RESEARCH ARTICLE

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

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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 better predicted by land use and socio-economic variables than climatic variables and biodiversity, although 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.

Conclusions: The drivers of spatiotemporal variation in virus discovery rates vary in different regions of the world. Within regions virus discovery is driven mainly by land-use and socio-economic variables; climate and biodiversity variables are consistently less important predictors than at a global scale. Potential new discovery hotspots in 2010–2019 are identified. Results from the study could guide active surveillance for new human-infective viruses in local high-risk areas.

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Editor's evaluation

This study will be of interest to readers in the field of virus discovery. This study attempts to identify predictors of human-infective RNA virus discovery and predict high risk areas in a recent period in the United States, China, and Africa using an ecological modeling framework. The study has potential to inform future discovery efforts for human-infective viruses.

Introduction

RNA viruses are the primary cause for emerging infectious diseases with epidemic potential, given that they have a high rate of evolution and high capacity to adapt to new hosts (***Woolhouse et al., 2016***). In recent decades, infectious diseases caused by severe acute respiratory syndrome coronavirus (SARS-CoV), Middle East respiratory syndrome coronavirus (MERS-CoV), Bundibugyo Ebola virus and SARS-CoV-2 present major threats to the health and welfare of humans (***Albariño et al., 2013***; ***Ksiazek et al., 2003***; ***Mackay and Arden, 2015***; ***World Health Organisation, 2020***). Detection of formerly unknown human-infective RNA viruses in the earliest stage after the emergence are essential for controlling the infections they cause. Measures to implement early detection include not only advanced diagnostic techniques (***Lipkin and Firth, 2013***), but more importantly the idea where to look for them (so-called hotspots) (***Morse, 2012***).

Socio-economic, environmental, and ecological factors related to both virus natural history and research effort have been found to affect the discovery of emerging RNA viruses (***Jones et al., 2008***; ***Morse, 2012***; ***Rosenberg, 2015***; ***Zhang et al., 2020***). However, these factors are highly spatially heterogeneous, making the generality of any associations with discovery debatable. For example, the United States, China, and Africa have experienced different rates of socio-economic, environmental, and ecological changes in the last one hundred years. The United States has always had better resources to discover new viruses. For example, the Rockefeller Foundation—a U.S. foundation—supported the discovery of 23 arboviruses in Latin America, Africa, and India in 1951–1969 (***Rosenberg et al., 2013***). China has seen urban land coverage more than double and GDP per capita increase by seven times since the 1980s (***Ritchie, 2018***; ***Roser, 2013***). Nine out of 223 human-infective RNA viruses have been originally discovered in China, and all were discovered after 1982 (***Zhang et al., 2020***). In contrast, effective surveillance is challenging in less developed regions such as large parts of Africa given resource constraints (***Petti et al., 2006***).

There have been no previous comparisons of the specific predictors for RNA virus discovery in different regions. In this study, we applied a similar methodology from our previous study of global patterns of discovery of human-infective RNA viruses (***Zhang et al., 2020***) to investigate 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, using three new virus discovery data sets. We also mapped discovery probability in three regions in 2010–2019 using the fitted models and historical predictors. According to findings from our previous study (***Zhang et al., 2020***), the main predictors for virus discovery at the global scale were GDP-related. This suggests that the patterns of virus discovery we have identified may have been largely driven by research effort rather than the underlying biology. In this study, by focusing on more restricted and homogenous regions where the research effort is less variable, we expected to identify predictors more associated with virus biology.

Materials and methods

Data sets of human-infective RNA viruses in three regions

We performed an ecological study, and the subject of interest is each human-infective RNA virus species. With reference to a full list of human-infective RNA virus species (***Zhang et al., 2020***), we geocoded the first report of each in humans in the United States, China, and Africa separately. The latest version as of 31 December 2019 included 223 species (***Appendix 1—table 1***), with *Human torovirus* abolished and a new species—*Heartland banyangvirus*—added by International Committee on Taxonomy of Viruses (ICTV) in 2018 (***International Committee on Taxonomy of Viruses, 2018***). Data used in this study were not subsets of our previous global analysis; information on discovery locations and discovery dates for each virus species was re-collated for each specific geographical region.

We followed the same search terms, databases searched, and inclusion or exclusion criteria as our global data set for data collection (***Woolhouse and Brierley, 2018***). In each region, we established whether or not each virus species has been discovered in humans according to peer-reviewed literature. Reference databases included PubMed, Web of Science, Google Scholar, and Scopus. Two Chinese databases [i.e. China National Knowledge Infrastructure (CNKI) and Wanfang Data] were also searched when collecting data for China. Reference lists of relevant studies and reviews were also checked manually to find potential earlier discovery papers. The following key words were used for the retrieval: virus full name or abbreviations or virus synonyms; and human* or person* or case* or patient* or worker* or infection* or disease* or outbreak* or epidemic*; and region name (Chin* or Taiwan or Hong Kong or Macau; United States or US or USA or America*; Africa* or all African country names). Virus synonyms and abbreviations include early names used in the discovery paper and all subtypes provided by the ICTV online report (***International Committee on Taxonomy of Viruses, 2018***). Evidence which met the following criteria from peer-reviewed literatures were included: (a) Diagnostic methods for RNA virus infection in humans were clearly described, through either viral isolation or serological methods; (b) Specific virus species name or subtypes falling under that species were clearly provided; (c) Both natural infection and iatrogenic or occupational infections were accepted. Evidence which met the following criteria were excluded: (a) Uncertain species due to cross-reactivity with related viruses; (b) Diagnostic methods for virus infection were not specified; (c) Description of clinical symptoms or pathogenicity were not considered as human infection of one certain virus species; (d) Report of '[virus name]-like' or 'potential [virus name] infections'; (e) Intentional infections including experimental inoculation or vitro infections; (f) Non-peer-reviewed literature, including media reports, thesis, or unpublished data. Literature selection was performed by two individuals independently and discrepancies were resolved by discussion with a third individual.

We defined discovery location as where the initial human was exposed to/infected with the virus, as suggested in the first report of human infections from peer-reviewed literature. All locations were geolocated as precisely as possible using methods from our previous paper (***Zhang et al., 2020***). For each region, a polygon was created for those locations at administrative level 3 (county for the United States; city for China; for Africa, it varies between different countries) and above. Details of data types for virus discovery database in three regions was summarised in ***Appendix 1—table 2***. Although the majority of discovery locations in the United States and Africa involved point data and in China the majority involved polygon data at province level, the average number of grid cells per virus in three regions were similar. A bootstrap resampling procedure was developed for polygon data covering more than one grid cell (details below). Discovery date of human infection was defined as the publication year in the scientific literature.

Spatial covariates

As for our global analysis (***Zhang et al., 2020***), a suite of global gridded climatic, socio-economic, land use, and biodiversity variables (n=33) postulated to affect the spatial distribution of RNA virus discovery were compiled, each at a resolution of 0.5°/30" (except university count having a resolution at country level for Africa and at state/province level for the United States and China). Of these, GDP, GDP growth, and university were included to adjust for discovery effort as they could partially explain the infrastructure and technology that are available for virus research (***Zhang et al., 2020***). We reviewed and tested previous strategies researchers have used to adjust for discovery bias, including frequency of the country listed as the address for authors in scientific papers and frequency of publications for each pathogen from scientific databases (***Jones et al., 2008***; ***Olival et al., 2017***) but the results were not encouraging as the frequency of published papers from virus-related scientific journals is weakly linked to the published count of novel human-infective RNA virus (Appendix2, ***Appendix 3—figure 1***).

Data for the United States, China, and Africa were extracted by restricting the coordinates within each region. The definition, original resolution, and source of each variable were the same as our previous paper (***Zhang et al., 2020***). All predictors were aggregated from their original spatial resolution to 1°×1° resolution; data for climatic variables, population, GDP, and land use data without full

temporal coverage were extrapolated back to 1901; both following methods from our previous paper (***Zhang et al., 2020***).

Boosted regression trees modelling

We used a Poisson boosted regression trees (BRT) model to examine the relationship between discovery of RNA virus and 33 predictors for each 1° resolution of grid cell across each region separately, following codes from our previous study (***Zhang et al., 2020***) and one previous paper (***Allen et al., 2017***). As a tree-based machine learning method, the BRT model can automatically capture complex relationships and interactions between variables, and also can well account for spatial autocorrelation within the data (***Crase et al., 2012***). We compared Moran's I values of the raw virus data and the model residuals to estimate the ability of the BRT model to account for spatial autocorrelation (***Cliff and Ord, 1981***). In order to minimise the effect of spatial uncertainty of virus discovery data, we performed 1000 times bootstrap resampling for those discovery locations reported as polygons. We assumed each grid cell in the polygon has the equal chance to be selected, and for each virus record we selected one grid cell randomly from the polygon for each subsample. A ratio of 1:2 for presence to absence constituted each subsample, that is, for each grid cell with virus discovery, two grid cells with no discovery were randomly selected from 'virus discovery free' areas at all time points within the region. Take the United States as an example, each subsample included 95 grid cells with virus discovery and 190 with no virus discovery. We then matched the virus data with all predictors by geographical coordinates and decade (using the nearest decade for time-varying predictors). We assumed that the virus count in any given grid cell in each decade followed a Poisson distribution, and we calculated the virus discovery count in each grid cell by decade as the response variable.We also performed further sensitivity analyses by (i) matching virus discovery data and time-varying covariate data by year and (ii) testing for lag effects by matching virus discovery at year t and predictors at t-1 to t-5 year (Appendix4).

All BRT models were fitted in R v. 3.6.3, using packages dismo and gbm. BRT models require the user to balance three parameters including tree complexity, learning rate, and bag fraction. Tree complexity reflects the order of interaction in a tree; learning rate shrinks the contribution of each tree to the growing model; bag fraction specifies the proportion of data drawn from the full training data at each step. We set these parameters as recommended from ***Elith et al., 2008***, and make sure each resampling model contained at least 1000 trees. BRT models identified the final optimal number of trees in each model using a 10-fold cross validation stagewise function (***Elith et al., 2008***). The three parameter values of the optimal model as well as the mean optimal number of trees across 1000 replicate models for all three regions were summarised in ***Appendix 1—table 3***.

By fitting 1000 replicate BRT models, the relative contribution plots and partial dependence plots with 95% quantiles were plotted. We defined variables with a relative contribution greater than the mean (3.03%) as influential predictors in all three regions (***Shearer et al., 2018***). The partial dependence plots depict the influence of each variable on the response while controlling for the average effects of all the other variables in the model. The map of virus discovery probability across each region in 2010–2019 was derived from the means of the predictions of 1000 replicate models, using values of the 33 predictors in 2015. In order to show discovery hotspots, we converted the prediction map of virus count to a map of probability.

Two statistics were calculated to evaluate the model's predictive performance: (a) the deviance of the bootstrap model (***Elith et al., 2008***), (b) intraclass correlation coefficient (ICC) calculated from 50 rounds of 10-fold cross-validation, by following methods from our previous paper (***Zhang et al., 2020***). For the 10-fold cross-validation, we selected 50 data sets randomly from the 1000 bootstrapped subsamples. We took the first data set and partitioned into 10 subsets. For each round of 10-fold cross-validation, the unique combinations of nine subsets constituted the training sets and were used to fit models, and the remaining one was used as a test set to evaluate the predictive performance of the model. We repeated the same process as above for the remaining 49 data sets. One intraclass correlation coefficient (ICC) was calculated from each round of validation and the median with 95% quantiles across all 50 rounds was calculated. The ICC varies between 0 and 1, with an ICC of less than 0.40 representing a poor model, 0.40–0.59 representing a fair model, 0.60–0.74 representing a good model, and 0.75–1 representing an excellent model (***Cicchetti, 1994***).

Exploratory subgroup analyses distinguishing viruses firstly discovered in regions and those that had been discovered elsewhere in the world were performed. We used the same BRT modelling

approach as we described above, and relative contribution of each predictor was calculated for each subgroup. We were unable to perform subgroup analysis for China because only nine human-infective RNA viruses have been firstly discovered in it, and the BRT model cannot be fitted to a sample as small as 9.

R software, version 3.6.3 (R Foundation for Statistical Computing, Vienna, Austria) was used for all statistical analyses. All maps were visualised by using ArcGIS Desktop 10.5.1 (Environmental Systems Research Institute).

Results

The numbers of human-infective virus species discovered in the United States, China, and Africa up to October 2019 were 95, 80, and 107, respectively (***Appendix 1—table 1***). Most first discoveries have been in eastern United States (especially in areas around Maryland, Washington, D.C., and New York), eastern China (developed cities including Beijing, Hong Kong, Shanghai, and Guangzhou), and southern and central Africa (Pretoria and Johannesburg, South Africa; Borno State and Ibadan, Nigeria) (***Figure 1***). A total of 60 virus species were previously reported in all three regions, and 27, 12, 37 species were only found in the United States, China, and Africa, respectively (***Figure 2***). In all three regions, smaller proportions of viruses were vector-borne [United States: 23.2% (22/95); China: 21.3% (17/80); Africa: 27.1% (29/107)] and strictly zoonotic [United States: 30.5% (29/95); China: 16.3% (13/80); Africa: 33.6% (36/107)], compared to large proportions for both virus types at the global scale [vector-borne: 41.7% (93/223) and strictly zoonotic: 58.7% (131/223)] (***Figure 2***). The 60 shared species were also disproportionally vector-borne [11.7% (7/60)] and strictly zoonotic [7% (4/60), ***Figure 2***].

The discovery curves for the United States and Africa have seen a broadly similar pattern, with China lagging behind these two regions (***Figure 3***). The median time lag between the original discovery year of each virus in the world and the discovery year of each virus in each region was 0 [interquartile range (IQR): 2.5], 12 (IQR: 29.5), and 2 (IQR: 10.5) years in the United States, China, and Africa, respectively (***Appendix 3—figure 2***). In China, the time lag was noticeably shorter for viruses discovered after 1975 [before 1975: a median lag of 30.5 (IQR: 30.5) years; after 1975: 2.5 (IQR: 7) years, p value of Wilcoxon rank sum test < 0.001].

In the United States, six variables including three predictors related to land use [urbanized land: relative contribution of 35.8%, urbanization of cropland (i.e. the percentage of land area change from cropland to urban land): 8.0%, growth of urbanized land: 4.1%], two socio-economic variables (GDP growth: 10.0%; GDP: 5.7%), and one climatic variable (diurnal temperature change: 4.9%) were identified as important predictors for discriminating between locations with and without virus discovery (***Figure 4A***). The partial dependence plots shown in ***Appendix 3—figure 3*** suggested non-linear relationships between the probability of virus discovery and most predictors. All important predictors presented a positive trend over narrow ranges at lower values.

In China, twelve variables including four socio-economic variables (GDP: 12.7%, university count: 7.5%, GDP growth: 4.6%, population growth: 4.4%), five predictors involving land use [pasture: 8.3%, urbanized land: 8.1%, vegetation: 5.8%, cropland: 5.3%, urbanization of secondary land (the percentage of land area change from secondary land to urban land; secondary land is natural vegetation that is recovering from previous human disturbance): 3.3%], and three climatic variables (maximum precipitation: 4.5%, precipitation change: 3.8%, diurnal temperature range: 3.3%) were identified as important predictors for discriminating between locations with and without virus discovery (***Figure 4B***). GDP, urbanized land, university count, vegetation, GDP growth, maximum precipitation, population growth, and urbanization of secondary land presented a positive trend over narrow ranges at lower levels; pasture, cropland, precipitation change, and diurnal temperature range had non-monotonic/negative impacts, with highest risks at lower values (***Appendix 3—figure 4***).

