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An ecological assessment of the pandemic threat of Zika virus

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Keywords

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

23 **Summary**

24 The current outbreak of Zika virus poses a threat of unknown magnitude to human health¹. 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 uncertain²⁻⁴. 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 time⁷.
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.

44 **Main Text**

45 Following a twenty-fold upsurge in microcephalic newborns in Brazil tentatively linked to Zika
46 virus (ZIKV), the World Health Organization has declared an international health emergency¹.
47 Despite being profiled for the first time in 1947⁸, Zika remains poorly characterized at a global
48 scale. Thus, the present pandemic expansion in the Americas poses a threat of currently unknown
49 magnitude. Closely related to dengue fever, Zika conventionally presents as a mild infection,
50 with 80% of cases estimated to be asymptomatic⁹. The cryptic nature of infection has resulted in
51 sporadic documentation of the disease and rarely includes spatially explicit information beyond
52 the regional scale¹⁻⁴. This greatly limits the confidence with which statistical inferences can be
53 made about the expansion of the virus. With an estimated 440,000-1,300,000 cases in Brazil in
54 2015⁹, and continuing emergence of new cases in Central America and, most recently, the United
55 States, assessing the full pandemic potential of the virus is an urgent task with major
56 ramifications for global health policy.

57
58 Current evidence portrays the global spread of ZIKV as a basic diffusion process facilitated by
59 human and mosquito movement, a hypothesis supported by the frequency of infected traveler
60 case studies in the Zika literature¹⁰⁻¹³. Tracing phylogenetic and epidemiological data has
61 revealed the expansion of ZIKV has occurred in a stepwise process through the South Pacific,
62 moving the disease from Southeast Asia into French Polynesia and the Philippines, and
63 subsequently to Easter Island¹⁻⁴. ZIKV is conjectured to have dispersed into South America as
64 recently as three years ago from the last of those locations, and the virus is presumed not to be at
65 a biogeographic equilibrium in the Americas. With cases in the ongoing outbreak in Colombia,
66 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 uncertain⁷.

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 fever¹⁴), 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 model¹⁵ 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 fever¹⁶). 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 niche¹⁷ (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 ones¹⁹) 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 America⁶.

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 Asia²⁰, 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 regions²¹, 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 directly¹². Additionally, antibodies against Zika
147 have been observed in several rodent and livestock species in Pakistan²², as well as several large
148 mammal species, including orangutans, zebras, and elephants²³. 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 pathogens²⁴. 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 disease²⁶. 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

168 **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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175

176 **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
182 available at www.nature.com/reprints. The authors declare no competing financial interests.

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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 remainder¹, 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 dengue⁴, 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 distributions⁷, we downloaded monthly average NDVI layers for each month
267 in 2014 from the NASA Earth Observations TERRA/MODIS data portal⁸, 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

320 **References**

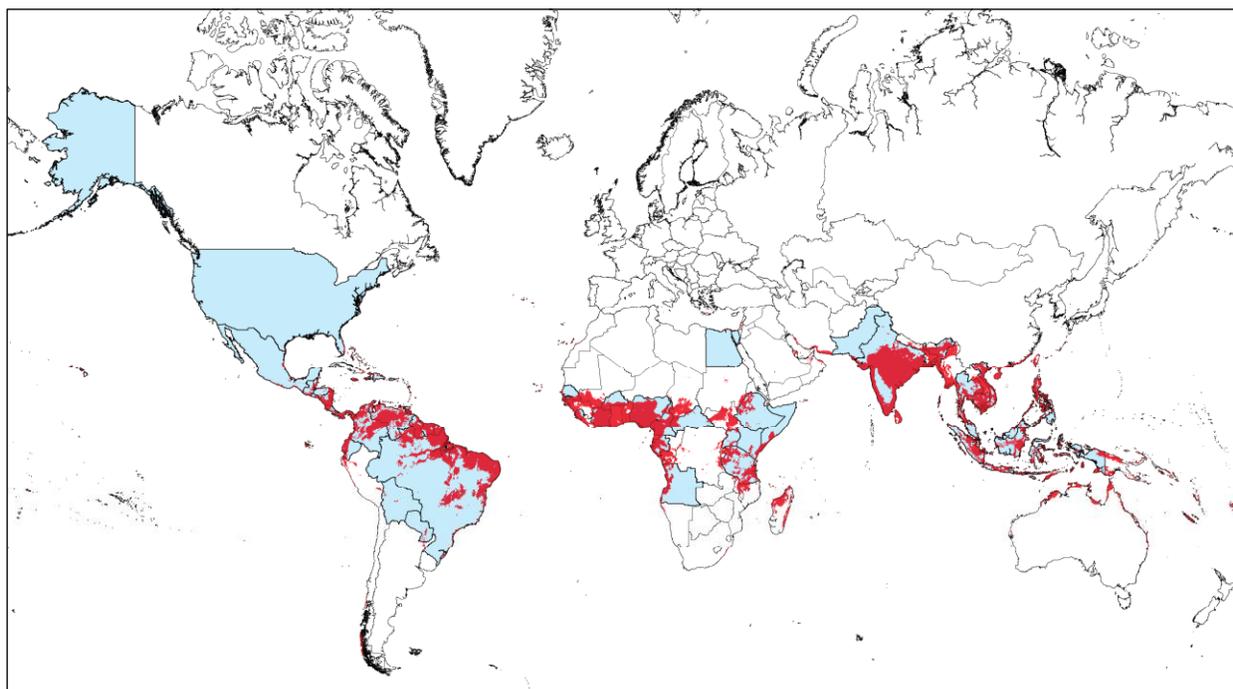
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348 **Figures and Tables**

