1   **Title**

2   Predictors of human-infective RNA virus discovery in the United States, China and Africa,

3   an ecological study

4   **Authors**

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Abstract

Background The variation in the pathogen type as well as the spatial heterogeneity of predictors make the generality of any associations with pathogen discovery debatable. Our previous work confirmed that the association of a group of predictors differed across different types of RNA viruses, yet there have been no previous comparisons of the specific predictors for RNA virus discovery in different regions. The aim of the current study was to close the gap by investigating whether predictors of discovery rates within three regions—the United States, China and Africa—differ from one another and from those at the global level.

Methods Based on a comprehensive list of human-infective RNA viruses, we collated published data on first discovery of each species in each region. We used a Poisson boosted regression tree (BRT) model to examine the relationship between virus discovery and 33 predictors representing climate, socio-economics, land use, and biodiversity across each region separately. The discovery probability in three regions in 2010–2019 was mapped using the fitted models and historical predictors.

Results The numbers of human-infective virus species discovered in the United States, China and Africa up to 2019 were 95, 80 and 107 respectively, with China lagging behind the other two regions. In each region, discoveries were clustered in hotspots. BRT modelling suggested that in all three regions RNA virus discovery was best predicted by land use and socio-economic variables, followed by climatic variables and biodiversity, though the relative importance of these predictors varied by region. Map of virus discovery probability in 2010–2019 indicated several new hotspots outside historical high-risk areas. Most new virus species since 2010 in each region (6/6 in the United States, 19/19 in China, 12/19 in Africa) were discovered in high risk areas as predicted by our model.

35   ***Conclusions*** The drivers of spatiotemporal variation in virus discovery rates vary in different

36   regions of the world. Within regions virus discovery is driven mainly by land-use and socio-

37   economic variables; climate and biodiversity variables are consistently less important

38   predictors than at a global scale. Potential new discovery hotspots in 2010–2019 are

39   identified. Results from the study could guide active surveillance for new human-infective

40   viruses in local high risk areas.

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Introduction

44 RNA viruses are the primary cause for emerging infectious diseases with epidemic potential,

45 given that they have high rate of evolution and high capacity to adapt to new hosts

46 (Woolhouse et al., 2016). In recent decades, infectious diseases caused by severe acute

47 respiratory syndrome coronavirus (SARS-CoV), Middle East respiratory syndrome

48 coronavirus (MERS-CoV), Bundibugyo Ebola virus and SARS-CoV-2 present major threats

49 to the health and welfare of humans (Albarino et al., 2013; Ksiazek et al., 2003; Mackay et al.,

50 2015; World Health Organisation, 2020). Detection of formerly unknown human-infective

51 RNA viruses in the earliest stage after the emergence are essential for controlling the

52 infections they cause. Measures to implement early detection include not only advanced

53 diagnostic techniques (Lipkin et al., 2013), but more importantly the idea where to look for

54 them (so-called hotspots) (Morse et al., 2012).

55 Socio-economic, environmental, and ecological factors related to both virus natural history

56 and research effort have been found to affect the discovery of emerging RNA viruses (Jones

57 et al., 2008; Morse et al., 2012; Rosenberg, 2015; Zhang et al., 2020). However, these factors

58 are highly spatially heterogeneous, making the generality of any associations with discovery

59 debatable. For example, the United States, China, and Africa have experienced different rates

60 of socio-economic, environmental, and ecological changes in the last one hundred years. The

61 United States has always had better resources to discover new viruses. For example, the

62 Rockefeller Foundation—a U.S. foundation—supported the discovery of 23 arboviruses in

63 Latin America, Africa, and India in 1951–1969 (Rosenberg, 2015). China has seen urban land

64 coverage more than double and GDP per capita increase by seven times since the 1980s

65 (Ritchie, 2018; Roser, 2013). Nine out of 223 human-infective RNA viruses have been

66 originally discovered in China, and all were discovered after 1982 (Zhang et al., 2020). In

4

67   contrast, effective surveillance is challenging in less developed regions such as large parts of

68   Africa given resource constraints (Petti et al., 2006).

69   There have been no previous comparisons of the specific predictors for RNA virus discovery

70   in different regions. In this study, we applied a similar methodology from our previous study

71   of global patterns of discovery of human-infective RNA viruses (Zhang et al., 2020) to

72   investigate whether predictors of discovery rates within three regions—the United States,

73   China and Africa—differ from one another and from those at the global level, using three

74   new virus discovery data sets. We also mapped discovery probability in three regions in

75   2010–2019 using the fitted models and historical predictors. According to findings from our

76   previous study (Zhang et al., 2020), the main predictors for virus discovery at the global scale

77   were GDP-related. This suggests that the patterns of virus discovery we have identified may

78   have been largely driven by research effort rather than the underlying biology. In this study,

79   by focusing on more restricted and homogenous regions where the research effort is less

80   variable, we expected to identify predictors more associated with virus biology.

81   **Materials and Methods**

82   *Data sets of human-infective RNA viruses in three regions*

83   We performed an ecological study, and the subject of interest is each human-infective RNA

84   virus species. With reference to a full list of human-infective RNA virus species (Zhang et al.,

85   2020), we geocoded the first report of each in humans in the United States, China, and Africa

86   separately. The latest version as of 31 December 2019 included 223 species (**Table 1S**), with

87   *Human torovirus* abolished and a new species—*Heartland banyangvirus*—added by ICTV in

88   2018 (International Committee on Taxonomy of Viruses, 2018). We defined discovery

89   location as where the initial human was exposed to/infected with the virus, as suggested in

90   the first report of human infections from peer-reviewed literature.

91   We followed the same search terms, databases searched, and inclusion or exclusion criteria as

92   our global data set for data collection (Woolhouse et al., 2018). Reference databases included

93   PubMed, Web of Science, Google Scholar, and Scopus. Two Chinese database [i.e. China

94   National Knowledge Infrastructure (CNKI) and Wanfang Data] were also searched when

95   collecting data for China. Reference lists of relevant studies and reviews were also checked

96   manually to find potential earlier discovery papers. The following key words were used for

97   the retrieval: virus full name or abbreviations or virus synonyms; and human* or person* or

98   case* or patient* or worker* or infection* or disease* or outbreak* or epidemic*; and region

99   name (Chin* or Taiwan or Hong Kong or Macau; United States or US or USA or America*;

100   Africa* or all African country names). Virus synonyms and abbreviations include early

101   names used in the discovery paper and all subtypes provided by the ICTV 10th report (*Full*

102   *ICTV Online (10th) Report: https://talk.ictvonline.org/ictv-reports/ictv_online_report/*).

103   Evidence which met the following criteria from peer-reviewed literatures were included: (a)

104   Diagnostic methods for RNA virus infection in humans were clearly described, through either

105   viral isolation or serological methods; (b) Specific virus species name or subtypes falling

106   under that species were clearly provided; (c) Both natural infection and iatrogenic or

107   occupational infections were accepted. Evidence which met the following criteria were

108   excluded: (a) Uncertain species due to cross-reactivity with related viruses; (b) Diagnostic

109   methods for virus infection were not specified; (c) Description of clinical symptoms or

110   pathogenicity were not considered as human infection of one certain virus species; (d) Report

111   of '[virus name]-like' or 'potential [virus name] infections'; (d) Intentional infections

112   including experimental inoculation or vitro infections; (e) Non-peer-reviewed literature,

113   including media reports, thesis, or unpublished data. Literature selection was performed by

114   two individuals independently and discrepancies were resolved by discussion with a third

115   individual.

116   All locations were geolocated as precisely as possible using methods from our previous paper

117   (Zhang et al., 2020). For each region, a polygon was created for those locations at

118   administrative level 3 (county for the United States; city for China; for Africa, it varies

119   between different countries) and above. Details of data types for virus discovery database in

120   three regions was summarised in **Table 2S**. The majority of discovery locations in the United

121   States and Africa involved point data, while in China the majority involved polygon data at

122   province level. A bootstrap resampling procedure was developed for polygon data covering

123   more than one grid cell (details below). Discovery date of human infection was defined as the

124   publication year in the scientific literature.

125   *Spatial covariates*

126   As for our global analysis (Zhang et al., 2020), a suite of global gridded climatic, socio-

127   economic, land use, and biodiversity variables (n=33) postulated to affect the spatial

128   distribution of RNA virus discovery were compiled, each at a resolution of 0.5°/30" (except

129   university count having a resolution at country level for Africa and state/province for the

130   United States and China). Data for the United States, China and Africa were extracted by

131   restricting the coordinates within each region. The definition, original resolution, and source

132   of each variable were the same as our previous paper (Zhang et al., 2020). All predictors were

133   aggregated from their original spatial resolution to 1°×1° resolution; data for climatic

134   variables, population, GDP, and land use data without full temporal coverage were

135   extrapolated back to 1901; both following methods from our previous paper (Zhang et al.,

136   2020).

137   *Boosted regression trees modelling*

138   We used Poisson boosted regression trees (BRT) model to examine the relationship between

139   discovery of RNA virus and 33 predictors for each 1° resolution of grid cell across each

7

140 region separately, following codes from our previous study (Zhang et al., 2020) and one

141 previous paper (Allen et al., 2017). As a tree-based learning method, BRT model can

142 automatically capture complex relationships and interactions between variables, and also can

143 well account for spatial autocorrelation within the data (Crase et al., 2012). We compared

144 Moran's I values of the raw virus data and the model residuals to estimate the ability of the

145 BRT model to account for spatial autocorrelation (Cliff et al., 1981). In order to minimise the

146 effect of spatial uncertainty of virus discovery data, we performed 1000 times bootstrap

147 resampling for those discovery locations reported as polygons. We assumed each grid cell in

148 the polygon has the equal chance to be selected, and for each virus record we selected one

149 grid cell randomly from the polygon for each subsample. A ratio of 1:2 for presence to

150 absence constituted each subsample, i.e., for each grid cell with virus discovery, two grid

151 cells with no discovery were randomly selected from 'virus discovery free' areas at all time

152 points within the region. Take the United States as an example, each subsample included 95

153 grid cells with virus discovery and 190 with no virus discovery. We then matched the virus

154 data with all predictors (using the nearest decade for time-varying predictors). We assumed

155 that the virus count in any given grid cell in each decade followed a Poisson distribution, and

156 we calculated the virus discovery count in each grid cell by decade as the response variable.

157 All BRT models were fitted in R v. 3.6.3, using packages dismo and gbm. BRT models

158 require the user to balance three parameters including tree complexity, learning rate, and bag

159 fraction. Tree complexity reflects the order of interaction in a tree; learning rate shrinks the

160 contribution of each tree to the growing model; bag fraction specifies the proportion of data

161 drawn from the full training data at each step. We set these parameters as recommended from

162 Elith et al (Elith et al., 2008), and make sure each resampling model contained at least 1000

163 trees. BRT models identified the final optimal number of trees in each model using a 10-fold

164 cross validation stagewise function (Elith et al., 2008). The three parameter values of the

165   optimal model as well as the mean optimal number of trees across 1000 replicate models for

166   all three regions were summarised in **Table 3S**.

167   By fitting 1000 replicate BRT models, the relative contribution plots and partial dependence

168   plots with 95% quantiles were plotted. We defined variables with a relative contribution

169   greater than the mean (3.03%) as influential predictors in all three regions (Shearer et al.,

170   2018). The partial dependence plots depict the influence of each variable on the response

171   while controlling for the average effects of all the other variables in the model. The map of

172   virus discovery probability across each region in 2010–2019 was derived from the means of

173   the predictions of 1000 replicate models, using values of the 33 predictors in 2015. In order to

174   show discovery hotspots, we converted the prediction map of virus count to a map of

175   probability.

176   Two statistics were calculated to evaluate the model's predictive performance: a) the

177   deviance of the bootstrap model (Elith et al., 2008), b) infraclass correlation coefficient (ICC)

178   calculated from 50 rounds of ten-fold cross-validation, by following methods from our

179   previous paper (Zhang et al., 2020). For the ten-fold cross-validation, we selected 50 data sets

180   randomly from the 1000 bootstrapped subsamples. We took the first data set and divided into

181   ten subsets. For each round of ten-fold cross-validation, the unique combinations of 9 subsets

182   constituted the training sets and were used to fit models, and the remaining one was used as a

183   test set to evaluate the predictive performance of the model. We repeat the same process as

184   above for the remaining 49 data sets. One intraclass correlation coefficient (ICC) was

185   calculated from each round of validation and the median with 95% quantiles across all 50

186   rounds was calculated. The ICC varies between 0 and 1, with an ICC of less than 0.40

187   representing a poor model, 0.40–0.59 representing a fair model, 0.60–0.74 representing a

188   good model, and 0.75–1 representing an excellent model (Cicchetti, 1994).

189   Exploratory subgroup analyses (distinguishing viruses firstly discovered in regions and those

190   that had been discovered elsewhere in the world) were performed. We used the same BRT

191   modelling approach as we described above, and relative contribution of each predictor was

192   calculated for each subgroup. We were unable to perform subgroup analysis for China

193   because only 9 human-infective RNA viruses have been firstly discovered in it, and BRT

194   model cannot be fitted to a sample as small as 9.

195   The R software, version 3.6.3 (R Foundation for Statistical Computing, Vienna, Austria) was

196   used for all statistical analyses. All maps were visualised by using ArcGIS Desktop 10.5.1

197   (Environmental Systems Research Institute).

198   **Results**

199   The numbers of human-infective virus species discovered in the United States, China and

200   Africa up to October 2019 were 95, 80 and 107 respectively (**Table 1S**). Most first

201   discoveries have been in eastern United States (especially in areas around Maryland,

202   Washington, D.C., and New York), eastern China (developed cities including Beijing, Hong

203   Kong, Shanghai, and Guangzhou), and southern and central Africa (Pretoria and

204   Johannesburg, South Africa; Borno State and Ibadan, Nigeria) (**Figure 1**). A total of 60 virus

205   species were previously reported in all three regions, and 27, 12, 37 species were only found

206   in the United States, China, and Africa respectively (**Figure 2**). In all three regions, smaller

207   proportions of viruses were vector-borne [United States: 23.2% (22/95); China: 21.3%

208   (17/80); Africa: 27.1% (29/107)] and strictly zoonotic [United States: 30.5% (29/95); China:

209   16.3% (13/80); Africa: 33.6% (36/107)], compared to large proportions for both virus types at

210   the global scale [vector-borne: 41.7% (93/223) and strictly zoonotic: 58.7% (131/223)]

211   (**Figure 2**). The 60 shared species were also disproportionally vector-borne [11.7% (7/60)]

212   and strictly zoonotic [7% (4/60), **Figure 2**].

