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An ecological assessment of the pandemic threat of Zika virus

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4 Colin J. Carlson[1*†], Eric R. Dougherty[1†], Wayne Getz[1,2]

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13 **Affiliations:**

14 [1]Department of Environmental Science, Policy, and Management, University of California,

15 Berkeley, 130 Mulford Hall, Berkeley, CA 94720, USA

16 [2] School of Mathematical Sciences, University of KwaZulu-Natal, South Africa.

17 *Corresponding author: cjcarlson@berkeley.edu.

18 †These authors contributed equally to this work.

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20 **Keywords**

21 Zika viral disease (ZIKV), flavivirus, climate change, ecological niche modeling, species

22 distribution modeling

23 **Summary**

24 The current outbreak of Zika virus poses a threat of unknown magnitude to human health[1]. While

25 the range of the virus has been cataloged growing slowly over the last 50 years, the recent

26 explosive expansion in the Americas indicates that the full potential distribution of Zika remains

27 uncertain[2-4]. Moreover, most current epidemiology relies on its similarities to dengue fever, a

28 phylogenetically closely related disease of unknown similarity in spatial range or ecological

29 niche[5,6]. Here we compile the first spatially explicit global occurrence dataset from Zika viral

30 surveillance and serological surveys, and construct ecological niche models to test basic

31 hypotheses about its spread and potential establishment. The hypothesis that the outbreak of

32 cases in Mexico and North America are anomalous and outside the ecological niche of the

33 disease, and may be linked to El Nino or similar climatic events, remains plausible at this time[7].

34 Comparison of the Zika niche against the known distribution of dengue fever suggests that Zika

35 is more constrained by the seasonality of precipitation and diurnal temperature fluctuations,

36 likely confining the disease to the tropics outside of pandemic scenarios. Projecting the range of

37 the diseases in conjunction with vector species (*Aedes africanus*, *Ae. aegypti*, and *Ae. albopictus*)

38 that transmit the pathogens, under climate change, suggests that Zika has potential for northward

39 expansion; but, based on current knowledge, Zika is unlikely to fill the full range its vectors

40 occupy. With recent sexual transmission of the virus known to have occurred in the United

41 States, we caution that our results only apply to the vector-borne aspect of the disease, and while

42 the threat of a mosquito-carried Zika pandemic may be overstated in the media, other

43 transmission modes of the virus may emerge and facilitate naturalization worldwide.

Main Text

Following a twenty-fold upsurge in microcephalic newborns in Brazil tentatively linked to Zika

virus (ZIKV), the World Health Organization has declared an international health emergency[1].

Despite being profiled for the first time in 1947[8], Zika remains poorly characterized at a global

scale. Thus, the present pandemic expansion in the Americas poses a threat of currently unknown

magnitude. Closely related to dengue fever, Zika conventionally presents as a mild infection,

with 80% of cases estimated to be asymptomatic[9]. The cryptic nature of infection has resulted in

sporadic documentation of the disease and rarely includes spatially explicit information beyond

the regional scale[1-4]. This greatly limits the confidence with which statistical inferences can be

made about the expansion of the virus. With an estimated 440,000-1,300,000 cases in Brazil in

2015[9], and continuing emergence of new cases in Central America and, most recently, the United

States, assessing the full pandemic potential of the virus is an urgent task with major

ramifications for global health policy.

Current evidence portrays the global spread of ZIKV as a basic diffusion process facilitated by

human and mosquito movement, a hypothesis supported by the frequency of infected traveler

case studies in the Zika literature[10-13]. Tracing phylogenetic and epidemiological data has

revealed the expansion of ZIKV has occurred in a stepwise process through the South Pacific,

moving the disease from Southeast Asia into French Polynesia and the Philippines, and

subsequently to Easter Island[1-4]. ZIKV is conjectured to have dispersed into South America as

recently as three years ago from the last of those locations, and the virus is presumed not to be at

a biogeographic equilibrium in the Americas. With cases in the ongoing outbreak in Colombia,

El Salvador, Guatemala, Paraguay, and Venezuela, and by November of last year, as far north as

67   Mexico, Puerto Rico, and the continental United States, the full potential distribution of the

68   disease remains unknown. Moreover, alternative explanations for the disease's expansion remain

69   unconsidered; most notably, the role of climate change in Zika's expansion is uncertain[7].