In Africa, ten variables including two socio-economic variables (GDP growth: 21.2%, GDP: 13.0%), seven predictors related to land use (urbanized land: 9.4%, growth of cropland area: 5.6%, urbanization of cropland: 5.5%, growth of urbanized land: 5.1%, urbanization of pasture: 3.8%, vegetation, 3.7%, cropland: 3.2%), and one biodiversity variable (mammal species richness: 3.1%) were identified as important predictors for discriminating between locations with and without virus discovery (***Figure 4C***). All important predictors presented a positive trend over narrow ranges at lower positive values, except mammal species over a large range (***Appendix 3—figure 5***).

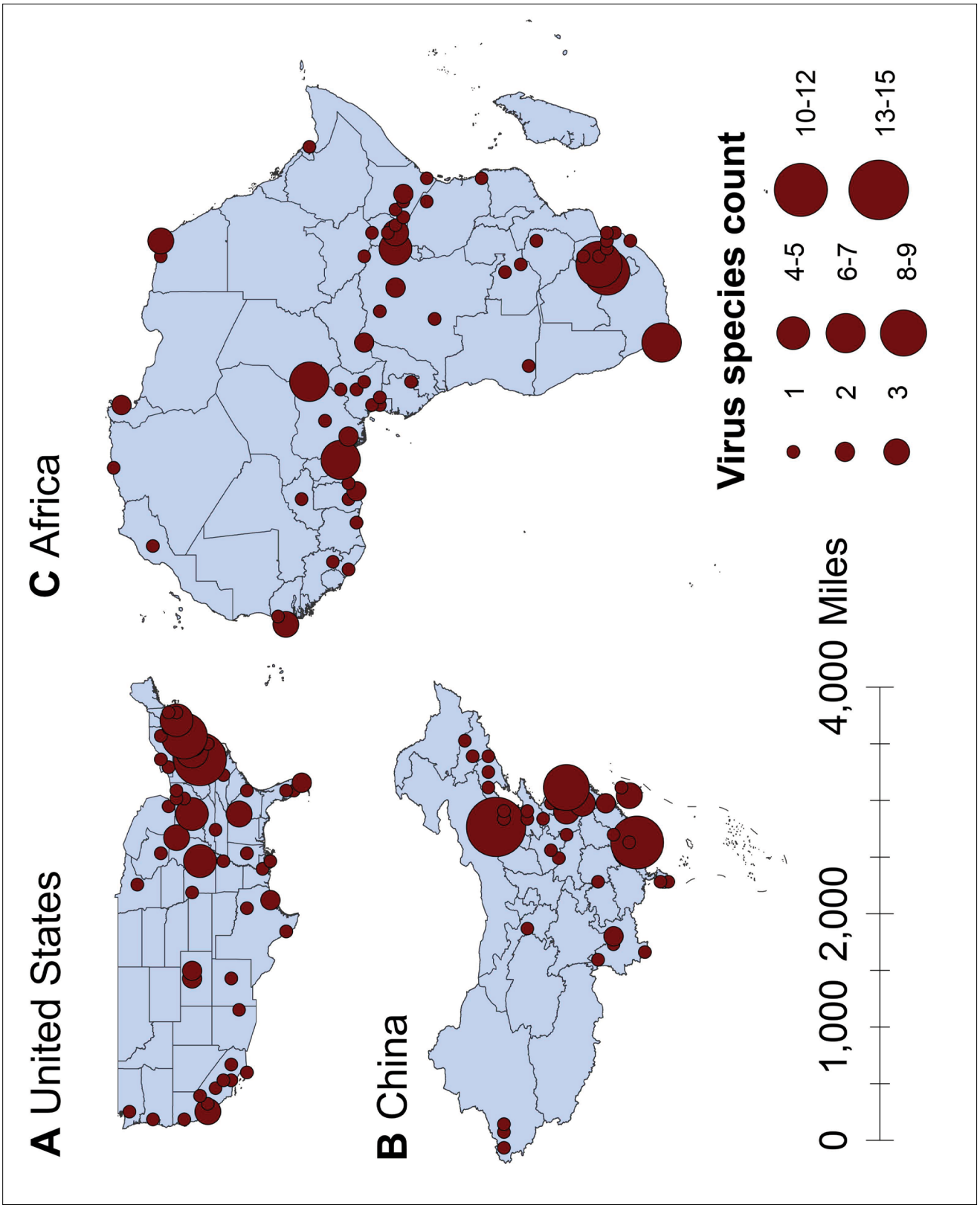

Figure 1. Spatial distribution of human-infective RNA virus discovery in three regions, 1901–2019. (**A**) United States. (**B**) China. (**C**) Africa. Red dots represent discovery points or centroids of polygons, with the size representing the cumulative virus species count.

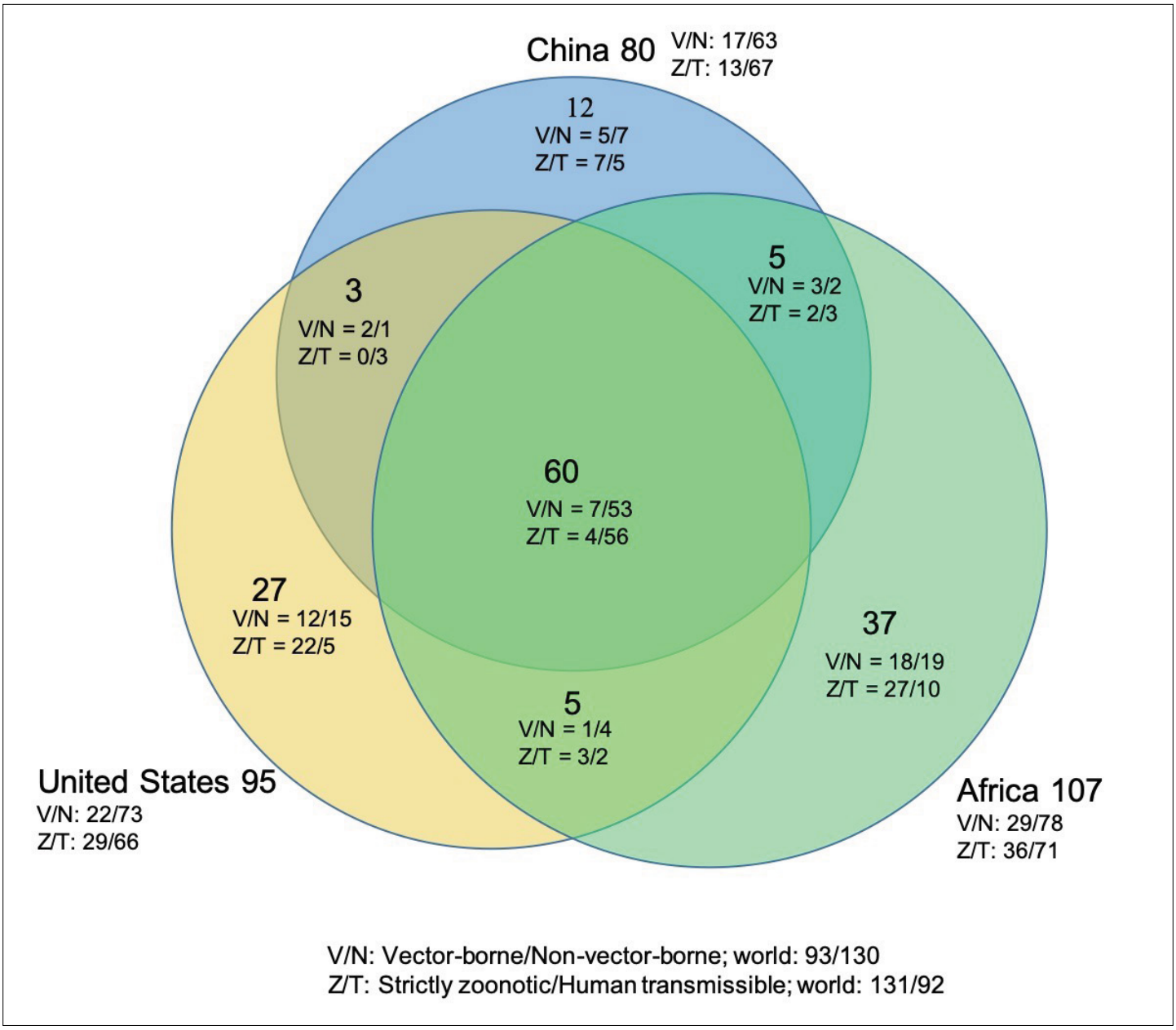

Figure 2. Shared human-infective RNA virus species count in three regions. Under/By the species count the ratios of vector-borne (**V**) to non-vector-borne (**N**) viruses and strictly zoonotic (**Z**) to human transmissible (**T**) viruses were shown.

Our BRT models reduced Moran's I value below 0.15 in all three regions (***Appendix 3—figure 6***), suggesting that BRT models with 33 predictors have adequately accounted for spatial autocorrelations in the raw virus data in all three regions. The model validation statistics for each region are shown in ***Appendix 1—table 4***. Combining these measures, our BRT model predictions range from fair to good (***Cicchetti, 1994***). In our sensitivity analyses based on data matched by year (***Appendix 3—figure 7***) and 1–5 year lag (results of 1 year lag shown in ***Appendix 3—figure 8***), though there were several changes of relative contribution, the top predictors were broadly consistent with our main model based on data matched by decade (***Figure 4***).

In comparison with the whole world, human-infective RNA virus discovery was more associated with land use and socio-economic variables than climatic variables and biodiversity in all three regions (***Figure 5***). The comparison of four groups of predictors between three regions showed that: the greatest contribution of climatic variables to the discovery of human-infective RNA viruses was in

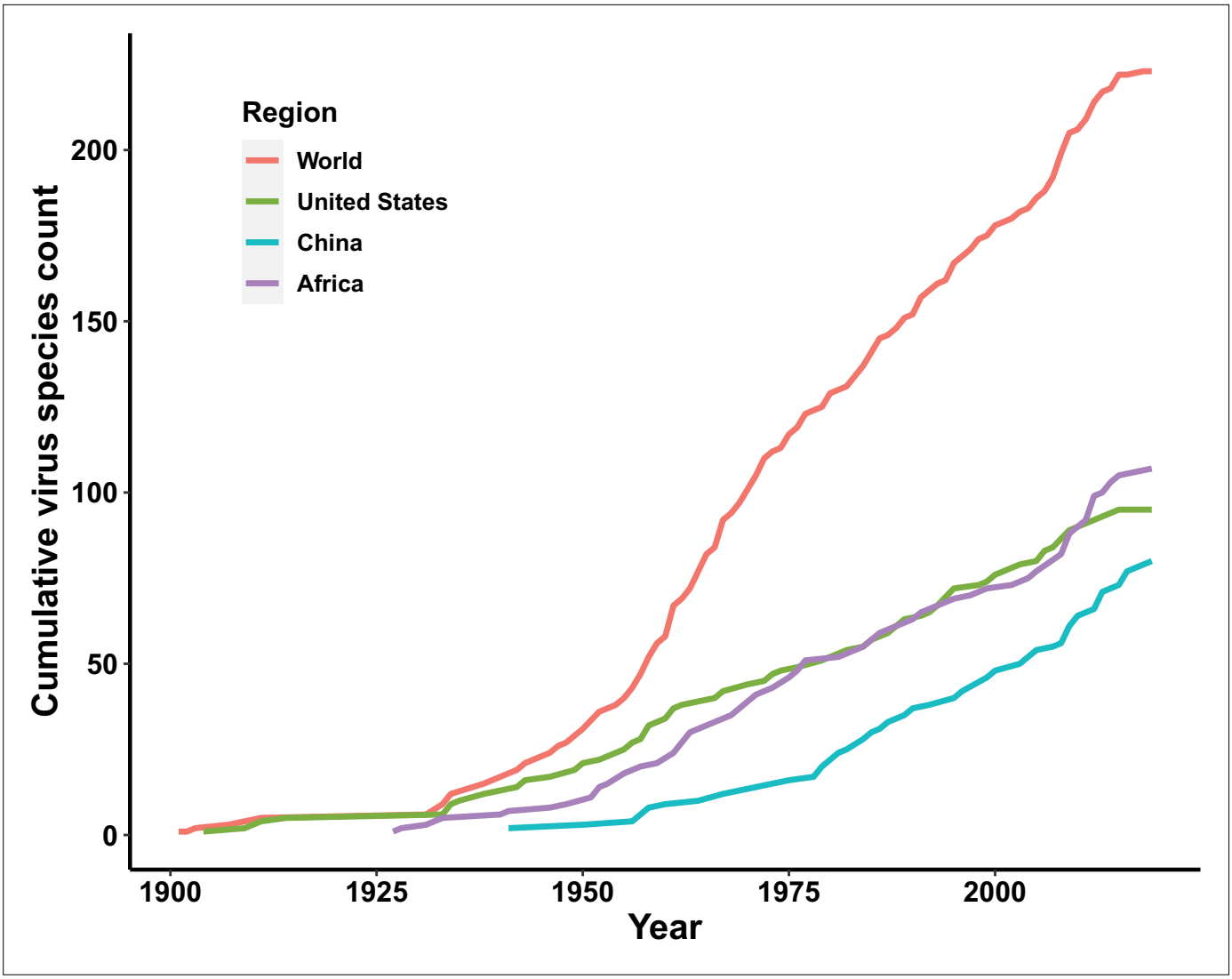

Figure 3. Discovery curve of human-infective RNA virus species in three regions and the world.

China; the greatest contribution of land use was in the United States; the greatest contribution of socio-economic variables and biodiversity was in Africa and least in the United States.

We mapped human-infective RNA virus discovery probability in 2010–2019 for the three regions, based on the fitted BRT models and values of all 33 predictors in 2015 (***Appendix 3—figure 9*** to ***Appendix 3—figure 11***). Outside contemporary risk areas where human-infective RNA viruses were previously discovered in the United States (***Figure 1A***), we predicted high probabilities of virus discovery across southern Michigan, central-Northern Carolina, central Oklahoma, southern Nevada, and north-eastern Utah (***Figure 6A***). Outside contemporary risk areas where human-infective RNA viruses were previously discovered in China (***Figure 1B***), we predicted high probabilities of virus discovery across other eastern China area as well as two western areas including south-central Shaanxi and north-eastern Sichuan (***Figure 6B***). Outside contemporary risk areas where human-infective RNA viruses were previously discovered in Africa (***Figure 1C***), we predicted high probabilities of virus discovery across northern Morocco, northern Algeria, northern Libya, south-eastern Sudan, central Ethiopia and western Democratic Republic of the Congo (***Figure 6C***). 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 (85% percentiles of predicted probability across each region) as predicted by our model. Of all the 37 (United States: 6; China: 19; Africa: 12) viruses discovered in high-risk areas in 2010–2019,

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 boosted regression tree models, with whiskers indicating minimum and maximum and black dots indicating outliers.