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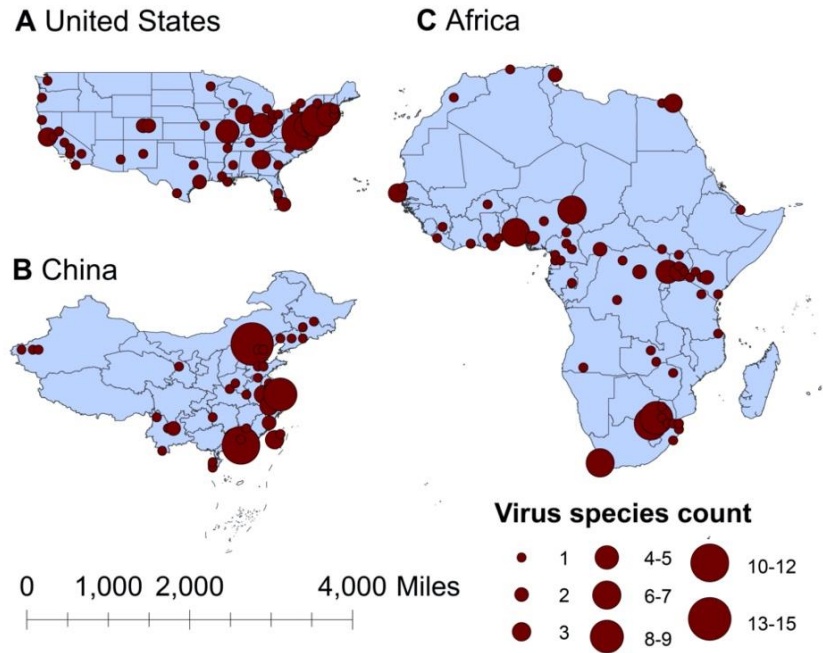
Figure 1 Spatial distribution of human-infective RNA virus discovery in three regions, 1901–2019. A, United States. B, China. C, Africa. Red dots represent discovery points or centroids of polygons, with the size representing the cumulative virus species count.

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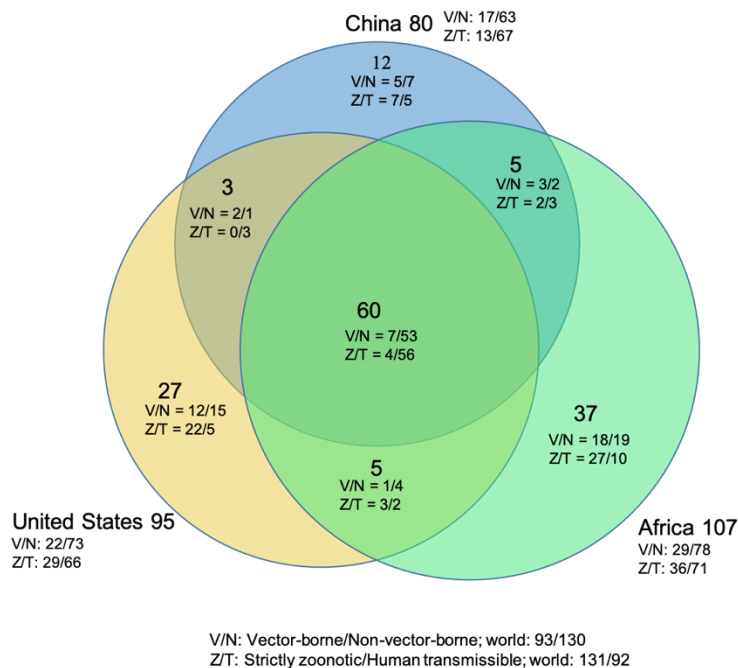
Figure 2 Shared human-infective RNA virus species count in three regions. Under/By the species count the ratios of vector-borne (V) to non-vector-borne (N) viruses and strictly zoonotic (Z) to human transmissible (T) viruses were shown.

11

221   The discovery curves for the United States and Africa have seen a broadly similar pattern,

222   with China lagging behind these two regions (**Figure 3**). In comparison with the world, the

223   median time lag of the virus discovery was 0 [interquartile range (IQR): 2.5], 12 (IQR: 29.5)

224   and 2 (IQR: 10.5) years in the United States, China and Africa, respectively (**Figure 1S**). In

225   China, the time lag was noticeably shorter for viruses discovered after 1975 [before 1975: a

226   median lag of 30.5 (IQR: 30.5) years; after 1975: 2.5 (IQR: 7) years, p value of Wilcoxon

227   rank sum test < 0.001].
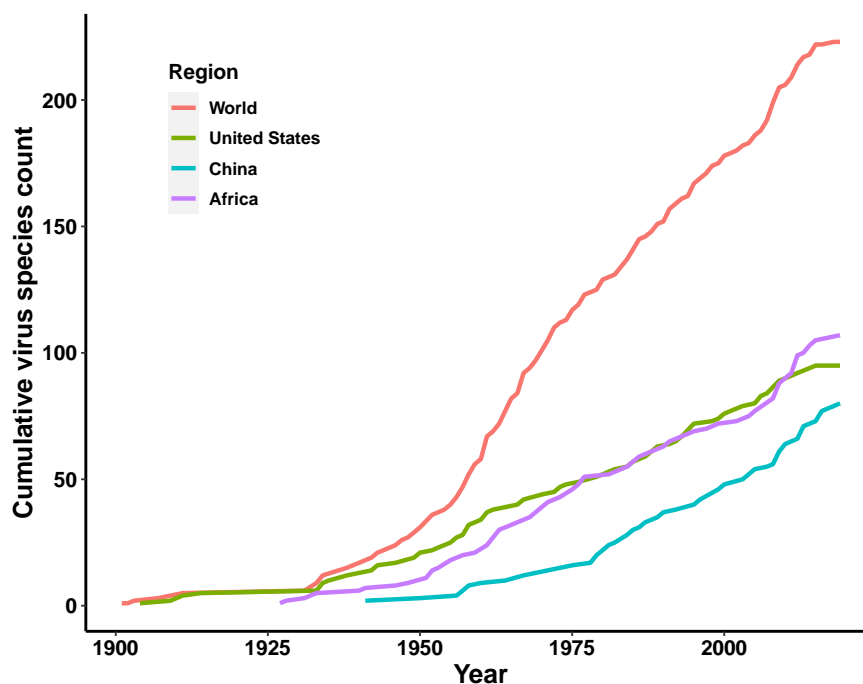
228

229   **Figure 3 Discovery curve of human-infective RNA virus species in three regions and the world**

230   In the United States, six variables including three predictors related to land use [urbanized

231   land: relative contribution of 35.8%, urbanization of cropland (i.e. the percentage of land area

232   change from cropland to urban land): 8.0%, growth of urbanized land: 4.1%], two socio-

233   economic variables (GDP growth: 10.0%; GDP: 5.7%), and one climatic variable (diurnal

234   temperature change: 4.9%) were identified as important predictors for discriminating between

235   locations with and without virus discovery (**Figure 4A**). The partial dependence plots shown

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236   in **Figure 2S** suggested non-linear relationships between the probability of virus discovery

237   and most predictors. All important predictors presented a positive trend over narrow ranges at

238   lower values.

239   In China, twelve variables including four socio-economic variables (GDP: 12.7%, university

240   count: 7.5%, GDP growth: 4.6%, population growth: 4.4%), five predictors involving land

241   use [pasture: 8.3%, urbanized land: 8.1%, vegetation: 5.8%, cropland: 5.3%, urbanization of

242   secondary land (the percentage of land area change from secondary land to urban land;

243   secondary land is natural vegetation that is recovering from previous human disturbance):

244   3.3%], and three climatic variables (maximum precipitation: 4.5%, precipitation change:

245   3.8%, diurnal temperature range: 3.3%) were identified as important predictors for

246   discriminating between locations with and without virus discovery (**Figure 4B**). GDP,

247   urbanized land, university count, vegetation, GDP growth, maximum precipitation,

248   population growth, and urbanization of secondary land presented a positive trend over narrow

249   ranges at lower levels; pasture, cropland, precipitation change, and diurnal temperature range

250   had non-monotonic/ negative impacts, with highest risks at lower values (**Figure 3S**).

251   In Africa, ten variables including two socio-economic variables (GDP growth: 21.2%, GDP:

252   13.0%), seven predictors related to land use (urbanized land: 9.4%, growth of cropland area:

253   5.6%, urbanization of cropland: 5.5%, growth of urbanized land: 5.1%, urbanization of

254   pasture: 3.8%, vegetation, 3.7%, cropland: 3.2%), and one biodiversity variable (mammal

255   species richness: 3.1%) were identified as important predictors for discriminating between

256   locations with and without virus discovery (**Figure 4C**). All important predictors presented a

257   positive trend over narrow ranges at lower positive values, except mammal species over a

258   large range (**Figure 4S**).

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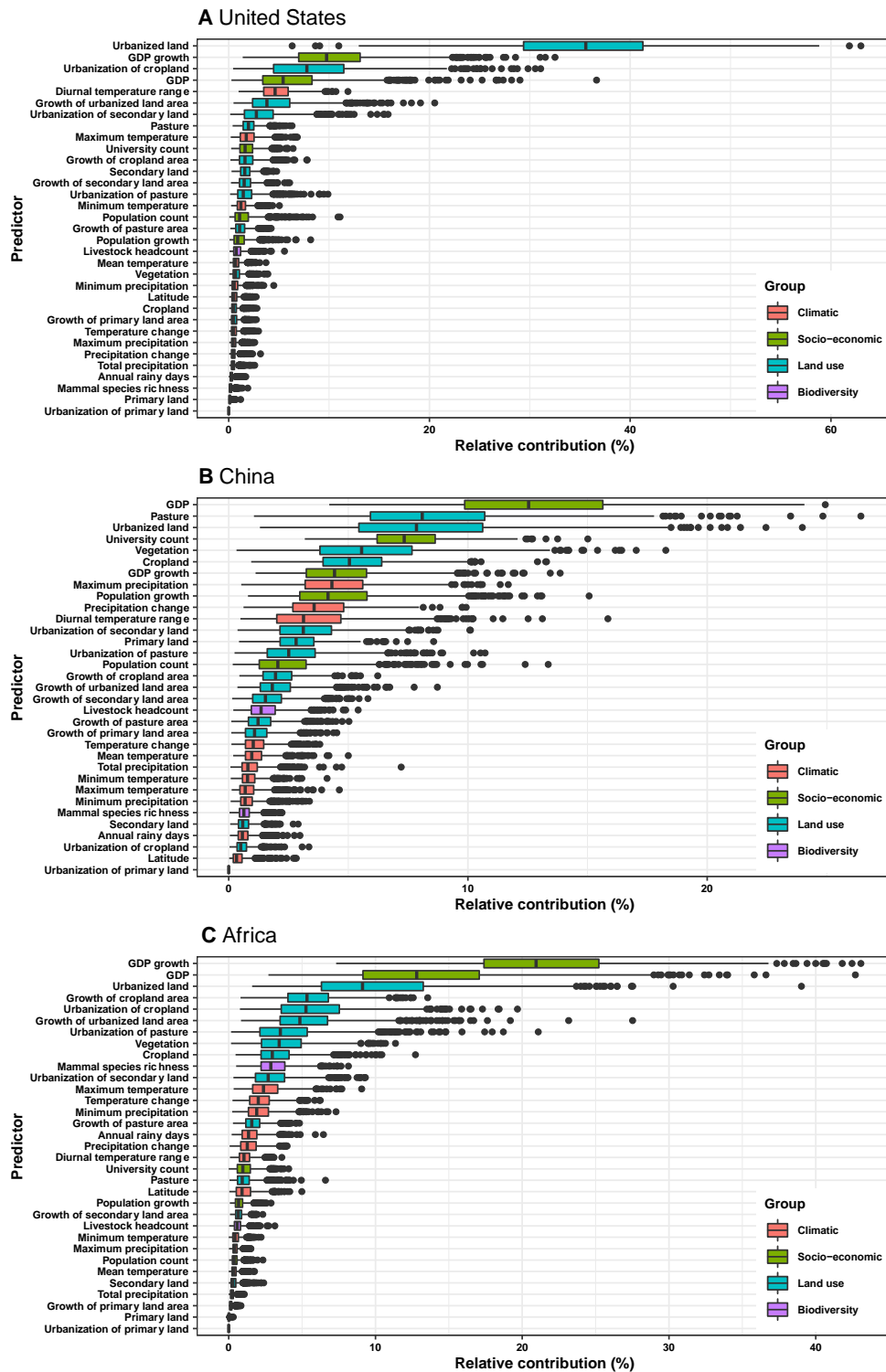
Figure 4 Relative contribution of predictors to human-infective RNA virus discovery in three regions. A, United States. B, China. C, Africa. The boxplots show the median (black bar) and interquartile range (box) of the relative contribution across 1000 replicate models, with whiskers indicating minimum and maximum and black dots indicating outliers.

264   Our BRT models reduced Moran's I value below 0.15 in all three regions (**Figure 5S**),

265   suggesting that BRT models with 33 predictors have adequately accounted for spatial

266   autocorrelations in the raw virus data in all three regions. The model validation statistics for

267   each region are shown in **Table 4S**. Combining these measures, our BRT model predictions

268   range from fair to good (Cicchetti, 1994).

269   In all three regions, human-infective RNA virus discovery was best predicted by land use and

270   socio-economic variables, followed by climatic variables and biodiversity (**Figure 5**),

271   whereas virus discovery was more associated with climatic variables and biodiversity at the

272   global level. The comparison between three regions showed that: climatic variables

273   contributed most to the discovery of human-infective RNA viruses in China; land use

274   contributed most to the discovery in the United States; socio-economic variables and

275   biodiversity contributed most to the discovery in Africa and least to discovery in the United

276   States.
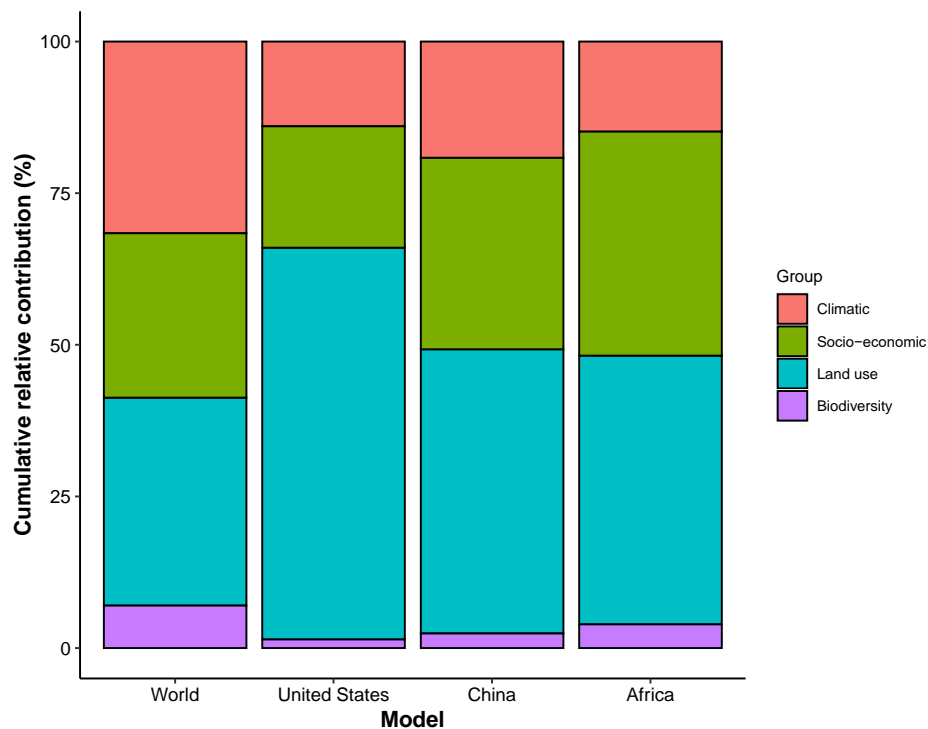
277

278   **Figure 5 Cumulative relative contribution of predictors to human-infective RNA virus discovery by**

279   **group in each model of different regions.** The relative contributions of all explanatory factors sum to 100% in

280   each model, and each colour represents the cumulative relative contribution of all explanatory factors within

281   each group.