70

71   We present three competing hypotheses that describe the path of expansion that Zika could take,

72   based on evaluations of the ecological niche of the virus within and outside of its vectors. If the

73   Zika niche is indistinguishable from that of its *Aedes* vectors (as is essentially the case for

74   dengue fever[14]), future range expansions should match mosquito ranges. On the other hand, if

75   Zika has a transmission niche that is constrained by climatic factors within the ranges of its

76   mosquito vectors, its range may be much more limited—with, as we show below, possible

77   confinement to the tropics. In this case, the expansion of Zika into North America represents one

78   of two processes: a steady range expansion driven by climatic shifts, or an anomalous event

79   driven by human dispersal or extreme weather events. To test these hypotheses, we present the

80   first spatially explicit database of Zika occurrences from the literature and an ecological niche

81   model[15] using that data to map the potential distribution of the virus.

82

83   Our dataset includes 64 of the known occurrences of the disease – a combination of clinical cases

84   and seropositivity surveys in humans and mosquitoes. Spanning seven decades, these data have

85   not previously been compiled nor explicitly geo-referenced, and emergency modeling efforts for

86   diseases of special concern are often published with fewer occurrences (cf. a 2004 model using

87   12 points for Ebola viral disease and only four for Marburg fever[16]). Ensemble modeling also

88   vastly improves the predictive power with datasets of this sort (Extended Data Fig. 1-5), and

89   reduces the associated error. Our final model combines seven methods with a variable set chosen

90   from bioclimatic variables and a vegetation index to minimize predictor covariance. The

91   ensemble model performs very well (AUC = 0.994; Fig. 1), and strongly matches most

92   occurrences including the hotspots of Brazilian microcephaly. It also predicts additional regions

93   where Zika is as yet unrecorded, but where further inquiry may be desired (in particular,

94   Southern Sudan and the northern coast of Australia). Our model indicates that certain

95   occurrences, like the 1954 report from Egypt and almost all North American cases, are likely

96   outside the stable transmission niche[17] (i.e., persistent over time) of the virus. Moreover, we note

97   that visual presentation of cases at the country level may make the range of the virus appear far

98   larger than our models suggest (see Fig. 1). Projecting niche models to the year 2050 suggests

99   that expansion of Zika's niche outside the tropics is an unlikely scenario, independent of vector

100   availability (Fig. 2d). However, significant westward expansion in South America and eastward

101   expansion in Africa implies that Zika may continue to emerge in the tropics.

102

103   Recently published work by Bogoch *et al.*[6] uses an ecological niche model for dengue as a proxy

104   for the potential full distribution of ZIKV in the Americas, presenting findings in terms of

105   potential seasonal vs. full-year transmission zones. While that approach has been effectively

106   validated for dengue transmission in mosquitoes, using a model of one disease to represent the

107   potential distribution of another emerging pathogen is only a placeholder, and is particularly

108   concerning given the lack of evidence in our models that ZIKV and dengue have a similar niche

109   breadth. To evaluate the similarity of Zika and dengue, we built another niche model using the

110   dengue occurrence database compiled by Messina *et al.*[18]. Comparing the two niche models

111   reveals that the two niches are significantly different (Schoener's $D = 0.256$; $p < 0.02$; Extended

112   Data Fig. 6). While the two occupy a similar region of global climate space, Zika is more strictly

113 tropical than dengue, occupying regions with higher diurnal temperature fluctuations and

114 seasonality of precipitation (Fig. 2a). Moreover, our future projections for dengue (which

115 strongly agree with previously published ones[19]) show an expansion out of the tropics that is not

116 shared with Zika (Fig. 2, 3). These results call into question the applicability of dengue niche

117 models used to project a significant future range for Zika in North America[6].

118

119 Given the ecological nonequivalence of Zika and dengue, and the occurrence of Zika cases

120 outside our predicted suitable range for the virus, the 2016 Zika outbreak may be in ephemeral

121 rather than stable parts of the Zika transmission niche due to anomalous climatic conditions.

