origin. As the most thoroughly studied
406 vertebrate, humans are known as the only natural host for at least three and possibly five
407 African plasmodia (Liu *et al.*, 2010; Rutledge *et al.*, 2017; Arisue *et al.*, 2021; Daron *et al.*,
408 2021), and possibly one nematode (Laurence, 1989; Small *et al.*, 2019). This may be an
409 underestimate since humans are among the youngest vertebrate species. With over 5,000
410 vertebrate species in Africa (~1,400 mammals (Burgin *et al.*, 2018), 2,401 birds (Lepage, 2021)
411 and 1,648 reptiles (Tolley *et al.*, 2016) and ~600 amphibians (Channing & Rodel, 2019)), a
412 conservative estimate would be around 15,000 MBPs, suggesting that only ~1% of the total
413 African MBP diversity is currently known. Thus, pathogen and vector discovery, as well as
414 identifying their reservoir hosts would be highly productive endeavor, especially if targeting
415 lesser-known vertebrates and mosquitoes. The global emergence of “benign” zoonotic
416 pathogens such as ZIKV, CHIKV, and WNV illustrate the need for comprehensive knowledge of
417 the MBPs, including those transmitted among wild animals by unknown vectors. Targeting
418 mosquito subgenera with a high fraction of African species that presumably had longer time to
419 be co-opted as vectors by African pathogens, such as species of *Eretmapodites*, *Catageomyia*
420 (*Aedes*), *Neomelaniconion* (*Aedes*), *Albuginosus* (*Aedes*), *Hopkinsius* (*Aedes*), *Maillotia*
421 (*Culex*), and *Barraudius* (*Culex*) might yield many new MBPs. The network of mosquitoes and
422 MBPs defined by their significant co-occurrence in the same countries (Fig. S2) identifies
423 putative sylvatic vectors (Supp. Results and Discussion).

424 The area occupied by African mosquitoes and MBPs: drivers and implications

425 With a quarter of the species occupying a single country, ~50% in 1–3 countries, and only 5% or
426 less present in >25 countries (Fig. 2), most mosquitoes and MBPs occupy relatively small
427 ranges. Endemicity in African mosquitoes is lower than that reported globally (50%) (Foley *et al.*,
428 2007), probably because African islands were excluded from our analysis. Based on the
429 median total area occupied by a mosquito and a species of MBP (see Results), their typical
430 ranges cover 10% and 7% of continental Africa, respectively. These range sizes can be
431 approximated by squares with sides of 1,760 km and 1,500 km, respectively. The distributions
432 of range size in African mosquitoes and MBPs are strikingly similar, although the mosquito
433 median is larger than that of the MBPs (see Results), suggesting that most African MBPs are
434 transmitted by one or just a few narrow-range mosquitoes in sylvatic cycles among their wild
435 host species. MBPs with one or few mosquito vectors are probably specialized to these vector
436 species and vertebrate hosts, whose ranges ultimately limit pathogen spread. Therefore,
437 adapting to multiple vector species is likely a prerequisite for initiating range expansion in MBPs
438 (see more below) and given the small number of domesticated mosquitoes (Fig. 2a).
439 Considering that the majority of the MBPs circulate in wild vertebrates (Fig. 1c) in a relatively
440 small area, this state might have represented the original phase of today’s most widespread
441 MBPs (Fig. 2b), which have since undergone range expansion. This may also apply to MBPs
442 that will emerge in the future (below).

443
444 Surprisingly, most species of *Aedes*, *Anopheles*, and *Culex* occupy a typically small area (1–3
445 countries), whereas the widespread outlier species (>30 countries) include *Ae. aegypti*, *Ae.*
446 *vitattus*, *Cx. quinquefasciatus*, and ten *Anopheles* species, e.g., the primary malaria vectors *An.*
447 *gambiae*, *An. arabiensis*, and *An. funestus*, as well as the more zoophilic *An. pharoensis*, *An.*
448 *squamosus*, *An. coustani*, *An. ziemanni*. (Fig. 2a). These species feed preferentially on people
449 and/or domestic animals and are well adapted to the domestic environment. Notably, at least six
450 of these thirteen species were intercepted at high altitudes (40–290 m above ground) in the
451 Sahel of Mali (Huestis *et al.*, 2019), indicating that windborne long-range migration is a common
452 trait of these exceptionally widespread species, as for other insects (Pedgley *et al.*, 1995;

453 Reynolds *et al.*, 2006; Chapman *et al.*, 2012; Drake & Reynolds, 2012). The high proportion of
454 widespread *Anopheles* species suggests faster adaptation to domestic environment and/or
455 increased dispersal capacity. These traits may mutually reinforce each other because the
456 widespread presence of domestic settings minimize the risk of ending long-range migration in
457 an inhospitable habitat.

458 Similarly, the exceptionally widespread MBPs whose range exceed 20 countries include only
459 nine species (Fig. 2). Except for WNV, which is transmitted between wild birds, six are
460 transmitted between people: PLFLC and PLVIX (>30 countries), PLOVL, DENV, YFV, and
461 CHIKV, whereas RVFV and anthrax are transmitted between domestic animals. All these MBPs
462 are vectored by one or more of the most widespread mosquitoes: the human plasmodia are
463 primarily vectored by *An. gambiae*, *An. arabiensis*, *An. funestus*, (as well as by *An. coluzzii* that
464 occupies West and parts of Central Africa) and secondarily by *An. pharoensis*, *An. squamosus*,
465 *An. coustani*, and *An. ziemanni*. Likewise, DENV, YFV, and CHIKV are vectored primarily
466 among people by *Ae. aegypti*, whereas RVFV is transmitted among domestic animals by
467 several species including *Ae. vitattus*, *Cx. quinquefasciatus*, *An. pharoensis*, *An. squamosus*,
468 and *An. coustani* (Linthicum *et al.*, 1985; Seufi & Galal, 2010; Tantely *et al.*, 2015; Braack *et al.*,
469 2018). WNV is also transmitted by multiple mosquito vectors, including *Cx. quinquefasciatus*
470 and *An. rufipes* (Braack *et al.*, 2018; Ndiaye *et al.*, 2018). Finally, anthrax which is only
471 secondarily transmitted by mosquitoes (mechanically) is transmitted among domestic and wild
472 animals primarily via ingestion and inhalation of the bacteria from soil or plants, and can be
473 transported hundreds of kilometers by domestic or wild host animals, e.g., vultures, elephants
474 (Purdon *et al.*, 2018; Phipps *et al.*, 2019). The role of mosquitoes and other flies (Turell &
475 Knudson, 1987) in transporting anthrax should not be disregarded. Indeed, an outbreak of the
476 mechanically transmitted myxomatosis (caused by Myxoma virus) was attributed to windborne
477 mosquitoes flying from Australia to Woody Island, a distance of 320 km (Garrett-Jones, 1950).
478 This observation adds to others in support of pathogens transmitted by windborne mosquitoes
479 over long distances (Garrett-Jones, 1962; Sellers, 1980; Kay & Farrow, 2000; Reynolds *et al.*,
480 2006; Huestis *et al.*, 2019; Sanogo *et al.*, 2021). These results suggest that the key features of
481 the few exceptionally widespread MBPs include transmission among people or domestic
482 animals, as well as adaptation to at least one of the exceptionally widespread mosquito vectors,
483 and often to other mosquito vectors that may be important to maintain the virus in sylvatic
484 cycles.

485 These results assume that the distributions of the mosquitoes and (the known) MBPs is sound.
486 More comprehensive surveillance is expected to add distribution records and shift some of our
487 species to the right side of the L-shaped distributions (Fig. 2). The fraction of country endemics
488 will probably decrease, but the L-shaped distribution may remain, because many newly
489 described MBPs of wild vertebrates with modest ranges will be added. Considering that only
490 part of a country is actually included in most species' ranges, accurate location data may
491 identify these parts, thus the net change in the typical range may be modest.

492 *Diversity, endemism and composition of mosquitoes and MBPs across the continent*

493 Consistent with ample evidence on the decrease of species richness with latitude, including
494 studies of worldwide mosquitoes and general parasites and pathogens (Guernier *et al.*, 2004;
495 Foley *et al.*, 2007; Wilkerson *et al.*, 2021), African mosquito and MBP diversities measured by
496 species richness are similarly concentrated along the equatorial forest peaking in Central Africa.
497 A secondary high "ridge" of high diversity stretches along the eastern coast from Kenya to South
498 Africa, whereas the lowest diversities are found across North Africa (Fig. 3). Mosquito and MBP
499 exhibit corridors of moderate species-richness along the Sahel (Mauritania to Chad), and

500 between Central Africa and both East and Southern Africa (Fig. 3). These corridors' continuity
501 and association to areas of seasonal aridity - inhospitable to mosquitoes, attest that they
502 represent natural features (below). Unlike species richness, mosquito endemism reveals two or
503 three hotspots, whereas surrounding countries possessed few or no endemic species (Fig. 4).
504 Endemic mosquito species are concentrated in the Cameroon and South Africa, followed by
505 Uganda, Kenya, Tanzania, Angola and the DRC. The African equatorial forest, which is known
506 for its high biodiversity combines stable conditions with diverse habitats, large area, and
507 mountains (>1,000 m above sea level) that promote speciation and accumulation of species
508 adapted to cooler habitats that found refuge in higher elevation (Lomolino 2020). Thus, higher
509 rates of speciation, lower rates of extinction, and high ecosystem diversity can explain the high
510 richness and endemism of mosquitoes, MBPs (Figs. 3 and 4), and vertebrate species (Burgess
511 et al. 2004). Somewhat different constellations of these factors extend the East and Southern
512 Africa around the Rift System, which can also explain its high biodiversity (Burgess et al. 2004).

513 Unlike the higher richness and higher endemism region of Central Africa, the markedly low ratio
514 of endemism to richness across Sahelian countries (Figs. 3 and 4) suggest a fauna with high
515 propensity for long-range migration, which allow these mosquitoes to benefit from the
516 ephemeral habitats that provide ideal conditions during the short Sahelian wet season
517 (Reynolds & Riley, 1988; Pedgley *et al.*, 1995; Drake & Reynolds, 2012; Huestis *et al.*, 2019;
518 Florio *et al.*, 2020). Indeed >40 species of mosquitoes were intercepted at high altitudes (40–
519 290 m above ground) in the Sahel of Mali alone, representing ~50% of the documented
520 mosquito fauna (Huestis et al. 2019, and Yaro et al. unpublished), as predicted around seasonal
521 ecosystems (Southwood, 1962; Drake & Gatehouse, 1995; Florio *et al.*, 2020). Conversely, the
522 high endemism/richness ratio in equatorial regions (Figs. 3 and 4) suggests a lower propensity
523 for long range migration.