282   We mapped human-infective RNA virus discovery probability in 2010–2019 for the three

283   regions, based on the fitted BRT models and values of all 33 predictors in 2015 (**Figure 6S**–

284   **Figure 8S**). Outside contemporary risk areas where human-infective RNA viruses were

285   previously discovered in the United States (**Figure 1A**), we predicted high probabilities of

286   virus discovery across southern Michigan, central-Northern Carolina, central Oklahoma,

287   southern Nevada, and north-eastern Utah (**Figure 6A**). Outside contemporary risk areas

288   where human-infective RNA viruses were previously discovered in China (**Figure 1B**), we

289   predicted high probabilities of virus discovery across other eastern China area as well as two

290   western areas including south-central Shaanxi and north-eastern Sichuan (**Figure 6B**).

291   Outside contemporary risk areas where human-infective RNA viruses were previously

292   discovered in Africa (**Figure 1C**), we predicted high probabilities of virus discovery across

293   northern Morocco, northern Algeria, northern Libya, south-eastern Sudan, central Ethiopia

294   and western Democratic Republic of the Congo (**Figure 6C**). Most new virus species since

295   2010 in each region (6/6 in the United States, 19/19 in China, 12/19 in Africa) were

296   discovered in high-risk areas (85% percentiles of predicted probability across each region) as

297   predicted by our model. Of all the 37 (United States: 6; China: 19; Africa: 12) viruses

298   discovered in high-risk areas in 2010–2019, 13 (United States: 2; China: 7; Africa: 4) viruses

299   were discovered at the potential new hotspots where there have not been any virus

300   discoveries before 2010.

A United States

C Africa

B China

0 1,000 2,000   4,000 Miles

▲ virus location

Probability
High : 0.89

Low : 0.01

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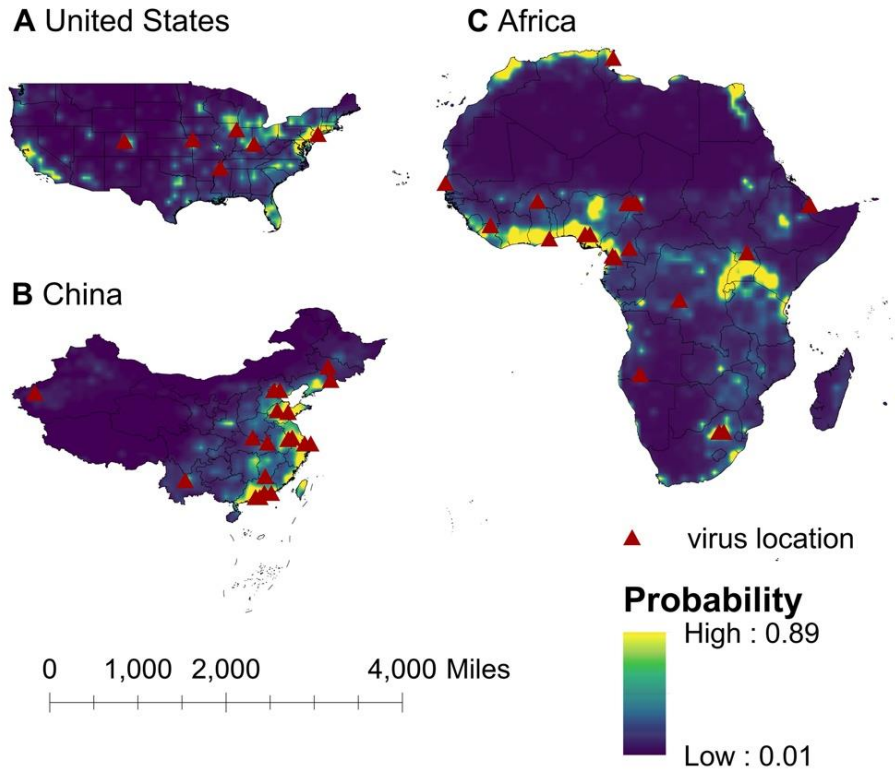
Figure 6 Predicted probability of human-infective RNA virus discovery in three regions in 2010–2019. A, United States. B, China. C, Africa. The triangles represented the actual discovery sites from 2010 to 2019, and the background colour represented the predicted discovery probability.

305 Based on our subgroup analysis (distinguishing viruses firstly discovered in regions and those

306 that had been discovered elsewhere in the world), discoveries of human-infective RNA

307 viruses firstly discovered from either United States or Africa were better predicted by

308 climatic and biodiversity variables, while discoveries of viruses that had been discovered

309 from elsewhere in the world were better predicted by socio-economic variables (**Figure 9S**).

Discussion

311 To our knowledge, this analysis represents the first investigation of human-infective RNA

312 virus discovery in three large regions of the world which have experienced distinct socio-

313 economic, ecological and environmental changes over the last 100 years. In total, 95 human-

314 infective RNA virus species had been found in the United States; 80 in China; 107 in Africa.

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315   The discovery maps of human-infective RNA virus in the three regions indicated areas with

316   historically high discovery counts: eastern and western United States, eastern China, and

317   central and southern Africa. BRT modelling suggested that the relative contribution of 33

318   predictors to human-infective RNA virus discovery varied across three regions, though

319   climatic and biodiversity variables were consistently less important in all three regions than at

320   a global scale. We mapped the probability of human-infective RNA virus discovery in 2010–

321   2019 which would continue to be high in historical hotspots but, in addition, we identified

322   several new hotspots in central-eastern and southwestern United States, eastern and western

323   China, and northern Africa. These results offer a tool for public health practitioners and

324   policy-makers to better understand local patterns of virus discovery and to invest efficiently

325   in surveillance systems at the local level.

326   In all three regions, GDP and/or GDP growth were identified as important predictors for virus

327   discovery, especially in Africa where GDP and GDP growth were identified as the leading

328   predictors. This is consistent with our previous analysis that GDP and GDP growth play a

329   major role in discovering viruses (Zhang et al., 2020). In general, sufficient economic, human

330   and material resources, the availability of advanced infrastructure and technology, and greater

331   research capabilities in the relative higher-income areas enable the virus discovery

332   (Rosenberg et al., 2013). That this effect applied both within one continent and within single

333   countries such as the United States and China suggested that most virus discoveries were

334   likely passive, i.e. the viruses were detected when they arrived in a location with the

335   resources to detect them. This is plausible because in all regions in our study, human-

336   transmissible viruses accounted for the larger proportion, and our previous analysis suggested

337   richer areas were more likely to first capture transmissible viruses (e.g. Influenza virus,

338   Rhinovirus, Rabies lyssavirus, Measles morbillivirus, Mumps orthorubulavirus, Rubella virus,

339   and Norwalk virus) capable of spreading to multiple areas (Zhang et al., 2020). Temporally,

340   in China the rate of discovery increased after economic growth accelerated in the 1980s

341   (**Figure 3**). We note in publications describing first virus discoveries that most historical

342   virus discoveries in Africa received support from the United States and Europe, and this may

343   explain why Africa saw an increased number of virus discoveries after 1950—30 years

344   earlier than China (**Figure 3**). Notably, in China the relative contribution of GDP growth to

345   virus discovery was not as substantial as that in Africa. In contrast, university count was

346   found to be associated with virus discovery, suggesting virus discovery likely being a

347   significant area of research in Chinese universities. Our model also suggested the overall

348   socio-economic factors contributed less in the United States than other two regions. The

349   possible explanation is that the socio-economic level across the whole United States is

350   relatively high and homogenous.

351   Predictors other than GDP and university count are likely to be linked to virus natural history.

352   In all three regions, the area of urban land and further urbanization made great contribution to

353   virus discovery. This reinforced previous studies that urbanization was linked to the detection

354   of new human pathogens through the denser urban population, increased human-wildlife

355   contact rate, spill-over of human infection from enzootic cycle, and the contamination of the

356   urban environment with microbial agents (Hassell et al., 2017; Olival et al., 2017; Weaver,

357   2013). In the United States, land use contributed most to virus discovery in comparison to

358   other regions—urbanized land, urbanization of cropland, and growth of urbanized land alone

359   had a relative contribution of 47.9%. However, the leading role of urbanization to virus

360   discovery in the United States remains unclear. There might be many factors contributing to

361   this, e.g. the underlying relationships between urbanization and economic growth as well as

362   population growth, but we can't untangle these from this study.

363 Consistent with our previous work, population growth was identified as a less prominent

364 predictors (Zhang et al., 2020). In China, population growth—though with greater influence

365 than other regions—contributed less than urbanized land and three other land types on virus

366 discoveries. This reinforces our previous interpretation that urbanization brings larger

367 changes on human living environment than human population size/growth, and therefore may

368 have influenced virus discovery more greatly.

369 Climate had less influence on human-infective RNA virus discovery in all three regions in

370 comparison to other predictors, in contrast to virus discovery at a global scale (Zhang et al.,

371 2020). The underlying reason may be that the proportion of vector-borne viruses—whose

372 distribution and abundance is strongly associated with the impact of climate on vector

373 populations (Li et al., 2014)—in all three regions (United States: 23.2%; China: 21.3%;

374 Africa: 27.1%) were less than that in the world (41.7%) (**Figure 3**). Vector-borne viruses

375 tend to have more restricted global ranges, so are less likely to appear in a study of any one

376 region (Zhang et al., 2020).

377 In addition, a relative smaller proportion of strictly zoonotic viruses in three regions (United

378 States: 30.5%; China: 16.3%; Africa: 33.6%) than that in the world (58.7%) (**Figure 2**) made

379 biodiversity contribute less to virus discovery in the three regions than in the world (Zhang et

380 al., 2020). With exposure to denser mammals played a slightly larger role in virus discovery

381 in Africa than in China and the United States (**Figure 6S–Figure 8S**).

382 Our discovery probability maps for 2010–2019 in three regions captured most historical

383 hotspots, though several small new areas in central-eastern and southwestern United States,

384 eastern and western China, as well as northern Africa would also make greater contribution to

385 virus discovery (**Figure 6**). Our model has a good predictive ability, given 84% (37/44) new

386 virus species in 2010–2019 were discovered in high-risk areas we have defined—85%

387   percentiles of discovery probability within each region. Further, 35% (13/37) of those viruses

388   discovered in high-risk areas since 2010 were discovered at the potential new hotspots where

389   there had not been any virus discoveries in the past.

390   Our subgroup analyses suggested in both the United States and Africa, discoveries of viruses

391   firstly discovered in regions were more likely to be associated with climatic and biodiversity

392   variables while discoveries of viruses had been discovered elsewhere in the world were more

393   likely to be associated with socio-economic variables. This is plausible, again because after a

394   novel virus was discovered elsewhere in the world, it is usually areas with a higher socio-

395   economic level firstly capture the virus in the local region.

396   This study had limitations. First, one common problem for data collected from literature

397   review is the time lag between virus discovery and publication, in which case the virus data

398   are likely to be matched to covariates in later decades. Second, we acknowledge that it is

399   possible we have not identified the earliest report for some well-known viruses such as

400   yellow fever virus, measles virus, especially in the post-vaccination era. Third, we were

401   unable to identify robust and comprehensive data for all three regions on virus discovery

402   effort, although we interpret GDP and university count as being an indirect measure of

403   resources available for this activity.

404   The study adds to our previous study (Zhang et al., 2020) in several ways. First, we firstly

405   construct data sets of human-infective RNA virus discovery reflecting the viral richness in

406   three broad regions of the world. Second, we reduced the heterogeneity of the predictors by

407   focusing on regions, including those predictors reflecting the research effort. Research effort

408   is less variable within restricted regions and therefore has less effect on virus detection. This

409   implies our predicted hotspots stand closer to the virus geographic distribution in nature.

410   Third, the predicted hotspots derived from regional analysis have a higher precision than at a

411   global scale, e.g. specific areas in the United States and China were identified as hotspots

412   from regional analysis, rather than the whole eastern area from the global analysis. This helps

413   target areas for future surveillance.

414   In conclusion, a heterogeneous pattern of virus discovery-driver relationships was identified

415   across three regions and the globe. Within regions virus discovery is driven more by land-use

416   and socio-economic variables; climate and biodiversity variables are consistently less

417   important predictors than at a global scale. We mapped with good accuracy that in 2010–

418   2019 three regions where human-infective RNA viruses had previously been discovered

419   would continue to be the discovery hotspots, but in addition, several new areas in each region

420   would make great contribution to virus discovery. Results from the study could guide active

421   surveillance for new human-infective viruses in high risk areas.

422   **Author contributions**

423   Feifei Zhang, Conceptualization, Data preparation, Formal analysis, Methodology, Validation,

424   Visualization, Interpretation, Writing - original draft, Writing - review and editing; Margo

425   Chase-Topping, Methodology, Interpretation, Writing - review and editing; Chuan-Guo Guo,

426   Data preparation, Methodology, Validation, Interpretation, Writing - review and editing;

427   Mark E.J. Woolhouse, Conceptualization, Methodology, Interpretation, Writing - original

428   draft, Writing - review and editing, Funding Acquisition.

429   **Competing interests**

430   The authors disclose no conflicts of interest.

437   **Data availability**

438   The authors confirm that all data or the data sources are provided in the paper and its

439   Supplementary Materials. The final datasets and codes used for the analyses are available via

440   figshare at https://doi.org/10.6084/m9.figshare.15101979.