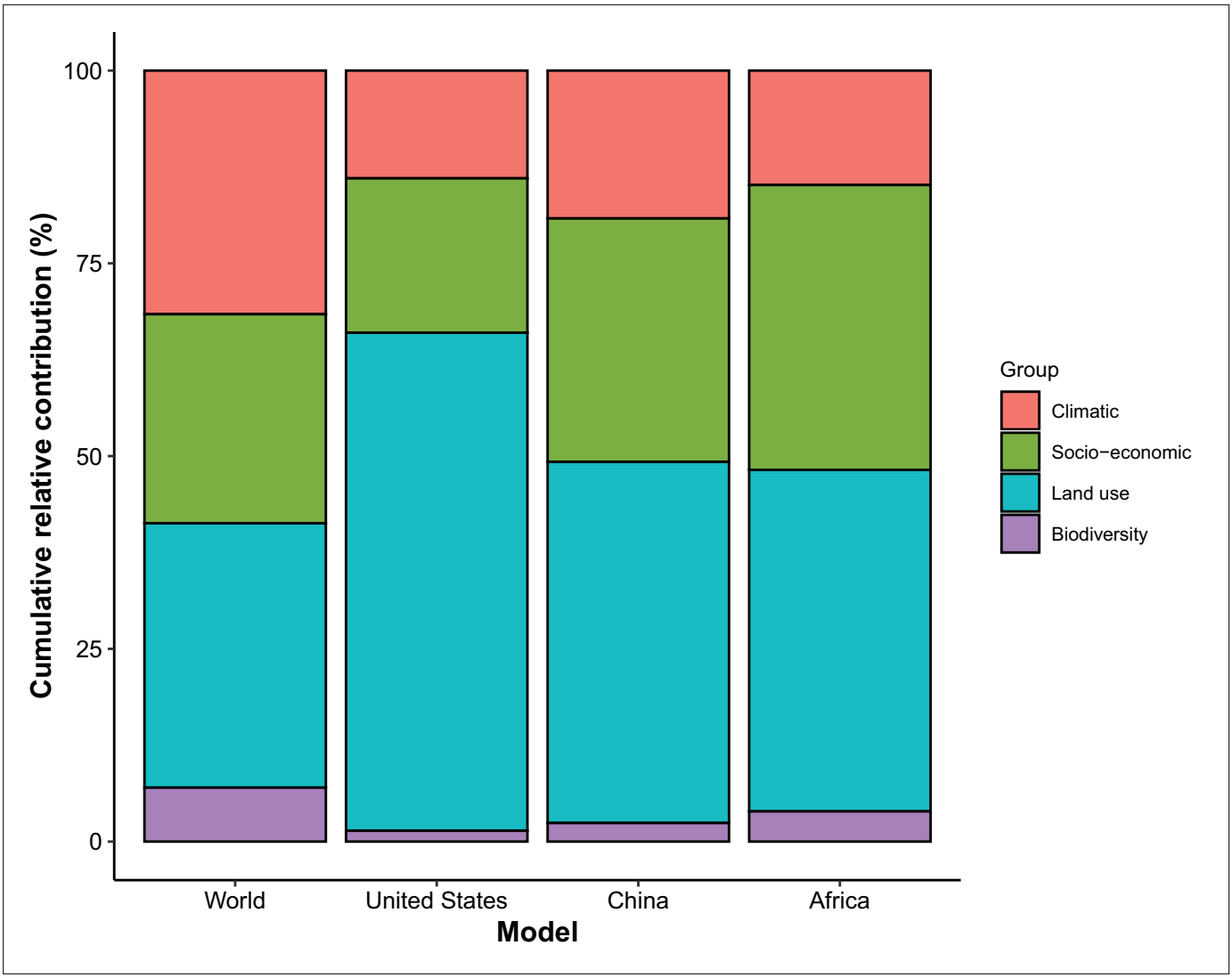

Figure 5. Cumulative relative contribution of predictors to human-infective RNA virus discovery by group in each model of different regions. The relative contributions of all explanatory factors sum to 100% in each model, and each colour represents the cumulative relative contribution of all explanatory factors within each group.

13 (United States: 2; China: 7; Africa: 4) viruses were discovered at the potential new hotspots where there have not been any virus discoveries before 2010.

Based on our subgroup analysis distinguishing viruses firstly discovered in regions and those that had been discovered elsewhere in the world, discoveries of human-infective RNA viruses first discovered from either United States or Africa were better predicted by climatic and biodiversity variables, while discoveries of viruses that had been discovered from elsewhere in the world were better predicted by socio-economic variables (***Appendix 3—figure 12***).

Discussion

To our knowledge, this analysis represents the first investigation of human-infective RNA virus discovery in three large regions of the world which have experienced distinct socio-economic, ecological and environmental changes over the last 100 years. In total, 95 human-infective RNA virus species had been found in the United States; 80 in China; 107 in Africa. The discovery maps of human-infective RNA virus in the three regions indicated areas with historically high discovery counts: eastern and western United States, eastern China, and central and southern Africa. BRT modelling suggested that

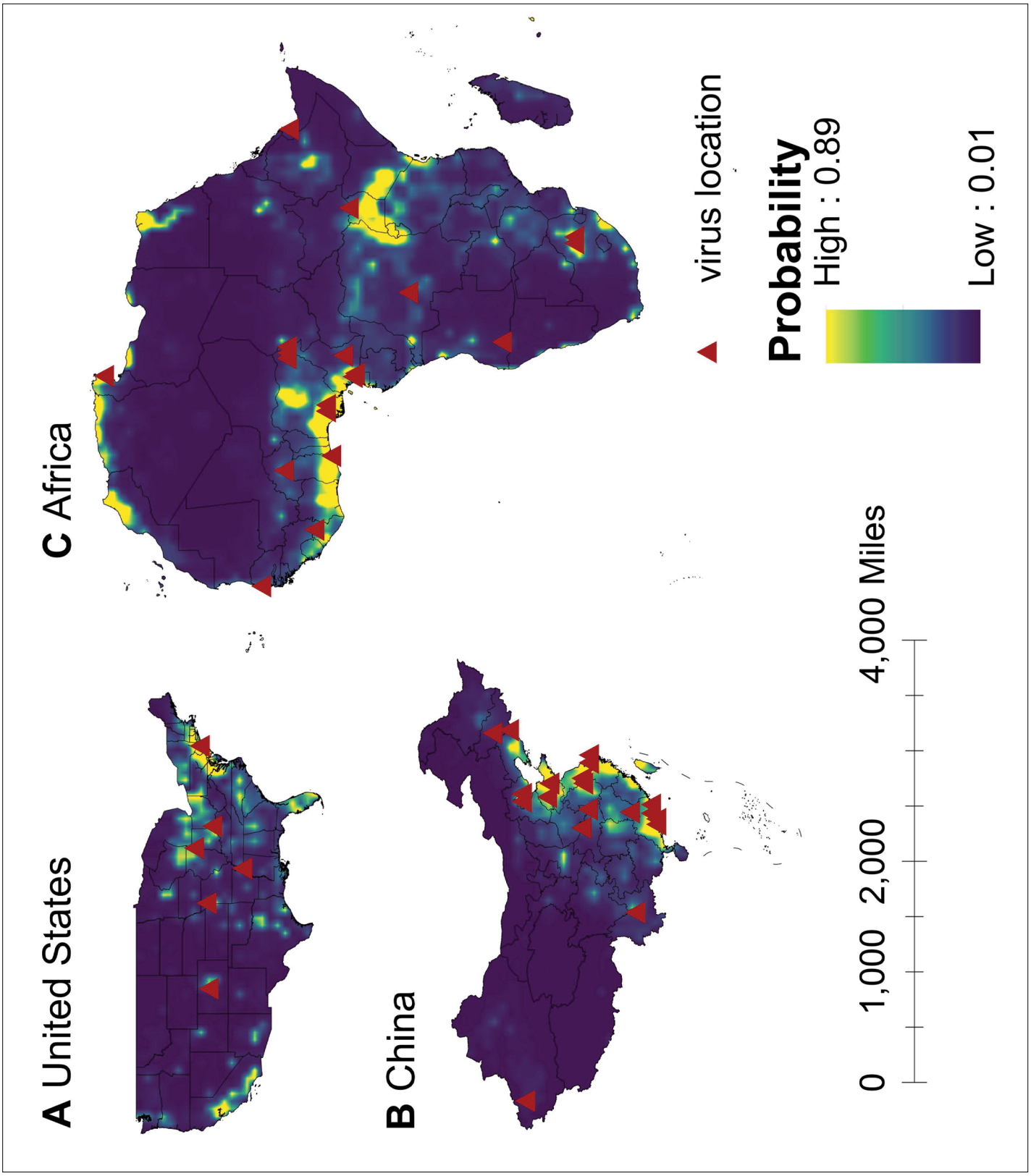

Figure 6. Predicted probability of human-infective RNA virus discovery in three regions in 2010–2019. (A) United States. (B) China. (C) Africa. The triangles represented the actual discovery sites from 2010 to 2019, and the background colour represented the predicted discovery probability.

the relative contribution of 33 predictors to human-infective RNA virus discovery varied across three regions, though climatic and biodiversity variables were consistently less important in all three regions than at a global scale. We mapped the probability of human-infective RNA virus discovery in 2010–2019 which would continue to be high in historical hotspots but, in addition, we identified several new hotspots in central-eastern and southwestern United States, eastern and western China, and northern Africa. These results offer a tool for public health practitioners and policymakers to better understand local patterns of virus discovery and to invest efficiently in surveillance systems at the local level.

In recent decades, factors that drive pathogen discovery have been comprehensively studied, e.g., (***Morse, 2012***). In general, evidence has come from three forms of analyses: analysis of single emergence event such as SARS, AIDS, and Ebola (***Parrish et al., 2008***), quantifying the spillover (or host switching/cross-host transmission) risk using traits of both hosts and viruses (***Kreuder Johnson et al., 2015***; ***Olival et al., 2017***; ***Pulliam and Dushoff, 2009***), and record of first emergence/discovery event in humans globally over time (***Allen et al., 2017***; ***Jones et al., 2008***; ***Zhang et al., 2020***). Of these, the latter form of analyses have linked the distribution of emerging infectious diseases across the globe to ecological, environmental, and socio-economic factors, predicted the high-risk areas for discovery of emerging zoonoses, and helped identify priority regions for investment in surveillance systems for new human viruses (***Allen et al., 2017***; ***Jones et al., 2008***; ***Zhang et al., 2020***). In addition to these analyses, our current regional analyses identified more precise hotspots for virus discovery in three large regions of the world. Because zoonotic viruses are responsible for most historical endemics and epidemic diseases, several projects such as the Global Virome project (GVP), the PREDICT project, and the Vietnam Initiative on Zoonotic Infections (VIZIONS) were launched to construct a comprehensive data set of unknown viruses with epidemic potential from specific animals likely to harbour high-risk viruses, humans having a high contacting rate with animals, and animal-human interfaces with high spill-over probability (***Carroll et al., 2018***; ***Morse, 2012***; ***Rabaa, 2015***). These hotspots analyses indicate priority regions for surveillance for new viruses for these projects.

In all three regions, GDP and/or GDP growth were identified as important predictors for virus discovery. This is consistent with our previous analysis that GDP and GDP growth play a major role in discovering viruses (***Zhang et al., 2020***). In general, sufficient economic, human and material resources, the availability of advanced infrastructure and technology, and greater research capabilities in the relative higher income areas enable the virus discovery (***Rosenberg et al., 2013***). That this effect applied both within one continent and within single countries such as the United States and China suggested that most virus discoveries were likely passive, that is, the viruses were detected when they arrived in a location with the resources to detect them. This is plausible because in all regions in our study, human-transmissible viruses accounted for the larger proportion, and our previous analysis suggested richer areas were more likely to first capture transmissible viruses (e.g. Influenza virus, Rhinovirus, Rabies lyssavirus, Measles morbillivirus, Mumps orthorubulavirus, Rubella virus, and Norwalk virus) capable of spreading to multiple areas (***Zhang et al., 2020***). Temporally, in China the rate of discovery increased after economic growth accelerated in the 1980s (***Figure 3***). We note in publications describing first virus discoveries that most historical virus discoveries in Africa received support from the United States and Europe, and this may explain why Africa saw an increased number of virus discoveries after 1950—30 years earlier than China (***Figure 3***). Notably, in contrast to Africa, university count was found to be associated with virus discovery in China, suggesting virus discovery likely being a significant area of research in Chinese universities. Our model also suggested the overall socio-economic factors contributed less in the United States than other two regions. The possible explanation is that the socio-economic level across the whole United States is relatively high and homogenous.

Predictors other than GDP and university count are likely to be linked to virus natural history. In all three regions, the area of urban land and further urbanization made great contribution to virus discovery. This reinforced previous studies that urbanization was linked to the detection of new human pathogens through the denser urban population, increased human-wildlife contact rate, spill-over of human infection from enzootic cycle, and the contamination of the urban environment with microbial agents (***Hassell et al., 2017***; ***Olival et al., 2017***; ***Weaver, 2013***). In the United States, land use contributed more to virus discovery than in other regions—urbanized land, urbanization of cropland, and growth of urbanized land alone had a relative contribution of 47.9%. It is possible that land use change in the US is driving both the emergence of novel viruses and their discovery, as has been

suggested for Heartland virus (**Mansfield et al., 2017**; **Savage et al., 2013**) and several hantaviruses (**Hassell et al., 2017**).

Climate had less influence on human-infective RNA virus discovery in all three regions in comparison to other predictors, in contrast to virus discovery at a global scale (**Zhang et al., 2020**). The underlying reason may be that the proportion of vector-borne viruses—whose distribution and abundance is strongly associated with the impact of climate on vector populations (**Li et al., 2014**)—in all three regions (United States: 23.2%; China: 21.3%; Africa: 27.1%) were less than that in the world (41.7%) (**Figure 3**). Vector-borne viruses tend to have more restricted global ranges, so are less likely to appear in a study of any one region (**Zhang et al., 2020**).

In addition, a relatively smaller proportion of strictly zoonotic viruses in three regions (United States: 30.5%; China: 16.3%; Africa: 33.6%) than that in the world (58.7%) (**Figure 2**) made biodiversity contribute less to virus discovery in the three regions than in the world (**Zhang et al., 2020**). With exposure to a higher density of mammals played a slightly larger role in virus discovery in Africa than in China and the United States (**Appendix 3—figure 9** to **Appendix 3—figure 11**).

Our discovery probability maps for 2010–2019 in three regions captured most historical hotspots, though several small new areas in central-eastern and southwestern United States, eastern and western China, as well as northern Africa would also make greater contribution to virus discovery (**Figure 6**). Our model has a good predictive ability, given 84% (37/44) new virus species in 2010–2019 were discovered in high-risk areas we have defined—85% percentiles of discovery probability within each region. Further, 35% (13/37) of those viruses discovered in high-risk areas since 2010 were discovered at the potential new hotspots where there had not been any virus discoveries in the past.

Our subgroup analyses distinguishing viruses firstly discovered in regions and those that had been discovered elsewhere in the world suggested in both the United States and Africa, discoveries of viruses firstly discovered in regions were more likely to be associated with climatic and biodiversity variables while discoveries of viruses had been discovered elsewhere in the world were more likely to be associated with socio-economic variables. This is plausible, again because after a novel virus was discovered elsewhere in the world, it is usually areas with a higher socio-economic level that first capture the virus in the local region.

This study had limitations. First, one common problem for data collected from literature review is the time lag between virus discovery and publication, in which case the virus data are likely to be matched to covariates in later decades. Second, we acknowledge that it is possible we have not identified the earliest report for some well-known viruses such as yellow fever virus, measles virus, especially in the post-vaccination era. Third, we were unable to identify robust and comprehensive data for all three regions on virus discovery effort (e.g. government transparency, laboratory infrastructure and technology), although we interpret GDP and university count as being an indirect measure of resources available for this activity. Previous studies have tried to use the bibliographic data to correct for the discovery effort (;). However, this strategy worked less well for our data as the frequency of published paper from virus-related scientific journals has only a weak link to publications on novel human-infective RNA virus (**Appendix 3—figure 1**).

The study adds to our previous study (**Zhang et al., 2020**) in several ways. First, we firstly construct data sets of human-infective RNA virus discovery reflecting the viral richness in three broad regions of the world. Second, we reduced the heterogeneity of the predictors by focusing on regions, including those predictors reflecting the research effort. Research effort is less variable within restricted regions and therefore has less effect on virus detection. This implies our predicted hotspots stand closer to the virus geographic distribution in nature. Third, the predicted hotspots derived from regional analysis have a higher precision than at a global scale, for example, specific areas in the United States and China were identified as hotspots from regional analysis, rather than the whole eastern area from the global analysis. This helps target areas for future surveillance.

In conclusion, a heterogeneous pattern of virus discovery-driver relationships was identified across three regions and the globe. Within regions virus discovery is driven more by land use and socio-economic variables; climate and biodiversity variables are consistently less important predictors than at a global scale. We mapped with good accuracy that in 2010–2019 three regions where human-infective RNA viruses had previously been discovered would continue to be the discovery hotspots, but in addition, several new areas in each region would make great contribution to virus discovery. Results from the study could guide active surveillance for new human-infective viruses in high-risk areas.