122 Specifically, El Nino Southern Oscillation (ENSO) events drive outbreaks of dengue in the

123 Americas and in Southeast Asia[20], and we conjecture that the 2016 ENSO event may be

124 responsible in large part for the severity of the ZIKV outbreak in North and Central America, a

125 hypothesis also raised by Paz *et al.*[7] in response to Bogoch *et al.*[6]. While wind-dispersed

126 mosquitoes carrying infections can be responsible for the introduction of diseases to new

127 regions[21], reported cases in the United States have all been contracted sexually or while traveling

128 abroad to regions with endemic outbreaks, further supporting the tropical constraint hypothesis.

129 However, the rapid expansion during the current outbreak beyond the boundaries of the stable

130 transmission niche indicates that regions outside our modeled range may support transmission

131 during anomalous periods of climatic flux, but will not necessarily enable naturalization of the

132 pathogen in the future. This highlights one of the most important limitations of this work, as

133 ecological niche models relate occurrence to climate, while disease drivers may operate at the

134 temporal scale of weather.

135

136   While the potential for rare, weather-driven outbreaks should not be overlooked, our models

137   imply that it is premature to expect Zika naturalization as an eventuality in North America.

138   Without more definitive information on the basic biology of Zika, however, the confidence with

139   which niche models can forecast pandemics is limited. In particular, we draw attention to recent

140   evidence suggesting Zika persistence may depend on wildlife reservoirs in addition to human

141   hosts and mosquitoes. Primates have been suggested as the primary candidate clade, because the

142   Zika flavivirus was first isolated in a rhesus macaque in the Zika Forest in Uganda. But as rhesus

143   macaques do not occur on the African continent, and were captive there for inoculation

144   experiments, the primate reservoir hypothesis remains unsupported. A 2015 case of an Australian

145   presumed to have contracted Zika from a monkey bite while traveling in Indonesia, however,

146   indicates that primates may transmit the virus directly[12]. Additionally, antibodies against Zika

147   have been observed in several rodent and livestock species in Pakistan[22], as well as several large

148   mammal species, including orangutans, zebras, and elephants[23]. The potential for any North

149   American wildlife species to play host to Zika is, at the present time, entirely unknown, and the

150   infection of alternate hosts could potentially support new regions of stable transmission.

151

152   From the limited data in existence, we conclude that the global threat of a specifically vector-

153   borne Zika pandemic, though devastating, may be limited to the tropics. However, sexual

154   transmission of Zika infections may still facilitate a significant outbreak in the United States and

155   other previously unsuitable regions, particular under evolutionary processes that select for the

156   most directly transmissible strains of pathogens[24]. A case of sexual transmission in Texas has

157   been suspected in the 2016 outbreak, and two previous reports of likely sexual transmission of

158   ZIKV originate from 2011 and 2015[3,25], though these seem to have been overlooked in most

159   press coverage, which has presented the case of sexual transmission in Texas as a novel facet to

160   the disease. Even if the Zika cases in the United States represent a rare spillover outside of the

161   mosquito-borne viral niche, sexual transmission could create a new, unbounded niche in which

162   the virus could spread. We draw attention to the potential parallels with simian and human

163   immunodeficiency virus (SIV/HIV), for which a sexually transmitted pandemic has

164   overshadowed the zoonotic origin of the disease[26]. With Zika's asymptomatic presentation and

165   the overall confusion surrounding its basic biology and transmission modes, we caution that its

166   potential for a sexually-transmitted global pandemic cannot be overlooked in the coming months.

167

Supplementary Information

169   Supplementary Information is linked to the online version of the paper at

170   www.nature.com/nature.

171

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Author Contributions

177   C.J.C. and E.R.D. collected the data, ran the models and wrote the first draft. All authors edited

178   and approved the final text submitted for review.

179

180   **Author Information**

181   Data presented in the paper are available in Table S1. Reprints and permissions information is

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183   Correspondence and requests for materials should be addressed to C.J.C.

184   (cjcarlson@berkeley.edu)

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239

240 **Methods**

241 Occurrence data for Zika virus was compiled from the literature from studies dating as far back

242 as the original discovery of the virus in Zika Forest, Uganda in 1947. Special attention was paid

243 to correctly attributing cases of travelers to the true source of infection. Locality data was

244 extracted from a set of clinical and survey papers, and georeferenced using a combination of

245 Google Maps for hospitals and the Tulane University GEOLocate web platform for the

246 remainder[1], which allows for the attribution of an uncertainty radius to points only identified to a

247 regional level. Sixty four points were used in the final models presented in our paper after

248 limiting our results to only locations that could be estimated within 75 km (Extended Data: Table

249 S1). To our knowledge, this spatially explicit database is the most inclusive dataset currently in

250 the literature.