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503

1 Supplementary materials

2 *Supplementary tables*

3 Table 1S Summary of the human-infective RNA virus data sets in the United States, Africa and China

Species	Original discovery year	United States					China					Africa				
		Reported?	Discovery year	location	Lat	Lon	Reported?	Discovery year	location	Lat	Lon	Reported?	Discovery year	location	Lat	Lon
Argentinian mammarenavirus	1958	No					No					No				
Brazilian mammarenavirus	1994	Yes[1]	1995	New Haven, Connecticut	41.31	-72.93	No					No				
Cali mammarenavirus	1971	Yes[2]	1974	Houston, Texas	29.76	-95.37	No					No				
Chapare mammarenavirus	2008	No					No					No				
Guanarito mammarenavirus	1991	No					No					No				
Lassa mammarenavirus	1970	Yes[3]	1970	New Haven, Connecticut	41.31	-72.93	No					Yes[3]	1970	Lassa, Borno State, Nigeria	10.69	13.27
Lujo mammarenavirus	2009	No					No					Yes[4]	2009	Lusaka, Zambia	-15.39	28.32
Lymphocytic choriomeningitis mammarenavirus	1934	Yes[5]	1934	St. Louis county, Missouri	38.61	-90.41	No					No				
Machupo mammarenavirus	1964	No					No					No				
Mobala mammarenavirus	1985	No					No					Yes[6]	1985	Bouboui and Gomoka village, Boali town, Central African Republic	4.89	18.14
Whitewater Arroyo mammarenavirus	2000	Yes[7]	2000	Alameda County, California	37.60	-121.72	No					No				
Mamastrovirus 1	1975	Yes[8]	1981	Martin County, California	40.22	-123.10	Yes[9]	1981	Guangzhou, Guangdong	23.13	113.26	Yes[10]	1981	Lebowa, South Africa	-23.5	29.5
Mamastrovirus 6	2008	Yes[11]	2009	St. Louis, Missouri	38.63	-90.20	Yes[12]	2010	Hong Kong	22.40	114.11	Yes[13]	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mamastrovirus 8	2009	Yes[14]	2009	St. Louis, Missouri	38.63	-90.20	Yes[15]	2013	Nanjing, Jiangsu and Lanzhou, Gansu	31.95	118.78	Yes[13]	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mamastrovirus 9	2009	Yes[16]	2009	Accomack and Northampton Counties, Virginia	37.71	-75.81	Yes[17]	2019	Jinan, Shandong	36.68	117.11	Yes[13]	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mammalian 1 orthobornavirus	1985	Yes[18]	1985	Philadelphia, Pennsylvania	39.95	-75.17	Yes[19]	1999	Taiwan	23.70	120.96	Yes[20]	1992	Rural area of East Africa	-1.28	34.53
Mammalian 2 orthobornavirus	2015	No					No					No				

Virus																
Norwalk virus	1972	Yes[21]	1972	Norwalk, Ohio	41.24	-82.62	Yes[22]	1995	Henan	33.88	113.48	Yes[23]	1993	Pretoria, Gauteng province, South Africa	-25.75	28.23
Sapporo virus	1980	Yes[24]	1988	Houston, Texas	29.76	-95.37	Yes[24]	1988	Shanghai	31.23	121.47	Yes[25]	1997	Pretoria, Gauteng province, South Africa	-25.75	28.23
Vesicular exanthema of swine virus	1998	Yes[26]	1998	Corvallis, Oregon	44.56	-123.26	No					No				
Alphacoronavirus 1	2007	No					No					No				
Human coronavirus 229E	1966	Yes[27]	1966	Chicago, Illinois	41.88	-87.63	Yes[28]	1975	Kunming, Yunnan	25.07	102.68	Yes[29]	1998	Kumasi, Ghana	6.70	-1.62
Human coronavirus NL63	2004	Yes[30]	2005	New Haven, Connecticut	41.31	-72.93	Yes[31]	2005	Hong Kong	22.40	114.11	Yes[32]	2008	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Betacoronavirus 1	1967	Yes[33]	1967	Bethesda, Maryland	38.98	-77.09	Yes[31]	2005	Hong Kong	22.40	114.11	Yes[34]	2011	Pretoria, Gauteng province, South Africa	-25.75	28.23
Human coronavirus HKU1	2005	Yes[35]	2006	New Haven, Connecticut	41.31	-72.92	Yes[36]	2005	Hong Kong	22.40	114.11	Yes[34]	2011	Pretoria, Gauteng province, South Africa	-25.75	28.23
Middle East respiratory syndrome-related coronavirus	2012	Yes*[37]	2014	Lake county, Indiana	41.45	-87.37	Yes*[38]	2015	Huizhou, Guangdong	23.09	114.40	Yes*[39]	2014	Monastir, Tunisia	35.79	10.82
Severe acute respiratory syndrome-related coronavirus	2003	Yes*[40]	2003	Atlanta, Georgia	33.75	-84.39	Yes[41]	2003	Hong Kong	22.40	114.11	Yes[42]	2004	Pretoria, Gauteng province, South Africa	-25.75	28.23
Human torovirus (been abolished)	1984	No					No					No				
Bundibugyo ebolavirus	2008	No					No					Yes[32]	2008	Bundibugyo and Kikyo town, Bundibugyo District, Western Uganda	0.71	30.06
Reston ebolavirus	1991	Yes[43]	1991	Reston, Fairfax County, Virginia	38.96	-77.35	No					No				
Sudan ebolavirus	1977	No					No					Yes[44]	1977	Maridi, South Sudan	4.91	29.45
Tai Forest ebolavirus	1995	No					No					Yes[45]	1995	Abidjan, Cote-d'lvoire	5.36	-4.01
Zaire ebolavirus	1977	No					No					Yes[46]	1977	Yambuku village, Democratic Republic of the Congo	2.83	22.22
Marburg marburgvirus	1968	Yes*[47]	2009	Denver county, Colorado	39.55	-105.78	No					Yes[48]	1975	Johannesburg, South Africa	-26.20	27.90
Aroa virus	1971	No					No					No				
Bagaza virus	2009	No					No					No				
Banzi virus	1959	No					No					Yes[49]	1959	Maponde's Kraal(Usutu river), South Africa	-26.52	31.67
Cacipacore virus	2011	No					No					No				
Dengue virus	1907	Yes[50]	1914	Savannah, Georgia	32.02	-81.12	Yes[51]	1967	Southwest Taiwan	23.06	120.59	Yes[52]	1927	Durban, KwaZulu-Natal Province, South Africa	-29.86	31.02

Virus	Year		Year	Location	Lat	Long		Year	Location	Lat	Long		Year	Location	Lat	Long
Edge Hill virus	1985	No					No					No				
Gadgets Gully virus	1991	No					No					No				
Ilheus virus	1947	No					No					No				
Japanese encephalitis virus	1933	Yes*[53]	1953	Waltham, Massachusetts	42.38	-71.24	Yes[54]	1941	Beijing	40.01	116.41	Yes[55]	2017	Cunene, Angola	-16.28	15.28
Kokobera virus	1964	No					No					No				
Kyasanur forest disease virus	1957	No					Yes[56]	2009	Hengduanshan Mountain, Yunnan	27.50	99.00	Yes[57]	2014	Djibouti, Republic of Djibouti	11.57	43.15
Langat virus	1956	No					No					No				
Louping ill virus	1934	Yes[58]	1934	New York	40.71	-74.01	No					No				
Murray Valley encephalitis virus	1952	No					No					No				
Ntaya virus	1952	No					No					Yes[59]	1952	Bwamba county, Uganda	0.75	30.02
Omsk hemorrhagic fever virus	1948	No					No					No				
Powassan virus	1959	Yes[60]	1973	Middlesex County, New Jersey	40.54	-74.37	No					No				
Rio Bravo virus	1962	Yes[61]	1962	Dallas city, Texas	32.78	-96.80	No					No				
Saint Louis encephalitis virus	1933	Yes[62]	1933	St. Louis City, Missouri	38.63	-90.20	No					No				
Tembusu virus	1975	No					Yes[63]	2013	Shandong	36.40	118.77	No				
Tick-borne encephalitis virus	1938	Yes*[64]	1979	Cleveland, Ohio	41.51	-81.69	Yes[65]	1956	Bali village, Wuchang, Heilongjiang	44.91	127.16	No				
Uganda S virus	1952	No					No					Yes[66]	1952	Bwamba county, Uganda	0.75	30.02
Usutu virus	2009	No					No					No				
Wesselsbron virus	1957	No					No					Yes[67]	1957	Lake Simbu region, Maputaland, KwaZulu-Natal, South Africa	-27.36	32.32
West Nile virus	1940	Yes[68]	2001	New York	40.71	-74.01	Yes[69]	2013	Jiashi County, Xinjiang	39.58	77.18	Yes[70]	1940	Omogo, West Nile district, Uganda	0.42	33.21
Yellow fever virus	1901	Yes[71]	1904	Laredo, Texas	27.51	-99.51	Yes*[72]	2016	Beijing	40.01	116.41	Yes[73]	1928	Larteh, Ghana	5.94	-0.07
Zika virus	1952	Yes*[74]	2011	Northern Colorado	39.55	-105.78	Yes*[75]	2016	Gan County, Ganzhou city, Jiangxi	25.86	115.02	Yes[76]	1952	Zika, Uganda	0.12	32.53
Hepacivirus C	1989	Yes[77]	1989	Emeryville, California	37.83	-122.29	Yes[78]	1990	Qidong county, Jiangsu	31.88	121.72	Yes[79]	1990	Johannesburg, South Africa	-26.20	27.90
Pegivirus C	1995	Yes[80]	1995	Chapel Hill, North Carolina; Rochester, Minnesota; Dallas,	35.91	-79.06	Yes[81]	1996	Beijing	40.01	116.41	Yes[80]	1995	Cairo, Egypt	30.04	31.24

Virus	Year	Detected	Year	Location	Lat	Long	Detected	Year	Location	Lat	Long	Detected	Year	Location	Lat	Long
				Texas												
Pegivirus H	2015	Yes[82]	2015	New York city, New York	40.71	-74.01	Yes[83]	2018	Guangzhou, Guangdong	23.13	113.26	Yes[84]	2019	Ebolowa, Cameroon	2.92	11.15
Pestivirus A	1988	Yes[85]	1989	Whiteriver, Arizona	33.83	-109.97	No					Yes[86]	1988	Zambia	-13.13	27.85
Andes orthohantavirus	1996	No					No					No				
Bayou orthohantavirus	1995	Yes[87]	1995	Louisiana	30.98	-91.96	No					No				
Black creek canal orthohantavirus	1995	Yes[88]	1995	Miami-Dade County, Florida	25.76	-80.34	No					No				
Choclo orthohantavirus	2000	No					No					No				
Dobrava-Belgrade orthohantavirus	1992	No					No					No				
Hantaan orthohantavirus	1978	No					Yes[89]	1980	Zhejiang	29.14	119.79	No				
Laguna Negra orthohantavirus	1997	No					No					No				
Puumala orthohantavirus	1980	No					No					No				
Sangassou orthohantavirus	2010	No					No					Yes[90]	2010	Sangassou village, Macenta district, Forest Guinea	8.24	-9.32
Seoul orthohantavirus	1982	Yes[91]	1987	Mississippi	32.57	-89.88	Yes[92]	1982	Jiangsu	33.14	119.79	Yes[93]	1986	Jos, Nigeria	9.90	8.86
Sin Nombre orthohantavirus	1993	Yes[94]	1993	New Mexico	34.52	-105.87	No					No				
Thailand orthohantavirus	2006	No					No					No				
Thottopalayam thottimvirus	2007	No					No					No				
Tula orthohantavirus	1996	No					No					No				
Orthohepevirus A	1983	Yes*[95]	1987	Los Angeles County, California	34.05	-118.24	Yes[96]	1989	Kashi county, Kashi city, Xinjiang	39.46	75.99	Yes[97]	1985	Medea town, Algeria	36.26	2.75
Orthohepevirus C	2018	No					Yes[98]	2018	Hong Kong	22.40	114.11	No				
Crimean-Congo haemorrhagic fever orthonairovirus	1967	No					Yes[99]	1985	Bachu, southern Xinjiang	39.79	78.55	Yes[100]	1967	Kisangani, Tshopo province, Democratic Republic of the Congo	0.53	25.19
Dugbe orthonairovirus	1969	No					No					Yes[101]	1969	Ibadan, Nigeria	7.35	3.88
Nairobi sheep disease orthonairovirus	1969	No					No					Yes[102]	1991	Mombasa; Malindi; and Kilifi, Coast Province, Kenya	-3.34	39.57
Thiafora orthonairovirus	1989	No					No					No				
Influenza A virus	1933	Yes[103]	1935	Philadelphi, Pennsylvania	39.95	-75.17	Yes[104]	1950	Beijing	40.01	116.41	Yes[105]	1951	Johannesburg, South Africa and Cape Town, South Africa	-26.20	27.90
Influenza B virus	1940	Yes[106]	1940	Irvington village, Greenburgh town,	41.03	-73.87	Yes[107]	1957	Beijing	40.01	116.41	Yes[108]	1970	Arusha, Arusha Region, Tanzania	-3.37	36.69

				Westchester County, New York												
Influenza C virus	1950	Yes[109]	1950	Ann Arbor city, Michigan	42.28	-83.74	Yes[110]	1957	Beijing	40.01	116.41	Yes[111]	1968	Johannesburg, South Africa	-26.20	27.90
Dhori thogotovirus	1985	No					No					No				
Thogoto thogotovirus	1969	No					No					Yes[101]	1969	Ibadan, Nigeria	7.35	3.88
Avian orthoavulavirus 1	1943	Yes[112]	1943	Washington, D. C.	38.91	-77.04	No					No				
Hendra henipavirus	1995	No					No					No				
Nipah henipavirus	1999	No					No					No				
Canine morbillivirus	1955	Yes[113]	1955	Buffalo, New York	42.89	-78.88	No					No				
Measles morbillivirus	1911	Yes[114]	1911	Washington, D. C.	38.91	-77.04	Yes[115]	1958	Beijing	40.01	116.41	Yes[116]	1963	Dakar, Senegal	14.72	-17.47
Human respirovirus 1	1958	Yes[117]	1958	Washington, D. C.	38.91	-77.04	Yes[118]	1964	Zhejiang	29.14	119.79	Yes[119]	1963	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Human respirovirus 3	1958	Yes[117]	1958	Washington, D. C.	38.91	-77.04	Yes[120]	1987	Guangzhou, Guangdong	23.13	113.26	Yes[119]	1963	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Achimota pararubulavirus 2	2013	No					No					Yes[121]	2013	Volta, Ghana	6.05	0.37
Human orthorubulavirus 2	1956	Yes[122]	1956	Cincinnati, Ohio	39.10	-84.51	Yes[123]	1975	Nanjing, Jiangsu	31.95	118.78	Yes[124]	1967	Accra, Ghana	5.60	-0.19
Human orthorubulavirus 4	1960	Yes[125]	1960	Bethesda, Maryland	38.98	-77.09	Yes[126]	2005	Hong Kong	22.40	114.11	Yes[127]	2010	Ndiop village, Sine Saloum region, Senegal	15.18	-16.74
Mammalian orthorubulavirus 5	1959	Yes[128]	1959	Stanford, California	37.42	-122.17	No					No				
Menangle pararubulavirus	1998	No					No					No				
Mumps orthorubulavirus	1934	Yes[129]	1934	Nashville, Tennessee	36.16	-86.78	Yes[130]	1958	Beijing	40.01	116.41	Yes[131]	1955	Johannesburg, South Africa	-26.20	27.90
Simian orthorubulavirus	1968	No					No					No				
Sosuga pararubulavirus	2014	No					No					Yes[132]	2014	-	3.76	32.82
Tioman pararubulavirus	2007	No					No					No				
Bunyamwera orthobunyavirus	1946	Yes[133]	1964	Southern Florida	26.92	-81.21	No					Yes[134]	1946	Bwamba County, Uganda	0.75	30.02
Bwamba orthobunyavirus	1941	No					No					Yes[135]	1941	Bwamba county, Western Province of Uganda	0.75	30.02
California encephalitis orthobunyavirus	1952	Yes[136]	1952	Kern county, California	35.49	-118.86	Yes[137]	1984	Longhua, Shanghai	31.22	121.43	Yes[138]	1961	Uganda	1.37	32.29
Caraparu orthobunyavirus	1961	No					No					No				