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Author contributions

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Additional files

Supplementary files

- Transparent reporting form

Data availability

The authors confirm that all data or the data sources are provided in the paper and its Supplementary Materials. The final datasets and codes used for the analyses are available via figshare at https://doi.org/10.6084/m9.figshare.15101979.

The following dataset was generated:

Author(s)	Year	Dataset title	Dataset URL	Database and Identifier
Zhang F	2021	Supporting data and R scripts for: Predictors of human RNA virus discovery in the United States, China and Africa	https://doi.org/10.6084/m9.figshare.15101979	figshare, 10.6084/m9.figshare.15101979

The following previously published dataset was used:

Author(s)	Year	Dataset title	Dataset URL	Database and Identifier
Woolhouse MEJ, Brierley L	2017	Epidemiological characteristics of human-infective RNA viruses	http://dx.doi.org/10.7488/ds/2265	Edinburgh DataShare, 10.7488/ds/2265

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Appendix 1

Appendix 1—table 1. Summary of the human-infective RNA virus data sets in the United States, Africa, and China.

		United States					China					Africa				
Species	Original discovery year	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 ***Barry et al., 1995***	1995	New Haven, Connecticut	41.31	--72.93	No					No				
Cali mammarenavirus	1971	Yes ***Buchmeier et al., 1974***	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 ***Buckley and Casals, 1970***	1970	New Haven, Connecticut	41.31	--72.93	No					Yes ***Buckley and Casals, 1970***	1970	Lassa, Borno State, Nigeria	10.69	13.27
Lujo mammarenavirus	2009	No					No					Yes ***Briese et al., 2009***	2009	Lusaka, Zambia	--15.39	28.32
Lymphocytic choriomeningitis mammarenavirus	1934	Yes ***Armstrong and Lillie, 1934***	1934	St. Louis county, Missouri	38.61	--90.41	No					No				
Machupo mammarenavirus	1964	No					No					No				
Mobala mammarenavirus	1985	No					No					Yes ***Georges et al., 1985***	1985	Bouboui and Gomoka village, Boali town, Central African Republic	4.89	18.14
Whitewater Arroyo mammarenavirus	2000	Yes ***Enserink, 2000***	2000	Alameda County, California	37.60	--121.72	No					No				
Mamastrovirus 1	1975	Yes ***Oshiro et al., 1981***	1981	Martin County, California	40.22	--123.10	Yes ***Xu et al., 1981***	1981	Guangzhou, Guangdong	23.13	113.26	Yes ***Dowling and Wynne, 1981***	1981	Lebowa, South Africa	--23.5	29.5
Mamastrovirus 6	2008	Yes ***Finkbeiner et al., 2009c***	2009	St. Louis, Missouri	38.63	--90.20	Yes ***Chu et al., 2010***	2010	Hong Kong	22.40	114.11	Yes ***Kapoor et al., 2009***	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mamastrovirus 8	2009	Yes ***Finkbeiner et al., 2009a***	2009	St. Louis, Missouri	38.63	--90.20	Yes ***Wang et al., 2013***	2013	Nanjing, Jiangsu and Lanzhou, Gansu	31.95	118.78	Yes ***Kapoor et al., 2009***	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mamastrovirus 9	2009	Yes ***Finkbeiner et al., 2009b***	2009	Accomack and Northampton Counties, Virginia	37.71	--75.81	Yes ***Tao et al., 2019***	2019	Jinan, Shandong	36.68	117.11	Yes ***Kapoor et al., 2009***	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Mammalian 1 orthobornavirus	1985	Yes ***Rott et al., 1985***	1985	Philadelphia, Pennsylvania	39.95	--75.17	Yes ***Chen et al., 1999***	1999	Taiwan	23.70	120.96	Yes ***Bode et al., 1992***	1992	Rural area of East Africa	--1.28	34.53
Mammalian 2 orthobornavirus	2015	No					No					No				
Norwalk virus	1972	Yes ***Kapikian et al., 1972***	1972	Norwalk, Ohio	41.24	--82.62	Yes ***Fang et al., 1995***	1995	Henan	33.88	113.48	Yes ***Taylor et al., 1993***	1993	Pretoria, Gauteng province, South Africa	--25.75	28.23
Sapporo virus	1980	Yes ***Nakata et al., 1988***	1988	Houston, Texas	29.76	--95.37	Yes ***Nakata et al., 1988***	1988	Shanghai	31.23	121.47	Yes ***Wolfaardt et al., 1997***	1997	Pretoria, Gauteng province, South Africa	--25.75	28.23
Vesicular exanthema of swine virus	1998	Yes ***Smith et al., 1998***	1998	Corvallis, Oregon	44.56	--123.26	No					No				
Alphacoronavirus 1	2007	No					No					No				
Human coronavirus 229E	1966	Yes ***Hamre and Procknow, 1966***	1966	Chicago, Illinois	41.88	--87.63	Yes ***Virus Research Group of Kun Number 323 Unit, The Chinese People's Liberation Army, 1975***	1975	Kunming, Yunnan	25.07	102.68	Yes ***Hays and Myint, 1998***	1998	Kumasi, Ghana	6.70	--1.62
Human coronavirus NL63	2004	Yes ***Esper et al., 2005***	2005	New Haven, Connecticut	41.31	--72.93	Yes ***Chan et al., 2005***	2005	Hong Kong	22.40	114.11	Yes ***Smuts et al., 2008***	2008	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Betacoronavirus 1	1967	Yes ***McIntosh et al., 1967***	1967	Bethesda, Maryland	38.98	--77.09	Yes ***Chan et al., 2005***	2005	Hong Kong	22.40	114.11	Yes ***Venter et al., 2011***	2011	Pretoria, Gauteng province, South Africa	--25.75	28.23
Human coronavirus HKU1	2005	Yes ***Esper et al., 2006***	2006	New Haven, Connecticut	41.31	--72.92	Yes ***Woo et al., 2005***	2005	Hong Kong	22.40	114.11	Yes ***Venter et al., 2011***	2011	Pretoria, Gauteng province, South Africa	--25.75	28.23

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Middle East respiratory syndrome-related coronavirus	2012	Yes* ***Bialek et al., 2014***	2014	Lake county, Indiana	41.45	--87.37	Yes* ***Gao and Song, 2015***	2015	Huizhou, Guangdong	23.09	114.40	Yes* ***Abroug et al., 2014***	2014	Monastir, Tunisia	35.79	10.82
Severe acute respiratory syndrome-related coronavirus	2003	Yes* ***Charles M, 2003***	2003	Atlanta, Georgia	33.75	--84.39	Yes ***Peiris et al., 2003a***	2003	Hong Kong	22.40	114.11	Yes ***Chiu et al., 2004***	2004	Pretoria, Gauteng province, South Africa	--25.75	28.23
Human torovirus (been abolished)	1984	No					No					No				
Bundibugyo ebolavirus	2008	No					No					Yes ***Smuts et al., 2008***	2008	Bundibugyo and Kikyo town, Bundibugyo District, Western Uganda	0.71	30.06
Reston ebolavirus	1991	Yes ***Miranda et al., 1991***	1991	Reston, Fairfax County, Virginia	38.96	--77.35	No					No				
Sudan ebolavirus	1977	No					No					Yes ***Bowen et al., 1977***	1977	Maridi, South Sudan	4.91	29.45
Tai Forest ebolavirus	1995	No					No					Yes ***Le Guenno et al., 1995***	1995	Abidjan, Cote-d'Ivoire	5.36	--4.01
Zaire ebolavirus	1977	No					No					Yes ***Johnson et al., 1977***	1977	Yambuku village, Democratic Republic of the Congo	2.83	22.22
Marburg marburgvirus	1968	Yes* ***Centers for Disease Control and Prevention, 2009***	2009	Denver county, Colorado	39.55	-- 105.78	No					Yes ***Gear et al., 1975***	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 ***Smithburn et al., 1959***	1959	Maponde's Kraal(Usutu river), South Africa	--26.52	31.67
Cacipacore virus	2011	No					No					No				
Dengue virus	1907	Yes ***Lavinder and Francis, 1914***	1914	Savannah, Georgia	32.02	--81.12	Yes ***Clarke et al., 1967***	1967	Southwest Taiwan	23.06	120.59	Yes ***Edington, 1927***	1927	Durban, KwaZulu-Natal Province, South Africa	--29.86	31.02
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* ***Perex-Pina and Merikangas, 1953***	1953	Waltham, Massachusetts	42.38	--71.24	Yes ***Yen, 1941***	1941	Beijing	40.01	116.41	Yes ***Simon-Loriere et al., 2017***	2017	Cunene, Angola	--16.28	15.28
Kokobera virus	1964	No					No					No				
Kyasanur forest disease virus	1957	No					Yes ***Wang et al., 2009***	2009	Hengduanshan Mountain, Yunnan	27.50	99.00	Yes ***Andayi et al., 2014***	2014	Djibouti, Republic of Djibouti	11.57	43.15
Langat virus	1956	No					No					No				
Louping ill virus	1934	Yes ***Rivers and Schwentker, 1934***	1934	New York	40.71	--74.01	No					No				
Murray Valley encephalitis virus	1952	No					No					No				
Ntaya virus	1952	No					No					Yes ***Smithburn, 1952***	1952	Bwamba county, Uganda	0.75	30.02
Omsk hemorrhagic fever virus	1948	No					No					No				
Powassan virus	1959	Yes ***Goldfield et al., 1973***	1973	Middlesex County, New Jersey	40.54	--74.37	No					No				
Rio Bravo virus	1962	Yes ***Suklin et al., 1962***	1962	Dallas city, Texas	32.78	--96.80	No					No				
Saint Louis encephalitis virus	1933	Yes ***Webster and Fite, 2009***	1933	St. Louis City, Missouri	38.63	--90.20	No					No				
Tembusu virus	1975	No					Yes ***Tang et al., 2013***	2013	Shandong	36.40	118.77	No				

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Tick-borne encephalitis virus	1938	Yes* ***Cruse et al., 1979***	1979	Cleveland, Ohio	41.51	--81.69	Yes ***Wang and Zhao, 1956***	1956	Bali village, Wuchang, Heilongjiang	44.91	127.16	No				
Uganda S virus	1952	No					No					Yes ***Dick and Haddow, 1952***	1952	Bwamba county, Uganda	0.75	30.02
Usutu virus	2009	No					No					No				
Wesselsbron virus	1957	No					No					Yes ***Smithburn et al., 1957***	1957	Lake Simbu region, Maputaland, KwaZulu-Natal, South Africa	--27.36	32.32
West Nile virus	1940	Yes ***Nash et al., 2001***	2001	New York	40.71	--74.01	Yes ***Li et al., 2013***	2013	Jiashi County, Xinjiang	39.58	77.18	Yes ***Smithburn et al., 1940***	1940	Omogo, West Nile district, Uganda	0.42	33.21
Yellow fever virus	1901	Yes ***Guiteras, 1904***	1904	Laredo, Texas	27.51	--99.51	Yes* ***Chen and Lu, 2016***	2016	Beijing	40.01	116.41	Yes ***Stokes et al., 1928***	1928	Larteh, Ghana	5.94	--0.07
Zika virus	1952	Yes* ***Foy et al., 2011***	2011	Northern Colorado	39.55	--105.78	Yes* ***Sun et al., 2016***	2016	Gan County, Ganzhou city, Jiangxi	25.86	115.02	Yes ***Dick, 1952***	1952	Zika, Uganda	0.12	32.53
Hepacivirus C	1989	Yes ***Choo et al., 1989***	1989	Emeryville, California	37.83	--122.29	Yes ***Xu et al., 1990a***	1990	Qidong county, Jiangsu	31.88	121.72	Yes ***Kew et al., 1990***	1990	Johannesburg, South Africa	--26.20	27.90
Pegivirus C	1995	Yes ***Simons et al., 1995***	1995	Chapel Hill, North Carolina; Rochester, Minnesota; Dallas, Texas	35.91	--79.06	Yes ***Wang et al., 1996***	1996	Beijing	40.01	116.41	Yes ***Simons et al., 1995***	1995	Cairo, Egypt	30.04	31.24
Pegivirus H	2015	Yes ***Kapoor et al., 2015***	2015	New York city, New York	40.71	--74.01	Yes ***Wang et al., 2018***	2018	Guangzhou, Guangdong	23.13	113.26	Yes ***Rodgers et al., 2019***	2019	Ebolowa, Cameroon	2.92	11.15
Pestivirus A	1988	Yes ***Yolken et al., 1989***	1989	Whiteriver, Arizona	33.83	--109.97	No					Yes ***Giangaspero et al., 1988***	1988	Zambia	--13.13	27.85
Andes orthohantavirus	1996	No					No					No				
Bayou orthohantavirus	1995	Yes ***Morzunov et al., 1995***	1995	Louisiana	30.98	--91.96	No					No				
Black creek canal orthohantavirus	1995	Yes ***Ravkov et al., 1995***	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 ***Lee et al., 1980***	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 ***Klempa et al., 2010***	2010	Sangassou village, Macenta district, Forest Guinea	8.24	--9.32
Seoul orthohantavirus	1982	Yes ***Forthal et al., 1987***	1987	Mississippi	32.57	--89.88	Yes ***Song et al., 1982***	1982	Jiangsu	33.14	119.79	Yes ***Tomori et al., 1986***	1986	Jos, Nigeria	9.90	8.86
Sin Nombre orthohantavirus	1993	Yes ***Nichol et al., 1993***	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* ***De Cock et al., 1987***	1987	Los Angeles County, California	34.05	--118.24	Yes ***Huang et al., 1989***	1989	Kashi county, Kashi city, Xinjiang	39.46	75.99	Yes ***Belabbes et al., 1985***	1985	Medea town, Algeria	36.26	2.75
Orthohepevirus C	2018	No					Yes ***Sridhar et al., 2018***	2018	Hong Kong	22.40	114.11	No				
Crimean-Congo haemorrhagic fever orthonairovirus	1967	No					Yes ***Yen et al., 1985***	1985	Bachu, southern Xinjiang	39.79	78.55	Yes ***Simpson et al., 1967***	1967	Kisangani, Tshopo province, Democratic Republic of the Congo	0.53	25.19