524 The landscape of endemism of MBPs shows a focal hotspot in Central African Republic,
525 towering over all countries (Fig. 4). This exceptional endemism is difficult to reconcile solely by
526 the effect of species richness and country's area (a determinant of the latter, Fig. 4) or the high
527 biodiversity of the equatorial forest. In part, it might be explained by biased sampling; for
528 example, research centers on yellow fever were established over 90 years ago in Nigeria and
529 Uganda, leading to the discovery of new viruses e.g., WNV, ZIKV, and Semliki Forest virus
530 (SFV). Within two decades, additional virus research centers were established in South Africa,
531 Egypt, Ivory Coast, Senegal, Central African Republic, Kenya, Tanzania, DRC, and Sudan
532 (Rosenberg *et al.*, 2013; Vasilakis *et al.*, 2019). More arbovirus surveillance was carried out
533 around these centers, leading to differences in virus diversity among countries. Regional
534 differences in diversity cannot be reconciled with these centers because the centers were
535 distributed across all regions. Between-region variation in surveillance effort is much smaller
536 than that between countries, therefore, regional analysis is used to test the main country-based
537 results. For example, the higher fraction of region vs. country endemism (40% vs. 25%) of the
538 mosquito and MBP species, finding 60% of the mosquitoes and MBPs in one or two regions,
539 and only 3% (mosquitoes) and 11% (MBPs) across the continent (Fig. 5) are consistent with
540 country-based results. Additionally, despite sharing ecozones and biomes across our regions
541 (Burgess *et al.*, 2004), the regional analysis revealed compositional heterogeneity in mosquitoes
542 and MBPs across the continent (Figs. 5, 6). The country dendrograms based on composition of
543 mosquitoes and MBPs generally clustered together countries of the same subdivisions (Fig. 6).
544 Remarkably, the clustering of regions into subdivisions based on the composition of the
545 mosquito and MBP faunas were nearly identical (Fig. 6). Similar to plant and vertebrate
546 biogeographical results (Burgess *et al.*, 2004) our sub-Saharan Africa and North Africa divisions
547 (Fig. 6) match the Palearctic and the Afrotropical faunal realms and highlight the Sahara as a
548 geographic barrier. Clustering West and Central Africa regions together, separately from the

549 cluster of East and Southern Africa (Fig. 6) fits also with the vertebrate biogeographical
550 landscapes including those of mammals and birds (Burgess *et al.*, 2004). Our West and Central
551 regions share the Sudanian, Sahelian and Equatorial (Guinean-Congolian) zoogeographical
552 zones whereas our East and Southern Africa regions overlap with the Zambebian and South
553 African zoogeographical zones (Linder *et al.*, 2012). The high mountains along the Rift System
554 probably contribute to the separation between the East and Central regions. The clustering of
555 countries based on mosquito composition indicated a subdivision of our West and Central
556 African regions into Sudano-Sahelian and Equatorial subregion as indicated by grouping of
557 Chad with Niger and Ivory Coast with Central African Republic (Fig. 6) showing correspondence
558 between our results and the zoogeographical zones identified by Linder *et al.* (2012). Altogether
559 these corresponding patterns add support for a strong bio-geographical signal in our results.

560 As for the distribution of range area (above), the regional composition of the MBPs was nearly
561 identical to that of the mosquitoes, raising the question “Has MBPs geographical organization
562 been shaped primarily by their mosquito vectors or by their vertebrate hosts?” Although both
563 hosts and vectors limit the MBPs range, there is some evidence supporting a greater role for the
564 mosquito vectors. Both mammals and birds exhibit large areas of high species richness and
565 endemism in East Africa and in smaller areas in Central, West, and Southern Africa (Burgess *et al.*
566 *et al.*, 2004), unlike African mosquitoes and MBPs. Likewise, the Sudano-Sahelian area from
567 Senegal to Sudan exhibits the second highest level of African mammals endemism (Burgess *et al.*
568 *et al.*, 2004). In birds, aside from a hyper-endemic area in East Africa, the remainder of the
569 continent is nearly devoid of endemics (Burgess *et al.*, 2004) as expected from the most mobile
570 terrestrial vertebrate class. Although salient biodiversity features of MBPs are more similar to
571 mosquitoes than to mammals and birds, resolving this question requires data on species
572 richness and endemism using the same unit area, which is beyond our analysis and data.

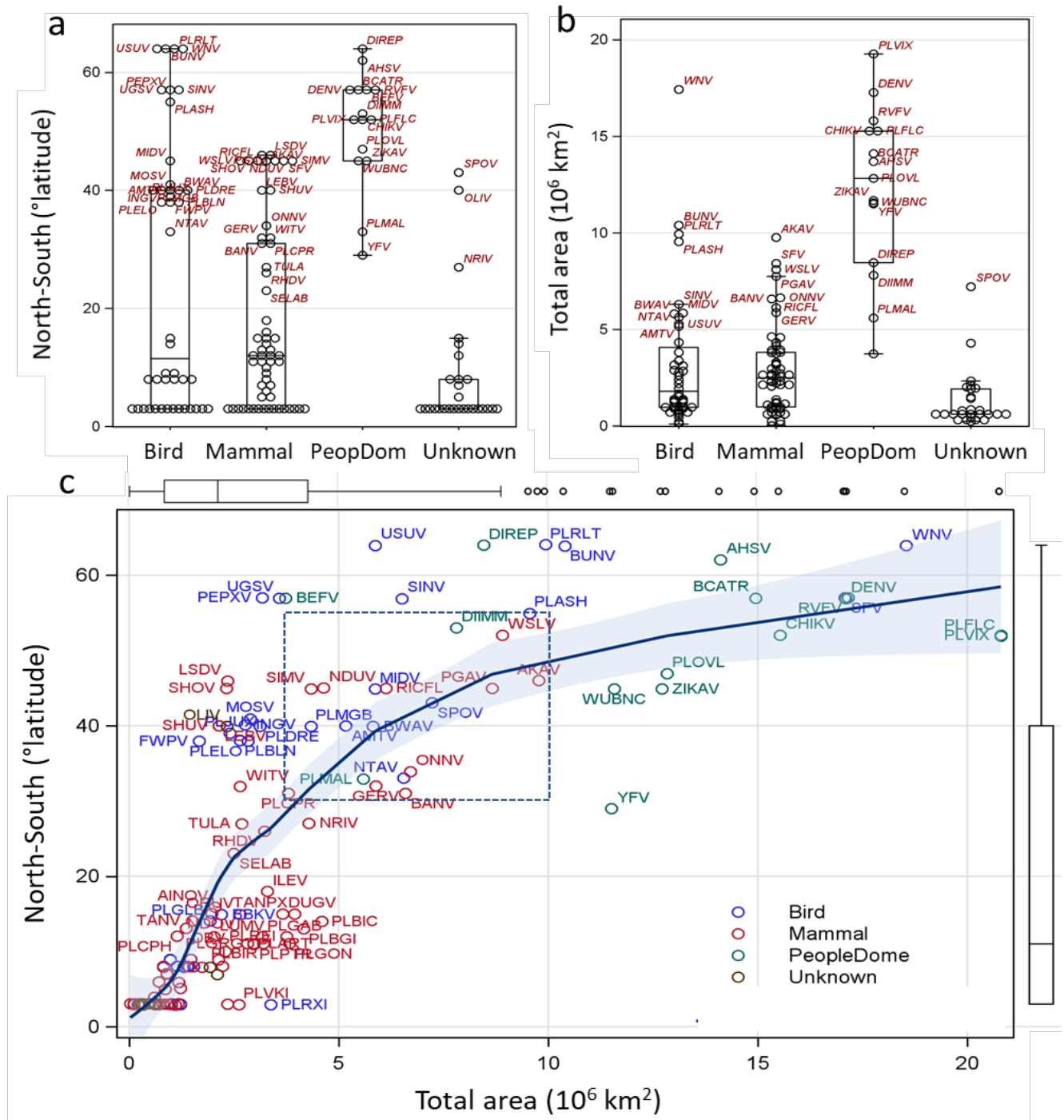
573 **A model of MBD range expansion and predicting emerging MBDs of the future**

574 The high similarity in geographic organization of African MBPs and mosquitoes (Figs. 2–6 and
575 S1a), and the facts that most MBPs circulate in wild vertebrate hosts (Fig. 1d) within a narrow
576 distributional range – remarkably similar to that of mosquitoes (Fig. 2) – suggest that typically,
577 MBPs are vectored by one or few mosquito species. Unlike this ‘original state’ of African MBPs,
578 human malarias, YFV, WNV, RVFV, ZIKAV and CHIKV represent a small subset of
579 exceptionally widespread African MBDs, many of which have expanded across the continent
580 and beyond. Following Wolfe and colleagues (Wolfe *et al.*, 2007), the biogeographical
581 differences observed between the ‘original’ and the ‘emergent states’ points to a plausible
582 process leading to range expansion of MBDs. The last phase of this range expansion includes
583 continuous transmission (i) between people or domestic animals, (ii) by vectors that feed
584 preferentially on these hosts and are themselves exceptionally widespread, e.g., human malaria
585 (*An. gambiae*, *An. arabiensis*, *An. funestus* among others) and chikungunya (*Ae. aegypti*). The
586 preceding phase would include a capacity to circulate in humans or domestic animals for a
587 single season or a few years, depending whether vector populations are perennial or seasonal
588 (Sellers, 1980; Linthicum *et al.*, 1999; Diallo *et al.*, 2005; Hanafi *et al.*, 2010). How rapidly does
589 the ‘original state’ develop into the widespread ‘emergent phases’? Unlike pathogens that are
590 directly transmitted among hosts, the dependence of MBPs on both wild vertebrate and
591 mosquito vector species (that blood-feed preferentially on reservoir species), range expansion
592 requires sequential adaptations to achieve transmissibility by new vectors that expand the
593 breadth of the MBP host species. Host and vector switching typically face fitness tradeoffs
594 linked to specialization on particular host and vector species (Hellgren *et al.*, 2007; Joy *et al.*,
595 2008; Vasilakis *et al.*, 2009; Molina-Cruz *et al.*, 2013b, 2013a, 2015, 2020; Ricklefs *et al.*, 2017).
596 Thus, we expect that a typical range expansion of MBP requires a longer intermediate phase
597 than a directly transmitted pathogen. Evidence in support of such a slow process is found in the

598 rare occasions in which avian plasmodia (and other haemosporidia) found in migrant birds could
599 be established in resident birds in both the Northern and Southern Hemispheres (Hellgren *et al.*,
600 2007; Ricklefs *et al.*, 2017). During the intermediate phase, the number of vectors and host
601 species slowly increase, facilitating a gradual increase in the geographical range of the MBP.
602 Once the MBP attains transmissibility into and from human or domestic animals by at least one
603 of the domesticated vectors, the transition into the last phase is complete and a rapid final range
604 expansion is expected worldwide.