349

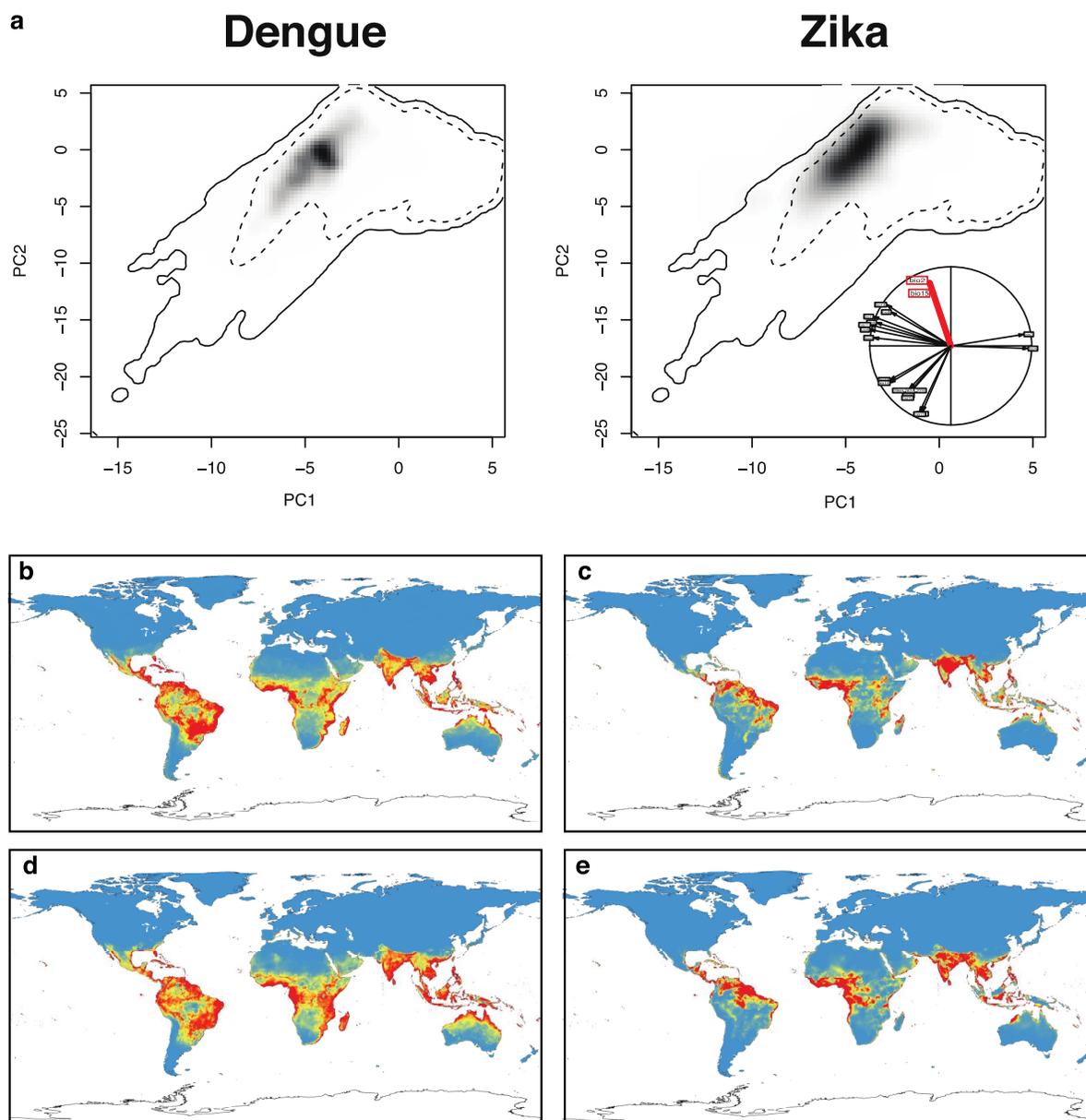
350 **Figure 1.** The global distribution of case reports of Zika virus (1947 to February 2016) broken
351 down by country (blue shading) and an ensemble niche model built from occurrence data (red
352 shading). Our model predicts occurrence in part of every shaded country; it is clear that
353 displaying cases at country resolution overstates the distribution of the virus, especially in the
354 Americas (for example, Alaska).