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Dugbe orthonairovirus	1969	No					No					Yes ***Causey et al., 1969***	1969	Ibadan, Nigeria	7.35	3.88
Nairobi sheep disease orthonairovirus	1969	No					No					Yes ***Morrill et al., 1991***	1991	Mombasa; Malindi; and Kilifi, Coast Province, Kenya	--3.34	39.57
Thiafora orthonairovirus	1989	No					No					No				
Influenza A virus	1933	Yes ***Francis and Magill, 1935***	1935	Philadelphi, Pennsylvania	39.95	--75.17	Yes ***Chang and Chiang, 1950***	1950	Beijing	40.01	116.41	Yes ***Isaacs and Andrews, 1951***	1951	Johannesburg, South Africa and Cape Town, South Africa	--26.20	27.90
Influenza B virus	1940	Yes ***Francis, 1940***	1940	Irvington village, Greenburgh town, Westchester County, New York	41.03	--73.87	Yes ***Wen and Chu, 1957***	1957	Beijing	40.01	116.41	Yes ***Montefiore et al., 1970***	1970	Arusha, Arusha Region, Tanzania	--3.37	36.69
Influenza C virus	1950	Yes ***Francis et al., 1950***	1950	Ann Arbor city, Michigan	42.28	--83.74	Yes ***Zhang, 1957***	1957	Beijing	40.01	116.41	Yes ***Joosting et al., 1968***	1968	Johannesburg, South Africa	--26.20	27.90
Dhori thogotovirus	1985	No					No					No				
Thogoto thogotovirus	1969	No					No					Yes ***Causey et al., 1969***	1969	Ibadan, Nigeria	7.35	3.88
Avian orthoavulavirus 1	1943	Yes ***Burnet, 1943***	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 ***Karzon, 1955***	1955	Buffalo, New York	42.89	--78.88	No					No				
Measles morbillivirus	1911	Yes ***Goldberger and Anderson, 1911***	1911	Washington, D. C.	38.91	--77.04	Yes ***Tang et al., 1958***	1958	Beijing	40.01	116.41	Yes ***Baylet et al., 1963***	1963	Dakar, Senegal	14.72	--17.47
Human respirovirus 1	1958	Yes ***Chanock et al., 1958***	1958	Washington, D. C.	38.91	--77.04	Yes ***Chen et al., 1964***	1964	Zhejiang	29.14	119.79	Yes ***Taylor-Robinson and Tyrrell, 1963***	1963	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Human respirovirus 3	1958	Yes ***Chanock et al., 1958***	1958	Washington, D. C.	38.91	--77.04	Yes ***Yu et al., 1987***	1987	Guangzhou, Guangdong	23.13	113.26	Yes ***Taylor-Robinson and Tyrrell, 1963***	1963	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Achimota pararubulavirus 2	2013	No					No					Yes ***Baker et al., 2013***	2013	Volta, Ghana	6.05	0.37
Human orthorubulavirus 2	1956	Yes ***Chanock, 1956***	1956	Cincinnati, Ohio	39.10	--84.51	Yes ***Pathogen biology research group, Jiangsu new medical college, 1975***	1975	Nanjing, Jiangsu	31.95	118.78	Yes ***Balestrieri et al., 1967***	1967	Accra, Ghana	5.60	--0.19
Human orthorubulavirus 4	1960	Yes ***Johnson et al., 1960***	1960	Bethesda, Maryland	38.98	--77.09	Yes ***Lau et al., 2005***	2005	Hong Kong	22.40	114.11	Yes ***Niang et al., 2010***	2010	Ndiop village, Sine Saloum region, Senegal	15.18	--16.74
Mammalian orthorubulavirus 5	1959	Yes ***Schultz and Habel, 1959***	1959	Stanford, California	37.42	--122.17	No					No				
Menangle pararubulavirus	1998	No					No					No				
Mumps orthorubulavirus	1934	Yes ***Johnson and Goodpasture, 1934***	1934	Nashville, Tennessee	36.16	--86.78	Yes ***Wang et al., 1958***	1958	Beijing	40.01	116.41	Yes ***Bayer and Gear, 1955***	1955	Johannesburg, South Africa	--26.20	27.90
Simian orthorubulavirus	1968	No					No					No				
Sosuga pararubulavirus	2014	No					No					Yes ***Albariño et al., 2014***	2014	-	3.76	32.82
Tioman pararubulavirus	2007	No					No					No				
Bunyamwera orthobunyavirus	1946	Yes ***Work, 1964***	1964	Southern Florida	26.92	--81.21	No					Yes ***Smithburn et al., 1946***	1946	Bwamba County, Uganda	0.75	30.02
Bwamba orthobunyavirus	1941	No					No					Yes ***Smithburn et al., 1941***	1941	Bwamba county, Western Province of Uganda	0.75	30.02
California encephalitis orthobunyavirus	1952	Yes ***Hammon and Reeves, 1952***	1952	Kern county, California	35.49	--118.86	Yes ***Gu et al., 1984***	1984	Longhua, Shanghai	31.22	121.43	Yes ***Bardos and Sefcovicova, 1961***	1961	Uganda	1.37	32.29
Caraparu orthobunyavirus	1961	No					No					No				

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
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 ***Williams et al., 1965***	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 ***Moore et al., 1975***	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* ***Liu et al., 2016***	2016	Beijing	40.01	116.41	Yes ***Daubney et al., 1931***	1931	Rift Valley of Kenya Colony	--0.28	36.07
Sandfly fever Naples phlebovirus	1944	No					No					Yes ***Sabin, 1951***	1951	Cairo, Egypt	30.04	31.24
Heartland banyangvirus	2012	Yes ***McMullan et al., 2012***	2012	Andrew and Nodaway Counties, Missouri	39.82	--94.59	No					No				
Huaiyangshan banyangvirus	2011	No					Yes ***Zhang et al., 2011***	2011	Huaiyangshan	31.37	115.39	No				
Uukuniemi phlebovirus	1970	No					No					No				
Human picobirnavirus	1988	Yes ***Grohmann et al., 1993***	1993	Atlanta, Georgia	33.75	--84.39	Yes ***Rosen et al., 2000***	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 ***Luo et al., 1999***	1999	Guangzhou	23.13	113.26	Yes ***Donia and Youssef, 2002***	2002	Alexandria Governorate, Egypt	30.74	29.74
Cardiovirus A	1947	Yes ***Jonkers, 1961***	1961	New Orleans, Louisiana	29.95	--90.07	Yes ***Feng et al., 2015***	2015	Changchun, Jilin	43.87	125.34	Yes ***Dick and Best, 1948***	1948	Entebbe, Uganda	0.05	32.46
Cardiovirus B	1963	Yes ***Jones et al., 2007***	2007	San Diego, California	32.72	--117.16	Yes ***Cheng et al., 2009a***	2009	Lanzhou, Gansu	36.06	103.79	Yes ***Zoll et al., 2009***	2009	Cameroon	5.03	12.40
Cosavirus A	2008	No					Yes ***Dai et al., 2010***	2010	Shanghai	31.23	121.47	Yes ***Kapusinszky et al., 2012***	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus B	2008	No					Yes ***Yang et al., 2016***	2016	Zhenjiang, Jiangsu	32.19	119.43	No				
Cosavirus D	2008	No					No					Yes ***Kapusinszky et al., 2012***	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus E	2008	No					No					Yes ***Kapusinszky et al., 2012***	2012	Maiduguri, Borno State, Nigeria	11.83	13.15
Cosavirus F	2012	No					No					No				
Enterovirus A	1949	Yes ***Sickles and Dalldorf, 1949***	1949	New York	43.30	--74.22	Yes ***Xiao et al., 1985***	1985	Tianjin	39.34	117.36	Yes ***Bayer and Gear, 1955***	1955	Johannesburg, South Africa	--26.20	27.90

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Enterovirus B	1949	Yes ***Sickles and Dalldorf, 1949***	1949	Wilmington	39.74	--75.54	Yes ***Wu et al., 1960***	1960	Fuzhou, Fujian	26.07	119.30	Yes ***Patz et al., 1953***	1953	Middelburg, Transvaal, South Africa	--25.77	29.46
Enterovirus C	1909	Yes ***Flexner and Lewis, 1909***	1909	New York city, New York	40.71	--74.01	Yes ***Yen and Hsü, 1941***	1941	Bejing	39.90	116.41	Yes ***Hudson and Lennette, 1933***	1933	Monrovia, Liberia	6.29	--10.76
Enterovirus D	1967	Yes ***Schieble et al., 1967***	1967	Berkeley, California	37.87	--122.27	Yes ***Shanghai Eye and Skin Disease Prevention and Treatment Institute, 1979***	1979	Shanghai	31.23	121.47	Yes ***Mirkovic et al., 1973***	1973	Morocco	31.79	--7.09
Enterovirus E	1961	Yes ***Moscovivci et al., 1961***	1961	Denver, Colorado	39.74	--104.99	No					No				
Enterovirus H	1965	No					No					No				
Rhinovirus A	1953	Yes ***Price, 1956***	1956	Baltimore, Maryland	39.29	--76.61	Yes ***Guangzhou Institute of Medicine and Health, 1975***	1975	Guangzhou, Guangdong	23.13	113.26	Yes ***Taylor-Robinson, 1963***	1963	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Rhinovirus B	1960	Yes ***Hamre and Procknow, 1961***	1961	Chicago, Illinois	41.88	--87.63	Yes ***Xiang et al., 2008***	2008	Beijing	40.01	116.41	Yes ***Briese et al., 2008***	2008	Pretoria, Gauteng province, South Africa	--25.75	28.23
Rhinovirus C	2006	Yes ***Lamson et al., 2006***	2006	New York city, New York	40.71	--74.01	Yes ***Lau et al., 2007***	2007	Hong Kong	22.40	114.11	Yes ***Briese et al., 2008***	2008	Pretoria, Gauteng province, South Africa	--25.75	28.23
Erbovirus A	2005	No					No					No				
Hepatovirus A	1973	Yes ***Feinstone et al., 1973***	1973	Bethesda, Maryland	38.98	--77.09	Yes ***Microbiology Research Group of Shanghai First Medical College and Laboratory of Shanghai Sixth People's Hospital, 1978***	1978	Shanghai	31.23	121.47	Yes ***Szmuness et al., 1977***	1977	Dakar, Senegal	14.72	--17.47
Aichivirus A	1991	Yes ***Chhabra et al., 2013***	2013	Cincinnati, Ohio	39.10	--84.51	Yes ***Yang et al., 2009***	2009	Shanghai	31.23	121.47	Yes ***Sdiri-Loulizi et al., 2008***	2008	Monastir, Tunisia	35.77	10.82
Parechovirus A	1958	Yes ***Ramoz-alverz and Sabin, 1958***	1958	Cincinnati, Ohio	39.10	--84.51	Yes ***Shan et al., 2009***	2009	Shanghai	31.23	121.47	Yes ***Kapusinszky et al., 2012***	2012	Ouagadougou, Burkina Faso	12.24	--1.56
Parechovirus B	2003	No					No					No				
Salivirus A	2009	Yes ***Greninger et al., 2009***	2009	Northern California	38.84	--120.90	Yes ***Shan et al., 2010***	2010	Shanghai	31.23	121.47	Yes ***Li et al., 2009***	2009	Maiduguri, Borno State, Nigeria	11.83	13.15
Avian metapneumovirus	2011	Yes ***Kayali et al., 2011***	2011	Memphis, Tennessee	35.15	--90.05	No					No				
Human metapneumovirus	2001	Yes ***Falsey et al., 2003***	2003	Rochester, New York	43.16	--77.61	Yes ***Peiris et al., 2003b***	2003	Hong Kong	22.40	114.11	Yes ***Madhi et al., 2003***	2003	Johannesburg, South Africa	--26.20	27.90
Human orthopneumovirus	1957	Yes ***Chanock et al., 1957***	1957	Baltimore, Maryland	39.29	--76.61	Yes ***Kun Number 323 Unit, the Chinese People's Liberation Army, 1975***	1975	Kunming, Yunnan	25.07	102.68	Yes ***Doggett, 1965***	1965	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Colorado tick fever virus	1946	Yes ***Florio et al., 1946***	1946	Denver, Colorado	39.74	--104.99	Yes ***Yang et al., 1996***	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				
Lebombo virus	1975	No					No					Yes ***Moore et al., 1975***	1975	Ibadan, Nigeria	7.38	3.95
Orungo virus	1976	No					No					Yes ***Tomori et al., 1976***	1976	Ibadan, Nigeria	7.38	3.95
Mammalian orthoreovirus	1954	Yes ***Ramos-Alvarez and Sabin, 1954***	1954	Cincinnati, Ohio	39.10	--84.51	Yes ***Zhao et al., 1995***	1995	Xuzhou, Jiangsu	34.26	117.19	Yes ***Malherbe et al., 1963***	1963	Johannesburg, South Africa	--26.20	27.90
Nelson Bay orthoreovirus	2007	No					Yes* ***Cheng et al., 2009b***	2009	Hong Kong	22.40	114.11	No				
Rotavirus A	1973	Yes ***Kapikian et al., 1976***	1976	Washington, D. C.	38.90	--77.04	Yes ***PaPa et al., 1979***	1979	Beijing	40.01	116.41	Yes ***Tomori et al., 1976***	1976	Johannesburg, South Africa	--26.20	27.90
Rotavirus B	1984	Yes ***Eiden et al., 1985***	1985	Baltimore, Maryland	39.29	--76.61	Yes ***Hung et al., 1984***	1984	Jinzhou, Liaoning	41.10	121.13	Yes ***Nakata et al., 1987***	1987	Kenya	--0.02	37.91
Rotavirus C	1986	Yes ***Jiang et al., 1995***	1995	Providence, Rhode Island	41.82	--71.41	Yes ***Qiao et al., 1999***	1999	Beijing	40.01	116.41	Yes ***Sebata and Steele, 1999***	1999	Pretoria, Gauteng province, South Africa	--25.75	28.23

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Rotavirus H	1987	No					Yes ***Wang et al., 1987***	1987	Huaihua, Hunan Province	27.55	109.96	No				
Banna virus	1990	No					Yes ***Xu et al., 1990b***	1990	Xishuangbanna, Yunnan Province	21.90	100.80	No				
Primate T-lymphotropic virus 1	1980	Yes ***Poiesz et al., 1980***	1980	Bethesda, Maryland	38.98	--77.09	Yes ***Hung et al., 1984***	1984	Shenyang, Liaoing	41.80	123.38	Yes ***Williams et al., 1984***	1984	Ibadan, Nigeria	7.38	3.95
Primate T-lymphotropic virus 2	1982	Yes ***Kalyanaraman et al., 1982***	1982	Seattle, Washington	47.61	--122.33	Yes ***Ma et al., 2013***	2013	Henan and Hubei	32.21	112.96	Yes ***Delaporte et al., 1991***	1991	Franceville, Gabon	--1.63	13.60
Primate T-lymphotropic virus 3	2005	No					No					Yes ***Calattini et al., 2005***	2005	Océan department, South Province, Cameroon	2.50	10.50
Human immunodeficiency virus 1	1983	Yes ***Safai et al., 1984***	1984	Washington, D. C.	38.90	--77.04	Yes ***Chang et al., 1986***	1986	Hong Kong	22.40	114.11	Yes ***Brun-Vézinet et al., 1984***	1984	Kisangani, Tshopo province, Democratic Republic of the Congo	0.53	25.19
Human immunodeficiency virus 2	1986	Yes* ***Centers for Disease Control, 1988***	1988	New Jersey	40.06	--74.41	Yes* ***Yan et al., 2000***	2000	Fuzhou, Fujian	26.07	119.30	Yes ***Kanki et al., 1986***	1986	Dakar, Senegal	14.72	--17.47
Simian immunodeficiency virus	1992	Yes ***Khabbaz et al., 1992***	1992	Atlanta, Georgia	33.75	--84.39	No					Yes ***Calattini et al., 2005***	2005	Cameroon	7.37	12.35
Central chimpanzee simian foamy virus	2012	No					No					Yes ***Rua et al., 2012***	2012	Near Dja Nature Reserves, Southern Cameroon	4.50	13.50
Eastern chimpanzee simian foamy virus	1971	No					No					Yes ***Achong et al., 1971***	1971	Kenya	--0.02	37.91
Grivet simian foamy virus	1997	No					No					No				
Guenon simian foamy virus	2012	No					No					Yes ***Rua et al., 2012***	2012	Near lolodrof, Southern Cameroon	3.23	10.73
Taiwanese macaque simian foamy virus	2002	No					Yes ***Huang et al., 2012***	2012	Yunnan	25.18	101.86	No				
Australian bat lyssavirus	1998	No					No					No				
Duvenhage lyssavirus	1971	No					No					Yes ***Meredith et al., 1971***	1971	Pretoria, Gauteng province, South Africa	--25.75	28.23
European bat Yeslyssavirus	1989	No					No					No				
European bat 2 lyssavirus	1986	No					No					No				
Irkut lyssavirus	2013	No					Yes ***Liu et al., 2013***	2013	Tonghua county, Jilin	41.68	125.76	No				
Mokola lyssavirus	1972	No					No					Yes ***Familusi et al., 1972***	1972	Ibadan, Nigeria	7.38	3.95
Rabies lyssavirus	1903	Yes ***Black and Powers, 1910***	1910	Southern California	34.57	--116.76	Yes ***Wu, 1981***	1981	Beijing	40.01	116.41	Yes ***Wilhelm and Alexis, 1933***	1933	Carolina, Mpumalanga, South Africa	--26.07	30.12
Bas-Congo tibrovirus	2012	No					No					Yes ***Grard et al., 2012***	2012	Mangala village, Boma Bungu Health Zone, Democratic Republic of Congo (DRC)	--4.04	21.76
Ekpoma Yestibrovirus	2015	No					No					Yes ***Stremlau et al., 2015***	2015	Irrua, Edo State, Nigeria	6.74	6.22
Ekpoma 2 tibrovirus	2015	No					No					Yes ***Stremlau et al., 2015***	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				