605
606 Accordingly, a larger than typical geographical range is a marker of a MBP in the intermediate
607 phase (above), in which the MBP has expanded its vector and/or vertebrate range. Except for
608 small coastal ecozones, the African biogeographical units are typically wider across their east-
609 west axis than across their north-south axis (Burgess 2004), suggesting that the longer the
610 north-south dimension of a MBP's range, the more likely it is to be transmitted by multiple vector
611 species across multiple host species. Hence, we propose that MBP total range size, estimated
612 as the sum of the area (of the countries) in their range and maximal north-south length of their
613 range be used to gauge its range expansion phase. Whereas these range size measures are
614 expected to be largest in MBPs circulating among humans and domestic animals and smallest
615 for those circulating in wild mammals, it is less clear if MBPs circulating in wild birds are larger
616 than those of wild mammals. Both measures were larger for MBPs circulating in humans and
617 domestic animals for the median and the 75th quantile (area: $P < 0.0001$, $t > 8$ $df = 116$, north-south:
618 $P < 0.0001$, $t > 5$ $df = 116$, Figs. 7a, 7b), but no significant differences were found between MBPs
619 circulating in mammals and birds even using one side test (area: $P > 0.31$, $t < 0.11$ $df = 116$, north-
620 south: $P > 0.11$, $t < 1.2$ $df = 116$, Figs. 7a, 7b). Contrary to our expectation, the north-south distance
621 seems to "saturate" faster than the total area (Fig. 7), indicating that it may be more sensitive to
622 early range expansion than to later stages of MBD range expansion. The total area of most
623 MBPs transmitted among humans or domestic animals (undergone range expansion, $N = 15$)
624 cover area $10\text{--}20 \times 10^6$ km² and their north-south distance spans $40\text{--}60^\circ$, whereas the majority
625 of MBPs (>90) cover $<4 \times 10^6$ km² and north-south distance $>15^\circ$ (Fig. 7c). Except eight MBPs
626 transmitted among wild birds that have a long north-south distance, 30 MBPs occupy
627 intermediate ranges covering area $4\text{--}10 \times 10^6$ km² and north-south distance of $20\text{--}50^\circ$ (Fig. 7c).
628 Accordingly, this group is enriched with species that are currently at the intermediate phase of
629 range expansion. This model enables identification of putative MBPs with elevated risk for range
630 expansion such as Usutu (USUV), Wesselsbron (WSLV), Akabane (AKAV), Spondweni virus
631 (SPOV), and ONNV, which are elevated for both measures (Fig. 7c). This approach putatively
632 identifies expanding pathogens during the intermediate phase of range expansion even before
633 they infect humans or domestic animals. Monitoring changes in geographical range as well as
634 the MBP host range and vector range would be key to evaluating these aspects of disease
635 emergence. Validating this biogeographical ranking with independent risk predictions will
636 increase confidence in the subset of MBPs of elevated risk. For example, the number of vectors
637 and hosts in which a pathogen is found in and the numbers it can be transmitted from may be
638 used as independent markers of the MBP's prospects to undergo further range expansion.
639 Experimental evidence about the pathogen compatibility and capacity for transmission e.g.,
640 (Haddow *et al.*, 2016) with the most widespread vectors and domestic hosts (Fig. 2), will further
641 augment the risk assessment. Development and testing of such models will advance
642 understanding and predictive capacity of range expansion as a component of disease
643 emergence. Evaluation of the pathogenicity and impact that a MBP would have on human and
644 domestic animals are beyond the scope of this analysis, but the possibility of increased
645 virulence linked to transmissibility in these new hosts by domesticated vectors, e.g., ZIKV –
646 should not be ignored.

647 Figure 7. Ranking of African mosquito-borne pathogens by their range area and maximum north-south distance to
 648 estimate their phase of range expansion. a) Variation between host groups in north-south distance (latitude degrees)
 649 and b) Variation between host groups total range area (10^6 km^2). c) relationship between MBP's total area (10^6 km^2 ;
 650 X-axis) and the maximum north-south distance (degrees latitude; Y-axis) using local regression (loess and 95% CLM)
 651 on all MBDs (N= 150). Box plots along axes display distributions of corresponding variables. Acronym of MBPs are
 652 given for those with total area larger than 2.5 or north-south longer than 5° and colors denote host group (birds are
 653 used if birds and mammals are thought to act as natural hosts). Box draws attention to putative MBPs at intermediate
 654 phase of range expansion (excluding MBPs of birds and domestic animals, see text).



656 METHODS

657 The database and our analysis refer to continental Africa (surrounded by the Mediterranean Sea
658 to the north, the Indian Ocean to the east and the Atlantic Ocean to the west), excluding all
659 islands (e.g., Cape Verde, Comoros, Madagascar, Mauritius, Seychelles, São Tomé and
660 Príncipe) because island biogeography requires consideration of multiple factors, such as
661 distances to the nearest mainland and to other islands, historical formation of the island,
662 existence of past terrestrial bridges, etc., which deserve a separate treatment. Very few records
663 of mosquitoes and MBPs can be found for Eswatini, Lesotho, South Sudan and Western
664 Sahara. Moreover, parts of their records are included in their previous political affiliations, e.g.,
665 South Sudan in Sudan. Therefore, these countries are not listed in our analysis; instead, our
666 analysis, pertains to 45 countries, with few countries that subsumed those in the past and still
667 “contain” their records, e.g., “Sudan and South Sudan” being used (Table S1). Because
668 countries differ in surveillance effort, grouping neighboring countries into regions minimizes
669 variation in surveillance effort variability and was used to test country-based patterns. Unlike the
670 geopolitical regions with the same names, our five regions were defined to maximize distances
671 among regions, accommodate latitudinal variation, and minimize inter-region enclaves (Fig. 5).

672 Our African mosquito distribution data (Supp. File 1) was initially generated based on the global
673 distribution lists, updated to 2017 (Wilkerson *et al.*, 2021). We updated records of anophelines
674 in sub-Saharan countries (Irish *et al.*, 2020), and culicines following country-specific lists
675 recently published for Mali (Tandina *et al.*, 2018), Mauritania (Lemine *et al.*, 2017), Morocco
676 (Trari *et al.*, 2017), and incorporated records for southern African countries (Jupp, 1996).
677 Information on global diversity of mosquitoes was recently updated (Wilkerson *et al.*, 2021) and
678 allowing reconciliation of species identifications that were later revised, e.g., *Culex tigripes* and
679 *Lutzia tigripes* or *An. arabiensis* and *An. gambiae*. Subspecies were not included in our data.

680 The mosquito-borne pathogen (MBP) distribution data was generated based on hundreds of
681 references listed in Supp File 2, providing they met the three criteria as follows: A peer-reviewed
682 scientific source (or a source, e.g., the CDC arbovirus catalogue, listed in peer-reviewed
683 sources) reported that the MBP has been i) naturally transmitted in continental Africa, ii) to a
684 terrestrial vertebrate host, iii) by mosquito vector, to the extent that this mode of transmission is
685 recognized to have an epidemiological role, even if other mode(s) of transmission play a greater
686 role. Our database includes information whether mosquito role in the MBP transmission is
687 secondary or primary and whether it is biological or mechanical. Strains or any sub-species
688 definitions were not included in our analysis. To ascertain accuracy of our MBP records, we
689 compared our data with the CRORA database (*Centre de Référence OMS sur la Recherche*
690 *des Arbovirus et des Fièvres Hémostatiques (CRORA)*): www.pasteur.fr/recherche/banques/CRORA
691 (discontinued since 2015) and the EID2 database (Wardeh *et al.*, 2015) (as of September 2021)
692 among other sources. Only records that met our above criteria were included in our database.
693 By confining our records to continental Africa, the term endemic refers to a species found in one
694 African country (or region, when specified), however, although uncommon, the species may be
695 also found outside continental Africa.

696 Information on land mass of the World and of continental African countries (The-World-Bank,
697 2021) were used to calculate the proportion of area of continental Africa from the land worldwide
698 and total area per species. Accordingly, the total area of the worldwide and continental Africa
699 we used are 148,568,946.1 and 296,63,582.0. Global coordinates central position of each
700 African country (Google Developers, 2021) were used to computed maximum north-south range
701 distances for each MBP.

702

703 **Data analysis**

704 Goodness of fit χ^2 tests implemented by Proc Freq (SAS Institute, 2012) were used to assess if
705 diversity in a particular area was higher than predicted by the relative size of the area. Exact
706 tests were used if expected values were smaller than 5. Confidence intervals (distribution free)
707 of medians were computed using Proc Univariate (SAS Institute, 2012) based on order statistics
708 (ranks). Person correlation, linear, and quadratic regression models to relate biodiversity
709 measures with country area were implemented by Proc Reg (SAS Institute, 2012). Quantile
710 regression implemented by Proc Quantreg (SAS Institute, 2012) extends the general linear
711 model for estimating conditional change in the response variable across its distribution as
712 expressed by quantiles, rather than its mean (though the median is similar to the mean in
713 symmetric distributions). It does not assume parametric distribution (e.g., normal) of the random
714 error part of the model, thus it is considered semiparametric. The value of this analysis is that it
715 allows us to address variation among the medians of various groups and also across quantiles
716 even when the mean and the median are unchanging. The parameters estimates in linear
717 quantile regression models are interpreted as in typical general linear models, as rates of
718 change adjusted for the effects of the other variables in the model for a specified quantile (Cade
719 and Noon 2003). We used matrices of presence absence of mosquitoes or MBPs to compute
720 matrices of Jaccard distances between regions or countries (separately), using Proc Distance
721 (SAS Institute, 2012) and used the Ward method in Proc Cluster with height measured by R^2
722 (the proportion of variance accounted by the clusters) to produce and plot dendrograms.