Virus	Year	Col3	Year	Location	Lat	Long	Col8	Year	Location	Lat	Long	Col13	Year	Location	Lat	Long
Catu orthobunyavirus	1961	No					No					No				
Guama orthobunyavirus	1961	No					No					No				
Guaroa orthobunyavirus	1959	No					No					No				
Kairi orthobunyavirus	1967	No					No					No				
Madrid orthobunyavirus	1964	No					No					No				
Marituba orthobunyavirus	1961	No					No					No				
Nyando orthobunyavirus	1965	No					No					Yes[139]	1965	Kisumu, Kenya	-0.09	34.77
Oriboca orthobunyavirus	1961	No					No					No				
Oropouche orthobunyavirus	1961	No					No					No				
Patois orthobunyavirus	1972	No					No					No				
Shuni orthobunyavirus	1975	No					No					Yes[140]	1975	Ibadan, Nigeria	7.38	3.95
Tacaiuma orthobunyavirus	1967	No					No					No				
Wyeomyia orthobunyavirus	1965	No					No					No				
Candiru phlebovirus	1983	No					No					No				
Punta Toro phlebovirus	1970	No					No					No				
Rift Valley fever phlebovirus	1931	No					Yes*[141]	2016	Beijing	40.01	116.41	Yes[142]	1931	Rift Valley of Kenya Colony	-0.28	36.07
Sandfly fever Naples phlebovirus	1944	No					No					Yes[143]	1951	Cairo, Egypt	30.04	31.24
Heartland banyangvirus	2012	Yes[144]	2012	Andrew and Nodaway Counties, Missouri	39.82	-94.59	No					No				
Huaiyangshan banyangvirus	2011	No					Yes[145]	2011	Huaiyangshan	31.37	115.39	No				
Uukuniemi phlebovirus	1970	No					No					No				
Human picobirnavirus	1988	Yes[146]	1993	Atlanta, Georgia	33.75	-84.39	Yes[147]	2000	Lulong County, Hebei	39.94	116.94	No				
Equine rhinitis A virus	1962	No					No					No				
Foot-and-mouth disease virus	1965	No					Yes[148]	1999	Guangzhou	23.13	113.26	Yes[149]	2002	Alexandria Governorate, Egypt	30.74	29.74
Cardiovirus A	1947	Yes[150]	1961	New Orleans, Louisiana	29.95	-90.07	Yes[151]	2015	Changchun, Jilin	43.87	125.34	Yes[152]	1948	Entebbe, Uganda	0.05	32.46
Cardiovirus B	1963	Yes[153]	2007	San Diego, California	32.72	-117.16	Yes[154]	2009	Lanzhou, Gansu	36.06	103.79	Yes[155]	2009	Cameroon	5.03	12.40
Cosavirus A	2008	No					Yes[156]	2010	Shanghai	31.23	121.47	Yes[157]	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus B	2008	No					Yes[158]	2016	Zhenjiang, Jiangsu	32.19	119.43	No				

Virus	Year		Year	Location	Lat	Long		Year	Location	Lat	Long		Year	Location	Lat	Long
Cosavirus D	2008	No					No					Yes[157]	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus E	2008	No					No					Yes[157]	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus F	2012	No					No					No				
Enterovirus A	1949	Yes[159]	1949	New York	43.30	-74.22	Yes[160]	1985	Tianjin	39.34	117.36	Yes[131]	1955	Johannesburg, South Africa	-26.20	27.90
Enterovirus B	1949	Yes[159]	1949	Wilmington	39.74	-75.54	Yes[161]	1960	Fuzhou, Fujian	26.07	119.30	Yes[162]	1953	Middelburg, Transvaal, South Africa	-25.77	29.46
Enterovirus C	1909	Yes[163]	1909	New York city, New York	40.71	-74.01	Yes	1941	Bejing	39.90	116.41	Yes[164]	1933	Monrovia, Liberia	6.29	-10.76
Enterovirus D	1967	Yes[165]	1967	Berkeley, California	37.87	-122.27	Yes[166]	1979	Shanghai	31.23	121.47	Yes[167]	1973	Morocco	31.79	-7.09
Enterovirus E	1961	Yes[168]	1961	Denver, Colorado	39.74	-104.99	No					No				
Enterovirus H	1965	No					No					No				
Rhinovirus A	1953	Yes[169]	1956	Baltimore, Maryland	39.29	-76.61	Yes[170]	1975	Guangzhou, Guangdong	23.13	113.26	Yes[171]	1963	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Rhinovirus B	1960	Yes[172]	1961	Chicago, Illinois	41.88	-87.63	Yes[173]	2008	Beijing	40.01	116.41	Yes[174]	2008	Pretoria, Gauteng province, South Africa	-25.75	28.23
Rhinovirus C	2006	Yes[175]	2006	New York city, New York	40.71	-74.01	Yes[176]	2007	Hong Kong	22.40	114.11	Yes[174]	2008	Pretoria, Gauteng province, South Africa	-25.75	28.23
Erbovirus A	2005	No					No					No				
Hepatovirus A	1973	Yes[177]	1973	Bethesda, Maryland	38.98	-77.09	Yes[178]	1978	Shanghai	31.23	121.47	Yes[179]	1977	Dakar, Senegal	14.72	-17.47
Aichivirus A	1991	Yes[180]	2013	Cincinnati, Ohio	39.10	-84.51	Yes[181]	2009	Shanghai	31.23	121.47	Yes[182]	2008	Monastir, Tunisia	35.77	10.82
Parechovirus A	1958	Yes[183]	1958	Cincinnati, Ohio	39.10	-84.51	Yes[184]	2009	Shanghai	31.23	121.47	Yes[157]	2012	Ouagadougou, Burkina Faso	12.24	-1.56
Parechovirus B	2003	No					No					No				
Salivirus A	2009	Yes[185]	2009	Northern California	38.84	-120.90	Yes[186]	2010	Shanghai	31.23	121.47	Yes[187]	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Avian metapneumovirus	2011	Yes[188]	2011	Memphis, Tennessee	35.15	-90.05	No					No				
Human metapneumovirus	2001	Yes[189]	2003	Rochester, New York	43.16	-77.61	Yes[190]	2003	Hong Kong	22.40	114.11	Yes[191]	2003	Johannesburg, South Africa	-26.20	27.90
Human orthopneumovirus	1957	Yes[192]	1957	Baltimore, Maryland	39.29	-76.61	Yes[193]	1975	Kunming, Yunnan	25.07	102.68	Yes[194]	1965	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Colorado tick fever virus	1946	Yes[195]	1946	Denver, Colorado	39.74	-104.99	Yes[196]	1996	Nanjing, Jiangsu	31.95	118.78	No				
Eyach virus	1980	No					No					No				
Corriparta virus	1967	No					No					No				
Great Island virus	1963	No					No					No				

Virus	Year	Detected	Year	Location	Lat	Long	Detected	Year	Location	Lat	Long	Detected	Year	Location	Lat	Long
Lebombo virus	1975	No					No					Yes[140]	1975	lbadan, Nigeria	7.38	3.95
Orungo virus	1976	No					No					Yes[197]	1976	Ibadan, Nigeria	7.38	3.95
Mammalian orthoreovirus	1954	Yes[198]	1954	Cincinnati, Ohio	39.10	-84.51	Yes[199]	1995	Xuzhou, Jiangsu	34.26	117.19	Yes[200]	1963	Johannesburg, South Africa	-26.20	27.90
Nelson Bay orthoreovirus	2007	No					Yes*[201]	2009	Hong Kong	22.40	114.11	No				
Rotavirus A	1973	Yes[202]	1976	Washington, D. C.	38.90	-77.04	Yes[203]	1979	Beijing	40.01	116.41	Yes[197]	1976	Johannesburg, South Africa	-26.20	27.90
Rotavirus B	1984	Yes[204]	1985	Baltimore, Maryland	39.29	-76.61	Yes[205]	1984	Jinzhou, Liaoning	41.10	121.13	Yes[206]	1987	Kenya	-0.02	37.91
Rotavirus C	1986	Yes[207]	1995	Providence, Rhode Island	41.82	-71.41	Yes[208]	1999	Beijing	40.01	116.41	Yes[209]	1999	Pretoria, Gauteng province, South Africa	-25.75	28.23
Rotavirus H	1987	No					Yes[210]	1987	Huaihua, Hunan Province	27.55	109.96	No				
Banna virus	1990	No					Yes[211]	1990	Xishuangbanna, Yunnan Province	21.90	100.80	No				
Primate T-lymphotropic virus 1	1980	Yes[212]	1980	Bethesda, Maryland	38.98	-77.09	Yes[205]	1984	Shenyang, Liaoing	41.80	123.38	Yes[213]	1984	Ibadan, Nigeria	7.38	3.95
Primate T-lymphotropic virus 2	1982	Yes[214]	1982	Seattle, Washington	47.61	-122.33	Yes[215]	2013	Henan and Hubei	32.21	112.96	Yes[216]	1991	Franceville, Gabon	-1.63	13.60
Primate T-lymphotropic virus 3	2005	No					No					Yes[217]	2005	Océan department, South Province, Cameroon	2.50	10.50
Human immunodeficiency virus 1	1983	Yes[218]	1984	Washington, D. C.	38.90	-77.04	Yes[219]	1986	Hong Kong	22.40	114.11	Yes[220]	1984	Kisangani, Tshopo province, Democratic Republic of the Congo	0.53	25.19
Human immunodeficiency virus 2	1986	Yes*[221]	1988	New Jersey	40.06	-74.41	Yes*[222]	2000	Fuzhou, Fujian	26.07	119.30	Yes[223]	1986	Dakar, Senegal	14.72	-17.47
Simian immunodeficiency virus	1992	Yes[224]	1992	Atlanta, Georgia	33.75	-84.39	No					Yes[217]	2005	Cameroon	7.37	12.35
Central chimpanzee simian foamy virus	2012	No					No					Yes[225]	2012	Near Dja Nature Reserves, Southern Cameroon	4.50	13.50
Eastern chimpanzee simian foamy virus	1971	No					No					Yes[226]	1971	Kenya	-0.02	37.91
Grivet simian foamy virus	1997	No					No					No				
Guenon simian foamy virus	2012	No					No					Yes[225]	2012	Near lolodrof, Southern Cameroon	3.23	10.73
Taiwanese macaque simian foamy virus	2002	No					Yes[227]	2012	Yunnan	25.18	101.86	No				
Australian bat lyssavirus	1998	No					No					No				
Duvenhage lyssavirus	1971	No					No					Yes[228]	1971	Pretoria, Gauteng province, South Africa	-25.75	28.23
European bat Yeslyssavirus	1989	No					No					No				
European bat 2	1986	No					No					No				

lyssavirus															
Irkut lyssavirus	2013	No					Yes[229]	2013	Tonghua county, Jilin	41.68	125.76	No			
Mokola lyssavirus	1972	No					No					Yes[230]	1972	Ibadan, Nigeria	7.38	3.95
Rabies lyssavirus	1903	Yes[231]	1910	Southern California	34.57	-116.76	Yes[232]	1981	Beijing	40.01	116.41	Yes[233]	1933	Carolina, Mpumalanga, South Africa	-26.07	30.12
Bas-Congo tibrovirus	2012	No					No					Yes[234]	2012	Mangala village, Boma Bungu Health Zone, Democratic Republic of Congo (DRC)	-4.04	21.76
Ekpoma Yestibrovirus	2015	No					No					Yes[235]	2015	Irrua, Edo State, Nigeria	6.74	6.22
Ekpoma 2 tibrovirus	2015	No					No					Yes[235]	2015	Irrua, Edo State, Nigeria	6.74	6.22
Alagoas vesiculovirus	1967	No					No					No			
Chandipura vesiculovirus	1967	No					No					No			
Cocal vesiculovirus	1964	No					No					No			
Indiana vesiculovirus	1958	Yes[236]	1958	Beltsville, Prince George's County, Maryland	39.05	-76.90	No					No			
Isfahan vesiculovirus	1977	No					No					No			
Maraba vesiculovirus	1984	No					No					No			
New Jersey vesiculovirus	1950	Yes[237]	1950	Madison, Wisconsin	43.07	-89.40	No					No			
Piry vesiculovirus	1974	No					No					No			
Barmah Forest virus	1986	No					No					No			
Chikungunya virus	1956	Yes*[238]	2006	Minnesota	46.44	-93.36	Yes[51]	1967	Southwest Taiwan	23.06	120.59	Yes[239]	1956	Newala district, Tanzania	-10.64	39.24
Eastern equine encephalitis virus	1938	Yes[240]	1938	Southwestern Massachusetts	42.19	-73.09	No					No			
Everglades virus	1970	Yes[241]	1970	Homestead, Florida	25.47	-80.48	No					No			
Getah virus	1966	No					Yes[242]	1992	Baoting County, Hainan	18.98	109.83	No			
Highlands J virus	2000	Yes[243]	2000	Florida	27.66	-81.52	No					No			
Madariaga virus	1972	No					No					No			
Mayaro virus	1957	Yes*[244]	1999	Ohio	40.42	-82.91	No					No			
Mosso das Pedras virus	2013	No					No					No			

Virus	Year															
Mucambo virus	1965	No					No					No				
Ndumu virus	1961	No					No					Yes[245]	1961	Ndumu, Maputaland, KwaZulu-Natal, South Africa	-26.93	32.26
Onyong-nyong virus	1961	No					No					Yes[246]	1961	Entebbe, Uganda	0.05	32.46
Pixuna virus	1991	No					No					No				
Rio Negro virus	1993	No					No					No				
Ross River virus	1972	No					Yes[247]	1999	Hainan	19.16	109.94	No				
Semliki Forest virus	1979	No					No					Yes[248]	1990	Bangui, Central Africa	4.36	18.58
Sindbis virus	1955	No					No					Yes[249]	1955	Cairo, Egypt	30.04	31.24
Tonate virus	1976	No					No					No				
Una virus	1963	No					No					No				
Venezuelan equine encephalitis virus	1943	Yes[250]	1943	New York	40.71	-74.01	No					No				
Western equine encephalitis virus	1938	Yes[240]	1938	Fresno, California	36.75	-119.77	No					No				
Whataroa virus	1964	No					No					No				
Rubella virus	1942	Yes[251]	1942	Washington, D. C.	38.91	-77.04	Yes[252]	1979	Hangzhou, Zhejiang	29.87	119.33	Yes[253]	1963	Cape Town, Western Cape Province, South Africa	-33.90	18.57
Hepatitis delta virus	1977	Yes[254]	1979	New Jersey	40.06	-74.41	Yes[255]	1980	Taipei, Taiwan	24.96	121.51	Yes[256]	1984	Harare, Zimbabwe	-17.83	31.03

4 Notes: Yes denotes the virus was ever discovered from the region; * denotes the virus was ever discovered from the region, but imported from other regions; No denotes the
5 virus   species has never been discovered from the region; The lat and long denote the coordidate of discovery points or centroids of polygons

6 **Table 2S Resolution and covered grid cells for virus discovery data**

		Polygon data			Point data	Total
		Country level	State/Province level	City/County level		
United States	Virus counts	NA	14 (14.7%)	11 (11.6%)	70 (73.7%)	95
	Gridded cell counts	NA	189	12	72[*]	273
China	Virus counts	NA	22 (27.5%)	47 (58.7%)	11 (13.8%)	80
	Gridded cell counts	NA	161	70	12[*]	243
	Virus counts	7 (6.5)	5 (4.7%)	15 (14.0%)	80 (74.8%)	107
Africa	Gridded cell counts	307	22	17	80	426

7 [*]Grid cell counts here include viruses first detected in multiple points from the literature, NA, not applicable

8 **Table 3S Model parameters**

Model	Tree complexity	Learning rate	Bag fraction	No. of trees
United States	2	0.0020	0.5	1430
China	2	0.0035	0.5	1473
Africa	2	0.0030	0.5	1446

9 **Table 4S Model validation statistics for analyses in three regions**

Model	% of deviance explained (95% quantiles)	ICC (95% quantiles)
United States	50.5% (44.3%−56.8%)	0.66 (0.60−0.70)
China	42.0% (32.4%−50.8%)	0.52 (0.41−0.60)
Africa	42.4% (34.2%−50.0%)	0.51 (0.44−0.62)