Appendix 1—table 1 Continued on next page

Appendix 1—table 1 Continued

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
Indiana vesiculovirus	1958	Yes ***Patterson et al., 1958***	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 ***Hanson et al., 1950***	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* ***Centers for Disease Control and Prevention, 2006***	2006	Minnesota	46.44	--93.36	Yes ***Clarke et al., 1967***	1967	Southwest Taiwan	23.06	120.59	Yes ***Ross, 1956***	1956	Newala district, Tanzania	--10.64	39.24
Eastern equine encephalitis virus	1938	Yes ***Howitt, 1938***	1938	Southwestern Massachusetts	42.19	--73.09	No					No				
Everglades virus	1970	Yes ***Ehrenkranz et al., 1970***	1970	Homestead, Florida	25.47	--80.48	No					No				
Getah virus	1966	No					Yes ***Li et al., 1992***	1992	Baoting County, Hainan	18.98	109.83	No				
Highlands J virus	2000	Yes ***Meehan et al., 2000***	2000	Florida	27.66	--81.52	No					No				
Madariaga virus	1972	No					No					No				
Mayaro virus	1957	Yes* ***Tesh et al., 1999***	1999	Ohio	40.42	--82.91	No					No				
Mosso das Pedras virus	2013	No					No					No				
Mucambo virus	1965	No					No					No				
Ndumu virus	1961	No					No					Yes ***Kokernot et al., 1961***	1961	Ndumu, Maputaland, KwaZulu-Natal, South Africa	--26.93	32.26
Onyong-nyong virus	1961	No					No					Yes ***Williams and Woodall, 1961***	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 ***Xu et al., 1999***	1999	Hainan	19.16	109.94	No				
Semliki Forest virus	1979	No					No					Yes ***Mathiot et al., 1990***	1990	Bangui, Central Africa	4.36	18.58
Sindbis virus	1955	No					No					Yes ***Taylor et al., 1955***	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 ***Casals et al., 1943***	1943	New York	40.71	--74.01	No					No				
Western equine encephalitis virus	1938	Yes ***Howitt, 1938***	1938	Fresno, California	36.75	-- 119.77	No					No				
Whataroa virus	1964	No					No					No				
Rubella virus	1942	Yes ***Habel, 1942***	1942	Washington, D. C.	38.91	--77.04	Yes ***He et al., 1979***	1979	Hangzhou, Zhejiang	29.87	119.33	Yes ***Selzer, 1963***	1963	Cape Town, Western Cape Province, South Africa	--33.90	18.57
Hepatitis delta virus	1977	Yes ***Rizzetto et al., 1979***	1979	New Jersey	40.06	--74.41	Yes ***Rizzetto et al., 1980***	1980	Taipei, Taiwan	24.96	121.51	Yes ***Crocchiolo et al., 1984***	1984	Harare, Zimbabwe	--17.83	31.03

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 virus species has never been discovered from the region; The lat and long denote the coordidate of discovery points or centroids of polygons

Appendix 1—table 2. Resolution and covered grid cells for virus discovery data.

		Polygon data				
		Country level	State/Province level	City/County level	Point data	Total
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
Africa	Virus counts	7 (6.5%)	5 (4.7%)	15 (14.0%)	80 (74.8%)	107
	Gridded cell counts	307	22	17	80	426

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

Appendix 1—table 3. 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

Appendix 1—table 4. Model validation statistics for analyses in three regions.

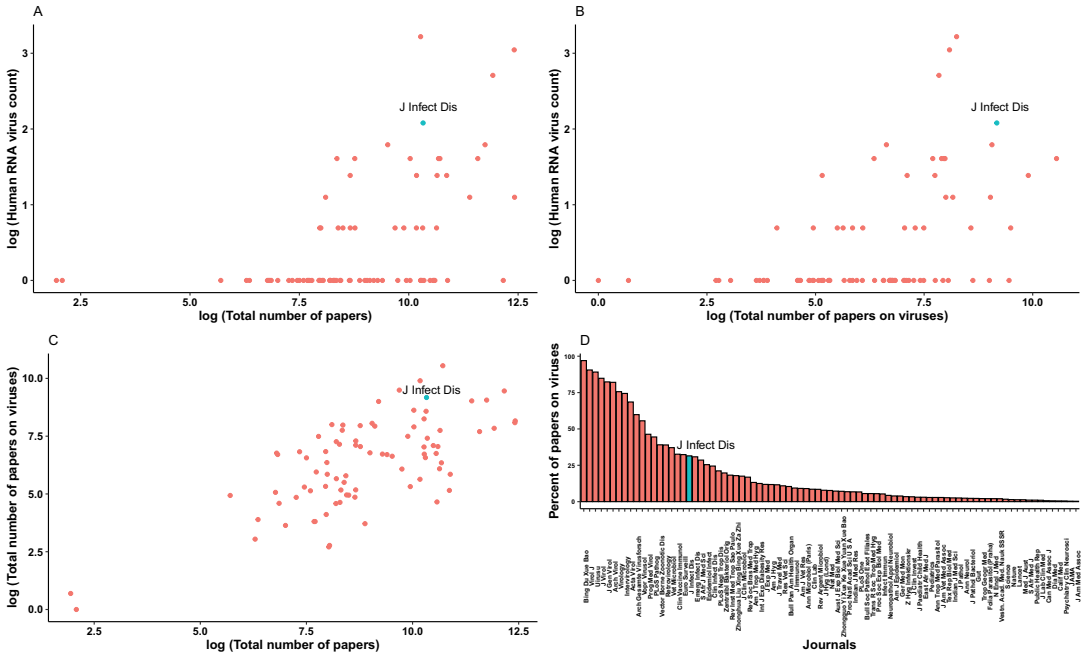
Model	% of deviance explained (95% quantiles)	ICC (95% quantiles)
United States	50.5% (44.3%–56.8%)	0.66 (0.60–0.70)
China	42.0% (32.4%–50.8%)	0.52 (0.41–0.60)
Africa	42.4% (34.2%–50.0%)	0.51 (0.44–0.62)

ICC, intraclass correlation coefficient

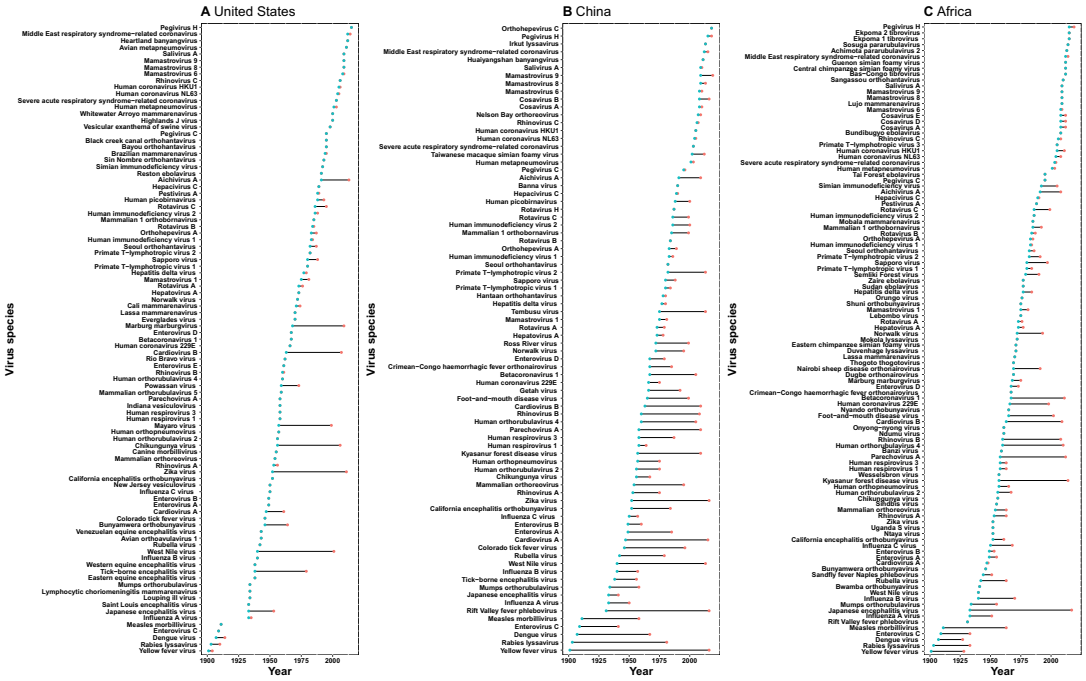
Appendix 2

We considered using bibliographic data to adjust for discovery effort, but rejected this strategy after some exploratory tests. ***Jones et al., 2008*** estimated the discovery effort for emerging infectious diseases (EID) by calculating the number of papers published by each country (denoted by the address for every author) in the Journal of Infectious Diseases (JID) since 1973. The hypothesis is that countries publishing more papers in JID are likely to discover more EID events. We tested whether this method worked for our analysis by plotting the relationship between published human-infective RNA virus count and total number of papers from all journals which published on human-infective RNA viruses in Web of Science (as of 21 Feb 2018). Both the total number of papers (***Appendix 3—figure 1A***) and total number of papers on viruses (***Appendix 3—figure 1B***) were weakly linked to the published human virus count in our database, though the number of papers did have a positive relationship with the number of papers on viruses (***Appendix 3—figure 1C***). We also noted that papers in JID (highlighted in blue in ***Appendix 3—figure 1***) may not be able to fully explain the discovery efforts for newly discovered viruses. ***Olival et al., 2017*** adjust for the discovery effort by searching the number of publications for each of 586 virus species they have studied using a keyword search by virus name in PubMed and Web of Science. We found the results using this method were similar to that of ***Jones et al., 2008***. ***Allen et al., 2017*** derived a different index for discovery bias, based on the spatial distribution of place names in peer-reviewed biomedical literature. The disadvantage of this method is that it may not represent the discovery effort, as many place names are not related to zoonotic viruses.