723

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734 position, policy or decision unless so designated by other documentation.

735

736 **Supplemental Information**

737

738 Supplemental Results and Discussion

739 Table S1: Genera and subgenera of mosquitoes in continental Africa

740 Table S2: African countries included in this analysis: area and centroid coordinates

741 Supp. Data File 1: African mosquito faunal list per country (to be included with publication in refereed
742 journal)

743 Supp. Data File 2: African mosquito-borne pathogens: Acronym, taxonomical affiliation, transmission
744 mode, and distribution by country, with references (to be included with publication in refereed journal)

745

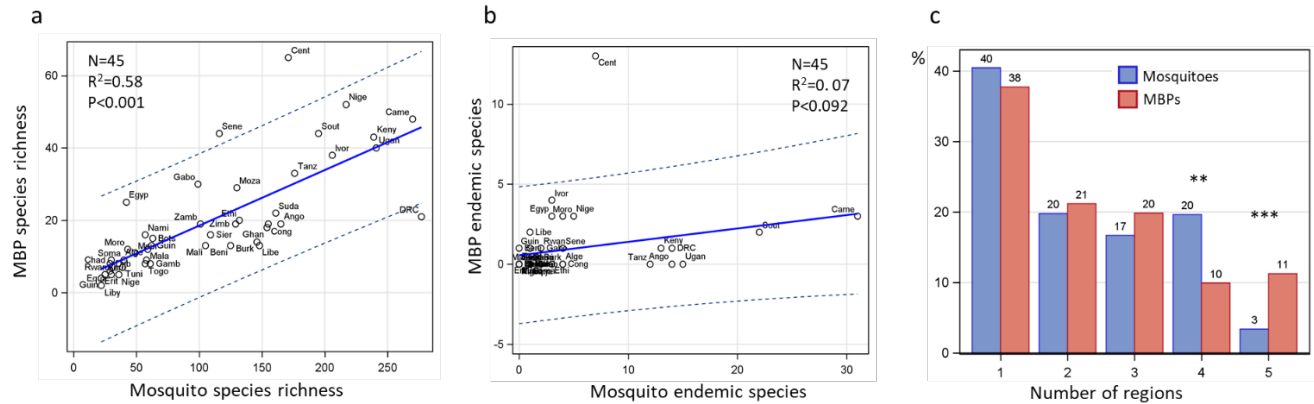
746

747 **Supplemental Results and Discussion**

748 The similarity in species richness of MBPs and mosquitoes (Fig. 3) is also expressed by the
749 high positive correlation coefficient between these indices ($r= 0.76$, $N= 45$, $P< 0.001$ Fig. S1a),
750 although the correlation in species endemism was far lower ($r= 0.26$, $N= 45$, $P= 0.09$, Fig. S1b).
751 Because conventional pathogen detection requires species-specific diagnostic test that have
752 been developed for common and widespread pathogens, endemic pathogens are expected to
753 be under-detected. Furthermore, this weak correlation may also reflect sampling effort inequality
754 of uncommon MBPs among countries (see Main text).

755 Although the overall regional distributions of mosquitoes and MBPs are very similar (Fig. 5), the
756 differences (Fig. S1c) reveal a higher fraction of cross-Sahara MBPs (found in all five regions),
757 whereas a higher fraction of mosquitoes is found across sub-Saharan Africa ($P< 0.01$, Fig. S1c).
758 This pattern suggests that relatively few MBPs, albeit more than mosquitoes, are transported by
759 their vertebrate host(s) across the Sahara. Additionally, MBPs that have been recently
760 introduced into Africa, e.g., DENV, may have been arrived into multiple parts of the continent,
761 and being already adapted to the domestic environment, may have spread rapidly. Unlike
762 pathogens that are easily transported by human and domestic animals, fewer mosquitoes
763 represent this subgroup, e.g., *Ae. albopictus* and *An. stephensi*.

764 **Fig. S1.** Congruence between MBPs and mosquitoes in country diversity (a), endemism (b) and
765 in the number of regions occupied (c). The relationship between MBPs and mosquitoes in
766 species richness (a) and endemism (b) is shown using a linear regression (blue solid line) and
767 95% CI for individual observations (countries, dotted line) with corresponding statistics. Names
768 of countries are abbreviated to the first four letters. c) Differences in the distribution of the
769 number of regions occupied by mosquitoes and MBPs in percent (above bars). Statistically
770 significant differences (determined using 2x2 heterogeneity χ^2 tests) are shown by asterisks: **
771 and *** denote $P<0.01$ and $P<0.001$, respectively.



773 Mechanical transmission of MBPs by mosquitoes is usually disregarded by vector biologists,
 774 because it is not the primary mode of pathogen transmission (Fig. 1c), which perpetuates this
 775 attitude despite limited information about it. In Africa, only pox viruses and bacteria are reported
 776 to be transmitted mechanically by mosquitoes (Fig. 1c). The epidemiological contribution of
 777 mosquito transmission of these MBPs in short- and long-range spread of the pathogens is
 778 poorly known (but see main text), as well the extent of the vector range used by these
 779 pathogens. Further study and surveillance of pathogens transmitted mechanically by
 780 mosquitoes (especially bacteria) would reveal new grounds.

781 Geographical assemblages of mosquitoes and MBPs

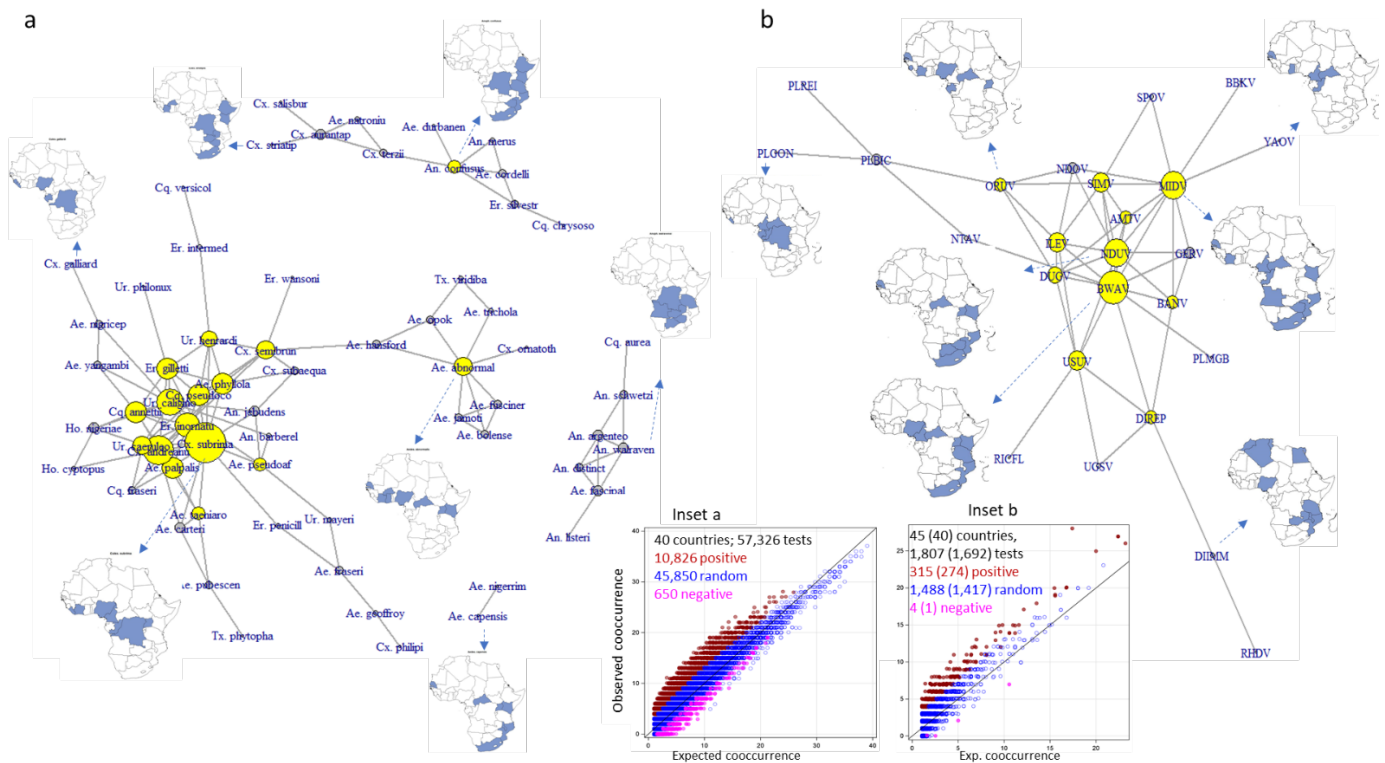
782 Species that co-occur more than expected by chance define regional assemblages that can
 783 underlie similar ecological preferences or co-dependence. We used Veech co-occurrence index
 784 (Veech, 2013) to evaluate which pairs of species co-occur positively across countries (joint
 785 country occurrence is higher than expected by chance), negatively (joint country occurrence is
 786 lower than expected by chance), or randomly (joint country occurrence is not different than
 787 expected by chance). Considering the whole continent (45 countries), the results revealed that
 788 73% of the mosquito pairs were random, 24% were positive ($P<0.05$), and 3% were negative
 789 ($P<0.05$, $N= 57,847$ testable species pairs). North Africa might have inflated significant
 790 associations because only 5% of species are found across the Sahara. Excluding the North
 791 African countries, reduced the fraction of significant associations: 19% (10,826) positive and 1%
 792 (650), negative (80% showing random associations, $N= 57,326$ species pairs, Fig. S2a: inset)
 793 across 40 countries. Negative co-occurrence in mosquitoes were especially common in
 794 *Anopheles* (78%) and *Culiseta* (6%), both within and across genera, whereas positive co-
 795 occurrences between species pairs were distributed across all genera (not shown). Such
 796 negative association suggests adaptive speciation in distinct environments, where assemblages
 797 are unique, and therefore not overlapping in species composition. *Anopheles* and *Culiseta* have
 798 the highest fraction of African species among the genera (except *Eretmapodites*, which is
 799 mostly equatorial; see Results), suggesting extensive speciation in Africa and distinct
 800 environment that supports this explanation.