251

252 Occurrence data for the other species included in our study were compiled from the literature.

253 For *Aedes africanus*, we used a dataset of 99 points downloaded from the Global Biodiversity

254 Informatics Facility (www.gbif.org). GBIF's coverage of *Aedes aegypti* and *Aedes albopictus*

255 was however deemed to be lacking; occurrences for those species was taken from the previously

256 published work of Kraemer *et al.*[2,3] Messina *et al.*'s database was used for dengue[4], as it has been

257 previously published in *Scientific Data* and used with great success to generate a global

258 distribution model.[5] Both of these datasets were reduced down to point-only data (i.e., polygons

259 of occurrence were excluded), leaving 5,216 points for dengue and 13,992 and 17,280 points for

260 *Ae. aegypti* and *Ae. albopictus* respectively.

261

262   We used the WorldClim data set BIOCLIM at 2.5 arcminute resolution to provide all but one of

263   our climate variables.[6] The BIOCLIM features 19 variables (BIO1-BIO19) that summarize

264   trends and extremes in temperature and precipitation at a global scale. Given the relevance of the

265   normalized difference vegetation index (NDVI) in previous studies of dengue and as a predictor

266   of vector mosquito distributions[7], we downloaded monthly average NDVI layers for each month

267   in 2014 from the NASA Earth Observations TERRA/MODIS data portal[8], and averaged those

268   twelve layers to provide a single mean NDVI layer. Species distribution models were executed

269   using the BIOMOD2 package in R 3.1.1, which produces ensemble species distribution models

270   using ten different methods: general linear models (GLM), general boosted models or boosted

271   regression trees (GBM), general additive models (GAM), classification tree analysis (CTA),

272   artificial neural networks (ANN), surface range envelope (SRE), flexible discriminant analysis

273   (FDA), multiple adaptive regression splines (MARS), random forests (RF), and maximum

274   entropy (MAXENT).[9] Models were run individually for Zika (ZIKV), dengue (DENV), *Ae.*

275   *aegypti, Ae. albopictus,* and *Ae. africanus.*

276

277   To address colinearity in the environmental variable set, we produced a correlation matrix for

278   our 20 variables, and identified each pair with a correlation coefficient > 0.8. For each species,

279   we ran a single ensemble model with all ten methods and averaged the variable importance for

280   our 20 predictors across the methods (See Table S2-S6). In each pair we identified the variable

281   with the greater contribution, and we produced species-specific reduced variable sets used in the

282   final published models by eliminating any covariates that universally performed poorer than their

283   pairmate. Based in this criteria, we excluded the following variables for each species to reduce

284   colinearity:

285   •   ZIKV: BIO5, BIO9, BIO12, BIO14

286   •   DENV: BIO3, BIO5, BIO12, BIO17

287   •   *Ae. aegypti:* BIO6, BIO8, BIO12, BIO17

288   •   *Ae. africanus:* BIO5, BIO6, BIO12, BIO17

289   •   *Ae. albopictus:* BIO8, BIO9, BIO16, BIO17

290   The AUC of every model run with reduced variable sets is presented in Table S7. We found no

291   significant correlation between NDVI and any individual BIOCLIM variable, so NDVI was

292   included in every model of current distributions. We ran five iterations of each reduced variable

293   set model and eliminated any prediction methods from the ensemble with an AUC of lower than

294   0.95, so that the final model had only included the best predicting models. This was found to

295   only leave the RF method for DENV, so a cutoff of 0.9 was applied in that case, to keep the

296   ensemble approach constant across datasets. The final models were run with the following

297   methods with ten iterations using an 80/20 training-test split in the final presentation:

298   •   ZIKV: GLM, GBM, GAM, ANN, FDA, MARS, RF

299   •   DENV: GLM, GBM, GAM, FDA, MARS, RF, MAXENT

300   •   *Ae. aegypti:* GLM, GBM, GAM, CTA, ANN, FDA, MARS, RF

301   •   *Ae. africanus:* GLM, GBM, GAM, CTA, ANN, FDA, MARS, RF

302   •   *Ae. albopictus:* GLM, GBM, GAM, CTA, FDA, MARS, MAXENT, RF

303   The importance of variables of the reduced model set for each are presented in Table S8-S12.

304

305   To project the distribution of the species under climate change, we reran each model with the

306   previously chosen method and variable sets but excluding NDVI, for which we did not feel we

307   could appropriately simulate future values. BioClim forecasts were taken from WorldClim using

308   the Hadley Centre Global Environmental Model v. 2 Earth System climate forecast (HadGEM2-

309   ES) predictions for representative climate pathway 8.5 (RCP85), which, within that model,

310   represents a worst case scenario for carbon emissions and climate warming.[10] All five species'

311   models were retrained on current climate data and projected onto forecasts for the year 2050, the

312   results of which are shown in Figure 3. Finally, to compare the niche of dengue and Zika, we

313   used the R package ecospat, which uses principal component analysis to define the position of

314   species' ecological niche relative to background environmental variation[11,12]. We excluded BIO5

315   and BIO12 from our analysis as they were included in neither of the final models for the

316   diseases; niche similarity tests were run 100 times with 100 iterations each. The results of that

317   analysis are presented in Figure S1, which shows both the one-directional similarity test and the

318   bidirectional equivalence test.

319

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347

348   **Figures and Tables**

349

350   **Figure 1.** The global distribution of case reports of Zika virus (1947 to February 2016) broken

351   down by country (blue shading) and an ensemble niche model built from occurrence data (red

352   shading). Our model predicts occurrence in part of every shaded country; it is clear that

353   displaying cases at country resolution overstates the distribution of the virus, especially in the
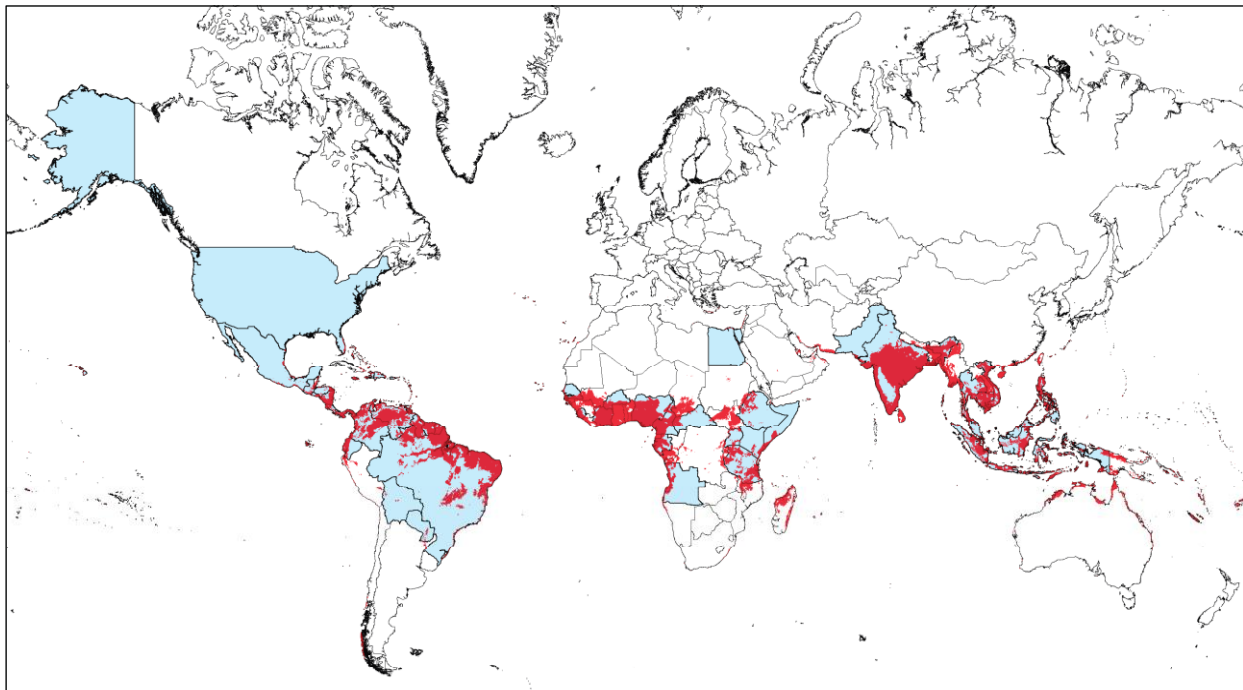
354   Americas (for example, Alaska).