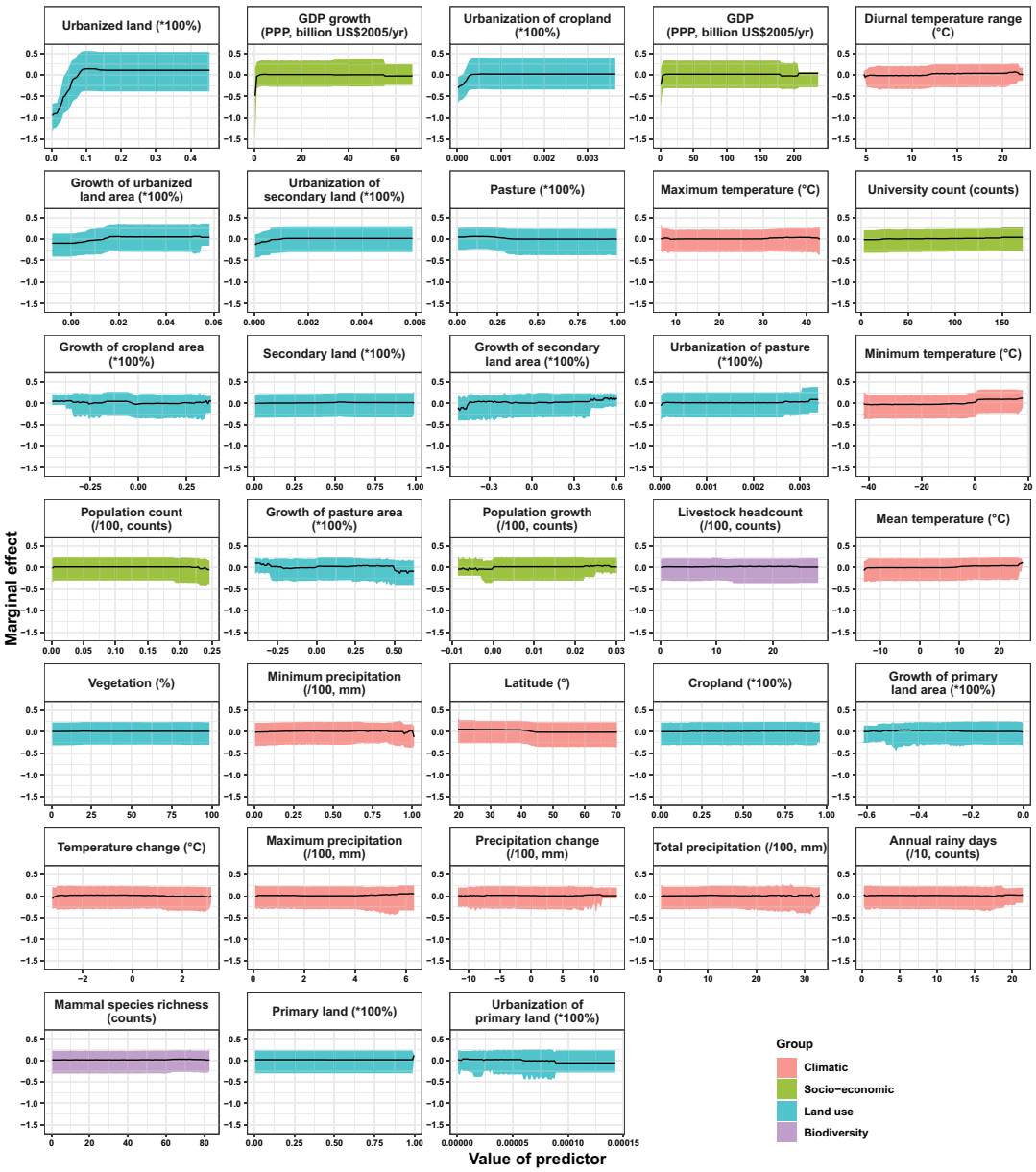
Appendix 3



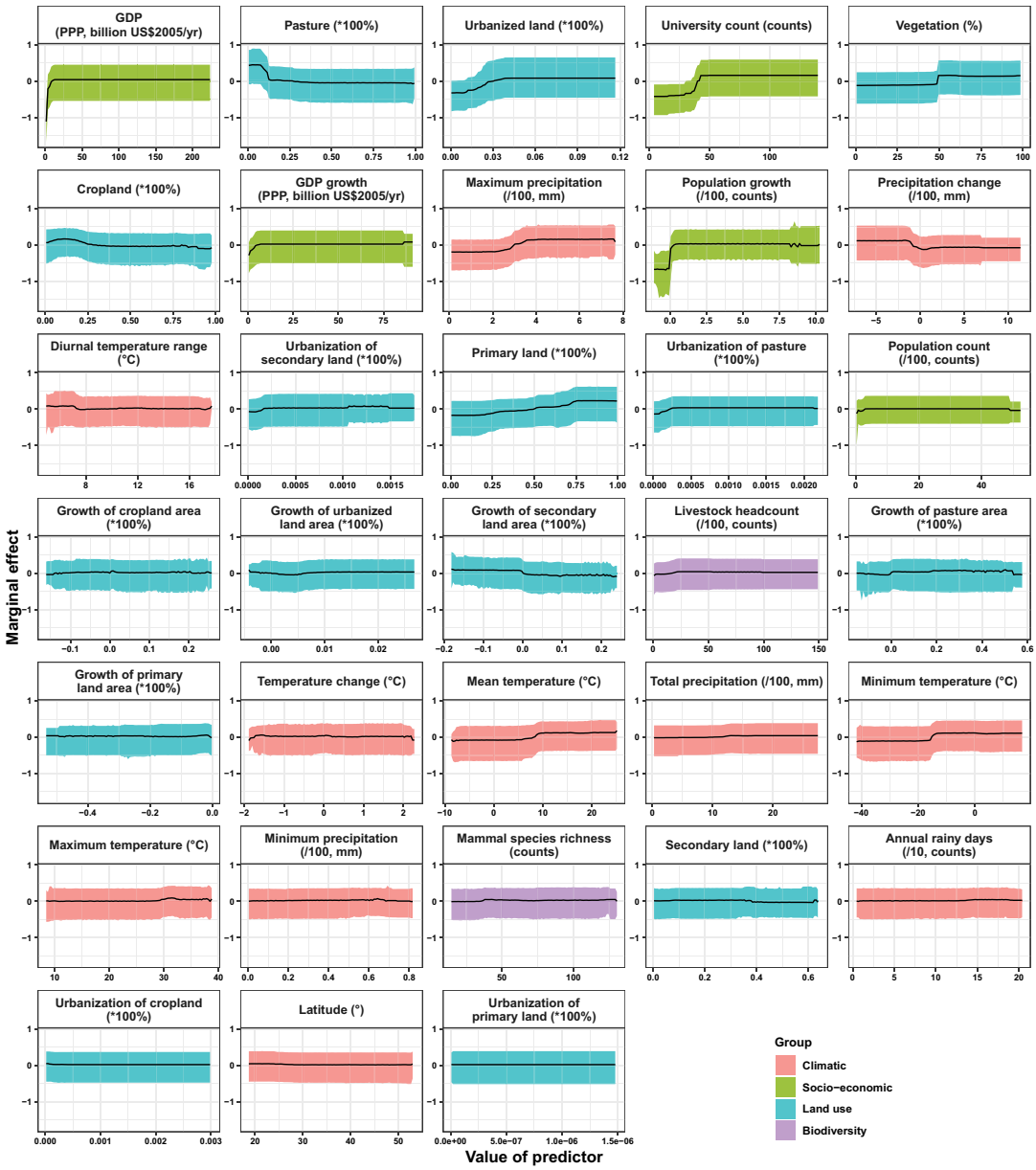
Appendix 3—figure 1. Relationship between published human-infective RNA virus count and total number of papers from the journals which published all human-infective RNA viruses in Web of Science. (A) Total number of papers vs. published human virus count; (B) Total number of papers on viruses vs. published human virus count; (C) Total number of papers vs. total number of papers on viruses; (D) Percent of papers on viruses in each journal. Journal of Infectious Diseases (JID) is highlighted in blue.



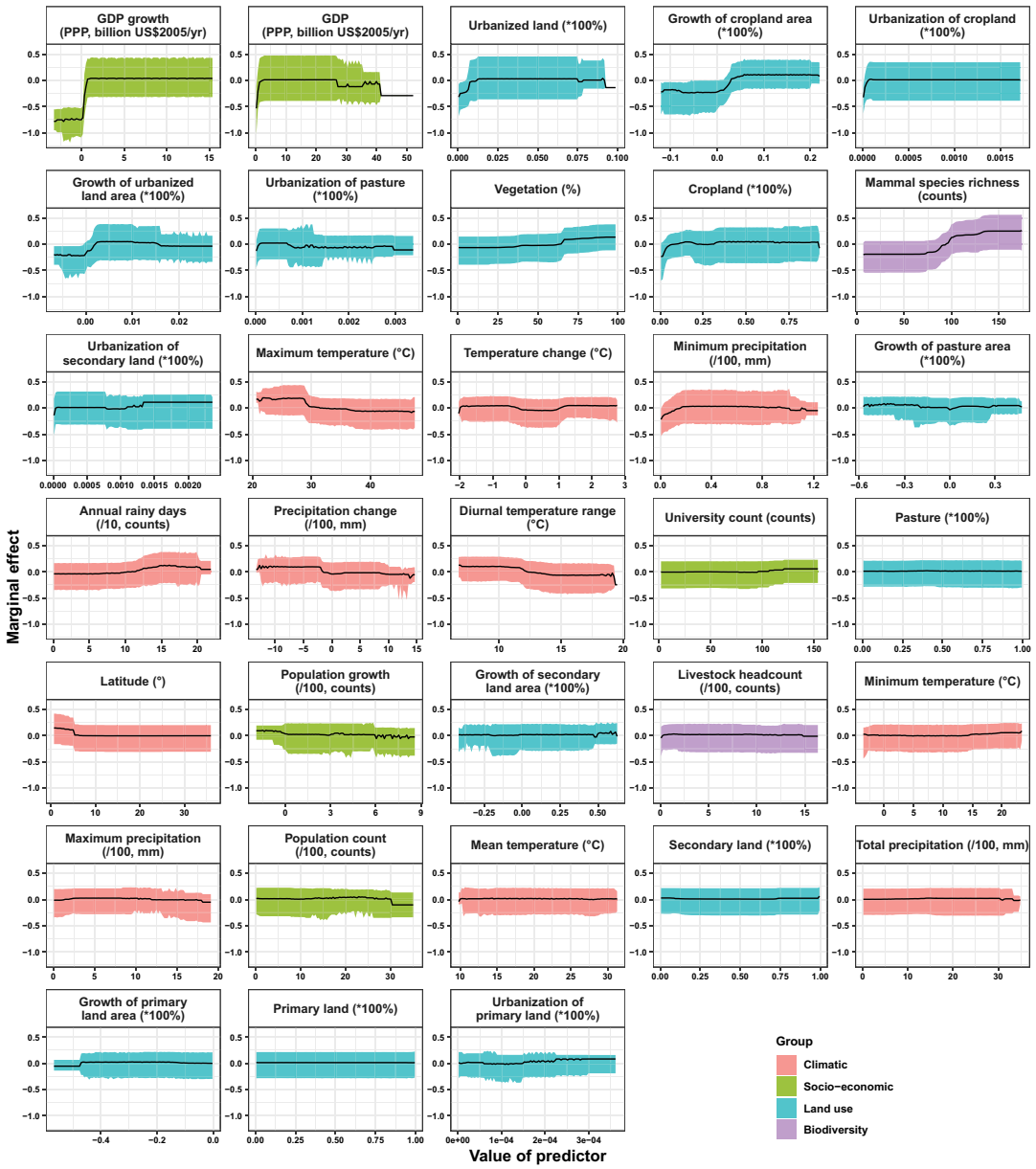
Appendix 3—figure 2. Time lag of human-infective RNA virus discovery between the three regions and the world. (A) United States. (B) China. (C) Africa. The blue dots represent the original discovery year of each virus in the world; the red dots represent the discovery year of each virus in three regions; and the segments between them represent the time lag.



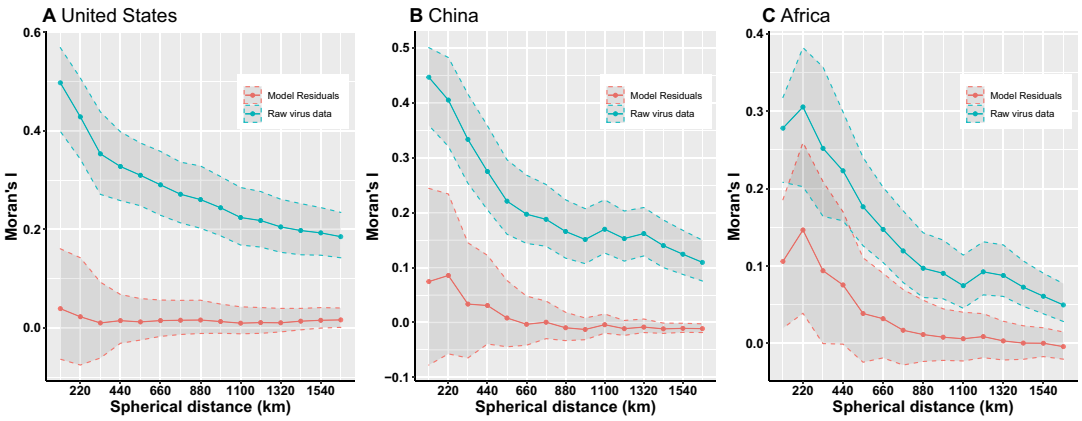
Appendix 3—figure 3. Partial dependence plots showing the influence on human-infective RNA virus discovery for all predictors in the Unites States. Partial dependence plots show the effect of an individual predictor over its range on the response after factoring out other predictors. Fitted lines represent the median (black) and 95% quantiles (coloured) based on 1000 replicated boosted regression tree models. Y axes are centred around the mean without scaling. X axes show the range of sampled values of predictors.



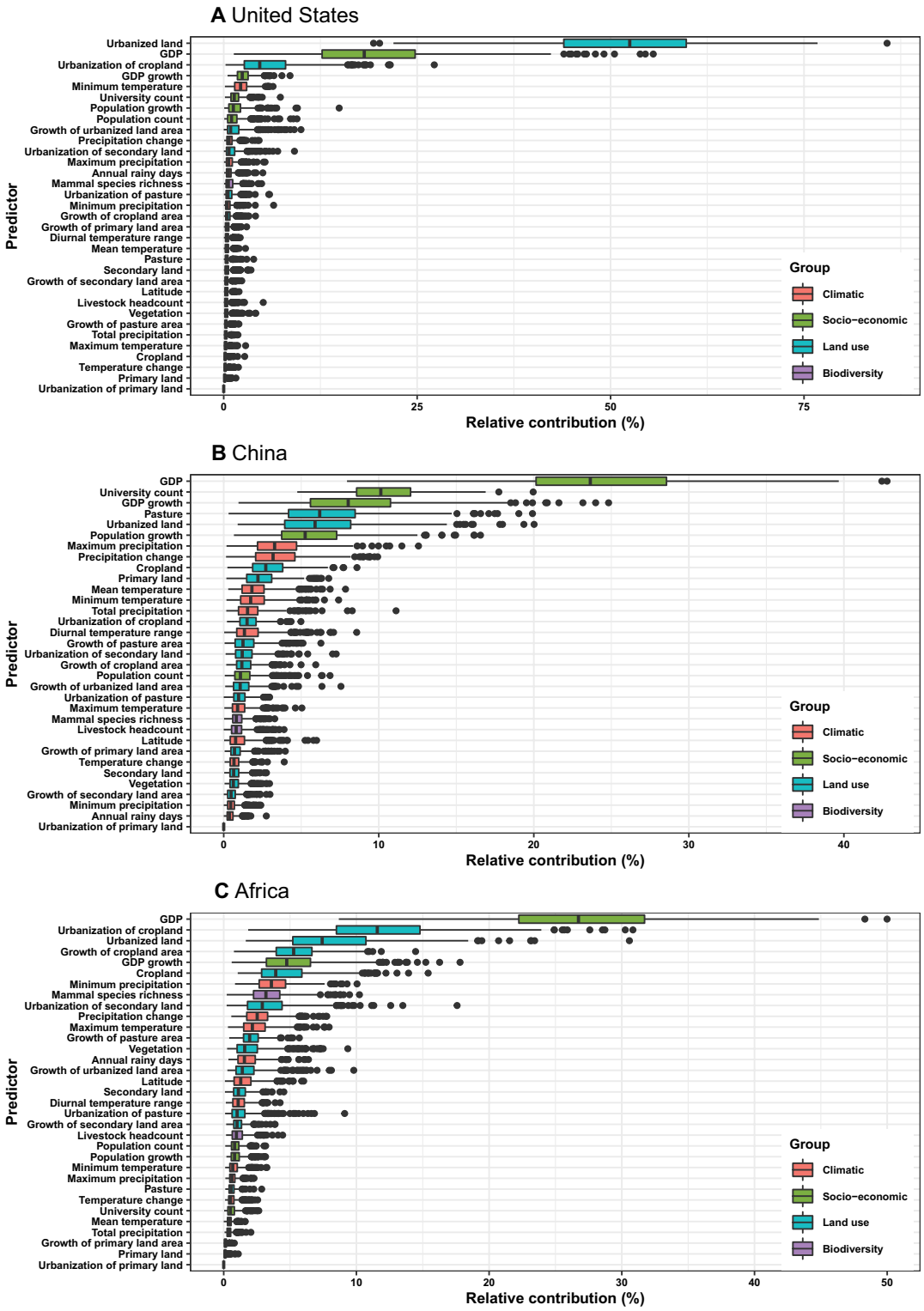
Appendix 3—figure 4. Partial dependence plots showing the influence on human-infective RNA virus discovery for predictors in China. Partial dependence plots show the effect of an individual predictor over its range on the response after factoring out other predictors. Fitted lines represent the median (black) and 95% quantiles (coloured) based on 1000 replicated boosted regression tree models. Y axes are centred around the mean without scaling. X axes show the range of sampled values of predictors.



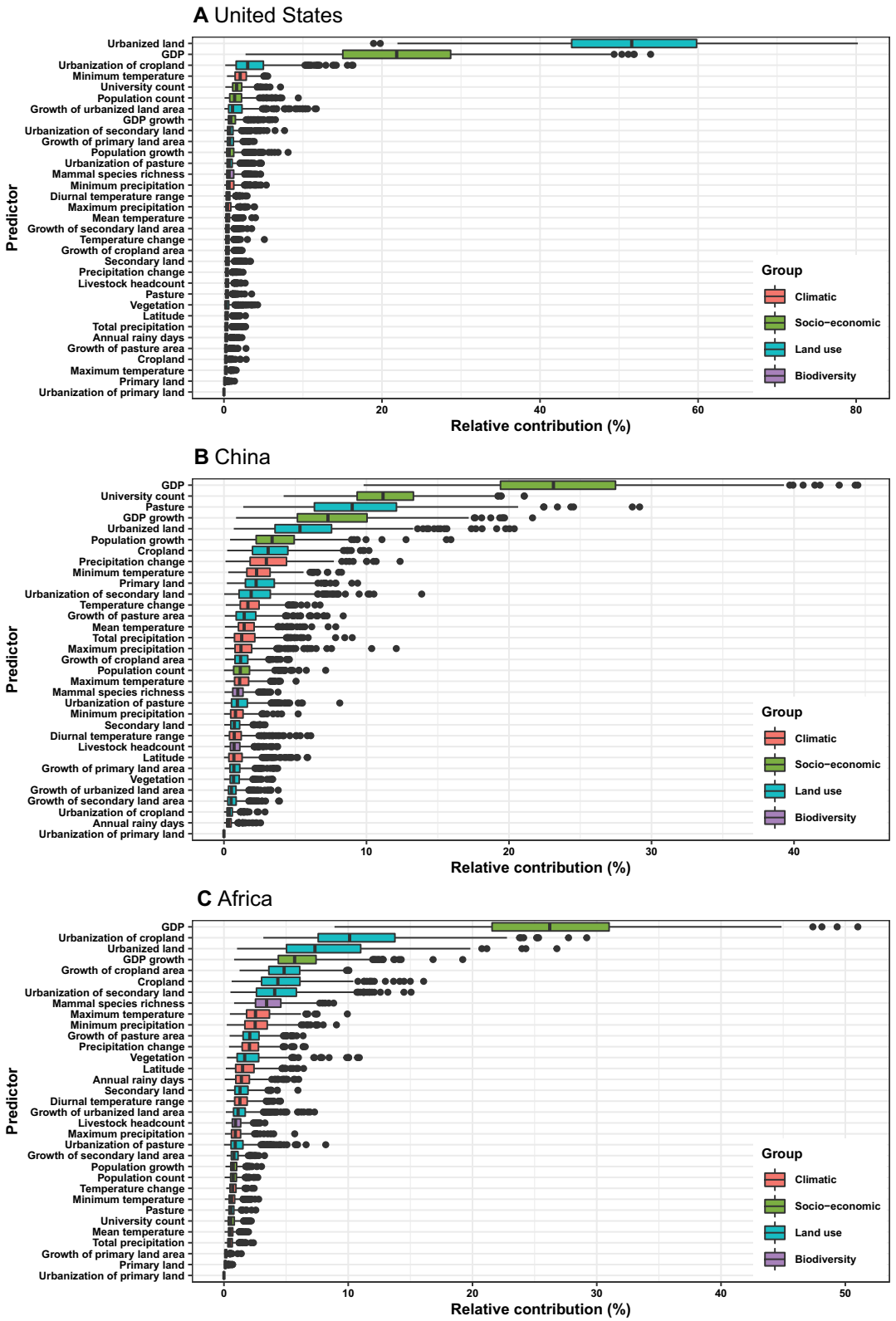
Appendix 3—figure 5. Partial dependence plots showing the influence on human-infective RNA virus discovery for all predictors in Africa. Partial dependence plots show the effect of an individual predictor over its range on the response after factoring out other predictors. Fitted lines represent the median (black) and 95% quantiles (coloured) based on 1000 replicated boosted regression tree models. Y axes are centred around the mean without scaling. X axes show the range of sampled values of predictors.