801 Considering MBPs in the whole continent, 17.4% (315) of the pairs were positive and 0.2% (4)
 802 were negative out of a total of 1,807 testable pairs (Fig. S2b: inset). Because 17% of species
 803 are found across the Sahara, rather than the corresponding 5% of the mosquitoes (above),
 804 North African countries were included in subsequent analyses. Unlike the negative co-occurring
 805 MBP pairs, the number of positive co-occurring MBP pairs is far higher than that expected by
 806 chance (2.5%).

807 To visualize the organization of mosquito assemblages, defined by the co-occurrence analysis,
 808 positively co-occurring pairs of narrow-range species (5-10 countries) were included in a
 809 network consisting 119 pairs (Fig. S2a). The mosquito network exhibited four disjointed
 810 components, reflecting distinct assemblages: (i) Western-Central Africa cluster represented by
 811 *Cx. subrima* (main) with an equatorial cluster represented by *Ae. abnormalis*, (ii) Southern-East
 812 Africa represented by *An. confusus*, (iii) Southern-Central Africa, represented by *An. walravensi*,
 813 and (iv) a small widespread assemblage, represented by *Ae. capensis* (Fig. S2a).

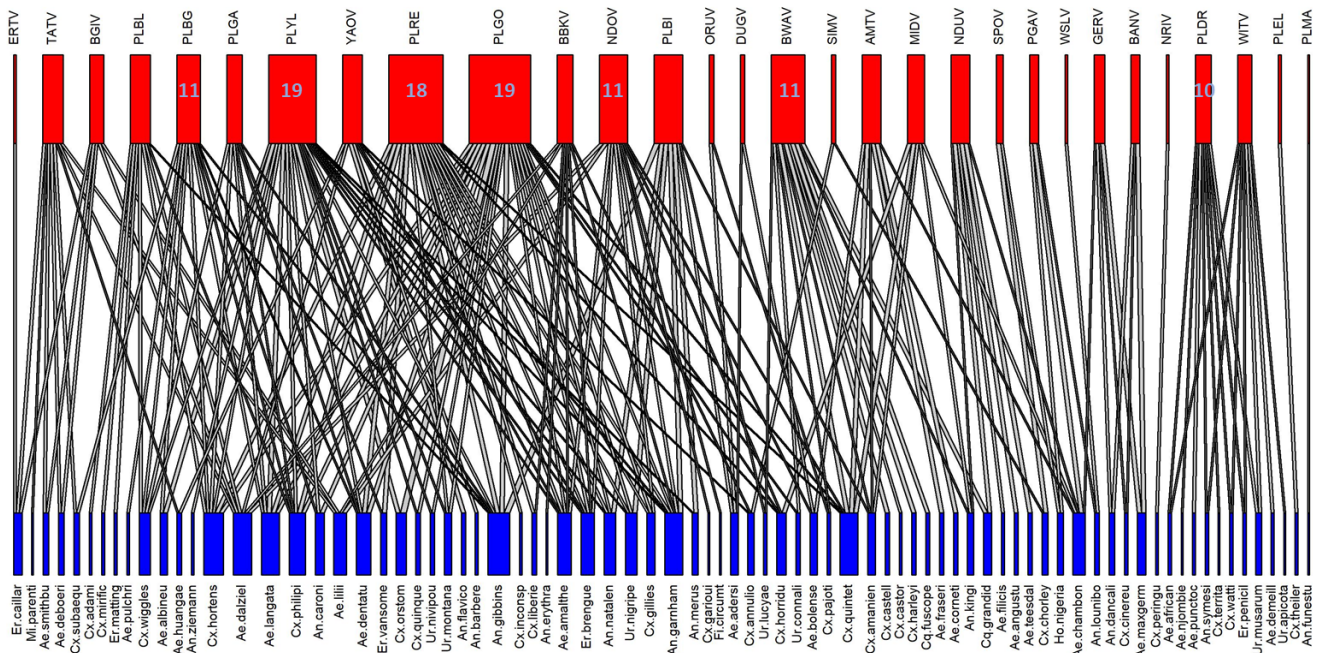
814 The network of 53 MBPs pairs consisting of 25 species, (5- 10 countries) presented a single
 815 component (Fig. S1b). While more densely connected than the mosquito network (density:
 816 0.177 vs. 0.059), distinct yet partly-overlapping assemblages are found in Southern-East and
 817 Central Africa represented by Bwamaba/Ndumu viruses (Fig. S2b, BWAV/NDUV), showing
 818 resemblance to the Southern-East Africa represented by *An. confusus*, a smaller equatorial
 819 assemblage represented by (ORUV), resembles the mosquito cluster represented by *Ae.*
 820 *abnormalis*, whereas the sub-Saharan MBP assemblage represented by Middleburg virus
 821 (MIDV) resembles the small, yet widespread mosquito assemblage represented by *Ae.*
 822 *capensis*.

823 **Figure S2.** Network of positively co-occurring pairs of mosquito (a) and MBP (b) species ($P < 0.05$), whose range is up
 824 to 10 countries (text). a) Node size proportional to its degree centrality (number of species it is significantly co-
 825 occurring with) yellow denotes >4 degrees). Distribution maps are drawn for species (broken arrows) with highest
 826 degree centrality within a component (cluster) as well as for arbitrary low-centrality species. Although North Africa
 827 was not included in the calculations of the co-occurrence for mosquitoes (text), it is included in the maps. Insets show
 828 the relationship between observed and expected joint co-occurrence (number of countries both species co-occur at)
 829 for mosquitoes (inset a) and MBPs (inset b). Positive pairs co-occur in more countries (observed) than expected
 830 denoted by the diagonal line and negative pairs co-occur in less countries than expected. Significantly positive and
 831 negative pairs are shown in red and magenta, respectively; nonsignificant pairs (random) are shown in blue.



833 Because mosquito transmission is the primary route of vertebrate infection in >90% of MBPs
834 (Fig. 1c), high vector-specificity is expected for sylvatic vectors, except for the poxviruses and
835 the three bacteria that rely on mechanical transmission. A bipartite network of mosquitoes and
836 MBPs based on the Veech index can reveal assemblages of mosquitoes and pathogens, which
837 might be different than their within-group assemblages. Albeit based on geography alone,
838 linking mosquitoes and MBPs may also help identify subset of putative sylvatic mosquito
839 vectors, which can be further refined applying other selective criteria. Veech co-occurrence
840 analysis (over the whole continent) revealed that 83% of the testable pairs were random, 16%
841 were positive and 1% were negative at $P < 0.05$ ($N = 21,342$ testable mosquito-MBP pairs).
842 Considering only highly positively co-occurring pairs ($P < 0.01$; note: 2.5% of the total tests at
843 each side are expected by chance), a bipartite network comprising of 30 MBPs and 80
844 mosquitoes with 194 links was plotted (Fig. S3). To simplify interpretation, mechanically-
845 transmitted MBPs and non-blood-feeding mosquitoes were excluded and only pairs in which the
846 pathogen joint co-occurrence was fully subsumed in that of the mosquito were retained. The
847 largest MBP-mosquito assemblages were from Central Africa: *Plasmodium gonderi* (PLGO with
848 19 mosquitoes), *Pl. reichenowi* (PLRE), followed by that in Southern-East and Central Africa
849 Bwamaba virus (BWAV, Figs. S2, S3).

850 Figure S3. Bipartite network of positively co-occurring pairs ($P < 0.01$) of MBP ($N = 30$, top-red)
851 and mosquito ($N = 80$, bottom-blue) to identify putative sylvatic vectors (see text). Note: mechanically-transmitted MBPs and non-blood-
852 feeding mosquitoes were excluded.



854 This network includes broad-ranging MBPs, e.g., *Pl. malariae*, whose range is subsumed only in
855 that of *An. funestus* (Fig. S3). On average each MBP is linked to 6.5 mosquitoes (median=6).
856 Because geographical overlap in MBP and mosquito distribution is the only basis for linking
857 them, the matrix included 5 non-bloodfeeding mosquitoes (*Mi. fraseri*, *Mi. moucheti*, *Tr. aeneus*,
858 *Tr. viridibasis*, and *Tr. wolfsi*, not shown). Likewise, the links between *Pl. reichenowi*, which is
859 thought to be transmitted exclusively by *Anopheles* mosquitoes also include 15 culicines.
860 Therefore, incorporating additional criteria such as *Anopheles* to filter among putative vectors of
861 a mammalian *Plasmodium* species, incorporating information on bloodmeal host range, and

862 permitting partial range overlap can produce a more accurate list of putative mosquito vector
863 species for surveillance and vectorial competence experiments. This approach can help
864 identifying the sylvatic vectors of many pathogens.

865

866 **Supplemental Methods**

867 The probabilistic model of species co-occurrence (Veech, 2013) was used to classify pairs of
868 species co-occurrence as negative, positive or random based on the probabilities that two
869 species would co-occur at a frequency less than or greater than the observed frequency if the
870 two species were distributed independently of one another among sites. Veech index is based
871 on an analytic probabilistic model using combinatorics to obtain the probability that two selected
872 species co-occur at any given number of sites among those sampled. The calculations were
873 coded in SAS (SAS Institute, 2012). Given the number of countries (sites) used in our data (40–
874 45), significant pairs could be classified at the $P < 0.05$ significance level, only if both ranges
875 cover at least 4 countries. We used Proc Gmap (SAS Institute, 2012) to generate maps.
876 Network plots and statistics were produced using the packages igraph (Csardi & Nepusz, 2006)
877 and bipartite (Dormann *et al.*, 2008) in R (R Core Team, 2016).