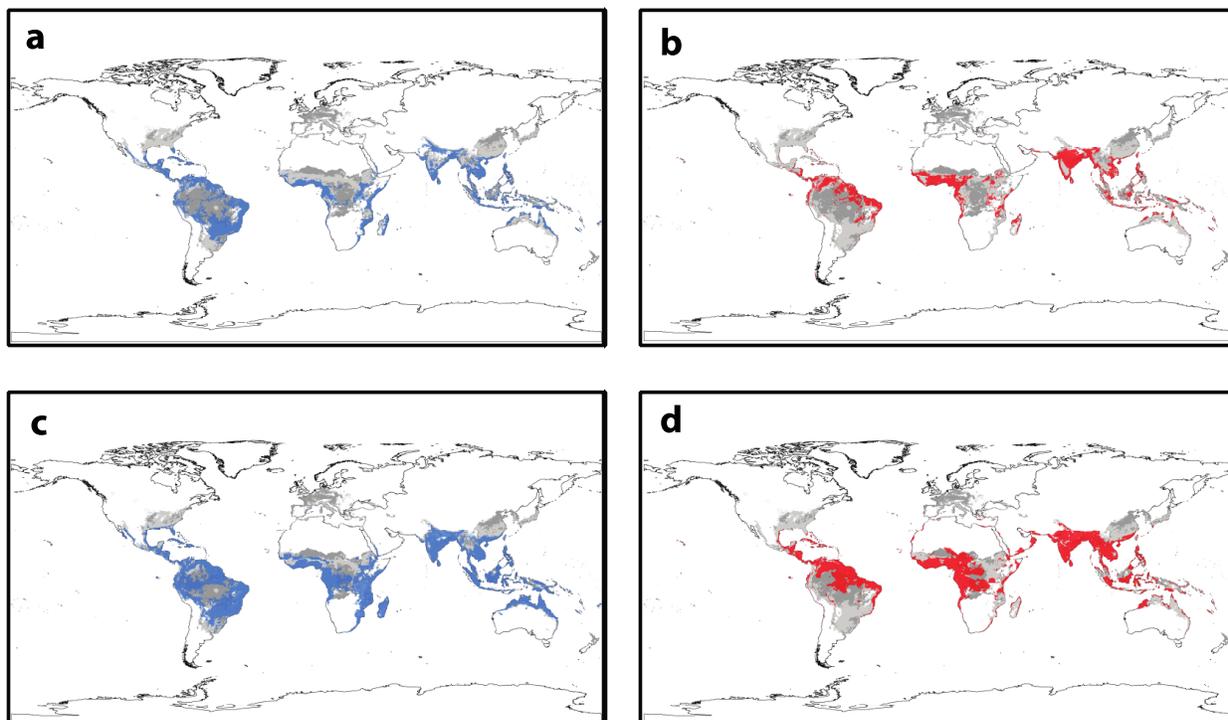
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357 **Figure 2.** The ecological niche of Zika and dengue in principal component space (a). Solid and
358 dashed lines are 100%/50% boundaries for all environmental data; principal component vectors
359 are shown in the bottom right. The red highlighted 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).



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:**

369

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

373

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