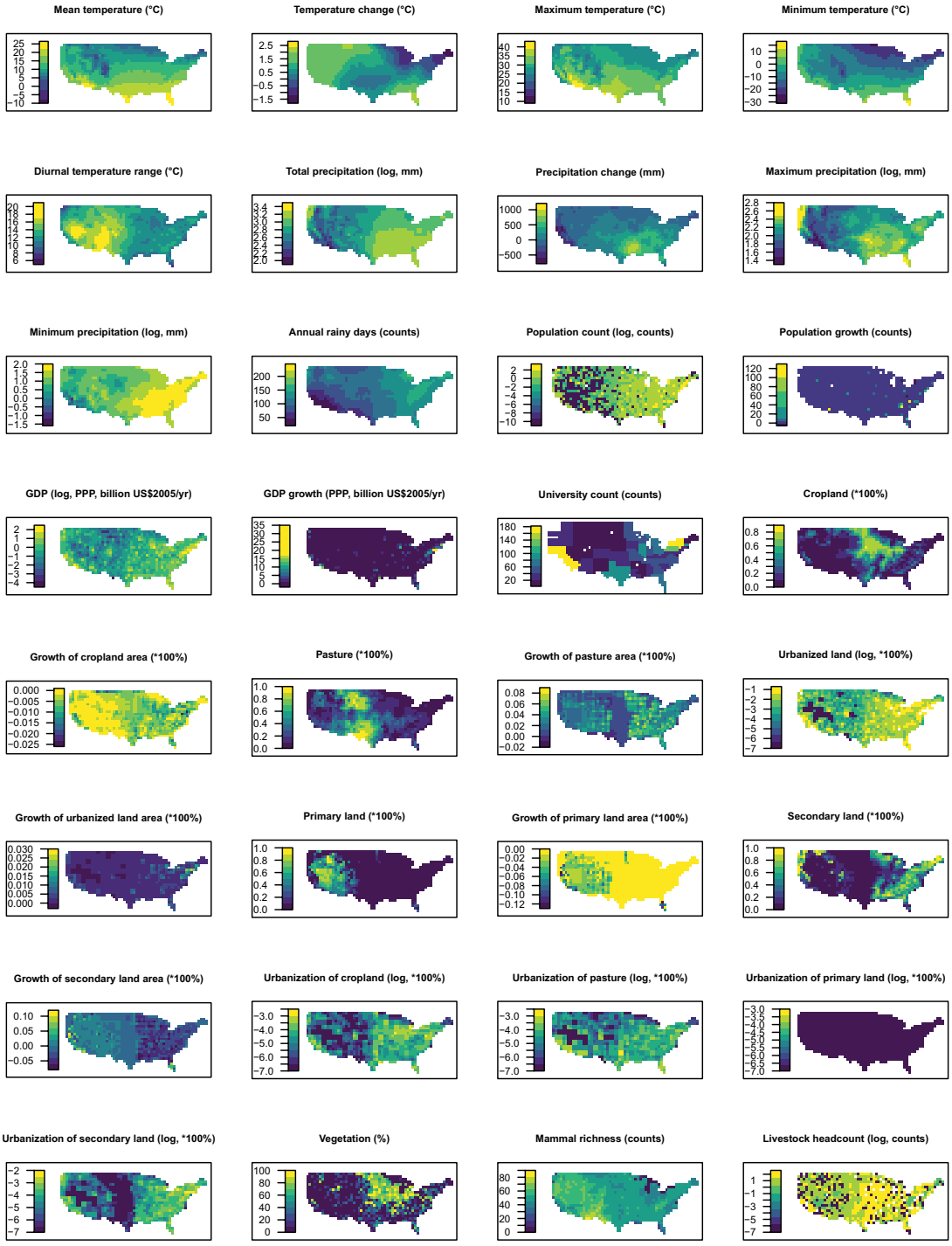
Appendix 3—figure 6. Moran's I across different spherical distances. (A) United States; (B) China; (C) Africa. The solid line and dots represented the median Moran's I value, and the grey area represented its 95% quantiles generated from 1000 samples (Blue: Raw virus data) or replicate boosted regression tree (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.



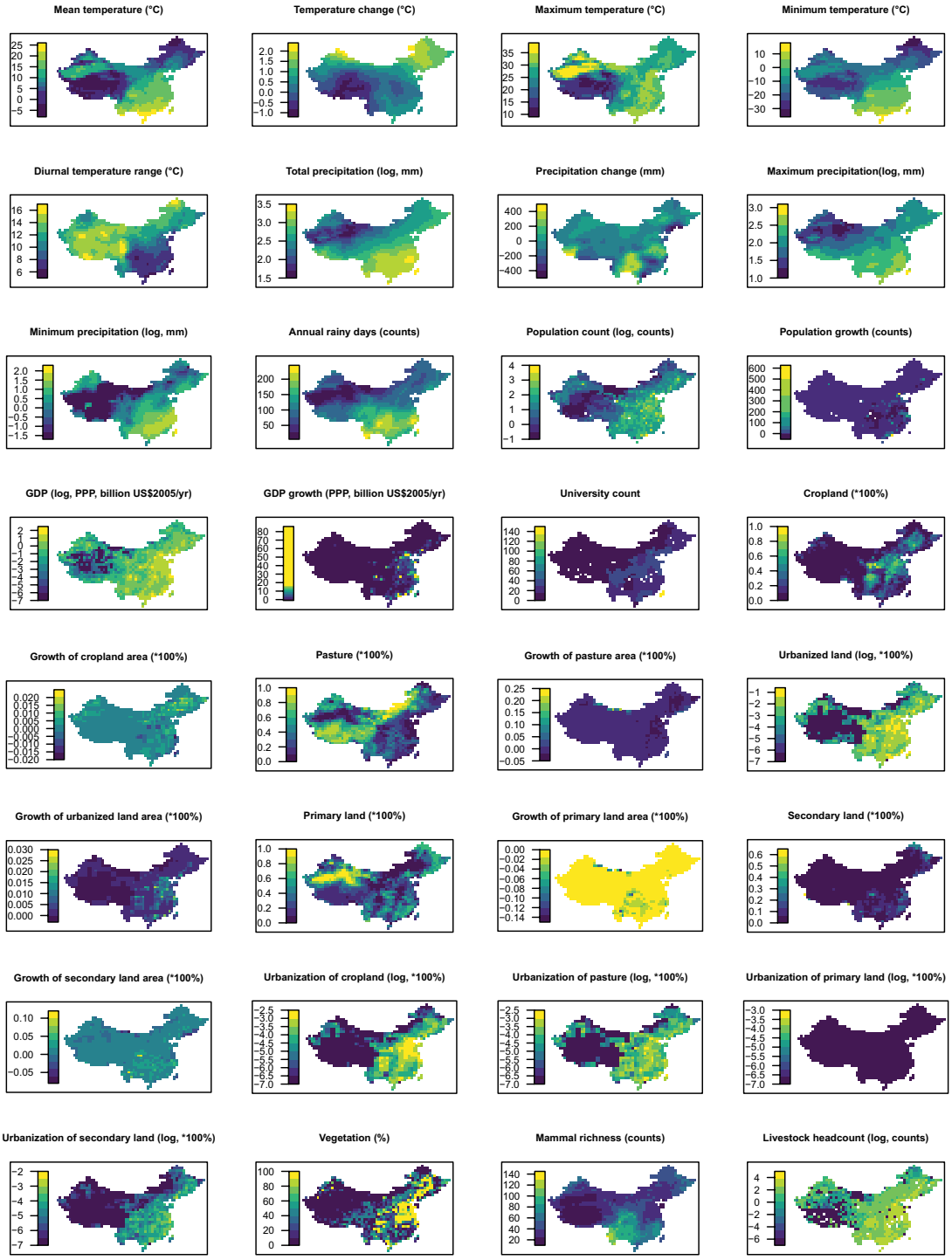
Appendix 3—figure 7. Relative contribution of predictors to human-infective RNA virus discovery in three regions. Virus discovery data were matched to time-varying covariate data by year. (A) United States. (B) China. (C) Africa. The boxplots show the median (black bar) and interquartile range (box) of the relative contribution across 1000 replicate boosted regression tree models, with whiskers indicating minimum and maximum and black dots indicating outliers.



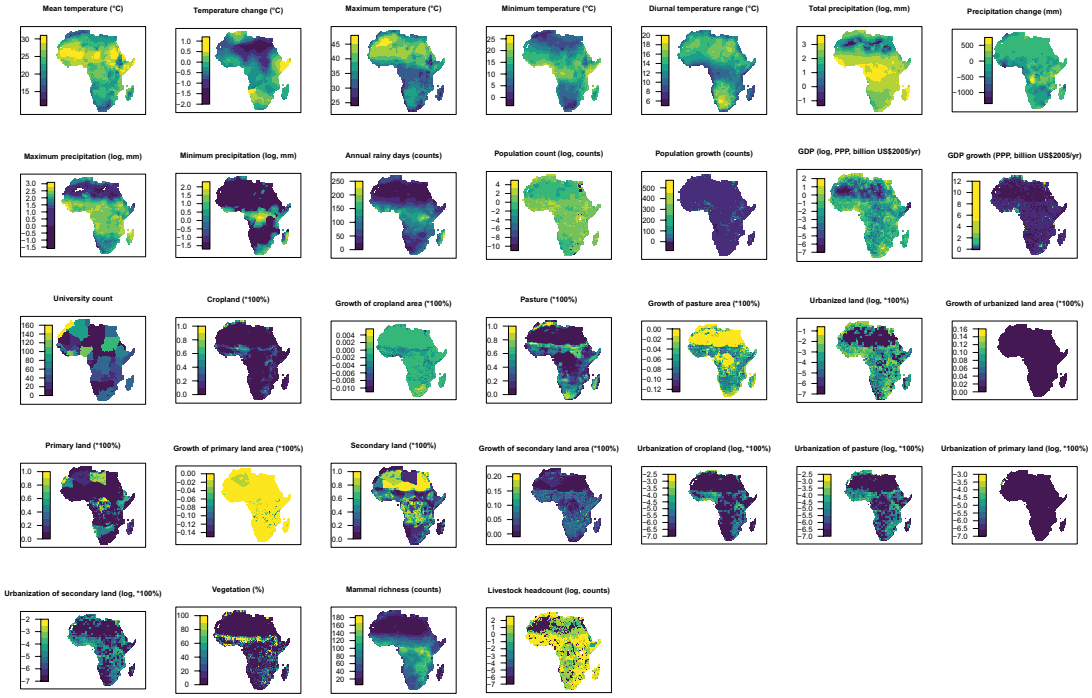
Appendix 3—figure 8. Relative contribution of predictors to human-infective RNA virus discovery in three regions. Virus discovery data at year t were matched to time-varying covariate data at year t-1. (A) United States. (B) China. (C) Africa. The boxplots show the median (black bar) and interquartile range (box) of the relative contribution across 1000 replicate boosted regression tree models, with whiskers indicating minimum and maximum and black dots indicating outliers.



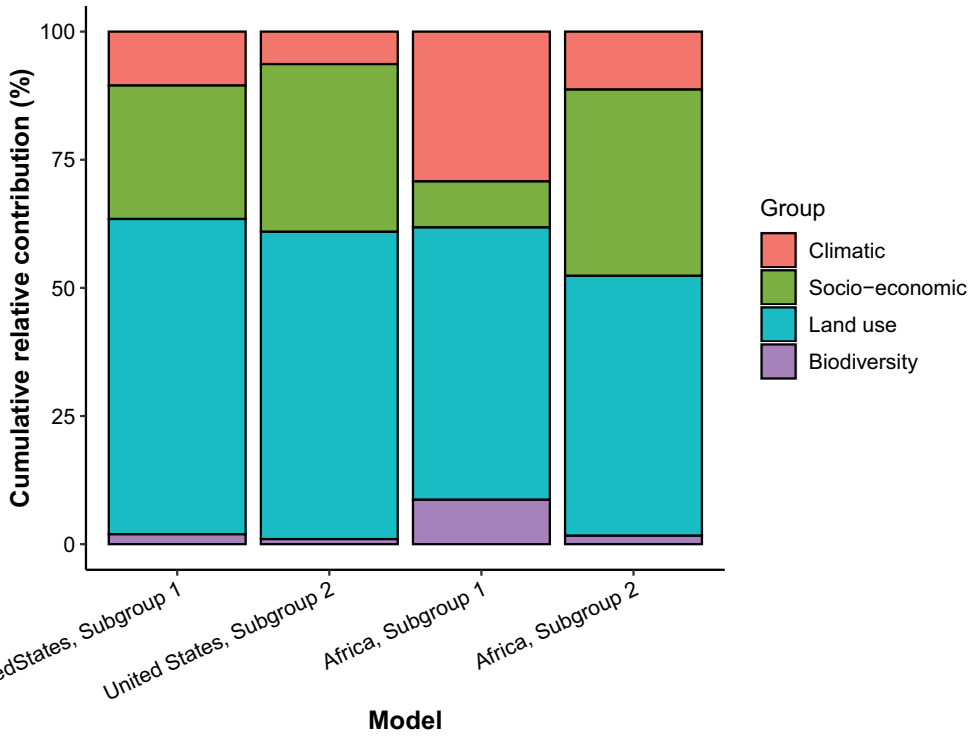
Appendix 3—figure 9. Distribution maps for 32 predictors in 2015 in the United States. The values of these explanatory variables and latitude in each grid cell were used to predict the virus discovery in the corresponding grid cell in the Unites States in 2010–2019. Explanatory variables were log transformed where necessary to get better visualization, not meaning they entered the model by logged values.



Appendix 3—figure 10. 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.



Appendix 3—figure 11. 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 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 entered the model by logged values.



Appendix 3—figure 12. 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. In the United States, virus count of Subgroup 1 and Subgroup 2 were 52 and 43, respectively. In Africa, virus count of Subgroup 1 and Subgroup 2 were 39 and 68, respectively. The relative contributions of all explanatory factors sum to 100% in each model, and each colour represents the cumulative relative contribution of all explan*atory factors within each group*.

Appendix 4

As covariates may vary within a decade and their effects on virus discovery were likely not immediate, we performed two further sensitivity analyses by (i) matching virus discovery data and time-varying covariate data by year and (ii) testing for lag effects by matching virus discovery at year t and predictors at t-1 to t-5 year. We collected yearly data for climatic variables and land use from the same sources used in the main analysis. Yearly population data at grid level before 1970 and GDP data before 1980 are not available, so we extrapolated them back to 1901 using the yearly growth rate at country level (Source: Our World in Data). For population, the WorldPop Project provides yearly gridded data for 2000-2020 (https://www.arcgis.com/home/item.html?id=56eb0f050c61434782f008a08331d23a), and we used the growth rate by grid to extrapolate values after 2000.