878 **Table S1.** Subgenera of mosquitoes in continental Africa with their number of species in the
879 continent and worldwide (Wilkerson *et al.*, 2021)

Genus	Subgenus	African species count	Worldwide species count
<i>Aedeomyia</i>	<i>Aedeomyia</i>	1	6
<i>Aedeomyia</i>	<i>Lepiothauma</i>	1	1
<i>Aedes</i>	<i>Acartomyia</i>	1	3
<i>Aedes</i>	<i>Aedimorphus</i>	40	65
<i>Aedes</i>	<i>Albuginosus</i>	9	9
<i>Aedes</i>	<i>Bifidistylus</i>	2	2
<i>Aedes</i>	<i>Catageiomyia</i>	29	29
<i>Aedes</i>	<i>Coetzeemyia</i>	1	1
<i>Aedes</i>	<i>Cornetius</i>	1	1
<i>Aedes</i>	<i>Dahlia</i>	2	3
<i>Aedes</i>	<i>Diceromyia</i>	8	8
<i>Aedes</i>	<i>Elpeytonius</i>	2	2
<i>Aedes</i>	<i>Fredwardsius</i>	1	1
<i>Aedes</i>	<i>Hopkinsius</i>	5	7
<i>Aedes</i>	<i>Mucidus</i>	6	14
<i>Aedes</i>	<i>Neomelaniconion</i>	24	28
<i>Aedes</i>	<i>Ochlerotatus</i>	12	186
<i>Aedes</i>	<i>Paulianius</i>	1	9
<i>Aedes</i>	<i>Polyleptiomyia</i>	1	2
<i>Aedes</i>	<i>Pseudarmigeres</i>	5	5
<i>Aedes</i>	<i>Pseudoalbuginosus</i>	1	1
<i>Aedes</i>	<i>Rusticoidus</i>	2	9
<i>Aedes</i>	<i>Skusea</i>	1	4
<i>Aedes</i>	<i>Stegomyia</i>	56	128
<i>Aedes</i>	<i>Vansomerensis</i>	3	3
<i>Aedes</i>	<i>Zavortinkius</i>	6	11
<i>Anopheles</i>	<i>Anopheles</i>	18	185
<i>Anopheles</i>	<i>Cellia</i>	121	225
<i>Anopheles</i>	<i>Christya</i>	2	2
<i>Coquillettidia</i>	<i>Coquillettidia</i>	23	44
<i>Culex</i>	<i>Afroculex</i>	1	1
<i>Culex</i>	<i>Barraudius</i>	3	4
<i>Culex</i>	<i>Culex</i>	63	200
<i>Culex</i>	<i>Culiciomyia</i>	15	54
<i>Culex</i>	<i>Eumelanomyia</i>	37	77
<i>Culex</i>	<i>Kitzmilleria</i>	1	1
<i>Culex</i>	<i>Lasiosiphon</i>	1	1
<i>Culex</i>	<i>Maillotia</i>	7	9
<i>Culex</i>	<i>Neoculex</i>	5	26
<i>Culex</i>	<i>Oculeomyia</i>	4	19

<i>Culiseta</i>	<i>Allotheobaldia</i>	1	1
<i>Culiseta</i>	<i>Culicella</i>	2	14
<i>Culiseta</i>	<i>Culiseta</i>	2	12
<i>Culiseta</i>	<i>Theomyia</i>	1	1
<i>Eretmapodites</i>	<i>n/a</i>	48	48
<i>Ficalbia</i>	<i>n/a</i>	4	8
<i>Hodgesia</i>	<i>n/a</i>	4	11
<i>Lutzia</i>	<i>Metalutzia</i>	1	6
<i>Malaya</i>	<i>Malaya</i>	6	12
<i>Mansonia</i>	<i>Mansonioides</i>	2	10
<i>Mimomyia</i>	<i>Etorleptomyia</i>	2	7
<i>Mimomyia</i>	<i>Mimomyia</i>	10	17
<i>Orthopodomyia</i>	<i>n/a</i>	4	36
<i>Toxorhynchites</i>	<i>Afrorhynchus</i>	12	19
<i>Toxorhynchites</i>	<i>Toxorhynchites</i>	8	51
<i>Uranotaenia</i>	<i>Pseudoficalbia</i>	30	150
<i>Uranotaenia</i>	<i>Uranotaenia</i>	18	121

880

881

882 **Table S2.** African countries included in this paper (N= 45), area, centroid position, and
 883 additional territories subsumed as used in this paper (Methods).

Country	Area (km ²)	Latitude	Longitude	Subsumes
Algeria	2381741	28.033886	1.659626	
Angola	1246700	-11.202692	17.873887	
Benin	112622	9.30769	2.315834	
Botswana	581726	-22.328474	24.684866	
Burkina Faso	274000	12.238333	-1.561593	
Burundi	27830	-3.373056	29.918886	
Cameroon	475442	7.369722	12.354722	
Central African Republic	622984	6.611111	20.939444	
Chad	1284000	15.454166	18.732207	
DRC	2344858	-4.038333	21.758664	
Djibouti	23200	11.825138	42.590275	
Egypt	1001449	26.820553	30.802498	
Equatorial Guinea	28051	1.650801	10.267895	
Eritrea	117600	15.179384	39.782334	
Ethiopia	1104300	9.145	40.489673	
Gabon	267668	-0.803689	11.609444	
Gambia	10380	13.443182	-15.310139	
Ghana	238534	7.946527	-1.023194	
Guinea	245857	9.945587	-9.696645	
Guinea-Bissau	36125	11.803749	-15.180413	

Ivory Coast	322460	7.539989	-5.54708	
Kenya	580367	-0.023559	37.906193	
Liberia	111369	6.428055	-9.429499	
Libya	1759540	26.3351	17.228331	
Malawi	118484	-13.254308	34.301525	
Mali	1240192	17.570692	-3.996166	
Mauritania	1030700	21.00789	-10.940835	
Morocco	710850	31.791702	-7.09262	Western Sahara
Mozambique	801590	-18.665695	35.529562	
Namibia	825418	-22.95764	18.49041	
Niger	1267000	17.607789	8.081666	
Nigeria	923768	9.081999	8.675277	
Republic of Congo	342000	-0.228021	15.827659	
Rwanda	26798	-1.940278	29.873888	
Senegal	196723	14.497401	-14.452362	
Sierra Leone	71740	8.460555	-11.779889	
Somalia	637657	5.152149	46.199616	
South Africa	1221037	-30.559482	22.937506	Eswatini and Lesotho
Sudan & South Sudan	2505813	12.862807	30.217636	Sudan and South Sudan
Tanzania	945203	-6.369028	34.888822	
Togo	56785	8.619543	0.824782	
Tunisia	163610	33.886917	9.537499	
Uganda	236040	1.373333	32.290275	
Zambia	752614	-13.133897	27.849332	
Zimbabwe	390757	-19.015438	29.154857	

884

References

- 885 Arisue, N., Honma, H., Kume, K. & Hashimoto, T. (2021) Progress in understanding the
886 phylogeny of the *Plasmodium vivax* lineage. *Parasitology international*, **87**.
- 887 Bensch, S., Hellgren, O. & Perez-Tris, J. (2009) MalAvi: a public database of malaria parasites
888 and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages.
889 *Molecular Ecology Resources*, **9**, 1353–1358.
- 890 Binder, S., Levitt, A.M., Sacks, J.J. & Hughes, J.M. (1999) Emerging infectious diseases: Public
891 health issues for the 21st century. *Science*, **284**, 1311–1313.
- 892 Braack, L., Gouveia De Almeida, A.P., Cornel, A.J., Swanepoel, R. & Jager, C. De. (2018)
893 Mosquito-borne arboviruses of African origin: Review of key viruses and vectors. *Parasites and*
894 *Vectors*, **11**, 29.
- 895 Burgess, N.D., Hales, J.D., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., *et al.* (2004)

- 896 *Terrestrial eco-regions of Africa and Madagascar: A conservation assessment*. World Wildlife
897 Fund, United States, Island Press, Washington D.C.
- 898 Burgin, C.J., Colella, J.P., Kahn, P.L. & Upham, N.S. (2018) How many species of mammals
899 are there? *Journal of Mammalogy*, **99**, 1–14.
- 900 Burke, D. (1998) The evolvability of emerging viruses. In *Pathology of Emerging Infections 2*
901 (ed. by Nelson, A.M. & Horsburg, R.C.J.). American Society for Microbiology, Washington, DC,
902 USA, pp. 1–12.
- 903 CDC. (2019) Arbovirus Catalog [WWW Document]. URL
904 <https://wwwn.cdc.gov/arbocat/VirusBrowser.aspx> [accessed on .
- 905 Channing, A. & Rodel, M.-O. (2019) *Field Guide to the Frogs & Other Amphibians of Africa*.
906 Penguin Random House South Africa.
- 907 Chapman, J.W., Bell, J.R., Burgin, L.E., Reynolds, D.R., Pettersson, L.B., Hill, J.K., *et al.* (2012)
908 Seasonal migration to high latitudes results in major reproductive benefits in an insect.
909 *Proceedings of the National Academy of Sciences*, **109**, 14924–14929.
- 910 Collins, W.E. & Jeffery, G.M. (2005) Plasmodium ovale: Parasite and disease. *Clinical*
911 *Microbiology Reviews*, **18**, 570–581.
- 912 Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research.
913 *InterJournal*, **Complex Sy**, 1695.
- 914 DaMassa, A.J. (1966) The role of Culex tarsalis in the transmission of fowl pox virus. *Avian*
915 *Diseases*, **10**, 57.
- 916 Daron, J., Boissière, A., Boundenga, L., Ngoubangoye, B., Houze, S., Arnathau, C., *et al.*
917 (2021) Population genomic evidence of Plasmodium vivax Southeast Asian origin. *Science*
918 *advances*, **7**.
- 919 Diagne, M.M., Ndione, M.H.D., Gaye, A., Barry, M.A., Diallo, D., Diallo, A., *et al.* (2021) Yellow
920 Fever Outbreak in Eastern Senegal, 2020–2021. *Viruses 2021, Vol. 13, Page 1475*, **13**, 1475.
- 921 Diallo, D., Sall, A.A., Buenemann, M., Chen, R., Faye, O., Diagne, C.T., *et al.* (2012) Landscape
922 ecology of sylvatic chikungunya virus and mosquito vectors in southeastern senegal. *PLoS*
923 *Neglected Tropical Diseases*, **6**, 1–14.
- 924 Diallo, D., Sall, A.A., Diagne, C.T., Faye, O., Faye, O., Ba, Y., *et al.* (2014) Zika virus
925 emergence in mosquitoes in Southeastern Senegal, 2011. *PLoS ONE*, **9**.
- 926 Diallo, M., Nabeth, P., Ba, K., Sall, A.A., Ba, Y., Mondo, M., *et al.* (2005) Mosquito vectors of the
927 1998-1999 outbreak of Rift Valley Fever and other arboviruses (Bagaza, Sanar, Wesselsbron
928 and West Nile) in Mauritania and Senegal. *Medical and Veterinary Entomology*, **19**, 119–126.
- 929 Dormann, C., Gruber, B., interaction, J.F.- & 2008, undefined. (2008) Introducing the bipartite
930 package: analysing ecological networks. *biom.uni-freiburg.de*, **8**.
- 931 Drake, V.A. & Gatehouse, A.G. (1995) *Insect migration: tracking resources through space and*