10 ICC, infraclass correlation coefficient

11

Supplementary Figures
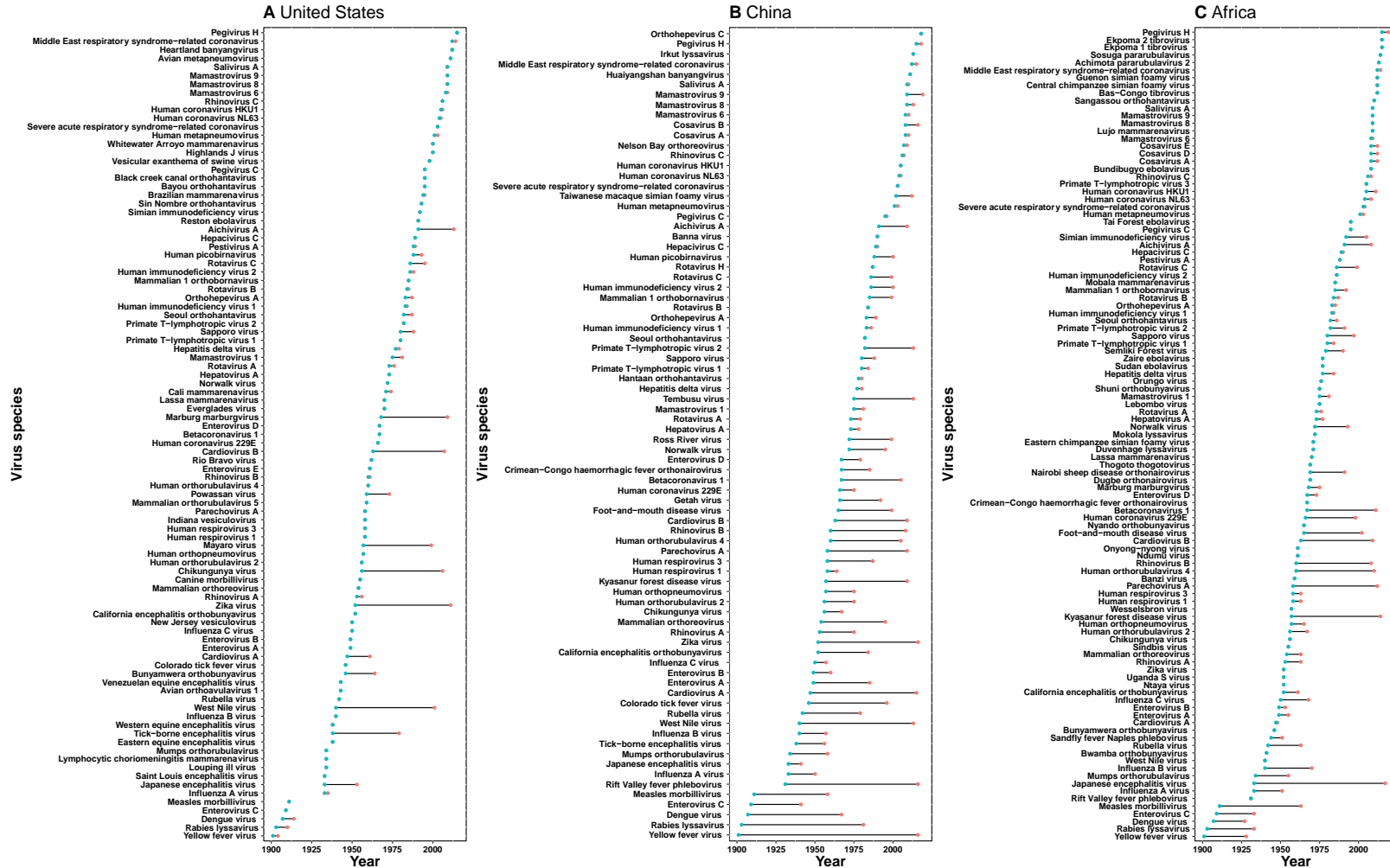
Figure 1S Time lag of human-infective RNA virus discovery between the three regions and the world. A, United States. B, China. C, Africa. The blue dots represent the original discovery year of each virus in the world; the red dots represent the discovery year of each virus in three regions; and the segments between them represent the time lag.
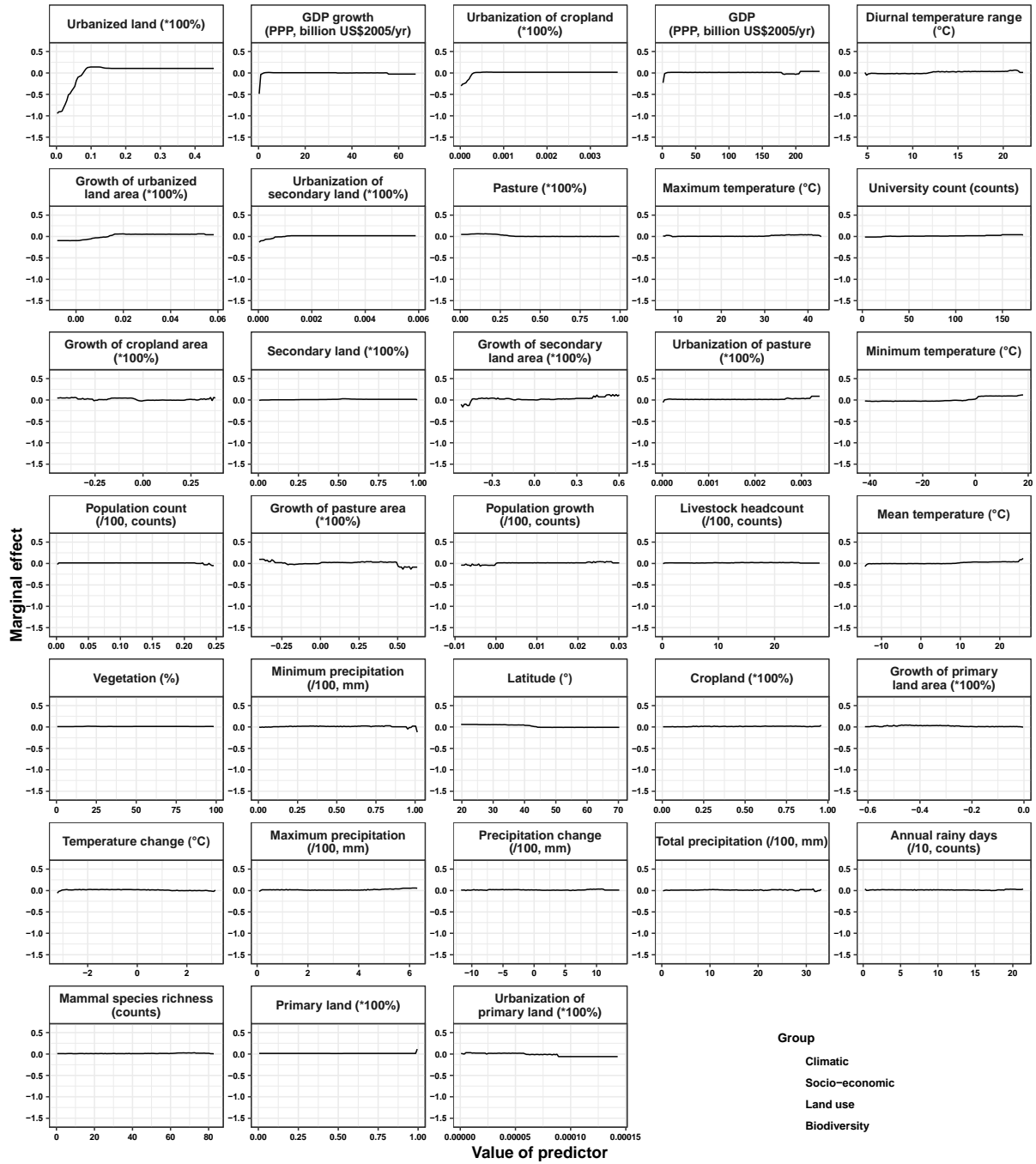
16
17 **Figure 2S Partial dependence plots showing the influence on human-infective RNA virus discovery for all**
18 **predictors in the Unites States.** Partial dependence plots show the effect of an individual explanatory factor
19 over its range on the response after factoring out other explanatory factors. Fitted lines represent the median
20 (black) and 95% quantiles (coloured) based on 1000 replicated models. Y axes are centred around the mean
21 without scaling. X axes show the range of sampled values of explanatory factors.

13
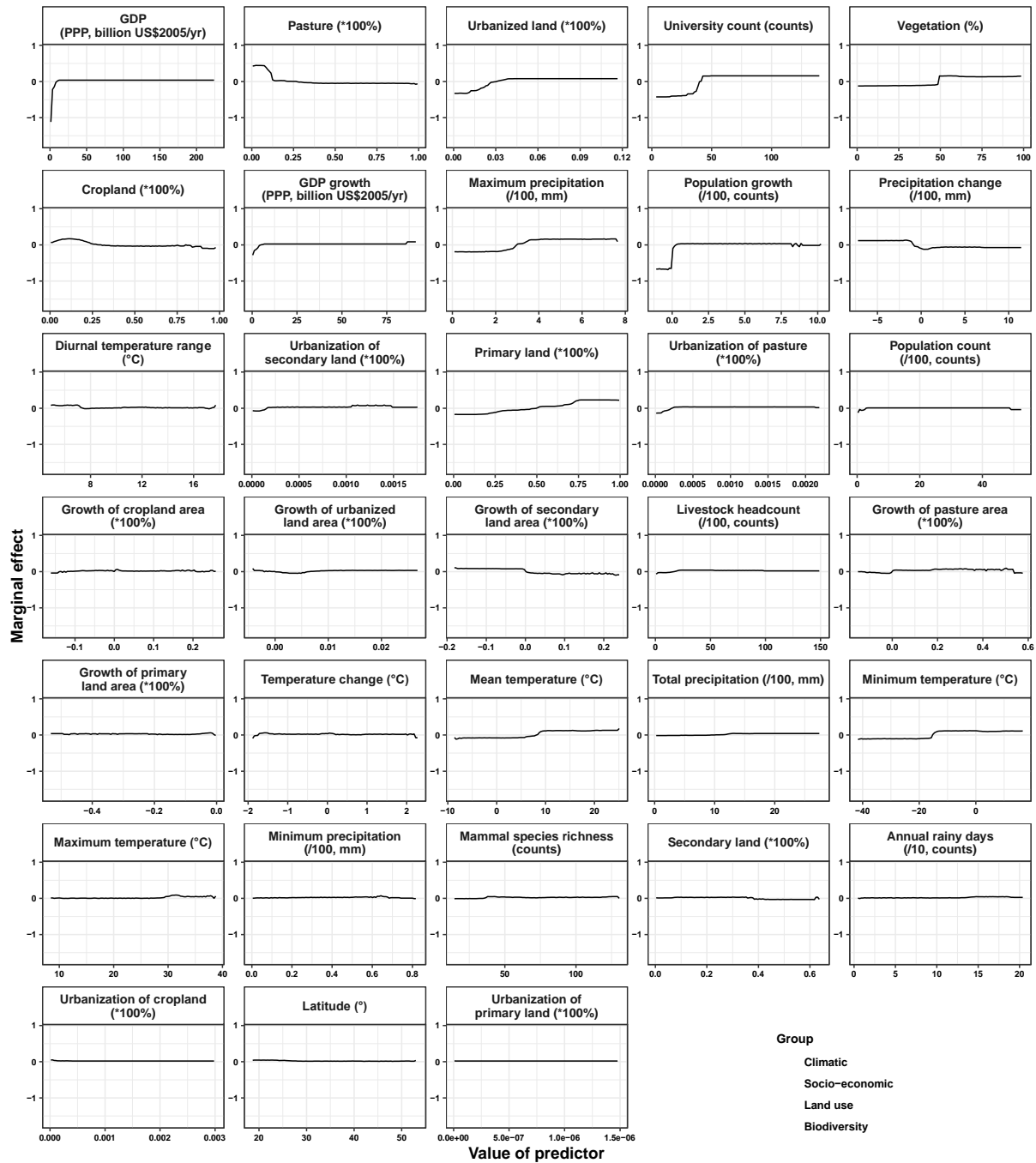
Figure 3S Partial dependence plots showing the influence on human-infective RNA virus discovery for all risk factors in China. Partial dependence plots show the effect of an individual explanatory factor over its range on the response after factoring out other explanatory factors. Fitted lines represent the median (black) and 95% quantiles (coloured) based on 1000 replicated models. Y axes are centred around the mean without scaling. X axes show the range of sampled values of explanatory factors.

28
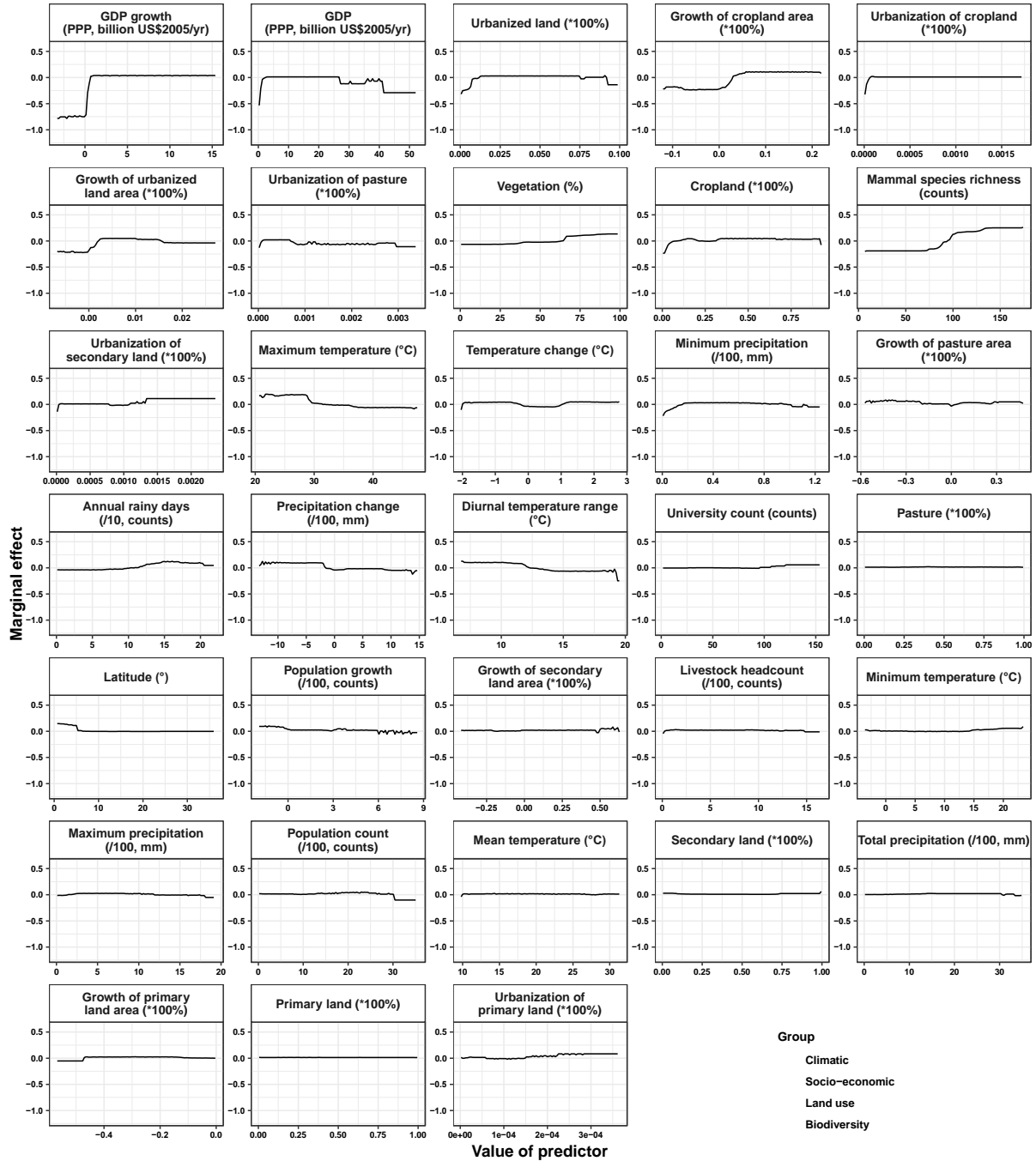
Figure 4S Partial dependence plots showing the influence on human-infective RNA virus discovery for all risk factors in Africa. Partial dependence plots show the effect of an individual explanatory factor over its range on the response after factoring out other explanatory factors. Fitted lines represent the median (black) and 95% quantiles (coloured) based on 1000 replicated models. Y axes are centred around the mean without scaling. X axes show the range of sampled values of explanatory factors.