355

356

357   **Figure 2.** The ecological niche of Zika and dengue in principal component space (a). Solid and

358   dashed lines are 100%/50% boundaries for all environmental data; principal component vectors

359   are shown in the bottom right. The red highlighted arrow shows the direction of mean diurnal

360   temperature range and precipitation seasonality. The differences in their niches are evident in the

361   current (b,c) and future (d,e) projections of our niche models for dengue (b,d) and Zika (c,e).
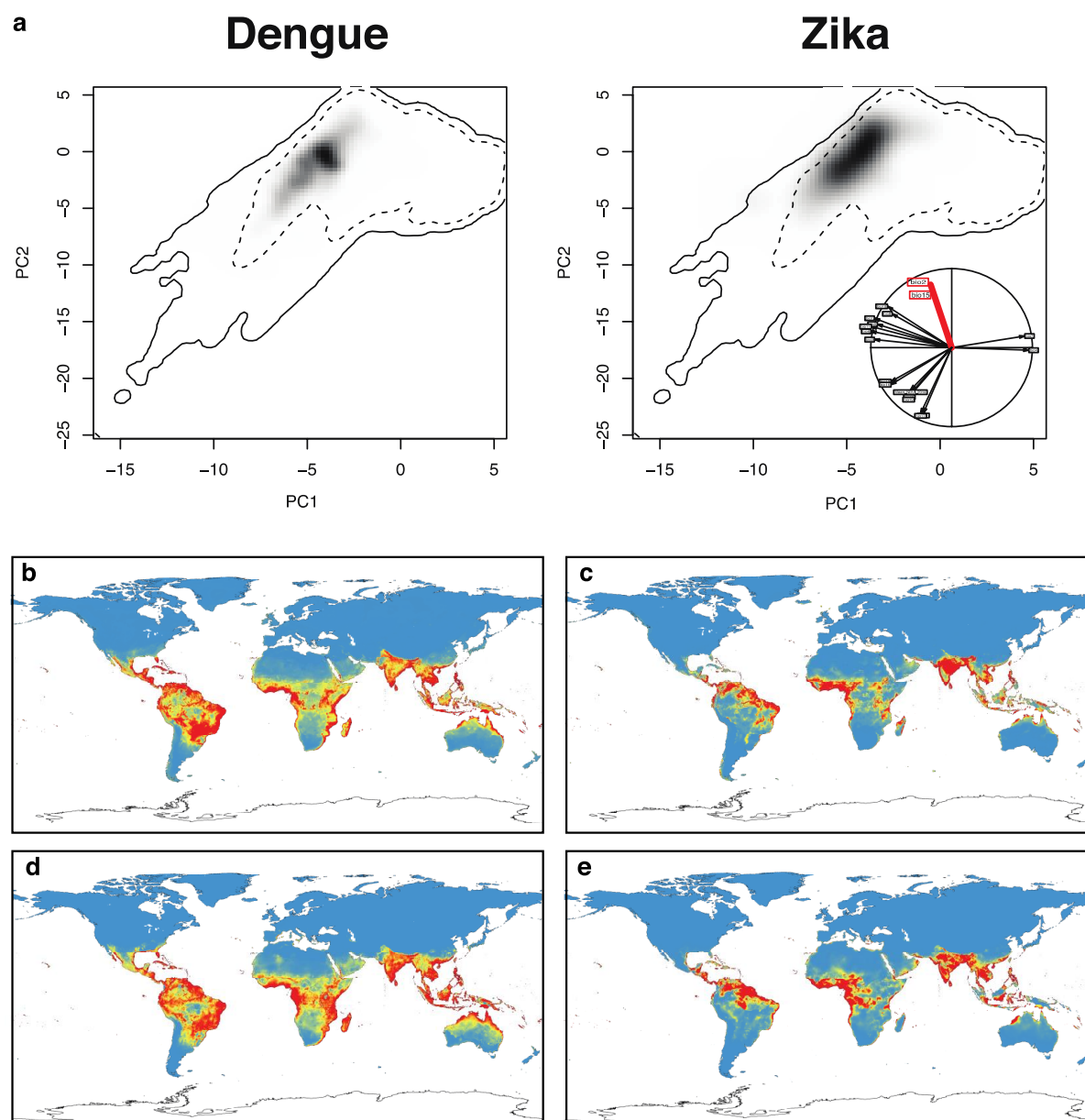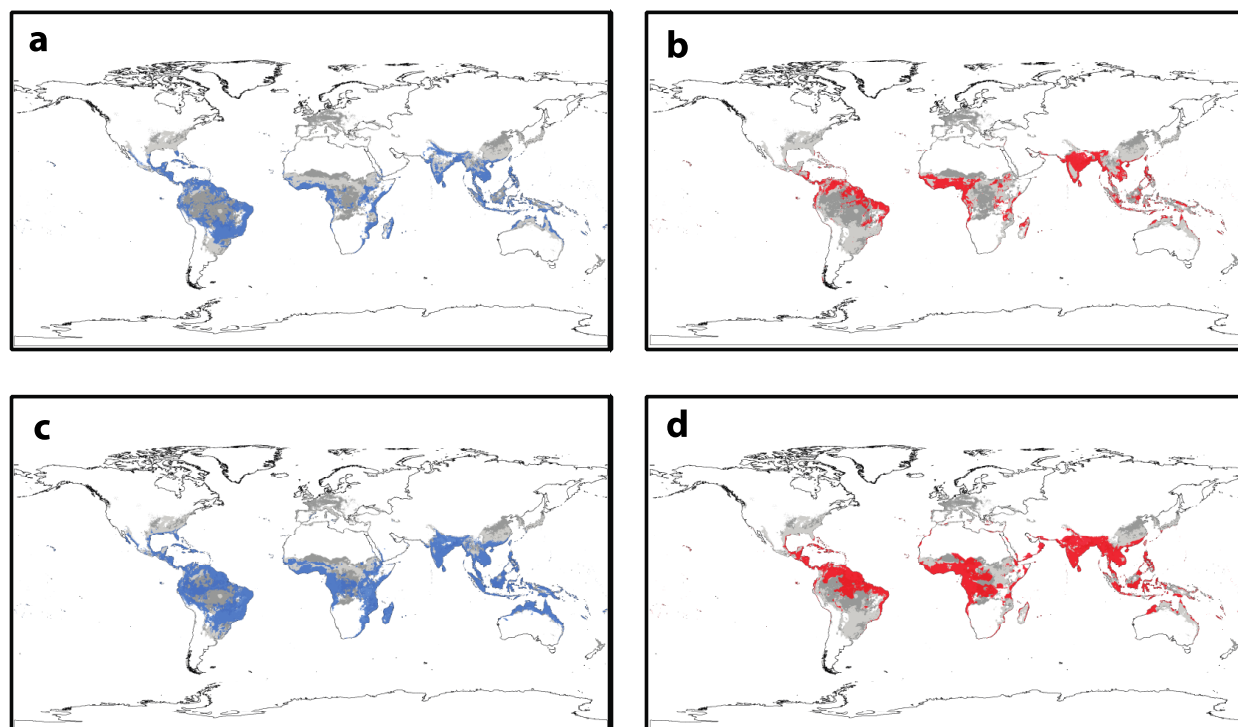

362

363 **Figure 3.** The estimated distribution of Zika (red) and dengue (blue) based on current (a, b) and

364 2050 climate projections (c, d), compared against the current (light grey) and future distribution

365 of all three mosquito vectors (a-d).

366

367

368   **Extended Data:**

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370   **Extended Data Figure 1 |** Final ensemble model for Zika virus

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372   **Extended Data Figure 2 |** Final ensemble model for dengue fever

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374   **Extended Data Figure 3 |** Final ensemble model for *Aedes aegypti*

375

376   **Extended Data Figure 4 |** Final ensemble model for *Aedes africanus*

377

378   **Extended Data Figure 5 |** Final ensemble model for *Aedes albopictus*

379

380   **Extended Data Figure 6 |** Niche overlap between ZIKV and DEV