- 932 *time*. Cambridge University Press, New York.
- 933 Drake, V.A. & Reynolds, D.R. (2012) *Radar entomology : observing insect flight and migration*.
934 CAB International., Wallingford, UK.
- 935 Epelboin, Y., Talaga, S., Epelboin, L. & Dusfour, I. (2017) Zika virus: An updated review of
936 competent or naturally infected mosquitoes. *PLOS Neglected Tropical Diseases*, **11**, e0005933.
- 937 Faulde, M.K., Spiesberger, M. & Abbas, B. (2012) Sentinel site-enhanced near-real time
938 surveillance documenting West Nile virus circulation in two Culex mosquito species indicating
939 different transmission characteristics, Djibouti City, Djibouti. *Journal of the Egyptian Society of*
940 *Parasitology*, **42**, 461–474.
- 941 Faye, O., Ba, Y., Faye, O., Talla, C., Diallo, D., Chen, R., *et al.* (2014) Urban Epidemic of
942 Dengue Virus Serotype 3 Infection, Senegal, 2009 - Volume 20, Number 3—March 2014 -
943 Emerging Infectious Diseases journal - CDC. *Emerging Infectious Diseases*, **20**, 456–459.
- 944 Fenollar, F. & Mediannikov, O. (2018) Emerging infectious diseases in Africa in the 21st
945 century. *New Microbes and New Infections*, **26**, S10.
- 946 Florio, J., Verú, L.M., Dao, A., Yaro, A.S., Diallo, M., Sanogo, Z.L., *et al.* (2020) Diversity,
947 dynamics, direction, and magnitude of high-altitude migrating insects in the Sahel. *Scientific*
948 *Reports 2020 10:1*, **10**, 1–14.
- 949 Foley, D.H., Rueda, L.M. & Wilkerson, R.C. (2007) Insight into Global Mosquito Biogeography
950 from Country Species Records. *Journal of Medical Entomology*, **44**, 554–567.
- 951 Fontenille, D., Traore-Lamizana, M., Diallo, M., Thonnon, J., Digoutte, J.P. & Zeller, H.G. (1998)
952 New vectors of Rift Valley fever in West Africa. *Emerging infectious diseases*, **4**, 289–293.
- 953 Garrett-Jones, C. (1950) A dispersion of mosquitoes by wind. *Nature*, **165**, 285–285.
- 954 Garrett-Jones, C. (1962) The possibility of active long-distance migrations by *Anopheles*
955 *pharoensis* Theobald. *Bulletin of the World Health Organization*, **27**, 299–302.
- 956 Google Developers. (2021) Countries: Public data [WWW Document]. URL
957 https://developers.google.com/public-data/docs/canonical/countries_csv [accessed on .
- 958 Guernier, V., Hochberg, M.E. & Guégan, J.F. (2004) Ecology drives the worldwide distribution of
959 human diseases. *PLoS Biology*, **2**.
- 960 Haddow, A.D., Nasar, F., Guzman, H., Ponlawat, A., Jarman, R.G., Tesh, R.B., *et al.* (2016)
961 Genetic Characterization of Spondweni and Zika Viruses and Susceptibility of Geographically
962 Distinct Strains of *Aedes aegypti*, *Aedes albopictus* and *Culex quinquefasciatus* (Diptera:
963 Culicidae) to Spondweni Virus. *PLOS Neglected Tropical Diseases*, **10**, e0005083.
- 964 Hanafi, H., Warigia, M., Breiman, R.F., Godsey, M., Hoel, D., Lutomiah, J., *et al.* (2010) Rift
965 Valley Fever Virus Epidemic in Kenya, 2006/2007: The Entomologic Investigations. *The*
966 *American Journal of Tropical Medicine and Hygiene*, **83**, 28–37.
- 967 Hellgren, O., Waldenstrom, J., PerezERÉZ-Tris, J., Szoll, E., Si, Ö., Hasslequist, D., *et al.*

- 968 (2007) Detecting shifts of transmission areas in avian blood parasites — a phylogenetic
969 approach. *Molecular Ecology*, **16**, 1281–1290.
- 970 Huestis, D.L., Dao, A., Diallo, M., Sanogo, Z.L., Samake, D., Yaro, A.S., *et al.* (2019) Windborne
971 long-distance migration of malaria mosquitoes in the Sahel. *Nature*, **574**, 404–408.
- 972 Irish, S.R., Kyalo, D., Snow, R.W. & Coetzee, M. (2020) Updated list of Anopheles species
973 (Diptera: Culicidae) by country in the Afrotropical Region and associated islands. *Zootaxa*,
974 **4747**, 401–449.
- 975 Jones, K.E., Patel, N.G., Levy, M.A., Storeygard, A., Balk, D., Gittleman, J.L., *et al.* (2008)
976 Global trends in emerging infectious diseases. *Nature*, **451**, 990.
- 977 Joy, D.A., Gonzalez-Ceron, L., Carlton, J.M., Gueye, A., Fay, M., McCutchan, T.F., *et al.* (2008)
978 Local adaptation and vector-mediated population structure in Plasmodium vivax malaria.
979 *Molecular Biology and Evolution*, **25**, 1245–1252.
- 980 Jupp, P. & McIntosh, B. (1990) Aedes furcifer and other mosquitoes as vectors of chikungunya
981 virus at Mica, northeastern Transvaal, South Africa. *J Am Mosq Control Assoc.*, **6**, 415–420.
- 982 Jupp, P.G. (1996) *Mosquitoes of Southern Africa: Culicinae and Toxorhynchitinae*. Ekogilde
983 Publishers.
- 984 Karabatsos, N. (1985) *International Catalogue of Arboviruses, including certain other viruses of*
985 *vertebrates*. 3rd edn. Am Soc Trop Med Hygi for the Subcommittee on Information Exchange of
986 the Am Comm on Arthro born viruses., San Antonio, Texas.
- 987 Kay, B.H. & Farrow, R.A. (2000) Mosquito (Diptera: Culicidae) Dispersal: Implications for the
988 Epidemiology of Japanese and Murray Valley Encephalitis Viruses in Australia. *Journal of*
989 *Medical Entomology*, **37**, 797–801.
- 990 Kligler, I.J., Muckenfuss, R.S. & Rivers, T.M. (1928) Transmission of fowl-pox by mosquitoes.
991 *Proc. Soc. Exptl. Biol. Med.*, **26**, 128–9.
- 992 Kyalo, D., Amratia, P., Mundia, C.W., Mbogo, C.M., Coetzee, M. & Snow, R.W. (2017) A geo-
993 coded inventory of anophelines in the Afrotropical Region south of the Sahara: 1898-2016.
994 *Welcome Open Research*, **2**, 57-.
- 995 Laurence, B.R. (1989) The global dispersal of bancroftian filariasis. *Parasitology Today*, **5**, 260–
996 264.
- 997 Lemine, A., Lemrabott, M., Ebou, M., Khadijetou, L., Salem, O., Khyarhoum, O., *et al.* (2017)
998 Mosquitoes (Diptera: Culicidae) in Mauritania: A review of their biodiversity, distribution and
999 medical importance. *Parasites and Vectors*, **10**.
- 1000 Lepage, D. (2021) Avibase - The World Bird Database [WWW Document]. URL
1001 <https://avibase.bsc-eoc.org/checklist.jsp?region=AFC> [accessed on .
- 1002 Linder, H.P., Klerk, H.M. de, Born, J., Burgess, N.D., Fjeldså, J. & Rahbek, C. (2012) The
1003 partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal*
1004 *of Biogeography*, **39**, 1189–1205.

- 1005 Linthicum, K.J., Anyamba, A., Tucker, C.J., Kelley, P.W., Myers, M.F. & Peters, C.J. (1999)
1006 Climate and satellite indicators to forecast Rift Valley fever epidemics in Kenya. *Science (New*
1007 *York, N.Y.)*, **285**, 397–400.
- 1008 Linthicum, K.J., Davies, F.G., Kairo, A. & Bailey, C.L. (1985) Rift Valley fever virus (family
1009 Bunyaviridae, genus Phlebovirus). Isolations from Diptera collected during an inter-epizootic
1010 period in Kenya. *J Hyg (London)*, **95**, 197–205.
- 1011 Liu, W.M., Li, Y.Y., Learn, G.H., Rudicell, R.S., Robertson, J.D., Keele, B.F., *et al.* (2010) Origin
1012 of the human malaria parasite *Plasmodium falciparum* in gorillas. *Nature*, **467**, 420-U67.
- 1013 Lomolino, M. V. (2020) *Biogeography A Very Short Introduction*. First. Oxford University Press,
1014 Oxford, UK.
- 1015 Molina-Cruz, A., Canepa, G.E., Kamath, N., Pavlovic, N. V., Mu, J., Ramphul, U.N., *et al.* (2015)
1016 *Plasmodium* evasion of mosquito immunity and global malaria transmission: The lock-and-key
1017 theory. *Proceedings of the National Academy of Sciences*, **112**, 15178–15183.
- 1018 Molina-Cruz, A., Canepa, G.E., Silva, T.L.A. e, Williams, A.E., Nagyal, S., Yenkoidiok-Douti, L.,
1019 *et al.* (2020) *Plasmodium falciparum* evades immunity of anopheline mosquitoes by interacting
1020 with a Pfs47 midgut receptor. *Proceedings of the National Academy of Sciences*, **117**, 2597–
1021 2605.
- 1022 Molina-Cruz, A., Garver, L.S., Alabaster, A., Bangiolo, L., Haile, A., Winikor, J., *et al.* (2013a)
1023 The human malaria parasite Pfs47 gene mediates evasion of the mosquito immune system.
1024 *Science*, **340**, 984–987.
- 1025 Molina-Cruz, A., Lehmann, T. & Knöckel, J. (2013b) Could culicine mosquitoes transmit human
1026 malaria? *Trends in Parasitology*.
- 1027 Morse, S.S., Mazet, J.A., Woolhouse, M., Parrish, C.R., Carroll, D., Karesh, W.B., *et al.* (2012)
1028 Prediction and prevention of the next pandemic zoonosis. *The Lancet*, **380**, 1956–1965.
- 1029 Nanfack Minkeu, F. & Vernick, K.D. (2018) A Systematic Review of the Natural Virome of
1030 Anopheles Mosquitoes. *Viruses 2018, Vol. 10, Page 222*, **10**, 222.
- 1031 Ndiaye, E.H., Diallo, D., Fall, G., Ba, Y., Faye, O., Dia, I., *et al.* (2018) Arboviruses isolated from
1032 the Barkedji mosquito-based surveillance system, 2012-2013. *BMC Infectious Diseases*, **18**, 1–
1033 14.
- 1034 Njabo, K.Y., Cornel, A.J., Sehgal, R.N.M., Loiseau, C., Buermann, W., Harrigan, R.J., *et al.*
1035 (2009) *Coquillettidia* (Culicidae, Diptera) mosquitoes are natural vectors of avian malaria in
1036 Africa. *Malaria Journal*, **8**, 1–12.
- 1037 Pedgley, D.E., Reynolds, D.R. & Tatchell, G.M. (1995) Long-range insect migration in relation to
1038 climate and weather: Africa and Europe. In *Insect Migration: Tracking resources through space*
1039 *and time* (ed. by Drake, V.A. & Gatehouse, A.G.). Cambridge University Press, New York, pp.
1040 3–30.
- 1041 Perkins, S.L. (2014) Malaria's Many Mates: Past, Present, and Future of the Systematics of the
1042 Order Haemosporida. *Journal of Parasitology*, **100**, 11–25.