15
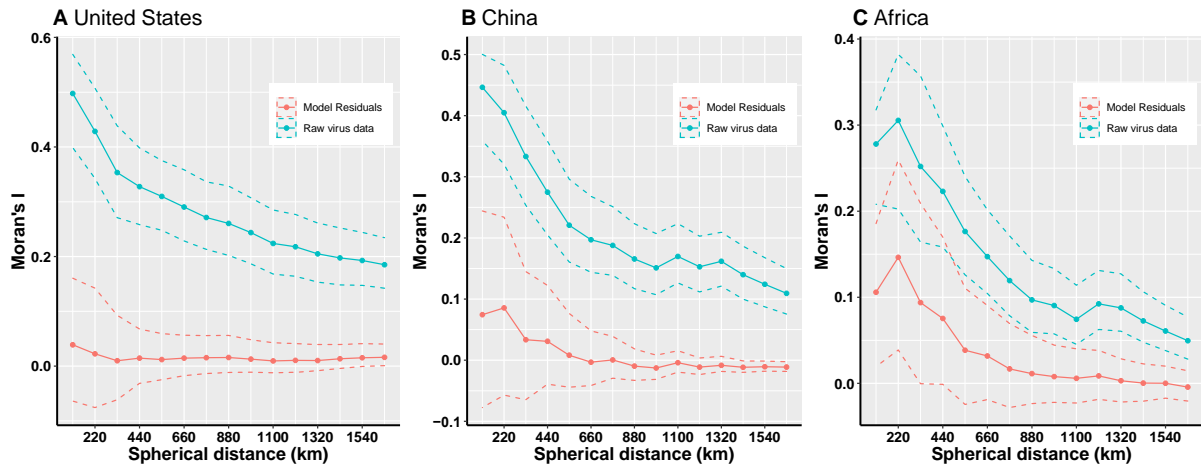
Figure 5S Moran's I across different spherical distances. A, United States; B, China; C, Africa. The solid line and dots represented the median Moran's I value, and the grey area represented its 95% quantiles generated from 1000 samples (Blue: Raw virus data) or replicate BRT models (Red: Model residuals). We used the fixed spherical distance as the neighbourhood weights—as there is no general consensus for selecting cut-off values, we chose spherical distances ranging from one time to fifteen times of distance of 1° grid cell at the equator, i.e. 110km to 1650km, considering the area of three regions. Our BRT models reduced Moran's I value from a range of 0.19–0.50 for the raw virus data to 0.009–0.04 for the model residuals in the United States A), 0.11–0.45 to -0.01–0.09 in China B), 0.05–0.31 to -0.004–0.15 in Africa C), suggesting that BRT models with 33 predictors have adequately accounted for spatial autocorrelations in the raw virus data in all three regions.
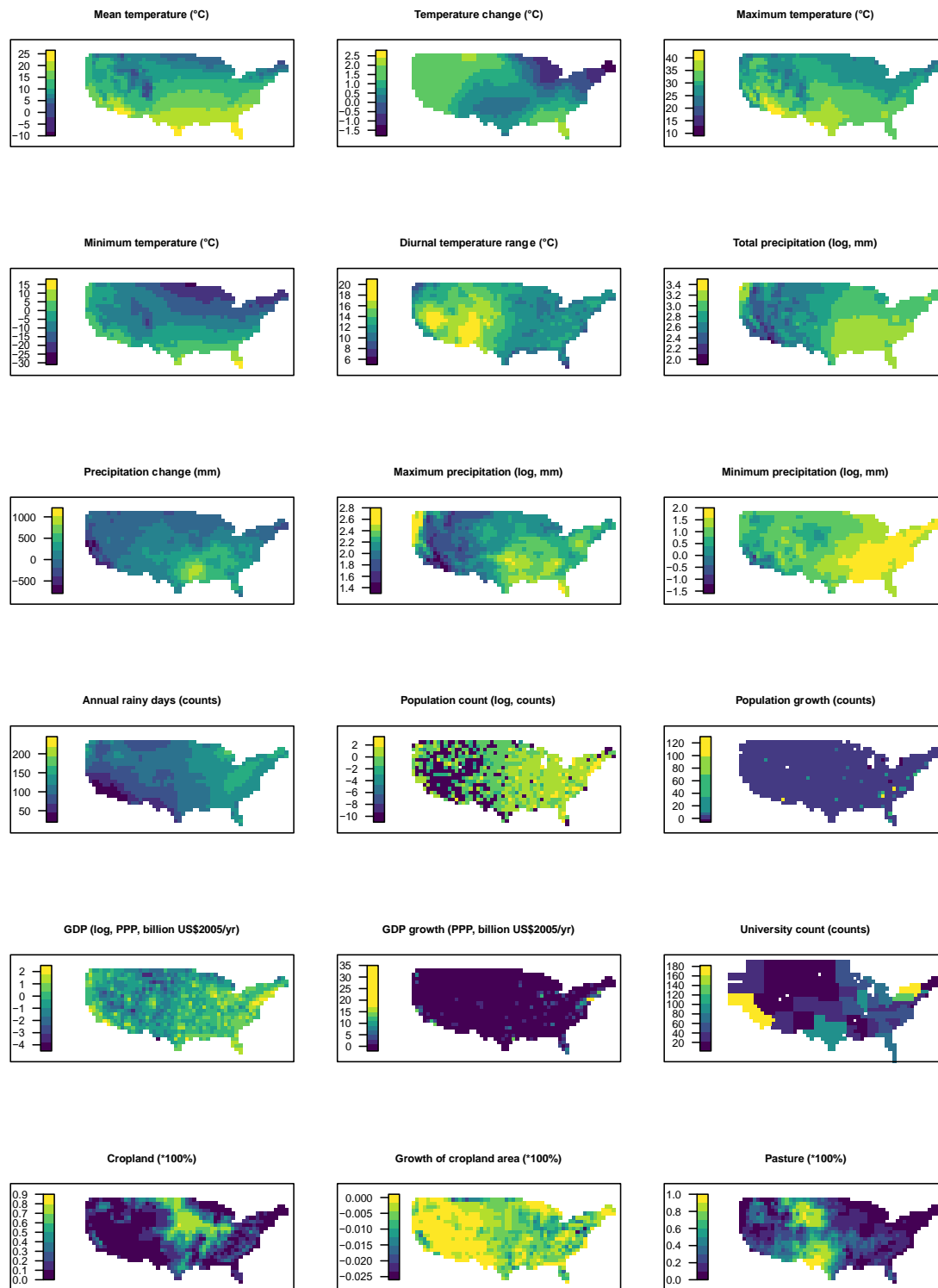
Figure 6S Distribution maps for 32 predictors in 2015 in the United States. The values of these explanatory variables and latitude in each grid cell were used to predict the virus discovery in the corresponding grid cell in the Unites States in 2010–2019. Explanatory variables were log transformed where necessary to get better visualization, not meaning they entered the model by logged values.
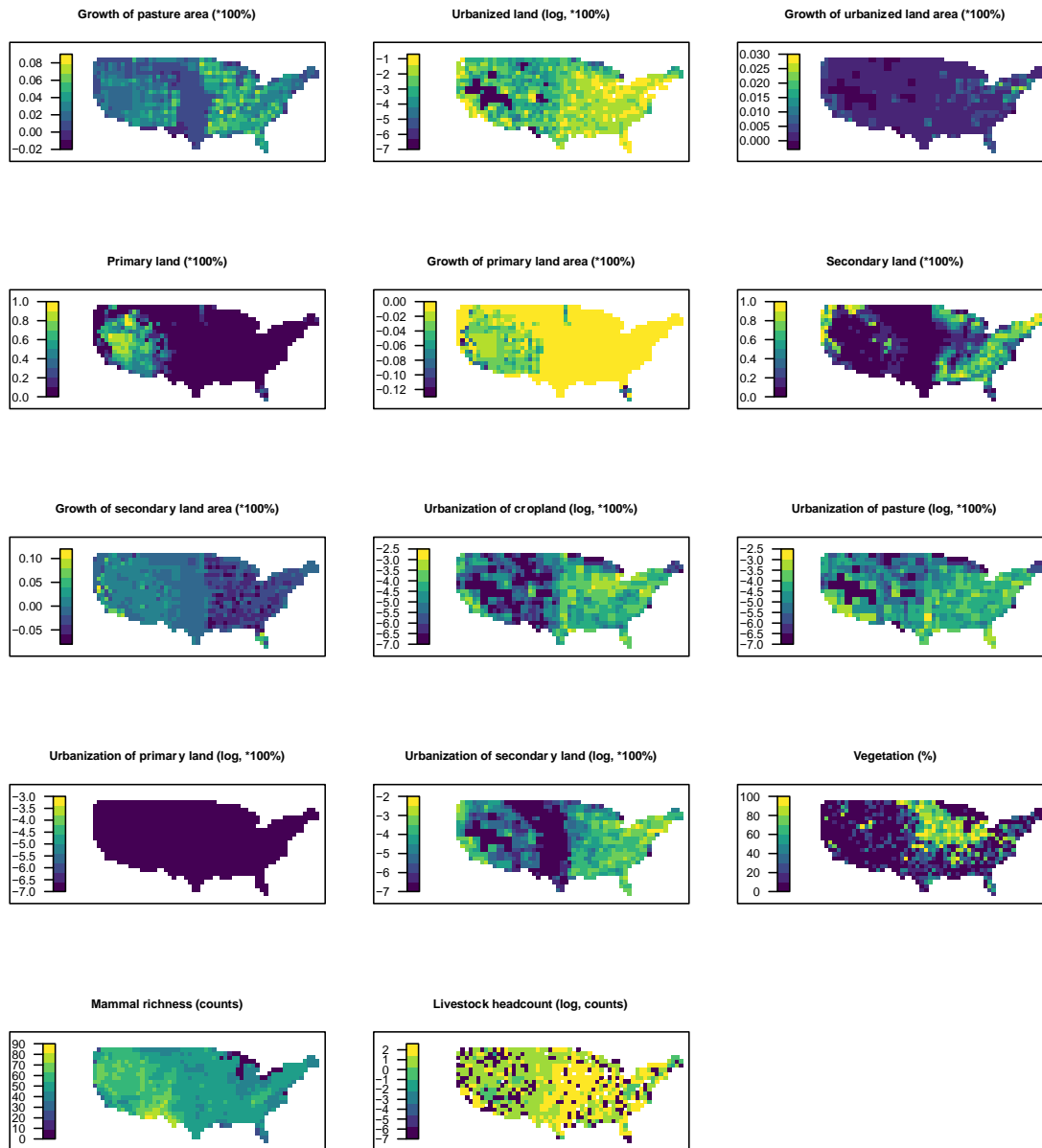
50
51   **Figure 6S Continued**