- 1043 Perkins, S.L. (2018) Malaria in Farmed Ungulates: an Exciting New System for Comparative
1044 Parasitology. *mSphere*, **3**.
- 1045 Phipps, W.L., López-López, P., Buechley, E.R., Opper, S., Álvarez, E., Arkumarev, V., *et al.*
1046 (2019) Spatial and Temporal Variability in Migration of a Soaring Raptor Across Three
1047 Continents. *Frontiers in Ecology and Evolution*, **7**.
- 1048 Purdon, A., Mole, M.A., Chase, M.J. & Aarde, R.J. van. (2018) Partial migration in savanna
1049 elephant populations distributed across southern Africa. *Scientific Reports 2018 8:1*, **8**, 1–11.
- 1050 R Core Team. (2016) R: A Language and Environment for Statistical Computing.
- 1051 Reynolds, D.R., Chapman, J.W. & Harrington, R. (2006) The migration of insect vectors of plant
1052 and animal viruses. *Advances in virus research*, **67**, 453–517.
- 1053 Reynolds, D.R. & Riley, J.R. (1988) A migration of grasshoppers, particularly *Diaboloocatantops*
1054 *axillaris* (Thunberg) (Orthoptera: Acrididae), in the West African Sahel. *Bulletin of Entomological*
1055 *Research*, **78**, 251–271.
- 1056 Ricklefs, R.E., Medeiros, M., Ellis, V.A., Svensson-Coelho, M., Blake, J.G., Loiselle, B.A., *et al.*
1057 (2017) Avian migration and the distribution of malaria parasites in New World passerine birds.
1058 *Journal of Biogeography*, **44**, 1113–1123.
- 1059 Rosenberg, R. (2015) Detecting the emergence of novel, zoonotic viruses pathogenic to
1060 humans. *Cellular and Molecular Life Sciences*, **72**, 1115–1125.
- 1061 Rosenberg, R., Johansson, M.A., Powers, A.M. & Miller, B.R. (2013) Search strategy has
1062 influenced the discovery rate of human viruses. *Proceedings of the National Academy of*
1063 *Sciences of the United States of America*, **110**, 13961–13964.
- 1064 Rutledge, G.G., Böhme, U., Sanders, M., Reid, A.J., Cotton, J.A., Maiga-Ascofare, O., *et al.*
1065 (2017) Plasmodium malariae and P. ovale genomes provide insights into malaria parasite
1066 evolution. *Nature 2017 542:7639*, **542**, 101–104.
- 1067 Sanogo, Z.L., Yaro, A.S., Dao, A., Diallo, M., Yossi, O., Samaké, D., *et al.* (2021) The effects of
1068 high-altitude windborne migration on survival, oviposition, and blood-feeding of the African
1069 malaria mosquito, Anopheles gambiae s.l. (Diptera: Culicidae). *Journal of Medical Entomology*,
1070 **58**.
- 1071 SAS Institute. (2012) SAS software for Windows Version 9.4.
- 1072 Sellers, R.F. (1980) Weather, host and vector--their interplay in the spread of insect-borne
1073 animal virus diseases. *The Journal of hygiene*, **85**, 65–102.
- 1074 Service, M.W. (Ed.). (2001) *Encyclopedia of Arthropod-transmitted Infections*. 1st edn. CAB
1075 International., New York.
- 1076 Seufi, A.E.M. & Galal, F.H. (2010) Role of Culex and Anopheles mosquito species as potential
1077 vectors of rift valley fever virus in Sudan outbreak, 2007. *BMC Infectious Diseases*, **10**, 1–8.
- 1078 Small, S.T., Labbé, F., Coulibaly, Y.I., Nutman, T.B., King, C.L., Serre, D., *et al.* (2019) Human

- 1079 Migration and the Spread of the Nematode Parasite *Wuchereria bancrofti*. *Molecular Biology*
1080 *and Evolution*, **36**, 1931–1941.
- 1081 Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological*
1082 *Reviews*, **37**, 171–211.
- 1083 Swei, A., Couper, L.I., Coffey, L.L., Kapan, D. & Bennett, S. (2020) Patterns, Drivers, and
1084 Challenges of Vector-Borne Disease Emergence. *Vector-Borne and Zoonotic Diseases*, **20**,
1085 159–170.
- 1086 Tandina, F., Doumbo, O., Yaro, A.S., Traoré, S.F., Parola, P. & Robert, V. (2018) Mosquitoes
1087 (Diptera: Culicidae) and mosquito-borne diseases in Mali, West Africa. *Parasites & Vectors*, **11**,
1088 467.
- 1089 Tantely, L.M., Boyer, S. & Fontenille, D. (2015) A Review of Mosquitoes Associated with Rift
1090 Valley Fever Virus in Madagascar. *The American Journal of Tropical Medicine and Hygiene*, **92**,
1091 722.
- 1092 Taylor, L.H., Latham, S.M. & Woolhouse, M.E.J. (2001) Risk factors for human disease
1093 emergence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **356**, 983–
1094 989.
- 1095 The-World-Bank. (2021) Data: Land Area [WWW Document]. URL
1096 <https://data.worldbank.org/indicator/AG.LND.TOTL.K2> [accessed on .
- 1097 Tolley, K.A., Alexander, G.J., Branch, W.R., Bowles, P. & Maritz, B. (2016) Conservation status
1098 and threats for African reptiles.
- 1099 Trari, B., Dakki, M. & Harbach, R.E. (2017) An updated checklist of the Culicidae (Diptera) of
1100 Morocco, with notes on species of historical and current medical importance. *Journal of Vector*
1101 *Ecology*, **42**, 94–104.
- 1102 Turell, M.J. & Knudson, G.B. (1987) Mechanical transmission of *Bacillus anthracis* by stable
1103 flies (*Stomoxys calcitrans*) and mosquitoes (*Aedes aegypti* and *Aedes taeniorhynchus*).
1104 *Infection and Immunity*, **55**, 1859–1861.
- 1105 Twohig, K.A., Pfeffer, D.A., Baird, J.K., Price, R.N., Zimmerman, P.A., Hay, S.I., *et al.* (2019)
1106 Growing evidence of *Plasmodium vivax* across malaria-endemic Africa. *PLOS Neglected*
1107 *Tropical Diseases*, **13**, e0007140.
- 1108 Vasilakis, N., Deardorff, E.R., Kenney, J.L., Rossi, S.L., Hanley, K.A. & Weaver, S.C. (2009)
1109 Mosquitoes put the brake on arbovirus evolution: Experimental evolution reveals slower
1110 mutation accumulation in mosquito than vertebrate cells. *PLoS Pathogens*, **5**.
- 1111 Vasilakis, N., Tesh, R.B., Popov, V.L., Widen, S.G., Wood, T.G., Forrester, N.L., *et al.* (2019)
1112 Exploiting the Legacy of the Arbovirus Hunters. *Viruses 2019, Vol. 11, Page 471*, **11**, 471.
- 1113 Veech, J.A. (2013) A probabilistic model for analysing species co-occurrence. *Global Ecology*
1114 *and Biogeography*, **22**, 252–260.
- 1115 Villinger, J., Mbaya, M.K., Ouso, D., Kipanga, P.N., Lutomia, J. & Masiga, D.K. (2017)

- 1116 Arbovirus and insect-specific virus discovery in Kenya by novel six genera multiplex high-
1117 resolution melting analysis. *Molecular Ecology Resources*, **17**, 466–480.
- 1118 Wardeh, M., Risley, C., McIntyre, M.K., Setzkorn, C. & Baylis, M. (2015) Database of host-
1119 pathogen and related species interactions, and their global distribution. *Scientific Data* **2:1**,
1120 **2**, 1–11.
- 1121 Weaver, S.C., Chen, R. & Diallo, M. (2020) Chikungunya virus: Role of vectors in emergence
1122 from enzootic cycles. *Annual Review of Entomology*, **65**, 313–332.
- 1123 Weaver, S.C., Winegar, R., Manger, I.D. & Forrester, N.L. (2012) Alphaviruses: Population
1124 genetics and determinants of emergence. *Antiviral Research*, **94**, 242–257.
- 1125 WHO, W.H.O. (2020) Vector-borne diseases [WWW Document]. URL
1126 <https://www.who.int/news-room/fact-sheets/detail/vector-borne-diseases> [accessed on 2020].
- 1127 Wilkerson, R.C., Linton, Y.-M. & Strickman, D. (2021) *Mosquitoes of the World*. Vol. 1 & 2.
1128 Johns Hopkins University Press, Baltimore.
- 1129 Wolfe, N.D.N., Dunavan, C.C.P. & Diamond, J. (2007) Origins of major human infectious
1130 diseases. *Nature*, **447**, 279–283.
- 1131 Woolhouse, M.E.J. & Gowtage-Sequeria, S. (2005) Host range and emerging and reemerging
1132 pathogens. *Emerging Infectious Diseases*, **11**, 1842–1847.
- 1133