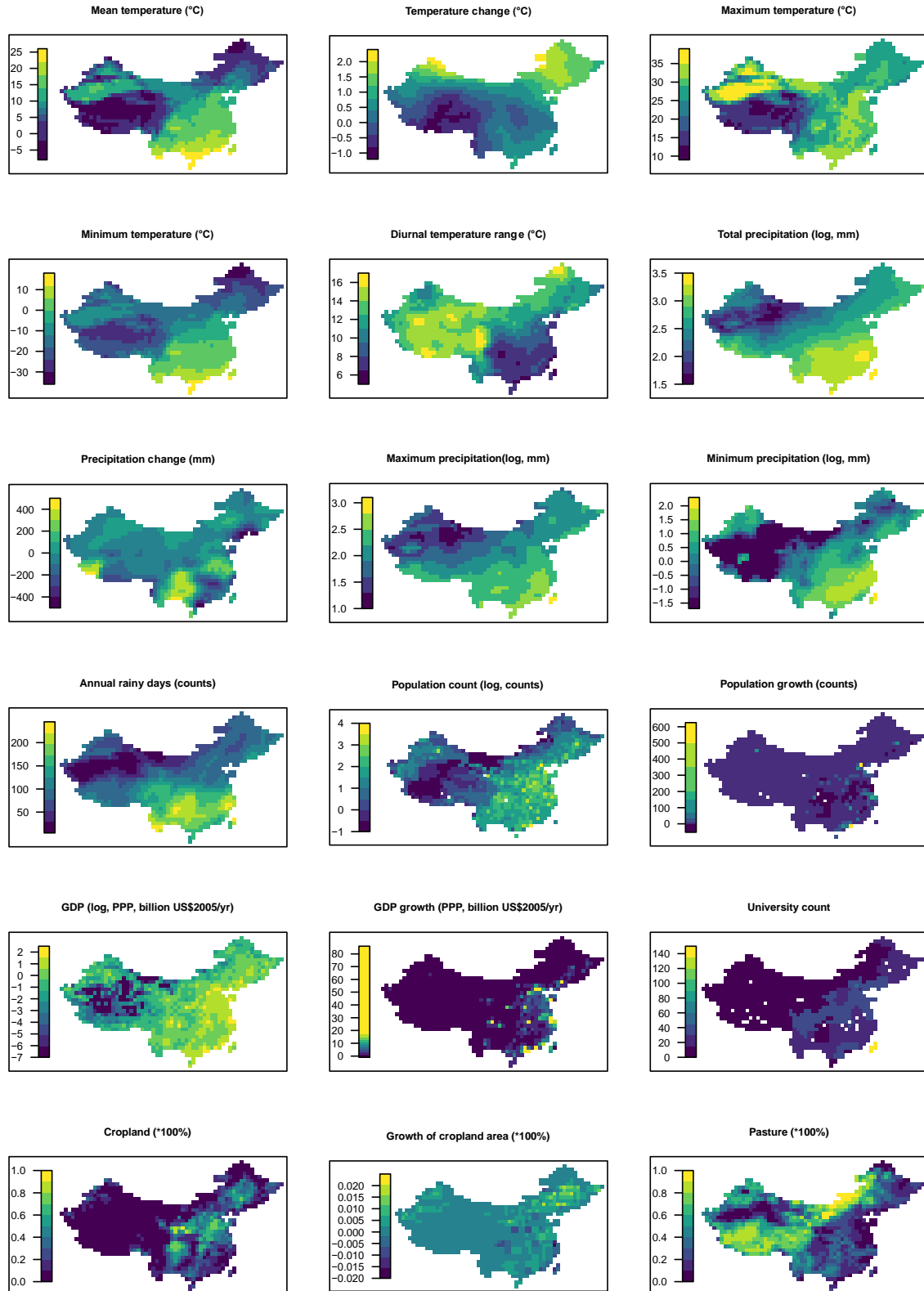
Figure 7S Distribution maps for 32 predictors in 2015 in China. The values of these explanatory variables and latitude in each grid cell were used to predict the virus discovery in the corresponding grid cell in China in 2010–2019. Explanatory variables were log transformed where necessary to get better visualization, not meaning they entered the model by logged values.
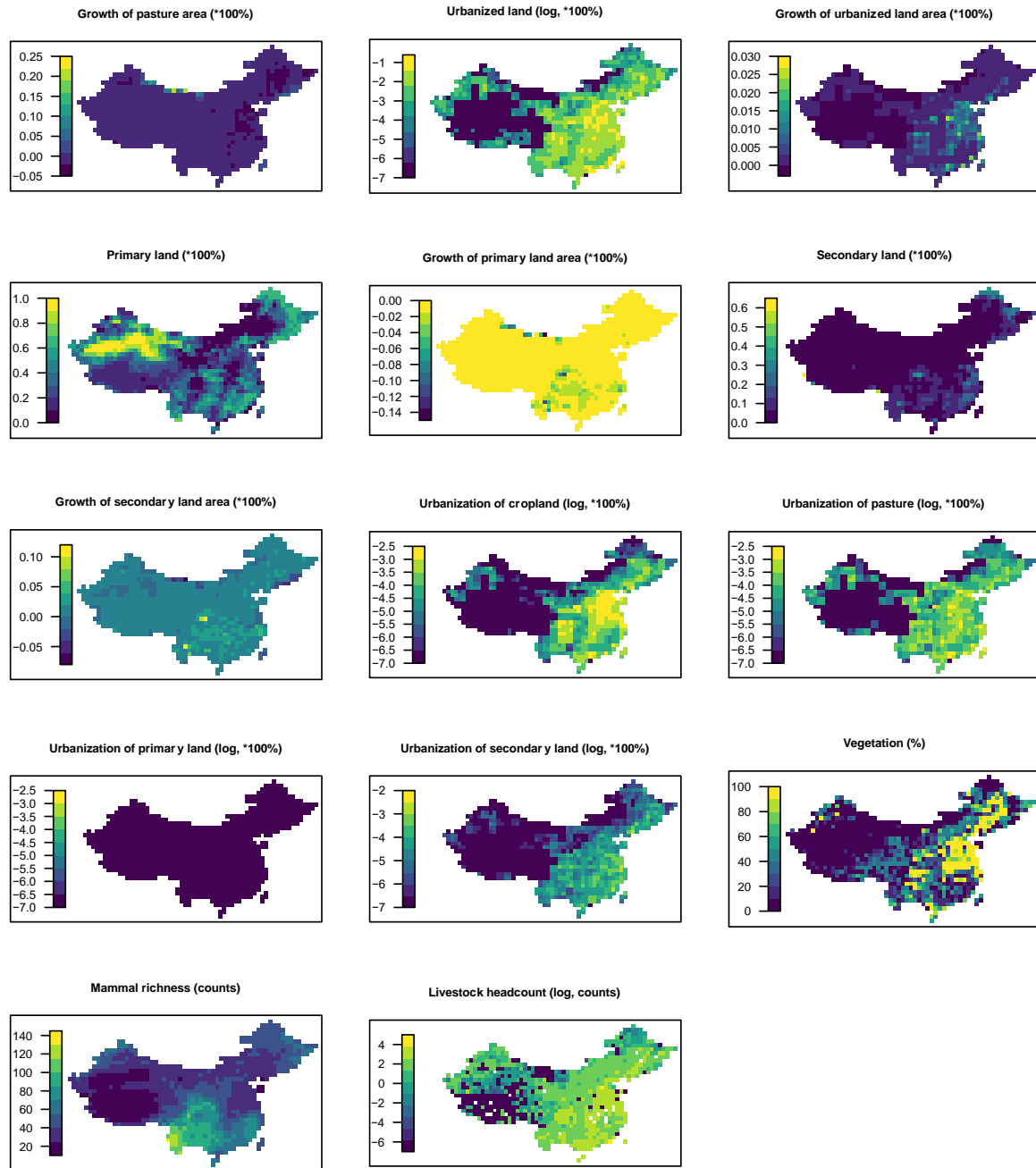
57
58 **Figure 7S Continued**
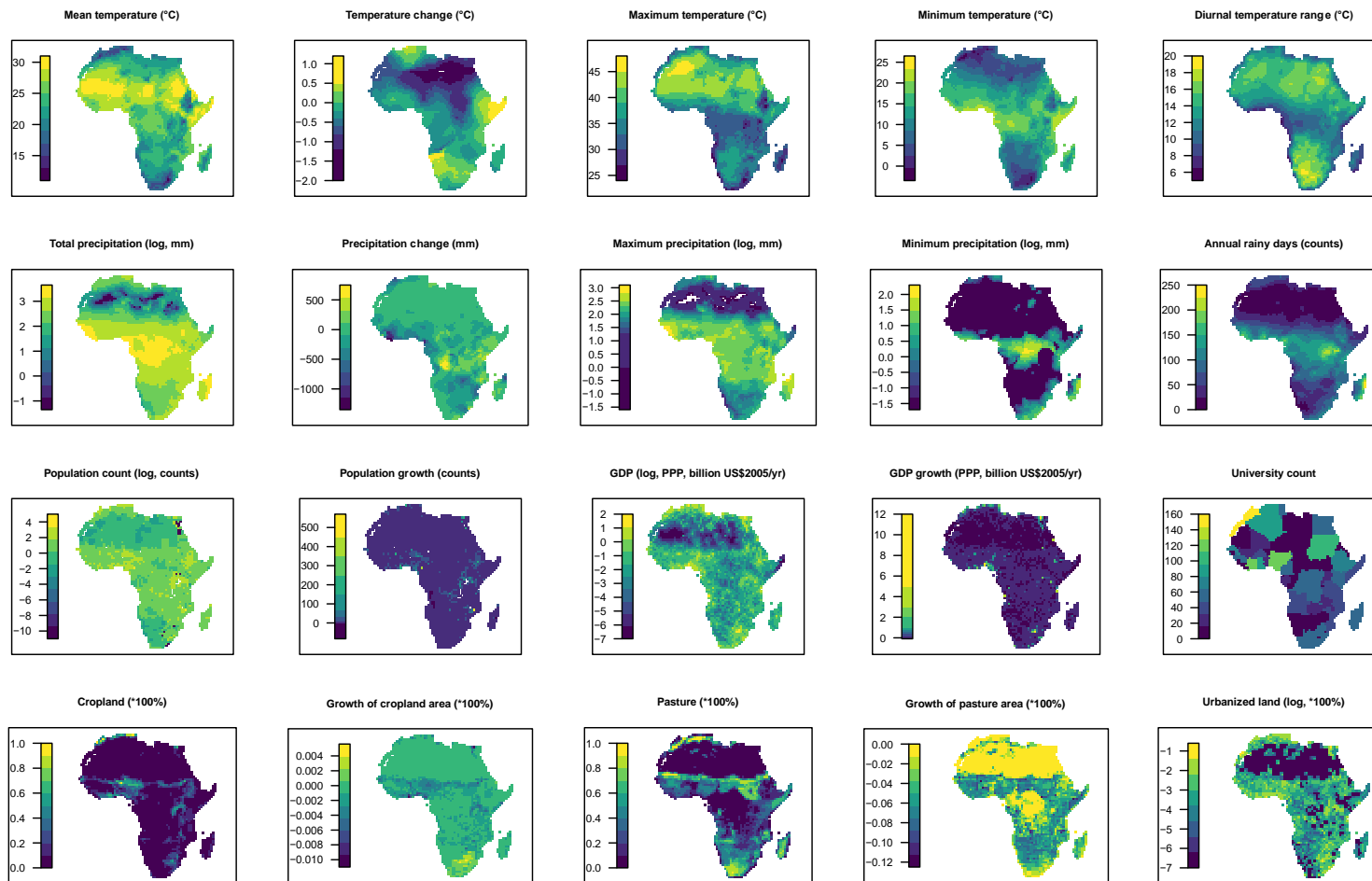
59
60 **Figure 8S Distribution maps for 32 predictors in 2015 in Africa.** The values of these explanatory variables and latitude in each grid cell were used to predict the virus
61 discovery in the corresponding grid cell in Africa in 2010–2019. Explanatory variables were log transformed where necessary to get better visualization, not meaning they
62 entered the model by logged values.
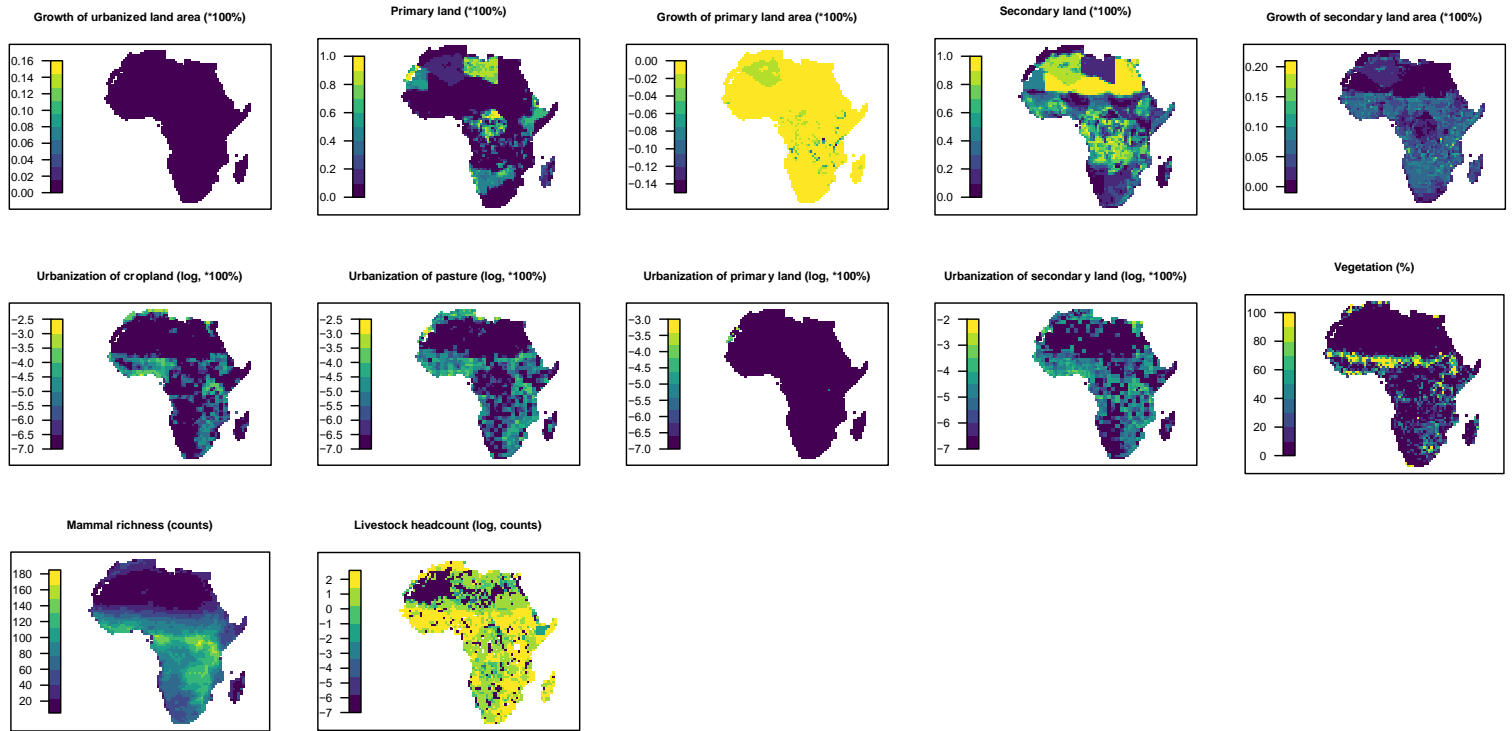
63
64 **Figure 8S Continued**
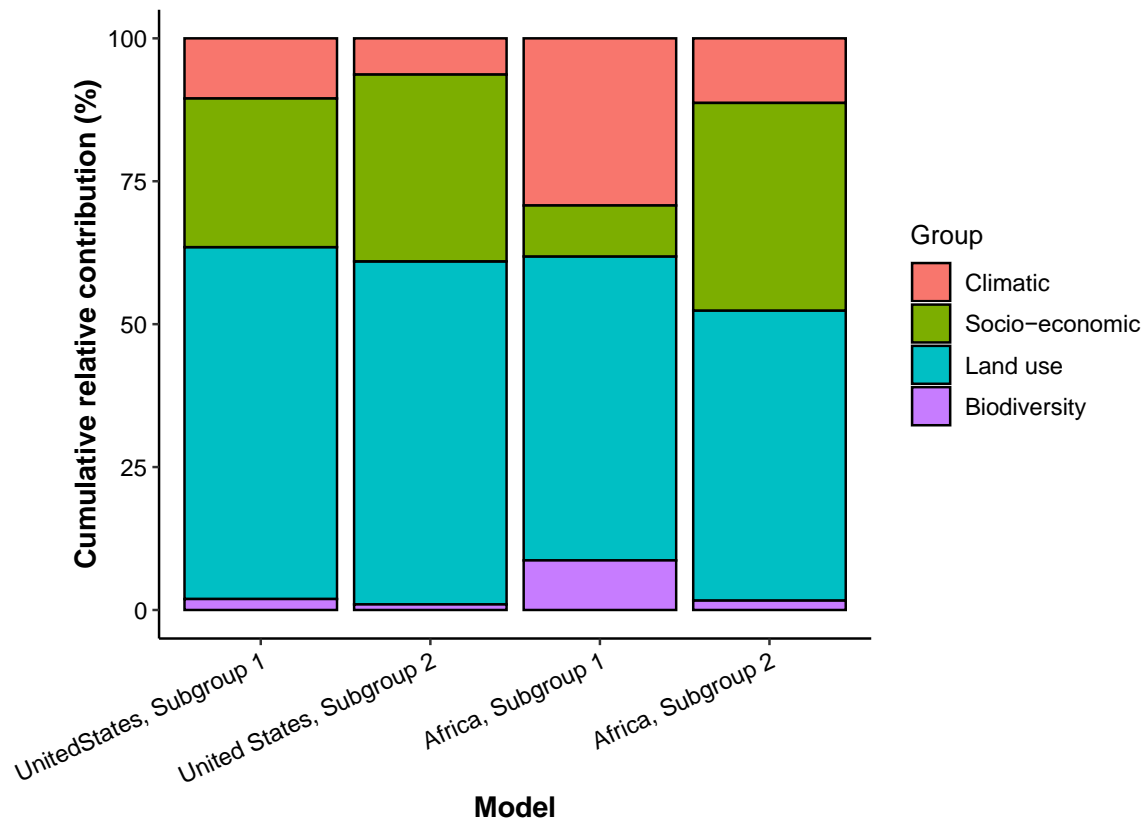
Figure 9S Cumulative relative contribution of predictors to human-infective RNA virus discovery by group in each model of subgroups. Subgroup 1 represents viruses firstly discovered from the region (United States or Africa); Subgroup 2 represents viruses firstly discovered elsewhere in the world. The relative contributions of all explanatory factors sum to 100% in each model, and each colour represents the cumulative relative contribution of all explanatory factors within each group.

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